NEST SITE FIDELITY AND NEST SITE SELECTION OF LOGGERHEAD, *CARETTA CARETTA*, AND LEATHERBACK, *DERMOCHELYS CORIACEA*, TURTLES IN KWAZULU-NATAL, SOUTH AFRICA

By

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DECLARATION

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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

Loggerhead and leatherback sea turtles nest on the beaches of the north-eastern portion of Kwazulu-Natal within the iSimangaliso Wetland Park. Loggerheads place ~60 % of all nests within an 8 km stretch of beach, whereas leatherbacks tend to space their nests more evenly along the entire length of the monitoring area. The study aimed to determine nest site fidelity of loggerheads and leatherbacks (using four decades of nesting data housed by Ezemvelo KZN Wildlife) and the factors that influence nest site selection of both species within the 56 km of turtle monitoring area (32N to 100S) and the 5 km area of high-density loggerhead nesting (0N to 12N). The effectiveness of nest site selection was then determined through the hatching success of loggerheads over the 5km area (0N to 12N). Results showed that loggerheads show a high degree of nest site fidelity (~3 km) with nest site fidelity of individuals increasing over subsequent seasons of nesting, as well as these individuals using the same stretches of beach for nesting (the most popular area being 1N to 4N for repeat nesters). Leatherbacks displayed nest site fidelity of ~9 km and this did not increase over successive seasons of nesting. In terms of nest site selection, loggerheads and leatherbacks both avoided areas where low shore rock was present, whereas both species preferred nesting on beaches of intermediate morphodynamic state. Leatherback nesting was significantly higher in areas with wider surf zones. Both species were able to surpass the high water mark when nesting as nests below this point would be almost certainly doomed. Hatching success of loggerheads was comparative to high (83 %) relative to other studies, however, nest success varied across the beach from beacon 1N to 12N. Areas where highest nest success was observed were not areas of highest nest density presumably due to artificial lighting. Results from this study increase our understanding of the evolutionary biology of loggerhead and leatherback turtles in South Africa and the effectiveness of loggerhead nest site selection through hatching success.

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CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION

Sea turtles are a relatively unique group amoung the reptiles as they are the only truly marine reptiles with the exception of some sea snakes. Among the seven species of sea turtles, habitats utilised range from pelagic waters of temperate regions to tropical continental shelf waters, with the main limiting factor to distribution being climate and specifically temperature (Hendrickson 1980). Sea turtles remain tied to land, as they are dependent on land incubation of their eggs and therefore have to come ashore to oviposit eggs to incubate under certain temperature and sand conditions. Like their terrestrial counterparts, the general body structure of sea turtles is box-like, with hard outer carapaces used as defence mechanisms against predators, but sea turtles are unable to withdraw their heads and other extremities into the carapace which makes them vulnerable, especially when on land (Hendrickson 1980).

Reproduction and nesting of sea turtles shares some characteristics with land tortoises but on the whole tends to be very complex. At the onset of the nesting season, male and female sea turtles begin migrations to their respective rookeries. The ability of sea turtles to return to their respective rookeries, defined as natal homing, season after season has been well documented through the study of tag returns as well as females returning to natal rookeries (Carr & Carr 1972; Bowen *et al.* 1989; Bowen *et al.* 1992; Bowen *et al.* 1993; Bass *et al.* 1996; Miller *et al.* 2001; Lee *et al.* 2007). The difficulty associated with these studies ranging from hatchling stage through to adulthood of sea turtles is the adequate long-term marking of the hatchlings (Bowen *et al.* 1989; Dutton *et al.* 1999). Notching of the marginal scales i.e. mutilation tagging of newly hatched loggerheads in South Africa, started by Hughes in the 1970s (Hughes 1971), overcame the challenge of tagging newly hatched sea turtles with external tags (Hughes 1989; Baldwin *et al.* 2003). This ongoing study yielded conclusive results that (at least some) females return to their natal beaches to nest when mature.

The challenge has remained how sea turtles manage to return to their beaches of incubation. Two theories have been proposed to explain how sea turtles navigate back to natal beaches from feeding grounds, which could be thousands of kilometres away; "natal homing'", the programming or imprinting of hatchlings with a particular scent, inclination angle or intensity of the magnetic field at the rookery (Bowen *et al.* 1993; Lohmann *et al.* 2008) or "social facilitation", neophytes (first-time nesters) follow older, more experienced females to nesting grounds from foraging areas and imprint on the rookery (Dutton *et al.* 1999). The answer is still unclear but is likely to be a combination of these factors, rather than one in isolation.

The timing of the nesting seasons depends on the geographical position of the rookery and coincides with warmer months. Nesting seasons in the southern hemisphere are from October to March and May to August in the northern hemisphere (Hughes 1989; Miller *et al.* 2001), whereas nesting of sea turtles in the tropics can occur throughout the year (McAllister *et al.* 1965; Hughes 1989). The majority of female sea turtles usually return only every second or third season to nest, with very few females returning yearly (Boulon *et al.* 1996; Hughes 1996; Miller *et al.* 2001). The number of nests oviposited per season and the number of eggs laid per nest are species dependent, ranging from one to six nests for loggerheads, *Caretta caretta* Linnaeus (Miller *et al.* 2001), and can be as high as 11 nests per season for leatherbacks, *Dermochelys coriacea* Linnaeus (Kamel & Mrosovsky 2004).

Once females have navigated back to their natal beaches, a nesting area needs to be selected by the female based on cues or previous knowledge of the area known as nest site fidelity. Olfactory cues that are biological in nature such as metabolite derivatives from hundreds of successful nests, or chemical cues from the erosion of the substratum where minerals are transported by water bodies adjacent to the nesting beach, may attract females to respective rookeries (Hughes 1989). However, the cues that attract nesting females to the precise location of nest placement remain speculative. Nesting females are success stories as they hatched successfully from the beach and therefore may follow cues that were acquired as a hatchling, whatever these cues might have been.

The size of the stretch of beach that a female may use for placing her eggs is dependent on the size of the rookery and the species in question. Tag returns of green turtles have shown the existence of a highly accurate method of placing different nests in close relation to one another (Carr & Carr 1972; Bowen *et al.* 1989). Between-species studies have shown that green turtles are stricter in nest placement (1.8 km apart) than hawksbill turtles (3 km apart) in Mexico (Xavier *et al.* 2006). Loggerheads have also been shown to exhibit a high degree of accuracy by one female placing eight clutches in one season within a 15.9 km stretch of beach in Casey Key, Florida (Tucker 2009). Leatherbacks, the biggest of all species of sea turtles, have been shown to be the least strict in nest placement, much less so than hard-shelled turtles, as leatherbacks have been observed to nest up to 40 km away from previous nest sites (Hughes 1989).

If there was no existence of nest site fidelity, no turtle nesting rookeries would exist as sea turtles would lack “homing drive” to natal rookeries and be content nesting on any stretch of beach where they hauled out. Without natal homing, mate location and nesting patterns would be more random which would be energetically expensive or unsuccessful. If nest site fidelity did not exist, male and female sea turtles would face the challenge of locating one another as there would be no mating aggregations in waters off the rookeries. Mating patterns would be different to the current ones displayed and mating would instead have to occur on the feeding grounds, as these would be the only common areas shared by both males and females. Mating aggregations of sea turtles have been shown to occur with male turtles showing fidelity season after season to specific courtship areas off the rookery (Pandav *et al.* 2000; Tripathy & Pandav 2007). Furthermore, sea turtle eggs require specific conditions for successful incubation (Miller *et al.* 2001; Wallace *et al.* 2007). The temperature of sand governs the development of sea turtle eggs, with average temperatures below 20^0C (Hughes 1989) and above 35^0C causing a cessation of development (Miller *et al.* 2001). Therefore, nest site fidelity homes sea turtles to nesting in areas where temperature facilitates the successful incubation of eggs. The existence of nest site fidelity may also aid in the defence of the nests against predation pressure as a single nest on its own has a high probability chance of being predated while six or seven clumped nests have considerably less chance of being predated upon. Female sea turtles gain the advantage of sparing energy with the existence of nest site fidelity as they do not have to actively seek males to copulate with and assess different stretches of beach per nest or even across multiple nesting seasons.

Within a turtle rookery where sea turtles display high nest site fidelity, a female sea turtle places nests with the number being species and population specific (Miller *et al.* 2001). Within this stretch of beach, females discriminate on local conditions to select the most suitable environment for placing nests that will facilate nesting, incubation and presumably hatching although it is not clear what these characteristics are or how they are selected. Factors that have been investigated with reference to nest site selection are: intertidal slope (Eckert 1987; Wood & Bjorndal 2000; Garmestani *et al.* 2000), 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 type, pH (Garmestani *et al.* 2000), salinity (Wood & Bjorndal 2000), sand softness, beach length, beach height (Kikukawa *et al.* 1999) and the presence of reefs or rocks (Mortimer 1995). Therefore, nest site selection can be defined as the non-random placement of nests or eggs within a pre-defined area by a female turtle.

Results from nest site selection studies have often varied from rookery to rookery with no factors consistently affecting nest site selection to the same degree per rookery. All current nest site selection studies have failed to examine nest site selection of sea turtles from a beach ecosystems perspective by not examining the entire littoral active zone such as characteristics of the intertidal zone; the surf zone including the presence of subtidal reef and intertidal rock distribution, beach morphodynamic characteristics (including wave height, grain size, slope, etc.), beach width, back-beach width, vegetation cover. Beach morphodynamic type ultimately describes the interplay of the features of beach ecosystems. For example; the intertidal slope is determined by grain size and wave height, with coarser sand creating a steeper beach face (i.e. the more reflective), with a shorter distance for a turtle to crawl to reach a "safe" nest site above the high water mark (Wright & Short 1984; Mortimer 1995; Benedet *et al.* 2004). The beach morphodynamic type also describes the general pattern of the surf zone with short or no surf zone width associated with reflective beaches (McLachlan & Brown 2006).

The most important consequence of nest site selection is hatching success of a clutch of eggs or nest success. Nest site selection is thus highly important in terms of hatching success however, other factors also contribute to this success but are beyond the scope of the current study. These are the intrinsic factors such as the species of sea turtle in question (Miller *et al.* 2001; Antworth *et al.* 2006; Xavier *et al.* 2006), female fertility (Miller *et al.* 2001; Bell *et al.* 2003) and embryonic mortality (Bell *et al.* 2003). Extrinsic factors that will affect nest site selection and thus nest success are sand grain size (Maloney *et al.* 1990; Ralph *et al.* 2005) and associated with grain size is slope (Wright & Short 1984; Benedet *et al.* 2004; McLachlan & Brown 2006), intertidal width and the distance of a nest from the vegetation zone and the tidal zones (Eckert 1987).

Failing to lay nests in the "correct" area on the beach may result in hatchling or nest mortality. Placement of a nest too near to the high water mark or below the high water mark could result in inundation of the nest (Wood & Bjorndal 2000). Inundation near the end of the incubation period may be lethal to the developing hatchlings as it may decrease the oxygen content as well as drown the hatchlings (Miller *et al.* 2001). Nesting too far inland could result in increased desiccation of the nest, misorientation of the hatchlings and predation of females, eggs and hatchlings (Wood & Bjorndal 2000; Kamel & Mrosovsky 2004). Placement of nests near vegetation may also prove to be lethal to the incubating eggs as plant roots may penetrate nests thereby destroying eggs (Kamel & Mrosovsky 2004). This study will focus on extrinsic factors.

THESIS OUTLINE

All content chapters are written as stand-alone chapters to assist with the successive publication and therefore repetition may be evident from one chapter to the next.

Chapter 2: The aim of this chapter is to describe the study site and provide the context of the South African long-term monitoring and protection programme. This chapter describes all aspects of the nesting beaches of the turtles as well as the full details of data collection in the monitoring programme which is conducted independently of this project, but of which the data provides the basis to much of this thesis. Details such as history of conservation and the iSimangaliso Wetland Park are also discussed.

Chapter 3: This chapter aims to define and describe nest site fidelity of loggerheads, *Caretta caretta*, and leatherbacks, *Dermochelys coriacea*, in South Africa. This chapter details nesting of loggerheads and leatherbacks monitored from 1965/66 season through to the 2007/08 season. Key questions dealt with in this chapter are: (1) whether nest site fidelity exists for loggerheads and leatherbacks; (2) whether nest site fidelity changes during the season for either species; (3) whether nest site fidelity changes between seasons for either species.

Chapter 4: The aim in this chapter is to identify criteria used for nest site selection by loggerheads, *Caretta caretta*, and leatherbacks, *Dermochelys coriacea*, in South Africa. Key issues to be dealt with in this chapter are possible reasons as to why sea turtles haul out onto the particular stretch of beach where they do, and why they place their nests where they do.

Chapter 5: The key question to be addressed in this chapter is the implications of the criteria used for nest site selection by loggerheads on hatching success. It will thus evaluate the effectiveness of site selection of loggerheads, *Caretta caretta*, through hatching success. This chapter follows on from Chapter 4 and deals with the hatching and emergence success of loggerhead hatchlings based on the site selection criteria for each nest.

Chapter 6: Is the synthesis and conclusions. This chapter summarises and discusses all the main findings in each of the content chapters and explains the processes and cues involved in the selection of a stretch of beach for loggerheads and leatherbacks to the hatching success of loggerheads. It describes nesting in relation to current threats.

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CHAPTER 2

STUDY SITE AND THE SOUTH AFRICAN TURTLE MONITORING PROGRAMME.

INTRODUCTION

The turtle nesting beaches of Kwazulu-Natal, South Africa form the southern most nesting rookery of loggerhead and leatherback sea turtle populations globally (-27S). Nesting in South Africa is restricted to the north-eastern coast of Kwazulu-Natal (McAllister *et al.* 1965; Hughes *et al.* 1967) in the iSimangaliso Wetland Park. The iSimangaliso Wetland Park, a world heritage site since 1999, listed for its natural attributes, including the sense of place, rich biodiversity and rare and threatened species (iSimangaliso Authority 2009). One of the goals of this world heritage site, in addition to conservation, is the stimulation of economic development of the adjacent region and the empowerment of local communities (iSimangaliso Authority 2009). The long-standing goal has been conservation which started through a Ramsar agreement being signed in 1971 (Mountain 1990), specifically to provide recognition to the turtle nesting beaches and the coral reefs of Tongaland (Baldwin *et al.* 2003). Two marine protected areas were proclaimed before the establishment of the iSimangaliso Wetland Park; the St. Lucia Reserve (now a marine protected area, MPA) which extends from Cape Vidal (-28.120S 32.555E) in the south, to north of the Ngoboseleni stream where the Maputaland Marine Reserve (also an MPA) extends northwards to the Mozambican border (Marine Living Resources Act 1998). Both marine protected areas extend three nautical miles seawards from the high water mark (Marine Living Resources Act 1998).

The ocean current dominating the north-eastern coast of South Africa, and hence dominating marine life on the eastern seaboard, is the Agulhas current which flows along the continental shelf to conclude at the southern tip of Africa (Schumann & Orren 1980; Lutjeharms & Ansorge 2001). This is a warm water current (Lutjeharms 2001) with temperatures near the core peaking at 28^0C in summer (Schumann & Orren 1980). The Agulhas current is fast flowing with speeds ranging 5.4 km/hr to 7.2 km/hr (Schumann & Orren 1980; Lutjeharms 2001). A significant aspect of the current is the ability to sweep hatchlings in this body of warm water in a southerly direction towards the tip of Africa (Baldwin *et al.* 2003) with some warm water eddies spinning off into the cold Benguela current along the west coast of southern Africa, assumed to draw hatchlings along.

The turtle nesting beaches of South Africa are characterized by a narrow intertidal strip constituting mainly silica sand (Hughes 1996; Baldwin *et al.* 2003). The coastline is medium to high energy (Baldwin *et al.* 2003) due to a very narrow continental shelf and characterized by small, asymmetric (half-heart shaped) sandy bays approximately 5 km in length (McAllister *et al.* 1965; Hughes 1996). The southern ends of the bays are protected by rocky headlands with few rocks situated within the bays (McAllister *et al.* 1965). The main beach morphodynamic state occurring in the iSimangaliso Wetland Park is intermediate beaches with some coarse grained, steep reflective beaches (Harris 2008). The back-beaches are bordered by high, ancient secondary dunes stabilized by sub-tropical coastal dune forest. Some stretches of the coast are characterized by mobile, wind-blown dunes (McAllister *et al.* 1965).

STUDY SITE

The beach component of iSimangaliso Wetland Park extends for approximately 200 km along the east coast from the Mozambican border in the north to Cape Vidal (-28.120S 32.555E) in the south (Fig. 2.1). The turtle monitoring area falls within the borders of the iSimangaliso Wetland Park and extends from the Kosi Estuary mouth at turtle beacon number 32N, N for north, (-26.897S 32.880E) to Mabibi at 100S, S for south, (-27.347S 32.743E) in the south (Fig. 2.2). The high-density loggerhead nesting area is a 5 km stretch of coast that forms the core of the turtle monitoring area and extends from 0N (-27.012S 32.866E) to 12N (-26.968S 32.874E) as seen by Fig. 2.3 where nesting numbers of loggerheads and leatherbacks from 1965/66 to 2006/07 are shown.

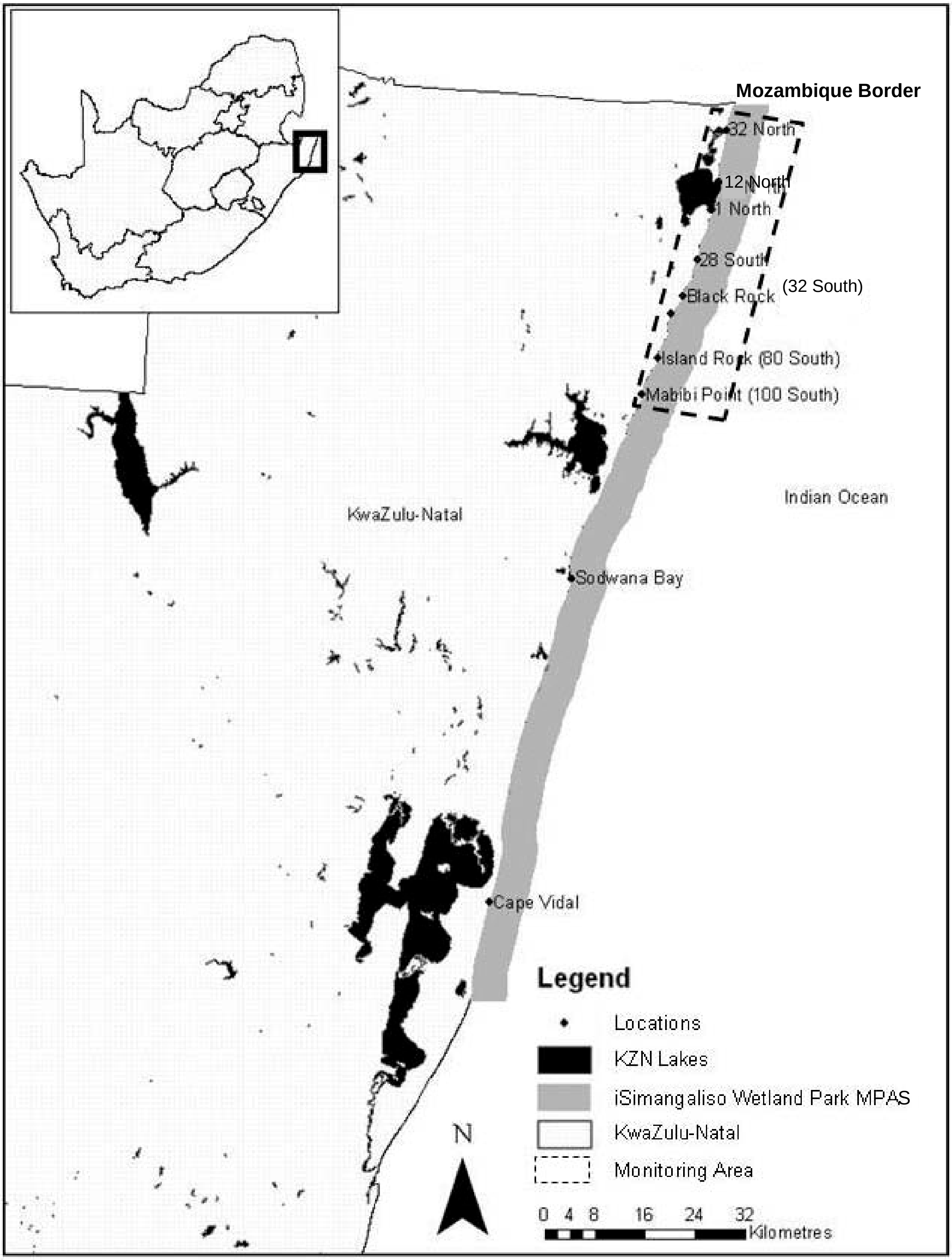

Fig. 2.1. The iSimangaliso Wetland Park showing the extent of the MPAs and the turtle monitoring area in the north.

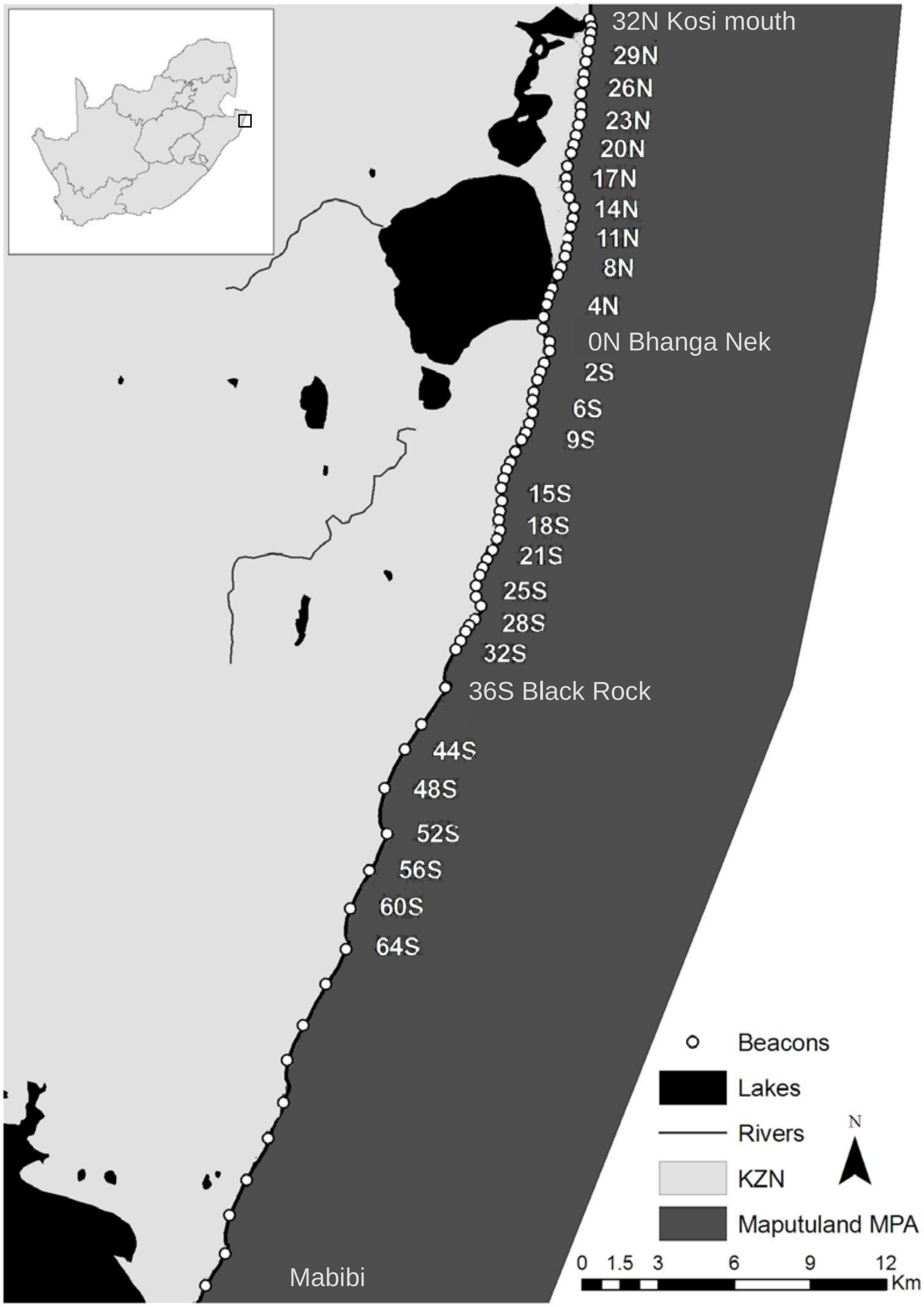

Fig. 2.2. The turtle monitoring area (32N to 100S) showing monitoring beacons along the coastline.

The entire monitoring area is marked with sequentially numbered marker poles at 0.4 km intervals. All beacons north of the research base at Bhanga Nek, 0N (Fig. 2.2.) are marked as North while all beacon numbers to the south of Bhanga Nek are marked as South. Past 28S, only one-mile (1.6 km) beacon posts are present and continue to Mabibi at 100S.

The study site consists of two components, the 56 km turtle monitoring area and the 5 km high-density turtle nesting area (Fig. 2.3). The high-density nesting area consists of very narrow dune corridor due to the presence of the Kosi lake system of which the edge of the largest lake, Lake Manzanyama can be seen (Fig. 2.3.). The dunes adjacent to beacons 1N and 2N are the narrowest between the lake and the beach, which is also the section that is regularly eroded. A bush camp adjacent to beacons 2N and 3N causes some disturbance with artificial lighting from some informal campsites. The unvegetated beach-dune interface is uniform in width up to beacon 10N but starts to widen from here onwards to beacon 12N. The beach at beacons 11N and 12N are characterised by unvegetated, wind-blown dunes. The dunes at beacons 1N to 3N are small, vegetated primary dunes covered by *Ipomea* and *Scaevola*. The area from beacon 3N through to 5N is backed by established higher primary dunes with some alien *Cassuarina* trees stabilising the beach-dune interface. From 5N through to 10N, no wind blown dunes are apparent (Fig. 2.3.). Some inshore rocks protect the beach at beacons 9N and 10N, which can make this section inaccessible to sea turtles during low tides. At extreme low spring tides rocks are visible from beacon 7N onwards to 10N.

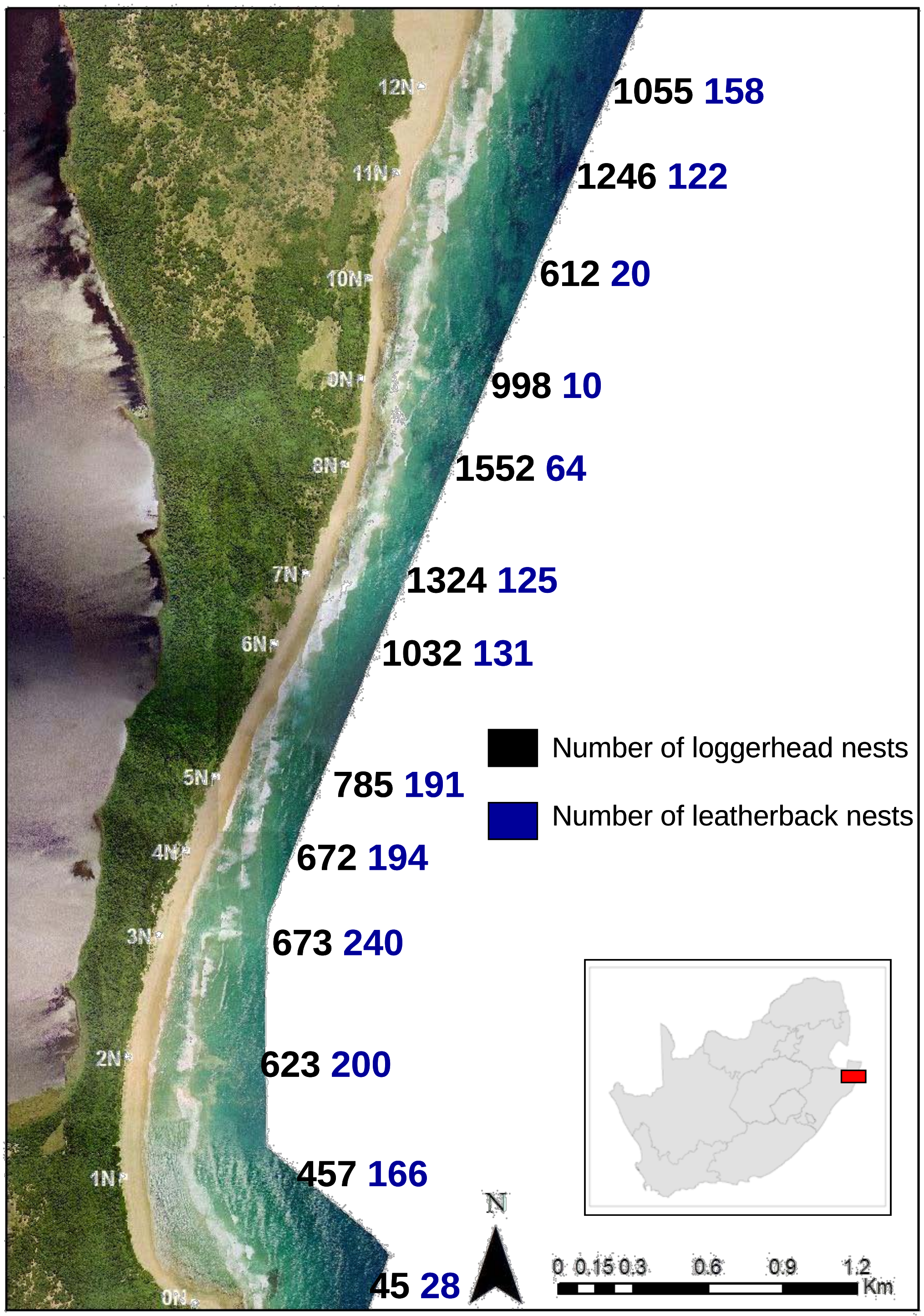

Fig. 2.3. The high-density loggerhead nesting area with the beacons shown at 0.4 km intervals and number of loggerheads and leatherbacks nests laid from 1965/66 to 2006/07.

THE SOUTH AFRICAN LONG-TERM TURTLE MONITORING PROGRAMME

Background

Loggerhead and leatherback nesting around South Africa was first discovered by Smith in 1849 (Hughes 1989; Hughes 1996; Baldwin *et al.* 2003). The first law against the killing of sea turtles in South Africa was passed in 1916, however subsistence harvesting still occurred and decreased the numbers further (Hughes 1989). It was not until the 1960s that serious action was taken to protect turtles and with that the South Africa turtle monitoring and protection programme was initiated in 1963 (Hughes 1989; Hughes 1996; Baldwin *et al.* 2003), thus making it one of the longest running, consistently sampled monitoring and protection programmes for loggerheads and leatherbacks in the world (Wilson & Humphrey 2004; Nel & Lawrence 2007). Initially monitoring was restricted to an 8 km stretch of beach from the research station at Bhanga Nek to Kosi mouth estuary. This includes all the northern beacons, and is still used as the Index area for interannual nesting comparisons. The area was later expanded to the current monitoring area which spans 56 km. Turtle conservation was later enhanced by enclosing the turtles nesting habitat into formal conservation areas and by the proclamation of two marine protected areas, St. Lucia Marine Reserve and Maputaland Marine Reserve (McAllister *et al.* 1965; Hughes 1996).

The monitoring and protection programme has resulted in the growth of loggerhead nesting numbers in South Africa (Hughes 1989; Baldwin *et al.* 2003; Nel 2008; Nel 2009). The number of loggerheads per year is approximately four times greater than at the start of the programme with the latest season report showing between 500 to 600 females nesting annually in the iSimangaliso Wetland Park (Nel 2009). The leatherback population has increased since the inception of the monitoring programme, with only five leatherbacks seen in 1966 (Hughes 1989). The leatherback population has grown to approximately 60 nesting females per year

(Hughes 1989; Nel 2008; Nel 2009), keeping in mind that there was restricted monitoring effort in the early years however, this figure is still extremely low with the nesting population being very small.

Monitoring protocol

The monitoring protocol has been consistent for the entire duration of the programme, and has been conducted by a combination of foot and vehicle patrols. When turtles are encountered, the species is identified, curved carapace length (CCL), curved carapace width (CCW), or straight carapace length (SCL) and straight carapace width (SCW) recorded. The straight line measurements are only recorded in the case of loggerheads using "giant" callipers and curved measurements are made using a soft tape measure, and are routinely only measured for leatherbacks. All size measurements are made to the nearest millimetre. Other data that are collected are the date and time, flipper tag number, location to the nearest beacon number and whether the female nested or not. Tag scarring is recorded as calloused and notch codes in the case of loggerheads are recorded. Notch codes were applied in unique codes per year which are now used to identify when the female hatched from these beaches. For example, in 1971/72, 5000 loggerhead hatchlings had the first carapace scale to the left of the tail removed with a leather punch and therefore would have the notching code of one left, 1L (Hughes 1989). Notching was soon increased to a double-notch code as it was evident that single scars could be interpreted as natural. All turtles encountered are double-tagged (since 2007/08) with two titanium flipper tags, in the front flippers for loggerheads and hind flippers for leatherbacks. Each track scored is cancelled (with a giant "S" through the track) once data is collected so that duplication of data does not occur.

The data from the long-term turtle monitoring programme forms a useful basis to assess aspects of the nesting behavior and ecology of loggerheads and leatherbacks in the east Africa.

The data as previously mentioned, includes valuable information about turtles and their nesting sites. With the aid of the long-term turtle monitoring database (~45 years), it is possible to determine nest site fidelity of loggerheads and leatherbacks based on tag numbers of females returning to nest in the monitoring area of the iSimangaliso Wetland Park and beacon numbers as the proxy for distance between nests of individuals. These data are used for chapter 3 and 4 of the thesis with additional data collected per objective in these chapters.

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CHAPTER 3

NEST SITE FIDELITY OF LOGGERHEADS, *CARETTA CARETTA*, AND LEATHERBACKS, *DERMOCHELYS CORIACEA*, IN SOUTH AFRICA.

ABSTRACT

Nest site fidelity is the successive placement of nests by the same individual at a distance smaller than the area offered or available to nest in. Nest site fidelity was determined using a long-term dataset for loggerhead and leatherback turtles nesting in South Africa. *Within-season* nest site fidelity was defined as the mean distance of one nest relative to another within the same season, whereas *between-season* analysis evaluated if within-season nest site fidelity per individual (measured in distance) remained constant over multiple seasons. *Across-season* nest site fidelity evaluated if the same stretches of beach were used by individuals over multiple seasons. Loggerheads displayed high *within-season* nest site fidelity (~ 3 km) which was higher than leatherbacks (~ 9 km) and it remained relatively constant over time for both populations. A *between-season* nest site fidelity assessment showed that loggerheads were able to reduce the distance between successive nests over successive seasons but the same result did not hold true for leatherbacks; instead nest site fidelity remained constant between seasons for individuals. *Across-season* nest site fidelity suggested that loggerheads “learn” where to nest as there was substantial overlap in areas used among seasons. Leatherbacks did not show any “learning” ability across seasons. The strategy of “learnt” nest site fidelity favours loggerhead females with numbers increasing over successive seasons, conversely leatherback numbers seem stagnant and not on the increase.

INTRODUCTION

Nest site fidelity studies have been conducted across a number of egg-laying taxa, including spiders (Hoefler & Jakob 2006), birds (Jenkins 1993; Ryabitsev & Alekseeva 1998; Gonzales-Solis *et al.* 1999) and sea turtles (Carr & Carr 1972; Hays & Sutherland 1991; Nordmoe *et al.* 2004). Nest site fidelity definitions generally assume that subsequent nests are or should be in close proximity to the previous nest to show some form of selection (Hughes 1989; Gonzales-Solis *et al.* 1999; Miller *et al.* 2001) but there is no one distance or ratio of distance that signifies nest site fidelity, within or across species. When comparing nest site fidelity across species or taxa, the coefficient of variation (i.e. distance between nests in relation to available area) is a more effective way of assessing nest site fidelity. Available nesting areas for small animal species, such as ants and spiders, may be far smaller than the area or distance used by birds and sea turtles which are “free ranging”, larger species, but they may be equally specific, and discriminatory within that smaller area as to the placement of nests or eggs. Migratory species, such as birds or turtles, travelling several hundreds of kilometres at a time may have no difficulty travelling many kilometres between nest sites (Hughes 1989; Georges *et al.* 2007; Witt *et al.* 2008). However, on the scale of used area to available area it may be equally specific to smaller species.

Defining nest site fidelity even within a taxon is complicated. In the case of sea turtles, one of the complications at hand is beach length as this defines the length of a rookery. Nesting rookeries can be defined as stretches of beach with similar beach characteristics and separated from other such areas by a cessation of turtle nests or a major obstacle separating the areas. Complications of beach length and nest site fidelity can be typified by island versus mainland rookeries. Island rookeries may be smaller than mainland rookeries and therefore if a female returns faithfully to a beach 2 km in size where nesting occurs over the whole 2 km stretch compared to the same situation on a 200 km rookery, could she be said to show higher fidelity? It has to be taken into account that both sea turtles nesting on island and mainland rookeries show homing behaviour to their respective rookeries, however one has the ability to show higher selectivity compared to the other. Therefore the definition of nest site fidelity in this thesis is the choice to restrict nesting to a specific area within the available area. Examples of sea turtle nesting can be used to validate the definition such as loggerheads nesting in North Carolina that tend to space their nests by 4.8 km on a 16 km rookery (Webster & Cook 2001). Green turtles have been documented to display spatial intervals of between 0.4 km and 1.2 km on a 35 km beach in Tortuguero (Carr & Carr 1972). Therefore, beach or rookery length in terms of sea turtle nesting behaviour implies an important consequence for nest site fidelity because of the difference in available nesting sites associated with short and long rookeries. Further complications include rookeries that span over two countries such as South Africa and Mozambique (Baldwin *et al.* 2003) that are artificially separated by national borders. From a sea turtle perspective, national borders are meaningless. National borders should not affect sea turtle nesting in any way and sea turtles may even affect decisions in the establishment of transboundary parks (Georges *et al.* 2007).

The purpose of nest site fidelity in sea turtle ecology is relatively unclear. A possible suggestion is to maintain genetic perpetuity in nesting populations. However, due to the lack of maternal care in sea turtles (McAllister *et al.* 1965; Hendrickson 1980), they are forced to maximize every effort of the nesting process by primarily selecting a stretch of beach that is favourable for the development and hatching of turtles. The only possible way that a female turtle would know if a stretch of beach was favourable or not, was if she successfully incubated and hatched from that very beach. Much genetic evidence exists for female turtles returning faithfully to their natal beaches as well as a study where marginal scales were notched (Hughes 1989; Bowen *et al.* 1989; Bowen *et al.* 1992; Bowen *et al.* 1993; Bass *et al.* 1996; Baldwin *et al.*

2003; Lee *et al.* 2007). Possible explanations as to how or why sea turtles find and recognize their specific rookery and favourable nesting sites include ideas on nesting success versus learned behaviour. The first theory is called “precise natal philopatry” where population-specific genetic programming or imprinting of hatchlings is responsible for natal homing (Bowen *et al.* 1993; Lee *et al.* 2007). The most obvious example is that the females are success stories themselves as they originated from the beaches (Mitrus 2006) and therefore have imprinted or have been the genetically programmed for a particular beach and hence natal homing. The second theory is called “social facilitation” where first time inexperienced nesters follow experienced nesters from the feeding grounds to the nesting beaches and then imprint on the rookery for future nesting (Bowen *et al.* 1993; Dutton *et al.* 1999). Different cues may be sensed by the females to inform them of the specific stretch of beach where they nest once they have reached the rookery. An example of this type of cue would be olfactory cues (Carr & Carr 1972; Hughes 1989). The olfactory cues may be chemical or biological in origin derived from either minerals transported in the water or a pheromone derived from successful nests (Hughes 1989). A possibility is that the pheromone that is detected results from the metabolites derived from developing embryos or the mucus that is deposited with the clutches of eggs and after several centuries of nesting, the beaches may be impregnated with the pheromone (Hughes 1989).

The placement of nests by a female in relation to her other nests is important as there may be advantages and disadvantages associated with differing degrees of nest site fidelity (Carr & Carr 1972; Eckert *et al.* 1989). Animals that show high nest site fidelity may be a result of having knowledge of the area itself and in particular the adjoining foraging areas and predator refuges (Shields 1984; Ryabitsev & Alekseeva 1998). Animals such as some sea turtles species showing high fidelity to an area may gain an advantage over those showing lower fidelity in terms of time and energy spent on searching for suitable nest sites and mates if reproductive aggregations are associated with the species in question (Carr & Carr 1972; Pandav *et al.* 2000).

The converse is that high nest site fidelity may pose a problem in areas that are prone to changing conditions or are unstable (Eckert *et al.* 1989; Ryabitsev & Alekseeva 1998). In this case, species that show low nest site fidelity are able to adapt and seek out new nesting sites (Ryabitsev & Alekseeva 1998) and possibly colonize new nesting areas (Hays & Sutherland 1991). There is virtually no way to track this in sea turtles, especially on a long stretch of beach such as South Africa. Therefore nest site fidelity studies need to be conducted within, between and across seasons.

The sea turtle nesting area in South Africa is to some extent unique. There is 200 km of almost continuous beach available for nesting to loggerheads and leatherbacks, which extends into Mozambique for about another 100 km (Hughes 1996). Within the 56 km turtle monitoring area, Nel (2008) indicated an uneven distribution of loggerhead and leatherback nesting. The majority of loggerheads tend to concentrate nest (~62 % of all nests per season north of Botelier Point, 0N) while the remaining ~38 % of loggerheads nests are dispersed in a comparatively even manner along the remaining section of the monitoring area (Nel 2008). In comparison, the population of leatherbacks spread their nests in a relatively even manner with ~36 % of all nests north of Botelier Point (0N) and the remaining ~64 % of nests south of this point (Nel 2008). The question remains as to how specific individuals of both species are to these areas. Nest site fidelity can determine the extent of the unevenness of nesting of the two species of turtles in South Africa.

The purpose of this study was thus to determine if the distribution of loggerhead and leatherback nesting over the past 40 years of turtle monitoring is even or uneven. Furthermore, if it is uneven: 1) establish if nest site fidelity, measured in kilometres and defined as the distance used by individuals within a season (as opposed to the area available), exists in loggerheads and leatherbacks nesting in South Africa, 2) to determine if nest site fidelity patterns are consistent between seasons and 3) determine if the same nesting areas are preferred from season to season over the past 45 years, including high density and low density years (across season fidelity).

MATERIALS AND METHODS

The data used for this section of the study was the long-term turtle monitoring database housed at Ezemvelo KZN Wildlife. This is turtle monitoring data at “low resolution”, meaning a maximum accuracy of 400 m, with nests scored to a beacon number, 400 m apart. The monitoring programme and protocol is described in detail in Chapter 2. All statistical analyses were done using Statistica version 8 (2009).

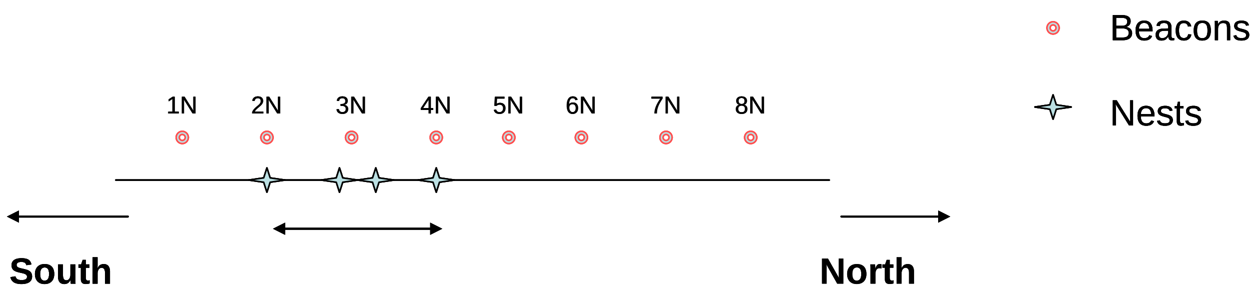
Evenness of nesting

Potential hotspots were identified by comparing the number of nests per beacon per season. This also made it possible to see if any large-scale changes in nesting over time had occurred. This was done for each species. A chi-square analysis was run to see if the nesting distribution was equal along the beach and if not, what the hotspot areas were.

Within-season nest site fidelity

Within-season nest site fidelity analyses only made use of tagged individuals that were recorded to have nested more than once in a particular season. The distance over which a female laid all her clutches per season was calculated as the distance between the “outer” beacons – i.e. furthest north and south. Once the nesting distance was calculated it was divided by the number of times a female nested within the area (Fig. 3.1.). This was used as an index of nest site fidelity for each individual per species within a season.

A Pearson-product moment correlation was used to detect if the within-season nest site fidelity was dependent on the number of individuals analysed per season. One-way ANOVAs were used to establish if there were any changes in nest site fidelity (measured in kilometres) over time by using seasons as the grouping variable and nest site fidelities as the dependent variables. Only seasons where all beacons from 32N to 100S were monitored were used for analyses to ensure consistency (thus only seasons after 1972/73). If any significant results were obtained through one-way ANOVAs, a post-hoc Tukey HSD test was conducted to determine which of the seasons were significantly different.



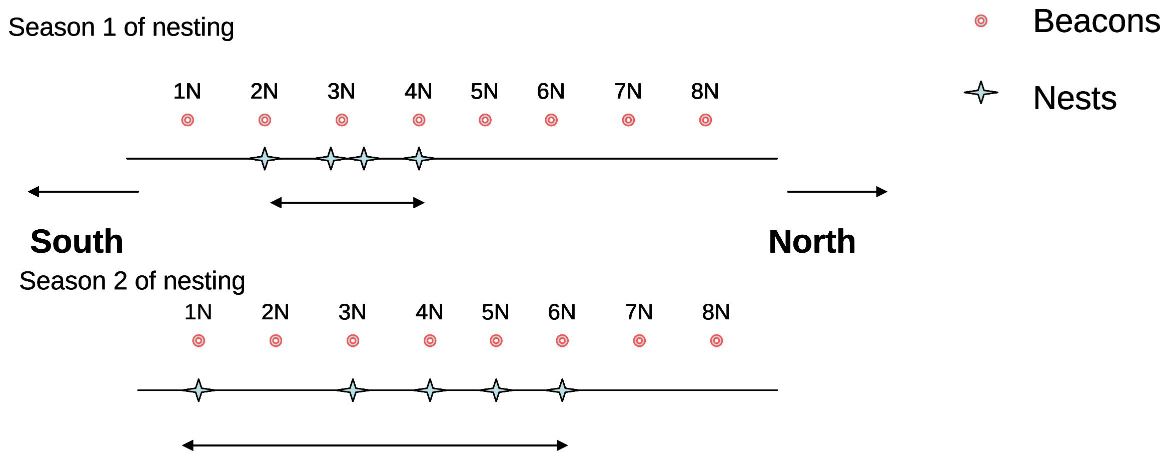
Nesting at beacons 2N to 4N
∴ 2 beacons x 0.4 km
= 0.8 km / 4 nests
= 0.2 km nest site fidelity

Fig. 3.1. An example of within-season nest site fidelity for an individual turtle within the study area with beacons and arbitrary data shown.

Between-season nest site fidelity

Between-season nest site fidelity was determined by identifying all the females that nested for two or more seasons. Within-season nest site fidelity for each female per season was calculated (as previously) and then averaged over the number of seasons that a female nested (Fig. 3.2). Nest site fidelity per individual for the second, third, fourth and fifth seasons of nesting was also compared.

One-way ANOVAs were used to determine if any significant differences existed between nest site fidelity and number of seasons an individual nested. The season number (one, two, three, four or five) was used as the grouping variable, whereas the within-season nest site fidelity per individual was used as the dependent variable. If any significant results were obtained a post-hoc Tukey HSD test was conducted to determine which seasons were significantly different.

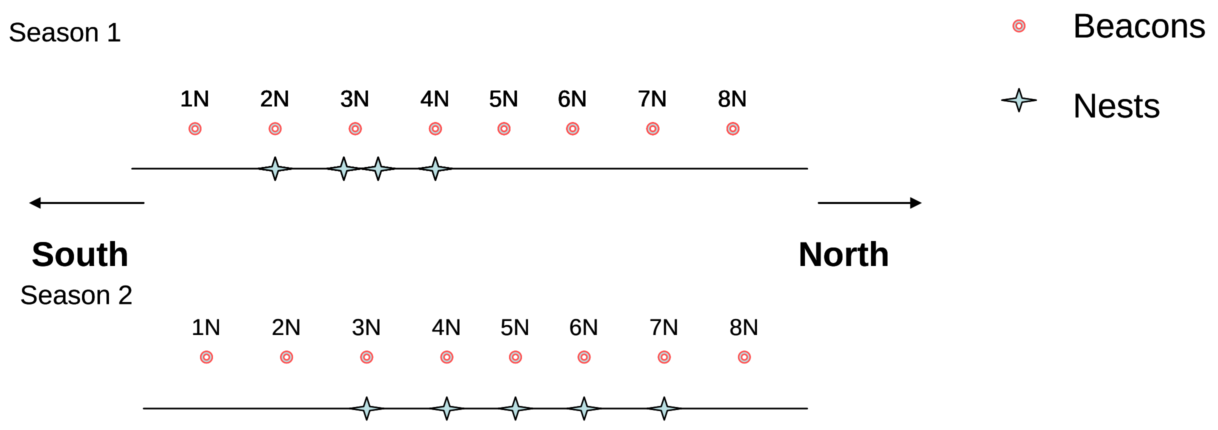


Within-season nest site fidelity: season 1 = 0.2 km
Within-season nest site fidelity: season 2 = 0.4 km
∴ 0.2 km + 0.4 km = 0.6 km
∴ 0.6 km / 2 seasons = 0.3 km between season nest site fidelity

Fig. 3.2. An example of between-season nest site fidelity for an individual turtle within the study area with beacons and arbitrary data shown.

Across-season nest site fidelity

Across-season nest site fidelity was evaluated by combining the results obtained from within and between-season comparisons and evaluating the consistency of these results. This was done by assigning maximum and minimum beacon numbers to nests placed by individual females across all seasons (Fig. 3.3). The difference in beacon numbers was calculated within-season for females for each respective season of nesting and then multiplied by 0.4 km (beacon accuracy). Differences were averaged over the number of seasons where nesting occurred. Secondly, the range of nesting over all seasons was determined from the maximum (most southerly nest) to the minimum (most northerly nest), multiplied by 0.4 km and averaged over the number of seasons nested by an individual. If the same area was consistently used between seasons the within-season and across-season comparison should be similar. If different areas were used for nesting between seasons, the across-season differences would be greater (Fig. 3.3).



Season 1:
4 – 2 = 2 * 0.4 km
= 0.8 km
Season 2:
7 – 3 = 4 * 0.4 km
= 1.6 km

∴ 0.8 km + 1.6 km = 2.4 km / 2 nesting seasons
= 1.2 km

Across season nesting range (maximum – minimum):

∴ 7 – 2 = 5 * 0.4 km
= 2 km
□ 2 km / 2 nesting seasons
= 1 km

1 km < 1.2 km, ∴ Nest site fidelity is shown

Fig. 3.3. An example of across-season nest site fidelity for an individual turtle within the study area with beacons and arbitrary data shown.

Data analysis involved determining if across-season nest site fidelity exists for loggerheads and leatherbacks. This was done by comparing the average within-season range of distance (i.e. 0.8 km was used for four nesting events) versus the across-season range of distance using a paired-sample t-test. One-way ANOVAs were used to compare the average nesting range between individuals that nested for two, three, four and five seasons (in the case of loggerheads). For this analysis, season number was the grouping variable while the average nesting range, across-season nest site fidelity, was the dependent variable.

High-resolution data

Data were collected over two nesting seasons (December 2007 and 2008) over a 5 km area to assess if nest site fidelity existed at a resolution finer than 400 m as this is a restriction imposed by the long-term data set. This higher resolution data were obtained by using GPS coordinates (accuracy ± 5 m) for each nest. This data were used to determine how turtles, specifically loggerheads, spread their nests along the beacons.

RESULTS

Evenness of nesting

Loggerhead nesting along the rookery was uneven ($X^2_{0.05,\ 32} = 48119.37$, $p < 0.01$) with females preferring the area north of beacon 16S (Fig. 3.4.). Immediately either side of beacon 0N was preferred among loggerheads with nests in these areas totalling more than 800 over the duration of constant monitoring effort (season 1973/74 onwards). The highest concentration of loggerhead nests was between beacons 4N to 15N where 11335 nests have been placed since 1973/74. The most popular cluster of beacons was 8N to 11N where in excess of 4000 nests have been laid by loggerheads. Towards the south of the monitoring area, loggerhead nesting decreased with fewer nests situated per beacon compared to the areas north of Bhanga Nek (0N).

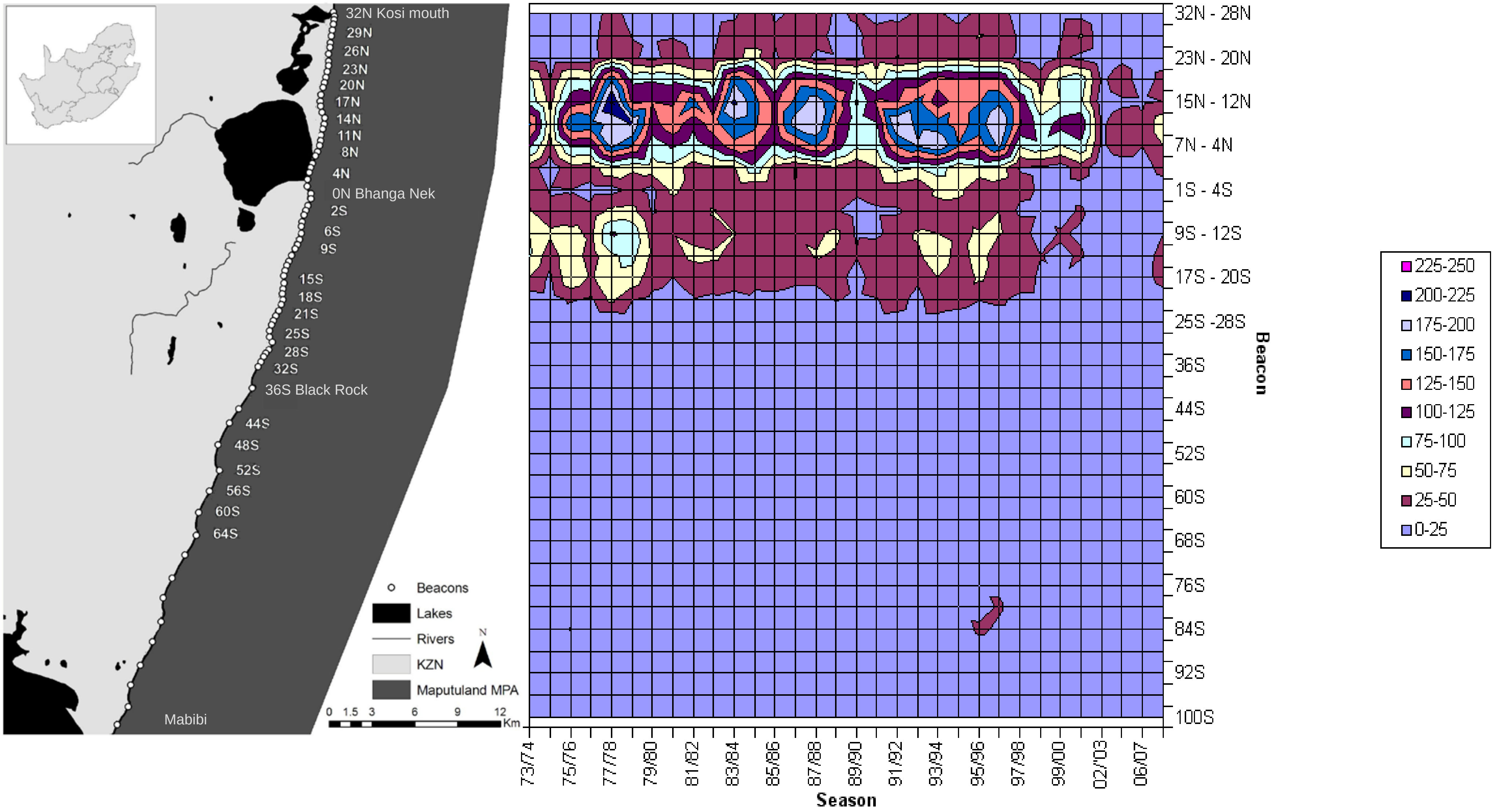


Fig. 3.4. Relative nesting intensity of loggerheads across time (1973/74 to 2007/08) and space (56 km monitored).

The lowest densities of loggerheads nests occurred from beacon 32S to 52S with fewer than 100 nests placed per beacon over the duration of consistent monitoring effort.

Leatherback nesting intensity appeared to be more evenly distributed than the distribution of nesting events for loggerheads (Fig. 3.5.). Leatherback nesting intensity was uneven in the monitoring area ($X^2_{0.05,\ 32} = 3362.5$, $p < 0.01$) with the most preferred leatherback nesting areas around beacons 72S and 92S where 724 and 753 leatherbacks have nested since the 1973/74 season respectively. In the 1995/96 season, a total of 65 leatherback nests were placed at 92S alone. The beacons with the lowest leatherback nesting intensity were 20N to 23N and 5S to 8S where totals of only 77 and 76 nests have been recorded since 1973/74.

It is thus clear that neither leatherback nor loggerhead nests are placed evenly along the 56 km monitoring area. Loggerheads have one particular preferred area, north of Botelier Point (or Bhanga Nek 0N), whereas leatherbacks use approximately four different areas consistently throughout the monitoring area. The question is thus to see if the animals are specific to one area, or bay, (i.e. display nest site fidelity) or if they move between these areas.

Nesting patterns between December 2007 and December 2008 were similar in terms of areas being utilized for nesting by loggerheads and leatherbacks from beacon 0N to 12N (Fig. 3.6.). In December 2007, the most preferred nesting area for loggerheads was beacon 7N with 22 % of all nests placed there. No nests were laid at beacon 0N in December 2007 while beacons 1N to 3N had the lowest percentage of nests (1.37 % per beacon). Nesting across beacons for loggerheads in December 2007 was uneven ($X^2_{0.05,\ 11} = 59.88$, $p < 0.01$). In December 2008, beacon 6N was the most preferred beacon for loggerhead nesting with 13.7 % of nests laid at this beacon followed by beacons 7N and 8N that received 11.87 % of nesting each. Lowest number of nests were observed at 0N (1.37 %) and 4N (3.19 %) respectively. Nesting across beacons 0N to 12N was also uneven in December 2008,

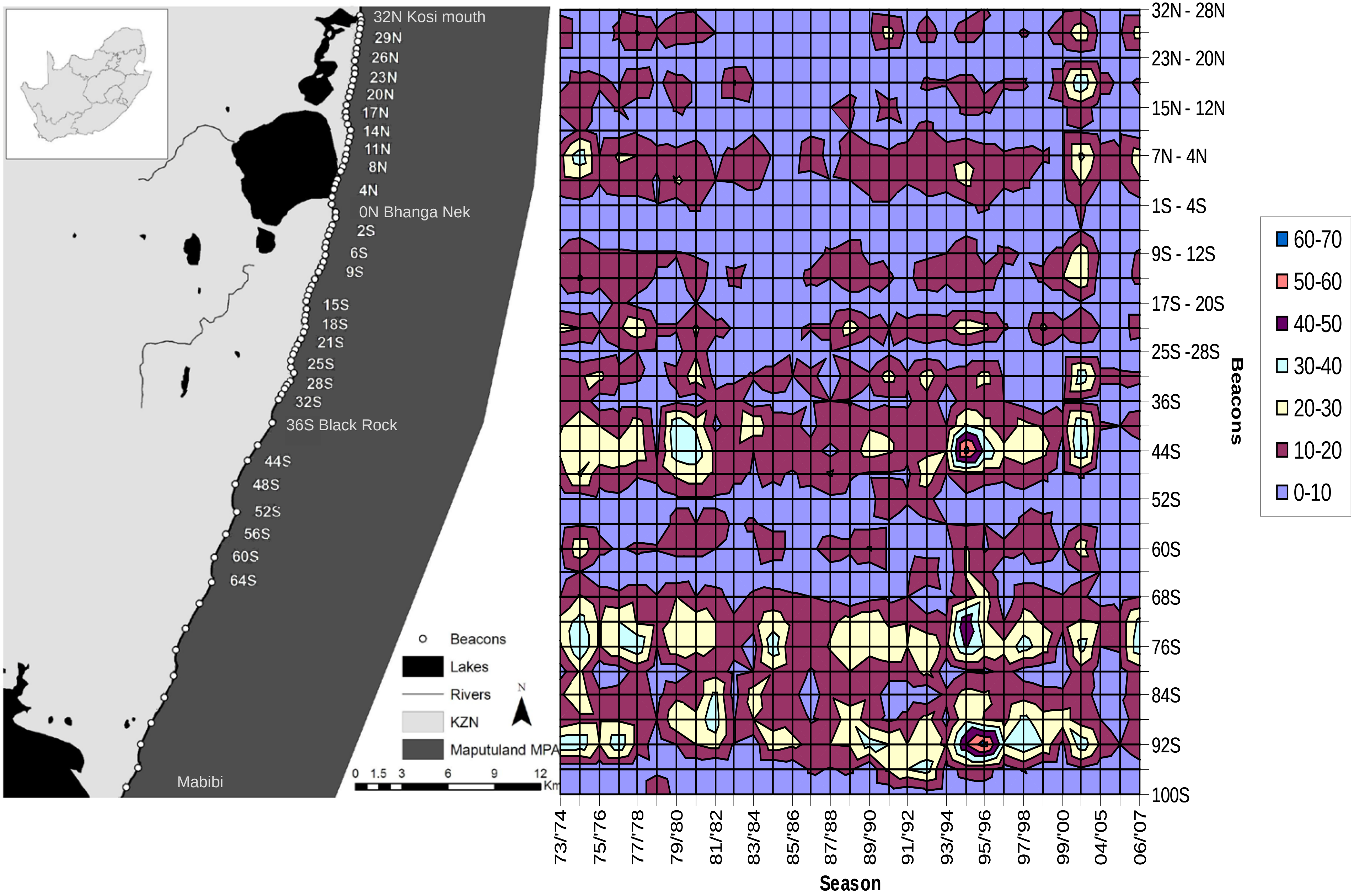


Fig. 3.5. Relative nesting intensity of leatherbacks across time (1973/74 to 2007/08) and space (56 km monitored).

($X^2_{0.05, 11} = 28.26$, $p = 0.005$). Leatherback nesting in December 2007 was divided between two beacons; beacon 4N which received 75 % of nesting whereas 11N received 25 %. Nesting was therefore uneven across all beacons, ($X^2_{0.05, 11} = 658.33$, $p < 0.01$) as well as across beacons where leatherback nesting occurred within the season ($X^2_{0.05, 11} = 25$, $p < 0.01$). Leatherback nesting in December 2008 occurred over beacons 2N, 3N and 11N. Beacon 11N was the only common beacon between the two seasons. Nesting across beacons 0N to 12N was uneven as only three beacons were used ($X^2_{0.05, 11} = 308.\ 33$, $p < 0.01$) however, nesting across the three beacons in December 2008 was even, $X^2_{0.05, 11} = 0.000$, $p = 1.00$).

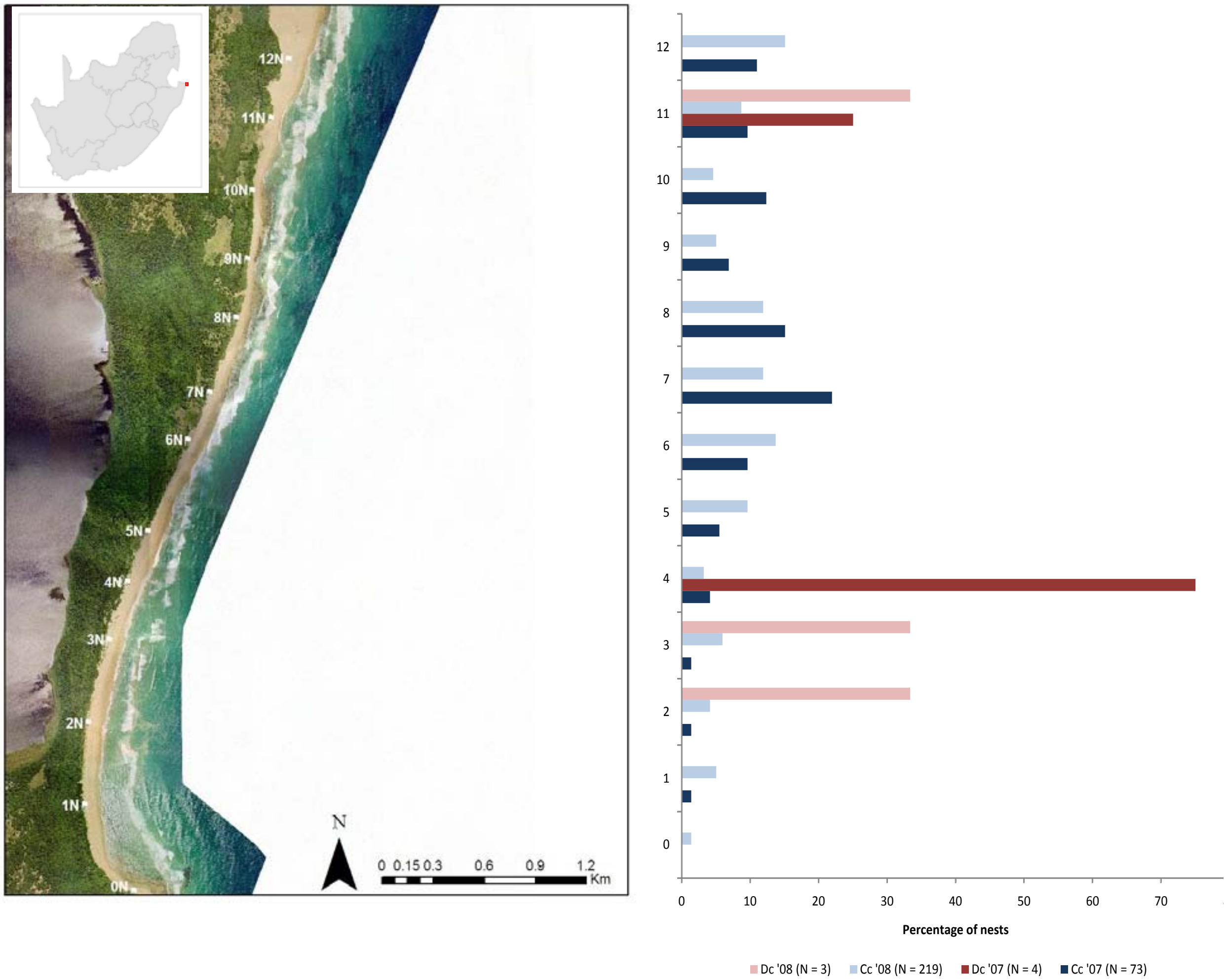


Fig 3.6. Loggerhead (Cc) and leatherback (Dc) nest distribution (%) between beacons 0N and 12N for two weeks in December 2007 and again in 2008.

Within-season nest site fidelity

The average nest site fidelity measure for loggerheads over the entire time period of monitoring was 3.51 ± 0.09 km (n = 4100, mean ± standard error). The range of nest site fidelity was 0 km to 49.6 km, indicating that there are individuals that are able to move substantial distances between nest sites, however the proportion of individuals doing so was very small. A very small fraction, 0.44 % (n = 18), of loggerheads nested more than 40 km from previous nest sites. The proportion of loggerheads nesting more than 5 km from a previous nest was also small with only 19.39 % (n = 795) of the population doing so. Nest site fidelity was independent of the number of individuals tested per season, (r = -0.21, p = 0.23) and similar from one season to the next. Slight increases and decreases in nest site fidelity were evident from season to season but not significantly so ($F_{0.05\ (1),\ 32,\ 4068}$ = 1.15, p = 0.26).

In South Africa, leatherbacks showed lower nest site fidelity compared to loggerheads over the study period. The average nest site fidelity of leatherbacks in South Africa was 9.71 ± 0.29 km (n =953) and there was no correlation between the number of leatherbacks that nested two or more times per season and nest site fidelity (r = 0.01, p = 0.96). The furthest that two nests were placed apart by one individual leatherback was 46.4 km, however the proportion of leatherbacks placing nests more than 40 km apart was also small (1.15 %, n = 11). The highest number of individuals, 64.64 % (n = 616) placed their nests within 10 km of one another. There were no statistical differences for leatherbacks between nest site fidelity and the different seasons of monitoring ($F_{0.05\ (1),\ 32,\ 921}$ = 1.29, p = 0.14).

Between-season nest site fidelity

Between-season nest site fidelity investigated whether the same animal used smaller sized areas across different seasons of nesting and not the same area across seasons. The lowest nest site fidelity was shown by loggerheads that were reported to nest for only one season. This was a mean distance of 3.69 ± 0.1 km (n = 3177, mean ± standard error) between nesting events (Fig. 3.7.). Loggerhead females that nested for more than one season showed higher nest site fidelity with the highest nest site fidelity shown by females that nested for five seasons, 1.12 ± 0.17 km (Fig. 3.7.). There was a significant difference (p = 0.02) between the nest site fidelity of loggerheads that nested for only one season compared to two or more seasons ($F_{0.05\,(1),\ 4,\ 3697}$ = 4.67, p = 0.001). It is apparent that loggerheads improve nest site fidelity in subsequent seasons of nesting (Fig. 3.7.).

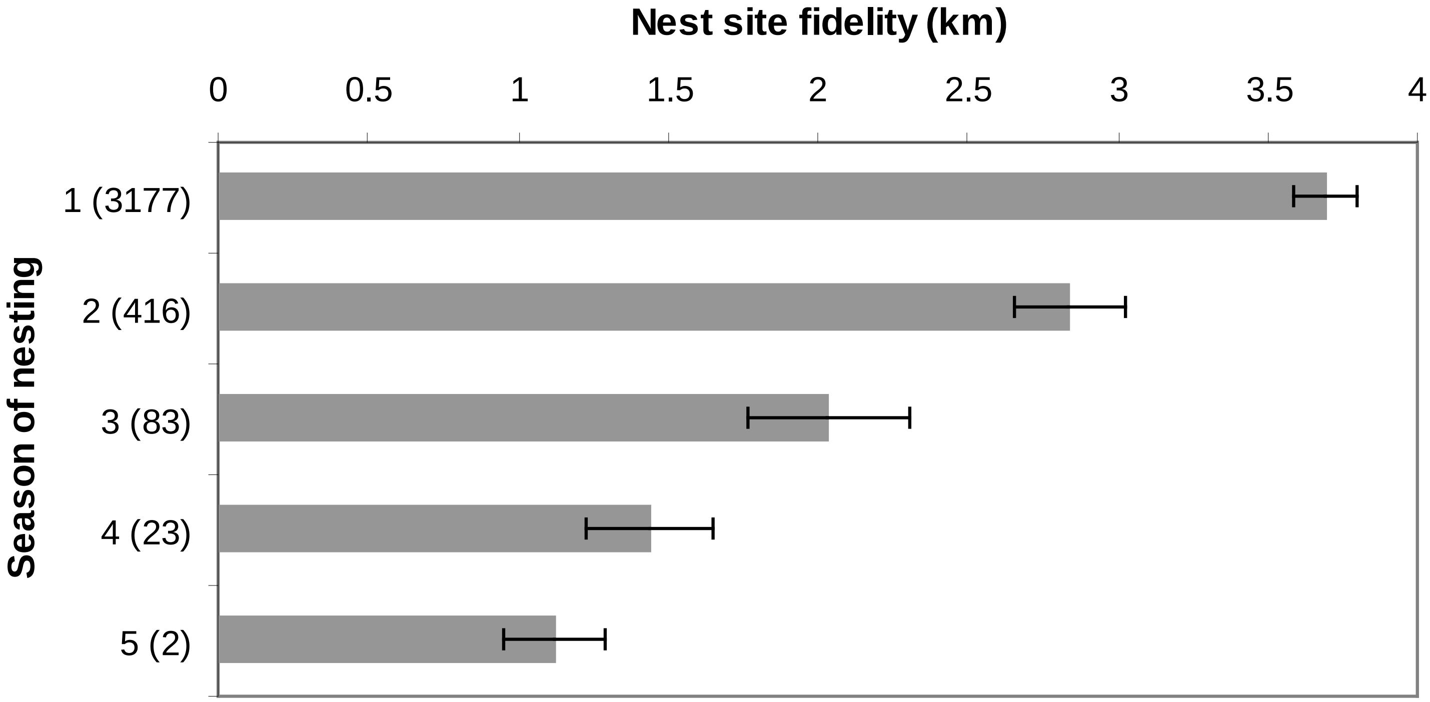


Fig. 3.7. Nest site fidelity (mean ± S.E.) of loggerheads that nested for multiple seasons. The number of animals used (n) are in parentheses after the number of seasons nested.

Unlike loggerheads (Fig. 3.7.), leatherbacks do not improve nest site fidelity in subsequent seasons of nesting (Fig. 3.8.). The nest site fidelity of leatherbacks that nested over multiple seasons are all similar and range between 9.51 ± 0.34 km (one season nesters) and

9.79 ± 0.94 km (for three season nesters). The highest nest site fidelity was shown by leatherback females that nested for four seasons, 6.61 ± 1.86 km (Fig. 3.8.) however, this was not significantly higher than nest site fidelity shown by leatherbacks that nested for one, two or three seasons and has fairly low replication, with high variability ($F_{0.05\ (1),\ 3,\ 834}$ = 0.26, p = 0.86).

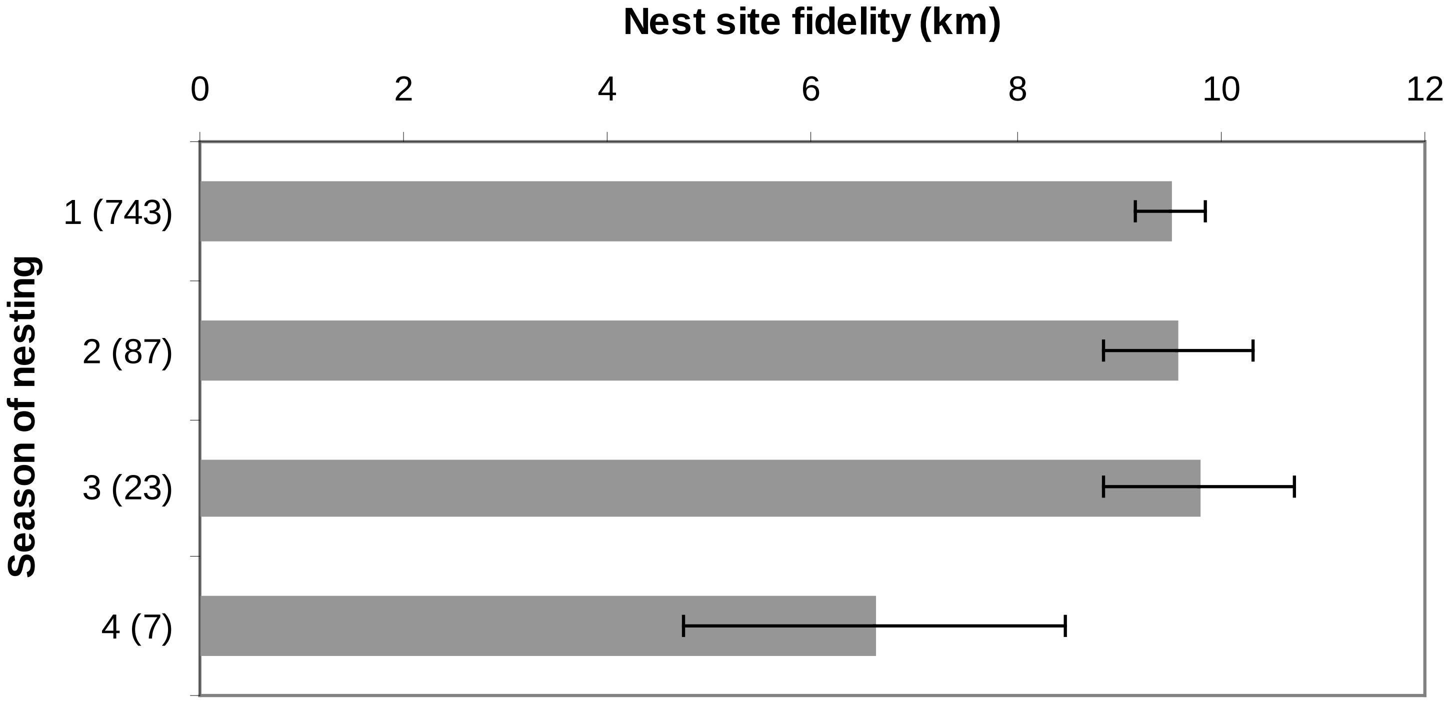


Fig. 3.8. Nest site fidelity (mean ± S.E.) of leatherbacks that nested for multiple seasons. The number of animals used (n) are in parentheses after the number of seasons nested.

Across-season nest site fidelity

Across-season nest site fidelity compares overlap in areas used between nesting seasons. Loggerhead across-season nest site fidelity or areas used were similar or smaller than those used within seasons (Fig. 3.9.), indicating overlap in areas used among seasons, ($t_{0.05\ (2),\ 524}$ = 4.11, p = 0.0001). Therefore, across-seasons loggerheads are able to successfully return to areas that they utilized in previous seasons for nesting, and are able to decrease the area significantly ($F_{0.05\ (1),\ 3,\ 520}$ = 6.54, p = 0.000) between the second and third (p = 0.002) and the second and fourth seasons (p = 0.002) of nesting. The most popular stretch of beach used by loggerheads for nesting across seasons was 4N to 11N (2.8 km).

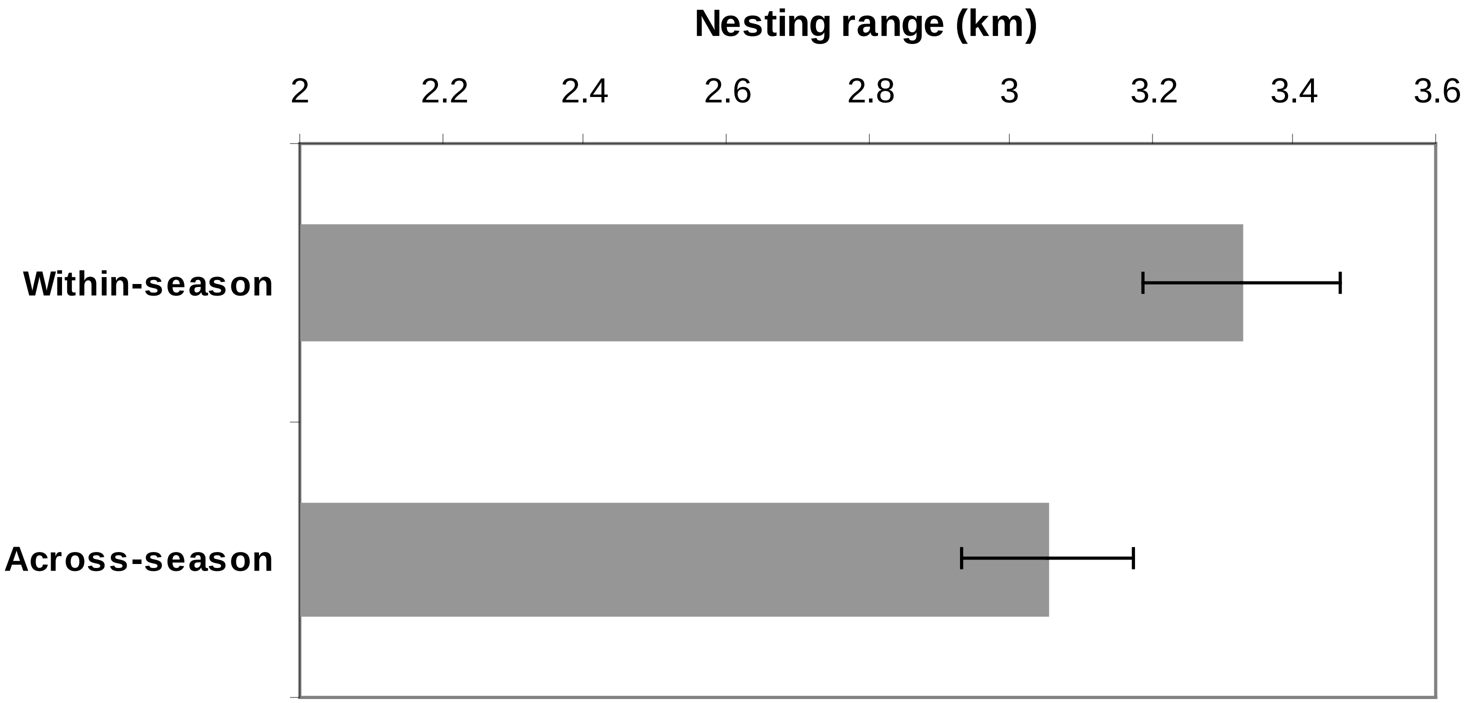


Fig. 3.9. The average nesting range (in kilometres) of loggerheads within-season and across-seasons.

Across-seasons, leatherbacks become more specific in the area used (Fig. 3.10.) if they nest over multiple seasons with a significant increase in nest site fidelity after one season ($t_{0.05\ (2),\ 117}$ = 3.99, p = 0.0001) but not subsequent seasons ($F_{0.05\ (1),\ 2,\ 117}$ = 1.5, p = 0.23). The area used by leatherbacks is somewhat larger than the area used by loggerheads and is located approximately 5.6 km from the loggerhead high-density area. The area most frequented by leatherback nesting events according to across season analyses is beacon 10S to 44S (13.6 km).

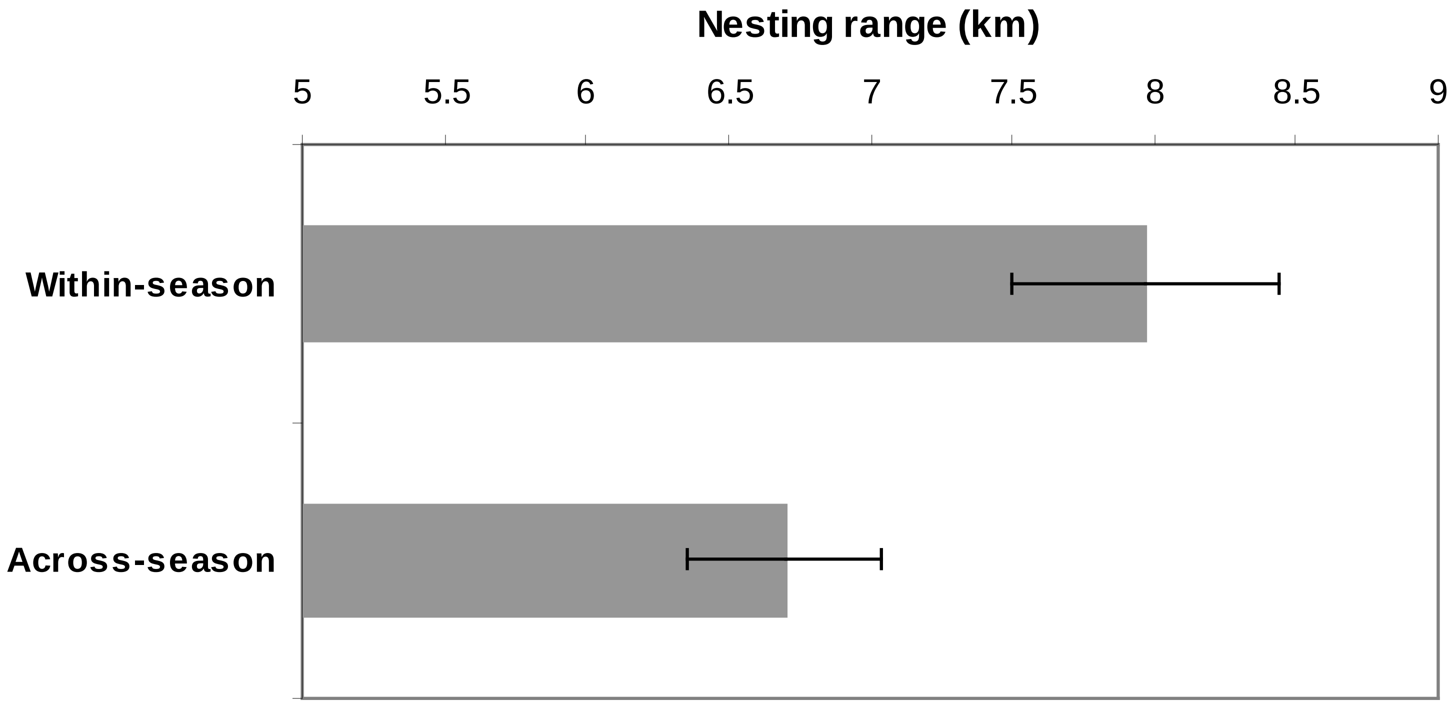


Fig. 3.10. The average nesting range (in kilometres) of leatherbacks within-season and across-seasons.
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High-resolution data

No same individuals were observed nesting within the loggerhead high-density area (0N to 12N) during the two-week study period therefore it is impossible to assign nest site fidelity of individuals to any distance smaller than 0.4 km (the distance beacons are placed apart in the loggerhead high-density area). The GPS data (high-resolution data) however can represent the spatial distribution of loggerhead and in some cases leatherback nests (Fig. 3.11.). From beacons 0N to 2N, loggerhead nests are evenly distributed across the beacons with the first sign of clumping at beacon 3N, thereafter, nests are evenly distributed until beacon 9N. Between beacons 9N and 10N, loggerhead nests are sparsely distributed, with the lowest concentration of nests placed between these beacons. Nests are in high concentration beyond beacon 10N and evenly spread along the beach length. The placement of leatherback nests in this area is sparse (n = 4) and therefore patterns of nest placement cannot be inferred. Loggerheads have no preference for certain areas within beacons and appear to spread nests evenly throughout the high-density area. Therefore, nest site fidelity analyses cannot be faulted as there are no preferred hotspots of nesting within the high-density area.

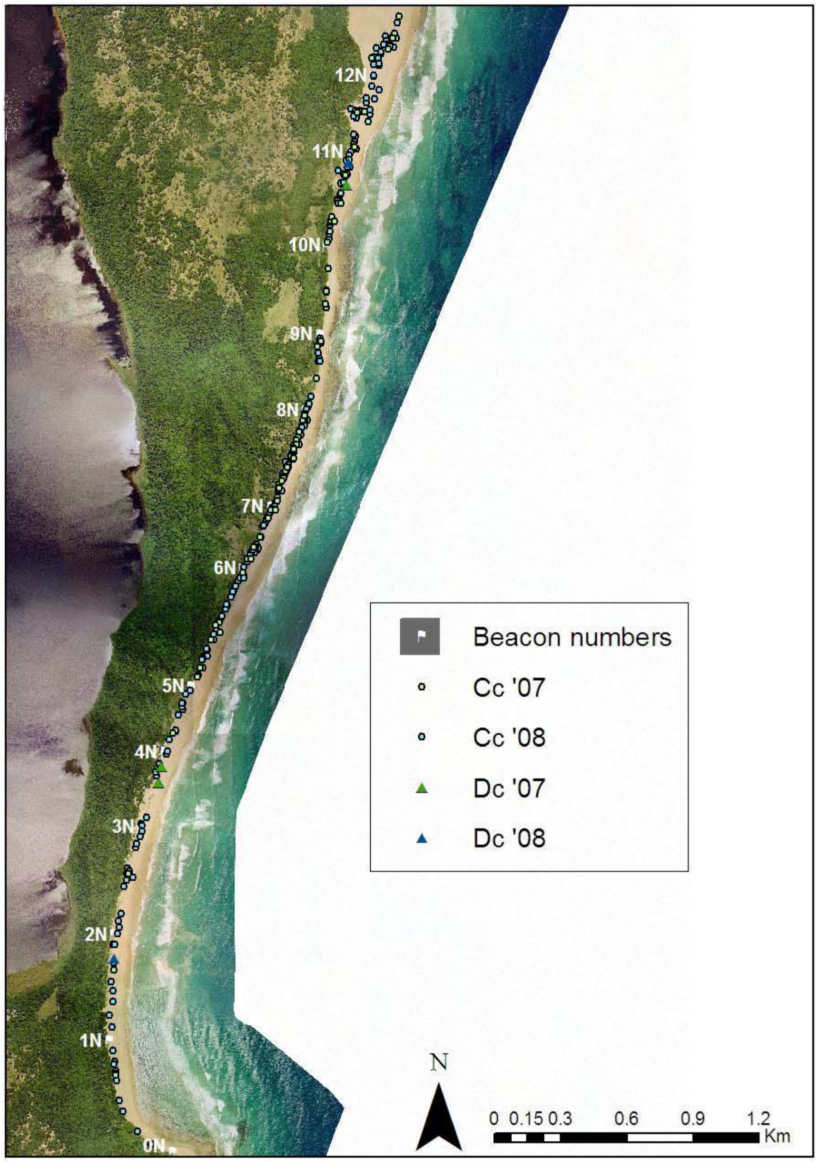

Fig. 3.11. Distribution of loggerhead (Cc) and leatherback (Dc) nests for 2 weeks in December 2007 and 2008. Nest co-ordinates are accurate to ~5 m.

DISCUSSION

Loggerhead and leatherback nest distribution along the length of the monitoring area was uneven with areas of highest nest concentrations for both species being different. The highest concentration of loggerhead nesting occurred from beacon 4N to 16N (Fig. 3.4.). The area from 0N to 32N provided an important region for loggerheads as approximately 60 % of all loggerhead nests were laid in this area with a more or less even spread of the other 40 % of nests across the balance of the monitoring area (Nel 2008; Nel 2009). The position of the Kosi Lake system seems to play an important role in the attracting loggerheads to the beaches in the northern sector of the monitoring area, although the mechanism is not known (Hughes 1989). Hughes (1989) suggested that the freshwater of the lakes possibly causes mineral transport from the groundwater outflow and this may act as a cue attracting male and female turtles. Male loggerheads that previously hatched from the high-density loggerhead area may follow the same cues as the females and once there may show fidelity to a mating area such as that demonstrated by olive ridley sea turtles (Pandav *et al.* 2000). Males may therefore stay in areas where they know females would be drawn to, therefore enhancing their chances of mating.

Leatherbacks display different nest distribution to loggerheads. Instead of concentrating nests in a specific area (i.e. the northern sector of the monitoring area) as loggerheads do, leatherbacks spread their nests more or less evenly along the beach with some preference to four bays (Fig. 3.5.). No statements on leatherback nesting outside of the 56 km monitoring area can be made. The index area (0N to 32N) presents nesting sites for approximately 30 % of leatherback nests while the other 70 % of leatherback nests are spread throughout the remainder of the monitoring area (Nel 2008; Nel 2009). Leatherback nesting is highest around beacons 72S and 92S. Unlike the loggerheads that seem to use chemical cues to locate their nesting areas, leatherbacks seem to use deep water access to the beach and areas that are free of major reef systems as cues (Eckert 1987; Hughes 1989; Mortimer 1995). Therefore, leatherbacks may select areas based on practicality to manoeuvre their large bodies instead of chemoreception. This may be problematic for male leatherbacks seeking females to copulate with as there are no cues for the males to follow to locate females adjacent to the nesting beaches. In time, the situation faced by leatherbacks may lead to the allee effect where a population at low densities is subjected to low recruitment and high mortality and therefore results in a slow or non existent rate of recovery of the species (Courchamp *et al.* 1999).

Within the high-density loggerhead nesting area as highlighted by the uneven spread of nests (Fig. 3.4.) the percentage nest distribution is evenly distributed with loggerheads utilizing beacons to a similar extent between the consecutive seasons (Fig. 3.6.). In 2007, beacons 7N and 8N were the most preferred beacons for nesting activity of loggerheads while in 2008, along with the before mentioned beacons, beacon 6N was also among the beacons receiving the highest amount of nesting. In both years nesting at beacon 0N was the lowest by loggerheads. These results are in agreement with those by Hughes (1989) that loggerheads have high-density nesting beacons within the high-density nesting area (0N to 12N). Nesting of leatherbacks between beacons 0N to 12N during December 2007 and 2008 was uncommon. The placement of the nests was constant at beacon 11N between the two consecutive seasons and beacons 2N and 4N also received leatherback nesting. From the results of the leatherbacks, very little can be deduced.

Once female turtles home to their natal beaches, they are presented with two challenges; to find a mate and to repeatedly find a suitable stretch of beach to nest. Both male and female sea turtles undertake extensive migrations back to their nesting grounds from foraging areas (Hughes 1989; Miller *et al.* 2001). Copulation then takes place at sea, with males showing fidelity to courtship areas from one season to the next (Pandav *et al.* 2000; Miller *et al.* 2001;

Tripathy & Pandav 2007). Once mated, females need to select suitable areas for nesting that will not endanger them, and will ensure successful hatching of their eggs. In South Africa, the loggerhead population shows nest site fidelity of ~3 km with no significant change in this distance from one season to the next. Other studies have confirmed the existence of high nest site fidelity by loggerheads (Miller *et al.* 2001; Webster & Cook 2001; Xavier *et al.* 2006). However, direct comparisons between various loggerhead populations present a challenge as not all rookeries are the same length. South Africa presents a fairly unique situation of 200 km of uninterrupted, fairly uniform beach available for nesting. Therefore bearing this in mind, for loggerheads to place nests at a distance of ~3 km shows high nest site fidelity.

Much the same as loggerheads, the leatherback population in South Africa is presented with the same beach length of 200 km to nest and yet are able to maintain nest site fidelity of ~9 km within the monitored area from season to season. Leatherbacks show lower nest site fidelity than loggerheads in South Africa but for animals that have been said to show low nest site fidelity, if any at all (Hughes 1989; Nordmoe *et al.* 2004), 9 km seems high. Hughes (1989) found that leatherbacks are able to nest up to 40 km from a previous nest site. The same result was also found by the current study although the proportion of animals doing so is very small compared to those nesting less than 10 km from previous nest sites. Eckert (1987) showed that leatherbacks in the U.S. Virgin Islands show high nest site fidelity by placing nests an average of approximately 0.6 km from the first nest of the season. The difference between the South African rookery and the rookery in the U.S. Virgin Islands is 197.6 km as the island rookery is only 2.4 km in length (Eckert 1987). Thus ~9 km over a 200 km stretch of beach versus 0.6 km over a 2.4 km stretch of beach.

Among bird species, differences in nest site fidelity patterns also arise (Ryabitsev & Alekseeva 1998) as they do for the turtle species in South Africa. Some bird species are termed conservative, showing high nest site fidelity, as for loggerheads (Ryabitsev & Alekseeva 1998) whereas, some bird species showed low nest site fidelity as for leatherbacks and were thus more opportunistic in finding nest sites (Ryabitsev & Alekseeva 1998). Stable environments and having knowledge of the area (such as predation risk) promote high nest site fidelity particularly in birds (Jenkins 1993; Gonzales-Solis *et al.* 1999). This may also be the case in loggerhead turtles in South Africa. Animals have the ability to visually recognise areas and therefore orientate themselves according to olfactory and visual cues that they encounter (Hoefler & Jakob 2006). Turtles may use landmarks (olfactory cues), guiding cues such as chemicals for example, to guide them to rookeries and thereafter make use of beacons (visual cues) which may be the features of the coastline that they visually recognise (Hoefler & Jakob 2006). In doing so, sea turtles would have the ability to "learn" which areas are favourable for nesting especially if previous nesting experiences were successful (i.e. she could mount the beach with ease, no predators or people disturbed her, she didn't have to crawl a long distance and the nest could be excavated with ease). The results from the between-season and across-season nest site fidelity demonstrated that loggerheads seem to 'learn' what stretches of beach to use for nesting in subsequent seasons of nesting along the beach (Fig. 3.7. and 3.9.). Similar results were observed on Bald Head Island where a female loggerhead returned to nest in the same area as she did in previous seasons (Webster & Cook 2001).

Leatherbacks do not show the same patterns of between-season and across-season nest site fidelity as the loggerheads. It appears that they don't "learn" where to nest in subsequent seasons of nesting (Fig. 3.8. and 3.9.). This may stem for the fact that leatherbacks show less nest site fidelity than loggerheads and that cues are not thought to be followed as in the loggerheads (Hughes 1974; Hughes 1989). Therefore leatherbacks may be using sites that seem practical in terms of deep water and reef-free approaches (Eckert 1987; Hughes 1989; Mortimer 1995). This may be a result of the larger size of leatherbacks which make them less vulnerable to terrestrial predators, as can be seen in the great nesting success that they have in terms of haul outs to nesting. Leatherbacks nest nine out of ten times when they emerge, whereas loggerheads only nest five out or ten times (Nel 2008).

The South African population of loggerheads and leatherbacks form excellent study species for nest site fidelity. Sea turtles are long-lived and therefore observing more than one season of nesting would be possible assuming incidental mortality rates were not high and therefore remigrations could occur in stable numbers. Knowing that the nest distribution of both species was uneven along the monitoring area, nest site fidelity studies of within, between and across seasons showed that the different populations showed fidelity to different areas and at different levels. Loggerheads have increased since the monitoring programme started with a 2.5 times increase in the number of nests per season whereas leatherbacks have shown little population growth since the start of the programme (Nel 2008). A possible explanation for this is that animals showing high nest site fidelity have a base for consistent population structure (Ryabitsev & Alekseeva 1998) as ~60 % of the loggerhead population nesting within the same area whereas leatherbacks scatter nests uniformly within and outside the monitoring area.

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CHAPTER 4

NEST SITE SELECTION OF LOGGERHEADS, *CARETTA CARETTA*, AND LEATHERBACKS, *DERMOCHELYS CORIACEA*, IN SOUTH AFRICA.

ABSTRACT

Nest site selection is the non-random placement of nests or eggs by a female. The placement of nests by sea turtles is critical as there is no parental care in sea turtles, and the only way to ensure continuation of a gene is by optimizing nest success (and so demonstrates fitness). Nest site selection of loggerheads and leatherbacks was tested at two levels in South Africa; firstly on a coarse-scale along the coast (56 km monitoring area) where effects of surf zone width, inshore rocks, beach morphodynamic type, slope, beach width and back-beach width were tested on nest site selection and secondly, a high-resolution analysis within a bay (5 km high-density loggerhead area) testing the effects of pH, mean grain size and the distance of the nest to the vegetation line and high water mark. Physical factors that affected nest site selection were inshore rocks and the beach morphodynamic state. Intermediate beaches (i.e. medium grain size and moderate slopes) were preferred by both loggerhead and leatherback turtles. Leatherbacks tended to come ashore on beaches with wider surf zones. No other factors investigated affected nest site selection of either species. In most instances, both species nested above the high water mark. A short coming of the study is the uniformity of the beach morphodynamic state along the area, and is thus difficult to demonstrate cause and effect. However, as there are clear hotspots in nesting it is concluded that these hotspots are not the result of beach characteristics.

INTRODUCTION

Once turtles have selected a stretch of beach to nest on, they need to select sites to haul out on and ultimately deposit a clutch of eggs on the beach (Miller *et al.* 2001). The selection of an oviposition site by a female involves a trade-off between the cost of searching for a suitable nesting site and the reproductive benefits of choosing a “successful” site (Wood & Bjorndal 2000). As there is no parental care in sea turtles, this is the only choice a mother can make to maximize the chances for her offspring. Furthermore, the fitness of the parents is then directly affected by the success of the nest site selected by the female as hatchlings are the future gene carriers of their parents (Resetarits 1996; Wood & Bjorndal 2000). Nest site selection can thus be defined as the non-random placement of eggs by an individual female turtle along a stretch of beach or area to maximize her chances of nesting and hence successfully produce offspring (Wilson 1998; Kamel & Mrosovsky 2005).

Many physical factors have been shown to influence, facilitate or dictate nest site selection in sea turtles. These factors include coastal geomorphology, bathymetry of the surf zone and dimensions of the beach (Stancyk & Ross 1978; Eckert 1987; Hays *et al.* 1995; Kikukawa *et al.* 1999; Garmestani *et al.* 2000; Miller *et al.* 2001; Mazaris *et al.* 2006). Coastal geomorphology includes features of the coastline such as the incidence of sheltered bays and rocky headlands. Closely linked to the coastal geomorphology is the bathymetry of the surf zone. Features in the surf zone include rocks, depth or slope and the width of the surf zone. Sea turtles, especially leatherbacks, seem to prefer approaches that are obstacle or rock free (Eckert 1987; Mortimer 1995). The absence of inshore rocks allows sea turtles to avoid impeding injury to the female coming ashore, especially at low tide, and the increased number of hatchlings predated on along rocky shores or shallow reefs (Mortimer 1995; Garmestani *et al.* 2000). Deep water access has been said to be preferred by sea turtles (Hughes 1974; Mortimer 1995) however, no mention of how deep the water should be or the slope of the intertidal zone has been mentioned. Mortimer (1995), suggested that beaches selected by leatherbacks tend to be steep, indicating reflective beach types (Wright & Short 1984; Benedet *et al.* 2004) Reflective beaches ensure shorter crawl distances for sea turtles to reach the high water mark (Mortimer 1995). With reflective beaches, there are very small or no surf zones present compared to dissipative beaches (which dissipates wave energy in the surf) that have gentle slopes (McLachlan & Brown 2006).

Dimensions of a beach are governed by grain size, wave action and tide range (for full description on beach morphodynamic states see McLachlan & Brown 2006). These factors interact to create different morphodynamic conditions which can easily be assessed using intertidal slope. Slopes of beaches can be used to classify beaches along a continuum of beach types from ultra-dissipative, through intermediate (four states) to reflective (Wright & Short 1984; McArdle & McLachlan 1992; Benedet *et al.* 2004; McLachlan & Brown 2006). Reflective beaches are classified by steep slopes and coarse grained sand, dissipative beaches are characterised by gentle slopes and fine sand and intermediate beaches, which is between these extremes, form the medium states which are temporally variable with changing wave regimes (Wright & Short 1984; McArdle & McLachlan 1992; Benedet *et al.* 2004; McLachlan & Brown 2006). For sea turtles, sand grain size may be of equal importance to slope in nest site selection (Stancyk & Ross 1978). However, the grain size of sand is more important from a nest digging perspective and gas diffusion while eggs are incubating (Mortimer 1995). Tide ranges on reflective beaches tend to be smaller than on dissipative beaches (McLachlan & Brown 2006). Dissipative beaches being the flatter of the two extreme states, allow for the tide to move further up the beach than reflective beaches (McLachlan & Brown 2006). Wider beaches tend to offer more of a choice of conditions along the width of the beach (Mazaris *et al.* 2006) as elevation, temperature, moisture and organic content changes with the distance from the sea (Miller *et al.* 2001).

Vegetation in proximity to the nest may affect various aspects of hatchling development such as body size, hatching and emergence success, sex ratios and vulnerability to predators (Resetarits 1996; Miller *et al.* 2001; Kamel & Mrosovsky 2005; Mitrus 2006; Kamel & Mrosovsky 2006). The type and density of vegetation may cool sand temperatures and therefore decrease the overall incubation temperature (Wilson 1998). Nests situated closer to vegetation have a higher probability of being predated (Eckert 1987) and vegetation, especially roots, may impede digging efforts by females (Kamel & Mrosovsky 2004). Experiments on leatherback hatchlings showed that when placed in vegetation, they became misorientated as their line of vision to the ocean was obscured by the vegetation (Kamel & Mrosovsky 2004). Misorientation may also be evident when females nest behind dunes (Mazaris *et al.* 2006). Along with the risk of misorientation of hatchlings high up on the beach, comes changes in temperature and moisture (Miller *et al.* 2001) and therefore higher chances of desiccation and predation (Wood & Bjorndal 2000) as the hatchlings would have longer distances to crawl to the ocean.

The two disadvantages associated with nesting too low down on the shore are that nests may be inundated during spring tides (decreasing the incubation temperature or “drowning” the eggs or hatchlings) or that nests are eroded (Wood & Bjorndal 2000) exposing eggs or hatchlings prematurely. Sudden inundation of a nest near the hatching phase may kill the entire clutch by decreasing the oxygen supply when the demand is the highest (Miller *et al.* 2001). Inundation of the nest may alter the sex ratio of hatchlings as sea turtles are temperature sex dependant (Maxwell *et al.* 1988; Hughes 1989; Maloney *et al.* 1990; Miller *et al.* 2001).

The objective of this chapter was to identify factors that encourage or discourage nesting in loggerhead and leatherback turtles. Specific factors that were assessed were the presence of inshore rocks, surf zone width, intertidal slope, beach and back-beach width and dune characteristics. In the high-density loggerhead nesting area, the average grain size of the sand and pH was evaluated as well as the distances of the nests from the vegetation and the track length above the high-water mark to the nest.

MATERIALS AND METHODS

Nest site selection of turtles was determined using the monitoring area of 56 km for a coarse-scale analysis. The high-density loggerhead nesting area (~5 km) within the 56 km monitoring area was used for a higher resolution analysis in an attempt to identify specific physical factors that facilitate loggerhead nesting in this area as distribution is not uniform throughout (Chapter 3).

Coarse-scale data collection

Nesting data from the 2000/01 season to the 2007/08 season were used for the large scale investigation of haul out sites and nest selection sites. The nesting data were obtained from the Ezemvelo KZN Wildlife long-term monitoring database. The reason for the selection of nesting data was due to the SPOT 5 imagery used being from the year 2005. Therefore any large-scale changes would be avoided by using seasons that were timed close to the imagery used. From the Spot 5 imagery used in ArcGIS version 9.2, the following were measured: the position of the inshore rocks, surf zone width, slope (using a digital elevation model), beach and back-beach width per beacon along the beach. The beaches were mapped according to beach morphodynamic state (see (Harris 2008). The area used for this investigation was the 56 km monitoring area (see Fig. 2.1., Chapter 2). GPS positions of loggerhead and leatherback nests from December 2007 and 2008 were used for the investigation on the effects of inshore rocks on nesting.

All statistics were performed using Statistica version 8 (Statsoft). To determine if any of these factors had an effect on nest site selection of turtles, physical factors were correlated (Pearson-product moment) with nesting numbers. These factors were evaluated both in terms of haul outs and successful nesting events. The factors that were investigated were slope, beach width and the back-beach width. The back-beach is defined as the area between the spring high tide mark and the dune base. Nesting directly in line with inshore rocks as opposed to next to them and preference for beach morphodynamic type were determined using chi-square analyses.

High-resolution data collection

During the nightly patrols, track length of every emerged turtle, and distance to the vegetation line from the nest or false crawl of the turtle, were measured using a flexible tape measure however, measurements were accurate to 0.5 m as the environment was extremely variable. Track length of a turtle was tide-dependent as it was the measurement from the tide mark to the nest and therefore was only possible to record when the tide was receding. The beach cover around the nest was scored as either open sand or vegetated. Vegetation was classified as any live leaf, stem or root material in the vicinity of the nest.

Grain size and pH were measured once-off at each beacon (see Chapter 2 for site descriptions of beacons). Surface sand was used for pH analysis by mixing 5g of sand with 50 ml distilled water for ten minutes. The pH was measured using a Hannah instrument, model HI 964400. For the grain size analysis, sand samples taken above the high water mark were washed over a 63 µm sieve to eliminate salt and silt particles and dried at 80^0C for 24 hours. Dried samples were sieved using standard dry sieving techniques (McLachlan & Brown 2006). Average grain size was obtained using Gradistat V7 (Blott & Pye 2001).

The high-resolution data analysis was restricted to loggerhead nesting as only 11 leatherback nests were encountered during the two week data collection period, an insufficient number for statistical purposes. All statistical analyses were conducted in Statistica version 8 (Statsoft). One-way ANOVAs were conducted on nest numbers per beacon and the distance to vegetation. Chi-square analysis was used to compare nest numbers in the between open sand and vegetated areas and t-tests were used to compare distance to vegetation between to samples for nested versus not nested tracks. Correlations were conducted for the pH and average grain size per beacon against the number of nests per beacon.

RESULTS

Correlation analyses showed only one significant correlation between physical factors, haul outs and nesting of both species. Leatherback haul out increased with wider surf zones, ($r = 0.329$, $p = 0.005$; Table 4.1.). More leatherback haul outs (678 at beacon 72S and 774 at beacon 92S) were evident near the southerly limit of the monitoring area, which were characterised by wider surf zones (230 m and 239 m at beacons 72S and 92S respectively). The number of leatherbacks ($n = 5$) nesting in the high-density loggerhead area during December 2008 was too low to conduct any meaningful statistical tests with regards to pH and mean grain size. Loggerhead turtle haul outs and nesting indicated no dependence on any of the physical factors measured.

Table 4.1. Results of correlation analyses between nesting numbers of loggerheads and leatherbacks and a suite of physical factors. ** denotes significant results ($p < 0.05$).

Physical factor	*Range*	*Loggerheads*		*Leatherbacks*	
		r	p	r	p
Surf Zone width	30 – 269 m	0.06	0.96	0.33	0.005**
Slope	1:10 – 1:18	0.11	0.39	0.33	0.79
Beach width	14 – 252 m	-0.05	0.68	0.09	0.49
Back-beach width	11 – 226 m	-0.00	0.99	0.06	0.65
pH	6.6 – 8.5	0.48	0.12	-	-
Mean grain size	202 –404µm	0.15	0.63	-	-

Loggerheads prefer nesting on beaches that are intermediate compared to reflective and those characterised by the presence of low shore rock, ($X^2_{0.05,\ 2} = 11544.31$, $p = 0.000$; Fig. 4.1a to c). A total of 12605 loggerhead nests were laid on intermediate beaches between season 2000/01 and 2007/08, whereas only 2859 and 2193 nests were laid on reflective beaches and those characterised by low shore rock respectively in the same nesting seasons. The number of loggerheads nesting on intermediate beach types in the monitoring area (32N to 100S) may however be artificially high as a result of the high-density loggerhead area between 0N and 12N and the high incidence of intermediate beaches along the monitoring area (Fig. 4.1a.). No comparison between beach morphodynamic types could be made in the high-density loggerhead area as the area is uniform in beach type with the exception of low shore rock present at beacons 9N and 10N where nesting numbers were correspondingly lower than elsewhere within the area. Nonetheless, when the high-density loggerhead nesting area was excluded from the analysis it is still apparent that loggerheads prefer to nest on intermediate beaches ($n = 7183$) as opposed to reflective beaches ($n = 2859$) and beaches characterised by low shore rock ($n = 1171$, $X^2_{0.05,\ 2} = 5144.96$, $p = 0.000$).

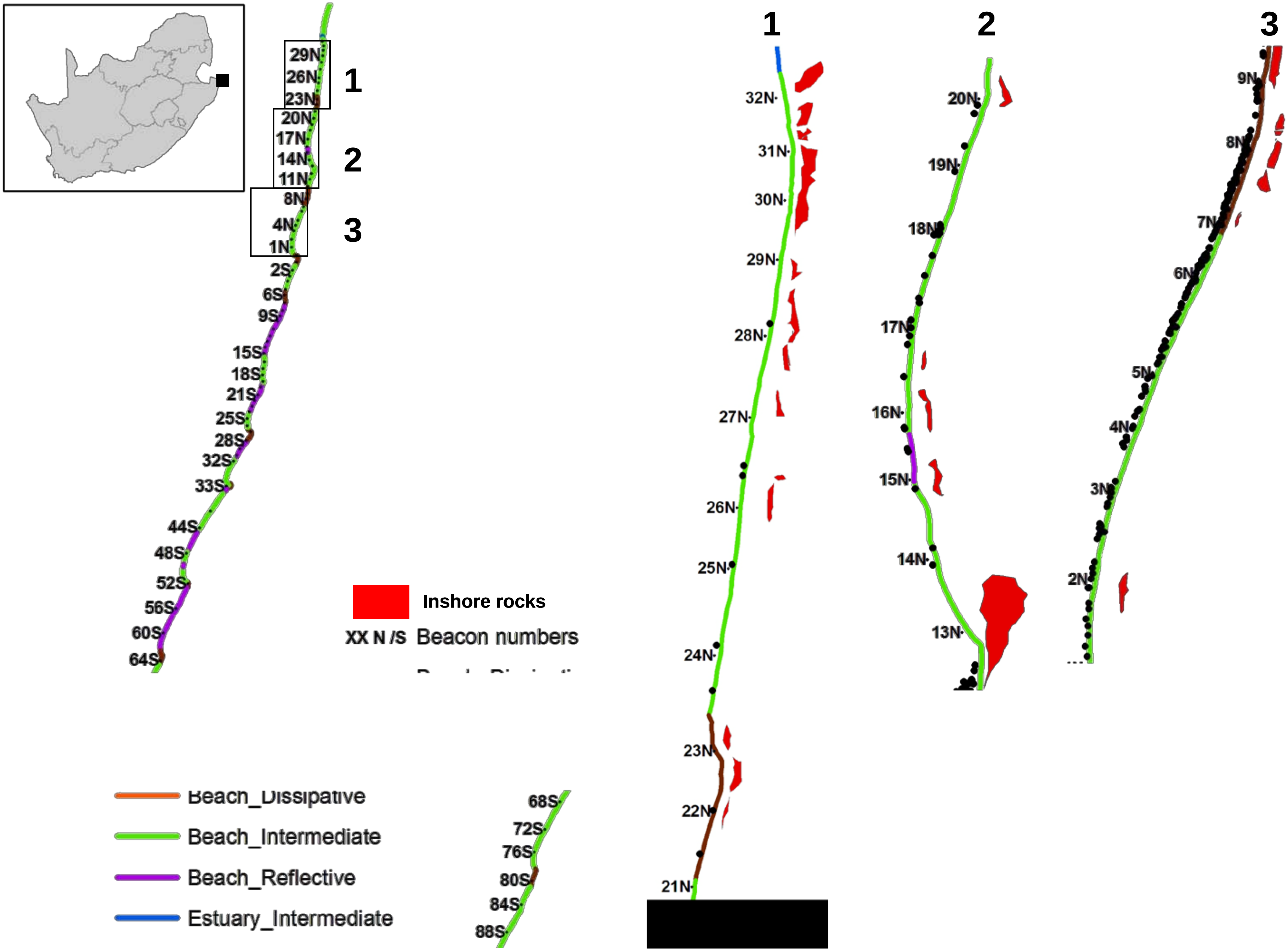

Fig. 4.1a. Distribution of loggerhead nests (black dots) from 32N to 1S in relation to inshore rocks and beach morphodynamic type.

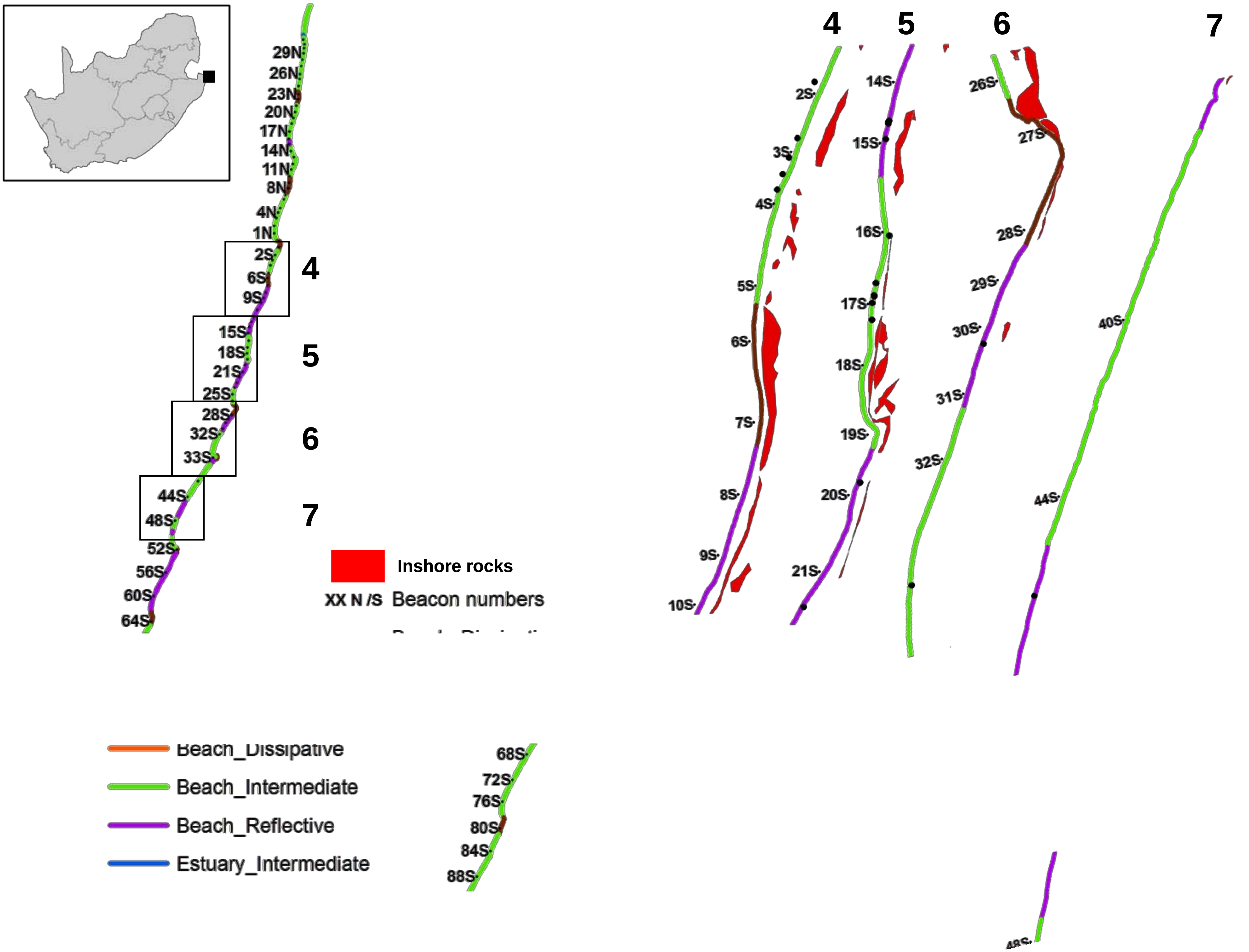

Fig. 4.1b. Distribution of loggerhead nests (black dots) from 2S to 48S in relation to inshore rocks and beach morphodynamic type.

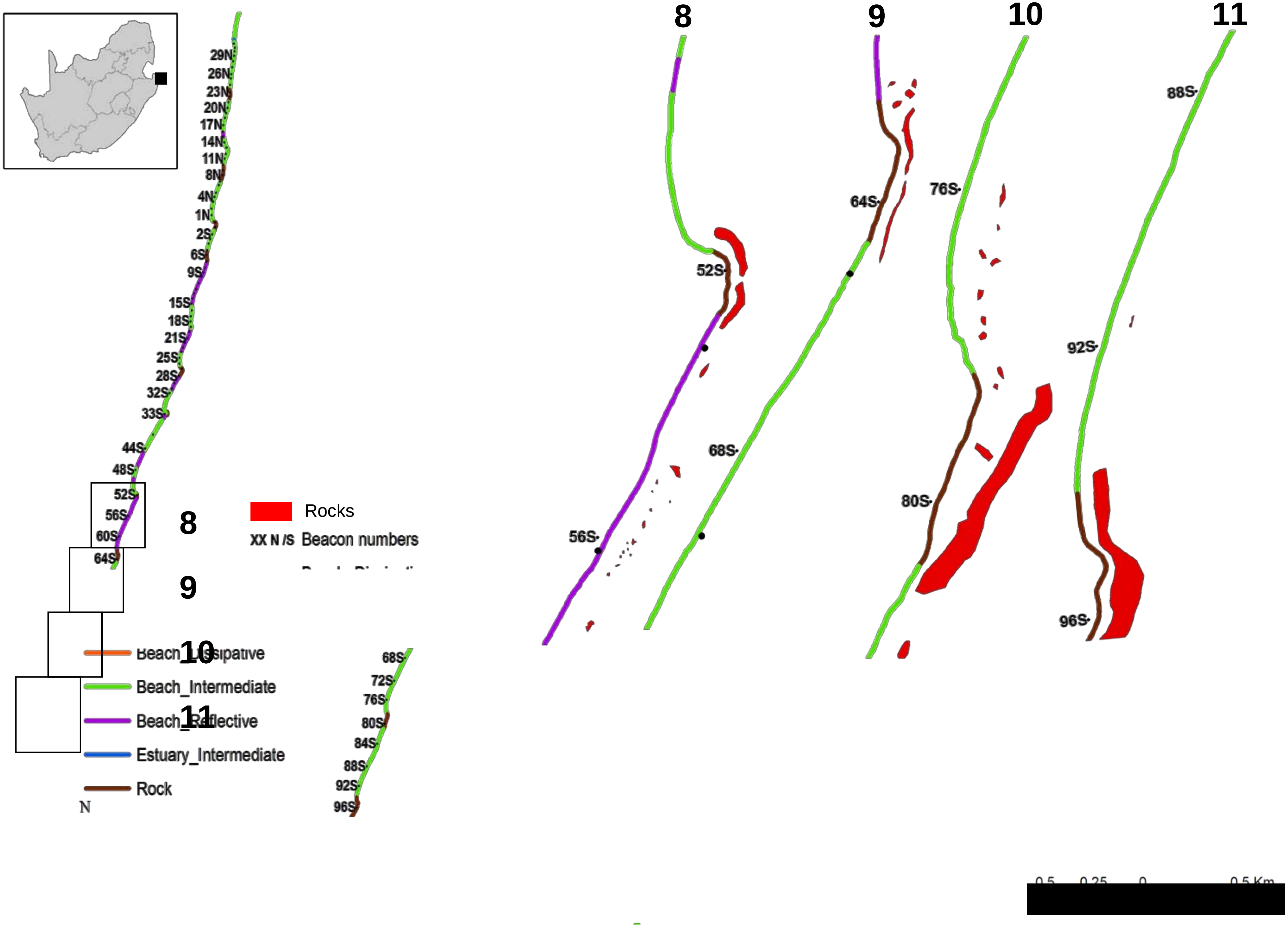

Fig. 4.1c. Distribution of loggerhead nests (black dots) from 52S to 100S in relation to inshore rocks and beach morphodynamic type.

If rocks pose no problem to sea turtles nesting then the number of turtles nesting on beaches directly in line with rocks should be equal to numbers nesting either side of rocks. However, this was not the case. Most loggerhead nests were placed on stretches of beach situated between inshore rocks and not directly behind them suggesting that loggerheads avoid nesting in most places where inshore rocks are present. This finding was enforced by the fact that loggerhead nesting is not equal directly in line with rocks and adjacent to rocks, ($X^2_{0.05, 1} = 87.04$, $p = 0.000$).

The most preferred beach type used for leatherback nesting in the turtle monitoring area (32N to 100S) were intermediate beaches with 3032 nests placed on this beach type from season 2000/01 to 2007/08. Reflective beaches and beaches characterised by low shore rock were used to a lesser degree (1019 and 530 nests respectively) than intermediate beaches for leatherback nesting, ($X^2_{0.05, 2} = 2302.27$, $p = 0.000$). Within the study period, December 2007 and 2008, no leatherback nests were laid on beaches where low shore rocks were present although not all stretches of beach were monitored as consistently as beacon 0N to 12N. However, within the area 0N to 12N, no leatherback nests were recorded on beaches (beacons 9N and 10N) where low shore rock was present (Fig. 4.2a). Some stretches of beach received no leatherback nesting during the study period such as beacon 2S to 36S, however, beyond 36S towards 100S leatherback nesting became apparent on reflective beaches (Fig. 4.2b and c). Significantly different surf zone widths ($F_{0.05\ (1),\ 2,\ 77} = 3.37$, $p = 0.04$) associated with different beach types, reinforce the fact that leatherbacks prefer intermediate beaches for nesting.

Four out of 17 leatherback nests were directly in line with inshore whereas the remaining nests were placed on stretches of beach situated between inshore rocks or adjacent to inshore rocks. The pattern observed from Fig. 4.2a, 4.2b and 4.2c suggests that inshore rocks pose a problem to leatherbacks. Therefore, there is uneven nesting with respect to leatherbacks and rocks and areas adjacent to rocks ($X^2_{0.05, 1} = 8.05$, $p = 0.005$).

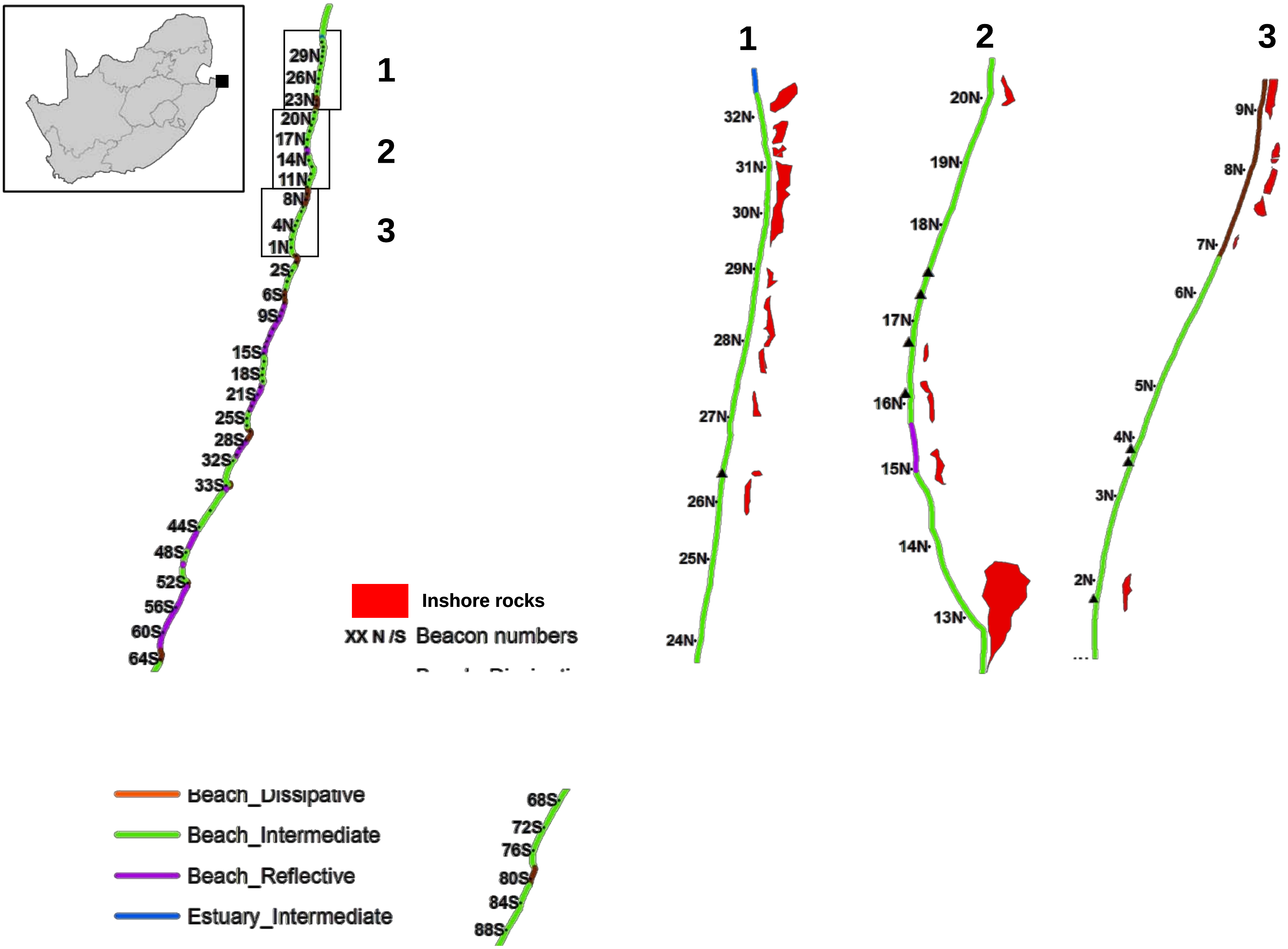

Fig. 4.2a. Distribution of leatherback nests (black triangles) from 32N to 1s in relation to inshore rocks and beach morphodynamic type.

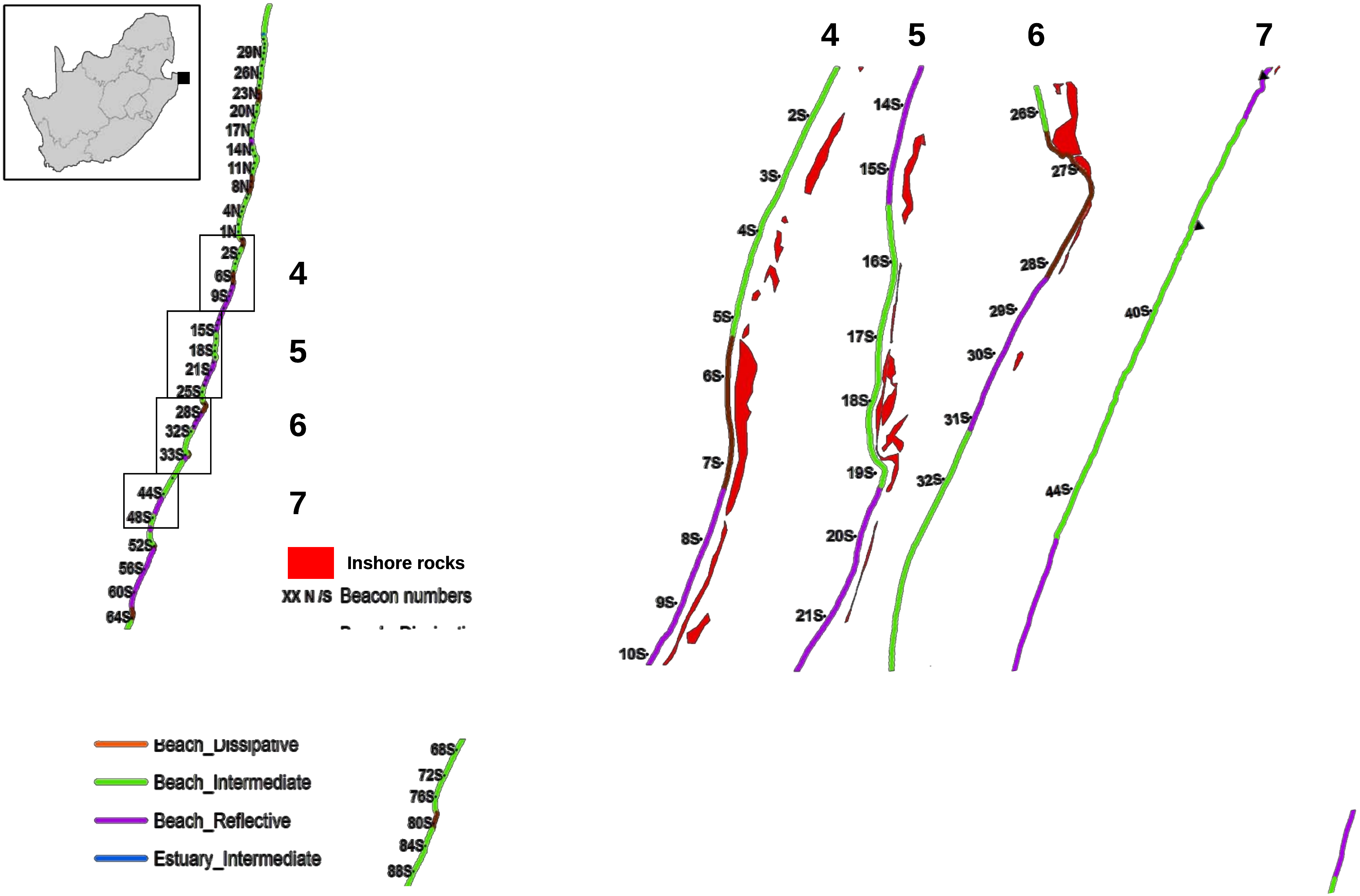

Fig. 4.2b. Distribution of leatherback nests (black triangles) from 2S to 48s in relation to inshore rocks and beach morphodynamic type.

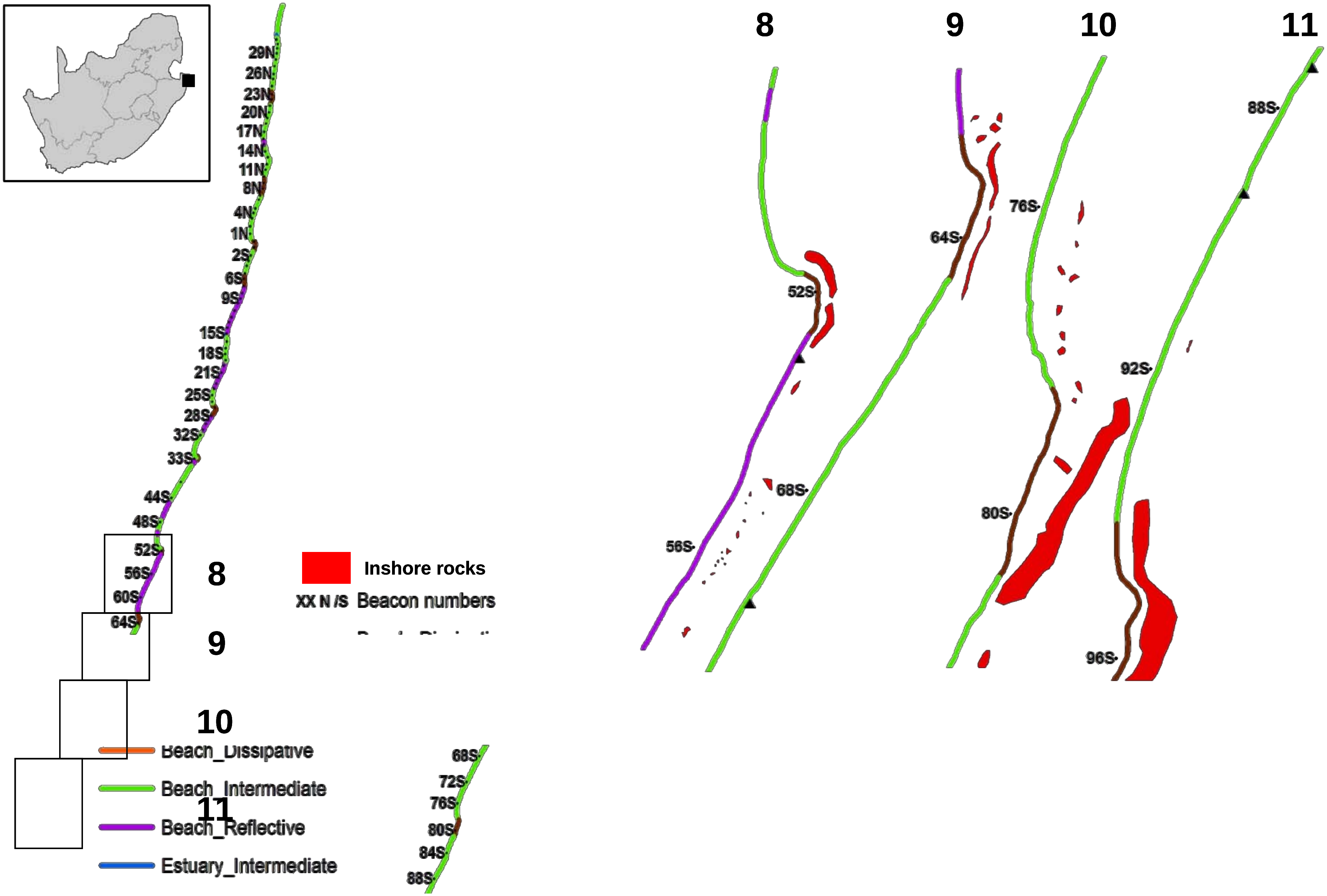

Fig. 4.2c. Distribution of leatherback nests (black triangles) from 52S to 100S in relation to inshore rocks and beach morphodynamic type.

The majority of loggerheads in December 2008 preferred to nest in close proximity to the vegetation line with the mean distance to the vegetation 11.96 ± 0.73 m (mean ± standard error). The distribution of nest position in relation to the vegetation line was skewed towards the vegetation ($g_1 = 3.43$, $p < 0.01$). Some nests were laid in excess of 100 m from the vegetation, however, beaches differed in width and it was possible to nest a great distance from the vegetation line in some areas. A strong correlation was observed between the back-beach width and the distance that a nest was placed from the vegetation line, ($r = 0.86$, $p = 0.00$).

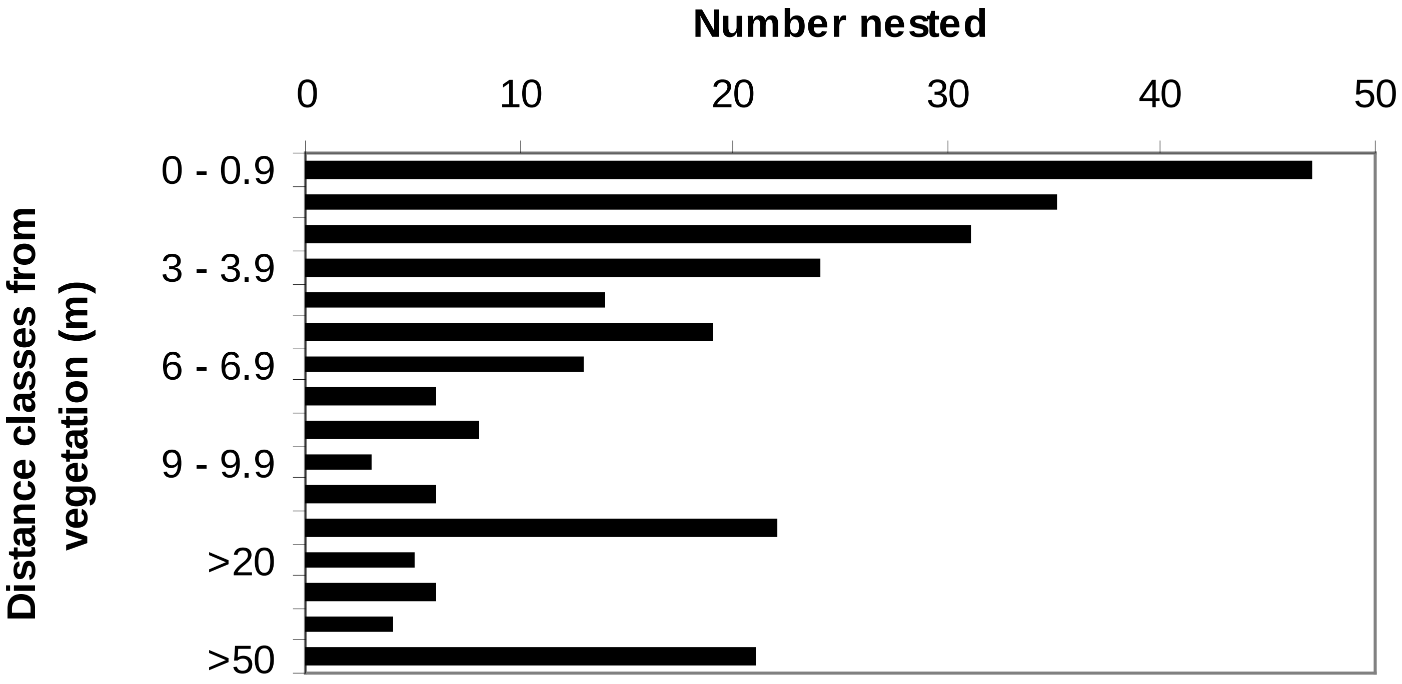

Fig. 4.3. Nesting sites of loggerheads (N = 264) in relation to the vegetation line (0m).

Unequal nesting of loggerheads occurred between the vegetation and the open sand ($X^2_{0.05,\,1} = 25$, $p = 0.000$) with the majority of nests occurring in the open sand. Nests laid in open sand totalled 75 % of all nests laid with the remaining 25 % laid in “vegetation”. This included any signs of vegetation close to the nest whether in the form of roots or plants such as *Ipomea* and *Scaevola.* All 11 leatherback nests were placed in open sand showing a strong preference among leatherbacks for open sand.

Most loggerhead false crawls were in the region of beacon 0N with a 33 % chance of a female actually nesting in this area when crawling out (Fig. 4.4.). Consequently 0N is the beacon where the field ranger station is based and continuous foot traffic is evident. The chance of a nest resulting from a crawl was highest at beacon 11N with ~79 % of crawls resulting in nests. Interestingly, the chance of nesting occurring at one of the most popular beacons of the season, 8N was relatively low (~42 %). Beacon 7N, the other most popular beacon, showed a higher chance of nests resulting from crawls (~63 %) than beacon 8N. The chances of nests resulting from crawls by loggerheads is even between 0N and 12N, ($X^2_{0.05,\ 12}$ = 33.22, p = 0.0009). Therefore, the incidence of false crawls is random and not due to specific conditions on any section on the beach but rather a result of disturbance.

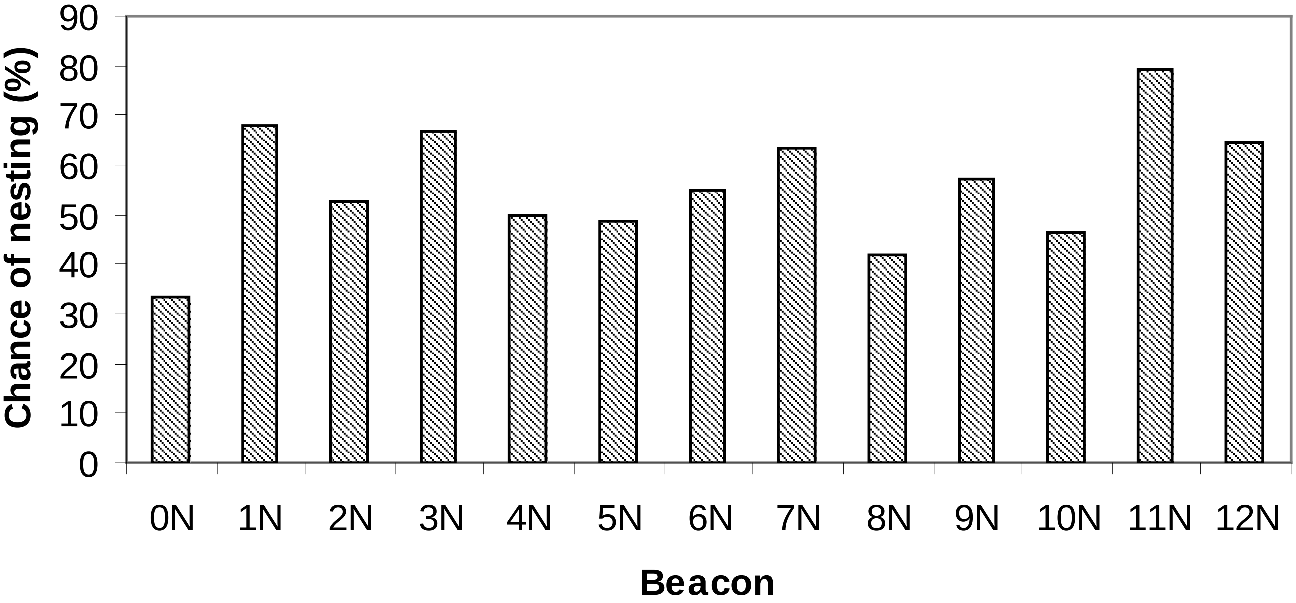

Fig. 4.4. The ratio of nested to not nested loggerheads in the sampling area (0N to 12N) during December 2008.

Loggerheads nested closer (11.96 ± 1.46 m) to the vegetation than the leatherbacks (21.11 ± 7m) as seen in Fig. 4.5. There is however no significant difference in the distance nested from the vegetation line between the two species ($t_{0.05\ (2),\ 273} = -1.26$, $p = 0.208$). Loggerheads tend to nest a significantly greater distance above the high water mark than the leatherbacks ($t_{0.05\ (2),\ 270} = 2.21$, $p = 0.03$) and loggerheads overall seem to crawl further up the beach than leatherbacks when the track lengths of the two species were compared. Loggerheads crawl a mean distance of 40.17 ± 16.85 m to nest while leatherbacks only crawl 20.13 ± 3.46 m in comparison. The difference between the lengths of the tracks was significant, $t_{0.05\ (2),\ 139} = 2.64$, $p = 0.009$.

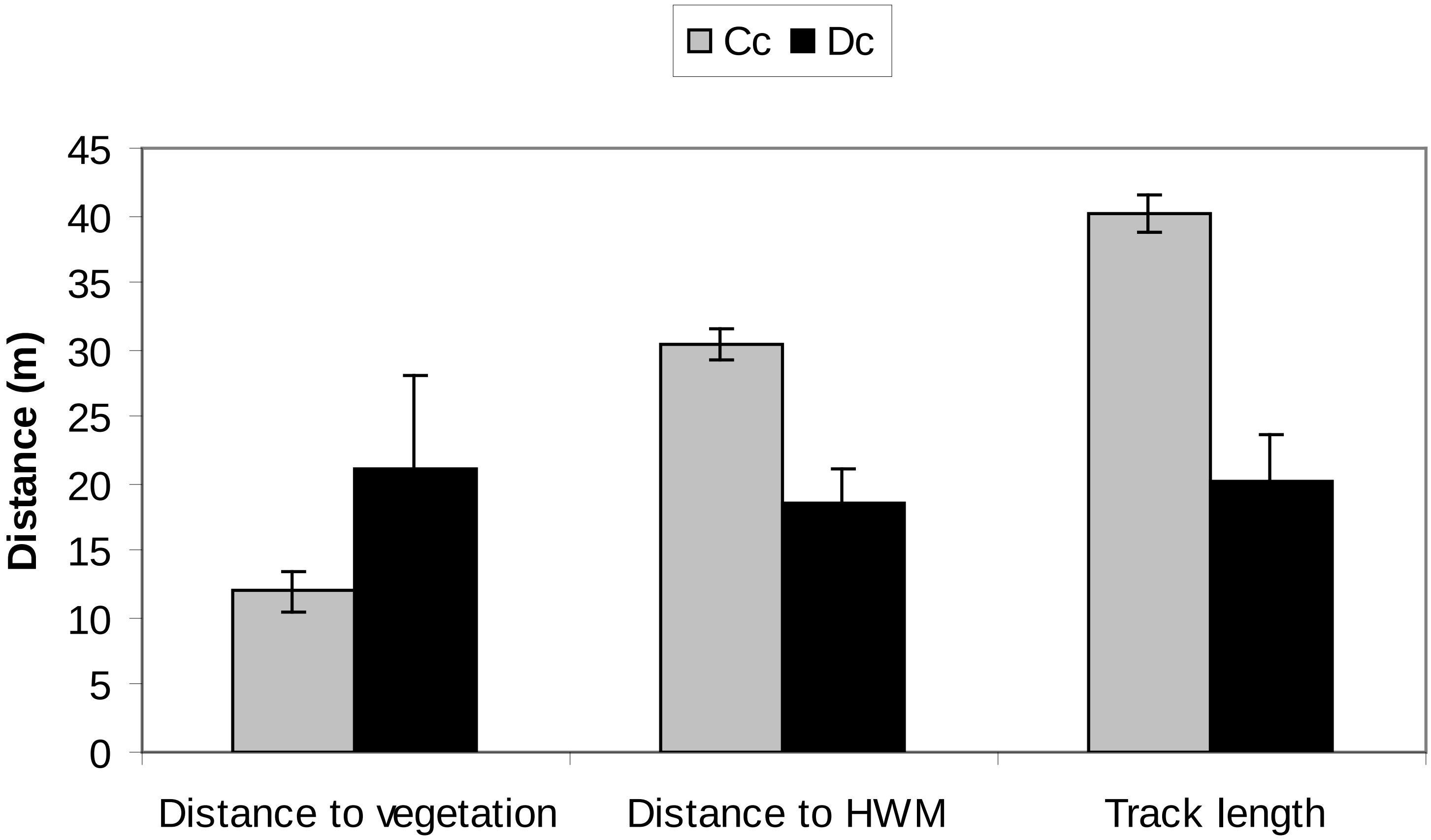

Fig. 4.5. Comparison of distances from the vegetation line, the high water mark and the track length between loggerheads (Cc), n = 264 and leatherbacks (Dc), n = 11. Bars represent standard error bars (SE).

DISCUSSION

For a beach to qualify as a good nesting beach, there are criteria that need to be met (Mortimer 1995). Among physical factors, slope has been shown to play an important role in nest site selection of sea turtles (Mortimer 1995; Wood & Bjorndal 2000; Garmestani *et al.* 2000). Sea turtle nesting in South Africa did not confirm results of other nest site selection studies (Table 4.1), as there was no significant correlation between the number of nests and slope per beacon. The pH and mean grain size of the sand did not affect placement decisions of loggerheads in December 2008 and this confirmed the results from other studies based on pH and beach sand characteristics (Stancyk & Ross 1978; Mortimer 1995; Garmestani *et al.* 2000). Kikukawa *et al.* (1999) however found that sand compaction was an important property considered by nesting turtles, but is highly variable depending on moisture level. In the current study, both pH and mean grain size (more conservative measures) were only measured over a short stretch of beach (~5 km) of similar beach type (mostly intermediate with some low shore rock present at some beacons, Fig. 4.1a). Perhaps conclusive results could be achieved if pH and mean grain size were measured along the entire length of the monitoring area. However, beach morphodynamic state works as a proxy for grain size and therefore the effect of grain size has been sampled indirectly. In the current study, leatherbacks selected beaches to haul out with wider surf zones (Table 4.1). This can be explained by the tendency of leatherbacks selecting intermediate beach types above reflective beaches and beaches where low shore rock is present. Intermediate beaches have wider surf zones than reflective beaches (McLachlan & Brown 2006). Both species preferred intermediate beaches, however, loggerheads nested more frequently on beaches characterised by low shore rock than leatherbacks (Fig. 4.1 and 4.2). This could be explained by the presence of the high-density loggerhead nesting area where loggerheads are facilitated by high-tide emergences and hard carapaces making it easier for them to crawl over rocks.

Beaches that are fronted by inshore rocks may be inaccessible for turtle nesting or may be threatening to turtles attempting to haul out in these areas (Mortimer 1995). Loggerheads and leatherbacks in this study both avoided beaches that were obstructed with low-lying inshore rocks (fig 4.1 and 4.2 respectively). Loggerheads do not however appear to be as affected by inshore rocks as leatherbacks. Loggerheads may in fact prefer beaches with rock outcrops (Hughes 1974) as it may be associated with the final orientation of the sea turtles before beaching, as suggested by Kikukawa *et al.* (1999) in the Okinawa Islands. The same results can be seen by the high loggerhead nesting density at beacons 1N to 2N, 6N to 8N and 10N to12N. The before mentioned areas are all adjacent to inshore rocks. Perhaps the freshwater outflows from the lake in this vicinity act as the overall homing cue but rocks are used for orientation by loggerheads (Hughes 1989; Kikukawa *et al.* 1999). Due to leatherbacks being the larger of the two species and with live skin covering the shell, makes them more vulnerable to injury on rocks (Mortimer 1995). For this reason, in this study and in other studies, leatherback nesting beaches are unprotected by offshore reefs (Eckert 1987; Mortimer 1995).

In the current study, loggerheads nested in close proximity to vegetation with the distribution of nests skewed towards the vegetation. A similar result was found for loggerheads by Hays (2004), where they selected to nest close to the supralittoral vegetation. It was found that some nests were placed in excess of 50 m and even 100 m from vegetation and these were nests that were placed at beacon 12N respectively. The beach is wider (approximately 150 m) in this area and consists of wind-blown dunes and therefore vegetation is situated a substantial distance from the high water mark (see Chapter 2, fig 2.3.). It would therefore be near impossible for a loggerhead to nest at or in the vegetation at beacon 12N. If vegetation is present on a stretch of beach that can be easily reached by loggerheads, they may nest near to it but if there is no vegetation, loggerheads may place their eggs in open sand as was observed for 75 % of loggerhead nests. Turtles that nest nearer to the vegetation are likely to have greater nest success as the eggs are at 'safe' distances from the high water mark therefore; the risk of inundation and erosion by tides is less. However, if turtles were to nest in the vegetation it would almost certainly impede digging efforts by the females as the roots act as obstacles (Mortimer 1995; Hays *et al.* 1995; Kamel & Mrosovsky 2004). Not only will the roots obstruct the nesting females, they will obstruct emerging hatchlings and possibly penetrate the nest and destroy eggs (Wood & Bjorndal 2000; Kamel & Mrosovsky 2004). Leatherbacks showed the same trend as loggerheads by placing 100 % of all their nests within open sand compared to vegetation and this was also observed for leatherbacks in French Guiana by Kamel & Mrosovsky (2004).

The ratio of nested to not nested events of loggerheads suggests that false crawls are random and not caused by a physical factor on the beach such as sand grain size, slope and/ or vegetation. Instead, random effects may include disturbances by humans, artificial lighting and collapsed nests. During the summer months many tourists are attracted to the area of Bhanga Nek especially in the region of 0N to 3N where informal campsites and officer's houses are situated. Campsites and field officers' houses use artificial lighting during the sea turtle nesting season. Artificial lighting has been shown to deter sea turtles from nesting (Mortimer 1995; Steyermark *et al.* 1996; Kikukawa *et al.* 1999; Witherington 1999; Antworth *et al.* 2006) and this explains the fraction of turtles that did not nest (and only displayed false crawls) along the 0N stretch of beach. A possible mitigation for the future is that lights emitting short wavelengths (yellow and red) be used as an alternative as they are weakly detected by turtles (Witherington 1999).

Loggerheads and leatherbacks showed no significant difference between the distances a nest is placed in relation to vegetation. However, loggerheads crawl significantly further above the high water mark and they have significantly longer overall track lengths compared to leatherbacks. Loggerheads are capable of crawling in excess of 100 m to reach a suitable site to nest (Hughes 1989) and therefore would be expected to crawl longer distances from the high water mark and have longer overall track lengths when compared to leatherbacks that are approximately five times their size. Hughes (1989) suggested that loggerheads do almost always surpass the high water mark when nesting and leatherback females have responded to the pressure of nests being inundated by tides by nesting at intermediate distances from the high water mark. However, the distance above the HWM that a nest is placed seems unimportant for loggerheads (Hughes 1989). Hughes (1989) suggested that turtles may be able to distinguish between the temperatures of the sand in the intertidal and supratidal areas so that they know when it is ‘safe’ to excavate a nest.

The strategy employed by loggerheads seems to select for the factors that favour nest survival such as nesting above the high water mark but not nesting too close to the vegetation so that roots can destroy the nest or so that vegetation can shade the nest. Loggerheads, being much lighter and smaller of the two species, possibly have more of a choice of nest sites as such as they are able to move with ease to seek nesting sites when compared to leatherbacks. Vegetation as a visual cue may therefore be a driver for nesting to occur in loggerheads. Leatherbacks on the other hand seem to nest on the beach with ease once they have found a suitable site to haul out on. Leatherbacks are responding to wider surf zones and the lack of inshore rocks. Therefore, leatherbacks may be selecting the haul out site instead of a nesting site on the beach as such, however, they must have some means of knowing when they are above the high tide mark.

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CHAPTER 5

THE EFFECTIVENESS OF NEST SITE SELECTION OF LOGGERHEAD TURTLES, *CARETTA CARETTA*, MEASURED THROUGH HATCHING SUCCESS

ABSTRACT

Hatching success of sea turtles is primarily affected by three factors; intrinsic factors such as turtle species, fertility and embryonic mortality; extrinsic factors such as environmental conditions which include temperature, rainfall and sediment moisture content, vegetation type and density and gas exchange within the nest; and then random factors which include predation of nests. Hatching and emergence success of loggerheads were measured in the high-density loggerhead nesting area over a 5 km stretch of beach along with the measurement of a suite of environmental factors at the time of oviposition. This was conducted during the 2008/09 nesting and hatching season in Maputaland, Kwazulu Natal. Hatching and emergence success did not correlate with any of the environmental variables measured. Nest success (defined as the percentage of nests that produce hatchlings) measured from beacon 0N to 12N, was not uniform along the beach. Nest success was highest at beacons 2N and 3N, which was disproportionably high along this section of coast compared to the number of nests laid. There is a small potential for human conflict with nesting as there is some artificial lighting shining onto the beach in the region of beacons 2N and 3N. Thus, overall nest success and hatchling production would be enhanced if this conflict could be eliminated and adult females allowed to nest undisturbed at the most successful nesting site.

INTRODUCTION

After a female turtle selects a site to nest, she digs a body pit followed by an egg chamber and deposits eggs into the funnel-shaped chamber. This site selected by a female is of critical importance for the development and survival of the embryos, and is the only control that she has over the incubation success of her offspring (Kamel & Mrosovsky 2004). Three suites of factors affect the incubation success of nests or eggs. Firstly, the intrinsic factors which are factors associated with the fitness of individual turtles including species (Miller *et al.* 2001; Antworth *et al.* 2006; Xavier *et al.* 2006), female fertility (Miller *et al.* 2001; Bell *et al.* 2003) and embryonic mortality (Bell *et al.* 2003) which involves the embryo and not the female as such. Extrinsic factors are the environmental conditions in and around the nest to which the female has limited or no control over. These factors include temperature (Wilson 1998; Miller *et al.* 2001; Wallace *et al.* 2004), vegetation type and density, moisture content of sand and rainfall (Kraemer & Bell 1980; McGehee 1990; Wood & Bjorndal 2000; Miller *et al.* 2001), sand grain size and *in situ* gas concentrations (Maloney *et al.* 1990; Ralph *et al.* 2005). Predation acts as a random factor as female turtles have no control over predators and it is impossible to predict which nests may or may not be predated and to what extent.

Hatching success of sea turtles is species- and population specific (Miller *et al.* 2001) with hawksbill and green turtles demonstrating the highest hatching success of all sea turtle species. Hawksbills have hatching success values as high as 87 % - 89 %, laying clutch sizes between 137 and 149 eggs per clutch (Kamel & Mrosovsky 2005; Xavier *et al.* 2006). Green turtles show similar hatching success values to hawksbills ranging 86 % to 89 % (Fowler 1979; Xavier *et al.* 2006) and produce between 118 to 130 eggs per clutch (Antworth *et al.* 2006; Xavier *et al.* 2006). All loggerheads populations worldwide have hatching success of approximately 80 % producing an average of 112 eggs per clutch (Miller *et al.* 2001). The fertility of loggerhead eggs exceeds 80 % and can be as high as 95 % (Miller *et* *al.* 2001). Of all sea turtles species, leatherbacks show the lowest hatching success with most studies at various leatherback rookeries estimating hatching success of about 50 % with few cases exceeding this value (Bell *et al.* 2003; Wallace *et al.* 2004; Ralph *et al.* 2005). A value of 71.6 % hatching success was achieved under laboratory conditions (Bell *et al.* 2003). The fertility rate of leatherbacks is thought to be high with 93 % of all eggs fertilised (Bell *et al.* 2003). Fertility is thus excluded as an explanation for the low hatching success in this species. Embryonic mortality is reported as a concern for this critically endangered species as this leads to the low hatching success (Bell *et al.* 2003). Causes for embryonic mortality may include maternal reproductive health, chemical contaminants in females transferred to eggs or bacterial infections of the eggs (Bell *et al.* 2003).

Extrinsic factors such as vegetation and rainfall have the potential to affect incubation temperature and therefore the incubation period of a clutch. Fowler (1979), later confirmed by Wilson (1998), found that eggs placed in open areas incubated faster, and hatched sooner, than those in shaded sites. This was also discovered to hold for freshwater turtles (Wilson 1998). Increased distance from the vegetation showed increased nest success for snapping turtles (Kolbe & Janzen 2002).

The minimum temperature for successful incubation of sea turtle eggs is ~25^{0}C with the maximum temperature in Australia being 33^{0}C, and 34^{0}C in the USA (Miller *et al.* 2001). At 25^{0}C, the incubation period for loggerheads is approximately 13 weeks as opposed to six and a half weeks of incubation at 33^{0}C or 34^{0}C (Miller *et al.* 2001). Temperature is not only responsible for the sex determination and incubation time but also affects gas exchange of the embryos (Wallace *et al.* 2004). The oxygen demand of the embryos increases due to the faster developmental rates at higher temperatures (Miller *et al.* 2001) with oxygen gradients becoming higher from the centre to the periphery of the nest (Ralph *et al.* 2005).

Plant roots can penetrate nest chambers and destroy eggs (Kamel & Mrosovsky 2004) or prevent hatchlings from leaving the nest (*pers. obs.*). The seaward movement of hatchlings is guided by visual cues (Godfrey & Barreto 1995) and may be obscured by vegetation. Hatchlings that emerge or are released in vegetation, have difficulty moving towards the ocean (Kamel & Mrosovsky 2004) with some hatchlings moving landwards and never reaching the sea (Godfrey & Barreto 1995). Hatchings released on open sand showed a different trend to those released in vegetation by orientating towards the sea (Godfrey & Barreto 1995). Misorientation of hatchlings leads to longer periods of time spent on land, greater energy expenditure and greater risk to predation and desiccation (Godfrey & Barreto 1995; Wood & Bjorndal 2000).

Sea turtle eggs are cleidoic and therefore are dependent on the uptake of moisture from the environment (Miller *et al.* 2001). It would thus be favourable for females to lay clutches at an optimum sand moisture content of 25 % (McGehee 1990). Too much moisture adversely affects nests by drowning the embryos (Wood & Bjorndal 2000) as does too little moisture by desiccating the eggs, leading to hatching failure (McGehee 1990). Rainfall and inundation of nests by tides near the end of incubation can suffocate eggs (Kraemer & Bell 1980) by reducing the oxygen availably when the oxygen demand is highest (Miller *et al.* 2001). The sediment moisture may also indirectly affect the incubation period (McGehee 1990) by reducing sand temperatures during rainfall (Kraemer & Bell 1980). Rainfall or increased moisture may also affect emergence success as it impedes digging efforts by hatchlings as compaction of the sand increases (Kraemer & Bell 1980).

Predation is a factor that has the ability to alter hatching success of clutches dramatically. Physical excavation of nests and stealing of eggs or infestations may reduce the number of eggs left in the nest or the number of eggs that may hatch. In Tortuguero, wild dogs have become major predators of turtle nests whereas ghost crabs burrow into nests to feed on eggs and/or hatchlings (Fowler 1979). Smaller organisms such as fly larvae and ants also feed on turtle eggs and particularly dead or weakened hatchlings (Fowler 1979; McGowan *et al.* 2001). It was suggested that shallower nests and those in closer proximity to the high water mark are at higher risk of infestation by dipteran larvae (McGowan *et al.* 2001) whereas those in vegetated areas were more prone to ant infestations (Fowler 1979). However, there is no way for female turtles to protect their nests from predation other than disguising the nest when laid. Predation on turtle nests in South Africa has not been documented extensively, especially not quantitatively in recent years, but predators reported to feed on turtle nests include feral dogs, water mongooses, genets, water monitors and ghost crabs (Hughes 1989).

Most studies that have focused on hatching success of loggerheads focussed on factors affecting incubation conditions (Bustard & Greenham 1967; Fowler 1979; Peters *et al.* 1994; Skoufas 2005), however, few have investigated hatching success from a female turtle nest site selection point of view. The aim of this chapter was to determine hatching success and emergence success of loggerheads based on factors that females discriminate for or against when selecting a nest site. The physical factors tested to evaluate hatching and emergence success that a female may select for were: slope, grain size, pH, distance above the high water mark (HWM), distance to vegetation and vegetation cover or density. Leatherbacks were excluded as only two leatherbacks nested in the sampling area during the study period.

MATERIALS AND METHODS

Beach characteristics

Grain size and pH were measured once-off at each beacon i.e. every 0.4 km along a ~5 km stretch of beach (0N to 12N). Surface sand was used to analyse pH. A sample of 5 g of sand was stirred with 50 ml distilled water for ten minutes. The pH was measured using a Hannah instrument, model HI 964400. For the grain size analysis, sand samples were washed over a 63 µm sieve to eliminate silt and salt particles and dried at 80^0C for 24 hours. Dried samples were sieved using standard dry sieving techniques (McLachlan & Brown 2006). Average grain size was obtained using Gradistat version 7 (Blott & Pye 2001). Slope was measured using standard beach methods (McLachlan & Brown 2006). The beach cover around the nest was scored as either open sand or vegetated. Vegetation was classified as any live leaf, stem or root material in the vicinity of the nest.

Hatching success

The GPS coordinates of all loggerhead nests were recorded over a two week, peak nesting period in December 2008. Along with the GPS coordinates, factors that may indicate site selection (preference) such as distance to the vegetation, distance to the high water mark and vegetation type were recorded for each nest.

The hatching of the GPS marked nests were monitored over a three-week period in February 2009. Evening patrols were conducted with the intent of encountering hatchlings so that nests that they originated from could be positively identified. Nests were clearly marked with wooden stakes and left undisturbed for another four days to allow all hatchlings that remained in the chamber to emerge naturally. After the four day interval had passed, nests were excavated carefully and all of the contents were removed from the nest chamber. All egg shells of 50% or more were placed together and counted as one egg (Miller 1999).

All hatched, unhatched eggs and hatchlings were compared and the number of hatchlings that emerged successfully from the nest was calculated using the following formulas:

Hatching success (%) = (# shells / # shells + # UD + # UH + # UHT + # P) * 100 where: UD = Undeveloped, UH = Unhatched, Unhatched term and P = depredated (Miller 1999)

Emergence success (%) = (# shells – (# L + # D) / # shells + # UD + # UH + # UHT + # P) *100 where: L = hatchlings live in nest and D = Hatchlings dead in nest (Miller 1999)

Nest success (%) = (# hatched nests / # predated + # depredated nests) * 100

Data analysis

The position of December 2008 and February 2009 nests were spatially mapped in ArcGIS 9.3 to illustrate the distribution and density of excavated and predated nests. Hatching and emergence success data were overlaid with physical beach characteristics as per information collected in December 2008. Hatched nests were plotted with a 5 m buffer as this reflects the accuracy of the GPS. December 2008 and February 2009 nests i.e. laid versus hatched nests were paired. Statistics were conducted on the data using Statistica version 8. Analysis included Chi – square to determine the evenness of nest success and hatching and emergence success across beacons 0N to 12N, as well as chances of nests resulting from crawls along the 5 km stretch. Correlations (Pearson – product moment) were extensively used to determine if there was dependence of one factor on another in terms of hatching and emergence success versus slope, pH and average grain size per beacon, hatching success versus emergence success, hatching and emergence success versus clutch size, hatching and emergence success versus distance from vegetation and the high water mark. T – tests were used to compare hatching and emergence success in the open sand to hatching and emergence success in vegetation as well as the length of the incubation period in vegetation and open sand.

RESULTS

There were no significant differences between hatching success per beacon. Therefore, hatching and emergence success across beacon 0N to 12N were even ($\chi^2_{0.05,\ 11}$ = 7.89, p = 0.72 and $\chi^2_{0.05,\ 11}$ = 9.38, p = 0.58 respectively). Overall hatching success of the loggerheads across beacon 1N to 12N was 82.93 ± 1.88 % (n = 100, mean ± standard error) and emergence success 79.11 ± 2.04 % (n = 101). Nests contained an average of 99.8 ± 2.21 eggs with 152 the maximum number of eggs in a nest and 48 the minimum number of eggs. There was a negative correlation between hatching success and clutch size (r = -0.24, p = 0.01). No correlation was found between emergence success and the clutch sizes of the nests (r = -0.1, p = 0.32). There was a strong positive correlation between hatching success and emergence success (r = 0.83, p = 0.000).

There was no correlation between mean grain size and hatching success between beacons 1N to 12N (r = 0.007, p = 0.98). Correlations also indicated no relationship between slope and hatching success and emergence success and between pH and hatching success and emergence success (r = 0.18, p = 0.57 and r = -0.05, p = 0.88 respectively) see Table I. Females did not select nest sites based on grain size, pH and slope but rather beach morphodynamic type and rocks (Chapter 4). Not limiting the study to 5 km may yield more conclusive results on hatching success and beach morphodynamic type.

Hatched nests excavated in February 2009 (Fig. 5.1a and 5.1b) were not evenly distributed among the beacons 1N to 12N ($\chi^2_{0.05,\ 11}$ = 47.62, p = 0.000) with greater abundances of hatched nests at beacons 8N (21), 7N (14), 4N (13) and 2N (12). Nests were clumped along the stretch of beach 7N and 8N compared to beacons 11N, 12N, 1N and 2N. The lowest numbers of hatched nests occurred around beacon 10N and 0N. The highest number of predated nests occurred around beacons 4N and 5N and 10N and 11N with fewer nests predated at 6N, 7N and 12N. The remaining beacons 1N to 3N and 8N showed no signs of predation of nests.

Table 1. Beach characteristics and hatching and emergence success per beacon with the mean ± standard error shown.

Beacon	*Slope (V:H)*	*Grain size (µm)*	*pH*	*Number of nests*	*Clutch size (mean ± S.E)*	*Hatching success (%)*	**Emergence success (%)**
1N	1:13	321	8.1	1	82	97.56	97.56
2N	1:11	367	8.49	12	97.42 ± 6.34	82.17 ± 5.75	80.69±6.01
3N	1:17	272	8.36	8	98.88 ± 5.59	90.15 ± 3.31	89.57 ± 3.3
4N	1:13	292	8.37	13	104.86 ± 6.08	91.46 ± 1.85	87.01 ± 2.33
5N	1:13	202	7.72	8	93.13 ± 12.02	81.2 ± 6.23	79.32 ± 5.83
6N	1:11	265	8.18	7	88.29 ± 11.11	81.19 ± 4.88	78.43 ± 5.35
7N	1:18	328	8.67	14	96.63 ± 5.69	77.68 ± 6.15	74.6 ± 5.8
8N	1:12	3335	8.42	21	103.52 ± 5.5	80.46 ± 3.97	73.08 ± 5.33
9N	1:10	286	8.28	1	124	87.1	87.1
10N	1:14	279	8.2	2	111.5 ± 26.16	70.84 ± 38.17	69.77 ± 36.67
11N	1:11	247	8.46	6	98.83 ± 7.47	93.98 ± 2.00	93.2 ± 2.18
12N	1:15	404	8.19	7	107.43 ± 5.77	92.4 ± 2.09	81.94 ± 7.37

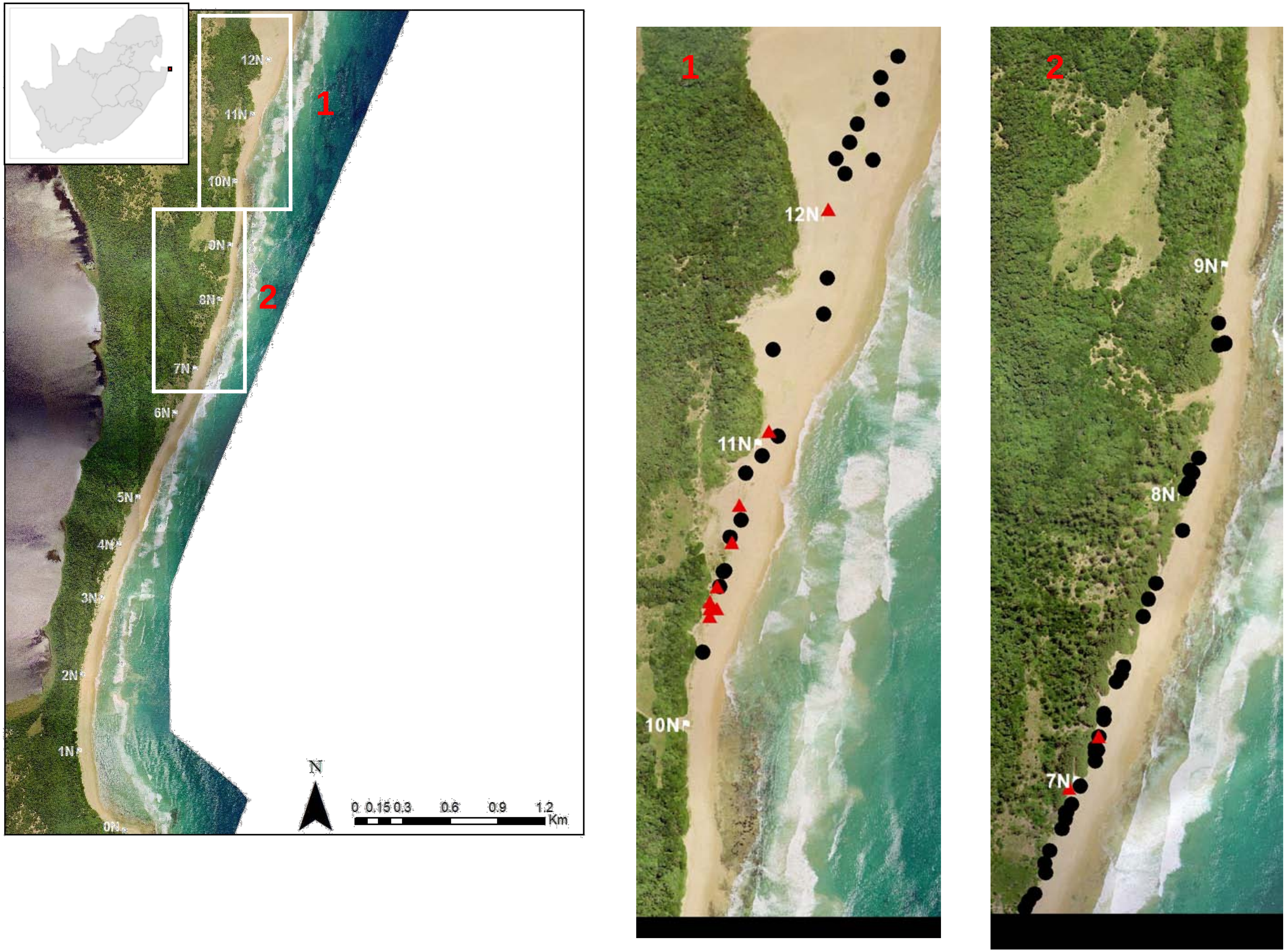

Fig. 5.1a. Distribution of hatched loggerhead nests to predated loggerhead nests from beacon 12N to beacon 7N.

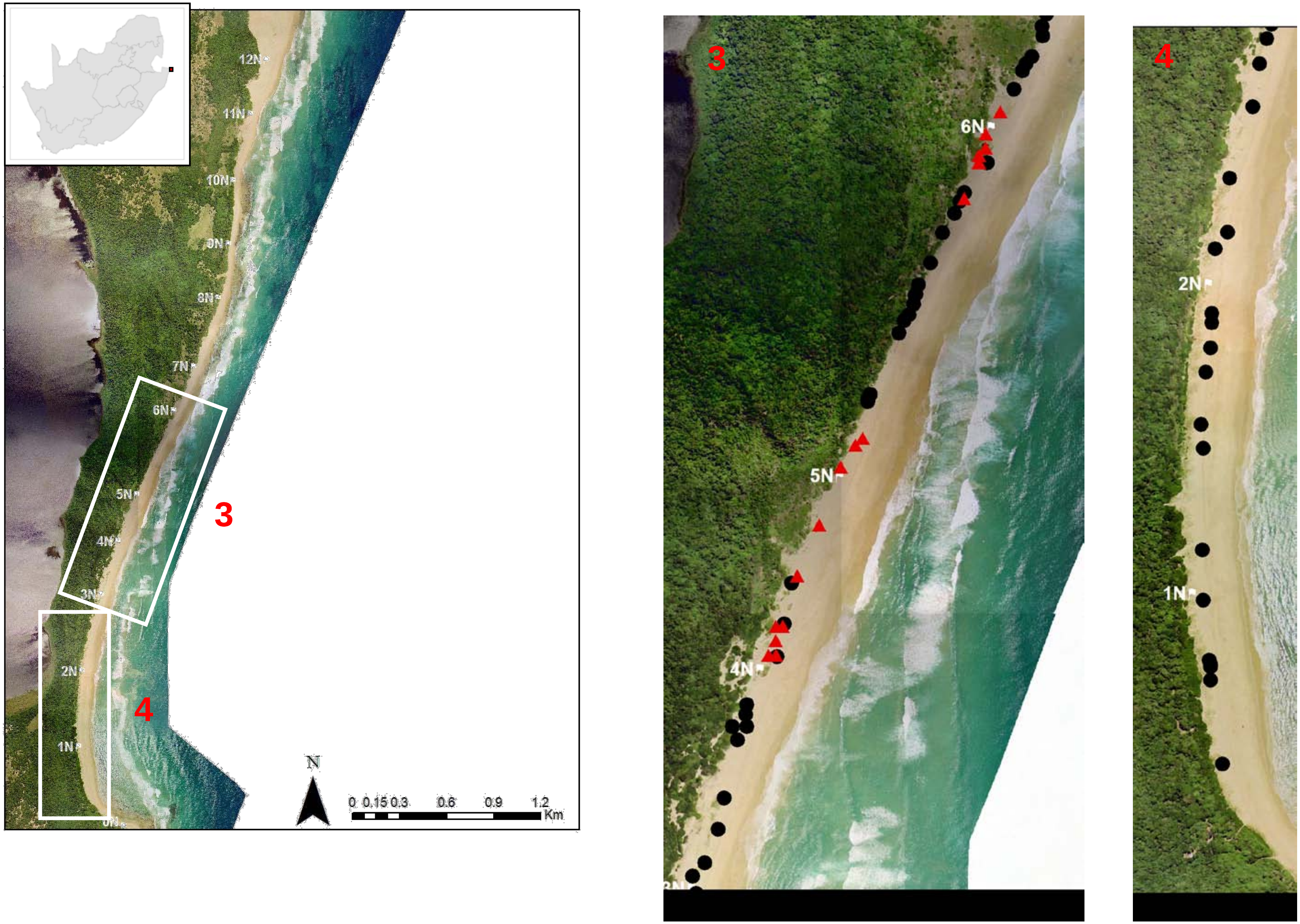

Fig. 5.1b. Distribution of hatched loggerhead nests to predated loggerhead nests from beacon 6N to beacon 1N.

Nest success was not even across beacons 1N to 12N ($X^2_{0.05, 11}$ = 98.85, p = 0.000). The lowest nest success was evident at beacons 9N and 10N were the nest success was 33.3 % and 28.6 % respectively (Fig. 5.2). Other beacons showing lower nest success were beacons 1N and 11N that both had success rates of 50 %. The highest nest success was that of nests placed at beacons 2N and 3N where there was a 100 % success rate among the nests. The beacon with the highest density of loggerhead nests, beacon 8N, also had a relatively high level of nest success amoung the nests, namely 90.9 %. The overall nest success of all nests was 65.0 ± 7.29 % (mean ± standard error).

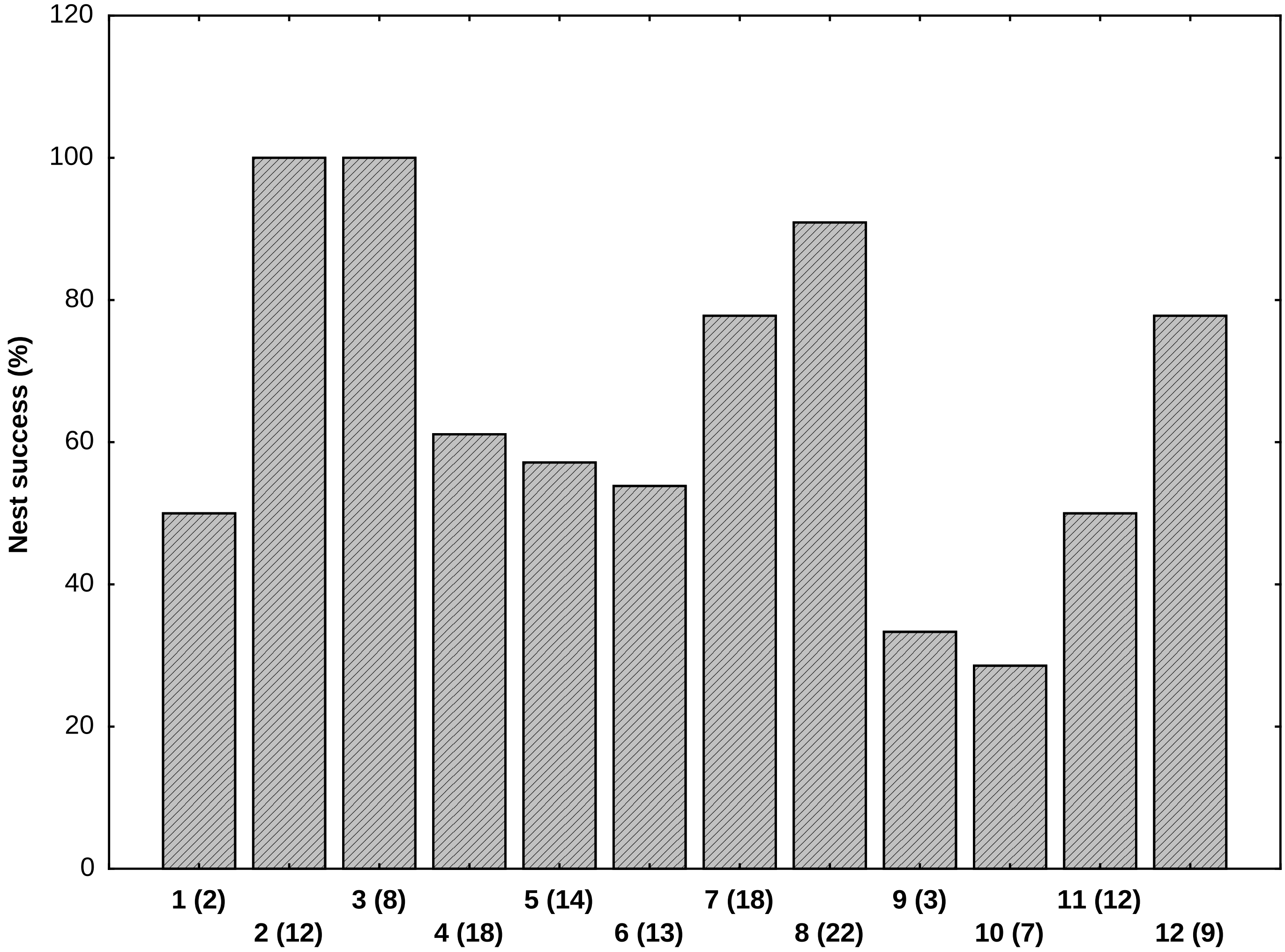

Fig. 5.2. Nest success of loggerhead nests along the sampling area (beacon 0N to 12N). Shown in brackets after the beacon number is number of nests per beacon.

Hatching success and emergence success showed no significant relationships between distances from vegetation although the highest values were observed in nests that were more than 9 m from vegetation (95.9 ± 15.03 %). There was no correlation between the distance from vegetation and hatching success, ($r = 0.13$, $p = 0.4$). Emergence success mirrored trends of hatching success and no correlation was observed between distance from vegetation and emergence success ($r = 0.82$, $p = 0.61$). In terms of distance above the high water mark (HWM), highest hatching success was observed at two areas above the HWM, one at 31 – 35 m above the HWM where hatching success was 95.2 ± 2.23 % and the other at 41 – 45 m above the HWM where hatching success was 95.72 ± 2.98 %. The highest figures observed for emergence success were 89.59 ± 9.1 % and 94.56 ± 1.47 % respectively. There was no correlation between hatching success and the distance above the HWM ($r = 0.16$, $p = 0.3$) or emergence success and the distance above the HWM ($r = -0.07$, $p = 0.65$). The position above the high water mark or distance to vegetation does not affect hatching success due to the uniformity of conditions. However, the importance lies in whether the nest is laid above or below the HWM.

Hatching success of loggerheads was very similar in the open sand compared to vegetation ($t_{0.05\ (2),\ 37} = 0.5$, $p = 0.62$) although the variability in vegetation was much higher (Fig. 5.3.). The average hatching success in the open sand was 83.37 ± 4.04 % ($n = 32$) while in vegetation hatching success was 79. 06 ± 9.37 % ($n = 10$). Emergence success of hatchlings in vegetation (78.22 ± 9.24 %) was also similar to that of the hatchlings in the open sand (77.92 ± 4.11 %, Fig. 5.3).

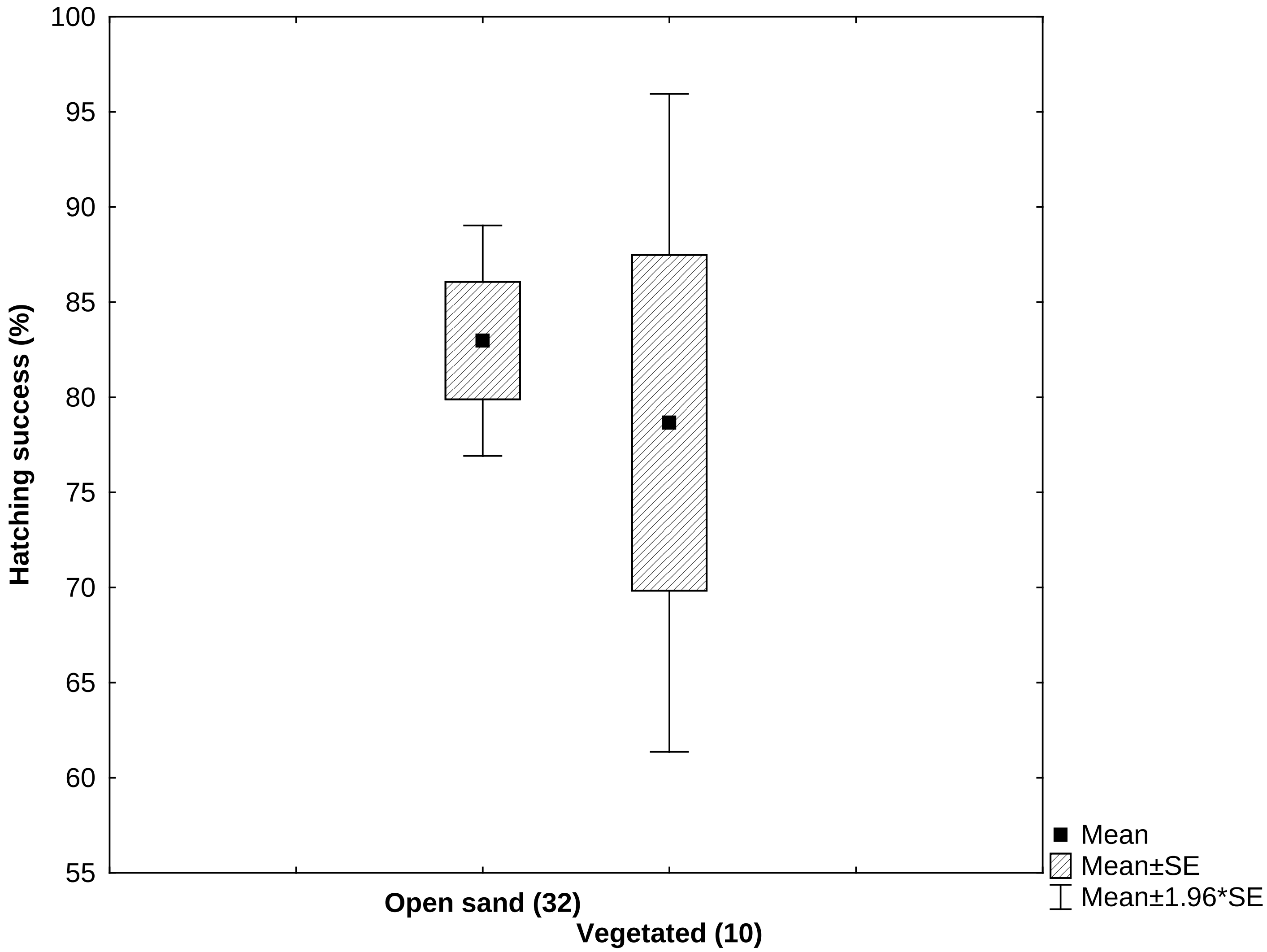

Fig. 5.3. Hatching success of loggerhead nests in open sand versus vegetated areas. Number of nests are indicated in brackets.

The average incubation period for loggerheads across the beach was 66.83 ± 1.15 days (n = 35). The longest incubation period of all the nests that were recorded was 82 days and this nest was situated in open sand. The shortest incubation period was 58 days and this nest was also recorded in open sand. Incubation periods tended to be of shorter duration in the vegetated areas than in the open sand as seen in Fig. 5.4. The average incubation period in the vegetation was 64.67 ± 1.25 days (n = 6) with the longest duration in this area 68 days compared to 82 days in the open sand. Nests in the open sand incubated for an average of 67.28 ± 1.36 days (n = 29). There is no significant difference in the incubation period between the open sand nests and the nests that were situated in vegetated areas ($t_{0.05\,(2),\,33}$ = 0.87, p = 0.87) due to high variability.

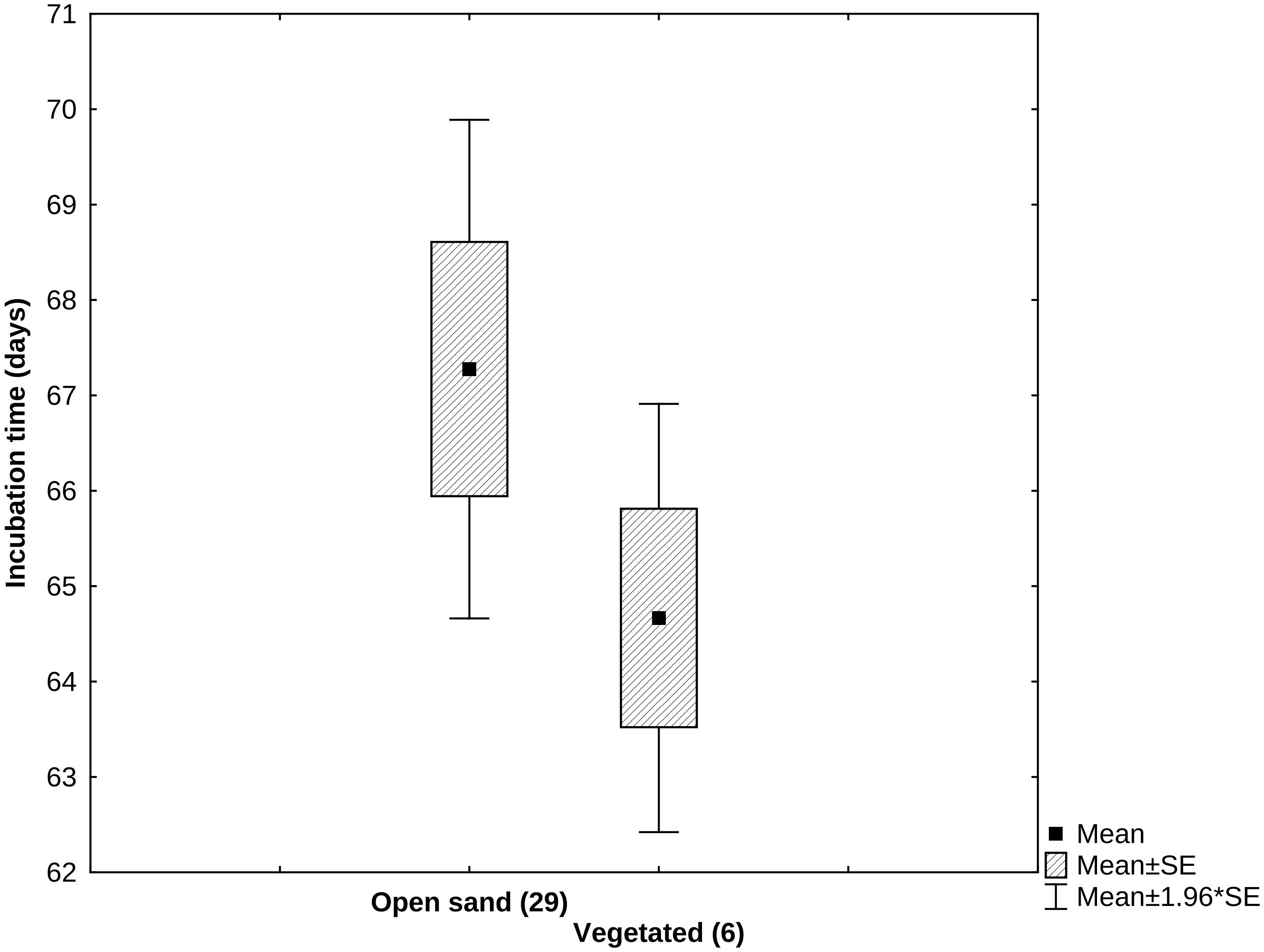

Fig. 5.4. Incubation period of loggerhead nests in open sand and vegetated areas. Number of nests per area are indicated in brackets.

There was no clear indication as to which nests would be more prone to nest predators such as ants, worms, honey badgers and small felines. Predated nests appear to be both closer to vegetation (4.7 ± 1.4 m) than non-predated nests (9.9 ± 5.25 m) and closer to the HWM (29.9 ± 3.71 m) than non-predated nests (33.7 ± 3.25 m). There were no significant differences expressed between the distance from the vegetation of predated (n =

15) and non-predated (n = 40) nests ($U_{0.05\ (2),\ 15,\ 39}$ = 285, p = 0.89) and between the distance from the HWM of predated and non-predated nests ($U_{0.05\ (2),\ 15,\ 39}$ = 232, p = 0.25).

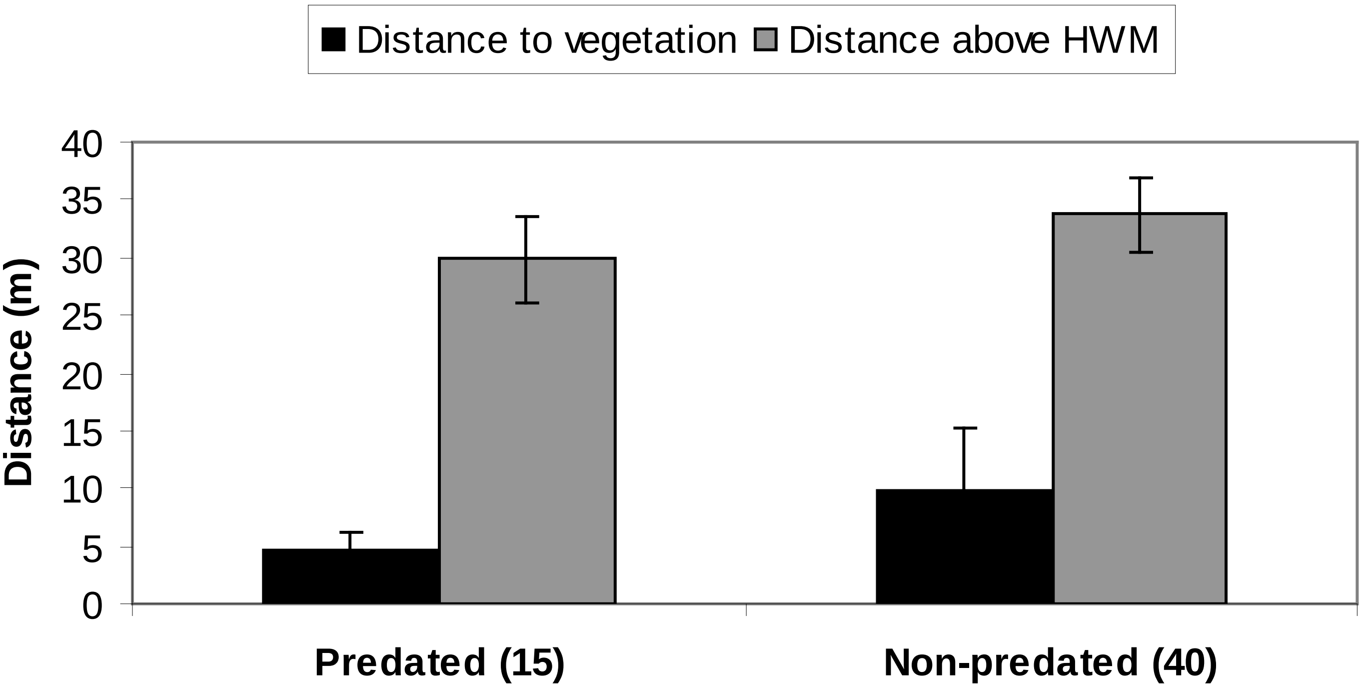

Fig. 5.5. Average distance to vegetation and HWM of predated and non-predated loggerhead nests. Error bars represent standard error (SE).

DISCUSSION

All beacons (1N to 12N) showed high hatching and emergence success compared to other studies focusing on hatching success (Table I). Some of the estimates may be unusually high as only one or two nests were recorded for a particular beacon. The larger the number of nests the more accurate the estimate of hatching success. Hatching success for loggerheads in South Africa was 82.93 ± 1.88 % with emergence success being slightly lower at 79.11 ± 2.04 % with these two being highly correlated as expected (Miller *et al.* 2001). Hatching success in South Africa was higher than in Turkey, 77 ± 26 % (Peters *et al.* 1994) and Greece, 65.1 % (Skoufas 2005) with the results closer to the general estimate made by Miller *et al*. (2001) for loggerhead populations around the world. Compared to other species of sea turtles, loggerheads have a near even hatching success to green turtles (83 %) as found by Fowler (1979) and a higher hatching success when compared to leatherbacks (Bell *et al.* 2003; Wallace *et al.* 2004; Ralph *et al.* 2005).

Clutch sizes vary between different clutches as well as within and between turtle populations around the world (Miller *et al.* 2001). Results from the current study showed that the average clutch size of loggerheads in South Africa was 99.85 ± 2.21 eggs which is less than the average number of eggs (112.4) mentioned by Miller *et al.* (2001). Clutch size estimates from the current study confirm results from Florida and Turkey were clutch sizes were 98.5 ± 1.7 eggs and 90.3 ± 27.2 eggs respectively (Peters *et al.* 1994; Antworth *et al.* 2006). A study by Skoufas (2005) in Greece indicated higher clutch sizes (up to 127.4 eggs) for loggerheads as compared to South Africa’s population. The larger clutch sizes of loggerheads in Greece may be owed to the fact that they have lower hatching success (65.1 %) than other rookeries and this may be a reproductive strategy employed by these loggerheads to increase the number of hatchlings and ultimately the number of loggerheads that return to nest in the future (Skoufas 2005) or there is a growing proportion of inexperienced nesters.

Hatching success and emergence success were not found to be dependent on any of the physical parameters such as slope, average grain size and pH, that females could possibly use as factors to select sites. This may be due to the physical parameters not differing from one beacon to the next (Table I). This was also found to be the case in a study by Wood and Bjorndal (2000). However, their explanation for the situation was that egg mortality and factors such as environmental conditions, that cannot be controlled by female turtles, may alter hatching success so that it does not reflect the original selection by females. The hatching success for loggerheads in South Africa is high and is not of concern for the future survival of the species at present. Further study of physical factors and hatching success across the whole monitoring area of 56 km could however show a different result as the beach topography and physical factors (mean sand grain size, pH and slope) could change over a larger scale. It should be kept in mind that loggerhead nesting varies considerably over this stretch of beach (32N to 100S) and this high-density area (0N to 12N) was pre-selected due to its success.

Across the beacon from dune base towards the sea, hatching success did not differ significantly with the highest hatching success at more than 9 m from the vegetation and emergence success highest at 1 m and 6 m from the vegetation. This differs from Wilson (1998) who found that survivorship of embryos in nests increased towards the vegetation for freshwater turtles. Hatching success and emergence success were similar between the open sand and the vegetation. This could reflect that differences between nest sites, such as vegetation cover, do not affect development of embryos (Kamel & Mrosovsky 2005). These results confirm those found by Kolbe & Janzen (2002) and Kamel & Mrosovsky (2005).

Another aspect that vegetation has been shown to affect is the incubation time of nests (Fowler 1979; Wilson 1998; Kolbe & Janzen 2002). Eggs that are placed in open sand areas were found to incubate faster and therefore hatch sooner as opposed to those in vegetated areas that may be shaded (Wilson 1998). The results from the current study are not in agreement with those found by Wilson (1998) as the term ‘vegetation’ may have differed between the two studies. The vegetation in the study area was sparse and short and consisted of plant roots, *Ipomoea brasiliensis* and *Scaevola plumieri*, with no large trees present in the immediate vicinity of the nests that would shade them for extended periods of time. Therefore, there is no significant difference observed in the current study between the vegetated and open areas as the vegetation had little influence on the incubation temperature.

Distance to the high water mark (HWM) has been indicated as a factor in determining nest success or whether a nest hatches at all (Kamel & Mrosovsky 2004; Kamel & Mrosovsky 2005). The concern associated with nest success and the HWM is the incidence of inundation of the nest by sea water (Wood & Bjorndal 2000; Kamel & Mrosovsky 2004; Kamel & Mrosovsky 2005). Inundation of the nest is risky in terms of sudden decreased temperatures that may affect metabolic processes and sex determination, erosion of the nest and a reduction in oxygen availability near the end of incubation, resulting in the entire clutch suffering mortality (Wood & Bjorndal 2000; Miller *et al.* 2001). The previous statements could be used to explain the low occurrence of nests that hatched between beacons 9N and 10N. The nests in this area were subjected to storm swells that forced the HWM up to the border of the vegetation and therefore would have inundated most, if not all, nests in that region. In terms of hatching and emergence success, no results from other studies based on the same criteria were found in terms of distance to the HWM except for that of Kamel and Mrosovsky (2005) who stated that emergence success decreased towards the HWM. The same result being apparent in this study however, not significant.

Nest success varied along the beach with nest success of 100 % at beacons 2N and 3N. However, this is not the area that has the highest number of nests placed per season which means that the maximum number of hatchlings is not leaving the rookery every year. The main reason as to why fewer nests are placed in this area is presumably due to the artificial lights that occur in this area. Loggerheads have been shown to avoid areas of artificial lighting (Mortimer 1995; Steyermark *et al.* 1996; Kikukawa *et al.* 1999; Witherington 1999; Antworth *et al.* 2006). Hatchlings are attracted towards light sources (Hughes 1989; Bourgeois *et al.* 2009) and therefore hatchlings that hatch in these areas may be attracted to the lights instead of the sea (pers. obs.). This may then increase the amount of time that hatchlings may be out of water and therefore may be subjected to dehydration and increased predation.

No pattern was observed between the predated and non-predated nests in terms of open sand and vegetation and distances from the vegetation or the HWM. A study by McGowan *et al*. (2001) showed that the distance to the HWM had a significant effect on whether predation by fly larvae occurred or not. Nests further from the HWM were less prone to infestation due to the greater distance from the debris accumulated on the HWM (McGowan *et al.* 2001). However, nests closer to vegetation and further inland were also prone to natural predation (Wood & Bjorndal 2000). Of importance to note is the difference in predator species between the two areas. Closer to the vegetation predators are primarily honey badgers and ants (Fowler 1979; Hughes 1989) while those closer to the HWM ghost crabs and fly larvae are the main predators (McGowan *et al.* 2001). According to Hughes (1989), predated nests did not contribute a significant proportion of the nests during the entire season (4 %). Predation is a form of sea turtle mortality on eggs or hatchlings therefore should be seen as an important factor. A suggestion is that records are kept on predation of nests and the predator be identified in each case so that the biggest threat in terms of predation may be singled out and mitigated. For example placing baskets over nests to maximize the number of eggs safely incubated and hatchlings emerging.

Loggerheads in South Africa have high rates of hatching success and emergence success. These nests are able to incubate and hatch safely due to the protection afforded by the iSimangaliso Wetland Park. It seems that females place nests in positions that facilitate the hatchlings to orientate towards the ocean. If this is in fact the case, meaning there is a clear line of sight to the ocean for the hatchlings (Godfrey & Barreto 1995), they only have to contend with terrestrial predators to reach the sea successfully. However, if the line of sight from the nest to the ocean is obstructed by dunes or vegetation hatchlings (Kamel & Mrosovsky 2005), may face not only terrestrial predators but also dehydration and the possibility of never reaching the ocean (Godfrey & Barreto 1995). Nests also need to be placed where they will not be inundated by tides or storm swell. It is thus concluded that the only clear site selection criterion that seems to be influencing the hatching and emergence success of loggerheads in the high-density loggerhead nesting area (0N - 12N) is the placement of nests above the HWM.

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CHAPTER 6

SYNTHESIS AND CONCLUSIONS: NESTING ECOLOGY OF LOGGERHEADS AND LEATHERBACKS IN SOUTH AFRICA

INTRODUCTION

Sea turtles begin long migrations back to natal rookeries at the onset of nesting seasons when they are reproductively prepared (Hughes 1989; Bowen *et al.* 1993; Miller *et al.* 2001; Lee *et al.* 2007). The timing of this is seasonal and coincides with warmer water and air temperatures (McAllister *et al.* 1965; Hughes 1989). Homing to rookeries could occur in two ways; social facilitation and natal philopatry (Bowen *et al.* 1992; Bowen *et al.* 1993; Bass *et al.* 1996; Dutton *et al.* 1999; Lee *et al.* 2007). Of the two theories, natal philopatry has received the most evidence supporting it. It may occur through either population-specific genetic programming to a specific rookery or environmental imprinting (Bowen *et al.* 1989). A feature of natal philopatry is that there is a lack of gene flow within species across rookeries and therefore all rookeries are genetically variable (Bowen *et al.* 1989; Dutton *et al.* 1999; Lee *et al.* 2007).

Once back at the natal rookeries, sea turtles begin mating. Some male sea turtles show fidelity to specific courtship areas off the natal beaches season after season and therefore females would know where to find males (Pandav *et al.* 2000; Tripathy & Pandav 2007). It is possible that the males follow the same cues as the females as they were once hatchlings on the beach themselves. After mating, males return to foraging grounds and females remain at the nesting grounds (Miller *et al.* 2001). Female sea turtles have the ability to store sperm and therefore are able to produce a number of clutches within a season depending on the species (McAllister *et al.* 1965; Hughes 1989; Bowen *et al.* 1992; Nordmoe *et al.* 2004; Wallace *et al.* 2007).

South Africa has two nesting species of sea turtles, namely loggerheads and leatherbacks. The nesting season begins in October and ends in March (Hughes 1989) although the number of females nesting in the last two months of the season is small. Females begin nesting by selecting a stretch of beach following cues (possibly olfactory) to place their clutches of eggs (Bowen *et al.* 1989; Wilson 1998; Wood & Bjorndal 2000; Miller *et al.* 2001). Once the stretch of beach is selected (nest site fidelity), females need to refine their choices by choosing specific sites along the stretch of beach to haul out and ultimately find a "suitable" nest site to place their eggs, termed nest site selection (Wood & Bjorndal 2000; Miller *et al.* 2001). The eggs remain incubating in the nest for approximately 60 days (Hughes 1989; Bowen *et al.* 1993; Nordmoe *et al.* 2004) with the peak hatching period in South Africa during February and March. When nests have completed incubation, if the female was successful in her selection of a nest site, approximately 50 % to 80 % of the eggs oviposited (species and population dependent) should hatch and slightly less should emerge (Miller *et al.* 2001; Nordmoe *et al.* 2004). Once hatchlings have emerged and reached the sea successfully, they too should one day return to this same beach either to mate and/or nest.

SELECTING STRETCHES OF BEACH – NEST SITE FIDELITY

Nest site fidelity was defined at the start of the thesis as the ability to restrict nesting to a specific stretch of beach that is smaller than the stretch of beach available. South Africa has a somewhat unique situation in terms of beach choice for nesting sea turtles as there is almost 200 km to choose from (Hughes 1996). Therefore, sea turtles nesting in South Africa would have a greater opportunity to disperse but also conversely to show higher specificity than sea turtles nesting on island rookeries where stretches of beach are often less than 5km in length.

Loggerheads showed a very high degree of nest site fidelity by placing nests ~3 km apart. A small fraction (0.44 %) of females nested up to 40 km apart whereas the majority of females (80.61 %) nested within 5 km of previous nest sites. With the proportion of females nesting in excess of 40 km apart being so small, showed that these nesting "inaccuracies" were limited events. From one nesting season to the next (between-season nest site fidelity), nest site fidelity improves and individuals become more accurate in nest placement (by increasing nest site fidelity) between seasons. Across seasons, loggerhead individuals are able to return to the same stretch of beach used in previous seasons enforcing the fact that loggerheads “learn” where to nest from one season to the next.

Loggerheads are specific in selection of stretches of beach as approximately ~60 % of the entire population nest in a relatively small area (0N to 32N) adjacent to Lake Manzamyama (Nel 2008; Nel 2009). It is thought that this lake is what attracts the majority of loggerheads to nest in this area (Hughes 1989) and the results from the current study also suggest that a “cue” for loggerheads nesting in this region of the South African rookery must exist. Further studies should focus on this cue, whatever it may be, and ensure that it remain in a pristine condition if it is for instance the outflows from the lake adjacent to the nesting beach.

Leatherbacks follow a strategy of placing nests further apart than loggerheads, ~9 km, and the population as a whole is more evenly spread across the 56 km monitoring area than loggerheads. It must however be stressed that the results for leatherbacks are only an indication of nest site fidelity within the 56 km turtle monitoring area as they are known to nest outside of this area (Hughes 1996; Nel 2008) and therefore data from nesting outside of the monitoring area would not have been captured. Nest site fidelity of leatherbacks may be a consequence of females selecting areas based on practicality rather than fresh water outflows as a cue. Leatherbacks showed little indication of learning where to nest both between and across seasons. This supports the idea that leatherbacks do not follow the same cues as loggerheads and therefore are not able to refine their choices during subsequent seasons.

CHOICES, CHOICES – NEST SITE SELECTION

How females select their nest sites within a stretch of beach chosen seems straight forward. Both loggerheads and leatherbacks select nesting areas away from inshore rocks and this is due to injury to the animals coming ashore and the higher amount of predators associated with rocky areas (Eckert 1987; Mortimer 1995; Garmestani *et al.* 2000). However, loggerheads were suggested to select areas adjacent to inshore rocks as these help with the final orientation to beaches (Hughes 1989; Kikukawa *et al.* 1999). This is possible as much nesting occurred around beacons 7N and 8N and these areas are both associated with intertidal rock but are still accessible to sea turtles at low tide. The beach type selected for by both leatherback and loggerheads is of an intermediate morphodynamic state. This may be due to the high occurrence (45 %) of intermediate beaches in comparison to reflective and dissipative beaches along the Kwazulu-Natal coast (Harris 2008). Along with the selection of intermediate beach types by leatherbacks, they select haul out sites with wider surf zones. This reflects the selection of intermediate beaches as they were shown to have significantly wider surf zones than reflective beaches and beaches characterised by low shore rock. The same did not hold for loggerheads.

Once on the beach, both populations of turtles do not seem to respond to any other cue other than the high water mark. If nests are placed below the high water mark, they will be destroyed by inundation and erosion (Hughes 1989; Wood & Bjorndal 2000; Miller *et al.* 2001). If the stretch of beach has been selected through nest site fidelity, and it is only 3 km long for instance, the chances of change in beach conditions along this area are small compared to a 56 km area where the chances of change are larger. Therefore once a loggerhead has nested in a certain area in a season, she will not need to assess the area at a later nesting event and with them showing increased nest site fidelity across and between seasons, the need to assess the beach again may be needless. Turtles must have therefore evolved a mechanism of informing them when they have surpassed the high water mark.

THE ULTIMATE GOAL – HATCHING SUCCESS

If females nest successfully and the nest hatches successfully, overall the female was successful in her task of nesting. Hatching success for loggerheads in South Africa was high overall (~83 %) and there is an indication of high fertility of females from the results. Nest success was not spread evenly across the area at Bhanga Nek where few nests were placed in the areas of 100 % (beacons 2N and 3N) nest success. The majority of nests were placed at 8N where nest success was 90 %. This is a high success rate however, if more nests were placed in the region of 2N and 3N, even more hatchlings would be successfully recruited from the South African rookery.

EVOLUTIONARY BIOLOGY

Nest site fidelity drives to the heart of sea turtle biology, and natural selection. Without nest site fidelity, sea turtle populations would probably not nest at rookeries as we know them today as no homing drive would be generated through nest site fidelity. Sea turtles would have no need to home back to natal areas and any beach could be deemed “successful” for incubation within limits. For instance, temperature is a major factor limiting sea turtle distribution and therefore nesting occurs in the tropics and subtropics as it is however, not strictly conforming to rookeries. The genetic status of individuals would most likely not conform to certain populations and populations would not be isolated at present day. The purpose of the genetic isolation would possibly be the imprinting or genetic programming that occurs on hatchlings to a specific rookery so that turtles come back to this rookery when reproductively active.

As a result of a high degree of nest site fidelity of loggerheads in South Africa, all nests are placed relatively close to one another. Most females belonging to the loggerhead population in South Africa will be in close proximity as ~60 % of all loggerhead nests within a season are laid between 0N and 32N (Nel 2008; Nel 2009). With high densities of females occurring in this area, males would presumably be attracted to the same area by cues and females. Once mated, females can select a nest site and through having nested and had successful oviposition without being injured by rocks, not having to crawl far and with difficulty, hindered in digging efforts by the sand, preyed upon, disturbed by humans, and observing other females in the area, loggerhead females may “learn” where to nest by laying subsequent nests within and between seasons in the same area. The evolutionary advantage of learning where to nest is that hatching success should be favourable especially with the placement of many loggerhead nests in the same area as predation on single nests will be lowered. The incidence of predation on hatchlings may also be lower if more than one nests hatches on the same evening as well as predation on nesting females which is the principle used by olive ridley turtles nesting in arribadas. Females are also able to conserve energy as they do not have to actively search and assess each new nest site. In doing so, females become more well acquainted with stretches of beach.

Leatherbacks show a lower degree of nest site fidelity however, high in terms of the area of beach provided for nesting. Leatherbacks presumably follow different cues to loggerheads and follow cues based on practicality. The advantage of the strategy employed by leatherbacks is that spreading of nests as a population decreases the threat of total eradication of a season’s nests with one disturbance (oil spill, storm swells). If disturbances are prevalent during one nesting season, leatherbacks could easily adjust nesting sites, unlike loggerheads that are inflexible in nest placement. In light of predation on nests, leatherbacks may be more at risk as there is no clumping associated with the distribution of nests along the rookery. Therefore if one leatherback is solitary and some distance from surrounding nests, there is an increased risk that the nest will be predated.

Nest site fidelity of sea turtles dictates nest site selection. Once a stretch of beach is identified and selected, nest site selection will take place within this section. Females have two considerations when nesting; their safety and the safety of their nests. Having already assessed the beach through a positive nesting experience, a female can select a nest site based on her knowledge of the area. The factor that seems to be of the utmost importance when selecting a site to place the nest is the high water mark. Turtles seem to surpass the high water mark and once past this point there seems to be very little that influences the decision of the placement of the nest. Nest site selection in terms of high water shows evolutionary potential (Kamel & Mrosovsky 2004). If the sea-level were to rise, sea turtles would be able to adjust nest sites according to the level of the high water mark (Kamel & Mrosovsky 2004) should there be enough beach available.

Nest site selection dictates hatching success of nests. If the nest site is favourable, hatching success should be high assuming female fertility, sperm viability and no embryonic mortality. If the nest hatches successfully, and is not predated upon or washed away by tides, hatchlings should return to the very beach where they once hatched as this is the only beach that they will know which is successful for incubation and that they have been genetically "programmed" to return to.

CONSERVATION IMPLICATIONS

Nest site fidelity of sea turtle populations can assist in the identification of core areas for conservation. In the case of loggerheads in South Africa, the area 4N to 11N was used consistently by individuals nesting in subsequent seasons. Nel (2008, 2009) showed that the area from 0N to 32S had 60 % of all nests placed in this area. Thus, the area is of high conservation priority. The importance of this area raises the issue of artificial lighting. In the summer months, the months that coincide with turtle nesting in South Africa, informal campsites and field ranger houses use artificial lighting from dawn to approximately 10 pm. Female turtles avoid areas where artificial lighting is present (Mortimer 1995; Steyermark *et al.* 1996; Kikukawa *et al.* 1999; Witherington 1999; Antworth *et al.* 2006) and furthermore, hatchlings are attracted towards light sources (Hughes 1989; Bourgeois *et al.* 2009). Results from the current study showed that false crawls of loggerheads were random but highest in the area where lighting is prevalent at beacon 0N. Another problem is that nest success is 100 % at both beacons 2N and 3N and therefore if more turtles were allowed the opportunity to nest in this area without disturbance, more hatchlings may ultimately be hatched from the rookery. A suggestion is that management actions be taken to reduce the amount of artificial lighting in the area of 2N and 3N to allow more loggerheads and possibly leatherbacks to nest in this area.

Nest site fidelity may be an important tool in determining the effects of climate change on nesting sites of sea turtles. Any major shifts could be recognised especially working with individual turtles and their between and across season nest site fidelity to determine if there are any changes in these. The current study showed no evidence of changes in the rookery, however, along with these results, future results may suggest different trends.

CONCLUSION

There is the uttermost importance in selecting sites that the female would deem “successful” for the development of her embryos as there is a lack of parental care of nests and offspring. Sea turtles may have therefore reverted to strategies whereby placing many eggs per nest to try and increase the number of hatchlings that survive to adulthood (Hendrickson 1980) and then repeatedly nest in close proximity to this site to further enhance the chances of her offspring.

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