

# Estimating the complex patterns of survey availability for loggerhead turtles

Joshua M. Hatch<sup>1</sup>  | Heather L. Haas<sup>1</sup> | Christopher R. Sasso<sup>2</sup> |  
 Samir H. Patel<sup>3</sup> | Ronald J. Smolowitz<sup>3</sup>

<sup>1</sup>NOAA National Marine Fisheries Service, NEFSC, Woods Hole, MA 02543, USA

<sup>2</sup>NOAA National Marine Fisheries Service, SEFSC, Miami, FL 33149, USA

<sup>3</sup>Coonamessett Farm Foundation, 277 Hatchville Road, East Falmouth, MA 02536, USA

## Correspondence

Joshua Hatch, NEFSC, NOAA Fisheries, 166 Water Street, Woods Hole, MA 02543, USA.  
 Email: [joshua.hatch@noaa.gov](mailto:joshua.hatch@noaa.gov)

## Funding information

Interagency Agreements M14PG00005, M10PG00075, and M19PG00007 with the United States Department of the Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center and the United States Department of the Interior, Bureau of Ocean Energy Management; Sea Scallop Research Set Aside Program administered by the Northeast Fisheries Science Center

## Abstract

Successful management strategies are important for conservation and allow accurate surveying and monitoring of populations for presence, abundance, and trend. This becomes challenging for cryptic, low-density species, and for animals that have complicated life histories where not every stage of the life cycle can be surveyed effectively. We used information from animal-borne data loggers to characterize the dive-surfacing behavior of cryptic loggerhead turtles (*Caretta caretta*) in the northwest Atlantic from 2009–2018. Our data covered a large geographic area off the east coast of North America, and allowed us to present estimates for and variation in 3 metrics that can be used to assess availability bias affecting visual surveys: average dive duration, average surface duration, and the proportion of time at the surface. We used a stochastic partial differential equation approach to construct spatiotemporal regression models for the availability bias metrics. Model predictions showed pronounced individual, spatial, and spatiotemporal (seasonal) variation among the 245 turtles. Overall, we estimated an average dive duration of  $14.5 \pm 1.36$  minutes (SE), an average surface duration of  $15.1 \pm 2.77$  minutes, and an average proportion of time at the surface of 0.50 (95% CI = 0.41–0.59). We made predictions of the 3 availability bias metrics on a 20-km  $\times$  20-km grid and further used predictions to explore seasonal variations. Our results contribute new insights into loggerhead turtle behavior

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society. This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

and provide information that enables survey counts to be translated into more accurate abundance estimates.

#### KEYWORDS

availability bias, behavior, *Caretta caretta*, loggerhead turtles, northwest Atlantic, spatiotemporal regression

When animals are cryptic or elusive, it dramatically complicates conservation efforts. The difficulty associated with studying cryptic species often leaves their underlying distribution, abundance, and behavior unknown. Animals that are difficult to see are vulnerable to unintentional harm from a variety of anthropogenic activities (Howell et al. 2008, Crum et al. 2019, National Oceanic and Atmospheric Administration [NOAA] 2020), and mitigation measures such as conservation engineering solutions or time area conservation measures can be complicated to implement with so much uncertainty associated with behavior and distribution (Shumway 1999). Effectively monitoring cryptic and elusive populations is difficult and resource intensive (McNew and Handel 2015), particularly when accurate abundance information is needed.

For cryptic and elusive wildlife, animal-borne data loggers (biologgers) are often used to augment field surveys to describe distribution and estimate abundance. Distance sampling (Buckland et al. 2001) and density surface modeling (Miller et al. 2013) are 2 of the most commonly used approaches for estimating animal density and abundance. These methods assume, by default, that animals will always be visible to the observers. If animals are not available to be seen (e.g., because they are submerged, underground, or otherwise out of the observer's field of view; Laake et al. 1997), then density and abundance will be underestimated. This problem of biased density and abundance estimates because of animal availability is known as availability bias. Data obtained from biologgers include valuable information on behavior, which can then be used to correct density and abundance estimates for availability bias. In a marine context, knowledge about the average dive and surface duration, or the proportion of time at the surface, can aid in developing these corrections (Laake et al. 1997, Barco et al. 2018, Sparks and DiMatteo 2020).

Patterns of availability and detectability are often oversimplified (i.e., assumed to be uniform across space and time) because of data limitations, but unaccounted for heterogeneity in availability or detection can cause additional bias in abundance estimates (Marsh and Sinclair 1989, Cubaynes et al. 2010, Innes et al. 2014, Fuentes et al. 2015, Merrick and Koprowski 2017). Variation in availability to visual observers has been reported for many taxa: snakes (Boback et al. 2020), ungulates (Samuel et al. 1987), dolphins (Sucunza et al. 2018), large whales (Jaquet et al. 2000, Hodgson et al. 2017), sirenians (Edwards et al. 2007, Pollock et al. 2009), and sea turtles and tortoises (Thomson et al. 2012, 2013; Couturier et al. 2013). Even estimating the abundance in a relatively small geographic area can be severely hampered by seasonal differences in the amount of time animals are available to be seen (Ganley et al. 2019).

Sea turtle dive-surfacing behavior, like marine mammals, can be regulated by their need to breathe and by their behavioral mode, life stage, and environmental factors (Mansfield et al. 2014, Patel et al. 2015); however, hard-shelled sea turtles are ectothermic and rely on external heat sources to maintain their internal body temperature (Pough 1980). To some extent, turtles can produce heat through metabolism (Sato et al. 1995) and retain some of it because of their large body mass (Paladino et al. 1990, Sato 2014) and blood-flow patterns (Hochscheid et al. 2002). But because of this need to thermoregulate, sea turtles may represent the complicated end of the spectrum for marine vertebrates when it comes to estimating availability to visual observers.

The complex nature of sea turtle dive-surfacing behavior can lead to results that are site-specific, ambiguous, and highly variable. For example, green turtles (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*) in Western Australia (Thomson et al. 2012) have availability correction factors that are highly heterogeneous, with larger corrections in colder, deeper waters. Other researchers have reported no significant correlation between sea temperature and time spent near the surface for a pooled dataset from green turtles at multiple locations (Fuentes et al. 2015). Similarly, a study that classified basking as extended surface times, exceeding 10 minutes, was unable

to describe any general temporal or spatial pattern because of the variability in individual turtle behavior (Hochscheid et al. 2010). These diverse, and sometimes contradictory, results highlight the need for behavioral data from the spatial and temporal areas of interest.

The United States Atlantic shelf region is home to potentially the world's largest population of loggerhead turtles, known as the Northwest Atlantic Distinct Population Segment, which is protected by the United States Endangered Species Act. Only 1 other management region (Northwest Indian Ocean) has comparable nesting numbers (Willson et al. 2020), and these 2 regions combined account for 90% of global loggerhead nesting (Witherington et al. 2009). Previous aerial surveys have estimated that between approximately 40,000 and 60,000 loggerheads seasonally inhabit the northwest Atlantic, particularly the Mid-Atlantic Bight, and between approximately 500,000 and 1,000,000 inhabit the South Atlantic Bight (Northeast Fisheries Science Center [NEFSC] and Southeast Fisheries Science Center [SEFSC] 2011). These may be underestimates, indicating the need for improved calculations of availability bias, because stable isotope analysis and satellite telemetry distribution data indicate that 30–50% of loggerheads that nest and reside along the United States eastern seaboard seasonally forage within the Mid-Atlantic Bight (Ceriani et al. 2017). The abundance of loggerheads in shelf waters of the United States coupled with protections mandated by the Endangered Species Act focuses attention on potential impacts of various marine anthropogenic activities (e.g., fishing, offshore wind energy development). For these reasons, federal agencies are interested in improved estimates of loggerhead distribution and abundance in this region.

We used data from animal-borne data loggers to characterize the dive-surfacing behavior of loggerhead turtles in the northwest Atlantic by calculating estimates for and variation in 3 metrics that can be used to assess availability bias: average dive duration, average surface duration, and the proportion of time at the surface. Because of the heterogeneity in dive-surfacing behavior observed in other sea turtle populations and our own observations of loggerheads, we expected that variability in the dive-surfacing behavior of loggerheads in the Northwest Atlantic population would be appreciable and at least partially described by spatial and temporal components.

## STUDY AREA

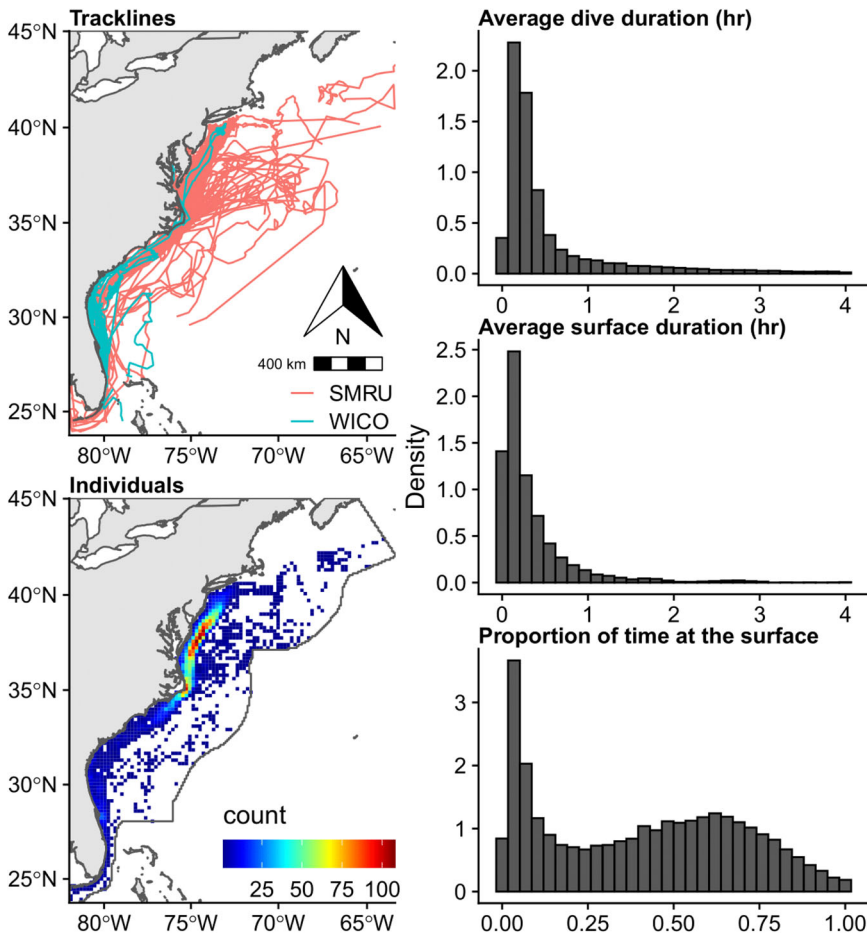
The study area ranged from Atlantic Canada to Florida, USA, and extended from the coastline to roughly 200 nautical miles (~370 km) from shore, covering 1,195,017 km<sup>2</sup> of neritic and oceanic environments (Figure 1). Loggerhead turtles undergo extensive seasonal migrations, with highest densities of tracks from tagged individuals typically occurring along the continental shelf (Winton et al. 2018). These more densely populated regions roughly correspond to the Northeast and Southeast Continental Shelf Large Marine Ecosystems (LMEs). Both LMEs are characterized by temperate climates and moderate to high productivity, and support a wide variety of commercial fisheries and protected species (Aquarone 2009, Aquarone and Adams 2009).

## METHODS

### Data

We tagged loggerhead turtles between 2009 and 2018 with Sea Mammal Research Unit (SMRU) and Wildlife Computer (WICO) satellite relay data loggers (SRDLs) under permits issued by the National Marine Fisheries Service following standard protocols detailed elsewhere (Patel et al. 2018). To avoid errant behavior by loggerhead turtles post-release, we excluded transmitted records occurring within the first 24 hours of tag deployment from analysis.

The SMRU SRDLs recorded average dive and surface duration and proportion of time at the surface. The tags calculated the average dive duration from all individual dive-cycle records that ended in a 4- or 6-hour interval, with only a sample of those summarized records being transmitted by the tag and successfully received by the satellite.



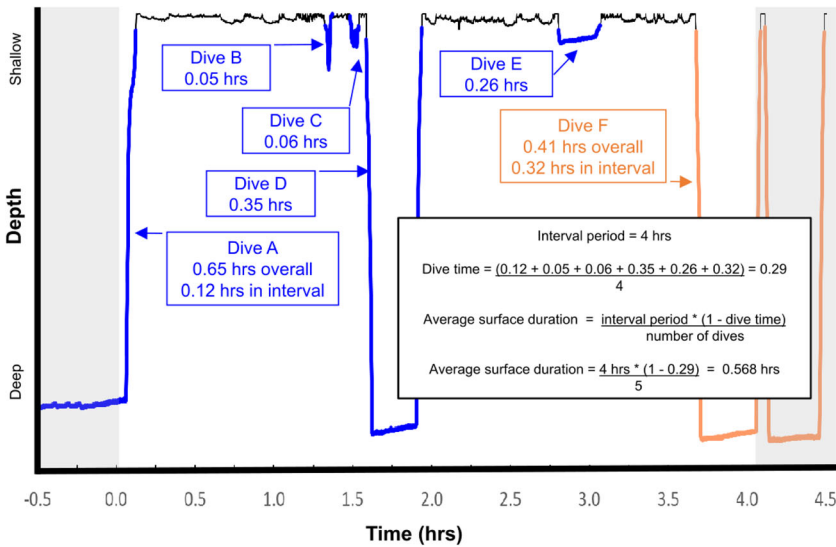
**FIGURE 1** Track lines of the 245 loggerhead turtles tagged with satellite relay data loggers (SMRU = Sea Mammal Research Unit, WICO = Wildlife Computers), 2009–2018, within the study area off the east coast of North America (black outline), number of satellite-tagged individuals summarized over the prediction grid with a cell size of 20 km × 20 km, and histograms of average dive (~3% of values were >4 and are not shown) or surface duration (~1% of values were >4 and are not shown) and proportion of time at the surface across individuals.

Individual dive cycles were programmed to start when the SMRU SRDLs were wet and >1.5 m deep for 20 seconds and end when dry or <1.5 m deep. We then calculated the average surface duration as the amount of time not spent in a dive divided by the number of dives that occurred within a 4- or 6-hour interval (Table 1; Figure 2). The WICO SRDLs recorded proportion of time at the surface, and other predetermined depth bins, over 4-hour intervals with a 24-hour on and 72-hour off transmission duty cycle. Although, data collection by the WICO tags occurred continuously. To align with the SMRU SRDL definition of a dive, we considered the proportion of time spent at depths  $\geq 2$  m as the dive time (Table 1). In summary, only the SMRU SRDLs recorded information on dive and surface duration, whereas both the SMRU and WICO SRDLs recorded information on the proportion of time spent at the surface.

We filtered the SRDL data to remove potentially erroneous records and to exclude intervals that occurred primarily at night (i.e., we kept records if  $\geq 75\%$  of the interval time occurred during the day). We used only daytime records because these coincided with aerial surveys. We then linked values for average duration and proportion of time at the surface to hourly interpolated locations from tracks reconstructed using continuous time correlated random walk movement models (Winton et al. 2018). To provide a single spatial coordinate per datum, we averaged the hourly interpolated locations that occurred within an interval. Prior to fitting the continuous time correlated random walk, we removed approximate

**TABLE 1** Description of pertinent variables recorded by the satellite relay data loggers (SRDLs). The transmitted column flags variables that were calculated by the tags and then transmitted via satellite (yes) or were calculated by hand after the fact (no). We deployed 245 SRDLs on loggerhead turtles off the east coast of North America, 2009–2018.

Variable	Description	Transmitted
Dive duration	Calculated by the tag as the amount of time between the start of a dive (when the depth remains >1.5 m for 20 seconds) and the end of a dive (when the tag is dry or the depth <1.5 m).	No
Average dive duration	Calculated by the tag as the average dive duration for dives that ended in the interval period, regardless of which interval period they began in.	Yes
Dive time	Calculated by the tag as the proportion of time spent in a dive during the interval period.	Yes
Number of dives	Calculated by the tag as the number of dives that ended in the interval period.	Yes
Average surface duration	Calculated <i>post hoc</i> as (interval period × (1 – dive time) / number of dives).	No
Proportion of time at the surface	Calculated by the tag as the proportion of time spent at the surface during the interval period.	Yes



**FIGURE 2** Example of how time and depth data were recorded by the satellite relay data loggers (SRDLs) and processed into dive and surface durations. The thin black line shows time depth data, which has been somewhat manipulated to better illustrate the types of dive and surface behavior that may occur within an interval period. The bright blue line shows dives that ended in this interval period. The orange line shows dives that ended in the next interval period. We deployed 245 SRDLs on loggerhead turtles between 2009 and 2018 off the east coast of North America.

locations if they duplicated a date-time stamp, had poor location quality, plotted on land, or were flagged as improbable using a speed filter (i.e., max. swimming speed of 5 km/hr). We did not interpolate hourly locations from reconstructed tracks over time gaps >3 days. We then re-projected all spatial coordinates into an oblique Mercator projection with a central line that roughly coincided with the long axis of the eastern United States.

For a single retrieved SMRU tag, we compared the summarized dive and surface durations to averaged time-depth-recording (TDR) values to verify the method used to calculate average surface duration was

**TABLE 2** Number of satellite relay data loggers deployed annually on loggerhead turtles in the South Atlantic Bight, Mid-Atlantic Bight, and Georges Bank by the Coonamessett Farm Foundation (CFF), Northeast Fisheries Science Center (NEFSC), and Southeast Fisheries Science Center (SEFSC) off the east coast of North America, 2009–2018.

Year	CFF	NEFSC	SEFSC	Total
2009	2			2
2010		14	30	44
2011	10	16		26
2012	15	15		30
2013	10	6	29	45
2014	13	5		18
2015	8	2		10
2016	5	16		21
2017	14	9		23
2018	10	16		26
Total	87	99	59	245

reasonable. Comparison between the summarized SRDL and averaged TDR values (Appendix A) suggested the 2 were reasonably similar (Figure A1).

We used a stochastic partial differential equation (SPDE) approach to construct the spatiotemporal regression models of average dive or surface duration and proportion of time at the surface (Appendix B; Lindgren et al. 2011). We chose the SPDE approach to provide smooth, spatially explicit maps of the 3 availability bias metrics (average dive, surface duration, and proportion of time at the surface) that can be used to broadly describe dive and surface behavior, and to develop correction factors for abundance estimates. In this way, we properly accounted for the individual, spatial, and temporal variability and autocorrelation inherent in georeferenced dive-surfacing behavior data generated by the animal-borne data loggers (NEFSC and SEFSC 2011). The number of SRDLs deployed in any given year was not sufficient to explore interannual trends (Table 2), so we pooled data across years to focus on differences among months. We conducted data wrangling (Pebesma 2018, Wickham et al. 2019, Hijmans 2020), analyses (Kristensen et al. 2016), and figures (Auguie and Antonov 2017, Nychka et al. 2017, South 2017, Wickham et al. 2019, Wilke 2019, Wickham and Seidel 2020) using the statistical software R (R Core Team 2019).

## Prediction surfaces

We placed predictions from the spatiotemporal regression models onto a 20-km × 20-km grid that spanned the study area from Atlantic Canada to Florida with the same oblique Mercator projection as the re-projected data. The prediction surfaces were calculated as

$$\frac{\text{Duration}}{\mathbb{E}(y)} = \mu_{k,l} \quad \frac{\text{Proportion}}{\mathbb{E}(y)} = \frac{\tau + \mu_{k,l}}{1 + \nu + \tau}$$

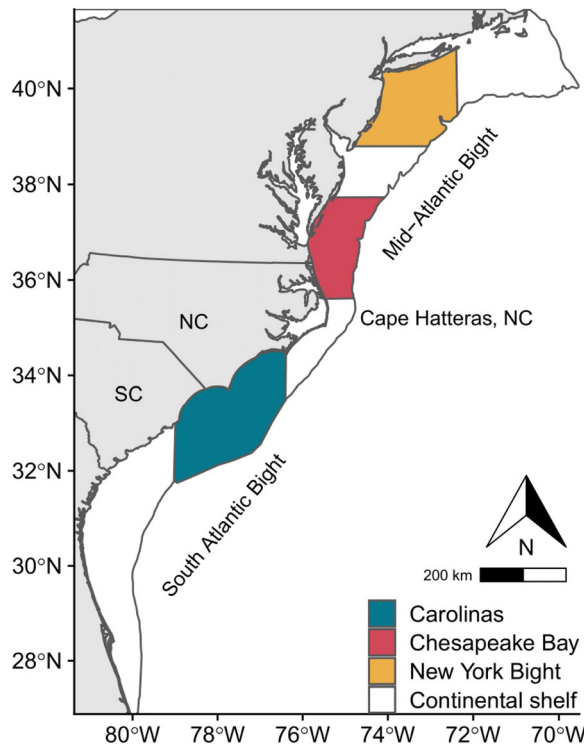
where  $\mathbb{E}(y)$  represents the expected value of the data for an average individual at a location ( $k$ ) and month ( $l$ ),  $\mu$  is the estimated mean, and  $\nu$  and  $\tau$  are estimated parameters that define the beta-inflated distribution (Appendix B).

We obtained the standard errors of the predicted values using the delta method (Kristensen et al. 2016). We then masked the prediction surfaces and removed grid cells from the prediction surfaces by buffering the averaged locations by the maximum estimated spatial decorrelation range, which represents the distance beyond which the observations are essentially uncorrelated. We masked the prediction surfaces to avoid interpolated values outside of the seasonal range boundaries for loggerhead turtles in the northwest Atlantic.

We further summarized prediction surfaces at 2 spatial scales to develop time series of monthly quantiles (i.e., 0.025, 0.50 [median], and 0.975) for the 3 availability bias metrics to describe seasonal patterns. We selected the spatial scales to summarize the continental shelf and 3 smaller areas along the United States Atlantic coast. The 3 smaller areas represent neritic regions off the coasts of the Carolinas, Chesapeake Bay, and the New York Bight (Figure 3). We focused on the continental shelf because this area had the most data and the most scientific and management interest. The majority of aerial survey effort occurs on the shelf, with the 3 smaller areas representing regions that are heavily managed for commercial fishing and ocean and wind energy development.

## RESULTS

We deployed SRDLs on 245 loggerhead turtles in the South-Atlantic Bight, Mid-Atlantic Bight, or Georges Bank between 2009 and 2018 in partnership with the Coonamessett Farm Foundation, Northeast Fisheries Science Center, and Southeast Fisheries Science Center (Table 2; Figures S1–S2, available in Supporting



**FIGURE 3** Regions used to summarize predictions of the 3 availability bias metrics (average dive duration, average surface duration, and proportion of time at the surface) using quantiles. We generated predictions from spatiotemporal regression models using data from up to 245 satellite-tagged loggerhead turtles collected between 2009 and 2018 off the east coast of North America.

Information). Loggerhead turtle sizes (standard carapace lengths) ranged between 51 cm and 100 cm ( $\bar{x} = 72 \pm 9$  cm [SD]).

All 3 spatiotemporal regression models successfully converged, with positive definite Hessian matrices and maximum gradient components  $<0.001$ . Residual diagnostic plots also indicated that the spatiotemporal regression models fitted the data reasonably well. The ability of our developed spatiotemporal regression models to characterize observed behavior of tagged loggerhead turtles was supported by high Spearman rank correlation coefficients, which ranged from 0.59 to 0.74, between the observed and fitted values for the 3 models.

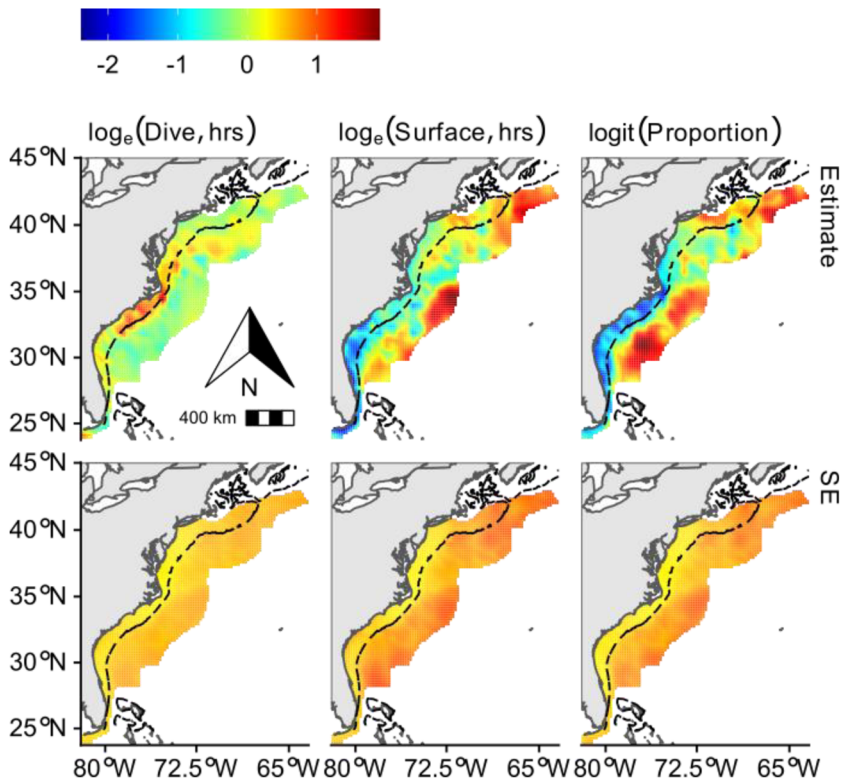
All 3 availability bias metrics displayed considerable individual, spatial, and spatiotemporal variation in predictions of dive-surfacing behavior for loggerhead turtles inhabiting the northwest Atlantic. The large values for the marginal spatial standard deviations demonstrated pronounced spatial variation for all 3 of the availability bias metrics (Table 3; Figure 4). Spatiotemporal variation was also evident (Table 3), indicating seasonal variation in the spatial distributions (Figures S3–S8, available in Supporting Information). Behavioral differences were apparent between periods of overwintering and summer foraging (Figure 5).

## Average dive duration

The majority of summarized dive durations (70%) were  $<30$  minutes long, with a maximum of 13.5 hours (Figure 1). Overall, the average dive duration was estimated to be approximately 14.5 minutes  $\pm$  1.36 minutes (SE; Table 3), with noticeable individual differences in dive time with estimates that ranged between 6.53 and 31.07 minutes.

**TABLE 3** Parameter estimates from spatiotemporal regression models fitted to behavior data obtained from up to 245 satellite relay data loggers deployed on loggerhead turtles between 2009 and 2018 off the east coast of North America.

Parameter	Observed	Estimate	SE
Average dive duration (hr)			
Intercept ( $\beta_0$ )—overall average		0.2422	0.0226
Spatial decorrelation range		117 km	10 km
Marginal spatial standard deviation		0.6310	0.0650
Marginal spatiotemporal standard deviation		0.9665	0.0394
Average surface duration (hr)			
Intercept ( $\beta_0$ )—overall average		0.2524	0.0461
Spatial decorrelation range		190 km	17 km
Marginal spatial standard deviation		1.0960	0.0875
Marginal spatiotemporal standard deviation		0.7877	0.0451
Proportion of time at the surface			
Probability of 0 ( $p_0$ )	0.0033	0.0033	0.0002
Probability of 1 ( $p_1$ )	0.0020	0.0020	0.0002
Probability of (0, 1) ( $p_2$ )	0.9948	0.9948	0.0003
Spatial decorrelation range		206 km	18 km
Marginal spatial standard deviation		1.0417	0.0793
Marginal spatiotemporal standard deviation		0.7245	0.0407



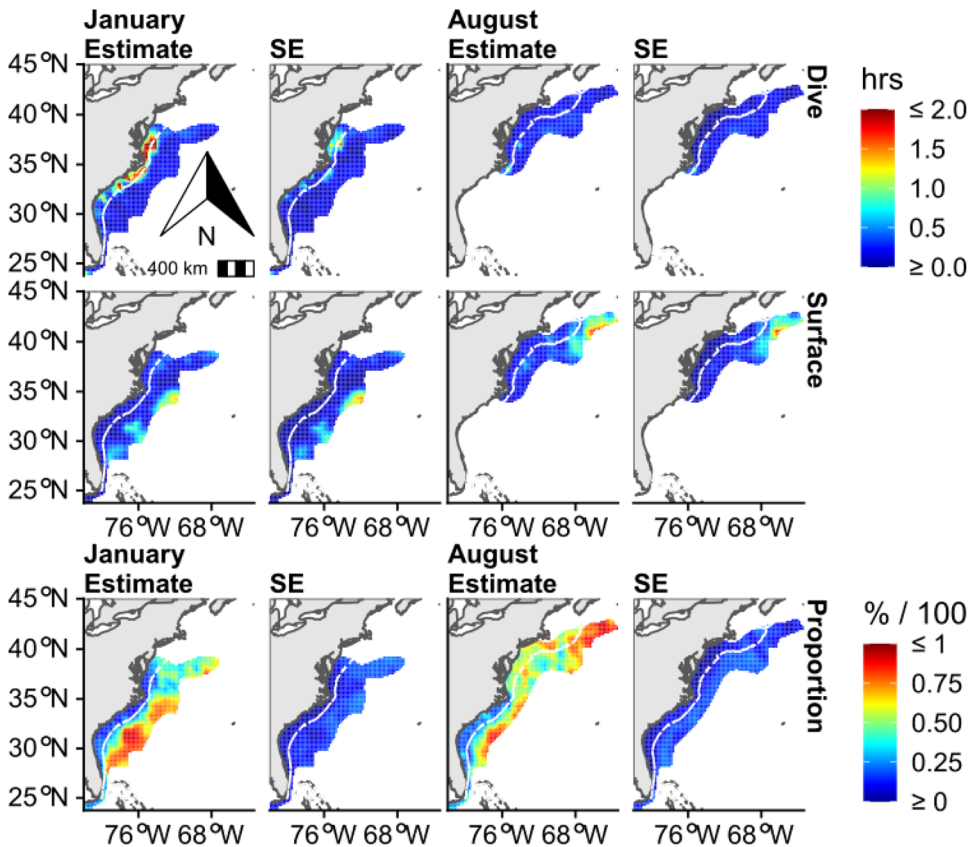
**FIGURE 4** Estimates of the spatial random effects and standard errors on the  $\log_e$  scale for the spatiotemporal regression models of average dive or surface duration and the logit scale for the spatiotemporal regression model of proportion of time at the surface using data from up to 245 satellite-tagged loggerhead turtles collected off the east coast of North America, 2009–2018. The black, dashed line denotes the 200-m isobath.

Spatially, the predicted average dive durations were higher inshore, compared to offshore areas defined by bottom depths >200 m (Figure 4); although, this pattern was less apparent north of Cape Hatteras, North Carolina. The longest dives appeared to be concentrated along the continental shelf near the coasts of North and South Carolina (Figures 3 and 4). Additionally, longer dives were predicted farther south in January, relative to the shorter dives in August along the Mid-Atlantic Bight (Figure 5). We also estimated significantly greater spatiotemporal than spatial variation for the estimated average dive durations, with a relative increase in the marginal standard deviations of roughly 1.5 times (Table 3).

Seasonally, along the continental shelf, the average dive duration was highest during October–May, relative to the warmer summer months of June–September (Figure 6). More variability in average dive duration occurred from October–May, with sharp declines in this pattern during summer (Figure 6). The longest dives occurred farther south in the Carolinas and Chesapeake Bay regions, following a similar seasonal pattern as demonstrated across the entire continental shelf (Figure 6). In the New York Bight area, average dive duration was relatively more stable with consistently shorter dives throughout the year, again with slightly longer dives from October–May (Figure 6).

### Average surface duration

The majority of summarized surface durations (79%) were <30 minutes long, with a maximum of 6 hours (Figure 1). Overall, the average surface duration was estimated to be approximately  $15.1 \pm 2.77$  minutes (SE);

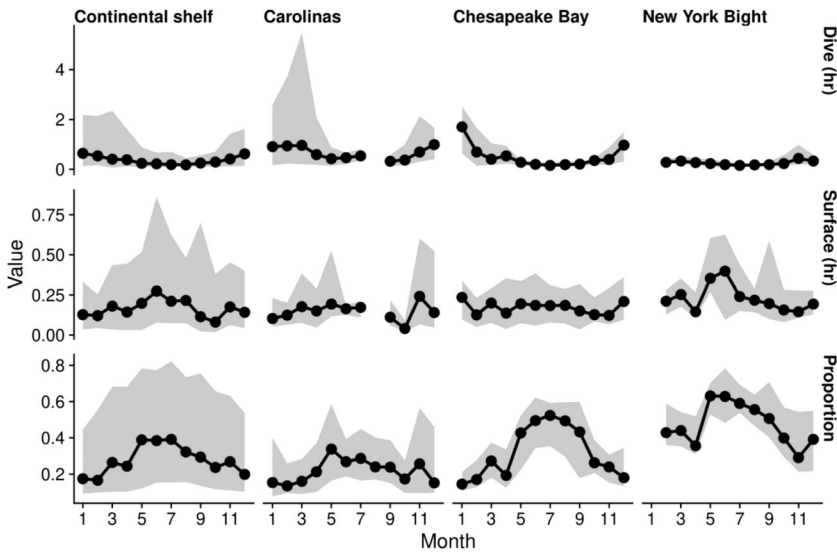


**FIGURE 5** Predictions and standard errors for the average dive duration, average surface duration, and average proportion of time at the surface from the spatiotemporal regression models using data from up to 245 satellite-tagged loggerhead turtles off the east coast of North America, January and August, 2009–2018. The white, dashed line denotes the 200-m isobath. The color scale for predictions of average dive duration, with roughly 2% of values being >2 hours.

Table 3), with noticeable individual differences in surface time with estimates that ranged between 4.65–65.85 minutes.

Spatially, the predicted average surface durations were higher offshore, compared to inshore areas defined by bottom depths <200 m (Figure 4). Although, this pattern was less apparent north of Cape Hatteras. At least for shelf waters, there was a strong latitudinal gradient in the predicted average surface durations (Figure 4). We also estimated significantly greater spatial than spatiotemporal variation for the predictions, with a relative increase in the marginal standard deviations of roughly 1.4 times (Table 3). In contrast to the average dive duration, there was less of an apparent trend in the predictions between January and August (beyond the inshore-offshore differences already mentioned; Figure 5).

Seasonally, along the continental shelf, the average surface duration was highest during the warmer late spring and summer months of May–September, relative to the months of October–April (Figure 6). Although, this seasonal pattern was less pronounced than that of the average dive duration given the more consistent variability across months (Figures S5–S6). Even with the more muted seasonal pattern, the latitudinal gradient across regions was still apparent. Generally, the longest surfacings occurred farther north in the New York Bight region, with shorter surface durations near the Chesapeake Bay and shelf waters off the Carolinas (Figure 6).



**FIGURE 6** Quantiles (i.e., black dots = 0.5 quantile [median], with the shaded areas representing the 0.025 and 0.975 quantiles) for predictions of average dive duration, average surface duration, and average proportion of time at the surface from the spatiotemporal regression models using data from up to 245 satellite-tagged loggerhead turtles on the Continental Shelf, New York Bight, Chesapeake Bay, and the Carolinas regions off the east coast of North America. We omitted quantiles if we did not have data for  $\geq 75\%$  of the cells in a region and month.

### Proportion of time at the surface

The average proportion of time at the surface was estimated to be approximately 0.50 (95% CI = 0.41–0.59), with noticeable individual differences in dive-surfacing behavior with estimates that ranged between 0.25 and 0.68. Roughly 58% of the observed proportions of time at the surface were  $\leq 0.50$ , with a maximum value of 1.0 indicating that a turtle was at the surface 100% of the time over an interval period (Figure 1).

Spatially, the predicted proportions of time at the surface were higher offshore, compared to inshore areas defined by bottom depths  $< 200$  m (Figure 4); although, this pattern was less apparent north of Cape Hatteras. We also estimated significantly greater spatial than spatiotemporal variation for the predictions, with a relative increase in the marginal standard deviations of roughly 1.4 times (Table 3).

In January, for shelf waters, turtles spent less time at the surface compared to August, which was especially pronounced for parts of the mid-Atlantic (Figure 5). There was also a more uneven spatial distribution for areas north of Cape Hatteras in August, possibly a reflection of low sample size in the far northeast fringes of the range (Figure 5).

Seasonally, along the continental shelf, the proportion of time at the surface was highest during the warmer late spring and summer months of May–September, relative to the months of October–April (Figure 6). There was also more consistency in variation across months, similar to the average surface duration (Figures S7–S8). The seasonal pattern demonstrated across the entire continental shelf (Figure 6) was also reflected in the Carolinas, Chesapeake Bay, and New York Bight regions to varying degrees (Figure 6). The farther north the region, the more distinct the dive-surfacing behavior was for the summer months relative to the rest of the year, along with more time spent at the surface overall (Figure 6).

## DISCUSSION

In some times and areas, the diving and surfacing behavior of loggerhead turtles can make it difficult to detect their presence. During winter in coastal regions near the Chesapeake Bay and in the shelf waters off North and South Carolina, the median predicted value for the duration of a loggerhead turtle's dive was close to or exceeded 1 hour (Figure 6). Short surface durations and small proportions of time at the surface were estimated to occur in the South Atlantic Bight during winter (Figure 5). Similar to other reptiles, the cryptic behavior of loggerhead turtles means that it may not be appropriate to infer species absence from an absence of sightings (Kéry 2002, Hartel et al. 2008). This behavior can leave loggerhead turtles vulnerable to risks associated with marine use and development such as vessel strikes (Foley et al. 2019), underwater explosions (Keevin and Hempten 1997), and dredging (Ramirez et al. 2017) because they are not readily observed at the surface.

A subset of the dives, particularly in winter, were unusually long and are consistent with brumation. This pattern of longer dives in winter is compatible with previous studies (Hochscheid et al. 2005, Arendt et al. 2012) and with the concept of unique overwintering behavior (Braun McNeill et al. 2020). Our maximum observed average dive duration of 13.5 hours, and 108 other average dives ( $\leq 1\%$  of total average dives), exceeded the previously reported longest dive (i.e., 8 hr; Hochscheid et al. 2007). We caution, however, that the data examined here have been summarized and relayed via satellite; therefore, there is more uncertainty in this dataset compared to higher resolution data from archival time-depth recorders. These very long dives complicate traditional surveys and mitigation methods that rely on observing turtles at the surface.

The satellite-tagged loggerhead turtles spent a significant amount of time at-depth and out of view of visual observers. Loggerhead turtles spent roughly 51% of an average dive-surfacing cycle at the surface, with the estimated average dive and surface durations being approximately equal (Table 3). This was further corroborated by an estimate of 50% time being spent at the surface for an average individual, as described by the zero-one inflated beta regression (Table 3). Both results align well with similar values reported for availability of telemetered loggerhead turtles near the Chesapeake Bay (Barco et al. 2018). Barco et al. (2018) reported that telemetered turtles in the deep, ocean stratum (the stratum that most closely matched our study) during the spring and summer months spent roughly 54% and 61% of their time at the surface, respectively. Loggerhead turtles in that study also exhibited a strong seasonal signal in surface time. This conclusion was echoed in our results, with strong inshore-offshore and seasonal gradients in dive-surfacing behavior.

Visual availability is important for translating surface abundance into total water-column abundance and for propagating uncertainty in dive-surfacing behavior. In fitting the average dive and surface duration models, we did not consider the within-interval variability that is averaged out in the summary statistics transmitted by the SRDLs. We used those summary statistics to fit the models, which then provided predictions over the gridded study area (Figure 5). Uncertainty in the predictions of average dive and surface duration, then, will likely be underestimated to some degree, but by how much is currently unknown. An avenue for further research lies in propagating the within-interval variation through to the predictions and exploring individual dive profiles as opposed to the binned data analyzed here.

Line-transect surveys often explicitly address biases associated with variation in detectability (such as through mark-resight approaches using double observers), but variation in availability has the potential to affect abundance estimates to an even larger degree. For example, preliminary estimates of total loggerhead turtle abundance in the northwest Atlantic differed by about an order of magnitude (NEFSC and SEFSC 2011) when availability was explicitly considered. This difference was largely attributed to the developed correction factors for availability bias that varied substantially between spatial strata used in the survey design (NEFSC and SEFSC 2011). The spatial strata may have been too coarse to resolve representative correction factors for availability, especially given the identified gradients in behavior among the telemetered turtles from this study. A key conclusion of the NEFSC and SEFSC (2011) study was that further analysis was required to resolve the most appropriate correction factors and their uncertainty, along with the collection of additional data to better characterize dive-surfacing behavior over the northwest Atlantic.

Heterogeneity in availability is not uncommon for marine animals, and has been noted for mammals (Marsh and Sinclair 1989, Pollock et al. 2009), sharks (Nykänen et al. 2018), and particularly sea turtles (Thomson et al. 2012, 2013, Barco et al. 2018). Prior researchers reported differences in surface time for sea turtles based on demographics (Cardona et al. 2005), environmental gradients (Thomson et al. 2013, Barco et al. 2018), and space and time (Barco et al. 2018). This suggests applying uniform correction factors for availability may lead to biased estimates of abundance, with the degree of bias being study-dependent. For sea turtles that spend a variable amount of time underwater, this makes refining availability bias correction factors to appropriate spatiotemporal scales very important (Barco et al. 2018).

The apparent heterogeneity and patchiness in availability of loggerhead turtles (Figures 4 and 5) may be partially related to the lack of data in certain times and areas (Figure 1). Fewer satellite-tagged loggerhead turtles ventured off the continental shelf during the study period, resulting in varying sample sizes for the number of tagged individuals present across the region in any given month (Figure 1, S2). The inclusion of individual, spatial, and spatiotemporal random effects can help alleviate some of these concerns, as the modeled interdependence in the data can inform areas with data gaps or deficiencies. In areas with data from only a few tagged individuals, the possibility remains that the behavior of those individuals strongly influenced the prediction surfaces. Prediction uncertainties, to some extent, will reflect this low sample size through higher standard error estimates but will be unable to clarify to what extent the behavior from a few tagged individuals is representative of the larger population.

The underlying behavior of cryptic and elusive animals is important for conservation beyond effective monitoring programs supported by surveys. An understanding of where and when protected species are likely to occur can assist with efforts to reduce interactions with fisheries (Howell et al. 2008), prevent fatal collisions with transiting vessels (Crum et al. 2019), and mitigate impacts of military readiness activities (NOAA 2020). Beyond these examples, several emerging issues (e.g., climate change, aquaculture, power generation) in the marine environment will also require a better understanding of habitat use and behavior to accurately characterize and potentially quantify mortality and morbidity risk imposed on marine wildlife (Bolten et al. 2019).

Animal-borne data loggers allow for data collection of dive-surfacing behavior over extended periods of time and over important environmental gradients and habitats that are essential for delineating availability of animals to survey platforms. Future researchers can add value by investigating the mechanistic process underlying the patterns we observed here. Knowing more about the mechanistic processes may provide insights into future patterns with expected changes in climate (Santidrián Tomillo and Spotila 2020) and energy development scenarios (Bailey et al. 2014, which urged mechanistic studies linked to wind development). Like other air-breathing marine animals, patterns of sea turtle availability to visual observers may be related to a variety of predictive or explanatory variables including those related to migration, forage, and abiotic factors that affect sea turtle physiology (Crawford et al. 2020).

## MANAGEMENT IMPLICATIONS

Accounting for potential biases in aerial and shipboard line-transect surveys is important for the creation of accurate and precise abundance estimates used to evaluate population recovery of threatened and endangered marine species. A notable potential bias is availability, and when availability to visual surveys is heterogeneous in time and space, applying uniform correction factors may lead to biased estimates of abundance. Our current analysis represents an improvement to practices in surface density modeling where uniform correction factors are applied over broadly defined strata or where estimates of availability from external studies are applied to new regions. If the variability we observed in loggerhead turtle behavior is indicative of variability in the behavior of other species, caution should be exercised when considering the use of highly aggregated or unrepresentative data to estimate availability in other marine or terrestrial animals. We recommend that our estimated availability bias metrics for loggerhead turtles be integrated with

line-transect survey data to improve population estimates that can support decisions on threat assessments, research priorities, and recovery actions to ensure persistence of this important northwest Atlantic sub-population. Further research comparing modeling approaches that estimate availability of loggerhead turtles to visual survey platforms would also be beneficial, and may help to explore the heterogeneity and patchiness found in the prediction surfaces of the availability metrics and the potential implications of that patchy variability on resulting density models. We also recommend collecting additional data on loggerhead turtle behavior using animal-borne data loggers to help resolve availability in times and areas where data were sparse, particularly in offshore waters deeper than 200 m and east of 72°W.

## ACKNOWLEDGMENTS

We thank J. Gutowski and the captains, crew, and scientists on the F/V Kathy Ann and F/V Ms Manya for their expert field work. We have had numerous contributions from varying scientists and appreciate their efforts, in particular the contributions from E. Matzen, L. Crowe, L. Siemann, M. Weeks, and M. Winton. We thank D. Palka for helpful comments on an earlier version of the manuscript. This study was funded in part by the scallop industry Sea Scallop Research Set Aside program administered by the Northeast Fisheries Science Center and the United States Department of the Interior, Bureau of Ocean Energy Management through Interagency Agreements M14PG00005, M10PG00075, and M19PG00007 with the United States Department of the Commerce, National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS), Northeast Fisheries Science Center (NEFSC).

## CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

## ETHICS STATEMENT

All work was conducted under Endangered Species Act permits issued to the Northeast Fisheries Science Center, the Southeast Fisheries Science Center, or the Coonamessett Farm Foundation (1551, 1576, 14249, 16556, 18526).

## DATA AVAILABILITY STATEMENT

The derived data products are available on a GitHub repository at [https://github.com/NEFSC/READ-PSB-TE-Hatch\\_et\\_al\\_2022\\_jwildlmanage](https://github.com/NEFSC/READ-PSB-TE-Hatch_et_al_2022_jwildlmanage).

## ORCID

Joshua M. Hatch  <http://orcid.org/0000-0002-1857-530X>

## REFERENCES

- Aquarone, M. C. 2009. XV-51 Southeast US continental Shelf: LME# 6. The UNEP large marine ecosystem report: a perspective on changing conditions in LMEs of the world's regional seas. UNEP Regional Seas Report and Studies 182: 689–698.
- Aquarone, M. C., and S. Adams. 2009. XIX-61 Northeast US Continental Shelf: LME# 7. The UNEP large marine ecosystems report: a perspective on changing conditions in LMEs of the world's regional seas. UNEP Regional Seas Report and Studies Number 182. United Nations Environment Programme, Nairobi, Kenya.
- Arendt, M. D., A. L. Segars, J. I. Byrd, J. Boynton, J. D. Whitaker, L. Parker, D. W. Owens, G. Blanvillain, J. M. Quattro, and M. A. Roberts. 2012. Distributional patterns of adult male loggerhead sea turtles (*Caretta caretta*) in the vicinity of Cape Canaveral, Florida, USA during and after a major annual breeding aggregation. *Marine Biology* 159:101–112.
- Auguie, B., and A. Antonov. 2017. gridExtra: miscellaneous functions for “grid” graphics. R package version 2.3. <https://CRAN.R-project.org/package=gridExtra>

- Banerjee, S., A. E. Gelfand, A. O. Finley, and H. Sang. 2008. Gaussian predictive process models for large spatial datasets. *Journal of the Royal Statistical Society B* 70:825–848.
- Bailey, H., K. L. Brookes, and P. M. Thompson. 2014. Assessing environmental impacts of offshore wind farms: lessons learned and recommendations for the future. *Aquatic Biosystems* 10:1–13.
- Barco, S. G., M. L. Burt, R. A. DiGiovanni, Jr., W. M. Swingle, and A. S. Williard. 2018. Loggerhead turtle *Caretta caretta* density and abundance in Chesapeake Bay and the temperate ocean waters of the southern portion of the Mid-Atlantic Bight. *Endangered Species Research* 37:269–287.
- Boback, S. M., M. G. Nafus, A. A. Yackel Adams, and R. N. Reed. 2020. Use of visual surveys and radiotelemetry reveals sources of detection bias for a cryptic snake at low densities. *Ecosphere* 11:e03000.
- Bolten, A. B., L. B. Crowder, M. G. Dodd, A. M. Lauritsen, J. A. Musick, B. A. Schroeder, and B. E. Witherington. 2019. Recovery Plan for the Northwest Atlantic Population of the loggerhead sea turtle (*Caretta caretta*) second revision (2008), assessment of progress toward recovery. National Marine Fisheries Service and United States Fish and Wildlife Service, Washington, D.C., USA.
- Braun McNeill, J., L. Avens, A. Goodman Hall, I. Fujisaki, and A. R. Iverson. 2020. Foraging and overwintering behavior of loggerhead sea turtles (*Caretta caretta*) in the western North Atlantic. *Marine Ecology Progress Series* 641: 209–225.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating the abundance of biological populations. Oxford University Press, Oxford, United Kingdom.
- Cardona L., M. Revelles, C. Carreras, M. San Félix, and A. Aguilar. 2005. Western Mediterranean immature loggerhead turtles: habitat use in spring and summer assessed through satellite tracking and aerial surveys. *Marine Biology* 147: 583–591.
- Ceriani, S. A., J. F. Weishampel, L. M. Ehrhart, K. L. Mansfield, and M. B. Wunder. 2017. Foraging and recruitment hotspot dynamics for the largest Atlantic loggerhead turtle rookery. *Scientific Reports* 7:1–3.
- Couturier, T., M. Cheylan, A. Bertolero, G. Astruc, and A. Besnard. 2013. Estimating abundance and population trends when detection is low and highly variable: a comparison of three methods for the Hermann's tortoise. *Journal of Wildlife Management* 77:454–62.
- Crawford, J. A., M. J. Dreslik, S. J. Baker, C. A. Phillips, and W. E. Peterman. 2020. Factors affecting the detection of an imperiled and cryptic species. *Diversity* 12:177.
- Crum, N., T. Gowan, A. Krzysan, and J. Martin. 2019. Quantifying risk of whale–vessel collisions across space, time, and management policies. *Ecosphere* 10:e02713.
- Cubaynes, S., R. Pradel, R. Choquet, C. Duchamp, J. M. Gaillard, J. D. Lebreton, E. Marboutin, C. Miquel, A. M. Reboulet, C. Poillot, et al. 2010. Importance of accounting for detection heterogeneity when estimating abundance: the case of French wolves. *Conservation Biology* 24:621–626.
- Douma, J. C., and J. T. Weedon. 2019. Analysing continuous proportions in ecology and evolution: a practical introduction to beta and Dirichlet regression. *Methods in Ecology and Evolution* 10:1412–1430.
- Edwards, H. H., K. H. Pollock, B. B. Ackerman, J. E. Reynolds, III, and J. A. Powell. 2007. Estimation of detection probability in manatee aerial surveys at a winter aggregation site. *Journal of Wildlife Management* 71:2052–2060.
- Foley, A. M., B. A. Stacy, R. F. Hardy, C. P. Shea, K. E. Minch, and B. A. Schroeder. 2019. Characterizing watercraft-related mortality of sea turtles in Florida. *Journal of Wildlife Management* 83:1057–1072.
- Fuentes, M. M. P. B., I. Bell, R. Hagihara, M. Hamann, J. Hazel, A. Huth, J. A. Seminoff, S. Sobtzick, and H. Marsh. 2015. Improving in-water estimates of marine turtle abundance by adjusting aerial survey counts for perception and availability biases. *Journal of Experimental Marine Biology and Ecology* 471:77–83.
- Ganley, L. C., S. Brault, and C. A. Mayo. 2019. What we see is not what there is: estimating North Atlantic right whale *Eubalaena glacialis* local abundance. *Endangered Species Research* 38:101–113.
- Hartel, T., K. Öllerer, L. Farczády, C. I. Moga, and R. Băncilă. 2008. Using species detectability to infer distribution, habitat use and absence of a cryptic species: the smooth snake (*Coronella austriaca*) in Saxon Transylvania. *Acta Scientiarum Transylvanica* 16:101–116.
- Hefley, T. J., K. M. Broms, B. M. Brost, F. E. Buderman, S. L. Kay, H. R. Scharf, J. R. Tipton, P. J. Williams, and M. B. Hooten. 2017. The basis function approach for modeling autocorrelation in ecological data. *Ecology* 98:632–646.
- Hijmans, R. J. 2020. raster: geographic data analysis and modeling. R package version 3.0-12. <https://CRAN.R-project.org/package=raster>
- Hochscheid, S., F. Bentivegna, M. N. Bradai, and G. C. Hays. 2007. Overwintering behaviour in sea turtles: dormancy is optional. *Marine Ecology Progress Series* 340:287–298.
- Hochscheid, S., F. Bentivegna, A. Hamza, and G. C. Hays. 2010. When surfacers do not dive: multiple significance of extended surface times in marine turtles. *Journal of Experimental Biology* 213:1328–1337.

- Hochscheid, S., F. Bentivegna, and G. C. Hays. 2005. First records of dive durations for a hibernating sea turtle. *Biology Letters* 1:82–86.
- Hochscheid, S., F. Bentivegna, and J. R. Speakman. 2002. Regional blood flow in sea turtles: implications for heat exchange in an aquatic ectotherm. *Physiological and Biochemical Zoology* 75:66–76.
- Hodgson, A., D. Peel, and N. Kelly. 2017. Unmanned aerial vehicles for surveying marine fauna: assessing detection probability. *Ecological Applications* 27:1253–1267.
- Howell, E. A., D. R. Kobayashi, D. M. Parker, G. H. Balazs, and J. J. Polovina. 2008. TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endangered Species Research* 5:267–278.
- Innes, S., M. P. Heide-Jørgensen, J. L. Laake, K. L. Lairde, H. J. Cleator, P. Richard, and R. E. Stewart. 2014. Surveys of belugas and narwhals in the Canadian High Arctic in 1996. *NAMMCO Scientific Publications* 4:169–190.
- Jaquet, N., S. Dawson, and E. Slooten. 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. *Canadian Journal of Zoology* 78:407–419.
- Kéry, M. 2002. Inferring the absence of a species: a case study of snakes. *Journal of Wildlife Management* 66:330–338.
- Keevin, T. M., and G. L. Hempen. 1997. The environmental effects of underwater explosions with methods to mitigate impacts. U.S. Army Corps of Engineers, St. Louis District, St. Louis, Missouri, USA.
- Kristensen, K., A. Nielsen, C. W. Berg, H. Skaug, and B. M. Bell. 2016. TMB: automatic differentiation and laplace approximation. *Journal of Statistical Software* 70:1–21.
- Laake, J. L., J. Calambokidis, S. D. Osmeck, and D. J. Rugh. 1997. Probability of detecting harbor porpoise from aerial surveys: estimating  $g(0)$ . *Journal of Wildlife Management* 61:63–75.
- Lindgren, F., H. Rue, and J. Lindström. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. *Journal of the Royal Statistical Society Series B* 73:423–498.
- Mansfield, K. L., J. Wyneken, W. P. Porter, and J. Luo. 2014. First satellite tracks of neonate sea turtles redefine the 'lost years' oceanic niche. *Proceedings of the Royal Society B: Biological Sciences* 281:20133039.
- Marsh, H., and D. F. Sinclair. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *Journal of Wildlife Management* 84:1017–1024.
- McNew, L. B., and C. M. Handel. 2015. Evaluating species richness: biased ecological inference results from spatial heterogeneity in detection probabilities. *Ecological Applications* 25:1669–1680.
- Merrick, M. J., and J. L. Koprowski. 2017. Should we consider individual behavior differences in applied wildlife conservation studies? *Biological Conservation* 209:34–44.
- Miller, D. L., M. L. Burt, E. A. Rexstad, and L. Thomas. 2013. Spatial models for distance sampling data: recent developments and future directions. *Methods in Ecology and Evolution* 4:1001–1010.
- Miller, D. L., R. Glennie, and A. E. Seaton. 2020. Understanding the stochastic partial differential equation approach to smoothing. *Journal of Agricultural, Biological and Environmental Statistics* 25:1–16.
- National Oceanic and Atmospheric Administration [NOAA]. 2020. Taking marine mammals incidental to the U.S. Navy training and testing activities in the Northwest Training and Testing (NWTT) study area. Federal Register 85(219):72312–72469.
- Northeast Fisheries Science Center [NEFSC] and Southeast Fisheries Science Center [SEFSC]. 2011. Preliminary summer 2010 regional abundance estimate of loggerhead turtles (*Caretta caretta*) in northwestern Atlantic Ocean continental shelf waters. U.S. Department of Commerce, Northeast Fisheries Science Center Reference Document 11-03, Woods Hole, Massachusetts, USA.
- Nychka, D., R. Furrer, J. Paige, and S. Sain. 2017. fields: tools for spatial data. R package version 10.3. <<https://github.com/NCAR/Fields>>
- Nykänen, M., M. Jessopp, T. K. Doyle, L. A. Harman, A. Cañadas, P. Breen, W. Hunt, M. Mackey, O. Ó Cadhla, D. Reid, and E. Rogan. 2018. Using tagging data and aerial surveys to incorporate availability bias in the abundance estimation of blue sharks (*Prionace glauca*). *PLoS ONE* 13:e0203122.
- Paciorek, C. J., S. J. Goring, A. L. Thurman, C. V. Cogbill, J. W. Williams, D. J. Mladenoff, J. A. Peters, J. Zhu, and J. S. McLachlan. 2016. Statistically-estimated tree composition for the northeastern United States at Euro-American settlement. *PLoS ONE* 11:e0150087.
- Paladino, F. V., M. P. O'Connor, and J. R. Spotila. 1990. Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* 344:858–60.
- Pateiro-Lopez, B., and A. Rodriguez-Casal. 2019. alphahull: generalization of the convex hull of a sample of points in the plane. R package version 2.2. <https://CRAN.R-project.org/package=alphahull>
- Patel, S. H., S. G. Barco, L. M. Crowe, J. P. Manning, E. Matzen, R. J. Smolowitz, and H. L. Haas. 2018. Loggerhead turtles are good ocean-observers in stratified mid-latitude regions. *Estuarine, Coastal and Shelf Science* 213:128–36.
- Patel, S. H., S. J. Morreale, A. Panagopoulou, H. Bailey, N. J. Robinson, F. V. Paladino, D. Margaritoulis, and J. R. Spotila. 2015. Change-point analysis: a new approach for revealing animal movements and behaviors from satellite telemetry data. *Ecosphere* 6:1–3.

- Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data. *R Journal* 10:439–446.
- Pollock, K. H., H. Marsh, I. R. Lawler, and M. W. Allredge. 2009. Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. *Journal of Wildlife Management* 70: 255–262.
- Pough, F. H. 1980. The advantages of ectothermy for tetrapods. *American Naturalist* 115:92–112.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramirez, A., C. Y. Kot, and D. Piatkowski. 2017. Review of sea turtle entrainment risk by trailing suction hopper dredges in the US Atlantic and Gulf of Mexico and the development of the ASTER decision support tool. U.S. Department of the Interior, Bureau of Ocean Energy Management, Sterling, Virginia, USA.
- Rigby, R. A., and D. M. Stasinopoulos. 2010. A flexible regression approach using GAMLSS in R. London Metropolitan University, London, United Kingdom.
- Roberts, J., B. Best, L. Mannocci, E. Fujioka, P. N. Halpin, D. L. Palka, L. P. Garrison, K. D. Mullin, T. V. N. Cole, C. B. Khan, et al. 2016. Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. *Scientific Reports* 6: 22615.
- Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian models using integrated nested Laplace approximations (with discussion). *Journal of the Royal Statistical Society Series B* 71: 319–392.
- Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. *Journal of Wildlife Management* 51:622–630.
- Santidrián Tomillo, P., and J. R. Spotila. 2020. Temperature-dependent sex determination in sea turtles in the context of climate change: uncovering the adaptive significance. *BioEssays* 42:2000146.
- Sato, K. 2014. Body temperature stability achieved by the large body mass of sea turtles. *Journal of Experimental Biology* 217:3607–3614.
- Sato, K., W. Sakamoto, Y. Matsuzawa, H. Tanaka, S. Minamikawa, and Y. Naito. 1995. Body temperature independence of solar radiation in free-ranging loggerhead turtles, *Caretta caretta*, during inter-nesting periods. *Marine Biology* 123: 197–205.
- Shumway, C. A. 1999. A neglected science: applying behavior to aquatic conservation. *Environmental Biology of Fishes* 55: 183–201.
- South, A. 2017. *r.naturalearth*: world map data from Natural Earth. R package version 0.1.0. <https://CRAN.R-project.org/package=r.naturalearth>
- Sparks, L. M., and A. D. DiMatteo. 2020. Loggerhead sea turtle density in the Mediterranean Sea. NUWC-NPT Technical Report 12, 360. Naval Undersea Warfare Center Division, Newport, Rhode Island, USA.
- Sucunza, F., D. Danilewicz, M. Cremer, A. Andriolo, and A. N. Zerbini. 2018. Refining estimates of availability bias to improve assessments of the conservation status of an endangered dolphin. *PLOS ONE* 13:e0194213.
- Thomson, J. A., A. B. Cooper, D. A. Burkholder, M. R. Heithaus, and L. M. Dill. 2012. Heterogeneous patterns of availability for detection during visual surveys: spatiotemporal variation in sea turtle dive–surfacing behaviour on a feeding ground. *Methods in Ecology and Evolution* 3:378–387.
- Thomson, J. A., A. B. Cooper, D. A. Burkholder, M. Heithaus, and L. M. Dill. 2013. Correcting for heterogeneous availability bias in surveys of long-diving marine turtles. *Biological Conservation* 165:154–161.
- Thorson, J. T. 2019. Guidance for decisions using the Vector Autoregressive Spatio-Temporal (VAST) package in stock, ecosystem, habitat and climate assessments. *Fisheries Research* 210:143–161.
- Warren, D. L., N. Matzke, and T. L. Iglesias. 2020. Evaluating presence-only species distribution models with discrimination accuracy is uninformative for many applications. *Journal of Biogeography* 47:167–180.
- Wickham, H., M. Averick, J. Bryan, W. Chang, L. D'Agostino McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, et al. 2019. Welcome to the Tidyverse. *Journal of Open Source Software* 4:1686. <https://doi.org/10.21105/joss.01686>
- Wickham, H., and D. Seidel. 2020. *scales*: scale functions for visualization. R package version 1.1.1.1. <https://CRAN.R-project.org/package=scales>
- Wilke, C. O. 2019. *cowplot*: streamlined plot theme and plot annotations for 'ggplot2'. R package version 1.0.0. <https://CRAN.R-project.org/package=cowplot>
- Willson, A., B. Witherington, R. Baldwin, M. Tiwari, T. Al Sariri, A. Al Kiyumi, A. Al Harthi, M. S. Willson, A. Al Bulushi, G. Al Farsi, et al. 2020. Evaluating the long-term trend and management of a globally important loggerhead population nesting on Masirah Island, Sultanate of Oman. *Frontiers in Marine Science* 7:666.

- Winton, M. V., G. Fay, H. L. Haas, M. Arendt, S. Barco, M. C. James, C. Sasso, and R. Smolowitz. 2018. Estimating the distribution and relative density of satellite-tagged loggerhead sea turtles using geostatistical mixed effects models. *Marine Ecology Progress Series* 586:217–32.
- Witherington, B., P. Kubilis, B. Brost, and A. Meylan. 2009. Decreasing annual nest counts in a globally important loggerhead sea turtle population. *Ecological Applications* 19:30–54.

Associate Editor: Cynthia Paszkowski.

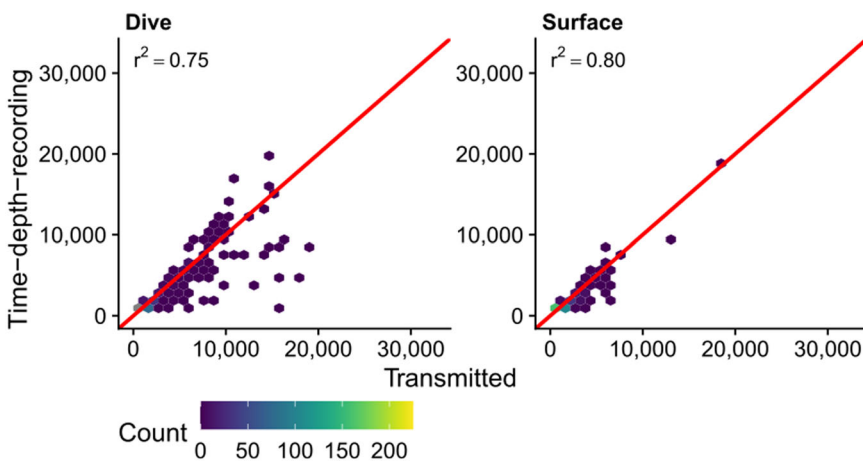
## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Hatch, J. M., H. L. Haas, C. R. Sasso, S. H. Patel, and R. J. Smolowitz. 2022. Estimating the complex patterns of survey availability for loggerhead turtles. *Journal of Wildlife Management* 86:e22208. <https://doi.org/10.1002/jwmg.22208>

## APPENDIX A: COMPARISON BETWEEN TRANSMITTED AND HAND-CALCULATED DURATION STATISTICS FOR A SINGLE TAG

The SMRU SRDLs summarized dive or surface duration over 4- or 6-hour intervals for 186 loggerhead turtles tagged between 2009 and 2018 off the east coast of North America. For a single tag, we compared the transmitted summary statistics for dive and surface duration to those manually calculated from the retrieved TDR. To the extent practicable, we processed the TDR in a manner similar to that of the information transmitted by the SRDL during deployment. Overall, the summarized dive or surface duration had high correspondence between the transmitted and manually calculated numbers, as shown by the high  $r^2$  values (Figure A1). Any disagreement between the 2 is likely a result of misalignment when linking numbers by date and time, as transmitted durations are binned by 4- or 6-hour intervals.



**FIGURE A1** Comparison between summarized dive or surface duration (seconds) transmitted by the satellite relay data loggers and calculated from the time-depth-recording for a single tag deployed on a loggerhead turtle off the east coast of North America in 2013. The red line denotes 1:1 agreement. Numbers were hexagonally binned with color indicating count.

**APPENDIX B: SPATIOTEMPORAL MODELS**

There are multiple approaches available to model the autocorrelation inherent to the satellite telemetry data used in this study. Two commonly cited approaches for modeling autocorrelated data are generalized linear mixed models (GLMMs) and generalized additive models (GAMs; Hefley et al. 2017). The GLMM framework accounts for autocorrelation by including random effects terms, modeling the latent spatial and spatiotemporal structures through specification of the covariance matrices that partially define the random effects distributions (Hefley et al. 2017). On the other hand, GAMs tend to model the autocorrelation as 1-dimensional or 2-dimensional basis-penalty splines specified within the definition of the mean structure (Hefley et al. 2017). The spatiotemporal regression models developed in this study are GLMMs or like GLMMs, in the case of the zero-one inflated beta regression (Douma and Weedon 2019), that make use of the SPDE approach to include and estimate the latent spatial and spatiotemporal random effects (Lindgren et al. 2011). Recent work by Miller et al. (2020) reported that the SPDE approach can be interpreted as a basis-penalty smoother, suggesting that the SPDE approach and more commonly applied GAMs (Roberts et al. 2016) have conceptual linkages. In this sense, we might anticipate that the SPDE and GAM approaches would be similar, although the degree of similarity would depend on how the basis-penalty smooths are defined (Hefley et al. 2017, Miller et al. 2020).

**Detailed description of the spatiotemporal regression models**

We constructed the spatiotemporal regression models using a SPDE approach. Lindgren et al. (2011) first introduced the SPDE approach and provides further explanation on the underlying mechanics, while Miller et al. (2020) provide a useful interpretation of the SPDE approach as a smoothing penalty allowing practitioners to better understand, adapt, and implement these types of approaches in disciplines that are familiar with basis-penalty smoothers.

We decided not to include environmental covariates in our spatiotemporal regression models for several reasons. First, we wished to avoid concerns about dependence on covariate values in subsequent analyses that may use our data products (i.e., avoid induced circular reasoning; Paciorek et al. 2016). Second, we wished to avoid the additional challenges of covariate selection and uncovering the appropriate functional forms of selected covariate effects, which is not trivial and requires further research. Finally, as has been noted elsewhere, spurious correlations can result between environmental predictors and the response variable when there is spatial autocorrelation (Warren et al. 2020). As a result, we decided to focus on the spatial and temporal components in this analysis and left the question of environmental and non-environmental predictors for future studies.

**Average dive and surface durations**

To estimate the average dive and surface durations, we assumed the summarized durations followed a Gamma distribution with density

$$\text{Gamma}(y \mid \alpha, \beta) = \frac{1}{\beta^\alpha \Gamma(\alpha)} y^{\alpha-1} e^{-y/\beta},$$

where  $\Gamma$  is the gamma function,  $\alpha$  is the shape parameter, and  $\beta$  is the scale parameter. We assumed a Gamma distribution because the summarized durations could only take on values greater than zero. More formally,

$$\bar{y}_{i,j,k,l} \sim \text{Gamma}\left(\alpha \times n_i, \frac{\mu_{j,k,l}}{\alpha \times n_i}\right),$$

where  $\bar{y}$  is the average dive or surface duration for summarized record  $i$  with sample size  $n$  from individual  $j$  at location  $k$  during month  $l$ . We modeled the mean response as:

$$\mu_{j,k,l} = \exp(\beta_0 + b_j + \Omega(s_k) + E_l(s_k)),$$

where  $\beta_0$  is the intercept,  $b_j$  is the individual random effect, and  $s_k$  is the spatial coordinate.

### Proportion of time at the surface

To estimate the average proportion of time at the surface, we assumed the proportions followed a beta-inflated distribution with density (Rigby and Stasinopoulos 2010)

$$\text{BEINF}(y \mid \mu, \sigma, \nu, \tau) = \begin{cases} p_0 & \text{if } y = 0 \\ (1 - p_0 - p_1) \frac{1}{B(\alpha, \beta)} y^{\alpha-1} (1 - y)^{\beta-1} & \text{if } 0 < y < 1, \\ p_1 & \text{if } y = 1 \end{cases}$$

where  $B(\cdot)$  is the Beta function,  $\alpha$  and  $\beta$  are shape parameters,  $\mu = \alpha/(\alpha + \beta)$ ,  $\sigma = (\alpha + \beta + 1)^{-1/2}$ ,  $p_0$  is the probability of 0,  $p_1$  is the probability of 1,  $p_2 = 1 - p_0 - p_1$  (i.e., probability between 0 and 1),  $\nu = p_0/p_2$ , and  $\tau = p_1/p_2$ . We assumed a beta-inflated distribution because the proportions arose from continuous time and included values of 0 and 1. More formally,

$$y_{i,j,k,l} \sim \text{BEINF}(\mu_{j,k,l}, \sigma, \nu, \tau),$$

where  $y$  is the fraction of time spent at the surface for record  $i$  from individual  $j$  at location  $k$  during month  $l$ . We then modeled the  $\mu$  as:

$$\mu_{j,k,l} = \text{logit}^{-1}(\beta_0 + b_j + \Omega(s_k) + E_l(s_k)),$$

where  $\beta_0$  is the intercept,  $b_j$  is the individual random effect, and  $s_k$  is the spatial coordinate.

For both regression models, the  $\Omega$  represents a continuous spatial process and the  $E$  represents changes to that continuous spatial process ( $\Omega$ ) over time (i.e., months). If it is assumed that both  $\Omega$  and  $E$  follow multivariate normal distributions with zero mean vectors and Matérn covariance functions (i.e., Gaussian random fields [GRFs] sampled at finite points), then the continuous spatial processes can be approximated as the weak solutions to SPDEs that produce Markovian GRFs (GMRFs; Lindgren et al. 2011). In brief, the SPDE approximation of a GRF, with some relatively non-restrictive assumptions, is a GMRF defined as a weighted sum of piecewise linear basis functions over a triangulated mesh with the same spatial domain as the continuous spatial process (Lindgren et al. 2011). The advantage of using a GMRF is that it is computationally more efficient and allows for the use of sparse matrix operations.

While each observed location could be specified as a node in the triangulated mesh, we selected a reduced number of locations referred to as knots in a predictive process approach (Banerjee et al. 2008). We maximized the number of knots before encountering computational difficulties (Thorson 2019), which translated into roughly 600 knots that were regularly spaced inside an  $\alpha$ -hull that spanned the domain of the averaged spatial coordinates (Pateiro-Lopez and Rodriguez-Casal 2019, Thorson 2019). We then used the R-INLA software to create the triangulated mesh and the sparse matrices needed for the SPDE approximation (Rue et al. 2009). We specified the Matérn functions for the spatial and spatiotemporal processes with fixed smoothness parameters and a shared scale parameter,  $\kappa$  (Winton et al. 2018). The spatial decorrelation range can then be approximated using  $\sqrt{8}/\kappa$ , where  $\kappa$  is an estimated parameter (Lindgren et al. 2011). We fitted the spatiotemporal regressions to the data using the statistical software R (R Core Team 2019) and Template Model Builder (TMB; Kristensen et al. 2016). We explored model performance using residual diagnostic plots.