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MARINE MAMMAL RESPONSE TO ECOSYSTEM VARIABILITY IN MONTEREY
BAY, CALIFORNIA

2
A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Julia Burrows

December 2009

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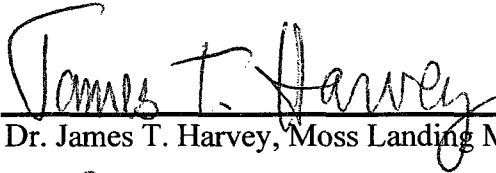
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The Undersigned Thesis Committee Approves the Thesis Titled
MARINE MAMMAL RESPONSE TO ECOSYSTEM VARIABILITY IN
MONTEREY BAY, CALIFORNIA

by

Julia Burrows

APPROVED FOR MOSS LANDING MARINE LABORATORIES



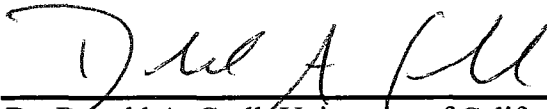
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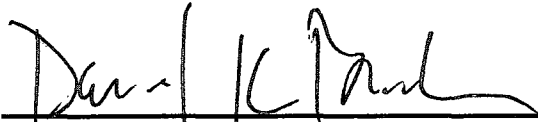
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ABSTRACT

MARINE MAMMAL RESPONSE TO ECOSYSTEM VARIABILITY IN MONTEREY BAY, CALIFORNIA

by Julia Burrows

The coastal upwelling ecosystem near Monterey Bay, California is an extremely productive, yet variable, ecosystem and an important foraging area for mobile, apex predators, such as marine mammals. Longer-term studies are required to better understand how marine mammals respond to temporal environmental variability; however, few of these studies exist. We conducted monthly shipboard line-transect surveys in Monterey Bay from 1997 to 2007, concurrent with hydroacoustic and oceanographic sampling. Twenty-two species of marine mammals were identified, and monthly and annual densities were calculated for the 12 most commonly sighted species. Densities varied among years, whereas species richness remained relatively constant. Marine mammals were most evenly distributed but least dense during the anomalous upwelling conditions of 2005 and least even but still dense during the 1997/1998 El Niño event. No single environmental variable consistently predicted the densities of cetacean species, and variables expected to be good predictors explained only a minimal amount of variability. Incorporating temporal lags into analyses improved predictive capabilities of upwelling index, chlorophyll, and primary productivity, but a more comprehensive prey collection methodology may also have improved predictive power. Through long-term monitoring programs, we can expand our understanding of how environmental variability affects top predators and become better prepared for future oceanic change as it occurs.

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INTRODUCTION

Eastern boundary currents, such as the California Current, are among the most productive ecosystems in the world (Hickey 1979, Glantz & Thompson 1981). Productivity is driven by local-forcing coastal upwelling (Barber & Smith 1981, Carr & Kearns 2003) and larger-scale oceanic circulation patterns (such as El Niño/La Niña events). Upwelling in the California Current is initiated when northwest winds along the North American west coast combine with Coriolis force to create offshore Ekman transport of surface waters, resulting in the movement of cool, nutrient rich waters to the surface (Barber & Smith 1981, Huyer 1983, Service et al. 1998). Nutrients brought to the euphotic zone induce phytoplankton blooms, which increases productivity at multiple trophic levels (Hutchings et al. 1995, Pennington & Chavez 2000).

In coastal upwelling ecosystems, there is a temporal lag between the onset of physical oceanographic changes and the biological response to those changes. Increases in the strength of upwelling winds precede decreases in sea surface temperatures (SSTs), which precede increases in chlorophyll fluorescence (Service et al. 1998). Chlorophyll is often used as an index of primary production (Smith et al. 1982, Kahru & Mitchell 2008), which is a measure of food availability for grazers. Increases in chlorophyll (primary production) precede increases in zooplankton abundance, which ultimately precede the arrival of top predators, such as marine mammals (Marinovic et al. 2002, Burtenshaw et al. 2004, Littaye et al. 2004, Croll et al. 2005).

In addition to seasonal coastal upwelling, interannual variability resulting from El Niño/La Niña events influences productivity in the California Current (Barber & Chavez

1983, Chavez et al. 2002). El Niño events are typically associated with a delayed and shortened upwelling season (Bograd et al. 2009), increased SSTs, a deepening of the thermocline, reduced nutrient availability, and decreased primary production (Barber & Chavez 1983, Hayward 1993, Lenarz et al. 1995, Chavez 1996, Chavez et al. 2002, Marinovic et al. 2002). La Niña events often follow El Niño's and result in a cooler, more productive environment (Chavez et al. 2002, Marinovic et al. 2002).

Physical and biological oceanographic variables associated with upwelling and El Niño/La Niña events influence the abundance and distribution of mid-trophic level prey species (Fiedler et al. 1986, Lenartz et al. 1995, Marinovic et al. 2002, Brodeur et al. 2006) and ultimately apex predators, such as marine mammals (Sydeman & Allen 1999, Benson et al. 2002, Burtenshaw et al. 2004, Keiper et al. 2005, Lowry & Forney 2005). Oceanographic variables are often used to predict marine mammal abundance and distribution (Smith et al. 1986, Littaye et al. 2004, Tynan et al. 2005, MacLeod et al. 2007, Grémillet et al. 2008) because they require relatively less cost and effort to obtain than prey data. However, prey availability (or a combination of prey and oceanographic variables) is likely the best predictor of predator density, because predators distribute in a manner that tracks their prey (Weinrich et al. 1997, Benoit-Bird & Au 2003).

Environmental variability may not only affect the density and distribution of species, but also diversity. Researchers who have examined the effect of interannual environmental variability on diversity have reported increased species diversity and richness in the North Pacific during El Niño years, and attributed the increases to the northward movement of species typically associated with warmer waters (Benson et al.

2002, Worm et al. 2005, Hooff & Peterson 2006). A similar, yet longer-term, poleward expansion of southern species and associated increase in biodiversity in higher latitudes already is occurring (or is predicted to occur) as the world's oceans warm (Hughes 2000, Beaugrand et al. 2002, Hyrenbach & Veit 2003, Whitehead et al. 2008). The response of species to shorter-term variability, such as delayed and weakened seasonal upwelling (Snyder et al. 2003) or El Niño events, may be the best predictor of how these species will respond to longer-term oceanographic change, such as ocean warming (Trathan et al. 2007). Understanding how environmental variability affects species density and diversity is an important step in anticipating changes that may occur in species composition and ecosystem functioning over longer time periods.

Many researchers have studied the movements or distribution of individual species throughout a season or several years (Sydeman & Allen 1999, Friedlaender et al. 2006, Weise et al. 2006), without monitoring changes in species composition over longer time periods (decades). In this study we attempted to determine how a community of top predators was affected by environmental variability and to establish if these effects were consistent through time. To accomplish this objective we (1) documented changes in marine mammal density and diversity in Monterey Bay, California throughout an 11-year period (1997-2007), (2) tested for differences in marine mammal density and diversity (richness and evenness) between years with warmer and cooler oceanic conditions, (3) examined the effects of environmental and prey predictor variables on monthly marine mammal density and occurrence patterns, and (4) incorporated temporal lags of environmental predictor variables into analyses.

We hypothesized that marine mammal species typically associated with cooler water would be present in greater densities during years dominated by cooler oceanic conditions (stronger upwelling, lesser SSTs), and species typically associated with warmer water would be present in greater densities during years dominated by warmer oceanic conditions (lesser upwelling, greater SSTs). We expected that a greater diversity of marine mammal species would be associated with warmer-water years. Additionally, we hypothesized that the most direct trophic link (prey) would be the best predictor and thus explain the greatest amount of variability in marine mammal density when compared with environmental predictor variables. We also expected that there would be temporal lags between maxima in environmental predictor variables and maxima in marine mammal densities, and that incorporating time lags into analyses would improve predictive capabilities.

METHODS

Study area

Monterey Bay, located off the central California coast, is the largest bay (approximately 1200 km²) on the west coast of the United States completely open to the ocean (Benson et al. 2002, Croll et al. 2005; Fig. 1). The Monterey Submarine Canyon, one of the largest canyons in the world (Shepard 1973), divides the bay into two nearly equal shallower shelves (up to 140 m deep and 10-15 km wide), with deeper waters over the canyon in the center of the bay (Greene et al. 2002; Fig. 1). Monterey Bay is influenced seasonally by a coastal upwelling plume that originates approximately 30 km

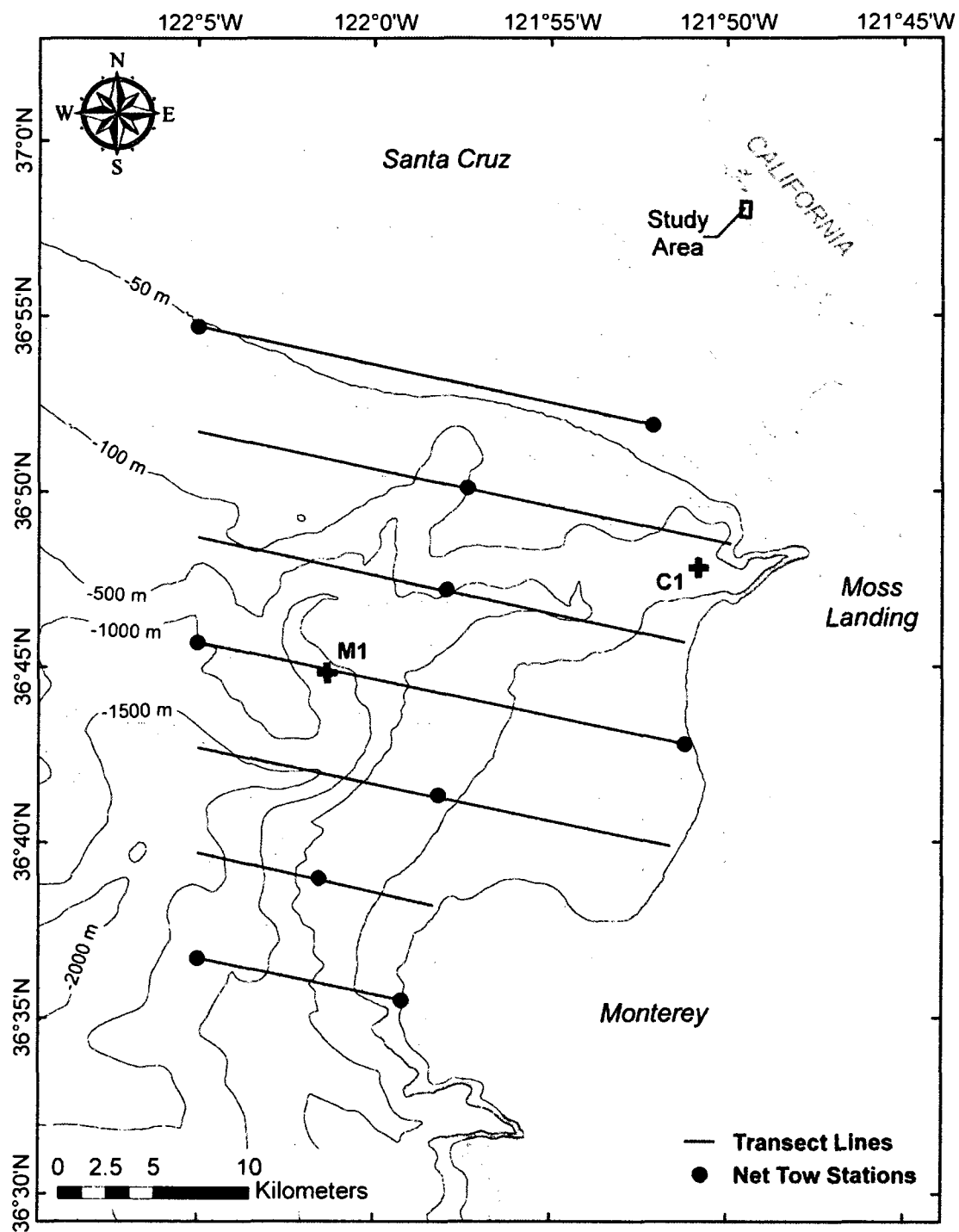


Figure 1. Monterey Bay study area with marked transect lines, euphausiid (krill) net tow stations, and C1 & M1 oceanographic sampling stations. Bathymetric contours of Monterey Submarine Canyon also shown.

north of the bay at Point Año Nuevo (Rosenfeld et al. 1994). Upwelling winds off the central California coast usually begin in March and continue through August; with periods of wind relaxation (Send et al. 1987) becoming more frequent during July and August (Pennington & Chavez 2000). A short transitional oceanic period occurs from late-August through November, when winds continue to relax and SSTs increase until a warmer, less productive winter Davidson Current season begins in December and persists through February (Skogsberg 1936, Skogsberg & Phelps 1946, Pennington & Chavez 2000).

Line transect field methods

Monterey Bay was divided into seven transect lines which were surveyed for marine mammals throughout the 11-year study (Benson et al. 2002, Croll et al. 2005; Fig.1). Transect lines ranged in length from 10 km (5.4 nautical miles; nmi) to 25 km (13.5 nmi), and totaled approximately 126 km (68 nmi). The entire survey area encompassed approximately 909 km². The location of the first line was randomly chosen from a 3-minute latitudinal range, after which each line was spaced 5.5 km (3 nmi) apart for uniform coverage of the bay (Benson et al. 2002). Beginning in September 2006, the first line was no longer randomly selected and the same grid of seven lines was surveyed during subsequent months. Surveys were conducted at a ship speed of 18.5 km per hour (10 knots) from the 55 m (30 fathom) isobath WNW to 122.083°W longitude. Surveys were completed during two consecutive days each month from May through November 1997-2007, with additional surveys in January and March 2003-2007. Lack of funding during 2007 meant surveys were conducted only one day a month (five transect lines

totaling 82 km) and no surveys occurred during June, September, and October 2007.

Surveys were occasionally postponed or cancelled due to persistent inclement weather.

Two observers stationed on top of the bridge (4.3 m above sea level, except for March and July 2007 when observers were 5.66 m above sea level) searched for marine mammals from the trackline to 90° abeam of the ship using Fujinon 7x50 binoculars (with a compass and reticle scale in the oculars). A third centrally located observer searched mainly with the naked eye on the trackline near the ship (binoculars were used to aid in species identification), while a fourth person entered sightings into a laptop computer using the program SeeBird_WinCruz (Holland 2008) with direct input from the ship's GPS. When a sighting occurred, all observers assisted with species identification (to the lowest taxonomic level) and abundance estimation. Time, latitude, longitude, species, number of individuals, cue (body, blow), method (eye, binoculars), compass bearing, and number of reticle marks down from the horizon were recorded. Environmental conditions (fog or rain, visibility in miles, wind direction and speed, swell direction and speed, horizontal and vertical sun position, and Beaufort sea state) were continually updated throughout the survey.

Monthly density estimates

Marine mammal densities were calculated from line transect data using Distance software (Thomas et al. 2006). Sightings from May through November 1997-2007, and January and March 2003-2007 were included in analysis to obtain the global detection function ($g(x)$ = the probability of detecting an animal, given that it is at distance "x" from the line; Buckland et al. 2001). Radial distances of marine mammal groups to the

trackline were obtained using binocular reticle measurements and the platform (observer eye) height using the formula of Lerczak & Hobbs (1998). Calculations were performed in a Microsoft Excel function obtained from the National Marine Mammal Laboratory website (<http://www.afsc.noaa.gov/nmml/>). Radial distances for sightings made using the land/ocean interface as a reticle reference rather than the true horizon (sky/ocean) were adjusted using the military analyst toolset in ArcMap (ArcGIS 2006).

Perpendicular distance (x) from the trackline was computed from the radial distance (r) and the angle (θ) between the trackline and the marine mammal group ($x = r * \sin(\theta)$).

Densities of marine mammals were estimated using the Multiple Covariate Distance Sampling (MCDS) analysis engine in Distance and were based on the following equation:

$$\hat{D} = \frac{\sum_{i=1}^n s_i / \hat{p}_i}{2wL}$$

where \hat{D} is the density estimate (animals per km²), n is the number of marine mammal groups detected; s_i is the size of the i^{th} group; w is the truncation distance and half-width of the transect, L is the total line length, and \hat{p}_i is the estimated probability of detecting the i^{th} group (Buckland et al. 2001, Buckland et al. 2004).

Detection probability was estimated from the detection function ($g(x)$), which was fitted to the observed perpendicular distances using Distance software. A detection function is composed of a key function and optional adjustment function (cosine, simple or hermite polynomial), which are series expansion terms. Both half-normal (Hn) and hazard-rate (Hr) key functions were considered:

$$\text{Hn: } g_i(x) = e^{\frac{-x^2}{2\sigma_i^2}}$$

$$\text{Hr: } g_i(x) = 1 - e^{\left(\frac{-x}{\sigma_i}\right)^{-p}}$$

where p is an exponent parameter and σ_i is a scale function that can change based on the observation-specific values of covariates (e.g. group size, sea state etc.) and estimated parameters. As σ_i increases the detection probability increases. The observation-specific detection probability is computed as:

$$p_i = \int_0^w g_i(x) \frac{1}{w} dx.$$

The truncation distance (w) was set for each species such that approximately 5% of the most distant sightings were excluded (Buckland et al. 2001). Only survey effort that occurred in acceptable Beaufort sea states (0-4) and swell heights (1-8 feet) were included in analyses. Additionally, only non-collinear covariates with a significant effect on perpendicular distance were considered as covariates in MCDS (Beaufort sea state, swell height, visibility, and group size). Beaufort was treated as a factor with discrete levels 0-4, whereas all other covariates were continuous variables (non-factors).

Observer was not included as a covariate because there were more than 200 volunteer observers during the 11-year study. Because more experienced observers were likely better at detecting marine mammals than less experienced observers, not including observer as a covariate added to the random error in the density estimates.

A sequence of models with different sets of covariates were examined, with the addition of series expansion terms (cosine, simple or hermite polynomial) to assist in

minimizing Akaike's Information Criterion (AIC; Akaike 1973). Model convergence was more difficult to achieve using all combinations of covariates and adjustments (i.e. too many parameters) for species with fewer sightings. In these cases, the best model was chosen from models including only one covariate and no adjustments, or no covariates (null model). Additionally, to achieve model convergence using the Hr key function in MCDS, starting values for the Hr parameter estimates were manually selected using those calculated from the Hn model for the same species, with the power parameter coefficient set to two.

The expected value for group size ($\hat{E}(s)$) was estimated as the mean of observed group size when size was not included as a covariate in the detection model (i.e. observed mean group size did not change with distance). When probability of detection (p_i) was a function of group size, then the following estimator was used to adjust for size-bias:

$$\hat{E}(s) = \sum_{i=1}^n \frac{s_i}{\hat{p}_i} / \sum_{i=1}^n \frac{1}{\hat{p}_i}.$$

Although Distance Sampling methods assume certain detection on the trackline (i.e. $g(0) = 1$), it is likely some animals were not seen (perception bias) or submerged (availability bias) as the vessel passed, resulting in an underestimation of true density. However, because the aim of this study was to compare relative densities of animals in the same area through time, consistent underestimation should not affect results. Additionally, because it was not possible to include uncertainty associated with density calculations in subsequent statistical analyses with environmental and prey variables, variance estimates for monthly densities were not determined.

Annual density and diversity

Once monthly density estimates were obtained, species richness, species evenness, species densities, and total density were calculated for each year 1997-2006 (2007 was excluded from diversity calculations due to reduced effort that year). Species richness (S) was defined as the total number of marine mammal species identified each year, including rare species. Species evenness was calculated for each year using the 12 most abundant species (with enough sightings to obtain density estimates) by first calculating species diversity using the Shannon-Weiner index (H):

$$H = -\sum_{i=1}^s (p_i)(\log p_i)$$

where p_i is the proportion of total sample belonging to the i th species. Shannon's equitability (E_H , evenness) was then calculated as:

$$E_H = \frac{H}{\log S}$$

where S is the annual species richness of the 12 most abundant species (hereafter focal species). Shannon's equitability index for species evenness quantifies the numerical equality of the annual densities of each of the 12 focal species. An E_H value of one indicates complete evenness (i.e. all 12 species were present in equal densities). Because of the difficulties associated with identifying common dolphins in the field, long-beaked (*Delphinus capensis*) and short-beaked (*Delphinus delphis*) common dolphins were treated as one species for evenness calculations. Mean annual density and standard error (SE) for each focal species were calculated from monthly density estimates (May-Nov),

and total annual density was calculated by summing the mean annual densities of the 12 focal species.

Prey and environmental variables

Prey data were collected concurrently with marine mammal line transect data. From May 1997 through May 2003 a Simrad EY500 digital echosounder configured with a 200 kHz hull-mounted single-beam transducer (ping interval of two seconds) was used for collection of prey data. This model was replaced in June 2003 by a Simrad EK60 digital echosounder operated at 200 kHz with a split beam transducer. The echosounder was calibrated once per year using the standard sphere method (Johannesson and Mitson 1983). Echograms were generated from backscatter data, stored on a laptop computer, and subsequently analyzed following methods described in Hewitt & Demer (1993) and Croll et al. (1998). Euphausiids (krill) and fish schools were identified using Echoview software (SonarData 2007) based on the strength and morphology of backscattering aggregations. The nautical area scattering coefficient (NASC) for krill was calculated for each km of survey effort to a depth of 5 m above the ocean floor (for depths less than 200 m) or 200 m (for depths greater than 200 m), and mean NASC (krill backscatter; $\text{m}^2 \text{km}^{-2}$) was determined for each survey month. Fish schools detected in the same depth range were enumerated and the number per kilometer surveyed also was determined for each survey month. Plankton net tows were conducted at 6-10 sampling stations to verify that backscatter aggregations were correctly identified and to determine krill abundance ($\# 1000 \text{ m}^{-3}$; Marinovic et al. 2002; Fig. 1).

Two chlorophyll (Chl) and primary production (PP) datasets were used in this study. The first was obtained from surface water samples (following methods recommended by Fitzwater et al. 1982 to avoid trace metal contamination) collected at the M1 (36.747°N, 122.022°W) and C1 (36.797°N, 121.847°W) sampling stations (Fig. 1) during Monterey Bay Aquarium Research Institute's (MBARI) time series cruises (which occurred at approximately 21 day intervals). Chlorophyll-a concentrations (hereafter *in situ* Chl; mg Chl m⁻³) were determined using the conventional fluorometric technique of Holm-Hansen et al. (1965) and Lorenzen (1966), with a modified extraction procedure described by Venrick & Hayward (1984). Primary production, or carbon fixation (hereafter *in situ* PP; mg C m⁻³ d⁻¹), was measured as the rate of uptake of the radioactive isotope ¹⁴C during a 24-hour incubation period in natural light conditions (Pennington & Chavez 2000). The second set of Chl and PP data were calculated from satellite measurements of spectral reflectance (ocean color) obtained from the Japanese Ocean Color and Temperature Scanner (OCTS; Jan-Jun 1997), NASA's Sea-viewing Wide Field-of-View Sensor (SeaWiFS; Oct 1997-Jun 2002) and combined NASA's SeaWiFS and Moderate Resolution Imaging Spectrometer (MODIS) Aqua satellites (Jul 2002-Dec 2007). Remotely sensed data for July through September 1997 were not available. Mean monthly Chl-a (hereafter remote Chl; mg Chl m⁻³; 1 km pixel resolution) and mean monthly depth-integrated net primary production, total primary production minus losses due to phytoplankton respiration, (hereafter remote PP; mg C m⁻² d⁻¹; 9 km pixel resolution) were determined for a 9 x 9 km box around the M1 mooring using the Ocean Chlorophyll 4 version 4 (OC4v4) algorithm for remote Chl (O'Reilly et al. 1998) and the

Vertically Generalized Production Model (VGPM) for remote PP (Behrenfeld & Falkowski 1997, Kahru et al. 2009). The VGPM also used SST (°C; 9 km pixel resolution) obtained from OCTS (Jan-Jun 1997), Advanced Very High Resolution Radiometer (AVHRR) Pathfinder (Oct 1997-Jun 2002), and MODIS Aqua (Jul 2002-Dec 2007) satellites.

Additional environmental variables used included SST and upwelling index (UI). Mean monthly SSTs (°C) were calculated from a continuous record of temperature at one meter depth at the MBARI M1 mooring (Fig. 1). Mean monthly UIs ($\text{m}^3 \text{sec}^{-1} 100 \text{m}^{-1}$); measures of wind-driven offshore Ekman transport derived from six-hourly synoptic surface atmospheric pressure fields) from 36°N 122°W were obtained from NOAA's Pacific Fisheries Environmental Laboratory website (<http://www.pfeg.noaa.gov/>).

Statistical analyses

Warmer vs. cooler years

To determine if mean annual SST and UI affected annual marine mammal density and diversity, years were grouped into two categories based on similarities in physical oceanographic conditions: cooler (lesser SSTs and greater UIs) and warmer (greater SSTs and lesser UIs). Years with clearly lesser UI and greater SST pairings (1998, 2004, 2005, and 2006) were categorized as warmer years and years with clearly greater UI and lesser SST pairings (1999, 2001, 2002, and 2007) were categorized as cooler years (Fig. 2). Discriminate function analysis was then used to categorize years without a clear grouping (1997, 2000, and 2003). A two-tailed Student's t-test was used to determine if species richness, species evenness, species densities, or total density differed between cooler and

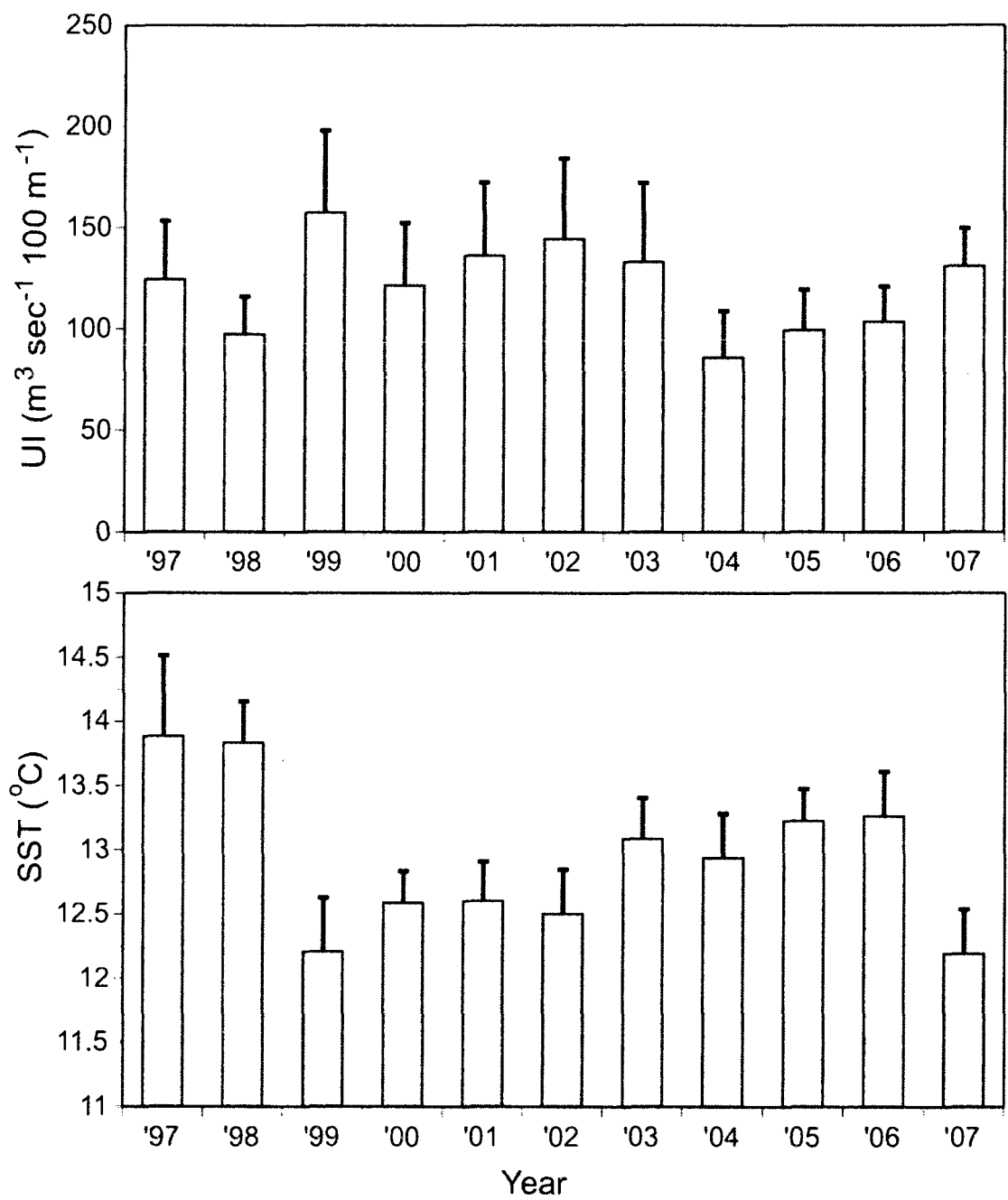


Figure 2. Annual means and standard errors for upwelling indices (UI) and sea surface temperatures (SSTs) in Monterey Bay, Jan-Dec 1997-2007.

warmer years. The assumption of normality was tested using a Kolmogorov-Smirnov (KS) test and the assumption of homoscedasticity was tested using Levene's test. If variances were heteroskedastic, unequal variance t-tests were performed. Results from unequal variance t-tests were confirmed with a randomization test using Resampling Stats software (Resampling Stats, Inc. 2003). One analysis included all years surveyed ($n = 11$) and another included only the years used to create the discriminate function ($n = 8$). An additional analysis was performed grouping years as strong upwelling (1999, 2000, 2001, 2002) and weak and/or delayed upwelling (2004, 2005, 2006; as described in California Cooperative Oceanic Fisheries reports, CalCOFI, <http://www.calcofi.org/>), but excluding El Niño years. When the null hypothesis was not rejected, effect size was calculated using G*Power software (Faul et al. 2007) for a two-tailed t-test with an alpha of 0.05, a power of 0.8, and $n = 5$ in each group (for species richness and evenness) or $n = 5$ for warmer years and $n = 6$ for cooler years (for total density and species densities). Effect size was then multiplied by the pooled standard deviation (for homoskedastic variables only) to determine the difference in means that would have been detected statistically.

Monthly density and occurrence predictors

Relationships between prey and environmental variables, and density and occurrence (presence/absence) patterns, were examined for the six most abundant cetaceans. Pinnipeds were not included because their life history characteristics likely had a greater impact on their densities than environmental and prey variables. For example, California sea lions (*Zalophus californianus*) breed off southern California and

Mexico during the summer (Odell 1975), which results in decreased sea lion densities in central California at the time when upwelling and productivity typically increase. All statistical analyses were conducted using SYSTAT (SYSTAT Software Inc. 2007) or SPSS (SPSS Inc. 2007) software at an alpha level of 0.05.

The original data were divided into two datasets as recommended by Fletcher et al. (2005). For the first dataset, least squares multiple regressions were used to assess the effects of environmental and prey variables (UI, SST, *in situ* Chl, *in situ* PP, remote Chl, remote PP, krill backscatter, krill abundance, and fish regions) on cetacean densities (when cetaceans were present). For the second dataset, multiple binary logistic regressions were used to test for effects of the same predictor variables on cetacean occurrence. Requirements for inclusion in the final model were based on likelihood-ratio statistics. Plots of linear regression residuals were screened to assess linearity and homoscedasticity. One-sample KS tests were used to assess normality of predictor and response variables for all analyses, and non-normal variables were log-transformed to achieve normality. The assumption of independence was tested using a Durbin-Watson D statistic, and monthly cetacean densities that were temporally autocorrelated were transformed using the first-order autocorrelation parameter (ρ) as described by Neter et al. (1996).

Data were screened for multicollinearity through a forward stepwise multiple regression procedure. Changes in the F ratio or changes in the magnitude or direction of the regression coefficients from one step to the next were used as indicators of multicollinearity. Variance Inflation Factors (VIFs), measures of the extent to which

variance of the regression coefficients increased due to multicollinearity (Neter et al. 1996), were calculated for each predictor variable. Statistical multicollinearity existed if VIFs were greater than two, or when significant variables became insignificant when another correlated predictor was added to the model (due to variance inflation; Graham et al. 2003). In these situations, the correlated predictor explaining the least amount of variability was removed from the analysis (for similar logic see Ainley et al. 2005). Statistical multicollinearity was not a major issue in this study because either only one or two uncorrelated predictor variables were significant thus included in the same regression model, or predictor variables were lagged one, two, or three months thereby breaking most correlations between predictors.

Pearson correlation analyses were used to determine the most appropriate temporal lag between environmental variables and monthly cetacean densities (when cetaceans were present). Environmental variables were lagged zero, one, two, and three months prior to a density observation. The time lag with the greatest absolute value for the correlation was selected as the appropriate temporal lag for each environmental predictor variable (UI, SST, *in situ* Chl, *in situ* PP, remote Chl, and remote PP). Because marine mammal sightings occurred May through November, data for correlation analyses were limited to seven months per year. Forward stepwise multiple regression analyses were performed once time lags were identified and predictor variables were appropriately adjusted.

For binary logistic regression analyses, used to determine if predictor variables had a significant effect on cetacean occurrence, equal sample sizes were required to

obtain a balanced model that predicted each outcome (presence or absence) with equivalent accuracy. To equate sample size, “ n ” random subsamples were drawn from the category (presence or absence) with the most sightings such that “ n ” equaled the number of samples in the category with the lesser number of sightings. For example, sample size for blue whales (*Balaenoptera musculus*) was originally 18 present and 46 absent, thus 18 data points were subsampled from the absent category and all data points in the present category were used in every subsample for a final sample size of 36. Subsamples also were taken for harbor porpoises (*Phocoena phocoena*; originally 44 present/19 absent; final $n = 38$), humpback whales (*Megaptera novaeangliae*; originally 52 present/14 absent; final $n = 28$), Risso’s dolphins (*Grampus griseus*; originally 39 present/24 absent; final $n = 48$), Dall’s porpoises (*Phocoenoides dalli*; originally 27 present/36 absent; final $n = 54$), and Pacific-white sided dolphins (*Lagenorhynchus obliquidens*; originally 30 present/33 absent; final $n = 60$). Logistic regression analyses were repeated five times for each species using different subsamples.

RESULTS

Monthly density estimates

Twenty-two species of marine mammals were identified during the 11-year study (Table 1). Monthly densities were calculated in Distance Sampling for ten species with enough sightings ($n > 55$) to obtain a single global detection function (Table 2). Monthly densities also were calculated for common dolphins (*Delphinus spp.*) and northern right whale dolphins (*Lissodelphis borealis*) from a shared model with additive swell height,

Table 1. Number of sightings for all marine mammal species identified in Monterey Bay, May-Nov 1997-2007.

Species	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
Baird's beaked whale (<i>Berardius bairdii</i>)				1	1		1				
Blue whale (<i>Balaenoptera musculus</i>)	2	1	1	7	4	20	31	10	2		
Bottlenose dolphin (<i>Tursiops truncatus</i>)	2	1							1		
California sea lion (<i>Zalophus californianus</i>)	307	165	182	241	193	207	197	79	51	120	51
Cuvier's beaked whale (<i>Ziphius cavirostris</i>)									1		
Dall's porpoise (<i>Phocoenoides dalli</i>)	15	10	14	3	3	6	6	14	3	6	5
Elephant seal (<i>Mirounga angustirostris</i>)	3	14	8	4	4	1	5	1	10	5	
Fin whale (<i>Balaenoptera physalus</i>)	1	2					3				
Fur seal (<i>Callorhinus ursinus</i>)		1							3		1
Gray whale (<i>Eschrichtius robustus</i>)			4							1	
Harbor porpoise (<i>Phocoena phocoena</i>)	17	20	52	11	9	36	33	16	26	17	12
Harbor seal (<i>Phoca vitulina</i>)	8	26	16	6	18	20	30	7	21	11	4
Humpback whale (<i>Megaptera novaeangliae</i>)	21	47	48	53	20	35	25	18	30	23	21
Killer whale (<i>Orcinus orca</i>)			1	2				1	2	1	
Long-beaked common dolphin (<i>Delphinus capensis</i>)	5	10		2	4	1					
Minke whale (<i>Balaenoptera acutorostrata</i>)	2		1								
Northern right whale dolphin (<i>Lissodelphis borealis</i>)			5	3	2	4	6	2	3	4	
Pacific white-sided dolphin (<i>Lagenorhynchus obliquidens</i>)	8	19	31	32	11	22	15	5	2		1
Risso's dolphin (<i>Grampus griseus</i>)	3	4	5	9	5	40	14	18	12	25	3
Sea otter (<i>Enhydra lutris</i>)	10	24	10	14	14	33	50	35	56	21	3
Short-beaked common dolphin (<i>Delphinus delphis</i>)	5	2									
Steller sea lion (<i>Eumetopias jubatus</i>)						1		1			1

Table 2. Multiple Covariate Distance Sampling (MCDS) results for 12 focal marine mammal species, May-Nov 1997-2007, and Jan & Mar 2003-2007. Species, number of observations (n), key function (Hr = hazard-rate, Hn = half-normal), power parameter coefficient (standard error; SE), intercept (Int.) of the scale parameter, covariate coefficients for SH = swell height, V = visibility, GS = group size, and B0-B3 = Beaufort levels 0-3 (for models with Beaufort, the intercept of the scale parameter is Beaufort 4), adjustment type (herm poly = hermite polynomial, cos = cosine) and number (#), adjustment coefficient, average probability of detection (P), 5% truncation distance (W), and goodness of fit KS p-value (GOF KS p; $\alpha = 0.05$) from the model used to obtain species density estimates.

Species	n	Key Fct.	Power coef. (SE)	Int. (SE)	SH coef. (SE)	V coef. (SE)	GS coef. (SE)	B0 coef. (SE)	B1 coef. (SE)	B2 coef. (SE)	B3 coef. (SE)	Adj. type (#) coef. (SE)	P (SE)	W (km)	GOF KS p
California sea lion (<i>Zalophus californianus</i>)	1777	Hr	2.103 (0.664)	0.104 (0.009)	-0.071 (0.027)	0.092 (0.032)		0.751 (0.189)	0.578 (0.130)	0.238 (0.122)	0.055 (0.131)	herm poly (1) 0.188 (0.054)	0.351 (0.007)	0.580	0.134
Sea otter (<i>Enhydra lutris</i>)	334	Hn		0.087 (0.018)		0.085 (0.047)		0.549 (0.489)	0.851 (0.475)	0.831 (0.469)	0.406 (0.481)		0.470 (0.020)	0.646	0.708
Humpback whale (<i>Megaptera novaeangliae</i>)	319	Hr	2.072 (1.621)	0.215 (0.035)				0.942 (0.514)	0.786 (0.295)	0.933 (0.283)	0.691 (0.283)		0.370 (0.018)	1.820	0.750
Harbor porpoise (<i>Phocoena phocoena</i>)	249	Hr	3.907 (3.500)	0.162 (0.036)	-0.081 (0.046)	0.079 (0.053)		0.572 (0.363)	0.807 (0.317)	0.745 (0.322)	0.192 (0.330)		0.540 (0.026)	0.665	0.932
Harbor seal (<i>Phoca vitulina</i>)	168	Hr	4.276 (4.610)	0.104 (0.012)				0.943 (0.640)	0.437 (0.283)	0.137 (0.282)	0.172 (0.334)		0.637 (0.031)	0.250	0.969
Risso's dolphin (<i>Grampus griseus</i>)	144	Hr	2.564 (2.816)	0.157 (0.026)		0.180 (0.085)	0.012 (0.005)						0.468 (0.031)	0.927	0.792
P. white-sided dolphin (<i>Lagenorhynchus obliquidens</i>)	141	Hn		0.232 (0.039)		0.157 (0.072)	0.007 (0.005)					cos (2) 0.251 (0.138) 0.208 (0.125)	0.377 (0.026)	0.954	0.964
Dall's porpoise (<i>Phocoenoides dalli</i>)	79	Hn		0.110 (0.032)				-0.063 (1.206)	1.293 (0.698)	0.805 (0.662)	0.846 (0.681)		0.422 (0.048)	0.708	0.750
Blue whale (<i>Balaenoptera musculus</i>)	74	Hn		0.681 (0.064)									0.501 (0.043)	1.681	0.491
Elephant seal (<i>Mirounga angustirostris</i>)	55	Hr	2.039 (0.619)	0.165 (0.048)									0.388 (0.067)	0.642	0.999
Common dolphin ^a (<i>Delphinus spp.</i>)	67	Hn		0.838 (3.742)	-0.321 (0.243)		0.001 (0.001)						0.519 (0.062)	0.927	0.838
N. right whale dolphin ^a (<i>Lissodelphis borealis</i>)				1.251 (0.647)											

^a *Delphinus spp.* ($n = 39$) and *L. borealis* ($n = 28$) observations were pooled to fit a common model with additive swell height, group size, and species effects. Intercept value reported for *L. borealis* is the species coefficient (SE). The baseline scale for *Delphinus spp.* is 0.8383 and for *L. borealis* it is $0.8383 \cdot \exp(1.251)$. Densities were calculated from individual detection functions, but pooled values are reported under common dolphin heading.

group size, and species effects (Table 2). Sightings for long-beaked and short-beaked common dolphins were combined for density estimates due to small sample sizes and difficulty distinguishing them in the field.

The best models chosen for California sea lions, elephant seals (*Mirounga angustirostris*), harbor porpoises, humpback whales, and sea otters (*Enhydra lutris*), were those that minimized AIC. The best models chosen for the remaining species excluded models with the lesser AIC if those models violated assumptions or produced unexpected results. For example, models with numeric covariates with a coefficient counter to expectation, such as positive swell height coefficient for harbor seals (*Phoca vitulina*) or negative visibility coefficients for Dall's porpoises and common dolphins/northern right whale dolphins, were disregarded and the next best model was chosen. Coefficients with a sign opposite of expectation likely occurred by chance alone, resulting from unequal sample size distribution across all levels of a covariate. Adjustment terms were not included in the final model for Risso's dolphin density because the probability of detection at zero distance with a simple polynomial adjustment was greater than one, violating the assumption of certain detection on the trackline. The best half-normal model was chosen over hazard-rate models for Pacific white-sided dolphins and Dall's porpoises to avoid fitting the spike in sightings at zero distance, likely due to responsive movement of these species towards vessels (Williams & Thomas 2007). The model minimizing AIC for blue whales included Beaufort coefficients that did not increase from Beaufort 4 to Beaufort 0 as was expected (i.e. the distance at which animals were detected should have increased in lesser Beaufort sea states), and thus the next best model

was chosen. Beaufort coefficients were mostly positive, changing the scale of the detection function and increasing the distance at which objects could be detected.

Annual density and diversity

Densities of the 12 focal species varied among years (Fig. 3), although mean species richness remained relatively constant (13.7 ± 0.396 (SE) species per year; Fig. 4). Species richness varied by only four species during the ten-year period, and was 15 (greatest richness observed) during 1997, 1998, and 2005 (Fig. 4). Marine mammals were most evenly distributed, but least dense during 2005, and least even, but dense during 1997 and 1998 (Fig. 4). The greatest total density of marine mammals occurred during 1997, 1998, and 2007 (Fig. 4). California sea lions, Dall's porpoises, harbor porpoises, harbor seals, humpback whales, Risso's dolphins, and sea otters were sighted every year, and elephant seals were sighted every year but 2007 (Fig. 3). Northern right whale dolphins were absent in 1997, 1998, and 2007, and present in greatest densities during 1999 (Fig. 3). Pacific white-sided dolphins were present in greatest densities from 1999-2002, and decreased densities during 1997, 1998, and 2003-2007 (Fig. 3). Common dolphins were present in greatest densities and were the most abundant species of marine mammal during 1997 and 1998, but were sighted infrequently or absent in subsequent years (Fig. 3). Blue whales were present in greatest densities during 2003, and least densities or absent from 1997-1999 and 2005-2007 (Fig. 3). Risso's dolphins were present in decreased densities during 1997 and 1998, but were almost ten-times as dense during 2002 (Fig. 3).

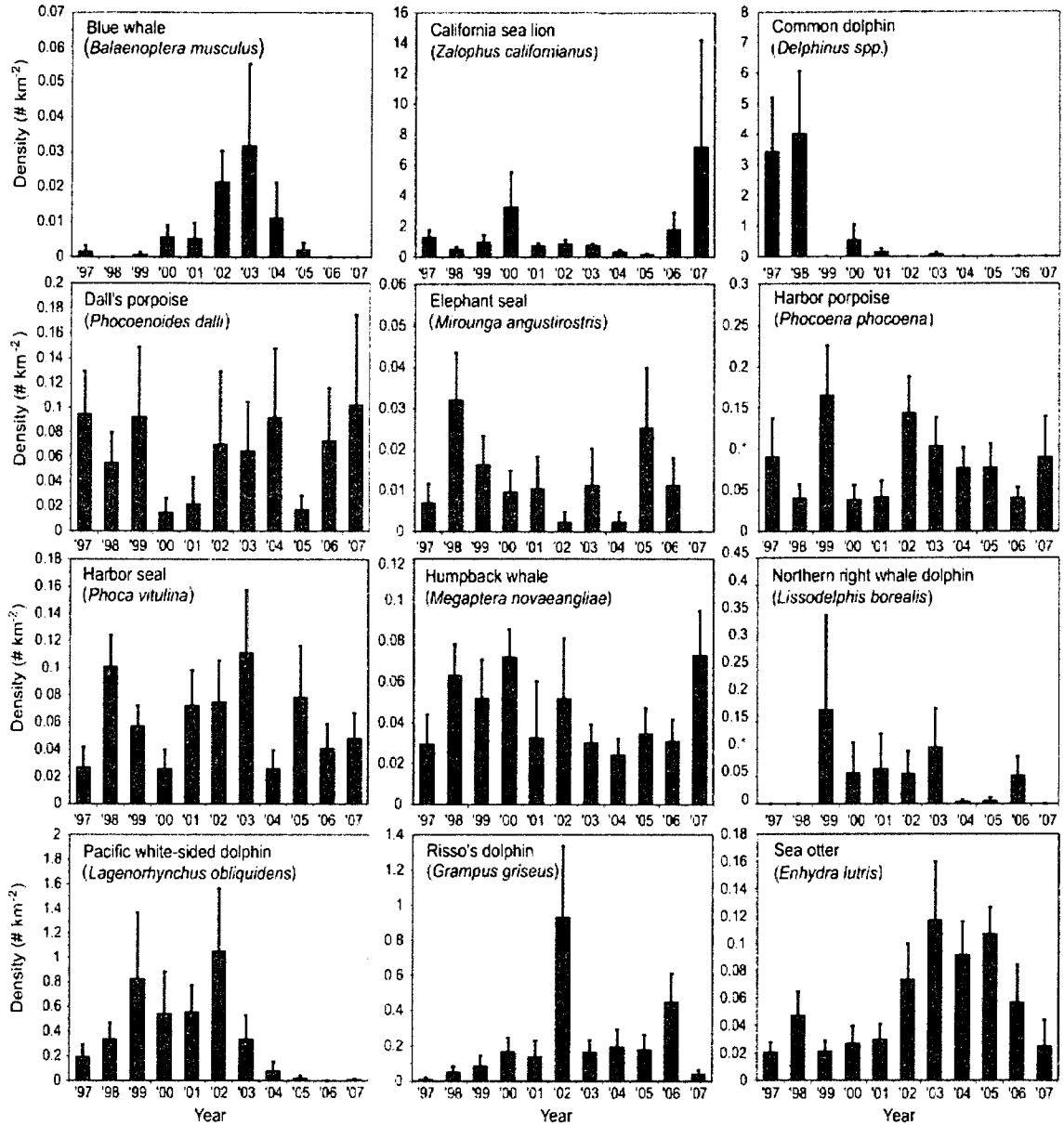


Figure 3. Annual mean densities and standard errors for 12 focal marine mammal species identified in Monterey Bay, May-Nov 1997-2007. Note different scales on y-axis.

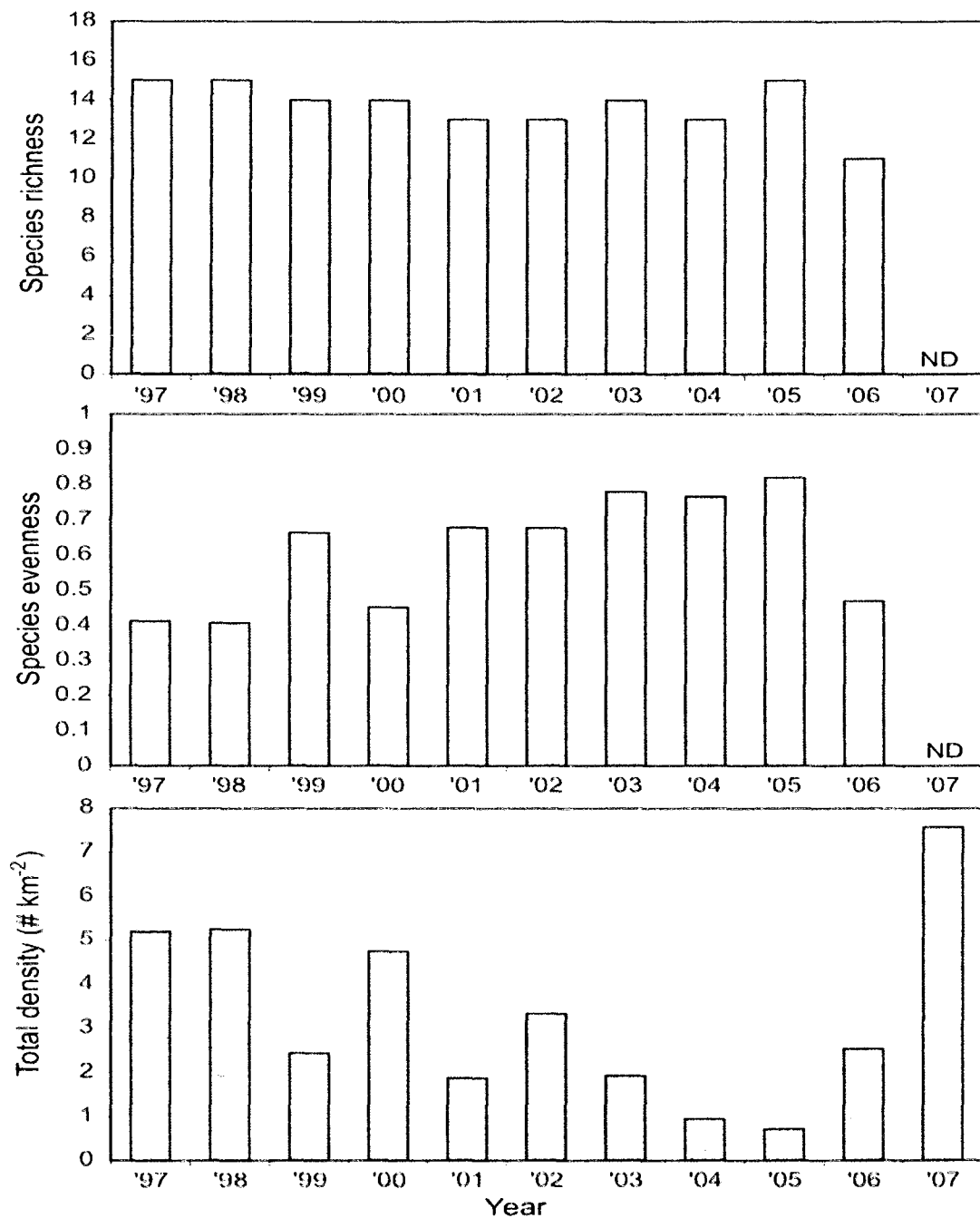


Figure 4. Species richness, species evenness, and total density for marine mammal species identified in Monterey Bay, May-Nov 1997-2007. Species richness was determined for all species sighted, including rare species, whereas species evenness (Shannon's equitability index) and total density were determined for only 12 focal species. Species richness and evenness were not calculated for 2007 due to reduced effort that year (ND = no data).

Warmer vs. cooler years

Discriminate function analysis indicated that warmer and cooler year groupings were significantly different based on UIs and SSTs ($n = 8$, $F = 29.847$, $p = 0.002$), and generated scores ($-15.863 + 0.626 \cdot \text{SST} - 0.864 \cdot \text{UI}$) to categorize the remaining years as warmer (1997) or cooler (2000, 2003). Species richness, species evenness, and total density did not differ significantly between the two groups (Table 3). Pacific white-sided dolphins and northern right whale dolphins were the only species with significantly greater densities in cooler years, although northern right whale dolphin densities were only marginally significant (Table 3). No species had significantly greater densities in warmer years (Table 3). Randomization tests performed on heteroscedastic response variables (species richness, blue whale, common dolphin, and elephant seal densities) confirmed non-significant results of unequal variance t-tests. Performing the same analyses using only the eight most disparate years (used to develop the discriminate function) did not yield significant results. Performing the same analyses excluding El Niño years produced significant results for Pacific white-sided dolphins only (results not shown). The calculated mean differences necessary to detect significant differences in species evenness ($n = 10$), total density ($n = 11$), and species densities ($n = 11$) between warmer and cooler years were approximately 2-17 times greater than the actual observed mean differences (Table 3). Calculations were not performed for species richness, blue whale, common dolphin, or elephant seal densities because effect size for heteroskedastic variables could not be computed using G*Power.

Table 3. T-test results for differences in species richness, species evenness, total density, and species densities between warmer and cooler years. Mean (standard error; SE), sample size (n), t -statistic (t), p -value (p), and observed mean differences reported. Calculated mean differences were determined using G*Power for a two-tailed t -test with $\alpha = 0.05$ and power = 0.8. Asterisk (*) indicates significant results ($\alpha = 0.05$).

Species	Warmer year mean (SE)	n	Cooler year mean (SE)	n	t	p	Obs. mean diff.	Calc. mean diff.
Species Richness ^a	13.800 (0.800)	5	13.600 (0.245)	5	0.239	0.821	0.200	
Species Evenness	0.575 (0.090)	5	0.650 (0.054)	5	0.717	0.494	0.075	0.336
Total density	2.932 (0.987)	5	3.654 (0.900)	6	0.541	0.602	0.722	4.207
Blue whale ^a (<i>Balaenoptera musculus</i>)	0.003 (0.0002)	5	0.011 (0.005)	6	1.389	0.211	0.008	
California sea lion (<i>Zalophus californianus</i>)	0.821 (0.309)	5	2.298 (1.056)	6	1.231	0.250	1.477	3.779
Common dolphin ^a (<i>Delphinus spp.</i>)	1.489 (0.917)	5	0.129 (0.086)	6	1.477	0.212	1.360	
Dall's porpoise (<i>Phocoenoides dalli</i>)	0.066 (0.014)	5	0.061 (0.015)	6	0.259	0.802	0.005	0.065
Elephant seal ^a (<i>Mirounga angustirostris</i>)	0.016 (0.006)	5	0.008 (0.002)	6	1.176	0.288	0.007	
Harbor porpoise (<i>Phocoena phocoena</i>)	0.065 (0.011)	5	0.097 (0.021)	6	1.266	0.237	0.032	0.248
Harbor seal (<i>Phoca vitulina</i>)	0.055 (0.015)	5	0.065 (0.012)	6	0.554	0.593	0.010	0.178
Humpback whale (<i>Megaptera novaeangliae</i>)	0.037 (0.007)	5	0.052 (0.008)	6	1.498	0.168	0.016	0.033
N. right whale dolphin (<i>Lissodelphis borealis</i>)	0.012 (0.010)	5	0.075 (0.024)	6	2.267	0.050*	0.063	
P. white-sided dolphin (<i>Lagenorhynchus obliquidens</i>)	0.126 (0.062)	5	0.553 (0.149)	6	2.453	0.037*	0.427	
Risso's dolphin (<i>Grampus griseus</i>)	0.177 (0.077)	5	0.255 (0.137)	6	0.471	0.649	0.079	0.525
Sea otter (<i>Enhydra lutris</i>)	0.065 (0.016)	5	0.049 (0.016)	6	0.701	0.501	0.016	0.070

^a Indicates unequal variance t-test used.

Monthly density predictors

Linear regression results (non-lagged) indicated that humpback whale and Risso's dolphin densities could be predicted using environmental or prey variables. Log krill backscatter and *in situ* Chl had a significant effect on log humpback whale density using the *in situ* dataset, whereas log krill backscatter was the only significant predictor of log humpback whale density using the remote-sensed dataset (Table 4, Fig. 5). Upwelling index was the only environmental variable with a significant effect on log Risso's dolphin density using either dataset (Table 4, Fig. 5). None of the (non-lagged) environmental variables significantly predicted log transformed blue whale ($n = 19$), Dall's porpoise ($n = 31$), harbor porpoise ($n = 51$), or Pacific white-sided dolphin ($n = 34$) densities.

The time frame in which cetaceans responded to environmental predictors varied among species (Fig. 6). *In situ* Chl (lagged three months; Fig. 6) was the only significant predictor of log Dall's porpoise density using the *in situ* dataset (Table 4, Fig. 5), whereas remote PP (lagged three months; Fig. 6) was the only significant predictor of log Dall's porpoise density using the remote-sensed dataset (Table 4). The significance of remote PP in predicting Dall's porpoise density was driven by one outlier, which if removed resulted in a non-significant outcome. Log krill backscatter (no lag) was the only significant predictor of log humpback whale density using either dataset (Table 4, Fig. 5). *In situ* PP (lagged three months; Fig. 6) was the only significant predictor of Pacific white-sided dolphin density using the *in situ* dataset (Table 4, Fig. 5), whereas none of the environmental variables tested significantly predicted Pacific white-sided dolphin

Table 4. Significant least squares multiple regression results predicting log transformed cetacean densities using environmental and prey variables. Regression coefficients (coef.) and standard errors (SE), sample size (n), adjusted r^2 , F or t statistic, and p -values ($\alpha = 0.05$) reported. Number of months lagged shown in parentheses after predictor variables.

<i>In situ</i> Chl and PP dataset							
Not lagged	Significant predictors	Coef.	(SE)	n	r^2	Statistic	p -value
Humpback whale density (<i>Megaptera novaeangliae</i>)	full model			54	0.208	$F = 7.961$	<0.001
	constant	-2.104	(0.240)			$t = 8.749$	<0.001
	log krill backscatter	0.250	(0.070)			$t = 3.729$	<0.001
	<i>in situ</i> Chl	-0.036	(0.016)			$t = 2.230$	0.030
Risso's dolphin density (<i>Grampus griseus</i>)	full model			41	0.139	$F = 7.477$	0.009
	constant	-0.574	(0.087)			$t = 6.566$	<0.001
	upwelling index	0.002	(0.0007)			$t = 2.734$	0.009
Remote Chl and PP dataset							
Not lagged							
Humpback whale density (<i>Megaptera novaeangliae</i>)	full model			55	0.141	$F = 9.890$	0.003
	constant	-2.151	(0.244)			$t = 8.818$	<0.001
	log krill backscatter	0.217	(0.069)			$t = 3.145$	0.003
Risso's dolphin density (<i>Grampus griseus</i>)	full model			41	0.139	$F = 7.477$	0.009
	constant	-0.574	(0.087)			$t = 6.566$	<0.001
	upwelling index	0.002	(0.0007)			$t = 2.734$	0.009
<i>In situ</i> Chl and PP dataset							
Lagged							
Dall's porpoise density (<i>Phocoenoides dalli</i>)	full model			31	0.157	$F = 6.575$	0.016
	constant	-1.261	(0.119)			$t = 10.633$	<0.001
	<i>in situ</i> Chl (3)	0.048	(0.019)			$t = 2.564$	0.016
Humpback whale density (<i>Megaptera novaeangliae</i>)	full model			55	0.141	$F = 9.890$	0.003
	constant	-2.151	(0.244)			$t = 8.818$	<0.001
	log krill backscatter (0)	0.217	(0.069)			$t = 3.535$	0.003
P. white-sided dolphin density (<i>Lagenorhynchus obliquidens</i>)	full model			32	0.131	$F = 5.568$	0.024
	constant	-0.737	(0.200)			$t = 3.684$	<0.001
	<i>in situ</i> PP (3)	0.002	(0.001)			$t = 2.383$	0.024
Risso's dolphin density ^a (<i>Grampus griseus</i>)	full model			36	0.340	$F = 19.000$	<0.001
	constant	-0.809	(0.103)			$t = 7.828$	<0.001
	upwelling index (1)	0.003	(0.0007)			$t = 4.358$	<0.001
Remote Chl and PP dataset							
Lagged							
Dall's porpoise density ^b (<i>Phocoenoides dalli</i>)	full model			31	0.125	$F = 5.271$	0.029
	constant	-1.272	(0.138)			$t = 9.211$	<0.001
	remote PP (3)	0.00009	(0.00004)			$t = 2.296$	0.029
Humpback whale density (<i>Megaptera novaeangliae</i>)	full model			55	0.141	$F = 9.890$	0.003
	constant	-2.151	(0.244)			$t = 8.818$	<0.001
	log krill backscatter (0)	0.217	(0.069)			$t = 3.145$	0.003
Risso's dolphin density ^a (<i>Grampus griseus</i>)	full model			36	0.340	$F = 19.000$	<0.001
	constant	-0.809	(0.103)			$t = 7.828$	<0.001
	upwelling index (1)	0.003	(0.0007)			$t = 4.358$	<0.001

^a Sea surface temperature was excluded from analysis due to multicollinearity.

^b Significant results for remote PP (lagged 3 months) are driven by one outlier. If outlier is removed, results become non-significant.

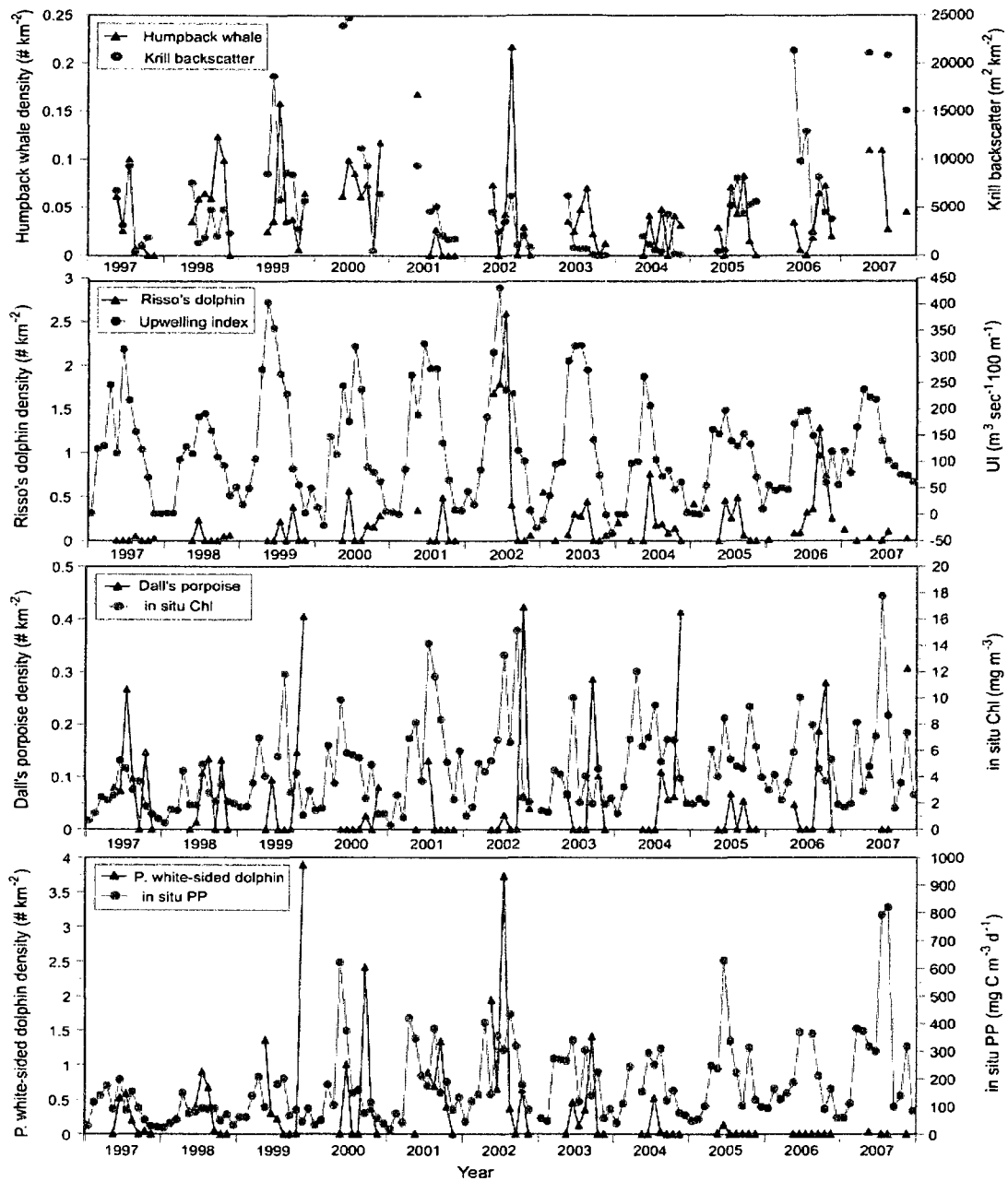


Figure 5. Relationship between significant environmental and prey predictor variables (●) and cetacean densities (▲) for humpback whales (*Megaptera novaeangliae*) and krill backscatter, Risso's dolphins (*Grampus griseus*) and upwelling index (UI), Dall's porpoises (*Phocoenoides dalli*) and *in situ* chlorophyll (Chl), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and *in situ* primary production (PP). Each point is a monthly observation for Jan-Dec (UI, *in situ* Chl, and *in situ* PP), or May-Nov (krill backscatter and cetacean densities) 1997-2007.

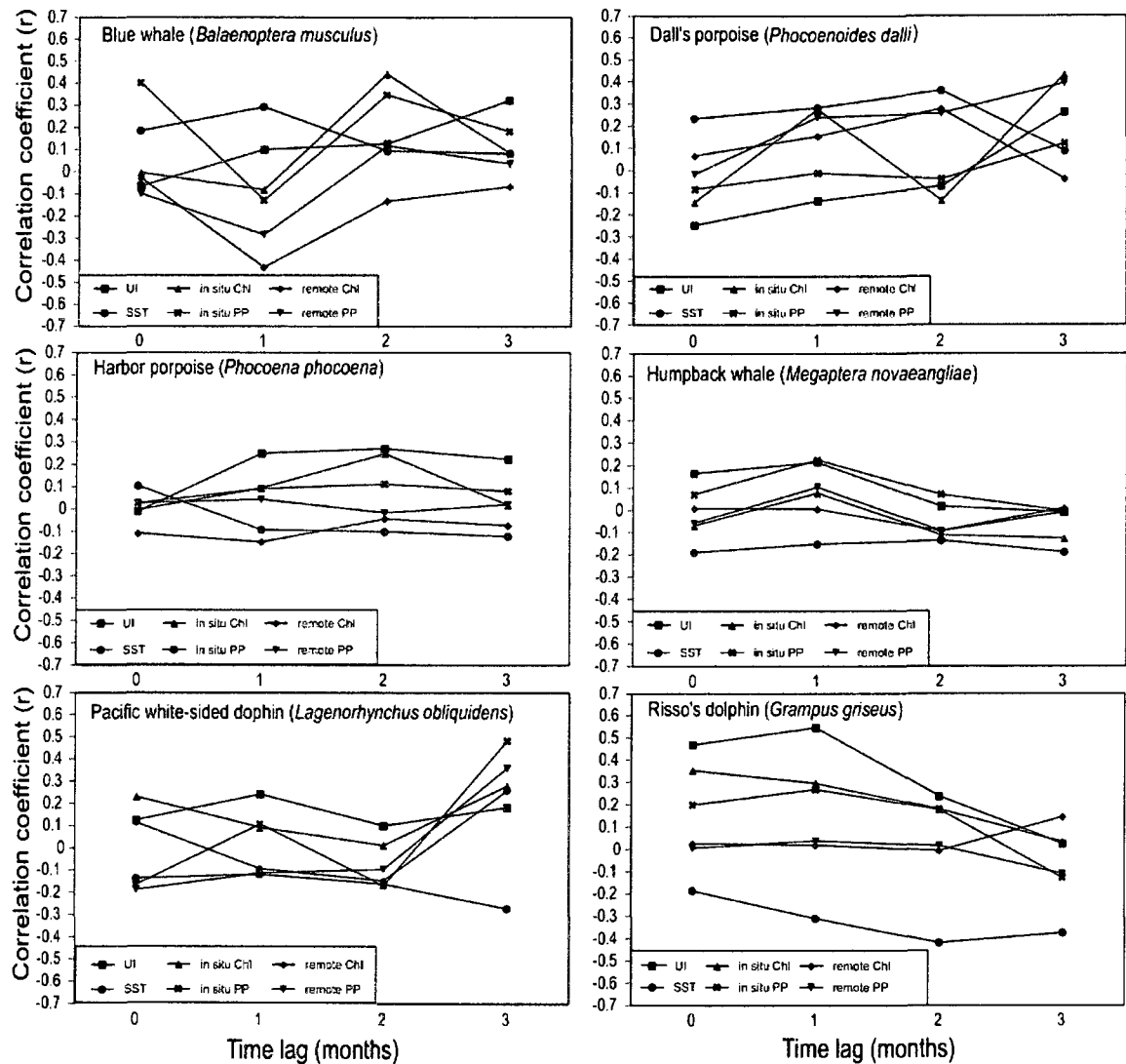


Figure 6. Pearson's partial correlation coefficients (at zero, one, two, and three month time lags) for environmental variables (upwelling index; UI (■), sea surface temperature; SST (●), *in situ* chlorophyll; Chl (▲), *in situ* primary production; PP (✱), remote Chl (◆), and remote PP (▼)) and cetacean densities (when cetaceans were present).

density ($n = 32$) using the remote-sensed dataset. Upwelling index (lagged one month; Fig. 6) was the only significant predictor of log Risso's dolphin density using either dataset (Table 4, Fig. 5). Sea surface temperature (lagged two months; Fig. 6) also had a significant effect on Risso's dolphin density, but was collinear with UI thus excluded from analyses ($VIF > 2$). None of the lagged environmental variables significantly predicted log blue whale ($n = 19$) or harbor porpoise ($n = 52$) densities using either dataset.

Harbor porpoise, Pacific white-sided dolphin, and Risso's dolphin densities and predictor variables required transformation to reduce temporal autocorrelation for both analyses (non-lagged and lagged), whereas blue whale and humpback whale monthly densities were not autocorrelated in either analysis. Dall's porpoise densities and predictor variables required transformation to reduce temporal autocorrelation for non-lagged analysis, but transformation was not required when time lags were considered.

Monthly occurrence predictors

Results from binary logistic regressions were inconsistent among the five subsampled analyses. It was not possible to provide reliable predictive models for blue whales, harbor porpoises, humpback whales, or Risso's dolphins. Significant predictors existed for all four species, but not for all five subsampled analyses. The only consistent results indicated that there were no significant predictors in any of the five subsampled analyses for blue whale or Risso's dolphin occurrence using the remote-sensed dataset.

Significant predictors existed for all five subsampled analyses for Dall's porpoise and Pacific-white sided dolphin occurrence, but different combinations of predictors were

significant for different subsamples. Only the predictors which were consistently significant in all five subsamples were reanalyzed using non-subsampled data. Non-subsampled results were good representations of subsampled results because sample sizes were nearly equal for these two species. Collinear predictor variables UI, SST, and *in situ* Chl were removed from analysis of the Dall's porpoise *in situ* dataset and SST was removed from analysis of the Dall's porpoise remote-sensed dataset. No evidence of multicollinearity existed in either Pacific white-sided dolphin analysis. *In situ* PP significantly predicted Dall's porpoise occurrence using the *in situ* dataset, whereas UI significantly predicted Dall's porpoise occurrence using the remote-sensed dataset (Table 5). Upwelling index and SST significantly predicted Pacific white-sided dolphin occurrence using the *in situ* dataset, whereas UI and remote Chl significantly predicted Pacific white-sided dolphin occurrence using the remote-sensed dataset (Table 5).

DISCUSSION

Warmer vs. cooler years

Species evenness and total density

The lack of statistically significant differences in marine mammal species evenness and total density between warmer and cooler years is likely a result of the inconsistent community response of marine mammals to similarly grouped years. For example, although 1997/1998 (El Niño event) and 2005 (delayed and weakened seasonal upwelling) were classified as warmer years based on oceanographic conditions, the response of marine mammals differed between years. Therefore, grouping years as

Table 5. Significant binary logistic regression results predicting cetacean occurrence (presence/absence) using environmental and prey variables. Abbreviations are for sample size (n) and Hosmer and Lemeshow goodness of fit (H&L GOF) test. Coefficient (coef.) standard errors are in parentheses and $\alpha = 0.05$ for all statistical analyses.

Statistic	Dall's porpoise (<i>Phocoenoides dalli</i>)		P. white-sided dolphin (<i>Lagenorhynchus obliquidens</i>)	
	<i>In situ</i> dataset	Remote dataset	<i>In situ</i> dataset	Remote dataset
n presence	27	27	30	30
n absence	36	36	33	33
Omnibus Chi-squared	7.846	6.456	14.308	19.078
Omnibus p -value	0.005	0.011	0.001	<0.001
-2 log likelihood	78.200	79.590	72.886	68.116
Nagelkerke r^2	0.157	0.131	0.271	0.349
H&L GOF Chi-square	8.408	5.182	11.969	6.058
H&L GOF p -value	0.395	0.738	0.153	
% correct absence	69.4	72.2	72.7	75.8
% correct presence	55.6	55.6	56.7	73.3
% correct overall	63.5	65.1	65.1	74.6
constant: coef. (SE)	0.861 (0.514)	0.799 (0.517)	-11.208 (4.467)	-0.596 (0.616)
constant: odds ratio	2.365	2.224	0.00001	0.551
UI: coef. (SE)		-0.007 (0.003)	0.014 (0.004)	0.012 (0.004)
UI: odds ratio		0.993	1.014	1.012
SST: coef. (SE)			0.671 (0.300)	
SST: odds ratio			1.957	
Remote Chl: coef. (SE)				-0.275 (0.097)
Remote Chl: odds ratio				0.760
<i>In situ</i> PP: coef. (SE)	-0.006 (0.002)			
<i>In situ</i> PP: odds ratio	0.994			

warmer or cooler without considering the initial mechanism of variability (El Niño versus anomalous upwelling) may not be an effective method of categorization. Marine mammal communities appear to have responded slightly differently each year to the various combinations of factors affecting the ecosystem.

Although grouping years as warmer or cooler may not be effective for some analyses, our dataset enabled a comparison of the community response of marine mammals between the 1997/1998 El Niño event and the anomalous upwelling year of 2005. During 2005, warmer than average SSTs (throughout spring and summer), decreased primary production and zooplankton abundance (Mackas et al. 2006, Schwing et al. 2006, Barth et al. 2007), and reduced catches of mid-trophic level fish species (Brodeur et al. 2006) occurred off the west coast of North America. Previous researchers reported that the biological effects of the anomalous oceanic conditions of 2005 were limited to central California through southern British Columbia (northern California Current; Brodeur et al. 2006, Mackas et al. 2006, Sydeman et al. 2006) and documented positive zooplankton anomalies (Mackas et al. 2006) from Point Conception, California south to Baja, Mexico (southern California Current). Thus, it is likely that decreased total density of marine mammals in Monterey Bay during 2005 resulted from the redistribution of more mobile species to areas outside the region affected by the upwelling anomaly. Indeed, densities of wider-ranging species (e.g. blue whales, Dall's porpoises, and Pacific white-sided dolphins) decreased in Monterey Bay during 2005, whereas densities of more resident species (e.g. harbor porpoises, harbor seals, and sea otters) remained unchanged or increased from the previous year.

Increased total densities of marine mammals during the 1997/1998 El Niño event can be attributed to the marked increased density of common dolphins during those years, in addition to the aggregation of cetaceans species in a narrow nearshore area of increased productivity (Benson et al. 2002). Although productivity was reduced in Monterey Bay during the 1997/1998 El Niño event compared with other years, there was still sufficient nutrient availability nearshore to support some primary production (Kudela & Chavez 2000, Chavez et al. 2002). Therefore, during basin-wide decreases in productivity (El Niño events) mobile top predators may be more likely to aggregate nearshore and less likely to redistribute north-south, to the extent that may have occurred during the anomalous upwelling conditions of 2005.

Species richness

The lack of a statistically significant difference in species richness between warmer and cooler years and the similarity of species richness among all years are indications that species richness may not be a good measure of species diversity in this study. There were important changes in species composition between years that were not evident when only species richness was examined. Species richness did not vary much among years because the presence of regularly occurring species (California sea lions, Dall's porpoises, elephant seals, harbor porpoises, harbor seals, humpback whales, Risso's dolphins, and sea otters) and different rare species totaled approximately the same richness every year. In other words, despite changes in the composition of species among years the total number of species sighted was similar for all years. Additionally, richness may not be a good measure of diversity because extreme differences in species

evenness occurred between 1997/1998 and 2005, whereas species richness was identical in all three years.

Individual species densities

Densities of Pacific-white sided dolphins and northern right whale dolphins were significantly greater during cooler years, whereas no species were present in significantly greater densities during warmer years. Greater densities of the two cold-temperate species during cooler years likely resulted from the southward movement of these species with cooler-waters. Barlow & Forney (2007) found similar increased abundances of Pacific-white sided dolphins and northern right whale dolphins off California during the cooler-water year of 1996, but reported no consistent variation in the abundance of common dolphins or Risso's dolphins with warm and cold-water years. We also found that warm-temperate common dolphins were not present in greater densities during warmer years and attribute this result to the fact that common dolphins did not respond consistently to like-years. The drastic increase in common dolphin densities seen in this study during the 1997/1998 El Niño event, did not occur again in subsequent warmer years (during 2004, 2005, and 2006 no common dolphins were sighted). It is likely that during the 1997/1998 El Niño event, large groups of common dolphins moved north with warmer waters in search of prey, whereas during 2004, 2005, and 2006 common dolphins remained in their normal habitat further south (southern California to Mexico) because it was largely unaffected by the upwelling anomalies (Peterson et al. 2006).

The lack of significantly greater densities of any species during warmer years may be attributed to the fact that species responded differently depending on the mechanism

of variability (El Niño or anomalous upwelling). It also is possible that non-significant results may simply be a consequence of small sample sizes. Although 11 years is a reasonably long time series, given the amount of variability in the system, we may have lacked the ability to detect significant differences if they existed. The mean differences statistically detectable were considerably greater than those actually observed, in some cases even greater than what might be biologically realistic. If the calculated mean differences we were able to detect were, in fact, biologically unrealistic, it is possible that there was a difference between years that was not detected statistically.

Prey variables as density predictors

Prey availability may have had a greater effect on marine mammal densities than oceanographic variables. For example, densities of Risso's dolphins (which feed almost exclusively on squid) increased dramatically in Monterey Bay during 2002, concurrent with a marked increase in Humboldt squid (*Dosidicus gigas*) abundance (Zeidberg & Robison 2007). Additionally, market squid (*Loligo opalescens*) fisheries landings in Monterey Bay in 2002 exceeded the previous record by 58% in a near unprecedented record-setting year (CDFG 2003). Thus the increase in Risso's dolphin density in Monterey Bay during 2002 may have been a direct result of increased prey availability that year.

Although we were unable to quantify squid availability during this study, acoustic backscatter and abundance measurements of krill, a major prey source of blue and humpback whales, were collected. Results support the hypothesis that the closest trophic linkage to top predators, in this case mean krill backscatter, would be the best predictor of

humpback whale density. Previous researchers primarily examining the relationship between baleen whales and krill found a similar association between predators and prey (Reid et al. 2000, Benson et al. 2002, Murase et al. 2002, Friedlaender et al. 2006).

The lack of significance of mean krill backscatter in predicting blue whale density was an unexpected finding, particularly because blue whales forage almost exclusively on krill, whereas humpback whales forage on krill and small schooling fishes. We thus would have expected krill backscatter to be a better predictor of blue whale density than humpback whale density. Previous researchers using acoustic backscatter as a measurement of krill abundance have reported blue whales were associated with seasonally dense aggregations of krill (Croll et al. 1998, Fiedler et al. 1998, Croll et al. 2005). It is possible that there was a relationship between blue whale density and mean krill backscatter, but because there were fewer sightings of blue whales than humpback whales, we simply did not have enough statistical power to detect it. It also is possible that because of their large size and consequently greater prey requirements, blue whales may need extremely dense aggregations of krill in which to forage. Prior studies in Monterey Bay support this idea and reported blue whales foraged on krill aggregations orders of magnitude greater than krill densities in the remainder of the bay (Schoenherr 1991, Croll et al. 2005). Consequently, a measure such as maximum krill backscatter may have been a better predictor of blue whale density than mean krill backscatter used in this study.

The lack of a significant predictive relationship between krill abundance (calculated from net tows) and humpback whale or blue whale densities was another

unexpected finding that may be due to the nature of the sampling technique used. Net tows to collect krill specimens were limited to certain sampling stations, whereas hydroacoustic data were collected continuously while the ship was underway. It is possible that hydroacoustic data produce a more representative estimate of prey availability over a larger spatial area (as in this study), and net tow data are better suited for studies requiring accurate high-resolution prey information over a very small spatial area.

Although hydroacoustic backscattering strength has proved useful when assessing krill availability as marine mammal prey, the number of fish schools per kilometer surveyed as determined from hydroacoustic data may not be effective in assessing fish availability. Fish schools did not predict the densities of any of the piscivorous cetacean species studied (Dall's porpoises, harbor porpoises, humpback whales, or Pacific white-sided dolphins), although previous researchers have reported a significant relationship between forage fish abundance and baleen whale abundance (Payne et al. 1986, Piatt et al. 1989, Weinrich et al. 1997). The poor association between fish schools and piscivorous cetaceans may have resulted from our inability to conduct trawls to verify backscattering aggregations were correctly identified as fish (due to the expense and time involved). We were thus unable to estimate fish species, density, or biomass. Additionally, more fish schools (i.e. increased encounter rate) did not necessarily indicate increased density or biomass of fish, because many fish may have been concentrated in few large aggregations. Furthermore, all fish schools identified may not have served as suitable prey for marine mammals because much of the prey identified as fish may have

been too large or an inferior prey species. Thus, although identifying fish schools per kilometer surveyed using hydroacoustic data is a relatively quick and easy method of estimating marine mammal prey when compared with other more time consuming techniques (e.g. net tows), it appears to be too crude of an estimate to have any meaningful predictive power in this study.

Environmental variables as density predictors

Environmental variables had a significant effect on the densities of some cetacean species, but not others. Risso's dolphins were the only species significantly affected by upwelling (with a time lag of one month improving the correlation) and also were the only species that fed almost exclusively on squid. Because of their rapid growth and short lifespan, squid are extremely responsive to changes in environmental conditions, such as UI and SST (Jackson & Domeier 2003, Zeidberg et al. 2006). Market squid, which spawn annually in Monterey Bay during the upwelling season, form a key component of a relatively short trophic system consisting of upwelling, phytoplankton, krill, and squid (Mangel et al. 2002, Ish et al. 2004). Therefore, it is possible that UI significantly predicted Risso's dolphin density because UI was a good predictor of squid size and abundance (Jackson & Domeier 2003, Zeidberg et al. 2006).

Chlorophyll (*in situ*) or primary production (*in situ* or remote) had a significant effect on Dall's porpoise, humpback whale, and Pacific white-sided dolphin densities, but remote Chl did not affect the densities of any cetacean species studied. The lack of significance of remote Chl was surprising, considering it has been used frequently by researchers to describe habitat associations for cetaceans on various spatial and temporal

scales (Smith et al. 1986, Jaquet et al. 1996, Moore et al. 2002, D'Amico et al. 2003, Burtenshaw et al. 2004). Due to the ephemeral nature of primary productivity blooms and subsequent consumption or offshore advection, monthly means used in this study may have been inadequate to detect the fine-scale effects of Chl or PP on top predators. Thus the lack of significance of remote Chl and the minimal amount of variability explained by the *in situ* and remote datasets may have been the result of a temporal mismatch in the sampling regimes of cetaceans and environmental variables.

Adjusting environmental variables to account for the temporal lag from the initiation of upwelling to the arrival of foraging cetaceans improved the predictive capabilities of models for some odontocete species. Although previous researchers have acknowledged the importance of time lags to mysticetes, few have recognized their effect on odontocetes. Burtenshaw et al. (2004) observed a time lag of several months between spring chlorophyll blooms and the northward migration of blue whales in the northeast Pacific Ocean and Croll et al. (2005) reported a time lag of several months between seasonal increases in primary production and the arrival of blue whales in Monterey Bay. In this study, we also found a three-month time lag, indicative of the time required for primary production to move up the trophic links and attract enough prey species to affect top predator densities. Because Chl and PP did not significantly predict Dall's porpoise or Pacific white-sided dolphin densities without time lags, and did have a significant effect when lags were incorporated, results indicate that time lags may be important to consider when building predictive models for odontocetes, in addition to mysticetes.

The lack of significant predictors for the density of another odontocete species, harbor porpoise, may have resulted from incomplete sampling of their habitat or the less mobile nature of this species. Field survey effort extended to a depth of 55 m (approximately 5 km from shore), whereas harbor porpoise reside mostly in shallow (< 55-60 m), neritic waters (Gaskin 1984, Barlow 1988, Carretta et al. 2000). By sampling only the outer edge of their habitat, we may have been unable to detect changes in harbor porpoise density if they did occur. It also is possible that densities did not change with environmental conditions because harbor porpoise in Monterey Bay constitute a resident population (Calambokidis & Barlow 1991, Carretta et al. 2007). Resident animals would be less likely to move large distances in search of prey and more likely to remain in Monterey Bay despite poor environmental conditions.

Monthly occurrence predictors

Inconsistent logistic regression results for four of the six cetacean species studied indicated that it was not possible to predict cetacean occurrence (presence/absence) with the given predictor variables and sample sizes. Because the two species with nearly equal (thus largest) sample sizes yielded consistently significant results and other species with lesser sample sizes yielded inconsistent results, it is most likely that the samples were insufficient to detect consistently significant predictors given the amount of variability in the system. However, even models that significantly predicted Dall's porpoise and Pacific white-sided dolphin occurrence did not do so with great accuracy.

In situ PP and UI (remote dataset) were the only variables included in the final Dall's porpoise occurrence model, although any of the collinear variables (UI, SST, *in*

situ Chl, or *in situ* PP) could have been used. The negative coefficients for UI and *in situ* PP indicate that as those predictors decreased below a certain threshold level, Dall's porpoise moved into Monterey Bay. It is possible that decreased productivity throughout the California Current forced Dall's porpoises to congregate in nearshore regions of increased productivity relative to the offshore environment. This effect would be similar to the response of cetaceans during El Niño years discussed previously (Benson et al. 2002).

Results from Pacific white-sided dolphin logistic regression analysis are difficult to explain biologically. The mathematical sign of the partial regression coefficient for UI was positive for Pacific white-sided dolphins, whereas it was negative for Dall's porpoises. Results from *in situ* and remote analyses indicate that as upwelling intensity exceeded a certain threshold level, Pacific white-sided dolphins moved into Monterey Bay. This response of Pacific white-sided dolphins to increased upwelling intensity was expected if upwelling increased the abundance of their prey, but the positive partial regression coefficient for SST and negative coefficient for remote Chl were surprising. Because partial regression coefficients describe the amount of change in the response variable for a unit change in the predictor, when all remaining predictor variables are held constant, it is possible that given a certain level of increased upwelling, Pacific white-sided dolphins responded to slightly warmer waters or lesser Chl levels. It also is possible that these results occurred by chance alone, thus should be interpreted cautiously. More conclusive occurrence predictors may have been obtained if a larger spatial area was studied (i.e. California Current).

Conclusions

Monterey Bay is a small region within the larger California Current, which is a temporally and spatially dynamic system. Marine mammals are wide-ranging predators that respond to prey resources over a large spatial area. By tracking a community of top predators in Monterey Bay during an 11-year period, we have documented interannual changes in marine mammal density and diversity resulting from ecosystem variability. We found that the community response of marine mammals differed depending on the mechanism of variability (El Niño or anomalous upwelling events) and that by grouping years as warmer and cooler years we were unable to detect statistical differences in density (for most species) or diversity (richness and evenness). We believe prey is the best predictor of cetacean density and that a more comprehensive prey collection methodology may have improved our results. Environmental variables explained some degree of variation in the densities of certain species, but lagging environmental variables helped improve predictive power. No single environmental variable was superior in predictive ability and many variables expected to be good predictors explained only a minimal amount of variability. Our limited explanatory ability is likely a result of the synergistic effect of environmental forces including, but not limited to, local (upwelling) and basin-wide (El Niño/La Niña) phenomena. Each species of marine mammal appears to have responded slightly differently to the unique combination of environmental factors.

As the world's climate continues to change, the need to better understand the effects of environmental variability on the oceans top predators is becoming increasingly

important. Longer-term datasets are crucial in helping to achieve this goal, yet few marine mammal datasets span over a decade. With 11 years of data, a large number by most standards, we have only just begun to understand the processes affecting the movements and habitat use of these animals. There is still much to be learned from an even longer time-series covering a larger spatial area. Through long-term monitoring programs, we should improve our understanding of how environmental variability affects ecosystem functioning and be better prepared for future oceanic change as it occurs.

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