



Reduction of sea turtle population recruitment caused by nightlight: Evidence from the Mediterranean region



Charalampos Dimitriadis^{a,*}, Ivoni Fournari – Konstantinidou^{b,c}, Laurent Sourbès^a, Drosos Koutsoubas^{a,b}, Antonios D. Mazaris^c

^a National Marine Park of Zakynthos, El. Venizelou 1, 29100 Zakynthos, Greece

^b Department of Marine Science, Faculty of Environment, University of the Aegean, 81000 Mytilene, Lesvos Island, Greece

^c Department of Ecology, School of Biology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece

ARTICLE INFO

Keywords:

Sea-finding
Coastal lighting
Marine turtles
Disorientation
Light pollution

ABSTRACT

The spread of artificial night lighting is increasingly acknowledged as a major threat to global biodiversity. Identifying and exploring the impacts of nightlight pollution upon species behavior, ecology and population dynamics could enhance conservation capacity. Sea turtle hatchlings emerge from nest at night and use visual cues to direct towards the brightest and lowest horizon, eventually leading them to the sea. Nightlight pollution could alter the cues perceived, disorienting the fragile hatchlings. We examined the level of artificial lighting and orientation patterns of sea turtles hatchling, in Zakynthos Island, Greece, one of the main nesting rookeries of the loggerheads (*Caretta caretta*) in the Mediterranean Sea. We analyzed movement patterns of 5967 hatchlings from 230 nests, and demonstrate that nightlight pollution could reduce population recruitment by more than 7%, suggesting that mitigation measures should become a high conservation priority. Our results further suggest that the responses of sea turtle hatchlings to artificial nighttime lighting could vary significantly depending on various factors, either anthropogenic or natural. Local conditions operating at the nesting site level determine the fine scale responses of hatchlings, thus conservation measures should be drawn in respect to site-specific properties.

1. Introduction

The coastline represents an attractive zone for the establishment of various economic activities (IPCC, 2007; Halpern et al., 2008). Still, the development and increased utilization have come together with new threats for coastal biodiversity (Lotze et al., 2006; Coll et al., 2012) and for the organisms which temporary use the coastal habitat (e.g. marine mammals, seabirds, estuarine fish, sea turtles) for resting, foraging or reproduction. Yet, the ability to quantify the impacts of coastal threats is critical for prioritizing conservation actions (Beger et al., 2010; Micheli et al., 2013).

Coastal development has accelerated the spread of artificial nightlights. As a result, over the last years, an increased number of studies had explored the impacts of artificial night lighting upon the behavioral and physiological ecology of amphibian, reptile, bird, mammal, invertebrate and fish species inhabiting the coastal realm (e.g. Rich and Longcore, 2006; Gaston et al., 2015; Davies et al., 2014, 2015; Troy et al., 2011; Becker et al., 2013; Luarte et al., 2016). The impacts of artificial nightlights are often translated as a disruption of foraging,

reproductive, navigation, orientation, dispersal and migration behavior, as an increased risk of predation and fitness reduction (Perry and Fisher, 2006). Artificial night sky brightness is therefore accounted as driver affecting population viability and dynamics (Gaston and Bennie, 2014). This is actually the reason why nightlight pollution is increasingly acknowledged as an additional threat for biodiversity and thus should be treated as a modern challenge for global conservation and management (Gaston et al., 2014; Davies et al., 2014).

Sea turtles are charismatic megafauna for which the impact of artificial nighttime lighting has been tested both experimentally and empirically (e.g. Witherington and Martin, 1996; Tuxbury and Salmon, 2005; Thums et al., 2016). Adult female sea turtles lay their nests in the coastal beaches at the close vicinity where they were born several decades ago. The hatchlings emerge from nest at night and use visual cues which will drive them towards the brightest and lowest horizon, eventually directing them to the sea (Kawamura et al., 2009; Limpus and Kamrowski, 2013). As artificial nighttime lighting overrules the effect of natural visual cues (Witherington and Martin, 1996) it can directly (light sources visible from the beach) and indirectly (sky-glow

* Corresponding author.

E-mail address: xdimitriadis@marine.aegean.gr (C. Dimitriadis).

caused by inland light sources not directly visible from the beach) disrupt the sea-finding orientation of the hatchlings (e.g. Tuxbury and Salmon, 2005; Limpus and Kamrowski, 2013; Berry et al., 2013). For the fragile hatchlings, the loss of orientation could lead to mortality due to exhaustion, dehydration, and exposure to predators. Nightlight pollution could therefore lead to reduction of population recruitment (Lorne and Salmon, 2007).

Each nesting beach has distinct topographical features (e.g. slope, width, silhouettes that back the shore) which could alter the cues for orientation perceived by sea turtle hatchlings. The visual behavior of sea turtle hatchlings could also differ between populations of the same species (Fritsches, 2012). Alternatively, sea turtles have shown different intrinsic abilities with respect to nesting site microenvironment features [e.g. thermal adaptive differentiation to finer scale nesting conditions (Weber et al., 2011); varying thermal tolerance of embryos (Howard et al., 2014); varying pivotal sex determination temperatures (Hays et al., 2014)]. Yet, the diversity of local conditions along with the fine scale adaptive potential could lead to differences in the level of exposure, the sensitivity of responses and the vulnerability of different population to nightlight pollution.

Despite these concerns, there is a lack of estimates regarding how the impact of hatchlings' disorientation due to artificial nighttime lighting could be translated to reduced recruitment. Similarly, there is a gap in the spatial extent of relevant studies along the distribution of sea turtle nesting sites. For example, in the Mediterranean region that currently hosts 45 major nesting sites of loggerheads and 13 of green turtles (Almanidou et al., 2016; Casale and Margaritoulis, 2010) such evidence is very scarce (but see Peters and Verhoeven, 1994).

Here, we attempt to contribute to this research, by providing quantitative evidence on the responses of loggerhead sea turtle hatchling to artificial night sky brightness in the Mediterranean region. We investigate hatchling orientation patterns and light pollution level at both light impacted and naturally dark nesting beaches of the National Marine Park of Zakynthos (NMPZ), Greece. The NMPZ hosts one of the most important nesting rookeries of loggerhead turtles in the Mediterranean, while it is subjected to intense tourism activities annually, with the peak tourist period synchronized with the middle of sea turtle reproduction period. The objectives of this study are twofold. First, we aim to provide insights on sea turtle hatchling responses to lighting from an underrepresented region. Second, we attempt to identify the degree to which specific measures are needed to be taken for mitigating potential impacts of nightlight pollution upon this critical nesting aggregation.

2. Methodology

2.1. Study area

The study was conducted at the nesting beaches of loggerhead sea turtles, *Caretta caretta*, located within the boundaries of the NMPZ, eastern Mediterranean (Fig. 1). The rookery contains 6 nesting beaches with a total length of approximately 6 km. All beaches are enclosed within the boundaries of the NMPZ which was established in 1999 as the first protected area in the Mediterranean focusing mainly on the protection of sea turtles. Measurements of nighttime lighting and observations of sea-finding orientation patterns were conducted to the 5 nesting beaches (i.e. Kalamaki, Crystal, Sekania, Gerakas and Marathonisi) which support more than 85% of the nesting activity. These nesting beaches have different environmental conditions (e.g. beach slope, width, length) and are subjected to different human use and thus pressures (Katselidis et al., 2012).

In NMPZ the nesting activity of loggerheads is taking place from late May to early August with the incubation duration ranging from 51.3 to 69.8 days (Margaritoulis, 2005). The island of Zakynthos is an international tourist destination; annually more than 800,000 people are visiting the beaches located within the boundaries of the NMPZ, and use

the facilities (e.g. settlements, hotels, resorts, shops, bars, airport) hosted along the coastline (Appendix A). Therefore, a high overlap in the hatchling emergence period and the peak of the tourist period (during August) is taking place subsequently raising conservation challenges.

2.2. Field work

2.2.1. Light pollution assessment

Measurements of nighttime lighting were conducted during the 2014 nesting period. In order to ensure comparability of patterns and processes across the nesting rookery, a strict protocol was followed for the nighttime light measurements. The nesting beaches were divided into 12 stations which were identified to share similar topographical characteristics and level of exposure to artificial light sources (Management Agency of the NMPZ, 2008). For each one of these stations, one-off nighttime lighting measurements were taken under the absence of cloud cover between 11:00 and 12:00 p.m. during the new moon phase of August (i.e. no moon light) (Kamrowski et al., 2015). The nests which were laid within the boundaries of a given station were characterized by its nightlight properties.

At each sampling station the following parameters were recorded: a) 360° bearing of the coastal lighting and the brightest sources of light visible from the beach, b) 360° bearing of sky-glow (degrees) and its strongest sources and c) light intensity (average of 4 successive point measurements) at each station. Given that hatchlings are oriented by using a visual 'cone of acceptance' from 0 to 30° in the vertical level, light intensity at each sampling station was measured at an elevation of 15° from the beach surface (Limpus and Kamrowski, 2013). The mean light intensity at a nesting beach level was then produced as the average of the measurements taken at each station. Measurements were conducted by means of a portable light meter (WETEKOM ST-8820), compass and GPS.

2.2.2. Orientation patterns and nest environment

To delineate the potential impact of nighttime lighting upon hatchling sea-finding orientation, we reported movement patterns of hatchlings emerged from 230 nests by visiting the nesting beaches during the dawn from August to October 2014. Hatchling tracks were counted and their routes were recorded by using a GPS (at 5 m intervals).

When more than 15 hatchling tracks were found to originate from the same nest we used the fan mapping method (Salmon and Witherington, 1995; Pendoley, 2005) (Fig. 2). In this respect, we measured the angle (North direction was used as reference point) of the right and left outer tracks of the fan, the modal direction and the direct line from the nest to the sea (shortest route to the sea). Bearings were recorded by means of a compass at distance of 5 m from the nest (Kamrowski et al., 2015). These measurements were used to provide a set of hatchling sea-finding orientation metrics for each nest: a) fan spread defined as the difference of compass bearings between the outside arms of the track fan, b) offset angle defined as the difference between the modal direction and the bearing of the most direct line to the sea (i.e. shortest distance from the nest to the sea bearing), and (c) mean offset from the sea direction defined as the difference between the bearings of the two outer arms of the track fan and the direct line to the sea (indicating skew pattern of the tracks). To list a sea-finding orientation behavior as disturbed we used two alternative thresholds (see Salmon and Witherington, 1995): the offset angle been higher than 30° and/or the fan spread angle been higher than 90°.

Irrespectively of the number of tracks found at each nest (i.e. both for the cases of more or less than 15 tracks), bearings and routes of the stray tracks (i.e. hatchling tracks found in a different direction to the bulk of the nest) were reported, but they were not included in the fan mapping method (Pendoley, 2005). The routes of the stray tracks were recorded individually when they were less than 5 while their main

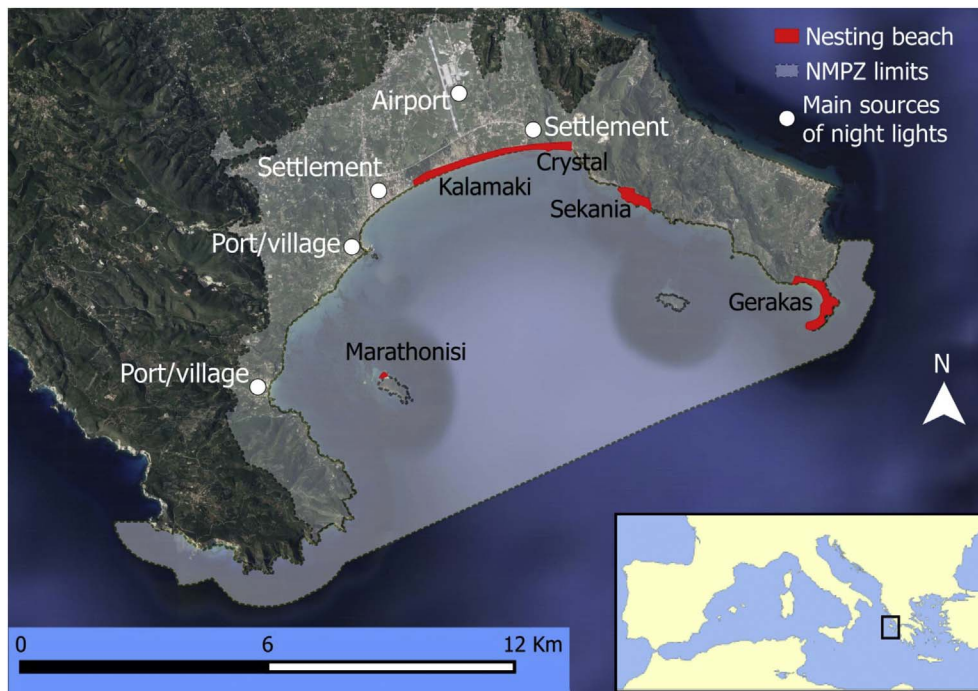


Fig. 1. Map of the marine protected area (MPA) of the National Marine Park of Zakynthos (NMPZ) indicating the nesting beaches that were surveyed and the main sources of night lights at regional level.

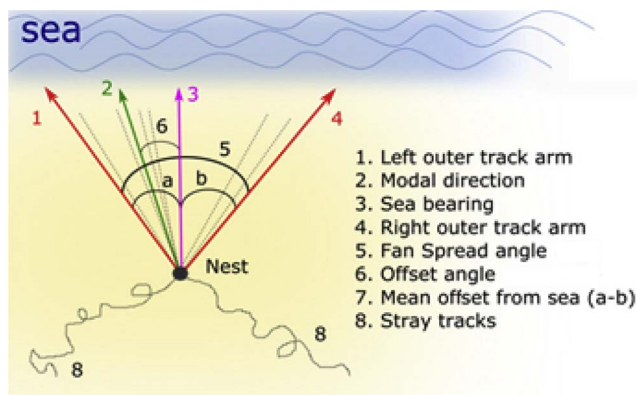


Fig. 2. Diagram of the fan mapping method for hatched nests indicating the measured and calculated angles and bearings (modified from Berry et al., 2013).

direction (i.e. average direction of the tracks) was recorded in cases of more than 5 stray tracks per nest.

For each nest a series of parameters which can have a potential effect on the perception of nighttime lighting by hatchlings were recorded, including the exact geographic position of the nest, the straight distance to the sea (m), the presence of vegetation, sand dunes and other beach furniture in a radius of 20 m around the nest. Beach slope was also reported, at the onset of the hatching period, at various distance intervals for each nesting beach (38 transects traversing beach width placed according to beach morphology changes and length) by using a digital theodolite (LEICA SPRINTER 100). Finally, for each hatched nest the moon phase at the night of hatchlings' emergence was also reported.

2.3. Data analyses

We used the non-parametric Kruskal-Wallis test to investigate for any potential differences in the night light intensity measurements between the nesting beaches. Pair-wise comparisons were performed by applying post-hoc tests after Nemenyi (package PMCMR in R; Pohlert, 2014).

We used Rao's spacing test that checks for significant directionality of movement patterns (circular data) to examine whether the hatchling movements uniformly directed around the nest. This analysis was performed for offset and fan spread angles. We also used Watson Williams test which can compare mean angles in two or more samples, to investigate for significant displacements and directional patterns of the spread of tracks in relation to the direct line to the sea (mean offset from the sea). To investigate for any significant association between the offset angle and the spread of tracks, we used the circular correlation for angular variables. Prior to the implementation of parametric tests (i.e. Watson-Williams test) data fit to von Mises distribution was checked by the use of Watson's U^2 test'. The former analyses were performed at the nest level and then aggregated to nesting beach level while all circular statistics were carried out in R by using the package Circular (Agostinelli and Lund, 2017). Spearman's rank - order correlation coefficient was employed to check for any significant association between the number of stray tracks and the light intensity measurements (derived by each sampling station) at rookery level.

We used Generalized Additive Models (GAM) to test the relationship between the basic directional pattern of hatchings, as been defined by the offset angle, and beach features, at a rookery level. GAMs were implemented by using the mgcv library in R, version 3.3.0. The GAM applied non-parametric smoothers to predictor variables and additively calculated the response upon the dependent variable. A Gaussian distribution was selected using an identity link function. Predictor variables included in the models were: exposure to artificial nightlight, distance of nest to the sea, moon phase, beach slope, presence of sand dunes backing the nest and existence of beach furniture between nest and light source. For the analyses, barriers identified between the nest and the light sources were grouped together. After a preliminary analysis on the non-linear effects, smoothing terms were applied to distance of nest to the sea, beach slope and moon phase.

3. Results

We found significant differences in the intensity of artificial nighttime lighting between nesting beaches (Kruskal - Wallis test, $H = 36.6$, $p < .01$), with the values of light measurement ranging from 0.01 to 0.08 LUX (Fig. 3). Pairwise comparisons revealed that the longer

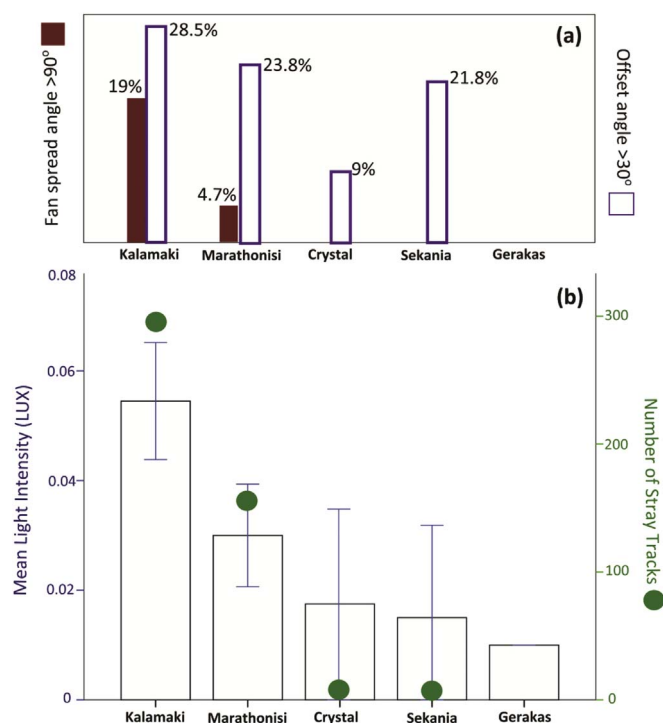


Fig. 3. (a) Percentage of hatchling tracks with a disrupted sea-finding behavior (fan spread and offset angle greater than 90° and 30°, respectively) and (b) mean light intensity measurements (error bars represent 99% confidence intervals of mean) and number of stray tracks at each nesting beach.

nesting beach (i.e. Kalamaki) was the most exposed to nightlight than the other nesting beaches ($p < .05$ in all cases) while the second smallest and most isolated nesting beach (i.e. Gerakas) was a naturally dark beach during nighttime ($p < .05$ in all cases).

In total we reported movement patterns of 5967 loggerhead hatchlings. For all study beaches, Rao's spacing test demonstrated significant deviation of movement patterns from uniformity (in all cases, for both offset and fan spread angle $p < .01$). The significant orientation was not however always directed towards the sea, with evidence on significant displacements detected when comparing Modal vs Sea bearing direction and Sea bearing vs the left and right outer arms of the fan for nests located at the most nightlight polluted beaches (i.e. Kalamaki, Marathonisi and Crystal) (in these cases Watson Williams test $p < .01$). In these nesting beaches hatchling orientation patterns were skewed towards the brightest sources of light (i.e. westward at Kalamaki and Crystal beach, northward at Marathonisi beach) (Fig. 4, Table 1). On the other hand, orientation patterns did not significantly depart from the sea direction for nests located at beaches with limited or null exposure to nightlight pollution (i.e. Sekania and Gerakas, respectively) (in these cases Watson Williams test $p > .05$). According to the metrics used (Table 1), the higher disruption of sea-finding was detected at the most light impacted beaches (Fig. 3). In this respect at the lightest nesting beach (i.e. Kalamaki) offset and fan spread angle presented values over the acceptable threshold of sea-finding disruption for the 28.5% and 19% of the nests studied, respectively.

Circular correlation analyses revealed a significant positive relationship between mean offset of the straight line to the sea and the spread of tracks ($p < .01$), at the three nesting beaches with the increased light intensity (i.e. Kalamaki, Marathonisi and Crystal). No significant relationship between the two variables, was detected in the two beaches (i.e. Gerakas and Sekania) with the limited or null exposure to nightlight pollution (in both cases $p > .05$).

In total we detected 450 stray tracks (7.5% of the total reported tracks). The number of stray tracks was found to be significantly related

with light intensity levels (Spearman's $r_s = 0.79$; $p < .001$) at rookery level with the most light impacted nests resulting in a higher number of stray tracks (Fig. 3). Moreover, at the most light polluted nesting beaches (i.e. Kalamaki, Marathonisi), the majority of the stray tracks was orientated towards the brightest sources of light (westward and northward, respectively). In some extreme cases, hatchlings (108 stray tracks) were found to move directly to the back of the beach towards the sand dunes or to crawl in circular/irregular paths, lacking any kind of orientation pattern (i.e. central part of Kalamaki beach) (Fig. 5).

Offset angle was significantly affected by the nightlight intensity, moon phase and beach slope (GAM: adjusted $R^2 = 0.34$, deviance explained 36.3%). The offset angle increased at higher nightlight intensities (estimate: 113, $p < .01$). Likewise, offset angle was significantly related to the smoothed variable describing moon phase ($F = 4.25$, $p < .05$), decreasing while moving from new to full moon. The relationship of offset angle with slope, even though significant ($F = 10.963$, $p < .01$) did not show a clear relationship; spread angle declined as moving from negligible to slight slopes and increased at steeper slopes (Fig. 6).

4. Discussion

Overall, our analyses revealed strong evidence on a significant impact of artificial nighttime lighting upon hatchling sea-finding orientation. As far as we are aware, our study is the first to provide quantitative evidence on the impact of nightlight upon sea turtle hatchlings in the Mediterranean region. Protected areas are expected to be highly vulnerable to the increasing global threat of artificial nighttime lighting (Gaston et al., 2015), a finding that seems to hold for the only Marine Protected Area in the Mediterranean that was established with the main objective to protect sea turtles and their nesting habitats and it is managed by a Management Agency. It is therefore imperative to transfer this outputs into management initiatives and policy decisions.

The prioritization of conservation efforts and the political pressure towards the application of specific measures largely depend on the ability to quantitatively assess the impact of any threat of interest. So a critical question for sea turtle conservation is whether the hatchling sea-finding disruption due to nightlight pollution could have any effect on the recruitment of the populations. Assuming a mean number of 106 eggs per nest in Zakynthos rookery, 73.6% of them will be hatched (defined as hatching success) and 68.9% will successfully emerge the nest (defined as hatching emergence success) (Margaritoulis et al., 2011). This means that from a clutch of 106 eggs, less than 54 hatchlings might eventually manage to face the last step before entering the sea. In our analyses we found that 7.5% of hatchling tracks studied were heavily disoriented (stray tracks), thus having a limited potential to enter the sea. Considering this 7.5% of stray tracks, we find that less than 40 (~38%) of the eggs laid will have the chance to result to hatchlings which will manage to enter the sea. This estimate is rather conservative since it ignores that almost 20% of the mass nest emergences (more than 15 hatchlings) at rookery level resulted to hatchlings' crawls that can be reported as disrupted from sea-finding (i.e. offset angle $< 30^\circ$). The prolonged crawling duration on the beach weakens the ability to respond to cues used for sea-finding while it also compromises their swimming orientation away from the shore (Lorne and Salmon, 2007), thus further impairing survival probability.

In relevant studies, the level of the disrupted seaward orientation due to artificial lighting is often reported offering the basis for comparisons. For example, in comparison to our findings a higher percentage of loggerhead hatchling were found to deviate from seaward direction in Florida nesting sites (Salmon and Witherington, 1995), while a lower percentage was detected at the Australian rookeries (Berry et al., 2013; Kamrowski et al., 2014). Still, given the differences in the reproductive features (i.e. performance and output) obtained at a population or even at a nesting rookery level, any such comparison could

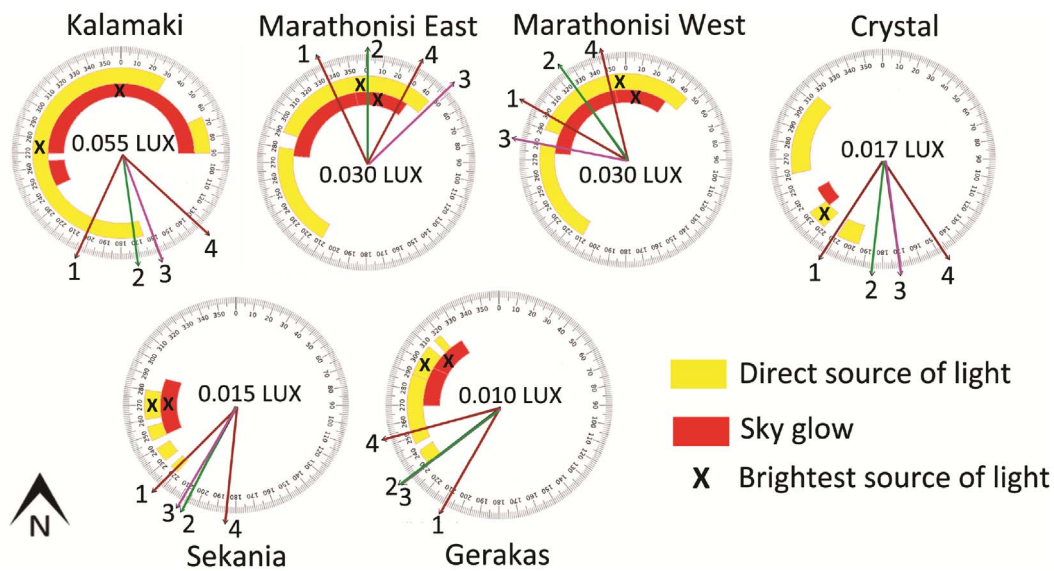


Fig. 4. Average bearings of the fan mapping method metrics (1 and 4: left and right outer arm of the fan, respectively; 2: modal direction of hatchlings and 3: shortest sea bearing) in conjunction with the bearings of direct sources of lights visible from the beach and the sky glow (the bearings of the brightest sources of light are also presented along with the average light level intensity per nesting beach).

offer only limited conservation information. On the contrary, given that models developed to assess population trends and dynamics require accurate estimates on survival rates (Chaloupka, 2002; Mazaris et al., 2005; Mazaris and Matsinos, 2006), the inclusion of disrupted seaward orientation trends into an overall recruitment rate could serve such modeling efforts often used to prioritize and direct conservation initiatives.

Maintaining naturally dark conditions at the nesting sites is the best and most highly recommended management strategy against light pollution impacts on sea turtles (Rivas et al., 2015). Still, any such target might not be realistic particularly in highly touristic or industrial areas. Alternatively, mandatory mitigation measures could include the elimination of the unnecessary lights, the reduction of the luminaire wattage to the minimum required for function, the use of long wavelength lights, the shielding of light sources that are directly visible from the beach and the elimination of all upward-directed lighting (Salmon, 2003). Complementary measures may also include the shading of the nests from night lights, the preservation and enhancement of sand dunes and beach vegetation (e.g. Bourgeois et al., 2009; Karnad et al., 2009; Pendoley and Kamrowski, 2016) as well as the active engagement and participation of the local society, visitors and stakeholders in artificial nighttime lighting reduction initiatives (Kamrowski et al., 2014). The recurrent monitoring and evaluation of artificial nighttime lighting impacts particularly on the most light-polluted nesting beaches is also highly recommended.

Our results suggested that orientation ability of sea turtle hatchlings is determined by synergistic interactions and joint effects of multiple drivers. Therefore, analyzing orientation patterns or drawing mitigation measures by relying solely on nighttime lighting, offers an epi-

phenomenological approach which disregards the complexity of other critical natural or artificial cues. In this respect the moon light has previously been reported, as it was also the case in our study, to be among the factors that are influencing the sea finding ability of the hatchlings (e.g. Tuxbury and Salmon, 2005; Berry et al., 2013). Similarly, the environmental heterogeneity at a nesting beach level (e.g. nest position and beach morphology) does actually compose a complex but unique mosaic of ordination cues, suggesting that effective measures should be designed at a local scale (Limpus and Kamrowski, 2013; Kamrowski et al., 2014). For example even if we recognized that the slope of the nesting beach significantly altered orientation behavior of loggerheads hatchlings in Zakynthos, this relationship was not linear, gradually leading to different responses. A plausible explanation of this pattern could be that nesting beaches in this rookery have rather gentle slopes and thus other factors operating at smaller spatial scales might further alter hatchling' sea-finding ability.

Micro-topographic beach features such as depressions that parallel the tide line (e.g. Marathonisi nesting beach) might act as traps for hatchlings (since the perceived lowest horizon elevation for a hatchling in the bottom of the depression is in a parallel direction to the sea line) forcing them to wander for long distances along the sea line (Fig. 5b) (Limpus and Kamrowski, 2013). Such local effects on hatchling' sea-finding ability also suggest that mitigation measures should be taken even if artificial night lighting is not the primary reason of a disrupted sea-finding behavior.

In some nesting rookeries, the effect of night light pollution seemed to be highly detrimental (e.g. Witherington and Martin, 1996), while in others it has been reported as moderate or minor (e.g. Bourgeois et al., 2009; Kamrowski et al., 2014; Rivas et al., 2015). To cover all factors

Table 1
Hatchlings orientation indices at Zakynthos nesting rookery and night light intensity levels during the 2014 nesting season.

	Nesting beach				
	Kalamaki	Marathonisi	Crystal	Sekania	Gerakas
Mean Light Intensity (LUX) ± standard deviation	0.055 ± 0.017	0.030 ± 0.007	0.017 ± 0.009	0.015 ± 0.005	0.010
Mean fan spread angle (95% confidence intervals of mean)	68.7 (60.0–77.5)	52.8 (40.9–64.7)	64.1 (51.3–76.9)	41.8 (34.8–48.9)	46.6 (32.2–54.9)
Range of fan spread angle	30–135	30–105	35–85	20–75	20–65
Mean offset angle (95% confidence intervals of mean)	16.1 (13.6–18.5)	45.7 (35.6–55.7)	17.9 (16.1–19.8)	11.4 (9.2–13.6)	5.7 (5.7–5.7)
Range of offset angle	0–65	20–85	0–50	0–50	0–20
Orientation Skew Pattern	West	North	West	Sea	Sea

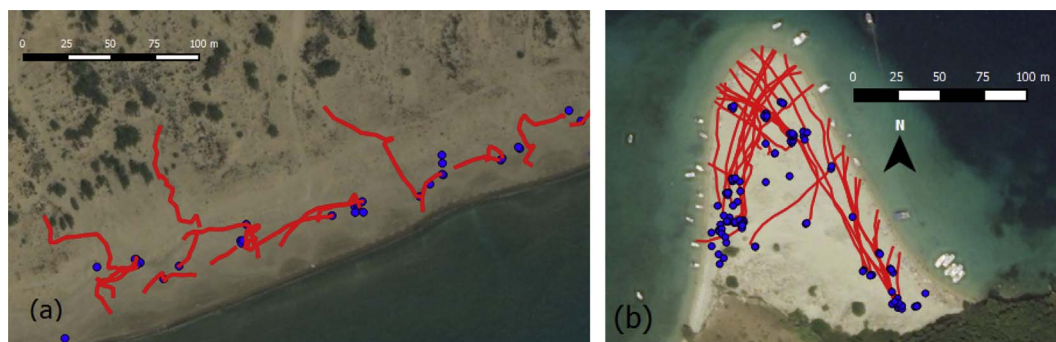


Fig. 5. Directional paths of the stray tracks found in the two most light - impacted nesting beaches of Zakynthos (a: central part of Kalamaki beach and b: Marathonisi beach) (blue dots indicate nests and red lines the routes of the stray tracks). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

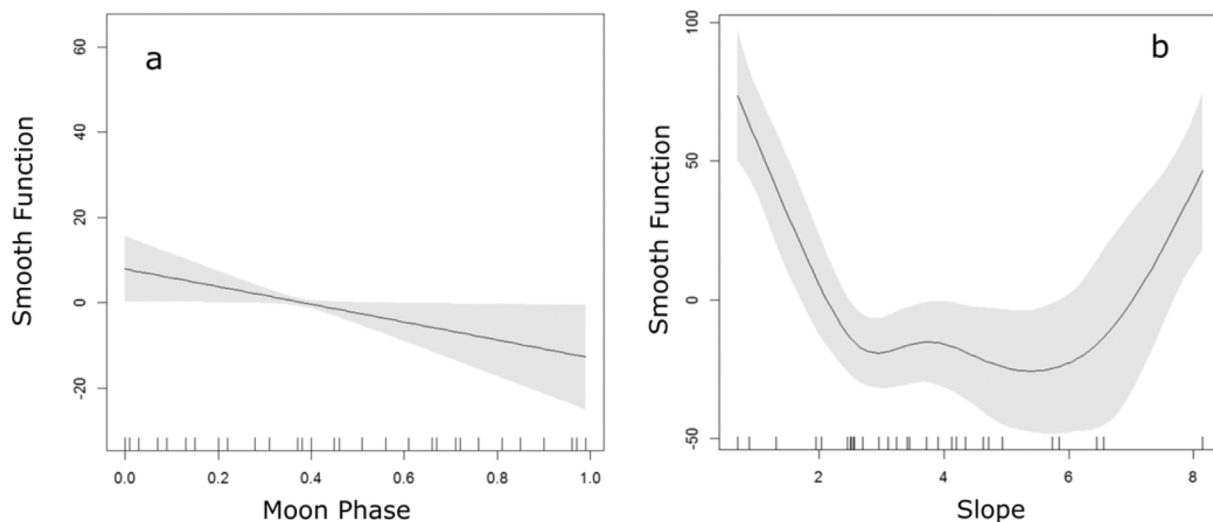


Fig. 6. Relationships, derived from GAMs, illustrate responses between smoothed components of the predictors used (a: moon phase and b: slope) against offset angle; shaded area indicates 95% confidence intervals.

affecting the seaward orientation of sea turtle hatchlings adequately, experimental and field work studies need to be expanded. For example, night light's characteristics such as their wavelength and polarization might also have an impact on the sea-finding orientation ability of sea turtle hatchlings (Witherington and Bjørndal, 1991; Rivas et al., 2015). From an evolutionary perspective, the intra-nest synchronous emergence of sea turtle hatchlings has been considered as an adaptive mechanism against predation (Santos et al., 2016); thus it might be worthy to detect whether a potential differentiation in orientation patterns between consecutive emergences from the same nest could hinder an adaptive value of reproductive synchrony. Further research is also required to evaluate the in-water performance and survival probabilities of hatchlings entering water from different angles. Yet, under the complexity that inherent the evaluation of the synergetic or antagonistic impacts of different environmental features and nightlight properties upon hatchling orientation, and while a pile of information gaps need to be compiled, we suggest that site-specific studies could serve as the first step towards a more effective protection and conservation (e.g. Simões et al., 2017).

Artificial nighttime lighting is expanding worldwide while it is even prevalent and increasing within the Marine Protected Areas (Davies et al., 2016), subsequently raising conservation challenges for a variety

of protected species and valuable habitats. In the case of the NMPZ, one of the main nesting rookeries of the loggerhead sea turtles in the Mediterranean region, the reduction of recruitment caused by artificial night lights raise the need for immediate and proactive conservation initiatives. Recent evidence on the recovery of many sea turtle populations around the globe, suggests that conservation efforts taken at the nesting beaches could be highly effective (Mazaris et al., 2017). We suggest that mitigation measures towards reducing the impacts of artificial nightlight upon hatchlings or adult turtles must be embedded within the recurrent protection activities and planning undertaken at a nesting site level.

Acknowledgments

This study was supported by the Management Agency of the National Marine Park of Zakynthos in the framework of the project 'Monitoring of the oviposition of the loggerhead sea turtle *Caretta caretta* in Laganas Bay' funded by the European Regional Development Fund (ERDF) and National resources (Operational Programme 'Environment and Sustainable Development' under the NSRF 2007–2013). We would also like to thank the referees for their valuable comments that substantially improved the manuscript.

Appendix A

Table A

List of the main artificial nightlight sources that are directly (indicated as '+') or indirectly (indicated as '-') (as night sky glow) visible from the nesting beaches.

Main sources of light	Nesting beach				
	Kalamaki	Marathonisi	Crystal	Sekania	Gerakas
Laganas Settlement (bars, hotels, shops etc)	+, -	+, -	-	+, -	
Airport	-	-	-	-	
Kalamaki road and settlement	-	-	-	-	
Agios Sostis port and village	+, -	+, -		+, -	
Keri port and village	-	+, -		-	
Zakynthos town (-)	-	-			
Hotels, taverns (+)	+		+		

References

- Agostinelli, C., Lund, U., 2017. R package 'circular': circular statistics (version 0.4-93). <https://r-forge.r-project.org/projects/circular/>.
- Alpanidou, A., Schofield, G., Kallimanis, A.S., Türkozan, O., Hays, G.C., Mazaris, A.D., 2016. Using climatic suitability thresholds to identify past, present and future population viability. *Ecol. Indic.* 71, 551–556. <http://dx.doi.org/10.1016/j.ecolind.2016.07.038>.
- Becker, A., Whitfield, A.K., Cowley, P.D., Järnegren, J., Næsje, T.F., 2013. Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *J. Appl. Ecol.* 50, 43–50. <http://dx.doi.org/10.1111/1365-2664.12024>.
- Beger, M., Grantham, H.S., Pressey, R.L., Wilson, K.A., Peterson, E.L., Dorfman, D., Mumby, P.J., Lourival, R., Brumbaugh, D.R., Possingham, H.P., 2010. Conservation planning for connectivity across marine, freshwater, and terrestrial realms. *Biol. Conserv.* 143, 565–575. <http://dx.doi.org/10.1016/j.biocon.2009.11.006>.
- Berry, M., Booth, D.T., Limpus, C.J., 2013. Artificial lighting and disrupted sea-finding behaviour in hatchling loggerhead turtles (*Caretta caretta*) on the Woongarra coast, south-east Queensland, Australia. *Aust. J. Zool.* 61, 137–145. <http://dx.doi.org/10.1071/ZO13028>.
- Bourgeois, S., Emmanuelle, G., Viallefond, A., Boussamba, F., Deem, S.L., 2009. Influence of artificial lights, logs and erosion on leatherback sea turtle hatchling orientation at Pongara national park, Gabon. *Biol. Conserv.* 142, 85–93. <http://dx.doi.org/10.1016/j.biocon.2008.09.028>.
- Casale, P., Margaritoulis, D., 2010. *Sea Turtles in the Mediterranean: Distribution, Threats and Conservation Priorities*. IUCN, Gland, Switzerland.
- Chaloupka, M., 2002. Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecol. Model.* 148, 79–109. [http://dx.doi.org/10.1016/S0304-3800\(01\)00433-1](http://dx.doi.org/10.1016/S0304-3800(01)00433-1).
- Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W., et al., 2012. The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. *Global Ecol. Biogeogr.* 21, 465–480. <http://dx.doi.org/10.1111/j.1466-8238.2011.00697.x>.
- Davies, T.W., Coleman, M., Griffith, K.M., Jenkins, S.R., 2015. Night-time lighting alters the composition of marine epifaunal communities. *Biol. Lett.* 11. <http://dx.doi.org/10.1098/rsbl.2015.0080>.
- Davies, T.W., Duffy, J.P., Bennie, J., Gaston, K.J., 2014. The nature, extent, and ecological implications of marine light pollution. *Front. Ecol. Environ.* 12, 347–355. <http://dx.doi.org/10.1890/1523-1739.2013.12.347>.
- Davies, T.W., Duffy, J.P., Bennie, J., Gaston, K.J., 2016. Stemming the tide of light pollution encroaching into marine protected areas. *Conserv. Lett.* 9, 164–171. <http://dx.doi.org/10.1111/conl.12191>.
- Fritsches, K.A., 2012. Australian loggerhead sea turtle hatchlings do not avoid yellow. *Mar. Freshw. Behav. Physiol.* 45, 79–89. <http://dx.doi.org/10.1080/10236244.2012.690576>.
- Gaston, K.J., Bennie, J., 2014. Demographic effects of artificial nighttime lighting on animal populations. *Environ. Rev.* 22, 323–330. <http://dx.doi.org/10.1139/er-2014-0005>.
- Gaston, K.J., Duffy, J.P., Gaston, S., Bennie, J., Davies, T.W., 2014. Human alteration of natural light cycles: causes and ecological consequences. *Oecologia* 176, 917–931. <http://dx.doi.org/10.1007/s00442-014-3088-2>.
- Gaston, K.J., Duffy, J.P., Bennie, J., 2015. Quantifying the erosion of natural darkness in the global protected area system. *Conserv. Biol.* 29, 1132–1141. <http://dx.doi.org/10.1111/cobi.12462>.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., et al., 2008. A global map of human impact on marine ecosystems. *Science* 319, 948–952. <http://dx.doi.org/10.1126/science.1149345>.
- Hays, G.C., Mazaris, A.D., Schofield, G., 2014. Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Front. Mater. Sci.* 43, 1–9. <http://dx.doi.org/10.3389/fmars.2014.00043>.
- Howard, R., Bell, I., Pike, D.A., 2014. Thermal tolerances of sea turtle embryos: current understanding and future directions. *Endanger. Species Res.* 26, 75–86. <http://dx.doi.org/10.3354/esr00636>.
- IPCC, 2007. Intergovernmental panel for climate change. IPCC fourth assessment report: climate change 2007. working group II: impacts, adaptation and vulnerability. https://www.ipcc.ch/publications_and_data/ar4/wg2/en/ch6s6-2-2.html.
- Kamrowski, R.L., Limpus, C., Pendoley, K., Hamann, M., 2015. Influence of industrial light pollution on the sea-finding behaviour of flatback turtle hatchlings. *Wildl. Res.* 41, 421–434. <http://dx.doi.org/10.1071/WR14155>.
- Kamrowski, R.L., Sutton, S.G., Tobin, R.C., Hamann, M., 2014. Potential applicability of persuasive communication to light-glow reduction efforts: a case study of marine turtle conservation. *Environ. Manag.* 54, 583–595. <http://dx.doi.org/10.1007/s00267-014-0308-9>.
- Karnad, D., Isvaran, K., Kar, C.S., Shanker, K., 2009. Lighting the way: towards reducing misorientation of olive ridley hatchlings due to artificial lighting at Rushikulya, India. *Biol. Conserv.* 142, 2083–2088. <http://dx.doi.org/10.1016/j.biocon.2009.04.004>.
- Katselidis, K.A., Schofield, G., Stamou, G., Dimopoulos, P., Pantis, J.D., 2012. Females first? Past, present and future variability in offspring sex ratio at a temperate sea turtle breeding area. *Anim. Conserv.* 15, 508–518. <http://dx.doi.org/10.1111/j.1469-1795.2012.00543.x>.
- Kawamura, G., Naohara, T., Tanaka, Y., Nishi, T., Anraku, K., 2009. Near ultraviolet radiation guides the emerged hatchlings of loggerhead turtles *Caretta caretta* (Linnaeus) from a nesting beach to the sea at night. *Mar. Freshw. Behav. Physiol.* 42, 19–30. <http://dx.doi.org/10.1080/10236240802663580>.
- Limpus, C.J., Kamrowski, R.L., 2013. Ocean-finding in marine turtles: the importance of low horizon elevation as an orientation cue. *Behaviour* 150, 863–893. <http://dx.doi.org/10.1163/1568539X-00003083>.
- Lorne, J.K., Salmon, M., 2007. Effects of exposure to artificial lighting on orientation of hatchling sea turtles on the beach and in the ocean. *Endanger. Species Res.* 3, 23–30. <http://dx.doi.org/10.3354/esr003023>.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., et al., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312, 1806–1809. <http://dx.doi.org/10.1126/science.1128035>.
- Luarte, T., Bonta, C.C., Silva-Rodriguez, E.A., Quijón, P.A., Miranda, C., Farias, A.A., Duarte, C., 2016. Light pollution reduces activity, food consumption and growth rates in a sandy beach invertebrate. *Environ. Pollut.* 218, 1147–1153. <http://dx.doi.org/10.1016/j.envpol.2016.08.068>.
- Management Agency of the Zakynthos National Marine Park, 2008. *Sea Turtle Nesting Beach Scientific Research Programme*. Technical Report. NMPZ, Zakynthos, Greece, pp. 163.
- Margaritoulis, D., 2005. Nesting activity and reproductive output of loggerhead sea turtles, *Caretta caretta*, over 19 seasons (1984–2002) at Laganas Bay, Zakynthos, Greece: the largest rookery in the Mediterranean. *Chelonian Conserv. Biol.* 4, 916–929.
- Margaritoulis, D., Rees, A.F., Dean, C.J., Riggall, T., 2011. Reproductive data of loggerhead turtles in Laganas Bay, Zakynthos Island, Greece, 2003–2009. *Mar. Turt. Newsl.* 131, 2–6.
- Mazaris, A., Fiksen, Ø., Matsinos, Y.G., 2005. Using an individual based model for assessment of sea turtle population viability. *Popul. Ecol.* 47, 179–191. <http://dx.doi.org/10.1007/s10144-005-0220-5>.
- Mazaris, A., Matsinos, Y.G., 2006. An individual based model of sea turtles: investigating the effect of temporal variability on population dynamics. *Ecol. Model.* 194, 114–124. <http://dx.doi.org/10.1016/j.ecolmodel.2005.10.006>.
- Mazaris, A.D., Schofield, G., Gkazinou, C., Alpanidou, V., Hays, G.C., 2017. Global sea turtle conservation successes. *Sci. Adv.* 3, e1600730. <http://dx.doi.org/10.1126/sciadv.1600730>.
- Micheli, F., Levin, N., Giakoumi, S., Katsanevakis, S., Abdulla, A., Coll, M., Fraschetti, S., Kark, S., Koutsoubas, D., Mackelworth, P., Maiorano, L., Possingham, H.P., 2013. Setting priorities for regional conservation planning in the Mediterranean Sea. *PLoS One* 8. <http://dx.doi.org/10.1371/journal.pone.0059038>.
- Pendoley, K., Kamrowski, R.L., 2016. Sea-finding in marine turtle hatchlings: what is an appropriate exclusion zone to limit disruptive impacts of industrial light at night? *J. Nat. Conserv.* 30, 1–11. <http://dx.doi.org/10.1016/j.jnc.2015.12.005>.
- Pendoley, K.L., 2005. *Sea Turtles and the Environmental Management of Industrial Activities in North West Western Australia*. Ph.D. Thesis. Murdoch University, Perth.
- Perry, G., Fisher, R.N., 2006. Night lights and reptiles: observed and potential effects. In: Rich, C., Longcore, T. (Eds.), *Ecological Consequences of Artificial Night Lighting*. Island Press, Washington, pp. 169–191.
- Peters, A., Verhoeven, K.J.F., 1994. Impact of artificial lighting on the seaward orientation of hatchling loggerhead turtles. *J. Herpetol.* 28, 112–114.

- Pohlert, T., 2014. The pairwise multiple comparison of mean ranks package (PMCMR). R package. <http://CRAN.R-project.org/package=PMCMR>.
- Rich, C., Longcore, T., 2006. *Ecological Consequences of Artificial Night Lighting*. Island Press, Washington.
- Rivas, M.L., Tomillo, P.S., Uribeondo, J.D., Marco, A., 2015. Leatherback hatchling sea-finding in response to artificial lighting: interaction between wavelength and moonlight. *J. Exp. Mar. Biol. Ecol.* 463, 143–149. <http://dx.doi.org/10.1016/j.jembe.2014.12.001>.
- Salmon, M., Witherington, B.E., 1995. Artificial lighting and seafinding by loggerhead hatchlings: evidence for lunar modulation. *Copeia* 4, 931–938. <http://dx.doi.org/10.2307/1447042>.
- Salmon, M., 2003. Artificial night lighting and sea turtles. *Biologists* 50, 163–168.
- Santos, R.G., Pinheiro, H.T., Martins, A.S., Riul, P., Bruno, S.C., Janzen, F.J., Ioannou, C.C., 2016. The anti-predator role of within-nest emergence synchrony in sea turtle hatchlings. *Proceedings of the Royal Society B: Biological Sciences* 283 (1834), 20160697. <http://dx.doi.org/10.1098/rspb.2016.0697>.
- Simões, T.M., da Silva, A.C., de Melo Moura, C.C., 2017. Influence of artificial lights on the orientation of hatchlings of *Eretmochelys imbricata* in Pernambuco, Brazil. *Zoologia* 34, 1–6. <http://dx.doi.org/10.3897/zoologia.34.e13727>.
- Thums, M., Whiting, S.D., Reisser, J., Pendoley, K.L., Pattiaratchi, C.B., Proietti, M., Hetzel, Y., Fisher, R., Meekan, M.G., 2016. Artificial light on water attracts turtle hatchlings during their near shore transit. *R. Soc. Open Sci.* 3, 160142. <http://dx.doi.org/10.1098/rsos.160142>.
- Troy, J.R., Holmes, N.D., Green, M.C., 2011. Modeling artificial light viewed by fledgling seabirds. *Ecosphere* 2, 1–13. <http://dx.doi.org/10.1890/ES11-00094>.
- Tuxbury, S.M., Salmon, M., 2005. Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. *Biol. Conserv.* 121, 311–316. <http://dx.doi.org/10.1016/j.biocon.2004.04.022>.
- Weber, S.B., Broderick, A.C., Groothuis, T.G., Ellick, J., Godley, B.J., Blount, J.D., 2011. Fine-scale thermal adaptation in a green turtle nesting population. *Proc. R. Soc. Lond. B Biol. Sci.* 279, 1077–1084. <http://dx.doi.org/10.1098/rspb.2011.1238>.
- Witherington, B.E., Bjørndal, K.A., 1991. Influence of wavelength and intensity on hatchling sea turtle phototaxis: implications for sea-finding behavior. *Copeia* 1991, 1060–1069.
- Witherington, B.E., Martin, R.E., 1996. *Understanding, Assessing, and Resolving Light-pollution Problems on Sea Turtle Nesting Beaches*. Florida Marine Research Institute technical report TR2, 1-73.