

BALEEN WHALE DISTRIBUTION RELATIVE TO SURFACE TEMPERATURE AND ZOOPLANKTON ABUNDANCE OFF SOUTHERN CALIFORNIA, 2004–2008

LISA M. MUNGER, DOMINIQUE CAMACHO, ANDREA HAVRON, GREG CAMPBELL,
JOHN CALAMBOKIDIS, ANNIE DOUGLAS, JOHN HILDEBRAND

Scripps Institution of Oceanography
University of California, San Diego
9500 Gilman Drive mailcode 0205
La Jolla, California 92093-0205
lmunger@ucsd.edu

ABSTRACT

We investigated the spatial and temporal variation in distributions of three large baleen whale species off southern California in relation to sea surface temperature (SST) and zooplankton displacement volume using Geographic Information System (GIS) software. Data were collected on sixteen California Cooperative Oceanic Fisheries Investigations (CalCOFI) quarterly cruises (lines 77–93) from July 2004–March 2008. The most frequently sighted large whales were humpback whales (*Megaptera novaeangliae*, 67 sightings), fin whales (*Balaenoptera physalus*, 52 sightings), and blue whales (*Balaenoptera musculus*, 36 sightings). Blue and humpback whale sightings peaked in summer (July/August) and fin whales were most frequently seen in summer and fall, consistent with known migratory patterns. In spring through fall, whale sighting locations were associated with colder SST and greater zooplankton abundance levels compared to averages from random locations on the trackline. These results support the hypothesis that foraging distributions of large whales are linked to cold surface temperatures, which may indicate processes that enhance prey production and accumulation, such as upwelling or advection of productive water within the California Current. However, winter distributions of whales presumed to be migrating do not appear to be related to the habitat variables we analyzed, and may be harder to predict based on oceanographic data. The frequency of CalCOFI cruises provides us with high temporal resolution and an ongoing, long time series compared to other survey efforts, allowing comparison between seasons and years that will increase our understanding of these top predators and their response to habitat variability within an important subregion of the California Current Ecosystem.

INTRODUCTION

Baleen whales are highly mobile apex predators that feed on spatially patchy, ephemeral aggregations of zooplankton. Several baleen whale species seasonally forage and migrate within the productive and dynamic California Current Ecosystem (CCE), which varies markedly on seasonal, interannual and multi-year timescales (Hickey 1979; Hayward and Venrick 1998; Mullin et al. 2000;

Brinton and Townsend 2003; Chhak and Di Lorenzo 2007; Keister and Strub 2008). California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises, conducted offshore of southern California every three months, provide an excellent platform to observe temporal variation in whale distribution in relation to zooplankton abundance and other habitat variables. The data provided by these frequent surveys and extensive oceanographic measurements may aid in developing predictive models of whale occurrence as a useful management and conservation tool in southern California, a region heavily used by humans for military, industrial, and other activities.

Cetacean surveys have been conducted on each CalCOFI cruise since July 2004 using both visual and acoustic detection methods (Soldevilla et al. 2006; Douglas et al. in prep.¹). The most frequently sighted baleen whales during these and other surveys off southern California are blue (*Balaenoptera musculus*), fin (*B. physalus*), and humpback (*Megaptera novaeangliae*) whales, all within the family Balaenopteridae (rorquals) (Smith et al. 1986; Soldevilla et al. 2006; Barlow and Forney 2007). Blue whales off California feed exclusively on euphausiids (krill) (Fiedler et al. 1998a), whereas the diets of fin whales and humpback whales include krill as well as copepods, cephalopods, and small schooling fish such as sardines, herring and anchovies (Clapham et al. 1997; Fiedler et al. 1998a; Flinn et al. 2002).

Baleen whales in the eastern North Pacific Ocean forage primarily in summer and typically migrate to lower-latitude breeding and calving grounds in winter, although wintering grounds and movement patterns are not well known for all proportions of each population (Forney and Barlow 1998; Mate et al. 1999; Etnoyer et al. 2006). Whaling records from the early 20th century and recent surveys over the past twenty years indicate that blue and fin whales are most abundant off the coast of California in summer and fall (but seen occasionally in winter), whereas humpbacks are near the coast in sum-

¹Douglas, A. et al. *In prep.* Seasonality, diversity and density of marine mammal species present off Southern California, based on sighting data collected on quarterly California Cooperative Oceanic Fisheries Investigations cruises 2004–2008.

mer but further offshore in winter (Clapham et al. 1997; Forney and Barlow 1998). However, recent cetacean survey effort off California has been seasonally biased, conducted primarily from ships in summer through fall (Barlow and Forney 2007), except for two winter aerial surveys conducted in 1991 and 1992 (Forney and Barlow 1998). Continuous, year-round acoustic monitoring off southern California corroborates that blue whales are present in summer and fall and are rare or absent at other times of year (Burtenshaw et al. 2004; Oleson et al. 2007), whereas fin whale calls are detected year-round with the greatest abundance in summer through fall (Oleson 2005).

The foraging distributions of baleen whales off California vary depending on where and when their prey are concentrated, which is largely determined by marine ecosystem features and dynamic climatic and oceanic processes. Circulation within the Southern California Bight is characterized by the cold, equatorward-flowing California Current (CC) centered about 200–300 km offshore, and the strengthening in summer to fall of the Southern California Eddy and Southern California Countercurrent, which brings warm water northward along the coast (Lynn and Simpson 1987; Hickey 1992). In the CCE, wind-driven coastal upwelling in spring promotes high primary productivity (as indicated by chlorophyll concentration) followed by a subsequent increase in zooplankton production that reaches a peak in adult biomass after a time lag of one to four months (Hayward and Venrick 1998). This time lag corresponds to the interval between peak surface chlorophyll concentration and peak whale abundance off California (Burtenshaw et al. 2004; Croll et al. 2005). As upwelled, productive waters are advected southward by the CC, dense euphausiid patches may develop in areas where bottom topography and/or other features (such as eddies and fronts) contribute to retention, such as in Monterey Bay (Croll et al. 2005), and around the Channel Islands (Fiedler et al. 1998a). Keiper et al. (2005) recorded greater marine mammal sighting rates during periods of upwelling relaxation that led to stronger stratification in early to late-spring surveys, and hypothesized that these conditions contribute to stabilization and aggregation of prey.

Climatic oscillations on annual and multiyear timescales contribute to variability in production within the CCE and hence distribution of whales. For example, cetacean surveys in Monterey Bay during the late 1990s documented decreased balaenopterid whale abundance during the 1997 onset of El Niño, when krill acoustic backscatter was low, and then a sharp increase in whales as krill abundance slowly increased in 1998 (Benson et al. 2002). The authors hypothesized that the sharp increase in whale numbers within the bay was due to

whales concentrating in inshore productive areas while offshore krill abundance remained low through the El Niño event. Over the past couple of decades, large-scale population assessment surveys conducted by the U.S. National Marine Fisheries Service (NMFS) provide evidence for blue whales shifting foraging grounds outside of the California-Oregon-Washington study area (Barlow and Forney 2007; Barlow et al. 2008a²). This shift in blue whale distribution may be associated with the overall declining trend in zooplankton displacement volumes off California since the 1990s (Goericke et al. 2007; McClatchie et al. 2008). However, NMFS surveys are conducted every three to five years primarily in summer and fall, and as such do not capture seasonal variability between years.

The CalCOFI program has conducted four cruises per year since 1949 that presently measure over 20 meteorological, oceanographic and biological variables. Since 2004, CalCOFI cruises have included systematic marine mammal visual and acoustic surveys, providing an opportunity to investigate the relationship of top marine predators to these numerous habitat variables. Previous studies in the CCE have found that baleen whale distributions are related to season and environmental variables including bathymetry, sea surface temperature, salinity, location of fronts, chlorophyll concentration, and acoustic backscatter (Smith et al. 1986; Burtenshaw et al. 2004; Keiper et al. 2005; Tynan et al. 2005; Etnoyer et al. 2006). However, habitat models are often limited by small sample sizes due to infrequent surveys/low numbers of sightings, lack of data during winter months when surveys are not typically conducted, and/or by availability of oceanographic data. For example, many studies incorporate bathymetry and remotely-sensed ocean-surface data from satellites because these data are widely available, but assumptions are required to explain physical and biological mechanisms by which surface production is transferred to macrozooplankton in dense aggregations needed to support apex predators.

This paper provides a preliminary, descriptive overview of spatiotemporal patterns in selected habitat variables and cetacean distributions within the Southern California Bight. We examined two habitat variables measured in situ during CalCOFI cruises, sea surface temperature (SST) and zooplankton displacement volume, in relation to concurrent whale sightings data. We selected sea surface temperature due to its potential to indicate physical mechanisms that lead to either production (e.g. upwelling or advection of cold, nutrient-rich water) or

²Barlow J., J. Calambokidis, and K. A. Forney. 2008a. Changes in blue whale and other cetacean distributions in the California Current Ecosystem: 1991–2008. In California Cooperative Oceanic Fisheries Investigations annual conference 2008: Troublesome Trends or Meandering Variability?, J. Heine, ed. San Diego, CA.

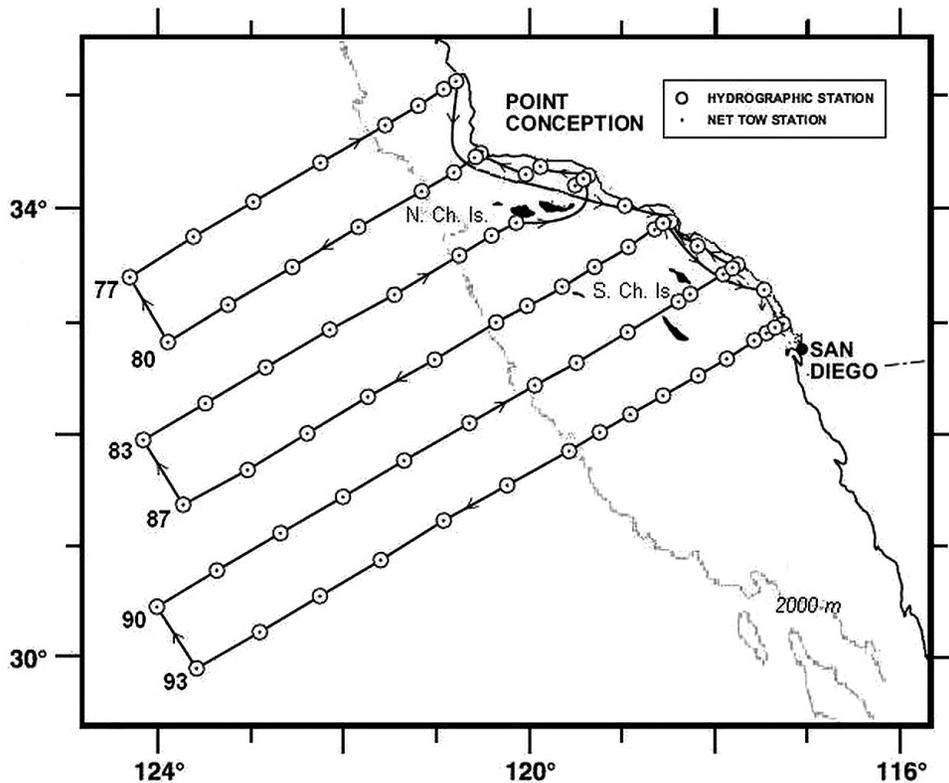


Figure 1. CalCOFI study area showing numbered ship tracklines, hydrographic and net tow stations, and northern and southern Channel Islands. 2000 m depth contour shown in grey. Figure altered from McClatchie et al. (2005).

concentration of prey (e.g. along temperature fronts or eddies). Total macrozooplankton displacement volume (a proxy for macrozooplankton abundance), is not a direct measure of krill abundance but is the best currently available dataset to represent foraging conditions for higher trophic levels. Identifying potential patterns and linkages between whale distributions, prey, and oceanographic variables will allow the formulation of hypotheses that can be tested using more rigorous statistical methods.

MATERIALS AND METHODS

Data collection

Data were collected during CalCOFI cruises off southern California (Figure 1) from July 2004 through March 2008 using Scripps Institution of Oceanography RVs *New Horizon* (NH), *Roger Revelle* (RR) and the National Oceanic and Atmospheric Administration (NOAA) RV *David Starr Jordan* (JD). Two trained marine mammal observers were posted on the bridge wings (NH, 8.1 m above water), flying bridge (JD, 11 m), or 03 level (RR, 13.2 m) and equipped with 7×50 power binoculars to locate and identify cetaceans as the ship transited between stations at 10 knots. Ship time constraints did not allow deviation from the trackline to approach unidentified cetaceans; however, “big eye” binoculars (25×50

power) were used in November 2004 and all cruises since July 2005 (JD and RR had constant access, NH had restricted access) to aid in species identification at long distances (Soldevilla et al. 2006). Mammal observers recorded sighting information including species, group size (estimated by consensus), behavior, weather and sea state; the latter two variables were also recorded periodically independent of sightings. Survey effort was curtailed in sea state Beaufort 6 or greater, or when visibility was reduced to less than 1 km. Mammal observers recorded opportunistic sightings during poor conditions and/or while on station, but these were not used in this analysis.

Sea surface temperature (SST) and other ocean-surface data were collected at approximately 2 m depth using the ship hull-mounted system and Seabird Electronics SBE-21 thermosalinograph or similar. Underway data were collected at 30-second intervals and processed with 10-minute time resolution. Underway data were not available as of this study from winter 2007 (CC0701JD) and winter and spring 2008 (CC0801JD and CC0803JD); for these cruises we analyzed on-station temperature data from CTD sensors and bottles.

Zooplankton were sampled at CalCOFI stations with a standard oblique plankton tow to 210 m (bottom depth permitting) using Bongo paired 505 µm mesh nets with

71 cm diameter openings. Total zooplankton volumes (ml) were standardized to water volume (per 1000 cubic meter strained volume). For this analysis, we removed high outlier zooplankton displacement volumes likely due to overabundance of gelatinous species (A. Hays pers. commun.³).

Data analysis

We used Geographic Information Systems (GIS) software to analyze whale sightings in relationship to oceanographic data. Zooplankton displacement volumes, SST, and sightings of blue, fin, humpback, and unidentified baleenopteric whales were uploaded into ArcGIS 9.2 and analyzed using Geostatistical Analyst. Zooplankton volume and SST coverages were created using two interpolation methodologies. A universal Kriging analysis was applied to the 10-minute averaged underway SST data, accounting for a northwest directional second-degree polynomial trend in temperature (Royle et al. 1981; Oliver and Webster 1990; ESRI 2008). An Inverse Distance Weighted (IDW) analysis (Watson and Philip 1985; ESRI 2008) was applied to data collected at CalCOFI stations because of smaller sample size and greater spacing between data points. Station data analyzed using IDW included zooplankton displacement volumes and CTD bottle temperature data for cruises 0701, 0801, and 0803. To ensure that the different interpolations produced similar contour maps for underway data and station data, we down-sampled underway SST data for four cruises (one each season) at intervals mimicking station spacing, and compared the IDW and Kriging products by performing a paired Student *t*-test (Sokal and Rohlf 2001) using surface temperatures extracted at random locations from each coverage. The results were not statistically significant and we proceeded with IDW analysis of bottle SST for the three cruises for which underway data were unavailable.

Whale sighting locations recorded while observers were on effort were overlaid onto zooplankton displacement volume and SST coverages to produce contour maps for each cruise. Line segments representing visual search effort were constructed and depicted on contour maps. Zooplankton displacement volume and SST were extracted for each whale sighting location for each cruise. We pooled these interpolated zooplankton and SST values by season and compared the values at whale sighting locations to those at the same number of random locations generated along survey effort track-lines, using a nonparametric Mann-Whitney U test for $n > 20$ (Sokal and Rolf 2001).

TABLE 1
 Large baleen whale sightings, combined by season,
 in CalCOFI southern California region
 (lines 93 through 77), July 2004–March 2008.

	Winter	Spring	Summer	Fall	Total
Blue Whale	0	0	31	5	36
Fin Whale	3	4	23	22	52
Humpback Whale	0	13	36	18	67
Unidentified Baleen Whale	22	10	54	51	137
Total	25	27	144	96	292

RESULTS

The sighting rates of blue, fin, and humpback whales varied seasonally and spatially. The number of large baleen whale sightings (including unidentified to species) was greatest in summer and fall (tab. 1). Blue and humpback whale sightings were most frequent during summer cruises (July–August); fin whales were seen with almost equal frequency in summer and fall (October–November). Blue whales were not seen in winter (January–February) or spring (March–April), whereas fin whales were observed year-round and humpback whales were frequently seen in spring and fall. Unidentified baleen whale sightings accounted for about 38% of the total sightings in spring and summer, 53% in fall, and 88% in winter (tab. 1). Humpback whale sightings were predominantly on the shelf (<2000 m depth; see fig. 1), concentrated near Point Conception and the Channel Islands, whereas blue and fin whale distributions extended further offshore (fig. 2). Douglas et al.¹ provide a more detailed analysis of cetacean seasonality and inshore/offshore patterns observed during CalCOFI cruises.

Winter baleen whale sightings, predominantly unidentified and fin whales, were sparse and occurred both inshore and offshore (of the 2000 m isobath) (fig. 2A). Winter and spring were characterized by cold SST and low zooplankton biomass throughout most of the study area (fig. 2A, B). Winter whale distributions did not differ noticeably between years. During spring, SSTs remained cold overall, with the coldest temperatures generally in the nearshore region from Point Conception to the northern Channel Islands, although cold temperatures extended further offshore in 2007 and 2008 (fig. 2B). Zooplankton biomass increased somewhat in spring relative to winter and the greatest displacement volumes were generally along the coast (fig. 2B). Nearly all whale sightings that took place in spring were inshore, again with no noticeable interannual variation, particularly given the reduced survey effort in spring 2007 and 2008 (fig. 2B).

Summer whale sightings were associated with elevated zooplankton levels, which corresponded to cold SSTs near Point Conception and to the south (fig. 2C). Cold surface water within the central CalCOFI area was

³Amy Hays. pers. commun. NOAA Fisheries Southwest Fisheries Science Center. 3333 Torrey Pines Road, La Jolla, California 92037.

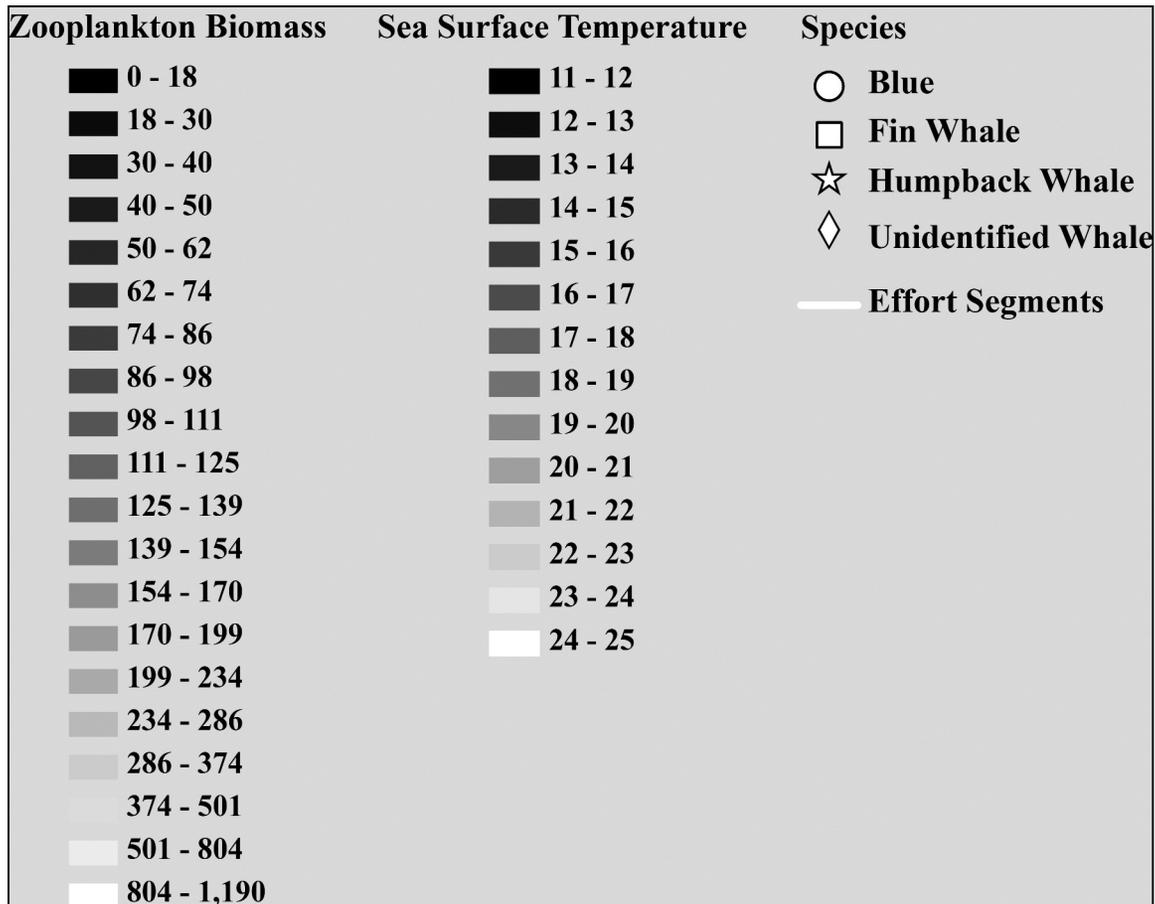


Figure 2. Legend: Zooplankton biomass = total zooplankton displacement volume, ml/1000 m³ strained. Sea surface temperature in degrees Celsius. Following four pages: Whale sightings overlaid on contour maps of SST (left) and zooplankton biomass (right), A) winter cruises, 2005–2008, B) spring cruises, 2005–2008, C) summer cruises, 2004–2007, D) fall cruises, 2004–2007.

centered further offshore in summer than in spring, just seaward of the Channel Islands. In summer 2004, zooplankton abundance was high throughout the central part of the study area; this was reflected by more dispersed, offshore whale sightings (fig. 2C). In contrast, whale sightings in 2007 were clustered around Point Conception, where zooplankton abundance was greatest and more tightly restricted. The Southern California Countercurrent was also strongest in summer (Hickey 1979, 1992; Lynn and Simpson 1987), resulting in warm coastal water and lower zooplankton levels in the southeastern portion of the bight; however, several whale sightings (blue and unidentified whales) occurred along the southern California coast in 2006 and 2007 (fig. 2C). Blue and fin whale summer distributions included both southern (87–93) and northern (77–83) lines, whereas humpbacks were only seen north of line 83 during summer cruises (fig. 2C).

In fall, SSTs remained warm throughout much of the study area (fig. 2D). Fall zooplankton displacement volumes were low overall (see Goericke et al. 2005, 2007; Peterson et al. 2006; McClatchie et al. 2008) and whale

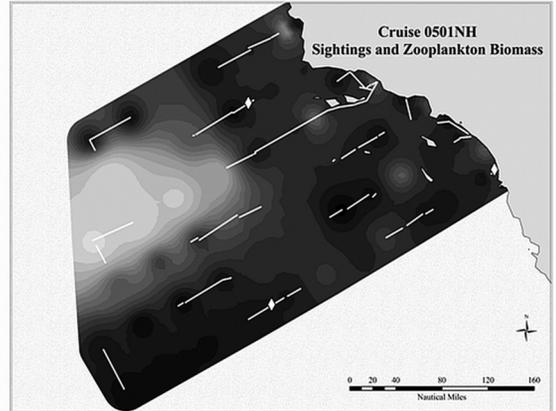
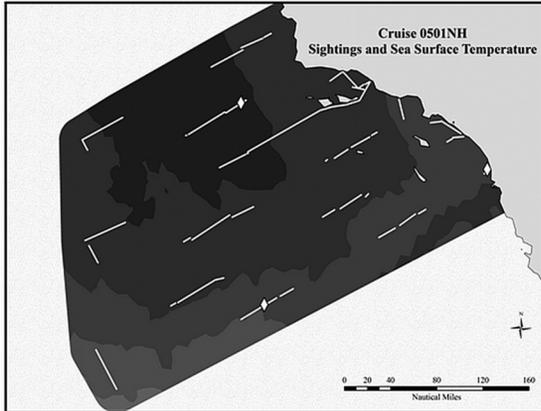
sightings occurred primarily in cool water near shore and islands, with some scattered sightings offshore on southern lines. During three of the four fall cruises, a cluster of blue and fin (2004, 2005) or unidentified whales (2007) were sighted offshore along lines 77 and 80 (fig. 2D). A southward transit along the outer Channel Islands in fall 2006 resulted in numerous sightings, but was not repeated in other cruises and cannot be compared with other seasons or years.

Average SST at whale sightings in summer through fall was colder than the average from random locations along effort trackline, with the greatest difference in summer (fig. 3A). The exception to this was in summer 2006, when the mean SST at whale sightings was almost 1°C greater than average from random locations. Summer whale sighting locations also corresponded to greater zooplankton displacement volumes on average more than to random locations (fig. 3B). Most of the winter and spring data points in Figure 3 are based on small sample sizes (number of sightings < 10).

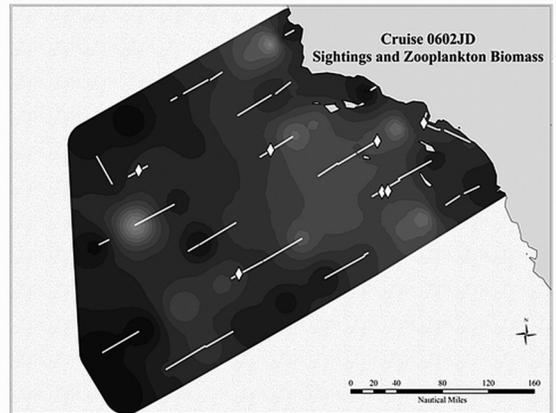
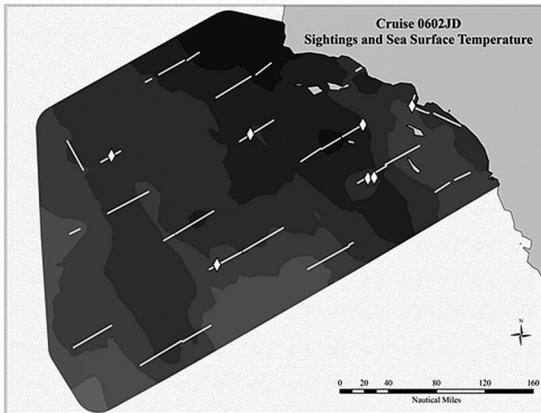
Pooling data by season showed significant differences in median SST and zooplankton displacement volumes

A) winter

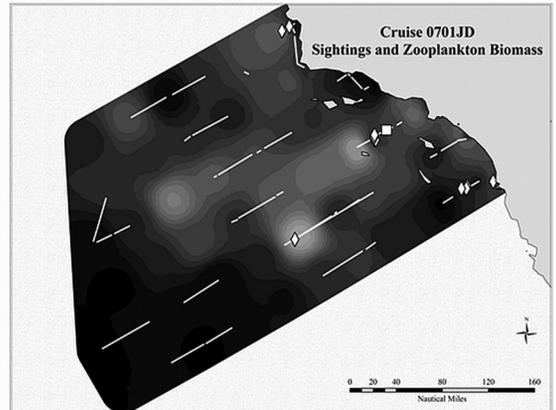
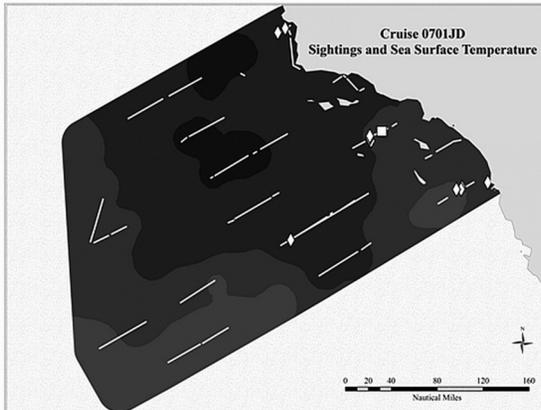
2005



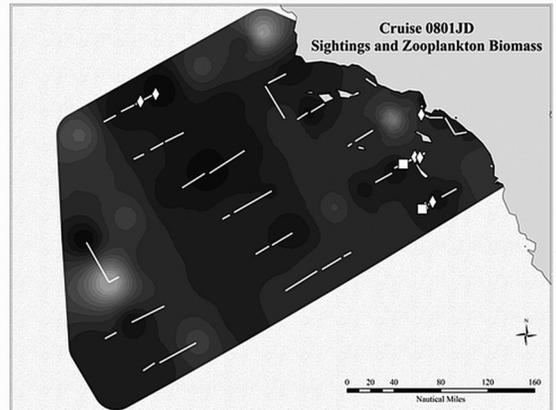
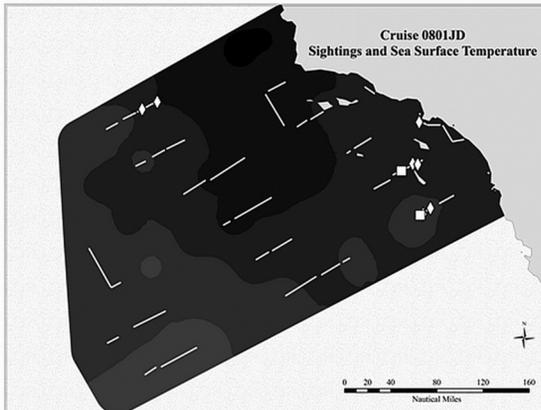
2006



2007

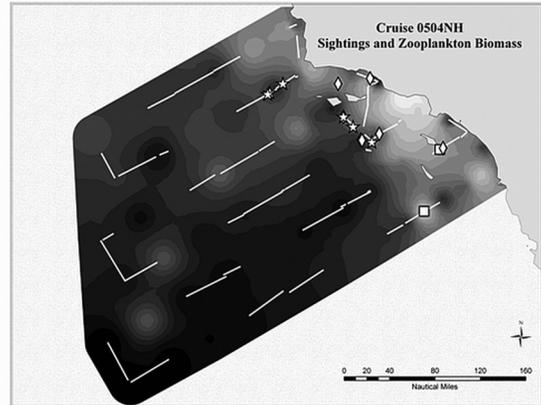
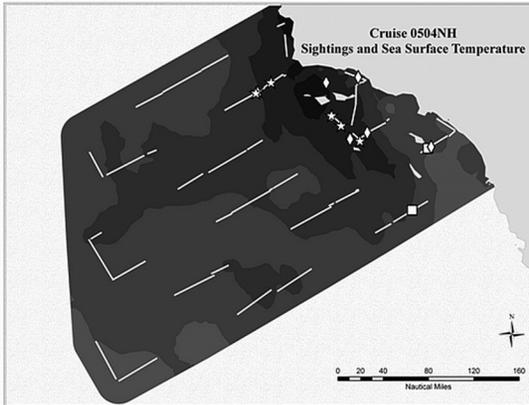


2008

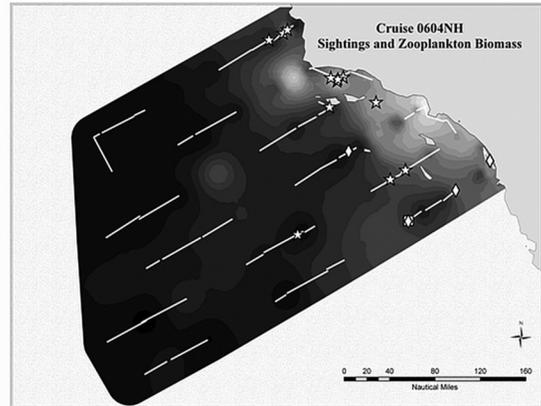
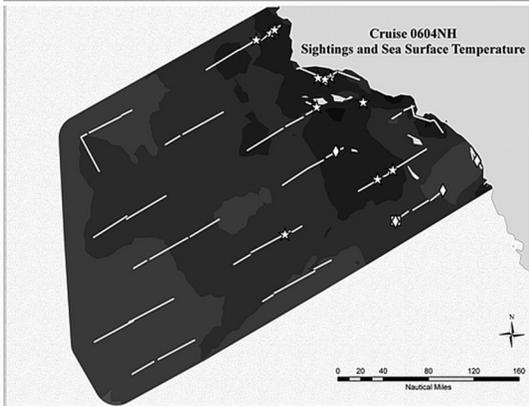


B) spring

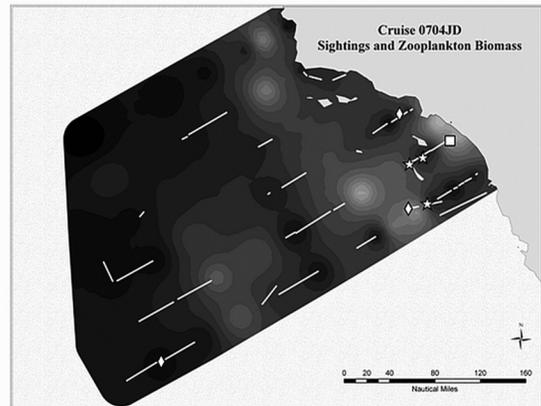
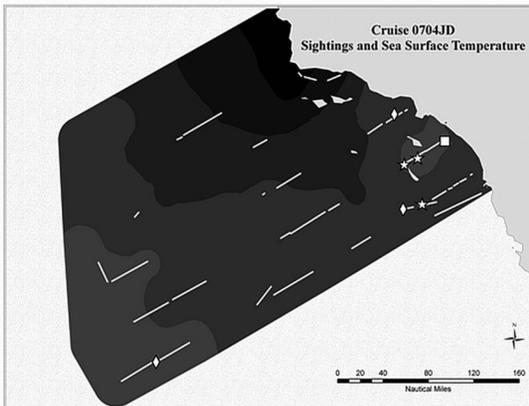
2005



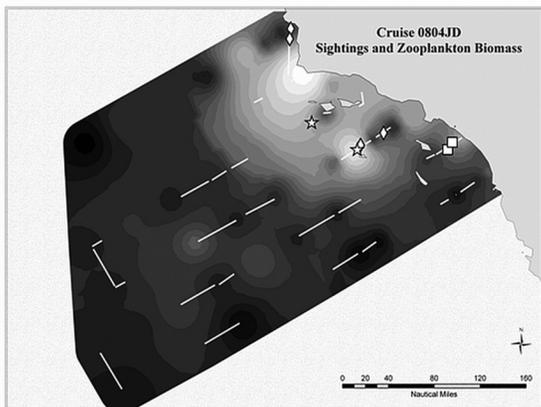
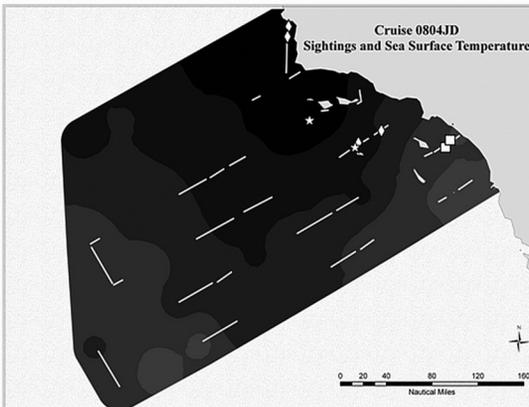
2006



2007

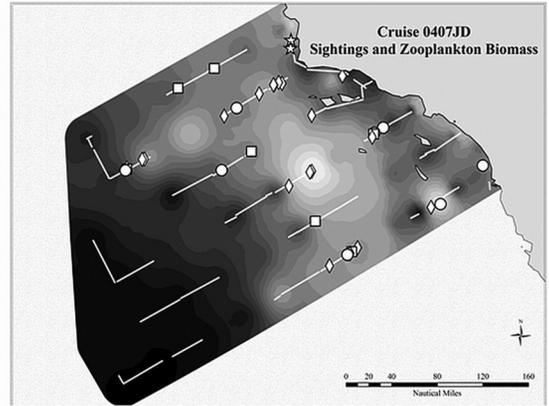
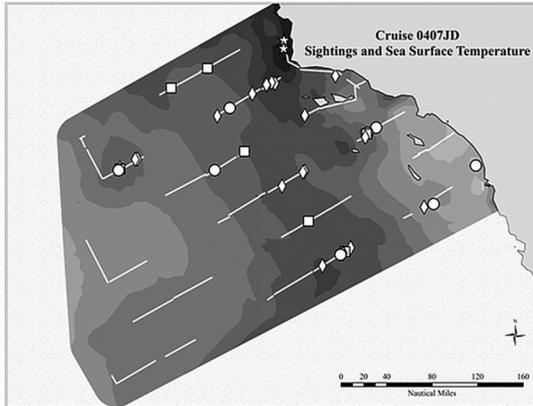


2008

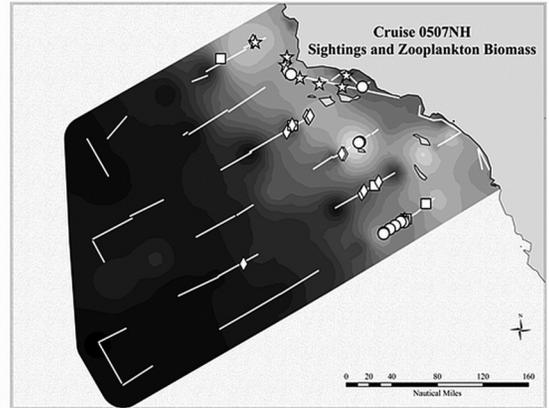
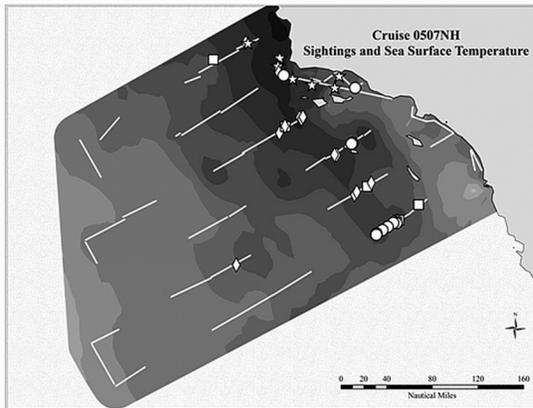


C) summer

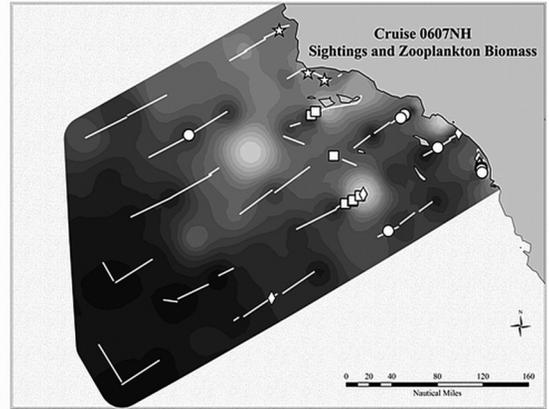
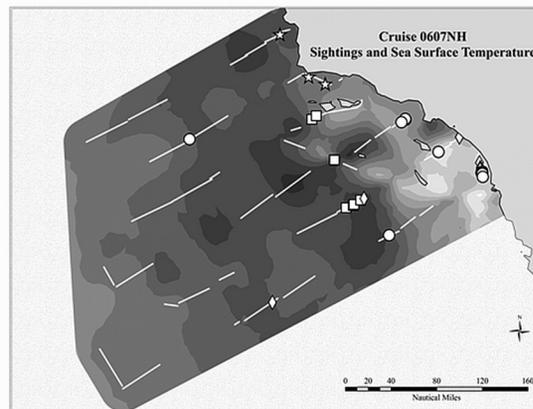
2004



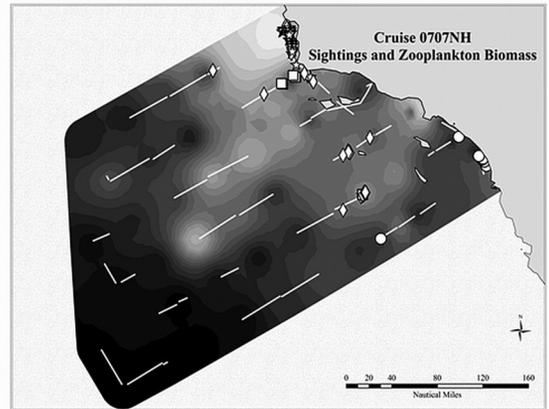
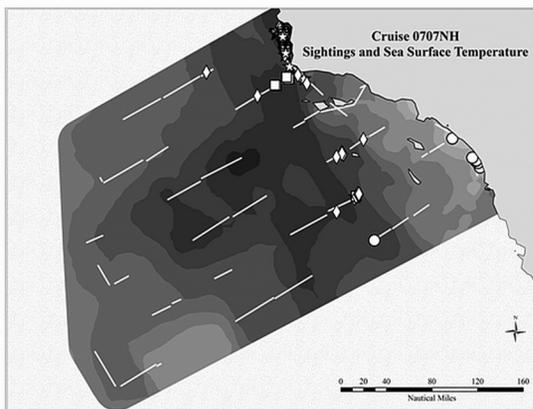
2005



2006

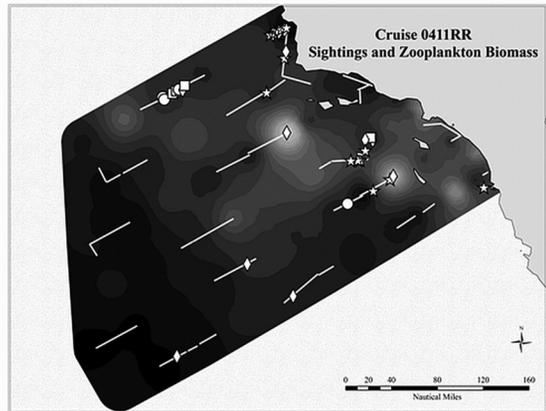
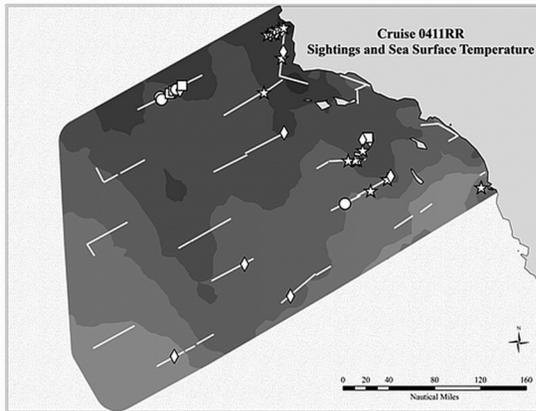


2007

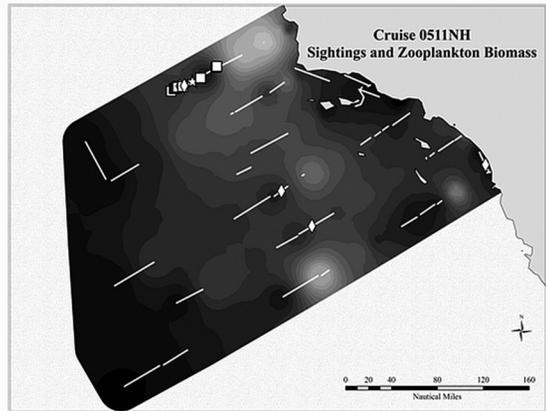
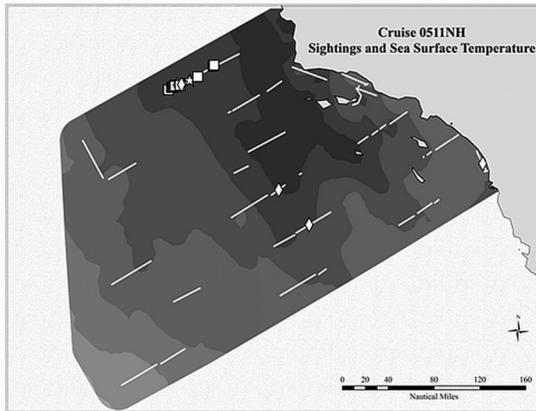


D) fall

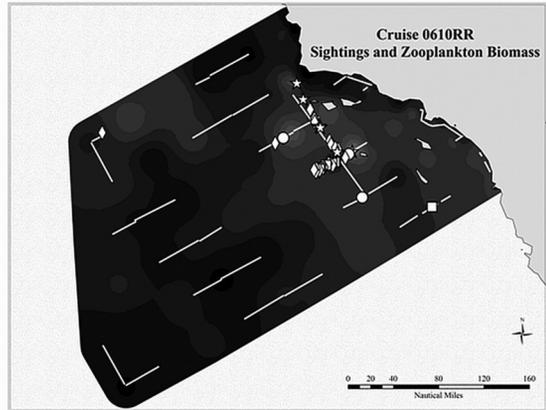
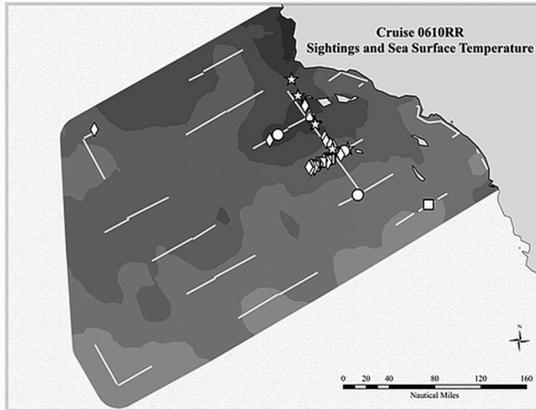
2004



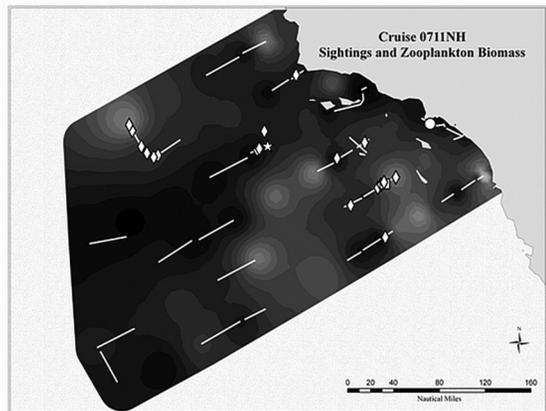
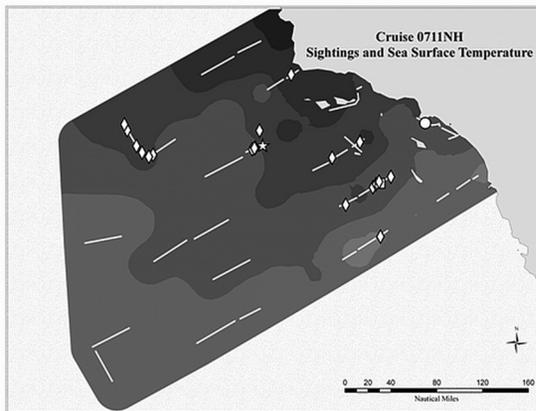
2005



2006



2007



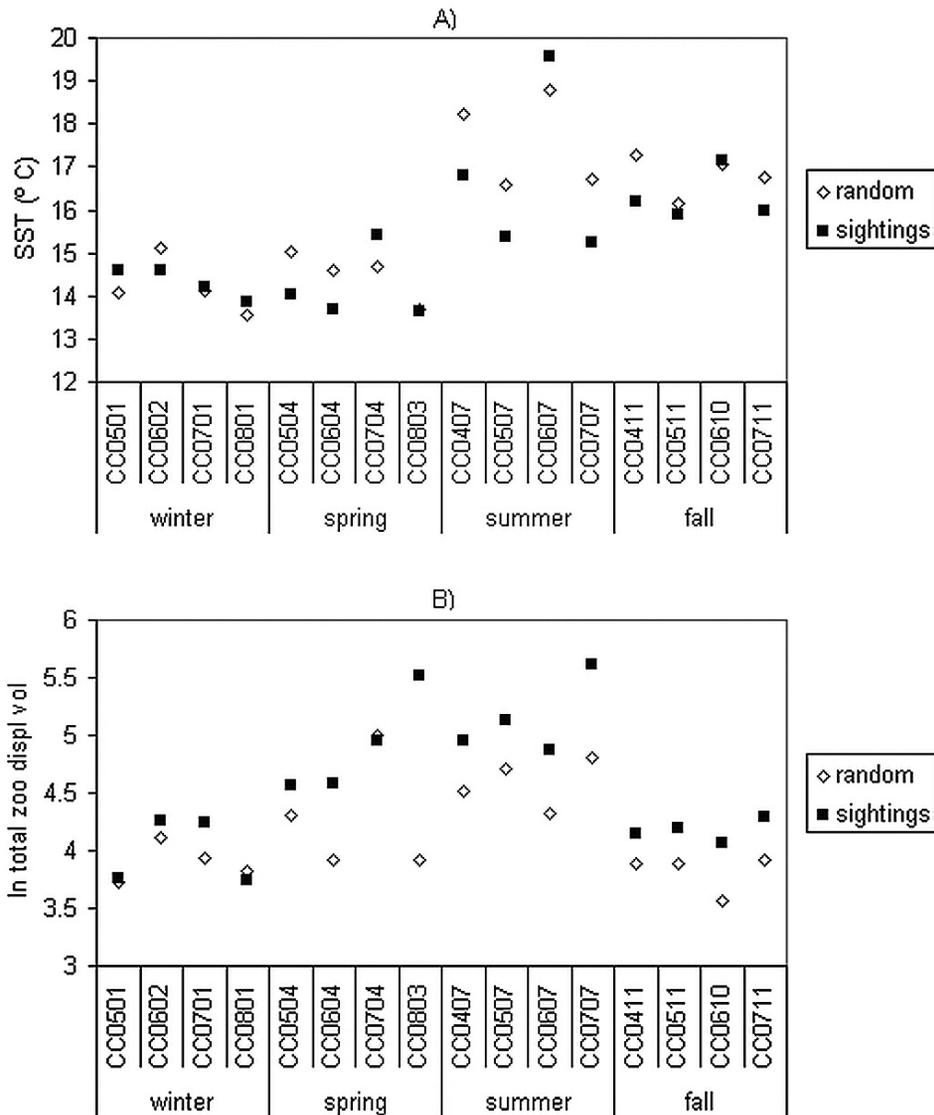


Figure 3. A) Mean SST for random locations along effort trackline (open diamonds) and at whale sightings (filled squares). B) Natural logarithm of mean total zooplankton displacement volume at random locations and whale sightings.

at whale sightings compared to random trackline locations in spring, summer, and fall, but not winter (fig. 4). Relevant statistical quantities are given in Table 2.

DISCUSSION

The summer peak in large whale sightings and their association with high zooplankton displacement volumes during that time indicate that blue, fin, and humpback whales use the Southern California Bight (SCB) primarily as summer foraging habitat, consistent with historic and recent observations (Forney and Barlow 1998; Fiedler et al. 1998a; Barlow and Forney 2007). However, fin whales and unidentified large whales were present year-round in the SCB, with a more scattered offshore distribution in winter. These findings are not new; how-

TABLE 2
 Summary of Mann-Whitney U test results comparing SST and zooplankton volumes extracted at whale sightings to random locations (number of random locations equal to number of sightings), pooled by season.

Season	Variable	n	Sum of ranks	t _u (Mann-Whitney U-test, n > 20)	p-value
Winter	SST	25	624	-0.252	0.801
Winter	Zooplankton Vol	25	611	-0.505	0.614
Spring	SST	27	904	2.785	< 0.01
Spring	Zooplankton Vol	27	526	-3.737	<< 0.01
Summer	SST	144	24394	5.074	<< 0.01
Summer	Zooplankton Vol	144	15309	-7.781	<< 0.01
Fall	SST	96	10438	3.048	< 0.01
Fall	Zooplankton Vol	96	7234.5	-5.270	<< 0.01

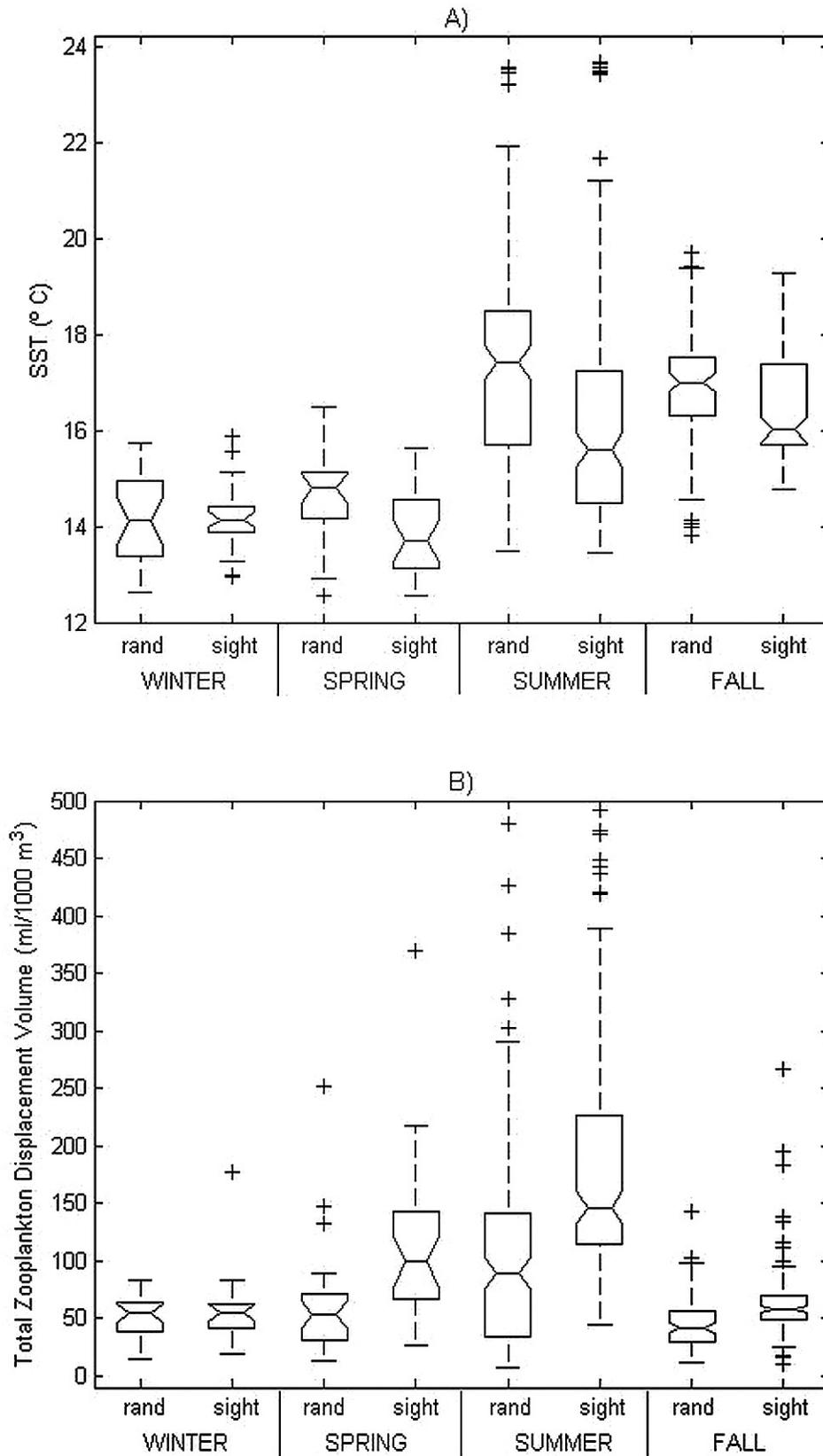


Figure 4. Notched box plots showing lower quartile, median, and upper quartile values of A) SST and B) zooplankton displacement volumes at random locations (rand) and whale sightings (sight). No overlap in notches indicates significant difference ($p < 0.05$) between medians. Dashed whiskers show extent of data to 1.5 times the interquartile range. In plot B (zooplankton), five outliers (plus symbols) > 500 ml/1000 m^3 in summer not shown.

ever, they reflect more recent (2004–08), ongoing, and repetitive seasonal effort than broad-scale, population assessment surveys to date (e.g. Forney and Barlow 1998; Barlow and Forney 2007).

The high proportion of unidentified sightings in winter may be related to generally poorer sighting conditions, i.e. weather and sea state, during that time of year, particularly in the offshore region. Although weather and sea conditions are typically at their worst in spring, most sightings were close to shore or islands and potentially were in relatively calmer water. Unidentified winter and spring sightings were likely to include fin whales and humpbacks as they have been visually and acoustically detected off California during those times of year (Forney and Barlow 1998; Norris et al. 1999; Oleson 2005), whereas blue whales were only rarely detected in early winter and late spring (Oleson et al. 2007).

In summer, whale sightings were generally associated with high zooplankton displacement volumes and cold surface water. The exception to this was during summer 2006, when surface temperatures were warm inshore throughout the SCB and whale sightings were in warmer-than-average surface water. Although the overall zooplankton abundance in summer 2006 was lower than usual, perhaps due to delayed and weak upwelling (Goericke et al. 2007), whale sightings were nonetheless associated with greater than cruise-average zooplankton displacement volumes. The general pattern of whales and zooplankton being associated with cold surface temperatures or gradients in SST may be indicative of conditions leading to zooplankton production, e.g., upwelling and advection of cold, nutrient-rich water, or mechanisms that entrain and concentrate zooplankton, such as fronts and eddies.

The macrozooplankton sampling and analysis methods were not specifically geared toward measuring krill abundance, and several caveats apply when drawing associations between total zooplankton displacement volumes and whale foraging conditions. Net samples were not sorted to taxon as of this study, and may have included some gelatinous organisms as well as prey items such as copepods and euphausiids. We attempted to exclude samples that likely contained abundant gelatinous organisms based on our communication with scientists who had collected samples, but presence of gelatinous organisms in the remaining data could have skewed total zooplankton biomass volumes to appear richer in potential prey than they really were. In addition, sighting data and random points for comparison both occurred only during daytime. Krill are therefore likely to have been underrepresented in total macrozooplankton biomass due to their capability to avoid nets, particularly in daylight, and potential for vertically-migrating krill and other crustaceans to be concentrated during the day at

greater depth than net deployments (Brinton 1967; Everson and Bone 1986; Ianson et al. 2004). Finally, whale observation effort and zooplankton sampling did not take place on exactly the same scales. Visual search efforts were conducted while in transit, whereas zooplankton sampling took place at stations 37 or 74 km apart and therefore may have missed zooplankton patchiness on finer spatial scales. A better method for estimating euphausiid densities may be to measure acoustic backscatter near-continuously (Sameoto et al. 1993; Fiedler et al. 1998b; Fielding et al. 2004). Acoustic backscatter was not measured by the RV *New Horizon*, which conducted most of the summer cruises, although backscatter data at some frequencies were collected on other cruises by the RVs *David Starr Jordan* and *Roger Revelle*. In winter 2009, a Simrad EK-60 acoustic echosounder was installed on the RV *New Horizon*, and will enable better characterization of euphausiid densities with greater spatial resolution.

During the past two decades, populations of baleen whales that forage or migrate in the California Current Ecosystem have increased and/or continue to increase (Calambokidis and Barlow 2004; Barlow and Forney 2007). At the same time, average total zooplankton displacement volumes (per CalCOFI cruise) off California have been declining from 1984–98 and 1999–present levels (Goericke et al. 2007; McClatchie et al. 2008). Shifts in whale distribution may be partly in response to such trends in zooplankton availability. For example, blue whales, abundant around the Channel Islands in the 1990s (Fiedler et al. 1998a), have been decreasing in density off southern California since 1997 (Barlow and Forney 2007). This is likely due to redistribution of animals that previously fed off California, potentially to more northerly feeding areas off British Columbia and in the Gulf of Alaska (Barlow et al. 2008a, Calambokidis et al. 2009), or southward to habitats off Baja California (Calambokidis et al. 1990; Tershy et al. 1990; Rice 1974) or Central America (Wade and Friedrichsen 1979; Reilly and Thayer 1990; Wade and Gerrodette 1993). During the CalCOFI cruises in 2005, fin whales were seen more frequently in northern offshore areas than in the 1990s, and blue whales were more dispersed northward along the U.S. west coast (Peterson et al. 2006), perhaps also related to prey distribution. Barlow et al. 2008b calculated that at their currently estimated abundance, baleen whales in the California Current Ecosystem require about 4% of the net primary production to sustain the prey that they consume. As cetacean populations continue to increase, it will be of value to understand how climate variability and long-term trends affect primary production, as well as the mechanisms that lead to secondary production and prey concentration within the CCE.

This study was mainly descriptive, rather than quan-

titative, as a first step toward using CalCOFI data to examine patterns in large baleen whale distributions and marine ecosystem variables off southern California. Based on these results, we hypothesize that large baleen whale distributions are negatively correlated with sea surface temperature and positively correlated with zooplankton biomass during foraging season. We also hypothesize that whale foraging distributions off southern California shift depending on location and temporal shifts therein of the California Current and coastal upwelling centers. Some recurring high densities of whale sightings, such as offshore on northern lines (77–80) in fall, are not clearly related to either of the variables mapped in this study, and warrant further examination. Analyses are underway to investigate CalCOFI cetacean diversity and encounter rates in relation to season, depth, and distance to shore and shelf break (Douglas et al.¹). Subsequent analyses should incorporate additional environmental variables, including remotely-sensed data as well as in situ measurements, to elucidate habitat use using more rigorous statistical techniques and potentially to aid in estimating whale densities (de Segura et al. 2007). Including acoustic backscatter measurements of prey density on future cruises will also provide a more direct link for examining whale responses to habitat variation.

CONCLUSIONS

Habitat models are a useful tool for understanding how whales interact with dynamic marine ecosystems and respond to prey patchiness and temporal variability. Federally-sponsored marine mammal surveys off California are designed to estimate population abundance over their entire seasonal range, and are conducted primarily in summer and fall every three to five years over a broad area spanning the U.S. west coast (Barlow and Forney 2007; Forney and Barlow 1998). In contrast, CalCOFI provides a platform to observe marine mammals at a smaller geographic scale with greater temporal resolution. As of the submission of this manuscript, marine mammal surveys have been conducted on 20 CalCOFI cruises since 2004, and the number of CalCOFI baleen whale sightings is beginning to exceed those reported in the southern California region in NMFS population assessment surveys for some species (e.g., for humpback whales). Augmenting the CalCOFI marine mammal time series and increase sighting sample size by continuing marine mammal observations aboard seasonal CalCOFI cruises will improve our understanding of whale habitat use off southern California and allow us to test predictions about whale occurrence in relation to different oceanographic variables. Southern California marine ecosystems are affected by a variety of human uses (shipping, fishing, military, industrial, etc.), and predictive models of whale distribution may become a valu-

able management tool for whale populations with whom we share this productive and complex ecosystem.

ACKNOWLEDGMENTS

We thank the many people who have made this research possible. Marine mammal observers and acousticians included Melissa Soldevilla, Robin Baird, Veronica Iriarte, Autumn Miller, Michael Smith, Ernesto Vasquez, Laura Morse, Karlina Merckens, Suzanne Yin, Nadia Rubio, Jessica Burtenshaw, Erin Oleson, E. Elizabeth Henderson, and Stephen Claussen, whose memory we honor. We also thank CalCOFI and SWFSC scientists Dave Wolgast, Jim Wilkinson, Amy Hays, Dave Griffith, Grant Susner, and Robert Tombley; ship crew, research technicians, MARFAC Staff; and two anonymous reviewers whose suggestions helped to improve the quality of this manuscript. Funding and project management was provided by Frank Stone, Ernie Young, and Linda Petitpas at the Chief of Naval Operations, division N45, the Office of Naval Research, and Curt Collins at the Naval Post Graduate School.

LITERATURE CITED

- Barlow, J., and K. A. Forney. 2007. Abundance and population density of cetaceans in the California Current ecosystem. *Fish. Bull.* 105:509–526.
- Barlow, J., M. Kahru, and B. G. Mitchell. 2008b. Cetacean biomass, prey consumption, and primary production requirements in the California Current ecosystem. *Mar. Ecol. Progr. Ser.* 371:285–295.
- Benson, S. R., D. A. Croll, B. 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 La Niña 1999. *Prog. Oceanogr.* 54:279–291.
- Brinton, E. 1967. Vertical Migration and Avoidance Capability of Euphausiids in California Current. *Limnol. Oceanogr.* 12:451–483.
- Brinton, E., and A. Townsend. 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 50:2449–2472.
- Burtenshaw, J. C., E. M. Oleson, J. A. Hildebrand, M. A. McDonald, R. K. Andrew, B. M. Howe, and J. A. Mercer. 2004. Acoustic and satellite remote sensing of blue whale seasonality and habitat in the Northeast Pacific. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 51:967–986.
- Calambokidis, J., and J. Barlow. 2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. *Mar. Mamm. Sci.* 20:63–85.
- Calambokidis, J., G. H. Steiger, J. C. Cubbage, K. C. Balcomb, C. Ewald, S. Kruse, R. Wells, and R. Sears. 1990. Sightings and movements of blue whales off central California 1986–88 from photo-identification. Report of the International Whaling Commission (Special Issue 12). pp. 343–348.
- Calambokidis, J., J. Barlow, J. K. B. Ford, T. E. Chandler, and A. B. Douglas. 2009. Insights into the population structure of blue whales in the eastern North Pacific from recent sightings and photographic identifications. *Mar. Mamm. Sci.* (DOI:10.1111/j.1748-7692.2009.00298.x).
- Chhak, K., and E. Di Lorenzo. 2007. Decadal variations in the California Current upwelling cells. *Geophys. Res. Lett.* 34, L14604.
- Clapham, P. J., S. Leatherwood, I. Szczepaniak, and R. L. Brownell. 1997. Catches of humpback and other whales from shore stations at Moss Landing and Trinidad, California, 1919–1926. *Mar. Mamm. Sci.* 13:368–394.
- Croll D. A., B. Marinovic, S. Benson, F. P. Chavez, N. Black, R. Ternullo, and B. R. Tershy. 2005. From wind to whales: trophic links in a coastal upwelling system. *Mar. Ecol. Progr. Ser.* 289:117–130.
- De Segura A. G., P. S. Hammond, A. Cañadas, and J. A. Raga. 2007. Comparing cetacean abundance estimates derived from spatial models and design-based line transect methods. *Mar. Ecol. Progr. Ser.* 329:289–299.

- ESRI. 2008. ArcGIS Desktop Help 9.3 <http://webhelp.esri.com/>. Environmental Systems Research Institute, Inc.
- Etnoyer, P., D. Canny, B. R. Mate, L. E. Morgan, J. G. Ortega-Ortiz, and W. J. Nichols. 2006. Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 53:340–358.
- Everson, I., and D. G. Bone. 1986. Effectiveness of RTM-8 system for sampling krill swarms. *Polar Biol.* 6:83–90.
- Fiedler, P. C., S. B. Reilly, R. P. Hewitt, D. Demer, V. A. Philbrick, S. Smith, W. Armstrong, D. A. Croll, B. R. Tershy, and B. R. Mate. 1998a. Blue whale habitat and prey in the California Channel Islands. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 45:1781–1801.
- Fiedler, P. C., J. Barlow, T. Gerrodette. 1998b. Dolphin prey abundance determined from acoustic backscatter data in eastern Pacific surveys. *Fish. Bull.* 96:237–247.
- Fielding, S., G. Griffiths, and H. S. J. Roe. 2004. The biological validation of ADCP acoustic backscatter through direct comparison with net samples and model predictions based on acoustic-scattering models. *ICES J. Mar. Sci.* 61:184–200.
- Flinn, R. D., A. W. Trites, E. J. Gregr, and R. I. Perry. 2002. Diets of fin, sei, and sperm whales in British Columbia: An analysis of commercial whaling records, 1963–1967. *Mar. Mamm. Sci.* 18:663–679.
- Forney, K. A., and J. Barlow. 1998. Seasonal patterns in the abundance and distribution of California cetaceans, 1991–1992. *Mar. Mamm. Sci.* 14:460–489.
- Goericke, R., E. Venrick, A. Mantyla, S. J. Bograd, F. B. Schwing, Huyer A, Smith RL, Wheeler PA, Hooff R, Peterson WT, Chavez F, Collins C, Marinovic B, Lo N, Gaxiola-Castro G, Durazo R, Hyrenbach KD, Sydeman WJ. 2005. The State of the California Current, 2004–2005: Still Cool? *Calif. Coop. Oceanic Fish. Invest. Rep.* 46:32–71.
- Goericke, R., E. Venrick, T. Koslow, W. J. Sydeman, F. B. Schwing, S. J. Bograd, W. T. Peterson, R. Emmett, J. R. L. Lara, G. G. Castro, J. G. Valdez, K. D. Hyrenbach, R. W. Bradley, M. J. Weise, J. T. Harvey, C. Collins, and N. C. H. Lo. 2007. The State of the California Current, 2006–2007: Regional and Local Processes Dominate. *Calif. Coop. Oceanic Fish. Invest. Rep.* 48:33–66.
- Hayward, T. L., and E. L. Venrick. 1998. Nearsurface pattern in the California Current: coupling between physical and biological structure. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 45:1617–1638.
- Hickey, B. M. 1979. The California current system—hypotheses and facts. *Prog. Oceanogr.* 8:191–279.
- Hickey, B. M. 1992. Circulation over the Santa Monica-San Pedro Basin and Shelf. *Prog. Oceanogr.* 30:37–115.
- Ianson, D., G. A. Jackson, M. V. Angel, R. S. Lampitt, and A. B. Burd. 2004. Effect of net avoidance on estimates of diel vertical migration. *Limnol. Oceanogr.* 49:2297–2303.
- 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. *Mar. Ecol. Prog. Ser.* 289:285–306.
- Keister, J. E., and P. T. Strub. 2008. Spatial and interannual variability in mesoscale circulation in the northern California Current System. *J. Geophys. Res.—Oceans* 113, C04015.
- Lynn R. J., J. J. Simpson. 1987. The California Current System—The seasonal variability of its physical characteristics. *J. Geophys. Res.—Oceans* 92:12947–12966.
- Mate B. R., B. A. Lagerquist, J. Calambokidis. 1999. Movements of North Pacific blue whales during the feeding season off southern California and their southern fall migration. *Mar. Mam. Sci.* 15:1246–1257.
- McClatchie, S., R. Goericke, J. A. Koslow, F. B. Schwing, S. J. Bograd, R. Charter, W. Watson, N. Lo, K. Hill, J. Gottschalk, M. L'Heureux, Y. Xue, W. T. Peterson, R. Emmett, C. Collins, G. Gaxiola-Castro, R. Durazo, M. Kahru, B. G. Mitchell, K. D. Hyrenbach, W. J. Sydeman, R. W. Bradley, P. Warzybok, and E. Bjorkstedt. 2008. The State of the California Current, 2007–2008: La Niña Conditions and Their Effects on the Ecosystem. *Calif. Coop. Oceanic Fish. Invest. Rep.* 49:39–76.
- Mullin, M. M., E. Goetze, S. E. Beaulieu, and J. M. Lasker. 2000. Comparisons within and between years resulting in contrasting recruitment of Pacific hake (*Merluccius productus*) in the California Current System. *Can. J. Fish. Aquatic Sci.* 57:1434–1447.
- Norris, T. F., M. McDonald, and J. Barlow. 1999. Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *J. Acoust. Soc. Amer.* 106:506–514.
- Oleson, E. M. 2005. Calling behavior of blue and fin whales off California. Ph.D., University of California, San Diego.
- Oleson, E. M., S. M. Wiggins, and J. A. Hildebrand. 2007. Temporal separation of blue whale call types on a southern California feeding ground. *Anim. Behav.* 74:881–894.
- Oliver, M. A., and R. Webster. 1990. Kriging: a method of interpolation for geographical information systems. *Int. J. Geograph. Inform. Sci.* 4:313–332.
- Peterson, W. T., R. Emmett, R. Goericke, E. Venrick, A. Mantyla, S. J. Bograd, F. B. Schwing, R. Hewitt, N. Lo, W. Watson, J. Barlow, M. Lowry, S. Ralston, K. A. Forney, B. E. Lavaniegos, W. J. Sydeman, D. Hyrenbach, R. W. Bradley, P. Warzybok, F. Chavez, K. Hunter, S. Benson, M. Weise, and J. Harvey. 2006. The State of the California Current, 2005–2006: Warm in the North, Cool in the South. *Calif. Coop. Oceanic Fish. Invest. Rep.* 47:30–74.
- Reilly, S. B., and V. G. Thayer. 1990. Blue whale (*Balaenoptera musculus*) distribution in the eastern tropical Pacific. *Mar. Mam. Sci.* 6:265–277.
- Rice, D. W. 1974. Whales and whale research in the eastern North Pacific. *In* The whale problem: A status report, W. E. Schevill, ed. Harvard University Press, Cambridge, MA. 170 00 195 pp.
- Royle, A. G., F. L. Clausen, and P. Frederiksen. 1981. Practical Universal Kriging and automatic contouring. *Geo-Processing* 1:377–394.
- Sameoto, D., N. Cochrane, and A. Herman. 1993. Convergence of Acoustic, Optical, and Net-Catch Estimates of Euphausiid Abundance—Use of Artificial-Light to Reduce Net Avoidance. *Can. J. Fish. Aquatic Sci.* 50:334–346.
- 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. *Mar. Biol.* 91:385–402.
- Sokal, R. R. and F. J. Rohlf. 2001. *Biometry: Third Edition*. New York: W.H. Freeman and company.
- Soldevilla, M. S., S. M. Wiggins, J. Calambokidis, A. Douglas, E. M. Oleson, and J. A. Hildebrand. 2006. Marine mammal monitoring and habitat investigations during CalCOFI surveys. *Calif. Coop. Oceanic Fish. Invest. Rep.* 47:79–91.
- Tershy, B. R., D. Breese, and C. S. Strong. 1990. Abundance, seasonal distribution and population composition of balaenopterid whales in the Canal de Ballenas, Gulf of California, Mexico. Report of the International Whaling Commission (Special Issue 12):369–375.
- Tynan, C. T., D. G. Ainley, J. A. Barth, T. J. Cowles, S. D. Pierce, and L. B. Spear. 2005. Cetacean distributions relative to ocean processes in the northern California Current System. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 52:145–167.
- Wade, L. S., and G. L. Friedrichsen. 1979. Recent sightings of the blue whale, *Balaenoptera musculus*, in the northeastern tropical Pacific. *Fish. Bull.*, U.S. 76: 915–919.
- Wade, P. R., and T. Gerrodette. 1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. Report of the International Whaling Commission 43:477–93.
- Watson, D. F., and G. M. Philip. 1985. A refinement of inverse distance weighted interpolation. *Geo-Processing* 2:315–327.