ARTICLE

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Species distribution modeling of deep-diving cetaceans

Paul C. Fiedler[1] | Elizabeth A. Becker[1,2] | Karin A. Forney[1,3] | Jay Barlow[1] | Jeff E. Moore[1]

[1]NOAA Fisheries, Southwest Fisheries Science Center, La Jolla, California

[2]ManTech International Corporation, Solana Beach, California

[3]Moss Landing Marine Laboratories, San Jose State University, Moss Landing, California

Correspondence
Paul Fiedler, Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA 92037.
Email: pfiedler1@gmail.com

Abstract

Species distribution models (SDMs) have been developed and extensively validated for diverse cetaceans within the California Current Ecosystem off the West Coast of the United States. These studies have recognized the challenges associated with developing robust models for deep-diving cetaceans—sperm whales and beaked whales—thus limiting the accuracy of predictions for management and ecological understanding. In this study, we explore whether additional biologically relevant predictor variables can improve models for deep-divers. These variables are related to the oxygen minimum layer and phytoplankton and micronekton biomass and could influence prey availability for cetacean top predators. We found that the addition of these variables improved the performance of SDMs for sperm whales, as well as for some more common baleen whale and dolphin species, but that the accuracy of deep-diver models was nevertheless poor. The sightings data sets for deep-diving cetaceans have small sample sizes compared to other cetaceans, and sightings are distributed nearly randomly across the study area and model domain. These factors hinder the development of useful environmentally driven models of spatial distribution.

KEYWORDS
beaked whale, California Current, species distribution model, sperm whale

1 | INTRODUCTION

Species distribution models (SDMs) that predict abundance or presence of animals from environmental variables are widely used to explain and predict both spatial and temporal variations of marine populations (Melo-Merino et al., 2020; Redfern et al., 2006). These models are potentially useful in managing impacts to marine species due to climate change, natural variation in the environment, and human activities such as ship strikes, naval exercises, entanglement in fishing gear, and noise (Becker et al., 2019; Bombosch et al., 2014; Eguchi et al., 2017; Hazen et al., 2017; Redfern et al., 2013). SDMs have been developed and improved over many years for California Current cetaceans off the West Coast of the United States (Becker et al., 2010, 2014, 2016, 2017, 2020; Forney et al., 2012).

While SDMs have been shown to accurately predict the distributions of many cetacean species in the California Current, models for some species have been consistently unsatisfactory. These are primarily for the deep-diving whales—sperm whales (*Physeter macrocephalus*) and beaked whales—species that tend to be sighted infrequently and have widespread distributions within the study area. The performance of species distribution models is known to be affected by sample size (Wisz et al., 2008) and by the prevalence of occupied samples (Santika, 2011; Sor et al., 2017). Even for presence-only models, with no observed absences, prevalence as the fraction of the study area occupied affects model performance (van Proosdij et al., 2016). Fiedler et al. (2018) found that models of more widespread whales in the eastern tropical Pacific tend to be less informative about what determines patterns of distribution, irrespective of the number of sightings.

Another likely contributor to the poor model performance for these species is that the environmental variables available to the SDMs largely describe ocean surface and near-surface habitat. Deep-diving species are almost certainly responding principally to habitat characteristics at depth, which are not accurately represented in the SDMs due to the challenges of sampling and accurately modeling the deeper ocean habitat. A recent paper by Virgili et al. (2022) found that predictor variables reflecting the deep-water habitat of beaked whales and sperm whales can help explain their distributions in the Bay of Biscay. The objectives of this paper are (1) to investigate whether SDMs of cetaceans can be improved by identifying potentially more relevant predictors and (2) to examine the characteristics of species and survey data that influence the performance of SDMs for a diverse suite of cetaceans, including deep-diving species and more shallow-water feeders.

SDMs for the California Current were developed for the deep-diving Baird's beaked whale (*Berardius bairdii*), Cuvier's beaked whale (*Ziphius cavirostris*), and sperm whale. For sperm whales, we constructed models for three categories of sightings, which could reflect potential differences in the distributions of males and females (Rice, 1989): all sightings, sightings of single whales (likely mature males), and sightings of groups (mostly females and juvenile males).

For comparison, SDMs were also developed for species that feed at shallower depths: blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), Risso's dolphin (*Grampus griseus*), striped dolphin (*Stenella coeruleoalba*), short-beaked common dolphin (*Delphinus delphis delphis*), long-beaked common dolphin (*Delphinus delphis bairdii*), Dall's porpoise (*Phocoenoides dalli*), and northern right whale dolphin (*Lissodelphis borealis*). SDMs previously built for these species have performed well based on cross-validation (Barlow et al., 2009; Becker et al., 2010; Forney, 2000; Forney et al., 2012) and predictions on novel data sets (Barlow et al., 2009; Becker et al., 2012, 2014, 2019; Calambokidis et al., 2015; Forney et al., 2012).

1.1 | Species overview

We summarize information on the distributions and diets of the species examined, from Würsig et al. (2018) and sources therein and from the U.S Pacific Marine Mammal Stock Assessment Report (Carretta et al., 2020).

Beaked whales are rare, oceanic cetaceans about which little is known. They feed on deep water squid, fish, and to a lesser extent, crustaceans. Baird's beaked whale is found in deep waters and along the continental slopes of the North Pacific, primarily along the continental slope from late spring to early fall in our study area. Cuvier's beaked whales are the most commonly seen beaked whale in our study area. They have the widest distribution of any of the beaked whales and are found globally in tropical and temperate waters over the continental slope and beyond.

Sperm whales are cosmopolitan. Adult males are typically observed as single individuals and range to higher latitudes than do the larger groups of females and juveniles. Both males and females are found year-round within the California Current Ecosystem, during winter mostly south of 40°N, where they feed on mesopelagic and deep-sea squid, and occasionally fish.

Blue whales are cosmopolitan; the eastern North Pacific population winters off southern Mexico and Central America and migrates along the coast of California and north for summer feeding on aggregations of euphausiids. Fin whales are cosmopolitan in subtropical and subarctic waters, with a hiatus in tropical waters. Humpback whales are globally cosmopolitan. They migrate to coastal feeding grounds at mid- and high latitudes during summer.

Common dolphins are common in warm-temperate and coastal waters worldwide. In the eastern Pacific, they range from the California Current and offshore south into eastern equatorial waters and along the coast of Peru and northern Chile. Short-beaked common dolphins are the most abundant cetacean in our study area and are widely distributed in waters off California and Oregon. Long-beaked common dolphins are generally found in shallower, warmer water closer to the coast from central California south along Baja California. Both subspecies feed on a variety of prey, including small mesopelagic fishes and squids and epipelagic schooling species such as small scombroids, clupeoids, and market squids; foraging dives to 200 m have been recorded.

Risso's dolphins and striped dolphins are found in warm-temperate, subtropical, and tropical waters worldwide, off the continental shelf. Risso's dolphins tend to dive deeply, feeding mainly on deep-water mesopelagic cephalopods such as squid, octopus, and cuttlefish, presumably at night to exploit vertically migrating prey. Striped dolphins consume pelagic and mesopelagic fish and squid. Dall's porpoise and northern right whale dolphins are both cold-water species endemic to deeper waters of the North Pacific Ocean as far south as the latitude of southern California and Japan. Both species move toward the southern end of our study area during colder winter months or cool-water years. Prey items include schooling pelagic fishes, mesopelagic fishes, and squids.

2 | METHODS

2.1 | Survey data

Cetacean sighting data were collected within waters of the California Current Ecosystem (CCE) along the U.S. West Coast from 1991 to 2018 (Table 1) using standardized line-transect distance sampling methods (Buckland et al., 2001). The study area covers waters off the entire West Coast of the United States out to 300 nautical miles (556 km) offshore, although not all surveys covered the entire area (Table 1). When combined across years, the surveys provided comprehensive coverage of waters throughout the CCE study area (Figure 1). Only on-effort data collected in Beaufort sea state conditions ≤5 within the study area were used in model development.

All surveys followed similar line-transect protocols (see Barlow, 2016; Barlow & Forney, 2007; Becker et al., 2020; Henry et al., 2020) and are briefly summarized here. Cetacean sightings were made by skilled observers on the flying bridge deck (~10 m height) of NOAA research vessels, using 25 × 100 big-eye binoculars (a data recorder also contributed observations using naked eye or 7 × 50 handheld binoculars). Vessels moved at ~10 kn. Principal data recorded for each sighting included distance and direction from the vessel, from which perpendicular sighting distance was calculated, and group size. If the group of animals was within 3 nautical miles (5.6 km) of the trackline, the ship would typically divert from the transect line and go "off-effort" to approach the animals for accurate group size estimation and species identification. All observers independently provided best, high, and low group size estimates, as well as the proportional makeup of species in the case of multispecies groups.

To prepare data for modeling, continuous portions of on-effort survey tracklines were divided into approximate 5-km segments using methods described by Becker et al. (2010). The total number of species-specific sightings and associated average group size estimates were assigned to each segment. In distance sampling, "effective strip widths" are estimated from the perpendicular sighting distance data to calculate animal density. We used methods of

TABLE 1 Cetacean and ecosystem assessment surveys and effort conducted within the California Current Ecosystem study area during 1991–2018. Regions covered within the study area: CA/OR/WA = California/ Oregon/Washington, CenCA = central California, SoCA = southern California, Baja = Baja California, Mexico. Samples are the number of approximate 5-km on-effort segments of the survey trackline.

Survey	Dates	Effort (km)	Region	Samples
CAMMS91[a]	Jul–Nov 1991	10,353.6	California	2,250
PODS93[b]	Jul–Nov 1993	6,437.4	California/Baja California	1,434
ORCAWALE96[c]	Jul–Nov 1996	15,530.8	CA/OR/WA	3,179
ORCAWALE01[d]	Jul–Dec 2001	10,343.4	CA/OR/WA	2,139
CSCAPE05[e]	Jul–Dec 2005	10,221.9	CA/OR/WA	2,119
ORCAWALE08[f]	Jul–Nov 2008	12,242.3	CA/OR/WA	2,537
DELPHINUS09[g]	Sept–Dec 2009	4,389.1	CenCA/SoCA/Baja California	979
CalCurCEAS14[h]	Aug–Dec 2014	10,205.4	CA/OR/WA	2,210
CCES18[i]	June–Dec 2018	9,554.7	Canada/CA/OR/WA/Baja	2,050
Total		89,278.6		18,897

[a]Hill & Barlow (1992)
[b]Mangels & Gerrodette (1994)
[c]von Saunder & Barlow (1999)
[d]Appler et al. (2004)
[e]Forney (2007)
[f]Barlow et al. (2010)
[g]Chivers et al. (2010)
[h]Henry et al. (2015)
[i]Henry et al. (2020).

Barlow et al. (2011) to find effective strip width for each species in this study. For this purpose, sighting data were truncated (Buckland et al., 2001) at a distance of 5.5 km perpendicular to the trackline for the delphinids and large whales, 4.0 km for small whales (Baird's and Cuvier's beaked whales), and at 3.0 km for Dall's porpoise.

2.2 | Environmental predictor variables

Two categories of predictor variables were considered (see Table 2 for list with data sources). The first category consisted of physical variables, which included both fixed geographic and dynamic oceanographic variables. The fixed variables were bottom depth (*depth*) and distance to shelf edge (*dist2edge*). Dynamic surface oceanographic variables included surface temperature (*temp*), surface salinity (*sal*), sea surface height (*ssh*), wind speed (*wspd*), wind stress curl (*wsc*), and wind divergence (*wdiv*). Dynamic subsurface oceanographic variables were derived from temperature and salinity profiles (Table 2) and included isothermal layer depth (*ild*, depth of $temp - 0.5°C$), thermocline depth (*td*), and stratification (*sdt*). The thermocline was defined as the depth interval that included the upper decile (the greatest 10%) of 1-m temperature gradients in a 0–300-m temperature profile. Thermocline depth was the weighted mean of the depths of this set, with each depth weighted by the value of the 1-m temperature gradient at that depth. Stratification was indexed as the standard deviation of temperature in the near-surface layer, 0–300 m (Fiedler, 2010). A *temp-sal* interaction term was also considered to represent differences among surface water masses in the California Current system: Pacific Subarctic Water, Eastern North Pacific Central Water, Equatorial Pacific Water, and Coastal Upwelled Water (McClatchie, 2014).

The second category consisted of biological predictor variables and variables that are related to biological processes. These variables should be more proximate determinants of predator distribution as they can directly represent or influence prey availability. We used hypoxic depth (*dhypox*, depth of dissolved oxygen <63 µmol/L),
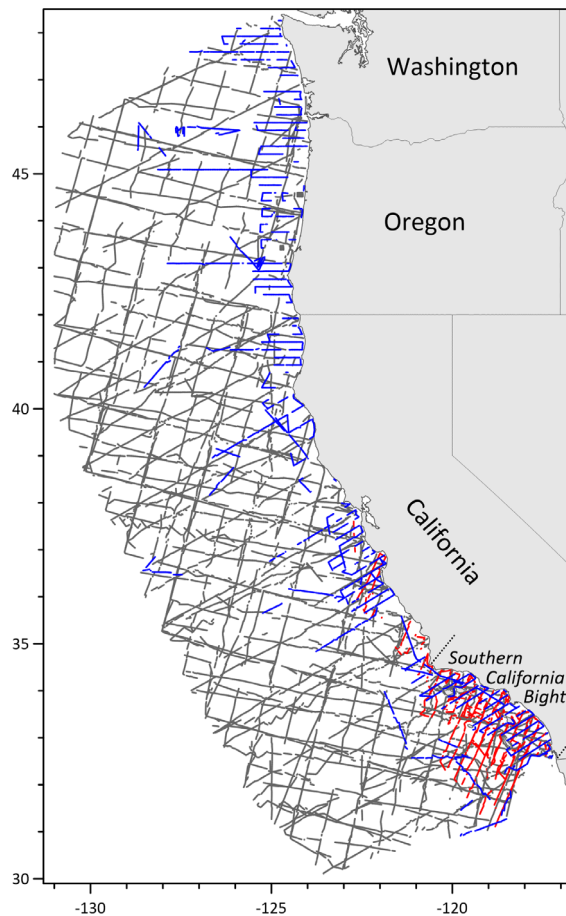
FIGURE 1 Completed transects for the Southwest Fisheries Science Center systematic shipboard surveys conducted between 1991 and 2018 in the California Current Ecosystem study area. The lines show on-effort transect coverage in Beaufort sea states of 0–5. Surveys with limited coverage: DELPHINUS09 (red), CCES18 (blue).

minimum dissolved oxygen concentration (*mino2*), integrated chlorophyll (*chlint*), epipelagic micronekton biomass (*epi_mnk*), mesopelagic micronekton biomass (*meso_mnk*) and total plankton biomass (*total_pk*). Variations in the deep oxygen minimum layer are known to affect the distribution of mesopelagic organisms (Gilly et al., 2013; Koslow et al., 2014). Many marine SDMs use surface chlorophyll because it is readily available from satellite data sets and represents a proxy metric for phytoplankton and phytoplankton production at the base of the pelagic food web. However, for top predators, phytoplankton is at least two trophic levels removed from prey. We used integrated chlorophyll from the same global ocean biogeochemistry hindcast model that provided water column dissolved oxygen data (CMEMS GLOBAL_REANALYSIS_BIO_001_029; Table 2). In our study, we also considered model-based estimates of zooplankton and micronekton biomasses (Lehodey et al., 2010) from a global ocean low- and mid-trophic level biomass content hindcast (SEAPODYM-LMTL, available in CMEMS GLOBAL_REANALYSIS_BIO_001_033; Table 2). Micronekton includes forage organisms in the epipelagic and mesopelagic layers, marked by nominal depths equal to 1.5 and 10.5 times the euphotic zone depth (45 and 120 m near the coast to 315 and 840 m at the oceanic extreme of the study area). SEAPODYM differentiates six categories of micronekton based on depth and diurnal migration. We found that the summed micronekton biomasses in the epipelagic and mesopelagic depth layers at any time of day, *epi_mnk* and

TABLE 2 Predictor variables considered for SDMs of CCE cetaceans. Spatial resolution for all predictors, either as available or derived, was 0.25° × 0.25°. Temporal resolution for all dynamic variables was monthly (see footnotes); periods of available data are listed under Years.

Name	Description	Source	Years
Physical variables: fixed			
depth	bottom depth (m)	ETOPO1[a] (Amante & Eakins, 2009)	—
dist2edge*	distance to shelf edge (km)	Harris et al. (2014)	—
Physical variables: dynamic			
temp	surface temperature (°C)	ECMWF Ocean Reanalysis System 5[b]	1979–2018
sal	surface salinity (psu)	https://www.cen.uni-hamburg.de/en/icdc/	
ild*	isothermal layer depth (m)		
td	thermocline depth (m)		
sdt*	stratification (°C)		
ssh	sea surface height (cm)		
wspd	wind speed (m/s)		
wsc	wind stress curl (N/m^3)		
wdiv	wind divergence (s^{-1})		
Biological variables			
dhypox	hypoxic depth (m)	Copernicus Marine Service (CMEMS),	1993–2019
mino2	minimum dissolved oxygen, log(µmol/L)	GLOBAL_REANALYSIS_BIO_001_029[c]	
chlint	integrated chlorophyll (mg/m^2)	https://resources.marine.copernicus.eu/	
epi_mnk	epipelagic micronekton biomass (g/m^2)	Copernicus Marine Service (CMEMS), GLOBAL_MULTIYEAR_BGC_001_033[d]	1998–2019
meso_mnk	mesopelagic micronekton biomass (g/m^2)	https://resources.marine.copernicus.eu/	
total_pk*	total plankton biomass		

Note: Predictor variables marked with * were not included due to high cross-correlations with other predictors.
[a]1 arc-minute data smoothed by 2-D convolution (Matlab function *conv2*).
[b]0.25°, monthly mean data.
[c]0.25°, weekly data averaged monthly.
[d]0.25°, daily data averaged monthly.

meso_mnk, were highly correlated ($r = +0.67$), but used mesopelagic micronekton biomass (*meso_mnk*) as a predictor variable for the deep-diving species and epipelagic micronekton biomass (*epi_mnk*) for the other species.

Predictor variable values were spline-interpolated for each effort segment's geographical midpoint and, for dynamic variables, day of observation. Monthly climatological data (monthly means for the available years) were used for early years that were not covered by the biological variables data sets: 1991 for *dhypox*, *mino2* and *chlint*; 1991, 1993, and 1996 for *epi_* and *meso_mnk*. This may have compromised the performance of models that use these variables. However, preliminary modeling using only the post-2000 surveys that are covered by these data sets, with 35% less effort and 29% fewer sightings, resulted in less satisfactory model predictions, especially for species with low numbers of sightings.

Cross-correlation values of predictor variables in the survey effort segment samples varied in absolute values between 0.00 and 0.81 (Figure 2). Three of the potential predictor variables (*dist2edge*, *sdt*, and *total_pk*) were not offered in the models because they were highly correlated ($|r| > 0.6$) with several other variables. Two of the biological variables that were retained as potential predictors (*dhypox* and *chlint*) show high correlations with physical
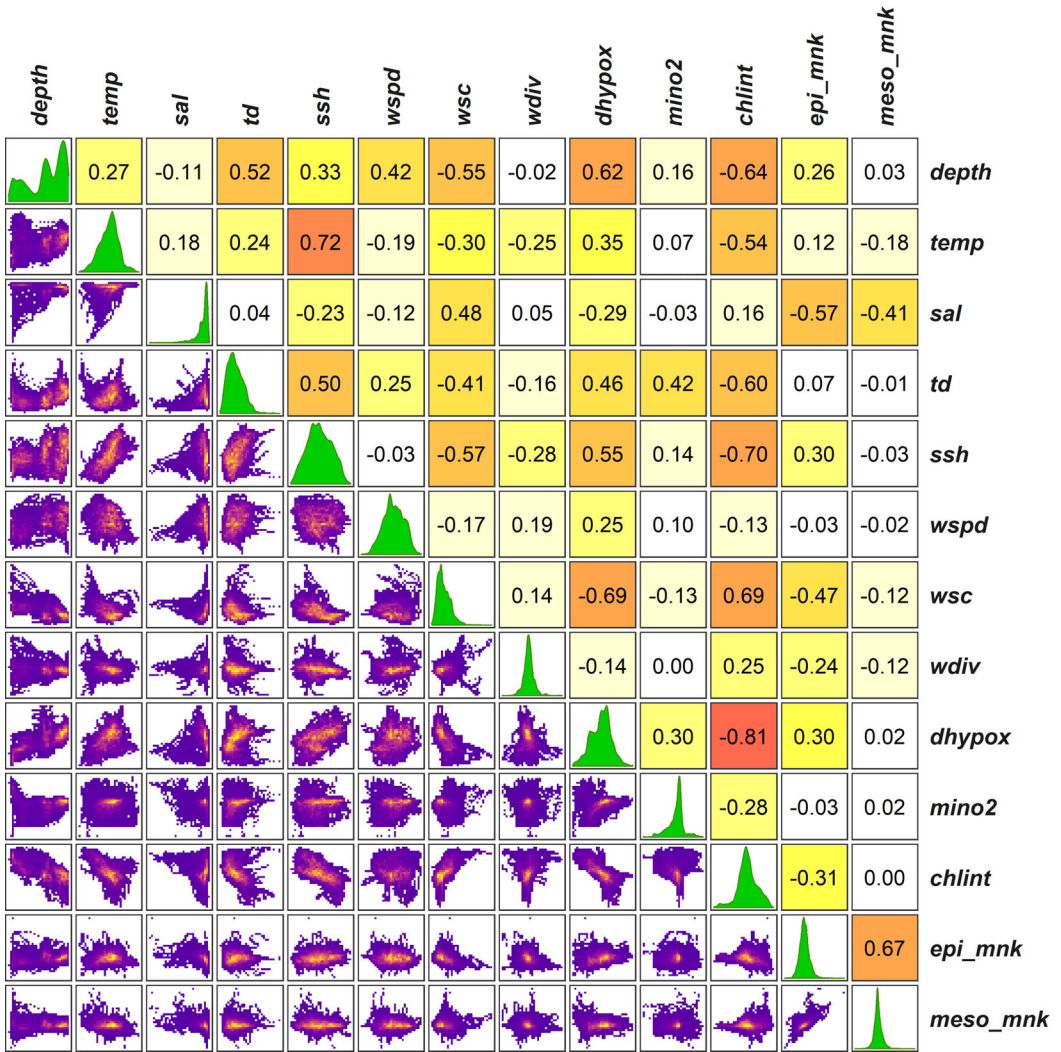
FIGURE 2 Matrix showing Spearman correlations (above diagonal) and scatterplots (below diagonal) among the predictor variables in 5-km survey segments ($N = 18{,}929$). Green curves on the diagonal are frequency distributions of segment values for each variable.

variables because of functional relationships between biological processes and the environment. Climatological (mean) maps of the retained predictor variables are in Appendix S2 (Figures S1 and S2).

2.3 | Species distribution models

Generalized additive models (GAM; Wood, 2017) were developed in R (v. 4.0.5; R Core Team, 2020) using the package "mgcv" (v. 1.8–31; Wood, 2011). Methods largely followed those described in Becker et al. (2016, 2020) and are summarized here. Model predictions were calculated by averaging the predictions for each year calculated from the spatial fields of the static covariates and, for dynamic covariates, the August–November mean fields.

One of two modeling frameworks was used for each taxon. For whales and some dolphin species, a single-response GAM was fit for the number of individuals per transect segment as the response variable. All transect

segments were used, regardless of whether they included sightings. A Tweedie distribution was used to account for overdispersion (Miller et al., 2013), as this distribution has been shown to be effective for modeling cetacean densities in numerous other studies, including several that used the same data set as in our study (Becker et al., 2019, 2020, 2022; Roberts et al., 2016; Sigourney et al., 2020; Warwick-Evans et al., 2022). As detailed below, the effective area searched on each segment was included as an offset in the encounter rate models. Therefore, the model prediction is encounter rate of individuals, equivalent to density (individuals/km^2).

For many species of dolphins that have large and variable group sizes, separate models for encounter rate of sightings (sightings/km^2) and group size (individuals per sighting) have been found to perform better than a single model of individuals/km^2. Encounter rate models for sightings/km^2 were built as described above for the single model of individuals/km^2. Group size models were built using only those segments that included sightings, with the natural log of group size as the response variable, and a Gaussian link function. A tensor product smooth of latitude and longitude (Wood, 2003) was the only predictor variable included in the group size models. Density in a model cell is the predicted encounter rate (sightings/km^2) multiplied by the predicted group size. This model scheme will be referred to as a "product model." Based on comparisons of single-response and product model performances (Table S1), single-response models were used for striped dolphin and northern right whale dolphin; product models were used for long- and short-beaked common dolphin, Risso's dolphin, and Dall's porpoise.

In all models, restricted maximum likelihood (REML) was used to obtain parameter estimates (Marra & Wood, 2011). The shrinkage approach of Marra & Wood (2011) was used to potentially remove terms from each model by modifying the smoothing penalty, allowing the smooth effect to be shrunk to zero. Additionally, to avoid overfitting, a backwards iterative selection process was used to remove covariates that had p-values > .05 (Redfern et al., 2017; Roberts et al., 2016).

The natural log of the effective area searched (A) was included as an offset in the encounter rate models. The value of A for segment i is:

$$A_i = 2 \cdot L_i \cdot ESW_i \cdot g(0)_i \qquad (1)$$

where L_i is the length of the effort segment i, ESW_i is the effective strip half-width, and $g(0)_i$ is the probability of detection on the transect line. Following the methods of Becker et al. (2020), species-specific and segment-specific estimates of both ESW and $g(0)$ were incorporated into the models based on the recorded detection conditions on that segment. In Equation 1, the effective area searched is multiplied by two to account for observers searching on both sides of the transect line. During the 2018 survey, coastal fog and other conditions occasionally prohibited visual observations on one side of the ship, so that cetacean sighting data were collected on only one side of the transect line. These portions of reduced effort were systematically recorded in the data set and the effective area searched was reduced accordingly along these segments, i.e., the constant was changed to a "1" in Equation 1.

Model performance was evaluated using the true skill statistic (TSS). TSS measures the ability of the predictions to discriminate between presence and absence (occupied and unoccupied sites). TSS is equal to sensitivity + specificity −1, where sensitivity is the true-positive rate and specificity is the true-negative rate (Allouche et al. 2006). TSS can be calculated for density models using the sensitivity-specificity sum maximization approach to obtain thresholds for species presence (Liu et al., 2005). We calculated TSS using the "evaluate" command in the R package "dismo" (v.1.1.4). This evaluation was run 1,000 times with a random selection of absences (segments with no sightings) equal to the number of sightings. TSS values range from −1 to 1, where a positive score indicates better than random skill at discriminating presence and absence. Differences in mean TSS for model comparisons were tested by an unpaired t-test of the two sets of 1,000 values.

We supplemented the statistical assessment of model performance by calculating the Model:LT ratio, a measure of bias in the abundance estimate generated by the SDM. Model:LT compares the model's abundance estimate from segment-predicted densities (Model) to a standard line-transect estimate (LT) derived from the same segment observations used for modeling (Becker et al., 2017). Although there is no statistical threshold for significance, values departing from

1 indicate potential bias of model-based estimates compared to design-based (line-transect) estimates of density. We assessed model predictions visually by the correspondence between maps of predicted density and observed sightings during the 1991–2018 cetacean surveys. We also report deviance explained for the GAMs; for the dolphin species modeled as the product of group encounter rate and group size, the sum of the deviances explained is reported.

The relative importance or contribution of predictor variables to a model prediction was estimated as in Thuiller et al. (2009). For a given GAM, each of the selected variables was randomly permuted before being used to calculate a prediction surface. The correlation of the original prediction with the prediction using a permuted variable is related to the importance of the permuted variable; permuting an unimportant variable will change the prediction only slightly and result in a high correlation, while permuting an important variable will result in more change in the prediction and a lower correlation. This permutation was repeated 1,000 times. The scores of variable importance are equal to 1 minus the mean correlation, rescaled to sum to 1 across all predictor variables.

Prevalence, the fraction of the study area or the fraction of samples that is occupied, is often used to quantify the distribution of observations that might influence species distribution model performance. Our surveys were designed for uniform coverage of the survey area, which was usually, but not always, the entire study area. 89.7% of the 2,054 0.25° model cells in the study area were sampled at least once. However, cetaceans are not always detected where they are present on a shipboard line-transect survey. The probability of detecting an animal that is directly on the survey trackline (g(0) in Equation 1) ranges from 0.224 to 0.708 for our species (Barlow, 2015). Therefore, we did not estimate prevalence to characterize species distributions. An alternative measure of the aggregation or randomness of observations is the Clark-Evans aggregation index (R), a crude measure of clustering or ordering of a point pattern (Clark & Evans, 1954). R is the ratio of the observed mean nearest-neighbor distance to the expected nearest-neighbor distance for randomly distributed points. Thus, $R < 1$ indicates clustering or aggregation, $R \approx 1$ indicates randomness, while $R > 1$ indicates an even or dispersed distribution.

3 | RESULTS

3.1 | Does adding biological predictors improve model performance for deep-diving cetaceans?

SDMs were built for the three deep-diving taxa (Figure 3). The models for sperm whale groups were very similar to those for all sperm whales (singles and groups). The model for single sperm whales predicted a nearly flat density surface throughout the study area. Therefore, we will report only the results for Baird's beaked whale, Cuvier's beaked whale and sperm whale (sightings of both singles and groups).

Added biological predictors (Table 3) improved SDM performance for sperm whale, but not for Cuvier's or Baird's beaked whale. The sperm whale model added *dhypox* and *mino2* with a combined importance of 30% (Table 4). A significant increase in TSS indicated better performance for the model with added biological predictors. Visually, both models predicted the highest densities in some areas that do not correspond to the densest aggregations of sightings, with the exception of the aggregation off the coast of northern California. The model with added biological variables predicted a high density of sperm whales all along the continental slope off California (Figure 3a).

The performance of the Cuvier's beaked whale model, with depth as the only predictor, was low as measured by TSS; deviance explained was only 3.2%. Model:LT was close to one, indicating no model bias. Visually, the model predicted very low densities on the continental shelf, consistent with the absence of sightings (Figure 3b). Higher densities are predicted along the continental shelf off California and in deeper waters offshore.

Biological predictors were also not selected for the SDM of Baird's beaked whale, but this model had the best accuracy of the deep-diving taxa, with the highest TSS value. The most important predictors were *wsc* and *depth*, along with *td*, *ssh*, and *temp-sal*. The model prediction map shows a strong aggregation along the continental slope
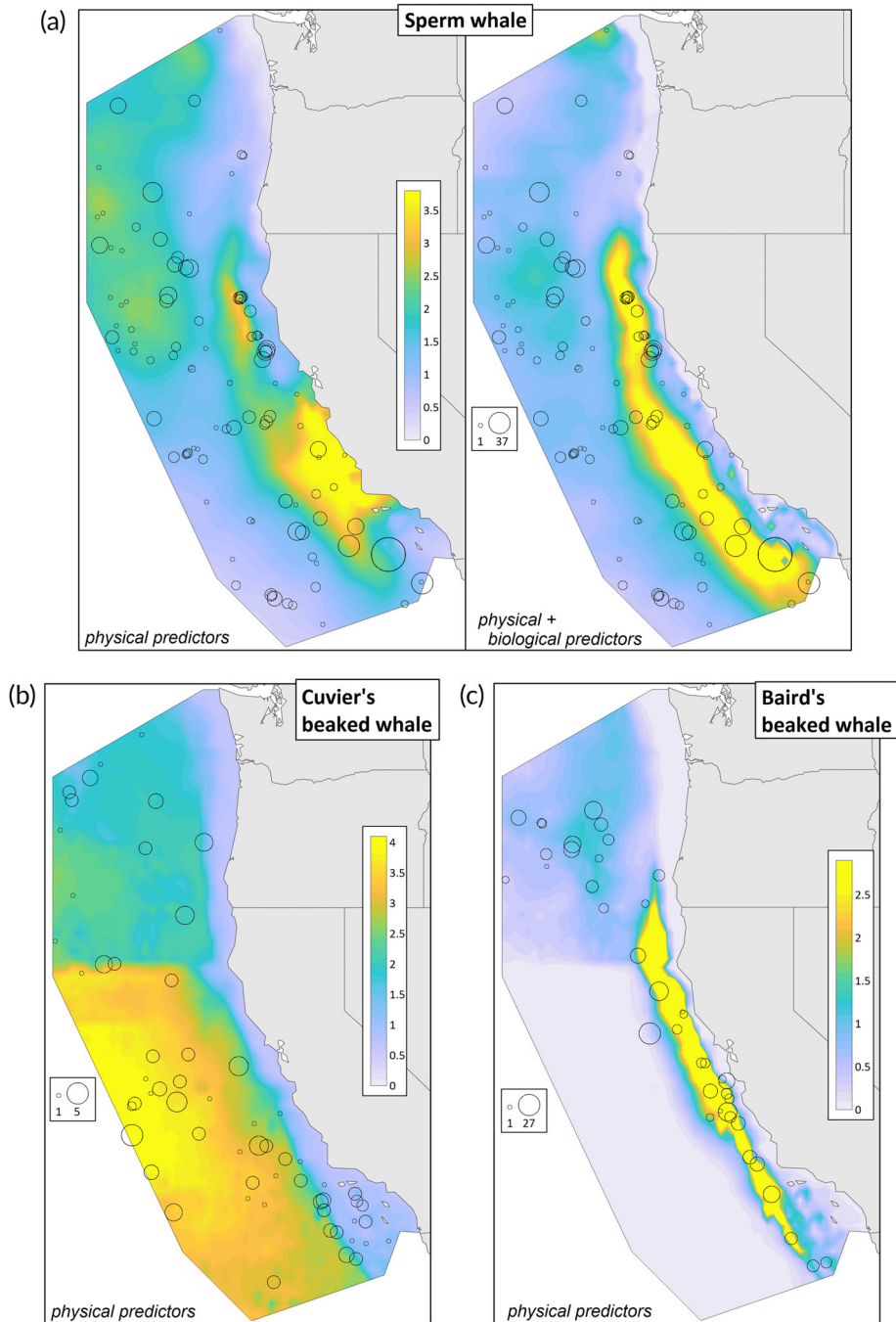
FIGURE 3 Predictions of density (animals/1,000 km²) for deep-diving cetaceans—(a) sperm whale, (b) Cuvier's beaked whale, and (c) Baird's beaked whale—using only physical oceanographic variables (*physical predictors*) and with added biological variables if any were selected (*physical + biological predictors*). Circles mark sightings, with circle size proportional to group size.

off California, even more pronounced than for sperm whale, with a broader distribution in deeper water to the north, where there is complex bathymetry at water depths similar to the continental slope (2,000–3,000 m; see Figure S1), consistent with the observed sightings (Figure 3b).

TABLE 3 Significant predictor variables and their relative importance in GAMs predicting density of deep-diving cetaceans using physical predictor variables only (*phys*) and using added biological predictor variables (*phys + biol*, shaded).

	Physical variables									Biological variables			
	depth	*temp*	*sal*	*temp-sal*	*td*	*ssh*	*wspd*	*wsc*	*wdiv*	*dhypox*	*mino2*	*chlint*	*meso_mnk*
Sperm whale													
phys		.33	.21		.06	.16		.24		—	—	—	—
phys + biol					.06			.65		.12	.18		
Cuvier's beaked whale													
phys	1.0									—	—	—	—
phys + biol	1.0												
Baird's beaked whale													
phys	.25			.05	.17	.09		.44		—	—	—	—
phys + biol	.25			.05	.17	.09		.44					

TABLE 4 Performance of GAMs in predicting density of deep-diving cetaceans using physical predictor variables only (*phys*) and using added biological predictor variables (*phys + biol*).

	TSS	Model:LT	Dev.expl.
Sperm whale			
phys	.142	1.035	.151
phys + biol	.190***	1.027	.163
Cuvier's beaked whale			
phys	.172	1.054	.032
phys + biol			
Baird's beaked whale			
phys	.599	1.085	.402
phys + biol			

Note: TSS = true skill statistic, asterisks indicate significantly greater TSS; Model:LT = ratio of model abundance estimate to standard line-transect estimate; Dev.expl. = deviance explained.
***$p < .0001$.

3.2 | Does adding biological predictor variables improve model performance for other cetaceans?

The same two model types, with and without biological predictors, were fit to data for three baleen whale and six dolphin species for which GAM SDMs have performed well in other studies (Barlow et al., 2009; Becker et al., 2010, 2012, 2014, 2019; Calambokidis et al., 2015; Forney, 2000; Forney et al., 2012). In general, these species have more sightings than the deep-diving taxa. Models for all of these species retained biological predictors when they were offered (Table 5). As expected, these models exhibited better performance (Table 6) than those for the deep-diving taxa (Table 4).

The blue whale model was not improved by the addition of biological predictors, as measured by TSS, although *dhypox*, *chlint*, and *epi_mnk* were selected as significant predictors with a combined relative importance of 40%.

TABLE 5 Significant predictor variables and their relative importance in GAMs predicting density of other cetacean species using physical predictor variables only (*phys*) and using added biological predictor variables (*phys + biol*, shaded).

	Physical variables									Biological variables			
	depth	temp	sal	temp-sal	td	ssh	wspd	wsc	wdiv	dhypox	mino2	chlint	epi_mnk
Blue whale													
phys	.24	.04	.04	.24	.27	.11			.06	—	—	—	—
phys + biol	.11	.19	.04	.09	.04	.08			.05	.02		.16	.22
Fin whale													
phys	.19	.26		.15	.07	.23	.12			—	—	—	—
phys + biol	.12	.25	.01	.11	.04	.14	.08	.01			.03	.17	.03
Humpback whale													
phys	.21	.30		.06	.10	.04	.01	.28		—	—	—	—
phys + biol	.08	.29			.02	.04	.02	.26				.18	.12
Common dolphin, short-beaked													
phys	.18	.19	.17	.31	.04	.04		.07		—	—	—	—
phys + biol	.09	.33	.10	.21	.02			.01		.10			.14
Common dolphin, long-beaked													
phys	.25	.22	.30	.16			.01	.06		—	—	—	—
phys + biol	.24	.09	.11	.15		.08	.01			.21			.10
Risso's dolphin													
phys	.91					.01		.08		—	—	—	—
phys + biol	.80	.02						.03				.15	
Striped dolphin													
phys	.37	.21	.03	.26	.10			.02		—	—	—	—
phys + biol	.20		.07	.30		.20				.09		.08	.06
Dall's porpoise													
phys	.14	.28	.28	.19	.04	.07				—	—	—	—
phys + biol	.09	.15	.36	.15	.02	.14			.01	.02			.07
Northern right whale dolphin													
phys	.50	.48						.02		—	—	—	—
phys + biol	.15	.39				.05	.04	.10		.11		.15	

Visually, both models correctly predicted higher densities off southern and central California, and also at some locations along the coast of northern California and southern Oregon (Figure 4a). However, the model with added biological variables seemed to better predict the high densities off southern and central California, while the model with only physical variables tended to overpredict higher densities along the coast to the north. Despite these local prediction biases, Model:LT values were close to one.

The fin whale model was improved by the addition of biological predictors, selecting *mino2*, *chlint*, and *epi_mnk* with a combined relative importance of 23%. TSS increased significantly, indicating improved performance. Differences in the model prediction maps are subtle (Figure 4b). Both maps emphasize high density in a wide band adjacent

TABLE 6 Performance of GAMs in predicting density of other cetacean species using physical predictor variables only (*phys*) and using added biological predictor variables (*phys* + *biol*).

	TSS	Model:LT	Dev.expl.
Blue whale			
phys	.444***	1.053	.231
phys + *biol*	.410	1.048	.250
Fin whale			
phys	.292	1.119	.214
phys + *biol*	.308***	1.119	.241
Humpback whale			
phys	.744	1.012	.570
phys + *biol*	.761***	1.018	.562
Common dolphin, short-beaked			
phys	.319	1.224	.139
phys + *biol*	.336***	1.218	.145
Common dolphin, long-beaked			
phys	.883*	0.236	.486
phys + *biol*	.876	0.229	.518
Risso's dolphin			
phys	.472	0.998	.111
phys + *biol*	.481**	0.998	.132
Striped dolphin			
phys	.488	1.412	.317
phys + *biol*	.487	1.389	.369
Dall's porpoise			
phys	.588***	0.971	.324
phys + *biol*	.528	0.971	.327
Northern right whale dolphin			
phys	.405	0.888	.433
phys + *biol*	.412	1.017	.422

Note: TSS = true skill statistic, asterisks indicate significantly greater TSS; Model:LT = ratio of model abundance estimate to standard line-transect estimate; Dev.expl. = deviance explained for the GAMs of encounter rate of individuals or of groups plus group size (short- and long-beaked common dolphin, Risso's dolphin, Dall's porpoise).
*p < .01.**p < .001.***p < .0001.

to the coast along southern and central California. From northern California north, density is lower in this band and near zero close to the coast. With the addition of biological predictors, the prediction map is visually more consistent with the distribution of sightings at the northern extreme of this higher-density band.

The humpback whale model was improved by the addition of the biological predictors *chlint* and *epi_mnk* with a combined relative importance of 30%. TSS increased significantly, indicating improved performance. The resulting prediction maps are similar; both show higher density near the coast, in agreement with observed sightings, but this pattern includes high density along the coast of northern California where there are few sightings (Figure 4c). The prediction with added biological variables appears less consistent with the sightings off central Oregon, but more consistent with the sightings off northern California and at the northwestern end of the Southern California Bight.
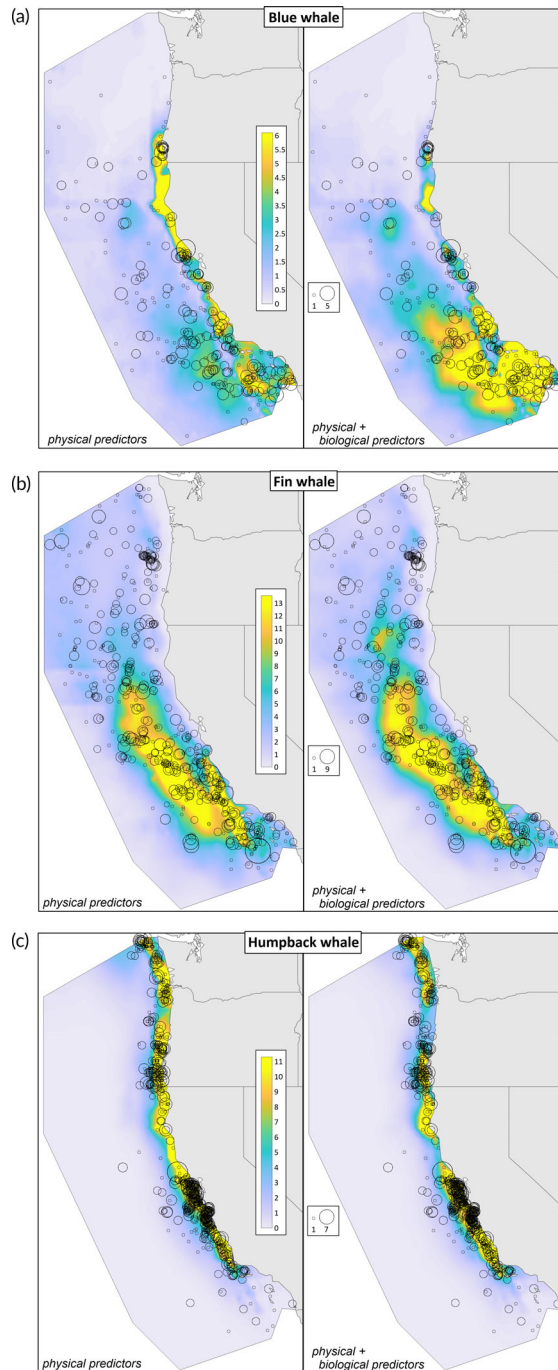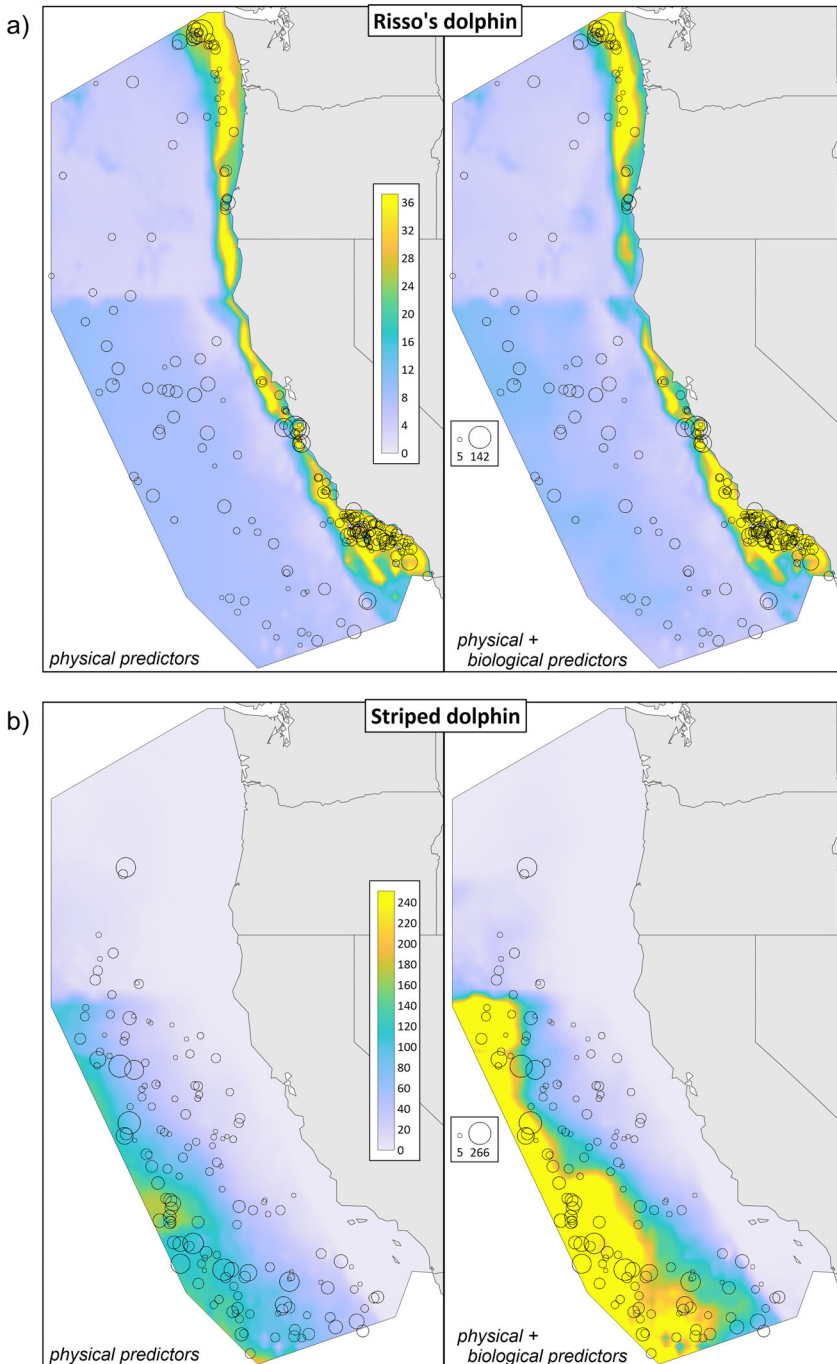
FIGURE 4 Predictions of density (animals/1,000 km^2) for baleen whales—(a) blue whale, (b) fin whale, and (c) humpback whale—using only physical oceanographic variables (*physical predictors*) and with added biological variables (*physical + biological predictors*). Circles mark sightings, with circle size proportional to group size.

Among dolphins, the short-beaked common dolphin model added the biological predictors *dhypox* and *epi_mnk*, with a combined relative importance of 24%; TSS increased significantly, indicating improved performance. Both prediction maps show highest densities in the Southern California Bight and high density offshore of central California;
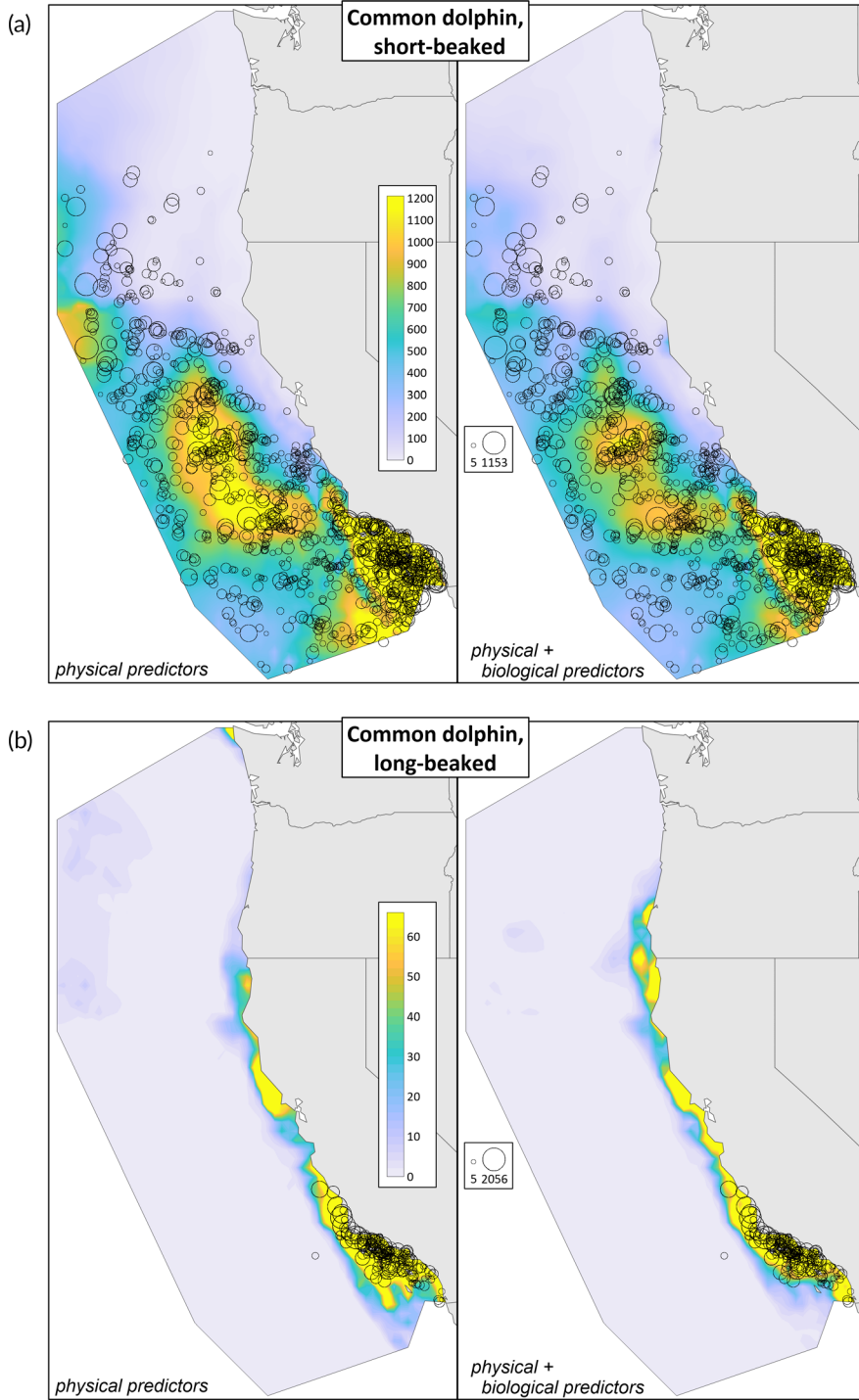
FIGURE 5 Predictions of density (animals/1,000 km²) for two subspecies of common dolphin—(a) short-beaked and (b) long-beaked—using only physical oceanographic variables (*physical predictors*) and with added biological variables (*physical + biological predictors*). Circles mark sightings, with circle size proportional to group size.

FIGURE 6 Predictions of density (animals/1,000 km²) for other cetacean species—(a) Risso's dolphin, (b) striped dolphin, (c) Dall's porpoise, and (d) northern right whale dolphin—using only physical oceanographic variables (*physical predictors*) and with added biological variables (*physical + biological predictors*). Circles mark sightings, with circle size proportional to group size.
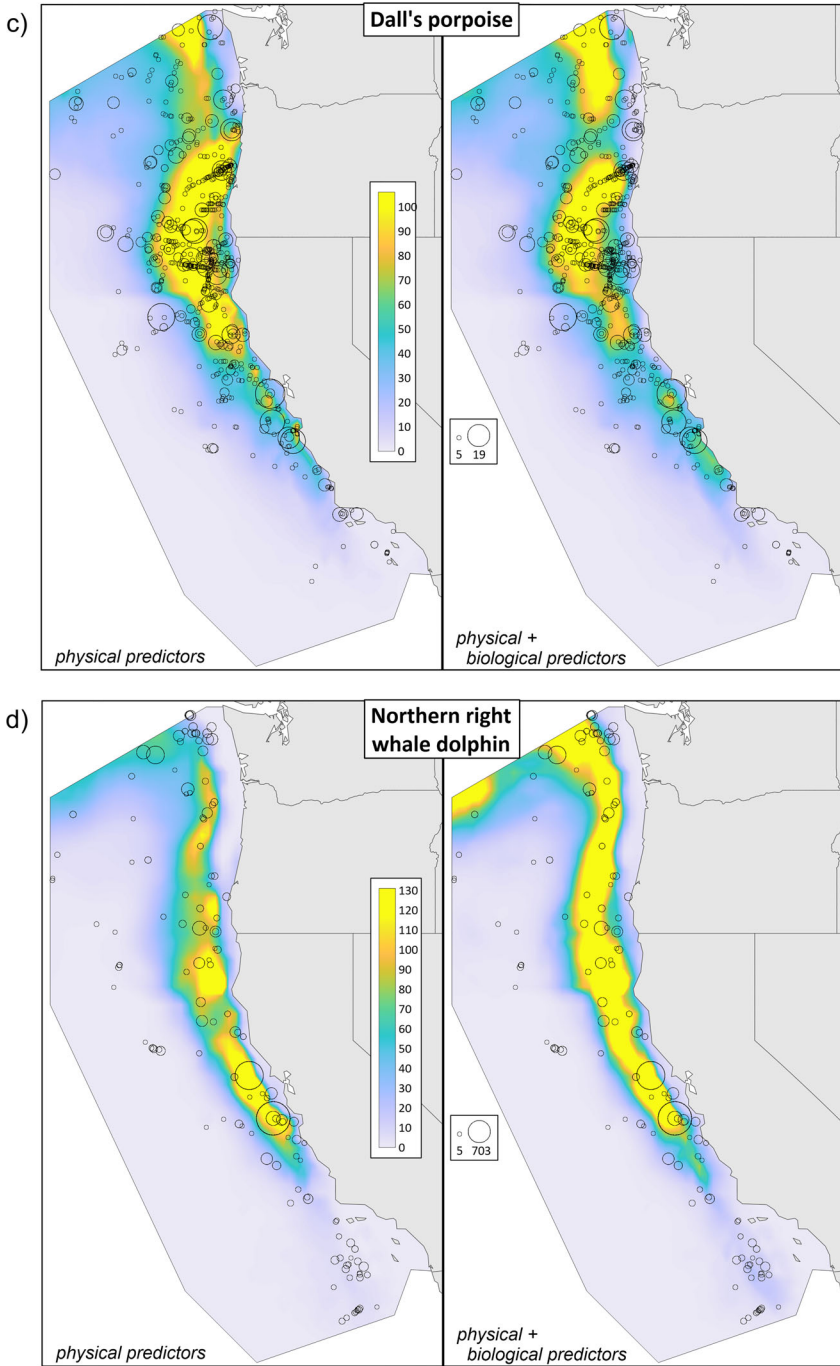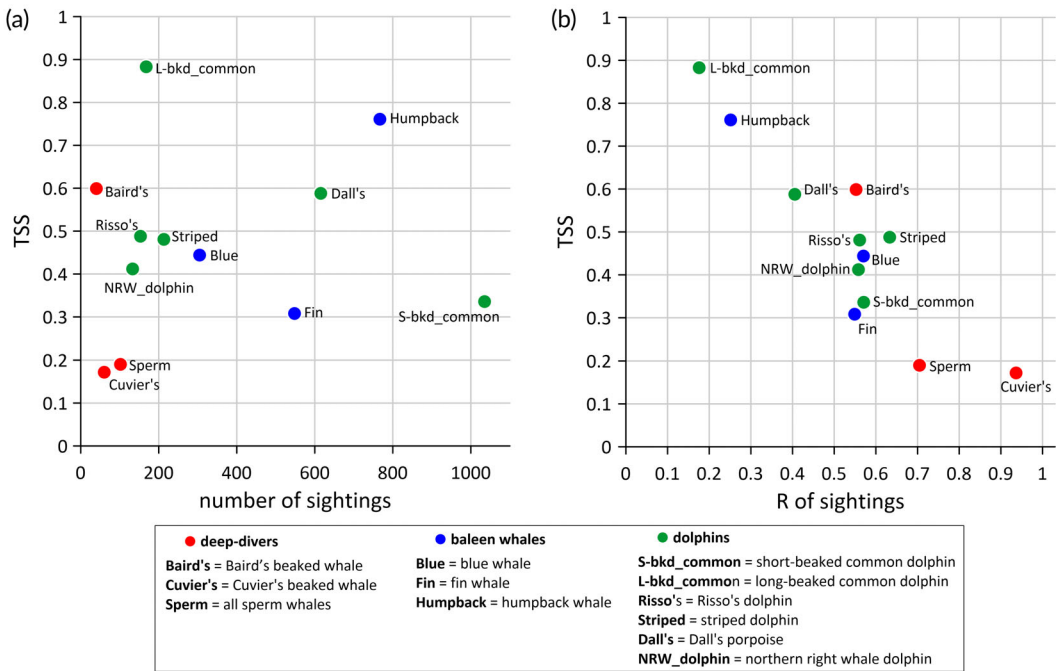
FIGURE 6 (Continued)

only slight differences in minor details can be seen between the maps (Figure 5a). Model:LT values are slightly greater than one, using the product model scheme, but would be even greater using the single model scheme (Table S1).

FIGURE 7 Model performance metric TSS (true skill statistic) versus (a) number of sightings, and (b) aggregation index (*R*) of sightings.

The long-beaked common dolphin model added the biological predictors *dhypox* and *epi_mnk* with a combined relative importance of 31%; TSS decreased significantly, suggesting impaired performance. Both models correctly predict high densities along the coast of southern and central California; the model with added biological predictors was more consistent with the sightings in this area (Figure 5b). Both models erroneously predicted higher densities farther north along the coast, but this error was less extensive for the model with only physical predictors. Model:LT was not close to 1 for either model, perhaps because only a small part of the study area was occupied by this species.

The Risso's dolphin model added the biological predictor *chlint* with a relative importance of 15%; TSS increased significantly, indicating improved performance. Both models correctly predict high densities in two coastal regions— (1) the Southern California Bight and along the coast of central California, and (2) the coast of Washington and northern Oregon—as well as moderate densities offshore of the California coast (Figure 6a). The model with only physical predictors erroneously predicted higher densities along the coast of northern California and southern Oregon, between the two high-density regions. Both models erroneously predict a local extension of the higher densities in the Southern California Bight into offshore waters towards the south.

The striped dolphin model added the biological predictors *dhypox*, *chlint*, and *epi_mnk*, with a combined relative importance of 23%. TSS did not change significantly, indicating no improvement in performance, although improvement was suggested by a Model:LT closer to one and an increase in deviance explained. Prediction maps for both models show an overall higher density in the southern offshore quarter of the study area (Figure 6b). Predicted densities are slightly higher in this region with the addition of biological variables, but both prediction maps are consistent with sightings.

The Dall's porpoise model added the biological predictors *dhypox* and *epi_mnk*, with a combined relative importance of 9%. TSS decreased significantly, indicating impaired performance. The pattern of the prediction map changed only slightly with the addition of biological variables, although predicted densities were considerably higher. Both prediction maps show highest densities off northern California and southern Oregon, with lower densities next to the coast (Figure 6c). Moderate predicted densities extend to the south along the central California coast and to the north off

Washington. Another high-density center is predicted at the northernmost corner of the study area; predicted densities here are much higher with the addition of biological predictors, perhaps the decrease in TSS.

The northern right whale dolphin model added the biological predictors *dypox* and *chlint*, with a combined relative importance of 26%. TSS increased significantly, indicating improved model performance. Both prediction maps correctly show high density along the continental shelf off northern California, but neither one predicts higher densities corresponding to the sightings offshore of southern California (Figure 6d). The prediction of the model with added biological variables is more consistent with the sightings at the northern corner of the study area off Washington and northern Oregon.

3.3 | What other factors affect cetacean SDM performance?

The deep-diving taxa have the lowest number of sightings (Figure 7a). The model performance metric TSS is not significantly related to the number of sightings (Pearson $r = 0.055$). In contrast (Figure 7b), TSS declines markedly ($r = -0.864$) as the aggregation index R increases from <1 (clustered) towards 1 (random). The lowest-performing SDMs are for the deep-diving sperm whale and Cuvier's beaked whale, which are both distributed nearly randomly. The SDM for Baird's beaked whale performs relatively well, even compared to models for the other cetacean species at intermediate levels of R between 0.4 and 0.65.

4 | DISCUSSION

Selection of appropriate predictor variables is an important part of building SDMs to explain or predict distributions of animals in space and time. A variable with explanatory power is not appropriate or useful if it is not relevant to the life processes of the species under study. Fourcade et al. (2017) showed that models using pseudo-predictors, derived from the graphic patterns of paintings that are in no way relevant to the environment, can be as effective at predicting species distributions as models using real predictors. Of course, such predictions are neither informative about causation nor useful in predicting changes driven by dynamic variables.

We offered biological predictors that could either represent or influence, more proximately than do physical variables alone, the availability of prey in the foraging environment of deep-diving cetaceans. This addition slightly improved the performance of SDMs for sperm whales, but not beaked whales, although model performance was still lower compared to the other cetacean species for which previous models exhibit strong explanatory and predictive performance. Biological predictors did not improve the performance of the SDM for Baird's beaked whale, which performed relatively well with only physical variables. For the nine other cetacean species, biological predictors improved performance for five, impaired performance for one, and had mixed or no effects on performance for three. We also developed models using only biological predictors, but their performance was considerably worse than models using physical variables as well.

The model prediction maps presented here (Figures 3–6) are very similar to those in Becker et al. (2020) for species in which biological predictors did not improve model performance (beaked whales, blue whale, striped dolphin). Most of the models that retained added biological variables gave predictions that were generally consistent with observed sightings (the deep-diving sperm whale, and most of the other whale and dolphin species). The exception was long-beaked common dolphin; our model predicted high densities along the coast far north of the Southern California Bight and outside of this species' normal range (Carretta et al., 2011; Gerrodette & Eguchi, 2011). Becker et al. (2020) used a spatial term (bivariate spline of longitude and latitude) that constrained the predicted distribution to this species' normal range off central and southern California.

We used predictor variables, both physical and biological, that have plausible effects on feeding or other life processes. Forage availability is difficult to assess at spatial scales relevant to cetaceans by in situ sampling, and

predictive models rarely go beyond zooplankton. This is a limitation that pervades SDMs of marine predators. Some previous studies have used biological predictors related to prey availability in cetacean species distribution models, but results have been inconsistent. In a recent paper, Virgili et al. (2021) investigated the use of SEAPODYM micronekton estimates in SDMs of ziphiid beaked whales and sperm whales in the North Atlantic basin. The authors found that these predictors were not selected for the beaked whale model and only marginally improved performance for the sperm whale model. They suggest that the epipelagic and mesopelagic micronekton might not represent prey utilized by these deep-diving predators. Similarly, our results likewise show that SEAPODYM mesopelagic micronekton estimates are not useful in models for deep-diving sperm whales and beaked whales; however, epipelagic micronekton estimates are at least a useful proxy for SDMs of many other cetaceans (Table 5). Pérez-Jorge et al. (2019) found that SEAPODYM estimates of meso-zooplankton biomass, but not micronekton, were useful predictors for distributions of surface-feeding baleen whales tracked in the North Atlantic. We did not use this variable because it was highly correlated with *chlint*, which represents primary producer biomass.

Multifrequency acoustic backscatter data offer another way to estimate the distribution of prey organisms. Such data have been used in studies of foraging by cetacean predators at fine spatial scales (Benoit-Bird & Au, 2003; Cade et al., 2021; Hazen et al., 2009), but are not extensive enough to be used for predicting distributions over larger scales.

The question remains why does predicting the distribution of deep-diving cetaceans remain more difficult than predicting that of the other species? Undoubtedly, it would help to have direct observations or accurate and detailed model estimates of the environment at the depths where these predators are feeding. For the present, however, does sample size or spatial distribution influence modeling success?

SDMs of species that are less widely distributed within the model domain, and thus have lower prevalence in sampled sites, are known to have higher TSS values (Allouche et al., 2006). A higher model performance (TSS) for species that are more aggregated (lower R), or less widespread throughout the study area, means that the model is better able to discriminate between presence and absence in geographical space, essentially because there are more observed zeros in a portion of the niche space that is distinct from the portion that is occupied. As a result, there is a pattern in geographic space that can be statistically explained by niche variables. An abundant species can be cryptic or hard to detect, like beaked whales, and thus have relatively few sightings in surveys. For a species that is either truly rare, or more abundant but rarely detected, if the few sightings are widespread over a study area, as for beaked whales or sperm whales, the aggregation index will indicate a near random distribution. On the other hand, an abundant and easily detectable species, like the humpback whale, can have a low prevalence if it has a strong preference for a small part of the study area. Humpbacks migrate to the U.S. West Coast during summer to feed on krill and small fish over the continental shelf (Calambokidis et al., 2015).

Model performance in our study is not dependent on the number of sightings (Figure 7a). Cuvier's beaked whales and sperm whales have very few sightings in our data and the lowest SDM performance. In contrast, Baird's beaked whale has the smallest number of sightings but a SDM performance better than most species. The poor performance of SDMs for Cuvier's beaked whales and sperm whales is not fully explained by the low number of sightings in the study area. The distribution of those few sightings throughout the study area also impairs model performance.

We argue that the widespread distribution of these species impairs model performance (Figure 7b). For all species, model performance declines as the distribution of sightings becomes less aggregated. Cuvier's beaked whales and sperm whales have the least aggregated sightings and the worst model performance. Random spatial patterns can be parsimoniously predicted without any covariates (e.g., with a homogeneous distribution over the study area), thereby limiting the scope for inferring the importance of these covariates. A species with a small number of sightings can have an aggregated spatial pattern: Baird's beaked whale had the smallest number of sightings (40), yet they were aggregated similarly to several dolphin species and the SDM accurately predicted their aggregation along the continental slope off California and near the seamounts associated with the Juan de Fuca Ridge off Oregon.

4.1 | Caveats and limitations

As with all modeling studies, there are caveats and limitations, particularly relating to spatial and temporal scales of the data and to species distribution patterns.

The CCE study area is dominated by onshore-offshore gradients (Figures S1 and S2). At the large scale of the study area as a whole, cetaceans tend to be distributed either offshore or along the coast, with some showing latitudinal tendencies in addition to the onshore-offshore preferences. We used monthly 0.25° fields of predictor variables. This coarse scale is not appropriate for studying responses to small-scale environmental features such as fronts, mesoscale eddies or forage patches (Benoit-Bird & Lawson, 2016; Palacios et al., 2013). The surveys were not designed for this kind of study; tracklines within a survey year were separated by ∼100 km and weeks to months. Therefore, the distribution patterns resolved by the sampling were on scales of at least 0.25° in space and about 1 month in time.

On the other hand, our California Current study area covers a small part of the geographic ranges of the resident or migratory cetaceans sighted during our summer–fall surveys. Some species are distributed widely and the study area is only a small area within a global range. For others, the study area is at a latitudinal edge of a smaller range that extends well beyond either to the north or south. Thus, as for nearly all studies and applications using SDMs, the models based on our California Current survey data do not encompass the entire range of these species in either geographical or environmental space. With our data, we cannot address questions such as why seasonal migrators visit the region or what factors determine global range limits.

A spatial term (bivariate spline of longitude and latitude) was not included in our models, although it has improved the performance of SDMs for certain purposes (Becker et al., 2019; Cañadas & Hammond, 2008; Forney et al., 2012; Hedley & Buckland, 2004; Tynan et al., 2005; Williams et al., 2006). As discussed above, our predicted distributions are very similar to those in Becker et al. (2020) for most species. They used a fixed spatial term in their models, which can be useful for some purposes, such as avoiding potential interactions of fishery operations or ship traffic with cetaceans. However, the inclusion of a spatial term is not useful for explaining the ecological factors influencing the distribution of animals or for predicting responses to a changing environment.

4.2 | Conclusions

Species distribution models are used for a variety of science and management objectives, including abundance estimation, mitigation of bycatch and vessel strike threats, elucidation of community and ecosystem structure, and prediction of effects of climate change. The selection of predictor variables depends on the purpose of the prediction. If understanding or future projection are an objective, predictor variables should be selected with some ecological relevance. However, data availability constrains choices of predictor variables. Modelers of top predator distributions commonly bemoan the lack of data on prey abundance. We were able to improve the performance of models of deep-diving cetaceans by including variables related to prey availability, but these models still did not perform as well as we had hoped. For models of other whale and dolphin species that feed at or near the surface, some of these variables were always selected as predictors along with physical variables, but did not always improve model performance. Useful spatial–temporal data on near-surface and deeper prey will hopefully become available in the future through higher-resolution modeling of biogeochemical processes and trophic interactions.

The deep-diving cetaceans that have been challenging to model successfully have other characteristics that hinder model performance. Fewer sightings that are nearly randomly distributed will not result in a useful environmentally-driven model of spatial distribution. Models that combine observations from multiple data sources—visual sightings, acoustic detections, and tag records—may offer additional inference for such cryptic species. Other tools can help us understand how these species use their environment and to manage anthropogenic and climate-related threats to their welfare, for example monitoring of abundance, bycatch, or life history parameters.

AUTHOR CONTRIBUTIONS

Paul C. Fiedler: Formal analysis; writing – original draft. **Elizabeth A. Becker:** Methodology; writing – review and editing. **Karin Forney:** Methodology; writing – review and editing. **Jay Barlow:** Conceptualization; investigation. **Jeffrey Moore:** Investigation; writing – review and editing.

ORCID

Paul C. Fiedler https://orcid.org/0000-0002-4792-1013
Karin A. Forney https://orcid.org/0000-0002-9195-4701
Jay Barlow https://orcid.org/0000-0001-7862-855X

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