



Increased nesting, good survival and variable site fidelity for leatherback turtles in Florida, USA



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ABSTRACT

Despite facing serious threats of extinction in the Eastern Pacific, the leatherback turtle (*Dermochelys coriacea*) appears to be thriving in the Atlantic basin based on increasing nest counts at several rookeries. In particular, Florida's nest numbers have been increasing by 10.2% per year since standardized counts began in 1979. The US Recovery Plan for leatherbacks calls for vital rates and population parameters to be determined for the three leatherback rookeries under US jurisdiction: St. Croix (USVI), Puerto Rico, and the east coast of Florida. Based on mark-recapture data gathered over eleven years, we determined important population parameters for nesting female leatherbacks at Juno Beach, one of the most densely nested beaches in Florida. Average annual survival was 88.9%. The average female nesting population size for Juno Beach is estimated at 100 ± 41 individuals each season; statewide we expect the estimate to be higher. The average remigration interval was 2.7 ± 1.0 years. In addition, we report observed clutch frequency (2.1 ± 1.4 clutches/year), estimated clutch frequency (4.4 ± 1.1 nests/year), and observed inter-nesting period (10.2 ± 1.3 days between nests). The probability of observing an individual female at least once during the season was 73.0%, likely due to variable site fidelity, even though sea turtles do exhibit natal homing. Using opportunistic observations at additional beaches, we found that 72 females observed nesting within the Juno Beach study area were also observed nesting outside the study area. Thirty-three individuals laid clutches both inside and outside the survey area within a single season; these nests were separated by as much as 463.5 km. Although the population in Florida is relatively small compared to other rookeries throughout the Western Atlantic, it is increasing at such a rapid pace that it has the potential to become more important regionally, thereby contributing to the abundance of leatherbacks in the Atlantic.

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1. Introduction

Understanding population demography for long-lived marine animals is important for evaluating and predicting what changes may occur in populations under climate change scenarios, or how changes in vital rates may affect the viability of threatened

species. For species being managed specifically for recovery, and for implementing good planning and management objectives, assessing the capacity of a population to grow depends on understanding vital rates. For example, in a study of a declining harbor seal (*Phoca vitulina*) population, using satellite telemetry and tags, Hanson et al. (2013) demonstrated that the decline was not likely due to an increase in pup mortality but rather changes in adult survival were the likely cause. Similarly, Regehr et al. (2010) assessed vital rates for polar bears (*Ursus maritimus*) over several years and evaluated how differences in annual ice cover would affect adult survival and breeding probability. Long-term mark-recapture

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studies represent an investment in understanding complexities and variation in life history characteristics and parameters. In particular, these studies are especially useful for long-lived, iteroparous and capital breeders that may not breed annually and whose vital rates are closely coupled to environmental conditions.

Sea turtles, all species of which are listed under the US Endangered Species Act (ESA, 1973), have complex life histories requiring multiple habitats for various life stages. Additionally, sea turtles are long-lived and migrate long distances across international boundaries. These factors have made it difficult to collect population parameters to gain a full understanding of their life history and then to plan for recovery or management. Addressing research objectives in recovery plans is essential for managing these threatened species because basic population parameters must be established to provide the framework under which to focus conservation efforts and funding.

The leatherback turtle (*Dermochelys coriacea*) is the largest turtle in the world, nesting globally on subtropical and tropical beaches. These turtles deposit their eggs on open, dark beaches, generally above the high tide line (Mrosovsky, 1983; Whitmore and Dutton, 1985; Kamel and Mrosovsky, 2004). They nest approximately every nine to 10 days within a season (internesting interval) (Miller, 1997) and on average, return every two to three years (remigration interval) (Miller, 1997). Depending on the population, they may lay up to 14 nests each during a single nesting season (clutch frequency) (Girondot and Fretey, 1996) but the average is generally five or six nests per year (van Buskirk and Crowder, 1994). Once considered Critically Endangered worldwide by the International Union for the Conservation of Nature (IUCN, 2012), leatherback status varies by population and is now considered Vulnerable globally, while still facing various natural and anthropogenic threats depending on locality. Because they migrate long distances between foraging and nesting grounds, these turtles face potential risks to survival during all life stages. It is therefore essential to determine nesting trends, evaluate threats and estimate population parameters such as survival rates and abundance to manage this species effectively. In the Eastern Pacific, the leatherback faces a population crisis and it is only because long-term studies have been done that it has been possible to study population dynamics and to derive estimates for critical parameters, unfortunately even if the purpose is to document declining populations there. In the Atlantic basin, the leatherback is experiencing a quite different reality, with most small populations increasing rapidly and large populations maintaining their size or increasing slightly (Turtle Expert Working Group, 2007; Stewart et al., 2011).

The need to establish baseline life history data for leatherbacks in the USA was first specifically outlined in a National Marine Fisheries Service (NMFS) stock assessment report (NMFS-SEFSC, 2001), and again in a 2007 report (Turtle Expert Working Group, 2007). More recently it was recommended by the Committee on the Review of Sea-Turtle Population Assessment (National Research Council, 2010) that vital rates for sea turtle populations in the United States be determined for developing more accurate assessments of population status and for predicting the capacity of species to recover. Specific objectives for each leatherback population at three US rookeries (Culebra, Puerto Rico; St. Croix, US Virgin Islands; east coast of Florida) were described in the 1992 recovery plan. Initially, the NMFS was only able to complete a preliminary stock assessment of leatherback turtles in US waters because the appropriate data (survival rates, remigration interval, internesting interval, and population size) simply did not exist for leatherbacks nesting in the US. Since the leatherback recovery plan was written (NMFS and USFWS, 1992), good information has been published on two important US rookeries (St. Croix, USVI and Puerto Rico), based on long term monitoring of leatherback nesting and individual turtle identification. Population vital rates have been lacking for

Florida to date, with the exception of nest counts and resulting rough estimates of population size. The current recovery plan requires that by 2017 an increase in the number of leatherbacks or the number of nests must be evident to meet the objective of recovery, however the current status must be evaluated. Efforts to determine population sizes for sea turtles have been hampered by the difficulty in counting individuals within populations. Assessing stocks on nesting beaches has been constrained by the very nature of sea turtle life history; they exhibit extensive variability in the regularity with which they nest and setting up research in remote locations has proven difficult.

Florida's beaches are extensive (>500 km on the east coast) and provide important nesting habitat for loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and leatherback turtles each summer. The number of leatherbacks currently nesting in Florida is unknown. Previous population size estimates derived from nest numbers and clutch frequency data ranged from 10–15 individuals (Carr, 1952) to 16–31 individuals nesting each year (Meylan et al., 1995). Leatherback nesting has been recorded in 20 of 34 coastal counties, although the densest nesting occurs in three contiguous counties (Palm Beach, Martin, and St. Lucie) along ~200 km of the Atlantic coastline. These counties have received 83.8% of all leatherback nesting recorded in the state since 1979 (Stewart et al., 2011). Palm Beach County has the highest proportion of nests (38.7%) followed by Martin County (32.1%) and St. Lucie County (13.0%) (Stewart et al., 2011). Some nesting occurs along the panhandle (FWRI, 2007), and sporadic nesting has been documented along the beaches of Georgia, South Carolina, and North Carolina (Rabon et al., 2003). Leatherback nest counts have increased dramatically at $10.2 \pm 1.9\%$ per year over the past 30 years in Florida (Stewart et al., 2011).

The purpose of this study was to estimate a nesting population size for Florida by sampling a portion of the coastline where leatherbacks regularly nest. We aimed to develop empirical estimates for life history parameters such as remigration interval, internesting interval, clutch frequency (observed and estimated), and to derive estimates of population size. Because sea turtles are long-lived and are assumed to have long reproductive lives with thousands of offspring each having low survival, adult survival should be relatively high; we were able to estimate this parameter for the Florida rookery. In addition, we had an opportunity to document the distance that an individual leatherback may travel between nests (to spread reproductive risk), thus quantifying the potential nesting range of individual females.

2. Materials and methods

2.1. Study site and leatherback tagging

Leatherback turtles were observed during nightly (2100–0600 h) patrols from mid-March to late June each year from 2001–2011; this covers ~95% of the nesting season annually. Using all-terrain vehicles (ATVs), the team surveyed a 19.4 km segment of Florida's east coast at the Juno Beach study area from Jupiter Inlet (26°56'36"N, 80°04'15"W) south to Lake Worth Inlet (26°46'24"N, 80°01'53"W) (Fig. 1). Nesting turtles were approached after egg deposition had begun and all flippers were inspected for existing metal or plastic tags or tagging scars. Turtles were also thoroughly examined using a Passive Integrated Transponder (PIT) tag reader (Destron Fearing Pocket Reader-EX or similar) passed over each flipper and the neck. For each turtle, curved carapace length and width were measured according to procedures in Bolten (1999), and any distinguishing marks or injuries were noted. If the turtle had no identifying characters or tags, it was marked with tags for subsequent identification. Following

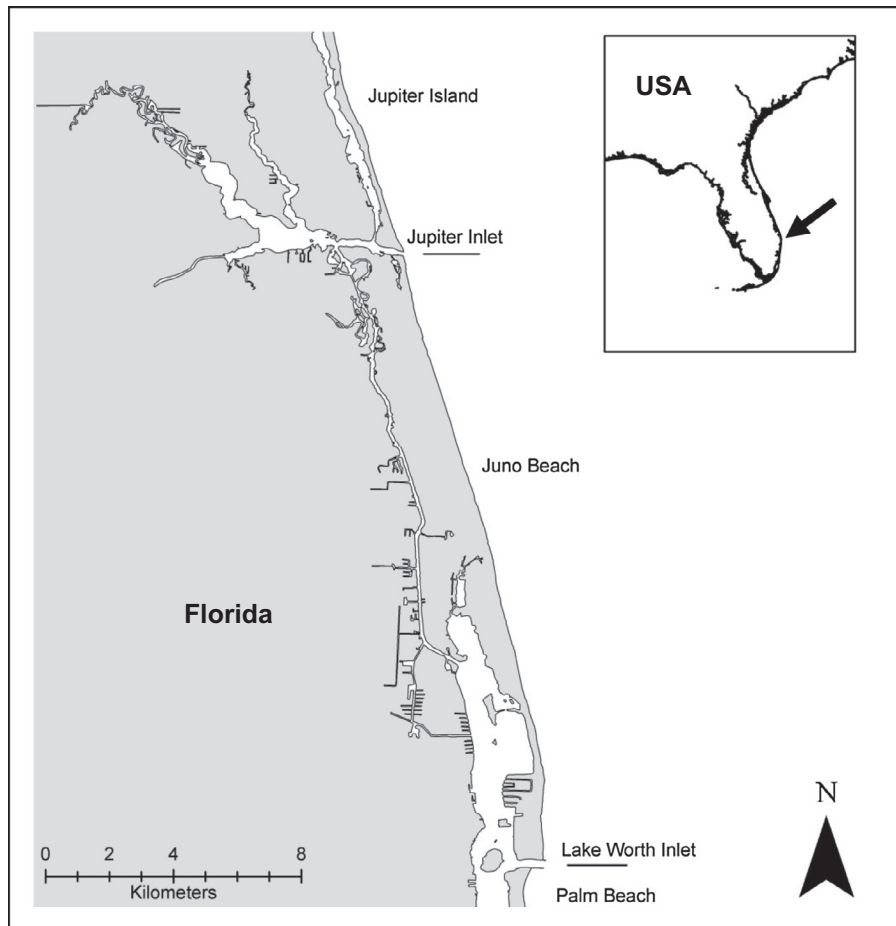


Fig. 1. Map showing the study area of Juno Beach, FL, bounded to the north by Jupiter Inlet and to the south by Lake Worth Inlet. Inset shows Florida within the southeastern USA.

procedures outlined in the Marine Turtle Conservation Guidelines (Florida Fish and Wildlife Conservation Commission, 2007), tagging sites were prepared before metal tags (Inconel style 681; National Band and Tag Co., Newport, KY) were applied to both rear flippers and a PIT tag (125 kHz or 134 kHz; Digital Angel Corporation, St. Paul, MN) was injected into the right front shoulder muscle of each turtle. Triple tagging (2 flipper tags and a PIT tag) ensured redundant identification methods for unique individuals. Upon resighting of an individual, each turtle's tags were carefully checked and recorded, and then compared to a master list while in the field to correct any inconsistencies; the chance of misidentification of an individual was negligible. We wanted to minimize any error due to tag loss or failure because this may result in the overestimation of the number of nesting turtles and associated parameters (Rivalan et al., 2005a). Although there were no known instances of complete loss of all three tags on any turtle as no turtles were observed with tag scars on both rear flippers and the lack of a PIT tag, it is possible that a few turtles may have lost all identification. If turtles had lost one or more flipper tags, they were replaced. When we encountered turtles carrying tags that we had not applied, we contacted the Cooperative Marine Turtle Tagging Program (CMTTP) of the Archie Carr Center for Sea Turtle Research (ACCSTR, University of Florida) and requested the original tagging data. Opportunistic leatherback sightings were also made at Hutchinson Island, Jupiter Island, Boca Raton, and Ft. Pierce. Additionally, researchers from the University of Central Florida conducting nightly surveys at the Archie Carr National Wildlife Refuge (ACNWR) encountered several tagged females.

2.2. Nesting parameters

The remigration interval based strictly on raw observations and not accounting for detection probability (see below) was calculated for each female that was marked and then resighted some time later by counting the number of years from first to last encounter and then dividing by the number of total years that the turtle was observed. Observed clutch frequency (OCF) was defined as the number of clutches we observed per female during one nesting season (eggs confirmed for each clutch) for all turtles, and the mean was calculated for the eleven year study period. Because observed clutch frequency may depend on survey effort and the distance traveled by an individual turtle during the nesting season, we also calculated individual estimated clutch frequency (ECF) following methods described previously (Reina et al., 2002; Price et al., 2004). For turtles observed multiple times and in multiple locations, but on dates longer than one typical nesting interval apart (i.e., 8–13 days), we took the final observed nesting date for an individual, calculated the number of days since the first observed nest, divided this value by the mean observed internesting period (OIP) and added one for the first nest (Reina et al., 2002; Price et al., 2004).

2.3. Mark-recapture analysis (Open Robust Design Multi-Strata option)

For each individual female an encounter history was constructed for the eleven-year period. We structured our sampling

according to the Open Robust Design Multi-Strata option (ORD-MS; Kendall and Bjorkland, 2001; Kendall and Nichols, 2002), which was initially a combination of mark-recapture designs by Schwarz and Stobo (1997) and Kendall et al. (1997). This modeling approach assumes Markovian (non-random) breeding probability, because whether a turtle nests in a given year may be dependent on whether she nested in a previous year or not. The model also relaxes some assumptions about the population closure within primary sampling periods, allowing turtles to enter and exit the population once during a primary sampling session (nesting season = March to July annually) while assuming that there is no death or new recruitment within that season. Although the study area in this work represents the epicenter of leatherback nesting in Florida, females do use other beaches outside the study area for nesting (see below). However, we would consider the choice of beach by female to be random and each female would have a positive probability of choosing Juno Beach at least once per nesting season. The detection probability (p) in this case would be equivalent to the availability of a particular female within the study area during a secondary sampling period times the probability that she will be detected. In effect then, each nesting season the population is considered closed, meaning that any females choosing to breed that season would be entering the nesting population once and leaving it once per season. In other words, once the female becomes a nester for the year, she does not transition to a non-nesting state until after the nesting season is over. Between primary sessions (years), the population is considered open, because females may or may not become part of the nesting population the following year. The ORD-MS model is especially appropriate for nesting sea turtle populations because these turtles generally skip one or more years following nesting before they can return to the nesting beach (Miller, 1997) and as such, they are not available for capture during their off-year (Markovian state transitions). Within the first of two strata described in the model are the turtles that are females at the nesting beach. In the second stratum, which is unobservable, a female may be an adult turtle and still be a member of the breeding population, but she may not be present at the nesting beach. The survival rate of the individuals that are skipping one or more years after nesting is assumed to be the same as the survival rate for nesting turtles, since in the unobservable state parameters cannot be estimated as these turtles are never seen. Other basic mark-recapture assumptions within the model include: (1) tags are not lost or misidentified, (2) all individuals encountered during one observation period survive to the next observation period within each season and (3) turtles are equally catchable, whether tagged or untagged.

Leatherback nesting season in Florida typically lasts from early March through late June, with the peak of nesting occurring during the last two weeks of May (Meylan et al., 1995; Stewart et al., 2011). Under the ORD-MS, each discrete nesting season that we surveyed represented a primary sampling session ($n = 11$). We divided each nesting season (primary sampling session) into 13 secondary sampling periods of nine days each. Leatherbacks nest approximately every nine to 10 days (Miller, 1997) and since many of the females at Juno Beach nested at nine-day intervals, it was appropriate to structure the yearly encounter histories in nine-day segments. This maximized the number of encounters that we could use for each individual's capture history. In addition, this allowed us to use the residence time (as a derived parameter) as a proxy for the number of clutches laid per season, even if we did not observe that turtle for every single nest that she laid within a particular season. Therefore, each individual female had an encounter history with 143 encounter sessions of nine days each, over eleven years.

To generate population parameters, we constructed models regarding survival and breeding probabilities. We used Program

MARK 6.1 (White and Burnham, 1999) to run the ORD-MS model. From individual turtle capture histories we derived estimates for average annual survival, conditional breeding probability (probability that a turtle will nest in any particular year, given she nested or did not in the previous year), probability that a turtle that just laid a clutch returns to lay another clutch, and capture probability (in our case the product of the probability a turtle chooses our study area to lay a clutch and the probability of detection given that she uses our study area). From all models tested, the one that best fit the data was selected based on Akaike's Information Criterion (AICc) and comparison of the models was done using normalized AICc weights (Burnham and Anderson, 2004; Cooch and White, 2014). Derived estimates of annual nesting population size and residence time accounting for detection probability (i.e., number of nests per season per individual) (Kendall, 2006) were also generated in each model. We calculated the probability of encountering an individual at least once during the nesting season (p^*) by dividing the number of turtles observed at Juno Beach by the estimates of annual population size.

2.4. Nesting range

Throughout the eleven-year study, many individuals were encountered only once along the surveyed beach during a single nesting season. Because we suspected that these turtles were nesting additional times outside the 19.4 km study area, we quantified the potential nesting range for individual turtles. We obtained records of individuals observed nesting on other beaches from the Cooperative Marine Turtle Tagging Program (CMTP) that had been originally tagged on Juno Beach. These events were recorded by trained individuals conducting morning nesting surveys as well as researchers conducting nightly tagging surveys and coastal construction monitoring. We plotted all nest locations (ArcMap 10.0; ESRI, Redlands, CA) and then calculated the straight-line distance between each individual's recorded nests within a single season.

3. Results

3.1. Leatherback turtles and nest parameters

A total of 466 individual turtles were identified and tagged over eleven nesting seasons (primary sampling periods). For each year, the proportion of newly captured turtles and the proportion of recaptured turtles are listed in Table 1. The proportion of recaptures has increased to 65.9% in 2011. Of the 466 individuals, 73% (340) were recaptured at least once during the study. Since 2003, there have been 17 turtles that nested in consecutive years and one turtle that nested 3 years in a row. The average remigration

Table 1

For each year of the survey (nesting season), the number of individual turtles encountered, the number of those that were newly captured, and the proportion that were recaptured individuals. A total of 466 individuals were tagged from 2001–2011.

Year	Total captured	Total new	Recaptures (%)
2001	27	27	0.0
2002	45	44	2.2
2003	69	53	23.2
2004	34	22	35.3
2005	76	40	47.4
2006	44	20	54.5
2007	104	50	51.9
2008	61	28	54.1
2009	133	74	44.4
2010	113	65	42.5
2011	126	43	65.9

interval for turtles marked and resighted ($n = 198$) was 2.7 ± 1.0 years (Table 2) with a range of 1–5.5 years; the most commonly observed remigration interval was 2.0 years. The mean size of individual females for this rookery was published previously (151.8 ± 6.63 cm CCL, 109.2 ± 5.0 cm CCW; Stewart et al., 2007). Although we observed up to 8 nests per female in a season, the overall observed clutch frequency for all turtles was 2.1 ± 1.4 nests/year and the estimated clutch frequency (4.4 ± 1.9 nests/year) were based on turtles seen multiple times during one nesting season (2001–2011) (Table 2). Despite efforts to observe every turtle nesting, we observed 80.3% of nesting events in eleven years (1708 of 2097 nests, based on day-time nest counts following our surveys) in the 19.4 km study area, so observed and estimated clutch frequency may be slightly underestimated.

3.2. Mark-recapture analysis – ORD-MS

From the models tested using the ORD-MS option in MARK 6.1, the most appropriate one based on Akaike's Information Criterion (AICc) for the 466 turtle encounter histories was Model M; there was virtually no support for any of the other models tested (Table 3). Specific parameter estimates of Model M are given in Table 4. Average annual survival was constant over the period at $88.9 \pm 1.2\%$. The probability that a turtle would transition from being a nester in one year to a non-nester the following year varied over time and ranged from 86.5% in 2006 to 100% in 2001, 2002 and 2007; the average transition probability was 95.3%. Breeding probability for a turtle that had skipped nesting in one year to become a nesting turtle the next year also varied by time and ranged from 41.4% to 92.7% (average = 64.5%). Using the conditional breeding probabilities while taking detection probability into account, we estimated the remigration interval to be 2.5 years, which is slightly lower (and more realistic) than our estimate based on the raw observations of remigration interval. Estimates

Table 2
A summary of population parameters for the Florida nesting population of leather-back turtles.

Parameter	Mean (\pm SD)	n	References
Curved carapace length (CCL)	151.8 ± 6.6 cm	174	Stewart et al. (2007)
Curved carapace width (CCW)	109.2 ± 5.0 cm	174	Stewart et al. (2007)
Remigration interval	2.7 ± 1.0 years	198	This study
Observed clutch frequency	2.1 ± 1.4 nests/yr	831	This study
Estimated clutch frequency	4.4 ± 1.9 nests/yr	478	This study
Interesting period	10.2 ± 1.3 days	578	This study

Table 3
Model M was supported by the empirical data; there was no support for additional models. Model ID, structure, AIC values, model likelihood, the number of parameters estimated and the deviance for each model are listed.

ID	Structure	AICc	Δ AICc	AICc Weight	Likelihood	Parameters	Deviance
M	$\Phi^*(.) \gamma''(t) \gamma'(t) \beta(tt) \Phi(tt) p(..)$	9889.53	0	0.993	1.000	167	9520.63
N	$\Phi^*(.) \gamma''(t) \gamma'(t) \beta(tt) \Phi(tt) p(tt)$	9899.55	10.02	0.007	0.007	243	9336.14
Q	$\Phi^*(t) \gamma''(t) \gamma'(t) \beta(tt) \Phi(t) p(..)$	9904.05	14.52	0.001	0.001	113	9662.55
O	$\Phi^*(.) \gamma''(t) \gamma'(t) \beta(tt) \Phi(t) p(..)$	9909.19	19.66	0.000	0.000	107	9681.33
S	$\Phi^*(.) \gamma''(.) \gamma'(.) \beta(tt) \Phi(t) p(..)$	9910.32	20.79	0.000	0.000	97	9704.99
T	$\Phi^*(.) \gamma''(t) \gamma'(t) \beta(t) \Phi(t) p(..)$	9946.07	56.54	0.000	0.000	41	9862.09
R	$\Phi^*(.) \gamma''(.) \gamma'(.) \beta(tt) \Phi(t) p(..)$	9964.29	74.76	0.000	0.000	95	9763.43
L	$\Phi^*(t) \gamma''(t) \gamma'(t) \beta(..) \Phi(tt) p(..)$	10043.37	153.84	0.000	0.001	89	9855.87
K	$\Phi^*(.) \gamma''(t) \gamma'(t) \beta(..) \Phi(tt) p(..)$	10153.66	264.13	0.000	0.000	85	9975.01

Note: Φ^* = survival, γ'' = breeding probability for nesters, γ' = breeding probability for non-nesting adult females, β = entry probability, Φ = probability of remaining at the study site, and p = capture probability (after Kendall and Bjorkland (2001)). Dots represent time constant variables, while t represents time variable parameters.

Table 4
Parameter estimates from Model M: annual survival (Φ^*), probability of skipping a year after nesting (γ''), probability that a turtle that has skipped nesting in one year becomes a nester the following year (γ'), the average annual probability of remaining in the study area from one secondary sampling period to the next (Φ), the probability of a turtle entering the study area during a particular sampling period (β), and capture probability (p). The mean, standard error and lower and upper 95% confidence intervals are given.

Parameter	Estimate	SE	Lower	Upper
Φ^*	0.889	0.012	0.863	0.911
γ''_{01}	1.000	0.000	1.000	1.000
γ''_{02}	1.000	0.000	1.000	1.000
γ''_{03}	0.928	0.041	0.796	0.977
γ''_{04}	0.874	0.070	0.667	0.960
γ''_{05}	0.960	0.028	0.852	0.990
γ''_{06}	0.865	0.065	0.684	0.950
γ''_{07}	1.000	0.000	1.000	1.000
γ''_{08}	0.979	0.021	0.863	0.997
γ''_{09}	0.968	0.018	0.905	0.990
γ''_{10}	0.954	0.023	0.883	0.983
γ''_{02}	0.927	0.113	0.330	0.997
γ''_{03}	0.414	0.122	0.209	0.654
γ''_{04}	0.523	0.079	0.371	0.671
γ''_{05}	0.492	0.095	0.315	0.671
γ''_{06}	0.702	0.070	0.551	0.819
γ''_{07}	0.694	0.101	0.472	0.851
γ''_{08}	0.649	0.076	0.490	0.781
γ''_{09}	0.713	0.093	0.505	0.858
γ''_{10}	0.692	0.076	0.528	0.819
Φ_1	0.700	0.115	0.444	0.957
Φ_2	0.734	0.114	0.479	0.989
Φ_3	0.800	0.107	0.562	1.038
Φ_4	0.892	0.037	0.809	0.975
Φ_5	0.862	0.040	0.774	0.950
Φ_6	0.896	0.038	0.812	0.980
Φ_7	0.929	0.028	0.868	0.991
Φ_8	0.891	0.051	0.777	1.004
Φ_9	0.827	0.053	0.709	0.945
Φ_{10}	0.629	0.090	0.428	0.829
Φ_{11}	0.322	0.093	0.115	0.528
Φ_{12}	0.126	0.090	-0.075	0.327
β_1	0.090	0.025	0.035	0.146
β_2	0.141	0.036	0.060	0.221
β_3	0.138	0.047	0.032	0.243
β_4	0.123	0.035	0.045	0.201
β_5	0.104	0.037	0.021	0.187
β_6	0.063	0.016	0.028	0.097
β_7	0.108	0.025	0.052	0.164
β_8	0.091	0.024	0.038	0.145
β_9	0.058	0.019	0.016	0.100
β_{10}	0.036	0.014	0.006	0.067
β_{11}	0.017	0.007	0.001	0.033
β_{12}	0.006	0.005	-0.005	0.018
p	0.350	0.012	0.328	0.374

Note: Although both the probability of remaining from one period to the next (Φ) and the probability of entry (β) varied by year, they are shown here as averages per secondary sampling session.

of the probability of remaining at the study site between secondary periods (Φ) varied both between years and between secondary periods (annual averages by secondary period are shown in Table 4). The probability that a turtle remained in the area from one secondary period to the next was very high during early periods of the season and then dropped off quickly at secondary period ten (Φ_{10}). This period corresponds with dates between May 31 and June 8, which immediately follows peak nesting in Florida. The probability of entering the study site also varied by year and by secondary period (annual averages shown in Table 4), but the highest probabilities of entering were between periods 2 and 5 (between March 20 and April 24). Finally, the probability of an individual female being available at Juno Beach during any secondary period during the season times the probability of being encountered (p) was constant at $35.0 \pm 1.2\%$.

Derived estimates of Model M included annual estimated nesting population size and residence time (i.e., number of nests per season per individual); these are listed in Table 5. The average annual nesting population affiliated with Juno Beach varied through the years, from a low of 50.7 ± 4.4 turtles in 2004 to a high of 149.3 ± 4.5 nesting females in 2011. On average, there were 100 ± 41 nesting turtles each year from 2001–2011. The average residence time (in our case, the number of secondary sampling sessions for which an individual turtle was present over the nesting season) that was estimated by Model M was 4.3 ± 1.1 secondary sampling sessions. Each 9-day secondary sampling session is the equivalent of an internesting period, meaning that a turtle could only be observed nesting once during this time. The residence time was in close agreement with our individual estimated clutch frequency that was calculated directly from observations of individual turtle nests (4.4 ± 1.9 nests/year). The probability that an individual was detected at least once in a nesting season was 73.0%.

3.3. Nesting range

Over 11 seasons, a high proportion (42.6%) of individual turtles were only seen once in a single nesting season (but may have been seen in a subsequent season), 28.8% were seen twice and 28.6% were observed nesting three or more times and we suspected that

Table 5

Derived parameter estimates from Model M in MARK (Open Robust Design Multi-Strata option) for annual estimated population size of nesting turtles (N^{\wedge}), and residence time (i.e., number of nests per individual or estimated clutch frequency).

Parameter	Year	Estimate	SE	Lower	Upper
N^{\wedge}	2001	50.92	5.02	41.07	60.77
N^{\wedge}	2002	71.12	5.50	60.35	81.90
N^{\wedge}	2003	102.36	5.53	91.52	113.19
N^{\wedge}	2004	50.66	4.37	42.11	59.22
N^{\wedge}	2005	95.65	4.69	86.45	104.85
N^{\wedge}	2006	59.86	3.81	52.39	67.33
N^{\wedge}	2007	137.65	5.67	126.53	148.78
N^{\wedge}	2008	79.00	4.37	70.44	87.57
N^{\wedge}	2009	154.29	4.92	144.66	163.93
N^{\wedge}	2010	148.93	5.39	138.37	159.50
N^{\wedge}	2011	149.27	4.52	140.41	158.13
Residence	2001	2.21	0.39	1.44	2.99
Residence	2002	2.95	0.42	2.13	3.76
Residence	2003	3.46	0.38	2.71	4.20
Residence	2004	3.89	0.64	2.64	5.14
Residence	2005	4.75	0.47	3.83	5.67
Residence	2006	4.35	0.58	3.22	5.47
Residence	2007	4.48	0.39	3.72	5.24
Residence	2008	4.66	0.51	3.65	5.67
Residence	2009	6.10	0.41	5.29	6.91
Residence	2010	4.48	0.36	3.79	5.18
Residence	2011	5.80	0.40	5.02	6.58

turtles only seen a few times within a season were nesting outside the study area. From 2001 to 2011, 72 individual turtles were encountered 117 times on beaches outside our 19.4 km survey area. These encounters occurred on beaches along the east coast of Florida and Georgia and were documented by researchers conducting research projects or morning nesting surveys. Thirty-three individuals were encountered both inside and outside our survey area within a single season (Table 6). The maximum observed distance south of our survey range was 111.8 km when a turtle initially tagged on Juno Beach nested on Miami Beach 18 days after first being encountered. The maximum observed distance north of our survey area was 463.5 km. This turtle was observed nesting on St. Simon's Island, GA, 45 days after she was tagged on Juno Beach.

4. Discussion

The number of individual leatherbacks nesting in Florida at Juno Beach is far greater than the previous estimates (10–31 turtles; Carr, 1952; Meylan et al., 1995) for all of Florida. This is evident from the number of tagged turtles and from the annual estimated population size results derived from the mark-recapture analysis. Through tagging alone, 466 individual turtles were identified. The population size for nesting females affiliated with Juno varied from 51 to 149 annually; this reflects the variation we see in remigration intervals for individual turtles (turtles may skip 1–2 years before re-nesting). Overall, we found that there are an average of 100 ± 41 females nesting annually at Juno Beach (estimated using encounter histories in ORD-MS). If the survey was expanded to cover more of the Florida beaches and the encounter probability

Table 6

For 33 turtles that laid clutches within the local study area (Juno Beach) and outside the study area (Distant Beach) within a single season, the respective dates of oviposition (Local date, Distant date) and the distance between nesting locations (km) are given.

Turtle #	Local date	Distant date	Distant Beach	Distance (km)
1	5/8/2004	5/26/2004	Hutchinson Isl.	39.9
2	6/14/2004	5/26/2004	Boca Raton	51.9
3	3/30/2005	4/10/2005	Hutchinson Isl.	37.5
4	4/1/2005	5/5/2005	Palm Beach	21.9
5	4/2/2005	4/20/2005	Miami Beach	111.1
6	4/3/2005	5/17/2005	Palm Beach	18.8
7	4/4/2005	3/15/2005	Hutchinson Isl.	41.0
8	4/18/2005	6/5/2005	Melbourne	117.9
9	4/19/2005	4/28/2005	Hutchinson Isl.	44.9
10	4/19/2005	4/9/2005	Hutchinson Isl.	41.9
11	4/20/2005	4/29/2005	Hutchinson Isl.	42.6
12	5/8/2005	6/6/2005	Melbourne	123.4
13	5/11/2005	4/10/2005	Hutchinson Isl.	43.0
14	5/18/2005	4/7/2005	Hutchinson Isl.	39.1
15	5/1/2007	5/31/2007	Jupiter Island	7.0
16	5/19/2007	6/16/2007	Melbourne	136.8
17	5/21/2007	4/8/2007	Jupiter Island	28.4
18	6/24/2007	7/16/2007	Jupiter Island	14.1
19	4/15/2008	5/30/2008	Melbourne	128.6
20	5/9/2008	6/24/2008	Jupiter Island	24.0
21	5/14/2008	6/2/2008	Melbourne	132.7
22	6/4/2008	5/26/2008	Melbourne	120.7
23	3/18/2009	5/15/2009	Boca Raton	47.9
24	4/20/2009	6/4/2009	St. Simon's, GA	463.5
25	6/2/2009	6/12/2009	Jupiter Island	11.5
26	5/26/2010	6/5/2010	Jupiter Island	16.7
27	5/30/2010	5/19/2010	Melbourne	130.8
28	6/3/2010	6/27/2010	Melbourne	123.8
29	4/11/2011	5/25/2011	Melbourne	124.2
30	4/14/2011	4/24/2011	Melbourne	120.8
31	5/13/2011	5/22/2011	Jupiter Island	17.9
32	6/4/2011	5/25/2011	Hutchinson Isl.	41.8
33	6/14/2011	6/24/2011	Melbourne	109.1

(p) improved through better detection, we suggest that the total population size for Florida should be significantly greater.

Long-lived, late-maturing animals with high adult survival tend to be iteroparous (Stearns, 1992) and this strategy is particularly beneficial in unpredictable environments because it enhances an individual's ability to spread reproductive risk through time and space. The ability of leatherbacks to spread their reproductive risk quite widely along dynamic beaches is reflected in the probability of encountering an individual at Juno Beach at least once during the nesting season (73.0%). This is lower than encounter probability estimates for leatherbacks at St. Croix (100%; Dutton et al., 2005) and for hawksbill turtles at Jumby Bay, Antigua (100%; Kendall and Bjorkland, 2001), where the primary nesting beaches are more discrete and limited in distance than are the beaches in Florida. By definition, leatherback nesting habitat is dynamic, highly erosional, and may shift entirely over the course of short- and long-term time scales (Bacon, 1970; Pritchard, 1971; Mrosovsky, 1983; Eckert, 1987). Pritchard (1979) even suggested that leatherbacks choose a beach type rather than a particular location. Our lower detection probability is likely due to the broad choices that leatherbacks have when nesting in Florida. Although many individuals appear to choose Juno more often than not, others tend to be seen only once per season there. As we did not see every nest being deposited (1708 observed of 2097), it is possible that we missed seeing those individuals choosing Juno only once per season, thus lowering our encounter probability (p). Using distance measurements between nests for individual turtles encountered on other beaches within a season, we found that leatherbacks nesting in Florida have the potential to nest at broad spatial scales (up to 463.5 km between nests) and that some turtles may exhibit low site fidelity to a particular beach. It is difficult to characterize the full nesting range of an individual using opportunistic recaptures. Leatherbacks are tagged with small (26 mm \times 8 mm) Inconel tags along the trailing edge of the rear flippers. These tags are almost impossible to observe without handling the animal. PIT tags are not readable without expensive scanners. Trained personnel looking specifically for tagged turtles on a few beaches reported all of the recaptures. In the eleven years of the study, no tags were reported by beachgoers encountering turtles along the nesting beach at night. This lower level of site fidelity that some leatherbacks may exhibit was evident in a study by Thorson et al. (2012). They attributed a lack of apparent population recovery for leatherbacks in South Africa to lower detection probability in their surveys. They hypothesized that the population may in fact be increasing in size but also undergoing a range expansion with the turtles nesting further to the north and south, thus decreasing the detection probability on traditionally surveyed beaches. In combination with nest counts and tagging nesting females, current satellite technology is likely the best tool for examining the complete nesting range that leatherbacks may exhibit in particular populations. We used satellite tracking for several turtles nesting on Juno Beach. Four of the turtles reported as encounters outside of our survey area were actively tracked to a distant nesting beach via satellite and VHF technology. We recommend the use of high-precision satellite tracking to further explore nesting range and site fidelity for other populations.

At Juno Beach, the probability that a turtle entered the study area (β ; Table 4) was variable by year but generally highest (14.1%) for period 2 (March 20–28), although periods 3–5 (March 29–April 24) also had similar entry probabilities. Interestingly, there was another increase in the entry probability during periods 7–8 (10.8–9.1%; May 4–21), which is when the peak of nesting begins and when we see a small pulse of turtles that have not been seen earlier in the season. Although anecdotal, these turtles are often not tagged and are smaller than the average size of nesting females at Juno Beach. The probability of a turtle remaining at

the study site from one secondary sampling period (9-day interval) to the next was high (Table 4, Φ values) until the 9th sampling period (31 May–8 June). This indicates that once a turtle arrives at the nesting beach, she is likely to remain in the area for the duration of that nesting season, and is probably laying many clutches during that time.

Our finding that many turtles (43%) were observed nesting only once (one-time nesters) within a season in our study area contrasts with only 8.8% one-time nesters over 2.25 km on the island of Culebra, Puerto Rico (Tucker and Frazer, 1991). At Juno Beach, patrols covered approximately 10% of the nesting habitat most used by leatherbacks in Florida, which is about 200 km long. The mean observed clutch frequency (OCF) at Juno Beach (2.1 ± 1.4 clutches/nesting season) is extremely low relative to what is expected for a turtle of this size and iteroparous life history (van Buskirk and Crowder, 1994) and low when compared to clutch frequencies observed at other beaches. For example, at Sandy Point National Wildlife Refuge (St. Croix, USVI), which is a short (2.4 km) and densely-nested beach, the average observed clutch frequency was 5.3 nests per season over fifteen years (Boulon et al., 1996), and at Culebra (Puerto Rico), OCF ranged from 5.2 to 7.0 clutches per season over four years (Tucker and Frazer, 1991). Similar to our study, on the beach at Babunsanti, Suriname, OCF was 1.6 ± 1.0 clutches per season (Hilterman and Govere, 2005), although their survey effort and the distance covered were less than in this study. However, when we look at estimated clutch frequencies (ECF), we found values that are more likely to reflect the true clutch frequency of these turtles. The ECF calculated solely from nesting dates of tagged turtles (4.4 ± 1.9 clutches/nesting season), was confirmed by the derived estimates of residence time (i.e., clutches laid per female, 4.3 ± 1.1 clutches/nesting season) from the most parsimonious model in MARK (Model M). Although the residence time varied annually and corresponded to 2 nests per female in 2001 (we had low detection that year) to 6 nests per female in 2009, the estimates generally approximated the ECF calculations. In our case, clutch frequency is still likely to be underestimated because turtles may have chosen another beach for their first or last nests and this could not be accounted for in our models. In French Guiana, Rivalan et al. (2005b) used stopover duration analysis (and different assumptions of when the first and last nests occurred) to estimate that leatherbacks laid between 8.7 and 11.4 nests per season depending on an individual's remigration interval (2 vs. 3 years respectively).

If one takes the mean number of nests in Florida for the decade from 2001–2010 (mean = 942 nests/year) (Stewart et al., 2011; FWC, 2011) and divides it by the OCF or ECF to derive the annual population size, the results are very different. Using an OCF of 2.1 and an ECF of 4.4, we can estimate population sizes of 449 or 214 annual nesting females based on an average annual nest count of 942. The stock assessment for leatherbacks in the Atlantic (Turtle Expert Working Group, 2007) used a 'reasonable' global estimate for clutch frequency of 5, which would result in a yearly population size for Florida of 188 nesting females. The difference in estimated population size based on OCF (2.1 nests/year = 449) is more than twice the population size using the global average clutch frequency (5 nests/year = 188). For small rookeries, this may not be an issue, but when trying to estimate global abundance, the range of values may have remarkably wide confidence intervals. With such a large margin of error, our ability to manage endangered or threatened species to a particular goal becomes very difficult. If the estimate of the number of individuals is so highly variable, it is nearly impossible to set target goals for a species to be delisted and the credibility in our estimates decreases dramatically. Underestimating clutch frequency leads to an overestimate of nesting female abundance when the number of females is extrapolated from nest counts alone. This may lead to an overly

optimistic view of population status and recovery (Turtle Expert Working Group, 2007). Clutch frequencies calculated from tag returns alone will always be underestimated because it is difficult and costly to monitor the entire coastline habitat at night. Additionally, total saturation tagging where no turtles are missed is highly unlikely, and in some areas, tag loss may be a concern (Rivalan et al., 2005a), but striving for a major sampling effort (at least for the peak of nesting) is recommended for robust estimates and good performance of models. Abundance calculations are always best when they are based on marking or tagging and following individuals through time. In a study of loggerheads on a barrier island in Georgia, USA, Pfaller et al. (2013) cautioned that depending on nest counts and female counts alone without also accounting for detection probability (p) may lead to the wrong conclusions about population status (e.g., an increasing number of nests and females observed may not mean that the population is increasing if the detection probability is decreasing).

We found that the adult female survival rate at Juno Beach (88.9%) was very similar to the survival rate for leatherbacks nesting on St. Croix (89.3%; Dutton et al., 2005). In French Guiana, Rivalan et al. (2005b) divided nesting leatherbacks into two survival groups; transients were newly marked females while previously marked individuals made up the other group. They found a survival rate of 0.50 for the transients and a survival rate of 0.91 for previously marked turtles. They reported that survival rates may have been adjusted downward because they could not fully account for permanent emigration (i.e., low site fidelity for some individuals). Similarly, Pilcher and Chaloupka (2013) reported a survival rate of 0.46 for transients and a survival rate of 0.85 for previously marked leatherbacks nesting in Papua New Guinea. Here, they attributed lowered survival rates to lower site fidelity and also a lower probability (0.41) for an individual to transition to breeding status after one skipped year. We found no support for differential survival rates in our models for transients vs. previously marked turtles. Whether these survival rates (>85%) for previously marked turtles would be considered adequate for sustaining or growing the population is not known conclusively however both the Florida and St. Croix populations are currently increasing at a good pace (Dutton et al., 2005; Stewart et al., 2011). Other marine capital breeders have similar survival rates. In an increasing elephant seal population at Año Nuevo, California, a 40-year mark-recapture dataset showed that annual survival for females of breeding age was over 80% and close to 90% for the majority of adult life (Condit et al., 2014). In another marine species exhibiting skipped reproduction after a successful year, the wandering albatross (*Diomedea exulans*) was shown to have high annual survival (>80% to >95%) over a 36-year mark-recapture study (Gauthier et al., 2012). These studies of species with similar life history traits (skipped reproduction, long life) suggest that a survival rate of 89% may indeed be adequate for population growth. More years of mark-recapture data will allow us to examine variation in annual survival rates and other demographic parameters. Having estimates of parameters such as reproductive life span, age to maturity and longevity would allow us to better evaluate the survival rate for what might be adequate for growing or sustaining a population.

The remigration interval for turtles nesting in Florida (2.7 years based on raw observations and 2.5 years based on Model M) is similar to that seen for St. Croix (both places had a mode = 2 years; Dutton et al., 2005) and not particularly surprising given the high breeding probability for turtles in our study making the transition from the non-nesting to the nesting state the following year (64.5%; Table 4). In contrast, Pilcher and Chaloupka (2013) found that the probability of a turtle transitioning to nesting after a skipped year was only 41% and they also found that the probability of a turtle skipping two years after nesting was quite high at 59%.

Florida-nesting turtles may not always skip a year or two before nesting again; 3.6% of turtles tagged at Juno Beach returned in consecutive years to nest (one turtle returned in 3 consecutive years). The potential is therefore quite good for these turtles to have high reproductive output over fairly short periods of time and this is an aspect of the nesting ecology that should be explored further. At St. Croix, due to the relocation of nests that would have been lost to erosion and an exponentially increasing number of nesting females, hatchling production has risen from 2000 to over 49,000 since the project began. The remigration rates at these two Atlantic leatherback rookeries (Florida and St. Croix) contrast starkly with remigration intervals calculated for Playa Grande, Costa Rica. There, turtles return on average every 3.7 years (Wallace et al., 2006) and their reproductive output is much lower (Reina et al., 2002). Eastern Pacific turtles however, are facing different environmental conditions than turtles in the Atlantic (Wallace et al., 2006; Saba et al., 2007) so meaningful comparisons are difficult to make.

In conclusion, this study addressed important objectives needed for continuing management by directly calculating average annual nesting population size, survival rates and remigration intervals for leatherbacks along the east coast of Florida and it is the first study to do so on the basis of empirical data collected from nesting females. Developing population parameters for use in an updated recovery plan was the initial goal of this study, and several important parameters have now been estimated. The use of emerging and sophisticated mark-recapture models tailored for specific animals that take into account the biology of the animal are incredibly useful and valuable. Choosing the right analytical design helps minimize bias and reduces error of parameters that are being estimated. The ORD-MS design (Kendall and Bjorkland, 2001) seems appropriate for future population studies of turtles on nesting beaches to avoid biases in survival rates and other parameters because of the nature of sea turtle reproductive biology (i.e., skipping a year following nesting). These methods have proven to be useful for other marine species as well.

To develop a complete picture of the status of the leatherback in US waters and on nesting beaches, we recommend continuing the long-term studies at St. Croix and in Florida. In addition, a similar summary from the other major nesting beaches within US jurisdiction (throughout Puerto Rico, Culebra and Vieques) would be most useful and informative. Long-term studies such as these are critical tools for detecting changes in populations and may provide estimates of parameters that may inform management decisions and refine population models.

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