Orientation of Leatherback Turtle Hatchlings, *Dermochelys coriacea* (Vandelli, 1961), at Sandy Point National Wildlife Refuge, US Virgin Islands

by

Violeta Villanueva Mayor

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Approved by:

_____   _____
Juan G. González Lagoa, Ph.D.   Date
Member, Graduate Committee

_____   _____
Allen R. Lewis, Ph.D.   Date
Member, Graduate Committee

_____   _____
Mónica Alfaro, Ph.D.   Date
Chairman, Graduate Committee

_____   _____
Dallas E. Alston, Ph.D.   Date
Representative of Graduate Studies

_____   _____
Carmen T. Porrata, M.S.   Date
Acting Director of the Department

_____   _____
L. Antonio Estévez, Ph.D.   Date
Director of Graduate Studies

Abstract

Leatherback hatchling orientation was assessed for the first time at Sandy Point National Wildlife Refuge (SPNWR), US Virgin Islands. The median angle and range of tracks, moon condition, and date were recorded shortly after hatchling emergences. Experiments recording individual crawl-directions were also conducted during no moon and full moon conditions. Data were analyzed using circular statistical procedures with a significance level of 0.05. When the moon was not visible, hatchling dispersion was significantly wider throughout the entire beach. Furthermore, where lights were directly visible, hatchlings significantly deviated from a straight path to the sea toward those lights. Consequently, hatchlings were exposed to additional predation and used up energy needed for their offshore migrations. The critical times for orientation disruption were given for a lunar month and critical areas for hatchling management were identified. A comprehensive light-management strategy was recommended.

Key words: Artificial lighting, *Dermochelys coriacea*, leatherback hatchlings, orientation disruption, sea turtles, US Virgin Islands

Resumen

La orientación de las crías de laúd se valoró por primera vez en el Refugio Nacional de Vida Silvestre de Sandy Point (RNVSSP), Islas Vírgenes de Estados Unidos. La mediana y el rango de las huellas, las condiciones de la luna y la fecha se registraron poco después de las emergencias. También se realizaron experimentos registrando la dirección de las crías durante condiciones de luna llena y sin luna. Los datos se analizaron usando procedimientos estadísticos para datos circulares con un nivel de significancia de 0.05. Cuando no había luna la dispersión de las crías fue significativamente más amplia en toda la playa. Además, cuando las luces artificiales fueron visibles directamente, las crías se desviaron del camino directo al mar en dirección a esas luces. Como consecuencia, las crías estuvieron más expuestas a la depredación y consumieron energía necesaria para la migración hacia aguas profundas. Se proporcionaron las horas críticas de desorientación para el mes lunar y se identificaron las áreas críticas para el manejo de crías. Se recomendó un plan completo para el manejo de las luces.
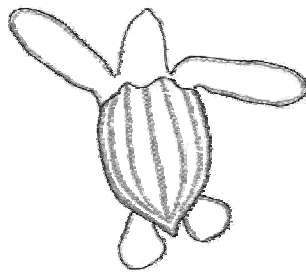
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Violeta Villanueva Mayor
November 2002.

"Aunque tengo mil arrugas,
como todas las tortugas,
soy buscada, soy amada,
pero no me gusta nada.
Pues me quieren para sopa,
para bolsos, cinturones
y también para jabones.
Cada día somos menos,
en los mares ya no abundo.
Algún día no quedarán
mas tortugas en el mundo..."

"Nota de una tortuga", Anónimo

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Introduction

The endangered leatherback sea turtle, *Dermochelys coriacea* (Vandelli, 1761), is a migratory pelagic reptile that lays its eggs on tropical and subtropical beaches. Clutches contain on average 80 yolked eggs (Boulon et al., 1996) that are buried in the sand at a depth of about 75 cm. The eggs hatch approximately two months later, and the hatchlings dig up out of the nest column by social facilitation among siblings (Carr and Hirth, 1961). The drop of sand temperature experienced at dusk stimulates the mostly nocturnal emergence of hatchlings (Miller, 1997; Mrosovsky, 1968; Witherington et al., 1990). The hatchlings may emerge in stages, the first wave being the largest of approximately 20 to 70 hatchlings (Witherington, 1986). The emergence is followed by a period of high activity, called the "hatchling frenzy", at which the hatchlings crawl seaward and swim out to the open sea (Lohmann et al., 1997).

Emerging hatchlings primarily use visual cues to orient themselves toward the sea, termed "sea finding". Hatchlings tend to follow the brightest direction within species-specific horizontal and vertical angles of acceptance (Salmon and Wyneken, 1990; Verheijen and Wildschut, 1973). Light closest to the horizon plays the greatest role in determining orientation direction (Salmon et al., 1992). Many nesting beaches have a relatively simple topography with an open stretch of sand backed by trees and vegetation. This gives a brightness difference between the open seaward horizon and the darker tree line and landmass (Mrosovsky, 1970). In

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addition, water reflects more moonlight and starlight than land (Lohmann and Lohmann, 1996), enabling hatchlings to find the sea when it cannot initially be seen (Mrosovsky, 1970).

Under natural conditions, hatchlings crawl directly from the nest to the sea. However, the sea-finding behavior is usually disrupted if artificial light sources can be seen from the nesting beach (Mann, 1978; Witherington and Martin, 1996). Artificial lighting alters natural conditions by creating a beach environment in which one direction is much brighter than all others, usually toward the land (Lohmann et al., 1997). For sea turtles, this light pollution is best described as misinformation. Any deviation of hatchlings from their shortest path to the sea increases their vulnerability to dehydration, exhaustion, and predation (Mann, 1978; McFarlane, 1963; Philibosian, 1976; Van Rhijn, 1979).

The nesting grounds under United States jurisdiction that support the largest population of leatherback turtles are located within the Sandy Point National Wildlife Refuge (SPNWR), St. Croix, US Virgin Islands. The refuge's nesting beaches are protected from development; however, lights from the adjacent town, Frederiksted, may be affecting hatchlings during their seaward crawls. For management purposes it is vital to document hatchling orientation and identify critical areas for management, so actions can be taken to maximize hatchling recruitment into the population.

The purpose of this investigation was to assess for the first time the seaward orientation of hatchling leatherback turtles at SPNWR. The specific objectives were:

1)   To describe the nocturnal orientation of emerging leatherback hatchlings at SPNWR.

2)   To compare the orientation of hatchlings under "full moon" and "no moon" conditions by means of orientation experiments.

3)   To identify critical areas for management at SPNWR based on orientation disruption, hatching success, and number of adult landings.

4)   To recommend hatchling management-strategies for SPNWR.

Literature Review

Sea-finding mechanisms

Since the early 1960's, considerable progress has been made in characterizing the mechanisms that guide turtle hatchlings from their nests to the sea. The most detailed descriptions of this sea-finding behavior have come from observations on loggerhead (*Caretta caretta* Linnaeus, 1758) and green (*Chelonia mydas* Linnaeus, 1758) turtles.

Hatchlings emerge *en masse* from the nest (Carr and Hirth, 1961; Witherington et al., 1990) and immediately crawl seaward. Among the features that may influence the sea-finding behavior are visual cues, beach slope, sound, and vibration (Mrosovsky and Kingsmill, 1985; Salmon et al., 1992; Van Rhijn, 1979). However, experiments have demonstrated that hatchlings, including leatherbacks, primarily use visual cues, which include light intensity, wavelength, and objects or their silhouettes (McFarlane, 1963; Mrosovsky and Carr, 1967; Mrosovsky and Shettleworth, 1974, 1975).

In absence of any visible light, loggerhead and green turtle hatchlings oriented themselves down slope in experimental arenas. However, when exposed to illumination, the visual cues used by loggerheads and greens weakened or even superseded slope cues during sea finding (Salmon et al., 1992). Green turtle hatchlings released on a beach with their eyes covered crawled in circles or random

directions, unable to orient themselves accurately (Mrosovsky and Shettleworth, 1968, 1975).

Under natural light conditions hatchlings accurately find the sea. Studies suggested that they find the shortest path by crawling toward the brighter open horizon, which is often in the direction of the sea (Mrosovsky and Carr, 1967; Mrosovsky and Shettleworth, 1968). Objects such as bushes, dunes, and trees elevate the horizon and darken the view landward (Van Rhijn, 1979).

In laboratory experiments green turtle and loggerhead hatchlings were tested in a circular arena in which one side had a low, dimly illuminated horizon and the other a higher, brighter horizon. The turtles consistently moved toward the lower, dimmer light (Salmon et al., 1992). Thus, orientation appears to depend on both the brightness of the light and its elevation. Turtles moved seaward by crawling toward the lowest illuminated horizon and only chose the brightest light when the horizon elevation was similar in all directions (Salmon et al., 1992). The orientation of green turtle and leatherback hatchlings is usually poor when crawling from nests surrounded by vegetation. They move more slowly with no significant orientation (Godfrey and Barreto, 1995).

The assessment of brightest direction depends on the visual angle of acceptance of hatchlings, which varies among species. The horizontal angle of acceptance was found to be approximately 180° for three species: loggerhead, olive ridley *(Lepidochelys olivacea* Eschscholtz, 1829), and green turtle. The vertical

angle was between 10° below and 30° above the horizon for loggerheads and just "a few degrees" for greens and olive ridleys (Salmon and Wyneken, 1990; Verheijen and Wildschut, 1973). This means that light closest to the horizon plays the greatest role in determining orientation direction. Thus, high sources of light, such as occasionally the moon and the sun, have relatively little effect on orientation (Salmon and Wyneken, 1990; Verheijen and Wildschut, 1973).

Some controversy exists as to whether the rising or setting sun or moon affects sea finding in hatchlings. Van Rhijn (1979) reported that the sun on the horizon affected loggerhead, green, and hawksbill (*Eretmochelys imbricata* Linnaeus, 1766) turtles insignificantly. On the other hand, Mrosovsky (1970) reported that green and hawksbill turtles reacted to the position of the sun by deviating from the shortest path to the water.

Light preference and behavioral responses to specific wavelengths differed among four species tested. Green, hawksbill, and olive ridley sea turtles were attracted to light in the near ultraviolet to yellow region of the spectrum (360 to 600 nm), but were indifferent to light in the yellow-orange to red region (630 to 700 nm). In contrast, loggerheads showed an aversion to light in the green-yellow to yellow region of the spectrum (560 to 600 nm) (Dickerson and Nelson, 1988; Mrosovsky and Carr, 1967; Witherington and Bjorndal, 1991).

Leatherback sea turtles have the peculiarity to occasionally make small and quickly executed circles during their seaward course, named 'orientation circles'

(Carr and Ogren, 1959). Mrosovsky and Shettleworth (1975) suggested that orientation circles depend on slight differences in the sea-finding mechanisms of leatherbacks when compared to other sea turtles. Such differences were found in fields of view, sensitivity to changes in illumination, after-effects of visual stimulation, and influence of speed of movement (Mrosovsky and Shettleworth, 1975).

Orientation and artificial lighting

Artificial lighting visible from a nesting beach can easily disrupt sea-finding behavior, causing "misorientation" (locomotion on a straight path, but in a direction other than toward the sea) or "disorientation" (hatchlings lacking directed orientation) (Salmon and Witherington, 1995). Artificial light fields with high directivity often elicit "light-trapping" responses in animals, an abnormal behavior occurring when an orienting nocturnal animal approaches an artificial light source and becomes blinded to all else (Verheijen, 1958).

Artificial lighting does not necessarily have blinding characteristics when perceived from a distance. For instance, hatchlings beneath an artificial light source circle as if blinded, but hatchlings at a few meters from the source often crawl directly toward it. On occasion hatchlings may crawl for hundreds of meters toward distant lighting. Thus, to hatchlings on a dark beach, an artificial light source or its radiation may become a supernormal stimulus that ambiguously indicates the seaward direction. At such high levels of stimulation, hatchlings may ignore shape

cues and other features of the beach, or perhaps not even perceive them (Lohmann et al., 1997).

Generally, artificial lighting and its radiation increase the time hatchlings spend on the beach, allowing higher mortality due to overexposure to predators, dehydration, exhaustion, and other causes (Mann, 1978; McFarlane, 1963; Philibosian, 1976; Van Rhijn, 1979). At SPNWR, the most common predators are yellow-crowned night-herons (*Nyctanassa violacea*), ghost crabs (*Ocypode quadrata*), mongooses (*Herpestes aropunctatus*), and feral dogs (*Canis domesticus*) (McDonald-Dutton et al., 2000).

The light of the moon has an apparent effect on the degree of sea-finding disruption caused by artificial lighting. Experiments on urbanized beaches in Florida and northern Cyprus demonstrated that fluctuations in background illumination from the moon, and not an attraction to the moon itself, restored normal sea-finding orientation in loggerhead and green turtles (Irwin et al., 1998; Salmon and Witherington, 1995). Moonlit nights have high levels of ambient light that reduce the attraction to artificial light sources (Salmon and Witherington, 1995). Furthermore, results suggested that there is a reciprocal relationship between the "strength" of the trapping light source and the magnitude of background lighting required to negate it (Salmon and Witherington, 1995). However, at some beach sites, even full-moon illumination may be insufficient to counter the effects of strong artificial lighting (Salmon and Witherington, 1995).

Methods

Study site

Research was conducted at Sandy Point National Wildlife Refuge (SPNWR), located in the southwestern corner of St. Croix, US Virgin Islands (17° 41' N, 64° 54' W). Sandy Point supports the largest nesting population of leatherbacks under US jurisdiction (Eckert, 1987). Sandy point was designated as Critical Habitat in 1978 under the auspices of the Federal Endangered Species Act and was acquired as a National Wildlife Refuge in 1984 by the US Fish and Wildlife Service. The primary goals have been to protect and enhance the population of leatherback turtles.

The refuge's 5 km shoreline is demarcated with numbered stakes every 20 m. Habitat suitable for nesting leatherbacks extends approximately 2.8 km and is delimited by near shore reef and rock on the north shore, and a gradual diminution of sandy beach to the south.

The nesting beach patrolled was divided into three sectors: sector I facing southeast (stake numbers 65 to 139), sector II southwest (140 to 174), and sector III northwest (175 to 205). The adjacent town Frederiksted and its suburbs are located northeast of the refuge (Fig. 1). Facing seaward, its lights are directly visible to the left at sector I and to the right at sector III. At sector II the city lights are only indirectly visible as reflection above the vegetation.
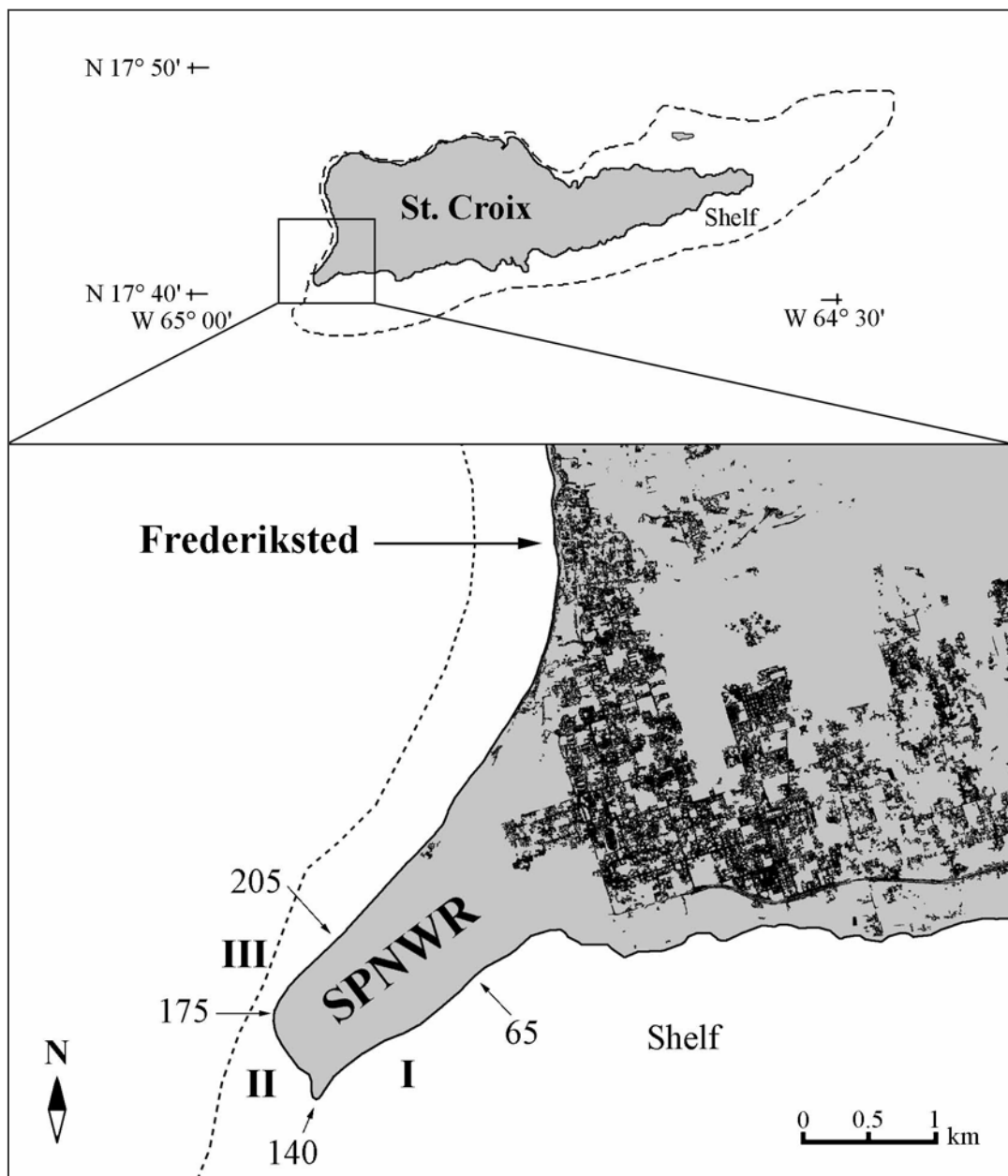
Figure 1. Study area at Sandy Point National Wildlife Refuge (SPNWR), located in the southwestern corner of St. Croix, US Virgin Islands. The beach was divided into three sectors: sector I (stake numbers 65 – 139), sector II (140 – 174), and sector III (175 – 205). Dark areas indicate urban development and gray areas land.

The eastern area (sector I), known as the windward side, has a narrow backshore that is partly covered with wave-deposited sea grasses and gorgonians. The western area (sectors II and III), also known as the leeward side, has a relatively wide and sandy backshore. The shelf edge lies within several kilometers from the windward side and within a few hundred meters from the leeward side. The sand is mostly biogenic, consisting of marine organic derived material.

Annual erosion and buildup cycles are unpredictable in all sectors. However, during the leatherback nesting-season, erosion primarily occurs between markers 123 to 164 and accretion between 165 to 180 (Eckert, 1987). At Sandy Point these cycles could result in annual nest losses of 45 to 65 % (Eckert, 1987). Thus, diring the past 20 years, researchers and conservationists have relocated clutches prone to erosion to sectors I and III (Dutton, pers. com.). All other nests have been left *in situ*.

The number of leatherbacks nesting at SPNWR has significantly increased from an average of 36 adults per season (range = 18 – 55) during the first 15 years to an average of 111 adults per season (range = 42 – 186) in the last 6 years (Boulon et al. 1996; McDonald-Dutton et al., 2000, 2001, Alexander, pers. com.) (Fig. 2). Nests were laid primarily in sectors II and III, however due to the relocation efforts, most nests incubated in sector III.
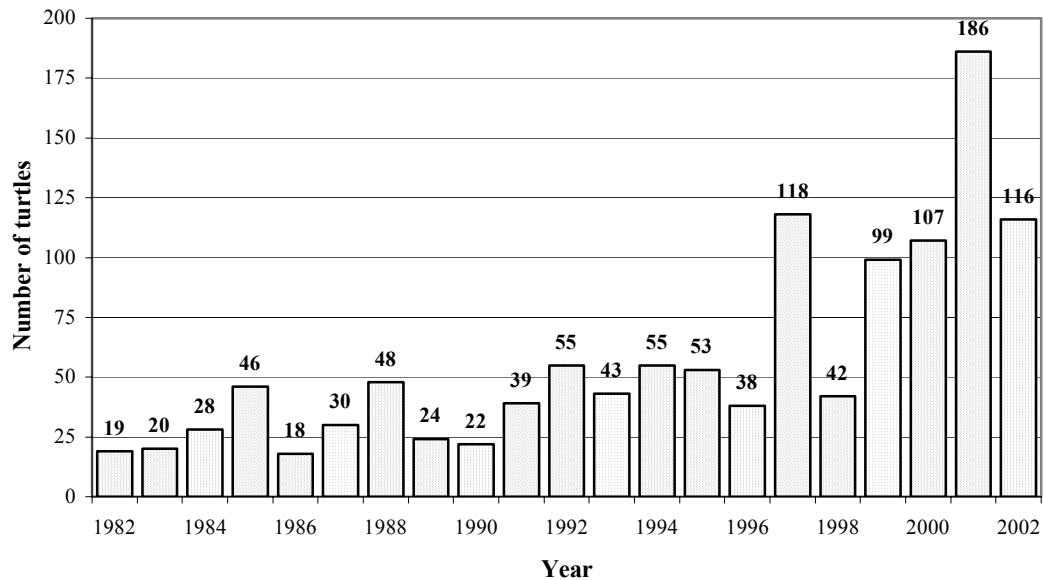
Figure 2. Annual number of female leatherbacks nesting at Sandy Point National Wildlife Refuge from 1982 to 2002.

The beach vegetation primarily consists of low shrubs and small trees represented by sea grape (*Coccoloba uvifera*), wild tamarind (*Leucaena leucocephala*), casha (*Acacia tortuosa*), and manchineel (*Hippomane mancinella*). The vegetation is dense and at night it appears as an unbroken silhouette when viewed from the sea.

Data collection

Hourly beach patrols were conducted from stake 65 to 205 from 20:00 to 04:00 hours every night during the months of April to August 2001. The location of each leatherback landing was recorded and nest locations were triangulated from the two nearest stakes. Hatchlings emerged after an average incubation time of 63.8 days (McDonald-Dutton et al., 2001).

Shortly after the emergence of a randomly selected nest, a circular arena (4 m in diameter) centered on the nest was drawn into the sand and the following data collected:

1)   Median angle: bearing from the nest to the center of the densest cluster of tracks, dividing the tracks into two equal-sized groups. The bearing was defined as the clockwise angle (0 to 359º) starting in the direction facing opposite to the shortest path to the sea (Fig. 3a). Thus, hatchlings crawling toward the sea had a bearing of 180°.

2)   Track range: angle (1 to 360º) defined as the smallest portion of the circle's circumference that contains all tracks crossing the arena's boundary (Fig. 3b).

3)   Date, time, and nest location: triangulation from the nearest two stakes.

4)   Moon condition (not visible, quarter, half, three quarters, or full moon) and artificial lights and their direction when facing the sea (not visible, visible to the left, or visible to the right).

At beach areas where few or no nests were located, the following "median/range" experiment was conducted under "moon not visible" and "full-moon" conditions. Hatchlings were collected at the beginning of the emergence period and transported in a dark plastic box to a selected site above the high tide line. Twenty hatchlings were placed into a 5 cm deep depression located in the center of a cleared circular arena drawn into the sand, 4 m in diameter. After all

turtles had crossed the boundary the above data were collected. Those that failed to locomote within five minutes were excluded from analysis. Hatchlings were used once and released at a suitable site shortly after the experiment.
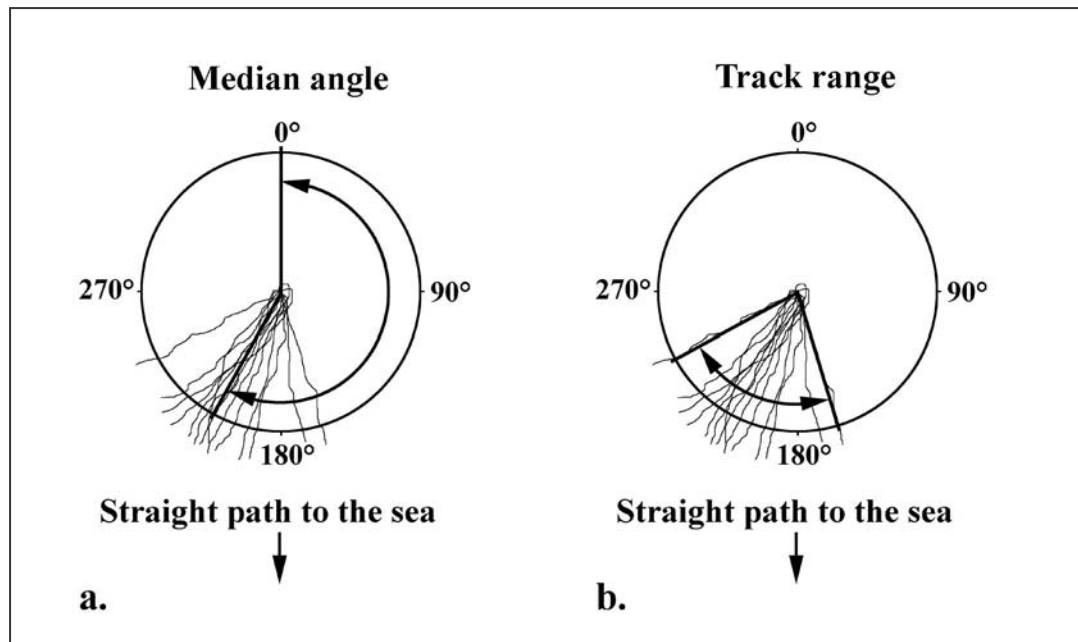
Figure 3. Median angle (a) and track range (b) for *in situ* nest emergences and "median/range" experiments.

Additional orientation experiments, called "mean/dispersion" experiments, were conducted under "no moon" and "full moon" conditions during the nesting seasons 2001 and 2002. Hatchlings were collected at the beginning of the emergence period and transported in a dark plastic box to a selected site at sectors II and III. Twenty hatchlings were released in groups of five at the center of a cleared circular arena drawn into the sand, 4 m in diameter. The arena was divided into 32 intervals of 11.25°, with 0° toward the vegetation. The intervals were

demarcated by wooden stakes and numbered clockwise (Fig. 4). The intervals at which hatchlings left the arena were recorded and the tracks erased. Hatchlings that failed to locomote within five minutes were excluded from analysis. At the end of the experiment the data were summarized in a frequency table. All hatchlings were used once and released at a suitable site shortly after.
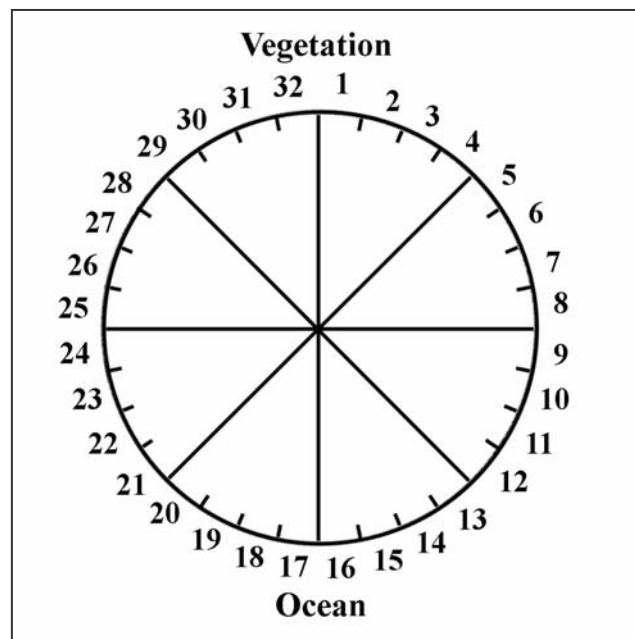
Figure 4. Arena-setup of "mean/dispersion" experiments. The circle measured 4 m in diameter and each interval had an angle of 11.25°.

Random *in situ* nests were excavated and the content categorized to determine percent hatching success, defined as number of hatched shells divided by number of yolked eggs.

Global Positioning System (GPS) readings were taken from each stake and at 10 m increments along the vegetation and high water line. GPS readings were

downloaded to an IBM compatible laptop computer using TOPO!GPS (National

Geographic Holdings, Inc.) and then imported to ArcView GIS 3.2a

(Environmental Systems Research Institute, Inc.). Ambient light readings were

taken using a Cal-Light 400 precision lightmeter (The Cooke Corporation).

Data analysis

Data recorded from emerging hatchlings and from the "median/range"

experiments were used to describe their nocturnal orientation. First, the median

angle and the track range were tested for significant correlation with the moon

phase. Each of the three beach sectors was tested separately since the light

conditions were not comparable (Fig. 1). Based on the date of emergence, the moon

phase was converted into a scale that ranged from 0 to 14 days to the closest full-

moon night (= X) and then into angular directions ranging from 0° to 336° (= a),

where $k = 15$ time units (Equation 1). Emergences that occurred before moon rise

or after moon set were grouped with new-moon data. Nonparametric angular-

angular correlation was used to test for significance (Zar, 1999).

$$a = \frac{(360°)(X)}{(k)} \tag{1}$$

Second, the deviation of the median angle from a straight path to the sea

and the track range were tested for independence from the moon phase. The

deviation from the straight path to the sea was defined as the absolute value

obtained by subtracting 180° from the median angle. The angles of deviation were

grouped into three categories: 0 - 14°, 15 - 29°, and ≥ 30°. The track ranges were

grouped into two categories: 0 - 89° and $\geq$ 90°. The moon phases were grouped into five categories: full, three-quarter, half, quarter, and no moon. The frequencies were summarized in 3 x 5 and 2 x 5 contingency tables, respectively, and tested for independence using chi-square (X^2) statistics (Zar, 1999). The contingency tables were subdivided as necessary to develop additional hypotheses (Zar, 1999). The results were graphed in *mosaic* display (Friendly, 1994), where prominent differences (> 30 %) from the expected frequencies were highlighted.

Third, deviation of the median angle from a straight path to the sea and track range were averaged within 15 stake intervals in sector I and within 5 stake intervals in sectors II and III. Deviation of median angle and track range were grouped into three (0 – 14°, 15 – 29°, and $\geq$ 30°) and two (0 – 89° and $\geq$ 90°) classes, respectively, and then according to the moon conditions (no moon and full moon) plotted on maps using ArcView GIS 3.2a.

Data obtained from the "mean/dispersion" experiments were used to compare the behavior of hatchlings specifically under "no moon" and "full moon" conditions. Standard circular statistical procedures, with a significance level of 0.05, were used to analyze the data (Zar, 1999). First, a group mean-angle ($\bar{a}$), dispersion (r), and the circular standard deviation (CSD) were calculated for each experiment. The value r has no units and ranges from 0 (when there is so much dispersion that a mean angle cannot be described) to 1 (when all the data are

concentrated at the same direction). Then, the Rayleigh's test for circular uniformity was used to check for significant orientation within each experiment.

Second, a 99.9 % confidence interval for each group mean angle ($\bar{a}$) was calculated to test for significant differences from a straight path to the sea. It was necessary to decrease the significance level from 0.05 to 0.001 to compensate for multiple testing-error. A difference was detected when the specified value lay outside the confidence interval.

Third, a second-order mean angle (namely the mean of a set of means) was calculated for the different moon conditions and sectors. A nonparametric one-sample second-order analysis was applied to test for significant orientation. Then, the nonparametric Watson's U^2 two-sample test was used to determine significant differences between mean angles.

Fourth, the Wallraff (1979) procedure of analyzing angular distances was applied to test for differences in dispersion between moon conditions. The angular distances of the two samples were then pooled and ranked for application of a two-tailed Mann-Whitney test.

The hatching success data were tested for significant differences among sectors using the Kruskal-Wallis test for non-parametric analysis of variance (Zar, 1999). A non-parametric multiple comparisons-test for unequal sample sizes and tied data was used to determine between which of the samples significant differences occurred (Zar, 1999). Hatchling success was averaged within 15 stake

intervals in sector I and within 5 stake intervals in sectors II and III. Hatchling

success was grouped into three adequate categories and then plotted on a map using

ArcView GIS 3.2a.

Chi-square statistic was used to test for equal distribution of leatherback

landings along the beach (Zar, 1999). The number of adult leatherback landings for

the 2000 nesting season were summed within 15 stake intervals in sector I and

within 5 stake intervals in sectors II and III, grouped into three adequate categories,

and then plotted on a map using ArcView GIS 3.2a.

Critical areas for hatchling management at SPNWR were defined as areas

with significant hatchling orientation disruption and high hatchling production. The

5 to 15 stake intervals were ranked based on the sum of scores of each of the four

variables 'deviation of the median angle from a straight path to the sea', 'track

range', 'hatching success', and 'number of adult landings' (Table 1). Thus,

intervals with a high sum of scores were classified as critical areas for hatchling

management. Critical areas where then plotted on a map using ArcView GIS 3.2a.

Table 1. Score designation for the different categories within the four variables
used to define critical areas for hatchling management.

	Deviation of the median angle			Track range		Hatching success			Number of adult landings		
Category	0-14°	15-29°	$\geq 30°$	1-89°	$\geq 90°$	low	med	high	low	med	high
Score	0	1	2	0	1	0	1	2	0	1	2

Results

During the 2001 nesting season, 1008 nests were recorded at SPNWR. Nesting activities started on March 11 and ended on August 4. Peak nesting period was from May 6 to 26. Hatchling emergences peaked in July. Median angle, track range, and moon conditions were recorded at 197 hatchling emergences and 37 "median/range" experiments. A total of 480 hatchlings were released during 24 "mean/dispersion" experiments.

Median angle and moon phase were significantly correlated at sectors II ($r_{(aa)s}$ = 0.057; n = 55; 0.02 < P < 0.05) and III ($r_{(aa)s}$ = 0.042; n = 135; P < 0.01) (Fig. 5). Track range and moon phase were significantly correlated at sector III ($r_{(aa)s}$ = 0.023; n = 135; 0.02 < P < 0.05) (Fig. 6).

Deviation of the median angle from a straight path to the sea was dependent of the moon phase in sectors I (X^2 = 24.712, df = 8, 0.001 < P < 0.005) and III (X^2 = 43.085, df = 8, P < 0.001). Track range was dependent of the moon phase in sector III (X^2 = 11.134, df = 4, 0.025 < P < 0.05) (Appendix I). Subdividing the contingency tables revealed that median angle and track range were independent of some moon phases, which allowed for pooling of the data (Figs. 7 and 8).

The deviation of the median angle and the track-range maps showed that the greatest orientation disruption occurred during no moon conditions, especially in areas where lights were directly visible (Figs. 9 to 12).
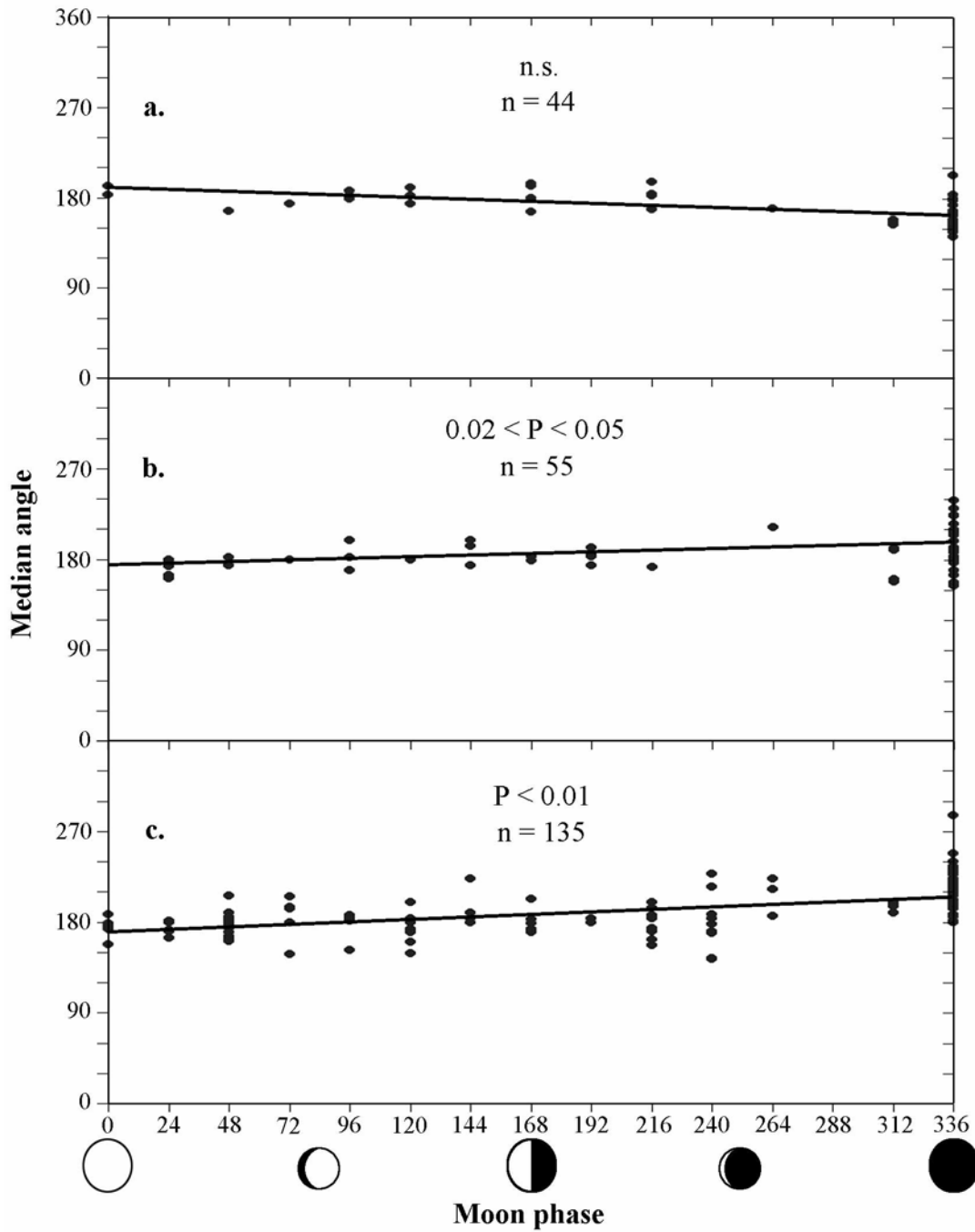
Figure 5. Nonparametric angular-angular correlations between median angle and moon phase at sectors I (a), II (b), and III (c). The white and black circles represent full and new moon, respectively.
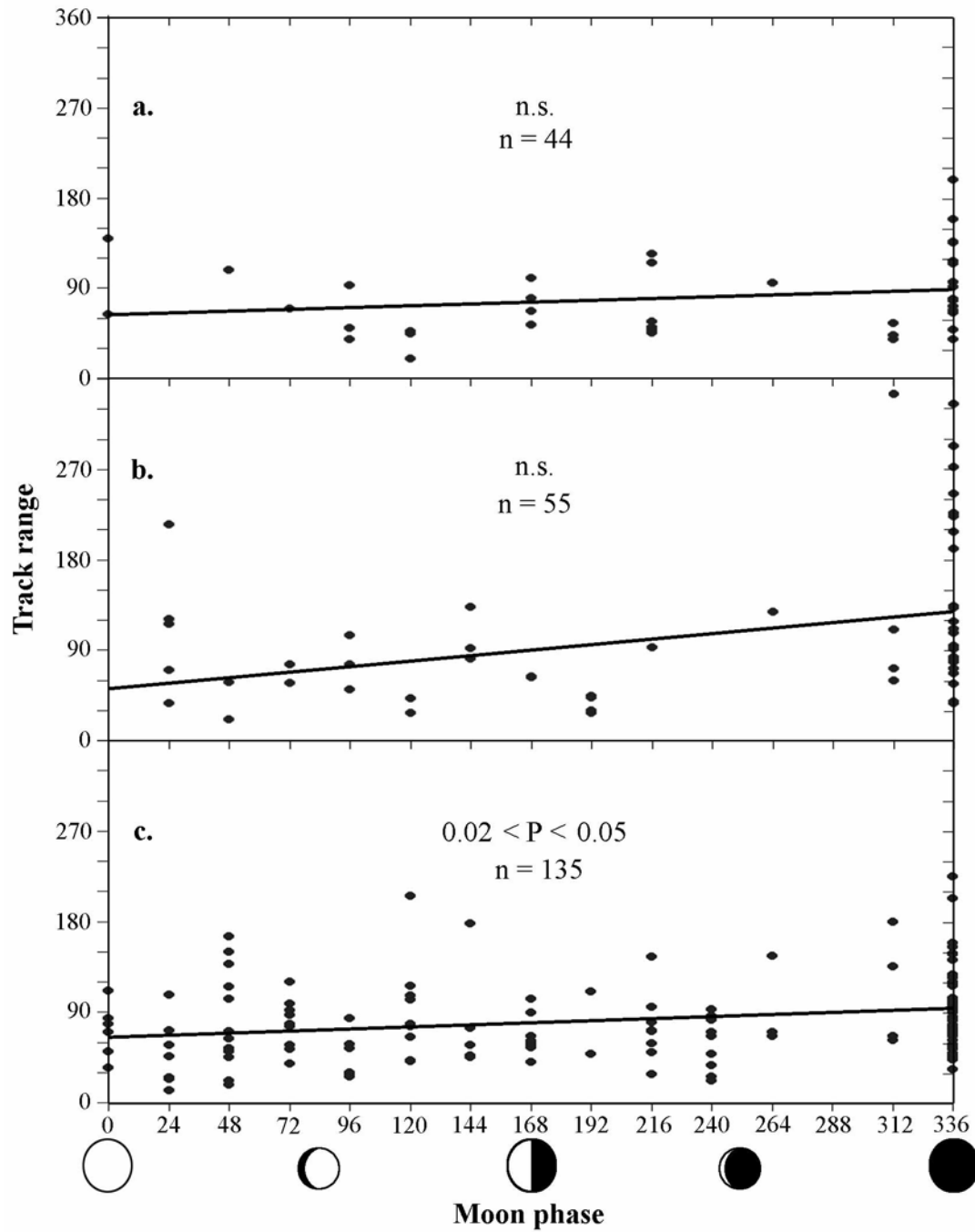
Figure 6. Nonparametric angular-angular correlations between track range and moon phase at sectors I (a), II (b), and III (c). The white and black circles represent full and new moon, respectively.
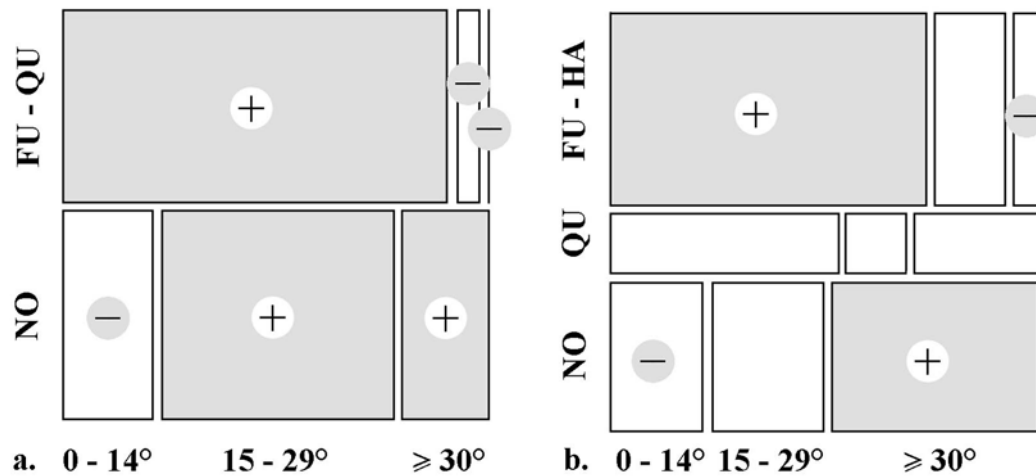
Figure 7. Mosaic display of the contingency tables for median angle and moon phase at sectors I (a) and III (b). Differences greater than 30 % from the expected frequencies are highlighted with positive or negative signs. NO indicates no moon conditions. Full moon (FU) through quarter moon (QU) phases and FU through half moon (HA) phases were pooled due to their independence of the median angle.
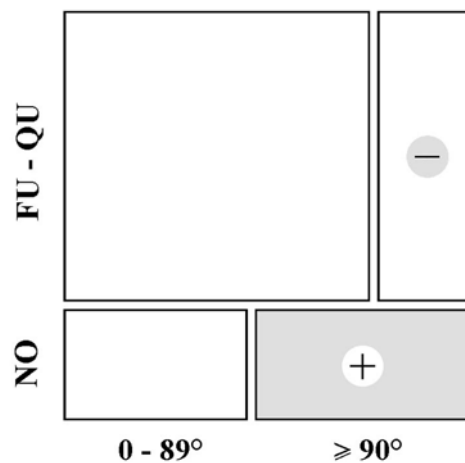
Figure 8. Mosaic display of the contingency table for track range and moon phase at sector III. Differences greater than 30 % from the expected frequencies are highlighted with positive or negative signs. NO indicates no moon conditions. Full moon (FU) through quarter moon (QU) phases were pooled due to their independence of the track range.
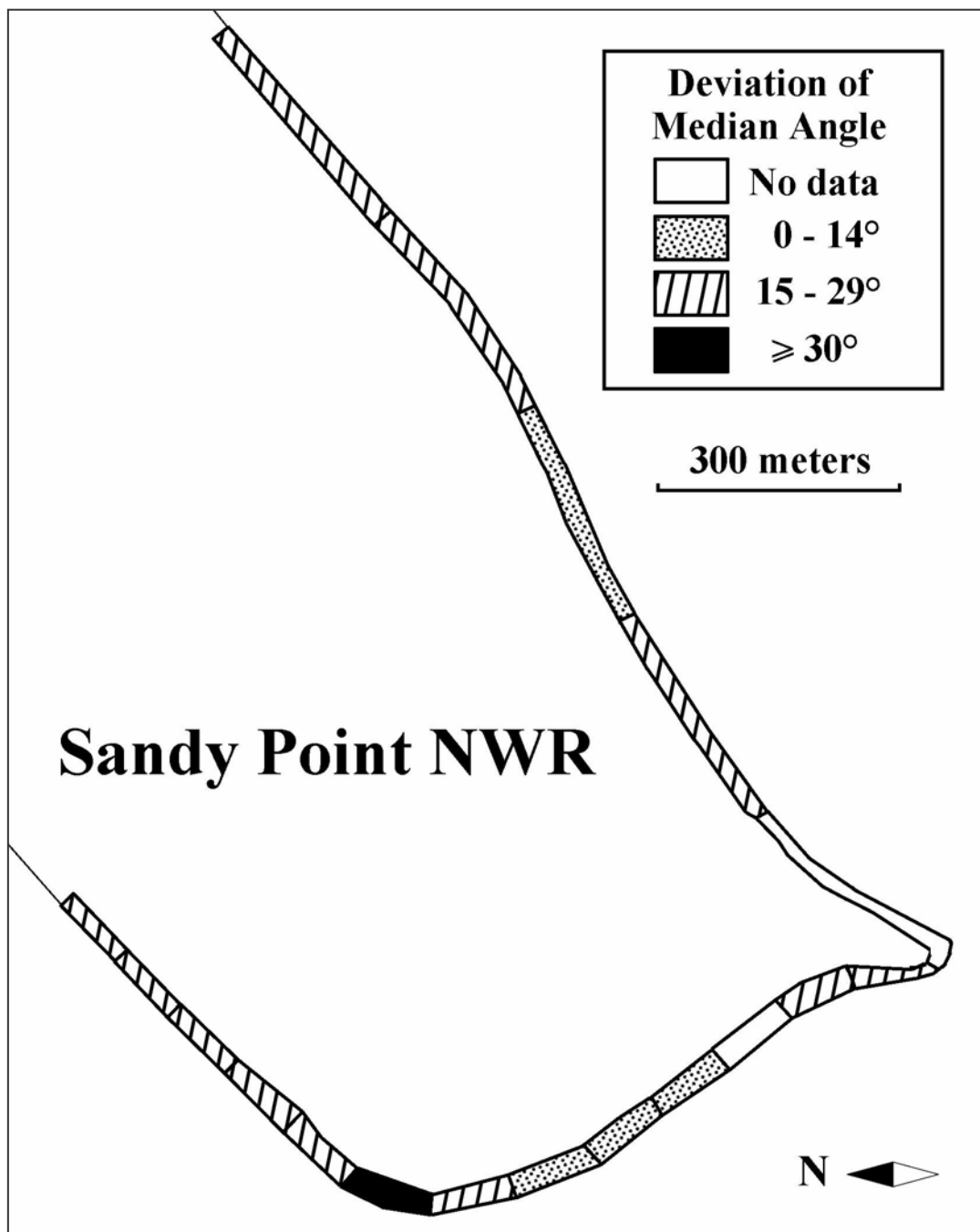
Figure 9. Mean deviation of the median angle from a straight path to the sea within 5 to 15 stake intervals during no moon conditions.
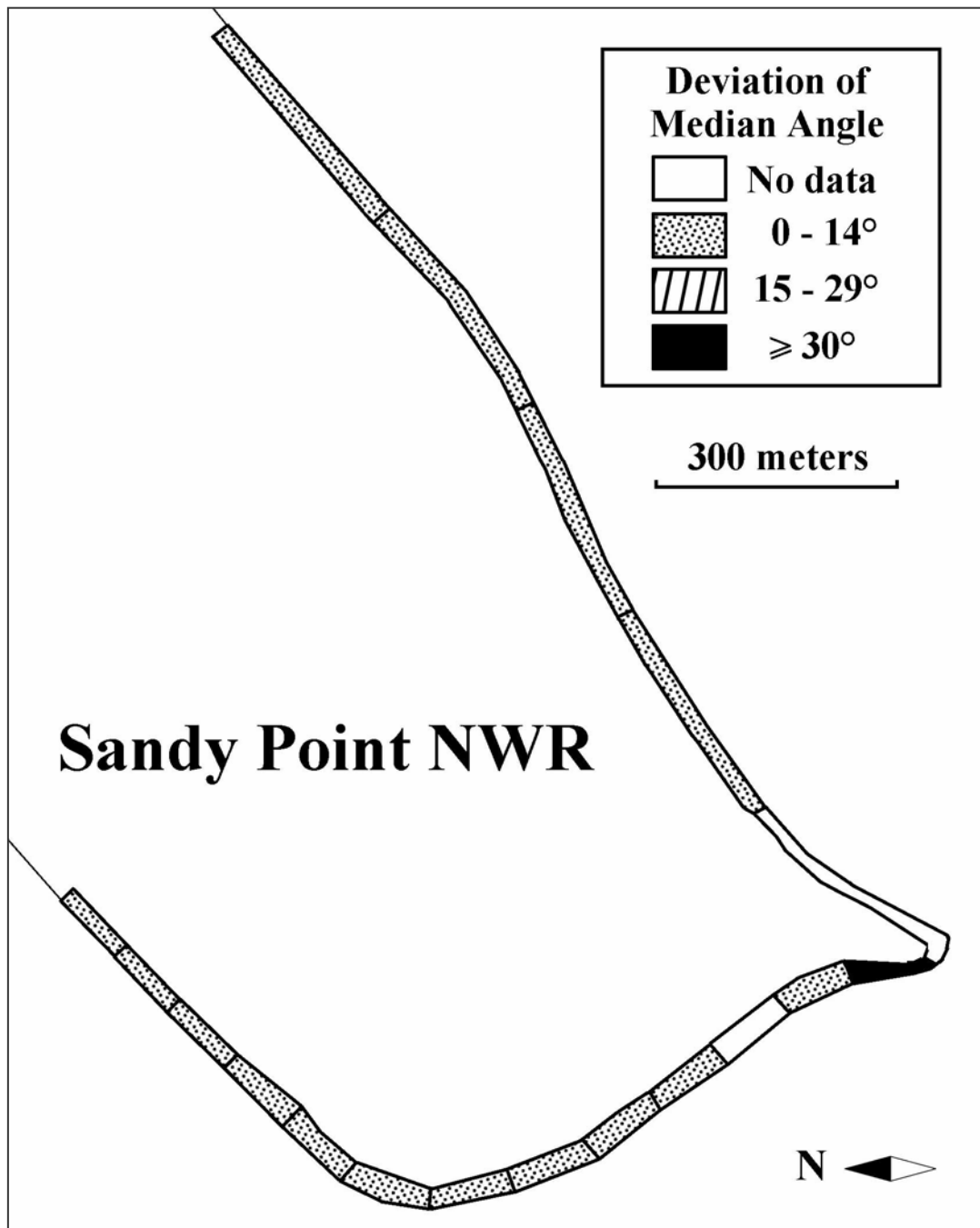
Figure 10. Mean deviation of the median angle from a straight path to the sea within 5 to 15 stake intervals during full moon conditions.
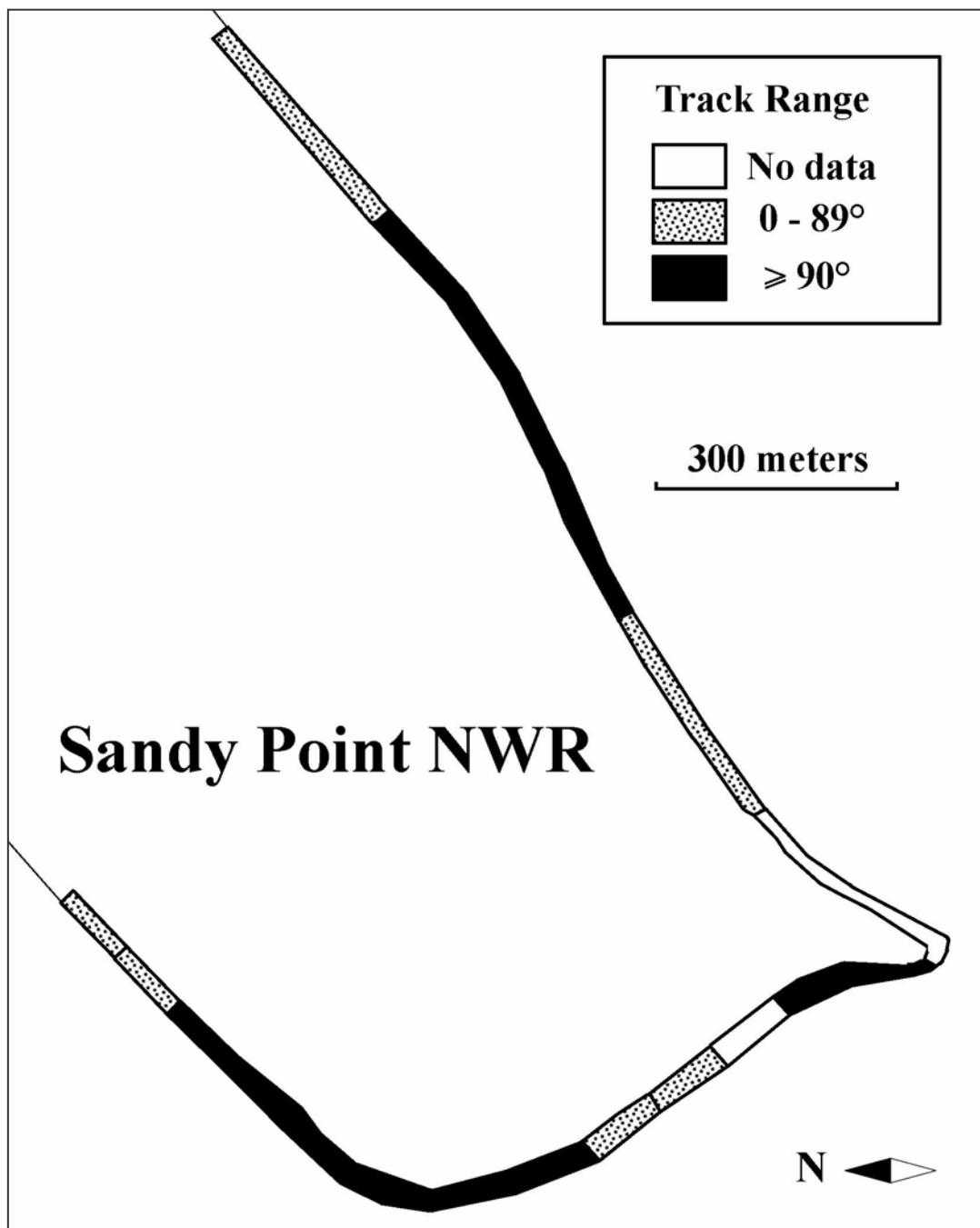
Figure 11. Mean track range within 5 to 15 stake intervals during no moon conditions.
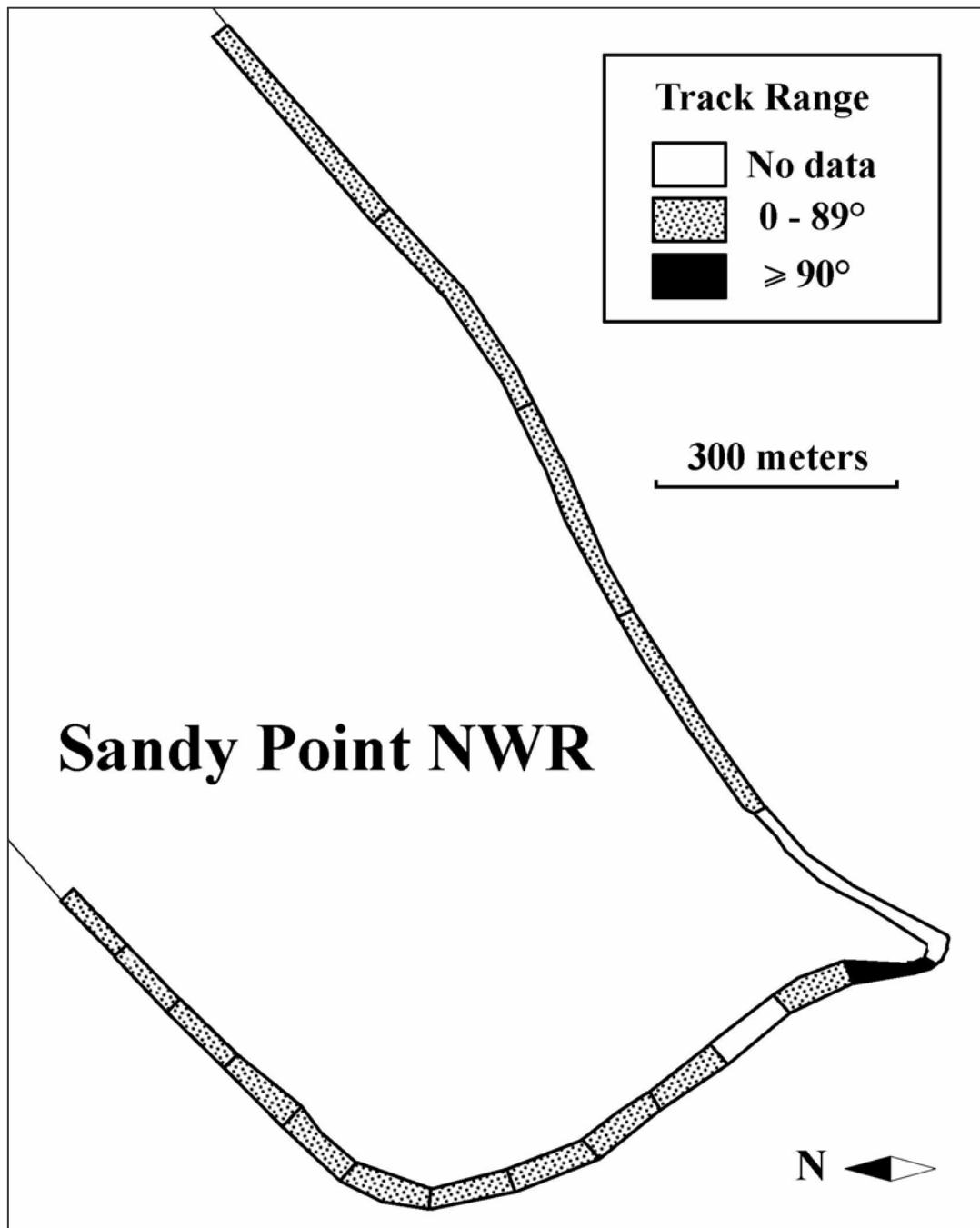
Figure 12. Mean track range within 5 to 15 stake intervals during full moon conditions.

In all "mean/dispersion" experiments hatchlings were significantly oriented ($P < 0.001$). During no-moon conditions at sector III, five out of six group mean angles significantly deviated from a straight path to the sea to the right (Table 2).

Table 2. Group mean angle ($\bar{a}$), dispersion (r), circular standard deviation (CSD), and 99.9 % confidence limits (L_1 = lower limit, L_2 = upper limit) for groups of 20 leatherback hatchlings. Asterisks indicate significant difference from a straight path to the sea.

		Sector II					Sector III					
Moon	Arena	$\bar{a}$	r	CSD	L_1	L_2	Arena	$\bar{a}$	r	CSD	L_1	L_2
No	1	177.7	0.95	18.9	161	194	1	223.8	0.94	20.3	206	242 *
	2	168.4	0.70	48.3	125	212	2	225.5	0.94	20.9	207	244 *
	3	173.0	0.95	19.1	156	190	3	203.3	0.82	36.6	169	237
	4	174.1	0.76	42.9	135	213	4	231.8	0.91	25.4	208	255 *
	5	171.2	0.78	40.2	135	208	5	212.6	0.90	25.8	189	236 *
	6	169.9	0.83	34.5	137	203	6	225.6	0.84	33.7	193	258 *
Full	1	186.7	0.93	21.2	168	206	1	179.4	0.97	14.0	167	192
	2	169.6	0.94	19.7	152	187	2	178.3	0.96	16.1	164	192
	3	186.5	0.92	22.9	166	207	3	175.0	0.99	9.7	167	183
	4	177.1	0.95	18.1	161	193	4	180.8	0.95	18.9	164	198
	5	178.9	0.95	18.7	162	195	5	173.2	0.98	10.6	164	182
	6	175.5	0.94	19.5	158	193	6	180.1	0.95	18.0	164	196

Second-order mean angles were significantly oriented ($P < 0.001$). The second-order mean angles at sector III were significantly different between full and no moon conditions ($U^2 = 0.27$, $n_1 = n_2 = 6$, $P < 0.02$) (Table 3).

Table 3. Second-order group mean angle ($\bar{a}$), dispersion (r), and circular standard deviation (CSD).

	Sector II			Sector III		
Moon	$\bar{a}$	r	CSD	$\bar{a}$	r	CSD
No	172.6	0.83	35.3	220.8	0.87	29.2
Full	179.0	0.93	21.0	177.7	0.96	15.3

Dispersion of hatchlings was significantly different between no moon and full moon conditions at sectors II ($Z_c = 2.202$, $n_1 = n_2 = 120$, $0.01 < P < 0.05$) and III ($Z_c = 5.703$, $n_1 = n_2 = 120$, $P < 0.001$) (Appendix II).

Overall *in situ* hatching success was 63.8 % (SE = 1.6, n = 264). Mean hatching success was highest at sector I (mean = 69.0 %, SE = 3.5 %, range = 0.0 – 97.1 %, n = 61), followed by sector II (mean = 65.5 %, SE = 3.4 %, range = 0.0 – 100.0 %, n = 57) and sector III (mean = 60.9 %, SE = 2.2 %, range = 0.0 – 96.5 %, n = 146). Hatching success at sector I was significantly higher than at sector III (Q = 2.754, k = 3, $0.01 < P < 0.05$) (Appendix III). Mean hatching success within 5 to 15 stake intervals ranged from 35.9 to 83.3 % (Table 4, Fig. 13).

Leatherbacks landed primarily in sectors II (47 %) and III (35 %). Those sectors were significantly preferred over sector I ($X^2 = 381.8$, df = 1, P < 0.001, n = 760). Of 760 activities, 545 resulted in egg deposition. However, due to annual erosion in sector II, most nests were relocated to sector III. The number of adult

leatherback landings within 5 to 15 stake intervals ranged from 9 to 77 females (Fig. 14).

Table 4. Mean hatching success within 5 to 15 stake intervals. HS = hatching success.

Sector I			Sector II			Sector III		
Stakes	HS (%)	n	Stakes	HS (%)	n	Stakes	HS (%)	n
65 – 79	65.4	8	140 - 144	N/A	0	175 - 179	60.2	28
80 – 94	67.4	18	145 - 149	N/A	0	180 - 184	55.3	23
95 - 109	67.6	24	150 - 154	35.9	2	185 - 189	61.9	40
110 - 124	76.2	9	155 - 159	49.7	4	190 - 194	62.2	23
125 - 139	83.3	2	160 - 164	65.9	13	195 - 199	63.1	21
			165 - 169	60.8	13	200 - 205	63.9	11
			170 - 174	72.6	25			

Of the 18 beach intervals at SPNWR, 6 were identified as critical areas for hatchling management (sum of scores = 4 – 6) (Fig. 15).

Light measurements at all beach sectors and all ambient conditions were below or equal to the detection limit of the lightmeter (0.1 cd/m^2).
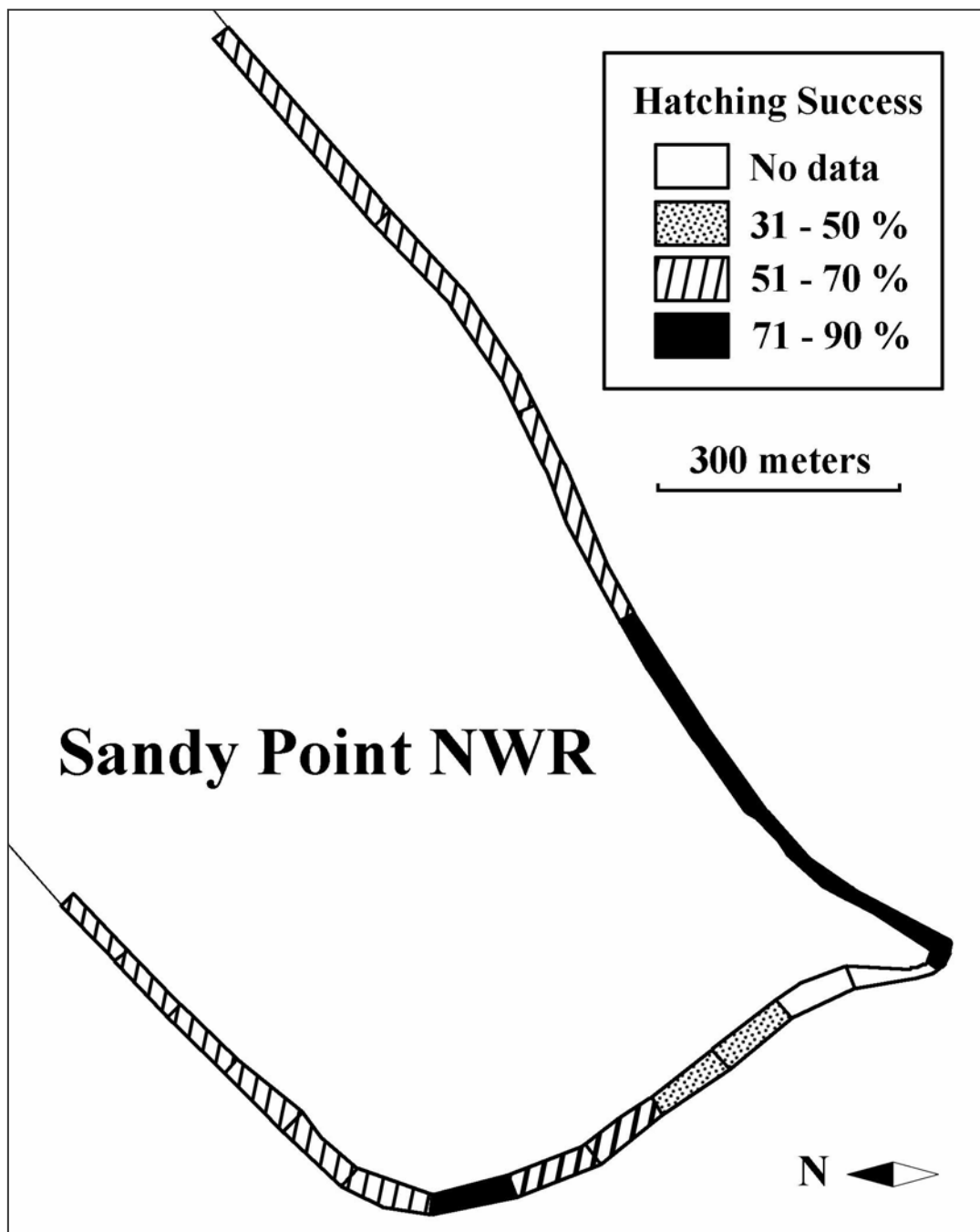
Figure 13. Mean hatching success within 5 to 15 stake intervals.
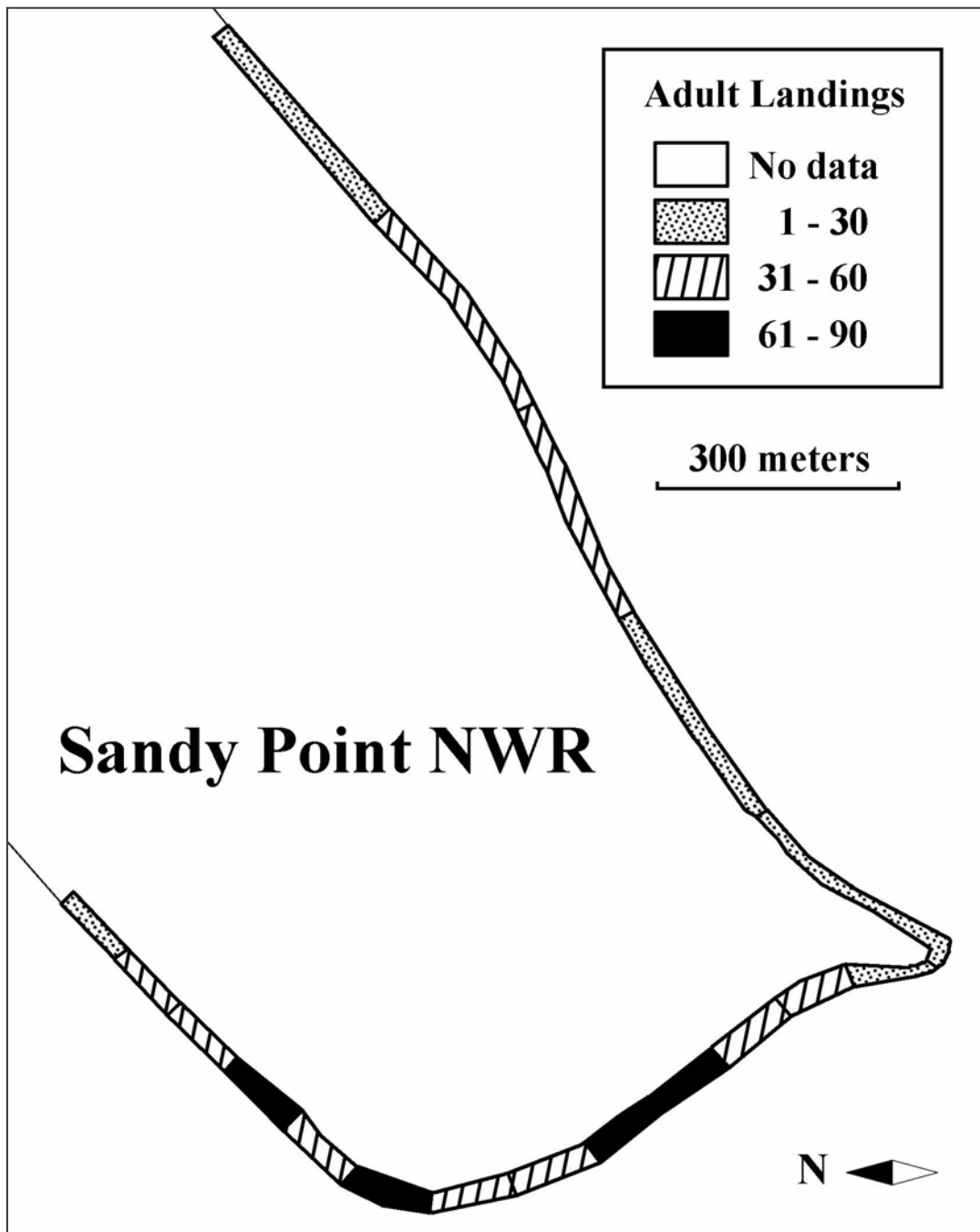
Figure 14. Number of adult leatherback landings within 5 to 15 stake intervals.
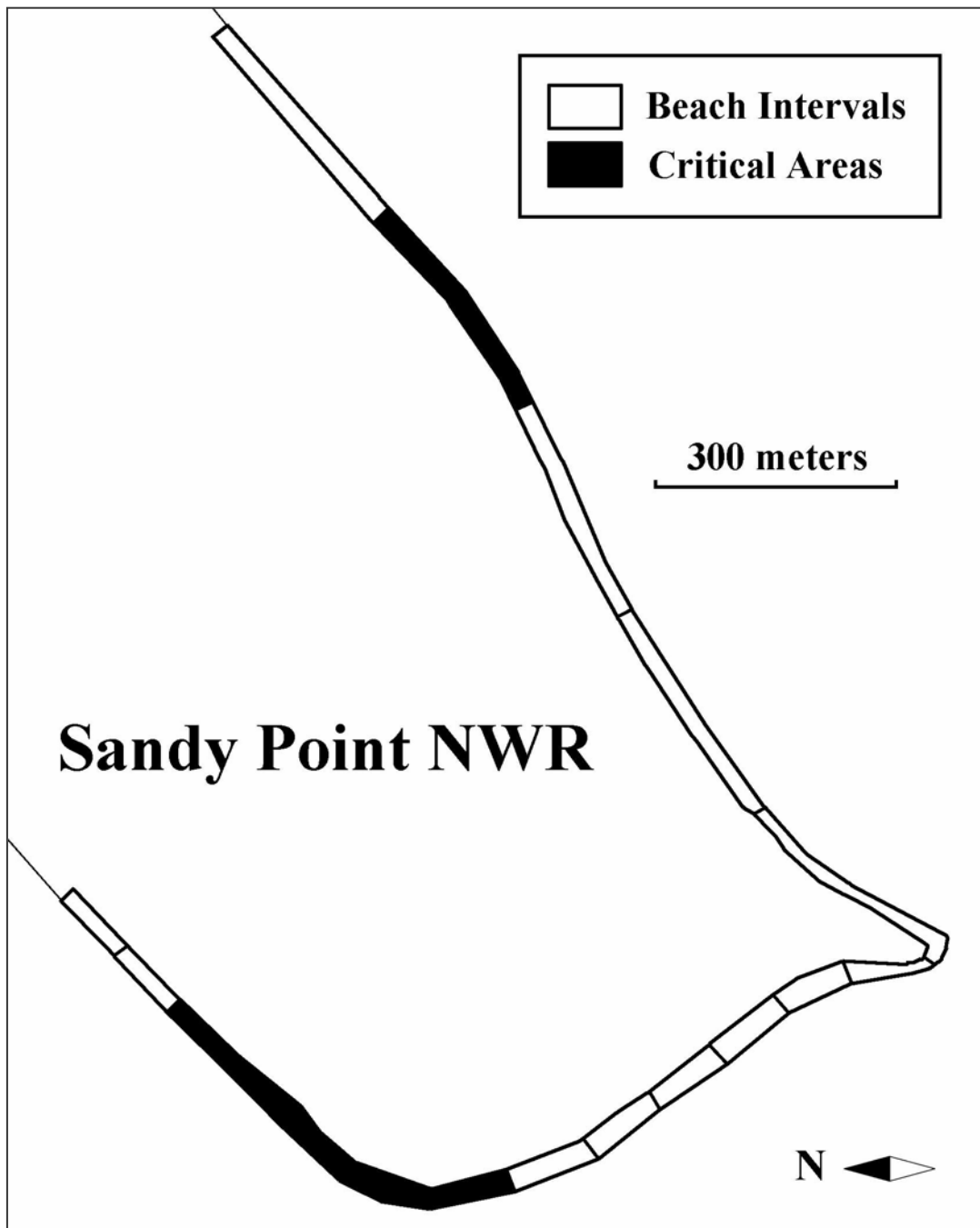
Figure 15. Critical areas for hatchling management based on orientation disruption, hatching success, and number of adult landings.

Discussion

Artificial lighting visible from a nesting beach potentially disrupts the sea-finding orientation of hatchlings (McFarlane, 1963). Hatchlings tend to either deviate from a direct path to the sea in direction of the light source or spread into different directions, uncertain and confused to where the ocean is. The former was estimated either by the median or the mean angle, the latter by the range or dispersion.

At Sandy Point, the significant correlation found between median angle and moon phase, indicated that hatchling orientation-disruption depended on the sector and the moonlight intensity. At sectors II and III, the city lights and their reflection in the sky seemed to attract hatchlings during new moon conditions (median angles > 180°). Conversely, the presence of the moon lowered the relative brightness of the artificial lights to an extent where normal sea-finding orientation was restored (median angles around 180°). This is in accordance with results published for loggerhead and green turtle hatchlings (Irwin et al., 1998; Mann, 1978; Mrosovsky and Carr, 1967; Verheijen, 1958). In general, artificial light-intensity decreases with increasing levels of background illumination, until it approaches natural conditions, where light from celestial sources is scattered by the atmosphere and by surface reflection, "smoothing out" variation (Salmon and Witherington, 1995). At sector III several median angles were smaller than 180°, suggesting that the hatchlings were attracted to the moon positioned in the opposite direction of

Frederiksted. At sector I no significant correlation was detected. This may be due to the moon positioned in the same direction as the artificial lights. Furthermore, less direct light was visible at sector I than III, resulting in smaller deviations from a straight path to the sea.

The significant correlation found between track range and moon phase at sector III, indicated that hatchlings were not only misdirected, but also confused by the lights of Frederiksted, causing them to spread out more strongly when approaching new moon conditions. At sectors I and II it seemed that the artificial lights were too weak to significantly increase track ranges.

Deviation of the median angle from a straight path to the sea was significantly dependent on moon phase at sectors where artificial lights were directly visible (I and III). The dependence rose primarily from the difference between no moon and moon conditions. Deviation was independent of full, three-quarters, and half moon conditions. This may help to explain why no significant correlation was found in sector I. Deviation was not dependent on moon phase in sector II, where lights were only indirectly visible. This may seem contradictory to the significant correlation of median angle and moon phase seen previously; however, the data points were correlated within a narrow range, mostly within the $0 - 14°$ class. Therefore, there was a significant correlation but hardly any deviation from a straight path.

The significant dependence of track range on moon phase found in sector III resulted from the difference between no moon and moon conditions. Thus, the lights of Frederiksted significantly augmented the track range during no moon conditions, whereas any visible moon restored it to "normal" levels again.

The analysis of the "mean/dispersion" experiments strengthened the results obtained from the *in situ* nest-emergences and the "median/range" experiments. During no moon conditions mean angles deviated significantly toward the visible lights from Frederiksted and its suburbs. The deviation of the second-order mean angle was 41°, surprisingly high for a beach located over 1.5 km from light sources. Witherington and Martin (1996) came to the conclusion that artificial lights visible to a person standing anywhere on the nesting beach are likely to cause problems for the sea turtles nesting there. Hatchling orientation disruption may be even higher for nests laid closer to Frederiksted. At high levels of artificial light-stimulation hatchlings may ignore natural sea-finding cues, or not even perceive them (Lohmann et al., 1997). This problem occurs on beaches with beachfront development (Katselidis and Dimopoulos, 2000; Mann, 1978) or where highways run parallel to the beach (McFarlane, 1963; Witherington, 1992).

The "mean/dispersion" experiments also showed that independent of the direct visibility of artificial lights, dispersion was significantly larger during no moon than full moon conditions. Thus, during no moon conditions at sector II, hatchling mean direction was toward the sea, but their dispersion was significantly

larger than "normal", resulting in hatchlings crawling into the vegetation or in circles. Mann (1978) found that the orientation of greens and loggerheads was often correct, even though diffused light over the landward horizon was more intense than that over the sea, however he did not investigate dispersion.

Recording median angle and range allowed for easy orientation assessment of hatchlings based on their tracks. Its disadvantage however was that individual tracks could not be differentiated from each other. Thus, important information was lost and the power of statistical analysis was reduced. However, the more detailed "median/dispersion" experiments were labor intensive and demanded handling of hatchlings.

Both methods revealed similar results that orientation disruption occurred primarily during no moon conditions. The times when no moon is visible during a lunar month can be calculated. Combined with the peak of hatchling emergence at SPNWR (approximately 19:00 to 24:00 hours) (pers. obs.), this presents a critical time of orientation disruption (Fig. 16).

In situ hatching success was significantly higher at sector I than III despite the high variation within sectors. However, these results would have been different if nests prone to erosion had not been relocated. Nevertheless, it suggests that environmental factors, such as oxygen and water availability, temperature, and bacteria levels, may have been more favorable at sector I than III. Because leatherback nesting-sites are located at high energy and cyclically eroding beaches

(Eckert, 1987), mean hatching success per sector and overall hatching success may

vary significantly among seasons (Boulon et al., 1996).
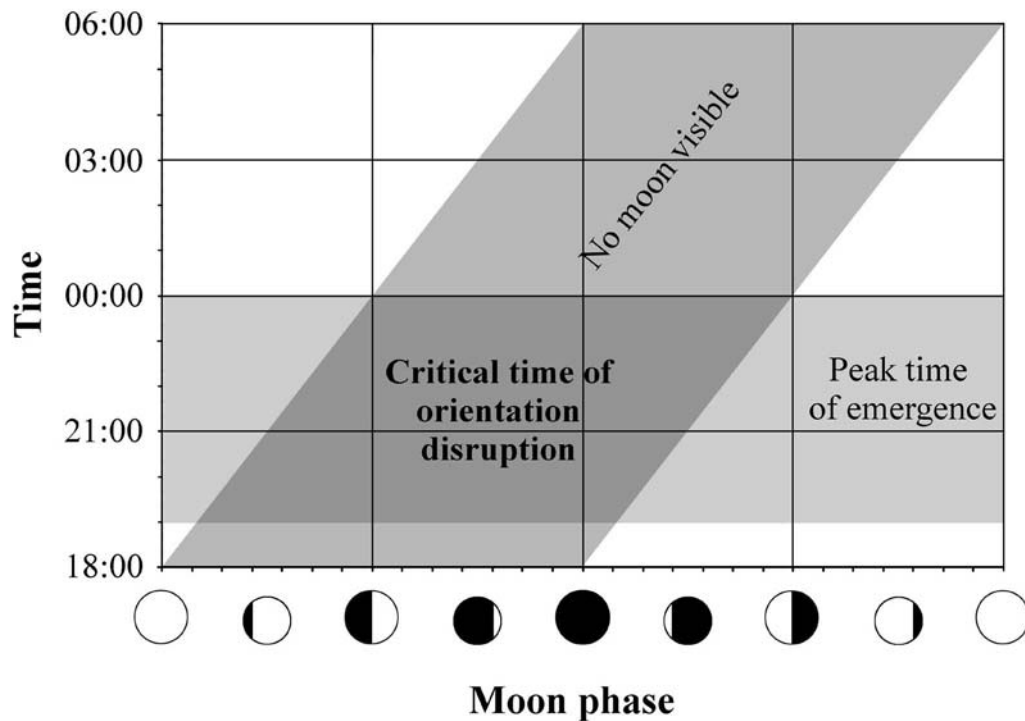
Figure 16. Critical times of orientation disruption during a lunar month. White circles represent full moon and the black circle new moon.

Leatherbacks preferred to nest on the leeward side (sectors II and III), as

they had in previous years (Eckert, 1987). This side offers two major advantages:

first, there is an easy, unobstructed deep-water access, which also minimizes the

time hatchlings have to swim over the predator-rich insular shelf, and second, there

is a wide, sandy beach with little vegetation growth and debris. Unfortunately, a

large part of the beach (marker 123 to 164) is prone to annual beach erosion, where

hatching success would result close to zero without relocation efforts.

Since the light measurements were equal or below the detection limit of the

lightmeter (0.1 cd/m^2) and artificial lighting could only be seen at a far distance or

indirectly, light intensity at SPNWR was considered low. Nevertheless, the lights

significantly affected hatchling orientation. On beaches with beach front

development, such as in Barbados, light measurements reached 5.5 cd/m^2 and were

high enough to discourage adult turtles from nesting (Woody et al., 2000). Also, it

has been documented that the intensity of the ballpark lights of Frederiksted were

strong enough to attract sea turtle hatchlings onto the game field (Philibosian,

1976). To mitigate this problem, in 1997 baffles were installed on the stadium and

ballpark lights, which noticeably decreased the amount of light reaching the beach.

However, severe storms damaged some of the baffles and knocked others loose,

thus they still need replacement (McDonald, et al., 2000).

Observations in nesting leatherbacks indicate that, similar to hatchlings,

these turtles rely on vision to find the sea (Mrosovsky and Shettleworth, 1975).

Witherington (1992) described how nesting greens and loggerhead were

misdirected by artificial lighting. At SPNWR, a few adult turtles attempting to

return to the sea after nesting have been observed crawling parallel to the water in

an apparent response to light. Because females may abandon their landing attempts

while still in the water (Witherington, 1992), the full impact of artificial lighting on turtles may be underestimated.

Six critical areas for hatchling management were identified at SPNWR, based on the following variables: orientation disruption during no moon conditions, hatching success, and adult landing-site preference. Together with the critical times of orientation disruption, they provide a helpful tool for conservation-project managers to effectively allocate personnel and equipment to assist hatchlings during their sea finding.

Nevertheless, it is important to address the causes of orientation disruption. Different management alternatives have been proposed to lessen the effects of artificial lighting. They include lights-off regulations, reducing light wattage, lowering, shielding, or redirecting luminaries, using motion sensitive lighting, and enhancing beach profile (Patrick and Watson, 1998; Raymond, 1984; Witherington, 1999; Witherington and Martin, 1996). Although these approaches are effective for beachfront light-sources, they do not deal with inland lights that reflect in the sky. These measures need to extend island-wide. Thus, a comprehensive light-management strategy would include: first, prevent any further light-source development in proximity to SPNWR; second, conduct intense public awareness campaigns; third, implement long-term educational programs at schools and the University of the Virgin Islands; fourth, establish a center for technical support to which questions and concerns can be addressed; fifth, persuade the government to

adopt light management legislation; sixth, enforce the environmental laws; and seventh, further monitor hatchling orientation disruption at SPNWR and other nesting beaches.

Although the present study has demonstrated the importance of the moon condition on leatherback hatchling orientation, the great degree of individual variation within categories in comparison to the variation among categories indicates there may be important factors influencing hatchling orientation not considered in this study. Examples that may need to be addressed are the exact position of the moon at the moment of emergence, cloud cover, the nest position in relation to vegetation or debris, the large and small-scale beach profile around the nest, beach slope, distance to the sea, or the mean fitness within a clutch.

Furthermore, this study is limited to the orientation of hatchlings shortly after emergences. However, orientation cues may change once turtles are on their path to the sea or in the water (Salmon and Lohmann, 1989). There are indications that beach lighting may influence hatchling orientation at sea (Frick, 1976; Mann, 1978; Witherington, 1990). At SPNWR confused hatchlings have been found crawling back onto land after reaching the water (pers. obs.). Hatchling mortality caused by artificial lighting is difficult to detect and probably underestimated. Hatchlings that enter the sea after a period of wandering on the beach may have a lower rate of survivorship due to increased energy consumption on land, which

instead should have been used to actively swim to the open sea (Lohmann and Lohmann, 1996).

The relocation of threatened nests has been a main management tool to increase hatchling production. With the growing number of nesting females at SPNWR, careful selection of relocation sites is important to avoid high nest densities, which can result in oxygen depletion and high bacteria load, and negatively affect hatching success (Ackerman, 1997). Furthermore, this abnormal concentration of hatchlings in a relatively small area may result in an increase of land and in-water predators (Frick, 1976; Wyneken et al., 1998). Thus, it is recommended to liberate the hatchlings of relocated nests at their original location. In this way, the original intent of leatherbacks to spread their reproductive effort in space and time is re-established.

Conclusion

For the first time it was documented that the artificial lights from Frederiksted and its suburbs significantly disrupted the orientation of leatherback hatchlings at SPNWR. When the moon was not visible, hatchling dispersion was significantly wider throughout the entire beach. Furthermore, where lights were directly visible, hatchlings significantly deviated from a straight path to the sea toward the lights. Consequently, hatchlings were exposed to additional predation and used energy needed for their offshore migrations.

The critical times of orientation disruption were given for a lunar month. Furthermore, the critical areas for hatchling management were identified based on the variables orientation disruption, hatchling success, and adult landing-site preference. Emphasis was put on the importance to reduce the causes of orientation disruption and a comprehensive light-management strategy was recommended.

Although the moon condition was a key factor in determining the effects of artificial lights on hatchling orientation, individual variation within categories indicated the presence of other factors. For further conservation efforts to be effective, these factors need to be determined. Future studies also should address the effects of artificial lighting on hatchling orientation in the sea.

Bibliography

Ackerman R. A. 1997. The nest environment and the embryonic development of sea turtles. In: P. L. Lutz and J. A. Musick (editors). The biology of sea turtles, pp. 83-106. CRC Press, Boca Raton, Florida.

Albrecht, M. 1998. Influence of post hatching captivity on activity and orientation of sea turtle hatchlings. In: Byles, R. and Y. Fernandez (compilers). Proceedings of the sixteenth annual symposium on sea turtle biology and conservation, pp. 8-10, NOAA Tech. Mem. NMFS-SEFSC-412.

Anderson, P. K. 1958. The photic responses and water-approach behavior of hatchling turtles. Copeia 1958: 211-215.

Baijal, V. S. 1996. Protecting endangered species: GIS decision support system. In: Heit, M, H. D. Parker, and A. Shorteid (editors). GIS application in natural resources 2, pp. 469-472. GIS World Books, Fort Collins.

Boulon, R. H., P. Dutton, and D. L. McDonald. 1996. Leatherback turtles (*Dermochelys coriacea*) on St. Croix, U.S. Virgin Islands: fifteen years of conservation. Chelonian Conserv. Biol. 2: 141-147.

Carr, A. and H. Hirth. 1961. Social facilitation in green turtle siblings. Anim. Behav. 9: 68-70.

Carr, A. and L. Ogren. 1959. The ecology and migrations of sea turtles, 3. *Dermochelys* in Costa Rica. Am. Mus. Nov. (1958): 1 - 29.

Dickerson D. D. and D. A. Nelson. 1988. Use of long wavelength lights to prevent disorientation on hatchling sea turtles. In: Schroeder, B. A. (compiler). Proceedings of the eighth annual symposium on sea turtle biology and conservation, pp. 19-21, NOAA Tech. Mem. NMFS-SEFSC-214.

Eckert K. L. 1987. Environmental unpredictability and leatherback sea turtle (*Dermochelys coriacea*) nest loss. Herpetologica 43: 315-323.

Friendly, M. 1994. Mosaic displays for multiway contingency tables. J. Amer. Statist. Assoc. 89: 190-200.

Frick, J. 1976. Orientation and behaviour of hatchling green turtles (*Chelonia mydas*) in the sea. Anim. Behav. 24: 849-857.

Godfrey, M. H. and R. Barreto. 1995. Beach vegetation and seafinding orientation of turtle hatchlings. Biol. Conserv. 74: 29-32.

Irwin, M. S., B. J. Godley, and A. C. Broderick. 1998. The effect of anthropogenic lighting on marine turtles in northern Cyprus. In: Byles, R. and Y. Fernandez (compilers). Proceedings of the sixteenth annual symposium on sea turtle biology and conservation, pp. 71-74. NOAA Tech. Mem. NMFS-SEFSC-412.

Katselidis, K. and D. Dimopoulos 2000. The impact of tourist development on loggerhead nesting activity at Daphni, Zakynthos, Greece. In: Abreu-Grobois, F. A., R. Briseño-Dueñas, R. Márquez, and L. Sarti. (compilers). Proceedings of the eighteenth annual symposium on sea turtle biology and conservation, pp. 75-77 NOAA Tech. Memo. NMFS-SEFSC-436.

Lohmann, K. J. and C. M. F. Lohmann. 1996. Orientation and open-sea navigation in sea turtles. J. Exper. Biol. 199: 73-81.

Lohmann, K. J., B. E. Witherington, C. M. F. Lohmann, and M. Salmon. 1997. Orientation, navigation and natal beach homing in sea turtles. In: P. L. Lutz and J. A. Musick (editors). The biology of sea turtles, pp. 107-135. CRC Press, Boca Raton, Florida.

Mann, T. M. 1978. Impact of developed coastline on nesting and hatchling sea turtles in Southeastern Florida. Flor. Mar. Res. Publ. 33: 53-55.

Mayor, P. A. 1998. Nesting of the leatherback turtle (*Dermochelys coriacea*) at Las Baulas and Santa Rosa National Park and population estimations for the entire Pacific coast of Costa Rica. Master's Thesis, Swiss Federal Institute of Technology (ETH). 58 pp.

McDonald-Dutton, D., A. Barragan, P. A. Mayor, V. Villanueva-Mayor, and R. Boulon. 2000. Tagging and nesting research on leatherback turtles (*Dermochelys coriacea*) on Sandy Point, St. Croix, U.S. Virgin Islands. Ann. Rept. US Fish Wildl. Ser. Pc-PNR-091-2000. 28 pp.

McDonald-Dutton, D., V. Villanueva-Mayor, J. L. Alexander, S. T. W. Deishley, and W. Coles. 2001. Tagging and nesting research on leatherback turtles (*Dermochelys coriacea*) on Sandy Point, St. Croix, U.S. Virgin Islands. Ann. Rept. US Fish Wildl. Ser. Pc-PNR-091-2001. 32 pp.

McFarlane, R. W. 1963. Disorientation of loggerhead hatchlings by artificial road lighting. Copeia 1963: 153.

Miller, J. D. 1997. Reproduction in sea turtles. In: P. L. Lutz and J. A. Musick (editors). The biology of sea turtles, pp. 51-81. CRC Press, Boca Raton, Florida.

Mrosovsky, N. 1968. Nocturnal emergence of hatchling sea turtles: control by thermal inhibition of activity. Nature 220: 1338-1339.

Mrosovsky, N. 1970. The influence of the sun's position and elevated cues on the orientation of hatchling sea turtles. Anim. Behav. 18: 648-651.

Mrosovsky, N. 1978. Effects of flashing lights on sea-finding behavior of green turtles. Behav. Biol. 22: 85-91.

Mrosovsky, N. and A. Carr. 1967. Preference for light of short wavelengths in hatchling green sea turtles, *Chelonia mydas*, tested on their natural nesting beaches. Behaviour 28: 217-231.

Mrosovsky, N. and S. F. Kingsmill. 1985. How turtles find the sea. Z. Tierpsychol. 67: 2367-256.

Mrosovsky, N. and S. J. Shettleworth. 1968. Wavelength preferences and brightness cues in the water finding behaviour of sea turtles. Behaviour 32: 211-257.

Mrosovsky, N. and S. J. Shettleworth. 1974. Further studies of the sea-finding mechanism in green turtle hatchlings. Behaviour 51: 195-208.

Mrosovsky, N. and S. J. Shettleworth. 1975. On the orientation circle of the leatherback turtle, *Dermochelys coriacea*. Anim. Behav. 23: 568-591.

Oliver, L. J., M. Salmon, J. Wyneken, R. Hueter, and T. W. Cronin. 2000. Retinal anatomy of hatchling sea turtles: anatomical specializations and behavioral correlates. Mar. Behav. Physiol. 33:233-248.

Patrick, L. and K. Watson. 1998. A lighting plan for a beachfront development. In: Epperly, S. P. and Braun, J. (compilers). Proceedings of the seventeenth annual symposium on sea turtle biology and conservation, pp. 242. NOAA Tech. Mem. NMFS-SEFSC-415.

Philibosian, R. 1976. Disorientation of hawksbill turtle hatchlings, *Eretmochelys imbricata*, by stadium lights. Copeia 1976: 824.

Raymond, P. W. 1984. Sea turtle hatchling disorientation and artificial beachfront lighting. Center for Environmental Education, Washington, D. C. 72 pp.

Richardson, J. I., 1999. Priorities for studies of reproduction and nest biology. In: Eckert, K. L., K. A. Bjorndal, F. A. Abreu-Groboism and M. Donnelly (editors). Research and management techniques for the conservation of sea turtles, pp.9-11. IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Salmon, M. and K. J. Lohmann. 1989. Offshore orientation by loggerhead hatchlings. In: Eckert, S. A., K. L. Eckert, and T. H. Richardson (compilers). Proceedings of the ninth annual symposium on sea turtle biology and conservation, pp. 41. NOAA Tech. Mem. NMFS-SEFSC-232.

Salmon, M. and B. E. Witherington. 1995. Artificial Lighting and seafinding by loggerhead hatchlings: evidence for lunar modulation. Copeia 1995: 931-938.

Salmon, M. and J. Wyneken. 1990. Do swimming loggerhead sea turtles (*Caretta caretta* L.) use light cues for offshore orientation? Mar. Behav. Physiol. 17: 233-246.

Salmon, M., J. Wyneken, E. Fritz, and M. Lucas. 1992. Seafinding by hatchling sea turtles: role of brightness, silhouette and beach slope as orientation cues. Behaviour 122: 56-77.

Van Rhijn, F. A. 1979. Optic orientation in hatchlings of the sea turtle, *Chelonia mydas*. I. Brightness: not the only optic cue in sea-finding orientation. Mar. Behav. Physiol. 6: 105-121.

Verheijen, F. J. 1958. The mechanisms of the trapping effect of artificial light sources upon animals. Archives Neerlandaises de Zoologie 13: 1-178.

Verheijen, F. J. and J. T. Wildschut. 1973. The photic orientation of hatchling sea turtles during water finding behaviour. Netherlands J. Sea Res. 7: 53-67.

Wallraff, H. G. 1979. Goal-oriented and compass-oriented movements of displaced homing pigeons after confinement in differentially shielded aviaries. Behav. Ecol. Sociobiol. 5: 201-225.

Whitmore, C. P. and P. H. Dutton. 1985. Infertility, embryonic mortality and nest-site selection in leatherback and green sea turtles in Suriname. Biol. Conserv. 34: 251-272.

Witherington, B. E. 1986. Human and natural causes of marine turtle clutch and hatchling mortality and their relationship to hatchling production on an important Florida nesting beach. Master's thesis, Univ. Central Florida, Orlando. 141 pp.

Witherington, B. E. 1990. Photopollution on sea turtle nesting beaches: problems and next-best solutions. In: Richardson, T., J. Richardson, and M. Donnelly (compilers). Proceedings of the tenth annual symposium on sea turtle biology and conservation, pp. 43-45. NOAA Tech. Mem. NMFS-SEFSC-278.

Witherington, B. E. 1992. How are hatchling sea turtles able, and unable, to locate the sea? In: Salmon, M. and J. Wyneken (compilers). Proceedings of the eleventh annual symposium on sea turtle biology and conservation, pp. 127-130. NOAA Tech. Mem. NMFS-SEFSC-302.

Witherington, B. E. 1999. Reducing threats to nesting habitat. In: Eckert, K. L., K. A. Bjorndal, F. A. Abreu-Grobois, and M. Donnelly (editors). Research and management techniques for the conservation of sea turtles, pp. 179-183. IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Witherington, B. E. and K. A. Bjorndal. 1991. Influences of wavelength and intensity on hatchling sea turtle phototaxis: implications for sea-finding behavior. Copeia 1991: 1060-1069.

Witherington, B. E. and R. E. Martin. 1996. Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches. FMRI Technical Report TR-2. Florida Marine Research Institute, St. Petersburg, Florida, 73 pp.

Witherington, B. E., K. A. Bjorndal, and C. M. McCabe. 1990. Temporal pattern of nocturnal emergence of loggerhead turtle hatchlings from natural nests. Copeia 1990: 1165-1168.

Witherington, B. E., C. Crady, and L. Bolen. 1995. A hatchling orientation index for assessing orientation disruption from artificial lighting. In: Keinath, J., D. Barnard, J. Musick, and B. Bell (compilers). Proceedings of the fifteenth annual symposium on sea turtle biology and conservation, pp. 344-347. NOAA Tech. Mem. NMFS-SEFSC-387.

Woody, K. K., J. Horrocks, and L. A. Vermeer. 2000. Factors influencing within-beach nest distribution in hawksbill turtles. In: Abreu-Grobois, A., R. Briseño-Dueñas, R. Márquez-Millá, and L. Sarti-Martínez (compilers). Proceedings of the eighteenth annual symposium on sea turtle biology and conservation, pp. 170-171. NOAA Tech. Mem. NMFS-SEFSC-436.

Wyneken, J., L. De Carlo, L. Glenn, M. Salmon, D. Davidson, S. Weege, and L. Fisher. 1998. On the consequences of timing, location, and fish for hatchlings leaving open beach hatcheries. In: Byles, R. and Y. Fernandez (compilers). Proceedings of the sixteenth annual symposium on sea turtle biology and conservation, pp. 155-156. NOAA Tech. Mem. NMFS-SEFSC-412.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Inc. Upper Saddle River, New Jersey, 663 pp.

Appendices

Appendix I. Contingency tables for median angle and track range. FU = full moon, TQ = three-quarters moon, HA = half moon, QU = quarter moon, NO = no moon, Obs = observed frequency, Exp = expected frequency, v = degrees of freedom.

Contingency table (3 x 5) for median angle at sector I.

Deviation		FU	TQ	HA	QU	NO	Total
0-14°	Obs	3	7	4	6	5	25
	Exp	1.7045	3.9773	2.2727	3.9773	13.0682	
15-29°	Obs	0	0	0	1	13	14
	Exp	0.9545	2.2273	1.2727	2.2273	7.3182	
>=30°	Obs	0	0	0	0	5	5
	Exp	0.3409	0.7955	0.4545	0.7955	2.6136	
Total		3	7	4	7	23	44
$v =$	8	$X^2 =$	24.712	0.005 < P < 0.001			

°

Contingency table (3 x 5) for median angle at sector II.

Deviation		FU	TQ	HA	QU	NO	Total
0-14°	Obs	5	6	8	1	14	34
	Exp	4.3273	4.3273	5.5636	1.2364	18.5455	
15-29°	Obs	2	1	1	0	10	14
	Exp	1.7818	1.7818	2.2909	0.5091	7.6364	
>=30°	Obs	0	0	0	1	6	7
	Exp	0.8909	0.8909	1.1455	0.2545	3.8182	
Total		7	7	9	2	30	55
$v =$	8	$X^2 =$	11.672	n.s.			

Contingency table (3 x 5) for median angle at sector III.

Deviation		FU	TQ	HA	QU	NO	Total
0-14°	Obs	20	17	13	11	11	72
	Exp	13.8667	12.8000	8.0000	10.6667	26.6667	
15-29°	Obs	6	5	1	3	14	29
	Exp	5.5852	5.1556	3.2222	4.2963	10.7407	
>=30°	Obs	0	2	1	6	25	34
	Exp	6.5481	6.0444	3.7778	5.0370	12.5926	
Total		26	24	15	20	50	135
$v =$	8	$X^2 =$	43.085	P < 0.001			

Contingency table (2 x 5) for track range at sector I.

Range		FU	TQ	HA	QU	NO	Total
		Moon phase					
0-89°	Obs	1	5	3	1	7	17
	Exp	1.3600	3.4000	2.7200	0.6800	8.8400	
>=90°	Obs	1	0	1	0	6	8
	Exp	0.6400	1.6000	1.2800	0.3200	4.1600	
Total		2	5	4	1	13	25
$v =$	4	$X^2 =$	4.408	n.s.			

Contingency table (2 x 5) for track range at sector II.

Range		FU	TQ	HA	QU	NO	Total
		Moon phase					
0-89°	Obs	3	6	6	0	9	24
	Exp	3.5294	4.2353	4.9412	1.4118	9.8824	
>=90°	Obs	2	0	1	2	5	10
	Exp	1.4706	1.7647	2.0588	0.5882	4.1176	
Total		5	6	7	2	14	34
$v =$	4	$X^2 =$	8.609	n.s.			

Contingency table (2 x 5) for track range at sector III.

Range		FU	TQ	HA	QU	NO	Total
		Moon phase					
0-89°	Obs	19	17	12	13	14	75
	Exp	17.5676	16.2162	10.1351	10.1351	20.9459	
>=90°	Obs	7	7	3	2	17	36
	Exp	8.4324	7.7838	4.8649	4.8649	10.0541	
Total		26	24	15	15	31	111
$v =$	4	$X^2 =$	11.134	$0.05 < P < 0.025$			

Appendix II. Two-sample testing of angular dispersion.

Testing of angular dispersion between no moon and full moon conditions at sectors II and III.

Ho. The dispersion of hatchlings during no moon conditions is not different to full moon conditions.

Ha. The dispersion of hatchlings during no moon conditions is different to full moon conditions.

	Sector II	Sector III
Mann-Whitney statistic (U)	6019	4147
N	120	120
Summation of ties	90528	127860
Mean of U distribution	7200	7200
Standard error of U distribution	536.01	535.28
Normal distribution statistic corrected for continuity (Z_c)	2.20	5.70
	$0.05 < P < 0.01$	$P < 0.001$
	Reject Ho.	Reject Ho.

Appendix III. Nonparametric analysis of variance and multiple comparison procedure for hatching success.

Nonparametric ANOVA table used to test for significant differences in hatching success among sectors.

Ho. Percent hatching success is the same in all sectors.

Ha. Percent hatching success is not the same in all sectors.

		Sector I	Sector II	Sector III
n		61	57	146
Sum of ranks (R)		9395.5	7777.0	17807.5
Groups of tied ranks (m)	39			
Kruskal-Wallis statistic (H)	7.7765			
Correction factor for tied ranks (C)	0.9999			
Corrected value of H (Hc)	7.7776			
Reject Ho.	$0.01 < P < 0.05$			

Nonparametric multiple comparisons table to determine between which of the samples significant differences occur.

Ho. Percent hatching success is the same between sectors.

Ha. Percent hatching success is not the same between sectors.

Sectors	3	2	1
R	17807.5	7777.0	9395.5
n	146	57	61
Mean R	121.97	136.44	154.02

Comparison	Difference	Standard Error	Q	Conclusion
1 vs. 3	32.06	11.64	2.75	Reject Ho.
1 vs. 2	17.59	14.07	1.25	Accept Ho.
2 vs. 3	14.47	11.92	1.21	Accept Ho.