Loggerhead marine turtles (*Caretta caretta*) nesting at smaller sizes than expected in the Gulf of Mexico: Implications for turtle behavior, population dynamics, and conservation

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Abstract

Estimates of parameters that affect population dynamics, including the size at which individuals reproduce, are crucial for efforts aimed at understanding how imperiled species may recover from the numerous threats they face. In this study, we observed loggerhead marine turtles (*Caretta caretta*) nesting at three sites in the Gulf of Mexico at sizes assumed nonreproductive in this region (≤87 cm curved carapace length-notch [CCL-n]). These smaller individuals ranged from 74.0 to 86.9 cm CCL-n, and the proportion of smaller nesting loggerheads was 0.13 across three study sites: Gulf Shores, AL; Dry Tortugas National Park, Florida (FL); and Everglades National Park (ENP), FL. The greatest proportion of smaller nesters was observed at ENP at 0.24. Tracking data indicated that the smaller nesters migrated shorter distances and swam in shallower waters compared to the larger nesting loggerheads (>87 cm CCL-n) in our dataset. These results provide valuable information on two of the smallest subpopulations of NW Atlantic loggerheads and understudied ENP turtles. Our results have potential applications in the classification and interpretation of stranding limits and bycatch estimates, population modeling (e.g., stage durations and fecundity), and understanding threats and subpopulation recovery efforts for multiple subpopulations of this imperiled species.

KEYWORDS
Bayesian hierarchical behavior-switching state-space model, *Caretta caretta*, curved carapace length, Gulf of Mexico, foraging, loggerhead, marine sea turtles, migration, size at reproduction

1 INTRODUCTION

Understanding the demography of imperiled species is crucial to countering the threats they face and supporting their recovery. Population (or subpopulation) models rely on accurate estimates of demographic parameters that affect population persistence (Heppell, 1998; Heppell, Crowder, Crouse, Epperly, & Frazer, 2003; Piacenza, Balazs,
Hargrove, Richards, & Heppell, 2016), including age at maturity, duration of life stages, and reproductive output (Caswell, 2006; Crouse, Crowder, & Caswell, 1987). However, demographic parameters for small subpopulations may differ from estimates from larger subpopulations (Hatch, Haas, Richards, & Rose, 2019; Richards et al., 2011), and substantial variation in reproductive traits can exist among subpopulations of the same species (van Buskirk & Crowder, 1994). Furthermore, animals can exhibit plasticity in both size at maturity and fecundity (Gotthard & Nylin, 1995; Kuparinen & Merila, 2007), which can affect demographic rates and the ability of a species to recover from declines (Piacenza et al., 2016). Elasticity analysis, which evaluates the relative input of each vital rate (age-specific survival and fecundity) to the annual population (or subpopulation) growth rate, also indicates that subpopulations of the same species can have varying elasticity patterns (Heppell, 1998). For marine sea turtles, the focus of our study, evidence exists for variation in elasticity patterns (Heppell, 1998) and reproductive traits (van Buskirk & Crowder, 1994) within a single species. This calls for the need to understand subpopulation-specific demography to assess the growth, recovery, and success of imperiled (and often small) subpopulations of marine turtles, which also face numerous threats.

Loggerhead marine turtles (Caretta caretta) in the Northwest Atlantic Ocean are part of a distinct population segment (DPS) listed as federally threatened under the U.S. Endangered Species Act (ESA, 1973, as amended). In total, there are nine DPSs that all together represent loggerhead marine turtles globally; they are differentiated based on ecology, distributions, genetics, and movements and allow for the unique assessment of risks, endangered status, and recovery objectives and criteria for each DPS (Conant et al., 2009). The Northwest Atlantic Ocean DPS is comprised of five recovery units (or subpopulations) outlined in the Recovery Plan that vary in size: the Northern, Peninsular Florida (FL), Dry Tortugas (DRTO), Northern Gulf of Mexico, and Greater Caribbean Recovery Units (RU). Nesting trends for Northwest Atlantic loggerhead, which affect overall species persistence, indicate either a declining trend, no trend, or unknown trend (NMFS-USFWS, 2008; TEGA, 2009; Witherington, Kubilis, Brost, & Meylan, 2009). For example, data show declining loggerhead nesting trends in the Northern Gulf of Mexico (1995–2007; NMFS-USFWS, 2008), Peninsular FL (1989–2008; NMFS-USFWS, 2008), and DRTO (2001–2009; Richards et al., 2011). And, more recent data through 2018 indicate a lack of significant nesting trend for the Northern Gulf of Mexico and Peninsular FL, with insufficient data for DRTO (Bolten et al., 2019). The presence of either a negative trend or no trend in nesting numbers indicates that these RUs are not meeting Recovery Objectives and Demographic Recovery Criteria in the Northwest Atlantic Ocean loggerhead Recovery Plan (Bolten et al., 2019). Globally, the loggerhead sea turtle is classified as vulnerable, is decreasing in numbers, and populations are severely fragmented (Casale & Tucker, 2017), and recommendations exist for regional assessments of extinction risk for marine turtle species (Seminoff & Shanker, 2008; Wallace et al., 2010), including for that of the loggerhead marine turtle.

Loggerhead marine turtles in the Northwest Atlantic Ocean face numerous threats. In-water threats include anthropogenic activities such as fisheries bycatch (Bolten et al., 2019; Hart et al., 2018a; Hays, Broderick, Godley, Luschi, & Nichols, 2003; Iverson, Benscoter, Fujisaki, Lamont, & Hart, 2020), ship strikes (Casale et al., 2010), energy development (e.g., oil spills; Henkel, Suryan, & Lagerquist, 2014; Vander Zanden et al., 2016; Bolten et al., 2019), and plastics (Bolten et al., 2019). Other threats are harmful algal blooms (HABs; Hart et al., 2018a; Bolten et al., 2019) and climate change (Bolten et al., 2019), including sea level rise (Conant et al., 2009). There are also numerous threats to nesting habitat, such as anthropogenic development, beach traffic (pedestrian and vehicular), lighting on beaches, erosion control structures that inhibit nesting movements, beach erosion, beach pollution, and sand extraction (Conant et al., 2009; NMFS-USFWS, 2008). Threats to the loggerhead marine turtles can vary based on life stage and in their impact on population (or subpopulation) growth rates (Bolten et al., 2011).

Evaluating proposed management actions to respond to these threats requires accurate estimation of vital rates, including size at sexual maturity. Understanding the size at which females achieve sexual maturity can affect stage durations in population models (Heppell, 1998; Piacenza et al., 2016), bycatch estimates (Gulf Coast Ecosystem Restoration Council, 2013), and incidental stranding limits (ISLs; Hart, Mooreside, & Crowder, 2006). Comprehending the size at sexual maturity may also affect how Recovery Objectives, Demographic Recovery Criteria, and Recovery Actions defined in the Recovery Plan for the Northwest Atlantic Ocean DPS of loggerhead marine turtles are achieved (NMFS-USFWS, 2008).

In this study, we observed nesting loggerhead marine turtles that were below the standard size that is considered as reproductive in this region (curved carapace length-notch [CCL-n] ≤ 87 cm). The size classification for reproductively mature females is reported as >87 cm CCL-n in various studies and in the Recovery Plan for the Northwest Atlantic Ocean DPS of loggerhead marine turtles (adults defined as >87 cm CCL-n in Witherington, 1986; Bjornsdal, Bolten, & Martins, 2000; Bjornsdal et al., 2001; NMFS, 2001; NMFS-USFWS, 2008). Because this size threshold of 87 cm CCL-n is used in various research and management applications, we quantified the proportion of nesting loggerhead
females that were \( \leq 87 \text{ cm} \) CCL-n at three sites in the Gulf of Mexico from 2011 to 2019. Because the smaller size of these nesting females may also have implications for subpopulation demography (e.g., fecundity), space-use behavior, and potential exposure to threats (e.g., fisheries bycatch, boat strikes), we also compared inter-nesting migration, and foraging characteristics between these smaller reproductive females and those that are \( >87 \text{ cm CCL-n} \), using satellite tracking. Our goals were to (1) quantify the frequency at which these smaller reproductive turtles nest (ratio of smaller nesters to total nesters) across multiple recovery units of the Northwest Atlantic Ocean loggerhead marine turtle DPS, and (2) to assess potential differences in space-use behavior between the smaller female reproductive loggerheads and their larger counterparts, given size differences in the two groups.

2 | METHODS

2.1 | Study sites and data collection

In the Gulf of Mexico, we sampled, tagged, took size measurements, and satellite-tracked nesting loggerhead females from 2011 to 2019 at three sites that represent different segments of Northwest Atlantic loggerhead marine turtle population (Caretta caretta): Gulf Shores, Alabama (AL; 30.228°N, 87.852°W), Dry Tortugas National Park (DRTO; 24.629°N, 82.873°W), and Everglades National Park (ENP; 25.142°N, 81.109°W) following established protocols (Hart, Guzy, & Smith, 2021; Hart, Lamont, Sartain, & Fujisaki, 2014; Hart, Lamont, Sartain, Fujisaki, & Stephens, 2013; NMFS-SEFSC, 2008). These nesting subpopulations each comprise an individual Recovery Unit (RU, as mentioned earlier) for the Northwest Atlantic loggerhead marine turtle DPS, and (2) to assess potential differences in space-use behavior between the smaller female reproductive loggerheads and their larger counterparts, given size differences in the two groups.

We categorized nesting females as smaller if CCL-n was \( \leq 87 \text{ cm} \), as measured from the midline anterior point (nuchal scute) to the midline posterior notch. The 87 cm division between subadults and adults represents a conservative division applied in numerous other studies (Bjorndal et al., 2000, 2001; NMFS, 2001; Witherington, 1986). The use of CCL-n is recommended for assessing CCL, because there is greater variability in CCL-tip because of deviation of the measuring tape from the midline (Bjorndal & Bolten, 1989; Bolten, 1999) and turtle carapace injuries from factors such as ship strikes.

2.2 | Proportion of smaller-sized nesters

We determined the proportion of these smaller nesting loggerheads at each study site, and the mean CCL-n of reproductive female loggerheads that were \( \leq 87 \text{ cm} \) CCL-n and \( >87 \text{ cm CCL-n} \), across all sites (\( n = 352 \) total turtles). To quantify if the proportion of smaller loggerhead nesters varied by site and year, we fit generalized linear models (GLMs) with a binomial distribution, and applied model selection using AICc in the MuMIn package (Barton, 2020) and determined \( R^2 \) in the performance package (Lüdecke, Makowski, Waggoner, & Patil, 2020) in the program R (version 4.0.3; R Core Team, 2020). We fit a null model, a model with year as covariate, a model with site as a covariate, and a model with both year and site as covariates. Lastly, we also determined the size threshold defining female reproductive loggerheads at which 10, 5, 2.5, and 1% of our observed nesters would be classified as smaller-sized.

2.3 | Satellite tracking and switching state-space modeling

We fitted platform terminal transmitters (PTTs; SPOT5, SPOT6, or SPLASH10; Wildlife Computers, Redmond, WA) to loggerhead females after they nested (\( n = 110 \) turtles), according to established protocols (NMFS-SEFSC, 2008) and methods outlined in Hart et al. (2014, 2018b, 2021); methods were approved by Institutional Animal Care and Use Committee Protocol (see Acknowledgments for more details). All tagged turtles were released within 2 hr at their capture location. Satellite location data were downloaded via Satellite Tracking and Analysis Tool (STAT; Coyne & Godfrey, 2005; accessible via SEATURTLE.ORG Inc. [www.seaturtle.org] prior to July 2014, and via the Wildlife Computers Portal [www.wildlifecomputers.com] after July 2014). The satellite-based Argos system was used to collect the satellite location data, and location data were assigned
accuracy estimates (CLS, 2015) using Kalman filtering (CLS, 2015; Kalman, 1960). Satellite locations were excluded if they were classified into location class (LC) Z, indicating no location error estimate was available. We summarized the data until the transmitters stopped delivering information or until the time of data analyses: September 17, 2020.

We estimated the location and behavioral mode for each turtle by fitting a Bayesian hierarchical behavioral-switching state-space model (hDCRWS model; hierarchical first difference correlated random walk switching model) to the marine turtle satellite data using the R package bsam (Jonsen, 2016; Jonsen, Bestley, Wotherspoon, Sumner, & Flemming, 2017; Jonsen, Mills Flemming, & Myers, 2005) using a time step of 24 hr (1 point per day). This type of switching state-space model (SSM) estimates movement parameters jointly across all individuals to improve behavioral state estimation, and accounts for location error. Behavioral modes based on SSM output were defined as either “area-restricted searching” or “transiting” (Jonsen et al., 2013; Jonsen, Myers, & James, 2007), the former represented by locations with comparatively shorter step lengths and greater turning angles (tortuous tracks) and the latter represented by comparatively longer step lengths and smaller turning angles (less turning, straighter movement). The models were fit by the R package bsam by calling JAGS (R package rjags; Plummer, 2019) to run the Markov chain Monte Carlo (MCMC) algorithm. We ran two independent parallel chains of MCMC, used adaptive sampling for the first 3500 iterations, and discarded 3500 additional samples as the burn-in. We then drew 10,000 samples from the posterior distribution, and thinned by 5 to reduce within-chain autocorrelation, resulting in 2,000 posterior samples for inference. To avoid fitting the SSM to satellite tracks with temporal gaps, where long temporal gaps lead to less informed SSM trajectories, we defined a threshold gap size of 20 days for each turtle, above which the gap period was removed and trajectory was split and re-estimated. Multiple trajectories (separated by a temporal gap in satellite data) for the same turtle were re-combined after SSM (see previous application of this method in Hart, Lamont, Iverson, & Smith, 2020). The minimum number of locations in a split trajectory was set to 50, and split trajectories with fewer than 50 locations were omitted. In addition to running the SSM with a 24 hr time step, we also ran the SSM using both a time step of 12 and 8 hr and spatially compared the outputs. We opted for the timestep of 24 hr to reduce autocorrelation in the modeled locations (in one case we supplemented an SSM migration point from the 8 hr time step output because we observed a clear migration path that was short in duration).

### 2.4 Behavioral characteristics

After we delineated each SSM turtle track into area-restricted searching or transiting modes, we characterized the SSM locations representing migration path (transiting) and the foraging locations (area-restricted searching) for each turtle. Because all turtles in this dataset were tagged after nesting, we used date of last beach encounter, a plot of cumulative distance traveled versus deployment duration (e.g., Hart et al., 2021; Tucker, MacDonald, & Seminoff, 2014), and mode assigned by SSM to delimit migration and foraging behavioral modes. We also visually inspected each SSM track and compared it to the corresponding satellite track for quality assurance. We identified the first migration date, last migration date, first foraging date, and last foraging date of each turtle, where the foraging period is represented by the locations after the last migration date.

Location filters to the SSM data were applied to account deviations in the location data that may not have represented in-water turtle movements during each behavioral mode. We filtered out SSM locations that fell on land, locations that represented movement speeds >5 kph during foraging, or locations that fell in waters deeper than -200 m (neritic zone delineation) during foraging. Loggerheads are typically located in water within the continental shelf, shallower than 200 m deep (Hawkes et al., 2011). Additionally, if the turtle exhibited a stopover during migration (two or more consecutive days of area-restricted searching locations during migration) or a foray during foraging (two or more consecutive days of transiting locations during foraging), we excluded these points.

We determined the nesting interval between nesting events in a given season for turtles with available data; identification of nesting events followed protocol outlined in Hart, Zawada, Fujisaki, and Lidz (2010). First, we compiled all nesting encounters observed on the ground. Next, we filtered satellite data before the start of migration to include only the highest quality locations (LC 1–3; CLS, 2015) that occurred close to or on land (within the error estimate for each LC class), that were clustered during a short-time span, and occurred during night-time hours; in some rare cases lower quality locations (LC A–B) were used to infer nesting if they were clustered in time, space, and occurred at night (Tucker, 2010; Vincent, McConnell, Ridoux, & Fedak, 2002). These filtered satellite locations were used to infer nesting events only if they met location, clustering, and time-based criteria outlined above. We combined these inferred nesting events with known nesting events observed on the beach, and determined nesting interval as the days between nesting events.

To assess whether migration and foraging traits differed between smaller nesting loggerheads that were ≤87 cm
CCL-n and those that were >87 cm CCL-n, we calculated the following behavioral characteristics from the SSM tracks: the length of the migration path (km), the mean depth along the migration path (m), the depth at the foraging centroid (m), and the distance to shore from the foraging centroid (km). We determined migration path distance by converting the migration SSM points to a line, and calculating the length of the line. We determined foraging centroids for each turtle using the geometric center (arithmetic mean position) of the foraging SSM points. All depth calculations were conducted using the ETOP01 Bedrock cell-registered bathymetry (Amante & Eakins, 2009) and the shoreline layer used was the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG; Wessel & Smith, 1996). All depth and distance calculations were made in ArcGIS 10.7.1 (ESRI, 2019; Data Management, Analysis, Tracking Analysis, and Spatial Analyst toolboxes) and all summary statistics were calculated in R using the package dplyr (Wickham, François, Henry, & Müller, 2020).

To evaluate whether migration and foraging characteristics varied based on turtle size category (≤87 cm or >87 cm CCL-n), we ran two sets of linear regression models: one for migration traits (n = 99 turtles) and one for foraging traits (n = 110 turtles). For the migration traits, we assessed whether the migration path distance and the depth along the migration path varied according to size and site. For the foraging traits, we assessed whether the distance to shore from the foraging centroid and the depth at the foraging centroid varied according to size and site. All migration and foraging response variables were ln-transformed (natural logarithm) because their distributions were positively skewed (mean > median); we used absolute values of depth variables in the models. We also generated kernel density estimate plots (equivalent to a smoothed histogram) for each migration or foraging response variable to visually compare the distribution of values (the area under the curve is equal to 1) for each behavioral trait (Venables & Ripley, 2002) in the R package ggplot2 (Wickham, 2016).

3 | RESULTS

3.1 | Proportion of smaller-sized nesters

The total number of individually sampled turtles was 352 (AL: n = 157, DRTO: n = 161, ENP: n = 34). The CCL-n of the smaller-sized nesting loggerhead females ranged from 74.0 to 86.9 cm (n = 44, mean size = 84.4 cm, median size = 85.5 cm, SD = 2.9). For comparison, the CCL-n of larger nesters ranged from 87.3 to 108.9 cm (n = 308, mean size = 94.9 cm, median size = 94.5 cm, SD = 4.9; Figure 1; see Benscoter & Hart, 2021). The mean proportion of smaller nesters was 0.13 across all sites. Model selection, determined via AICc and model weight (ω), indicated that the top two models were the site model and the null model. Although, there was not a high level of differentiation between the site and null model in terms of AICc (ΔAICc < 1 between the site model and the null model), the site model had greater model weight and slightly higher R² compared to the null model (Lüdecke, Makowski, Waggner, & Patil, 2020), therefore we present the site model as the top model (AICc = 266.75, df = 3, ω = 0.56; see Tables S1a and S1b, Supporting Information). The site model indicated that the proportion of smaller-sized nesters varied according to site, where the proportion of nesting females ≤87 cm CCL-n was higher at ENP compared to AL (the intercept, z = 2.20, p = 0.02). The greatest proportion of smaller-sized reproductive loggerheads was observed at ENP (0.24; n = 8 out of 34 turtles), then DRTO (0.13; n = 21 out of 161 turtles), followed AL (0.10; n = 15 out of 157 turtles; Figure 2).

We also determined the threshold size defining female reproductive loggerheads at which 10, 5, 2.5, and 1% of our observed nesters would be classified as smaller-sized. This exercise revealed that the size thresholds at which 10, 5, 2.5, and 1% of the turtles in our data set would be classified as smaller-sized nesters were 86.5, 85.3, 82.4, and 79.3 cm CCL-n, respectively.

![Figure 1](https://example.com/figure1.png)

**Figure 1** Histogram showing the sizes of female reproductive loggerhead turtles (Caretta caretta; curved carapace length-notch, CCL-n) nesting at three sites in the Gulf of Mexico: Gulf Shores, Alabama, Dry Tortugas National Park, Florida (FL), Everglades National Park, FL; the black line represents the threshold between the smaller (≤87 cm CCL-n, n = 44) nesting females and the larger (>87 cm CCL-n, n = 308) size class, where the standard size considered as reproductive for loggerhead females in this region is >87 cm CCL-n (as defined in Witherington, 1986; Bjorndal et al., 2000, 2001; NMFS, 2001; NMFS-USFWS, 2008).
3.2 Behavioral characteristics

Of all the reproductive female loggerheads tagged at the three sites, 110 turtles were also satellite-tracked and had data to calculate inter-nesting ($n = 95$), migration ($n = 99$), and foraging characteristics ($n = 110$) (see Benscoter & Hart, 2021). The inter-nesting interval for smaller-sized nesters was 12.1 days ($\pm 2.1$ SD for $n = 13$ turtles) and 13.0 days for the nesters >87 cm CCL-n ($\pm 2.0$ SD for $n = 81$ turtles). There were differences between the smaller reproductive females and their larger (>87 cm CCL-n) counterparts in behavioral traits, particularly for migration (Figure 3). The mean migration path distance was shorter for the smaller (mean = 142.9 m, 95% CI: 81.5–250.3 m) versus the larger (mean = 362.1 m, 95% CI: 291.2–450.4 m) nesters ($R^2 = 0.09$; $t = -3.09$, $p < 0.01$). The mean depth along the migration path was shallower (less negative) for smaller (mean = −21.7 m, 95% CI: −9.7 to −48.3 m) versus the larger (mean = −69.4 m, 95% CI: −50.8 to −94.7 m) nesters ($t = -2.65$, $p < 0.01$; $R^2 = 0.06$; Figure 3a,b). We also observed the general patterns that smaller reproductive loggerheads foraged at more shallow depths and foraged closer to shore compared to larger nesters, but the 95% confidence intervals between the two size classes of turtles overlapped for the estimates of these response variables ($p > 0.05$; Figure 3c,d). Although we accounted for site in our models, we did not observe a consistent significant effect of site for the behavioral models; therefore, we present the pooled estimate of the migration and foraging behavioral traits in Figure 3 based on the size effect alone.

4 DISCUSSION

In this study, we observed that 13% of the loggerheads nesting on beaches at three sites in the Gulf of Mexico were smaller than the standard size considered as a reproductive female for this species in this region ($\leq$87 cm CCL-n; sites: Gulf Shores [AL], DRTO [FL], and ENP [FL]). For loggerheads nesting at ENP, the proportion of smaller-sized nesters was 24%. We also determined that the size thresholds potentially defining reproductive loggerhead females at which 10, 5, 2.5, and 1% of the turtles in our data set would be classified as smaller-sized were 86.5, 85.3, 82.4, and 79.3 cm CCL-n, respectively.
respectively. This exercise provided a preliminary evaluation of how the proportion of smaller-sized reproductive loggerhead females could change if the size threshold classifying adult reproductive female loggerheads shifted. We caution however, that our data set is from three of the five RUs for Northwest Atlantic Ocean DPS of loggerhead marine turtles, and we sampled during only a portion of the nesting season. Longer duration studies that continue to evaluate the proportion of loggerheads nesting at smaller sizes that what is typically considered reproductive may lend to increased understanding of the size female loggerheads begin reproducing in this region. For example, Phillips, Stahelin, Chabot, and Mansfield (2021) recently determined that the minimum size interval (the range of values from the smallest individual up to two standard deviations below the mean) of mature loggerhead females nesting at Archie Carr National Wildlife Refuge from 1982 to 2019 was 70.6–83.2 CCL-n (n = 9855 turtles; size conversion equations obtained from NOAA-NMFS, 2009). Coordination with studies such as Phillips, Stahelin, et al. (2021) to include a broader spatial and temporal coverage of the Northwest Atlantic Ocean DPS of loggerhead marine turtles is necessary to fully evaluate the appropriate size threshold defining reproductive female loggerheads in this region.

The smaller reproductive females in our data set behaved differently than their larger counterparts, specifically they exhibited shorter migration distances and migrated along shallower depths compared to the larger (>87 cm CCL-n) reproductive females. In general, the probability of migrating is associated with body size (mass) for swimming and walking species (birds and mammals; Soriano-Redondo, Gutiérrez, Hodgson, & Bearhop, 2020). Here, we observed a similar pattern within species, where longer migration distances were
associated with larger-individuals, and short migration
distances were associated with smaller individuals.
Variation in movement behavior of individuals in a given pop-
ulation or subpopulation may potentially expose
individuals to different threats (e.g., exposure to fisheries,
boat strikes, algal blooms), and understanding behavioral
differences between different sizes of nesting loggerhead
females is valuable for recognizing how current regula-
tions offer protection for reproductive female loggerhead
turtles.

Our results have potential implications for the classi-
fication of reproductive adults in bycatch estimates and
incidental stranding limits (ISLs). Understanding the
number of strandings in the mature (i.e., adult) age class
is an important component of species management for
imperiled marine reptiles that are susceptible to human
and environmental threats. Whether an individual is cat-
egorized as an adult in a stranding occurrence effects
ISLs and the application of ISLs into fisheries manage-
ment to reduce bycatch (Hart et al., 2006). Currently, the
RESTORE Act aims to reduce bycatch (Gulf Coast Eco-
system Restoration Council, 2013) and the classification
of reproductive individuals in bycatch estimates is
applied based on our understanding of what size defines
a reproductive adult. The size classification in bycatch
estimates also may affect whether recovery criteria in the
Recovery Plan for the Northwest Atlantic Ocean DPS of
loggerhead marine turtles (NMFS-USFWS, 2008) are
being met.

The smaller size at reproduction can also affect popu-
lation demography. Although development of population
models for loggerheads is limited by knowledge gaps in
species biology (Heppell, 1998), in particular for the early
oceanic life stage (National Research Council, 1990), the
size at maturity affects reproductive attributes and re-
productive success in marine turtles. The size at reproduc-
tion can affect clutch size (smaller clutch size for smaller
marine turtles; Broderick, Glen, Godley, & Hays, 2003)
and the number of clutches produced in a reproductive
season (more clutches produced in larger animals; Brost
et al., 2015). Similarly, body size is positively correlated
with traits such as egg size and overall reproductive effort
in marine turtles (van Buskirk & Crowder, 1994). The
small size of nesting loggerhead females in this study is
notable because of their imperiled statuses and the low
population sizes (i.e., hundreds not thousands) of the
DRTO and Northern Gulf of Mexico (Gulf Shores, AL)
RUs, where small turtle size may limit the ability to
recover from population declines or environmental per-
turbations (e.g., oil spills). We also provide valuable infor-
mation on loggerheads nesting at ENP, which are
understudied component of the Peninsular FL
RU. Variation in the size at reproduction within each
distinct subpopulation can affect life stage durations and
fecundity estimates, is important for accurately modeling
subpopulation and population dynamics, and may also
affect movement behavior.

The trends observed here may apply to other hard-
shelled marine turtles in other locations. For example,
for female green turtles (Chelonia mydas) tagged and
satellite-tracked after nesting in the Galápagos Archipel-
ago (Ecuador), the largest turtles exhibited different
migration and foraging behavioral patterns compared to
the smallest turtles, whereby the largest turtles performed
oceanic migrations to neritic foraging areas and the
smallest turtles remained in the Galápagos (Seminoff
et al., 2008). Similarly, for loggerhead turtles satellite-
tagged after nesting at Keewaydin Island, FL, larger tur-
tles migrated to the northern Gulf of Mexico and the
Bahamas and foraged in those locations, and smaller tur-
tles remained near the nesting beach in south Florida
and foraged locally (Phillips, Addison, Sasso, & Mansfield, 2021). The differences in movement behavior
between turtles of different sizes have implications for
managing the diverse threats that occur in shallow
coastal areas versus deeper oceanic zones. For example,
the management of nearshore marine areas for recrea-
tional and commercial use may not currently protect
areas that smaller reproductive loggerheads use, if des-
ignated based on larger turtle movement information.
Furthermore, there exists a greater impact of anthro-
ogenic drivers in ocean areas that are shallow and near
the shore (Halpern et al., 2008), including areas that
loggerheads use.

There is evidence for variation in marine turtle size
for female Northwest Atlantic loggerhead marine turtles.
The size of nesting loggerheads in this study ranged from
74.0 to 108.9 cm CCL-n (n = 352), which suggests our
turtles are smaller than other Northwest Atlantic logger-
heads. For example, nesting loggerhead females from
Archie Carr NWR (Peninsular FL RU) ranged from 82.3
to 114.5 CCL-n (n = 46; Evans, Carthy, & Ceriani, 2019);
size conversion equations obtained from NOAA-
NMFS (2009). However, a recent study by Phillips,
Stahelin, Chabot, and Mansfield (2021) documents
mature loggerheads as small as 70.6 CCL-n nesting at
Archie Carr National Wildlife Refuge (n = 9855 turtles
from 1982 to 2019; size conversion equations obtained
from NOAA-NMFS, 2009). Nesting female loggerheads
from the Northern RU for Northwest Atlantic logger-
heads ranged from 80.2 to 111.4 CCL-n (n = 64; Griffin
et al., 2013). Moreover, the CCL-n size range of the
nesting population at Blackbeard Island National Wild-
life Refuge in Georgia (Northern RU) ranged 84.6–
111.1 cm (from 2001 to 2008; Cason, 2009). Another pop-
ulation in coastal Georgia ranged from 94.6 to 114.9 cm
(Kraemer, 1979). All of these studies report a larger minimum and maximum size of nesting female loggerheads compared to the turtles we observed, except for Phillips, Stahelin, et al. (2021). However, many of them also have observations of female loggerheads nesting at sizes less than 87 cm CCL-n.

Size data across various sites in the Gulf of Mexico (from NOAA-NMFS, 2009) show a similar pattern of a broad range of sizes representing the size of first-time (neophyte) nesters for loggerheads, indicating high variation in marine turtle size. Putative first-time loggerhead nesters in the Peninsular FL Subpopulation were smaller (mean size = 95.4 CCL-n, \( n = 300 \)) compared to putative first-time nesters in the Northern (mean = 98.0 CCL-n, \( n = 158 \)) and Greater Caribbean (mean = 97.2 CCL-n, \( n = 368 \)) RU. Data on loggerheads on the SE U.S. coast show a wide range of sizes in neophyte nesters, ranging from 80.4 to 115.0 CCL (\( n = 826 \); Scott, Marsh, & Hays, 2012; TEWG, 2009). The minimum size of sexual maturation estimated (via skeletochronological analysis) for loggerheads along the Atlantic coast of the United States was 78.5 cm CCL (mean = 96.3, max = 108.6, \( n = 32 \); Avens et al., 2015; size conversion equations obtained from NOAA-NMFS, 2009; Avens et al., 2013). It is notable that other studies also report loggerheads nesting at sizes less than the 87 cm CCL threshold for which loggerhead females in this region are considered sexually mature. However, the smallest size of sexually mature females in many of these other studies are still larger than those we report (smallest size in this study = 74.0 cm CCL).

Our results provide an interesting parallel to research in the Mediterranean, where observed sizes of reproductive loggerheads are very small. The minimum, mean, and maximum size at sexual maturity for nesting female loggerheads in the Mediterranean was reported as 66.4, 69.0, and 84.7 cm CCL, respectively (summarized in Avens et al., 2015; Casale, Mazaris, Freggi, Vallini, & Argano, 2009; Casale, Conte, Freggi, Cioni, & Argano, 2011; Casale, Mazaris, & Freggi, 2011; Piovano et al., 2011). Tiwari and Bjorndal (2000) reported smaller body sizes in Mediterranean loggerheads, compared to other loggerheads in Brazil and FL (east coast of FL). The smaller body size of Mediterranean turtles may be explained in part by latitude, where a negative correlation was observed between body size and latitude (Tiwari & Bjorndal, 2000), and could be related to factors such as growth rate.

The smaller sizes of nesting loggerhead females in the three RUs in the Northwest Atlantic may be indicative of slower growth rates and/or maturation at younger ages, which may represent a shorter juvenile stage for these turtles. Interestingly, Bjorndal et al. (2013) report a decline in growth rates in Northwest Atlantic loggerheads from 1997 to 2007. Both slower growth rates and maturation at younger ages have potential implications for the timing of ontogenetic shifts, the age structure of the population, reproductive success, and ultimately population dynamics. Numerous other marine ectotherms show maturation at younger ages and sizes from stressors such as fisheries (Hutchings & Reynolds, 2004; Morita & Fukuwaka, 2007; Piacenza et al., 2016) and warming (Audzijonyte et al., 2016; Daufresne, Lengfellner, & Sommer, 2009; Jonsson, Jonsson, & Finstad, 2013; Ohlberger, 2013); fisheries bycatch is identified as the greatest marine threat to the Northwest Atlantic Ocean loggerhead marine turtle DPS (Bolten et al., 2019).

The size and number of females that are reproducing in the population is vital to understanding how Recovery Objectives, Demographic Recovery Criteria, and Recovery Actions defined in the Recovery Plan for the Northwest Atlantic Ocean DPS of loggerhead marine turtles are being met (NMFS-USFWS, 2008). Recovery Objectives in the Recovery Plan include increasing the number of nests per recovery unit, associated increases in nesting females with nest number increases, minimizing fisheries bycatch, and minimizing trophic changes from fisheries harvest and habitat alteration (NMFS-USFWS, 2008). There are also Demographic Recovery Criteria related to nest numbers and rates of increase, and ensuring that neritic strandings do not increase at a greater rate than in-water abundance trends for similar age classes (NMFS-USFWS, 2008). Recovery Actions include monitoring nesting and in-water trends, and implementing measures to minimize bycatch. If these Recovery Objectives, Criteria, and Actions are evaluated based on the threshold size greater than 87 cm CCL-n representing mature females, these evaluations may not accurately represent what is occurring in the population. The life history of the loggerhead marine turtle is complex, and different threats are shown to interact with different life stages for this species (Bolten et al., 2011). Therefore, differences in maturation size and behavior (and consequently other potential factors such as reproductive output, stage durations, space use over time) can interact with different threats, and the relative importance each threat poses to the population growth rate (Bolten et al., 2011). Understanding the risk of each threat to population recovery has been identified as crucial to the success of recovery actions and reaching recovery objectives for imperiled species (Bolten et al., 2011). Wide-ranging marine species show inter-population variation in life history traits and population dynamics that merit management specific to individual populations (Wallace et al., 2010). This is especially important for species such as sea turtles because their intrinsic traits of longevity,
large body size, late maturity, low fecundity, rarity, and high market value make them particularly vulnerable to and prone to extinction (He et al., 2017).

When we compared the proportion of smaller-sized reproductive females between sites in our study, the site model indicated that ENP had a greater proportion of smaller-sized reproductive females compared to AL. Although the site model represented the lowest AICc, highest ω, highest $R^2$, and had a significant effect of site ($p = 0.02$), we note that there was not a high degree of differentiation between the site model and the null model in terms of the AICc ($Δ$AICc <1 between the site model and the null model), and the $R^2$ value was low for the site model ($R^2 = 0.04$). However, the mean proportion of smaller-sized reproductive females was 0.13 across all sites, and ranged from 0.10 at AL to 0.24 at ENP, which we think alone is a crucial finding. The primary aim of this study is to document the presence and frequency of female loggerhead turtles that are nesting at sizes smaller than what is typically considered reproductive for this species in this region, which is evident across all three study sites. The sampling frequency and duration in this data set only covers a portion of the nesting season, therefore future efforts to increase sample sizes and sample locations could allow researchers to better understand the frequency of smaller-sized reproductive females both spatially and temporally in the Northwest Atlantic Ocean loggerhead DPS.

Our behavioral models had low $R^2$ values (range: 0.06–0.09). We find this unsurprising, as the response variables we used are affected by a number of complex ecological and evolutionary factors in addition to turtle size, and it was not our goal to capture those other factors. Turtle size was a better predictor of migration traits than of foraging traits: the two migration trait response variables had a mean $R^2 = 0.08$, while the two foraging trait response variables had a mean $R^2 = 0.02$ and were not significant (although the foraging depth trait had a $p$-value of .06). While size clearly does not predict turtle migration traits extremely well, our finding that size alone can explain nearly 8% of the variation in migration in our data set is important. Notably, we did not observe any small-sized reproductive loggerheads migrating long distances or migrating in the deeper water; all of the smaller-sized reproductive turtles migrated shorter distances in shallow water across the entire study period (2011–2019). We did not observe any smaller reproductive females migrating across the FL Straits to the Bahamas or Cuba, or across the Gulf of Mexico to the Yucatan Peninsula, as observed in the larger (>87 cm CCL-n) reproductive loggerheads. Similarly, the smaller-sized reproductive turtles did not forage at the deeper end of foraging depths observed in our data set. The smaller reproductive female turtles also foraged close to shore, with the exception of 1 individual, which we believe contributed to the high confidence interval around the foraging distance to shore variable. The minimum values for migration distance, migration depth, foraging depth, and foraging distance to shore all pertained to the smaller-sized loggerheads. Variation in migration patterns based on turtle size can affect the degree and duration these turtles interact with threats such as fisheries and boat strikes, their overlap in space use with marine protected areas, and use of habitat areas (Shimada, Limpus, Jones, & Hamann, 2017). It would be valuable for other studies on the Northwest Atlantic Ocean loggerhead marine turtle DPS and for this RMU to examine the proportion of smaller-sized nesters and their migration and foraging behavioral characteristics to increase our understanding of how trends in proportion of smaller nesters and their behavior may vary across space and time, and how they interact with threats, habitat use patterns, and marine protected area delineations.

The observation that female loggerheads are nesting at smaller sizes than typically considered reproductive for this species in this region is important and has numerous conservation and management implications, especially given that loggerhead marine turtles face many threats to recovery, ranging from in-water threats (e.g., fisheries bycatch, climate change, oil spills, ingestion of plastics) to nesting habitat threats (e.g., anthropogenic development, beach erosion, sea-level rise). We also provide analyses that aim to decipher patterns related to the proportion of these small females nesting over space and time, as well as behavioral patterns that may differ for these smaller-bodied reproductive females. However, most importantly, the observation of smaller-sized loggerhead females nesting at three sites in the Gulf of Mexico has crucial conservation and management implications, including classification of turtle strandings, bycatch estimates, developing population models (e.g., stage durations, fecundity), understanding population trends, and the ability to monitor and meet recovery objectives for this species. Future studies investigating the degree to which these smaller females are reproducing could provide critical information to resource managers. The sampling we conducted at each study site in our data set occurs during a portion of the nesting season (1–3 weeks per year depending on the site in our study). Greater sampling frequency, duration, and extent (e.g., different spatial areas) could help differentiate possible patterns in the ratio of smaller reproductive females and their behavior across space and time. The application of more in-depth studies across all of the RU’s within this Northwest Atlantic Ocean DPS on the proportion and behavior of smaller reproductive females may have serious
implications for long-term population recovery of the imperiled loggerhead marine turtle.

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CONFLICT OF INTEREST
The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS
Allison M. Benscoter led the analyses and writing and contributed to design. Brian J. Smith contributed to data acquisition, design, analyses, and writing. Kristen M. Hart led the conception and design, secured funding and permits, led the data acquisition, and contributed to analyses and writing. All authors contributed to the revision and preparation of the final version.

DATA AVAILABILITY STATEMENT
Data are accessible via ScienceBase repository, via the following DOI link: https://doi.org/10.5066/P96S4B8P

ETHICS STATEMENT
All methods were approved by Institutional Animal Care and Use Committee Protocol (USGS-Southeast Ecological Science Center: USGS-WARC-GNV #2011-05 and #2019-14 and the United States National Park Service SER-BISC-BUIS-DRTO-EVER-Hart-Sea Turtles-Terrapins-2018-A2). All appropriate permits were obtained (see Acknowledgments section).

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