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**MARINE MAMMALS OFF CENTRAL CALIFORNIA RELATIVE TO
HYDROGRAPHY; 1986-94, 1997-99**

A Thesis

Presented to

The Faculty of the Department of Moss Landing Marine Laboratories

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Carol Ann Keiper

December 2001

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ABSTRACT

MARINE MAMMALS OFF CENTRAL CALIFORNIA RELATIVE TO HYDROGRAPHY 1986-94, 1997-99

By Carol Ann Keiper

Variability of upwelling, coupled with larger scale processes (El Niño/La Niña), affects productivity and the distribution of fish and marine mammals. Marine mammal and environmental data gathered using standard strip transect methodology were used with CTD and mid-water trawl data collected off central California from Bodega Bay to Monterey Bay 1986-1999 (except 1995-96). Distributional patterns of marine mammals relative to hydrography were investigated using Geographical Information System, Percent Similarity Index (PSI), multiple logistic regression, and principal component analyses. Differences in species composition and presence/absence of marine mammals likely were related to significant differences in ocean structure resulting from local and large-scale processes. Distribution of the dominant species (California sea lion, northern fur seal, Pacific white-sided dolphin, Dall's porpoise, harbor porpoise, and humpback whale) was related to bathymetry and changing oceanographic and biological conditions that affected their prey.

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INTRODUCTION

The waters off central California between Pt. Reyes and Cypress Pt. are part of the large scale California Current System, a major eastern boundary current, and are regarded as one of the major upwelling regions of the world (Bakun 1996). The hydrography is characterized by seasonal changes associated with upwelling that varies both spatially and temporally (Husby & Nelson 1982, Brink 1983, Huyer 1983, Schwing et al. 1991, Smith 1992). Spatial features of upwelling include fronts (Brink 1983, Dykstra et al. 1984, Traganza et al. 1981, Rosenfeld et al. 1993) that separate cooler, more saline productive water from warmer, less saline off-shore water (Huyer et al. 1990, Schwing et al. 1991, Breaker & Broenkow 1994); meandering jets, which carry some of the nutrient water offshore (Strub et al. 1991); mesoscale eddies that occur within the larger water masses (Schwing et al. 1991, Strub et al. 1991); and coastal boundary zones (Breaker & Gilliland 1981, Parrish et al. 1981, Huyer 1983). Distinct zones often are marked by a sharp temperature gradient between the interface of offshore and upwelled waters (Herman & Denman 1979, Brink 1983, Traganza et al. 1983, Breaker & Mooers 1986, Armstrong et al. 1987, Huyer et al. 1990).

Upwelling features that persist or recur are linked to interactions among bathymetry, coastal topography, water flow, and wind (Denman et al. 1981, Brink 1983, Huyer 1983, Schwing et al. 1991). Upwelled water may either extend into the California current creating well defined plumes of cold filaments (Traganza et al. 1981, Chelton et al. 1987) or can be centered on topographical features such as canyons and capes (Traganza et al. 1981, Brink 1983, Kelly 1985, Breaker & Mooers 1986). The irregular

coastline of California results in irregular upwelling patterns and often, in areas near capes, plumes are associated with coastal topography (Denman & Powell 1984, Kelly 1985) creating upwelling centers (Brink 1983, Traganza et al. 1981, Tracy 1990, Schwing et al. 1991, Rosenfeld et al. 1993, Lenarz et al. 1995). Upwelling centers associated with coastal headlands of California occur off Pt. Reyes, Pt. Año Nuevo, and Pt. Sur (Schwing et al. 1991, Rosenfeld et al. 1993, Breaker & Broenkow 1994, Lenarz et al. 1995).

The onset of the upwelling season (spring through late summer) off central California is variable from year to year and is marked by the “spring transition” (Huyer et al. 1990). A sudden strengthening of the northwest wind occurs during a week or less (Breaker & Mooers 1986), which, in combination with the rotation of the earth, produces offshore transport of surface water. This surface water is replaced by nutrient-rich cooler water from depths of approximately 50 to 100 meters. Oscillations between upwelling favorable winds, wind relaxation, and wind reversals result in various stages of upwelling intensity, duration, relaxation, and persistence (Traganza et al. 1983, Schwing et al. 1991, Rosenfeld et al. 1993). Many of the effects of upwelling can extend beyond the zone of active upwelling, and a single upwelling event of several days duration may change the oceanographic regime for several months (Huyer 1983).

The timing of upwelling may affect production cycles and location of nutrients, plankton, and fish. Upwelling plumes result in localized regions of increased productivity (Hunt & Schneider 1987, Schwing et al. 1991, Parker 1996, Chavez et al. *in press*). The relaxation between upwelling events allows nutrient-rich water to accumulate downwind

of the upwelling zone (Send et al. 1987), and increases primary production and higher trophic levels (Denman & Powell 1984). If upwelling is intense and sustained, organisms and nutrients are transported offshore before production cycles are completed (Denman & Powell 1984). If upwelling is not intense and sustained, phytoplankton blooms can occur during the relaxation periods between upwelling events, resulting in increased stocks of zooplankton and ultimately fish (Denman & Powell 1984). Although the peak upwelling season is May through June (Baltz 1997), it can occur in winter (Huyer 1983, Strub et al. 1987). Off central California, upwelling and ocean mixing during winter months is important for food-web development (Ainley et al. 1993).

The waters off central California also are affected by large time and space scale processes associated with El Niño Southern Oscillation (ENSO) events (McLain 1983, Barber & Chavez 1983, Breaker & Mooers 1986, Hayward 1993, Lenarz et al. 1995, Ramp et al. 1997, Schwing et al. 1997, Lynn et al. 1998). El Niño events may result in reduced vertical advection of nutrients and a warmer, deeper upper mixed layer that reduces nutrient enrichment derived from local wind-driven Ekman transport.

The central California coastal upwelling region (from Cape Blanco to Pt. Conception) is dominated by migratory pelagic stocks of sardine (*Sardinops sagax*), hake (*Merluccius productus*), jack mackerel (*Trachurus symmetricus*), anchovy (*Engraulis mordax*) and rockfish (*Sebastes* spp.; Parrish et al. 1981). Because changing oceanographic conditions affect the distribution, year class strength, abundance, reproduction, and survival of prey (Parrish et al. 1981, Ainley et al. 1993, Larson et al. 1994, Hernandez-Vazquez 1994, Horne & Smith 1997, Saunders & McFarlane 1997,

Schwing et al. 1997, Lynn et al. 1998, Hayward et al. 1999), these changing conditions affect the availability of prey to marine mammal predators.

Schools of cephalopods, which are prey for marine mammals, occur in coastal and offshore waters (Cailliet et al. 1979, Fiscus et al. 1989). *Loligo* occurs year-round off California, and moves inshore to spawn in shallow waters, with a peak in Monterey Bay from May through July. Except for *Loligo opalescens*, patterns of distribution and abundance of cephalopods are unknown (Black 1994).

With more than one third of the world's cetacean species and six species of pinnipeds, central California is well known for its abundance and diversity of marine mammals (Bonnell et al. 1983, Dohl et al. 1983, Calambokidis et al. 1989). Distributions of cetaceans vary with factors such as distance from land (Dohl et al. 1983, Allen 1994, Barlow 1995); depth and bathymetric features, such as continental slope and shelf waters (Huber et al. 1980, Dohl 1983, Kenny & Winn 1986, Allen 1994, Tynan 1996); areas of high relief (Hui 1979); edges of submarine canyons (Schoenherr 1991); water temperature (Dohl et al. 1983, Leatherwood et al. 1980, Black 1994, Allen 1994); concentrations of oceanic chlorophyll (Smith et al. 1986); upwelling-modified waters (Reilly & Thayer 1990); and season (Dohl et al. 1983, Calambokidis et al. 1988, 1990, Barlow 1995).

Patterns of cetacean abundance and habitat use also have been described in relation to the abundance of their primary prey, with concentrations of cetaceans and prey occurring in mid-shelf habitats or along shelf edges (Kenny & Winn 1986, Dolphin 1987, Schoenherr 1991). For example, depending on available krill or schooling fish,

humpback whale (*Megaptera novaeangliae*) is concentrated near the Farallones during some summer months (Calambokidis et al. 1991), along the shelf, south of the Farallones in other months and years (Allen 1994), or more concentrated between Cordell Bank and Bodega Canyon (Calambokidis et al. 1989, 1990, 1991). Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and Dall's porpoise (*Phocoenoides dalli*) feed on northern anchovy, Pacific hake, Pacific saury (*Cololabis saira*), and cephalopods of the family Gonatidae that are found in the epipelagic (0 to 200 m) and mesopelagic (200 to 1000 m) zones (Stroud et al. 1981). Harbor porpoise (*Phocoena phocoena*) are found inshore of the shelf-break on the continental shelf (Szczepaniak 1987) where they feed on northern anchovy, juvenile rockfish, Pacific hake, Pacific Tomcod (*Microgadus proximus*), and *Loligo* (Jones 1981, Allen 1994).

The temporal distribution of some cetaceans varies among species. Although year-round residents, densities of harbor porpoise throughout the study area vary with season (Dohl 1983, Brueggeman et al. 1992) and hydrographic conditions (Szczepaniak 1987, Allen 1994, Forney 2000). Densities of harbor porpoise were greatest in autumn south of San Francisco and inside Monterey Bay (Dohl 1983). Dall's porpoise exhibit seasonal north-south and inshore-offshore shifts (Dohl 1983), and humpback whale distribution varies among years with concentrations moving from the Farallon Islands to Cordell Bank and Bodega Canyon (Calambokidis et al. 1989, 1990, 1991, Kieckhefer 1992).

Six species of pinnipeds inhabit central California, including the California sea lion (*Zalophus californianus*), Steller sea lion (*Eumetopias jubatus*), northern fur seal

(*Callorhinus ursinus*), Guadalupe fur seal (*Arctocephalus townsendi*), Pacific harbor seal (*Phoca vitulina richardsi*), and the northern elephant seal (*Mirounga angustirostris*; Bonnell et al. 1983). Some of the factors that explain the distribution of pinnipeds are distance to shelf-break and land (Allen 1994, Brueggeman 1992), bathymetric features (Bonnell et al. 1983), prey type and abundance (Ainley et al. 1982, Allen 1994), and season (Bonnell et al. 1983). Although sighted near the coast, more sightings of California sea lions occur in waters overlying the continental shelf (Antonelis & Fiscus 1980, Bonnell et al. 1983, Allen 1994). Elephant seals occur over the continental shelf and slope (Bonnell et al. 1983), in deeper water over the slope, and in the pelagic zone (Allen 1994). The northern fur seal is the most pelagic of the three otariids; when they are away from the breeding grounds, this species is dispersed widely throughout the open ocean south to about 32°N (Kenyon & Wilke 1953, Stroud et al. 1981, York 1987). They are most numerous along the continental slope, beyond the shelf break (Antonelis & Fiscus 1980, Allen 1994) and are present off California from January through June (Antonelis & Fiscus 1980, Kajimura 1984, Allen 1994).

During spring, greater densities of pinnipeds occur over the Monterey canyon, Pioneer and Guide seamounts, and Cordell Bank (Bonnell et al. 1983). Pinniped densities are related mostly to the presence of California sea lions, with greatest densities occurring in the spring over the shelf (Bonnell et al. 1983), depending on year. Pinnipeds generally feed on a variety of prey found in nearshore, mid-shelf, or offshore waters, and include some seasonally abundant small schooling fish such as Pacific hake (Allen, 1994), northern anchovy, jack mackerel, squid (Kenyon & Wilke 1953, Morejohn

et al. 1978, Stroud et al. 1981, Lowry et al. 1990), myctophids (Allen 1994), and epipelagic and mesopelagic fishes (Antonelis & Fiscus 1980, Antonelis et al. 1983).

Because the spatial and temporal features of upwelling may influence the timing of food web development and the location of prey resources, these features may influence the occurrence patterns of marine mammals. The temporal and spatial distribution of marine mammals is likely related to the timing of upwelling, with greater numbers of marine mammals expected near upwelling centers during relaxation phases.

In this study, I investigated the occurrence of marine mammals and hydrographic features associated with mesoscale ocean structure resulting from upwelling off the coast of central California from Bodega Bay south to Cypress Point.

The following hypotheses were tested:

1. ocean structure is less stratified both horizontally and vertically before the onset of the upwelling season than during the upwelling season with sea surface temperature significantly warmer, thermocline depth significantly deeper, Δt significantly lower, and (25.8 kg m^{-3} isopycnal) significantly deeper;
2. ocean structure changes significantly within an upwelling season, with sea surface temperature significantly cooler during active upwelling and, as upwelling relaxes, ocean structure is more stratified and thermocline depth is significantly shallower, Δt significantly greater, and Σt (25.8 kg m^{-3} isopycnal) significantly shallower;

3. the distribution (presence/absence) of marine mammals along tracklines is non-random;
4. marine mammal sighting rates are greater within surface upwelling zones than outside of surface upwelling zones; and
5. there is a significant association between marine mammals and ocean habitat variables (sea surface temperature, thermocline depth, Delta-t, Sigma-t (25.8 kg m^{-3} isopleth, and wind speed) with presence of marine mammals significantly associated with relatively warmer sea surface temperatures and well-stratified ocean conditions and absence of marine mammals associated with relatively cool sea surface temperatures and less-stratified ocean conditions.

METHODS

The study area included 54,000 sq. km off central California, from Bodega Bay (38.32° N) to Cypress Pt. (36.58° N), and from the coast to approximately 250 km offshore (Fig. 1). Data were collected using strip transect methods of Tasker et al. (1984) as modified by Ainley and Boekelheide (1983), on cruises in early spring (April, 1987-1988, February-March 1992, and March 1993-1994), and peak upwelling periods or late spring (May-June, 1986-1994, 1997-1999). Strip width was 0.3 km for pinnipeds and 0.8 km for cetaceans. Cruises were conducted on the R/V David Starr Jordan, a research vessel of the National Oceanic and Atmospheric Administration (NOAA) during rockfish assessment cruises conducted by the National Marine Fisheries Service (NMFS), Tiburon Laboratory. During each annual cruise, three consecutive "sweeps" (repeated sampling) of the survey area grid were performed during a period of approximately 7 to 10 days. The marine mammal sighting data were collected during one or two of these sweeps and a total of 19,489 km² were surveyed along 24,361 km of track lines (Table 1). The following data associated with sightings were collected every 15 minutes from dawn to dusk when the ship was underway between CTD stations: ocean depth (nearest 1 m), distance to nearest land mass (nearest km), sea surface salinity (nearest 1 ‰) and sea surface temperature (nearest 1°C) measured by a Seabird thermosalinometer, wind direction (nearest 10°), and wind speed (kts/hr).

The term sample unit refers to each 15-minute segment (at 10 kts this was four km) along the transect line. Because successive sample units may not be independent, an analysis of adjacent sample units was performed in the following way: the proportion of

pairs of sample units containing no animals present (A), animals present in one of the pairs (PA), and animals present in both pairs (P) were calculated for distances of zero to five sample units apart. Paired sample units at these distances were tested for significance with SPSS RxC Crosstabs Pearson Chi-square and Likelihood ratio tests. Alpha levels were equal to 0.025 to avoid Type I errors (Tabachnick & Fidell 1996). The results showed no significant differences for any combination of pairs ($p < 0.05$); therefore, adjacent units were considered independent for subsequent analyses.

Spatial and temporal survey effort was unequal among years. Therefore, trackline maps were created and visually inspected and years with similar spatial and temporal survey effort (1992-1994, and 1997-1999) were selected for final analysis. Because the ship's speed was not always 10 kts, and distance traveled was not always four km, sample units were not equal. Therefore, before any investigations, lengths of sample units per survey period were calculated (lengths ranged from 0.6 km to 10.3 km). To determine if unequal sample unit length might bias the results, kilometers traversed per sample unit was included as a variable in a preliminary multiple logistic regression analysis. Because length of sample units was significantly associated with presence/absence of marine mammals (indicating the likelihood of presence of marine mammals increased as sample unit size increased) only sample units 2.6 to 6.0 km (± 2 standard deviations) in length were used in analyses.

Ocean Habitat

Due to skewed distributions, nonparametric statistics were used to test for temporal differences in sea surface temperature (SST) data. Sea surface temperature

differences among early and late survey periods and among all late survey periods were tested for significance using Kruskal-Wallis one-way ANOVA. Sea surface temperature differences within an upwelling season were tested for significance using the Kolmogorov-Smirnov Z test.

ArcView 3.2, Geographical Information System (GIS) software from Environmental Science Research Institute (ESRI, Redlands, CA), and the Spatial Analyst Extension (an ESRI software product), were used to investigate spatial differences in sea surface temperature (SST) among surveys. Sea surface temperature grids and isotherms were created at a scale of four kilometers (sample unit scale) and the Inverse Distance Weighted interpolation method was used to create sea surface temperature maps. Distance to upwelling plumes was calculated with the Find Distance function, and boundary zones of 15 km were drawn around upwelling polygons. An upwelling plume was defined as a relatively cool pool of water (-1 standard deviation from the mean sea surface temperature of the study area derived from shipboard data) that emanated from upwelling centers near Pt. Reyes and Pt. Año Nuevo. An upwelling zone was defined as a surface plume of cool water and waters within 15 km of the plume. Because surface fronts were defined as a two-degree change in sea surface temperature in 20 km distance (Brown et al. 1995), 15 km was selected as a reasonable distance for potential fronts associated with surface plumes of cooler water. Advanced Very High Resolution Radiometry (AVHRR) images acquired from the NOAA Coast Watch Group in La Jolla, California, were used to verify location of upwelling plumes (available for 1993-1994 and

1997-1999), and GIS was used to calculate the area and perimeter of upwelling plumes present during survey periods.

Conductivity-Temperature-Depth (CTD) data for 1992-94 and 1997-99 were acquired from the National Marine Fisheries Service (Tiburon, CA). Data were collected from casts conducted every 16 km at standard sampling stations (Fig. 1) using methods of Sakuma et al. (1996). A MATLAB computer program (Adams 1998, Moss Landing Marine Labs) was used to extract the following variables from each CTD station: (1) depth at the top of the most dominant thermocline, defined as the inflection point in the temperature profile at which the greatest change in temperature occurred over 20 m with a potential range from the surface to 180 m depth, (2) Delta-t was used as an estimate of the vertical component of the temperature gradient calculated as the temperature difference (nearest 0.1°C) between the top of the dominant thermocline to a point 20 m below it (Spear et al. 2001); and (3) depth of the 25.8 kg m⁻³ isopycnal (potential density anomaly surface). Thermocline depth and Delta-t were selected (as variables) because of their association with stratification and biological productivity. Water column stratification varies between upwelling (a mixing or destabilizing process) and relaxation (a stratification or stabilizing process; Gargett 1997). A deep thermocline and low Delta-t indicate weakly stratified ocean conditions, whereas a shallow thermocline and high Delta-t indicate strongly stratified ocean conditions. The 25.8 kg m⁻³ isopycnal is an isopleth consistently found in the upper 100 meters of seawater off central California (10 year climatology; Baltz 1997) that indicates salient seawater density characteristics

associated with upwelled water. The spatial distribution of this density is also a proxy for stratification and was selected (as a variable) because of its association with the dominant thermocline (Baltz 1997). This density isopleth rises and falls in response to wind stress, wind stress curl, wind relaxation events, and may vary with distance from shore (Baltz 1997). Higher density water nearshore, often associated with well-known upwelling centers, is an important upwelling signature: strong upwelling, with greater Ekman transport, results in denser water closer to the surface (a shallower 25.8 kg m^{-3} isopleth) and advection of denser water further offshore. Weaker upwelling and/or El Niño conditions results in a deeper 25.8 kg m^{-3} isopleth and indicates lighter water (usually warmer) near the surface (Baltz 1997). In this study, the term Sigma-t refers to this isopleth. For each CTD cast, the MATLAB program successively differentiated each temperature value from the surface to a maximum depth of 200 m, identified all inflection points, and then selected the inflection point depth with the largest Delta-t over 20 m. Each cast was visually inspected for inconsistencies and aberrant data were omitted from analyses. Because distributions were skewed, extracted CTD variables were tested for significant differences using a Kruskal-Wallis test and imported into ArcView. The Spatial Analyst Extension was used to map the CTD station locations, thermocline depth, Delta-t, and the 25.8 isopleth during 1992-94 and 1997-99. Vertical oceanographic variables at a scale of 16 km were interpolated with the Inverse Distance Weighted method to 4 km (sample unit scale). ArcView Spatial Analyst Reclassify Function was used to generate mean ($\pm$ SD) gridded cell counts for CTD variables. Reclassified cell counts were used to calculate mean ($\pm$ SD) proportions for thermocline depth, Delta-t,

and Sigma-t to provide a more complete view of the geographical extent of variables associated with vertical ocean structure.

The daily and monthly time series of upwelling index for 36° N 122° W (south of the study area) and 39° N 125° W (north of the study area) were obtained from the Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov/products/PFEL) and were used to identify the phasing and intensity of upwelling during survey periods. The upwelling index is a measure of offshore Ekman transport, and thus upward vertical motion near the coast, the main features of the upwelling process. Upwelling indices were expressed in metric tons per second per 100 m of coastline, and used as a measure of upwelling intensity and degree of variability. Positive values indicated upwelling (equatorward wind stress and offshore transport) and negative values indicated downwelling (onshore advection accompanied by a downward displacement of water). A comparison of upwelling indices before and during survey periods was used to provide insight into factors influencing ocean structure and marine mammal occurrence.

Bathymetry

ArcView 3.2 was used to map the bathymetry data acquired from U.S. Geological Survey (USGS) in Menlo Park, California. The bathymetric contours off central California have the following documentation: Datum: nad27; Projection: geographic; map scale: 1:250,000; arc increments 10 to 200 at 10 m intervals, 200-4000 at 50 m intervals. The bathymetric contours were optically scanned from the NOAA 1:250,000 charts for the area; the average mean distance between points was 250 m with

an average standard deviation of 184 m. Data files in dBase IV (Borland International, Scotts Valley, CA) format were imported into ArcView, and location of marine mammal sightings and sea surface isotherms derived from shipboard measurements were mapped and layered with the bathymetry data. All GIS map projections were UTM (Universal Transverse Mercator) 1983 zone 10.

Marine Mammal Distribution

The presence and absence of marine mammals per sample unit along track lines was tested for a non-random distribution. The binomial frequency distribution of animals present in paired sample units (PP), an animal present in one of the pairs (AP_PA), and no animals present (AA) was calculated for adjacent sample units and tested for significant differences between observed and expected frequencies. A coefficient of dispersion (CD) was calculated to quantitatively indicate the distribution by comparing the variance to mean ratio to one, with a 95% confidence zone of random dispersal (Fowler et al. 1998). If the observed CD was greater than the expected CD the distribution was most likely clumped; if observed CD was less than the expected CD, the distribution was most likely uniform; and if the observed and expected $CD \approx 1$, the distribution was most likely stochastic.

The occurrence of marine mammals relative to season and sea surface temperatures was investigated. Sighting rates, (expressed as the number of sightings per 100 km traversed), were calculated for all survey periods and tested for normality and homoscedacity. A two-sample t-test was used to test for significant differences among early and late spring survey sighting rates and among pinniped and cetacean sighting

rates. The grand mean of sea surface temperature (12.26°C; n = 19) was used to define warm (>12.26°C) and cool (<12.26°C) water survey periods. Because variances were not equal, a Mann Whitney U (Zar 1984) was used to test for significant differences in sighting rates between warm and cool water periods.

Proportions of sightings of species present during survey periods were calculated and graphed. Species composition was compared for each late spring survey period among years, and survey periods within years, using a percentage similarity index (PSI, Silver 1975): $PSI = \sum \text{minimum}(P1iP2i)$ where $P1i$ and $P2i$ are relative number of sightings of species from survey periods “1” and “2”, respectively. The value of the index ranges from 0 to 1.00 with values increasing as the similarity in species composition and in relative number of sightings of species increases between two survey periods. A significance level was arbitrarily set at 0.70 for a significantly similar index. Marine mammal species sighted infrequently were grouped for PSI analysis: gray whale (*Eschrichtius robustus*), minke whale (*Balaenoptera acutorostrata*), sei whale (*Balaenoptera borealis*), and unidentified Balaenopterids were mysticete sp.; common dolphin (*Delphinus capensis*), Risso’s dolphin (*Grampus griseus*), northern right whale dolphin (*Lissodelphis borealis*), killer whale, Cuvier’s beaked whale (*Ziphius cavirostris*), and unidentified odontocetes were odontocete sp.; and Steller sea lion (*Eumetopias jubatus*), northern elephant seal (*Mirounga angustirostris*), harbor seal (*Phoca vitulina*), and unidentified seals/sea lions were pinniped sp. Numerically dominant species were selected for the PSI analyses.

Marine Mammals and Ocean Habitat

Marine mammal sighting locations were mapped over sea surface isotherms and surface upwelling zones and were visually evaluated to assess trends among survey periods. ArcView was used to quantify sightings associated with the Pt. Reyes and Pt. Año Nuevo upwelling zones, and species were identified that occurred within and out of upwelling zones. A two-sample t-test was used to test for significant differences in sighting rates within and out of surface upwelling zones

Interpolated GIS maps of thermocline depth, Delta-t, and the 25.8 isopleth were overlaid with sighting locations and evaluated visually for trends. Vertical structures were linked to mammal sighting location and surface environmental data and exported for statistical analysis.

To determine which oceanographic variables were related to the presence and absence of marine mammals, SPSS version 10.0 was used to perform a backward stepwise multiple logistic regression based on the likelihood-ratio statistic. The binary dependent variable was the presence and absence of the numerically dominant marine mammals (cited above) and the continuous independent variables were depth of water, sea surface temperature, thermocline depth, Delta-t, Sigma-t (25.8 kg m^{-3}), and wind speed. Because logistic regression is sensitive to extremely high correlations among predictor variables (Tabachnik & Fidell 1996) the continuous predictor variables were screened for multicollinearity using a Pearson Correlation and correlated ($r > 0.60$) variables were not included in the analysis. Because the presence of an animal occurred

in only 25% of the sample units analyzed (number sample units with animal present divided by total number sample units, 736/2906), models performed well on the absence of animals. To more clearly explain the patterns revealed in logistic regression results, Principal Component Analysis (PCA) was used to investigate details among ocean habitat variables associated with the presence of marine mammals, and to assess the total variance and importance of each ocean habitat variable associated with marine mammal presence. PCA combines the ocean habitat variables into a set of factors and quantifies the total variance of ocean habitat variables associated with the presence of marine mammals. The factors (or components) are defined by the high-loading variables (component loadings). The higher the component loading, the more important the variable is in explaining the variance observed. Only component loadings ≥ 0.300 were interpreted as ecologically significant (Tabachnick & Fidell 1996). To reveal patterns of discrete assemblages, differences in PCA factor scores between species were tested for significance with a Kruskal-Wallis test (due to unequal variances) and Games and Howell multiple comparison tests (Day & Quinn 1989) were used to identify significant differences among paired comparisons.

Mid-water Trawls

Data regarding northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), Pacific hake (*Merluccius productus*), rockfish (*Sebastes* sp, shortbelly rockfish (*Sebastes jordani*), and *Loligo*, mid-water trawls conducted at night during survey periods (1992-94, 1997-99) were acquired from Tiburon Laboratories at the National

Marine Fisheries Service. Although spatial and temporal differences were too great for a direct comparison between mid-water trawls and marine mammal surveys, these data were used as a proxy for biological conditions and potential prey available to marine mammals. Catch Per Unit Effort (CPUE; number fish per number hauls), effort (number of hauls), and frequency of occurrence (FO; presence of each species/haul) were calculated.

RESULTS

Ocean Habitat

Sea surface temperatures were significantly different ($p < 0.001$), interannually, between early and late spring surveys during 1986-88 and 1992-94 and significantly different ($p < 0.001$) interannually between late spring surveys of 1986-1994 and 1997-1999 (Kruskal-Wallis one way ANOVA; Fig. 2 & 3). Mean sea surface temperatures during early spring surveys were $10.8^{\circ}\text{C} \pm 0.9$ SD (1987) to $13.8^{\circ}\text{C} \pm 0.5$ SD (1992), whereas mean sea surface temperatures during late spring survey periods were $9.6^{\circ}\text{C} \pm 0.9$ SD (1999) to $14.0^{\circ}\text{C} \pm 1.2$ SD (1997). Early spring sea surface temperatures were cooler than late spring in 1986 and 1987, similar in 1988, 1992 and 1993, and warmer in 1994. Sea surface temperatures of late spring during 1986, 1987, 1992, 1993, 1997 and 1998 were significantly warmer than 1988, 1989, 1994, and 1999. During 1999, Sweep 3 was significantly warmer than Sweep 1 ($p < 0.001$).

Qualitative comparisons between sea surface temperatures, wind speed, and daily mean upwelling index values indicated cooler sea surface temperatures coincided with

stronger wind speeds and relatively high upwelling index values, and warmer sea surface temperatures coincided with lesser wind speeds and relatively low upwelling index values (Table 2, Fig. 2 & 3). Except for 1986 and 1987, mean wind speed was less during early spring surveys than late spring surveys. For example, the relatively low wind speeds for early spring 1992-1993 coincided with negative upwelling indices and relatively warm sea surface temperatures. During late spring, the relatively high values of upwelling index coincided with greater wind speeds and cooler sea surface temperatures (1994 and 1999), whereas relatively lesser values of upwelling index coincided with relatively warmer sea surface temperatures and lesser wind speeds (1997 and 1998). The greatest difference in mean wind speed during late spring survey periods occurred between 1986 and Sweep 1 of 1999 (Fig. 3). Mean wind speed was more than twice as strong in 1999 (Sweep 1) than 1986. Comparisons of the spatial distribution of wind speed indicated no clear off-shore/inshore patterns were evident. In some cases (1992 and 1997) maps of wind data indicated a weak tendency for alongshore winds to increase offshore.

During 1992-1999 surveys, depth of thermocline, Delta-t, and depth of the 25.8 kg m⁻³ isopleth were significantly different among years and seasons with the Kruskal-Wallis one-way ANOVA ($p < 0.001$). The marked changes in vertical ocean structure in early and late spring coincided with marked changes in values upwelling index (Table 2). There were deeper thermoclines and less stratified ocean structure during early spring surveys (when upwelling index values were low or negative) than late spring surveys (when upwelling index values were relatively greater). The greatest difference in mean depth of the dominant thermocline between early and late spring occurred in 1993

(Fig. 4). During early spring of 1993, mean thermocline depth was twice as deep as late spring; 78% of the early spring survey area contained thermocline depths of 53.8 to 85.8 m, whereas 75% of the late spring survey area contained thermocline depths of 10.2 to 41.9 m. Mean 25.8 kg m^{-3} isopleth depth in early spring was almost twice as deep as late spring; in early spring of 1993, 69% of the survey area contained 25.8 kg m^{-3} isopleth depths of 93 to 121 m, whereas 64% of the survey area during late spring of 1993 contained 25.8 kg m^{-3} isopleth depths of 45 to 91 m. Delta-t in late spring increased almost two-fold compared with early spring; 68% of the area in early spring contained Delta-t values of 1.4°C to 2.0°C , whereas 69% of the area contained Delta-t values of 2.1°C to 3.5°C in late spring. Among late spring surveys, thermocline depths of 1998 (coincident with relatively low upwelling index values) and Sweep 1 of 1999 (coincident with relatively high upwelling index values) were deeper than all other surveys (Table 2). The greatest difference in mean depth of the dominant thermocline between late spring surveys occurred in 1997 and 1998 (Table 2). During late spring of 1998, mean thermocline depth was three times as deep as late spring of 1997; 67% of the 1998 survey area contained thermocline depths of 9 to 48 m, whereas 83% of the 1997 survey area contained thermocline depths of 3.9 to 18 m. In late spring of 1998, mean isopleth depth was 20 meters deeper, and Delta-t was less than in late spring of 1997. Although upwelling indices were relatively low during both years, the 1998 survey occurred near the end of a strong El Niño event.

During Sweep 1 and 3 of 1999, depth of thermocline and Delta-t, varied significantly (Kolmogorov-Smirnov Z test; $p < 0.001$). During 1999 (Sweep 1), mean

thermocline depth was more than twice as deep as during Sweep 3 (Table 2, Fig. 5); 76% of the survey area contained thermocline depths of 25.6 m to 68.9 m during Sweep 1, whereas 78% of the survey area contained thermocline depths of 6.3 to 30 m during Sweep 3. During Sweep 1, mean Delta-t values were approximately half the values of Sweep 3; 68% of the survey area during Sweep 1 contained Delta-t values of 0.3°C to 0.8°C, whereas 70% of the survey area during Sweep 3 contained Delta-t values of 1.0°C to 1.6°C. Because 25.8 kg m⁻³ isopycnal was only present during Sweep 3, no comparisons were conducted with this variable.

Marine Mammal Distribution

Twenty-two species of marine mammals were observed (five of which could only be identified to genus) including four species of mysticetes, eight species of odontocetes, five species of pinnipeds, and one species of fissiped (Table 3). Fifty-four percent of sightings were pinnipeds, 36% odontocetes, 9% percent mysticetes, and 0.5% mustelids. Numerically dominant species were California sea lion, northern fur seal, Pacific white-sided dolphin, Dall's porpoise, harbor porpoise, and humpback whale.

Marine mammals were widely distributed on and off the continental shelf and along the shelf-break during early and late spring surveys (Fig. 6 & 7). Generally, harbor porpoise were sighted near-shore and on the shelf (mean depth 60 m $\pm$ 56 SD, Fig. 6d & 7d), Pacific white-sided dolphins were sighted along the shelf-break (mean depth 1,042 m $\pm$ 864 SD; Fig. 6a & 7a), northern fur seals were observed in deep water (mean depth 2,789 m $\pm$ 1299 SD, Fig. 6b & 7b), California sea lions (mean depth 303 m $\pm$ 620 SD, Fig. 6e & 7e), humpback whales (mean depth 608 m $\pm$ 807 SD, Fig. 6f & 7f), and Dall's

porpoise (mean depth 877 m $\pm$ 1335 SD, Fig. 6c & 7c) were observed throughout the survey area.

Marine mammal sightings were not equally distributed among sample units along track lines during 1992 to 1994, 1997, 1998, and 1999 survey periods. Observed and expected binomial frequency distributions of the presence and absence of marine mammals per sample were significantly different for all survey periods ($p < 0.025$). Except for 1997 (when the observed Coefficient of Dispersion index (CD) was less than the expected, indicating the distribution was uniform), marine mammals displayed a clumped distribution.

Sighting rates of marine mammals did not differ significantly ($p > 0.05$) between early and late spring surveys regardless of year (Fig. 8). There were no significant differences between mean pinniped and mean cetacean sighting rates during early spring ($t = -0.84$, $df = 10$, $p > 0.05$), and no significant differences between mean pinniped and mean cetacean sighting rates during late spring survey periods ($t = 0.01$, $df = 22$, $p > 0.05$).

Although numerically dominant species (California sea lion, northern fur seal, Dall's porpoise, harbor porpoise, Pacific white-sided dolphin, and humpback whale) were sighted during most early and late spring surveys, percentages of each species varied (Fig. 9 & 10). Early spring species composition was significantly similar ($PSI > 70.0$) during 1987 and 1988, 1986-1994, and 1992-1993, with northern fur seals being seen more frequently during 1992 and 1993 (Table 4, Fig. 9). Pinniped species composition during early and late spring changed markedly in 1992 and 1993 with northern fur seals

seen more frequently in early spring, whereas California sea lions were seen more frequently in late spring. Species composition also was not similar between early and late spring surveys for other years (PSI=56.0 in 1986, PSI = 45.0 in 1987, PSI = 41.0 in 1988, PSI = 37.0 in 1992, PSI = 64.0 in 1994).

Species composition during late spring was significantly similar for 1992 and 1993, and for 1992 and 1998 (El Niño years) with California sea lions seen more frequently (PSI >70.0; Table 5, Fig. 10). Species composition also was significantly similar (PSI >70.0; Table 5, Fig. 10) in 1991, 1997, and 1999 Sweep 3 with northern fur seals, Dall's porpoise and humpback whales seen more frequently. Species composition during Sweep 1 of 1999 was markedly different than 1988, 1990, and 1992 with Pacific white-sided dolphin seen more frequently in 1999 and Dalls porpoise seen more frequently in 1988 and 1990.

Marine Mammals and Ocean Habitat

Sighting rates were correlated positively with mean sea surface temperatures (Pearson Correlation Coefficient = 0.57, $p < 0.01$; Fig. 11), but there were no significant differences ($p > 0.05$) in sighting rates during warm-water ($>12.26^{\circ}\text{C}$) and cool-water ($<12.3^{\circ}\text{C}$) surveys. During late spring surveys, the least sighting rate (3.1 sightings per 100 km traversed) occurred during 1988, a relatively cool-water period (mean $11.0^{\circ}\text{C} \pm 0.9$ SD), whereas the greatest sighting rate (15.5 sightings per 100 km traversed) occurred during 1997, a relatively warm-water period (mean $14.0^{\circ}\text{C} \pm 1.2$ SD). This pattern, however, was not observed during early spring surveys where the greatest sighting rate (8.2 sightings per 100 km traversed) occurred during 1992, a relatively

warm-water period (mean $13.7^{\circ}\text{C} \pm 0.5$ SD), and the least sighting rate (2.1 sightings per 100 km traversed) also occurred during a relatively warm-water period (1994; mean $13.0^{\circ}\text{C} \pm 0.3$ SD).

There are two considerations in interpreting results of the stepwise logistic regression analyses. First, there was a significant correlation (>0.60) between the depth of Sigma-t (depth of the 25.8 kg m^{-3} isopleth) and thermocline depth, and between Delta-t and thermocline depth ($>.60$). Therefore, when thermocline depth was included in an analysis, Sigma-t and Delta-t were excluded, and when Sigma-t and Delta-t were included, thermocline depth was excluded. Second, marine mammals were observed in only 25% of the 2,906 sample units, therefore, multiple logistic regression models tended to predict conditions associated with absence rather than presence. Because the thermocline depth model did not perform well, only the Sigma-t model was used in the final analysis. When all species were combined for the 1992-1998 survey periods, stepwise logistic regression indicated three variables were important for predicting presence and absence of marine mammals: depth of water, wind speed, and Sigma-t (Table 6). For all species combined, the Sigma-t model indicated that as wind speed increased, the likelihood that animals were present or seen decreased and, as the depth of Sigma-t increased, the likelihood that animals were present decreased. Depending on species, most marine mammals generally were found where Sigma-t depths were relatively shallow and wind speeds were low, however, some species were found where Sigma-t was deeper and when wind speeds were greater.

For each species, stepwise results indicated wind speed was significant for all but California sea lion. Sea surface temperature was significant in predicting presence of Dall's porpoise and harbor porpoise indicating Dall's porpoise were found in relatively cooler water whereas harbor porpoise were found in relatively warmer water. Dall's porpoise however, also were found in warmer water. Depth of water was significant for predicting presence for all but Pacific white-sided dolphin, indicating these dolphins were found over the shelf-break where they were present in shallow and deep water depending on their relative position to the shelf break. Northern fur seals were found off the continental shelf in deeper water, whereas harbor porpoise, California sea lions, and humpback whales were found on the continental shelf in shallower water.

There was a significant correlation (>0.60) between thermocline depth and Delta-t, and Sigma-t and thermocline depth, when associated with presence of marine mammals. Therefore, variables used for Principal Component Analysis (PCA) were depth of water and Sigma-t, Delta-t, sea surface temperature, and wind speed. Presence of all mammals combined yielded two ocean habitat descriptors (factors) that explained 68.4% of the variance observed (Table 7). Factor 1 indicated that presence of different marine mammal species was dependent on water depths and depth of Sigma-t, and Delta-t values. Factor 2 indicated that presence of marine mammals species was dependent on sea surface temperatures and wind speed (Fig. 12).

Factor scores, representing a suite of variables for each sighting of each species were plotted (Fig. 13) and both factor scores were significantly different among dominant species (Factor 1 and Factor 2: Chi-square $p < 0.001$). Pairwise multiple comparison

tests indicated northern fur seal and Dall's porpoise factor scores were significantly different than factor scores of all other species and were found in deeper depths of water. Northern fur seals also were found where Sigma-t depths were deeper, sea surface temperature was warmer, and wind speed was reduced, whereas Dall's porpoise were found in a range of ocean habitat conditions (cool and warm sea surface temperatures, reduced and stronger wind speeds, high and low Delta-t, and moderate to deep depths of Sigma-t). California sea lions were found in a variety of sea surface temperatures, however, their occurrence differed from northern fur seals because they occurred in shallower water, shallower Sigma-t and greater Delta-t. Harbor porpoise also were found in shallower depths of water, warmer sea surface temperatures, reduced wind speed, shallower Sigma-t, and greater Delta-t. Pacific white-sided dolphins and humpback whales were found where there were moderate depths of water and Sigma-t values, moderate sea surface temperatures, and greater Delta-t values.

Mapping results of surface and vertical structure overlaid with sighting locations supported the descriptive and multivariate statistical results. Comparisons of GIS generated maps indicated distinct similarities and differences among and within years. For example, mapped sea surface isotherms for early and late spring survey of 1993 (Fig. 14), verified by composite AVHRR images (Fig. 15), indicated marked contrasts in surface ocean structure. During early spring surveys in 1993, no upwelling plumes were present, sea surface temperatures were relatively warm, and sighting rates were relatively low (5.6 sightings/100 km traversed). In contrast, during late spring of 1993 (El Niño year), although sea surface temperatures were relatively warm ($13.9^{\circ}\text{C} \pm 2.0 \text{ SD}$), sea

surface isotherms and the AVHRR image indicated presence of upwelling near Pt. Reyes and Pt. Año Nuevo that coincided with greater sighting rates (8.4 sightings /100 km traversed).

During late spring surveys, maximum upwelling and coincident cold-water plumes were present near Pt. Reyes for all surveys, whereas plume presence near Pt. Año Nuevo was more variable (seven of 13 late spring surveys; Table 8). The persistent, relatively large upwelling plume (mean = $2,110 \text{ km}^2 \pm 1005 \text{ SD}$, $n = 12$) near Pt. Reyes varied from 4.7 to 23% of the survey area, whereas the Pt. Año Nuevo upwelling plume was only 0.1 to 6% of the survey area (mean = $191 \text{ km}^2 \pm 286 \text{ SD}$, $n = 8$; Table 8). Plume perimeter at Pt. Reyes (mean = $290 \text{ km} \pm 64 \text{ SD}$) and Pt. Año Nuevo (mean = $51 \text{ km} \pm 38 \text{ km SD}$) also varied among survey periods. During Sweep 1 of 1999, 34% of the survey area contained a large plume near Pt. Reyes that extended along the coast to Pt. Año Nuevo creating the largest cool-water plume ($6,142 \text{ km}^2$) observed among all late spring survey periods.

Sighting rates during late spring surveys were greater within than outside surface upwelling zones in seven of 13 survey periods (Fig. 16), however, these results were not statistically significant ($t = 0.115$, $df = 24$, $p > 0.05$). Although there were no correlations between sighting rates and plume area (Pearson Correlation Coefficient = -0.079 , $p = 0.797$) or perimeter (Pearson Correlation Coefficient = -0.272 , $p = 0.369$), sighting rates and mean upwelling indices during 1992-1994 and 1997-1999 surveys were negatively correlated (Pearson Correlation Coefficient = -0.876 , $p = 0.01$; $n = 7$). Cetacean sightings in upwelling zones were greater than pinniped sightings in seven of 13

survey periods, whereas pinnipeds were sighted more frequently than cetaceans within upwelling zones during the 1992-93 El Niño years (Table 9). Sixty-six percent of pinniped sightings within upwelling zones were California sea lions; 42% of cetacean sightings were Dall's porpoise, and 22% were harbor porpoise.

During late spring surveys, sighting rates were greater when relatively cool upwelling plumes were present and water was stratified, as noted by relatively warm sea surface temperatures, relatively shallow depths of thermocline and Sigma-t, relatively high Delta-t, and relatively low upwelling index values (Tables 2 & 10). Survey maps of late spring for 1993 provided examples of the relationships between locations of sightings and ocean structure. During late spring of 1993, relatively high sighting rates coincided with presence of upwelling plumes and relatively warm sea surface temperatures (Fig. 14b). Ocean conditions were relatively stratified as indicated by relatively shallow thermocline depth and Sigma-t (Fig. 17a,b), relatively high Delta-t, and relatively low upwelling index values (Table 2). In contrast, the map for Sweep 1 of 1999 provided an example of fewer sightings that coincided with weakly stratified ocean structure: presence of upwelling plumes, relatively cool sea surface temperatures, relatively deep thermocline depth, reduced vertical temperature gradients, the greatest mean wind speed of all surveys, and greater upwelling indices (Table 2, Fig. 18a,b). Maps of Sweep 1 and 3 1999 also are examples of the marked changes in ocean structure and sighting rates that occurred within an upwelling season. Although upwelling plumes were present during both survey periods, the area of the surface upwelling zone in Sweep 1 (34% of survey area) was almost three times as great as the area of the surface upwelling zone

(12% of survey area) in Sweep 3 (Fig. 18a,b). During Sweep 1, the lesser sighting rates coincided with significantly cooler sea surface temperatures, greater wind speeds, and ocean structure that was less stratified. The greater sighting rates observed during Sweep 3 coincided with relatively warmer sea surface temperature, a reduction in mean wind speed, and ocean structure that was more stratified than during Sweep 1 (Tables 2 & 10).

Mid-water Trawls

Species composition of mid-water trawls, Catch Per Unit Effort (CPUE), and frequency of occurrence (FO) of northern anchovy, Pacific sardine, Pacific hake, rockfish spp., and squid varied markedly among late spring survey periods (Fig. 19, 20, & 21). During 1993 and 1997, the relatively high CPUE coincided with relatively warmer water, and well-stratified ocean conditions. Hake was the numerically dominant species during 1993 and 1997, and occurred in greater than 40% of the hauls in 1993 and 70% of the hauls in 1997. However, proportions and frequency of occurrence of hake also were relatively high during 1994 and 1999 coincident with relatively low CPUE (<200 fish per haul), relatively cooler water, and weakly stratified ocean conditions. CPUE was markedly reduced in a strong El Niño year (1998) when 50% of the total catch was sardine and in cool-water years (1994 and 1999) when either no sardines were caught (1994) or proportions were < 10% (1999).

DISCUSSION

Off central California, upwelling is the dominant process that drives development of the California Current food web (Glantz & Thompson 1981), and due to the phasing of the upwelling process, ocean conditions vary both seasonally and annually. During early spring surveys, conditions reflected those that occur during the Davidson Current season, a time when winds are southerly, and horizontal and vertical temperature gradients are reduced (Bolin & Abbot 1963, Chavez et al. 1991). The “spring transition”, a time when southward winds along the west coast of North America increase as a result of the strengthening and shifting of the North Pacific high pressure system, often occurs sometime from mid-March (Kosro et al. 1991) through April (Breaker & Mooers 1986), but can occur as early as February (Strub et al. 1987). Before the spring transition, ocean structure during March 1993 and 1994 included less spatial variability; relatively constant sea surface isotherm distributions; absence of upwelling plumes; relatively uniform temperatures to considerable depths; deep thermocline and Sigma-t, and relatively low upwelling index values (Fig. 22) that are characteristic of the Davidson Current season (Kosro et al. 1991, Schwing et al. 1994). The San Francisco Bay plume, another typical temporal feature, extended west-southwest from the Golden Gate (Schwing et al. 1991), during the 1993 and 1994 surveys.

In contrast to early spring surveys, late spring surveys were conducted during the peak of the upwelling season (May-June, Baltz 1997; Fig. 22), and observed surface features and vertical structure reflected well-established upwelling conditions off central

California. Hydrography during late spring surveys was affected by the onset, intensity, duration, and relaxation of upwelling events, coupled with mesoscale effects of El Niño and La Niña (Schwing et al. 1991, 1997, Parker 1996, Sakuma et al. 1994, 1995, 1996, Baltz 1997, Ralston et al. 1999, Steger 2000). Although ocean structure was similar during all late spring surveys (presence of plumes with relatively dense water on the continental shelf), the variability in local short-term wind forcing (Fig. 23), and anomalies in large-scale atmospheric and ocean forcing (Hayward et al. 1994, Schwing et al. 1997, Lynn et al. 1998) resulted in distinct differences in surface plumes and vertical structure. In a three-year study, Parker (1996) found the Pt. Reyes filament (plume) was persistent (observed throughout the upwelling season and in each year surveyed), and upwelled water extended offshore and equator-ward. In my study, plumes of upwelled water near Pt. Reyes were observed during all late spring surveys; however, the Pt. Año Nuevo plumes were less persistent. Parker (1996) also found the response to upwelling-favorable winds at Pt. Año Nuevo and Pt. Reyes was different: the Pt. Año Nuevo plume only occurred during periods of prolonged upwelling winds and quickly dissipated as winds decreased, whereas the Pt. Reyes plume persisted despite lack of winds (Parker 1996). These conditions may have caused the observed differences in mapped sea surface isotherms: Pt. Reyes and Pt. Año Nuevo plumes were coincident in only 7 of the 13 late spring survey periods. The observed denser water over the continental shelf, with dense water shoaling near-shore and deeper off shore, (coincident with the surface plumes) indicated effects of the upwelling process (Baltz 1997).

On a local scale, differences in ocean structure also were the result of two basic hydrographic states, upwelling and relaxation (Send et al. 1987, Rosenfeld et al. 1993). Oscillations occur between persistent equator-ward, alongshore wind and wind relaxation events. Upwelling favorable winds strengthen and relax at 3 to 10 day (Schwing et al. 1991) or 20-day intervals (Baltz 1997), and multiple upwelling-relaxation events occur from approximately March to September. Steger (2000) found that each time wind relaxations were observed, surface waters in the Gulf of the Farallones became fresher and warmer. Furthermore, the persistent recurring circulation feature at Pt. Reyes (Parker 1996, Baltz 1997), allowed recently upwelled water to mix with older upwelled water, and circulation patterns allow this water to be retained within distinct boundaries that persist during relaxation events (Parker 1996). Most of the Gulf of the Farallones is in the upwelling shadow of the Pt. Reyes upwelling center (Ralston et al. 1999). During relaxation, weaker winds allow the warmer California Current water to move shoreward, whereas upwelling centers at Pt. Reyes and to a lesser extent Pt. Año Nuevo, continue to be a source of relatively cold water that pulses intermittent injections of nutrients into the region (Parker 1996). During this study, differences in distribution and size of upwelling plumes and vertical structure observed during late spring surveys reflected these upwelling and relaxation events (Fig. 23). Husby & Nelson (1982) reported strong similarities among thermocline depth and Δt and the timing and intensity of upwelling, the upwelling index, and wind, similarities also observed in this study. Strong winds and relatively greater upwelling indices before and during surveys resulted in cooler sea surface temperatures, a relatively broad extension of the upwelling plumes,

and relatively weak stratification, whereas relatively mild upwelling before surveys (with weaker winds and relaxation of upwelling during time of surveys) coincided with a relative reduction in size of surface upwelling plumes, stronger stratification, shallower thermocline depth and Sigma-t (25.8 kg m^{-3}), and greater vertical temperature gradients, features consistent with a decrease in upwelling.

A comparison of surveys in 1994, and 1999 provided examples of marked variability of upwelling intensity within an upwelling season. The upwelling during late spring 1994 was an example of a typical upwelling signal, with recently upwelled water, relatively cool temperature ranges, and a relatively high upwelling index throughout the survey period (Fig. 15 & 23), indicating this was a relatively intense upwelling phase. During Sweep 1 of 1999, the mean weekly upwelling index ($215 \text{ m}^3/\text{s}/100\text{m}$ of coastline; Fig. 23) indicated more intense upwelling than during 1994, and was an example of larger scale effects on local upwelling conditions. The cold water that was encountered ($\sim 7.5^\circ\text{C}$) coincided with La Niña, and Ralston et al. (1999) reported the low temperatures encountered in the Pt. Reyes plume during Sweep 1 were the lowest in 17 years of observation. During the 1999 upwelling season, La Niña conditions were evident along the entire coast, and upwelling anomalies were among the greatest in over a 50-year record of the upwelling index (Bograd et al. 2000, Hayward et al. 1999, Schwing et al. 2000). Within the survey area, the large ($6,142 \text{ km}^2$) upwelling plume extended along the coast and coincided with relatively high winds and upwelling index values and weak stratification (Fig. 23, Table 2). A comparison of Sweep 1 and 3 of

1999 provided an example of intense upwelling followed by a brief period of relaxation within a short time scale (2-week period): a marked reduction in upwelling just before Sweep 3 (Fig. 23) followed by an increase and relaxation during the survey, resulted in warmer sea surface temperatures and more stratified ocean structure during Sweep 3.

In contrast to surveys conducted during intense upwelling, surveys conducted during 1993, 1997, and 1998 occurred during periods of relaxation or reduced upwelling (Fig. 23). For example, just before the survey period in 1993, Sakuma et al. (1994) reported conditions were downwelling favorable indicating a significant relaxation event had occurred (Parker 1996). The 1993 survey is an example where brief periods of weak upwelling (evident in the sea surface isotherms and upwelling index) were preceded by relaxation of upwelling (Fig. 23) that resulted in increased stratification. The survey periods in 1997 and 1998 also were examples of upwelling conditions during relaxation events (Fig. 23). Early in 1997, before the survey period, upwelling indices were greater than normal along northern California, but by May, upwelling was reduced dramatically along the entire coast (Schwing et al. 1997). During surveys, daily upwelling indices for 1997 and 1998 were relatively low, indicative of weak upwelling (Fig. 23). However, regional effects of El Niño off San Francisco also were evident, with sea surface temperatures above seasonal norms during 1993 (Hayward et al. 1994, Sakuma et al. 1994), 1997, and 1998. Ocean structure during these surveys reflected local upwelling/relaxation events coupled with large-scale effects of an El Niño.

Large-scale El Niño events off central California have been well studied (Barber and Chavez 1983, McLain & Thomas 1983, Hayward 1993, Lenarz et al. 1995, Ramp et al. 1997, Schwing et al. 1997, Lynn et al. 1998), and result in warmer sea surface temperatures and depressed thermoclines that reduce nutrient enrichment derived from local wind-driven Ekman transport. El Niño events that occurred during survey periods (1986-87, 1992-93, 1997-98) varied in intensity and duration (Rasmusson & Carpenter 1982, Wolter 1987, Wolter & Timlin 1998), and off central California, arrived as a series of pulses that traveled up the coast (Ramp et al. 1997). The warmer water during early and late spring 1992-1993 was the result of a continuation of the El Niño during 1991-1993 (Sakuma et al. 1994), and the late spring surveys also provided an example of the persistent Pt. Reyes plume, evident even during El Niño conditions (Schwing et al. 1997). During the late spring survey of 1993, thermocline depth was not depressed significantly, and 69% of the survey area in 1993 contained the greatest vertical temperature gradient of all late spring surveys used in the analysis, indicating well-stratified conditions because of relaxed winds. However, surveys conducted in 1997 and 1998 occurred just before (1997) and just at the end (1998) of an El Niño. The multivariate El Niño index indicated the El Niño of 1997/98 was one of the strongest on record since 1957, however, in its early stages impacts were small in the North Pacific (Lynn et al. 1998). The strong upwelling that occurred early during 1997 mitigated the effects of downwelling (Schwing et al. 1997), and although the Pt. Reyes plume was present and sea surface temperatures were elevated in both years, vertical structure was well-stratified in 1997 (before the onset of El Niño) and markedly depressed during 1998

(after El Niño). This resulted in relatively greater fish catches and marine mammal sighting rates during 1997, and low fish catches with relatively high marine mammal sighting rates during 1998. These surveys provided an example of the effects of timing/intensity of local events coupled with the timing/intensity of large-scale events on biological conditions.

Prey potentially available to marine mammals during early spring, such as northern anchovy, Pacific hake, and Pacific sardine, are schooling fishes seasonally abundant in the California Current System that spawn several times per year for several years. These fishes are distributed from British Columbia, Canada, to Baja, Mexico, and encompass regions of different seasonal sea surface temperatures, productivity, and zooplankton biomass (Saunders & McFarlane 1997). They spawn during winter and spring, and to reduce the effects of advection and potential loss of eggs and larvae offshore, spawning may take place before the spring transition (Parrish et al. 1981, Bakun & Parrish 1982). During winter, when upwelling is reduced or mild, juvenile rockfish are less likely to be advected offshore or affected by turbulence (Ainley et al. 1993). Northern anchovy spawn off southern California from December to April; however, off California, anchovy eggs and larvae are present throughout the year along the entire coast (Hernandez-Vazquez 1994). Pacific sardines also spawn off southern California (Feb-June with peaks in May-June) and off Baja (Feb-May with peaks in March). Hake, one of the most abundant fish species along the west coast of North America (Horne & Smith 1997), migrate annually between spawning grounds (off Cape

Mendocino to Baja California) and summer feeding grounds (located from central Oregon to northern Vancouver Island; Saunders & McFarlane 1997). Spawning occurs seaward of the shelf break between January and March off southern California; during the northward migration, adults move towards shore, where they feed along the coastal shelf and slope off California, Oregon, and Washington and are potential prey for marine mammals.

During late spring, marine mammal prey are affected by upwelling intensity and relaxation. Because relaxation events incubate nutrient rich water and can result in food web development, upper trophic level marine predators are affected by the onset, intensity, and relaxation of upwelling (Schwing et al. 1991, Rosenfeld et al. 1994, Parker 1996, Baltz 1997). Local upwelling patterns and their effects on trophic levels have been well documented (Sakuma et al. 1995, Parker 1996, Hayward et al. 1999, Ralston et al. 1999). The persistent pulsed injections of nutrient-rich upwelled water from Pt. Reyes and Pt. Año upwelling centers are linked to the unique features of the coastal capes, points, and bathymetry, resulting in complex mixtures of water masses with a long residence time, creating pockets along the coast where high productivity can occur (Parker 1996). During active, intense upwelling, chlorophyll, total production, and sea surface temperatures are relatively low, but nitrate is high (Pennington et al. 2000). Depending on local conditions, high concentrations of chlorophyll develop near shore and are exported offshore and downstream from upwelling centers (Chavez et al. *in press*) or offshore of the wind-driven coastal upwelling region (Schwing et al. 1997). In

the Gulf of the Farallones, the spatial and temporal distribution of primary productivity is highly variable and influenced by the Pt. Reyes upwelling filament (Ralston et al. 1999). Sweep 1 of 1999 (strong upwelling) provided an example of intense upwelling that resulted in offshore transport of nutrients and phytoplankton (phytoplankton was primarily off the shelf; Ralston et al. 1999). Furthermore, oscillations between upwelling favorable winds and relaxations in the wind field result in weekly fluctuations of phytoplankton abundance (Ralston et al. 1999), and during relaxation or moderate upwelling intensity, high chlorophyll coincides with greater larval fish abundances, coupled with medium to large adult biomass (Denman & Powell 1984, Cury et al. 1995). Depending on intensity of upwelling events, larval northern anchovy, hake, or rockfish may be advected off shore (Cury et al. 1995; Parrish 1981, Ainley et al. 1993, Horne & Smith 1997), whereas during relaxation events, when warm water flows poleward from the Gulf of the Farallones, this region is an important retention area for plankton and fish larvae that become concentrated in the relaxation flow south of Pt. Reyes (Wing et al. 1998). Furthermore, Larson et al. (1994) found retention and onshore movement of all sizes of rockfish during relaxation of upwelling, and distribution of juvenile rockfish correlated with a sharp, shallow thermocline with several species and size groups abundant above the sharp thermocline. The 1993 and 1997 surveys provided examples of relaxation or reduced upwelling events that coincided with relatively high CPUE and relatively well-stratified ocean conditions whereas the 1994 and 1999 Sweep 1 and 3 surveys provided examples of intense upwelling that coincided with relatively low CPUE

(NMFS mid-water trawls), and weakly stratified and well-mixed ocean conditions (1999).

El Niño events that affect central California also result in short-term and long-term effects on prey resources. Several decades of studies on northern anchovy and sardines (Lenarz et al. 1995) indicated significant correspondence between the climatology of the California Current System and fluctuations in population structure. During 1997-98, ocean climate changes associated with El Niño affected distributional patterns of hake, northern anchovy, and sardine. During 1998, hake shifted north, anchovy abundance and spawning area (coupled with a response to El Niño) continued to decrease, and sardine egg distribution was greater off central California than southern California during spring of 1997/98 (Hayward et al. 1999). In this study, the lowest CPUE (NMFS trawl surveys) of all surveys used in this comparison occurred during the strong El Niño of 1998, with low abundances of anchovy, sardine, hake, rockfish, and squid, consistent with studies cited above. These shifts in distribution and fluctuations in population structure lead to variation in the food supplies available to marine mammals.

Marine Mammal Distribution and Ocean Habitat

Marine mammals are mobile, patchily distributed predators, and seasonal north-south shifts or inshore-offshore shifts in distribution of the six dominant species off central California has been well documented (Antonelis & Fiscus 1980, Kajimura 1980, Bonnell 1983, Dohl et al. 1983, Black 1994, Calambokidis et al. 1988, 1989, 1990, 1991, Forney & Barlow 1998, Forney 2000). Seasonal shifts in distribution of pinnipeds and

cetaceans are related to large-scale oceanographic events (El Niño/La Niña), migrations (e.g. humpback, California sea lion, and northern fur seal), or movements in response to warm or cool-water conditions related to shifting prey (e.g. Dall's porpoise, harbor porpoise, Pacific white-sided dolphin). A comparison of early spring surveys of 1992 and 1993 with early spring of 1994 provided examples of the striking variation in sightings of northern fur seal that probably was caused by shifts in distribution related to an El Niño. Northern fur seals from San Miguel Island and the Pribilof Islands migrate to central California (Kajimura 1980, Kenyon & Wilke 1953, Pyle et al. 2001). During autumn, adult female and juvenile northern fur seals migrate into water over the continental shelf and slope of the eastern North Pacific and congregate in areas of abundant food supply (Antonelis & Perez 1984). Greatest numbers occur off central California during February and March, and as their northward migration begins in April and May, abundance declines (Kajimura 1984). Off California, important prey species of northern fur seals are northern anchovy (Kajimura 1984), Pacific hake, and market squid (Antonelis & Perez 1984). Because northern fur seals are opportunistic and feed on a wide range of seasonally abundant prey, greater numbers of northern fur seals sighted during early spring 1992-1993 indicated northern fur seals may have responded to an increase in prey availability off central California, whereas fewer sightings in the early spring of 1994 indicated they may have been feeding further north.

Northern fur seal sighting patterns also may have been affected by sighting conditions during surveys. The probability of detecting small inconspicuous animals such

as northern fur seals, Dall's porpoise, and harbor porpoise is a function of sea state conditions (Barlow 1988, Barlow & Forney 1994). Because wind speed and upwelling indices during the early spring 1994 were greater than those during 1992-93, these conditions may have resulted in under counting these small inconspicuous species. It also should be noted that wind speed was a significant variable in PCA and logistic regression. However, because survey effort during early spring of 1994, was approximately half the effort during early spring of 1992-1993 (Table 1), sighting rates and species composition patterns may be too incomplete for meaningful comparisons.

During late spring surveys, when upwelling plumes were present, the data were not consistent with my hypothesis that more sightings would occur within than outside of upwelling zones. No clear pattern in location of sightings or sighting rates relative to upwelling plumes was evident. Because the plume areas were not adequately surveyed, the lack of a clear pattern may be a function of sample design. Another possibility is the criteria used to define upwelling zones may not have been sufficiently linked to subsurface features. In this study, cool water plumes used to identify upwelling zones represented surface structure only. Consideration of vertical structure may have provided a more complete definition. Parker (1996) found the Pt. Reyes plume fluctuated in location and magnitude on a synoptic scale, and fluctuations did not appear linked to the wind field. Because the Pt. Reyes filament is driven by responses to the topography of the local coastline coupled with Ekman transport, surface upwelling plumes and subsurface density structure considered collectively may be a more

meaningful representation of the coastal upwelling signature used to define an upwelling zone at Pt. Reyes. Indeed, many of the effects of upwelling (e.g. modified temperature distribution, density distribution, nutrient distribution), may reflect the importance of a three-dimensional circulation (Breaker & Mooers 1986) that may extend well beyond the zone of active upwelling (Huyer 1983). Several other important considerations related to the unique features of the Pt. Reyes upwelling region include the Pt. Reyes Headlands, that deflect currents and winds creating an “upwelling shadow” (Steger et al. 2000), a continental shelf that widens to almost 50 km, and unique circulation features. Steger et al. (2000) reported complex circulation features that included newly upwelled water, oceanic water, San Francisco Bay outflow water, and a mixture of these three types. Circulation also included submesoscale eddy activity associated with the Pt. Reyes upwelling region, and a strong poleward Slope Counter Current, all providing additional support of the importance of a three-dimensional consideration of this region.

Although all six dominant species of marine mammals were sighted during most late spring survey periods, distinct differences in sighting rates and species composition likely reflected fluctuations in oceanographic conditions and subsequent prey availability. The Sigma-t logistic model indicated reduced wind speed and a shallow Sigma-t were associated with presence of marine mammals and sea surface temperature, wind speed, Delta-t, Sigma-t, and depth of water were interpreted as ecologically significant for interpreting where marine mammals were present.

During late spring, marine mammals would benefit from increases in foraging opportunities if prey densities increase as upwelling relaxes. Prolonged calm winds possibly result in concentration or stabilization of prey whereas prolonged strong winds may result in the dispersal of prey. Based on logistic models and PCA, greater sighting rates coincided with relaxed or reduced upwelling, stratified ocean conditions, and greater trawl catches, conditions that may have stabilized or concentrated marine mammal prey. In contrast, lesser sighting rates coincided with intense upwelling, well-mixed ocean conditions, and lesser trawl catches, conditions that may have dispersed marine mammal prey. These conditions indicated a strong association between the timing of upwelling processes, stable prey resources, and marine mammal sightings.

The 1997 and 1998 survey periods also were examples of the strong association between the timing of both local and large-scale events and ocean structure. The late spring survey of 1997 was an example of ocean conditions during relaxation of upwelling, just before the onset of the strong El Niño of 1998. The upwelling index was the lowest of all late spring surveys and coincided with a thermocline depth that was the shallowest of all surveys and the second highest Delta-t values. The relatively well-stratified ocean conditions of the 1997 survey coincided with a relatively high CPUE (with hake the predominant species), and the highest sighting rates of marine mammals of all surveys. During early 1997, values of chlorophyll and primary productivity were distributed normally; however, values declined towards shore by the oceanic season (Chavez et al. *in press*). By the 1997-1998 Davidson Current season, values of

chlorophyll were relatively low and failed to develop during the strong El Niño of 1998 (Chavez et al. 2000). During 1997, distribution of sardine eggs was greater off central California than southern California, with a broad, off shore extent (Lynn et al. 1998). The greater sighting rates of marine mammals probably were a result of the productive conditions that occurred during this survey period.

In contrast, the late spring survey of 1998 was an example of ocean conditions just after one of the largest El Niños in more than 50 years (Hayward et al. 1999). During 1998, the California Current was pressed against the coast, and during April-May, upwelling was unusually weak (Lynn et al. 1998) with a depressed thermocline and Sigma-t, and weak vertical temperature gradients. The spatial distribution of primary productivity was limited to shelf and near-shore coastal regions (Ralston et al. 1999, Chavez et al. *in press*) and except for a narrow band nearshore (approximately 50 km), values were extremely low (Chavez et al. *in press*). Distribution of sardine eggs also was narrow and near the coast (Lynn et al. 1998). Abundance of macrozooplankton was the lowest in 50 years of the CalCOFI time series (Lynn et al. 1998), and CPUE of only 61 fish/haul was one of the lowest during my study period. Catches of all rockfish were the least since 1983, when the NMFS trawl surveys began (Hayward et al. 1999). Because spawning hake shift north during warm-water years and south during cold-water years (Horne & Smith 1997), the low abundance of hake in 1998 indicated hake might have shifted to the north during that El Niño (Hayward et al. 1999). Despite the apparent low productivity, sighting rates during 1998 were the second highest of all surveys. This

indicated marine mammals were either moving through the survey area during the survey period, or were responding to localized prey patches that were limited to the shelf and near-shore regions (Lynn et al. 1998, Ralston et al. 1999). A relatively large school (approximately 1,300) of common dolphins (a warm temperate species sighted only three times during all years surveys were conducted) was sighted during 1998, reflecting this species shift in distribution in response to seasonal and interannual changes in ocean conditions reported by Forney & Barlow (1998) and Forney (2000).

The variability in cetacean and pinniped species composition reflected well-documented temporal and spatial movement patterns. Pacific white-sided dolphins and Dall's porpoise, temperate-water species with distinct seasonal north-south shifts in distribution off central California (Forney 2000), were species that were sighted during cool-water (and relatively intense upwelling) periods as well as warm-water (and reduced/relaxed upwelling) periods. Pacific white-sided dolphins are present year round; however, group size changes with season, with smaller mean group size during the cooler upwelling season and larger group size during the warmer, oceanic season (Black 1994). I observed similar patterns: during intense upwelling (1999 Sweep 1), mean group size was only 4.8 animals per sighting. During the 1997 warmer water survey, however, sighting rates were 0.8 sightings per 100 km traversed and mean group size was 24.6 animals per sighting (Table 10). Greater group size was coincident with higher catches of squid, hake, and rockfish (NMFS mid-water trawls), prey of Pacific white-sided dolphins. Pacific white-sided dolphins are opportunistic predators that feed on abundant

fishes and cephalopods; fluctuations in sightings indicated these dolphins might have been responding to changes in prey availability related to timing of upwelling or effects of El Niño. The relatively high variability in ocean habitat variables associated with Pacific white-sided dolphin sightings may explain PCA and logistic regression results that indicated no significant association with ocean habitat variables. However, Black (1994) found relative abundance of dolphins was greatest near the shelf-break and up to 10 km beyond it, in Carmel Bay, and near the northern rim of Monterey Submarine Canyon. Black (1994) also found Pacific white-sided dolphins were more abundant and occurred closer to the shelf-break when sea surface temperature anomaly was high.

The variability of Dall's porpoise sightings reflected seasonal shifts in their distribution. Greater number of sightings and sighting rates of Dall's porpoise during cool water periods is consistent with other studies. Barlow & Gerrodette (1996) and Forney (2000) found greater abundances and greater encounter rates of Dall's porpoise off California during cool water years. Dall's porpoise shift southward during cooler water periods (Barlow & Forney 1998), and the variability in sighting rates among survey periods observed during this study may be attributed to these shifts in distribution. Dall's porpoise eat Pacific hake, northern anchovy, Pacific saury, and cephalopods of the family Gonatidae (Stroud et al. 1968); greatest numbers of sightings occurred during 1994 and 1997, which coincided with relatively high catches of Pacific hake (NMFS mid-water trawls). Although the greatest number of sightings occurred in the 1994 cool-water, relatively intense upwelling period, it is possible these results may be due to more

extensive survey coverage in the cool-water plume area during the 1994 late spring survey. Furthermore, relatively strong winds during the intense upwelling surveys likely affected the probability of sighting small, inconspicuous animals on tracklines (Barlow 1988, Barlow & Forney 1994). For example, sightings of Dall's porpoise ($n = 3$ sightings), harbor porpoise ($n = 0$), and northern fur seal ($n = 0$), were relatively low or zero during the relatively intense upwelling survey of 1999, a time when mean wind speed was $20 \text{ kts} \pm 5.8 \text{ SD}$. During Sweep 3 of 1999, an increase in sightings of these species coincided with reduced wind speed (mean $11 \text{ kts} \pm 7.5 \text{ SD}$).

Sufficient information was not available to make comparisons of occurrence patterns of harbor porpoise among late spring survey periods. Area surveyed did not always cover the coastal habitat of harbor porpoise. Nevertheless, variables strongly associated with presence of harbor porpoise (sea surface temperature, wind speed, depth of water, Sigma-t and Delta-t) indicated an association with warmer-water relaxation phases during 1992-1993 that may have been related to availability of prey.

The population of humpback whales that feed off California, Oregon, and Washington, migrate from coastal Mexico and Costa Rica. Although they are sighted from islands located in the study area in all months (Pyle & Gilbert 1996), they are more frequently sighted off central California from March through November with peaks in summer and fall (Calambokidis et al. 1996). Humpback whales respond to oceanographic conditions on many time and space scales that were not measured during this study. The variability in humpback whale sightings during the upwelling seasons of

my study, however, was consistent with the variability in sightings of humpback whales reported by Calambokidis et al. (2000). Relatively greater sighting rates of humpback whales during 1997 and 1998 occurred during surveys with markedly different ocean conditions. During 1997, before the onset of an El Niño, well-stratified ocean structure and relatively high mid-water trawl fish catches (the second highest of all surveys) indicated relatively stable prey resources in the survey area. Although 1998 was an El Niño year, near-shore studies in Monterey Bay (Benson et al. *in press*, Chavez et al. *in press*,) revealed unique conditions during this El Niño that resulted in a narrow band of productivity near the coast. In this study, sightings of humpbacks were greater on the shelf indicating whales may have been searching for and possibly finding prey closer to shore. However, the CPUE and frequency of occurrence of fishes in regions where NMFS fish trawl catches were conducted were one of the lowest of all surveys used in this comparison. The greater humpback whale sightings reported in this study during 1997-1998 were consistent with greater number of sightings reported by Calambokidis et al. (2000) near the Farallon Islands during May (coincident with this study), where humpback whales were sighted along the 200 m depth contour. The relatively greater sighting rates during 1997 and 1998 indicated humpback whales were either traveling through the survey area en route to other feeding regions or they were responding to available prey. Fewer sightings in 1999, consistent with Calambokidis et al. (2000), indicated humpback whales were not yet in the area feeding or were more dispersed.

In general, the seasonal occurrence of California sea lions is linked to spring and fall movements related to pre-breeding and post-breeding. In contrast to surveys conducted during intense upwelling phases, greater numbers of California sea lions were sighted during surveys conducted during relaxation and El Niño conditions (1992-1993 and 1997-1998). This pattern likely reflected their migration north in response to a reduction of local food resources and changes in availability of prey during El Niño years (Trillmich & Ono 1991). Bonnell & Ford 1987 reported that in non-El Niño years, 18% of the population was likely to be at sea, whereas during an El Niño year, perhaps as high as 54% of the population is at sea. Results from this study, also indicated during El Niño years California sea lions spent more time at sea possibly looking for food. Peak numbers of California sea lions also occurred on the Farallon Islands during 1983, 1992, 1997-1998 (Sydeman & Allen 1999). Greater number of sightings of California sea lions near haul-out sites on the Farallon Islands and Año Nuevo during the relatively warm-water surveys (and fewer sightings during cool-waters with less stratified conditions) likely reflected either a response to availability of prey or prey searching. Although sea surface temperature was not strongly associated with the presence of California sea lions (logistic regression results), plots of PCA factor scores for California sea lions indicated California sea lions were sighted in warmer SST, in shallow and deep thermocline depths, variables associated with warmer water surveys during relaxation events (1997) or El Niño events (1998).

In this study, northern fur seals were present where depth of water and Sigma-t were relatively deep, sea surface temperatures were relatively warm, and wind speed was relatively low. Although York (1991) found no significant positive correlation between SST and oceanic survival during the period that the fur seals are at sea during their first four years, Kajimura (1979) suggested that distribution and migration routes of young fur seals were strongly affected by ocean currents and prevailing wind regimes. The striking differences in sightings of northern fur seals during late spring surveys (for example 1997 and 1998) indicated this species might have been responding to changes in prey availability associated with the El Niño. The greatest proportion of fur seal sightings (> 30%) and relatively high sighting rates (5.2 sightings/100 km traversed) occurred during the late spring of 1997. CPUE (NMFS mid-water trawls) also was relatively high in 1997 with a predominance of Pacific hake, prey consumed by northern fur seals, whereas during 1998, CPUE was the lowest of all surveys with low proportions of Pacific hake. The relatively few sightings of fur seals during 1998, coincident with relatively low CPUE for NMFS trawl surveys, indicated northern fur seals might have been feeding in other regions, resulting in fewer seals feeding in the survey area. During 1997 and 1998, however, low pup production and high pup mortality was reported on San Miguel Island (DeLong & Melin 1999) and on Bogoslof Island (Ream et al. 1999), and effects of the 1997-1998 El Niño resulted in almost total mortality of the 1997 cohort of northern fur seals. The absence of fur seals in 1998 surveys, therefore, may have been the result of a decline in the total numbers of fur seals. Patterns of occurrence of northern fur seals were consistent with sightings on the South Farallon Islands (Pyle et al. 2001). Increased

arrivals of northern fur seals on South Farallon Islands occurred during years preceding the major El Niño events of 1992-93 and 1997-98, followed by decreased arrivals and/or breeding activity during and after these events.

Species distribution maps for 19 survey periods during 1986-1994, and 1997-1999 indicated species-specific distributions relative to depth that was consistent with other published surveys (Huber et al. 1980, Dohl et al. 1983, Barlow 1988, Calambokidis et al. 1988, 1989, 1990, 1996, 2000, Kieckhefer 1991, Brueggeman et al. 1992, Allen 1994, Black 1994, Barlow et al. 1995, Forney & Barlow 1998). With the exception of a few studies (Allen 1994 and Calambokidis et al. 1988, 1989, 1990, 1991, 1996, 2000); however, shipboard or aerial surveys were short term (one to three seasons, or one to three years). This longer-term study indicated long-term consistent patterns of distributions. Pacific white-sided dolphins and northern fur seals were distributed along the shelf-break and seaward of the 200 m isobath. Dall's porpoise were more widely distributed along the shelf-break with concentrations near Cordell Bank. Humpback whales were distributed on the shelf and seaward of the 200 m isobath, whereas, harbor porpoise were on the shelf. California sea lions were distributed on the shelf and along the shelf-break with concentrations near haul-out sites at Pt. Reyes, the Farallon Islands, and Pt. Año Nuevo (Allen 1994, Sydeman & Allen 1999). The offshore, pelagic distribution of northern fur seals and Dall's porpoise during the six early spring surveys reflected the increase in offshore area surveyed during those surveys. Logistic regression results indicated depth of water was an important variable for northern fur seals,

California sea lions, humpback whales, harbor porpoise and Dall's porpoise. Depth of water also was significant to all species in PCA.

In this study, the long-term data sets regarding hydrography, environmental variables, and marine mammal sightings, incorporated with GIS, provided an integrated perspective of the temporal and spatial mesoscale variability in ocean structure and occurrence of marine mammals off central California. The GIS overlays in this study indicated details of the temporal and spatial relationships between sighting locations, bathymetry, and surface and subsurface ocean structure. Throughout the survey area, the most frequently sighted pinnipeds were California sea lions and northern fur seals and the most frequently sighted cetaceans were Pacific-white sided dolphins, Dall's porpoise, harbor porpoise, and humpback whales. During the upwelling season, within persistent surface upwelling zones, the most frequently sighted mammals were Dall's porpoise, harbor porpoise, and California sea lions. Fluctuations in pinniped and cetacean sightings coincided with periodic variations in upwelling and relaxation, resulting in variations in ocean structure, coupled with inter-decadal variations in large-scale processes associated with El Niño and La Niña events. Although distribution of the numerically dominant species was related to bathymetry, marine mammal occurrence patterns also were related to changing local and large-scale oceanographic and biological conditions that affected their prey.

Cool water upwelling plumes (during the upwelling season) entrained in continental shelf waters due to relaxation events, downstream of upwelling centers, can

provide a suitable habitat for marine mammals and their prey. The spatial limitations of this study (constrained by NMFS traditional gridded transects) precluded sampling surface plumes and shelf-break fronts. More site-specific sampling near fronts (both surface and vertical) would provide important knowledge about direct relationships between these physical features and the distributional patterns of marine mammals and their prey. The temporal limitations of this study (conducted only during the upwelling season) precluded an understanding of the long-term seasonal effects of upwelling. It would be useful to expand the surveys to also sample during summer and fall and include integrated, multi-disciplinary sampling of hydrography, marine mammals, and their prey. This would provide a more complete understanding of the seasonal biological effects of the upwelling process, particularly around Pt. Reyes, the Farallon Islands, Cordell Bank, and Bodega Canyon.

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Table 1. Kilometers traversed (KMT) and area surveyed (km²; based on strip width of 0.8 km) during survey periods. Early spring surveys were conducted in April 1986-1988, in February-March 1992, and in March 1993-94. All late spring surveys were conducted in May-June. Two surveys conducted in 1999 were Sweep 1, 10-16 May (1999_1) and Sweep 3, 28 May - 3 June (1999_3).

YEAR	MONTH	KMT (km)	AREA (km ²)
1986	April	865.3	692.2
1986	May-June	1997.0	1597.6
1987	April	1133.6	906.9
1987	June	1542.2	1233.7
1988	April	644.6	515.7
1988	May	925.5	740.4
1989	May-June	1082.4	866.0
1990	May-June	1496.3	1197.0
1991	May-June	2305.6	1844.5
1992	Feb.-Mar.	1785.1	1428.1
1992	June	2245.0	1796.0
1993	March	1548.6	1238.9
1993	June	1375.2	1100.2
1994	March	860.5	688.4
1994	June	1086.2	869.0
1997	May	907.3	725.8
1998	May	853.0	682.4
1999_1	May	765.0	612.0
1999_3	May-June	943.0	754.4
Total		24,361.5	19,489.1

Table 2. Summary of ocean structure and environmental conditions during early and late spring survey periods. Percent area for thermocline depth (DEP), Sigma-t (SIGMAT), and Delta-t (DELTAT) were derived from GIS measurements using ArcView Spatial Analyst Reclassify Function (see Methods). Years with asterisk (*) are El Niño years. All means are reported with $\pm$ 1 standard deviation. Surveys with no plumes present are indicated by N/A. Data not in CTD casts are reported as NAN.

OCEAN STRUCTURE	EARLY SPRING				LATE SPRING						
	1992*	1993*	1994		1992*	1993*	1994	1997*	1998*	1999_1	1999_3
SURFACE											
mean SST	13.75 $\pm$ 0.48	13.04 $\pm$ 0.49	13.03 $\pm$ 0.30		14.04 $\pm$ 1.10	13.92 $\pm$ 1.95	11.4 $\pm$ 1.33	14.0 $\pm$ 1.21	13.4 $\pm$ 0.60	9.6 $\pm$ 0.80	10.97 $\pm$ 0.84
area cool water plume (km ²)	N/A	N/A	N/A		3106	1557	3345	1638	3688	6142	2224
perimeter cool water plume (km)	N/A	N/A	N/A		397	415	272	260	314	558	185
proportion (%) cool water plume area	N/A	N/A	N/A		16	9	19	9	23	34	12
VERTICAL											
mean DEP (m)	36.5 $\pm$ 25.47	70.42 $\pm$ 21.1	61.23 $\pm$ 14.28		25.6 $\pm$ 25.7	22.4 $\pm$ 17.94	24.7 $\pm$ 20.2	10.81 $\pm$ 9.16	33.74 $\pm$ 20.0	43.71 $\pm$ 35.67	18.43 $\pm$ 1.74
DEP % area	60%	77%	53%		51%	75%	52%	83%	77%	77%	78%
mean SIGMAT (m)	110 $\pm$ 18	109 $\pm$ 18.6	91 $\pm$ 10.4		70.18 $\pm$ 33.5	64 $\pm$ 26.47	19.71 $\pm$ 24.08	46.05 $\pm$ 27.09	72 $\pm$ 20.0	NAN	22.9 $\pm$ 19.54
SIGMAT % area	63%	70%	70%		71%	70%	70%	70%	63%	NAN	NAN
mean DELTAT (°C)	1.73 $\pm$ 0.40	1.68 $\pm$ 0.44	1.57 $\pm$ 0.32		2.48 $\pm$ 0.84	2.96 $\pm$ 1.11	1.89 $\pm$ 0.87	2.7 $\pm$ 0.68	1.66 $\pm$ 0.47	0.67 $\pm$ 0.36	1.26 $\pm$ 0.43
DELTAT % area	72%	68%	70%		62.30%	69%	59%	63%	71%	68%	70%
WIND SPEED											
(mean) kts	9.4 $\pm$ 6.9	11.22 $\pm$ 4.8	14.97 $\pm$ 6.0		15.3 $\pm$ 6.1	16.4 $\pm$ 7.3	19.6 $\pm$ 5.8	14.4 $\pm$ 1.2	16 $\pm$ 5.1	20.1 $\pm$ 5.8	11 $\pm$ 7.5
UPWELLING											
INDEX (daily mean at 39° N 125° W)	-28	-8	49		137	103	155	42	94	215	230

Table 3. Species, number of sightings, and number of marine mammals observed during surveys conducted off central California 1986 -1999 (except 1995 -1996). Also listed are codes used to abbreviate species in various other tables and figures.

Species	Common name	Codes	Number of sightings	Number of animals
<i>Mysticetes</i>				
<i>Eschrichtius robustus</i>	Gray whale	WHGR	10	38
<i>Megaptera novaeangliae</i>	Humpback whale	WHUM	109	242
<i>Balaenoptera acutorostrata</i>	Minke whale	WMIN	14	18
<i>Balaenoptera borealis</i>	Sei whale	WSEI	2	2
<i>Balaenoptera spp.</i>	Unidentified balenopterid	WHAL	9	11
<i>Odontocetes</i>				
<i>Dolphin spp.</i>	Unidentified dolphin	DOLP	14	29
<i>Delphinus capensis</i>	Common Dolphin	DOCO	5	1,407
<i>Lagenorhynchus obliquidens</i>	Pacific White-sided dolphin	DOPW	145	1,603
<i>Grampus griseus</i>	Risso's Dolphin	DORI	26	207
<i>Lissodelphis borealis</i>	Northern Right whale dolphin	DORW	16	259
<i>Phocoena phocoena</i>	Harbor porpoise	POHA	134	327
<i>Phocoenoides dalli</i>	Dall's porpoise	PODA	239	1,011
<i>Porp spp.</i>	Unidentified porpoise	PORP	2	3
<i>Orcinus orca</i>	Killer whale	WKIL	5	12
<i>Beaked whale spp.</i>	Unidentified beaked whale	WHBK	5	19
<i>Ziphius cavirostris</i>	Cuvier's beaked whale	WBCU	2	8
<i>Pinnipedia</i>				
<i>Zalophus californianus</i>	California sea lion	SLCA	344	862
<i>Eumetopias jubatus</i>	Northern sea lion	SLNO	14	28
<i>Callorhinus ursinus</i>	Northern fur seal	FSNO	356	518
<i>Mirounga angustirostris</i>	Northern elephant seal	SENE	109	111
<i>Phoca vitulina</i>	Harbor seal	SEHA	51	51
<i>pinniped spp.</i>	Unidentified pinniped	PINN	4	4
<i>Fissipedia</i>				
<i>Enhydra lutris</i>	Sea otter	OTTS	13	15
Total all species			1,628	6,785

Table 4. Percentage similarity indices (PSI, Silver 1975) of species composition for early (n = 15 and late (n = 15) spring surveys. Significantly similar years (>0.70) indicated by asterisk (*).

	EARLY SPRING					LATE SPRING				
	1987	1988	1992	1993	1994	1987	1988	1992	1993	1994
1986	0.67	0.67	0.58	0.58	*0.74	1986	0.62	*0.71	0.55	0.53
1987		*0.79	0.66	0.57	0.63	1987	0.46	0.58	0.49	0.60
1988			0.51	0.48	0.65	1988		0.44	0.36	0.56
1992				*0.87	0.53	1992			*0.81	0.65
1993					0.55	1993				0.57

Table 5. Percent Similarity Index (PSI, Silver 1975) between years (1987-1999) using species composition for each late spring survey period. Similarity in species composition between years was considered significantly similar if $PSI \geq 0.70$ (as indicated by *), or dissimilar if $PSI \leq 0.30$ (as indicated by a +). Sweep 1 and 3 of 1999 are indicated by 1999_1 and 1999_3.

	1987	1988	1989	1990	1991	1992	1993	1994	1997	1998	1999_1	1999_3
1986	0.62	*0.72	*0.71	*0.76	0.62	0.55	0.53	0.38	0.48	0.40	0.34	0.53
1987		0.46	0.60	0.57	0.65	0.58	0.49	0.60	0.53	0.45	0.59	0.49
1988			0.48	*0.70	0.50	0.44	0.36	0.56	0.39	0.25	+0.18	0.37
1989				0.52	0.48	0.46	0.36	0.66	0.50	0.48	0.52	0.58
1990					0.66	0.57	0.45	0.65	0.56	0.36	+0.22	0.61
1991						0.58	0.46	0.46	*0.79	0.43	0.31	*0.75
1992							*0.81	0.65	0.63	*0.74	0.32	0.53
1993								0.57	0.45	0.63	+0.24	0.40
1994									0.53	0.53	0.40	0.54
1997										0.59	0.33	*0.80
1998											0.33	0.48
1999_1												0.36

Table 6. Regression coefficients for 25.8 kg m^{-3} (Sigma-t) model using a backwards stepwise multiple logistic regression of habitat variables: depth of water (DPT), sea surface temperature (SST), wind speed (WSP), Sigma-t and Delta-t. Significance was tested for presence/absence of all marine mammals combined, and with dominant species only, during 1992-1994, and 1997-1998 survey periods. Significance levels of * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$ are shown. Blank indicates coefficient was not significant.

SIGMAT MODEL	Pacific						
	all mammals	white-sided dolphin	northern fur seal	Dall's porpoise	harbor porpoise	California sea lion	humpback whale
DPT	*.000		***.001	*.000	***.008	***.001	***.001
SST				***.409	***.655		
WSP	***.055	*.051	***.074	***.080	***.096		*.051
SIGMAT	***.010				***.017	***.012	*.013
DELTAT					***.1455		

Table 7. Factor loadings for PCA Sigma-t model habitat variables sampled during 1992-1998 surveys. Ecologically significant variables (*) are interpreted as component loadings with absolute values ≥ 0.300 . Codes for ocean habitat variables are as follows: depth of water (DPT), sea surface temperature (SST), wind speed (WSP), Delta-t (DELTAT), and Sigma-t (SIGMAT).

	FACTOR LOADINGS	
	1	2
DPT	*0.785	0.077
SST	-0.042	*0.900
WSP	-0.266	*-0.644
DELTAT	*-0.689	*0.489
SIGMAT	*0.870	0.164
% Variance explained	38.42	29.95

Table 8. Upwelling plume perimeter (km) and area (km²) during late spring 1986-1994, and 1997-1999 surveys. Asterisk (*) indicates no plume was present near Pt. Año Nuevo (AN) during survey periods. Double asterisk (**) indicates Pt. Reyes (PR) plume and Pt. Año Nuevo plume were combined. ArcView Spatial Analyst Extension was used to calculate measurements and relative proportion of PR and AN plume area. Two surveys were conducted in 1999 (1999_1, 1999_3).

Plume Perimeter (km)	1986	1987	1988	1989	1990	1991	1992	1993	1994	1997	1998	1999_1	1999_3
Pt.Reyes	242	377	281	260	288	330	397	379	272	152	314	558	185
Pt.Año Nuevo	*	13	114	*	29	37	*	36	*	*	108	**	*
Plume Area (KM ²)													
Pt.Reyes	1153	1849	1633	707	2009	3311	3106	1530	3345	1065	3688	6142	2224
Pt.Año Nuevo	*	10	725	*	26	42	*	27	*	573	*	**	*
Total survey AREA	12296	15658	11459	14958	14362	18923	19403	17422	17368	18309	16000	18064	18064
Proportion PR plume area	0.094	0.118	0.143	0.047	0.140	0.175	0.160	0.088	0.193	0.058	0.231	0.340	0.123
Proportion AN plume area	*	0.001	0.063	*	0.002	0.002	*	0.002	*	0.031	*	**	*

Table 9. Number of sightings of cetaceans and pinnipeds in upwelling zones by species and by year during late spring survey periods. Asterisk (*) indicates El Niño years.

CETACEANS	YEAR														
	86*	87*	88	89	90	91	92*	93*	94	95	96	97*	98*	99	
<i>B. acutorostrata</i>	3	1		2						no surveys					
<i>E. robustus</i>							1						1		
<i>B. griseus</i>				1		5									
<i>L. borealis</i>	3	2						1							
<i>L. obliquidens</i>	9							2	1			2	3	11	
<i>M. novaenangliae</i>	1				1	1	2	1	1			6	15		
<i>O. orca</i>								1				2			
<i>P. dalli</i>	19	5	11	6	20	5	5	1	16			3	2	2	
<i>P. phocoena</i>	6		1	4	5	1	9	18	5			1			
<i>Unidentified dolphin</i>	2														
Total number sightings	30	19	12	15	26	12	17	24	23			14	21	13	
Total all species	147	193	48	31	104	35	32	86	114			42	61	56	
Total number species	4	5	2	5	3	4	4	5	4			5	4	2	
PINNIPEDS															
<i>C. ursinus</i>	6	1	1	1	2	4	4						3		
<i>E. jubatus</i>	2	1	2		2	4	2	1	2						
<i>M. angustirostris</i>					2		2	4				3			
<i>P. vitulina</i>	4		1		5	3	3	6				1			
<i>Z. californianus</i>	3	3			8	7	41	38	12			18	11		
<i>Unidentified pinniped</i>												2			
Total pinniped sightings	15	5	4	1	19	18	52	49	14			22	16	0	
Total all species	61	6	3	1	25	18	167	104	43			49	17	0	
Total number species	4	3	3	1	5	4	5	4	3			3	3	0	

Table 10. Summary of sighting rates (sigs/100 kmt) and number of sightings of marine mammals during 1992-1994 and 1997-1995 Years with asterisk (*) are El Niño years. Note sighting rates for the numerically dominant species in parentheses. Pacific white-sided dolphin mean group size indicated in second parentheses. Surveys with no plumes present are indicated by N/A.

SIGHTING RATES	EARLY SPRING			LATE SPRING						
	1992*	1993*	1994	1992*	1993*	1994	1997*	1998*	1999 1	1999 3
In Survey Area	8.2	5.6	2.1	9.9	8.4	5.9	15.5	13.4	4.4	6.3
In surface upwelling zones	N/A	N/A	N/A	10.99	9.83	8.08	11.78	16.97	5.9	2.47
Outside surface upwelling zones	N/A	N/A	N/A	9.52	6.8	4.3	17.37	13.27	3.8	6.93
Number Cetacean Sightings and (sigs/100 km)										
<i>B. acutorostrata</i>	1					2				
<i>E. robustus</i>	1			2				1		
<i>G. griseus</i>			2	4				2	1	1
<i>L. borealis</i>		1			4	1		3		
<i>L. obliquidens</i>	1		4	21	11	12	8	6	21	6
	(0.06)(5)		(0.2)(10)	(0.9)(7.4)	(0.8)(6.5)	(1.1)(4.6)	(0.8)(24.6)	(0.7)(21.5)	(2.7)(4.8)	(0.6)(8.0)
<i>M. novaeangliae</i>	1	4		12	2	1	21	29	3	9
	(.05)	(0.2)		(0.5)	(0.1)	(.09)	(2.3)	(3.4)	(0.4)	(0.9)
<i>O. orca</i>	18	14	4	15	2	18	14	4	3	7
<i>P. dalli</i>	(1.0)	(0.9)	(0.4)	(0.6)	(0.1)	(1.7)	(1.5)	(0.5)	(0.4)	(0.7)
<i>Z. cavirostris</i>		1					1			
<i>D. capensis</i>	17	5		13	20	5	2	2		7
<i>P. phocaena</i>	(0.9)	(0.3)		(0.5)	(1.5)	(0.5)	(0.2)	(0.2)		(0.7)
unidentified whale				1			1	2	3	
Unidentified dolphin/porpo										
Number Pinniped Sightings and (sigs/100km)										
<i>C. uralinus</i>	88	53		21		3	47	7		21
	(4.9)	(3.4)	5 (0.5)	(0.9)		(0.3)	(5.2)	(0.8)		(2.2)
<i>E. jubatus</i>				6	2	2				
<i>M. angustirostris</i>	6	5	1	16	13		10	2		
<i>P. vitulina</i>	2	1		9	6	2	3	1		
<i>Z. californianus</i>	10	3		100	54	18	30	51	1	7
	(0.5)	(0.1)	2 (0.2)	(4.5)	(3.9)	(1.6)	(3.3)	(5.9)	(0.1)	(0.7)
Unidentified pinniped							1	1	1	1

Figure 1. Study area (early spring survey perimeter depicted by dashed line and late spring survey perimeter depicted by solid line) off central California indicating location of CTD stations during early spring surveys (open circles) and late spring surveys (solid triangles) and depth (m).

Figure 2. Mean sea surface temperature (SST; solid square with solid line) and mean wind speed (solid triangle with dashed line) during early (a) and late (b) spring 1986-88, 1992-94 survey periods. Vertical bars are ± 1 standard deviation. See Table 2 for wind speed standard deviations.

Figure 3. Mean sea surface temperature (SST; solid square with solid line) and mean wind speed (WSP; solid triangle with broken line) derived from shipboard data during late spring survey periods. Bars (vertical lines) are -1 standard deviation and represent criteria used to define and map surface upwelling plumes for each survey period. See Table 2 for mean wind speed standard deviations.

Figure 4. Frequency histograms of extracted thermocline depth (m), Delta-t (°C), and depth (m) of 25.8 kg m⁻³ isopleth comparing data collected during early (n = 69) and late (n = 65) spring surveys of 1993.

Figure 5. Frequency histograms of extracted thermocline depth (m), and Delta-t (°C), comparing data collected during late spring surveys of 1999 Sweep 1 and 3.

Figure 6. Sighting locations of (a) Pacific white-sided dolphin, (b) northern fur seal, (c) Dall's porpoise, (d) harbor porpoise, (e) California sea lion, and (f) humpback whale during early spring surveys of 1986-1988, and 1992-1994.

Figure 7. Sighting locations of (a) Pacific white-sided dolphin, (b) northern fur seal, (c) Dall's porpoise, (d) harbor porpoise, (e) California sea lion, and (f) humpback whale during late spring surveys of 1986-1994, and 1997-1999.

Figure 8. Sighting rates of marine mammals during early and late spring survey periods 1986-1994 and 1997-1999. Numbers over bars are kilometers traversed. Solid black bars indicate number cetacean sightings per 100 km traversed; hatched bars indicate number pinniped sightings per 100 km traversed.

Figure 9. Relative proportions of sightings of northern fur seal (FSNO), California sea lion (SLCA), Dall's porpoise (PODA), harbor porpoise (POHA), Pacific white-sided dolphin (DOPW), and humpback whale (WHUM) during early (a) and late (b) spring surveys. Harbor seal, northern elephant seal, Steller sea lion, beaked whale, killer whale, northern right whale dolphin, Risso's dolphin and common dolphin were grouped as 'other'.

Figure 10. Relative proportions of sightings of northern fur seal (FSN), California sea lion (SLCA), Dall's porpoise (PODA), harbor porpoise (POHA), Pacific white-sided dolphin (DOPW), humpback whale (WHUM), during late spring surveys of 1986-1999. Harbor seal, northern elephant seal, Steller sea lion, beaked whale, killer whale, northern right whale dolphin, Risso's dolphin, common dolphin, minke whale, and gray whale were grouped as 'other'.

Figure 11. Scatter plot of number of sightings per 100 km traversed and mean sea surface temperature by season (clear triangle = early spring surveys, solid triangle = late spring surveys).

Figure 12. Distribution of factor scores of dominant species (Pacific white-sided dolphin, Dall's porpoise, harbor porpoise, northern fur seal, California sea lion, and humpback whale) as defined by the factors of Principal Component Analysis for 1992-94 and 1997-98 survey periods.

Figure 13. Distribution of factor scores for Pacific white-sided dolphin (a), Dall's porpoise (b), Harbor porpoise (c), northern fur seal (d), California sea lion (e), and humpback whale (f) as defined by the Factors of Principal Component Analysis for 1992-1998 survey periods.

Figure 14. Sea surface isotherms overlaid with locations of marine mammal sightings during 1993 early (a; March 2-13) and late (b; June 3-12) spring surveys. Pinnipeds are represented by solid circle and cetaceans by a cross. Surface upwelling zones include relatively cool water plumes and a 15-km boundary (bolded line) around the plumes.

Figure 15. Composite AVHRR images for early and late spring 1993 and 1994. Data are from NOAA-11 satellite passes (1993 early spring $n = 43$, 1993 late spring $n = 37$, 1994 early spring $n = 23$, 1994 late spring $n = 16$). Data values represent temperature in degrees C times 10; cooler colors are cooler temperatures.

Figure 16. Sighting rates (sightings per 100 km traversed) of marine mammals outside (hatched bar) and within (solid bar) the Pt. Reyes and Pt. Año Nuevo surface upwelling zones. Numbers over bars are kilometers traversed within and outside of zones.

Figure 17. Depth (m) of thermocline (a) and depth (m) of Sigma-t (b) overlaid with marine mammal sighting locations during 1993 late spring surveys. Bolded line is boundary of surface upwelling zone that includes relatively cool water plumes and a 15-km boundary around the plumes.

Figure 18. Sea surface isotherms overlaid with marine mammal sighting locations during 1999 Sweep 1 (a; 10-16 May), and Sweep 3 (b; 28 May - 3 June). Surface upwelling zones include relatively cool water plumes and a 15-km boundary (bold line) around the plumes.

Figure 19. Proportion of anchovy, sardine, hake, rockfish, shortbelly rockfish, and *Loligo* in mid-water trawls conducted by NMFS, Tiburon Laboratories from 1992 to 1994 and 1997 to 1999.

Figure 20. Effort as number of hauls (solid black square and dashed line) and CPUE number of fish per haul (solid triangle and solid line) for fishes and squid in mid-water trawls conducted at night by NMFS, Tiburon Laboratories from 1992 to 1994, 1997 to 1999 during late spring survey periods.

Figure 21. Frequency of occurrence of anchovy, sardine, hake, rockfish, shortbelly rockfish, and *Loligo* in mid-water trawls conducted at night by NMFS, Tiburon Laboratories, from 1992 to 1994, and 1997 to 1999 during survey periods.

Figure 22. Time series of monthly mean upwelling index from 1 January 1992 to 31 December 1994 and 1 January 1997 to 31 December 1999 at 39° N 125° W. Arrows indicate time of survey periods.

Figure 23. Time series of daily upwelling index at 39° N 125° W (solid line) and 36° N 122° W (dashed line) for May-June 1992-94 and 1997-99 indicating upwelling index before and during surveys north and south of the survey area.