Environmental cues and sensory preferences directing the nesting process in loggerhead turtles, *Caretta caretta*, nesting in Maputaland, South Africa

By

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Submitted in fulfilment of the requirements for the degree of Masters of Science in the department of Zoology at the Nelson Mandela Metropolitan University

January 2012

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Declaration

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Declaration

In accordance with Rule G 4.6.3, I hereby declare that the above-mentioned dissertation is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

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Abstract

Animals use their senses for everything on an immediate, and day to day fashion – detecting danger, finding food, finding mates among other activities. In sea turtles and other migratory species senses are used for long-distance migrations. Senses such as smell, vision and hearing, have been studied experimentally under laboratory conditions but seldom have been investigated in the field. This thesis takes a combination of field and laboratory experiments and investigates some of the hypotheses involved in natal homing and nest site selection. The loggerhead's nesting distribution in Maputaland is distinct with characteristic high and low density nesting areas which are consistent from year to year. Investigations by earlier researchers on these beaches suggested that beach characteristics, such as beach morphodynamic type and beach width, do not appear to influence the beaches at which loggerheads emerge to nest. The high density nesting area (with approximately 440 loggerhead emergences/km) have similar beach characteristics as the low density nesting area (with <50 loggerhead emergences/km). It is therefore suggested that there is another cue that drives nest site selection. It can either be related to a physical characteristic not yet realised, or is a non-physical (but chemical or biological) cue. This dissertation aims to identify the sensory inputs received during the nest selection process, as well as sea-finding ability after nesting. To investigate the mechanism causing the high-density as opposed to the low-density nesting area, three potential drivers were investigated namely: chemical imprinting (as a natal beach cue), ambient and artificial light (as deterrents) and social facilitation (as a learned behaviour). It was also attempted to identify the strength of the most common senses – vision, hearing and smell. As animal ethics restricts interfering with emerging or nesting turtles, the strengths of these senses were tested during sea-finding by adult loggerheads. The results indicate that sulfide concentrations appear to be used as chemical cues for nesting as these concentrations are elevated (>150%) in the high density nesting beaches compared to the low density nesting beaches within and among seasons however further investigations are required. Artificial light (range: 0.045–0.5 lux) is an active deterrent of female emergences while ambient light, even under extreme conditions such as lightning during electric storms (up to 8.2 lux), appears to have no observable influence on the spatial or temporal distributions of emergences. Social facilitation appears unlikely as a primary nest site selection factor for loggerheads. It may however, play a minor secondary role to preferred areas or hotspots. Sea-finding in post-nesting female loggerheads appears to be driven exclusively by visual cues such as the light horizon, with minimal to no influence from other cues (the sound of the breakers, slope or smell of the ocean) which solidify the visual system's use in sea-finding. This research on the nest site selection of loggerheads and the sensory systems involved in this process has added valuable information to the limited pool of knowledge already present and has created a solid framework on which further investigations can be based. Future work in this field should focus on integrating a suite of sensory stimuli and cues to receive a greater understanding of the sensory systems used in nest site selection.

Keywords: imprinting, light, loggerhead sea turtle, natal homing, nest site selection, social facilitation

Acknowledgements

Firstly, I would like to thank Ronel Nel for her continued assistance and support throughout the process of this dissertation. She has contributed significantly to this project and her input was always appreciated. I would also like to thank Deo Winter for his continued input on methods and the statistical analyses. Further thanks go to Dave Schoeman and Lorenz Hauser for their contributions to the statistics of this project.

Special thanks go to Linda Harris who has assisted in many GIS problems and in aiding in the creation of all the maps in this dissertation. Further acknowledgements go to all the assistants that were more than willing to collect data for this project. These are in no particular order: Robyn Holm, Jenny Tucek, Linda Harris, Anje De Wet, Nora Weyer, Julia Walbruhl, and Nathan Robinson.

I would also like to thank the iSimangaliso Wetland Park authority and Ezemvelo KwaZulu-Natal for allowing this project to happen. Eric Mhlaba, and the field rangers, of Ezemvelo deserve a special mention as they were always around to assist in any problems encountered in the field. A large section of this dissertation would not be possible without the permission from the Bayworld Aquarium in Port Elizabeth, South Africa, which allowed me to perform my experiments on their loggerheads. A huge thank you to Malcolm Smale, Michelle du Toit, and Steve Warren for their continued input at all stages of the Bayworld experiments. A further thank you to Malcolm Smale for use of his personal equipment for the duration of the Bayworld experiments.

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Chapter 1: General Introduction

Introduction

Sea turtles are marine reptiles that inhabit neritic and oceanic environments in the tropics and subtropics (Bolten 2003). They are a highly migratory species travelling large distances throughout their lives (Lohmann *et al.* 1999). Loggerhead turtles (*Caretta caretta*), like other sea turtles, begin the oceanic part of life with a pelagic phase where they inhabit oceanic currents for about 10 years. This is termed the 'lost years' because of the many unknowns in distribution and destination of these migrations (Reich *et al.* 2007). After a decade, they return to coastal (neritic) waters as juveniles, using magnetic cues to find foraging habitat in the very general vicinity of their natal beaches (Avens & Lohmann 2004, Luschi *et al.* 2007, Lohmann *et al.* 2008), where they undergo a dietary change from pelagic coelenterates to benthic crustaceans and molluscs. These turtles remain in coastal waters until they reach maturity which is when they initiate the long distance migrations to their breeding sites (Hopkins-Murphy *et al.* 2003).

Natal homing

All adult sea turtle species perform natal homing migrations between their foraging and nesting grounds often traversing thousands of kilometres (i.e. leatherbacks) to the beaches they hatched upon (Hughes 1996, Luschi *et al.* 1998, Papi *et al.* 2000, Schroeder *et al*. 2003, Craig *et al.* 2004). It is suspected that a suite of cues are used for these migrations, one of which is geomagnetic cues (Lohmann *et al.* 1999, Lohmann 2007, Lohmann *et al.* 2007, Fuentes-Farias *et al.* 2008). Sea turtles are able to detect both inclination angle and intensity of the earth's magnetic field allowing the sea turtle to position them on the globe (Lohmann *et al.* 1999, Fuentes-Farias *et al.* 2008). However, magnetically-inhibited green turtles still return to their foraging grounds, from their nesting grounds, without any apparent difficulties suggesting that geomagnetic cues are not important in at least post-nesting migrations (Papi *et al.* 2000). Furthermore, there are considered other cues that are equally important in these natal homing migrations although these cues are unknown (Benhamou *et al.* 2011).

It is possible that natal homing is not only selecting for the general vicinity of the nesting beach but may be specific to a selected section of the nesting beach (Fuentes-Farias *et al.* 2008, Botha 2010). There is evidence to suggest that female loggerheads nesting in

Maputaland, South Africa, increase their nest site fidelity (i.e. become more accurate) with increased return nesting seasons (Botha 2010). Nest site fidelity (i.e. specificity of the area used for repeated nesting) is approximately 3.7 km in neophyte (i.e. first time) nesters and shrinks to approximately 1.5 km in fourth season nesters. This is remarkable as these loggerheads have over 150 km of beaches available for nesting (Nel 2008). There is thus a clear preference for specific sites and the increased specificity through repeat nesting suggests that nest site selection is a learned process.

Environmental cues and nest site selection

Although geomagnetic cues are suspected to be used for the migrations from foraging grounds to nesting grounds i.e. intermediate to long-distance homing (Lohmann *et al.* 1999, Lohmann 2007, Lohmann *et al.* 2007, Fuentes-Farias *et al.* 2008), it is unlikely that these cues may be used in fine-scale, localized nest site selection (Kenneth Lohmann, pers. comm.) Therefore, other cues must be guiding nest site selection, as is the case for loggerheads in Maputaland. Sea turtle senses potentially used for nest site selection include geomagnetism (Fuentes-Farias *et al*. 2008), vision (Witherington 1992), hearing (Wyneken 2001) and olfaction (Owens *et al.* 1982, Grassman *et al.* 1984, Grassman 1993, Mrosovsky 2007, see appendix A for details on these sensory systems). These senses may be used independently or as a suite of inputs to provide navigational information/direction.

Environmental and beach characteristics that have been investigated as drivers of nest site selection include the presence of reefs or rocks (Mortimer 1995), the cover of various vegetation types (Mazaris *et al.* 2006, Serafini *et al.* 2009) intertidal slope (Eckert 1987, Garmestani et al. 2000, Wood & Bjorndal 2000, Mazaris *et al.* 2006, Serafini *et al.* 2009), length and width of the beach (Mazaris *et al.* 2006), sand and clay colour (Mazaris *et al.* 2006), sand pH (Garmestani et al. 2000, Mazaris *et al.* 2006), soil texture (Mazaris *et al.* 2006), sand organic content (Mazaris *et al.* 2006) and substratum type (Mazaris *et al.* 2006). Specific beach variables measured on the nesting beaches in Maputaland include presence/absence of inshore rocks, surf-zone width as a proxy for wave exposure, beach morphodynamic type (see McLachlan & Brown 2006 for definitions), slope, beach width, back-beach width, pH and mean grain size (Botha 2010). Botha (2010) showed that the number of nesting loggerheads is not strongly correlated with any of the beach features (with the exception of intertidal rock) and hence assumed to be relatively unimportant as drivers of nest site selection. However, it was not surprising that there was no correlation between the number of nesting loggerheads and the beach morphodynamic features (such as surfzone width, wave height and period, and grain size) because Harris *et al.* (2011) found that these beach morphodynamic features are too uniform to create morphodynamic types other than intermediate-reflective.

Visual cues may act in many different ways in the selection of a nesting site. For example, physical features such as the presence of dune fields, reefs and rocks, which presumably provide visual cues, may be a selection or avoidance factor. High dunes, creating dark beaches may be attractive, whereas turtles may avoid beaches on rocky headlands or with low-lying rock as these can provide obstacles. Maputaland loggerheads specifically avoid rocky outcrops in the shallow inshore especially during low tide (Botha 2010). Further, when emerging onto the beach or while on the beach, sea turtles are disturbed by the presence of people, especially those with lights (pers. obs.). Further evidence exists that adult females emerging onto beaches to nest avoid artificially illuminated beaches illustrating a reduced number of nesting numbers on these illuminated beaches (Proffitt *et al.* 1986, Witherington 1992, Salmon 2003, Mortimer 2004). Artificial lights also have a major effect on hatchlings as naive sea-seeking hatchlings orientate towards the brightest light assuming it to be the light horizon (Salmon & Witherington 1995, Salmon *et al.* 1995, Tuxbury & Salmon 2005, Bourgeois *et al.* 2009). In the presence of artificially illuminated beaches, the brighter direction instead lies landward of the beach, often misorientating hatchlings which results in desiccation and predation (Mortimer 2004).

The effect of natural ambient light on adult nesting turtle behaviour is not well documented. Pike (2008) used full/new moon phase as a proxy for light intensity as a nesting cue and found little influence of varying moon phases on nesting frequency. However, these light intensities were not quantified but were estimated from moon phases alone. Furthermore, changing weather conditions, such as cloud cover, would alter the light intensity at any one time resulting in inaccurate results. Vision thus seems to be a potentially valuable sense for nest site selection although more to indicate unsuitable habitat, obstacles or for the avoidance for potential threats. Therefore further investigation is needed into the effect of ambient light on nesting distributions both spatially and temporally.

Social facilitation

Social facilitation plays a role in almost all organism's behaviour in some or other form ranging from the highly social groupings and interactions of dolphins, the schooling behaviour of some fish species, to the lives of solitary organisms. Examples of social facilitation are the copied behaviour of spotted hyena where individuals copy social defecating among other activites (Glickman *et al.* 1997) and cattle eating the same plants as conspecifics by copying (Ralphs *et al.* 1994). It is suggested that social facilitation operate among sea turtle females preparing to nest; neophyte nesters (first-time nesters) that are not familiar with the nesting grounds will follow experienced individuals (those that have nested before) to the nesting grounds (Hendrickson 1958, Owens *et al.* 1982). The mechanism of trailing is speculated to be an attraction to a pheromone secreted by Rathke's gland (Ehrenfeld & Ehrenfeld 1973, Weldon & Tanner 1990, Rostal *et al.* 1991, Plummer & Trauth 2009). This gland that has been speculated to be used in conspecific communication and is situated ventrolaterally in the auxiliary, inguinal and inframarginal regions of the plastron and it excretes a carbohydrate-protein (Ehrenfeld & Ehrenfeld 1973, Weldon & Tanner 1990, Rostal *et al.* 1991). There are no results from published literature on sea turtles that have investigated the informative ability of these pheromones and therefore the purpose of these glands remains speculative (Plummer & Trauth 2009).

Chemical imprinting hypothesis

Another method of nest site selection using the olfactory sense has been suggested and is currently the leading hypothesis for specific natal homing (i.e. chemical imprinting hypothesis). Chemical imprinting has been demonstrated to operate in salmon (Nevitt & Dittman 1999) and penguins (Wright *et al.* 2011). Regardless of the popularity of this hypothesis, there is limited published literature on the topic and hardly any involving sea turtles (Hendrickson 1958, Owens *et al.* 1982). The chemical imprinting hypothesis states that emerging hatchlings (from the nest chamber) and hatchling moving down the beach to the water, identify and remember (or imprint) the unique scent of their natal beach (Hendrickson 1958, Owens *et al.* 1982). The origin of this scent or the time at which it is imprinted is unknown. When returning as adults, they use the imprinted scent to find their natal nesting beaches. This scent is presumably detectable from the water either because it originated in the water, or it seeps into the water through the groundwater of the beach or it is present as an airborne cue.

A good example of natal homing is that of the green turtle migration to Ascension Island. The intermediate portions of these migrations are thought to be driven by geomagnetic cues (Benhamou *et al.* 2011) until they reach the scented plume (waterborne or airborne) of the island where they would then use this to find the island (Koch *et al.* 1969). This may also occur on continental nesting beaches if specific areas have distinctive scents and these scents are detectable by the sea turtles using them. In the case of migrating chum salmon it is speculated that the cue may be generated by vegetation growing on the banks and the scent leaching into the water (Yamamoto & Ueda 2009; Ishizawa *et al.* 2010). However, results from the literature on chemical imprinting are inconclusive, especially for sea turtles. Because of sea turtle's IUCN endangered listing, experiments centred on handling adult sea turtles are restricted by ethical considerations not to interfere with nesting ability or survivorship. The ideal experiment would require manipulating gravid females before nesting however, this is not an option.

The majority of published literature on chemical imprinting in sea turtles focuses on juveniles and hatchlings (Owens *et al.* 1982, Grassman *et al.* 1984) because of the ease in acquiring and moving smaller individuals. Further, these studies are focussed laboratory studies and therefore conducted under controlled environments. One such study used hatchlings imprinted to various artificial chemicals in the nest chambers and after hatching (Owens *et al.* 1982). These hatchlings were then given a choice of imprinted and non-imprinted scents to which they selected the imprinted scent more often than any other scent. Another study (by Grassman *et al.* 1984) on juveniles in a similar experimental setup as the previous example however, used the scent of natal beach sand instead of artificial chemicals. The results from this study suggest that sea turtles imprinted to a specific nesting beach are affiliated with the smell of their natal beaches (natal beach scent) as juveniles. However, whether this is used in natal homing or specific nest site selection is unknown.

A sea turtle's sense of hearing or auditory ability has been suggested to be used as a natal homing cue in some populations (Mrosovsky, 1972; Luschi *et al.* 1996, Lohmann 2007). These are usually populations that nest on islands such as Ascension Island in the Atlantic

Ocean. Low frequency sounds originating from wave action on beaches can be heard by fish and molluscs among other marine animals (Stocker 2002) and can potentially be used by sea turtles to find nesting islands or continents. Sea turtle populations that nest on larger continents are less likely to find their specific nesting beaches because the waves from the whole coast would assumedly be similar and therefore sea turtles would be unable to identify their specific nesting beaches. However low frequency sounds from waves on continents may be used as a primary cue to find the continent if these sea turtles are migrating across oceanic waters.

Sea-finding behaviour

Once adult sea turtles have selected a nesting beach to nest upon and have finished the nesting process, they need to find their way back to the ocean. There is scant evidence for adult sea-finding behaviour however, what does exist suggests that adults use visual cues (Ehrenfeld & Carr 1967). Hatchling sea-finding, however, has been extensively studied and it is assumed that the mechanism of sea-finding in adults and hatchlings will be similar. Therefore the results from hatchling sea-finding are discussed here in light of adult sea-finding behaviour. Hatchlings are known to orientate towards the brighter light and often is the case where coastal developments, fishermen and other sources of artificial light attract these hatchlings leading them away from the ocean (Peters & Verhoeven 1994, Salmon 2003, Bourgeois *et al.* 2009, Karnad *et al.* 2009). Under natural conditions, the brighter sea surface and the darker dune silhouette are used for sea-finding (Salmon *et al.* 1992, Salmon & Witherington 1995, Bartol & Musick 2003). However when the sea surface is not the brighter direction, the lower silhouette (which is usually the sea surface) is primarily used for sea-finding (Salmon *et al.* 1992, Bartol & Musick 2003).

Implications of nest site selection

The obvious outcome of nest site selection is emergence success which is usually the indirect measure of nesting success. For example, if a female places all her clutches below or near the high water mark, then the emergence success of hatchlings will be low and the nesting success will also be low (Botha 2010). Nest site selection is thus an important process for gravid females because it depicts reproductive success of the individual. Further, sea turtles have temperature dependent sex determination and nest placement has major implications for hatchling sex ratios (Kamel & Mrosovsky 2005). Many sea turtle programs have been/are involved with actively relocating nests that are most likely to become inundated during tidal events or in an attempt to establish a new or previously lost nesting ground (Carr 1967, Wyneken *et al.* 1988, Godfrey & Baretto 1995, Dutton *et al.* 2003, Bell *et al.* 2005, Kornaraki *et al.* 2006, Mrosovsky 2007). This reinforces the importance of nest site selection in sea turtles. Lastly, the chemical imprinting hypothesis, as described above, is often assumed to be the driver of natal homing migrations. This hypothesis has been used as a mechanism to imprint hatchlings to these beaches in an attempt to establish a new nesting population (Bell *et al.* 2005, Mrosovsky 2007). Therefore nest site selection is of great importance to the ecology and conservation of sea turtles however there is a limited amount of information on the topic to provide accurate accounts.

Dissertation outline

Each chapter will investigate a specific sense and the potential cues associated with each sense together with their underlying theories of navigation.

To set the scene for the dissertation a thorough description of the Maputaland sea turtle monitoring program, the beaches hosting the program and the methods for data collection are provided in Chapter 2; Study Site. A subset of the data from this long-term monitoring program is present or at least referred to in every other chapter. All aspects of the monitoring program and influencing factors to the monitoring program and to aspects of this dissertation are discussed.

The aim of Chapter 3 is to outline olfactory imprinting and to evaluate if olfactory imprinting is present in loggerhead populations in Maputaland. This is done by performing orientation experiments on captive adults and hatchlings in the field as well as measuring nutrient levels in the groundwater/swash along the coast that hatchlings may use as cues to imprint on and subsequently use as adults to find their natal beaches.

The effect of ambient and artificial lights on loggerhead nesting emergence in Maputaland is discussed in Chapter 4. This chapter aims to determine the spatial and temporal effects of ambient and artificial light on nesting emergences. Light intensities along the nesting beaches are quantified and related to hotspots for nesting emergences. Various weather conditions, such as full moon and lightning storms are also evaluated in terms of changes in light intensity and the potential effects it may have on turtle nesting.

Chapter 5 will deal with the social facilitation hypothesis and whether it is used in nest site selection. The long-term loggerhead monitoring program is analysed in terms of clustered emergences as a proxy of social facilitation. Initial and subsequent nest placements are also investigated in light of the social facilitation hypothesis.

Understanding the sensory cues used in sea-finding, after nesting, may provide valuable information for sensory perception. It may also provide insight into the cues potentially used for nest site selection and therefore these are the aims of Chapter 6: discover the primary and potential cues used in sea-finding behaviour in adult loggerheads.

The final chapter, Chapter 7, provides a holistic view of the sensory biology of sea turtles and concludes on the findings from all the other chapters. The most likely drivers of nest site selection are discussed with a further discussion on the importance of understanding nest site selection.

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Chapter 2: Study site and the South African sea turtle monitoring program

Study site

The Maputaland beaches (previously Tongaland) in Northern KwaZulu-Natal, South Africa, are the southernmost nesting grounds of sea turtles in the world (≈27°S). These nesting grounds are frequented by both loggerhead (*Caretta caretta* L.) and leatherbacks (*Dermochelys imbricata* L.). Loggerheads nest on South African beaches (<1000 nesting females.yr^{-1}) more often than leatherbacks (<100 nesting females.yr^{-1}). This site falls within the UNESCO world heritage site, i.e. the iSimangaliso Wetland Park (iSimangaliso, Fig. 2.1). This world heritage site was proclaimed in 1999 and is an amalgamation of terrestrial and two marine protected areas (MPAs), namely the Maputaland and the St Lucia Marine Reserves. The sea turtle nesting beaches and the reef systems were key reasons for the proclamation of this area as a marine reserve (Mountain 1990, Hughes 2010). The park boundary extends three nautical miles seawards and provide protection to the natural habitat of this area including a rich biodiversity together with rare and endangered species.

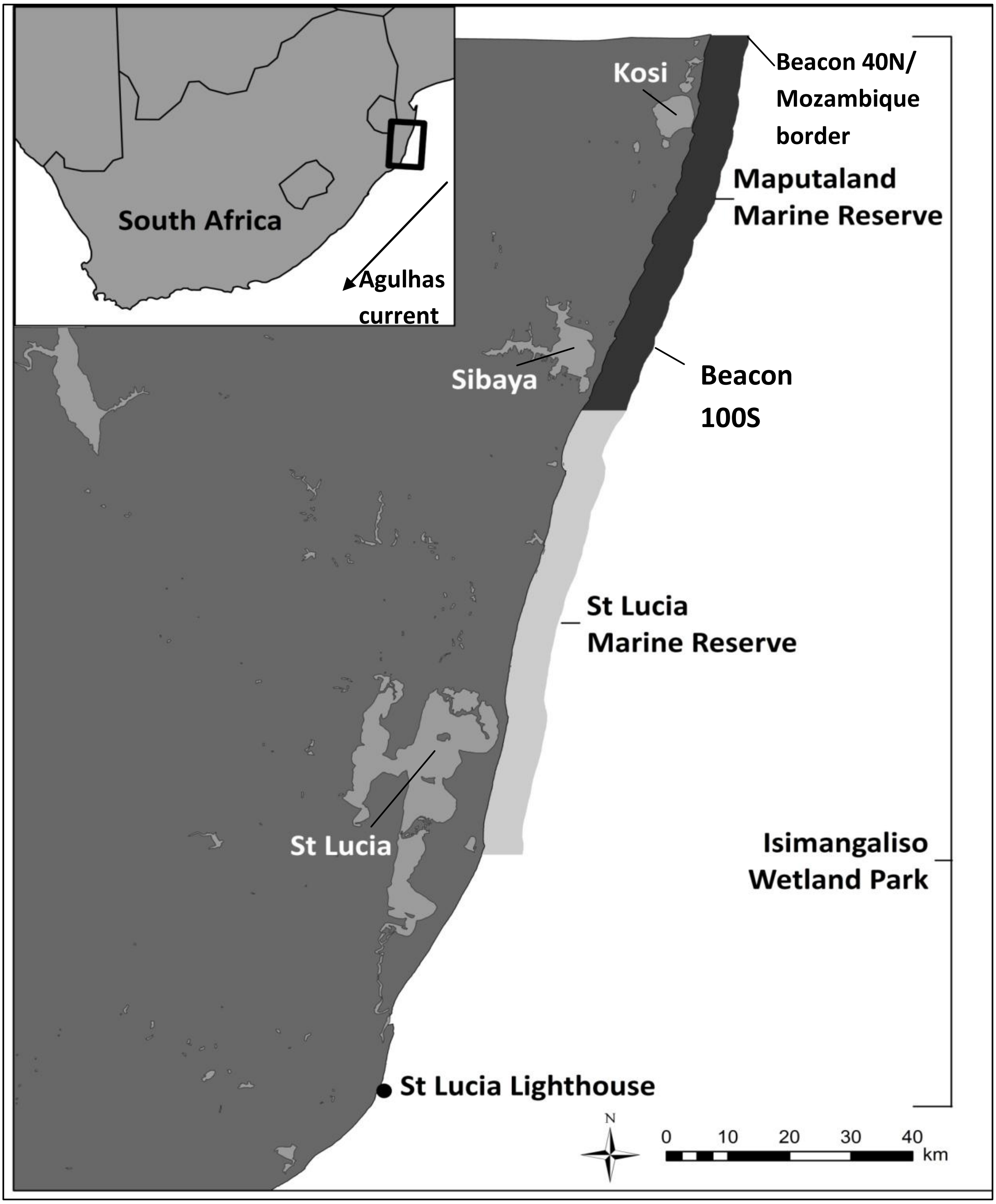

Figure 2.1: Map illustrating the position of the iSimangaliso Wetland Park with the St Lucia marine reserve and the Maputaland marine reserves within South Africa. Mozambique is situated north-east of South Africa. Labels in white are the names of the major coastal lakes/estuaries.

The climate of the study site is tropical to subtropical with a mean annual ambient temperature of 21°C (van Wyk & Smith 2001). Rainfall is highly variable with 60 % of the approximately 1200 mm per annum falling in the summer months of November to March (van Wyk 1996, van Wyk & Smith 2001). Prevailing winds are northerly (Wright *et al.* 2000). Climate along the east coast of South Africa is heavily influenced by the Agulhas current (Rouault *et al.* 2002).

The warm Agulhas current flows southwards extending to the southern tip of Africa (Schumann & Orren 1980, Lutjeharms & Ansorge 2001). The peak surface temperatures of the Agulhas current adjacent to the nesting beaches, off northern KZN, is approximately 28° C in summer with minimum temperatures of 21° C in winter (Schumann & Orren 1980). The maximum speed of this current off Maputaland is 1.5 $m.s^{-1}$ (Schumann & Orren 1980). Often offshoots of the Agulhas current form clockwise vortices that run northerly and parallel to the coast (Duncan 1970, Harris 1978), which describes the general movement of the nearshore waters off the Maputaland nesting beaches (Hughes 1974). The Agulhas current carries post-nesting females, hatchlings and sick, weak juvenile or adult sea turtles south along the east coast of South Africa where they sometimes strand (Baldwin et al. 2003, Nel 2008).

Maputaland is a high-energy coastline with the dominant wave action from the south east (Hughes 1996) which results in the characteristic morphology of the coastline made up of consecutive bays and rocky points (Hughes 1996). The beach morphodynamic type of the nesting beaches in Maputaland is predominantly intermediate (medium sand grain size and slope) with mixed shores and some rocky outcrops (Harris *et al.* 2011). The beaches are backed by large, pristine dune systems stabilized by thicket and dune forest (Mountain 1990, Hughes 1996, Botha 2010). The intertidal and subtidal areas are characterised by irregular rocks which reduces the ability of sea turtles to nest on these beaches, especially at low tide (Botha 2010). Offshore tropical reefs, the only tropical reefs in South Africa, are also present, scattered along the iSimangaliso coast (Mountain 1990, Sink *et al.* 2011). These reefs are very productive and have incredible diversity and therefore provide refugia for many organisms. Sea turtles are thought to use these areas as foraging grounds as well as protective habitats during inter-nesting periods (Brazier *et al.* 2011).

iSimangaliso is home to three large fresh water systems, namely, Kosi Bay, Lake Sibaya and Lake St Lucia. St Lucia lies south of the sea turtle monitoring area and is not described in this dissertation. Lake Sibaya is the largest freshwater lake in South Africa and is present behind the dunes at the southern end of the monitored sea turtle nesting area. Lake Sibaya has no opening to the ocean and the only input is from rainfall and inflow from the aquifers while water loss occurs through evaporation and groundwater seepages (Taylor 2003). These groundwater seepages can be quite substantial as Lake Sibaya is a perched lake with a substantial hydrological head (Guy Bates pers. comm.). Kosi Bay, which is actually an estuary, is a combination of four tidal shallow, warm 'lakes' lying adjacent to the coast behind highly vegetated natural dunes (Allanson & van Wyk 1969, Mountain 1990, Kyle 1999). It is fed by two main rivers and consists of swamps and sedge-beds (Mountain 1990). This lake is also adjacent to the highest density of nesting beaches for loggerheads within the South African nesting area (Fig. 2.2). Furthermore, this highest interannual density nesting distribution is consistently situated adjacent to the Kosi Lake. The Kosi lake system is primarily freshwater with saltwater mixing closer to the mouth, which is generally open throughout the year (Mountain 1990, Harris *et al.* 1995, Hart 1995).

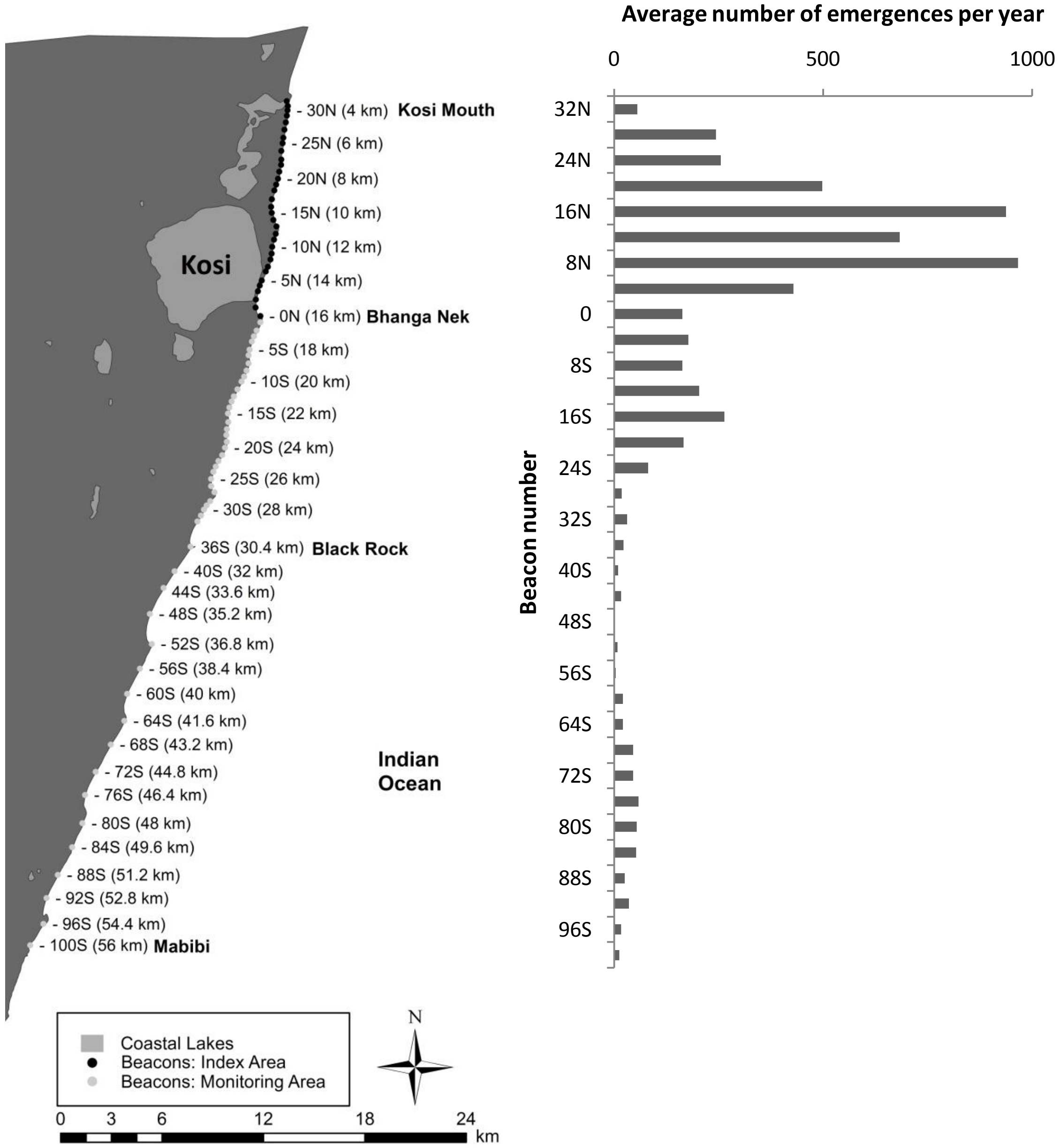

Figure 2.2: Map with associated number of emergences per beacon illustrating the annual nesting distributions with their close proximity to the Kosi lake systems. Each single beacon number represents 400 m.

Aquifers present along the coastal areas of KZN are described by Campbell *et al.* (1992) and Meyer *et al.* (2001) as mainly siltstone and sandstone formations known as the Maputaland Group. These aquifers are the largest in South Africa (Mkhwanazi 2010). The Maputaland coastal aquifers transport groundwater to the ocean under the dune systems (Meyer *et al.* 2001). This groundwater may be influenced by the coastal lakes because these lakes are extensions of the aquifer (Meyer *et al.* 2001, Mkhwanazi 2010). This is the reasoning behind the theory that nesting turtles use cues from these groundwater seepages from the Kosi Bay system to locate their nesting beaches (Hughes 1974).

South African monitoring program

Exploitation of sea turtles in the South Western Indian Ocean (SWIO) has occurred since approximately 50 000 years ago (Frazier 2007). This exploitation peaked in the 1900's (Hughes 1989) and sea turtle populations in the SWIO began to collapse from overexploitation by commercial fisheries. However, subsistence harvesting was the greatest threat to Maputaland's loggerheads and leatherbacks which remained a large threat for the South African populations until the Natal Ordinance, in 1916, which prohibited the killing of sea turtles (Hughes 1989). In 1960, further legislature was created to increase the protection to sea turtles in South Africa which led to the creation of the monitoring program in 1963 (Hughes 1989). The purpose of this monitoring program is therefore to provide protection to nesting loggerheads and leatherbacks, and to obtain information on population numbers and dynamics. An increase in understanding of their life histories will enhance the effectiveness of conservation efforts (Hughes 2010). This program is still operating, making it one of the longest running quantitative sea turtle monitoring programs in the world (Wilson & Humphrey 2004; Nel & Lawrence 2007).

Initially the monitored area extended north from the research hut at Bhanga Nek to the Kosi estuary mouth (≈12.8 km). The monitored area has subsequently extended further south to Mabibi (≈40 km). Due to the number of nests north of the Kosi estuary mouth and the border, protection and monitoring was extended all the way to the Mozambique border (≈3.2 km) totalling an area of 56 km (Hughes 1996, Nel 2009). Beacons are used to record an approximate geographical position of each nest. These beacons are painted poles placed, approximately 400 m apart on the dune ridge for easy identification. Beacon poles exist at every beacon between 40 N and 40 S however from beacon 40 S to 100 S, the beacon poles are 1600 m (1 mile) apart. Therefore these geographical locations are recorded in a lower resolution.

Annual monitoring of the nesting females and emerging hatchlings of loggerheads and leatherbacks (by Ezemvelo KZN Wildlife) begins in mid-October until mid-March (Nel 2009). Peak nesting and hatching times are December and February, respectively (Nel 2009). Approximately 2600 loggerhead- and 250 leatherback nests are laid per year (Nel 2009). These numbers are stable for leatherbacks and are increasing for loggerheads.

Monitoring takes place in the form of foot and vehicle patrols (Hughes 1996). Twice-nightly foot patrols are performed by locals every night (starting at 19h00) and in the morning (starting at 06h00) to encounter nesting females and to obtain a count of tracks from emergences from the previous night respectively. These monitors have set areas to patrol and extend from 40N (Fig. 2.1) at the Mozambique border to approximately 60S. Vehicle patrols are conducted primarily through two concessionaire's (monitoring 58S-100S) every nightly (Nel 2009). Data collected that are relevant for this dissertation include date, time, geographic position (beacon number) and whether the turtle nested or not (Hughes 1996). Date is measured to the previous night if the recordings occur post-midnight; time is recorded in a straight forward manner while geographic position is recorded as to the nearest beacon pole.

Since there is virtually no coastal developments in Maputaland, disturbances of nesting turtles and emerging hatchlings are considered few. The major disturbances are vehicle and foot patrols together with guided tours run by the local community (Nel 2008). These events introduce artificial lights onto the beaches at night and have been known to disturb nesting events and interfere with hatchling sea-finding behaviour (Proffitt *et al.* 1986, Mortimer 2004, Bourgeois *et al.* 2009). A major, constant artificial light source present on the nesting beaches is the research and ranger houses at beacon 0 (Bhanga Nek). The light spreads across the beach and nesting rarely occurs in this area, even though these lights are powered from a diesel generator that usually only operates until 22h00.

Conclusion

Loggerhead nests are highly concentrated in an 8 km stretch of beach out of a potential 150 km and this preferred area is restricted to the beaches adjacent to Kosi Lake. The reason for this selection is unknown although speculations have been made. One of these speculations is that nest site selection often appears to be near an artificial body of water (Hughes 1974), in this case, the Kosi lake system. Possible scent cues, perceived by the loggerheads, attract them to nest on these beaches. These scents may enter the oceans through aquifers present below the lakes and the dunes which carry groundwater and lake water under the dunes and into the surf zone.

Maputaland’s coastline is considered a pristine environment, protected since the mid 1970s, and now a world heritage site. It hence has very little coastal developments or the disturbances associated with them. Coastal developments and the light sources projecting onto beaches are known to deter gravid females from nesting (Proffitt *et al.* 1986, Mortimer 2004, Bourgeois *et al.* 2009). However, diffuse ambient light is very important for orientation for both adults and hatchlings. Maputaland is thus an ideal area to test the effect of both ambient and artificial light intensities on the nesting behaviour of loggerheads.

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Chapter 3: Olfactory imprinting of loggerhead sea turtles

An image of loggerhead hatchlings making their way down the beach to begin their offshore migration. This is one of the possible time frames that hatchlings imprint on their natal beaches to return here as adults.

Abstract

The olfactory imprinting hypothesis in sea turtles has been a point of controversy and there is scant evidence to date to confirm that olfactory imprinting is the driver for nest site selection in sea turtles. The aims of this chapter are to determine the origin and nature of potential chemical attractants, and their relationship to the loggerhead nesting distribution in Maputaland. To answer these questions, sulfide (mg.l^{-1}), nitrate (mg.l^{-1}), nitrite (mg.l^{-1}) and salinity (ppt) concentrations were measured along 14 groundwater stations with samples obtained at the effluent line[1]. These nutrient concentrations were correlated to the number of emergences alongshore. Furthermore, experiments were conducted to monitor the movements of captive loggerheads (Bayworld Aquarium, Port Elizabeth), and hatchlings in the field after the introduction of their natal beach scent into the experimental chamber. A comparison was made between orientation before (control) and with beach sand scent (treatment) into the water to determine whether they orientated towards this chemical scent. Nitrate, nitrite pre- and post nesting salinity concentrations do not appear to influence nest site selection. Pre- and post nesting season sulfide concentrations (mg.l^{-1}) were not correlated with the number of emergences per beacon. However, when a correlation was performed on the skewed sulfide concentrations (each sulfide concentration was compared to the number of emergences of the beacon directly north of it i.e. sulfide concentrations of 4N were compared to the number of emergences at beacon 8N) post-nesting sulfide concentrations (mg.l^{-1}) correlated to the number of emergences. Captive sub-adults and adults, and wild-caught loggerhead hatchlings did not navigate towards their natal beach scent when natal beach-scented water was introduced into the experimental tank. These turtles were always positioned and orientated towards the seaward side of the pool. With the introduction of a food scent or the natal beach scent, the accuracy with which the adults and the hatchlings orientated towards the unidentified cue decreased. This was considered a response to the introduction of the chemical cue. The experiments were therefore successful but a stronger or a more directional cue would potentially provide more results. Therefore olfactory imprinting to a natal scent appears to occur in Maputaland loggerheads however further research is required to further investigate olfactory imprinting.

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[1] The effluent line is the intersection of the water table and the sand surface to create a “glassy layer”.

Introduction

Sea turtles, like migratory birds and salmon, are marvelled at for their impressive migrations and pin-point navigational feats (Lohmann *et al.* 2008a). All these animals perform long-distance natal homing migrations between foraging and nesting/breeding grounds often thousands of kilometres apart (Carr & Carr 1972, Nordmoe *et al.* 2004). Pacific salmon however are semelparous and perform only a single migration in their lifetime but with a phenomenal level of accuracy (Nevitt & Dittman 1999). These long-distance migrations are guided by different cues for each group of animal adapted to specific environments. Salmon (*Oncorhynchus kisutch*) for example are able to detect the earth's magnetic field and are suspected to use this as an initial driver of natal homing (Ogura *et al.* 1992, Lohmann *et al.* 2008b). Once near the natal stream/river, salmon use unique chemical signatures of their natal stream, to which they imprinted as juveniles, to find and move up the correct stream to reproduce (Scholz *et al.* 1976, Nevitt *et al.* 1994, Dittman & Quinn 1996, Nevitt *et al.* 1996).

A very similar form of navigation has been suggested for sea turtles. Geomagnetic cues are thought to be the intermediate-distance drivers of sea turtle natal homing migrations (Lohmann *et al.* 2004, Cain *et al.* 2005, Luschi *et al.* 2007, Benhamou *et al.* 2011) whereas the final part of the homing migration is (hypothesised to be) guided by local cues such as beach scents i.e. the olfactory imprinting hypothesis (Owens *et al.* 1982, Grassman *et al.* 1984, Grassman 1993, Mrosovsky 2007). This hypothesis states that hatchlings emerging from their nests identify and remember the unique scent of their natal beach and subsequently return to these beaches as adults to nest (Carr & Carr 1972).

For turtles to perform these natal homing migrations they need to be able to detect odours in their environment even at a distance from the source. Manton *et al.* (1972) and Endres *et al.* (2009) demonstrated that loggerheads are able to detect both airborne and waterborne odours. Previous artificial imprinting experiments in multiple-choice situations have proven that sea turtles actively select scents for which they have been imprinted (Owens *et al.* 1982, Grassman *et al.* 1984). Kemp's ridley hatchlings collected from the Rancho Nuevo nesting beaches in Mexico were transported to and allowed to crawl down the Padre Island beaches in Texas and then transported to the Galveston head-starting program which have seen returns to areas near the imprinted beaches, albeit only a few (Fontaine & Shaver

2005) suggesting that olfactory imprinting may be the driver of these nest site selections. Similar results were obtained for green turtles imprinted in a similar way at the Cayman Turtle Farm (Mrosovsky 2007). Therefore chemical imprinting appears to be a plausible mechanism to redirect turtles back to their natal beaches.

The real puzzle in these large scale migrations is the accuracy with which animals return to their nesting grounds or even specific patches within their nesting grounds (Limpus *et al.* 1992, Botha 2010). Consistent nesting distribution patterns are found along sea turtle nesting beaches with gradients of high and low nesting density (Hughes 1974). It is thus suspected that specific, smaller-scale cues affect nest selection as opposed to homing behaviour. It is unclear though whether the fine-scale selection is habitat-, chemical- cue driven, directed by social interactions of turtles, or a combination of all. A further complicating factor is that Botha (2010) discovered that the home ranges of nesting female loggerheads decrease (i.e. become more specific/accurate) with repeat nesting seasons. This suggests that more experienced nesters may be able to select better nesting beach patches based on their previous experience. This suggests that there may be clear chemical cues that they select for, possibly before they emerge onto the beach.

The selection of a particular habitat is a function of habitat heterogeneity and the preference for specific habitats within the range available (Morris 1992). Beach characteristics globally have been investigated to identify preferred habitats driving nest site selection. These selection factors include intertidal slope (Eckert 1987, Garmestani et al. 2000, Wood & Bjorndal 2000, Mazaris *et al.* 2006), distance of nests to vegetation and the high water mark (Hays et al. 1995; Kamel & Mrosovsky 2004; Kamel & Mrosovsky 2005; Xavier et al. 2006), sand pH (Garmestani et al. 2000, Mazaris *et al.* 2006), and the presence of reefs or rocks (Mortimer 1995). The results of these studies are inconsistent and may suggest that individual populations have different preferences or that the range of physical features available are not different enough to be detectable (to scientists). Similar beach characteristics were investigated (by Botha 2010) as drivers of nesting for loggerheads in Maputaland. Loggerheads preferred intermediate beaches (medium slope and grain size) and avoided beaches with presence of inshore rocks. No relationship was obtained with other physical variables (surf zone width, inshore rocks, beach morphodynamic type, slope, beach width and back-beach width, sand pH, mean grain size and the distance of the nest to the vegetation line and high water mark, Botha 2010). However, beaches with apparently very similar beach characteristics have a wide range of nesting densities suggesting that beach characteristics per se are not the reason for the preference to the high density nesting area. It is thus suspected that there is another driver other than beach morphodynamics responsible for the nesting distribution on Maputaland beaches.

Grassman *et al.* (1984) suggest that beaches have unique chemical and/or biologically-derived scents that turtles detect. These scents have many possible origins such as decaying eggs in nest chambers, from pheromone-enriched mucous secreted by females during nesting, or to local chemical cues (air- or waterborne) originating and unique to the area (Hughes 1989). Scents originating from the nesting process or from decaying nests are suspected to last among seasons to be used by the initial nesters of the next season (Hughes 1989). According to Hughes (1974), nesting beaches are often backed by large bodies of water. These may be mangroves swamps, lagoons, coastal lakes and the like. Interestingly Maputaland’s high density nesting beaches are backed by these large coastal lake systems (Kosi Lake). Hughes (1989) stated that groundwater seepages may transport minerals that may be used as cues to nesting sea turtles. The same would be true for sulphides or hormone proteins conserved among seasons.

Aquifers at Stinson beach, California, are estimated to discharge between 0.1 – 0.5 L.min^{-1}.m^{-1} freshwater into the surf during spring tides, and 1.2 – 4.7 L.min^{-1}.m^{-1} during neap tides (de Sieyes *et al.* 2008). This freshwater contains high concentrations of nutrients (de Sieyes *et al* 2008). The Maputaland aquifer, which is linked to the coastal Kosi Lake systems in northern KwaZulu-Natal (South Africa), is thus likely to discharge freshwater onto the beach through the groundwater containing chemicals and nutrients specific to the lake and beach. These chemicals may be recognized by loggerheads as their natal beach scent. This cue may originate from the lakes or on the beach and either way end up in the ocean. Very little is known about imprinting (Owens *et al.* 1982) and which cues may be used for this process.

The aims of this chapter are to identify chemicals that could produce a natal beach scent and to measure the concentrations of these potential chemical cues along the shore, as well as solicit a response, if any, of captive and field-caught loggerheads to these scents. To do this, two sets of data were obtained: i) the nutrient concentrations of groundwater samples were taken from the effluent line and related to the number of emerging loggerheads; ii) orientation experiments on captive and wild-caught loggerheads were performed to determine their position and orientation movements in the presence (and absence) of a gradient of natal beach scent.

Materials & Methods

In Situ Nutrient Levels

The chemicals used in natal homing and nest site selection are unknown but these chemicals have been suggested to originate from nearby coastal bodies of water, in this case, Kosi Lake (Hughes 1974, Hughes 1989). To determine the chemicals used in nest site selection, sulfide ($mg.l^{-1}$), nitrate ($mg.l^{-1}$), nitrite ($mg.l^{-1}$) and salinity (ppt) concentrations (collectively called *in situ* nutrient levels from here on) were tested along the shore. Sulfide concentrations ($mg.l^{-1}$) were measured because it is derived from the breakdown of organic material under anoxic conditions. In lakes and in sediment it is often due to salinity and temperature stratification preventing mixing with oxygen rich waters/sand on the surface (Jorgensen 1980). Nitrates are a natural by-product of protein breakdown and are important for the growth of algae (Fig. 3.1, Golterman *et al.* 1975). Increased levels of nitrates are often associated with excessive surface runoff into rivers and estuaries due to fertilizers and other forms of pollution (Golterman *et al.* 1975). Nitrites are formed by the aerobic decomposition of ammonia (which originated from proteins such as sea turtle egg proteins) and the anaerobic decomposition of nitrates by bacteria (Fig. 3.1, Kirchmann & Witter 1989). Therefore nitrates and nitrites were measured (in $mg.l^{-1}$) to determine whether their levels were detectable and whether they were higher (or lower) in the area of the high density nesting beaches (0-32N).

If nest site selection cues are derived from previous nesting events, then it could be assumed that there is a positive feedback mechanism whereby nesting females in a specific area would subsequently attract others, reinforcing a specific area to be an attractive nesting area. Early- (10-15 November 2011) and late (or post)-nesting season samples (6-30 April 2011) of *in situ* nutrient levels were collected in an attempt to identify possible cues as well as the origin thereof. Groundwater samples were used to measure the concentrations of the *in situ* nutrient levels because this would be the entry point of the waterborne cues into the surf (Hughes 1974, Hughes 1989).

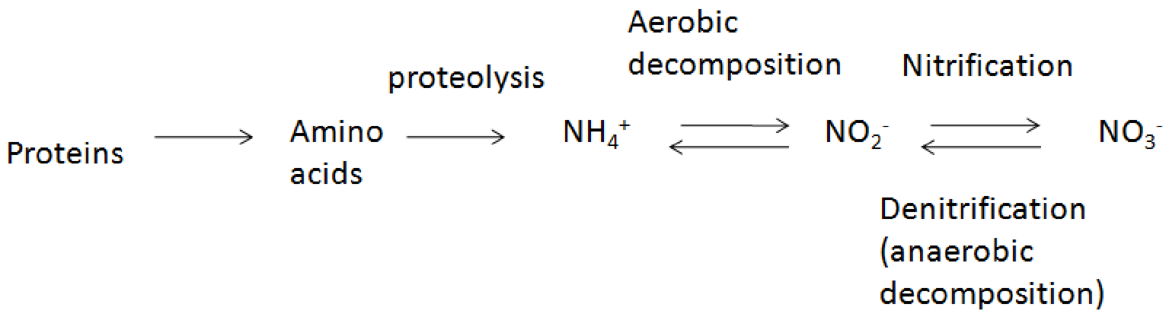

Figure 3.1: Illustration of a simplified nitrogen cycle that may be present on sea turtle nesting beaches. This figure illustrates the creation of both nitrite and nitrate together with its breakdown.

To measure the potential *in situ* nutrient concentrations, groundwater samples were collected along the Maputaland coast (Fig. 3.2). Samples were collected across the high and the low density nesting areas so that a comparison could be made between these two areas. Furthermore, water samples from Kosi Lake and Kosi estuary mouth were also collected. The groundwater samples were collected during spring low tide to ensure that the samples collected were indeed groundwater seepage and not dominated/diluted by sea water. This groundwater is suspected to have originated or at least contain a proportion of freshwater from Kosi Lake through aquifer flow. Due to the physical distance that needed to be covered it was not always possible to collect samples on spring tide. When samples were not taken on spring events, the samples were still collected at the lowest available tide and above the saturation zone to ensure that the samples came from the water table. Water samples from the Kosi lake and estuary mouth were collected from the surface waters near the lake/estuary banks (Fig. 3.2).

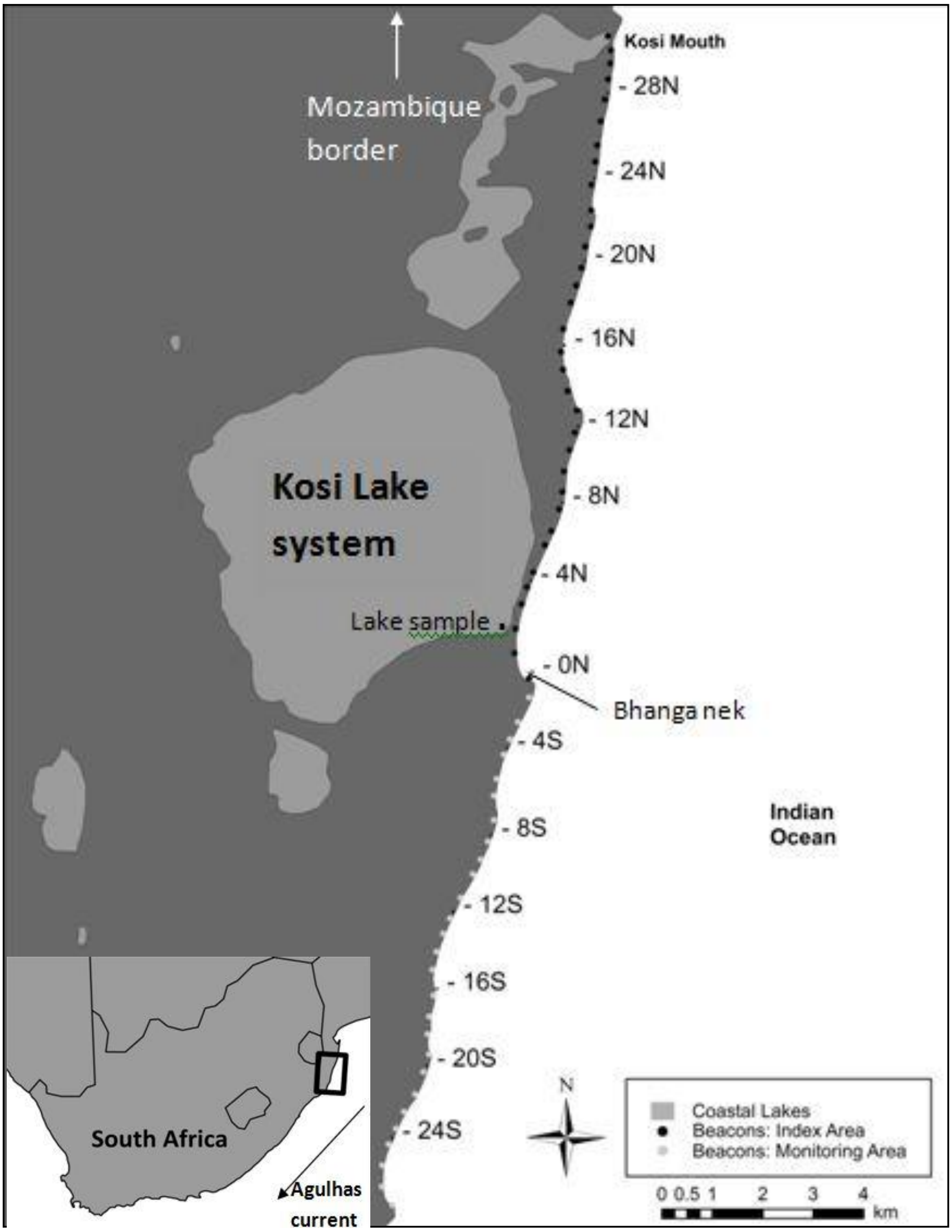

Figure 3.2: Distribution of the sites used to collect 15 sets of samples of *in situ* nutrient concentrations taken along shore (and one on the edge of the lake) with an indication of the beacon nearest to each sampling station.

There were two sampling trips that took place; one pre-nesting season (November 2011) and the other post-nesting season (April 2011). Three replicates for sulfide and salinity each were collected for the pre-nesting season. Three replicate set of samples of sulfide, nitrate and nitrite were collected, and seven replicates for salinity were collected along the beach for the post-nesting season samples. Nitrate and nitrite were not re-sampled because of the results of the post-nesting season and the lack of variation between these. Estuary mouth and lake samples are independent of nesting or spring tides and hence were collected when convenient during the pre- and post nesting sampling events mentioned above.

Groundwater samples were collected at every fourth beacon (≈1.6 km) along the coast for 20.8 km (Fig. 3.2) by excavating a hole at the effluent line (Fig. 3.3), down to the groundwater table, and taking approximately 50 ml sample of the groundwater. These samples were stored in plastic bottles and the lids sealed to prevent air from contaminating the sample. The variables were measured as soon as possible after their collection (always within 24 hours) and each sample was re-measured 10 times with the average of these re-measurements being the final value per replicate. Sulfide, nitrate and nitrite concentrations (mg.l^{-1}) of the groundwater were measured using a hand-held Lamotte SMART2 colorimeter (code 1919). The *in situ* nutrient concentrations were analysed using the low range test kits for sulfide (range of measurements: 0-1.50 mg.l^{-1}; Product code 3654-01-SC), nitrate-nitrogen (range of measurements: 0-3.00 mg.l^{-1}; Product code 3649-SC) and nitrite-nitrogen (range of measurements: 0-0.80 mg.l^{-1}; code 3650-SC). Salinity was measured using SelecTech meter with salinity attachment (SelecTech Salt Testr 11). The salinity attachment initially available was limited to measurements of salinity up to 10 ppt. This salinity meter was only used for the post-nesting concentrations. The pre-nesting salinities were measured using the more accurate Crison CM35+ Conductivity meter with the Crison 50 63 conductivity probe. This equipment setup was calibrated before use and also calibrated to the SelecTech conductivity meter for comparable measurements.

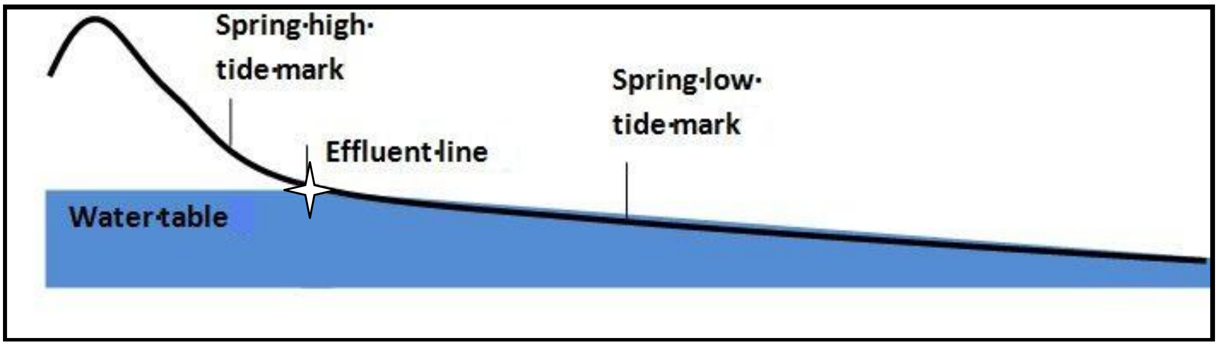

Figure 3.3: Diagram to illustrate the position of the effluent line where the *in situ* nutrient samples were collected illustrated by a star in the figure.

Pearson product moment correlations were performed between the *in situ* nutrient concentrations and the number of emergences per beacon for the 2010/2011 nesting season (Ezemvelo, unpublished data). This was done using the Analysis ToolPak in Microsoft Excel 2010, and interpretation using ZAR (1999). The geographic position of each female that emerged onto the beach was recorded to the nearest beacon (400 m intervals). Therefore to correlate the number of emergences with the concentrations of the *in situ* nutrient concentrations (per 1.6 km intervals) the emergence count for every 4th beacon i.e. only the beacons where water samples were obtained were used. The data for both these correlations were adhered to the requirements of correlations by testing for normality (D' Agostino-Pearson test) and homoscedasticity (Bartlett's test). Beacon 0 was removed from the analyses because females tend not to nest here, probably due to the presence of rocky shore and artificial lights, and this would interfere with the results.

To further determine the effect of Kosi Lake on the loggerhead nesting distribution, the straight line distances between the shoreline of each beacon and the lake shore were measured. This was done remotely using satellite imagery from Google Earth 2007. The shortest straight line distance between the beach high tide mark and the lake shore was measured and linearly correlated to nutrient concentrations using Microsoft Office Excel 2010 Add-in Data Analysis Toolpak.

Orientation Experiments

Captive Animals

The second hypothesis investigated is that loggerheads navigate towards their natal beach scent cues as suggested by the imprinting hypothesis. Natal beach scent originates from a unique combination of organic and other chemicals trapped in the nesting beach sand. It is assumed that the highest density of loggerhead nesting sites coincides with the largest or most concentrated release of natal beach scent. Therefore, sand and groundwater laced with the natal beach scent was obtained from holes at the effluent line dug at beacon 8N. These samples were not collected closer to the waterline because the sand below the effluent line was diluted with seawater from wave surge. The natal sand-water mix was flushed over a 50 µm mesh with distilled water with a fixed ratio of distilled water to four volumes of natal wet sand (e.g. 1 litre of distilled water per 4 litres of wet sand). The filtrate was frozen to preserve possible proteins or volatile substances in the samples for later use in experiments with captive animals at Bayworld Aquarium, Port Elizabeth. These scented water blocks were subsequently thawed to room temperature for use in the experiments using sub-/adult loggerheads. It was also the intent to analyse the chemical compounds in the natal sands but was opted against as it could literally contain hundreds of chemical compounds without any surety as to the ecological value of each compound (Frost C, NMMU, pers. comm.).

The experimental pool used in Bayworld Aquarium was circular with a diameter of 9 m and a maximum depth of 2 m (Fig. 3.4). There was a 1.2 m wide step along the edge the pool with an average height of 0.5 m. This step therefore did not interfere with a turtle swimming on the surface. The pool was also equipped with a gate on one side used to flush the tank. After each experimental run fresh filtered sea water was pumped into the experimental pool to clear all turtle waste and food and sand scents. During each experiment the pool gate remained water-tight and the pump turned off to prevent stirring of the water.

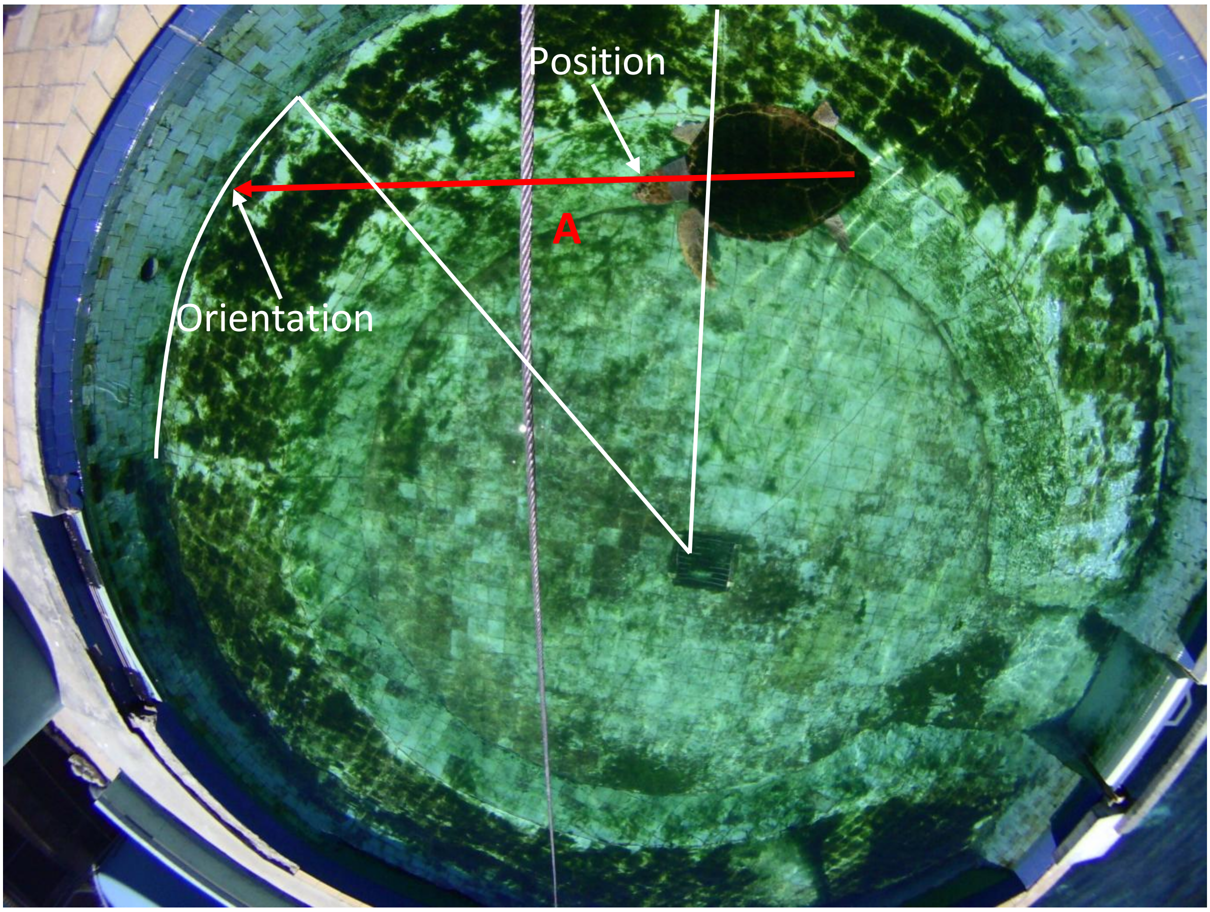

Figure 3.4: A photograph taken illustrating the experimental procedure and the means of collecting data on the position and orientation of one of the captive loggerheads from Bayworld Aquarium.

Experiments on captive loggerheads were performed between the 20 October– 3 November 2010 which is during the migration of Maputaland loggerheads to their nesting beaches to reproduce. Maputaland was assumed to be the natal beach of the loggerheads in Bayworld as these turtles were collected from strandings along the South African coast and it is estimated that approximately 75 % of all loggerheads in South Africa are from Maputaland's nesting beaches (Nel 2010). These experiments were performed by placing a single loggerhead at a time in the circular pool and allowing the turtle to acclimate to the pool overnight. Experimental observations began in at 08h00 and ended at the latest at 14h00. Observations were made for three treatments: pre-cue as a control, post-first-cue and post-second-cue. The first cue was always the natal beach scent and the second cue was a food scent which was used to test the method because theoretically they would navigate towards food.

Observations were recorded for the movements of the loggerheads using a wide-angle camera (GoPro digital camera) which took a single photo every five seconds. The camera was attached to a horizontal pole positioned centrally above the pool facing downwards. Each experiment was 20 minutes long resulting in approximately 240 digital photos per experiment per turtle. These were later analysed for orientation and position within the tank by dividing the pool into nine equal wedges (40° each) and recording the position and orientation every five seconds (Fig. 3.4). Position refers to the section of the pool the turtle was situated in. Orientation was recorded by extending a straight line from the posterior to the anterior edge of the carapace and extending this line to the side of the pool (Fig. 3.4). The turtles often rested on the bottom of the tank and these data points were removed from analyses.

Observation of the loggerheads began with a 20 minute pre-experimental (control) observation which was used for comparison to the two treatments (sand and pilchard scent) observations. The first cue was introduced after a 10 minute rest time (i.e. 30 minutes after the start of the pre-experimental observations) followed by the second food cue, also after a 10 min rest time. Once these experiments were completed, the turtle was removed and measured for straight and curved carapace length and width (SCL, SCW, CCL and CCW in mm) and mass (kg).

The position of the introduction of the scent cues was random and performed as inconspicuously as possible to avoid disturbing the turtle. This was done by extending a 3 m long plastic pipe to the relevant side of the pool. When the cue was introduced, the tip of the pipe was allowed to enter the water and the cue (2 litres) was poured down the pipe, over approximately one minute, into the pool. Different pipes were used for the different cues and the pipes were thoroughly rinsed between experiments. The only disturbance would then have been the entrance of the water into the pool which was short and considered negligible. The perimeter of the pool was blocked off to prevent passer-bys from disturbing the experiment. [Ethical clearance was obtained for this section of the chapter from the Nelson Mandela Metropolitan University (Ref no. A1O-SCI-ZOO-007)].

The position and orientation of the loggerheads were measured relative to the cue introductions. The point of cue introduction was set to 0° and mean angles were positive for clockwise angles and negative for anti-clockwise angles (i.e. -180° to 180°). Circular statistics were performed on orientation experiments. Rayleigh's test (*z*) for circular uniformity was used to determine if there was a significant mean direction and the one-sample circular test was used to determine if the mean direction of the individual was significantly different from the section of cue introduction. Statistical procedures adhered to were from Zar (1999) and performed in Microsoft Excel 2010.

Field Experiment

Captive animal experiments were repeated but as ethics clearance was rejected for manipulative experiments on gravid females, hatchlings were used instead.

Capture and treatment of hatchlings

Loggerhead hatchlings were collected from Maputaland's nesting beaches during the hatching season (28 February 2011 – 8 March 2011) as they emerged from nests between beacon 0 and 12N (5 km). These hatchlings were allowed to crawl down the beach up until the surf where they were recollected and carried back to the research hut at beacon 0. The stage that hatchlings imprint on is unknown however, they spend up to four days in the sand between hatching from their eggs and emerging (Witherington *et al.* 1990) from the nest chamber which appears to be the most likely time for them to imprint to a scent. This is why hatchlings were allowed to experience all the natural stages of sea-finding excluding swimming through the surf offshore stage. Collecting hatchlings at this stage would make it far more difficult and costly. Hatchlings used in these experiments were from a single nest each night (i.e. siblings) and were released immediately after the experiment.

Experimental Design

Hatchlings were expected to navigate towards/away from their natal beach scent. To test this, similar experiments as those performed on captive animals were repeated on hatchlings. The same method of collecting water containing the natal beach scent was used here as before. However the pool used for hatchlings was smaller with a diameter of 1.1 m and a depth of 0.25 m which was filled with water to a depth of 0.15 m. The water for this pool was taken from the adjacent ocean. An inherent problem with this method is that the water may be impregnated with the natal beach scent. Therefore, in an attempt to eliminate or reduce possible scents in this water, it was allowed to stand in the sun for approximately 8 hours which is assumed to reduce the concentration of volatile compounds in the water as well as reduce any other possible protein scents which may interfere with the experiment (Andy Dittman, NOAA, pers comm.).

The hatchlings were placed into the pool for 20 minutes before the experiment was started to allow the hatchlings to acclimate to the water. Control observations were performed for 20 minutes after this acclimation period so that a comparison to the post-cue release could be made. Experimental setup and procedure was similar to the captive experiments. Differences include the pool was divided into eight sections (45° each) rather than nine and experiments were performed at night to reduce light effects on position due to the phototactic nature of the hatchlings (Proffitt *et al.* 1986, Mortimer 2004, Bourgeois *et al.* 2009). Experiments were restricted to moonless nights to further reduce the effect of light cues on orientation. As no/little light was present photographic recording of orientation was not possible. Only the position per hatchling (per wedge) was recorded using a pair of night vision goggles (Tevion NV3) and vocal recording data onto a tape recorder which was later transcribed. Natal beach scent was introduced into the pool over a period of approximately one minute to create a gradient. Statistical methods were similar to the captive orientation experiments (Rayleigh's z-test for uniformity, one-sample circular test) except only position was recorded without orientation.

Results

In situ nutrient levels

Pre-nesting season sulfide concentrations ranged from 0.002–0.009 mg.l^{-1} while post-nesting season sulfide concentrations ranged from 0.002–0.017 mg.l^{-1} (Fig. 3.5). Nitrate concentrations ranged from 0.10–0.32 mg.l^{-1} (Fig. 3.5) while nitrites, on the other hand, ranged from 0.04-0.11 mg.l^{-1}(Fig. 3.6). Salinity was stable across the season with pre-nesting season salinities ranging 5.55–5.66 ppt and post-nesting season salinities ranging 5.68–5.78 ppt and thus were marginally higher (Fig. 3.7). Sulfide concentrations were consistently low with an average of 0.004 mg.l^{-1} for pre-nesting season and 0.008 mg.l^{-1} for post-nesting season. Lake ($t = 0.61$; $p = 0.55$; $df = 13$) and estuary mouth ($t = 0.74$; $p = 0.47$; $df = 13$) samples of sulfide concentrations were not different from groundwater samples (Fig. 3.5). Concentrations of nitrate in the lake water were not significantly different from the groundwater samples ($t = 0.74$; $p = 0.47$; $df = 13$) while nitrate concentrations in the estuary mouth were significantly larger than the groundwater samples ($t = 4.35$; $p \ll 0.05$; $df = 13$). Nitrite concentrations of the lake ($t = 4.72$; $p \ll 0.05$; $df = 13$) and the estuary mouth ($t = 5.72$; $p \ll 0.005$’ $df = 13$) were significantly higher than the groundwater samples (Fig. 3.6). However, salinity was significantly lower in lake samples than groundwater samples (Fig. 3.7, $t = 6.98$; $p \ll 0.005$; $df = 13$).

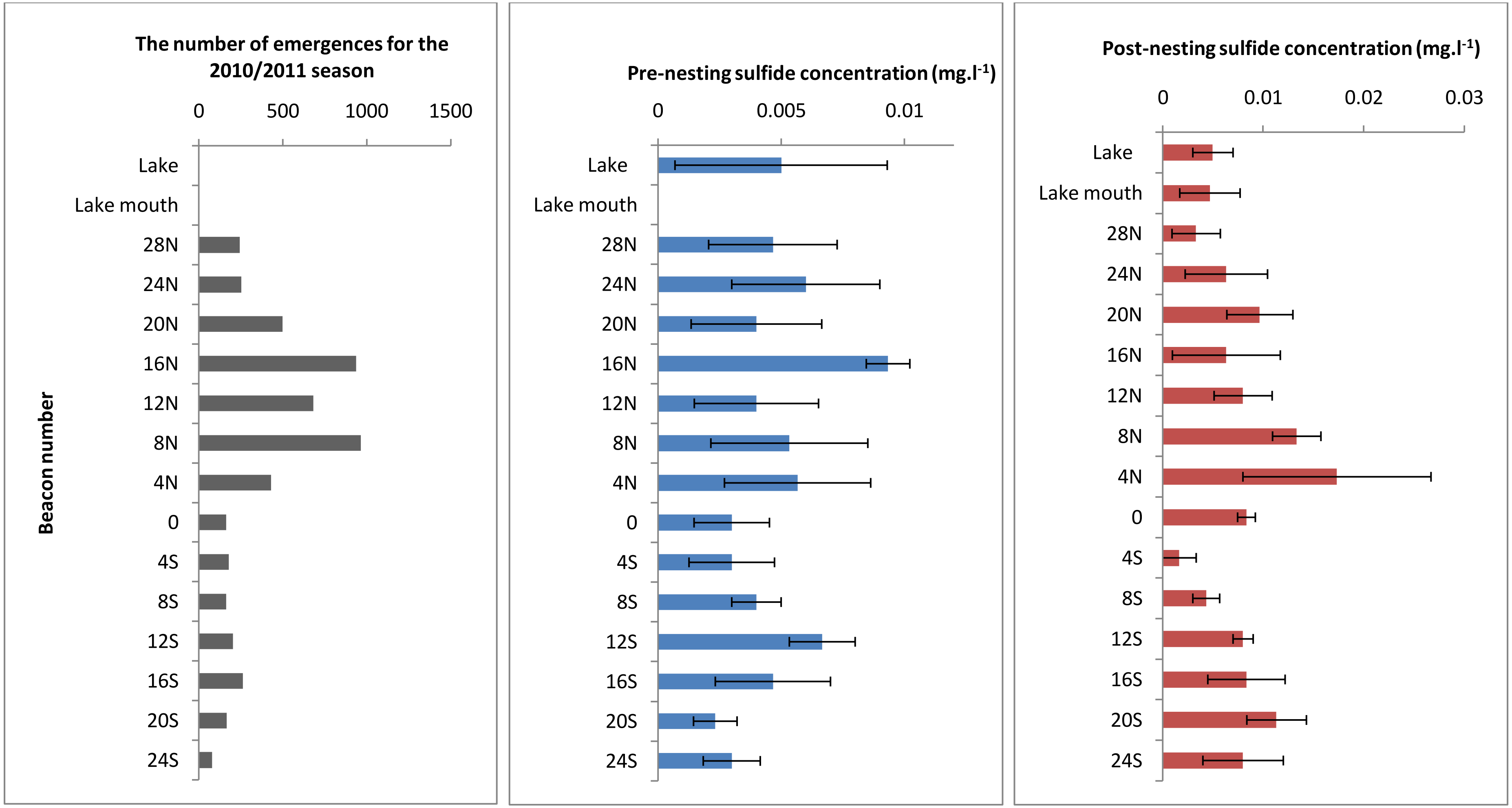

Figure 3.5: Pre-nesting and post-nesting season sulfide concentrations (mg.l^{-1}) along the nesting beaches. Data presented as means ± standard error. Graph on left illustrates the distribution of loggerhead emergences per sampling site for the 2010/2011 nesting season.

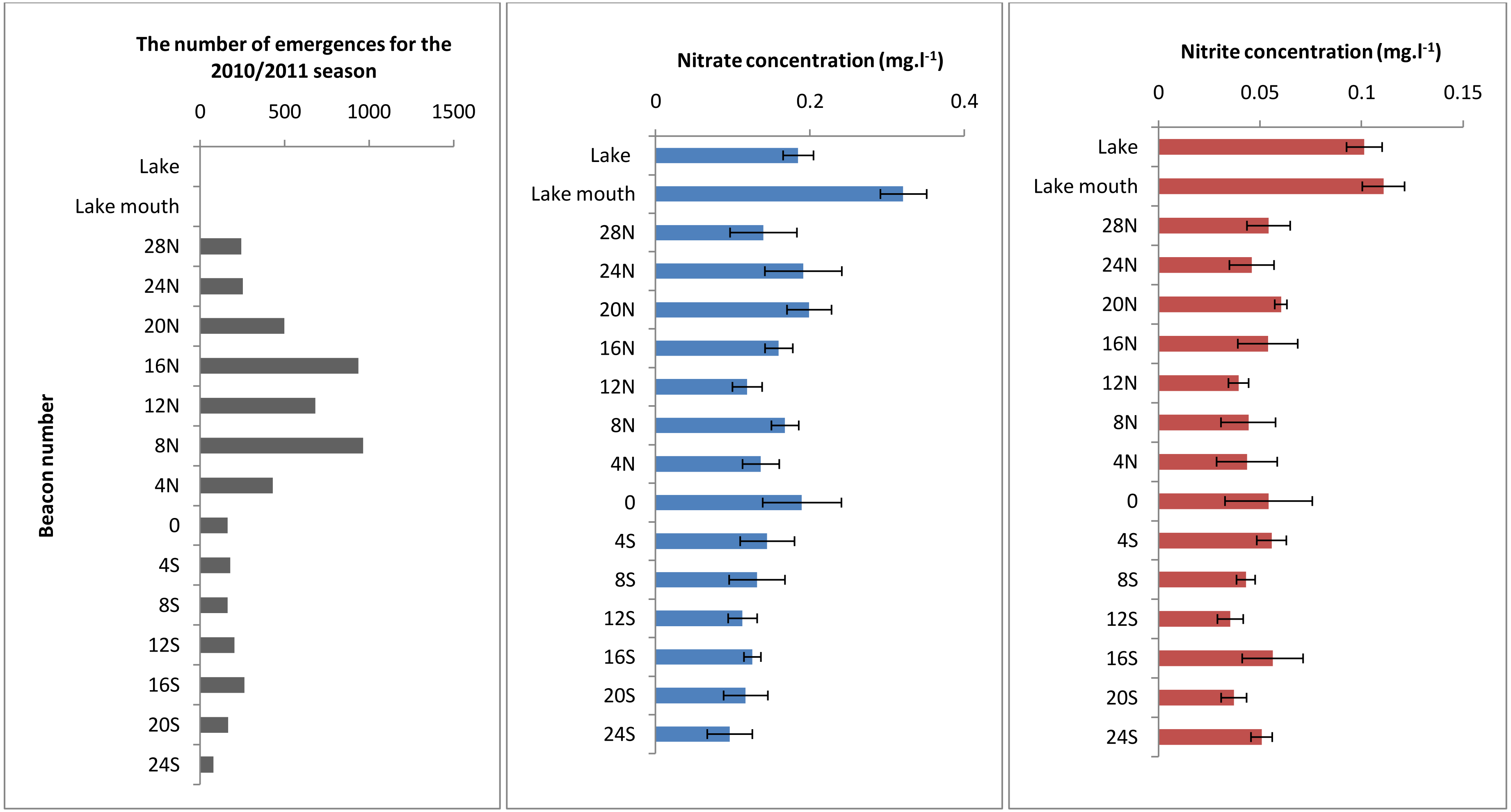

Figure 3.6: Nitrate and nitrite concentrations (mg.l^{-1}) along the nesting beaches. Data presented as means ± standard error. Graph on left illustrates the distribution of emergences per sampling site for the 2010/2011 nesting season.

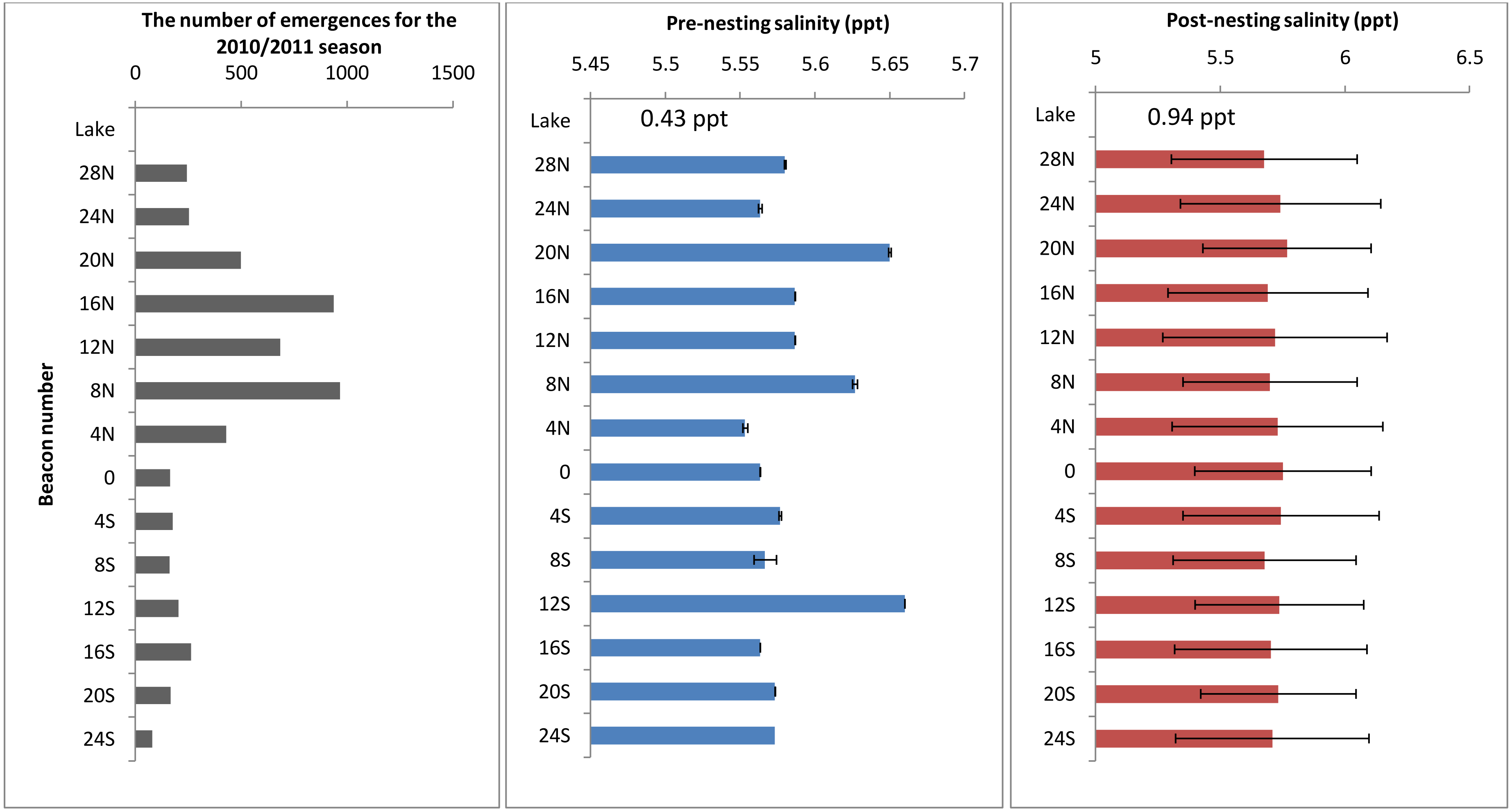

Figure 3.7: Pre-nesting salinity and post-nesting season salinity concentrations (ppt) along the nesting beaches. Data presented as means ± standard error. Graph on left illustrates the distribution of emergences per sampling site for the 2010/2011 nesting season.

The distribution of the number of emergences of loggerhead in Maputaland was highly variable between beacons with the characteristic high density between 5N and 19N and low density nesting areas outside of this range (Fig. 3.6 left panel). The highest density area received 111-364 emergences per beacon (across the 2010/2011 nesting season) with reducing densities on either side. The peak of the sulfide concentration (0.017 $mg.l^{-1}$ for post-nesting) was at beacon 4N while the peak in the number of female emergences (364 emergences in 2010/2011 season) was at beacon 8N. The sulfide concentrations ($mg.l^{-1}$) were linked to the number of emerging females but with a spatial lag in the southerly direction (Fig. 3.5); In other words, when the number of emergences from beacon 8N were correlated with sulfide concentrations ($mg.l^{-1}$) at beacon 4N and the number of emergences from beacon 4N were correlated to sulfide concentrations from beacon 0 (Fig. 3.5) then, post-nesting season sulfide concentrations were significantly correlated to this lagged nesting distribution (Fig. 3.8b; $r = 0.79$, $p < 0.005$). This correlation did not hold for direct comparison between the number of emergences (Fig. 3.8a, b; $r = 0.28$; $p = 0.33$) and sulphide concentration. The reason for using this lagged nesting distribution is that there is a northward flowing current which would displace the potential chemical plume originating from a specific section of the beach resulting in attracted sea turtles nesting further north where the scent has been extended to. Further pre-nesting season sulfide concentrations were not significantly correlated to lagged (Fig. 3.8a; $r = 0.10$; $p = 0.72$) or the direct comparison of the number of emergences (Fig. 3.8a; $r = 0.43$; $p = 0.13$). Pre- and post nesting season sulfide concentrations were also not correlated to distance from the lake ($r = 0.489$; $p = 0.09$ and $r = 0.22$; $p = 0.48$ respectively).

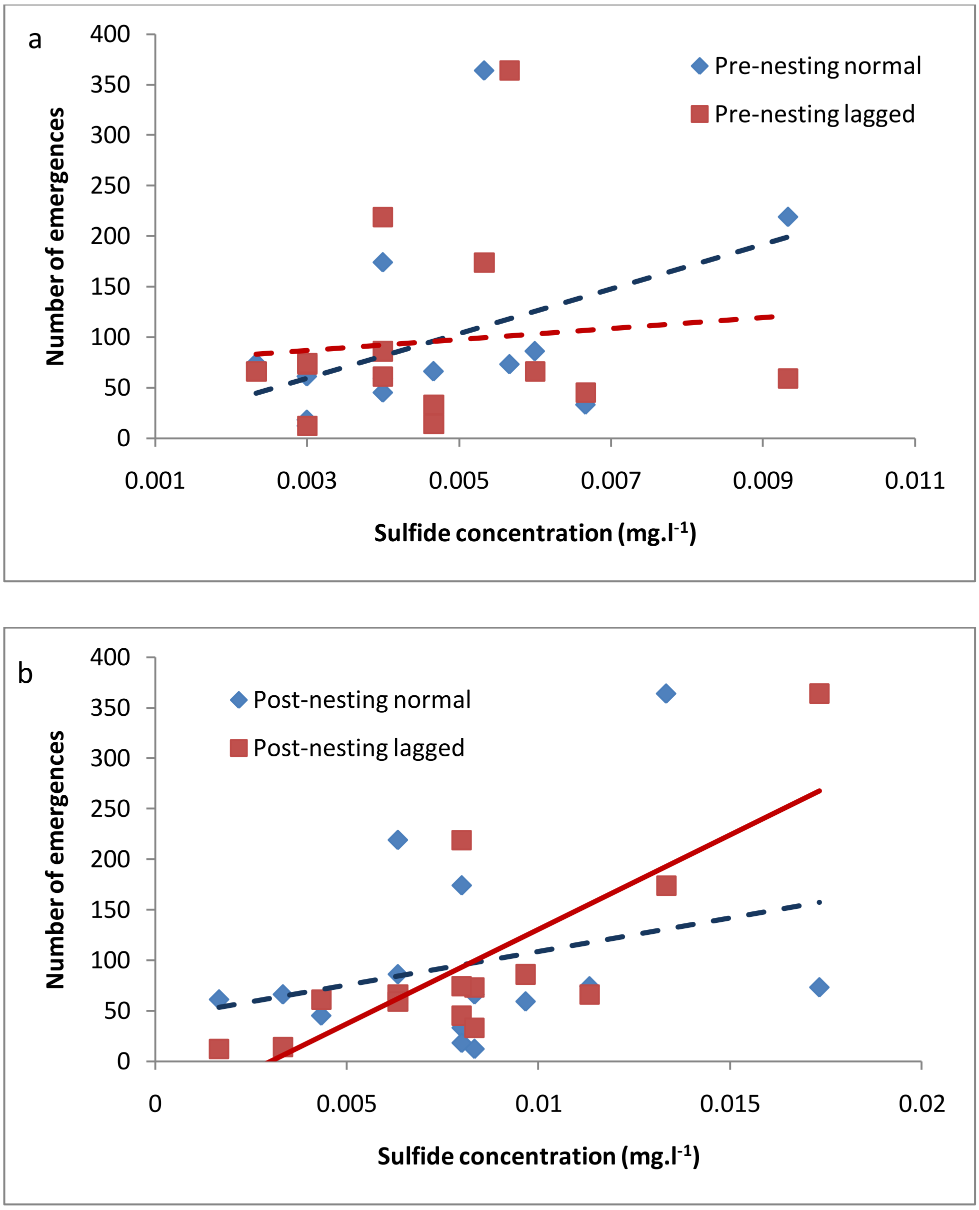

Figure 3.8: Correlations between a) pre- and b) post-nesting sulfide concentrations with the number of emergences per sampling site for 2010/2011 season with a direct correlation with the same beacon numbers (pre- and post-nesting normal) and a lagged correlation with beacon numbers (pre- and post-nesting lagged) as described in the text.

Nitrate and nitrite concentrations were not significantly correlated with the number of emergences per sampling site for the 2010/2011 nesting season (r = 0.34; p = 0.26 and r = 0.10; p = 0.75 respectively). However, nitrate concentrations were significantly correlated with distance from the lake (Fig. 3.9; r = 0.63; p = 0.02) while nitrite concentrations were not (r = 0.12; p = 0.70). Both pre- (r = 0.38; p = 0.19) and post-nesting (r = 0.2; p = 0.49) salinities were not significantly correlated with the number of emergences for the 2010/2011 season.

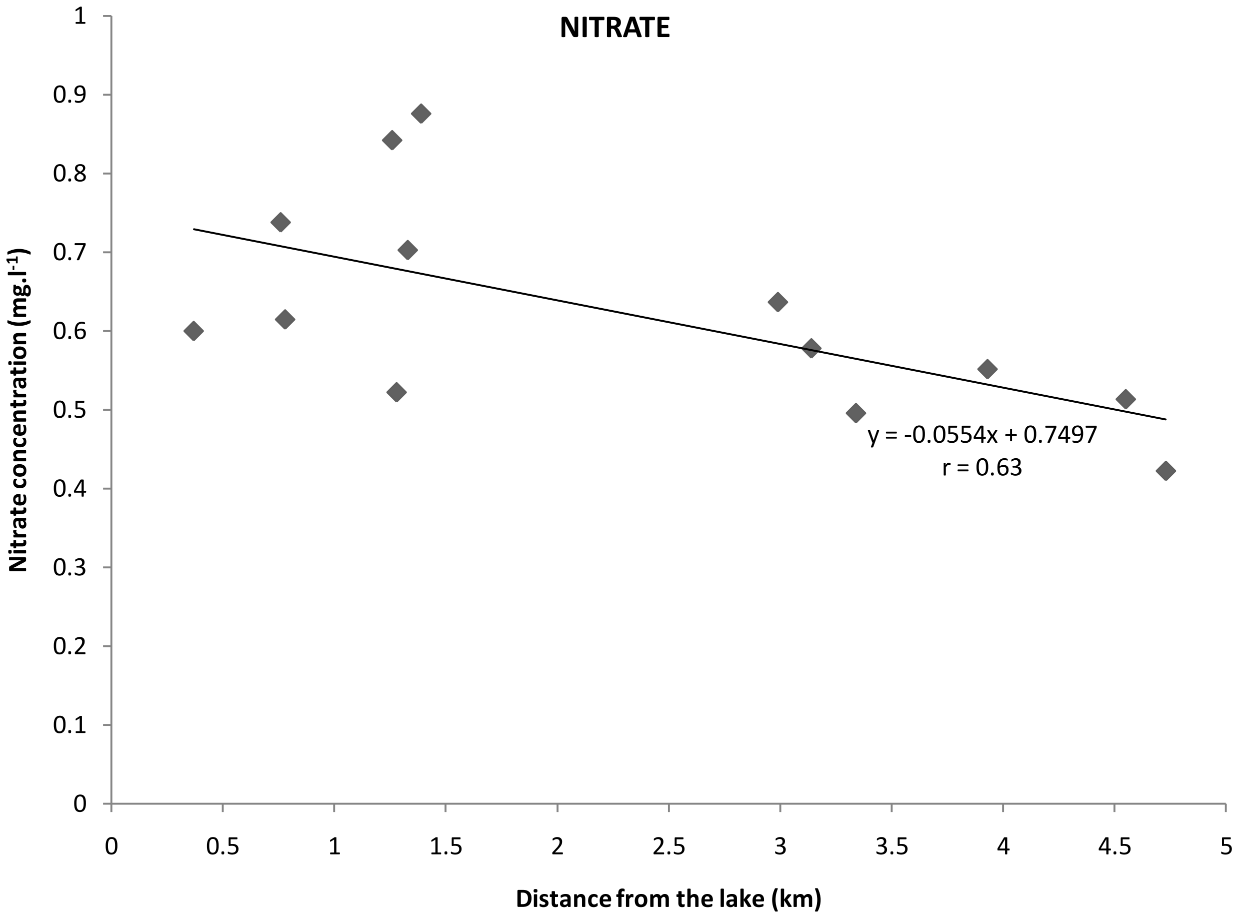

Figure 3.9: Correlation of nitrate concentrations (mg.l^{-1}) and distance from the lake.

Orientation Experiments

Captive Animals

A total of four loggerheads were available and used in the navigation experiments (Table 3.1). Two of these were adults, a male and a female, and the other two were sub-adults and therefore sex was unknown. These loggerheads were originally taken to Bayworld Aquarium because they were found stranded on nearby beaches and often injured. Two of the turtles had missing limbs. The duration that these loggerheads have been at Bayworld is also highly variable ranging from 1-33 years. Neither, age, sex nor captivity or injury should be a deterrent to attraction to their natal beach scent.

Table 3.1: Biological Information of the captive turtles from Bayworld Aquarium used in the experiments.

	Turtle 1 (Georgina)	Turtle 2 (Garreth)	Turtle 3 (Stompie)	Turtle 4 (Proppie)
SCL (mm)	950	845	696	386
SCW (mm)	770	672	590	318
CCL (mm)	1003	930	764	438
CCW (mm)	882	826	713	400
Mass (kg)	136	120.5	55.2	10.595
Sex	Female	Male	Unknown*	Unknown*
Disability	No front-right flipper	None	No hind flippers	None
Time at Bayworld (years)	1	33	5	1.75

* Both of these are immature turtles and hence impossible to identify the gender without an internal (laparoscopic) investigation.

Turtle 3 was the only turtle to exhibit a significant change in position towards the area where the sand cue was introduced (Table 3.2). However, turtle 3 was not significantly orientated towards the sand scent cue and neither were any of the other turtles. Furthermore, Turtle 3 was also the only turtle to significantly change its position and orientation towards the pilchard scent. Further examination of the position and orientation data did not reveal any time-related changes in position possibly driven by cue dilution. The general orientations of all four turtles were towards 80°-160° regardless of presence of any cues (Fig. 3.10). This coincides with the position of the ocean, across the road from Bayworld Aquarium. Therefore these turtles did not navigate towards the introduced cues but appear to be orientating based on external factors. However, the accuracy of the means of the control is greater than after the natal beach sand or the pilchard scent was introduced. Therefore it appears as if the animals detected the cue, strayed from their preferred section of the pool, but that the cue was not consistent (prolonged) enough or provides a strong enough directional factor to guide them to an alternative point in the pool.

Table 3.2: Results on position and orientation of captive animals from Bayworld Aquarium tested without a cue (Control), with a sand scent and a food cue (pilchard).

	Position				**Orientation**			
Turtle No.	1	2	3	4	1	2	3	4
Pre-experiment (Control)								
N	83	0	225	205	83	0	221	139
Mean position (°)	97.9 ± 16.4		80.7 ± 6.6	113.5 ± 10.4	119.5 ± 55.1		53.0 ± 11.5	85.0 ± 11.9
Distance from cue (°)	NA	NA	NA	NA	NA	NA	NA	NA
Sand scent cue								
N	86	130	138	47	86	130	136	47
Mean position (°)	177.2 ± 43.7	99.9 ± 32.8	46.3 ± 15.9	74.1 ± 6.6		108.3 ± 48.1	22.3 ± 13.6	70.0 ± 11.7
Distance from cue (°)	57.2	59.9	6.3*	74.1		68.3	-17.7	70.0
Pilchard scent cue								
N	18	19	116	79	18	19	94	79
Mean position (°)	242.1 ± 4.4	110.9 ± 26.2	121.6 ± 17.4	74.1 ± 4.4	345.8 ± 16.0	118.2 ± 42.3	148.2 ± 46.6	68.5 ± 5.4
Distance from cue (°)	122.1	70.9	1.6*	34.1	-134.2	78.2	28.2*	28.5

Angles for ‘distance from cue’ represent the difference between where the cue was introduced and the mean angle of orientation/position, with confidence intervals. Blank cells represent circular uniformity and therefore do not have a mean position. N is the number of images used in each observation. An asterisk represents a significant selection of the specific cue.

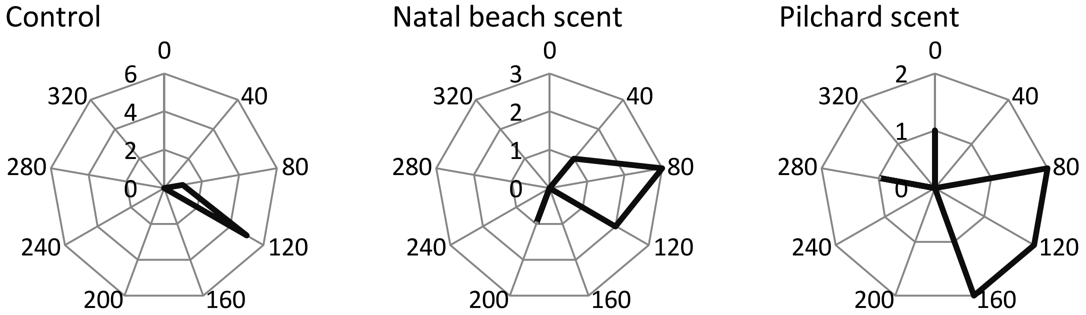

Figure 3.10: Summary of mean position and orientation for the experiments on captive loggerheads. Values are sums of mean angles. Position and orientation were grouped per treatment of control, natal beach scent, pilchard scent.

Field Orientation Experiment

None of the 17 hatchlings used in these experiments orientated significantly towards the introduced sand scent cue (Table 3.3). However, the majority of hatchlings tended to navigate towards the 180° to 360° (Fig. 3.11). Hatchlings orientated towards the ocean side of the pool much like the results in the captive turtle experiments; however the hatchling experiments were in the absence of light. Therefore it appears that hatchlings are also orientating based on external factors. Similar to the captive loggerhead experiments, the accuracy of the hatchlings control experiment was greater than when the natal beach scent was introduced suggesting confusion or an attempt to react to this scent.

Table 3.3: Position of hatchlings for pre-experiments together with positions after the introduction of sand scent cue. The last column gives the difference between the mean angles of the position of the hatchling minus the point of sand cue introduction. Blank cells represent circular uniformity and therefore do not have a mean position.

Hatchling number	Control		Sand scent cue		
	N	Position	N	Position	Mean position – cue introduction
1	88	311.5° ± 19.8°	84		
2	83		85		
3	86	239.1° ± 7.7°	86	193.2° ± 6.9°	121.8°
4	84	190.1° ± 11.4°	83	207.5° ± 7.2°	107.5°
5	167		167		
6	165	1.7° ± 32.3°	166		
7	84	0.0° ± 6.2°	165	317.8° ± 4.6°	-132.2°
8	165	268.1° ± 23.0°	164	213.2° ± 13.6°	-101.8°
9	166		167	300.1° ± 46.5°	-149.1°
10	158	309.6° ± 17.1°	166	282.5° ± 56.4°	-167.6°
11	169	191.2° ± 20.2°	167	162.5° ± 12.7°	-107.5°
12	167	124.6° ± 25.0°	167	155.6° ± 12.4°	-159.4°
13	168	240.0° ± 40.2°	165	271.0° ± 6.4°	91.0°
14	166	228.2° ± 19.1°	166	241.6° ± 25.2°	-118.4°
15	169		168	248.6° ± 24.0°	
16	166	318.9° ± 22.6°	168	351.0° ± 33.3°	126.0°
17	167	211.5° ± 49.7°	157	5.0° ± 23.6°	50.0°

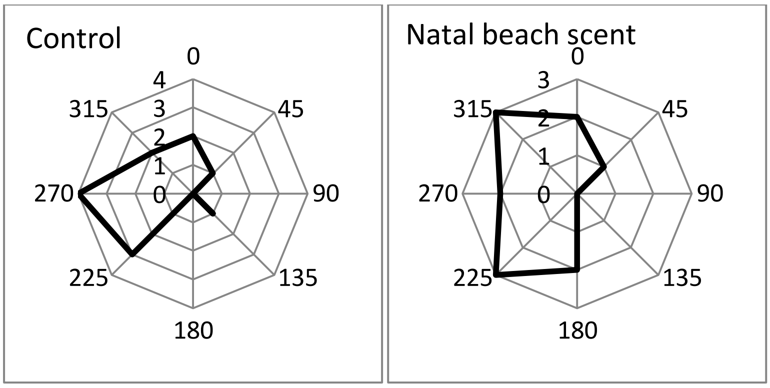

Figure 3.11: Mean positions of hatchlings for the control experiment and natal sand scent experiment. Values are sums of mean angles. Position and orientation were grouped per treatment of control and natal beach scent.

Discussion

None of the variables measured in this paper were significantly correlated to the number of emergences per sampling site except for post-nesting sulfide concentrations (mg.l^{-1}) with a spatial displacement (or lag) to the number of emergent females. Pre-nesting season sulfide concentrations were on average 60% lower than post-nesting season sulfide concentrations and this increase may be a result of decomposition of nests. Decaying organic matter, potentially originating from nests laid during the nesting season, will produce nutrients including sulfides. This organic decay may be the reason sulfide concentrations are higher in the post-nesting compared to pre-nesting season. Further, Hughes (1989) suggests that cues for nest site selection may originate from the previous year's nests in the form of mucous secreted by nesting females, decomposing eggs or other chemical releasing processes. This seems to be the case for the sulfides that remain in the sand among seasons as is seen in these results. Therefore sulfides are a potential long-lasting cue driving nest site selection.

Return nesters or experienced nesters are known to reach nesting beaches and begin laying before neophyte nesters (Ezemvelo, Unpublished Data). These experienced nesters have already been imprinted or have a memory of a favourable nesting beach and therefore these experienced nesters will setup the cue on a favourable beach for neophyte nesters that arrive later in the season. This may play a crucial role in, unintentionally increasing the sulfide concentrations (mg.l^{-1}) in the groundwater before neophyte nesters arrive so that they know where to nest by following these cues. There may be an increase in decomposition rates due to increased temperatures during the nesting season resulting in more nutrients being released however this is purely speculative. A more likely explanation is that sulfides remain between seasons and are therefore used as a nest site selection cue. Nitrite and salinity do not have any influence on nest site selection.

The association of large coastal bodies of water with high density nesting beaches was first noted by Hughes (1974), where he suggested that these water bodies may be the origin of nest site selection cues. However, only nitrate concentrations were correlated with distance from the lake. This may suggest that the nitrates originate from the lake and appear in the groundwater on the beach through aquifers. However, nitrate concentrations in the lake were much lower than those in the groundwater which suggests that nitrates may originate in the aquifer, in the groundwater, or in the beach itself. Meiofauna, protozoa and bacteria are known to change the nutrient concentrations of the beaches (McLachlan *et al*. 1981). Therefore, nutrient concentrations observed in the groundwater may have been influenced by beach fauna. Furthermore, the increase in the nitrate and sulfide concentrations in the high nesting density area may be a result of the larger number of nests laid in the high nesting density areas once again suggesting that previous nesting events create nest site selection cues.

The decrease in accuracy of mean positions and orientations of captive experiments and, to a lesser degree, the hatchling field orientation experiments, with the presence of natal scent or pilchard scent (for captive experiments) suggests that turtles detect and are attracted by the natal scent but that the origin is uncertain and the concentration too small. The expanded distribution seems to be a result of turtles detecting and moving around, but then not finding and returning to the preferred position. Perhaps a stronger gradient i.e. a more concentrated scent would have provided a stronger result for these experiments.

Interestingly, both captive and field-caught sea turtles used in these position and orientation experiments were generally orientated towards the ocean side of the pools. These results are interesting for the captive experiments as these loggerheads have been captive for variable amounts of time and the ocean is not visible from the turtle’s position in the experimental pool. It is also, unlikely that the turtles can hear or discern direction of the waves from their position. Potentially, these turtles were orientating towards another cue that is unknown. Available cues include the sun's position in the sky (only captive experiments), celestial cues (only hatchlings), brighter horizon (only hatchlings), olfactory cues (both) and magnetic cues (both).

It may be possible that the sun rising in the east coincides with the position of the ocean for the sub-adult and adult experiments to be used as a navigational cue. The azimuth of the sun has been used by freshwater turtles to find orientation (DeRosa & Taylor 1980) and may also be used by sea turtles although this has not been well-studied. Further, celestial cues (such as stars) present after sunset for hatchling experiments may have provided directional cues. The smell of the ocean may also appeal to the sea turtles resulting in their orientation towards this source. However this is considered an unlikely cue as it would depend on the wind direction and even when there was an offshore or alongshore wind, orientation was always towards the ocean. Geomagnetic cues may potentially be used in much the same way as was found for young loggerhead sea turtles in the Atlantic Ocean (Lohmann & Lohmann 1996). These loggerheads were able to detect and use the earth's magnetic field to navigate in the correct direction to remain in the North Atlantic gyre. Loggerheads used in the present experiments may have used geomagnetic cues to head in the correct direction towards the ocean.

The hatchling experiments were performed on the beach and there are a number of possible reasons for their orientation towards the ocean: 1) dune silhouettes as well as the research hut were visible at certain sections of the pool and may have provided visual sea-finding cues, 2) celestial cues may be used for orientation, 3) hatchlings use magnetic cues to determine position and direction (Lohmann & Lohmann 1996, Fuxjager *et al.* 2011) and therefore they may have used these to swim seawards in the pool. This last point is complicated because Lohmann & Lohmann (1996) and Goff *et al.* (1998) and suggest that magnetic cues are established only after passing through the surf and experiencing the wave propagation. The hatchlings used in these experiments were only allowed to enter the intertidal swash at which stage they were removed immediately and placed in to the experimental pool and therefore it is assumed that they were not able to establish magnetic orientation.

If the nest site selection cue does indeed originate from the coastal lakes, or sulphide being pushed into the ocean through the groundwater, then preservation of these lakes with a reasonable ecosystems functioning and freshwater discharge is critical to the continued existence of nesting sea turtles in South Africa. Anthropogenic activities along the South African coast are increasing substantially resulting in a subsequent increase in the associated pollution and exploitation of coastal resources (Reid *et al.* 2005). Among these are the water abstraction from aquifers, lakes and fresh groundwater. Furthermore, climate change scenarios predict that rainfall patterns will change resulting in an increase need for extraction from reliable water sources (Reid *et al.* 2005), including aquifers. Therefore if chemical imprinting is linked to the lakes or the groundwater discharge on nesting beaches, then coastal biochemistry will be an important consideration for coastal management.

The hypothesis of chemical imprinting has never been proven to occur in sea turtles and it remains a hypothesis for the mechanism of natal homing and nest site selection. The results from this study suggest that nutrients present in the sand/groundwater may be present within and between seasons and is a possible cue in nest site selection although the interaction with the number of emergences is not a simple one and further investigation is necessary. Therefore chemical imprinting is plausible however further research is needed.

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Chapter 4: The effect of ambient and artificial lights on loggerhead nesting emergences in South Africa

Two images of examples of ambient and artificial light sources present on nesting beaches (Images from http://www.photos8.com & http://4.bp.blogspot.com).

Abstract

Lights present on nesting beaches have major implications for sea turtle nesting behaviour. The effects of artificial lights on nesting beaches have been well documented however the effect of quantitatively measured ambient lights has never been investigated. Therefore the aims of this chapter were to determine the effect of ambient light intensities on the number of emerging females both spatially and temporally and further solidify the negative effect of artificial lights on the distribution of emergences of females onto beaches. Ambient and artificial light intensities were measured during the nesting season and related to the number of emergences both per night and per location. Other influencing variables (moon phase, cloudcover and presence of lightning) were recorded to determine the effect of these on light intensities and further on the number of emergences. Light intensities were not correlated to the number of emergences per night for seaward, skyward and landward measurements or for alongshore distances. Further, combined moon phase and cloudcover were significantly correlated with light intensity but not with the number of emergences. The presence of lightning significantly elevated light intensities, however nights with the presence of lightning never altered the number of emergences per night or per sampling site from the averages per night. Artificial light sources exhibited elevated light intensity recordings up to 1000 m away from the source with a reduced number of emergences in this area. Therefore it appears that ambient light intensity is not used as a cue for female emergence. The deterrent effects of artificial lights present on Maputaland's nesting beaches are evident in the reduction of the number of emergences in the near vicinity of these lights and mitigatory measures will be beneficial to restore previously illuminated nesting beaches.

Introduction

The life history of sea turtles is inextricably linked to the beach environment (Carr *et al.* 1966). Adult females crawl up beaches to deposit their eggs and subsequently return to the ocean. Hatchlings then emerge from these nests at night and navigate towards the ocean to begin their offshore migrations (Lohmann *et al.* 1990). Adults and hatchlings use natural ambient light available to find the ocean (Moein Bartol & Musick 2003). Literature investigating adult sea-finding behaviour is scarce, and even though experiments have been conducted on all species of sea turtles, the actual mechanism of orientation was assumed (light horizon for sea finding) to be the same among all species and classes.

Hatchling orientation has been studied most extensively and therefore the findings from these studies will be discussed in light of adult sensory abilities. Sea-finding orientation is influenced to varying degrees by light intensity (Salmon *et al*. 1992, Karnad *et al.* 2009), landward silhouettes (dark-dune silhouettes) (Salmon *et al*. 1992, Salmon & Witherington 1995), wavelength of light (Levenson *et al.* 2004, see appendix A for wavelength preferences), ambient light (Tuxbury & Salmon 2005) and beach slope (Salmon *et al*. 1992). Hatchlings are attracted to the brightest light even if this happens to be an artificial light source in a landward direction (Salmon *et al.* 1992, Salmon & Witherington 1995). Landward silhouettes are found in the form of large dune systems (Salmon *et al.* 1992), large stands of vegetation (Karnad *et al.* 2009) or even in some cases, as large buildings which create the type of silhouettes required for sea-finding by hatchlings (Salmon *et al.* 1995).

Hatchlings with colour filters (to alter the perceived wavelength) covering their eyes were able to find the ocean with varying degrees of success (Ehrenfeld & Carr 1967). Further experiments with different colour filters by Witherington & Bjorndal (1991) suggest that loggerheads are xanthophobic thus opposed to yellow-orange light. They are also attracted to lights of lower wavelengths and are able to detect lights at least in the range of 360 nm – 700 nm. More intense ambient light have been found to reduce the effect of artificial lights on hatchling orientation (Tuxbury & Salmon 2005). Under natural conditions, emerged sea turtle hatchlings orientate towards the brighter sea surface, away from darker landward silhouettes (Salmon *et al.* 1992, Moein Bartol & Musick 2003). Therefore various aspects of light influence the orientation ability of sea turtle hatchlings. When light cues are confusing or not available, alternative cues such as beach slope may be used to direct hatchlings

(Mora & Robinson 1982, Salmon *et al.* 1992) but it is not always used or effective (Daniel & Smith 1947, Mrosovsky & Shettleworth 1968). Unfortunately, beach slope is not reported in these investigations so little can be concluded on this.

In recent years turtle nesting beaches have been overwhelmed by artificial lights from coastal developments, overnight fishermen and other night beach users (Peters & Verhoeven 1994, Bourgeois *et al.* 2009, Karnad *et al.* 2009) such as turtle researchers (Pers. obs.). Artificially illuminated beaches are known to deter adult females from nesting (Proffitt *et al*. 1986, Witherington 1992a, Mortimer 2004) presumably due to the possible perceived increase in predation risk. Hatchlings are positively phototactic which means they orientate towards these artificial lights situated on or to the landward side of the dune resulting in hatchlings moving away from the ocean. This inland search causes higher mortality rates due to desiccation, exhaustion and increased predation (Mortimer 1979, Witherington & Bjorndal 1991, Peters & Verhoeven 1994, Witherington & Martin 2003, Mortimer 2004, Bourgeois *et al.* 2009). According to Tuxbury & Salmon (2005) the competitive cue hypothesis states that disorientation and misorientation occur when observed artificial cues are similar or greater in intensity than natural cues respectively. Artificial lights present on a beach, are almost always brighter than natural light and therefore the cue to be homed in on/away from. The implications of artificial lights on sea turtles life history are thus large and important to understand.

Only a few artificial lights are present on Maputaland's loggerhead nesting beaches (pers. obs.). The main, and constant artificial light sources include the collection of the research hut and park rangers' houses at beacon 0 and the police camp at Beacon 76S. The generators at both these facilities are shut down before midnight. Mobile, flashing lights include the torch lights used by the turtle monitors, researchers, guided turtle tours, concessionaire's vehicle tours and fishermen which move up and down the nesting beaches (Nel 2009). The number of turtle emergences seems to have decreased in the adjacent area since the construction of the research and park rangers' camps (Ezemvelo unpublished data). Due to the lack of artificial light interference, Maputaland is the ideal area for research on natural light cues.

Research on sea turtle nest site selection generally focuses on physical beach characteristics (see Miller *et al.* 2003 for a summary). However, this chapter will investigate the effect of light intensity on emergence and nest site selection. The only study to investigate moon phase as an emergence/nest site selection cue was Pike (2008). However this study did not quantify light intensity but only assumed light intensity from moon phase. The results from Pike's (2008) study suggest that moon phase is not a strong cue for emergence/nest site selection. To date no clear attractant/deterrent has been identified (other than artificial light) driving nest site selection.

The aims of this study were to investigate the deterrent and attractive effects of spatial (alongshore) and temporal variation in light intensities on loggerhead nesting distributions in Maputaland. To do this, three key points will be addressed: 1) compare light intensity of landward, skyward and seaward horizons between nights with different light conditions and at different beacons to relate these conditions with the number of female emergences per night and per beacon respectively. 2) Explain variations of light intensity by relating this to cloudcover, moon phase, and the presence of lightning and lastly, 3) determine the negative effect of artificial light sources on female emergences by measuring these light intensities at increasing distances from the light source and relating this to the nesting distribution.

Methods

Photometer

Light measurements to the beach, dunes, and sky horizons were recorded using a photometer (Extech Instruments: Model 401036) (Fig. 4.1). The wavelength sensitivity of this photometer resembles that of the loggerheads' eyes (Fig. 4.2) and therefore this device was considered a close approximation of what a loggerhead would see. The photometer has a broad input for measuring light (±180°) and can measure intensities in the range of 0.01 – 20000 lux. The accuracy of these measurements as indicated by the manufacturer is to 3 % with a repeatability of 2 %. The spectral sensitivity curve of the photometer follows that of the International Commission on Illumination (CIE) photopic curve (human eye response) which closely resembles the spectral sensitivity curve of the loggerhead retina as discovered by Levenson *et al.* (2004) (Fig. 4.2).

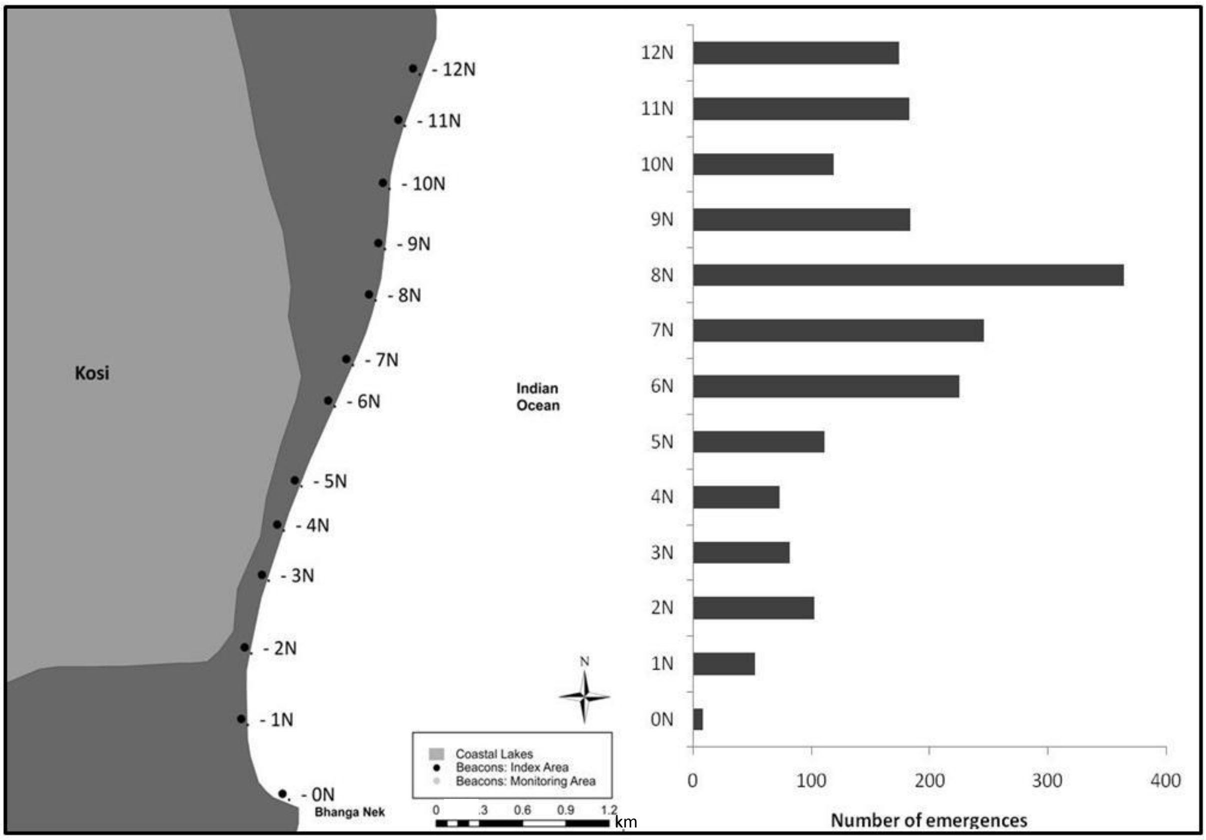


Figure 4.1: Map of the sampled sites for light intensity in Maputaland, South Africa, together with accompanying number of emergences for the 2010/2011 season. The changing width, height and vegetation density of the dune field is expected to result in varying grades of light intensity.

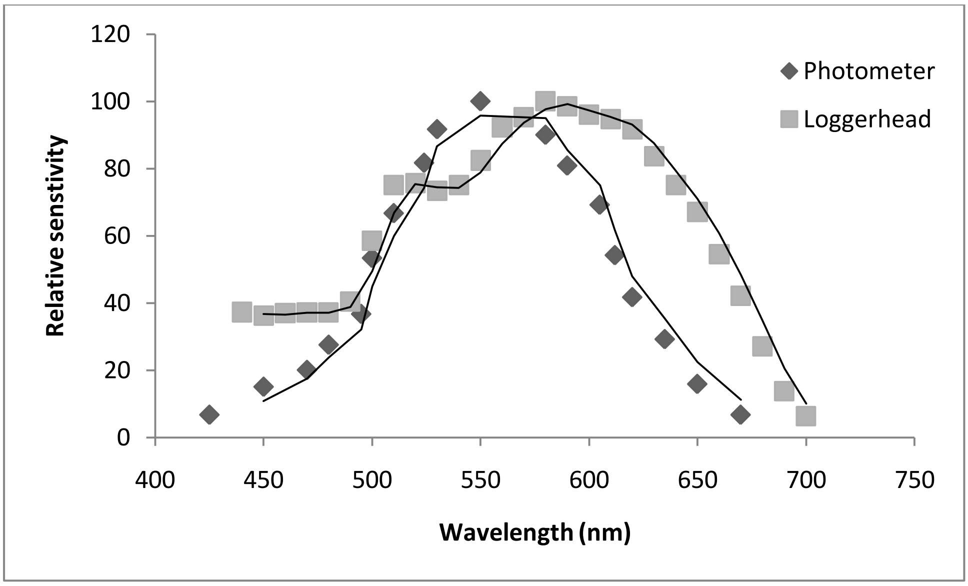


Figure 4.2: Spectral sensitivity or visible range of the Extech photometer (Model 401036) and the loggerheads' eye (from Levenson *et al.* 2004).

Data collection and manipulation

Landward, skyward and seaward light intensities were collected during the nightly nesting and hatching monitoring foot patrols in Maputaland, South Africa on two separate occasions (weather permitting) between the 13th – 29th December 2010 and the 27th February-19th March 2011. Measurements were taken at 400 m intervals (roughly equivalent to the distance among adjacent beacons) within the high density index area (beacon 0-12N = approximately 4.8 km) along the loggerhead nesting beaches (Fig. 4.1). Each light intensity reading, measured in lux, included the sea-, sky- and landward directions while standing on the midshore. The light sensor was pointed in the appropriate direction with a fully straightened arm and held as still as possible. The maximum light intensity measurement recorded over ten seconds was used for each direction. Other variables recorded were lightning (absence/presence) and cloud cover (in quarters). Moonrise and moonset times as well as moon phase was retrieved from the South African Navy Tide Tables. The new (0), quarters (0.5) and full (1) moon phases were scored. The phases between these set values were assumed to scale continuously and were calculated as the difference in phase divided by the number of days between the next phase. Recordings taken on new moons and when the moon was not present (e.g. due to complete cloudcover) were assumed to have the same effect on light intensities and both were classified as new moon. Additional data (distance from light and light intensity) were collected when the lights from the research and ranger accommodation at beacon 0 were visible. Analyses of light intensity were performed with regards to beacon numbers, date, lightning events, moon phases and cloud cover. Measurements prior to 20h30 and after 03h30 were removed from analyses due to the sun's influence. Recordings where lightning was present were removed from all analyses except where lightning was investigated.

Pearson product moment correlations between the number of female emergences and light intensities (lux), spatially and temporally, were investigated using Analysis ToolPak in Microsoft Excel 2010. An Analysis of Variance (ANOVA) was used after inspecting the data and ensuring no major deviation from normality and homoscedasticity. ANOVA was used to determine whether there was a significant difference among the three directional measurements. A Pearson product moment correlation analysis between the average landward and seaward light intensities and the number of emergences per night was performed to quantify the brighter sea surface and the darker dune silhouette that is used by hatchlings to find the ocean (Bourgeois *et al*. 2009). Light intensity recordings were also correlated to cloudcover and moon phases. The D' Agostino-Pearson test for normality and the Bartlett's test for homoscedasticity was used to test the data for normality and homoscedasticity respectively. Cloudcover and moon phase were expected to have an antagonistic effect and therefore a combination of cloudcover and moon phase was used by adding these 0-1 scale variables together. Zero in both variables was set to represent the expected lowest light intensities (full cloudcover and new moon). This combined variable was then correlated to the number of emergences. The effect of lightning on light intensity recordings was determined using t-tests after determining that there were no major deviations from normality or homoscedasticity. All statistics were performed using Microsoft Excel 2010.

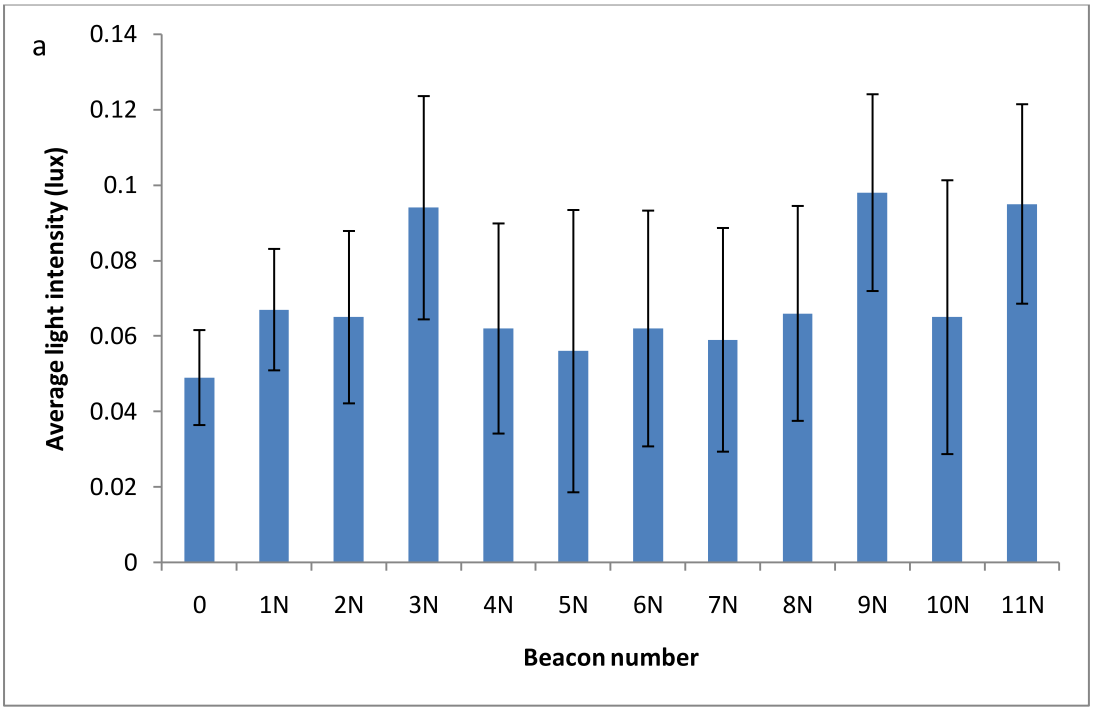
To illustrate the light intensities of two common artificial light sources, a headlamp and the lights present at the research hut (Beacon 0) were measured from multiple distances to determine the effect these have on light measurements and to compare them to ambient light intensities. In both cases, the light sensor of the photometer was directed towards the headlamp and the house for maximum intensity readings.

Results

Light intensities measured between 20h30 and 03h30 and excluding lightning events and artificial lights along the beach ranged from 0.01 to 0.32 lux. The maximum light intensities measured during the presence of lightning were 0.4 lux for seaward, 8.04 lux for skyward and 1.14 lux for landward. The light intensities measured for full moon phases ranged from 0.01 lux to 0.25 lux.

Spatial and temporal light intensities

There were no significant correlations between the number of emergences and average light intensities per beacon ($r = 0.037$; $p > 0.5$, Fig. 4.3a,b) as well as for seaward ($r = 0.22$; $p > 0.05$), skyward ($r = 0.23$; $p > 0.05$) or landward measurements ($r = 0.08$; $p > 0.5$). There was also no significant correlation between the number of emergences and the average light intensities per night ($r = 0.05$; $p > 0.4$, Fig. 4.4) as well as for seaward ($r = 0.25$; $p > 0.1$), skyward ($r = 0.34$; $p > 0.1$) and landward measurements ($r = 0.00$; $p > 0.5$). Further, there was no significant correlation between the average number of emergences for the 2010/2011 nesting season and light intensities per 30 minute period for seaward ($r = 0.13$; $p > 0.5$), skyward ($r = 0.06$; $p > 0.5$), or landward measurements ($r = 0.31$; $p > 0.1$). No significant difference was found between the average light intensities for seaward, skyward and landward measurements ($F = 0.03$; $p > 0.5$). The differences between seaward and landward light intensities were not significantly correlated with the number of emergences per day ($r = 0.52$; $p > 0.1$).



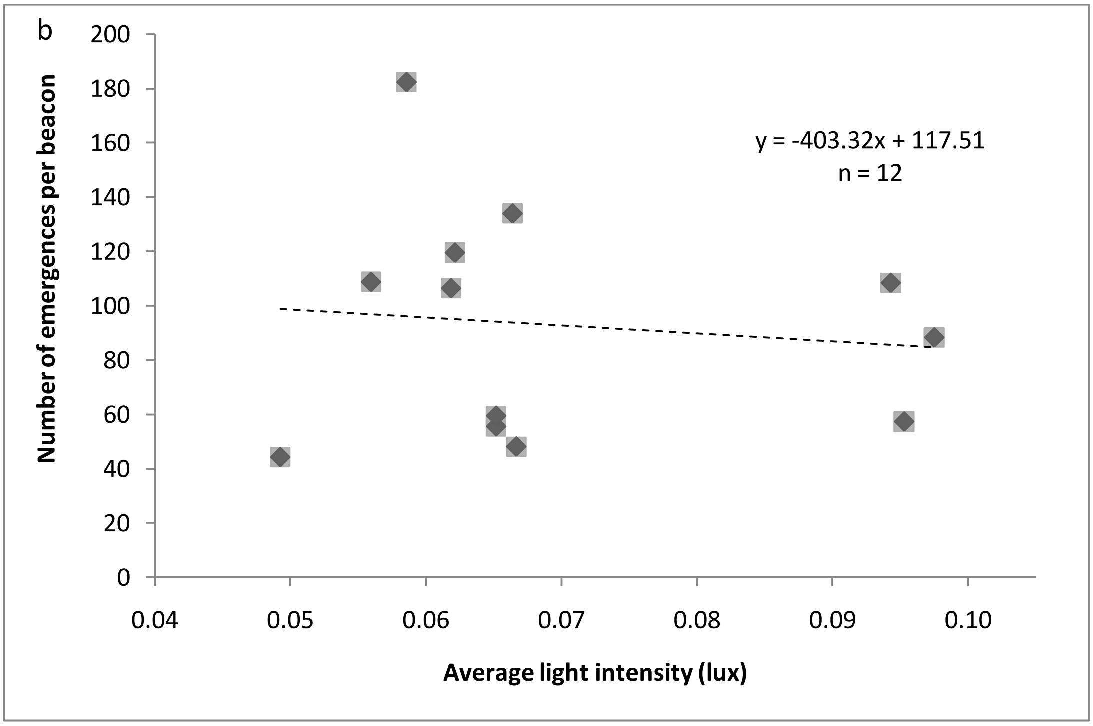


Figure 4.3: The a) average light intensity per beacon with associated standard error bars and the b) number of emergences per beacon correlated with the average light intensity of sea-, sky- and landward measurements.

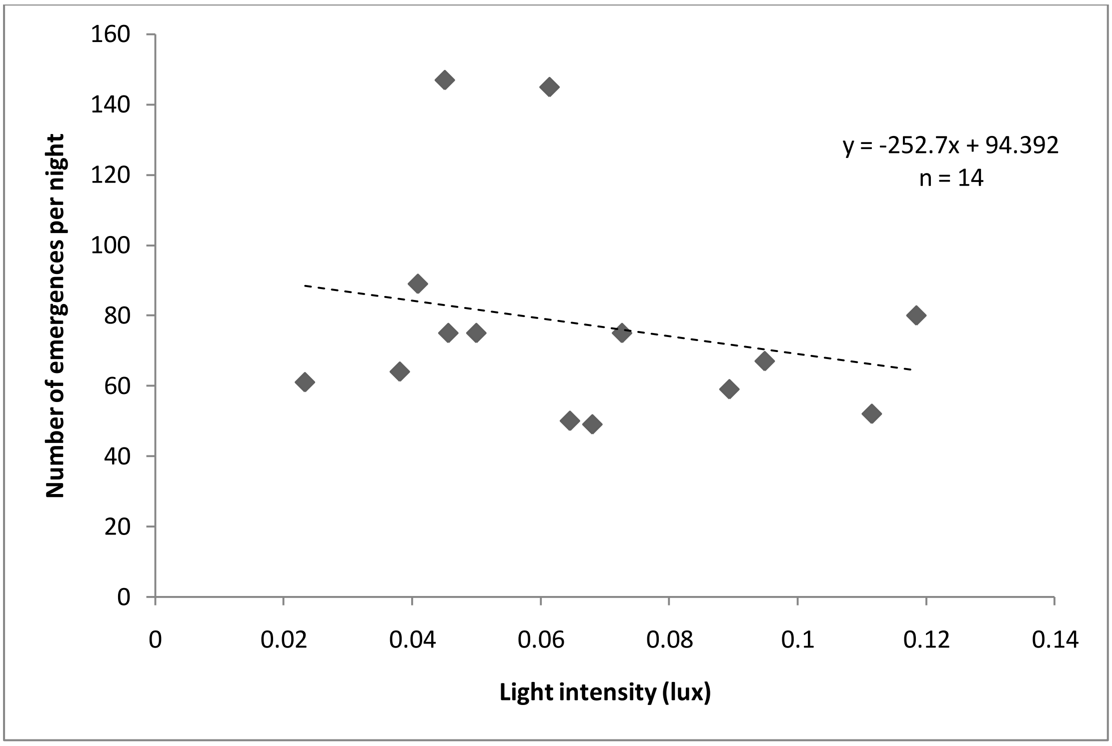


Figure 4.4: The number of emergences per night correlated with the average light intensity of sea-, sky- and landward measurements.

Influencers of light intensity

Average light intensities were not significantly correlated with cloudcover (seaward: $p > 0.5$; skyward: $p > 0.1$; landward: $p > 0.1$) or with moon phase (seaward: $p > 0.1$; skyward: $p > 0.05$; landward: $p > 0.1$). However, when the cloudcover and the moon phase were combined as a single variable, there was a significant correlation for seaward and skyward light intensities (Seaward: $r = 0.75$; $p < 0.05$; skyward: $r = 0.71$; $p < 0.05$; landward: $r = 0.44$; $p > 0.1$, all $n = 10$). Also, the number of emergences was not correlated to the combined cloudcover and moon phase variable ($r = 0.10$; $p > 0.5$, Fig. 4.5). Lightning was found to significantly elevate light intensity readings for seaward ($t = 2.28$; $p < 0.05$; df = 334), skyward ($t = 4.32$; $p < 0.01$; df = 339) and landward measurements ($t = 5.97$; $p < 0.01$; df = 338), with skyward light intensities during lightning being much higher than the others (Fig. 4.6). However none of these nights with lightning significantly altered the number of emergences from the average ($t = 0.08$, $p = 0.94$, df = 27).

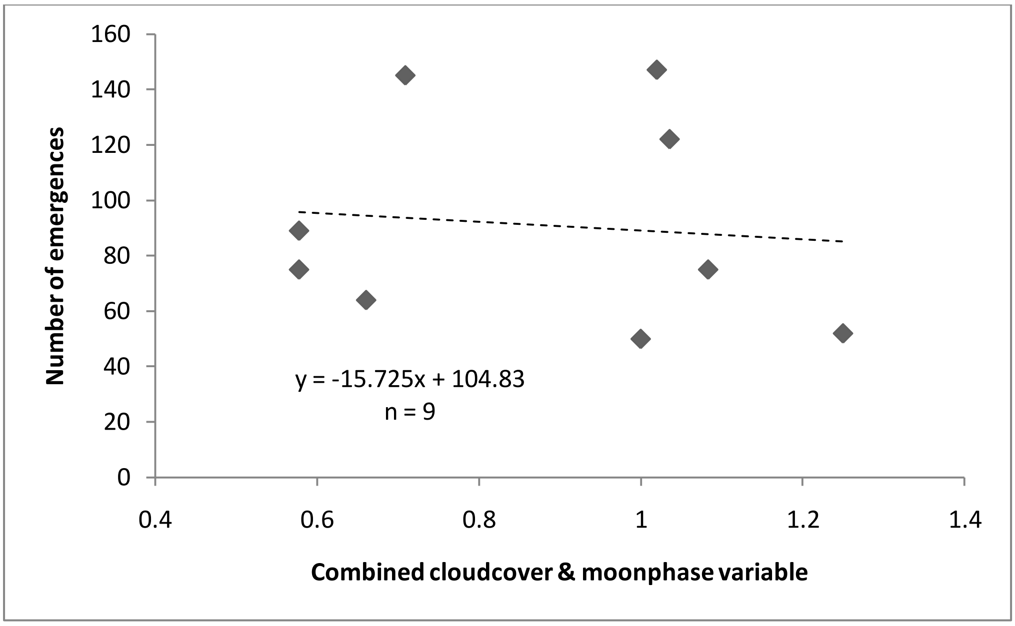


Figure 4.5: The number of emergences correlated with the combined cloudcover and moon phase variable.

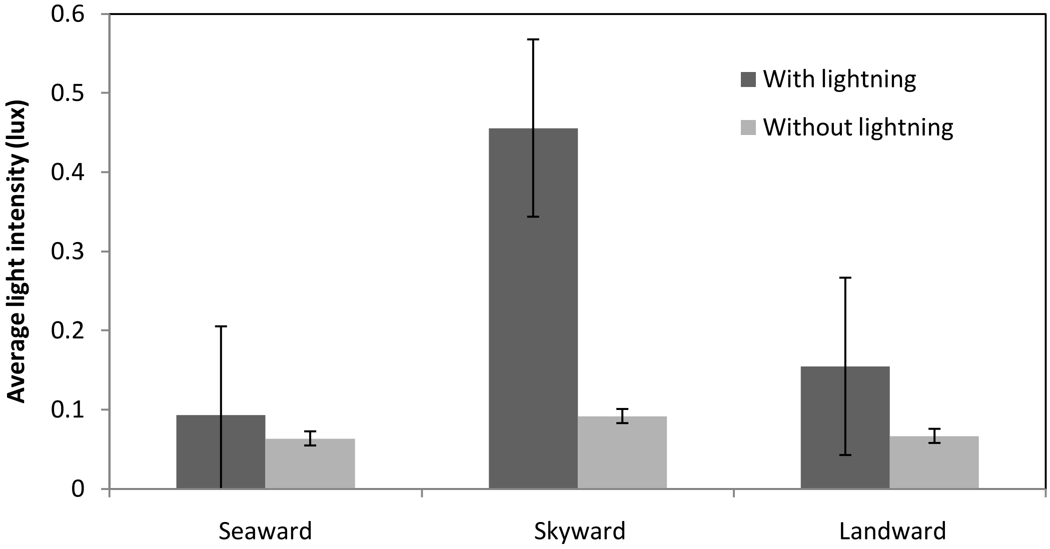


Figure 4.6: The effect of lightning on light intensity readings for seaward, skyward and landward directions. Error bars denote 1 SE.

Artificial light sources

Artificial light intensity (lux) recordings decreased exponentially with an increase in the distance to the source (Fig. 4.7). However, the same exponential decrease in light intensity was not found for the research house lights (Fig. 4.8). This may be a result of the mixture of light sources and the relatively low intensities that were recorded at distances and the interference of ambient light with these. Direct comparison of measurements suggest that the light intensity of a headlamp measured from 50 m is roughly equivalent to that of the house lights with the light screens open at 200 m, or the house lights with blinds closed at 5 m.

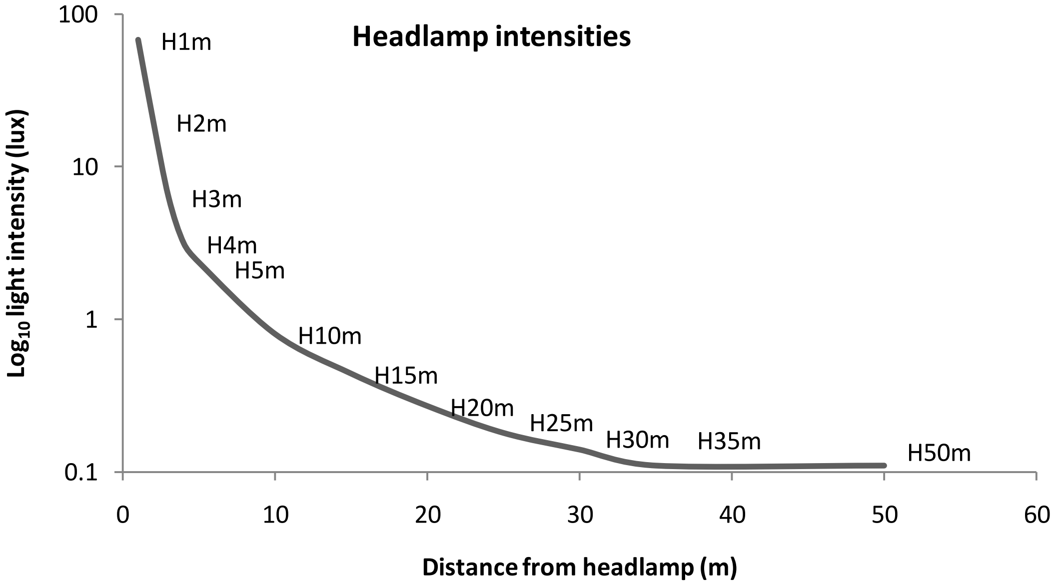


Figure 4.7: Light intensities (lux) of a headlamp (e.g. H1m – headlamp from 1m away) measured at varying distances from the source.

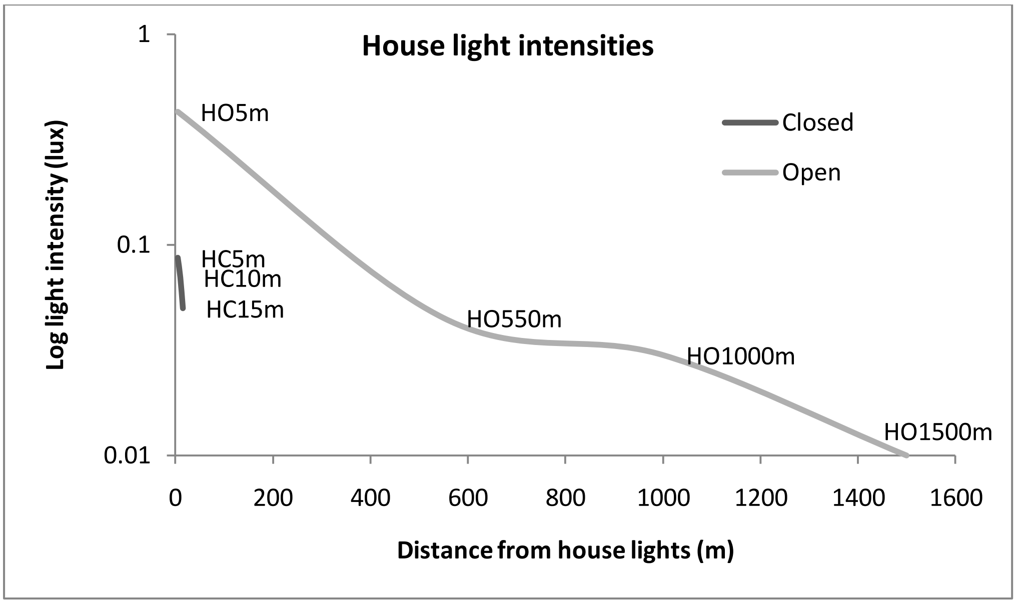


Figure 4.8: Light intensities (lux) of the research hut (e.g. HO5m = House with curtains/blinds Open from 5m away, HC5m = house with closed curtains from 5m away) measured from varying distances from the source.

Discussion

Spatial and temporal distributions of light intensities were not correlated to loggerhead emergences. This leads to the initial conclusion that ambient light intensities as experienced under these conditions are not important drivers for turtle emergences. One of the conditions that was investigated was a combined cloudcover and moon phase variable. This variable had a significant effect on light intensity but had no effect on nesting emergences. These results suggest that the cloudcover and moon phase variable can be used as indicators of light intensity although nesting emergence is not dependent on these variables. Another investigated driver was the presence of lightning. Lightning significantly increased the light intensity measurements. However, the presence of lightning did not have any effect on the number of emergences. Regardless, variations in light intensity observed had no noticeable effect on the number of emergences.

Hatchling sea-finding studies suggest that they orientate towards the brighter sea surface and away from the dark dune silhouette (Salmon *et al.* 1992, Salmon & Witherington 1995, Moein Bartol & Musick 2003). It would be assumed, then, that adults use the same cues to find the ocean after nesting, and one would consequently expect a gradient in light intensity to exist from land to sea. However there was no statistically significant difference between the measurements of seaward, skyward and landward light intensities. Nonetheless, this does not necessarily mean that the perceived light intensities of sea turtles do not differ and there are several explanations as to why, which are described below.

Firstly, sea turtles have a field of vision of 180° horizontal with only 60° vertical (Witherington 1992b, Witherington 1997) while the photometer is able to detect an area of 180° both horizontally and vertically. This suggests that the photometer will pick up a greater proportion of the sky when measuring landward and seaward directions, introducing a bias in the measurements. Secondly, light measurements are only taken for a fraction of the night while the number of emergences is taken for the entire night. Therefore changing weather conditions during the night will not always be recorded (with varying times of onset and duration). Thirdly, it is suspected that hatchling sea turtles use more than one cue and do not always orientate towards the brighter horizon (Salmon *et al.* 1992, Moein Bartol & Musick 2003, Fuentes-Farias *et al.* 2011). This reinforces the argument that hatchlings primarily orientate away from high dune silhouettes and toward the brighter sea surface (Salmon *et al.* 1992, Moein Bartol & Musick 2003). Fourthly, directional light intensity differences that sea turtles eyes are able to detect are possibly too small for the light meter to detect. Lastly, it appears that emerging females do not discriminate between natural light conditions but avoid artificially illuminated beaches (Witherington 1992a).

It is well known that artificial lights present on nesting beaches reduces the number of emergences on those beaches (Proffitt *et al*. 1986, Witherington 1992a, Salmon 2003, Mortimer 2004). Light intensities were found to decrease exponentially with distance from the headlamp with an inconsistent decrease in intensity from the house lights. The light intensities of the house at approximately 500 m were roughly equivalent to the average ambient light intensity. However, anecdotal observations of hatchlings orientating towards the house from distances up to 1500 m away have been noted. There are a few explanations for these observations. Firstly, point-source lights have a large effect on hatchling orientation (Philibosian 1976). Secondly, ambient light intensity plays a large role in the orientation of hatchlings. Bright ambient lights can diminish the effects of artificial lights on hatchling orientation by decreasing the contrast between point-source lights (Salmon &

Witherington 1995, Tuxbury & Salmon 2005, Bourgeois *et al.* 2009). Thirdly, hatchlings may be able to detect light intensity variations below those detectable by the photometer used in these experiments. Fourthly, the light sensor used in these experiments has a wider angle of acceptance than the sea turtle eye (Witherington 1992b, Witherington 1997) and a single point-source light, which appears bright, may be diluted by the more abundant dark area. Regardless, the number of emergences directly adjacent to the artificial light source is reduced and therefore an avoidance to nest near illuminated beaches is seen. Unfortunately there is no simple measure of light intensity for artificial lights that will suggest an influence on nesting or hatchling orientation because of the intricate interactions between artificial and ambient lights (Witherington & Martin 2003).

A possible short-coming in these results is the temporal variations in light intensity measurements and variables and nesting emergences. For example, if lightning occurs for a fraction of a night and light intensities are recorded for the same time period but turtle emergences are taken for the entire night, it will be impossible to detect whether turtles are avoiding emerging during the lightning events and emerging after the storm, or if lightning truly has no effect on their emergence.

Another study investigating the effect of tides on the number of emergences in Maputaland discovered that the onset of darkness was a more important cue for initiation of nesting rather than tidal phase (Scheun 2011). Most loggerhead emergences occurred at 20h00 which was suggested to be a possible predator avoidance mechanism and related to the onset of darkness. Furthermore, the artificial light sources present on Maputaland's beaches are turned off at 23h00 suggesting that these light sources overlap with the peak nesting times and potentially deter the majority of potential nesting females from nesting on these illuminated beaches.

One hypothesis put forward by Bowen *et al.* (2005) for freshwater turtles is that nesting may not require specific environmental variables once the temperature of the water is warm enough. They would then not rely on environmental variables but would simply nest when they were physiologically ready to nest again. This mechanism may be similar for marine turtles in that they nest when the temperature is correct and future nesting events are simply based on physiological need to nest rather than prevailing conditions. Also, nesting may be initiated at the start of darkness and any variation in light intensities after nightfall will have little effect on nesting behaviour. Therefore this hypothesis suggests that the light cues investigated in this dissertation may not have any implications for nesting behaviour, except perhaps, for the initiation of nesting at nightfall.

In conclusion, ambient light variability does not appear to influence the number of emergences but other environmental variables such as the onset of darkness, not investigated in this dissertation, may be a more influential cue that initiates nesting. Artificial lights on Maputaland nesting beaches are limited to a very small section of the beach and are usually turned off at 23h00 although the effect of this on emergences is evident by the reduced number of emergences on adjacent beaches. Covering these artificial lights to prevent them from shining onto the nesting beaches may potentially provide valuable habitat for nesting loggerheads. However, with over 150 km of nesting beaches to nest upon, these management interventions may be unimportant for this particular area.

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Chapter 5: The prevalence of social facilitation in nest site selection for loggerheads

An image of a sea turtle that appears to be swimming together which is the crux of this chapter (Image from http://cdn.c.photoshelter.com/img-get/I0000TDWbVLLd000/s/850/850/Turtles-in-the-shallows.jpg with permission from the photographer, Steve De Neef).

Abstract

Social facilitation involves the behavioural influence of one individual on another. For adult sea turtles it is a following behaviour whereby inexperienced nesters follow experienced individuals to nest sites. However, very little work has been performed on this subject and therefore it remains a possible hypothesis for nest site selection in sea turtles. The aims of this chapter were firstly to determine if the nesting distribution by female loggerheads was even, random or clumped (using Morisita's index of clumping). If this nesting distribution is clumped, then the second aim would be to determine whether the clumping was hotspot driven (thus a preferred area) or randomised within the high density area (spatially variable over time). The final aim was to determine if individual loggerheads nest on the same sites among seasons or if they vary among seasons. To do this, nesting data from 1981-2008 were analysed. The nightly nesting distribution was found to be highly clumped with 82.5% of nights having a Morisita's index >1.5. However these grouping events mostly occurred in the high density nesting areas at consistent beacons (Beacons 4N to 20N) which suggests the grouping are hotspot driven rather than random/clumped. Further, 32.2% of individuals return to nest within 1 km of their previous season's average nesting location. Therefore this nesting distribution appears hotspot driven and social facilitation plays an insubstantial role in spatial selection of the nest site for the Maputaland loggerheads, especially for experienced nesters. However it may be possible that social facilitation plays a different role, such as guiding neophytes to the nesting ground or a minor role in nest site selection, and may have a temporal signal which was not possible to test with the existing data set as not every turtle individual is encountered.

Introduction

Social facilitation is defined as the influence of individuals on each other's behaviours (Allport 1924, Zajonc 1965). Social facilitation is found almost everywhere in life where more than one individual is present in a particular area at one time. The social behaviour of human beings has often been studied in terms of social facilitation. One example of social facilitation is given by Chen (1937) and reviewed in Zajonc (1965) and states that an ant will be more efficient at nest-building when in the presence of another ant than when it is alone. There are many more examples of social facilitation occurring in many different organisms all using different mechanisms, such as: following behaviour with the use of trailing pheromones in ants (Tumlinson *et al.* 1971); shoaling in fish using the impulses detected through the lateral lines of conspecifics (Bleckmann 1993); and facilitation of learning through conspecifics especially in mammals (Klein & Zentall 2003). On farms it is used to avert livestock from certain poisonous foods (Ralphs & Provenza 1999). However, social facilitation is an emerging field in behavioural studies and there is still much to discover.

The social facilitation model for sea turtles was proposed by Hendrickson (1958) and states that reproductively inexperienced sea turtles follow experienced conspecifics to nesting grounds. If a positive nesting experience is encountered, the inexperienced sea turtle will subsequently fix onto that particular site for future nesting events. This hypothesis is based on the simple notion that inexperienced nesters wandering around may encounter experienced nesters and follow them to appropriate nesting sites (Hendrickson 1958).

Sea turtles have three potential ways of detecting conspecifics. Firstly, there is visual identification. Visual cues will only be possible in intimately associated groups due to limited visibility exacerbated by turbidity in the marine environment. This form of following may be significant for olive ridleys during (mass synchronised nesting) arribada events, but it is not likely for loggerheads as they do not characteristically group (Carr 1967, Plotkin *et al.* 1995, Bernado & Plotkin 2007). However, sea turtle shaped decoys have been used to attract and catch sea turtles in nets (Caillouet 1995) suggesting that visually-driven association or attraction may be possible. Secondly, grouping may be driven by scents or pheromones originating from conspecifics. Rathke's gland, an exocrine gland on the plastron of loggerheads among others sea turtles, has been suggested to excrete a protein-based pheromone which may potentially play a role in conspecific communication (Ehrenfeld &

Ehrenfeld 1973, Wyneken 2001, Lewis *et al.* 2007). Thirdly, vocalization and hearing is a potential means of broadcasting and detecting conspecifics, respectively. However, there has been very little research on sea turtles on this subject, and so this is method is purely speculative.

Groups of sea turtles (particularly green and olive ridley turtles) have often been observed in the waters of foraging grounds and on their way to nesting grounds (Carr 1967, Carr 1986, Dash & Karr 1990). It is suspected that the majority of courtship grounds are situated just off the nesting beaches, in which case both males and females will migrate to these areas to reproduce, thereby facilitating reproduction (Limpus 1993, Godley *et al.* 2002). Further, the olive ridleys nest in massive synchronised events termed arribadas and large numbers of these species are found in groups adjacent to nesting beaches (Hughes & Richard 1974, Dash & Karr 1990). These arribada events are synchronised to a particular cue that is unknown. There has been much speculation to what this cue may be and one of these speculations is social facilitation (Owens *et al.* 1982). This may be driven by secretions from the rathke's gland as mentioned above. Maputaland loggerheads have been found to remain very close to the shore (barely exceeding 30 m depth contour) between nesting events, and just off the high density nesting beaches (Vogt 2011), suggesting a close association with other loggerheads. This close association of loggerheads is a key component for the social facilitation of following to nest sites.

One of the advantages of this kind of following behaviour ascribed by the social facilitation hypothesis is an increased chance of locating mates (Owens *et al.* 1982). This will be facilitated by the increased movements of an adult beginning its first migration to its nesting grounds (Owens *et al.* 1982). Further, if social facilitation is indeed the driver of nest site selection, then this may potentially provide a means of fixing or imprinting to a specific nesting site, which will then be repeated for future generations (Owens *et al.* 1982).

The limited amount of literature on the social facilitation model on sea turtles does not include loggerheads, although an assumption is made that the process is likely similar among species. The literature generally concludes that social facilitation is unlikely for the following reasons. Genetic analyses of populations that share feeding grounds but have different nesting grounds have shown that the populations are genetically distinct from each other, suggesting that these populations do not interbreed (Cowen 1990, Meylan *et al.* 1990, Bowen *et al.* 1994, Bass *et al*. 1996). If this is viewed in light of the social facilitation hypothesis, then it would be assumed that individuals who share feeding grounds would follow experienced individuals to their nesting grounds. If there was no preference by the neophyte nesters to follow an experienced individual of a specific population, then it can be assumed that following would occur randomly to each nesting grounds and an even distribution of neophytes would occur at both nesting grounds. Furthermore, green turtles from a head-starting program in the Cayman Islands were found nesting on the imprinted island (Bell *et al.* 2005). This suggests that social facilitation is unlikely to occur for this population as the number of emergences is estimated in the range of 2–8 turtles per season and these green turtles would probabilistically follow the majority of turtles from more populated nesting grounds because of their larger numbers. Therefore, following of experienced sea turtles by inexperienced individuals (i.e. social facilitation) is unlikely from foraging grounds to nesting grounds for at least some populations.

In spite of this, the application of the social facilitation model in sea turtles is often discussed as an explanation for natal homing migrations to nesting grounds. There is some anecdotal evidence that suggests that this model may also operate on a finer scale such as in nest site selection within a nesting area. Observations of large groups of gravid females emerging within a short amount of time of each other have been observed on Maputaland's loggerhead nesting beaches (pers. obs.). These grouped nesting events characteristically consist of a large percentage of the total number of females emerging at night within a short time period (while the first individual is still nesting) and a small spatial area (<200 m). Therefore this chapter investigates social facilitation within a single nesting ground (Maputaland) and the role it may play in this grouping effect of nesting loggerheads. It is expected that the number of emergences will reveal a spatially and temporally visible grouping effect on these nesting beaches. There has been no previously published literature that investigated the social facilitation model within a single nesting ground.

The aim of this chapter is to determine whether the characteristic nesting distribution found in Maputaland's nesting beaches is a result of group nesting events driven by the process of social facilitation. This will be obtained by answering the following questions; 1) is the spatial nesting distribution even, random or clumped? 2) If clumped, is it repeatedly clumped in the same area (i.e. hotspot or preferred area driven) or is it randomly clumped (i.e. spatially variable). 3) If it is hotspot driven – do the same turtles prefer the same sites between different seasons, or do the preferred sites change between seasons potentially implying social facilitation)? 4) Is the nesting distribution within the high density nesting area consistently clumped in the same areas?

Methods

Field Data Collection

To determine if loggerheads in Maputaland are emerging in groups due to social facilitation, data from the Ezemvelo database were used. This database includes recorded emergence time and position of loggerhead sea turtles per night, although only a small fraction of the animals are encountered. The position data per emergence were recorded between set distances which are represented in the database as beacon numbers. Beacon numbers used were limited to beacons 32N and 32S which include the high and low nesting density areas and the monitoring effort has been consistent for this area throughout the monitoring programme. Only data for the seasons 1981 to 2008 were used for analyses because the effort pre-1981 was inconsistent. Further, data analyses were limited to the peak nesting month for each season i.e. December to eliminate the lower number of emergences at the start and end of the season.

Data were collected by pairs of monitors assigned to monitor specific sections of the nesting beaches. Monitoring methods (specific to this chapter) involve morning (06h00) foot patrols, which cover on average 15 beacons (approximately 6 km) per pair of monitors, where they record all the tracks/emergences for the previous night. Nesting emergence data were recorded to beacon number and date, with locations accurately to 400 m as before, representing the nearest beacon. Data were sorted so that each night represented a replicate, resulting in 863 nights of data with an average of 31.7 nesting turtles per night.

Evaluating Clumpedness

To determine if clumping of emergences occurred, Morisita's index was used (Morisita 1959). This index is the scaled probability that any two points chosen at random will occur in the same sampling unit – in this case within a beacon.

Morisita's Index: $(I_m) = \frac{n\sum x(x-1)}{n\bar{x}\,(n\bar{x}-1)}$ where *n* = is the total number of individuals sampled in all quadrants/beacons; *x* = sum of all individuals and $\bar{x}$ = mean number of individuals in all quadrants/beacons.

Morisita's index (I_m) was calculated per season to determine if clumpedness varied with time. Further, Morisita's index was calculated per night and the results were illustrated using a mean Morisita's index with standard error frequency histogram to give an indication of clumping of loggerhead emergences. If $I_m = 0$ it suggests the data are uniformly distributed; $I_m = 1$ indicates that the nesting events are randomly distributed; $I_m > 1$ means data tend toward clumping, with the greater the I_m value, the more clumped the distribution (Morisita 1959).

Hotspot Identification

Clumping of nesting distribution does not necessarily equate to social facilitation. In order to assess if social facilitation was indeed driving nest site selection, the results needed to be distinguished into hotspot grouping (consistent areas of clumping) or random groupings (driven by social facilitation). Hotspot grouping occurs when groups are consistently concentrated in a particular area in the high density nesting area. The nesting preference may be influenced by the beach or reef characteristics (or some other cue discussed in previous chapters). Grouping derived from social facilitation would have spatially variable groupings per night, which will persist even in the high density area, but will "move" randomly between beacons per night. It may thus be a combination of these two factors (hotspots and social facilitation) driving nest site selection, but the exact drivers are very difficult to establish. To distinguish between these two drivers, the maximum number of emergences per any one night, as well as the beacon at which this occurred was recorded for each night. This serves to single out the most selected site/beacon per night. In the case where the highest number of emerging loggerheads occurs simultaneously on two beacons in a single night, both beacon numbers were recorded. Where the highest number of emerging loggerheads occurred on three beacons on the same night, it was assumed that there was no clear selection of nest site and the night was discarded. A Pearson product moment correlation was performed between the frequency of the maximum number of emerging females per beacon per night and the average number of emergence per beacon per night of the 1981-2008 nesting seasons. D' Agostino-Pearson and Bartlett's test were performed to determine whether the data adhered to the normality and homoscedasticity assumptions of a Pearson product moment correlation.

Further investigations were made into individual nest site fidelities. Botha (2010) discovered that nest site fidelity became more accurate with an increase in the number of seasons a turtle nested. This increase in accuracy is assumed to be associated with an increase in 'experience' of the preferred nesting beaches. This is suspected to work in much the same way as human memory (hence not social facilitation), whereby the landscape is unknown upon a first visit (or the first time in many years), but demonstrates familiarity with subsequent returns. If it is easy to navigate to – it will be reselected and if not, it will be avoided (presumably). To test this hypothesis (of increased nest site fidelity over time), data from tagged loggerheads that nested in more than two seasons were extracted. The difference in individual geographical nest site selections between seasons were measured by averaging all the beacon numbers that were used from each season and calculating the distances between these averages. Difference (in beacons) in average nest site selections (average beacon) between the first season and later seasons were recorded as well as to consecutive seasons.

Further investigations into the individual nest site fidelity and location were performed to determine if individuals returned to the same location as previous seasons and if these areas fall within the high density nesting area. These analyses were performed on tagged loggerheads. Only flipper-tagged loggerheads that have emerged in at least three seasons and have been observed at least three times per season (i.e. tag recordings) were used. This reduced the total number of individuals to 159. Nest location (beacon) was translated to distance from the Mozambique border, which allows for a linear distance measurement (in kilometres). These linear distance used per individual per season from the border was calculated and then averaged for each season and plotted.

The existence of a high density nesting area (beacons 0-32N) immediately suggests a strong area influence (as discussed in Chapter 3, which may be derived from previous nesting and lake water signals), i.e. hotspot-driven nesting. However, social facilitation may play a role in reinforcing nest site selection within the preferred nesting area. For example, the high-density area may have specific stimuli that attract loggerheads to the area, but nest site selection within this large area (high density area) may be driven by social facilitation. To test this, the beacon which has the highest number of nesting upon it per night was recorded per night. These were then used to create a frequency plot and correlated to the average nesting distribution (average nesting numbers per individual beacon) between the seasons 1981-2008. Therefore if the maximum number of emerging females varies per beacon per night, there will only be a weak (if any) correlation between the frequency of beacons with the maximum number of emergences per night and the average nesting distribution between the seasons 1981-2008.

Results

Average Morisita's indices per season ranged from 2.6 to 7.3 with an average of 3.8 (Fig. 5.1). These numbers suggest a highly clumped distribution throughout seasons with considerable variance. Morisita's index per night of loggerhead emergences also averaged 2.5 with a range of 0.05-22.8. Of the 852 nights of emergence data, only 2.5% of the nightly emergences were considered uniformly distributed (0-0.5), 15% were random (0.5-1.5) and 82.5% were clumped (>1.5) according to Morisita's index (Fig. 5.2). Further, approximately 24.8% of the emergences per nights had a Morisita's index greater than 3 which suggests highly clumped distributions.

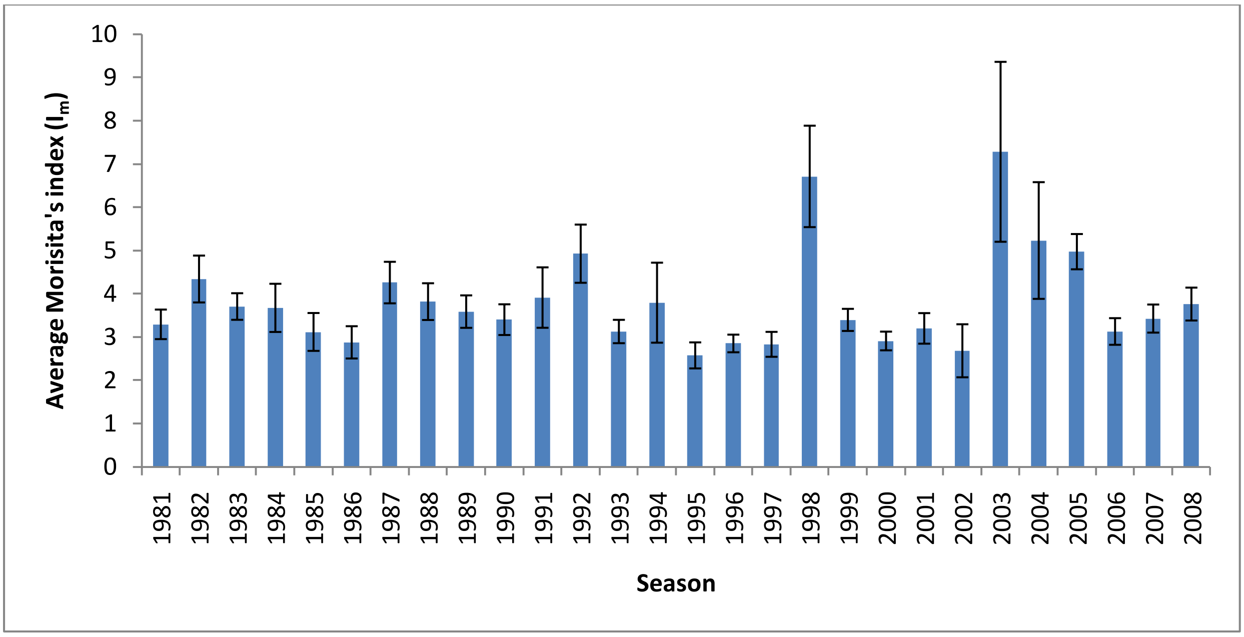

Figure 5.1: The average Morisita's index calculated per season with accompanying standard error bars.

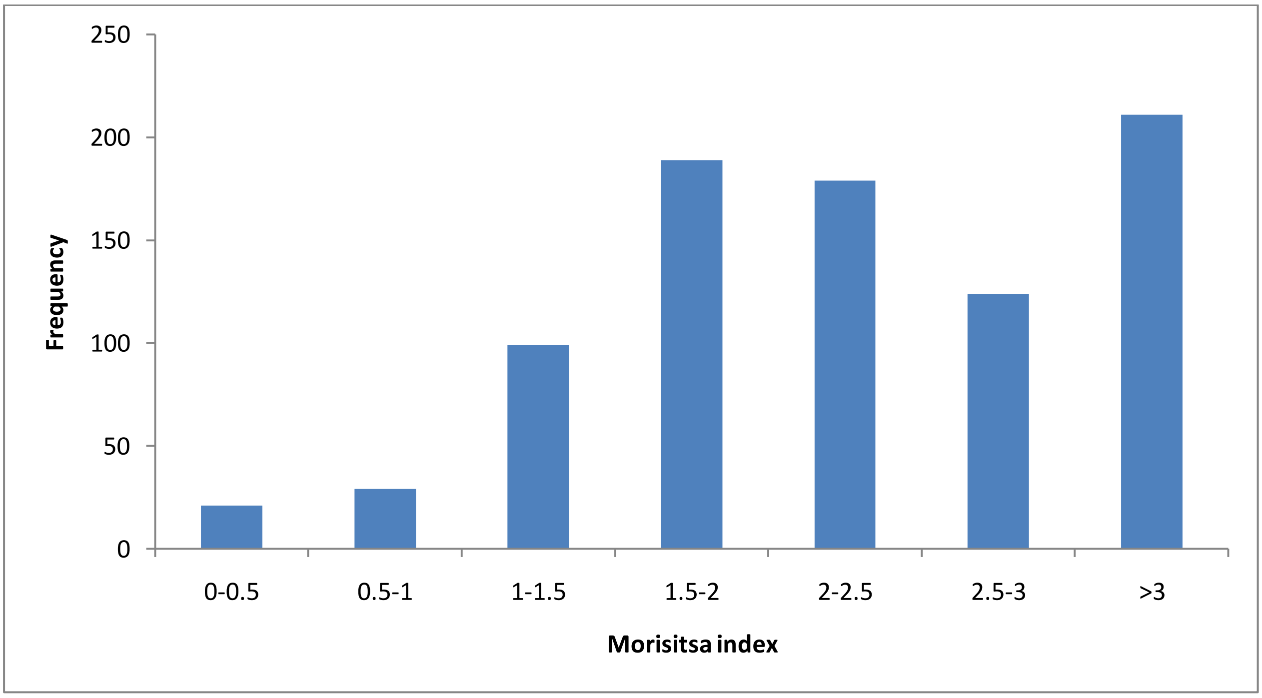

Figure 5.2: Frequency histogram of the Morisita's index values calculated per night for each December between 1981–2008. (I_m=0 indicates a uniform distribution, I_m=1 denotes a random distribution and $I_m > 1$ shows data tends toward clumping, and the greater the I_m value, the more clumped the distribution (Morisita 1959)).

The beacons with the maximum frequency of emergences per night are significantly correlated to the average number of emergences per beacon from 1981-2008 seasons (Fig. 5.3; r = 0.93; p << 0.05, n = 863). This was not dependent on the number of emergences per night and therefore was not density dependent. Therefore it appears that it is the largest clumping per night that creates the characteristic nesting distributions for the entire season, which is also consistent between seasons

Individual analyses for distances between the first season of nesting and subsequent seasons indicated that the majority of individuals (>71%) nest within 1-5 km from the average location of their first nesting season (Fig. 5.4). The total monitored area consists of 56 km and there appears to be a definite selection process occurring. Further comparisons among consecutive seasons found similar results with 78%-83% of nesting to overlap with the middle of the nesting location (calculated as the average distance) ranging 1-5 km (Fig. 5.5).

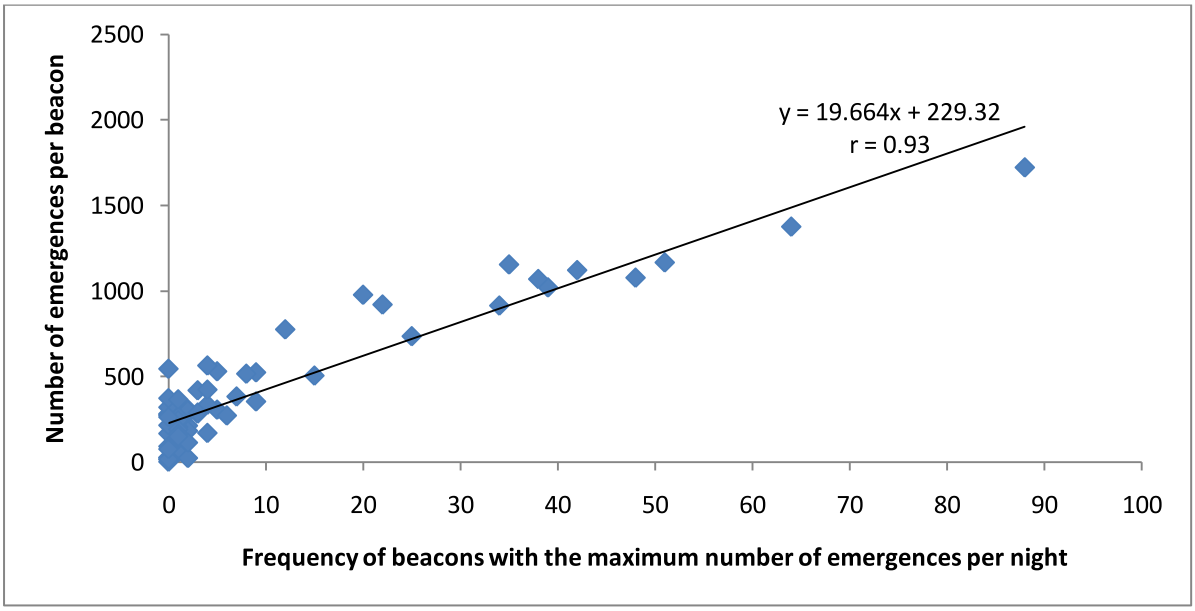

Figure 5.3: Correlation of the frequency of the beacons with the largest number of emerging females per night with the average number of emerging females per beacon (32N – 32S) for 1981-2008 nesting seasons. N = 227 for season 1, 2 and 3; N= 222 for season 4; N = 82 for season 5.

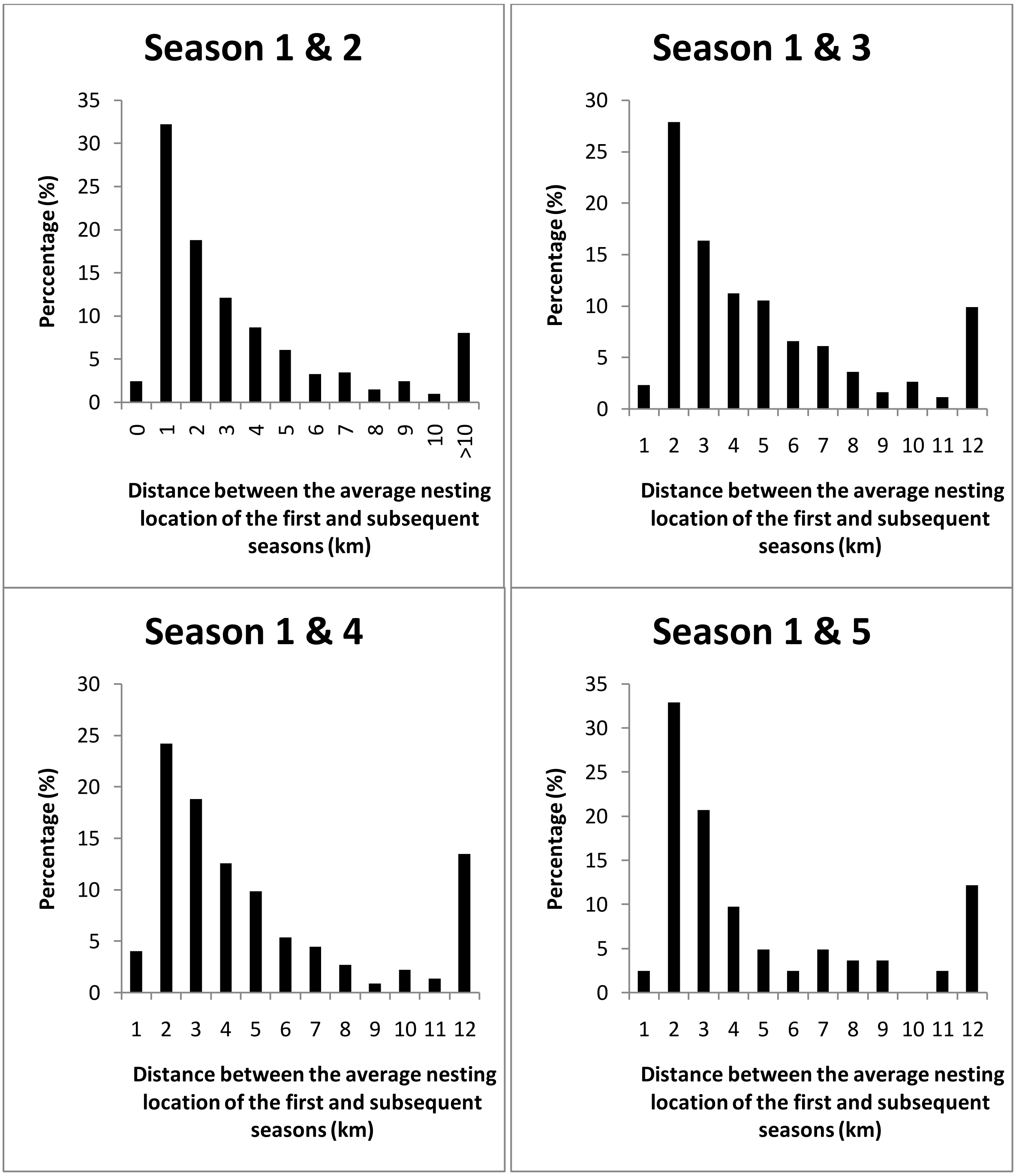

Figure 5.4: The percent distribution of the middle nesting distances between the first recorded nesting season of each individual (season 1) and subsequent nesting seasons (season 2, 3, 4 and 5). N = 227 for season 1, 2 and 3; N= 222 for season 4; N = 82 for season 5.

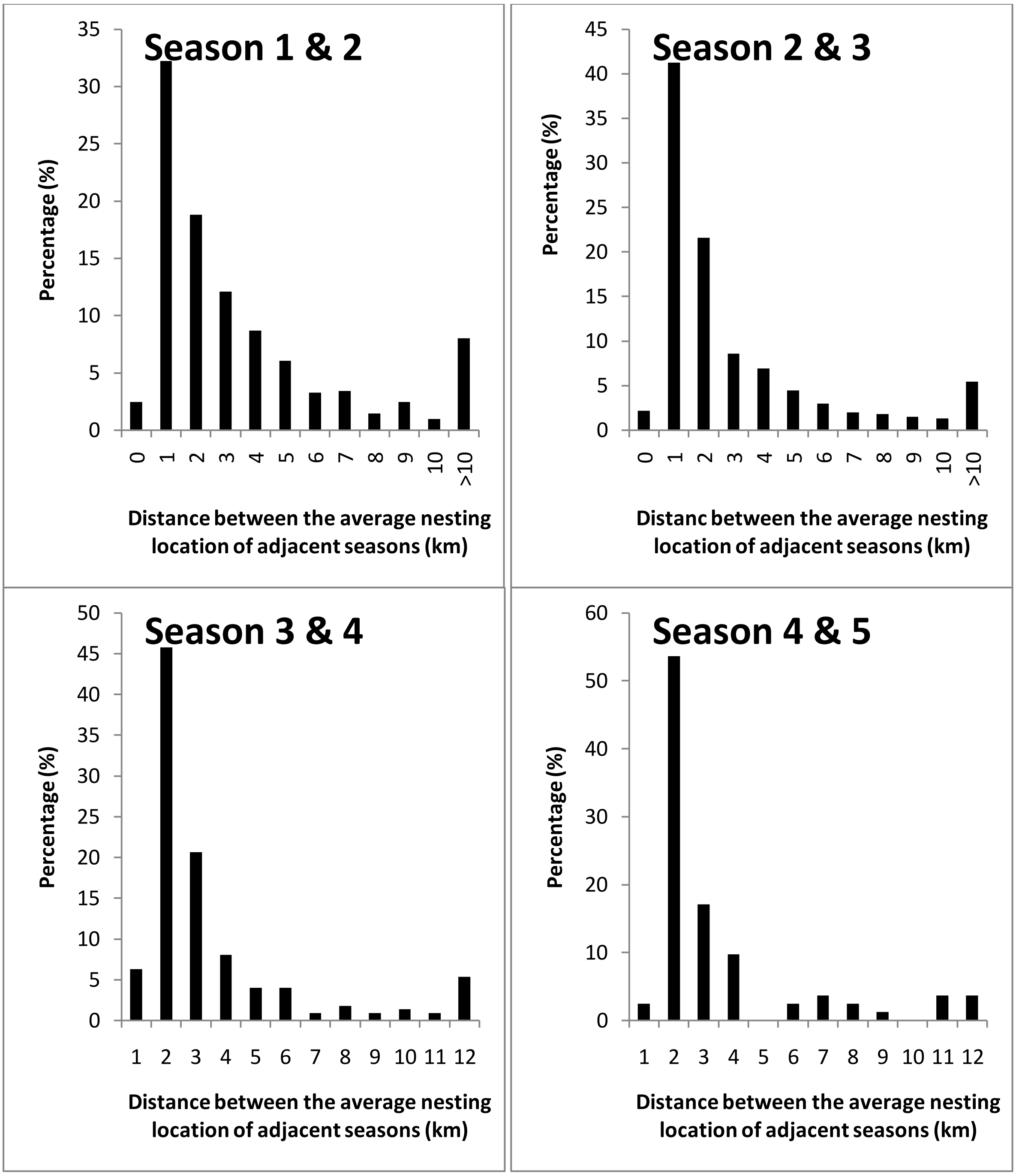

Figure 5.5: The percent distribution of the middle nesting distances between adjacent nesting seasons of each individual. N = 227 for season 1, 2 and 3; N= 222 for season 4; N = 82 for season 5.

A total of 159 tagged individuals were used for the analyses of geographic location of subsequent nesting seasons. The majority of the middle (mean) nesting locations (62.3%) were within the high density nesting area (Fig. 5.6), leaving 37.7% of the mean nesting locations outside of the high density nesting area. This corresponds with the general distribution of all nesting individuals. The standard error (SE) bars in Fig. 5.6 are highly variable between individuals, although the majority of the spread of the nesting per individuals is less than 1 km (76%). Furthermore, the standard error of nesting distance per individual in the high density nesting area are significantly smaller than those outside of the nesting area for the whole nesting range ($t = 2.51$; $p < 0.05$; $df = 157$) and the consistently spaced range of 40N to 40S ($t = 4.93$; $p << 0.05$, $df = 157$), also evident in Fig. 5.6.

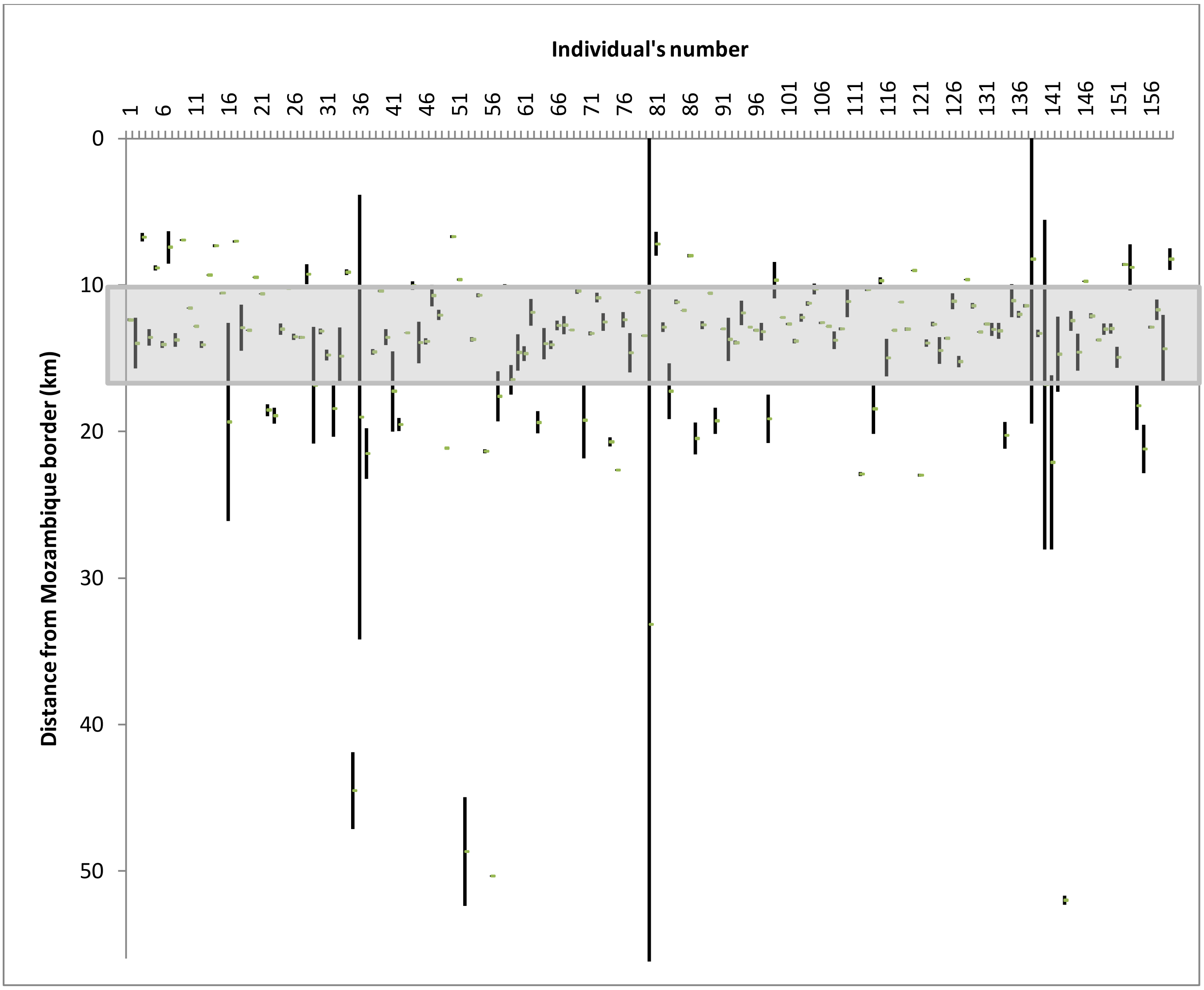

Figure 5.6: Individual middle nesting position with SE bars for the entire history of each individual with more than three nesting seasons and each season with at least 3 recordings of tag numbers. Each mean and SE bar represents that of all the seasons. The grey bar represents the high density nesting area (>100 nests per beacon per season). Some SE bars extend beyond the figure borders.

The maximum frequency of nesting in the high density nesting (beacon 0-32N) was significantly correlated to the number of emerging females (Fig. 5.7, r = 0.94; p << 0.05). This suggests that nesting within the high density nesting area is focussed in the same particular area from year to year.

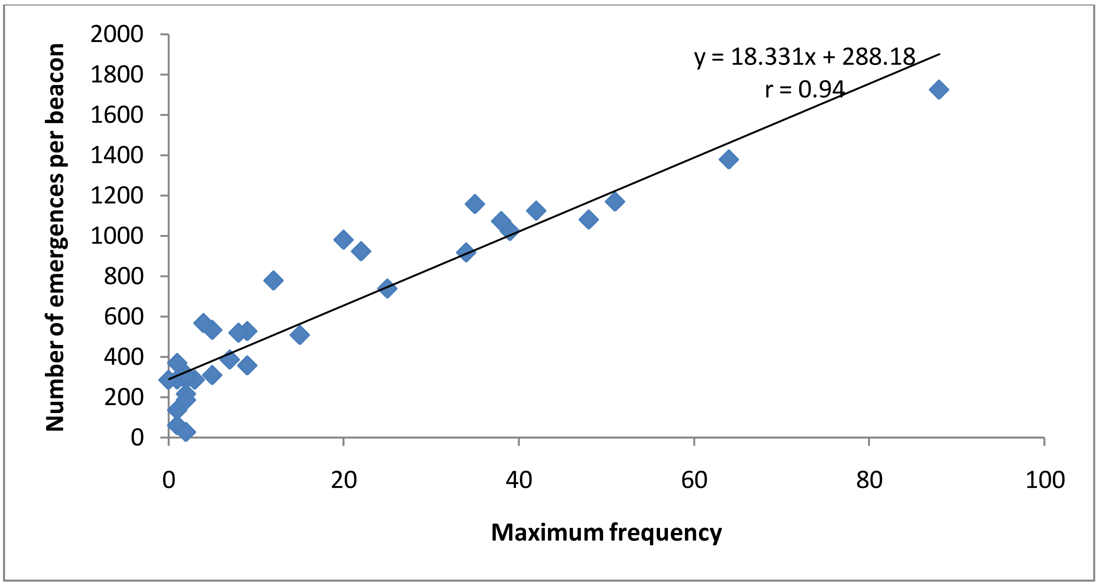

Figure 5.7: Correlation between the maximum frequency (as in figure 5.3) and the average the number of emerging females between 1981 and 2008, limited to beacons within the high density nesting area (beacons 0-32N).

Discussion

It is clear that loggerhead nesting distributions in Maputaland are non-random. A large majority of nesting distributions per night had Morisita's indices larger than three, indicating a high degree of clumping. These results are consistent with what was expected under the social facilitation hypothesis. However, the frequencies of beacons with the maximum number of emergences per night were highly similar to the total number of emergences per season, suggesting that there is a specific beach selection taking place. This means that nest clumps were not randomly distributed but were focussed at hotspots, signifying a nest site selection process that is unique to this particular area. Therefore it appears that social facilitation has a limited or negligible (measureable) effect on nest site selection (under the current experimental conditions).

Individual nest site fidelity between seasons was found to be very selective, with a very large percentage of nesting occurring within 5 km of that during previous seasons. These results suggest that there is a very strong selection for nest sites, and that individuals return to the same beaches in subsequent years. Botha (2010) discovered that Maputaland loggerheads have more accurate nest site fidelity as their number of return seasons increases (i.e. as they become more experienced nesters). Combining these two results, it appears that Maputaland loggerheads have a specific preference for nest sites, which gets more refined the more times they return to nest.

It is also interesting to note that loggerheads that nest in the high density nesting area have far smaller standard errors (i.e. greater nest site fidelity) than loggerheads that nest outside of the high density nesting area. This result suggests that loggerheads are more accurate in their nest site selections if they nest in the high nesting density area. Perhaps this is an indication that loggerheads nesting outside of the (apparently more favourable) high density area are moving around more looking for a more suitable beach to nest upon. However, when examining the individual nesting patterns, it is found that some individuals demonstrate strong nest site fidelity even if it is (far) outside the high density area.

There are a number of possible explanations for these results. Firstly, it appears likely that social facilitation and conspecific interactions during nest site selection does not occur. This is supported by the hotspot-driven nest site selection seen in the present loggerhead nesting distribution. Furthermore, loggerheads are not considered social animals and grouping is therefore unlikely (Carr 1967, Plotkin *et al.* 1995). This does not mean that social information sharing or facilitation is not or cannot be used by loggerheads, because complicated social information transfer has been found to occur among conspecifics of other non-social animals (e.g. Pasqualone & Davis 2011). Unfortunately, however, the oceanic life history of sea turtles has made it difficult to study their social interactions.

Secondly, it may be possible that the effect of social facilitation on nesting site selection is masked by a more dominant driver, such as an attractive nesting cue (such as sulfides – see Chapter 3) present on nesting beaches. This hypothesis is quite possible as this cue would theoretically attract females to their natal beaches resulting in a hotspot-driven distribution. It is also possible that nest site selection is a learned process and more experienced nesters will be able to find better beaches than inexperienced individuals. Botha's (2010) results are in support of this hypothesis illustrating smaller nest site fidelity with an increase in the number of return seasons for females.

Alternatively, social facilitation may have played a significant historical role in the establishment of the hotspot, resulting in the present observed nesting distribution. This nesting distribution may have arisen through a series of logical processes, with positive reinforcement. It may be assumed that the beach with the largest survival rate is the beach with the greatest number of hatchlings that survive to maturity. Therefore, under natal homing, it is expected that the largest number of females will nest on the beach with the highest survival rate because it produced the largest number of mature females from previous generations. This process would be repeated and reinforced over time and ultimately result in an apparent high density nesting area. Furthermore, under the social facilitation hypothesis, the majority of the inexperienced females would statistically follow experienced individuals to the high density nesting area and further reinforce the creation of the hotspot.

The lack of knowledge and understanding of natal homing migrations and nest site selection make it difficult to isolate the influence of social facilitation on nest site selection from that of the other drivers. Social facilitation may operate at sea by bringing inexperienced nesters to natal grounds or even causing congregations on particular reefs, which is manifested as a hotspot in the number of emergences. While the social facilitation hypothesis is not falsified in this study, the results strongly suggest that social facilitation does not appear to play a substantial role in current nest site selection of loggerhead sea turtles in Maputaland.

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Chapter 6: Sensory input and sea-finding behaviour in adult loggerheads

Abstract

Sea-finding ability of post-nesting females has rarely been studied and the few results that exist are often contradictory. The aim of this chapter is to determine the sensory systems used (in this case for sea-finding) in loggerheads. To do this, visual, olfactory and auditory systems were inhibited separately to assess the function of each sense. Post-nesting females were intercepted at night on the beach on the crawl back to the ocean. The appropriate sensory system was inhibited in turn and the turtle was rotated to face along-shore. The initial choice and the time taken to reach the ocean were recorded. Only individuals with their visual system inhibited (9 individuals) indicated any disorientation; they moved in any direction, while all other turtles (nine or ten individuals) in experimental and control groups moved directly seawards. Furthermore, the time taken to reach the ocean was <1 min for all turtles in all experimental and control groups except for (visually) blinded turtles with an average time to reach the ocean of 6.6 minutes. Therefore it appears that the visual system is the sole driver of sea-finding behaviour. However, at some stage, other cues may become more important for sea-finding. These results give valuable insight into the sensory capabilities of sea turtles.

Introduction

Nest site selection and the cues used in nest site selection have been largely studied in sea turtles. However, sea-finding of nesting adults has focussed only on visual stimuli. Hatchlings are thought to use multiple cues for finding the ocean once they have emerged from the nest chamber (Hirth 1971). Understanding the full suite of sensory cues used in sea-finding behaviour could provide valuable insight into the sensory basis and capabilities of sea turtles also used in homing and emergence.

Post-nesting sea-finding behaviour of sea turtles have been investigated in terms of directional visual stimuli, light intensity and wavelength preferences (Ehrenfeld & Carr 1967, Ehrenfeld 1968, Mrosovsky & Shettleworth 1968, Witherington & Bjorndal 1991). Results from these studies state that visual stimuli act as a primary cue for sea-finding. Secondary cues however, such as olfactory cues and sound have rarely been investigated. Vision of sea turtles in air is considered myopic (Ehrenfeld & Koch 1967) providing minimal visual cues other than general light and dark areas. These secondary cues could be important in exceptionally dark conditions when light gradients may not be discernable. Evidence exists that suggests that on exceptionally dark nights, hatchlings have been unable to find the ocean supposedly due to a lack of visual stimuli (Daniel & Smith 1947). Further, a blind adult olive ridley successfully nested in Costa Rica. This suggests that vision is not necessarily required in natal homing, nesting or for sea-finding (Mora & Robinson 1982). These reports also suggest that visual cues are not the exclusive sensory system used in adult nesting and sea-finding. However, there are further observations of hatchlings being unable to find the ocean on extremely dark nights suggesting that visual cues are essential for sea-finding (Mrosovsky & Shettleworth 1968).

Orientation in hatchlings has been more extensively studied, but because the mechanism of orientation in hatchlings and adults are assumed to be similar, it is appropriate to discuss hatchling abilities to better understand adult sea-finding. Sea-finding orientation in hatchlings may be influenced, to varying degrees, by light intensity (Mrosovsky 1972, WItherington & Bjorndal 1991, Salmon *et al.* 1992, Karnad *et al.* 2009), wavelength (Witherington & Bjorndal 1991, Levenson *et al.* 2004), landward silhouettes (Salmon *et al.* 1992, Salmon & Witherington 1995, Lohmann & Lohmann 1996), background illumination or ambient light (Tuxbury & Salmon 2005) and beach slope (Salmon *et al.* 1992). Primarily, hatchlings orientate away from the higher silhouette but if this cue is unavailable, then they orientate towards the brighter direction which is usually the ocean (Salmon *et al.* 1992, Bartol & Musick 2003). If however, light intensity and silhouettes are not present or usable, then slope is used (Salmon *et al*. 1992). Further, hatchlings with one eye or both eyes blind-folded resulted in circuitous routes heading towards the uncovered eye or not being able to find the ocean respectively (Carr & Ogren 1960, Mrosovsky & Shettleworth 1968, Mrosovsky & Shettleworth 1974). Hatchlings with colour filters covering their eyes were able to find the ocean with varying degrees of success (Ehrenfeld & Carr 1967).

Auditory stimuli have rarely been studied in terms of sea-finding behaviour (see Appendix A for background on auditory system). Standora *et al.* (1999) suggested that leatherback hatchlings potentially use acoustic stimuli (such as the sound of crashing waves) to find the ocean after emergence from their nests. However, olive ridley hatchlings, under the same experimental setup, appeared to ignore acoustic stimuli and instead used a fixed compass heading to find the ocean (Standora *et al.* 1999). Different species may thus respond differently to the same cues. Further, these experiments were performed on hatchlings but have never been bench marked for adults which may use a different set of cues because of different experiences of the beach/surf environment.

Sand-smelling is often thought to occur after emergence on a nesting beach as a form of confirmation that the correct beach was chosen to nest upon (Hendrickson 1958, Carr *et al.* 1966, Hughes 1974). This hypothesis has never been tested and the importance of olfactory cues in the nesting process is unknown. The possibility could also exist that with onshore winds, smelling the ocean could be used as a potential or alternative cue, in the absence of clear visual cues to find the ocean. Another possibility is the low frequency sounds such as those generated by crashing waves which can be heard at a distance (even in poor light) by both marine mammals and sea turtles (Garces *et al.* 2006). These low frequency sounds have even been connected with island finding ability in sea turtles although it is still speculation (Mrosovsky 1972, Luschi *et al*. 1996, Hays *et al.* 2003). It is therefore logical to conclude that these sounds may be a potential source of sea-finding cues.

It appears that visual stimuli are very important primary cue for sea-finding in hatchlings and adults, but that secondary cues including sound, smell and slope may be used when the visual cues are unavailable. However, the influences of olfaction and audition have never been investigated as potential cues in sea-finding, especially in adults, nor ranked against each other as a level of importance. Therefore this chapter aims to rediscover the influence of visual cues and investigate olfactory and auditory cues potentially used in sea-finding in adults, and if possible rank the cues against each other. This will be attempted by taking post-nesting adults and blocking out each of the senses (eyes, ears, and smell) and test the effectiveness (both in terms of direction and time) in orientating to the ocean.

Methods

To test sea-finding in adult loggerheads, females heading back to the ocean after a nesting event or attempting to nest were intercepted. Morphometric information was obtained (while the females were nesting) and tag numbers read. If the female was untagged a new tag was applied. The flipper tag code provides the complete nesting history of the female to give an indication of nesting experience – within and between seasons.

Experimental Design

One of three sensory-inhibiting experiments was performed per individual blocking out the eyes, ears or smell. This was done by i) blindfolding turtles by padding both eyes to inhibit all visual stimuli, or ii) by playing music using noise-cancelling headphones directly onto the heads of turtles to disguise the sound of the ocean, or iii) by spraying $ZnSO_4$ into the nares of the turtle to temporarily inhibit olfaction (following the protocol suggested by Manton *et al.* 1972). Controls of these experiments were performed by applying the same gear to the heads of the turtles but only partially so that the senses were still fully functioning. This was done to ensure that behaviour was not modified due to the presence of the gear but that it is due to the absence of each cue. The control were thus conducted by i) placing all the gauze patches of tape to the turtle's head without actually covering the eyes, ii) placing headphones over the tympanic membrane of the turtle but not playing any sounds, iii) spraying salt water instead of $ZNSO_4$ into the nares.

The exact design of the visually-inhibiting blindfolds consisted of sterile eye gauze patches designed to fit over the human eye which were strapped over the eyes to the head using non-adhesive, sports underwrap, followed by duct tape. This was to keep the blindfold in place and also to ensure that all light was blocked out – although the turtles close their eyelids when an object gets close (pers. obs.). The strappings over the eyes were made as loose as possible to prevent any damage to the eyes. The headphones used to disguise the sound of the ocean were only strapped using duct tape if it was required as for many of the experiments they remained in position on the head without support. The selected music was from the band 'As I Lay Dying' and was selected because of its constant sound and noise cancelling effect on human ears. The $ZnSO_4$ was sprayed twice into each nare of the turtle using a spray attachment that created a fine mist. This was assumed to enter the entire nasal cavity and come into contact of all surfaces.

Sixty female loggerheads (ten per control and ten per treatment) were intercepted at the mid-shore. Once the gear was applied, the turtle was rotated to face along the beach, parallel to the shore. The direction in which the animal was turned was random to account for handedness. The initial directional choice of seaward (correct choice), landward (wrong choice) or along-shore (no choice) was recorded as well as the time (in minutes) taken to determine the correct direction. The initial choice of direction was taken in hind-sight when a clear directed movement to the ocean was taken and not confused with a random wandering which coincidentally headed towards the ocean. The slope was recorded from the start of the experiment along the initial path the turtle took. This would then record the slope that the turtle experienced during its initial movements. To measure slope, the distance down the beach (5 m was used) and the height difference was used by dividing the height by the length.

Wind direction was also recorded to determine if it affected the initial choice of loggerheads' movements down the beach. This was done using a two-sample t-test in Microsoft Excel 2010 after determining if these data conform to normality and homoscedasticity. Further, a chi-square analysis was performed on the frequency data obtained to determine if the seaward orientation was more likely selected than landward or along-shore. This was also performed Microsoft Excel 2010. D' Agostino-Pearson normality test was performed on the data before performing the chi-square test.

Results

In total 54 individuals were used in these experiments. All individuals appeared to be in good health and capable of using all their senses. A range of slopes were used for these experiments ranging from 0.24 to -0.02 (Table 6.1). The time taken for an individual to reach the ocean ranged from <1 minute to over 10 minutes with no sign of reaching the ocean in which case the experiment was terminated and the gear removed.

Every individual tested initially chose correctly, i.e. a seaward direction, except for experiments involving the inhibition of the visual system (Table 6.1). The initial orientation of the visually inhibited turtles were roughly equally divided between seaward and landward with one individual continuing to move along-shore for a considerable distance in the direction they were orientated for the experiment (Fig. 6.1, Table 6.1).

Table 6.1: Specific information on individual loggerheads used in the sea-finding experiments.

Turtle #	Date (Nov. 2011)	Slope (h/l)	Initial choice	*Time to reach ocean (min)	Initial facing direction	Turtle #	Date (Nov. 2011)	Slope (h/l)	Initial choice	Time to reach ocean (min)	Initial facing direction
Visual control						**Visual experiment**					
1	10	0.23	Sea	1	N	1	5	0.10	Sea	1	S
2	19	0.02	Sea	1	N	2	7	0.03	Sea	10	S
3	20	0.08	Sea	1	S	3	8	0.03	Land	4	N
4	20	0.11	Sea	1	S	4	10	0.13	Sea	6	N
5	21	0.09	Sea	1	S	5	9	0.05	Land	7	N
6	25	0.09	Sea	1	S	6	13	0.04	Land	6	S
7	27	0.24	Sea	1	N	7	18	0.11	Along	4	N
8	27	0.06	Sea	1	S	8	19	0.11	Land	9	S
9	27	0.07	Sea	1	N	9	19	0.08	Land	9	S
						10	27	0.07	Sea	10	N
Olfactory control						**Olfactory experiment**					
1	6	0.12	Sea	1	S	1	6	0.14	Sea	1	S
2	15	0.13	Sea	4	N	2	6	0.04	Sea	1	S
3	15	0.08	Sea	1	N	3	7	0.03	Sea	1	N
4	15	0.11	Sea	1	N	4	8	-0.02	Sea	1	N
5	20	0.09	Sea	1	N	5	9	0.05	Sea	1	S
6	22	0.09	Sea	1	S	6	11	0.05	Sea	1	S
7	22	0.13	Sea	1	N	7	12	0.03	Sea	1	S
8	22	0.09	Sea	1	S	8	13	0.06	Sea	1	N
9	23	0.21	Sea	1	N	9	20	0.00	Sea	1	N
10						10	24	0.07	Sea	1	S
Auditory control						**Auditory experiment**					
1	12	0.05	Sea	1	S	1	6	0.05	Sea	1	S
2	13	0.02	Sea	1	S	2	8	0.06	Sea	1	N
3	18	0.08	Sea	1	N	3	11	0.05	Sea	1	N
4	19	0.14	Sea	1	S	4	12	0.04	Sea	1	N
5	21	0.09	Sea	1	N	5	12	0.05	Sea	1	S
6	24	0.08	Sea	1	S	6	6	0.05	Sea	1	N
7	25	0.08	Sea	1	S	7	8	0.06	Sea	1	N
8	25	0.07	Sea	1	S	8	27	0.07	Sea	1	S

If time to reach the ocean is equal to one, this means that the turtle was able to find the ocean in minute or less.

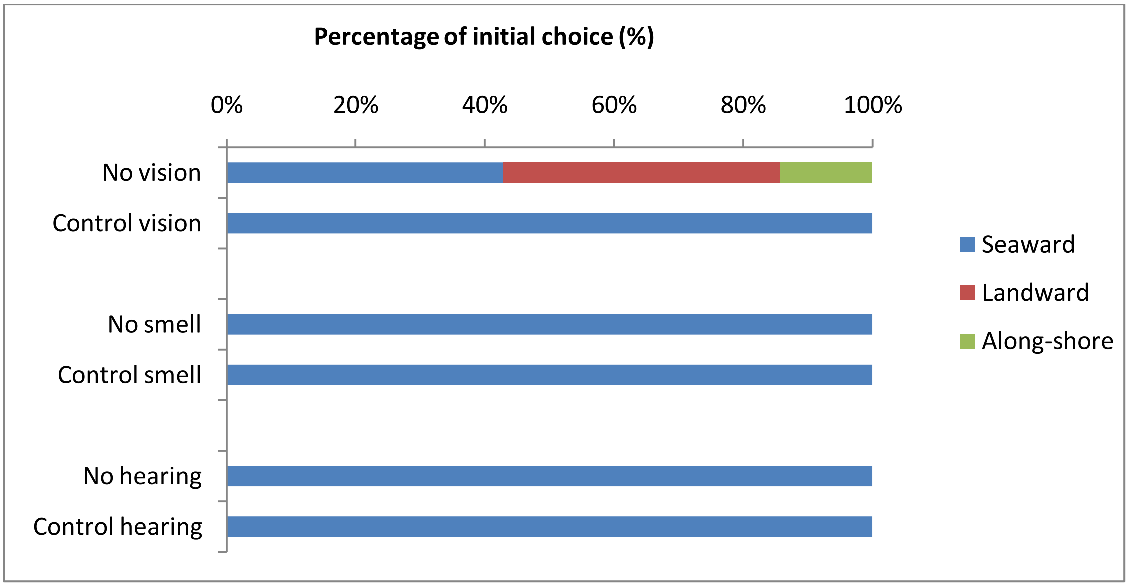

Figure 6.1: Percentage of the initial directional choices of loggerheads with different sensory systems inhibited (n =54).

Visually inhibited turtles were unable to find the ocean within the first minute nine out of ten times (Table 6.1, Fig. 6.2). However, once the blindfolds were removed, the turtles orientated directly towards the ocean without any difficulties and all reached the ocean within the first minute. Four individuals appeared to have found the ocean only after nine minutes and more of being blind-folded although this is thought to be due to chance and random movements. The control group for the visually inhibited experiments were always able to find the ocean without any apparent difficulties. Experimental and control groups for olfactory and auditory cues were always orientated towards the ocean and subsequently found the ocean within the first minute (Table 6.1, Fig. 6.2). Loggerheads that were exposed to steeper slopes were found to head seaward significantly more often that those exposed to gentler slopes ($t = 1.26$; $p = 0.25$; $df = 7$). However the sample size for this was very small (three and six individuals respectively) and therefore these results are more likely a result of too few samples. Southerly winds were found not to significantly alter the chance loggerheads initially chose to move landwards ($X^2 = 0.28$; $p = 0.90$). However, one particular night with exceptionally strong along-shore winds and heavy rain, where one olfactory control experiment was performed, the turtle’s movements were slow and although the initial orientation was still towards the ocean. Further, slope appeared to have no influence on time to find the ocean or on the initial directional choice with a total experimental range of 0.24 to -0.02. The range of slopes for the visual experiments was 0.13 to 0.03 with the visual control group exposed to 0.24 to 0.00 (Table 6.1).

Anecdotal observations of head lifting behaviour were recorded for almost all instances during experimentation. However, these appeared to have an increased frequency in the experiments where the loggerheads were blind-folded than in other experimental groups.

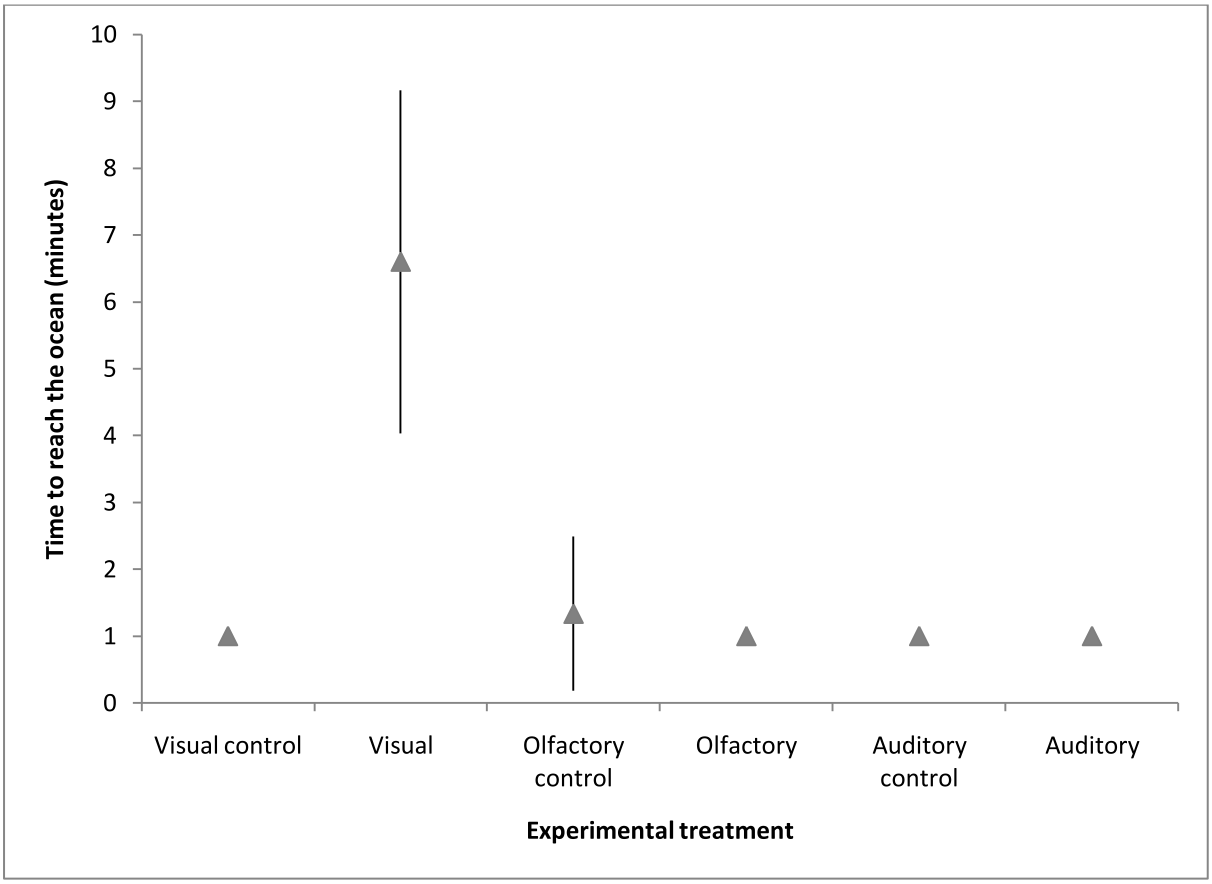

Figure 6.2: The average time taken for each experimental group to reach the ocean.

Discussion

Adult sea turtles appeared to be unable to find the ocean, other than by chance, without the use of visual cues. These results were tested on a range of slopes and wind directions which suggests that these are not important orientation cue used in sea-finding. These results are similar to what was found for Ehrenfeld & Carr (1967) and Mrosovsky &

Shettleworth (1968). However, results from Mrosovsky & Shettleworth (1974), Van Rhijn (1979) and Salmon *et al.* (1992) found that hatchling loggerheads and green turtles were able to use the slope of the beach in the absence of visual cues. Further, slopes as gentle as 1° were detectable by hatchlings (Van Rhijn 1979). Olfactory and auditory cues appear to have little influence in sea-finding (at least over the time scale tested). However, the only individual that was able to find the ocean was on an intermediate slope (0.10). It is unlikely that the slope is the reason for finding the ocean but was merely a coincidence because other visually inhibited individuals were unable to find the ocean on a wider range of slopes.

Individuals with inhibited sound and olfactory capabilities were able to find the ocean without any apparent difficulties, and did so within the first minute. This is ascribed to the primary use of visual cues in sea-finding leaving these other two cues as unused secondary cues. However when the visual system is inhibited, individuals found the ocean only after an average of 6.6 minutes suggesting that even in the absence of visual cues, olfactory and auditory cues have little to no influence on sea-finding. Perhaps the blind sea turtle that nested and found the ocean successfully (as mentioned in the introduction, Mora & Robinson 1982) had heightened sensory perception for its other senses because it was blind and therefore was able to find the ocean without any problems. However, it would have had time to adapt. Another potential explanation is that sea turtles are able to find the ocean using any number of cues but because the loggerheads used in these experiments were handled and disorientated, they were in a stressed and fearful state of mind which potentially added to lack of ability to find the ocean. Adding to this, Van Rhijn (1979) found that green turtle hatchlings that were blindfolded for 24 hours tended to use the slope as a sea-finding cue which may suggest that the adults used in this experiment could potentially use slope but under less handling-induced stress, and with some time to adapt.

These results suggest that visual cues are paramount for sea-finding in adult loggerheads (in the short term). Vision in sea turtles is considered myopic suggesting that specific objects are not discernable but that light and dark horizons can potentially be used for orientation (Ehrenfeld 1968, Akesson 1996). Therefore, even though vision in air is minimal for sea turtles, it is still a very important cue for orientation in, at least, the terrestrial portion of their life histories. Olfactory and auditory cues are not considered important for sea-finding in adult loggerheads.

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Chapter 7: General conclusions

Introduction

The nesting distribution of loggerhead turtles in Maputaland, South Africa, is uneven with a clear high density nesting area suggesting more favourable nesting conditions. However the reason for this selection is unknown. The purpose of this dissertation was to determine the reason behind this nest site selection and to investigate the current hypotheses together with the available cues and sensory capabilities of loggerheads. Nest site selection in loggerheads (and other sea turtles) has been extensively studied in the form of physical environmental factors, resulting in controversial conclusions for different populations. However nest site selection in Maputaland does not appear to be related to these environmental factors particularly beach characteristics and therefore this dissertation aimed to cover a wider, often understudied set of selection cues. These include, chemical imprinting, the presence of ambient and artificial lights and social facilitation.

Chemoreception

Chemical cues have long been suggested as being the drivers for nest site selection and among consistent nesting patterns in sea turtles (Owens *et al.* 1982, Grassman *et al.* 1984, Grassman 1993, Mrosovsky 2007). However, very little work has been done to test this hypothesis. This dissertation investigated this topic, to some extent, to better understand chemical imprinting in nest site selection.

The consistent annual nesting distribution in Maputaland suggests that there is a strong attraction to a section of the available nesting beaches preferred by loggerheads to nest upon. One particular hypothesis that may explain this preference is familiarity through olfactory imprinting. Sulfide concentrations found in the groundwater on the beach are highest within the high density nesting area which can provide a strong nest site selection cue. These results suggest that sulfides are not concentrated at the beginning of the season but increases during the season. This can either be formed through the decomposition of the eggs in the nest chamber which finds its way into the groundwater, or the lake water in the groundwater may become anoxic due to higher temperatures (and increased nutrients) and subsequently higher decomposition rates. Orientation experiments performed, showed no strong selection for the natal beach scent, but when the natal scent was introduced to the experimental pool, there was a reaction from the individuals; the accuracy of orientation and position of these turtles decreased suggesting a response to the natal beach scent. These sulfides may be used for within- and between season nest site selection cues however further investigations are required.

Ambient and artificial lights

The effect of ambient light intensities on nesting emergences has only been investigated once, (by Pike 2008) and these light intensities were not quantified but merely estimated from moon phase. The results from Pike (2008) found that ambient light intensities had little influence on nesting. With this being stated, artificial light intensities are well-known to deter nesting females, and previous work has found that nesting distributions shift away from these light sources. Results from this study confirmed that ambient light intensities have little influence on spatial or temporal nesting patterns. Cloud cover, moon phase and lightning significantly alter the light intensity experienced on the beach however; they have no effect on the number of emergences. Nevertheless, the effect of artificial light intensities is evident in the reduced number emergences at beacons near these artificial light sources. This has major management implications and mitigation to these impacts can easily be overcome.

Social facilitation

The social facilitation hypothesis has not been well received by sea turtle biologists and is often not even considered in the process of nest site selection, although the importance at sea should not be discarded just because it is understudied or poorly understood. If social facilitation plays a significant role in nest site selection, it would have major implications for conservation and future attempts to establish new nesting populations. The results obtained from this dissertation suggest that social facilitation is an unlikely driving factor in nest site selection but it may have a secondary importance. This process is self-perpetuating with neophyte nesters becoming experienced nesters continuing the process. In this way, the nesting distribution would be maintained throughout time.

Sea-finding

Previous studies investigating sea-finding for adult and hatchling sea turtles found that visual cues are the primary drivers for orientation. In some instances, slope may also have been used. Results from this study found that visual cues are primary cues and that slope has little influence on sea-finding. The sea turtle visual system is considered myopic and only light intensity variations are detectable out of water. Therefore, it is stated that sea turtles orientate away from the dark dune silhouette and towards the brighter sea surface. Olfactory and auditory cues do not appear to be used in sea-finding and they appear to have little value as secondary cues when visual systems are inhibited.

Concluding remarks

From the abovementioned sensory cues, the only definite influence of nest site selection was artificial lighting and these had a negative effect on adult nesting behaviour. The chemical imprinting hypothesis may potentially have an influence in nest site selection, however further investigations are required to entirely elucidate this hypothesis.

Favourable beaches may not actually exist within a nesting ground but they may merely be a factor of convenience and all the investigated variables for nest site selection may be unimportant for nest site selection. For example, there are inshore reefs present along the entire nesting grounds with increased frequencies towards the northern sections (Sink *et al.* 2011). Home range analyses from satellite tag data of eight loggerheads revealed that the inter-nesting movements of these individuals were focussed in the area between beacon 7N and 17N with offshore movements barely exceeding the 30 m depth isobath (Vogt 2011). This area may provide a safe habitat for inter-nesting females during the nesting season. Therefore it is possible that there would be an increased number of emerging loggerheads in this area, in comparison to the rest of the coastline that is adjacent to the nesting beaches. Gravid females would then simply move to the nearest nesting beach adjacent to these reefs, and variations in nesting patterns may simply be due to water movements and currents. Coincidentally, the area adjacent to the increase in the number of reef structures is also the high density nesting beaches for loggerheads. A simple diving survey may be sufficient to investigate this hypothesis.

Another potential explanation for the current nest site selection is oceanic currents. The consistent nesting distribution and the individual return nesters that appear to select the same or similar beaches from previous nesting events both within and between seasons may be driven by prevailing currents. Perhaps these currents are consistent and the gravid females merely swim to the beach of least resistance, which in this case could be the weakest currents or a particular beneficial current direction. Investigating currents at the nesting beaches may be a valuable means to further elucidate the driver of nest site selection. Also, the near-shore waters off the high density nesting beaches may be an area with the least amount or weakest currents providing loggerheads that remain near the coast with an area which they could use relatively little energy in remaining in this area. Monitoring currents and flow regimes of the waters adjacent to the nesting beaches would provide insight into this hypothesis.

Visual cues that may be discernable during the life history of sea turtles and that may also be used as orientation cues may be in the form of physical landmarks whereby memories of these landmarks are created and used in subsequent migrations to navigate (Carr & Ogren 1960, Carr 1967, DeRosa & Taylor 1980). Further, landmarks may be used to find specific nesting beaches and therefore be important in nest site selection. Unfortunately, there are few publications on this mechanism of homing and it can therefore not be excluded as a potential source of homing cues.

Sea-finding appears to be driven by a single sensory system (visual) which is considered a weak system for sea turtles when used in air. However visual cues are often the most reliable cues on nesting beaches and therefore they have remained the dominant drivers of sea-finding. The use of the visual system for sea-finding reinforces the idea that spatial learning of potentially distinct landmarks may be used for natal homing and subsequent nest site selection (Lopez *et al.* 2003). However, these visual cues would have to be detectable to a turtle’s eye out of water which is considered a weak sense (Ehrenfeld & Koch 1967, Ehrenfeld 1968).

The drivers of nest site selection investigated in this dissertation were considered in isolation however more than likely they are not used exclusively. It is expected that different cues are used under different conditions. This dissertation attempted to isolate the drivers to determine whether they were detectable and further, used during orientations and navigations. Therefore further studies could investigate a suite of drivers in unison and attempt to discover the suite of drivers of sensory orientation and navigation however the scale of this project would be enormous if all potential variables were included.

This dissertation has been of significant value by contributing to the discovery of nest site selection and the sensory perception of sea turtles. This project has contributed to an increasing field of knowledge with regards to the scarcity of evidence.

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Appendix A

Sea turtle sensory systems

Sea turtles have many sensory systems that are used throughout their lives for navigation. This section will only focus on four to give the appropriate background for this dissertation. These include geomagnetism, smell, vision and hearing all situated in the head of sea turtles (Fig. 1).

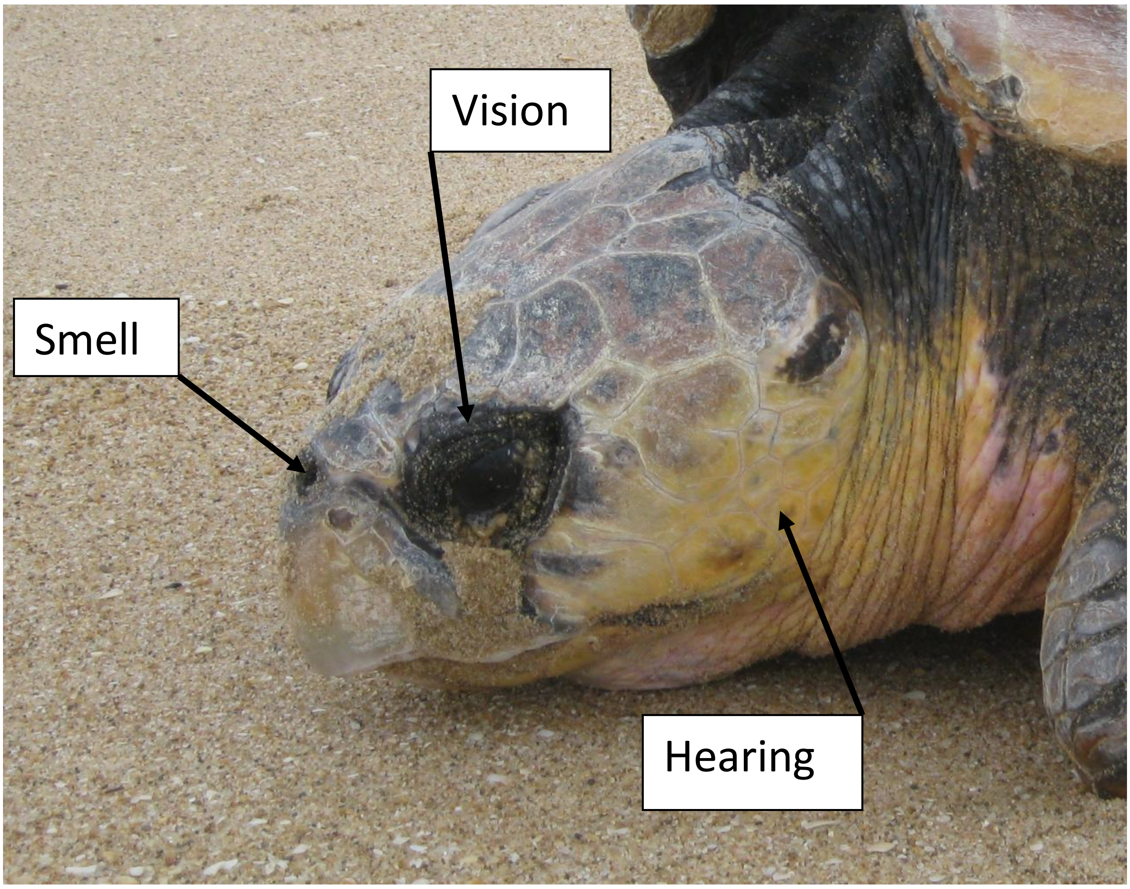

Figure 1: The head of a loggerhead turtle indicating the external features housing each of the sensory systems – smell, vision and hearing.

Geomagnetism

The earth has unique magnetic fields that are detectable to humans with equipment such as a compass. Some animals have internal mechanisms to detect these magnetic fields that provide them with information on position and orientation. The commonly reported compound used to detect the magnetic fields is magnetite which is also found in sea turtles (Kirschvink 1980, Perry *et al.* 1985, Kirschvink *et al.* 2001, Walker *et al.* 2002). A good visual illustration of the potential mechanism in which these magnetite compounds work may be found in Walker *et al.* (2002). Essentially, the presence of a magnetic field opens up certain ion channels of a cell allowing a change in the receptor potential of the cell (Walker *et al.* 2002).

Behavioural studies have revealed that perception of the magnetic field is important for sea turtle migrations. Hatchlings require the perception of the earth's magnetic field to remain within large oceanic circulations (Lohmann & Lohmann 1996, Fuxjager *et al.* 2011). Juvenile and adult sea turtles also use the earth's magnetic field during large-distance migrations (Lohmann *et al.* 2008a, Lohmann *et al.* 2008b). Therefore the earth's magnetic field is very important for navigation in sea turtles. However, there are studies which suggest that the earth's magnetic field is not always used in navigational feats (Papi *et al.* 2000) suggesting that magnetoreception may only be used in some aspects or certain areas of navigation (Benhamou *et al.* 2011).

Smell

The external morphological features facilitating smell of turtles are two nostrils (olfactory) and the mouth (gustatory). These two systems are used for different functions, namely smell and taste. Investigations performed by Manton *et al.* (1972) revealed the sensory systems in the nasal cavity rather than those in the mouth were used for a series of behavioural experiments. Within the nasal passage, there are two different types of tissue namely: olfactory and vomeronasal. These two pathways are differentiated through their neural pathways where the olfactory system is connected to the main olfactory bulb (MOB) in the central nervous system through the olfactory nerve while the vomeronasal system is linked to the accessory olfactory bulb (AOB) through the vomeronasal nerve (Fig. 2). The olfactory and vomeronasal epithelium in the nasal cavity are also non-overlapping (Saito *et* *al.* 2000). Through dye experiments, it was found that after the turtle submerged, the olfactory epithelium remained dry while the vomeronasal epithelium was wet (Saito *et al.* 2000, Southwood *et al.* 2008). Further studies were performed by Endres *et al.* (2009) who discovered that sea turtles are able to detect odours above-water. Therefore, the locations of the two epitheliums in the nasal cavity suggest that they are used to detect odours in different mediums.

The vomeronasal system has often been suggested as a pheromone receptor in other organisms (Mason *et al.* 1989, Liman 1996, Wirsig-Wiechmann 2002) and therefore if this is the same for sea turtles, then pheromones would more than likely be detectable in the liquid medium. However, substantial evidence exists to suggest that, not only are the olfactory receptors able to detect some pheromones, but that the vomeronasal receptors are also able to detect general odours such as protein odours originating from prey items (Halpern & Martinez-Marcos 2003, Baxi *et al.* 2006).

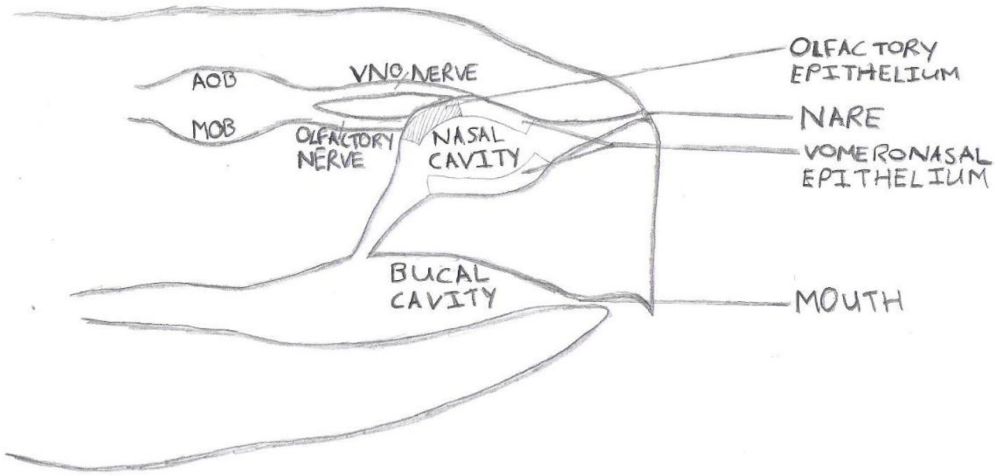

Figure 2: Illustration of the olfactory and vomeronasal epithelium in the nasal cavity of a sea turtle together with the associated pathways. AOB – Accessory olfactory bulb; MOB – Main olfactory bulb.

Vision

Sea turtles have two eyes in either side of their heads. Their sight is considered myopic out of water (Ehrenfeld & Koch 1967). This suggests that the sea turtle's ability to see out of water is poor and they are only able to distinguish light and dark with little ability to discern shapes. Another interesting anatomical feature of the sea turtle's is their very small lenses and pupils for their body size (Northmore & Granda 1991). This would suggest that they have a reduced ability to detect dim lights (Mathger *et al.* 2007) which is intriguing because during hatching and nesting, they use slight changes in brightness to navigate towards the ocean (Bartol & Musick 2003).

Sea turtles have well developed visual systems (Levenson *et al.* 2004) with their eye's are adapted for shallow marine habitats (except for the leatherback, Levenson *et al.* 2004). Their eyes contain four cone photoreceptors (Mathger *et al.* 2007) which, through behavioural studies, provided a response in the spectral range from 440 – 700 nm (as in Fig.4.2, Levenson *et al.* 2004). Colour discrimination is enhanced through the presence of coloured oil droplets present in the photoreceptors (Fig. 3; Levenson *et al.* 2004). These act as filters to alter the sensitivity of cones to different wavelengths and broaden the range of colour perception (Liebman & Granda 1975, Vorobyev 2003, Levenson *et al.* 2004). However sea turtles have weak receptiveness in higher wavelengths (red light) of 650 nm (Levenson *et al.* 2004). Yet, sea turtles have the capacity to detect wavelengths as low as 320 nm which falls within the ultraviolet (UV) range (Witherington & Bjorndal 1991, Ventura *et al.* 1999, Mathger *et al.* 2007). However, the purpose of detecting UV light in sea turtles in unknown (Levenson *et al.* 2004).

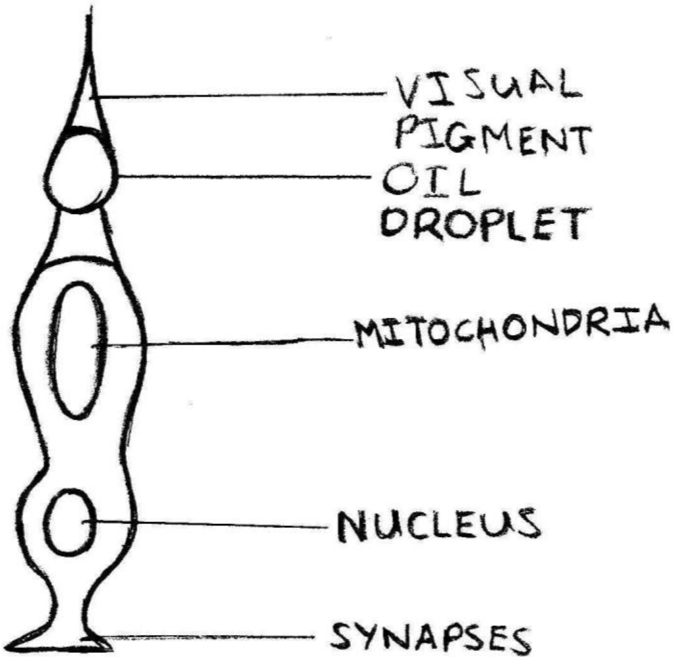

Figure 3: Illustration of a photoreceptor in the turtle retina.

Hearing

Sea turtles have internal ears with a tympanum consisting of an extension of the facial tissue with a layer of fat underneath the tympanum (Fig. 4; Moein Bartol & Musick 2003). This is considered an adaptation to living in water with a speculated increase in sound perception however sea turtles are also able to hear on land (Lenhardt *et al.* 1985). The layer of fat underneath the tympanum is suggested to be highly specialised for underwater hearing (Ketten *et al.* 1999) however there is also evidence to suggest that the fat layer and the tympanum are simply there as a sound release mechanism but the true pathway of hearing in sea turtles is still unknown (Moein Bartol & Musick 2003). Loggerhead's sensitivity to sound was measured using auditory brainstem responses (ABRs) and it was found that juveniles exposed to varying frequencies respond in the range of 250 – 1000 Hz with the peak at 250 Hz (Moein Bartol *et al.* 1999). Hearing capabilities of sea turtles appear to be dependent on size classes because the sensitivity between juveniles and sub-adults green turtles was considerably different (Moein Bartol & Ketten 2006). Furthermore, sound sensitivity of sea turtle's ears is different for in-water and on land (Moein Bartol & Musick 2003, Moein Bartol & Ketten 2006).

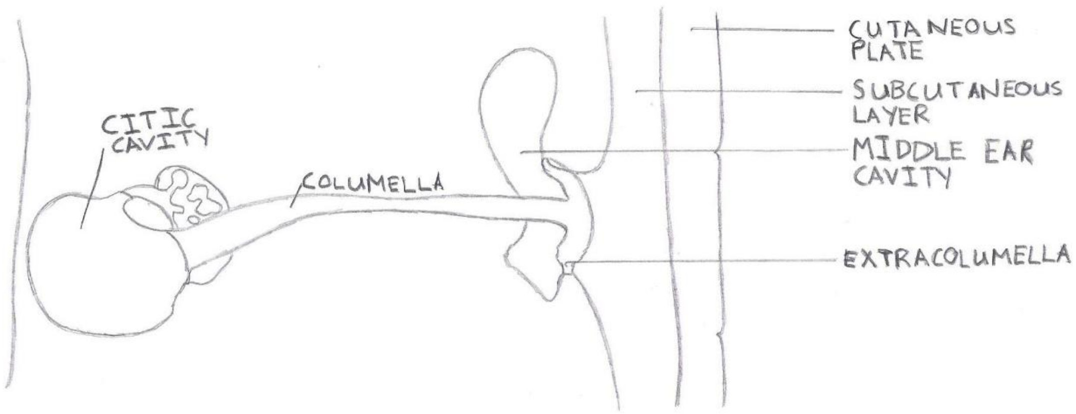

Figure 4: Internal anatomy of a sea turtle ear.

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