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Introduction

The Hawaiian Islands Cetacean and Ecosystem Assessment Survey (HICEAS) 2017 was conducted in waters within the United States (U.S.) Exclusive Economic Zone (EEZ) around the Hawaiian Archipelago (henceforth "Hawaiian EEZ" for brevity) from 6 July through 1 December 2017 (Yano et al. 2018). The primary objective of this line-transect survey was to collect cetacean sighting data to support the derivation of cetacean density estimates using both design-based analyses and habitat modeling techniques. This report summarizes the results of the habitat modeling effort. The design-based estimates are described separately in Bradford et al. (in review).

Habitat models, or species distribution models (SDMs), have been recognized as valuable tools for estimating the density and distribution of cetaceans and assessing potential impacts from a wide range of anthropogenic activities (e.g., Gilles et al. 2011; Goetz et al. 2012; Hammond et al. 2013; Redfern et al. 2013). SDMs for nine cetacean species have been developed for waters in the central North Pacific, including U.S. EEZ waters around the Hawaiian Islands, from ship-based, line-transect survey data collected by the Pacific Islands Fisheries Science Center (PIFSC) and Southwest Fisheries Science Center (SWFSC) between 1997 and 2012 (Forney et al. 2015). The models provided spatially explicit density predictions at a 25 km × 25 km grid resolution for pantropical spotted dolphin (*Stenella attenuata*), striped dolphin (*S. coeruleoalba*), spinner dolphin (*S. longirostris*), rough-toothed dolphin (*Steno bredanensis*), common bottlenose dolphin (*Tursiops truncatus*), false killer whale (*Pseudorca crassidens*), short-finned pilot whale (*Globicephala macrorhynchus*), sperm whale (*Physeter macrocephalus*), and Bryde's whale (*Balaenoptera edeni*).

To develop improved and updated SDMs, sighting data from HICEAS 2017 were combined with previous line-transect survey data collected within waters of the Hawaiian EEZ from 2002 to 2016. The majority of these data were from the two previous HICEAS efforts, the first in 2002 (Barlow 2006) and the second in 2010 (Bradford et al. 2017). In contrast to previous modeling efforts that included survey data from a broader region of the central Pacific Ocean (Becker et al. 2012; Forney et al. 2015), the current SDMs were built only with survey data collected within waters of the Hawaiian EEZ. Habitat models were developed to derive spatially explicit estimates of species density specific to the Hawaiian EEZ based on previously established methods that allow for the incorporation of segment-specific estimates of detection probability (Becker et al. 2016). Potential habitat variables included bathymetric depth, distance to islands, and a suite of dynamic surface and subsurface outputs from an ocean circulation model. The habitat-based models of cetacean density developed in this study represent an improvement over the previous models developed by Forney et al. (2015) because they more accurately account for variation in detection probabilities, provide finer-scale density predictions (~9 km × 9 km grid resolution), and better account for uncertainty in the resulting study area abundance estimates. In addition, they include dynamic subsurface variables that were not available for the previous models. Further, increases in sample sizes allowed us to develop a new habitat model for Risso's dolphin (*Grampus griseus*).

Methods

Survey data

Cetacean sighting data used to build the SDMs were collected within waters of the Hawaiian EEZ from 2002 to 2017 (Table 1) using line-transect methods (Buckland et al. 2001). Only on-effort data collected in Beaufort Sea State conditions ≤6 within the study area were used in model development. When combined across years, the surveys provided comprehensive coverage of waters throughout the study area (Figure 1).

Table 1. Cetacean and ecosystem assessment surveys and effort conducted within the Hawaiian EEZ during 2002–2017.

Cruise number	Period	NOAA Ship	Region
1621	Jul–Dec 2002	*David Starr Jordan*	Hawaiian Archipelago
1622	Oct–Dec 2002	*McArthur*	Hawaiian Archipelago
1629	Jul–Nov 2005	*McArthur II*	Central Pacific Islands[1]
1641	Aug–Dec 2010	*McArthur II*	Hawaiian Archipelago
1642	Sep–Oct 2010	*Oscar Elton Sette*	Hawaiian Archipelago
1108	Oct–Nov 2011	*Oscar Elton Sette*	Palmyra Atoll[1]
1203	Apr–May 2012	*Oscar Elton Sette*	Palmyra Atoll[1]
1303	May–Jun 2013	*Oscar Elton Sette*	Northwestern Hawaiian Islands
2016	Jun–Jul 2016	*Oscar Elton Sette*	Main Hawaiian Islands
2017	Jul–Oct 2017	*Oscar Elton Sette*	Hawaiian Archipelago
2017	Aug–Dec 2017	*Reuben Lasker*	Hawaiian Archipelago

[1] Transit portions located within the Hawaiian EEZ were used.

The survey protocol was the same for all years (see Barlow 2006; Kinzey et al. 2000) with the exception of adjustments made to the collection of false killer whale data beginning in 2010 (Bradford et al. 2014; 2017; Yano et al. 2018). Survey protocols are briefly summarized here. Each survey used a NOAA research vessel with a flying bridge and a team of 6 experienced visual observers. For each rotation, 3 observers stationed on the flying bridge of the ship visually searched for and recorded cetacean sightings between 0 and 90 degree to port and starboard using standard line-transect protocols. Port and starboard observers searched with pedestal-mounted 25 × 150 binoculars and a center-stationed third observer searched by eye or with handheld 7 × 50 binoculars. When cetaceans were detected within 3 nmi (5.6 km) of the trackline, the sighting was recorded (along with distance and direction from the vessel, from which perpendicular sighting distance was calculated), and the ship would then typically divert from the transect line and go “off effort” to approach the animals and enable more accurate estimation of group size and species identification. All observers independently provided best, high, and low group size estimates. The best estimates were averaged (i.e., arithmetic mean) for each species to obtain a single group size estimate for each sighting. Systematic survey effort was conducted along predetermined tracklines at an average survey speed of 18.5 km/hr. During transit between tracklines, transits to or from port, or deviations from pre-determined tracklines for other purposes, the visual observers generally maintained standard data collection protocols.

Although such non-systematic effort is generally not used to derive encounter rate for design-based density estimates, it is incorporated into the SDM as the uneven distribution of effort can be accounted for within the statistical framework (Hedley and Buckland 2004).

Changes in survey protocol for false killer whales over the study period necessitated a more complex analytical approach for this species. A detailed account of the methodical approach and results for false killer whales are provided in Bradford et al. (2020), though the results for this species are replicated in this report to provide a comprehensive summary of all available habitat-based density models derived from HICEAS 2017.

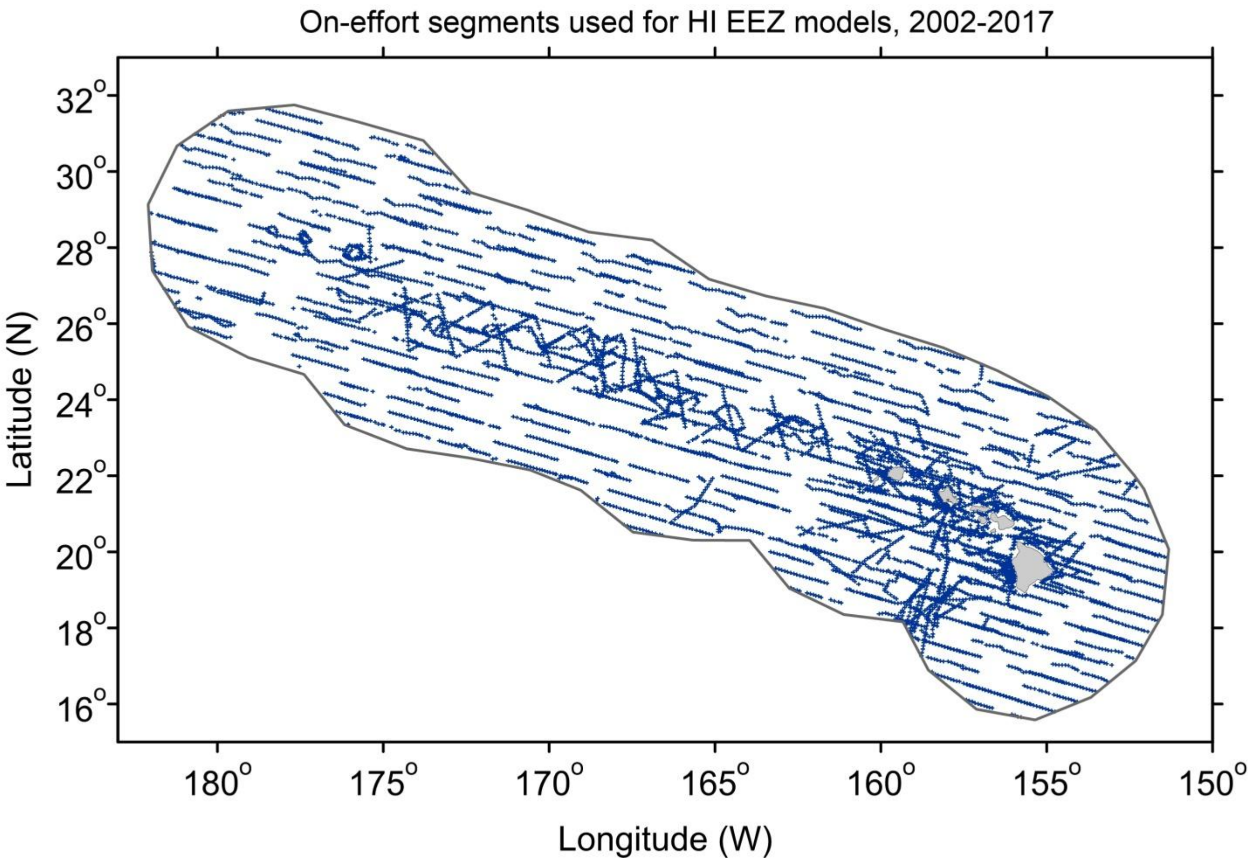

Figure 1. Effort segments from the 2002–2017 Southwest Fisheries Science Center and Pacific Islands Fisheries Science Center line-transect ship surveys used for modeling. The blue lines show on-effort modeling segments completed in Beaufort sea states of 0–6.

Environmental predictor data

To create samples for modeling, continuous portions of on-effort (systematic and non-systematic) survey tracklines were divided into approximate 10-km segments using methods described by Becker et al. (2010). Species-specific sightings and their associated average group size estimates were retained with each segment and habitat covariates were derived based on the segment's geographical midpoint. Sighting data were truncated at 5.5 km perpendicular to the trackline to eliminate the most distant groups and maintain consistency with the species-specific effective-strip-width (*ESW*) estimates derived by (Barlow et al. 2011) and used in this study to estimate density.

Outputs from the Hybrid Coordinate Ocean Model (HYCOM; Chassignet et al. 2007) were used as dynamic predictor variables in the habitat models. HYCOM products include a global reanalysis that assimilates multiple sources of data in product development (including satellite and in situ), and outputs from HYCOM have been widely used and widely tested.[1] Daily averages for each variable served at the 0.08-degree (~9 km) horizontal resolution of the HYCOM output were used in the models. The suite of potential dynamic predictors included sea surface temperature (SST) and its standard deviation (sd(SST)), calculated for a 3 × 3-pixel box around the modeling segment midpoint), mixed layer depth (MLD, defined by a 0.5 °C deviation from the SST), sea surface height (SSH), sd(SSH), salinity (SAL), and sd(SAL). Distance to land and water depth (m) were also included as potential predictors, derived from the ETOPO1 1-arc-min global relief model (Amante and Eakins 2009) and obtained for the midpoint of each transect segment.

A spatial term (longitude × latitude) was also included in the suite of potential predictors because SDMs that explicitly account for geographic effects have exhibited improved explanatory performance (Becker et al. 2018; Cañadas and Hammond 2008; Forney et al. 2015; Hedley and Buckland 2004; Tynan et al. 2005; Williams et al. 2006). The inclusion of a spatial term may result in more robust models, particularly for species with smaller sample sizes, but prohibit predictions outside the study area.

Although it is possible to include a year term as a covariate within an SDM to explicitly capture population trends (e.g., Becker et al. 2018), year was not incorporated into the present modeling effort. The limited number of survey years and small sample sizes available within the study area prevent robust assessment of population trends, so temporal terms were not included in the list of potential predictor variables.

Habitat models

Generalized Additive Models (GAM; Hastie and Tibshirani 1990) were developed in R (v. 3.4.1; R Core Team, 2017) using the package "mgcv" (v. 1.8-17; Wood 2011). Methods largely followed those described in Becker et al. (2016) and are summarized here. One of two modeling frameworks was used for each species, depending on its group size characteristics. For species with large and variable group sizes (all species except Bryde's whales), separate encounter rate and group size models were developed. Encounter rate models were built using all transect segments, regardless of whether they included sightings, using the number of sightings per segment as the response variable and a Tweedie distribution to account for overdispersion (Miller et al. 2013). Group size models were built using only those segments that included sightings, using the natural log of group size as the response variable, and a Gaussian link function. For the species with small group sizes (Bryde's whales), GAMs were fit using the number of individuals per transect segment as the response variable using all transect segments, and a Tweedie distribution to account for overdispersion. The full suite of potential habitat predictors was offered to both the encounter rate and single response GAMs. A tensor product smooth of latitude and longitude (Wood 2003) was the only predictor variable included in the

[1] https://www.hycom.org/

group size models given its success in previous SDMs (Becker et al. 2016) and observed geographic differences in group sizes for many delphinid species (Barlow 2015; Cañadas and Hammond 2008; Ferguson et al. 2006). Although mgcv is robust to correlated variables (Wood 2008), distance to land and depth (absolute correlation = 0.59) were offered to the models separately.

In all models, restricted maximum likelihood (REML) was used to optimize the parameter estimates (Marra and Wood 2011). Potential variables were excluded from the model using a shrinkage approach that modifies the smoothing penalty, allowing the smooth to be identically zero and removed from the model (Marra and Wood 2011). Additionally, to avoid overfitting, variables that had P-values > 0.05 were also removed and then the models refit to ensure that all remaining variables had P-values < 0.05 (Redfern et al. 2017; Roberts et al. 2016). The natural log of the effective area searched (described below) was included as an offset in both the single response and encounter rate models.

Predictions from the final model were incorporated into the standard line-transect equation (Buckland et al. 2001) to estimate density (*D*; number of animals per km^2):

$$D_i = \frac{n_i \cdot s_i}{A_i} \tag{1}$$

where *i* is the segment, *n* is the number of sightings, *s* is the average group size, and *A* is the effective area searched:

$$A_i = 2 \cdot L_i \cdot ESW_i \cdot g(0)_i \tag{2}$$

where *L* is the length of the effort segment, *ESW* is the effective strip half-width, and *g(0)* is the probability of detection on the transect line. Following the methods of Becker et al. (2016), 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 using coefficients estimated by (Barlow et al. 2011) for *ESW* and Barlow (2015) for *g(0)*. For those segments where the average Beaufort sea state was 0 (< 1% of the segments), *g(0)* was assumed to = 1, i.e., that all animals directly on the transect line were detected.

Model performance was evaluated using established metrics, including the following: the percentage of explained deviance, the area under the receiver operating characteristic curve (AUC; Fawcett 2006), the true skill statistic (TSS; Allouche et al. 2006), and the visual inspection of predicted and observed distributions during the 2002–2017 cetacean surveys (Barlow et al. 2009; Becker et al. 2010; Becker et al. 2016; Forney et al. 2012). The AUC discriminates between true-positive and false-positive rates, and values range from 0 to 1, where a score of >0.5 indicates better than random discrimination. TSS accounts for both omission and commission errors and ranges from −1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random. To calculate TSS, the sensitivity-specificity sum maximization approach (Liu et al. 2005) was used to obtain thresholds for species presence. In addition, the model-based abundance estimates for the Hawaiian EEZ based on the sum of individual modeling segment predictions were compared to standard line-transect estimates derived from the same data set used for modeling in order to assess potential bias in the habitat-based model predictions. The standard line-transect estimates were derived from the 2002–2017 survey data using Equations (1) and (2) above, but without the inclusion of habitat predictors.

The encounter-rate and group-size habitat relationships derived from the complete 2002–2017 data set were used to predict spatially explicit density values for the Hawaiian EEZ study area, given the environmental conditions specific to the 2002, 2010, and 2017 HICEAS effort periods. Model predictions were made on separate environmental conditions for every third day (tri-daily) during the 2002, 2010, and 2017 survey periods, thus taking into account the varying oceanographic conditions during the 2002–2017 cetacean surveys. Daily predictions have been used for similar models developed for the California Current Ecosystem (Becker et al. 2018); however, given that the physical oceanographic properties of waters around the Hawaiian Archipelago are defined by larger-scale processes (Mann and Lazier 2005), a coarser temporal resolution was selected for this study area. The separate tri-daily predictions were then averaged across the 2002–2017 survey period to produce spatial grids of average species density at 9-km^2 resolution within the study area. The final prediction grids thus provide a "multi-year average" of predicted tri-daily cetacean species densities. The tri-daily predictions were also used to create individual yearly averages for 2002, 2010, and 2017. The prediction grid was clipped to the boundaries of the approximate 2,447,635-km^2 Hawaiian EEZ study area.

The model-based abundance estimates were calculated as the sum of the individual grid cell abundance estimates, which were calculated by multiplying the cell area (in km^2) by the predicted grid cell density, exclusive of any portions of the cells located outside the Hawaiian EEZ or on land. Area calculations were completed using the R packages *geosphere* and *gpclib* in R (version 2.15.0, The R Foundation for Statistical Computing 2012).

Variance in study area abundance and density was estimated by combining uncertainty from four sources: environmental variability, group size, *g(0)*, and *ESW*. In highly dynamic ecosystems such as the California Current, variation in environmental conditions has been shown to be one of the greatest sources of uncertainty when predicting density as a function of habitat variables (Barlow et al. 2009; Forney et al. 2012). Although such variation is not expected to be as substantial for the Hawaiian EEZ, spatially explicit measures of uncertainty based on environmental variability were calculated as pixel-specific standard errors using the full set of tri-daily predictions. The pixel-specific standard errors were then used to derive an overall study area estimate of environmental variance using standard methods. The variance in group size was estimated based on the variation in observed group sizes using standard statistical formulae. Uncertainty in *g*(0) was estimated using the variance estimates for this parameter weighted by the proportion of survey effort conducted within each of the Beaufort sea state categories and estimated based on 10,000 bootstrap values. Beaufort-specific values of *ESW* used for this analysis were based on multiple covariates that influence cetacean detection (Barlow et al. 2011), but not all required variance components were available for analytical or simulation-based variance estimation. Therefore, the uncertainty in *ESW* was approximated as the variance in *ESW* for the average sea state (Beaufort 4) within the survey data (Barlow 2015). Although sea state is a major factor influencing *ESW*, this approximation will underestimate the variance of *ESW* by a small amount. These four sources of uncertainty were combined using the delta method (Seber 1982) to provide an overall measure of variance for the model-based study area abundance estimates. GAM parameter uncertainty was not included in the combined uncertainty measures because robust statistical methods for dealing with the dependence among the various sources of uncertainty were not available. One component of GAM parameter uncertainty is the stochastic variance in the number of groups or animals that will be sighted relative to the expectation given other model parameters. This variation is driven largely by the proportion of study area that is observed and the detection probability of the animals and will be higher for species that are rarer or have a more clustered distribution. The derivation of spatially explicit variance measures that account for these combined sources of uncertainty in an SDM is statistically complex and an area of active research[2]. For the models here, uncertainty will be under-estimated somewhat, but the most important sources of uncertainty are likely accounted for, especially for those species with larger sample sizes.

[2] U.S. Navy, Living Marine Resources Project 31. DenMod: Working Group for the Advancement of Marine Species Density Surface Modeling, https://www.navfac.navy.mil/content/dam/navfac/Specialty Centers/Engineering and Expeditionary Warfare Center/Environmental/lmr/LMRFactSheet_Project31.pdf

Results

The habitat-based density models were developed for 8 species using 71,530 km of on-effort survey data collected between 2002 and 2017 within the Hawaiian EEZ. The majority of this effort was from the 2002, 2010, and 2017 HICEAS surveys (59,768 km), and the remainder was from surveys of smaller regions within the study area or transits through the study area to other locations (Table 1). The number of sightings within the species-specific truncation distances and available for modeling ranged from 30 to 95 (Table 2). In addition to these 8 species, a habitat model was also developed for false killer whale, as described by Bradford et al. (2020), with the model outputs replicated in the Appendix for a comprehensive summary of all species SDMs from the HICEAS 2017 effort. Forney et al. (2015) developed a habitat model for spinner dolphin for waters of the central Pacific[3]. A new model for this species was not developed because of the small number of spinner dolphin sightings within Hawaiian EEZ waters (12 total for the 2002–2017 surveys).

Table 2. Number of sightings and average group size (Avg. GS) of cetacean species observed in the Hawaiian EEZ during the 2002–2017 shipboard surveys listed in Table 1 for which habitat-based density models were developed. All sightings occurred while on systematic and non-systematic effort in Beaufort Sea States ≤6 within the species-specific truncation distances (see text for details).

Common name	Taxonomic name	# Sightings	Avg. GS
Pantropical spotted dolphin	*Stenella attenuata*	69	61.82
Striped dolphin	*Stenella coeruleoalba*	65	39.66
Rough-toothed dolphin	*Steno bredanensis*	58	22.08
Common bottlenose dolphin	*Tursiops truncatus*	40	18.07
Risso's dolphin	*Grampus griseus*	30	18.64
Short-finned pilot whale	*Globicephala macrorhynchus*	95	25.61
Sperm whale	*Physeter macrocephalus*	81	7.94
Bryde's whale	*Balaenoptera edeni*	41	1.41

The most commonly selected predictor variables for encounter rate models of individuals (Bryde's whales) or groups (all other species) were MLD, bathymetric depth, and the smooth of latitude and longitude (Table 3). SSH, SST, and the standard deviation of SST were also selected in some of the models, yet salinity did not enter any of the models. The model of group size for all species except Bryde's whales included a tensor product smooth of latitude and longitude.

[3] The Forney et al. (2015) model for spinner dolphin was used to derive a density estimate for the Hawaii pelagic stock of spinner dolphins within the Hawaiian Islands EEZ in U.S. Department of the Navy. 2017. Quantifying acoustic impacts on marine mammals and sea turtles: Methods and analytical approach for phase iii training and testing. San Diego, CA: Naval Undersea Warfare Center.

Table 3. Summary of the final single response (Bryde's whale) and encounter rate (all other species) models built with the 2002–2017 survey data. Variable abbreviations are as follows: SST = sea surface temperature, SSTsd = standard deviation of SST, MLD = mixed layer depth, SSH = sea surface height, depth = bathymetric depth, dist = distance to land, LON = longitude, and LAT = latitude. All models were corrected for effort with an offset for the effective area searched (see text for details). Performance metrics included the percentage of explained deviance (Expl. Dev.), the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), and the ratio of observed to predicted density for the study area (Obs:Pred).

Species	Predictor variables	Expl. Dev.	AUC	TSS	Obs:Pred
Pantropical spotted dolphin	MLD + dist + LON:LAT	18.21	0.82	0.51	0.97
Striped dolphin	SSTsd + MLD + depth + LON:LAT	35.09	0.72	0.35	1.02
Rough-toothed dolphin	depth + LON:LAT	14.34	0.75	0.40	0.98
Bottlenose dolphin	SSTsd + depth	55.90	0.86	0.66	0.79
Risso's dolphin	MLD + depth + LON:LAT	18.54	0.84	0.54	1.05
Short-finned pilot whale	SSTsd + SSH + depth + LON:LAT	22.67	0.85	0.58	1.00
Sperm whale	SST + LON:LAT	12.02	0.70	0.29	1.00
Bryde's whale	SST + MLD + LON:LAT	17.10	0.80	0.52	1.00

Deviance explained by the models was variable, ranging from approximately 12% to 56% (Table 3). AUC values for all models were greater than 0.7 and the majority were greater than 0.8, indicating that the models did a good job discriminating between true-positive and false-positive results. The TSS values, which account for both omission and commission errors, were more variable, ranging from 0.29 (sperm whale) to 0.66 (common bottlenose dolphin). All models had observed: predicted density ratios close to 1, indicating that the sum of the segment-based density predictions were successful at capturing overall abundance in the study area as derived from design-based line-transect methods.

The multi-year average density surface maps generally captured observed distribution patterns as illustrated by actual sightings during the 2002–2017 surveys (Appendix). Strong island associations were evident for pantropical spotted dolphin, rough-toothed dolphin, common bottlenose dolphin, and short-finned pilot whale (Figure A 1, Figure A 3, Figure A 4, Figure A 6), consistent with observations (Baird 2013; Baird et al. 2009; Baird et al. 2008), predictions from prior density models (Forney et al. 2015), and formal recognition of island-associated stocks for pantropical spotted dolphins and common bottlenose dolphins (see Carretta et al. 2018). With the exception of Bryde's whale, overall geographic patterns of predicted density were similar between 2002, 2010, and 2017. The Bryde's whale model showed substantial differences in distribution patterns between the three years, though with a consistent lower density region near the main Hawaiian Islands (Figure A 8). Overall sighting rates of Bryde's whale during the three HICEAS efforts were markedly different (Table 4) likely reflecting a fluctuating distribution of the whales relative to habitat or prey distribution within the broader region.

Although geographic variations in density between HICEAS years were small for most species, overall Hawaiian EEZ-wide density did vary for all species other than rough-toothed dolphins (Table 4). The SDM for rough-toothed dolphin included only static variables—depth and the spatial longitude:latitude interaction term, such that it is not possible to predict changes in distribution using this model based on environmental variability.

Four sources of uncertainty (i.e., environmental variability, group size, *g(0)*, and *ESW)* were combined to provide an overall measure of variance for the model-based study area abundance estimates (Table 5). Since GAM parameter uncertainty was not specifically accounted for, the overall CV estimates of study area abundance are considered biased-low. The greatest source of uncertainty for all models was from the estimate of trackline detection probability (*g(0)*), while the source contributing the least was from environmental uncertainty due to temporal changes in habitat during the span of the survey periods. Variability in environmental conditions did not contribute to the variance estimate for rough-toothed dolphin since the best model for this species included only static terms (i.e., depth and longitude:latitude).

Table 4. Multi-year (2002-2017) average and annual model-predicted estimates of abundance and density (100 km-2), and corresponding coefficient of variation (CV) within the Hawaiian EEZ. Annual estimates are predicted from the full model using the habitat characteristics in that year. Log-normal 95% confidence intervals (CIs) apply to abundance estimates only. Also shown is the total number of sightings (N) during each of the survey years and the total for 2002, 2010, and 2017. The N for All years is inclusive of all surveys listed in Table 1.

Species	Period	N	Model abundance	Model density	CV	Low 95% CI	High 95% CI
Pantropical spotted dolphin	All years	69	47,692	1.95	0.156	35,175	64,663
	2002	10	47,608	1.95	0.153	35,341	64,134
	2010	12	48,662	1.99	0.154	36,023	65,735
	2017	22	47,464	1.94	0.159	34,808	64,722
Striped dolphin	All years	65	35,901	1.47	0.229	23,045	55,928
	2002	12	35,817	1.46	0.220	23,384	54,861
	2010	21	36,886	1.51	0.222	24,004	56,681
	2017	16	35,179	1.44	0.233	22,416	55,209
Rough-toothed dolphin	All years	58	72,195	2.95	0.480	29,589	176,153
	2002	14	72,195	2.95	0.443	31,489	165,521
	2010	16	72,195	2.95	0.467	30,245	172,328
	2017	14	72,195	2.95	0.490	29,100	179,108
Bottlenose dolphin	All years	40	13,831	0.57	0.391	6,608	28,948
	2002	11	13,279	0.54	0.372	6,553	26,907
	2010	15	13,706	0.56	0.377	6,709	27,999
	2017	2	14,395	0.59	0.395	6,829	30,341
Risso's dolphin	All years	30	6,867	0.28	0.214	4,534	10,401
	2002	5	6,916	0.28	0.208	4,623	10,346
	2010	10	6,174	0.25	0.204	4,159	9,165
	2017	10	7,385	0.30	0.221	4,817	11,322
Short-finned pilot whale	All years	95	14,269	0.58	0.178	10,088	20,184
	2002	16	15,198	0.62	0.171	10,900	21,191
	2010	24	15,343	0.63	0.169	11,039	21,326
	2017	16	12,607	0.52	0.183	8,826	18,008
Sperm whale	All years	81	5,523	0.22	0.351	2,833	10,769
	2002	25	5,707	0.23	0.344	2,961	10,998
	2010	26	5,497	0.22	0.342	2,863	10,555
	2017	14	5,387	0.22	0.370	2,668	10,878
Bryde's whale	All years	41	656	0.03	0.209	437	982
	2002	10	562	0.02	0.209	375	842
	2010	28	822	0.03	0.204	554	1,220
	2017	2	602	0.02	0.215	397	913

Table 5. Coefficient of variation (CV) for individual parameter estimates across the full study period (2002-2017). Environmental variability (Envt. Var.), group size (GS), g(0), and effective strip width (ESW).

Species	Envt. Var.	GS	*g(0)*	ESW
Pantropical spotted dolphin	0.002	0.102	0.114	0.033
Striped dolphin	0.003	0.092	0.198	0.070
Rough-toothed dolphin	0.000	0.101	0.465	0.063
Common bottlenose dolphin	0.008	0.159	0.354	0.039
Risso's dolphin	0.006	0.107	0.180	0.042
Short-finned pilot whale	0.004	0.078	0.157	0.034
Sperm whale	0.003	0.092	0.334	0.052
Bryde's whale	0.006	0.051	0.197	0.046

Discussion and Conclusions

The present analysis provides the most comprehensive treatment of model-based density for this study area. The new SDMs are an improvement over prior modeling efforts for the Hawaiian EEZ because they more accurately account for variation in detection probabilities by using segment-specific estimates of both *ESW* and *g(0)*, they provide finer-scale density predictions (~9 km × 9 km grid resolution), and they include additional years of survey data for the study area. Unlike the previous models presented by Forney et al. (2015), which included sightings from the Eastern Tropical Pacific to increase sample size, the models presented here are specific to the Hawaiian EEZ. Further, the increase in sample size allowed for the development of a new habitat model for Risso's dolphin. The dynamic environmental predictors included in the previous models were limited to surface variables, while a subsurface variable (mixed layer depth) was available and included as a key predictor in four of the new models (Table 3). Brodie et al. (2018) found that including dynamic subsurface variables that quantify the structure of the water column significantly improved the explanatory performance of habitat models, and this study is consistent with these findings.

Model selection uncertainty was estimated for the previous Hawaiian EEZ models using a jack-knife approach (Forney et al. 2015) but did not include measures of uncertainty for parameters such as group size, *g(0)*, or *ESW* that were accounted for by this study. Although treated more comprehensively, variance in the model-based study area abundance estimates was underestimated in the present study as well, since uncertainty in the model parameters was not included in the variance estimation process. Methods to derive spatially explicit variance measures that account for the major sources of SDM uncertainty are currently in development.

The distribution patterns predicted with these SDMs for 2002 and 2010 were broadly similar to those predicted by Forney et al. (2015) for species with strong island-associations (pantropical spotted dolphin, rough-toothed dolphin, common bottlenose dolphin, and short-finned pilot whale), as well as for Bryde's whale, and to a lesser extent for sperm whale. Geographic differences were apparent in the density maps for striped dolphin, particularly for 2002 when the current models predicted highest densities in the northwest portion of the Hawaiian EEZ, as well as offshore waters around the main Hawaiian Islands, consistent with actual sighting locations, whereas the Forney et al. (2015) predictions were relatively low in these regions.

High seasonal and interannual variability in cetacean abundance and distribution patterns have been observed and predicted from habitat models that were developed for waters in the California Current Ecosystem (Barlow and Forney 2007; Becker et al. 2018; Becker et al. 2017; Forney and Barlow 1998; Forney et al. 2012). The California Current Ecosystem is defined by high oceanographic variability at multiple temporal and spatial scales (Hickey 1979). Dynamic oceanographic processes around the Hawaiian Islands occur on larger spatial and temporal scales than those of eastern boundary currents (Mann and Lazier 2005), so the lower inter-annual variability in density predictions exhibited in this study is not unexpected, particularly for the island-associated species (e.g. Figure A 1, Figure A 4). The greatest variability in distribution patterns between years was for Bryde's whale (Figure A 8), consistent with results from the previous habitat modeling study (Forney et al. 2015). Bryde's whales are thought to move broadly within ocean basins (Kato and Perrin 2018) and have shifted their distribution in other regions in response to changing oceanic conditions (Kerosky et al. 2012).

Although the available sample size within the Hawaiian EEZ is reasonable for constructing habitat-based density models for the presented species, it is inadequate for examination of changes in population abundance over time, other than those predicted by changes in the environment. Population trends can be explicitly captured by an SDM by including a year term in the model (e.g., Becker et al. 2016), but more years of data, larger sample sizes, and potentially more information on factors affecting abundance are required than are currently available for the species presented here. Because a temporal term was not included in the models, the annual variability in abundance is likely under-estimated.

Comparison of model and design-based estimates

These models predict some inter-annual variability in the abundance estimates for all species except rough-toothed dolphin, for which the habitat covariates included in this models were limited to static predictors (i.e., depth and longitude:latitude). Stock-specific, design-based uniform density estimates also were produced for all species sighted on systematic survey effort during HICEAS 2002, 2010, and 2017 and are presented in Bradford et al. (in review). For all but two modeled species, the design-based estimates apply to a Hawaiian EEZ-wide stock; however, pantropical spotted dolphins and common bottlenose dolphins are represented by several island-associated stocks within the Hawaiian Archipelago (see Carretta et al. 2018), such that the design-based estimate for these species applies to the pelagic stock only. The influence of insular stock sightings within the pantropical spotted dolphin and common bottlenose dolphin habitat-based models make comparisons to the design-based estimates difficult, as the density patterns represented by the models likely represent a hybrid of the habitat characteristics of both insular and pelagic stocks. Although it is inappropriate to use the current species-level spotted and bottlenose dolphin habitat-based model estimates for Stock Assessment Reports, the models are still useful for examining overall distribution and density for the species in other contexts.

For species with EEZ-wide stock delineations, comparison of the design-based and habitat-based abundance estimates is instructive (Figure 2). For all species, the abundance estimates resulting from the habitat-based models are more stable over the 3 survey years than the design-based, uniform estimates. This stability is largely because the habitat predictors are derived from the multi-year data set within the modeling framework, combined with an implicit assumption of the time-independent model that overall population size contributing animals to the study area is constant through time. The design-based estimates are based on the realized encounter rates within each year (see details of the design-based methodology in Bradford et al. in review).The latter are subject to greater variation, because sampling error and patchiness in the environment and animal distribution can result in single year abundance estimates that are more variable than long-term trends in animal abundance might suggest (Moore and Barlow 2014). In contrast, habitat-based models can serve to smooth across annual variation in observed encounter rates, resulting in less variability between years, with much of the remaining variance largely attributed to environmental variability rather than to low single year sample size (Barlow et al. 2009; Forney et al. 2012). Thus, the multi-year habitat-based models assume that 1) the identified species-habitat associations are persistent across survey years and 2) cetacean density and distribution are primarily driven by changes in the extent and spatial distribution of habitat within the study area. Although it is possible to include annual trend terms in habitat-based models, if the available time-series is sufficiently long and sample sizes are robust (e.g., Becker et al. 2018), the limited sample sizes and survey years in this study were not sufficient to include a meaningful yearly trend in the habitat-based model.

As a result of the increased sampling variation associated with annual encounter rate estimates rather than a combined habitat-based encounter rate, the design-based estimates have broader confidence intervals than those predicted by the SDM. In most cases, however, the design-based confidence intervals fully encompass the point estimate and 95% CIs predicted by the SDMs (Figure 2). The only notable exception to this pattern is for Bryde's whales, where the point estimate of abundance derived from the design-based approach is outside of the 95% CI of the SDM-derived estimate in 2002 and 2010 and lower than the 95% CI of the SDM in 2017, although the tails of the confidence intervals estimated for the two approaches overlap in all years. As with most SDMs presented here, the annual abundance estimates are more similar than those derived from the design-based approach. Further, the confidence intervals for the 2017 design-based estimates do not overlap those from 2002 or 2010. The large differences in the design-based estimates are explored further in Bradford et al (in review); however, it is likely that the variation in the design-based estimates illustrates both annual variation in Bryde's whale distribution and abundance from habitat and potentially other factors in the Hawaiian EEZ, as well as the effects of encounter rate variability when estimating abundance of species with low sighting rates (Moore and Barlow 2014).

In contrast, SDM-predicted annual estimates for rough-toothed dolphins are quite similar, in their point estimates and CIs, to those derived from the design-based analysis (Figure 2). The similar point estimates are likely due to the reliance on only static variables within the SDM, while the broader confidence intervals are largely driven by the high *g(0)* CV (Table 5).

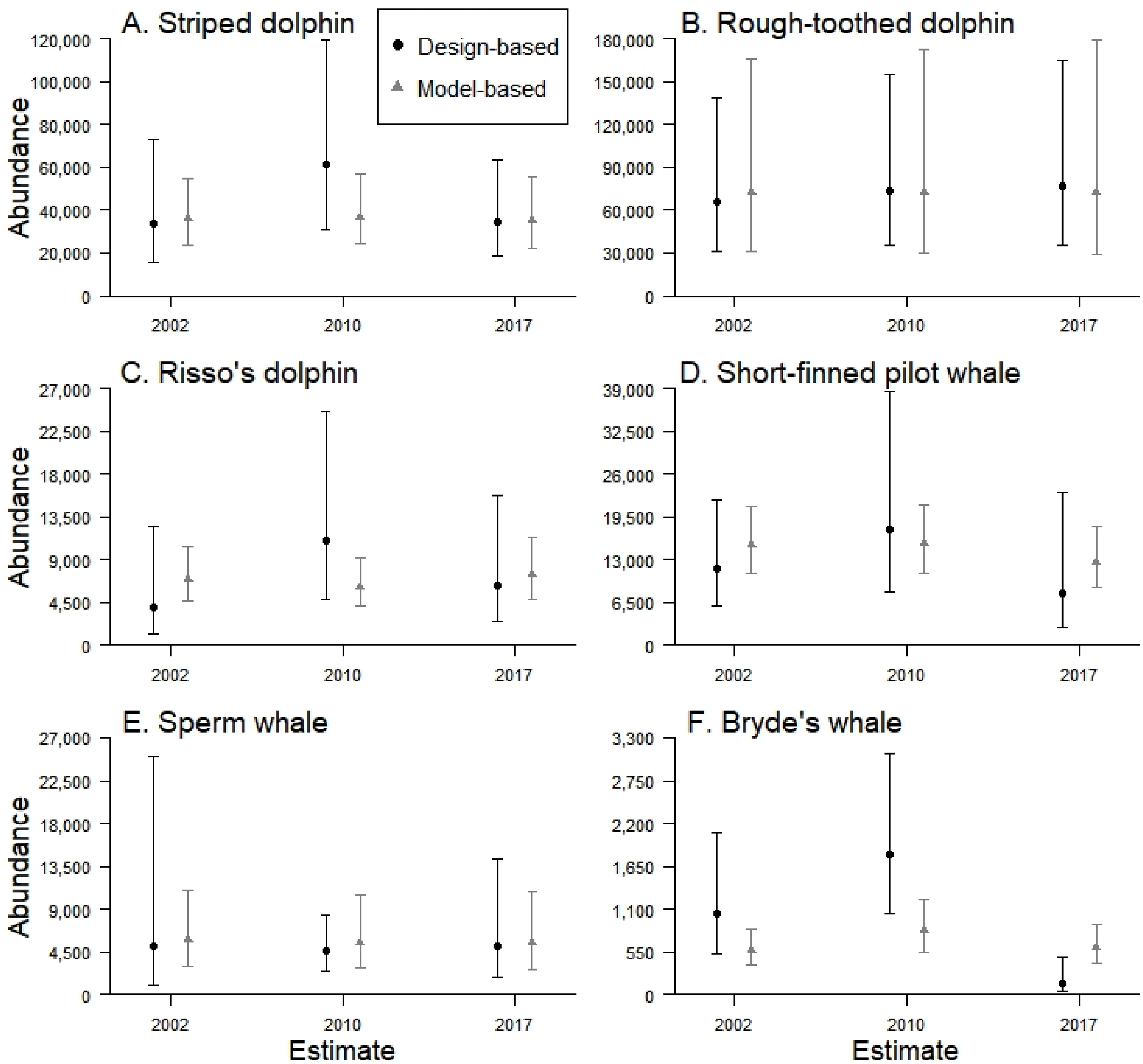

Figure 2. Comparison of design-based and model-based estimates of abundance for modeled species for each HICEAS year (2002, 2010, 2017).

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Appendix: Species Density Maps

Maps depict predicted average density (animals 100 km^{-2}) and the standard deviation (SD) of density derived from the habitat-based density models for the multi-year average, as well as the predicted average density for each HICEAS survey year (2002, 2010, 2017). Panels show average (AVG) density predictions on the environmental conditions for all years (top panel), as well as each individual year (2002, 2010, and 2017). Predictions are shown for the study area (2,447,635 km^2). Black dots in all the average plots show actual sighting locations from the respective ship surveys.

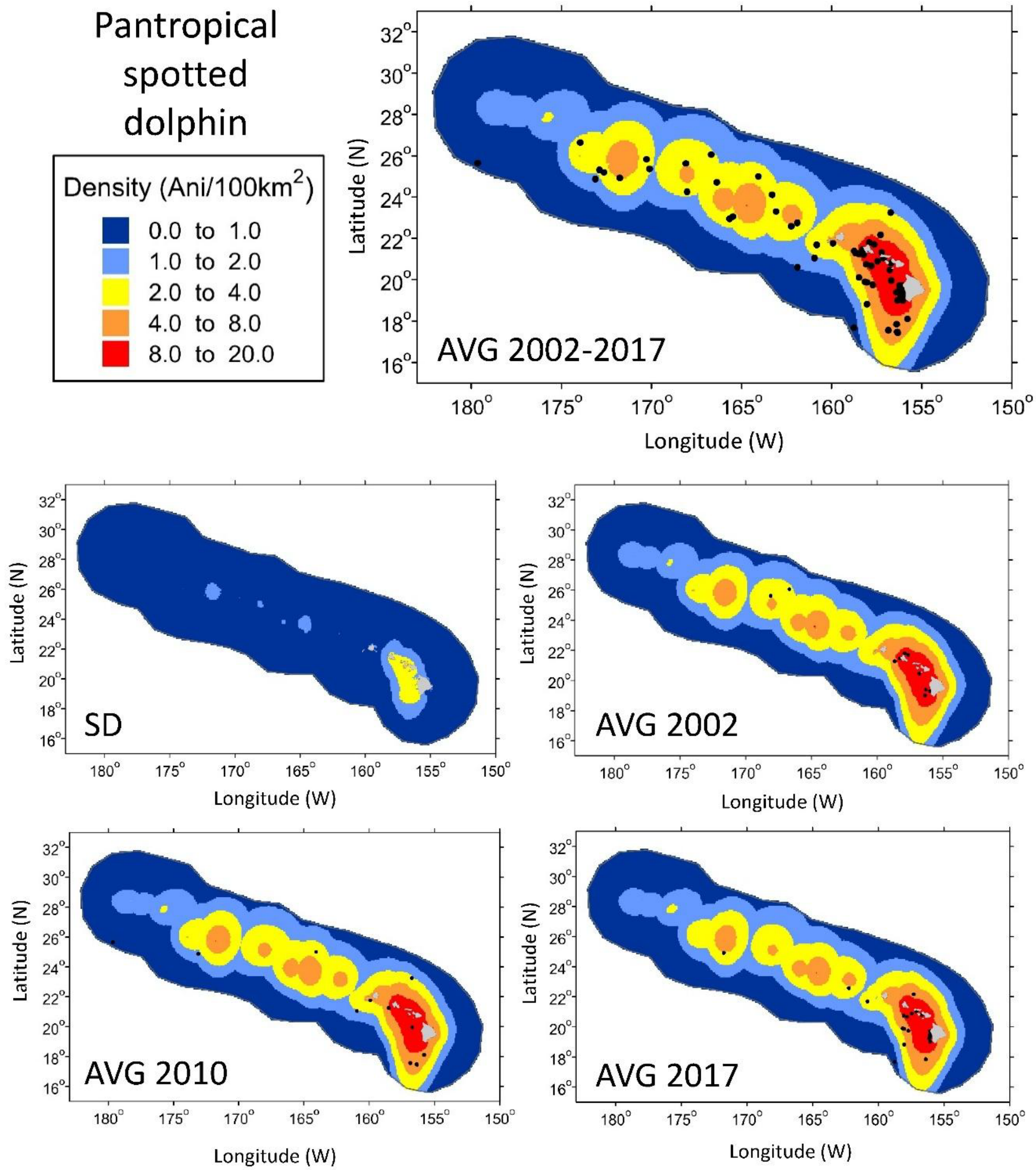

Figure A 1. Habitat-based density model output for pantropical spotted dolphin (*Stenella attenuata*).

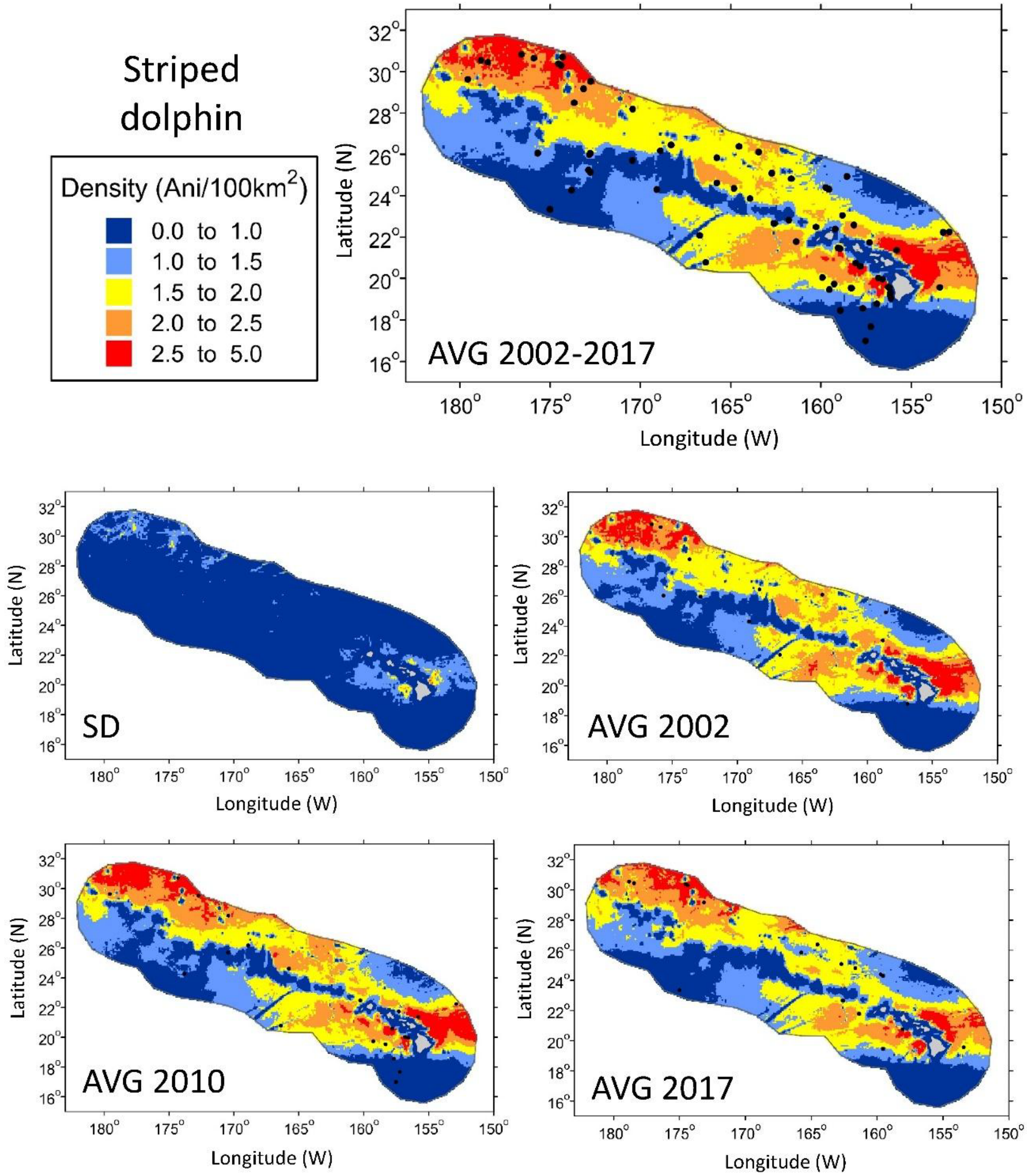

Figure A 2. Habitat-based density model output for striped dolphin (*Stenella coeruleoalba*).

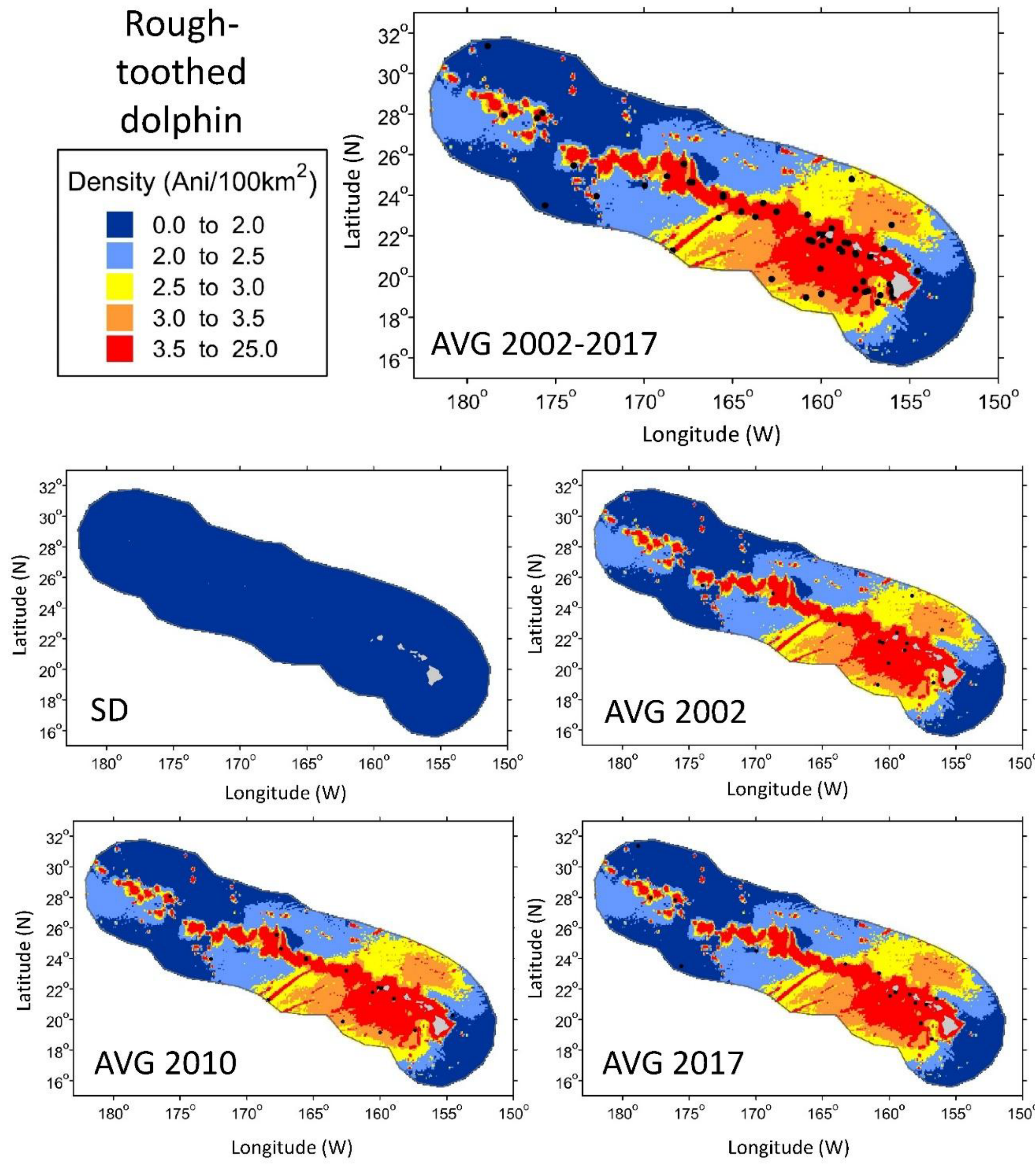

Figure A 3. Habitat-based density model output for rough-toothed dolphin (*Steno bredanensis*).

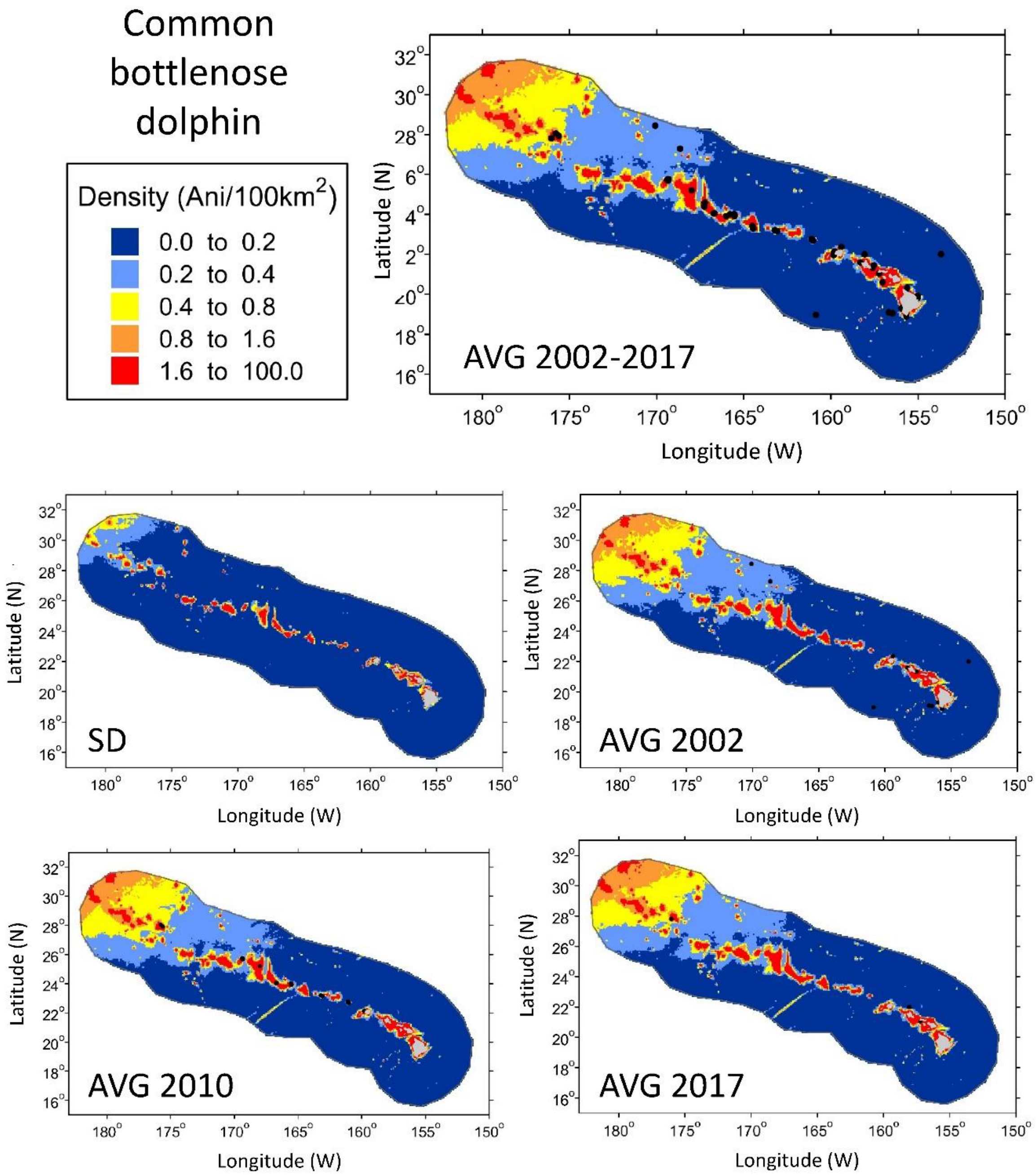

Figure A 4. Habitat-based density model output for common bottlenose dolphin (*Tursiops truncatus*).

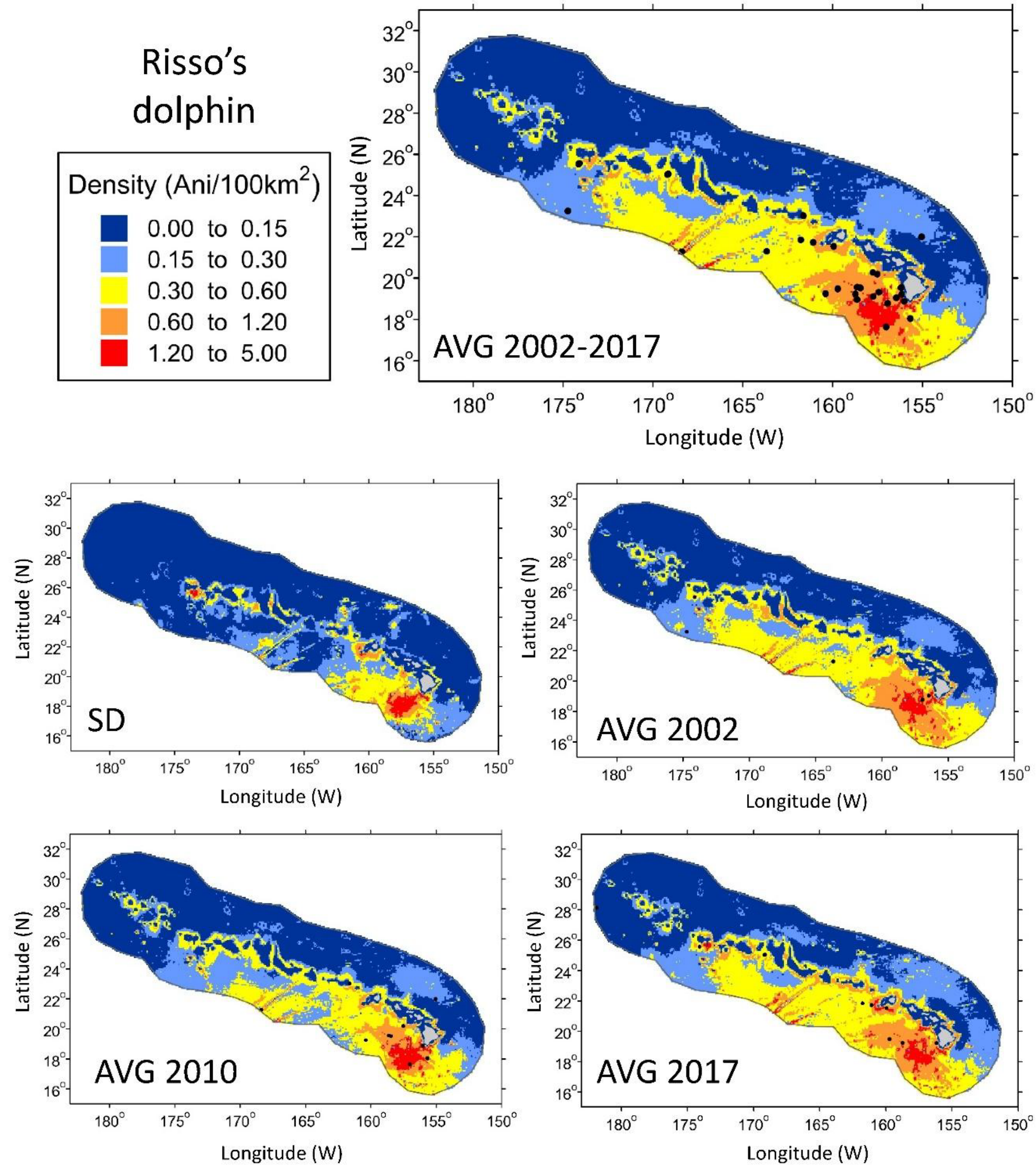

Figure A 5. Habitat-based density model output for Risso's dolphin (*Grampus griseus*).

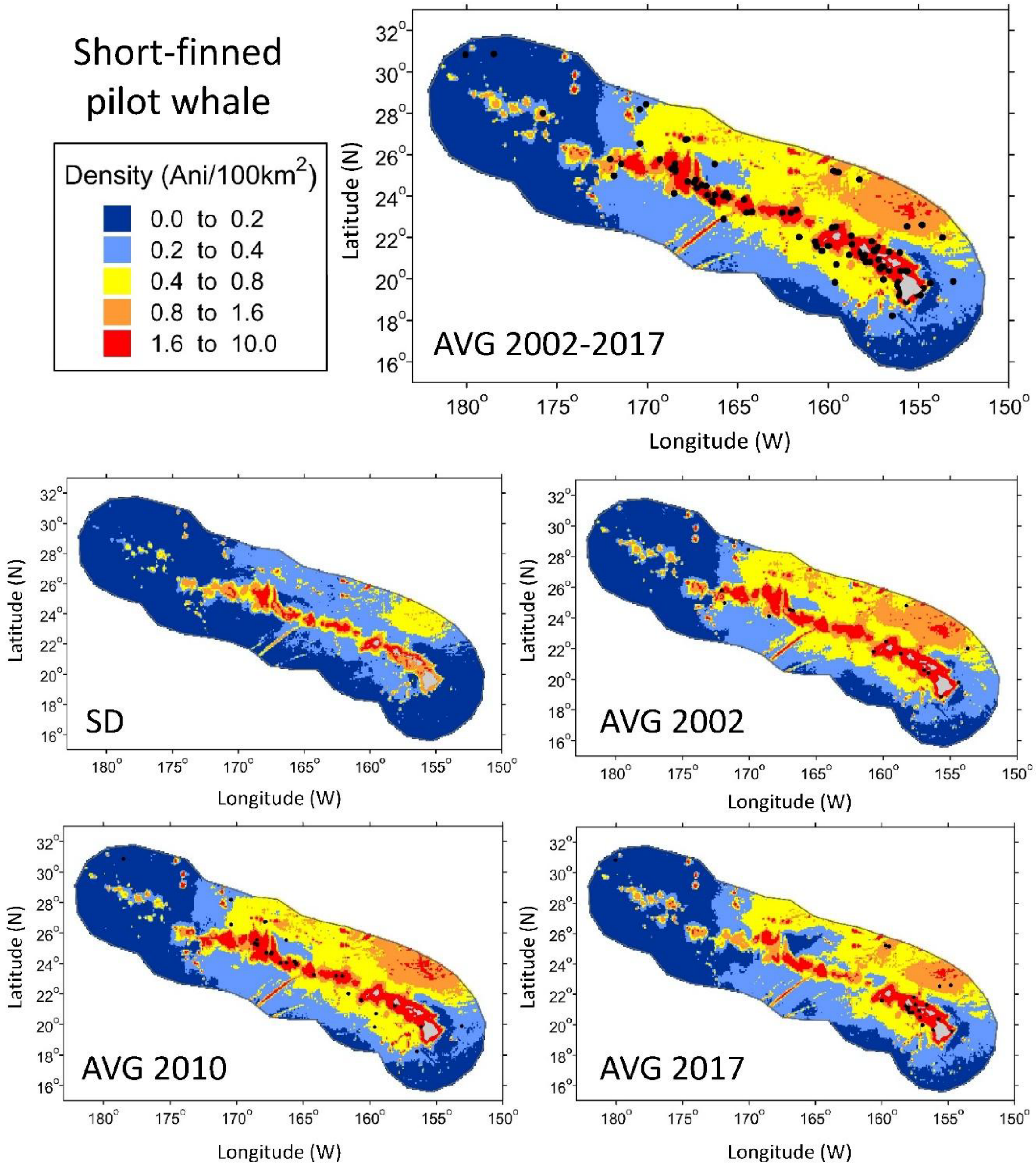

Figure A 6. Habitat-based density model output for short-finned pilot whale (*Globicephala macrorhynchus*).

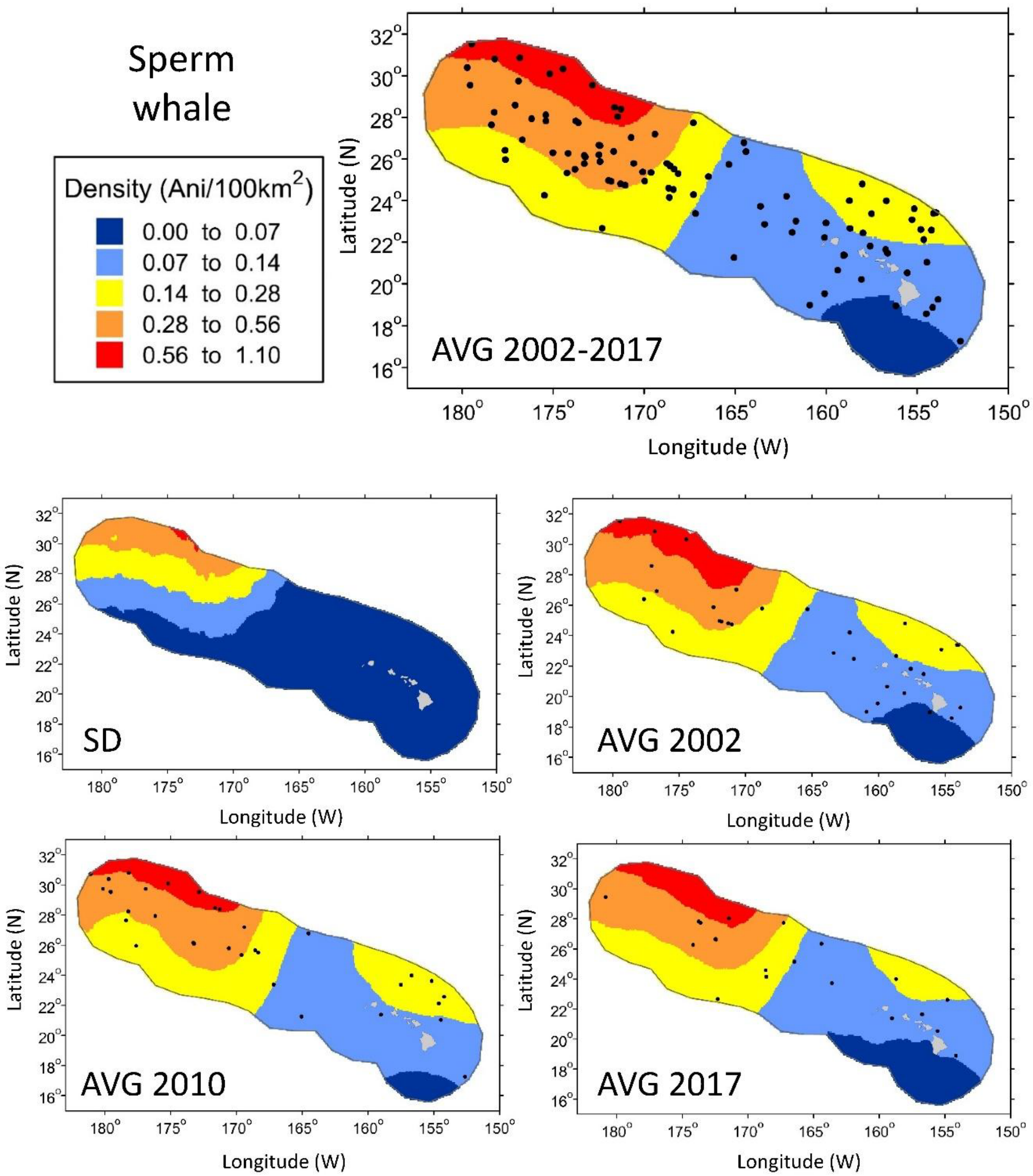

Figure A 7. Habitat-based density model output for sperm whale (*Physeter macrocephalus*).

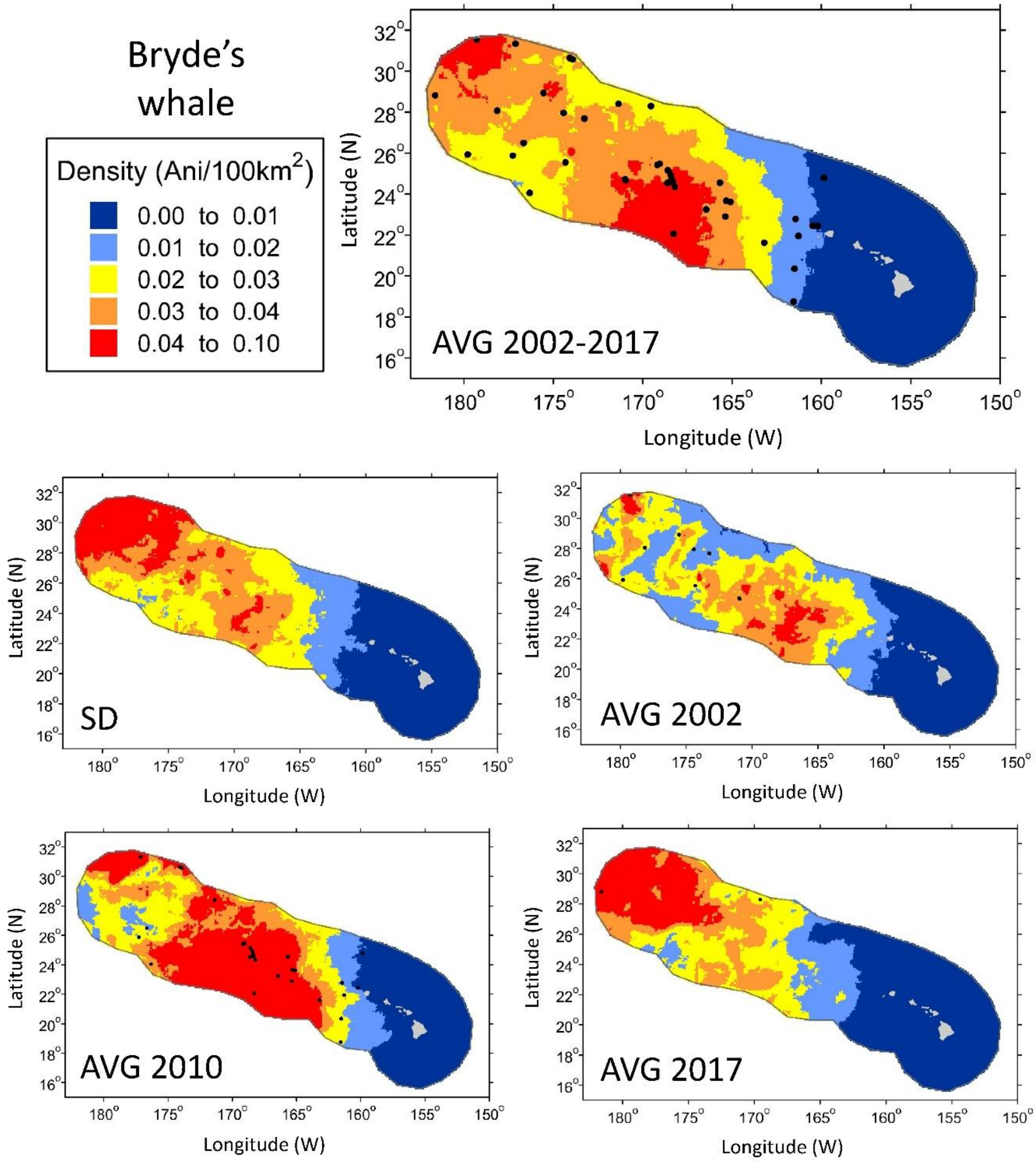

Figure A 8. Habitat-based density model output for Bryde's whale (*Balaenoptera edeni*).

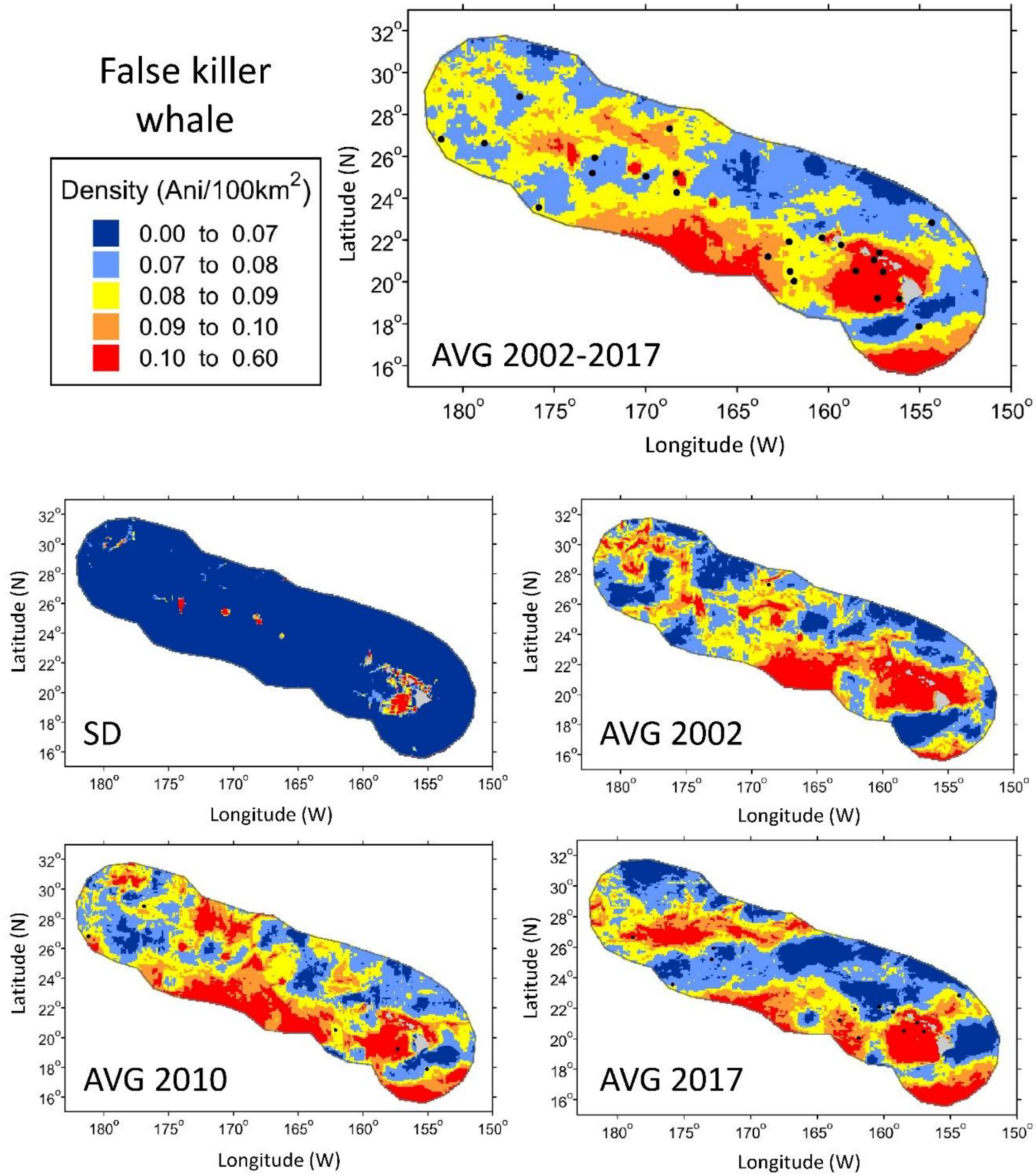

Figure A 9. Habitat-based density model output for false killer whale (*Pseudorca crassidens*) for the Hawaiian EEZ from the habitat-based density model for pelagic false killer whales in the central Pacific study. Reproduced from Bradford et al. (2020).