Sea turtle nesting patterns in Florida vis-à-vis satellite-derived measures of artificial lighting

Zachary A. Weishampel, Wan-Hwa Cheng & John F. Weishampel

Department of Biology, University of Central Florida, Orlando, Florida, USA

Keywords
Artificial light, DMSP, light pollution, marine turtles, nest surveys, simultaneous autoregressive modeling

Abstract
Light pollution contributes to the degradation and reduction of habitat for wildlife. Nocturnally nesting and hatching sea turtle species are particularly sensitive to artificial light near nesting beaches. At local scales (0.01–0.1 km), artificial light has been experimentally shown to deter nesting females and disorient hatchlings. This study used satellite-based remote sensing to assess broad scale (~1–100s km) effects of artificial light on nesting patterns of loggerhead (Caretta caretta), leatherback (Dermochelys coriacea) and green turtles (Chelonia mydas) along the Florida coastline. Annual artificial nightlight data from 1992 to 2012 acquired by the Defense Meteorological Satellite Program (DMSP) were compared to an extensive nesting dataset for 368, ~1 km beach segments from this same 21-year period. Relationships between nest densities and artificial lighting were derived using simultaneous autoregressive models to adjust for the presence of spatial autocorrelation. Though coastal urbanization increased in Florida during this period, nearly two-thirds of the surveyed beaches exhibited decreasing light levels (N = 249); only a small fraction of the beaches showed significant increases (N = 52). Nest densities for all three sea turtle species were negatively influenced by artificial light at neighborhood scales (<100 km); however, only loggerhead and green turtle nest densities were influenced by artificial light levels at the individual beach scale (~1 km). Satellite monitoring shows promise for light management of extensive or remote areas. As the spectral, spatial, and temporal resolutions of the satellite data are coarse, ground measurements are suggested to confirm that artificial light levels on beaches during the nesting season correspond to the annual nightlight measures.

Introduction
As humans appropriate the terrestrial surface of the earth, areas of total natural darkness are becoming increasingly rare (Bogard 2014). Though perhaps not as feared as chemical forms of pollution, light pollution (excessive and/or misdirected light) may have significant negative impacts on wildlife (e.g., Hölker et al. 2010). Artificial light disrupts animal (amphibian, bird, fish, mammal, reptile and invertebrate) physiology and behavior, which affects their ability to orient, communicate, forage and reproduce (Longcore and Rich 2004; Rich and Longcore 2006). Organisms that live on earth’s surface have evolved within the constraints of regular diel and seasonal light cycles that have been interrupted by the glow created by artificial light. Light pollution is fundamentally a form of habitat degradation—a primary cause of biodiversity loss (Tilman et al. 1994).

The two sea turtle families (Cheloniidae and Dermochelyidae) have persisted for >100 million years (Naro-Maciel et al. 2008). The seven species that comprise these families are listed as Vulnerable (1), Endangered (2), Critically Endangered (3) and Data Deficient (1) by the International Union for Conservation of Nature (IUCN 2015). As a slowly maturing, long-lived taxon, sea turtles have had only a few generations to adapt to the widespread appearance of artificial lighting along the coast since the patent of the electric light bulb in 1880. Sea turtles occupy land for a minuscule fraction of their lives: when they incubate as eggs then crawl to the ocean.
as hatchlings and, if adult female, when they return to their natal beaches to nest. Both of these life-history-defining activities are primarily nocturnal for six of these species and the influence of artificial light on these behaviors are well documented (see Witherington and Martin 2003 for a summary).

When sea finding after emergence, hatchlings often become mis- or disoriented in the presence of artificial light (Peters and Verhoeven 1994; Salmon et al. 1995; Tuxbury and Salmon 2005). Artificial light from behind the beach, interferes with the normal, visual cues of starlight or moonlight reflecting off the water (Salmon 2006). In Florida, this has been projected to lead to thousands of hatchling deaths annually as they wander away from the ocean (Salmon 2003). For adult females, experimental field studies (at 10–100 m scales) on Florida and Costa Rica beaches showed the presence of mercury vapor lights (multiple spectral peaks between 400 and 700 nm) inhibited loggerhead and green turtle nesting, respectively (Witherington 1992). This negative effect was not apparent with low pressure sodium lamps (spectral peak at 590 nm; Witherington 1999). Deterring gravid females leads to denser nest congregations on darker beaches, which may increase depredation rates and divert hatchlings from more suitable dispersal-related nearshore features (Hamann et al. 2011).

Remote sensing is used to map extensive and inaccessible areas and over time can be used to monitor habitat change (Pettorelli et al. 2014). For sea turtles, airborne and satellite data have been used to map beach morphology (e.g., Long et al. 2011; Yamamoto et al. 2012), sea surface temperature (e.g., Hawkes et al. 2007; Weishampel et al. 2010), sargassum movements (e.g., Witherington et al. 2012; Hu et al. 2015), and recently artificial lighting (e.g., Magyar 2008; Kamrowski et al. 2012, 2014a). A series of Australian studies showed trends in satellite-derived artificial lighting on nesting beaches of five sea turtle species around the continent (Kamrowski et al. 2012, 2014a). These studies focused on population management units of the different species that include stretches of coastline (>100 km) and represent important nesting beaches, but did not directly relate artificial light levels to annual nest numbers on specific beaches. However, an eastern Mediterranean study summed loggerhead and green turtle nest counts over a 19-year period and found that nest density negatively related to two satellite-derived measures of artificial light intensity (from 2003 to 2007) on 190, 1-km beaches along the coastline of Israel (Mazor et al. 2013).

Because of systematic nest surveying efforts over the last 26 years across >320 km of Florida beaches and a 21-year archive of satellite-derived nightlight imagery, we can directly compare year-to-year nesting and artificial light patterns. Where the maximum combined nest density in the Israeli study was <10 nests km\(^{-1}\) year\(^{-1}\), several monitored Florida beaches have densities that exceed 700 loggerhead, 100 green turtle, and 10 leatherback nests km\(^{-1}\) year\(^{-1}\). This study’s primary objectives were to: (1) use satellite data to identify coastal light pollution trends on key Florida nesting beaches from 1992 to 2012 and with nest survey records (2) assess broad scale (1–100s km) artificial lighting effects on nocturnal nesting patterns of the three predominant sea turtle species in Florida.

### Materials and Methods

#### Study area and species

Approximately 90% of all sea turtle nesting in the continental United States occurs in Florida (FWC 2015a). The three main sea turtles that nest in Florida in decreasing nest numbers are loggerheads (Caretta caretta; family Cheloniidae), green turtles (Chelonia mydas; family Cheloniidae), and leatherbacks (Dermochelys coriacea; family Dermochelyidae). Florida possesses the highest number of loggerhead nests in the Western Hemisphere, the highest number of nesting green turtles in the United States, and is the only continental state where leatherbacks regularly nest (FWC 2015a). In 1996 the IUCN designated loggerheads as endangered; the U. S. Fish and Wildlife Service (USFWS) lists Florida populations as threatened. These populations have been fluctuating over the last 30 years (Witherington et al. 2009). Florida loggerheads nest between April and September laying 4–7 nests (~115 eggs per nest) and return approximately to the same beach area every 2–4 years (Ceriani et al. 2015). In 2004 the IUCN categorized Green turtles as endangered. Though listed as endangered by the USFWS, Florida green turtle populations have been exponentially increasing (Chaloupka et al. 2008) since the 1980s; they nest at 2–4-year intervals between June and September and lay ~3–5 nests (~135 eggs per nest) each season. In 2013 the IUCN listed leatherbacks as vulnerable; the USFWS lists the Florida populations as endangered. Florida leatherback populations have been steadily increasing (Stewart et al. 2011); they nest between March and August laying 5–7 nests per season (~80 eggs per nest), returning every 2–3 years.

In terms of physiological responses to light, differences among species are somewhat unclear. Based on the anatomical, optical eye geometries, though universally not well-adapted for vision in dim light conditions, leatherbacks are more sensitive to low light intensities than loggerheads and green turtles (Fritsches and Warrant 2013). Loggerhead and green turtles have similar visual pigment
spectral peak locations, but the magnitudes of the peaks differ between the species. Though possessing similar visual pigments, leatherbacks have a higher sensitivity at shorter wavelengths (Crognale et al. 2008) reflecting their lifestyle that involves deeper dives than loggerheads and green turtles. Moreover, adult leatherbacks also have a slower temporal, visual resolution than loggerheads and green turtles, suggesting adaptations for dimmer (deeper) water (Southwood et al. 2008).

Sea turtle nesting survey data

To conserve these species as mandated by the 1973 Endangered Species Act, the Florida Fish and Wildlife Conservation Commission (FWC) collaborates with the USFWS to monitor nesting patterns across the state. In 1989, the FWC established the Index Nesting Beach Survey (INBS). The INBS (FWC 2015b) follows standard protocols where FWC-trained surveyors and volunteers traverse specific beaches every morning during nesting season (15 May to 31 August) and record nesting by species based on track and digging characteristics. Witherington et al. (2009) divided the Florida coast into eight survey regions, Northeast, Central Northeast, Central East, Central Southeast, Southeast, South, Southwest, and Northwest (Fig. 1). Though these geographic regions may possess similar environmental factors (e.g., ocean currents, sea surface temperatures), they do not correspond to genetic subdivisions of the sea turtle populations as shown for loggerheads which are estimated to have seven different subunits for Florida (Shamblin et al. 2011). A total of 27 beaches comprising 368, ~1 km segments, from six survey regions have been monitored consistently, using INBS standards since the program’s inception. Five more beaches (126, ~1 km segments) from the Gulf coast have been added since 1992; however, these were not included in this analysis. The 368 beaches analyzed here do not include any from the South (which represents the Everglades and Florida Keys) and Northwest (Florida panhandle) survey regions.

We acquired the INBS sea turtle nesting data from the FWC Fish and Wildlife Research Institute for 1992–2012 to coincide with the satellite data described below. The FWC data consisted of 7,728 nesting tallies per species (368 beach segments × 21 years). We calculated annual nest density for the state, each region, and each INBS beach segment for each species (Figs. 2 and 3) using segment lengths from the FWC-provided ArcGIS shapefiles. In a similar approach as Witherington et al. (2009), to better visualize the data and simplify spatial analyses, we coarsely estimated distances along the coastline (not considering fractal properties; Jiang and Plotnick 1998) from the midpoint of each INBS segment in ArcGIS and spatially transformed the nesting (and artificial light data) from latitude–longitude coordinates into 1-dimensional, 953.2-km long transects comprised of the 368 sample points from Ft. Clinch (NE 0 km) to Sanibel Island (SW 953.2 km) going clockwise around the state (Fig. 3). This

Figure 1. Map of study area along the Florida coast. Nesting regions with numbers of beaches and beach segments that were analyzed are designated.
transformation ignores the coastline along bays with narrow inlets and produces minor distortions as the distance light travels differs from the distance a sea turtle swims from one beach to the next.

Artificial lighting data

The Defense Meteorological Satellite Program (DMSP) Operational Linescan System (OLS) monitors weather for the United States Air Force. Visible and infrared sensors (440–940 nm) collect 3000 km swaths of data, covering the earth twice daily. To detect clouds at night, the visible signal is intensified. This enables light detection at the planet surface (see Elvidge 2014 for examples using nighttime lights data). Nighttime, cloud-free data (without solar glare, moonlight, and auroral effects) are mapped into a latitude-longitude grid with an equatorial pixel size of ~1 km. The pixel size around Florida is closer to 800 m. We used the stable lights product, which removes ephemeral events such as fires and background noise (NOAA 2015a). We downloaded DMSP imagery data from 1992 to 2012 from the NOAA National Geophysical Data Center (now the National Centers for Environmental Information) using the recommended six satellite sources for the years that Kamrowski et al. (2014a) used for their 19-year study. Because there is no on-board calibration, sensitivity may change over the lifespan of the satellite as well as differ among satellites. To compensate for this, we used the second-order regression models developed by Elvidge et al. (2014) to intercalibrate the time series of night light data. We rescaled the annual 6-bit data from 0 to 100 with 0 representing total darkness and 100 representing complete light saturation for the period of detection.

Figure 4A shows the average light value for each pixel from 1992 to 2012. Urban areas, for example, Jacksonville, Miami, and Tampa-St. Petersburg, are large red amorphous features representing maximum light (saturated) values. We used the insectlinerst command in the Geospatial Modelling Environment (Beyer 2014) software package to calculate the yearly artificial light value for each beach segment weighted by the portion of the segment in a DMSP raster. As done with the nesting data, we calculated the change in light over the 21-year period by region (Fig. 5) and examined the average light levels by INBS segment (Fig. 6).

Data analysis and statistical modeling

Trends in artificial light were calculated based on the slope of the linear regressions of the light levels for each INBS beach segment over the 21-year period. To determine the influence of artificial light (X) and other possible contributing factors on nest density (Y), we followed a multi-model selection approach. But as was found with nesting data on a ~40-km INBS subsample (Weishampel et al. 2003) and is common with species distribution data (Kissling and Carl 2008; Miller 2012), we anticipated that nesting, as well as artificial light patterns, would not be spatially independent, that is, they would exhibit spatial autocorrelation (SAC). This assumption that spatially closer values will be more related than spatially distant values is, in part, caused by site fidelity and philopatry of nesting sea turtles and by the non-random location and sprawling growth patterns of cities. To measure the extent of SAC across different distances (i.e., correlograms) between INBS locations, we calculated Moran’s I using the software program GS+ (Gamma Design Software)
Because the presence of SAC violates assumptions of sample independence, we used simultaneous (or spatial) autoregressive (SAR) models that account for the influence of SAC in the models. Following analyses of simulated SAC data using a variety of spatial regression approaches (Dorman et al. 2007; Kissling and Carl 2008; Beale et al. 2010), we used a spatial error model (SARerr). The SARerr model expands on the basic generalized least squares model ($Y = X\beta + \epsilon$; where $\beta$ is a vector of the slopes of predictors X and $\epsilon$ is the error term) with the term $\lambda W \mu$, where $\lambda$ is the spatial autoregression coefficient, $W$ is the spatial weights matrix, and $\mu$ is the spatially dependent error term (Dorman et al. 2007). Because independent variables (e.g., artificial light) can also be autocorrelated, at scales different from the dependent variable, we used a mixed SARerr model or spatial Durbin error model (errorsarlm command with an “emixed” error type in the spdep package in R; Bivand 2015) which adds spatially lagged predictors. As nest density for a given year at a specific INBS beach location may relate to regional or statewide fluctuations, which are most conspicuous with green turtles (Fig. 2), these were also included as predictors (Table 1). Resulting SARerr models comprised of different predictors were compared using the Akaike Information Criterion (AIC). An analysis of model residuals was performed to assess where the regression models over- and under-predicted nest densities and to compare species nesting patterns. The effectiveness of the SARerr
models were assessed by comparing autocorrelation patterns (using Moran’s I) of the models’ residuals to those of their corresponding generalized least squares models.

Results

Trends in light levels on surveyed beaches

Though most urban areas grew over this 21-year period as shown by the positive slopes (light increases) around the cities (Fig. 4B), trends in artificial light along the nesting beaches were variable, but mostly showed decreases (Fig. 7). Some beach communities seemingly had no artificial light mitigation policies allowing light to increase (e.g., Amelia Island, Wabasso Beach, Jupiter Island); others very conscientiously reduced artificial light (e.g., Ft. Matanzas, Merritt Island, Sanibel Island); while others basically maintained the status quo which was typically relatively dark (e.g., Canaveral National Seashore) or exceedingly bright (e.g., Miami Beach).

Spatial autocorrelation of coastal artificial light levels and nest densities

Artificial light was significantly positively autocorrelated at scales <20 km and ~50 km (Fig. 8), using a Moran’s I value of ±0.2 as a rough cutoff of significance (P < 0.05). This indicates that variables exhibit neighborhood effects in these ranges and are not spatially independent. Nest densities for all three species and artificial light exhibited strong SAC patterns. Loggerhead, green turtle, and leatherback nest densities were significantly positively autocorrelated at <40, <20, and <50 km scales, respectively (Fig. 9). Thus, using a mixed \( \text{SAR}_{err} \) model that considers autocorrelation associated with both independent variables (artificial light) and dependent (sea turtle nest density) as reflected by the model error term was appropriate.

Simultaneous autoregressive (SAR) model selection

Prior to multiple regression analyses, sea turtle nest densities and artificial light values were log-transformed to obtain normal distributions. Based on the lowest AIC value, the most informative (best fit and most parsimonious) \( \text{SAR}_{err} \) models (highlighted in dark gray in Table 2) for all three sea turtle species included artificial light on the nesting beach (\( \text{Artificial Light} \)), overall annual nest density by species (\( \text{Statewide Density} \)), and the spatially autocorrelated term (with a lag distance up to 100 km) for artificial light.
light \(\text{lag100Artificial\_Light}\). The second most informative models (highlighted in light gray in Table 2), which were also consistent for the three species, dropped the \text{lag100Artificial\_Light} term. The remaining eight models had much higher AIC values as did others with smaller (50 km) and larger (150 km) lag distances (not shown).

For all species, the spatial auto-regressive (neighborhood effect) terms associated with the model error (\(\lambda\), which is on a \(-1\) to \(+1\) scale) were all highly \((P < 0.001)\) significant and the resulting SAR models were also significantly different (as shown by the Wald statistic) and more informative (as shown by the lower AIC) than the corresponding ordinary least squares (OLS) models (Table 3). Though the best models as determined by AIC were the same, the significance of the individual predictors differed by species. To summarize:

- The two spatially autocorrelated variables \(\text{lag100Artificial\_Light}\) and the \(\lambda\) coefficient associated with the error terms) were significant \((P < 0.001)\) for all species. The \text{lag100Artificial\_Light} predictor was negatively related to nest density at the beach segment scale for all species.
- \text{Artificial\_Light} values at the INBS beach segment locations were significant and negatively related to nest densities for loggerhead \((P < 0.001)\) and green turtles \((P = 0.007)\), but did not show a relationship with leatherback nest densities.
- \text{Statewide\_Density} values were significant \((P = 0.007)\) and negatively related only to green turtle nest density at the beach segment scale. This may relate to their widely fluctuating, somewhat biennial nesting patterns found in Florida (Fig. 2).

**Analysis of SAR_{err} model residuals**

A comparison of autocorrelation of the residuals between linear models and the SAR_{err} models showed that the levels were consistently lower for the SAR_{err} models (Table 3). Residuals of the most informative SAR_{err} models (Table 2) indicated how well the regression models predicted nest densities for the 368 beach segments. For loggerheads and green turtles, residuals were within \pm 6 nests per km (Figs. 10A and B), which show the models to be accurate given their high nest densities (Figs. 3A and B). For leatherbacks, however, residuals were within \pm 3 nests per km (Fig. 10C), which is not as notable, given their relatively low densities (Fig. 3C). This may

---

**Table 1.** List of simple and spatially-autocorrelated (lag_{100}) predictor variables used to estimate nest density patterns separately for loggerhead, leatherback, and green turtles on the INBS beaches from 1992 to 2012.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artificial_Light</td>
<td>Annual DMSP intensity values of pixels that intersected with INBS beach segments weighted by the proportion of the length of the segment that occurred in each pixel</td>
</tr>
<tr>
<td>Regional_Density</td>
<td>Annual average nest density on INBS beach segments for each of the six regions surveyed consistently from 1992 to 2012</td>
</tr>
<tr>
<td>Statewide_Density</td>
<td>Annual average nest density for all INBS beach segments</td>
</tr>
<tr>
<td>lag_{100}Artificial_Light</td>
<td>Annual levels of spatially autocorrelated light levels that occur within 100 km of a particular INBS beach segment</td>
</tr>
<tr>
<td>lag_{100}Regional_Density</td>
<td>Annual levels of spatially autocorrelated regional density levels that occur within 100 km of a particular beach segment</td>
</tr>
</tbody>
</table>

The SAR_{err} model by default includes the spatially autocorrelated error that may be associated with the dependent variable (i.e., nest density).
reflect their lower densities and more fluctuating nesting patterns (Fig. 9C).

The regression models fairly consistently over-predicted nest densities for well-lit heavily urbanized areas (e.g., Atlantic-Jacksonville and Miami Beaches) and beaches near inlets (e.g., Wabasso Beach, Ft. Pierce Inlet, St. Lucie Inlet, Sanibel Island) while under-predicting others (e.g., South Brevard, Hutchinson Island, Jupiter Island, Juno Beach, MacArthur State Park). This suggests additional environmental (e.g., human activities, ocean currents) or biological (e.g., historic philopatry) variables are influencing the nesting patterns.

Though all general nesting patterns were similar, based on an analysis of the residuals, loggerhead and green turtle nesting, with respect to artificial light, behaved more alike than compared to those of leatherbacks (Fig. 11). This was not unexpected given the resemblance of average nesting patterns, especially between loggerhead and green turtles across the INBS segments (Fig. 3).

Figure 7. Artificial light trends on INBS beach segments from 1992 to 2012. Red and blue bars designate increasing and decreasing light levels, respectively.

Figure 8. Spatial autocorrelation patterns of artificial light on INBS beaches. Orange lines are the annual levels and the black line is the average from 1992 to 2012.

Figure 9. Spatial autocorrelation patterns of (A) loggerhead, (B) green turtle, and (C) leatherback nest densities on INBS beaches. Colored lines are the annuals levels and the black lines are the averages from 1992 to 2012.
Table 2. Summary of SARerr model selection to predict nest densities for the three species at the 368 INBS beaches for the 1992–2012 period.

<table>
<thead>
<tr>
<th>Predictor variables (X)</th>
<th>Total parameters estimated</th>
<th>Loggerhead</th>
<th>Green turtle</th>
<th>Leatherback</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AIC</td>
<td>ΔAIC</td>
<td>AIC</td>
<td>ΔAIC</td>
</tr>
<tr>
<td>Artificial_Light</td>
<td>4</td>
<td>23 246</td>
<td>5 214</td>
<td>23 383</td>
</tr>
<tr>
<td>Artificial_Light + Statewide_Density</td>
<td>5</td>
<td>18 123</td>
<td>91</td>
<td>17 976</td>
</tr>
<tr>
<td>Artificial_Light + Regional_Density</td>
<td>5</td>
<td>19 830</td>
<td>798</td>
<td>21 723</td>
</tr>
<tr>
<td>Artificial_Light + Statewide_Density + Regional_Density</td>
<td>6</td>
<td>19 815</td>
<td>783</td>
<td>21 723</td>
</tr>
<tr>
<td>Artificial_Light + lag100Artificial_Light</td>
<td>5</td>
<td>23 243</td>
<td>5 211</td>
<td>23 360</td>
</tr>
<tr>
<td>Artificial_Light + Statewide_Density + lag100Artificial_Light</td>
<td>6</td>
<td>18 032</td>
<td>0</td>
<td>17 860</td>
</tr>
<tr>
<td>Artificial_Light + Regional_Density + lag100Artificial_Light</td>
<td>7</td>
<td>19 614</td>
<td>1 582</td>
<td>21 564</td>
</tr>
<tr>
<td>Regional_Density + lag100Regional_Density</td>
<td>5</td>
<td>20 056</td>
<td>2 024</td>
<td>21 862</td>
</tr>
<tr>
<td>Regional_Density + Statewide_Density + lag100Artificial_Light + lag100Regional_Density</td>
<td>6</td>
<td>20 042</td>
<td>2 010</td>
<td>21 861</td>
</tr>
</tbody>
</table>

Lower AIC values indicate the best fit and most parsimonious models (dark gray is the lowest, followed by the lighter gray). AIC, Akaike information criterion.

Table 3. Parameters from the most informative SARerr models shown in Table 2 that predict (A) loggerhead, (B) green turtle, and (C) leatherback nest densities.

A. Predictors (X) for loggerhead nest density

| Coefficient (B) estimates | Standard error | z-value | Pr(>|z|) |
|---------------------------|----------------|---------|---------|
| (Intercept)               | 2.109          | 1.032   | 2.043   | 0.041  |
| Artificial_Light          | -0.090         | 0.009   | -9.723  | <0.001 |
| Statewide_Density         | 0.006          | 0.007   | 0.857   | 0.392  |
| lag100Artificial_Light    | -0.371         | 0.038   | -9.807  | <0.001 |
| k                         | 0.961          | 0.003   | 306.85  | <0.001 |

Wald statistic 94 157; P-value < 0.001
AIC for SARerr:AIC for OLS 18 032:30 671
Avg Moran’s I of residuals <100 km for SARerr:OLS 0.11:0.56

B. Predictors (X) for green turtle nest density

| Coefficient (B) estimates | Standard error | z-value | Pr(>|z|) |
|---------------------------|----------------|---------|---------|
| (Intercept)               | 1.270          | 0.335   | 3.793   | <0.001 |
| Artificial_Light          | -0.025         | 0.009   | -2.691  | 0.007  |
| Statewide_Density         | -0.057         | 0.020   | -2.896  | 0.003  |
| lag100Artificial_Light    | -0.406         | 0.037   | -10.921 | <0.001 |
| k                         | 0.957          | 0.003   | 278.52  | <0.001 |

Wald statistic 77 572; P-value < 0.001
AIC for SARerr:AIC for OLS 17 860:29 912
Avg Moran’s I of residuals <100 km for SARerr:OLS 0.03:0.27

C. Predictors (X) for leatherback nest density

| Coefficient (B) estimates | Standard error | z-value | Pr(>|z|) |
|---------------------------|----------------|---------|---------|
| (Intercept)               | 0.266          | 0.105   | 2.537   | 0.011  |
| Artificial_Light          | 0.001          | 0.005   | 0.129   | 0.897  |
| Statewide_Density         | -0.014         | 0.085   | -0.170  | 0.865  |
| lag100Artificial_Light    | -0.078         | 0.018   | -4.242  | <0.001 |
| k                         | 0.909          | 0.007   | 132.88  | <0.001 |

Wald statistic 17 658; P-value < 0.001
AIC for SARerr:AIC for OLS 8518.6:13 604
Avg Moran’s I of residuals <100 km for SARerr:OLS 0.11:0.24

Parameters and tests highlighted in gray represent statistically significant relationships (P < 0.05).
Over the 21-year period from 1992 to 2012, Florida’s human population grew by more than 5.7 million (U. S. Census Bureau 2015). Following general United States trends, much of this growth occurred along the coast (NOAA 2015b). Thus, it was assumed that most nesting beaches would exhibit an increase in artificial light associated with increasing urbanization. However, 67.7% (N = 249) of INBS beaches showed a decrease in satellite-derived artificial light, 14.1 (N = 52) showed an increase, and the remaining 18.2% (N = 67) showed little change.

Some U.S. National Parks (and National Seashores like Canaveral National Seashore; Fig. 4) with active light management strategies have been shown to provide a refuge from light pollution (Manning et al. 2015).

As found in the Mediterranean study (Mazor et al. 2013), the presence of artificial light was negatively associated with nest numbers. Unlike Mazor et al. (2013), SAC associated with nest densities and artificial light played an important role in the regression models. The artificial light level for the pixels that included the nesting beaches was found to be a significant predictor of loggerhead and green turtle nest densities and at broader scales for nest densities of all three species (Table 3). Leatherbacks were less impacted than loggerheads and green turtles by artificial lighting, a trait which was also noted by Walker (2010). Long-range effects associated with sky glow from

Figure 10. Distribution of SARerr model residuals from INBS beaches for (A) loggerhead, (B) green turtle, and (C) leatherback nest densities. Positive and negative values correspond to model under- and over-predictions, respectively.
sources as far as 18 km away have been shown to influence nesting flatback (*Natator depressus*) turtles (Hodge et al. 2007). Thus, light from nearby urban areas, not at the specific nesting beach, may be a factor in determining the spatial patterns of nesting.

The satellite-derived artificial light measures undoubtedly confound other potential factors associated with urbanization (e.g., noise, chemical pollution, per cent of adjacent impervious surfaces, nighttime beach activity; Southwood et al. 2008; Taylor and Cozens 2010) that could also influence nesting. In addition to light, Mazor et al. (2013) found human population density and infrastructure to be negatively related to nest numbers. Though satellite nightlight data have been correlated to human population density in coastal zones (e.g., Small and Nicholls 2003), obtaining annual human density numbers (and other urbanization metrics) for areas surrounding specific Florida beaches is difficult as census (and land use) surveys are less frequent. It is likely that the model over-prediction for Miami Beaches may reflect additional urban factors that were not included.

Even though the SAR$_{err}$ models developed in this study did not incorporate a litany of potential contributing factors (e.g., sea surface temperature, ocean currents, beach renourishment, shoreline armoring) in addition to satellite-derived artificial light, they nonetheless provided fairly accurate predictions of nest density as shown by the relatively small residuals (Fig. 10).

Undoubtedly some of the model error relates to the spatial, temporal, and spectral resolution limitations of the DMSP OLS sensors and available data. A fundamental question that remains is to what extent does the satellite capture the light environment that is being experienced by the nesting female? The 800 m resolution of the DMSP pixel is much coarser (probably by an order of magnitude) than the width of most Florida nesting beaches (Reece et al. 2013). Hence, light from sources not directly exposed on the beach are included. Furthermore, beaches may be shaded by vegetation, buildings, dunes, escarpments or simply protected from direct light because of the beach slope. Thus, additional metrics that incorporate beach morphology and adjacent 3-dimensional structures (e.g., condominiums and trees) perhaps using LiDAR (Long et al. 2011) could be developed to improve predictions. An examination of the artificial light trends and model residuals may show beaches that should be examined to determine what management policies (e.g., light ordinances, beach use restrictions, dune construction features, tree or other light blocking structures) may be contributing to higher and lower than expected nest densities.

As the Stable Light DMSP product is an annual measure, it includes time periods outside the nesting seasons of the turtles. Artificial light activities on beaches may differ during different times of the year. Some local municipalities have ordinances that restrict lighting on the beaches during nesting season (FWC 2015c). Contrarily, human beach activity may increase during the summer months during the prime nesting season of loggerhead and green turtles. If the temporal resolution of the satellite data were finer, these seasonal changes corresponding to nesting periods could be more precisely captured. To perhaps support a future study, monthly nightlight data from the more light sensitive, finer spatial resolution Visible Infrared Imaging Radiometer Suite (VIIRS) are currently being distributed, but the archive only begins in 2014. Also some light ordinances permit “turtle friendly” light wavelengths (i.e., red light). However, DMSP OLS data are not divided into spectral bands that would allow differentiation of turtle friendly versus unfriendly

---

**Figure 11.** Two-species comparisons, that is, (A) loggerheads and green turtles, (B) loggerheads and leatherbacks, and (C) green turtles and leatherbacks, of SAR$_{err}$ model residuals for the INBS beaches. Model residuals were converted to z-scores to account for the differences in nest densities.
wavelengths. To further investigate the results, a ground truth effort using light-sensitive instruments that directly compares ambient nighttime on the beach (e.g., Pendoley et al. 2012; Verutes et al. 2014; Constant 2015) to the DMS OLS values is warranted.

In Florida, the general increases in sea turtle nesting for all three species (Fig. 2) suggest that artificial lighting may not be critically impairing these populations or the adopted artificial light mitigation policies may be successful which may be reflected by the general decreasing light trends on the INBS beaches (Fig. 7). However, nesting females represent only one side of the equation. Artificial lighting effects on hatchlings may not be manifest in nest density measures and may not be apparent until decades later. This study identified pixels that subsume nesting beaches where there are a variety of artificial light levels as well as areas where light has been increasing or decreasing. To determine if there is an impact, hatchling dis and misorientation and mortality rates should be assessed on a cross-section of these beaches representing different satellite-derived light levels. Furthermore, flatback hatchlings have been shown to be influenced by sky-glow that originates from 15 km away (Kamrowski et al. 2014b); thus, Florida hatchlings may also be affected by distance light.

The long-term sea turtle nest monitoring effort by FWC permitted an extensive, year-to-year analysis of broad-scale sea turtles nesting patterns in relation to artificial light for these important Western Hemisphere breeding grounds. This study, along with its predecessors (Kamrowski et al. 2012, 2014a; Mazor et al. 2013), shows promise that satellite measures of artificial light can be used to help guide not only statewide, but global management of light pollution for sea turtles including the other three predominantly nocturnally nesting species, i.e. flatback, hawksbill (Eretmochelys imbricata), and olive ridley (Lepidochelys olivacea) as well as other light-sensitive species.

Acknowledgments

We are grateful for the nesting data provided by the Florida Fish and Wildlife Conservation Commission’s Florida Marine Research Institute and the artificial nightlight satellite data provided by NOAA made available through the U.S. Department of Defense. The research benefited from suggestions provided by Beth Brost, Simona Ceriani, Robert Hardy, Tomo Hirama, and Anne Meylan from the FWC, members of the UCF Geospatial Analysis and Modeling of Ecological Systems (GAMES) Lab and attendees at the International Sea Turtle Symposium in Malamuna, Mugla-Turkey and the International Symposium on Research/Conservation and Future Prospects of Sea Turtles in Taiwan. We also thank Anthony Weishampel for assistance with the R programming and statistical analyses and two anonymous reviewers for helpful suggestions.

References


