Nest site selection and nest site fidelity in sea turtles

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by

Michaela King

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Supervisor: Prof. Ronel Nel

Co-supervisors: Dr Diane le Gouvello & Dr Linda Harris

Declaration

Full name: Michaela Jade King

Student number: 216044464

Qualification: Master's in Science (Zoology)

Declaration:

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

Signature:

Date: 06-03-2023

Abstract

Nest site selection and fidelity have many ultimate and proximate benefits and are thus found in many species, including sea turtles. Reproductively mature female sea turtles exhibit large-scale homing to rookeries where nest site selection and fine-scale fidelity to specific sites on rookeries for clutch placement (within and across nesting seasons) takes place. Environmental features (in-water, on-shore, and further inland) act as cues for nest site selection and nest site fidelity and operate across spatial and temporal scales. Nest site selection and nest site fidelity constitutes one of the only parental investments for oviparous reptiles during the reproductive process before digging a nest, depositing a clutch, and covering the nest again. Owing to the limited parental care and maternal investment by sea turtles, nest site selection and nest site fidelity will have implications for incubation and the quality and quantity of the resultant offspring that in turn can affect reproductive success and fitness. Should inappropriate nest site selection and fidelity at an individual level be found fixed within a population as a maladaptive habitat choice, then this could impact the abundance of the sea turtle population in the long-term. A decrease in sea turtle nesting abundance could be critical considering the low conservation status of many populations in various regional management units.

The population-level nest site selection and individual level nest site fidelity behaviour were tested for loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles from iSimangaliso Wetland Park. The rookery, on the north-eastern coast of South Africa, consists of ~200 km of mostly continuous (i.e., not segmented) beach with heterogenous coastal features. The overall aim of this thesis is to disentangle nest site selection using a spatial data set that extends further into the off-shore bounds of rookery (not covered in many other studies) and to compare nest site fidelity for loggerheads and leatherbacks in a South African rookery between species and across time.

Chapter 2 aimed to compare the nesting distribution of both loggerhead and leatherback populations along the iSimangaliso Wetland Park rookery and determine which coastal features can potentially drive the nesting distribution of each population. Objectives to disentangle nest site selection behaviour included: 1) describing and comparing the differences in nesting distribution of each population; 2) investigating spatio-temporal consistency of nesting of each population using 54 years of monitoring data; and 3) determining the coastal features along-shore and across-shore associated with the nesting preferences of each population using a General Niche-Environment System Factor Analysis (GNESFA) in R version 4.2.1 based on spatial data of nest locations and coastal features in ArcMap 10.7. The aim of chapter 3 was to compare the nesting behaviour and nest site fidelity among individuals within each population The objectives for nest site fidelity (within each population) included: 1) comparing the nest site fidelity of individuals in each population; 2) comparing the nest site fidelity of experienced versus less experienced (i.e., neophyte) nesters; and 3) comparing the nest site fidelity of emergence sites and nesting sites between and within species.

Results for nest site selection showed that loggerheads had an uneven distribution congregating in the north and sparse distribution in the south, compared with leatherbacks who showed a more evenly dispersed distribution with a few hotspots scattered throughout the rookery. The number of nesting loggerheads was also greater than the number of leatherbacks and both populations' emergences were spatially and temporally consistent. GNESFA results suggest that both populations select nesting areas close to coral reefs and dissipative intermediate beach types. Loggerheads had stronger preferences than leatherbacks did, and selected specifically for southern coral communities, and northern estuarine lakes but selected against reflective beaches and rocky shores. Leatherbacks were less specific in their preferences and selected for vegetated nesting areas with sand-dominated mixed shores and selected against both northern estuarine lakes and southern freshwater lakes.

Results for nest site fidelity showed that loggerheads had greater nest site fidelity (i.e., nests placed closer together) than that of leatherbacks. Loggerhead experienced nesters also had significantly greater nest site fidelity than neophyte nesters and this was reflected in significant improvement in nest site fidelity of individuals over time. Leatherbacks had no significant difference in nest site fidelity between turtles of different nesting experience and no significant change in nest site fidelity of individuals over time. Fidelity between emergence sites (including false crawls) and nesting sites did not differ for loggerheads or leatherbacks, indicating that selection for nesting habitat is more decisive before the haul out and where loggerheads and leatherbacks are emerging from the water is their preferred location for nesting regardless of if false crawls are committed.

Nest site fidelity and nest site selection are dynamic among sea turtles, with interspecific and intraspecific variation and sometimes change within individuals. However, both high and low nest site fidelity, as well as specialized or generalized approaches to nest site selection can impact the reproductive success of individuals and the reproductive fitness of populations. While reproductive success or fitness was not measured in this study, results obtained in the dissertation provide a basis for future studies and presents more questions as to why the nesting populations differ in their population recovery following equal conservation effort.

Contents

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CHAPTER 1: INTRODUCTION

Like species such as Pacific Salmonids (Lohmann, Putman, et al. 2008) or the Atlantic puffin (Coulson 2016), sea turtles display a behaviour pattern known as natal homing. Natal homing is initial homing event when animals return to their birthplace to reproduce themselves. In reproductive seasons following the initial natal homing event, successive homing occurs to the same site. However, the return of these animals to their natal streams and beaches has received some attention in evolutionary discussions, not only in the context of why and how they do this, but also once they are at the natal rookery or stream, how do they select specific breeding sites, and do so repeatedly?

Sea turtles are marine organisms, but females undergo an obligatory terrestrial phase when nesting on land (Lutz et al. 2002a). It has been argued that as a result of their own successful hatching on their natal beach, incubation conditions were previously suitable and thus there is a reasonable chance that their own reproductive efforts will be successful (Lohmann et al., 2013). The patterns of selecting a nesting site upon arriving at a natal beach, and doing so repeatedly, however have been less studied. This is in part due to the size of the nesting beaches either being small, e.g., on islands (Patino-Martinez et al., 2022) or fragmented (Leighton et al., 2008). It is rare to have long, uninterrupted, unspoilt nesting beaches to nest on (as is the case in South Africa).

Once arriving at the natal beach or rookery, a nesting female will select a site to nest at (nest site selection). She will repeat this nest site selection process several times in the nesting season with the frequency and interval depending on the species (Robinson et al., 2022). These consecutive clutches may be placed in close spatial proximity to previously placed nests within the same season or from a previous season and relative to the total area available, thus exhibiting some loyalty to specific areas of the rookery (Botha, 2010). The selection process is critical as successful nest site selection represents the only parental input (other than the nutrients provided in each egg; Miller, 1997) provided by sea turtles toward their offspring's success (Hughes and Brooks, 2006). Sea turtles thus do not provide care for their offspring other than choosing a perceived appropriate nesting site, digging out a nest, depositing a clutch of eggs, and covering the nest from predators. Inappropriate nest site selection can result in failed egg development, hatching, or emergence success. Frequently failed nesting reduces an individual female's reproductive output over her reproductive lifetime and thus decreases overall fitness. (Serafini et al., 2009, Patrick and Weimerskirch, 2017).

Homing (successive returning after the initial natal homing) bringing turtles back to their breeding grounds operates at a macroscale, whereas nest site selection and nest site fidelity are at a meso- and microscale. Depending on how sea turtles are choosing where to nest repeatedly across these scales, there may be consequences for their reproductive fitness and thus ecological and evolutionary significance for nest site selection and nest site fidelity. By impacting reproductive fitness, nest site selection and nest site fidelity will also impact the conservation and management of sea turtle species. However, very little is known about the potential along-shore and across-shore coastal features acting as proximate and ultimate drivers of nest site selection at the population and individual levels.

Proximate and ultimate drivers of nest site selection

Proximate drivers provide immediate benefits to individuals like saving energy by limiting search time, whereas the ultimate drivers are those that have direct fitness consequences for populations over many generations (Mayor et al., 2009, Hildén, 1965). The ultimate and proximate drivers affecting nest site selection behaviours are better studied in birds (Burger, 1987, Regehr et al., 1998, Ardia et al., 2006). For example, the concept that environmental temperature and social cues affects nest site selection and that nest site selection then impacts reproductive success, as seen in Piping Plovers (*Charadrius melodus*) (Burger, 1987, Ardia et al., 2006). Additionally, studies in birds have also shown that nest site selection can also incur anti-predator benefits which also has consequences for increased clutch size, hatchling rate and fledgling rate which increases reproductive benefits (Burger, 1987, Regehr et al., 1998). The concepts investigated in birds and other animal studies are relevant and applicable to sea turtles. However, owing to the spatial separation of juvenile and adult feeding grounds, migration routes and nesting habitats these drivers will operate on different spatial scales. Additionally, both proximate and ultimate drivers may affect sea turtle's nest site selection and nest site fidelity (Burger, 1987, Regehr et al., 1998, Ardia et al., 2006) and will thus impact their reproductive fitness on long-term and short-term temporal scales.

An example of a proximate driver for homing in sea turtles is the benefit of congregating offshore in courtship areas prior to nesting; creating high-density aggregations of males and females which reduces the energetic cost of finding a mate (Long, 2013, Theissinger et al., 2009). Considering the energetic cost of long distance migration from the foraging areas (Shimada et al., 2020, Shimada et al., 2021) and fasting or low food consumption during the nesting season (Smith, 2010), plus the female's energy investment during vitellogenesis (Hamann et al., 2002), saving energy by not having to search for mates or nesting sites is beneficial. These local (proximate) drivers provide immediate benefit to sea turtles such as saving energy, enhanced egg development, or hatchling survivorship.

Ultimate drivers confer long-term benefits leading to improved fitness for the nesting female and so her offspring (Wilson, 1998). An example of an ultimate driver for nest site selection in sea turtles is observed in olive ridley sea turtles (*Lepidochelys olivacea*) on arribada beaches with synchronized mass nesting (Kalb, 1999). The predator satiation hypothesis (Sweeney and Vannote, 1982) is applied when turtles saturate the nesting beach with an abundance of nests within the same time in the nesting season which reduces the probability of each individual nest being raided, or hatchlings being consumed by predators. A female returning to an area where her hatching and previous nesting attempts were successful implies favourable environmental conditions. Favourable conditions for sea turtle nesting includes a sandy rather than a rocky coast, a suitable climate, and temperatures facilitating development of sea turtle embryos (Davenport, 1997, Janzen, 1994, Laloë et al., 2014) and functional sex ratios in a population.

Given the long-lived and slow-maturing nature of sea turtles and the dynamic nature of land habitats, ultimate drivers are not always stable; previously suitable conditions may be lost over time. Nesting environments change rapidly or may be disturbed through storms, beach erosion, or coastal development, such that environmental conditions are no longer suitable for successful egg development but are still homed to and selected for by mature nesting females (Kolbe and Janzen, 2002). Such incidents may lead to an ecological trap (Pike, 2013, Buderman et al., 2020).

Ecological traps occur when individuals repeatedly make maladaptive habitat choices leading to reduced success despite higher-quality habitats being available, based on previously reliable cues that are no longer useful due to environmental changes (Schlaepfer et al., 2002). Examples include the unchanged selection of foraging habitat by seabirds despite detrimental environmental change, as noted after a dam collapse caused increased arsenic and cadmium bioaccumulation in seabird tissue in eastern Brazil (Nunes et al., 2022). A second example found in sea turtles is the migration of immature loggerheads to preferred winter foraging grounds in the North-East Atlantic, which are at times thermally unsuitable with sudden temperature drops (and predicted to become more unstable and unsuitable with climate change), which leads to many of the smaller juveniles stranding after undergoing cold-stunning (Chambault et al., 2021). Additionally in sea turtles, hatchlings orientate to the lighter horizon, irrespective if it is natural light or the artificial (street) light horizon dragging them inland as observed in Florida (Lorne and Salmon, 2007, Erb and Wyneken, 2019).

The effect of poor habitat choices can be buffered in the short term through large population size (Schlaepfer et al., 2002), e.g., metapopulation dynamics, migration rates and ecological traps inferred for Little Bustard, *Tetrax tetrax*, populations in western France (Morales and Bretagnolle, 2022, Morales et al., 2005). An additional maladaptive habitat choice buffer is eventual behavioural adaptation. Adaptive behaviours have been observed in projected southward distribution shifts of loggerheads in Northwest Atlantic Ocean under the threat of climate change (Patel et al., 2021).

However, ecological traps could become evolutionary traps should the maladaptive behaviour choice persist (Schlaepfer et al., 2002). Evolutionary traps can arise through two scenarios (Schlaepfer et al., 2002); one occurs when the original cue is followed but the environment has detrimentally changed such that the original cue no longer reflects the original habitat, as seen in mayflies ovipositing on asphalt roads rather than ponds as both polarize light horizontally (Kriska et al., 1998). The second scenario arises when the environment and cue followed changes, but the changed cue elicits the same response as the original cue. An example of this second scenario is found in Cuban treefrogs where males attempt to mate with dead females found on roads following vehicular-induced mortality (Meshaka Jr, 1996) that reduces reproductive output and wastes reproductive energy. Most commonly, evolutionary traps are triggered by anthropogenic disturbances to environments such as the introduction of exotic species or expansions in agricultural areas (Robertson et al., 2013).

Theories behind natal homing

Natal homing, nest site selection, and nest site fidelity are driven by responses to external cues and stimuli experienced by individuals (Mayor et al., 2009, Hildén, 1965). These cues may be biotic (e.g., physiology and symbioses), varying from socialization with conspecifics and responses to predators or competitors (Regehr et al., 1998, Morris, 2003) to abiotic, environmental cues (e.g., temperature or light) for finding shelter and food (Cudworth and Koprowski, 2011, Hildén, 1965). For sea turtles specifically, there are many theories explaining the environmental cues behind broad-scale homing, i.e., homing of sea turtles to their rookery of origin (Lohmann et al., 2013). These theories include orientation to the earth's geomagnetic field, following ocean currents and following odour plumes (Lohmann et al., 2013, Painter and Plochocka, 2019).

Magnetic fields

The earth's magnetic field acts as a navigational cue directing movement and even causes a change in orientation at certain locations along turtle migratory routes (Lohmann et al., 2013, Lohmann et al., 2008). The earth's magnetic field is a grid-based rather than a map-based navigational process as animals respond to gradients of force rather than a guided migratory path using familiar landmarks (Bingman and Cheng, 2005). Many species orientate during long-distance migrations using magnetic fields; classic examples include Arctic tern (*Sterna paradisaea*) migrating from Greenland to either the West African or Brazilian coast (Egevang et al., 2010), monarch butterflies (*Danaus plexippus*) navigating from eastern USA and south-eastern Canada to the mountains of central Mexico (Chapman et al., 2015), and sea turtles, like the leatherbacks migrating across the Pacific from South China to the California Current Ecosystem and from the Indonesian sea to the Tasman Front (Benson et al., 2011)

Luschi et al. (2020) described a biphasic homing strategy for displaced loggerheads. Mediterranean loggerheads initially appeared confused when moved from a familiar location to an unfamiliar one further away, after which they then orientated directionally by (presumably) aligning with the earth's magnetic field and moved in an almost straight line towards the nesting beach. Directional homing was also noted in other studies for loggerheads from other rookeries on Cyprus (Broderick et al., 2007, Hays et al., 2014) and Zakynthos Island (Hays et al., 2014) and green turtles from Ascension Island (Hays et al., 2002, Broderick et al., 2007). These islands are small, isolated land masses relative to larger continental rookeries and may therefore require less fine-scale homing to locate specific nesting areas on the islands but more difficult broad-scale homing while migrating to the island or continental land mass. Supporting this, these same studies in the Mediterranean and at Ascension Island show that upon arriving on the coast, movement becomes less directed as sea turtles search for nesting habitats (Luschi et al., 2020, Hays et al., 2002, Broderick et al., 2007). Thus, magnetic fields are homing cues that may be useful at a macroscale to find land masses and the general proximity of the nesting beach. Magnetic homing is too crude for fine-scale orientation and nest site selection (Luschi et al., 2020, Mouritsen, 2018). Once close to, or on the coast, alternative cues must be used.

Odour plumes and ocean currents

Water composition varies between freshwater bodies and oceanic waters owing to processes occurring within freshwater bodies such as breakdown of anoxic organic matter and run-off after agricultural fertilization (Brazier, 2012, Golterman, 1975). When land-based sources such as lakes, estuaries, and groundwater empty into the sea, odour plumes and the compounds within them can be found in oceanic water bodies far from the freshwater origin (Koch et al., 1969). The transport of compounds such as sulphide, nitrite, and nitrate creating the plumes is due to diffusion and convection through winds and currents (Koch et al., 1969) that can then be detected by marine organisms. The use of olfactory cues for homing has been studied in the migration of anadromous fish; Salmonids and lampreys migrate from the open ocean to estuaries using olfactory cues to navigate upriver to spawning areas (Putman et al., 2013, Sutterlin and Gray, 1973, Bett and Hinch, 2016). Freshwater cues are however flow- and current-dependent, and vary in strength and direction, affecting homing efficiency.

For sea turtles, individuals from various nesting populations have returned to nesting beaches from both up-current and down-current foraging areas despite the odour plume only occurring in one direction. At Ascension Island, the South Equatorial counter current flows eastward containing the odour plume towards Africa (Koch et al., 1969), but returning green turtle females foraging off Brazil return successfully from the west without using the odour plume (Brown, 1990). There are species that home successfully but are unlikely to use aquatic odour plumes; marine birds and insects use aerial odour plumes cues (Mouritsen, 2018). Thus, while freshwater odour plumes are a likely cue for homing, it is used on a more localized scale than magnetic fields and the mechanisms for fine-scale orientation in sea turtles still needs to be investigated.

A multi-modal approach or combination of cues at different spatial scales is necessary to direct homing (Endres et al., 2016, Painter and Plochocka, 2019). However, environmental cues may not be the only external cues triggering homing. Social interactions with conspecifics may also play a role in facilitating natal homing.

Social facilitation

Social facilitation is the increase in the frequency or investment of a behaviour performance when in the presence of conspecifics (Ogura and Matsushima, 2011) through the social transfer of information (Nicol, 1995). For example, birds like the Australian fairy tern (*Sternula nereis*) follow audio-visual cues of the songs of conspecifics during nest site selection. Fairy terns nest in the presence of conspecifics, as it is concluded that the presence of conspecifics indicates suitable nesting grounds for the gregarious species (Greenwell et al., 2021).

In sea turtles, the “social facilitation” hypothesis suggests that younger, first-time nesters follow more experienced females back to rookeries and use social cues from other females when selecting nesting habitat (Owens et al., 1982). Social facilitation is not mutually exclusive with the natal homing strategies (discussed above) and may operate in combination. Testing these (natal homing and social facilitation) hypotheses is difficult because of logistical challenges; it requires following individuals over their life cycle, large distances travelled, and large numbers due to the high mortality of younger age classes (Bjorndal et al., 2001, Tucek et al., 2014, Van Buskirk and Crowder, 1994). However, kinship relationships have provided some insight in distinguishing the viability of the natal homing and social facilitation hypotheses.

If social facilitation operates randomly and in isolation with no natal homing, then migration of sea turtles from mixed-stock foraging grounds to rookeries would result in high female-mediated gene flow between rookeries and mixed-stock on nesting grounds (Bowen et al., 1993, Bowen et al., 1992). If genes in specific rookeries are “unique”, then the natal homing is more dominant (Lutz et al., 1986, Lutz et al., 2002a). Early studies tested these with the use of mitochondrial DNA. Female green turtles feeding in Brazilian seagrass pastures in the presence of other green turtles nested separately on rookeries in Suriname and Ascension Island (Pritchard, 1976, Carr, 1975). Mitochondrial DNA results indicated some genetic components of each rookery were unique and thus provided evidence for some natal homing rather than just social facilitation. The same was observed for green turtle females from Heron and Raine Island rookeries feeding on the Great Barrier Reef. (Encalada et al., 1996, Bowen et al., 1992).

Regardless of the environmental and social cues, natal homing and homing following the initial return to natal areas are critical processes within the reproductive cycle of many species. For sea turtles, large-scale homing is only the first step of their breeding migration. To complete the nesting process, even finer scale cues on the beach need to be used by nesting female sea turtles to select where on the beach to dig out nests and place her clutches of eggs.

Nest site selection

Nest site selection depends on cues obtained from the interaction of internal (i.e., turtle sensory input) and external factors (e.g., physical beach characteristics). Some cues may be more important than others at different times during the nesting process (i.e., in-water cues may be more important when arriving at the beach and moving through the intertidal zone while beach factors may be more important after hauling out, crawling across the beach and digging out a nest, etc.). Cues may act in combination with each other either synergistically or antagonistically, i.e., a cue might be dependent on another cue to impact nest site selection, such as odour plume flow and current direction (Brazier, 2012).

Physical characteristics of beaches influencing nest site selection and nesting success

Many different beach characteristics may act as cues after arriving at a nesting area and deciding where to emerge, crawl across the beach, and dig an egg chamber to possibly deposit a clutch. The emergence may result in a nesting event or a false crawl, i.e., failed nesting attempt, and thus not every time a turtle emerges does it result in a clutch being placed (Leech, 2008). Mesoscale along-shore and microscale across-shore characteristics of beaches may thus influence turtles' finer-scale nest site selection after homing. These physical characteristics are dependent on beach morphodynamic states which take into consideration that the morphology of beaches is a continuum (Brown and McLachlan, 2002, Wright and Short, 1984). Beach morphodynamic states are determined by three primary factors: tidal regime, sand grain size, and wave climate. These three factors are used to determine whether a beach is on the continuum of two extreme forms, dissipative or reflective, or somewhere in between as intermediate (Wright and Short, 1984). High-energy beaches tend towards dissipative while low-energy beaches tend to be reflective (Brown and McLachlan, 2002, McArdle and McLachlan, 1992, Short, 1999, Benedet et al., 2004). Beach morphodynamic states are important abiotic factors that will affect turtle nest site selection and various anthropogenic factors can also have negative impacts of a turtle's ability to nest.

When sea turtles first arrive at a nesting beach, human settlement and the associated artificial lighting, as well as rocks and reefs in the intertidal zone act as deterrents to the nesting efforts (Witherington and Bjorndal, 1991, Witherington and Martin, 2000, Mortimer, 1995, Brazier, 2012). Artificial lighting negatively affects nesting females by disturbing them on emergence and disorientating adult females trying to return to sea after nesting (Witherington and Bjorndal, 1991, Lohmann and Lohmann, 1996). Light reflections (or light horizon) off the sea surface are used to guide females and hatchlings to the sea after nesting and emergence, respectively. Artificial lights, behind the beach, disorient hatchlings to move inland and can cause a "light trapping" effect (Nelson and Dickerson, 1988, Clark, 1989). Additionally, rocks and reefs, especially when exposed at low tide, make crawling up the beach or down the beach an obstacle (Kaska et al., 2010). These structures can inflict injury to the softer plastron and under-skin and can also act as deterrents to nesting females and hatchlings (Crespo-Picazo et al., 2013).

After hauling out successfully from the ocean, sea turtles will crawl up the beach to the back-shore taking cues from the high shore environment. The slope of a beach is a function of the beach morphodynamic types and is used as a nesting cue to obtain appropriate nest elevation to prevent nest inundation too close to the high-water mark in nest site selection (Cuevas et al., 2010, Lutz et al., 2002, Wood and Bjorndal, 2000). Additionally, coastal vegetation acts as a cue for nesting in some turtle species such as loggerheads that nest at the vegetation line (Karavas et al., 2005), and hawksbill sea turtles that nest into and under vegetation (Kamel and Mrosovsky, 2005, Kamel and Mrosovsky, 2006). Upon reaching beach vegetation, nesting females may then proceed with digging out a body pit and an egg chamber where eggs will be deposited before being covered again with substrate by the female (Mazaris et al., 2009).

The characteristics of the substrate around the eggs is one of the factors (other than moisture, oxygen concentration air temperature and salinity) that will determine nest incubation success and hatchling emergence success. Substrate characteristics such as compaction and sand grain size act as cues for nest site selection (Carr and Ogren, 1959, Carr et al., 1966, Mann, 1978). However, sand characteristics affect the vulnerability of the substrate to coastal erosion (Grant and Beasley, 1998, Koch et al., 2007, Pfaller et al., 2009, Rivas et al., 2016). Coastal erosion also affects nest site selection through the development of impassable dune scarps or berms that prevent nesting females from reaching the upper shore (Rivas et al., 2016).

Nets site selection will occur each time an adult female nester is ready to lay a clutch of eggs within the rookery. However, the placing of clutches within and between nesting seasons may be honed to a specific area on the beach. On smaller rookeries located on islands, nest site fidelity to specific sites in a rookery may not be conspicuous. On relatively larger rookeries (some being hundreds of kilometres long), choosing specific areas to nest when the entire rookery is available implies nest site fidelity for some nesting areas compared to others.

Nest site fidelity

Nest site fidelity, also known as nest site fixity (Carr and Carr, 1972) or tenacity (LeBuff Jr, 1974, Weishampel et al., 2003) can be defined as the “successive placement of nests by the same individual at a distance smaller than the area offered or available to nest in” (Botha, 2010). Many species display site fidelity to breeding grounds, such as jumping spiders (*Phidippus clarus*) that have been observed repeatedly returning to their own webs among many offered. Similar observations of returning to specific sites for breeding have been noted in other species such as birds, including black terns, *Caledonia’s niger*, which showed a 66% fidelity rate for breeding sites despite unstable environments with unfavourable weather conditions (Atamas and Tomchenko, 2020), and nurse sharks, *Ginglymostoma cirratum,* with known individuals returning to the same mating grounds for periods of up to 28 years (Pratt Jr et al., 2022).

Nest site fidelity has also been seen in sea turtles (Kamel and Mrosovsky, 2006, Botha, 2010, Nordmoe et al., 2004, Kamel and Mrosovsky, 2004); nesting individuals place successive clutches in relative proximity to each other within a reproductive period. Individuals with a high nest site fidelity have nests placed closer together and thus have a smaller distance between them. Individuals exhibiting low nest site fidelity have nests placed further apart.

Both high and low nest site fidelity have advantages depending on the environment in which the individual nests. Stable environments favour high nest site fidelity as less time and energy is needed to search for new locations with a small chance of reproductive failure (Vergara et al., 2006). Low nest site fidelity is favoured in unstable environments. Spreading nests among areas with different levels of stability will offer a range of the conditions under which the eggs will develop and thus spread the risk of clutches failing (Eckert, 1987, Flint et al., 2014). Low nest site fidelity is preferred by opportunistic individuals/species that colonize new nesting areas. When previously favourable sites become unfavourable, opportunistic species thrive and colonizing new locations lends itself towards population persistence (Hays and Sutherland, 1991) providing the behavioural response to nest site fidelity is at an appropriate temporal scale (Schmidt, 2004). Behavioural responses have been observed in the expansion of the kemp's ridley (*Lepidochelys kempii*) nesting range from Tamaulipas, Mexico (an area that was modelled to be under threat from climate change and increasing overlap with human development) to undeveloped coastal areas of Florida (Pike, 2013). However, nest site fidelity patterns are not universal among all sea turtle species.

Different species of sea turtles differ in their nest site fidelity; leatherbacks (*Dermochelys coriacea*), for example, are found to have relatively low nest site fidelity. Leatherbacks in Florida may place nests more than 450 km apart in the same nesting season (Stewart et al., 2014), whereas species such as green turtles (Miller, 1997, Lutz et al., 2002b) and flatback sea turtles (Lutz et al., 2002b, Parmenter, 1994, Limpus et al., 1984), have "consistent" nest site fidelity with successive nests placed in close proximity. Olive ridley (*Lepidochelys olivacea*) sea turtles are unique as they exhibit different strategies on different beaches; they use low nest site fidelity in non-synchronous nesting populations (Kalb, 1999) but place nests closer together during synchronous mass nesting, called arribadas (Plotkin et al., 1995, Kalb, 1999). Difference in fidelity for arribadas was observed in Costa Rica, where arribada nests were more spatially clumped and aggregated than non-arribada nests, with six times more nests found on average for arribada nests in the same along-shore distance as non-arribada nests (Ruthig, 2019).

Describing nest site fidelity and nest site selection depends on individual identification as well as long-term monitoring of the population, and noting the areas along a rookery where sea turtles nest (Webster and Cook, 2001). Therefore, the South African nesting populations of loggerhead and leatherback turtles provide a good case study to test nest site selection and nest site fidelity as a result of consistent monitoring efforts (since 1963 up to the present) and individual tagging. Owing to the length of the rookery (~300 km), the nesting sites chosen compared to the entire length of beach available is more apparent.

South African perspective and context

South African turtles and the monitoring program

Sea turtle populations worldwide have been separated into biologically distinct spatial units known as Regional Management Units (RMUs) (Wallace et al., 2010). Population(s) of sea turtles of different species making up RMUs are distinguished from each other biogeographically and genetically taking into account different areas of biological importance (i.e., foraging, nesting, migration routes, etc.). These units are relevant to aid the conservation and management of sea turtles (Wallace et al., 2010). For example, species are listed globally according to the IUCN red list categories, but the species' threat status in local management units may differ from the global threat status based on local population size and threats faced. Leatherback sea turtles in the South Western Indian Ocean are Critically Endangered (Tiwari et al., 2013), and loggerheads are Near Threatened (Nel and Casale, 2015). Globally, these species are both listed as Vulnerable (Wallace et al., 2013, Casale and Tucker, 2017). The largest proportion of both of these species have rookeries located in South Africa, nesting in the iSimangaliso Wetland Park (Nel et al., 2013).

The iSimangaliso Wetland Park is one of the longest running turtle monitoring programs in the world, monitoring leatherback and loggerhead sea turtles since 1963 (Nel et al., 2013). The nesting grounds form part of a marine area that was declared a World Heritage site in 1999. The two contiguous marine protected areas (MPA; St Lucia and Maputoland) were expanded to iSimangaliso MPA in 2019, and is one of the biggest MPAs in South Africa as well as a recognized Ecologically or Biologically Significant Marine Area (EBSA) and Indian Ocean and South-East Asia (IOSEA) marine turtle area (Harris et al., 2022). The Park is now a continuous terrestrial to marine protected area, with estuarine areas and coral reefs utilized by non-nesting sea turtle species (Hughes, 1974). The two nesting species are not identical in their reproductive biology.

The two turtle species nesting along the South African north-have contrasting features. Loggerheads (Fig. 2.1a) are smaller in weight and size, have a lower reproductive output (produce approximately 100 eggs in 3 - 5 clutches a season) and have nesting hotspots in the northern part of the rookery (Botha, 2010). Leatherbacks (Fig. 2.1b) are larger in size, have a greater reproductive output (produce approximately 105 eggs in 6 - 8 clutches a season), and have more evenly distributed nesting sites all along the coast (Botha, 2010, Nel et al., 2013, Harris et al., 2015). Since the implementation of the turtle monitoring program in 1963, the loggerhead population has increased while the leatherback population increased initially and then plateaued despite both species making use of the same nesting beach resources (Nel et al., 2013).

Sea turtles are ecologically and economically valuable to iSimangaliso Wetland Park. The turtles deposit eggs in oligotrophic sandy shores, thereby providing nutrient inputs to the beach system (Le Gouvello et al., 2017). In iSimangaliso, sea turtles are protected by rangers, paid monitors and are viewed by tourists through low-cost and high-end tourism concessions, providing employment for rural communities living in and nearby the Park (Poultney and Spenceley, 2001). Declines in the South African sea turtle nesting abundance would thus have negative ecological and economic consequences.

Previous studies on beach characteristics driving nest site selection and nest site fidelity in South Africa

Hughes (1974) was the first to describe sea turtle nesting patterns in South Africa. He noted the preference of loggerhead nests to the northern beaches around Kosi lakes, without testing for a potential mechanism or drivers of this behaviour. Brazier (2012) attempted to identify compounds associated with estuarine and freshwater groundwater out-welling entering the sea alongshore that could be used as a homing cue to nesting females. Brazier (2012) also tested the relative importance of visual, auditory, and olfactory senses used by turtles post-nesting. He found that visual cues are dominant to sound or smell in sea finding and inferred that sulphur from groundwater may have a directional signal in directing nesting females toward particular areas on the beach as it had a high correlation. Thus, Brazier’s (2012) results were mostly inconclusive; not providing direct, substantial evidence to explain previous observations by Hughes (1974) of loggerhead nesting on beaches near Kosi lakes.

Botha (2010) first described the nest site selection and nest site fidelity patterns of loggerhead and leatherback turtles in iSimangaliso. Results from the study confirmed that loggerhead nests are aggregated in the northern parts of the Park (with 60% of nests found within an 8km-stretch; Botha, 2010) while leatherbacks had a more uniform distribution with nests spread more evenly along the entire length of the monitored area. Botha (2010) also described some beach characteristics potentially driving the nest site selection of each species. She noted that both species preferred intermediate beaches and avoided areas of low inshore rock, with leatherbacks additionally preferring beaches with wide surf zones. Botha (2010) also found that the mean distance between clutches of the same loggerhead individual were placed about 3 km from each other. Leatherback nests were, on average, about 9 km apart from each other. More interestingly, Botha (2010) also suggested that loggerheads improved in nest placement, with distances between nests shrinking each season, while leatherback nest distances did not shrink. Considering the available beach length of ~ 300 km across the South African and Mozambique border, ‘accuracy’, less than 10 km (which may be two adjacent bays) is still a relatively high nest site fidelity for both species. However, the study by Botha (2010) used only intertidal and supratidal features to describe nesting behaviour, and this from a data set with a limited spatial (56 km) and temporal extent (8 years).

Dissertation outline

The overall aim of this thesis is to disentangle nest site selection using a spatial data set that extends further into the off-shore bounds of the rookery (not covered in many other studies) and to compare nest site fidelity for loggerheads and leatherbacks in a South African rookery between species and across time. This dissertation will revisit the aims and objectives of Botha (2010) but with an expanded data set and using newer analytical techniques. The study will use the larger long-term monitoring data set (54 463 nesting events over 55 years, courtesy of Ezemvelo KZN Wildlife) along with fine-scale resolution spatial data set representing coastal ecosystem types (Harris et al., 2019), which includes offshore, shore, back-shore (foredunes), and inland aquatic (lakes) types. This map therefore includes marine and terrestrial ecosystem types previously ignored in analyses regarding turtle nest site selection. The content chapters of this dissertation will investigate the following:

Chapter 1 - Introduction: The aim of this chapter is to (briefly) review literature on the current state of knowledge on sea turtle nest site selection and nest site fidelity, as it relates to the South African context.

Chapter 2 - Nest site selection of loggerheads and leatherbacks: This chapter aims to compare the nesting distribution of both loggerhead and leatherback populations along the iSimangaliso Wetland Park rookery and determine which coastal features can potentially drive the nesting distribution of each population. Key questions include: 1) What is the nesting distribution for loggerheads and leatherbacks in South Africa? 2) Are these nesting distributions consistent in space and time? and 3) Which coastal features are associated with the nesting distributions?

Chapter 3 - Nest site fidelity of loggerheads and leatherbacks: This chapter aims to compare the nesting behaviour and nest site fidelity among individuals within each population. Key questions are: 1) Which species has the highest nest site fidelity? 2) Does nest site fidelity differ between neophyte and experienced nesters? And 3) Is the decision on where to nest made before hauling out or after hauling out?

Finally*, **Chapter 4 - Synthesis and conclusion:*** This chapter provides a summary of findings across the dissertation content chapters. The aim of this chapter is to discuss how nesting of individuals is indicative of population nest site selection, how coastal features impact sea turtle nest site selection and nest site fidelity, and how nest site selection and nest site fidelity affect reproductive fitness.

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CHAPTER 2: LOGGERHEAD AND LEATHERBACKS NESTING HABITAT SELECTION

Abstract

Mature sea turtles exhibit large-scale natal philopatry between foraging areas and their natal rookeries. Upon arrival at the rookery, turtles choose where to place each clutch through a process of nest site selection. The selection of each of the nesting sites is critical for ensuring reproductive success as it constitutes the only parental investment of nesting females aside from producing the eggs. This chapter aimed to examine nest site selection by loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) turtles in iSimangaliso Wetland Park in South Africa and how these spatial patterns are correlated with coastal features including subtidal (i.e., coral reef) and surf conditions (e.g., surf zone width) as well as visible (like vegetated dunes) and hidden (like lake presence) coastal features. Nesting distribution patterns for 55 seasons (for each species) and the coastal features were coded to a set of coastal units using ArcGIS 10.7. Coastal units were each a mile long to align with markers (beacons) used along the shore. A General Niche-Environment System Factor Analysis (GNESFA) run in R version 4.2.1 suggested that loggerheads select for coral reef habitat and dissipative-intermediate beach morphodynamic type while leatherbacks select mixed shore and dune vegetation and avoid the non-visual cue, lake presence (hidden behind a dune cordon). The specificity of site selection differed between species, with stronger selection by loggerheads than by leatherbacks. It was concluded that both visible terrestrial and subtidal features are used (positively or negatively) during nest sit selection for the cues driving loggerhead and leatherback nesting choices even though specific mechanisms weren’t identified.

Introduction

Animals exhibit many different breeding strategies and reproductive behaviours to optimise reproductive success. One such strategy is broad-scale homing to reproductive sites. A variety of taxa including Chinook salmon, *Oncorhynchus tshawytscha*, (Dittman et al., 2010), red mason bees*, Osmia rufa*, (Steffan-Dewenter and Schiele, 2004) and Leach's storm-petrel, *Oceanodroma leucorhoa* (Blackmer et al., 2004), return to the same location from which they hatched from (e.g., a specific stream, beach or vegetation patch) to complete their own reproductive cycle. Female sea turtles also exhibit homing to the beaches from which they hatched but are migratory, travelling among foraging grounds and courtships areas alongside males before travelling to nesting areas (Lohmann et al., 2013).

The rookeries used by the nesting females will (generally) be on the same beaches from which they emerged as hatchlings (i.e., their natal rookery) where nesting females will place successive clutches of eggs in the sandy substrate. Nest site selection is “the placement of eggs by females at sites that differ from random sites within a delimited area” (Wilson, 1998) and occurs each time a clutch of eggs is laid. The nest site selection on a rookery is critical in determining reproductive success (Kolbe and Janzen, 2002). Nests placed in inappropriate locations may result in failed egg development, or failed hatching and/or emergence (Miller et al., 2003). If nest site selection is inappropriate for the majority of individuals in a nesting population over multiple generations, this may result in decreased reproductive output and success and ultimately the decline in abundance of the population (Pfaller et al., 2009).

For sea turtles, nest site selection occurs on two scales: Firstly, macroscale philopatry which is the migration of adult sea turtles back to their nesting grounds (Lohmann and Lohmann, 1996, Putman et al., 2012, Hays and Sutherland, 1991) from different bioregions or ocean basins. Explanations of cues directing natal philopatry and successive homing of sea turtles include the use of geomagnetic fields (Luschi et al., 2007, Lohmann et al., 2008, Brothers and Lohmann, 2015), chemical imprinting on substances found at the natal rookery (Endres et al., 2016, Grassman and Owens, 1981, Owens et al., 1982, Lohmann et al., 2013) and social facilitation (Carr and Hirth, 1961) where neophytes (or inexperienced nesters) follow older, more experienced females to rookeries (see Chapter 1). The second scale of nest site selection is at the mesoscale, which is the longshore nest site selection. A series of cues including rocks and reefs in the intertidal zone may either act as an obstacle and be avoided (Mortimer, 1995, Schofield et al., 2017) or potentially act as a visual cue from the surf back-line before the turtle hauls out onto the beach. Additionally, artificial lighting (Salmon, 2003) and seashore vegetation on the back-shore (Hannan et al., 2007) may be used to guide nesting at a mesoscale. There are also microscale abiotic factors (such as moisture, sand grain size or organic content) and biotic effects (such as genes, physiology and predation), which are often measured as drivers of nest site selection but are unknown to an emerging turtle (Mortimer, 1990, De Vos, 2018).

Environmental variation exists among the rookeries used by sea turtles in what cues are present and selected for by sea turtles; nesting hawksbills in the West Indies (Horrocks and Scott, 1991) and loggerhead sea turtles in Sekania (Schofield, 1996) display a preference for vegetation, whereas hawksbills on Arembepe beach in north-eastern Brazil do not have a clear preference for nesting in vegetation (Serafini et al., 2009). Loggerheads from the same rookery on Boa Vista Island in Cape Verde showed high variability in their nest site selection with regards to nesting distance from vegetation and the high water mark (Martins et al., 2022). However, turtles that were larger in size (it was inferred that larger individuals are older, and therefore more experienced) showed better repeatability in their nest site selection from the same Cape Verde population (Martins et al., 2022).

Rookeries also differ in size and therefore nest site fidelity (accuracy) may differ among locations. Turtles may nest on islands with very short beaches, such as the green turtle rookeries comprising cays and islands of the northern Great Barrier Reef that range in size between 0.02 -0.3 km^2 (Fuentes et al., 2010) or Sekania beach that is 650 m long, on Zakynthos Island (Karavas et al., 2005). Other rookeries, however, are a continuous, long beach such as the satellite island of Klein Bonaire (6 km^2) and the main island (288 km^2) of Bonaire in the Caribbean (Fish et al., 2005), or iSimangaliso with continuous beaches stretching for hundreds of kilometers (with no physical boundaries). Nest site fidelity may therefore be expressed in terms of the available habitat rather than just distance among successive nesting events. For the South African loggerheads and leatherbacks nesting population, there is seasonal nesting on a long, continuous beach (~300 km) within the warmer months (October – February) of the year (Nel et al., 2013, Botha, 2010).

Hughes (1974) observed uneven nesting distributions for the two nesting species in South Africa suggesting species-specific preferences; he noted that loggerhead nests were congregated on the beaches adjacent to the Kosi lakes system. This is similar to the congregated nesting of green turtles down-current of river outflows in Costa Rica (Richard and Hughes, 1972). Botha (2010) re-investigated nesting patterns of loggerhead and leatherback turtles in South Africa and confirmed that the distribution described initially (by Hughes 1974) persisted for more than 40 years. Loggerhead nesting was concentrated in the northern section of the iSimangaliso Wetland Park around Kosi lakes, with 60% of nests in only 8 km of the beach (Botha, 2010). Conversely, leatherbacks had a more dispersed distribution, with nests spread more evenly along the beach. Botha (2010) also attempted to identify physical characteristics of beaches (such as grain size, slope, and surf zone width) associated with the nest site selection of each species. She found that leatherbacks nested on beaches with wide surf zones (beaches with intermediate morphodynamic states), whereas loggerheads nested in the absence of inner shelf rock, absence of dune vegetation (i.e., open sand) and on intermediate beach morphodynamic types. The study by Botha (2010) was however limited in the scope and results were informative but inconclusive.

Hughes (1974) also speculated that loggerhead spatial distribution was related to olfactory compounds associated with the estuarine and freshwater systems entering the sea via the groundwater. Some other sea turtle rookeries are also backed by freshwater bodies, such as the Curral Velho wetland behind the João Barrosa beach in Cabo Verde Archipelago (Martins et al., 2022). However, not all rookeries have a distinct freshwater or estuarine water body feature that may act as a cue. Brazier (2012) attempted to identify some compounds that could orientate nesting turtles. Sulphide (S_2^-) concentrations was the only tested compound that varied directionally along the shore. He reported a directional plume from the lake that could be used as a potential cue. However, Brazier's (2012) results did not provide substantial and direct evidence to support the previous hypothesis, unlike other studies done on green turtles at Ascension Island (Koch et al., 1969, Carr, 1975) and studies on olfactory cue used for homing in other species such as Salmonids (Sutterlin and Gray, 1973, Dittman et al., 2010). Studies on olfactory cues have also been done on blacktip sharks, *Carcharhinus limbatus* in Terra Ceia Bay, Florida whereby yearlings will return to developmental areas within the bay even when displaced and older juveniles individuals with unblocked olfaction demonstrate annual philopatry to the bay during spring (Gardiner et al., 2015).

The aim of this study is thus to analyse a broad range of coastal features potentially driving nest site selection by loggerhead and leatherback sea turtles within a ~300-km long rookery (of which only 83 km is monitored) in South Africa. The specific objectives are to 1) review stability of nesting distribution of loggerhead and leatherback sea turtles in space and time (1965-2019 nesting seasons) by comparing the longshore distribution over time and identify consistent nesting "hotspots"; 2) characterize the mesoscale coastal features present/absent along the shore (in one-mile units) and across-shore (from the surf to secondary dunes within each coastal unit); and 3) analyse nesting distribution per population along with the coastal features. It was hypothesized that spatially variable coastal features act as cues for turtle nest site selection depending on the species because of species-specific preferences for some coastal features over others. Thus, it is predicted that nesting is not random and there are high-use and low-use areas that differ between the two species.

Methods

Ethics statement

Original data collection for each year (from 2009 - 2020) was conducted under the authority of the Nelson Mandela University (previously Nelson Mandela Metropolitan University) Animal Ethics Committee and DEA/DFFE collection permits to the NMU sea turtle research program (NMU Animal Ethics: A09-SCIZOO-005, A11-SCI-ZOO-013 A13-SCI-ZOO-011, A16-SCI-ZOO-014 A18-SCI-ZOO-006 and Department of Environment/Department of Fisheries, Forestry and Environment's Research Permits: RES2009/08, RES2010/55, RES2011/41, RES2012/24, RES2013/10, RES2014/64, RES2015/69, RES2016/69 RES2017/73; RES2018/68; RES2019/05; RES2020/102; RES 2021/14.). The long-term data used (1965 onwards) were collected under the legal (monitoring) mandate of Ezemvelo KZN Wildlife and iSimangaliso Wetland Park. The data used within this study are secondary data with permission from the data custodians.

Study Site

This study was undertaken in the northern section of iSimangaliso Wetland Park (Fig. 2.1), a UNESCO World Heritage Site, with both marine and terrestrial components (Fig. 2.2a). The study area is located in the Delagoa Bioregion between Cape Vidal (South Africa) and Bazaruto Archipelago in Mozambique (Sink et al., 2005, Porter et al., 2017, Massingue et al., 2014). The subtropical climate (Eeley et al., 2001) is under the influence of the warm Agulhas Current which originates from the Indo-Pacific Region and then flows south-westerly. This current is fast-flowing (5.4-7.2 km.h^{-1}), with core temperatures nearing 28°C in summer (Schumann and Orren, 1980, Lutjeharms and Ansorge, 2001).

The nesting habitat along the South African coastline is not homogenous in its physical characteristics. The straight north-south orientation of the coast is structured by a series of shallow bays, each 4 – 5 km in length, with the bays interposed with rocky headlands consisting of dune rock (Hughes, 1996) on the low shore. These bays contain exposed, silica-dominated sandy beaches (Hughes, 1974), even on the back-shore of headlands. These are high-energy intertidal shores that mostly constitute intermediate to reflective beach types (Harris et al., 2019). Low-shore areas contain rockpools (Fig. 2.2b) formed within sandstone platforms (McCarthy, 1967).

The back-shore is bound by high, narrow coastal dunes (Von Maltitz et al., 1996) that reach elevations over 80 m near the Mfolosi-St. Lucia estuary in the south and mostly parabolic, forested dunes (Tinley, 1985) with occasional narrow vegetated primary dunes (Fig. 2.2c). The coastline is backed by a few (but significant) land-based water sources, notably freshwater Lake Sibaya in the south and the estuarine Kosi lakes in the north (Walther and Neumann, 2011), the latter of which consists of four joined bodies of water that are connected to the sea via the Kosi estuary (Fig. 2.2d) (Kyle, 1995). Within brackish water bodies, such as the Kosi Estuary, exists mangrove forests with species such as *Avicennia marina* and *Bruguiera gymnorrhiza* (Naidoo, 2016).

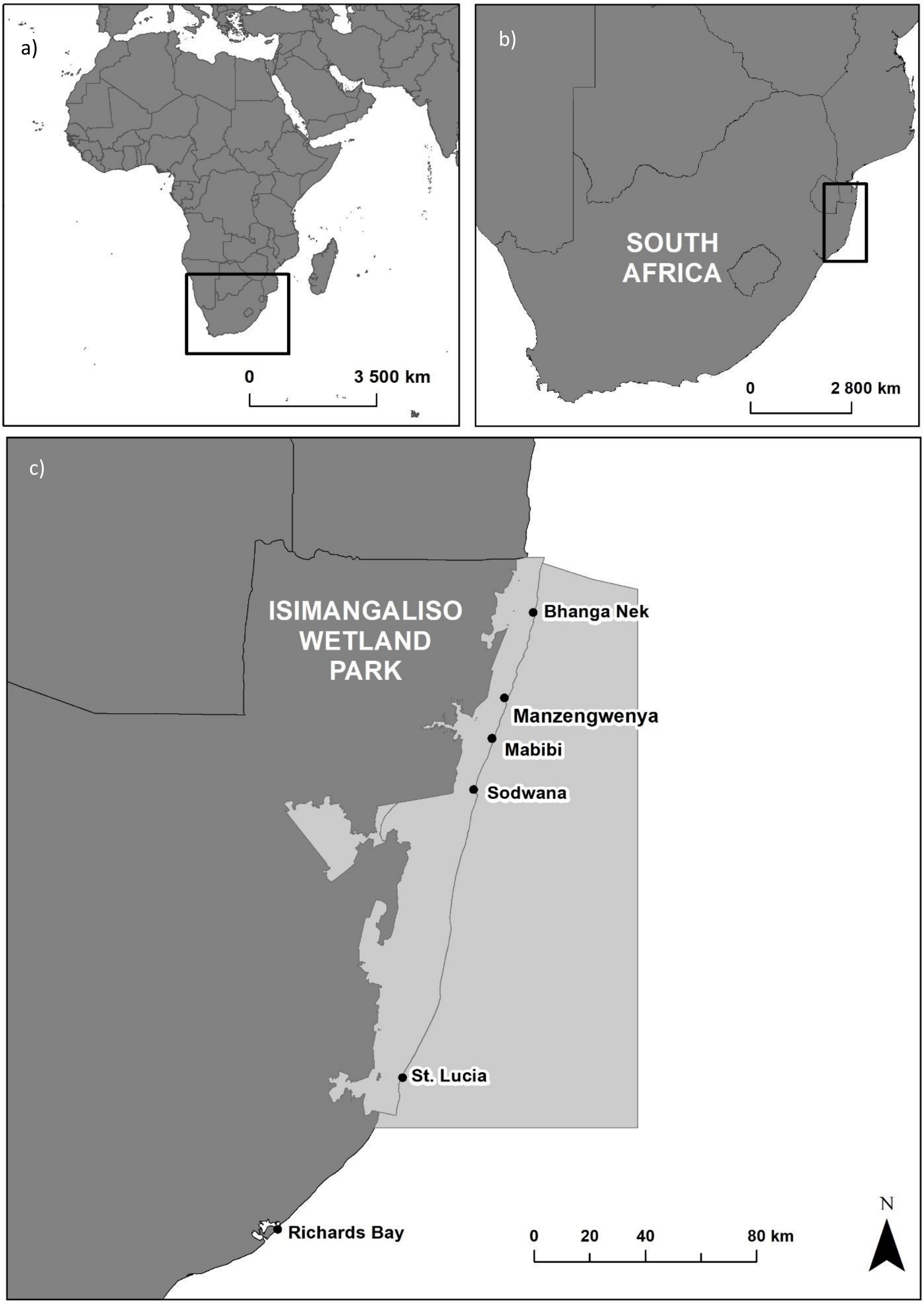

Figure 2.1: Study site panel indicating a) location relative to other countries, b) location relative to the whole South Africa and c) location of the iSimangaliso Wetland Park, including terrestrial components and offshore extent of the Park, relative to other locations within KwaZulu-Natal province.

Figure 2.2: Heterogenous habitat along iSimangaliso Wetland Park shoreline with a) Overhead view of the coastline with dune cordon, coastal forest, and intertidal zone (Max and Osana St John, March 2020), b) Sandstone tidal pools (Linda Harris, July 2016), c) Dune vegetation along the shore (Andy Coetzee, January 2020) and d) Kosi Estuary (Osana and Max St John, March 2020)

Long-term nest monitoring

Ezemvelo KZN Wildlife (formerly known as Natal Parks Board) has monitored the annual sea turtle nesting activity in iSimangaliso MPA with (mostly) consistent effort since 1963. The set index area running 8 km north from Bhanga Nek has been monitored the most consistently. The monitoring by Ezemvelo has recently been expanded to include the beaches south of Bhanga Nek from Mabibi to Sodwana Bay. Two species namely loggerheads (*Caretta caretta*) (Fig. 2.3a) and leatherbacks (*Dermochelys coriacea*) (Fig. 2.3b) nest on these shores and are monitored, with green turtle and hawksbill turtles being year-round residents in coastal waters but rarely coming ashore.

In 1963, South Africa still used Imperial units, and so the beach was divided up into mile units (1.6 km) with the high nesting density area subdivided into quarter-mile units (400 m, Fig. 2.4a). Each female's emergence is therefore recorded to the nearest beacon (in quarter or one-mile units), the flipper tags reported, as well as size, species, nested (or not), and previous tag scarring to discriminate first-time nesters (neophytes) from experienced breeders. A more extensive description of all monitoring protocols can be found in Nel et al. (2013).

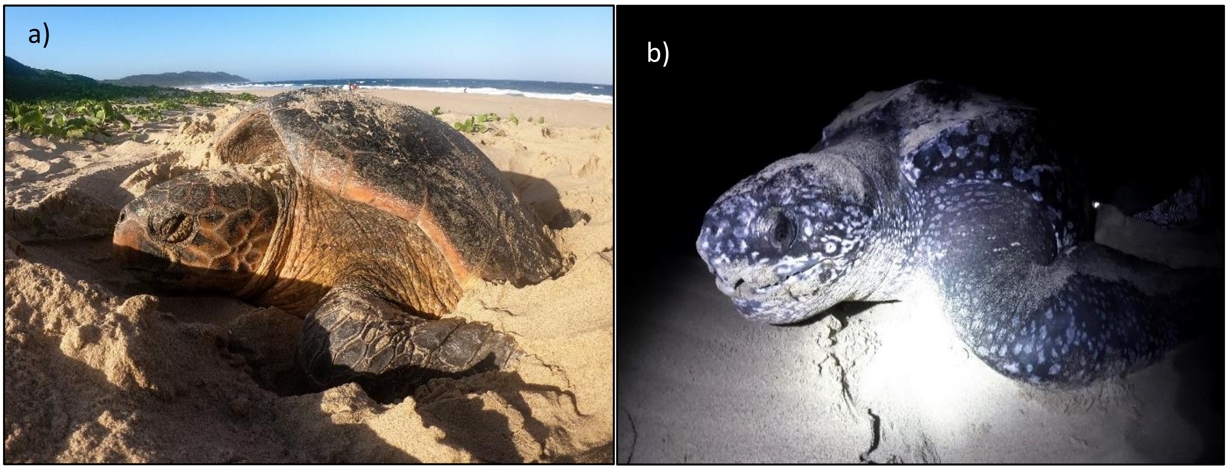

Figure 2.3: Study species used in the dissertation, a) loggerheads, Caretta caretta, and b) leatherbacks, Dermochelys coriacea.

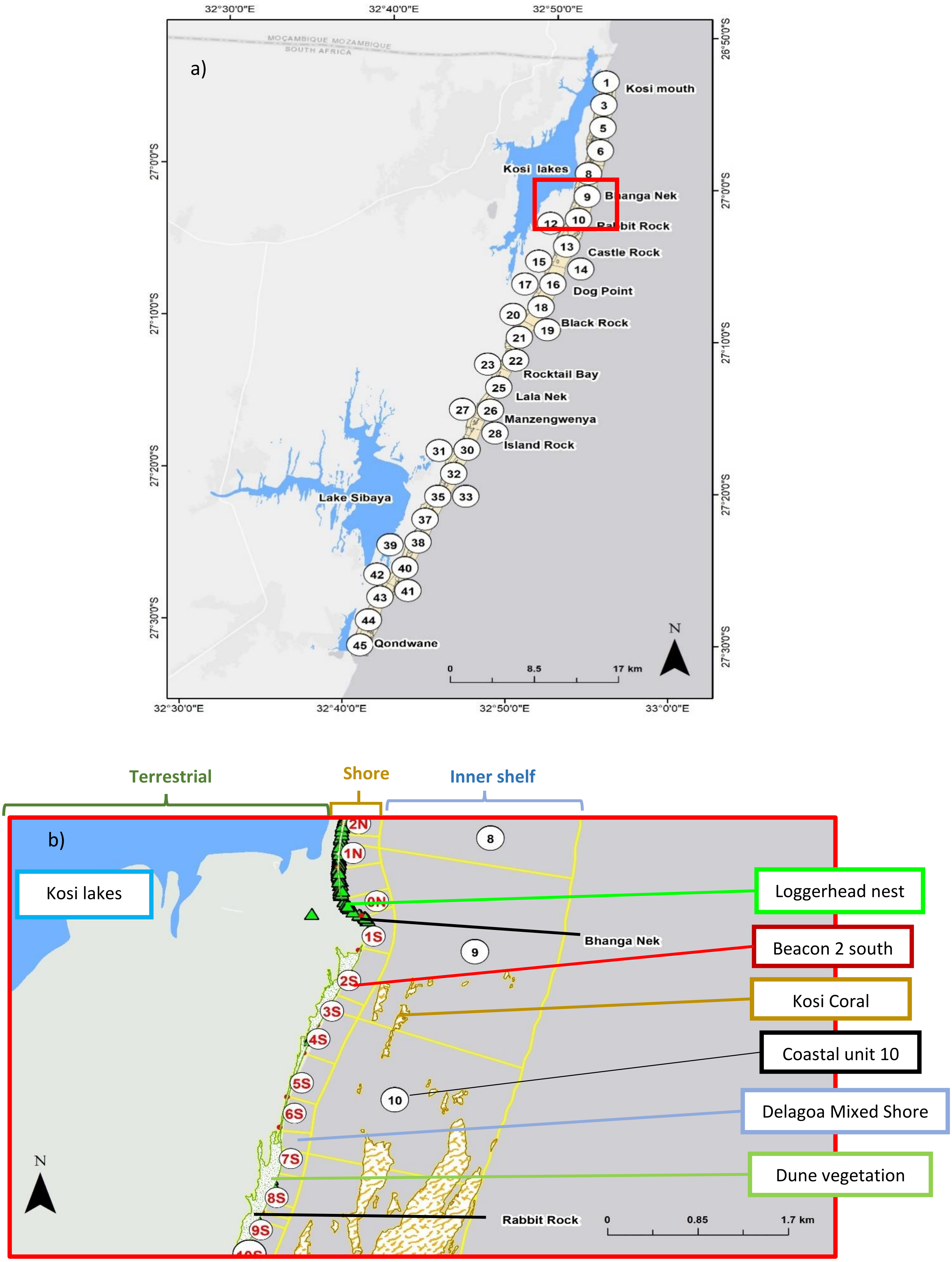

Figure 2.4: a) Map of the study area with labelled landmarks and coastal unit 1 to coastal unit 45 (1-mile units) with red square indicating position of b) coastal unit 8 to coastal unit 11 with ecosystem types, nesting locations, beacons, backshore lakes and nearshore Kosi Coral Community reef.

Temporal and spatial patterns in nest distributions

The stability of the nesting distribution per species over time (Obj.1) was investigated using contour plots in R 4.2.1 (R Core Team, 2021) per one-mile coastal units. See Table 2.1 for explanation on using coastal units over quarter-mile units (described above). The frequency of female emergences per species in the long-term monitoring area (Kosi Estuary at beacon 32N i.e., coastal unit 2 to Mabibi at beacon 100S, i.e., coastal unit 32) per year, from 1965/66 to 2019/20 was plotted per beacon over time. Spatial and temporal consistency of nesting distribution was prioritized as investigating nesting distributions that are unstable alongshore across space and time with static coastal features would impact reliability and analysis of results.

Temporal trends

Data were non-normal for both species' distribution across coastal units (Anderson-Darling test: loggerhead A = 184.14, leatherback A = 60.171, $p << 0.001$ in both cases) and lacked homogeneity of variances between coastal units (Fligner-Killeen test: loggerhead $X^2 = 160.57$, leatherback $X^2 = 205.93$ $p << 0.001$ in both cases). Thus, a non-parametric test was used to test whether sea turtle emergences were consistent over 55 seasons

Spatial trends

Data were non-normal for both species' distribution across coastal units (Anderson-Darling test: loggerhead A = 337.12, leatherback A = 153.26, $p << 0.001$ in both cases) and lacked homogeneity of variances between coastal units (Fligner-Killeen test: loggerhead $X^2 = 1228.4$, leatherback $X^2 = 788.39$ $p << 0.001$ in both cases). Thus, a non-parametric test was used to test whether sea turtle emergences were consistent among the coastal units.

Table 2.1: Brief description of the attributes (i.e., coastal features and coastal units) determined using ArcGIS and Google Maps and the methods used to procure data for each attribute. All attributes are from the South African Coastal Ecosystem Map (Harris et al., 2019) except lakes and estuaries that are from Van Deventer et al. (2018) and intertidal zone, from Harris (2012).

Attribute	Method/Rule
Coastal unit	Beacons (poles embedded into the sand) were placed along-shore in 1963 at the start of the turtle monitoring program and were approximately a quarter mile apart in the area with high turtle nest density, and one mile apart in the low-density areas. Coastal units were constructed to be one-mile long because this was the smallest unit that could be consistently applied across the rookery.
Ecosystem types	Within each one-mile long coastal unit, the total area (m^2) of each coastal unit was calculated or derived from the National Biodiversity Assessment (NBA) data set. Then the proportion of each beach morphodynamic type (BMT) and other ecosystem types (e.g., Sodwana coral communities, Kosi coral communities and seashore vegetation on the NBA Ecosystem Type map) within each coastal unit was calculated. Delagoa mixed shore was separated into mixed shore that was mostly sand-dominated and that which was mostly rock-dominated.
Lakes and estuaries	Water bodies (i.e., Kosi lakes and Lake Sibaya) mapped in the 2018 South African Inventory of Inland Aquatic Ecosystems (SAIIAE) map were cut perpendicularly to the back-shore to connect with pre-existing coastal unit lines. These cut portions of lakes and estuarine water bodies were then used to determine the distance (in metres) from the dune base of a coastal unit to the nearest lake or estuarine water body within each coastal unit.
Rocks	Historical Google Earth images were compared with the ecosystem types mapped in the Coastal Ecosystem Map to make sure all rocky areas were captured.
Dune hummocks and inner shelf rocks	Using ArcMap, the proportion (%) of the total length of each coastal unit containing dune hummocks was measured. The same was done where inner shelf rocks were present in a coastal unit.
Back-shore and Intertidal zone width	Within each coastal unit, the length and area of the intertidal zones and back-shore (zone of shore above the high-water mark only acted upon by severe storms between the beach face and dune base) was determined using the Coastal Ecosystem Map and then the average width (m) of the back-shore and intertidal zone per coastal unit calculated by dividing the area by the length calculated in ArcMap.

Identifying potential drivers of nest site selection

Data preparation

The coast was described by characterizing the dominant coastal features (using ArcMap 10.7 and Google Earth) in one-mile coastal units (see Table 2.1). The features were plotted using Google imagery and South Africa National Integrated Coastal Map by Harris et al. (2019) (Fig. 2.4b). Initially, 26 coastal features were measured within each coastal unit, but variables that were highly correlated (e.g., area of coral reef versus the proportion of the inner shelf of each coastal unit containing coral reef) within a correlation matrix were discarded. Methods for plotting and mapping environmental variable for the coastal units is described in Table 2.1 with 18 final coastal features being considered in total (see Table 2.2 for labelling of coastal features).

Table 2.2: Key to coastal features used to describe each coastal unit.

Key		
Label	***Environmental variable name***	***Data type and unit***
Ecosystem types		
DMixSA	Delagoa mixed shore (sand-dominated)	Area (m^2)
RDMixSA	Delagoa mixed shore (rock-dominated)	Area (m^2)
DVExpRS	Delagoa very exposed rocky shore	Area (m^2)
NDDISA	Natal-Delagoa dissipative-intermediate sandy shore	Area (m^2)
NDISA	Natal-Delagoa intermediate sandy shore	Area (m^2)
NDRSA	Natal-Delagoa reflective sandy shore	Area (m^2)
Other coastal features		
KCoCA	Kosi Coral Community	Area (m^2)
SCoCA	Sodwana Coral Community	Area (m^2)
LPLowRock	Low inshore rock	Proportion of total length of coastal unit (%)
PHumm	Dune hummocks	Binary (presence/absence)
Headl	Rocky headland	Binary (presence/absence)
InTw	Intertidal zone	Width (m)
BackSw	Back-shore	Width (m)
VegA	Seashore Vegetation	Area (m^2)
LED	Lake or estuarine water body	Distance from dune base (m)
WBA	Water bodies	Area (m^2)
KosiLP	Kosi bay lakes	Binary (presence/absence)
SibLP	Lake Sibaya	Binary (presence/absence)

General-Niche Environment System Factor Analysis

Comparison of the nesting distribution for each species and the distribution of coastal features in each coastal unit was done using a GNESFA (General Niche-Environment System Factor Analysis) in R version 4.2.1 (R Core Team, 2021) which is a Design I analysis (i.e., animals are not individually identified; the availability and habitat use are measured at a scale of the population) in adehabitatHS package (Basille et al., 2008, Calenge, 2011, Calenge, 2013, Thomas and Taylor, 1990). A GNESFA consists of three separate analyses: 1) a FANTER (Factor Analysis of the Niche Taking the Environment as the Reference), whereby the relative availability of each nesting habitat along the rookery is used as the reference for the graphical exploration of the association between available habitat and the distribution or occurrences, 2) a MADIFA (Mahalanobis Distances Factor Analysis) whereby the utilization weights (i.e., the number of nesting females found emerging in each nesting area along the nesting beach) is the reference distribution; and 3) an ENFA (Ecological Niche Factor Analysis whereby the availability and the utilization weights are used). In combination, these three will inform on habitat selection (FANTER), habitat suitability (MADIFA) and habitat rarity with species tolerance, i.e., how adaptable species are to changes in the environment (ENFA). For more details see Appendix 1 and Calenge (2011). All three analyses use one if not both concepts of marginality and specialization within the analysis. Habitat specialization refers to the restriction or narrowness of the niche relative to the available environment (Calenge and Basille, 2008, Caruso et al., 2015, Neupane et al., 2019). Marginality refers to the central tendency or preference of the individual, population, or species from within an available possibility in an environment. Marginality is formally measured as the absolute difference between global mean distribution divided by 1.96 standard deviation of the global distribution of the focal species (Basille et al., 2008, Calenge and Basille, 2008, Neupane et al., 2019).

A GNESFA requires three data sets; i) a list of the coastal features data (qualitative and/or quantitative measures) contained within each coastal unit (described in Tables 1 & 2 and Fig. 2.4a), ii) the availability of the habitat/niche features (each coastal unit is equally available to the study species in this investigation). Lastly, iii) the proportion of each unit used e.g., abundance of species. A combination of these indicators highlights rare habitats and disproportionate high use thereof. Abundance of loggerheads and leatherbacks was obtained during long-term monitoring and beacon numbers in the monitoring data set were converted into coastal units. In this study abundance was the proportion of total emergences per species from across the entire study area found within each coastal unit. Additional information on each GNESFA analyses can be found in Appendix 1.

Outlying Means Index Analysis

Comparison of the nesting distribution of individual females from each species and the relationship with specific coastal features was done using an Outlying Means Index analysis (OMI analysis in R version 4.2.1 (R Core Team, 2021) using the adehabitatHS package (Calenge and Basille, 2008). Data used for the OMI analysis includes i) a centred list of the coastal features (qualitative and/or quantitative measures) contained within each coastal unit (described in Tables 1 & 2 and Fig. 2.4a) and ii) the proportion of each unit used. The OMI analysis was first described by Dolédec et al. (2000) as an approach to study habitat selection of individuals. It is a Design II analysis, meaning that it is used to assess habitat use by identified individuals (Basille et al., 2008, Calenge, 2011, Calenge, 2013) although it is now more commonly used to compare habitat use in community assemblages across multiple species rather than multiple individuals (Heino, 2005, Randa and Yunger, 2006, Mérigoux and Dolédec, 2004, Dolédec et al., 2000).

The OMI analysis considers the niche position and niche breadth of the data entered into the analysis and assigns a quantitative and tolerance value respectively (Heino, 2005). These OMI values are derived from the marginality of the habitat distribution (defined as the squared Euclidean distance between the mean conditions utilized vs the mean conditions available) across the study area (Dolédec et al., 2000, Heino, 2005, Saccò et al., 2020). The individuals with high OMI values occupy marginal niches (i.e., rarer and less available habitat) relative to the rest of the community. Low OMI values (i.e., low marginality values) indicate occurrence within common habitats. Species tolerance measures the amplitude in the distribution of each species along the environmental gradients sampled within the study area (Heino, 2005). High tolerance values indicate that a species is a generalist rather than specialist and can persist in a broad range of environments (i.e., has a wide niche breadth) and vice versa (Heino, 2005, Saccò et al., 2020).

OMI values and tolerance values for each species were both non-normal (Anderson Darling test: $p < 0.05$), with OMI values lacking homogeneity of variances between species (Fligner Killeen test: $p < 0.05$) while homogeneity of variances for species did exist for tolerance values (Fligner Killeen test: $p > 0.05$). Thus, a non-parametric test was used to test if the values of OMI and tolerance differed significantly between loggerheads and leatherbacks.

Results

Temporal and spatial patterns in nest distributions

Temporal trends

A non-parametric Kruskal-Wallis test was done to investigate whether sea turtle emergences were consistent over 55 seasons (1965 – 2020) using 166 729 loggerhead emergences and 18 612 leatherback emergences. The null hypothesis that the ranks of the groups (i.e., the average number of emergences in each nesting season) are the same was rejected for loggerheads ($X^2 = 460.23$, $p \ll 0.01$) and leatherbacks ($X^2 = 333.75$, $p \ll 0.01$) as $p < 0.05$ for both species, indicating interannual variation. A comparison of the number of tracks in the 8-km long index area (Fig. 2.5a & 1.5b) from 1965 to 2020, indicates a directional trend that loggerhead emergences increased over time from 1965 and peaked in 2015, with a decline between 2015 and 2019 (mean ± SD: 3473.3 ± 932.6). Leatherbacks increased initially but emergences remained constant from 1970 onwards with an overall mean of 72.2 tracks (±28.4 SD) in the index area per season.

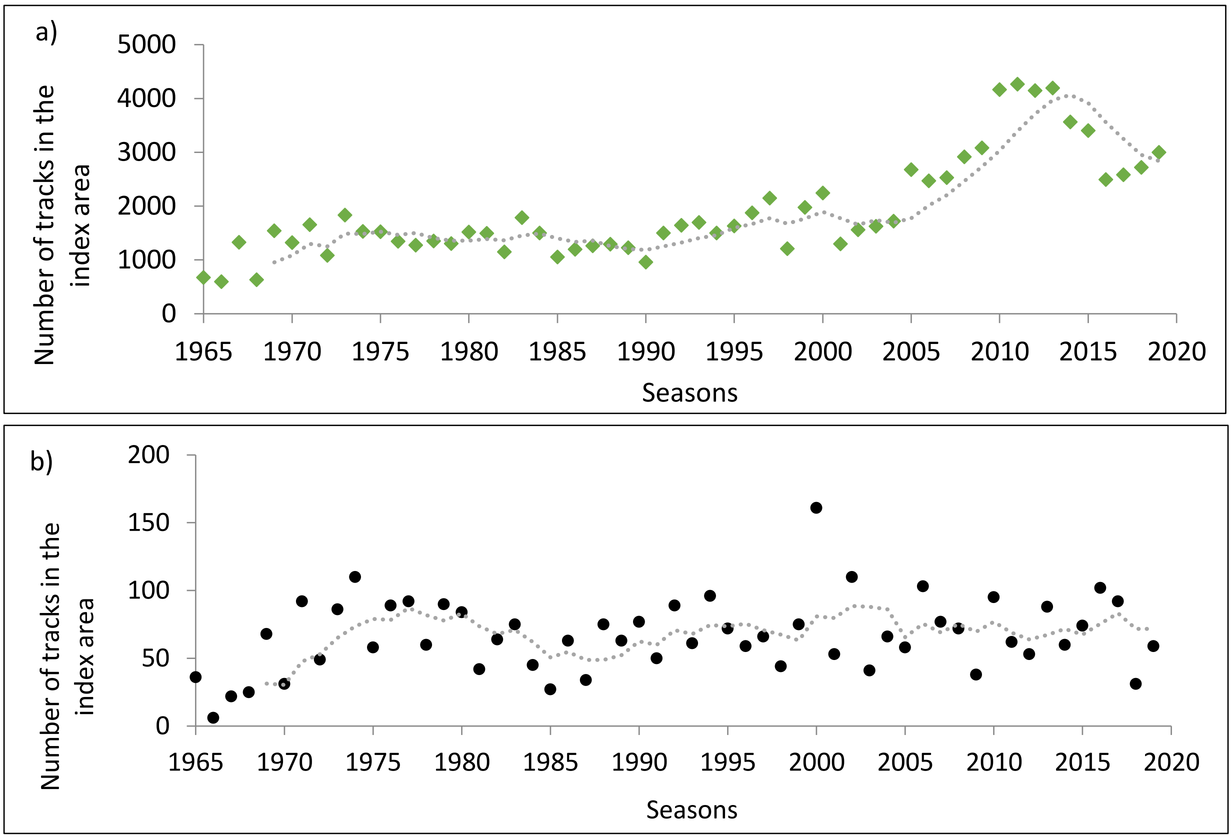

Figure 2.5: Number of tracks for loggerheads (a) and leatherbacks (b) from the 8-km long index area to compare long term abundance trends. Trend line is a 5-year moving average.

Spatial trends

A non-parametric Kruskal-Wallis test was done to investigate whether sea turtle emergences (averaged across all seasons) were equal across the different coastal units. The null hypothesis that the ranks of the groups (i.e., average number of emergences in each coastal unit) are the same was rejected for loggerheads ($X^2 = 3112.7$, $p < 0.01$) and leatherbacks ($X^2 = 2092.3$, $p < 0.01$) as $p < 0.05$ for both species. Thus, both loggerheads and leatherbacks seem to have clear hotspots of nests. Loggerheads had the highest abundance in the north (between coastal units 3 and 15, Kosi Mouth to Dog Point) with a peak at around coastal unit 7, north of Bhanga Nek (Fig. 2.6a) whereas leatherback emergences were more evenly distributed along the coastline (Fig. 2.6b) but still peaking at coastal units 8, 12, 27 and 32 (which are Bhanga Nek, Rabbit Rock, Manzengwenya, and Mabibi).

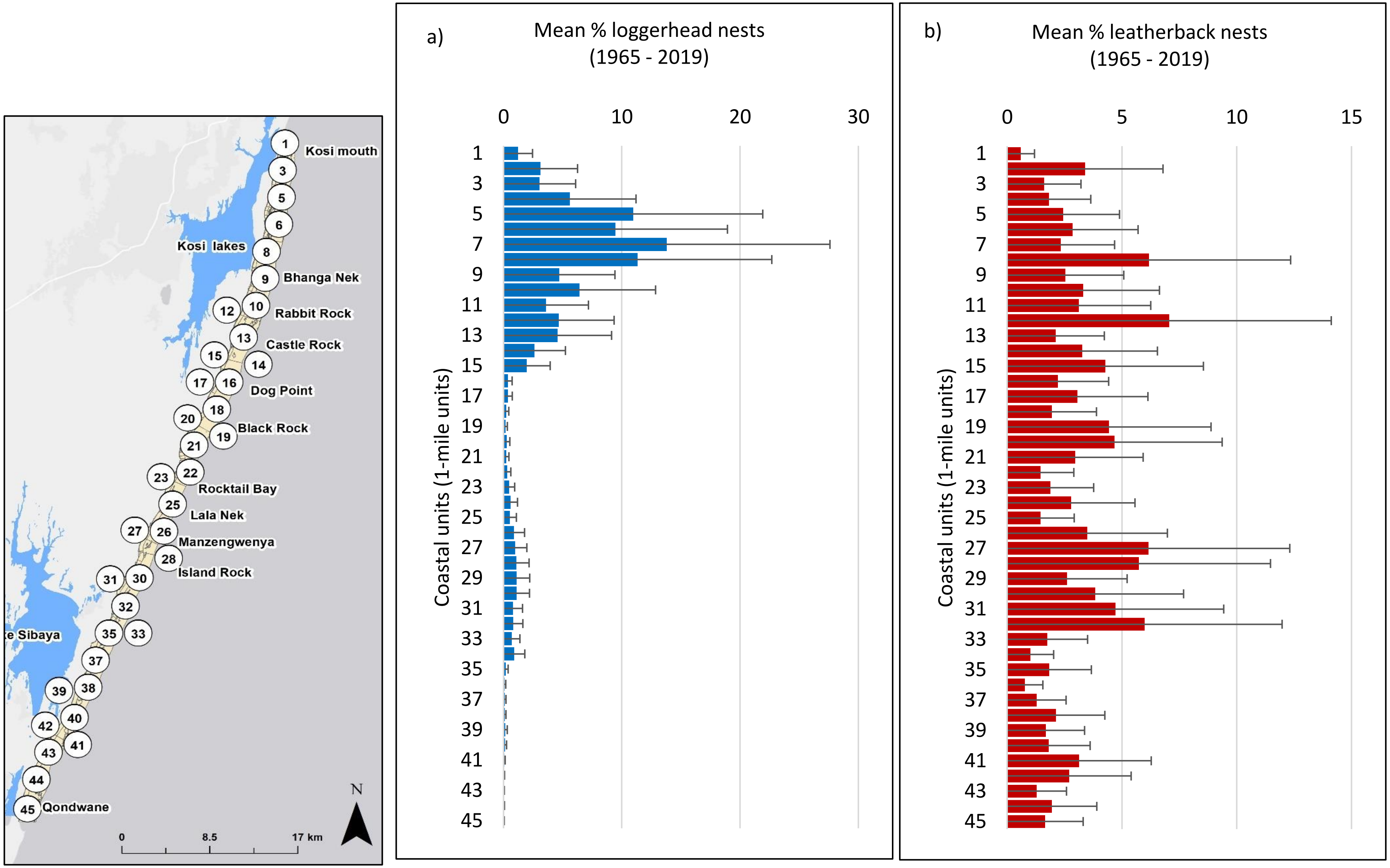

Figure 2.6: Mean proportion (SE) of emergences across all seasons of a) loggerheads and b) leatherbacks nesting within each coastal unit (n = 166 729 for loggerheads and n = 18 612 for leatherbacks).

Patterns of nest distributions in both space and time

Spatio-temporal stability of sea turtle nesting distribution was inspected using contour plots (Fig. 2.7 and 1.8). The loggerhead nesting distribution expanded with a growth in the population, but the hotspots remained around coastal unit 4 (two miles south of Kosi mouth) to coastal unit 8 (one mile north of Bhanga Nek; Fig. 2.7a). Leatherback nesting was more diffused along the coastal units (Fig. 2.8a), but their nest hotspots were also consistent over time. Hotspots were less intense in both species in the years with lower abundances. Both species (Fig. 2.7 and 1.8) showed different overall extent for the first decade which is attributed to restricted sampling effort that was later expanded, in addition to increased conservation activity. However, the hotspots appear consistent in space (at the same location) over time.

To reduce the effect of short-term interannual variation and variable sampling effort, but identify possible shifts in distribution over time, data were summed per half decade (Fig. 2.7b and 1.8b). The spatial stability of both leatherback and loggerhead nesting remained over time when considered in half decades. Loggerhead nesting abundance (Fig. 2.7b) was concentrated around coastal units 4 - 8 (from Bhanga Nek to north halfway between Bhanga Nek and Kosi mouth) whereas leatherback nesting was distributed along the entire coastline with six hotspots (around coastal units 2, 12, 14, 20, 28 and 32; Fig. 2.8b).

The number of loggerhead tracks in coastal units 4 - 8 increased from <2000 sea turtles nesting here per half decade at the onset of monitoring (1965 - 1969) to 3000 - 4000 in more recent seasons (2015 - 2019). Coastal unit 35 (south of Island Rock but before Sodwana) was also noticeably used in later years with higher nesting abundance. Leatherback numbers increased only marginally and plateaued at 50 - 150 nests per half decade for each hotspot (from 1965 onward) (Fig. 2.7 & 1.8).

Given the stability in nesting distribution with each species using the same location (or coastal units) over time, the entire nesting data set (1965 - 2019) was then included in the analyses to identify potential drivers of nest site selection, without needing to account for temporal aspects. The coastal units were also coded with features that persist over time (like lakes, reefs, and beach morphodynamic types) that could potentially be used for navigation and orientation.

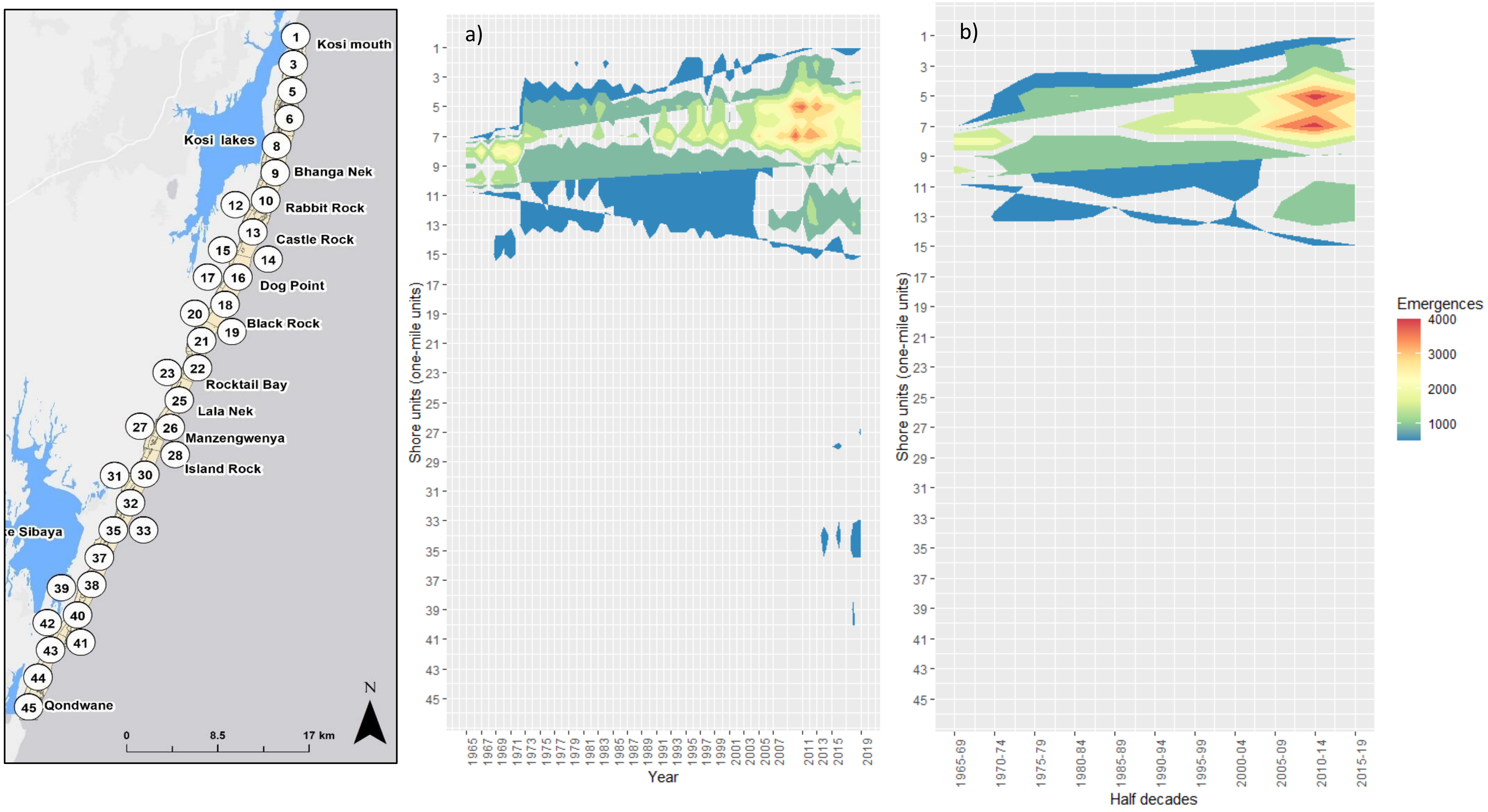

Figure 2.7: Change in distribution of nesting female loggerheads a) annually and b) every half decade along the South African coastline from the beacons closest to the Mozambique border (Coastal unit 1) to further south away from the border (Coastal unit 45). Different colours on the contours represent loggerhead abundance measured as the number of emergences.

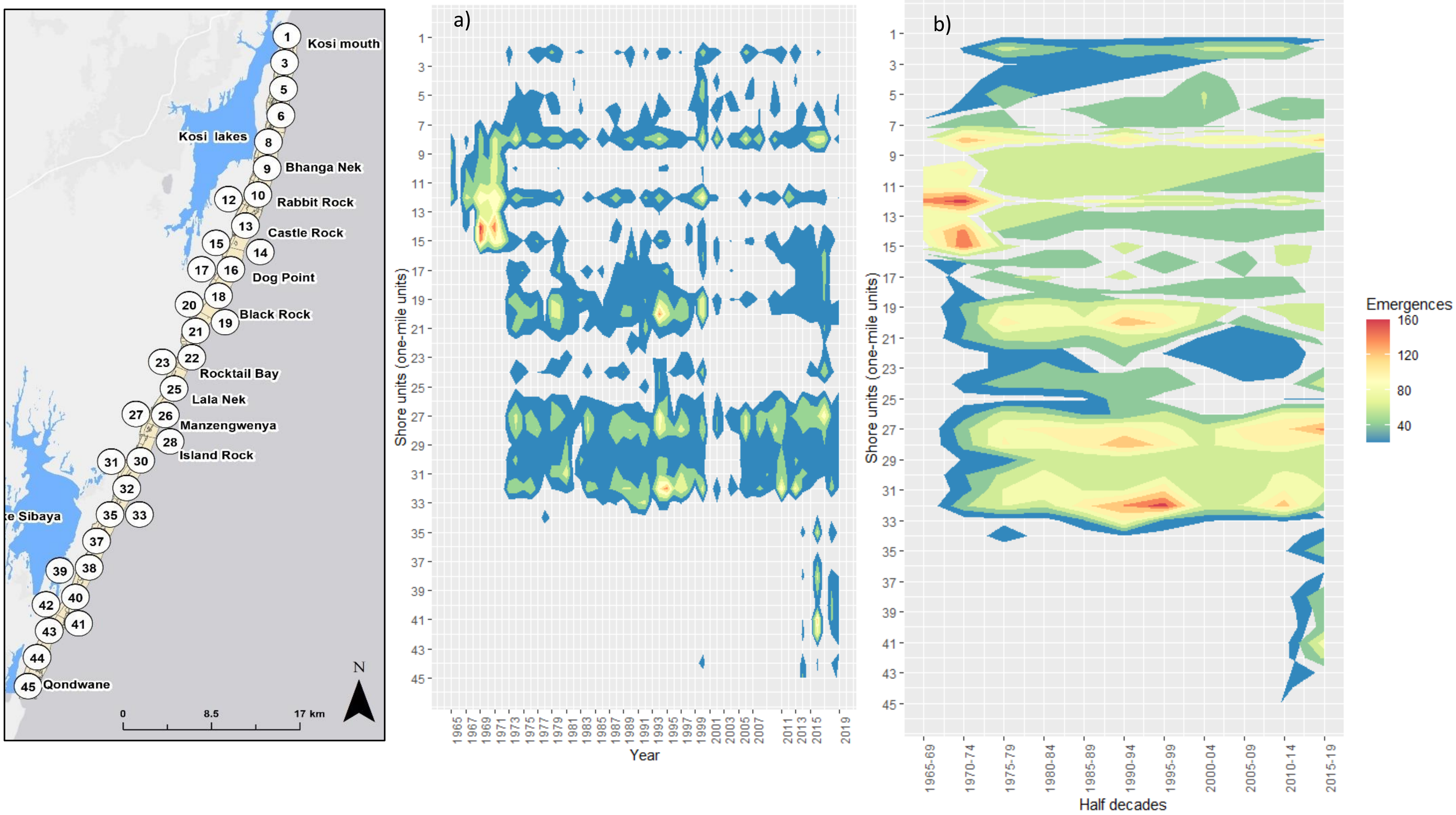

Figure 2.8: Change in distribution of nesting female leatherbacks a) annually and b) every half decade along the South African nesting from the beacons closest to the Mozambique border (Coastal unit 1) to further south away from the border (Coastal unit 45). Different colours on the contours represent leatherback abundance measured as the number of emergences.

Potential drivers of nest site selection

When visually comparing the nesting distribution of loggerheads and leatherbacks, the differences were apparent (Fig. 2.9). Loggerhead nesting was most dense near Kosi lakes (at Bhanga Nek) and coral reefs in the northern part of the rookery with a declining density northward and southward of Kosi estuary mouth. In comparison leatherback nesting was denser around Bhanga Nek (with narrow dunes), the central area of the rookery north and south of Island Rock and around Manzengwenya and Black Rock (between the two lakes).

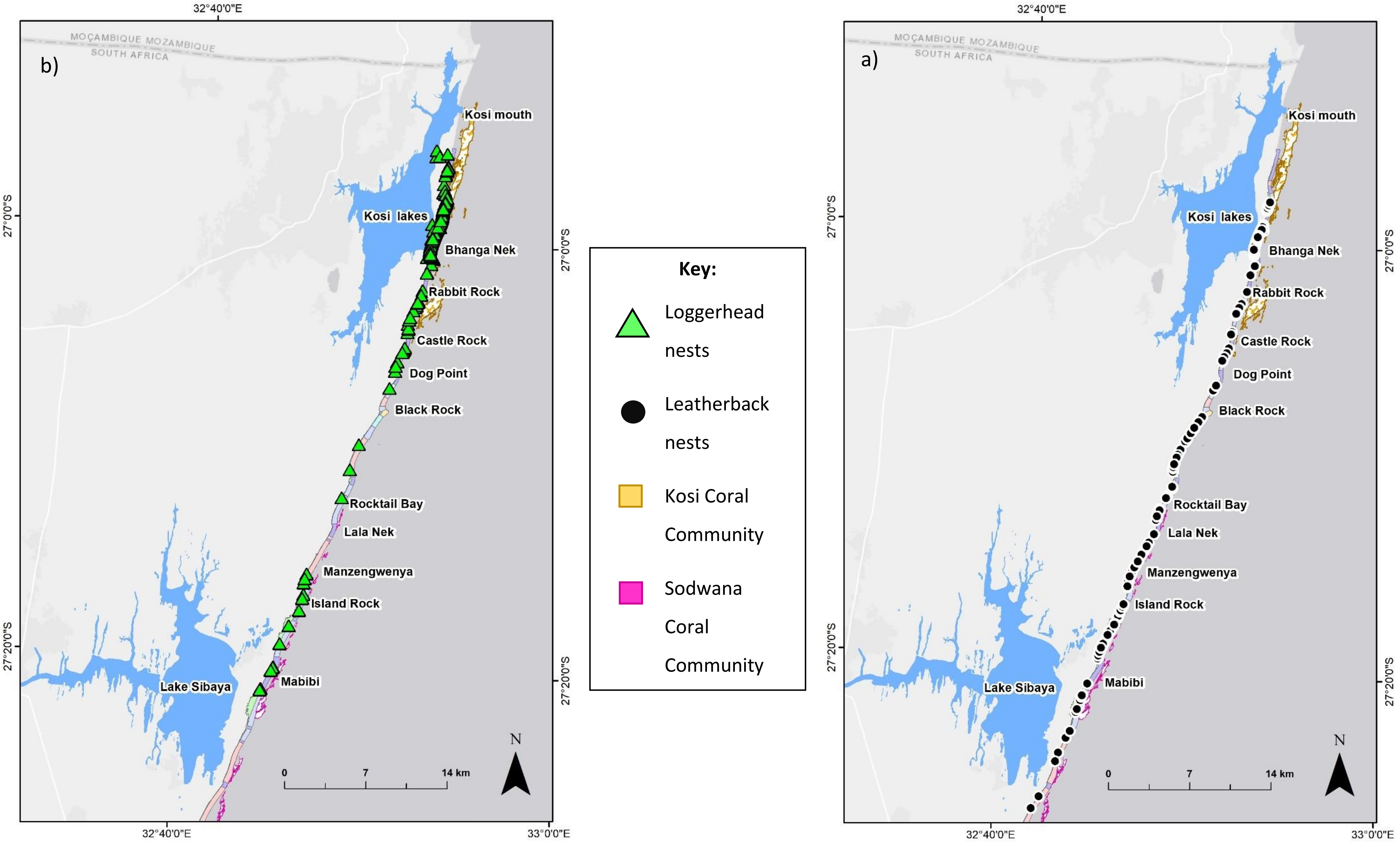

Figure 2.9: Map of a) loggerhead and b) leatherback nests relative to landmarks along the rookery and locations of lakes and reefs.

General-Niche Environment System Factor Analysis

Within the FANTER analysis (measuring habitat selection/relative use) as well as ENFA (habitat rarity), and MADIFA (measuring habitat suitability/niche similarity to local conditions), correlations (See Appendix 2) values close to zero indicate that the variable is of average importance. Positive or negative correlations indicate deviation from the mean with positive values indicating a preference for the variable and negative values indicating an avoidance of that environmental variable. A Monte Carlo Permutation Test for randomization for each species (with 1000 simulations and a two-sided alternative hypothesis) were not significant (i.e., $p > 0.05$) for the FANTER analyses and the first components of the MADIFA analyses. Only the second component of the MADIFA for loggerheads was significant (Table 2.3). However, the components with eigenvalue breaks on the eigenvalue diagrams still provided graphical information for analysing relationships between species distribution and the available and utilized coastal features. Thus, these components with eigenvalue breaks (FANTER: first and last components; MADIFA and ENFA: first two components) were still used in the analysis.

*Table 2.3: P-values for the Monte Carlo permutation tests for randomization with 1000 simulations. Bold values with ** indicates significant results.*

		Loggerheads p-values	Leatherbacks p-values
FANTER	first component	0.61	0.90
	last component	0.16	0.67
MADIFA	first component	0.11	0.10
	second component	**0.02****	0.07

Loggerheads

The first factor (i.e., x-axis, indicating selection or preference) of the FANTER analysis (Fig. 2.10a) had the strongest positive correlations (Table 2.4) with water body size (m^2) that is backing the coastal unit ($\gamma_1 = 0.48$) with a particular preference for the Kosi lakes ($\gamma_1 = 0.46$). The most negative correlation occurred with distance (m) between the dune base and nearest lake or estuary within the coastal unit ($\gamma_1 = - 0.35$), with the highest preference at the shortest distance between the lake and dunes and avoidance of areas where this distance increases. There was also a small negative correlation with the presence of the freshwater body Lake Sibaya ($\gamma_1 = -0.25$) and presence of dune hummocks ($\gamma_1 = -0.21$), indicating slight avoidance of these features. The niche distribution was multimodal (i.e., non-normal), implying multiple variables can be identified as affecting the shape of the niche (Fig. 2.10b). The last factor of the FANTER (where specialization is maximized, y-axis of Fig. 2.10a) showed strong correlations with Sodwana coral communities ($\gamma_x = 0.92$) and sand-dominated Delagoa mixed shore ($\gamma_x = 0.49$), and weaker negative correlations with rocky headlands ($\gamma_x = -0.18$) and inner shelf rock ($\gamma_x = -0.17$). It was concluded that loggerheads selected for shores adjacent and close to large estuarine water bodies, specifically Kosi lakes, and nesting locations close to Sodwana Coral Community but selected against nesting areas with rocky headlands or dune hummocks.

The ENFA outputs measuring rare habitats used, showed a strong positive correlation on the first axis (i.e., the marginality component on the abscissa indicating preferences of loggerheads – see Appendix 1, Fig. 2.10c) for the Sodwana coral communities ($\gamma_{marg} = 0.90$) and a minor positive correlation (Table 2.4) with sand-dominated Delagoa mixed shore ($\gamma_{marg} = 0.49$). Weak negative correlations for the first factor were associated with rocky headlands ($\gamma_{marg} = -0.17$), dune hummocks ($\gamma_{marg} = -0.17$) and the Natal-Delagoa reflective sandy shore ($\gamma_{marg} = -0.15$). The second factor (the first specialization component, y-axis Fig. 2.10c) had the largest positive, but relatively small, contribution from the Natal-Delagoa dissipative-intermediate shore ($\gamma_{spec1} = 0.21$). The coastal features with very strong negative contributions to the second factor were for Delagoa very exposed rocky shore ($\gamma_{spec1} = - 0.95$) followed by Natal-Delagoa reflective shore ($\gamma_{spec1} = -0.60$). Thus, preference for Sodwana Coral Community and avoidance of dune hummocks and rocky headlands contributed the most to marginality (i.e., niche position) and the loggerheads' specialization (i.e., niche breadth) indicated that the population was not tolerant to variation in area of Natal-Delagoa very exposed rocky shore and Natal-Delagoa reflective shore (i.e., loggerhead niche was restricted on a limited range for these shore types with a mean shift towards smaller areas of these shore types). Therefore, smaller areas of these shore types restricted the niche of loggerheads.

The first two factors of the ENFA analysis (i.e., the marginality and the first factor of specialization) explained 44% of the total variances and the inclusion of the third factor (second factor of specialization) explained 55% of the total variances. The eigenvalue of the first axis of specialization was 23.9 which reflects that the variance of the available background was approximately 24 times the variance of the used habitat and thus the ecological niche was much narrower than the available background habitat.

The first component (x-axis of Fig. 2.10d) of the MADIFA analysis measuring habitat suitability, i.e., how similar the ecological niche used by loggerheads is to the available habitat, showed a strong positive correlation (Table 2.4) with Sodwana Coral Community ($\gamma_1 = 0.98$) and a minor positive correlation with the sand-dominated Delagoa mixed shore ($\gamma_1 = 0.45$). The strongest negative correlation was associated with the presence of Kosi lakes ($\gamma_1 = -0.25$) and the proportion of the coastal unit length containing inner shelf rock ($\gamma_1 = -0.25$) and rocky headlands ($\gamma_1 = -0.22$). For the second component of the MADIFA (y-axis, Fig. 2.10d, there was a strong positive correlation with Natal-Delagoa dissipative-intermediate sandy shore ($\gamma_2 = 0.50$) and minor negative correlations with Kosi lakes presence ($\gamma_2 = -0.39$), water bodies area ($\gamma_2 = -0.32$), intertidal width ($\gamma_2 = -0.32$) and inner shelf rock ($\gamma_2 = -0.32$). It was concluded that habitat suitability varied along the rookery for loggerheads that used areas with Sodwana coral communities and Natal-Delagoa dissipative-intermediate shores that were abundant, but also preferred areas near Kosi lakes that were localised and not available across the rookery.

Table 2.4: Summary of loggerhead (top) and leatherback (bottom) GNESFA results showing components of each analysis and the coastal features with the strongest (±0.5 in bold) positive and negative correlations in each component.

FANTER			**ENFA**			**MADIFA**		
Loggerhead								
First factor	+	Water bodies (area): 0.48; Kosi lakes (presence): 0.46	Marginality component	+	**Sodwana coral communities (area): 0.90**	First Factor	+	**Sodwana coral communities (area): 0.98**
	-	Dune base in coastal unit to nearest lake or estuary (distance): -0.35		-	Dune hummocks (presence): -0.17; Headlands (presence): -0.17		-	Kosi lakes (presence): -0.25; coastal unit with inner shelf rock (proportion): -0.25
Last factor	+	**Sodwana coral communities (area): 0.92**	First specialization component	+	Natal-Delagoa dissipative-intermediate shore (0.21)	Second Factor	+	**Natal-Delagoa dissipative-intermediate shore (area): 0.50**
	-	Headlands (presence): -0.18; Dune hummocks (presence): -0.17		-	**Delagoa Very Exposed Rocky shore (area): -0.95;** **Natal-Delagoa reflective shore (area): -0.60;** **Intertidal zone (width): -0.56**		-	Kosi lakes (presence): -0.39; Water bodies (area): -0.32; Intertidal zone (width): -0.32; coastal unit with inner shelf rock (proportion): -0.32
Leatherback								
First factor	+	**Dune vegetation (area): 0.54**	Marginality component	+	Dune to nearest lake or estuary (distance): 0.38	First Factor	+	Dune base to nearest lake or estuary (distance): 0.40
	-	Natal-Delagoa reflective shore (area): -0.18; Kosi lakes (presence): -0.18		-	Water bodies (area): -0.44		-	Water bodies (area): -0.49
Last factor	+	Dune base in coastal unit to nearest lake or estuary (distance): 0.40	First specialization component	+	Delagoa mixed shore (area): 0.39; Kosi lakes (presence): 0.32	Second Factor	+	**Delagoa mixed shore (area): 0.59**
	-	Water bodies (area): -0.47; Lake Sibaya (presence): -0.25		-	Sodwana coral communities (area): -0.47; Back shore (width): -0.37; Vegetation (area): -0.36		-	Back shore (width): 0.37; Natal-Delagoa dissipative-intermediate shore (area): -0.36; Vegetation (area): -0.35

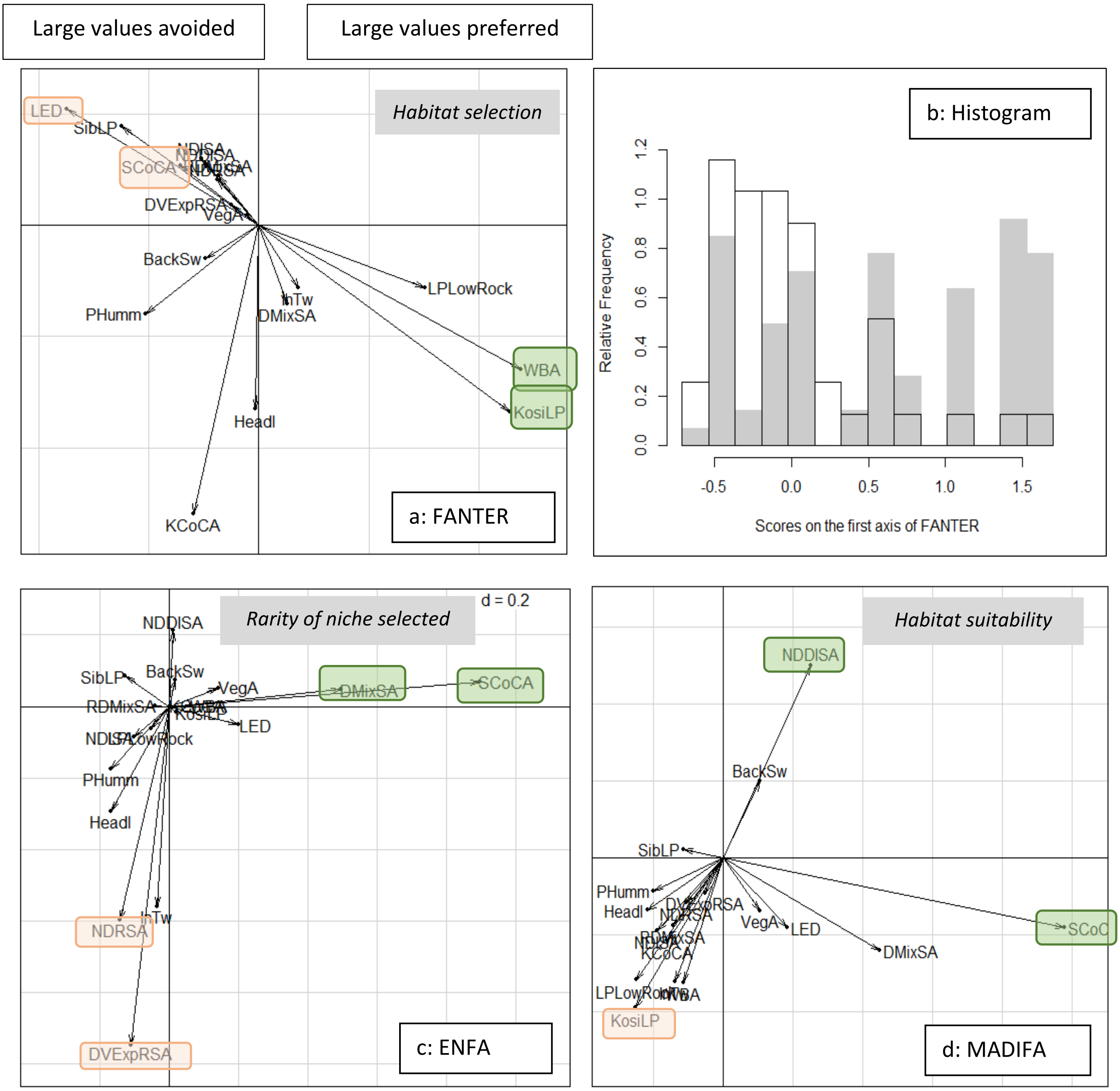

Figure 2.10: Plots of the GNESFA for loggerheads, formed by the a) first and last factors for the FANTER with gridlines separated by a distance of 0.1, and b) Histograms of the coordinates of the available background and of the used habitat on the first component of the FANTER c) marginality and specialization planes of the ENFA with gridlines separated by a distance of 0.2, d) first and second factors of the MADIFA with gridlines separated by a distance of 0.2. Key for labels are given in Table 2.1. Variables highlighted in green showed high positive values for the analysis and values in orange had high negative values.

Leatherbacks

The results for leatherbacks were less clear and somewhat contradictory. The first factor of the FANTER analysis (x-axis, Fig. 2.11a) for leatherbacks had a positive correlation (Table 2.5) with the presence of vegetation ($\gamma_1 = 0.54$). Small negative correlations were associated with the Natal-Delagoa reflective sandy shore (area; $\gamma_1 = -0.18$), Kosi lakes presence ($\gamma_1 = -0.18$) and intertidal width ($\gamma_1 = -0.16$). The first factor of FANTER, indicated a multimodal niche distribution and thus there are multiple variables that can be identified as affecting the shape of the niche (Fig. 2.11b). The last factor of the FANTER (indicating specialization, y-axis Fig. 2.11a) for leatherbacks was weakly correlated to the distance from the dune base to the lake ($\gamma_x = 0.40$) and to Natal-Delagoa dissipative-intermediate shores ($\gamma_x = 0.27$) but had a weak negative correlation with water bodies ($\gamma_x = -0.47$) including Lake Sibaya ($\gamma_x = -0.25$) and dune hummocks ($\gamma_x = -0.19$). Thus, leatherbacks were weakly selecting for areas that were vegetated and near water bodies but weakly avoided areas directly adjacent to Lake Sibaya or Kosi lakes or that were Natal-Delagoa reflective sandy shore types.

The first component of the ENFA analysis (i.e., the axis where marginality/niche position is maximized, Fig. 2.11c) had a weak positive correlation (Table 2.5) with distance between the dune base and lake ($\gamma_{marg} = 0.39$) and a minor positive correlation with the Natal-Delagoa dissipative-intermediate shore ($\gamma_{marg} = 0.24$) and sand-dominated Delagoa mixed shore ($\gamma_{marg} = 0.20$). A weak negative correlation was found with water bodies ($\gamma_{marg} = -0.44$) and Lake Sibaya ($\gamma_{marg} = -0.25$). The second factor (i.e., the ordinate where specialization is maximized; Fig. 2.11c), had the strongest positive contribution from the area of sand-dominated Delagoa mixed shore ($\gamma_2 = 0.39$) and the presence of Kosi lakes ($\gamma_2 = 0.32$). The strongest negative contribution came from Sodwana coral communities ($\gamma_2 = -0.47$), back-shore width ($\gamma_2 = -0.37$), vegetation (area; $\gamma_2 = -0.36$) and Natal-Delagoa dissipative-intermediate shore ($\gamma_2 = 0.\text{-}31$). Thus, leatherback marginality (used niche vs available habitat) was contributed to mostly by the avoidance of areas directly adjacent to large water bodies. Leatherback specialization (i.e., niche breadth) indicated that the population was weakly intolerant to variation in sand-dominated Delagoa mixed shores and vegetated areas within the same habitat also near Kosi lakes, Sodwana Coral Community and wide back-shores. There was a mean shift towards sand-dominated Delagoa mixed shore and Kosi lakes mostly affecting the position of the available niche relative to the used niche on the coast.

The first two factors of the leatherback ENFA analysis (i.e., the marginality and the first factor of specialization) explained 19% of the total variance and the inclusion of the third factor (second factor of specialization) explained 27% of the total variance. The eigenvalue of the first axis of specialization was 2.1 which reflects that the variance of the available background was approximately two times the variance of the used habitat and thus the ecological niche was narrower (or half) than the available background habitat.

For the MADIFA analysis (Fig. 2.11d, the first component had the highest positive correlation (Table 2.4) with the distance between the dune base and lakes ($\gamma_1 = 0.40$) and Natal-Delagoa dissipative-intermediate sandy shores ($\gamma_1 = 0.28$). Small negative correlations were associated with the area of water bodies ($\gamma_1 = -0.49$) and the presence of Lake Sibaya ($\gamma_1 = -0.25$). The second component had a strong positive correlation with the sand-dominated Delagoa mixed shore ($\gamma_1 = 0.59$) and minor positive correlation with Kosi lakes ($\gamma_1 = 0.20$). Weak negative correlations were found with back-shore width ($\gamma_{spec1 =}$ -0.37), Natal-Delagoa intermediate shore ($\gamma_{spec1} = -0.36$), presence of vegetation ($\gamma_{spec1} = -0.35$), and Sodwana Coral Community ($\gamma_{spec1} = -0.30$). These coastal features had the largest effect on the position of the available niche relative to the used niche. It was concluded that habitat suitability varied along the nesting beach for leatherbacks (i.e., not all areas are equally suitable along the beach). Leatherbacks used areas close to lakes or estuaries, and with sand-dominated Delagoa mixed shores that were largely available and thus more optimal. Leatherbacks also preferred largely vegetated areas with Natal-Delagoa dissipative-intermediate shore and wider back-shores but that were not largely available relative to the entire rookery area.

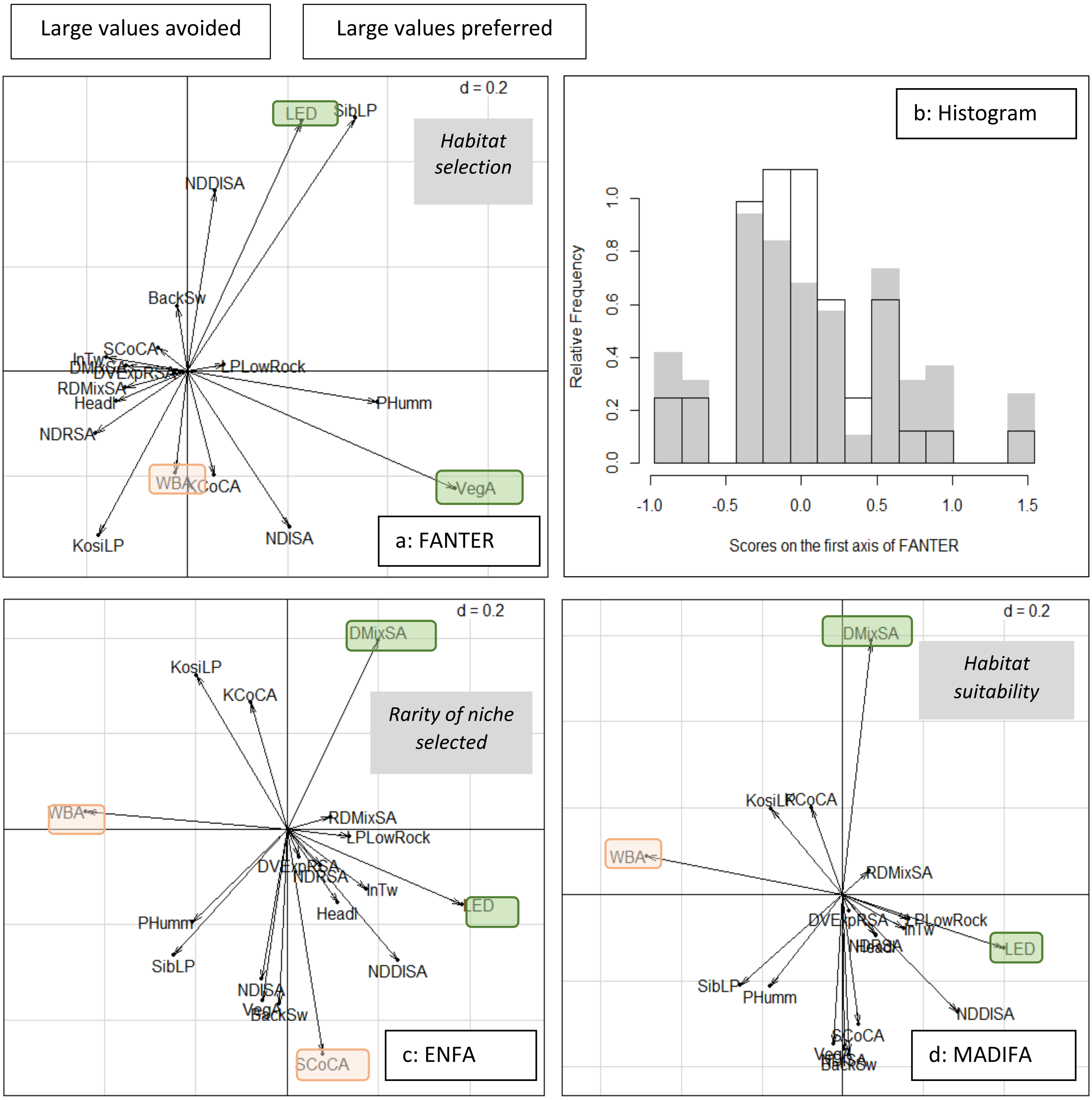

Figure 2.11: Plots of the GNESFA for leatherbacks formed by the a) first and last factors for the FANTER with gridlines separated by a distance of 0.1, b) Histograms of the coordinates of the available background and of the used habitat on the first component of the FANTER c) marginality and specialization planes of the ENFA with gridlines separated by a distance of 0.2, d) first and second factors of the MADIFA with gridlines separated by a distance of 0.2 and. Key for labels is given in Table 2.1.Variables highlighted in green showed high positive values for the analysis and values in orange had high negative values.

Comparison between species and analyses

The GNESFA results for loggerheads and leatherbacks suggests that loggerheads have much stronger preferences than leatherbacks. Coral communities and beach types (specifically Natal-Delagoa mixed shores and Natal-Delagoa dissipative-intermediate shores) were the most influential coastal features for loggerhead emergences (i.e., were preferred during the habitat-selection process), whereas leatherback distribution was weakly affected by the presence of lakes, coral communities, and size of water bodies.

For both loggerhead and leatherbacks, the FANTER and MADIFA analyses were significantly correlated (Table 2.5), especially on the specialization (niche breadth) component (both species $p \ll 0.001$). Thus, there is an agreement between what is preferred by each species (FANTER) and what the environment offers (MADIFA).

Table 2.5: Correlations between components of the FANTER, ENFA and MADIFA results for loggerheads and leatherbacks.

x	y	Correlation coefficient	p-value	t-value	df
Loggerheads					
FANTER first component	ENFA marginality component	-0.05	0.842	-0.202	16
FANTER last component	ENFA first specialization component	0.36	0.139	1.559	16
FANTER first component	**MADIFA second component**	-0.49	**0.0387**	-2.252	16
FANTER last component	**MADIFA first component**	0.94	**<< 0.001**	11.394	16
ENFA marginality component	MADIFA second component	-0.13	0.607	-0.524	16
ENFA first specialization component	MADIFA first component	0.31	0.216	1.287	16
Leatherbacks					
FANTER first component	ENFA marginality component	-0.22	0.379	-0.9044	16
FANTER last component	ENFA first specialization component	-0.14	0.571	-0.578	16
FANTER first component	**MADIFA second component**	-0.49	**0.039**	-2.250	16
FANTER last component	**MADIFA first component**	0.997	**<< 0.001**	52.310	16
ENFA marginality component	MADIFA second component	0.01	0.962	0.049	16
ENFA first specialization component	MADIFA first component	-0.18	0.480	-0.724	16

Outlying Means Index analysis

OMI values (i.e., marginality, niche position) were higher on average for loggerheads than for leatherbacks, although leatherbacks had higher tolerance values on average than loggerheads did (Table 2.6). Lower OMI values for leatherbacks indicated that individuals are more dispersed throughout the study area compared to loggerheads, which were influenced more by a subset of measured coastal features. Higher tolerance of leatherbacks indicated they were more generalist than loggerheads that were more specialized relative to leatherbacks, i.e., leatherbacks had a broader nesting niche and loggerheads a narrower nesting niche.

A non-parametric Kruskal-Wallis test was conducted to test whether the values of OMI and tolerance differed significantly between loggerheads and leatherbacks. Both the OMI values (Kruskal-Walls: $X^2 = 51.598$, $p < 0.01$) and tolerance values (Kruskal-Walls: $X^2 = 19.443$, $p < 0.01$) had p-values below 0.05, therefore the null hypothesis of means being the same for each group (i.e., species) was rejected. Thus, the OMI values and tolerance values differed significantly between loggerheads and leatherbacks.

Table 2.6: Means of results for the OMI analysis. x̄ OMI = mean of outlying mean index (i.e., marginality) values that indicates niche position. x̄ Tol = mean Tolerance index values that indicates niche breadth. x̄ Rtol = mean of residual tolerance values. Italicized columns represent the percentage of variability corresponding to a specific statistic

Species	**x̄ OMI**	**x̄ Tol**	**x̄ Rtol**	***x̄ OMI***	***x̄ Tol***	***x̄ Rtol***
Loggerhead	8.136998	0.691329	5.537929	*57.07246*	*4.479042*	*38.4515*
Leatherback	2.889759	1.364986	11.03534	*19.02727*	*8.6*	*72.37727*

Discussion

This study aimed to investigate coastal features potentially used to guide nest site selection by loggerhead and leatherback turtles in iSimangaliso. Suitable nesting sites directly affects reproductive success in oviparous reptiles that do not provide parental care beyond nest site choice (Hughes and Brooks, 2006). The nest site selection process of sea turtles at their nesting grounds is generally poorly documented, and most nest site selection studies only focus on features above the low tide mark. This study is one of the first to incorporate coastal features extending below the intertidal zone, i.e., in-water features, into analyses on sea turtle nest site selection. Female turtles choose a location by interacting with a combination of complex abiotic and biotic factors acting as nesting cues (Hays et al., 1995, Kikukawa et al., 1999, Mayor et al., 2009, Weishampel et al., 2006). These cues could be physical (like reef presence), chemical (like freshwater odours) or visual (like dune skyline or vegetation colour) and may extend from the inner shelf to in-land areas past coastal vegetation.

The hypothesis that spatially variable coastal features act as cues for turtle nest site selection depending on the species because of species-specific preferences for some coastal features over others was accepted; there were hotspots for each species and results were more striking for loggerheads, but both species had preferences for specific areas along the shore that persisted over time. Further, coastal features are not evenly distributed, and both species appear to have preferences for specific features although it seemed much stronger for loggerheads turtles.

Spatial-temporal stability in nest distributions

Loggerhead nests were aggregated in the northern section of iSimangaliso near Kosi lakes, whereas leatherback nests were more dispersed. The high abundance in the first decade of monitoring among coastal units 5-8 could be interpreted as a sampling bias because of the initially limited extent of turtle monitoring effort. However, when the monitoring program stabilised and expanded after 1974, the recorded distribution expanded for both species. There was also a slight shift in nesting distribution away from Botelier Point (headland at Bhanga Nek, coastal unit 9) with the establishment of a ranger station and presumably increased tourism traffic on the beach. Foot traffic and light pollution from accommodation for tourism peaks at the same time as turtle nesting, thus potentially causing a disturbance to nesting. Tourism negatively impacting sea turtle nesting was observed with green turtles and tourists in Costa Rica (Jacobson and Lopez, 1994). During times when tourists were more commonly found on the beach, sea turtle nesting was reduced by 30% as a result of the disturbance. The longshore distributions in nests (objective 1) are in agreement with the results from Botha (2010), even with the expanded data set, confirming that loggerhead nesting is more intense in the northern part of the rookery and leatherback nesting is diffused along the rookery.

Potential drivers of nest site selection

Homing sea turtles eventually travel close inshore (Shimada et al 2016), and this is presumably the same for loggerheads returning to iSimangaliso. Subtidal features, like Sodwana Coral Community, would be characteristic cues along the way. Loggerheads showed relatively strong positive correlations with reef complexes, compared with that of other coastal features. Similar results were also found with satellite tagging of the same population by Harris et al. (2015). This suggests that the presence of certain reef communities will provide at least a visual cue at sea (Shimada et al., 2016), but probably also an audible cue from other reef species (Lobel, 2013), and shelter during inter-nesting intervals. Coral reefs also provide refuge from predators, places to rest and also cleaning stations to remove epibionts on the shells of nesting females (Nolte et al., 2020, Schofield et al., 2017). Visual cues were found to be important for sea finding for post-nesting females (Brazier, 2012), and coral reefs and inshore rocks can form important visual cues for sea turtles returning to the same rookery every two to three years (Shimada et al., 2020).

After arriving in the nearshore area off a nesting beach, female sea turtles must make decisions on a suitable area to haul out on to nest when a clutch is ready to be laid. Beach morphodynamic state and beach width (i.e., back-shore and intertidal widths of the beach, sand grain size, and wave energy in the surf zone) can differ in extremes according to beach morphodynamic types (Harris et al., 2011, Short, 2012, Jackson and Short, 2020). Reflective beaches have higher energy surf zones and have shorter across-shore widths than intermediate beaches that have characteristics between reflective and dissipative types. Dissipative-intermediate beaches are less extreme than dissipative beaches, having less energetic surf zone, longer wave periods and finer sands (Short, 2006). Dissipative-intermediate beaches are wider than the reflective extreme but not as wide as the dissipative extreme (Short, 2012). The width of the beach and wave action intensity in the surf zone as they relate to beach morphodynamic types is relevant for sea turtles; wider beaches and stronger wave action will require more energy to haul out and crawl across the beach, especially in species which crawl across the beach until they reach vegetation often growing on dune bases such as loggerheads (Karavas et al., 2005) and green sea turtles (Kamel and Mrosovsky, 2006).

Beach morphodynamic types were also a coastal feature that was correlated with the distribution of the nesting population of both species, specifically the preference for Natal-Delagoa dissipative-intermediate beach type and avoidance of Natal-Delagoa reflective shore by loggerheads (Botha,

2010) and leatherback preference for sand-dominated Delagoa mixed shore. Loggerheads prefer wide beaches with flatter slopes; as was reported for loggerhead populations by Garmestani et al. (2000) in Florida and by Mazaris et al. (2006) in Zakynthos of Greece. Studies on leatherbacks report that although they can use wide beaches such as those studied by Sivasunder et al. (1996) in Andaman and Rutland islands, they make use of steeper beaches on undeveloped sections of Playa Granda in Costa Rica (Roe et al., 2013) and high-energy surf zone beaches such as Trinidad in the West Indies (Bacon, 1970, Tucker, 1990) that tend to be narrower.

After hauling up the beach and committing to a nesting site, dune vegetation may act as the next cue to initiate digging of a nest chamber. Contrary to expectation, leatherback nest site selection was strongly correlated with dune vegetation (even though they don't nest close to, or in, vegetation) rather than loggerheads that seem to crawl until they encounter dune vegetation (King, 2019). Other studies also show that loggerheads nest near or within dune vegetation (Karavas et al., 2005, Hannan et al., 2007, Garmestani et al., 2000), whereas leatherbacks nest on open sand generally no closer than two metres from the dune vegetation (Botha, 2010, Sivasunder and Devi Prasad, 1996), as it seems to lower nest productivity (Conrad et al., 2011). This was also found in the Virgin Islands (Conrad et al., 2011), Costa Rica (Nordmoe et al., 2004, Neeman et al., 2015), Suriname (Whitmore and Dutton, 1985) and Andaman Islands of India (Sivasunder and Devi Prasad, 1996). These studies suggest that it is unlikely that dune vegetation is acting as a direct, tactile cue in nest site selection as it does with other species such as loggerheads and hawksbills (Leighton et al., 2008). However, dune vegetation may act as a visual cue for leatherbacks. Female turtles nesting along Florida beaches avoided areas of the beach without exposure to artificial light that were backed by tall buildings (Salmon, 2003). Considering that turtle vision is myopic out of water (Ehrenfeld and Koch, 1967), patches of vegetation may be similar to tall buildings, or create visible colour/shade contrasts of light and dark areas detectable by sea turtles (Brazier, 2012).

Water bodies behind a dune corridor is not visible from the ocean shore but yet presumably affect nest site selection by olfactory plumes permeating through the groundwater or through estuarine out-welling (Hughes, 1974), similar to the cue followed by salmon species where freshwater meets oceanic water (Sutterlin and Gray, 1973). Migrating green turtles follow a freshwater plume back to its source from Ascension Island over 2000 km away (Koch et al., 1969). However, odour plumes are not the only cue (if it is indeed a cue) as sea turtles have returned from both up-current and down-current foraging sites despite an odour plume only occurring in one direction. This was observed for green turtles in Costa Rica (Carr, 1986), loggerheads in Florida (Meylan et al., 1983), kemp's ridley's at Rancho Nuevo in Mexico (Carr, 1963) and loggerheads along the Great Barrier Reef (Limpus et al., 1992).

Hughes (1996), however, noted the correlation between the turtle nest locations and beaches backed by the Kosi lakes. After the initial study by Hughes (in 1974), water bodies, like Kosi lakes and Lake Sibaya, are still important for nesting but the mechanism of how it affects nest site selection is still unknown. Brazier (2012) attempted to investigate the mechanism where sea turtle emergences were correlated to the chemical components within fresh groundwater influx but found no meaningful effect. The only directional and possible attractional effect was sulphide in the shallow surf zone water. He concluded that turtle emergences were correlated to the sulphide concentrations further along-shore rather than directly where they hauled out. However, the loggerhead nesting has the highest density at the smallest distance between the Kosi lakes and the shore and tapers in both direction to the estuary mouth and Dog Point (Fig. 2.6a). It was therefore assumed that the cue percolates in through the ground water rather than through estuarine out-welling, or by an aerial olfactory cue. The microscale level (i.e., low level) of information being perceived by turtles during the process of nest site selection may be more intricate and complex than it seems, considering the directional effect of lakes and groundwater influx on nesting distribution despite their location offshore, unseen by sea turtles.

Implications for sea turtle fitness

Loggerheads overall had a stronger preference for specific environmental features than leatherbacks, or the features for which they select are more localised/concentrated. The nesting strategy of leatherbacks seen in South Africa has also been described in the scattered nesting-hypothesis (Tucker, 1990, Mrosovsky, 1983) where nests of leatherbacks are without spatial preference (i.e., lacking an area along the nesting beach where nesting is concentrated). The proximate driver behind scattered-nesting is to reduce each individual nests' chances of failing within unstable nesting environments through bet-hedging (Cohen, 1966, Giesel, 1976). However, Tucker (1990) investigated whether this scattered-nesting persists on stable and unstable nesting beaches such as the Culebra and St Croix nesting beaches respectively and found that even in nesting areas with stable conditions, nesting was still scattered.

Studying sea turtle habitats use during foraging and courtship is logistically more difficult, than protecting and observing adults females when they come to nest considering the obligate terrestrial component for sea turtle nesting (Shimada et al., 2021, Shimada et al., 2020). Understanding what features are selected for along nesting beaches may be useful for management decisions about what environmental features of a nesting rookery need to be protected. If back-shore or in-water features guide nest site selection but only beach components are protected, it could lead to nest failure should these unprotected features be lost or compromised with anthropogenic coastal development.

Indiscriminate building of harbour walls or beach armouring (Dugan et al., 2008) as well as beach renourishment (Steinitz et al., 1998) that alter sandy beach characteristics (like grain size) may alter nest site success. Reduced nesting frequency (Steinitz et al., 1998) and emergence success (Trindell et al., 1998) following beach nourishment was reported for loggerheads nesting in Florida. However, in other rookeries such as Raine Island, beach renourishment as a method for beach re-profiling has been successful in increasing green turtle hatchling output (Smithers and Dawson, 2023).

From the results of this study, the South African loggerhead nesting population can be described as specialists having narrower nesting niches. Comparatively, leatherbacks are generalists with a much broader nesting niche. A population of spatial specialists may incur lower reproductive costs with higher nest site fidelity at an individual level (Patrick and Weimerskirch, 2017). Seeking out a specific nesting site with certain environmental conditions (presumably, conditions that will allow for nest development, hatching and emergence success) and then placing consecutive nests close to the initially chosen nesting site, result in less energy spent searching for nesting sites (Tripathy and Pandav, 2008). Studies on leatherback and green turtle nest site selection in Equatorial Guinea have shown that differences in nest site selection impacted hatching success (Veelenturf et al., 2022). Spatial generalists will not be as selective , incurring a higher energetic cost per nest, but may find more ecological benefit in unstable, dynamic environments where nest perturbation is likely (Byer and Reid, 2022). By not exhibiting high nesting nest site fidelity, spreading the nests over areas with varying conditions, there is a better chance that some nests will survive a perturbation event (Eckert, 1987). Nest site fidelity at an individual level will be investigated further in the following chapter.

Conclusions

To conclude, the nesting distribution of both species was consistent on a spatio-temporal scale with loggerhead nesting being more concentrated in a hotspot in the northern part of the rookery while leatherback nesting was more evenly distributed with more hotspots spread out along the coastline. Coral reefs, certain beach morphodynamic types (dependent on the species), dune vegetation and lakes and estuaries were all positively associated with the population-level nest site selection of leatherbacks and loggerheads, even though the correlations and thereby selection was stronger for loggerheads. While the study looked at what coastal features, both along-shore and across-shore, were relatively important for these species’ nest site selection, it did not investigate mechanisms responsible for selection. However, linking the variability of coastal features to sea turtle nesting is vital for implementing management decisions especially on nesting beaches where more than one species nests. Should nest site selection and reproductive success of individuals over multiple generations be compromised, then this could result in a nesting population decline that would be detrimental considering the threatened nature of sea turtle populations globally.

Appendix 1

The FANTER is used for identifying the 1) habitat specialization of a species (i.e., the restriction or narrowness of the species niche relative to the available environment (Calenge and Basille, 2008, Caruso et al., 2015, Neupane et al., 2019), 2) the marginality of the species (i.e., the central tendency or preference of the individual, population or species from within an available possibilities in an environment, formally measured as the absolute difference between global mean divided by 1.96 standard deviation of the global distribution of the focal species) (Basille et al., 2008, Calenge and Basille, 2008, Neupane et al., 2019) and 3) how coastal features affect the shape of the niche such that it is unimodal or multimodal.

The ENFA removes the choice of whether the utilization weights or availability weights will be the distribution chosen as the reference. This analysis is symmetrical in that the spherical shape applies to both the availability and utilization distributions and both act as the reference and the focus (Calenge and Basille, 2008, Caruso et al., 2015, Neupane et al., 2019). The first factor extracted by the analysis displays the marginality coefficient (ranging from positive one to negative one) (Caruso et al., 2015) thereby allowing for the species niche (i.e., marginality) and the restriction of the species niche (i.e., specialization) to be maximized and indicates rarity of the environmental characteristics selected by the species in the study area. While the ENFA is complimentary to the FANTER (it identifies bimodal niches) (Neupane et al., 2019, Calenge and Basille, 2008) and allows for the development of habitat suitability maps like the MADIFA, the ecological space experiences loss of one dimension that may lead to loss of important biological information. The orthogonality constraints in the factor analysis may thus cause erroneous interpretation because marginality is not significant causing biased specialization results (Neupane et al., 2019). However, assuming that both the presence and available background are symmetrical and unimodal, the marginality and specialization of a species can be distinguished by ENFA.

The MADIFA is used for determining where the direction of the ecological space occurs such that the characteristics of the environment are furthest from the optimum of the species and whether the habitat is used by the species (Calenge and Basille, 2008, Caruso et al., 2015, Neupane et al., 2019), resulting in the focus of the analysis being the utilization weights and the reference and centring of the analysis being on the availability weights. Thus it can be identified what the species 'considers' in terms of what is available to it and whether the environment is suitable (close to the niche) or not suitable (far away from the niche) (Calenge and Basille, 2008). This analysis is used for creating habitat suitability maps. The ecological niche has a theoretically spherical shape and the curvature of the ecological space indicates the deviation of the species optimal to the available environment (Neupane et al., 2019). For niche restriction, marginality and specialization are combined into a single measure.

Compared to other studies using GNESFA done in areas such as national parks or protected areas using relocation and tracking data (Neupane et al., 2019, Caruso et al., 2015, Calenge and Basille, 2008), 100% of the area analysed within this study was both utilized and available for the study species. Thus, the GNESFA was done using presence-only data which is possible with the adehabitatHS package (Caruso et al., 2015, Basille et al., 2008, Calenge and Basille, 2008).

Appendix 2

Table A2.1: Component loadings of loggerhead and leatherback GNESFA analyses. Significant values (≥0.5 or ≤-0.5) are in bold and the key for coastal features is found in Table 2.1.

	FANTER				ENFA				MADIFA			
	Loggerhead		Leatherback		Loggerhead		Leatherback		Loggerhead		Leatherback	
Coastal features	First factor	Last factor	First factor	Last factor	First factor	Second factor	First factor	Second factor	First factor	Second factor	First factor	Second factor
DMixSA	0.05	0.49	-0.12	0.12	0.49	0.05	0.20	0.39	0.45	-0.24	0.07	**0.59**
RDMixSA	-0.07	-0.05	-0.12	0.08	-0.04	0.00	0.10	0.03	-0.14	-0.17	0.06	0.05
DVExpRSA	-0.05	-0.10	-0.03	0.02	-0.11	**-0.95**	0.03	-0.06	-0.05	-0.09	0.02	-0.04
NDDISA	-0.10	0.05	0.06	0.27	0.01	0.21	0.24	-0.28	0.25	**0.50**	0.28	-0.27
NDISA	-0.10	-0.12	0.20	-0.02	-0.10	-0.09	-0.06	-0.31	-0.19	-0.19	0.00	-0.36
NDRSA	-0.07	-0.14	-0.18	0.08	-0.14	**-0.60**	0.07	-0.08	-0.11	-0.11	0.08	-0.09
WBA	0.48	0.04	-0.02	-0.47	0.06	0.00	-0.44	0.04	-0.11	-0.32	-0.49	0.09
KCoCA	-0.12	-0.02	0.05	-0.08	0.00	0.00	-0.08	0.27	-0.16	-0.22	-0.08	0.20
SCoCA	-0.14	**0.92**	-0.06	0.05	**0.90**	0.07	0.08	-0.47	**0.98**	-0.18	0.04	-0.30
LPLowRock	0.30	-0.08	0.07	0.16	-0.05	-0.06	0.14	-0.01	-0.25	-0.32	0.16	-0.06
PHumm	-0.21	-0.17	0.38	-0.19	-0.17	-0.18	-0.21	-0.20	-0.20	-0.08	-0.18	-0.21
Headl	-0.01	-0.18	-0.14	0.09	-0.17	-0.29	0.11	-0.15	-0.22	-0.14	0.08	-0.10
InTw	0.07	-0.05	-0.16	0.16	-0.03	**-0.56**	0.17	-0.13	-0.14	-0.32	0.15	-0.08
BackSw	-0.10	0.03	-0.02	0.00	0.02	0.07	-0.02	-0.37	0.11	0.20	0.02	-0.37
VegA	-0.02	0.14	**0.54**	-0.03	0.14	0.05	-0.05	-0.36	0.11	-0.14	-0.02	-0.35
LED	-0.35	0.20	0.23	0.40	0.20	-0.05	0.38	-0.16	0.18	-0.18	0.40	-0.12
KosiLP	0.46	-0.02	-0.18	-0.19	0.02	-0.02	-0.20	0.32	-0.25	-0.39	-0.18	0.20
SibLP	-0.25	-0.13	0.34	-0.25	-0.13	0.09	-0.25	-0.27	-0.11	0.02	-0.25	-0.21

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CHAPTER 3: NEST SITE FIDELITY OF LOGGERHEAD AND LEATHERBACK INDIVIDUALS IN SOUTH AFRICA

Abstract

Repeated nesting behaviour and patterns of individual nesters over time will be indicative of the overall population behaviour. However, individual behaviour is not always consistent over time and space both within the same nesting season and across multiple seasons. While populations persist because of nesting success leading to successful egg development, hatching and emergence, not every individual's nesting attempt is successful. At times, individual females may emerge out of the water and not successfully crawl up the beach and instead decide to turn back, before even moving across the beach and attempting to dig a nest. Regardless of when a female turns back, the failure to nest after emerging out of the surf zone is considered a "false crawl". The question remains, however: are false crawls energetically costly mistakes, or simply a trade-off between energy used to haul-out and energy used for offspring provisioning? This chapter aims to compare the nesting behaviour and nest site fidelity among individuals within each population of loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles within iSimangaliso Wetland Park. Using 55 years of nesting data, the nesting history of 16 664 loggerheads and 2 691 leatherbacks was reconstructed with records of where and when (i.e., the season and nesting event number within the season) an individual emerged and whether the nesting attempt was successful. By comparing nest site fidelity between species and among years, it was determined which species is placing their nests closer together and whether nesting experience impacts the precision of nest placement. The nest site fidelity of nesting events was also compared to the site fidelity of emergences (where false crawls are included with nesting events) across seasons. By comparing fidelity of emergences and nesting events, it could indicate whether sea turtles are selecting where they wish to nest before hauling out or after. Results indicated that spatially, loggerheads have higher fidelity than leatherbacks and are placing their nests closer together along the beach. Temporally, nest site fidelity improved with experience for loggerheads but not for leatherbacks, thus loggerheads exhibit some learning behaviour across nesting seasons. However, site fidelity of emergence locations and nesting locations didn't differ for both loggerheads and leatherbacks. Thus, for both species, there is decision-making for clutch placement prior to hauling out and where they emerge along the beach is where they have selected to nest. While fidelity and change in fidelity with experience are not the same between species, both low and high fidelity have positive and negative implications for sea turtle reproductive fitness.

Introduction

Various species display nest site fidelity, including insects, e.g., red mason bees (*Osmia rufa*) (Steffan-Dewenter and Schiele, 2004), birds e.g., white storks (*Ciconia ciconia*) (Vergara et al., 2006) or black terns (*Chlidonias niger*) (Atamas and Tomchenko, 2020) and sea turtles (Kamel and Mrosovsky, 2006, Botha, 2010, Nordmoe et al., 2004, Kamel and Mrosovsky, 2004). Sea turtle nest site fidelity is determined by examining the distance placed between nests along the natal rookery, the beach where a reproductively mature female turtle hatched herself and returns to from foraging areas for nesting. Depending on the nature and stability of the environment in which the eggs are placed, the fidelity of a sea turtle within and across seasons may impact reproductive fitness. Repeatedly successful reproduction within populations is essential to maintain sea turtle abundance in different regional management units (Wallace et al., 2010).

Nest site fidelity operates at an individual rather than population level, with the relative proximity between nests of the same individual as the metric. Individuals with a high nest site fidelity have nests placed closer together and thus have a smaller distance between them whereas individuals with low nest site fidelity have nests placed further apart. Both high and low nest site fidelity can be advantageous, depending on the environment and conditions in which the individual is nesting. When nesting and mating are aggregated for a species and conditions are stable, high nest site fidelity is the favoured strategy because less time and energy is needed to place nests closer together and the chances of reproductive failure are reduced (Vergara et al., 2006). However, in unstable environments low nest site fidelity is favoured in spreading nests between areas that may differ in their level of stability (Eckert, 1987, Flint et al., 2014). Low nest site fidelity is also better for opportunistic individuals colonizing new nesting areas (Hays and Sutherland, 1991).

Nest site fidelity varies within sea turtle species among populations nesting at different rookeries. Leatherbacks (*Dermochelys coriacea*), the largest species, generally have low nest site fidelity (Lutz et al., 2002) whereas smaller species such as green turtles (Miller, 1997, Lutz et al., 2002) and flatbacks (Lutz et al., 2002, Parmenter, 1994, Limpus et al., 1984) have higher nest site fidelity. Olive ridleys (*Lepidochelys olivacea*) exhibit within-species variability in nest site fidelity; non-synchronous nesting populations exhibit low nest site fidelity (i.e., nests sites are geographically distant from each other) (Kalb, 1999) but females nesting in arribadas (i.e., *en masse* synchronous nesting) place nests closer together and thus have higher nest site fidelity (Plotkin et al., 1995, Kalb, 1999).

Within individuals, fidelity does not always imply every nesting attempt is a success. Emergence sites are all locations where a turtle hauls out. However, emergences from the surf zone may result in either completing a nesting event or committing a false crawl, whereby before completing nesting the attempt is terminated (Miller, 1997). Committing a false crawl and terminating a nesting attempt may occur any time between hauling out, crawling up the beach, digging a nest and depositing eggs in the dug-out chamber before covering the nest up. Multiple factors have been studied as possible causes of false crawls. Some factors may be purely environmental, such as sand being too hard and compacted (following heavy rain, spring tide or beach renourishment) to dig up leading to the female abandoning the nesting attempt (Ozan, 2011). However, most studies have focused on anthropogenic influences, such as the foot-traffic on the beach, the effects of obstructions including beach armouring (Hirsch et al., 2022) and revetments (Byrd, 2022) or light pollution (Rychener, 2022). Anthropogenic structures might even indirectly influence environmental conditions, as observed by Byrd (2022) for Jekyll Island revetments. In areas with revetments, loggerheads had significantly higher false crawls and environmental factors were significantly different in revetment areas. While the iSimangaliso rookery in South Africa is mostly unspoiled, lacking coastal development and heavy foot traffic, there are still false crawls committed by the nesting species.

Botha (2010) investigated nest site selection and nest site fidelity of loggerhead and leatherback turtles in the iSimangaliso Wetland Park, South Africa, over four consecutive seasons. The mean distance between successive loggerhead nests was about 3 km from each other over four consecutive seasons whereas leatherback nests were on average about 9 km from each other also over four consecutive seasons (Botha 2010). Loggerheads improved nest site fidelity, with experienced individuals gradually having smaller distances between their nests each season. Repeat-nesting leatherbacks, however, did not reduce the distance between nests with experience. Considering the available along-shore length of the rookery’s mostly continuous stretch of beach, Botha (2010) considered this high nest site fidelity for both species. Since Botha’s (2010) study was undertaken, a decade’s worth of additional data on loggerhead and leatherback nesting have been collected at a greater spatial scale, providing an opportunity to repeat her analyses, test whether the findings still hold, and look for new insights into individual loggerhead and leatherback nest site fidelity.

The study aim was to determine and compare individual-level nest site fidelity of two turtle species and whether it differs with nesting experience, and between nested and emergence events. The specific objectives were to 1) Calculate the average distance between an individual’s nests (per species); 2) to determine if nest site fidelity changes with experience; and 3) determine if site fidelity of actual nest sites is different from site fidelity using all emergences. It was hypothesized that loggerhead individuals are more specialized in their nest site selection while leatherback individuals have a more generalist approach, individuals integrate and utilize learned information about the nesting environment with repeated nesting attempts and that nesting attempts are made based on areas selected before hauling out. Thus, it was predicted that nest site fidelity would be lower for loggerheads, individual sea turtles' nesting site fidelity improves with nesting experience and that site fidelity would differ between emergence and nesting events.

Methods

Ethics statement

The data used in this chapter were collected under the authority of the Nelson Mandela University (NMU; previously Nelson Mandela Metropolitan University) Animal Ethics Committee, DEA/DFFE collection permits for the NMU sea turtle research program, and under the legal (monitoring) mandate of Ezemvelo KZN Wildlife and iSimangaliso Wetland Park. For full details see Chapter 2.

Study Site

The study site was the same as in Chapter 2.

Reconstructing individual turtle's nesting histories

The nesting history of 16 664 loggerheads and 2 691 leatherbacks was reconstructed (total of 54 455 nesting events) for each season from 1965 - 2020 using the low-resolution but long-term monitoring data collected by Ezemvelo KZN Wildlife. For each year it was recorded when and which individuals were seen, whether the sighted individual nested or false crawled (i.e., hauled up on the beach but did not nest), and where the emergence was located. Numbering of sequential nesting events and emergences were done according to the sequence in which individuals or tracks were sighted on a temporal scale. Emergences were referenced to the nearest along-shore beacon, with beacons placed every quarter mile or mile and numbered relative to their position north or south from the research station at Bhanga Nek (see Fig. 2.5, Chapter 2). The emergence locations relative to each beacon was also recorded, allowing for the construction of each emergence location relative to the coastal units (see chapter 1 methods for how beacons were used to determine coastal units). Thus, accuracy for distances recorded is to the nearest mile.

Determining nest site fidelity of loggerheads and leatherbacks in South Africa

Using the reconstructed nesting histories with false crawls excluded (i.e., only nesting events used), the distance between all pairwise combinations of nests laid by the same female was measured for 13 595 loggerheads and 2 547 leatherbacks (i.e., the distance between first sighted to the second sighted nest, first to the third nest, second to the third nest…etc). See Figure 3.1 for details. A large median distance between nests implies low nest site fidelity (i.e., nests are placed far apart) whereas a smaller nesting distance implies higher nest site fidelity. The median distances between all nests per individual for each species was averaged and compared. The number of turtles used in the analysis was lower than in the database as nesting events with missing data were excluded and only nesting events were used (i.e., individuals who were recorded as committing false crawls only and not nesting were excluded).

Data were non-normal for both species' average median distance between nests (Anderson-Darling test: loggerhead A = 813.29, leatherback A = 52.42, p << 0.001 in both cases) and lacked homogeneity of variances between species (Fligner-Killeen test: X2 = 901.33, p << 0.001). Additionally, sample size of loggerheads and leatherbacks differed. Thus, a non-parametric test was used to test whether average loggerhead and leatherback median nesting distance was the same.

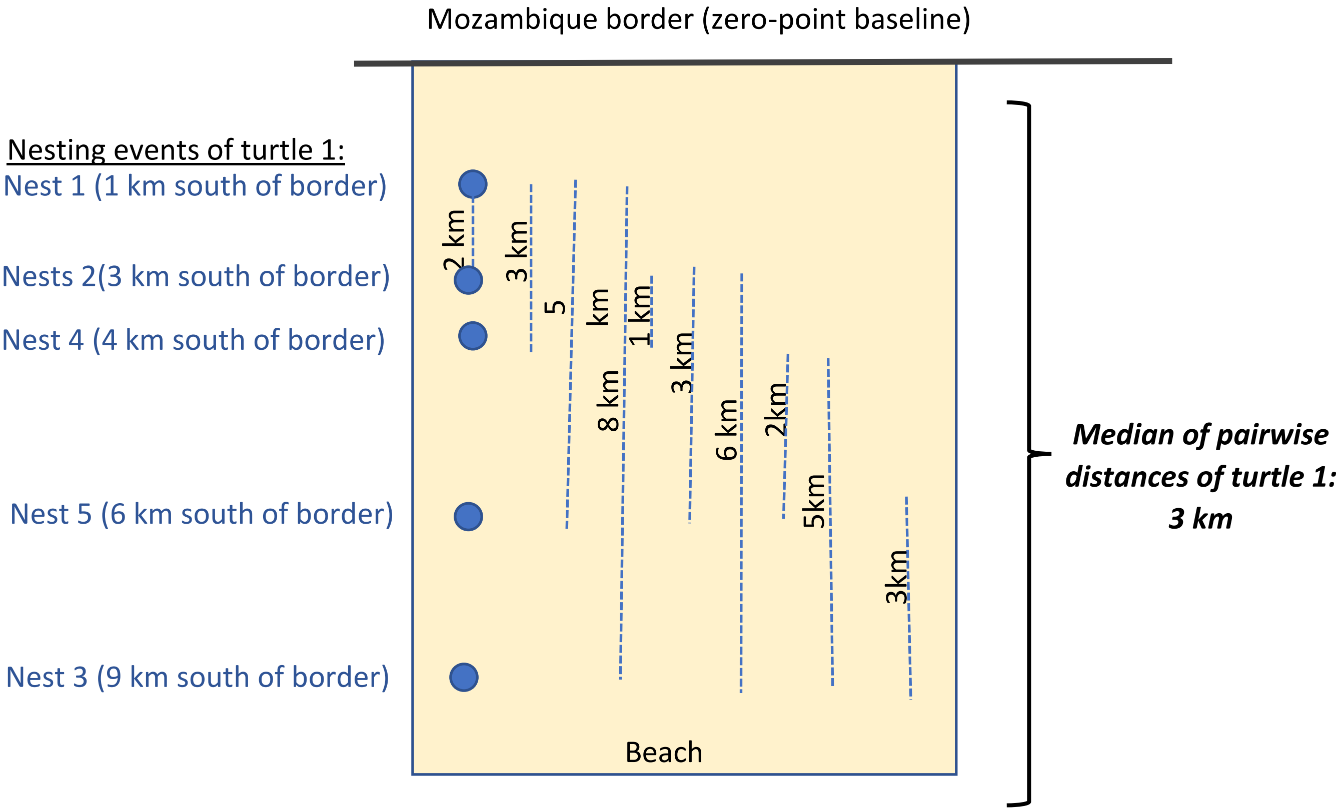

Figure 3.2 Illustration depicting the method for calculating pairwise distances between nests per individual turtle. The median of all the pairwise distances between nests was then taken.

Determining among-season nest site fidelity: changes in fidelity with nesting experience

The previously reconstructed history with false crawls excluded was used (loggerhead n = 13 595 individuals, leatherback n = 2 547 individuals) to investigate if nest site fidelity changes with nesting experience (among seasons). Median pairwise distances between nests per individual per season was calculated. With the average median pairwise nesting distance as a proxy, the nest site fidelity was compared between inexperienced (potentially first-time nesters, i.e., neophytes) and experienced (i.e., repeat) nesters between seasons up to seven seasons.

Data for nest site fidelity data across seasons were non-normally distributed for both loggerheads and leatherbacks (Anderson-Darling test: loggerhead A = 878.26, leatherback A = 62.61; $p << 0.001$ in both cases). There was also a lack of homogeneity of variance across seasons for loggerheads (Fligner-Killeen test: $X^2 = 248.59$, $p << 0.001$) but not for leatherbacks ($X^2 = 14.07$, $p = 0.03$). Thus, a non-parametric test was used to determine whether the average median distance between nests for neophytes and more experienced nesters is the same

Comparing emergence site fidelity with sea turtle nest site fidelity

The method used was identical to that described above comparing change in nest site fidelity with nesting experience. However, all emergences (false crawls and nesting events) median pairwise emergence distances per individual, per season, were averaged and compared with the average median pairwise nesting distances of nesting events only. Site fidelity comparing emergence and nesting events with sufficient replication only extended up to five seasons.

Emergence site fidelity data were not normally distributed for both loggerheads (Anderson-Darling test: loggerhead A = 1421.60) and leatherbacks (Anderson-Darling test: leatherback A = 101.05, both $p << 0.001$). There was also a lack of homogeneity across seasons for both species (Fligner-Killeen test: loggerhead $X^2 = 429.28$, leatherbacks $X^2 = 87.308$, both species $p << 0.001$). Thus, a non-parametric test was used to determine whether neophyte and more experienced nesters median pairwise emergence distance averages are the same.

Site fidelity data across seasons for nesting events and across seasons for emergences were not normal for both loggerheads and leatherbacks (Anderson-Darling test: loggerhead nesting events A = 872.03, $p << 0.001$ and emergences A = 1229, $p << 0.001$; leatherbacks nesting events A = 61.8, $p << 0.001$ and emergences A = 55.75, $p << 0.001$). There was homogeneity of variance between nesting events and emergences median distance for both loggerheads and leatherbacks (Fligner test: loggerheads $X^2 = 0.07$, $p = 0.79$; leatherbacks $X^2 = 0.72$, $p = 0.39$). Thus, a non-parametric test was used to test whether median distances of emergence sites and median distance of nesting sites were the same across seasons.

Results

Determining nest site fidelity of loggerheads and leatherbacks in South Africa

Using the nesting locations of individual turtles from each species in 1965-2020, average nest site fidelity across individuals of each species was calculated (Fig. 3.2) with pairwise distance between nests as a proxy for nest site fidelity. Loggerheads had an average median distance between nests of 5.3 km (SD = 8.40, n = 13 595) and leatherbacks an average median of 15.4 km (SD = 14.75, n = 2 547), thus loggerhead individuals place their nests closer together than leatherback individuals do. A non-parametric Kruskall-Wallis test was thus done to test the null hypothesis that the two species have the same means of nest site fidelity ($X^2 = 968.81$ and $p << 0.001$). Nest site fidelity was significantly different per species, as $p < 0.05$ and thus the null hypothesis was rejected.

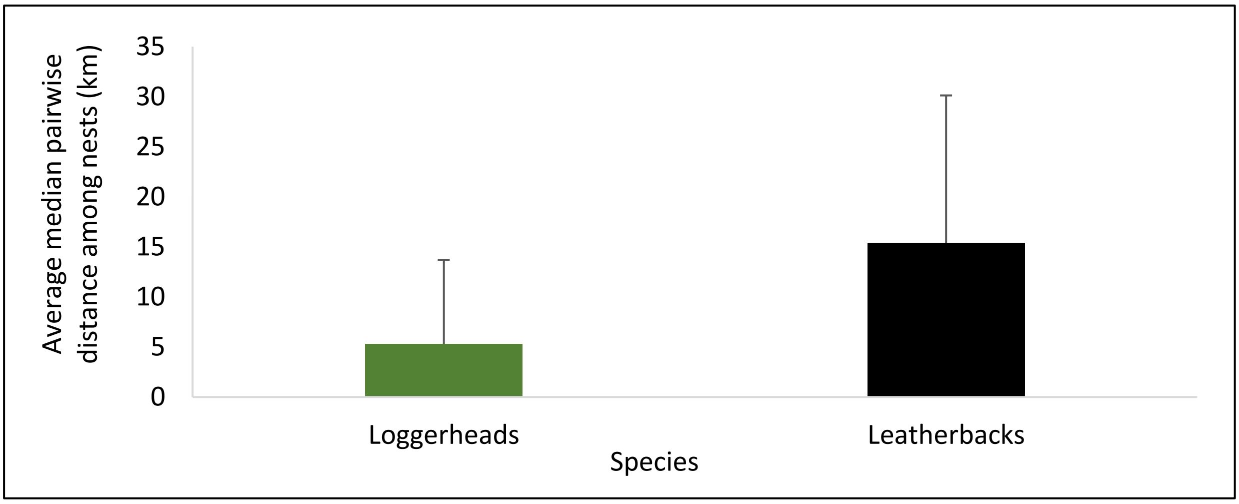

Figure 3.3: Comparing nest site fidelity for loggerheads (n = 3 595) and leatherbacks (n = 2 547) nesting during 1965 – 2020, measured as the average median (SD) pairwise distance between nests per individual, across seasons.

Determining among-season nest site fidelity: changes in fidelity with nesting experience

For both species, there are more neophytes than the number of more experienced individuals seen nesting repeatedly in multiple seasons (i.e., nesting for two or more seasons) (Fig. 3.3). The average median pairwise distance between nesting events for loggerhead neophytes (n = 4 932) and most experienced nesters. i.e., nested for seven seasons (n = 11), was 4.89 km and 1.45 km respectively (Fig. 3.3a), and for leatherbacks it was 14.45 km (neophyte n = 998) and 9.60 km (most experienced total n = 3) respectively (Fig. 3.3b). Thus, neophyte nesters had a lower nest site fidelity than the most experienced nesters for both species, but loggerhead neophyte and experienced nesters had nests closer together and were more abundant than leatherbacks.

A non-parametric Kruskal-Wallis test was done for each of the two species testing the null-hypothesis that the average median distance across nesters with different seasons of experience is the same. For loggerheads, the Kruskal-Wallis test results were $X^2 = 112.03$ and $p << 0.001$ and for leatherbacks the results were $X^2 = 7.81$ and $p = 0.25$. $P < 0.05$ for loggerheads but not for leatherbacks, null hypothesis was thus rejected only for loggerheads but accepted for leatherbacks. Loggerheads therefore had significantly different nest site fidelity among individuals who nested for different numbers of seasons (i.e., different years of experience gained) while there was no significant difference for leatherbacks.

A post-hoc Dunn test (using the Holm correction to adjust p; Table 3.1) showed that overall, loggerhead neophytes have a significantly different fidelity than more experienced loggerhead nesters that nest in later seasons (all combinations of first season nesters to any later seasons except the last season, adjusted $p < 0.05$; Z test-statistics for each season combination in Table 3.1). Potentially, the lack of significant difference between neophytes and the most experienced nesters (i.e., nested for seven seasons) may be because of a small sample size for the most experienced individuals (n = 11) based on findings from Figure 3.3a. It is likely that with additional individuals for the last season, there would be a significant difference. Results for post hoc test comparing experienced individuals (i.e., nested for 2 – 4 seasons) with even more experienced individuals (i.e., nested for 5 – 6 seasons) with most experienced individuals were all insignificant (i.e., $p > 0.05$; Table 3.1).

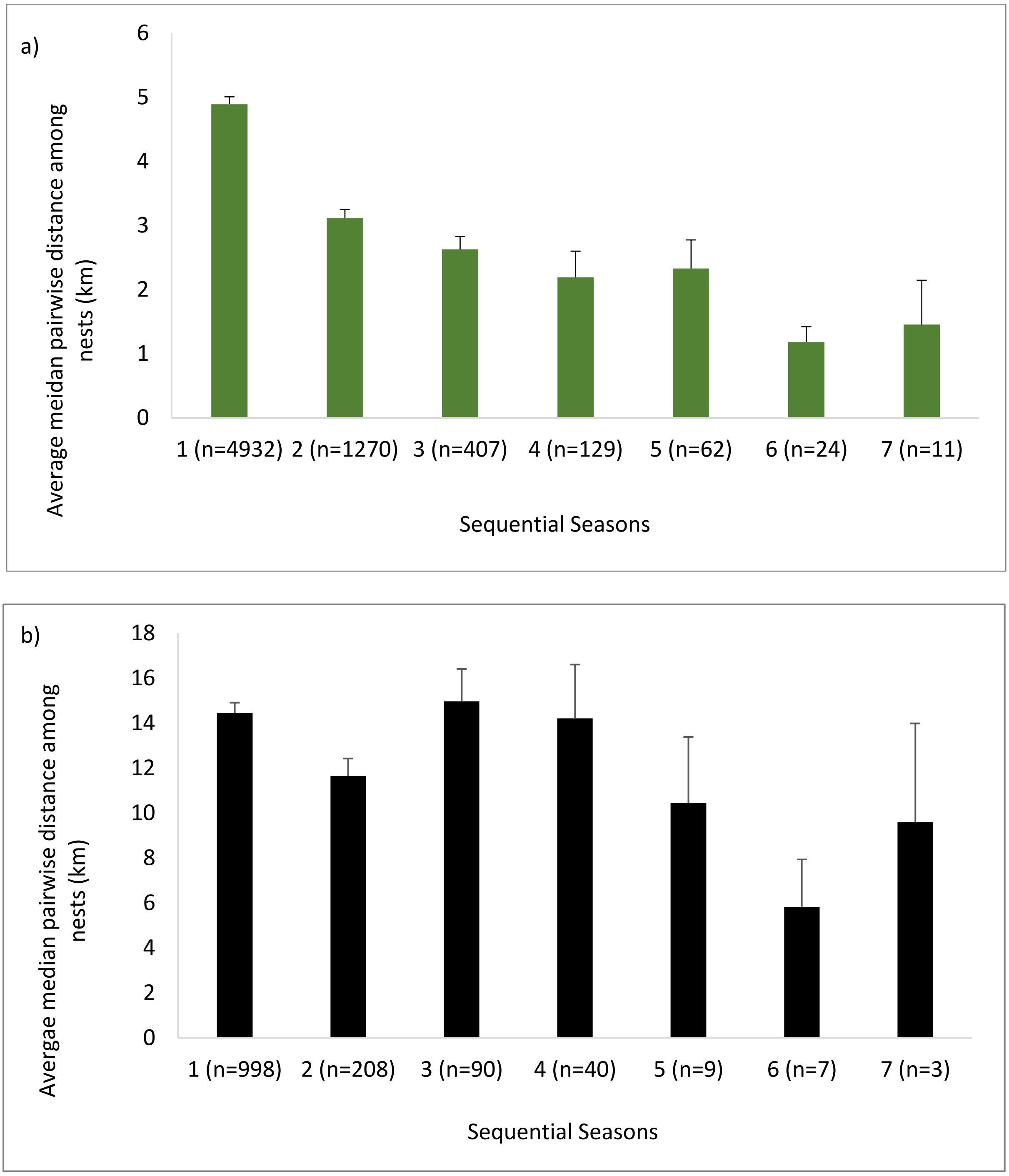

Figure 3.3: Differences in median (SE)distance between nests of neophytes (only one season) versus more experienced nesters (up to seven seasons) for a) loggerheads and b) leatherbacks in subsequent seasons. Value in brackets indicate sample for each season.

*Table 1.1: Results of post hoc Dunn test (with Holm correction for adjusted p) for loggerheads following significant Kruskall-Wallis test. Values with ** and bold indicate significant values at p < 0.05. Z = Dunn test statistic.*

Season Combinations	Z	Unadjusted p values	Adjusted p values
Season 1-Season 2	6.092	****<< 0.001**	****<< 0.001**
Season 1-Season 3	6.191	****<< 0.001**	****<< 0.001**
Season 1-Season 4	5.570	****<< 0.001**	****<< 0.001**
Season 1-Season 5	3.062	****0.002**	****0.03513315**
Season 1-Season 6	3.376	****<< 0.001**	****0.01323695**
Season 1-Season 7	2.381	****0.017**	0.241
Season 2-Season 3	2.240	****0.025**	0.326
Season 2-Season 4	3.301	****<< 0.001**	****0.01637836**
Season 2-Season 5	1.535	0.125	1
Season 2-Season 6	2.422	****0.015**	0.231
Season 2-Season 7	1.741	0.082	0.817
Season 3-Season 4	1.756	0.079	0.869
Season 3-Season 5	0.529	0.597	1
Season 3-Season 6	1.769	0.077	0.923
Season 3-Season 7	1.308	0.191	1
Season 4-Season 5	-0.682	0.495	1
Season 4-Season 6	0.873	0.383	1
Season 4-Season 7	0.707	0.480	1
Season 5-Season 6	1.246	0.213	1
Season 5-Season 7	1.001	0.317	1
Season 6-Season 7	0.077	0.939	0.939

Comparing site fidelity of nest events and all emergences

Average median pairwise distance of all emergences for loggerheads for neophyte ($n = 4464$), and most experienced nesters (nested for five seasons; $n = 56$), was 4.72 km and 3.31 km (Fig. 3.4a) respectively while leatherbacks was 14.37 km (neophyte $n = 498$) and 8.47 km (most experienced $n = 6$) respectively (Fig. 3.4b). Thus, neophyte nesters had a higher median pairwise distance (thus lower nest site fidelity) than the most experienced nesters for both species, but loggerhead neophyte and most experienced nesters had a smaller distance between emergences (i.e., higher emergence-site fidelity) than leatherbacks.

A non-parametric Kruskal-Wallis test was done for each of the two species, testing the null-hypothesis that the median pairwise emergence distance averages are the same across individuals with varying experience (i.e., varying number of seasons seen emerging). The Kruskal-Wallis test results (loggerhead $X^2 = 221.65$ and leatherbacks $X^2 = 98.33$, $p << 0.001$ for both species) indicated significant differences between neophytes and more experienced individuals. For both species $p < 0.05$ and null hypothesis was rejected, thus loggerheads and leatherbacks had significant differences in the fidelity of across individuals with varying number of seasons they were seen emerging.

A non-parametric Friedman rank sum test was used to test the null hypothesis that the median treatment effects (i.e., including false crawls for emergences) of the population are the same (i.e., median distances between emergences and nesting events don't differ), with median distance averages per season acting as replicate blocks to the treatment groups. Median treatment effects were not significantly different between nesting events and emergences for both loggerheads ($X^2 = 1.80$, $p = 0.18$) and leatherbacks ($X^2 = 0.2$, $p = 0.65$). Thus, the null hypothesis was accepted with $p > 0.05$ for both species and there was no significant difference in the median distance between emergence sites and nesting sites for both loggerheads and leatherbacks.

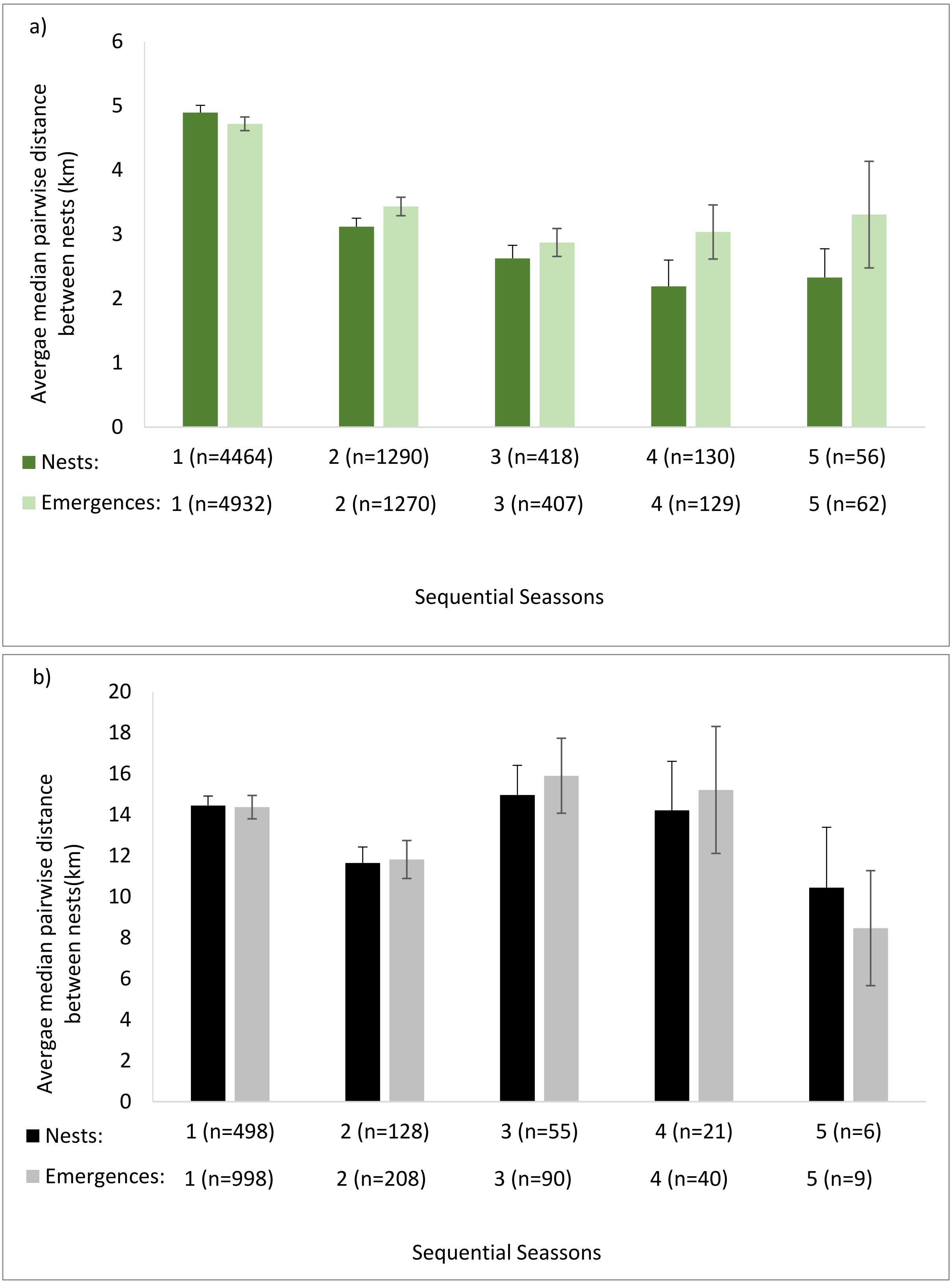

Figure 3.4: Comparing a) loggerhead and b) leatherback average median (SE) pairwise distance between nesting events and all emergences with false crawls included across seasons. Values in brackets indicate sample size for each season.

Discussion

This study aimed to compare individual-level nest site fidelity behaviour and patterns of two turtle species and whether it varies with nesting experience and between actual nest events and all emergences. The hypotheses that loggerhead individuals are more specialized in their nest site selection while leatherback individuals have a more generalist approach, individuals integrate and utilize learned information about the nesting environment with repeated nesting attempts and that nesting attempts are made based on areas selected before hauling out were accepted. Nest site fidelity differed between loggerheads and leatherbacks and between individuals with varying nesting experience for loggerheads but not for leatherbacks. The median distance between all emergence events and only nesting events did not differ for both species and thus fine-scale nest site selection for consecutive clutch placement seems to occur prior to the beach crawl for both species.

Nest site fidelity of species

Loggerheads have higher nest site fidelity than leatherbacks, supported by Botha's (2010) findings from the same nesting population. Loggerheads are generally inferred as being spatial specialists and having high nest site fidelity (<10 km); e.g., on the East Florida coast (Ehrhart, 1980) and in Australia (Limpus, 1985). However, there are also loggerhead populations with slightly lower nest site fidelity, such as the 35-km long rookery on Maio Island, where 77% of loggerheads laid repeated clutches within 15 km of prior nesting sites both within and between nesting seasons (Patino-Martinez et al., 2022). Other loggerhead rookeries have even lower nest site fidelity, such as the population in the Gulf of Mexico where the mean distance between nests was found to be 27.5 km, with 46% of sampled turtles nesting >5 km from their original nesting site (Hart et al., 2013). Similar results of low nest site fidelity have also been seen on Wassaw Island (11 km in length), where inter-island shifting resulted in low nest site fidelity. Approximately 60% of the sea turtles identified for tag return were seen once on Wassaw and were only seen again on neighbouring islands (Williams and Frick, 2008).

Like loggerheads, there is also high intraspecific variation within and across leatherback rookeries. Leatherbacks generally have poor nest site fidelity; on Juno Beach, Florida, leatherback nests were placed 78.03 km apart with the maximum distance between nests of one individual's nests being 463.4 km (Stewart et al., 2014). Contrary to this, however, leatherbacks nesting in Costa Rica repeatedly show fidelity to the Playa Grande beach that is 3.6 km in length rather than using the other available beaches suitable for nesting in the Parque Nacional Marino Las Baulas (Santidrián Tomillo et al., 2007).

Comparing nest site fidelity of the same species between rookeries is difficult as rookery length and rookery characteristics differ across different nesting beaches. Although the average loggerhead nest site fidelity (5.3 km) in this study was higher than the average leatherback nest site fidelity (15.4 km), both species have relatively high nest site fidelity for the South African rookery considering that the rookery just in South African iSimangaliso Wetland Park is ~200 km of beach with mostly continuous conditions (some bays are separated by rocky headlands) suitable for nesting (Hughes, 1974, Nel et al., 2013).

Among-season nest site fidelity: changes in fidelity with nesting experience

Differences in nest site fidelity with nesting experience was also found for loggerheads nesting in Zakynthos, Greece (Katselidis et al., 2005). On the Zakynthos rookery, which was divided into six different beach sections (each about 6 km in length), neophytes used more sections of the nesting beaches (average of three) than the experienced nesting females who used only two of the six sections on average (Katselidis et al., 2005). This is a large difference considering the average length of each beach section. Higher nest site fidelity of more experienced loggerhead nesters and lower nest site fidelity of neophytes was also observed in Florida (Tucker, 2010) and Georgia (Richardson, 1982).

The change in loggerhead individual behaviour supports a hypothesis of "learned" behaviour, resulting in higher nest site fidelity with more experience. This "learning" might be individual (i.e., an individual gets better at perceiving environmental cues over time in terms of quality and availability) (Martins et al., 2022) or socially facilitated (i.e., nesters become better at following social cues from other turtles on where to nest) (Carr and Hirth, 1961). Whatever the mechanism, this "learning" does indicate that with nesting experience, loggerhead individuals do reduce the distance between their nests and become more accurate in their nest site placement relative to previously placed sites.

For leatherbacks in the South African rookery, the lack of change in nest site fidelity with experience may be because of intrapopulation variation in environmental feature preferences resulting in varying nest site selection along-shore (Kamel and Mrosovsky, 2004, Wallace and Saba, 2009, Palomino-González et al., 2020). From satellite tagging it seems like some turtles remain close to the coast during the inter-nesting period ("coastal clingers"), while others occupy pelagic waters ("ocean rovers") (Harris et al., 2015). Coastal clingers had a higher nest site fidelity and tended to nest in the monitoring area of the rookery, while ocean rovers had lower fidelity and tended to nest outside of the monitoring area (Harris et al., 2015). Coastal factors exposed to coastal clingers and pelagic factors experienced by ocean rovers would vary in availability and quality between the two groups and thus could impact the cues they have available or prefer when selecting nesting sites. Potentially, the coastal clingers could have greater nest site selection capabilities owing to their proximity to the coast while ocean rovers are selecting nesting areas on wherever physical characteristics of deeper oceans (e.g., currents) takes them. However, in this study these two groups were not differentiated between when investigating the change in nest site fidelity over time.

Comparing site fidelity of nest events and all emergences: implications of temporal and spatial specificity

Two scenarios can apply when comparing the average distance among all emergence sites and the average distance among nesting sites: In the first scenario, the distance between emergence and nesting sites doesn't differ which implies that females haul out on preferred nesting locations even when conditions on the beach are non-conducive to nesting. The alternate scenario is that distance between emergence sites does differ from that of nesting sites which implies that where they haul out is not always the preferred nesting location. Thus, the selection of nesting sites may be more decisive before hauling out for the first scenario, or more decisive after hauling out for the second scenario. The results from this study lends support to the first scenario noting the caveat of outliers with using median pairwise distances instead of means.

In this study, the fidelity of emergence sites across consecutive seasons was compared to the fidelity of nest sites across the same number of seasons for loggerheads and leatherbacks (Fig. 3.4). The site fidelity for all emergence sites did not differ significantly from that of nesting events for loggerheads or leatherbacks (i.e., the first scenario). A lack of difference in distance between emergence sites and nesting sites may imply that the available information used for nest site selection (either from social cues or environmental conditions) which impacts fidelity has already been integrated. Thus, the areas are selected for nesting before hauling out.

Interestingly, nesting rates reported by Nel et al. (2013) for the same nesting populations, indicate loggerheads nest ~55% of the time they haul out while leatherbacks nest ~91% of the time. Comparatively, loggerheads are committing false crawls at a much higher rate, but still emerging where they wish to nest. Why would loggerheads incur unnecessary energetic costs by turning around only to come up at the same place but at a different time relative to leatherbacks? A possible explanation for this lies in the comparable size and inter-nesting intervals of each population. The scaling of energy used for migratory swimming with body size has been inferred by Wyneken (2017). Thus for a different type of locomotion, beach haul-outs, loggerheads smaller size (Miller, 1997) may incur less energetic cost per haul-out relative to leatherbacks. Loggerheads are also more flexible with their 13—15 days inter-nesting intervals than leatherbacks with a stricter ~10 day interval (Nel et al., 2013). Furthermore, loggerheads are more specialized in their nest site selection with narrower nesting niches while leatherbacks have a generalist approach with wider nesting niches (Chapter 2). Thus, despite both species emerging where they want to nest, leatherbacks may not be committing as many false crawls because they are more energetically constrained by their size and lack a temporal buffer in their inter-nesting intervals. They have to undergo the nesting process to completion almost every single time they emerge from the surf zone.

Potentially, features visible, audible or smelled from sea seem more important for nest site fidelity than on-shore features (like grain size). The potential importance of in-water features is highlighted as well in Chapter 2, whereby there was a strong nest site selection for in-water features such as reefs, especially for loggerheads. In-water features may provide visual, e.g., reefs, rocks, and sand banks, (Schofield et al., 2017) auditory, i.e., wave action and reef organisms, (Lobel, 2013) and olfactory cues, i.e., groundwater seepage from freshwater or estuarine sources (Hughes, 1974). A lack of fine-scale selection for beach features (geomorphic and vegetation) was observed by Kelly et al. (2017) for loggerheads in Eastern Australia. The importance of visual/physical in-water features for loggerheads is supported by tracking information at Zakynthos Island, with females targeting specific areas such as cleaner stations during nesting seasons (Schofield et al., 2017). Nordmoe et al. (2004) did observe some on-shore environmental feature selection for leatherbacks at Playa Grande where only the across-shore features (i.e., fine-scale beach environmental beach characteristics) was significantly selected for while along-shore selection (i.e., broad-scale) in beach zones did not indicate any nest site fidelity to specific locations. However, the effect of tidal extremes (i.e., at their peaks; high and low) as an in-water feature has been reported to affect the nesting behaviour of leatherbacks in Costa Rica (Palomino-González et al., 2020).

Implications for sea turtle fitness

An individual’s fitness is measured by the number of offspring produced successfully (Arlt and Pärt, 2007, Kamel and Mrosovsky, 2005), and factors that enhances this output for the individual and the population thus confer ecological and evolutionary benefits. The benefits and disadvantages obtained from nest site fidelity differ between individuals and among populations with high or low nest site fidelity; neophytes had lower reproductive output (clutch frequencies) than experienced nesters in studies on green turtles at Tortuguero and Ascension Island (Bjorndal, 1980, Mortimer and Carr, 1987). Similar findings have occurred for leatherbacks; the comparative reproductive output (clutch size and frequency) being higher for experienced leatherback nesters than neophytes in Puerto Rico (Tucker and Frazer, 1991). Contrary to these studies is the findings by Carroll et al. (2022) that neophyte loggerheads in Georgia had higher hatching success than experienced nesters despite the nests of neophytes and experienced nesters having the same measured environmental conditions. Thus, the higher nest site fidelity of experienced loggerheads may increase reproductive output (Pfaller et al., 2009), but this may not always be the case. However, lower nest site fidelity (apparent for neophyte loggerheads and leatherbacks in this study), may also be beneficial.

In unstable, dynamic environments, some areas will have a higher risk of nest perturbation or adult mortality than others (Eckert, 1987, Byer and Reid, 2022). However, chances of placing all nests in the same location with a high risk of reproductive failure is reduced through a “bet-hedging” strategy (Arlt and Pärt, 2007). By spreading nests along-shore, i.e., exhibiting lower site fidelity, the risk of nest perturbation is reduced for each nest (Patino-Martinez et al., 2022). Thus, turtles may incur reproductive benefits if they don’t place all their eggs in one basket, or rather, one nesting area, in unstable nesting habitat. If this is extensive in a population (especially small populations) it can impact a population’s reproductive fitness (Troëng and Chaloupka, 2007). However, the ‘bet-hedging’ strategy implies that turtles are aware of past reproductive failures or successes, which is difficult to support since turtles do not interact with nests or hatchlings once a nest has been placed, the eggs covered, and females have returned to sea.

Results of the study have implications for the management and conservation of sea turtles, especially within the broad South-west Indian Ocean (SWIO) region. The possible pre-haul-out selection of in-water features by loggerheads emphasizes the importance of protecting sea turtle nesting areas beyond the visible on-shore region where nests are placed. Should off-shore, in-water features be deterministic in the nest site selection process then off-shore areas need to be included in spatial planning to conserve the contiguous onshore-offshore habitat integrity. In South Africa, as of 2019, the marine protected area (MPA) was expanded including expansions of the previous Maputoland and St. Lucia MPAs such that in-water features are currently included in the protected iSimangaliso Wetland Park (Kirkman et al., 2021) with a 34 NM offshore extent (Republic of South Africa, 2019). While the effect of fidelity on reproductive success and therefore reproductive fitness has been discussed, this study did not explicitly analyse reproductive success with nest site fidelity. Thus, the results of this investigation suggest a future study on the possible link between nest site fidelity and reproductive success.

Conclusions

To conclude, loggerheads have relatively high nest site fidelity and improve their nest site fidelity with experience. Leatherbacks place nests further apart, i.e., have relatively low nest site fidelity, and do not improve nest site fidelity with experience. Both species are however hauling out in areas preferred for nesting, suggesting that nest site selection happens in the intertidal zone before emerging. While both high and low nest site fidelity has advantages within different reproductive strategies, relative differences in nest site fidelity and nest site selection between loggerheads and leatherbacks may be affecting reproductive fitness. However, the correlation between fidelity and fitness was not done for this study and future studies need to focus on analysing the effect of nest site fidelity on reproductive success.

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CHAPTER 4: SYNTHESIS AND CONCLUSION

Sea turtles, like many other species (Steffan-Dewenter and Schiele, 2004, Blackmer et al., 2004, Dittman et al., 2010), perform long migrations from foraging areas to courtship and breeding areas (Shimada et al., 2021, Shimada et al., 2020) during warm, summer periods. After mating female sea turtles return to natal rookeries to nest, depositing clutches of eggs along sandy beaches in an obligatory terrestrial phase of the reproductive cycle (Miller, 1997). Return to the rookery is done on a broad scale known as homing (Lohmann et al., 2013, Lohmann et al., 1999), whereby the rookery the female returns to is the same rookery from which she was hatched. Upon arriving at the rookery, finer-scale selection on where to nest occurs through a process of nest site selection (Hays et al., 1995) and the repeated laying of clutches in close proximity to each other implies a nest site fidelity within the rookery (Carr and Carr, 1972, Katselidis et al., 2005, Botha, 2010). Nest site selection and nest site fidelity are vital for reproductive success as it constitutes the only parental investment within a sea turtle’s reproductive strategy (Hughes and Brooks, 2006). Should nest site selection be inappropriate and repeated across individuals for multiple seasons, in turn resulting in failed egg development, hatching and/or emergence then this may impact population abundance (Wallace and Saba, 2009, Bowen et al., 1993, Santidrián Tomillo et al., 2007, Thorson et al., 2012).

With previous findings in mind, this study aimed to investigate the nest site selection of loggerheads and leatherbacks at a population and individual level. Objectives for investigating nest site selection behaviour (Chapter 2) included: 1) describing and comparing the differences in nesting distribution of each population; 2) investigating spatio-temporal consistency of nesting of each population using 54 years of monitoring; and 3) determining the coastal features along-shore and across-shore associated with the nesting preferences of each population using a General Niche-Environment System Factor Analysis (GNESFA) and spatial data of coastal features in ArcMap 10.7. Objectives for nest site fidelity (Chapter 3) included 1) comparing the nest site fidelity of individuals in each population; 2) comparing the nest site fidelity of neophyte versus more experienced nesters; and 3) comparing the nest site fidelity of emergence sites and nesting sites within and between species.

Nest site selection of loggerheads and leatherback populations in South Africa

Chapter 2 demonstrated that nest site selection (i.e., choosing a place to haul out along the rookery) differed between the two nesting populations. Despite the limitations of uneven monitoring effort across spatial and temporal scales, nesting distributions for both species were temporally and spatially consistent, with loggerheads having a higher occurrence of emergences annually than leatherbacks throughout the study period as a result of their higher abundance. The loggerhead population had a northern nesting distribution, with a nesting hotspot around the Kosi lakes and mouth while leatherbacks had various “hotspots” (i.e., areas with greater emergences relative to other equally available areas along the rookery) along the shore, with some peaks in the middle of the rookery but with a mostly dispersed distribution along-shore.

Nest site preferences differed between the species in terms of what was selected for and avoided and the strength of their selection for or against certain coastal features. Loggerheads preferred nesting areas near the Kosi lakes, with dissipative-intermediate sandy shores as well as southerly located coral communities (i.e., Sodwana coral reefs) and avoided rocky shores and reflective sandy shores. Leatherbacks preferred sand-dominated mixed shores, vegetated nesting areas and avoided areas directly backed by either Lake Sibaya or Kosi Lakes. Overall, loggerhead preferences were stronger than those of leatherbacks and shore types, lakes and coral reefs were more prominent within nest site preferences than other coastal features.

While preference for certain coastal features was evident, mechanisms behind why these features were selected were not investigated in this study and thus can only be inferred. Selection for water bodies may be due to the attractional effect of the compounds they release through river mouths or groundwater (Hughes, 1974, Koch et al., 1969). Dissipative shores or intermediate shores may be less energetically costly to haul out on (as turtles do not feed during the reproductive season and thus have a limited amount of energy available to nest) owing to the lower-energy surf zone compared to reflective beaches and rocky shores (Maxwell et al., 2014). Lastly, coral reefs may provide acoustic and visual cues (Lobel, 2013) and areas for shelter, resting and cleaning (Forbes, 1996, Grossman et al., 2006, Schofield et al., 2017) between nesting attempts. Harris et al. (2015) also observed through satellite tagging that South African loggerheads tend to remain near inner shelf reef structures.

Results were representative of general knowledge of the study site and nesting populations; however, some improvements could be made for future studies. To account better for spatially and temporally inconsistent monitoring, results for spatio-temporal consistency could have focused on only the index area in the last 25 years rather than the large spatial and temporal extent used for the investigation. In terms of coastal variables, an analysis incorporating finer-scale across-shore variables (e.g., sand grain size, moisture, slope, dune vegetation density) alongside along-shore features would be a useful addition to the niche modelling. The GNESFA was illustrative for results and integrated multiple environmental variables but was complicated in its interpretation. Thus, the use of more simplistic niche modelling relative to the questions being asked could also be incorporated when looking ahead for follow-up studies.

Nest site fidelity of loggerheads and leatherback individuals in South Africa

Chapter 3 results illustrated that individual nesting behaviour and effect of nesting experience differed between loggerheads and leatherbacks but was similar pre-haul out. Loggerhead individuals were on average placing their nests 5.3 km apart while individual leatherback nests were on average separated by 15.4 km. Thus, loggerheads had greater nest site fidelity than leatherbacks. However, considering the relatively large size (~300 km) of the continuous rookery across South Africa and Mozambique, both loggerheads and leatherbacks show high nest site fidelity compared to the total area available to nest (Hughes, 1974, Nel et al., 2013).

There was a significant difference in nest site fidelity with nesting experience for loggerheads, with experienced nesters placing their nests closer together than neophytes. This indicates a “learning” in loggerheads that resulted in their nest site fidelity improving over time. The concept of “learning” behaviour resulting in differences in nest site fidelity between neophytes and more experienced nesters has also been observed for loggerheads in other rookeries at Zakynthos island (Katselidis et al., 2005), Florida (Tucker, 2010) and Georgia (Bell and Richardson, 1978). Results from this study showing that more experienced individuals with higher fidelity may have better reproductive output was also found for green turtles at Ascension Island (Mortimer and Carr, 1987) and Tortuguero (Bjorndal, 1980) and for leatherbacks in Puerto Rico (Tucker and Frazer, 1991). However, contradictory results were found for loggerheads in Georgia, whereby neophytes had higher hatching success than experienced nesters despite both having equal environmental nesting conditions (Carroll et al., 2022). There was no difference in nest site fidelity between neophytes and more experienced nesters for leatherbacks.

The nest site fidelity of emergence locations to nesting locations did not differ for loggerheads or leatherbacks. Both species are emerging where they prefer to nest, and this potentially indicates a fine-scale level of decision-making prior to the haul out of the individuals. Possibly, the results indicated that if decision-making is more implicit before hauling out then in-water features may be more important than previously considered during the selection process. In-water features may be essential as they provide auditory (Lobel, 2013), visual (Schofield et al., 2017) and olfactory cues (Hughes, 1974) during the nest site selection process. This can be inferred from the studies of sea turtle nesting behaviour and in-water coastal features at other rookeries in Eastern Australia (Kelly et al., 2017) Playa Grande island (Nordmoe et al., 2004) and other islands in Costa Rica (Palomino-González et al., 2020). However, more studies need to investigate this by incorporating intertidal features into their analyses.

Results were limited by the accurate identification of tagged individuals over time. Thus, the findings were limited by the assumption that all individuals were identified correctly within and between seasons. Individuals are double tagged, however in the event that both tags are lost a re-nester may have instead been identified as a neophyte. Suggestions for future studies within not only the South African rookery but also other rookeries would be the implementation of GPS monitoring for nesting sites and the Fastloc satellite tagging of individuals early in the season. By tagging turtles early, their nesting behaviour and inter-nesting behaviour would be useful to review the nest site selection process and its implications for fidelity prior to the haul-out. An interesting expansion on the results obtained in this study would be the analysis of nest site fidelity with females' size, health, and reproductive output as a proxy for fitness. These suggestions highlight the importance of maintaining long-term monitoring for evaluating population trends and the effectiveness of conservation measures.

Reproductive fitness and evolutionary biology: implications of nest site selection and fidelity?

Since the implementation of the sea turtle monitoring program in 1963, there has been a disparate population response to equal conservation efforts for loggerheads and leatherbacks in South Africa. The number of emergences, used as a proxy for the number of nesting females over time has increased exponentially over time for loggerheads, while leatherbacks increased initially but have since plateaued (Nel, 2006, Nel, 2009, Nel et al., 2013). Differences in nesting success and hatching success are evident within the iSimangaliso Wetland Park populations, with loggerheads showing greater hatching success (73% for loggerheads versus 70% for leatherbacks) and overall nesting success (89% for loggerheads versus 78% for leatherbacks) (De Wet, 2012). However, these differences occur despite leatherbacks having less false crawls owing to their larger size and lack of temporal buffering in their inter-nesting intervals (nesting ~91% of the time they haul out compared to ~55% for loggerheads) and greater reproductive output (Nel et al., 2013) in terms of clutch frequency (7-8 clutches for leatherbacks and 3-4 clutches for loggerheads) since the number of eggs per species is more or less the same (mean of 104 and 105 for loggerheads and leatherbacks respectively). So, it appears that reproductive success is not responsible for the lower recovery of the leatherback population and causes may thus be at a different life stage in the water (foraging, migration, juvenile age class etc.; Miller 1997).

In species other than sea turtles, including those with parental investment and care outside of site selection, choices on nest site selection and nest site fidelity impact reproductive success and consequently also impacts their reproductive fitness (Arlt and Pärt, 2007, Kamel and Mrosovsky, 2005). In bird species, such as Black Terns (Atamas and Tomchenko, 2020) Buffleheads (Gauthier, 1990), Black Oystercatchers (Hazlitt and Butler, 2001), and White Storks (Vergara et al., 2006), individuals that return to the same sites they used previously incurred greater reproductive success in terms of hatching and survival past fledgling phase than individuals who used different sites. This may be due to familiarity with the area for resource acquisition (Vergara et al., 2006), finding mates (Schieck and Hannon, 1989) or avoiding predators (Schmidt, 2001) which reduces energetic costs during reproductive periods. Individuals choosing different nesting sites or who had lower nest site fidelity experienced lower reproductive success.

Studies have linked nest site selection and nest site fidelity with reproductive success in sea turtle species; consequences of nest site selection for reproductive fitness have been found with loggerheads and hawksbill sea turtles in Brazil, whereby hatching success was correlated differently with various coastal features chosen within the nest site selection (Serafini et al., 2009). Differences in nest site selection of individuals of the same species have also impacted the reproductive success for green turtles in Turkey (Turkozan et al., 2011), whereby individuals nesting in vegetated areas had higher hatching success. Nesting experience and its impact on nest site fidelity impacted the clutch frequencies of loggerheads and green turtles at Ascension Island (Mortimer and Carr, 1987) and leatherbacks in Puerto Rico (Tucker and Frazer, 1991).

However, reproductive fitness was not directly analysed in this study with nest site fidelity and nest site selection and only along-shore beach features influencing nest site selection were analysed. Leatherbacks may have lower hatching success than loggerheads as a result of across-shore features, such as distance from the high water mark being insufficient to prevent over-washing during storm events (Maden et al., 2022) or high tides (Carpio et al., 2022) in nests placed very low on the shore. Over-washing may subsequently cause nest inundation, which often causes egg development or hatching or emergence to fail, depending on how long the eggs have been developing at the time of inundation (Lyons et al., 2022). Factors off-shore causing adult mortality such as fisheries bycatch (Harris et al., 2018) and pollution (plastic, oil, etc.) (Hoarau et al., 2014) could also impact population abundance. In 2000 alone, around 50 000 leatherbacks were caught as bycatch in pelagic longline fisheries within the Pacific Ocean alone (Lewison et al. 2004) and is reflected in the reduction of returning nesters each year for nearby rookeries for the Pacific (Spotila et al. 2000). These factors operating synergistically could then reflect in the lack of population growth of leatherbacks compared to loggerheads when both populations are under the same conservation effort. The findings of this study provide a good basis for future studies to correlate and compare the impact of fidelity and nest site selection with reproductive success for loggerheads and leatherbacks in the rookery as well as analysing the off-shore impacts affecting sea turtle population recovery.

Conclusion

Nest site selection and nest site fidelity are important aspects of sea turtle reproduction as they constitute the only parental input. The aim of this study was to disentangle nest site selection using a spatial data set that extends further into the off-shore bounds of rookery not covered in many other studies and to compare nest site fidelity for loggerheads and leatherbacks in a South African rookery between species and across time. The reproductive strategy differed at population and individual levels at the rookery and may be triggered by a variety of cues operating on different scales. Loggerheads had more specific nest site selection, higher fidelity and learned with experience to improve fidelity while leatherbacks had a generalist approach to nest site selection, relatively low fidelity and did not learn with experience. Both species are hauling out and emerging along the rookery where they prefer to nest even if they commit a false crawl. However, both nest site selection and nest site fidelity may impact individual turtles' reproductive success and nesting population reproductive fitness.

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