

Abstract—The link between ocean temperature and spatial and temporal distribution patterns of 8 species of small cetaceans off Southern California was examined during the period 1979–2009. Averages and anomalies of sea-surface temperatures (SSTs) were used as proxies for SST fluctuations on 3 temporal scales: seasonal, El Niño–Southern Oscillations (ENSO), and Pacific Decadal Oscillations (PDO). The hypothesis that cetacean species assemblages and habitat associations in southern California waters co-vary with these periodic changes in SST was tested by using generalized additive models. Seasonal SST averages were included as a predictor in the models for Dall’s porpoise (*Phocoenoides dalli*), and common dolphins (*Delphinus* spp.), northern right whale dolphin (*Lissodelphis borealis*), and Risso’s dolphin (*Grampus griseus*). The ENSO index was included as a predictor for northern right whale, long-beaked common (*Delphinus capensis*), and Risso’s dolphins. The PDO index was selected as a predictor for Dall’s porpoise and Pacific white-sided (*Lagenorhynchus obliquidens*), common, and bottlenose (*Tursiops truncatus*) dolphins. A metric of bathymetric depth was included in every model, and seafloor slope was included in 5 of the 9 models, an indication of a distinctive spatial distribution for each species that may represent niche or resource partitioning in a region where multiple species have overlapping ranges. Temporal changes in distribution are likely a response to changes in prey abundance or dispersion, and these patterns associated with SST variation may foreshadow future, more permanent shifts in distribution range that are due to global climate change.

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Effects of fluctuations in sea-surface temperature on the occurrence of small cetaceans off Southern California

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Cetaceans are higher-trophic-level marine predators whose movement patterns and habitat preferences are typically related to the distribution of their prey (Wishner et al., 1995; Gowans et al. 2007). Unlike baleen whales, small cetaceans (porpoises, dolphins, and small-toothed whales) generally do not undertake ocean-scale annual migrations to track prey or to move between breeding and feeding grounds. Rather, small cetaceans may display a high degree of site fidelity, or they may move seasonally inshore and offshore or along regional-scale coastlines (Leatherwood et al., 1984; Dohl et al., 1986; Shane et al., 1986; Forney and Barlow, 1998).

Although many small cetacean species may overlap in any one region of their total range, they often

differ in their occurrence or habitat-use patterns, perhaps reflecting competitive exclusion or niche partitioning. This separation of habitat and resources often occurs along depth, slope, and sea-surface temperature (SST) gradients (Reilly, 1990; Forney, 2000; Ballance et al., 2006; MacLeod et al., 2008). Habitat preferences likely reflect differences in preferred prey. Dolphins may follow prey habitats as they shift not only seasonally but through large-scale climate-driven changes such as the El Niño–Southern Oscillation (ENSO) or the Pacific Decadal Oscillation (PDO) (Shane, 1995; Defran, 1999; Benson et al., 2002; Ballance et al., 2006).

We examined the distribution and relative abundance of multiple species of small cetaceans across shifting temperature regimes off South-

ern California by using a unique coupled cetacean-oceanographic long-term data set. This data set enables a rare opportunity to assess interdecadal changes in cetacean distribution over a broad spatial extent. The co-occurrence of cold- and warm-water cetacean species makes this location an ideal one at which to examine potential effects of climate variation on regional distribution patterns at different temporal scales (intra-annual, annual, and decadal).

The Southern California region represents the convergence of warm- and cold-water masses and supports populations of both warm- and cold-water, small cetacean species (Forney and Barlow, 1998). During the summer, the cold, equatorward flowing California Current system has a seasonal maximum (7.8 Sverdrups [Sv], ~ 7.8 million $\text{m}^3 \text{ s}^{-1}$). The California Current turns shoreward (poleward) at approximately 32°N and becomes the California Countercurrent. The California Countercurrent and California Undercurrent also have a seasonal maximum in late summer and into the fall and, therefore, dominate the Southern California Bight, with a combined maximum transport in October of 1.8 Sv. The California Undercurrent reaches its minimum (0.8 Sv) and turns equatorward in the spring. The California Countercurrent turns equatorward then as well; therefore, all flow through the Southern California region becomes equatorward in the spring, allowing the California Current to dominate and transport cooler water farther south (Hickey, 1993; Hickey et al., 2003).

In the California Current system, strong El Niño years in the positive ENSO phase have been linked to increased downwelling, warmer SSTs, and a deepening of the thermocline observed off Southern California (Sette and Isaacs, 1960; McGowan, 1985; Caldeira et al., 2005). During the warm, positive phase of the PDO, the California Current is weakened and the Countercurrent is strengthened. This intensified current brings warmer waters farther north and west into and beyond the Southern California region, creating warm SST anomalies along the California coast. In contrast, during the cool, negative PDO phase, the California Current is stronger, bringing cool water farther south and east into the region (Mantua and Hare, 2002). A PDO regime shift from cool to warm occurred around 1977, before our study, and a shift back to a cool PDO may have occurred during the last decade starting in 1998–99 (Peterson and Schwing, 2003; Zhang and McPhaden, 2006; Wang et al., 2010).

Two long-term sets of ship-based surveys have been conducted in Southern California waters, making it an ideal region for this investigation. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has been conducting quarterly cruises that have sampled a breadth of oceanographic and lower-trophic-level biological data since 1949. Marine bird and mammal observations were added in 1987 (Hyrenbach and Veit, 2003; Sydeman, et al., in press). The NOAA Southwest Fisheries Science Center (SWFSC) also regularly has

conducted marine mammal abundance surveys that have included this region since 1979.

Changes in SST have been linked to changes in all levels of the food web, from immediate phyto- and zooplankton responses to lagged alterations in numbers, diet, and even reproductive success of higher-level organisms, such as fishes, seabirds, and marine mammals (Tibby, 1937; Hubbs, 1948; McGowan, 1985; McGowan et al., 2003; Sydeman et al., in press). It follows that small cetacean populations would respond to such variations in SST, likely as a response to changes in prey populations, as has been shown for seabirds (Hyrenbach and Veit, 2003). In addition, population-level responses to these fluctuations in temperature may predict their reaction to future ocean conditions as global ocean temperatures rise.

We investigated such responses by 8 species of small cetaceans across 30 years, using SST averages and anomaly indices as a proxy for environmental variation on 3 temporal scales: seasonal (yearly), ENSO (2–7 years) and PDO (~ 30 years). We predicted that patterns in small cetacean occurrence and distribution within Southern California waters would follow similar trends reported for seabirds (Hyrenbach and Veit, 2003; Yen et al., 2006; Sydeman et al., in press) and other cetaceans (Forney and Barlow, 1998; Becker et al., 2012). For small cetaceans off Southern California, the following trends were predicted: 1) species assemblages will differ depending on the dominant SST regime, 2) cold-water-associated species will be more abundant and broadly distributed when cold-water conditions prevail, 3) warm-water-associated species will dominate during warm-water conditions, and 4) the latter 2 patterns will be compounded when SST fluctuations co-occur on multiple scales.

Materials and methods

Study area and survey methods

Our study area was situated between 117°W and 125°W longitude and from 30°N to 35°N latitude (Fig. 1) and includes the Southern California Bight as well as deeper offshore waters. The Southern California Bight is a region of complex bathymetric features, including the Channel Islands and a series of deep basins and shallow ridges (Dailey et al., 1993). Beyond the steep 2000-m slope lies the ocean basin, with a mean depth of >3500 m. Three regions, associated with depth, were defined in the analyses for this study (Fig. 1): 1) the inshore and island region (with a mean depth <1100 m and a maximum depth <2000 m); 2) the slope region (with a mean depth of 1000–3200 m and a depth range of 500–3500 m); and the offshore region (with a mean depth >3500 m and a maximum depth >4000 m). The terms for these three regions will be used throughout the study.

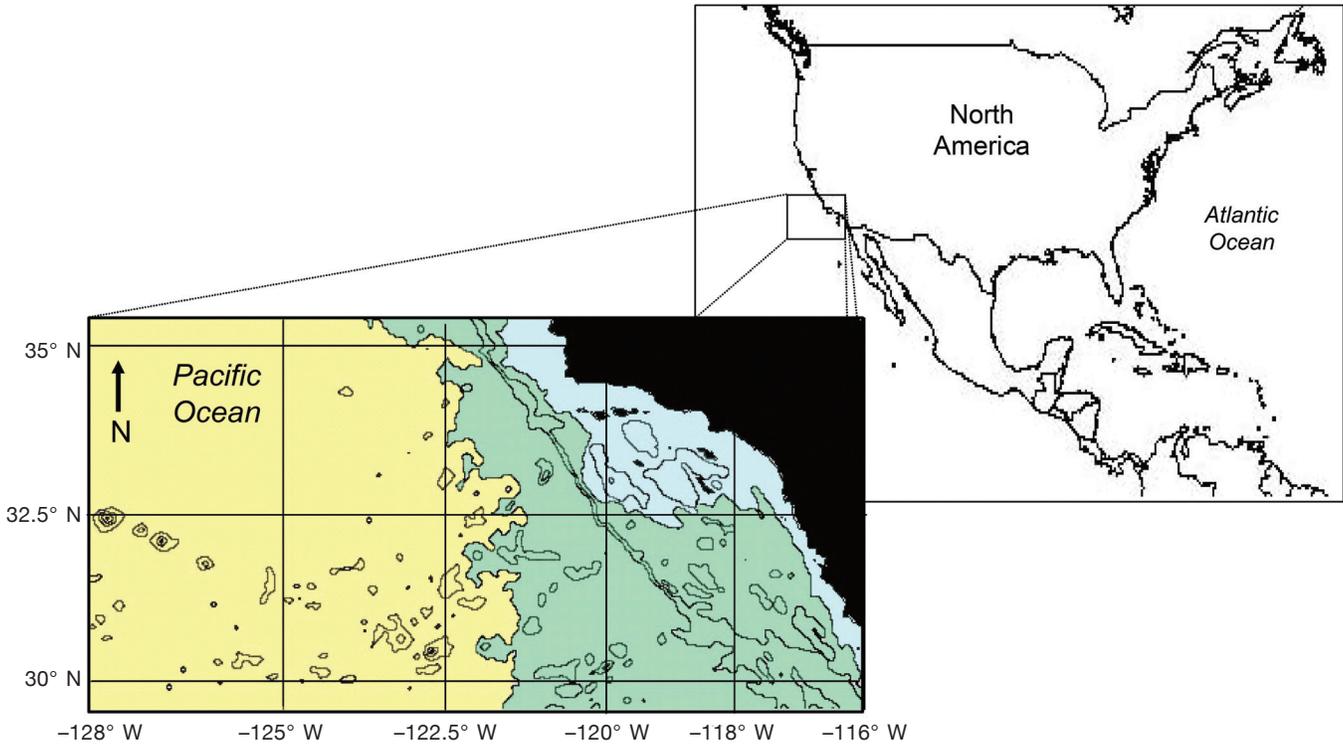


Figure 1

Map of the study area located off Southern California in the eastern North Pacific Ocean, south of Point Conception and incorporating the Channel Islands, in which small cetacean distributions were recorded during 1979–2009. Colored areas indicate 500-m depth contours. The blue area (mean depth <1100 m, maximum depth <2000 m) was considered the inshore and island region, the green area (mean depth of 1000–3200 m, within a depth range of 500–3500 m) was considered the slope region, and the yellow area (mean depth >3500 m, maximum depth >4000 m) was considered the offshore region.

We analyzed data from visual sightings of marine mammals from 105 separate survey cruises conducted by both CalCOFI and SWFSC from 1979 to 2009 (Fig. 2). During CalCOFI cruises from May 1987 to April 2004 (CalCOFIa) marine mammals were recorded as part of standardized CalCOFI top predator surveys that were focused primarily on marine birds. The strip-transect methods of Tasker et al. (1984) were followed. Observations were made with the naked eye by a single observer stationed on one side of the flying bridge or outside the main bridge. Marine mammals were recorded only if they occurred within the 300-m strip transect used for birds or within 1000 m of the vessel for large cetaceans. Each CalCOFI transect line extended from directly in front of the ship to 90° on the observation side. Group sightings of marine birds and mammals were summarized into 3-km bins, with the latitude and longitude determined for the centroid of each bin. Additional details of field methods are provided in Veit et al. (1996; 1997), Hyrenbach and Veit (2003), and Yen et al. (2006).

In July 2004, 2 dedicated marine mammal visual observers were added to the CalCOFI cruises (CalCOFIb), and a standard line-transect protocol replaced the strip-transect protocol (Burnham et al., 1980; Buckland

et al., 2001). A complete description of survey methods can be found in Soldevilla et al. (2006). Each observer monitored a 90° field of view from bow to abeam, one on each side of the ship, and alternated between scanning with Fujinon¹ 7×50 binoculars (Fujifilm Corp., Tokyo) and with the naked eye. Survey effort was calculated on the basis of latitude and longitude at the start and end of each trackline.

For all CalCOFI surveys, observations were made on daytime tracklines between stations, and no visual observation effort was conducted while the vessel was stationary. All visual effort was conducted in sea state conditions rated 5 or less on the Beaufort scale. Data used for analyses were generally from 4 surveys per year from 1987 to 2009, 1 survey per season (typically in the same month but with some variation). In 5 of these years, only 3 surveys were conducted. In 1998, surveys were carried out monthly to capture a time series of oceanographic measures in a strong El Niño year. However, to be consistent across all years for purposes of analysis, these cruise data were combined into

¹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

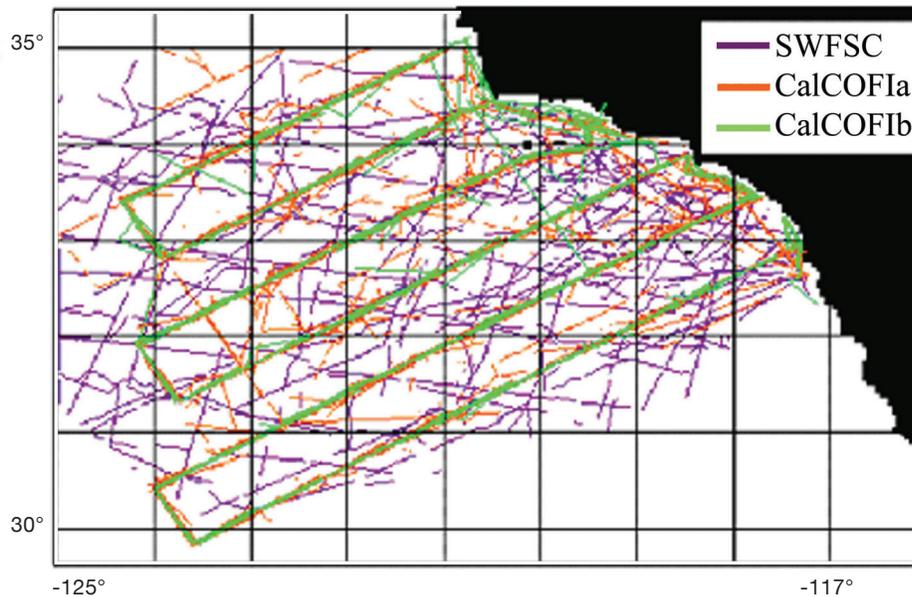


Figure 2

Transect lines surveyed for all studies of small cetaceans off Southern California in 1979–2009. Orange lines indicate surveys conducted during California Cooperative Oceanic Fisheries Investigations (CC) cruises from 1987 to 2004, green lines indicate CC surveys conducted from 2004 to 2009, and purple lines indicate surveys conducted by the NOAA Southwest Fisheries Science Center (SWFSC) from 1979 to 2009. Black lines indicate latitude and longitude in 1° increments, which were used to create the grid sections for analyses in the generalized additive models.

4 quarters (winter, spring, summer, and fall; see the next section, *Environmental data*, for details). A full summary of surveys, along with total effort (in kilometers) and sightings per year for all species is provided in Appendix I.

Data for analyses also came from 10 different SWFSC cruises, conducted primarily in the summer and fall (from July through November) from 1979 through 2005 and covering an area that included Southern California waters (Appendix I). For SWFSC cruises, standard line-transect protocols were followed, as described in Barlow and Forney (2007) and Kinzey et al.² The latter cruises had 3 observers on the flying bridge, 2 of whom used “big eye” 25×150 binoculars to scan 90° from bow to abeam on either side of the flying bridge. The third observer monitored the entire forward 180° with 7×50 binoculars and the naked eye. Survey effort (in kilometers) was calculated either from the latitude and longitude positions at the start and end of each trackline (1979–84 surveys) or from latitude and longitude positions recorded approximately every 10 min along the track (1991–2005 surveys).

Eight species of small cetaceans were examined in

this analysis. The 3 warm-temperate and tropical species were short-beaked common dolphin (*Delphinus delphis*), long-beaked common dolphin (*D. capensis*), and striped dolphin (*Stenella coeruleoalba*). The 3 cold-temperate species were Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), northern right whale dolphin (*Lissodelphis borealis*), and Dall’s porpoise (*Phocoenoides dalli*). The remaining 2 species were considered cosmopolitan, distributed globally in tropical and temperate waters: Risso’s dolphin (*Grampus griseus*) and bottlenose dolphin (*Tursiops truncatus*) (Reeves et al., 2002).

All bottlenose dolphin sightings in this study were presumed to be offshore animals because most coastal animals remain within about 1 km from the shore (Hanson and Defran, 1993) and surveys were conducted at least 5–10 km from the coast. In addition to their individual species’ models, short- and long-beaked common dolphins were combined into an additional *Delphinus* species category because the 2 species were not recognized formally as distinct until 1994 (Heyning and Perrin, 1994). Furthermore, they were not distinguished on SWFSC cruises before 1991 or on CalCOFI cruises before August 2004. Therefore, the data sets for long-beaked and short-beaked common dolphin are smaller than the data sets for all other species, and the data set for *Delphinus* spp. consists of all combined common dolphin sightings from all cruises.

² Kinzey, D., P. Olson, and T. Gerrodette. 2000. Marine mammal data collection procedures on research ship line-transect surveys by the Southwest Fisheries Science Center. NOAA Southwest Fisheries Science Center, Admin. Rep. LJ-00-08, 32 p.

Environmental data

Three variables were used to represent variations in SST on different temporal scales: quarterly SST averages, ENSO indices, and PDO indices. Monthly averaged SST data from 1985 to 2009 were from NOAA Advanced Very High Resolution Radiometer (AVHRR) Pathfinder satellite data, which have a spatial resolution of ~4.1-km (<http://www.nodc.noaa.gov/Satellite-Data/pathfinder4km>). For 1981–84, NOAA AVHRR data (multichannel averaged SST with a 5.7-km resolution) were also used. No satellite data were available before 1981; therefore, a missing data filter and a single imputation method were used to create values for 1979 and 1980 with the mean of the SSTs for the other years (Hastie, 1991; Nakagawa et al., 2001).

With Windows Image Manager, vers. 6 (WimSoft, San Diego, CA), seasonal SST averages were calculated from the monthly SST data. These SST averages were estimated for each quarter and each grid cell (see the following paragraph) for the period 1979–2009 (spring: February–April; summer: May–July; fall: August–October; winter: November–January). NOAA ENSO anomaly data, derived from the Oceanic Niño Index as a 3-month running mean of SST anomalies from 1971 to 2009 in the Niño 3.4 region (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml), were used as a proxy for ENSO for 1979–2009. The Niño 3.4 region is centered on the equator; therefore, the index indicates the relative strength of the ENSO event rather than SST anomaly values for Southern California waters. PDO anomaly data, averaged for the period from 1900 to 2009, from the University of Washington (<http://jisao.washington.edu/pdo>) were used as a proxy for the PDO regime from 1979 to 2009. The PDO index is derived from a monthly averaged SST for North Pacific waters poleward of 20°N.

Depth data were taken from the NOAA National Geophysical Data Center's ETOPO2 2-min global relief database (<http://www.ngdc.noaa.gov/mgg/fliers/06mkg01.html>). The study area was divided into 52 grid cells of 1° (111 km or 60 nmi) latitude by 1° longitude, leading to grid cell areas that ranged from 2940 to 3120 km². The gridded depth data were then assigned to each of the grid cells, and minimum, maximum, and mean depth values were calculated for each grid cell, along with the maximum seafloor slope per cell. These large grid cells correspond to approximately one day of effort for each of the surveys and were designed to be large enough to smooth out the mesoscale features that occur on shorter temporal and spatial scales than were of interest here. Although mesoscale features, such as fronts or eddies, are often observed to be hotspots for marine mammals, the multidecadal data set used in our study allowed for a synoptic examination of changing distribution patterns throughout the study area.

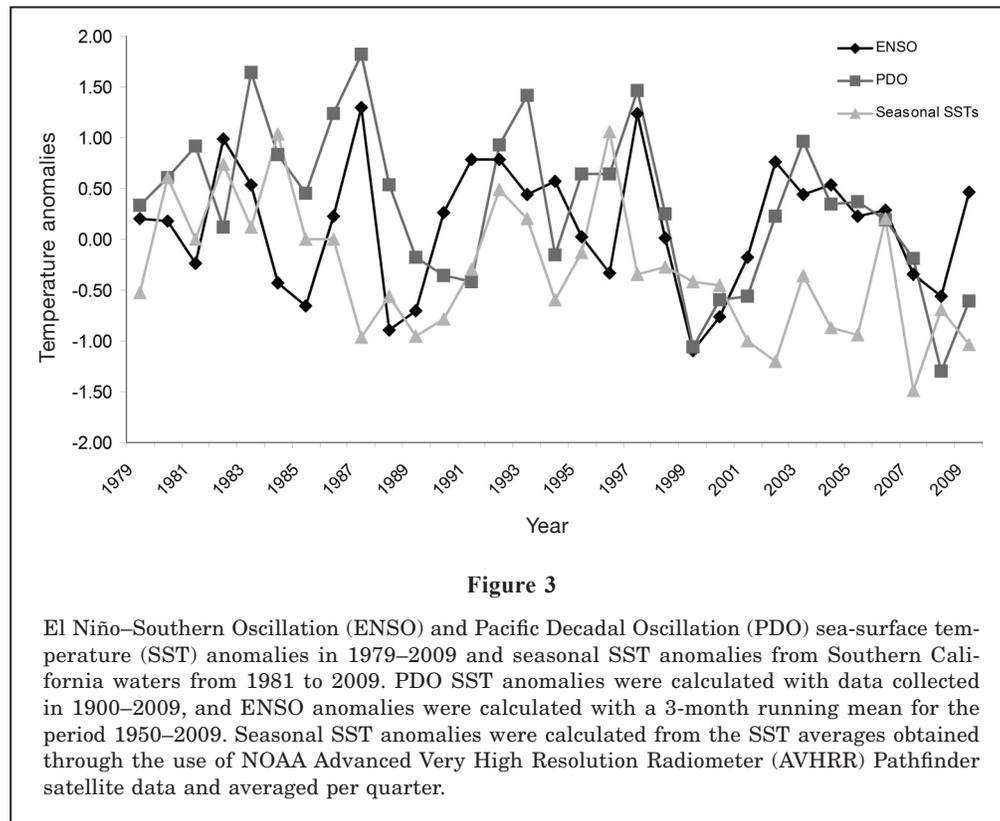
Modeling cetacean sighting rates

Generalized additive models (GAMs) of species sighting rates as a function of the temperature data and depth values were created with the mixed GAM computational vehicle (mgcv) package in R software, vers. 2.14.2 (R Core Team, 2012) (Hastie and Tibshirani, 1990; Wood, 2006). GAMs use a link function to relate the predictor variables to the mean of the response variable. GAMs also allow nonparametric functions to be fitted to the predictor variables through the use of a smoothing function to describe the relationship between the predictor and the response variables (Hastie and Tibshirani, 1990).

For model development, the grid cells described previously were used as data units, and all effort, sighting, and seasonal SST data were calculated for each cell. This approach allowed for the normalization of spatial and temporal differences in survey data. The type of survey was included as a categorical variable to account for differences in sighting rates due to survey method and platform. For example, because many vessels of different heights were used and heights for some vessels were not reported, standardization of observations for platform heights was not possible. Survey types included SWFSC (1979–2005), CalCOFIa (1987–2004), and CalCOFIb (2004–09). For each survey type, the number of group sightings of each species within each 1° cell, standardized by the log of the amount of effort per cruise (in kilometers), was modeled by assuming a Poisson distribution with a log link function.

Potential predictor variables in the model were the following: seasonal SST averages of each grid section (SeasAv); ENSO index (ENSO); PDO index (PDO); the mean (DepthMean), minimum (DepthMin), and maximum (DepthMax) depth (in meters) for each grid section; the maximum slope for each grid section (Slope); and the quarter (Quarter) as a categorical variable for identification of interannual patterns. Although sea state has been shown to be an important predictor of sighting rates in other cetacean habitat and trend models (Becker, 2007), the condition of the sea surface was not recorded in early CalCOFI observations and, therefore, sea state was not included in this analysis. Instead, only data recorded when the sea state was rated 0–3 on the Beaufort scale during SWFSC cruises and later CalCOFI cruises were used to standardize for differences in survey effort and, thus, make the different platforms as comparable as possible.

We used the number of group sightings, rather than the number of individuals, as our measure of relative encounter rate, essentially creating encounter rate models of group sightings per unit (kilometer) of survey effort (SPUE) (Bordino et al., 1999; Stockin, 2008). A correlation analysis of annual rates of group sightings in relation to mean group size per year



also was conducted to determine whether group size correlated with the number of groups encountered.

To select predictor variables for inclusion in each model, a likelihood-based smoothness selection method, instead of a traditional stepwise method, was applied with the restricted maximum likelihood (REML) criterion (Patterson and Thompson, 1971; Wood, 2006). Each predictor variable was tested for inclusion in the model with a tensor product approach coupled with a smoothing function defined by a cubic regression spline with shrinkage. The best model was selected on the basis of a combination of the information-theoretic descriptor Akaike's information criterion (AIC; Akaike, 1976) and REML. Next, an interactive term selection method was applied to sequentially drop the single term with the highest nonsignificant P -value and then refit the model until all terms were significant. The best-fit model was therefore one that minimized AIC and maximized REML and the explained deviance and that included only significant predictor variables. In addition, the ENSO, PDO, and seasonal SST averages, as well as each of the depth metrics, were tested for correlation if more than one of them was included in a model as a significant predictor. These variables were then included together only if they were not correlated. If the variables were correlated, then only the most significant variable remained in the final model.

Results

Sea-surface temperature for the study area over the period 1979–2009 ranged from 12.7°C to 19.4°C, with a mean of 16.2°C. Overall averaged seasonal anomalies ranged from –1.5°C to 1.1°C around the mean (Fig. 3). In comparison, seasonal anomalies by grid section ranged from –3.8°C to 3.4°C. Years with a strong positive PDO (index > 1) were 1983, 1987, 1993, 1997, and 2003, and a strong negative PDO (index < –1) occurred in 1999 and 2008 (Fig. 3). Strong positive ENSO years were 1982–83, 1987–88, 1991–92, 1997–98, and 2002–03, and strong negative ENSO years were 1988–89 and 1999–2000 (Fig. 3). No long-term trends in SST were apparent in our data given the levels of seasonal and ENSO variation observed. However, a linear regression of PDO anomaly data shows an overall negative trend in the last 30 years: coefficient of multiple determination (R^2) = 0.215, P = 0.009. This pattern is likely a result of the PDO regime switch in the last decade (Overland et al., 2008; Hodgkins, 2009).

The correlation analysis revealed that annual sighting rates and mean group size were not correlated for any of the species examined. This finding indicates that, although species may be encountered with varying frequency across years, the number of individual animals per group does not change in a correlated way. For example, if more groups of a given species were

Table 1

The final best-fit generalized additive models are presented here for each of the 8 species of small cetaceans investigated for this study in Southern California waters in 1979–2009. Also included are the restricted maximum likelihood (REML) score, explained deviance (Expl. dev.), and residual degrees of freedom (df) for each model. See Appendix 2 for the *P*-values of each variable in these models. The 8 species were the short-beaked common dolphin (*Delphinus delphis*), long-beaked common dolphin (*D. capensis*), Risso's dolphin (*Grampus griseus*), northern right whale dolphin (*Lissodelphis borealis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Dall's porpoise (*Phocoenoides dalli*), striped dolphin (*Stenella coeruleoalba*), and bottlenose dolphin (*Tursiops truncatus*); a third model for common dolphins incorporated data for both the short- and long-beaked common dolphins. Variable abbreviations: DepthMin=minimum depth (m), DepthMean=mean depth (m), MaxDepth=maximum depth (m), SeasAv=seasonal averaged sea-surface temperature, ENSO=El Niño–Southern Oscillation, and PDO=Pacific Decadal Oscillation.

Species	Final model	REML	Expl. dev.	Residual df
Short-beaked common dolphin	Quarter + Slope + DepthMean + SeasAv	754.0	23.9%	642
Long-beaked common dolphin	Quarter + DepthMax + ENSO + SeasAv	211.7	57.4%	652
Both common dolphins	Quarter + SurveyType + Slope + DepthMax + PDO + SeasAv	2751.8	32.5%	2415
Risso's dolphin	Quarter + SurveyType + Slope + DepthMean + ENSO + SeasAv	644.7	36.6%	2421
Northern right whale dolphin	SurveyType + DepthMax + ENSO + SeasAv	270.3	26.1%	2428
Pacific white-sided dolphin	Quarter + SurveyType + Slope + DepthMean + PDO	706.2	21.2%	2419
Dall's porpoise	Quarter + SurveyType + Slope + DepthMean + PDO + SeasAv	726.8	27.5%	2423
Striped dolphin	SurveyType + DepthMin	88.3	41.8%	2437
Bottlenose dolphin	SurveyType + Slope + DepthMean + PDO	376.0	46.4%	2429

encountered in a year, the group size would not necessarily also increase or decrease.

The best-fit models are shown in Table 1. Values for explained deviance ranged between 21.2% and 57.4% across species. A summary of group sighting rates is given in Table 2. Six of the 9 models included the Quarter variable, indicating intra-annual variation in the SPUE for each species. Of the 9 models, 7 models included the SurveyType variable; the 1987–2004 CalCOFI cruises ranked lowest and the SWFSC cruises ranked highest in sighting numbers for most species. Of the 9 models, 6 models included the seasonal SST average variable, and 7 models also included either the PDO or ENSO index. The latter results indicate the importance of those temperature fluctuations on small cetacean distribution. All models also included at least one depth metric, previously shown to be an important predictor variable for Southern California cetaceans (e.g., Becker, 2007). Finally, 5 of the 9 models included slope as a predictor.

Common dolphins

Three different models were used for common dolphins: both species of common dolphin in a single

combined category, short-beaked common dolphin, and long-beaked common dolphin. The similarities in the model results for both common dolphins and the short-beaked common dolphin indicate that the data for the combined category likely are dominated by sightings of short-beaked common dolphins. Common dolphins were associated with seasonal SSTs of about 14–18°C in all 3 models, indicating possible avoidance of extremely warm or cold temperatures (Fig. 4). For all common dolphin groups, most sightings occurred in the summer and fall, and generally the fewest sightings occurred in the spring. Depth was an important predictor of common dolphin distribution in all 3 models, and slope was included in the models for the combined category and the short-beaked common dolphin. Long-beaked common dolphins were found almost exclusively inshore, and sightings of short-beaked common dolphins and dolphins in the combined group were recorded both inshore and offshore in areas with shallow slopes. The model for both common dolphins combined showed a very slight increase in sightings with negative PDO anomalies, although the overall response was fairly flat (Fig. 4).

Table 2

Summary of sightings, including the number of cruises conducted by the California Cooperative Oceanic Fisheries Investigations and the NOAA Southwest Fisheries Science Center in which each species was encountered and the total number of groups sighted in 1979–2009 in Southern California waters for each studied species of small cetacean: short-beaked common dolphin (*Delphinus delphis*), long-beaked common dolphin (*D. capensis*), Risso's dolphin (*Grampus griseus*), northern right whale dolphin (*Lissodelphis borealis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Dall's porpoise (*Phocoenoides dalli*), striped dolphin (*Stenella coeruleoalba*), and bottlenose dolphin (*Tursiops truncatus*). Because the short- and long-beaked common dolphins were not recognized formally as distinct until 1994, data for both species were used in a combined category in analyses.

Species	Number of cruises	Number of groups
Short-beaked common dolphin	29	387
Long-beaked common dolphin	22	93
Both common dolphins	105	1537
Risso's dolphin	74	227
Northern right whale dolphin	32	71
Pacific white-sided dolphin	62	217
Dall's porpoise	64	240
Striped dolphin	22	28
Bottlenose dolphin	50	180

Risso's dolphin

Risso's dolphins were largely observed inshore, although they were occasionally observed offshore and in areas of shallow depths and steep slope, as shown in the partial residuals plots for depth and slope (Fig. 5). Sightings peaked slightly during warmer seasonal SSTs, around 18°C, but occurred least frequently in the summer. ENSO also was included in the model and indicated slightly more sightings during positive ENSO phases.

Striped dolphin

Striped dolphins are a tropical and warm-temperate species associated with warm water masses, and dolphins of this species were predominantly observed offshore of the 2000-m depth contour with a deep minimum depth (Fig. 5). Because of this strong offshore distribution, only 28 groups were sighted during 22 cruises. This low number of sightings is in part due to the limitation of including only sightings made in sea states rated 3 or less on the Beaufort scale; because most striped dolphin sightings occurred offshore, many were made in higher-rated sea states and were, therefore, not included. Because of that exclusion, most sightings included for analyses came from data collect-

ed during later SWFSC (1991–2005) cruises, making Survey Type an important predictor variable.

Bottlenose dolphin

Bottlenose dolphin groups tended to display a strong inshore and island association. They generally were sighted over the continental shelf, although they were occasionally observed farther offshore, as shown in the depth residuals plots (Fig. 5). The PDO variable was significant, indicating that a slight increase in sightings occurred with negative PDO anomalies.

Northern right whale dolphin

Northern right whale dolphin is 1 of 3 cold-temperate species strongly associated with the California Current system. Therefore, the extent of this species into the Southern California study area was expected to correlate with cold-water intrusions. Sightings were associated with cool SSTs as expected. However, sightings were associated also with both positive and negative ENSO anomalies. Groups of northern right whale dolphins showed a strong association with the slope region, with most sightings located at depths between 2000 and 4000 m, as shown in the depth residuals plot (Fig. 6).

Dall's porpoise

Sightings of Dall's porpoise, another cold-temperate species, peaked during the spring, fall, and winter (Fig. 6), and groups of Dall's porpoises were associated with cool SSTs. However, they were associated with slightly positive PDO phases, as well. They were distributed inshore and offshore, in areas of slightly shallower slopes, as shown in the depth and slope residuals plots.

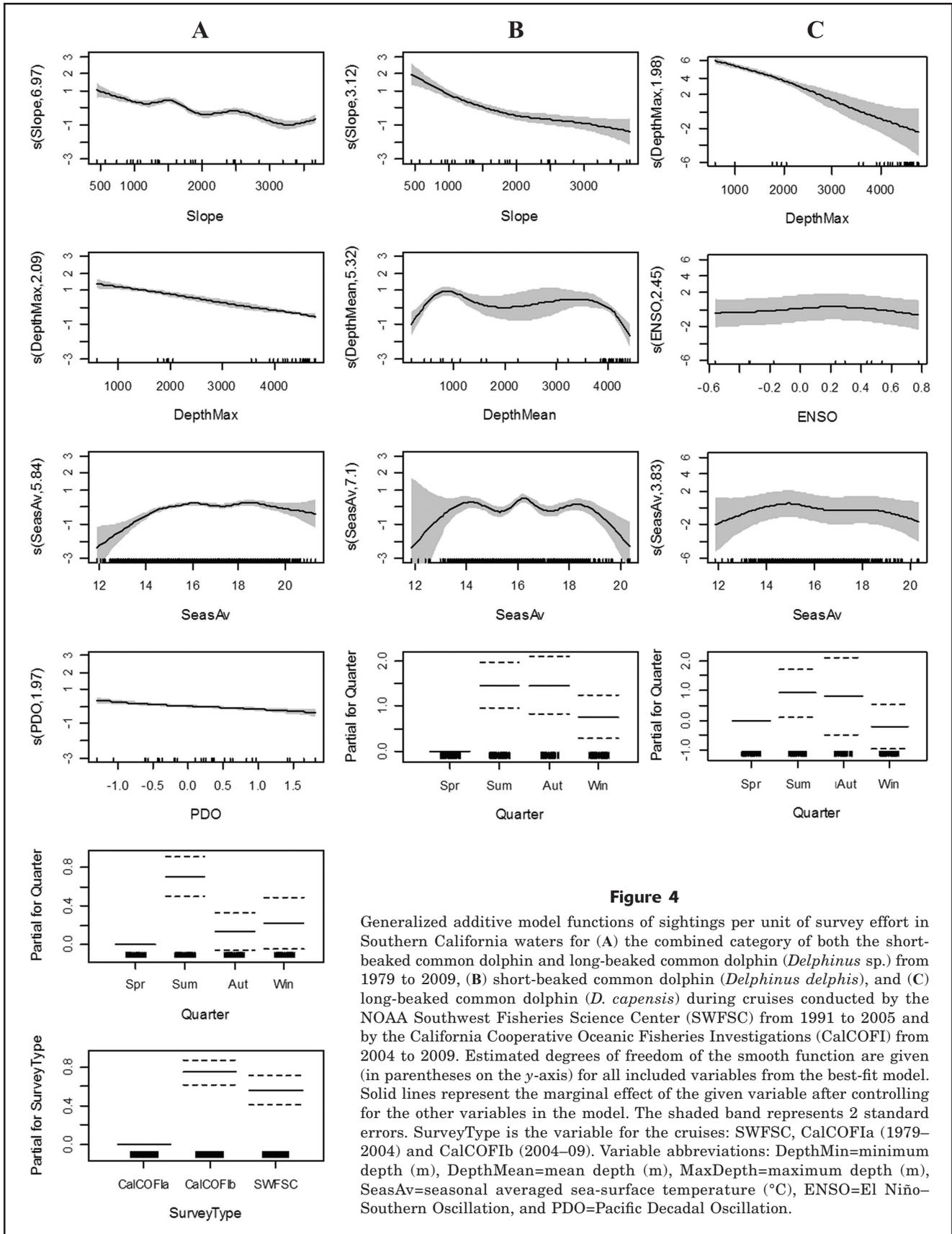
Pacific white-sided dolphin

Results were unexpected for Pacific white-sided dolphin, the final cold-temperate species the sighting rates of which were anticipated to increase in cooler temperatures. Sightings peaked slightly during the spring quarter when the water temperature was cooler. However, they also exhibited an association with slightly positive PDO indices (Fig. 6). This species was distributed largely inshore, as shown in the depth residuals plot.

Discussion

Patterns of seasonal sea-surface temperatures

Patterns of encounter rate related to seasonal SSTs were largely consistent with past studies within this region



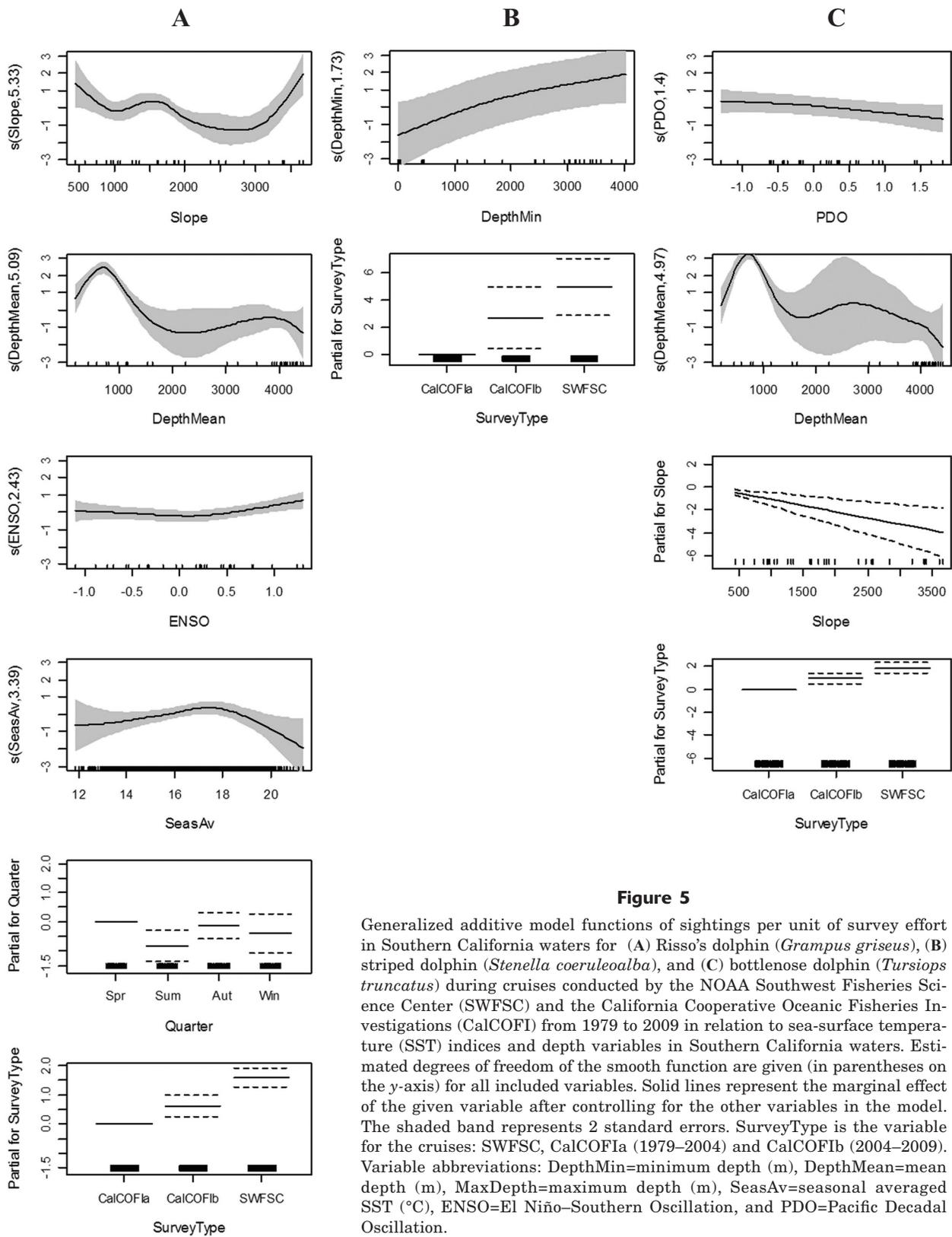


Figure 5

Generalized additive model functions of sightings per unit of survey effort in Southern California waters for (A) Risso's dolphin (*Grampus griseus*), (B) striped dolphin (*Stenella coeruleoalba*), and (C) bottlenose dolphin (*Tursiops truncatus*) during cruises conducted by the NOAA Southwest Fisheries Science Center (SWFSC) and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) from 1979 to 2009 in relation to sea-surface temperature (SST) indices and depth variables in Southern California waters. Estimated degrees of freedom of the smooth function are given (in parentheses on the y-axis) for all included variables. Solid lines represent the marginal effect of the given variable after controlling for the other variables in the model. The shaded band represents 2 standard errors. SurveyType is the variable for the cruises: SWFSC, CalCOFIa (1979–2004) and CalCOFIb (2004–2009). Variable abbreviations: DepthMin=minimum depth (m), DepthMean=mean depth (m), MaxDepth=maximum depth (m), SeasAv=seasonal averaged SST (°C), ENSO=El Niño–Southern Oscillation, and PDO=Pacific Decadal Oscillation.

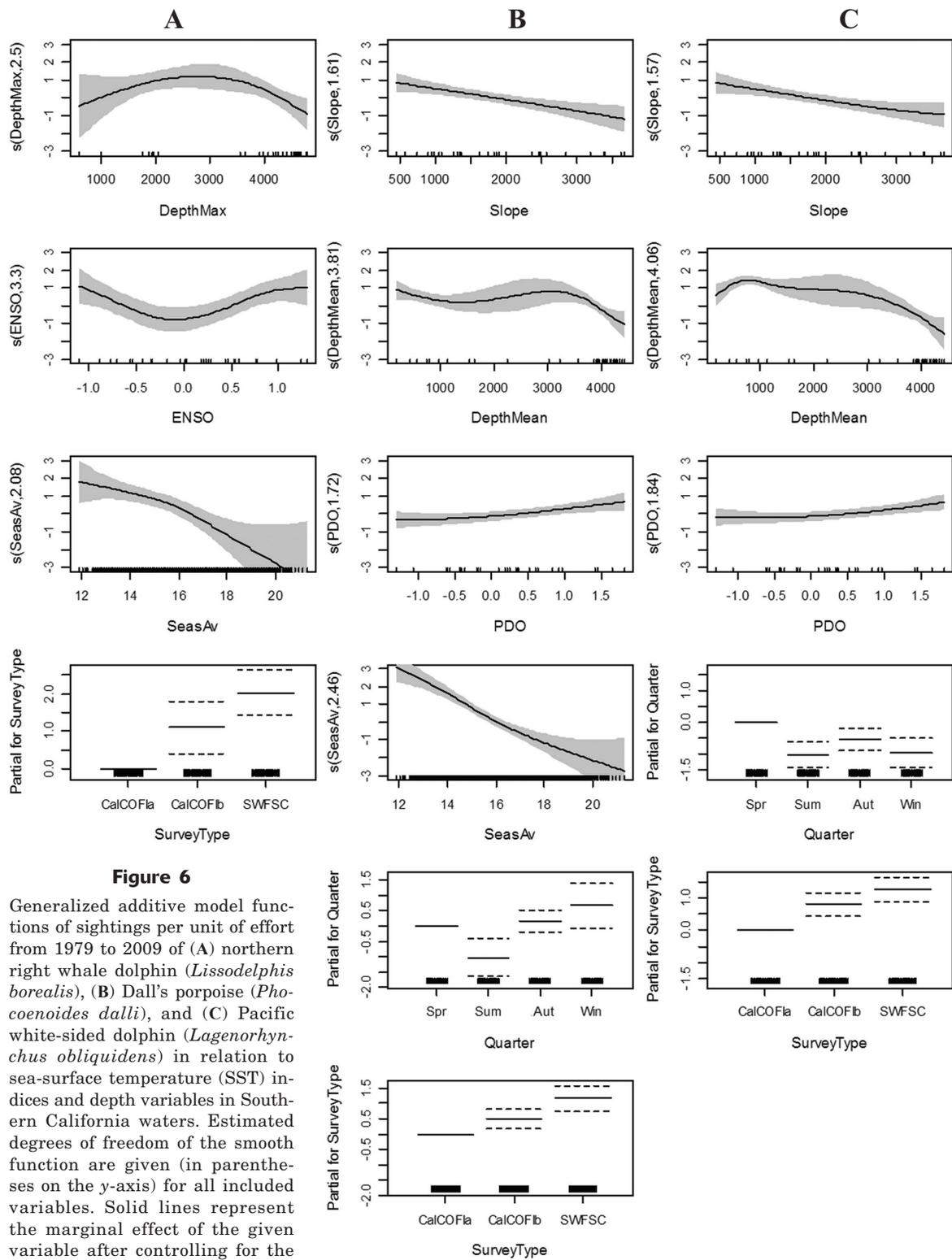


Figure 6

Generalized additive model functions of sightings per unit of effort from 1979 to 2009 of (A) northern right whale dolphin (*Lissodelphis borealis*), (B) Dall’s porpoise (*Phocoenoides dalli*), and (C) Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) in relation to sea-surface temperature (SST) indices and depth variables in Southern California waters. Estimated degrees of freedom of the smooth function are given (in parentheses on the y-axis) for all included variables. Solid lines represent the marginal effect of the given variable after controlling for the other variables in the model. The shaded band represents 2 standard errors. SurveyType is the variable for the cruises: SWFSC, CalCOFIa (1979–2004) and CalCOFIb (2004–09). Variable abbreviations: DepthMin=minimum depth (m), DepthMean=mean depth (m), MaxDepth=maximum depth (m), SeasAv=seasonal averaged SST (°C), ENSO=El Niño–Southern Oscillation, and PDO=Pacific Decadal Oscillation.

(e.g., Dohl et al., 1986; Barlow, 1995; Forney and Barlow, 1998; Forney, 2000; Barlow and Forney, 2007; Becker, 2007). Risso's and common dolphins preferred waters of intermediate and warmer temperature (14–20°C) (Forney, 2000; Reeves et al., 2002; Becker, 2007). In contrast, sightings of Dall's porpoises, Pacific white-sided dolphins, and northern right whale dolphins peaked in the cool spring season or with cool SSTs. In addition, long-beaked common, bottlenose, and Risso's dolphins and Dall's porpoises showed a preference for inshore or island-associated waters. Short-beaked common and Pacific white-sided dolphins were observed both inshore and slightly offshore. Northern right whale dolphins were associated with the slope region, and striped dolphins were observed only in deep offshore waters. The relationship between SST and depth is complex and difficult to separate, and these models likely oversimplify the observed trends. However, these results do seem to indicate some habitat or resource partitioning is occurring because these small cetacean species presumably follow preferred water conditions and prey.

Although the seasonal distribution patterns here are generally consistent with those found by Forney and Barlow (1998) for temperate species, an increase in common dolphin sightings was observed in that study in winter rather than in summer for 1991–92. In contrast, a summer peak in sightings for common dolphins was found by Dohl et al. (1986). Our results, however, support the findings of both of these studies. ENSO was included as a predictor in the model for the long-beaked common dolphin. The strong El Niño that occurred in 1991–92 may explain the increase in winter sightings for common dolphins in the surveys conducted by Forney and Barlow (1998) over that time period. If the winter of 1991–92 was uncharacteristically warm, then there may have been more common dolphins present than usual at that time of year. In contrast, the 1975–78 surveys conducted by Dohl et al. (1986) overlapped with the 1976–77 PDO regime shift from cool to warm; this shift could account for the increase in common dolphins during the warmer summer months of 1975–78.

Patterns of temperature oscillation

Temperature fluctuation patterns like ENSO, PDO, and the North Atlantic Oscillation have been documented to affect the prey of marine animals. An example of this effect is the strong relationship between the North Atlantic Oscillation, the life cycle of the copepod *Calanus finmarchicus*, and the recruitment of larval Atlantic Cod (*Gadus morhua*) that prey on copepods (Stenseth et al., 2002). Atlantic Cod in turn are a major food source for the gray seal (*Halichoerus grypus*), and *Calanus* spp. are an important prey for the North Atlantic right whale (*Eubalaena glacialis*) (Wishner et al., 1995; Mohn and Bowen, 1996). Calanoid copepods in the California Current system also have exhibited population-level step changes in abundance in response to

strong ENSO events and PDO shifts (Rebstock, 2002). For example, during the PDO phase switch in the late 1970s, 28% of the copepod species sampled increased in abundance. In contrast, around 1990 a biological step change occurred in copepod populations, when 28% of the species declined in abundance.

Population fluctuations of small pelagic fishes, such as anchovies (*Engraulis* spp.) and Pacific Sardine (*Sardinops sagax*), are also correlated strongly with both ENSO and PDO indices in the California Current system and in the Peru–Chile Current (Tibby, 1937; Hubbs, 1948; Niquen and Bouchon, 2004; Lehodey et al., 2006). These fish species are prey for many species of cetaceans in the California Current, including the short- and long-beaked common dolphins, bottlenose dolphin, Pacific white-sided dolphin, and Dall's porpoise (e.g., Stroud et al., 1981; Walker and Jones, 1993; Heise, 1997; Amano et al., 1998; Osnes-Erie, 1999).

Isolated instances of cetaceans changing their distribution patterns have been noted during and after strong climatic events. One example is the permanent expansion of the northern extent of the range of coastal bottlenose dolphins along the California coast during the 1982–83 El Niño (Defran et al., 1999). Another example is the increased abundance of humpback whales (*Megaptera novaeangliae*) in Monterey Bay during the 1997–98 El Niño (Benson et al., 2002). SST fluctuations have been shown to affect the distribution and community composition of seabirds in the California Current system as well (Hyrenbach and Veit, 2003; Yen et al., 2006). A decline of 2% per year in overall seabird density was recorded for the last 25 years—a drop that was attributed to declines in nearshore abundance of forage fishes (Sydeman et al., in press).

The models for most species included the PDO and ENSO indices as significant variables, although they were not strong predictors in most cases. During positive PDO and ENSO phases, upwelling and productivity decrease while water temperature increases, particularly as warm equatorial waters are pushed poleward and the California Current system is found closer inshore (Sette and Isaacs, 1960; McGowan, 1985). These conditions may explain the apparent association of the Dall's porpoise and Pacific white-sided dolphin with positive PDO indices. These species may be pushed closer to shore by the contraction of the California Current, or they could be concentrating in the remaining areas of productivity, as has been hypothesized for the increase in rorquals in Monterey Bay during the 1997–98 El Niño (Benson et al., 2002).

Alternately, the patterns observed here may reflect changes that occur in other parts of these species' ranges. For example, during negative, cool PDO phases, the overall range of warm-temperate species may contract southward; therefore, a slight increase in the number of common dolphins and even bottlenose dolphins may occur during this phase. Likewise, if the cold-temperate species range as far south as Baja during negative PDO and ENSO periods, then their ranges

may contract northward during positive PDO phases, leading to an increase in sightings of Dall's porpoises and Pacific white-sided dolphins in Southern California waters.

Implications in regard to climate change

We have demonstrated changes in distributions of small cetaceans on scales of months to decades. Despite a limited understanding of the mechanisms behind those changes, the model results may help create a basis for understanding the potential effect of climate change upon these species. Studies of climate change in the California Current system indicate that, in addition to increasing temperatures, a rise in atmospheric carbon dioxide levels is predicted to lead to more intense upwelling (Bakun, 1990; Snyder et al., 2003), stronger thermal stratification, and a deepening of the thermocline (Roemmich and McGowan, 1995). These changes may alter large-scale circulation patterns (Harley et al., 2006). Fluctuations in these physical mechanisms will lead to changes in ecosystem dynamics and biodiversity from primary producers to top predators (Sydeman et al., 2001; Harley et al., 2006; Hooff and Peterson, 2006).

Globally, species associated with sea ice or with highly limited ranges are the most obvious species to be affected by changing ocean temperatures and sea levels (Moore and Huntington, 2008). However, even pelagic species, such as the ones discussed here, are likely to be affected (Learmonth et al., 2006; Simmonds and Elliott, 2009). For example, as water temperatures off Scotland increased, the abundance of common dolphins increased, whereas the number of white-beaked dolphins (*Lagenorhynchus albirostris*), which are associated with cold water, decreased. Such trends could indicate a poleward shift in range for both species (MacLeod et al., 2005; Simmonds and Isaac, 2007). In addition, an influx of cold freshwater in the northern Gulf of Mexico in 2011 may have contributed to an unusually high mortality rate in bottlenose dolphins (Charmichael, et al. 2012).

We predicted that the ranges of the common dolphins, Risso's dolphin, and bottlenose dolphin would expand northward as ocean temperatures warmed, especially as seasonal, ENSO, and PDO events were compounded (e.g., a positive PDO with a positive ENSO). Conversely, we predicted that the ranges of the Pacific white-sided dolphin, northern right whale dolphin, and Dall's porpoise would contract poleward and inshore. These patterns have held true for observations made during previous shorter-term studies. For example, Dall's porpoises and Pacific white-sided dolphins dominated the odontocete species assemblage off central California in the decade before the strong El Niño of 1997–98 (Benson et al., 2002; Keiper et al., 2005).

Keiper et al. (2005) noted that during the strong El Niño of 1997–98 there was a deepened thermocline, a narrow, inshore distribution of Pacific Sardine eggs, and

an overall decrease in abundance of macrozooplankton. During that El Niño, sightings of Dall's porpoises were greatly reduced, whereas common and Risso's dolphin sightings increased. Furthermore, Pacific white-sided dolphin sightings decreased after this period, while sightings of common (particularly the long-beaked species) and bottlenose dolphins increased (Keiper et al., 2005).

However, over the longer-term, our study showed an association of the Pacific white-sided dolphin and Dall's porpoise with positive PDO indices, of common and bottlenose dolphins with negative PDO indices, and of the northern right whale dolphin with positive ENSO indices. These results indicate a more complicated relationship between distribution patterns and SST than we allowed for in our initial predictions or that has been observed on shorter temporal scales. Continued monitoring efforts should be made to ensure that future changes in distribution or reproductive success are documented.

Model considerations

The results presented here provide insight into long-term distribution trends of small cetaceans over several decades. The results are both supported by and build upon the current knowledge base for these species. Nonetheless, we recognize some caveats to this study that warrant discussion.

The PDO and ENSO indices were developed with the use of broad regions of the Pacific. Therefore, they may not reflect precisely the specific dynamics of the Southern California study area. The seasonal SSTs, although averaged for each grid section and quarter, were also still quite broad, as was the selected size of grid cells. However, this scope was used intentionally to capture the large temporal- and spatial-scale dynamics of these changing SST patterns, rather than to examine meso-scale dynamics on shorter temporal scales. In addition, the SST, ENSO, and PDO variables have the potential to be correlated, as the indices are similar over time. A correlation analysis was conducted, and correlations between ENSO and PDO and between seasonal SSTs and PDO were detected for some species. In those cases, they were not included together, and only the most significant predictors were included.

Only one cruise occurred per year before 1987. To account for potential differences between Survey Types, we repeatedly reran each model while randomly dropping out data from different years. The results indicated that the models were robust against missing years of data, and the variation in the number of surveys per year did not affect the results. The survey methods from each Survey Type were quite different, making it a challenge to combine these data sets. However, by using only the group SPUE and by limiting our sightings to the ones made in sea states of 3 or less on the Beaufort scale, we tried to make the data as comparable as possible.

The inclusion of the Survey Type variable in most models reflects some of those differences in survey effort. The CalCOFI cruises in 1987–2004 consistently ranked lowest in sighting numbers for all species although those surveys had the most effort. This ranking was likely due to a single observer who covered both birds and mammals with a smaller effective strip width rather than to the multiple observers dedicated to monitoring marine mammals for the other 2 types of surveys.

The SWFSC cruises had the highest number of observations for 6 of the 7 models in which they were included, although those cruises had less effort than the CalCOFI cruises. The high number of observations may have been due to optimal sighting conditions during the SWFSC cruises, which were largely conducted in summer and fall. In addition, big eye binoculars were used on SWFSC cruises but were not used regularly on CalCOFI cruises. In another difference in Survey Type, CalCOFI surveys always were conducted in passing mode in which the survey vessel does not leave the transect line when animals are sighted, but SWFSC ships operated in closing mode and could deviate from the transect line to confirm species.

Finally, we used the number of groups sighted rather than the number of individuals observed as our metric for encounter rate. The correlation analysis did not indicate a strong relationship between the number of groups encountered and the size of the group for any of the modeled species. Therefore, our models may have misidentified trends if a change in group size as a response to any of these variables had better explanatory power than the overall encounter rates.

Conclusions

The models presented in this study indicated that fluctuations in SST regimes influenced the distribution of small cetaceans. However, the relationships were not as straightforward as predicted. The observed complexities likely are related to effects of SSTs on prey and subsequent responses by cetaceans. Dolphins have been shown previously to be sensitive to changes in SST and to shift their distributions in response to regime oscillations like ENSO. However, this study is the first one to model responses to multiple temperature shifts over a long time period for a variety of cetacean species in this region of the California Current system.

The resulting models were unique to each of the 8 species studies. This finding indicates that each species is characterized by a distinct pattern in habitat occurrence related to SST dynamics in this study area, despite the overlap in the overall distributions of the examined species in the Southern California study area. Results herein can be used to begin to predict the future distribution of these small cetaceans throughout the waters off Southern California. Results also provide a tool to understand, as global climate change

intensifies, potential responses of these species to rising ocean temperatures and the ecological mechanisms responsible for those responses.

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Appendix I

Search effort (in linear kilometers) and number of groups seen for each species on each of the surveys conducted by the NOAA Southwest Fisheries Science Center (SWFSC) and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and included in the analyses for this study. El Niño cruises were combined into seasons for analyses. Seasons are defined as follows: spring was February–April, summer was May–July, fall was August–October, and winter was November–January. Species abbreviations are as follows: Dsp=*Delphinus*

sp.; Dd=*Delphinus delphis*; Dc=*Delphinus capensis*; Gg=*Grampus griseus*; Lb=*Lissodelphis borealis*; Lo=*Lagenorhynchus obliquidens*; Pd=*Phocoenoides dalli*; Sc=*Stenella coeruleoalba*; Tt=*Tursiops truncatus*. NA=not available. The SWFSC cruises are as follows: CAMMS=The California Marine Mammal Survey; PODS=Population of Delphinus Stocks; ORCAWALE=Oregon, California, Washington Line-Transect and Ecosystem cruise; CSCAPE=The Collaborative Survey of Cetacean Abundance and the Pelagic Ecosystem.

Cruise	Year	Quarter	Dsp	Gg	Lb	Lo	Pd	Sc	Tt	Dd	Dc	Effort (km)
CalCOFI												
CC198705	1987	Spring	5	1	0	0	4	0	3	NA	NA	1559
CC198709	1987	Summer	9	4	0	5	0	0	3	NA	NA	1704
CC198711	1987	Fall	3	1	0	1	2	0	3	NA	NA	1468
CC198801	1988	Winter	3	2	0	2	3	0	3	NA	NA	1501
CC198804	1988	Spring	3	1	4	0	0	0	3	NA	NA	1346
CC198808	1988	Summer	15	0	0	0	3	0	3	NA	NA	1810
CC198810	1988	Fall	3	7	0	0	9	0	3	NA	NA	1420
CC198901	1989	Winter	2	0	1	0	2	0	3	NA	NA	1338
CC198904	1989	Spring	1	0	0	3	7	0	3	NA	NA	1596
CC198907	1989	Summer	25	3	1	1	1	0	3	NA	NA	1932
CC198911	1989	Fall	11	4	1	1	4	0	3	NA	NA	1496
CC199003	1990	Winter	1	0	1	0	1	0	3	NA	NA	407
CC199004	1990	Spring	13	0	0	5	3	1	3	NA	NA	1509
CC199007	1990	Summer	18	2	0	0	1	0	3	NA	NA	1887
CC199011	1990	Fall	5	3	0	1	4	0	3	NA	NA	1349
CC199101	1991	Winter	3	1	0	1	3	0	3	NA	NA	1332
CC199103	1991	Spring	7	2	0	1	5	0	3	NA	NA	1162
CC199107	1991	Summer	28	0	0	2	0	0	3	NA	NA	1668
CC199109	1991	Fall	12	2	0	0	0	0	3	NA	NA	1635
CC199201	1992	Winter	5	1	2	3	1	0	3	NA	NA	1265
CC199204	1992	Spring	5	2	0	1	2	0	3	NA	NA	2427
CC199207	1992	Summer	18	1	1	2	1	0	3	NA	NA	1437
CC199209	1992	Fall	5	0	0	0	2	0	3	NA	NA	1625
CC199301	1993	Winter	10	1	0	1	1	0	3	NA	NA	1249
CC199303	1993	Spring	9	2	0	0	0	0	0	NA	NA	1630
CC199308	1993	Summer	9	0	0	0	0	0	0	NA	NA	1843
CC199310	1993	Fall	2	1	0	0	2	0	0	NA	NA	1549
CC199401	1994	Winter	12	2	2	0	4	0	1	NA	NA	1369
CC199403	1994	Spring	2	0	0	0	0	0	0	NA	NA	1552
CC199410	1994	fall	15	6	0	2	0	0	2	NA	NA	1590
CC199501	1995	Winter	15	2	0	0	1	0	0	NA	NA	1331

Cruise	Year	Quarter	Dsp	Gg	Lb	Lo	Pd	Sc	Tt	Dd	Dc	Effort (km)
CC199504	1995	Spring	12	2	0	0	2	0	0	NA	NA	1629
CC199507	1995	Summer	26	1	0	2	1	0	0	NA	NA	1900
CC199510	1995	Fall	9	1	0	1	0	0	0	NA	NA	1589
CC199604	1996	Spring	6	1	0	0	1	0	1	NA	NA	1214
CC199608	1996	Summer	8	0	0	3	0	0	0	NA	NA	1729
CC199610	1996	Fall	4	0	0	0	0	0	0	NA	NA	1434
CC199701	1997	Winter	7	8	1	5	3	0	0	NA	NA	1442
CC199707	1997	Summer	25	3	0	0	1	0	2	NA	NA	1724
CC199709	1997	Fall	9	1	0	2	0	0	1	NA	NA	1511
CC199712	1997	El Niño 1	2	3	0	0	0	0	0	NA	NA	361
CC199801	1998	Winter	10	1	0	0	0	0	0	NA	NA	696
CC199803	1998	El Niño 2	6	2	0	4	1	0	1	NA	NA	701
CC199804	1998	Spring	13	1	0	2	0	0	1	NA	NA	1491
CC199805	1998	El Niño 3	14	0	0	1	1	0	2	NA	NA	818
CC199806	1998	El Niño 4	14	1	1	2	0	0	1	NA	NA	812
CC199807	1998	Summer	25	0	0	1	0	0	1	NA	NA	1652
CC199809	1998	Fall	9	1	0	0	0	0	0	NA	NA	1499
CC199810	1998	El Niño 5	21	0	0	1	0	0	0	NA	NA	1308
CC199904	1999	Spring	9	1	3	3	1	0	0	NA	NA	1633
CC199908	1999	Summer	33	2	0	0	0	0	1	NA	NA	1457
CC199910	1999	Fall	17	1	0	0	1	0	0	NA	NA	1212
CC200004	2000	Spring	9	0	0	3	5	0	2	NA	NA	1667
CC200007	2000	Summer	9	0	0	10	1	0	3	NA	NA	1754
CC200010	2000	Fall	9	0	2	4	1	0	2	NA	NA	1425
CC200101	2001	Winter	7	2	0	1	1	0	0	NA	NA	1434
CC200104	2001	Spring	5	2	1	1	2	0	0	NA	NA	1428
CC200107	2001	Summer	16	0	0	0	0	0	0	NA	NA	1547
CC200110	2001	Fall	25	3	0	5	0	0	0	NA	NA	1322
CC200201	2002	Winter	7	4	3	0	3	0	1	NA	NA	1172
CC200203	2002	Spring	6	0	0	5	4	0	0	NA	NA	1454
CC200207	2002	Summer	23	1	0	2	2	0	4	NA	NA	1741
CC200211	2002	Fall	7	0	0	0	0	0	0	NA	NA	1443
CC200301	2003	Winter	14	2	0	1	2	0	0	NA	NA	1712
CC200304	2003	Spring	6	3	1	7	12	0	0	NA	NA	3503
CC200307	2003	Summer	16	4	1	0	1	0	0	NA	NA	1680
CC200310	2003	Fall	12	0	0	0	0	0	0	NA	NA	1542
CC200401	2004	Winter	16	1	0	0	4	0	5	NA	NA	1380
CC200403	2004	Spring	13	6	3	7	14	0	0	NA	NA	2301
CC200407	2004	Summer	21	2	0	6	1	2	0	16	0	2003
CC200411	2004	Fall	19	2	0	6	0	0	2	8	8	1552
CC200501	2005	Winter	16	2	1	4	3	0	0	11	1	1376
CC200504	2005	Spring	7	4	6	13	4	0	2	0	4	2024
CC200507	2005	Summer	64	0	0	3	0	0	0	16	18	2264
CC200511	2005	Fall	32	5	1	1	1	0	1	10	7	1357
CC200602	2006	Winter	4	0	0	4	0	0	7	6	4	1292
CC200604	2006	Spring	6	3	2	3	8	0	3	1	1	2070
CC200607	2006	Summer	53	0	0	0	0	0	0	41	3	1964
CC200610	2006	Fall	17	0	1	3	1	1	4	11	2	1731
CC200707	2007	Winter	42	7	0	1	0	0	0	14	10	2180
CC200711	2007	Spring	22	0	2	2	1	0	1	12	0	1630
CC200701	2007	Summer	20	1	0	1	7	0	0	14	0	1454
CC200704	2007	Fall	9	4	1	2	9	0	2	2	1	900
CC200801	2008	Winter	15	4	1	5	4	0	0	8	0	1264
CC200803	2008	Spring	19	2	2	6	22	0	2	13	2	1182
CC200808	2008	Summer	31	1	0	1	0	0	6	10	3	1224
CC200810	2008	Fall	30	2	0	2	0	0	1	21	1	1505
CC200901	2009	Winter	30	1	0	0	13	0	4	18	3	1273
CC200903	2009	Spring	14	0	0	0	2	0	1	5	4	707
CC200907	2009	Summer	34	7	0	0	0	1	7	9	9	931
CC200911	2009	Fall	12	2	1	1	1	0	0	6	1	713
SWFSC 564	1979	Sept-Oct	17	8	1	1	2	1	3	NA	NA	1662

Cruise	Year	Quarter	Dsp	Gg	Lb	Lo	Pd	Sc	Tt	Dd	Dc	Effort (km)
646	1980	June–July	8	0	0	0	2	0	3	NA	NA	2045
798	1982	April	16	15	11	8	16	0	3	NA	NA	1842
674	1983	Dec	19	7	0	18	4	0	3	NA	NA	562
905	1984	Dec	42	13	1	10	3	0	3	NA	NA	1179
CAMMS	1991	July–Oct	50	8	10	0	0	6	3	45	2	4210
PODS	1993	July–Oct	23	3	0	0	0	4	1	21	0	2610
ORCAWALE	1996	Aug–Nov	30	6	1	9	0	6	4	24	2	3936
ORCAWALE	2001	July–Dec	20	7	0	2	0	1	7	16	1	2540
CSCAPE	2005	Aug–Dec	42	2	0	0	6	5	4	29	6	2951

Appendix 2

The effective degrees of freedom (EDF) and P -values for each of the parameters included in the generalized additive model of sightings per unit effort in Southern California waters in 1979–2009 for each studied species of small cetacean: short-beaked common dolphin (*Delphinus delphis*), long-beaked common dolphin (*D. capensis*), Risso's dolphin (*Grampus griseus*), striped dolphin (*Stenella coeruleoalba*), bottlenose dolphin (*Tursiops truncatus*), northern right whale dolphin (*Lissodelphis borealis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), and Dall's porpoise (*Phocoenoides dalli*). Because the short- or long-beaked

common dolphins were not recognized formally as distinct until 1994, data for both species were used in a combined category in analyses. Note that no EDF was available for the 2 parametric variables (Quarter and SurveyType). SurveyType is the variable for the cruises, which were conducted by the NOAA Southwest Fisheries Science Center and the the California Cooperative Oceanic Fisheries Investigations. Variable abbreviations: DepthMin=minimum depth (m), DepthMean=mean depth (m), MaxDepth=maximum depth (m), SeasAv=seasonal averaged sea-surface temperature (°C), ENSO=El Niño–Southern Oscillation, and PDO=Pacific Decadal Oscillation. NA=not available.

Species	Parameter	EDF	P -value
Both common dolphins	Quarter	NA	<0.01
	SurveyType	NA	<0.01
	Slope	6.97	<0.01
	DepthMax	2.09	<0.01
	SeasAv	5.87	<0.01
	PDO	1.97	<0.01
Short-beaked common dolphin	Quarter	NA	<0.01
	Slope	3.12	<0.01
	DepthMean	5.32	<0.01
	SeasAv	7.1	<0.01
Long-beaked common dolphin	Quarter	NA	0.02
	DepthMax	1.98	<0.01
	SeasAv	2.46	0.03
	ENSO	3.82	0.03
Risso's dolphin	Quarter	NA	<0.01
	SurveyType	NA	<0.01
	Slope	5.33	<0.01
	DepthMean	5.09	<0.01
	ENSO	2.43	<0.01
	SeasAv	3.39	0.01

Species	Parameter	EDF	P -value
Striped dolphin	SurveyType	NA	<0.01
	DepthMin	1.73	<0.01
Bottlenose dolphin	SurveyType	NA	<0.01
	DepthMean	4.97	<0.01
	PDO	1.4	0.03
Northern right whale dolphin	SurveyType	NA	<0.01
	DepthMax	2.51	<0.01
	ENSO	3.32	<0.01
	SeasAv	2.19	<0.01
Pacific white-sided dolphin	Quarter	NA	<0.01
	SurveyType	NA	<0.01
	Slope	1.57	<0.01
	DepthMean	4.06	<0.01
Dall's porpoise	PDO	1.84	0.01
	Quarter	NA	<0.01
	SurveyType	NA	<0.01
	Slope	1.61	<0.01
	DepthMean	3.81	<0.01
	PDO	1.74	0.01
SeasAv	2.83	<0.01	