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National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Science Center

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Predictive Modeling of Cetacean Densities in the California Current Ecosystem based on Summer/Fall Ship Surveys in 1991- 2008.

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ABSTRACT

We use data from six ship-based cetacean and ecosystem assessment surveys in the California Current Ecosystem (CCE) to update habitat-based density models for 11 species and one small-beaked-whale guild. We previously had modeled cetacean density as a function of oceanic variables for the same 12 species/guild using data collected during four line-transect ship surveys conducted in the CCE in summer and fall of 1991, 1993, 1996, and 2001. An independent set of survey data collected in the summer and fall of 2005 was used to validate the models. These estimates were incorporated into a web-based system that allows users to estimate cetacean density within any user-defined region within the CCE study area. In this study, data from an additional line-transect survey conducted in 2008 were pooled with the 1991-2005 data and used to re-build the habitat-based density models. We also refit the 1991-2008 data to the previous “best” models to compare model performance. The additional year of data provided increased sample sizes and a greater range of oceanic conditions for robust model development. Predicted densities for each year were smoothed and then averaged to produce a composite grid that represents our best estimate of CCE cetacean density over the past 20 years. The final model predictions were used to update the web-based system and also provided to the U.S. Navy to help assess potential impacts from their at-sea training and testing activities.

INTRODUCTION

To ensure compliance with U.S. regulations including the Endangered Species Act and the Marine Mammal Protection Act, the Navy and others who conduct major activities in the marine environment (e.g., oil and gas production) must estimate the number of marine mammals that might be affected by their at-sea activities. Typically these activity areas are much smaller than the broad-scale study areas generally used to estimate cetacean abundance. Along the U.S. West Coast, the abundance of many cetaceans has been estimated based on ship surveys conducted during the summer and fall since 1991 (Barlow 1995; Barlow 2003; Barlow and Forney 2007). Cetacean densities are generally estimated using line-transect methods (Buckland et al. 2001), and the resulting estimates are often used in stock assessment research, for which cetacean abundance is presented for very large geographic strata (e.g., waters off California, Oregon, and Washington; Carretta et al. 2012). Stratified line-transect analyses can provide density estimates for smaller areas, such as the Southern California Bight (e.g., Barlow and Forney 2007); however, the associated reduction in sample size (i.e., the number of cetacean sightings) often prohibits such stratified estimates.

Habitat-based density models allow predictions of cetacean densities on a finer spatial scale than traditional line-transect analyses because cetacean densities are estimated as a continuous function of habitat variables (e.g., sea surface temperature, seafloor depth, distance from land, etc.; Redfern et al. 2006). Within the modeled study area, cetacean densities can be predicted wherever these habitat variables can be measured or estimated. In a previous study (Barlow et al. 2009; Forney et al. 2012), we modeled cetacean density as a function of oceanic variables for 11 species and one small-beaked-whale guild in the California Current Ecosystem (CCE). Cetacean sighting data used to develop the models were collected by the Southwest Fisheries Science Center (SWFSC) on four systematic line-transect surveys during the summer and fall of 1991, 1993, 1996, and 2001 (Fig. 1). To evaluate predictive power, a separate set of survey data collected in 2005 was used for cross-validation (i.e., models were built with the 1991-2001 data and used to predict densities for the novel 2005 year). Following model selection and validation, the best models were then re-fit to include the additional year of data. Predictions from the final models were incorporated into a web-based system that allows users to

estimate cetacean density and associated coefficients of variation within any user-defined area within the CCE study area. The web site (<http://serdp.env.duke.edu>) is currently hosted by Duke University.

In this study, we pooled data from the most recent CCE line-transect survey conducted in 2008 (Fig. 2) with the 1991-2005 data to re-build the habitat-based density models. Additional data from the 2008 cruise served to increase sample sizes and provide a greater range of oceanic conditions for model development. Consistent with the previous study (Barlow et al. 2009; Forney et al. 2012), models were built for striped dolphin (*Stenella coeruleoalba*), short-beaked common dolphin (*Delphinus delphis*), Risso's dolphin (*Grampus griseus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), northern right whale dolphin (*Lissodelphis borealis*), Dall's porpoise (*Phocoenoides dalli*), sperm whale (*Physeter macrocephalus*), fin whale (*Balaenoptera physalus*), blue whale (*B. musculus*), humpback whale (*Megaptera novaeangliae*), Baird's beaked whale (*Berardius bairdii*), and a small-beaked-whale guild (including Cuvier's beaked whale, *Ziphius cavirostris*, and beaked whales of the genus *Mesoplodon*). Analysis methods largely followed those used for the original analyses, although for each species/guild we compared both a "rebuilt" model (all predictor variables considered during model building) and a "refit" model (our previous "best" models refit to the 1991-2008 dataset). Models were evaluated based on a collection of quantitative and qualitative methods, and final models were selected based on their ability to capture known distributions for each species. Density predictions from the selected models were then used to update the web-based system.

MATERIALS AND METHODS

Cetacean Survey Data

Cetacean sighting data used to construct the habitat-based density models were collected within the 1,141,800 km² CCE study area from late July through early December of 1991, 1993, 1996, 2001, 2005, and 2008 using established SWFSC line-transect survey methods that were consistent on all surveys (Kinzey et al. 2000; Barlow and Forney 2007; Barlow 2010). The observer team consisted of six individuals who had previous experience searching and identifying marine mammals at sea. Each observer rotated every 40 minutes among starboard

observer, port observer, and data recorder positions that were located on the flying bridge of the ship. The starboard and port observers searched for animals using pedestal-mounted 25x150 binoculars while the data recorder searched using unaided eye and 7x50 handheld binoculars. Marine mammals were identified to the species level whenever an observer could make a determination with certainty. Otherwise, animals were identified to the lowest taxonomic level possible (e.g., “beaked whale”). Minimum, maximum, and “best” group size estimates were recorded confidentially by each of the observers who saw the group (Kinzey et al. 2000). We used only on-effort sightings made on systematic transect lines and identified to species (with the exception of a small-beaked-whale group, for which we relied on genus identification) for building the models. Group size estimates used for modeling were calculated as the average of all observers’ “best” estimates; if no “best” estimate was recorded, we used the average of the minimum estimates.

To create samples for modeling, cetacean survey data from the 2008 shipboard survey were separated into continuous transect segments of approximately 5-km length as described by Becker et al. (2010) and as had been done previously for the 1991-2005 survey data (Barlow et al. 2009; Forney et al. 2012). Species-specific sighting information (number of encounters, mean group size) and environmental data (described below) were assigned to each segment based on the segment’s geographical midpoint.

***In situ* Oceanographic Data**

In addition to cetacean sighting data, oceanographic variables were measured during the 1991-2008 surveys, some of which were included as potential habitat predictors in the density models. Sea surface salinity (SSS) was recorded continuously at 0.5- to 2- minute intervals from a thermosalinograph and averaged over 5-km intervals to reduce both the number of observations and the discrepancy in sample spacing along and between transects. Mixed layer depth (MLD; the depth at which temperature is 0.5°C less than surface temperature) was estimated from expendable bathythermograph (XBT) and conductivity-temperature-depth (CTD) casts collected three to five times per day. Surface chlorophyll (CHL; mg m⁻³) was estimated at the same stations from the surface bottle on the CTD or from bucket samples analyzed by standard techniques (Holm-Hansen et al. 1965). Details of the sampling protocols are described in Barlow et al. (2010).

SSS, MLD, and CHL measurements were interpolated to obtain continuous spatial grids of the *in situ* oceanographic habitat variables (surface chlorophyll values were log-transformed to normalize the data for interpolation). In our original analysis, five interpolation methods were compared and kriging was found to be the optimal method for smoothing habitat variables (see Barlow et al. 2009 for details). Kriging was used to create yearly spatial grids for the five CCE surveys (1991, 1993, 1996, 2001, and 2005). The method was used in this study to create SSS, MLD, and CHL grids from the 2008 survey data. Values of SSS, MLD, and CHL for each segment midpoint were estimated from the interpolated yearly fields using Surfer's (Version 9, Golden Software, Inc., 2009) *residual* command.

Remotely Sensed Oceanographic Data

In addition to the *in situ* measurements, remotely sensed sea surface temperature (SST) data (National Oceanic and Atmospheric Administration/National Environmental Satellite, Data, and Information Service/Pathfinder v5) and measures of its variance were included as potential habitat predictors, using 8-day running average SST composites (Becker et al. 2010). Dynamic oceanic processes such as upwelling, fronts, and eddies often result in surface SST gradients between colder upwelled water and warmer surface waters. Our original analysis used the coefficient of variation of SST in the models to capture these gradients. However, it has been suggested that these gradients are more accurately captured by the standard deviation of SST, SD(SST). We used SD(SST) in these analyses.

Additional Habitat Variables

Water depth, bathymetric slope, and distance to the 2,000m isobath were also included in the models as potential predictors. This isobath represents the transition from slope waters to the abyssal plain and is an important habitat feature for many cetacean species (Barlow et al. 2009; Becker et al. 2010; Forney et al. 2012). Water depth in each segment was obtained from the ETOPO2 2-minute global relief data (U.S. Department of Commerce 2006). Bottom slope was calculated as the magnitude of the bathymetry gradient using the gradient operator tool in GMT (Generic Mapping Tools, Wessel and Smith 1998). Distance to the 2,000m isobath from each segment midpoint was estimated using the ArcGIS (Version 9.2, ESRI, Inc.) *near* command. For most species, we used negative values of distance to the 2000m isobath in waters shallower

than 2,000m to differentiate shelf/slope from abyssal plain waters. The only exception to this rule was for Baird's beaked whale; because this species is closely associated with the shelf break and equally likely to be on either side of it, absolute distance to the 2000-m isobath was more ecologically meaningful. Average Beaufort sea state on each segment was also included as a predictor to account for potential biases due to changes in detection probability (Barlow et al. 2001); segments with average sea state values exceeding Beaufort 5 were not included in this analysis.

Analytical Methods

The analytical methods used to build the habitat-based density models were similar to those used previously for the CCE (Barlow et al. 2009; Becker et al. 2010, 2012a; Forney et al. 2012) and are briefly summarized here.

We used generalized additive models (GAMs; Hastie and Tibshirani 1990) for each species/guild to relate encounter rate (number of sightings) and group size in each segment to the habitat variables described above: SST, SD(SST), SSS, MLD, log-transformed CHL (lnCHL), water depth (depth), bathymetric slope (slope), distance to the 2,000m isobath, and Beaufort sea state. Separate encounter rate and group size GAMs were built for each species using the *step.gam* function in the statistical software package S-PLUS (Professional Edition Version 6.1, Release 1 for Windows, Insightful Corp., 2001). We used a stepwise forward/backward variable selection procedure in which each model was fit three 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 (AIC; Akaike 1973) was used in *step.gam* as the basis for selecting the variables included in each model and the degrees of freedom for the cubic smoothing splines. A maximum of three 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). All variables and the highest degrees of freedom for each variable found in any candidate model within two AIC units of the best model were included in the final model (Becker et al. 2012a).

Encounter rate models were built using all transect segments, regardless of whether they included sightings, while group size models were built using only those segments that included sightings. For the encounter rate models, we fit Poisson GAMs in which overdispersion was

corrected using a quasi-likelihood model. Segment length was included as an offset term in the models to account for the varying length of our segments and 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 (Ferguson et al. 2006).

Density (number of animals per km²) 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):

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

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 zero 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 survey data (Barlow 2003). For many species, 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. Final density predictions were based on the average observed Beaufort sea state during the survey years, to match the average conditions under which the $f(0)$ and $g(0)$ estimates were derived (see Barlow et al. 2009, Becker et al. 2010 for further details).

In addition to the models built using the full suite of predictor variables as described above (hereafter the “rebuilt models”), a second set of encounter rate and group size models was developed for each species/guild by re-fitting the “best” model selected in our previous analysis to the 1991-2008 dataset (Barlow et al. 2009; Forney et al. 2012). The “refit models” were developed by forcing the previous models’ variables and associated degrees of freedom on the combined 1991-2008 dataset. The only exception to this was for fin whales. Fin whale abundance has increased during the range of the survey period (Barlow and Forney 2007; Moore and Barlow 2011), so models were rebuilt and refit using only survey data from 1996-2008 to represent more current conditions.

This process provided us with two sets of candidate models (i.e., a rebuilt model and a refit model) for each species/guild. The segment-specific predictions from both sets of models were interpolated to the entire CCE study area using inverse distance weighting as described by Becker et al. (2010). Grids were created for each of the six individual survey years, and the individual grid cells were averaged across all years to calculate mean species density and its variance.

To identify the best models, we compared explained deviance, average squared prediction error (ASPE; Hastie & Tibshirani 1990), and ratios of observed to predicted densities. Observed and predicted densities (defined as the encounter rate multiplied by the group size) were calculated for each segment and summed for all segments within a year and for all years. The within-year metrics provide an indication of the model's ability to predict interannual variability in species abundance, which is one of the largest sources of variance in the CCE study area (Forney and Barlow 1998; Barlow et al. 2009; Becker et al. 2010; Forney et al. 2012). The accuracy of the spatial patterns of predicted density were evaluated using observed to predicted density ratios calculated for eight geographic strata within the CCE study area (Fig. 3): four north-south strata consistent with those used for line-transect abundance estimation (Barlow & Forney 2007), and an offshore-onshore division at the 2,000-m isobath, as a proxy for the shelf-break. The four north-south strata include waters off Oregon and Washington (322,200 km² north of 42°N), northern California (258,100 km² south of 42°N and north of Point Reyes at 38°N), central California (243,000 km² between Point Conception at 34.5°N and Point Reyes), and southern California (318,500 km² south of Point Conception). Finally, sighting locations from the 1991-2008 surveys were plotted on the multi-year average density grids, because the human eye can be superior to statistics for comparing patterns (Wang et al. 2004). These maps were evaluated by experts knowledgeable about cetacean ecology in the CCE, and final models were selected based on their ability to capture known distributions for each species. Density predictions from the selected models were then used to update the web-based system so that users could access the most recent data.

RESULTS

The rebuilt models were selected as the final best models for all of the species/guild with the exception of the sperm whale, for which the refit model was selected (Table 1). The variables entering the final rebuilt encounter rate models (Table 1 and Fig. 4) were similar to those included in our previous models (see Table 21 in Barlow et al. 2009), although for many of the variables, the degrees of freedom for the smoothing splines increased. The variables included in the final rebuilt group size models for all species were also similar, although there tended to be a greater number of variables included in the updated models (Table 1 and Fig. 5). The percentage of deviance explained ranged from 4% (sperm whale) to 43% (humpback whale) for the encounter rate models and from 3% (short-beaked common dolphin) to 38% (northern right whale dolphin) for the group size models (Table 2). Model performance as indicated by ASPE differed among species (Table 2), but for the group size models these differences in part reflect the range of species-specific group sizes (e.g., short-beaked common dolphins tend to occur in highly variable groups of up to thousands of animals while blue whales are usually found singly or in small groups).

There was relatively good agreement between the ratios of observed to predicted density for all species summarized over all years for the entire study area (Tables 3 and 4). Most ratios were within 10% of unity except for fin whales. This deviation was likely caused by overestimation of fin whale density during the earlier years (particularly 1991; Table 3), because fin whale abundance has increased markedly in the CCE during the study period and the models were built using only 1996-2008 (Barlow and Forney 2007; Moore and Barlow 2011). Similar to previous analyses, the individual yearly ratios are highly variable, reflecting the reduced predictive ability for any specific year, in part due to smaller sample sizes resulting from data stratification (Barlow et al. 2009; Becker et al. 2010; Forney et al. 2012). The geographically stratified density ratios also show large variability, both among species and among strata (Table 4).

Density plots comparing observed sighting locations to the yearly predictions confirm the high interannual variability in species distribution within the CCE study area (Barlow et al. 2009; Becker et al. 2010; Forney et al. 2012) and demonstrate that the models were effective at capturing this variability (Fig. 6). The multi-year average density plots incorporate this

interannual variability and were broadly effective at capturing general distribution patterns of the 12 modeled cetacean species and small-beaked-whale guild (Fig. 7). Similar to our past study (Barlow et al. 2009; Forney et al. 2012), uncertainty in model predictions (Fig. 8) tended to be higher off Oregon and Washington where there were only four years of data (the 1991 and 1993 surveys were conducted off California only; Fig. 1).

DISCUSSION

The results of this study provide our best estimate of average cetacean density and distribution over the past 20 years within the California Current region off the U.S. west coast. Our previous best estimates were based on models built with the 1991-2001 data and then refit to include the additional 2005 data; the models in this study were developed with two additional years of systematic survey data (2005 and 2008). The additional data provided increased sample sizes and a greater range of oceanic conditions for robust model development, as was evident in the selection of the “rebuilt” vs “refit” models for all but one species. The multi-year averaged density plots reflect mean cetacean densities, taking into account both the varying oceanographic conditions and different levels of sampling coverage achieved during the six cetacean surveys. In the absence of forecast predictions (Becker et al. 2012a) or current, real-time survey data, these model predictions provide our best expectation of average species distribution patterns. However, patterns of cetacean distribution and abundance in any given year can be markedly different from the average, particularly in the highly dynamic CCE.

The model for fin whales built with only the 1996-2008 survey data exhibited better overall performance than the model built with the full 1991-2008 dataset, as evident from plots of sighting locations and comparisons of the precision of the yearly and regional observed to predicted density ratios. The standard error of the yearly density ratios for models built with the 1991-2008 data was higher (0.20 vs. 0.17), as was the standard error of the regional ratios (0.21 vs. 0.20). Although the study area ratio of observed to predicted density for the 1996-2008 model was not within 10% of unity, this deviation was likely caused by overestimation of fin whale density during the earlier years (particularly 1991; Table 3). It is difficult to detect trends in cetacean abundance due to high levels of uncertainty in yearly estimates and a correspondingly low statistical power to detect trends (Taylor and Gerrodette 1993; Forney 1999;

Taylor et al. 2007). However, a recent study using Bayesian hierarchical modeling indicates that the abundance of fin whales in the CCE study area increased during the 1991-2008 survey period, most likely from *in situ* study area population growth combined with distribution shifts (Moore and Barlow 2011). Our models rebuilt using survey data from 1996-2008 represented the more recent conditions. This provides a unique example whereby increased sample size did not equate with increased model performance because of a confounding population increase.

The multi-year density maps provide the most recent spatially explicit estimates of average CCE cetacean density and variance. The smoothed maps are available online at <http://serdp.env.duke.edu>. Studies planned for the future include the evaluation of additional remotely sensed predictor variables, incorporating the area searched to account for detection differences (Becker et al. 2012b), predicting on habitat-based pixels rather than transect segments, and evaluating the ability of the broad-scale CCE habitat models to predict cetacean densities at finer spatial extents such as the Southern California Bight.

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Table 1. Predictor variables included in the final rebuilt (RB) or refit (RF) encounter rate (ER) and group size (GS) models for the 1991-2008 survey data. The expression $s(x,n)$ indicates a non-parametric spline of the variable x with n degrees of freedom. Variable abbreviations are as follows: SST = sea surface temperature, SD(SST) = standard deviation of SST, SSS = sea surface salinity, MLD = mixed layer depth, $\ln\text{CHL}=\ln(\text{surface chlorophyll concentration})$, depth = water depth, slope = bathymetric slope, dist = distance to the 2,000m isobath, beauf = Beaufort sea state, offset = offset($\ln(\text{effective distance searched in km})$).

Common Name (Scientific name)	Model	GAM
Striped dolphin (<i>Stenella coeruleoalba</i>)	RB	ER $s(\text{depth}, 3) + s(\text{SST}, 2) + \text{beauf} + \text{offset}$ GS $\text{slope} + \text{dist} + \text{MLD} + s(\ln\text{CHL}, 2)$
	Short-beaked common dolphin (<i>Delphinus delphis</i>)	ER
GS		$s(\text{SST}, 3) + \text{SSS}$
Risso's dolphin (<i>Grampus griseus</i>)	RB	ER $s(\text{depth}, 2) + s(\text{SST}, 3) + s(\text{beauf}, 2) + \text{offset}$ GS $\text{slope} + \text{SST} + \text{MLD}$
	Pacific white-sided dolphin (<i>Lagenorhynchus obliquidens</i>)	ER
GS		$\text{depth} + \text{SSS} + s(\text{beauf}, 3)$
Northern right whale dolphin (<i>Lissodelphis borealis</i>)	RB	ER $s(\text{depth}, 3) + s(\text{SST}, 3) + s(\text{SSS}, 3) + s(\text{MLD}, 2) + s(\ln\text{CHL}, 3) + s(\text{beauf}, 3) + \text{offset}$ GS $s(\text{SST}, 2) + \text{SD}(\text{SST}) + \text{MLD} + \ln\text{CHL} + s(\text{beauf}, 2)$
	Dall's porpoise (<i>Phocoenoides dalli</i>)	ER
GS		$s(\text{slope}, 3) + s(\text{SST}, 2) + \text{SSS} + s(\text{MLD}, 2) + \text{beauf}$
Sperm whale (<i>Physeter macrocephalus</i>)	RF	ER ² $s(\text{depth}, 2) + s(\text{CV}(\text{SST}), 3) + s(\ln\text{CHL}, 3) + s(\text{beauf}, 2) + \text{offset}$ GS $s(\text{dist}, 2) + \text{SST}$
	Fin whale (<i>Balaenoptera physalus</i>)	RB ¹
Blue whale (<i>Balaenoptera musculus</i>)		RB
	Humpback whale (<i>Megaptera novaeangliae</i>)	RB
Baird's beaked whale (<i>Berardius bairdii</i>)		RB
	Small-beaked-whale guild (<i>Ziphius cavirostris</i> & <i>Mesoplodon</i> spp.)	RB

*Absolute distance to the 2,000m isobath included based on known distribution patterns (see text for details)

¹Model built with 1996-2008 survey data

²The refit model used the coefficient of variation (CV) of SST instead of the SD(SST)

Table 2. Average squared prediction error (ASPE) and the percentage of deviance explained (Exp Dev) by the final encounter rate and group size models for each species. For taxonomic names, see Table 1.

Species	Encounter Rate Model		Group Size Model	
	ASPE	Exp Dev	ASPE	Exp Dev
Striped dolphin	0.05	9.2%	2,851	31.9%
Short-beaked common dolphin	0.62	13.2%	53,965	3.2%
Risso's dolphin	0.07	11.0%	695	15.6%
Pacific white-sided dolphin	0.08	25.1%	32,784	34.3%
Northern right whale dolphin	0.05	18.6%	9,802	37.9%
Dall's porpoise	0.20	39.6%	7.8	12.0%
Sperm whale	0.08	4.0%	65.8	9.6%
Fin whale	0.14	16.3%	3.2	8.2%
Blue whale	0.12	17.3%	0.78	9.8%
Humpback whale	0.09	42.6%	2.1	9.5%
Baird's beaked whale	0.03	15.1%	21.5	35.7%
Small-beaked-whale guild	0.07	6.5%	0.71	15.5%

Table 3. Ratios of observed to predicted density (defined as the encounter rate multiplied by the group size) for each survey year and for all years combined. The standard error of the ratios (SE) was calculated using the values from the individual years. For taxonomic names, see Table 1.

Species	Survey Year						All years	SE
	1991	1993	1996	2001	2005	2008		
Striped dolphin	1.30	0.76	0.30	0.97	1.49	0.59	0.91	0.18
Short-beaked common dolphin	0.58	1.32	0.90	0.70	1.64	0.95	0.99	0.16
Risso's dolphin	1.49	1.22	1.28	0.93	0.46	0.38	0.94	0.19
Pacific white-sided dolphin	0.08	0.26	1.15	0.51	1.76	0.85	0.93	0.25
Northern right whale dolphin	0.82	0.56	0.69	0.93	3.27	0.65	1.06	0.43
Dall's porpoise	0.91	0.61	1.35	0.82	0.91	0.80	1.02	0.10
Sperm whale	0.37	2.26	0.63	1.10	1.49	0.78	1.04	0.28
Fin whale	0.19	0.75	0.65	0.76	1.30	1.24	0.82	0.17
Blue whale	0.99	1.99	1.46	0.34	0.73	0.39	0.99	0.26
Humpback whale	1.10	2.34	0.82	0.98	0.75	1.29	1.00	0.24
Baird's beaked whale	0.00	3.72	0.50	0.69	1.08	1.13	1.03	0.53
Small-beaked-whale guild	1.20	1.68	1.00	0.55	0.61	0.97	0.99	0.17

Table 4. Ratios of observed to predicted density (defined as the encounter rate multiplied by the group size) for the California Current Ecosystem geographic strata (refer to Fig. 3 for locations). The standard error of the ratios (SE) was calculated using the values from the individual strata. A ratio of 0 indicates that there were no sightings of the species/guild within the stratum during any of the 1991-2008 surveys. Note that “All strata” reflect values for the entire study over all years and are thus identical to the “All years” ratios in Table 3. For taxonomic names, see Table 1.

Species	Geographic Strata								All strata	SE
	1	2	3	4	5	6	7	8		
Striped dolphin	0.00	0.00	1.31	0.00	0.57	0.00	1.02	0.40	0.91	0.18
Short-beaked common dolphin	0.10	0.00	1.43	0.05	1.10	0.59	0.75	1.10	0.99	0.19
Risso’s dolphin	0.52	0.94	1.04	0.24	1.41	1.10	0.94	1.05	0.94	0.13
Pacific white-sided dolphin	0.55	1.36	1.45	0.58	1.03	0.41	0.00	0.57	0.93	0.18
Northern right whale dolphin	0.75	0.51	0.66	0.55	3.81	0.65	0.28	0.16	1.06	0.42
Dall’s porpoise	0.85	1.02	1.26	0.85	0.77	1.51	0.21	0.74	1.02	0.14
Sperm whale	0.76	0.52	1.79	0.00	0.32	0.15	1.09	3.67	1.04	0.43
Fin whale	1.08	0.96	0.70	0.06	0.76	2.07	0.66	0.80	0.82	0.20
Blue whale	0.16	0.19	0.75	1.94	0.92	1.24	1.47	0.83	0.99	0.21
Humpback whale	0.98	0.95	0.46	0.83	1.33	1.50	0.43	0.25	1.00	0.16
Baird’s beaked whale	1.12	1.70	1.03	0.00	1.18	5.89	0.32	0.22	1.03	0.67
Small-beaked-whale guild	1.04	0.90	0.89	0.00	1.39	0.00	0.81	1.00	0.99	0.18

Figure 1. Completed transects for the Southwest Fisheries Science Center shipboard surveys conducted from late July through early December 1991/93, 1996, 2001, and 2005 off the U.S. West Coast. Thick transect lines were surveyed in Beaufort sea states of 0 to 2 and thin lines in Beaufort 3 to 5. Black lines on all maps indicate the boundaries of four geographic strata used for line-transect abundance estimation (Barlow and Forney 2007).

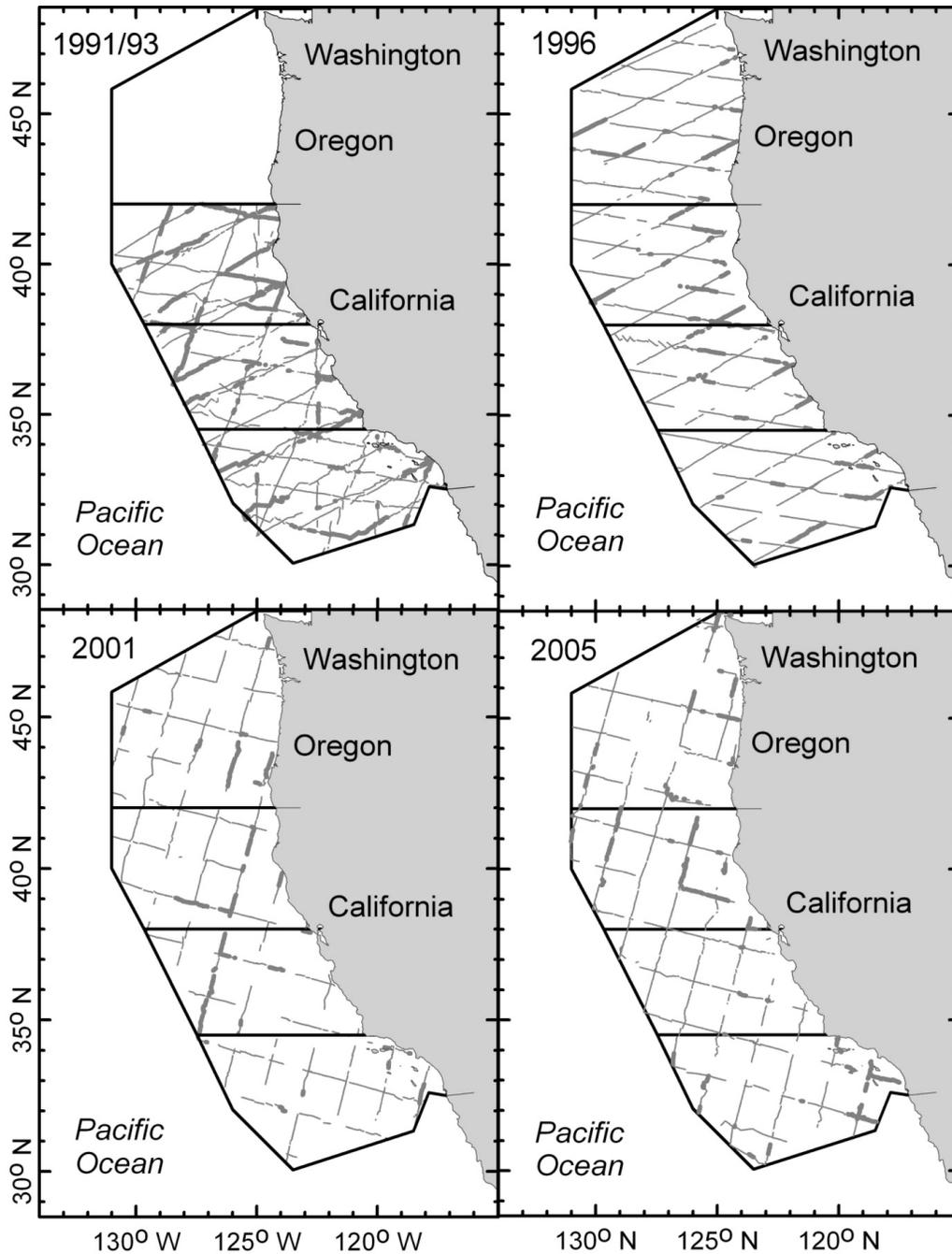


Figure 2. Completed transects for the Southwest Fisheries Science Center shipboard survey conducted 29 July through 30 November 2008 off the U.S. West Coast.

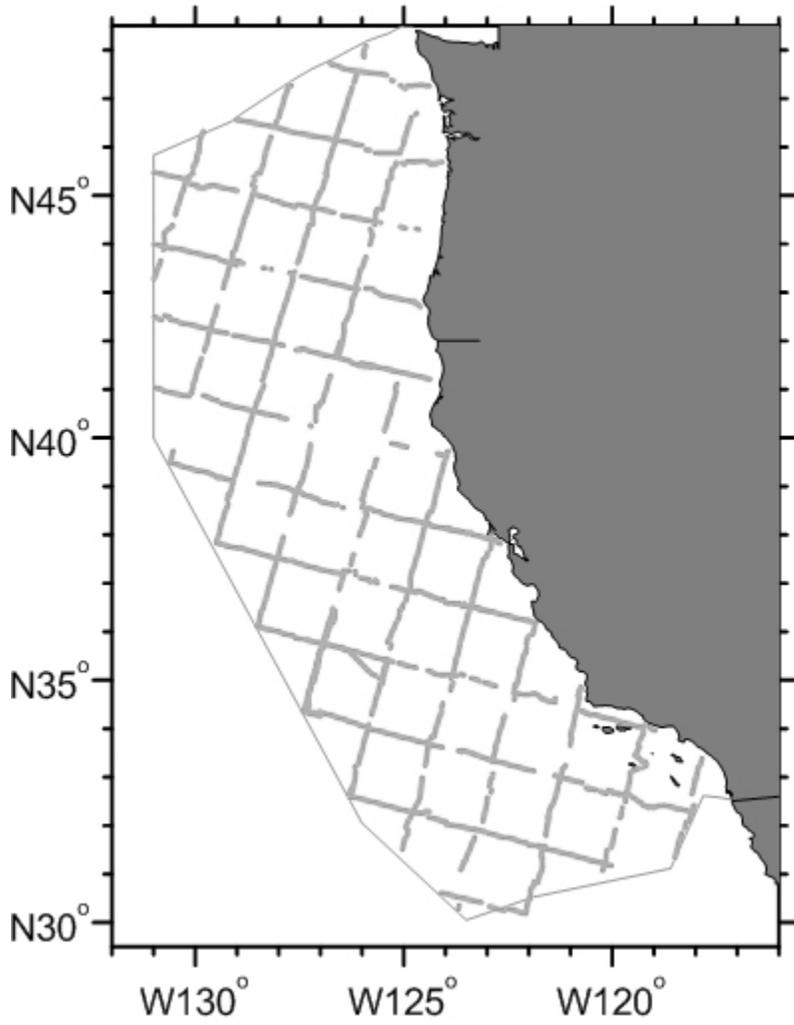


Figure 3. Eight geographic strata used to evaluate the accuracy of the spatial patterns of predicted density: the four north-south strata are consistent with those used for line-transect abundance estimation (Barlow and Forney 2007) and an offshore-onshore division occurs at the 2,000m isobath.

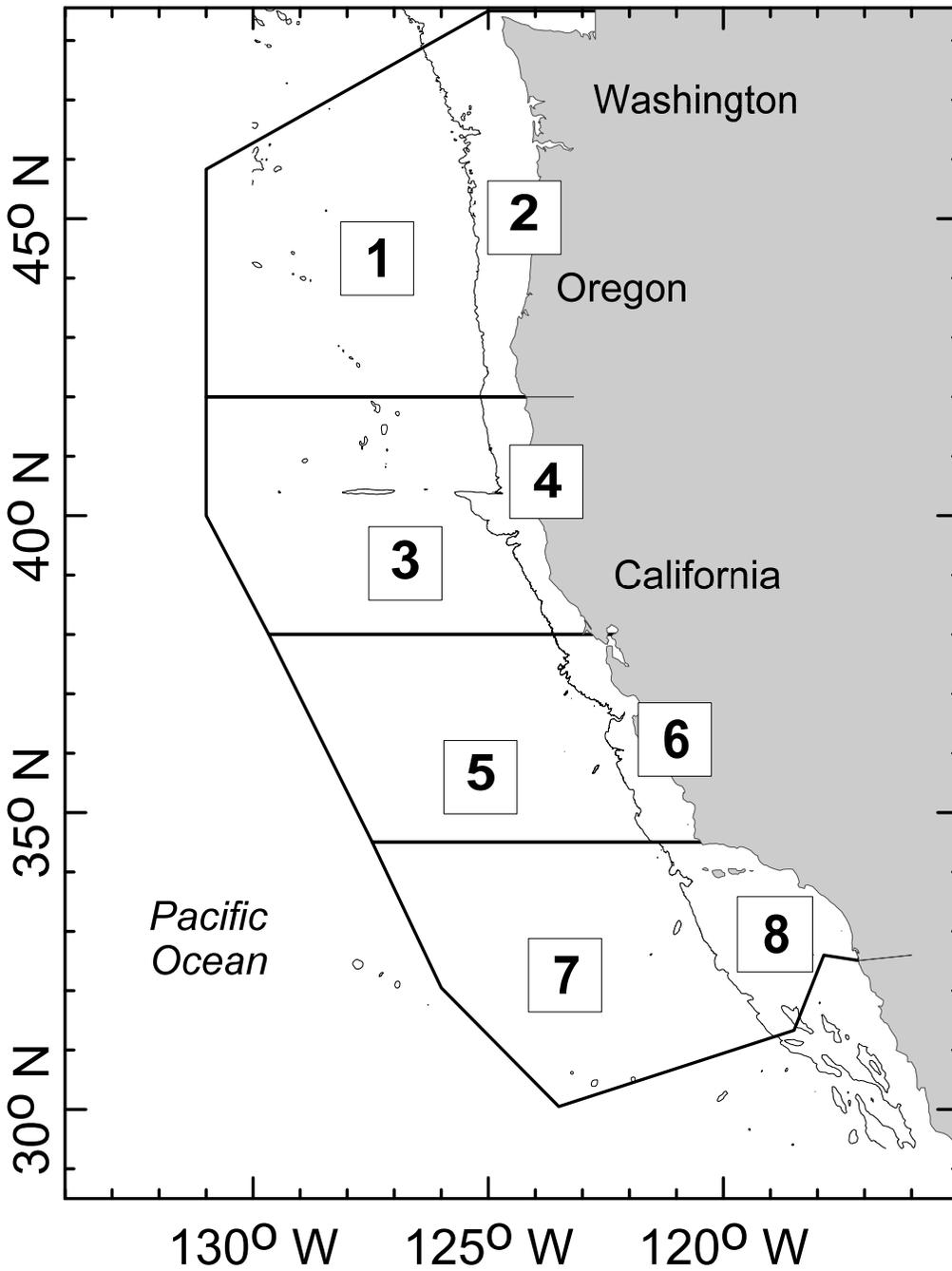
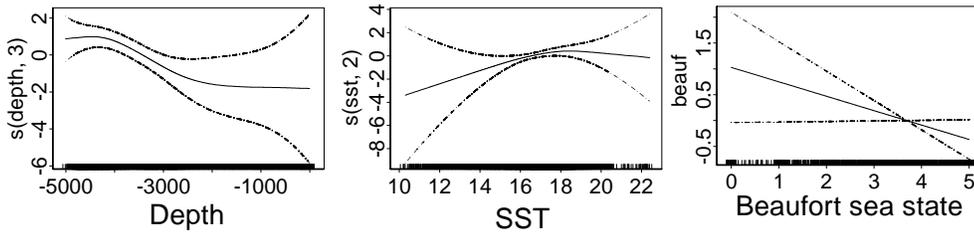


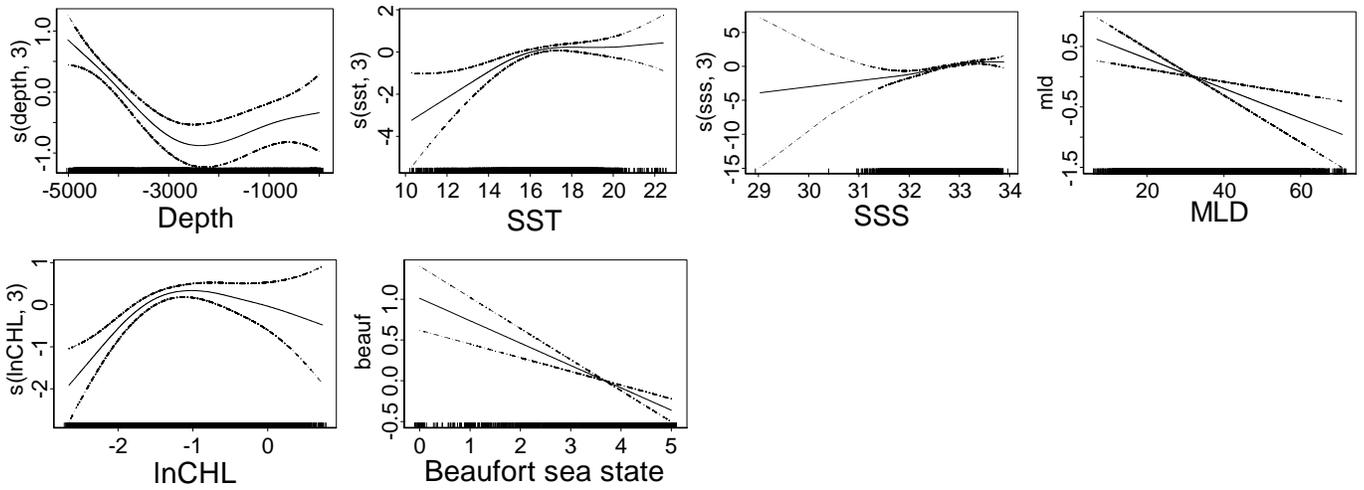
Figure 4. Encounter rate model functions for (a) striped dolphin, (b) short-beaked common dolphin, (c) Risso's dolphin, (d) Pacific white-sided dolphin, (e) northern right whale dolphin, (f) Dall's porpoise, (g) sperm whale, (h) fin whale, (i) blue whale, (j) humpback whale, (k) Baird's beaked whale, and (l) the small-beaked-whale guild. Models were constructed with both linear terms and smoothing splines having up to three degrees of freedom. Degrees of freedom for nonlinear fits are in the parentheses on the y-axis. Potential predictor variables included sea surface temperature (SST), the standard deviation of SST (SD(SST)), sea surface salinity (SSS), mixed layer depth (MLD), log-transformed CHL (lnCHL), water depth (depth), bathymetric slope (slope), distance to the 2,000m isobaths (dist), and Beaufort sea state (beauf). Data points for each variable are shown as tick marks on the x-axes. The y-axes represent the term's (linear or spline) function. Zero on the y-axis corresponds to no effect of the predictor variable on the estimated response variable (encounter rate). Scaling of y-axis varies among predictor variables to emphasize model fit. The dashed lines reflect 2x standard error bands (i.e., 95% confidence interval). For taxonomic names, see Table 1.

Figure 4

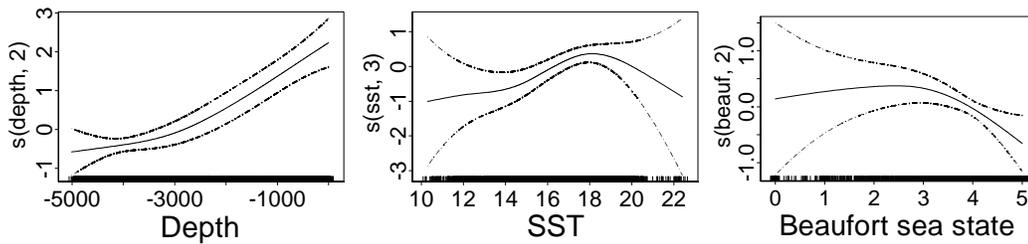
A) Striped Dolphin



B) Short-beaked Common Dolphin



C) Risso's Dolphin



D) Pacific White-sided Dolphin

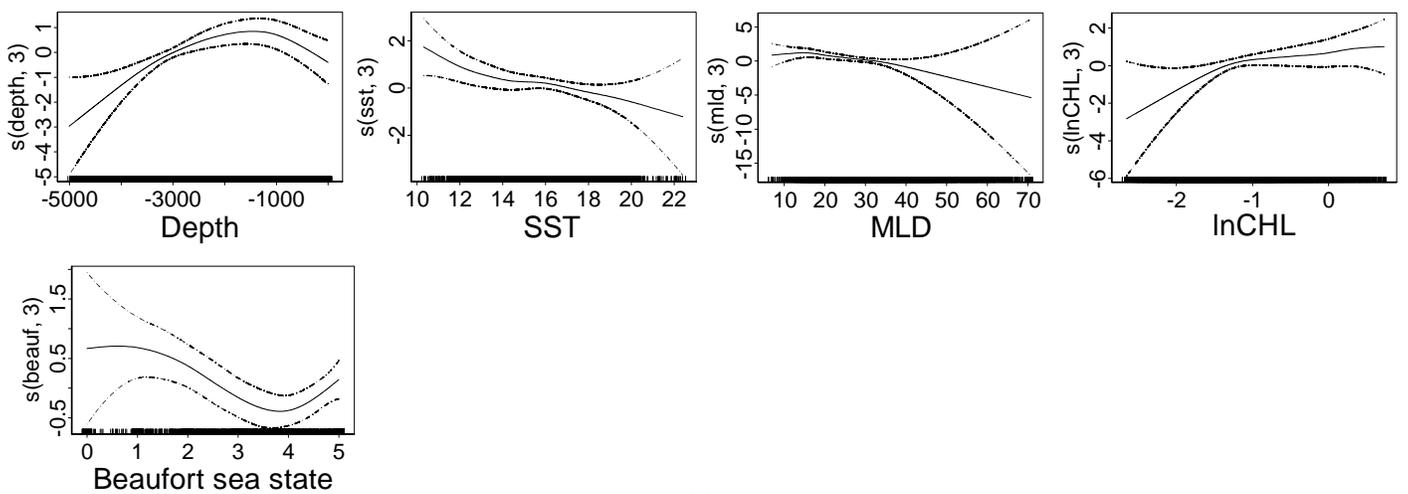
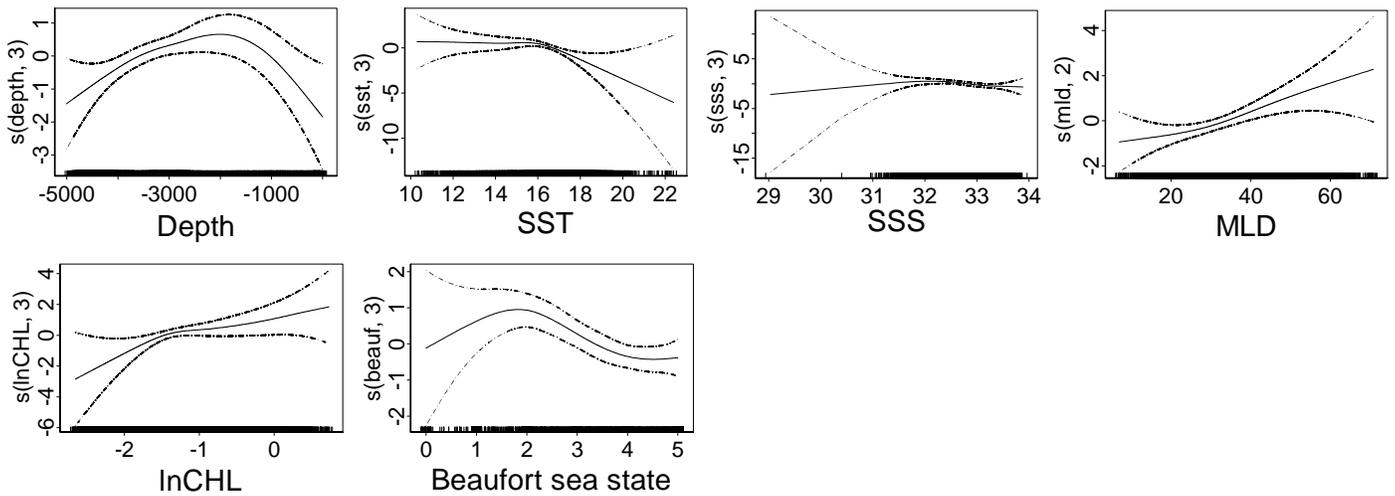
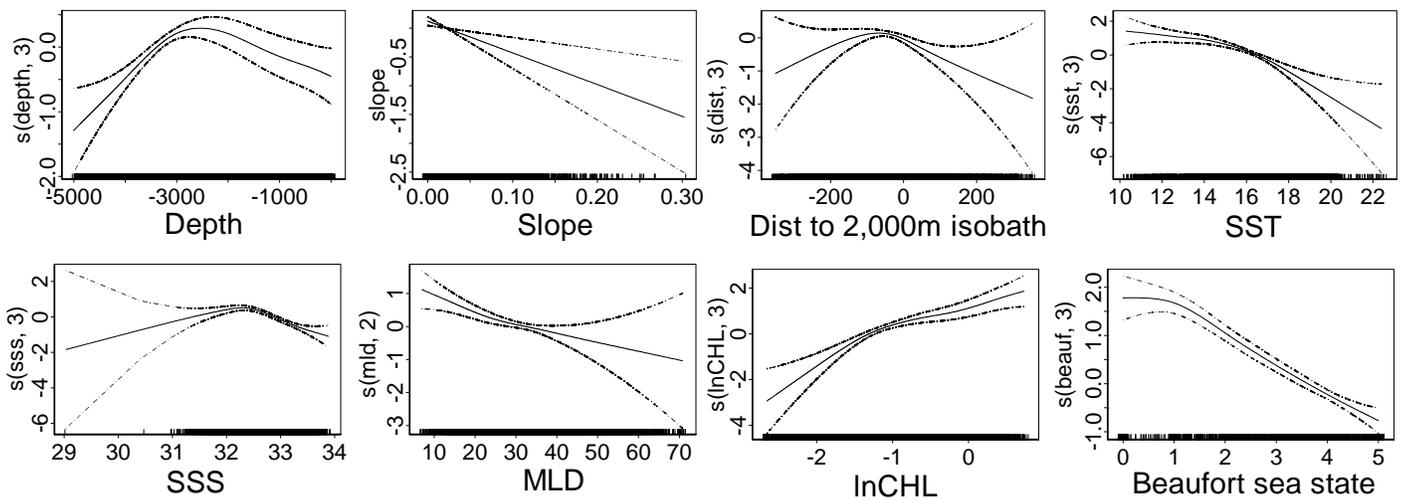


Figure 4 (cont.)

E) Northern Right Whale Dolphin



F) Dall's Porpoise



G) Sperm Whale

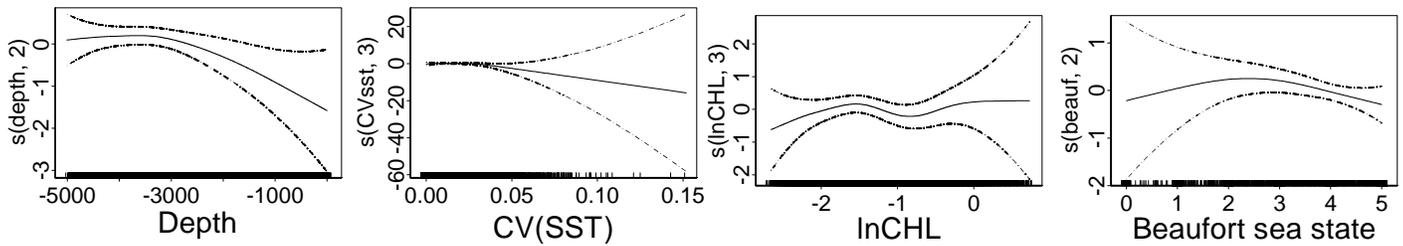
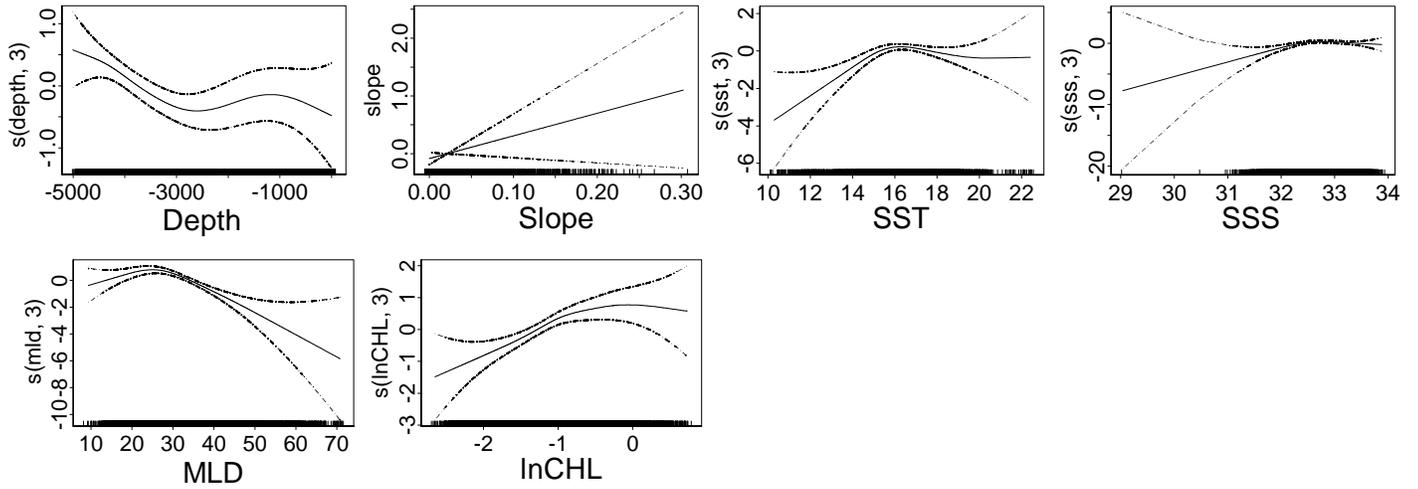
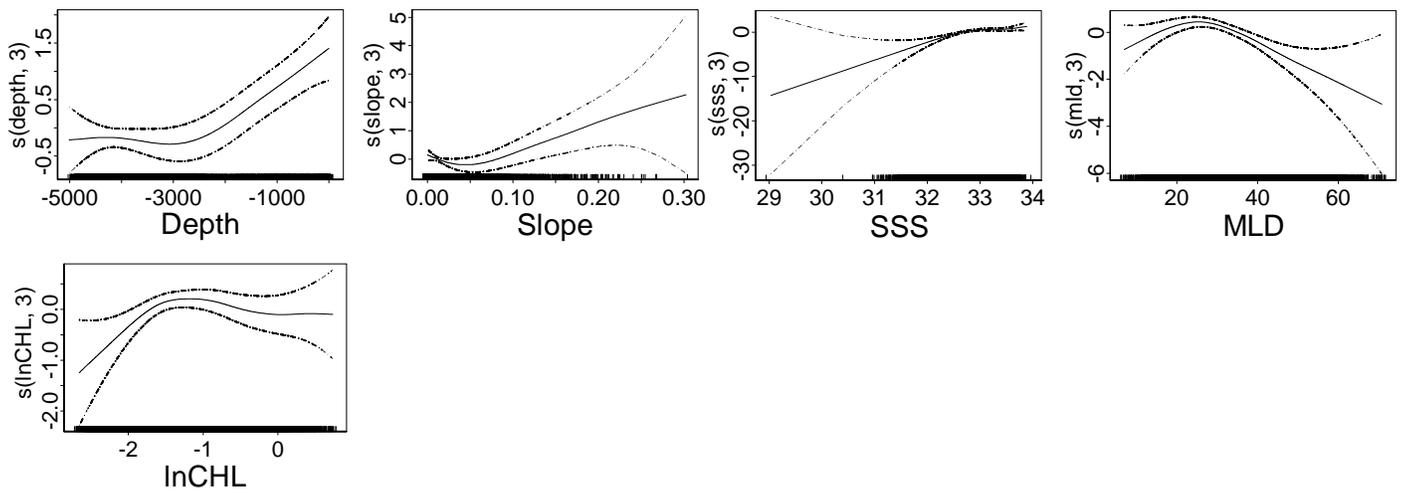


Figure 4 (cont.)

H) Fin Whale



I) Blue Whale



J) Humpback Whale

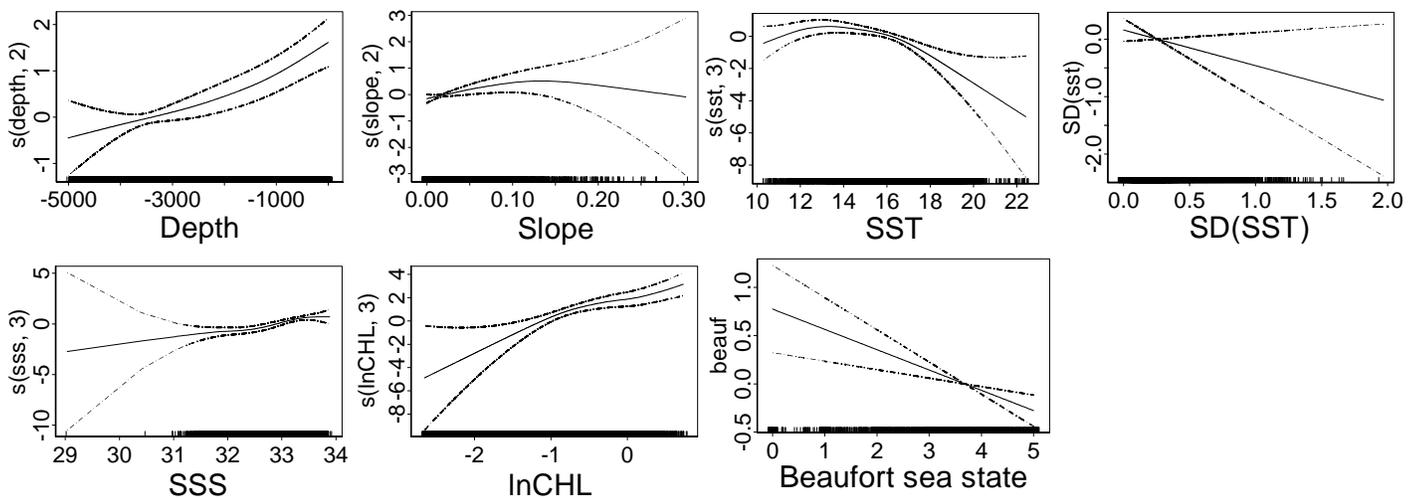
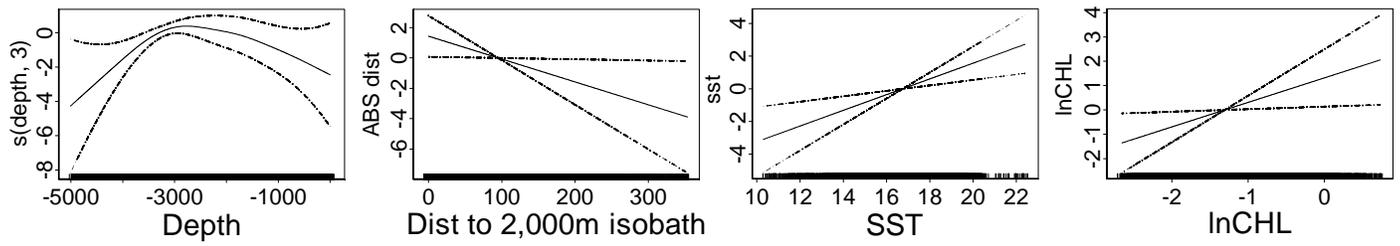


Figure 4 (cont.)

K) Baird's Beaked Whale



L) Small Beaked Whales

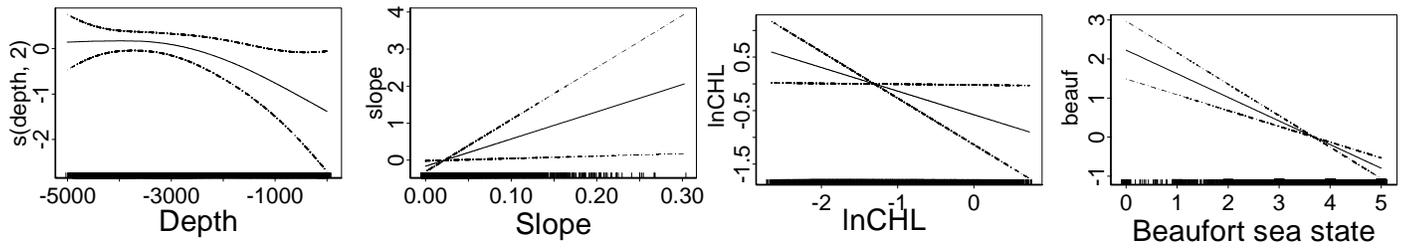
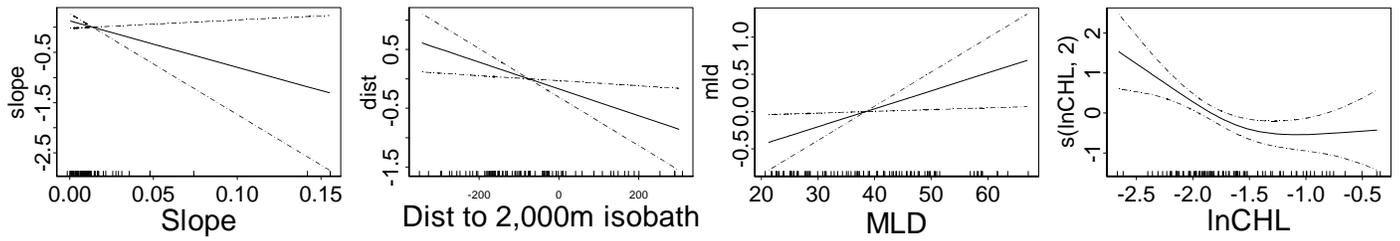


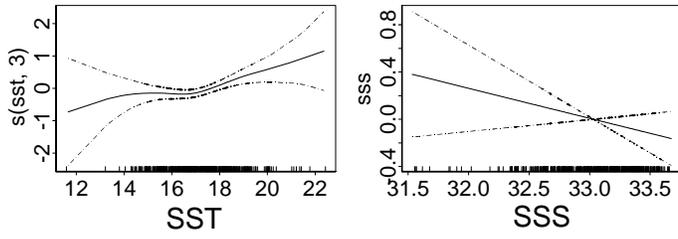
Figure 5. Group size model functions for (a) striped dolphin, (b) short-beaked common dolphin, (c) Risso's dolphin, (d) Pacific white-sided dolphin, (e) northern right whale dolphin, (f) Dall's porpoise, (g) sperm whale, (h) fin whale, (i) blue whale, (j) humpback whale, (k) Baird's beaked whale, and (l) the small-beaked-whale guild. Models were constructed with both linear terms and smoothing splines having up to three degrees of freedom. Degrees of freedom for nonlinear fits are in the parentheses on the y-axis. Potential predictor variables included sea surface temperature (SST), the standard deviation of SST (SD(SST)), sea surface salinity (SSS), mixed layer depth (MLD), log-transformed CHL (lnCHL), water depth (depth), bathymetric slope (slope), distance to the 2,000m isobaths (dist), and Beaufort sea state (beauf). Data points for each variable are shown as tick marks on the x-axes. The y-axes represent the term's (linear or spline) function. Zero on the y-axis corresponds to no effect of the predictor variable on the estimated response variable (group size). Scaling of y-axis varies among predictor variables to emphasize model fit. The dashed lines reflect 2x standard error bands (i.e., 95% confidence interval). For taxonomic names, see Table 1.

Figure 5

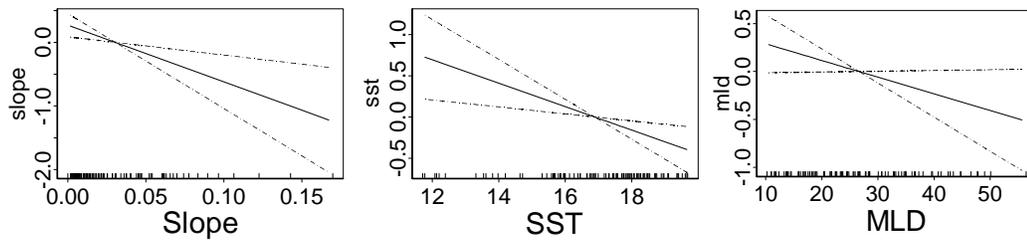
A) Striped Dolphin



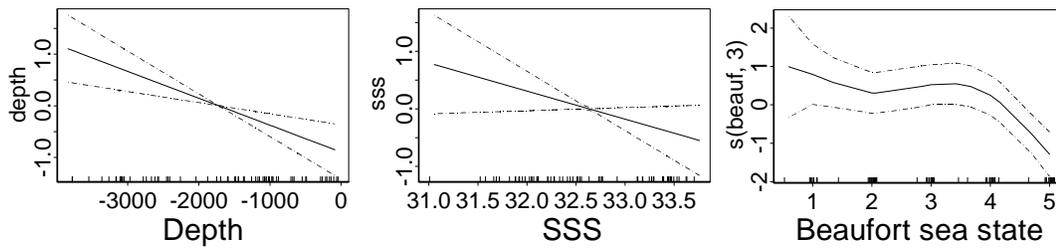
B) Short-beaked Common Dolphin



C) Risso's Dolphin



D) Pacific White-sided Dolphin



E) Northern Right Whale Dolphin

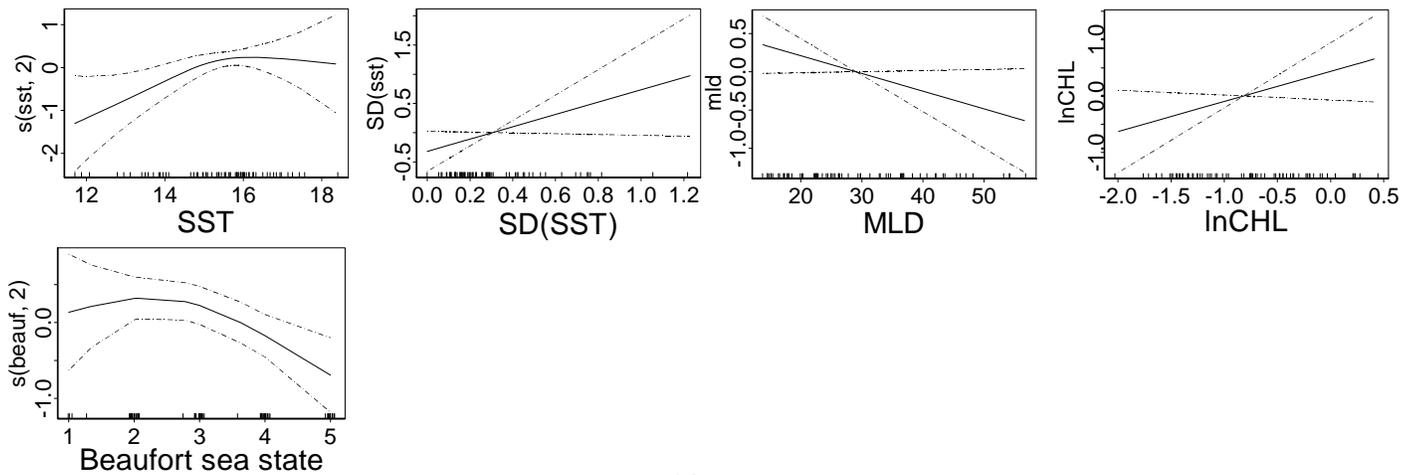
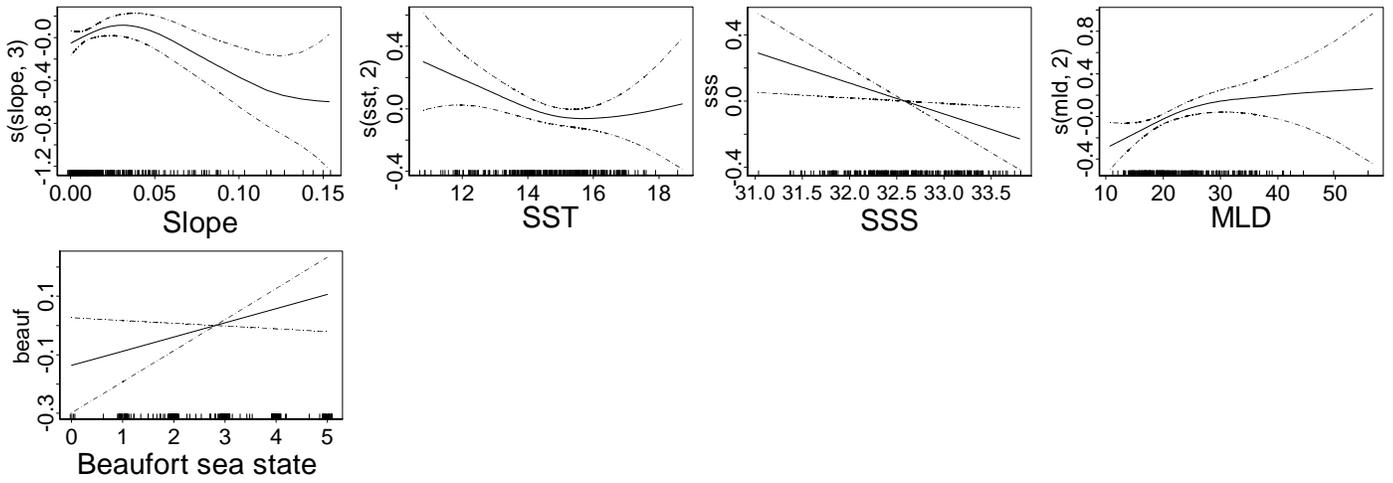
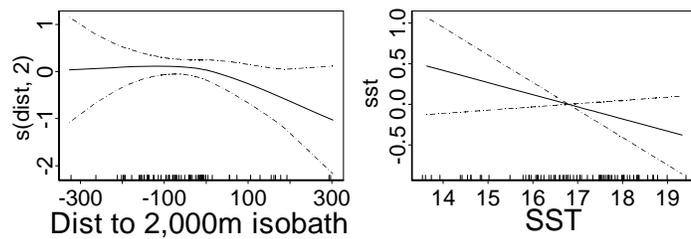


Figure 5 (cont.)

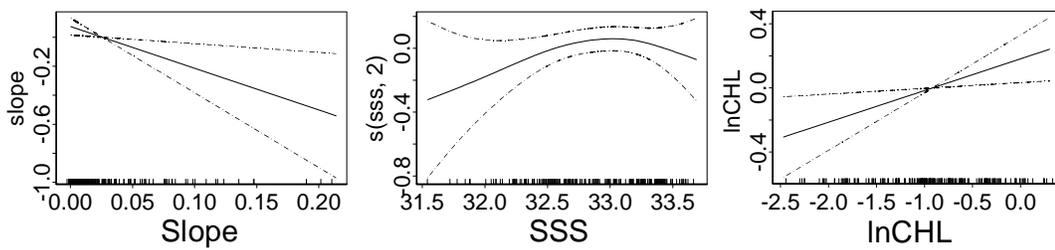
F) Dall's Porpoise



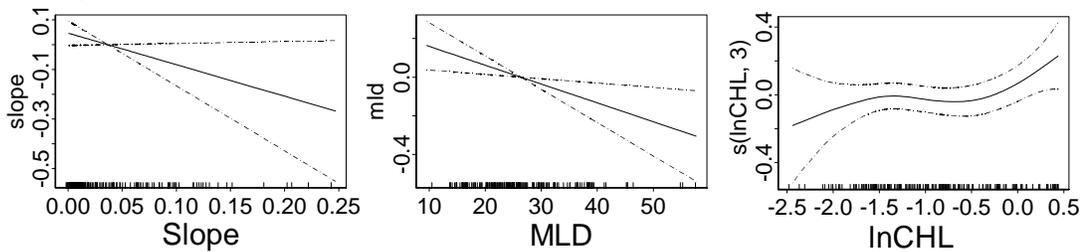
G) Sperm Whale



H) Fin Whale



I) Blue Whale



J) Humpback Whale

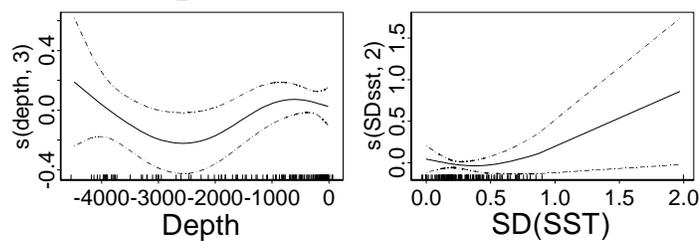
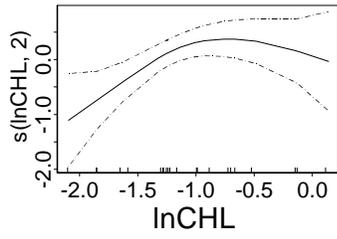


Figure 5 (cont.)

K) Baird's Beaked Whale



L) Small Beaked Whales

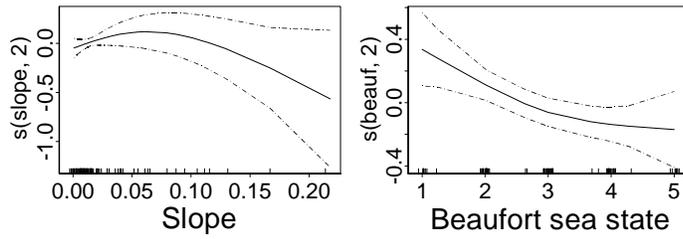
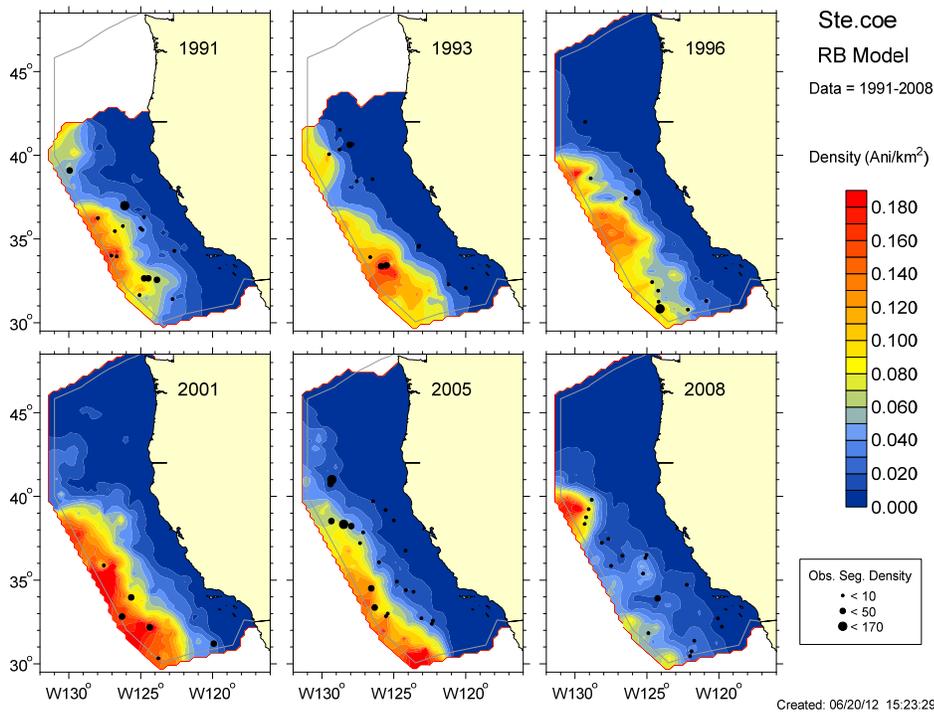
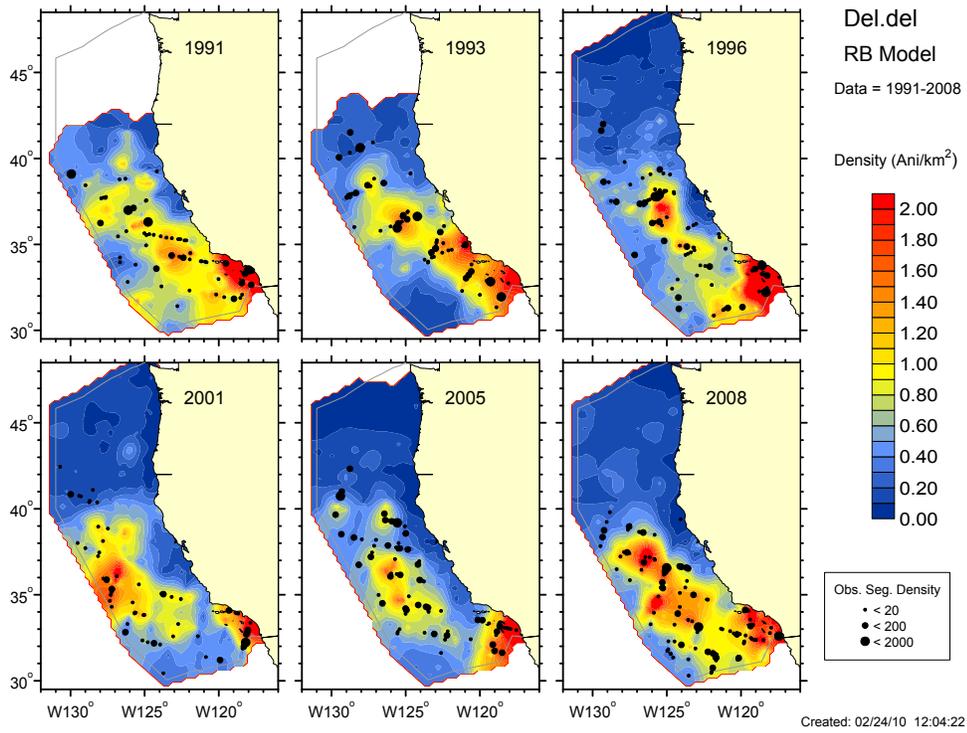


Figure 6. Predicted yearly densities based on the final California Current Ecosystem rebuilt (RB) or refit (RF) models for: (a) striped dolphin, (b) short-beaked common dolphin, (c) Risso’s dolphin, (d) Pacific white-sided dolphin, (e) northern right whale dolphin, (f) Dall’s porpoise, (g) sperm whale, (h) fin whale, (i) blue whale, (j) humpback whale, (k) Baird’s beaked whale, and (l) the small-beaked-whale guild. Predicted values were smoothed using inverse distance weighting (see text for details). Black dots show actual sighting locations, with larger dots representing more animals (Obs. Seg. Density). The surveys in 1991 and 1993 did not cover waters off Oregon and Washington. For taxonomic names, see Table 1.

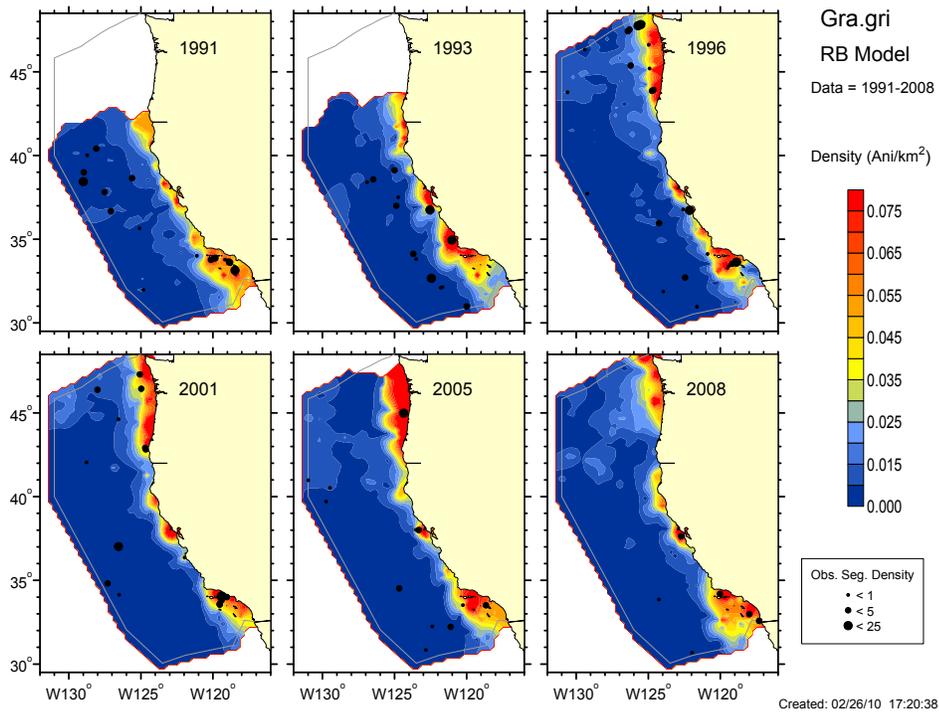
a) Striped dolphin



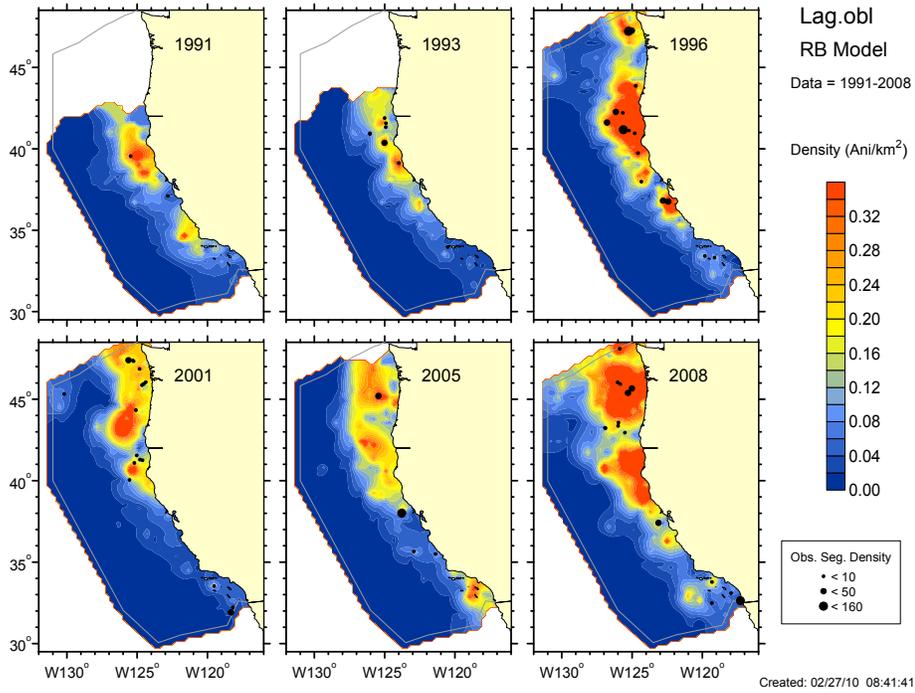
b) Short-beaked common dolphin



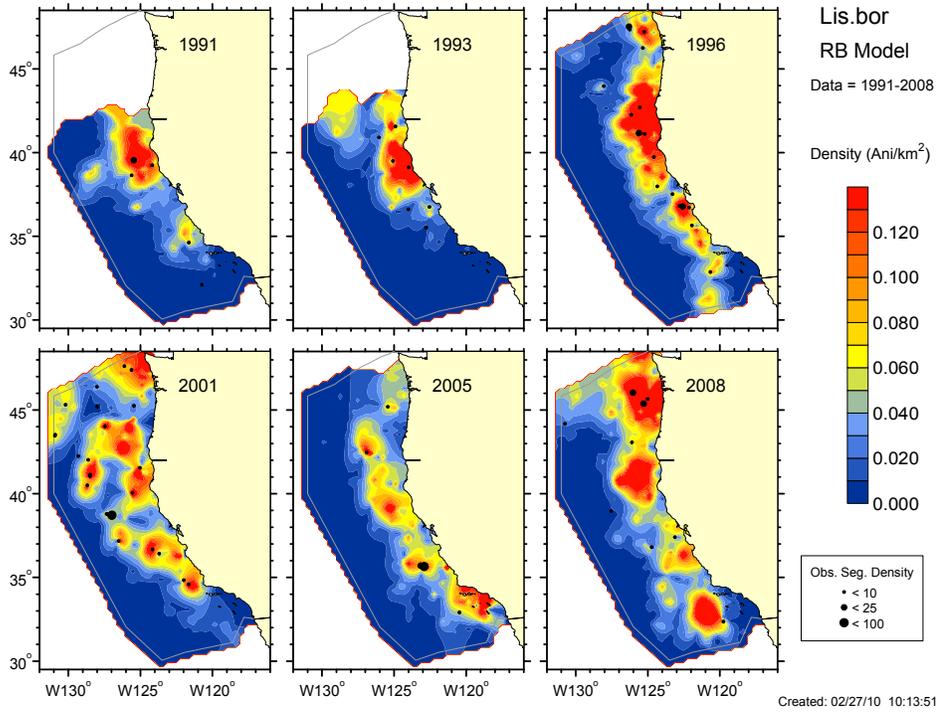
c) Risso's dolphin



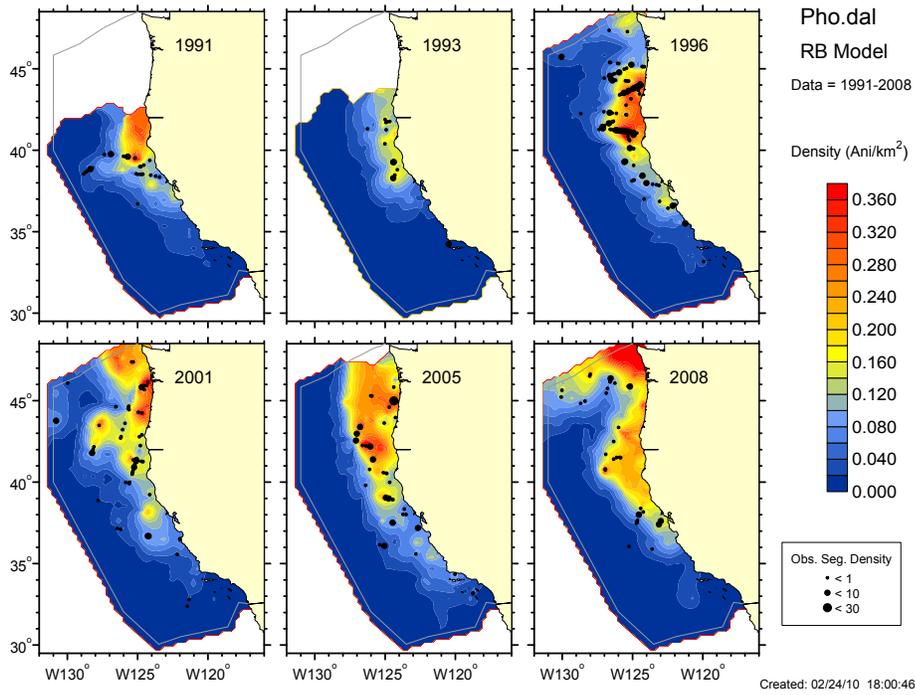
d) Pacific white-sided dolphin



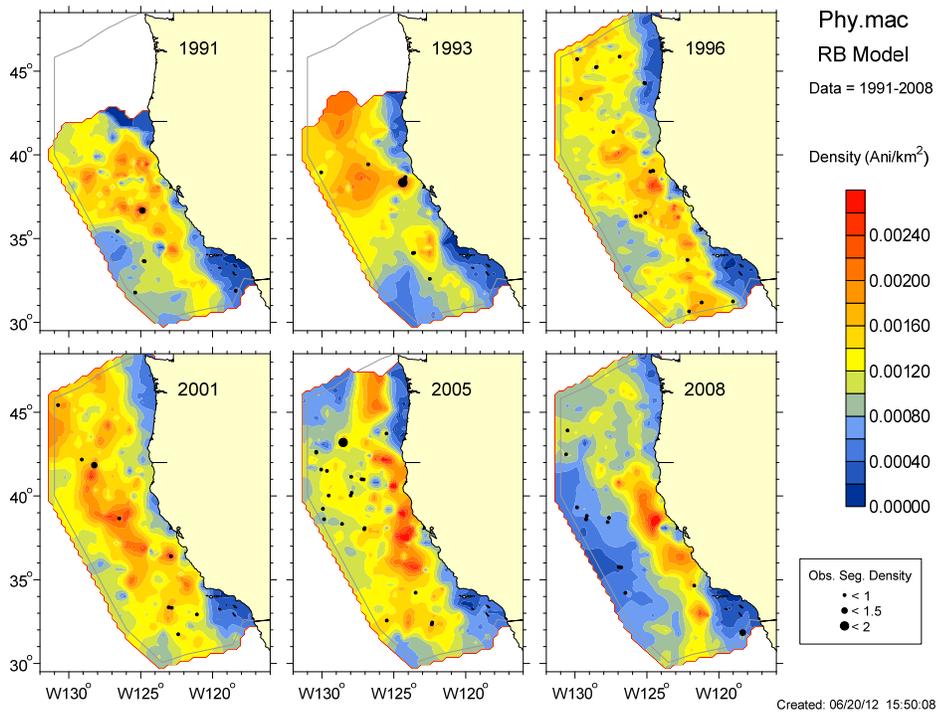
e) Northern right whale dolphin



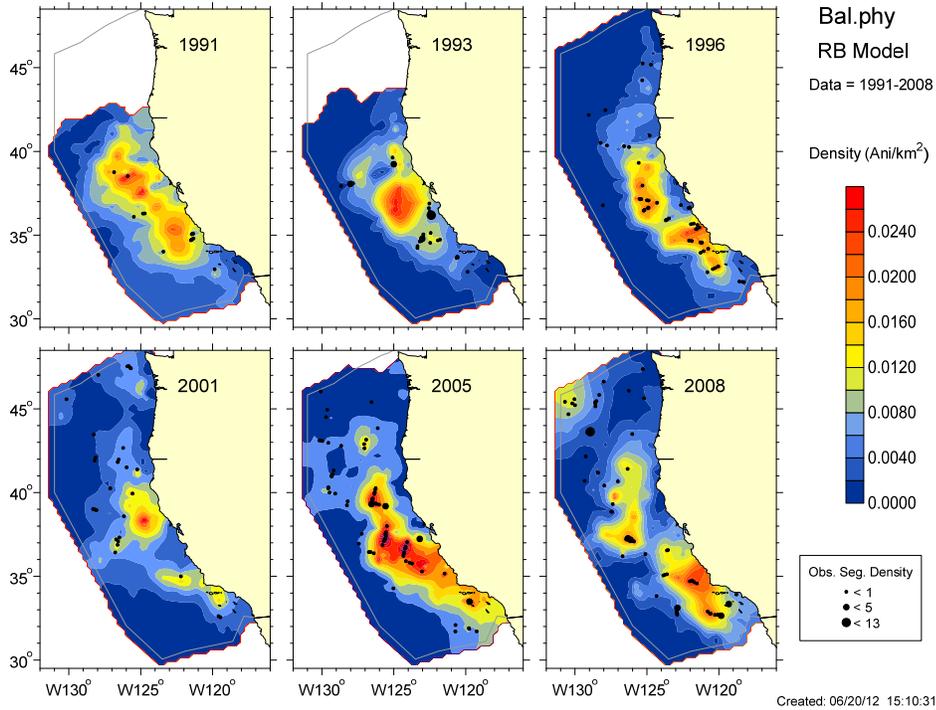
f) Dall's porpoise



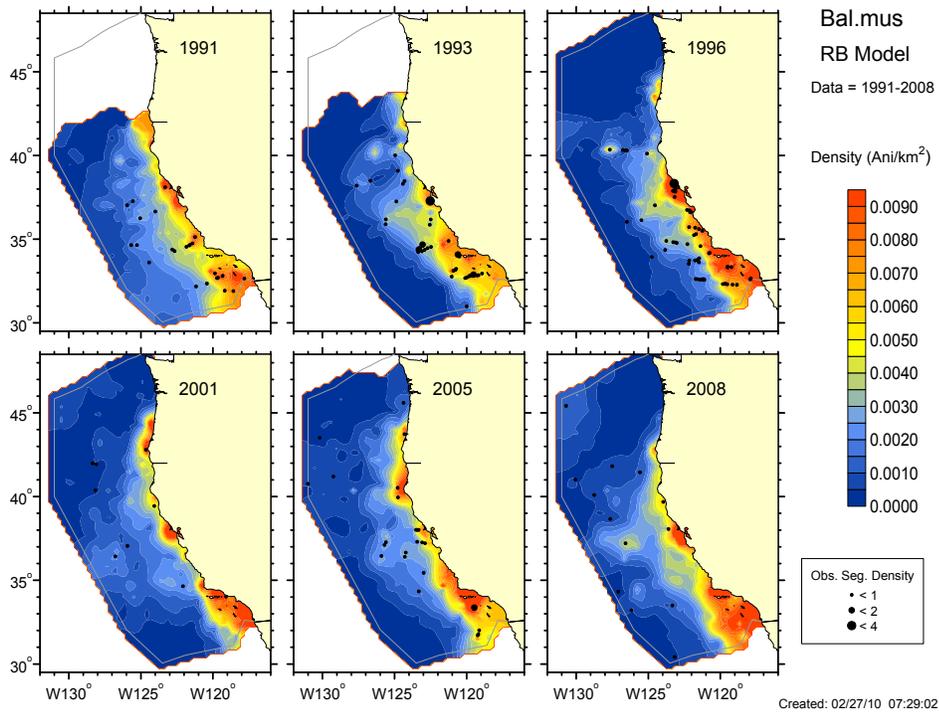
g) Sperm whale



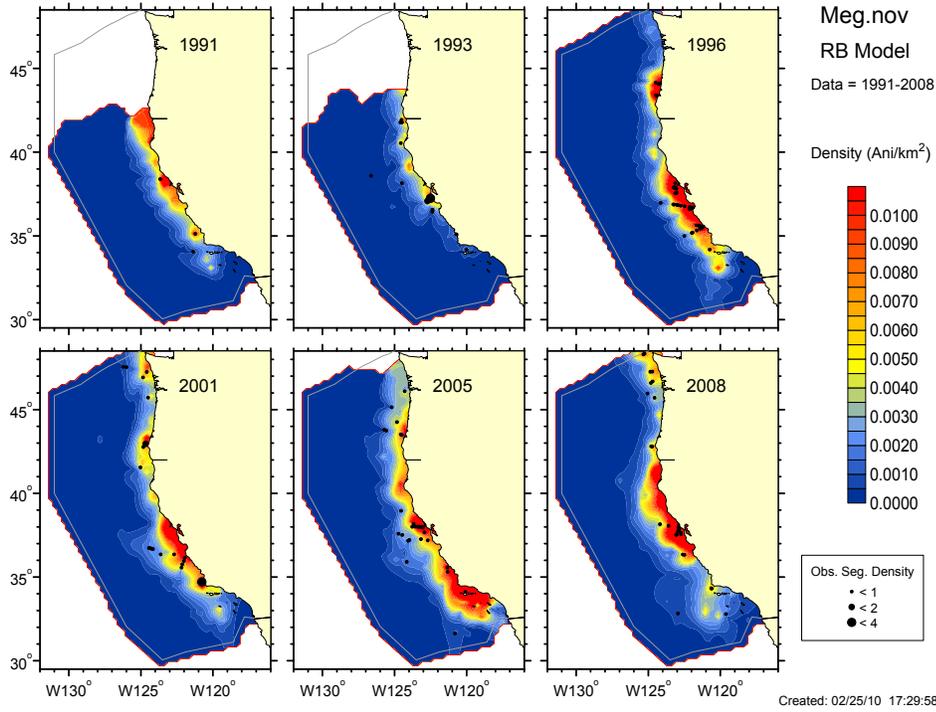
h) Fin whale



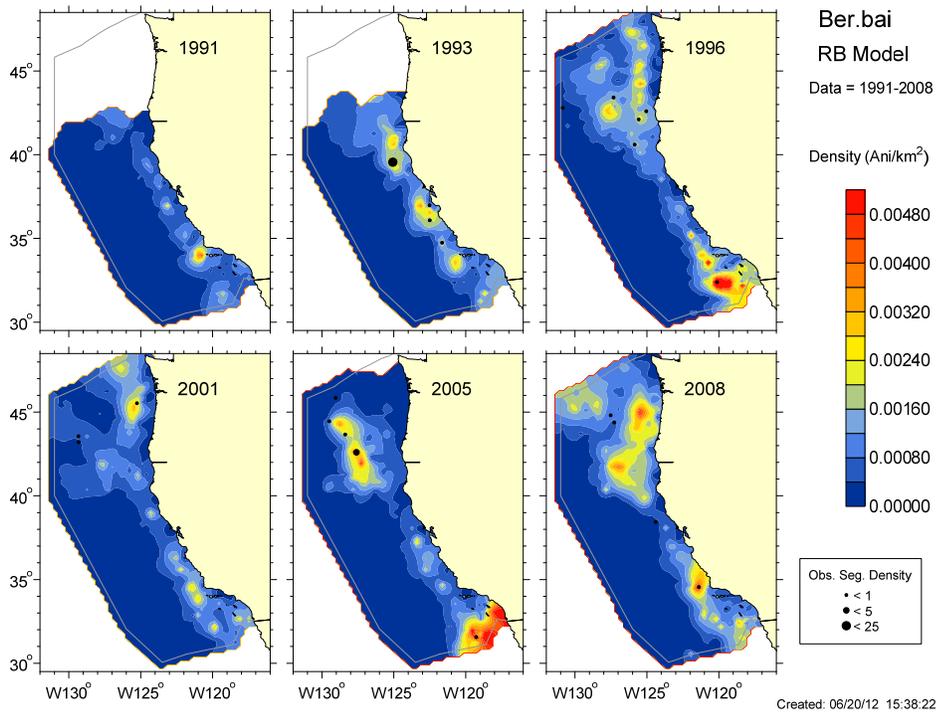
i) Blue whale



j) Humpback whale



k) Baird's beaked whale



l) Small-beaked-whale guild

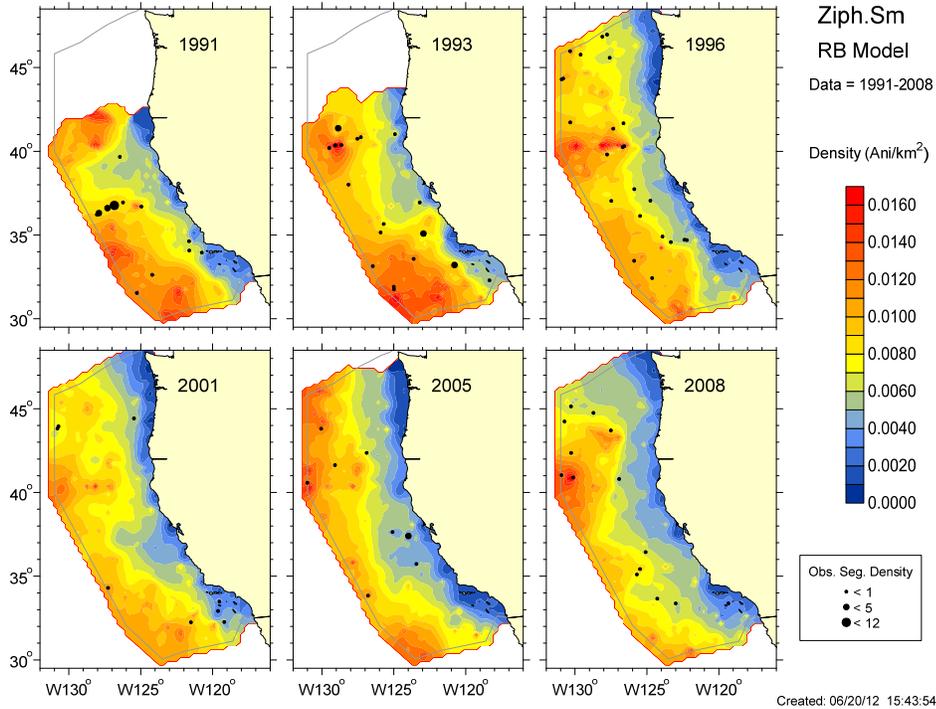
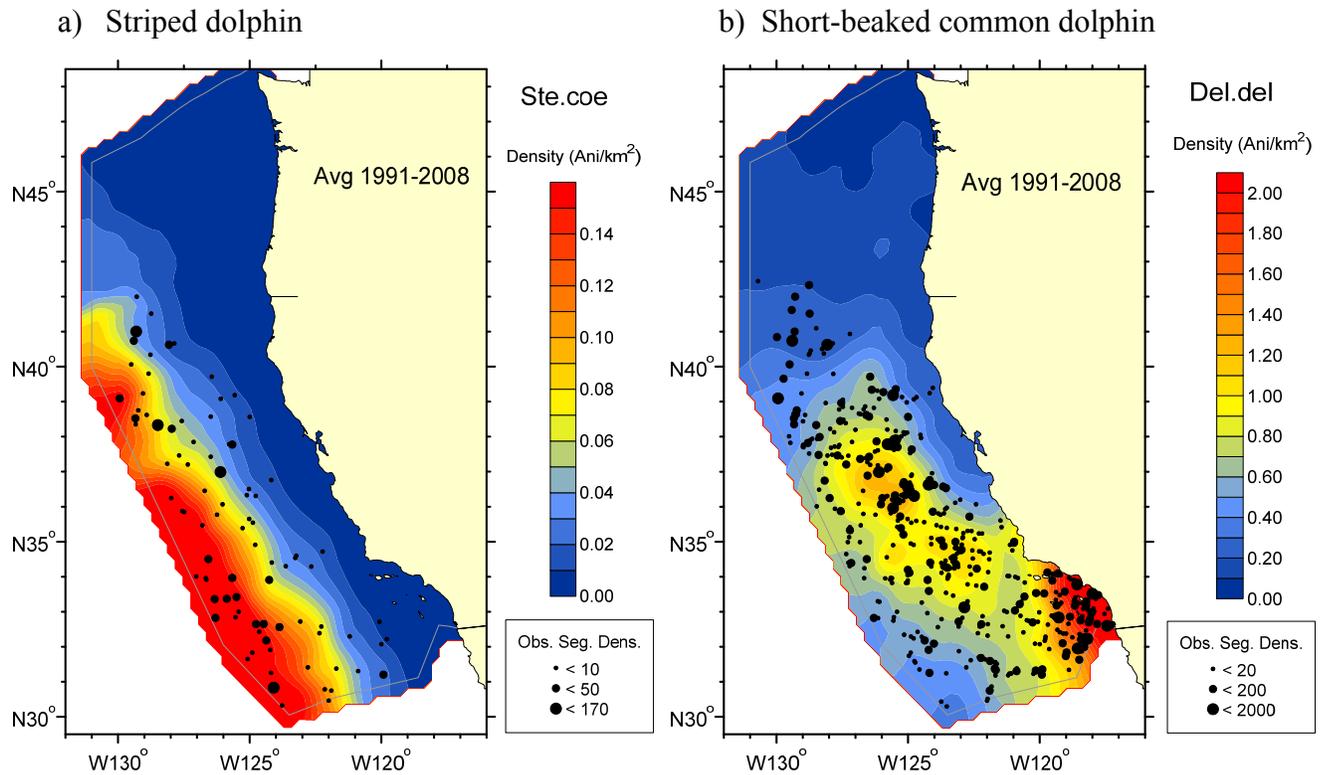
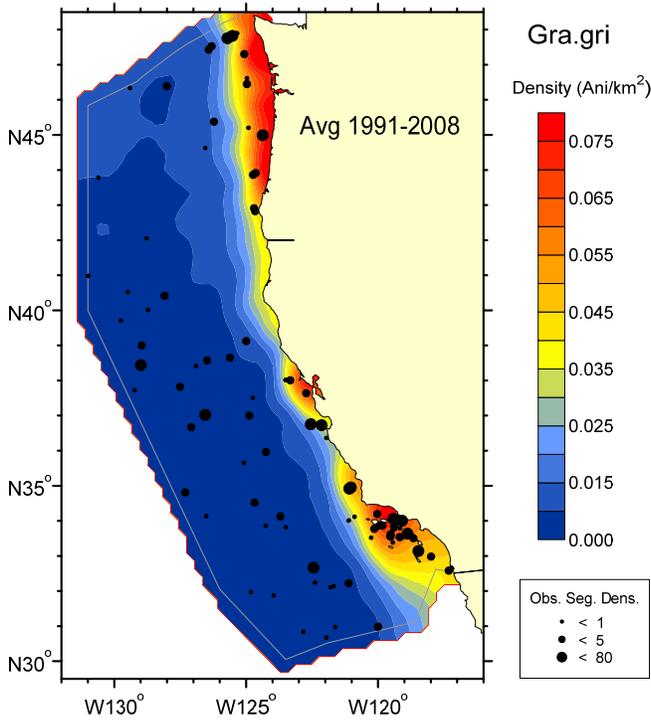


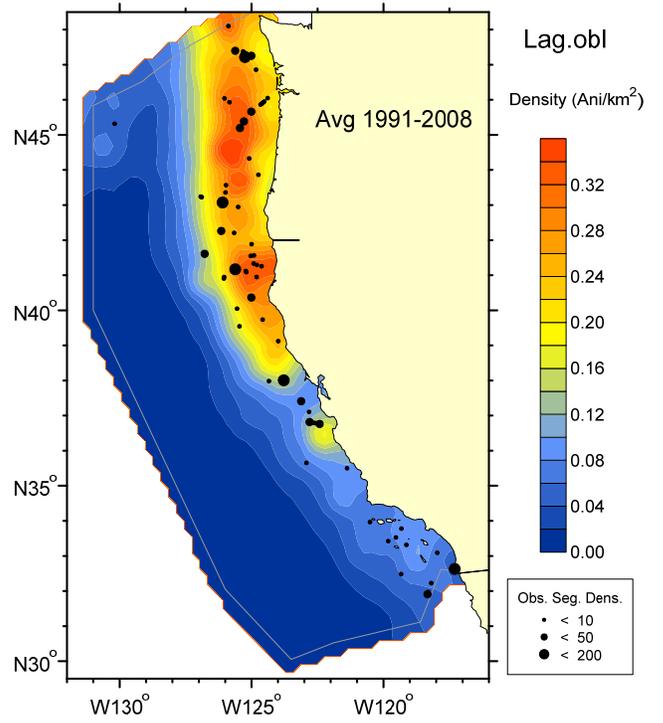
Figure 7. Predicted average density based on the final California Current Ecosystem rebuilt or refit models for: (a) striped dolphin, (b) short-beaked common dolphin, (c) Risso’s dolphin, (d) Pacific white-sided dolphin, (e) northern right whale dolphin, (f) Dall’s porpoise, (g) sperm whale, (h) fin whale, (i) blue whale, (j) humpback whale, (k) Baird’s beaked whale, and (l) the small-beaked-whale guild. Predicted values for each survey year were interpolated using inverse distance weighting; these maps represent the average of the yearly interpolations (see text for details). Black dots show actual sighting locations, with larger dots representing more animals (Obs. Seg. Dens.). For taxonomic names, see Table 1.



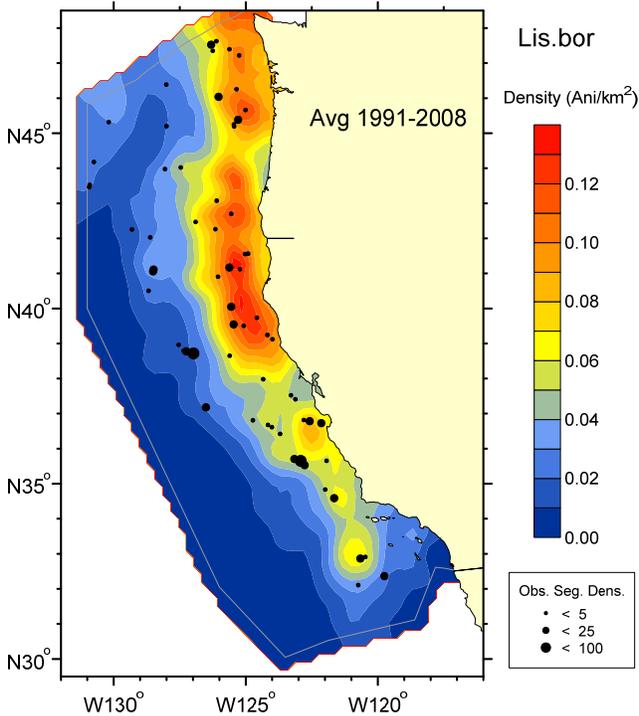
c) Risso's dolphin



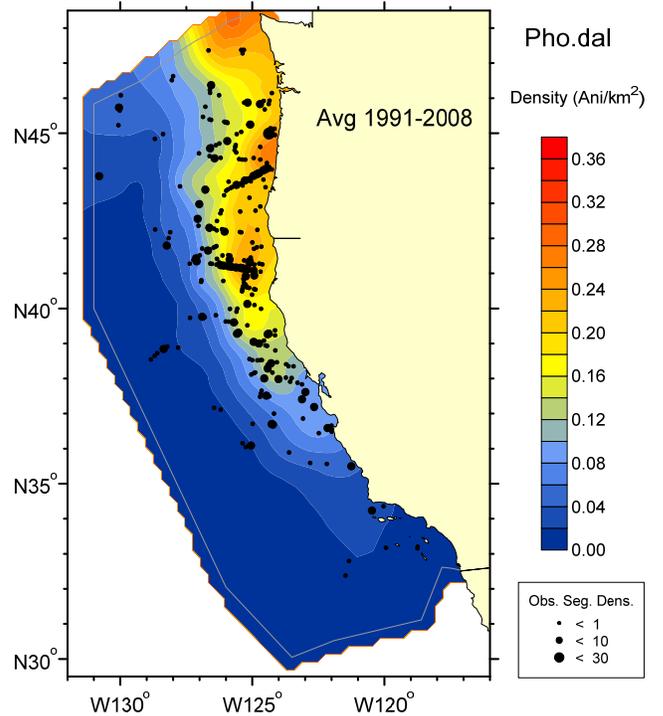
d) Pacific white-sided dolphin



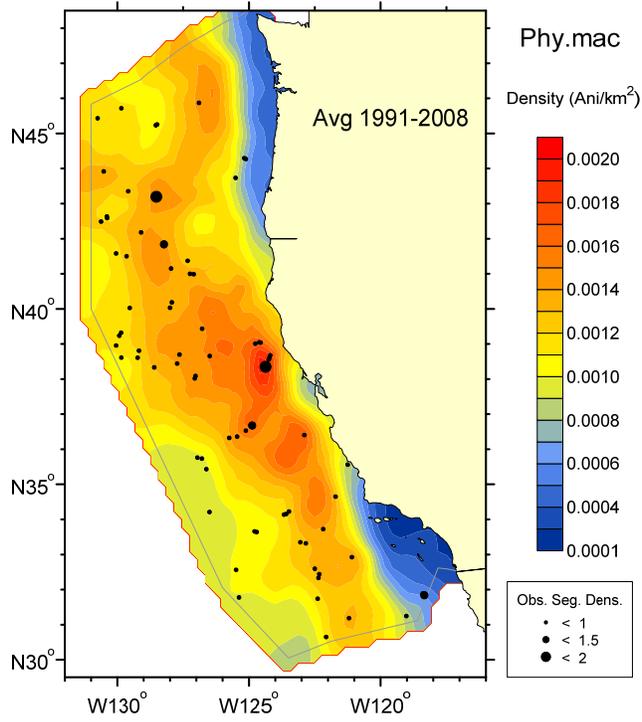
d) Northern right whale dolphin



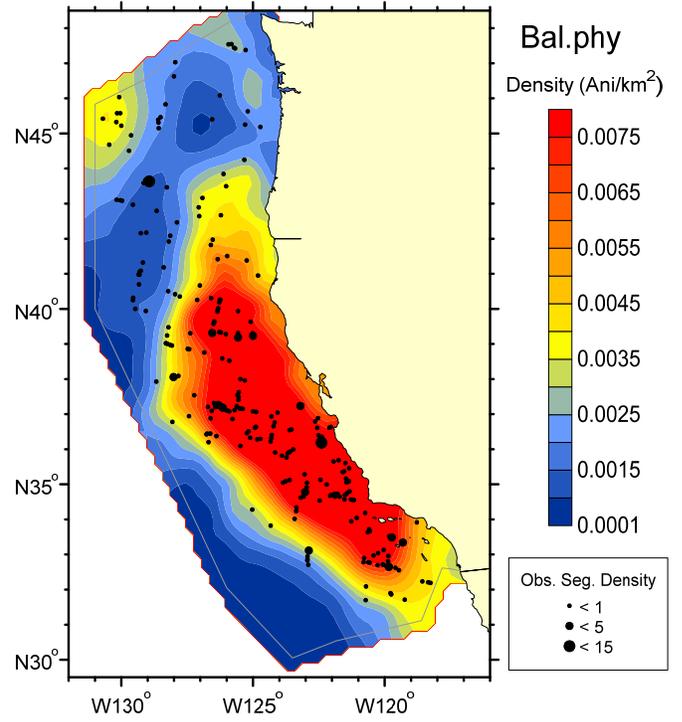
f) Dall's porpoise



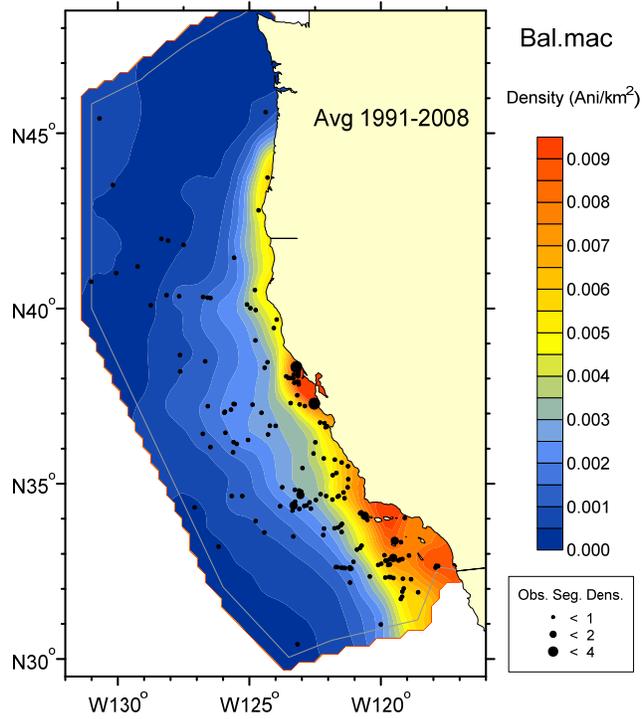
g) Sperm whale



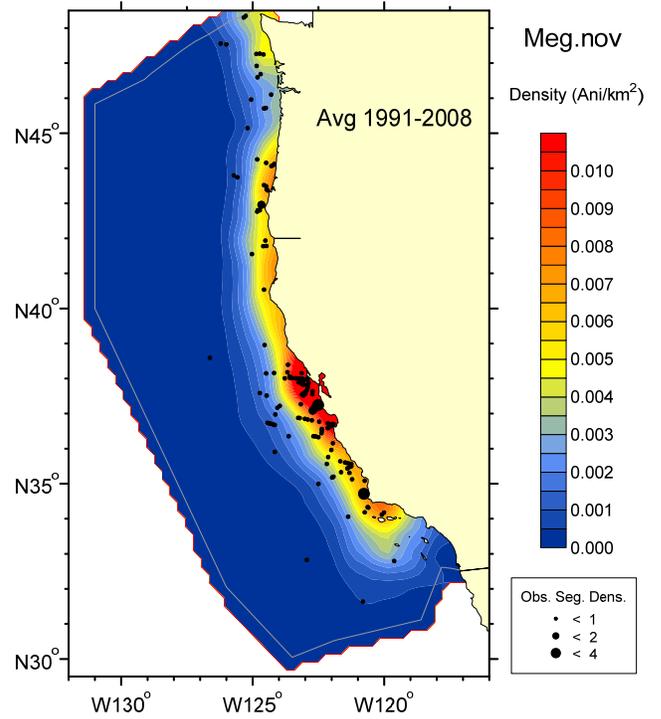
h) Fin whale



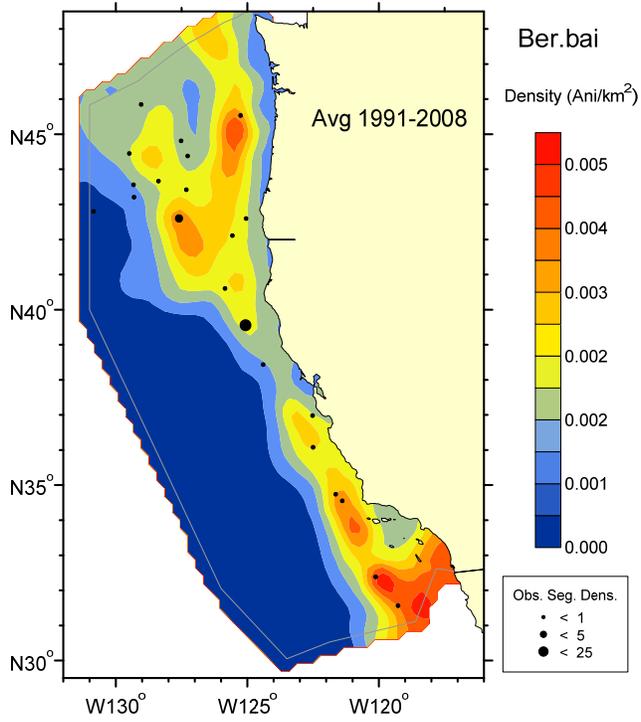
i) Blue whale



j) Humpback whale



k) Baird's beaked whale



l) Small-beaked-whale guild

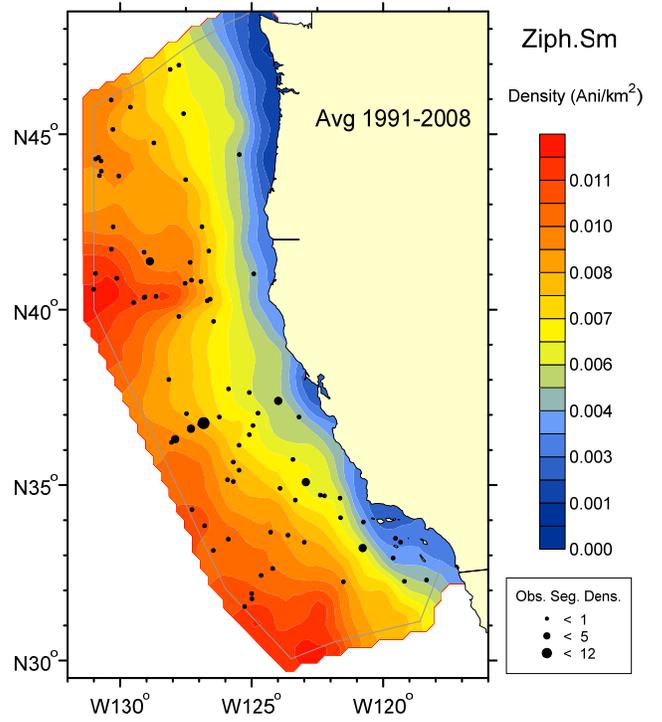
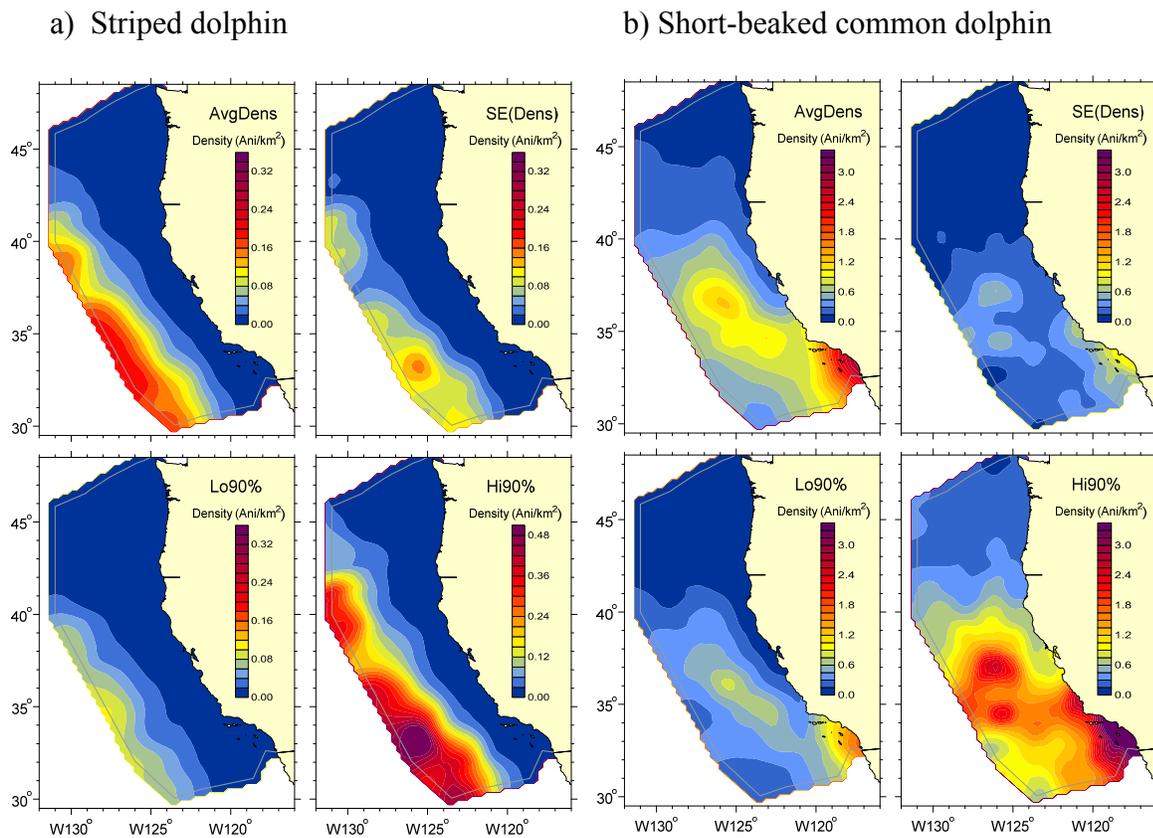
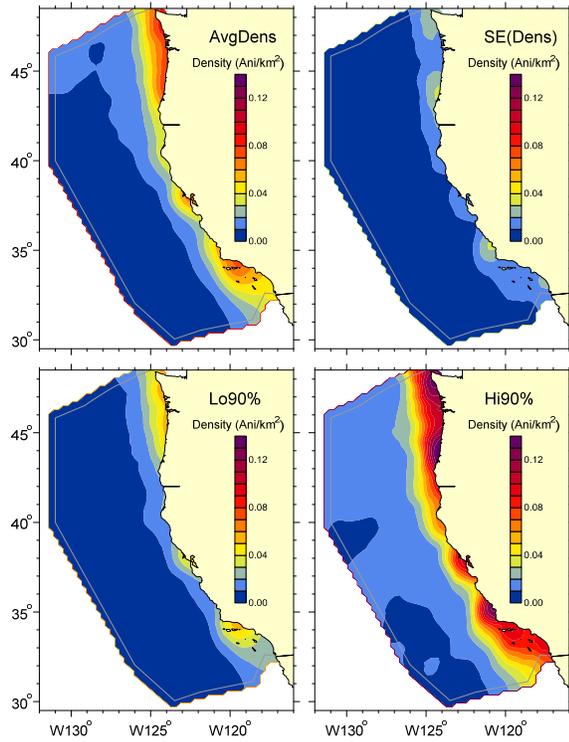


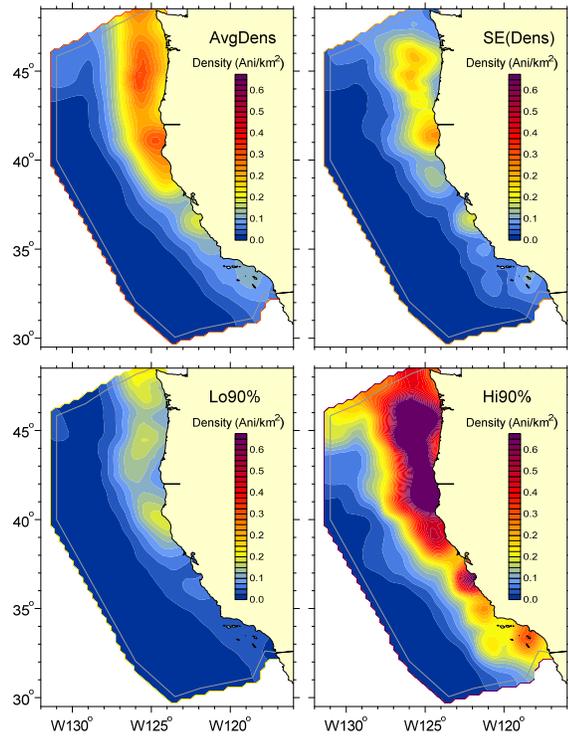
Figure 8. Predicted average density (AveDens), standard error (SE(Dens)), and upper and lower lognormal 90% confidence limits(Lo90% and Hi90%) based on the final California Current Ecosystem rebuilt or refit models for: (a) striped dolphin, (b) short-beaked common dolphin, (c) Risso’s dolphin, (d) Pacific white-sided dolphin, (e) northern right whale dolphin, (f) Dall’s porpoise, (g) sperm whale, (h) fin whale, (i) blue whale, (j) humpback whale, (k) Baird’s beaked whale, and (l) the small-beaked-whale guild. Predicted values for each survey year were interpolated using inverse distance weighting (see text for details). Grid cells for each of the individual survey years were then averaged across all years to calculate average species density; standard errors and upper and lower lognormal 90% confidence limits were calculated from the grid cell averages and variances using standard formulae. For taxonomic names, see Table 1.



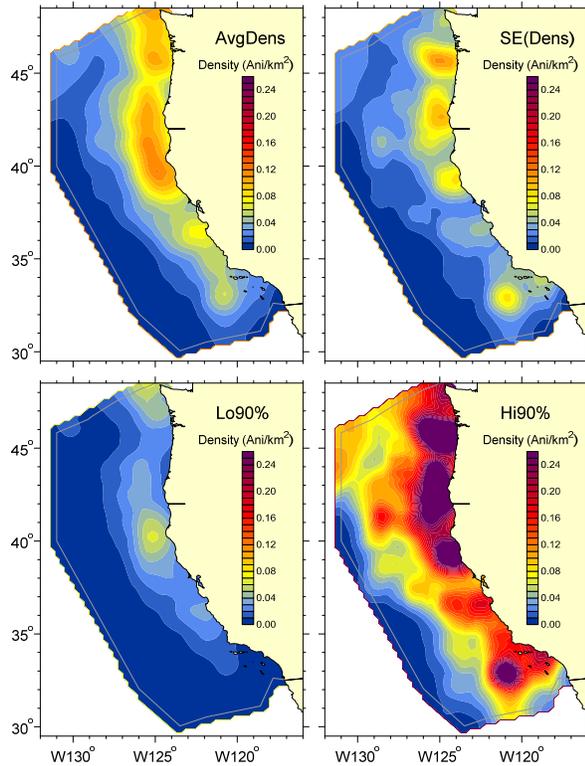
c) Risso's dolphin



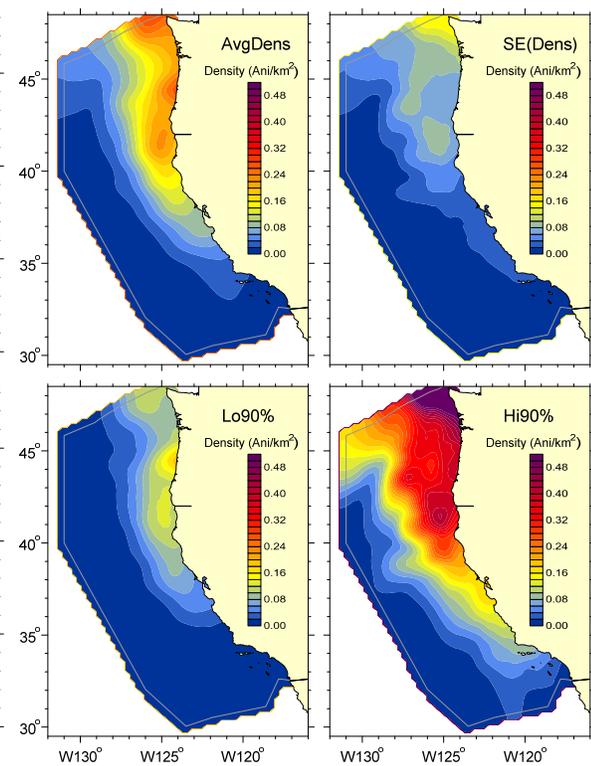
d) Pacific white-sided dolphin



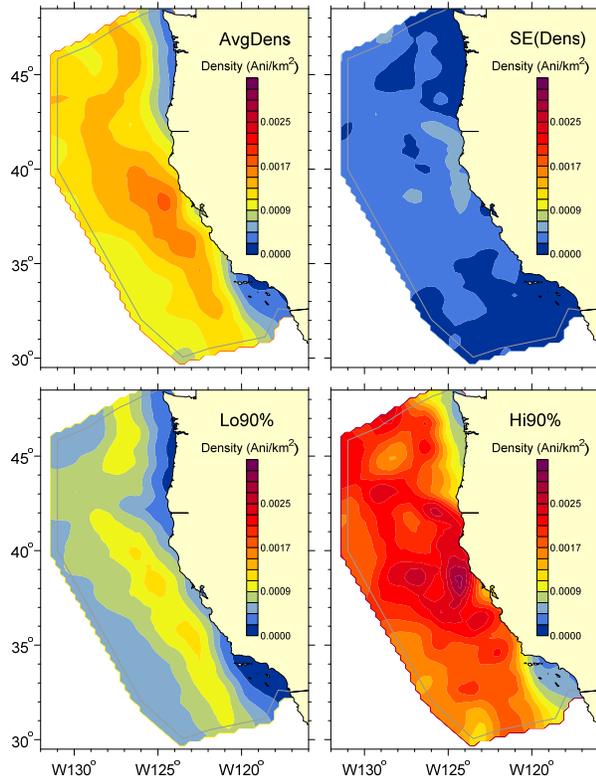
e) Northern right whale dolphin



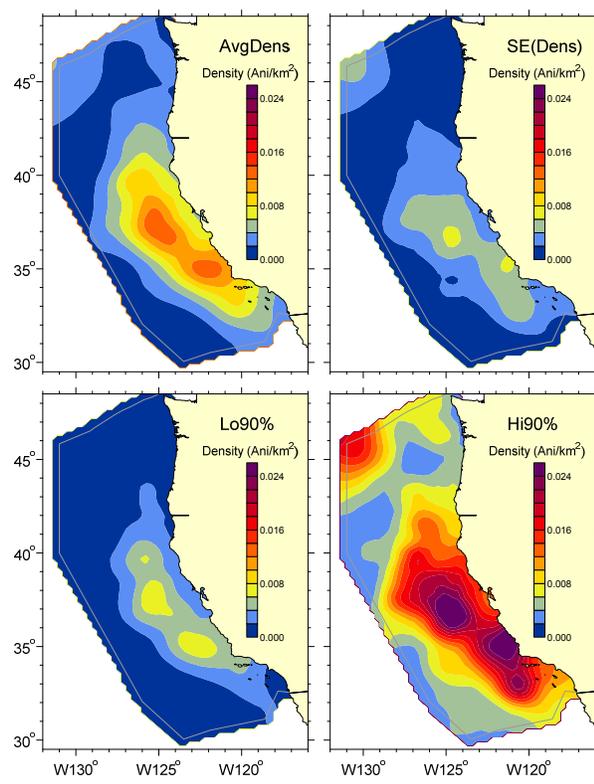
f) Dall's porpoise



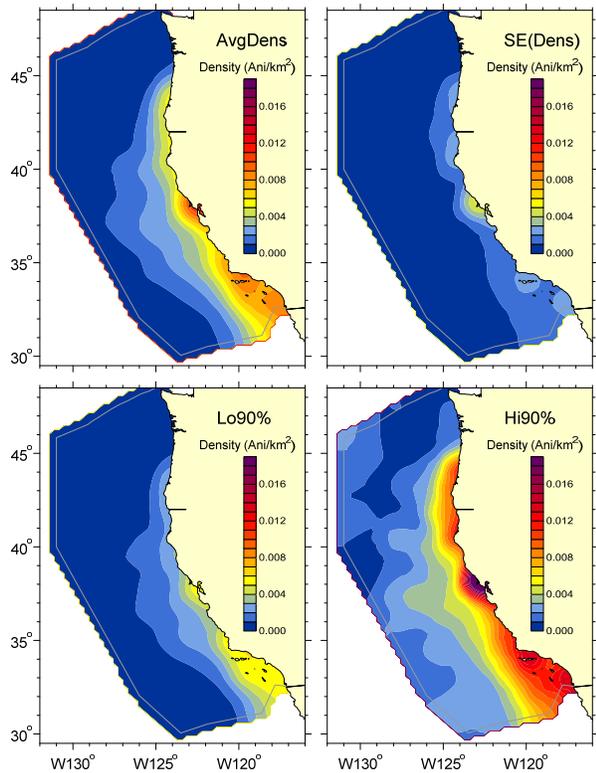
g) Sperm whale



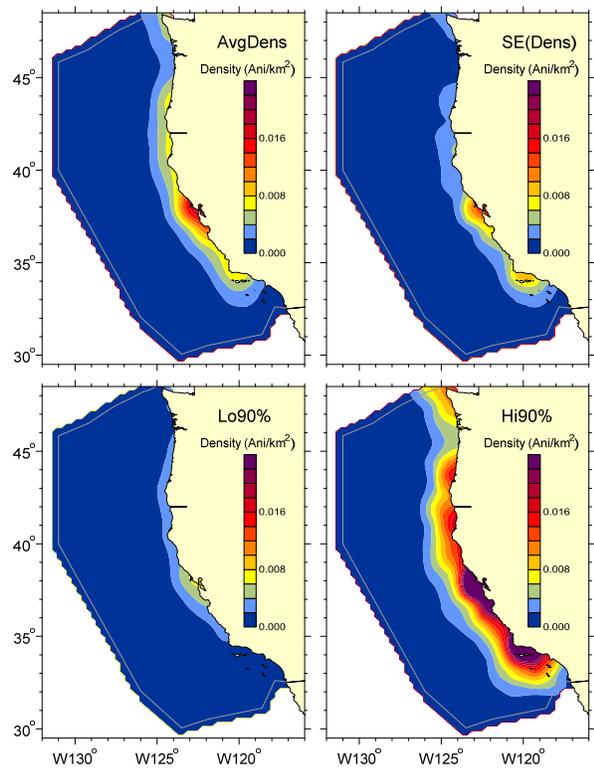
h) Fin whale



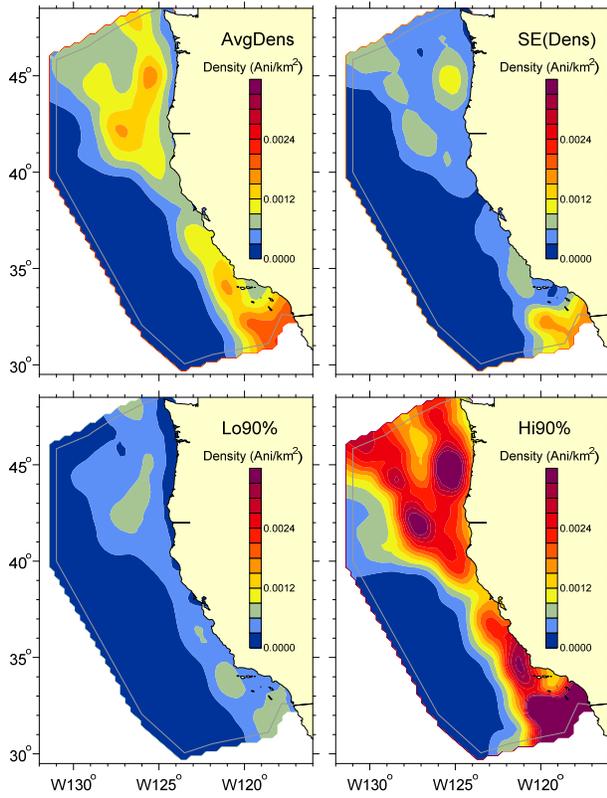
i) Blue whale



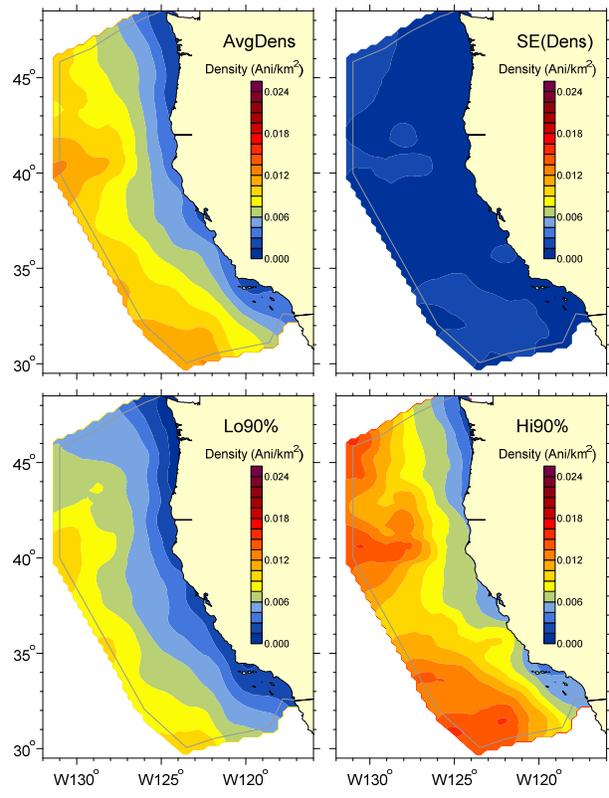
j) Humpback whale



k) Baird's beaked whale



l) Small-beaked-whale guild



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