

Using Data from Satellite Telemetry and Nesting Beach Monitoring to Improve Estimates of Marine Turtle Clutch Frequency

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Abstract

Population abundance data is often used to define species' conservation status. Abundance of marine turtles is typically determined using information from nesting beach monitoring such as clutch frequency and remigration interval of nesting females. However, studies have shown that clutch frequency determined solely from nesting beach monitoring data can be underestimated. To obtain reliable estimates of clutch frequency 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, whilst state space modelling of satellite telemetry data indicated the departure date of turtles, allowing calculations of residence length at breeding site and therefore estimation of clutch frequency based on interesting intervals. Nesting females were estimated to nest up to six times within the nesting season and had an average clutch frequency of 4.7 nests per female. This estimate is almost twice larger than previous estimates based only on beach monitoring. The new estimates of clutch frequency will allow for more reliable population abundance estimates for this critically endangered population. Further, to guide future estimates of marine turtle clutch frequency methods to estimate clutch frequency were compared and their advantages and biases were discussed. Our approach and findings highlight the need for reconsideration of how clutch frequency is commonly determined for marine turtle populations and the use of beach monitoring data and satellite telemetry for estimations of clutch frequency.

1. Introduction

Population abundance data is one of the key parameters used in population assessments to evaluate and determine a species' conservation status (IUCN, 2017a; Willians et al., 2011), 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 may be difficult to determine, particularly for species with high dispersal, and when different life stages and genders are not equally available for counting (Bradbury et al. 2008). Further, some species may utilize a variety of areas spatially within a region, being residents to core areas, and /or also migrate between locations, being transient in some locations (e.g., often only being observed once at specific locations), biasing counts and abundance estimates (Chaloupka and Limpus 2002; Clavel et al. 2008).

This is the case for marine turtles, where estimates of species abundance should consider information on hatchlings, juveniles, sub-adults and adults from both sexes (Chaloupka and Limpus 2001; Rees et al. 2016). However, determining abundance across life stages is hard, especially for some life stages, such as the first few years of hatchlings, since limited information is available for this life stage (Putman et al. 2020). Further, until marine turtles reach maturity males and females cannot be distinguished visually, making it difficult to determine the gender of individuals and determine numbers for each sex individually (Meylan et al. 2011). Males are also more difficult to encounter and count as they remain in the oceanic environment for their entire life, and do not come ashore as nesting female turtles, with exception of cold-

water regions, where they come ashore to bask, such as in the Galapagos (Maxwell et al. 2014) and Hawaii (Whittow and Balazs 1982). Additionally, marine turtles use a variety of areas across each of their life-stages, having residence in some locations (e.g., foraging areas) but being transient in others (e.g., migratory corridors) (Chaloupka and Limpus 2002; Prince and Chaloupka 2012).

As a result of these factors the easiest, least expensive and most used method to estimate marine turtle abundance is to utilize counts of the number of nests and breeding females at nesting beaches (National Research Council, 2010; Mazaris et al., 2017). The fact that breeding individuals within a population aggregate in particular areas for reproduction makes it easier to count individuals that may disperse across the vast marine realm (Godley et al. 2010). Marine turtles lay several clutches within a nesting season, with intervals between seasons from one to several years, these remigration interval (RI) varies amongst individuals, populations and species (Miller 1997; Troëng and Chaloupka 2007; Warden et al. 2017). A snapshot of the number of females nesting in a given season within a population, can be estimated using the total number of nests across all nesting sites used by that population in that season divided by the number of nests that individuals laid (clutch frequency) (Johnson and Ehrhart 1996; Broderick et al. 2002). However, this approach is simplistic and doesn't account for the uncertainty in this reproductive rate parameter (Ceriani et al. 2019). Combining this information with the known RI allows the estimation of abundance of nesting females (Hays 2000; Broderick et al. 2002; Ceriani et al. 2019; Casale and Ceriani 2020). Both RI and clutch frequency are difficult to determine. RI requires that individual turtles be seen once during the reproductive season, while clutch frequency depends 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 information on clutch frequency is challenging for two reasons. First, the nests can be spatially separated by more than 100 km requiring for night tagging monitoring to occur across large spatial extents to encounter turtles (Tucker 2010; Shamblin et al. 2017), which is logistically difficult and often unfeasible. Second, tagging loss may cause individuals to be counted more than once and bias clutch frequency estimations (Hays 2000; Rivalan et al. 2005). Satellite telemetry as well as genetic capture-recapture fingerprinting has improved the ability to detect when marine turtles return to beaches for nesting events improving estimates of clutch frequency (Tucker 2010; Esteban et al. 2017; Shamblin et al. 2017; Tucker et al. 2018; Rees et al. 2020). 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). However, most of the population abundance estimates from 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; Troëng and Rankin, 2005; Witherington et al., 2009). This is the case for hawksbill turtles (*Eretmochelys imbricata*) nesting in the South Atlantic, in particular in Brazil which has the largest hawksbill turtle nesting density in the region (Marcovaldi et al. 2007; Santos et al. 2013). Thus, to obtain more accurate estimation of population abundance of hawksbill turtles nesting in Brazil there is the need to revisit clutch frequency numbers. Here, we combined beach monitoring data with satellite telemetry data to reassess clutch frequency for hawksbill turtles that nest in the southern coastline of Rio Grande do Norte, Brazil, an important region for this

critically endangered species. Further, we provide comparisons among several methods to estimate clutch frequency and discuss the advantages and biases from data collected from each approach to inform future studies that aim to estimate marine turtle clutch frequency.

2. Material And Methods

2.1 Study site and approach

Clutch frequency was determined by combining information from nesting beach monitoring and from satellite telemetry obtained at three hawksbill turtle nesting beaches (Chapadão, 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). This population is part of the Southwest Atlantic Regional Management Unit (RMU) (Wallace et al. 2010) and is classified as critically endangered by the International Union for the Conservation of Nature (IUCN) Redbook (IUCN, 2017b) and by the Brazilian Red List of Threatened Species (Marcovaldi et al. 2011).

2.2 Study design

Morning beach monitoring for marine turtle activity (e.g., nests and false crawls) was conducted daily from November 1st to May 30th during the 2014/2015 and the 2018/2019 nesting season. Each record was identified as a nest or false crawl, but for this study we only considered information from nests. As well as morning beach monitoring, during each of these five nesting seasons, intensive monitoring was conducted nightly from the 10th December to 15th April, which accounts for 93.4% of nesting across the season. Sunrise in the region occurs around 4:30 am and 81% of nesting records occurs before midnight (Nakamura et al. 2019), thus night 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, hawksbill turtles were intercepted after egg-laying, checked for Inconel tags (number 681 National Band and Tag Company), and if none were present, they were tagged in both front flippers. Curved carapace length (CCL ± 0.1 , cm) was measured with a flexible tape from notch to tip (Marcovaldi and Marcovaldi 1999). After the 15th 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) all the nests were excavated after hatching, to confirm the species for the nesting event.

Nesting females encountered during the night monitoring were randomly selected for attachment of platform transmitting terminals (PTT; N = 35), and 10 of them were tracked in two consecutive nesting seasons with a new PTT (Table S1). Six PTT models were used for our study (Table S1; mass in g;

dimensions [length x width x height]: 12 SPOT-293A – 119 g – 72x54x24 mm, 6 SPOT-375 – 136 g – 99x55x21 mm, 8 SPLASH10-F-296A – 195 g – 86x85x29 mm, 3 SPLASH10-F-334 – 450 g – 112x63x62 mm, manufactured by Wildlife Computers (Redmond, WA, USA), and 4 Kiwi-Sat K2G 376D – 240 g – 136x44x59 mm, 2 Kiwi-Sat K2G 376D – 360 g – 138x78x50 mm manufactured by Sirtrack (Havelock North, New Zealand). 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., In press). Turtles in the study site take at least 40 minutes to successfully nest, therefore FastGPS were set to enter haul-out cycle after 20 minutes when the wet/dry sensor was dry and exited haul-out after 30 seconds 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 minutes 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 sampling interval, ranging from one to four locations per hour, enabling the detection of nesting attempts. In cases where subsequent haul-out 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.

For individual clutch frequency estimation, we selected a subset (N = 18) of satellite tracked females that nesting monitoring data indicated laid their first clutch during the first portion of the nesting season (Fig. S1). We selected turtles that nested by the end of January as indicated by data from the monitoring activities, to avoid considering turtles that nested previously during the nesting season (Fig. S1), which represents 24% of the clutches laid (Fig. S1). PTT deployment for the selected turtles identified to have nested in January, took place in December/January (N = 8) February and April (N = 10; Table 1; Fig. 2). Among the subset of tracked females, 11 PTTs (Kiwi-Sat and SPOT models) relied on ARGOS positions while the 7 SPLASH models included FastGPS and haul-out data (Table 1).

2.3 Clutch frequency estimates

Observed clutch frequency estimates (OCF) was based on information obtained during nesting beach monitoring and determined as the number of times that each individual nesting turtle was encountered nesting successfully during the nesting season throughout our monitoring activities.

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 (ECF_b) based on the beach monitoring data. For example, if we had an interval of 30 days between the encounters of a turtle, we assumed that one unobserved nesting event occurred, for intervals of 45 days we assumed that two unobserved nesting events occurred (Johnson and Ehrhart 1996; Broderick et al. 2002; Briane et al. 2007; Santos et al. 2013). In order 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 at our study site during the relevant period were from other identified individual turtles it meant that the

assumed nest occurred elsewhere outside of our study site. However, if occurred nesting events existed 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 the nest occurred at our study site.

To estimate clutch frequency (ECF_s) using the data from the subset of satellite tagged turtles and from nesting beach monitoring the length of residency at the breeding site was divided by the average internesting interval after the first clutch was laid as suggested by Esteban et al. (2017). Hence the individual residency length (IRL_s), was first determined by fitting a hierarchical state-space modeling (SSM) (Jonsen et al. 2006) using location estimates for each 6 hour 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, FastlocGPS 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 (Wotherspoon et al. 2017) in R v.3.5.1 (R Core Team 2018). As 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. In the ten cases where the turtle was detected nesting during beach monitoring prior to satellite tag instrumentation, we added the number of days since it was first recorded nesting within that season to the calculation of the IRL_s at the breeding site. Similarly, two females (ID 13 and 25) started migration immediately after instrumentation, however, they were detected by the nesting beach monitoring when they nested earlier in the season allowing us to estimate their residence period at the breeding site (Fig. 2). For the cases ($N = 3$) that 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) towards its foraging site (second polygon), allowing us to determine their residency length (Fig. S2).

For comparison purposes, we also calculated the individual residence (IRL_b) length based on beach monitoring data, as the difference in days between the last and first nests recorded for all individuals ($N = 122$), excluding the transient turtles, that is, those observed only once ($N = 88$). We further compared IRL_b as well as the number of transient turtles from the first portion of the nesting season with those that started to nest later in the season, that is, with first nesting from February onwards. 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 nesting monitoring ($N = 210$), and the average departure date based on SSM ($N = 32$) or home range inspection ($N = 3$; IDs 13, 16 and 16*). December 1st was considered day zero for each nesting season since nesting for this populations typically starts early in

December (Santos et al. 2013). The difference in days between averages of first nesting and departure were used to estimate PRL at the breeding site. Similarly, to the ECF_s calculation described above, we used PRL to obtain a clutch frequency estimate for the nesting population (ECF_{PRL}) dividing PRL by the average internesting interval and adding 1 clutch to take into account the first nest.

To further inform future studies that aim to estimate marine turtle clutch frequency, we compared the ECF_b based on beach monitoring solely with ECF_s based on the combination of beach monitoring data with satellite telemetry using a paired t-test and determined the number of unobserved nests by beach monitoring. Similarly, we compared residence length that incorporated data from satellite telemetry (IRL_s) with those obtained from beach monitoring solely (IRL_b).

We compared IRL_s and ECF_s for the individual turtles tracked in two subsequent nesting seasons, however we did not make any comparative statistics as the sample size was small ($N = 4$). We also evaluated the efficiency of satellite telemetry in determining nesting events based on the haul-out data in comparison to the nesting records by beach monitoring and length of residence period at the breeding site.

3. Results

3.1 Nesting activity

Between 33 to 51 (average 42 ± 7.5) individual nesting hawksbill turtles were encountered each season during the beach monitoring conducted at our study site, with in average 124 ± 8 (range 114 – 138) nests per season (Table S2). Of the individuals encountered during the beach monitoring, 41% were transient and seen nesting only once during the nesting season within our study site (Table S3). The average IRL_s for the subset of tracked hawksbill turtles at the breeding site was 55.9 ± 11.8 days (range 31 – 76 days; Table 1; Fig. 2), whereas the PRL at the breeding site was estimated to be 52.6 days (Table S4). 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%) (Figs. S3 and S4).

The overall average IRL_b was 44.1 ± 16.7 days (range 13 – 82 days), significantly smaller than IRL_s (Paired t test, $t_{17} = 12.86$, p-value <0.001). Average IRL_b for turtles that nested by the end of January was 48.9 ± 16.1 days (range 14 – 82 days; $N = 67$) and with first nesting from February onwards was 38.3 ± 15.6 days (range 13 – 82; $N = 55$); the two values significantly differed (Paired t test, $t_{54} = 7.14$, p-value <0.001). Transient turtles among turtles seen in the first portion of the nesting season were 33.1% ($N = 99$) whilst from February onwards was 50.5% ($N = 111$).

The IRL_s 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 IDs 3 and 4, and 12 and 15 days shorter for IDs 7 and 11, respectively (Table 1; Fig. 2).

3.2 Clutch frequency estimates

Based on information obtained from beach monitoring, the average OCF was estimated to be 3.3 ± 1.4 clutches per female (median = 4 clutches per female; Table 1) and the average ECF_b was estimated to be 3.9 ± 1.5 clutches per female (median = 4 clutches per female; Table 1). Based on data from beach monitoring and satellite telemetry the estimated average ECF_s was 4.7 ± 0.8 clutches per female (range 3.1 – 6.1 clutches per female; median = 4.9 clutches per female; Table 1). Average ECF_b was significantly smaller than ECF_s (Paired t test, $t_{17} = 2.83$, p-value = 0.012). The PRL produced average ECF_{PRL} of 4.5 clutches per female. For individuals tracked in two consecutive nesting seasons, ECF_s was the same in both nesting seasons for IDs 3 and 4, while for IDs 7 and 11 there was a difference of one nest between the two seasons (Table 1).

Table 1. Subset of turtles selected for platform transmitting terminals (PTT) deployment. CCL = curve carapace length, OCF = observed clutch frequency, ECF_b = estimated clutch frequency based on beach monitoring data, ECF_s = estimated clutch frequency based on beach monitoring data and satellite telemetry information. Departure date - indicate 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 to departure dates. *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.

Turtle ID	PTT Model	CCL (cm)	First documented nest date	Departure date	IRL (days)	OCF	ECF _b	ECF _s
1	SPLASH10-F-296A	91.2	1/28/15 ⁺	3/14/15	45	4	4	4
2	SPOT-293A	86.1	1/28/15 ⁺	3/28/15	59	3	5	4.9
3	SPOT-293A	88.9	1/19/15 ⁺	3/18/15	58	4	5	4.9
3*	SPLASH10-F-296A	88.4	1/16/18	3/19/18	61	2	4	5.1
4	SPLASH10-F-296A	86.3	1/19/15 ⁺	3/20/15	60	4	5	5
4*	SPLASH10-F-296A	88	12/26/17	3/2/18	66	3	4	5.4
7	SPLASH10-F-296A	95.5	1/17/16	3/20/16	63	5	5	5.2
7*	SPOT-375	95.7	1/27/18	3/19/18	51	4	4	4.4
8	SPOT-293A	98.1	1/21/16	3/8/16	47	1	1	4.1
9*	SPLASH10-F-334	86.5	1/14/19	3/25/19	70	5	5	5.7
10	SPOT-293A	82.8	1/25/16 ⁺	3/9/16	44	3	4	3.9
11	SPOT-293A	86.4	1/28/16 ⁺	3/14/16	46	4	4	4.1
11*	Kiwi-Sat K2G 376D	86.3	1/24/19	2/24/19	31	2	3	3.1
13	SPOT-293A	84.4	1/25/16 ⁺	3/29/16	64	5	5	5.3
19	SPOT-375	93.3	12/19/18	2/14/19	56	1	1	4.7
20	SPOT-375	85.2	12/28/18	2/6/19	40	1	1	3.7
21	Kiwi-Sat K2G 376D	95	1/18/19 ⁺	3/28/19	69	4	5	5.6
25	SPLASH10-F-334	97.2	1/24/19 ⁺	4/10/19	76	5	6	6.1

3.3 Assessment of information obtained from nesting beach monitoring and satellite telemetry

Nesting females were encountered by the monitoring team for most (82.6%) of the nests recorded in our study during our monitoring activities (Table S2). When calculating the ECF_b (Table 1), 11 nests were assumed to have occurred based on internesting interval (Table S5). 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

interesting period (i.e., records in which the female was not observed) (Table S6). 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 S6).

Satellite telemetry information typically complemented nesting data from our monitoring efforts, for instance three individuals (IDs 8, 19 and 20) were observed nesting only once during our beach monitoring (Table S5). However, satellite telemetry data indicated that residence length at the breeding site was compatible with at least three other nesting events at our study sites during the nesting season (Fig. 2). Further, we assumed that three nests occurred outside our study site; however, information from haul-outs obtained from the FastGPS tags indicate that one of them actually occurred at our study site but was missed by the beach monitoring (Table S6; A7). Nevertheless, two nesting events observed during the nesting monitoring were not recorded or transmitted by information obtained from haul-out from one of the 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.

4. Discussion

Combined data from nesting beach monitoring and satellite telemetry allowed us to provide robust estimates of average clutch frequency for hawksbills turtles nesting in Rio Grande do Norte state, Brazil, with estimates ranging from 3.3 when using observed data from beach monitoring to 4.7 when combining the beach monitoring data with satellite telemetry. Larger clutch frequency estimations when using satellite telemetry and data from nesting turtles opposed to only using data from nesting beach is reflective of previous studies (Rees et al. 2010; Tucker 2010; Weber et al. 2013; Esteban et al. 2017; Tucker et al. 2018). Larger clutch frequency numbers, when estimating number of nesting females, results in a lower estimate of nesting female numbers, as the total number of clutches is divided by a larger denominator (Mazaris et al. 2008). That is why clutch frequency is considered a key demographic parameter to marine turtles and when not accurately estimated may lead to inflated estimation of nesting females. Despite the importance of clutch frequency estimates, this parameter has been rarely estimated for Atlantic hawksbill turtles, with disparities in estimations, based on beach monitoring, between continental rookeries (less than three clutches per females) 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, since it is typically easier to encounter all nesting females at smaller, geographically isolated beaches, which is usually the case at islands. As turtles nesting at continental beaches may nest within a region, there is the possibility that they may be nesting at adjacent beaches to those surveyed. Nevertheless, although evidence exists that hawksbill turtles nesting in islands exhibit strong site fidelity (Levasseur et al. 2019), evading from the original site to other near islands can also occur (Iverson et al. 2016), making challenging to obtain unbiased clutch frequency estimates with beach monitoring data solely. Clutch frequency using satellite

telemetry has been calculated for nesting hawksbill turtles in the Dominican Republic (between 2–4 clutches); however, the selection of individuals for these estimations may have included females that nested previously in the season, underestimating clutch frequencies (Revuelta et al. 2015).

The temporal scale of monitoring, and consequently data inclusion into estimates, affects clutch frequency estimates; thus, care should be taken to ensure that the whole nesting season is incorporated into such estimations. 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 occurs during the first nesting event of the breeding season or prior. Indeed, disparities in clutch frequency estimations 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 an estimated 3.9 clutches for ECF_b . However a ECF_b 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 clutch estimations, Rivalan et al. (2006) estimated clutch frequency in leatherback turtles 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 stopover duration on birds (Schaub et al. 2001; Efford 2005) and further adapted to improve estimation of clutch frequency in leatherback turtles (*Dermochelys coriacea*) 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). Futures studies can 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).

Residence length, a parameter that might be used to calculate clutch frequency (Esteban et al. 2017; Kendall et al. 2019) also requires knowledge of the first and last nesting event for individual nesting turtles. Residence length at a site is a result of the cumulative sum of each turtle internesting interval, from first to last nesting event (Esteban et al. 2017). Several factors may influence the internesting and residence length of turtles 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 the turtle to conclude/start 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; this could be in the same night, but often in the following night(s) (see Hamann et al., 2002). If false crawls occur repeatedly, the extended internesting intervals will increase residence length. Second, temperature influences physiology, with warmer waters causing internesting intervals to decrease (Sato et al. 1998; Hays et al. 2002). 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). Also linked to physiology, the water limitation hypothesis has been suggested to influence the length of internesting interval (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). Lastly, the process of PTT attachment may influence nesting turtle behavior, in particular if the turtle is displaced to another area for the instrumentation and further release, which was not the case for this study (see Luschi et al., 2003, 1996).

Our estimates for residence length that incorporated data from satellite telemetry were close to each other IRL_s of 55.9 ± 11.8 days (range 31–76 days; $N = 18$) and the PRL of 52.6. It is interesting to note that this single number (PRL) was estimated based on the difference between average date for first nesting event from beach monitoring ($N = 210$), which includes turtles seen only once (transients), and the average date from departure from satellite telemetry ($N = 35$) (Fig. S4). The longest residence length (85 days) at a breeding site recorded for hawksbill turtle using satellite telemetry was observed in the US Virgin Islands ($N = 30$; 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 are 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 the female hawksbill turtle was tracked from the foraging site towards the breeding site are scarces 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). Even though, with recent technological advancement satellite tags have the ability 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 benefit from satellite tracking studies.

Our IRL_b comparison for turtles from the first portion of the nesting season was higher than that for turtles starting the season from February onwards, suggesting that early nesters may have higher clutch frequency. For other species such as many 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 two years, as the remigration interval for hawksbill turtles is typically two 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 to leave, this could be determined with laparoscopy or ultrasound (Pilcher et al. 2020). 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). On the other hand, resident turtles that do not need to allocate energy to large migrations may nest more times during the season or exhibit smaller remigration interval (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.

The spatial extent of sampling, and data inclusion, also needs to be considered for clutch frequency estimation. It is very common for projects to report their nest count for their specific study site (Mascarenhas et al. 2004; Marcovaldi et al. 2007; Camillo et al. 2009; Moura et al. 2012; Santos et al. 2013). However, our study highlights that the use of clutch frequency data to estimate abundance of nesting females based on nest counts should only be used when the whole population is considered, in a more comprehensive way (see Ceriani et al., 2019). For instance, if we use our $ECF_s = 4.7$ to infer number of nesting females within our study sites for the year with highest number of nests ($18/19 = 138$ nests), the result would be 29 females. However, in that season 48 individual females were encountered, with 33% of transient turtles (16 females; Table S2) that also used adjacent beaches to nest (Santos et al. 2013). There are studies with hawksbill turtles that exclude transient turtles for the calculation of clutch frequency (Beggs et al. 2007). Using this approach for the previous example, the estimation would result in 3.9 clutches per female, which is the same ECF_b that we obtained; however, if we just divide the total number of clutches by the number of individual females observed, it would result in 2.9 clutches per female. Therefore, sampling a fraction of the population will always require dealing with 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 S5 and S6). Tidal regime 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 S6) 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, tidal regime is an important factor to consider when designing monitoring surveys and interpreting nesting information. Additionally, despite the fact that most hawksbills turtles nest at night, a few nests occur 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).

Our results indicate that beach monitoring data combined with satellite telemetry information may fine tune clutch frequency estimation for marine turtles. However, it is important to consider that if the interesting habitat for hawksbill turtles is very close to the shoreline (e.g. less than 1 km), detecting nesting events through satellite telemetry will require tags with fine scale resolution, which are usually costly (Esteban et al. 2017). Thus it is suggested that residence length should be used as indicator of clutch frequency, such approach would allow for sample sizes to be higher through the use of lower resolution cheaper satellite tags. Our approach and suggestions although applied to hawksbill turtles nesting in Rio Grande do Norte, should be considered for other nesting locations in Brazil (e.g., Bahia, Piauí, Paraíba, Pernambuco, Alagoas and Sergipe states), which would allow for nesting numbers to be estimated for this endangered genetically discrete population.

Declarations

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Compliance with Ethical Standards Biodiversity authorization and information system (SISBio) issued the data collection license 42760, respecting Brazilian animal care regulations. All authors declare no competing interests.

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), beach monitoring data is available upon request from the corresponding author and with permission of IBAMA and ICMBio.

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Figures

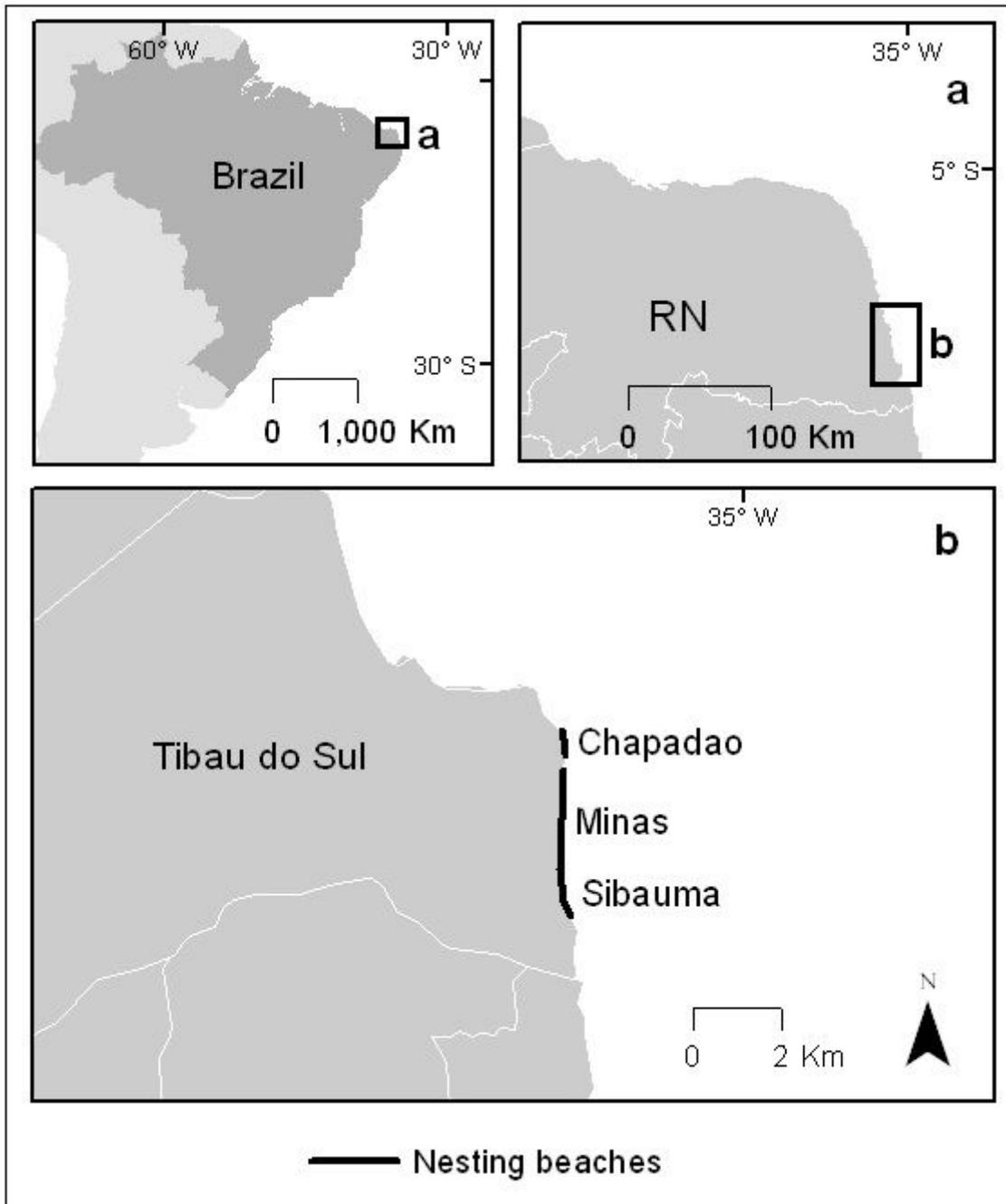


Figure 1

Study sites in Brazil, at the southern coastline of Rio Grande do Norte (RN) state (A), where data was obtained at Tibau do Sul municipality to determine clutch frequency for hawksbill turtles (B) across three nesting beaches in the region. Km = kilometers.

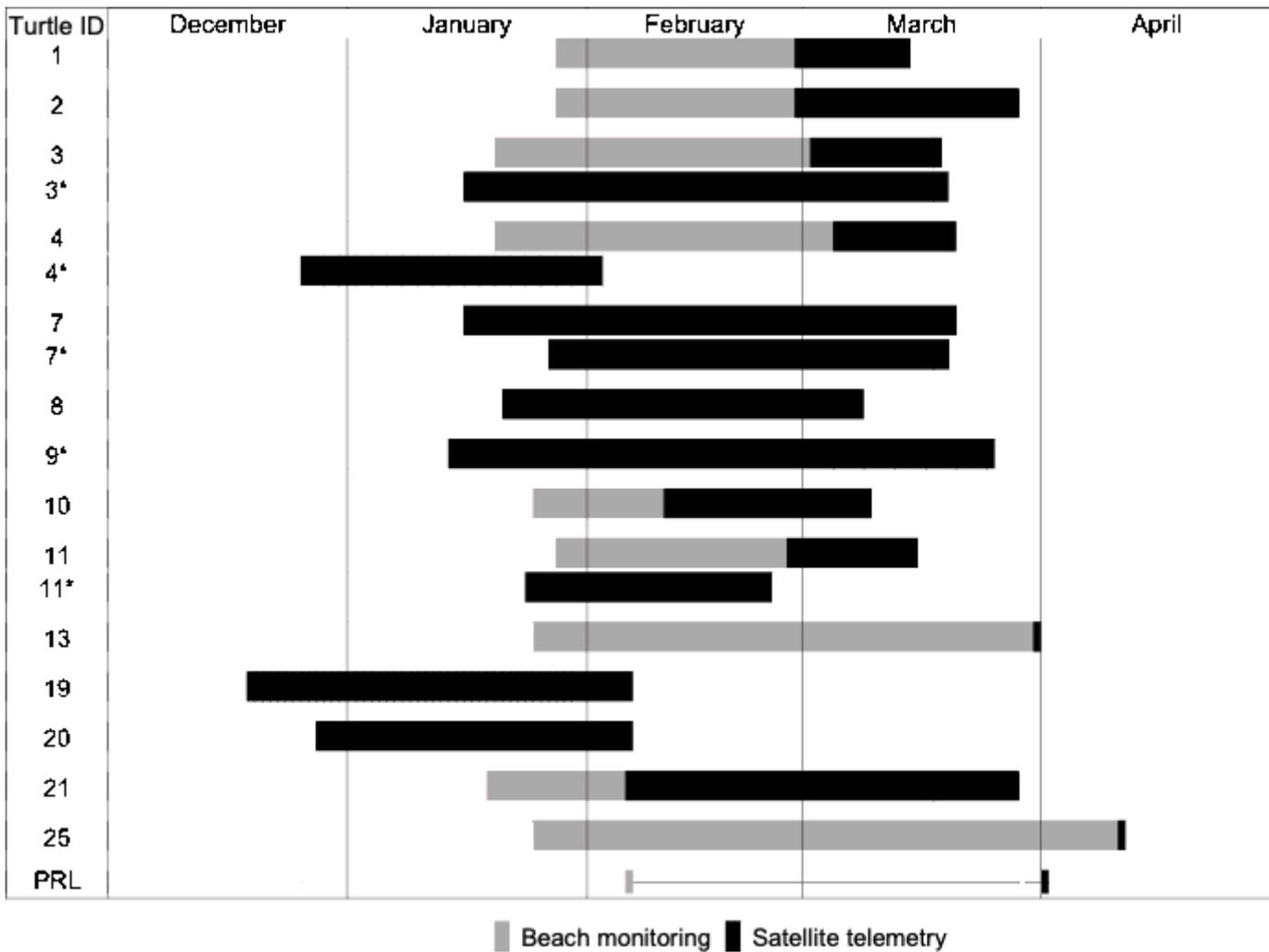


Figure 2

Residence length at the breeding site for nesting hawksbill turtles obtained by a combination of data from beach monitoring and satellite telemetry. Individual residence length (IRL) at the breeding site is presented for 18 platform transmitting terminals (PTTs) 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.

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