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Ryan Bonner
Coastal Carolina University

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The Impact of Photopollution on Nesting Loggerhead Sea Turtles (*Caretta caretta*) along the
Grand Strand, South Carolina

by
Ryan Bonner

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Requirements for the Degree of Master of Science in
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Approved by: _____

Dr. Eric Koepfler, Thesis Advisor

Dr. Kevin Godwin, Committee Member

Dr. Scott Parker, Committee Member

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Introduction

Human population growth and development is greatly skewed towards coastal regions, with 44 % of the world's human population living within 150 kilometers of the ocean (UN Atlas of the Oceans, 2015). In South Carolina, the population of coastal Horry County has grown by over 37% since the year 2000 and possesses the most rapid growth rate in the state (U.S Census Bureau, 2014). With this development comes photopollution, a periodic or chronic increase in ambient illumination that results in environmental degradation for local organisms (Longcore & Rich, 2004). The influence of photopollution is expected to intensify concurrently with coastal development, and photopollution associated with heavily developed coastlines is known to exhibit a wide variety of harmful effects on surrounding natural systems. In the United States, coastal light intensity is estimated to be increasing at a rate of 6% per year (Cinzano et al., 2001). Impacts range from misorientation and disorientation of affected species to the disruption of behavioral patterns adapted to natural periods of light and dark. For example, the adverse effects of night lighting on birds have been well documented over the past century. While predominately active during the day, many species of birds undergo migrations at night. Illumination of tall structures such as communication towers (Brewer & Ellis, 1958) and light houses (Hansen, 1954) have caused in increased mortality for birds during these nocturnal migrations through collisions. Birds have also been observed to be attracted to artificial light and tend to stay within sight of light sources they encounter, indirectly lowering survivability by extending or delaying the migration period or by altering the migration route (Rich & Longcore, 2006).

Predominately nocturnal species may also exhibit negative changes in behavior when exposed to artificial light. A study of the impact of night lighting on nocturnal sugar gliders (*Petaurus breviceps*) found that exposure to light resulted in significantly decreased activity and foraging levels (Barber-Meyer, 2007). Sugar glider foraging behavior was observed to be altered by exposure to illumination as low as 7 lux. While frog species may benefit from enhanced foraging opportunities due to higher insect concentrations in lighted areas, they may also suffer from increased mortality (Perry et al., 2008). Frogs feeding in illuminated areas are at a greater risk of being struck by vehicles (Baker, 1990), and their eyes are slow to adapt to changing light levels, leading to reduced vision when moving between areas of varying light intensity (Cornell & Hailman, 1984). A study of grey frog (*Hyla chrysoscelis*) foraging abilities in enhanced lighting conditions found that the ability of frogs to locate and consume prey was diminished when exposed to lighting brighter than natural moon illumination (Buchanan, 1993).

The negative effects of photopollution on sea turtles have been particularly well established (Salmon, 2003). Hatchlings are known to experience disorientation and misorientation when attempting to navigate to the ocean when exposed to artificial light sources immediately following emergence (Witherington & Bjorndal, 1991a; Salmon, 2003; Berry et al., 2013). In regions where urban development borders nesting beaches, hatchlings may be attracted inland, resulting in significant juvenile mortality (Witherington & Martin, 1996). Adult female sea turtles are also vulnerable to photopollution along coastlines. Nesting turtles emerge from the sea at night and prefer dark nesting sites (Mann, 1978). Nesting attempt frequency by green and loggerhead sea turtles has been demonstrated to be decreased on beaches illuminated with white lighting (Witherington, 1992). Nesting turtles

tended to avoid exiting the water along experimentally lighted sections of undeveloped coastline in favor of nearby unlit nesting sites. When nesting on lighted beaches, turtles are known to prefer “shaded” areas provided by tall artificial structures (Salmon, 2003). Aside from beach lighting, other nesting cues following emergence are nonvisual and include temperature and beach geomorphology (Stoneburner & Richardson, 1981).

Inability to locate a suitable nesting site or encountering a disturbance during nest construction may result in an aborted nesting attempt known as a “false crawl.” False crawls have been observed to increase in frequency relative to successful nesting attempts along developed coastlines (Williams-Walls et al., 1983). Nesting turtles are most likely to be disturbed between emergence from the ocean and excavation of the nesting cavity (Hirth & Samson, 1987). During this phase, flashlight beams (Carr & Giovannoli, 1957) and other human activity (Witherington & Martin, 2000) within the field of vision of a nesting turtle have been reported to be enough to result in false crawls. Turtles are less likely to abandon nesting if disturbed during oviposition but have been observed to spend drastically less time covering and camouflaging nests before returning to the sea. Witherington & Martin (2000) reported witnessing nesting green turtles return to the water within five minutes following egg-laying when disturbed by groups of humans with flashlights instead of the average of 50 minutes this species typically spends exhibiting nest-covering behavior. Nests are likely put at greater risk of exposure to temperature extremes and predation by the abbreviation of this activity. Murphy (1985) noted that repeatedly unsuccessful nesting turtles chose increasingly distant and unsuitable nesting sites on successive attempts. Females may also release eggs into the ocean

when unable to find suitable nesting sites, as they have been observed to do so when confined to pens during the nesting season (Witherington & Martin, 2000).

The nature of photopollution directly ties it to human development and activity, making it difficult to separate and quantify the negative impacts of night lighting from other anthropogenic factors. Night lighting on nesting beaches indirectly inhibits nesting by increasing the probability of human activity and disturbance (Carr & Giovannoli, 1957), with lighting more likely to be present in areas with greater human population density and will draw more human activity than nearby unlit beaches. A study of nesting sea turtles in Florida discovered that nesting density increased as nearby human population density decreased (Weishampel et al., 2003). A separate study in Japan determined that nesting density was positively correlated with distance from local settlements (Kikukawa et al., 1999). Brei et al. (2014) noted that the presence of docks and the number of nearby potential hotel occupants (quantified using number of available hotel beds) correlated with decreased nesting activity while the presence of roads and ports did not. A satellite-based study of the relationship between night lighting and nesting sea turtles in Israel found that night-lighting was best able to explain nesting distribution when compared with other potential anthropogenic threats (Mazor et al., 2013). Night-lighting exists alongside and facilitates most nocturnal human activity that can potentially result in nesting disturbance and act as a deterrent to nesting turtles in the absence of other stressors. The impact of photopollution on both adult and hatchling sea turtles serves to directly and indirectly limit nesting success and reduce the survivability of these species.

One of the largest marine reptiles, the loggerhead sea turtle (*Caretta caretta*) is found in temperate and tropical oceans around the world (Marine Turtle Specialist Group 1996). Loggerheads are vulnerable to a variety of anthropogenic threats including night-lighting, coastal development (Prunier et al., 1993), incidental bycatch (Lewison et al., 2004), and ingestion of marine debris (Tomas et al., 2002). Loggerheads are currently classified as “endangered” by the IUCN (Marine Turtle Specialist Group, 1996). On the east coast of in the United States, loggerhead nesting sites are primarily located in the Carolinas, Georgia, and Florida (Ehrhart et al., 2003). The bulk of this loggerhead nesting population (approximately 90%) is found in Florida (Ehrhart et al., 2003). Sex determination in loggerhead hatchlings is controlled primarily by nest temperatures (Limpus et al., 1985). Nests exposed to temperatures lower than 26 ° C will produce predominantly male hatchlings while temperatures greater than 32 ° C will result in females (Limpus et al., 1985). Intermediate temperatures will produce a mixture of both sexes. Warmer average temperatures present along Florida nesting beaches has been observed to lead to a significantly higher proportion of female hatchlings relative to males (Hanson et al., 1998). As a result, the less populated, cooler northern nesting sites in the Carolinas are disproportionately important to the regional loggerhead population for their role in the production of male hatchlings (Hanson et al., 1998). Protection of these northern sites will be required to maintain sufficient sex ratios and the long-term survivability of the population. To this end, an understanding of the effects of photopollution on nesting adult female loggerhead nesting site selection will be critically important to preserving habitat quality and associated reproductive success as urbanization of coastlines continues.

Mazor et al. (2013) note that while the impact of photopollution on nesting sea turtles has been well explored on small spatial scales through case studies and experiments in laboratory settings, few studies have examined this relationship over broader spatial scales (i.e., 10 - 100 km). The goal of this study was to characterize the onshore light field presented to nesting turtles on a regional scale along a developed stretch of South Carolina coastline and to quantify how photopollution intensity impacts loggerhead nesting density derived from historical nesting data ("Sea Turtle Nest Monitoring System," 2015). These findings will facilitate the identification of vulnerable nesting sites, direct sea turtle conservation efforts in the region, and provide guidance for management and conservation of loggerheads, and other endangered sea turtles, throughout the world.

Methods

Experimental Design

The study site extended from the Little River inlet to southern Pawleys Island, encompassing most of South Carolina's coastal Grand Strand region (Figure 1). 74 sites were selected at approximately 1 km intervals across the study area and each site was visited once. At each site, all measurements were collected from a location at a distance of 20 m downslope from the primary dunes. The 360° light field was divided into twelve 30° horizontal intervals using a compass. Onshore light measurements were recorded at two inclination angles of 5° and 15° relative to the horizon at each horizontal interval. These inclination angles represent the lower and middle thirds, respectively, of the onshore field of view of a nesting sea turtle emerging from the water (Lutz & Musick, 1996). Offshore light measurements were taken at

the 5° inclination angle. Each measurement was taken in triplicate using a Unihedron Sky Quality Meter-L mounted on a tripod approximately 1.5 meters tall. Sky Quality Meters are portable, low-light photometers capable of measuring mean sky brightness at specific angles and have been used to successfully characterize photopollution intensity in urban settings (Pun & So, 2012). The half width at half maximum of the angular sensitivity of the Sky Quality Meter-L is approximately 10°, and the sensitivity to a point source approximately 19° off-axis is a factor of 10 lower than on-axis (“Sky Quality Meter-L,” 2015). A level was used to adjust the vertical angle of the Sky Quality Meter between measurements. Measurement units were initially recorded in magnitudes/arcsecond² and were converted to cd/m², the SI unit for luminance. All measurements were collected between June and October, 2014, between 9:00 p.m. and 12:00 a.m. following the conclusion of astronomical twilight. One site in Pawleys Island was selected to be sampled twice, once during a full moon and once during a new moon to test variation in light intensity due to changing lunar cycle. Nesting density data from 2009 - 2014 was collected by the South Carolina Department of Natural Resources and SCUTE, a local volunteer sea turtle monitoring organization, and was available from Seaturtle.org (“Sea Turtle Nest Monitoring System,” 2015). Six years of nesting data were used to provide temporal replicates for each region. The data used is available to the public and is organized into eleven sub-regions within the Grand Strand area. NOAA VIIRS satellite imagery data was also used to examine coastal photopollution within the study area and to determine consistency between ground-based and satellite sampling methodology. Imagery was a composite of moonless and cloudless night skies for May 2014 at a spatial resolution of 500m/pixel. Satellite imaging may most accurately represent anthropogenic lighting within a region by controlling for the influence of natural light,

but it is unable to account for natural or artificial obstructions that would alter light intensity visible to nesting turtles and cannot be used to determine variation in light intensity between vertical or horizontal angles for an observer on the ground.

Statistical Analysis

All data was analyzed using SPSS statistics software using a stated a priori 95% confidence interval. The following specific tests were conducted:

1. Light Intensity at the 5° Inclination Angle v. Sea Turtle Nesting Density
2. Light Intensity at the 15° Inclination Angle v. Sea Turtle Nesting Density
3. Satellite Imaging Light Intensity v. Sea Turtle Nesting Density
4. Light Intensity at the 5° Inclination Angle v. Satellite Imaging Light Intensity
5. Light Intensity at the 5° Inclination Angle v. 15°
6. Onshore Light Intensity v. Offshore Light Intensity
7. Full Moon Light Intensity v. New Moon Light Intensity between developed and undeveloped sites
8. Peripheral Onshore Light Intensity v. Central Onshore Light Intensity between developed and undeveloped sites
9. Coefficient of Variation for Onshore Light Intensity between developed and undeveloped sites

For comparisons between light intensity and sea turtle nesting data, sampling sites were averaged into eleven sub-regions to match the spatial format of the nesting density data. The three most shoreward angles at each site (e.g., 315°, 285°, 255°) were averaged to compare the

relationship between shoreward light intensity at 5° and 15° inclination angles and loggerhead nesting density during 2009-2014. Onshore and offshore light intensity datasets were compared to illustrate differences between light fields presented to female turtles ascending to and descending from nest sites. Satellite imaging and photometer photopollution measurements were compared at each of the 74 study sites. As measurement sites were not identical between the two methodologies, the average of the two closest satellite sites was used to obtain an equivalent value for each photometer site. A log transformation of both data sets was conducted. Three developed and three undeveloped sites, each from different sub-regions, were selected to explore variation between light intensity recorded at all angles of the onshore light field. Undeveloped sub-regions were defined as locations with limited permanent anthropogenic presence relative to the rest of the region. The three developed sites chosen were the brightest sites from the three most highly developed regions, Myrtle Beach, North Myrtle Beach, and Surfside Beach. The three undeveloped sites chosen were the darkest sites recorded from Huntington Beach State Park, Waites Island, and Pawleys Island. A coefficient of variation was calculated for each location to allow for the examination of shoreward light variability between developed and undeveloped sub-regions. Logarithmic regression analysis was used to test the relationships between light intensity and nesting data. As parametric assumptions for all data sets were not met (e.g., data was not normally distributed), nonparametric Mann Whitney U or Kruskal Wallis tests were used for analysis of variance.

Results

Average nesting density differed significantly (Kruskal-Wallis , $df = 10$, $F = 34.927$, $p < 0.001$) across all sub-regions (Figure 2). Average onshore light intensity at the 5° inclination angle was characterized for seventy-four sites in the Grand Strand region (Figure 3). Both 5° onshore light intensity (Kruskal-Wallis, $df = 11$, $F = 413.72$, $p < 0.001$) and 15° onshore light intensity (Kruskal-Wallis, $df = 11$, $F = 427.87$, $p < 0.001$) averages significantly varied between sub regions (Table 1).

Average onshore light intensity was found to be significantly higher (Mann-Whitney U , $N = 1332$, $F = 362488.5$, $p < 0.001$) than average offshore light intensity for the mean of the three most shoreward angles at each of the seventy-four sites (Figure 4). Total average onshore 5° light intensity was significantly higher (Mann-Whitney U , $F = 197867$, $p = 0.001$) than average 15° light intensity across all sub-regions (Figure 5). Average onshore 5° light intensity was also compared to average 15° light intensity within sub-regions (Table 2). The difference between light intensity between both inclination angles was not significant at Waites Island (Mann-Whitney U , $F = 929$, $p = 0.500$), Huntington Beach State Park (Mann-Whitney U , $F = 1027$, $p = 0.907$), and Pawleys Island (Mann-Whitney U , $F = 1737$, $p = 0.227$). The difference between light intensity between both inclination angles was significant at North Myrtle Beach (Mann-Whitney U , $F = 7756$, $p = 0.034$), Briarcliff Acres (Mann-Whitney U , $F = 96$, $p = 0.037$), Myrtle Beach (Mann-Whitney U , $F = 10328$, $p = 0.001$), Myrtle Beach State Park (Mann-Whitney U , $F = 18$, $p = 0.047$), Surfside Beach (Mann-Whitney U , $F = 886$, $p > 0.001$), Garden City Beach (Mann-

Whitney U , $F = 38$, $p > 0.001$), North Litchfield (Mann-Whitney U , $F = 65$, $p = 0.002$), and Litchfield by the Sea (Mann-Whitney U , $F = 90$, $p = 0.023$).

Nesting density was strongly negatively correlated (Logarithmic Regression, $R^2 = 0.79$, $p < 0.001$) with mean onshore 5° light intensity (Figure 6). 15° onshore light intensity was also found to be negatively correlated (Logarithmic Regression, $R^2 = 0.76$, $p < 0.001$) with nesting density (Table 3, Figure 7). A similar correlation (Logarithmic Regression, $R^2 = 0.83$, $p < 0.001$) was found between the spectral radiance data collected through satellite imaging and nesting density (Table 3, Figure 8). The satellite imaging data set was also found to be moderately correlated (Linear Regression, $R^2 = 0.54$, $p < 0.001$) with the ground-based light intensity data (Figure 9).

Variation between full moon and new moon light intensity was examined at onshore and offshore angles (Figure 10). Light intensity was found to be significantly (Mann-Whitney U , $F = 18.0$, $p = 0.050$) higher for both onshore light intensity and offshore light intensity (Mann-Whitney U , $F = 0$, $p < 0.001$) during the full moon compared with the new moon, although the magnitude of this difference was much greater for offshore light intensity (Table 1). Light intensity at all measured onshore angles was compared at six sites from different sub-regions (Figure 11). Average light intensity was significantly (Mann-Whitney U , $F = 442.5$, $p = 0.030$) greater at the peripheral shoreward angles relative to central angles for the three undeveloped (Pawleys Island, Waites Island, and Huntington Beach State Park) sites, while the opposite trend was observed (Mann-Whitney U , $F = 121$, $p < 0.001$) for the three developed (Myrtle Beach, North Myrtle Beach, and Surfside Beach) sites (Figure 12). The average 5° onshore light

intensity coefficient of variation was also found to be higher for the three developed sites than for the three undeveloped locations (Figure 13).

Discussion

Over a span of five months, coastal light intensity was quantified along the Grand Strand of South Carolina (Figure 2). Our results provide a critical baseline for monitoring regional anthropogenic impacts on sea turtle nesting distribution and possess a number of implications for conservation efforts. The negative correlation we observed between light intensity and average nest density (Figure 6) is consistent with the findings of similar photopollution studies (Carr & Giovannoli, 1957; Witherington, 1992; Mazor et al., 2013; Brei et al., 2014). The most heavily developed sub-region, Myrtle Beach, exhibited the lowest nest density along with onshore photopollution intensity a full order of magnitude higher than the next brightest sub region. The highest nesting densities occurred in undeveloped sub-regions and nesting density was observed to decline dramatically in the presence of low amounts of anthropogenic light (Figure 6). Maximum light intensity was found to be skewed towards the most shoreward angles in developed sites and towards peripheral angles in undeveloped sites. Developed locations also experienced greater variation in light intensity between onshore angles relative to undeveloped locations. These characteristics may influence sea turtle nesting site selection by drawing them toward sites with brighter peripheral onshore angles relative to the most shoreward angles even along urbanized coastlines. Developing an understanding of this behavior would improve our ability to predict nesting patterns in regions where sea turtles are

not presented with preferred low-light nesting beaches and would be a worthy topic for further research.

The results of this study emphasize the importance of maintaining undeveloped stretches of coastline for use as nesting habitat, as even lightly developed sub-regions where photopollution was low expressed dramatic declines in nesting density. In Florida, adult loggerhead sea turtles are known to continue nesting on heavily urbanized coastlines if undeveloped habitats are available by preferentially nesting beneath the shade offered by palm trees or tall structures such as hotels (Salmon et al., 1995a). However, anthropogenic structures do not offer a consistent barrier for illumination the way natural barriers do, and hatchlings from nests in these regions frequently experience very high levels of disorientation and/or misorientation (Salmon et al., 1995b). While misdirection of hatchlings following nest emergence is not currently considered a serious issue in South Carolina and has yet to be quantified, the impact of photopollution will likely intensify as the coastal human population increases and development continues. Our findings show significantly greater average light intensity is present at the lower 5° onshore inclination angle than at 15°. Within each sub-region, the difference between light intensity at 5° and 15° was found not to be statistically significant only at Waites Island, Huntington Beach State Park, and Pawleys Island, three of the least developed sub-regions sampled. Variation in light intensity between the two measured inclination angles may possess significance for conservation efforts. As the lowest third of a nesting sea turtle's field of vision is consistently brightest in urbanized areas, nesting turtles could potentially be protected from a large amount of anthropogenic light through the construction or maintenance of relatively low-lying natural barriers such as dunes and

vegetation along developed coastlines that provide consistent barriers against anthropogenic illumination, particularly in areas that lack tall structures. Both inclination angles possessed similar relationships with nesting density, suggesting that light intensity present anywhere within the onshore field of vision of a nesting turtle is capable of resulting in negative impacts.

The onshore light field was found to be significantly brighter than the offshore light field for nearly all of the sub-regions in the study area (Figure 4). The offshore light intensity was only able to significantly exceed onshore light intensity at Pawleys Island where the majority of sites were sampled during a clear night with a full moon. While changes in lunar cycle do have an effect on both onshore and offshore light intensity, the impact of this variation is dwarfed by that of the onshore artificial glow present along heavily developed coastlines, which was observed to be several orders of magnitude higher than undeveloped analogs. In addition, Lohmann et al. (1997) note that the lunar cycle does not affect sea turtle nesting behavior. These results challenge the current paradigm of the manner photopollution negatively impacts hatchling turtles. If hatchlings possess a tendency to utilize the brightest light source to assist in the location of the ocean following emergence from the nest, the onshore light field is typically the brightest even in the absence of any human development. That hatchlings are still frequently disoriented or misoriented when exposed to high light intensity suggests that the relationship between artificial light and hatchling navigational ability has not been fully explored. Further attempts to quantify hatchling navigational impairment in the Grand Strand region would help to illuminate the mechanisms of this phenomenon if compared to regions in which there are high levels of hatchling misorientation and disorientation.

Similar studies have recently utilized satellite technology to obtain light intensity data over wide spatial areas for a single moment in time in order to control for temporal variation (Brei et al., 2014). The primary advantage of the ground-based study is that it can analyze the coastal light field at angles that most accurately represent the field of vision of nesting sea turtles emerging from the water and can take account for coastal features such as structures and sand dunes that may block line of sight. The increased ease of controlling for temporal variables may result in satellite imaging becoming standard for photopollution studies on regional scales. Comparisons between ground and satellite data could be used to help verify the reliability of photopollution data collection using satellite-imaging. The results for both sampling methods used in this study were moderately correlated (Figure 9) and suggest that both methodologies are of comparative effectiveness. The existing variation between the two data sets was likely caused in part by temporal fluctuation from our ground-based data collection. As the average photopollution measurements of the two closest satellite sites was used to find an equivalent value for each of our 74 photometer sites, additional variation may have resulted for sites that possess a high degree of light intensity variation over small spatial scales (i.e. approximately 0.5 km). Satellite imaging is also able to record light intensity that may be reduced or blocked by the presence of natural or artificial structures from the perspective of a photometer located on the beach. For photopollution studies over smaller spatial scales, ground-based light intensity surveys may be more accurate than satellite studies where researchers have the resources to control for the effects of temporal variability, as satellite imaging does not directly measure light intensity present in the field of view of a nesting turtle (Lutz & Musick, 1996).

The impact of light intensity cannot be fully separated from that of interrelated anthropogenic threats such as nesting habitat degradation resulting from coastal development and disturbance caused by human activity on nesting beaches. The light intensity measured in this study is therefore primarily used as an indicator for quantifying all anthropogenic impacts on nesting turtles that are facilitated by or associated with coastal night lighting. Light intensity was only measured for the visible spectrum, and no distinction was made between night lighting coloration. Loggerhead sea turtles are capable of distinguishing between colors, and hatchlings are known to be particularly averse to yellow lighting (Witherington & Bjorndal, 1991b).

A limitation of this ground-based study was the inability to control for temporal light intensity variation. Light intensity surveys were limited by tidal and weather conditions as well as volunteer availability, resulting in a field work period that spanned five months. This experiment did not control for variation in ambient light levels originating from coastal building occupancy or cloud coverage during this period.

The effectiveness of our comparisons of photopollution intensity and sea turtle nesting density was inhibited by the relative coarseness of the nesting density data. All sea turtle nesting data was recorded by geographic sub-region. These sub-regions vary in size and surveyor effort. In addition, sea turtle nests discovered in developed areas in the Grand Strand region are typically relocated to undeveloped sites. The tendency of nesting sea turtles to return to their natal beaches (Luschi et al., 2003) could potentially lead to an observable decline

in nesting density in developed regions unrelated to the direct effects of photopollution on nesting success or the survivability of hatchling turtles as relocated populations mature.

Our findings demonstrate a negative correlation between photopollution and loggerhead sea turtle nesting density in the Grand Strand region of South Carolina. Loggerhead nesting declines dramatically along stretches of coastline exposed to chronic night lighting. In addition, we reveal significant differences in the characteristics of the onshore light field between developed and undeveloped locations that may play a role in nest site selection and could help to inform conservation efforts. Continuing to closely monitor and address coastal photopollution trends on both small and regional spatial scales will be essential to ensure the long-term preservation of the regional loggerhead sea turtle nesting population.

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Tables and Figures

Tested Variables	Test	Test Statistic	N	df	Significance
Nests v. Sub-Region	Kruskal-Wallis	34.927	65	10	0.000
Onshore Light 5° v. 15°	Mann-Whitney	197867	1332		0.001
Offshore Light 5° v. Onshore Light 5°	Mann-Whitney	362488.5	1332		0.000
Onshore Light New Moon v. Full Moon	Mann-Whitney	18	18		0.050
Offshore Light New Moon v. Full Moon	Mann-Whitney	0	18		0.000
Onshore Light 5° v. Sub Region	Kruskal-Wallis	413.72	666	11	0.000
Onshore Light 15° v. Sub Region	Kruskal-Wallis	427.871	666	11	0.000
Central v. Peripheral Light (Developed)	Mann-Whitney	121	63		0.000
Central v. Peripheral Light (Undeveloped)	Mann-Whitney	442.5	54		0.030

Table 1: Nonparametric statistical test results for photopollution and sea turtle nesting data sets.

Sub-Region	Test Statistic	Standardized Test Statistic	N	Significance
Waites Island	929	-0.674	90	0.500
North Myrtle Beach	7756	-2.114	270	0.034
Briarcliff Acres	96	-2.089	36	0.037
Myrtle Beach	10327.5	-3.315	324	0.001
MBSP	18	-1.99	18	0.047
Surfside Beach	885.5	-3.518	108	< 0.001
Garden City Beach	38	-4.392	90	< 0.001
Huntington Beach State Park	1027	0.117	90	0.907
North Litchfield	65	-3.071	36	0.002
Litchfield by the Sea	90	-2.279	36	0.023
Pawleys Island	1737	-1.208	126	0.227

Table 2: Mann-Whitney *U* statistical test results for comparisons between onshore light intensity at 5° and 15° inclination angles for individual sub-regions.

Tested Variables	Equation	Test Statistic	df	R ²	Significance
Nests/km v. Onshore Light 5°	Logarithmic	33.553	10	0.79	< 0.001
Nests/km v. Onshore Light 15°	Logarithmic	28.237	10	0.76	< 0.001
Nests/km v. Satellite Spectral Radiance	Logarithmic	43.845	10	0.83	< 0.001
Satellite/Sky Quality Meter	Linear	85.767	73	0.54	< 0.001

Table 3: Regression analysis statistical test results.

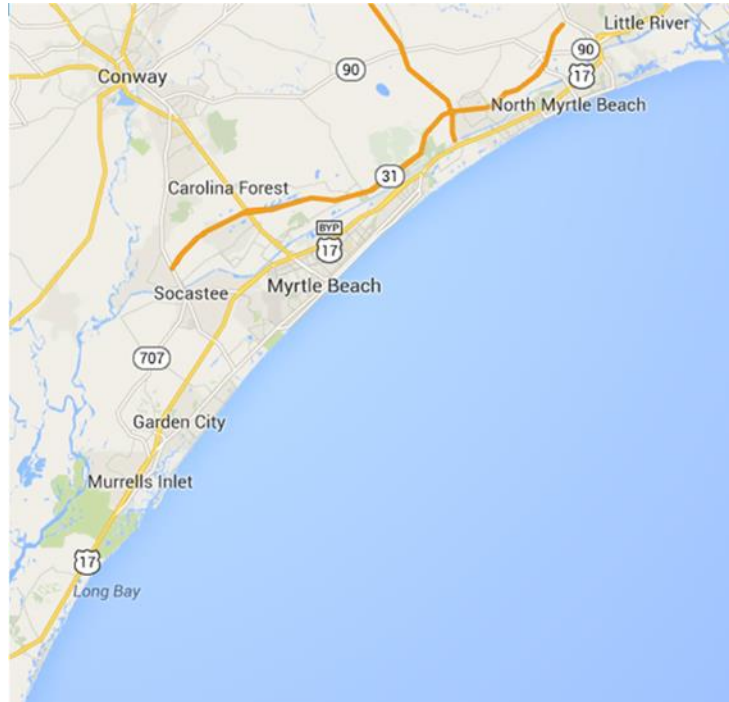


Figure 1: The study area comprises the Grand Strand region of South Carolina and extends from Little River Inlet in the north to Pawleys Island in the south (Google Maps, 2014).

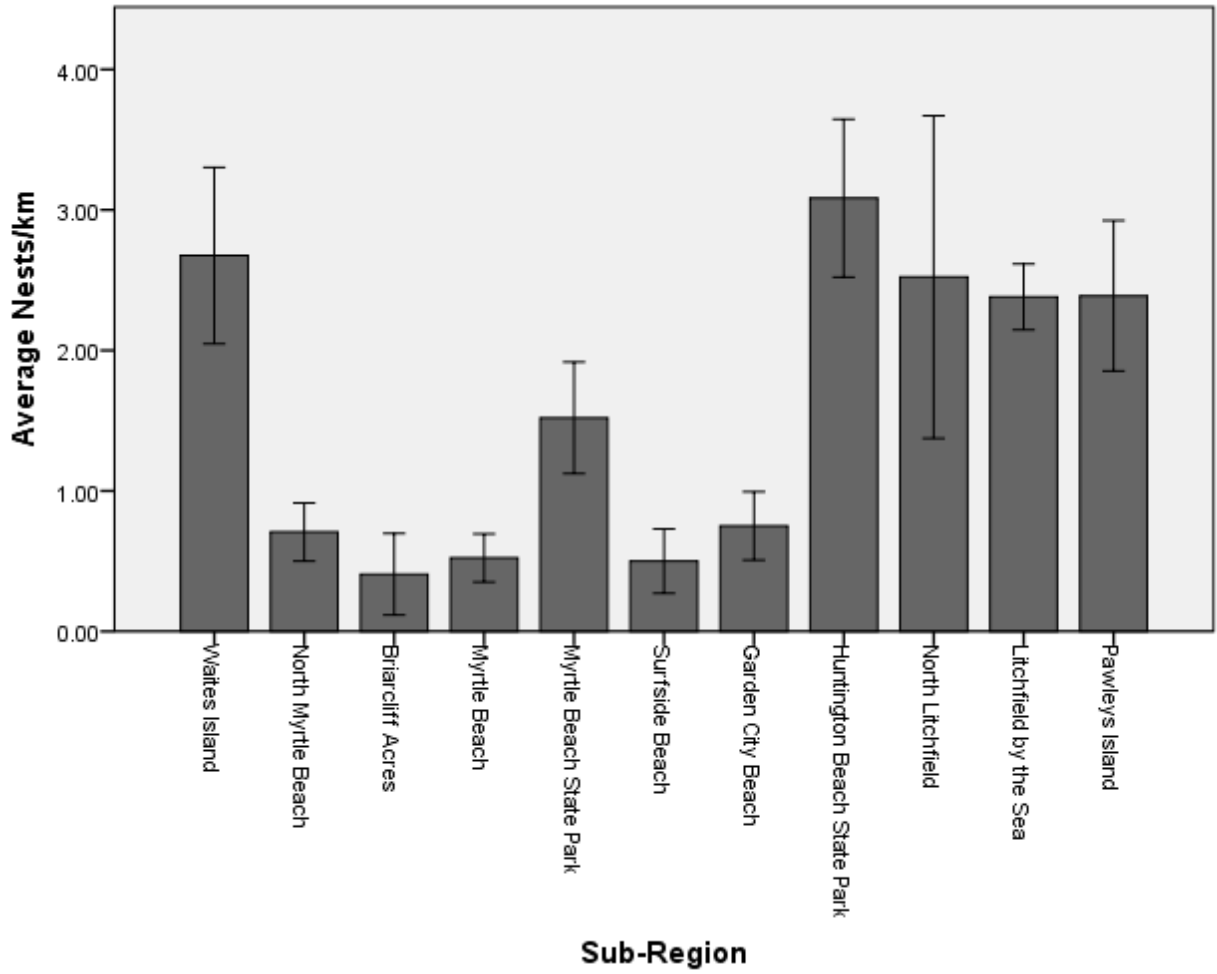


Figure 2: Average nests/km for 11 Grand Strand sub-regions. Error bars represent one standard error.

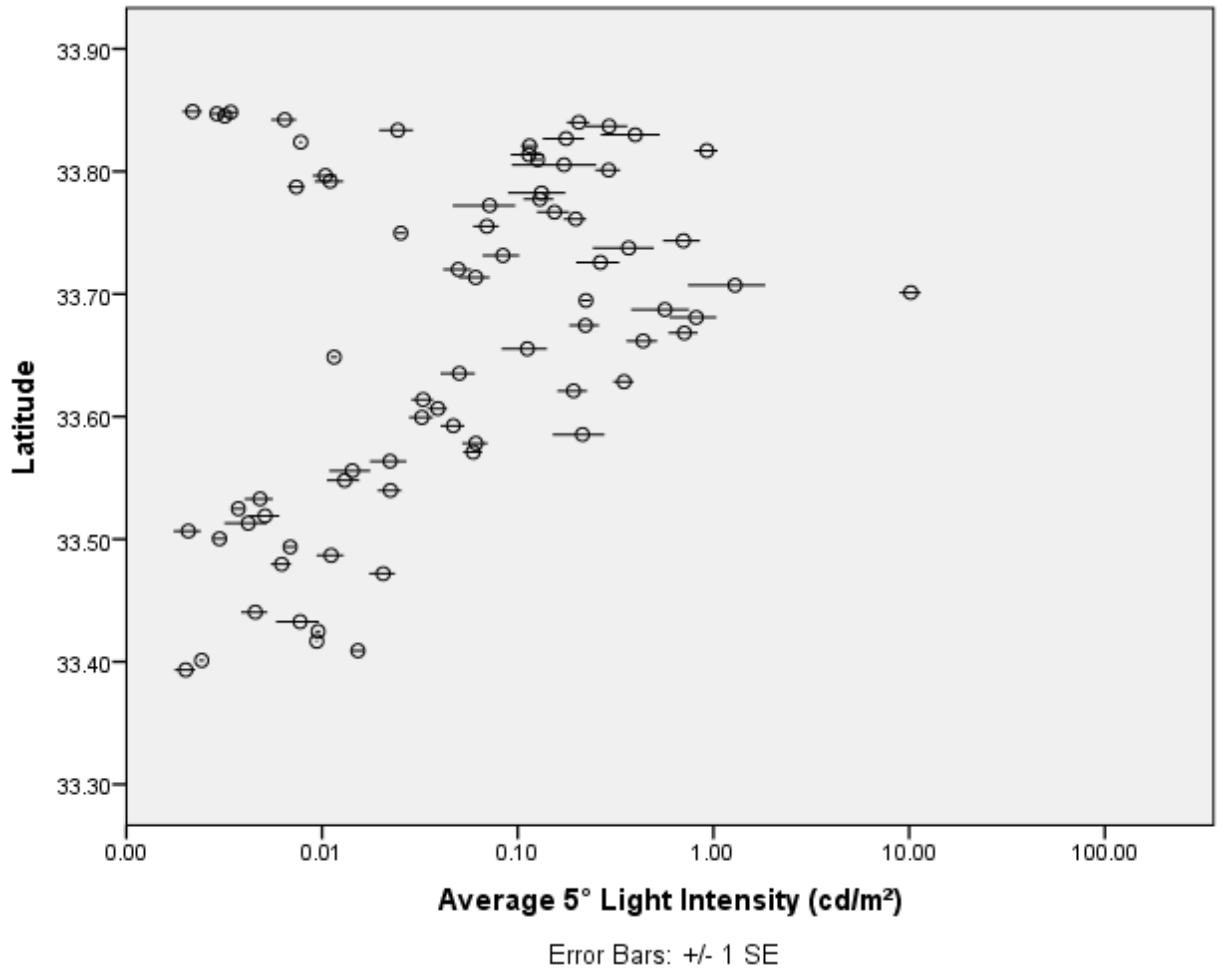


Figure 3: Latitude v. average onshore 5° light intensity (cd/m^2) for 74 Grand Strand sites. Error bars represent one standard error.

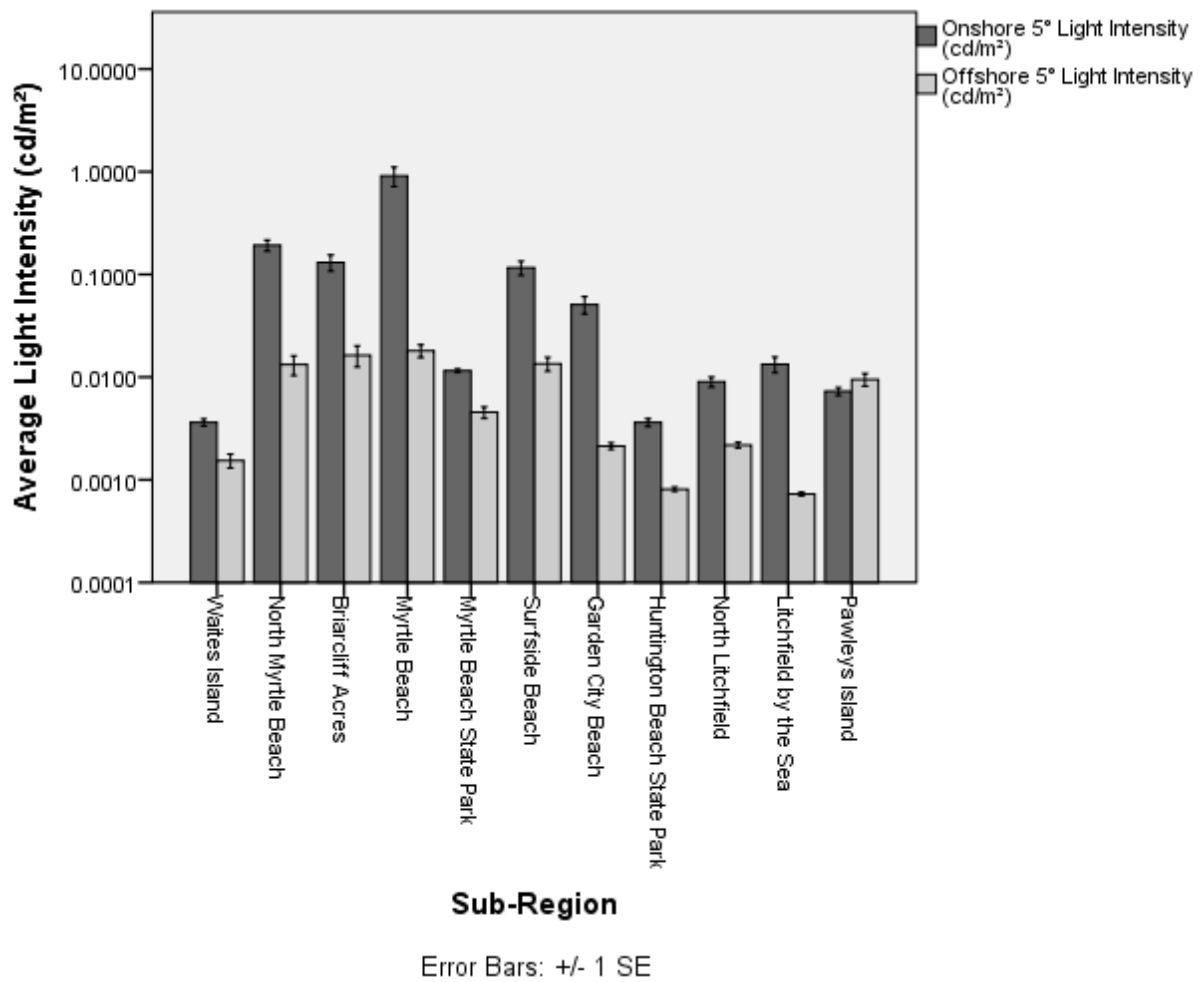


Figure 4: Average onshore and offshore light intensity (cd/m^2) at the 5° inclination angle for 11 Grand Strand sub-regions. Error bars represent one standard error.

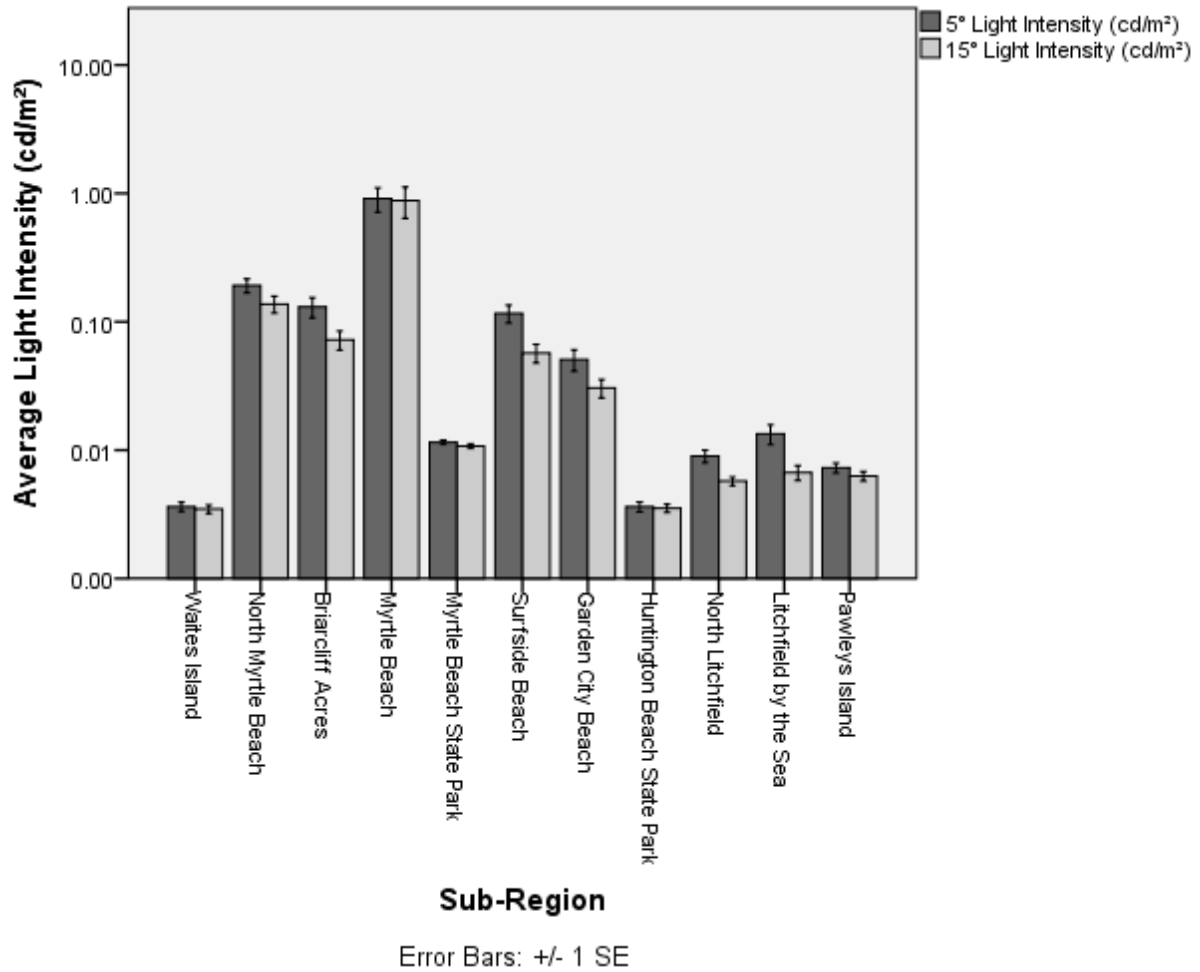


Figure 5: Average onshore 5° and 15° light intensity (cd/m²) means for 11 Grand Strand sub-regions. Error bars represent one standard error.

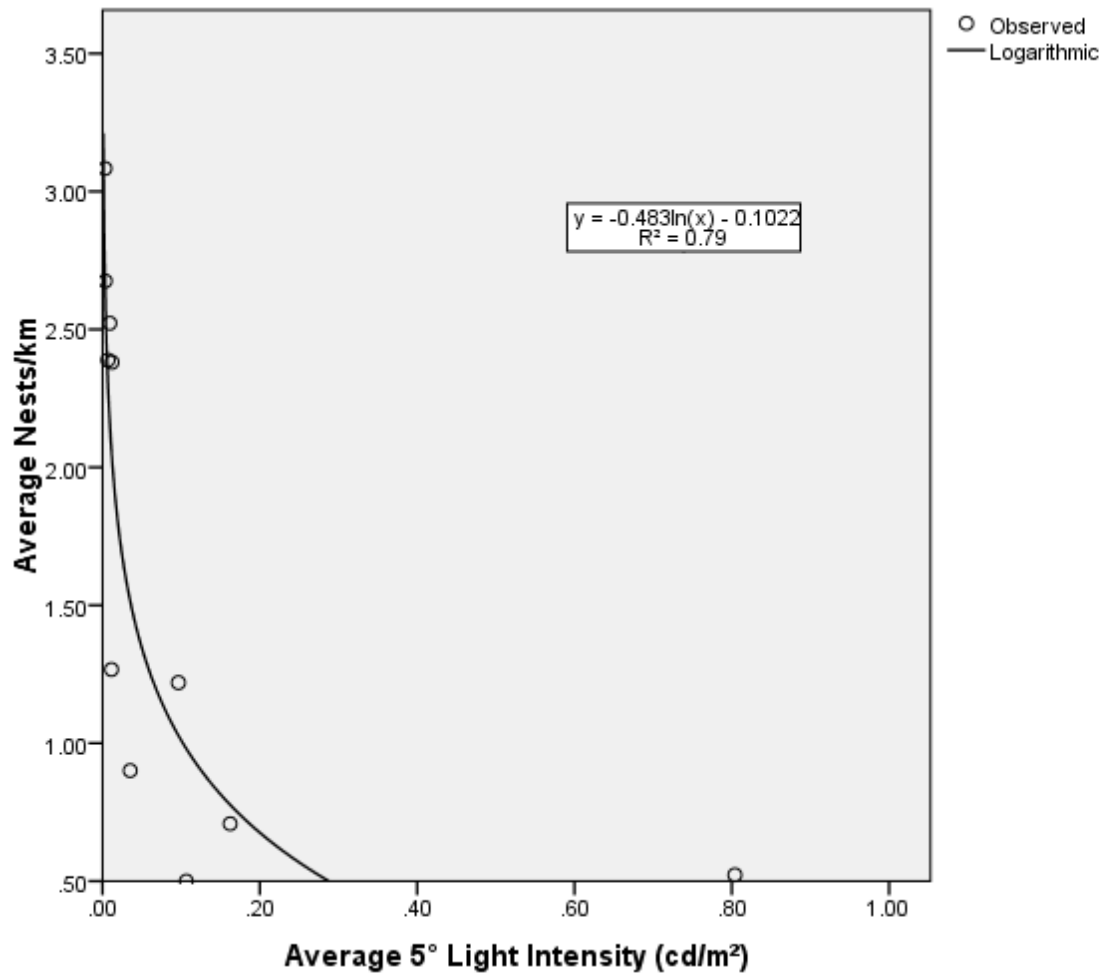


Figure 6: Average number of nests/km for 2009-2014 v. average onshore 5° light intensity (cd/m²).

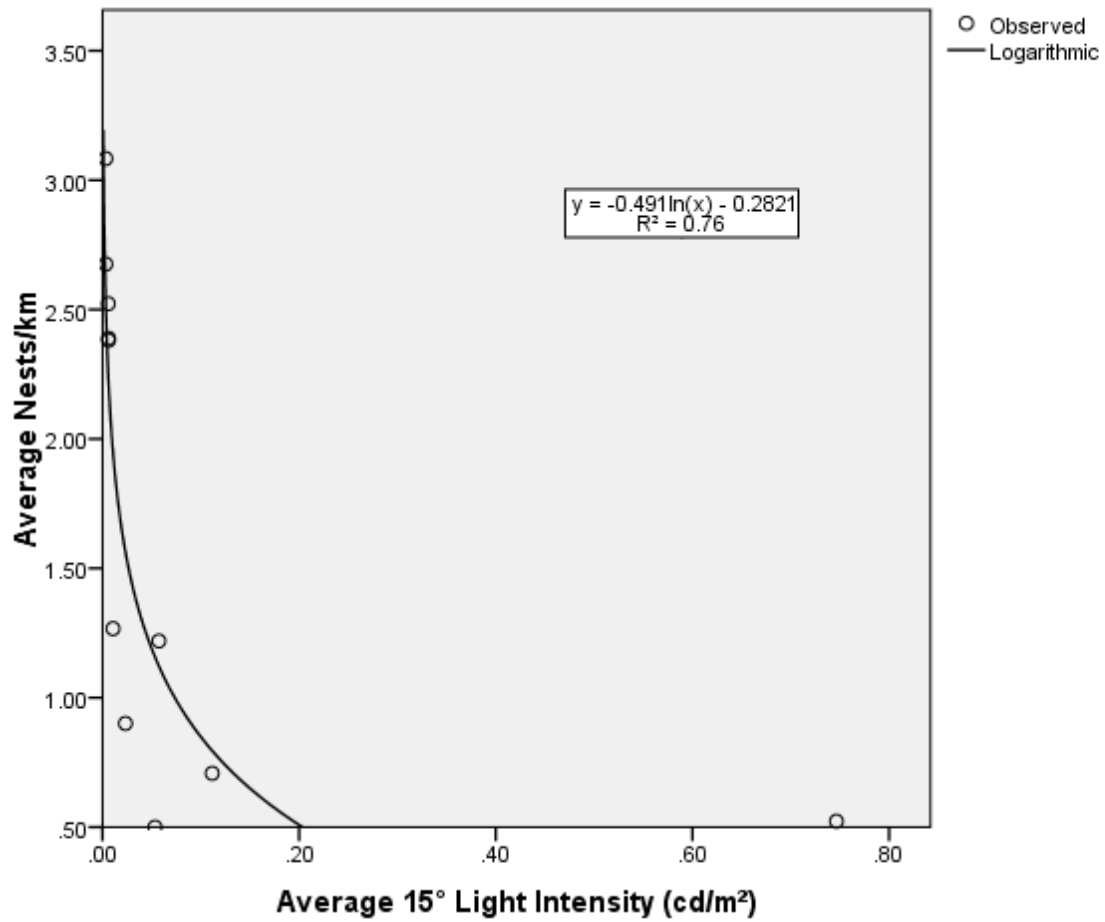


Figure 7: Average number of nests/km for 2009-2014 v. average onshore 15° light intensity (cd/m²).

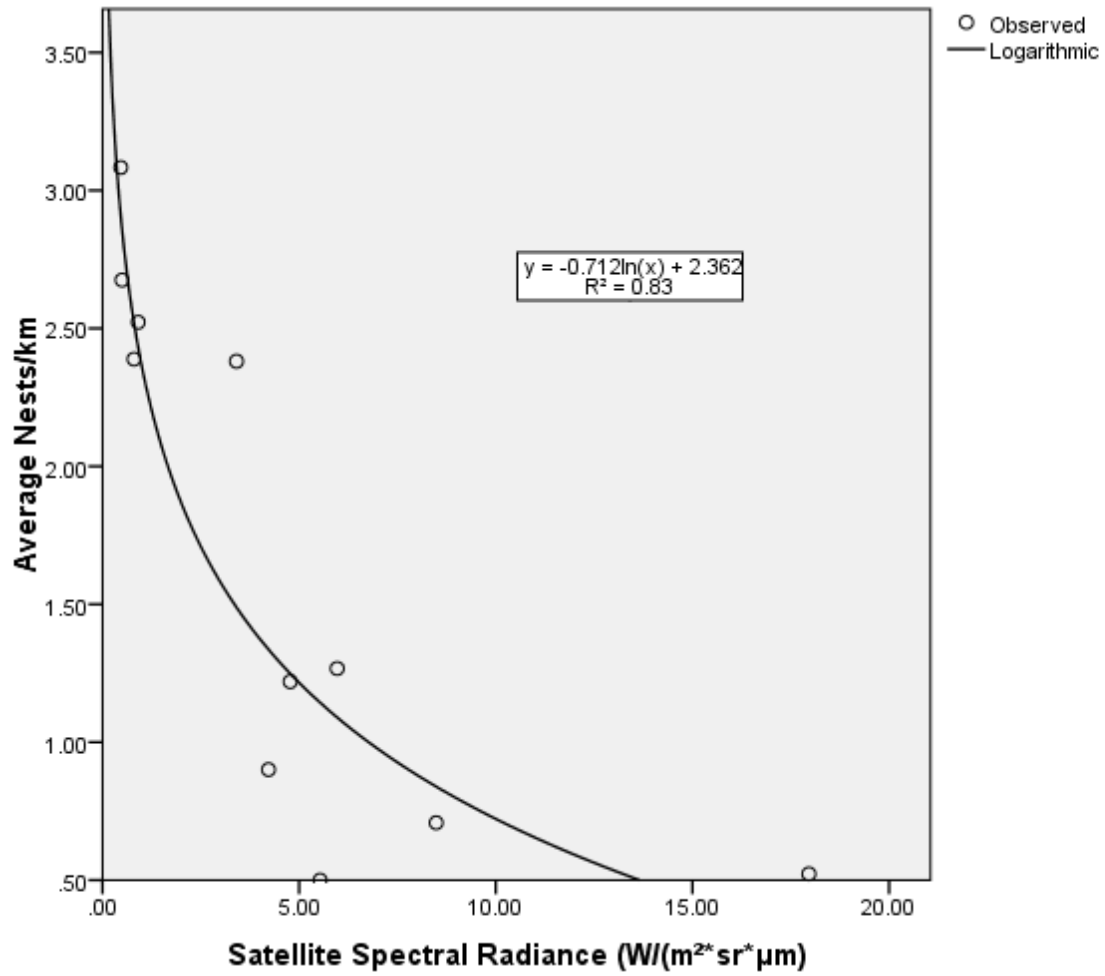


Figure 8: Average number of nests/km for 2009-2014 v. satellite spectral radiance (W/(m²*sr*µm)).

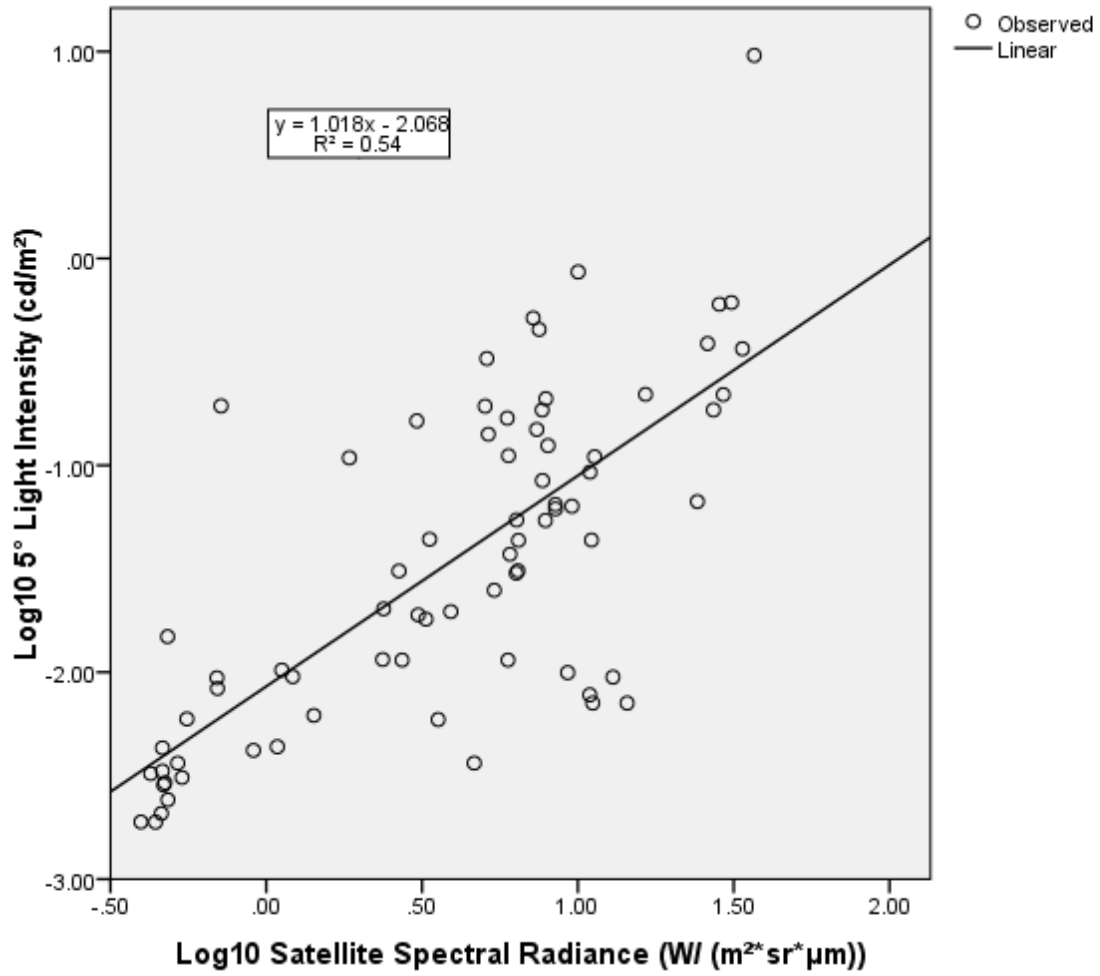
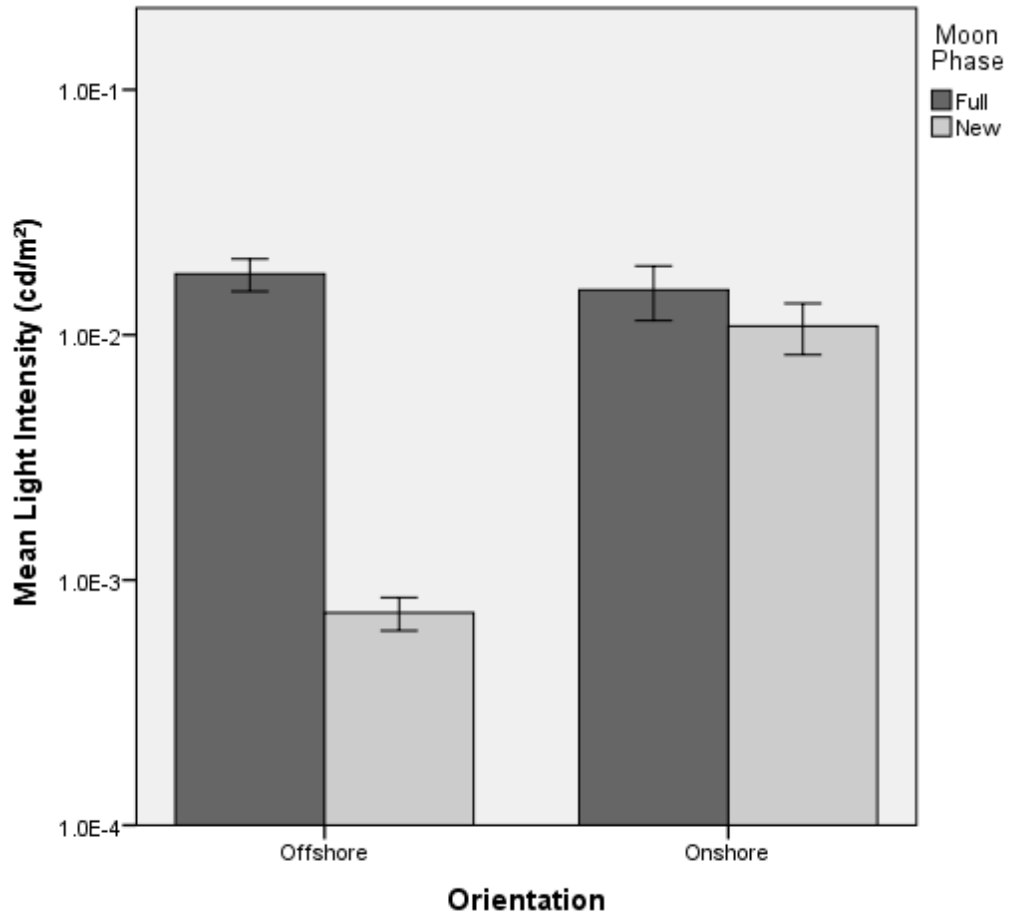


Figure 9: Log10 5° onshore light intensity (cd/m²) v. log10 satellite spectral radiance (W/ (m²*sr*µm)) for 74 Grand Strand sites.



Error Bars: +/- 1 SD

Figure 10: Mean 5° light intensity (cd/m²) for one Pawleys Island site by orientation during a full moon and a new moon. All measurements were taken at the 5° angle of inclination.

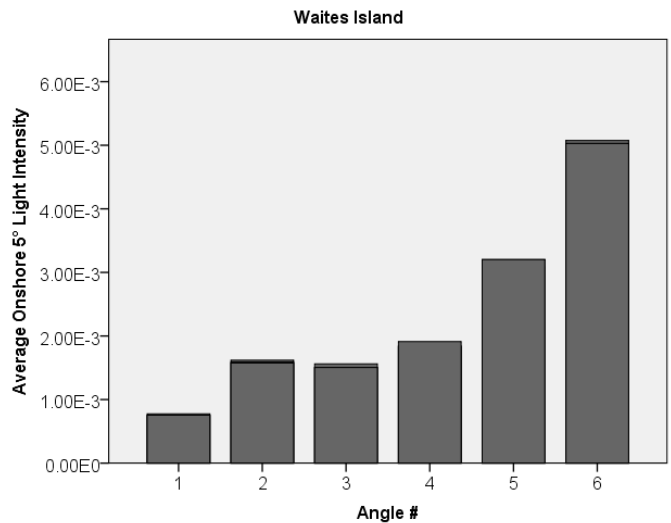
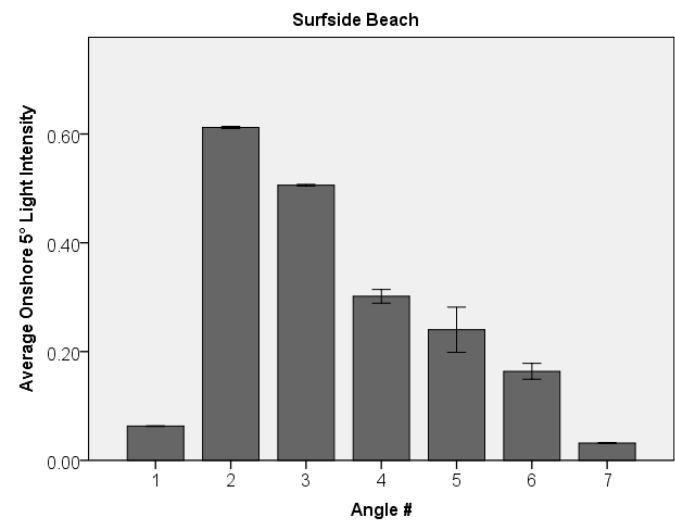
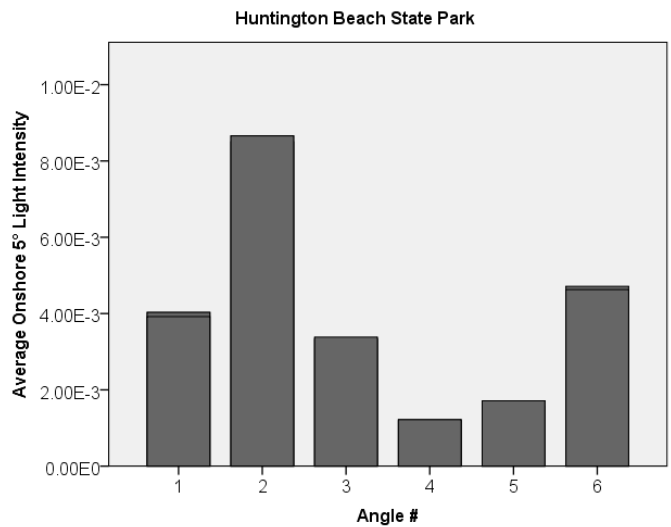
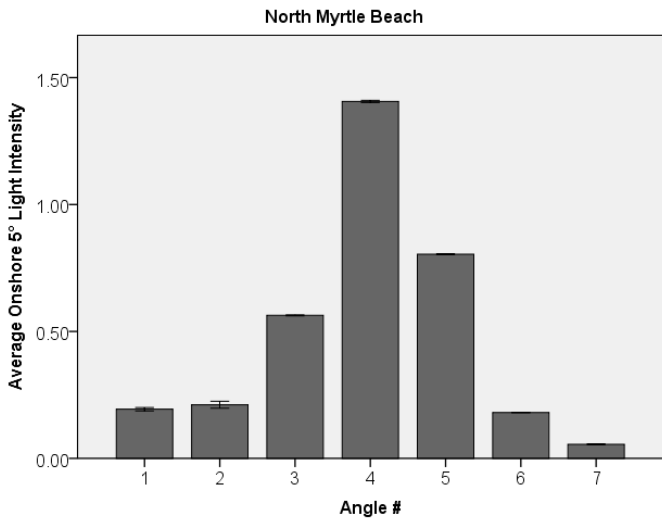
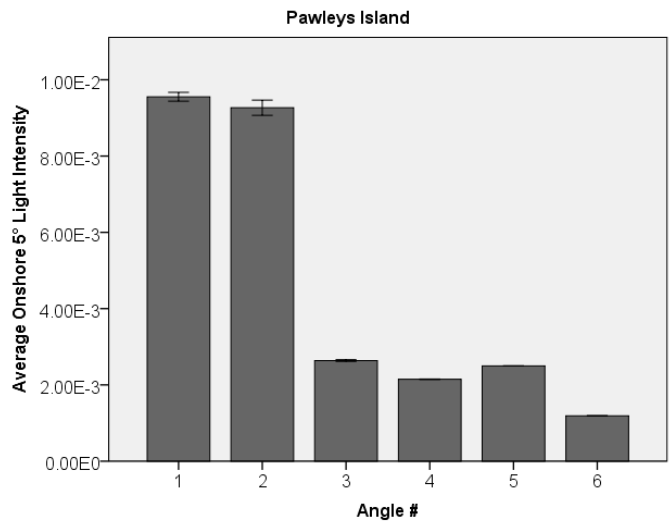
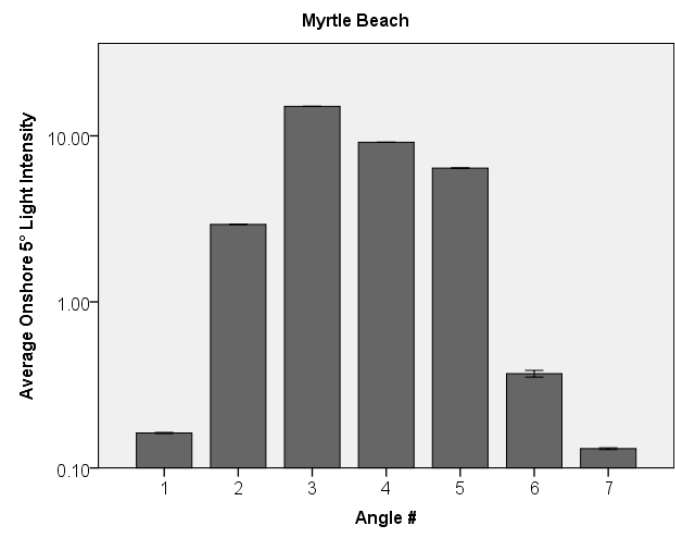


Figure 11: Average onshore light intensity (cd/m^2) at the 5° angle of inclination for all measured onshore angles at six sites. The brightest site at Myrtle Beach, North Myrtle Beach, and Surfside Beach and the darkest site at Pawleys Island, Waites Island, and Huntington Beach State Park

are displayed. Angles 1, 2, 6, and 7 represent peripheral angles, while angles 3, 4, and 5 represent central angles at sites with a total of seven onshore angles. Angles 1, 2, 5, and 6 represent peripheral angles, while angles 3 and 4 represent central angles at sites with a total of six onshore angles. Average 5° onshore light intensity (cd/m^2) is higher for central angles relative to peripheral angles for the developed sites. Error bars represent one standard error.

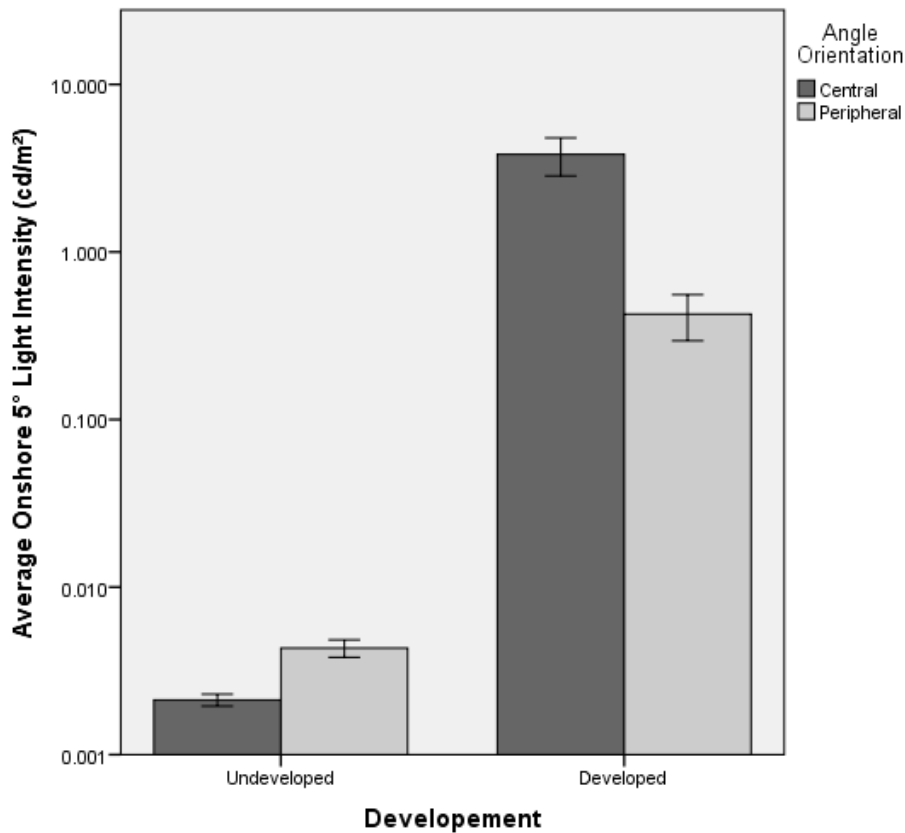


Figure 12: Average 5° onshore light intensity (cd/m^2) at central and peripheral angles for three highly developed sites (Myrtle Beach, North Myrtle Beach, and Surfside Beach) and three undeveloped sites (Pawleys Island, Waites Island, and Huntington Beach State Park). Error bars represent one standard error.

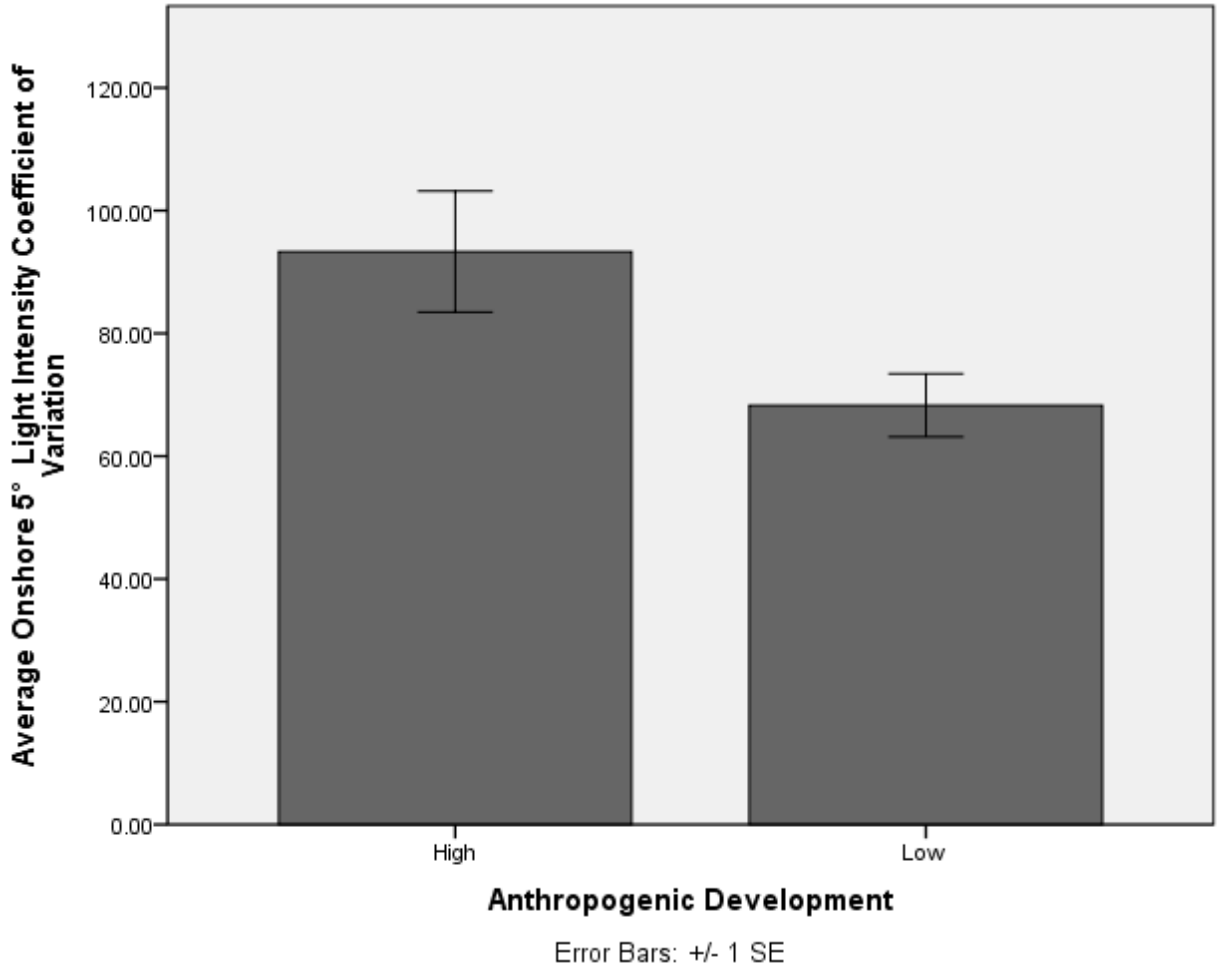


Figure 13: Average 5° onshore light intensity (cd/m^2) coefficient of variation for three highly developed sites (Myrtle Beach, North Myrtle Beach, and Surfside Beach) and three undeveloped sites (Pawleys Island, Waites Island, and Huntington Beach State Park). Error bars represent one standard error.