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Abstract

We report results of ecosystem studies in Monterey Bay, California, during the summer upwelling periods, 1996–99, including impacts of El Niño 1997–98 and La Niña 1999. Random-systematic line-transect surveys of marine mammals were conducted monthly from August to November 1996, and from May to November 1997–99. CTDs and zooplankton net tows were conducted opportunistically, and at 10 predetermined locations. Hydroacoustic backscatter was measured continuously while underway to estimate prevalence of zooplankton, with emphasis on euphausiids, a key trophic link between primary production and higher trophic level consumers.

The occurrences of several of the California Current’s most common cetaceans varied among years. The assemblage of odontocetes became more diverse during the El Niño with a temporary influx of warm-water species. Densities of cold-temperate Dall’s porpoise, Phocoenoides dalli, were greatest before the onset of El Niño, whereas warm-temperate common dolphins, Delphinus spp., were present only during the warm-water period associated with El Niño. Rorqual densities decreased in August 1997 as euphausiid backscatter was reduced. In 1998, as euphausiid backscatter slowly increased, rorqual densities increased sharply to the greatest observed values. Euphausiid backscatter further increased in 1999, whereas rorqual densities were similar to those observed during 1998. We hypothesize that a dramatic reduction in zooplankton biomass offshore during El Niño 1997–98 led to the concentration of rorquals in the remaining productive coastal upwelling areas, including Monterey Bay. These patterns exemplify short-term responses of cetaceans to large-scale changes in oceanic conditions. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The distribution, abundance, and foraging success of top trophic level predators in marine systems, such as sharks, seabirds, pinnipeds, and cetaceans, are determined by large-scale oceanographic patterns and their effects on prey distribution and abundance (Ainley, Sydeman, & Norton, 1995; Ainley, Veit, Allen, Spear, & Pyle, 1995; Forney, 2000; Kenney, Winn, & Macaulay, 1995; Pyle, Klimley, Anderson, & Henderson, 1996; Smith, Dustan, Au, Baker, & Dunlap, 1986; Sydeman & Allen, 1999; Tynan, 1997). Variability in the physical features can be seasonal (Barber & Smith, 1981; Hutchings, Pitcher, Probyn, & Bailey, 1995; Reid, Roden, & Wyllie, 1958), interannual, (e.g. El Niño; Barber & Chavez, 1983), and decadal (McGowan, Cayan, & Dormann, 1998). Such perturbations bring changes in nutrient upwelling, primary productivity, and zooplankton biomass within coastal upwelling systems (Chavez, 1996; Lenarz, Schwing, Ventresca, Chavez, & Graham, 1995; McGowan et al., 1998).

Marine vertebrates respond to ocean variability in a number of ways, including changes in survival and fecundity (Ainley, Sydeman, et al., 1995; Fiedler, Methot, & Hewitt, 1986; Yoklavich, Loeb, Nishimoto, & Daly, 1996) and shifts in distribution (Forney, 2000; Forney & Barlow, 1998; Tynan, 1999). Several studies have demonstrated that shifts in the distribution of birds and mammals can be linked to changes in availability of their prey, including fish, cephalopods, and zooplankton (Ainley, Spear, Allen, & Ribic, 1996; Fiedler et al., 1998; Piatt et al., 1999). While the effects of El Niño events on pinniped movements and population dynamics have been well documented along the North American west coast (Sydeman & Allen, 1999; Trillmich & Ono, 1991), few data are available regarding responses of cetaceans (Reilly & Fiedler, 1994; Tynan, 1999; Wells et al., 1990).

This study documents the effect of habitat variability on the cetacean assemblage occurring in a coastal upwelling area within the California Current, spanning both the strongest El Niño recorded during the 20th century and the subsequent La Niña. The study area is located in Monterey Bay, California (36° 45’ N, 122° 00’ W) (Fig. 1), the largest bay (approximately 1200 km²) on the US West Coast, that is entirely open to the ocean. Water temperature, current patterns, and primary production in the upper water column in Monterey Bay are strongly influenced by springtime wind-driven upwelling north of the bay (Paduan & Rosenfeld, 1996; Rosenfeld, Schwing, Garfield, & Tracy, 1994), leading to high levels of primary production and zooplankton biomass (Pennington & Chavez, 2000; Rosenfeld et al., 1994; Service, Rice, & Chavez, 1998). Monterey Bay is further distinguished by the presence of the Monterey Submarine Canyon, a canyon of similar dimensions as the Grand Canyon (Shepard, 1973), creating a unique combination of deep-sea and nearshore environments. In this study, we document how changes in the physical dynamics and lower-trophic level biological responses during El Niño 1997–98 and La Niña 1999 led to changes in the distribution and abundance of baleen whales (rorquals) and smaller cetaceans (odontocetes) in the Monterey Bay upwelling ecosystem.
2. Methods

2.1. Field methods

Our study area comprised approximately 909 km$^2$. Twenty-seven shipboard line-transect surveys were conducted monthly from August to November 1996 and May to November 1997–99. Each survey consisted of seven transect lines, beginning at the 55-m (30-fathom) isobath and extending WNW to 122° 05.00′ W longitude, totaling approximately 126 km (68 nm). Each line ranged in length from 10 km (5.4 nm) to 22 km (11.9 nm) (Fig. 1). The location of the northern-most line was selected randomly from within a 3-min latitudinal range, and subsequent lines were spaced 5.5 km (3 nm) apart toward the south to provide uniform and representative coverage of the area. A single survey was typically completed during two consecutive days. While the ship was moving along the transect line, three observers located atop the pilot house, 4.3 m above sea level, searched for marine mammals with the aid of 7×50 binoculars fitted with a compass and reticle markings. Line-transect methods (Buckland, Anderson, Burnham, & Laake, 1993) were used, with sighting distances calculated from the compass bearings and reticle readings. Surveys were conducted at a ship speed of 18.5 km/h (10 knots) in acceptable surface conditions (Beaufort sea states 0–5) and satisfactory visibility (1–7 km). Sighting information and environmental conditions were recorded and updated throughout the survey with a laptop computer connected to a GPS receiver. Marine mammals were identified to the lowest possible taxonomic level.

Zooplankton backscatter was measured along tracklines using a Simrad EY-500 echosounder operating at 200 kHz with a ping interval of 2 s. The echosounder system was calibrated before and after each survey year using the standard sphere method (Johannesson & Mitson, 1983). Identification of acoustic targets
was confirmed periodically by plankton tows using paired 0.7 m bongo nets fitted with 333 µm mesh (Marinovic, Croll, Gong, Benson, & Chavez, 2002). Ocean temperature profiles were obtained at predetermined stations (Fig. 1) with a SEABIRD® 19 conductivity-temperature-depth (CTD) probe lowered to a depth of 200 m or to within 10 m of the bottom.

2.2. Analytical methods

2.2.1. Cetacean density

Cetacean abundance was estimated using standard line-transect analysis (Buckland et al., 1993). Owing to sample size limitations, it was necessary to pool sightings of different species for estimation of the probability density function, \( f(x) \). Species having similar detection properties (body size, group sizes, behavior) were subjectively combined and then evaluated using a Kolmogorov–Smirnov test of perpendicular distance distributions. Only species whose distributions were not significantly different were combined in the final analyses. For each species group, the program DISTANCE (Laake, Buckland, Anderson, & Burnham, 1996) was used to evaluate models of perpendicular distance. Data were truncated to eliminate 4–6% of the most distant sightings, and stratifications by sea state and group size were investigated. Half-normal, hazard, and uniform models including cosine adjustments were evaluated. The model that minimized Akaike’s Information Criteria (AIC) (Akaike, 1973) was selected for each species group. The remainder of the analyses were conducted using the program ABUND4 developed by Barlow (1995), because this program more effectively allows for multi-species calculations when performing stratified analyses. Cetacean densities, \( D \), were calculated for each species as:

\[
D = \frac{n f(0)}{2L}
\]

where \( n \) is the number of sightings, \( s \) is the average group size, \( f(0) \) is the probability density function evaluated at zero perpendicular distance (km\(^{-1}\)), and \( L \) is the length of transect surveyed (km).

Temporal patterns of density were investigated for species with adequate sample sizes. The three most common rorquals, blue (\textit{Balaenoptera musculus}), fin (\textit{B. physalus}), and humpback whales (\textit{Megaptera novaeangliae}) forage on many of the same prey items (Croll et al., 1998; Fiedler et al., 1998; Kieckhefer, 1992; Schoenherr, 1991); therefore, they were combined into a single ‘rorqual’ category for analysis. Gray whales (\textit{Eschrichtius robustus}) were included in this category because they were observed foraging on krill during the only month in which they were sighted, May 1999. The most frequently encountered odontocetes included in the temporal density comparisons were the cold-temperate Dall’s porpoise (\textit{Phocoenoides dalli}) and the warm-temperate common dolphins (Heyning & Perrin, 1994). Field identification of the two species of common dolphins was not always possible. Therefore, sightings of the long-beaked common dolphin (\textit{Delphinus capensis}), short-beaked common dolphin (\textit{D. delphis}), and unidentified common dolphin, (\textit{Delphinus} sp.) were combined for analyses. To evaluate temporal patterns of the odontocete assemblage, encounter rates of schools were compared for all species regardless of sample size. This, in effect, normalized each species’ temporal pattern to its mean school size and allowed interspecific patterns to be detected more effectively.

2.2.2. Hydroacoustic and oceanographic data analyses

Analysis of acoustic data followed the methodology of Croll et al. (1998) and Hewitt and Demer (1993). Echograms were generated from the sampled data set, and portions of the echogram were attributed to echos of krill based on the morphology and density of backscattering aggregations. Although acoustic backscatter can be attributable to a variety of zooplankton and fish species, the accuracy of krill characterization criteria used in this study was verified by 38, discrete-depth, targeted zooplankton tows in areas where backscatter was attributed to euphausiids (Marinovic et al., 2002). Euphausiid surface area backscatter
was calculated for each 0.93-km (0.5 nmi) transect segment, integrated to 200 m. Average krill density for the entire survey was estimated as the mean of the individual segment values. The maximum krill value observed on all segments during each survey was obtained as a measure of euphausiid density within aggregations. This may be important because whales forage in areas of highest relative euphausiid density (Croll et al., 1998; Fiedler et al., 1998; Gendron, 1992; Schoenherr, 1991; Tershy, 1992). During three surveys (19 August 1996, 25 November 1996 and 18 August 1997), krill density estimates were not available.

CTD profiles were processed using standard SEABIRD® software, bin-averaged at 1-m intervals. Mixed layer was defined as the layer between the surface and the depth at which the rate of change in temperature was greatest. Mixed layer depth and thermocline slope were averaged across hydrographic stations to calculate a synoptic index for each survey. Depth of the 10 °C isotherm was estimated only from deep-water CTD casts (>100 m). Average sea-surface temperature (SST) and its standard deviation, a measure of within survey spatial variability, was estimated for each survey from all CTD stations.

To investigate the relationships between species densities and measured environmental variables, a step-wise multiple regression was performed on log-transformed densities for the 24 surveys having complete environmental data. Potential predictors included average krill, maximum krill, mixed layer depth, thermocline slope, depth of the 10 °C isotherm, average SST, and standard deviation of SST. Correlated predictor variables were not simultaneously allowed in the regression model to avoid co-linearity. The level of significance was set to $\alpha=0.05$ for all tests.

3. Results

3.1. Oceanographic patterns

A detailed account of the evolution of El Niño 1997–98 is given by Chavez et al. (2002). Physical effects of El Niño were apparent in the SST record obtained at mooring M1 (Fig. 1) during the period August 1997 through September 1998, after which La Niña conditions developed (Fig. 2A). The M1 SST values were highly correlated ($r^2=0.97$) with average SST values obtained from the CTD stations during our surveys. In August–November 1996, SST was low and increased slightly throughout the season, with a drop in November (mean for all surveys=13.2 °C, SD=0.53). During early summer 1997, SST was similar to values observed in 1996, but increased abruptly between the July and August surveys (13.9 to 17.1 °C), yielding a higher and more variable average SST for the survey season (15.6 °C, SD=1.7). Temperatures were elevated but variable from May through November 1998 (seasonal average 14.1 °C, SD=1.2). The lowest SST observed in our study occurred in May 1999, followed by a gradual warming through October (seasonal average 13.4 °C, SD=1.2). Although the average depth of the mixed layer increased as the seasons progressed in 1996 and 1997, it remained shallow (2–15 m) during 1998 and most of 1999. Particularly shallow mixed layer depths (2–10 m) were recorded during August–September 1996, May, July, and September 1997, May–July 1998, and May–October 1999. In all years except 1998, the mixed layer deepened in November (1996: 25 m, 1997: 41 m, 1998: 13 m, and 1999: 45 m). Depth of the 10 °C isotherm also increased within the survey season in all years except 1998 (Fig. 2C), when the isotherm rose to shallower depths in October. The 10 °C isotherm reached the deepest depths (>120 m) during the late summer and fall (late November 1996, August–November 1997, September 1998, and November, 1999).

3.2. Biological patterns

Ninety-five percent of the 38 targeted net tows yielded high krill volumes, and were composed primarily of krill verifying the accuracy of our euphausiid backscatter characterization criteria. Four species of
Fig. 2. Sea surface temperature (A); rorqual density (●, B) and average euphausiid surface area backscatter (□, B); common dolphin density (●, C) and depth of 10 °C isotherm (line, C); and Dall’s porpoise density (●, D) during the study period, August 1996–November 1999. Vertical bars indicate one standard error for estimates of cetacean density and euphausiid backscatter.

euphausiid dominated the samples: *Euphausia pacifica*, *Thysanoessa spinifera*, *Nematoscelis difficilis* and *Nyctiphanes simplex* (Marinovic et al., 2002). *Nyctiphanes simplex* was only observed during the warm water period associated with El Niño. Euphausiid backscatter was greatest at cooler SSTs, generally when <15 °C (Fig. 2B), and least when SSTs peaked at ~17 °C (August–November, 1997). The greatest levels of krill backscatter were observed in fall 1998 and spring 1999 with the onset of La Niña conditions.

Cetacean densities were estimated based on the selected detection function models and stratification criteria that minimized AIC. Half-normal or hazard rate models, with up to two cosine adjustments, were selected for all species groups (Table 1). Large whales did not require stratification by group size or sea state. Dolphin sightings were stratified into small groups (1–40) and large groups (>40), with small groups further stratified by sea state. Dall’s porpoise analyses were stratified by sea state.

Densities of large whales reflected patterns of euphausiid backscatter (Fig. 2B). Rorqual densities, dominated by humpback whales, were high during August 1996, May through July 1997, and most of 1998 and 1999. Greater densities corresponded to colder SST before 1998 and during 1999; however, densities of rorquals were also elevated during 1998 when SST was high. During late summer and fall 1997, when El Niño was most apparent, krill backscatter was low and few rorquals were present. A significant relation-
Table 1
Species groups, truncation distances, detection function models, and group size and sea state strata used for line-transect density calculations.

<table>
<thead>
<tr>
<th>Species group</th>
<th>Truncation distance (km)</th>
<th>Selected model</th>
<th>n</th>
<th>Group size</th>
<th>Beaufort sea state</th>
<th>f(0)</th>
<th>C.V.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rorquals</td>
<td>3.0</td>
<td>Half-normal (1)</td>
<td>177</td>
<td>All</td>
<td>0–4</td>
<td>1.087</td>
<td>0.060</td>
</tr>
<tr>
<td>Dolphins</td>
<td>1.0</td>
<td>Half-normal</td>
<td>53</td>
<td>0–40</td>
<td>0–2</td>
<td>1.750</td>
<td>0.109</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Half-normal (2)</td>
<td>34</td>
<td>0–40</td>
<td>3–4</td>
<td>2.762</td>
<td>0.222</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hazard (1)</td>
<td>21</td>
<td>&gt;40</td>
<td>0–4</td>
<td>1.362</td>
<td>0.115</td>
</tr>
<tr>
<td>Dall’s porpoise</td>
<td>1.0</td>
<td>Half-normal</td>
<td>22</td>
<td>All</td>
<td>0–1</td>
<td>1.878</td>
<td>0.160</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hazard (1)</td>
<td>63</td>
<td>All</td>
<td>2–4</td>
<td>4.354</td>
<td>0.153</td>
</tr>
</tbody>
</table>

n=number of sightings for each species group. f(0) is the probability density function evaluated at zero perpendicular distance (see Eq. (1)); C.V. is the coefficient of variation of f(0).

ship was identified between rorqual densities and maximum krill backscatter (p=0.0002, r^2=0.47, Table 2). Blue whales were absent during the warm water period corresponding to El Niño conditions (Fig. 3). Humpback whales dominated the rorqual assemblage in all years, and were commonly encountered over Monterey Canyon. Although they were initially scarce during the early period of El Niño in 1997 (Fig. 3), they were widespread in Monterey Bay during the late stages of El Niño in 1998 and during La Niña 1999. Fin whales were seen infrequently during 1996–98 and were not observed in 1999. Gray whales appeared only during May 1999 (La Niña) when they were observed feeding on large surface swarms of Thysanoessa spinifera.

Species composition among odontocetes, as measured by the encounter rate of schools (Fig. 4), reflected changes in SST (Fig. 2A). During the cool conditions that existed before the onset of El Niño in August 1997, temperate species dominated the odontocete assemblage: Dall’s porpoise, harbor porpoise (Phocoena phocoena), and Pacific white-sided dolphin (Lagenorhynchus obliquidens). As SST increased in August 1997, warm-temperate species that previously had been virtually absent became conspicuous: common dolphins and Risso’s dolphin (Grampus griseus). In 1999, temperate species dominated the assemblage

Table 2
Stepwise regression results for models of log-transformed cetacean density relative to measured environmental variables. Variables tested included log(average krill backscatter), log(maximum krill backscatter), SST, standard deviation of SST, depth of mixed layer, thermocline slope, and depth of 10 °C isotherm (Z10)

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rorquals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>23</td>
<td>19.5</td>
<td>0.0002</td>
</tr>
<tr>
<td>Log(maximum krill)</td>
<td>1</td>
<td>19.5</td>
<td>0.0002</td>
</tr>
<tr>
<td>Error</td>
<td>22</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R^2=0.47</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common dolphins</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>23</td>
<td>11.4</td>
<td>0.0027</td>
</tr>
<tr>
<td>Z10</td>
<td>1</td>
<td>11.4</td>
<td>0.0027</td>
</tr>
<tr>
<td>Error</td>
<td>22</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R^2=0.34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dall’s porpoise</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No variables</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

No variables significant
again, as cooler oceanographic conditions returned during La Niña. Density estimates were calculated for the most frequently encountered odontocetes, common dolphins and Dall’s porpoise, to examine potential effects of environmental correlates. The stepwise regression analysis (Table 2) indicated a significant positive relationship between densities of common dolphins and the depth of the 10 °C isotherm (Fig. 2C). This corresponded to the appearance of common dolphins as the warm surface layer deepened with the onset of El Niño in 1997, and in late summer of 1998 (Chavez et al., 2002). In contrast, none of the tested environmental variables explained a significant proportion of the variability in Dall’s porpoise densities. Although densities were greater before El Niño (Fig. 2D), Dall’s porpoise were seen consistently throughout the study period.
4. Discussion

4.1. Rorquals

With the arrival of El Niño in 1997, Monterey Bay experienced decreased upwelling, increased water temperatures, and increased mixed layer depth (Chavez et al., 2002). Whilst primary productivity was depressed, zooplankton abundance remained fairly high and cetacean abundances, particularly rorquals, also were high. Off California, rorquals forage in areas characterized by dense aggregations of *Euphausia pacifica*, *Thysanoessa spinifera*, and *Nyctiphanes simplex* (Croll et al., 1998; Fiedler et al., 1998; Kieckhefer, 1992; Schoenherr, 1991). Blue whales generally feed exclusively on krill (reviewed in Perry, DeMaster, & Silber, 1999) whereas humpback and fin whales also forage on small schooling fish in our study area (Clapham, Leatherwood, Szczepaniak, & Brownell, 1997). The abundance of rorquals in Monterey Bay during 1996–99 paralleled patterns of krill abundance. Few whales were present during the initial stages of El Niño (summer 1997) when krill abundance was low. Seasonally, whale abundance was greater during the summer and early fall periods of increased krill abundance, although the magnitude of this response varied among years (Fig. 2B). For example, euphausiid aggregations in late 1998 were not markedly larger than those measured before El Niño and were below levels recorded in 1999, but peak whale densities during 1998 were the greatest observed during the 4-year study.

The ability of marine mammals to forage at varying trophic levels and switch prey can obscure patterns of local abundance relative to oceanographic and lower trophic-level processes. Prey switching between krill and schooling fish likely complicated patterns in humpback whale abundance. The regression model (Table 2) explained <50% of the variability in rorqual density, implying that other, unmeasured factors (such as fish abundance) may have influenced the observed patterns. It is also possible that rorquals were responding to environmental factors at scales greater than those measured in this study, i.e. insufficient prey abundance outside the study area may have caused whales to aggregate disproportionately in the only remaining productive areas, including Monterey Bay, during 1998.

Local patterns of upwelling-favorable winds and their effect on primary and secondary production during
the El Niño are described elsewhere in this volume (Chavez et al., 2002; Marinovic et al., 2002). The frequency and amplitude of upwelling events were reduced during El Niño 1997–98 throughout central California waters, and productivity was limited to a narrow zone along the coast. Although primary productivity was depressed within our study area, the reduction in productivity was greater beyond 50 km from shore (Chavez et al., 2002). Thus, nearshore areas such as Monterey Bay may have represented an ‘oasis’ of productivity for both zooplankton (Marinovic et al., 2002) and rorquals (this study). This hypothesis is consistent with previously observed patterns within Monterey Bay during El Niño 1991–93 (Kudela & Chavez, 2000).

In addition to total krill abundance, patch structure may have played a role in the distribution of rorquals. The regression results (Table 2) indicated that maximum krill density, a measure of the density of krill within patches, was the most significant predictor of whale density. This is consistent with previous studies of baleen whales and their prey (Fiedler et al., 1998; Wishner, Schoenherr, Beardsley, & Chen, 1995). High euphausiid backscatter can be caused either by a high density of individuals or by a predominance of larger life stages (Greene, Stanton, Wiebe, & McClatchie, 1991; Hewitt & Demer, 1993; Simard & Lavoie, 1999). Rorquals in Monterey Bay could have been targeting both dense aggregations of krill and aggregations that contained a greater proportion of larger adults; both types of aggregations were observed in net samples (Marinovic et al., 2002), but they could not be differentiated in the hydroacoustic record. Euphausiids from blue whale fecal samples collected in the Santa Barbara Channel, California, were larger than those in corresponding net samples (Croll et al., 1998). In a study of whale foraging ecology off southern California, Fiedler et al. (1998) speculated that blue whales targeted adult euphausiids.

4.2. Odontocetes

Odontocetes off central California feed on a wide array of fishes and cephalopods (Jefferson, 1988; Jones, 1981; Osnes-Erie, 1999). Although we did not measure prey abundance for odontocetes, the effects of the oceanographic perturbation caused by El Niño were nonetheless apparent in the odontocete assemblage. Following the onset of El Niño 1997–98, both the diversity and abundance of odontocetes in Monterey Bay increased. The increase in diversity (Fig. 4) was caused by an influx of warm-water species, particularly common dolphins, coupled with the persistence of temperate species typically found off central California, such as Dall’s porpoise, harbor porpoise, and Pacific white-sided dolphins. This increase in abundance was driven largely by the appearance of large schools of 500–1000 common dolphins.

Previous studies along the California coast found that temperate and warm-water odontocetes change their distribution and abundance as oceanographic conditions vary both seasonally (Forney & Barlow, 1998) and interannually (Forney, 2000). SST was a significant predictor of common dolphin and Dall’s porpoise abundance off California in 1991–96 (Forney, 2000). Although oceanographic conditions were a significant predictor of common dolphin abundance in our study, hydrographic variables did not explain patterns of Dall’s porpoise observed in Monterey Bay during 1996–99. This may relate to the fact that Dall’s porpoise are regular constituents of the marine fauna of Monterey Bay (Jefferson, 1991), whereas common dolphins are intermittent visitors.

The movements of cetaceans and other mobile marine predators are driven primarily by changes in prey resources, (Angel, 1994). Odontocetes feed on a diverse array of prey species, including small fishes and cephalopods whose abundances are difficult to measure directly when conducting marine mammal surveys. However, prey species often respond directly to physical oceanographic conditions, particularly at lower trophic levels (Angel, 1994; Fiedler et al., 1986; Marinovic et al., 2002). For this reason, oceanographic properties, such as sea surface temperature and chlorophyll, have been used as proxies when modeling cetacean distribution patterns (Smith et al., 1986; Forney, 2000). The correlation between common dolphin densities in Monterey Bay and oceanographic conditions suggests that the prey base may have changed during the El Niño to include species not otherwise available. By inference, prey species consumed by
Dall’s porpoise may have persisted throughout the period, or prey switching enabled Dall’s porpoise to remain in Monterey Bay despite the changing oceanographic conditions.

The results of this study shed light on the local effects of El Niño and La Niña on cetaceans in this upwelling system, but it is important to understand the scale of this study in relation to the scales at which the physical and biological processes operate. Long-lived mobile marine predators, such as marine mammals, seabirds, and predatory fishes, generally respond to oceanographic perturbations at much larger temporal and spatial scales (Angel, 1994). Thus, observations made in a particular region could be driven by unmeasured oceanographic events in other areas.

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