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Declining Reproductive Parameters Highlight Conservation Needs of Loggerhead Turtles (*Caretta caretta*) in the Northern Gulf of Mexico

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Abstract. – Marine turtles in the Gulf of Mexico are at risk due to many anthropogenic threats including habitat degradation, commercial fishing, and petroleum activities. The severity of this risk was made apparent in 2010 with the occurrence of the Deepwater Horizon oil spill. The objectives of this study were to assess long-term trends in abundance and reproductive parameters for this genetically distinct nesting group. From 1994 to 2010, morning surveys were conducted along 3 beaches on the St Joseph Peninsula, Florida, including within our primary study site on Cape San Blas. Nest abundance on all 3 beaches declined by at least 47% ($p < 0.01$). Mean nesting success on Cape San Blas was 40% and also declined ($p = 0.002$). Mean clutch size was 108 and mean emergence success was 58%. Throughout the study there were no changes in clutch size and emergence success. We found that nesting characteristics for the northern Gulf of Mexico subpopulation appear similar to those from other loggerhead turtle nesting groups in the southeastern United States in some ways, such as emergence success, timing of peak nesting, and incubation duration and different in other ways such as nesting success. Variation in some of the parameters may indicate turtles among the different nesting groups experience different environmental conditions. The severity of declines in nest abundance and the low nesting success reported for this small subpopulation suggest potentially serious consequences for this nesting group.

Key Words. – Reptilia; Testudines; Cheloniidae; clutch size; emergence success; marine turtles; nest abundance; nesting

Loggerhead turtles (*Caretta caretta*) that nest along the Gulf of Mexico coast face many threats to survival including commercial fishing (NMFS 2008), pollution (Alam and Brim 2000), boat-related mortalities (Sobin 2008), and loss of nesting habitat (Lamont and Carthy 2007; Hawkes et al. 2009; Witherington et al. 2009). Marine animals in this region face the additional and serious threat of the largest oil spill in US history. Because of these threats, Bjorndal et al. (2011) suggest critical data, including demographic and abundance parameters, must be collected to assess and limit long-term declines in populations. In addition, the most recent report by the Turtle Expert Working Group (TEWG) highlights as a top priority the identification of population parameters for all loggerhead nesting groups (TEWG 2009).

One of the largest nesting aggregations of loggerhead turtles in the Atlantic basin is found along the southeastern United States where about 80% of all nesting occurs and 90% of all hatchlings are produced (TEWG 2009). The large contribution of this region to the global population highlights the importance of understanding the status of this group. Genetic studies have divided the Western Atlantic loggerhead nesting group into 5 subpopulations: 1) northern (Florida/Georgia border to southern Virginia), 2) peninsular Florida (Florida/Georgia border through Pinellas County, Florida), 3) Dry Tortugas (islands west of Key West, Florida), 4) northern Gulf of Mexico (Franklin County, Florida, through Texas), and 5) greater Caribbean (all other nesting beaches throughout the Caribbean and Mexico) (Encalada et al. 1998; TEWG 2009; Shamblin et al. 2011). Studies have indicated that the abundance of loggerhead nests along the Atlantic coast and in southwestern Florida is declining (Dodd and Mackinnon 2008; TEWG 2009; Witherington et al. 2009). Continued declines in these numbers was a primary factor prompting a proposal for elevating the level of protection for loggerheads in the United States (USFWS and NMFS 2010) and in the recent designation of 9 distinct population segments of loggerheads as either Endangered or Threatened (Wallace et al. 2010; USFWS and NMFS 2011), thereby highlighting the importance of developing population assessments for each of these subgroups.

Assessments of abundance are difficult for long-lived and wide-ranging species such as marine turtles (Frazer 1983; Crouse et al. 1987; Heppell et al. 2000, 2003; Witherington et al. 2009). The life cycle for the loggerhead turtle requires multiple habitats and spans ocean basins: eggs are deposited on beaches, hatchlings remain in oceanic currents, juveniles use coastal bays, and adults migrate across oceans (Dodd 1988). Therefore, population assessments for marine turtles are typically

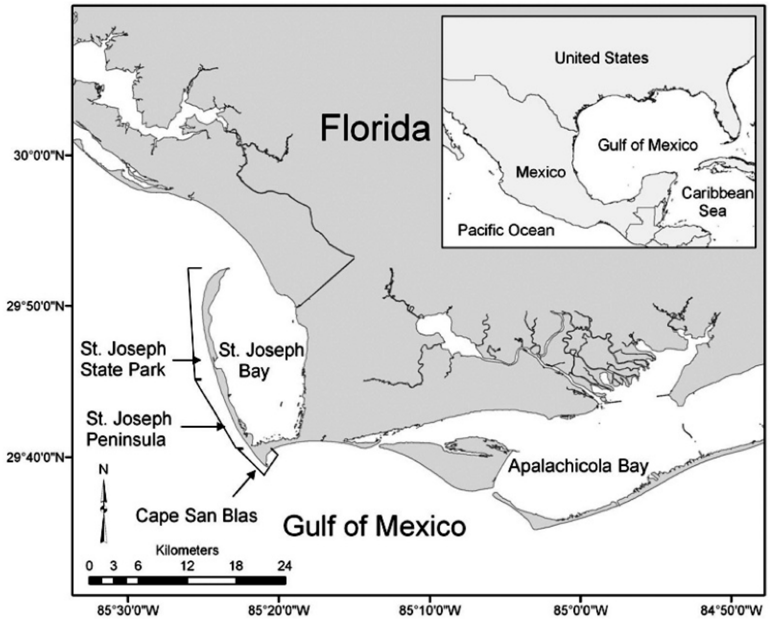

Figure 1. Three nesting beaches on the St Joseph Peninsula, Florida, located in the northern Gulf of Mexico, where reproductive parameters for loggerhead turtles were collected from 1994 to 2010.

generated using data from the most accessible life-history stage, nesting females, using parameters such as nest abundance, clutch size, and emergence success (Dodd and McKinnon 2008; Witherington et al. 2009; Bolten et al. 2011). Unfortunately, these data have previously been lacking for turtles nesting in the northern Gulf of Mexico, thereby making population assessments for this nesting group difficult (Wallace et al. 2010). Our goals were to examine temporal trends in nesting and hatching parameters for loggerhead turtles in the northern Gulf of Mexico, including abundance, nest success, clutch size, and emergence success over a 17-yr period.

METHODS

Study Site. — We conducted intensive nesting surveys and calculated emergence success from 1994 to 2010 along 5 km of beach on Eglin Air Force Base property along Cape San Blas (CSB), Florida, which represents the southern tip of the St Joseph Peninsula (SJP). This area supports one of the greatest nesting densities of loggerhead turtles in the northern Gulf of Mexico (Lamont and Carthy 2007). Nest abundance data from adjacent beaches on 7 km of the SJP and along 16 km of beach within T.H. Stone Memorial St Joseph State Park (SJSP; data made available by T. Spector, Florida State Parks; Fig. 1) were also used to calculate trends.

Nesting and Hatching Surveys. — Surveys were conducted every morning during the nesting season from 1 May to 1 November on foot, all-terrain vehicle, or 4-wheel drive vehicle. All turtle crawls were identified to species and egg clutches were located. Four wooden stakes were placed around the clutch, and flagging was wrapped around the stakes. On CSB, intensive morning surveys began in 1994 and data collected included number of crawls, number of nests, clutch size, incubation period, and emergence success. On SJP, annual nest abundance data were available from 1995, whereas in SJSP data were available beginning in 1996. All surveys followed standard protocol established by the Florida Fish and Wildlife Conservation Commission (FWC 2007; http://www.myfwc.com/media/418106/Seaturtle_Guidelines.pdf).

We defined nesting success as a proportion of the total number of nests to the total number of crawls. On CSB, nests were excavated 3 d posthatching or after 75 d of incubation. The total number of eggs in the clutch was assessed during nest relocation. Clutches were relocated landward of the original nest site if they were immediately threatened by erosion or long-term inundation. Incubation length was defined by calculating the number of days between deposition (determined during morning survey) and the date of first emergence (determined by presence of hatchling tracks). If rain or high winds could have obscured those first signs of emergence, nests were not included in analyses. To calculate the number of hatchlings that emerged from the nest, the number of dead hatchlings found within the nest was subtracted from the total number of hatched eggs. Emergence success was defined as the number of hatchlings that emerged from the nested divided by the total number of eggs deposited in the nest, following Johnson et al. (1996).

Analyses. — We first examined the temporal trends in annual nest abundance along all 3 beaches using a Poisson regression. For CSB, we also examined variation in nest abundance by month (May–August) and temporal trends in monthly nest abundance and clutch size using Poisson regression.

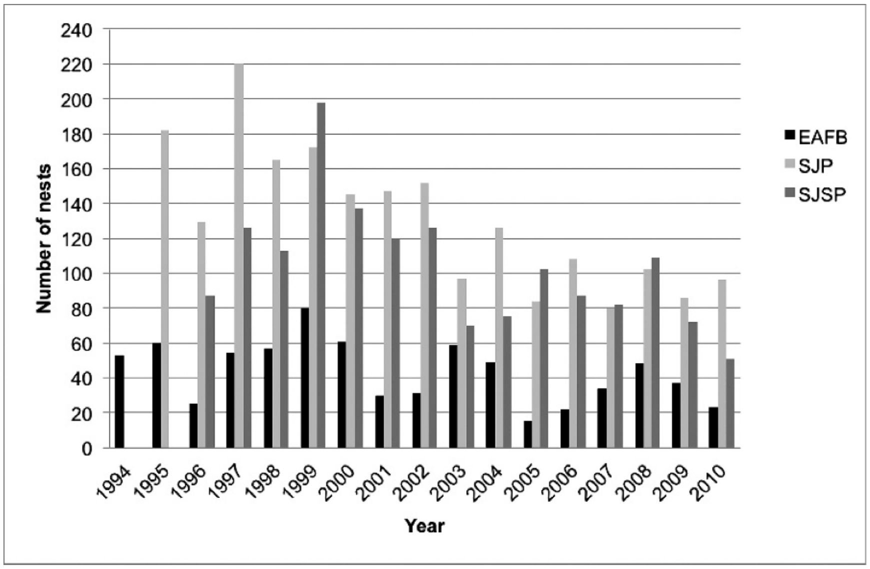

Figure 2. The number of nests laid per year on adjacent beaches along the St Joseph Peninsula (SJP), Florida, in the northern Gulf of Mexico: Eglin Air Force Base (EAFB) property on Cape San Blas from 1994 to 2010, the SJP from 1995–2010, and within St. Joseph State Park (SJSP) from 1996 to 2010.

Nesting success was modeled using year and month as independent variables. Emergence success was modeled with year and month effects. Both nest success and emergence success were analyzed using logistic regression. We used the GENMOD procedure of SAS 9.2 for Poisson and logistic regressions and used an α-level of 0.05 to assess significance of covariate effects.

RESULTS

At all 3 sites on the SJP, the number of nests significantly declined over time; based on the fitted model, the estimated decline was 46.8% (1994–2010), 55.8% (1996–2010), and 46.8% (1995–2010) declines in CSB ($N_{nest} = 4.106 - 0.039 \times$ year, $p_{slope} < 0.01$), SJP ($N_{nest} = 5.359 - 0.055 \times$ year, $p_{slope} < 0.01$), and SJSP ($N_{nest} = 5.073 - 0.045 \times$ year, $p_{slope} < 0.01$; Fig 2).

The mean number of crawls that occurred along CSB was 109, with 43 (8.7 nests/km) of those crawls resulting in a nest and 63 (12.6/km) resulting in no nest (Table 1). During the entire study period only 1 nest was deposited in September, therefore this data point was combined with August. The mean number of nests laid in May (3) and August (2) was smaller than the mean number laid in July (20; $p < 0.01$; Table 2); however the mean number deposited in June (19) was similar to the mean number laid in July.

Mean nesting success was 40.1% with greatest success (56%) occurring in 1999 and lowest success (23%) occurring in 2006. Nesting success did not differ within the season ($p > 0.05$; Table 1) but there was a significant declining trend in nesting success throughout the study ($p < 0.01$; Table 1).

Loggerheads deposited a mean of 108 eggs in each nest (Table 1). There was no change in clutch size

Table 1. Summary of estimated nesting parameters for loggerhead turtles nesting along 5 km of beach on Cape San Blas, Florida, in the northern Gulf of Mexico from 1994 to 2010.

Nesting parameters	*n*	Mean	SE	Range
Total number of nests	738	43.4	4.3	15–80
Total number of crawls	1805	109.0	8.0	56–181
Total number of false crawls	1067	62.8	4.9	33–121
Nesting success (%)	738	40.1	2.2	23–56
Clutch size	171	108	1.5	40–168
Emergence success (%)	360	58.1	2.0	0–100
Incubation length (days)	386	60.6	0.3	50–89

Table 2. Estimated model parameters for nest abundance and clutch size using Poisson regression, and nest success and emergence success using logistic regression on 5 km of beach on Cape San Blas, Florida, in the northern Gulf of Mexico from 1994 to 2010. For the month effect, July (the most active nesting month) was used as the base month.

Nesting parameters	Variable	Estimate	SE	χ^2	*p*
Number of nests	Year	−0.0386	0.0076	25.85	< 0.001
	May	−2.0529	0.1620	160.61	< 0.001
	June	−0.0427	0.0781	0.30	0.585
	August	−2.1006	0.1655	161.18	< 0.001
Clutch size	Year	−0.0002	0.0007	0.10	0.753
	May	0.0439	0.0162	7.30	0.007
	June	0.0108	0.0082	1.73	0.188
	August	0.0058	0.0177	0.11	0.741
Nest success	Year	−0.0313	0.0104	9.06	0.003
	May	−0.3690	0.2031	3.30	0.069
	June	−0.1100	0.1032	1.14	0.286
	August	0.6619	0.2286	0.53	0.465
Emergence success	Year	−0.0009	0.0016	0.34	0.558
	May	0.3787	0.0328	133.64	< 0.001
	June	0.6718	0.0174	1,494.29	< 0.001
	August	−0.4212	0.0414	103.67	< 0.001

Table 3. Summary of reproductive parameters showing mean number of nests/km, nesting success, clutch size, emergence success, and incubation length from loggerhead turtle nesting beaches throughout the southeastern United States, including within our study site on 5 km of beach in the northern Gulf of Mexico (Cape San Blas, Florida). A dash mark (-) indicates no data were available for that parameter. Time periods for data collection at each site differ.

Geographic area	Number of nests/km	Nesting success (%)	Clutch size	Emergence success (%)	Incubation length
Cape San Blas, Florida: 1994–2010	8.7	40	108	58.1	61
Bald Head Island, North Carolina (Rush 2003; Hawkes 2007; Hedges 2007)	7.1	48	118	82.9	60
Brevard County, Florida (Bagley et al. 1998)	634.0	59	-	54.7	-
Sarasota, Florida (Tucker et al. 2009)	46.4	53	-	76.1	53
Cape Canaveral, Florida (Antworth et al. 2006)	86.7	56	99	-	-
Georgia statewide (Dodd and Mackinnon 2008)	11.1	59	-	55.7	60
Everglades, Florida (Davis and Whiting 1997)	-	81	100	-	55
Palm Beach County, Florida (EAI 2008)	673.6	45	107	73.6	51

throughout the study ($p = 0.30$; Table 2). However, clutch size of nests deposited in May tended to be smaller ($p < 0.01$; Table 2) and those deposited in August tended to be larger ($p < 0.01$; Table 2) than those deposited in July.

Mean emergence success was 58% (Table 1). There was no significant trend in emergence success during the study period ($p = 0.56$; Table 2); however, there were monthly differences with greater emergence success in May and June than in July and lower emergence success in August than in July ($p < 0.01$; Table 2). Eggs incubated for an average 61 d before hatching (Table 1).

DISCUSSION

Results of this study support those of Witherington et al. (2009) who suggest a decline in loggerhead nesting along the Atlantic coast and in southwestern Florida; however the dramatic decline in nest abundance along the SJP and in nesting success along CSB suggest this small subpopulation in the northern Gulf of Mexico may also be at risk. Estimated declines in nest abundance on the Atlantic and southwestern coasts of Florida ranged from 29% to 37% between 1989 and 2006 (Witherington et al. 2009), whereas abundance of nests along the northern Gulf of Mexico declined by almost half from 1994 to 2010. This nesting group is one of the smallest subgroups within the larger southeastern US nesting population and the number of females contributing to this subpopulation is unknown. It is believed that extinction of a species occurs when mortality rates exceed reproductive replacement over a sustained period (Sodhi et al. 2009). If this large decline in nest abundance along the northern Gulf of Mexico is an indication of loggerhead mortality and if nesting success is used to define reproductive replacement, then there may be serious consequences for this nesting group. Findings from our study highlight the urgent conservation needs for this nesting group.

We also found that nesting characteristics for the northern Gulf of Mexico subpopulation appear similar to those of other loggerhead turtle nesting groups in the southeastern United States in many ways, such as emergence success, timing of peak nesting each season, incubation duration, and clutch size, but different in nesting success (Table 3). During our study, nesting occurred most often in June and July, which coincides with peak nesting throughout the southeastern United States (Weishampel et al. 2004; Antworth et al. 2006). Emergence success within our study site also appears to be similar to that reported on other nesting beaches in the southeastern United States including in Brevard County, Florida, and along the southwest Florida coast (Ehrhart et al. 2003; Tucker et al. 2009). Emergence success is often affected by sand characteristics (Fadini et al. 2011) such as hardness (Kudo et al. 2001) and mean particle diameter (Mortimer 1990). Clutch size fell within the range reported for other studies (Hedges 2007; EAI 2008). Because clutch size has been linked to turtle size, this suggests turtles nesting in the northern Gulf are of similar size to those nesting throughout the southeastern United States (Frazer and Richardson 1985; Hays and Speakman 1993; Broderick and Godley 1996). Our study site is a natural beach that has never been nourished, therefore sand characteristics may be optimal for successful hatchling incubation and emergence. Finally, because incubation duration is determined by incubation temperatures, incubation duration at our study site appeared more similar to durations reported for cooler, northern nesting beaches such as those in North Carolina (Rush 2003) and Georgia (Dodd and Mackinnon 2008). Incubation durations on warmer beaches, such as those in southwestern Florida (Tucker et al. 2009) and the Everglades, Florida (Davis and Whiting 1977), appear to be longer.

Although some aspects of loggerhead reproduction appear similar between the northern Gulf of Mexico and other nesting groups in the southeastern United States population, nesting success appeared to be lower than that reported for many other beaches in the southeastern United States, including those in Georgia and Brevard County, Florida (Hawkes et al. 2005; Antworth et al. 2006; Brock et al. 2009; Tucker et al. 2009; Witherington et al. 2009). Low nesting success indicates increased false crawling behavior. False crawling behavior has been linked to activities such as turtle walks (Johnson et al. 1996), artificial lighting (Stoneburner and Richardson 1981), and changes in beach substrate due to nourishment (Raymond 1984). However because the beach along CSB is uninhabited and has never been nourished, false crawling behavior at our study site may not be attributed to direct anthropogenic causes. Turtles attempting to nest may also be disturbed by predators, such as coyotes and raccoons, thereby causing them to false-crawl (Shoop et al. 1985). From 1994 to 1997, coyote depredation of turtle nests on CSB was fairly common and resulted in destruction of approximately 20%–40% of nests each year. However in 1998, consistent predator control activities began on Eglin Air Force Base and within nearby SJSP, which has since reduced predation of turtle nests at our study site to a handful (~ 5–10) of eggs taken each year by ghost crabs (*Ocypode quadrata*), fish crows (*Corvus ossifragus*), and fire ants (*Solenopsis invicta*; Parris et al. 2002). Because nesting success did not improve following initiation of predator control, it indicates that predators are not causing turtles to false-crawl on CSB.

It has been suggested that turtles use cues located both offshore and onshore to identify nesting sites. Offshore factors include the presence of reefs and rocks (Hughes 1974), magnetic fields (Lohmann and Lohmann 1996), and olfactory cues (Carr 1972), whereas onshore cues such as temperature, salinity, slope, moisture, width, and sand type have been suggested to influence nest site selection (Johannes and Rimmer 1984; Provancha and Ehrhart 1987; Kikukawa et al. 1996; Garmestani et al. 2000; Wood and Bjorndal 2000). Our study site on CSB is located on a highly dynamic cape spit. This area experiences one of the greatest rates of natural erosion in Florida (Lamont and Carthy 2007). Perhaps the dynamic nature of the nearshore environment off CSB blurs cues used in nest site selection. Lack of offshore cues may result in a greater number of false crawls if turtles must come onshore to assess site selection.

Quantitative demographic analyses require large amounts of data on life-stage–specific parameters such as survival, growth and fertility, migration, and on the effects of environmental variability on these parameters (Groom and Pascual 1998; Heppel et al. 2003). Loggerhead turtles nesting in the northern Gulf of Mexico experience different environmental variables than those that nest along the Atlantic coast, therefore the strategies they use to optimize reproduction most likely differ. Results from our study demonstrate that parameters among nesting groups within one population can vary greatly (Wallace et al. 2010), which highlights the importance of gathering life-history parameters for development of accurate population models and effective conservation strategies. This is particularly important for this group of loggerhead turtles that, due to large declines in nest abundance and decreasing nest success, requires immediate management and conservation action.

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LITERATURE CITED

ALAM, S.K. AND BRIM, M.S. 2000. Organochlorine, PCB, PAH, and metal concentrations in eggs of loggerhead sea turtles (*Caretta caretta*) from northwest Florida, USA. Journal of Environmental Science and Health B 35:705–724.

ANTWORTH, R.L., PIKE, D.A., AND STINER, J.C. 2006. Nesting ecology, current status, and conservation of sea turtles on an uninhabited beach in Florida, USA. Biological Conservation 130:10–15.

BAGLEY, D.A., UONG, L.T., DANNER, A.B., HIRAMA, S., WICK, L.A., AND EHRHART, L.M. 1998. Marine turtle nesting at the Archie Carr National Wildlife Refuge in 1997. In: Abreu-Grobois, F.A., Briseno-Duenas, R., Marquez, R., and Sarti, L. (Eds.). Proceedings of the Eighteenth International Sea Turtle Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-436, US Department of Commerce.

BJORNDAL, K.A., BOWEN, B.W., CHALOUPKA, M., CROWDER, L.B., HEPPELL, S.S., JONES, C.M., LUTCAVAGE, M.E., POLICANSKY, D., SOLOW, A.R., AND WITHERINGTON, B.E. 2011. From crisis to opportunity: better science needed for restoration in the Gulf of Mexico. Science 331:537–538.

BOLTEN, A.B., CROWDER, L.B., DODD, M.G., MACPHERSON, S.L., MUSICK, J.A., SCHROEDER, B.A., WITHERINGTON, B.A., LONG, K.J., AND SNOVER, M.L. 2011. Quantifying multiple threats to endangered species: an example from loggerhead sea turtles. Frontiers in Ecology and the Environment 9:295–301.

BROCK, K.A., REECE, J.S., AND EHRHART, L.M. 2009. The effects of artificial beach nourishment on marine turtles: differences between loggerhead and green turtles. Restoration Ecology 17:297–307.

BRODERICK, A.C. AND GODLEY, B.J. 1996. Population and nesting ecology of the green turtle, *Chelonia mydas*, and the loggerhead turtle, *Caretta caretta*, in northern Cyprus. Zoology in the Middle East 23:27–46.

CARR, A. 1972. The case for long-range chemoreceptive piloting in Chelonia. NASA SP-262, pp. 469–483.

CROUSE, D.T., CROWDER, L.B., AND CASWELL, H. 1987. A stage based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.

DAVIS, G.E. AND WHITING, M.C. 1977. Loggerhead sea turtle nesting in Everglades National Park, Florida, USA. Herpetelogica 33:18–28.

DODD, M.G. 1988. Synopsis of the biological data on the loggerhead sea turtle: *Caretta caretta* (Linnaeus, 1758). US Department of Interior, US Fish and Wildlife Service.

Dodd, M.G. and Mackinnon, A.H. 2008. Loggerhead turtle nesting in Georgia, 2008. Annual report submitted to US Fish and Wildlife Service for grant E-5-Amendment 8, Coordination of loggerhead sea turtle nest protection in Georgia.

EAI (Ecological Associates, Inc.) 2008. Sea turtle monitoring and studies. Tequesta, Palm Beach, County, Florida. Results of 2008 nesting season. Final report for Palm Beach County, FL Department of Environmental Resources Management.

Ehrhart, L.M., Bagley, D.A., and Redfoot, W.E. 2003. Loggerhead turtles in the Atlantic Ocean: geographic distribution, abundance, and population status. In: Bolten, A.B. and Witherington, B.E. (Eds.). Loggerhead Sea Turtles. Washington, DC: Smithsonian Books, pp. 157–174.

Encalada, S.E., Bjorndal, K.A., Bolten, A.B., Zurita, J.C., Schroeder, B., Possardt, E., Sears, C.J., and Bowen, B.W. 1998. Population structure of loggerhead turtle (*Caretta caretta*) nesting colonies in the Atlantic and Mediterranean as inferred from mitochondrial DNA control region sequences. Marine Biology 130:567–575.

Fadini, L.S., Silva, A.G., and Ferreira-Junior, P.D. 2011. Sedimentary characteristics and their effects on hatching success and incubation duration of *Caretta caretta* (Testudines: Cheloniidae) in Espirito Santo, Brazil. Zoologia 28:312–320.

Florida Fish and Wildlife Conservation Commission (FWC). 2007. Marine Turtle Guidelines. Available at: www.myfwc.com/media/418106/seaturtle_guidelines.pdf.

Frazer, N.B. 1983. Survivorship of adult female loggerhead sea turtles, *Caretta carreta*, nesting on Little Cumberland Island, Georgia, USA. Herpetologica 39:436–447.

Frazer, N.B. and Richardson, J.I. 1985. Annual variation in clutch size and frequency for loggerhead turtles, *Caretta caretta*, nesting at Little Cumberland Island, Georgia, USA. Herpetologica 41:246–251.

Garmestani, A.S., Percival, H.F., Portier, K.M., and Rice, K.G. 2000. Nest-site selection by the loggerhead sea turtle in Florida's Ten Thousand Islands. Journal of Herpetology 34:504–510.

Groom, M.J. and Pascual, M.A. 1998. The analysis of population persistence: an outlook on the practice of viability analysis. In: Fiedler, P.L. and Karciva, P.M. (Eds.). Conservation Biology for the Coming Decade. Second edition. New York: Chapman and Hall, pp. 4–27.

Hawkes, L.A. 2007. Ecology and conservation of the loggerhead sea turtle (*Caretta caretta*). PhD Dissertation, University of Exeter, Exeter, United Kingdom.

Hawkes, L.A., Broderick, A.C., Godfrey, M.H., and Godley, B.J. 2005. Status of nesting loggerhead turtles *Caretta caretta* at Bald Head Island (North Carolina, USA) after 24 years of intensive monitoring and conservation. Oryx 39:65–72.

Hawkes, L.A., Broderick, A.C., Godley, M.H., and Godley, B.J. 2009. Climate change and marine turtles. Endangered Species Research 7:137–154.

Hays, G.C. and Speakman, J.R. 1993. Nest placement by loggerhead turtles, *Caretta caretta*. Animal Behavior 45:47–53.

Hedges, M.E. 2007. Development and application of a multistate model to the northern subpopulation of loggerhead sea turtles. MS Thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Heppell, S.S., Caswell, H., and Crowder, L.B. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Heppell, S.S., Crowder, L.B., Crouse, D.T., Epperly, S.P., and Frazer, N.B. 2003. Population models for the Atlantic loggerhead. In: Bolten, A.B. and Witherington, B.E. (Eds.). Loggerhead Sea Turtles. Washington, DC: Smithsonian Books, pp. 255–253.

Hughes, G.R. 1974. The sea turtles of southeast Africa. 1. Status, morphology and distribution. Republic of South Africa Oceanographic Research Institute, Investigation Report 35.

Johannes, R.E. and Rimmer, D.W. 1984. Some distinguishing characteristics of nesting beaches of the green turtles, *Chelonia mydas* on North West Cape Peninsula, Western Australia. Marine Biology 83:149–154.

Johnson, S.A., Bjorndal, K.A., and Bolten, A.B. 1996. Effects of organized turtle watches on loggerhead (*Caretta caretta*) nesting behavior and hatchling production in Florida. Conservation Biology 10:570–577.

Kikukawa, A., Kamezaki, N., Hirate, K., and Ota, H. 1996. Distribution of nesting sites of sea turtles in Okinawajima and adjacent islands of the Central Ryukyus, Japan. Chelonian Conservation and Biology 2:99–101.

Kudo, H., Murakami, A., and Watanabe, S. 2001. Effects of sand hardness and human beach use on emergence success of loggerhead sea turtles on Yakushima Island, Japan. Chelonian Conservation and Biology 4:695–696.

Lamont, M.M. and Carthy, R.R. 2007. Response of nesting sea turtles to barrier island dynamics. Chelonian Conservation and Biology 6:206–212.

Lohmann, K.J. and Lohmann, C.M.F. 1996. Orientation and open-sea navigation in sea turtles. Journal of Experimental Biology 199:73–81.

Mortimer, J.A. 1990. The influence of beach sand characteristics on the nesting behavior and clutch survival of green turtles (*Chelonia mydas*). Copeia 1990:802–817

NMFS (National Marine Fisheries Service). 2008. Estimated takes of sea turtles in the bottom longline portion of the Gulf of Mexico reef fish fishery July 2006 through 2007 based on observer data. NMFS Southeast Fisheries Science Center Contribution PRD-07/08-15, September 2008. 21 p.

NMFS and USFWS (National Marine Fisheries Service and US Fish and Wildlife Service). 2010. Recovery plan for the Northwest Atlantic population of the loggerhead sea turtle (*Caretta caretta*). Second revision. National Marine Fisheries Service.

Parris, L.B., Lamont, M.M., and Carthy, R.R. 2002. Increased incidence of red imported fire ant (Hymenoptera: Formicidae) presence in loggerhead sea turtle (Testudines: Cheloniidae) nests and observations of hatchling mortality. Florida Entomologist 85:514–517.

Provancha, J.A. and Ehrhart, L.M. 1987. Sea turtle nesting trends at Kennedy Space Center and Cape Canaveral Air Force Station, Florida, and relationships with factors influencing nest site selection. In: Witzell, W.N. (Ed.). Ecology of East Florida Sea Turtles: Proceedings of the Cape Canaveral, Florida Sea Turtle Workshop Miami, Florida, 26–27 February 1985, NOAA Technical Report NMFS 53, pp. 33–44.

Raymond, P.W. 1984. The effects of beach restoration on marine turtle nesting in south Brevard County, Florida. MS Thesis, University of Central Florida, Orlando, FL.

Rush, M.P. 2003. An evaluation of nest relocation as a loggerhead sea turtle (*Caretta caretta*) management technique in North Carolina. MS Thesis, Duke University, Durham, NC.

Shamblin, B.M., Dodd, M.G., Bagley, D.A., Ehrhart, L.M., Tucker, A.D., Johnson, C., Carthy, R.R., Scarpino, R.A., McMichael E., Addison, D.S., Williams, K.L., Frick, M.G., Ouellette, S., Meylan, A.B., Godfrey, M.H., Murphy, S.R., and Nairn, C.J. 2011. Genetic structure of the southeastern United States loggerhead turtle nesting aggregation: evidence of additional structure within the peninsular Florida recovery unit. Marine Biology 158:571–587.

Shoop, C.R., Ruckdeschel, C.A., and Thompson, N.B. 1985. Sea turtles in the southeast United States: nesting activity as derived from aerial and ground surveys, 1982. Herpetologica 41:252–259.

Sobin, J.M. 2008. Diving behavior of female loggerhead turtles (*Caretta caretta*) during their internesting interval and an evaluation of the risk of boat strikes. MS Thesis, Duke University, Durham, NC.

Sodhi, N.S., Brook, B.W., and Bradshaw, C.J.A. 2009. Causes and consequences of species extinctions. In: Levin, S.A., Carpenter, S.R., Godfray, H.C.J., Kinzig, A.P., Loreau, M., Losos, J.B., Walker, B., and Wilcove, D.S. (Eds.). The Princeton Guide to Ecology. Princeton, NJ: Princeton University Press, pp. 514–520.

Stoneburner, D.L. and Richardson, J.I. 1981. Observations on the role of temperature in loggerhead turtle nest site selection. Copeia 1981:238–241.

Tucker, A.D., Welsh, R., Mazzarella, K., Garrett, K., and Hirsch, S. 2009. Sea turtle monitoring, nest evaluation and protection measures for Casey Key 2009. Mote Marine Laboratory, Technical Report No. 1434.

TEWG (Turtle Expert Working Group). 2009. An assessment of the loggerhead turtle population in the western North Atlantic. NOAA Technical Memorandum NMFS-SEFSC -575.

USFWS and NMFS (US Fish and Wildlife Service and National Marine Fisheries Service). 2010. Endangered and threatened species; proposed listing of nine distinct population segments of loggerhead sea turtles as endangered or threatened. US Federal Register 75:12598–12656.

USFWS, NMFS (US Fish and Wildlife Service & National Marine Fisheries Service). 2011. Endangered and threatened Species: determination of nine distinct population segments of loggerhead sea turtles as endangered or threatened. US Federal Register 76:58868–58952.

Wallace, B.P., Dimatteo, A.D., Hurley, B.J., Finkbeiner, E.M., Bolten, A.B., et al. 2010. Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLoS ONE 5: e15465.

Weishampel, J.F., Bagley, D.A., and Ehrhart, L.M. 2004. Earlier nesting by loggerhead sea turtles following sea surface warming. Global Change Biology 10:1424–1427.

Witherington, B.E., Kubilis, P., Brost, B., and Meylan, A. 2009. Decreasing annual nest counts in a globally important loggerhead sea turtle population. Ecological Applications 19: 30–54.

Wood, D.W. and Bjorndal, K.A. 2000. Relation of temperature, moisture, salinity, and slope to nest site selection in loggerhead sea turtles. Copeia 2000:119–128.

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