Sea level rise, land use, and climate change influence the distribution of loggerhead turtle nests at the largest USA rookery (Melbourne Beach, Florida)

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ABSTRACT: Anthropogenic climate change adds to the existing suite of threats to species, such as habitat degradation, by increasing extinction risk and compromising the ability of species to respond adaptively to these stressors. Because threats from anthropogenic climate change often interact synergistically with other threats, integrated assessments of the factors and processes that affect species persistence and distribution are required. We assessed the influence of coastal land use and climate change (specifically sea level rise) on the spatial distribution of nests within the largest loggerhead *Caretta caretta* marine turtle rookery in the Atlantic Ocean, at Melbourne Beach, Florida, from 1986 to 2006. We generated a multiple regression model based on climate change, sea-level rise and land use that describes 47% of the spatial variation in loggerhead nesting. Nests have shifted northward (likely in response to warming temperatures), away from intensive coastal development, and, surprisingly, toward areas of increased erosion. Using the Bruun Rule (an approximation of the response of the shoreline profile to sea level rise), we modeled the impacts of sea level rise of 0.25 and 0.5 m in conjunction with extrapolations of coastal development and a continued northward shift in nest distribution. We project up to a 43% decrease in beach area from 1986 to a future with 0.5 m of sea level rise and predict that loggerhead nesting will shift northward and become increasingly crowded on narrowing beaches. An implication of this study is that areas currently protected for large rookeries may not overlap with their future distributions.

KEY WORDS: *Caretta* · Climate change · Sea level rise · Beach erosion · Sea turtle · Coastal development · Bruun Rule

INTRODUCTION

Anthropogenic climate change (IPCC 2007) poses significant threats to biodiversity (Cahill et al. 2013, Foden et al. 2013), particularly because it is occurring in the midst of the Earth's sixth mass extinction (Barnosky et al. 2011), where the adaptive capacity of

species is compromised by habitat destruction, invasive species, and other pressures such as direct human persecution. The stresses from anthropogenic climate change often interact synergistically with other threats (Harley et al. 2006, Root & Schneider 2006, Russell et al. 2009), which suggests a need for integrated assessment of the factors and processes

that threaten species persistence. Considering the influence of climate on species without accounting for other factors, such as habitat loss and degradation, barriers to dispersal, and altered interspecific interactions, may result in unrealistic projections and often underestimates threats and extinction risk (Burgman et al. 1993, Dawson et al. 2011, Urban et al. 2012). Successful conservation requires an understanding of the relationships between species, their environment, and the factors that determine their distribution in light of climate change. This is particularly true in coastal areas, where human land use and density are typically intense, because the impacts of changing temperature and precipitation, habitat loss/degradation, and sea level rise combine to squeeze species 'between the devil and the deep blue sea' (Harris & Cropper 1992, Noss 2011).

The spatial scale of climate and species distribution modeling, relative to conservation efforts, is also critical to consider. Conservation biologists produce niche envelope models and related tools to help planners understand potential future species distributions, given various scenarios of climate change (Pearson & Dawson 2003, Hijmans & Graham 2006, Wiens et al. 2009). Although these models are useful, their predictions pose challenges because, for many species, the predicted future distribution is outside of existing protected areas, where human land use often precludes occupancy (see Halpin 1997). Conservation planning for climate change in the form of warming temperatures and sea level rise should focus on spatial scales of relevant protected areas and potential movement corridors among them, even when those areas constitute only a small portion of the species' total range.

For marine turtles, new stressors from anthropogenic climate change such as warming temperatures, sea level rise, and the increased frequency of extreme weather events add to historic threats such as habitat destruction. Sea level rise exacerbates coastal erosion of sandy beaches on which marine turtles lay their eggs (Fish et al. 2005, 2008, Baker et al. 2006, Hawkes et al. 2007, Poloczanska et al. 2009, Witt et al. 2010). Climate change can also increase the incidence of storms that erode or inundate nests (Pike & Stiner 2007, Van Houtan & Bass 2007, Fuentes & Abbs 2010, Mousavi et al. 2011), lead to incubation temperatures that alter sex ratios or hatching success (Godley et al. 2001, Hawkes et al. 2007, Poloczanska et al. 2009, Fuentes et al. 2010b, 2011, Hays et al. 2010, Witt et al. 2010, Katselidis et al. 2012), decrease nesting success (Tiwari et al. 2006, Fuentes et al. 2010a,c), and potentially alter the sea surface tem-

perature cues females use to determine when and where to nest (Weishampel et al. 2004, 2010).

Although marine turtles have experienced tremendous shifts in climate and sea level (Kominz et al. 1998, Paillard 2006) over their evolutionary histories and have responded by shifting their distributions to more suitable habitat (Bowen et al. 1994, Reece et al. 2005), their ability to respond to current climate change is compromised by reduced numbers because of human activities and ongoing threats to habitat (Mazaris et al. 2009). For example, coastal development can reduce beach area and render beaches inhospitable to turtles by disrupting nesting adults or disorienting hatchlings as they move from the beach to offshore currents (Witherington & Bjorndal 1991, Salmon et al. 1995). Coastal land use can also prevent the natural migration of beach habitat in response to climate change (Mazaris et al. 2009).

Because marine turtles exhibit regional nest site fidelity (Bjorndal et al. 1983), conservation efforts have focused heavily on protecting nesting beaches (NMFS & USFWS 1991, Witherington 2003). However, protected nesting areas are static, whereas populations and the biotic and abiotic factors on which they depend are spatially and temporally dynamic. Tracking studies in the Mediterranean have shown the potential for the loggerhead marine turtle *Caretta caretta* to alter nesting distributions over small spatial scales in response to climate change, suggesting that relatively small, static protected areas may not meet the nesting needs of adults with spatially and temporally dynamic preferences (Schofield et al. 2010). Thus, it is critical to determine if the beaches currently protected for marine turtle nesting will be suitable over the next several decades.

Here, we empirically assess changes in human land use and climate (including sea level rise) in the largest loggerhead rookery in the USA, at Melbourne Beach, Florida, within a protected area over a 20 yr period from 1986 to 2006. We used multiple regression models to evaluate which combination of factors best explains spatial heterogeneity in the distribution of loggerhead nests within the protected area, while accounting for model uncertainty. To understand how these changes might influence the spatial distribution of loggerhead nests in the future, we modeled shoreline recession in response to sea level rise over the next 20 to 50 yr. We use our model of beach erosion in combination with extrapolated trends in land use to predict how sea level rise over the next several decades will affect the spatial distribution of nests. This study represents a detailed assessment of a globally critically important logger-

head rookery and an evaluation of suggested management strategies for marine turtles. Our approach is broadly applicable to marine turtles and other species threatened by the interacting threats of human land use patterns and climate change.

MATERIALS AND METHODS

Case study: the loggerhead turtle and the Archie Carr National Wildlife Refuge

Currently, loggerhead marine turtle nesting in Florida is clustered around protected areas such as the Archie Carr National Wildlife Refuge (ACNWR; www.fws.gov/archiecarr), which is located on a barrier island along Florida's east coast. One of the largest protected areas for marine turtles, ACNWR was created in 1991 to protect critical beach habitat for turtles, including one of the world's largest loggerhead rookeries (Ehrhart et al. 2003). ACNWR spans approximately 20 km of beach on the relatively narrow (<1 km wide on average) barrier island of Florida's east coast, with its southern terminus near Sebastian Inlet. Coincident with federal protection of the loggerhead as threatened under the Endangered Species Act in 1978 and subsequent creation of AC-NWR, the number of nesting loggerheads increased by approximately 30%, from 9300 in 1980 to 12 233 in 2010 (FWC; http://myfwc.com/research/wildlife/sea-turtles/nesting/). Despite comprising roughly 2% of Florida's coastal beaches, approximately 1 of every 6 of Florida's loggerhead turtles nests on this 20 km stretch of protected shoreline, and this area has the highest density of loggerhead nesting in the Western Hemisphere (Ehrhart et al. 2003). Sea level rise is a particularly severe threat within ACNWR because of the relatively narrow barrier islands, where inland retreat of the beach is impeded by either anthropogenic development or lack of space. We chose this study site because of its global importance and its exposure to multiple threats, including climate change and land use, and because the University of Central Florida (UCF) Marine Turtle Research Group has been engaged in a long-term monitoring program at this site since the early 1980s.

Loggerhead nest placement and changes in the distribution of nests

Our study site included a 20 km stretch of beach separated into 0.5 km beach sections at ACNWR in Melbourne Beach, Florida. We assessed the beach characteristics that loggerheads in ACNWR prefer using a database of 650 nests sampled between 2007 and 2011. Nests were randomly sampled temporally and spatially following the methodology of a long-term study by the UCF Marine Turtle Research Group. For each nest, we measured the estimated position between the 2 closest 0.5 km landmarks using both visual cues and GPS. The exact coordinates of each nest were not recorded for the full duration of the study, but rather we recorded their placement relative to the nearest two 0.5 km landmarks. All analyses are based on 0.5 km sections of beach as the smallest longshore spatial unit, which is adequate for our purposes. For each nest, we also measured the distance from the clutch to the mean high water (MHW) mark and to the base of the dune (where beach width was the sum of the latter 2 measurements). Measurements to the dune stopped at the vertical dune face. Measurements to the MHW line stopped at the middle of the highest high tide line visible on the beach (as marked by a line of fine debris deposited on the sand). We tested for a linear correlation between beach width and distance from the nest to MHW to determine if turtles altered nest placement above the high tide line depending on the total beach width. We also evaluated the relationship between the distances of nests from MHW and the frequency of nests washed out by erosion and the relationship between beach width and nest washout frequency.

To depict the spatial distribution of nests, the UCF Marine Turtle Research Group recorded the total number of nests during daily morning surveys for each 0.5 km section of beach over the entire nesting season (approximately May through August) of each year from 1986 to 2006. This time period begins with the earliest available nesting surveys and ends prior to major nourishment (manual deposition of sand) projects in the refuge that artificially altered beach widths, dune shape, and dune placement, potentially influencing the spatial distribution of nesting.

Changes in latitude

Average mean global temperatures (IPCC 2007) and average summer temperatures in Florida are increasing at a rate of 0.02°C per decade (Von Holle et al. 2010). As reviewed in Bellard et al. (2012), 2 potential responses to temperature increases in North America are for species to shift upslope in elevation (not an option for marine turtles) or north in

latitude or to alter their phenology. Although there is no documented recent trend, loggerheads at ACNWR have been shown to alter their nesting phenology (Weishampel et al. 2010) in relation to warmer sea surface temperatures. To assess evidence for latitudinal (e.g. northward) shift in nest deposition, we conducted a linear regression for each beach section, where the independent variable was year and the dependent variable was the total proportion of ACNWR nesting observed in that 0.5 km section, yielding a measurement of slope for each beach section. The slope is the trajectory (increasing, decreasing, or constant) in the proportion of nesting in that beach section, where a positive slope indicates an increase in the proportion of nesting from 1986 to 2006, a negative slope indicates a decrease in the proportion of nesting, and a non-significant relationship indicates no net change in the proportion of nesting throughout the study period. The proportion of total nesting for the study area was used to remove the effect of annual variation in the total number of nests.

Influence of land use change in ACNWR

We assessed the number and the annual change in linear meters of beachfront structures (hereafter frontage), defined as buildings (i.e. houses, condominiums, and public buildings) and lighted/paved parking lots, between the beach and Highway A1A across 20 km of ACNWR. We assume that the beachfront area is related to the probability of human interactions with marine turtles on the beach and the lighting potential of built structures, which are known to negatively impact nesting adult turtles as well as hatchlings (Witherington & Bjorndal 1991, Mazor et al. 2013). In addition, structures built on the dune prevent the natural migration of beaches inland in response to sea level rise. Although nesting data spanned the time period from 1986 to 2006, information on beach frontage was only available for 1983, 1994, and 2006. Measures of beach frontage were taken for every 0.5 km section of beach based on aerial and satellite imagery. A linear regression between frontages from 1983 to 1994 was used to infer frontage in 1986 for comparison with nesting and beach width data. For 1983, we georeferenced aerial photos of Brevard County provided by the Florida Department of Transportation (scale 1:2400) in ArcMap (ESRI 2010) and digitized all structures as polygons and all 0.5 km markers as points. For 1994 and 2006, we used high-resolution

Google Earth satellite imagery, digitized all structures and points in Google Earth, and then imported these into ArcMap for comparison of structures across time. Frontage was measured using the measure tool in ArcMap and Google Earth, with cross-validation to ensure equivalent measures of the same structures. Analyses with and without parking lots or by counting the number of structures versus frontage in meters did not qualitatively affect our results. An alternative metric to consider might be lighting potential (see Mazor et al. 2013), because some structures have 'turtle-friendly' lighting while others do not, but these data were not available for historical analysis.

Historical sea level rise

We assessed beach narrowing in ACNWR from 1986 to 2006 using measurements taken from the Florida Department of Environmental Protection (FDEP), Bureau of Beaches and Coastal Systems (BBCS). Approximately every 4 yr, representatives of FDEP BBCS take georeferenced measurements of beach widths from the MHW line to the dune line at 100 m increments. We used measurements taken from 1986 and overlaid them with markers laid at 0.5 km intervals throughout ACNWR. At each of the 40 markers, we used the measurement tool in ArcGIS v10 to measure the distance from the dune line to the MHW line. In the FDEP BBCS data, GPS points were taken only for the MHW points (not the dune line). To recreate the dune line, we overlaid high-resolution aerial images with a 0.3 m bare earth lidar-derived digital elevation map (DEM) acquired from FDEP and traced the dune profile. The distance from the recreated dune line to the georeferenced MHW points was, on average, less than 0.2 m different from the width recorded by FDEP BBCS. The result of this analysis was a MHW line recreated from 1986 and 40 measurements of beach width. We repeated this analysis to recreate the MHW line in 2006. To assess the degree of beach erosion at each landmark between 1986 and 2006, we performed 2 measurements: first, we computed the distance between the 1986 and 2006 MHW points (this measurement is independent of any reconstructed dune line and yields an estimate of the amount of shoreline erosion); second, we measured the change in beach width (calculated as distance from the MHW line to the traced contour line) over the same period. This analysis yields an estimate of historical and recent beach widths over a 20 yr period. Because the 2

measurements were similar, we report only measurements from the MHW line to the traced contour line (using the alternative dataset did not qualitatively alter our results).

Projected beach widths over the next 50 yr

The Bruun Rule (Bruun 1962) is a useful tool for modeling shoreline recession in response to sea level rise. The Bruun Rule is based on 2 assumptions: (1) the active beach profile extends out to a depth where bed sediments are no longer significantly transported by wave action; and (2) the volume of sand eroded in the upper shoreface is conserved and deposited offshore while the beach profile maintains its shape. Coastal geologists and engineers have been using the Bruun Rule for nearly 5 decades (Ranasinghe & Stive 2009) and have validated its predictions (Rollason et al. 2010). It is an integral component to many contemporary coastal management applications and is the basis of theoretical models that predict coastal response. The Bruun Rule assumes that wave heights and periods will not change with a rise in sea level, as Ruggiero (2013) suggests they may, in which case the frequency of coastal flooding and erosion will increase. Nevertheless, evidence supporting the theory includes wave tank experiments (Schwartz 1965, 1967) and long-term studies of coastal profiles in eastern Lake Michigan (Hands 1983) and of the Virginia shoreline of the Chesapeake Bay (Rosen 1978). However, the Bruun Rule should be considered a first approximation of shoreline recession (DECCW 2010), and any predictions should be considered broad estimates (Ranasinghe & Stive 2009). The Bruun Rule can be tested by comparing long-term rates of shoreline change with rates of sea level rise to determine if sea level rise is correlated with beach erosion at a given location (Zhang et al. 2011).

The Bruun Rule predicts shoreline recession under a given sea level increase from the relationship:

$$R = S \frac{L^\star}{b + h^\star} \tag{1}$$

where S is the rise in mean sea level, b is the elevation of the dune, $h^\star$ is the depth of closure, and $L^\star$ is the distance to the depth of closure. To determine the location and elevation of the dune face at each landmark, we compared a 3 m lidar-derived DEM with aerial photography. Elevations ranged from 2.72 to 7.16 m (MSL) and correspond well with dune elevations determined by the US Geological Survey using high-resolution laser altimetry data for the Mel-

bourne area, which ranged from 3.5 to 7.5 m (MSL) (Elko et al. 2002). The depth of closure is considered the most landward depth at which bed sediments are no longer significantly transported between the nearshore and the offshore (Dean & Dalrymple 2002). It can be determined through beach profile surveys or predictive equations that use knowledge of the local significant wave height and wave period. Dean & Grant (1989) determined position-dependent depths of closure along the Florida coastline and reported a depth of approximately 4.89 m (MSL) at Melbourne Beach. Because the study area does not span a large distance relative to the wave characteristics, this depth was considered fixed for all landmarks. The distance that the active profile extends out to the depth of closure, $L^\star$, was determined by identifying the 4.89 m contour through use of a bathymetric DEM assembled from NOAA National Ocean Service hydrographic surveys. The distance was measured from the MHW line (the landward boundary of the active profile) to the depth of closure contour at each landmark.

The shoreline recession at each landmark was calculated for 0.25 and 0.5 m of sea level rise. These values were chosen based on an expectation of 1 m of sea level rise by 2100, roughly corresponding with 0.25 m by 2020 and 0.5 m by 2050 (Pfeffer et al. 2008, Vermeer & Rahmstorf 2009, Strauss et al. 2012), which are shorter timeframes more amenable to planning than a time horizon of 2100. Because the Bruun Rule is a cross-shore predictive model, it does not take into account any erosion or deposition caused by longshore transport. The presence of Sebastian Inlet 2.5 km south of the first landmark is far enough away to not have a direct impact on erosion or deposition for this study area, since the landmarks are outside of the inlet's flood and ebb shoals. We also calculated the total beach area as the area of polygons created by the MHW and dune line for each beach segment. We report on the total area of beach and the proportion that remains after projected sea level rise.

Inferring the influence of man-made structures and sea level rise on the spatial distribution of nests

We developed multiple regression models to determine the relative importance of human land use changes, sea level rise, and latitudinal shifts on the spatial distribution of nests within ACNWR. Because the number of loggerhead nests deposited statewide and within ACNWR varies non-linearly (Weisham-

pel et al. 2003, Witherington et al. 2009; see supplement and Fig. S1 in the supplement, available at www.int-res.com/articles/suppl/m493p259_supp.pdf), we used the proportion of total nests deposited in each beach section as the response variable in our multiple regression. This proportion is highly correlated across years (Weishampel et al. 2003), and we incorporate this into our model, with year as the first predictor variable. Additional predictors included annual measures for each 0.5 km section for latitude, beach width from 1986 to 2006, and meters of beach frontage for human-built structures from 1986 to 2006. First, we conducted a multiple regression analysis using the *lm* function in R (R Core Development Team 2009) with all 4 predictor variables and their interaction effects. Second, we executed stepwise reduction and addition to identify the best model, including several models with interaction effects (reported in results), using the *step* function from MASS (Venables & Ripley 2002). Third, we tested for collinearity among predictor variables and between the model residuals and predictors. We calculated the relative importance of each of the predictor variables and interaction effects examined using the *calc.relimp* function in the relaimpo package in R (http://prof.beuth-hochschule.de/groemping/relaimpo). We used corrected Akaike's information criterion (AIC$_c$) values to identify the best-fit model, defined as 4 or more AIC$_c$ units greater than the next best-fitting model (Burnham & Anderson 2002).

Predicting future changes in the distribution of loggerhead nests

We estimated the future distribution of loggerhead nests within ACNWR based on trends inferred over the last 20 yr. We used the best-fit model inferred from historical data to predict where future nesting would occur. First, we validated the model by using it to predict what proportion of nesting would occur in each beach segment for 2011, for which we have recorded data. For extrapolated values, latitude remained constant. Land use was projected by taking the average number of structures added to each beach segment per year over the 20 yr study period and projecting out to 2020 and 2050, ensuring that the projections would not exceed the maximum beach frontage given the space available and average structure size. For the 2011 validation model, beach widths were predicted by extrapolating from a linear regression of beach width and year. Following

validation of the model, we applied it to predictions for 2020 and 2050, only in this case beach widths were changed to projections using the Bruun Rule conversions described above for 0.25 and 0.5 m of sea level rise. Projections also were made assuming that no new structures were built after 2011. We report on the number of nests projected within each 0.5 km beach segment and uncertainty surrounding those estimates.

To further investigate the potential impacts of beach erosion as predicted by the Bruun Rule, we assessed impacts of crowding nests on ever-narrowing beaches as the probability that 2 or more nests would overlap in space. We calculated total beach area in 1986 and 2006 and with 0.25 (2020) and 0.5 m (2050) of sea level rise by multiplying the beach width at each 0.5 km marker by 500 m. We calculated available nesting sites using a loggerhead nest footprint of 979 cm^2. This is based on a nest diameter of 28.9 cm (Tiwari & Bjorndal 2000) plus 2 standard deviations (6.4 cm) to encompass 95% of nest width, which equals a 35.3 cm diameter or 1765 cm radius, or a footprint of 979 cm^2. We computed the available nesting sites as beach area per 0.5 km section divided by the loggerhead nest footprint. Because green turtles also nest on these beaches, their impact was assessed using a footprint of equal size (Bustard & Tognetti 1969). For 1986 and 2006, we used the number of nests deposited and beach area available for nesting, but for 2020 and 2050 estimates, we used the multiple regression model predictions and the beach area available based on Bruun Rule projections. Our regression model predicts the proportion of nesting in each beach section but not the total number of nests, so we multiplied these proportions by the average number of nests deposited per year from 1986 to 2011. We used the average value because of the non-linearity of nesting numbers through time (see supplement). Stirling's approximation was used to calculate the probability of a loggerhead or green turtle disturbing an existing loggerhead nest:

$$P(A) = \left(\frac{n}{n-k} \right)^{n-k+0.5} e^{-k} \tag{2}$$

where n = the number of available nesting sites, k = the number of loggerhead and green turtle nests (computed as loggerhead equivalents), $P(A)$ = the probability that no 2 nests overlap. These calculations represent a first approximation of nest crowding. Although nest crowding is currently only considered for arribadas, or mass-coordinated nesting

beaches (e.g. Cornelius et al. 1991), it may become an increasingly important consideration on highly eroded beaches.

RESULTS

Loggerhead nest placement and changes in the distribution of nests

The proportion of total nests within each 0.5 km section of beach varies geographically within and between years from 1986 to 2006 (Table S1 in the supplement). Based on data from 650 nests marked in ACNWR between 2007 and 2011, the distance that turtles place their nests above the MHW line is strongly correlated with beach width (p < 0.0001, R^2 = 0.62), which indicates that loggerheads place their nests further from the high tide line on wider beaches than they do on narrower beaches. In other words, there is no set distance beyond the high tide line that acts as a cue for nest deposition; rather, loggerheads tend to nest in the middle of the beach, irrespective of beach width. The majority of nests (88%) are deposited on beaches between 12 and 25 m wide. However, upwards of 80% of beaches were between 12 and 25 m wide between 2007 and 2011, so it is unclear if the tendency to nest on the wider beaches indicates a preference for wide beaches or availability of beach habitat. Nests deposited on narrower beach segments were not more likely to suffer destructive erosion from wave action. A linear regression between beach and the arcsine-transformed proportion of nests washed out shows no significant correlation (p = 0.62). Nevertheless, as expected, the highest proportion of washouts occurred among nests deposited within zero to 5 m of the MHW line (17.7%), irrespective of the total width of the beach. Because very few beach segments are currently limited to 5 m in width, nest loss to washouts has not historically been a major threat to loggerheads in ACNWR. The slope of the beach may be an important factor in the probability of nest washout, as steeper beaches provide a shorter distance for the turtle to crawl before finding nesting habitat above the high water line. Our data clearly demonstrate that loggerheads tend to deposit their nests in the middle of the beach, irrespective of beach width, and since this finding was consistent across our sampling area, where beach slope is not constant (Hays 2012), this pattern is presumably irrespective of beach slope as well. However, slope measurements were not available for direct examination of this relationship.

Changes in latitude

Overall, nesting in most of the beach sections in the northern end of the refuge increased while those in the south decreased, suggesting a northward shift in loggerhead nesting within ACNWR. The change in the proportion of ACNWR nesting between 1986 and 2006 is presented for each beach section in Fig. 1 (data in Table S1 in the supplement).

Influence of land use change in ACNWR

Beach development (frontage) increased by 160% in ACNWR between 1986 and 2006. This increase was slightly greater from 1983 to 1994 than from 1994 to 2006. Most of the increase occurred on the central and southern portions of the refuge (Fig. 2).

Historical beach widths and sea level rise

Beach erosion or reduction in width was spatially heterogeneous. Most, but not all, sections of the beach narrowed over the 20 yr study period, with an average decrease of 3.22 m of beach width, or 0.16 m yr^{-1} (Fig. 3, Fig. S2 in the supplement). A linear regression between the change in beach width and latitude revealed that beach width decreased more in the northern end than in the southern end of ACNWR (p = 0.001, R^2 = 0.25, slope = 0.39 m km^{-1}).
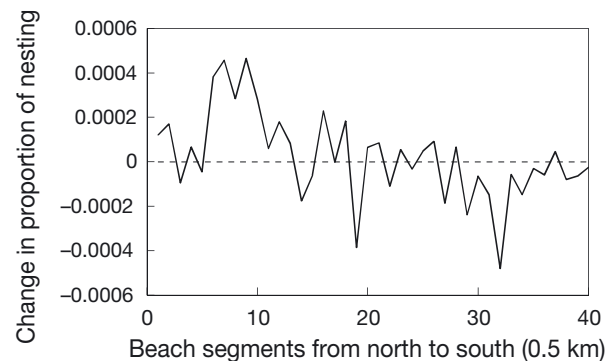

Fig. 1. Change in the proportion of nests deposited in each of the forty 0.5 km beach segments of the Archie Carr National Wildlife Refuge (ACNWR) from 1986 to 2006 (zero change denoted with dashed line). Beach segments are oriented in increasing order from north to south. Positive values on the *y*-axis mean that the proportion of nesting in that segment increased, and negative values mean that it decreased relative to other beach segments. The linear regression between latitude and the change in the proportion of nests from 1986 to 2006 was significant (p = 0.0007, R^2 = 0.24), consistent with a historical shift toward a greater proportion of ACNWR nesting in the north end of the refuge
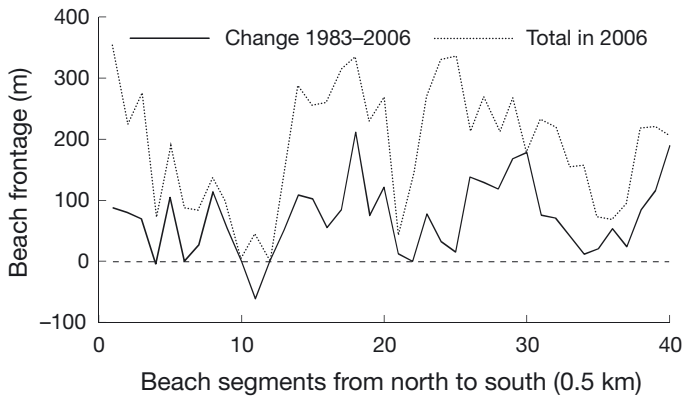
Fig. 2. Change in, and total meters of, beach frontage occupied by man-made structures (houses, condominiums, and lighted/paved parking lots), with zero denoted by horizontal dashed line. The solid line depicts the inferred change in meters of frontage between 1986 and 2006 (inferred because datapoints were 1983, 1994, and 2006) for each beach segment. The dotted line depicts the total meters of frontage in 2006. Note that although there is much overlap, some beach segments with the highest housing density (segments 23 to 25) have only modest increases in the number of structures over the study period
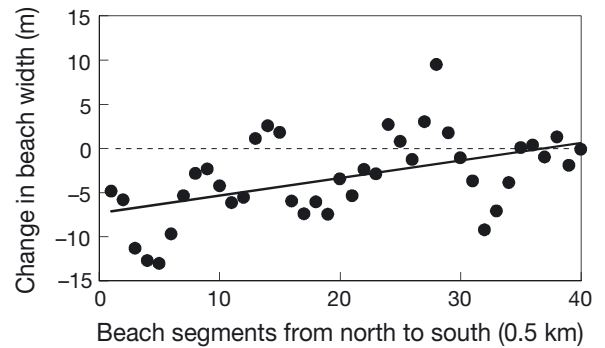
Fig. 3. Change in beach width for each 0.5 km segment of the Archie Carr National Wildlife Refuge from 1986 to 2006, with zero change denoted by dashed line. Linear regression revealed a significant association between reduction in beach width and latitude, with a greater beach narrowing in the north than in the south of the refuge (p = 0.0029, R^2 = 0.2, slope = 0.33 m km^{-1}). Some regions increased in beach width

Projected beach widths over the next 50 yr

Similar to the historical erosion analysis (Fig. 3), the northern end of the study area is expected to experience more erosion than the southern end (Fig. 4). In comparison with measured historical erosion rates, the average beach width decreased by 3.22 m over a 20 yr period. The average rate of sea level rise measured by tide gauges in the Florida Keys is 2.2 mm yr^{-1} from 1913 to 2006 (Maul & Martin 1993; http://tidesandcurrents.noaa.gov). Projecting this rate of erosion to 0.25 m of sea level rise gives a shoreline erosion of 18.52 m since 1986, which suggests that the 12.2 m of erosion modeled by the Bruun Rule may be a conservative estimate. Table 1 summarizes the variation in recession, volume of eroded sand, and corresponding cost of nourishment per cubic yard for the east coast of the USA (Valverde et al. 1999). Fig. 5 presents the projected change in total area of beach from approximately 0.99 million m^2 in 1986 to approximately 0.57 million m^2 in 2050 with 0.5 m of sea level rise, a 43% reduction in potential nesting habitat.
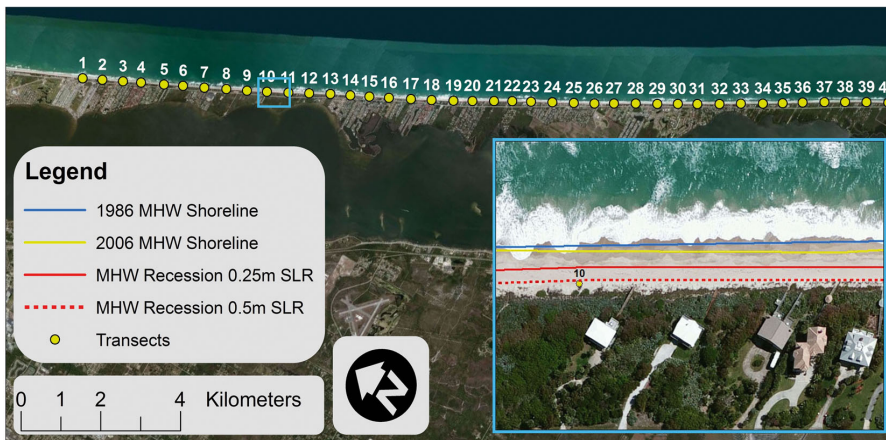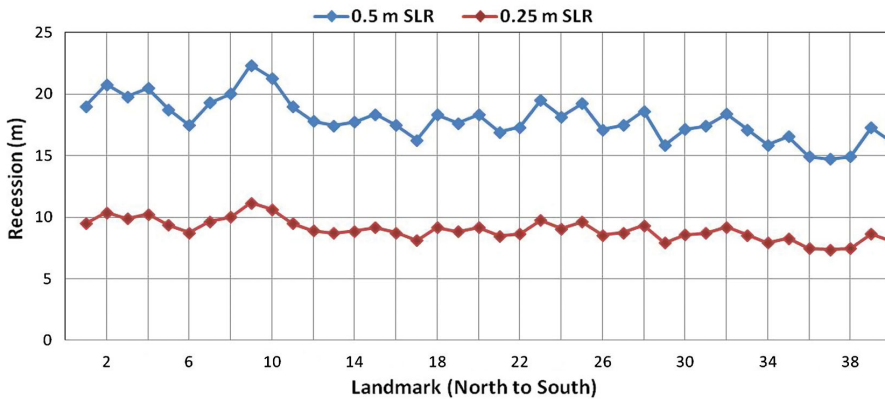

Fig. 4. Study site with 0.5 km section markers and Bruun Rule modeled predictions of beach recession projected from 2006 to a future with 0.25 and 0.5 m of sea level rise (SLR). The inset depicts the mean high water (MHW) lines for an example section of beach

Table 1. Recession (post 2006), volume of eroded sand, and corresponding cost of nourishment based on the average cost of nourishment per cubic yard on the east coast of the USA (Valverde et al. 1999), for 2 projections of sea level rise (SLR)

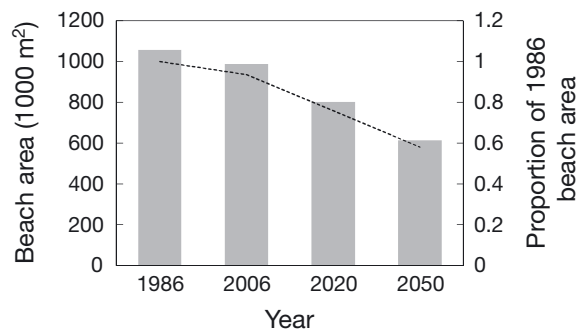| SLR (m)	Recession (m)	Volume eroded (m^3 m^{-1})	Potential cost of nourishment (millions)
0.25	6.8–11.1	73.3–111.0	$10–$15
0.5	13.6–22.3	146.5–222.0	$20–$30

Fig. 5. Total beach area calculated for 1986 and 2006, and predicted for 2020 and 2050 corresponding to 0.25 and 0.5 m of sea level rise, respectively. Also shown is the proportion of 1986 beach area remaining (dashed line), with a 43% reduction in potential nesting habitat by 2050

Inferring the influence of man-made structures and sea level rise on the spatial distribution of nests

The multiple regression model identified 12 factors (including main and interaction effects) as the best model for describing the spatio-temporal distribution of nests in ACNWR from 1986 to 2006 (Table 2). The relative importance of each main effect is given in Table 3. The model describes 47% of the spatial heterogeneity in nesting through time (Table 2). This is substantial predictive power, given that the spatial precision of natal homing in loggerheads is on the order of tens to hundreds of kilometers (Bowen et al. 2004, 2005), making the spatial distribution of their nests inherently difficult to predict. The strongest predictors were latitude and the interaction of latitude and beach width, which combined account for 71% of the model's predictive power (Table 3). We validated the model by predicting the spatial distribution of nests in 2011, for which the true distribution is known. The predicted distribution matches the observed distribution in most areas (Pearson's correlation coefficient = 0.78; Fig. 6), and no spatial bias exists in mismatches between predicted and observed nest distributions. We report on diagnostics of the regression model in Text S1 in the supplement.

Table 2. Results (Akaike's information criterion [AIC] and ΔAIC scores, adjusted R^2 values, and number of parameters in the model) of model-fitting analyses for 8 candidate models predicting the spatial pattern of nests in the Archie Carr National Wildlife Refuge from 1986 to 2006. Y = year, L = latitude, BW = beach width, LU = land use or number of structures; colons indicate interaction effects, and asterisks indicate combined main and interaction effects. The best-fit model was identified by both stepwise model addition and reduction and is superior to the next best-fitting model by more than 5 corrected Akaike's information criterion (AIC_c) units (a difference in AIC_c values of >4 units is considered strong; Burnham & Anderson 2002)

Model	AIC	ΔAIC_c	R^2	N
Y*L*BW+LU+Y:LU+L:LU+ Y:L:BW+Y:L:LU+L:BW:LU	−6694	0	0.472	12
Y*L*BW*LU	−6689	5	0.471	15
Y*L*BW	−6580	114	0.392	7
Y*L*LU	−6492	202	0.325	7
Y*BW*LU	−6196	498	0.039	7
Y*LU	−6171	523	0.006	3
Y*BW	−6187	507	0.024	3
Y*L	−6367	327	0.213	3

Table 3. Relative importance of each factor from the multiple regression model predicting the spatial distribution of nests. The R^2 contribution averaged over orderings among regressors (Lindeman et al. 1980, Chevan & Sutherland 1991) is abbreviated R^{2cont} and sums to 0.472, the overall adjusted R^2 for the best model from Table 2

Main effect	R^{2cont}
Latitude	0.192
Latitude: Beach width	0.142
Latitude: Land use	0.069
Year: Latitude	0.036
Beach width	0.012
Latitude: Beach width: Land use	0.009
Year: Land use	0.004
Year: Latitude: Land use	0.004
Year: Latitude: Beach width	0.0020
Land use	0.001
Year: Beach width	0.0010
Year	0.0003

Predicting future changes in nest distribution

Our predictions of the spatial distribution of nests in 2020 and 2050 (with 0.25 and 0.5 m of predicted sea level rise, respectively) indicate a continued northward shift in nesting within ACNWR. Fig. 6 depicts the spatial distribution of nesting from 1986 through projections to 2050. In 1986, nesting was evenly distributed from north to south, but by 2006, nesting had shifted to higher proportions in the north
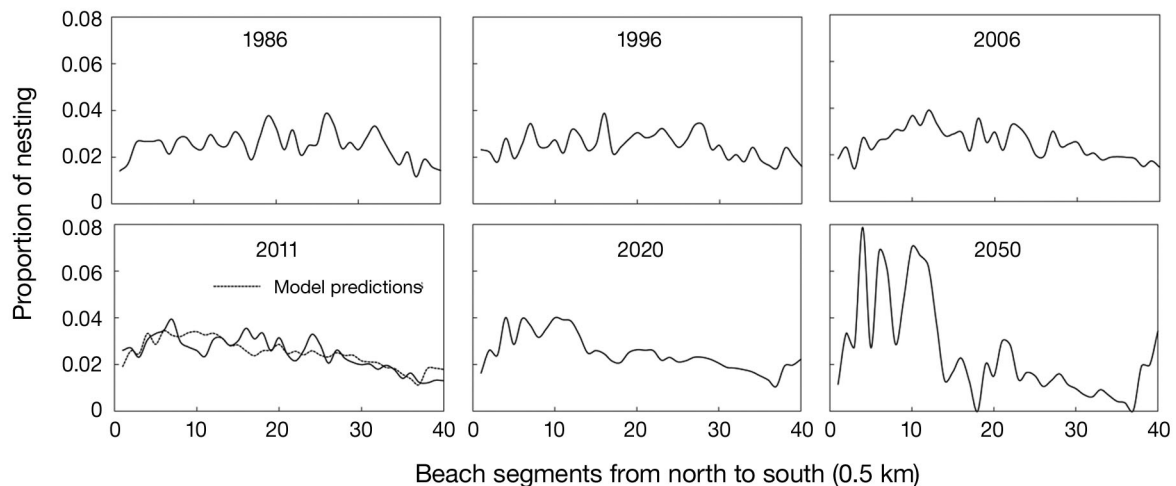
Fig. 6. Proportion of nesting in the Archie Carr National Wildlife Refuge (ACNWR) in each of forty 0.5 km beach sections oriented from north to south (left to right). From 1986 to 2006, the proportion of nesting steadily increased in the northern sections and decreased in the southern sections, becoming more pronounced by 2011. Also shown in the 2011 plot is our validation of the multiple regression model parameterized using data from 1986 to 2006 and predicting the 2011 spatial distribution of nests (dotted line), explaining 80.5% of the variation. Also presented are multiple regression model predictions of the spatial distribution of nests in 2020 and 2050, assuming continued trends in land use and sea level rise of 0.25 and 0.5 m, respectively. Predictions under no changes in land use and confidence intervals surrounding predictions are provided in Figs. S3 to S5 in the supplement (available at www.int-res.com/articles/suppl/m493p259_supp.pdf)

than in the south. These changes were more pronounced by 2011 and, based on our predictions, become dramatic by 2050. The projected increases at the southern terminus of the study area reflect the fact that the southernmost 1.5 km historically held the widest beaches (Fig. S2 in the supplement), providing a refuge for nesting. Despite greater erosion in the northern sections of ACNWR, loggerhead nesting is shifting north, although the projected increases in the northern end of the refuge are not homogenous (Fig. 6). This is because some areas, such as the northernmost sections 1 and 3, were relatively narrow historically (Fig. S2 in the supplement), are projected to show larger than average losses by erosion (Fig. 4), and have a high rate of increase in man-made structures (Fig. 2); thus, they are not projected to increase in the proportion of nests as much as other northern sections. This overall trend of a northward shift is maintained even under the assumption that the number of structures remains fixed at 2011 levels (which would be a very conservative estimate of land use; Fig. S3 in the supplement). Figs. S4 & S5 in the supplement include confidence intervals surrounding these predictions. Although we cannot demonstrate a broader northward shift in the range of all Florida nesting aggregations or show that temperatures vary consistently through time across the latitudes we sampled, a northward shift in nesting is consistent with migration toward cooler

temperatures in response to global warming. Irrespective of the cause, the nesting aggregation we studied is shifting northward. This pattern was not clear from 1986 to 1996 but became increasingly pronounced between 1996 and 2006 and distinct by 2011 (Fig. 6).

Sea level rise and erosion are predicted to decrease beach widths in ACNWR by an average of 12.2 m by 2020 with 0.25 m of sea level rise and 21.2 m by 2050 with 0.5 m of sea level rise. Assuming that the total number of loggerhead and green turtle nests remains relatively constant, we can predict the probability that 2 or more nests will overlap as nests become increasingly crowded on a narrowing beach. The average probability of a single incidence of nest overlap in a given year throughout the study period from 1986 to 2006 was low (<0.2, average = 0.10; lowest in the southern 5 km of ACNWR) but otherwise fairly constant. The average probability of overlap in 2020 (0.25 m sea level rise) and 2050 (0.5 m sea level rise) increases to $p = 0.29$ and 0.35, respectively (Fig. S6 in the supplement). The potential for nest overlap in the future increases to high probabilities ($p = 0.5$ to 1.0) in regions with projected increases in the proportion of nesting and reductions in beach area, particularly at the northern edge of the refuge (Fig. S6 in the supplement). These probabilities ignore the impact of 'false nests', which are nest cavities dug by adult females without the deposition of

eggs, the counting of which would increase the esti-mated probability of nest overlap. Given these and other uncertainties, the actual estimated probability of nest overlap is less important than the magnitude of the increase from historical patterns (1986 to 2006) to 2020 or 2050, which is dramatic in the northern end of the refuge (from 0.2 to 1.0 in some areas).

DISCUSSION

From 1986 to 2006, ACNWR experienced a steady increase in beachfront housing (169% over 20 yr; Fig. 2), while beach widths narrowed on average by 3.22 m (0.16 m yr^{-1}; Figs. 3 to 5). Coincident with these changes, the spatial distribution of loggerhead nests shifted to the north (Figs. 1 & 6). One antici-pated effect of a warming climate in North America is that loggerhead nesting aggregations would either shift northward or the phenology of nesting would change (Hawkes et al. 2007, Witt et al. 2010). The loggerhead aggregation at ACNWR was previously examined and found to show mixed evidence for phenological shifts (Weishampel et al. 2004, 2010). The northward shift in nesting may reflect a response to the increasing average summer temperatures observed in Florida over the same timeframe (Maul & Sims 2007, Von Holle et al. 2010), but this warming pattern is spatially heterogeneous at fine scales (Maul & Sims 2007), and it is unclear if there is a con-sistent temperature change gradient across ACNWR over the timeframe examined in our study. Latitude explains only 19.6% of the variation in the spatial distribution of nests (Table 3), and this pattern does not appear to extend statewide or even across the east coast of Florida, as an examination of statewide nesting shows a fairly stable distribution (Withering-ton et al. 2009). Instead, a more complicated pattern emerges whereby land use, beach width, year, and latitude (and their interaction effects) combine to explain 47% of the variation in the distribution of nests (Table 2).

Our projections of future beach erosion are appro-ximately double the historical rate, assuming a sea level rise of 0.25 m by 2020 and 0.5 m by 2050 (Fig. 4). Projected rates of beach narrowing would range between 0.36 and 0.33 m yr^{-1}, corresponding to a 25 and 43% decrease in beach area, respectively (Fig. 4). The magnitude of erosion predicted by our model is similar to that predicted for other marine turtle nesting beaches in the Caribbean (Fish et al. 2005, 2008), Hawaii (Baker et al. 2006), and Australia (Fuentes et al. 2010c). Our multiple regression model

fitted to historical data, validated, and extrapolated out to 2020 and 2050 (Fig. 6) predicts a continued and exaggerated shift of loggerhead nesting densities northward, where losses of beach area because of sea level rise are expected to be most severe. The implications of these predictions are that nests may become increasingly crowded and potentially shift beyond the boundaries of ACNWR. If these trends continue, increased competition for nest space may occur, particularly in beach segments predicted to increase in their proportion of total ACNWR nests (Fig. S6 in the supplement). Despite these reductions in beach widths, even at 0.5 m of sea level rise, the average beach width in ACNWR is estimated at 29.2 m, which based on our historical analysis of log-gerhead nest placement is still sufficiently wide to protect nests from storm surge and tidal inundation. Nevertheless, storm surge from major hurricanes is predicted to become more intense in the coming decades (Grinsted et al. 2013), and, thus, although this beach width may have protected nests from inundation historically, it may be insufficient in the future.

These threats may not be insurmountable; logger-head turtles as a lineage have experienced climate change throughout their evolutionary history, includ-ing more rapid and extreme changes in climate and sea level than current patterns or those predicted over the next 100 yr. The most extreme predictions for 2100 include 6 m of sea level rise (Schubert et al. 2006, reviewed in Strauss et al. 2012) with 2 to 5°C of warming (IPCC 2007), whereas during the last inter-glacial period 120 000 yr ago, sea levels were 5.5 to 9 m higher than current levels (Dutton & Lambeck 2012). Moreover, sea level rise during some periods since the last glacial maximum was more than 10 times the current rate (Savarese et al. 2002, Dono-ghue 2011, Gregoire et al. 2012). Historically, logger-head populations from more temperate regions of the western Atlantic shifted their distributions to climatic refugia in the Yucatan and potentially in South America (Reece et al. 2005); they then expanded their range to recolonize the southeastern coast of the USA as conditions again became favorable (Bowen et al. 1994).

The combination of climate change and human-imposed threats and population reductions, how-ever, has reduced the capacity of loggerheads to adapt to environmental changes as they might have in the past. Although it is possible that the large areas of undeveloped coastline north of ACNWR can facilitate a northward shift in this nesting aggregation, a number of factors suggest that this

may not be likely. First, marine turtles prefer to nest on beaches with a steep slope, high wave energy, and large sand grain size (Ackerman 1997), which are all present at ACNWR. Beaches to the north of the refuge, for example in Cocoa Beach, New Smyrna Beach, and Daytona Beach, are generally broader, less sloped, and of a finer sand grain size that shows greater compaction and moisture retention (Provancha & Ehrhart 1987, Mayhew & Parkinson 2007), which are not ideal for marine turtle nesting. Thus, the edaphic factors that make ACNWR an ideal marine turtle nesting beach are not necessarily present elsewhere (albeit much more research is needed). In addition, a northward migration would place nests closer to Port Canaveral and associated rock jetties, which have historically increased erosion on beaches to the south (Douglass 2002). Thus, although it is possible that ACNWR loggerhead aggregation will shift north beyond the borders of the refuge and find suitable habitat, this is not a certainty. On the other hand, Pike (2013) developed niche models for all 7 species of marine turtles, with 2 implications highly relevant to this study. First, the impacts of climate change vary by species and likely by populations within species; thus, it is important to focus on individual rookeries or protected areas, as we have done here. Second, the study indicated that loggerheads have the broadest climatic tolerances of all marine turtle species, leaving some room for optimism that large-scale shifts in their nesting distribution may not be necessary.

Other factors not measured in our study could potentially explain changes in the spatial distribution of nests that we observed. For example, although beach lighting is not the only impact from beachfront structures, it is a major factor (Witherington & Bjorndal 1991, Witherington 2003, Mazor et al. 2013). However, not all houses have similar lighting impacts because of variation in the size and height of the structure, local vegetation and topography, and potential use of turtle-friendly lighting. Beach slope is another important factor in determining suitable nesting habitat (Hays 2012). The steeply sloped beaches of ACNWR protect incubating nests from seasonally high tides and storm surge, but it is unclear how the slopes of beaches have changed in the past or will change in the future. Our analysis examined beach width and area, which are clearly important, but slope is a factor that should also be addressed in future work. Other potentially important factors that may predict the spatial distribution of loggerhead nests include edaphic properties of the sand, offshore currents and bathymetry, distance from human settlements, presence of lagoon systems, wave energy, and oceanic currents.

Numerous strategies have been suggested for helping marine turtles adapt to the threats from climate change considered in our study, as reviewed by Fuentes et al. (2012). Our study emphasizes the synergism of climate change factors with existing stressors such as land use and beach erosion, which pose the greatest threat to many nesting aggregations, including turtles at ACNWR. Similarly, Fuentes et al. (2012) acknowledge the need to first reduce existing stressors to enhance the adaptive capacity of populations to cope with climate change stressors. Table S2 in the supplement lists all 20 recommendations compiled by Fuentes et al. (2012) and our assessment of the feasibility and benefit of their implementation in ACNWR. Overall, we suggest that the greatest benefit to loggerheads and other marine turtles nesting in ACNWR would derive from a 4-fold strategy to (1) limit construction near beaches and require existing construction to use turtle-friendly lighting, either through regulations or purchasing of private inholdings; (2) impose rolling easements on existing private lands; (3) ban future and remove existing shoreline-hardening structures; and (4) plan urban growth to redirect development away from existing (and future) nesting areas.

Additional strategies such as removal of nests for artificial incubation, coloring sand, or shading nests will often be untenable given the spatial scale, costs, and density of nests at ACNWR. Beach nourishment projects have been implemented on the beach berm north of the refuge (Brock et al. 2009) and on the dune within the refuge (Carthy 1996), but given the costs (Valverde et al. 1999; Table 1) and diminishing returns of these efforts (most last <10 yr), we do not recommend these projects except as a temporary fix for areas where beach widths are <10 m, as these areas are highly prone to nest washouts from wave action and storm surge. We suggest that the only viable strategy is managed retreat of human infrastructure from the dune, which will allow beaches to naturally migrate inland (Mcglashan 2003, Bush et al. 2004). Fish et al. (2008) surveyed 11 beaches in Barbados and showed that preventing construction within 90 m of the beach resulted in minimal loss of beach habitat, assuming that beaches could naturally migrate inland at a rate that keeps pace with sea level rise. Such a strategy could potentially require massive infrastructure costs, as Route A1A is in many areas within 90 m of the beach/dune interface. However, given conservative predictions of 0.5 to 2 m of

sea level rise by 2100 (Pfeffer et al. 2008, Vermeer & Rahmstorf 2009, Strauss et al. 2012), armoring of the shoreline to protect roads and associated residential, commercial, and governmental infrastructure in their current configuration may be untenable.

The results of our study provide testable predictions about the distribution of loggerhead turtle nests in ACNWR in a future with sea level rise, increased land use intensity, and continued warming temperatures. Although this refuge is a key protected area for loggerheads, green turtles, and leatherbacks in Florida and globally, our study area encompasses only 20 km of beach, compared to 1067 km of beach coastline in Florida alone. Future research should investigate the impacts and predictive power of land use, sea surface temperature, climate change, sea level rise, and erosion (such as erosion near artificial inlets, jetties, and piers) on the spatio-temporal distribution of nests statewide. Identifying the specific beach characteristics (slope, grain size, wave energy, etc.) that nesting aggregations prefer is another key objective for future research. Two major initiatives, the Statewide Nesting Beach Survey and the Index Nesting Beach Survey, have tracked the number and timing of loggerhead nesting throughout Florida since 1979 and 1989, respectively. Future studies should continue to harness these datasets (e.g. Witherington et al. 2009) to focus on trends in the total numbers of nests but also include the spatial distribution of those nests and the factors influencing them.

LITERATURE CITED

Ackerman RA (1997) The nest environment and the embryonic development of sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 83–106

Baker JD, Littnan CL, Johnston DW (2006) Potential effects of sea level rise on the terrestrial habitats of endangered and endemic megafauna in the northwestern Hawaiian Islands. Endang Species Res 2:21–30

Barnosky AD, Matzke N, Tomiya S, Wogan GOU and others (2011) Has the Earth's sixth mass extinction already arrived? Nature 471:51–57

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377

Bjorndal KA, Meylan AB, Turner BJ (1983) Sea turtles nesting at Melbourne Beach, Florida, I. Size, growth and reproductive biology. Biol Conserv 26:65–77

Bowen BW, Kamezaki N, Limpus CJ, Hughes GR, Meylan AB, Avise JC (1994) Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. Evolution 48:1820–1828

Bowen BW, Bass AL, Chow SM, Bostrom M and others (2004) Natal homing in juvenile loggerhead turtles (*Caretta caretta*). Mol Ecol 13:3797–3808

Bowen BW, Bass AL, Soares L, Toonen RJ (2005) Conservation implications of complex population structure: lessons from the loggerhead turtle (*Caretta caretta*). Mol Ecol 14:2389–2402

Brock KA, Reece JS, Ehrhart LM (2009) The effects of artificial beach nourishment on marine turtles: differences between loggerhead and green turtles. Restor Ecol 17: 297–307

Bruun P (1962) Sea-level rise as a cause of shore erosion. Proc Am Soc Civil Eng. J Waterw Harb Div 88:117–130

Burgman MA, Ferson S, Akçakaya HR (1993) Risk assessment in conservation biology. Chapman & Hall, London

Burnham KP, Anderson DR (2002) Model selection and mixed model inference: a practical information-theoretic approach. Springer, New York, NY

Bush DM, Neal WJ, Longo NJ, Lindeman KC and others (2004) Living with Florida's Atlantic beaches: coastal hazards from Amelia Island to Key West. Duke University Press, Durham, NC

Bustard HR, Tognetti KP (1969) Green sea turtles: a discrete simulation of density-dependent population regulation. Science 163:939–941

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, Hua X and others (2013) How does climate change cause extinction? Proc R Soc Lond B Biol Sci 280:20121890

Carthy RR (1996) The role of the eggshell and nest chamber in loggerhead turtle (*Caretta caretta*) egg incubation. PhD dissertation, University of Florida, Gainesville, FL

Chevan A, Sutherland M (1991) Hierarchical partitioning. Am Stat 45:90–96

Cornelius SE, Ulloa MA, Castro JC, Mata del Valle M, Robinson DC (1991) Management of olive ridley sea turtles (*Lepidochelys olivacea*) nesting at Playas Nancite and Ostional, Costa Rica. In: Robinson JG, Redford KH (eds) Neotropical wildlife use and conservation. University of Chicago Press, Chicago, IL, p 231–251

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. Science 332:53–58

Dean R, Dalrymple R (2002) Coastal processes with engineering applications. Cambridge University Press, Cambridge

Dean RG, Grant J (1989) Development of methodology for thirty-year shoreline projections in the vicinity of beach nourishment projects. Division of Beaches and Shores, Tallahassee, FL

DECCW (Department of Environment, Climate Change and

Water) (2010) Guidelines for preparing coastal zone management plans. New South Wales Department of Environment, Climate Change and Water, Sydney

Donoghue J (2011) Sea level history of the northern Gulf of Mexico coast and sea level rise scenarios for the near future. Clim Change 107:17–33

Douglass SL (2002) Saving America's beaches: the causes of and solutions to beach erosion. World Scientific Publishing, River Edge, NJ

Dutton A, Lambeck K (2012) Ice volume and sea level during the last interglacial. Science 337:216–219

Ehrhart LM, Bagley DA, Redfoot WE (2003) Loggerhead turtles in the Atlantic Ocean: geographic distribution, abundance, and population status. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Institution Press, Washington, DC, p 157–174

Elko NA, Sallenger AH, Guy K, Morgan KLM (2002) Barrier island elevations relevant to potential storm impacts: 2. South Atlantic. US Geological Survey Open-File Report 02-0288

ESRI (Environmental Systems Resource Institute) (2010) ArcMap 10.1. ESRI, Redlands, CA

Fish MR, Cote IM, Gill JA, Jones AP, Renshoff S, Watkinson AR (2005) Predicting the impact of sea-level rise on Caribbean sea turtle nesting habitat. Conserv Biol 19: 482–491

Fish MR, Cote IM, Horrocks JA, Mulligan B, Watkinson AR, Jones AP (2008) Construction setback regulations and sea-level rise: mitigating sea turtle nesting beach loss. Ocean Coast Manag 51:330–341

Foden WB, Butchart SHM, Stuart SN, Vié JC and others (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS ONE 8:e65427

Fuentes MMPB, Abbs D (2010) Effects of projected changes in tropical cyclone frequency on sea turtles. Mar Ecol Prog Ser 412:283–292

Fuentes MMPB, Dawson JL, Smithers SG, Hamann M, Limpus CJ (2010a) Sedimentological characteristics of key sea turtle rookeries: potential implications under projected climate change. Mar Freshw Res 61:464–473

Fuentes MMPB, Hamann M, Limpus CJ (2010b) Past, current and future thermal profiles of green turtle nesting grounds: implications from climate change. J Exp Mar Biol Ecol 383:56–64

Fuentes MMPB, Limpus C, Hamann M, Dawson J (2010c) Potential impacts of projected sea-level rise on sea turtle rookeries. Aquat Conserv Mar Freshw Ecosyst 20: 132–139

Fuentes MMPB, Limpus CJ, Hamann M (2011) Vulnerability of sea turtle nesting grounds to climate change. Glob Change Biol 17:140–153

Fuentes MMPB, Fish MR, Maynard JA (2012) Management strategies to mitigate the impacts of climate change on sea turtle's terrestrial reproductive phase. Mitig Adapt Strategies Glob Change 17:51–63

Godley BJ, Broderick AC, Mrosovsky N (2001) Estimating hatchling sex ratios of loggerhead turtles in Cyprus from incubation durations. Mar Ecol Prog Ser 210:195–201

Gregoire LJ, Payne AJ, Valdes PJ (2012) Deglacial rapid sea level rises caused by ice-sheet saddle collapses. Nature 487:219–222

Grinsted A, Moore JC, Jevrejeva S (2013) Projected Atlantic hurricane surge threat from rising temperatures. Proc Natl Acad Sci USA 110:5369–5373

Halpin PN (1997) Global climate change and natural-area protection: management responses and research directions. Ecol Appl 7:828–843

Hands EB (1983) The Great Lakes as a test model for profile responses to sea level changes. In: Komar PD (ed) CRC handbook of coastal processes and erosion. CRC Press, Boca Raton, FL, p 167–189

Harley CDG, Randall Hughes A, Hultgren KM, Miner BG and others (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Harris LD, Cropper WPJ (1992) Between the devil and the deep blue sea: implications of climate change for Florida's fauna. In: Peters RL, Lovejoy TE (eds) Global warming and biological diversity. Yale University Press, New Haven, CT, p 309–324

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2007) Investigating the potential impacts of climate change on a marine turtle population. Glob Change Biol 13: 923–932

Hays A (2012) Determining the impacts of beach restoration on loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*) nesting patterns and reproductive success along Florida's Atlantic coast. MSc thesis, University of Central Florida, Orlando, FL

Hays GC, Fossette S, Katselidis KA, Schofield G, Gravenor MB (2010) Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. Conserv Biol 24:1636–1643

Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. Glob Change Biol 12:2272–2281

IPCC (Intergovernmental Panel on Climate Change) (2007) Climate change 2007: the physical science basis. In: Solomon S, Qin D, Manning M, Chen Z and others (eds) Contribution of Working Group I to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge

Katselidis KA, Schofield G, Stamou G, Dimopoulos P, Pantis JD (2012) Females first? Past, present and future variability in offspring sex ratio at a temperate sea turtle breeding area. Anim Conserv 15:508–518

Kominz MA, Miller KG, Browning JV (1998) Long-term and short-term global Cenozoic sea-level estimates. Geology 26:311–314

Lindeman RH, Merenda PF, Gold RZ (1980) Introduction to bivariate and multivariate analysis. Scott, Foresman, Glenview, IL

Maul GA, Martin DM (1993) Sea level rise at Key West, Florida, 1846–1992: America's longest instrument record? Geophys Res Lett 20:1955–1958, doi:10.1029/93-GL02371

Maul GA, Sims HJ (2007) Florida coastal temperature trends: comparing independent datasets. Fla Sci 70: 71–82

Mayhew TA, Parkinson RW (2007) Holocene evolution of the barrier island system, east-central Florida. Fla Sci 70: 383–397

Mazaris AD, Matsinos G, Pantis JD (2009) Evaluating the impacts of coastal squeeze on sea turtle nesting. Ocean Coast Manag 52:139–145

Mazor T, Levin N, Possingham HP, Levy Y, Rocchini D, Richardson AJ, Kark S (2013) Can satellite-based night lights be used for conservation? The case of nesting sea turtles in the Mediterranean. Biol Conserv 159:63–72

Mcglashan DJ (2003) Managed relocation: an assessment of

its feasibility as a coastal management option. Geogr J 169:6–20

Mousavi M, Irish J, Frey A, Olivera F, Edge B (2011) Global warming and hurricanes: the potential impact of hurricane intensification and sea level rise on coastal flooding. Clim Change 104:575–597

NMFS (National Marine Fisheries Service), USFWS (US Fish and Wildlife Service) (1991) Recovery plan for U.S. population of the loggerhead turtle. NMFS, Washington, DC

Noss RF (2011) Between the devil and the deep blue sea: Florida's unenviable position with respect to sea level rise. Clim Change 107:1–16

Paillard D (2006) What drives the ice age cycle? Science 313: 455–456

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr 12: 361–371

Pfeffer WT, Harper JT, O'Neel S (2008) Kinematic constraints on glacier contributions to 21st-century sea-level rise. Science 321:1340–1343

Pike DA (2013) Climate influences the global distribution of sea turtle nesting. Glob Ecol Biogeogr 22:555–566

Pike DA, Stiner JC (2007) Sea turtle species vary in their susceptibility to tropical cyclones. Oecologia 153: 471–478

Poloczanska ES, Limpus CJ, Hays GC (2009) Vulnerability of marine turtles to climate change. In: Sims DW (ed) Advances in marine biology, Vol. 56. Academic Press, Burlington, VT, p 151–211

Provancha J, Ehrhart L (1987) Sea turtle nesting trends at Kennedy Space Center and Cape Canaveral Air Force Station, Florida, and relationships with factors influencing nest site selection. In: Witzell WN (ed) Ecology of east Florida sea turtles: proceedings of the Cape Canaveral, Florida, sea turtle workshop, Miami, FL, February 26–27, 1985. NOAA Technical Report NMFS 53, p 33–44

R Core Development Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ranasinghe R, Stive M (2009) Rising seas and retreating coastlines. Clim Change 97:465–468

Reece JS, Castoe TA, Parkinson CL (2005) Historical perspectives on population genetics of three marine turtle species. Conserv Genet 6:235–251

Rollason V, Patterson D, Huxley C (2010) Assessing shoreline response to sea level rise: an alternative to the Bruun Rule. Proc 19th NSW Coastal Conf, Nov 10–12, 2010, Batemans Bay, New South Wales

Root TL, Schneider SH (2006) Conservation and climate change: the challenges ahead. Conserv Biol 20:706–708

Rosen PS (1978) A regional test of the Bruun Rule on shoreline erosion. Mar Geol 26:M7–M16

Ruggiero P (2013) Is the intensifying wave climate of the U.S. Pacific Northwest increasing flooding and erosion risk faster than sea level rise? J Waterw Port Coast Ocean Eng 139:88–97

Russell BD, Thompson JAI, Falkenberg LJ, Connell SD (2009) Synergistic effects of climate change and local stressors: CO_2 and nutrient-driven change in subtidal rocky habitats. Glob Change Biol 15:2153–2162

Salmon M, Tolbert, MG, Painter DP, Goff M, Raymond R (1995) Behavior of loggerhead sea turtles on an urban beach. II. Hatching orientation. J Herpetol 29:568–576

Savarese L, Tedesco LP, Mankiewicz C, Shrake L (2002) Late Holocene sea level rise in southwest Florida: implications for estuarine management and coastal evolution. Proc 15th Keck Res Symp in Geology, April 2002, Amherst College, Amherst, MA

Schofield G, Hobson VJ, Lilley MKS, Katselidis KA, Bishop CM, Brown P, Hays GC (2010) Inter-annual variability in the home range of breeding turtles: implications for current and future conservation management. Biol Conserv 143:722–730

Schubert R, Schellnhuber HJ, Buchmann N, Epiney A and others (2006) The future oceans — warming up, rising high, turning sour. German Advisory Council on Global Change, Berlin

Schwartz ML (1965) Laboratory study of sea-level rise as a cause of shore erosion. J Geol 73:528–534

Schwartz ML (1967) The Bruun theory of sea-level rise as a cause of shore erosion. J Geol 75:76–92

Strauss BH, Ziemlinski R, Weiss JL, Overpeck JT (2012) Tidally adjusted estimates of topographic vulnerability to sea level rise and flooding for the contiguous United States. Environ Res Lett 7:014033

Tiwari M, Bjorndal KA (2000) Variation in morphology and reproduction in loggerheads, *Caretta caretta*, nesting in the United States, Brazil, and Greece. Herpetologica 56: 343–356

Tiwari M, Bjorndal KA, Bolten AB, Bolker BM (2006) Evaluation of density-dependent processes and green turtle *Chelonia mydas* hatchling production at Tortuguero, Costa Rica. Mar Ecol Prog Ser 326:283–293

Urban MC, Tewksbury JJ, Sheldon KS (2012) On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proc Biol Sci 279:2072–2080

Valverde HR, Trembanis AC, Pilkey OH (1999) Summary of beach nourishment episodes on the U.S. east coast barrier islands. J Coast Res 15:1100–1118

Van Houtan KS, Bass OL (2007) Stormy oceans are associated with declines in sea turtle hatching. Curr Biol 17: R590–R591

Venables W, Ripley B (2002) Modern applied statistics with S. Springer, New York, NY

Vermeer M, Rahmstorf S (2009) Global sea level linked to global temperature. Proc Natl Acad Sci USA 106: 21527–21532

Von Holle B, Wei Y, Nickerson D (2010) Climatic variability leads to later seasonal flowering of Floridian plants. PLoS ONE 5:e11500

Weishampel JF, Bagley DA, Ehrhart LM, Rodenbeck BL (2003) Spatiotemporal patterns of annual sea turtle nesting behaviors along an east central Florida beach. Biol Conserv 110:295–303

Weishampel JF, Bagley DA, Ehrhart LM (2004) Earlier nesting by loggerhead sea turtles following sea surface warming. Glob Change Biol 10:1424–1427

Weishampel JF, Bagley DA, Ehrhart LM, Weishampel AC (2010) Nesting phenologies of two sympatric sea turtle species related to sea surface temperatures. Endang Species Res 12:41–47

Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. Proc Natl Acad Sci USA 106:19729–19736

Witherington BE (2003) Biological conservation of loggerheads: challenges and opportunities. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithson-

ian Books, Washington DC, p 295–311

Witherington BE, Bjorndal KA (1991) Influences of artificial lighting on the seaward orientation of hatchling logger-head turtles *Caretta caretta.* Biol Conserv 55:139–149

Witherington B, Kubilis P, Brost B, Meylan A (2009) Decreasing annual nest counts in a globally important loggerhead sea turtle population. Ecol Appl 19:30–54

Witt MJ, Hawkes LA, Godfrey MH, Broderick AC (2010) Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. J Exp Biol 213:901–911

Zhang K, Dittmar J, Ross M, Bergh C (2011) Assessment of sea level rise impacts on human population and real property in the Florida Keys. Clim Change 107:129–146