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Estimating the distribution and relative density of satellite-tagged loggerhead sea turtles using geostatistical mixed effects models

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ABSTRACT: Movement and location data collected via satellite-linked telemetry tags are often used to inform spatial conservation measures for threatened marine populations. Most applied telemetry studies aim to reconstruct the continuous utilization distribution underlying reported locations to characterize the relative intensity of space use. However, commonly applied space use estimators do not directly estimate the underlying distribution of interest and, perhaps more importantly, ignore correlations in space and time that may bias estimates. Here we describe how geostatistical mixed effects models, which explicitly account for spatial and/or temporal correlation using Gaussian random fields, can be applied to estimate utilization distributions from satellite telemetry data. We use simulation testing to compare the performance of the proposed models with several conventional space use estimators. Our results suggest that geostatistical mixed effects models outperform conventional estimators when the number of tag transmissions changes over time, a common source of bias in satellite telemetry studies that is rarely addressed. We illustrate this approach via application to satellite telemetry location observations collected from 271 large juvenile and adult loggerhead sea turtles in the western North Atlantic from 2004 to 2016. We demonstrate how such models can be used to predict the overall spatial distribution of tagged individuals, as well as seasonal shifts in densities at smaller time scales. For tagged loggerheads, overall predicted densities were greatest in the shelf waters along the US Atlantic coast from Florida to North Carolina, but monthly predictions highlight the importance of summer foraging habitat in the Mid-Atlantic Bight.

KEY WORDS: *Caretta caretta* · Utilization distribution · Autocorrelation · Spatial point process · Spatiotemporal variation · Spatial smoothing · Home range

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INTRODUCTION

Management measures for endangered or threatened marine populations often rely on an understanding of a species' distribution and habitat use to identify overlap with potential sources of mortality. For highly migratory species such as loggerhead sea turtles *Caretta caretta*, the range of threats encountered shifts with habitats occupied seasonally and over the course of migration (Gardner et al. 2008,

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Finkbeiner et al. 2011, Lewison et al. 2014). Consequently, the effectiveness of management actions hinges on knowing where the species is likely to occur at any given point in time (Maxwell et al. 2011). Estimates of the relative density and distribution of large-bodied, obligate air-breathers such as sea turtles and marine mammals are often based on data collected during shipboard or aerial line transect surveys, which generally cover large geographic areas annually (Moore & Barlow 2013). Given the migratory habits of loggerheads (Griffin et al. 2013), the data generated during these surveys do not provide a sufficient basis for estimating the dynamic distribution of the species over the course of the year.

Data collected via satellite-linked telemetry tags are increasingly used to describe the distribution and migratory habits of marine turtle species (Godley et al. 2008). Satellite tags transmit signals that can be detected by overhead satellites when exposed to air, enabling geolocation of a tagged individual's location (CLS-Argos 2015). In contrast to infrequent, discontinuous line transect surveys, satellite tags can be programmed to sample turtle behavior every day of the year, and can represent the location of animals even as transient relationships with the environment (e.g. salinity, depth) change with physiological demands imposed by migration and fluctuating food sources. Most applied telemetry studies attempt to characterize space use by reconstructing the underlying spatial probability distribution (typically referred to as the utilization distribution; Van Winkle 1975) from available discrete location observations. Though this is their implicit aim, the most commonly applied space use estimators (i.e. kernel density estimators and minimum convex polygons; Calenge 2006) do not directly estimate the underlying continuous process of interest. Instead, they bound or smooth over the distribution of reported locations to approximate the underlying distribution, precluding predictive inference (Diggle et al. 2013).

Perhaps more importantly, conventional estimators weight each observed location equally, ignoring correlations in space and time that have the potential to bias estimates of space use (Whitehead & Jonsen 2013, Fleming et al. 2015). Receipt of satellite tag transmissions is limited by battery life and other sources of signal loss (e.g. biofouling; Hays et al. 2007) and varies with seasonal shifts in behavior (e.g. increased dive times during winter or basking during summer; Hays et al. 1999). As a result, the number of estimated locations received from tagged individuals changes, and generally decreases, over time. Thus, estimates of the relative intensity of space use generated using conventional methods are often biased towards the time and location of tagging operations, where the number of reported locations is typically greatest (Whitehead & Jonsen 2013). This issue and its potential ramifications have been largely ignored in studies describing marine animal densities from tagging data (though see Whitehead & Jonsen 2013), in part due to a lack of analytical techniques available to address this source of bias.

Spatiotemporal point process models have recently been proposed as a means to estimate spatial distributions from satellite telemetry data while accounting for temporal autocorrelation (Johnson et al. 2013). Conceptually, this approach considers the density of reported locations as a discrete realization of an underlying, spatially continuous but varying (i.e. inhomogeneous) intensity function that shifts over time (Aarts et al. 2012, Johnson et al. 2013, Thorson et al. 2016). Existing applications have focused on modeling the spatial intensity of the point process as a function of spatially referenced covariates (Johnson et al. 2013), which may not adequately account for the correlation structure of the data if a critical covariate is omitted. Geostatistical mixed effects models (also referred to as log Gaussian Cox processes; Diggle et al. 2013), which model point process intensity as a function of spatial random effects using Gaussian random fields, can be used to characterize the latent spatial structure without the need to specify covariates. These models are rooted in well-established generalized linear mixed modeling techniques (McCullagh & Nelder 1989, Pinheiro & Bates 2000), but explicitly account for spatial and/or temporal correlation by specifying that values sampled closely together in time or space are more similar than those sampled further apart. Shifts in distributions over time can be accounted for by the inclusion of additional random fields (Thorson et al. 2016), providing a theoretical basis for estimating the 'overall' spatial distribution underlying reported locations by integrating over time (Johnson et al. 2013).

Here, we apply geostatistical mixed effects models to estimate the distribution and relative density of tagged juvenile and adult loggerhead sea turtles in the western North Atlantic from satellite telemetry data collected from 2004 to 2016. After describing the loggerhead sea turtle data set, we review how conventional generalized linear models for counts can be extended to estimate both latent spatial and spatiotemporal variation in reported locations using Gaussian random fields. We then use simulation testing to compare the performance of space-time geostatistical mixed effects models with several com-

monly applied space use estimators and evaluate biases in the resulting estimates of space use. Finally, we apply a space-time geostatistical mixed effects model to estimate the relative density of 271 tagged loggerheads in the western North Atlantic and demonstrate how the full space-time model can be used to predict the overall spatial distribution, as well as seasonal shifts in densities.

METHODS

Loggerhead sea turtle tracking data

We used data from 271 satellite tags deployed on large juvenile and adult loggerheads in the northwest Atlantic by 6 tagging programs between 2004 and 2016 (Table 1). The specific tag model, set-up, and attachment method varied among the 6 tagging programs (see Haas et al. 2010, 2013, 2014, Weeks et al. 2010, Northeast Fisheries Science Center 2011, Arendt et al. 2012a–c, Coonamessett Farm Foundation 2012, 2013, Haas & Smolowitz 2012, Valenti & Smolowitz 2014, Cholewiak et al. 2015, Patel et al. 2015, 2016 and Barco & Lockhart 2017 for details of specific programs), but all tags transmitted location data via the Argos satellite system (CLS-Argos 2015). All but 17 of the turtles were wild-caught and tagged during the course of directed research; data from 15 tags deployed on rehabilitated turtles and 2 on loggerheads incidentally captured in pound nets that exhibited typical regional movements following release were also included. Tagging operations were conducted under appropriate permits (Coonamessett Farm Foundation and Northeast Fisheries Science Center: 1551, 1576, 14249, 16556, 18526; Fisheries and Oceans Canada: FRN-M-15-07; South Carolina Department of Natural Resources: 1540, Florida Marine Turtle Permit 163; Southeast Fisheries Science Center: 1551; Virginia Aquarium & Marine Science Center: 16134) following protocols detailed in reports (cited above) of each tagging program. Data collected from a subset of the tags deployed have been previously published in Arendt et al. (2012a–c) and Northeast Fisheries Science Center & Southeast Fisheries Science Center (2011).

Turtle locations were processed following standard guidelines for sea turtle tracking. Given the error associated with each Argos location, tracks of individual turtles were filtered based on a continuous-time correlated random walk model (Johnson et al. 2008, Albertsen et al. 2015), which describes the movement process as a function of the instantaneous

Table 1. Summary of Argos satellite tag deployments conducted by 6 loggerhead sea turtle *Caretta caretta* tagging programs in the western North Atlantic from 2004 to 2016. Mean straight carapace length (SCL) of tagged individuals, measured from notch to notch (cm), with range in parentheses, is also shown. SAB: South Atlantic Bight; MAB: Mid-Atlantic Bight; GB: Georges Bank

Tagging program	Tag model	Duty cycle	Turtles	Valid locations	Years	Region	SCL (cm): mean (range)	Days transmitting: median (range)
South Carolina Department of Natural Resources	Telonics ST-20, A2020	Continuous	72	43 414	2004–2015	SAB	79.0 (56.6–107.0)	148 (7–374)
Coonamessett Farm Foundation	Sea Mammal Research Unit Satellite Relay Data Logger	Continuous	59	146 261	2009–2016	MAB	73.0 (55.0–99.5)	274 (23–577)
Northeast Fisheries Science Center	Sea Mammal Research Unit Satellite Relay Data Logger	Continuous	58	116 440	2010–2015	MAB	71.2 (53.5–96.0)	250 (16–641)
		Continuous	2	1688	2015	GB	62.3 (67.0–72.3)	117 (116–117)
Southeast Fisheries Science Center	Wildlife Computers MK-10	24 h on 72 h off	56	32 847	2010–2013	SAB	69.5 (51.3–87.9)	118 (18–338)
Virginia Aquarium	Sea Mammal Research Unit Satellite Relay Data Logger	Continuous	21	33 380	2011–2015	MAB	69.5 (59.2–98.2)	188 (21–375)
Fisheries and Oceans Canada	Wildlife Computers SPLASH MK-10	Continuous	3	2472	2015	GB	56.4 (55.3–58.5)	94 (92–131)

velocity of the animal in each time step (see the Supplement at www.int-res.com/articles/suppl/m586p217_supp.pdf for details). Models were fitted to location data using functions modified from those provided by Albertsen al. (2015) in the software Template Model Builder (TMB; Kristensen et al. 2016), a recently developed package for R statistical software (R Core Team 2016) that makes use of automatic differentiation and Laplace approximation to efficiently fit complex random effects models. Prior to fitting, all location coordinates were re-projected into the oblique Mercator center projection centered on 35.0° N, 75.0° W using the R package 'rgdal' (Bivand et al. 2015).

Reconstructed tracks were then linearly interpolated onto a daily time step using the R package 'adehabitatLT' (Calenge 2006). This 'thinning' step was performed to avoid bias that may result from variation in tag duty cycles (Table 1) and for consistency with previous loggerhead tagging studies (TEWG 2009, Arendt et al. 2012a–c, Griffin et al. 2013). To avoid interpolating across areas and time periods without observations, individual tracks with position estimates separated by more than 3 d in time (the length of the longest 'off' period for tags that were duty cycled; Table 1) were divided into multiple, unlinked track segments. The resulting tracks thus represent daily turtle positions during each observation period (TEWG 2009).

Estimating relative densities using geostatistical mixed effects models

Our goal was to model spatial variation in the relative density of tagged juvenile and adult loggerheads over the course of the year in a way that would account for both the underlying correlation structure of telemetry data as well as the fact that the number of transmissions changed over time. Geostatistical mixed effects models, the approach we use here, have been described in detail elsewhere (Lindgren et al. 2011, Thorson et al. 2015, 2016) and so we provide only a brief review. We start with a Poisson generalized linear model (GLM) with a log link function to estimate the density of reported locations at a given site i (though other plausible distributions and link functions could also be applied). The notation we use here follows Thorson et al. (2015). We assume that n_i, the number of observed telemetry locations at site i, follows a Poisson distribution with mean and variance λ_i:

$$n_i \sim \text{Poisson}(\lambda_i) \quad (1)$$

In the simplest case, the number of locations reported at each site can be estimated as:

$$\log(\lambda_i) = \beta_0 + \log(a_i) \quad (2)$$

where β_0 is an intercept term representing the mean number of locations and a_i is the area associated with each site, which is included as an offset term to scale the expected counts into densities.

The above formulation implies that the densities of reported locations at each site are independent of those at all other sites and that the mean density is constant over time. However, we expect that densities at a given site will be more similar to those at neighboring sites than at distant sites. The above Poisson GLM can be extended using a Gaussian random field (GRF), to allow for this latent spatial variation between sites, s:

$$\log(\lambda_i) = \beta_0 + \log(a_i) + \Omega(s_i). \quad (3)$$

Here Ω denotes the GRF allowing for spatial variation in the expected number of reported locations at site i, which follows a mean-zero multivariate normal distribution:

$$\Omega \sim \text{multivariate normal}(0, \sigma_\Omega^2 \mathbf{C}_d) \quad (4)$$

where σ_Ω^2 is the marginal variance of Ω. $\mathbf{C}_d$ is the spatial correlation function between locations separated by a Euclidean distance of d, which is specified as a Matérn function with a smoothness parameter, ν, equal to 1 and a scaling parameter, κ, which is estimated (Lindgren et al. 2011). Together, these 2 terms represent the spatial covariance among locations, which we here assume to be isotropic (i.e. equal in both the north–south and east–west directions). The spatial correlation range (i.e. the distance at which observations can be considered approximately independent), ρ, can be empirically derived as $\sqrt{8}/\kappa$ (Lindgren et al. 2011).

For migratory animals like loggerheads, we also expect that regions of high density will shift over the course of the year. To account for temporal variation in the spatial distribution, the above model can be extended with a second GRF representing variation in Ω at time step t, denoted by E_t:

$$\log(\lambda_{i,t}) = \beta_0 + \log(a_i) + \Omega(s_i) + E_t(s_i), \quad (5)$$

where, as for Ω, E_t is assumed to follow a multivariate normal distribution with mean zero and spatial covariance given by $\sigma_E^2 \mathbf{C}_d$. Note that this specification implies that the correlation distance is stationary and time-invariant. As formulated here, Ω represents the marginal spatial distribution of the density field integrated over all time steps. That is, Ω provides an esti-

mate of the 'overall' spatial trend while accounting for changes in the spatial distribution over time. Shifts in time are represented as differences from the 'overall' spatial field (Ω) at each of t time steps. Using this approach, the time of tag transmissions is also considered random (Johnson et al. 2013, Thorson et al. 2016), which is appropriate when changes in transmission rates cannot be directly modeled (e.g. when transmission rates change due to unobservable changes in animal behavior or tag status), as is the case here.

Parameter estimation and spatial prediction

Variations in space and time are treated as random effects and are estimated using a stochastic partial differential equation approximation approach, which approximates a continuous GRF using a Gaussian Markov random field (see Lindgren et al. 2011 for details). In short, the approach approximates the full, continuous spatial field using weighted sums of piecewise linear basis functions, which are defined over the region of interest on a triangulated mesh (Lindgren et al. 2011); we use the R-INLA software to calculate the mesh and the sparse matrices used for this approximation (see Lindgren et al. 2011 and Lindgren & Rue 2015 for full details on mesh construction and the approximation). While each telemetry location could be specified as a mesh node, in most telemetry applications the large number of locations available will render such an approach computationally infeasible (Banerjee et al. 2008). For all simulations and applications conducted here, we use a predictive process approach, where spatial and seasonal fields are approximated at a series of gridded 'knots' (rather than at all available locations) to reduce dimensionality (Banerjee et al. 2008). We use the R package TMB (Kristensen et al. 2016) to estimate fixed effects parameters via non-linear optimization of the maximum marginal likelihood, which integrates across random effects using the Laplace approximation. The estimated fixed and random effects are then used to predict the distribution and relative density at each location within the study area. Readers interested in further details regarding the statistical theory underlying the models and specific details related to the spatial approximation and computational approaches are referred to Lindgren et al. (2011), Lindgren & Rue (2015), and Thorson et al. (2015). Code for fitting the models described here and conducting the simulations described below is provided on the first author's publicly available GitHub page (https://github.com/meganwinton).

Simulation testing

To test the performance of the spatiotemporal models described above when the number of tag transmissions changes over time, we conducted a simulation study. We used the space-time geostatistical mixed effects model and the R package 'RandomFields' (Schlather et al. 2015) to generate a continuous density field over a 30 × 30 unit-square grid assuming a mean intensity (β_0) of 0.05 reported locations per grid cell and a spatial GRF, Ω, with a marginal variance of 1 ($\sigma^2_\Omega = 1.0$) and a spatial range, ρ, of 15 grid cells. Shifts in densities over the course of 4 time steps (hereafter referred to as 'seasons') were simulated by the addition of a second GRF (E_t as described above) with $\sigma^2_E = 1.0$ and $\rho = 15$ grid cells.

We could have assumed that reported locations are generated as the realization of a Poisson process arising from each seasonal intensity field; however, this approach would not appropriately represent the serial correlation inherent in position estimates and ignores preferential selection of resources at the individual level. To account for this, we simulated the movement of 1 individual for 500 steps on each of the 4 seasonal fields using a Metropolis–Hastings inspired algorithm (Hastings 1970). The starting grid cell of each individual track was selected based on a random draw from a uniform distribution of grid cells. At each subsequent step, a grid cell within 2 cells of the current position was randomly selected; boundary effects were imposed by specifying that grid cells along the border were reflective. If the value of the underlying random field in the proposed grid cell was greater than that in the current grid cell, the individual moved to the new cell; to reflect searching behavior, movement also occurred if the value of the field in the current cell was less than the median of the entire field. If neither of those conditions were satisfied but the value in the proposed grid cell was at least half that of the current grid cell, the individual moved to the new cell with probability equal to the ratio of the values of the proposed and current cells. Within each grid cell, the position of each reported location was determined based on random draws from 2 uniform distributions representing variation in the east–west and north–south direction. To simulate decreasing numbers of transmissions over time, a subset of the generated locations was removed in the second (25%), third (50%), and fourth seasons (75%). The intensity of the simulated locations shifted in space and differed between seasons, which is typical of satellite tagging data.

We then applied the space-time geostatistical mixed effects model to the simulated location data to assess how well it recovered the underlying spatial field generating the observations. When fitting the space-time geostatistical mixed effects model, it was assumed that the 4 seasonal time steps were appropriately identified prior to fitting. Space-time models were fitted using functions modified from those provided in the supplementary material of Thorson et al. (2015) using the estimation methods described above.

We also applied 4 alternative space use estimators to compare their performance to that of the geostatistical mixed effects model: (1) the minimum convex polygon (Mohr 1947); (2) the conventional kernel density method (Worton 1989); (3) simple track densities; and (4) the Markov chain approach (Whitehead & Jonsen 2013). A brief description of each is provided here, but interested readers should consult the cited references for further details. Minimum convex polygons, which are the smallest possible convex polygon containing a specified proportion of the available telemetry locations (e.g. 50%), were estimated using functions in the R package 'adehabitatHR' (Calenge 2006). Conventional kernel density estimates were generated using default function settings in the same package; the approach estimates a bivariate kernel function over each location and averages the values of these functions over space (Calenge 2006). Track densities were estimated by summing the number of observed locations in each grid cell and dividing by the total number of locations; this corresponds to the simplest approximation of a multinomial resource selection function (McCracken et al. 1998). We also applied the Markov chain approach of Whitehead & Jonsen (2013), which can be used to produce unbiased measures of relative density from animal tracking data when movements among cells can be considered as a time-homogenous Markov chain.

We fit each of the 5 space use estimators considered to 100 simulated datasets. For comparison purposes, the simulated densities and the densities estimated using each method were scaled from 0 to 1 by conditioning the density in each grid cell on the total density generated using that method (i.e. the sum of the densities in all grid cells). The performance of each estimator was assessed by comparing the sum of absolute errors between estimators; error values were calculated by subtracting the value of the true underlying field in each grid cell from that estimated using each of the 5 methods in each iteration. We also compared the error in the area and percent overlap of the region corresponding to the smallest area encompassing 50% of the resulting probability distribution with that of the true underlying density field. This corresponds to the 50% home range metric often used to identify core use areas when conventional methods are applied (Calenge 2006). For each estimation method, the error in area was calculated as the difference between the number of grid cells included in the resulting core use area and that included in the true simulated field.

Method comparison via application to an individual loggerhead track

To illustrate how predictions from the space–time geostatistical mixed effects model differ from conventional methods when applied to an actual track, we applied each of the 5 space use estimators tested during the simulation study to locations reported from a 74 cm (curved carapace length) loggerhead that was tagged in the Mid-Atlantic Bight (MAB) in May 2012. This track was selected because the tag reported for almost an entire year (reporting 2061 locations until transmission ceased in May 2013) and captured the turtle's movements on summer foraging grounds in the MAB as well as the area in which it overwintered south of Cape Hatteras, North Carolina. Locations were binned by month (the time step we have found is most often requested by managers) and aggregated over the 10 km resolution Atlantic Marine Assessment Program for Protected Species (AMAPPS) spatial grid (area of each grid square = 100 km^2) in R using the 'sp' (Pebesma & Bivand 2005, Bivand et al. 2013) and 'raster' packages (Hijmans 2015). The AMAPPS grid was bounded by the coastline to constrain the loggerhead's space use to the ocean. To estimate the relative intensity of space use, a space–time geostatistical mixed effects model was fitted to counts of reported locations on a monthly time step as described above. The other 4 space use estimators were applied to aggregate locations on the AMAPPS spatial grid. The resulting densities from each method were scaled from 0 to 1, and the 50% core use area estimated as described for the simulations above.

Application to loggerhead tracking data

To estimate the relative density of the 271 tagged loggerheads over the course of the year, we fitted a space–time geostatistical mixed effects model to counts of daily loggerhead positions on a monthly time step. Under the assumption that tracks of indi-

vidual turtles represent independent Poisson processes, a model for multiple individuals can be obtained by pooling data; a combination of independent Poisson processes is also a Poisson process (Johnson et al. 2013). To account for differences in the duration of tag transmission between turtles, individual tracks in each month were weighted inversely according to the number of days transmitting. Daily weighted location estimates were binned by month and aggregated over a 40 km resolution version of the AMAPPS spatial grid (area of each grid cell = 1600 km^2) in R using the 'sp' (Pebesma & Bivand 2005, Bivand et al. 2013) and 'raster' packages (Hijmans 2015); given the broad geographic scale of interest for this application, we chose to use the larger resolution grid to speed computation time. Though several tagged turtles ventured into the Gulf of Mexico or further north, we only considered locations reported north of 25.0° N, south of 41.5° N, east of 81.5° W, and west of 65.0° W, which encompassed the area with the highest track densities. Prior to fitting, all location coordinates were re-projected into the oblique Mercator center projection centered on 35.0° N, 75.0° W using the R package 'rgdal' (Bivand et al. 2015).

Given the absence of data definitively indicating differences in the regional abundance of loggerheads at the time of tagging (Northeast Fisheries Science Center & Southeast Fisheries Science Center 2011), as well as differences in the number of tags deployed in the MAB and South Atlantic Bight (SAB) (Table 1, Fig. 1), we chose to weight tracks from tags deployed north and south of Cape Hatteras, North Carolina, equally. While 6 individual tagging programs were involved, there was a broad degree of overlap in the timing and location of tag deployments in the MAB and SAB due to collaborations between the Northeast Fisheries Science Center, Coonamessett Farm Foundation, and the Virginia Aquarium in the MAB, and between the Southeast Fisheries Science Center and the South Carolina Department of Natural Resources in the SAB (Fig. 1). To account for differences in the number of tag deployments between regions, the individually weighted tracks from turtles tagged in the SAB were scaled by the ratio of the number of daily locations available for turtles tagged in the MAB (which were higher in all months) to the number available for the SAB in each month; this gave equal weight to tags deployed in each region in each month. Tags deployed on or near Georges Bank were included with those deployed in the MAB due to low sample size (n = 5). A space-time geostatistical mixed effects model was fitted to the weighted dataset in R (R Core Team 2016) and TMB (Kristensen et al. 2016) as described above. Values for each monthly predicted field were scaled from 0 to 1 by conditioning the predicted value in each grid cell on the summed total in that month. Scaled fields were used to visualize the overall and monthly spatial distribution of tagged loggerheads over the 40 km resolution AMAPPS grid.

RESULTS

From 2004 to 2016, a total of 376 502 valid locations were reported by the 271 tags deployed (Table 1; Fig. 1). Tag reporting life ranged from 7 to 641 d (Table 1). Following track filtering and interpolation, a total of 55 803 daily loggerhead locations were available. The number of daily locations available in each month was highest from the summer through the fall, which reflected the timing of tag deployments; most tags were deployed in the spring or summer (Fig. 2). Tagged loggerheads primarily occupied the continental shelf from Long Island, New York, south to Florida, with some individuals making offshore excursions, often in the vicinity of the Gulf Stream (Fig. 1).

Simulation testing and method comparison

In simulated applications, the space-time geostatistical mixed effects models outperformed the 4 alternative space use estimators. The space-time model resulted in the lowest absolute error, and had the highest percent overlap with the 'true' core use area estimate (Fig. 3). Minimum convex polygons performed similarly to the space-time model in terms of estimating the size of the core use area, but resulted in the highest absolute error of all methods applied. On average, kernel density methods underestimated the size of the core use area, but performed reasonably well in terms of absolute error (Fig. 3). The track density and Markov chain estimates both performed poorly in comparison with the other methods. While the geostatistical mixed effects model did outperform the other 4 approaches overall, in 4 of the 100 simulations the predicted core use area was much larger than the true core area (Fig. 3b). In these instances, variation in the simulated seasonal fields was insufficient to estimate both the spatial and temporal variance parameters, resulting in uniform predictions over space in each time step.

Differences were also apparent when the 5 methods were applied to the track of an individual logger-

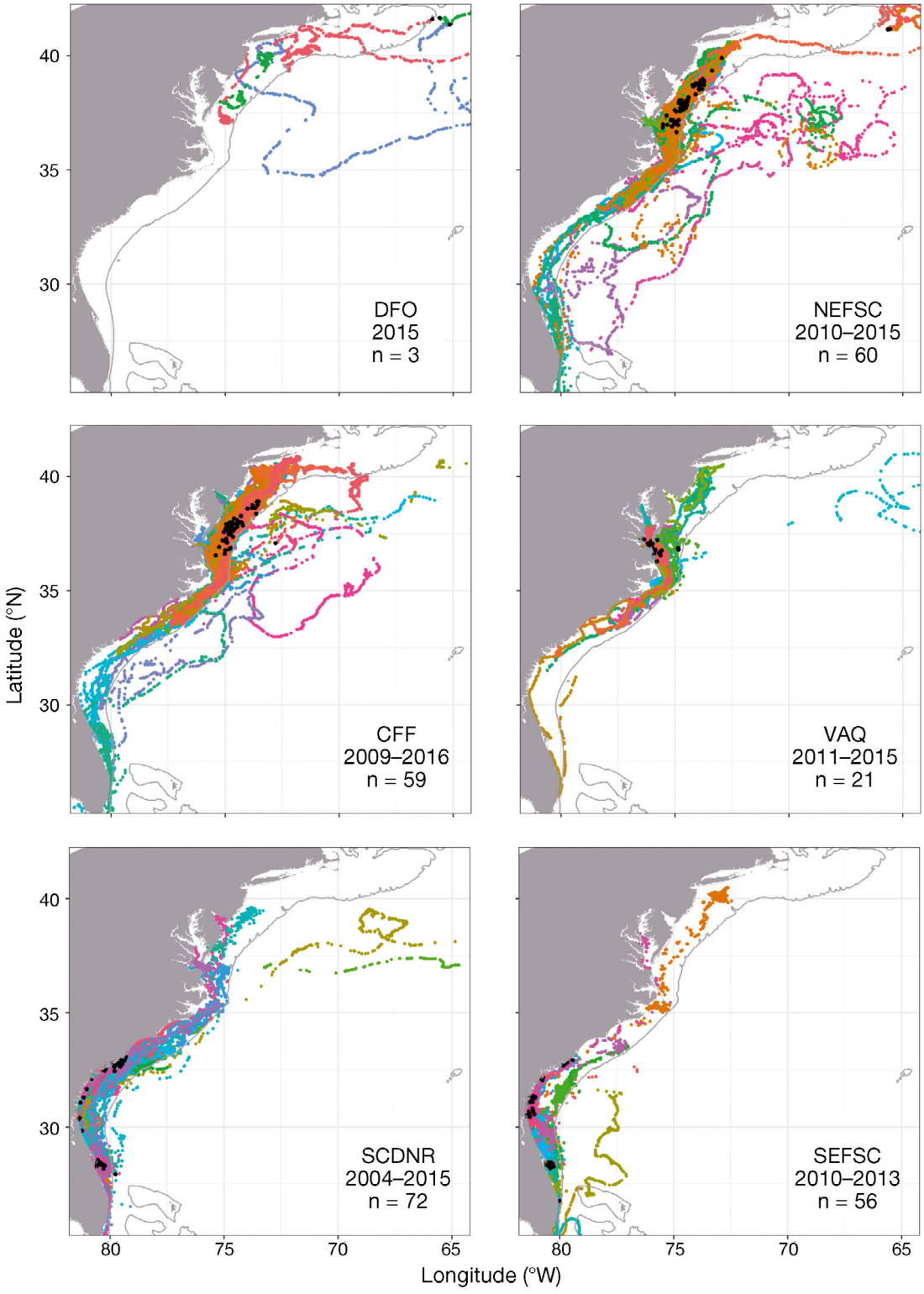

Fig. 1. Study area and reconstructed tracks from 271 large juvenile and adult loggerhead turtles tagged by 6 different tagging programs in the western North Atlantic from 2004 to 2016. Tracks of individual turtles are indicated by different colors. Tagging locations are indicated by black circles. The grey line denotes the 200 m bathymetric contour. DFO: Fisheries and Oceans Canada; NEFSC: NOAA Fisheries Northeast Fisheries Science Center; CFF: Coonamessett Farm Foundation; VAQ: Virginia Aquarium & Marine Science Center; SCDNR: South Carolina Department of Natural Resources; SEFSC: NOAA Fisheries Southeast Fisheries Science Center

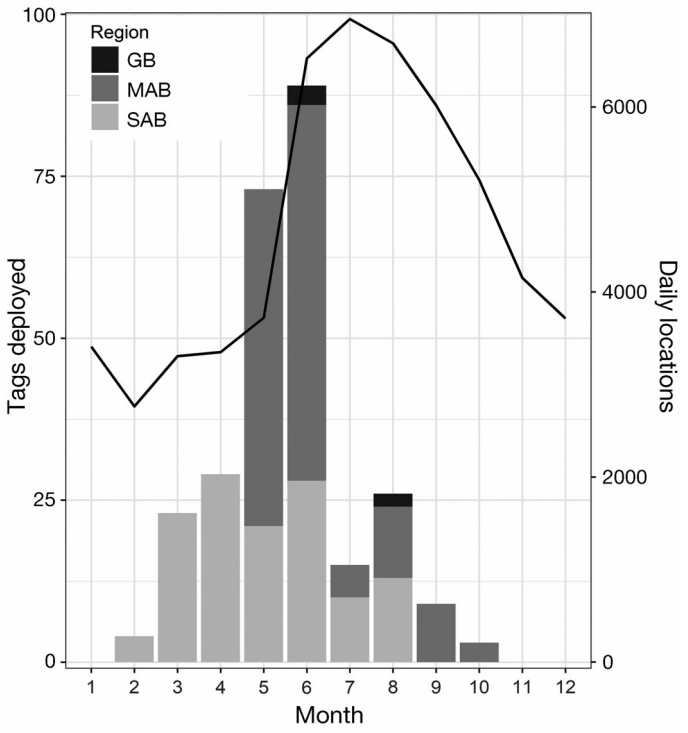

Fig. 2. Number of satellite tags (bars) deployed on 271 large juvenile and adult loggerheads in the western North Atlantic by month and region. The total number of daily locations available from tags deployed in all regions in each month is also indicated (black line). GB: Georges Bank; MAB: Mid-Atlantic Bight; SAB: South Atlantic Bight

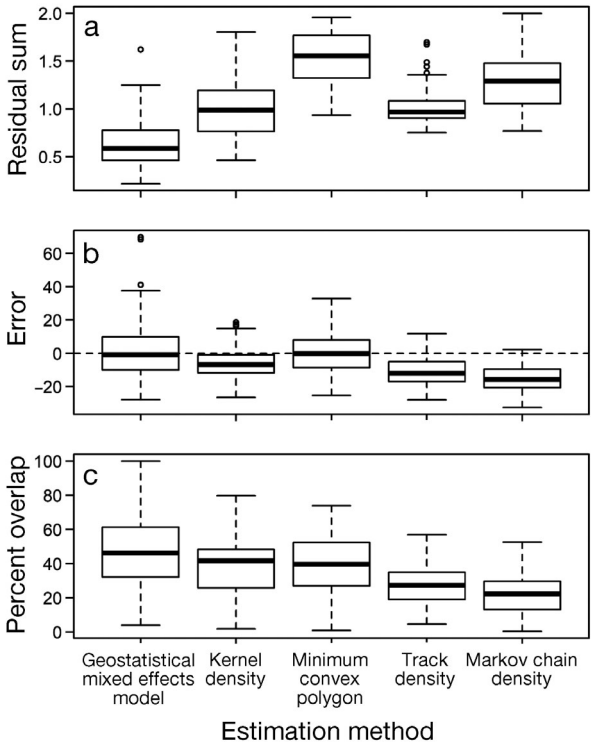

Fig. 3. Performance of 5 space use estimators applied to 100 simulated tracks generated as the realization of a latent spatiotemporal point process. For each boxplot, the thick black line in the middle represents the median, the top of the box the first quartile, the bottom of the box the third quartile, the whisker bars 1.5 times the interquartile range from the median, and the points are outliers. Individual panels represent (a) the sum of absolute error values; (b) the error in the area of the smallest region encompassing 50% of the resulting probability distribution, which corresponds to the 50% home range metric often used to identify core use areas; and (c) percent overlap with that of the true core area

head. Only the space-time geostatistical mixed effects model predicted a 50% core use area that encompassed both known foraging (off New Jersey) and overwintering areas (south of Cape Hatteras, North Carolina; Fig. 4). Core use areas identified using kernel density estimation and minimum convex polygons excluded the overwintering area, and that estimated using the Markov chain density method excluded the foraging area. The core use area identified by applying the track density estimation method did include both foraging and overwintering grounds, but the overwintering area was more disjointed than that predicted using the space-time geostatistical mixed effects model.

Relative densities of tagged loggerheads

Based on the fitted space-time geostatistical mixed effects model, the overall predicted spatial distribution of tagged loggerheads was concentrated along the US Atlantic shelf from central Florida to New Jersey (Fig. 5). The predicted density of tagged loggerheads remained relatively high across the shelf but generally declined north of New Jersey and at the shelf break. The areas with the highest overall predicted densities were off Cape Hatteras (North Carolina), Charleston (South Carolina), and Cape Canaveral (Florida). While high density regions did shift between months, these 3 coastal locations supported high densities of tagged loggerheads year-round. The overall predicted distribution was similar to that apparent from the reconstructed tracks (Fig. 1) but filled in the spatial gaps in offshore areas (Fig. 5).

Estimated fixed effects parameters suggested that variation in the spatial distribution over time was slightly greater than that in space (Table 2), which reflects the highly migratory behavior of loggerheads. The predicted monthly random fields (Fig. 5) indicated that tagged loggerheads were concentrated in continental shelf waters year-round but that densities shifted seasonally.

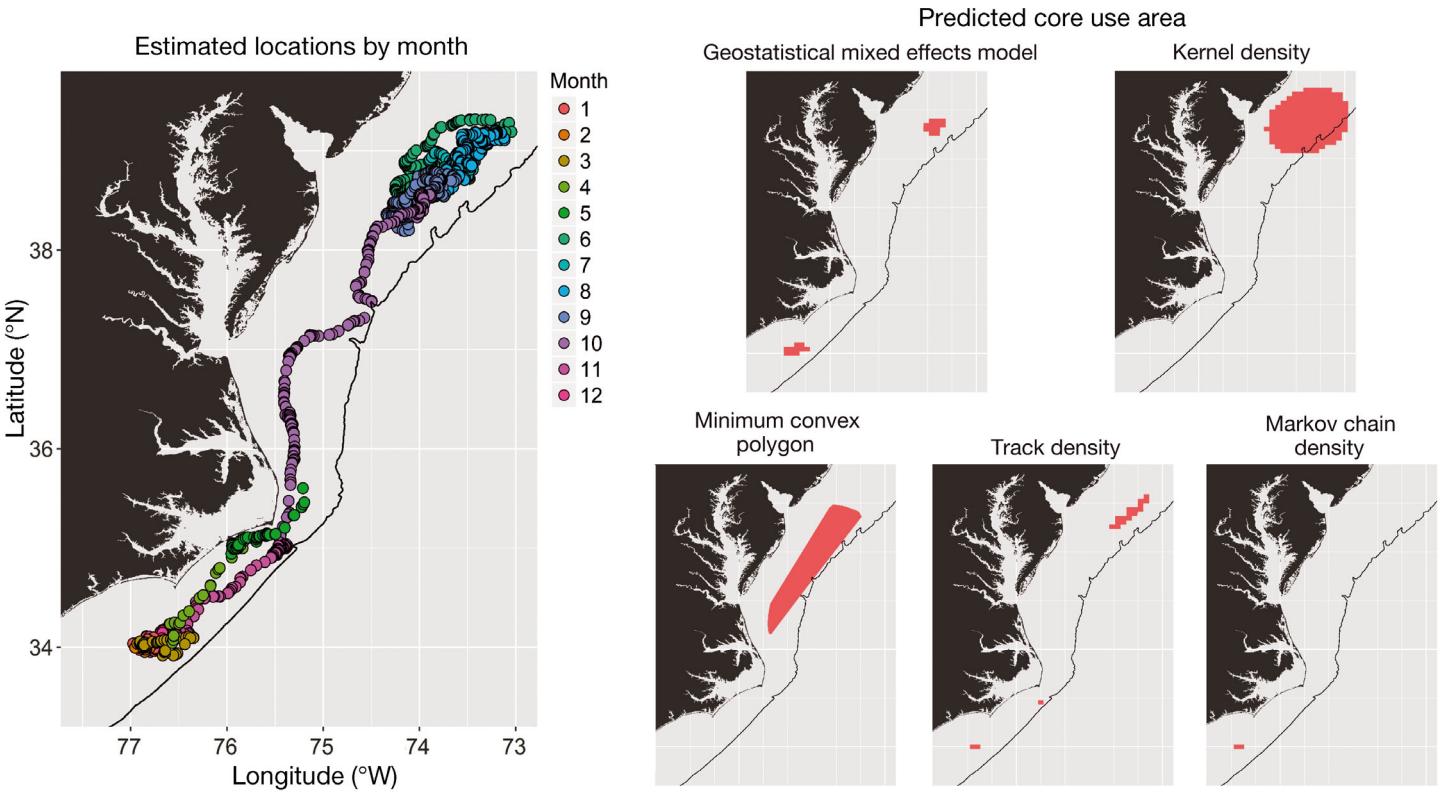

Fig. 4. Predicted 50% core use area from 5 space use estimators (right panels) applied to a 12 mo track of a 74 cm (straight carapace length) loggerhead sea turtle tagged in the mid-Atlantic in May of 2012 (left panel). The black line denotes the 200 m bathymetric contour.

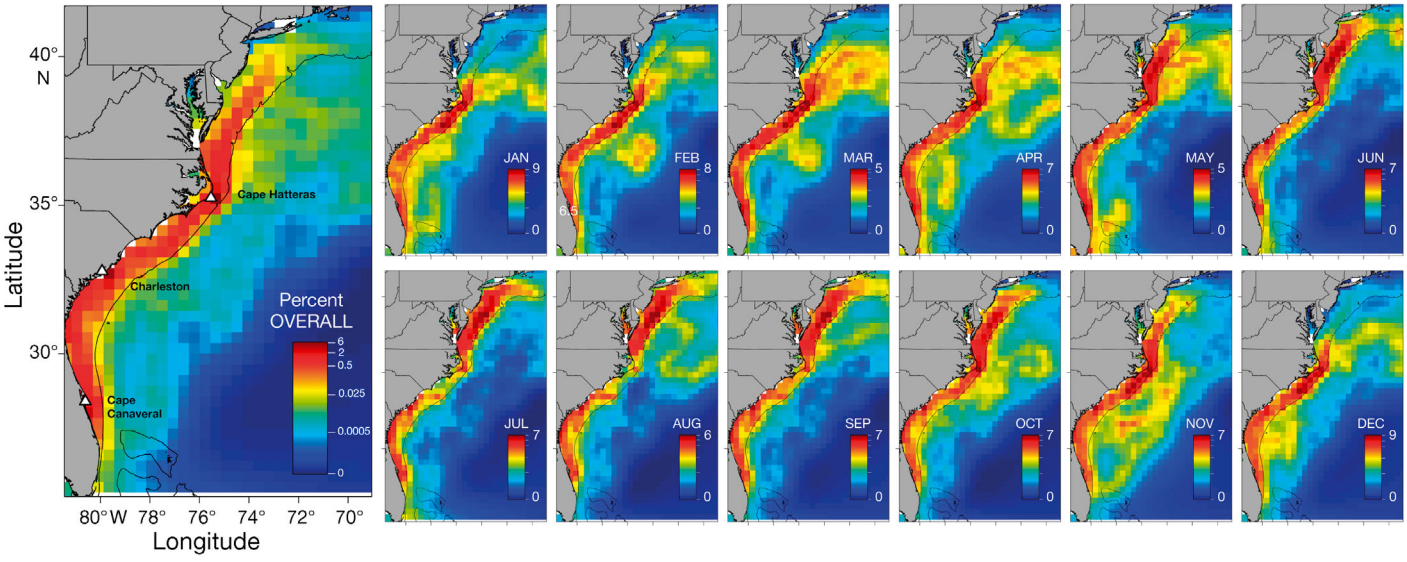

Fig. 5. Overall (left panel) and monthly (right panels) log density of tagged loggerhead sea turtles per 40 km resolution grid cell as predicted using a space-time geostatistical mixed effects model. Model predictions were based on daily locations of 271 large juvenile and adult loggerhead turtles tagged from 2004 to 2016. Predicted densities were scaled from 0 to 1 in each month for comparison purposes. The key indicates the proportion of the predicted density included in each grid cell. In each month, scale bars are consistent with the overall plot with the exception of the maximum value, which is indicated. The black line denotes the 200 m bathymetric contour. White triangles in the overall panel indicate the location of Cape Hatteras, North Carolina; Charleston, South Carolina; and Cape Canaveral, Florida

Monthly variation in the MAB was indicative of northward migration to known summer foraging grounds along the shelf in the MAB in the spring (March to May), with the reverse southward migration to overwintering areas in the fall (November to December). In the warmer spring and summer months (May to September), predicted densities of tagged turtles were highest in the shelf waters from Maryland to New Jersey. During cooler months (November to April), the highest densities in the MAB occurred on the shelf off of Cape Hatteras, North Carolina.

Predicted densities south of Cape Hatteras were not as seasonally variable and remained high in the shelf waters from Florida to North Carolina in all months (Fig. 5), which reflected the behavior of loggerheads tagged south of Cape Hatteras. Though a subset of individuals tagged in the SAB did migrate to foraging grounds in the MAB (Fig. 1), many remained in the general vicinity of their tagging location for the duration of tag transmission.

Table 2. Estimated parameters and standard errors from a space-time geostatistical mixed effects model fitted to daily locations for 271 loggerhead sea turtles satellite tagged in the western North Atlantic from 2004 to 2016. Note that ρ is empirically derived as described in 'Materials and methods'

Parameter	Estimate	Standard error
Intercept (β_0)	−8.13	0.98
Marginal spatial standard deviation (σ_Ω)	3.22	0.20
Marginal spatiotemporal standard deviation (σ_E)	3.49	0.26
Spatial correlation range (ρ)	403 km	27.9 km

DISCUSSION

The effectiveness of spatial conservation measures relies on an accurate description of a species' space use. Attempts to infer the relative intensity of space use from satellite telemetry data are often confounded by the inherently autocorrelated nature of the reported locations (Fleming et al. 2015) as well as the computational trade-offs associated with appropriately accounting for autocorrelation. In this study, we demonstrated that geostatistical mixed effects models can be used to account for bias associated with changes in the number of tag transmissions received over time (Whitehead & Jonsen 2013). Although our approach did not explicitly model serial correlation between reported locations, it can be used to account for both spatial and temporal correlation at a broader scale when analyzing large tracking datasets in a computationally efficient manner. Using geostatistical mixed effects models, we were able to predict the monthly distribution and relative density of tagged juvenile and adult loggerhead sea turtles in the western North Atlantic over the course of the year. By conditioning estimates on space and time, we estimated overall spatial variation in densities in a manner analogous to kernel density estimation, but in a predictive rather than ad hoc fashion (Diggle et al. 2013).

Our results suggest that tagged loggerheads inhabit the continental shelf along the US Atlantic from Florida to North Carolina year-round but also highlight the importance of summer foraging areas on the mid-Atlantic shelf. Previous satellite tagging studies have documented several different migration and foraging strategies among large juvenile and adult loggerheads in the US Atlantic (Mansfield et al. 2009, Arendt et al. 2012a–c, Griffin et al. 2013), which the monthly predicted distributions reflect. Some individuals remain in the SAB in thermally appropriate habitat year-round, or make smaller-scale migrations from nearshore summer habitat to warmer offshore waters bordering the Gulf Stream during the winter months (Hawkes et al. 2007, Arendt et al. 2012c, Ceriani et al. 2012, Griffin et al. 2013). Others travel between summer foraging areas in the MAB and overwintering grounds south of Cape Hatteras, North Carolina (Ceriani et al. 2012, Griffin et al. 2013). Areas where the shelf narrows, such as that with the highest overall predicted density of tagged loggerheads off Cape Hatteras, North Carolina, essentially 'funnel' loggerheads and other species during migrations between the MAB and SAB (Galuardi & Lutcavage 2012, Griffin et al. 2013, Kneebone et al. 2014).

Seasonal concentrations suggested by the monthly fields are also consistent with trends inferred from other data sources. Loggerhead bycatch rates remain relatively high south of 37° N year-round, but increase in the shelf waters from Virginia to New Jersey in the summer and fall as loggerheads migrate into and out of the MAB, with the highest aggregate encounter rates occurring off Cape Hatteras in the fall and winter (Warden 2011, Murray & Orphanides 2013). Shipboard and aerial survey sightings indicate loggerheads use habitats in the MAB from the summer into the fall but occur along the shelf from Florida to North Carolina throughout the year (TEWG 2009, Northeast Fisheries Science Center & Southeast Fisheries Science Center 2011). Surveys of

inshore waters have also recorded fluctuations in loggerhead sightings north of Cape Hatteras that correspond to seasonal migration patterns (Epperly et al. 1995).

While the seasonal occurrence of loggerheads in the MAB has been well-documented, the extent of the region's importance to the broader western North Atlantic population remains unclear. A preliminary analysis of aerial survey data collected in the summer of 2010 estimated that only 5% of the surveyed population occurred north of Cape Hatteras from June to September (Northeast Fisheries Science Center & Southeast Fisheries Science Center 2011). The analysis accounted for regional variation in surfacing behavior (based on percent surface time estimated from 34 of the tags analyzed here), but the authors recommended the collection of additional telemetry data given the limited sample size and the large estimated difference in median percent surface times between the SAB (7%) and MAB (57%); estimates of abundance derived from shipboard and aerial line transect surveys are extremely sensitive to percent surface time estimates (Buckland et al. 2015). Our results suggest that the MAB foraging grounds may support a larger proportion of the population, with over 50% of the predicted relative density of tagged loggerheads occurring north of Cape Hatteras from June to October.

Our estimate is likely driven, at least in part, by the selected weighting scheme. Given the absence of data definitively indicating regional differences in the overall abundance of loggerheads at the time of tagging, we chose to weight tracks from turtles tagged north and south of Cape Hatteras equally. Alternative weighting schemes could have resulted in either higher or lower regional density estimates. Weighting of different data sources has been much discussed in the fisheries stock assessment literature (Richards 1991, Francis 2011, Maunder & Punt 2013, Punt 2017), but there is little guidance available regarding weighting of telemetry datasets. The management implications of the selected weighting scheme certainly warrant further exploration, but were beyond the scope of the analysis conducted here.

It is important to stress that our results are only pertinent to the tagged population, and are therefore not necessarily reflective of relative abundance (Sippel et al. 2015). The number of tags deployed in each region was dictated by individual tagging programs, which predominantly targeted known loggerhead aggregation sites and migration corridors to maximize the efficiency of field operations (Fig. 1). While the spatiotemporal modeling approach we applied can be used to account for variation in the number of transmissions received from satellite tags over time, geostatistical approaches generally assume that the sampling process is independent of the continuous process underlying discrete observations (Diggle et al. 2010). For satellite telemetry data, this implies that animals 'sample' the overall area of interest and move between the resource-rich areas governing the continuous distribution of relative densities. Though multiple regions with suitable foraging or overwintering habitats may exist, individuals tagged in a particular location may exhibit fidelity to specific areas (Broderick et al. 2007). This could lead to oversampling of certain regions when tagging efforts are not distributed in proportion to abundance (Diggle et al. 2010).

Bias associated with the non-random nature of tag deployment was evident in the predicted distributions and highlights the need to consider existing knowledge of the spatial distribution of the population when designing tagging studies (Sippel et al. 2015). The discrete high use areas predicted off Charleston, South Carolina, and Cape Canaveral, Florida, were associated with tagging locations. Many of the loggerheads tagged in those regions appeared to be highly resident, remaining in the general vicinity of tagging for the duration of tag life (Arendt et al. 2012a–c). The majority of loggerheads tagged in the MAB were tagged in offshore shelf waters north of the Chesapeake Bay during their northward spring migration. Thus, loggerheads that occur in nearshore areas in the MAB may have been under-represented. Similarly, tags were not deployed evenly among regions and years, and so we were not able to examine inter-annual differences in the high density areas identified here, which likely vary over time (Kai et al. 2017). Despite the limitations of the available dataset, the predicted distribution represents a broad-scale synthesis of satellite tagging data available from in-water captures of loggerheads in the western North Atlantic, which is supported by trends inferred from other data sources as described above.

Here, our interest was the prediction of spatiotemporal variation in the density of tagged loggerheads, and so our application focused on the use of geostatistical mixed effects models as a model-based approach to spatial smoothing rather than on parameter estimation. However, models of this type have also been shown to produce less biased, more precise parameter estimates in other applications (Thorson et al. 2015), making them a potentially valuable tool for inferring relationships between environmental pro-

cesses and seasonal shifts in relative densities (Ono et al. 2016). In contrast to approaches used to indirectly infer associations between environmental drivers and conventional space-use estimators (Hooten et al. 2013), the model-based framework we used is well suited to directly link species distribution data with environmental variables (Thorson et al. 2015), which could be used as the basis for predicting the probability of loggerhead presence in areas not represented during tag deployment. Using a model-based approach confers the additional ability to quantify uncertainty in parameter estimates and the resulting predicted distributions, which may have important ramifications if model predictions are used as the basis for spatial management measures (Maxwell et al. 2011). While our goal here was to describe the overall spatial distribution of all loggerheads tagged by the 6 programs, inclusion of individual-specific information in such models would allow for the identification of variation in high density areas between sexes, maturity states, and size classes (Kai et al. 2017) to ensure that spatial conservation measures encompass areas important to multiple life stages. The models proposed are also compatible with the types of models applied to estimate relative densities from distance sampling data collected via shipboard or aerial line transect surveys, providing a logically consistent basis for integrating telemetry data into predictions of space use based on existing survey efforts (Royle et al. 2013).

It is important to consider how the choice of spatial and temporal scales of interest may influence interpretation when applying such models to satellite telemetry data (Johnson et al. 2013). While the modeling approach we used does not require gridding of location data (Lindgren et al. 2011), we used a gridded, predictive process approximation to reduce dimensionality and speed up computation (Banerjee et al. 2008). Previous work suggests that estimates based on a regular lattice of knots are generally robust, though the spacing of the selected grid limits the scale of spatial inference (Banerjee et al. 2008). We were interested in describing broad-scale changes in the intensity of space use and so chose a rather coarse discretization of space. In instances where fine-scale space use is of interest, grid spacing should be sufficiently small to provide information at the scale desired. Our selected grid cell size was much larger than the mean error estimated for all Argos location classes (see the Supplement for error estimates), and so we chose to filter locations prior to modeling densities to speed up computation. However, at small spatial scales this stepwise process may lead to bias. Future research should explore the inclusion of observation models to directly estimate location error within the models used here to address the potential for bias related to the choice of spatial scale.

Similarly, we chose to account for temporal variation by aggregating reported locations over a series of discrete monthly time steps rather than explicitly accounting for serial correlation in location estimates by modeling movement directly. Marine animals often undergo annual migrations to seasonal foraging or nursery grounds (Galuardi & Lutcavage 2012, Kneebone et al. 2014), meaning that autocorrelations in telemetry data tend to be cyclical and persist over long periods of time (Fleming et al. 2015). Thus, accounting for correlation at a broader temporal scale while also accounting for the latent spatial structure of the data may be sufficient when the goal is to describe large-scale space use. Though we chose to predict densities on a monthly time step requested by management groups, the time step selected could be decided upon in a less arbitrary manner based on inspection of autocorrelation functions or other diagnostics; future studies should investigate the implications of the selected time step on resulting estimates of space use. Alternatively, variation in time could be formulated in terms of behavior by incorporating a random effect for behavioral state (e.g. foraging or migrating), which could be informed via switching state-space (Jonsen et al. 2007) or hidden Markov models (Pedersen et al. 2011). However, when fine-scale habitat use is of interest, explicit modeling of both the movement and observation process (i.e. Argos geolocation error) would likely be required to more properly propagate uncertainty when inferring relationships with environmental drivers. Though computationally more intensive, our approach could be extended to model movement directly in a fashion similar to that applied by Johnson et al. (2013).

Our results represent a broad-scale synthesis of loggerhead satellite tagging data available from multiple research programs in the western North Atlantic. The predicted monthly distributions indicate that tagged loggerheads occur in the highest densities in shelf waters year-round, where the potential for overlap with human activities is high (Lewison et al. 2014). The high density areas identified here are based on over 10 yr of satellite tagging data, and represent the relative distribution of tagged loggerheads that may be expected on average in a given month. While this is certainly informative for developing spatial management strategies, a more mechanistic understanding of the spatiotemporal patterns de-

scribed here could be used to better predict where and when loggerheads would be expected to occur in response to changes in environmental conditions in a particular year. In addition to directly informing management actions, this information could also be used to optimize monitoring efforts (e.g. by informing the timing of aerial or shipboard surveys) and mitigate potential overlap between loggerheads and human activities.

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