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A HABITAT-BASED SPATIAL DENSITY MODEL FOR HARBOR PORPOISE (*Phocoena phocoena*) OFF OREGON AND WASHINGTON BASED ON 2021-2022 AERIAL SURVEYS

Karin A. Forney[1,2], Scott R. Benson[1,2], and Elizabeth A. Becker[3]

[1] NOAA Fisheries, SWFSC Marine Mammal and Turtle Division

[2] San Jose State University, Moss Landing Marine Laboratories

[3] Ocean Associates under contract to NOAA Fisheries
SWFSC Marine Mammal and Turtle Division

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A habitat-based spatial density model for harbor porpoise (*Phocoena phocoena*) off Oregon and Washington based on 2021-2022 aerial surveys

Karin A. Forney[1,2], Scott R. Benson[1,2], Elizabeth A. Becker[3]

[1] Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7544 Sandholdt Rd, Moss Landing, CA, United States

[2] Moss Landing Marine Laboratories, San Jose State University, 7544 Sandholdt Rd, Moss Landing, CA, United States

[3] Ocean Associates, Inc., under contract to the Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, 8901 La Jolla Shores Dr, La Jolla, CA 92037

ABSTRACT

This study presents new abundance estimates for harbor porpoise, *Phocoena phocoena*, within shelf waters of the outer coasts of Oregon and Washington, USA. Habitat-based spatial density models were developed to estimate the abundance of three harbor porpoise stocks in this region, based on aerial surveys conducted during August-September 2021 and 2022. Model results and spatial density maps show the greatest harbor porpoise densities within shallow waters and in waters with more uniform sea surface temperatures in the range of 14-16°C. The model-estimated abundance of 22,074 (CV=0.39) harbor porpoise within the range of the Northern Oregon/Washington Coast stock is very similar to the previous estimate of 21,487 (CV = 0.44) derived from 2010-2011 aerial surveys. A newly proposed Central Oregon stock, recommended for designation based on recent genetic studies, was estimated to contain 7,492 (CV = 0.42) harbor porpoises. The abundance of harbor porpoises within the reduced range of the Northern California/Southern Oregon stock, from which the Central Oregon stock was split, was estimated to be 15,303 (CV = 0.57). Combined these results provide updated abundance

estimates for three porpoise stocks and the first habitat-based density estimates for harbor porpoises along the U.S. West Coast.

INTRODUCTION

Harbor porpoise, *Phocoena phocoena*, are found in temperate nearshore waters of the northern hemisphere, including shelf waters (generally <200 m depth) of the Pacific coast of North America (Barlow 1988). Despite the continuous distribution of harbor porpoises along the U.S. West Coast, genetic studies identified significant differences between porpoises from multiple regions off California, Oregon, and Washington (Chivers et al. 2002, 2007). Since 2002 (Carretta et al. 2002), six stocks have been recognized in this region: Morro Bay, Monterey Bay, San Francisco-Russian River, Northern California/Southern Oregon, Northern Oregon/Washington Coast, and Inland Washington. More recently, Morin et al. (2021) provided evidence of additional population structure and recommended that the Northern California/Southern Oregon stock be further divided to separate animals north of about 43.2°N from those south of there. Forney et al. (2021) provided estimates of abundance and trends for the four harbor porpoise stocks found off California based on aerial surveys conducted during 1986-2016. Off Oregon and Washington, however, the most recent abundance estimates were derived from 2010-11 aerial surveys (Forney et al. 2014).

In this study, we present new harbor porpoise abundance estimates for Pacific waters off Oregon and Washington, based on aerial surveys conducted within about 40-50 km of the coast during August-September 2021 and 2022. The primary goal of those surveys was to assess the abundance, distribution, and habitat of leatherback turtles, *Dermochelys coriacea*; however, field methods followed standard aerial line-transect methodology (Buckland et al. 2001) that has been used during previous marine mammal and turtle aerial surveys (see Forney et al. 2014, 2021). The achieved survey coverage was fine-scale (1-4 minute latitudinal spacing) but heterogeneous, in part because of weather and airtime limitations, and in part because additional survey effort was conducted within areas of interest for leatherback turtle assessment. For this reason, a design-based analysis of harbor porpoise abundance would have required complex post-stratification. In contrast, habitat-based models of cetacean density and abundance can be developed from such heterogeneous survey data to obtain unbiased results (Hedley and Buckland 2004; Becker et al. 2020). Such models also allow interpolation (or careful extrapolation) to unsurveyed areas or time periods as long as sufficient coverage of similar habitat was available for model parameterization (Becker et al. 2014, 2018; Mannocci et al. 2015, 2017). Based on these considerations, we developed a novel habitat-based density model to estimate the spatial density and abundance of harbor porpoise within shelf waters (< 200m depth) off Oregon and Washington. Separate abundance estimates were derived for three harbor porpoise stocks, including the newly proposed Central Oregon stock (see Draft 2023 Stock Assessment Report).

METHODS

Study area and transect design

The survey area extended from just north of Cape Blanco, OR (43º N) to Cape Flattery, WA (48.4º). East-west transects extended from the coast to about 40-50km offshore, covering the majority of shelf waters. Based on daily weather conditions and logistic constraints, a subset of transect lines was selected for survey coverage each day. During the two field seasons (August 31 – September 24, 2021 and August 9 – September 5, 2022) most of the study area was surveyed, with the greatest coverage in areas where leatherback turtles or aggregations of their prey (brown sea nettles, *Chrysaora fuscescens*) were observed (Figure 1). Surveys were conducted under fair to excellent weather conditions (Beaufort sea states 0-4, variable cloud conditions including some overcast days).

Field methods

Field methods were identical to those used during previous harbor porpoise and leatherback surveys (Forney et al. 2014, 2021). Surveys were flown in a DeHavilland Twin Otter aircraft, at an altitude of about 198 m (650 ft) and airspeeds of 170-185 km/hr. The observer team consisted of two observers who searched from bubble windows on either side of the aircraft and a third observer who searched below the plane via a belly port at the rear of the aircraft. Viewing conditions (including Beaufort sea state, percent cloud cover, horizontal sun position, and a subjective assessment of visibility into the water) and sighting information (including species, number of animals, and declination angle measured with a Suunto™ hand-held clinometer), were verbally reported to a fourth team member who entered the details into a laptop computer with real-time GPS input. Marine mammals, sea turtles, and other species of interest (e.g., sea nettles, ocean sunfish, *Mola mola*, sharks) were recorded systematically. At the end of each survey day, the data were edited and error-checked for subsequent processing.

Data processing

For model development, transects were divided into approximate 1-km segments using the R package *swfscAirDAS* (Woodman 2022), following the approach of Becker et al. (2010) in which ‘extra’ sections of continuous effort were either added to another segment (if < 0.5 km) or considered a separate shorter segment (if ≥ 0.5 km). Only about 3% of segments were not 1 km. Data were restricted to include only survey effort collected under good to excellent survey conditions (Beaufort sea state ≤ 3 and cloud cover ≤ 25%) and within < 250 m water depth (to exclude a few deep-water areas that are not considered harbor porpoise habitat while including some data beyond the expected depth range of harbor porpoise for model fitting). Sightings beyond 300 m perpendicular distance to the transect line were truncated (eliminating 2.1% of the most distant sightings) based on a previous analysis of harbor porpoise survey data collected using the same methodology in this region (Forney et al. 2014). For the density predictions and abundance calculations, we established a 0.09-degree grid covering 26,974 km^2 within known porpoise habitat in shelf waters (< 200 m) off Oregon and Washington. The grid included the area from Cape Blanco south to the California/Oregon border, where no survey effort occurred during our study. This southward extension allowed us to estimate harbor porpoise abundance from the habitat-based model for the entire Pacific coast shelf region of Oregon and Washington, providing complementary coverage to the California abundance estimates presented in Forney et al. (2021).

Habitat covariates

Harbor porpoise densities are known to vary with water depth (Barlow 1988, Carretta et al. 2001), dropping off rapidly with increasing depth over scales of a few kilometers along the U.S. West Coast. Fine-scale bathymetric data were derived from the ETOPO1 1-arc min global relief model (Amante and Eakins 2009). Rugosity, calculated as the standard deviation of water depth within +/- 1 one pixel of each depth point, was also calculated to provide a measure of bathymetric slope. Various dynamic predictors have successfully been included in habitat-based models for cetaceans within the California Current Ecosystem (e.g., Becker et al. 2016, 2018, 2020) and for harbor porpoises in the North Sea (Gilles et al. 2016); however, only sea surface temperature (SST) is available at a sufficiently fine spatial scale to model harbor porpoise densities within the shallow shelf waters off Oregon and Washington. For this study, we derived SST from the 1-km resolution Multispectral Ultrahigh Resolution SST (mSST, Chin et al., 2017). Standard deviations of mSST were calculated at two spatial scales to capture frontal regions or mesoscale features: within +/- 4 pixels (9 x 9-km box; mSSTsd4) and within +/- 12 pixels (25 x 25-km box; mSSTsd12). Fixed spatial terms were not included in the model because we were interested in extending the model southward beyond the surveyed region to include all of the southern Oregon range of harbor porpoise and provide a stock-wide abundance estimate. All habitat covariates were extracted for each segment midpoint and prediction grid centroids.

Analysis methods

Prior to developing the habitat-based model, the R package *Distance* was used to estimate the detection function and corresponding effective half-strip width (*ESW*) (Buckland et al. 2001). Based on past analyses of harbor porpoise survey data collected using the same field methodology (Forney et al. 2014, 2021), a half-normal model with cosine adjustments was fit to the perpendicular sighting data, truncated at 300 m perpendicular distance (eliminating 2.1% of sightings). Analyses were conducted using multiple covariate distance sampling (MCDS) to allow for potential effects of Beaufort sea state on the detection function (Forney et al. 2014). The probability of detecting harbor porpoise groups on the transect line, $g(0) = 0.292$, CV = 0.366, was taken from the study of Laake et al. (1997), which used similar survey protocols. This value has also been used for previous studies estimating harbor porpoise abundance along the U.S. West Coast (Carretta et al. 2009; Forney et al. 2014, 2020). For each segment *i*, the effective area searched, A_i, was calculated following the methods of Becker et al. (2020), as the product of the segment length, the segment-specific *ESW* (based on Beaufort sea state), and $g(0)$:

$$A_i = 2 \cdot L_i \cdot ESW_i \cdot g(0)_i \tag{1}$$

Model development and selection

Habitat models were developed within the framework of Generalized Additive Models (GAM), using the package "mgcv" (v. 1.8-31; Wood 2011) in R (v. 4.2.2; R Core Team, 2022. Methods followed those previously developed for cetacean habitat models (Becker et al. 2016, 2020). The number of porpoises observed on each transect segment was the response variable, with water depth, mSST, and either mSSTsd4 or mSSTsd12 as potential covariates. The natural log of the effective area searched (A_i) was included as an offset. To account for overdispersion, Tweedie and negative binomial distributions were considered. Model parameter estimates were selected using restricted maximum likelihood (REML) and the shrinkage approach of Marra and Wood (2011).

Abundance and density estimation

The selected model was projected onto 122 daily covariate grids for all days of August-September 2021 and 2022 to obtain the average estimated number of porpoises and pixel-specific porpoise density, *D*. Stock-specific abundance estimates were derived by summing the average predicted number of porpoises for pixels within the range of each stock, with boundaries between stocks at 45°N and 43.2°N. Following the methods of Becker et al. (2016, 2020) the standard deviation of the daily predictions was calculated to estimate variability in porpoise density caused by environmental variation during the study period. Overall variance in abundance was estimated using the delta method by combining three sources of uncertainty according to the following formula:

$$CV(N_i) = \sqrt{CV^2(D) + CV^2(ESW) + CV^2(g(0))}, \tag{2}$$

where CV(*D*) = coefficient of variation of the model-based daily porpoise densities (*D*), CV(*ESW*) is derived from the Distance analysis above, and CV(*g(0)*) = 0.366 from Laake et al. (1997). Although more comprehensive methods of jointly estimating uncertainty from all key components (environmental variation, detection parameter uncertainty, model parameter uncertainty) were recently developed (Miller et al. 2022), the simplified delta method was preferable in our study because it allowed us to combine the Oregon abundance estimates with separate California estimates (Forney et al. 2020) to obtain a stock-wide abundance estimate for the Northern California/Southern Oregon stock (see Discussion below).

RESULTS

The complete August-September 2021-2022 survey effort resulted in a total of 14,858 km and 900 harbor porpoise sightings of 1,372 individuals. After excluding survey data that were unsuitable for harbor porpoise abundance estimation (e.g., sea states > 3, cloud cover > 25%, non-standard survey effort during faster transit flights, segments over deep water, and sightings beyond the 300-m truncation distance), the segment data used for model development included a total of 9,976 km of survey effort and 773 sightings of 1,187 harbor porpoises (Table 1). The complete surveys covered most of the study area from just north of Cape Blanco, OR to Cape Flattery, WA, but a few gaps were present within the modeling data set because of poor weather conditions (Figure 1). Nonetheless, a high level of coverage was achieved, including most of the suitable harbor porpoise habitat.

The detection functions modeled with and without Beaufort sea state as a covariate were similar (Δ AIC = 1.3, Table 2), and the model that included sea state was selected for further analysis to allow for segment-specific differences in porpoise detection as sea state conditions varied (Figure 2). The mean *ESW* was 158.3 m (CV=0.03), and estimated *ESW* values for Beaufort sea states of 0, 1, 2, and 3 were 167.5 m, 162.2 m, 156.9 m, and 151.6 m, respectively. This indicates about a 10% reduction in porpoise detection within the range of sea states included in this study (Beaufort sea states 0-3).

The best habitat-based density model for both Tweedie and negative binomial distributions included covariates depth, mSST, and mSSTsd12 (Table 3). Rugosity (the standard deviation of depth) was initially included as well but was excluded from the final model because it appeared to be overspecified and created pixelated artifacts along the shelf break. Functional plots and model metrics were similar for both model types (Figure 3), with the Tweedie models having slightly better metrics. For this reason, we selected the Tweedie Model 4 (see Table 3) for the spatial density distribution maps (Figure 4) and for abundance estimation. Spatial density estimates are dominated by a greater abundance of harbor porpoises in shallower waters, with some north-to-south variability based on the dynamic SST covariates. The daily variation across the 122-day study period (August and September 2021 and 2022) was greatest in the nearshore waters where porpoises were concentrated (Figures 1, 4). Stock-specific abundance estimates (Table 4) show the largest number of porpoises off Washington and northern Oregon and fewer animals off central and southern Oregon.

DISCUSSION

This study presents the first habitat-based spatial density and abundance estimates for harbor porpoises along the U.S. West Coast. Although the surveys were not specifically designed for harbor porpoises, the data collection protocols were the same as those used on past harbor porpoise surveys along the U.S. West Coast, and the habitat-based model allowed the data to be used for robust abundance estimation despite the heterogeneous coverage and spatial gaps. The dominant habitat covariate included in the model (depth) was consistent with previous studies that showed greater harbor porpoise numbers in shallow waters (e.g., Barlow 1988, Carretta et al. 2001, Calambokidis et al. 2004, Gilles et al. 2016). Our analysis further revealed that harbor porpoise densities were greater in waters of about 14-16°C, decreasing gradually in colder waters and more rapidly as water temperature increases (Figure 3). A small negative linear effect was also found with the standard deviation of SST at a scale of 25 × 25 km, suggesting that harbor porpoises off Oregon and Washington are associated with areas where SST is relatively uniform.

The habitat-based density model allowed informed, habitat-based extrapolation to regions not covered during the 2021-22 aerial surveys, including some shelf areas with survey gaps and the region south of Cape Blanco, OR. This provided gap-free abundance estimates for harbor porpoises along the entire outer coast of Oregon and Washington. The primary assumption for this extrapolation is that habitat associations are similar in surveyed and unsurveyed regions. While such extrapolation must always be done with care to avoid predictions outside of the covariate space used to build the model, studies have shown that habitat-based models can perform quite well when the covariate ranges are similar (Becker et al. 2014; Bouchet et al. 2019; Mannocci et al. 2015, 2017). In this study, the unsurveyed regions were ecologically similar to those that were surveyed (Spalding et al. 2007), providing support for the extrapolations. However, additional surveys within those areas would provide more robust abundance estimates in the future.

Uncertainty estimates in this study are based on the methods of Becker et al. (2016, 2020), which combine different variance components from environmental variability and detection parameters to estimate the overall uncertainty in abundance and density. Recently, methods have been developed to jointly estimate uncertainty stemming from a variety of sources, including habitat model covariates, detection parameters, and environmental variability within a single simulation framework (Miller et al. 2022, Becker et al. 2022). For this study, that approach was not practical because it would have confounded our ability to estimate the total abundance (and variance) of the Northern California/Southern Oregon stock by combining the southern Oregon estimate (this study) with the northern California abundance (Forney et al. 2021). The *g(0)* estimate from Laake et al. (1997) was used in both studies, but the integrated simulation framework would have prevented us from accounting for this joint variance component when combining variances from both regions. For this reason, a simpler variance calculation approach using the delta method was chosen. When additional survey data within the full range of the Northern California/Southern Oregon stock become available, the approach of Miller et al. (2022) would yield more inclusive uncertainty estimates for updated spatial densities and resulting abundance estimates throughout the entire stock range. Some additional uncertainty, which is not accounted for in the current analysis, derives from the application of fixed stock boundaries that assume porpoises do not move between stock regions, and the application of a *g*(0) estimate from a separate, prior study (Laake et al. 1997). While the uncertainty introduced by fixed stock boundaries is likely small relative to the confidence limits of the abundance estimates, the estimate of *g*(0) contributes a considerable amount of uncertainty (CV = 0.39). Future estimates of harbor porpoise abundance could potentially be improved if a more precise estimate of *g*(0) was obtained through additional studies.

The abundance estimates presented in this study are similar to the most recent previous estimates based on 2010-2011 aerial surveys (Forney et al. 2014). For the Northern Oregon/Washington Coast stock, Forney et al. (2014) estimated 21,487 (CV = 0.44) harbor porpoises, compared to our estimate of 22,074 (CV = 0.39). For coastal waters off Oregon south of 45°N, Forney et al. (2014) estimated 12,525 (CV = 0.48) harbor porpoises, while our two estimates within this region (separated by stock) are 7,492 + 3,143 = 10,635 total porpoises (Table 4). The habitat-based density model allowed us to estimate abundance separately by stock region, providing an abundance estimate for the proposed new Central Oregon harbor porpoise stock, and updated abundance estimates for the two other stocks found off Oregon and Washington. Minimum abundance estimates, defined as the lower 20th percentile of the estimated abundance, are provided in Table 4 to facilitate the preparation of updated stock assessment reports.

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Table 1. Summary of survey data used for modeling, including the total km surveyed, the number of harbor porpoise sightings, and the number of harbor porpoise individuals in Beaufort sea states 0-3 and with <= 25% cloud cover during the August-September 2021 and 2022 aerial surveys off Oregon and Washington.

Beaufort sea state	Km surveyed	No. porpoise sightings	No. porpoises
0	233	40	61
1	2,712	261	405
2	5,134	358	543
3	1,897	114	178
TOTAL	**9,976**	**773**	**1,187**

Table 2. Model fitting results for the half-normal detection function models. AIC = Akaike's Information Criterion, Δ AIC = difference in AIC between models, Mean *ESW* = average effective strip half-width for entire data set (in meters), CV(*ESW*) = coefficient of variation of *ESW*.

Covariate(s)	AIC	Δ AIC	Mean *ESW* (m)	CV(*ESW*)
None	-2098.3		158.4	0.03
Beaufort sea state	-2097.0	1.30	158.3	0.03

Table 3. Model summaries for harbor porpoise density models developed using Tweedie and negative binomial (Negbin) distributions. Greatest explained deviance (Expl. Dev.) and restricted maximum likelihood (REML), and smallest root-mean-squared-error (RMSE) and Akaike’s Information Criterion (AIC) are shown in **bold**, to show best model metrics. Based on the overall results, Model 4 was selected for abundance estimation. Covariate names are described in the methods section.

			Significance of covariates				**Model metrics**			
Model	**Distribution**	**Predictor variables**	**depth**	**mSST**	**mSSTsd4**	**mSSTsd12**	**REML**	**Expl. Dev.**	**RMSE**	**AIC**
1	Tweedie	Depth	<0.001				-3053.2	12.1%	0.5403	6098.7
2	Tweedie	depth + mSST	<0.001	<0.001			-3047.0	12.9%	0.5391	6078.6
3	Tweedie	depth + mSST+mSSTsd4	<0.001	<0.001	0.869		-3047.0	12.9%	0.5391	6078.6
4	**Tweedie**	**depth + mSST+mSSTsd12**	<0.001	<0.001		<0.001	**-3041.8**	**13.4%**	**0.5387**	**6065.4**
5	Negbin	Depth	<0.001				-3079.1	13.7%	0.5403	6148.9
6	Negbin	depth + mSST	<0.001	<0.001			-3075.0	14.7%	0.5393	6132.9
7	Negbin	depth + mSST+mSSTsd4	<0.001	<0.001	0.899		-3075.0	14.7%	0.5393	6132.9
8	Negbin	depth + mSST+mSSTsd12	<0.001	<0.001		<0.001	-3070.4	**15.3%**	0.5390	6120.6

Table 4. Abundance estimates (N) and coefficients of variation (CV) by harbor porpoise stock off Oregon and Washington. Individual CV components are also shown, including: CV(ENV) for the environmental variability from daily model predictions; CV(*ESW*) for the parameter uncertainty of the estimated effective strip half-width (this study); CV(*g0*) for the uncertainty of the trackline detection probability (Laake et al. 1997). Abundance estimates for the full stock range of the Northern California/Southern Oregon stock were estimated as the sum of those presented in this study and in Forney et al. (2021); CVs for the full stock range were estimated using standard variance formula (and taking into account that the same $g(0)$ estimate was applied in both studies). The minimum population size (N_{min}), defined within the Marine Mammal Protection Act and taken as the lower 20% percentile of a statistical abundance estimate, is also provided to facilitate the development of updated stock assessment reports. n/a = not available.

Harbor porpoise stock	**N**	**CV(N)**	**CV(ENV)**	**CV(*ESW*)**	**CV(*g0*)**	**N_{min}**
Northern Oregon/Washington Coast Stock	22,074	0.391	0.135	0.030	0.366	16,068
Central Oregon Stock	7,492	0.421	0.206	0.030	0.366	5,332
Northern California/Southern Oregon Stock	15,303	0.575	n/a	n/a	*0.366*	9,759
Southern Oregon (This study)	*3,143*	*0.464*	*0.283*	*0.030*	*0.366*	
Northern California (Forney et al. 2021)	*12,160*	*0.663*	n/a	n/a	*0.366*	

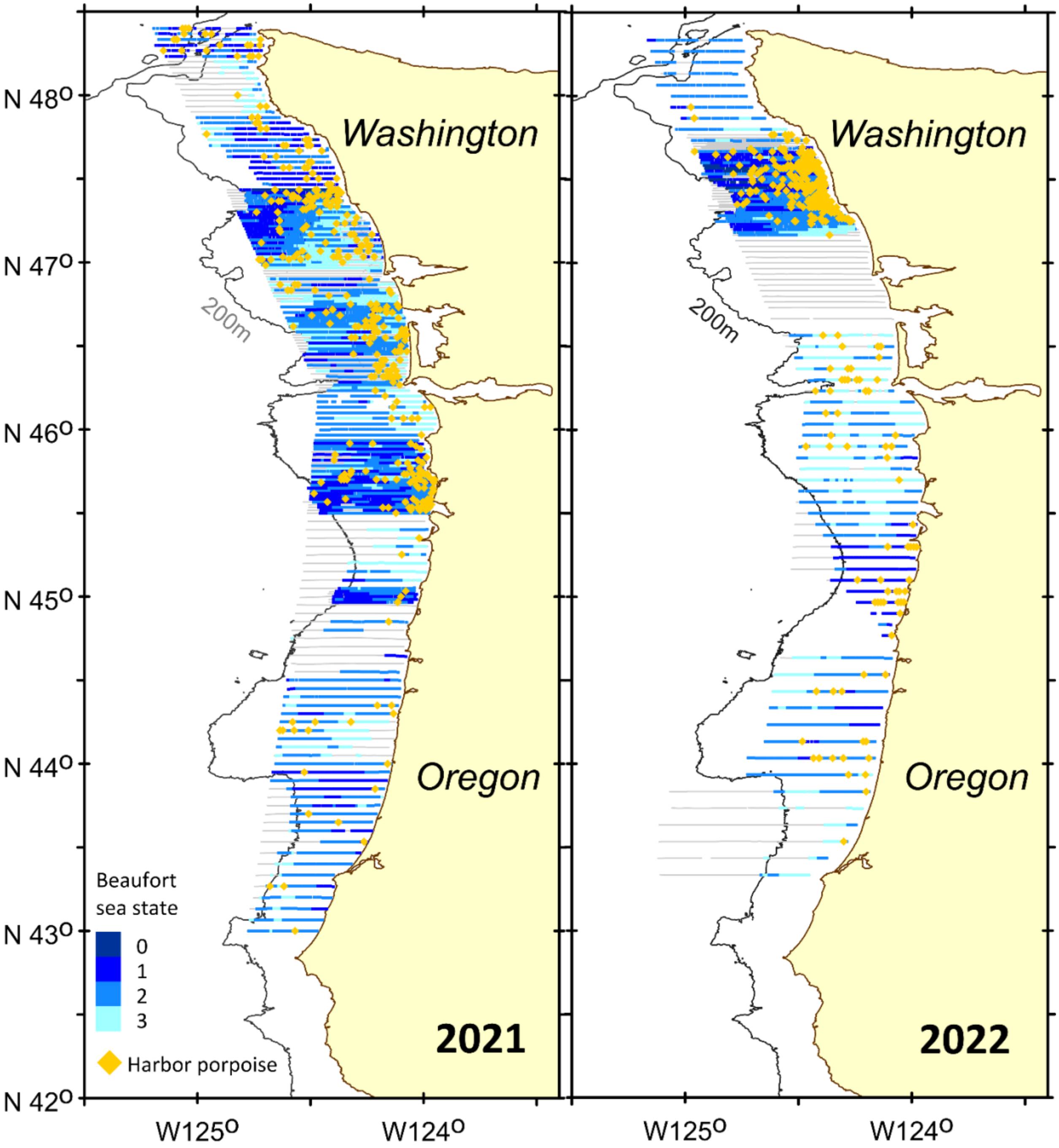

Figure 1. Survey coverage during the August 31 – September 24, 2021 (left) and August 9 – September 5, 2022 (right) leatherback turtle and marine mammal aerial surveys. Light gray lines show all survey transects flown, blue shades indicate the segments included in the modeling data file, color-coded by Beaufort sea state. Gold diamonds indicate harbor porpoise sightings. Note some transects were flown multiple times, especially off Washington where leatherback turtle habitat was identified.

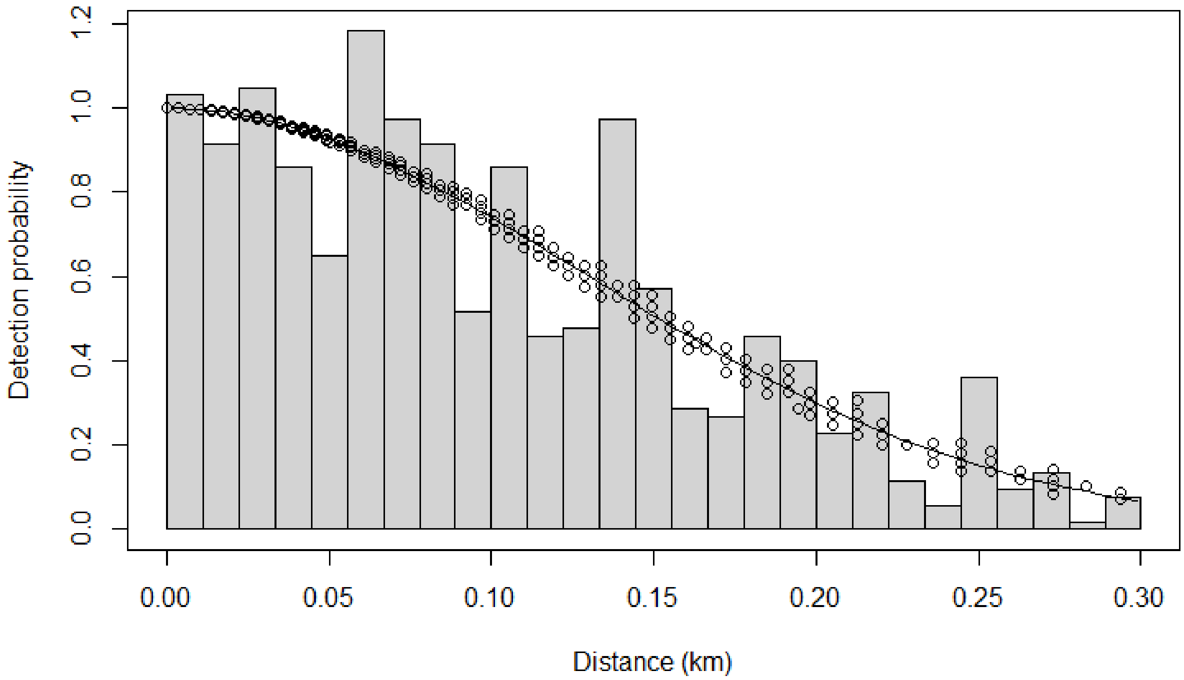

Figure 2. Half normal probability density function fit to perpendicular sighting distances for harbor porpoise sightings made during the 2021-2022 aerial surveys, with range of functional forms by sea state shown using open circles.

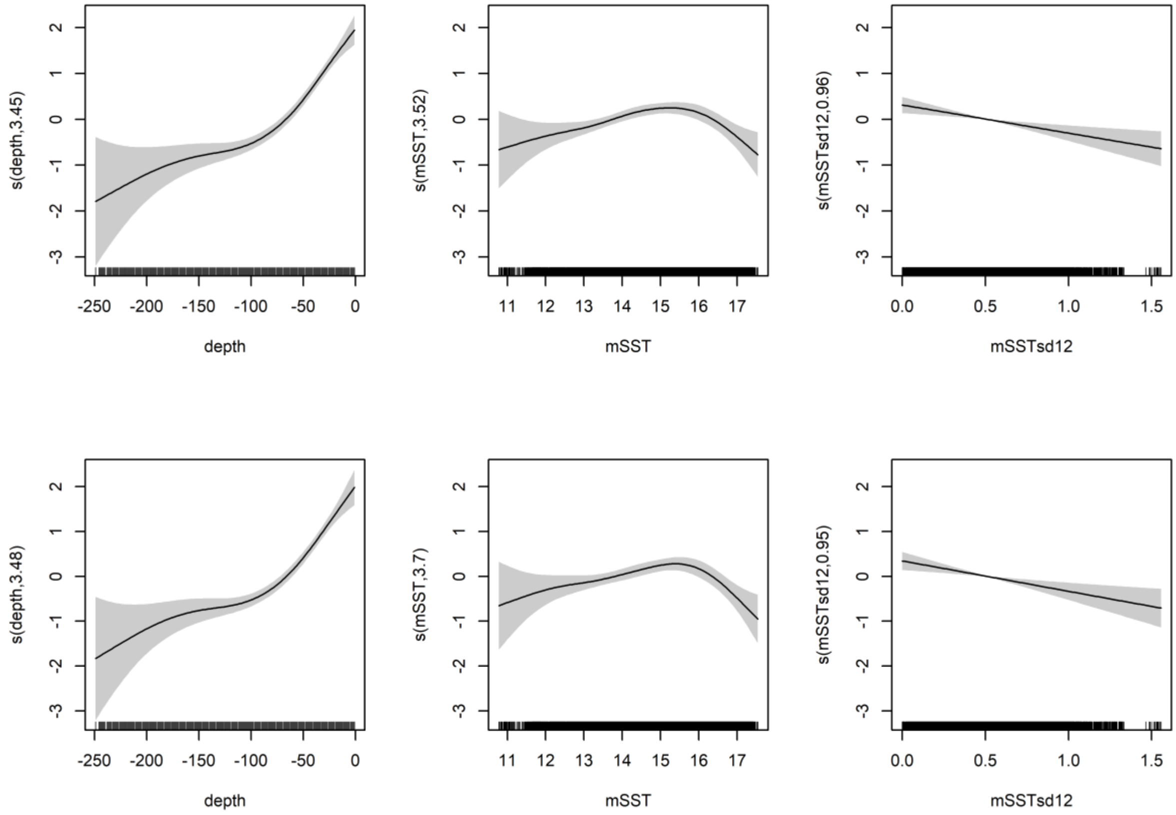

Figure 3. Functional plots (with smoothing degrees of freedom included in y-axis labels) for the covariates included in the best harbor porpoise density models using Tweedie (top row) or negative binomial (bottom row) distributions. Shading represents standard errors for the model fit; tick marks on x-axis indicate data values within the modeling data set. Key: depth = -bathymetric depth (m); mSST = sea surface temperature (°C), mSSTsd12 = standard deviation of sea surface temperature (°C) within a 25 x 25 km box around segment midpoint (+/- 12 pixels).

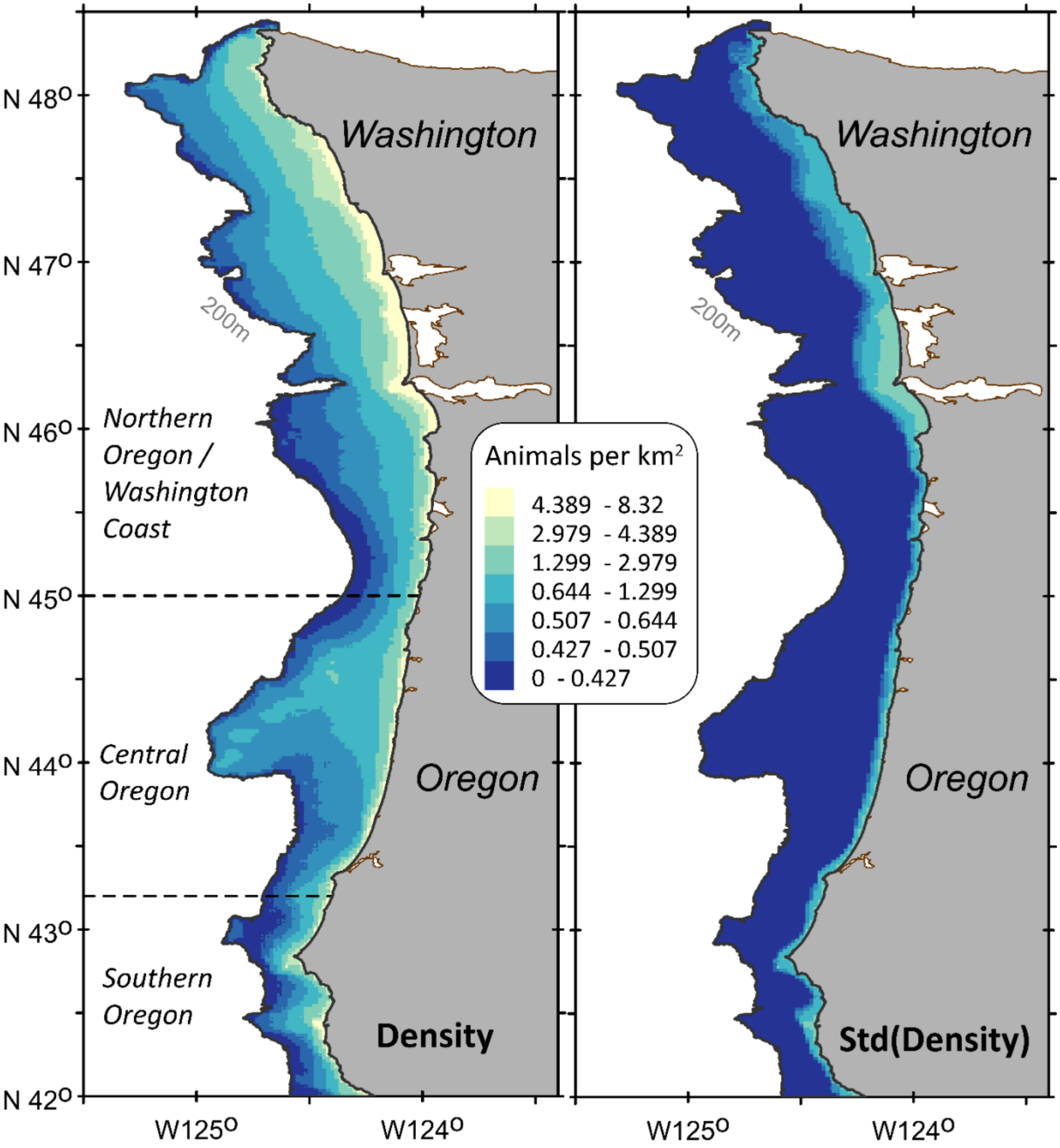

Figure 4. Spatial harbor porpoise densities (left) and standard deviation of estimated density during the study period (right) from the habitat-based density model derived in this study. Offshore study area boundary is the 200-m isobath, representing the continental shelf habitat inhabited by harbor porpoise in this region. Dashed lines indicate stock boundaries defined under the Marine Mammal Protection Act for the Northern Oregon/Washington Coast harbor porpoise stock, the proposed new Central Oregon harbor porpoise stock, and the Oregon portion of the range of the Northern California/Southern Oregon stock.