Assessment Of The Probability Of Loggerhead Sea Turtle (Caretta caretta) Recovery In The Northwest Atlantic Ocean Within 50 Years Of Federal And State Protection In The US

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Assessment of the probability of loggerhead sea turtle (*Caretta caretta*) recovery in the Northwest Atlantic Ocean within 50 years of federal and state protection in the U.S.

by

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Dedication

Under the radiance of a “Super moon” on May 5th, 2012, the shoreline at Melbourne Beach, FL was illuminated for what seemed like miles in either direction from our vantage point. My compadre (a six-year old named Bria) and I anxiously anticipated the amphibious assault that we knew was imminent. Despite our intense scanning, the loggerhead sea turtles appeared like magic; one instant nothing but wet sand for as far as the eye could see, and then ‘poof’, an ambling rock-like silhouette at the water’s edge. “Down there!” she exclaimed with elfin grace as we made our way down the beach.

With good friends who are authorized to interact with sea turtles nesting in the Archie Carr National Wildlife Refuge we appreciated how tough mother sea turtles must be. Eventually, though, a turtle kicking up sand and slowly depositing eggs while being harassed by mosquitos and fire ants paled in comparison to nature’s scavenger hunt that was unfolding before us: more sea turtles crawling ashore! On this night, la luna made it exceptionally easy to spot them, and more discoveries ensued. After about the eighth encounter, a dancing Bria exuberantly exclaimed, “This is the best day ever!” I smiled and nodded my head in agreement as I thought about the circuitous path that led me to this place, as well as imagined Bria returning with her brother, Caden, their mom, Michelle, and their own children in 30+ years when the 2012 cohort matured. This dissertation is dedicated to that memory; the prospect of creating a similar memory with my nephew, Noah, and niece, Sofia; and the hope that future sea turtle generations will continue to exhilarate future human generations for many more millennia.
Acknowledgements

“Two roads diverged in a wood, and I-
I took the one less traveled by,
And that has made all the difference.”

- Robert Frost, 1874–1963

I first read this poem in a high school English class and thoroughly enjoyed it. A few years later I was reminded of it when I matriculated at VMI and voluntarily forsake creature comforts and the contemporary college lifestyle to increase the probability of commissioning as an officer in the U.S. Navy, a career path that I ultimately declined and elected instead to become a marine scientist. Apparently I am a glutton for punishment because I have spent the past three years attempting to complete a Ph.D. program in Columbia, SC while managing four projects as a wildlife biologist with the SCDNR in Charleston, SC. However, now that the end of this experience is in sight, I reflect on it fondly and agree, again, that I followed a calling that has made a great deal of difference.

First and foremost, I wish to thank my committee for the strengths that they contributed that ultimately shaped the direction of this dissertation. As one of the original cast members of the regional sea turtle trawl survey in 2000, I’ve had a long-standing professional relationship with two of them for many years: Dr. David Owens taught me how to collect blood from sea turtles on my first day of work with SCDNR on 17 May 2000, and my interactions with my future major professor, Dr. Joe Quattro, began a few years later when my sea turtle trawl survey responsibilities increased.
Consequently, both of these gentlemen knew my scientific strengths as well as where improvements were most needed; as such, they challenged me accordingly to think more broadly and, when appropriate, with less conviction, for which I am grateful.

Conversely, my professional relationship with Dr.’s David Wethey, Ryan Rykaczewski, and Roger Sawyer is a direct result of acceptance into the Integrative Biology Program, and I could not have asked for better committee members. In addition to stimulating invigorating discussions in his Theoretical Ecology course, I thank David Wethey for regularly meeting with me to discuss preliminary analyses and contemplate additional analytical approaches, which benefited all of my dissertation chapters. I first approached Ryan Rykaczewski about serving on my committee given his interest in climate and trophic dynamics, and when I learned that he grew up in the land of loggerhead sea turtles it sealed the deal. In addition to his environmental background, Ryan refined my approach to management and analysis of large data sets. In spring 2015 we called an audible and added Roger Sawyer to the committee, and my only regret from that decision was that it didn’t occur sooner. As with all of my committee members, I discovered immediately that I thoroughly enjoyed talking science with Roger, and his research interests in developmental biology especially enhanced the analysis of long-term climate data in the last dissertation chapter.

Given my commuting approach to being a full-time student, my interactions with fellow graduate students were largely restricted to my cohorts in the Quattro lab and discussing publications in Theoretical Ecology. In the Quattro lab, I am grateful to Mark Roberts, who annually manages the process of assigning genetic haplotypes to sea turtle blood samples collected in the coastal trawl survey. Also in the Quattro Lab, I thank
Mohammad Al Jazza and Kate Levasseur for mental breaks to talk turtles and savor Arabian tea as time permitted during my stints at USC. Similarly, I thank Herrick Brown (Wethey Lab, and also a fellow SCDNR employee); Rachel Steward (Boggs lab); Brian Grieve (Rykaczewski lab); and Ben Belgrad, Eilea Knotts, and Zac Cannizzo (Griffin lab) for in-depth discussions in Theoretical Ecology that directly and indirectly helped shape the analytical development of this dissertation. Lastly, I thank Pat Earley, Peggy Breeland, and Amanda Polson-Zeigler for administrative support.

On the coast, I’m grateful to a host of folks who were invaluable in assuring me the best possible chance for success in this endeavor. First and foremost, I thank my supervisor, Dr. Michael Denson, who encouraged me to pursue this path; in all honesty it wasn’t even on my radar after having declined an offer to USC in 2004 and having an already overflowing plate of responsibilities. I am confident that the analyses contained herein would not be as strong (and in several cases wouldn’t even exist) without having enrolled in this program and subsequent interactions that ensued, so thank you for planting that seed. As that seed grew, my ability to multi-task diminished, particularly with field work, and I had to learn how to effectively delegate responsibility; thank you to Jeff Schwenter, Ellen Waldrop, Julie Dingle, and Paulette Mikell for rising to occasion. Jeff Schwenter also served as a great springboard for ideas as the analyses unfolded as well as conducted the testosterone radioimmunoassay to sex sea turtles captured in this survey, a vital role that Gaëlle Blanvillain and A. Michelle Lee also deserve thanks for regarding samples collected prior to 2010. I also thank Dawn Glasgow, a fellow SCDNR employee and USC IB program compatriot, for showing me the ropes and otherwise providing guidance as I navigated my way.
On the turtle trawl survey, I thank Captains Lindsey Parker, Richard Puterbaugh, and Marty Higgins of Brunswick, GA for their perspectives on various fisheries issues as a result of working the waters of the southeast U.S. for the past 40 years. I also thank Julia Byrd (SAFMC) and Dr. Al Segars, D.V.M., for their continued support to this study despite more pressing responsibilities and time demands. Numerous seasonal staff and vet students from multiple universities collected and processed sea turtle blood samples that were ultimately sent off to numerous laboratories for a plethora of analyses in addition to genetics (USC) and testosterone radioimmunoassay (CofC).

On the home front, I thank friends, family, and neighbors for being supportive and understanding that my time hasn’t really been my own for the past several years. And of course, I thank my furry children for providing a coping mechanism during what proved to be the most tumultuous of my life thus far, made worse by the loss of dear “Sparky”.

Federal funding for the trawl survey was provided by five grants administered through the “Southeast Sea Turtle” appropriation to the NMFS Southeast Regional Office (NA97FL0375; NA07FL0499; NA03NMF4720281; NA08NMF4720502; and NA13NMF4720182), and I thank Jeff Brown, Dennis Klemm, and David Bernhardt for their unwavering support (as well as Eileen Heyward, SCDNR, for grant management). Dr.’s Sherry Epperly and Chris Sasso (NMFS Southeast Fisheries Science Center) provided technical review of the trawl survey during the first 16 years of operation, and I look forward to continued design dialogue in the future. Sea turtle data collection was authorized under Section 10(A)(1)(a) permits 1245, 1540, and 15566; Florida Marine Turtle Permits 140 and 163); and Georgia Scientific Collection permits 1163 and 21303.
Abstract

Systematic implementation of sea turtle conservation measures have occurred in the U.S. since the 1970’s. As such, this dissertation assessed the probability that loggerhead sea turtles (*Caretta caretta*) in the NW Atlantic will meet or exceed recovery criteria in the minimum timeframe (i.e., 50 years) specified by the Recovery Plan. Mathematical modeling (Chapter 1) of a theoretical population resembling an important nesting assemblage in a stochastic environment for 200 years revealed broad (<20k to >106k) fluctuation in annual nest counts without extinction, as well as strong contemporary environmental influence on annual nest counts. Modeling also substantiated the importance of monitoring the relative abundance of juvenile females as the most reliable forecasting metric for nest count trajectories up to two decades into the future. In-water monitoring of loggerhead sea turtle demographic structure at a coastal foraging ground between South Carolina and north Florida suggests a shift away from a stable size distribution during 2000–2015, but which may eventually be tempered by the relative abundance of cohorts hatched near the turn of the last century (Chapter 2). The high relative abundance of juvenile females captured in this coastal trawl survey bodes well for sustained annual nest counts in the coming decade (Chapter 3). Slightly elevated female frequency among the smallest loggerhead sea turtles captured is consistent with a warming climate, but a 100-year association with the Atlantic Multi-decadal Oscillation suggests that reduced female production should begin to occur in the coming decade.
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List of Abbreviations

AMO……………………………………………………Atlantic Multi-decadal Oscillation
ANOVA…………………………………………………………Analysis of Variance
CI…………………………………………………………….Confidence Interval
CV………………………………………………………………Co-efficient of Variation
DPS………………………………………………………………Distinct Population Segment
ERA-20C……………….European Reconstruction Analysis, 20th Century (1900–2010)
ESA…….Endangered Species Act (of 1973; all U.S. sea turtles protected by it since 1978)
JRA-55………………….Japanese Reconstruction Analysis, 55 years (1958–2013)
NAO…………………………………………………………….North Atlantic Oscillation
NMFS…………………………………………………..National Marine Fisheries Service
NOAA…………………………………………….National Oceanic and Atmospheric Administration
NRC………………………………………………………..National Resources Council
PRU…………………………………………………Peninsular (Florida) Recovery Unit
SCDNR…………………………..South Carolina Department of Natural Resources
SCLmin…..Straight-line Carapace Length, minimum (nuchal notch to supracaudal notch)
SE………………………………………………………………Standard Error
SEMARNAT……………….Secretaría de Medio Ambiente y Recursos Naturales
USFWS…………………………………………..United States Fish and Wildlife Service
TED……………………………………………………..Turtle Excluder Device
Introduction

“In all things of nature there is something of the marvelous” (Aristotle, 384 to 322 B.C.)

Appreciation of the natural world spans civilizations (Schaefer, 2001); thus, it is reasonable to presume that a desire to protect such splendors has also existed for as long. However, given a genetic basis for diverse human personality (Nettle, 2006), it is also reasonable to presume that not all individuals in societies share this viewpoint. As such, philosophical differences among modern approaches to ecological stewardship are likely rooted in an ancient dilemma that has become more kinetic with exponential human population growth and subsequent resource competition (Holdren and Ehrlich, 1974).

The contemporary protectionist playbook for ensuring species diversity contains three central themes that differ principally in their degree of anthropogenic influence. Non-intervention promotes eliminating all anthropogenic interaction and letting nature take its course, for example, allowing barrier islands to migrate (Kaufman and Pilkey, 1983) vs. stabilizing beach dunes (Van der Meuler and Salman, 1996), as the latter tactic embodies preservation theory. Conservation is a broad term that includes management of anthropogenic disturbance as well as efforts to attempt to control species structure. Reduction of anthropogenic disturbance can be implemented on large scales to protect species diversity, for example, through the use of no-take marine reserves (Alcala and Russ, 2006) or by targeting the wanton mortality of certain species (Gilman et al., 2007). Conservation strategies to protect diversity by modifying species structure include species introductions (Gibbs et al., 2008), culling individuals (Takatsuki, 2009), or
otherwise altering reproductive outputs (Kirkpatrick and Turner, 1985). Culling restrictions in the absence of a perceived overpopulation problem are designed to harvest individuals at levels deemed sustainable for consumptive use, for example, by commercial (Martinet et al., 2007) and recreational (McPhee et al., 2002) fisheries.

In accordance with their complexity, a gradient also exists with regards to the ability to assess success and failure among non-intervention, preservation, and conservation strategies. Because non-intervention has no expected outcome, failure can only occur through the act of intervention. Preservation success is achieved by simple retention of the status quo, regardless of whether the outcome achieved a tangible ecological objective. Defining, and in turn measuring, success or failure of a conservation action is multi-faceted, but depends principally on objective perspective (Coen and Luckenbach, 2000; Brooks et al., 2006). The duration and extent of monitoring data (Brooks et al., 2006) is also of great importance, particularly relative to species generation times. Statistically, the size of the impacted population is also a crucial consideration, given that gain or loss of individuals in small populations has a disproportionate effect relative to large populations. Small populations, especially those that exist in a fragmented state, are also more susceptible to reduced genetic diversity and potentially, extinction (Wilcox and Murphy, 1985). For these reasons, long-lived, slow-growing, and highly migratory species such as sea turtles require high annual survival rates (Crouse et al., 1987; Arendt et al., 2013) for their continued existence.

Globally, seven sea turtle species remain from what was a large and diverse evolutionary radiation in the sub-Order Cryptodira (Meylan and Meylan, 1999). The plight of all sea turtle species involves common demise mechanisms as a result of
disturbance to and/or destruction of nesting beach habitat (Witherington, 1999); harvesting sea turtles and/or eggs for consumption (Witzell, 1994); the sale of sea turtle products (Mancini and Koch, 2009); and incidental mortality in a plethora of fisheries (Wallace et al., 2010a). With the exception of the flatback sea turtle (*Natator depressus*) which only occurs in northern Australia and for which sufficient population data are lacking, all other sea turtle species are listed as Vulnerable (2), Endangered (2), or Critically Endangered (2) by the IUCN Red List of Threatened Species (IUCN, 2013). In U.S. waters, all sea turtle species are federally protected under the 1978 Amendment to the U.S. Endangered Species Act (ESA) of 1973. Loggerhead sea turtles (*Caretta caretta*) remain managed as a threatened species under the ESA¹. Green sea turtles (*Chelonia mydas*) were originally managed as a threatened species since throughout the Atlantic Ocean except for breeding populations in Florida that was managed as endangered (NMFS and USFWS, 1991); however, the conservation status of this breeding aggregation was also changed to threatened in 2016 (81 FR 20057). Kemp’s ridley sea turtles (*Lepidochelys kempii*) have been managed as an endangered species since 1970; however, the second revision to the international recovery plan for this species anticipates that a down-listing (to threatened) nesting benchmark may be achieved by 2015 (NMFS et al., 2011). Leatherback sea turtles (*Dermochelys coriacea*) and hawksbill sea turtles (*Eretmochelys imbricata*) are both globally managed as endangered throughout their range (NMFS and USFWS, 1992, 1993).

Of the five sea turtle species common to the Northwest (NW) Atlantic Ocean, more is known about loggerhead sea turtles than any other species (Bolten, 2003a). The second largest loggerhead sea turtle rookery in the world occurs in Florida (NMFS and USFWS 2008), in close proximity to a large and well-studied spring breeding aggregation (Henwood, 1987; Arendt et al., 2012a). Roughly a month after the onset of mating season, female loggerhead sea turtles begin moving ashore to dig out chambers and deposit eggs in clutches of ~110 eggs, a process that will be repeated several times during a nearly two-month nesting window (Miller et al., 2003). Sex of sea turtles is determined by the nest chamber temperature, a reflection of air temperature and moisture content, during the nearly two-month incubation period (Carthy et al., 2003); cooler conditions favor male production, and a narrow (i.e., 5°C) critical temperature range exists for survival (Yntema and Mrosovsky, 1980). After nest emergence, hatchlings crawl frenetically to the water’s edge and then swim rapidly offshore until they reach down-welling lines where they seek cover in Sargassum mats (Witherington, 2002), and will ultimately be transported to the Northeast (NE) Atlantic Ocean and develop in the oceanic zone for the next decade (Bolten, 2003a,b). Upon returning to neritic habitats in the NW Atlantic Ocean, juvenile loggerheads forage in estuarine and nearshore coastal waters at water temperatures >20°C, but emigrate offshore, alongshore, and/or return to oceanic waters to over-winter (McClellan and Read, 2007; Mansfield et al., 2009; Arendt et al., 2012b). Growth rate data suggest that this annual cycle is repeated for nearly two decades before reaching sexual maturity (Braun-McNeill et al., 2008; Avens et al. 2013), after which the same seasonal foraging grounds likely continue to be utilized as adults.
given strong site fidelity exhibited by both juveniles (Avens et al., 2003; Arendt et al., 2012b,c) and adults (Hawkes et al., 2011; Arendt et al., 2012d; Ceriani et al. 2012).

A high degree of synchrony in temporal-spatial distribution patterns, especially when aggregation behavior occurs, increases a species’ vulnerability to population perturbations; however, management efforts that protect individuals while they inhabit vulnerable areas are also conducive to effective conservation (Griffin et al., 2013). In addition to protecting terrestrial nests during the past 38 years since sea turtles were added to the ESA, a suite of protective actions were systematically implemented which should have improved annual sea turtle survival rates at sea. The 1960’s were associated with “an even more aggressive era of foreign factory trawling near the U.S. coasts”\(^2\); however, by 1976, such practices were outlawed within 200 nm of the U.S. coastline as a result of the passage of the Magnuson Fishery Conservation Act. Shortly thereafter, attention was focused on improving sea turtle survival in domestic fisheries, with the shrimp trawl fishery in the southeast U.S. receiving the most scrutiny (NRC, 1990). Following a decade of deliberation and design evaluation, turtle excluder device (TED) regulations began being enforced in 1989, but more than another decade elapsed before the large contemporary style TED was required in 2003\(^3\). During the same period, a variety of modifications to longline fishing gear were evaluated to reduce encounters and/or increase survival rates for incidentally captured sea turtles and other protected


species (Watson and Kerstetter, 2006). Efforts to reduce sea turtle mortality in other coastal fisheries have also been recently emphasized (Murray, 2009, 2011).

The duration of time that this population has received protection is approaching the 50-year minimum in which recovery can be assessed (NMFS and USFWS, 2008). The period of dedicated protection of loggerhead sea turtles across all life history stages and most habitats encountered in the North Atlantic Ocean is slightly longer than most estimates of the age required for this species to reach maturity (Conant et al., 2009), but a decade less than the most conservative estimate of age to maturity (Scott et al., 2012). As such, if anthropogenic activities were responsible for the historical reduction of this species in the North Atlantic Ocean, then it is reasonable to presume that efforts to diminish anthropogenic impacts during the past 38 years should also produce discernible improvements in population metrics, as predicted >20 years ago by Crowder et al. (1994). Indeed, research catch rates of juvenile loggerheads in estuarine (Ehrhart et al., 2007; Epperly et al., 2007) and coastal (Arendt et al., 2012e,f) waters have increased since the 1990s. In 2012, annual nest counts by loggerhead sea turtles at Florida index nesting beach survey (INBS) beaches were comparable to levels observed in 1998 (Arendt et al., 2013), after which a 41% decline was observed through 2007 (Witherington et al., 2009). As such, loggerhead sea turtles associated with the NW Atlantic Distinct Population Segment (DPS) appear to have turned a corner and are on the slow road to recovery (Arendt et al., 2013; Griffin et al., 2013). However, without suitable demographic structure to sustain future nesting (Heppell, 1998; NRC, 2010), recent increases in annual nest counts and in-water catch rates may only represent an ephemeral phenomenon.
The importance of demographic structure for the continued existence of loggerhead sea turtles in the NW Atlantic is underscored by the observation that remigrants comprise ~90% of stable nesting assemblages (Arendt et al., 2013). As such, annual neophyte recruitment into an assemblage must offset annual remigrant attrition to prevent nesting assemblage decline. Therefore, this dissertation begins by establishing connectivity between annual nest counts and demographic structure, followed by an evaluation of temporal change in demographic structure for loggerhead sea turtles captured by trawling at an important coastal foraging ground since 2000. In Chapter 1, the relative importance of a suite of parameters on variability in annual nest counts is modeled, with emphasis on identifying the most likely mechanism(s) to explain the pattern observed for loggerhead sea turtle annual nest counts at Florida INBS beaches during 1989–2012 (Arendt et al., 2013). In Chapter 2, interactions between size, sex, and genetic haplotype distributions are evaluated in the context of assessing whether stable to increasing in-water catch rates reported for loggerhead sea turtles at this foraging ground (Arendt et al., 2012f) are predominantly driven by individual vs. population growth. In Chapter 3, temporal variability in the percent of female loggerhead sea turtles captured on this foraging ground are evaluated to determine if observed trends reflect sampling design, environmentally-mediated sex determination (Standora and Spotila, 1985), and/or changes in demographic structure that are predicted to occur with continued climate warming (Hawkes et al., 2007; Fuentes et al., 2009, 2010, 2011; Laloë et al., 2016).
Chapter 1. Mathematical modeling suggestions that long-term stable oscillations in
demographic structure and contemporary climate exert the greatest influence on nest
count variability for loggerhead sea turtles in the NW Atlantic Ocean.

Introduction

The awareness of five mass extinction events over the past 540M years and concern that a sixth such event is underway fuel demands for increased conservation actions to preserve contemporary species diversity (Barnosky et al., 2011). Geological evidence suggesting anoxia as a root cause of the Permian/Triassic mass extinction event (Wignall and Hallam, 1992) illuminates the physiological fragility of biota across taxa, further increasing biodiversity fears consequent to state shifts in the global carbon budget (Houghton, 2007). However, stable oscillations in species assemblages are both possible (Garfinkel and Sack, 1964; Maynard-Smith, 1974) as well as known to occur across taxa and ecosystems (Dunbar, 1960; Allen et al., 1977; Turchin and Taylor, 1992). Bottom-up regulation is a recurring theme that governs stable oscillations across studies, which as noted by Garfinkel and Sack (1964), may produce ecological systems with “distinctive time cycle lengths, resistant to perturbation.” Nevertheless, because at any given period in time it is difficult to distinguish between stable converging vs. stable diverging oscillations (Maynard-Smith, 1974), especially for long-lived and slow-growth species with relatively low reproductive outputs, it is understandable why conservative management frameworks for such species are strongly encouraged (Musick, 1999).
Long-lived, late maturing, and slow growing species may also exhibit complex life histories, further warranting conservative management approaches; sea turtles are a prime example. All seven extant sea turtle species hatch from eggs laid in terrestrial nests; egress to the ocean; and then develop in oceanic and neritic habitats (with pelagic and benthic foraging in the latter) that span the scale of ocean basins for 20+ years before reaching sexual maturity (Bolten, 2003a,b). This life history schedule provides ample researcher access to nesting females and their immediate progeny, but makes it exponentially more difficult to monitor other life history stages. Although collection of terrestrial population data is relatively straight-forward, interpretation of population implications is challenging for several reasons. First, reproduction is energetically costly; thus, most individual female sea turtles do not nest annually (Carr and Carr, 1970) in order to increase maternal investment and, in turn, the probability of offspring survival (Bull and Shine, 1979), and/or due to environmental constraints (Wallace et al., 2006). Second, variable nesting schedules (to include clutch frequency within a nesting year) across individuals may contribute to large inter-annual differences in the number of nests observed, making inference to the population size of adult females difficult at best (Carr and Carr, 1970; Hays, 2000; Solow et al., 2002; Tucker, 2010). Third, stability in top predator populations requires a steady supply of immature animals (Garfinkel and Sack, 1964); thus, the ability to reliably forecast future nesting from this data source should decrease as projection duration increases. Conversely, large juvenile loggerhead sea turtles (Crouse et al., 1987; Crowder et al., 1994) are reported to be the most important age group for maintaining long-term population viability. Therefore, the greatest utility of annual nest counts may be for monitoring post-hoc trends that represent the
confounding effects of numerous events that preceded nesting decades earlier, rather than as a reference data set for predicting future nesting trends.

International efforts to conserve sea turtles increased in earnest in the late 1970’s, with initial emphasis on annual nest monitoring and protection heavily promoted across species and populations. Consequently, multi-decadal data sets are now available at well-studied beaches from which trends in sea turtle nesting can be compared. Increasing annual nest counts for green sea turtle nesting assemblages are reported in Hawaii (Balazs and Chaloupka, 2004) and the Caribbean Sea (Bjorndal et al., 1999; Troëng and Rankin, 2005), but concerns remain that contemporary counts are well short of historical nesting assemblage sizes (Chaloupka, 2001; McClenachan et al., 2006). Mixed trends are reported for leatherback sea turtles nesting at study sites within the Caribbean Sea (Troënig et al., 2004; Dutton et al., 2005), but annual nest count declines are reported in the Eastern Pacific (Sarti et al., 1996; Sarti Martinez et al., 2007) which are attributed to both anthropogenic (Sarti et al., 1996; Lewison et al., 2004) and climate-mediated effects (Wallace et al., 2006; Saba et al., 2008). Annual nest counts for loggerhead sea turtles in Florida, USA increased during the 1980’s and 1990’s (Witherington et al., 2009; Ehrhart et al., 2014), declined in the first decade of the 21st Century (Witherington et al., 2009), but the then sharply increased early in the second decade (Arendt et al., 2013). Temporal trends in nesting are not widely available for other loggerhead populations, but stable nest count trends were reported at the largest rookery in the Mediterranean in the 1980’s and 1990’s (Margaritoulis, 2005). Limited data also suggest an increase in annual nest counts in the Cape Verde Archipelago early in the 21st century (Marco et al., 2012), the third largest loggerhead rookery after the Florida assemblage.
Concurrent with recent increases in loggerhead sea turtle nest counts in the southeastern U.S., interest in identifying the underlying mechanism(s) responsible for this trend has also piqued, particularly given climate implications on future nesting success. Weishampel et al. (2004) observed a 10-day shift (to earlier nesting onset) over a 15-year period concurrent with warmer sea surface temperatures; in addition to providing a potential mechanism to maintain highly female-biased sex ratios determined during incubation (Mrosovsky, 1994), temporal variability in the nesting season may also contribute to temporal variability in annual nest counts. Van Houtan and Halley (2011) reported a strong correlation between a 31-year lag in the Atlantic Multi-decadal Oscillation (AMO) and annual nest counts, from which they proposed that climatic conditions during the first year of life greatly influence long-term nesting trends. Arendt et al. (2013) demonstrated equal contemporary importance for the historical AMO and the contemporary North Atlantic Oscillation (NAO), but both climate indices were retained in the best predictive model despite never establishing a causal mechanism for either association. Remigration interval and/or clutch frequency are largely dismissed as explanatory mechanisms given non-significant temporal variability (Frazer and Richardson, 1985; Witherington et al., 2009; Tucker, 2010; Ehrhart et al., 2014, Phillips et al., 2014) reported across studies for the NW Atlantic Loggerhead DPS (NMFS and USFWS, 2008). However, because these parameters occur in the year of nesting vs. decades prior, they should greatly influence annual nest counts (Carr and Carr, 1977; Hays, 2000; Solow et al., 2002). As such, their relegation to parameters of secondary importance may be influenced by a priori knowledge of the importance of juvenile survival (Crouse et al., 1987; Crowder et al., 1994); awareness of historical and continued
anthropogenic threats (NRC, 1990; Wallace et al., 2010a); and similarity in parabolic periodicity between historical perturbation followed by conservation and contemporary nest count trajectory (Witherington et al., 2009; Arendt et al., 2013).

The NW Atlantic Loggerhead DPS is one of nine global DPSs (Conant et al., 2009), but one of only four listed as “threatened” vs. “endangered” (Federal Register 76(184): 58868). Five regional nesting recovery units are recognized within this DPS, with the Florida Peninsular Recovery Unit (PRU) comprising more than 80% of annual nest counts for the DPS (NMFS and USFWS, 2008). Arendt et al. (2013) reported that the demographic recovery criteria of 106,100 annual nests for this DPS could be achieved by 2030 if (a) survival trajectories were consistent with 5% annual population growth that Conant et al. (2009) reported to be plausible and (b) assuming no variability in survival trajectories across cohorts. Given improbability that either of these assumptions is likely to occur and/or be sustainable, and that annual nest counts have rapidly increased at PRU beaches since 2008, the present study was initiated. The first objective was to examine the relative sensitivity of simple and complex population models to a suite of parameters, with emphasis on the ability of parameter manipulation to reproduce the level of inter-annual variability recorded at Florida Index Nesting Beach Survey (INBS) beaches since 1989 (Witherington et al., 2009; Arendt et al., 2013). The second objective was to model temporal changes in theoretical nesting assemblages over a 200-year period in highly stochastic environments, and to subsequently determine the relative value of using abundance changes in various age classes to predict future nest counts. The third objective was to isolate the underlying mechanism(s) responsible for significant historical (AMO) and contemporary (NAO) associations with annual variability in loggerhead sea
turtle nest counts in Florida (Van Houtan and Halley, 2011; Arendt et al. 2013). The fourth objective was to conduct exploratory data analysis to evaluate the probability that both negative and positive anthropogenic activities since the 1930’s in oceanic and neritic habitats could have produced the oscillating pattern in nest counts at INBS beaches during 1982–2012 (Witherington et al., 2009; Arendt et al., 2013, Ehrhart et al., 2014).

Methods

Objective 1a: Simple model sensitivity

The first objective was completed using two distinct techniques. In the first approach, a stable age assemblage was created in MS Excel (Microsoft Office 2013; Redmond, CA) that generated 44,866 nests annually under the assumption of no variation across cohorts for any of the following 11 input parameters: Clutch size (CS); Ocean entry success (ES); Age 0 survival (A0); Percent female composition at the end of Age 0 (PF); Oceanic juvenile survival (OS); Oceanic stage duration (OD); Neritic juvenile survival (NE); Age at first maturity (AFM); Adult survival (AS); Remigration interval (RI); and Clutch Frequency (CF). The annual nest count reference (44,866) reflected the grand mean of the 1989–2012 annual nest counts evaluated by Arendt et al. (2013), plus the addition of 10 nests to ensure annual production of exactly 44,866 nests when stable values (described herein) for all 11 parameters were simultaneously considered. Annual nest production was calculated as the sum of neophyte and remigrant nesters divided by the remigration interval, the quotient of which was then multiplied by the clutch frequency. Neophyte nesters were computed as follows: 

\[
\text{Nests} \times \text{CS} \times \text{ES} \times \text{A0} \times \text{PF} \times \text{OS}^{(\text{OD} - 1)} \times \text{NE}^{(\text{AFM} - \text{OD})}.
\]

The number of remigrant nesters through age 77, the maximum age reported for this population based on skeletochronology data (Avens et al., 2015),
was computed as the number of individuals in each prior year multiplied by the adult survival rate. Integer values were used for all sea turtle ages.

To evaluate the relative importance of these 11 parameters, one value greater and one value less than the stable value for each parameter was considered (Table 1.1) which yielded 177,147 unique theoretical assemblages that were created as a Cartesian product in MS Access. To ensure reliable comparison among four parameters associated with the first year of life (CS, ES, A0, and PF), the same magnitude of variation (± 30%) was evaluated for each parameter. Variation around survival rates after the first year of life was limited by an upper boundary of 100%; thus, the maximum variation of 10% above the 90% stable value for adult survival was used to establish the amount of variation for oceanic and neritic juvenile stages accordingly. Neritic recruitment ranged from ages 8 to 12, reflecting the range of mean age at neritic recruitment for this population in recent decades (Bjorndal et al., 2000, 2003; Avens et al., 2013). Survival during the neritic juvenile phase was considered to be age-specific vs. habitat-specific to encompass flexible life history strategies but which are biased for neritic distribution (Witzell, 2002; McClellan and Read, 2007; Casale et al., 2008; Mansfield et al., 2009; Arendt et al., 2012b). Variation in age at first maturity reflected the mean and standard deviation (SD) modeled by the 2009 Global Status Review for this species (Conant et al., 2009). Clutch frequency and remigration interval were also based on parameters modeled by Conant et al. (2009), but with variation restricted to the smallest integer values possible given the disproportionate weight associated with each of these terms in the calculation of annual nest counts. Modeled variation in clutch frequency and remigration interval also encompassed the majority of variation reported in these parameters for this DPS across
studies (Bjorndal et al., 1983; Frazer and Richardson, 1985; Tucker, 2010; Ehrhart et al., 2014; Phillips et al., 2014). Sea turtle sex is determined by incubation temperature (Standora and Spotila, 1985); however, differential female mortality likely occurs during Age 0 given disparity between 9:1 female-biased ratios reported for loggerhead hatchlings in Florida (Mrosovsky, 1994) and 2:1 ratios reported for juvenile loggerhead sea turtles sampled from oceanic (Delgado et al., 2010) and neritic foraging grounds (Wibbels et al., 1991; Arendt et al., 2012c) for this DPS. As such, this study focused on variation in post-hatchling loggerhead sea turtle sex ratios.

Four metrics were analyzed for each of the 177,147 nest assemblage scenarios created under the assumption of no variation among cohorts within each assemblage: the frequency of production of at least 44,866 nests annually; the number of nests produced annually; the frequency of producing age 77 individuals; and the percent of the assemblage identified as neophyte nesters. The total number of scenarios that produced ≥44,866 nests was partitioned among the three value options (low, stable, high) for each parameter (Table 1.1), after which the percent difference in the number of events associated with the low and high values relative to the stable value was computed for each parameter. After first testing for normality, a Kruskal-Wallis (KW) test (α = 0.05) was performed in Minitab 15® (Minitab, Inc., State College, Pennsylvania) to determine if the distribution of frequencies associated with parameter values greater than or less than each parameter stable value were statistically similar. The mean of absolute differences for these two series was then computed for each parameter, after which they were ranked and analyzed descriptively. The total number of nests produced across the 177,147 scenarios was pooled into four categories: <30,000 nests, a reference point
slightly below the lowest annual nest count between 1989 and 2012 (Arendt et al., 2013); 30,000 to 60,000 nests, approximately the same range as annual nest counts analyzed by Arendt et al. (2013); between 60,000 and 106,100 nests, the upper boundary denoting the recovery threshold for this nesting population (NMFS and USFWS, 2008); and >106,100 annual nests. The number of scenarios associated with each parameter and value combination (33) was computed for each of these four annual nest count production groups, converted to a percent of each parameter and value combination, then expressed as a distribution to test (KW) for differences among the four groups. Chi-square contingency tests were used to test for differences among the four nest count groups with respect to the frequency of scenarios that produced age 77 nesters and the distribution of scenarios where neophyte nesters accounted for <15% versus ≥15% of the assemblage. Correlation tests were used to evaluate scenario frequency trends among the four groups.

**Objective 1b: Complex model sensitivity**

The second approach used for Objective 1 was to model the effects of differential temporal survival and maturity trajectories across cohorts for a 200-year observation period following a 77-year burn-in phase to stabilize the age structure (Ages 0 to 77). The same equation used to calculate age structure and nest counts for Objective 1a was also used for this model. In the 78th to 278th years of population existence the number of nests produced annually switched from a fixed value (44,866) to the number of nests produced by neophyte and remigrant nesters predicted to exist in each of these years. After confirmation of nest production stability through year 278, random values for years 78 to 278 were substituted for fixed values one parameter at a time to quantify the impacts to the 200 predicted annual nest counts. Random values in each year were
selected (MS Excel Sampling Tool) from a uniform distribution reflecting 199 evenly spaced intervals between the minimum and maximum values modeled for each parameter (Table 1.1). This process was repeated for all but age at neritic recruitment and age at first maturity, which remained fixed at 10 years and 30 years, respectively, due to deviation from the stable trajectory when these parameters were not fixed. Furthermore, when other parameter values were not compensated to achieve a new stable trajectory after altering age at neritic recruitment (8 vs. 12) and first maturity (25 vs. 35), the maximum range in predicted nests (28,991 to 71,130) exceeded the observed range in annual nests counts at Florida INBS beaches during 1989–2012 (Arendt et al., 2013).

Two annual nest count metrics were analyzed across 200-year model runs to assess variability among nine parameters: sequential year absolute difference and absolute range after 200 years. Due to a lagged response between changes in parameter values between the first year of life and maturity, calculation of sequential year differences was initiated once variability in predicted nest counts was first detected; as such, sample size for comparison of sequential year variability differed by up to 30 observations among parameters. Sequential year differences were treated as a distribution to evaluate statistical similarity among the nine parameters using a KW test. Absolute range in annual nest counts after 200 years consisted of a single minimum and maximum value for each parameter; thus, a Chi-square contingency test was used to detect statistical differences in nest count range among parameters. For both tests, a reference distribution for the 1989–2012 Florida INBS nest counts analyzed by Arendt et al. (2013) was also included. Bonferroni pairwise comparisons were used to assess differences in parameter distributions of sequential year absolute differences, with
emphasis on non-significant relationship with the Florida INBS nest count data. Chi-square tests were used to compare annual nest count range for each parameter relative to the annual range observed at Florida INBS beaches during 1989–2012.

**Objective 2: Sensitivity of nest counts and age structure to stochastic variability**

The model platform and 200-year duration used in Objective 1 was also used for Objective 2; the model run reported in Objective 1 constituted model run 1 in Objective 2, and two additional data sets were created in the same manner for model runs 2 and 3. Given 200 randomly selected values for each of nine parameters, the number of possible parameter combinations in one year alone was $7.1 \times 10^{190}$; thus, the purpose of Objective 2 was to evaluate generalized trends as opposed to examining all possible annual nest count distributions resulting from a highly stochastic environment. Furthermore, because modeled conditions would not likely occur universally across all habitats at each temporal iteration, annual values represented mean effects with the presumption of offsetting variance above and below annual values. In addition to predicting annual nest counts in a stochastic environment, this modeling approach also enabled assessment of temporal changes in age structure that preceded inter-annual nest counts. As such, this design presents a simplified approach to model stochastic effects on population viability relative to complex techniques such as Individual-Based Models (IBM’s) that require sophisticated software and computing power (Rose et al., 1993).

Statistical similarity in annual predicted nest count distributions and for sequential year changes (absolute magnitude) in predicted nest counts between model runs across the 200-year modeling period was assessed using KW tests and Bonferroni pairwise comparisons. A KW test was also used to assess differences in the percent neophyte
distribution among model runs. A One-Way Analysis of Variance (ANOVA) and Tukey Multiple Comparison test was used to assess statistical differences in the distribution of correlation co-efficient strength between predicted annual nest counts and the relative abundance of Age 0; oceanic; neritic; and remigrant females in the year of nesting and up to 40 years prior. Because abundance magnitude differed greatly among these four life history stages, annual abundance was expressed as a percent anomaly relative to the grand mean for each life history stage in each model run to standardize data series for correlation analysis and to facilitate greater ease of comparisons across life history stages.

**Objective 3**: Climate influence on nest counts and age structure

Unsmoothed (standard) monthly AMO data between 1856 and 2015 (long format) were uploaded from the Earth Systems Research Laboratory of the National Oceanic and Atmospheric Administration; [http://www.esrl.noaa.gov/psd/data/timeseries/AMO/](http://www.esrl.noaa.gov/psd/data/timeseries/AMO/) (accessed 29 November 2015). The AMO data were normalized as in Van Houtan and Halley (2011) and Arendt et al. (2013): a single annual value was created as the mean of monthly values between January and June plus the preceding December, from which the grand mean was subtracted and the resulting value divided by the grand SD, to generate a normalized series with a mean of 0 and a SD of 1.

Monthly (1950–2015) NAO index values were uploaded (6 January 2016) from the Climate Prediction Center of the NOAA National Weather Service [http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml](http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml); however, only March values in the year prior to nesting were used (Arendt et al., 2013).

Using data obtained between 1857 and 2015, 159 correlation tests were performed in MS Excel to evaluate temporal variability in co-efficient strength between sequential
24-year periods in the normalized AMO and loggerhead sea turtle nesting data at Florida INBS beaches during 1989–2012. Between 1887 and 1992, correlation tests were performed in MS Excel to evaluate temporal variability in co-efficient strength between sequential 24-year periods in each randomly generated model run (136 correlations each) and the normalized AMO.

Annual nest counts between 1857 and 2056 were predicted using the same random models described in Objective 2; however, AMO-adjusted values replaced random values for four parameters in the first year of life (CS, ES, A0, PF) and NAO-adjusted values replaced random values for CF and RI in the year of nesting. For both climate indices, a linear relationship was assumed between parameter values that contributed to the least number of nests produced during the cold phase of the index and that varied at evenly spaced increments until reaching maximum nest-producing values in the year with the warmest index score. AMO-adjusted values were substituted between 1857 and 2056; however, NAO-adjusted values were only substituted between 1951 and 2016 given index data set origin in 1950. Correlation tests were performed in MS Excel to evaluate model fit during 1989–2012 between the Florida INBS loggerhead sea turtle nest counts and each model run before and after parameter adjustments.

Objective 4: Anthropogenic influence on nest counts

The stable model platform used for the previous objectives was again used for Objective 4, but the temporal scope of the stable population was abbreviated to 1938 through 2012; this start date was selected to encompass 51 years prior to 1989, representing 90% of the all nesters. The focus of Objective 4 was to evaluate the potential for altered historical survival coinciding with periods of anthropogenic activities.
suspected to have influenced annual nest count trends. Because these activities would have been superimposed over environmental influences on nest counts, the best model fit identified in Objective 3 was treated as a base model upon which survival rates in neritic and oceanic realms were altered to simulate the impact of anthropogenic activities on the relative abundance of sea turtle age structure.

A step-wise parabolic relationship between 1955 and 1999 was evaluated to reflect general fisheries landings trends for shrimp (neritic) and tunas (oceanic) as well as systematic introduction and refinement of conservation measures such as TEDs in shrimp trawls and circle hooks and bait modifications for longline fishing gears (Watson and Kerstetter, 2006). Because sea turtle populations are susceptible to small perturbations (Crouse et al., 1987; Lewison et al., 2004), small deviations from stable values in juvenile survival (Table 1.1) for oceanic and neritic stages were considered as follows: 1955–1959 (-0.001); 1960–1964; (-0.005); 1965–1969 (-0.01); 1970–1974 (-0.03); 1975–1979 (-0.02); 1980–1984 (-0.01); 1985–1989 (-0.005); 1990–1994 (-0.001); 1995–1999 (-0.001). The same survival adjustment schedule was followed for adults except that the -0.01 reduction in survival remained between 1985 and 1999; decreased to -0.005 during 2000–2004; and then resumed stable values in 2005 to reflect the large TED requirement initiated in 2003. Correlation testing was used to assess association with 1989–2012 Florida INBS nest counts and all three models (base environmental fit; base + neritic survival; base + oceanic survival).

Results

Objective 1: Model sensitivity to parameter inputs

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A significant difference was not detected ($P = 0.562$) in the magnitude of deviation from stable nest count production when parameter values were increased vs. decreased values relative respective stable values; however, a distinct gradient in the magnitude of deviation was noted among parameters (Figure 1.1). Among the 11 parameters, neritic survival ranked first and resulted in a 73% mean change in the frequency of stable nest assemblages when this parameter value was deviated. Changes to adult survival (32%), age at first maturity (27%), and oceanic survival (27%) produced the next greatest deviation in the mean frequency of a stable trajectory (Figure 1.1). In contrast, deviation in the other seven parameters only produced mean changes of 5–10% in the frequency of a stable trajectory (Figure 1.1).

Theoretical nesting assemblages ($n = 177,147$ scenarios) created under the assumption of no variation in female survival trajectories across cohorts within each assemblage produced 22 nests to 28.3M nests (mean $\pm$ SE = 355,883 $\pm$ 2,263) annually. A significant difference ($H_3 = 92.97$, $P<0.001$) was noted in the frequency of annual nest count groupings produced: 41% $\pm$ 10% (median $\pm$ IQR) of scenarios produced $>106.1k$ nests; 39% $\pm$ 10% of scenarios produced $<30k$ nests; 11% $\pm$ <1% of scenarios produced 60 to 106.1k nests; and 10% $\pm$ <1% produced 30 to 60k nests (Table 1.2).

Fifty-seven percent of scenarios ($n = 101,160$) included at least one age 77 female, but a significant difference ($\chi^2_3 = 45376$, $P<0.001$) was detected in the ratio of events that included versus did not include at least one age 77 female across the four annual nest count groups. A significant correlation ($P = 0.058$, $r = 0.94$) was also noted between increased frequency of including age 77 females and increased nest counts; 27%
of scenarios that produced <30k nests included at least one age 77 female, compared to 83% of scenarios that produced >106.1k nests including at least one age 77 female.

Neophytes comprised 10.1 ± 0.0% (mean ± SE, range = 2.4 to 33.3%) of nesters, but were significantly different (χ² = 9936, P<0.001) across relative nest count groups with respect to the proportion of scenarios in which neophytes comprised <15% vs. ≥15% of nesters. Across groups, neophytes comprised <15% of nest assemblages for 52% of scenarios that produced <30k nests, but 79% of scenarios that produced >106.1k nests; a significant correlation (P = 0.058, r = 0.94) was noted between decreased prevalence of neophyte nesters and increased annual nest counts across these four groups.

A significant difference was detected (H₁₀ = 902, P<0.001) in the distribution of sequential year absolute differences in nest counts among parameters, with three groupings noted based on the Bonferroni pairwise comparisons and inter-quartile range (IQR; Figure 1.2). Randomly assigned values for remigration interval and clutch frequency produced sequential year differences in nest counts that were not statistically different from the magnitude of variation in the same metric at Florida INBS beaches during 1989–2012, but were statistically different from each other (Figure 1.2). Random changes in adult survival rate produced sequential year differences in nest counts that were greater than variability produced by random assignment of values for all other parameters (which did not differ from each other), but did not produce the level of sequential year variation observed in the Florida INBS data set. In contrast, random assignment of neritic survival was the only scenario that produced an annual nest count range that was not significantly different (χ² = 2.2, P = 0.137) from the range of annual
nests counts recorded at Florida INBS beaches during 1989–2012; random variation in all other parameters were significantly (P<0.001) different from the INBS data set.

**Objective 2: Sensitivity of nest counts and age structure to stochastic variability**

A significant difference was detected in annual nest counts ($H_2 = 243, P<0.001$) as well as the absolute magnitude of sequential year changes ($H_2 = 32.02, P<0.001$) predicted for three predominantly random data sets, none of which exhibited similar trajectories over the 200 year evaluation period (Figure 1.3).

In run 1, annual nest counts ranged from 25,780 to 141,804 (median = 49,402; IQR = 23,875; Figure 1.3), representing a deviation from the model origin nest count of -43% and +216%. Across sequential years, absolute differences in nest counts ranged from 14 to 51,344 (median = 10,889; IQR = 15,881).

In run 2, annual nest counts ranged from 11,938 to 83,038 (median = 34,084; IQR = 17,627; Figure 1.3), representing deviation from the model origin nest count of -73% to +85%. Across sequential years, absolute differences in nest counts ranged from 25 to 49,708 (median = 7,061; IQR = 12,968).

In run 3, annual nest counts ranged from 34,353 to 183,390 (median = 68,100; IQR = 32,584; Figure 1.3), representing deviation from the model origin nest count of -23% to +309%. Across sequential years, absolute differences in nest counts ranged from 4 to 93,477 (median = 13,904; IQR = 19,018).

Across all model runs, predicted annual nest counts were only <20k nests or >106.1k on 20 occasions (3.3%). Despite extensive variability in annual nest counts, the percent of neophyte nesters associated with annual nest counts was not significantly
different (H₂ = 0.2, P = 0.907) across model runs, and ranged from 2.0% to 36.9% (median = 9.8%; IQR = 5.8%).

Consistent temporal correlation trends were noted among model runs between shifts in the relative abundance of age 0, oceanic, neritic, and remigrant females 0 to 40 years prior to annual nest counts (Figure 1.4). Overall correlation co-efficient (r) strength ranged from -0.35 to 0.77 (mean = 0.15; SE = 0.01; n = 492), but was significantly different (F₄⁹₁ = 3.01, P = 0.030, r² = 0.01) among the four age groups as a result of lowest overall co-efficient distribution for Age 0 females. Temporal trajectories in mean correlation co-efficient strength also varied across the four age groups (Figure 1.4), but peaked as follows: Age 0 in the year of nesting (r = 0.67); oceanic juveniles in the year of nesting (r = 0.47); neritic juveniles 20 to 21 years prior to nesting (r = 0.50); and remigrant nesters in the year of nesting (r = 0.62).

**Objective 3: Climate influence on nest counts and age structure**

Between 1857 and 2015, correlation co-efficient strength between the normalized AMO and the 1989–2012 Florida INBS nest counts for loggerhead sea turtles ranged from -0.54 (1911–1934) to 0.66 (1957–1980), the latter corresponding to neophyte recruitment during 1987–2010 assuming a 30-year age at first maturity (Figure 1.5a). Between 1857 and 1992, correlation co-efficient strength between the normalized AMO and sequential 24-year spans for randomly generated annual nest counts ranged from -0.54 to 0.50 for model run 1, -0.59 to 0.63 for model run 2, and -0.77 to 0.60 for model run 3 (Figure 1.5b).

Mean (± SE) correlation co-efficient strength between randomly generated annual nest counts and 1989–2012 Florida INBS loggerhead sea turtle nest counts was 0.14 ±
0.07 (Figure 1.6). Replacement of random values with AMO-adjusted values (individually and all at once) for clutch size, ocean entry, Age 0 survival, and percent female composition improved correlation co-efficient strength, but differences among parameters were not discernible (Figure 1.6). Replacement of random values with NAO-adjusted values for clutch frequency and remigration interval further improved correlation co-efficient strength, with greatest improvement when both parameters were adjusted (Figure 1.6). Division of annual INBS nest counts by NAO-adjusted clutch frequency and then multiplication of this quotient by NAO-adjusted remigration interval produced an estimate of between 14,171 (2005) and 33,785 (2011) adult females that nested on these Florida beaches during 1989–2012; however, this estimated female population was not significantly different across years ($F_{23} = 0.35, P = 0.563, r^2 = 0.00$).

Objective 4: Anthropogenic influence on nest counts

Substitution of NAO-adjusted values for remigration interval and clutch frequency produced a correlation of $r = 0.52$ between the stable population trajectory and the 1989–2012 Florida INBS annual nest counts for loggerhead sea turtles (Figure 1.7a). When annual survival for neritic juveniles and adults was manipulated between 1955 and 2004 to simulate decreased survival in predominantly coastal neritic fisheries, correlation strength decreased to $r = 0.46$ and the overall trend reflected a steady decline vs. the trimoatal Florida INBS annual nest count trend (Figure 1.7b). When annual survival for oceanic juveniles was manipulated between 1955 and 1999 to simulate decreased survival in longline fisheries, correlation co-efficient strength increased to $r = 0.56$. Manipulation of oceanic survival produced a more oscillatory pattern than changes to neritic survival, but the predicted annual nest count decline began a decade earlier than
observed in the Florida INBS data set and a recovery response was less pronounced than predicted by NAO-adjustment of remigration interval and clutch frequency (Figure 1.7c).

**Discussion**

Conservation and management of natural resources are admirable endeavors, but effectively doing so is exceptionally challenging, especially for long-lived, slow-growing, and late-maturing species that require high annual survival rates to ensure existence (Musick, 1999). Conservation actions, whether voluntary or mandatory, represent a top-down control mechanism to minimize negative impacts associated with anthropogenic activities, which represent but one of many consumer levels in ecosystem trophic webs. While certainly laudable, such actions can only produce net improvements if they (a) address root causes; (b) do not create compounding effects; and (c) are implemented at sufficient scales to be influential. Consequently, management of natural resources reflects reactionary regulations given a penchant to implement restrictions when relative abundances for a species of interest decline, followed by deliberating the merits of relaxing restrictions when relative abundance indices return to pre-decline levels. The saga of sea turtle protection in the United States is a good example of this scenario.

After World War II, technological improvements to navigation equipment and fishing gear coupled with the petroleum revolution (Tyedmers, 2002; Ward and Hindmarsh, 2007) facilitated rapid expansion of fisheries to partially satisfy protein demands for exponentially growing human population (Holdren and Ehrlich, 1974). Because these fisheries operated in biologically productive waters across important developmental and foraging habitats for sea turtles, not surprisingly, mortality of sea turtles occurred. Given low relative sea turtle capture rates in fishery-independent trawl
surveys conducted by the National Marine Fisheries Service in the southeast U.S. between 1950 and 1976 (Bullis and Drummond, 1976), it was feared that sea turtle populations were becoming increasingly vulnerable to anthropogenic disturbances. Eventually, enough sea turtles were killed that all species became federally protected in the U.S. under the ESA by 1978. Over the next four decades, extensive monitoring of annual nest counts commenced in the southeast U.S., and a net increase in annual nest counts has occurred since 1978 for loggerhead (Witherington et al., 2009; Arendt et al., 2013; Ehrhart et al., 2014), green, and leatherback sea turtles. As evidenced by a request to resume limited indigenous harvest of green sea turtles in Hawaii (Chaloupka and Balazs, 2007), signs of recovery may be accompanied by interest in relaxing regulations. Given this observation, this study explored the merit of contemplating such action for the NW Atlantic Loggerhead DPS, which revealed several key findings discussed herein.

Survival of neritic juvenile female loggerhead sea turtles exerts the greatest long-term influence on annual nest count trends. Crouse et al. (1987) previously reached this conclusion using stage-based Leslie Matrix models, which Crowder et al. (1994) expanded to predict the potential benefits of requiring TEDs in shrimp trawls to increase survival of juvenile sea turtles in neritic habitats. Arendt et al. (2013) also reached the same conclusion through a less sophisticated matrix model to compare the relative importance of survival gauntlets experienced by sea turtles in the first year of life relative to all other years before reaching sexual maturity. In contrast to matrix modeling techniques that employ discrete probabilities, Mazaris et al. (2005; 2006a,b) reached a

different conclusion (i.e., that oceanic juveniles are most important) using individual-based models incorporating stochastic processes that were modeled for 200 years.

Therefore, the conclusion that neritic juvenile survival exerts the greatest influence on long-term nest count trends reached by the stochastic mathematical model in the present study and also modeled for 200 years is a very important finding. The main methodology discrepancy between the present study and the work of Mazaris et al. (2005; 2006a,b) stems from their pelagic juvenile survival rate of 0.6445 ±5%. In addition to being substantially lower than the 0.78 ±10% values modeled in the present study, the values modeled by Mazaris et al. (2005; 2006a,b) were originally associated with green sea turtle modeling for a 4–5 year oceanic phase (Chaloupka, 2002) as opposed to an eight year oceanic phase (Mazaris et al., 2005; 2006a,b). Consequently, the decline reported by Mazaris et al. (2005; 2006a,b) more likely represents a population growth rate (λ) <1.0 as opposed to the stochastic processes considered in their model, which is reinforced by the stable oscillations for random model runs revealed in the present study.

In addition to survival of neritic juveniles, the relative proportion of females on neritic foraging grounds is also important. Although manipulation of the percent of females in the cohort at the end of age 0 alone did not produce nest count variability of the magnitude seen at Florida INBS beaches during 1989–2012, interactions between this metric, variable survival rates, and initial cohort size should certainly influence the relative abundance of females in the population over time. This suggestion is substantiated by differential correlation co-efficient strength trajectories across life history stages; in contrast to age 0, oceanic juvenile, and remigrant females for which correlation strength and predicted nest counts declined with increasing lag duration.
before nesting, the strength of the correlation for neritic females steadily increased concurrent with lag duration (Figure 1.4). As such, this observation further supports the recommendation of Braun-McNeill et al. (2007) for temporal monitoring of sex ratios on foraging grounds, especially given greater potential for temporal variability in the percent of females produced on Florida beaches (Wyeneken and Lolavar, 2015), where roughly 80% of annual nesting for the NW Atlantic Loggerhead DPS occurs (NMFS and USFWS, 2008) than historically suspected (Mrosovsky, 1994). The potential for reduced ocean entry due to degraded locomotor function following incubation at exceptionally warm temperatures (Fisher et al., 2014) may also increase temporal variability in the percent of females in a cohort at the end of age 0. However, as demonstrated by Arendt et al. (2013) and reinforced herein, subtle changes in survival trajectory can greatly temper or exacerbate cohort abundance trajectories with sufficient elapsed time.

A definitive mechanism was not identified to explain the historical association with the AMO (Van Houtan and Halley, 2011; Arendt et al., 2013). Correlation strength between nest counts at Florida INBS beaches during 1989–2012 and predicted nest counts improved when parameters in the first year of life were adjusted to exhibit a linear relationship with the AMO; however, the extent of correlation co-efficient improvement was relatively minor (i.e., from 0.15 to 0.35) and differences between specific parameters were not evident. Greater temporal variability in hatching and emergence success are reported relative to clutch size for this assemblage (Ehrhart et al., 2014; Brost et al., 2015); however, because a high degree of variability in hatching and emergence success can occur at small spatial scales, these parameters may effectively be obtuse to regional climate influence. Incubation temperature can also vary considerably at small spatial
scales, notably due to the depth and moisture content of the incubation chamber (Booth and Astill, 2001) and the albedo of the overlying sand layer (Hays et al., 2001). Temperature is also a critical underlying metric associated with climate indices, and oscillations in temperature are suggested to generate temporal variation in cohort sea turtle sex ratios (Godfrey et al., 1996; Hays et al., 2003). However, without the ability to reliably age large numbers of sea turtles at sea, it is difficult to distinguish between preservation of temporal variability in the relative abundance of females as a result of conditions early in life vs. the consequence of survival trends later in life. Furthermore, since 1857 the AMO has oscillated smoothly with roughly 33 years per phase (Nye et al., 2014), whereas randomly generated model runs lacked defined periodicity; thus, the ability of random runs to achieve correlation strengths with the AMO similar to that between the AMO and INBS nest counts further supports the coincidence hypothesis.

Contrary to the historical association with AMO first reported by Van Houtan and Halley (2011), mean correlation with Florida INBS nest counts during 1989–2012 improved nearly four-fold when annual values for remigration interval and clutch frequency were scaled with the NAO. The influence of variable remigration interval on temporal variability in annual nest counts for green sea turtles in Costa Rica was first reported by Carr and Carr (1970), which was later suggested to have arisen from winter sea surface temperature anomalies (Solow et al., 2002). Although the NAO affects sea surface temperature, the greatest effect of the NAO is on winter pressure gradients and subsequent wind and current fields in response to shifts in the relative position of the center of a high atmospheric pressure zone over the Azores and a companion low pressure zone over Iceland (Hurrell, 1995). Positive values for the NAO are associated
with a stronger pressure gradient over the North Atlantic that in turn increases southerly flow in the southeast U.S. and shifts the northern wall of the Gulf Stream further north (Hurrell, 1995; Frankignoul et al., 2001). Ecological effects of the NAO are well documented in Europe (reviewed by Ottersen et al. (2000) and Drinkwater et al., 2003), where changes in plankton species assemblages differentially occur across water depths consequent to wind shear (Straile and Adrian, 2000; Straile 2002). Off the east coast of the United States, increased southwesterly wind flow induces coastal upwelling which in some regions exceeds the influence of fluid-driven water mass mixing (Glen et al., 2004). Given extensive geographic diversity in post-nesting foraging ground selection by loggerhead sea turtles originating from Florida (Ceriani et al., 2012; Hart et al., 2012; Pajuelo et al., 2012; Phillips et al., 2014), regional differences in NAO effects may be expected. However, given the high energy demand associated with the completion of the reproductive cycle for female loggerheads (Hamann et al., 2003), accessibility of high-quality energy sources should be a universal theme governing NAO effects on remigration interval and clutch frequency across foraging grounds (Broderick et al., 2001; Hamann et al., 2003).

Scaling remigration interval and clutch frequency to the NAO provided a superior explanation for the 1989–2012 Florida INBS nest pattern than historical perturbations in survival associated with anthropogenic activities and subsequent conservation actions. In the North Sea, systematic and cascading increases in the abundance of organisms across trophic levels occurred in the 1980’s in response to the NAO (Reid et al., 2001). During the same timeframe, annual nest counts for loggerhead sea turtles at the second largest loggerhead sea turtle rookery in the world also followed suit (Ehrhart et al., 2014), a trend
seen across INBS beaches for another decade before declining (Witherington et al., 2009) and then subsequently increasing again (Arendt et al., 2013). The inability to produce a superior fit for a 24-year nest count pattern (i.e., 1989–2012) when survival rates were adjusted for the perceived onset of anthropogenic disturbance underscores the importance of bottom-up processes (Garfield and Sack, 1964). Furthermore, given the ability of changes in oceanic survival to produce a relatively similar decline trajectory as observed during 2000–2007 (Witherington et al., 2009), a brief disruption to neritic recruitment several decades prior to nesting could certainly have contributed to the INBS pattern, but the mechanism would have to be rooted in natural causes given no indication of abatement in fisheries interactions with sea turtles in this realm (Lewison et al., 2004).

Temporal disagreement between fisheries interactions and recovery responses are also evident for leatherback sea turtles in the North Atlantic Ocean, which Lewison et al. (2004) report occur twice as frequently as in the North Pacific Ocean, where annual nest counts remain disconcertingly low (Sarti et al., 2007; Robinson et al., 2014). However, despite fisheries interactions with leatherback sea turtles occurring twice as often in the North Atlantic than in the North Pacific, pronounced annual increases in nest counts are reported for leatherback sea turtles in the North Atlantic5 (Robinson et al., 2014), further affirming the modeled conclusion of Garfield and Sack (1964) that the amount of protoplasm dictates the highest level predator that can be supported in any ecosystem. As such, indirect effects of fishing on biomass may actually pose a greater threat to sea turtle populations than gear interactions at the level of individual sea turtles (Heath, 2005).

The inter-connectivity of trophic energy uptake during foraging and subsequent annual nest counts is appreciated for leatherback (Wallace et al., 2006; Saba et al., 2008)
and loggerhead (Chaloupka et al., 2008a) sea turtles in the Pacific Ocean, but similar emphasis in the North Atlantic Ocean has predominantly been focused on leatherback sea turtles (Saba et al., 2008). Given the more rapid rate of ocean basin warming (and presumably also cooling) in the smaller North Atlantic Ocean relative to other ocean basins (Saba et al., 2016), the importance of bottom-up influences on sea turtle population viability in the NW Atlantic Ocean cannot be overstated. Therefore, it hoped that the results of the present study generated by modeling predominantly stochastic conditions will serve as a catalyst for placing increased emphasis on establishing ecological context when evaluating sea turtle population trends in the future. Specifically, it is necessary to recognize that due to environmental uncertainty, decreasing trends no more guarantee catastrophe than increasing trends guarantee survival despite conservation efforts. However, if multi-decadal trends truly reflect the occurrence of a stable oscillation, the more time that is spent in one phase of the cycle the greater the probability of future transition to the opposing phase. Lastly, because annual alone do not enable differentiation between historical catastrophe and demographic oscillation, there is a great need for holistic life history data sets.

The present study supports several recommendations regarding future changes for the management of sea turtles, with emphasis on NW Atlantic loggerhead sea turtles. First, the use of an upper limit to establish a benchmark for declaring a population recovered does not appear to be realistic, as evidenced by the modeled population only exceeding the de-listing criteria 3% of the time after 3 x 200 years in a stochastic system. Second, although annual nest counts varied considerably across model runs and years, a lower boundary was also evident below which annual nest counts rarely occurred, which
appears to provide a more realistic benchmark for monitoring population viability than an upper boundary. Only three model runs were completed in the present study given a focus on establishing a minimum sense of trend repeatability; thus, more rigorous modeling would be required to confidently determine an appropriate lower boundary for this population. Third, despite the variability in annual nest counts predicted across years and model runs, the underlying changes in population structure governing changes in annual nest counts were highly consistent. Robinson et al. (2014) recently reported on the importance of demographic change in regulating annual nest counts for leatherback sea turtles, but by design their definition of demographic change was restricted to shifts in the relative abundance of nesting females. While the trend reported by Robinson et al. (2014) is consistent with the relative importance of neophyte vs. remigrant nesters reported by Arendt et al. (2013) and reinforced in the present study, it neglects a key finding of Garfield and Sack (1964) that carnivores require a steady supply of juveniles to maintain populations. With regards to loggerhead sea turtles, the present study reached the same conclusion with a stochastic model that Crouse et al. (1987) reached with a discrete probability matrix model: large juveniles, which predominantly reside in neritic habitats, have the greatest long-term impact on the size of the nesting population. Yet, despite this relative importance, sea turtle recovery plans place disproportionate emphasis on annual nest counts as metrics to assess recovery (i.e., NFMS and USFWS 2008). For the reasons highlighted herein, it is strongly recommended that future versions of this and other recovery plans place at least equal to and preferably greater than emphasis on assessing the relative abundance and demographic structure of sea turtle foraging assemblages as has historically been allocated to monitoring nesting assemblages.
Table 1.1. Deviation around stable values for 11 parameters encompassing the life history of female loggerheads from egg to reproductively active adult was examined across numerous cohort structure contexts to elucidate each parameter’s relative influence on annual nest counts. Thirty percent deviation above and below model stable points was evaluated for each of four parameters in the first year of life (CS = clutch size; ES = ocean entry success; A0 = Age 0 survival; PF = percent female composition at the end of Age 0). Ten percent deviation above and below model stable points was evaluated for oceanic juvenile survival (OC), neritic juvenile survival (NE), and adult survival (AS). Deviation in oceanic stage duration (OD) and age at first maturity (AFM) occurred in Objective 1, but due to model structure the mean values for these parameters were used for all other objectives. Modest variability in clutch frequency (CF) and remigration interval (RI) for adult females was also evaluated.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>Increment, Obj. 2&amp;3</th>
</tr>
</thead>
<tbody>
<tr>
<td>CS</td>
<td>80.325</td>
<td>149.175</td>
<td>114.750</td>
<td>0.344</td>
</tr>
<tr>
<td>ES</td>
<td>0.377</td>
<td>0.701</td>
<td>0.539</td>
<td>0.002</td>
</tr>
<tr>
<td>A0</td>
<td>0.280</td>
<td>0.520</td>
<td>0.400</td>
<td>0.001</td>
</tr>
<tr>
<td>PF</td>
<td>0.462</td>
<td>0.858</td>
<td>0.660</td>
<td>0.002</td>
</tr>
<tr>
<td>OC</td>
<td>0.702</td>
<td>0.858</td>
<td>0.780</td>
<td>0.001</td>
</tr>
<tr>
<td>OD</td>
<td>8</td>
<td>12</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>NE</td>
<td>0.765</td>
<td>0.935</td>
<td>0.850</td>
<td>0.001</td>
</tr>
<tr>
<td>AS</td>
<td>0.810</td>
<td>0.990</td>
<td>0.900</td>
<td>0.001</td>
</tr>
<tr>
<td>AFM</td>
<td>25</td>
<td>35</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>CF</td>
<td>4</td>
<td>6</td>
<td>5</td>
<td>0.010</td>
</tr>
<tr>
<td>RI</td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>0.010</td>
</tr>
</tbody>
</table>
Table 1.2. Frequency of occurrence (%) of 177,147 scenarios evaluated in Objective 1 with respect to annual nest counts produced by a nesting assemblage with no variation across cohorts; parameter nomenclature is the same as used in Table 1.1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>&lt;30k nests</th>
<th>30 to 60k nests</th>
<th>60 to 106.1k nests</th>
<th>&gt;106.1k nests</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low</td>
<td>Stable</td>
<td>High</td>
<td>Low</td>
</tr>
<tr>
<td>CS</td>
<td>44.3</td>
<td>38.7</td>
<td>34.7</td>
<td>11.4</td>
</tr>
<tr>
<td>ES</td>
<td>44.4</td>
<td>38.7</td>
<td>34.7</td>
<td>11.4</td>
</tr>
<tr>
<td>A0</td>
<td>44.3</td>
<td>38.7</td>
<td>34.7</td>
<td>11.4</td>
</tr>
<tr>
<td>PF</td>
<td>44.3</td>
<td>38.7</td>
<td>34.7</td>
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</tr>
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<td>OC</td>
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<td>12.3</td>
</tr>
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</tr>
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<td>2.8</td>
<td>9.2</td>
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<tr>
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<td>22.7</td>
<td>12.3</td>
</tr>
<tr>
<td>RI</td>
<td>33.7</td>
<td>39.7</td>
<td>44.4</td>
<td>10.7</td>
</tr>
<tr>
<td>CF</td>
<td>42.5</td>
<td>39.0</td>
<td>36.2</td>
<td>11.2</td>
</tr>
</tbody>
</table>
Figure 1.1. Percent change in the frequency of occurrence of scenarios that produced stable to increasing annual nest counts under increased (dark bar) or decreased (light bar) value magnitudes relative to the stable model value for each parameter. X-axis legend as follows: Clutch size (CS); Ocean entry success (ES); Age 0 survival (A0); Percent female at the end of Age 0 (PF); Oceanic survival (OC); Initial oceanic stage duration (OD); Neritic survival (NE); Age at first maturity (AFM); Adult survival (AS); Remigration Interval (RI); and Clutch Frequency (CF).
Figure 1.2. Sequential year differences (bar-whisker series) and absolute range between minimum (gray dashed line) and maximum (black dashed line) nest counts produced by modeling randomly assigned values for nine parameters were evaluated in the context of variability observed at Florida index nesting beaches (INBS) during 1989–2012. The bar-whisker series contained the following metrics: median (black circle), inter-quartile range (gray bar), and minimum and maximum values (error bars). X-axis nomenclature was the same as Figure 1.1.
Figure 1.3. Predicted annual nest counts (y-axis) during a 200-year simulation for three model runs (1 = line with black diamonds; 2 = dashed black line; 3 = dashed gray line) based on randomly assigned values for nine parameters but fixed age at maturity and oceanic duration. Dashed horizontal line denotes the 106,100 annual nest recovery criteria for the Peninsular Florida Recovery Unit (NMFS and USFWS, 2008).
Figure 1.4. Temporal variability in correlation co-efficient strength (y-axis) between changes in the relative abundance of loggerhead sea turtle life history stages 0 to 40 years prior (x-axis) to predicted annual nest counts in the three model runs in Figure 1.3. Peak association with annual nest counts for loggerhead sea turtles in the first year of life (gray circle), during the initial oceanic phase (gray triangle), and as remigrant nesters (black diamond) occurred during the year of nesting; however, peak association for neritic juveniles (black square) occurred 20–21 years prior to nesting. Series values denote mean (symbol) and SE (error bars).
Figure 1.5. Extensive temporal variability in correlation co-efficient strength (y-axis, panel A) was noted between 136 consecutive 24-year spans in the normalized AMO data series (line) and the 1989–2012 Florida INBS loggerhead nest count trend; peak positive correlation \((r = 0.66)\) between 1957 and 1980 coincided with transition between warm and cool phases of the AMO (gray bars). Similar correlation co-efficient strength distributions (y-axis, panel B) were also noted between 24-year spans in the normalized AMO data series and three random model runs (run 1 = solid black line; run 2 = black dashed line; run 3 = dashed black line).
Figure 1.6. A gradient of improvement was noted in correlation co-efficient strength (r; y-axis) with loggerhead sea turtle nest counts on Florida INBS beaches (1989–2012) when random clutch size parameters were replaced with climate-mediated values. The least improvement was noted when AMO-mediated (cold phase = low values) values replaced (individually and all at once) random values for clutch size (CS), ocean entry success (ES), age 0 survival (A0), and the percent of females in the cohort at the end of age 0 (PF). The greatest improvement occurred with NAO-mediated values for clutch frequency (CF; cold phase = fewer nests) and remigration interval (RI; cold phase = longer intervals). Data series denotes mean (circle) ± SE (error bars).
Figure 1.7. Scaling only remigration interval and clutch frequency to the NAO (A) produced a correlation ($r = 0.52$) between the stable population trajectory (gray line) and annual nest counts for loggerhead sea turtles in Florida during 1989–2012 (dashed black line, all panels). The strength of this correlation was reduced ($r = 0.46$) when parabolic survival of neritic juveniles and adults during 1955–2004 was superimposed on the NAO-adjusted trajectory (B), but improved slightly ($r = 0.56$) when similar survival adjustments occurred in the oceanic realm (C)
Chapter 2. Temporal variability in demographic structure of loggerhead sea turtles at a critical coastal foraging ground: important insights for future management.

Introduction

Monitoring the demographic composition of populations is essential to identifying conservation concerns as well as documenting response to conservation actions. Demographic studies have provided a cornerstone for monitoring temporal changes in population structure for a diversity of organisms including plants (Hulme, 1998), insects (Carey, 1993), fish (Figueira, 2009), reptiles (Row et al., 2007), and mammals (Caro, 1999). While demographic data have largely been used for directing conservation efforts, as long-term data sets become available these data may also be used to assist with developing small-scale and sustainable consumption activities. For example, following determination that the green sea turtle stock in the Hawaiian island chain had rebounded to 83% of pre-exploitation levels, Chaloupka and Balazs (2007) indicated support for restoration of limited indigenous hunting. Few examples of recovery of sea turtles have emerged to date, but the findings of Chaloupka and Balazs (2007) highlight the value of long-term and concurrent monitoring of abundance and demographic parameters.

Demographic parameters of most importance to sea turtle conservation include size, sex, and natal origin. Skeletochronology has successfully been used to estimate sea turtle age (Zug et al., 1997, 2002, 2006; Avens et al., 2009, 2013, 2015), but the need for osteological samples almost exclusively restricts use of this technique to dead or
moribund specimens. Subsequently, size frequency distributions are more often used for relative delineation of life history stages (Crouse et al., 1987) and, in the case of recaptured individuals, for evaluating size-based growth rates (Limpus and Chaloupka, 1997; Schmid and Witzell, 1997; Braun-McNeill et al., 2008; Bjorndal et al., 2013).

Sexual dimorphism in adult male sea turtles is reported from tail elongation (Casale et al., 2005; Ishihara and Kamezaki, 2011) and shorter carapace lengths (Godley et al., 2002); however, for sexing immature sea turtles, testosterone radioimmunoassay is widely used (Owens et al., 1978; Wibbels et al., 1991; Gregory and Schmid, 2001; Braun-McNeill et al., 2007). Natal origins of sea turtles are traditionally assessed using mitochondrial DNA haplotypes (Encalada et al., 1998; Dutton et al., 2007), with rookery contributions to foraging grounds determined by mixed stock analysis (Roberts et al., 2005; Bolker et al., 2007; Bowen et al., 2007). More recently, nuclear DNA has been used to identify individual sea turtles on nesting beaches (Shamblin et al., 2011a), but could also be used to identify offspring (though with unknown hatch location and year) on foraging grounds.

To increase the probability that data are representative of the overall population, demographic data should be collected across a range of habitats and, in turn, life history stages. The general life cycle for loggerhead sea turtles consists of terrestrial nesting; nearly a decade of development in oceanic habitats; and the remainder of life is spent mostly in neritic habitats but with a flexible return to oceanic habitats (Witzell, 2002; McClellan and Read, 2007; Casale et al., 2008). Within the NW Atlantic Ocean neritic zone, loggerhead sea turtles occur in both estuarine and coastal ocean habitats along the entirety of the U.S. East Coast (Morreale et al., 2005; Ehrhart et al., 2007; Epperly et al., 2007; Warden, 2011; Arendt et al. 2012c,e). In addition to broad size structure, rookery
mixing is extensive within this neritic foraging ground complex (Bass et al., 2004; Bowen et al., 2004; Roberts et al., 2005), particularly north of Cape Canaveral, FL where disproportionate recruitment occurs relative to other foraging areas closer to natal origin (Bowen et al., 2004). Given a diversity of sizes, natal origin, and density of sea turtles within 100 km of shore, independent of water depth (Peckham et al., 2007; Baez et al., 2007), these areas are ideally suited for demographic studies.

Across studies, length frequency data for loggerhead sea turtles captured on foraging grounds in the NW Atlantic Ocean pre-date protection received under the ESA, and coarse synthesis of published data suggest an oscillating trend over the past 40 years. Between 1976 and 1979, the most prevalent size class captured in Mosquito Lagoon, FL measured 60 to 70 cm straight-line carapace length; the upper end of this size class also corresponded to the smallest adult females nesting on adjacent beaches in the first years of nest protection under the ESA (Mendonca and Ehrhart, 1982). Between 1982 and 1993, median size at a study area 27 km south in the Indian River Lagoon steadily declined from the mid 60-cm range to the upper 50-cm range (Ehrhart et al., 2007). During this same timeframe, most loggerhead sea turtles captured in coastal shipping channels measured 55 to 70 cm straight-line carapace length (Van Dolah and Maier, 1993; Schmid, 1995). Beginning in 1995, median size steadily increased for the next decade at the Indian River Lagoon study site (Ehrhart et al., 2007), an estuarine study site in North Carolina (Epperly et al., 2007), and in the Charleston, SC shipping channel relative to the early 1990’s (Arendt et al., 2012e). Assuming first recruitment to neritic from oceanic habitats between age 8 (Bjorndal et al., 2000) and 12 (Avens et al., 2013),
this increase in median size generally corresponds to the earliest cohorts to receive *in situ* nest protection and the first benefits of Turtle Excluder Devices (TEDs) in trawl nets.

Since 2000, the National Marine Fisheries Service has funded and permitted a trawl survey to randomly capture sea turtles in coastal waters across a 350-km latitudinal gradient on an important neritic foraging ground in the NW Atlantic Ocean (Bowen et al., 2004) to assess the relative abundance and demographic structure of sea turtles. Spatial clustering (Arendt et al., 2012c) and seasonal residence (Arendt et al., 2012b) independent of demographic attributes support use of this data set for assessing temporal trends for loggerhead sea turtles. Between 2000 and 2011, Arendt et al. (2012f) reported increased catch rates for loggerhead sea turtles measuring 75.1 to 80.0 cm minimum straight-line carapace length, but it is not known whether this increase represents an increase in abundance or continued survival and growth of dominant cohorts first detected in the 1990’s (Ehrhart et al., 2007). Therefore, the first objective of this study was to test the null hypothesis of no difference in size distribution between 2000 and 2015, with particular emphasis on assessing whether size classes prevalent in the preceding decade were merely growing with time and shifting the size distribution towards larger individuals. Given a 41% decline in nesting at Florida beaches between 1998 and 2007 where the majority of nesting for this species occurs in the NW Atlantic Ocean (Witherington et al., 2009), we would predict an exacerbated shift in size structure provided that survival remained high for size classes prevalent in the preceding decades. The second objective was to test the null hypothesis of no influence of sea turtle sex or genetic haplotype on potential change in size distribution between 2000 and 2015. The third objective was to generate a growth rate equation from tag-recapture and re-sighting
data, and to then evaluate the relative importance of demographic (size, sex, genetic haplotype) and temporal (capture and recapture year) attributes on growth rate. The fourth objective was to apply this growth rate equation to all loggerhead sea turtles captured in this trawl survey since 2000 to test the null hypothesis of no difference between predicted and observed size distributions in 2015. The fifth objective was to test the null hypothesis of no difference in size distributions in 2000 and 2015 from stable size distributions computed from applying growth rate equations to the stable age distribution for this population of loggerhead sea turtles (NMFS and USFWS, 2008).

**Methods**

*Sea turtle capture and handling*

Loggerhead sea turtles were captured by trawling (for gear description, see Arendt et al., 2012c,e,f) in coastal waters (4.6 to 13.7 m deep) between May and August. Because trawl nets were devoid of TEDs, bottom trawling time was limited to ≤30 minutes per ESA Section 10(A)(1)(a) permits 1245, 1540, and 15566 issued by the National Marine Fisheries Service, Office of Protected Resources. Trawling in 2000 to 2003 and again between 2008 and 2015 was conducted between latitude 33.1°N (Winyah Bay, SC) and 29.9°N (St. Augustine, FL; Figure 2.1). During 2004–2007, trawling was focused in the Charleston, SC (Arendt et al., 2012e) and/or Port Canaveral, FL (Arendt et al., 2012a) shipping channels; thus, size data from those years are excluded herein.

Processing of captured loggerhead sea turtles included collecting a suite of morphometric measurements (Bolten, 1999); however, here we only report minimum straight-line carapace length (SCLmin) measured to the nearest 0.1 cm with tree calipers. Where pre-existing injuries precluded accurate measurement of SCLmin, estimates of
SCLmin were obtained from maximum straight-line carapace width (SCW) according to the equation provided by Arendt et al. (2012f). Only data associated with the first capture event for five loggerhead sea turtles captured twice during the same sampling season were used for analyses.

Blood samples were collected from the dorsal cervical sinus of sea turtles using a 21-ga, 1.5” (3.8 cm) needle as described by Owens and Ruiz (1980). Blood samples consisted of a maximum of 45 ml total volume and did not exceed 10% of total blood volume based upon total weight as recommended by Jacobson (1998). Sea turtle sex was determined from circulating testosterone concentration measured by radioimmunoassay, a common practice with juvenile sea turtles (Owens et al., 1978; Wibbels et al., 1991; Delgado et al., 2010; Arendt et al., 2012c) that is reliable at water temperatures >23°C (Braun-McNeill et al., 2007). Through 2003, plasma testosterone concentrations <200 pg ml⁻¹ were identified as female; between 200 and 300 pg ml⁻¹ as undetermined; and >300 pg ml⁻¹ as male. Discontinuation of some of the original reagents for the assay in 2004 necessitated that this scale be adjusted after validation between new and old reagents. Between 2004 and 2013, sex was assigned as follows: female (<400 pg ml⁻¹); undetermined (400 to 500 pg ml⁻¹); and male (>500 pg ml⁻¹).

Whole blood samples for genetic determination (0.5 ml) were collected in heparin-free vacutainer tubes, prepped with a lysis buffer solution (0.8 ml), and stored at room temperature until analysis. Sample preparation methods prior to sequencing a 378-base pair fragment of the mitochondrial DNA (mtDNA) control region are described in detail by Roberts et al. (2005). Following sequencing, genetic haplotypes were
determined and compared with genetic haplotype distributions among regional rookeries (Encalada et al., 1998; Bowen et al., 2004).

Data analysis

Statistical analyses were performed in Minitab 15® (Minitab, Inc., State College, Pennsylvania) under the assumption of a significance level of $\alpha = 0.05$ after first checking all data distributions for normality.

For the first objective (i.e., temporal variability in size distribution), SCL$\text{min}$ for all loggerhead sea turtles captured in each year was expressed as a percentile distribution from 0 to 100 at one-percentile intervals. Conversion to percentile distributions transformed measurement data to a continuous scale which enabled assessment of distribution evenness (skewness) and peakedness (kurtosis) in MS Excel (Microsoft Corporation, Redmond, Washington); both metrics were then tested for temporal variability across years using linear regression. Logistical constraints and expanded data collection resulted in a 54% difference between peak sampling effort in 2003 (428 standard (30.5 m) net hours) and lowest sampling effort in 2015 (198 standard net hours). Accordingly, a significant decline ($F_{11} = 16.59$, $P = 0.002$, $r^2 = 0.58$) in the number of loggerhead sea turtles captured each year, and in turn sample size used to generate percentile distributions, also occurred. Thus, to test for potential sample size influence on observed size distributions across time, a theoretical size distribution representing every SCL$\text{min}$ measurement (0.1 cm intervals) between the minimum and maximum observed sizes between 2000 and 2015 was created; a random number of measurements were then selected for each year between 2000 and 2015 where the number of measurements sampled equaled the number used to generate percentile distributions in each year.
Regression was used to test for linearity in skewness and kurtosis for this theoretical size distribution between 2000 and 2015.

Percent change in SCLmin associated with each annual percentile increment was computed relative to the first year of the study (2000). Annual percent change values were pooled into five percentile groups (0-19th, 20th to 39th, 40th to 59th, 60th to 79th, and 80th to 100th), and the distribution of values was analyzed with a one-way ANOVA. Lack of overlap among 95% confidence intervals (CI) for each percentile group mean was used to assess statistical differences between groups; CI was computed as the standard error (SE) of each percentile group means multiplied by the appropriate t-statistic (Zar, 1996).

For the second objective (i.e., demographic influence on size distribution), each loggerhead sea turtle was assigned to one of the same five percentile groups above based on SCLmin measurement and the respective percentile distribution for each capture year. Percent female and percent CC-A1 metrics for each percentile group in each year were then computed given the prevalence of these sex and genetic haplotype assignments among captured sea turtles (Arendt et al., 2012c). Partitioning data by percentile groups versus discrete size classes ensured that annual percent sex and percent CC-A1 metrics were based on similar sample sizes across observed sizes. The inter-annual mean (± SE) values for percent female and percent CC-A1 were computed for each percentile group and mean values were then tested for statistical differences using linear regression. Correlation testing was used to test for relationships between the mean percent change in size and percent female or percent CC-A1 distributions across percentile groups.

For the third objective (i.e., growth rate equation), growth rates (cm yr⁻¹) for loggerhead sea turtles were computed by comparing SCLmin at capture and recapture
(within survey) or after being re-sighted alive (by other research programs), provided that at least nine months elapsed between measurements. Linear regression was used to statistically test for a relationship between annualized growth rates and SCLmin in the year of capture. Percent difference between observed and predicted sizes at recapture or re-sighting were computed for each loggerhead sea turtle and used to generate the growth rate equation. A One-Way ANOVA was then used to statistically test these percent difference values, as well as to test for differences in goodness of equation fit with respect to time elapsed between capture and recapture or re-sighting; percent difference values were pooled into three groups with nearly equal sample sizes between 9 months and 15 years at large. The influence of capture year and recapture or re-sighting year on annualized growth rates were also assessed with linear regression. Non-parametric KW tests were used to statistically evaluate the influence of genetic haplotype (0 = unknown, 1 = CC-A1, 2 = CC-A2, 3 = other) and sex (0 = unknown, 1 = female, 2 = male) on annualized growth rates.

For the fourth objective (i.e., identifying the mechanism for temporal size shift), the growth rate equation was applied annually to every SCLmin measurement between 2000 and 2014 to compute a theoretical size distribution for 2015. Correlation analysis was used to statistically compare the temporal distribution of mean growth rate with the median size of loggerhead sea turtles captured in each year to evaluate potential autocorrelation with capture and recapture or re-sighting year on growth rate. The complete percentile size distribution predicted for 2015 based on application of the growth rate equation at annual increments was then statistically compared to the observed size distribution in 2015 using a paired t-test. To test for potential sample size influence on
the predicted percentile size distribution, a subset of 500 and 100 theoretical sizes from the full 2015 distribution were randomly selected, expressed as percentile distributions, and then statistically compared to the observed size distribution in 2015 using paired t-tests or Mann-Whitney tests as appropriate.

To determine the necessary growth rates required to generate the observed size distribution in 2015 in the absence of recruitment, observed size for each percentile increment in each year between 2000 and 2014 was subtracted from the corresponding percentile size in 2015 and then divided by the number of years between that year and 2015. A 14-year mean (± 95% CI) was then computed for each percentile increment, and visually compared with the corresponding growth rate for each percentile increment based on the 2015 percentile distribution. For each percentile increment, non-overlap in 95% CI between the growth rate predicted by the equation computed in Objective 3 and the growth rate needed to achieve the 2015 percentile distribution without recruitment was used to assess a significant difference between the two percentile distributions.

For the fifth objective, a stable size distribution was calculated for loggerhead sea turtles ages 12 to 77 corresponding to neritic recruitment and maximum ages, respectively, per Avens et al. (2013, 2015). An exponential equation \((y = 12.746e^{-0.107x}; r^2 = 0.97)\) was fit for the same age subset in the stable age distribution (NMFS and USFWS, 2008), where \(y\) equaled the percent occurrence for each age \((x)\). A frequency distribution for ages 12 to 77 was then computed following modification of the exponent (from -0.107x to -0.1175x) so that the distribution summed to 100%. This frequency distribution was then used to compute the theoretical number of individuals in each age (and adjusted by one individual per age as needed) for a population with exactly 100,000
sea turtles. Size at age was computed from the growth rate equation in Objective 3 with a starting size of 55.3 cm SCLmin for age 12 (Avens et al., 2013); to ensure that the maximum predicted size by age 77 exceeded the largest loggerhead sea turtle captured in this survey between 2000 and 2015, a second growth trajectory was computed by accelerating the growth rate by 50% across all ages. The corresponding percentile distributions were then computed in MS Excel for both growth rate trajectories to approximate a stable size distribution reflective of age structure; where size was duplicated across percentiles, the distribution was smoothed by adding a fraction to each successive identical size where the fraction denoted the difference in size between the repeated size value and the next largest size value divided by the number of percentile increments associated with repeats. Mann-Whitney tests were used to statistically compare theoretical stable size and observed size structures in 2000 and 2015.

Results

A total of 1,894 SCLmin measurements (n = 108 to 209 per year) for loggerhead sea turtles captured by trawling on a coastal foraging ground between 2000–2003 and 2008–2015 were analyzed to assess temporal variability in size distributions. Minimum straight-line carapace ranged from 44.8 to 106.3 cm (median = 68.4 cm). Size distribution kurtosis ranged from -0.6 to 3.6 and declined significantly across years (F_{11} = 9.4, P = 0.012, r^2 = 0.43); however, kurtosis of randomly selected measurements (n = number of actual measurements per year) from a theoretical size distribution between minimum and maximum observed sizes did not (P = 0.461). Size distribution skewness ranged from 0.2 to 1.5 and also declined significantly across years (F_{11} = 35.08, P<0.001,
$r^2 = 0.76$); however, skewness of randomly selected measurements from the same theoretical size distribution sampled in the same manner as kurtosis did not ($P = 0.812$).

Annual differences in percentile distributions (at one-percentile increments = 1,110 observations) between 2001 and 2015 relative to the percentile distribution in 2000 ranged from -7.5% to 22.3% ($\text{mean} \pm \text{SE} = 6.8 \pm 0.1\%$). When pooled into five percentile groups, annual differences in percentile distribution relative to 2000 were significantly different ($F_4 = 96.02, P < 0.001$). No overlap in 95% CI occurred between the largest percentile size group and all other size groups, nor between the smallest size group and the 20th to 79th percentile size range (Figure 2.2).

Genetic haplotype was assigned for 1,529 loggerhead sea turtles. Across five percentile groups, the mean percent of loggerhead sea turtles exhibiting the CC-A1 haplotype ranged from 48% to 59%, but was not statistically significant ($P = 0.817$). Similarly, a non-significant correlation ($P = 0.087, R = -0.82$) was noted between mean change in percentile group size and the percent of loggerhead sea turtles exhibiting the CC-A01 haplotype (Figure 2.2).

Sex was assigned for 1,556 loggerhead sea turtles, with 68% classified as female. Across five percentile groups, the mean annual percent of female loggerheads ranged from 60% to 71%, and was significantly different ($F_4 = 11.40, P = 0.043, r^2 = 0.72$). A non-significant correlation ($P = 0.484, R = -0.42$) was noted between mean change in percentile group size and the percent of female loggerhead sea turtles (Figure 2.2).

Minimum straight-line carapace length for loggerhead sea turtles recaptured (45) or re-sighted by other in-water sampling programs (7) were used to calculate annualized growth rates (cm yr$^{-1}$). Loggerhead sea turtles were recaptured 4.5 ± 0.8 km (mean ± SE)
from where captured 0.7 to 15 years earlier, whereas re-sightings occurred 161.2 ± 71.2 km from where these loggerhead sea turtles were captured 5.4 to 13.9 years earlier.

Annualized growth rates (AGR) ranged from 0.0 to 2.2 cm yr\(^{-1}\) (mean ± SE = 0.9 ± 0.08 cm yr\(^{-1}\)), and were significantly different (F\(_{51} = 8.13, P = 0.006, r^2 = 0.12\)) with respect to SCL\(_{\text{min}}\) when tagged as evidenced by the following growth rate equation: \(\text{AGR} = 2.86 - (0.0288 \times \text{SCL}_{\text{min}})\). Percent differences between the observed and predicted sizes at recapture/re-sighting (Figure 2.3) ranged from -6.2% to 7.4% (mean ± SE = 0.2 ± 0.4%), but were not significantly different (P = 0.916) between loggerhead sea turtles at large <3 years (15); at large between 3 and 6 years (20); or at large between 7 and 15 years (17).

Significant differences were detected between annualized growth rates and the year tagged (F\(_{51} = 5.67, P = 0.021, r^2 = 0.08\)) as well as the year recaptured (F\(_{51} = 4.21, P = 0.045, r^2 = 0.06\)). A significant correlation (P = 0.001, R = -0.88) was also observed between median loggerhead size and mean theoretical growth rate based on observed size distributions between 2000 and 2015 (Figure 2.4). Annualized growth rates were not statistically different with respect to sex (P = 0.785) or genetic haplotype (P = 0.626).

The observed percentile size distribution in 2015 (Figure 2.5) was significantly different from the percentile distribution predicted for all loggerhead sea turtles measured through 2014 (T = -16.71, P<0.001); a percentile distribution for 500 randomly selected predicted sizes in 2015 (T = -14.77, P<0.001); and a percentile distribution for 100 randomly selected predicted sizes in 2015 (W = 8802, P<0.001). Excluding the two largest observed percentiles in 2015 that were 0.6 and 3.9 cm larger than predicted, observed percentiles were 0.5 to 8.5 cm smaller than predicted in 2015 (Figure 2.5).
In order for the observed size distribution in 2015 to have occurred without recruitment into the sampled population, annual growth rates would have needed to have been significantly (i.e., no 95% CI overlap) slower between 2000 and 2014 than was observed for recaptured loggerhead sea turtles for nearly half of the size distribution (Figure 2.6). Similar mean growth rate and/or overlap of 95% CI for the 55th through the 85th percentiles (Figure 2.6) suggests that size structure shifted with reduced recruitment; this percentile distribution encompassed 64.9 to 72.2 cm and 74.1 to 80.8 cm SCLmin loggerhead sea turtles in 2000 and 2015, respectively. Slow growth rates (and poor growth rate equation fit for loggerheads larger than recaptured) render interpretation of trends for the largest percentiles difficult; however, non-overlap of 95% CI may suggest modest recruitment into the adult population during 2000–2015.

Maximum size associated with two theoretical stable size distributions was 92.7 cm SCLmin for the growth rate equation computed in Objective 3 and 111.4 cm SCLmin when this growth rate equation was accelerated by 50% for ages 12 to 77 (Figure 2.7). The observed size distribution in 2000 was not statistically different (P = 0.258) from a stable size distribution based on the Objective 3 growth rate equation nor based on an accelerated version of this growth rate equation (P = 0.104). In contrast, the observed size distribution in 2015 was statistically different from a stable size distribution based on the Objective 3 equation ($W_{100} = 12782, P<0.001$) and a stable size distribution based on an accelerated growth rate equation ($W_{100} = 11514, P = 0.002$). Between these two growth rate equations, size at age 20 ranged from 64.5 to 69.1 cm SCLmin, which accounted for 23% (53rd to 75th percentiles) of captured loggerhead sea turtles in 2000, but only 15% (24th to 38th percentiles) of captured loggerhead sea turtles in 2015. Size at age
between these two growth rate equations ranged from 73.3 to 82.3 cm SCL min, which represented 6% (87th to 92nd percentiles) of loggerhead sea turtles captured in 2000, but 39% (54th to 92nd percentiles) of loggerhead sea turtles captured in 2015.

**Discussion**

Even in the absence of anthropogenic perturbation, populations ebb and flow along a continuum such that balance is denoted by a dynamic, versus a static state (Voltera, 1926). The ability to characterize such flux is intrinsically easier when phases pulse in short order, rather than over protracted schedules. However, with regards to long-lived, slow-growing, and late-maturing species that are quite vulnerable to anthropogenic disturbances (Musick, 1999), the ability to discriminate natural variability from acute stock stressors can be extremely difficult. Given greater magnitude in annual mortality for loggerhead sea turtles in neritic habitats of the NW Atlantic Ocean (≥11%; Conant et al., 2009) relative to annual growth (typically <3% change in size; Bjorndal et al., 2013; Avens et al., 2015; this study), temporal variability in size structure largely reflects initial cohort abundance and subsequent survival trajectories across decades. Accordingly, the observations presented herein represent one of the most holistic examinations of temporal shifts in size structure of foraging sea turtles reported, and illustrate the commitment to long-term monitoring that is necessary to comprehend demographic structure changes that precede annual nest counts by several decades.

Conversion of size distribution data to a percentile scale enabled computation of two critical metrics for assessing size distribution normality, which in turn were exceptionally informative. Between 2000 and 2015, the overall size range of loggerhead sea turtles captured in this trawl survey remained relatively static; however, greater
representation of multiple size classes was quantifiable as the size distribution became less biased towards singular, dominant size classes. Differential survival across decades, and in turn cohorts, provides the most logical explanation for size structure smoothing between 2000 and 2015. This suggestion is reinforced by small percent difference values between observed and predicted sizes at recapture or re-sighting for a limited number (52) of loggerhead sea turtles tagged and released in this study, suggesting stable size-based growth trajectories across cohorts. The suggestion of cohort effects was enhanced by computing multiple growth rate trajectories which in turn identified a standardized size range associated with each age that was evaluated between 2000 and 2015.

Increased carapace length was associated with all percentile classes between 2000 and 2015, but was most pronounced for the 40th to 79th percentiles. Greatest change in size distribution between 2000 and 2015 for percentile groups that should have experienced slower somatic growth indicates the occurrence of one or more of the following scenarios: natal homing concurrent with approaching sexual maturity (Bowen et al., 2004); high survival rates among older cohorts; and/or reduced recruitment of younger cohorts. Given slightly (but not significantly) reduced prevalence of the CC-A1 haplotype among loggerhead sea turtles in the 40th to 79th percentile group (Figure 2.2), significantly greater changes in size between 2000 and 2015 for these loggerhead sea turtles is not likely attributed to natal homing, especially considering the prevalence of the CC-A1 haplotype on beaches adjacent to the survey area (Bowen et al., 2004). Improved survival for older cohorts is suggested by an estimated increase in the relative occurrence of loggerhead sea turtles estimated to be age 30 in 2000 (6%, 1970 cohort) versus 2015 (39%, 1985 cohort). The increase in the relative proportion of older cohorts
is consistent with greater use of TEDs and increased survival as predicted by Crowder et al. (1994). Unfortunately, this trend of increased survival was not sustained for subsequent cohorts that should have received similar to enhanced protection from TEDs. Therefore, as also cautioned by Crowder et al. (1994), “new, or compensatory, sources of mortality” appear to have influenced the recovery response for loggerhead sea turtles on this foraging ground, with the most plausible explanations being food availability, marine debris ingestion, and/or predation (Witherington et al., 2009; Bjorndal et al., 2013).

Although unrealistic growth rates were required to achieve the smallest portion of the size distribution in 2015 without recruitment, significantly reduced neritic recruitment was evident for the 55th to 85th percentiles and is herein explored further.

Between 2000 and 2015, the size range associated with the 55th to 85th percentiles in 2015 corresponded to ages 18 to 28 for both stable size distribution trajectories, which corresponds to cohorts hatched between 1987 and 1997. Annual nest counts at Florida Index Nesting Beach Survey (INBS) beaches steadily increased between 1989 and 1998 (Witherington et al., 2009) as well as steadily increased through the 1980’s at the Archie Carr National Wildlife Refuge, which typically accounts for 25% of Florida INBS beaches (Ehrhart et al., 2014). Emergence success and hatchling production between 1987 and 1997 are not reported; however, a significant positive linear relationship between annual nest counts and hatchling production at Florida INBS beaches during 2002–2012 (Brost et al., 2015) suggests that hatching production should have also increased between 1987 and 1997. Therefore, consistent with the observation by Arendt et al. (2013) that changes in at-sea survival trajectories between age 0 and maturity can compensate for high or low nesting output, survival for some of the greatest annual
hatchling outputs produced on Florida beaches in the past 40 years appears to have been compromised after these cohorts entered the ocean, which begs the question, “why”?

Three general mechanisms exist for explaining reduced survival at sea and inferred reduced neritic recruitment by the 1987 to 1997 cohorts. The first mechanism addresses an acute gauntlet during the first 48 hours after entering the ocean, during which time loggerhead sea turtles swim frenetically towards the Gulf Stream where they seek shelter and foraging opportunities provided by buoyant Sargassum habitat (Witherington, 2002). Reduced terrestrial and aquatic motor skills for hatchling sea turtles are reported for incubation temperatures <28°C and >30°C (Fisher et al., 2014), which could in turn increase vulnerability to a guild of predators flanking nesting beaches (Stewart and Wyneken, 2004; Whelan and Wyneken, 2007) or otherwise deterring hatchlings from reaching the Gulf Stream. Similarly, despite earlier nesting by loggerhead sea turtles between 1989 and 2003 to compensate for a 2°C change in sea surface temperature (Weishampel et al., 2004), incubation conditions can still vary markedly across years due to precipitation (Wyneken and Lolavar, 2015). The highest proportion of females between 2000 and 2015 was consistently associated with the smallest percentile groups, but it is not possible to differentiate whether this observation is indicative of high female production at exceptionally warm temperatures coupled with high subsequent survival, or if reduced female prevalence among larger cohorts reflects increased precipitation during incubation (Wyneken and Lolavar, 2015). Given consistently low predation rates when hatchlings are most concentrated in shallow coastal waters (Stewart and Wyneken, 2004; Whelan and Wyneken, 2007) prior to rapid dispersal along individualized trajectories to reach common current features (Scott et al.,
mortality in this ephemeral gauntlet should only account for a small amount of decreased neritic recruitment by any cohort.

The second explanatory mechanism for apparent reduced neritic recruitment by the 1987 to 1997 cohorts considers the effect of natural mortality in oceanic habitats. Loggerhead sea turtles hatched in the southeast U.S. spend the first 8 to 12 years of life in oceanic habitats (Bjorndal et al., 2000; Avens et al., 2015), and based on size at age estimates become most vulnerable to interaction with longline fishing gears after age six (Bjorndal et al., 2000, 2003). As such, the greatest proportion of the oceanic phase should be associated with limited threats from fisheries mortalities, thus lending a great deal of support that, barring the ingestion of marine debris (see Schuyler et al., 2014), even natural survival is a challenge in the largely oligotrophic habitats of the oceanic realm. Bjorndal et al. (2003) demonstrated compensatory growth as a coping mechanism for high variability in oceanic food webs along convergent zones. Satellite telemetry also reveals that oceanic loggerhead sea turtles in the North Pacific (Polovina et al., 2006) and the North Atlantic (Mansfield et al., 2014) actively swim against currents and seek out optimal environmental conditions. Nevertheless, given that large scale processes in these habitats alter food web structure across decades (Nakata et al., 2001), it is reasonable to presume that annual survival rates are also equally variable in the oceanic realm.

The cumulative annual effects of fisheries by-catch are also superimposed on challenging survival conditions in oceanic habitats. In a global review (10 ocean basins, three gear types) of marine sea turtle by-catch between 1990 and 2007, Wallace et al. (2010a) reported the highest relative sea turtle interaction rates were associated with longline fisheries in the NW Atlantic Ocean. Although much of the early oceanic phase
of loggerheads hatched in the southeast U.S. occurs in the Eastern North Atlantic Ocean, oceanic habitats in the NW Atlantic Ocean appear to become increasingly important in later developmental years as loggerhead sea turtles prepare to transition to adjacent neritic habitats. Similar size distributions for loggerhead sea turtles in neritic habitats in the Northeast U.S. (Morreale et al., 2005) and among sea turtles captured by longline fisheries in adjacent offshore pelagic waters (Watson et al., 2005) suggest new neritic recruits may be especially vulnerable near the northern terminus of an important neritic foraging ground for loggerhead sea turtles in the NW Atlantic Ocean (Bowen et al., 2004), which could also greatly shape future size structures. Heightened awareness of sea turtle interaction and subsequent mortality in longline fisheries in the 1990’s prompted regulatory actions in the Atlantic (and Gulf of Mexico) pelagic longline fisheries, but these regulations were not implemented until between 2001 and 2004 (Finkbeiner et al., 2011). As such, reduction of loggerhead sea turtles in domestic longline fisheries in the NW Atlantic Ocean did not occur until roughly 15 years after TED regulations first went into effect, but concurrent with the large TED opening size requirement in 2003 (Finkbeiner et al., 2011). Approximately 30% of loggerhead sea turtles captured in neritic habitats during spring and summer and monitored with telemetry devices subsequently over-wintered in oceanic habitats in the NW Atlantic Ocean (McClellan and Read, 2007; Mansfield et al., 2009; Arendt et al., 2012c). Consequently, longline fisheries mortality may continue to contribute to the shaping of size structure in neritic habitats years after initial neritic recruitment.

Interpretation of temporal trends in size structure reported herein is based on the assumption of fixed growth trajectory across time where the dominant influence on
growth is sea turtle size. Although Avens et al. (2013, Supplement 1, Figure S3) demonstrated temporal variability in growth rate across a range of size classes using back-calculated somatic growth rates from humeral annuli, the relative change in growth rate among size classes was considerably less than the change in growth rate within size classes. Furthermore, the greatest within-size class variability was associated with oceanic loggerhead sea turtles <50 cm SCLmin which comprise a very small component of the neritic size structure considered in the present study, but also where stochastic environments and compensatory growth are to be expected (Bjorndal et al., 2003). With respect to the size range of loggerhead sea turtles commonly encountered on neritic foraging grounds, the within-size class temporal variability reported by Avens et al. (2013) were based on relatively few (n = 1 to 14) annual data points per size class (with smallest sample sizes typically associated with the earliest and latest observation years) and the use of broad (10-cm) size classes to increase annual sample size. Therefore, we conclude that methods used in the present study to examine temporal variability in foraging ground size structure have merit. We further suggest that despite the use of Generalized Additive and Generalized Additive Mixed Models used by Bjorndal et al. (2013) and Avens et al. (2015) to characterize temporal variability in growth rates, because these models did not simultaneously account for size and year, there is a high probability that overall growth rate changes across years reported in those published studies reflect auto-correlation between shifting size structure and subsequent overall growth rate as demonstrated in the present study (see Figure 2.4).

The findings reported herein reaffirm the importance of temporal monitoring of size distributions as well as sex and genetic composition of sea turtle populations on
foraging grounds. The study of population dynamics requires data on sex and age-specific abundance; thus, monitoring nest count trends alone is insufficient (Chaloupka and Limpus, 2001). Furthermore, as suggested by Crowder et al. (1994) and reiterated herein, annual nest count data as well as hatching success data do not automatically guarantee future recruitment into the nesting population given that survival at sea for several decades is required for all cohorts, irrespective of original cohort abundance. Although the use of large stranding data sets have some merit for evaluating temporal changes in population structure (Chaloupka et al., 2008b), data sets generated from live captures are most appropriate for demographic studies given known capture location (Hart et al., 2006), the possibility of future recapture, and the availability of intact specimens necessary for accurately measuring size. As revealed by the extensive work of Avens et al. (2013, 2015), the greatest utility of stranding data sets appears to be for aging and direct assessment of sex via gonadal observation. However, even though physical sample sizes can produce nearly 10 times as many annual somatic growth estimates, slow growth rates and the opportunistic nature of stranding events still require a commitment to long-term monitoring to ensure a suitable diversity in sizes/ages to assess temporal trends. The largest stranded animal examined by Avens et al. (2013) was 88.6 cm SCLmin, although Avens et al. (2015) complemented this data set with adult loggerhead sea turtles up to 108.2 cm SCLmin that also stranded. For comparison, the largest recaptured loggerhead sea turtle reported in the present study was 87.0 cm SCLmin. Therefore, a universal limitation for in-water and stranding data sets is access to a suitable number of large individuals to incorporate into growth rate equations.
Variability in morphological delineation of life history stages is reported across populations of loggerhead sea turtles around the world. For example, relative to loggerhead sea turtles in the NW Atlantic Ocean, neritic recruitment in the South Pacific Ocean occurs at larger sizes (Limpus et al., 1994) while nesting on beaches in the Mediterranean Sea is associated with small body sizes (Tiwari and Bjrndal, 2000). Therefore, temporal monitoring of size structure and the ability to comprehend and interpret influences in changes in size structure are essential for effective management of these long-lived species. Loggerhead sea turtles exhibit a type III survivorship curve, with low initial survival rates that improve with life history stage (Conant et al., 2009). However, as demonstrated herein, temporal variation in exposure to threats can alter survival trajectories across cohorts, further delaying the time required to recover sea turtle populations despite decades of effort spent on conservation (Crowder et al., 1994).

Size structure trended away from ‘stable’ between 2000 and 2015, but could eventually trend back towards ‘stable’ if survival rates remain high. In the short-term, however, sustained increases in nesting are likely given prevalence of older cohorts that will be followed roughly a decade later by recently recruited cohorts that appear to exhibit slightly greater female bias. The observations reported herein underscore the importance of demographic shifts governing population ecology, even for a species that was once feared to be headed towards extinction based largely on annual nest counts (Conant et al., 2009). In conclusion, the insights borne from the present study evoke encouragement that perhaps in the near future, loggerhead sea turtles in the NW Atlantic may eventually follow the example of green sea turtles in Hawaii (Chaloupka and Balazs, 2007) and receive the coveted label of ‘conservation success story’.
Figure 2.8. Loggerhead sea turtles were captured by trawling at randomly selected locations in coastal waters between Winyah Bay, SC (33.1°N) and St. Augustine, FL (29.9°N).
Figure 2.9. Change in loggerhead sea turtle size distribution (gray bars; first y-axis) between 2000 and 2015 was statistically similar across most size groups (x-axis) and was not correlated with the percent of loggerhead sea turtles in each group exhibiting the CC-A1 haplotype (circle) or that were female (diamond). Error bars denote 95% confidence intervals for inter-annual parameter means.
Figure 2.10. Differences between observed size (x-axis) and predicted size (y-axis) at recapture/re-sighting ranged from -6.2% to 7.4% (mean ± SE = 0.2% ± 0.4%), but were not statistically different between loggerhead sea turtles at large <3 years (gray circles), three to seven years (open diamonds), or seven to 15 years (black circles).
Figure 2.4. Temporal increase in median observed loggerhead size (gray bar, first y-axis) was auto-correlated (P = 0.001, R = -0.88) with a decrease in theoretical annualized somatic growth rate for measured loggerhead sea turtles (black circles, second y-axis) calculated by applying the growth rate regression equation to all loggerhead sea turtles measured in each capture year.
Figure 2.5. The observed size distribution in 2015 (diamonds) was statistically different (P<0.05) from theoretical size distributions predicted in 2015 by annually applying the growth rate regression equation to loggerhead sea turtle size measurements in each year of capture. Three predicted size distributions for 2015 were evaluated representing a distribution based on all sea turtles measured through 2014 (gray square); a sub-set of 500 randomly selected measurements (gray circle); and a sub-set of 100 randomly selected measurements (open circle).
Figure 2.6. Theoretical growth rates with respect to size distribution (x-axis) based on the regression equation for 52 recaptured and re-sighted loggerhead sea turtles (circles) were generally significantly faster than would have been required to achieve the size distribution observed in 2015 without recruitment for the smallest 50% of sea turtles (triangles). Similar growth rates between calculation methods for the 50th to 85th percentiles precluded distinction in size distribution shift in 2015 as a function of population size increase or growth of resident turtles. Error bars for gray triangles represent ±95% CI.
Figure 2.7. Observed size distribution in 2000 (black triangles) and 2015 (gray circles) were significantly different (P<0.001) from stable size distributions computed for the growth rate equation in Objective 3 (solid line) and a 50% faster growth rate trajectory (dashed line).
Chapter 3. Temporal variability in the frequency of female loggerhead sea turtles captured by trawling at an important foraging ground in the NW Atlantic Ocean and associations with historical climate.

Introduction

Population sex ratio is one of the most important demographic factors regulating the long-term viability of inter-breeding groups of organisms; a minimum number of females is needed to ensure sufficient offspring, but a relative number of males is also necessary for genetic diversity. In the case of genetically inherited sex, Fisher (1958) observed that males and females are not birthed equally, but rather that these differences are offset by sex-linked rates of reproduction and death. Where offspring sex is determined by environmental influences, Charnov and Bull (1989) contend that population sex ratio reflects differential fertilities (a relative measure of fitness) of males vs. females. More specifically, Charnov and Bull (1989) stipulate that the sex with lower mean fertility is “overproduced” in order to compensate for future environmental uncertainty and, thus, is akin to a limiting reagent in a chemical reaction. Because survival is not guaranteed for either sex, over-production of the least fit sex increases the probability that a sufficient number of individuals of this sex will exist at maturity to maintain a population. This conclusion is an especially important observation for long-lived and late-maturing species with environmentally-mediated sex determination such as globally distributed sea turtles.
Sea turtle sex is determined by the proportion of development (Georges, 1989) that occurs at different temperatures during the middle third of incubation in terrestrial nests (Standora and Spotila, 1985; Wibbels, 2003). Incubation temperatures reflect nest depth (Hanson et al., 1998), substrate properties (Mrosovsky and Provancha, 1992; Hays et al., 2001), diel cycles and meteorological events (Godfrey et al., 1996), metabolic heating (Godley et al. 2001a), and subsequent ambient gas (Ackerman, 1977) and nutrient (Bustard and Greenham, 1968) exchange. Incubation duration is typically 40 to 80 days and is inversely correlated with incubation temperature (Mrosovsky et al., 1999). The transition between all male (long, cool incubation periods) and all female clutches spans just a few degrees, with pivotal temperatures that produce equal numbers of each sex around 28-30°C for most sea turtle species (Wibbels, 2003). Georges et al. (1994) demonstrated that all female clutches could be produced at strongly male-biased temperatures when sufficient intra-daily variation occurred; however, the depth of most sea turtle nests generally limits diel temperature variation to inconsequential levels (Hanson et al., 1998; Godley et al., 2001a; Wibbels, 2003). When moisture is sufficient, all male clutches can be also produced above 30°C (Wyneken and Lolavar, 2015).

Temporal stability in sea turtle population sex ratios requires uniform distribution of nesting effort across a broad latitudinal gradient in the absence of climate shifts or concentrated nesting effort in a static environment. Among the seven extant sea turtle species, loggerhead sea turtles (*Caretta caretta*) exhibit the greatest latitudinal diversity in nesting, notably in the northern hemisphere (Wallace et al., 2010b). Subsequently, incubation temperatures for loggerhead sea turtles in the northern hemisphere span 18°C
(Matsuzawa et al., 2002) to 33.7°C (Godley et al., 2001a). Given the transitional range of temperatures for sex determination (Wibbels et al., 2003), if nesting effort occurred evenly across this temperature range, two males would be predicted for every female (Appendix A). When a generalized parabolic survival curve based on hatching and emergence success (Godley et al., 2001a; Matsuzawa et al., 2002; Conant et al. 2009) is superimposed on this temperature distribution, egg production declines but the predicted sex ratio remains static (Appendix A). As such, deviations from a 2:1 male-biased sex ratio either reflect disproportionate population nesting effort at female-biased temperatures and/or differential survival between males and females after hatching.

In light of environmentally mediated sex determination, predicted increases in global air temperatures (IPCC, 2013) could impact future sea turtle sex ratios. The direst prognoses suggest increased female bias that produces male-limited populations (Hawkes et al., 2007; Fuentes et al., 2010) and fewer total females consequent to reduced survival of eggs (Pike, 2014) and hatchlings (Yntema and Mrosovsky, 1982; Fisher et al., 2014). Under extreme temperature increases, nest selection behaviors (Mortimer, 1990; Wood et al., 2000) and an earlier initiation of the nesting season (Weishampel et al., 2004) could prove inadequate as compensation mechanisms, particularly if suitable nesting beach habitat is lost due to sea level rise and shoreline armoring (Fish et al., 2005; Fuentes et al., 2011). Air temperature changes in the northern hemisphere since the 1970s are unrivaled relative to the past 800 to 1400 years (IPCC, 2013); thus, an unprecedented opportunity to study potential sex ratio impacts on sea turtle cohorts also exists.

The loggerhead is the most common temperate sea turtle species in the northern hemisphere. In the NW Atlantic Ocean this species is listed as a “threatened” species
under the ESA and is managed as a single population with five regional recovery units (NMFS and USFWS, 2008). The first decade of life is generally spent in oceanic gyres (Bolten, 2003a,b; Avens et al., 2013) followed by recruitment to neritic habitats where the development continues for nearly two more decades before reaching sexual maturity (Conant et al., 2009). Hatchlings are strongly female-biased in central Florida (Mrosovsky and Provancha, 1992), the epicenter of nesting (Witherington et al., 2009), with less female-bias at higher latitudes (Mrosovsky, 1988). Substantial within-season variability in sex ratio occurs at higher latitudes (Mrosovsky et al. 1984), with less variability at lower latitudes (Mrosovsky and Provancha 1989, 1992). Reduced female bias with increased precipitation is also reported at tropical latitudes where precipitation is the primary driver of seasonal variability (Godfrey et al. 1996, Hays et al. 2003) as well as temperate latitudes where it is not (Wyneken and Lolavar, 2015).

Given the influence of temperature and precipitation on sea turtle sex determination and predicted warming trends for the foreseeable future, examination of temporal variability in contemporary sex ratios of loggerhead sea turtles in the NW Atlantic DPS is warranted. Since 2000, the National Marine Fisheries Services has supported a multi-state trawl survey to intensively sample coastal waters of the southeastern U.S. using a stratified random design. Catch rates (Arendt et al., 2012e,f) and spatial distributions (Arendt et al., 2012b,c) are reported, but to date demographic analyses have primarily addressed aggregate sex ratios and genetic haplotype distributions and/or tested for spatial influences (Arendt et al., 2012c,e). Therefore, the present study was initiated to evaluate temporal change in demographic structure. The first objective was to assess the importance of sample size on the range in temporal
variability in female frequency within and among sea turtle size groups captured in the coastal trawl survey. The second objective was to test the null hypothesis of no difference in temporal and spatial influences on theoretical incubation durations calculated from multi-decadal re-constructions of soil temperatures across the geographic range of nesting for this population in the NW Atlantic. The third objective was to test the null hypothesis of no correlation between temporal variability in theoretical incubation and two climate indices (AMO, NAO) that influence annual nest counts for loggerhead sea turtles in Florida (Van Houtan and Halley, 2011; Arendt et al., 2013).

Methods

Data collection and processing, sea turtles

Loggerhead sea turtle capture and processing was described in Chapter 2, and SCLmin was again only reported here. Blood samples for sex were also collected and processed as described in Chapter 2.

Data collection and processing, environmental data sets

Multi-decadal (1900–2010 and 1960–2013) reconstructions of nest temperature data were obtained for nine spatial areas (Table 3.1, Figure 3.1) encompassing 95% of the geographic range of annual nesting for loggerhead sea turtle nesting in the NW Atlantic Ocean (NMFS and USFWS, 2008): Cape Island, SC; Cumberland Island, GA; Anastasia State Park, FL; Daytona Beach, FL; Melbourne Beach, FL; Boca Raton, FL; Keywadin Island, FL; Siesta Key, FL; and Cape San Blas, FL.

Multi-decadal changes in nest temperatures at each area were estimated using a meteorological land surface model (Noah, Ek et al., 2003) along with multi-decadal meteorological reanalysis data (1960–2013; JRA-55, Kobayashi et al., 2015; 1900–2010;
ERA-20C, Stickler et al., 2014) obtained via the National Center for Atmospheric Research’s Research Data Archive (JRA-55: http://dx.doi.org/10.5065/D6HH6H41; ERA-20C: http://dx.doi.org/10.5065/D6VQ30QG). JRA-55 and ERA-20C data were available at 6-h intervals. Yearly time series of downwelling short and long wave radiation at the surface, wind speed at 10 m, air temperature at 2 m, relative humidity at 2 m, precipitate rate, and atmospheric pressure at the surface were used as forcing variables for the Noah land surface model. All data were bi-linearly interpolated in space from the model grid longitude and latitude of each area and linearly interpreted in time to 30-minute intervals. The soil at all areas was assumed to be sand with an albedo of 0.5 and a longwave emissivity of 0.8. There were 20 soil layers; the top five layers were 1 cm thick, the next 12 layers were 5 cm thick, and the bottom three layers were 10, 20, and 20 cm thick. The integration time was 30-min. The JRA-55 dataset was complete so it was possible to reconstruct soil temperatures for the entire period 1960–2013. The ERA-20C dataset was missing some variables in 1973, 1979, 1984, 1991, 1999, 2004, and 2008, so those years were omitted from the 1900–2010 reconstruction.

Centennial time series of daily mean, minimum, and maximum volumetric soil water (m$^3$ per m$^3$) time series were directly obtained from the ERA-20C data at the same areas for the uppermost (0 to 7 cm) model soil layer.

Unsmoothed (standard, long format) monthly values for the Atlantic Multidecadal Oscillation (AMO) were downloaded from the NOAA Earth Systems Research Laboratory; (http://www.esrl.noaa.gov/psd/data/timeseries/AMO/, accessed 29 November 2015). Because the AMO index is based on sea surface temperature anomalies, values vary depending on download date; however, correspondence between data set versions
also remains high (Arendt et al., 2013). Contrary to emphasis on winter and spring conditions prior to nesting (Van Houtan and Halley, 2011; Arendt et al., 2013), the present study focused on AMO data from April through November to correspond with the nesting and hatching season. Normalization of AMO data (1900 to 2013) was computed in the same manner as Van Houtan and Halley (2011) and Arendt et al. (2013): a grand mean was subtracted from each annual mean, and each corresponding annual value was divided by the grand standard deviation (SD); this produced a data series with a mean of 0 and a SD of 1.

Monthly (April –November) values for the North Atlantic Oscillation (NAO) were uploaded from the Climate Prediction Center of the NOAA National Weather Service (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml; accessed 13 December 2014). Annual means across months were used for analyses.

Statistical analyses, sea turtles

For all analyses, significance level (α) was 0.05 and statistical testing was performed using Minitab 15® (Minitab, Inc., State College, Pennsylvania, USA). Annual percentile size distributions were calculated in MS Excel (2013; Microsoft Office, Redwood City, California, USA) at one-percentile increments between minimum and maximum observed sizes, which were then used to assign all loggerhead sea turtles captured in each year to one of five percentile groups (min to 19th, 20th to 39th, 40th to 59th, 60th to 79th, 80th to max). The percent female composition and 95% confidence intervals (CI) for each size group in each year was computed; 95% CI were computed as the t-statistic (Zar, 1996) multiplied by the standard error (SE) which was computed as the square root of [(percent female) x (1 – percent female) / sample size]. Overlap in
95% CI was used to systematically pool data within and among size groups across years to generate the largest possible sample size for examining temporal variability in the frequency of female loggerheads captured by the trawl survey.

Statistical analyses, reconstructed soil temperatures

Theoretical incubation duration for each of nine spatial areas was calculated using the multi-decadal JRA-55 and ERA-20C reconstructions of soil temperature data in order to determine temporal anomalies among sites and years. A single depth layer was examined for each data set from which a mean daily temperature was calculated. For the JRA-55 data set we selected the 45-cm depth layer based on similarity with in situ data from Jensen Beach, FL (Hanson et al., 1998) and general correspondence to nest depths reported for this species (Godley et al., 2001a). For the ERA-20C data, larger grid size necessitated the use of a shallower depth layer to achieve similar daily temperature values for the nine areas of interest. For the 1 May to 2 September period of interest, mean daily temperature in the JRA-55 data was subtracted from each of 16 ERA-20C depth layers for each of nine spatial areas. For each area, the mean of each depth layer difference was divided by the standard error of depth layer difference. The mean of area index values across depth layers was plotted relative to the magnitude of change in these mean values between successive depth layers, which allowed visualization of the rate of change with increasing depth relative to the mean discrepancy in data set values across sites. From an inflection point on this graph the 15-cm layer was selected as the deepest possible depth. Cumulative degree days above 0°C were calculated for 125 days starting on each day between 1 May and 2 September in each year, corresponding to the primary nesting season for NW Atlantic loggerhead sea turtles.
Theoretical incubation duration for each of these 125 days per site per year was computed as the number of days elapsed between each initiation date and the date when the cumulative degree days equaled or exceeded 1,740; this threshold value was computed as 29°C (the pivotal sex determination temperature of loggerhead sea turtles in the NW Atlantic Ocean; Yntema and Mrosovsky, 1982; Mrosovsky, 1988) multiplied by 60 days, a central-tending incubation duration for this DPS (Mrosovsky, 1988).

Inter-annual mean theoretical incubation duration and the corresponding coefficient of variation (CV) was calculated for each of the 125 theoretical nest lay dates for each spatial area using the soil temperatures calculated with the Noah model using meteorological forcing from the JRA-55 and the ERA-20C data sets. Correlation tests were used to compare inter-annual mean daily incubation durations between data sets for each area. Linear regression was used to test for a significant relationship between incubation duration and latitude. Single linkage hierarchical cluster analysis was used to group areas based on percent similarity in inter-annual mean daily incubation durations in the JRA-55 and ERA-20C reconstructions.

Characterization of temporal anomaly distributions within each spatial area was carried out by computing a grand mean which was then subtracted from each annual mean and then multiplied by 100 to express this anomaly value as a percent deviation from the grand mean for each area. Annual percent deviations for each area were then multiplied by the fraction of annual loggerhead sea turtle nest counts associated with the region in which each spatial area occurred (Table 3.1). Nest count fractions were estimated from the 2nd Revision to the Recovery Plan for NW Atlantic Loggerhead Sea Turtles (NMFS and USFWS, 2008) and Witherington et al. (2009) which examined
temporal-spatial trends in Florida nest counts. Where two spatial areas occurred within the same DPS-weighting region, the fraction associated with each spatial area was halved so that the two areas summed to the full weight.

The annual sum of weighted spatial areas was computed for spatial groupings identified by cluster analysis, herein referred to as “DPS-weighted” anomaly values. Correlation testing was used to examine relationships between DPS-weighted anomaly series generated for each data set (i.e., JRA-55 and ERA-20C), to determine if only the greater temporal coverage ERA-20C data set could be used for testing associations with two climate indices (AMO, NAO). Correlation tests were used to evaluate relationships between the DPS-weighted anomaly series and two climate indices (AMO, NAO) at two levels: (a) inter-annual change and (b) cumulative change within each data series.

Inter-annual mean and coefficient of variation of maximum daily (1 May to 30 November) volumetric soil water in depth layer one (0 to 7 cm) was computed for each of nine areas. Differences among areas in annual cumulative volumetric soil water contents were compared (KW test). A grand mean of annual volumetric soil water content was computed for each area, which was then subtracted from each annual mean to evaluate temporal anomaly trends, and tested for differences among areas using a KW test. A single anomaly series was computed as the mean percent change across sites for each year and then tested for significant correlation with the AMO and NAO at both (a) inter-annual and (b) cumulative change levels.

**Results**

*In-water sea turtle captures*
Trawling in coastal waters between 2000 and 2013 captured a total of 1,556 loggerhead sea turtles for which sex was assigned, of which 1,056 (68% ± 5% CI) were classified as female based on circulating testosterone levels. Confidence interval range within and among size groups across years ranged from 23% to 47% annually, and from 13% to 18% across years for pooled data. Considerable overlap in 95% CI at all temporal levels examined precluded detection of statistical differences in the temporal capture frequency of female loggerhead sea turtles between 2000 and 2013; however, temporal oscillatory trends were noted across most size groups and overall (Figure 3.2).

Temporal anomalies in nest incubation duration and associations with climate

Mean theoretical incubation duration from re-constructed soil temperatures for nest lay dates between 1 May and 2 September at nine spatial areas encompassing >95% of nesting activity for loggerhead sea turtles in the NW Atlantic DPS was 75 days (CV = 0.6; n = 61,875) for the JRA-55 data set (1960 to 2013) and 85 days (CV = 0.5; n = 117,000) for the ERA-20C data set (1900 to 2010). However, across all areas, only 6% to 14% (JRA-55) and 5% to 48% (ERA-20C) of theoretical incubation durations spanned 40 to 80 days, which underscores the caveat that these data sets are better suited for examining temporal anomaly trends than for calculating precise incubation durations.

Year to year patterns in theoretical incubation duration were significantly correlated (P<0.001, r = 0.91 to 0.99) between data sets for each area (Appendix B). In both data sets, a linear seasonal decrease in theoretical incubation duration (slope = -0.8 to -0.2) was associated with four areas north of Cape Canaveral, FL; however, a parabolic to increasing seasonal pattern of theoretical incubation duration (slope = 0.0 to 0.3) was observed for the remaining five areas. A significant (F₈ = 48.45, P<0.001, r² = 0.86)
inverse relationship was noted between latitude and the seasonal change in incubation
duration as follows: Incubation duration (days per day) = 4.59 – (0.161 x latitude).

Hierarchical cluster analysis of inter-annual mean daily incubation duration
between 1 May and 2 September consistently generated two primary clusters across data
sets with respect to slope: the first cluster consisted of four negative slope areas located
north of Cape Canaveral, FL on the eastern seaboard (JRA-55 = 96 to 99% similarity;
ERA-20C = 98 to 99% similarity) herein referred to as ‘north’, while the second cluster
consisted of four areas along both coasts of peninsular Florida (JRA-55 = 96 to 99%
similarity; ERA-20C = 98 to 99% similarity) herein referred to as ‘south’. Assignment of
Cape San Blas, FL to a geographical cluster varied among data sets; in the JRA-55 data
set this area was assigned to the ‘south’ cluster (96% similarity), whereas in the ERA-
20C data set this area was assigned to the ‘north’ cluster (92% similarity). Given a
higher relative percent similarity score in the JRA-55 data set and closer proximity to
other ‘south’ areas, Cape San Blas was included as a ‘south’ area.

Temporal trends (1960–2010) in annual DPS-weighted incubation durations for
44 years common to the JRA-55 and ERA-20C were significantly correlated for ‘north’
(P<0.001, r = 0.83; Figure 3.3a,c) and ‘south’ (P<0.001, r = 0.68; Figure 3.3b,d) areas.
Among ‘north’ areas, annual DPS-weighted changes during these 44 universal years
ranged from -9% to 6% for the ERA-20C data set and -9% to 7% for the JRA-55 data set.
During the same period, annual DPS-weighted changes among ‘south’ areas ranged from
-47% to 37% for the ERA-20C data set and -38% to 65% for the JRA-55 data set.

An inverse relationship was noted between the AMO and all four DPS-weighted
incubation duration time series (Figure 3.4a,b). Correlation coefficients for three
significant (P<0.001) correlations were -0.35 (‘north’, cumulative anomaly); -0.48 (‘south’, annual anomaly); and -0.56 (‘north’, annual anomaly). There was a positive relationship between the NAO and all four DPS-weighted data series (Figure 3.4c,d). Three significant (P = 0.003 to 0.038) correlations were detected, with correlation coefficients of 0.31 (‘north’, cumulative anomaly); 0.36 (‘south’, cumulative anomaly); and 0.44 (‘north’, annual anomaly).

Between 1 May and 30 November, inter-annual variation in surface volumetric soil water accumulation ranged from 18 m$^3$ per m$^3$ (Daytona Beach, FL) to 32 m$^3$ per m$^3$ (Keywadin, FL and Boca Raton, FL), and a significant difference ($H_8 = 773.03; P<0.001$) was detected between areas (Figure 3.5). Inter-annual deviation from the grand mean within areas ranged from 30% (-18 to 12%) for Cape San Blas, FL to 83% (-52% to 31%) for Daytona Beach, FL; however, inter-annual deviation from the grand mean was not statistically different among areas ($H_8 = 2.15; P = 0.976$). Between 1900 and 2010, the mean anomaly series among areas was not significantly correlated with the AMO at the annual ($P = 0.087, r = -0.17$) nor the cumulative ($P = 0.786, r = -0.03$) change levels since 1900. Between 1960 and 2010, the mean anomaly series among areas was not significantly correlated with the NAO at the annual level ($P = 0.620, r = -0.08$) nor as a cumulative anomaly change since 1960 ($P = 0.201, r = -0.20$).

**Discussion**

During a period of observation representing nearly half the duration between hatching and age at first maturity for loggerhead sea turtles in the NW Atlantic Ocean (Conant et al. 2009), statistical temporal variation in the frequency of females captured was not detected due to large confidence intervals associated with annual data. However,
a general oscillatory trend in female frequency was noted overall, as well as a slight
decline in the female frequency among the smallest loggerhead sea turtles captured
between 2000 and 2013 (Figure 3.2a). Variation in annual confidence intervals for
pooled observations was comparable with annual variation of up to 15% reported for
hatchling sex ratios (Mrosovsky and Provancha, 1992; Wyneken and Lolavar, 2015) at
the epicenter of nesting for this population (Witherington et al., 2009). Godfrey et al.
(1996) predicted a wider range (20% to 90%) in inter-annual variation in cohort female
frequencies using reconstructed incubation temperatures for a single beach in Suriname;
however, this magnitude of variation across cohort proxies has never been reported for
loggerhead sea turtles captured on foraging grounds associated with this population
(Wibbels et al., 1991; Delgado et al., 2010).

Relative to other size groups, generally greater female frequency among the
smallest loggerhead sea turtles captured is consistent with warmer air temperatures since
1978 (IPCC, 2013) and, in turn, greater probability of female production. In addition to
increased probability of female production, exceptionally warm temperatures may
decrease hatchling survival in situ (Godley et al., 2001a; Matsuzawa et al., 2002) and
post-emergence (Fisher et al., 2014), which in turn could have potentially stabilizing
effects on sex ratios across cohorts. Although it was not possible to age loggerhead sea
turtles captured in this trawl survey, assuming a mean age of recruitment of 10 (Bjorndal
et al., 2000; Avens et al., 2013), new recruits between 2000 and 2010 originated from
cohorts associated with increasing annual nest counts, while new recruits since 2010
originated from cohorts associated with declining annual nest counts (Witherington et al.,
2009). Fisher et al. (2014) expressed concern for reduced female survival at
exceptionally warm nest temperatures; thus, when coupled with declining annual nest counts the probability of encountering small female loggerhead sea turtles should have decreased in later years of the survey. Although not statistically different, it is worth noting that females were less common among the smallest loggerhead sea turtles captured during 2008–2011 than during the first four years of the survey (Figure 3.2a).

Furthermore, because male and female loggerhead sea turtles are not spatially partitioned on this foraging ground (Arendt et al., 2012c) and given that both sexes exhibit site fidelity (Arendt et al., 2012b), differences in the prevalence of females among size groups should reflect incubation-level effects and/or differential survival among the sexes in the initial oceanic phase.

The potential for long-term, cyclical variability in gender bias across cohorts was supported by a significant correlation between the probability of producing females and the AMO for all nine areas for which theoretical incubation durations were analyzed. Association between the AMO and population abundance of a diversity of taxa is reported (Nye et al., 2014); however, the association between the AMO and annual nest counts for loggerhead sea turtles represents a ‘correlation without causation’ given that the underlying mechanism has never been identified (Van Houtan and Halley, 2011; Arendt et al., 2013; Chapter 1). Furthermore, as noted in Chapter 1, without known ages it is impossible to differentiate between cohort effects that persisted across years and contemporary sex distributions that represent the cumulative effects of time. However,
because warm phases of the AMO are associated with increased precipitation in central and south Florida\(^6\), the lack of a significant correlation between the AMO and surface soil water content is quite informative for sea turtle nest management. Although localized precipitation can acutely decrease incubation temperature and increase male clutch bias (Godley et al., 2001b; Matsuzawa et al., 2002; Wyneken and Lolavar, 2015), at broad scales it appears that temperature exerts the greatest influence on incubation temperatures, likely due to the episodic and localized nature of precipitation events (which are included in the soil temperature calculations).

Geographical groupings of four beaches north of Cape Canaveral, FL and five beaches south and west of this zoogeographic barrier underscores the relationship between coastal ocean temperatures and localized climate on adjacent beaches. In terrestrial systems, latitude and elevation exert critical influences on micro-climates (Richardson et al., 2004; Franco et al., 2006). In the present study, nest elevation above sea level was held constant and latitude ranged from 26°N to 33°N; however, areas did not cluster by latitude. Instead, three beaches in the Gulf of Mexico (Cape San Blas, Siesta Key, Keywadin) and two beaches in south and central Florida (Boca Raton, Melbourne) clustered together, suggesting a hydrographic connection to coastal waters of the Gulf of Mexico and the related Gulf Stream and Florida currents. On green sea turtle nesting grounds in Australia, Fuentes et al. (2009) demonstrated better model fits for nest sex ratio prediction when sea surface and air temperature were both included. In the present study, the influence of coastal microclimate was reinforced by the similarity of

\(^6\) Frequently asked questions about the Atlantic Multidecadal Oscillation (AMO), Question Number 6: How does the AMO effect Florida? Online (accessed 17 January 2016): http://www.aoml.noaa.gov/phod/amo_faq.php#faq_4
Melbourne Beach to Boca Raton which was more distant than Daytona Beach, but corresponded to a narrower continental shelf and in turn greater influence from the Gulf Stream (Olson et al., 1983).

Despite a more northerly distribution and nearly four times the range in latitude across areas, inter-annual trends in soil temperatures among four areas north of Cape Canaveral, FL exhibited a higher degree of similarity than five areas south and west of Cape Canaveral, FL (Figure 3). This observation suggests tremendous potential for influence on demographic structure, particularly with respect to genetics. Two dominant loggerhead haplotypes (CC-A1, CC-A2) account for more than 90% of all genetic haplotypes found on nesting beaches and foraging grounds in the NW Atlantic (Bowen et al., 2004; Arendt et al., 2012c). However, CC-A2 is extensively found in nests laid in the range associated with ‘south’ beaches in the present study and systematically declines in frequency with northward distance from Cape Canaveral, FL (Shamblin et al., 2011b). In contrast, CC-A1 is ubiquitously distributed throughout the nesting range of loggerhead sea turtles in the NW Atlantic, but it almost exclusively accounts for all nests laid north of Florida (Encalada et al., 1998; Bowen et al., 2004; Shamblin et al., 2011b). Therefore, more uniform inter-annual variation in sex ratio among nests laid by CC-A1 mothers should occur north of Cape Canaveral, FL which in turn should exaggerate the magnitude of sex ratio variability among cohorts. In contrast, greater intra-annual variability in CC-A2 sex ratio should dampen inter-annual oscillations to achieve greater temporal sex ratio stability. Given size-based differences in the prevalence of females and limited sample size following partitioning by size and year, we did not attempt to further partition
sample sizes by genetic haplotype to test this hypothesis; however, collaborative studies across regions may be able to do so if size-based trends were similar across study areas.

A near linear decrease in theoretical incubation duration during 1974–2013 as the AMO transitioned between cool and warm phases casts doubt on contemporary concerns that sea turtle populations are becoming irreversibly male-limited consequent to single trajectory climate change in the NW Atlantic Ocean (Hawkes et al., 2007). Assuming that multi-decadal oscillations are not unique to this ocean basin, large-scale climate oscillations may also be fueling similar demographic concerns worldwide (Chaloupka et al., 2008a; Fuentes et al., 2009, 2010, 2011). Since 1860, the AMO has alternated between warm and cool phases, with a full cycle periodicity of about 65 years (Nye et al., 2014). Given the length of the AMO period and a steady transition out of the last cool phase since 1974, it is reasonable to presume that the AMO should begin to transition back to the cool phase by 2020 and continue to do so for the next 20+ years, provided that overall predicted warming (IPCC, 2013) does not overwhelm the cool phase.

The next several decades may be especially important in sea turtle conservation, especially considering trends of increasing climate variability and extreme events (Hawkes et al., 2007; Chaloupka et al., 2008a; Fuentes et al., 2010; Laloë et al., 2016). Increased relative abundances on foraging grounds and/or annual nest counts on beaches are reported for multiple sea turtle species across ocean basins, suggesting potential improvement in population structure under contemporary climate conditions and/or the benefits of conservation actions enacted over the past 40 years (Chaloupka and Limpus, 2001; Balazs and Chaloupka, 2004; Dutton et al., 2005; Beggs et al., 2007; Arendt et al., 2013). Thus, provided that anthropogenic influences on survival remain stable, the
influence of the AMO on sea turtle populations should become easier to elucidate presuming that the AMO will soon transition back to the cool phase (Nye et al., 2014).

Cyclical variability in environmentally-mediated sex determination has profound implications for sea turtles and other long-lived species. Although the lowest prevalence of females was associated with the largest loggerhead sea turtles captured in this survey, increased catch rates for large juveniles nearing the transition to adulthood have been reported for this foraging ground (Arendt et al., 2012f). If increasing relative abundance of this size group is representative of the population, it could in part explain a surge in nesting on Florida beaches since 2008, which Arendt et al. (2013) demonstrated should be initiated by neophyte nesters. Presuming that annual survival rates do not decline below contemporary levels, slightly elevated (relative to other size groups) prevalence of females among smaller loggerhead sea turtles should also help to rebuild the nesting population as those sea turtles mature. Given connectivity between catch rates and demographic distributions on a coastal foraging ground surveyed regularly since 2000 (Arendt et al., 2012e) and nesting activity in Florida, continued monitoring of critical demographic metrics on foraging grounds in the southeast US is highly advisable, a sentiment previously expressed by Braun-McNeill et al. (2007). Much progress has been made in the fight to reverse the global decline of sea turtles, but as illustrated by the findings of Chapter 1 and reiterated herein, variable environmental conditions are predicted to exert long-term influences on population structure; thus, long-term monitoring of the relative abundance of juvenile female sea turtles is necessary for making informed management decisions.
Table 3.1. Spatial distribution of annual nesting for loggerhead sea turtles in the NW Atlantic Ocean, approximated from the 2nd Revision to the Recovery Plan for NW Atlantic Loggerhead Sea Turtles (NMFS and USFWS, 2008) and Witherington et al. (2009), was used to compute a weighted annual anomaly series for incubation duration among reconstructed soil temperature data sets located north vs. south and west of Cape Canaveral, FL. Four recovery units were represented as follows: Northern Gulf (NGRU), Dry Tortugas (DTRU), Peninsular Florida (PRU), and north of Florida (NRU).

<table>
<thead>
<tr>
<th>Nesting region</th>
<th>Recovery Unit</th>
<th>Soil Dataset Area</th>
<th>Est. annual nests</th>
<th>DPS-weight (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Texas to Alabama</td>
<td>NGRU</td>
<td></td>
<td>&lt;1%</td>
<td></td>
</tr>
<tr>
<td>Florida, Panhandle</td>
<td>NGRU</td>
<td>Cape San Blas</td>
<td>3680</td>
<td>2.9</td>
</tr>
<tr>
<td>Florida, Southwest</td>
<td>PRU</td>
<td>Siesta Key, Keywadin</td>
<td>7427</td>
<td>5.9</td>
</tr>
<tr>
<td>Dry Tortugas</td>
<td>DTRU</td>
<td></td>
<td>1100</td>
<td>0.9</td>
</tr>
<tr>
<td>Florida, Keys to Juno Beach</td>
<td>PRU</td>
<td>Boca Raton</td>
<td>14854</td>
<td>11.9</td>
</tr>
<tr>
<td>Florida, Juno Beach to Cape Canaveral</td>
<td>PRU</td>
<td>Melbourne</td>
<td>71087</td>
<td>56.9</td>
</tr>
<tr>
<td>Florida, Cape Canaveral to GA border</td>
<td>PRU</td>
<td>Dayton, Anastasia</td>
<td>12732</td>
<td>10.2</td>
</tr>
<tr>
<td>Georgia</td>
<td>NRU</td>
<td>Cumberland</td>
<td>1960</td>
<td>1.6</td>
</tr>
<tr>
<td>South Carolina</td>
<td>NRU</td>
<td>Cape Island</td>
<td>9240</td>
<td>7.4</td>
</tr>
<tr>
<td>North Carolina</td>
<td>NRU</td>
<td></td>
<td>2800</td>
<td>2.2</td>
</tr>
<tr>
<td>Virginia to New Jersey</td>
<td>NRU</td>
<td></td>
<td>&lt;1%</td>
<td></td>
</tr>
</tbody>
</table>

Total: 124880
Figure 3.1. Loggerhead sea turtles were captured by trawling in a coastal survey between Winyah Bay, SC (33.1°N) and St. Augustine, FL (29.9°N) during 2000–2003 and 2008–2013, nearly the same coastline as between Cape Island, SC (CPI), Cumberland Island, GA (CMB), and Anastasia State Park, FL (ANA). Soil temperatures from two reconstructed climate data sets (JRA-55, ERA-20C) were evaluated at these three areas as well as Daytona Beach, FL (DAY); Melbourne Beach, FL (MEL); Boca Raton, FL (BOC); Keywadin Island, FL (KEY); Siesta Key, FL (SIE); and Cape San Blas, FL (CSB) which collectively encompass >95% of range of nesting habitat for loggerhead sea turtles in the NW Atlantic population.
**Figure 3.2.** Annual female frequency (%) (black circle) and 95% confidence intervals (upper = black dashed line; lower = gray dashed line) for five loggerhead sea turtle size groups (A = min to 19th percentile; B = 20th to 39th percentile; C = 40th to 59th percentile; D = 60th to 79th percentile; E = 80th percentile to max) and overall (F).
Figure 3.3. Annual percent departure from the grand mean (y-axis) and DPS-weighted departure from the grand mean (secondary y-axis) was computed for nine spatial areas encompassing >95% of annual nesting for loggerhead sea turtles in the NW Atlantic to assess temporal trends in the probability of increasing (positive y-axis) or decreasing (negative y-axis) male-bias. Bars in panels A (ERA-20C) and C (JRA-55) correspond to four ‘north’ areas as follows: Cape Island, SC (red); Cumberland Island, GA (green); Anastasia State Park, FL (yellow); and Daytona Beach, FL (blue). Bars in panels B (ERA-20C) and D (JRA-55) correspond to five ‘south’ areas as follows: Melbourne Beach, FL (red); Boca Raton, FL (green); Keywadin, FL (yellow); Siesta Key, FL (blue); and Cape San Blas, FL (gray). In all panels, the black dashed line depicts the annual DPS-weighted impact associated with the bars and hence the secondary y-axis is scaled accordingly for ‘north’ and ‘south’ areas.
Figure 3.4. Annual DPS-weighted anomalies in incubation duration (closed circle) in the context of cumulative change since series origin (open circle) revealed a smooth temporal oscillation between 1900 and 2010 in reconstructed soil temperature data ‘north’ (panels A,B) and ‘south’ (panels C,D) of Cape Canaveral, Florida. Significant correlation was noted between the AMO (gray bars, panels A & C) and annual incubation duration anomalies for both ‘north’ and ‘south’ areas, but the AMO was only correlated with the cumulative anomaly for the ‘north’ area. Significant correlation was also noted between the NAO (gray bars, panels B & D) and annual incubation duration anomalies for both ‘north’ and ‘south’ areas, but the NAO was only correlated with the cumulative anomaly for the ‘south’ area.
Figure 3.5. Seasonal (1 May to 30 November) volumetric soil water at the different geographic areas (panel A) and aggregate (panel B) annual (black line, mean ± standard error) and cumulative (gray line) anomaly series. Soil water areas in panel A are denoted (top to bottom) as follows: black square (Cape San Blas, FL); gray circle (Cape Island, SC); open square (Anastasia, FL); open circle (Keywadin and Boca Raton, FL); gray triangle (Melbourne, FL); black triangle (Cumberland Island, GA); gray diamond (Siesta Key, FL); and black diamond (Daytona, FL).
Conclusions

Population cycles are well known in ecology, but the importance of cyclicality to extinction risk is less well understood. Anthropogenic contribution to extinction risk is also well documented; however, there is difficulty in distinguishing the importance of these two broad sources of influence when they overlap considerably. In fisheries biology, it is not uncommon to extrapolate data to estimate total impacts. For instance, Lewison et al. (2004) and Wallace et al. (2010a) examined rates of interactions between sea turtles and various fishing gears for a subset of the fisheries, and then extrapolated those rates using reasonable linear assumptions to estimate a cumulative annual impact. However, in addition to not knowing what fraction of the population was affected by the cumulative annual impacts, a fundamental flaw with this type of reasoning is that, due to variable demographic structure, population responses to perturbations are non-linear, particularly for long-lived species. It wasn’t until I built the model in Chapter 1 to examine across-cohort effects in response to stochastic conditions and small deviations in survival through anthropogenic activities that I fully appreciated the perils of linear thinking, which I am just as historically guilty of as the next person.

The influence of environmental regulation has received considerably more attention in the Pacific Ocean than in the Atlantic Ocean, both in general and with respect to sea turtles. Although Balazs and Chaloupka (2004) attribute the recovery of green sea turtles in Hawaii to restrictions on harvesting that occurred in the 1970’s, they also note that the recovery response occurred much sooner than anticipated, suggesting the
importance of factors other than just conservation actions. Similarly, Chaloupka (2001) reported variation in egg productivity among green sea turtle rookeries in Southeast Asia as a result of environmental stochastity and suggested the need to validate population models accordingly. Bottom-up regulation of foraging ground productivity and annual nesting for leatherback (Wallace et al., 2006; Saba et al., 2008) and loggerhead (Chaloupka et al., 2008a) sea turtles has also been demonstrated in the North Pacific Ocean. However, recent increases in leatherback sea turtle nesting in the NW Atlantic (Robinson et al., 2014) despite longline fishery interactions occurring twice as frequently in this basin as compared to the North Pacific (Lewison et al., 2004) reinforce that anthropogenic impacts are superimposed on environmental influences, not vice-versa.

The need to conduct in-water monitoring of relative abundance concurrent with demographic studies is well-documented (Braun-McNeill et al., 2007; NRC, 2010). However, because of greater expense and logistical demands associated with in-water research, a proliferation of coordinated studies has not manifested despite the best intentions of some resource management agencies for this to occur\(^7\). Consequently, only a handful of long-term in-water studies exist for examining temporal trends, with the longest running in-water studies located at the intake canal for the St. Lucie Power Plant\(^8\) near Jensen Beach, FL as well as in the Indian River Lagoon adjacent to the Archie Carr National Wildlife Refuge (Ehrhart et al., 2007). Other studies are characterized by intermittent sampling (Epperly et al., 2007); however, this approach is associated with

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substantial start-up costs due to the potential loss of personnel and vessel infrastructure during the lag periods in between sampling years. For this reason, the SCDNR has been very fortunate to receive annual federal funding to support the in-water data collection efforts which contributed greatly to this dissertation. Nevertheless, despite a generally favorable perception of the diversity of data collected by this trawl survey, funding is still allocated annually and as competition for funding resources increases, the possibility of reduced resources to conduct this in-water survey in the future increases. However, as illustrated by this dissertation, such course of action would be a mistake given that informed management of sea turtles requires more, not less, in-water data collection.

The overarching theme of this dissertation was to assess the probability that loggerhead sea turtles in the NW Atlantic Ocean could potentially be declared recovered within 50 years of protection under the Endangered Species Act. With regards to foraging grounds, the 2008 Revision to the Recovery Plan for this population stipulates just two demographic recovery requirements. First, “a network of in-water sites, both oceanic and neritic” must be “distributed across the foraging range….and monitoring is implemented to measure abundance (NMFS and USFWS, 2008).” Second, there must also be “statistical confidence (95%) that a composite estimate of relative abundance from these sites is increasing for at least one generation (NMFS and USFWS, 2008).” Capture and demographic data for some index sites began coincident with population protection (Mendoca and Ehrhart, 1982; Bjorndal et al., 2013), and in-water studies have been conducted at numerous locations across developmental habitats; thus, synthesis of available data sets is recommended as a surrogate data network to assess recovery, akin to pooling of nesting data used for the 2009 global status review (Conant et al., 2009).
Based on the suggestion of strong recruitment and survival of juvenile female loggerheads in the SCDNR-managed sea turtle trawl survey, the prognosis for stable to increased annual nest counts for loggerhead sea turtles over the next two decades appears to be favorable. However, mathematical modeling of a theoretical population resembling an important subset of the PRU (i.e., Florida INBS beaches) suggests that it is far less likely that annual nest count recovery criteria set for the PRU will be achieved. The long-term stable oscillation revealed in Chapter 1 suggests that the culmination of stochastic rather than unidirectional processes likely mediates the majority of variation in annual nest counts. Therefore, a paradigm shift in the delineation of recovery metrics is recommended that (a) places greater emphasis on monitoring the demographic structure of juveniles and (b) establishes an appropriate annual nest minima for maintaining nesting assemblages. Given that conservation actions work to minimize wanton mortality, there is no reason to discontinue them should any sea turtle species ever be officially de-listed from the ESA. In closing, even if conservation efforts during the past four decades effect are trumped by environmental influences, they have undoubtedly increased awareness of anthropogenic activities where greater environmental stewardship is needed, a social goal that has persisted since at least the time of Aristotle.
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Appendix A. Relationship between sex ratio and survival across the range of nest temperatures reported for loggerhead sea turtles. Assuming equal nesting effort (measured as 100 individuals) across the known range (Godley et al. 2001, Matsuzawa et al. 2002) of incubation temperatures (x-axis), the transition temperature range (black line) for loggerhead sea turtles in the NW Atlantic DPS (Yntema and Mrosovsky 1982) should produce a two males per female egg. When a theoretical survival curve (red line) configured to average 0.54 (i.e., the mean emergence success of Conant et al. (2009)) that peaks at the 29°C pivotal temperature of Yntema and Mrosovsky (1982) is superimposed on this theoretical nesting distribution, the number of eggs produced declines but the predicted sex ratio remains unchanged.
Appendix B. Inter-annual mean and CV for daily soil temperature and water content for nine spatially-distinct reconstructed data sets (JRA-55 and ERA-20C). In all panels, the black line denotes inter-annual mean and the gray line denotes inter-annual CV for theoretical incubation duration (days) between 1 May and 2 September during 1960–2013 (JRA-55, panel 1 for all series), 1900–2010 (ERA-20C, panel 2 for all series), or inter-annual mean and CV for maximum surface soil water (m$^3$ per m$^3$) content between 1 May and 30 November during 1900–2010 (ERA-20C, panel 3 for all series). Data were evaluated for nine geographic areas, ordered north to south/west, as follows: A = Cape Island, SC; B = Cumberland Island, GA; C = Anastasia State Park, FL; D = Daytona Beach, FL; E = Melbourne, FL; F = Boca Raton, FL; G = Keywaadin Island, FL; H = Siesta Key, FL; I = Cape San Blas, FL.
Appendix B, continued.
Appendix B, continued.