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Conservation hotspots for marine turtle nesting in the United States based on coastal development

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Abstract. Coastal areas provide nesting habitat for marine turtles that is critical for the persistence of their populations. However, many coastal areas are highly affected by coastal development, which affects the reproductive success of marine turtles. Knowing the extent to which nesting areas are exposed to these threats is essential to guide management initiatives. This information is particularly important for coastal areas with both high nesting density and dense human development, a combination that is common in the United States. We assessed the extent to which nesting areas of the loggerhead (*Caretta caretta*), the green (*Chelonia mydas*), the Kemp's ridley (*Lepidochelys kempii*), and leatherback turtles (*Dermochelys coriacea*) in the continental United States are exposed to coastal development and identified conservation hotspots that currently have high reproductive importance and either face high exposure to coastal development (needing intervention), or have low exposure to coastal development, and are good candidates for continued and future protection. Night-time light, housing, and population density were used as proxies for coastal development and human disturbance. About 81.6% of nesting areas were exposed to housing and human population, and 97.8% were exposed to light pollution. Further, most (>65%) of the very high- and high-density nesting areas for each species/subpopulation, except for the Kemp's ridley, were exposed to coastal development. Forty-nine nesting sites were selected as conservation hotspots; of those high-density nesting sites, 49% were sites with no/low exposure to coastal development and the other 51% were exposed to high-density coastal development. Conservation strategies need to account for ~66.8% of all marine turtle nesting areas being on private land and for nesting sites being exposed to large numbers of seasonal residents.

Key words: anthropogenic disturbance; conservation planning; green turtle (Chelonia mydas); *Kemp's ridley* (Lepidochelys kempii); *land tenure; leatherback turtle* (Dermochelys coriacea); *light pollution; loggerhead turtle* (Caretta caretta); *United States marine areas.*

INTRODUCTION

Coastal ecosystems have high ecological, economic, and cultural importance (Costanza et al. 1987, Martínez et al. 2007). They provide vital connections between aquatic and terrestrial habitats, serve as nutrient transfer zones between the ocean and terrestrial systems, and support many endangered species, comprising a high percentage of global biodiversity (Bouchard and Bjorndal 2000, Martínez et al. 2007). Coastal areas also contain many of the global centers of human population and economic activity, and are highly valued for the services and amenities they provide (Small and Nicholls 2003). Consequently, coastal areas are experiencing rapid human population growth and an increase in beachfront housing and infrastructure (Burak et al. 2004), which threaten the plants and animals that depend on these dynamic coastal habitats (Crain et al. 2009).

Marine turtles provide an instructive example of the potential conflicts between development and biodiversity in coastal areas. Coastal areas provide critical nesting

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habitat for marine turtles, which use the beach to lay their eggs (Fish et al. 2005). These habitats are crucial for the recruitment of hatchlings and, therefore, the persistence of populations (Pike 2013). However, many nesting areas are highly exposed to coastal development and its associated pressures, such as artificial lighting, human disturbance, shoreline armoring, beach compaction, noise, and pollution (Antworth et al. 2006, Kamrowski et al. 2012). These pressures jeopardize the quality of nesting areas, alter the behavior of both adults and hatchlings, and influence the reproductive output and success of marine turtles (Witherington 1992, Lorne and Salmon 2007, Harewood and Horrocks 2008, Berry et al. 2013). Further, nesting beaches exposed to human development tend to have higher levels of marine debris (Leite et al. 2014), which can be harmful to marine turtles (Bugoni et al. 2001, Nelms et al. 2015).

Coastal development can cause both direct and indirect loss of suitable nesting habitats (Fish et al. 2005), and exacerbates potential impacts from sea-level rise by preventing natural movement of beaches and landward recession of shorelines (Fish et al. 2008, Fuentes et al. 2010). Reduction of nesting areas may amplify density-dependent effects, and force female turtles to nest in smaller areas and closer to the sea, exposing nests to inundation, and hatchlings to the direct impacts of development (Fuentes et al. 2010, Katselidis et al. 2014).

Information on exposure of nesting beaches to threats from coastal development is particularly important for areas with both high nesting densities and dense housing development. Prime examples include a number of coastal shorelines in the United States (Weishampel et al. 2003, Antworth et al. 2006). Thus, the goal of our study was to develop a methodology to assess the extent to which nesting areas are exposed to coastal development. For this, we assessed the exposure of nesting areas, used by four species of marine turtles: the loggerhead (*Caretta caretta*), the green turtle (*Chelonia mydas*), the Kemp's ridley (*Lepidochelys kempii*), and the leatherback (*Dermochelys coriacea*) in the continental United States to coastal development. Night-time light from satellite imagery and United States census-sourced housing and population data were used as a proxy for coastal development.

Methods

Study area and marine turtle data

Loggerheads, greens, Kemp's ridleys, and leatherback marine turtles nest along beaches in the United States (Dodd 1988, Hirth 1997, Shaver and Caillouet 1998, Stewart et al. 2010). All four species are listed as either threatened or endangered under the Endangered Species Act, with the Kemp's ridley being the most endangered (NMFS and USFWS 2011*a*).

Most of the marine turtle nesting activity along the United States occurs in the Southeast (Fig. 1). The majority of loggerhead nesting activity extends from North Carolina's Atlantic coast to the Florida Gulf coast, with minimal nesting occurring westward to Texas and northward to Virginia (Dodd 1988). Along the southeastern Atlantic coast, ~90% of loggerhead nesting occurs in Florida (Dodd 1988). We considered six demographically distinct loggerhead nesting populations that nest in the continental United States between Alabama and Virginia: (1) northern Gulf of Mexico (NGM), which includes the northwestern Florida subpopulation and turtles nesting in Alabama, (2) central western Florida (CW), (3) southwestern Florida (SW), (4) southeastern Florida (SE), (5) central eastern Florida (CE), and (6) northern unit (N), which includes the northeastern Florida subpopulation and turtles nesting in Georgia, South and North Carolina, and Virginia (Shamblin et al. 2011, 2012). Green turtles nest primarily in Florida, with small numbers occurring in Georgia, South Carolina, and North Carolina, and non-mainland nesting (not considered here [Hirth 1997], Fig. 1). Florida is also an important area for leatherback nesting, with most nesting activity occurring along the Atlantic coast from Brevard to Broward counties (Stewart et al. 2010). Unlike the other species, Kemp's ridleys nest primarily along the southern Texas coast (Fig. 1), and in Mexico with sporadic nesting on both Florida's coasts. However, for this study we considered only Kemp's ridleys nesting areas in Texas (Plotkin 2007, NMFS and USFWS 2011*a*).

We obtained georeferenced locations of nesting areas ($n = 326$; loggerhead turtles $n = 314$; green turtles $n = 164$; leatherback turtles $n = 107$; Kemp's ridley $n = 10$), as well as information about the relative importance of each area from the Virginia Department of Game and Inland Fisheries, the North Carolina Wildlife Resources Commission, the South Carolina Department of Natural Resources, the Fish and Wildlife Research Institute of the Florida Fish and Wildlife Conservation Commission, the United States Fish & Wildlife Service Alabama Ecological Services Field Office, and the State of the World's Sea Turtles (SWOT) database hosted by OBIS-SEAMAP; Kot et al. 2013). We only included those sites where nesting activity was observed between 2010 and 2014 (hereafter referred to as the study period). Nesting area importance was based on nest density ($\text{nests}\cdot\text{km}^{-1}\cdot\text{yr}^{-1}$) averaged through the study period and relative for each species and distinct subpopulation. To obtain an indication of the importance of each nesting area for each species and subpopulation we employed density classifications of low, medium, and high for each species and subpopulation (as per the Florida State-wide Atlas of Sea Turtle Nesting Occurrence and Density). High-density beaches are those that have density values within the top 25% of the range of values; low-density beaches are those with the lowest 25% of density values; and beaches with densities between these two categories are medium-density beaches. To highlight the importance of the highest-density beaches, a category of very high density was assigned to the top three high-density beaches for each species/subpopulation. Only one

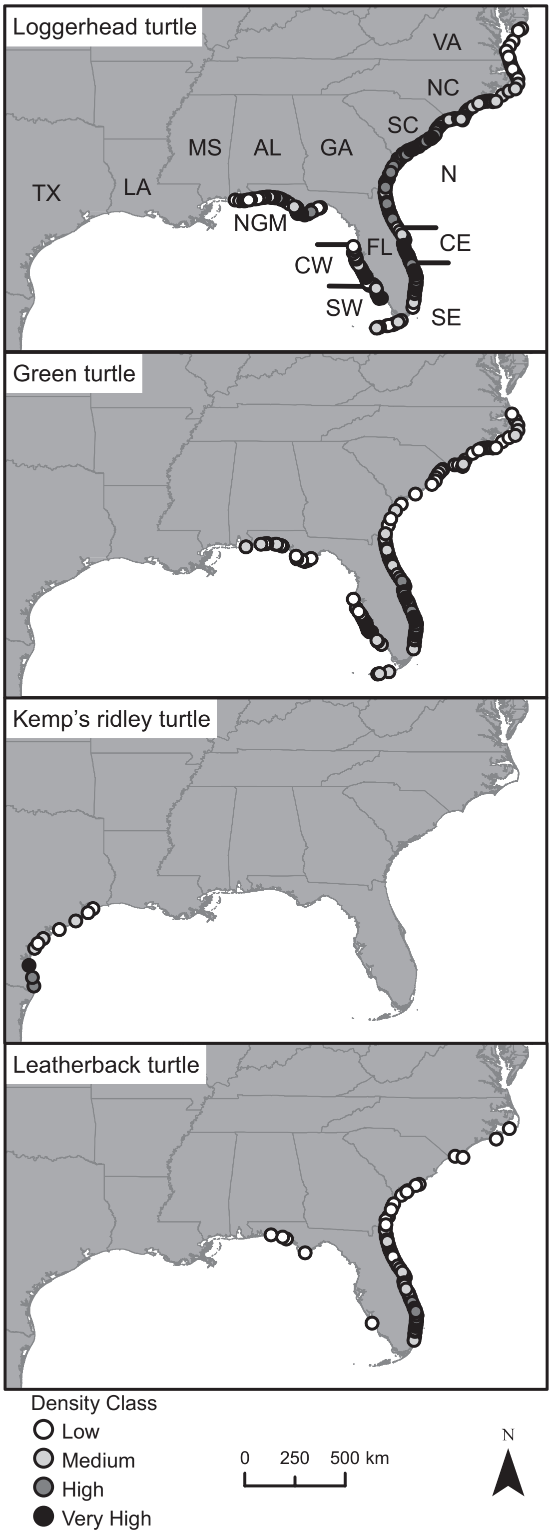

FIG. 1. Nesting areas within the United States considered for each marine turtle species/subpopulation and their relative density. Species were loggerhead (*Caretta caretta*), green (*Chelonia mydas*), Kemp's ridley (*Lepidochelys kempii*), and leatherback turtles (*Dermochelys coriacea*). For information on the categories of density utilized for each species/subpopulation see Table 1.

Kemp's ridley nesting beach was assigned a very high category because only 10 nesting beaches were considered for this species. Density categories for the loggerhead turtle were determined within each genetic subpopulation (as per Shamblin et al. 2011, 2012). Density categories for the green, Kemp's ridley, and leatherback turtles were assessed on a region-wide basis across their northwestern Atlantic range (Table 1).

Exposure to coastal development

To assess the exposure of nesting sites to coastal development, we analyzed: (1) intensity of night-time light measured from satellite imagery, as a proxy for coastal development (Sutton 1997); and (2) United States census-sourced housing and population data (count per block) to capture the number of people and their homes in the vicinity of beaches. We used a combination of ArcGIS software and Python scripting to buffer nesting sites and then extract values for light pollution (VIIRS), housing/population density (U.S. census data), and landownership (Protected Areas Database) around each nest area buffer. Values for these measures were obtained within 1 and 25 km of each nesting area, using a circular search radius, to obtain both a conservative and a high value of nesting area exposure to light, people, and homes.

Night-time light.—Night-time light can be used as a proxy of human population density, and thus coastal development (Sutton 1997). We used visible infrared imaging radiometer suite (VIIRS) night-time light data (2012) from the Earth Observation Group at the NOAA National Geophysical Data Center, in raster format, to determine the exposure of nesting areas to coastal development (light data *available online*).[14] The data consisted of VIIRS day/night band low-light imaging collected during nights with no moonlight, over two time periods, 18–26 April and 11–23 October 2012, with a broad field of view (3,000 km wide swath), 14-bit quantization, no saturation in urban areas, on-board radiometric-calibration, and an overpass time of approximately 01:30 every day (Elvidge et al. 2013). Grid cell resolution was 742 m, and radiances were measured in nW/(cm^2 × sr) (Baugh et al. 2013). The coarse resolution of the data does not take into account topographic features at the individual nesting areas, which may shield the region from light sources. We calculated maximum, and mean, radiance values within 1 and 25 km of each nesting site. Maximum values indicate the highest amount of light potentially reaching nesting areas, while mean values effectively "smooth out" the estimated amount of artificial light emitted within the buffer area. Thus, a high maximum value could indicate a single point source with high light values, whereas a high mean value indicate an overall high value for the region. In contrast to studies in Australia, where the coastline is less developed than in the United States (e.g., Kamrowski et al. 2012), we

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[14] http://ngdc.noaa.gov/eog/viirs/download_viirs_ntl.html

Table 1. Categories of density utilized for each species/recovery unit.

Species/Subpopulation	Number of nesting areas considered	Average density	Very high density	High density	Medium density	Low density
Loggerhead (*Caretta caretta*)						
Northern Gulf of Mexico (NGM)	47	2.18	8.74–11.32	2.06–7.88	0.89–1.92	0.13–0.85
Central western Florida (CW)	32	21.29	57.93–142.92	30.16–42.20	4.48–25.88	0.15–4.34
Southwestern Florida (SW)	17	14.02	23.63	22.47–22.54	7.30–20.88	0.43–5.41
Southeastern Florida (SE)	62	141.05	711.07–1013.34	175.00–493.40	5.33–168.07	0.13–5.00
Central eastern Florida (CE)	22	133.95	190.25–554.912	158.30–175.98	81.64–145.97	8.29–69.46
Northern unit (N)	134	7.76	44.31–103.56	11.42–25.11	1.17–11.31	0.01–1.06
Green turtle (*Chelonia mydas*)	164	15.38	244.29–355.77	6.00–190.96	0.05–5.75	0.01–0.04
Kemp's ridley turtle (*Lepidochelys kempii*)	10	0.24	0.97	0.25–0.75	0.03–0.17	0.01–0.02
Leatherback turtle (*Dermochelys coriacea*)	107	2.61	18.08–20.42	2.33–17.83	0.09–2.12	0.01–0.08
Overall (all nesting sites)	326	37.60	–	–	–	–

Notes: Nest density values (nests·km^{-1}·yr^{-1}) are based on total nest data from 2010 to 2014. Nest density classifications of low, medium, and high were developed according to quartile ranks. Very high classification was assigned to the three beaches for each species/recovery unit with highest nest density.

found little difference between maximum and mean values, which is why we present here mean values only.

We converted the VIIRS data into photometric (luminance) values (Kamrowski et al. 2012) based on the Standard Visibility Curve (CIE 1932). We chose this curve, which describes human sensitivity to light, because there is currently no corresponding curve available for marine turtles. Also, humans and marine turtles have similar visual sensitivity: both are sensitive to wavelengths across the visible spectrum, with peak sensitivity between 540 and 580 nm (Levenson et al. 2004, Narisada and Schreuder 2004, Horch et al. 2008). Thus, we converted radiance to luminance using appropriate values from the spectral luminous efficiency for human photopic vision (see Kamrowski et al. 2012), via the following equation:

$$X_{\mathrm{v}} = K_{\mathrm{m}} \int_{0}^{\infty} X_{\lambda} V_{\lambda} d_{\lambda}$$

where X_{V} represents the luminous intensity (cd/m^2), K_{m} is the constant scaling factor (683 for photopic vision; Hentschel 1994), X_{λ} is the corresponding radiant intensity (W·sr^{-1}·m^{-2}·nm^{-1}), V_{λ} is the curve for photopic vision, and λ is wavelength.

The conversion allowed us to determine the approximate amount of light present that would potentially be visible to marine turtles, given that turtles are not equally sensitive to all wavelengths of light (Palmer 1999, Narisada and Schreuder 2004). Once converted, we categorized each pixel according to the ratio between artificial light and natural night-time brightness below the atmosphere, using an average natural night-time brightness of 2.52×10^{-4} cd/m^2 (Cinzano et al. 2001). Artificial light is considered to be "light pollution" when lighting increases natural night-time brightness by more than 10% (or ~200×10^{-6} cd/m^2; categories 2–8 in Table 2; Smith 1979). To visualize and interpret the results, we used (Table 2) the same categories of light pollution as Cinzano et al. (2001) and Kamrowski et al. (2012; Table 2).

Table 2. Categories of light pollution, using ratios according to Cinzano et al. (2001) and Kamrowski et al. (2012)

Category	Luminance value (cd/m^2)	Ratio over natural brightness
1	0 to 2.5×10^{-6}	0–0.01
2	2.5×10^{-6} to 2.8×10^{-5}	0.01–0.11
3	2.8×10^{-5} to 8.3×10^{-5}	0.11–0.33
4	8.3×10^{-5} to 2.5×10^{-4}	0.33–1
5	2.5×10^{-4} to 7.6×10^{-4}	1–3
6	7.6×10^{-4} to 2.3×10^{-3}	3–9
7	2.3×10^{-3} to 6.8×10^{-3}	9–27
8	$>6.8 \times 10^{-3}$	>27

Housing and population density.—We obtained housing and population counts from the 2010 United States decennial census at block-level resolution (counts *available online*).[15] The United States census is a complete enumeration of houses, and provides data on houses and populations for fine-resolution polygons (blocks). Multiple apartments in one building are counted separately, but information about hotels and other structures are not included in the census. We also distinguished different housing types (i.e., seasonal houses, which are not permanently occupied and typically used for recreational purposes, and permanent residences).

Protected areas and tenure status

Information on land tenure was obtained from the United States Protected Areas Database (PAD) version 1.1 from the Conservation Biology Institute (data *available online*).[16] Land tenure was divided into five classes of public ownership (federal, state, local,

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[15] http://www2.census.gov/census_2010/04-Summary_File_1/

[16] http://protectedareas.databasin.org/galleries/4b2e6723283241bd84c42a649d2ec073

regional agency, joint ownership), two classes of private ownership (private, private conservation lands), and one class of Native American ownership. The area of each ownership class was calculated within 1 km of the midpoint of each nesting area.

Conservation hotspots

We identified two types of conservation hotspots for each species and subpopulation: (1) nesting areas with high nest density, high exposure to coastal development (>1,000 houses), i.e., areas that require intervention and are good candidates for targeted conservation and education initiatives to promote sustainable development, and (2) nesting areas with high nest density, low exposure to coastal development, i.e., areas that are good candidates to conserve and protect to ensure suitable nesting areas in the future. We also identified conservation hotspots areas that are important for multiple species of marine turtles.

Results

Exposure to light pollution

The vast majority (97.8%) of the marine turtle nesting sites studied were potentially exposed to light pollution (category 2–8; Table 2) within 1 km (Table 1). Indeed, all nesting areas for the NGM, CW, SW, SE, and CE loggerhead subpopulations were potentially exposed to light pollution, and 99.1% of nesting areas for leatherbacks, 97.6% for greens, 96.3% for the N loggerhead, and 80% for Kemp's ridley were potentially exposed to light pollution (Fig. 2, Table 3).

All the high-density leatherback nesting areas potentially had high exposure to light pollution (categories 7 and 8, within 1 km). The only leatherback nesting area without exposure to light pollution, Cape Hatteras/Ocracoke, North Carolina, had low nesting density. Similarly, all the high-density green turtle and loggerhead nesting areas for the NGM, CW, SW, SE, and CE subpopulations were potentially exposed to light pollution (Data S1). For the N loggerhead subpopulation, 93.9% of their high-density nesting areas were potentially exposed to light pollution, with only two high-density nesting sites, Sand Island and Lighthouse Island in South Carolina, potentially not exposed to light pollution. The most important nesting area for the Kemp's ridley (North Padre Island) was not exposed to light pollution within 1 or 25 km (Fig. 2).

Exposure to housing and people

The majority (81.6%) of the studied turtle nesting sites had one or more houses within 1 km, with an average of 576 houses and 507 people, of which 43.8% were seasonal houses (Table 3). Exposure to people and houses within 1 km of their nesting sites were particularly high for the SE loggerhead (96.8%), leatherback (89.7%), CW loggerhead (87.5%), green (84.9%), SW loggerhead (82.4%), the CE loggerhead (81.8%), the NGM loggerhead (78.7%), and the N loggerhead (73.9%; Table 3). These respective stocks were exposed on average, within 1 km of their nesting site, to 1,219 houses (range 0–5,640) and 1,326 people (range 0–5,378), 866 houses (range 0–5,640) and 864 people (range 0–5,378), 559 houses (range 0–1,887) and 488 people (0–2,234), 663 houses (range 0–5,640) and 631 (0–5,378), 807 houses 90–3,758) and 598 people (0–2,335), 668 houses (0–3,632) and 750 people (0–4,229), 406 houses (0–2,165) and 151 people (0–1,061), 334 houses (0–2,785) and 248 people (0–3,602; Data S1; Fig. 3). Half of the Kemp's ridley nesting sites were exposed to people and houses, with an average of 44 houses (0–270) and 21 people (0–155) within 1 km of their nesting sites. The most important Kemp's ridley nesting sites, North and South Padre Island, were not exposed to houses or people (Data S1).

All high- and very high-density nesting sites for leatherback turtles were exposed to people and houses (Data S1). Indeed, 44.8% of their high-density nesting areas, including two of their very-high nesting areas (Jupiter/Juno Beach, and Palm Beach Shores) were exposed, within 1 km, to more than 1,000 houses. Only one leatherback high-density nesting area (St. Lucie Inlet Preserve State Park) was not exposed to people or houses, and John D. MacArthur Beach State Park, another very high-density nesting site for leatherback turtles, had exposure to a small number of houses.

Two very high-density nesting sites for green turtles, Coral Cove Park and Tequesta Beaches, were exposed to more than 1,000 houses within 1 km of their nesting sites but five high-density green turtle nesting areas were not exposed to housing or people (Data S1).

All of the high and very high-density nesting sites for the CW, SW, SE, and CE loggerhead turtle subpopulations were exposed to housing and people within 1 km of their nesting sites. The N loggerhead turtle subpopulation had the highest proportion (27.3%) of high- and very high-density nesting sites not exposed to housing and people, including their highest nest density areas Cape Island and Lighthouse Island. Similarly, a high- and a very high-density NGM loggerhead nesting area (Cape St. George and St. Vincent National Wildlife Refuge) were not exposed to housing or people. However, some high-density nesting areas for both of these stocks are exposed to more than 1,000 houses; Hilton Head Island, a high-density nesting area for the N loggerhead turtle, and 14.9% of high- and very high-density nesting sites for the NGM subpopulation, were exposed to more than 1,000 houses within 1 km of their nesting site.

The SW loggerhead subpopulation was exposed to the highest proportion of seasonal houses (50.0%), and both a high- and another medium-density nesting site, North

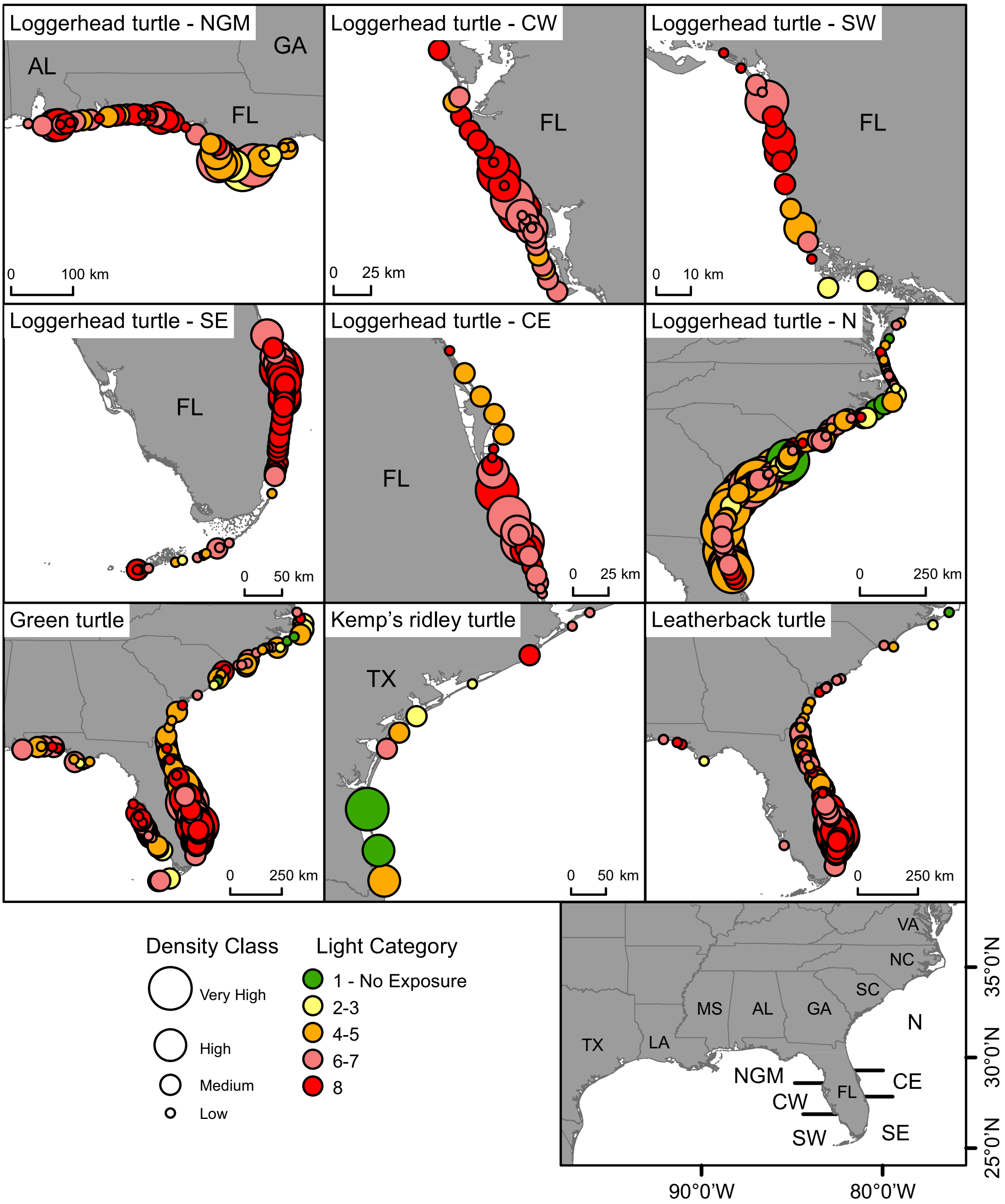

FIG. 2. Potential exposure of nesting areas to light pollution, within 1 km of each nesting site. Loggerhead subpopulations: northern Gulf of Mexico (NGM), central western Florida (CW), southwestern Florida (SW), southeastern Florida (SE), central eastern Florida (CE), and northern unit (N).

and South Keewaydin Island were exposed to more than 90% seasonal houses (Data S1). Eleven nesting sites for the N and NGM loggerhead subpopulations, which represent 8.2% and 23.4% of their nesting sites respectively, were exposed to more than 80% seasonal houses (Data S1).

Exposure to housing and people increased dramatically from within 1 to within 25 km of nesting areas. Across all

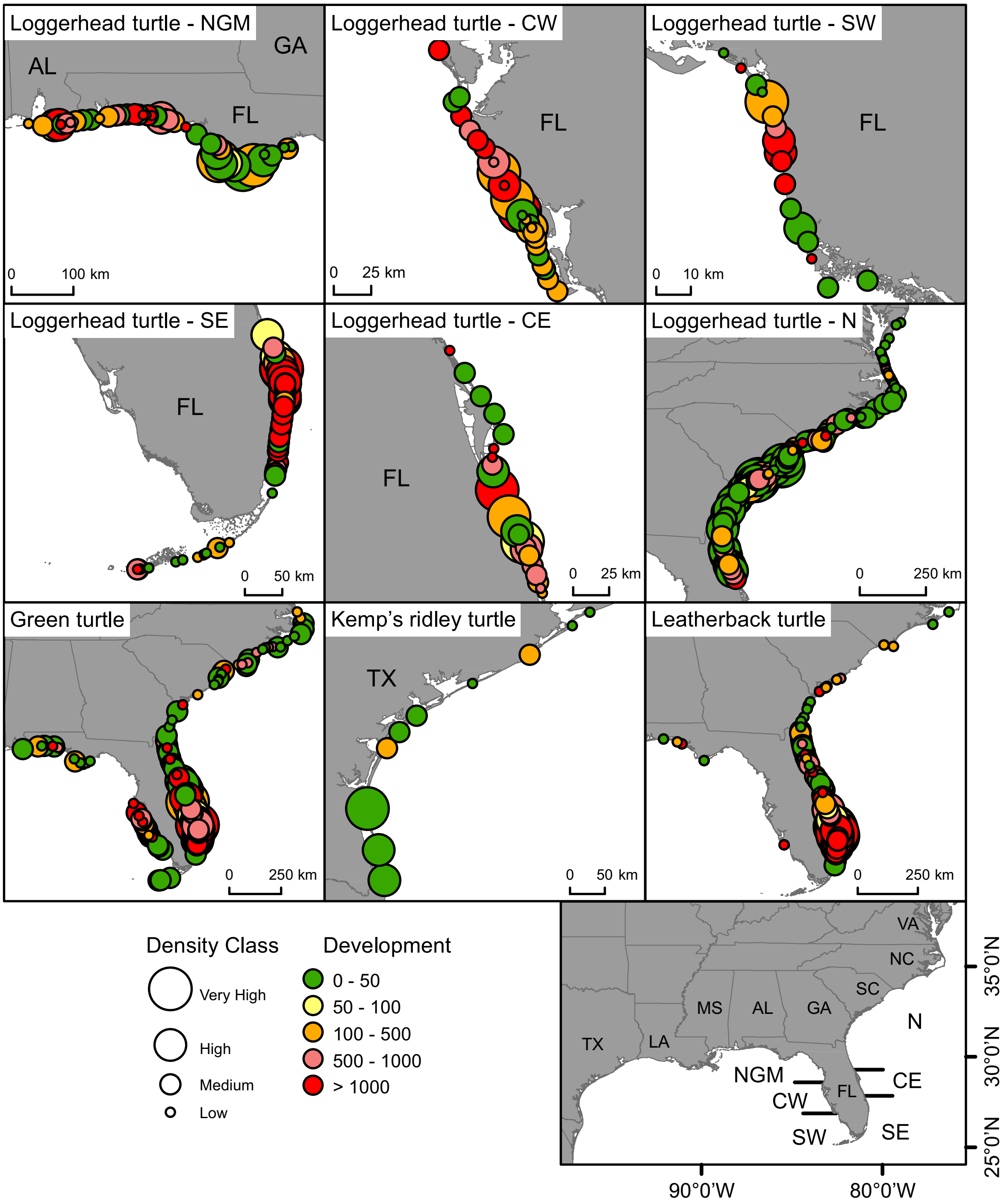

Fig. 3. Exposure of nesting areas to houses (development) within 1 km of each nesting site. Loggerhead subpopulations are as in Fig. 2.

species, exposure to housing and people increased on average more than 2,000 times, with nesting areas being exposed on average to 130,678 houses (range 0–965,661) and 248,293 people (range 0–2,148,655), within 25 km of their nesting sites (Data S1). When considering the exposure of nesting sites to housing and people within 25 km of each site, only one site, North Padre Island, was not exposed to houses or people (Data S1).

Table 3. Exposure of nesting areas and turtles to coastal development, coastal vulnerability, and shoreline change.

	Proportion of nesting areas exposed			Proportion of very high- and high-density nesting areas exposed†		
Species	Light pollution (%)	Houses/People (proportion of seasonal houses; %)	Privately owned land (%)	Light pollution (%)	Houses/People (proportion of seasonal houses; %)	Privately owned land (%)
Loggerhead						
NGM	100	78.7 (27.2)	62.7	100	81.82 (29.4)	51.1
CW	100	87.5 (38.5)	74.7	100	100 (33.1)	92.6
SW	100	82.4 (50.0)	54.1	100	100 (54.7)	74.7
SE	100	96.8 (33.8)	78.3	100	100 (38.3)	78.8
CE	100	81.8 (26.3)	62.2	100	100 (22.0)	49.1
N	96.3	73.9 (44.9)	62.8	93.9	72.7 (42.3)	51.5
Green turtle	97.6	84.9 (41.2)	64.0	100	87.8 (41.1)	71.5
Kemp's ridley turtle	80.0	50.0 (48.8)	72.5	0	0 (NA)	42.2
Leatherback turtle	99.1	89.7 (40.7)	69.2	100	96.3 (47.6)	80.6
Overall	97.8	81.6 (43.8)	66.8	90.9†	81.8 (34.1) †	66.7†

Notes: Abbreviations are as in Table 1. Results are for analysis conducted for exposure within 1 km of the nesting area. †Only includes sites with very high nesting density.

Land tenure

Most nesting sites (66.7%) were privately owned, and of these only 1.0% were private conservation lands (Table 3). The federal government owned 12.5% of the nesting sites, state governments 14.0%, local governments 1.4%, and 5.4% were jointly owned.

Private tenure covered 78.3% of nesting areas for the SE loggerhead, 74.7% for the CW loggerhead, 72.5% for the Kemp's ridley, 69.2% for leatherback, 64.0% for the green, 62.8% for the N loggerhead, 62.7% for the NGM loggerhead, and 62.2% for the CE loggerhead (Table 3). Most of the high- and very high-density nesting sites for the CW loggerhead (92.6%) and leatherback (80.6%) turtle were privately owned (Table 3); all of the very high nesting density sites for the CW loggerhead and one very high-density nesting site for the leatherback, Palm Beach Shores, were 100% privately owned (Data S1). In contrast, less than half of the high- and very high-density nesting sites for the CE loggerhead (49.1%) and the Kemp's ridley (42.2%) were privately owned (Table 3).

Conservation hotspots

We selected 49 nesting areas as conservation hotspots, and of those high-density nesting sites, 49% were sites with no or low exposure to coastal development and the other 51%were exposed to high coastal development (Data S1; Fig. 4). The majority (69.2%) of the high-development sites were in southeast Florida, whereas most of the undeveloped sites were in South Carolina (33.3%) and on the Gulf of Mexico coastline (45.4%) (Fig. 4). Seven areas had high- or very high-density nesting by loggerhead, green, and leatherback turtles, all of which had high development (Data S1).

Discussion

Our broadscale approach to identify conservation hotspots allowed us to compare multiple sites and species in a consistent way over a large spatial extent in order to inform on-the-ground assessment processes and aid conservation decisions (Myers et al. 2000, Mazor et al. 2013). An approach like ours is particularly useful for broadscale prioritization of conservation action and is a necessary precursor to site-level management (Mazor et al. 2013). Regional-scale priorities provide perspectives that are unavailable when working locally, but require interpretation to individual sites, with feedback to broad priorities when new data emerge (Pressey et al. 2013). Our analysis identified 49 conservation hotspots that currently have high reproductive importance and either face high exposure to coastal development, needing intervention, or have low exposure to coastal development, and are good candidates for continued and future protection. Seven of the conservation hotspots had high or very high nesting density for three species of marine turtles and were exposed to high levels of coastal development, thus intervention and protection of these areas may maximize conservation outcomes. Similar to these areas, we also found that most marine turtle nesting sites in the United States were exposed to high levels of coastal development, and, thus, are likely exposed to the multiple pressures associated with human presence (e.g. behavioral changes due to light pollution, disturbance of habitat, increased nest predation). Since our housing data set did not include hotels and other structures that were not residential houses/apartments and complexes, our results provide a conservative underestimation of numbers of houses that the nesting areas are exposed to. The night-time light data did not discriminate for structure type (i.e., hotels), so it provides an indication as a proxy of coastal development and also indicates that nesting areas in the United States are exposed to high levels of light pollution in many areas.

Our study is the first to consider such a diverse range of factors affecting multiple turtle species over a large spatial extent. Along with the need to determine areas being most exposed and potentially impacted, there is a need to better understand the actual effects of exposure on the reproductive output of marine turtles. Seminal work by Witherington and Bjorndal (1991) and Salmon et al. (1995), among others, showed that light pollution can deter marine turtles from emerging from the sea to nest and cause misorientation of hatchlings. However, only one study to date (Pike 2008) has explored the influence of coastal development and infrastructure at a broad scale on the reproductive success of marine turtles and reported that hatching success was higher on undeveloped beaches than on developed beaches. Anecdotal evidence suggests that coastal development and consequent increase in human presence may result in increased populations of raccoons and other species known to prey on marine turtle eggs and hatchlings (NMFS and USFWS 2011*b*). Nevertheless, more studies are necessary to better understand the causal links between coastal development, human population density, and marine turtle reproductive success.

Typically, marine turtle nesting is negatively correlated with light pollution, housing, and human density (Mazor et al. 2013, Reece et al. 2013, Roe et al. 2013). However, we found that some of the most important nesting areas for loggerhead, green, and leatherback turtles in the United States had a high exposure to these pressures. This might be an artifact of the lack of availability of undeveloped beaches. With increasing human populations, infrastructure, and light levels in coastal regions, the availability of beaches without exposure to coastal development has been reduced and will likely continue to diminish into the future (Pike 2008, Kamrowski et al. 2012). Marine turtles in the United States might have few options other than to nest on beaches close to development, and the use of heavily developed areas could indicate a certain level of disturbance adaptation (Marshall et al. 2014). Or simply, this may be an artifact of nest site fidelity; marine turtles often nest at the region of their birth (Miller 1997) and presumably may continue to return to their natal area until the habitat is totally gone. As development continues, it is important to understand the extent to which marine turtles can adapt to disturbance, whether there is a threshold to nest site fidelity and the degree to which beaches can be developed "sustainably" while maintaining suitable nesting areas (Roe et al. 2013). Persistence of suitable nesting habitat for marine turtles is crucial for reproduction and, thus, recruitment into the population. Suitable habitat is one of the key factors that can influence the resilience of

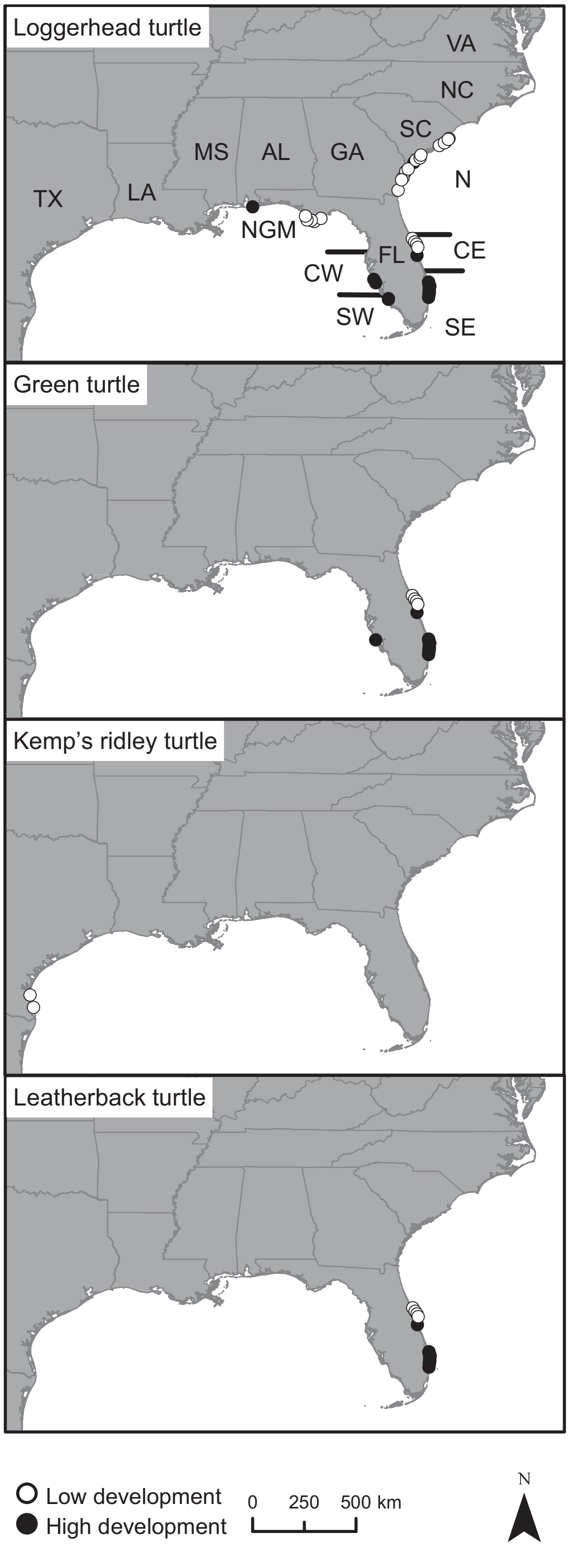

FIG. 4. Identified conservation hotspots. Loggerhead subpopulations are as in Fig. 2.

marine turtle populations to climate change (Fuentes et al. 2013). This highlights the need to maintain and protect important nesting areas and to identify (and legally protect) areas that can maintain suitable conditions for nesting into the future. It might be possible that nesting areas that currently are not important for marine turtles may become more important as marine turtles may shift their distribution as a response to projected climatic changes (Pike 2013).

Given that we used remotely sensed data, ultimately on-ground assessments of the reproductive output at nesting areas should be considered to identify the threshold of exposure at which coastal development affects marine turtle populations. For example, while several nesting areas in Florida have been identified as having high exposure to night-time lighting, many coastal counties and municipalities have lighting ordinances, with various levels of compliance and enforcement, that restrict the presence of visible light on the beach at night during months when marine turtles are nesting and hatchlings are emerging from nests (see http://myfwc.com/conservation/you-conserve/lighting/ordinances/). Our analyses may be useful to identify areas in Florida that should be ground-truthed, and highlight nesting areas in other states that should be assessed for presence of artificial lighting on the beach.

To address the potential effects of coastal development it is necessary to implement and enforce light-mitigation strategies (e.g., turtle-friendly lighting, vegetative barriers; Fuentes et al. 2012, Reece et al. 2013), reduce human disturbance to nesting areas (e.g., remove unattended material/properties in the beach: beach umbrellas, chairs, etc.), and leave beaches unaltered (e.g., limit/prohibit shoreline hardening structures; Sarah et al. 1998, Witherington et al. 2011). However, a combination of eroding coasts and development on these beaches has increased the demand for shoreline hardening structures in the United States coast, such as seawall and sloping rock revetments, which may reduce and/or degrade suitable nesting habitat (Witherington et al. 2011). Thus, it is crucial that setback regulations are established and enforced, that the construction of shoreline hardening structures are minimized and that construction in areas not yet developed are limited. Any management measure will need to take into account the threats that each nesting site is experiencing, land tenure, and whether houses are occupied permanently or seasonally (Knight 1999). Our study indicated that most (66.8%) turtle nesting areas across all species were on private land, and conservation there will require engagement with communities, public support, and most likely incentives (Fischer and Young 2007, Langpap and Kerkvliet 2012) to achieve the behavioral changes necessary to mitigate threats (Inglehart 1995). Gaining public support can be challenging (Lyytimäki and Rinne 2013), but can be helped by understanding relevant stakeholder beliefs and existing levels of local engagement with conservation efforts (Sutton and Tobin 2011, Kamrowski et al. 2015). Such knowledge can guide the development of "psychologically smart" communication with greater persuasive potential (Ockwell et al. 2009, Kamrowski et al. 2014). Relatedly, an average of 43.8% of houses at nesting sites are seasonally occupied, perhaps by people with different attitudes than permanent residents (Clendenning et al. 2005). Outreach and education efforts may have to be structured specifically to engage with seasonal residents and elicit their support for conservation actions. Finally, coastal residents can often play a positive role in conservation, despite contributing to coastal development (for an example, see Hopkins-Murphy and Seithel 2005). Thus efforts to encourage and engage the public with active participation in marine turtle conservation activities may help offset some of the negative impacts of coastal development.

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