

Improved female abundance and reproductive parameter estimates through subpopulation-scale genetic capture-recapture of loggerhead turtles

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Abstract Nest counts are often used as indices for nesting female abundance in marine turtle monitoring, but accurately interpreting nest count trends requires context on the scale of demographic connectivity and estimates of reproductive parameters. Weak nest site fidelity (NSF) relative to the scale of tagging effort may bias parameter estimates. The reproductive ecology of Northern Recovery Unit (NRU) loggerhead turtles (*Caretta caretta*) was assessed through subpopulation-scale genetic capture-recapture via clutch sampling from approximately 1000 km of coastline from Georgia to Maryland, USA (30.75–38.06°N and 75.24–81.45°W). Of 20,682 clutches recorded from 2010 to 2012, 20,222 sampled clutches were assigned to 5684 unique females through microsatellite genotyping. Approximately 73% of females detected laying multiple clutches deposited them within a 20-km span, suggesting the possibility of demographic structuring across NRU rookeries

that warrants further investigation. Estimated clutch frequencies (ECF) generated from open robust design modeling were 4.28 (4.02–4.54) in 2010, 4.63 (4.45–4.80) in 2011, and 4.57 (4.28–4.77) in 2012, and were significantly higher than observed clutch frequencies. ECF generated from single-island data were biased low by 23–50% relative to those from regional genetic tagging. Among females that nested at least once on a physical tagging beach, 54% also nested elsewhere, with 81% of these “permanently” emigrating during the nesting season. This pattern of relatively strong NSF, but distributed across multiple nearby islands, confounded modeling of detection in single-island datasets and highlights the need for regional coverage for generating robust estimates of demographic parameters for marine turtles.

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Introduction

Characterizing the breeding ecology and movements of imperiled species is critical for understanding demographic processes and optimizing conservation efforts (Hamann et al. 2010). However, quantifying connectivity

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and vital rates can be particularly challenging for species capable of extensive dispersal and migratory behavior. Variation in breeding site fidelity can have profound consequences for vital rate estimation, so determining the appropriate scale for assessing demographic parameters is an important consideration. Marine turtles with access to long stretches of essentially contiguous nesting habitats highlight these challenges in quantifying population connectivity and demographics (Tucker 2010). Loggerhead turtles have complex life cycles marked by ocean basin-scale dispersal as oceanic juveniles as well as seasonal and breeding migrations as adults (Bolten 2003), making it impossible to directly observe individuals throughout much of their life cycle. Nesting females represent the most easily accessible adults, but individual identification requires direct interception via hourly nocturnal patrols. Therefore, most marine turtle population assessments globally rely on morning nest count surveys, which are logistically less intensive. These nest counts are used as a proxy of adult female abundance by accounting for the average number of clutches laid per female each season and the mean remigration interval, the number of years between reproductive seasons for each respective population (National Research Council 1990). However, estimates of adult female population size may be confounded by fluctuations in clutch frequency and remigration intervals due to changes in food availability or quality (Witherington et al. 2009). It is therefore necessary to periodically assess reproductive vital rates such as clutch frequency and remigration intervals to properly interpret trends in nest counts over time (Schroeder et al. 2003; Richards et al. 2011).

Nocturnal tagging projects conducted on several southeastern United States beaches have addressed variation in clutch frequency and remigration intervals by measuring reproductive output of individual loggerheads (Schroeder et al. 2003). However, weak nest site fidelity (NSF, in this context the relative proximity of successive clutches laid by a female) relative to the geographic scale of monitoring efforts presents a significant challenge in generating robust vital rate estimates, particularly for clutch frequency (Schroeder et al. 2003). Approximately 66% of the individuals tagged on Wassaw Island, Georgia were seen only during their initial tagging and not afterward (Pfaller et al. 2013). Tag returns of Wassaw females indicate rare nesting dispersal as far north as Onslow Beach, North Carolina (~400 km north) and as far south as Cape Canaveral, Florida (~410 km south) (Williams and Frick 2008). The apparently weak NSF behavior exhibited by some proportion of individuals highlights the need for a regional approach to generate robust parameter estimates for loggerhead turtles. However, due to logistical or cost constraints, nocturnal patrols are generally limited to

single islands or discrete stretches of beach within larger matrices of available nesting habitat. Many islands have erosional areas that are difficult to negotiate during much of the tidal cycle, allowing females to escape detection while nesting in areas inaccessible to researchers.

Capture histories for individual females often exhibit temporal gaps longer than the typical expected inter-nesting interval of approximately 12–16 days (Frazer and Richardson 1985). One assumption is that these gaps represent unrecorded nests either because the female was able to nest without being identified on the tagging beach or temporarily left the study site to nest elsewhere. Correction factors have been applied to mark-recapture data that assume this inter-nesting periodicity is relatively fixed and consistent across the season. Corrected clutch counts for NRU loggerhead females vary from 2.8 to 4.2 clutches per female (Frazer and Richardson 1985). Mark-recapture models offer a more rigorous means of accounting for imperfect detection in clutch frequency estimation (Rivalan et al. 2006). However, the staggered arrival and departure of individual females at nesting beaches over the course of the nesting season violates assumptions of many classic mark-recapture models. The multistate open robust design (hereafter, MSORD) framework offers more flexibility in accounting for the staggered entry and exit at the study site and has emerged as a powerful tool in estimating demographic parameters for marine turtle populations (Kendall and Bjorkland 2001; Kendall and Nichols 2002). Derived parameters such as nesting female abundance and clutch frequency can be estimated based on detection probabilities across secondary capture occasions within each nesting season. When capture histories are constructed such that secondary capture periods span biologically relevant inter-nesting intervals, residence time at the nesting beach should produce a reasonable approximation of clutch frequency (Kendall and Bjorkland 2001). Although the MSORD approach has been widely applied in marine turtle studies, it is unclear whether it can effectively account for cases of “permanent” emigration that may occur at the scale of individual tagging beaches in generating robust clutch frequency estimates.

Advances in genetic techniques and modeling approaches have provided a novel opportunity to assess marine turtle demographic parameters. Genetic tagging through sampling a single egg from each clutch offers an approach to identify individual females responsible for each nest, which alleviates the need to directly intercept nesting females (Shamblin et al. 2011b). Freshly laid eggs that have incubated less than a day yield maternal genomic DNA based on comparisons between DNA derived from skin biopsies and egg shells of respective females (Shamblin et al. 2011b). We employed this method to genetically tag female loggerhead turtles representing the Northern Recovery Unit (NRU), the northernmost subpopulation of loggerhead turtles nesting from Georgia to

Maryland on the Atlantic coast of the United States. This discrete subpopulation was defined by mitochondrial haplotype frequency divergence relative to subpopulations nesting in Florida (NMFS and USFWS 2008). The NRU represents an ideal study population for capture-recapture because of low to moderate nesting densities relative to those in peninsular Florida, making it logistically feasible to sample all recorded nests on monitored beaches. We used subpopulation-scale genetic capture-recapture to generate more robust estimates of nesting female abundance and clutch frequency for the NRU subpopulation and to quantify NSF indices. We also compared estimated clutch frequencies (ECF) generated from single-island versus regional datasets to determine the efficacy of an MSORD approach in accounting for detection issues caused by variation in NSF that might occur in a typical marine turtle dataset generated from single beach/island data.

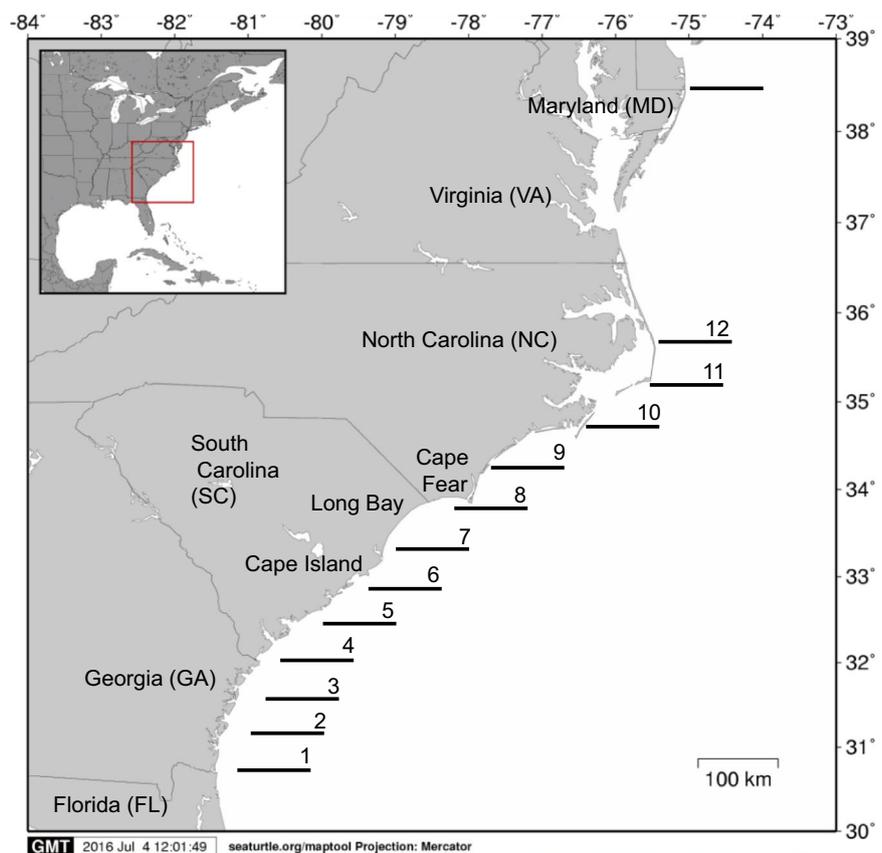
Materials and methods

Study site and sampling methods

Marine turtle nest monitoring projects obtained clutch samples from the Florida-Georgia border through the northern

extent of loggerhead turtle nesting in Maryland. Samples were collected from the majority of ocean-facing, barrier island beaches in the states of Georgia (GA), South Carolina (SC), North Carolina (NC), Virginia (VA), and Maryland (MD) from 2010 through 2012 (Table S-1 in Online Resource 1, Fig. 1). We surveyed in excess of 1000 km of beaches and approximately 93% of ocean-facing nesting habitat (Table S-1 in Online Resource 1). Survey start dates varied from late April to mid May depending on location and nesting phenology each year, but all projects that monitored daily commenced surveys by May 15th and continued through at least August 15th, surveying approximately 80% of ocean-facing beaches daily. Some beaches were not surveyed daily because of the difficulty of accessing nesting habitats on remote barrier islands during much of the tidal cycle and funding constraints (Table S-1 in Online Resource 1). However, most islands that were not monitored daily were surveyed at least weekly during peak nesting season, and known higher density beaches identified during pilot surveys were surveyed two to three times per week. Raccoon depredation was extensive on islands that were monitored at intervals greater than three days, increasing the probability that a clutch deposited within the previous week would be easily detected and sampled.

Fig. 1 Northern Recovery Unit loggerhead turtle nesting habitats sampled during the 2010 through 2012 nesting seasons. Bins delimited by parallel lines represent 0.45 decimal degree shifts in latitude used for finer scale analyses of nest site fidelity. The map was generated using the `maptool` function at www.seaturtle.org



The pilot study demonstrated that eggshells from freshly laid eggs yielded high-quality maternal DNA; however eggshells from partially or fully incubated eggs represented embryonic fingerprints, a mix of maternal and embryonic DNA, and/or had high allele dropout and amplification failure rates (Shamblin et al. 2011b). Therefore, projects that monitored daily attempted to collect a single viable egg from each clutch within 15 h of oviposition to provide the best opportunity for direct individual identification. On beaches monitored daily, surveyors rarely misidentified identified nesting crawls as non-nesting emergences but subsequently located clutches following nest depredation or hatchling emergence (~5%, Table S-2 in Online Resource 1). In those cases, we obtained shells from undeveloped eggs, used hatched eggshells, and/or dead embryo or hatchling tissue during nest inventories. Nests on the beaches that were not monitored daily suffered from high predation rates, so most often we salvaged depredated eggshells that had incubated for an unknown period prior to depredation. Where possible, we used eggs broken by predators, nesting females, or beach surveyors rather than sampling additional viable eggs. When fresh eggs were sampled, we discarded egg contents and retained only the shell. Surveyors on the three tagging beaches (Bald Head Island, NC; Wassaw Island, GA; and Jekyll Island, GA) collected 4-mm skin biopsies from the shoulder of nesting females following oviposition when they encountered nesting females; otherwise eggs were collected from clutches as previously described. Eggshells were stored in 95% ethanol prior to DNA extraction.

Individual identification

We extracted DNA using Qiagen DNEasy tissue extraction kits with modifications previously described (Shamblin et al. 2011b). Samples were genotyped using 18 microsatellite loci as previously described (Shamblin et al. 2007, 2009), with fragment analysis conducted at the Georgia Genomics Facility using a 3730xl DNA Analyzer (Applied Biosystems™). No significant linkage disequilibrium was detected among these loci in the original test data set (Shamblin et al. 2009). Primers for these loci were redesigned during the 2010—nesting season to overcome primer dimer contamination prior to the availability of dedicated post-PCR facilities (Table S-3 in Online Resource 1), and allele conversions were accomplished through re-genotyping of samples representing the allelic range of each marker. A pilot study previously identified allele dropout and the presence of extra non-maternal, presumably paternal, alleles as the two most common types of genotyping error (Shamblin et al. 2011b). Therefore, we tolerated low levels of genotyping error to satisfy the need to discriminate among related females without the requirement of extensive

re-genotyping. Unlike most studies that rely on non-invasive samples, the anticipated recapture rate was such that most individuals were expected to be present in the data set multiple times and at regular temporal intervals of eight or more days. Genotypes were compared using program CERVUS (Kalinowski et al. 2010) and any that perfectly matched across a minimum of ten loci and contained single allele mismatches at no more than two loci using the program were assigned to the same individual. The sibling non-exclusion probability of identity of the ten least informative markers in the dataset was 1.03×10^{-5} , providing strong discriminatory power among relatives even in the presence of this level of genotyping error. Samples that failed to match another sample or a consensus genotype by the end of each nesting season based on these criteria were re-extracted and re-genotyped. Re-extracted samples from the same clutch that matched one another based on the above criteria were considered new females. Three attempts were made to genotype a sample before considering it not assignable. Samples from depredated nests or nest inventories were initially treated as maternal to check for matches. In the absence of matches, they were treated as embryonic to assess potential for maternal parentage matches. Parentage analysis was performed using CERVUS (Kalinowski et al. 2010). First pass genotyping error was quantified through blind re-genotyping of randomly selected project samples. Final consensus genotypes across all individuals were analyzed in CERVUS to assess deviations from Hardy–Weinberg equilibrium and estimate null allele frequencies at each locus. More thorough descriptions of sample types and assignment methods are detailed in Online Resource 2.

Spatial analyses

To compare our results with previous marine turtle (NSF) studies, we generated two related intra-seasonal summary statistics at the state and NRU scales for each annual data set: mean distance between successive observed clutches (DBC) by each female and the mean distance between southernmost and northernmost clutches per female, or beach extent (BE). We used median nesting latitude as a spatially explicit metric to group females into bins for finer scale analyses of NSF. We partitioned bins by 0.45 decimal degrees of latitude, corresponding to approximately 50-km intervals that subdivided the study site into 18 bins (Fig. 1, Table S-4 in Online Resource 1). We chose this bin size based on the mean DBC and BE observed at the NRU scale (see Results) and the scale of spatial autocorrelation previously documented for loggerhead turtle nest counts (lag distances between 17 and 25 km) (Weishampel et al. 2003; Witherington et al. 2009). Bins 12 through 18 were pooled into a single group for analysis due to the small number of nesting females in this region.

For each bin, we calculated DBC, BE, and the proportion of multiple clutch females that had mean DBC of ≤ 5 km or ≤ 10 km and BE of ≤ 20 km to provide an index of high NSF females. The BE of 20 km was chosen to provide comparable data to a telemetry study that determined that 60% of clutches by central western Florida loggerhead females were deposited within a 20-km spread (Tucker 2010). Given the strong relationship between DBC and BE, we analyzed only BE to simplify comparisons of bin-level NSF. Annual variation within bins was tested via Kruskal–Wallis tests.

Capture-recapture modeling

We estimated annual nesting female abundance and mean clutch frequency using an MSORD approach (Kendall and Bjorkland 2001) as implemented in program MARK (White and Burnham 1999). Despite focus on intra-seasonal parameter estimates, we chose this framework to facilitate assessment of persistence at the study site as a function of the length of time an individual had already been there, its “age” at the study site in a given season (Kendall 2017). Three parameters were directly modeled: $pent$ the probability a female enters the study site to lay her first clutch of the season; ϕ persistence at the study site (the probability that a female will renest); and p , the detection probability across secondary capture periods. Nesting female population size and clutch frequency estimates were derived from the other parameters (Kendall 2017).

We divided loggerhead turtle nesting season into nine temporal bins of 14 days each and spanning the first and last nesting emergences recorded each nesting season following previous marine turtle mark-recapture methodology (Kendall and Bjorkland 2001). In any cases where two nests fell within the same bin but were detected eight or more days apart, one nest was moved into an adjacent empty bin. Inter-nesting intervals of eight days were rare, but were confirmed on the physical tagging beaches with large clutch sizes. Any clutches assigned to the same female but laid seven or fewer days apart were reanalyzed to confirm. These most often represented partial clutches involving disturbance during the initial nesting attempt. The partial clutches were combined into a single bin for clutch frequency analyses but were treated independently for spatial analyses. When precise lay dates were unknown, such as for nests initially recorded as non-nesting emergences, we estimated nesting emergence dates by assigning incubation periods of nearby clutches that hatched on similar dates. Binning of depredated nests on beaches with variable survey effort was accomplished manually through comparisons of survey logs and nesting emergence dates for other clutches assigned to the same female.

Several alternative models with constant and varying time dependent parameters were considered. In addition to constant and straight time variance across secondary periods, we considered smoothing functions: time since arrival (“age” at the study site), linear time, linear time since arrival, quadratic time, and quadratic time since arrival. Model ranking used the Quasi-likelihood Akaike’s Information Criterion corrected for small sample sizes (QAICc) as implemented in program MARK (White and Burnham 1999). Population and clutch frequency estimates were model-averaged. No explicit tests of goodness of fit exist for MSORD data structure (Kendall 2017), so we tested fit using a Cormack–Jolly–Seber data structure with a fully time-dependent global model using the median c -hat approach as implemented in program MARK (Cooch and White 2017). Model ranking and weighting were corrected for overdispersion by applying the median c -hat generated from the goodness of fit tests. We estimated nesting female abundance and clutch frequency for each annual dataset separately for each state as well as across the combined NRU dataset, following Kendall (2017).

Vital rates from single-island versus regional data

We characterized nesting movements and vital rates for individuals detected nesting on two tagging beaches in GA: Wassaw Island (~9 km consistently patrolled due to obstructions) and Jekyll Island (~10 km consistently patrolled due to obstructions). We assessed the proportion of individuals that were only detected nesting on each island, the proportion that nested on multiple islands, and the directionality of any detected inter-nesting movements. We compared clutch frequencies estimated from single-island nocturnal patrols with those generated from regional genetic capture-recapture for the same females to assess the effect of NSF on clutch frequency estimation in program MARK. The single-island data included only the detections in which personnel conducting tagging surveys encountered the female. As part of broader research and education objectives, project personnel monitored beaches nightly during the nesting season, applying flipper tags and passive integrated transponder tags to untagged females and recording tags for recaptured turtles (Williams and Frick 2008; Ondich and Andrews 2013). Non-nesting emergences by females that fell into any bins without observed nests were treated as clutches. The regional dataset included detections of all clutches by any female that nested on each tagging beach each year, including offsite clutches and any clutches laid on the tagging beach when the female was not observed during night patrols. The goal of this assessment was to compare clutch frequency estimates from the single-island datasets to those from the regional genetic datasets.

Results

Individual assignments and observed clutch frequency

Over the 2010 to 2012 nesting seasons, a total of 20,682 loggerhead turtle clutches were documented over the study area, of which 20,427 (99%) were sampled for genetics (Table S-2 in Online Resource 1). Two loci deviated from Hardy–Weinberg expectations, with null alleles likely accounting for one of these (Table S-3 in Online Resource 1). No variation was apparent across replicate runs for individual females at these two loci, so they were not expected to affect individual identification in any way. Genetic matches permitted individual assignments for 20,222 clutches (98% of those recorded and 99% of those sampled). The majority of unincubated egg samples (93%) produced clean maternal genotypes that directly matched other samples or turtle ID consensus genotypes. The first-pass, mean per-locus error rate was approximately 3% combined across all loci, and approximately 10% of samples did not meet minimum match criteria on the initial run due to failures or mismatches and were re-genotyped. A minority of freshly collected eggs (2%) had allele dropout issues or extra-maternal contamination that could not be resolved through re-genotyping and were assigned via parentage matches. A total of 5,684 unique females were empirically inferred (Table 1). Less than 2% of nesting females remigrated on annual cycles over the study period: 27 females nested both in 2010 and 2011, and 37 nested both in 2011 and 2012. Of these,

three females nested in all three years. Approximately 22% (392) of 2010 nesting females remigrated in 2012.

OCF ranged from one to seven clutches per female per season (Fig. S-1 in Online Resource 2). Mean OCF at the subpopulation scale ranged from 3.16 clutches per female ($n = 1,774$) to 3.46 clutches per female ($n = 1,973$) and was slightly higher in 2011 relative to 2010 and 2012 (Table 2). This pattern held for most of the state level annual comparisons as well. OCF was lower for NC than SC and GA in all three years (Table 2). The proportion of females detected laying a single clutch was consistent across years within states, but was higher for NC (26%) than GA and SC (15% each). The temporal distribution of lay dates for single-clutch females was roughly concordant with the overall temporal distribution of nesting in NC without obvious clustering at the beginning or end of nesting season, but there was some clustering toward the beginning of nesting season in SC in all years and GA in some years (Fig. S-2 in Online Resource 2).

Intra-seasonal nest site fidelity

Spatial data for intra-seasonal NSF analyses were available for 5044 nesting histories in which 4677 individual females were detected laying at least two clutches within a season. Recorded DBC and BE ranged from <0.1 to 723.8 km. The NRU DBC was 22.3 (± 54.0 SD) km and BE was 34.0 (± 75.8 SD) km. Of the 5,044 female-by-year nesting histories considered, 58% had DBC of less than 5 km and 78% had DBC of less than 20 km (Fig. 2).

Table 1 Unique female Northern Recovery Unit (NRU) loggerhead turtles identified nesting during the 2010 through 2012 nesting seasons based on microsatellite genotypes

	2010	2011
Georgia	546 (567, 563–571)	617 (635, 628–642)
South Carolina	1005 (1057, 1041–1073)	1169 (1227, 1200–1254)
North Carolina	326 (359, 350–367)	332 (354, 349–359)
Virginia	4	6
Maryland	1	
Northern Recovery Unit	1774 (1880, 1853–1908)	1973 (2065, 2042–2088)
	2012	Overall
Georgia	745 (781, 773–789)	1802
South Carolina	1397 (1453, 1438–1469)	3296
North Carolina	394 (428, 417–439)	995
Virginia	9	18
Maryland	1	2
Northern Recovery Unit	2388 (2525, 2494–2557)	5684

Rows do not sum to total because remigrant females appear in multiple years. Columns do not sum to NRU total because some females nested in multiple states. Numbers in parentheses represent model-averaged annual nesting female estimates and their 95% confidence intervals based on unconditional standard errors

Table 2 Clutch frequencies for Northern Recovery Unit (NRU) loggerhead turtles

	2010	2011	2012
Observed clutch frequency (OCF)			
Georgia	3.36 (3.24–3.47)	3.53 (3.41–3.65)	3.28 (3.18–3.39)
South Carolina	3.23 (3.13–3.32)	3.55 (3.47–3.64)	3.39 (3.31–3.47)
North Carolina	2.71 (2.56–2.86)	3.07 (2.91–3.23)	2.95 (2.80–3.12)
NRU	3.16 (3.09–3.23)	3.46 (3.39–3.53)	3.28 (3.22–3.34)
Estimated clutch frequency (ECF)			
Georgia	4.04 (3.86–4.22)	4.32 (3.96–4.68)	4.70 (4.38–5.03)
South Carolina	4.24 (4.00–4.49)	4.86 (4.62–5.11)	4.57 (4.15–5.00)
North Carolina	4.21 (3.85–4.58)	4.17 (3.88–4.46)	4.41 (3.99–4.82)
NRU	4.28 (4.02–4.54)	4.63 (4.45–4.80)	4.52 (4.28–4.77)

Observed clutch frequencies (OCF) by geographical extent and year are presented in the top panel. Estimated clutch frequencies (ECF) generated from open robust design model-averaging are presented in the bottom panel. Numbers in parentheses are 95% confidence intervals

Less than 6% of observed DBCs were in excess of 100 km. With respect to BE, 47% of observations were less than 5 km, and 73% were less than 20 km. Conversely, 10% had BEs of 100 km or more, and 4% had BEs in excess of 200 km.

At the individual bin level, NSF patterns were stable within bins across years (Table S-4 in Online Resource

1). Of the 12 inter-annual comparisons within bins, only bin 1 showed significant variation in BE across years ($H_2 = 17.01, P < 0.001$). Considering annual data sets separately, DBC varied from 6.8 ± 11.2 km ($n = 160$) to 101.2 ± 136.4 km ($n = 20$) within bins. All GA and SC bins had a mean DBC of ≤ 26.5 km, whereas all but one of the NC bins had a mean DBC of ≥ 28.2 km (Table S-4 in Online Resource 1). BE ranged from 12.5 ± 23.9 km ($n = 160$) to 137.7 ± 185.2 km ($n = 20$) across annual bins. As with DBC, BE of the southern six bins was ≤ 41.3 km, whereas the BE of all but one of the northern bins exceeded 43.4 km. This exception was bin 8 in 2010. When considered across the three seasons combined, BE was consistently higher for northern relative to southern bins (Fig. 3), with the break point occurring between bins 6 and 7, roughly corresponding to the southern extent of Long Bay that spans the coastline between Cape Island, SC and Cape Fear, NC (Fig. 1).

Population and clutch frequency estimation

Median c-hat estimates from CJS goodness of fit tests for the 12 spatial extent-by-year data sets ranged from 1.02 to 2.25. The best-supported models all included straight time variation in arrival probabilities across secondary periods. Models that incorporated linear or quadratic time functions on arrival probabilities were not well supported. Models incorporating these smoothing functions did perform slightly better with respect to modeling persistence probabilities, but time or time since arrival were present in top models for eight of the location-by-year data sets. In most cases, the best-supported

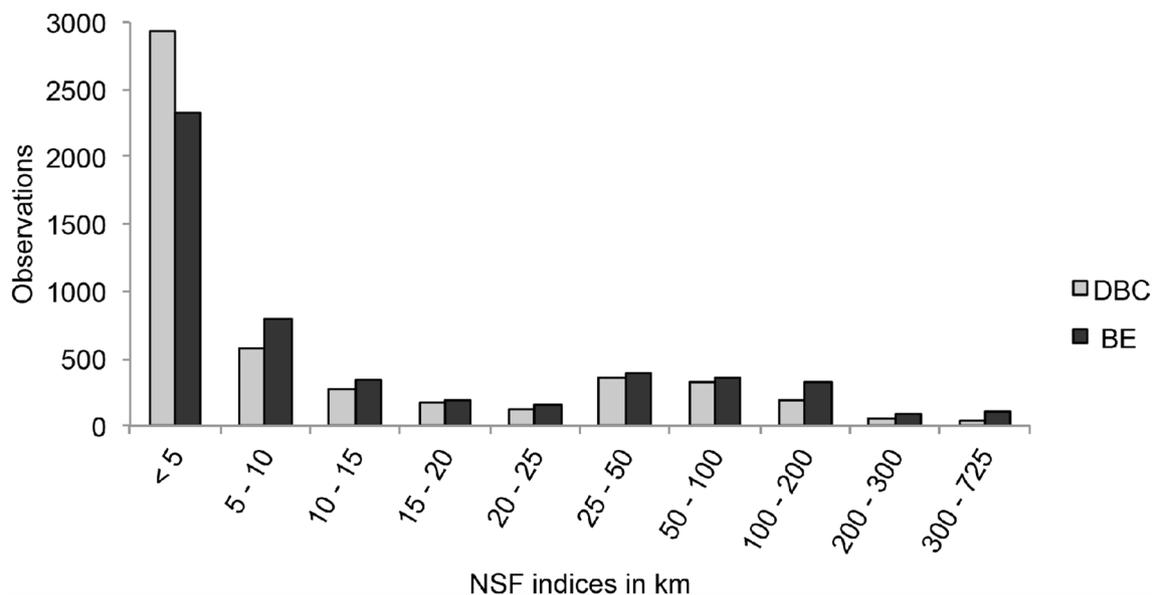


Fig. 2 Intra-seasonal nest site fidelity (NSF) indices for Northern Recovery Unit nesting females detected laying at least two clutches within a season. DBC is mean distance between clutches. BE is the distance between the most distant detected clutches within a season

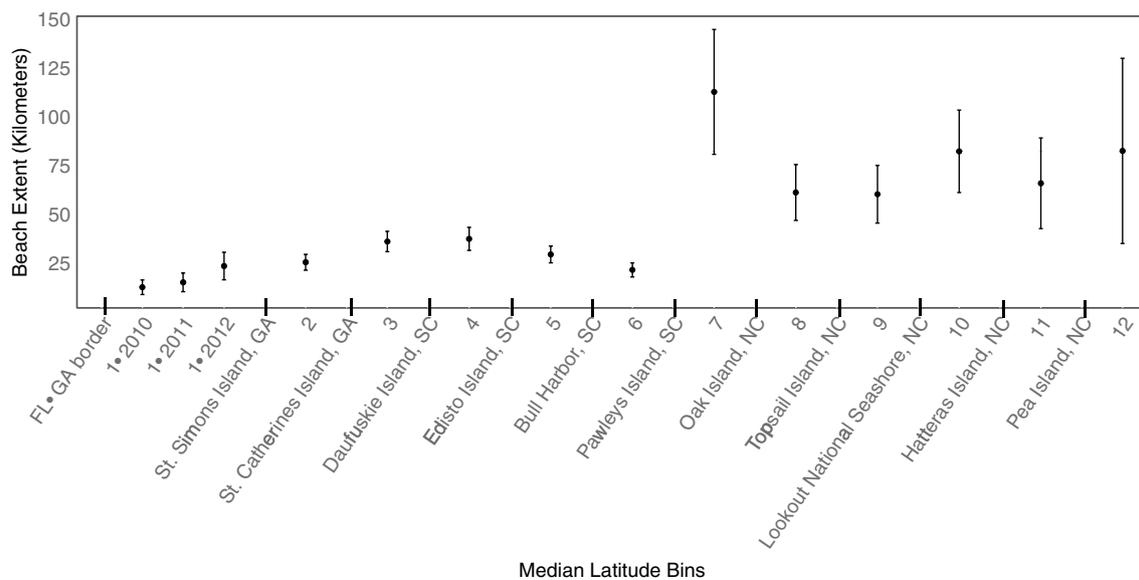


Fig. 3 Beach extent (the mean distance between the most distant clutches laid by individual females within each nesting season) in kilometers for Northern Recovery Unit loggerhead turtle females, based

on 0.45 decimal degree bins. Each female was assigned to a bin based on her median nesting latitude. Geographic locations of bin boundaries are indicated by *hash marks* on the *x-axis*

models also included time variation in detection probabilities (Table S-5 in Online Resource 1).

Annual nesting female population estimates from MSORD analyses were approximately 6% larger than empirically inferred counts (Table 1). MSORD-estimated ECFs were significantly higher than OCFs across all respective year-by-spatial pairwise comparisons, ranging from 4.28 to 4.63 clutches per female at the sub-population scale (Table 2).

Single-island versus regional comparisons

Between 44 and 64% of females that nested on a tagging beach also nested elsewhere during the same nesting season (Table 3). This resulted in 26–46% of assigned clutches laid by tagged females being deposited off of the tagging beaches. OCF for each of the six island-by-year physical tag datasets were significantly lower than OCF of the respective genetic tag datasets, resulting in downward biases of 26–49% relative to OCF generated from the regional genetic data (Table 3).

MSORD modeling of the physical tagging data did not alleviate this downward bias. ECFs from single-island datasets were significantly lower than their respective regional genetic ECF counterparts in five of the six comparisons (Table 3), biased low by 28–50%. Of the turtles that nested offsite of the tagging beach, a large majority (81%) “permanently” emigrated within the nesting season rather than returning to an initial nesting beach following emigration (Table 3). This resulted

in a large proportion of females being observed only once at the scale of the individual tagging beach (Fig. 4).

Discussion

Variation in intra-seasonal nest site fidelity

Dispersal may be defined as the displacement between a natal site and site of first breeding (natal dispersal) or the displacement between different breeding episodes (breeding dispersal) (Greenwood 1980). Our data limit inference of site fidelity to the context of breeding dispersal because the natal origins of the nesting females identified in the present study are unknown. Nonetheless, these NSF indices provide preliminary data on the potential scale of demographic connectivity across the rookeries comprising the NRU, in the absence of direct and indirect data on natal dispersal.

Loggerhead turtles are generally considered to exhibit strong NSF, with early assessments based on flipper tagging projects indicating that most females return to nest within 5 km of a previous nesting site (Schroeder et al. 2003). Our results confirm that a majority of nesting females exhibit relatively strong NSF within a nesting season, with approximately 47% of observed intra-seasonal BEs covering less than 5 km and 73% less than 20 km. Many females nested on multiple barrier islands, but did so within a relatively small region. Given this scale of NSF, local sources of mortality such as fisheries or development

Table 3 Nest site fidelity and clutch frequency metrics for females that nested on tagging beaches

	% Fem	% Mig	% Nests	Single-island OCF	Regional OCF	SI OCF bias (%)
Jekyll-2010	49	86	32	2.35 (2.00–2.70)	3.61 (3.29–3.93)	–34.9*
Jekyll-2011	44	82	26	3.02 (2.58–3.46)	3.90 (3.49–4.31)	–22.6*
Jekyll-2012	54	80	35	2.17 (1.86–2.48)	3.87 (3.56–4.18)	–43.9*
Wassaw-2010	64	82	42	2.23 (1.89–2.57)	3.70 (3.39–4.01)	–39.7*
Wassaw-2011	54	73	46	1.96 (1.67–2.25)	3.80 (3.52–4.08)	–48.4*
Wassaw-2012	59	84	41	1.95 (1.66–2.24)	3.17 (2.88–3.46)	–38.5*
				Single-island ECF	Regional ECF	SI ECF bias (%)
Jekyll-2010				3.19 (2.55–3.83)	4.54 (3.85–5.24)	–29.7*
Jekyll-2011				3.64 (3.01–4.26)	4.42 (3.92–4.92)	–27.5
Jekyll-2012				2.94 (1.50–4.38)	5.36 (4.76–5.96)	–45.1*
Wassaw-2010				2.63 (2.18–3.07)	4.51 (3.99–5.03)	–41.4*
Wassaw-2011				2.22 (1.45–3.00)	4.43 (4.02–4.83)	–49.9*
Wassaw-2012				3.23 (2.42–4.03)	5.61 (4.93–6.28)	–42.3*

% Fem is the proportion of females that nested off the tagging beach. % Mig is the proportion of females that nested offsite of the tagging beaches and that did not return to an original nesting site within the same season. % Nests is the proportion of detected clutches laid off the tagging beach by females that emerged at least once on a tagging beach. Single-island OCF is the mean observed clutch frequency based solely on single-island observation data along with 95% confidence interval. Regional OCF is the mean observed clutch frequency generated from complete tagging and genetic data along with 95% confidence interval. The biases represent single-island data relative to the complete regional dataset. ECF are the model-averaged estimated clutch frequency versions of these metrics estimated from multistate open robust design modeling in program MARK along with 95% confidence intervals

* Indicates significant difference between single-island and regional estimates

projects could have profound effects on local population recovery. Managers should consider the effect of strong NSF on local nesting populations when reviewing permits for activities that may result in adult female mortality.

Although a majority of females exhibited strong NSF, our indices suggested weaker NSF than those previously reported at the population scale by night patrols in the southeastern USA (DBC <7 km, Schroeder et al. 2003). The exception was a DBC of 17.5 km reported from Hutchinson Island, Florida, which was driven by a single female's long distance dispersal (Worth and Smith 1976). Breeding dispersal to distant beaches within or across seasons has been considered relatively rare (e.g., Bjørndal et al. 1983). Our results suggest that although these long distance relocations do comprise a small minority of inter-nesting movements, they are nonetheless more common than previously reported. The NRU DBC of 22 km and BE of 34 km are consistent with recent satellite telemetry results from northwestern Florida (DBC of 27.5 km) and central western Florida (BE of 28 km) indicating weaker NSF than previously characterized through flipper tagging studies (Hart et al. 2013; Tucker 2010). The telemetry and genetic capture-recapture results highlight the methodological advantages of regional approaches in capturing the full range of NSF behaviors in marine turtle populations that might go undetected from the perspective of a single nesting beach.

Studies of genetic structuring of mitochondrial DNA lineages have demonstrated that female marine turtles home to natal regions to nest (Jensen et al. 2013), and evidence suggests that loggerhead turtles navigate the open ocean and ultimately home to natal regions to nest via geomagnetic imprinting to the natal beach as hatchlings (Fuxjager et al. 2014; Brothers and Lohmann 2015). However, the precise scale of natal homing and the mechanisms underlying the final nesting beach selection process are not fully understood. Salmon use olfactory cues to complete this final phase of navigation (Dittman and Quinn 1996), and marine turtles are capable of detecting airborne and waterborne cues (Grassman et al. 1984; Endres et al. 2009). Navigation is likely a multi-phasic process and may require integration of multiple cues for final nesting beach selection (Endres et al. 2016). For NRU loggerhead females, NSF was lower in northern rookeries relative to southern ones with the apparent break corresponding to a marked transition in coastal geomorphology. Cape Island marks the southernmost of four cusped forelands (capes) that are spanned by large, concentric arcs of coastline. Cape Island exhibits significantly different geomorphology than the other prominent capes in the region, likely due to extensive erosion that has occurred over the last few centuries (Hayes and Michel 2008). Cape Island's beaches are steep, high-energy environments, representing some of the most erosional coastline in the state of SC. By contrast, Long

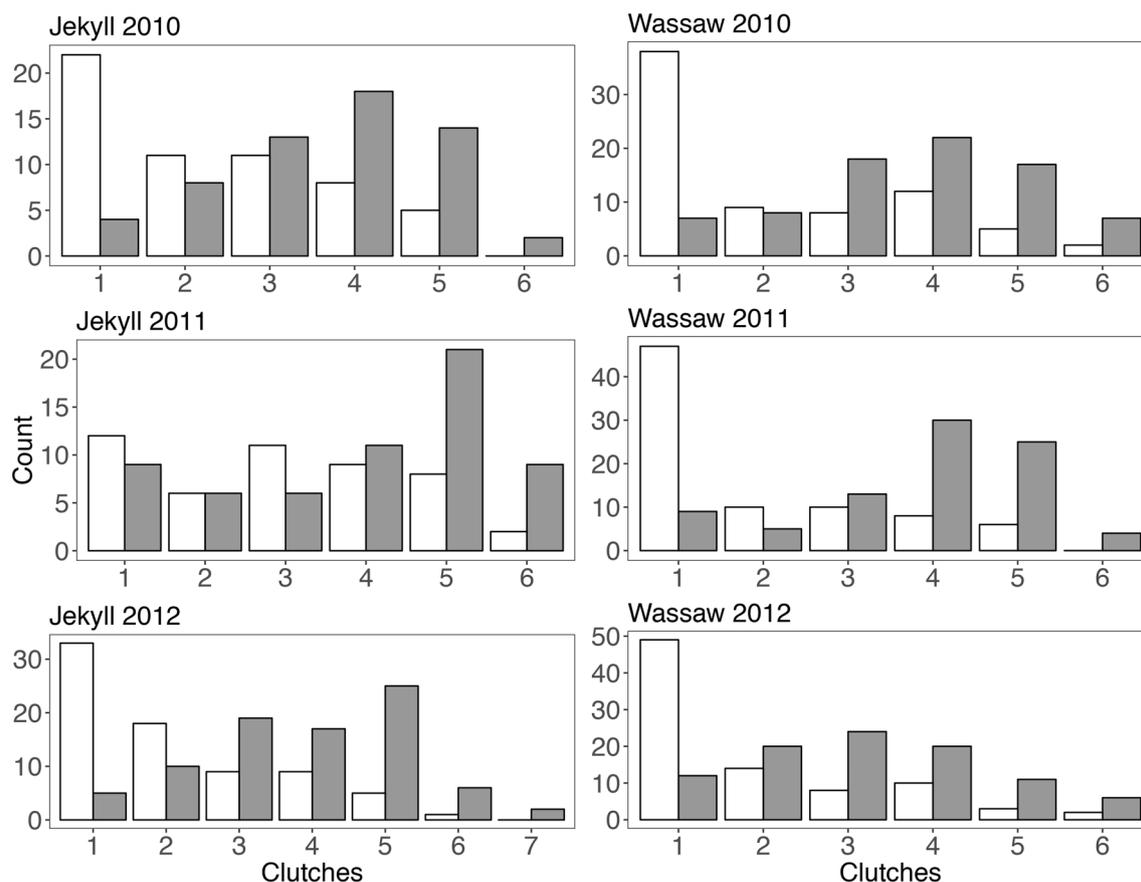


Fig. 4 Observed clutch frequency distributions for female loggerhead turtles nesting on Wassaw Island, Georgia and Jekyll Island, Georgia based on single-island and regional detections during the

2010 through 2012 nesting seasons. *Unfilled bars* represent detections from single-island data. *Gray bars* represent the regional genetic detections

Bay, which spans the SC and NC coasts between Cape Island and Cape Fear, represents a low energy environment (Hayes and Michel 2008).

Fine-scale spatial analyses of loggerhead turtle nesting densities on Florida index beaches revealed remarkable conservation of relative density peaks and valleys over a long time series, and the maintenance of these patterns was attributed to strong NSF of females to these particular nesting areas (Witherington et al. 2009). These spatial patterns in nesting densities reinforce the hypothesis that local cues, such as coastal geomorphology, may be important for marine turtle nesting beach selection (Putman et al. 2010; Shamblin et al. 2015). Loggerhead turtles nesting along the Atlantic coast of Florida appeared to prefer steeply sloped, coarse-grained beaches (Provancha and Ehrhart 1987). Analyses of the spatial distribution of emergences in northwest Florida suggested that female nest site selection was driven by the nearshore environment, with preferences for areas with steep offshore slope and the highest historical rates of erosion (Lamont and Houser 2014). Cape Island represents the densest rookery north of Florida

(NMFS and USFWS 2008) and its beaches are characterized by this steeply sloped, highly erosional habitat. Our results therefore suggest that local nesting beach selection cues may affect nesting densities by driving stronger NSF in areas with stronger cues. The presence of NSF variation within a single recovery unit highlights potential variation in population-scale NSF among stocks, which should be considered in demographic assessments.

Nesting female population size and clutch frequency estimates

Prior to this study, the most recent NRU nesting female population estimate was 3010 (95% confidence interval: 1540–4328) individuals based on nest counts from the 2001 through 2010 nesting seasons (Richards et al. 2011). The empirically derived count of 5687 females eclipses the previous estimate by a large margin. Higher population estimates generated by our study likely reflect population increases given increased nest counts over this period. As an example, loggerhead nest counts from comprehensive

surveys of GA beaches have been increasing at a rate of 2.9% annually from 1989 to 2016 (M. Dodd, Georgia Department of Natural Resources, unpublished data). However, even this new abundance estimate should be treated as a minimum because remigration intervals of three years or greater comprise a large proportion of the observed breeding intervals in Northwest Atlantic loggerhead turtle populations (48–70%) (Richards et al. 2011). Given the three-year span of the present study, a significant proportion of the adult female population likely did not nest during the study period and were therefore unavailable for detection. Analysis of a longer time series will be required to refine estimates of reproductive adult female abundance and assess remigration intervals for this subpopulation.

Researchers employing MSORD analysis of physical tagging data have reported a range of ECFs for subpopulations representing the Northwest Atlantic Distinct Population Segment, with the number of clutches per female estimated at 3.10 (2.05–4.14) in northwestern Florida (Lamont et al. 2014), 3.83 (3.61–4.04) in southwestern Florida (Phillips et al. 2014), and 2.44 (2.26–2.62) for Wassaw Island, GA females (Pfaller et al. 2013). Our higher NRU scale estimates of 4.28 (4.02–4.54) to 4.63 (4.45–4.80) clutches per female are more consistent with the 4.5 clutches per female inferred via satellite telemetry (Scott 2006), highlighting the value of increased detection by employing a regional perspective that more effectively captures the range of NSF exhibited within the NRU subpopulation.

Estimates of adult population size are critical for evaluating population status for conservation. For most marine turtle studies globally, nesting female population size is estimated by dividing nest counts by a mean ECF value; therefore, large variation in fecundity estimates can have a profound impact on population estimation (Tucker 2010). Frazer and Richardson (1985) reported annual corrected clutch frequencies for Little Cumberland Island, GA females that ranged from 3.06 to 4.18 over a 10-year period. This may represent biologically relevant variation in reproductive output related to foraging resources. Alternatively, these annual differences could be an artifact of detectability driven by variation in the relative proportions of weak and strong NSF females in each annual cohort. In this study, NRU OCF was higher in 2011 compared with 2010 and 2012, but ECF was not different across seasons. This suggests that at least some of the apparent annual variation previously reported may have arisen via differences in detection due to the limited geographic scope of the tagging studies. Dividing nest totals from 2010 through 2012 by the range of ECF from the three years resulted in an approximately 10% spread of nesting female population estimates, so the variation in ECF over the three-year period of the study had a relatively small effect on nesting population estimates. Nonetheless, periodically validating

clutch frequency at the subpopulation level is warranted, given its importance in generating robust abundance estimates (Richards et al. 2011).

Effects of nest site fidelity on parameter estimation

Variation in NSF at the individual level has been recognized as a significant challenge in generating robust clutch frequency estimates for marine turtles (Schroeder et al. 2003). Females observed laying only a single clutch comprise a significant proportion of the marked population in most marine turtle flipper-tagging studies globally (e.g. Broderick et al. 2002; Johnson and Ehrhart 1996; Rivalan et al. 2006; Pfaller et al. 2013; Lamont et al. 2014). Notable exceptions to this pattern are hawksbill turtles (*Eretmochelys imbricata*), which typically nest on pocket beaches and are considered to exhibit the strongest NSF and highest recapture rates among marine turtle species (Richardson et al. 2006). For example, hawksbills detected laying only a single clutch within a season at Jumby Bay, Antigua represented only 6% of females (Richardson et al. 1999). In contrast to all other loggerhead turtle nesting capture-recapture studies globally, females detected laying only a single clutch comprised a minority of the females in the present study, from 15 to 25% of each state cohort. However, it is still unclear whether single-clutch production could represent a real behavior in a minority of nesting females, possibly neophytes, or may arise entirely via imperfect detection or spatial coverage of nesting distributions. Continuation of the capture-recapture project would permit clutch frequency distribution comparisons between neophyte and remigrant females.

The discrepancy between observed and estimated clutch frequencies in NC relative to the other states highlights this potential detection issue. Females detected laying just one clutch were nearly twice as common (proportionally) in NC relative to SC and GA. These single-clutch observations from NC were not clustered at the beginning of the season, which might be expected in cases of mortality near the nesting beach. Nor were they clustered toward the end of the season, which might result from weak site fidelity females laying a final clutch on their way to northern foraging areas from nesting beaches south of our study site (see Ceriani et al. 2012, Pajuelo et al. 2012). OCFs were lower in NC compared to those in the south, but ECFs for NC were not lower with the exception of the 2011 NC versus SC comparison. Detection probabilities were consistently lower for NC than SC and GA. For example, the top models for both NC and GA in 2010 included constant detection probabilities across secondary periods with $p = 0.61$ for NC and $p = 0.81$ for GA.

It is difficult to account for this apparently lower detection probability on the basis of observation as the NC coast

was nearly completely covered by morning surveys spatially and temporally. Two islands, Masonboro and Lea-Hutaff (comprising ~2% of the NC coastline), were surveyed less than daily over the nesting season because of logistical constraints given the remote nature of the islands. Additionally, Brown's Island (~1% of the NC coast), which is part of the Marine Corps Base Camp Lejeune, was not surveyed at all due to the possibility of unexploded ordnance. One potential explanation is that some NC nesting emergences went undetected or were misidentified as non-nesting emergences. The northern half of the NC coast experiences higher wind speeds than in SC and GA (Elliott et al. 1986), which could perhaps lead to more nesting crawls being effaced before they can be detected on morning patrols. Alternatively, given that detection probability represents the product of detection and availability, some of these females may have been unavailable for detection because they also nested outside of the study area (Florida). We consider such a scenario unlikely given the strong regional structuring of mitochondrial DNA lineages across Florida's Atlantic coast (Shamblin et al. 2011a). Finally, it is possible that some apparently "missed" clutches actually represent extended inter-nesting intervals, given that inter-nesting intervals are inversely correlated to water temperatures within and across nesting populations (Sato et al. 1998; Hays et al. 2002). Of all NRU nesting habitats, NC would be most affected by colder temperatures caused by upwelling events given its closer proximity to the Gulf Stream relative to the other states. Future utilization of GPS telemetry coupled with temperature sensors would be one option for verifying the capture-recapture data and establishing ranges of inter-nesting intervals under different ocean conditions.

The MSORD framework provides a means of incorporating a transient effect on survival estimation to partially account for downward bias caused by permanent emigration (Monk et al. 2011), but current analytical approaches cannot fully account for transience in clutch frequency estimation. Comparisons between single-island and regional capture-recapture data clearly demonstrated downward biased clutch frequency estimates despite using the same MSORD approach to analyze both data sets. "Permanent" emigration represents a significant challenge for generating robust clutch frequency estimates even for marine turtles which have been considered to exhibit strong NSF, as most females were detected only once on a given tagging beach. Moreover, a longer time series will be required to assess inter-seasonal NSF and potential biases in remigration interval and adult female annual survival estimation.

Much of our foundational knowledge of marine turtle reproductive ecology has come from physical tagging projects on nesting beaches, and these remain critical for conservation and monitoring efforts. These projects

provide important life history and demographic data, as well as information that can only be obtained through direct interactions with nesting females, including but not limited to: morphometrics, reproductive physiology, nesting population and individual health assessments, and epibiota descriptions. Additionally, important ecological assessments and population viability projections involve direct observations of turtle behavior and their response to habitat quality, which involves studying not only their successful nesting events but their false crawls (non-nesting events). Further, and critically, conservation objectives related to endangered species recovery include increasing public awareness, which is a central focus of the tagging projects referenced in this project. In addition to the important public education benefits, many developed beaches require immediate intervention with onlookers in order to manage for successful nesting attempts.

Our analyses highlight the need for characterizing the relevant spatial scale for assessing individual movements and extrapolating to population-level demography. Despite recognition that most individual loggerheads exhibited relatively strong NSF, nesting on islands adjacent to the tagging beaches often lead to capture histories that failed to inform detection. We therefore encourage cautious inference of clutch frequency estimates using data generated from individual nesting beaches. Satellite telemetry offers one alternative for estimating clutch frequency and quantifying nest site fidelity. However, the expense of the transmitters and data processing necessarily limits sample sizes, potentially raising concerns about capturing a representative sample of the nesting population for transmitter deployment. Moreover, battery life and transmitter retention issues limit the utility of telemetry as a means of assessing inter-seasonal reproductive parameters. Genetic capture-recapture offers a novel tool for making these demographic inferences in marine turtle populations. Although this approach may not be feasible at the subpopulation scale long-term, having a snapshot of data at this scale identified the spatially explicit patterns of NSF that may have otherwise gone undocumented. These types of insights should prove valuable for choosing index sites for long-term monitoring in species that may be displaying cryptic behavioral polymorphisms that might not be recognized from smaller spatial perspectives. Future research should address the feasibility of an index beach sampling approach by determining the accuracy and precision of parameter estimates generated from various scales of spatial subsamples relative to the complete dataset. Long-term capture-recapture studies might best be achieved through a combination of physical tagging on core study beaches supplemented by genetic capture-recapture in adjacent buffer areas. Regardless of how individual identification data are generated, a

regional approach that integrates data from multiple nesting beaches will provide more robust inferences of reproductive parameter estimates in marine turtle populations.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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Human and animal rights statement All applicable national and institutional guidelines for the care and use of animals were followed (UGA Animal Care and Use Permit A2009 3-050 and permitted by the individual state sea turtle management agencies under the authority of the United States Fish and Wildlife Service).

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