esa ECOSPHERE

Conservation implications of sea turtle nesting trends: elusive recovery of a globally important loggerhead population

S. A. Ceriani,[1,†] P. Casale,[2] M. Brost,[1] E. H. Leone,[3] and B. E. Witherington[4]

[1]Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Saint Petersburg, Florida 33701 USA
[2]Department of Biology, University of Pisa, Pisa, Italy
[3]Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 1105 SW Williston Road, Gainesville, Florida 32601 USA
[4]Inwater Research Group, 4160 NE Hyline Dr., Jensen Beach, Florida 34957 USA

Citation: Ceriani, S. A., P. Casale, M. Brost, E. H. Leone, and B. E. Witherington. 2019. Conservation implications of sea turtle nesting trends: elusive recovery of a globally important loggerhead population. Ecosphere 10(11):e02936. 10.1002/ecs2.2936

Abstract. Understanding population status and trends is important for developing and evaluating management and conservation actions for threatened species. Monitoring population status of marine organisms is especially challenging. Because sea turtles come ashore to lay their eggs and nests are easily counted, these counts are commonly used as an index of abundance and population trends. Nest counts do not provide a direct index of adult female population abundance because females typically lay more than one nest per year and most do not reproduce every year. This study attempts for the first time to investigate the likelihood that observed fluctuations of nest counts represent inter-annual changes of the adult female population by accounting for uncertainty in reproductive rate parameters. We analyzed 30 yr of reproductive data from the largest nesting loggerhead sea turtle population worldwide, breeding in Florida (USA), and for the three Recovery Units and seven Management Units therein. Nest counts followed a general non-monotonic trend with wide fluctuations that corresponded to decreasing and increasing trends during short intervals. When we accounted for uncertainty in both clutch frequency and remigration interval, there was no evidence for an increasing or a declining trend in the breeding female population across the entire period. Despite extensive conservation efforts and protections for loggerheads in Florida and the wider USA, we did not find evidence of a strong population recovery. We recommend maintaining a high level of protection, addressing persistent anthropogenic threats, continued collection of rigorous nest-count data, and monitoring reproductive parameters to better link nest counts to adult female population abundance. Our results demonstrate the need for caution in using nest counts as a direct proxy for adult female population status, as it may lead to unsupported conclusions potentially detrimental to conservation. Therefore, we recommend to always translating nest trends to at least adult female trends, including uncertainty in reproductive parameters. Our approach can be exported to other populations, even where reproductive parameters are not available. Applying high parameter uncertainty obtained from other populations can help identifying unequivocal population changes; that is, nest trends unlikely justified by uncertainty and poor knowledge of reproductive parameters.

Key words: *Caretta caretta;* clutch frequency; nest count; Northwest Atlantic Distinct Population Segment; Northwest Atlantic Regional Management Units; population abundance; population trends; remigration interval; reproductive rate parameters.

Received 1 September 2019; accepted 19 September 2019; final version received 16 October 2019. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** simona.ceriani@myfwc.com

Introduction

Over the last five centuries, sea turtle populations have been so drastically reduced by anthropogenic activities that they may no longer fulfill their historical ecological roles (Jackson et al. 2001, Bjorndal and Jackson 2003). Although direct exploitation for meat and eggs has been reduced, several other anthropogenic threats continue to cause concern. These threats primarily include bycatch in fisheries (Wallace et al. 2013*a*), habitat loss (Fuentes et al. 2016, Nelson Sella and Fuentes 2019), pollution (Keller et al. 2012, Casale et al. 2016, Lauritsen et al. 2017), and climate change (Fuentes et al. 2011, Rees et al. 2016, Von Holle et al. 2019). Although there has been some improvement in bycatch in a few localized instances (Finkbeiner et al. 2011, Gilman and Huang 2017, Swimmer et al. 2017), the issue of bycatch is far from being resolved and continues to pose a serious threat to sea turtle recovery (Wallace et al. 2013*a*, Rees et al. 2016).

Understanding trends in population abundance for threatened species is important when developing or evaluating management and conservation actions. For sea turtles, and marine animals in general, monitoring population abundance is particularly challenging because of their scale of distribution, migratory nature, and cryptic early life stages. Sea turtles come ashore to lay egg clutches in nests (hereafter, nests), which can easily be counted along beaches. However, nests are an indirect representation of adult female abundance because females lay more than one nest per year and do not typically reproduce every year (Miller 1997). Moreover, females are only one part of the adult population, and adults are only a small fraction (~1%) of the total population (Crowder et al. 1994, Heppell et al. 1996, 2003*a*, Chaloupka and Limpus 2002, Casale and Heppell 2016). Furthermore, because sea turtles take decades to reach sexual maturity (Heppell et al. 2003*b*), any fluctuations observed in nest counts (and by extension, adult females) are the cumulative result of events (either threats or conservation measures) that occurred prior, either on the nesting beach or in the water. These limitations notwithstanding, nest counts have always been the most common, if not sole, index of sea turtle population abundance and trends (Carr et al. 1978, Meylan 1982, Schroeder and Murphy 1999, National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008, Witherington et al. 2009, Wallace et al. 2013*b*, Casale and Tucker 2017, Mazaris et al. 2017). Nest counts can be widely and systematically obtained, compared among study locations, and tracked over long time series.

Like other sea turtle species, the loggerhead turtle (*Caretta caretta*) is protected by various international treaties and agreements (e.g., the Convention on International Trade of Wild Flora and Fauna [CITES] Appendix S1) as well as national laws (e.g., U.S. Endangered Species Act, Canada Species at Risk Act). Of the 10 loggerhead Regional Management Units (RMU) identified by Wallace et al. (2010), the Northwest Atlantic is the largest (Casale and Tucker 2017). The Northwest Atlantic Loggerhead is listed as a Distinct Population Segment (DPS) under the U.S. Endangered Species Act. The main nesting beaches for this DPS are located in Florida, USA (89% of nests; Ceriani and Meylan 2017), and, therefore, monitoring reproductive effort in Florida is particularly important at both the population and species level.

The Florida Statewide Nesting Beach Survey (SNBS) program was launched in 1979 by the Florida Department of Natural Resources (now the Fish and Wildlife Research Institute [FWRI] of the Florida Fish and Wildlife Conservation Commission [FWC]) to monitor sea turtle nesting activity in the state. The program gradually expanded to include most of the state's sandy beaches (224 beaches and 1350 km surveyed in 2018). In 1989, FWC initiated the Florida Index Nesting Beach Survey (INBS) program to complement the SNBS. The INBS consists of a subset of SNBS beaches where surveyors follow a standardized protocol that ensures consistent monitoring effort (e.g., fixed start and end dates, fixed time window for daily early-morning surveys, and fixed survey boundaries). Surveyors at these beaches committed to a minimum of 10 yr of participation in the program, including standardized reporting and annual training workshops. The INBS program provides a reliable index of nesting activity in Florida and has been instrumental in assessing and monitoring the status of loggerheads (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008, Conant et al. 2009, Witherington et al. 2009).

Nesting on Florida index beaches showed an increase between 1989 and 1998 but a steep decline between 1998 and 2006, producing a net decrease over the 18-yr period (1989–2006) (Witherington et al. 2009). Witherington et al. (2009) considered it unlikely that the decrease observed in Florida nest counts was due to a change in reproductive rates. The nesting trend was hypothesized to represent a decline in the number of adult females in the population, and, of the various explanations considered, Witherington et al. (2009) suggested that bycatch in fisheries was the most plausible cause of the decline. This and other assessments of the Northwest Atlantic subpopulation prompted concern among scientists and managers that the largest nesting population in the Atlantic could be declining (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008, Conant et al. 2009). These concerns were particularly strong in the USA because the species had been listed under the Endangered Species Act (ESA) since 1978 and a variety of conservation measures aimed at recovering the species were implemented on nesting beaches and in the marine environment during the subsequent 30 yr. These conservation measures included protecting nesting habitat, reducing nest depredation, reducing beachfront lighting, and modifying fishing gears to reduce bycatch (including requirements to use Turtle Excluder Devices [TEDs] in the U.S. shrimp fishery and requiring large circle hooks and/or fish bait to reduce bycatch in certain sectors of the U.S. longline fisheries; National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008).

The cause(s) of the fluctuation in Florida loggerhead nest counts remains unclear. Assuming that loggerheads are not shifting nesting site to or from Florida—a realistic assumption given that Florida hosts by far the largest nesting aggregation in the Atlantic (Ceriani and Meylan 2017)—one key question is how much of the variability in nest counts is due to female population abundance and how much is due to other parameters such as reproductive effort. In this paper, we explore the extent to which estimates of adult female trends derived from nest counts are influenced by the uncertainty in two reproductive parameters—remigration interval (number of years between consecutive nesting seasons) and clutch frequency (number of clutches laid by a female in a given nesting year). This represents an extension to temporal series of the approach previously undertaken by Richards et al. (2011) to estimate the abundance of the Northwest Atlantic loggerhead population considered as static. We also address what the most effective management response should be in a system with inherent delay between causes and effects. Such a lag time is expected given that Northwest Atlantic loggerhead females reach sexual maturity at a minimum of 22.5–25 yr, with a mean of 36–38 yr (Avens et al. 2015), and nest counts are the cumulative result of events impacting females during that timeframe and thereafter.

The objectives of this study were to (1) provide updated nest counts of loggerheads on Florida index beaches over a 30-yr period (1989–2018) and, from these, (2) derive abundance estimates of annual nesting females and total adult females using the best available data on reproductive rates and incorporating the uncertainty around those two parameters, for the seven genetically distinct Management Units (Shamblin et al. 2012) and three Recovery Units (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008) present in Florida, (3) provide temporal trends of adult females over the last 30 yr based on currently available knowledge, and (4) discuss the implications for sea turtle conservation and management in Florida. Finally, we propose that the Northwest Atlantic loggerhead—one of the best-studied sea turtle populations in the world—can be used as a case study to inform other programs about the importance of long-term monitoring and the value of converting nest counts to turtle abundance estimates when assessing population trends.

Materials and Methods

Data collection

Nest counts were collected from 1989 to 2018 during early-morning surveys designed to detect the signs left by sea turtles that emerged the previous night. Trained surveyors used visible characteristics of tracks and nests to distinguish loggerhead nests from those of other sea turtle species (primarily green turtles, *Chelonia mydas,* and leatherback turtles, *Dermochelys coriacea*) and to distinguish nests from abandoned nesting attempts (techniques described by Schroeder and Murphy 1999, Florida Fish and Wildlife Conservation Commission 2016). Tracks were marked to prevent repeated counting. Surveys were conducted under two complementary monitoring programs, which differ in geographic and temporal coverage and methods—the Statewide Nesting Beach Survey program (SNBS) and Index Nesting Beach Survey program (INBS). The SNBS targets complete seasonal and geographic coverage, counts all tracks (above and below the recent tide-mark), and currently includes 224 beaches (Fig. 1), which represent most of the suitable nesting habitat along the sandy coastline, with survey gaps occurring only in the Everglades area and in some of the more remote keys in southernmost Florida. However, SNBS monitoring effort has varied over time: Beaches have been added, boundaries have fluctuated, and survey dates and frequency have varied. The INBS was developed to provide more rigorous data that would be appropriate to assess spatiotemporal nesting trends. Standardized surveys are conducted with consistent monitoring effort but at a finer spatial scale (beach zones < 1 km) with smaller geographic and seasonal coverage than SNBS beaches. The INBS consists of a subset of SNBS beaches (n = 36; Fig. 1), which are monitored daily from 15 May–31 August each nesting season. Additionally, counting effort is restricted to daily early-morning survey periods and to nests laid above the recent tide-mark in order to limit daily count bias from changing tidal cycles. To increase spatial resolution, the 36 INBS beaches are divided into permanent zones for a total of 517 zones (mean length 855 $\pm$ 264 m; range 152–3079 m). Surveys that were conducted after a missed survey day resumed only after nests from the missed days were marked as not-to-be counted to ensure counts accurately reflect the date the nest was laid.

Shamblin et al. (2012) identified demographically independent Management Units (MUs) within the Northwest Atlantic loggerhead population and, as a result, FWC assigned all SNBS and INBS beaches to one of the seven MUs occurring in Florida: (1) Northeast Florida (NE), (2) Central East Florida (CE), (3) Southeast Florida (SE), (4) Southwest Florida (SW), (5) Central West Florida (CW), (6) Northwest Florida (NW), and (7) Dry Tortugas (DRTO; Fig. 1). INBS beaches are spread throughout the principal nesting range of the loggerhead in Florida (Fig. 1); 27 of the 36 INBS beaches are considered core beaches because they have been monitored since the inception of the INBS program in 1989 and have been used in the previous nesting trend analysis (Witherington et al. 2009). These core beaches are located in five MUs: NE (n = 7), CE (n = 8), SE (n = 9), SW (n = 2), and CW (n = 1). We also included data from three additional INBS beaches located in the Gulf of Mexico that were added to the program in 1997 because they represent an additional MU (NW). While we included data from the DRTO MU (one INBS beach) for estimating the current number of adult females based on the last five years of nest counts (2014–2018), for the analysis over the 1989–2018 period we excluded these data along with five additional INBS beaches around the state where monitoring started later or has been intermittent, thus focusing on 30 of the 36 INBS beaches (465 zones) in six MUs (Appendix S1: Table S1). The U.S. Loggerhead Recovery Plan divides the Northwest Atlantic loggerhead Distinct Population Segment (DPS) into five Recovery Units (RUs) that are used to assess recovery status (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008). Three of these RUs are found in Florida: the Peninsular Florida RU (Florida/Georgia border south through Pinellas County, Florida), the Dry Tortugas RU (islands located west of Key West, Florida), and the Northern Gulf of Mexico RU (northwest Gulf coast of Florida through Texas, USA). The core beaches used in this study represent the Peninsular Florida RU, while the three additional INBS beaches in NW Florida represent the bulk of the Northern Gulf of Mexico RU.

Estimate of track identification error

We assumed that sea turtle tracks were conspicuous and unlikely to be missed if a beach was completely surveyed in accordance with established INBS survey protocols. However, we expected that the identification of species and track type would have error. Witherington et al. (2009) evaluated surveyors' ability to identify loggerhead tracks. We continued and expanded

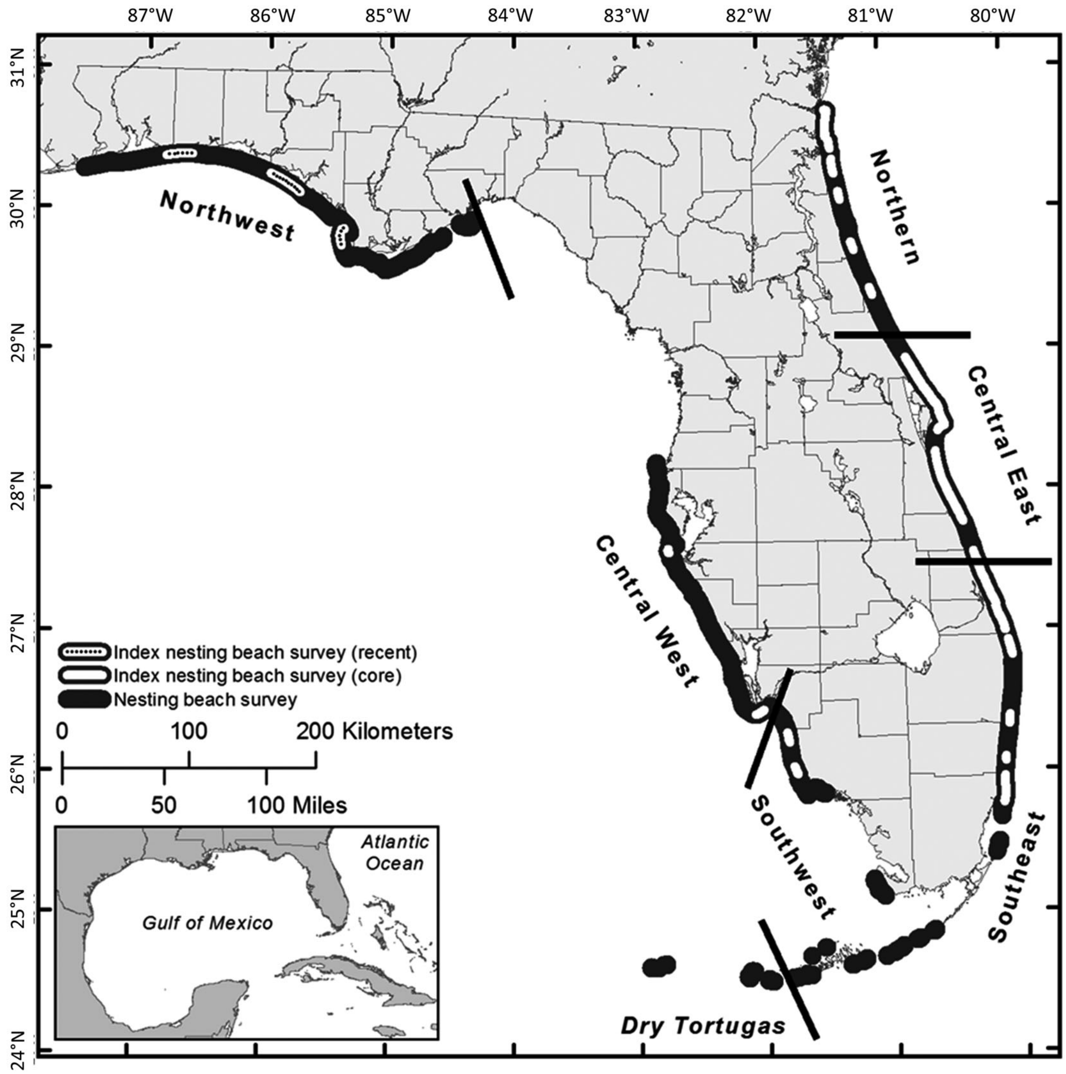

Fig. 1. Sea turtle nesting beaches in Florida where seasonal nest counts have been made. Black shoreline-shading represents all FWC Statewide Nesting Beach Survey (SNBS) beaches surveyed during the period 2014–2018. White shading represents the 27 core beaches of the FWC Index Nesting Beach Survey (INBS) program used in this study (1989–2018), while white-dotted shading represents the three INBS beaches in Northwest Florida that joined the program in 1997. All index beaches were surveyed daily for the INBS sampling season (15 May–31 August) each year. Black bars delineate boundaries between the loggerhead Management Units (MUs) found in Florida: Northeast (NE), Central East (CE), Southeast (SE), Dry Tortugas (DRTO), Southwest (SW), Central West (CW), and Northwest (NW). This study does not include the DRTO MU (one index beach) and five other index beaches around the state, where monitoring started later or has been intermittently. NE, CE, SE, SW, and CW MU combined make up the Peninsular Florida Recovery Unit (RU), while the NW MU represents the bulk of the Northern Gulf of Mexico RU and the DRTO MU is included in the Dry Tortugas RU.

the previous assessment by evaluating surveyors' ability to identify species (loggerhead vs. green turtle) and track type (nest vs. abandoned nesting attempt) during the 2015, 2017, and 2018 nesting seasons at 10 high nest density INBS beaches. During nighttime surveys, we directly observed and recorded the activity of females and placed a numbered flag by the track apex. A separate group of INBS surveyors assessed these pre-identified tracks during their regular surveys the following morning using only visible characteristics of the track. We calculated INBS surveyors' accuracy in interpreting tracks (i.e., identifying the species; discriminating between loggerhead nests and non-nesting attempts) as the ratio of correct/total and also estimated the associated 95% confidence intervals assuming a binomial distribution (Zar 1999).

Data analyses

Despite standardized effort, there are a small number of gaps in the survey data for INBS beaches. To correct for these lost days, we calculated an effort-adjusted nest count for each year according to the method described by Witherington et al. (2009). At one beach (Flagler Beach, NE MU), INBS surveys began in 1990, so we substituted the 1989 SNBS nest count (n = 63) for the 1989 INBS count, which likely represents a slight underestimate of the true nest count, given reduced monitoring effort in 1989. Similar to Witherington et al. (2009), we used restricted cubic splines, with a negative binomial regression model, to summarize the longitudinal trends in nests counts.

From nest counts, the number of adult females nesting in a specific year y (annual nesting females or ANF_y) was calculated as:

$$\mathrm{ANF}_y = \frac{n_y}{c} \tag{1}$$

where n_y is the total number of nests in year y, and c is the number of clutches laid by a female in a breeding year (i.e., clutch frequency). The total number of adult females in the population for year y (TF_y) was calculated as:

$$\mathrm{TF}_y = \mathrm{ANF}_y \times r \tag{2}$$

where r is the remigration interval (number of years between two consecutive nesting years). To estimate TF_y from n_y, we used a probabilistic resampling approach to account for the uncertainty in c and r. In doing this, we assumed that c and r do not co-vary. For each survey year y, we randomly drew 50,000 values of c from a normal distribution with mean = 5.4 and SD = 1.1. We drew this distribution of clutch frequency from Tucker (2010), who satellite tagged a total of 52 loggerheads on Casey Key (CW MU) between 2005 and 2009. Using these values of c, we generated 50,000 estimates of *ANF* for each survey year according to Eq. 1. Similarly, we calculated 50,000 estimates of TF with Eq. 2, by multiplying the ANF values described above with 50,000 random values of r drawn from a normal distribution with mean = 2.71 and SD = 0.91. We drew this distribution of remigration intervals from Bjorndal et al. (1983), who monitored 149 female loggerheads in CE Florida between 1972 and 1978. The mean and 95% confidence limits of TF were calculated as the mean and 2.5 and 97.5% empirical limits of the simulated distribution. We considered non-overlapping 95% CIs between two or more years as an unequivocal indication of a TF change. Finally, for each of the 50,000 temporal series of annual estimates of TF we fitted linear and exponential curves with the lm and nls functions of R, respectively, and calculated mean and 95% CIs of the slopes and of the annual growth rates, respectively. Keeping in mind that a constant linear or exponential trend across the entire monitored period represents a simplified and unlikely scenario, we considered cases with both 95% CIs increasing (or decreasing) as an unequivocal indication of a positive (or negative) TF trend.

Several studies have published remigration intervals for loggerheads in Florida (Ehrhart et al. 2014, Lamont et al. 2014, Phillips et al. 2014) but only three provide mean and SD for all the intervals (i.e., more than one for the same individual turtle). Two (Lamont et al. 2014, Phillips et al. 2014) were conducted in the NW and SW MU, respectively, and included long remigration intervals (up to 16 yr; probably due to imperfect detection) and consequently had wide SD. This may unduly increase uncertainty around the current estimates. Therefore, we used the values from Bjorndal et al. (1983) because they did not include long remigration intervals and were based on the CE MU, which is more representative of the entire Florida assemblage. However, Bjorndal et al. (1983) cautioned that coverage on the 11.2-km segment of Melbourne Beach in those early years was far from complete and Melbourne-tagged turtles were frequently documented nesting outside the study area, contributing to error in remigration interval data.

It is important to stress that the uncertainty we have addressed in c and r is based on simulations from one distribution. We assume that, while variable, these factors have remained stable throughout the study period and geographic range. It is possible that there have been trends in one, or both, of these parameters over the 30-yr period covered by this study.

All analyses were performed with R (R Development Core Team 2018), except effort-adjusted nest counts and restricted cubic spline models that were estimated with SAS v 9.4 (Cary, North Carolina, USA).

Results

A total of 2,152,238 and a subset of 1,410,846 loggerhead nests were observed on SNBS and INBS beaches from 1989 to 2018 (excluding Dry Tortugas), respectively. We estimated a total of 1,426,693 nests on INBS beaches after adjusting for effort (Table 1). Missed nests estimated by the adjustment for effort accounted for 1.1% of the total estimated nests (effort-adjusted), ranging from 0.1 to 1.4% in the five MUs of the core area, while they were 4.6% in the NW MU (Table 1). Unless otherwise specified, all the following analyses were performed on effort-adjusted nest counts (INBS). INBS surveyors correctly identified the species in 97.7% of 304 tracks (95% CI 95.3–99.1%) and true nests in 94.6% of 239 loggerhead tracks (95% CI 90.9–97.1%), which was comparable to the rate (91.3%) reported from the period 1993–1999 (Witherington et al. 2009), suggesting that surveyors' accuracy has remained consistently high over time.

Annual nest counts for 1989–2018 for the core INBS study area representing the Peninsular Florida RU, and for each MU, are shown in Figs. 2 and 3, respectively. In the core INBS sites (i.e., excluding the NW MU), nest totals ranged from 29,133 to 66,235 annually, with an annual mean ranging from 46 to 27,819 among the five MUs (Table 1). In the NW, MU nests ranged from 72 to 307 annually (1997–2018) with an annual mean of 169 nests. The core INBS nests in five MUs represented an average of 68% (SD 8%; range 52–81%) of the SNBS nest count from the same year and MUs. For the NW MU, this average was 16% (SD 3%; range 11–22%).

The mean number of annual nesting female turtles (ANF) estimated in the core INBS study area varied from 5655 (in 2007) to 12,873 (in 2016; Fig. 4). The wide 95% confidence intervals reflect the high level of uncertainty. The 95% confidence intervals did not overlap between some years in the NW, CW, SW, and NE MUs (Fig. 5), suggesting significant differences in ANF between those years. However, 95% confidence intervals overlapped widely in the most abundant MUs (CE & SE; Fig. 5) and do not provide strong evidence of differences. We found no indication of strong inter-annual differences in TF, based on the largely overlapping 95% confidence intervals in the sample of all core beaches (Fig. 6) and in all MUs except CW (Fig. 7). Moreover, the available data for the overall core beaches sample and for CE and SE are compatible with a nearly flat trend of the adult female population as well as with a moderate increase or decrease (Figs. 6, 7; Appendix S1: Figs. S1 and S2). For the overall core sample, the mean slope of the linear regression was $\beta = -55$ (95% CIs -517, 412) and the fitting annual growth rate was $g = 0.00934$ (95% CIs -0.02914, 0.05601). The fitting exponential curves of annual growth rates are shown in Appendix S1: Figs. S1 and S2 and values of slopes and annual growth rates for each MU are given in Table 2.

The total adult female population abundance estimated from the total annual nests observed (SNBS, including Dry Tortugas) in the most recent five years (average 2014–2018) was 51,319 (95% CIs 16,639–99,739) and ranged from 179 to 24,544 among the MUs (Table 3).

Discussion

Challenges in assessing population trends from nest counts

Annual loggerhead nest counts varied greatly in Florida between 1989 and 2018. While shorter time frames within the time series (e.g., before and after 2007) produced linear trends which may support both pessimistic (Witherington et al. 2009) and optimistic conclusions, the overall 30-yr pattern portrayed a general non-monotonic trend with wide fluctuations (max/min ratio = 2.3). This differs from the strong declining (e.g., Spotila et al. 2000, Tapilatu et al. 2013, Mazaris et al. 2017) or increasing trends observed elsewhere for loggerheads and other sea turtle species (Marcovaldi and Chaloupka 2007, Chaloupka et al. 2008, Mazaris et al. 2017).

Table 1. Annual average number of loggerhead turtle (*Caretta caretta*) nests documented by the FWC Statewide Nesting Beach Survey (SNBS) and Index Nesting Beach Survey (INBS) programs in Florida from 1989 to 2018, by Management Unit (MU).

	Annual average (range; total number of nests)						
	SNBS			INBS (Effort-Adjusted)			
MU	Annual average	Range	*n*	Annual average	Range	*n*	Adjustment (%)
Northeast	1213	590–2543	36,389	350	151–758	10,501	0.8
Central East	31,144	19,416–43,583	934,330	27,819	16,646–39,140	834,556	0.9
Southeast	31,803	20,826–57,587	954,081	18,911	11,986–28,144	567,327	1.4
Southwest	1139	189–2427	34,165	307	162–532	9203	0.5
Central West	5636	2047–14,054	169,083	46	10–164	1393	0.1
Total core (PFL RU)	70,935	44,511–120,013	2,128,048	47,433	29,133–66,235	1,422,980	1.1
Northwest (NGoM RU)	1100	552–2297	2,4190	169	72–307	3713	4.6
Total (entire period)	2,152,238			1,426,693			1.1

Notes: The total core represents the Peninsular Florida Recovery Unit (PFL RU), while the Northwest MU represents the bulk of the Northern Gulf of Mexico (NGoM) RU. The range of nests observed annually within each MU is provided in parentheses, along with the total number of nests observed in that region across all years. The % of nests potentially missed by direct observation and added in the effort-adjusted total is also shown (Adjustment). Data are provided for each MU, of which five represent the core Index sites monitored during the entire period, while Northwest (NW) was monitored since 1997.

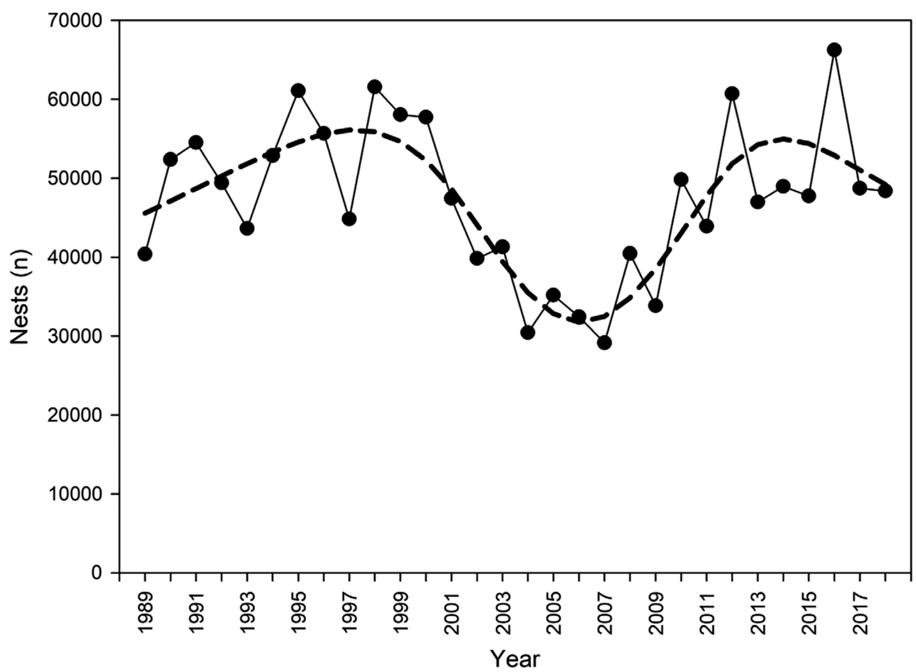

Fig. 2. Effort-adjusted number of loggerhead turtle (*Caretta caretta*) nests documented on the Florida Index Nesting Beach Survey (INBS) core beaches in the five Management Units (Northeast, Central East, Southeast, Southwest, Central West) from 1989 to 2018. The dashed line is a 6-knot restricted cubic spline curve fit via negative binomial regression, similar to Witherington et al. (2009).

In order to improve our understanding about the adult female trends possibly causing the observed nest trends, we implemented for the first time to a temporal series of nest counts an approach previously used for single-time estimates, that is, the inclusion of reproductive parameter uncertainty in the conversion from nest counts to adult females (Richards et al.

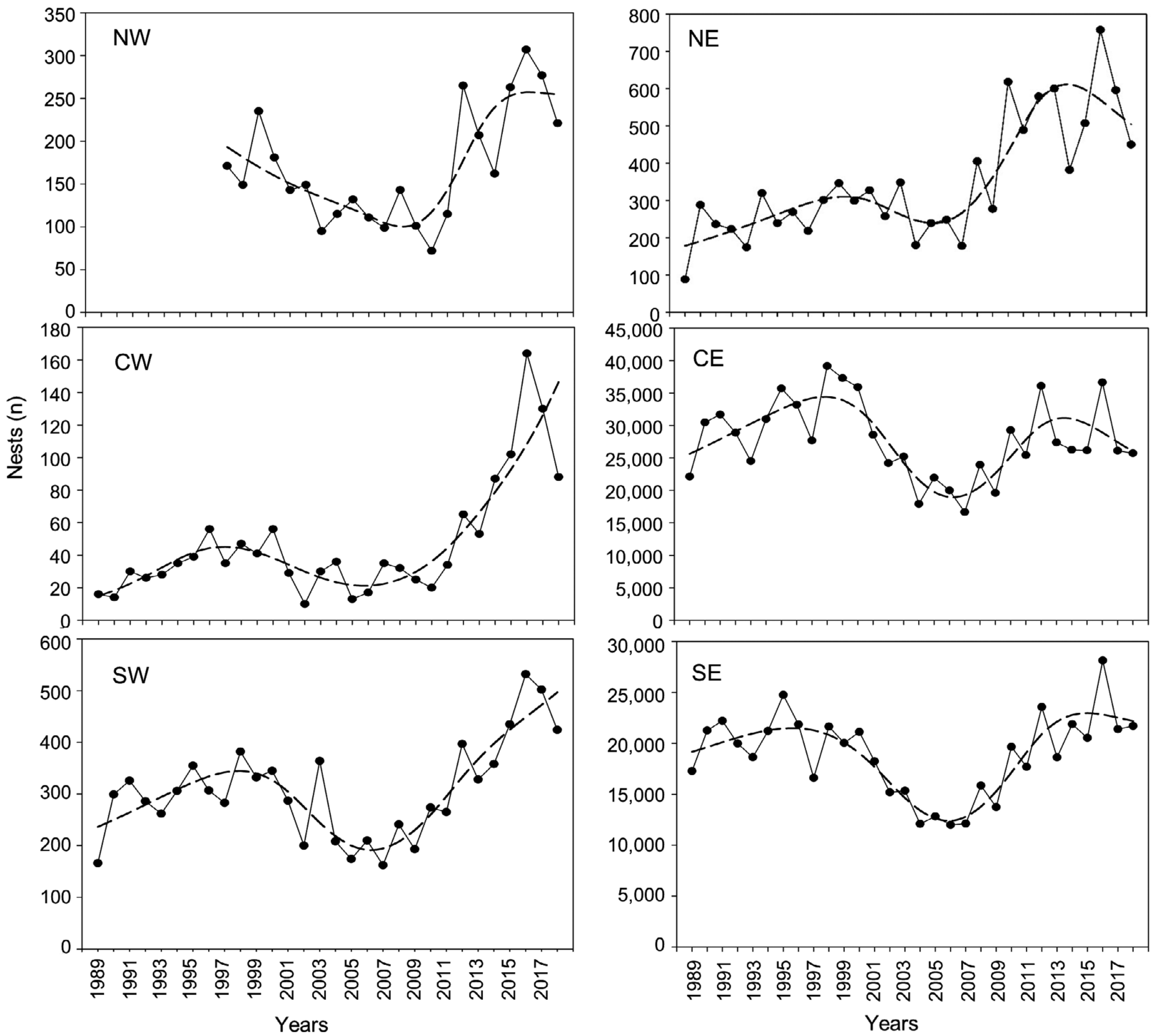

Fig. 3. Effort-adjusted number of loggerhead turtle (*Caretta caretta*) nests documented on the Florida Index Nesting Beach Survey (INBS) beaches within the six Management Units (MUs) of Florida (NW, Northwest, monitored only since 1997; CW, Central West; SW, Southwest; NE, Northeast; CE, Central East; SE, Southeast). The NW MU represents the bulk of the Northern Gulf of Mexico Recovery Unit (RU), while the other five MUs combined represent the Peninsular Florida RU. See Fig. 1 for MU geographic boundaries. The dashed line is a 6-knot restricted cubic spline curve fit via negative binomial regression, similar to Witherington et al. (2009).

2011). In spite of the marked changes in nest counts observed during the study period, we did not find clear evidence for either an increasing or decreasing adult female population trend over the 30-yr period. Results suggest breeding females are increasing at some MUs, but not at the two major MUs (CE and SE, which represented 82% of nesting in the last five years), and consequently at the statewide population.

Due to the paucity of robust data on average clutch frequency and remigration intervals in the literature, nest counts are commonly used as an index of adult female population abundance (Carr et al. 1978, Meylan 1982, Schroeder and Murphy 1999, National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008, Witherington et al. 2009, Wallace et al. 2013*b*, Casale and Tucker 2017, Mazaris et al. 2017). However, present

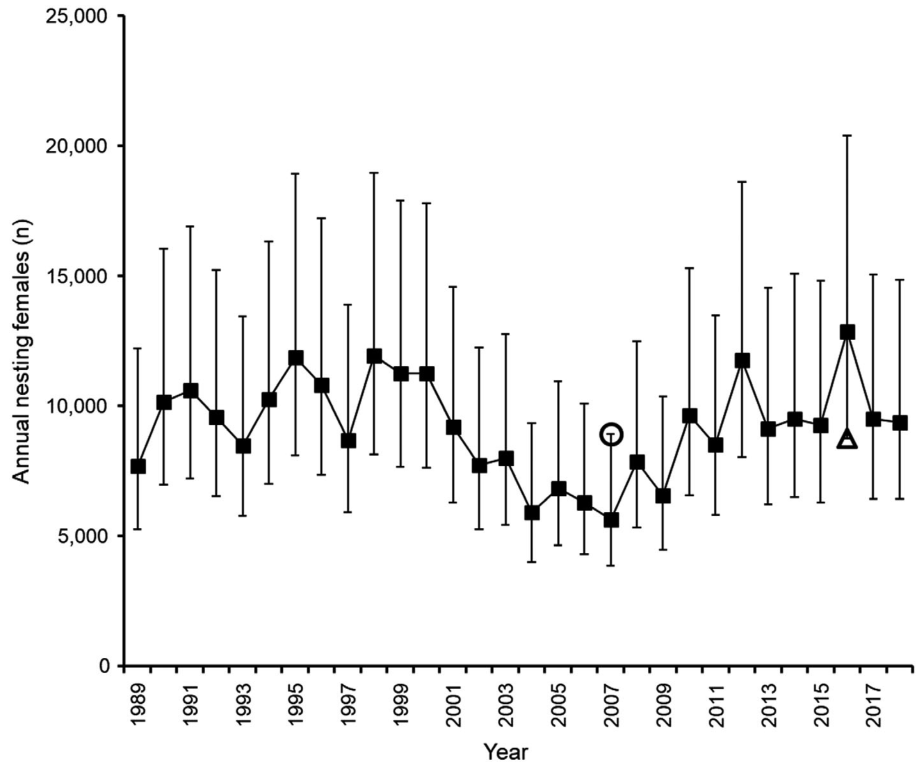

Fig. 4. Annual number of nesting female loggerhead turtles (*Caretta caretta*) in the five Management Units (MUs) of Florida that have been monitored since 1989 (Northeast, Central East, Southeast, Southwest, Central West), which combined represents the Peninsular Florida Recovery Unit (RU). Values are estimated from annual nest counts at FWC Index Nesting Beach Survey (INBS) core beaches and the number of nests per female per nesting season. Mean and 95% CIs (estimated from 50,000 replicates) are shown by closed squares and vertical bars, respectively. The maximum of the low 95% CIs and the minimum of the high 95% CIs are shown by a triangle and a circle, respectively. When the triangle is above the circle, 95% CIs of at least two years do not overlap suggesting some inter-annual differences and possible evidence of a trend. When the circle is above the triangle, all the 95% CIs overlap, suggesting no evidence of a trend.

results show that they may provide an imperfect picture of trends in the adult female population. To directly relate nest count to adult female population abundance, nest counts must be combined with reproductive data–clutch frequency (the number of nests made by each female in a season) and the proportion of females nesting in a given season (derived from remigration interval). A simple point estimate of average clutch frequency and remigration interval fails to capture the underlying variability in these conversion factors (Snover and Heppell 2009, Richards et al. 2011) and would simply mirror annual fluctuations of nest counts (Mazaris et al. 2017).

While our approach included uncertainty around clutch frequency and remigration intervals, due to the paucity of estimates for those parameters in the published literature, we were unable to consider annual variability in these measures (see also National Research Council 2010). Our approach can be easily exported to other populations, even where reproductive parameters are not available. Since the detection of trends depends on the variance and not on the mean of the reproductive parameters, applying high parameter uncertainty obtained from other populations would result in wide confidence intervals of the estimated adult female population. Under a conservative approach, non-overlapping confidence interval would suggest cases of unequivocal population changes, that is, when nest trends are unlikely

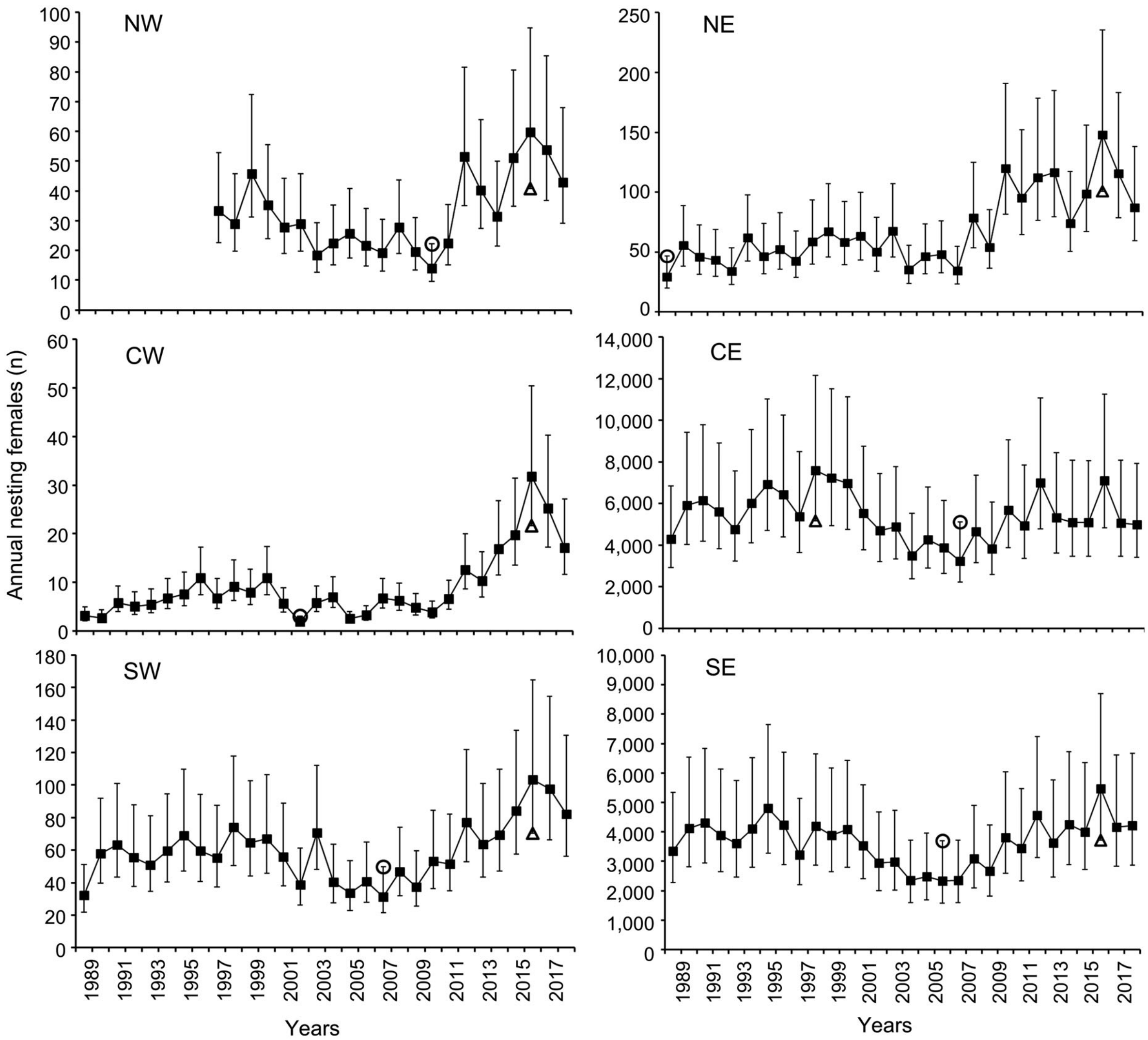

Fig. 5. Annual number of nesting female loggerhead turtles (*Caretta caretta*) in each of the six Management Units (MU) of Florida (NW, Northwest, monitored only since 1997; CW, Central West; SW, Southwest; NE, Northeast; CE, Central East; SE, Southeast). The NW MU represents the bulk of the Northern Gulf of Mexico Recovery Unit (RU), while the other five MUs combined represent the Peninsular Florida RU. Values are estimated from annual nest counts at FWC Index Nesting Beach Survey (INBS) beaches and the number of nests per female per nesting season. Mean and 95% CIs (estimated from 50,000 replicates) are shown by closed squares and vertical bars, respectively. The maximum of the low 95% CIs and the minimum of the high 95% CIs are shown by a triangle and a circle, respectively. When the triangle is above the circle, 95% CIs of at least two years do not overlap, suggesting some inter-annual differences and possible evidence of a trend. When the circle is above the triangle, all the 95% CIs overlap, suggesting no evidence of a trend. See Fig. 1 for MU geographic boundaries.

justified by uncertainty and poor knowledge of reproductive parameters.

Clutch frequency and remigration intervals are logistically difficult and expensive to measure, resulting in few published estimates. Clutch frequency requires near complete records of nesting behavior for individual females—records most reliably attainable with satellite telemetry data

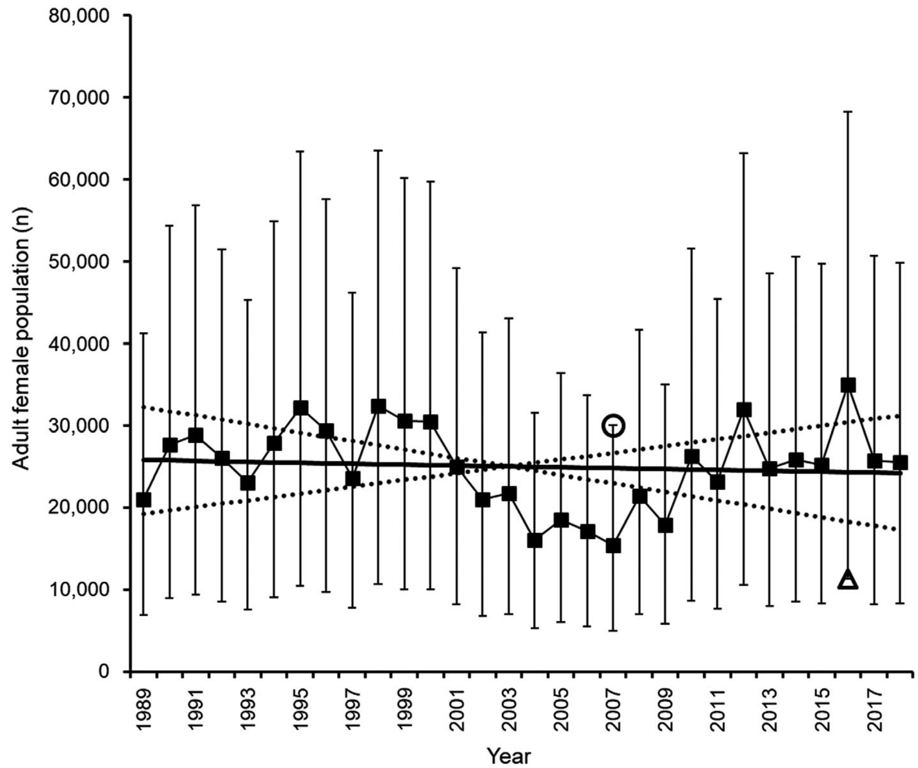

Fig. 6. Total adult female population abundance of loggerhead turtles (*Caretta caretta*) in the five Management Units of Florida monitored since 1989 (Central West, Southwest, Northeast, Central East, Southeast), which combined represents the Peninsular Florida Recovery Unit (RU). Values are estimated from annual nest counts at FWC Index Nesting Beach Survey (INBS) core beaches, number of nests per female per nesting season and interval between nesting years (both obtained through 50,000 randomly generated values; see text for details). Solid and dotted lines represent the mean and 95% CIs of the slope of the regression of the estimates (from 50,000 replicates). Other symbols as in Fig. 4.

for large populations (Tucker 2010, Esteban et al. 2017). A novel genetic approach was recently undertaken to determine accurate clutch frequency by identifying mothers from their clutches (Shamblin et al. 2017). Conversely, remigration intervals are best estimated with traditional capture–mark–recapture techniques. Assessing the proportion of breeding females in all the foraging grounds of a population is currently unfeasible. The use of satellite telemetry to estimate remigration interval is limited by the duration of the transmitters, usually much shorter than most remigration intervals. Multiple years of genetic fingerprinting, as suggested above, could theoretically provide data on remigration intervals as well. However, this approach would be limited to small populations, or small geographic scales, and would likely not be feasible for large populations, or at large geographic scales, such as the Florida loggerhead assemblage.

A disturbing lack of recovery of the world's largest loggerhead nesting assemblage

Our abundance estimate for adult female loggerheads nesting in Florida is higher than a previous estimate (Richards et al. 2011), partly due to an additional period of nest counts as well as different reproductive estimates. However, we did not find any unequivocal indication of population recovery—namely, an increasing trend in nest counts that "corresponds to an increase in number of nesting females (estimated from nests, clutch frequency,

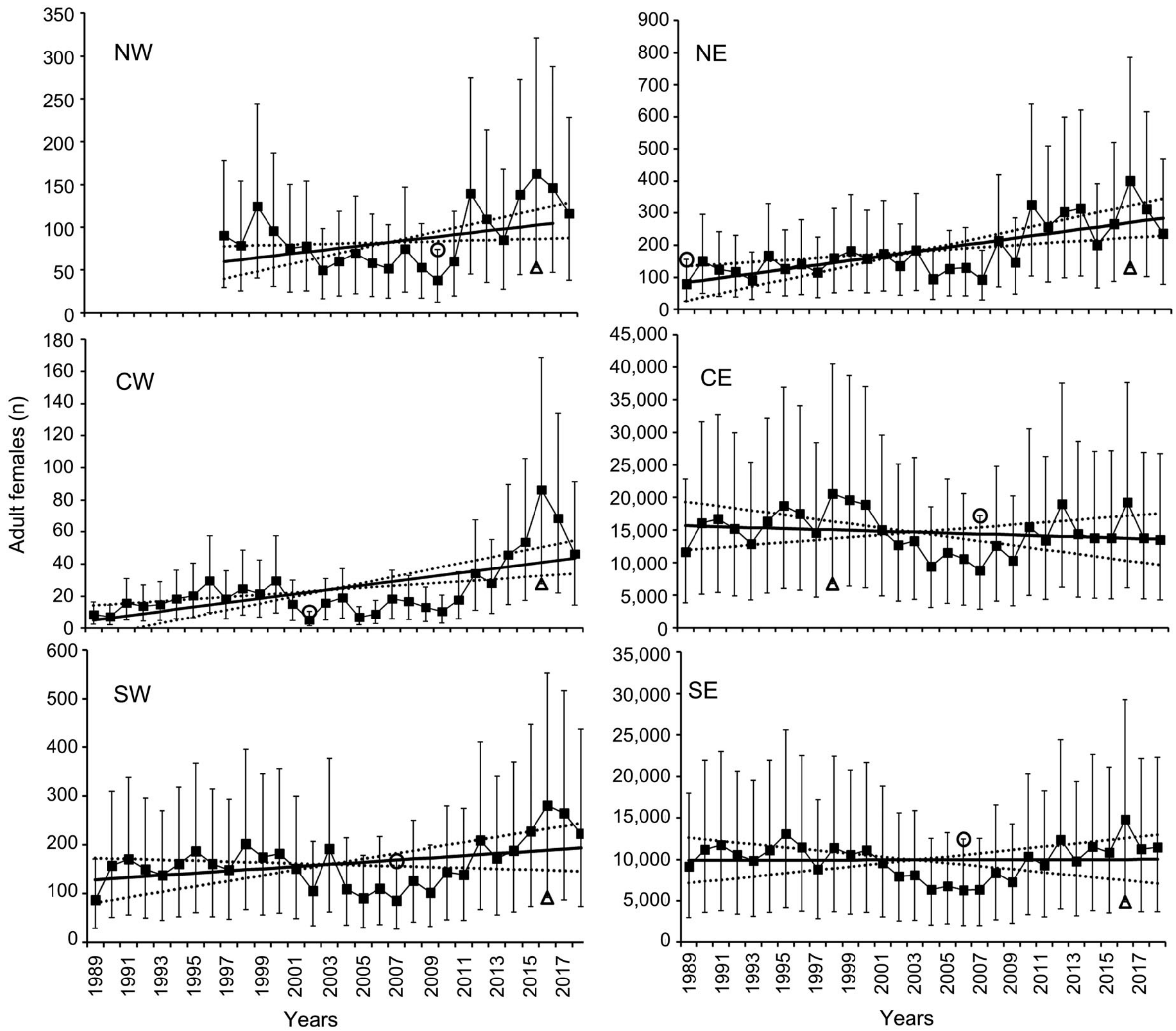

Fig. 7. Total adult female population abundance of loggerhead turtles (*Caretta caretta*) in each of the six Management Units (MUs) of Florida (see Fig. 5 for codes and definitions of MUs and Recovery Units). Values are estimated from annual nest counts at FWC Index Nesting Beach Survey (INBS) beaches, number of nests per female per nesting season, and interval between nesting years (both obtained through 50,000 randomly generated values; see text for details). Symbols as in Fig. 6.

and remigration interval)," as identified by the first demographic recovery criterion in the U.S. loggerhead recovery plan (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008).

We expected to find evidence of recovery given the extensive conservation efforts and protections that have targeted loggerheads in Florida, and the wider USA, for several decades (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008). These actions and protections mirror those for other sea turtle species that share Florida nesting beaches with loggerheads. In contrast to loggerhead nesting trends, nest counts for Florida green turtles have risen at an exponential rate (Chaloupka et al. 2008, Valdivia et al. 2019; FWC *unpublished data*). Such a long, monotonic increase is unlikely to be explained by variability in reproductive parameters alone. Threats uniquely affecting Florida's loggerhead population were discussed by Witherington et al. (2009) and National Marine

Table 2. Slopes and annual growth rates calculated from linear regression and exponential curves fitted on the estimates (50,000 replicates; see text) of loggerhead adult females for each Management Unit (MU) of the Florida assemblage.

	Linear regression mean slope (95% CIs)	Exponential curve mean annual growth rate (95% CIs)
Northeast	6.9 (3.3–11)	0.04948 (0.01544–0.09432)
Central East	−70.5 (−335.5 to 194.1)	0.01144 (−0.02634 to 0.05795)
Southeast	4.1 (−189 to 200.3)	0.00605 (−0.03513 to 0.0543)
Southwest	2.2 (−0.9 to 5.6)	0.0342 (−0.00108 to 0.08047)
Central West	1.3 (0.7–2.1)	0.06534 (0.02989–0.11216)
Total core	−55.2 (−517 to 412.3)	0.00934 (−0.02914 to 0.05601)
Northwest (NGoM RU)	2.4 (−0.7 to 5.6)	0.00827 (−0.05427 to 0.07766)

Table 3. Average annual number of loggerhead turtle (*Caretta caretta*) nests documented in Florida in the last 5-yr period (2014–2018) on FWC Statewide Nesting Beach Survey (SNBS) beaches across different Management Units (MUs) and the corresponding total number of adult females estimated.

MU	Nests (SNBS)	Total females mean (CI 95%)
Northeast	1852	974 (316–1885)
Central East	33,795	17,794 (5724–34,757)
Southeast	46,597	24,544 (7868–47,882)
Southwest	2036	1066 (341–2067)
Central West	11,150	5877 (1900–11,421)
Total Core (PFL RU)	95,342	50,280 (16,015–97,508)
Northwest NGoM RU)	1678	881 (284–1714)
Dry Tortuga (RU)	340	179 (58–350)
Total	97,447	51,319 (16,639–99,739)

Note: The total core represents the Peninsular Florida Recovery Unit (PFL RU), while the Northwest MU represents the bulk of the Northern Gulf of Mexico (NGoM) RU.

Fisheries Service and U.S. Fish and Wildlife Service (2008).

Several studies have attempted to explain proximal causes for the wide fluctuations in Florida loggerhead nest numbers and the decline observed from approximately 1999–2007 (Witherington et al. 2009, Van Houtan and Halley 2011, Arendt et al. 2013). Bjorndal et al. (2013) identified a simultaneous decline in growth rate of immature Northwest Atlantic loggerheads at the time nest counts were declining in Florida, which might reflect an effect of an environmental change on productivity, through slower growth rate, delayed sexual maturity, and/or decreased fecundity expressed as reduction in clutch frequency and longer remigration interval. Previous studies reached plausible but divergent conclusions (Van Houtan and Halley 2011, Arendt et al. 2013) underscoring our incomplete understanding of population trends and the demographic processes driving those trends. This lack of understanding is an impediment to projecting population trends and risk of extinction. Even when nest-count fluctuations reflect changes in population numbers, without an understanding of contributing demographic parameters, these patterns would require several cycles, spanning decades, to provide sufficient evidence to draw conclusions about population trends.

Implications for conservation and management

A comparison of recent five-year-annual-average loggerhead nest counts with comparable data from other regions (Casale and Tucker 2017) reveals that, worldwide, Florida is the most important nesting area for this species, likely hosting more than 40% of the nests laid globally. We point out that this concentration of nesting within a single geopolitical unit presents a global responsibility for federal, state, and local management authorities. Florida conservation agencies (principally FWC and county departments), beach management agencies (principally Florida Department of Environmental Protection and county departments), and federal agencies (principally National Oceanic and Atmospheric Administration, U.S. Fish and Wildlife Service, U.S. Army Corps of Engineers, and Bureau of Ocean Energy and Management) have critical roles in the conservation of loggerheads within the Northwest Atlantic RMU/DPS, with implications for the species' population as a whole. We further highlight the importance of Florida's CE and SE regions, which together host an average of 82% of Florida nests (35% and 48%, respectively).

We assume that the conservation actions implemented to protect loggerhead nests and nesting habitat and to reduce threats in the marine environment have played a role in the persistence of loggerheads in Florida. However, despite conservation efforts to date our results based on the best available knowledge do not demonstrate population recovery.

Based on our current findings and lack of understanding of drivers of the observed fluctuations in nest counts, we recommend maintaining a high level of protection, addressing persistent threats (fisheries bycatch, vessel strikes, habitat degradation/destruction) and improving our understanding of population dynamics, including changes in reproductive output. The only reliable estimate for clutch frequency in Florida was obtained from the CW MU (Tucker 2010), while the three estimates for remigration interval suitable for analyses are either limited due to inadequate survey coverage (Bjorndal et al. 1983) or from small MUs (Lamont et al. 2014, Phillips et al. 2014). Additional effort should be expended to provide consistent and reliable estimates of these parameters for each MU (in particular the most abundant ones: CE and SE) and to analyze and publish existing long-term datasets. We also believe it is critical to represent known levels of uncertainty when assessing, interpreting, and communicating nesting trends.

Ultimately, conservationists are interested in increasing or decreasing population trends. However, accurately interpreting nest-count trends requires context on the scale of demographic connectivity and estimates of reproductive parameters (clutch frequency and remigration interval; Tucker 2010, Shamblin et al. 2017). Incorporating variability in these two reproductive parameters will decrease the risk of (1) concluding the population has declined when it has not and (2) concluding the population has increased when it has not (see also Piacenza et al. 2017). While the former belief does not cause biological problems to the sea turtle population, the latter may well do so, if mechanisms and laws in place to protect a species are relaxed and support for monitoring and conservation programs is reduced.

Based on our simulations, we caution against unjustified optimism regarding global sea turtle conservation successes, such as recently suggested by Mazaris et al. (2017) in their meta-analysis of global sea turtle trends. It should be noted that in their estimates they either used nest counts or a single point estimate of annual breeding females (which mirrors the nest counts and fails to convey the range of variability and uncertainty of the estimates) to conclude that populations are increasing, but the majority (56% of 299) of the time series examined did not show any trend despite years, even decades, of conservation and management efforts. Similarly, the IUCN Red List assessments, most of which so far have been based on nest counts alone (Wallace et al. 2013*b*, Casale and Tucker 2017) could be improved by incorporating reproductive parameters and the related uncertainty in order to base the assessments on trends of adult females.

As emphasized by other authors (National Research Council 2010, Bjorndal et al. 2011, Warden et al. 2017), there is a need to develop in-water index programs and focus on integrating demography and abundance trends. Indexes of abundance at sea would have the advantage to monitor the bulk of population (juveniles) in real time and would perfectly complement nest counts.

The importance of annual nesting surveys

Uncertainties associated with converting nest numbers to numbers of adult females do not diminish the need to continue rigorous monitoring of sea turtle nesting activity. The homing behavior of sea turtles (Meylan et al. 1990) determines a metapopulation structure where Management Units for conservation can be identified and nest counts in an area are—by definition—related to a specific MU. Without nest counts, any exercise—like the present one—to estimate female population abundance and trends would be impossible. Under a precautionary approach, rapid decline of nest counts should prompt conservation action even in a context of uncertain population trends. We chose 95% confidence bars to represent annual estimates of nesting female numbers. Cautious resource managers may choose to assess annual changes under more narrow confidence limits, especially where the consequences of misinterpretation can be dire (many populations could be extirpated without ever having the data to unequivocally demonstrate they are in decline).

Moreover, long-term nesting monitoring programs provide the foundation and framework to collect and monitor demographic parameters and anthropogenic threats (Crain et al. 1995, Witherington and Martin 1996, Brock et al. 2009, Kamrowski et al. 2012, Ehrhart et al. 2014, Fuentes et al. 2016, Lauritsen et al. 2017, Nelson Sella and Fuentes 2019).

Conclusions and recommendations

Florida is the most important nesting area for loggerheads in the world and deserves special conservation management attention. Despite periods of increase and decrease in annual nest numbers over the 30 yr examined, clear evidence of a female population change over the study period or parts of it could not be detected once we accounted for uncertainty in reproductive parameters—clutch frequency and remigration interval. The cause(s) of the observed fluctuations in nest counts remains largely speculative. The current state of knowledge suggests that a strong population recovery—as the one expected from decades of conservation actions—has not occurred. Therefore, reducing existing protection or conservation attention to main threats like high-seas fisheries, coastal trawling, and vessel strikes (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008, Foley et al. 2019) is not justified.

We recommend (1) maintaining rigorous collection of sea turtle nest counts, which provide the basis for estimating female population size and reproductive output; (2) estimating sea turtle population trends by combining nest counts and reproductive parameters (clutch frequency and remigration interval), including uncertainty around them; (3) for populations where these parameters are not available, using values from other populations to provide preliminary information about the likelihood of unequivocal population changes; (4) pursuing good estimates of clutch frequency and remigration interval and their annual variation for each Florida MU, as well as for any sea turtle population; and (5) setting up long-term in-water programs for monitoring an index of abundance at sea, which could be integrated with nest counts to provide a more complete demographic assessment.

Acknowledgments

Nesting data were collected through a coordinated network of Florida Sea Turtle Permit Holders comprising individuals from Fort Clinch State Park (SP), Amelia Island Sea Turtle Watch, Amelia Island SP, Little Talbot Island SP, Beaches Sea Turtle Patrol, Guana Tolomato Matanzas National Estuarine Research Reserve Ft. Matanzas National Monument, Gamble Roger Memorial SRA and North Peninsula SP, Canaveral National Seashore, Merritt Island National Wildlife Refuge (NWR), Canaveral Air Force Station, UCF Marine Turtle Research Group, Sebastian Inlet SP, Archie Carr NWR, Fort Pierce Inlet SP, Inwater Research Group, Ecological Associates, Town of Jupiter Island, Marinelife Center of Juno Beach, Gumbo Limbo Nature Center, J.D. MacArthur Beach SP, John U. Lloyd SP (currently, Von D. Mizell-Eula Johnson State Park), Miami-Dade Parks and Recreation, Sanibel-Captiva Conservation Foundation, Delnor-Wiggins Pass SP, The Conservancy of Southwest Florida, St. Joseph Peninsula SP, Panama City Turtle Watch, and Eglin Air Force Base. The foundation of this network can be credited to A. Huff, C. Futch, and R. Witham. Data have been managed by W. Conley, B. Schroeder, A. Foley, B. Witherington, A. Meylan, B. Brost, and S. Ceriani. Guidance and permitting oversight for this network were provided by D. Arnold, C. Coogan, A. Foley, K. Frolich, A. Huff, M. Koperski, R. Mezich, C. Ryder, B. Schroeder, and R. Trindell. The Index Nesting Beach Survey program was established with guidance from A. Huff, E. Martin, A. Meylan, B. Witherington, E. Possardt, L. Ehrhart, C. Keske, and B. Schroeder. B. Schroeder played a key initial role in the successful coordination of this complex effort. G. Bruger, J. Hooper, and F. Bucci assisted with IT support; and C. Crady, L. Bolen, M. Broadstone, C. Koeppel, L. Lucas, R. Rivero, and R. Hardy helped with data editing and GIS. S. Ceriani, A. Meylan, T. Hirama, M. Koperski, T. Long, M. Wideroff, K. Minch, C. Lloyd, S. Schaf, L. Soares, M. Collins, E. Horner, K. Sella, and S. Burke assisted with the estimation of track identification error exercise (2015, 2017-2018). We thank A. Foley, A. Meylan, B. Schroeder, R. Hardy, and L. Soares for their comments on the manuscript. Funding for Florida sea turtle nest counts has come from the U.S. Fish and Wildlife Service and from the Marine Resources Conservation Trust Fund.

Literature Cited

Arendt, M. D., J. A. Schwenter, B. E. Witherington, A. B. Meylan, and V. S. Saba. 2013. Historical versus contemporary climate forcing on the annual nesting variability of Loggerhead Sea turtles in the Northwest Atlantic Ocean. PLOS ONE 8:e81097.

Avens, L., L. R. Goshe, L. Coggins, M. L. Snover, M. Pajuelo, K. A. Bjorndal, and A. B. Bolten. 2015. Age and size at maturation- and adult-stage duration for loggerhead sea turtles in the western North Atlantic. Marine Biology 162:1749–1767.

Bjorndal, K. A., B. W. Bowen, M. Chaloupka, L. B. Crowder, S. S. Heppell, C. M. Jones, M. E. Lutcavage, D. Policansky, A. R. Solow, and B. E. Witherington. 2011. Better Science Needed for Restoration in the Gulf of Mexico. Science 331:537–538.

Bjorndal, K. A., and J. B. C. Jackson. 2003. Roles of sea turtles in marine ecosystems: reconstructing the past. Pages 259–273 *in* P. L. Lutz, J. A. Musick, and J. Wyneken, editors. The biology of sea turtles. Volume II. CRC Marine Biology Series, CRC Press, Inc., Boca Raton, Florida, USA.

Bjorndal, K. A., A. B. Meylan, and B. J. Turner. 1983. Sea turtles nesting at Melbourne Beach, Florida, I. Size, growth and reproductive biology. Biological Conservation 26:65–77.

Bjorndal, K. A., et al. 2013. Temporal, spatial, and body size effects on growth rates of loggerhead sea turtles (*Caretta caretta*) in the Northwest Atlantic. Marine Biology 160:2711–2721.

Brock, K. A., J. S. Reece, and L. M. Ehrhart. 2009. The effects of artificial beach nourishment on marine turtles: differences between Loggerhead and Green turtles. Restoration Ecology 17:297–307.

Carr, A., M. H. Carr, and A. B. Meylan. 1978. The ecology and migration of sea turtles, 7. The west Caribbean green turtle colony. Bulletin of the American Museum of Natural History 162:1–46.

Casale, P., D. Freggi, V. Paduano, and M. Oliverio. 2016. Biases and best approaches for assessing debris ingestion in sea turtles, with a case study in the Mediterranean. Marine Pollution Bulletin 110:238–249.

Casale, P., and S. S. Heppell. 2016. How much sea turtle bycatch is too much? A stationary age distribution model for simulating population abundance and potential biological removal in the Mediterranean. Endangered Species Research 29:239–254.

Casale, P., and A. D. Tucker. 2017. *Caretta caretta* (amended version of 2015 assessment). The IUCN Red List of Threatened Species 2017: e.T3897A119333622. http://doi.org/10.2305/IUCN.UK.2017-2.RLTS.T3897A119333622

Ceriani, S. A., and A. B. Meylan. 2017. Caretta caretta (North West Atlantic subpopulation). The IUCN Red List of Threatened Species 2015: e.T84131194A84131608. https://doi.org/10.2305/iucn.uk.2015-4.rlts.t84131194a84131608.en

Chaloupka, M., K. A. Bjorndal, G. H. Balazs, A. B. Bolten, L. M. Ehrhart, C. J. Limpus, H. Suganuma, S. Troëng, and M. Yamaguchi. 2008. Encouraging outlook for recovery of a once severely exploited marine megaherbivore. Global Ecology and Biogeography 17:297–304.

Chaloupka, M. Y., and C. J. Limpus. 2002. Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. Marine Biology 140:267–277.

Conant, T. A., et al. 2009. Loggerhead sea turtle (Caretta caretta) 2009 status review under the U.S. Endangered Species Act. Report of the Loggerhead Biological Review Team to the National Marine Fisheries Service, August 2009.

Crain, D. A., A. B. Bolten, and K. A. Bjorndal. 1995. Effects of beach nourishment on sea turtles - review and research initiatives. Restoration Ecology 3:95–104.

Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea-turtle populations. Ecological Applications 4:437–445.

Ehrhart, L., W. Redfoot, D. Bagley, and K. Mansfield. 2014. Long-term trends in loggerhead (*Caretta caretta*) nesting and reproductive success at an important western Atlantic rookery. Chelonian Conservation and Biology 13:173–181.

Esteban, N., J. A. Mortimer, and G. C. Hays. 2017. How numbers of nesting sea turtles can be overestimated by nearly a factor of two. Proceedings of the Royal Society B: Biological Sciences 284:20162581. http://doi.org/10.1098/rspb.2016.2581

Finkbeiner, E. M., B. P. Wallace, J. E. Moore, R. L. Lewison, L. B. Crowder, and A. J. Read. 2011. Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. Biological Conservation 144:2719–2727.

Florida Fish and Wildlife Conservation Commission. 2016. Marine Turtle Conservation Handbook. https://myfwc.com/license/wildlife/marine-turtle-permit/

Foley, A. M., B. A. Stacy, R. F. Hardy, C. P. Shea, K. E. Minch, and B. A. Schroeder. 2019. Characterizing watercraft-related mortality of sea turtles in Florida. Journal of Wildlife Management 83:1057–1072.

Fuentes, M., C. J. Limpus, and M. Hamann. 2011. Vulnerability of sea turtle nesting grounds to climate change. Global Change Biology 17:140–153.

Fuentes, M. M. P. B., et al. 2016. Conservation hotspots for marine turtle nesting in the United States based on coastal development. Ecological Applications 26:2706–2717.

Gilman, E., and H. W. Huang. 2017. Review of effects of pelagic longline hook and bait type on sea turtle catch rate, anatomical hooking position and at-vessel mortality rate. Reviews in Fish Biology and Fisheries 27:43–52.

Heppell, S. S., L. B. Crowder, D. T. Crouse, S. P. Epperly, and N. B. Frazer. 2003*a*. Population models for Atlantic loggerheads: past, present, and future. Pages 255–273 *in* A. B. Bolten and B. E. Witherington, editors. Loggerhead sea turtles. Smithsonian Books, Washington, D.C., USA.

Heppell, S. S., M. L. Snover, and L. B. Crowder. 2003*b*. Sea turtle population ecology. Pages 275–306 *in* P. L. Lutz, J. A. Musick, and J. Wyneken, editors. The biology of sea turtles. Volume II. CRC Marine Biology Series, CRC Press, Boca Raton, Florida, USA.

Heppell, S. S., C. J. Limpus, D. T. Crouse, N. B. Frazer, and L. B. Crowder. 1996. Population model analysis for the loggerhead sea turtle, *Caretta caretta*, in Queensland. Wildlife Research 23:143–159.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Kamrowski, R. L., C. Limpus, J. Moloney, and M. Hamann. 2012. Coastal light pollution and marine turtles: assessing the magnitude of the problem. Endangered Species Research 19:85–98.

Keller, J. M., L. Ngai, J. B. McNeill, L. D. Wood, K. R. Stewart, S. G. O'Connell, and J. R. Kucklick. 2012. Perfluoroalkyl contaminants in plasma of five sea turtle species: comparisons in concentration and potential health risks. Environmental Toxicology and Chemistry 31:1223–1230.

Lamont, M. M., I. Fujisaki, and R. R. Carthy. 2014. Estimates of vital rates for a declining loggerhead turtle (*Caretta caretta*) subpopulation: implications for management. Marine Biology 161:2659–2668.

Lauritsen, A. M., P. M. Dixon, D. Cacela, B. Brost, R. Hardy, S. L. MacPherson, A. Meylan, B. P. Wallace, and B. Witherington. 2017. Impact of the Deepwater Horizon oil spill on loggerhead turtle *Caretta caretta* nest densities in northwest Florida. Endangered Species Research 33:83–93.

Marcovaldi, M. A., and M. Chaloupka. 2007. Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. Endangered Species Research 3:132–143.

Mazaris, A. D., G. Schofield, C. Gkazinou, V. Almpanidou, and G. C. Hays. 2017. Global sea turtle conservation successes. Science Advances 3: e1600730.

Meylan, A. 1982. Estimation of population size in sea turtles. Pages 135–138 *in* K. A. Bjorndal, editor. Biology and conservation of sea turtles. Smithsonian Institution Press, Washington, D.C., USA.

Meylan, A. B., B. W. Bowen, and J. C. Avise. 1990. A genetic test of the natal homing versus social facilitation models for green turtle migration. Science 248:724–727.

Miller, J. D. 1997. Reproduction in sea turtles. Pages 51–81 *in* P. L. Lutz and J. A. Musick, editors. The biology of sea turtles. CRC Marine Science Series, CRC Press, Boca Raton, Florida, USA.

National Marine Fisheries Service, and U.S. Fish and Wildlife Service. 2008. Recovery plan for the northwest Atlantic population of the loggerhead sea turtle (Caretta caretta). Second revision. National Marine Fisheries Service, Silver Spring, Maryland, USA.

National Research Council. 2010. Assessment of sea-turtle status and trends: integrating demography and abundance. The National Academies Press, Washington, D.C., USA.

Nelson Sella, K. A., and M. M. P. B. Fuentes. 2019. Exposure of marine turtle nesting grounds to coastal modifications: implications for management. Ocean & Coastal Management 169:182–190.

Phillips, K. F., K. L. Mansfield, D. J. Die, and D. S. Addison. 2014. Survival and remigration probabilities for loggerhead turtles (*Caretta caretta*) nesting in the eastern Gulf of Mexico. Marine Biology 161:863–870.

Piacenza, S. E., P. M. Richards, and S. S. Heppell. 2017. An agent-based model to evaluate recovery times and monitoring strategies to increase accuracy of sea turtle population assessments. Ecological Modelling 358:25–39.

R Development Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rees, A. F., et al. 2016. Are we working towards global research priorities for management and conservation of sea turtles? Endangered Species Research 31:337–382.

Richards, P. M., S. P. Epperly, S. S. Heppell, R. T. King, C. R. Sasso, F. Moncada, G. Nodarse, D. J. Shaver, Y. Medina, and J. Zurita. 2011. Sea turtle population estimates incorporating uncertainty: a new approach applied to western North Atlantic loggerheads Caretta caretta. Endangered Species Research 15:151–158.

Schroeder, B., and S. Murphy. 1999. Population surveys (ground and aerial) on nesting beaches. Pages 45–53 *in* K. L. Eckert, K. A. Bjorndal, F. A. Abreu-Grobois, and M. Donnelly, editors. Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, Washington, D.C., USA.

Shamblin, B. M., et al. 2012. Expanded mitochondrial control region sequences increase resolution of

stock structure among North Atlantic loggerhead turtle rookeries. Marine Ecology Progress Series 469:145–160.
Shamblin, B. M., et al. 2017. Improved female abundance and reproductive parameter estimates through subpopulation-scale genetic capture-recapture of loggerhead turtles. Marine Biology 164:138.
Snover, M. L., and S. S. Heppell. 2009. Application of diffusion approximation for risk assessments of sea turtle populations. Ecological Applications 19:774–785.
Spotila, J. R., R. D. Reina, A. C. Steyermark, P. T. Plotkin, and F. V. Paladino. 2000. Pacific leatherback turtles face extinction. Nature 405:529–530.
Swimmer, Y., A. Gutierrez, K. Bigelow, C. Barceló, B. Schroeder, K. Keene, K. Shattenkirk, and D. G. Foster. 2017. Sea turtle bycatch mitigation in U.S. longline fisheries. Frontiers in Marine. Science 4:260.
Tapilatu, R. F., P. H. Dutton, M. Tiwari, T. Wibbels, H. V. Ferdinandus, W. G. Iwanggin, and B. H. Nugroho. 2013. Long-term decline of the western pacific leatherback, dermochelys coriacea: a globally important sea turtle population. Ecosphere 4:25.
Tucker, A. D. 2010. Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: implications for stock estimation. Journal of Experimental Marine Biology and Ecology 383:48–55.
Valdivia, A., S. Wolf, and K. Suckling. 2019. Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. PLOS ONE 14:e0210164.
Van Houtan, K. S., and J. M. Halley. 2011. Long-term climate forcing in Loggerhead sea turtle nesting. PLOS ONE 6:e19043.
Von Holle, B., et al. 2019. Effects of future sea level rise on coastal habitat. Journal of Wildlife Management 83:694–704.
Wallace, B. P., C. Y. Kot, A. D. Dimatteo, T. Lee, L. B. Crowder, and R. L. Lewison. 2013*a*. Impacts of fisheries bycatch on marine turtle populations worldwide: toward conservation and research priorities. Ecosphere 4:40.
Wallace, B. P., M. Tiwari, and M. Girondot. 2013*b*. Dermochelys coriacea. IUCN Red List of Threatened Species. Version 2013.2. www.iucnredlist.org
Wallace, B. P., et al. 2010. Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLOS ONE 5:e15465.
Warden, M. L., H. L. Haas, P. M. Richards, K. A. Rose, and J. M. Hatch. 2017. Monitoring trends in sea turtle populations: Walk or fly? Endangered Species Research 34:323–337.
Witherington, B., P. Kubilis, B. Brost, and A. Meylan. 2009. Decreasing annual nest counts in a globally important loggerhead sea turtle population. Ecological Applications 19:30–54.
Witherington, B. E., and R. E. Martin. 1996. Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches. FMRI Technical Report TR-2. Florida Marine Research Institute, St. Petersburg, Florida, USA.
Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2936/full