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Sea turtle density surface models along the United States Atlantic coast

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ABSTRACT: Spatially explicit estimates of marine species distribution and abundance are required to quantify potential impacts from human activities such as military training and testing, fisheries interactions, and offshore energy development. There are 4 protected species of sea turtle (loggerhead, green, Kemp's ridley, and leatherback) commonly found along the east coast of the USA, our study area, and which require impact assessments. Data from 7 different survey organizations were used to create density surface models for the 4 sea turtle species utilizing 1.2 million km of line-transect surveys. A substantial portion (29.7%) of available sightings were not identified to the species level. Not including these sightings would underestimate density, so a conditional random forest model was used to assign unidentified sightings to species. Higher densities of loggerhead, green, and Kemp's ridley sea turtles were predicted south of the Outer Banks in cool months, transitioning northwards in late spring to occupy seasonal neritic habitats. The highest leatherback densities were predicted off the coasts of Georgia and Florida. Leatherbacks were also predicted throughout offshore areas. The predicted distribution patterns generally matched satellite tracking and strandings data, indicating the models reproduced established seasonal movements. Surveys rarely detect sea turtles smaller than 40 cm, so these age classes are not represented. The models are the first for the study area to apply availability bias estimates developed in or near the study area and attempt to classify unidentified sightings to the species level, providing an updated, critical tool for conservation management along the eastern seaboard.

KEY WORDS: Density · Abundance · Sea turtle · Classification · Availability bias

1. INTRODUCTION

Spatially explicit estimates of abundance and distribution are crucial to implement and assess effective conservation measures (Hooker et al. 2011). In the USA, estimates of the number of individuals potentially impacted by federal actions are required under federal laws and can only be derived from spatially

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explicit abundance estimates (United States Department of the Navy 2018). Developing spatially explicit abundance models for broadly ranging marine taxa can be challenging given the extensive range of seasonal and interannual migrations, the variability inherent in those migrations (Ceriani et al. 2014), and difficulties in detecting animals from observation platforms due to factors such as turbidity or long dive times. Sea turtles are no exception, as they only come to the surface intermittently. On the east coast of the USA, sea turtles are wide ranging due to seasonal water temperature changes, resulting in annual migrations between foraging areas (Eckert et al. 2006, Griffin et al. 2013, Barco et al. 2018a).

Density surface models (Miller et al. 2013) derived from line-transect survey data can be designed to estimate the abundance and distribution of broadly ranging marine megafauna (Forney et al. 2012, Roberts et al. 2015, DiMatteo et al. 2022a). Subsequently, density surface models can be employed to quantify the potential impacts of activities such as military training, energy exploration and development, fisheries bycatch, vessel collision, and dredging (United States Department of the Navy 2018, Bureau of Ocean Energy Management 2021). While local or subregional density surface models of marine megafauna are somewhat common (Barco et al. 2018b, Fortuna et al. 2018, Zoidis et al. 2021), basin-scale and regional density surface models are less common given the intensive surveying required over large spatial scales (Hammond et al. 2013, Becker et al. 2020, Benson et al. 2020, DiMatteo et al. 2022a, Roberts et al. 2023), but are needed for assessing human activities at those same scales.

Satellite tracking of target species can provide an important complement to broad-scale density surface models by validating seasonal changes in predicted distribution. Parameters important to density surface models not readily collected from line-transect survey platforms, such as availability bias, can be collected by satellite telemetry studies. However, while satellite tracking can augment capture-mark-recapture population models (Siegwalt et al. 2020, Stokes et al. 2023) and can inform animal distributions either directly (Jeffers & Godley 2016, Winton et al. 2018) or via habitat modeling (Patel et al. 2021, Roberts et al. 2021), even advanced species distribution modeling techniques (Liang et al. 2023) fall short of estimating absolute abundance, necessitating other techniques.

When considering spatially explicit abundance estimates, stratified estimates of animal abundance based on line-transect surveys (Buckland et al. 2001) may suffice for smaller areas. However, density surface models, which can predict distribution by relating density to the underlying environment, as well as abundance estimates (Miller et al. 2013), are needed for larger areas such as assessments that cover the east coast of the USA.

Four protected species of sea turtles (NOAA 1998, 2014a, Conant et al. 2009, National Marine Fisheries Service 2015) can be regularly found in the waters off the east coast of the USA: the loggerhead turtle *Caretta caretta*, green turtle *Chelonia mydas*, Kemp's ridley turtle *Lepidochelys kempii*, and leatherback turtle *Dermochelys coriacea*. Loggerhead turtles are the most common species in the study area. Some of the largest nesting rookeries in the world for loggerhead turtles are found in Florida (Ceriani et al. 2019). Green turtle nesting is an order of magnitude less than loggerhead turtles in the study area but is increasing (Brost et al. 2015, Florida Fish and Wildlife Commission Research Institute 2023). Kemp's ridley turtles are primarily distributed in the Gulf of Mexico, but some individuals migrate to the east coast of the USA to forage (Mansfield et al. 2002), and isolated nests have been documented. Leatherbacks nest throughout the wider Caribbean region, including Florida, and use the study area extensively to migrate to northern foraging areas (James et al. 2007).

In the last 2 decades, extensive line-transect surveys have been conducted by multiple organizations (see Table 1) on the east coast of the USA with the goal of assessing marine megafauna populations at sea, including sea turtles. The decades of line-transect surveys available in the study area provide an opportunity to generate multi-year averages of abundance and distribution for sea turtles, as has been done for several marine mammal taxa (Roberts et al. 2015) using a distance sampling framework (Hedley & Buckland 2004, Miller et al. 2013). Distance sampling (Buckland et al. 2001), the first stage of density surface modeling, accounts for decreasing sightablity of animals from the survey trackline by fitting detection functions.

Detection functions assume the probability of detecting an animal on the survey track is 1 (i.e. at a perpendicular distance of 0, or $g(0)$). This is rarely the case in practice, especially for diving animals like sea turtles, and is affected by 2 factors: (1) availability bias, which is failing to detect available animals directly on the survey trackline because of survey design or because they are hidden or submerged; and (2) perception bias, where observers fail to detect or cannot identify animals present at or near the surface due to survey conditions, such as sea state or human error (Pollock et al. 2006). To counteract this, animals can be tagged with time-depth recorders that can be used to estimate correction factors for availability bias by describing the proportion of time individuals are available at the surface to be detected. Double observer teams on surveying platforms can be used to estimate perception bias (Burt et al. 2014), and modeling approaches are available to attempt to classify unidentified sightings to relevant taxa.

The objectives of this research were to (1) classify unidentified sea turtle survey sightings using a machine-learning framework; (2) apply species-specific corrections for availability and perception bias; (3) use a generalized additive model (GAM) framework to generate a density surface model for each species; and (4) provide modeled predictions of density and associated uncertainty to inform conservation management of sea turtles on the eastern seaboard of the USA.

2. MATERIALS AND METHODS

2.1. Study area and available data

The study area (Fig. 1) covers the US east coast from Maine to the southern tip of Florida, seaward to the approximate border of the US Exclusive Economic Zone. This area is approximately 3300 km long and 370 km wide, with depths ranging from 0 to 5000 m. Line-transect survey data provided by 7 organizations (Table 1) from 2003 to 2019 were integrated into subsequent analyses and underwent extensive quality checks described in Sparks & DiMatteo (2023). The surveys covered approximately 1.2 million km of effort, split between 39 831 km of shipboard surveys and 1 151 880 km of aerial surveys (Fig. 1, Table 1, see Figs. S5–S7, S11–S13, S17–S19, & S23–S25 in the Supplement at www.int-res.com/articles/suppl/n053p227_supp.pdf for monthly effort).

Available sightings of sea turtles in the survey data (n = 25 202) were categorized as loggerhead *Caretta caretta*, green *Chelonia mydas*, Kemp's ridley *Lepidochelys kempii*, hawksbill *Eretmochelys imbricata*, leatherback *Dermochelys coriacea*, or unidentified turtle (Table 2). Loggerhead, green, and Kemp's ridley sea turtles have hard shells made of keratin and are referred to collectively throughout this study as 'hardshell' turtles.

Methods such as reviewing survey photographs, double observers, or circle-back techniques were used in some surveys, but not others, to confirm species assignments depending on survey protocols. Unidentified turtles accounted for 29.7% of sightings and were assumed to be hardshell turtle species, given the distinctive appearance and coloration of leatherback turtles, which have soft shells (Pritchard & Mortimer 1999). We used on-effort sightings with all requisite information in a distance sampling framework (Buckland et al. 2001) for detection function modeling. Both on- and off-effort sightings were utilized in the classification of unidentified sightings. In this study, we defined seasons as winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

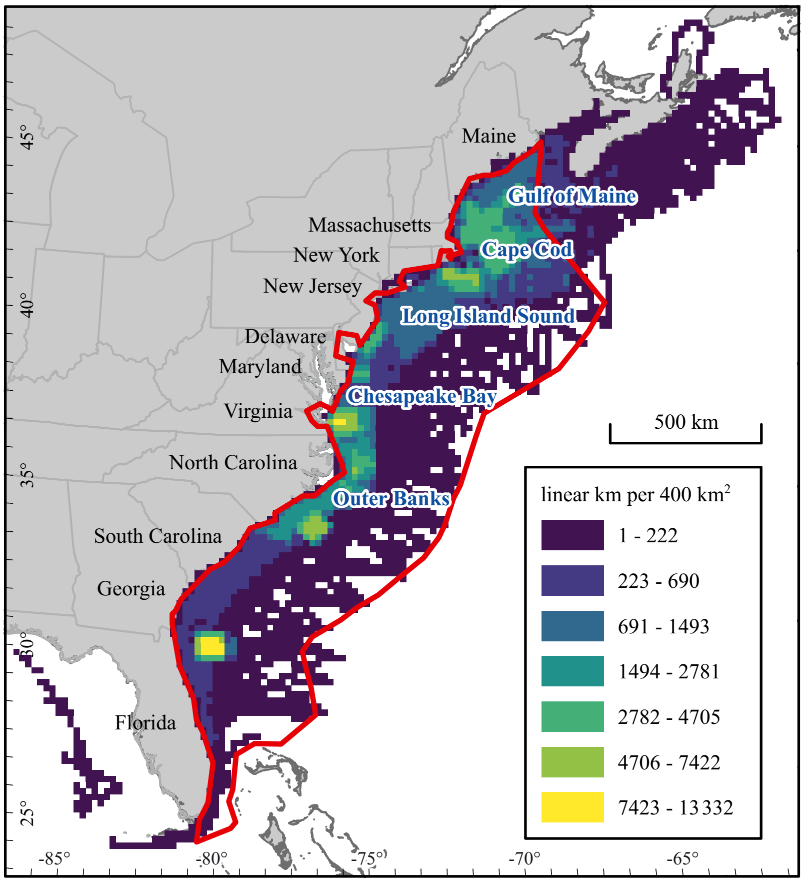

Fig. 1. Study area over which density surface model predictions were made (red polygon) and the amount of available line-transect survey data aggregated into 400 km^2 grid cells

Table 1. Summary of line-transect data incorporated into models by survey provider and program

Survey provider	Program	Platform	Effort (km)	Years	Months	Sightings	Source
Southeast Fisheries Science Center (SEFSC)	Atlantic marine assessment program for protected species (AMAPPS)	Boat	16 892	2011, 2013, 2016	Jun–Sep	198	Palka et al. (2017, 2021)
Northeast Fisheries Science Center (NEFSC)	AMAPPS	Boat	16 522	2011, 2013, 2014, 2016	Mar–Apr, Jun–Aug	30	Palka et al. (2017, 2021)
NEFSC	Pre-AMAPPS surveys	Boat	4011	2004, 2007	Jun–Aug	8	Mullin & Fulling (2003), Garrison et al. (2010), Palka (2006)
SEFSC	AMAPPS	Plane, bubble windows, altitude: 600 ft (183 m)	110 876	2010–2019	Jan–Dec	12 340	Palka et al. (2017, 2021)
SEFSC	Mid-Atlantic *Tursiops* survey (MATS)	Plane, bubble windows, 750 ft (229 m)	13 505	2004–2005	Jan–Mar, Jul–Aug	1158	NA
NEFSC	AMAPPS	Plane, bubble windows, 600 ft (183 m)	90 564	2010–2012, 2014–2019	Jan–Dec	695	Palka et al.(2017, 2021)
NEFSC	Pre-AMAPPS surveys	Plane, bubble windows, 600 ft (183 m)	34 558	2004, 2006–2008	Jun–Aug	511	Mullin & Fulling (2003), Garrison et al. (2010), Palka (2006)
NEFSC	North Atlantic right whale sighting survey (NARWSS)	Plane, bubble windows, 750 or 1000 ft (229 or 305 m)	471 722	2003–2017	Jan–Dec	143	Cole et al. (2007)
HDR Inc.	Navy marine species monitoring program	Plane, flat windows, 1000 ft (305 m)	6374	2018	Apr–Aug, Oct–Dec	218	McAlarney et al. (2018), Cotter et al. (2019)
New England Aquarium	Northeast large pelagic survey collaborative (NLPSC)	Plane, flat windows, 1000 ft (305 m)	43 309	2011–2015	Jan–Dec	161	Leiter et al. (2017), Stone et al. (2017)
Tetra Tech–New York State Department of Environmental Conservation (TT–NYSDEC)	New York Bight wind management (NYBWM)	Plane, bubble windows, 1000 ft (305 m)	57 303	2017–2018	Jan–Dec	290	Zoidis et al. (2021)
University of North Carolina Wilmington (UNCW)	Navy operating area surveys	Plane, flat windows, 1000 ft (305 m)	195 497	2009–2017	Jan–Dec	4739	McLellan et al. (2018), Read et al. (2014)
UNCW	Right whale surveys	Plane, flat windows, 1000 ft (305 m)	114 646	2005–2008	Jan–Jun, Oct–Dec	2935	Foley et al. (2019)
Virginia Aquarium & Marine Science Center (VAMSC)	Miscellaneous surveys in the mid-Atlantic	Plane, flat windows, 1000 ft (305 m)	56 942	2010, 2012–2017	Jan–Dec	1212	Barco et al. (2015), Mallette et al. (2017), Mallette et al. (2014, 2015)

Table 2. Summary of available survey sightings by species

Species	Count	Percentage
Loggerhead	15458	61.3
Green	598	2.4
Leatherback	1375	5.5
Kemp's ridley	297	1.2
Unidentified	7474	29.6
Total	25202	100

2.2. Environmental covariates

Environmental covariates (n = 27) with known or plausible connections to sea turtle habitat or physiological requirements were included as possible explanatory covariates for the species classification and density surface models (Table 3). Contemporaneous covariates rather than climatological covariates were selected on the premise that turtles respond more to ephemeral habitat features than long-term averages of environmental conditions (Howell et al. 2015, Mannocci et al. 2017). Covariates were also classified into one of 9 'families', such as depth or productivity, to assist with model selection (Table 3). We standardized covariates into a 10 × 10 km grid using a bilinear resampling method which was subsequently used for density model predictions.

2.3. Classification of unidentified sightings

We considered several options to apportion unidentified turtle sightings to species-specific models, which are detailed in Text S1 in the Supplement. We selected to classify the unidentified sightings using confirmed sightings in a machine-learning framework. This assumes the available environmental covariates can discriminate between species, for which there is some evidence (DiMatteo et al. 2022b), and that confirmed sightings were accurate.

Conditional random forests have been shown to be effective in classifying ambiguous sightings of mobile

Table 3. Candidate environmental covariates for density surface models. NA: not applicable

Name	Units	Type	Family	Temporal/spatial resolution
Depth	m	Static	Depth	NA / 15 arcsec
Distance to 1000 m isobath	m	Static	Depth	NA / 15 arcsec
Distance to 500 m isobath	m	Static	Depth	NA / 15 arcsec
Distance to shelf break	m	Static	Depth	NA / 30 arcsec
Distance to shore	m	Static	Depth	NA / 5 arcsec
Distance to canyons	m	Static	Features	NA / 30 arcsec
Distance to seamount	m	Static	Features	NA / 30 arcsec
Bottom slope	Degrees	Static	Slope	NA / 15 arcsec
Geostrophic zonal velocity from thermal wind	m s^{-1}	Dynamic	Geostrophic	Weekly / ¼ degree
Geostrophic meridional velocity from thermal wind	m s^{-1}	Dynamic	Geostrophic	Weekly / ¼ degree
Mixed layer depth	m	Dynamic	Productive depth	8 d / ¼ degree
Euphotic zone depth	m	Dynamic	Productive depth	Daily / 1/12 degree
Sea surface height	m	Dynamic	Sea surface height	Weekly / ¼ degree
Chlorophyll *a*	mg m^{-3}	Dynamic	Productivity	Daily / ¼ degree
Vertically integrated chlorophyll *a*	mg m^{-3}	Dynamic	Productivity	Daily / ¼ degree
Epipelagic micronekton	g m^{-2}	Dynamic	Productivity	Daily / 1/12 degree
Net primary	mg m^{-2} d^{-1}	Dynamic	Productivity	Daily / 1/12 degree
Zooplankton biomass	g m^{-2}	Dynamic	Productivity	Daily / 1/12 degree
Chlorophyll *a*	mg m^{-3}	Dynamic	Productivity	8 d / 9 km
Vertically integrated net primary productivity	mg m^{-3} d^{-1}	Dynamic	Productivity	Daily / ¼ degree
Net primary productivity	mg m^{-3} d^{-1}	Dynamic	Productivity	Daily / ¼ degree
Vertical generalized productivity model	mg m^{-3} d^{-1}	Dynamic	Productivity	8 d / 1080 × 2160 global grid cells
Bottom salinity	ppm	Dynamic	Salinity	Weekly / ¼ degree
Surface salinity	ppm	Dynamic	Salinity	Weekly / ¼ degree
Bottom temperature	°C	Dynamic	Temperature	8 d / ¼ degree
Sea surface temperature (night)	°C	Dynamic	Temperature	8 d / 9 km
Sea surface temperature (average)	°C	Dynamic	Temperature	8 d / ¼ degree

marine taxa (Roberts et al. 2018). The 'partykit' package version 1.2 (Hothorn & Zeileis 2015) in R version 4.0.2 (R Core Team 2022) was used to implement the conditional random forest model (Hothorn et al. 2006).

The environmental covariates (see Section 2.2) were candidate variables for classifying unidentified sightings, as were day of year, month, and latitude. The underlying environmental covariates were sampled at each confirmed sighting location. We fit candidate models by varying the method of splitting data into training and testing data sets, number of trees, depth of trees, bag fractions, and number of covariates to include in the model semi-systematically, with the goal of improving model accuracy. We selected the sampling strategy and model with the highest overall accuracy and retrained on the full data set of confirmed sightings. A single iteration of the selected model was implemented to classify unidentified sightings as loggerhead, green, or Kemp's ridley turtles.

2.4. Detection function modeling

We fit separate detection functions for each species by platform and survey program once the recommended 60 sighting threshold for fitting robust detection functions was met (Buckland et al. 2001). Survey programs were defined as a set of surveys provided by a single organization using the same survey protocols. Pooling sightings to fit a detection function (e.g. combining sightings from different survey programs) was instituted when a survey program did not have 60 sightings of a given species. Pooling between survey programs first occurred between similar platforms (such as survey height or flat versus bubble windows). If the 60 sighting threshold was still not met, pooling between species was considered. If a hardshell species was pooled, only sightings of other hardshell turtles were used, given the distinct appearance of leatherback turtles.

All surveys had survey condition covariates, such as Beaufort sea state, that allowed for multi-covariate distance sampling (Marques & Buckland 2004). Combinations of up to 3 survey condition covariates were attempted when fitting detection functions for both half-normal and hazard rate functions, which are the 2 most common types of detection functions (Buckland et al. 2001). Other tested covariates included year, month, group size, and whether the sighting was confirmed to species or was classified from an unidentified sighting.

We selected detection function models based on Akaike's information criterion (AIC). If models had similar AIC values (within 2), we selected the model based on goodness of fit (Cramer-von Mises and Kolmogorov-Smirnoff) and qualitative assessments of detection function plots. Additional details of our process for fitting detection functions and associated plots can be found in Sparks & DiMatteo (2023).

2.5. Corrections for $g(0)$

Availability bias estimates varied in temporal and spatial resolution. For loggerhead and leatherback turtles, availability bias estimates were based on time-depth recorders deployed in or near the study area. For Kemp's ridley and green turtles, availability bias estimates from a neighboring region were utilized because of a lack of adequate time-depth recorder data in the study area. These availability bias estimates are expressed as the proportion of time individuals are visible to observers (Table 4). Details of how the availability bias estimates were derived can be found in Text S1.

Perception bias estimates came from unpublished Atlantic marine assessment program for protected species (AMAPPS) and Gulf of Mexico marine assessment program for protected species (GOMMAPPS) data derived *in situ* from 2-observer team aerial surveys using mark-recapture distance sampling (Burt et al. 2014). We used perception bias estimates of 0.66 for loggerhead turtles, 0.52 for leatherback turtles, 0.32 for green turtles, and 0.56 for Kemp's ridley turtles, representing the proportion of sightings missed by observers.

Table 4. Summary of availability bias estimates and sources by species. NA: not applicable

Species	Spatial resolution	Temporal resolution	Availability bias estimate	Source
Loggerhead	20 km	Monthly	0.07–0.84	Hatch et al. (2022)
Green	NA	NA	0.19	Roberts et al. (2022)
Leatherback	NA	Monthly	0.07–0.52	Rider et al. (2022)
Kemp's ridley	NA	NA	0.17	Roberts et al. (2022)

2.6. Spatial models

We employed a GAM framework for all density surface models, fit with the R package 'mgcv' version 1.8 (Wood 2011). The response variable was density on survey segments, predicted with a Horvitz-Thompson estimator using the appropriate detection function, and adjusted for $g(0)$. Each GAM was fit using a Tweedie distribution, a maximum of 10 knots, and thin plate regression splines with shrinkage. For each species, models were fit to all segments from survey programs with sightings. The number of covariates to be included in each model and the number of models to fit and assess were limited in several ways *a priori*, which are detailed in Text S1. GAMs were assessed to ensure the included covariates were significant to a minimum p-value of 0.05, and GAM selection was made via restricted maximum likelihood.

We made predictions on the finest temporal scale of the selected covariates in each model (daily, weekly, etc.) and averaged them into monthly climatologies of density over the time span of the models. The green turtle model was limited to the last 10 yr of data to account for large increases in the nesting population in the study area during the last decade.

Estimates of the coefficient of variation (CV) for each model were generated from the GAM parameter uncertainty, both as surfaces covering the study area and as point estimates for the entire model made from the average of the grid cells from all predictions with non-zero density. Confidence intervals (CIs) were calculated for monthly and annual abundance estimates.

3. RESULTS

3.1. Classification of unidentified sightings

After removing leatherback turtle sightings, 16 353 confirmed sightings of hardshell species remained. The sightings were 94.5% loggerhead, 3.7% green, and 1.8% Kemp's ridley sea turtles.

The selected classification model had 1000 trees, gave equal weights to each species, and used the top 10 covariates from test models. The selected covariates, in order of decreasing importance, were epipelagic micronekton, sea surface temperature (8 d average), distance to shore, day of year, sea surface height, distance to seamount, surface salinity, vertically integrated net primary productivity, vertically integrated chlorophyll *a*, and latitude. The model's overall accuracy was 95.5%. Accuracy by species was 99.2% for loggerhead turtles, 40.5% for green turtles, and 18.2% for Kemp's ridley turtles. Applying the classification model to the unidentified sightings resulted in 7164 loggerhead turtles, 273 green turtles, and 37 Kemp's ridley turtle classified observations (Fig. 2). Readers interested in more visual detail of the classification model results are referred to Sparks

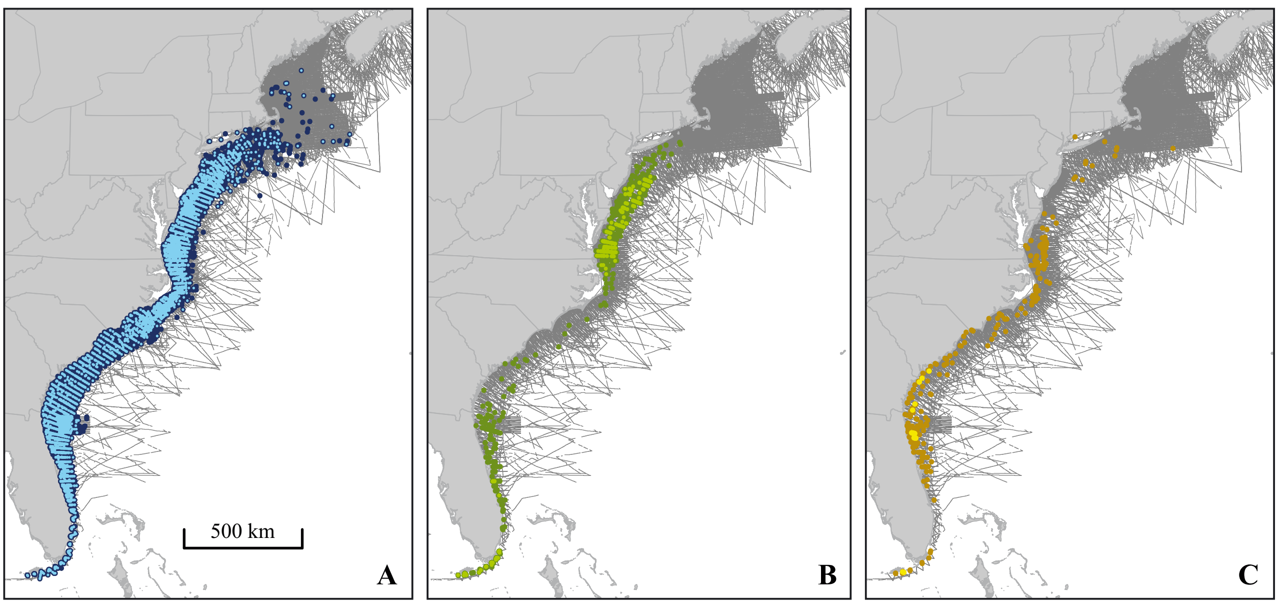

Fig. 2. Sightings identified to species overlaid with sightings classified by the conditional random forest model. Thin grey lines: survey effort tracks. (A) Confirmed (dark blue) and classified (light blue) loggerhead turtle sightings; (B) confirmed (dark green) and classified (light green) green turtle sightings; (C) confirmed (brown) and classified (yellow) Kemp's ridley turtle sightings

& DiMatteo (2023), which has full-page figures and seasonal breakdowns of these results.

3.2. Detection functions and density surface models

We fit a total of 31 detection functions: 14 for loggerheads, 6 for Kemp's ridleys, 2 for greens, 8 for leatherbacks, and one where Kemp's ridley and green turtle sightings were pooled for the same survey program. All detection functions performed adequately based on a review of the detection function plots, quantile–quantile plots, and model statistics. A summary of selected detection functions, included covariates, and truncation distances is provided in Table S1.

The environmental relationships reported for density surface models are specific to the species and region in question and may not be applicable elsewhere. Stated covariate preferences (e.g. high temperatures, deep waters, etc.) are subjective and relative to the sampled environment in the study area. Readers can refer to Figs. S1–S4 to view fitted covariate relationships, including rug plots of sampled values.

The selected loggerhead turtle density surface model included the depth, sea surface temperature (8 d average), sea surface height, bottom salinity, vertically integrated net primary productivity, euphotic zone depth, and latitude covariates. Deviance explained was 42.2%. Based on the selected model, loggerheads exhibited preferences for moderate to high bottom salinities, shallower depths, moderate euphotic zone depth, warm surface temperatures, and lower latitudes. A strong negative relationship was seen with depths associated with areas off the continental shelf and areas of low productivity. Most of the covariate space across the study area was well sampled by the observations except for deep waters off the continental shelf and high values of productivity. See the rug plots in Fig. S1.

The green turtle density surface model included the depth, sea surface temperature (8 d average), surface salinity, zooplankton biomass, euphotic zone depth, and latitude covariates. Deviance explained was 48.6%. Based on the selected model, green turtles exhibited preferences for shallow waters, deep productive depths, lower latitudes, moderate salinity, and warmer surface temperatures. A strong negative relationship was seen with depths associated with areas off the continental shelf, shallow euphotic zone depth, and areas of low productivity. Most of the covariates were well sampled, except for deep waters off the continental shelf (Fig. S2).

The Kemp's ridley turtle density surface model included the distance to shore, sea surface temperature (8 d average), surface salinity, zooplankton biomass, and latitude covariates. Deviance explained was 42.7%. Based on the selected model, Kemp's ridley turtles exhibited preferences for productive waters on the continental shelf and closer to shore, lower latitudes, moderate salinities, and warmer surface temperatures. A strong negative relationship was seen with areas of low productivity and cooler temperatures. Most of the covariates were well sampled, except for extreme low values of distance to shore (Fig. S3).

The leatherback turtle density surface model included distance to the 500 m isobath, sea surface height, surface salinity, euphotic zone depth, zooplankton biomass, sea surface temperature (nightly), and latitude covariates. Deviance explained was 32%, the lowest of all models. Distance to the 500 m isobath was selected rather than depth, reflecting the species' more offshore distribution compared to hardshell turtles.

Based on the selected model, leatherback turtles exhibited preferences for less productive waters on the continental shelf and slope, higher latitudes relative to hardshell species, moderate salinities, and warmer temperatures. Most of the covariates were well sampled, except for low values of distance to the 500 m isobath and high values of productivity (Fig. S4).

3.3. Predicted density and uncertainty

Terms such as low, medium, or high density or uncertainty are relative to the predicted values across the model under discussion and were assessed qualitatively based on our interpretation of maps of the monthly predictions. Referenced geographic locations are shown in Fig. 1. Uncertainty was generally higher offshore, where there was little survey effort, and where there were fewer sightings and was lower where there were many sightings. For hardshell species, this resulted in low uncertainty on the continental shelf south of Cape Cod and high uncertainty offshore and in the Gulf of Maine. For leatherback turtles, uncertainty was lowest in the Gulf Stream.

3.3.1. Loggerhead turtle predictions

Mean annual abundance for the loggerhead turtle density surface model was 193 423 (90% CI = 159 158–227 668). Mean monthly predicted abundance ranged from a high of 245 609 in February to a low of 135 066

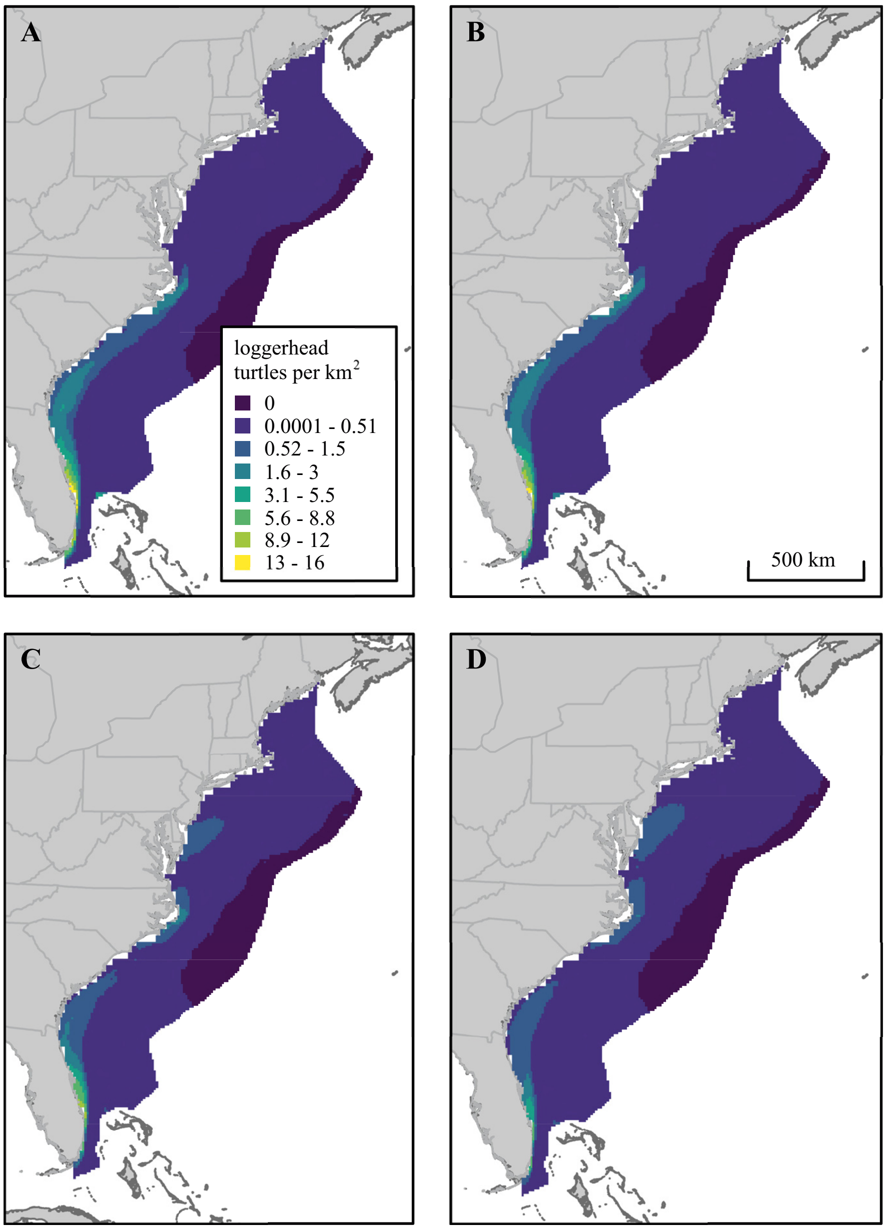

Fig. 3. Long-term predictions of loggerhead turtle density and distribution for select months: (A) January (abundance: 232 237; CI = 190 506–275 039), (B) April (abundance: 216 809; CI = 177 731–252 530), (C) July (abundance: 181 618; CI = 148 775–210 889), and (D) October (abundance: 141 748; CI = 115 173–167 429). The legend scale is applicable to this species only

in September and was generally higher in cool months (December–May) and lower in warm months (June–November).

Density was high off Florida year-round, with thousands of sightings in the area (Figs. S5–S7). An area south of the Outer Banks (Fig. 3A,B) was identified as a relatively higher-density region in cool months. Loggerhead turtles are predicted to move north of the Outer Banks in higher densities starting in May, with the furthest northward prediction of moderate density occurring in fall. Low but consistent density is predicted in all months north of Long Island and into the Gulf of Maine, which is supported by sightings data (Figs. S5–S7) and the literature (Brazner & McMillan 2008). Uncertainty was highest in waters off the shelf, which were poorly sampled. Mean CV was 1.5 in areas of non-zero density (Figs. S8–S10). High values of CV are almost exclusively in areas where there are few sightings and close to zero predicted density. CI is recommended rather than CV for a better understanding of the range of predictions for this species.

3.3.2. Green turtle predictions

Mean annual abundance for the green turtle density surface model was 63 674 (90% CI = 23 381–117 610). Mean monthly predicted abundance ranged from a high of 96 935 in July to a low of 49 720 in January and was generally higher in summer months (June–August) and lower in other months. These patterns were driven by a strong predicted preference for warm, shallow, productive waters and an avoidance of cooler, deeper waters.

Predicted density was high off Georgia and Florida year-round, particularly the Florida Keys. Green turtles were predicted to be in the mid-Atlantic from May until October, generally from Chesapeake Bay north to Long Island (Fig. 4). There were no sightings of green turtles north of Cape Cod, consistent with strandings data (Mass Audubon 2022, Figs. S11–S13). Green turtles were predicted to move south again starting in October, when northern waters begin to cool. Mean CV was 0.54 in areas of non-zero density (Figs. S14–S16).

The model predicted the presence of green turtles farther north than was supported by the available sightings or a review of satellite tracking data (Halpin et al. 2009). The following latitudinal cutoffs are recommended for use in management applications based on sightings and tracking data: winter, Cape Hatteras (Outer Banks); spring, the Delaware–Maryland border; summer and fall, Narragansett Bay. The cutoffs are applied in Fig. 4.

3.3.3. Kemp's ridley turtle predictions

Mean annual abundance for the Kemp's ridley turtle density surface model was 10 762 (90% CI = 2620–19 443). Mean monthly predicted abundance ranged from a high of 13 220 in October to a low of 8341 in August and was generally higher in spring and fall but only varied by a few thousand from month to month.

Predicted density was high off southern Georgia and northern Florida year-round, apparently driven by a cluster of sightings in the region (Fig. 5). Kemp's ridley turtles were predicted to be in the mid-Atlantic from May until November, generally from Chesapeake Bay north to Delaware Bay, and as far north as Long Island Sound in summer months (Figs. S17–S19). Kemp's ridley turtles were predicted to move south again starting in November, slightly later than green turtles. Mean CV was very high (3.8). These extremely high values of CV are almost exclusively in areas where there are no sightings and close to zero predicted density (Figs. S20–S22). CIs are recommended for better understanding the range of predictions, as there is little variation in predicted abundance in the areas of high CV.

Similar to green turtles, the following latitudinal cutoffs are recommended based on sightings and strandings data: winter, Pamlico Sound (Outer Banks); spring, the Delaware–Maryland border; summer and fall, slightly north of Cape Cod, based on the furthest north stranding data (Mass Audubon 2022). These cutoffs are used in Fig. 5.

3.3.4. Leatherback turtle predictions

Mean abundance for the leatherback turtle density surface model was 21 984 (90% CI = 10 049–33 600). Monthly predicted abundance ranged from a high of 54 329 in September to a low of 4655 in February and was generally higher in warm months (June–November) and lower in cool months (December–May; Figs. S23–S25). Leatherback turtles have the largest change between high and low abundance predictions of any species in this study, with monthly estimates spanning a full order of magnitude.

Leatherback turtles were predicted to be off the coast of Georgia and Florida year-round. (Fig. 6). Leatherback turtles were predicted throughout the entire study area, including offshore areas, except for a few isolated areas in June and July. Leatherbacks were predicted to be in the mid-Atlantic from June until November, generally from the Outer Banks north to Cape Cod, as well as offshore in the Gulf Stream in high numbers driven by the relationship with sea surface height. Mean CV was 0.70 (Figs. S26–S28).

4. DISCUSSION

This paper presents the first density surface models produced in over a decade for 4 species of sea turtles that span the entire east coast of the USA (United States Department of the Navy 2007) and the first to incorporate unidentified hardshell turtle sightings into species-specific models. For green turtles, this is the first time such a model has been published for the study area. Distribution of loggerhead turtles, the most abundant species in the study area, has been

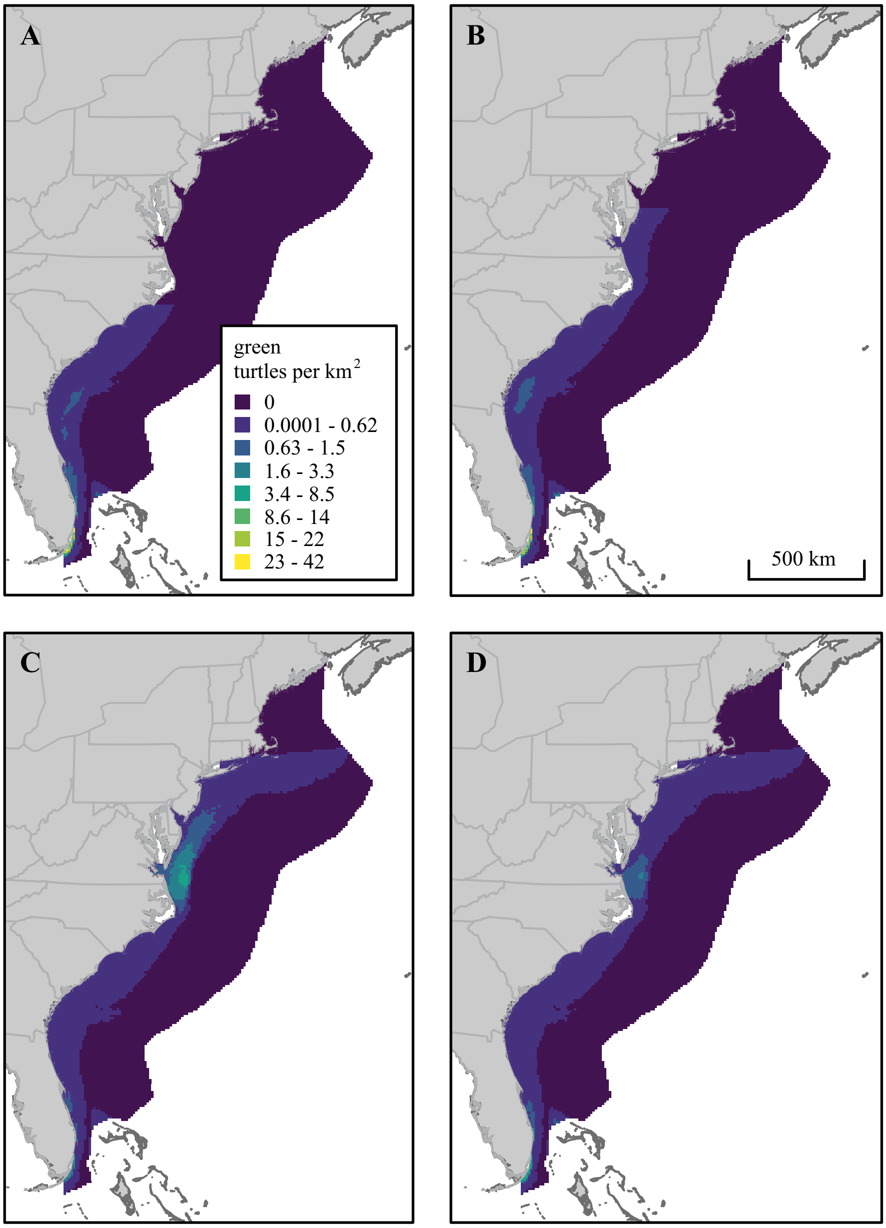

Fig. 4. Long-term predictions of green turtle density and distribution for select months: (A) January (abundance: 49 720; CI = 17 487–101 683), (B) April (abundance: 58 828; CI = 19 178–119 505), (C) July (abundance: 96 935; CI = 41 582–157 730), and (D) October (abundance: 55 656; CI = 21 359–97 393). The legend scale is applicable to this species only. Density was forced to zero north of the following latitudinal cutoffs: Cape Hatteras (Outer Banks) (A), the Delaware–Maryland border (B), and Narragansett Bay (C,D)

modeled more recently, though these efforts modeled relative abundance based on satellite-tracked animals (Winton et al. 2018) or were density surface models at smaller spatial scales (Barco et al. 2018b). As such, this study is a needed update to our understanding of the distribution and abundance of sea turtles on the east coast of the USA, where information was previously limited, outdated, or based on other data types. This paper supersedes the technical report (Sparks & DiMatteo 2023), with updated discussion and input from collaborators and coauthors.

The fact that most identified sightings in the survey record were loggerhead turtles may be driving the high accuracy of the machine-learning model for this species, or perhaps green and Kemp's ridley turtles' niches are too similar to discriminate with the available environmental covariates. DiMatteo et al. (2022b) found that loggerhead and Kemp's ridley turtles in

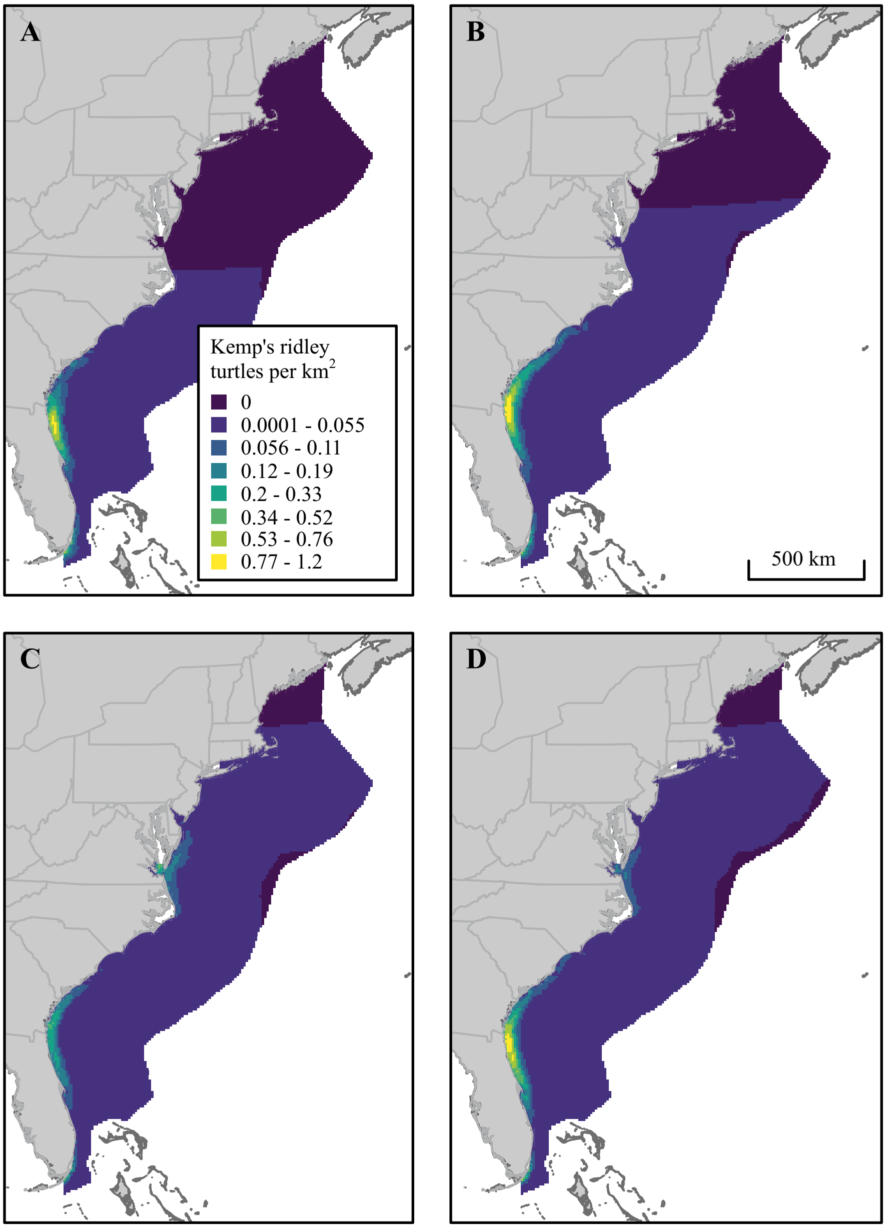

Fig. 5. Long-term predictions of Kemp's ridley turtle density and distribution for select months: (A) January (abundance: 9526; CI = 2501–17 023), (B) April (abundance: 12 707; CI = 3281–22 572), (C) July (abundance: 8901; CI = 1624–16684), and (D) October (abundance: 13220; CI = 3449–23 585). The legend scale is applicable to this species only. Density was forced to zero north of the following latitudinal cutoffs: Pamlico Sound (Outer Banks) (A), the Delaware–Maryland border (B), and slightly north of Cape Cod (C,D)

the Chesapeake Bay may occupy different ecological niches, with Kemp's ridley turtles apparently preferring shallower, more brackish habitats compared to loggerhead turtles. However, these differences may not be significant at the scale of the entire eastern USA, or environmental relationships for the 2 species in Chesapeake Bay may differ from the continental shelf and other nearshore areas. The low classification accuracy of the machine-learning model for Kemp's ridley and green turtles may contribute to underestimation for those species (and overestimation for loggerheads), as it is probable that some sightings that are actually these species are being erroneously classified as loggerheads. Several surveyors asserted that these species may in fact have a higher likelihood of being recorded as unidentified sightings compared to loggerheads, given their smaller size and coloration. Loggerhead turtles are generally orange- or reddish-

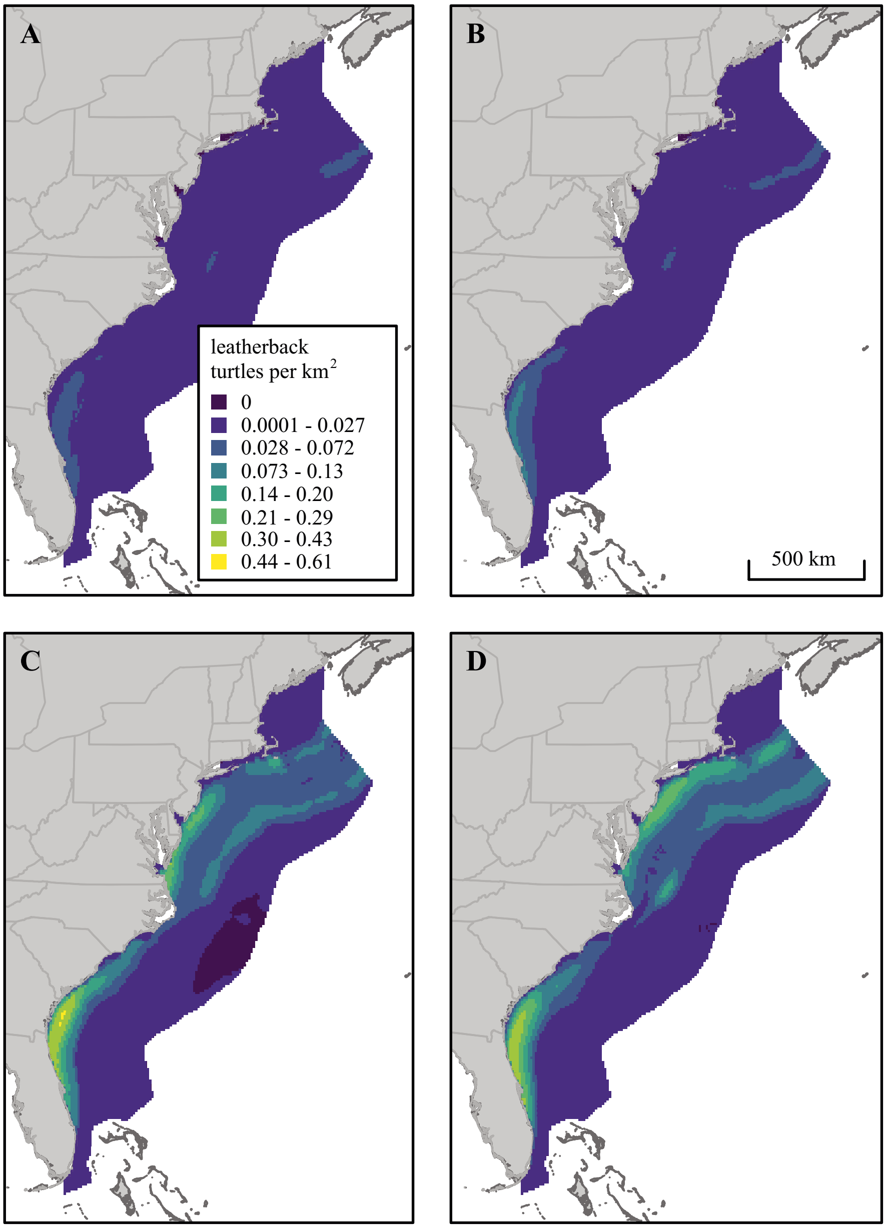

Fig. 6. Long-term predictions of leatherback turtle density and distribution for select months: (A) January (abundance: 5438; CI = 1340–9516), (B) April (abundance: 6740; CI = 2125–11 279), (C) July (abundance: 36 803; CI = 18 543–54 573), and (D) October (abundance: 40 177; CI = 18 598–61 118). The legend scale is applicable to this species only

brown, which stands out from seawater in many conditions, whereas green turtles are brown, buff, or green, and Kemp's ridleys are gray or olive-green (Pritchard & Mortimer 1999).

We tried to fit other classification models weighted towards green and Kemp's ridley turtles in an attempt to increase the accuracy for those 2 species. While accuracy for those 2 species was improved, it came at the expense of accuracy for loggerhead turtles, which resulted in hundreds of misclassifications in the testing data set. This tradeoff did not seem worthwhile, and the unequal weight models were dropped from consideration but remain an active research concern.

No surveys included in the study were designed to detect only turtles. All were multi-taxa surveys, which is common, usually targeting marine mammals in addition to turtles and occasionally sea birds. For both the Tetra Tech–New York State Department of Environmental Conservation (TT–NYSDEC) and North Atlantic right whale sighting (NARWSS) surveys, smaller marine mammals and sea turtles were logged when sighted per survey protocol, but the focus of the surveys was large whales, particularly North Atlantic right whales *Eubalaena glacialis*. Fitting detection functions by survey program should ameliorate differences in survey design and protocol. Indeed, we saw lower effective strip half widths for higher-altitude surveys compared to lower-altitude surveys (Sparks & DiMatteo 2023). However, higher-altitude aerial surveys, such as those designed with large whales in mind, may have a harder time detecting sea turtles, which are much smaller.

Based on discussions with survey providers, turtles smaller than 40 cm are likely being missed by surveys (regardless of altitude) to an unknown degree and represent a sizable proportion of the population of all sea turtle species. Observer trials of different-sized cutouts of various species of sea turtles of different size classes would be one method to estimate the proportion of smaller sea turtle size classes that are missed; however, to our knowledge, such experiments have not been undertaken in the study area. As such, these and other sea turtle density models underestimate density to an unknown, but currently unavoidable, extent. Future demographic modeling work similar to Putman et al. (2020) may provide an avenue to incorporate these small individuals into at-sea abundance estimates.

The selected density surface models exhibited plausible environmental relationships for all sea turtle species. For example, based on green turtles' preferred foraging on seagrass and macroalgae beds (Herren et al. 2018, Welsh & Mansfield 2022), selection for shallow, productive areas with high light penetration is plausible. The apparent preference of Kemp's ridleys for areas closer to shore than other sea turtle species could reflect the habitat of their preferred prey species on the east coast, the blue crab *Callinectes sapidus* (Burke et al. 1994, Seney & Musick 2005). The apparent preference of leatherbacks for unproductive waters potentially reflects a lag between primary productivity and the leatherback turtles' preferred gelatinous prey in the northeast Atlantic Ocean (Houghton et al. 2006, Witt et al. 2007).

Lower density predictions for the loggerhead model in June–November may be driven by lower productivity throughout most of the study area in those months, as a strong preference for productive areas was predicted by the model. Recall that when relating density to environmental covariates, density will vary as a function of those covariates. This seems more likely than large numbers of loggerhead turtles moving into and out of the study area seasonally. Though seasonal inshore versus offshore movements of loggerheads have been documented in the study area (McClellan & Read 2007), we posit the predicted environmental relationship to be the larger influence. High predicted loggerhead density off Florida reflects that region's importance as a nesting, post-nesting, overwintering, and transition area for both adults and juveniles (Ceriani et al. 2019).

The offshore patterns of predictions for leatherback turtles may reflect the east coast's importance as a migratory habitat, as turtles from the wider Caribbean region migrate to the Gulf of Mexico and North Atlantic Ocean basin seasonally to forage (Eckert 2006, Eckert et al. 2006, Sasso et al. 2021). Some foraging does occur in the study area (Dodge et al. 2014, 2018), which may be leatherback turtles stopping to feed on their long journey north or may reflect high-quality seasonal foraging habitat. Consistent seasonal foraging for male, female, juvenile, and adult leatherbacks has been documented in Canadian waters (James et al. 2005), and the waters of the study area are a primary route to reach those areas. The low predicted density in cool months may reflect leatherback turtles moving out of the study area after the summer breeding season to forage in North Atlantic waters (Eckert 2006, Eckert et al. 2006).

Predicted patterns of loggerhead and leatherback density reasonably match the underlying sightings and concur well with other, independent data sets such as satellite telemetry. Winton et al. (2018) presented a geostatistical mixed model of relative loggerhead turtle density based on 271 satellite-tagged individuals deployed in the region and predicted north–south movements similar to the loggerhead density surface model presented here. The Winton et al. (2018) paper did predict higher relative densities off the continental shelf in cool months compared to the density surface model, but the core distributions appear similar (Fig. 3). The drivers of the differences between the Winton et al. (2018) model and ours are unclear and could be sampling bias either from tracked individuals (in the case of the tracking study) or survey coverage (in the cause of ours), or may just reflect the different methodological frameworks of the 2 approaches.

Loggerheads are also regularly captured in fisheries off the coast of Nova Scotia (Brazner & McMillan 2008), supporting the presence of that species in the Gulf of Maine. The area south of Cape Hatteras has been designated as critical habitat for overwintering loggerhead turtles based on satellite telemetry data (NOAA 2014b) and was also identified by the density surface model as an area of relatively high density in those months.

Tracking data indicates the presence of leatherback turtles in the study area year-round (James et al. 2007, Dodge et al. 2014), including migrating through the study area in late summer and early fall. Migratory pathways span from close to the coastline to far offshore, beyond the boundaries of the study area (Eckert 2006, Eckert et al. 2006), offering support for the prediction of a substantial leatherback presence off of the continental shelf. Previous distribution modeling efforts for leatherback turtles in the area were limited to the continental shelf (Shoop & Kenney 1992, United States Department of the Navy 2007) and are much older, making comparisons uninformative.

Fewer supporting data sets exist for green and Kemp's ridley turtles in the region. The satellite tracks that do exist, as well as acoustic tagging data from the Chesapeake Bay, established timing of migration similar to that predicted by the spatial density models (Barco et al. 2018b). The models predicted green and Kemp's ridley turtles further north than is known from sightings and tracking data (e.g. in the Gulf of Maine). These predictions were at very low densities, generally less than 0.005 animals km^{-2}, and are likely artefacts of covariate relationships. As such, we recommend forcing the models to zero density per the cutoffs described in the results when using the models for management applications.

No previous distribution models for green sea turtles exist in the study area. The only previous distribution model for Kemp's ridley sea turtles is more than 10 yr old, only covers the continental shelf, and does not account for unidentified turtles, making comparisons challenging (United States Department of the Navy 2007).

CI ranges were substantial for green, Kemp's ridley, and leatherback turtles, all species with fewer sightings relative to loggerhead turtles. This uncertainty may indicate there are not enough sightings for these species to fit tight environmental relationships, or that the selected covariates had limited explanatory power for the species in question. Future models with more surveys included or with new generations of covariates that better describe the distribution of sea turtles may tighten uncertainty estimates.

Several sources of uncertainty and variability are not accounted for in the CV and CI estimates, which include environmental variability relative to GAM parameter uncertainty, detection function uncertainty, variability and uncertainty in the dive data and models used for availability bias estimates, measurement error in environmental covariates, and misidentification or misclassification of sightings, many of which are not regularly accounted for in density surface models but are important to understand. New methods of propagating some of those sources of uncertainty into GAM parameter CV estimates exist, particularly density function uncertainty, and are described in Bravington et al. (2021) and Miller et al. (2022) but were outside the scope of the project. The CV and CI estimates presented should be considered minimum estimates until future work can incorporate other sources of uncertainty.

Continual surveying is needed to ensure density surface models can be updated at appropriate intervals and limit the impact of using past data to predict future impacts. Suggested priorities for future work to improve the density surface models include incorporating more sources of uncertainty into the CV and CI estimates, creating spatial models of availability bias for the non-loggerhead turtle models, revisiting strategies to deal with unidentified sightings or updating the machine-learning model, platform-specific perception bias estimates and exploring reasons for differences in these estimates between species, and incorporating new survey types such as high-resolution imagery.

The density surface models discussed here are appropriate for use in spatially and temporally broad-scale planning and conservation initiatives, such as military training and readiness, offshore energy development, marine spatial planning on the scale of the eastern seaboard or subregions, critical habitat designations, fisheries mitigation, and other applications. The models should not be used for fine-scale planning (e.g. how many individuals are in a single grid cell) or where it is crucial to have population information from after 2019, as 2019 is the latest year of survey data incorporated, and the broad-scale nature of the models means that single grid cells may not replicate local conditions.

The density surface models provide an important complement to species distribution models derived from other data types such as satellite telemetry data and fisheries observation data. Estimates of in-water abundance data for these species are important to managers to complement abundance estimates derived from nesting data, and these models fill a critical knowledge gap in the region, which previously lacked up-to-date in-water abundance estimates for most species and areas.

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