



Using data from nesting beach monitoring and satellite telemetry to improve estimates of marine turtle clutch frequency and population abundance

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Abstract

Population abundance data are often used to define species' conservation status. Abundance of marine turtles is typically estimated using nesting beach monitoring data such as nest counts and clutch frequency (CF, i.e., the number of nests female turtles lay within a nesting season). However, studies have shown that CF determined solely from nesting beach monitoring data can be underestimated, leading to inaccurate abundance estimates. To obtain reliable estimates of CF for hawksbill turtles in northeastern Brazil (6.273356° S, 35.036271° W), the region with the highest nesting density in the South Atlantic, data from beach monitoring and satellite telemetry were combined from 2014 to 2019. Beach monitoring data indicated the date of first nesting event, while state-space modeling of satellite telemetry data indicated the departure date of turtles, allowing calculations of residence length at breeding site and CF estimates based on internesting intervals. Females were estimated to nest up to six times within the nesting season with CF estimates between 4.5 and 4.8 clutches per female. CF estimates were used to determine the number of nesting females at the study site based in two approaches: considering and not considering transient turtles. Our approach and findings highlight that transients heavily influence CF estimates and need for reconsideration of how this key parameter is commonly determined for marine turtle populations and the use of beach monitoring data and satellite telemetry for estimations of CF.

Keywords *Eretmochelys imbricata* · Transients · Endangered species · Sea turtle · Marine turtle · Brazil

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Introduction

Estimates of population abundance are one of the key parameters used in population assessments to evaluate and determine a species' conservation status (Williams et al. 2011; IUCN 2017) where low abundance or decreasing trends may indicate that a population is under threat and may need management intervention (Robins et al. 1999). Ideally, abundance estimates should consider all life stages from individuals within a population and be determined for both sexes (Schwarz and Seber 1999; Iijima 2020). However, this can be difficult to determine, particularly for species with high dispersal, and when different life stages and sexes are not equally available for counting (Bradbury et al. 2008). This is the case for marine turtles, which are highly migratory and utilize a variety of areas within a region, being residents to core areas (e.g., foraging areas), but being transient in some locations (e.g., often only being observed once at specific locations, such as migratory corridors), biasing

counts, and abundance estimates (Chaloupka and Limpus 2002; Clavel et al. 2008; Prince and Chaloupka 2012). As long-lived animals, determining marine turtle abundance across life stages is challenging, especially for life stages where limited information is available, such as the first few years following hatching (Putman et al. 2020). Juveniles and adult males are also more difficult to encounter and count as they remain in the marine environment for their entire life, and do not come ashore like nesting female turtles. As a result of these factors, the most common method to estimate marine turtle abundance is to utilize counts of the number of nests and breeding females at nesting beaches (Mazaris et al. 2008, 2017; National Research Council 2010).

Marine turtles lay several clutches within a nesting season, after that they do not migrate to breed again for one to several years. The number of clutches of eggs that each individual lays in a season is known as clutch frequency (CF), while the interval between seasons is known as remigration interval (Miller 1997; Tröng and Chaloupka 2007; Warden et al. 2017). Both metrics vary among individuals, populations, and species (Miller 1997; Tröng and Chaloupka 2007; Warden et al. 2017). A snapshot of the number of females nesting within a population in a given season can be extrapolated using the total number of nests across all nesting sites used by that population in that season divided by the average CF (i.e., $\text{nests/season} \div \text{nests/female/season} = \text{females/season}$; Johnson and Ehrhart 1996; Broderick et al. 2002). Accurate estimates of CF are critical, because the variation and uncertainty of estimates make it difficult to interpret trends in abundance estimated from clutch counts and CF (Ceriani et al. 2019). Accurate estimates of abundance therefore require robust estimates of CF. An extrapolation of the number of females nesting in a given season within a population can be generated using the total number of nests across all nesting sites used by that population in that season divided by the CF (Johnson and Ehrhart 1996; Broderick et al. 2002). Accurate estimates of CF are important, because the variation and uncertainty of previous estimates makes it difficult to interpret trends in abundance estimated from clutch counts and CF (Ceriani et al. 2019). Therefore, more robust estimates of CF are needed. However, accurate estimates of CF are difficult to determine during beach monitoring patrols as they depend on the detection or estimation of turtles returning to their nesting beaches during each nesting event throughout the nesting season (Briane et al. 2007; Pfaller et al. 2013; Weber et al. 2013). Obtaining this information is challenging, because nests can be spatially separated by several km, requiring that nighttime monitoring and tagging occur across large spatial extents to ensure that all turtles are encountered (Tucker 2010; Shamblin et al. 2017), which is logistically difficult and can result in insufficient coverage to ensure saturation-level monitoring. Indeed, it has been found that marine turtle

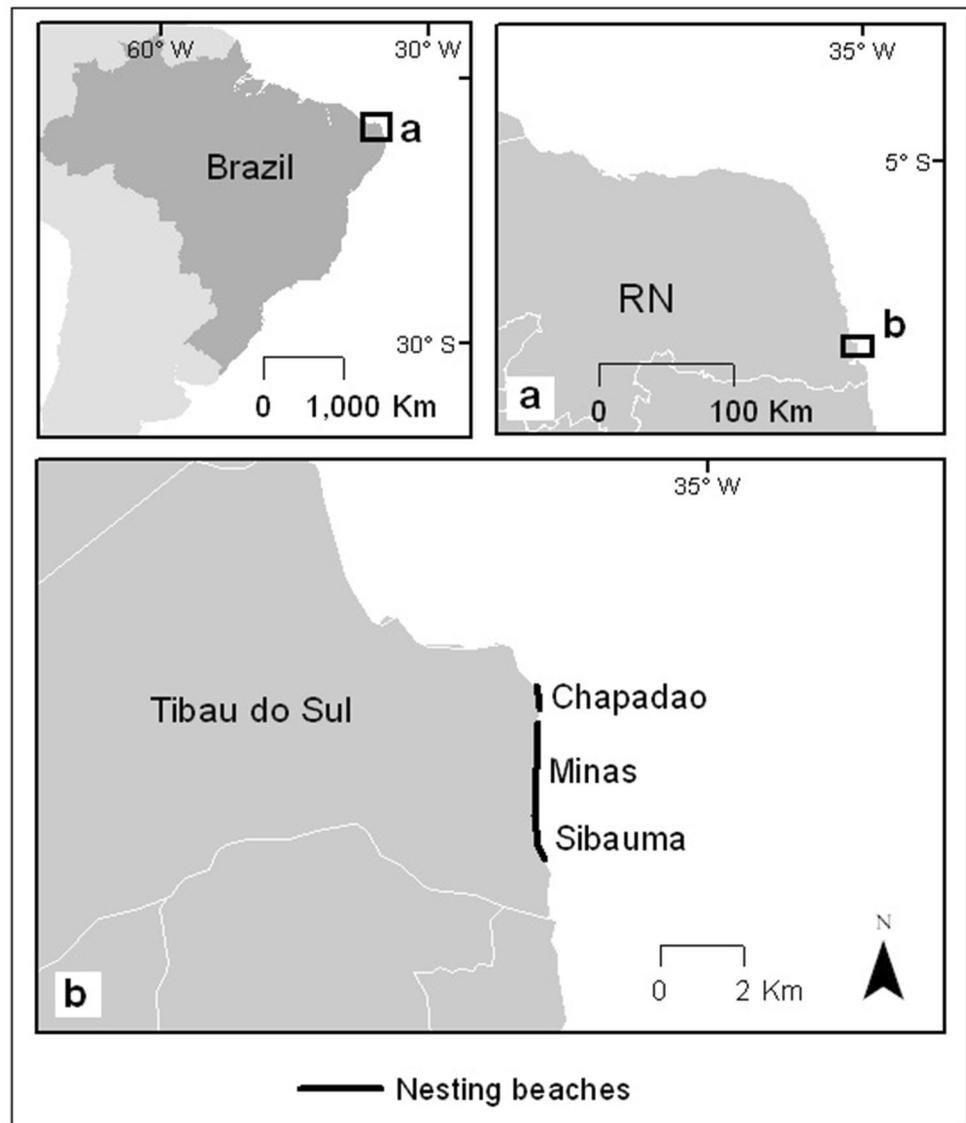
abundance estimates that rely solely on data from nesting beach monitoring can be overestimated by nearly a factor of two (Tucker 2010; Weber et al. 2013; Esteban et al. 2017). Satellite telemetry has improved the ability to detect when marine turtles return to beaches for nesting events, thereby improving estimates of CF (Tucker 2010; Esteban et al. 2017; Tucker et al. 2018; Rees et al. 2020). The use of genetic capture-recapture fingerprinting from freshly laid eggshells has also allowed population-wide estimation of CF across an extensive nesting area (Shamblin et al. 2017). However, most population abundance estimates of nesting females use solely information from beach monitoring (e.g., Almeida et al. 2011; Bjorndal et al. 1999; Johnson and Ehrhart 1996; Marcovaldi and Chaloupka 2007; Tröng and Rankin 2005; Witherington et al. 2009). This is the case for hawksbill turtles (*Eretmochelys imbricata*) nesting in the South Atlantic, Brazil, which have the highest hawksbill turtle nesting density in the region (Marcovaldi et al. 2007; Santos et al. 2013). Thus, to obtain more accurate estimation of annual breeder abundance of hawksbill turtles nesting in Brazil, there is the need to revisit estimates of CF. Here, we combined beach monitoring data with satellite telemetry data to reassess CF for hawksbill turtles that nest in the southern coastline of Rio Grande do Norte, Brazil, an important rookery for this critically endangered species (Marcovaldi et al. 2011). Furthermore, we estimate CF using several computational methods and discuss the advantages and biases of each approach to inform future studies that aim to estimate CF in marine turtles.

Materials and methods

Study site and population

Clutch frequency was estimated using information from nesting beach monitoring and satellite telemetry obtained at three hawksbill turtle nesting beaches (Chapadao, Minas and Sibauma; Fig. 1) in the Tibau do Sul municipality on the southern coastline of the state of Rio Grande do Norte, Brazil. The three beaches are interspersed by rocks, providing a contiguous nesting area of approximately 4 km in length (6.237295° S, 35.037489° W at the northernmost point and 6.273356° S, 35.036271° W at the southernmost point), with semidiurnal tide regime attaining a spring tide range of ± 3.2 m (Santos et al. 2016). This region hosts the highest nesting density of hawksbill turtles in the South Atlantic (Santos et al. 2013), and this population is part of the Southwest Atlantic Regional Management Unit (RMU) (Wallace et al. 2010). Although the classification needs updating and is currently under debate (Webb 2008), the species is classified as critically endangered by the International Union for the Conservation of Nature (IUCN) Redbook (IUCN 2021)

Fig. 1 Study sites in Brazil, along the southern coastline of Rio Grande do Norte (RN) state (a), where data were obtained at Tibau do Sul municipality to determine clutch frequency for hawksbill turtles (b) across three nesting beaches in the region



and by the Brazilian Red List of Threatened Species (Marcovaldi et al. 2011).

Beach monitoring

Morning beach monitoring for marine turtle activity (e.g., successful and unsuccessful nesting emergences) was conducted daily from 1 November to 30 May during each of the five nesting seasons between 2014/2015 and 2018/2019. Each record was identified as a successful (nest) or unsuccessful (false crawl). Unsuccessful nesting emergences occur when turtles come ashore but do not nest, and for the purposes of this study, we only considered information from successful nesting emergences, that is, when the turtle laid a clutch of eggs. In addition to morning beach monitoring, during each of these five nesting seasons, intensive nocturnal monitoring was conducted

from the 10 December to 15 April, which accounts on average for 93.4% of nesting across the season. Sunrise in the region during the study period occurs around 4:30 am. Nocturnal monitoring consisted of the beaches being patrolled by at least two people from 7 pm to 3 am to maximize the probability of encountering nesting turtles in our study sites. When encountered, turtles were intercepted after egg-laying, checked for the presence of tags, and if none were observed, each was tagged with Inconel tags (number 681 National Band and Tag Company) in both front flippers. Curved carapace length ($CCL \pm 0.1$, cm) was measured with a flexible tape from notch (external border of the nuchal scale) to tip (external border of the supracaudal scale; Marcovaldi and Marcovaldi 1999). After 15 April, night monitoring was conducted based on the internesting interval (15 ± 1.5 days) of turtles that had already been encountered laying at our study site (Santos

et al. 2010, 2013). Although 98% of nests in this region are of hawksbill turtles (Santos et al. 2013), nests for which the species of the female was not documented at the time they were deposited were excavated after hatching to confirm the species for the nesting event.

Satellite tags, attachment, and tracking

Twenty-five nesting females encountered by night monitoring were randomly selected for attachment of platform transmitting terminals (PTT), 10 of which were tracked in two consecutive nesting seasons with a new PTT ($N=35$ deployments; Table S1). Turtles selected for PTT attachment were restrained in a wood box as per Hart et al. (2010). The carapace was sanded and cleaned with isopropyl alcohol, and PTT was attached with epoxy, followed by anti-fouling paint following protocols by Santos et al. (2021).

Of the 35 PTT deployments, 24 relied on ARGOS positions and 11 included Fastloc-GPS positions. ARGOS positions are less accurate, and can deviate from 0.4 to 14.3 km from Fastloc-GPS positions, depending on the signal quality (Witt et al. 2010) and do not rely on haul-out wet/dry data to determine when a turtle is on the beach. Turtles in the study site take at least 40 min to successfully nest, therefore Fastloc-GPS were set to enter haul-out cycle after 20 min when the wet/dry sensor was dry and exited haul-out after 30 s if wet in the first nesting season (2014/2015). For the other nesting seasons (2015/2016 to 2018/2019), haul-out cycle was defined after 5 min to make it more sensitive to nesting attempts. If the turtle remained out of the water, haul-out messages were sent following the settings of the predefined Fastloc-GPS sampling interval, ranging from one to four locations per hour, enabling the detection of nesting attempts. In cases where subsequent haul-outs were detected, i.e., in consecutive days or even in the same night, the last haul-out position was used to represent the nesting event.

Estimating clutch frequency

Observed clutch frequency (OCF)

Observed clutch frequency estimates (OCF) were calculated based on information obtained during nightly beach monitoring and determined as the average number of times that each individual turtle was encountered nesting successfully during beach monitoring patrols. We calculated individual residence length based on beach monitoring data (IRL_{BM}), as the difference in days between the last and first nests recorded for all individuals ($N=122$), excluding the transient turtles, which were observed only once ($N=88$).

Estimated clutch frequency-beach monitoring (ECF_{BM})

For individual turtles for which the interval between nesting encounters, during our nesting monitoring, was greater than the range of a typical internesting interval (12–20 days; Santos et al. 2013), we assumed that turtles nested in that period and calculated an estimated clutch frequency based on the beach monitoring data (ECF_{BM}). To fill those gaps, we divided the observed interval by the average internesting interval of 15 days (Santos et al. 2013), using the nearest integer values only (Johnson and Ehrhart 1996; Broderick et al. 2002; Briane et al. 2007; Santos et al. 2013). For comparison purposes, ECF_{BM} was only calculated for the subset of 18 turtles that were satellite tagged and that laid at least one nest before 1 Feb (see below).

To investigate whether or not the assumed nesting event occurred within the study site, we analyzed all the nesting records that occurred between 12 and 20 days after the last nest in which the individual turtle was encountered within our site. If all the nesting records in the study site during the relevant period were from other identified individual turtles, it meant that the assumed nest occurred outside of the study site. However, if nesting events occurred where the individual turtle was not encountered/observed (i.e., nests missed by patrolling personnel and encountered by the track), it is possible that the nest was from the turtle in consideration, and therefore, we assumed that an unseen nest occurred in the study site.

Estimated clutch frequency-beach monitoring and satellite telemetry (ECF_{BM+ST})

Estimated clutch frequency was also estimated by combining data from beach monitoring and satellite telemetry (ECF_{BM+ST}). For ECF_{BM+ST} , we selected a subset ($N=18$) of satellite tracked females that beach monitoring data indicated laid their first clutch during the first portion of the nesting season (Fig. 2). The first portion of the season was defined as nesting events occurring before 1 February, which represents 24% of the clutches laid (Fig. 2). This criterion was established to avoid considering turtles that nested previously during the nesting season. PTT deployment for the selected turtles identified to have nested before 1 February, took place in December/January ($N=8$), February, and April ($N=10$; Table 1; Fig. 3). Among the subset of tracked females, 11 PTTs relied on ARGOS positions, while the 7 included Fastloc-GPS and haul-out data (Table 1).

To estimate ECF_{BM+ST} for each individual, we divided length of residency (days) by the average internesting interval for the population (15 days; Santos et al. 2010, 2013) as suggested by Esteban et al. (2017). For ECF_{BM+ST} , individual residence length (IRL_{BM+ST}) was calculated by subtracting the date that each of the selected

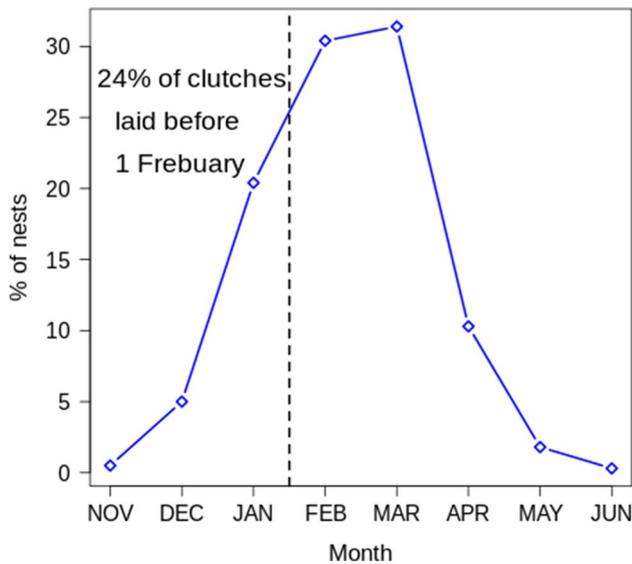


Fig. 2 Percentage of hawksbill turtle nests in Chapadao, Minas and Sibaua, on the southern coastline of the state of Rio Grande do Norte, Brazil across five nesting seasons (2014/2015 to 2018/2019; $N=622$ nests). Dashed line indicates the first portion of the nesting season, where 24% of clutches were laid before 1 February. All satellite tagged turtles selected for the estimation of clutch frequency ($N=18$ deployments) were observed nesting in the first portion of the nesting season to ensure that we maximized the probability that selected turtles were nesting for the first time within the season

individuals was encountered laying its first nest (identified during beach monitoring) from the date that those individuals departed the nesting area (estimated from satellite telemetry). Departure date was determined by fitting a hierarchical state-space model (SSM) (Jonsen et al. 2006) and using location estimates for each 6 h period from the satellite tags to determine when the turtles departed from the breeding site and started migration to their foraging areas. For this, we excluded location classes (LC) = Z, and retained LC = 3, 2, 1, 0, A, and B. When available, Fastloc-GPS locations were converted to LC = 3 and were combined with ARGOS data as in Wildermann et al. (2019). Behavioral modes were defined as ‘area-restricted searching’ (ARS) or ‘transiting’ (Jonsen et al. 2007), with the bsam package (Jonsen et al. 2017) in R v.3.5.1 (R Core Team 2018). Because the turtles were instrumented during the nesting season, the ARS behavior before ‘transiting’ behavior (migration) was linked to internesting and therefore used to indicate the residence period at the breeding site. The model that converged better was based on 40,000 iterations after a burn-in of 60,000 samples and thinned by ten to minimize within chain sample autocorrelation. We further excluded the data for migration and foraging as it was not relevant for this study. For the cases ($N=3$) where SSM did not detect behavioral changes associated with migration (i.e., local turtles), we inspected their

home range contours using OpenJUMP HoRAE program (Steiniger and Hunter 2013). The 95% contour from Scaled Line-Based Kernel Density for Movement Points function was used and the split in the home range output allowed us to identify the exact departure day when the turtle left the breeding site (first polygon) toward its foraging site (second polygon), allowing us to determine their residency length (Fig. S1).

In addition, we calculated population residence length (PRL) at the breeding site by determining the average day for the first nesting, based on information from beach monitoring for all turtles including ($N=210$) and also excluding transient turtles ($N=122$) and the average departure date based on SSM ($N=32$) or home range inspection ($N=3$; individuals 13, 16, and 16*; see Table 1 for * meaning). The first of December was considered day zero for each nesting season, since nesting for this population typically starts early in December (Santos et al. 2013). The difference in days between averages of first nesting and departure were used to estimate average PRL at the breeding site. Similar to the ECF_{BM+ST} calculation described above, we used PRL to obtain a clutch frequency estimate for the nesting population (ECF_{PRL}) dividing both PRL scenarios (with or without transient turtles) by the average internesting interval and adding one clutch to account for the first nest.

Estimates of nesting females

We used four approaches (ECF_{BM} , ECF_{BM+ST} , and both ECF_{PRL} with all turtles and non-transient turtles) to estimate the number of nesting females in our study site across two different scenarios. For the first scenario, we did not consider transient turtles in our calculations, and divided the total number of nests recorded by the ECF generated using each approach, to obtain an estimate of the nesting female population size for each approach. In our second scenario, transient turtles were considered and the number of nests per transient turtle (one nest for each turtle) was subtracted from the total number of nests before dividing it by the ECF generated using each approach. After this was done, the number of transient turtles was added to our value to account for the presence of transient turtles in our estimations. A one-way ANOVA followed by a Tukey’s range test was conducted to compare the number of nesting females across each approach and scenario at the $\alpha=0.05$.

Statistical comparisons

We compared IRL_{BM} and the number of transient turtles from the first portion of the nesting season with those that started to nest later in the season. To inform future studies that estimate marine turtle clutch frequency, we compared the ECF_{BM} with ECF_{BM+ST} using a paired t test. We

Table 1 Subset of turtles selected for platform transmitting terminals (PTT) deployment

Turtle ID	PTT model	CCL (cm)	First nest date (beach monitoring)	Departure date (satellite tracking)	IRL (days)	OCF	ECF _{BM}	ECF _{BM+ST}
1	Fastloc-GPS	91.2	2015-01-28 +	2015-03-14	45	4	4	4
2	ARGOS	86.1	2015-01-28 +	2015-03-28	59	3	5	4.9
3	ARGOS	88.9	2015-01-19 +	2015-03-18	58	4	5	4.9
3*	Fastloc-GPS	88.4	2018-01-16	2018-03-19	61	2	4	5.1
4	Fastloc-GPS	86.3	2015-01-19 +	2015-03-20	60	4	5	5
4*	Fastloc-GPS	88.0	2017-12-26	2018-03-02	66	3	4	5.4
7	Fastloc-GPS	95.5	2016-01-17	2016-03-20	63	5	5	5.2
7*	ARGOS	95.7	2018-01-27	2018-03-19	51	4	4	4.4
8 ^T	ARGOS	98.1	2016-01-21	2016-03-08	47	1	1	4.1
9	Fastloc-GPS	86.5	2019-01-14	2019-03-25	70	5	5	5.7
10	ARGOS	82.8	2016-01-25 +	2016-03-09	44	3	4	3.9
11	ARGOS	86.4	2016-01-28 +	2016-03-14	46	4	4	4.1
11*	ARGOS	86.3	2019-01-24 +	2019-02-24	31	2	3	3.1
13	ARGOS	84.4	2016-01-25 +	2016-03-29	64	5	5	5.3
19 ^T	ARGOS	93.3	2018-12-19	2019-02-14	56	1	1	4.7
20 ^T	ARGOS	85.2	2018-12-28	2019-02-06	40	1	1	3.7
21	ARGOS	95.0	2019-01-18 +	2019-03-28	69	4	5	5.6
25	Fastloc-GPS	97.2	2019-01-24 +	2019-04-10	76	5	6	6.1
Average/mean:		89.7			55.9	3.3	3.9	4.7

Departure date indicates the last record from the satellite telemetry before the turtle migrated to foraging areas. Individual residence length (IRL) was calculated by the difference in days between first documented nest and departure dates

CCL curve carapace length, OCF observed clutch frequency, ECF_{BM} estimated clutch frequency based on beach monitoring data, ECF_{BM+ST} estimated clutch frequency based on beach monitoring data and satellite telemetry information

*Indicates the second PTT deployment in the same individual turtle. + indicates that residence period was calculated by combining beach monitoring and satellite telemetry information, while entries without + were calculated only from satellite telemetry data. ^T indicates transient turtles

also determined the number of unobserved nests by beach monitoring. Similarly, we compared residence length that incorporated data from satellite telemetry (IRL_{BM+ST}) with those obtained from beach monitoring solely (IRL_{BM}). To allow comparisons between approaches, a 95% confidence interval (CI) for a Student's *t* distribution was calculated for the ECF_{BM} and ECF_{BM+ST} averages, as well as for the differences between the averages from dates of the first nesting and the departure to create an interval for PRL estimates, which was further used to indicate a confidence interval for ECF_{PRL}. Additionally, we compared IRL_{BM+ST} and ECF_{BM+ST} for the individual turtles tracked in two subsequent nesting seasons. However, the sample size was small ($N=4$) for statistical comparisons. We also evaluated the efficiency of satellite telemetry in determining nesting events from the haul-out data in comparison to the nesting records by beach monitoring and length of residence period at the breeding site.

Results

Nesting activity

On average, 42 ± 7.5 (range 33–51) individual nesting hawksbill turtles were encountered each season during the beach monitoring patrols that were conducted at our study site, with an average of 124 ± 8 (range 114–138) nests per season (Table S2). Of the individuals encountered during the beach monitoring, an average of $41.2 \pm 10.5\%$ (range 27.3–46.3%) were transient and seen nesting only once during the nesting season within our study site (Table S3). Among turtles initially seen during the first portion of the nesting season (Dec–Jan), 33.1% ($N=99$) were transient, while 50.5% ($N=111$) of turtles first seen during the second portion of the nesting season (Feb–Apr) were transient.

Residency length

For all non-transient turtles ($N=122$), the average for IRL_{BM} was 44.1 ± 16.7 days (range 13–82 days). For the subset of 18 satellite tracked turtles, the average for IRL_{BM+ST} was 55.9 ± 11.8 days (range 31–76 days;

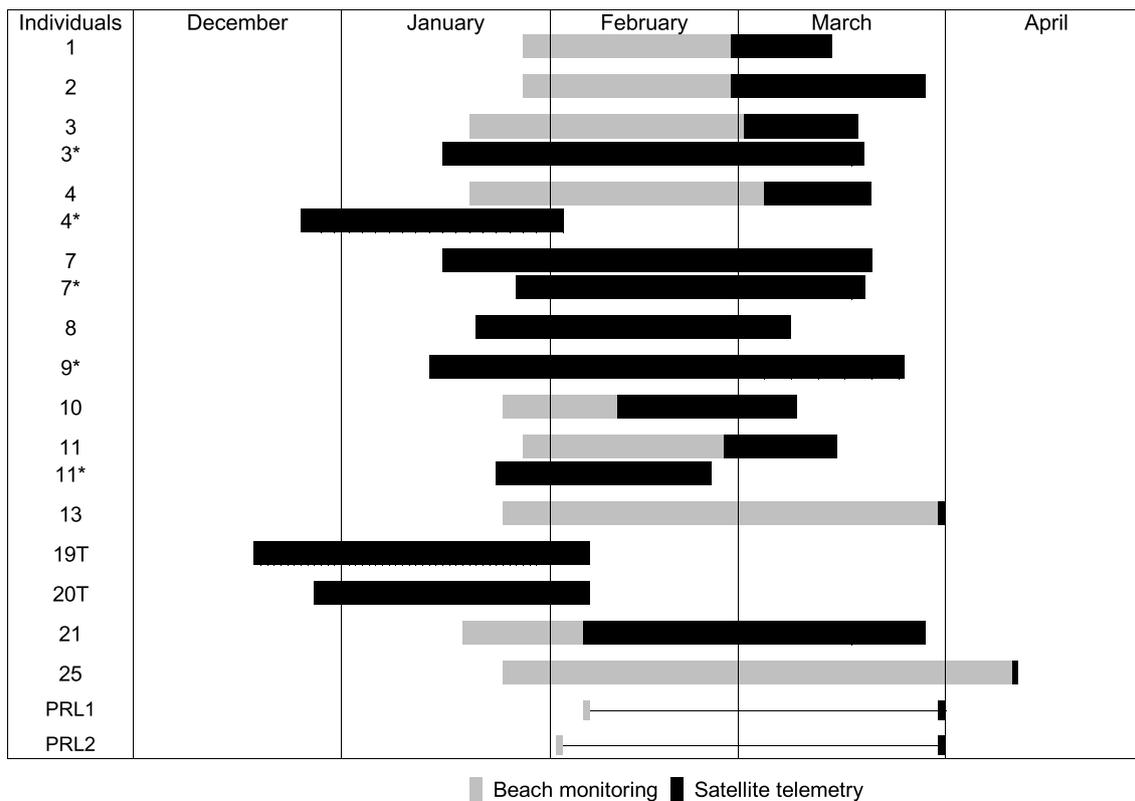


Fig. 3 Residence length at the breeding site for nesting hawksbill turtles obtained by a combination of data from beach monitoring and satellite telemetry. Eighteen platform transmitting terminals (PTTs) were deployed on 14 individual nesting hawksbill turtles and population residence length (PRL) in the southern coastline of Rio Grande

do Norte state, Brazil. * indicates the second deployment for the same individual turtle in consecutive seasons. PRL is based on beach monitoring (PRL1 including all individuals; $N=210$; and PRL2 non-transient individuals only; $N=122$) and satellite telemetry ($N=35$). T indicates transient turtles

Table 1; Fig. 3). IRL_{BM} was significantly less than IRL_{BM+ST} (paired t test, $t_{17} = 12.86$, p value < 0.001). Average IRL_{BM} for turtles that started nesting between Dec and Jan was 48.9 ± 16.1 days (range 14–82 days; $N=67$), while average IRL_{BM} started nesting between Feb–Apr was 38.3 ± 15.6 days (range 13–82; $N=55$); the two values were significantly different (paired t test, $t_{54} = 7.14$, p value < 0.001). The IRL_{BM+ST} for individuals tracked in two consecutive nesting seasons differed by a range of 3–15 days, with differences between the first and second year of three and six days longer, respectively, for individuals 3 and 4, and 12 and 15 days shorter for individuals 7 and 11, respectively (Table 1; Fig. 3).

For all turtles (including transient turtles) encountered during beach monitoring ($N=210$), the average date of each individual’s first nest documented during beach monitoring was 6 February (SD = 8 January–7 March; median = 4 February). Excluding transient turtles ($N=122$) from the analysis, the average date for first nest observed by beach monitoring was 2 February (SD = 7 January–28 February; median 29 January). For

all satellite tracking events ($N=35$ PPTs), the average of departure date estimated from SSM was 31 March (SD = 6 March–25 April). From these data, we estimated PRL to be 52.6 ± 4.1 days for all turtles (transients included), and 57.3 ± 1 days for non-transients only (Table 2). Most turtles departed from the breeding site in March (54.3%), but departures also occurred in February (8.6%), April (22.9%), and May (14.3%) (Fig. S2).

Clutch frequency

Average OCF was estimated to be 3.3 ± 1.4 clutches per female (range 1–5 clutches per female; median = 4 clutches per female; Table 1) and the average ECF_{BM} was estimated to be 3.9 ± 1.5 clutches per female (range 1–6 clutches per female; median = 4 clutches per female; CI 2.4–5.4 clutches per female; Table 1). Nesting females were encountered by the monitoring team for most (82.6%) of the nests recorded in the study during the monitoring activities (Table S2). When calculating the ECF_{BM} (Table 1), 11 nests were added based on long interesting

Table 2 Average date of first nesting event determined via beach monitoring for all turtles (transient turtles included) and for non-transient turtles in each nesting season and average departure date via state-space model of hawksbill turtles considering December 1st as day zero

	14/15	15/16	16/17	17/18	18/19	All seasons	Departure day	PRL at breeding site	ECF _{PRL}
All turtles									
Average	74.7	62.6	66.1	63.5	67.8	67.2	119.8	52.6 (43.4–61.8)	4.5 (3.9–5.1)
SD	32.4	29.4	27.2	27.9	29.5	29.3	25.0		
N	41	33	51	37	48	210	35		
Non-transients									
Average	66.6	59.0	63.3	55.4	66.2	62.5	119.8	57.3 (47.7–66.8)	4.8 (4.2–5.5)
SD	26.1	26.3	27.2	20.3	28.2	26.0	25.0		
N	22	24	24	20	32	122	35		

SD standard deviation, PRL population residence length, ECF_{PRL} average estimated clutch frequency for the population (confidence interval)

intervals (Table S4). Of those nests, three were assumed to occur outside of our study site, as there were no missed records by field personnel during the probable internesting period (i.e., records in which the female was not observed) (Table S5). Eight nests were assumed to have been missed by beach monitoring, since the females were not encountered during the monitoring patrols, but tracks were recorded during the relevant period that they were likely to nest (Table S5).

Based on the combination of data from beach monitoring and satellite telemetry, the average ECF_{BM+ST} was estimated to be 4.7 ± 0.8 clutches per female (range 3.1–6.1 clutches per female; median = 5 clutches per female; CI 3.9–5.5 clutches per female; Table 1). Average ECF_{BM} was significantly smaller than ECF_{BM+ST} (paired *t* test, $t_{17} = 2.83$, *p* value = 0.012). The PRL produced average ECF_{PRL} of 4.5 (CI 3.9–5.1) clutches per female for all turtles (transient turtles included) and 4.8 (CI 4.2–5.5) clutches per female for non-transient turtles (Table 2). For individuals tracked in two consecutive nesting seasons, ECF_{BM+ST} was the same in both nesting seasons for individuals 3 and 4, while for individuals 7 and 11, there was a difference of one nest between the two seasons (Table 1).

Discrepancies between beach monitoring and satellite telemetry

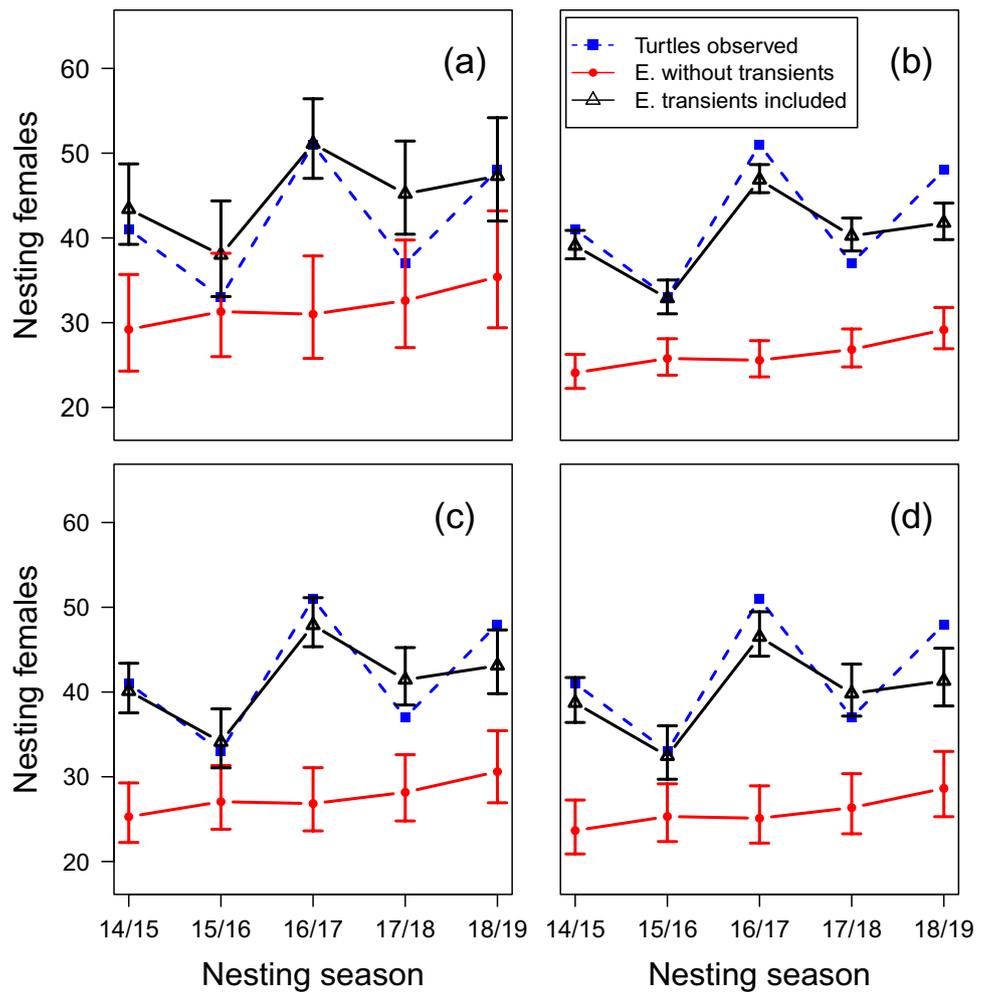
Satellite telemetry information typically complemented nesting data from our beach monitoring; three individuals (individuals 8, 19, and 20) were observed nesting only once during our beach monitoring (Table S4). However, satellite telemetry data indicated that residence length at the breeding site was compatible with at least three other nesting events during the nesting season (Fig. 3). These three transient turtles were equipped with ARGOS satellite tags only; as a result, we were not able to determine where the other nesting events occurred. Furthermore, we assumed that three nests occurred outside of our study site; however, haul-out

locations obtained from the Fastloc-GPS tags indicated that one of them actually occurred at our study site, but were missed by the beach monitoring (Table S5; A7). Indeed, all haul-out positions obtained from the Fastloc-GPS tags occurred in the study site. Nevertheless, two nesting events observed during the nesting monitoring were not recorded or transmitted by satellite tags (ID 9*; Table S5). Another two nests were assumed to be not recorded or transmitted by haul-outs; however, they were not confirmed by information from beach monitoring, since the period that individuals (ID 3* and 4*) remained at the breeding site (14 and 16 days) indicates that they probably nested but that it was not detected.

Estimates of nesting females

The average number of nesting females estimated without considering the presence of transient turtles for ECF_{BM} was 31.9 ± 2.3 , for ECF_{BM+ST} was 26.5 ± 1.9 , for ECF_{PRL} for all turtles was 27.6 ± 2.0 , and ECF_{PRL} for non-transients was 25.9 ± 1.9 . These average estimates were significantly different from the average number of nesting females observed during beach monitoring [$F(4,20) = 15.52$, $p = 0.000003$], with estimates from ECF_{BM} being the closest to the ones observed by beach monitoring (Fig. 4; Table Sup.6). The average number of nesting females estimated when including transient turtles for ECF_{BM} was 44.9 ± 4.8 , for ECF_{BM+ST} was 40.3 ± 5.0 , for ECF_{PRL} for all turtles was 41.33 ± 5.0 , and ECF_{PRL} for non-transients was 39.8 ± 5.1 . These average estimates were not different from the average number of nesting females observed during beach monitoring [$F(4,20) = 0.656$, $p = 0.629$], with ECF_{PRL} for all turtles having the best performance (closest to the observed value), followed by ECF_{BM+ST}, ECF_{PRL} for non-transients, and ECF_{BM} (Fig. 4; Table Sup.7).

Fig. 4 Number of nesting females observed during beach monitoring (blue dashed line) and estimates of nesting female numbers based on estimates of clutch frequency (ECF) without considering transient turtles (red line) and considering transient turtles (black line) obtained from: **a** beach monitoring (ECF_{BM}); **b** beach monitoring and satellite telemetry (ECF_{BM+ST}); **c** population residence length (PRL) for all turtles; **d** for PRL for non-transient turtles. Error bars indicate the 95% confidence interval around the averages. *E.* estimates



Discussion

Combined data from nesting beach monitoring and satellite telemetry allowed us to provide more robust estimates of average clutch frequency for hawksbills turtles nesting in Rio Grande do Norte state, Brazil and estimate population abundance for our study site. Estimates of clutch frequency ranged from 3.3 when using observed data from beach monitoring to 4.5–4.8 when combining the beach monitoring data with satellite telemetry. Higher estimates of clutch frequency when using satellite telemetry and data from nesting turtles opposed to only using data from nesting beach are reflective of previous studies (Rees et al. 2010, 2020; Tucker 2010; Weber et al. 2013; Esteban et al. 2017; Tucker et al. 2018). Higher estimates of clutch frequency, when extrapolating annual nest counts to number of nesting females, also result in lower estimates of nesting female abundance, as the total number of clutches is divided by a larger denominator (Mazaris et al. 2008). Consequently, since clutch frequency is considered a key demographic parameter for estimating marine turtle abundance, inaccurate estimates may mislead

population assessments. Below, we discuss several factors that may influence clutch frequency estimates, discuss associated conservation implications, and provide suggestions for future studies.

Residence length

Residence length represents the cumulative sum of each turtle internesting interval, from first to last nesting (Esteban et al. 2017), and might be used to calculate clutch frequency (Esteban et al. 2017; Kendall et al. 2019; Rees et al. 2020). This is especially useful when the internesting habitat for hawksbill turtles or other marine turtle species is close to the shoreline (e.g., less than 1 km), and detecting nesting events through satellite telemetry will require tags with finer scale resolution, which are usually costly (Esteban et al. 2017). However, for this, it is crucial to know the first and last nesting event for individual nesting turtles. Several factors may influence the internesting and residence length and should be considered. First, disturbances during nesting, such as lights, coastal construction, predators, human

activities, anthropogenic debris, sand compaction, or even other turtles, may prevent turtles concluding/starting nesting, causing unsuccessful attempts (Witherington 1992; Fuentes et al. 2016; Fujisaki and Lamont 2016; Drobles et al. 2019; Garrison and Fuentes 2019; Sella and Fuentes 2019). In these cases, the turtle returns to the sea and waits for the next opportunity to nest; either during the same or following night(s) (see Hamann et al. 2002). If unsuccessful nesting emergences occur repeatedly, the extended internesting interval will increase residence length. Second, temperature influences physiology, with warmer waters causing internesting intervals to be shorter (Sato et al. 1998; Hays et al. 2002). This affect may be influenced by geographical location, as well as differences between seasons and within a season (i.e., internesting interval might get shorter as the season progresses, assuming the temperatures increase as the season proceeds; Shimada et al. 2021). Behavior may also influence temperature, i.e., the turtles may select shallow warmer waters for breeding residence (see Fossette et al. 2012; Schofield et al. 2009). Third, also linked to physiology, the water-limitation hypothesis has been suggested to influence the length of internesting interval, in which water deposition in eggs is limited by desalination capacity (Price et al. 2019). Indeed, rehydration was theoretically suggested as responsible for mass recovery during the internesting interval (Santos et al. 2010) when gravid hawksbill turtles are fasting (Goldberg et al. 2013). Finally, the process of PTT attachment may influence nesting turtle behavior, in particular if the turtle is displaced to another area for the instrumentation and released elsewhere, which was not the case for this study (see Luschi et al. 2003, 1996). Despite residence length being heavily influenced by water temperature and nesting success (Miller 1997; Sato et al. 1998; Hays et al. 2002), which may vary across individuals, it can be used as a proxy to estimate clutch frequency allowing for sample sizes to be higher through the use of lower resolution, less expensive satellite tags.

Our estimates for residence length that incorporated data from satellite telemetry were close to each other IRL_{BM+ST} of 55.9 ± 11.8 days (range 31–76 days; $N=18$) and the PRL between 52.6 and 57.3 days (Table 2). The longest residence length (85 days) at a breeding site recorded for hawksbill turtle using satellite telemetry was observed in the US Virgin Islands (Hart et al. 2019). Because most satellite telemetry studies with nesting hawksbill turtles focus on migration and delineating foraging grounds (Cuevas et al. 2008; Van Dam et al. 2008; Hawkes et al. 2012; Moncada et al. 2012), those that included internesting intervals in their analyses have not typically been designed to track individuals since their first nesting event, and as a result, their residence length at the breeding site is likely to be underestimated (Troëng et al. 2005; Gaos et al. 2012; Marcovaldi et al. 2012; Pilcher et al. 2014; Nivière et al. 2018; Hart et al. 2019). Cases in which

female hawksbill turtles were tracked from the foraging site toward the breeding site are scarce in the literature (Hawkes et al. 2012; Iverson et al. 2016), and residence length at the breeding site has been provided for only one individual (Iverson et al. 2016). Despite recent technological advancement allowing satellite tags to last longer and store more data, problems with tag retention are still one of the biggest challenges to satellite telemetry studies (see Pilcher et al. 2020). Studies aiming to improve tag retention should be prioritized to gain more data from satellite tracking studies (Hart et al. 2021; Hays et al. 2021).

Our IRL_{BM} comparison for turtles from the first portion of the nesting season was higher than that for turtles starting the season later (from February onwards), suggesting that early nesters may have higher clutch frequency. For other species, such as some birds, the timing of arrival for the nesting season influences breeding success (Verhulst and Nilsson 2008; De Forest and Gaston 2010). Walcott et al. (2012) found that hawksbill turtles that arrive earlier in the nesting season occupy shallower waters, which may be associated with higher quality breeding residence habitats. In this sense, the arrival time for the breeding season may also influence residence selection, which possibly affects its length and therefore clutch frequency estimates. One way to investigate the possible influence of arrival timing during the nesting season on clutch frequency would be to deploy satellite transmitters before the females arrive at the breeding site. This would require the device to function for more than 2 years, as the remigration interval for hawksbill turtles is typically 2 years (Santos et al. 2013) or to attach the equipment in the foraging ground prior to migration (see Pilcher et al. 2020). However, selecting turtles at foraging grounds that will likely start migration to breeding areas is challenging, since it would require the identification of individuals that are reproductively “ready” by laparoscopy or ultrasound (Pilcher et al. 2020). In addition, nesting females from a particular rookery migrates to a variety of foraging grounds (Cuevas et al. 2008; Van Dam et al. 2008; Horrocks et al. 2011; Marcovaldi et al. 2012; Santos et al. 2021), and those from the same foraging region are likely to migrate to a nesting area at similar times than turtles that may be experiencing environmental conditions at a different site.

It is speculated that the longer the distance from the foraging ground to the breeding site, the more energy turtles will spend on migration (Enstipp et al. 2016), and therefore, less energy may be allocated to reproduction, resulting in smaller clutch frequency or clutch sizes (Patel et al. 2015). Conversely, resident turtles that do not need to allocate energy to large migrations may nest more times during the season or exhibit smaller remigration intervals (Ceriani et al. 2015; Vander Zanden et al. 2014). In addition, the quality of foraging grounds also plays a determinant role on energy accumulation and fecundity (Broderick et al. 2001; Vander

Zanden et al. 2014; Ceriani et al. 2015); however, possible impacts on clutch frequency remain unknown. Thus, if environmental changes are likely to influence the quality of foraging habitats over time (Hays 2000), there is the need to revisit demographic parameters such as clutch frequency and remigration interval from time to time.

Temporal scale

The temporal scale of monitoring, and consequently data inclusion into estimates, affects clutch frequency estimates. For this reason, care should be taken to ensure that the whole nesting season is incorporated into such estimates. For example, Rees et al. (2020) reported lower clutch frequency for turtles tracked later in the season. The clutch frequency using satellite telemetry calculated for nesting hawksbill turtles in the Dominican Republic (between 2 and 4 clutches) possibly may have included females that nested previously in the season, thereby underestimating clutch frequencies (Revuelta et al. 2015). Bio-logging tools such as radio or satellite telemetry are very helpful to keep track of internesting returns (Rees et al. 2010; Tucker 2010; Weber et al. 2013; Esteban et al. 2017; Tucker et al. 2018). However, it is important that device deployment takes place during the first nesting event of the breeding season or prior. Indeed, disparities in clutch frequency estimates can be observed between studies that use different sampling designs. For example, in our study, we only considered individuals nesting in the first portion of the nesting season to avoid including turtles that had nested previously within the season, with estimated 3.9 clutches for ECF_{BM} . However, an ECF_{BM} of 2.6 was estimated by Santos et al. (2013) at the same study sites when considering all individuals nesting over the course of the entire nesting season. This difference may be driven by the inclusion of turtles that may have nested previously within the nesting season.

Acknowledging that the first nesting event might not have been accounted for in clutch frequency estimation, Rivalan et al. (2006) estimated clutch frequency for leatherback turtles (*Dermochelys coriacea*) using an approach that considers that the turtle may have nested but not been observed prior to their first and after the last recorded nesting event. This approach was first designed to estimate stop-over duration in birds (Schaub et al. 2001; Efford 2005) and further adapted to improve estimation of clutch frequency in leatherback turtles using beach monitoring data (Rivalan et al. 2006). Despite the fact that we cannot ensure that the selected turtles for the present study have not nested previously, our approach of selecting individuals from the first portion of the nesting season reduces biases associated with individuals potentially nesting previously (see Esteban et al. 2017; Tucker 2010; Tucker et al. 2018). Future studies should use different approaches (e.g., ultrasonography, the

amount of fat in a turtles neck) to confirm the stage of nesting (Blanco et al. 2012; Walcott et al. 2012, 2013).

Spatial extent

Despite the importance of clutch frequency estimates, this parameter has been rarely estimated for Atlantic hawksbill turtles. Estimates based on beach monitoring that do exist show disparities between continental rookeries (less than three clutches per female) and island rookeries (4 to 5 clutches per female) (Garduño-Andrade et al. 1999; Xavier et al. 2006; Beggs et al. 2007; Kamel and Delcroix 2009; Kendall et al. 2019). This disparity is likely due to nests being missed during beach monitoring on continental beaches, since it is typically easier to encounter all or most nesting females at island beaches, which tend to be smaller and geographically isolated. As turtles nesting at continental beaches may nest within a wider region, there is a greater possibility of turtles nesting on adjacent beaches to those that are surveyed. Nevertheless, although evidence exists that hawksbill turtles nesting in islands exhibit strong site fidelity (Levasseur et al. 2019), leaving the original site in favor of other nearby islands can also occur (Iverson et al. 2016). This makes it challenging to obtain unbiased clutch frequency estimates with beach monitoring data alone.

It is important to also consider tidal regimes when considering clutch frequency, since it may play an important role on detectability, especially during high spring tides, as turtle tracks can be erased by waves. Indeed, the missed record A7 (Table S5) occurred during spring tide. In our study site, hawksbill turtles often (48%) nest below the highest spring tide line, as they crawl up the maximum possible path and come across a sand slope that is exposed to high spring tides (Santos et al. 2016). Thus, in areas where tides are not negligible, tidal regime is an important factor to consider when designing monitoring surveys and interpreting nesting information. Additionally, despite the fact that hawksbill turtles nest mostly at night, a few nests occur at any time during the day (A. J. B. S. personal communication), hindering the individual's detection, especially during spring tide periods. Strong winds and rain may also influence the detectability of marine turtle nests (Metcalf et al. 2015).

Conservation implications

Our work indicates that the integration of beach monitoring data with satellite telemetry information (such as residence length at the breeding site and haul-out locations) may refine clutch frequency estimates for marine turtles and consequently population abundance estimates. Importantly, when considering clutch frequency estimation, the spatio-temporal extent of sampling, and data inclusion, needs to be considered. Indeed, our study highlighted that the use of clutch

frequency data to estimate abundance of nesting females based on nest counts should only be used when the whole nesting population assemblage is considered (see Ceriani et al. 2019), which should include transient turtles. When sampling a fraction of the population, there is the need to account for biases from transient turtles. Sometimes, turtles are wrongly considered transient as a reflection of low detectability by beach monitoring (Pfaller et al. 2013). For example, in our study, even with an intensive monitoring effort, nests were missed, as was evidenced by the haul-out from female ID 4* (see Tables S4 and S5). In addition, the number of transient turtles may vary greatly between seasons; for example, the number of transient turtles was three times greater in 2016/2017 than in 2015/2016 (see Table S3). Some studies based on beach monitoring have excluded transient turtles when calculating clutch frequency for hawksbill turtles (Beggs et al. 2007) to avoid lowering average estimations by adding females that were likely to nest in adjacent beaches. To illustrate the implications of using such approach, we excluded transient turtles ($N=17$, Table S3) from the season with the highest number of nests (2018/19 with 138 nests; Table S2), and the ECF obtained was 3.9 clutches per female, which is the same ECF_{BM} that we obtained (Table 1).

Our estimates that accounted for transient turtles were much closer to the number of females observed nesting during beach monitoring than the estimates did not account for them (Fig. 4). With this in mind, the commonly used equation to calculate female turtles during a nesting season ($\text{clutches/season} \div \text{clutches/female/season} = \text{females/season}$) (Johnson and Ehrhart 1996; Broderick et al. 2002) seems very simplistic, as some nests are likely to belong to transient turtles. However, if one desires to use this approach, knowledge on the fidelity of individuals to their study site and the spatial extent of their nesting is needed, which will allow an assessment of whether transient turtles are present. If this assumption is not met, the number of transient turtles should be incorporated into calculations, by discounting the number of clutches that transients laid. All ECF approaches used to estimate the number of nesting females that incorporated transients outperformed approaches that did not consider transient turtles (Fig. 4). However, among the approaches that did not account for transient turtles, ECF_{BM} performed better, because the lower ECF biased by detectability compensated for the existence of transient turtles. Nevertheless, it is important to note that the number of females observed by beach monitoring represents a minimum estimate, as an average of 17% of nests were not observed; thus, the real number of females estimate for our study site is probably slightly higher than estimated here.

It is important to note that our study site represents an index area that is part of a larger monitored area for nesting hawksbill turtles in the southern coastline of Rio Grande do

Norte, Brazil, which extends 42 km (see Santos et al. 2013). This area as well as the Northern coast of Bahia (Marcovaldi et al. 2007) concentrates the highest number of nesting hawksbill turtles in Brazil; however, nesting occurs continuously along the whole Northeastern coastline (approximately 3000 km) covering several states: Piauí (Neto et al. 2021), Ceará (Santos et al. 2019), Rio Grande do Norte (Santos et al. 2013; Bomfim et al. 2021), Paraíba (Mascarenhas et al. 2004), Pernambuco (Moura et al. 2012), Alagoas (Simões et al. 2021), and Bahia (Marcovaldi et al. 2007; Camillo et al. 2009), with evidence that this continuous nesting range is used by a single genetic population (Vilaça et al. 2013; Arantes et al. 2020; Simões et al. 2021). The estimates from this study should provide a basis for future abundance estimates of hawksbill turtles for this important genetic unit. Despite the importance of these study results for the geographic area and species involved, the approaches we describe have a much broader applicability and can be applied to any marine turtle species to enhance estimation of clutch frequency and population abundance globally.

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Author contributions Conceptualization: AJBS and MMPBF, methodology: AJBS and Mariana MPBF, formal analysis and investigation: AJBS, writing—original draft preparation: AJBS, writing—review and editing: MMPBF, GC, and SC, data collection: AJBS, DHGV, and CB, and supervision: MMPBF.

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Data availability The satellite telemetry data that support the findings of this study are available from the Brazilian Environmental Agency (IBAMA—Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis) and ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade), and beach monitoring data are available upon request from the corresponding author and with permission of IBAMA and ICMBio.

Declarations

Conflict of interest All authors declare no conflict/competing interests.

Ethical approval Biodiversity authorization and information system (SISBio) issued the data collection license 42760, respecting Brazilian animal care regulations.

Informed consent All authors reviewed and agreed with the final version of this manuscript.

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