

Quantifying the impacts of future sea level rise on nesting sea turtles in the southeastern United States

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Abstract. Sandy beaches, a necessary habitat for nesting sea turtles, are increasingly under threat as they become squeezed between human infrastructure and shorelines that are changing as a result of rising sea levels. Forecasting where shifting sandy beaches will be obstructed and how that directly impacts coastal nesting species is necessary for successful conservation and management. Predicting changes to coastal nesting areas is difficult because of a lack of consensus on the physical attributes used by females in nesting site choice. In this study, we leveraged long-term data sets of nesting localities for two sea turtle species, loggerhead sea turtle, *Caretta caretta*, and green sea turtle, *Chelonia mydas*, within four barrier island National Seashores in the southeastern United States to predict future nesting beach area based on where these species currently nest in relation to mean high water. We predicted the future location of nesting areas based on a sea level rise scenario for 2100 and quantified how impervious surfaces will inhibit future beach movement, which will impact both the total available nesting area and the percentage of nesting area predicted to flood following a hurricane-related storm surge. Contrary to our expectations, those barrier islands with the greatest levels of human infrastructure were not projected to experience the greatest percentage of sea turtle nesting area loss due to sea level rise or storm surge events. Notably, loss of nesting beach areas will not have equal impacts across the four Seashores; the Seashore projected to have the least amount of total nesting area lost and percentage nesting area lost currently has the highest nesting densities of our two study species, suggesting that even low levels of beach loss could have substantial impacts on future nesting densities and disproportionate impacts on the population growth of these species. Our novel method of estimating current and future nesting beach area can be broadly applied to studies requiring a bounded area that encompasses the part of a beach used by nesting coastal species and will be useful in comparing future global nesting densities and population trajectories under projected future sea level rise and storm surge activity.

Key words: coastal nesting; coastal squeeze; global change; sea level rise; sea turtle; storm surge.

INTRODUCTION

Coastal areas face increasing impacts from multiple global change drivers (Jackson et al. 2001, Small and Nicholls 2003, Zhang et al. 2004, Harley et al. 2006, Vitousek et al. 2017). Increased global temperatures contribute to rising sea levels through thermal expansion of water and ice-sheet melting, with global sea level expected to rise between 0.52 and 0.98 m by 2100 if current emission trends continue (Church et al. 2013). Global sea levels over the last century have risen 1.5–1.9 mm/yr, with an acceleration to 2.8–3.6 mm/yr over the last two decades (Church et al. 2013). Global sea

level rise projections demonstrate scientific consensus that sea levels will continue to rise over the coming decades at a rate that likely exceeds historical rates (National Research Council 2012, Parris et al. 2012, Church et al. 2013, U.S. Global Change Research Program [USGCRP] 2018). One of the larger unknowns in predictions of sea level rise over the next century stems from the potential for rapid dynamic collapse of ice sheets, which could increase sea level rise to over 2 m by 2100 (Allison et al. 2009, Ritz et al. 2015, Kopp et al. 2017, Slater and Shepherd 2018, Bamber et al. 2019).

Concurrently, coastal areas face increasing pressure from coastal development (Small and Nicholls 2003). In the United States, it is estimated that approximately 60% of dry land within 1 m above tidal wetlands between Massachusetts and Florida are developed or planned to be developed (Titus et al. 2009). Beaches become narrower when sea level rise is combined with hard surfaces

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along the shoreline in the form of buildings, roads, and other shoreline structures; this beach narrowing is known as “coastal squeeze” (Fish et al. 2005, Mazari et al. 2009, Noss 2011). Historically, in the absence of human development, as sea levels rose, sandy beaches would shift landward (FitzGerald et al. 2008); however, when these beaches are adjacent to hard surfaces, this shift could be halted, preventing beach movement thus shrinking beach area (Noss 2011). At the same time, the severity of extreme weather events is increasing (Irish et al., 2014), potentially washing out beach areas, flooding the nests of beach nesting species (Van Houtan and Bass 2007), and changing beach morphology for future nesting seasons (Houser et al. 2015). The combined effects of these habitat-changing forces could decrease available habitat for species that rely on sandy beaches for part of their lifecycle (Von Holle et al. 2019).

Population decline and extinction are rarely the result of a single process (Brook et al. 2008, Mantyka-Pringle et al. 2012). Sea turtles, as long-lived and late-maturing species, are not expected to have the capacity to adapt to rapid anthropogenic changes (Awise et al. 1992, Hawkes et al. 2009, Hamann et al. 2013). Access to suitable sandy beaches for nesting is a critical determinant of species success. Female sea turtles must be able to find sandy beach habitat to dig nests and lay eggs in areas where the eggs will be undisturbed for the duration of incubation (approximately 60 d). Nest site location is a delicate balance of flooding and erosion risk if too close to the ocean (Mrosovsky 1983, Hays and Speakman 1993) and desiccation and depredation risk if too far inland (Witherington et al. 2009). The narrowing of sandy beaches due to coastal squeeze reduces habitat for females to oviposit (Reece et al. 2013), potentially causing females to nest closer to higher risk areas (Witherington et al. 2011). By impeding beach retreat, coastal squeeze may lead females to nest at lower elevations and closer to the high water line, putting these nests at increased flooding risk during high tide and storm events. If the same number of females are nesting in a smaller area, this increased density enhances risks of depredation, disease transmission, and the likelihood of females accidentally digging up a previously laid nest (Caut et al. 2006, Girondot et al. 2006, Tiwari et al. 2006, Leighton et al. 2010). Beyond direct density-dependent effects, beach width is an important environmental factor in female choice of nesting site, with females choosing not to nest on beaches below a certain width, though these preferences vary by species and population (Garmestani et al. 2000, Kaska et al. 2010, Zavaleta-Lizárraga and Morales-Mávil 2013, Randall 2015, Dunkin et al. 2016).

Nest placement is critical not only in terms of risks for flooding and depredation, but also for the nest microclimate, which determines whether eggs survive and hatch and the ratio of males to females as sex determination in sea turtles is temperature dependent (Mortimer 1990, Marco et al. 2018). The nest microclimate is influenced by the overall climate of the beach as well as the

placement of the nest in relation to the shoreline and vegetation (Kamel 2013, Swiggs et al. 2018). Because of the complexity of risks and signals associated with nest site placement, many hypotheses for how females choose an exact location have been proposed and tested with varying factors found to be significant across species and populations; these site characteristics include beach slope, temperature, salinity, distance to vegetation, distance to high water line, and beach width (see Wood and Bjorndal 2000, Mazari et al. 2006, Pike 2008, Zavaleta-Lizárraga and Morales-Mávil 2013). Interpreting the signals that female sea turtles are using in nest site selection is difficult because this is a complex, costly, multi-level decision for the animal. Beach choice, at some level, is determined by natal location, but where the nest is actually laid in terms of distance from high water line, vegetation, slope, and elevation varies by species and location (Wood and Bjorndal 2000). Without a consensus on what physical attributes determine where females choose to nest, it is difficult to model where on the landscape female sea turtles choose to nest. Modeling nesting areas is essential for predicting how nesting areas will change in the future in response to changes in the coastal habitat from climate change, sea level rise, and human development.

Just as there is no consensus on what attributes females use in nest site selection, there is also debate and system complexity in predicting how these beach characteristics will change and shift with rising sea levels and increased storm activity (Cooper and Pilkey 2004, Dean and Houston 2016, Ranasinghe 2016). Beach position and morphology is determined by, among other factors, the interplay of waves, currents, sea level, sand sources and sinks, longshore drift, and storm history (Ranasinghe 2016). Because of the complexities and unknowns in modeling both nest site choice and future beach morphology, accurately predicting future sea turtle nesting in a changing environment is extremely challenging (Von Holle et al. 2019).

Barrier islands are landforms where there will be a significant impact from rising sea levels (Moore et al. 2010), which will then affect key sea turtle nesting beaches. These systems are already deteriorating due to sea level rise (Penland et al. 1992, FitzGerald et al. 2008, Irish et al. 2010). Barrier islands will potentially migrate inland until they are absorbed by the mainland, alternatively, given the pace of sea level rise, they may shrink and eventually disappear (Stutz and Pilkey 2005). Barrier islands are not only important habitats for sea turtle nesting, but many are also developed for residential and recreational purposes, with some barrier islands, like many areas in the Outer Banks of North Carolina, having a high level of human infrastructure and development. Sea turtle nesting beaches on barrier islands face stressors from all directions between rising shorelines on both the open ocean and lagoon sides, physical human infrastructure, and the impacts that come with increasing human density and use (Fuentes et al. 2016).

Though barrier islands in the United States have a long history of human settlement, some portions have been congressionally designated as protected areas and are managed by the U.S. National Park system. National Seashores, part of the U.S. National Park system, provide large swaths of relatively undisturbed sea turtle nesting habitat (Pike 2008). Canaveral National Seashore in Florida supports approximately 200–6,000 green sea turtle, *Chelonia mydas*, and 3,000–5,000 loggerhead sea turtle, *Caretta caretta*, nests per year, as well as a smaller number of leatherback sea turtle, *Dermochelys coriacea*, and Kemp's ridley sea turtle, *Lepidochelys kempii* (data available online).² Preserved areas, like National Seashores, not only host large numbers of sea turtle nests (Nel et al. 2013), but these natural areas may also produce more viable hatchlings per nest that make it to the ocean compared to beaches with more human development and use (Kudo et al. 2003, Pike 2008, Fuentes and Hamann 2009, Kaska et al. 2010, Zavaleta-Lizárraga and Morales-Mávil 2013, Randall 2015).

Using over a decade of nesting locality information for loggerhead and green sea turtles across four barrier island National Seashores on the southeastern U.S. Atlantic coast between North Carolina and Florida, we projected the effects of sea level rise and current human infrastructure on available sea turtle nesting area. We hypothesize that the presence of stationary impervious surfaces, such as roads, will increase future loss of beach area critical to nesting sea turtles. We use four barrier island systems that are part of the U.S. National Park System with a gradient in the amount of human-made hard surfaces abutting nesting beaches to quantify the relationship between human development and loss of nesting area by 2100. We predict that those barrier islands experiencing the greatest coastal squeeze, resulting from beaches narrowing as sea levels rise and human infrastructure inhibits landward migration of beach systems, will have the greatest overall loss of sea turtle nesting area. We also predict that those beaches with greater coastal squeeze will face greater future flooding threats resulting from coastal squeeze forcing remaining nesting area to be closer to the future high water line, as compared to those National Seashores with less coastal squeeze. Alternatively, the morphology of the beaches and the height above sea level that sea turtles are currently nesting may play a large role in determining whether nests are currently and in the future predicted to be flooded. We employ a novel method to estimate nesting beach area based on records of where females are currently nesting. Beyond allowing us to predict where sea turtles may be nesting in the future given climate change, this method can be broadly applied to studies that require a bounded area that encompasses the part of a beach used by nesting coastal species.

METHODS

Study sites

We chose four barrier island National Seashores along the Atlantic coast that are part of the United States National Park Service: Canaveral National Seashore, Cumberland Island National Seashore, Cape Lookout National Seashore, and Cape Hatteras National Seashore (Fig. 1). All four Seashores have consistent annual nesting of loggerhead sea turtles with the densest concentration of nesting occurring at Canaveral National Seashore in Florida and decreasing with increasing latitude, the presence of other nesting sea turtle species also varies with latitude. These four Seashores have differing natural morphology and anthropogenic footprints (Table 1, Fig. 1).

Canaveral National Seashore (CANA), Florida (28.7864° N, 80.7542° W), established in 1975, consists of a long stretch of stable barrier beach backed by a single high dune ridge. At either end of the Seashore there is paved road access with parking areas and lifeguard stations; the center beach, Klondike, is only accessible by foot. This is the only Seashore we studied that also has a consistently high number of nesting green sea turtles.

Cumberland Island National Seashore (CUIS), Georgia (30.8586° N, 81.4525° W), established in 1972, is a single wide barrier island. Beach area is backed by dunes and steep cliffs with an upland oak maritime forest. This Seashore is accessible by ferry with limited daily admission and there is no development in proximity to the beach.

Cape Lookout National Seashore (CALO), North Carolina (34.8268° N, 76.3432° W), was created in 1966 with the purpose to preserve a natural barrier system “where ecological processes dominate” (National Park Service 2012). Like neighboring Cape Hatteras National Seashore, Cape Lookout is a narrow chain of barrier islands with wide, bare beaches and low dunes. Unlike Cape Hatteras, Cape Lookout has no bridge access; people and vehicles can only access the Seashore through ferries and personal watercraft. Vehicles are permitted on unpaved roads behind dunes as a means to access areas for beach driving.

Cape Hatteras National Seashore (CAHA), North Carolina (35.4137° N, 75.6506° W), is just north of Cape Lookout. Unlike Cape Lookout, Cape Hatteras' preserved area does not encompass the entirety of the barrier islands; instead, there are villages throughout the main islands that directly abut National Seashore beaches as well as paved roads connecting areas throughout the Seashore. Though there is substantial human development at risk from rising sea level and storm events, most erosion control was discontinued in the 1970s, with structures, like the iconic lighthouse, being relocated as the barrier island moves westward. Upkeep of artificial dunes created in the 1930s (Binkley 2007) as well as beach nourishment does occur intermittently across this system to protect roads and settlements (Dave Hallac, *personal communication*).

² <https://www.nps.gov/cana/learn/nature/sea-turtles.htm>

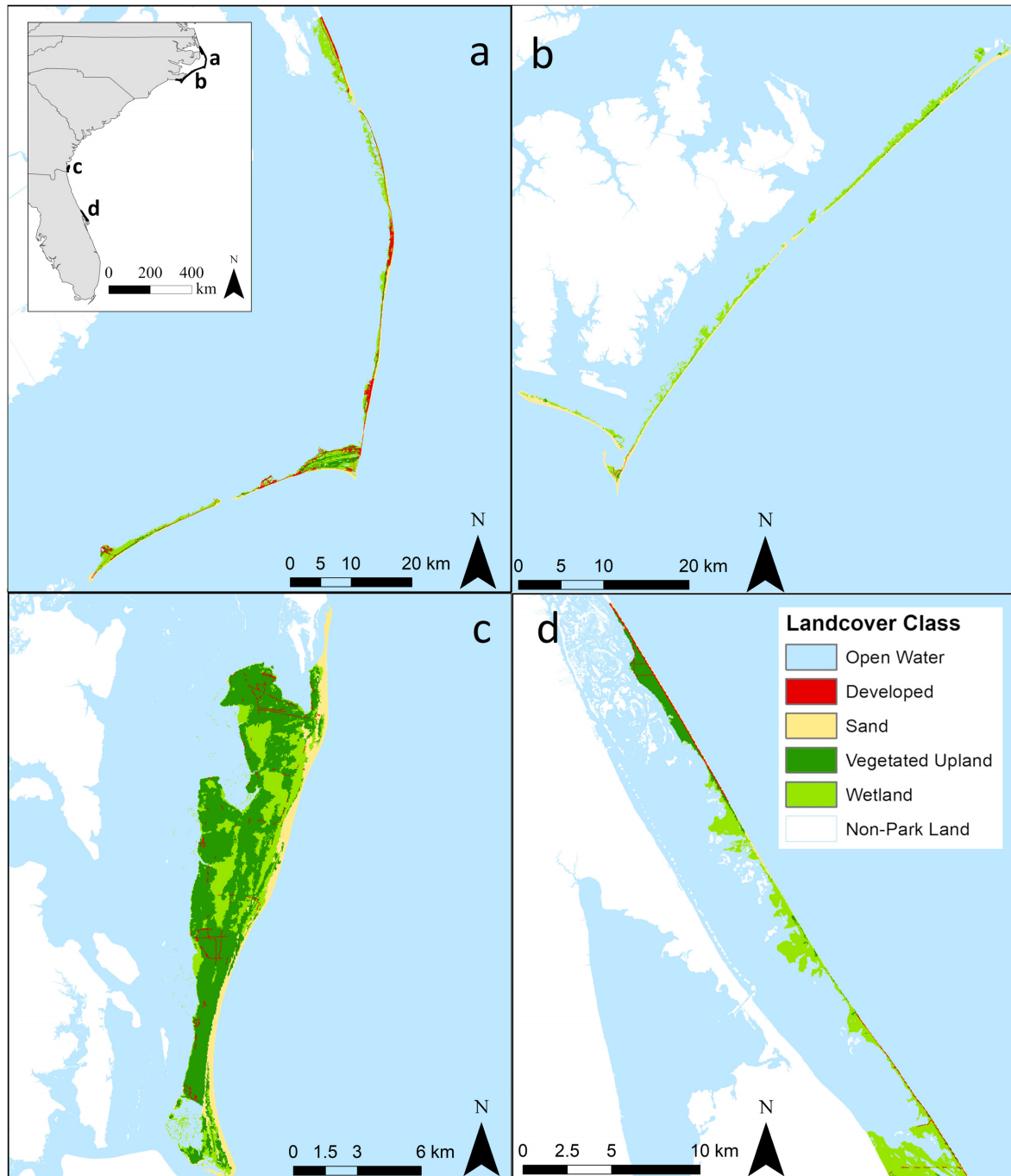


FIG. 1. Locations of four focal seashores with detailed maps of land cover for (a) Cape Hatteras, North Carolina (CAHA), (b) Cape Lookout, North Carolina (CALO), (c) Cumberland Island, Georgia (CUIS), and (d) Canaveral, Florida (CANA). This study focused on four National Seashores on the eastern coast of the United States. These Seashores differed in the amount of developed land, morphology, and latitude. Land cover data from the U.S. Geological Society’s 2011 National Land Cover Database; land cover classification has been simplified to five relevant classes.

Nesting data

We obtained nesting locations directly from each National Seashore. Nest locations were recorded by

trained volunteers and National Park Service biologists through daily, early morning surveys of all beaches. Nesting female sea turtles leave conspicuous marks in the sand that can be used to determine the species and

TABLE 1. Nearshore impervious surface development and human use across Seashores.

Seashore	Shoreline (km)	Road (km)	Village (km)	Developed shoreline (%)	2017 visitors
CAHA	124	103	20	99	2,433,703
CALO	94	53†		56†	399,357
CUIS	30	0		0	51,937
CANA	39	19		48	1,598,586

Notes: Overall shoreline length calculated from most recent high water vectors (see Table 2), road and village calculated from only the length parallel to the shoreline, estimated visitor numbers available from National Park Service (irma.nps.gov). CAHA, Cape Hatteras, North Carolina; CALO, Cape Lookout, North Carolina; CUIS, Cumberland Island, Georgia; CANA, Canaveral, Florida.

†Unpaved, sand roads.

location of a nest if eggs are deposited (Witherington et al. 2009). We made use of all nest locality data for the years in which Seashores used handheld GPS units for recording precise latitude and longitude (CANA 2013–2016, CUIS 2003–2017, CALO 2001–2015, CAHA 2005–2016).

We quantified the shortest distance between each nest site and high water line using the Near tool in ArcGIS (version 10.4). We used the mean high water line vector, retrieved from NOAA or USGS, for the year closest to the time when each nest was recorded (see Table 2 for years and sources). Based on the angle between nest point and shoreline, we were able to determine which nests were east of the high water line (below the high water mark) and recorded these as negative values. Using the “quantile” command in R version 3.4.2 (R Core Team 2017), we recorded a maximum value that 97.5% of the distances fall below and a minimum that 2.5% of the values fall above to encompass the middle 95% of the distances from the high water line for loggerheads in each Seashore and green turtles in CANA. We used this quantile approach, as distances form a normal distribution within each Seashore (Fig. 2). Each Seashore was analyzed separately to account for differences in beach width resulting from the underlying geology and natural processes, such as current and coastal evolution. We analyzed the cape areas within CALO and CAHA separately, because cape areas tend to accrue more sand, have wider beaches, and have more year-to-year high water line movement and sediment availability. We based the delineation for a “cape” area on a rectangle encompassing the area where the shoreline forms a distinctly concave shape as the directional orientation changes sharply from the roughly linear orientation of the rest of the island. CANA and CUIS do not have cape areas, and so the beach was analyzed as one for these two Seashores.

Beach area

We created polygons to approximate the area of beach that sea turtles are using for nesting. Using the buffer tool in ArcGIS, we created polygons of the areas that were greater than the minimum 2.5% distance from the mean high water line and less than the value for the upper

TABLE 2. High water location data years and sources by state.

Year	State	Source	URL
1997	NC	USGS	https://pubs.usgs.gov/of/2005/1326/metadata/North_Carolina/nc1997.htm
1999	GA	USGS	https://pubs.usgs.gov/of/2005/1326/metadata/Georgia/ga1999.htm
2002	GA	NOAA	https://www.ngs.noaa.gov/NSDE/
2009	NC	USGS	https://www.sciencebase.gov/catalog/item/58b8913ee4b01ccd5500c312
2014	NC	NOAA	https://www.ngs.noaa.gov/NSDE/
2017	All	NOAA	https://www.ngs.noaa.gov/NSDE/

Notes: Most recent (2017) high water vector retrieved from the Continually Updated Shoreline Project. Precise locality points for CANA nests were only available from 2013–present and thus only the most recent shoreline was used for Florida. NC, North Carolina; GA, Georgia.

97.5% of nesting distances. This method formed an area encompassing where 95% of nesting occurred in linear distance from the mean higher-high water line (MHHW), which represents the average of the daily high water heights over the last tidal epoch (1983–2001; polygon of MHHW line from Caffrey et al. 2018). This area could overlap the MHHW line to encompass the higher variability of the high water line in some Seashores as well as nesting that occurs below the MHHW line if the 2.5% minimum value was found to be below the high water line. Beach polygons were clipped by Seashore boundaries. Road, building, and parking lot areas (data from irma.nps.gov) were categorized as unsuitable for nesting. Road vectors were buffered by the road width quantified from GoogleEarth images; areas on the lagoon side of the road were also considered unsuitable and inaccessible to nesting females as they would require navigating across a road for both the nesting female and hatchlings. Because of the differences in accretion rates between the cape and non-cape areas within CALO and CAHA, if the nest placement in these regions was significantly different from non-cape regions, we created a separate polygon of the cape areas. We used an analysis of variance in R (version 3.4.2) to test whether there was a significant difference in the distance turtles were nesting from the high water line based on Seashore, cape regions within the Seashore, and species. To project future suitable nesting area, we carried

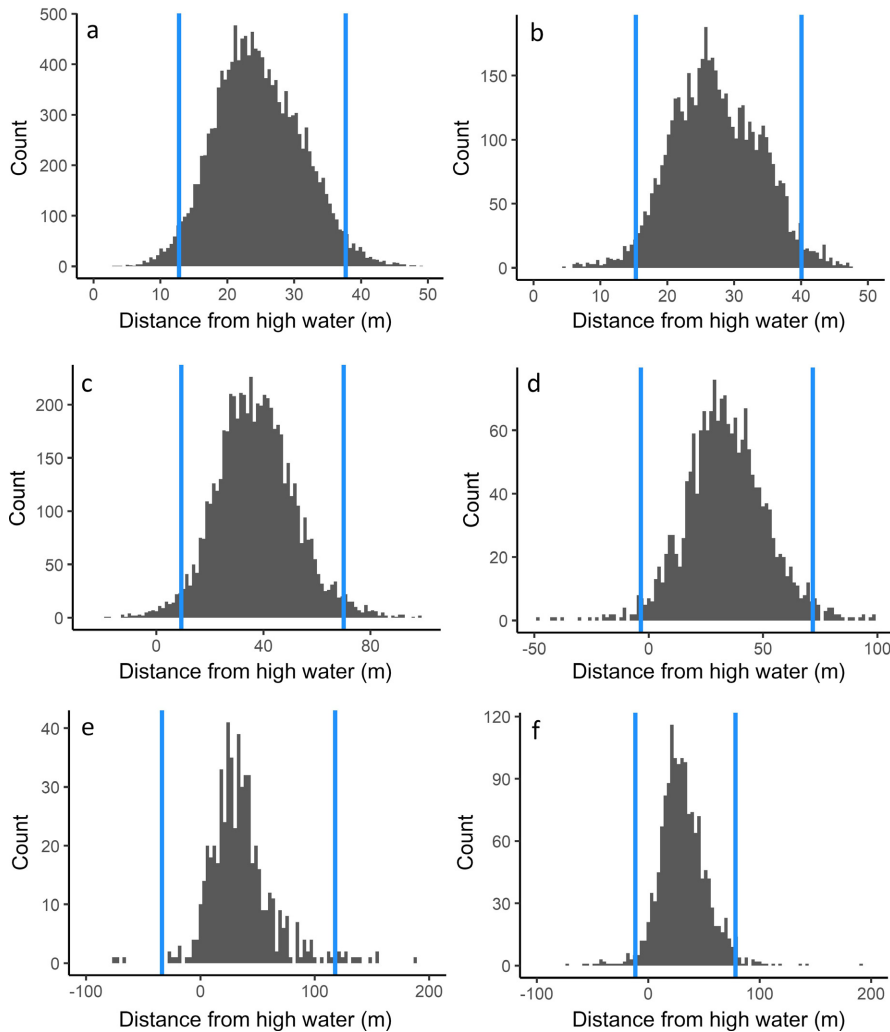


FIG. 2. Histograms of the distances between nest site and high water line for nests of loggerhead and green sea turtles at four National Seashores. (a) Loggerhead sea turtles at Canaveral National Seashore ($n = 14,273$), (b) green sea turtles at Canaveral National Seashore ($n = 5,143$), (c) loggerhead sea turtles at Cumberland Island National Seashore ($n = 5,962$), (d) loggerhead sea turtles at Cape Hatteras National Seashore ($n = 1,846$), (e) loggerhead sea turtles in the non-cape region of Cape Lookout National Seashore ($n = 1,536$), (f) loggerhead sea turtles in the cape region of Cape Lookout National Seashore ($n = 579$). Distance measured to high water based on high water line vector data for the closest year on record (Table 2). Beach area close to cape formation in CALO analyzed separately. Blue lines represent the lower (2.5%) and upper (97.5%) intervals.

out the same procedure of polygon creation using a high water line estimate for 2100 Representative Concentration Pathway (RCP) 8.5, which assumes business as usual for CO₂ emissions. Sea level rise estimates for 2100 were taken directly from Caffrey et al. (2018), who based their sea level rise estimates on the IPCC (Church et al. 2013) regional climate models (RCMs) downscaled to a spatial grid resolution of 1° × 1° from atmosphere–ocean general circulation models, this method assumes that islands do not migrate landward. We quantified areas available for nesting currently and in the future using Calculate Geometry in ArcGIS. To estimate average and maximum nest density, we used the nest counts provided by the Seashores along with the area estimated to be suitable for nesting.

We calculated the percent of nesting area in each Seashore that would be flooded by a Category 3 hurricane based on Caffrey et al.’s (2018) storm surge models, which rely on NOAA Sea, Lake and Overland Surges from Hurricanes (SLOSH) data. NOAA SLOSH models estimate potential storm surge height at current (most recent tidal datum) sea level (National Oceanic and Atmospheric Administration 2016), which is a conservative approach, as higher sea level and permanent inundation will change the fluid dynamics of a basin, the way waves propagate within a basin, the accretion and erosion rates, and the geomorphology of the coastline. The Caffrey et al. (2018) study only looked at future flooding, so we created polygons of current predicted flooding employing the same methodology using current sea

level. From this, we extracted and quantified the areas that were predicted to be suitable for nesting and were also above the storm surge line. We analyzed the current elevational distribution of sea turtle nests by extracting digital elevation values for nest sites from USGS digital elevation model (Caffrey et al. 2018). We used ANOVA and Tukey HSD post hoc tests to test first for a significant difference in nesting height between all Seashores and then to differentiate which Seashores were significantly different in nesting height from each other.

RESULTS

Current nesting area

Both species nesting in CANA had the lowest variation in nesting distance from the high water line, with nesting occurring on average closer to the mean high water line likely due to the beach at CANA being narrower than the other three Seashores. Loggerheads nested significantly closer to the mean high water line than green turtles (Table 3). In the two North Carolina Seashores, CALO and CAHA, minimum values for distance from high water line were negative, indicating that at least 2.5% of loggerheads nested below our referenced high water line on these beaches. Some of these nests may have been above the high water line, but appear below because high water line is not measured every year; this year-to-year variation in high water line is expected to be a more substantial issue for areas that have more variable shorelines, such as the cape regions. The wider range between minimum and maximum distances from mean high water (Fig. 2) for CAHA and CALO, and to a lesser extent CUIS, reflected the larger distances between dunes and high water line (based on digital elevation rasters and high water line vectors), indicating wider beach habitat available for sea turtle nesting in these Seashores. The North Carolina National Seashores have a more complex coastline made up of multiple barrier islands that do not lie along a single directional orientation. The combined effects of longer,

more complex shorelines and wider beaches in CAHA and CALO resulted in larger area estimates for current and future nesting areas. The large range of distances from mean high water for nesting turtles in the cape region of CALO further contributed to the larger estimated nesting area for this Seashore. For CAHA, we did not find a significant difference in nest site distance from high water line between cape and non-cape regions.

Though the barrier islands that make up CAHA and CALO had more available nesting area, CANA had the greatest number of annual nesting loggerhead and green sea turtles, likely because CANA is further south and within the core of the nesting ranges for these two species (Pike 2013). This was reflected in both the number of nests surveyed in each Seashore over the study years and the density of nests. The highest recorded density of nests during our study period was 3,816 nests/km² for loggerheads in CANA in 2012 and 1,505 nests/km² in 2013 for green turtles. The second-most southern Seashore, CUIS, had the second densest nesting of loggerheads (271 nests/km²). Although CAHA is slightly farther north than CALO, with a larger human footprint, we found a higher density of nests at CAHA (Table 4).

Future nesting area with sea level rise

We predicted that the Seashores with the largest human footprint, CANA and CAHA, would have the greatest nesting beach loss by 2100 because of coastal squeeze resulting from rising sea levels on the open ocean side and impervious surfaces, such as roads and settlements, on the landward side. In terms of total area lost, CAHA, which had the largest amount of human hard structure development, is predicted to have the greatest loss in overall area (Fig. 3, Table 5). However, in percentage of the total area that is predicted to be lost for each Seashore, CAHA is predicted to lose 5.2% of nesting area while CUIS, which had the smallest human footprint, is predicted to lose 6.7% of the nesting area (Fig. 3, Table 5); this loss is predicted to occur primarily at the northern and southern limits of the island (Fig. 4). CANA, which is located on part of a single barrier island, with roads extending for half of the beach length, had the least amount of predicted nesting beach loss in both total area and percentage. Nesting area for loggerheads does not intersect with roads presently or in the future (Fig. 4). We predicted that green turtles will lose more nesting beach area at CANA than loggerhead turtles will lose, because green turtles nest farther from the mean high water line (Fig. 2) and thus are likely to have more of their future nesting area restricted due to roads and rising lagoon water level.

Assuming the same number of sea turtles nest on these Seashores in the future, nesting densities will increase in areas that experience beach loss. If nesting counts in 2100 are equal to those currently experienced by each Seashore, CUIS will experience the largest magnitude increase in density with mean loggerhead density

TABLE 3. Average nest placement grouped by Seashore and species.

Seashore	Species	Average nest elevation (m)	Average distance from shore (m)
CAHA	loggerhead	2.34 ^A	33.26 ^A
CALO	loggerhead	2.33 ^A	31.45 ^B
CUIS	loggerhead	2.19 ^B	37.54 ^C
CANA	loggerhead	2.60 ^C	24.65 ^D
CANA	green turtle	2.85 ^D	27.31 ^E

Notes: Distance to high water was measured in relation to the closest available high water data source for nesting year (Table 2). Differences between Seashores and species were all significant ($P < 0.005$) based on ANOVA and Tukey post hoc tests, except for elevation differences between CAHA and CALO, which was not significantly different. Significant differences ($P \leq 0.005$) denoted by superscript letters.

TABLE 4. Nesting count and calculated density.

Seashore	Years	Species	Counts		Density (nests/km ²)			
			Maximum	Mean (SD)	Current		2100	
					Maximum	Mean (SD)	Maximum	Mean (SD)
CAHA	2005–2016	Cc	305	154 (82)	33	17 (9)	35	18 (9)
CALO†	2001–2015	Cc	229	177 (40)	24	19 (4)	25	20 (4)
CALO‡	2001–2015	Cc	229	177 (40)	24	19 (4)	25	19 (4)
CUIS	2003–2017	Cc	860	487(128)	479	271 (71)	512	290 (76)
CANA	2013–2016	Cc	5,120	3,742 (947)	5,221	3,816 (966)	5,299	3,873 (980)
CANA	2013–2016	Cm	4,148	1,467 (1,366)	4,256	1,505 (1,402)	4,369	1,545 (1,439)

Notes: Nest counts and averages based on park monitoring during the time period used in this study. Counts and density calculated for loggerhead sea turtles (Cc) across all four Seashores and green sea turtles (Cm) in CANA, the only park with >100 green turtles nesting annually. Density estimates based on number of nests and the nesting area quantified in this study. Future density reflects nest density assuming the same average number of turtles nest in 2100 as nested over the measurement period used in this study.

†Assumes dirt roads do not move from current placement and represent a barrier to sea turtle nesting.

‡Does not include dirt roads as a barrier.

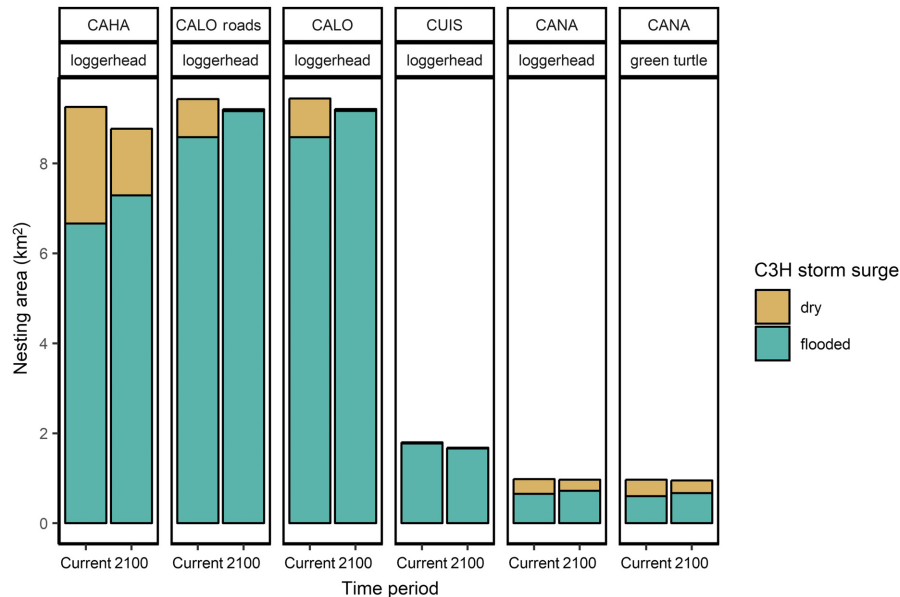


FIG. 3. Current and future (2100) total nesting area for each Seashore with the amount of that area estimated to be flooded from a storm surge associated with a Category 3 hurricane (C3H). Future area estimated based on sea level rise associated with RCP8.5 assuming beach movement; changes in total area between current (most recent tidal epoch 1983–2001) and 2100 time period were due to coastal squeeze from hard structures and rising lagoons. Green represents beach area that would be flooded from a storm surge associated with a Category 3 hurricane, currently and by 2100; light brown are areas not predicted to be flooded due to their elevation. Cape Lookout roads are unpaved and may not represent an impediment to sea turtle nesting and so we considered two scenarios: CALO roads, where unpaved roads were treated the same as roads at other seashores (impervious surfaces), and CALO, where roads were not included.

increasing from 271 to 290 turtles/km², based on this Seashore also having the greatest predicted loss of area by 2100 (Table 4, Fig. 3).

Future nesting area with storm surge

Based on historical storm surge activity, if a Category 3 hurricane came in the vicinity of these four Seashores, currently CUIS would be the most affected, with over

98% of the nesting beach area where 95% of nesting occurs predicted to experience flooding, followed by CALO, CAHA, and finally CANA, where less than 67% of nesting area is predicted to be flooded. Loggerhead nesting occurred at the lowest elevation in CUIS compared to the other three Seashores (Table 3, Fig. 3). We found that CALO would experience the greatest future flooding, with over 99% of nesting likely to be flooded by 2100, but this is not a substantial change as we

TABLE 5. Percentage of nesting area predicted to be lost by 2100.

Seashore	Shoreline development (%)	Species	Area lost (%)
CAHA	99	loggerhead	5.22
CALO†	56	loggerhead	2.50
CALO‡	5	loggerhead	2.48
CUIS	0	loggerhead	6.67
CANA	48	loggerhead	1.02
CANA		green turtles	2.06

Notes: Area predicted based on beaches shifting inland with rising sea level. Predicted loss of area resulted from squeeze between developed areas and rising shoreline as well as changes to island morphology due to rising sea level on multiple sides.

†Assumes dirt roads do not move from current placement and represent a barrier to sea turtle nesting.

‡Does not include dirt roads as a barrier, only buildings are included as barriers.

estimated that 91% of the current nesting area could be flooded with a Category 3 hurricane. At the neighboring Seashore, CAHA, we predicted a slightly larger change between current (72% flooded) and 2100 (83% flooded) nesting area.

Though they are in close proximity to each other, CAHA and CALO had different storm surge flooding risk currently and in the future. Nest sites in both Seashores occurred at a similar elevation (Table 3). However, based on USGS elevation data (Caffrey et al. 2018), the back beach areas of the islands that make up CAHA are higher in elevation than those at CALO. The Outer Banks barrier islands that make up CAHA and CALO naturally have low (<4 m height) intermittent dunes, which are seen on most of CALO, however at CAHA, the primary dune line reaches 4–7 m. Much of these higher dunes are the result of Civilian Conservation Corps work in the 1930s that has been maintained to protect infrastructure (Moore et al. 2010).

In CANA, green turtles nested further away from the mean high water line than loggerheads (Fig. 1, Table 3), so more of green turtle nesting area would be safe from flooding during a Category 3 hurricane, compared to loggerheads in the same Seashore. Regardless, we still predicted substantial flooding, with 62% of green turtle nesting area currently flooding with a Category 3 storm surge, and by 2100, we predicted that flooding would increase to 70% (Fig. 3).

DISCUSSION

We hypothesized that Seashores with greater hard infrastructure (CAHA and CANA) would experience greater nesting area loss by 2100 as a result of coastal squeeze. On the contrary, we found that most roads and other development are far enough away from the high water line that even with inland beach migration due to projected sea level rise, most sea turtle nesting grounds are not predicted to intersect roads. CUIS is predicted to

lose the greatest percentage of nesting area due to sea level rise, despite the fact that human activity and infrastructure are extremely restricted in this Seashore. The beach loss we report is based primarily on changes to the barrier island morphologies. With sea level rise, barrier islands face rising shorelines from multiple sides: the open ocean, as well as lagoon and tidal inlets, so it is the narrowest areas, low lying areas, and edges of barrier islands where we predict the greatest loss of nesting area due to sea level rise.

Our results indicate that the presence of roads, paved (CAHA and CANA) and unpaved (CALO), should not strongly inhibit present or future beach use by turtles. The inclusion of unpaved roads as a potential barrier in CALO did not have a substantial impact on our projected loss of beach area available for sea turtle nesting. Human development around roads and private inholdings may still deter nesting females (Kikukawa et al. 1999, Kaska et al. 2010, Nishizawa et al. 2013, Randall 2015), increase destruction of nests by predators attracted to human development (Lutcavage et al. 1997), and lower the ability of hatchlings to reach the ocean (Witherington and Bjorndal 1991, Salmon et al. 1995).

Beach loss and nest density

Though CANA has the smallest total nesting area, it is in the core nesting range of loggerhead sea turtles and thus has substantially more annual nesting than the other three Seashores, it was also the only site with consistently high (>100) annual numbers of nesting green sea turtles. This means that although we predict that CANA will lose the least amount of total nesting beach area as well as the smallest percentage of nesting beach area in the future due to sea level rise, this small loss has the potential to have the greatest impact on nesting sea turtle populations. Lower densities of nests at the other three Seashores implies that the number of nests is determined by climate and other environmental and historical factors rather than density dependence; a loss of nesting area in Georgia or North Carolina may not increase future nest densities to a point of being harmful to the populations as densities are currently well below carrying capacities calculated in other sea turtle systems (Caut et al. 2006, Girondot et al 2006, Tiwari et al. 2006, Mazaris et al 2009). For CANA, within the core loggerhead and green sea turtle nesting range, a loss of beach area is more likely to result in increased negative density effects, such as females digging up previously laid nests, disease spread, and predation; indicating negative implications for future population trajectories sustained by these beaches. With global climate change, nesting is expected to shift northward in the northern hemisphere (Pike 2013, Reece et al. 2013), CAHA, CALO, and CUIS having the potential to become increasingly important nesting grounds for both species; however, the relatively small predicted loss of suitable nesting area is

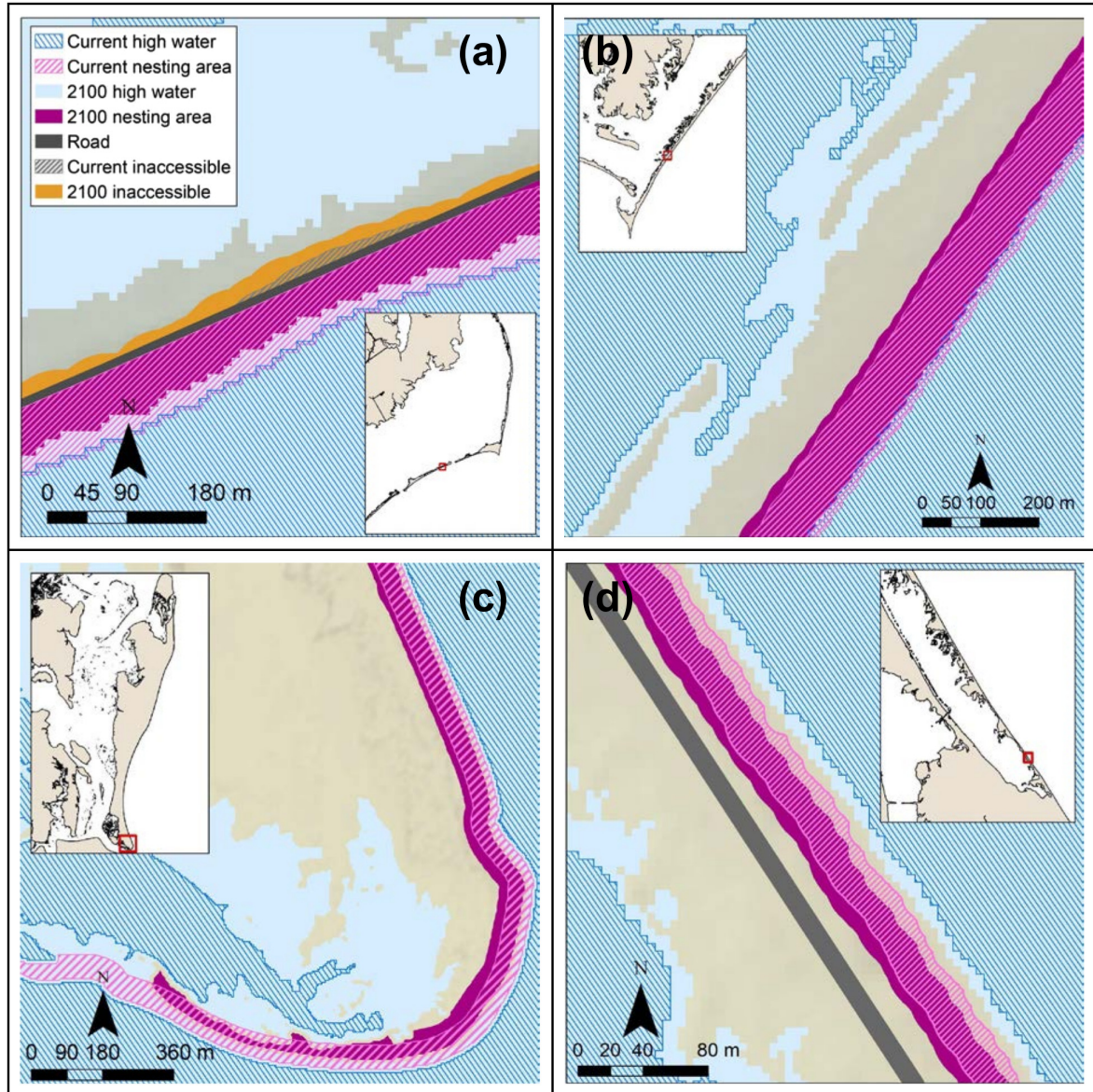


FIG. 4. Example maps for predicted current and future nesting area for loggerhead sea turtles within four National Seashores. (a) Cape Hatteras, an area predicted to experience coastal squeeze between rising sea level and roads, (b) Cape Lookout, a similarly shaped barrier island to Cape Hatteras without paved roads, (c) Cumberland Island, an area predicted to experience nesting loss due to rising sea level on multiple sides of the island, (d) Canaveral, nesting area was narrow and roads were set back far enough that we did not predict future coastal squeeze due to impervious surfaces.

unlikely to increase nesting density to the point of increasing density-dependent effects on the populations.

It is difficult to compare our density estimates of the number of nests per season per square kilometer to the literature because such measurements are rare. Without a standardized methodology for bounding nesting beach area, most studies are restricted to measuring nests per season per kilometer of shoreline. Our results demonstrate that the width of beach used by nesting females varies by species and location, making density measurements based on linear length of shoreline not comparable between

beaches and species. The number of nests for CANA per linear kilometer of shoreline ($131 \text{ nests} \cdot \text{km}^{-1} \cdot \text{yr}^{-1}$) is similar, though on the lower range of what is considered high density nesting at core rookeries for loggerheads, like Archie Carr National Wildlife Refuge where densities of $30\text{--}1,000 \text{ nests} \cdot \text{km}^{-1} \cdot \text{yr}^{-1}$ were reported by Witherington et al. (2011) and Boa Vista island where density ranged from 2.6 to over $1,000 \text{ nests} \cdot \text{km}^{-1} \cdot \text{yr}^{-1}$ depending on the beach reported by Marco et al. (2012). Nest density estimates using a linear measurement ignore variation in the width of the beach making these measurements less

comparable across space and time. The method we outline in this paper can be applied to any area with locality information on nests, which will hopefully result in greater quantification of density using area. We suggest that this method should be applied more widely in nesting studies to allow comparisons of sites over time, as well as to understand the relative impacts of habitat loss due to sea level rise and storm surge events.

Storm surge

Our analysis indicates that the CUIS nesting beaches are currently the most vulnerable to flooding from storm surge. The beach on Cumberland Island is relatively low lying, wide, and flat, backed in some areas by low dunes and in others by cliffs. At other Seashores, the proximity of dune formations to the high water line results in some nesting areas coinciding with dunes currently and in the future; these areas are more likely to be above storm surge levels with the potential for some nests to remain intact following hurricane impact. In the Outer Banks of North Carolina, we found that storm surge combined with sea level rise has the potential to impact the neighboring Seashores of CAHA and CALO differently. Though sea turtles are currently nesting at elevations that are not significantly different between the two Seashores, CAHA has more elevated area compared to CALO. The small difference in elevation appears to affect the amount of nesting areas predicted to flood currently and in the future. These future estimates of flooding should be interpreted with caution, as much of the area predicted to remain above storm surge during a Category 3 hurricane is based on the current locations of dunes, which are not expected to remain stationary with rising sea levels and changing storm patterns (Ranasinghe 2016).

The combination of increasing intensity of storm events and rising sea levels may mean that individuals and species that nest at a higher elevation are less susceptible to flooding. In our data set, green turtles nested at a higher elevation than loggerheads; Varela et al. (2018) also found that green sea turtles nested at a higher elevation than loggerheads, though in their study site in Northern Cyprus, both species nested at slightly lower average elevation than we recorded. They also concluded that because green turtle females dig deeper than loggerhead females, they may actually be at a similar risk of flooding even when nest placement is at a higher elevation.

These species will also be differentially affected by storm surge events because of the timing of their nesting. Loggerheads in the United States nest at the beginning of the summer, so their nests are less likely to experience the direct impacts of a storm surge, with hurricanes and storms typically occurring at the end of summer, although storm surge flooding will also dramatically alter the nesting beaches for future seasons, affecting all beach nesting species (Morton and Sallenger 2003).

Green turtles in the United States nest later in the year with nesting peaking during July and August followed by approximately 10 weeks of egg incubation, overlapping with the more extreme part of hurricane season (August through October); green turtle nests are more likely to be incubating during a tropical storm or hurricane event (Pike and Stiner 2007). Loggerhead nesting, at least in eastern Florida, is already shifting to earlier in the year and the nesting season is shortening with climate change (Pike et al. 2006, Weishampel et al. 2010), which may shift them further outside of tropical storm peril. Loggerhead populations in Brazil (Monsinjon et al. 2019), the Gulf of Mexico (Lamont and Fujisaki 2014) and the Mediterranean (Mazaris et al. 2008, Patel et al. 2016) have been recorded nesting earlier as well, this appears to be in response to increased sea surface temperature. Green turtles in Florida have also shifted median nesting date earlier with warming; however, their nesting season appears to be lengthening (Weishampel et al. 2010). Currently, CANA is the only Seashore that we studied with a large population of nesting green turtles and has the lowest predicted storm surge flooding from a Category 3 hurricane. Furthermore, the area of central Florida where CANA is located has historically lower storm density and a longer return rate (interval between storms) compared to the area in North Carolina where both CALO and CAHA are situated (data *available online*).³ Loggerhead sea turtles nesting on more northern beaches, like CAHA and CALO, nest later in the year, potentially putting these nests, which historically experience more storms, at a greater risk than loggerhead nests in Florida (Mazaris et al. 2013). Estimating reproductive effort lost to storm surge-related flooding requires taking into account nest placement, timing of nesting and storm events, and the frequency and timing of inundation events (Foley et al. 2006, Caut et al. 2010, Shaw 2013). Species-specific phenology, storm rates, and nesting density taken together appear to indicate that the threat of storm surge-related nesting loss is not as severe as indicated by looking at the percent area flooding across all Seashores. Future storm surge risk should be assessed in conjunction with changing phenology and shifting species distributions.

Differences in dune formation between Seashores will not only affect nest flooding during storms, but also how these beaches change following surge events. Storm surge and dune overwash events have long-lasting, complex impacts on beach morphology. How beaches change and when and whether they recover has to do with dune height pre-storm, beach profile, as well as the size and frequency of such events (Morton and Sallenger 2003, Houser et al. 2015). Smaller and discontinuous dunes, like those in CALO and CUIS, are more susceptible to overwash, which would move sediment to the inland- or lagoon-side of the island, making it unavailable for recovery (Houser et al. 2015). However, because

³ <https://www.nhc.noaa.gov/climo/>

the beach at CUIS is backed in many areas by cliffs and forest, rather than a lagoon or wetland, sediment may be less likely to be lost. In this Seashore, areas of concern remain in the northern and southern edges, which are not backed by upland vegetation and are the most susceptible to changes from both sea level rise and storm events. It was not within the scope of this study to model future long-term coastal evolution and nesting beach morphology at these four Seashores following storm events, but this is something that deserves future research and consideration given projections for sea level rise and storm activity.

Assumptions of modeling approach

For the purposes of this study, we restricted our analyses to current island topography and developed surfaces. The combined forces of sea level rise, storm surge, and increased erosion will change this landscape and require management decisions relating to the preservation of current beaches, roads, and other structures. This is already occurring at CAHA, where the narrowing of barrier islands and access needs of residents and visitors have forced the construction of the Rodanthe Bridge, which replaces part of Highway 12, going over the Pamlico Sound and bypassing Pea Island. Replacing on-island roads with bridges and ferries will mean less beach area lost due to coastal squeeze; however, these projects are costly. Efforts to retain current beach and dune locations in order to protect roads, buildings and recreational areas will inhibit natural beach migration and could ultimately lead to increased beach loss (Magliocca et al. 2011, Berry et al. 2013, Rogers et al. 2015). The barrier islands of the North Carolina Outer Banks are naturally low-lying islands with morphology governed by disturbance events. The beaches of CALO are more likely to shift naturally with changing sea level and storm flooding, while the surfaces and man-made dunes of CAHA make these beaches less resilient to storm overwash events (Magliocca et al. 2011), leading to the eventual narrowing of beaches at a greater magnitude than what we predict.

Our estimate of beach movement due to rising sea levels (0.68–0.79 m) is conservative (Caffrey et al. 2018). The combination of sea level rise and intermittent flooding due to storm events will likely result in a more pronounced beach retreat than what we modeled. Depending on the beach profile, particularly the presence and height of dunes and or cliffs, erosion and sediment loss from storm surge combined with sea level rise could result in sandy beach recession 50–100 times that of just sea level rise alone (Ranasinghe 2016). These effects are best estimated on a local level where sediment budgets and management actions can be included in morphodynamic models. Our goal was not to predict all coastal processes involved in future beach movement and loss at these four National Seashores, but rather present a method for bounding nesting area and testing

whether current levels of development within Seashores pose a threat to nesting beaches under a sea level rise scenario for 2100. This approach allowed us to standardize methods across four different regions in order to identify areas threatened by coastal squeeze as well as areas that are more resilient to aid future management decisions.

Static models, like the one used in this study, primarily rely on current elevation as input data and are useful for identifying barriers to beach migration like roads and buildings (Lentz et al. 2019). We used Caffrey et al.'s (2018) sea level rise modeling approach, which is a process-based model approach, estimating sea level rise based on the underlying physical processes using IPCC (Church et al. 2013) projections of sea level rise. This is a useful initial screening of shorelines most likely to experience beach loss from sea level rise by 2100. We acknowledge that this modeling approach does not capture all relevant coastal processes, including potential changes in longshore sediment transport, annual and decadal sea level trends, the effect of dune elevation (Plant et al. 2016), or other anthropogenic stressors. Areas we identified as having high nesting densities and high likelihood of future loss of beach warrant further investigation using more fine-scale baseline observations and modeling efforts to more accurately predict future habitat loss due to sea level rise. For example, process-based models such as Delft3D (Hydro-Morphodynamics 2017) and XBeach (Roelvink et al. 2009), which directly simulate hydrodynamics and sediment transport, would provide a quantitative assessment of future coastal erosion. Such investigations should include an analysis of the ability of specific sections of coast to migrate as well as predictions of the ability of these sea turtle species to change their habitat preferences.

In addition to the uncertainty in how sea level rise will affect specific sandy coastlines, there is still considerable uncertainty in the magnitude of sea level change in the next one hundred years. This uncertainty is largely driven by the speed and trajectory of ice sheet loss. Ice sheet loss has the potential to greatly increase the amount and speed of sea level rise. Recent work indicates that sea level rise by 2100 could plausibly reach 2 m (Bamber et al. 2019), over double the levels used for this study (0.68–0.79 m depending on the Seashore; Caffrey et al. 2018). Based on the current elevation and topography of the Seashores, a 2-m rise in sea level would drown all areas except for the dunes of CALO, CANA, and most of CAHA. This increased amount of sea level rise would also increase the extent of storm flooding and erosion. We chose a very conservative estimate of beach retreat that highlights areas that we can confidently say will be affected by coastal squeeze in the next hundred years based on current development, which allows us to compare loss at a broad scale between Seashores with different levels of human development. However, the methods developed for this study can be applied to any shoreline projection.

Applications

Continued research into the environmental cues that influence where female sea turtles choose to nest is necessary for our long term understanding of these species. However, because of the complexity of these environments and animals, creating models for nest choice based on all available information and then projecting this into the future is not feasible. Sea level rise is happening at a rapid pace and decisions on conservation priority areas and future coastal development need to be made at a concomitantly fast pace. The methodology that we outline in this paper is a pragmatic approach to delineating current and future areas on current nesting beaches where we predict loggerhead and green sea turtles will nest based on past nesting behavior and projected shoreline change. With these future projections, land managers can estimate where sea turtles are likely to be nesting in the next century, which can be used to inform decisions on the placement of new structures, including roads, many of which will need to be moved due to flooding. This method for delineating current nesting area is useful for creating a bounding area for studies modeling other aspects of the nesting environment, calculating density, and understanding and predicting spatial patterns.

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LITERATURE CITED

- Allison, I., R. B. Alley, H. A. Fricker, and R. H. Thomas. 2009. Ice sheet mass balance and sea level. *Antarctic Science* 21:413–426.
- Avise, J. C., B. W. Bowen, T. Lamb, A. B. Meylan, and E. Bermingham. 1992. Mitochondrial DNA evolution at a turtle's pace: evidence for low genetic variability and reduced microevolutionary rate in the Testudines. *Molecular Biology and Evolution* 9:457–473.
- Bamber, J. L., M. Oppenheimer, R. E. Kopp, W. P. Aspinall, and R. M. Cooke. 2019. Ice sheet contributions to future sea-level rise from structured expert judgment. *Proceedings of the National Academy of Sciences USA* 116:11195–11200.
- Berry, A., S. Fahey, and N. Meyers. 2013. Changing of the guard: adaptation options that maintain ecologically resilient sandy beach ecosystems. *Journal of Coastal Research* 9:899–908.
- Binkley, C. 2007. The creation and establishment of Cape Hatteras National Seashore: The Great Depression through Mission 66. Cultural Resources Division, Southeast Regional Office, National Park Service, Atlanta, Georgia, USA.
- Brook, B., N. Sodhi, and C. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23:453–460.
- Caffrey, M. A., R. L. Beavers, and C. Hoffman. 2018. Sea level and storm surge projections for the National Park Service. NPS/NRSS/NRR—2018/1648. National Park Service, Fort Collins, Colorado, USA.
- Caut, S., V. Hulin, and M. Girondot. 2006. Impact of density-dependent nest destruction on emergence success of Guianan leatherback turtles (*Dermochelys coriacea*). *Animal Conservation* 9:189–197.
- Caut, S., E. Guirlet, and M. Girondot. 2010. Effect of tidal overwash on embryonic development of leatherback turtles in French Guiana. *Marine Environmental Research* 69:254–261.
- Church, J. A., et al. 2013. Sea level change. Pages 1137–1216 in T. F. Stocker, et al., *The Physical Science Basis. Contribution of Working Group I on the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, New York, New York, USA.
- Cooper, J. A. G., and O. H. Pilkey. 2004. Sea-level rise and shoreline retreat: time to abandon the Bruun Rule. *Global and Planetary Change* 43:157–171.
- Dean, R. G., and J. R. Houston. 2016. Determining shoreline response to sea level rise. *Coastal Engineering* 114:1–8.
- Dunkin, L., M. Reif, S. Altman, and T. Swannack. 2016. A spatially explicit, multi-criteria decision support model for loggerhead sea turtle nesting habitat suitability: a remote sensing-based approach. *Remote Sensing* 8:573–22.
- Fish, M. R., I. M. Côté, J. A. Gill, A. P. Jones, S. Renshoff, and A. R. Watkinson. 2005. Predicting the impact of sea-level rise on Caribbean sea turtle nesting habitat. *Conservation Biology* 19:482–491.
- FitzGerald, D. M., M. S. Fenster, B. A. Argow, and I. V. Buynovich. 2008. Coastal impacts due to sea-level rise. *Annual Review of Earth and Planetary Sciences* 36:601–647.
- Foley, A. M., S. A. Peck, and G. R. Harman. 2006. Effects of sand characteristics and inundation on hatching success of loggerhead sea turtle (*Caretta caretta*) clutches on low-relief mangrove islands in southwest Florida. *Chelonian Conservation and Biology* 5:32–41.
- Fuentes, M. M. P. B., et al. 2016. Conservation hotspots for marine turtle nesting in United States based on coastal development. *Ecological Applications* 26:2708–2719.
- Fuentes, M. M. P. B., and M. Hamann. 2009. A rebuttal to the claim natural beaches confer fitness benefits to nesting marine turtles. *Biology Letters* 5:266–267.
- Garmestani, A. S., H. F. Percival, K. M. Portier, and K. G. Rice. 2000. Nest-site selection by the loggerhead sea turtle in Florida's Ten Thousand Islands. *Journal of Herpetology* 34:504–510.
- Girondot, M., A. D. Tucker, P. Rivalan, M. H. Godfrey, and J. Chevalier. 2006. Density-dependent nest destruction and population fluctuations of Guianan leatherback turtles. *Animal Conservation* 5:75–84.
- Hamann, M., M. M. P. B. Fuentes, N. Ban, and V. Mocellin. 2013. Climate change and marine turtles. Pages 353–378 in J. Wyneken, K. J. Lohmann, and J. A. Musick editors. *The biology of sea turtles*. Volume 3. CRC Press, Boca Raton, Florida, USA.
- Harley, C. D. G., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9:228–241.
- Hawkes, L. A., A. C. Broderick, M. H. Godfrey, and B. J. Godley. 2009. Climate change and marine turtles. *Endangered Species Research* 7:137–154.
- Hayes, G. C., and J. R. Speakman. 1993. Nest placement by loggerhead turtles, *Caretta caretta*. *Animal Behaviour* 45:47–53.
- Houser, C., P. Wernette, E. Rentschlar, H. Jones, B. Hammond, and S. Trimble. 2015. Post-storm beach and dune recovery:

- Implications for barrier island resilience. *Geomorphology* 234:54–63.
- Hydro-Morphodynamics. 2017. Version 3.15. Deltares, Delft, The Netherlands.
- Irish, J. L., A. E. Frey, J. D. Rosati, F. Olivera, L. M. Dunkin, J. M. Kaihatu, C. M. Ferreira, and B. L. Edge. 2010. Potential implications of global warming and barrier island degradation on future hurricane inundation, property damages, and population impacted. *Ocean and Coastal Management* 53:645–657.
- Irish, J. L., A. Sleath, M. A. Cialone, T. R. Knutson, and R. E. Jensen. 2014. Simulations of Hurricane Katrina 2005. Under sea level and climate conditions for 1900. *Climatic Change* 122:635–649.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.
- Kamel, S. J. 2013. Vegetation cover predicts temperature in nests of the hawksbill sea turtle: implications for beach management and offspring sex ratios. *Endangered Species Research* 20:41–48.
- Kaska, Y., E. Başkale, R. Urhan, Y. Katılmış, M. Gidiş, and F. Sari. 2010. Natural and anthropogenic factors affecting the nest-site selection of Loggerhead Turtles, *Caretta caretta*, on Dalaman-Sarıgerme beach in South-west Turkey. *Zoology in the Middle East* 50:47–58.
- Kikukawa, A., N. Kamezaki, and H. Ota. 1999. Factors affecting nesting beach selection by loggerhead turtles (*Caretta caretta*): a multiple regression approach. *Journal of the Zoological Society, London* 249:447–454.
- Kopp, R. E., R. M. DeConto, D. A. Bader, C. C. Hay, R. M. Horton, S. Kulp, M. Oppenheimer, D. Pollard, and B. H. Strauss. 2017. Evolving understanding of Antarctic ice-sheet physics and ambiguity in probabilistic sea-level projections. *Earth's Future* 5:1217–1233.
- Kudo, H., A. Murakami, and S. Watanabe. 2003. Effects of sand hardness and human beach use on emergence success of loggerhead sea turtles on Yakushima Island, Japan. *Chelonian Research* 4:695–696.
- Lamont, M. M., and I. Fujisaki. 2014. Effects of ocean temperature on nesting phenology and fecundity of the loggerhead sea turtle (*Caretta caretta*). *Journal of Herpetology* 48:98–102.
- Leighton, P. A., J. A. Horrocks, and D. L. Kramer. 2010. Predicting nest survival in sea turtles: when and where are eggs most vulnerable to predation? *Animal Conservation* 14:186–195.
- Lentz, E. E., N. G. Plant, and E. R. Thieler. 2019. Relationships between regional coastal land cover distributions and elevation reveal data uncertainty in a sea-level rise impacts model. *Earth Surface Dynamics* 7:429–438.
- Lutcavage, M. E., P. Plotkin, B. Witherington, and P. I. Lutz. 1997. Human impact on sea turtle survival. Pages 387–411 in P. I. Lutz, and J. A. Musick, editors. *The biology of sea turtles*. Volume 1. CRC Press, Boca Raton, Florida, USA.
- Magliocca, N. R., D. E. McNamara, and A. B. Murray. 2011. Long-term, large-scale morphodynamic effects of artificial dune construction along a barrier island coastline. *Journal of Coastal Research* 27:918–930.
- Mantyka-Pringle, C. S., T. G. Martin, and J. R. Rhodes. 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology* 18:1239–1252.
- Marco, A., et al. 2012. Abundance and exploitation of loggerhead turtles nesting in Boa Vista island, Cape Verde: the only substantial rookery in the eastern Atlantic. *Animal Conservation* 15:351–360.
- Marco, A., E. Abella, S. Martins, Ó. López, and J. Patino-Martinez. 2018. Female nesting behaviour affects hatchling survival and sex ratio in the loggerhead sea turtle: implications for conservation programmes. *Ethology Ecology and Evolution* 30:141–155.
- Mazaris, A. D., Y. G. Matsinos, and D. Margaritoulis. 2006. Nest site selection of loggerhead sea turtles: The case of the island of Zakynthos, W Greece. *Journal of Experimental Marine Biology and Ecology* 336:157–162.
- Mazaris, A. D., A. S. Kallimanis, J. Tzanopoulos, S. P. Sgardeelis, and J. D. Pantis. 2008. Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. *Journal of Experimental Marine Biology and Ecology* 367:219–226.
- Mazaris, A. D., G. Matsinos, and J. D. Pantis. 2009. Evaluating the impacts of coastal squeeze on sea turtle nesting. *Ocean and Coastal Management* 52:139–145.
- Mazaris, A. D., A. S. Kallimanis, J. D. Pantis, and G. C. Hays. 2013. Phenological response of sea turtles to environmental variation across a species' northern range. *Proceedings of the Royal Society B* 280:20122397.
- Monsinjon, J., M. Lopez-Mendilaharsu, P. Lara, A. Santos, M. A. G. dei Marcovaldi, M. Girondot, and M. M. P. B. Fuentes. 2019. Effects of temperature and demography on the phenology of loggerhead sea turtles in Brazil. *Marine Ecology Progress Series* 623:209–219.
- Moore, L. J., J. H. List, S. J. Williams, and D. Stolper. 2010. Complexities in barrier island response to sea level rise: insights from numerical model experiments, North Carolina Outer Banks. *Journal of Geophysical Research* 115:296–27.
- Mortimer, J. A. 1990. The influence of beach sand characteristics on the nesting-behavior and clutch survival of green turtles (*Chelonia mydas*). *Copeia* 1990:802–817.
- Morton, R. A., and A. H. Sallenger, Jr. 2003. Morphological impacts of extreme storms on sandy beaches and barriers. *Journal of Coastal Research* 19:560–573.
- Mrosovsky, N. 1983. Ecology and nest-site selection of leatherback turtles *Dermodochelys coriacea*. *Biological Conservation* 26:47–66.
- National Oceanic and Atmospheric Administration. 2016. Sea, lake, and overland surges from hurricanes. <http://www.nhc.noaa.gov/surge/slosh.phpMODELING>
- National Park Service. 2012. Foundation document: Cape Lookout National Seashore, North Carolina. U.S. Department of the Interior, Washington, DC, USA.
- National Research Council. 2012. Climate change: evidence, impacts, and choices. PDF booklet. The National Academies Press, Washington, DC, USA.
- Nel, R., A. E. Punt, and G. R. Hughes. 2013. Are coastal protected areas always effective in achieving population recovery for nesting sea turtles? *PLoS ONE* 8:e63525–12.
- Nishizawa, H., T. Noda, T. Yasuda, J. Okuyama, N. Arai, and M. Kobayashi. 2013. Decision tree classification of behaviors in the nesting process of green turtles (*Chelonia mydas*) from tri-axial acceleration data. *Journal of Ethology* 31:315–322.
- Noss, R. F. 2011. Between the devil and the deep blue sea: Florida's unenviable position with respect to sea level rise. *Climatic Change* 107:1–16.
- Parris, A., et al. 2012. Global Sea Level Rise Scenarios for the US National Climate Assessment. NOAA Tech Memo OAR CPO-1 1–37. Climate Program Office, Silver Spring, Maryland, USA.
- Patel, S. H., S. J. Morreale, V. S. Saba, A. Panagopoulou, D. Margaritoulis, and J. R. Spotila. 2016. Climate impacts on sea turtle breeding phenology in Greece and associated

- foraging habitats in the wider Mediterranean region. *PLoS ONE* 11:e0157170.
- Penland, S., S. J. Williams, D. W. Davis, A. H. Sallenger Jr, and C. G. Groat. 1992. Barrier island erosion and wetland loss in Louisiana. Pages 2–7 in S. J. Williams, S. Penland, A. H. Sallenger Jr., editors. Louisiana barrier island erosion study-atlas of barrier shoreline changes in Louisiana from 1853 to 1989: U.S. Geological Survey Miscellaneous Investigations Series I-2150-A. US Geological Survey, Reston, Virginia, USA.
- Pike, D. A. 2008. Natural beaches confer fitness benefits to nesting marine turtles. *Biology Letters* 4:704–706.
- Pike, D. A. 2013. Climate influences the global distribution of sea turtle nesting. *Global Ecology and Biogeography* 22:555–566.
- Pike, D. A., and J. C. Stiner. 2007. Sea turtle species vary in their susceptibility to tropical cyclones. *Oecologia* 153:471–478.
- Pike, D. A., R. L. Antworth, and J. C. Stiner. 2006. Earlier nesting contributes to shorter nesting seasons for the loggerhead sea turtle, *Caretta caretta*. *Journal of Herpetology* 40:91–94.
- Plant, N. G., E. R. Thieler, and D. L. Passeri. 2016. Coupling centennial-scale shoreline change to sea-level rise and coastal morphology in the Gulf of Mexico using a Bayesian network. *Earth's Future* 4:143–158.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ranasinghe, R. 2016. Assessing climate change impacts on open sandy coasts: a review. *Earth Science Reviews* 160:320–332.
- Randall, A. L. 2015. Nesting patterns of loggerhead sea turtles (*Caretta caretta*) in North Carolina (2005–2014). Thesis. University of North Carolina, Wilmington, Wilmington, North Carolina, USA.
- Reece, J. S., et al. 2013. Sea level rise, land use, and climate change influence the distribution of loggerhead turtle nests at the largest USA rookery (Melbourne Beach, Florida). *Marine Ecology Progress Series* 493:259–274.
- Ritz, C., T. L. Edwards, G. Durand, A. J. Payne, V. Peyaud, and R. C. A. Hindmarsh. 2015. Potential sea-level rise from Antarctic ice-sheet instability constrained by observations. *Nature* 528:115–118.
- Roelvink, D., A. Reniers, A. van Dongeren, J. van Thiel de Vries, R. McCall, and J. Lescinski. 2009. Modelling storm impacts on beaches, dunes and barrier islands. *Coastal Engineering* 56:1133–1152.
- Rogers, L. J., L. J. Moore, E. B. Goldstein, C. J. Hein, J. Lorenzo-Trueba, and A. D. Ashton. 2015. Anthropogenic controls on overwash deposition: evidence and consequences. *Journal of Geophysical Research: Earth Surface* 120:2609–2624.
- Salmon, M., M. G. Tolbert, D. P. Painter, M. Goff, and R. Reinert. 1995. Behavior of loggerhead sea turtles on an urban beach: Hatchling orientation. *Journal of Herpetology* 29:568–576.
- Shaw, K. R. 2013. Effects of inundation on hatch success of loggerhead sea turtle (*Caretta caretta*) nests. Thesis. University of Miami, Miami, Florida, USA.
- Slater, T., and A. Shepherd. 2018. Antarctic ice losses tracking high. *Nature Climate Change* 8:1025–1026.
- Small, C., and R. J. Nicholls. 2003. A global analysis of human settlement in coastal zones. *Journal of Coastal Research* 19:584–599.
- Stutz, M. L., and O. H. Pilkey. 2005. The relative influence of humans on barrier islands: humans versus geomorphology. *Reviews in Engineering Geology* 16:137–147.
- Swiggs, J., F. V. Paladino, J. R. Spotila, and P. S. Tomillo. 2018. Depth of the drying front and temperature affect emergence of leatherback turtle hatchlings from the nest. *Marine Biology* 165:1–10.
- Titus, J. G., D. E. Hudgens, D. L. Trescott, M. Craghan, W. H. Nuckols, C. H. Hershner, J. Kassakian, C. J. Linn, P. G. Merritt, and T. McCue. 2009. State and local governments plan for development of most land vulnerable to rising sea level along the US Atlantic coast. *Environmental Research Letters* 4:044008.
- Tiwari, M., K. A. Bjorndal, A. B. Bolten, and B. M. Bolker. 2006. Evaluation of density-dependent processes and green turtle *Chelonia mydas* hatchling production at Tortuguero, Costa Rica. *Marine Ecology Progress Series* 326:283–293.
- USGCRP. 2018. Impacts, risks, and adaptation in the United States: Fourth National Climate Assessment, Volume II. *IND*. R. Reidmiller, Avery, C. W., Easterling, D. R., Kunkel, K. E., Lewis, K. L. M., Maycock, T. K., and Stewart, B. C., editors. U.S. Global Change Research Program, Washington, D.C., USA.
- Van Houtan, K. S., and O. L. Bass. 2007. Stormy oceans are associated with declines in sea turtle hatching. *Current Biology* 17:R590–R591.
- Varela, M. R., A. R. Patrício, K. Anderson, A. C. Broderick, L. DaBell, L. A. Hawkes, D. Tilley, R. T. E. Snape, M. J. Westoby, and B. J. Godley. 2018. Assessing climate change associated sea-level rise impacts on sea turtle nesting beaches using drones, photogrammetry and a novel GPS system. *Global Change Biology* 2:21–10.
- Vitousek, S., P. L. Barnard, and C. H. Fletcher. 2017. Doubling of coastal flooding frequency within decades due to sea-level rise. *Scientific Reports*. 7:1399.
- Von Holle, B., et al. 2019. Effects of future sea level rise on coastal habitat. *Journal of Wildlife Management* 17:3644–11.
- Weishampel, J. F., D. A. Bagley, L. M. Ehrhart, and A. C. Weishampel. 2010. Nesting phenologies of two sympatric sea turtle species related to sea surface temperatures. *Endangered Species Research* 12:41–47.
- Witherington, B. E., and K. A. Bjorndal. 1991. Influences of wavelength and intensity on hatchling sea turtle phototaxis: implications for sea-finding behavior. *Copeia* 1991:1060–1069.
- Witherington, B., P. Kubilis, B. Brost, and A. Meylan. 2009. Decreasing annual nest counts in a globally important loggerhead sea turtle population. *Ecological Applications* 19:30–54.
- Witherington, B., S. Hiram, and A. Mosier. 2011. Sea turtle responses to barriers on their nesting beach. *Journal of Experimental Marine Biology and Ecology* 401:1–6.
- Wood, D. W., and K. A. Bjorndal. 2000. Relation of temperature, moisture, salinity, and slope to nest site selection in loggerhead sea turtles. *Copeia* 2000:119–128.
- Zavaleta-Lizárraga, L., and J. E. Morales-Mávil. 2013. Nest site selection by the green turtle (*Chelonia mydas*) in a beach of the north of Veracruz, Mexico. *Revista Mexicana de Biodiversidad* 84:927–937.
- Zhang, K., B. C. Douglas, and S. P. Leatherman. 2004. Global warming and coastal erosion. *Climatic Change* 64:41–58.

DATA AVAILABILITY

Data are available on Figshare: <https://doi.org/10.6084/m9.figshare.11743758.v2>