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A density surface model describing the habitat of the Critically Endangered Rice's whale *Balaenoptera ricei* in the Gulf of Mexico

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ABSTRACT: The newly recognized Rice's whale *Balaenoptera ricei* is among the most endangered large whale species in the world and primarily occupies a region near the continental shelf break in the northeastern Gulf of Mexico (GoMex). We analyzed visual line-transect survey data collected throughout the northern GoMex from 2003–2019 and developed spatially explicit density maps using a density surface modeling approach to examine relationships between Rice's whale density and bathymetric and oceanographic features. We identified water depth, surface chl *a* concentration, bottom temperature, and bottom salinity as key parameters that define the Rice's whale habitat. This is consistent with upwelling of cold, high-salinity water along the continental shelf break and seasonal input of high-productivity surface water originating from coastal sources. The dominant circulation patterns in the GoMex, including the presence of Loop Current eddies, lead to increased productivity and likely play a role in maintaining high densities of forage species needed to support Rice's whales. Extrapolation of the model suggests additional regions in Mexican waters of GoMex that may be suitable for Rice's whales. This study informs the designation of critical habitat as defined by the US Endangered Species Act and will assist in marine spatial planning activities to avoid additional anthropogenic impacts to Rice's whales associated with the development of wind energy and aquaculture.

KEY WORDS: Rice's whale · *Balaenoptera ricei* · Gulf of Mexico · Cetacean habitat model · Critical habitat

1. INTRODUCTION

The 'Bryde's whale complex' includes mysticete whales of genus *Balaenoptera* that occupy tropical and sub-tropical habitats in the world's oceans. While the taxonomy of this group is not fully resolved, the complex includes 2 previously recognized subspecies of the Bryde's whale, *B. edeni edeni* and *B. edeni brydei*, and the recently recognized species, *B. ricei* (Rice's whale, Rosel et al. 2021). The *B. edeni* subspecies occur in coastal and oceanic waters in the Atlantic, Pacific, and Indian oceans (Constantine et al. 2018, Rosel et al. 2021). Available genetic records indicate that *B. edeni brydei* occur in the western Atlantic Ocean off the coast of South America and the Caribbean (Luksenburg et al. 2015). Rice's whale was recently confirmed as genetically and morphologically distinct from other members of the complex (Rosel et al. 2021) and primarily occurs in the Gulf of Mexico (GoMex). It has recently been listed as endangered under the US Endangered Species Act (National Marine Fisheries Service 2019, 2021) and Criti-

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cally Endangered on the IUCN Red List (Rosel et al. 2022). The species is known to occur primarily within a small region near the continental shelf break in the northeastern GoMex off the west coast of Florida, USA, and it is the only resident baleen whale in the GoMex (see Fig. 1). There are also regular observations of Rice's whales in the central and western portions of the northern GoMex based on passive acoustic records (Soldevilla et al. 2022, 2024, Rosel et al. 2021). The current population estimate for Rice's whales is 51 individuals (95% CI: 20–130 individuals, Garrison et al. 2020), and the species is exposed to a number of threats in the highly industrialized northern GoMex, including vessel strikes, interactions with commercial fisheries, and exposure to industrial noise (Rosel et al. 2016, Soldevilla et al. 2017).

The Bryde's-like whales occur in a range of oceanic and coastal habitats and demonstrate diverse distribution and movement patterns. For example, Best (2001) documented distinct Bryde's whale populations along the southern coast of Africa that included a resident non-migratory population over the South Africa continental shelf and a pelagic population that migrated seasonally along the southwestern African coast. Non-migratory populations also occur in the Gulf of Haurki, New Zealand (Kato & Perrin 2009, Izadi et al. 2018), off the coast of Colombia (Pardo & Palacios 2006), southeastern Brazil (Lodi et al. 2015), and in the Gulf of California (Salvadeo et al. 2011). Seasonal range expansion and contraction, similar to that observed along the western coast of Africa, occurs in the Southern California Bight (Kerosky et al. 2012), and larger-scale seasonal movements likely occur in the western North Pacific (Watanabe et al. 2012).

Unlike most other mysticete whales, the Bryde's-like whales do not undertake large-scale seasonal migrations to feeding grounds in polar or temperate waters (Constantine et al. 2018) nor do they have distinct feeding and breeding grounds (Penry et al. 2011). Many other mysticete whales are characterized as 'capital breeders' (after Jonsson 1997, Stephens et al. 2009) that rely on high seasonal productivity to accumulate sufficient energy during a compressed feeding season to support calf production and have distinct feeding and calving seasons and habitats (e.g. humpback whales *Megaptera novaeangliae*, Braithwaite et al. 2015). In contrast, Bryde's-like whales are best characterized as 'income breeders' that rely upon consistent prey resources throughout the year to support the energetic costs of reproduction (Best 2001, Constantine et al. 2018, Izadi et al. 2018). Thus, it is essential that habitats that support these species have consistent, predictable, and high-energy prey resources to maintain survival and calf production.

The physical oceanographic conditions within the habitats of Bryde's-like whales are key to maintaining high productivity and concentrating prey items at densities that support efficient foraging. Bryde's-like whales exhibit a range of feeding strategies and prey preferences, and their diets include zooplankton (Carroll et al. 2019), euphausiids (Best 2001, Murase et al. 2007), and pelagic and mesopelagic fishes (Best 2001). Many populations rely upon small, schooling, pelagic fish species such as Pacific sardines *Sardinops sagax caeruleus* in the Gulf of California (Salvadeo et al. 2011), Japanese anchovy *Engraulis japonica* in the western Pacific (Murase et al. 2007, Watanabe et al. 2012), Brazilian sardine *Sardinella brasiliensis* and Atlantic thread herring *Opisthonema oglinum* off the coast of Brazil (Lodi et al. 2015, Tardin et al. 2017), and anchovies *E. mordax* and sardines *Sardinops sardax* along the Southern California Bight (Kerosky et al. 2012). Many of these prey species are associated with localized upwelling (e.g. Pardo & Palacios 2006, Weir et al. 2012, Tardin et al. 2017). Both the whales and their prey therefore occur where physiographic features, such as the continental shelf break (Corkeron et al. 2011), or oceanographic features, such as the Benguela Current along the African coast (Weir et al. 2012) and the Kuroshio Front in the western Pacific (Watanabe et al. 2012), maintain persistent upwelling and high prey density. In addition, seasonal changes in prey distribution and inter-annual variation related to the ENSO cycle may also drive variability in Bryde's-like whale ranges as the underlying distribution of prey changes (Best 2001, Salvadeo et al. 2011, Kerosky et al. 2012, Dwyer et al. 2016).

In this study, we utilize visual line-transect survey data collected in the northern GoMex during 2003–2019 to characterize the spatial distribution and habitat of Rice's whales. Physiographic features and physical oceanographic parameters obtained from both remote sensing platforms and hydrographic model outputs were used to develop spatially and temporally explicit models of animal density and identify the key environmental features that define the Rice's whale habitat. In addition to characterizing the unique features of their current known habitat, these models are also useful in identifying other regions of the GoMex where suitable Rice's whale habitat occurs. The study findings inform the designation of 'critical habitat', as defined under the US Endangered Species Act, and facilitate the development of protective measures to promote the conservation and recovery of the species.

2. MATERIALS AND METHODS

2.1. Visual survey data

Data on Rice's whale spatial distribution and abundance were collected during line-transect surveys aboard NOAA Ship 'Gordon Gunter' (a 68 m oceanographic research vessel) or NOAA Ship 'Pisces' (a 63 m oceanographic research vessel) conducted between 2003 and 2019 (Fig. 1). These surveys were primarily designed as line-transect surveys and were conducted along 'zig-zag' tracklines oriented perpendicular to bathymetry and covering deep waters of GoMex within the US exclusive economic zone. However, several surveys included directed effort within the Rice's whale core habitat (Table S1 in the Supplement at www.int-res.com/articles/suppl/n054p041_supp.pdf). Surveys followed standard methods for Southeast Fisheries Science Center (SEFSC) vessel-based visual line-transect surveys employing a single visual observer team stationed on a platform 13.9 m above the vessel's waterline and searching using 25 × 150 magnification 'bigeye' binoculars (e.g. Mullin & Fulling 2003, Garrison et al. 2020). The vessel position and environmental conditions that influence detection probability were recorded continuously throughout the survey. For each cetacean group sighting, the distance and bearing were recorded along with the species identification and number of animals. These methods are the same as those used to generate the abundance estimates for Rice's whales (Garrison et al. 2020).

Sightings were identified to the lowest taxonomic level possible. A baleen whale sighting was recorded as Rice's whales (originally identified as Bryde's whales *Balaenoptera edeni*) if the 3 ridges on the rostrum were observed to confirm the species. In more recent surveys, a baleen whale sighting was recorded as sei/Rice's whale *B. borealis/ricei* when a prominant falcate dorsal fin was observed, but it was not possible to confirm 3 rostral ridges, and as sei/Rice's/fin whale *B. borealis/ricei/physalus* when a dorsal fin was observed, or as unidentified baleen whale (*Balaenoptera* sp.) when it was not possible to make detailed observations other than body and head shape distinguishing the sighting from a sperm whale. While there have been occasional sightings and strandings

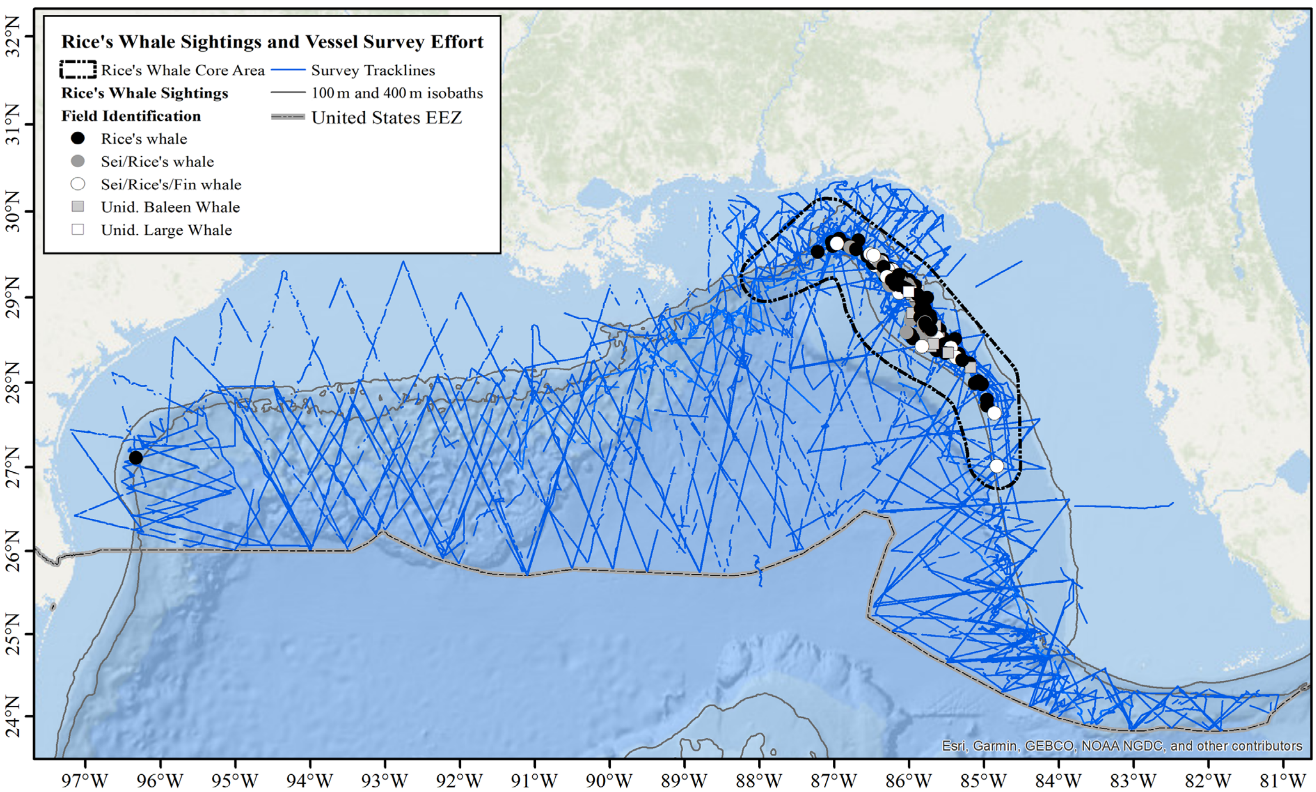

Fig. 1. Survey effort and Rice's whale/baleen whale sightings during Southeast Fisheries Science Center visual line-transect surveys conducted during 2003–2019. The Rice's whale 'core distribution area' (Rosel & Garrison 2022) is shown. EEZ: exclusive economic zone

of other baleen whales (e.g. North Atlantic right whale and fin whale) in the GoMex, there have been no confirmed sightings of other baleen whale species during SEFSC surveys in the Rice's whale core habitat in the last 30 yr. For this analysis, all baleen whale sightings within the core Rice's whale habitat area (Rosel & Garrison 2022; our Fig. 1) were presumed to be Rice's whales and included in the analysis (our Table S1).

2.2. Physiographic and oceanographic variables

Physiographic and oceanographic variables were used as explanatory variables in developing a spatially explicit density model (or density surface model [DSM]) for Rice's whales. Monthly averages of contemporaneous environmental variables were summarized within a hexagonal grid (Lambert azimuthal equal area projection; grid cell area: 40 km^2) initially developed by the US Environmental Protection Agency (White et al. 1992) that was expanded to cover the entire GoMex. Survey effort (km of trackline per cell) and the number of individual whales were also aggregated within each grid cell.

We obtained a digital map of the GoMex coastline from the full-resolution Global Self-consistent Hierarchical High-resolution Geography database (available from https://www.ngdc.noaa.gov/mgg/shorelines/, Wessel & Smith 1996). We also obtained a digital map of global seafloor geomorphic features (GSFM) created by Harris et al. (2014). GSFM is a collection of GIS vector maps of oceanic regions generated by the analysis of bathymetric contours derived from the Shuttle Radar Topography Mapping (SRTM30_plus) database (Becker et al. 2009). We estimated distance from the centroid of each hexagon in the grid to the features on the digital maps to obtain several derived variables: distance to shore, distance to the boundary of the continental shelf edge, and distance to canyons. Bottom depth and slope were extracted from the SRTM30_plus database with a 30 arcsecond (nominal) resolution.

Oceanographic variables (e.g. sea surface temperature [JPL MUR MEaSUREs Project 2015], chl *a* concentration [NASA Goddard Spaceflight Center 2022], bottom temperature, bottom salinity [Naval Research Laboratory 2022], sea surface height, and geostrophic currents) were used as dynamic covariates in the DSM and included both remotely sensed data and hydrographic model output (Table S2). We summarized each data source spatially by overlaying the hexagon grid and calculating the average for each cell at the highest temporal resolution available. Survey effort (km of trackline per survey) was also summarized within each grid cell, and contemporaneous environmental data were matched to effort segments in each grid cell. Effort segments were of variable length (median = 5.4 km, 1st quartile = 3.5 km, 3rd quartile = 6.8 km, min = 0.2 km, max = 34.9 km), and segment length was included as an offset term in the DSM to account for the effect of variable effort.

As an exploratory analysis, we investigated the univariate relationships between Rice's whale occurrence and each environmental variable. A Komolgorov-Smirnov test was used to compare the probability distribution of each variable on trackline segments where whales were observed against that on all of the segments sampled. Kernel density plots of the distribution of each variable were examined to evaluate selection for particular environmental conditions by Rice's whales. While these univariate relationships provide insight into potentially preferred environmental conditions, they do not account for the correlation between variables.

2.3. Detection probability

The detection probability within the surveyed strip was estimated using the distance analysis framework (Buckland et al. 2001) incorporating the effects of covariates on the sighting function (Marques & Buckland 2004, multi-covariate distance sampling [MCDS]). For each sighting, covariates evaluated for the detection model included sea state, glare, wind speed, swell height, and horizontal visibility. The form of the sighting function (hazard vs. half-normal) and the inclusion of covariates were evaluated using stepwise selection of terms and using the lowest Akaike's information criterion (AIC) among candidate models to select the most parsimonious model for the detection function. All analyses were conducted in the package 'mrds' (version 2.21, Laake et al. 2020) in the R statistical programming language. A correction for detection probability on the trackline for Rice's whales is not available, and therefore estimates of density are negatively biased. Due to short dive periods in Rice's whales (averaging 6–10 min; Soldevilla et al. 2017, Kok et al. 2023) and the slow-moving ship with long search distances, it is unlikely that individual whales within the survey strip would be submerged throughout the observation period. The probability of detection on the trackline for large whales at the surface (primarily sperm whales) for past SEFSC vessel surveys was 0.816 (coefficient of variation [CV] = 0.061; Garrison et al. 2020). It is unknown if this estimate is appropriate for Rice's whales; however, it suggests that the magnitude of this potential bias is small.

2.4. DSM

Spatially explicit maps of Rice's whale density were developed following the DSM approach described in Miller et al. (2013). Similar approaches have been applied to density maps for marine mammals based on line-transect survey data in the Atlantic and GoMex (Roberts et al. 2016) and along the US west coast (Becker et al. 2014, 2020). We followed the '2-stage' density modeling approach whereby detection probability is first estimated using the MCDS approach described in the previous paragraph. The detection probability, and therefore effective area searched, for each effort segment is predicted from the MCDS model based upon the average survey conditions experienced on the segment. The effective search area ($A_j p_j$) for each segment (j) is used as an offset term in a generalized additive model (GAM) that predicts counts of animals per segment (n_j) based upon smooth functions (f_k) of k covariates (z_k) with an intercept term (β_0):

$$n_j = A_j\, p_j \exp\left[\beta_0 + \sum_k f_k(z_k)\right] \quad (1) \text{ (Miller et al. 2013)}$$

GAMs were fit using the package 'mgcv' (version 1.18-42, Wood 2017) in the R statistical programming language. The GAM (method = 'reml', k = 10 for each variable) used a Tweedie distribution, which is appropriate for zero-inflated count data (Candy 2004, Miller et al. 2013). Model selection was performed using a training dataset including 80% of the survey effort (and associated sightings). The training dataset was selected to ensure that effort both inside and outside of the core Rice's whale habitat was represented (Fig. 1). Model predictive skill was evaluated using the remaining 20% of the data. Variable selection was performed by first fitting a 'full' model including all explanatory variables. 'Shrinkage smoothers' based on thin-plate regression splines were used to automatically select smooth function complexity and reduce the influence of uninformative variables (Wood et al. 2016). Model fit was assessed through evaluation of a Q-Q plot and a randomized quartile residual plot. Spatial patterns in residuals were examined to determine if the inclusion of a bivariate smooth of the strictly spatial terms would improve the explanatory and predictive power of the model. The final selected model included the significant explanatory terms, and the explanatory power of the reduced model compared to the full model was evaluated based on AIC and restricted maximum likelihood (REML) scores. The predictive skill of the resulting model was evaluated against the test dataset based upon a Kendall's tau rank correlation coefficient between predicted and observed values both for the entire survey area and within the core Rice's whale habitat.

Prediction maps were generated using monthly environmental parameters for the period 2015–2019. The posterior distribution of the GAM parameters was sampled 1000 times to generate a distribution of model coefficients that reflect the statistical uncertainty in the parameter estimation. Predictions of Rice's whale density were generated for each month in the 2015–2019 period based on each of these 1000 parameter sets. In this way, both inter-annual variability in environmental conditions and model uncertainty were included in the resulting samples. The uncertainty from the detection function was not propagated throughout the GAM, and therefore the total variance is underestimated. However, given the low CV of the estimated detection probability, this reflects a minor component of the overall uncertainty in density predictions. The monthly predictions were examined to identify sampled parameters that generated extreme predicted densities of Rice's whales, and these extreme values were excluded from the bootstrap sample prior to variance estimation. These extreme values, associated with density predictions orders of magnitude higher than the observed median, reflect projection of the model predictions into poorly sampled parameter space. The resulting trimmed distribution of realizations was used to summarize predicted average densities within seasons and to calculate metrics of uncertainty.

3. RESULTS

3.1. Sightings and habitat features

Rice's whale (and presumed Rice's whale) sightings occurred predominantly within the northeastern GoMex centered along the 200 m isobath (Fig. 1) and between the 100 and 400 m isobaths. A total of 152 groups of whales were observed, including 371 individual animals. The number of individuals per sighting ranged between 1 and 11 animals, with a mean group size of 2.4 (95% CI: 2.1–2.8). There was a single sighting of 1 Rice's whale outside of the core habitat during the summer of 2017 in a water depth of 263 m off the coast of Texas. Genetic analysis of a skin biopsy sample from the whale confirmed this animal to be a Rice's whale (Rosel et al. 2021).

Kernel density distributions of environmental variables at locations where whales were observed were compared to those from all survey effort to evaluate habitat selectivity (Fig. 2). Rice's whales were highly selective for water depth and were observed at a weighted (by number of whales) mean depth of 239 m (95% CI: 233–242 m), and 95% of all individuals were observed between depths of 188–326 m (Fig. 2A). These depths are on the inner portion of the shelf break, and so are therefore associated with low bottom slope areas. Whale distribution with respect to surface chl *a* concentration was also substantially different from the sampled environment, and the whales were most commonly observed at intermediate chl *a* concentrations that are above 'oceanic' levels (~0.1 mg m^{-3}, Fig. 2C). The weighted mean chl *a* concentration at locations where whales were observed was 0.335 mg m^{-3} (95% CI: 0.303–0.54 mg m^{-3}), and 95% of all observed individuals were observed at chl *a* concentrations between 0.097 and 1.42 mg m^{-3}. Finally, the bottom temperatures and bottom salinities where whales were observed were substantially different from those sampled (Fig. 2F). The weighted mean bottom temperature at whale locations was 14.6°C (95% CI: 14.4–14.7°C), and 95% of whales were observed at bottom temperatures between 12.4 and 16.7°C. The weighted mean bottom salinity for whale locations was 36.00 psu (95% CI: 35.97–36.01 psu), and 95% of whales were observed at bottom salinities between 35.67 and 36.23 psu (Fig. 2G).

3.2. Detection probability function

To estimate the probability of detection of Rice's whale groups during visual surveys, 106 groups that were sighted during 'on-effort' survey periods were analyzed using an MCDS approach. This analysis does not include a correction for the probability of detection on the trackline and therefore overestimates detection probability in the surveyed strip and consequently underestimates density. A right-truncation distance of 6000 m was selected based upon investigation of a histogram of detection distances, which resulted in removal of 5 sightings (4.7%) from the analysis. A half-normal key function including cosine adjustment terms was selected over a hazard rate model based upon AIC. Sea state, glare, wind speed, swell height, and horizontal visibility were considered as possible covariates in the detection function; however, the null model containing no covariates was preferred based upon AIC values. The final detection function fit the data well (Fig. 3, GoF test $\chi^2 = 1.93$, df = 7, p = 0.9634). The estimated probability of detection within the surveyed strip for Rice's whales was 0.427 (CV = 0.112).

3.3. DSM

The selected GAM included significant terms for $\log_e$(depth), $\log_{10}$(chl *a* concentration), sea surface temperature (SST), bottom temperature (Bottom.Temp), bottom salinity (Bottom.Sal), and surface geostrophic velocity (Gvel, Table 1). The reduced model had AIC and REML scores approximately equal to the full model, indicating that the inclusion of non-significant terms did not improve the explanatory power of the model. Both models were an improvement over the null model and had improved predictive power based upon the Kendall tau rank correlation coefficient between predicted and observed values in the testing dataset (Table 1). In all cases, the models predicted higher than expected numbers of Rice's whales in the training data set, but under-predicted the number of Rice's whales in the testing dataset (Table 1).

The selected model explained 54.9% of the deviance and included smooth terms with low degrees of freedom (Table 2). The Q-Q plot and plot of randomized quartile residuals indicate adequate fit and little bias. The GAM residual plots indicate a unimodal (2nd order) relationship between predicted numbers of animals and $\log_e$(water depth), bottom temperature, and $\log_{10}$(chl *a*) (Fig. 4) and linear relationships with bottom salinity and surface velocity. Higher densities are predicted at lower surface velocities, water depths between 150 and 300 m, bottom temperatures between 10 and 19°C, and surface chl *a* concentrations between 0.1 and 0.6 mg m^{-3}. These relationships were consistent with those observed in examination of the univariate relationships.

3.4. Rice's whale habitat and spatial distribution

Based upon monthly average environmental conditions between 2015 and 2019, the DSM predictions align closely to the observed spatial distribution of Rice's whales in their core habitat in the northeastern GoMex (Fig. 5), with the highest densities concentrated along the 200 m isobath, and non-zero predicted densities occurring between the 100 and 400 m isobaths. Higher densities were predicted during winter months (December–February), and this high-

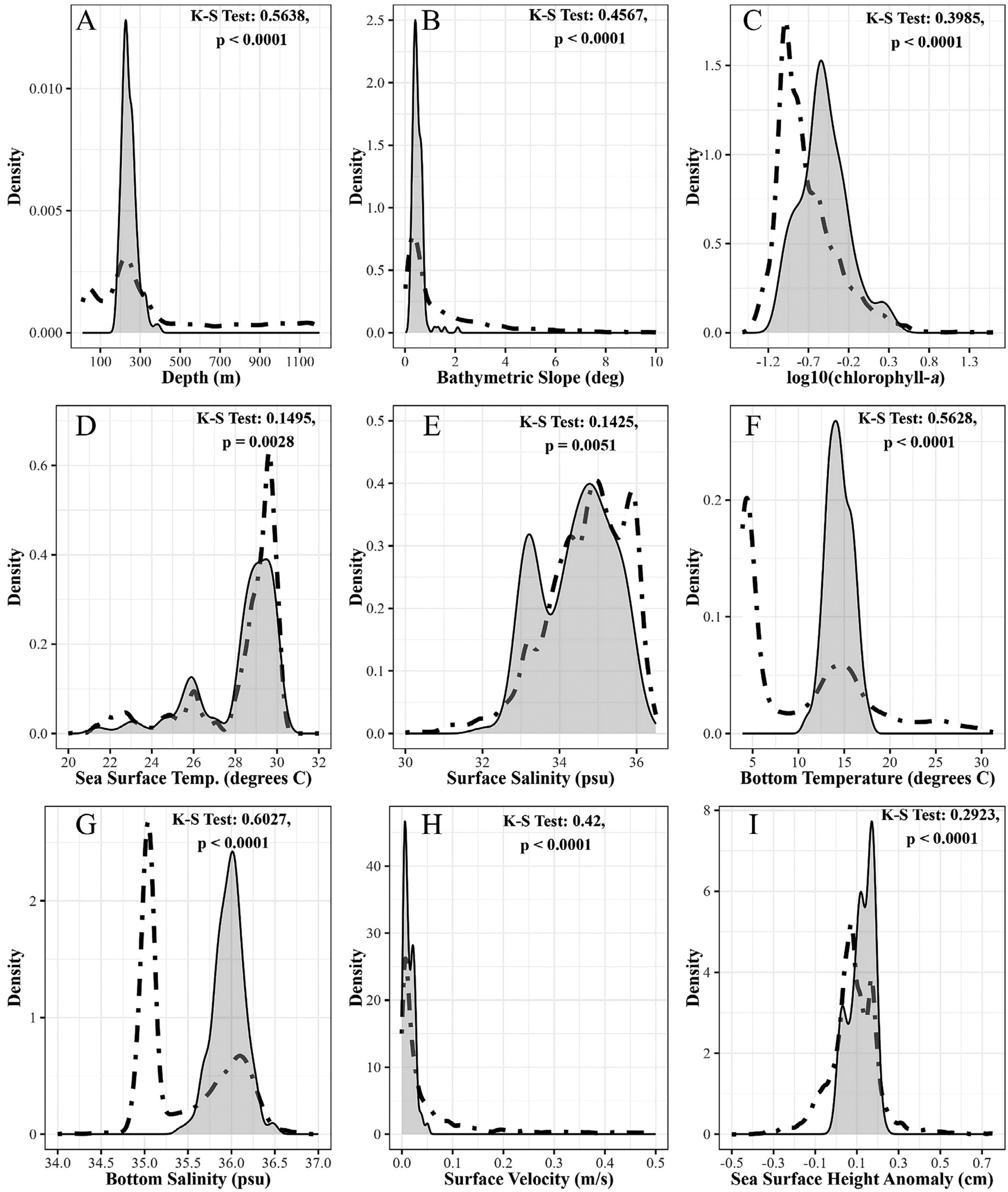

Fig. 2. Kernel density distribution of environmental variables at survey segments with Rice's whales (gray shading) compared to all surveyed segments (dotted line). Two-sample Kolmogorov-Smirnov (K-S) tests were used to compare the distributions for each variable: (A) depth, (B) bathymetric slope, (C) chl *a*, (D) sea surface temperature, (E) surface salinity, (F) bottom temperature, (G) bottom salinity, (H) surface velocity, (I) sea surface height anomaly

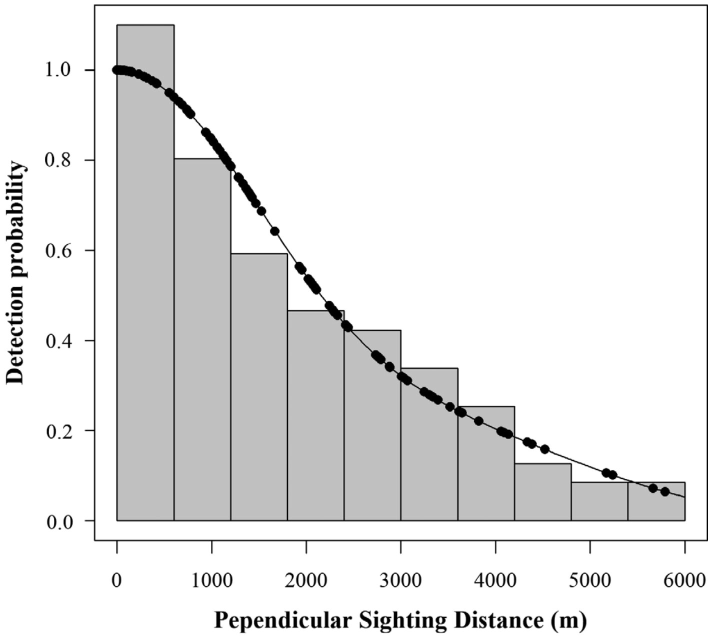

Fig. 3. Detection probability function for on-effort Rice's whale sightings during Southeast Fisheries Science Center visual line-transect surveys from 2003–2019. The selected sighting function included a half-normal key function with cosine adjustments and no covariates

density region extended through the majority of the habitat area (Fig. 5A). While there were relatively few sightings during winter months, there was also relatively little survey effort, so the predicted high densities of animals should be interpreted with caution. During spring (March–May), the highest predicted densities occurred in the northern portion of the habitat, and this distribution shifted southward during summer (June–August). During the fall (September–November), sightings and predicted densities were highest in the more central portion of the habitat (Fig. 5).

These seasonal patterns were related to changes in the distribution of physical and biological features in the core habitat, and in particular the seasonal input of chlorophyll during the spring and summer months. During a series of surveys conducted during 2018 and 2019 that surveyed intensively in the core habitat, Rice's whale sighting locations were correlated with these oceanographic features (Fig. 6). In each survey, Rice's whales occurred in a narrow band of bottom temperatures near 15°C near the 200 m isobath (Fig. 6). During the summer of 2018 and during June and July of 2019, sightings were concentrated more in the northern portion of the habitat where intermediate chl *a* concentrations occurred. In 2019, as the water with these intermediate chl *a* values moved further south, Rice's whale distribution also shifted further south (Fig. 6G,J). This summer distribution is contrasted with that during the fall of 2018 when there was lower overall production, and whales were localized in the central portion of the core area. The offshore presence of Loop Current eddies also influenced the circulation and the movement of higher-productivity waters. When a Loop Current eddy was present offshore of the habitat, there was along-shelf (southeastern flowing surface currents) advection of surface waters that moved higher-productivity shelf water south into the Rice's whale habitat. During the fall survey, when a Loop Current eddy was not

Table 1. Variable selection for generalized additive model of Rice's whale (RW) density. **Bold**: selected model. AIC: Akaike's information criterion; Bottom.Sal: bottom salinity; Bottom.Temp: bottom temperature; CHL: chl *a* concentration; Gvel: geostrophic velocity; REML: restricted maximum likelihood; SLA: sea level anomaly; SST: sea surface temperature; Surface.Sal: surface salinity; Predict/obs test: predicted and observed values in the testing dataset; Predict/obs train: predicted and observed values in the training dataset; Uvel: zonal surface velocity component; Vvel: meridional velocity component (see Table S2)

Model	Smooth terms	AIC	REML score	% Deviance explained	Predict/obs train	Predict/obs test	All cells Kendall tau (p-value)	RW habitat Kendall tau (p-value)
Full	log(Depth) + log(CHL) + SST + Uvel + Vvel + Gvel + Surface.Sal + Bottom.Temp + Bottom.Sal + SLA	730.35	373.2	55.2	193.5/162.3	69.7/97.5	0.1534 (<0.0001)	0.2208 (<0.0001)
Reduced	**log(Depth) + log(CHL) + Gvel + Bottom.Temp + Bottom.Sal**	**731.4**	**373.5**	**54.9**	**194.6/162.3**	**69.1/97.5**	**0.1534 (<0.0001)**	**0.2190 (<0.0001)**
Null	Offset only	908.1	451.9	0	192.4/162.3	53.1/97.5	0.0931 (<0.0001)	0.1500 (<0.0001)

Table 2. Parameters, degrees of freedom (df), and significance tests for the selected generalized additive model for Rice's whale density. Bottom.Sal: bottom salinity; Bottom.Temp: bottom temperature; CHL: chl *a* concentration; Gvel: geostrophic velocity (see Table S2); bs = "ts" indicates smoothing via thin plate regression splines allowing shrinkage (Wood et al. 2016)

Model formula: n.whales ~ offset(log(strip.area)) + s(log(Depth), bs = "ts") + s(logCHL, bs = "ts") + s(Gvel, bs = "ts") + s(Bottom.Temp, bs = "ts") + s(Bottom.Salinity, bs = "ts")
Family: Tweedie (p = 1.347)

Parametric term	Estimate	Std. error	*t*-value	p-value
Intercept	−20.647	6.972	−2.962	0.0031
Smooth terms	Effective df	Reference df	*F*	p-value
s(log(Depth))	2.495	9	1.157	0.0045
s(log(CHL))	2.148	9	0.939	0.0095
s(Gvel)	0.817	9	0.335	0.0542
s(Bottom.Temp)	2.386	9	0.925	0.0067
s(Bottom.Salinity)	0.692	9	0.243	0.0716

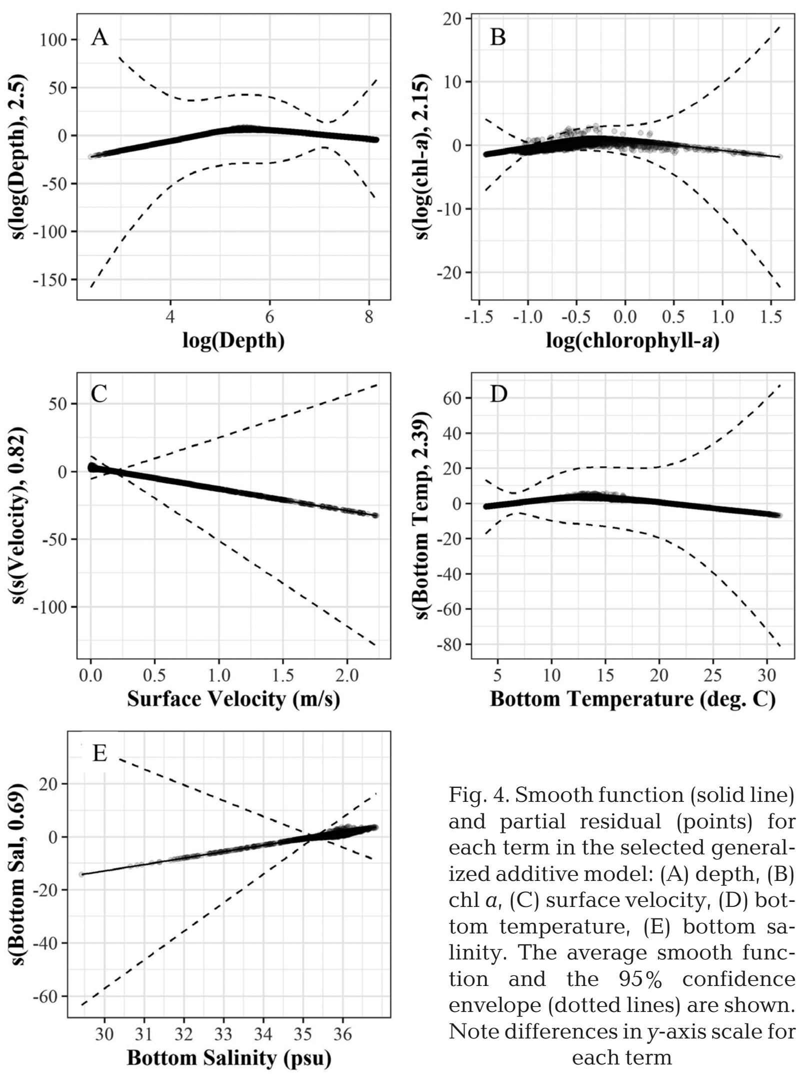

Fig. 4. Smooth function (solid line) and partial residual (points) for each term in the selected generalized additive model: (A) depth, (B) chl *a*, (C) surface velocity, (D) bottom temperature, (E) bottom salinity. The average smooth function and the 95% confidence envelope (dotted lines) are shown. Note differences in *y*-axis scale for each term

present, the net flow of surface water was to the northwest, moving lower-productivity oceanic waters shoreward into the habitat (Fig. 6D–F).

The Gulf-wide distribution of suitable habitat for Rice's whales generally is contained within the 100 to 400 m isobaths (Fig. 7A). In addition to the core habitat area, suitable Rice's whale habitat is predicted to occur in the central and western portions of the northern GoMex, including off the coast of Texas where the confirmed Rice's whale sighting occurred during the summer of 2017. While no data were collected in the southern GoMex during this study, similarities in habitat features allow the extrapolation of the model into these waters. Two notable areas with predicted high densities of Rice's whales in Mexican waters occurred in the southern Bay of Campeche and on the Campeche Bank north of the Yucatan Peninsula (Fig. 7A). Similarity in the topographic and oceanographic features of these regions with those of the core habitat in the northeastern GoMex suggest they may be areas that could support Rice's whale occurrence. The relatively high CV of these predictions should be noted. This uncertainty reflects model uncertainty, the relative rarity of Rice's whales, and environmental variability across months and years (Fig. 7B).

4. DISCUSSION

The DSM identifies environmental parameters that are important predictors of Rice's whale density, including bottom depth, bottom temperature and salinity, and surface chl *a* concentration. These environmental features are associated with the inner portion of the continental shelf break throughout the GoMex, and in particular within the area of the northeastern GoMex where predicted densities and occurrence of Rice's whales is highest. The intrusion of low-temperature, high-

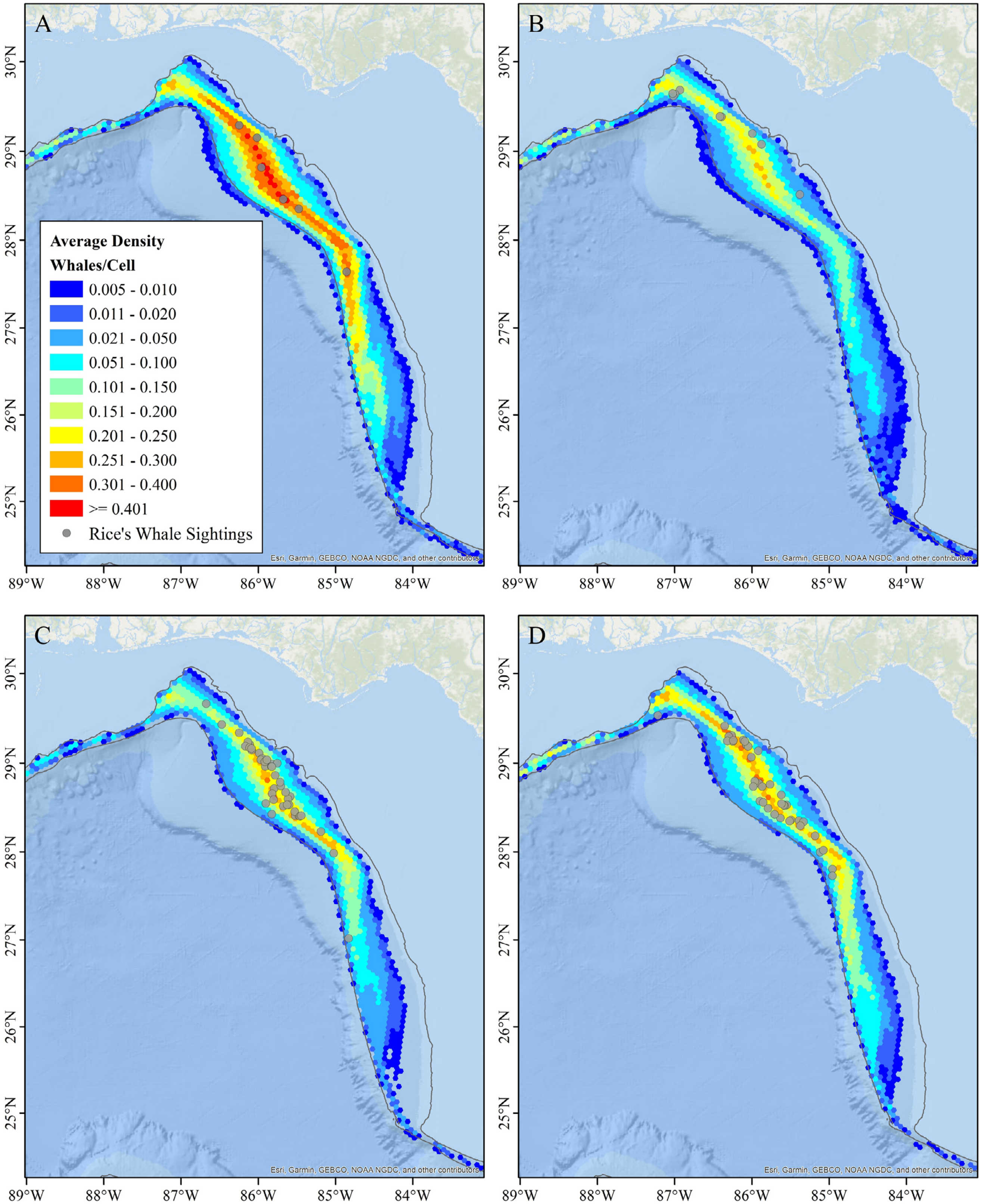

Fig. 5. Seasonal Rice's whale predicted density (whales per 40 km^2, grid cell area) reflecting average environmental conditions in each season from 2015–2019. The locations of Rice's whale sightings (black points) from large vessel surveys are shown along with the 100 and 400 m isobaths. (A) Winter (Dec–Feb), (B) spring (Mar–May), (C) summer (Jun–Aug), (D) fall (Sep–Nov)

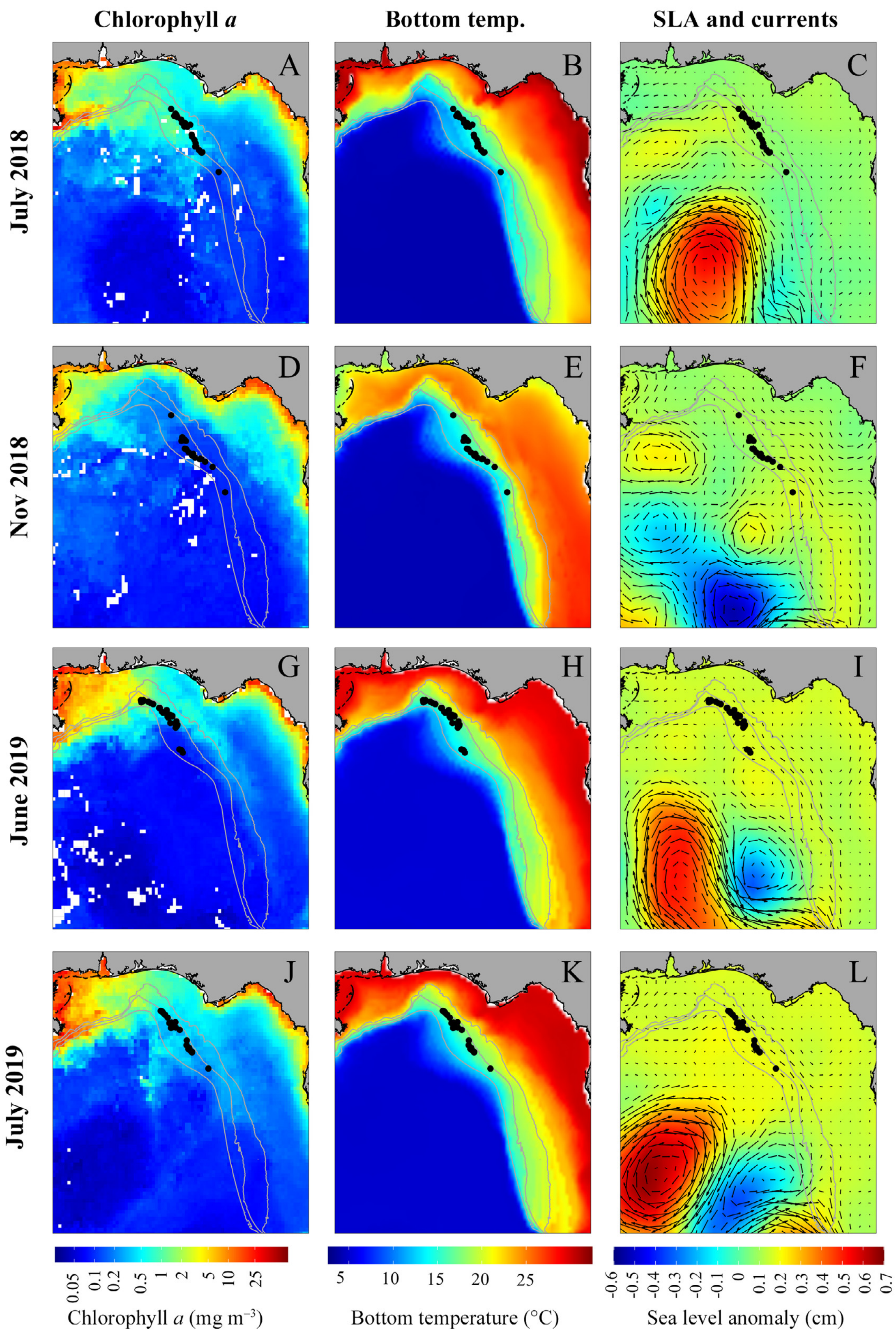

Fig. 6. Sightings of groups of Rice's whales (black points) and average oceanographic conditions during large vessel surveys conducted in (A–C) July 2018, (D–F) November 2018, (G–I) June 2019, and (J–L) July 2019. Vectors represent surface currents. SLA: sea level anomaly

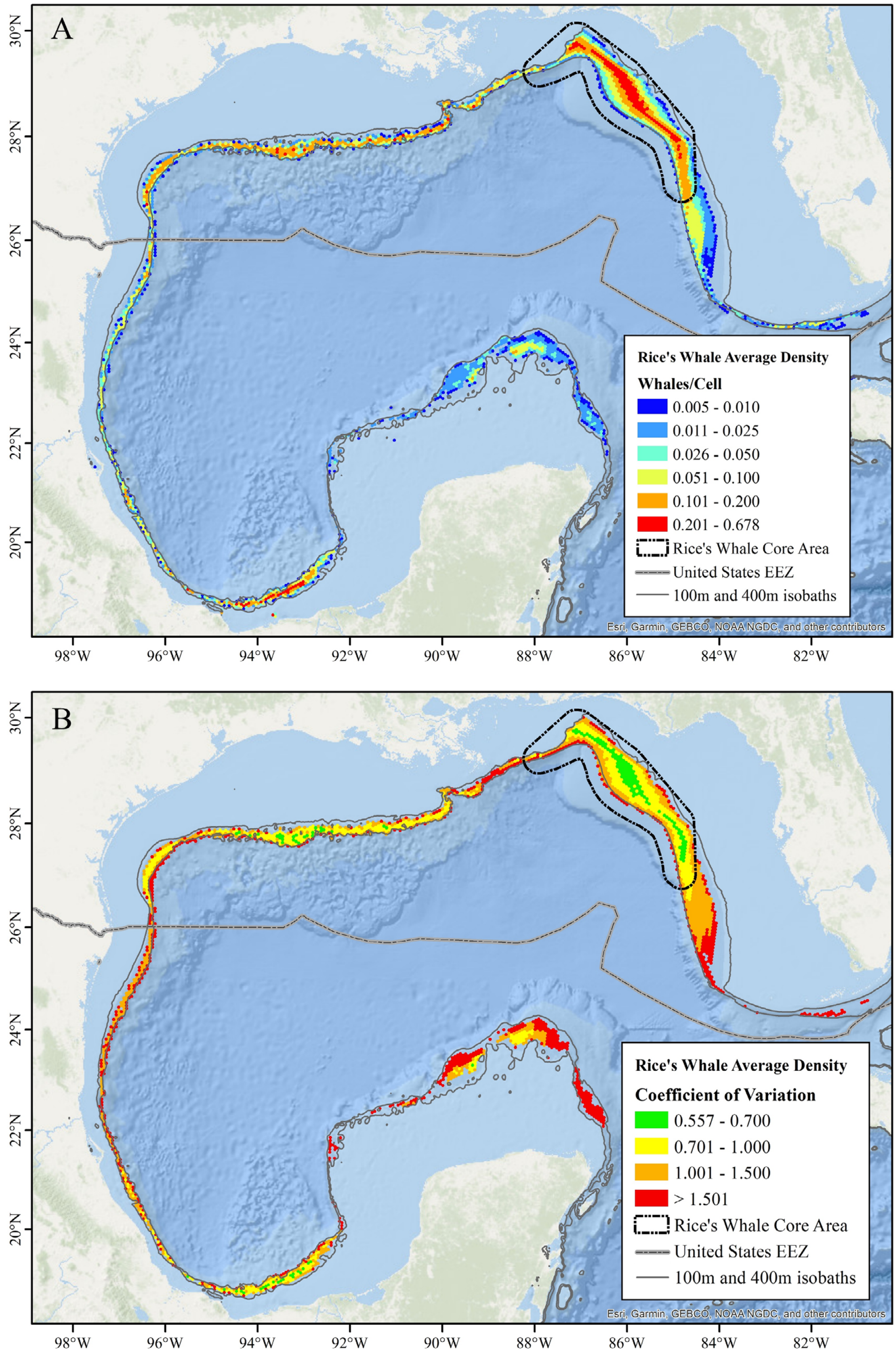

Fig. 7. Predicted average Rice's whale (A) density (whales per 40 km^2, grid cell area) and (B) coefficient of variation during 2015–2019. The long-term average and associated variance reflects both model uncertainty and variation in environmental predictors across months and years. EEZ: exclusive economic zone

salinity waters into bottom depths near 200 m is consistent with upwelling of water occurring off the shelf break shoreward bringing higher nutrient levels. This upwelling along the shelf break is driven by a combination of wind forcing and interactions with the Loop Current (Weisberg & He 2003, Weisberg et al. 2016). The resulting upwelling of nutrient-rich water onto the shelf results in increased primary productivity and is implicated in the dynamics of harmful algal blooms that occur frequently over the adjacent continental shelf (Walsh et al. 2003). In addition, this region experiences seasonal input of low-salinity surface water that is advected southeast from riverine sources in the central GoMex (Weisberg & He 2003). The high surface chl *a* levels in the spring and summer months represent an additional input of coastal productivity into the Rice's whale habitat. As with other Bryde's-like whales, these findings suggest that the complex physical oceanographic environment helps to maintain high local primary and secondary production necessary to sustain the Rice's whale population.

While the pelagic fish community is not well documented in this region, there are several species of fish that are present in the habitat area that are similar to Bryde's whale prey in other regions, including silver-rag drift fish *Ariomma bondi*, round herring *Etremeus teres*, ocean basses *Synagrops* spp., and argentines *Argentina striata* along with lanternfishes (family Myctophidae, Grace et al. 2010). Based upon data collected from archival suction cup tag deployments, Rice's whales conduct foraging dives throughout daylight hours and feed near the bottom on prey that undertake diel vertical migrations (Soldevilla et al. 2017, Kok et al. 2023). Echosounder data collected near foraging Rice's whales frequently indicate the presence of large aggregations of back-scattering organisms, likely swim-bladdered fish, near the bottom (SEFSC unpubl. data). Given their lunge-feeding behavior and the high energetic costs associated with diving and feeding in depths exceeding 200 m (Kok et al. 2023), it is probable that Rice's whales rely upon the presence of high-density patches of forage species. Analysis of carbon and nitrogen stable isotope data for Rice's whales and potential prey species indicate that Rice's whale diet is dominated by *Ariomma bondi*, which also has the highest energy density of available prey (Kiszka et al. 2023). The energetic costs of their feeding strategy necessitate high-energy and high-density prey in other rorqual whales (Goldbogen et al. 2011, Guilpin et al. 2019). It is likely that the complex oceanographic conditions within the Rice's whale habitat support both overall high productivity and formation of dense prey patches. Bottom-up physical processes are important in driving patch dynamics of small pelagic fishes. For example, along the coast of South Africa, upwelling processes were important in driving horizontal patchiness of prey that supported African penguin populations (McInnes et al. 2017). Similarly, a review of humpback whale habitat identified upwelling areas, high chl *a* concentration, and frontal systems that maintained high-density prey patches as important characteristics of feeding habitats (Meynecke et al. 2021).

The DSM predicts suitable Rice's whale habitats outside of their primary distribution area in the northeastern GoMex. Past sightings along the continental shelf break and strandings in the north-central and northwestern GoMex support this predicted habitat. A review of available stranding data from 1954–2012 indicated 22 strandings in the GoMex identified as *Balaenoptera edeni* (now identified as *B. ricei*), including several along the coast of Louisiana near the mouth of the Mississippi River and along the southern coast of Louisiana (for details and a map of historical strandings, please see Rosel et al. 2021). There were also 3 additional sightings from National Marine Fisheries Service (NMFS) surveys conducted during the early 1990s of baleen whales that could not be identified to species (Rosel et al. 2021). Moored passive acoustic monitoring units were placed seaward of the continental shelf break in the western and central GoMex during 2016–2017 to evaluate the presence of Rice's whales. Rice's whale vocalizations were detected persistently on these units with no apparent seasonality (Soldevilla et al. 2022). Additional passive acoustic monitoring studies off the coast of Texas during 2019–2020 also demonstrated frequent occurrence of Rice's whale vocalizations (Soldevilla et al. 2024). These observations, along with the confirmed visual sighting of a Rice's whale along the shelf break off Texas in the summer of 2017, support the use of these habitats as predicted by the DSM; however, additional passive acoustic and visual survey effort focused on the shelf-break region is needed to validate the predicted animal density outside of the northeastern GoMex habitat.

There is little visual survey data in Mexican waters available to assess the validity of the predicted occurrence of Rice's whales in the southern GoMex. One compilation of marine mammal sightings from opportunistic surveys between 1997 and 1999 indicated 1 baleen whale sighting that could not be confirmed to species (Ortega-Ortiz 2002, Rosel et al. 2016). A review of historical whaling fleet logbook information by Reeves et al. (2011) indicated takes of 'finback whales' in Campeche Bay and the Campeche Bank, which are considered likely to be Rice's whales, suggesting at least historical use of this habitat. As with the northeastern GoMex habitat, the Campeche Bank experiences upwelling associated with both local wind forcing and the remote influence of the Loop Current (Zavala-Hidalgo et al. 2003, Kurczyn et al. 2021). Rice's whales were detected on 14.9% of days during 2020–2022 in recently analyzed passive acoustic data from moorings seaward of the shelf break in Mexican waters of the GoMex ('Mexican Ridges', 23.1° N, 97.1° W; Soldevilla et al. 2024). These recent data help to validate the model predictions of suitable Rice's whale habitat in Mexican waters. Additional and ongoing study of the shelf-break region in southern GoMex waters is essential for understanding Rice's whale density, habitat use, and population size.

The tight coupling between oceanographic processes and Rice's whale habitat raises the prospect that climate change could have substantial impacts on their ecology and foraging dynamics. There has been a documented increase in water temperature in waters deeper than 2000 m in the western GoMex from 2003 to 2019 associated with increased temperature of the water spilling into the GoMex from the Caribbean and North Atlantic over the Yucatan Sill (Ochoa et al. 2021). A warming trend in bottom waters over the continental shelf in the north-central GoMex has also been documented, with an average annual increase of 0.051°C yr^{-1} between 1963 and 2015 (Turner et al. 2017). A projected reduction in Loop Current circulation associated with the slowing of the Atlantic Meridional Overturning Circulation (AMOC) may actually reduce the supply of warm water into the surface of the GoMex and offset air temperature-driven temperature increases (Liu et al. 2012). Changes in stratification and flow in the Yucatan Current are also expected to influence the rate of Loop Current eddy shedding (Moreles et al. 2021), which is critical to the circulation and advection of high-productivity water into the West Florida Shelf. Understanding how these complex changes may alter the available habitat for Rice's whales and their prey will be critical to predicting the long-term impacts of climate change on this vulnerable species.

The listing of Rice's whales under the US Endangered Species Act prompts the designation of 'critical habitat' which is defined as the key physical or biological features that are essential to the conservation of the species (US Endangered Species Act Section 3(5)(A)). The designation of critical habitat helps to reduce the risk that human activities will alter these habitat features and thereby threaten the conservation and recovery of the species. Our study describes the physical features that characterize Rice's whale critical habitat and points toward essential biological features, including high productivity and high prey density. Based upon these and other features, the US NMFS proposed to designate critical habitat for Rice's whales encompassing the region between the 100 and 400 m isobaths in US waters of the GoMex (National Marine Fisheries Service 2023a,b).

The GoMex is one of the most highly industrialized bodies of water in the world, particularly in the north-central and northwestern GoMex, where oil and gas energy development is extensive. As offshore wind energy development becomes more economically feasible, the US is considering the development of wind energy sites extending into the deep waters that include Rice's whale habitat in the central and western Gulf (US Department of the Interior — Bureau of Offshore Energy Management 2022). Aquaculture facilities are also being considered in the outer continental shelf waters of the GoMex. The Rice's whale habitat was considered in a suitability analysis of Aquaculture Opportunity Areas (Farmer et al. 2022), and several of the suitable areas are in close proximity to the predicted habitat in the central and western GoMex (Riley et al. 2021). The DSM developed here will continue to help inform marine spatial planning and support efforts to reduce impacts on Rice's whales and their habitats.

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