



One beach amongst many: how weak fidelity to a focal nesting site can bias demographic rates in marine turtles

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Abstract

In migratory marine species, demographic estimates are often generated from capture-mark-recapture (CMR) studies conducted at terrestrial breeding sites. However, when logistical difficulties limit the geographic area of these surveys, demographic estimates are vulnerable to biases. We compared demographic rates generated from CMR data of nesting loggerhead turtles (*Caretta caretta*) collected between 2010 and 2017 at one focal site (Wassaw Island, Georgia, USA; 31.89° N, 80.97° W) with estimates generated from the same group of turtles but including all other nesting events from adjacent sites in Georgia, South Carolina, and North Carolina. We found that estimates of annual recruitment at the focal site were overestimated: each year, 29–45% putative first-time nesters at the focal beach had, in fact, nested on a different beach in a previous season. Estimates of clutch frequency and breeding frequency generated at the focal site were biased low and skewed towards values of one, while estimates for remigration interval were not significantly over- or underestimated. Additionally, estimates of annual and total population productivity in terms of clutches, eggs, and hatchlings were underestimated by more than half at the focal site. Our results show how weak fidelity to a focal nesting/tagging site can affect demographic estimates in marine turtle populations and highlight the need to reconsider estimates from other populations that might be vulnerable to similar biases.

Keywords Marine turtles · Nest site fidelity · Capture-mark-recapture · Loggerhead sea turtle

Introduction

Accurate estimates of key demographic rates like recruitment and productivity are critical for evaluating the population status of threatened marine species and developing effective management strategies (Williams et al. 2002; NRC 2010). However, wide dispersal and cryptic habitat-use patterns often limit opportunities to collect these critical demographic data (Heppell et al. 1999). For many species of marine megafauna, including pinnipeds, seabirds, and marine turtles, opportunities arise when individuals aggregate at terrestrial breeding sites. Capture-mark-recapture (CMR) studies conducted at such sites have proved invaluable for population assessments of these species (Musick 1999), but weak or variable site fidelity complicates our ability to estimate accurate demographic rates when surveys do not encompass the entire breeding area (Tucker 2010; Shamblin et al. 2017). Failure to account for demographic biases associated with weak site fidelity to a sampling area

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can confound population assessments and mislead management decisions.

Accurate assessments of marine turtle populations are inherently challenging (Bolten 2003; NRC 2010). Long life spans, delayed sexual maturity, and transoceanic migrations make individuals inaccessible during most of their lives, especially as juveniles. Although in-water studies of marine turtles provide the most direct and complete assessments of population-wide demography and stability (Hamann et al. 2010), nesting beaches, where female turtles emerge from the ocean to lay eggs, have provided and will continue to provide the most accessible opportunities for monitoring population status and productivity over time (Meylan 1982; Eckert et al. 1999; Tucker 2010). Logistical difficulties, however, can limit the area covered by nesting beach surveys, causing the sampling area to be smaller than the nesting area as defined by the degree of individual nest-site fidelity (NSF)—the proximity of nesting events within and between breeding seasons (Tucker 2010; Shamblin et al. 2017, 2021). If NSF is weak relative to the sampling area, then a significant proportion of nesting events may occur away from a focal or index nesting site and estimates of key demographic rates would be prone to biases. Conversely, if NSF is strong and CMR studies conducted at focal nesting sites account for a large proportion of nesting events by breeding individuals, then the potential for demographic biases would be less of a concern.

Data from tag returns, satellite telemetry, and genetic CMR studies of marine turtles indicate that individual nesting ranges are often greater than expected, especially at continental nesting sites (i.e., not on oceanic islands) (e.g., Williams and Frick 2008; Tucker 2010; Esteban et al. 2017; Shamblin et al. 2017, 2021). In particular, loggerhead turtles (*Caretta caretta*) in the Northern Recovery Unit (NRU; NMFS and USFWS 2008) of the southeastern United States nest across ~ 1000 km of coastline from north Florida to Maryland and individuals deposit clutches on multiple nesting beaches within and between breeding seasons. Using genetic CMR via subpopulation-wide egg sampling, Shamblin et al. (2017, 2021) showed that while the majority of NRU females (> 70%) show relatively strong intra- and inter-seasonal NSF (< 20 km), the remainder of females deposit clutches ranging from 20 to 725 km apart. Prior to these studies, demographic rates used in population assessments were estimated from data collected at focal long-term monitoring sites, where nocturnal patrols intercept and mark nesting females with individualized tags (Frazer 1983; Hawkes et al. 2005; Ondich and Andrews 2013; Pfaller et al. 2013). However, at each long-term monitoring and tagging site in the NRU, the sampling area covered by nocturnal patrols is currently or was < 20 km in length (Shamblin et al. 2021), suggesting that a significant proportion of nesting events by females that were encountered at focal monitoring sites

likely occurred at adjacent unmonitored sites both within and between breeding seasons. Like other marine turtle monitoring programs around the world, CMR studies conducted at focal nesting sites that encompass only a portion of the nesting area, as defined by individual NSF, risk generating biased demographic estimates that can mislead conservation efforts.

The goal of this study was to compare demographic rates and metrics of population productivity estimated from data collected at a focal nesting/tagging site in the NRU (Wassaw Island, Georgia) with rates generated from the same group of turtles but including all other nesting events from adjacent sites in Georgia, South Carolina, and North Carolina (Fig. 1). The Caretta Research Project has monitored loggerhead nesting activity on Wassaw Island since 1973 (Williams and Frick 2001; Pfaller et al. 2013), representing one of the longest continuously running CMR programs for marine turtles in the world. More recently, the discovery that freshly laid eggshells contain maternal DNA has allowed for genetic CMR of individuals across almost the entire NRU nesting range, including Wassaw Island (Shamblin et al. 2011b, 2017, 2021). This scenario provides the unique opportunity to evaluate how weak or variable site fidelity to a focal terrestrial breeding site can affect demographic estimates in a threatened marine species.

Methods

Focal study site

Tagging and monitoring of nesting loggerhead turtles on Wassaw Island, Georgia, USA (31.89° N, 80.97° W; Fig. 1) was conducted by the Caretta Research Project (USFWS Permit No. 2018–2025 and GADNR Licensee No. 1000527963). During the loggerhead nesting season (May–August), nocturnal patrols were conducted by at least two research staff and up to eight volunteers from 2100 to 0600 h to intercept nesting females. Following oviposition or failed nesting, females were checked for and, if necessary, fitted with individualized tags. Inconel metal tags (style 681, National Band and Tag Company, Newport, Kentucky, USA) were fitted within the first, second or third large scale along the posterior edge of both front flippers and one Passive Integrated Transponder (PIT) tag (Trovan, Douglas, UK or Destron Fearing, St. Paul, Minnesota, USA) was implanted subcutaneously just proximal to the elbow region of the right front flipper. Tags were replaced if found to be lost upon recapture, such that every turtle (in most cases) returned to the water with the standard set of three tags (Pfaller et al. 2019).

Starting in 2008, genetic samples were collected from every female each season as part of larger regional and

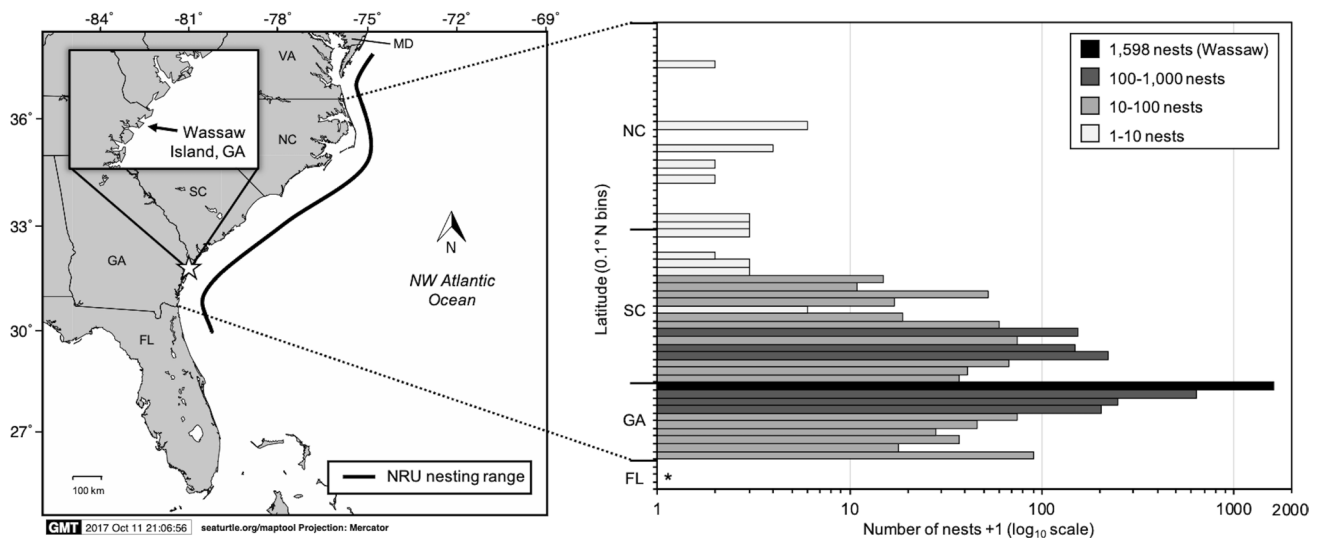


Fig. 1 Map showing the location of the Focal nesting/tagging site, Wassaw Island, Georgia, USA (31.89° N, 80.97° W; indicated by the star) and the primary nesting range for loggerheads in the Northern Recovery Unit (NRU). Graph showing the distribution of nesting events by 565 loggerheads that nested least once on Wassaw Island

between 2010 and 2017. Asterisk indicates that Florida was not included in NRU-wide genetic sampling. *FL* Florida, *GA* Georgia, *SC* South Carolina, *NC* North Carolina, *VA* Virginia, *MD* Maryland. Map was generated using the seaturtle.org Maptool (SEATURTLE.ORG Maptool 2002)

subpopulation-wide genetic studies (Shamblin et al. 2011b, 2017, 2021). Following oviposition or failed nesting, one 6-mm skin biopsy was collected from the shoulder region of each female one time per season (i.e., genetic samples were not collected during within-season recaptures of previously sampled females identified based on tags; see above). One eggshell was also collected from every clutch detected on Wassaw, regardless of whether or not the female was encountered or not (see below). All skin and eggshell samples were stored in 95% ethanol prior to DNA extraction and/or long-term storage.

NRU-wide genetic sampling

Starting in 2010, one eggshell sample was collected from every loggerhead clutch detected on nesting beaches between Georgia and Maryland, USA (~1000 km)—approximately 93% of ocean-facing nesting habitat was surveyed from May to August (80% daily). In most cases, freshly laid eggs were collected, emptied of their contents, and stored in 95% ethanol within 15 h of oviposition to preserve the maternal DNA and avoid embryonic contamination (Shamblin et al. 2011b). A small proportion of nests (5%) were detected greater than 15 h post-oviposition following nest depredation or hatchling emergence. In these cases, shells from undeveloped, hatched or predated eggs, and/or tissue from dead embryos or hatchlings were collected for genetic analysis. Whenever possible, eggs broken by predators, nesting females, or beach surveyors were used rather than sampling viable eggs. Procedures were permitted by the individual state sea turtle management

agencies under the authority of the United States Fish and Wildlife Service (North Carolina Wildlife Resources Commission, South Carolina Department of Natural Resources, and Georgia Department of Natural Resources).

Each eggshell sample collected from clutches detected across the NRU nesting range were genotyped and assigned a unique maternal identity. These samples include a small proportion of nesting events on Wassaw (5–10% nests/year), in which the female was not encountered (‘missed nests’) and eggshell samples provided the only means to identify the individual. Skin samples collected from females during their first encounter on Wassaw Island were also genotyped, which includes all untagged females and recaptured females originally tagged prior to 2008. Samples collected during subsequent recaptures of identifiable females (i.e., those with at least one tag) were not re-genotyped. DNA extractions were performed using QIAGEN DNEasy kits following protocol with modifications described by Shamblin et al. (2011b). Selected samples were genotyped using 18 microsatellite loci (described by Shamblin et al. 2007, 2009), with fragment analysis conducted at the Georgia Genomics Facility using a 3730xl DNA Analyzer (Applied Biosystems™).

Skin samples typically yielded high quality and quantity (> 20 ng/μl) DNA extracts, such that genotyping error rates generated from blind re-genotyping were very small (0.25%) (Shamblin et al. 2011b, 2017). Genotypes were compared using the program CERVUS (Kalinowski et al. 2010) and any that perfectly matched across a minimum of 10 loci and contained single allele mismatches at no more than two loci were assigned to the same individual. This buffer allowed us

to accommodate some genotyping failures and genotyping error (allele dropout and presence of non-maternal alleles in a small proportion of samples; Shamblin et al. 2011b) across samples without rerunning every sample until a complete genotype was obtained. The non-exclusion probability of sibling identity of the 10 least informative markers for these females was 1.03×10^{-5} , providing strong power for distinguishing even related individuals in the presence of low levels of genotyping error. Samples that failed to match a consensus genotype or another clutch by the criteria above at the end of each nesting year were subjected to a second round of DNA extraction and genotyping. See Shamblin et al. (2017) for more details on sample handling and genotyping methods.

Demographic rates

Demographic rates were estimated for the same set of individuals separated into two different datasets: (Focal) only nesting events documented on Wassaw Island and (All) all nesting events documented on Wassaw Island and across all other NRU nesting sites. The Focal dataset included nesting events on Wassaw in which individuals were identified via flipper tags, as well as a small proportion of nesting events in which individuals were missed but were subsequently identified via eggshell genotyping ('missed nests'; see above). Individuals in the All dataset were those documented nesting on Wassaw Island at least once during the study period (i.e., individuals in the breeding population that did not nest on Wassaw during the study period were not included in this study).

We quantified and compared four demographic rates between the Focal and All datasets, two within-season rates (1–2 below) and two between-season rates (3–4). Moreover, we quantified and compared three metrics of population productivity between the Focal and All datasets, each estimated both within each season and across all seasons combined (5):

1. *Recruitment*: Annual number and proportion of putative first-time nesters or new recruits to the breeding population (*termed* neophytes). In the Focal dataset, we classified turtles as 'neophytes' when they did not have tags or tag scars when first encountered on Wassaw or when a missed nest on Wassaw had a unique genotype never before detected on Wassaw. In the All dataset, clutches from 'neophytes' possessed a unique genotype that was eventually matched to a female after she was encountered on Wassaw, either during a subsequent nesting event in her first nesting season or in a subsequent season. When a turtle was detected nesting at a site other than Wassaw during her first nesting season, we classified her as a 'false neophyte' during her first season on Wassaw. For this metric, we excluded
2. *Clutch frequency*: Number of clutches laid by each turtle per season. We first estimated Observed Clutch Frequency (OCF) for both datasets using only *detected* clutches. However, because the interval between consecutive clutches is physiologically conserved within marine turtle populations (e.g., Wassaw loggerheads: mean \pm SD = 12.8 ± 1.8 days; Pfaller et al. 2013), past efforts to quantify clutch frequency often estimate Estimated Clutch Frequency (ECF) by adding *undetected* clutches when intervals between observed clutches are longer than expected (> 18 – 21 days; e.g., Frazer and Richardson 1985; Vander Zanden et al. 2014). Following a conservative approach used by Vander Zanden et al. (2014), we estimated ECF for both datasets by adding one clutch if two observed clutches were separated by ≥ 18 days; two clutches if two observed clutches were separated by ≥ 36 days; and three clutches if two observed clutches were separated by ≥ 54 days. The small proportion of clutches on Wassaw in which the female was not encountered and eggshell samples provided the only means to identify the individual ('missed nests') were included in the Focal dataset.
3. *Remigration interval*: Number of years between nesting seasons. Marine turtles rarely nest in consecutive years (remigration interval = 1). Instead, females skip one to several breeding seasons before *re*-migrating to breed again (remigration interval ≥ 2). In both datasets, females detected breeding during only one breeding season were, therefore, not included in calculations of remigration interval. Consequently, because some females that were detected remigrating once within the All dataset (remigration interval = 2) did not use Wassaw during both breeding seasons, fewer females were used to estimate remigration interval in the Focal dataset compared to the All dataset.
4. *Breeding frequency*: Number of breeding seasons per turtle during the 8-year study period. We excluded turtles that nested for the first time in 2016–2017 to avoid inflating the number of single breeding seasons, as these turtles would not have had an opportunity to re-migrate and breed more than once within the confines of the study period.
5. *Population productivity*: Number of clutches, eggs, and hatchlings produced per season (annual) and across all eight seasons combined (total). The number of eggs/clutch (i.e., clutch size) was estimated by either directly counting whole eggs when clutches were relocated shortly after deposition or by counting unhatched eggs and hatched eggshells following hatchling emergence. The number of hatchlings/clutch was estimated by mul-

tipling clutch size by emergence success (i.e., the proportion of eggs in each clutch that became viable hatchlings capable of emerging from the nest). The estimated number of eggs deposited and hatchlings produced in each clutch were summed across all clutches in each dataset.

Statistical analyses

We tested for differences in demographic rates estimated from the Focal and All datasets using an information criterion-based approach. We fit generalized linear models (GLMs) to each demographic variable and compared a null model, where we assumed no differences between the Focal and All datasets, to a model where demographic rates varied as a function of BEACH (i.e., Focal vs. All). Models were compared using Akaike's information criterion corrected for small sample sizes (AIC_C). Differences in AIC_C values (ΔAIC_C) between the best model (lowest AIC_C and highest Akaike weights) and the competing model were used to evaluate support for one model over another. When $\Delta AIC_C > 7$, then we concluded that there was strong evidence for one model over another (Burnham et al. 2011; Jerde et al. 2019). We used an evidence ratio to further evaluate the level of empirical support for each model comparison (Burnham et al. 2011). Post-hoc comparison were made using the R package emmeans (Lenth 2021).

For the proportion of neophytes estimated each season (recruitment), we fit a binomial distribution with a logit link function. Because the remaining demographic variables were count data (clutch frequency, remigration interval, and breeding frequency), we first fit a Poisson distribution with a log link function for each model and then checked for over- or under-dispersion. If over- or under-dispersion was detected, we refit the model with one of two distributions to compensate for unaccounted variation: a negative binomial distribution for over-dispersion (Hardin and Hilbe 2007) or a generalized Poisson distribution for under-dispersion (Joe and Zhu 2005). Models were fit in the R package glmTMB (Brooks et al. 2017). R code used to conduct these analyses are available on GitHub (http://github.com/constantin-george/Pfaller_et_al2021.git).

Results

A total of 565 unique individuals was identified using physical tags and multilocus genetic tags determined from DNA extracted from skin samples collected during each turtle's first encounter on Wassaw Island, the focal study site. On other beaches in Georgia, South Carolina, and North Carolina, we identified clutches laid by these individuals using the same multilocus genetic tags extracted from maternal

DNA found in the shell of freshly laid eggs (Fig. 1). In the Focal and All datasets, we detected the 565 individuals depositing 1,598 and 3,928 clutches, respectively (Table 1).

Within-season rates

For recruitment, or the percentage of neophyte turtles nesting each season, we found strong evidence that the inclusion of BEACH improved the model fit compared to the null model ($\Delta AIC_C = 72.2$; Table 2). The estimated proportion of recruits ($\pm 95\%$ profile CI) was 0.70 (0.66–0.74) at the focal site and 0.43 (0.39–0.47) when all nesting events were included (Fig. 2). The mean difference between the Focal and All datasets was 0.27 (Table 1). Each year 29–45% of putative first-time nesters were misclassified as neophytes ('false neophytes') at the focal site because they had in fact deposited clutches at other nesting sites during previous breeding seasons.

For both observed and estimated clutch frequency (OCF and ECF), we found strong evidence that the inclusion of BEACH improved the model fit over a null model ($\Delta AIC_C = 315.3$ and 384.9, respectively; Table 2). Model-estimated OCF ($\pm 95\%$ profile CI; N) was 2.25 clutches/turtle/season (2.15–2.35; 725) at the focal site and 3.54 clutches/turtle/season (3.44–3.64; 1,095) when all nesting events were included (Fig. 3a). Model-estimated ECF ($\pm 95\%$ profile CI; N) was 2.37 clutches/turtle/season (2.27–2.47; 725) at the Focal site and 3.91 clutches/turtle/season (3.80–4.02; 1,095) when all nesting events were included (Fig. 3b). Both OCF and ECF at the focal site were significantly underestimated (mean difference = 1.29 and 1.54 clutches/turtle/season, respectively) and skewed towards a modal value of one clutch/turtle/season (Table 1). Data are provided in Online Resource 1.

Between-season rates

We found weak evidence that the inclusion of BEACH improved the model fit for remigration intervals ($\Delta AIC_C = 2$; Table 1). The estimated remigration interval ($\pm 95\%$ profile CI; N) was 2.81 years (2.66–2.97; 162) at the focal site and 2.81 years (2.71–2.90; 527) when all nesting events were included (Fig. 4). The mean difference between Focal and All datasets was 0.01 years (Table 2).

We identified a total of 725 and 1,095 breeding seasons for the 565 turtles in the Focal and All datasets, respectively. For the number of breeding seasons per turtle between 2010 and 2017 (excluding turtles that nested for the first time in 2016–2017), we found strong evidence that the inclusion of BEACH improved the model fit over a null model ($\Delta AIC_C = 140.5$; Table 2). The estimated breeding frequency ($\pm 95\%$ profile CI; N) was 1.38 seasons/turtle (1.30–1.46; 470) at the focal site and 2.08 seasons/turtle (1.99–2.18; 470)

Table 1 Demographic rates for 565 loggerhead turtles estimated from nesting events documented on Wassaw Island (Focal) compared to nesting events documented across all NRU nesting sites (All) from 2010 to 2017 (data are provided in Online Resource 1)

Demographic rate	Parameter estimates ($\pm 95\%$ profile CI)		Comparisons/model statistics: mean diff., <i>p</i> value (<i>df</i> , test statistic)	Inference
	Focal	All		
Recruitment (2013–2017)				
Average proportion of neophytes/season	0.70 (0.66–0.74)	0.43 (0.39–0.47)	0.27, <0.0001 (8, <i>z</i> -ratio = 8.96)	Focal > All
Average number of neophytes/season	70.8	43.6	29–45% 'false neophytes'/season	Focal > All
Clutch frequency				
Average number of observed clutches/turtle/season (OCF)	2.25 (2.15–2.35)	3.54 (3.44–3.64)	1.29, <0.0001 (1817, <i>t</i> -ratio = –18.27)	Focal < All
Modal OCF	1	4	<i>no test or %</i>	Focal < All
Average number of estimated clutches/turtle/season (ECF)	2.37 (2.27–2.47)	3.91 (3.80–4.02)	1.54, <0.0001 (1817, <i>t</i> -ratio = –20.33)	Focal < All
Modal ECF	1	4	No test or %	Focal < All
Remigration interval				
Average number of years between seasons	2.81 (2.66–2.97)	2.81 (2.71–2.90)	0.01, 0.94 (686, <i>t</i> -ratio = 0.08)	Focal = All
Modal number of years between seasons	3	3	No test or %	Focal = All
Breeding frequency (2010–2017)				
Average number of breeding seasons	1.38 (1.30–1.46)	2.08 (1.99–2.18)	0.70, <0.0001 (937, <i>t</i> -ratio = –11.44)	Focal < All
Total number of breeding seasons	725	1,095	66.1% include Focal	Focal < All
Annual population productivity				
Average number of clutches/season	199.8	491.0	38–43% on Focal	Focal < All
Average number of eggs/season	20,540	47,960	38–46% on Focal	Focal < All
Average number of hatchlings/season	12,129	28,633	36–47% on Focal	Focal < All
Total population productivity (2010–2017)				
Total number of clutches	1598	3,928	40.7% on Focal	Focal < All
Total number of eggs	164,321	383,679	42.8% on Focal	Focal < All
Total number of hatchlings	97,935	229,067	42.4% on Focal	Focal < All

Parameter estimates ($\pm 95\%$ profile CI) were estimated from generalized linear models and back transformed from the log scale. Model statistics are presented for the BEACH model to show differences between the Focal and All datasets (see text and Table 2 for more details)

when all nesting events were included (Fig. 5). The mean difference between Focal and All datasets was 0.70 years (Table 1), indicating that, on average, nearly one nesting season per individual was missed at the focal site during the 8-year study period. Data are provided in Online Resource 1.

Population productivity

Estimates of annual population productivity in terms of clutches, eggs, and hatchlings were consistently underestimated at the focal site. Each year only 38–43% of clutches, 38–46% of eggs, and 36–47% of hatchlings produced by the 565 turtles were recorded at the focal site (Fig. 6). Similarly, estimates of total population productivity in terms of clutches, eggs, and hatchlings produced during the 8-year study period were underestimated at the focal site, with only 40.7% of clutches, 42.8% of eggs, and 42.4% of hatchlings produced between 2010 and 2017 being recorded at the focal site (Table 1; Fig. 6). Data are provided in Online Resource 1.

Discussion

The focal site in this study (Wassaw Island, Georgia), where a long-term nest monitoring and tagging program has been conducted since 1973, represented the predominant nesting site for turtles that used that site at least once during the 8-year study period (Fig. 1). However, because many turtles showed weak or variable NSF to Wassaw within and between breeding seasons, as revealed by subpopulation-wide genetic CMR, over half of all nesting events occurred away from the focal study site and were not accounted for in the Focal dataset. Consequently, we found that estimates of recruitment were overestimated and estimates of clutch frequency, breeding frequency, and population productivity were underestimated when only clutches deposited at the focal site were accounted for. Because biased estimates of key demographic rates, as well as metrics of population productivity, can mislead management decisions, it is critical for CMR studies to identify and account for the degree of site fidelity to a

Table 2 Model comparisons of demographic rates estimated from nesting events documented on Wassaw Island (focal) compared to nesting events documented across all NRU nesting events (All) by the same turtles ($N=565$)

Response	Conditional model	Distribution	Dispersion ^a	df	ΔAIC_C	Evidence ratio ^b	Akaike weights
Recruitment ^c	Null	Binomial	1	1	72.2	4.77e + 15	<0.001
	BEACH	Binomial	1	2	0		1
Obs. clutch frequency	Null	Generalized Poisson	0.85	2	315.3	2.92e + 68	<0.001
	BEACH	Generalized Poisson	0.78	3	0		1
Est. clutch frequency	Null	Generalized Poisson	0.93	2	384.9	3.80e + 83	<0.001
	BEACH	Generalized Poisson	0.82	3	0		1
Remigration Interval	Null	Generalized Poisson	0.44	2	0	2.71	0.73
	BEACH	Generalized Poisson	0.44	3	2.0		0.27
Breeding frequency	Null	Generalized Poisson	0.57	2	140.5	3.23e + 30	<0.001
	BEACH	Generalized Poisson	0.56	3	0		1

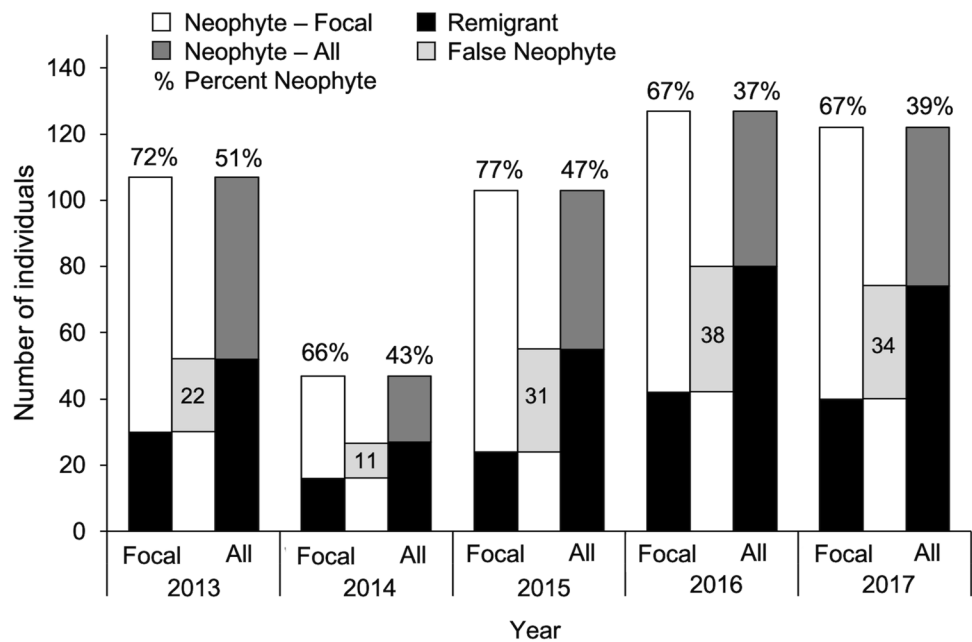
For each response variable, AIC_C values (Akaike’s information criterion corrected for small sample sizes) were compared between a null model, where we assumed no differences between the Focal and All datasets, and a model where demographic rates varied as a function of BEACH (i.e., Focal vs. All)

^aWhen the dispersion parameter is > 1 , there is evidence of over-dispersion, whereas values < 1 indicate under-dispersion. For the binomial model, the dispersion parameter is set to 1

^bThe evidence ratio is defined as $\exp(-1/2 * \Delta AIC_C)$ and where it is normalized so it sums to 1 it represents the Akaike weights. The evidence ratio indicates the support for the model with the lowest AIC_C over a competing model (e.g., support for the Null model of remigration intervals is 2.71 times that of the BEACH model)

^cRecruitment is the proportion of putative first-time nesters or neophytes detected each year

Fig. 2 Number and percentage of neophyte turtles (recruitment) relative to remigrants estimated from nesting events documented on Wassaw Island (Focal; white and black bars, respectively) compared to nesting events documented across all NRU nesting events (All; dark gray and black bars, respectively) by the same turtles between 2013 and 2017 (data are provided in Online Resource 1). Remigrant turtles that were misidentified as neophytes on Wassaw (termed ‘false neophytes’) are shown as light grey bars



sampling area and make efforts to expand the sampling area when individual NSF is comparably weak (NRC 2010; Pfaller et al. 2013; Shamblin et al. 2017). Moreover, past demographic estimates generated at focal nesting/tagging sites that encompass only a portion of the nesting area used by the nesting population within and between breeding seasons should be reevaluated and applied with caution.

Recruitment

Among CMR studies conducted at focal loggerhead tagging sites across the southeastern United States, putative first-time nesters or neophytes tend to comprise the majority of females encountered (Monk et al. 2011; Pfaller et al. 2013; Lamont et al. 2014; Phillips et al. 2014). Data collected at the focal tagging site in our study (Wassaw

Fig. 3 **a** Observed and **b** estimated clutch frequency generated from nesting events documented on Wassaw Island (Focal; white bars) compared to nesting events documented across all NRU nesting sites (All; black bars) from 2010 to 2017 (data are provided in Online Resource 1). Values in the captions represent back-transformed (log scale) parameters estimates ($\pm 95\%$ profile CI) from generalized linear models of each dataset

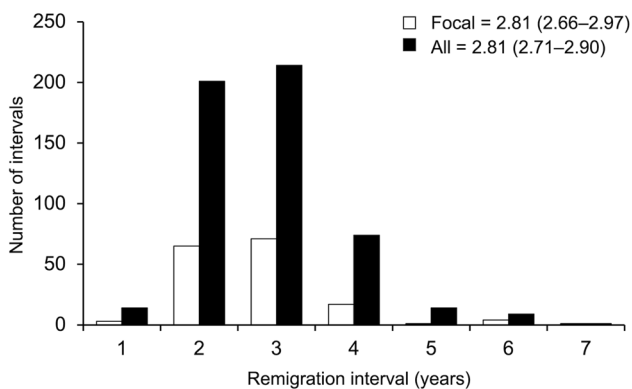
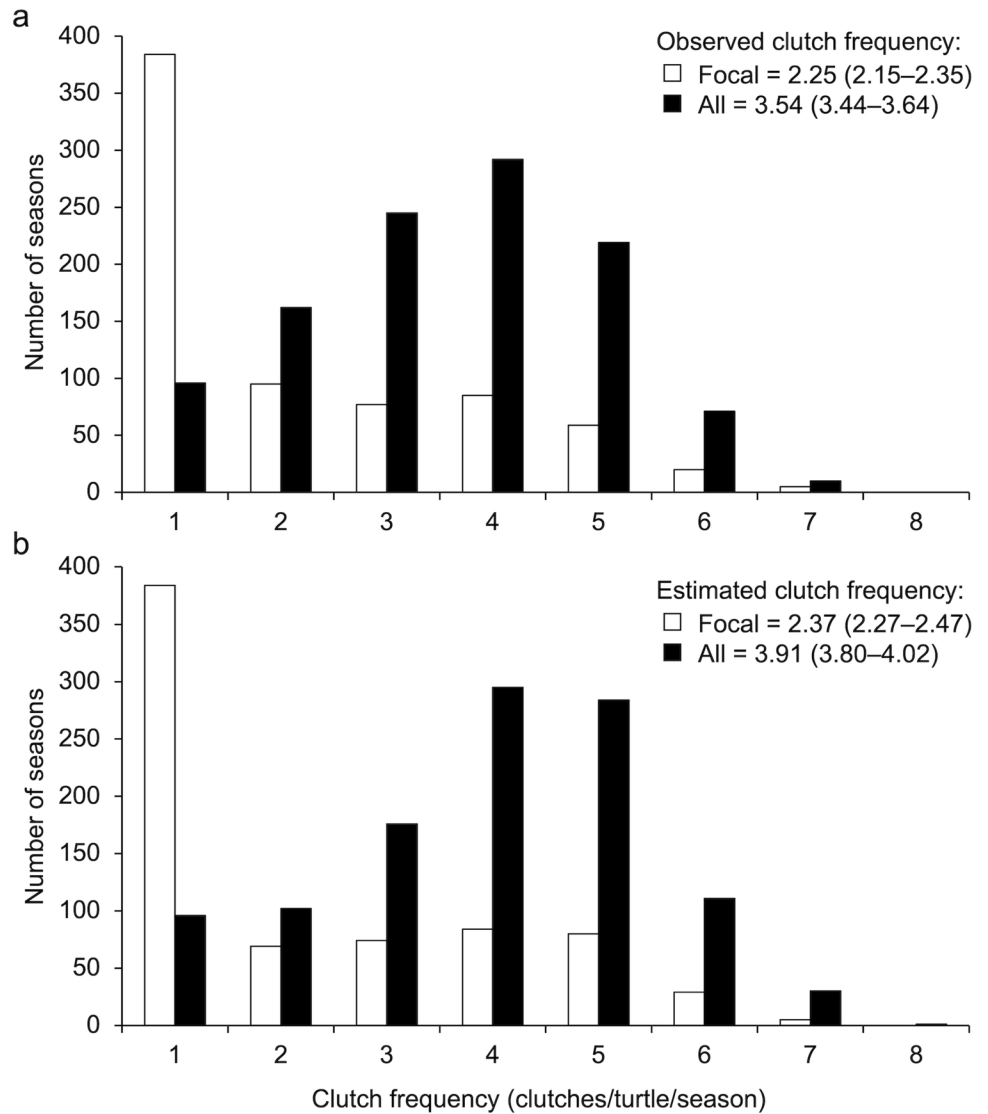


Fig. 4 Number of years between consecutive breeding seasons (remigration interval) estimated for nesting events documented on Wassaw Island (Focal; white bars) compared to nesting events documented across all NRU nesting sites (All; black) from 2010 to 2017 (data are provided in Online Resource 1). Values in the caption represent back-transformed (log scale) parameters estimates ($\pm 95\%$ profile CI) from generalized linear models of each dataset

Island) reflect the same pattern: putative neophytes comprised between 66 and 77% of the breeding population each season (Fig. 2). However, when we expanded our sampling area to include clutches deposited by the same group of turtles on beaches other than Wassaw, the percentage of neophyte turtles nesting each season decreased to less than 50% in every season except one—51% in 2013. Each year between 29 and 45% of females identified as neophytes on Wassaw had, in fact, deposited at least one clutch on a different beach during a previous breeding season. These ‘false neophytes’ were detected depositing up to six clutches on up to four different beaches, occasionally during two separate nesting seasons, prior to the first season that they were encountered on Wassaw. As we will discuss further below, failing to encounter individuals during their first breeding seasons can not only bias estimates of recruitment, but also estimates of individual productivity when a significant proportion of clutches, eggs, and

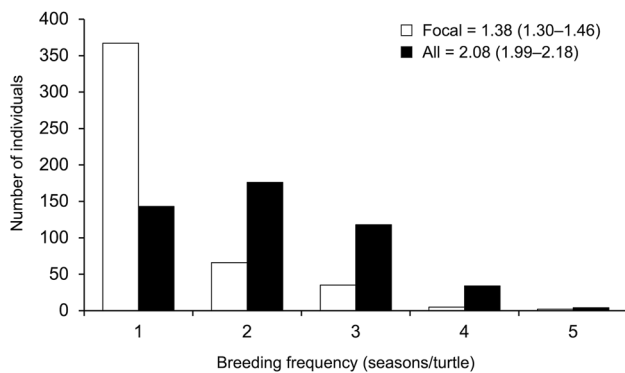


Fig. 5 Number of breeding seasons (breeding frequency) estimated for nesting events documented on Wassaw Island (Focal; white bars) compared to nesting events documented across all NRU nesting sites (All; black bars) between 2010 and 2017 (data are provided in Online Resource 1). Values in the caption represent back-transformed (log scale) parameters estimates ($\pm 95\%$ profile CI) from generalized linear models of each dataset. We excluded turtles that nested for the first time in 2016–2017 to avoid inflating the number of single breeding seasons, as these turtles would not have had an opportunity to remigrate during the study period

hatchlings are produced away from the focal tagging site during previous breeding seasons.

Measures of recruitment are important for determining population structure and interpreting trends in wildlife populations (Williams et al. 2002; NRC 2010). Recruitment into the breeding population is a critical life-history transition that is largely dependent on the environmental conditions that an individual experiences throughout juvenile development. For long-lived marine species, like marine turtles, this juvenile period may last one to several decades and may span entire ocean basins (Musick and Limpus 1997). The ability of juveniles to survive, find food, and avoid threats (natural and anthropogenic) dictates what proportion reach sexual maturity and eventually breeding status. For this reason, measures of recruitment are considered indicators of population health and the health of the habitats that support marine turtles (Stokes et al. 2014; Vander Zanden et al. 2014). Overestimating the annual number and proportion of neophytes at a focal tagging site may, therefore, falsely suggest that the environmental conditions that facilitate sexual maturity and recruitment are more favorable than they actually are. Accurate estimates of recruitment generated from CMR data collected at wider spatial scales that encompass the extent of individual NSF are critical for assessing population viability and managing ecological risk (Burgman et al. 1993).

In studies of marine turtle populations, failing to encounter and/or identify neophyte turtles during their first breeding season has important ramifications for generating accurate estimates of two key demographic rates: annual adult survival and age at sexual maturity. Estimates of annual adult survival, or the probability that an individual survives each

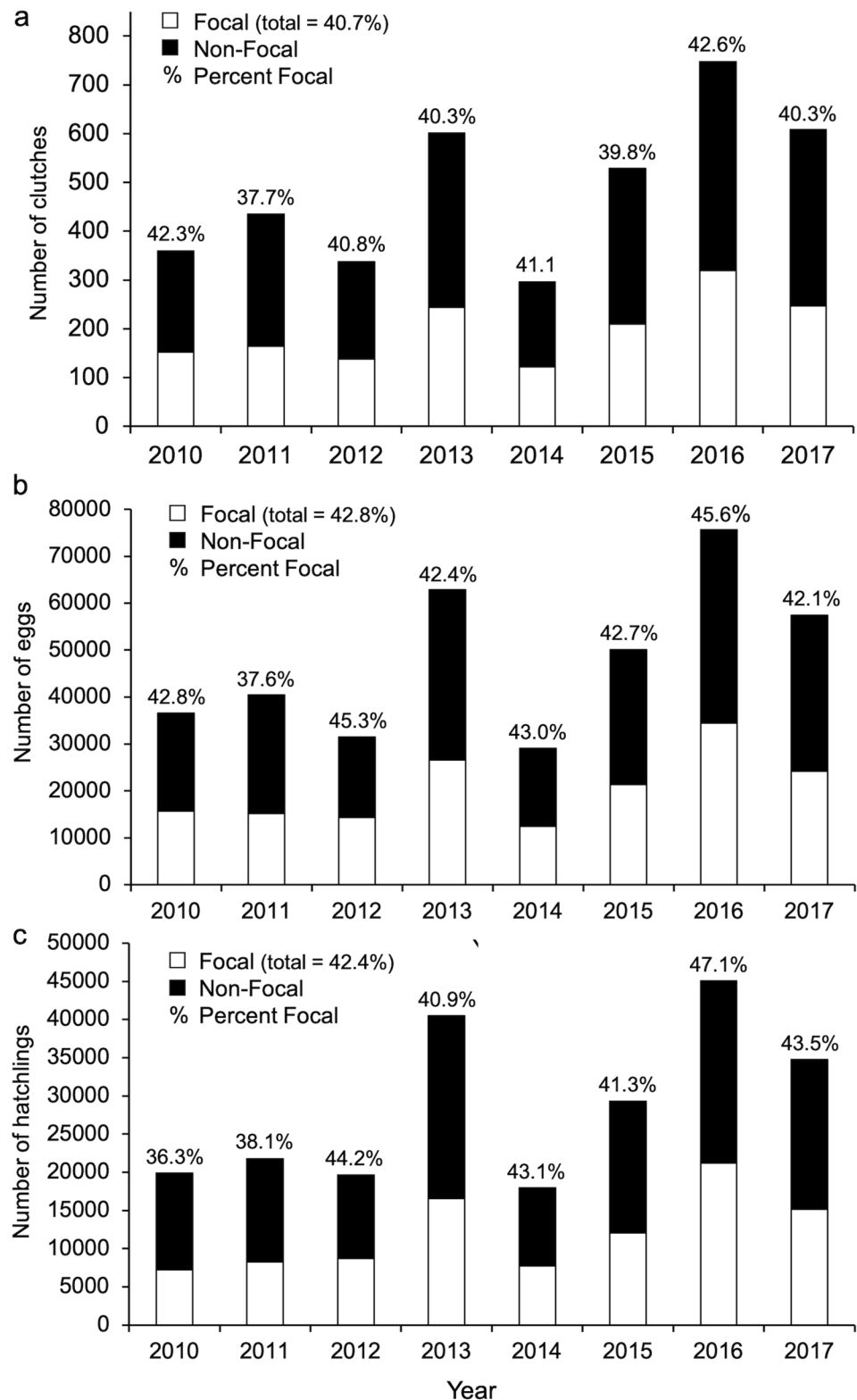
year of adult life, dictate the average number of years/seasons that each adult turtle is predicted to contribute to the breeding productivity of the population (Frazer 1983; Kendall and Bjorkland 2001). Accurate estimates of adult survival are, therefore, critical for evaluating threats and interpreting population trends (NRC 2010). Because estimates of annual adult survival are generated from inter-seasonal recaptures and marine turtles typically only breed once every 2–4 years (Miller 1997; Shamblin et al. 2021), failing to encounter a significant proportion of females at a focal tagging site during their first or even second breeding season can artificially truncate CMR histories for those individuals, causing the annual survival rate of the adult population to be biased low (Pfaller et al. 2018).

Age at sexual maturity (ASM) is an important but elusive parameter required for modeling population dynamics (Hep- pell et al. 1999, 2003). Studies that aim to determine the age- and stage-based structure of marine turtle populations frequently use measurements of neophyte body size collected at focal tagging sites as the baseline for size at sexual maturity (SSM; Scott et al. 2012; Avens et al. 2015). Estimates of ASM are then estimated by extrapolating juvenile growth trajectories toward estimates of SSM. Because loggerheads, as well as other marine turtles, grow relatively slowly as they approach sexual maturity (Bjorndal et al. 2013, 2017), minor differences in SSM can become magnified in resulting estimates of ASM (Avens et al. 2015). Unknowingly including body sizes of somewhat larger non-neophyte or remigrant turtles may, therefore, artificially increase estimates of ASM and affect the accuracy of population models. For this reason, correctly identifying neophyte status at focal tagging sites has important ramifications for understanding and conserving marine turtle populations.

Clutch frequency

Marine turtles are considered well-known for their seasonal fecundity and periodicity, in which females emerge multiple times per season to deposit large clutches of eggs at highly predictable intervals (Miller 1997). However, CMR data collected at focal tagging sites are not always consistent with this pattern. While some high-fidelity females are recaptured multiple times in a season (up to 6–10 times, depending on the species), the majority of females at many globally distributed tagging sites are encountered only once, resulting in average clutch frequencies that are closer to 2 rather than 4 or 5 (e.g., Alvarado-Díaz et al. 2003; Rivalan et al. 2006; Tucker 2010; Frey et al. 2014; Ekanayake et al. 2016). Given the discrepancy between what we expect and what we observe and the ramifications of generating inaccurate estimates of clutch frequency (see below), it is critical to evaluate potential sources of bias in CMR datasets collected at focal tagging sites.

Fig. 6 Number of **a** clutches, **b** eggs, and **c** hatchlings produced per season (annual population productivity) for nesting events documented on Wassaw Island (Focal; white bars only) compared to nesting events documented across all NRU nesting sites (Focal + Non-Focal; white + black bars) from 2010 to 2017 (data are provided in Online Resource 1)



At the focal tagging site in this study (Wassaw Island), we recorded 384 breeding seasons out of a total of 725 (53%) in which an individual deposited only one clutch, resulting in an OCF of 2.25 clutches/turtle/season ($\pm 95\%$ profile CI

2.15–2.35) and an ECF of 2.37 (2.27–2.97) (Fig. 3). However, when we included clutches deposited by the same group of turtles on beaches other than Wassaw, the percentage of single-clutch breeding seasons decreased to just

9% (96 out of a total of 1095), causing OCF to increase by 36% to 3.54 clutches/turtle/season (3.44–3.64) and ECF to increase by 39% to 3.91 clutches/turtle/season (3.80–4.02). Very similar results were found by Shamblin et al. (2017) for Wassaw during the 2010–2012 nesting seasons: average observed clutch frequency (OCF) on Wassaw ranged from 1.95 to 2.23, while average OCF for Wassaw + Non-Wassaw clutches ranged from 3.17 to 3.80. Because some females show high intra-seasonal NSF (47% < 5 km; Shamblin et al. 2017), they are more likely to be encountered at a focal tagging site during all or most of their nesting events. Conversely, females that exhibit weak NSF (27% > 20 km; Shamblin et al. 2017) relative to the sampling area covered by tagging patrols are more likely to be encountered only once at a focal tagging site. Such variable NSF among individuals clearly causes estimates of clutch frequency to be biased low and skewed towards one clutch/turtle/season when data from only a focal tagging site are analyzed. Moreover, the differences between OCF and ECF within each dataset were relatively small (0.12 in Focal and 0.37 in All) compared to the differences between the Focal and All datasets (1.29 for OCF and 1.54 for ECF). Therefore, adding undetected clutches between two observed clutches separated by a long interesting interval may improve estimates of clutch frequency, but it cannot overcome the limitations associated with weak or variable NSF to the focal tagging site.

Recent advances in statistical modeling and satellite telemetry have produced even higher estimates of clutch frequency for loggerheads in the Northwest Atlantic. The multistate open robust design (MSORD) statistical modelling framework is designed to estimate and account for changes in detection probability of animals at a given sampling location within and between sampling periods (Kendall et al. 1997; Schwarz and Stobo 1997; Kendall and Bjorkland 2001). The MSORD framework applied to CMR data collected at focal loggerhead tagging sites has produced average ECF values of 2.44 (2.26–2.62) on Wassaw Island (Pfaller et al. 2013), 3.83 (3.61–4.04) in southwestern Florida (Phillips et al. 2014), and 3.10 (2.05–4.14) in northwestern Florida (Lamont et al. 2014). However, when the MSORD approach was applied to subpopulation-wide CMR data in the NRU, ECF reached 4.28 (4.02–4.54) to 4.63 (4.45–4.80) depending on the year (Shamblin et al. 2017). Comparably high estimates of clutch frequency have been generated by counting nesting emergences of satellite-tracked females: 4.5 (4.12–4.88) in Georgia (Scott 2006) and 5.4 (5.1–5.7) in southwest Florida (Tucker 2010). In most cases, clutch frequency estimates generated at focal tagging sites are clearly biased low and skewed towards one clutch/turtle/season, even when the MSORD framework is used (e.g., Pfaller et al. 2013). Nevertheless, ECF estimates generated from Wassaw + Non-Wassaw CMR data in this study

were still somewhat lower than those from subpopulation-wide CMR modeling (Shamblin et al. 2017) and satellite telemetry (Scott 2006). These tools, therefore, might be better able to account for undetected clutches laid on monitored beaches or smaller unmonitored beaches within the extent of the sampling area (Georgia-Maryland), as well as those laid both early and late in the season and on beaches outside the sampling area in northeast Florida. Recent genetic evidence suggests that the NRU nesting area extends across the Georgia-Florida border, causing a small proportion of the total NRU nesting effort to fall outside the southern boundary of previous subpopulation-wide surveys (Shamblin et al. 2011a; BMS, unpubl data).

Biased estimates of clutch frequency can mislead management assessments of marine turtle populations that rely on annual clutch counts for estimating adult population abundance and monitoring population trends (e.g., Peninsular Florida; Richards et al. 2011). Because logistical limitations often prevent marking or identifying individual turtles on nesting beaches, estimates of clutch frequency are used as the conversion factor between annual clutch counts and annual breeder abundance (clutches/year ÷ clutches/turtle/year = turtles/year). However, when estimates of clutch frequency are either inaccurate or variable, resulting estimates of annual breeder abundance will reflect the same inaccuracy and/or uncertainty, thereby distorting population assessments (Esteban et al. 2017; Ceriani et al. 2019). When estimates of clutch frequency are biased low, as in our study, resulting estimates of annual breeder abundance will be overestimated. Applying the ECF estimates generated from the Focal and All datasets in this study (2.4 and 3.9, respectively) to the annual clutch counts recorded in the NRU between 2010 and 2015 (Shamblin et al. 2021), the resulting estimates of annual breeder abundance would be 38% lower using the All dataset value compared to the Focal dataset value (Table 3). Using an even higher clutch frequency estimate that is consistent with those generated from subpopulation-wide MSORD analyses and satellite telemetry (4.5; Scott 2006; Shamblin et al. 2017), the estimated annual breeder abundance would be 47% lower compared to that from the Focal dataset value (Table 2). Applying biased estimates of clutch frequency in this way can lead to significant misinterpretations of population size and stability, thereby undermining conservation efforts.

Remigration interval and breeding frequency

Due to the energetic costs associated with reproduction and reproductive migrations, marine turtles rarely breed in consecutive years (Schroeder et al. 2003). Thereafter, environmental conditions in foraging areas can impact the duration of an individual's remigration interval and, therefore, its breeding frequency during a fixed period of

Table 3 Recorded annual clutch counts in the NRU between 2010 and 2015 from Shamblin et al. (2021) converted to estimates of annual breeder abundance using three different values for estimated clutch frequency (ECF): focal, all, and high [asterisk indicates CF estimate consistent with Scott (2006) and Shamblin et al. (2017)]

Year	Clutches recorded (Shamblin et al. 2021)	Annual breeder abundance			Percentage change	
		Focal (ECF=2.4)	All (ECF=3.9)	High* (ECF=4.5)	Focal-all (%)	Focal-high (%)
2010	5770	2404	1479	1282	-38	-47
2011	6966	2903	1786	1548	-38	-47
2012	7946	3311	2037	1766	-38	-47
2013	8752	3647	2244	1945	-38	-47
2014	3834	1598	983	852	-38	-47
2015	8689	3620	2228	1931	-38	-47

time (Limpus and Nicholls 1988; Hays 2000; Solow et al. 2002; Vander Zanden et al. 2014). For loggerheads in the Northwest Atlantic, estimates of remigration interval range on average between 2 and 4.5 years (± 1 –2 years; Bjorndal et al. 1983; Tucker 2010; Lamont et al. 2014; Phillips et al. 2014), with average estimates for the NRU falling between 2.54 and 2.84 years (± 1 year; Richardson et al. 1978; Monk et al. 2011; Shamblin et al. 2021). The two estimates of average remigration interval in this study were very similar to previous NRU estimates and were not significantly different from each other: 2.81 years (2.66–2.97) in the Focal dataset and 2.81 years (2.71–2.90) when non-Focal clutches were accounted for in the All dataset. Estimates of remigration interval generated from CMR encounters on Wassaw were, therefore, more robust to biases associated with weak or variable NSF than other demographic parameters.

Unlike accurate estimates of clutch frequency, which require detecting females during most if not all clutches within a season, estimating remigration interval requires encountering each breeding female only once during a season (Schroeder et al. 2003; Shamblin et al. 2021). Remigration intervals estimated at focal tagging sites are, therefore, less affected by weak intra-seasonal NSF. Conversely, weak inter-seasonal NSF would only affect estimates of remigration interval for females with three or more documented breeding seasons: two seasons with at least one focal encounter separated by one or more seasons with no focal encounters. In effect, failing to detect a female during one breeding season (all non-focal clutches) between two detected breeding seasons (at least one focal clutch/year) would double her perceived remigration interval. During the 8-year study period, such scenarios were not sufficiently frequent to bias estimates of remigration interval generated from CMR data collected on Wassaw. Over longer study periods, however, more of these artificially long remigration intervals may be detected, leading to demographic biases. Until the potential for such biases is evaluated with additional years of data, estimates of remigration interval generated at focal tagging sites may still provide a strong basis for estimating the proportion of females breeding each year and

ultimately the total number of adult females in a population (Ceriani et al. 2019; Casale and Ceriani 2020).

More frequently, however, females in this study were encountered during one breeding season on Wassaw either before or after at least one season of breeding elsewhere. Because remigration interval cannot be estimated when a female is encountered during only one breeding season, these females were not included in the Focal dataset estimate of remigration interval. While not causing significant biases in estimates of remigration interval, failing to encounter some females during entire breeding seasons can cause significant biases in estimates of breeding frequency, as well as individual productivity (see below). During the 8-year period of this study, 371 breeding seasons (34%) were missed entirely at the focal tagging site, causing breeding frequency to be underestimated by almost one breeding season per turtle (1.38 seasons/turtle versus 2.08 seasons/turtle). Failing to encounter some females during entire breeding seasons can not only cause biases in estimates of breeding frequency and individual productivity, but it also artificially truncates the CMR histories of those females. Because marine turtles typically only breed once every 2–4 years (Miller 1997; Shamblin et al. 2021), missing one or more breeding season before or after encountering a female at a focal tagging site can reduce a female's perceived reproductive life by many years. Looking outside the 8-year study period, if such instances are sufficiently frequent in the breeding population, then estimates of reproductive longevity and annual adult survival will be biased low (Pfaller et al. 2018). Accounting for missed recruitment and permanent emigration associated with weak inter-seasonal NSF is, therefore, critical for generating accurate estimates of annual adult survival, a vital rate that is essential for assessments of marine turtle populations.

Contrary to the presumed longevity of marine turtles, many CMR studies around the world include a significant proportion of breeding females that were never recaptured after their initial tagging season or event, a phenomenon that Carr (1980) referred to as the “missing majority” (Shamblin et al. 2021). At the focal site in this study (Wassaw Island), Pfaller et al. (2013) found that between 1973 and 2011 only

167 out of 1,164 tagged females (14%) were recaptured during a subsequent breeding season. Similar unexpectedly low percentages, ranging from 7 to 33%, have been documented at other loggerhead tagging sites with at least 10 years of recapture data (Shamblin et al. 2021). In the Focal dataset in this study, out of 470 females that were first encountered between 2010 and 2015, only 108 (23%) were encountered remigrating at least once during the remainder of the study period (2011–2017; turtles encountered for the first time in 2016–2017 were excluded because these turtles would not have had an opportunity to remigrate during the study period). Conversely, when we included clutches deposited by the same group of turtles on beaches other than Wassaw, the number of turtles encountered remigrating increased to 332 (71%). A similar proportion of remigrant turtles (65%) was documented by Shamblin et al. (2021) from genetic CMR data collected across the vast majority of NRU nesting sites. While other factors may still cause some remigrant females to be missed (e.g., long remigration intervals, imperfect detection, and emigration to northeast Florida), weak fidelity to the focal tagging site in this study accounted for 62% of the “missing majority”. Especially at continental nesting sites (i.e., not on oceanic islands), low detection/re-detection rates associated with weak NSF can cause significant biases in demographic estimates. For this reason, past demographic estimates generated at focal tagging sites that encompass only a portion of the nesting area used by the breeding population should be reevaluated and applied with caution.

Population productivity

Measures of individual fecundity and population-wide productivity form the foundation for constructing population models and predicting population-level responses to perturbations (natural and anthropogenic) and management actions (Heppell et al. 1999, 2003). Because marine turtles exhibit slow growth and delayed sexual maturity, individuals that reach adulthood are expected to produce large numbers of offspring to balance the high cumulative mortality associated with decades of juvenile development (Stearns 1992; Heppell et al. 1999). Accurate estimates of population productivity are, therefore, critical for assessing whether hatchling production on nesting beaches is sufficient to maintain viable marine turtle populations. At the focal site in this study, the factors that biased estimates of clutch frequency (i.e., missed intra-seasonal clutches) and breeding frequency (i.e., missed breeding seasons) combine to dramatically underestimate the total number of clutches, eggs, and hatchlings produced by the breeding aggregation each year. During the 8-year study period, only 40.7% of clutches, 42.8% of eggs, and 42.4% of hatchlings produced by the 565 females were documented at the focal nesting/tagging site, while the remaining clutches, eggs, and hatchlings were produced elsewhere.

Consequently, on a per-individual basis, estimates of fecundity generated from data collected at the focal tagging site would be biased low by more than half. Population models applying such inaccurate estimates of per-female hatchling production risk misleading management actions by overestimating the rate of juvenile survival needed to maintain a stable adult population.

For many marine turtle populations, including NRU loggerheads, annual clutch counts collected at index nesting sites provide the primary basis for estimating population abundance and monitoring trends over time (Northwest Atlantic loggerheads: NMFS and USFWS 2008; Bolten et al. 2019; other marine turtle populations: e.g., Spotila et al. 2000; Balazs and Chaloupka 2004; Frey et al. 2014; Hamilton et al. 2015). Large population sizes, logistical constraints, and funding limitations frequently prevent saturation tagging of nesting females at index sites, thereby precluding direct estimates of breeder abundance. Consequently, annual breeder abundance is often estimated indirectly by dividing annual clutch counts by a single mean estimate of clutch frequency (Richards et al. 2011; see “Clutch frequency” section above). As mentioned above, when estimates of clutch frequency are either inaccurate or variable, resulting estimates of annual breeder abundance will reflect the same inaccuracy and/or uncertainty (Esteban et al. 2017; Ceriani et al. 2019). Additionally, however, if annual clutch counts at index sites account for only a portion of the clutches laid by females using that index site, then estimates of annual breeder abundance using this conversion equation will underestimate the true number of females breeding in a given year. Quantifying the proportion of clutches deposited outside an index sampling area by females using that index sampling area (i.e., the degree of fidelity to that site) is, therefore, important for avoiding biases in extrapolating breeding population abundance from annual clutch counts.

Similar caution should be used when interpreting population trends from annual clutch counts at index sampling sites. Temporal trends in annual clutch counts at index sites may indeed result from changes in breeder abundance driven by shifts in survival and/or recruitment. Over time, threats that reduce survival and recruitment can cause decreasing trends in annual clutch counts, while factors that enhance survival and recruitment can facilitate increasing trends. However, trends in clutch counts at index sites (either increasing or decreasing) may also result from changes in average fecundity and/or breeding periodicity (i.e., clutch frequency and remigration interval) associated with environmental fluctuations or from shifts in NSF, resulting from natural or anthropogenic modifications to the nesting habitat or surrounding coastal area. Without simultaneously evaluating temporal changes in breeding fecundity/periodicity or NSF of females depositing clutches on index sites, the underlying causes of temporal trends in clutch counts cannot

be identified. Accurate interpretations of the mechanisms causing changes in clutch counts are critical for evaluating population-level responses to perturbations (natural and anthropogenic) and developing effective management plans.

Summary

Starting in 2010, stakeholders from across the NRU nesting area began participating in a coordinated effort to individually genotype every loggerhead clutch deposited on nesting beaches between Georgia and Maryland, representing approximately 93% of ocean-facing nesting habitat (Shamblin et al. 2017, 2021). Clutches deposited in north-east Florida (Nassau, Duval, and St. John County) were included starting in 2016 (BMS, unpublished data). From the majority of detected clutches, hatching and emergence success were also quantified following hatchling emergence or failed incubation. In a unique situation for a moderately sized marine turtle nesting population (~ 7000 clutches/year) that uses an extensive nesting area (~ 1000 km), managers can now determine with reasonable confidence how many individual females breed each year and how many hatchlings are produced each year by those females. This highly concerted effort has provided unprecedented resolution into the demographics and productivity of this nesting population.

Using these subpopulation-wide genetic data and the saturation-tagging dataset amassed by the Caretta Research Project on Wassaw Island, our study highlights the potential biases of estimating demographic parameters from CMR data collected at a single focal nesting/tagging site. In summary, the biases identified in our study and their associated ramifications included:

- Overestimating the percentage of neophyte turtles nesting each season by 27%: 70% (Focal) and 43% (All). Overestimating annual recruitment can falsely suggest that the environmental conditions that facilitate sexual maturity are more favorable than they actually are. Moreover, failing to encounter most females during their first breeding season can cause estimates of annual adult survival probability to be biased low and estimates of SSM/ASM to be biased high.
- Overestimating the percentage of single-clutch breeding seasons by 44%: 53% (Focal) and 9% (All). Failing to encounter a significant proportion of females during all but one clutch per season can cause estimates of clutch frequency to be biased low (see next).
- Underestimating ECF by 39%: 2.37 clutches/turtle/season (Focal) and 3.91 clutches/turtle/season (All). Underestimating clutch frequency can cause population size to be overestimated when an average value of clutch frequency is used to convert annual clutch counts to annual breeder

abundance, thereby misleading population assessments and resulting in conservation efforts.

- Underestimating the total number of breeding seasons by all individuals and the average breeding frequency by 34%: 1.38 seasons/turtle (Focal) and 2.08 seasons/turtles (All). Failing to encounter females during entire breeding seasons can cause dramatic biases in per-individual and population-wide productivity (see below), but did not cause significantly biases in estimates of remigration interval.
- Underestimating the percentage of turtles that remigrated during the 8-year study period by 48%: 23% (Focal) and 71% (All). Failing to recapture females that remigrate can artificially truncate the perceived reproductive life spans and CMR histories of those individuals, causing the annual survival rate of the adult population to be biased low.
- Underestimating the total number of clutches, eggs, and hatchlings produced by all individuals by 59.3%, 57.2%, and 57.7%, respectively. Underestimating the cumulative productivity of a fixed number of individuals can cause biases in per-individual hatchling production, which can confound population models by overestimating the rate of juvenile survival needed to maintain a stable adult population. Moreover, failing to account for clutches produced away from an index nesting site by females using that site can cause biases in estimates annual breeder abundance when a single mean value of clutch frequency is used as the conversion between clutches and females.

For many marine turtle populations around the world, CMR data collected at focal/index nesting sites provide the only basis for estimating demographic rates and monitoring population trends. Exemplified by our study, failing to account for weak or variable individual NSF to a sampling area can jeopardize the accuracy of population assessments and mislead management decisions. For this reason, past assessments made from demographic data collected at focal nesting/tagging sites that encompass only a portion of the nesting area used by the nesting population within and between breeding seasons should be reevaluated and applied with caution.

Management recommendations

Effective management of marine turtle populations necessitates accurate estimates of key demographic rates that can be used to estimate and monitor population abundance at all life stages (NRC 2010). In-water studies, where both juveniles and adults can be surveyed, therefore, provide the most direct and complete assessments of population-wide demography and stability (Hamann et al. 2010). Unfortunately, however, monitoring marine turtle populations in

their foraging areas (both oceanic and neritic) remains challenging and, for many if not most populations, data collected at nesting beaches provide the only means of monitoring population trends. Progress in establishing a coordinated network of index in-water monitoring sites for NWA loggerheads is currently underway (NMFS and USFWS 2008; Bolten et al. 2019). However, until this is accomplished, the accuracy of demographic rates estimated from clutch counts and/or CMR data collected on nesting beaches is imperative for managers and policymakers to implement and evaluate effective management strategies.

For these data to continue to provide the most robust and accurate information available for guiding the conservation and management of NWA loggerheads, we recommend the following actions (listed in order of importance): (1) increase, or at minimum maintain, annual funding and support for the genetic CMR project to continue NRU-wide sampling of loggerhead clutches deposited between St. Johns County, FL and MD for at least an additional ten seasons, (2) initiate and provide annual funding for new subpopulation-wide genetic sampling of loggerhead clutches in other loggerhead Recovery Units, where feasible (e.g., Northern Gulf of Mexico RU and Dry Tortugas RU), (3) encourage periodic assessments of key demographic parameters from subpopulation-wide genetic data, including annual recruitment, clutch frequency, nest site fidelity (intra- and inter-seasonal), remigration interval, annual adult survival, annual breeder abundance, and total adult female abundance, (4) incorporate new estimates of key demographic rates into future management and recovery plans and replace past estimates generated from datasets that may be vulnerable to biases associated weak nest site fidelity (i.e., temporary and permanent emigration from a focal nesting/tagging site), and (5) integrate clutch count and genetic CMR data into a common cloud database server (e.g., Amazon QuickSight; <https://aws.amazon.com/quicksight/>) to harness the power of machine learning for analyzing population-wide patterns instantaneously, providing all stakeholders with the opportunity to explore the data and build visualizations to view and reference.

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Author contributions JBP and BMS conceived the study. K LW and CJN provided logistical support and funding. MGD, MHG, DBG, and SMP coordinated sample collection and provided nest metadata from their respective state monitoring programs. JBP and K LW collected

samples and provided nest metadata for Wassaw Island. JBP, SMW, and CCG collated nesting data, conducted analyses, and composed the manuscript with input from all other authors.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethics approval All applicable national and institutional guidelines for the care and use of animals were followed (University of Georgia Animal Care and Use Permits A2009 3–050 and A2015 01–011-Y1-A0 and permitted by the individual state sea turtle management agencies under the authority of the United States Fish and Wildlife Service).

Availability of data and material All data generated or analyzed during this study are provided in Online Resource 1.

Code availability Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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