

ABUNDANCE AND DISTRIBUTION OF MARINE MAMMALS IN NEARSHORE WATERS OF MONTEREY BAY, CALIFORNIA

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ABSTRACT

We studied the seasonal abundance and spatial distribution of marine mammals in nearshore waters (<1 km from shore) of Monterey Bay, California, during 1999 and 2000. The most abundant mammal was California sea lion, *Zalophus californianus*, followed by harbor porpoise, *Phocoena phocoena*, sea otter, *Enhydra lutris*, and harbor seal, *Phoca vitulina*. Seasonal abundance of harbor porpoise in the survey area was greatest during winter, pinnipeds were most abundant during autumn, and sea otters were most abundant during spring and autumn. California sea lions were more abundant in 2000 than in 1999. Harbor porpoise were found in water of lesser clarity than expected by chance, and sea lions were found more often in water of intermediate clarity. Distribution of sea otters and harbor seals were not affected by water clarity.

INTRODUCTION

At-sea abundance and distribution of marine mammals in California have been studied extensively (Dohl et al. 1983¹, Bonnell et al. 1983², Keiper et al. 2005). With few exceptions (Dohl et al. 1983³, Bonnell et al. 1983⁴, Forney and Barlow 1998, Lowry and Forney 2005), however, the seasonal abundance of marine mammals in California has not been assessed throughout the year. Telemetry studies have provided some

¹ Dohl, T.P., R.C. Guess, M.L. Duman, and R.C. Helm. 1983. Cetaceans of central and northern California, 1980-1983: status, abundance, and distribution. Unpublished Report, Pacific OCS Region, Minerals Management Service.

² Bonnell, M.L., M.O. Pierson, and G.D. Farrens. 1983. Pinnipeds and sea otters of central and northern California, 1980-1983: status abundance, and distribution. Unpublished Report, Pacific OCS Region, Minerals Management Service.

³ Ibid.

⁴ Ibid.

information on seasonal movements of marine mammals off California (LeBoeuf et al. 2000, Weise et al. 2006), but few data are available on the seasonal abundance of most species.

Similarly, whereas some aspects of habitat preference have been assessed, other aspects have received little research attention. Several researchers have reported on abiotic factors affecting the distribution of marine mammals at-sea, including sea-surface temperature, chlorophyll, oceanographic fronts, water depth, substrate, and proximity to the continental shelf break (Smith et al. 1986, Raum-Suryan and Harvey 1998, LeBoeuf et al. 2000, Baumgartner et al. 2001, Guinet et al. 2001, Johnston et al. 2005, Keiper et al. 2005). The relationship between water clarity and the at-sea distribution of gray whales, *Eschrichtius robustus*, was discussed briefly by Dohl et al. (1983⁵), however, this topic has been quantitatively assessed in only a few studies (Karczmarski et al. 2000, Bräger et al. 2003). Foraging ability of visual predators (e.g., sea lions) must be limited in very turbid water. Somewhat turbid water, however, may allow predators to more closely approach their prey without detection, as has been proposed for pursuit-diving seabirds (Ainley 1977, Henkel 2006). Foraging success of animals that locate their prey tactily (e.g., sea otters and harbor seals) or with echolocation (e.g., cetaceans) may be enhanced in turbid water, where prey are less able to detect predators. We hypothesized that harbor porpoise, which use echolocation (Carlstrom 2005), would be found most often in turbid water and that sea lions, which we presume to be visual predators (Levenson and Schusterman 1999), would occur in clearer water. Because sea otters and harbor seals likely forage both visually and tactily, we hypothesized that the distribution of these species would not be affected by water clarity.

METHODS

Study Area

We studied the distribution of marine mammals in nearshore waters of Monterey Bay, in central California (Fig. 1). Marine productivity in the Monterey Bay region is greatest in summer, after northwest winds drive coastal upwelling north of the bay, and cool, upwelled waters are advected into the bay, where surface circulation is cyclonic, flowing from south to north along shore (Breaker and Broenkow 1994, Paduan and Rosenfeld 1996). Temperature and chlorophyll values in summer usually are greatest in the northeast corner of Monterey Bay, where an “upwelling shadow” results in greater water residence times (Graham and Largier 1997, Pennington and Chavez 2000). Chlorophyll concentration and carbon uptake within Monterey Bay generally are greatest nearshore in autumn (Pennington and Chavez 2000). Although primary productivity is less in winter, some year-round upwelling occurs within Monterey Bay due to the orthographic effects of the steep Monterey Submarine Canyon (Breaker and

⁵ Ibid.

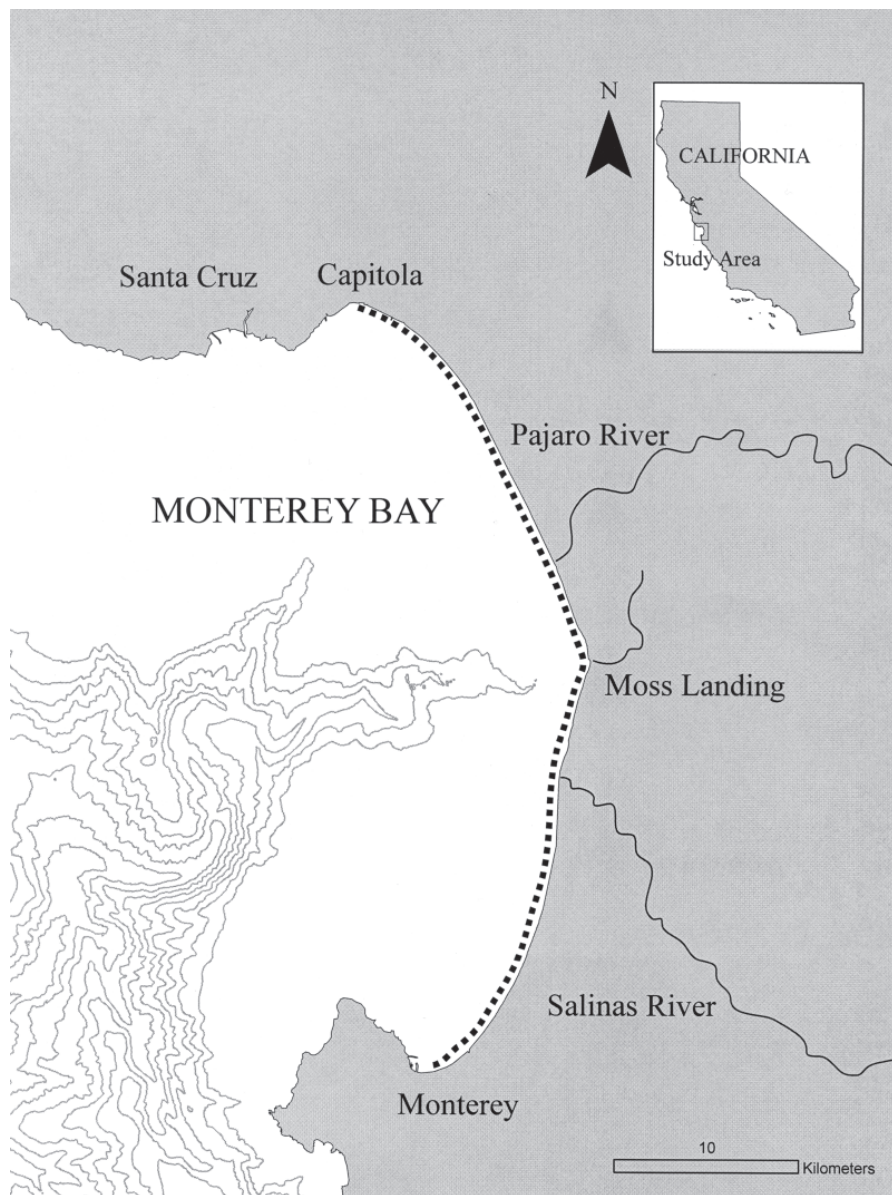


Figure 1. Study area, in Monterey Bay, California. Dashed line indicates approximate survey route.

Broenkow 1994). In very nearshore waters (generally less than 10 m depth), these oceanographic factors may have less effect on marine productivity than wave action and nutrient input from the Pajaro and Salinas rivers.

Three oceanographic seasons have been recognized for Monterey Bay: Upwelling (approximately March through August); Oceanic (September through November), in which warm surface water is advected into the bay; and Davidson Current (December through February) in which the warm north-flowing Davidson Current enters the bay (Bolin and Abbott 1963). These seasons can be indistinct, and vary considerably in timing and intensity from year to year (Pennington and Chavez 2000).

Field Methods and Analyses

We conducted 34 at-sea surveys for marine mammals for 2 years between 11 February 1999 and 19 March 2001. Transects were located parallel to shore, between 400 m and 800 m offshore (distance to shore varied as a result of surf conditions), between Capitola and Monterey (Fig. 1). Shoreline habitat in this area consisted entirely of sandy beach. The northern and southern sections of Monterey Bay were covered in 2 consecutive days. Combined length of transects was approximately 47 km. To minimize temporal autocorrelation, bay-wide transects were conducted at least 2 weeks apart.

Surveys were conducted from a 17-foot (5.2 m) open motorboat, traveling consistently at 15 km hr⁻¹ (8 knots). Observers recorded seals and sea lions within 50 m of both sides of the vessel, for a combined 100-m strip transect. Distance sampling (Buckland et al. 1993) was used to generate density data for harbor porpoises and sea otters. For these species, perpendicular distance from the survey trackline was estimated visually for each group of animals. Observers visually calibrated distance estimation before each survey using stationary objects at a known distance (e.g., distance between harbor jetties) to avoid observer bias. Because diving animals spend a considerable amount of time underwater, density estimates were likely underestimated (Laake et al. 1997, Lowry and Forney 2005). Surveys were conducted only in conditions of Beaufort 3 or less, to minimize the possibility of missing animals obscured by waves. Location and speed were determined using a hand-held Magellan Global Positioning System (GPS), and transects were allocated into 470, 100-m long contiguous quadrats.

Water clarity was recorded during nine surveys, primarily between December and April, when river discharge provided a wide range of turbidity values, but also during October 2000, when a plankton bloom in northern Monterey Bay resulted in a moderate range of turbidity values. Water clarity was measured every 5 s, using a Sea Tec 10 cm-beam transmissometer mounted off the side of the boat, approximately 1 m below the surface of the water. Water clarity measurements were recorded in units of DC voltage. Voltage was converted to Secchi depth based on a series of empirical observations of voltage and Secchi depth using a 30-cm diameter white Secchi disk ($\ln(\text{Secchi depth}) = 0.4287(\text{volts})^2 - 0.0852(\text{volts}) - 2.2142$; $R^2 = 0.94$). Water clarity values recorded during the entire study ranged from 0.2 m Secchi depth to 9.3 m.

To assess overall and seasonal abundance, density was calculated for each species each day. For pinnipeds, density was calculated as the number of animals detected within the 100 m strip divided by 4.7 km² (the total area sampled). For harbor porpoise and sea otter, we used the program DISTANCE version 5.0 (Buckland et al. 1993) to test a variety of curves to model the decrease in detectability with increasing distance, and chose the model with the best fit based on the lowest Akaike's Information Criterion (AIC) value (Burnham and Anderson 2002). DISTANCE uses this curve to determine the effective strip width (ESW). All missed detections inside the ESW equal the number of observed detections outside the ESW, meaning that density estimates using all observed data, and a sample area based on the ESW, represent actual density. For both species analyzed using DISTANCE, analyses were conducted by groups of animals, rather than individuals.

To test for effects of water clarity on distribution of mammals (by species), we combined all transect quadrats that contained that species into three categories of 0 to 3 m, 3 to 5 m, and >5 m Secchi depth (to provide categories sampled on multiple days with a roughly equal area of habitat surveyed), and calculated the number of animals occurring in each range of Secchi depth values, and the number that would be expected by chance alone based on habitat availability. These data (actual and expected number of animals in each category of water clarity) were then summed for all surveys on which that species was present, and a chi-square test was performed to test for differences between actual and expected distributions. Spatial autocorrelation (Keiper et al. 2005) was not an issue, because the sampling unit we used was total area occupied or not occupied by a given species. Because survey data were summed in these analyses, greater weight was given to surveys when mammals were abundant. The species being tested had to occur in at least three quadrats for inclusion in the analysis. Suitable spatial data were available only for sea otter, harbor seal, California sea lion, and harbor porpoise. Probability values <0.05 were considered significant. It should be noted that for all study species, "density" and "seasonal abundance" refer only to the relatively small area surveyed; patterns of seasonal abundance may reflect small-scale shifts in distribution (e.g., inshore to offshore) rather than changes in regional abundance. All mean values presented in the text are followed by + SD.

RESULTS

Only five species of marine mammal were detected on the 34 surveys. These were, in order of mean abundance, California sea lion, harbor porpoise, sea otter, harbor seal, bottlenose dolphin, *Tursiops truncatus*, and gray whale. Analyses of seasonal abundance and distribution relative to water clarity were limited to the four most abundant species.

California sea lions were recorded on 31 of 34 surveys, with a mean density of 3.1 (+5.1) animals km⁻². Sea lion density during 2000 (5.5 + 6.8) was five times greater than the density during 1999 (1.1 + 1.8), a significant increase ($t = 2.73$; $df = 29$; $P = 0.01$). Abundance was greatest during late summer (August to October; Fig. 2). Sea lion

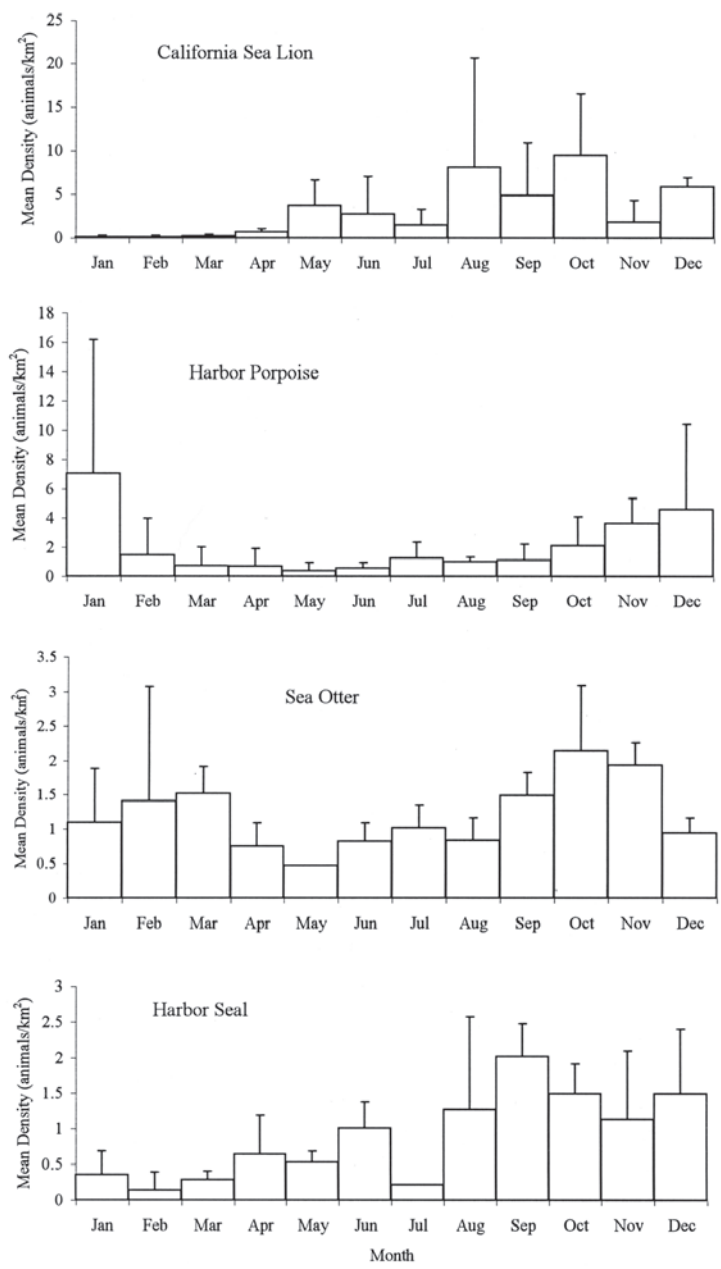


Figure 2. Monthly mean density (animals/km²) of California sea lions, harbor porpoise, sea otters, and harbor seals, in nearshore waters of Monterey Bay, 1999-2001. Error bars are one standard deviation.

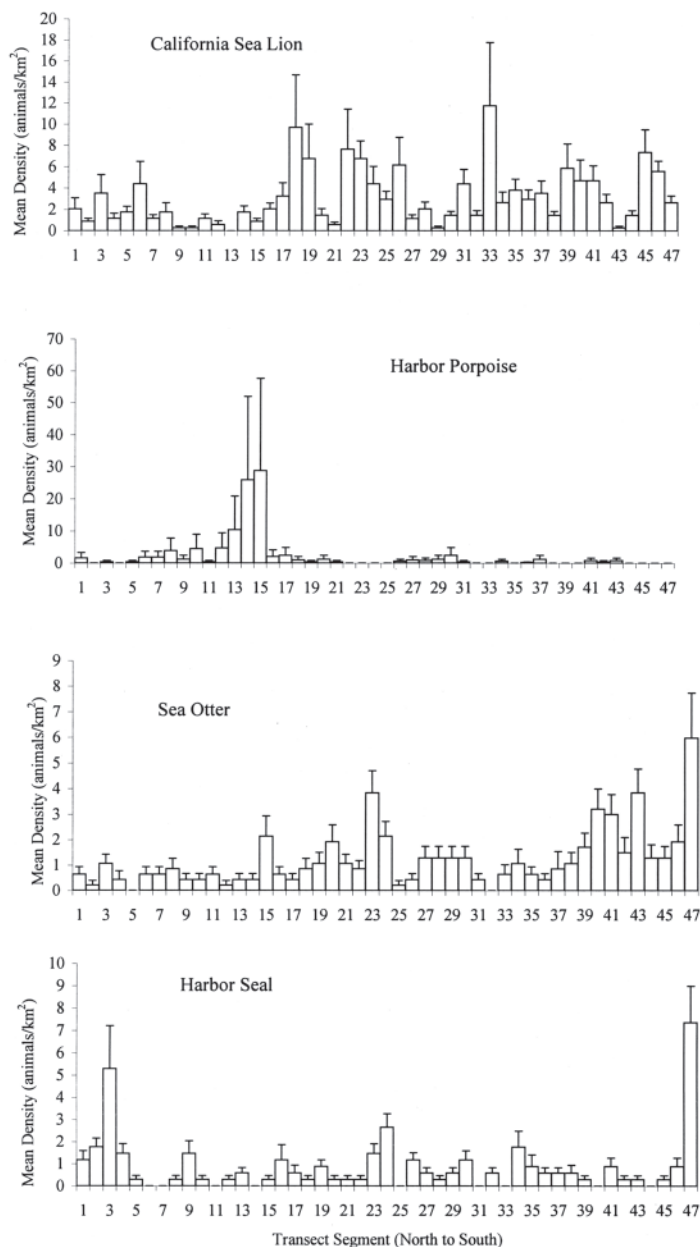


Figure 3. Spatial distribution (mean density per 1-km long transect segment) of California sea lions, harbor porpoise, sea otters, and harbor seals, along a continuous transect in nearshore waters of Monterey Bay. Reference points: segment 1 = Capitola; 18 = Pajaro River; 23 = Moss Landing Harbor; 29 = Salinas River Mouth; 47 = Monterey.

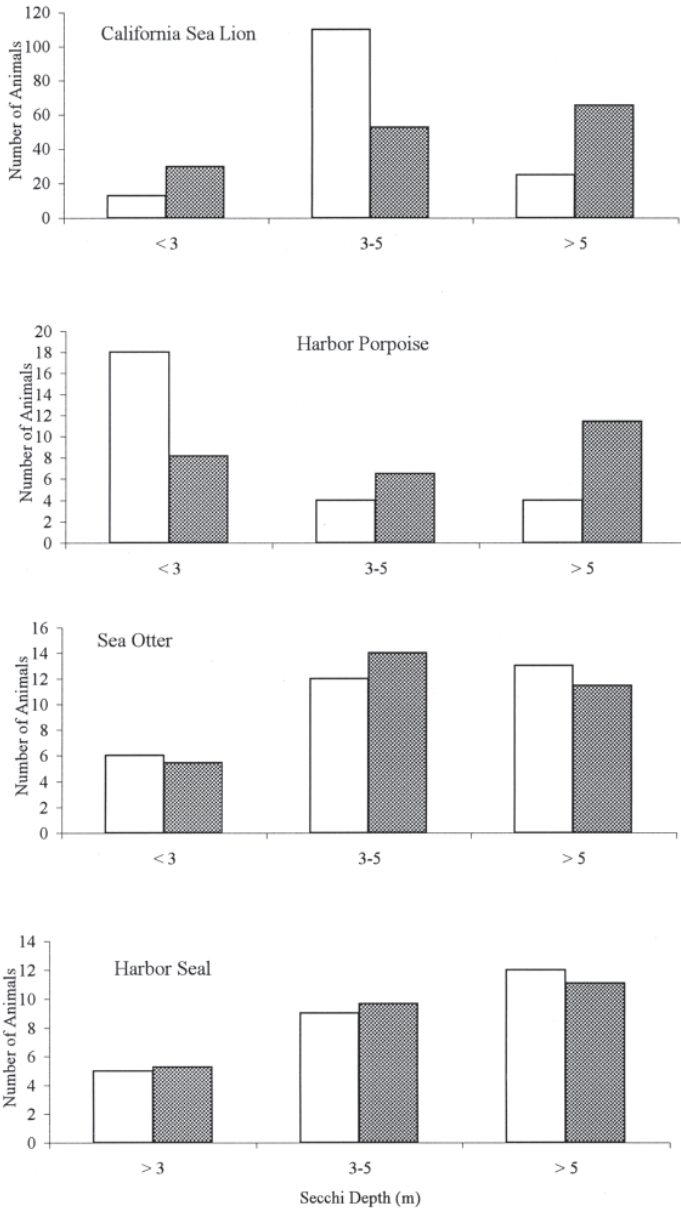


Figure 4. Observed (open bars) and expected (filled bars) distribution of California sea lions, harbor porpoise, sea otters, and harbor seals, relative to water clarity (Secchi depth) in nearshore waters of Monterey Bay.

abundance generally was greatest in the southern portion of the study area; greatest abundance occurred off the Pajaro and Salinas Rivers (transect segments 18 and 29; Fig. 3). Sea lions were found more often than expected in water of intermediate clarity (3-5 m; $\chi^2 = 96.7$; $df = 2$; $P < 0.001$; Fig. 4).

Harbor porpoise were recorded on 25 of 34 surveys, with a mean density of $2.0 (+ 3.3)$ animals km^{-2} . Effective strip width for porpoise was 137 m (95% CI = 60-78 m), based on a half-normal curve with one cosine adjustment. Data were binned into 20 m increments and truncated at 120 m, eliminating 13% of sightings ($n = 179$). Harbor porpoise abundance was greatest in winter (Fig. 2), and abundance on 6 January 2000, at 17.4 animals km^{-2} , was substantially greater than during other surveys. Porpoise were found almost exclusively north of the Pajaro River (Fig. 3). Harbor porpoise occurred more often than expected in the most turbid water available (< 3 m; $\chi^2 = 17.7$; $df = 2$; $P < 0.001$; Fig. 4).

Sea otters were recorded on all 34 surveys, with a mean density of $1.2 (+ 0.7)$ animals km^{-2} . Effective strip width for otters was 136 m (95% CI = 58-80 m), based on a hazard-rate curve with one cosine adjustment. Data were truncated at 120 m, eliminating 7% of sightings ($n = 196$). Sea otters were most abundant during autumn (October) and late winter or early spring (February-March; Fig. 2). Mean density was greatest at the southern end of the study area (near Monterey), and near Moss Landing, in the middle of the study area (Fig. 3). There was no relationship between water clarity and distribution of sea otters ($\chi^2 = 0.56$; $df = 2$; $P > 0.05$; Fig. 4).

Harbor seals were recorded on 30 of 34 surveys, with a mean density of $0.9 (+ 0.7)$ animals km^{-2} . Abundance was greatest during autumn (August to December; Fig. 2). Harbor seal density was greatest at the northern and southern ends of the study area, and moderate near Moss Landing (transect segment 23), and off the Pajaro (segment 18) and Salinas (segment 29) river mouths (Fig. 3). Regularly used harbor seal haul-outs were present in Elkhorn Slough (east of transect segment 23), on the "Cement Ship", a beached ship wreck at New Brighton State Beach (transect segment 3), and outside the study area to the south on the Monterey Peninsula. There was no relationship between water clarity and distribution of harbor seals ($\chi^2 = 0.13$; $df = 2$; $P > 0.05$; Fig. 4).

Bottlenose dolphins were recorded on 16 of 34 surveys, but sighting data were not adequate for generation of density estimates, due to a consistent distribution far from the transect line. Most sightings were well inshore of the transect line, at the outside edge of the surf zone. A maximum of 11 individuals was recorded on four surveys, indicating that this may have been the maximum group size using the study area. Bottlenose dolphins were recorded in every month except December. There was no clear trend between season and number of dolphins recorded, and dolphins occurred throughout the study area.

Gray whales were recorded only on 27 January 2000. One single adult and one adult with a yearling were recorded, all in the southern quarter of the study area. These animals were likely headed south on their annual migration.

DISCUSSION

Although considerable research has been conducted on marine mammals in the Monterey Bay area, few other local researchers have assessed seasonal abundance of mammals (Bonnell et al. 1983⁶, Dohl et al. 1983⁷, Sekiguchi 1995, Byrd 2001⁸, Lowry and Forney 2005), and none have tested for effects of water clarity on spatial distribution. To understand the ecology of even relatively common species, it is important to understand their basic natural history, including abundance and distribution patterns throughout the year, and for multiple years. The effect of water clarity on marine mammals is a topic which deserves greater research effort, especially in areas where anthropogenic effects may lead to alteration in amounts of suspended sediments in marine habitats.

Sea otters typically have fairly small home ranges, and in California, do not exhibit regular seasonal long-range migration (Riedman and Estes 1990). Sea otter territories are segregated by sex, with females occupying a large central area and males the periphery of the range (Jameson 1989). The seasonal pattern of abundance we observed in Monterey Bay is consistent with regional-scale movements of males during the spring/summer breeding season moving through areas occupied by females south of Monterey Bay then moving north of Monterey Bay to the periphery of the species' range in California (Bonnell et al. 1983⁹).

The density of sea otters (1.2 km⁻²) in nearshore Monterey Bay was slightly greater than the range-wide equilibrium density estimated for sandy beaches (0.95 – 1.1 km⁻²) by Laidre et al. (2001). Nevertheless, we did not observe large groups of animals foraging such as those (up to 17) observed in the 1970s by Stephenson (1977) in the same study area. It may be that the abundance of sea otters in Monterey Bay is related to the high quality of foraging habitat just outside the limits of our study, at Santa Cruz and Monterey, where abundant kelp beds are present, and within Elkhorn Slough, a large tidal embayment in the center of the study area, where bivalve prey are abundant (Kvitek et al. 1988).

Spatial distribution of sea otters corresponded loosely to regional centers of abundance near Monterey and at Elkhorn Slough, in Moss Landing. Sea otters, however, were found throughout the study area, which consisted entirely of sandy beach habitat. Although wave action, which is greater in southern Monterey Bay, can influence inshore/offshore distribution and species composition of benthic macrofauna (Oliver et al. 1980, Fleishack and de Freitas 1989), the greater abundance of otters near Monterey likely is related to the proximity to abundant kelp beds. Sea otters off sandy beaches in Monterey Bay historically fed on Pismo clams, *Tivela stultorum*, but this prey resource may no longer be widely available in Monterey Bay, as a result of heavy

⁶ Ibid.

⁷ Ibid.

⁸ Byrd, B.L. 2001. Abundance, distribution, food habits, and prey availability of the harbor porpoise (*Phocoena phocoena*) in northern Monterey Bay, California. M.S. Thesis, California State Univ., Stanislaus.

⁹ Ibid.

predation by otters during the 1970s (Stephenson 1977, Leet et al. 2001). Pismo clams historically were found primarily north of the Salinas River (Stephenson 1977), where we found sea otters now were less abundant. Currently, sea otters in Monterey Bay likely forage on other bivalve species and crabs, including *Blepharipoda occidentalis* and *Emerita analoga*, and occasionally, on market squid, *Loligo opalescens* (Riedman and Estes 1990). Sea otters may occasionally forage visually, but they are probably primarily tactile foragers, as evidenced by nocturnal foraging (Shimek 1977, Ralls et al. 1995, Wilkin 2003¹⁰). Thus, it is not surprising that there was no relationship between at-sea distribution of sea otters and water clarity.

Harbor seals and sea lions were most abundant in the study area during late summer and autumn. These findings were similar to those of Bonnell et al. (1983¹¹), who found that harbor seals were least abundant at sea during spring and early summer, when they were breeding on shore, and that abundance of juvenile and adult male California sea lions dispersing from southern California peaked in central California during late summer. These pinnipeds feed primarily on fish and squid (Morejohn et al. 1978, Harvey et al. 1995, Oxman 1995¹²), which likely are most abundant in nearshore Monterey Bay in summer and autumn, following a seasonal peak in chlorophyll (Pennington and Chavez 2000). Northern anchovy, *Engraulis mordax*, is an important prey for many marine mammals and birds in Monterey Bay, and a major prey item for these pinnipeds (Morejohn et al. 1978). Although the exact seasonal distribution of anchovies in Monterey Bay has not been studied, large shoals of anchovies often can be seen nearshore in summer and autumn (L. Henkel, unpubl. data). In southern California, Allen and DeMartini (1983) found that anchovies were most abundant nearshore in late summer, when sea surface temperature was greatest. Market squid, with spawning concentrations nearshore in southern Monterey Bay during summer, also are an important prey for birds and mammals (Morejohn et al. 1978, McInnis and Broenkow 1978).

Although other focus species were found in similar densities during 1999 and 2000, California sea lions were more abundant in 2000. This increase in sea lion abundance in nearshore waters was likely related to prey resources. Market squid catch per unit effort in Monterey Bay was greater in 2000 than in 1999 (Zeidberg et al. 2006). However, sea-surface temperature was significantly greater in Spring 2000 than in Spring 1999 (Henkel 2004), as 1999 was considered a strong “La Niña” year (Schwing et al. 2000). Greater sea surface temperature in Spring 2000 may have indicated greater water column stratification, and lower primary productivity, potentially leading to a reduction in abundance of prey species other than squid during summer. California sea lions may have been responding not to an increase in prey availability in the study area, but to

¹⁰ Wilkin, S.M. 2003. Nocturnal foraging ecology and activity budget of the sea otter (*Enhydra lutris*) in Elkhorn Slough, California. Unpubl. Masters Thesis, San Francisco State University.

¹¹ Ibid

¹² Oxman, D.S. 1995. Seasonal abundance, movements, and food habits of harbor seals (*Phoca vitulina richardsi*) in Elkhorn Slough, California. M.S. Thesis, California State University, Stanislaus.

a decrease in prey availability outside the study area. Given the typically greater prey availability in nearshore waters of Monterey Bay, sea lions may have responded to a decrease in prey abundance on a regional scale (e.g., the central coast of California) by moving to nearshore Monterey Bay. In Monterey Bay, prey may have been similarly reduced, but still may have been more abundant than elsewhere. Benson et al. (2002) found that during the 1998 ENSO event, some cetaceans were more abundant in Monterey Bay than normal, and proposed this was result of an “oasis” effect when productivity elsewhere was reduced. Sydeman and Allen (1999) similarly found that California sea lions were most abundant in central California during strong ENSO years. California sea lions are more transient than the three other focus species in this study, thus are more likely to exhibit shifts in distribution on a larger regional scale (Bonnell et al. 1983¹³).

Spatial distributions of harbor seals and sea lions were similar. Harbor seals were especially concentrated near haul-out sites near Capitola, Moss Landing, and Monterey. Both species also were found regularly off the two major river mouths in the study area, indicating that these areas are productive foraging areas. Eguchi (1998¹⁴) also found that radio-tagged harbor seals often occurred off these river mouths. Greater abundances of California sea lions in southern Monterey Bay may be related to seasonally abundant market squid in southern Monterey Bay (McInnis and Broenkow 1978), and to the presence of the nearby haul-out site at the Monterey Harbor breakwater.

Bay-wide distribution patterns of sea lions also may be related to water clarity. Sea lions occurred significantly less than expected in water of < 3 m Secchi depth. This turbid water occurred primarily in the northern portion of the study area. The significantly greater number of sea lions occurring in water of intermediate clarity indicates that foraging success of these visual predators may be limited at both extremes of water clarity. In turbid water, they may not be able to perceive their prey, but in clear water, their prey have more time between visual and physical contact in which to escape. Harbor seals, which had no relationship with water clarity, forage on more benthic fishes and invertebrates in Monterey Bay, and have the ability to forage tactily, using their vibrissae to track the hydrodynamic trails left by prey species (Denhardt et al. 2001). Oxman (1995¹⁵) found that harbor seals in the Monterey Bay area fed primarily on octopus, *Octopus rubescens*, a sessile benthic prey.

Seasonal abundance of harbor porpoise in Monterey Bay has been studied previously by Sekiguchi (1995) and Byrd (2001¹⁶). Both of these researchers indicated a seasonal peak in abundance during autumn (August to November). Dohl et al. (1983¹⁷), however, found that abundance in nearshore waters of Monterey Bay based

¹³ Ibid.

¹⁴ Eguchi, T. 1998. Morphology of the Pacific harbor seal (*Phoca vitulina richardsi*) using Elkhorn Slough, California, and their movements and diving behavior in the Monterey Bay area. M.S. Thesis, California State University, Fresno.

¹⁵ Ibid.

¹⁶ Ibid.

¹⁷ Ibid.

on aerial surveys was greater in winter, as it was in this study. These apparently contradictory findings likely are related to the area sampled, and variability in harbor porpoise distribution over a range of temporal scales. Sekiguchi (1995) conducted counts from shore near the Pajaro River, and Byrd (2001¹⁸) conducted surveys extending more than 10 km offshore. The disparity in patterns of seasonal abundance among these studies is likely related to small-scale shifts in distribution related to prey distribution at various temporal scales, from months to years. Forney (1999) found interannual differences in abundance of harbor porpoise occurring in nearshore and offshore waters, potentially related to sea-surface temperature. The apparent increase in harbor porpoise abundance we observed in nearshore waters of Monterey Bay during winter as did Dohl et al. (1983¹⁹) is presumably related to increased prey availability, or to decreased prey availability farther offshore. No data were available on seasonal patterns of prey availability in the study area.

The mean density of harbor porpoise during this study (2.0) was greater than that reported by Byrd (0.7; 2001²⁰), probably because we sampled only one stratum (500 m from shore) where harbor porpoise are common. Harbor porpoise populations off California are currently divided into four stocks, with about 1,600 animals in the Monterey Bay area stock (Caretta and Forney 2004²¹). On average, we observed less than 1% of this total, indicating that the area we sampled is a small proportion of the total habitat used by this population.

Harbor porpoise occurred in greater densities in nearshore waters of northern Monterey Bay, but the causes of this spatial distribution remain elusive (Dorfmann 1990²², Byrd 2001²³). Byrd (2001²⁴) found that abundance of northern anchovy, an important prey of harbor porpoise, was significantly greater north of the Pajaro River than to the south. Data on the distribution of market squid, probably the most important prey species for harbor porpoise, were not available (Byrd 2001²⁵), but squid are often most abundant in southern Monterey Bay (McInnis and Broenkow 1978). The spatial distribution of harbor porpoise relative to California sea lions appears to be inversely related, indicating possible spatial segregation of foraging areas by these two species (Fig. 3). The apparent segregation between harbor porpoise and sea lions may be related to water clarity: harbor porpoise were found in more turbid water than sea lions. Because harbor porpoise locate their prey (small fish and squid) using echolocation,

¹⁸ Ibid.

¹⁹ Ibid.

²⁰ Ibid.

²¹ Carretta, J.V., and K.A. Forney. 2004. Preliminary estimates of harbor porpoise abundance in California from 1999 and 2002 aerial surveys. SWFSC Administrative Report LJ-04-01, Southwest Fisheries Science Center, La Jolla, CA.

²² Dorfman, E.J. 1990. Distribution, behavior, and food habits of harbor porpoises (*Phocoena phocoena*) in Monterey Bay. M.S. Thesis, San Jose State University, San Jose, CA.

²³ Ibid.

²⁴ Ibid.

²⁵ Ibid.

we expected that their foraging success would be enhanced in turbid water where they could easily locate prey but their prey would not be able to see them (Abrahams and Kattenfeld 1997). Although we have no data on foraging success, we did find that harbor porpoise occurred significantly more often than expected in water of <3 m Secchi depth.

Few other researchers have studied the effects of water clarity on the distribution of cetaceans. Karczmarski et al. (2000), found the distribution of Indo-Pacific humpback dolphins, *Sousa chinensis*, was not affected by water clarity. Bräger et al. (2003) found that Hector's dolphins, *Cephalorhynchus hectori*, in New Zealand occurred more often in turbid water, although other factors, including water depth and sea-surface temperature also were important in predicting distribution. Although we also found that harbor porpoise occurred more often in turbid water, other factors may have affected the distribution of harbor porpoise and other species in this study. The study was designed to minimize the potentially confounding factors of water depth and distance from shore, but other factors, such as sea-surface temperature, substrate grain size, and wave action on adjacent beaches could potentially affect the distribution of marine mammals.

Few data were collected on the abundance and distribution of bottlenose dolphins in this study. Hansen and Defran (1993) found that 90% of bottlenose dolphin sightings off southern California occurred within 250 m of shore; similarly most sightings in this study were well inshore of the transect. Based on maximum counts, our data indicate a local group of approximately 11 bottlenose dolphins, about 5% of the coastal California stock (Carretta et al. 1998). This group size is similar to the mean group size of 17 animals reported by Feinholz (1996²⁶) based on surveys conducted in Monterey Bay in the early 1990s. Photographic identification studies have indicated that bottlenose dolphins in Monterey Bay do not represent a unique population, but are simply individuals that dispersed northward from the coastal population of southern California (Feinholz 1996²⁷, Defran et al. 1999). Although we lacked sufficient data to assess patterns of bottlenose dolphin distribution relative to water clarity, Feinholz (1996²⁸) found that they occurred preferentially off the mouth of the Pajaro River; this distribution could be related to turbidity created by the Pajaro River plume.

Most marine mammals were most abundant in nearshore waters of Monterey Bay during autumn and early winter. Spatial distribution varied among species, but "hot spots" included central Monterey Bay (between the Pajaro and Salinas rivers), the vicinity of Monterey Harbor, and for harbor porpoise, nearshore waters off Sunset State Beach, north of the Pajaro River. These areas presumably provide important foraging habitat for these mammals. Further research on factors affecting the distribution and abundance of marine mammals in Monterey Bay conducted over multiple years would provide greater insight into the ecology of these species.

²⁶ Feinholz, D.M. 1996. Pacific Coast Bottlenose Dolphins (*Tursiops truncatus gilli*) in Monterey Bay, California. M.S. Thesis, San Jose State University.

²⁷ Ibid.

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LITERATURE CITED

- Abrahams, M.V., and M.G. Kattenfeld. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioural Biology and Sociobiology* 40:169-174.
- Ainley, D.G. 1977. Feeding methods in seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. Pages 669-685 *in*: G.A. Llano, editor. *Adaptations within Antarctic ecosystems*. Smithsonian Institution, Washington, D.C.
- Allen, L.G., and E.E. DeMartini. 1983. Temporal and spatial patterns of nearshore distribution and abundance of the pelagic fishes off San Onofre-Oceanside, California. *Fishery Bulletin* 81(3):569-586.
- Baumgartner, M.F., K.D. Mullin L. N. May, and T.D. Leming. 2001. Cetacean habitats in the northern Gulf of Mexico. *Fishery Bulletin* 99(2):219-239.
- Benson, S.R., D.A. Croll, B. Marinovic, F.P. Chavez, and J.T. Harvey. 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997-98 and the La Niña 1999. *Progress in Oceanography* 54: 279-291.
- Bolin, R.L. and D.P. Abbott. 1963. Studies of the marine climate and phytoplankton of the central coastal area of California, 1955-1960. California Cooperative Fisheries Investigations Report 9:23-45.
- Bräger, S., J.A. Harraway, and B.F.J. Manly. 2003. Habitat selection in a coastal dolphin species (*Cephalorhynchus hectori*). *Marine Biology* 143:233-244.
- Breaker, L.C. and W.W. Broenkow. 1994. The circulation of Monterey Bay and related processes. *Oceanography and Marine Biology Annual Review* 32:1-64.
- Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake. 1993. Distance sampling: estimating abundance of biological populations. New York: Chapman and Hall.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. New York: Springer-Verlag.
- Carlstrom, J. 2005. Diel variation in echolocation behavior of wild harbor porpoises. *Marine Mammal Science* 21(1):1-12.
- Carretta, J.V., K.A. Forney, and J.L. Laake. 1998. The abundance of southern California coastal bottlenose dolphins estimated from tandem aerial surveys. *Marine Mammal Science* 14:655-675.
- Defran, R.H, D.W. Weller, D.L. Kelly, and M.A. Espinosa. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. *Marine Mammal Science* 15:366-380.
- Denhardt, G., B. Mauck, W. Hanke, and H. Bleckmann. 2001. Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). *Science* 293:102-104.

- Fleishack, P.C., and A.J. de Freitas. 1989. Physical parameters influencing the zonation of surf zone benthos. *Estuarine, Coastal, and Shelf Science* 28:517-530.
- Forney, K.A. 1999. Trends in harbor porpoise abundance off central California, 1986-95: evidence for interannual changes in distribution? *Journal of Cetacean Research and Management* 1(1):73-80.
- Forney, K.A., and J. Barlow. 1998. Seasonal patterns in the abundance and distribution of California cetaceans, 1991-1992. *Marine Mammal Science* 14(3):460-489.
- Graham, W.M. and J.L. Largier. 1997. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. *Continental Shelf Research* 17:509-532.
- Guinet, C., L. Dubroca, M.A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna, and J.P. Donnay. 2001. Spatial distribution of the foraging of female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology Progress Series* 219: 251-264
- Hansen, M.T. and R.H. DeFran. 1993. The behavior and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. *Aquatic Mammals* 19:127-142.
- Harvey, J.T., R.C. Helm, and G.V. Morejohn. 1995. Food habits of harbor seals inhabiting Elkhorn Slough, California. *California Fish and Game* 81(1):1-9.
- Henkel, L.A. 2004. Seasonal abundance of marine birds in nearshore waters of Monterey Bay, California. *Western Birds* 35(3):126-146.
- Henkel, L.A. 2006. Effect of water clarity on the distribution of marine birds in nearshore waters of Monterey Bay, California. *Journal of Field Ornithology* 77(2):151-156.
- Jameson, R.J. 1989. Movements, home range, and territories of male sea otters off central California. *Marine Mammal Science* 5(2):159-172.
- Johnston, D.W., A.J. Westgate, and A.J. Read. 2005. Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. *Marine Ecology Progress Series* 295:279-293.
- Karczmarski, L., V.G. Cockcroft, and A. McLachlan. 2000. Habitat use and preferences of Indo-Pacific humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa.
- Keiper, C.A., D.G. Ainley, S.G. Allen, and J.T. Harvey. 2005. Marine mammal occurrence and ocean climate off central California, 1986 to 1994 and 1997 to 1999. *Marine Ecology Progress Series* 289:285-306.
- Kvitek, R.G., A.K. Fukayama, B.S. Anderson, and B.K. Grimm. 1988. Sea otter foraging on deep-burrowing bivalves in a California coastal lagoon. *Marine Biology* 98(2):157-167.
- Laake, J.L., J. Calambokidis, S.D. Osmeck, and D.J. Rugh. 1997. Probability of detecting harbor porpoise from aerial surveys: estimating $g(0)$. *Journal of Wildlife Management* 61(1):63-75.
- Laidre, K.L., R.J. Jameson, and D.P. DeMaster. 2001. An estimation of carrying capacity for sea otters along the California coast. *Marine Mammal Science* 17(2):294-309.
- Le Boeuf, B.J., D.E. Crocker, D.P. Costa, S.B. Blackwell, P.M. Webb, and D.S. Houser. 2000. Foraging ecology of northern elephant seals. *Ecological Monographs* 70(3): 353-382.
- Leet, W.S, C.M. Dewees, R. Klingbeil, and E.J. Larson (eds.). 2001. California's living marine resources: a status report. Sacramento: California Department of Fish and Game, Sacramento.
- Levenson, D.H. and R.J. Schusterman. 1999. Dark adaptations and visual sensitivity in shallow and deep-diving pinnipeds. *Marine Mammal Science* 15(4):1303-1313.
- Lowry, M.S. and K.A. Forney. 2005. Abundance and distribution of California sea lions (*Zalophus californianus*) in central and northern California during 1998 and summer 1999. *Fishery Bulletin* 103:331-343.
- McInnis, R.R. and W.W. Broenkow. 1978. Correlations between squid catches and oceanographic conditions in Monterey Bay. *California Department of Fish and Game Bulletin* 169:7-9.

- Morejohn, G.V., J.T. Harvey, and L.T. Krasnow. 1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. California Department of Fish and Game Bulletin 169:67-97.
- Oliver, J.S., P.N. Slattery, L.W. Hulberg, and J.W. Nybakken. 1980. Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California. Fishery Bulletin 78(2):437-453.
- Paduan, J.D., and L.K. Rosenfeld. 1996. Remotely sensed surface currents in Monterey Bay from shore-based HF radar (Coastal Ocean Dynamics Application Radar). Journal of Geophysical Research 101(C9):20,669-20,686.
- Pennington, J.T., and F.P. Chavez. 2000. Seasonal fluctuations of temperature, salinity, nitrate, chlorophyll, and primary production at station H3/M1 over 1989-1996 in Monterey Bay California. Deep-Sea Research II 47:947-973.
- Ralls, K., B.B. Hatfield, and D.B. Siniff. 1995. Foraging patterns of California sea otters as indicated by telemetry. Canadian Journal of Zoology 73:523-531.
- Raum-Suryan, K.L. and J.T. Harvey. 1998. Distribution and abundance of and habitat use by harbor porpoise, *Phocoena phocoena*, off the northern San Juan Islands, Washington. Fishery Bulletin 96(4):808-822.
- Riedman, M.L., and J.A. Estes. 1990. The Sea Otter (*Enhydra lutris*): Behavior, Ecology, and Natural History. U.S. Fish and Wildlife Service Biological Report 90(14), Washington, D.C.
- Schwing, F.B., C.S. Moore, S. Ralston, and K.M. Sakuma. 2000. Record upwelling in the California Current in 1999. California Cooperative Fisheries Investigations Report 41:148-160.
- Sekiguchi, K. 1995. Occurrence, behavior and feeding habits of harbor porpoise (*Phocoena phocoena*) at Pajaro Dunes, Monterey Bay, California. Aquatic Mammals 21:91-103.
- Shimek, S.J. 1977. The underwater foraging habits of the sea otter, *Enhydra lutris*. California Fish and Game 63:120-122.
- Smith, R.C., P. Dustan, D. Au, K.S. Baker, and E.A. Dunlap. 1986. Distribution of cetaceans and sea-surface chlorophyll concentrations in the California Current. Marine Biology 91:385-402.
- Stephenson, M.D. 1977. Sea otter predation on Pismo clams in Monterey Bay. California Fish and Game 63(2):117-120.
- Sydeman, W.J., and S.G. Allen. 1999. Pinniped population dynamics in central California: correlations with sea-surface temperature and upwelling indices. Marine Mammal Science 15(2):446-461.
- Weise, M.J., D.P. Costa, and R.M. Kudela. 2006. Movement and diving behavior of male California sea lion (*Zalophus californianus*) during anomalous oceanographic conditions of 2005 compared to those of 2004. Geophysical Research Letters 33, L22S10:1-6.
- Zeidberg, L.D., W.M. Hamner, N.P. Nezlin, and A. Henry. 2006. The fishery for California market squid (*Loligo opalescens*) (Cephalopoda: Myopsida), from 1981 through 2003. Fishery Bulletin 104:46-59.

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