



Predicting seasonal density patterns of California cetaceans based on habitat models

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ABSTRACT: Temporal variability in species distribution remains a major source of uncertainty in managing protected marine species, particularly in ecosystems with significant seasonal or inter-annual variation, such as the California Current Ecosystem (CCE). Spatially explicit species–habitat models have become valuable tools for decision makers assisting in the development and implementation of measures to reduce adverse impacts (e.g. from fishery bycatch, ship strikes, anthropogenic sound), but such models are often not available for all seasons of interest. Broad-scale migratory patterns of many of the large whale species are well known, while seasonal distribution shifts of small cetaceans are typically less well understood. Within the CCE, species–habitat models have been developed based on 6 summer–fall surveys conducted during 1991 to 2008. We evaluated whether the between-year oceanographic variability can inform species predictions during winter–spring periods. Generalized additive models were developed to predict abundance of 4 cetacean species/genera known to have year-round occurrence in the CCE: common dolphins *Delphinus* spp., Pacific white-sided dolphin *Lagenorhynchus obliquidens*, northern right whale dolphin *Lissodelphis borealis*, and Dall's porpoise *Phocoenoides dalli*. Predictor variables included a combination of temporally dynamic, remotely sensed environmental variables and geographically fixed variables. Across-season predictive ability was evaluated relative to aerial surveys conducted in winter–spring 1991 to 1992, using observed:predicted density ratios, non-parametric Spearman rank correlation tests, and visual inspection of predicted and observed distributions by species. Seasonal geographic patterns of species density were captured effectively for most species, although some model limitations were evident, particularly when the original summer–fall data did not adequately capture winter–spring habitat conditions.

KEY WORDS: Cetacean abundance · Habitat-based density model · California Current · Remote sensing · Common dolphin · Pacific white-sided dolphin · Northern right whale dolphin · Dall's porpoise

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INTRODUCTION

The abundance and distribution of many pelagic species are highly variable on seasonal, interannual, and decadal time scales (Forney 1999, 2000, Pyper

& Peterman 1999, Maravelias et al. 2000, Rosenkranz et al. 2001, Koslow et al. 2002), and this temporal variability remains a major source of uncertainty in managing marine resources (Peterman & Bradford 1987, Forney et al. 1991, 2012, Edwards &

Perkins 1992, Taylor & Gerrodette 1993, Ralls & Taylor 2000). This is particularly important in dynamic regions like the California Current Ecosystem (CCE), which is defined by high variability at multiple temporal and spatial scales (Hickey 1979). Spatially explicit species-habitat models are increasingly recognized as valuable tools for assessing species distributions and recently have been used to develop conservation strategies for marine mammals (e.g. an *Endangered Species Research* Theme Section, 'Beyond marine mammal habitat modeling: applications for ecology and conservation,' was dedicated to this topic). The need for effective predictive models of cetacean occurrence and distribution has become more critical for marine resource managers who must select minimal-impact locations or seasons for an increasing number of human activities with the potential to harm cetaceans (e.g. vessel traffic, naval training, fisheries interactions). Quantitative cetacean-habitat models provide a means to assess potential impacts and inform conservation management decisions (Hooker et al. 1999, Cañadas et al. 2002, Torres et al. 2003, Kaschner et al. 2006, Barlow et al. 2009, Gerrodette & Eguchi 2011, Gilles et al. 2011, Becker et al. 2012a,b, Forney et al. 2012, Goetz et al. 2012, Keller et al. 2012, Redfern et al. 2013).

Habitat-based density models for cetaceans are typically based on sighting and oceanographic data collected during systematic line-transect surveys. Off the US west coast, the abundance of cetaceans was estimated from 6 shipboard line-transect surveys conducted by the Southwest Fisheries Science Center (SWFSC) from July to November 1991 to 2008, covering an area of approximately 1 141 807 km² (Barlow 2010). Cetacean sighting data from these surveys have been used to develop and validate habitat-based density models, which provide the best estimates of average cetacean density and distribution off the US west coast for summer and fall (hereafter 'summer' and 'summer models'; Barlow et al. 2009, Becker et al. 2012b, Forney et al. 2012).

Ideally, species-habitat models would be developed using sighting and corresponding environmental data specific to the period of interest. Rough weather conditions in the CCE make it difficult to collect shipboard line-transect data year-round, however, and few studies have assessed cetacean density and distribution in winter and spring (hereafter 'winter'). Most of the systematic survey data that exist for these seasons have been collected during aerial surveys (Dohl et al. 1983, Forney & Barlow 1998), which do not allow for the collection of complementary *in*

situ oceanographic data, and typically contain too few sightings to build and evaluate predictive habitat models. In the absence of sufficient winter survey data, it is important to evaluate the temporal range of predictions from the summer habitat models, particularly in a temporally dynamic environment. Broad-scale seasonal migratory patterns of many of the large whale species have been described (e.g. Calambokidis et al. 2000, 2009, Swartz et al. 2006, Barlow et al. 2011), and although pronounced seasonal distribution shifts of small cetaceans have been identified (Dohl et al. 1986, Green et al. 1992, 1993, Forney & Barlow 1998), they are typically not as well understood and may vary considerably from year to year.

Although the physical processes responsible for variation in local oceanographic conditions differ on seasonal (Reid et al. 1958, Barber & Smith 1981, Lynn & Simpson 1987), interannual (Barber & Chavez 1983, Schwing et al. 2000), and inter-decadal (McGowan et al. 1998, Mantua & Hare 2002) time scales, effects on sea surface temperature and other variables are similar (Chavez et al. 2003). If interannual variability in oceanographic conditions during summer is of a similar order of magnitude to seasonal variation, then it might be possible to predict winter population densities for cetacean species that are not highly migratory based on multi-year summer models and remotely sensed oceanographic data for the winter period. Predictive cetacean models primarily have been developed using habitat data that were collected *in situ*, but Becker et al. (2010) found that satellite-derived measures of sea surface temperature (SST) can be effective predictors of cetacean density, thus offering a means of predicting cetacean density and distribution when only remotely sensed environmental data are available.

In this study, we developed generalized additive models (GAMs; Hastie & Tibshirani 1990) to relate cetacean sighting data from shipboard surveys in the CCE during the summers of 1991 to 2008 to remotely sensed SST and static predictor variables. The resulting models were then used to predict cetacean distribution patterns based on remotely sensed environmental data for winter and spring 1991/92, a period when aerial surveys were conducted within a portion of the study area off California. Models were built for 3 small cetacean species and 1 genus that are known to be present year-round and had sufficient sightings during the winter aerial surveys to evaluate the habitat-based density models. The 3 small cetacean species are: Pacific white-sided dolphin *Lagenorhynchus obliquidens*,

northern right whale dolphin *Lissodelphis borealis*, and Dall's porpoise *Phocoenoides dalli*. Short-beaked common dolphins *Delphinus delphis* and long-beaked common dolphins *D. capensis* have similar pigmentation and morphology (Rosel et al. 1994), and were recorded only as *Delphinus* sp. during the aerial surveys (Forney et al. 1995, Forney & Barlow 1998), so the present analysis was conducted for the genus.

The aerial survey data were used to evaluate whether models constructed for summer using the extensive shipboard sighting data could predict broad distribution and density patterns during the winter period. This approach provided the advantages of a robust dataset for model construction (the shipboard data) and a test dataset during a different season for evaluation (the aerial survey data). The purpose of this study was to assess whether species–environment models developed using shipboard survey data collected during summer improve our ability to predict cetacean density for winter as compared to a 'null' model (i.e. density estimates derived from summer shipboard surveys without consideration of environmental data). Results are examined in light of known cetacean distribution patterns documented from previous California cetacean–habitat studies.

METHODS

Field methods

SWFSC US west coast shipboard surveys

Cetacean sighting data used to construct the predictive models were collected off the US west coast by SWFSC during the summer and fall (July through early December) of 1991, 1993, 1996, 2001, 2005, and 2008 using systematic line-transect methods (Buckland et al. 2001). Barlow & Forney (2007) provided detailed descriptions of the survey methods. The amount of survey effort varied among years, but transect coverage was roughly uniform throughout the study area (Fig. 1), and cetacean data collection procedures were consistent across all surveys (Kinzey et al. 2000, Barlow 2010). During daylight hours, 2 observers used pedestal-mounted 25×150 binoculars to search for marine mammals from the flying bridge of the ship. A third observer searched by eye or with 7× handheld

binoculars and recorded both sightings and survey conditions. When cetaceans were detected, the ship typically diverted from the transect line to estimate group size and identify the species present. All cetaceans sighted were identified to the lowest taxonomic level possible. To build the shipboard models, we used approximately 66 709 km of on-effort survey data (Fig. 1) collected in Beaufort sea states of 5 or lower.

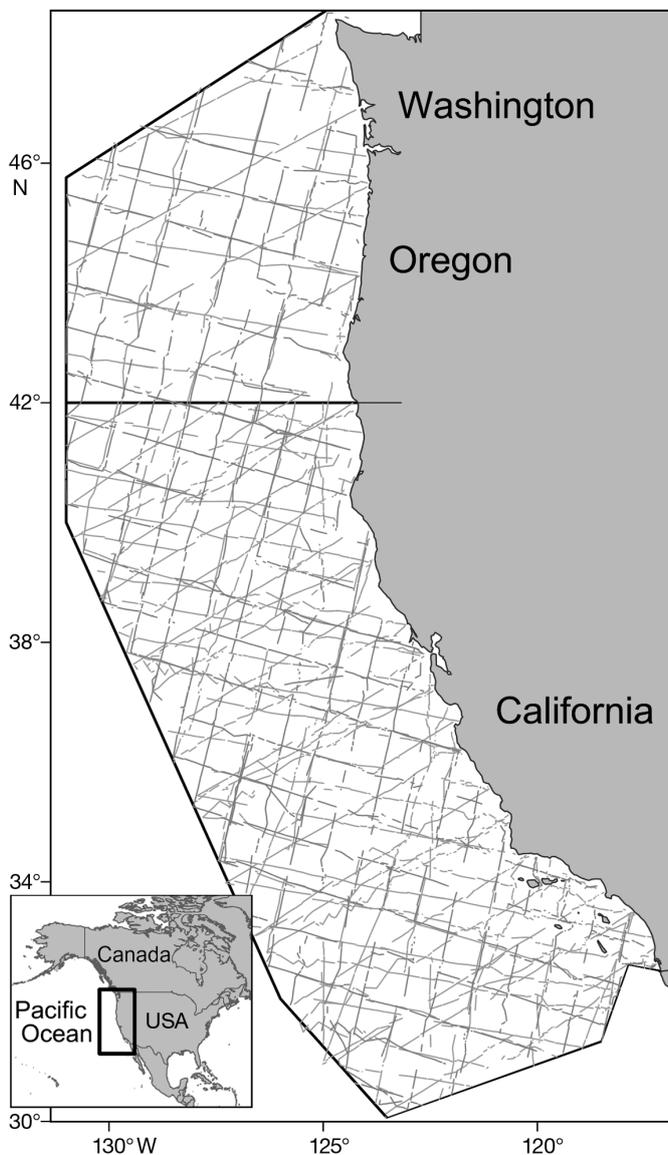


Fig. 1. Completed transects for the systematic shipboard surveys conducted during late July through early December 1991, 1993, 1996, 2001, 2005, and 2008 off the US west coast in Beaufort sea states of 0 to 5. The black line represents the boundary of the US west coast study area, with the horizontal division indicating the northern extent of the California study area. One degree of latitude = 111 km

SWFSC California aerial surveys

Cetacean sighting data were collected during aerial surveys conducted by SWFSC off California in March to April 1991 and February to April 1992. Detailed descriptions of aerial survey field methods have been published previously (Carretta & Forney 1993, Forney et al. 1995, Forney & Barlow 1998), and pertinent aspects are summarized here. The transects followed 2 overlapping grids designed to survey systematically along the entire California coast out to 185 km off central and northern California and 278 km off southern California (Fig. 2), encompassing approximately 264 000 km² of the nearshore portion of the shipboard study area off California. Aircraft were outfitted with 2 bubble windows for unobstructed lateral viewing and a belly port for downward viewing. The survey team consisted of 3 observers: 2 primary observers who searched through the left and right bubble windows and a secondary observer who used the belly window to search the trackline and report sightings missed by the primary team. In addition, a data recorder positioned next to the pilot recorded

sighting information and environmental conditions using a laptop computer connected to the aircraft's navigation system. When cetaceans were sighted, the aircraft circled over the animals to allow observers to identify species and estimate group size. Any additional sightings made after the aircraft had diverted from the trackline were not included in the present analysis.

Analytical methods

We examined the across-season predictive ability of the GAMs using a 2-step process in which (1) species-habitat models were constructed using the summer shipboard sighting data and associated environmental variables, and (2) the resulting models were used to predict cetacean encounter rates, group sizes, and densities based on environmental conditions during the winter aerial survey period. To create samples for modeling, cetacean survey data from the 6 shipboard surveys were separated into continuous transect segments of approximately 5 km length as described by Becker et al. (2010). The 5 km length was selected because the study area is characterized by strong cross-shore gradients (Palacios et al. 2006), and we wanted to be able to capture this variability in the static predictors. Following the guidelines of Buckland et al. (2001), sighting data were truncated at 3.3 km for the delphinids and 2.2 km for Dall's porpoise (Barlow 2003) to eliminate the most distant groups observed.

Species-specific sighting information (number of encounters, mean group size) and environmental data were assigned to each segment based on the segment's geographical midpoint. Environmental data included as potential predictor variables in the models were: satellite-derived estimates of SST, water depth, bathymetric slope, aspect (i.e. slope direction), and distance to the 200 m isobath. The 200 m isobath represents the shelf break for many areas of the California coast, and is a potentially important habitat feature for the species considered in the present analysis (Barlow et al. 2009, Becker et al. 2010, Forney et al. 2012). Bathymetric variables were derived from ETOPO1 (Amante & Eakins 2009), a 1 arc-minute global-relief model; we used negative values of the distance to the 200 m isobath in waters shallower than 200 m to differentiate shelf from slope waters. Slope and aspect were calculated using ArcGIS Spatial Analyst (Version 10.1, ESRI).

Satellite-based SST data derived using optimal interpolation methods (Reynolds & Smith 1994) were

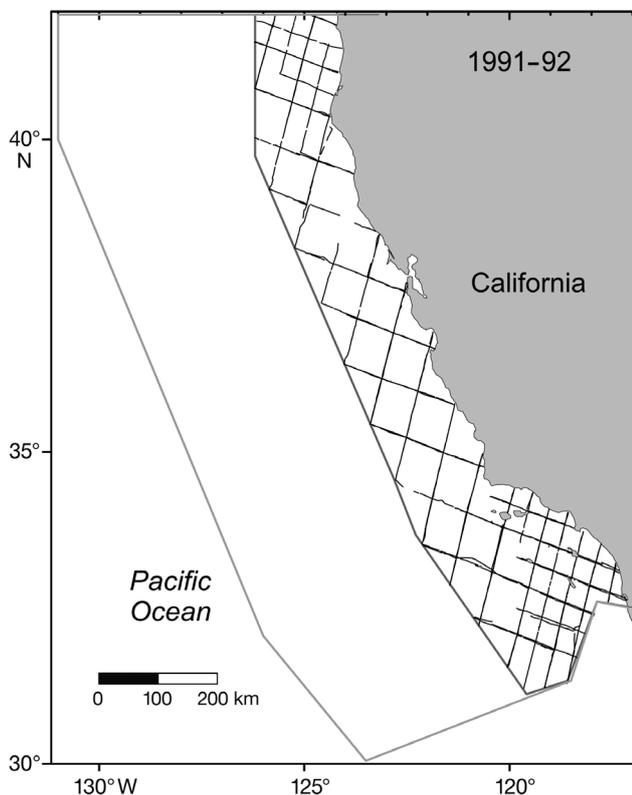


Fig. 2. Completed transects for the systematic aerial surveys conducted off California in March to April 1991 and February to April 1992. The light gray line west and offshore of the aerial study area marks the extent of the shipboard study area off California

used in the models as they provide a daily, gap-free SST product at 25 km spatial resolution (Reynolds et al. 2007). These ‘blended’ SST data combine *in situ* and infrared sensor measurements to virtually eliminate data gaps due to cloud cover, and have been used successfully in habitat-based density models for cetaceans (Becker et al. 2012a).

Average sea state (measured on the Beaufort scale) for each segment was included as a continuous predictor variable in our models to account for the variability in sighting conditions (Barlow et al. 2001), but segments with average sea state values exceeding Beaufort 5 were excluded from the analysis because small cetaceans cannot reliably be detected in sea states above Beaufort 5 (Barlow & Forney 2007). Although conventional line-transect analyses have generally restricted the analyses for Dall’s porpoise, the most cryptic species in this study, to include only calm conditions (Beaufort sea states 0–2; Barlow 2003, 2010, Barlow & Forney 2007), we included sea states up to Beaufort 5 when developing the habitat-based models because the limited segments with calm conditions did not cover the full range of habitats for Dall’s porpoise in the study area. For all species, sea state was included as a predictor variable within the models to account for detection differences.

Model structure and development

Detailed descriptions of the model-building process can be found in Barlow et al. (2009), Becker et al. (2010), and Forney et al. (2012); pertinent information is briefly summarized here. For each species/genus, we used GAMs to relate encounter rate (number of sightings) and group size to the habitat variables described above. The encounter rate and group size GAMs were built using the *step.gam* function in S+ (Version 8.2 for Windows, Tibco Software). We developed Poisson GAMs, in which overdispersion was corrected using a quasi-likelihood model, to fit the number of sightings for a given segment. Although the target segment length for modeling was 5 km, actual segment length varied slightly (see Becker et al. 2010); therefore, segment length was included as an offset term in the models to standardize each sample for effort. Group size models were built using the natural log of group size as the response variable and an identity link function, following the methods of Ferguson et al. (2006). Group size models were built using only those segments that contained sightings.

We used a stepwise forward/backward variable selection procedure in which each model was fit 3 times to ensure that all terms were tested and to improve the dispersion parameter estimate used to assess the final model (Ferguson et al. 2006). Akaike’s information criterion (Akaike 1973) was used in *step.gam* as the basis for selecting the variables and degrees of freedom for the cubic smoothing splines in each model. A maximum of 3 degrees of freedom in our smoothing splines was specified to capture non-linear relationships without adding unrealistic complexity to the functions (Forney 2000, Ferguson et al. 2006). We used the percentage of explained deviance to assess model fit and ratios of observed to predicted animals to assess the accuracy of the within-season (summer) predictions. Previous studies using these survey data and similar methods have validated the summer models using cross validation (Barlow et al. 2009, Becker et al. 2010, Forney et al. 2012), predictions on novel data sets (Barlow et al. 2009, Becker et al. 2012a, Forney et al. 2012), and expert opinion (Barlow et al. 2009, Becker et al. 2012b, Forney et al. 2012).

Density (D , ind. km⁻²) for each species was estimated by incorporating the final encounter rate and group size model results into the standard line-transect equation (Buckland et al. 2001):

$$D = \left(\frac{n}{L}\right) \times s \times \frac{1}{2 \times \text{ESW} \times g(0)} \quad (1)$$

where n/L is the predicted encounter rate (number of sightings per unit length of trackline in km), s is the predicted group size, ESW is the effective strip half-width in km, or $1/f(0)$ where $f(0)$ is the probability density function evaluated at 0 perpendicular distance (i.e. on the trackline), and $g(0)$ is the probability of detecting a group of animals on the trackline. We relied on published values of $f(0)$ (or ESW) and $g(0)$ for each species as estimated from a portion of the same summer survey data (Barlow 2003) and the specific winter survey data (Forney & Barlow 1998). For the delphinids, published $f(0)$ and $g(0)$ values were stratified by group size and, therefore, we weighted $f(0)$ and $g(0)$ values based on the number of small and large groups observed during the surveys for our density calculations. To account for potential seasonal differences in group size in our density estimates, the weighted correction factors were derived separately for each season for the entire study area, based on observed group sizes for all years pooled for the respective season. For Dall’s porpoise, published $f(0)$ and $g(0)$ values were available only for Beaufort conditions of 0 to 2. The appli-

cation of these $f(0)$ and $g(0)$ values in our study, which included sea states of 0 to 5, resulted in a downward bias in our density estimates for this species, but allows relative comparisons among seasons.

The segment-specific density predictions from the models were interpolated to the entire study area using inverse distance weighting as described by Becker et al. (2010). This weighting method gives points closer to each grid node greater influence than those farther away, and has been used in similar habitat-based density modeling studies (Ferguson et al. 2006, Barlow et al. 2009, Becker et al. 2012a,b, Forney et al. 2012). Grids were created for each of the 6 ship survey years, and the individual grid cells were averaged across all years to calculate mean species density and its interannual variance. Interannual variability in population density due to movement of animals within or outside of the study areas has been determined to be the greatest source of uncertainty in these models (Barlow et al. 2009, Forney et al. 2012), and we focused on this source of uncertainty to produce approximate estimates of variance and log-normal 90% confidence intervals for the summer spatial density estimates.

Evaluation of model predictive ability

Three different approaches were used to evaluate the between-season predictive ability of our summer models: (1) a nonparametric Spearman rank correlation test, (2) visual inspection of the observed winter sighting locations relative to the model-predicted density patterns, and (3) a comparison of the modeled density estimates to those derived from standard line-transect analyses ('observed densities') within the study area. For the correlation test, predictive ability was based on a comparison of the models' ranked predicted values across 6 geographic strata to those derived from the actual survey data for each species' encounter rate, group size, and density. To enable a rank analysis, we stratified the study area into 6 regions (Fig. 3). Point Arguello was selected as the dividing line between the northern and southern strata because the Point Arguello/Point Conception region is a known biogeographic boundary, marking the range limits of many marine species (Valentine 1973, Briggs 1974, Newman 1979, Doyle 1985). The northern and southern regions were further stratified roughly by water depth: shelf = waters from the coast to 200 m deep; slope = waters between 200 and 2000 m deep; and abyssal plain = waters deeper than 2000 m. Visual inspection of survey effort plots con-

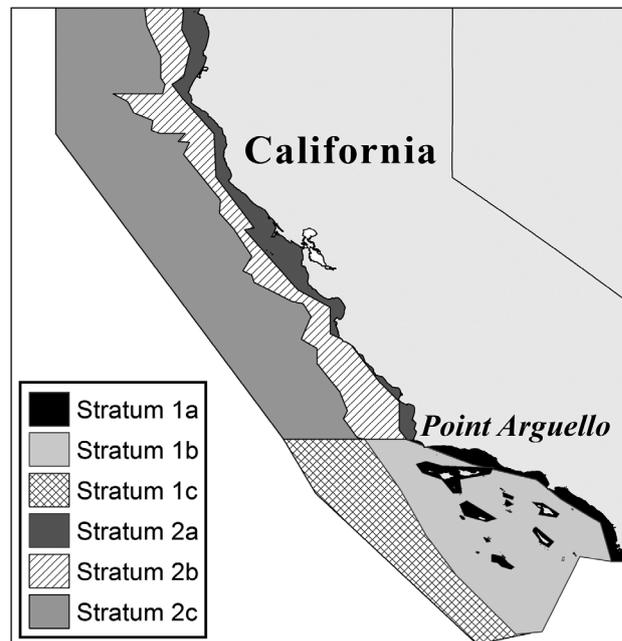


Fig. 3. Geographic strata used for the Spearman rank correlation tests

firmed that effort was relatively uniform within each stratum (i.e. to reduce potential bias resulting from concentrated effort in a portion of a stratum). Results from the Spearman rank correlation tests were compared to results obtained from a 'null' model, defined as the density derived from summer shipboard surveys without consideration of environmental data.

In addition to the rank correlation tests, the between-season predictive power of the summer models was evaluated using ratios of observed to predicted species abundance and comparisons of the predicted values to 95% confidence intervals of the observed values. The mean observed abundances were derived using line-transect analyses (Forney et al. 1995, Forney & Barlow 1998), and although these estimates are not necessarily unbiased, they are currently the standard measure used to estimate cetacean abundance. Bootstrap 95% confidence intervals were recalculated from the original line-transect analysis (Forney et al. 1995) using the BC_a method described by Efron & Tibshirani (1993) that allows for bias correction and acceleration.

Some differences in platform-specific biases deserve consideration when comparing densities estimated from aerial and shipboard survey data. The magnitude of availability bias (Marsh & Sinclair 1989) for all species is more important during aerial than shipboard surveys, given the shorter time that any given part of the ocean is in view (Forney &

Barlow 1998). During a shipboard survey, availability bias is minimal for the species considered in this analysis and almost negligible for *Delphinus* spp. that typically occur in large groups. Conversely, during aerial surveys, availability bias is likely for all species considered here, although it is considered to be relatively small for *Delphinus* spp. (Forney & Barlow 1998). Correction factors for perception bias (Marsh & Sinclair 1989) from the aerial surveys are available for the 4 taxa considered here; however, estimates of availability bias were made only for Dall's porpoise (Forney & Barlow 1998). The aerial survey abundance estimates for winter are thus expected to be biased low for Pacific white-sided dolphin and northern right whale dolphin.

To further evaluate the models' predictive ability, density estimates for each segment were smoothed on a grid resolution of approximately 25 km, and the resultant predictions of distribution and density were visually compared with actual sightings made during the winter aerial surveys. Smoothing was done using inverse distance weighting interpolation as described in the previous subsection for the modeled summer density estimates. The human eye is often superior to statistics for comparing patterns (Wang et al. 2004), particularly in data-limited cases where more advanced spatial methods cannot be used, and this approach provided a means to visually evaluate the models' between-season predictive power.

RESULTS

Barlow (2010) provided information on the search effort, number of species sighted, and associated line-transect abundance estimates for the 1991 to 2008 shipboard surveys. Similar information on the 1991 to 1992 aerial surveys was provided by Forney et al. (1995) and Forney & Barlow (1998). Our analysis included 1 warm-temperate/tropical genus (common dolphin) and 3 cold-temperate species (Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise), all known to be present year-round off California but exhibiting significant seasonal differences in abundance and/or distribution (Forney & Barlow 1998).

Summer models

For all taxa, the habitat relationships included in the final encounter rate GAMs built with the summer

shipboard data were similar to those observed in previous studies (Table 1, Fig. 4; Barlow et al. 2009, Becker et al. 2010, 2012b, Forney et al. 2012). Encounters with common dolphin were highest in the warmest waters in the study area, with encounters dropping substantially in water temperatures below about 16°C (Fig. 4a). A bimodal depth distribution was evident in the encounter rate GAM for common dolphin, with fewest encounters in waters approximately 2000 to 3000 m deep. The encounter rate models for Pacific white-sided dolphin and northern right whale dolphin were similar, both showing highest encounters in cooler waters over the continental shelf and slope, with a substantial drop in encounters in water temperatures greater than about 16°C (Fig. 4b,c). Highest encounters of Dall's porpoise occurred in cool northern shelf and slope waters, with encounters dropping substantially in water temperatures greater than approximately 17°C (Fig. 4d).

The percentage of deviance explained by both the encounter rate and group size models was similar to previous studies (Barlow et al. 2009, Becker et al. 2010, 2012b, Forney et al. 2012). The percentage of deviance explained by the encounter rate models ranged from 15% (northern right whale dolphin) to 34% (Dall's porpoise) and from 2% (common dolphins) to 30% (northern right whale dolphin) for the group size models (Table 2). Ratios of observed to predicted abundance summarized over all years for the entire study area indicate that the summer models accurately predicted the abundance of these 4 species during the summer season, as all ratios were within 3% of unity (Table 2).

Across-season predictive ability of summer models

Rank correlation tests

Despite the relatively high percentage of explained deviance for the Pacific white-sided dolphin and northern right whale dolphin group size models (29 and 30%, respectively), they were not effective at predicting spatial variability in group size during the winter, as indicated by the rank correlation test (Table 3). Conversely, the encounter rate model predictions for all species except northern right whale dolphin were better than the null model, and this difference was significant ($p < 0.05$) for both common dolphins and Dall's porpoise.

The summer models' ability to predict winter densities across geographic strata exceeded that of the

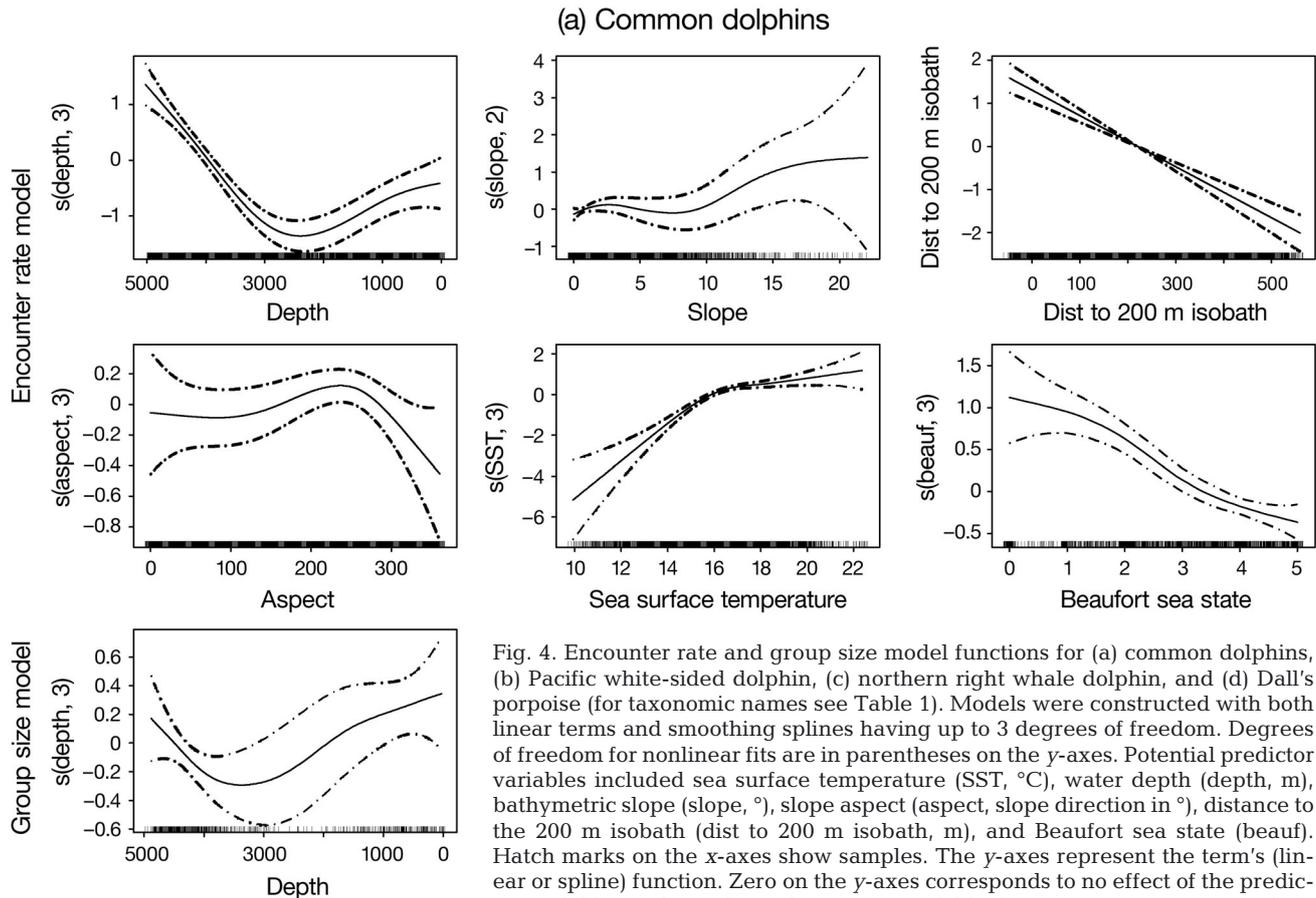


Fig. 4. Encounter rate and group size model functions for (a) common dolphins, (b) Pacific white-sided dolphin, (c) northern right whale dolphin, and (d) Dall's porpoise (for taxonomic names see Table 1). Models were constructed with both linear terms and smoothing splines having up to 3 degrees of freedom. Degrees of freedom for nonlinear fits are in parentheses on the y-axes. Potential predictor variables included sea surface temperature (SST, °C), water depth (depth, m), bathymetric slope (slope, °), slope aspect (aspect, slope direction in °), distance to the 200 m isobath (dist to 200 m isobath, m), and Beaufort sea state (beauf). Hatch marks on the x-axes show samples. The y-axes represent the term's (linear or spline) function. Zero on the y-axes corresponds to no effect of the predictor variable on the estimated response variable (encounter rate or group size). Scaling of y-axis varies among predictor variables to emphasize model fit. The dashed lines reflect 2× standard error bands (i.e. 95% confidence interval)

null model for 3 of the 4 taxa (common dolphins, northern right whale dolphin, and Dall's porpoise). For both the common dolphin and Dall's porpoise models, their ability to effectively predict spatial density patterns in winter was significantly better than the null model ($p < 0.05$; Table 3).

Visual inspection of density plots

Visual comparisons of predicted winter densities versus observed sightings from the aerial surveys suggest that the predictions were better than indicated by the coarse-scale rank correlation tests, as

Table 1. Predictor variables included in the final encounter rate (ER) and group size (GS) models for the 1991 to 2008 summer/fall survey data. The expression $s(x, n)$ indicates a non-parametric smoothing spline of the variable x with n degrees of freedom. GAM: generalized additive model, SST: sea surface temperature, depth: water depth, slope: bathymetric slope, aspect: slope aspect, dist200: distance to the 200 m isobath, beauf: Beaufort sea state, offset: $\text{offset}[\ln(\text{effective distance searched in km})]$

Species	Model	GAM
Common dolphins <i>Delphinus spp.</i>	ER	$s(\text{depth}, 3) + s(\text{slope}, 2) + \text{dist200} + s(\text{aspect}, 3) + s(\text{SST}, 3) + s(\text{beauf}, 3) + \text{offset}$
	GS	$s(\text{depth}, 3)$
Pacific white-sided dolphin <i>Lagenorhynchus obliquidens</i>	ER	$s(\text{depth}, 3) + \text{dist200} + s(\text{SST}, 3) + s(\text{beauf}, 3) + \text{offset}$
	GS	$s(\text{depth}, 3) + \text{dist200} + s(\text{beauf}, 3)$
Northern right whale dolphin <i>Lissodelphis borealis</i>	ER	$s(\text{depth}, 3) + s(\text{SST}, 3) + s(\text{beauf}, 3) + \text{offset}$
	GS	$s(\text{depth}, 2) + \text{dist200} + \text{aspect} + \text{SST} + s(\text{beauf}, 2)$
Dall's porpoise <i>Phocoenoides dalli</i>	ER	$s(\text{depth}, 3) + s(\text{slope}, 2) + s(\text{dist200}, 3) + s(\text{SST}, 3) + s(\text{beauf}, 3) + \text{offset}$
	GS	$s(\text{slope}, 3) + \text{dist200} + s(\text{SST}, 3) + \text{beauf}$

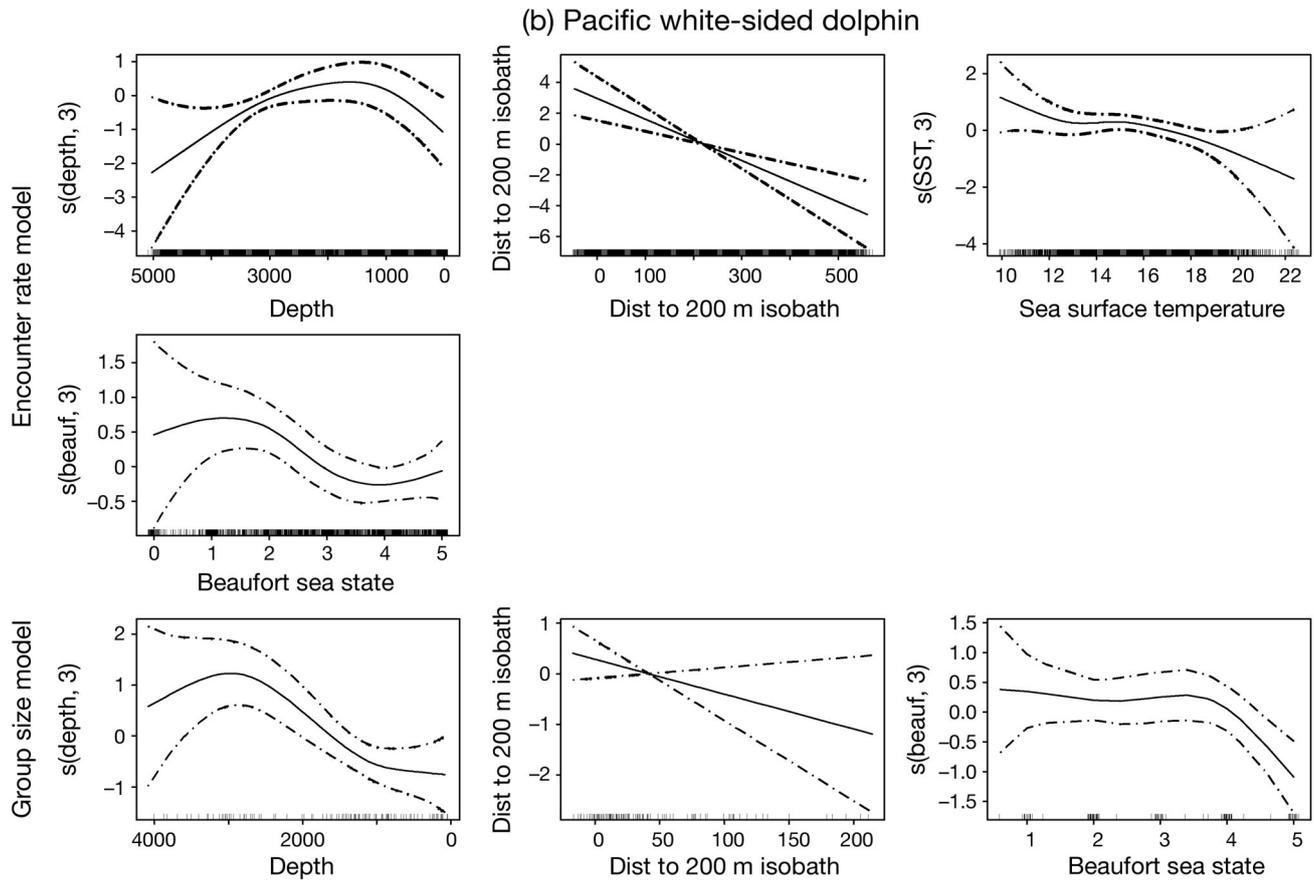


Fig. 4 (continued)

shifts in distribution were captured for all 4 taxa (Fig. 5). Further, for all but northern right whale dolphin, the winter predictions fell largely within the 90% confidence interval (as derived from interannual variability in summer density patterns) of the predictions based on the summer data, suggesting that interannual variability is comparable to seasonal variability for the remaining 3 taxa (Fig. 6).

Table 2. Percentage of deviance explained by the 1991–2008 encounter rate and group size models for each species, and the ratio of the observed to model-predicted study area density estimates for the summer/fall shipboard surveys (Obs/pred). Taxonomic names are given in Table 1

Species	Explained deviance		Obs/ pred
	Encounter rate model	Group size model	
Common dolphins	15.5	2.1	0.97
Pacific white-sided dolphin	23.5	29.1	0.98
Northern right whale dolphin	14.8	29.7	1.01
Dall’s porpoise	33.7	10.8	1.00

Observed:predicted abundance estimates

Winter abundance estimates predicted by the summer habitat models fell within the 95% confidence intervals of the standard line-transect analysis of the winter aerial survey data for all species except northern right whale dolphin, for which the modeled abundance estimate was more than 3 times higher than the line-transect point estimate (Table 4). The modeled abundance estimate for Dall’s porpoise was very similar to that derived using standard line-transect analyses, while the modeled abundance estimates for Pacific white-sided dolphin and common dolphins were lower than the line-transect derived estimates, and for the latter genus substantially so (almost half; Table 4).

DISCUSSION

In this study we evaluated whether summer/fall habitat-based density models developed based on multiple years of survey data can capture enough of

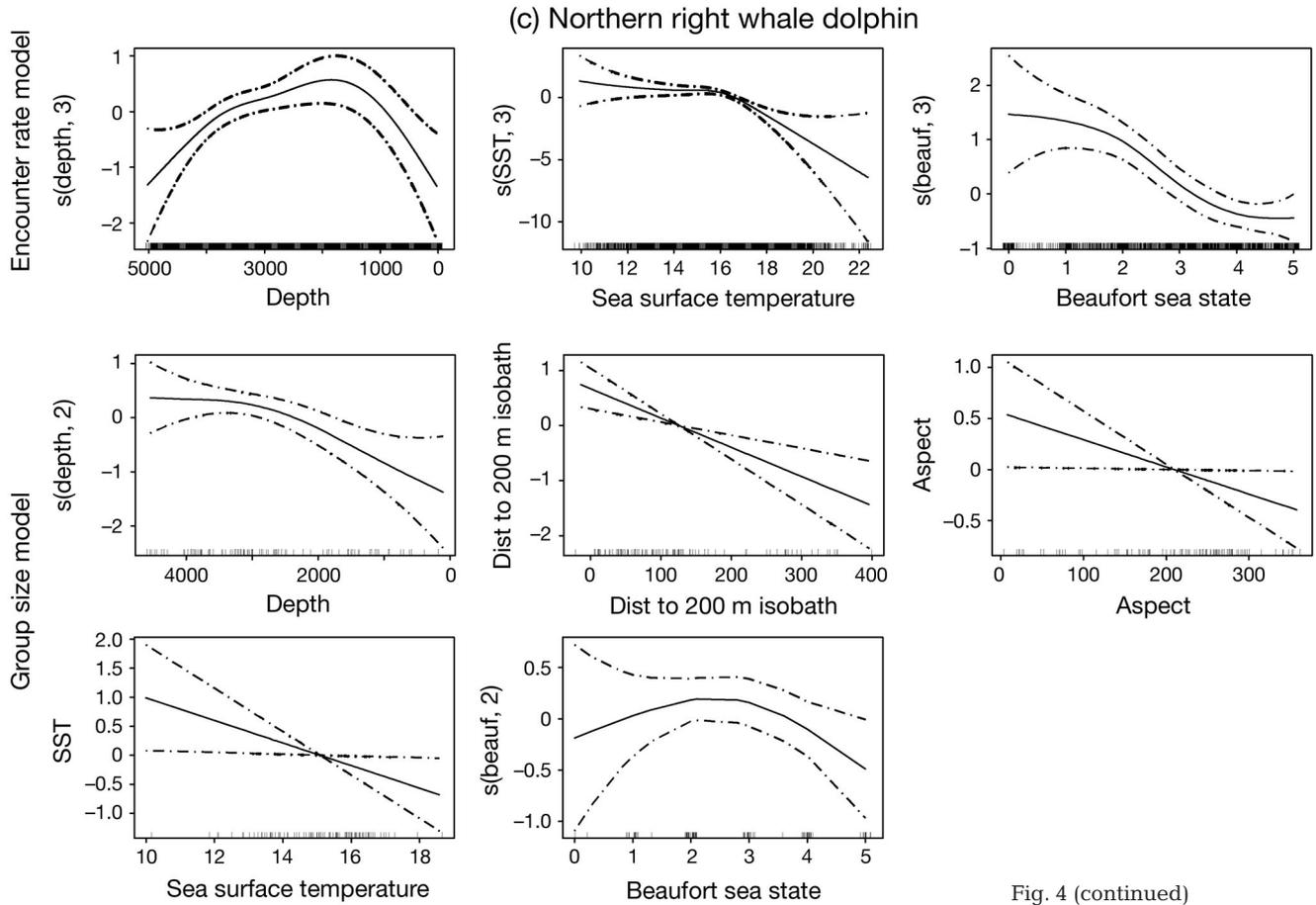


Fig. 4 (continued)

the temporal oceanographic variability to predict species density patterns during winter/spring periods. Based on the nonparametric rank correlation test, individual models for common dolphin, northern right whale dolphin, and Dall's porpoise provided increased ability to predict distribution patterns across seasons, while estimates based on a null model (observations

from the summer shipboard surveys) were better than the model predictions for Pacific white-sided dolphin. However, given the limited sample sizes and 6 geographic data pairs for the correlation test, statistical power is low. Comparisons of predicted densities to observed aerial survey sightings and model-predicted abundance estimates to those derived from standard

line-transect analyses suggest that the predictions were better than indicated by the rank correlation tests (Table 4, Fig. 5). All models showed good model fit (Table 2), emphasizing the importance of testing the explanatory power of a model prior to using it to make predictions on a novel dataset.

Because results varied by species, the models' ability to predict seasonal distribution patterns and capture known species–environment relationships are discussed separately for each species below.

Table 3. Summary of Spearman rank correlation coefficients (r). 'Null' values are those estimated from the summer/fall shipboard surveys using standard line-transect methods in the absence of environmental data. 'Model' values are the generalized additive models built with the summer/fall shipboard data predicting on environmental conditions during the winter/spring survey periods. The critical value at $\alpha = 0.05$ (1-tailed test) with 5 degrees of freedom is $r_{crit} = 0.829$ (i.e. values are significant if larger). Significant correlations are marked with an asterisk (*), and cases for which the model-predicted values did better than the null model are shown in **bold**. Taxonomic names are given in Table 1

Species	Encounter rate		Group size		Density	
	Null	Model	Null	Model	Null	Model
Common dolphins	0.757	0.986*	-0.300	0.443	0.586	0.986*
Pacific white-sided dolphin	0.429	0.486	0.486	-0.086	0.771	0.543
Northern right whale dolphin	-0.414	-0.200	0.414	0.143	0.300	0.314
Dall's porpoise	0.771	0.943*	0.086	-0.029	0.829	0.943*

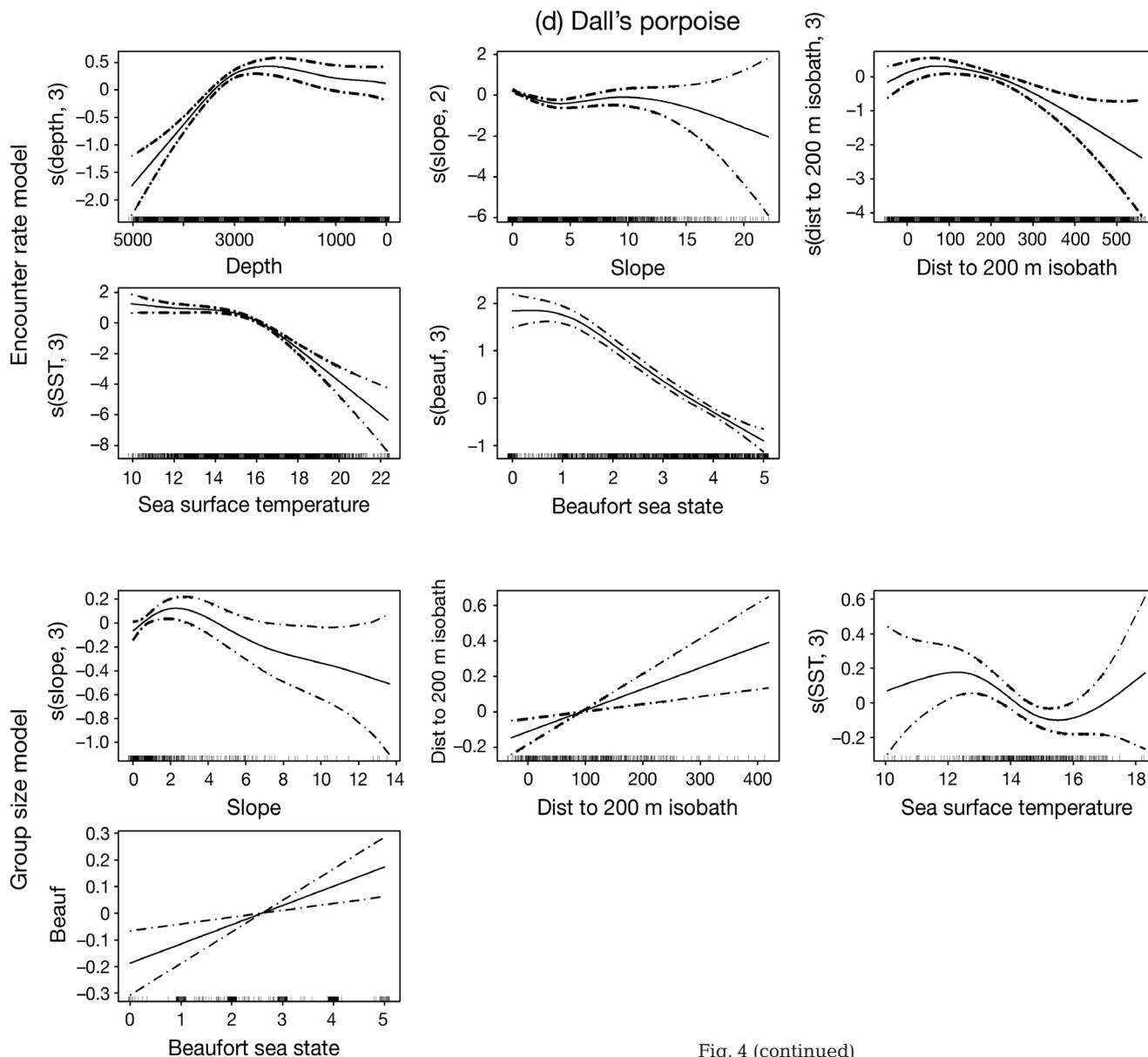


Fig. 4 (continued)

Delphinus spp.

Short-beaked and long-beaked common dolphins could not be reliably distinguished in the aerial surveys (Forney et al. 1995, Forney & Barlow 1998), so the present analysis was limited to the entire genus; however, given the nearshore range of long-beaked common dolphins (Heyning & Perrin 1994), most of the *Delphinus* spp. sightings from the surveys likely were short-beaked common dolphins. Significant seasonal differences in distribution have been documented for common dolphins off California; based on a statistical comparison of numbers of animals north

and south of Point Arguello, and inshore/offshore of the 2000 m isobath, Forney & Barlow (1998) identified a significant inshore/southerly shift in winter.

Predicted:observed density ratios for the total ship study area in summer were consistent with past modeling efforts (Barlow et al. 2009, Becker et al. 2010, 2012b, Forney et al. 2012), indicating within-season model robustness. These summer-based models effectively captured winter density patterns for the 6 geographic strata ($p < 0.05$; Table 3). Visual comparison of the density predictions also indicate that the model was able to identify the inshore and southerly shift in distribution observed during winter

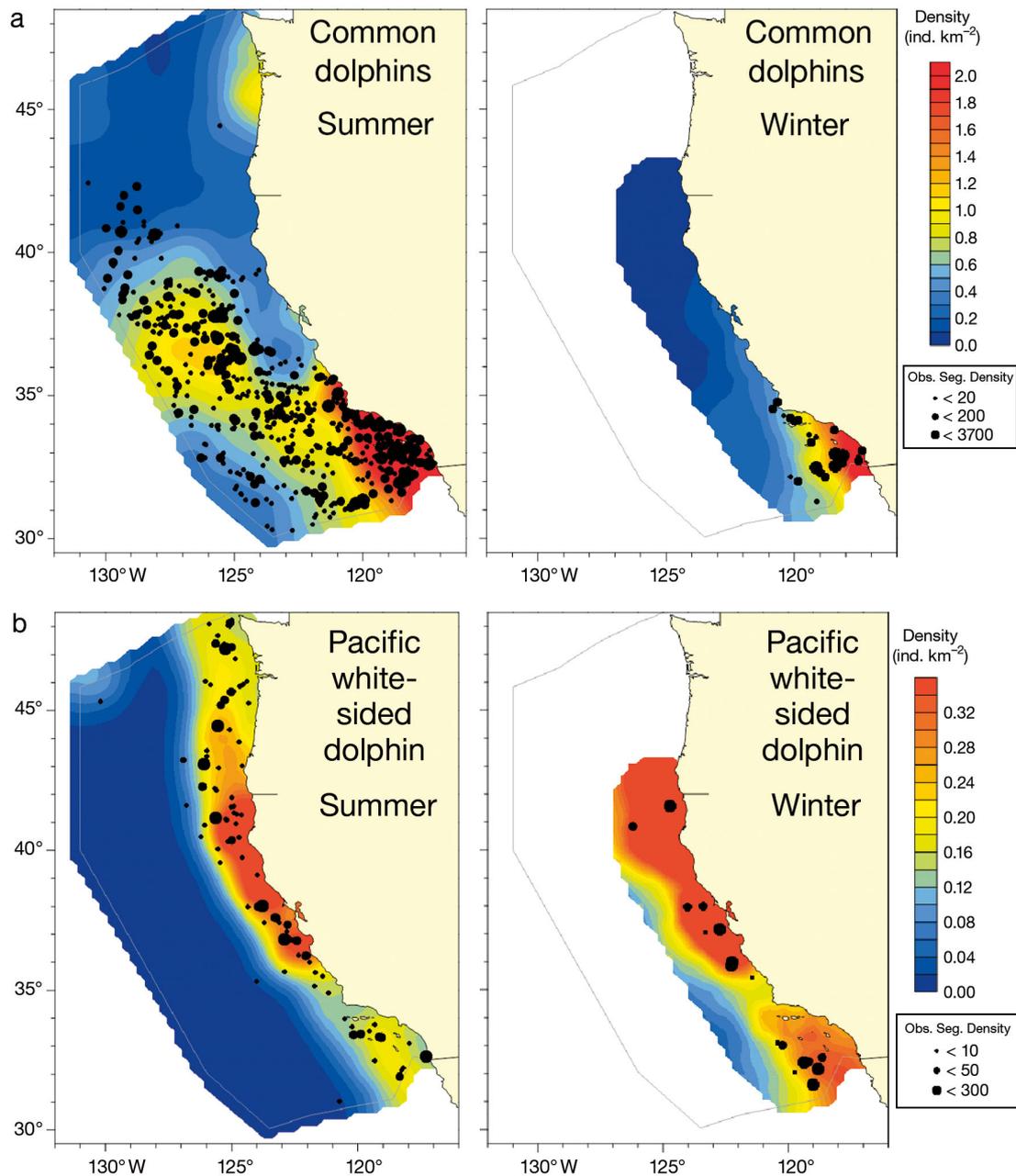


Fig. 5. Predicted densities from the summer/fall shipboard models based on summer/fall environmental data used for model building (left panels) and winter/spring environmental data (right panels), for (a) common dolphins, (b) Pacific white-sided dolphin, (c) northern right whale dolphin, and (d) Dall's porpoise. Predictions are shown for the study area (ship survey study area in left panels and aerial survey study area in right panels). Interpolation grids were created at a resolution of 25 km, using inverse distance weighting to the second power in Surfer software (Version 9). The light gray line west and offshore of the aerial study area (right panels) marks the extent of the shipboard study area. Red (blue) represents highest (lowest) predicted density, as shown in the species-specific density keys. Black dots show actual sighting locations for the summer/fall ship surveys (left panels) and winter/spring aerial surveys (right panels), with larger dots representing more animals per surveyed segment (Obs. Seg. Density). For taxonomic names see Table 1

1991/92, and the model predictions were notably different than those for summer, when *Delphinus* spp. were predicted well north of Point Arguello and farther offshore (Fig. 5a).

The study area abundance of common dolphins during winter, as estimated from model predictions, was about half of that derived from standard line-transect analyses but well within the line-transect

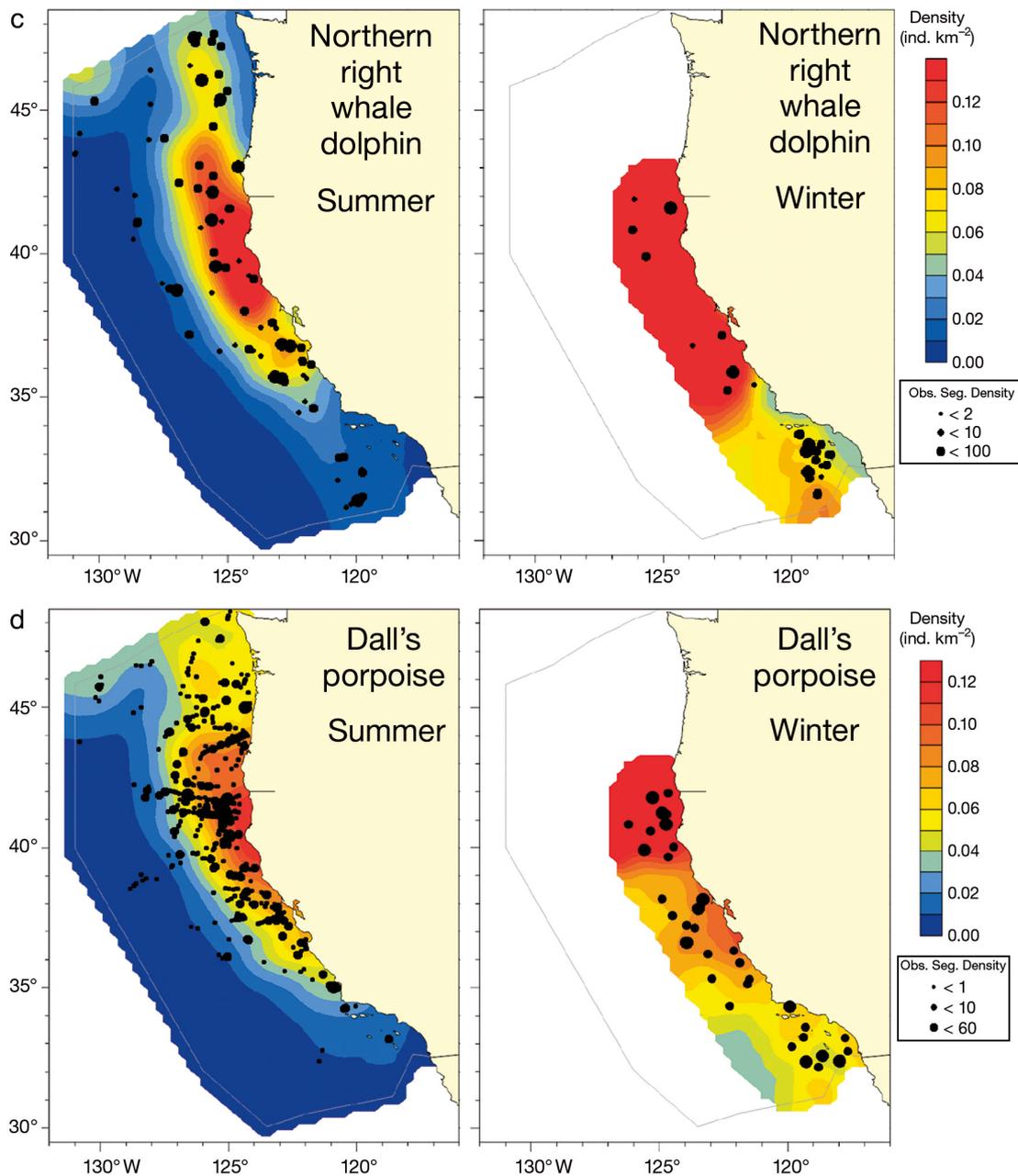


Fig. 5 (continued)

confidence limit (Table 4). Common dolphins typically occur in large groups, and availability bias is expected to be relatively small for the aerial surveys, but this would further increase the difference between the model- and survey-estimated values. The winter aerial surveys were conducted in 1991/92 during an El Niño year, when water temperatures off Southern California were anomalously high (Hayward 1993). Short-beaked common dolphins are a warm temperate to tropical species, and based on the models de-

veloped here as well as in previous studies (Barlow et al. 2009, Becker et al. 2010, 2012b, Forney et al. 2012), densities are greatest when waters are warmest (Figs. 4a & 5a). It is probable that there was a large influx of common dolphins into the study area in winter of 1991/92. The difference in abundance between the model estimate and the line-transect estimate could be caused by uncertainty in both estimates (within confidence limits), or it could be related to a potential El Niño-related influx of animals.

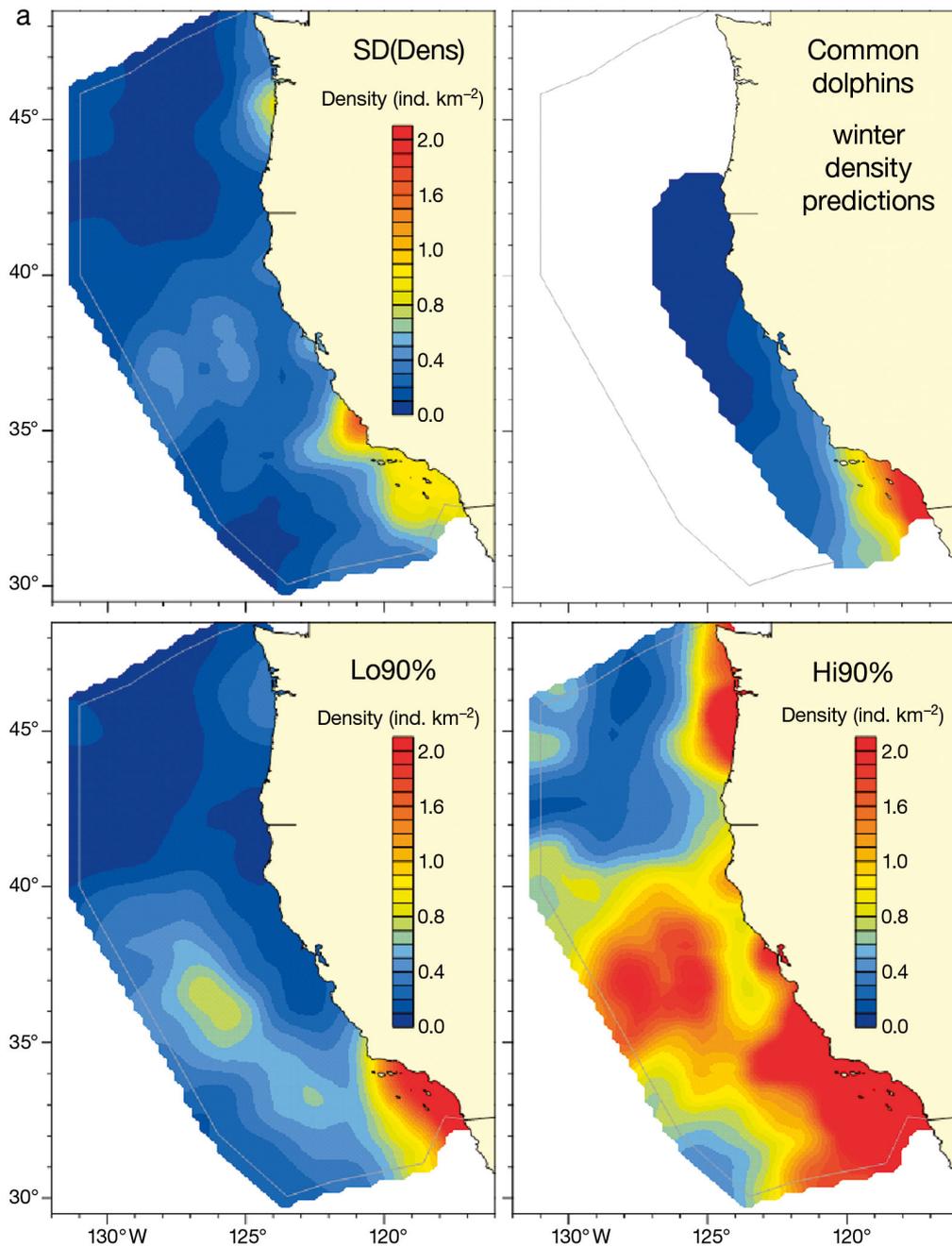


Fig. 6. Standard deviation (SD(Dens)), and upper and lower lognormal 90 % confidence limits (Lo90 % and Hi90 %) based on the summer/fall models predicted on summer environmental data, and winter/spring density predictions for: (a) common dolphins, (b) Pacific white-sided dolphin, (c) northern right whale dolphin, and (d) Dall's porpoise. Predicted values for each survey year were interpolated using inverse distance weighting (see 'Methods' for details). Grid cells for each of the individual survey years were then averaged across all years and SD and upper and lower lognormal 90 % confidence limits were calculated from the grid cell averages and variances using standard formulae. The light gray line marks the extent of the shipboard study area. Red (blue) represents highest (lowest) predicted density, as shown in the species-specific density keys. The density scale for the winter predictions has been scaled relative to the 90 % confidence limits. For taxonomic names see Table 1

The northern extent of short-beaked common dolphin distribution off the US west coast varies on an interannual basis but is generally south of 45° N latitude (Smith et al. 1986, Forney & Barlow 1998,

Hamilton et al. 2009). Interestingly, the average density predictions for summer showed an area of moderate density along the coast at approximately 45° N latitude (Fig. 5a), where, other than strandings

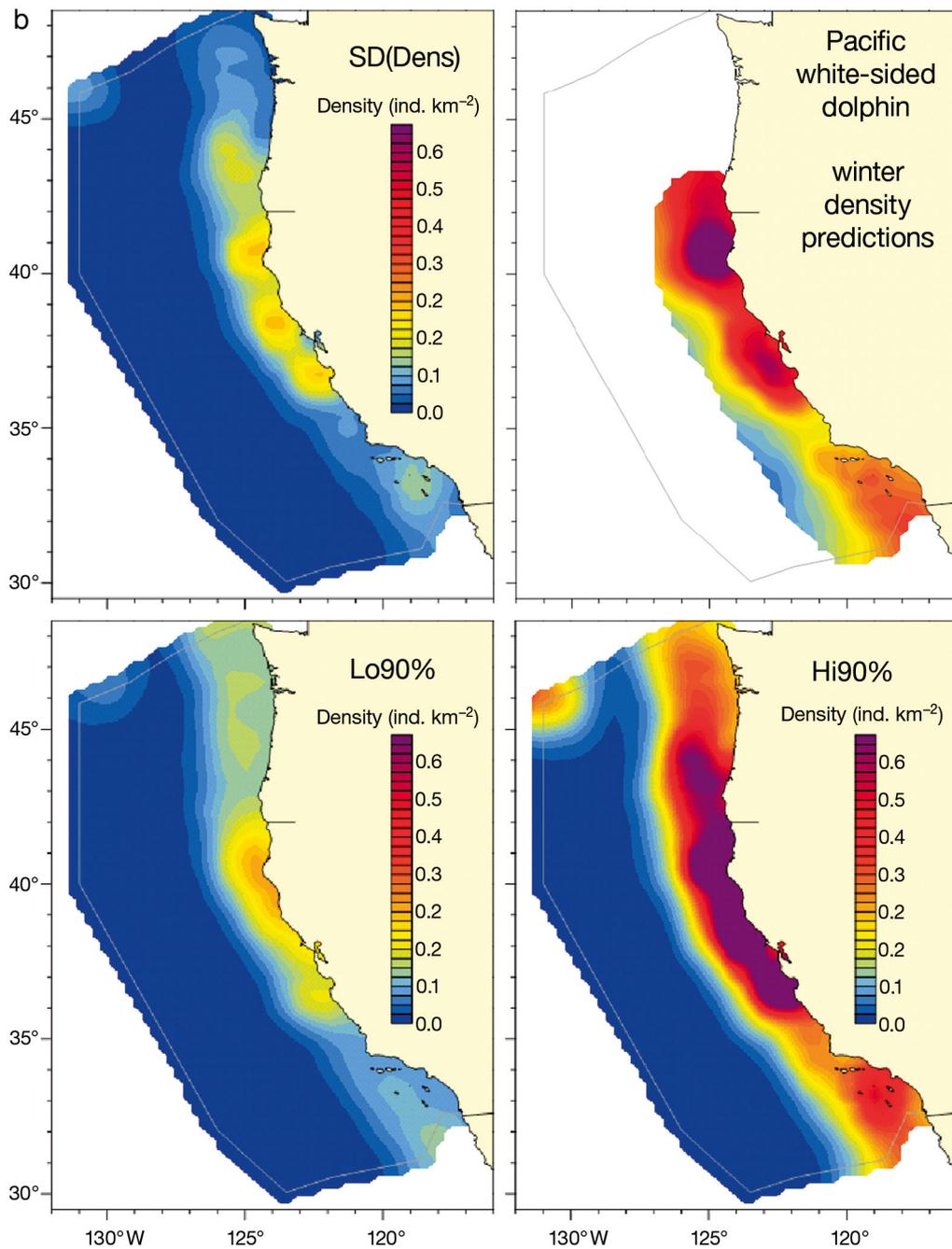


Fig. 6 (continued)

and occasional sightings, this species has not previously been documented (Barlow et al. 2009, Hamilton et al. 2009, Barlow 2010, Becker et al. 2012b, Forney et al. 2012). One group of approximately 40 short-beaked common dolphins was sighted off northern Washington at about 48°N latitude in 2005 (Forney 2007), but this was considered unusual. Short-beaked common dolphins are the most abun-

dant cetacean species off the US west coast (Barlow 2010), and their distribution shifts with changing oceanic conditions (Barlow et al. 2009, Becker et al. 2012b, Forney et al. 2012), but insufficient data are currently available to resolve whether this higher-density region identified by this summer model near 45°N has a biological basis or indicates potential mis-specification of the model.

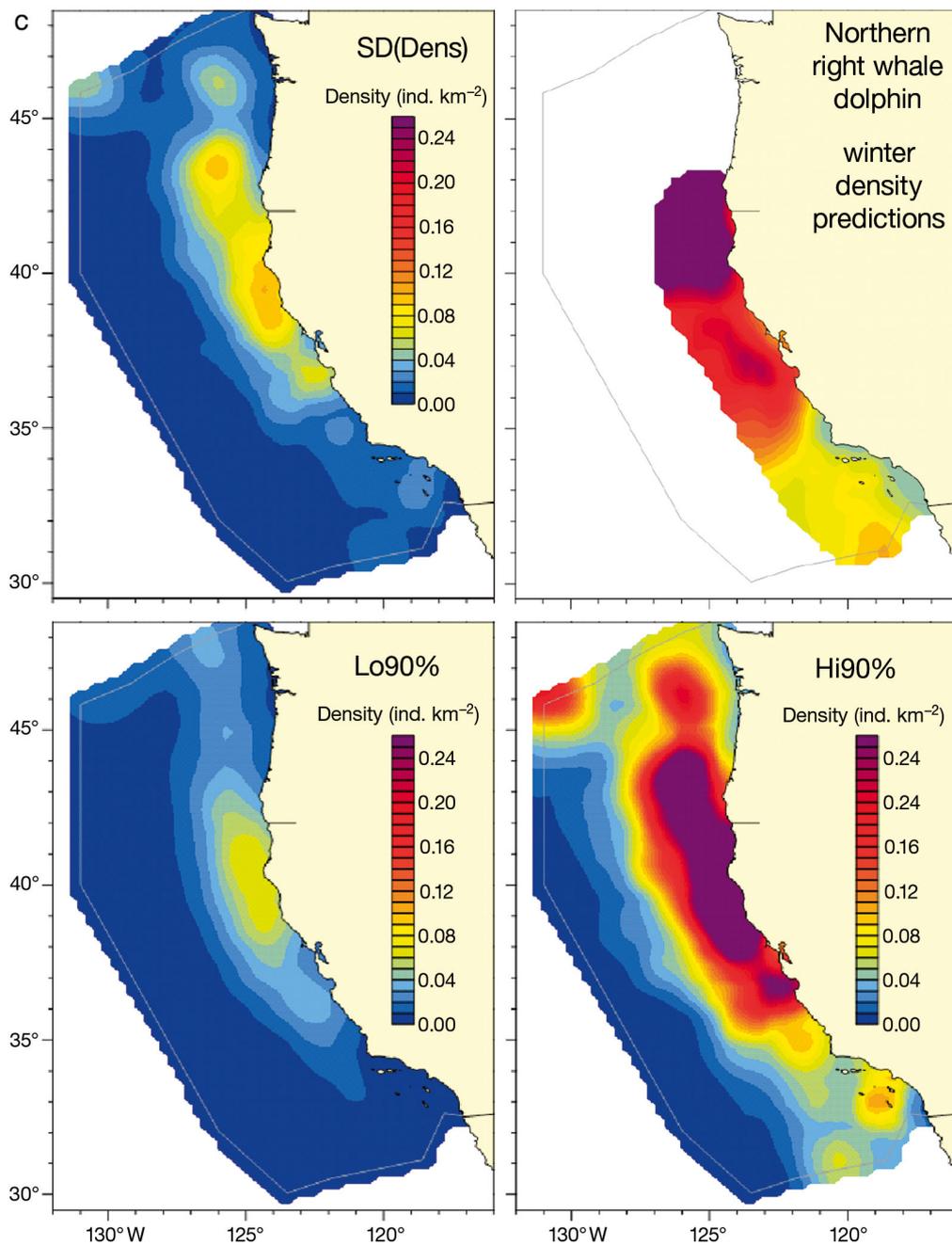


Fig. 6 (continued)

Pacific white-sided dolphin

Based on morphological and genetic evidence, 2 forms of Pacific white-sided dolphin occur in waters off California (Walker et al. 1986, Lux et al. 1997); however, they currently cannot be reliably distinguished in the field and are therefore treated together in the present analysis. Survey data indicate that the seasonal distribution of Pacific white-sided dolphins off the US west coast varies dramati-

cally, as animals move north into waters off Oregon and Washington during the summer months and south into southern California waters during the winter months (Green et al. 1992, Forney & Barlow 1998).

The stratum-specific modeled densities for Pacific white-sided dolphin failed to effectively predict winter density patterns as indicated by the rank correlation tests (Table 3). Visual inspection of the density plots for this species suggest that the mod-

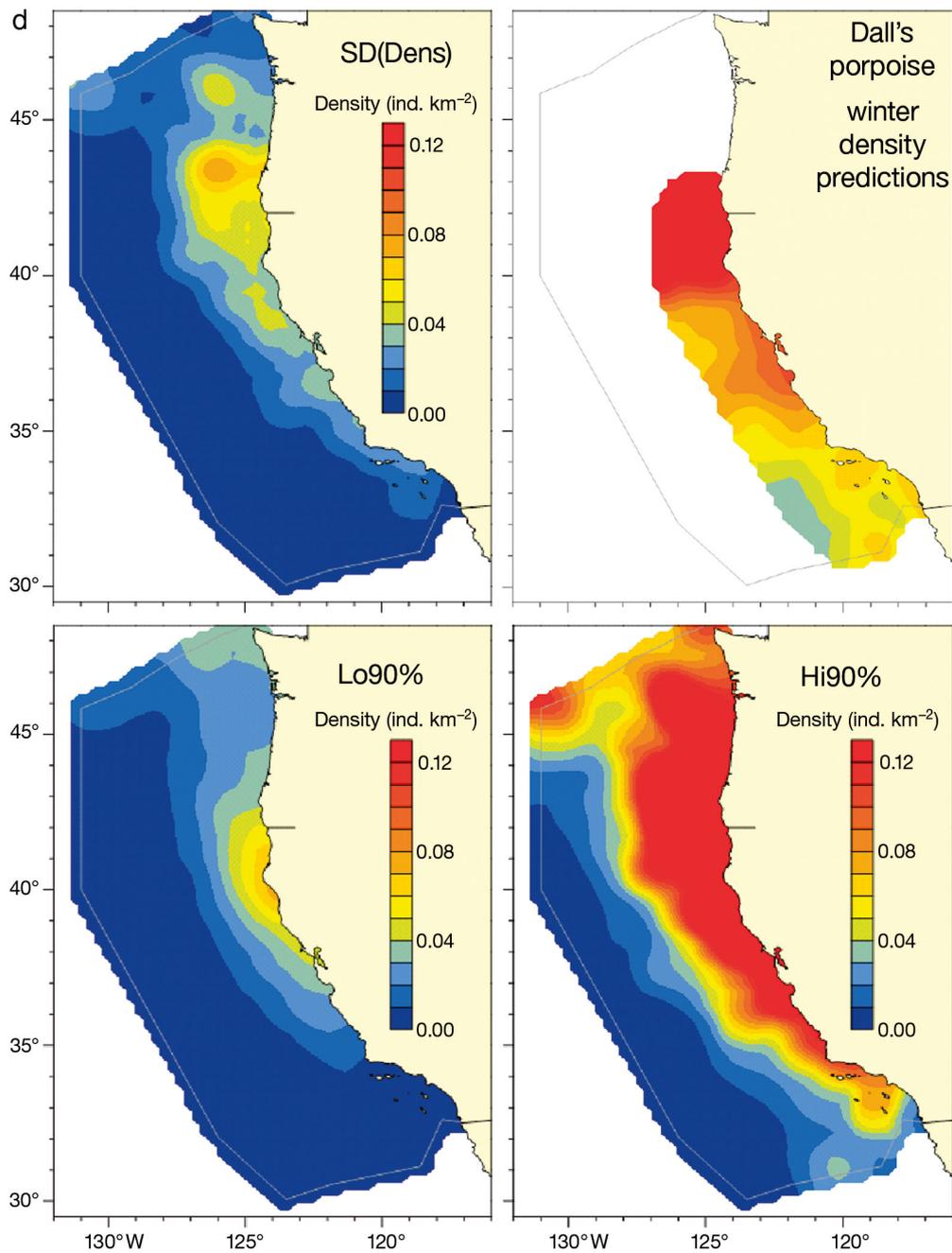


Fig. 6 (continued)

els' predictive ability was better than indicated, however, because greater densities were predicted south of about 33° N latitude, where large numbers of Pacific white-sided dolphins were sighted during the 1991/92 aerial surveys (Fig. 5b). Further, compared to the predicted density patterns in summer, a clear southerly shift in distribution is evident in the winter plot, indicating that the summer-based models more closely match the observed winter patterns.

The estimated winter abundance of Pacific white-sided dolphins based on model predictions was similar to (within 12% of) the estimate derived from standard line-transect analyses (Table 4). A higher proportion of animals is expected to be missed during aerial surveys due to availability bias, so the actual difference may be greater than indicated; however, Pacific white-sided dolphins commonly occur in large, asynchronously diving groups, so the magnitude of the aerial survey availability bias is expected to be small.

Table 4. Modeled abundance estimates (Model) and those derived from survey observations by Forney et al. (1995) using standard line-transect analyses (line-transect). Bootstrap confidence intervals (CIs, shown with lower and upper 95th percentiles) were recalculated from the original line-transect data using the BC_a method (Efron & Tibshirani 1993). Taxonomic names are given in Table 1

Species	Winter abundance estimates		Line-transect bootstrap CIs	
	Model	Line-transect	L95 %	U95 %
Common dolphins	156010	305694	124493	541163
Pacific white-sided dolphin	108338	121693	35625	261931
Northern right whale dolphin	66875	21332	9902	46147
Dall's porpoise	21841	26111	14919	46201

Northern right whale dolphin

Northern right whale dolphin is a cold-temperate species whose distribution shifts south into shelf waters of the Southern California Bight in the winter when waters are relatively cool (Dohl et al. 1978, Leatherwood & Walker 1979, Forney & Barlow 1998). Based on the stratum-specific density estimates, the model predictions were slightly better than those of the null model (Table 3), and visual inspection of the density plots for this species indicate that the model captured the winter distribution shift into shelf waters of the Southern California Bight (Fig. 5c). However, both the spatial range and absolute values of the winter density predictions extend outside the upper 90% confidence interval of the summer model in 2 regions: (1) in the Southern California Bight to the south and southwest of 34° N, and (2) north and northwest of 39° N where the winter plot suggests that the model is overpredicting density (Fig. 6c). This indicates that the range of interannual variability in oceanic conditions encompassed by the summer-based models did not adequately capture winter conditions, particularly for SST, which was a predictor in both the encounter rate and group size GAMs for northern right whale dolphin. Encounter rates and group sizes were predicted to be greatest within the coolest waters in the study area in summer (Fig. 3c); however, during summer the SST values ranged from 9.9 to 22.4°C, while winter SSTs ranged from 8.7 to 17.1°C. The model predictions for SSTs below the range of values observed during summer caused unreliable estimates for winter cool water conditions. This result highlights the need to avoid predicting out of the bounds of the variables used for model development.

Forney & Barlow (1998) identified a statistically significant difference in the abundance of northern right whale dolphin between summer and winter survey

periods off California, with more animals present during the cold water period. The estimated winter abundance of northern right whale dolphin based on model predictions was almost 3 times higher than the estimate derived from standard line-transect analyses, and well above the upper 95% confidence interval (Table 4). A higher proportion of animals is expected to be missed during the aerial surveys due to availability bias; however, it is unlikely that the magnitude of this bias would be large enough to account for the difference in model-predicted versus line-

transect-derived density estimates. The overestimate is likely the result of the models predicting outside the range of values used to build them as noted above. In summary, while the models exhibited some ability to predict seasonal shifts in distribution, more data collected over a range of oceanic conditions are needed to make the models robust and allow them to more accurately predict absolute abundance throughout the study area.

Dall's porpoise

Previous analyses of a portion of the cetacean sighting data used for this study found a statistically significant seasonal difference in the distribution of Dall's porpoise north and south of Point Arguello, documenting a southward shift during winter (Forney & Barlow 1998). The summer model's ability to capture the seasonal distribution shift was significant ($p < 0.05$) as indicated by the rank correlation test (Table 3). Visual comparison of the density predictions also indicate that the model was able to identify the southerly shift in distribution observed during winter 1991/92. Dall's porpoise was predicted to occur well south of Point Arguello, consistent with the winter survey sightings and notably different than the summer distribution pattern in the Southern California Bight (Fig. 5d).

The model-predicted abundance estimate for the winter study area was very similar to that derived from standard line-transect analyses, and well within the 95% confidence interval of the latter (Table 4). Availability bias was accounted for in the line-transect abundance estimate for Dall's porpoise (Forney & Barlow 1998), and this may have contributed to the similarity in estimates derived from the summer model predictions.

Seasonal predictions

In many regions with clearly distinctive seasonal differences (e.g. polar regions), it would not be appropriate to use models built with summer data in an attempt to make winter predictions. Across-season predictions also are not appropriate for highly migratory species, e.g. many baleen whales that are known to be absent from the study area during one season and present in another, unless this migratory pattern is included in the model. Social organization and behavioral aspects of species ecology may also confound the cetacean–habitat modeling approach, particularly when attempting to predict across seasons. In addition, anthropogenic activity may deter animals from preferred habitat, further confounding predictions from habitat models. For species present in an area year-round and known to have pronounced seasonal distribution shifts, the results of this study indicate that spatially explicit habitat models can be valuable tools for assessing species distributions in a temporally dynamic environment, although model accuracy is directly related to the degree to which the models can capture year-round habitat conditions.

A notable difference between our study and an initial evaluation of across-season predictive ability using a subset of these data (Becker 2007) was the number of sightings available to build and evaluate the models. The initial analysis relied on SST satellite data measured from passive infrared sensors (e.g. Pathfinder), which creates data gaps due to cloud cover. In the present study we used a more recent satellite-derived SST product that blends *in situ* and infrared sensor measurements and virtually eliminates data gaps due to cloud cover (Reynolds et al. 2007). On a species-specific basis, this increased the number of summer ship survey sightings available to build the models by up to 54% for the years included in the initial study (1991 to 2001) and increased the number of winter aerial survey sightings used to evaluate the predictions by up to 30%. Further, the present study included 2 additional years of ship survey data (2005 and 2008) and expanded the study area north to include waters off Oregon and Washington, thus including a broader range of environmental conditions for model development. These improvements resulted in more robust models, as demonstrated by the increased explanatory and predictive power of the models.

SST was the only dynamic environmental predictor variable included in the models used in the present study. Remotely sensed measures of chlorophyll could not be included because they were not avail-

able during 1991 to 1996, and satellite-derived salinity measurements have only been available since 2011. Further improvements to across-season predictions may be realized with the inclusion of additional environmental variables, particularly those that provide a more direct link to cetacean prey, such as zooplankton indices currently available from *in situ* data (Redfern et al. 2008, Barlow et al. 2009). Although the use of such predictors may improve model performance, collecting and processing *in situ* oceanographic data requires substantial time and expense, and predictive models that rely on *in situ* data may not be as useful to resource managers who are often required to make timely decisions related to protected species abundance and distribution. For cetacean species that require more complex habitat models that include predictor variables such as mixed layer depth and prey indices (Redfern et al. 2008, Barlow et al. 2009, Becker et al. 2012b, Forney et al. 2012), near real-time and forecast predictions from ocean circulation models (e.g. Chao et al. 2009) may provide a means to improve across-season predictions.

Methodology

Differences in species distribution may arise from variability in the number of groups in a given area or variability in group size, with potentially different environmental factors affecting the 2 parameters. To account for these differences, density estimates are typically derived from separate encounter rate and group size models using appropriate statistical distributions (Ferguson et al. 2006, Redfern et al. 2008, Barlow et al. 2009, Becker et al. 2010, 2012a,b, Forney et al. 2012). For species that typically occur in small groups (e.g. some baleen whales), the number of individual animals can be modeled as a single response variable (e.g. Redfern et al. 2013). Large variability in group size is evident for the delphinids addressed in this study, and hence we developed separate group size models. However, the lack of success in predicting group size in this and other studies (e.g. Ferguson et al. 2006, Redfern et al. 2008) suggests that either we are not including the appropriate environmental variables in our models or there are other non-environmental variables determining group size (e.g. social organization, predator protection, behavioral aspects; Reilly & Fiedler 1994). Future studies should evaluate alternative sampling distributions for modeling encounter rate and group size as a single response variable for species with large group size variability in order to better capture spatial patterns.

Implications for marine spatial planning

Effective pelagic conservation planning requires broad-scale information on species density across space and time, but management is often limited by the lack of data. This study was designed to evaluate the extent to which cross-season predictions might be valid within the CCE, a temporally dynamic environment. Results suggest that, although the processes of interannual and seasonal variability are different, interannual variability in the environmental parameters can be large enough to explain some of the variation in the seasonal distribution patterns of cetaceans in the waters off California. More importantly, models need to be developed using environmental parameters that include the full range of conditions for the temporal/spatial period they are predicting.

Ideally, cetacean survey data would be collected for the specific time period of interest and spatial habitat models built accordingly. However, in most areas cetacean survey data are biased towards summer (Kot et al. 2010). In the absence of actual survey data, results suggest that the seasonal geographic patterns of species density were captured effectively for most species, and demonstrate that there is potential to improve our decision-making through such models, but limitations and caveats must be considered. In this case, for marine planning activities that require an understanding of winter species distribution in order to assess and minimize potential impacts, the across-season predictions are more informative than the complete absence of data or the reliance on summer distribution patterns. In terms of estimating the total number of animals potentially exposed to a given anthropogenic activity, the model-derived density estimates would need to be applied cautiously on a species-by-species basis, with the recognition that in some cases the out-of-bound predictions could produce unrealistic results. For example, since the linear SST function in the group size model for northern right whale dolphins contributed to overpredictions of winter densities, a constant group size estimate could be used in concert with the encounter rate model to eliminate this effect on the density estimates. With the recognition of model limits, habitat-based density models can be valuable tools for assessing species distributions and informing pelagic management decisions.

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