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Defining the potential ecological roles of three sea turtle species (*Caretta caretta, Chelonia mydas* and *Eretmochelys imbricata*) along the eastern seaboard of South Africa

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Plagiarism Declaration

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Declaration:

In accordance with Rule G 5.6.3, I hereby declare that this dissertation is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

Signature:

Date: 17-11-2020

The truth isn't always beauty, but the hunger for it is.

- Nadine Gordimer

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Summary

Sea turtles were once key species, driving ecosystem processes and energy flows. The past decline in sea turtle abundance and subsequent loss of their ecological roles, however, has resulted in reduced ecosystem functionality through food web shifts and trophic cascades. Therefore, understanding the past and present ecological roles of sea turtles is identified as one of the global research priorities for sea turtle management and conservation. While South African sea turtles are relatively well-protected through the combination of a successful, long-term sea turtle conservation program and a series of coastal marine protected areas, the ecological roles of these turtles have never been investigated. This study aimed to evaluate the ecological roles of two non-breeding foraging species (*Chelonia mydas* and *Eretmochelys imbricata*) and one breeding species (*Caretta caretta*) along the eastern seaboard of South Africa. A multi-technique approach that incorporated the use of satellite telemetry, stable isotope analysis and stomach content analysis was implemented to examine key ecological features such as habitat use, trophic position and diet. Satellite tracks revealed that all species formed aggregations in the near-shore environment. While this is typical of the breeding species, the continual uses by the non-breeding foraging species are indicative of residency. Algae were the predominate food item for *C. mydas*, sponges for *E. imbricata*, while *C. caretta* stomachs contained molluscs and crustaceans, or were found to be empty, consistent with capital feeding during breeding. Stable isotope analyses indicated a geographic shift in feeding ecology of green turtles. All species were found to be feeding within similar trophic levels within their respective geographic regions. This study elucidates the importance of small-scale differential ecological roles fulfilled by sea turtles, strengthens the on-going conservation efforts and provides an ecological framework for future studies in the region.

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Chapter 1: General Introduction

1.1 Background

Sea turtles are marine reptiles that may have been more abundant in the past, based on historical harvest records (Hornell 1927, Hirth and Carr 1970, Mortimer 1984, Bjorndal 1982). Consequently, many conservation programs were initiated, realising the impacts of unprecedented harvest rates. South Africa has a long history of conservation, including that of sea turtles, with a number of significant increments to conservation in each decade (Nel et al. 2013a). Conservation efforts range from monitoring beaches, increased spatial protection, designating Ramsar sites, proclaiming a world heritage site and most recently, in August 2019, 20 new or extended Marine Protected Areas were declared (Government Gazette No. 42478) – some of these explicitly for the protection of sea turtles. However, much of this motivation was based on knowledge of resident vulnerable *Chelonia mydas* (green turtles) and critically endangered *Eretmochelys imbricata* (hawksbill turtles), and the presence of nesting near-threatened *Caretta caretta* (loggerhead turtles) and critically endangered *Dermochelys coriacea* (leatherback turtles) (IUCN Red List of Threatened Species). The South African nesting population, shared with Mozambique, of leatherback turtles has remained stable while loggerhead turtle populations have increased (Nel et al. 2013a). Although South Africa has signed up on every convention, there are basic research and monitoring programmes that have been reneged on. Other than Hughes (1974) and turtle data gleaned from shark net catches (Brazier et al. 2012), there is limited knowledge on green and hawksbill turtles along the eastern seaboard of South Africa. Essentially, these species are being protected without knowledge of their diet, distribution, residence, genetic relationships, or their ecological roles. Hence, the problem to be addressed in this dissertation is the lack of ecological knowledge of sea turtle species present along the eastern seaboard of South Africa. Key ecological traits such as habitat use and preference, diet, trophic position, and food web interactions will be assessed. With this knowledge, the effectiveness of the recently expanded MPAs in protecting and fulfilling the needs of sea turtle species in the region, can be assessed.

1.2 Ecological roles

Ecosystems are intricate and dynamic systems which depend on organisms fulfilling their ecological roles to maintain structure and functioning (Petersen et al. 1998). Ecosystems shift and evolve over time as organisms adapt differentially to changing conditions, sometimes altering ecosystems completely with potential overarching effects on their structure and function (Bjorndal and Bolten 2003, Jackson et al. 2001). Thus, understanding the ecological roles of organisms is imperative to understanding the overall functioning and structure of an ecosystem and its resilience, especially in light of unprecedented anthropogenic threats (Bjorndal and Bolten 2003, Jackson et al. 2001).

The ecological role of a species is a well-established concept and has long been described in literature, if not always directly. For example, Darwin in 1859 used the term "line of work" to describe the role and diversity of butterflies discovered in the Amazon (Chase and Leibold 2003). Presently, ecological roles are being highlighted as research focus areas across taxa. For example, Roff et al. (2016) investigated the ecological role of sharks on coral reefs and found that most reef-associated sharks function as mesopredators (mid-ranking predators) and not as apex predators (top predators), as previously thought. In East Asian waters, anthropogenic influences have created an ecosystem shift from dominance by fish to dominance by jellyfish as a consequence of overfishing and jellyfish blooms – the latter resulting from increased eutrophic conditions due to industrial and civil sewage discharge (Uye 2011). Overfishing of large teleosts in Fiji lead to increased coral-eating starfish which had deleterious cascading effects on reef-building corals and coralline algae (Dulvy et al. 2004). Such studies reiterate the necessity for understanding the function of species in ecosystems. In understanding a species' role by assessing key ecological traits such as its nutrition, reproduction and growth, we gain greater insight about underlying system processes and dynamics. These key ecological traits can also help elucidate patterns and behaviours that are drivers to a species' abundance and distribution and can thereby strengthen conservation efforts.

One of the major caveats of establishing an ecological role is the shifting baseline syndrome (Pauly 1995, León and Bjorndal 2002). This syndrome describes the tendency to use current population abundances as a baseline, while not accounting for past population abundances (Pauly 1995). The past population abundance at which ecological roles were fulfilled by a species is thus not fully appreciated (Bjorndal and Bolten 2003). The uncertainty of past species' population abundances compounded by current natural and anthropogenic threats make establishing ecological roles difficult.

One of the global research priorities for sea turtle management and conservation is to define the past and present ecological roles of sea turtles (Hamann et al. 2010, Lazar et al. 2011). The ecological roles ascribed from international literature suggest that sea turtles influence community diversity and structure by operating at multiple levels as predators (Goatley et al. 2012), prey (Heithaus et al. 2008), competitors (Pearson et al. 2013), substrate for epibionts (Pfaller et al. 2006), parasite and pathogen hosts (Altizer et al. 2011), nutrient transporters (Bouchard and Bjorndal 2000) and habitat modifiers (Lazar et al. 2011) at variable spatial and temporal scales.

Sea turtles facilitate unique ecological roles in habitats such as seagrass and coral reef ecosystems (McClenachan et al. 2006). It has been demonstrated that sea turtles are more effective reef herbivores (even at low densities) than reef fish (Goatley et al. 2012). Generally, sea turtles facilitate benthic diversity by stimulating seagrass bed growth, enabling space for corals to grow where sponges take over, as well as act as bioturbators in the system by actively reworking the sediment (Bjorndal and Jackson 2002). Burkholder et al. (2011) have also reported on individual diet specialization within populations, and even suggest the possibility that subsets of a population can display different ecological roles. Sea turtles also indirectly make significant nutrient contributions to nutrient-poor beaches through nesting and influencing beach food webs (Bouchard and Bjorndal 2000, Le Gouvello et al. 2017) and can act as ideal sentinel species, potentially increasing monitoring efficiency at the ecosystem level by acting as indicator species (Aguirre and Lutz 2004). This is possible as sea turtles use a range of habitats throughout their lives and interact with various threats throughout (Aguirre and Lutz 2004).

Sea turtles were once key species, driving ecosystem processes and energy flows (Bjorndal and Bolten 2003). However, the past decline in sea turtle abundance and subsequent loss of their ecological roles has resulted in reduced ecosystem functionality through drastic food web shifts and trophic cascades (Bjorndal and Bolten 2003). Defining these ecological roles will enable the assessment of potential threats that populations of current and future generations may encounter, and may provide an indication of ecosystem health (Aguirre and Lutz 2004, Pajuelo et al. 2012).

1.3 Life history

When defining the ecological roles of an organism, its entire ontogeny and not just its adult stage needs to be considered (Werner and Hall 1988). As remnants of their land-dwelling ancestors, female sea turtles come ashore to nest. Following the laying of eggs, hatchlings emerge and actively orientate and move themselves towards the sea where they begin their swim frenzy to reach the oceanic zone (Bolten 2003, Boyle 2006). Once a hatchling feeds, it is referred to as a post-hatchling (Boyle 2006). Depending on the species, post-hatchlings follow one of three developmental life history patterns (refer to Figure 1.1).

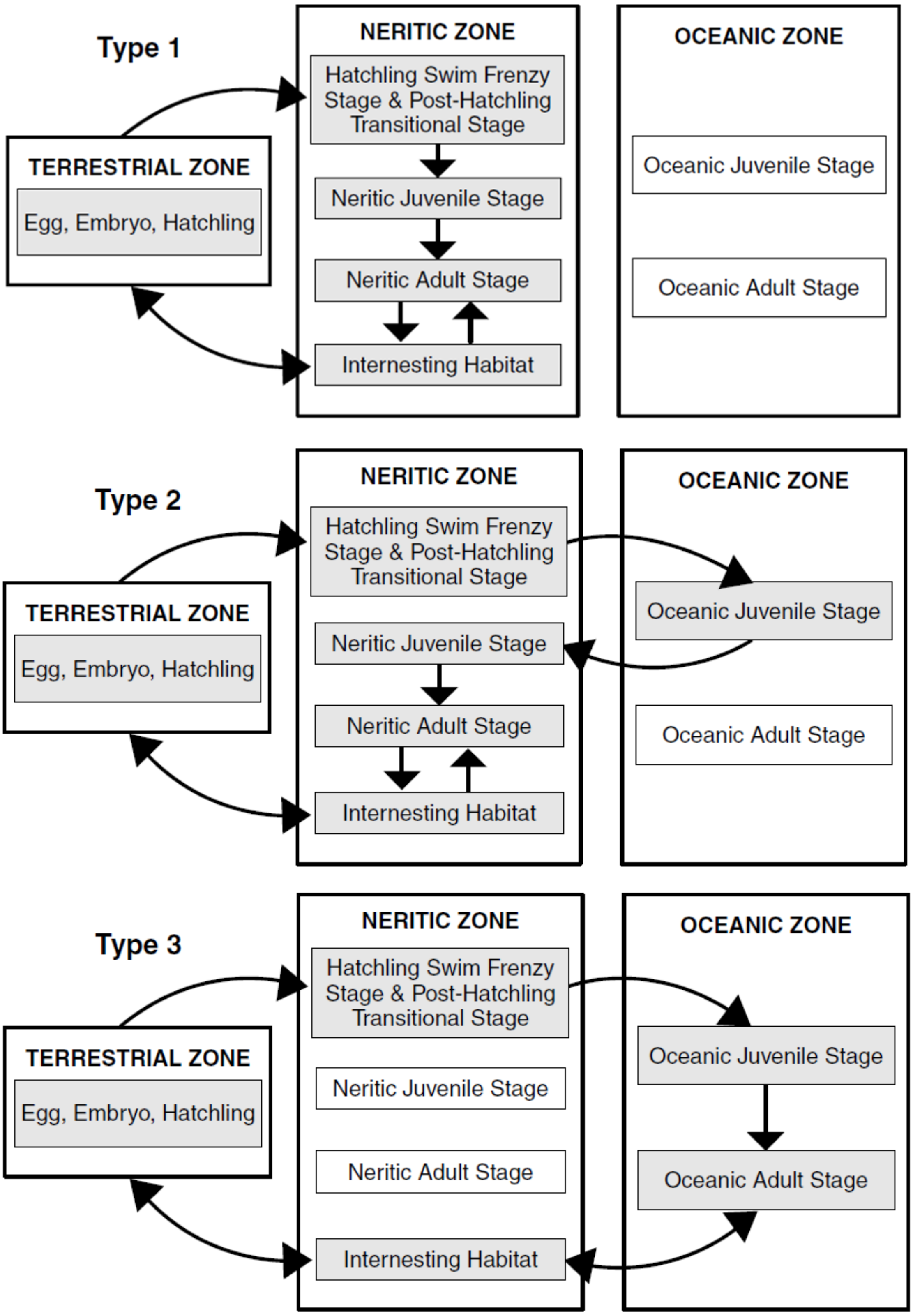

Figure 1.1. Basic life cycle of sea turtles (from Bolten 2003).

Type 1 life history pattern characterises sea turtles that complete their entire development in the neritic zone, with only one species, the Australian flatback turtle displaying this behaviour (Bolten

2003). Type 2 developmental pattern describes sea turtles that complete their early juvenile development (7-11.5 years) in the oceanic zone, then move into the neritic zone to complete their development and enter the adult stage (Bolten 2003). The Type 2 life history pattern is exhibited by most sea turtle species - loggerhead turtles, green turtles, hawksbill turtles and Kemp's ridley turtles (*Lepidochelys kempii*). Sea turtles that complete their entire development in the oceanic zone and only return to the neritic zone as adult females to nest, display the Type 3 life history pattern (Bolten 2003). Leatherback turtles exhibit the Type 3 developmental pattern while different subpopulations of olive ridley turtles (*Lepidochelys olivacea*) follow either the Type 2 or 3 life history pattern (Bolten 2003). Adult female sea turtles migrate between their foraging sites and their reproductive sites every 2-3 years to lay multiple clutches of eggs (Nel 2014). The period between successive nesting events within a season is known as the internesting period (Nel 2014). During the post-nesting period, female sea turtles begin the migration back to their foraging grounds.

1.4 Distribution

Sea turtles are some of the most widely distributed vertebrates, migrating long distances between foraging and nesting grounds and inhabiting a variety of niches throughout their complex life cycle (Biasatti 2004, Pike 2013). Global populations of all sea turtles are geographically and genetically distinct and need to be managed as Regional Management Units (RMUs) (Nel et al. 2013b, Wallace et al. 2010) (refer to Figure 1.2). RMUs need to be managed carefully and in accordance with prevalent threats as each distinct population is unique and irreplaceable. Sea turtles are therefore conservation-dependent and require further ecological elucidation to aid in restoring and/or maintaining the state of global populations.

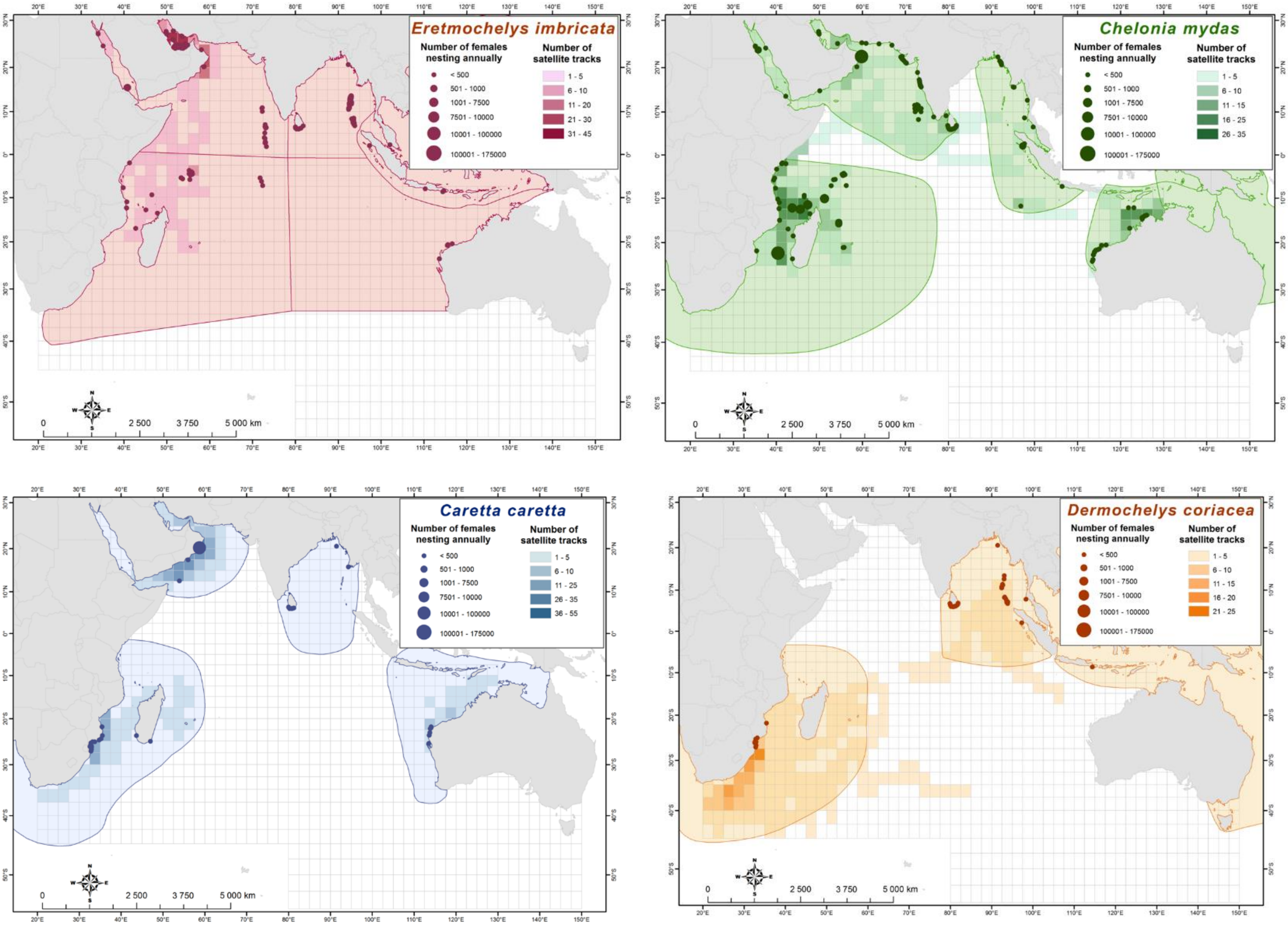

Figure 1.2 Regional management units (shaded areas) of four species of sea turtles nesting in the Indian Ocean arranged from the northern most nesters to southern-most nesters ; a) *Eretmochelys imbricata* (hawksbills) nesting in northern Mozambique north, b) *Chelonia mydas*, (green turtles) nesting on Europa Island and the central Mozambique coast, and c) *Caretta caretta* (loggerhead turtles) and d) *Dermochelys coriacea* (leatherback turtles) nesting in iSimangaliso, South Africa. Nesting sites are indicated by dots (Maps from Nel et al. 2013b.)

A central aspect to an organism's ecology is its movement in space and time (Ceriani et al. 2012). The advent of satellite tracking has vastly improved the knowledge of the spatio-temporal distribution and ecology of sea turtles at variable scale (Godley et al. 2008, Hawkes et al. 2012). Satellite tracking of sea turtles has been used to provide recent insight into migratory routes (Hawkes et al. 2012, Richardson et al. 2013, Varo-Cruz et al. 2013), foraging ecology (Carman et al. 2012, Casale et al. 2012, Ceriani et al. 2012) and high-use regions (Hart et al. 2013b, Hart et al. 2013c). The movement patterns of turtles within protected areas can be especially useful to aid in maintaining on-going conservation efforts (Hart and Fujisaki 2010). The satellite tracking studies in South Africa have mainly been conducted on the inter-nesting and post-nesting movements of female loggerhead and leatherback turtles (Hughes et al. 1998, Luschi et al. 2006). Home ranges and habitat use, particularly for the resident species, have not been reported.

1.5 Diet

Recognising the intrinsic link between an organism's physiology and its physical environment is necessary to understand movement ecology (Dalleau et al. 2019). Determining the diet of sea turtles, as well as their use of foraging grounds and of trophic resources is not only a fundamental goal of basic biology, but is also essential for effective population management (Tomas et al. 2001). Only one study to date has focussed on the diets of sea turtles present in South Africa (Hughes 1974) with no further ecological investigations, including trophic level positions.

The use of stomach content analysis is a common method of dietary studies and can provide valuable insight into foraging ecology (Boyle and Limpus 2008, Polito et al. 2011). Stomach content analysis is a direct approach, through removing and identifying prey items from the gut of turtles by dissection or through gastric lavages. However, this method only provides a snapshot of the animal's current diet and can underestimate the presence of soft-bodied prey (Polito et al. 2011).

Stable isotope analysis has become a popular, widely-used tool in ecology and can be used to infer trophic interactions, as well as supplement and complement information obtained from stomach content analysis (Burkholder et al. 2011). Stable isotope ratios of nitrogen (15N/14N; δ^{15}N) and carbon (13C/12C; δ^{13}C) are commonly used elements for dietary investigations and to infer trophic position. Through the digestion of organic matter, isotopic fractionation of these two elements occur, resulting in the enrichment of the heavier isotope in the consumer (Boyle and Limpus 2008). The enrichment factor between trophic levels for carbon is ~1% and ~3–5% for nitrogen. δ^{13}C is typically used to trace food sources where there are large variations in δ^{13}C, such as oceanic regions which have a lower δ^{13}C than coastal regions. δ^{15}N is used to infer trophic position, as consumers at a higher trophic level typically display a higher δ^{15}N value (Godley et al. 1998). By plotting δ^{13}C vs. δ^{15}N plots of turtles and their respective prey species, ecosystem trophic levels can be elucidated and prey that was previously underestimated in stomach content analysis can be accounted for. Stomach content analysis complements stable isotope analysis by elucidating similar trophic level prey contribution.

1.6 Sea turtle populations in South Africa

South Africa hosts five of the seven marine turtle species found globally; two nesting species, *Caretta caretta* (loggerhead turtles) and *Dermochelys coriacea* (leatherback turtles); two foraging species, *Eretmochelys imbricata* (hawksbill turtles) and *Chelonia mydas* (green turtles); and one vagrant occasional migratory species, *Lepidochelys olivacea* (olive ridley turtles) (Hughes 1974, Bourjea et al. 2008, Brazier et al. 2012, Nel et al. 2013a). All turtles found in South African waters fall within the South West Indian Ocean (SWIO) RMU and are at some of their southern-most distributions (Figure 1.2). The South African nesting loggerhead population is shared with Mozambique, both nesting and foraging occur along north-eastern seaboard of southern Africa (Nel et al. 2013a). The South African leatherback turtles are pelagic foragers and the most widely distributed species in the SWIO, nesting in southern Mozambique and north-east South Africa (Bourjea 2015). The foraging green turtle stock found in South Africa are known to be nesting at various central Indian Ocean islands, including but not limited to Madagascar and Seychelles (Bourjea 2015, Mortimer 2020). The foraging hawksbill turtle stock are the most equatorial species and nests mainly in the Seychelles and Chagos Archipelagos (Bourjea 2015, Mortimer 2020). Little is known about the rare, vagrant Olive Ridley turtle as this species has not been observed to feed or nest in South Africa (Bourjea 2015).

1.7 Threats and conservation

All seven species of sea turtles are listed on the IUCN Red List of Threatened Species. Their wide distribution coupled with elusive, cryptic behaviour makes sea turtles susceptible to a range of direct and indirect anthropogenic threats (Bolten 2003, Godley et al. 2008). These threats range from incidental fishery bycatch and habitat degradation or destruction to the targeted poaching of sea turtle eggs, meat and shells (Wallace et al. 2011, Hart et al. 2013a, Nel et al. 2013a).

South African sea turtles are relatively well-protected through the combination of a successful, long-running turtle conservation program established in 1963, and a series of coastal Marine Protected Areas (MPAs) (Nel et al. 2013a). Conservation efforts over the last five decades facilitated the recovery of the nesting population of loggerhead turtles, with the nesting number of females increased at an exponential rate (Nel et al. 2013a). However, the number of leatherback nesting females have remained stable in the region. Despite equal protection to both species, it is likely that the recovery of the leatherback population is hindered by offshore threats (Nel et al. 2013a).

Even though South African nesting sea turtles have been well documented through extensive monitoring for 53 years, the ecological roles of these animals have yet to be assessed. Further, ecological knowledge on the known resident hawksbill and green turtles is lacking. The majority of the research in the region has been solely focused on the conservation of nesting individuals. Only one study to date has partially documented the diet of loggerhead and green turtles in the region (Hughes

1974). Therefore, our understanding of these species and the roles they play in the environment are still largely unknown.

1.8 Rationale and dissertation outline

The aim of this research project is to define the potential ecological roles of three sea turtle species (*Caretta caretta*, *Eretmochelys imbricata* and *Chelonia mydas*) along the eastern seaboard of South Africa. To achieve this, various methodology techniques will be incorporated; namely satellite telemetry, stable isotope analysis and stomach content analysis. Key ecological traits such as distribution, habitat use and preference, diet, and isotopic niche will be assessed for loggerhead, green and hawksbill turtles in the region. Nesting loggerhead and non-nesting foraging green and hawksbill sea turtles were selected as the study species as they form aggregations in the neritic environment and are known to frequent the selected study sites. These sea turtle species exhibit the life history patterns depicted in Figure 1.3.

Chapter 1 provides a general introduction to the status quo of sea turtle populations in the SWIO. Chapters 2 and 3 are written as stand-alone research articles so there may be some repetition, however it is minimised.

Chapter 2 aims to (1) describe regional distribution, (2) construct and quantify home and core ranges and (3) identify benthic habitat preference for internesting loggerhead turtles, and foraging green and hawksbill turtles. It is hypothesized that these species would follow conventional restricted distribution (resident) patterns and display habitat preference focused on shallow reefs. As loggerhead turtles are in their internesting period, we hypothesize that these turtles would remain proximate to known nesting sites.

Chapter 3 aims to determine and quantify the i) diet and ii) isotopic niche of loggerhead, green and hawksbill sea turtles along the eastern seaboard of SA. It is hypothesised that respective sea turtle species from iSimangaliso and in the central and south of KZN will comply with their conventional diets, but with species-specific prey distributed along the east African seaboard. It is thus also predicted that green, hawksbill and loggerhead turtles will occupy different isotopic niches across different trophic levels, and fulfil different ecological roles.

Chapter 4 is a synthesis of the results from Chapters 2 and 3 and provides recommendations for future work.

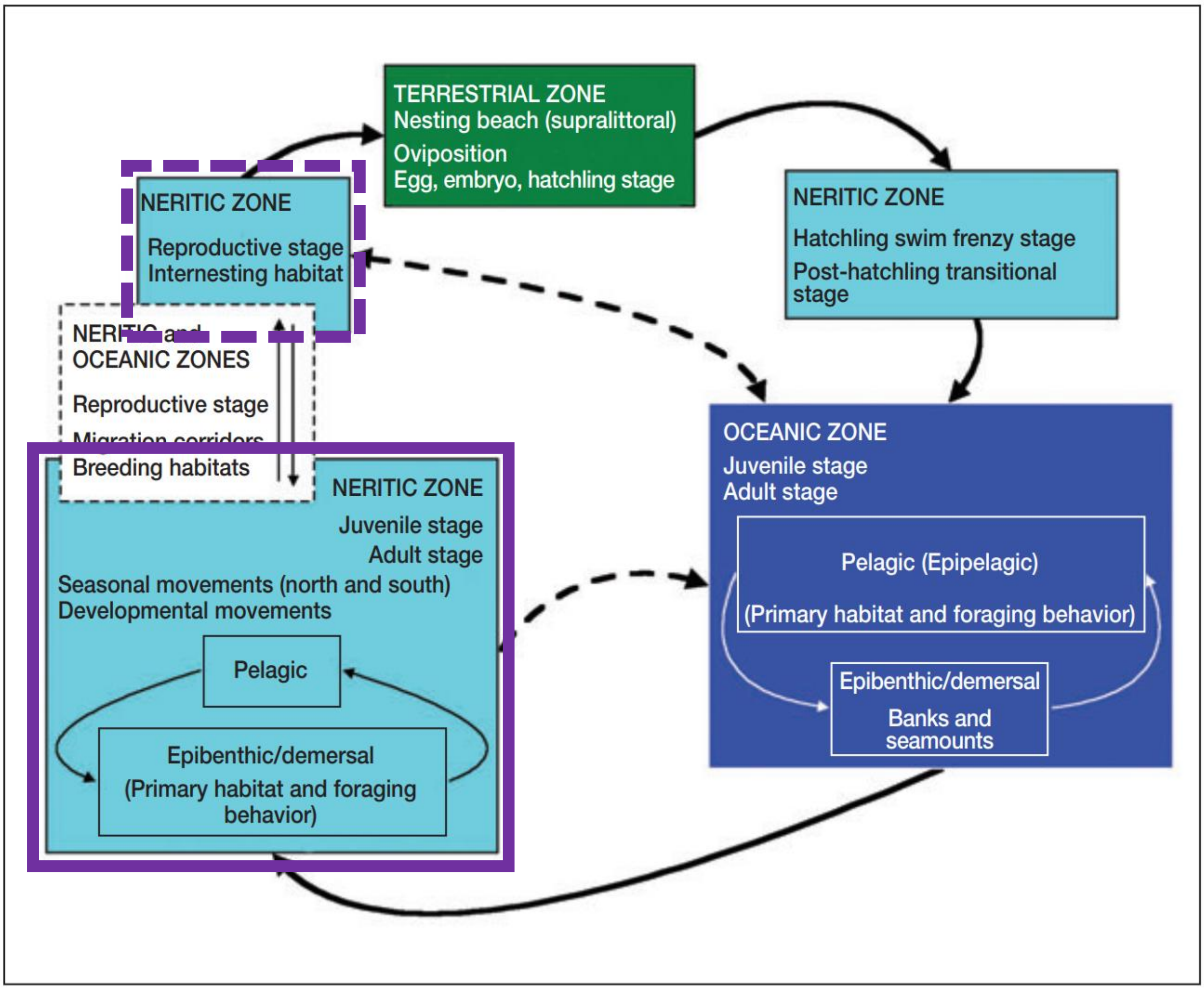

Figure 1.3 Ecology investigated for three species of sea turtles during the life history phases in the boxes outlined in purple. Only the internesting ecology of loggerheads is investigated as they are nesting in South Africa.

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Chapter 2: Distribution and habitat preference of loggerhead, green and hawksbill turtles along subtropical South Africa

2.1 Abstract

Satellite tagging is extensively used to identify the post-nesting dispersal of female turtles to their foraging grounds, using particular long-distance migratory routes. However, the distribution once at the foraging or nesting ground is much less known, as is the movement of immature turtles at their neritic developmental areas, especially in the Indian Ocean. These gaps hamper our understanding of sea turtle ecology, as well as the design of appropriate management options such as MPAs. For example, South Africa declared 20 new and/or expanded MPAs in 2019, but we do not know if these will serve the needs of non-nesting sea turtles or neritic phases of nesting species. The aims of the study were therefore to (1) describe regional distribution, (2) construct and quantify home and core ranges and (3) identify benthic habitat preference for internesting loggerhead turtles, and non-breeding green and hawksbill turtles, which are assumed to be more resident in South Africa. Loggerhead (n=9), green (n=5) and hawksbill (n=3) turtles were fitted with SPOT 5 (Wildlife Computers) or Kiwisat (Sirtrack) satellite tags, and standard morphometric measurements recorded. Satellite track duration across species for 17 turtles lasted 71-452 days ($\bar{x}$ = 173 ± 91 days), and were used to construct respective kernels for each tracked individual. These were overlaid with benthic habitat maps to identify habitat preference. The three species showed a high fidelity to tagging location with small home ranges. Of the 14 habitat types available, only six habitat types were used. These include sandy, estuarine and mixed shores, and inshore reefs, whereas most of the deeper reefs and canyons were not used. This study confirms the residence and habitat selection of three sea turtle species along the eastern seaboard of South Africa. Hence, the newly expanded iSimangaliso MPA is an effective conservation management tool for sea turtle species along the eastern seaboard of South Africa.

2.2 Introduction

Sea turtles are long-lived, late maturing marine reptiles with a peculiar life history divided between coastal-terrestrial habitat where they start their life, followed by an extended oceanic existence lasting for a decade, then an ontogenetic shift to neritic habitats (which can last for decades), until they mature and survive to do an occasional long-distance migrations to their natal beaches for breeding (Bolten et al 2003). There are multiple studies across all ocean basins that have tracked the adult migratory pathways (Rees et al. 2010, Read et al. 2014, Luschi et al. 2016, Hays and Hawkes 2018), and a few attempts at mapping the distribution of post-hatchlings (Mansfield et al. 2014, Scott et al. 2014, Mansfield et al. 2017). However, the least studied age classes are those of juvenile and subadult turtles with only a few studies (Mansfield et al. 2009, Peckham et al. 2011, Carman et al. 2012). Many of the studies that have tracked immature turtles are often following post-rehabilitation release after strandings or rehabilitated from fisheries catches (Dalleau et al. 2014). However, the aim of these studies is generally to track the success of recovery within the RMU these turtles come from (Dalleau et al. 2014). Very few of these aim to the investigate the ecology or local movements (home ranges) or habitat use of sea turtles.

An animal's home range, a fundamental biological concept (Seminoff et al. 2002, Kie et al. 2010), can be defined as the area traversed during routine activities, excluding erratic behaviour and migratory movement (Bailey 1984). Knowing an animal's home range enables the spatial identification of the core activity and habitat use areas, which allows for much more specific design of conservation areas so managers can focus conservation efforts to specific areas of resource use (Berube et al. 2012, Hart et al. 2012a). For example, Wall et al. (2005) used GPS technology to identify the home and core ranges of African elephants. While both the home and core ranges were within protected areas, the corridors used to traverse between the two ranges were outside the protected areas. Using satellite tracking technology, Jiguet and Villarubias (2004) identified home range sizes and habitat selection of black storks to afford better protection and management of breeding populations and their feeding habitats. As demonstrated by Maxwell et al. (2011), satellite tracking can be an effective tool to optimise conservation efforts for sea turtles. The internesting movements of olive ridley turtles in Central Africa were investigated in relation to current park protection boundaries and a proposed transboundary park between Gabon and the Republic of Congo. Within the current park boundary, only 44.6 % of high-density turtle areas were covered but the proposed transboundary park would incorporate 97.6 % of high-density areas (Maxwell et al. 2011). This highlights the importance of international co-operation and the establishment of transboundary protection to manage shared turtle populations, especially relevant as South Africa and Mozambique share sea turtle populations (Nel 2013).

South Africa maintains one of the most extensive, coastal and marine, turtle conservation programmes, providing the strongest space-based conservation protection available to two turtle species, loggerhead and leatherback sea turtles in iSimangaliso (Nel et al. 2013, Harris et al. 2015). The iSimangaliso Wetland Park, a UNESCO World Heritage Site, is situated along the north-eastern seaboard of KwaZulu-Natal, South Africa, and historically comprised of terrestrial reserves and two contiguous MPAs (St Lucia and Maputaland MPA). Both nesting species, loggerhead and leatherback females, are tagged and measured when ashore. Previous satellite tags have indicated that female loggerheads remain close inshore, adjacent to the nesting grounds during the internesting period (Harris et al. 2015), whereas leatherbacks have a more extensive distribution range and internesting movements. This extensive leatherback distribution was part of the motivation for an offshore and longshore extension of the iSimangaliso Protected Area (Harris et al. 2015). On 1 August 2019 (Government Gazette 42478), the newly revised iSimangaliso MPA came into effect with much extended boundaries (Figure 2.1a) which absorbed the previous marine reserves. In addition to this larger MPA, 19 other MPAs have been declared or existing MPAs expanded (See https://www.marineprotectedareas.org.za/).

Apart from the two nesting species, loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) turtles that nest along these MPAs, there is also a marked presence of two non-nesting sea turtle species, hawksbill (*Eretmochelys imbricata*) and green (*Chelonia mydas*) turtles. Juvenile and sub-adult green and hawksbill turtles are known to frequent the east African seaboard, suspectedly using it as a foraging/developmental ground (Bourjea et al. 2008, Brazier et al. 2012). They are also presumably linked to the populations of east African islands which they use as nesting grounds (Hickman 2017). However, except for sea turtle bycatch from bather protection nets (Brazier 2012), ad hoc stranding reports, anecdotal in-water observations by SCUBA divers of foraging activities (Nel pers. com), and preliminary genetic stock assignment (Hickman 2017) there is no robust quantitative empirical data to estimate population sizes or assess distribution, especially of green and hawksbill turtles.

Other studies have reported hawksbill turtles to have limited home ranges with small core areas, sometimes restricted to individual reefs and appear to be resident for extended periods (Ferreira et al. 2018). Similarly, green turtles seem to exhibit an affinity for nearshore shallow waters, close to reef systems (Williams et al. 2017). Loggerhead turtles exhibit strong site fidelity to their nesting areas during the internesting period (Harris et al. 2015). So, the internesting and post-nesting distribution of nesting loggerhead and leatherback turtles are known (Nel et al. 2013, Harris et al. 2015, Robinson et al. 2016), but home range and habitat use or preference, have not been described for loggerheads or any of the two non-nesting sea turtle species frequenting the subtropical Delagoa bioregion of South Africa.

The advent and evolution of satellite tracking technologies have vastly improved the knowledge of spatio-temporal distribution and associated ecology of a variety of taxa, ranging from insects and marine invertebrates to terrestrial vertebrates and marine megafauna, at various ecological scales (Godley et al. 2008, Hays et al. 2016). Knowledge of species movement informs the location, size and timing of potential conservation zones. Further, movement data can also assist with stock assessments and support the development of management and conservation strategies for species of concern (Hays et al. 2016, Jeffers and Godley 2016). The highly migratory nature of sea turtles makes satellite tracking a useful tool in identifying key areas of habitat use that are essential to understanding population dynamics (Hart et al. 2014a). Although sea turtles are extensively studied by remote tracking (Godley et al. 2008), there is a lack of robust spatial and temporal data for the Indian Ocean, that hampers our understanding of sea turtle ecology in the region (Casale et al. 2012, Varo-Cruz et al. 2016). Informing this knowledge gap and establishing an ecological baseline for foraging species (see Stokes et al. 2019) is therefore imperative to improve our understanding of sea turtle ecology, their specific ecological roles in the marine environment, and strengthening on-going conservation efforts within MPAs.

Sea turtles may act as keystone species on foraging areas (Bjorndal and Bolten 2003, Luschi et al. 2006) providing essential ecological functions and resilience to the ecosystem. Consequently, research directed at various life stages will help elucidate green and hawksbill turtle distribution patterns. Determining distribution patterns will contribute to the conservation of these species throughout the Western Indian Ocean (WIO) region. The aims of the study were therefore to (1) describe regional distribution, (2) construct and quantify home and core ranges and (3) identify benthic habitat preference for internesting loggerhead turtles, and foraging green and hawksbill turtles. Green and hawksbill turtles will be satellite tagged for the first time in the region – therefore we hypothesize that these species would follow conventional restricted distribution (resident) patterns and display habitat preference focused on shallow reefs. As loggerhead turtles are in their internesting period, we hypothesize that these turtles would remain proximate to known nesting sites.

2.3 Materials and Methods

Ethics statement

Ethics clearance for the attachment of satellite tags on hard-shelled sea turtles was obtained from the Nelson Mandela University Animal Ethics Committee: A13-SCI-ZOO-012, and with the permission of, and in collaboration with the Department of Environmental Affairs (permit no. RES2012/24) and under research agreement with iSimangaliso Wetland Park and Ezemvelo KZN Wildlife.

Study Area

All satellite tag deployments took place from the iSimangaliso Wetland Park (Figure 2.1a). The benthic and coastal habitat for this study region can be classified into seven ecozones within three marine ecoregions (Figure 2.1b); namely the Natal (inshore, shelf and shelf edge), Delagoa (inshore, shelf and shelf edge) and Southwestern Indian (upper bathyal) Ecoregions (Sink et al. 2012). The habitat types within the distribution range of iSimangaliso is broadly categorized as being dominated by sandy and reef habitats interspersed with mixed shores and to a lesser extent, exposed rocky coasts and canyons leading offshore into the upper bathyal of the southwest Indian Ocean.

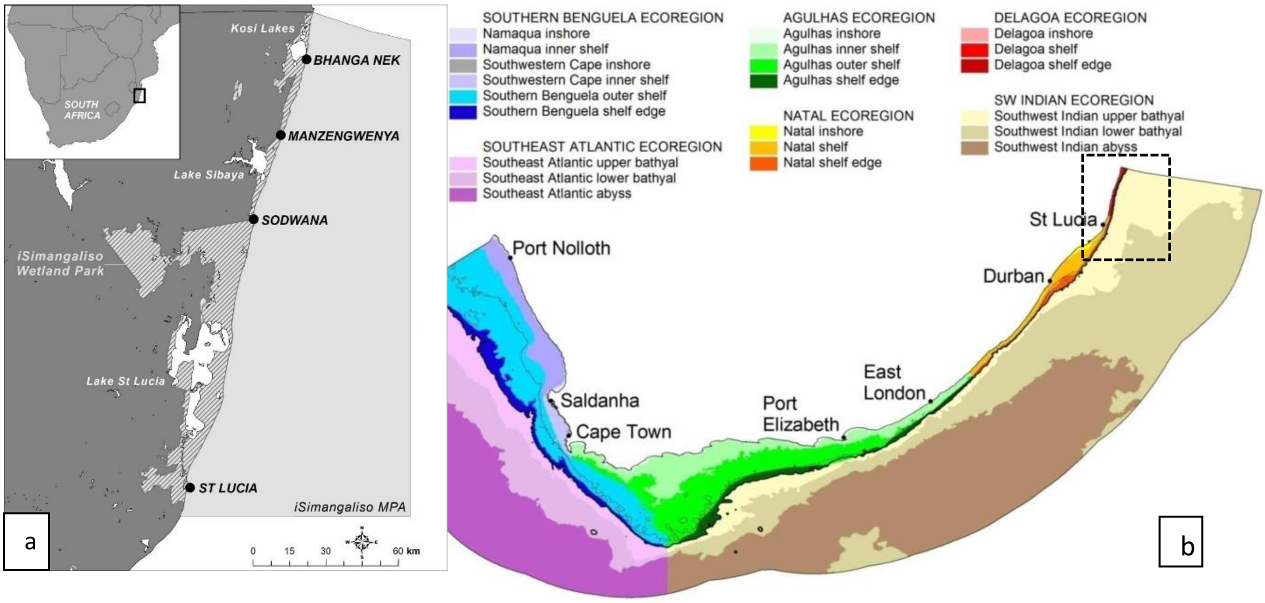

Figure 2.1 a) Study site map indicating the iSimangaliso MPAs. (Map by Diane Le Gouvello.) Shaded area on land indicates the terrestrial reserves within the iSimangaliso Wetland Park. b) Benthic and coastal habitat map for the study region (stippled block) as per Sink et al., (2012). Satellite tagging of loggerhead individuals were done at Bhanga Nek, whereas green and hawksbill turtles were tagged at Sodwana with a registered and practical boat launch site.

Data collection

Individual nesting loggerhead females (n=9) were opportunistically fitted with SPOT 5 (Wildlife Computers) or Kiwisat (Sirtrack) satellite tags during night monitoring patrols at Bhanga Nek in the December 2010/2011 season. Green (n=5) and hawksbill (n=3) immature and sub-adult individuals were captured on SCUBA (following Ehrhart and Ogren 1999) at Sodwana in January and October 2013. All satellite tags were fitted directly onto the hard shell at the highest point of the second central scute (Zbinden et al. 2008, Ceriani et al. 2012) using a marine grade epoxy and anti-fouling paint applied post-attachment. Satellite tags were linked to Service Argos and were set to run continuously (24 $h.d^{-1}$). Standard morphometric measurements of straight (SCL) and curved (CCL) carapace lengths were recorded for all individuals (Table 2.1). Coded metal flipper tags were applied to the inner trailing end of the anterior flippers of previously untagged or only single flipper tagged individuals to add to our conservation database.

Table 2.1 Metadata and tracking duration for all individuals. Females were tagged on the beach as nesting females, immature turtles have an unknown sex, and the sub-adult females were assumed as there was no elongation yet of the tail at this near-fully grown size.

Species	ID	Sex	CCL (cm)	Tracking Duration (Days)
Loggerhead turtles	66387	Female	86.2	153
	66347	Female	79	183
	66312	Female	83.3	203
	66290	Female	91	71
	105319	Female	86.8	231
	105318	Female	86.8	241
	105317	Female	88.2	190
	105316	Female	92	84
	105315	Female	84.8	207
Green turtles	119369	Female	95	73
	119368	Immature	62	101
	119363	Sub Adult Female	98.4	87
	119366	Immature	81.6	134
	119367	Immature	63.4	192
Hawksbill turtles	105314	Immature	79.2	184
	119362	Immature	76.5	452
	119370	Immature	79	150

Data filtering and analyses

Argos data for all species were filtered in Movebank (www.movebank.org) using the Distance, Angle and Rate (DAR) filter (Douglas et al. 2012) and following parameters from Harris et al. (2015) for loggerhead sea turtles (representative of hard-shelled turtles). The user-defined parameters in the DAR filter allow for improved accuracy of the track by 50-90 % (Douglas et al. 2012), while retaining a larger proportion of the data that would otherwise be filtered by removing lower quality location estimates (Harris et al. 2015). The filtered data were plotted in ArcGIS 10.4 (ESRI) with points on land and those from migrations (away from the resident or inter-nesting areas) removed. Individuals with fewer than 30 location estimates overall were excluded from further analysis because there were insufficient data to plot reliable kernel home ranges (Seaman et al. 1999). Kernel density is a non-parametric method that allows for the estimation of high-use (core) areas within a home boundary by weighting observations (Worton 1989, Hart and Fujisaki 2010) and can be useful in assessing habitat selection (Seaman et al. 1999). Fixed kernel home ranges with the smoothing factor (h) determined per individual using least-squares cross-validation (LSCV) (Seaman and Powell 1996, Hart et al. 2012a) were constructed in ArcView 3.3 (ESRI) using the Animal Movement Extension (Hooge et al. 1999), with 95 % and 50 % utilisation distributions (UDs) used to estimate overall home and core area range respectively.

Habitat preference was performed as a design II study, where individuals are identified and their respective use of resources measured, but availability of resources are measured at a population level (Manly et al. 2007). It was assumed that the area used by all (tracked) individuals was available to each individual for respective species. This “available habitat”/species buffer was delineated by creating a buffer of the shoreline by a distance of the farthest offshore location, and cutting it perpendicular to the shore at the southern- and northern-most points. The South African marine and coastal benthic habitat map (Sink et al. 2012) was clipped by the species buffer (to represent available habitats), as well as all of the home (95 %) and core (50 %) utilisation distributions (to represent used habitat). The species’ buffers and utilisation distributions were then projected into the Universal Transverse Mercator (UTM) using the World Geodetic System (WGS) 84 projection (Zone 36 S for KwaZulu–Natal). The area (km^2) of available and used benthic habitats (habs and per habitat, hab$_x$) were calculated using spatial statistical tools in ArcGIS 10.4 (ESRI). A modification of the Mills and Gorman (1997) preference index (PI) formula, which incorporates Duncan (1983) log transformation for index normality, was calculated as follows:

$$PI = \log\left(\frac{Area\ of\ hab_x\ within\ a\ kernel\ \div\ Area\ of\ all\ habs\ within\ a\ kernel}{Area\ of\ hab_x\ within\ species\ buffer\ \div\ Area\ of\ all\ habs\ within\ species\ buffer}\right)$$

The applied modification uses areas of the kernel home and core range as an alternative to number of observations or location point estimates, as the error associated with Argos data make these point estimates unreliable. Therefore, the areas associated with the kernels (at both the home and core range level) were used as a more accurate proxy of habitat utilization and would be a truer representation in terms of preference. A PI value equivalent or greater than 0.3 indicates preference for a particular habitat, whereas a value lower than 0.3 indicates avoidance (Mills and Gorman 1997). Simple linear regression analyses were conducted per species to determine if there were significant associations between area (at 50% and 95% UD) and sea turtle size (represented by the CCL). Data were appropriately log transformed to satisfy assumptions of linearity. All data satisfied assumption tests for normality and homoscedasticity ($p>0.05$).

2.4 Results

Spatial Distribution

Satellite track duration for 17 turtles of all three species lasted 71 - 452 days ($\bar{x}$ = 173 ± 91 days) and produced a total of 10 707 filtered location estimates which were used to construct respective kernels for each tracked individual (Figures 2.2-2.4).

Home and Core Ranges

The delineated study areas constructed for all species (“species buffer”), based on the extent of the farthest offshore and northern- and southern- most location estimates, indicate that loggerheads have the overall largest total distribution area (4 002.7 km^2). This distribution ranges from 15.0 km south of Sodwana Bay to the South African-Mozambique border, falling within both the “old” Maputaland and St Lucia MPAs, and extends 43 km offshore into the upper bathyal of the southwest Indian Ocean. However, it is evident from individual loggerhead kernels (Figure 2.2.) that this distribution range is an accumulation of conspecific variability. Individual loggerhead home ranges (95 % UD) reveal much smaller areas (29 - 211 km^2, $\bar{x}$ = 111 ± 70 km^2) and show a greater affinity to the region proximate to Bhanga Nek where they were tagged. Loggerhead core range (50 % UD) indicate that the species exhibits an affinity to the coasts (“coastal clingers”) and rarely venture beyond the Delagoa sandy shelf edge and into the upper bathyal while at the breeding sites.

Green turtles had the smallest overall total distribution area (86.5 km^2) and were closely associated to the coast of Sodwana (Figure 2.3), extending 8.0 km north and 6.3 km south of the region. Apart from one individual (ID: 119367), all green turtles appeared to utilize the same area of the coast in their core range (50 % UD). Green turtle 119363, the largest of all green turtles, had a more extensive home and core range area (15.2 km^2 and 2.9 km^2 respectively) in comparison to all other individual's home and core range areas ($\bar{x}$ = 4.0 ± 1.7 km^2, $\bar{x}$ = 0.5 ± 0.2 km^2 respectively).

Hawksbills appeared to utilize a similar area as green turtles in the Sodwana region but with a slightly broader spatial use (17.5 km north, 9.3 km south) and had an overall total distribution area of 509.3 km^2. Hawksbill turtle 105314 also displayed a more extensive home and core range (39.8 km^2 and 5.0 km^2 respectively) relative to the two other individuals ($\bar{x}$ = 9.3 ± 0.17 km^2, $\bar{x}$ = 1.3 ± 0.39 km^2). Interestingly, hawksbill turtle 105314, like green turtle 119363, both with more extensive home and core range area, was the largest individual tagged. Both of these turtles were also the only turtles to venture onto the Delagoa canyons within a subset of their home range (95 % UD). The SPOT 5 tags were not equipped with depth data and therefore it is not clear if they actually dived into the canyons. A regression analysis of size and area indicated that area for the kernels at both the home and core range (50 % and 95 % UD respectively) were not significantly ($p > 0.05$) associated with sea turtle curved carapace length (Table 2.2). However, this may be a function of the small sample sizes.

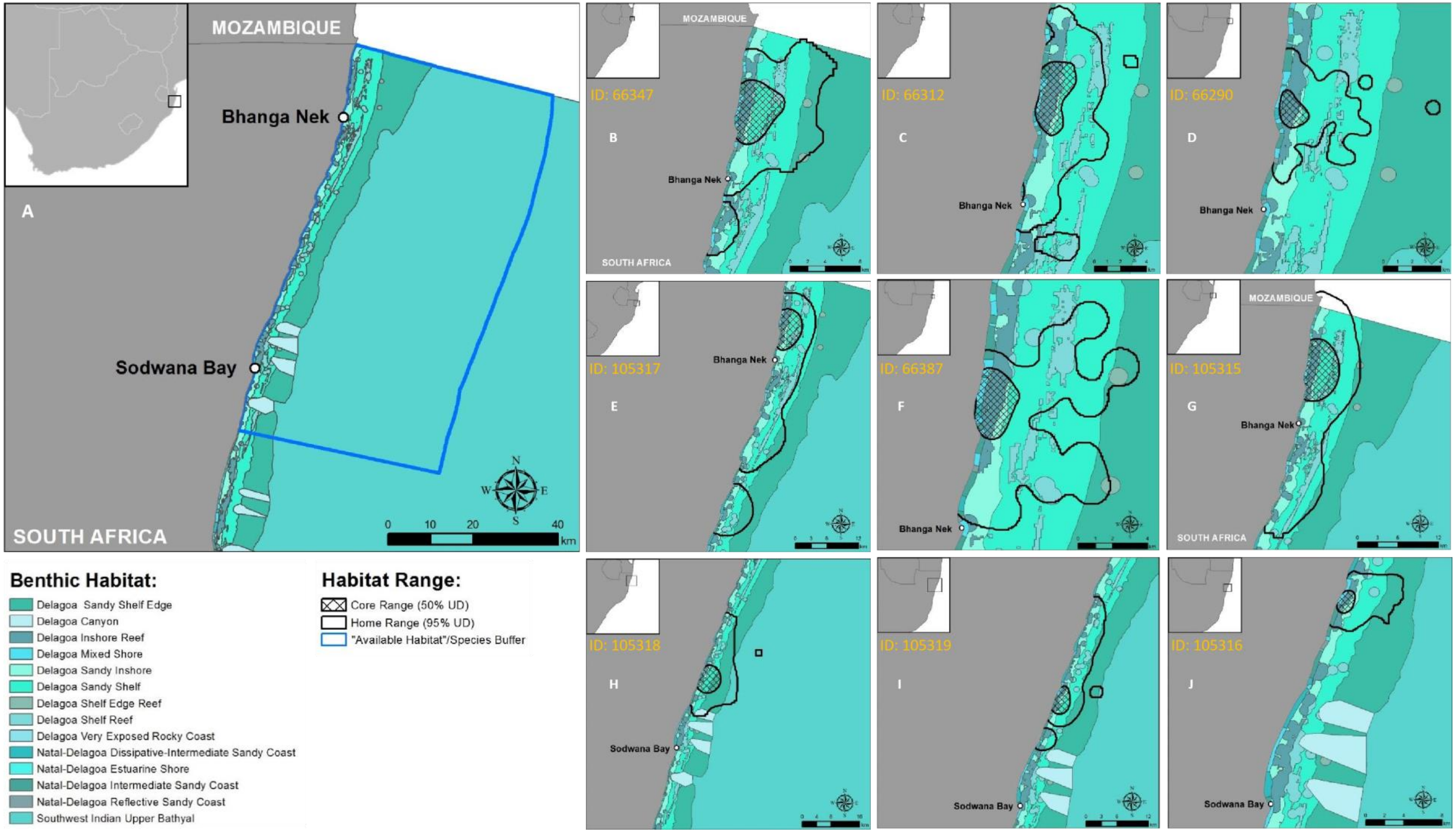

Figure 2.2 Habitat range of loggerhead turtles overlaid on the SA marine and coastal benthic habitat map: (A) the delineated study area indicating the full extent of the loggerhead turtle distribution, representing the available habitat to all individuals. (B-J) The habitat used indicated by the home (95 % UD) and core range (50 % UD) for each individual.

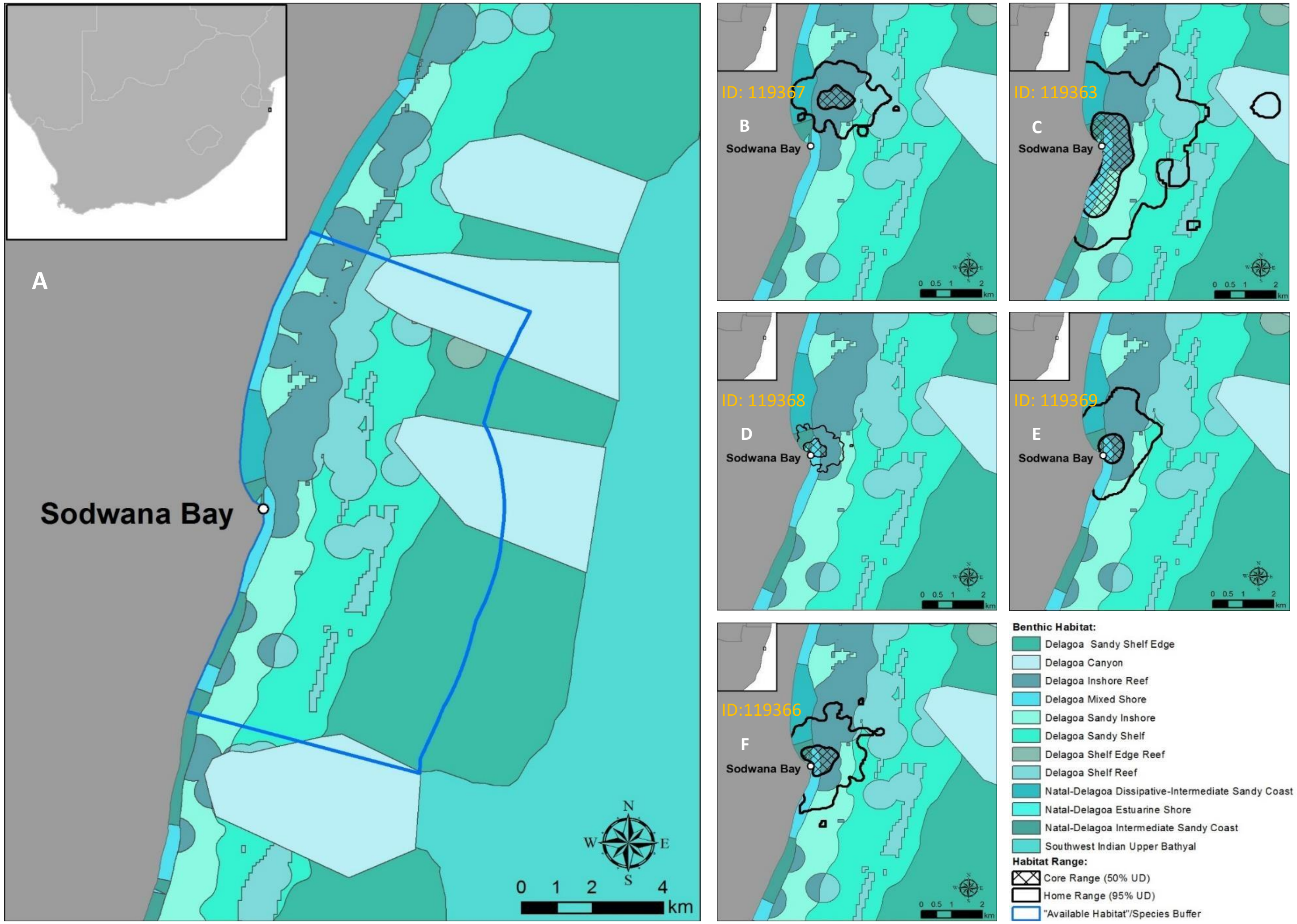

Figure 2.3 Habitat use of five green turtles overlaid on the SA marine and coastal benthic habitat map: (A) the delineated study area indicating the full extent of the green turtle distribution, representing the available habitat to all individuals. (B-F) The habitat used indicated by the home (95 % UD) and core range (50 % UD) for each individual.

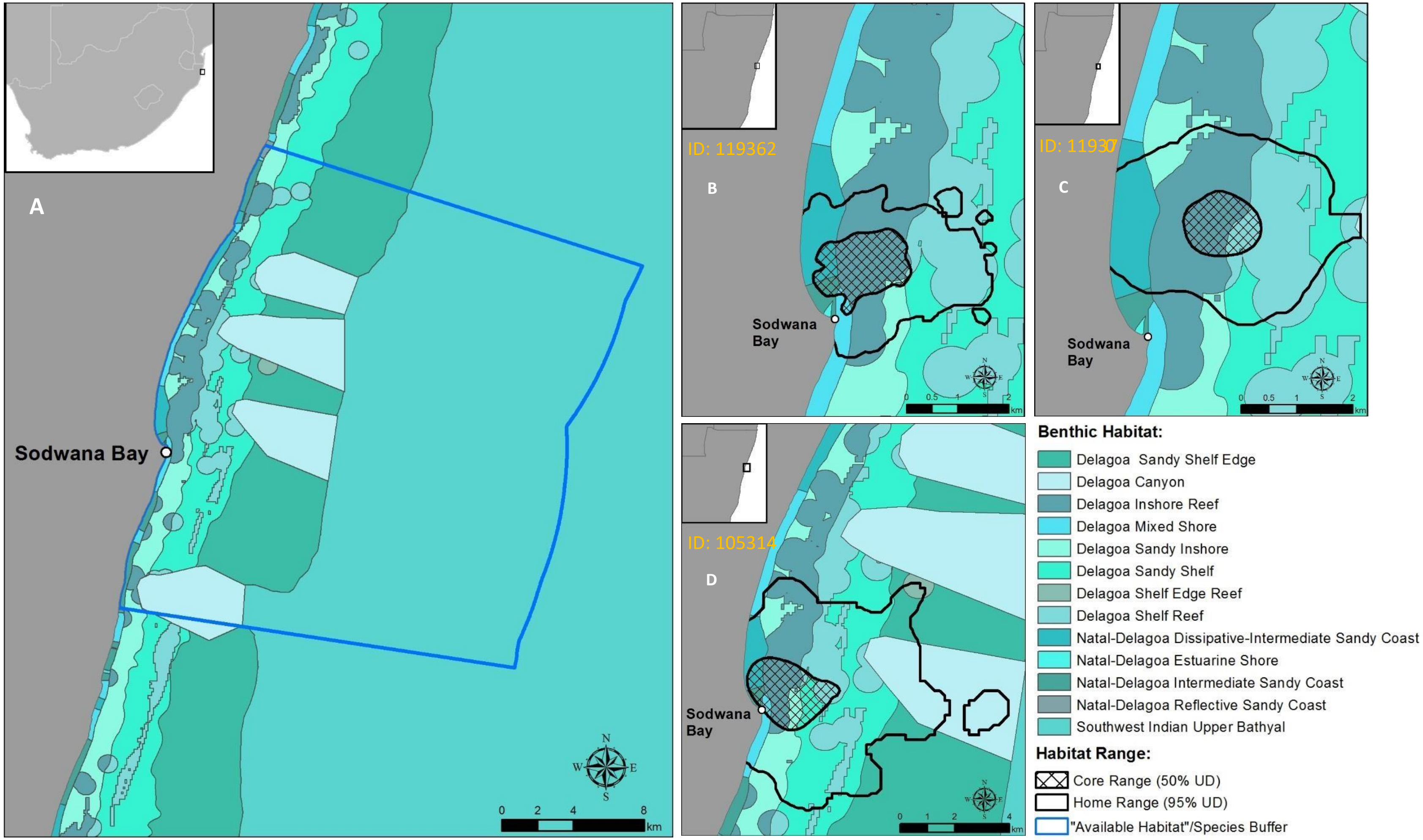

Figure 2.4 Habitat range of three hawksbill turtles overlaid on the SA marine and coastal benthic habitat map: (A) the delineated study area indicating the full extent of the hawksbill turtle distribution, representing the available habitat to all individuals. (B-D) The habitat used indicated by the home (95 % UD) and core range (50 % UD) for each individual.

Table 2.2 Regression analyses of loggerhead, green and hawksbill sea turtle size (CCL) and respective areas (km^2) of habitat use at the home (95 % UD) and core (50 % UD) ranges

		F	**P**	**R^2**
Loggerhead (n=9)	Home Range	2.429	0.163	0.258
	Core Range	4.667	0.068	0.400
Green (n=5)	Home Range	4.421	0.126	0.596
	Core Range	3.063	0.178	0.505
Hawksbill (n=3)	Home Range	0.479	0.615	0.324
	Core Range	0.246	0.707	0.198

Habitat Preference

The cumulative habitat use of all individuals for the three species ("available habitat"/species buffers) encompassed a total of 14 benthic habitats; loggerhead turtles occurred in all 14 habitats, hawksbill turtles in 13 habitats and green turtles in 12 habitats (Figures 2.2-2.4A). Loggerheads exhibited preference (PI ≥ 0.3; see Table 2.3) for 64% of these available habitats within their home range (95% UD), with the highest preferences (or most time spent) in the Natal-Delagoa Reflective Sandy Coast (PI = 0.99), Delagoa Mixed Shore (PI = 0.98) and the Delagoa Inshore Reef (PI = 0.98). The loggerhead core range (50 % UD) showed more selectivity with nine benthic habitats available, for which seven habitats were frequented. The highest preferences (at 50 % UD) were allocated to the Delagoa Mixed Shore (PI = 1.44), Delagoa Inshore Reef (PI = 1.38), Natal-Delagoa Intermediate Sandy Coast (PI = 1.03) and the Delagoa Sandy Inshore (PI = 0.97).

Table 2.3 Mean benthic habitat preference index (PI) of loggerhead, green and hawksbill sea turtles within their home (95 % UD) and core (50 % UD) ranges. Three highest scores per species are shaded. Benthic habitat in boldface is that most frequently selected by all three species.

Benthic Habitat	**Loggerhead PI**		**Green PI**		**Hawksbill PI**	
	Home Range	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**
Delagoa Mixed Shore	**0.98***	**1.44***	0.17	**0.84***	**0.42***	0.27
Delagoa Very Exposed Rocky Coast	0.29	-	-	-	-	-
Natal-Delagoa Dissipative-Intermediate Sandy Coast	**0.70***	**0.53***	**0.67***	0.04	**1.10***	**0.59***
Natal-Delagoa Estuarine Shore	**0.30***	-	**1.00***	**1.55***	**0.95***	**0.59***
Natal-Delagoa Intermediate Sandy Coast	**0.97***	**1.03***	0.00	**0.67***	0.00	0.27
Natal-Delagoa Reflective Sandy Coast	**0.99***	0.17	-	-	-	-
Delagoa Inshore Reef	**0.98***	**1.38***	**0.56***	**0.60***	**0.94***	**1.30***
Delagoa Sandy Inshore	**0.90***	**0.97***	0.04	0.08	**0.36***	0.21
Delagoa Shelf Reef	**0.82***	**0.38***	0.00	0.00	**0.96***	**0.70***
Delagoa Canyon	0.03	-	0.00	-	0.00	-
Delagoa Shelf Edge Reef	0.23	-	-	-	0.25	-
Southwest Indian Upper Bathyal	0.00	-	-	-	-	-
Delagoa Sandy Shelf	**0.94***	**0.58***	0.00	-	**0.31***	0.00
Delagoa Sandy Shelf Edge	0.04	0.05	-	-	0.00	-

***Denotes preference (PI≥0.3)**

- Habitat not available

Green turtles showed selectivity for nine available habitats in their home range (95 % UD), of which only three were preferred: Natal-Delagoa Estuarine Shore (PI = 1.00), Natal-Delagoa Dissipative-Intermediate Sandy Coast (PI = 0.67) and Delagoa Inshore Reef (PI = 0.56). Green turtle showed preference for four habitats in their core range (50 % UD): Natal-Delagoa Estuarine Shore (PI = 1.55), Delagoa Mixed Shore (PI = 0.84), Natal-Delagoa Intermediate Sandy Coast (PI = 0.67) and Delagoa Inshore Reef (PI = 0.60).

Hawksbill turtles, like loggerheads, showed preference for 64% of the available habitats within their home range (95 % UD), with the highest preferences for the Natal-Delagoa Dissipative-Intermediate Sandy Coast (PI = 1.10), Delagoa Shelf Reef (PI = 0.96) and the Natal-Delagoa Estuarine Shore (PI = 0.95). However, the core range (50 % UD) indicates less preference (50%) for the available habitats than that of the home range, with the highest preferences allocated to the Delagoa Inshore Reef (PI = 1.30), Delagoa Shelf Reef (PI = 0.70), Natal-Delagoa Dissipative-Intermediate Sandy Coast (PI = 0.59) and the Natal-Delagoa Estuarine Shore (PI = 0.59).

2.5 Discussion

The aim of the study was to describe the distribution of nesting loggerhead, and non-nesting green and hawksbill turtles, including their high-use areas (home vs core range), and relate these to the habitats they frequent. These results provide the first insight to the distribution, habitat use and preferences of green and hawksbill sea turtles in South African waters, although the description is currently limited to iSimangaliso, as these were the areas chosen by the turtles after they were tagged. Home ranges for loggerhead turtles which also use this region during their reproductive period, was also restricted to very specific locations in the Park.

Spatial Distribution

Loggerhead turtle home ranges have a high affinity to the coast during its internesting period; home ranges showed substantial individual variation in the offshore extent, but core range region for all individuals tended to be near the coast (Figures 2.2-2.4). This is further implied by the habitat preference index which shows a selection for a range of near-shore benthic habitats and an active avoidance to benthic habitat types further away from the coast. This aligns well with the establishment of loggerheads as coastal species that remain in proximity of nesting beaches during the internesting period (Hart et al. 2014b, Harris et al. 2015). The majority of tracked individuals show a core range affinity to the region just north of Bhanga Nek. This area is a recognised nesting hotspot for loggerheads in the region (Hughes 1974, Nel et al. 2013). This compact distribution could also provide evidence that this loggerhead population does not forage during the internesting period. While it is generally accepted that loggerheads do not forage during the internesting period, there have been cases reported to support the alternative where loggerhead turtles were found to forage during their internesting period (Hart et al. 2013).

Green turtles show a strong affinity to the nearshore area with individuals displaying site fidelity to the Sodwana region within their core ranges. Such aggregations and compact use of the coast by green turtles have been frequently noted suggesting a substantial carrying capacity with sufficient resources to be commonly shared (Brill et al. 1995, Renaud et al. 1996, Whiting and Miller 1998, Makowski et al. 2006). However, large variations in movement and home range patterns have also been recorded globally for green turtles, indicating a high degree of plasticity in behaviour (Carman et al. 2012, Christiansen et al. 2016). These variations in movement and home range have been described as adaptations to the local environmental conditions which includes factors such as resource availability and seasonal temperatures (Carman et al. 2012, Fujisaki et al. 2016).

Hawksbills, like green turtles, display a high affinity to the coast and site fidelity to the Sodwana region. There is considerable overlap in the distributions of tracked individuals at both the home and core ranges. These compact distribution patterns have also been reported for foraging hawksbills from other studies (Scales et al. 2011, Berube et al. 2012, Hart et al. 2012b). However, there have been reported cases of variability in distribution. As with green turtles, this variability in distribution indicates a plasticity in hawksbill life history (Gaos et al. 2011). The extensive offshore region, which includes a considerable portion of the Southwest Indian upper bathyal, found within the species buffer was not prevalent in any of the individual home or core ranges. This implies that these extended excursions offshore were irregularities in behaviour and may be caused by changes in local environmental conditions (e.g. cold water wedging in), or predator avoidance (Heithaus et al. 2008).

Home and Core ranges

Loggerheads occupy relatively small home ($\bar{x}$ = 111 ± 70 km^2) and core ($\bar{x}$ = 17 ± 12 km^2) ranges for most of the internesting period (mean track duration = 174 ± 60 days). There is considerable variation in home and core ranges of internesting loggerhead populations reported from other studies. The largest loggerhead internesting aggregation in the Gulf of Mexico had a mean core range of 62 ± 28 km^2 (Hart et al. 2013), while the smallest loggerhead internesting sub-population in the western Atlantic had a mean core range of 142 ± 117 km^2 (Hart et al. 2014a). The Mediterranean Greek island loggerhead population of Zakynthos had a mean core range of 10 km^2 with both breeding males and females restricted to the coastline (Schofield et al. 2010), similar to the results of the current study.

Green turtles were tracked for an average of 117 ± 47 days and utilised a mean home range area of 6.24 ± 5.23 km^2 in the Sodwana Bay region. A more intimate home (4.00 ± 1.74 km^2) and core (0.52 ± 0.27 km^2) range would be attained with the exclusion of the extensive movement from a single individual (ID 119363). The extensive movement of this individual may just be exploratory in nature as the core range still overlaps with other individuals of the species. There is considerable overlap in the core range of most green turtles, which is similar for six juvenile green turtles tracked along a near-shore reef in Southeast Florida (Makowski et al. 2006). These turtles displayed a compact mean core range of 0.49 ± 0.39 km^2. Green turtles from the Dry Tortugas, Florida and the Gulf of California, Mexico showed larger mean core ranges of 1.3 - 18.9 km^2 (Fujisaki et al. 2016) and 4.09 - 32.31 km^2 (Seminoff et al. 2002) respectively. Carman et al. (2012) demonstrated the vast plasticity in green turtle behaviour when subpopulations of juveniles from the southwest Atlantic revealed core ranges of 1176 - 4987 km^2. Due to the compact nature of home range areas used relative to the mean track distribution, it is inferred that this behaviour is a strong indication of residency to the region for the juvenile green turtles described in this study. Christiansen et al. (2017) used visual examinations to identify foraging ground areas by noting the cease in persistent directional travelling and the back and forth movement within a relatively restricted area. Therefore, it was concluded that juvenile green turtles in the current study can be classified as resident coastal foragers.

The three hawksbills in this study utilized a mean home range of 19 ± 18 km^2 and core range of 2 ± 2 km^2 over an average track duration of 262 ± 165 days. The home and core range area are more than halved by the exclusion of the extensive movements from a single individual, hawksbill 105314 (9.30 ± 0.17 km^2, 1.33 ± 0.39 km^2 respectively). Like the green turtle ID 119363, hawksbill ID 105314's movement may just be exploratory in nature because its core range still overlaps with other individuals of the species. These small home and core ranges, usually maintained around an area of 1 km^2, are well documented in the literature (van Dam and Diez 1998, Scales et al. 2011, Berube et al. 2012). These compact home ranges are usually attributed to the availability of abundant food resources and shelter in the region. However, larger variations in home ranges do occur, indicating plasticity in the behaviour of the species (Ferreira et al. 2018). These larger variations in home range are usually attributed to patchy distribution of resources, habitat configuration and life history stage (Hart et al. 2012b, Marcovaldi et al. 2012). Like green turtles, hawksbills can also be classified as resident coastal foragers due to their long-term high site fidelity to the Sodwana region.

Habitat Preference

Loggerhead turtles were encountered in a range of benthic habitats with their home and core ranges limited to nearshore, shallow habitats, while 'avoidance' was shown for benthic habitats further away from the coast. This observation supports the evidence that loggerheads, while in the study region, prefer coastal habitats and remain close to their nesting beaches during the internesting period (Hart et al. 2014b). The use of a wide variety of benthic habitat types within the near-shore region indicates that loggerhead turtles seemingly show no preference. This could potentially be attributed to the effect of minimal movement during the energetically demanding process of nesting and wanting to remain proximate to the nesting site.

Green turtles exhibited preference for a small range of sandy and reef habitats within their home and core ranges. In the core range, higher preference is directed to the sandy benthic habitat types with the Natal-Delagoa Estuarine Shore having the highest preference. Seasonally, this was also the case for juvenile green turtles from the southwest Atlantic that spent the most time foraging in estuarine areas (Carman et al. 2012). Most studies show foraging juvenile green turtles to be closely associated with sandy bottoms and reefs where food resources (such as algae and seagrass) and shelter (such as reef ledges) are abundant (Brill 1995, Makowsi et al. 2006). Patches of seagrass and algae do exist on these benthic habitats in the study region (R. Nel, pers. com), but its availability is sporadic and/or unmapped, so it is difficult to conclude the association between juvenile green turtles and their preference for sandy benthic habitats.

Hawksbill turtles had a strong preference for reef regions within their core range, in particular the Inshore and Shelf Edge Reefs. It is well established that hawksbill turtles show a strong affinity to reef habitats in which they forage and rest (Scales et al. 2011, Marcovaldi et al. 2012). Some studies have even made use of tools like acoustic telemetry in collaboration with satellite telemetry to reveal high resolution habitat utilization within these systems (Scales et al. 2011, Hart et al. 2012b). Hawksbill turtles showed almost equal preference for the Natal-Delagoa Dissipative-intermediate Sandy Coast and estuarine shore. This provides further evidence of hawksbill turtle plasticity and indicates that the species are not obligate coral reef inhabitants and can display variations in habitat use and diet (Bjorndal and Bolten 2010, Hart et al. 2012b).

Findings

The geographical split among the nesting and resident foraging species can be attributed to their respective ecological needs as indicated by the species' habitat preference within their respective home ranges. Green and hawksbill turtles would most likely exploit regions with more abundant food and available shelter, whereas loggerhead distribution may be more driven by hormonal cues facilitating the nesting process (Brazier, 2012). However, it may also be a function of sampling location and effort, as juvenile green turtles are regularly sited by snorkelling off Bhanga Nek, whereas hawksbills are very scarce at this location (pers. obs).

The overlap in home ranges of green and hawksbill turtles has important ecological implications for the region. Greens and hawksbills have been shown to co-exist in the same ecosystem while fulfilling different ecological roles within these systems. Green turtles are grazers which forage on algal turfs, while hawksbill turtles are browsers which forage on leathery macroalgae; both functional groups of grazers and browsers play a pivotal role in maintaining the healthy state of coral reefs (Goatley et al. 2012). The combined habitat use of these two species was inferred to be greater than that of reef fish in maintaining the reefs in which they occurred (Goatley et al. 2012). This level of functionality reinforces the notion of sea turtles as keystone species (Luschi et al. 2006). Considering this, the implications for the study region are profound, given the scale of home ranges exhibited and the deficiency of ecological data for green and hawksbill turtles at a population level.

The findings emphasise the need for more research for sea turtle species in the study region. A more robust sample size for tracked individuals would help further elucidate sea turtle distributions in terms of home and core ranges, as well as their preferences for certain habitats. Associated depth data would also help identify areas of use. Increased sample size is also especially important as there are associated errors in accuracy due to the nature of Argos tags. Other techniques such as diet and stable isotope analysis can be used to help complement satellite tracking data and provide a better picture of these animals' ecology.

2.6 Conclusion

The three species that occur within iSimangaliso Wetland Park showed a particular affinity to the area where they were tagged, i.e. two coastal locations, Bhanga Nek and Sodwana. The nesting loggerhead turtles display high site fidelity to the Bhanga Nek coast and remain in the inshore region proximate to the high nesting density "hotspot" region. The two foraging species, green and hawksbill turtles, show prolonged, high site fidelity to the Sodwana (Jesser Point) region and were initially thought to be transient and frequent the region using it only as a foraging/migration corridor. However, results from the current study indicates that both species are, in fact, coastal resident foragers in the iSimangaliso MPA with extreme local site fidelity.

The current research thus provides important spatial distribution data relevant to the conservation of these species. With the resident behaviour during the developmental phase it is necessary to protect resources also for these non-nesting turtle species within the MPA. The iSimangaliso Wetland Park, along the eastern seaboard of South Africa thus provides protection for nesting loggerhead and resident (mostly immature) green and hawksbill foraging sea turtles, with these residents contributing to the maintenance of healthy reefs and reef ecology.

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2.8 Supplementary Material

APPENDIX 1 Number of filtered points used to construct kernels with smoothing factor (h) for each individual

Species	ID	Number of location estimates used to construct kernels	h "smoothing factor"
Loggerhead	66387	38	0.008305
	66347	85	0.017839
	66312	137	0.008605
	66290	71	0.005365
	105319	101	0.01482
	105318	200	0.027155
	105317	222	0.025158
	105316	176	0.006213
	105315	522	0.030629
Green	119369	503	0.002608
	119368	1644	0.00683
	119363	451	0.00328
	119366	1826	0.001366
	119367	1457	0.00119
Hawksbill	105314	635	0.005721
	119362	1884	0.001435
	119370	755	0.002905

APPENDIX 2 Raw Preference Index (PI) of all individuals within the home (95 % UD) and core (50 % UD) ranges for loggerhead turtles

Benthic Habitat	**66387**		**66347**		**66312**		**66290**		**105319**		**105318**		**105317**		**105316**		**105315**	
	Home Range	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**
Delagoa Mixed Shore	0.97	1.74	0.97	1.26	1.10	1.53	1.24	1.36	0.93	1.43	0.65	1.08	0.87	1.35	1.19	1.93	0.93	1.26
Delagoa Very Exposed Rocky Coast	-	-	-	-	-	-	-	-	-	-	-	-	1.28	-	-	-	1.35	-
Natal-Delagoa Dissipative-Intermediate Sandy Coast	0.62	1.23	0.38	0.72	0.65	0.74	0.63	0.78	1.20	-	0.87	-	0.92	0.74	0.57	-	0.43	0.60
Natal-Delagoa Estuarine Shore	-	-	1.41	-	-	-	-	-	-	-	-	-	-	-	-	-	1.28	-
Natal-Delagoa Intermediate Sandy Coast	0.86	0.98	0.96	1.14	1.12	1.24	1.17	-	1.00	1.47	0.76	1.09	0.89	1.02	1.02	1.17	0.98	1.19
Natal-Delagoa Reflective Sandy Coast	0.84	-	1.09	-	0.85	-	1.00	-	1.04	-	0.74	0.97	1.14	1.11	-	-	1.19	-0.55
Delagoa Inshore Reef	0.88	1.62	0.93	1.28	1.10	1.59	1.19	1.73	1.08	1.31	0.75	0.87	0.95	1.24	1.02	1.55	0.92	1.26
Delagoa Sandy Inshore	0.85	1.04	0.81	0.65	1.02	0.83	0.87	1.09	1.03	1.18	0.76	0.92	0.98	1.00	0.88	1.35	0.94	0.70
Delagoa Shelf Reef	0.99	-	0.83	0.95	1.08	0.45	0.72	-	0.73	-	0.54	0.11	1.05	0.92	0.42	-	1.03	1.01
Delagoa Canyon	-	-	-	-	-	-	-	-	-	-	0.28	-	-	-	-	-	-	-
Delagoa Shelf Edge Reef	1.50	-	1.21	-	-	-	-	-	-	-	-0.96	-	-0.26	-	-	-	0.59	-
Southwest Indian Upper Bathyal	-	-	-	-	-	-	-	-	-1.89	-	-0.82	-	-	-	-	-	-	-
Delagoa Sandy Shelf	1.04	0.50	0.98	1.01	0.97	0.74	1.03	0.43	0.88	0.91	0.65	0.94	0.95	0.96	0.91	-1.30	1.04	1.00
Delagoa Sandy Shelf Edge	-0.16	-	0.28	-	-	-	-0.67	-	0.22	-	0.61	0.47	0.03	-	0.43	-	-0.41	-

APPENDIX 3 Raw Preference Index (PI) of all individuals within the home (95 % UD) and core (50 % UD) ranges for green turtles

Benthic Habitat	**119369**		**119368**		**119363**		**119366**		**119367**	
	Home Range	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**
Delagoa Mixed Shore	0.59	1.08	0.74	1.21	0.27	0.95	0.58	0.98	-1.31	-
Natal-Delagoa Dissipative-Intermediate Sandy Coast	0.75	-	0.44	-	0.66	0.18	0.60	-	0.89	-
Natal-Delagoa Estuarine Shore	1.24	1.99	1.79	2.47	0.75	1.47	1.24	1.83	-	-
Natal-Delagoa Intermediate Sandy Coast	0.54	0.73	1.05	0.98	0.35	0.68	0.55	0.94	-3.08	-
Delagoa Inshore Reef	0.63	0.62	0.65	0.31	0.25	0.48	0.57	0.65	0.68	0.92
Delagoa Sandy Inshore	0.21	-	-0.31	-	0.40	0.42	0.34	-	-0.45	-
Delagoa Shelf Reef	-1.16	-	-	-	0.18	-	-0.70	-	0.17	-1.19
Delagoa Canyon	-	-	-	-	-0.61	-	-	-	-	-
Delagoa Shelf Edge Reef	-	-	-	-	-	-	-	-	-	-
Delagoa Sandy Shelf	-0.59	-	-	-	-0.13	-	-0.43	-	-0.55	-
Delagoa Sandy Shelf Edge	-	-	-	-	-	-	-	-	-	-

APPENDIX 4 Raw Preference Index (PI) of all individuals within the home (95 % UD) and core (50 % UD) ranges for hawksbill turtles

Benthic Habitat	**105314**		**119362**		**119370**	
	Home Range	**Core Range**	**Home Range**	**Core Range**	**Home Range**	**Core Range**
Delagoa Mixed Shore	0.56	0.81	0.71	-	-	-
Natal-Delagoa Dissipative-Intermediate Sandy Coast	0.73	1.09	1.27	0.67	1.28	-
Natal-Delagoa Estuarine Shore	1.11	1.77	1.74	-	-	-
Natal-Delagoa Intermediate Sandy Coast	0.02	0.81	0.66	-	-0.80	-
Natal-Delagoa Reflective Sandy Coast	-	-	-	-	-	-
Delagoa Inshore Reef	0.66	1.11	1.10	1.44	1.05	1.34
Delagoa Sandy Inshore	0.53	0.62	0.28	-	0.28	-
Delagoa Shelf Reef	0.80	0.66	1.00	0.44	1.08	1.00
Delagoa Canyon	0.17	-	-	-	-1.77	-
Delagoa Shelf Edge Reef	0.75	-	-	-	-	-
Southwest Indian Upper Bathyal	-	-	-	-	-	-
Delagoa Sandy Shelf	0.64	0.45	0.03	-1.79	0.24	-1.30
Delagoa Sandy Shelf Edge	-0.20	-	-	-	-	-

Chapter 3: Diets and isotopic niches for three hard-shelled sea turtles in subtropical South Africa

3.1 Abstract

Understanding feeding ecology of species and the trophic interactions throughout an ecosystem provides insights into understanding ecosystem resilience, which is especially relevant under prevailing natural and human-induced environmental change. The aim of this study is to determine and quantify the diet and isotopic niche of loggerhead, green and hawksbill sea turtles along the eastern seaboard of SA using stomach content and stable isotope analyses. Stomachs of loggerhead (n=27), green (n=13) and hawksbill turtles (n=2) contained prey items following their respective conventional diets. Loggerhead diet mainly constituted crustaceans and molluscs. Green turtle diet comprised mainly chlorophyta and rhodophyta, but tunicates and cnidarians were also found frequently in their diet. While hawksbill turtles sample size was low, individuals contained poriferans and other benthic invertebrates. Individual specialization was noted for 4 loggerhead individuals. Stable isotope data revealed a geographic split in green turtle populations, with one population foraging at a higher trophic level and closer inshore. Species within the same geographic region appear to forage within a similar trophic level.

3.2 Introduction

The seemingly simple act of animal feeding, which includes the processes of finding, eating, and digesting food is a highly complex animal function directed by behavioural traits, morphology, physiology and ecology i.e., the interactions among predators, prey and competitors (Brodeur et al. 2017, Goatley et al. 2012, Lazar et al. 2011). An organism's diet provides the essential nutrition which affects the individuals' life history and demographic characteristics such as growth rate, migration timing and reproductive success (Bjorndal 1997, Carman et al. 2013, Jones and Seminoff 2013), whereas feeding ecology determines the distribution, abundance and demographics of individuals and so stocks/populations/species (Brodeur et al. 2017). Understanding feeding ecology of species and the trophic interactions throughout an ecosystem provides insights into understanding ecosystem resilience, which is especially relevant under prevailing natural and human-induced environmental change (Bjorndal 1985). It is expected that sea turtles play an important role in ecosystem functioning, but it is difficult to generalise these roles as there are major differences in the foraging ecology of these species.

Sea turtles have a complex life history, with an ontogenetic shift in diet when they recruit as early juveniles from the oceanic zone to the neritic zone (Bolten 2003). Conventionally, loggerhead turtles are carnivores, feeding on an extensive range of benthic invertebrates, at shallow to moderate depths from both rocky and sedimentary habitats (Godley et al. 1997, Plotkin 1993). Green turtles are considered to be primarily herbivorous foraging on seagrasses and algae (Mortimer 1982), mainly in shallow water from intertidal depths of 10 meters (Bjorndal 1997). Hawksbill turtles feed on primarily benthic invertebrates and are considered to be almost exclusively spongivorous (Meylan 1988, Ferreira et al. 2018). However, there is growing evidence of foraging behaviour plasticity at various levels of organisation and at different spatial scales for all these species (Figgener et al. 2019). This necessitates an investigation into "local" turtle populations with the concomitant dietary preferences, to understand their functional role in proximate and distant ecosystems.

The South West Indian Ocean (SWIO) hosts 5 species of sea turtles, all regarded as threatened (www.IUCNredlist.org): loggerhead turtles (*Caretta caretta*), green turtles (*Chelonia mydas*), hawksbill turtles (*Eretmochelys imbricata*), leatherback turtles (*Dermochelys coriacea*) and olive ridley turtles (*Lepidochelys olivacea*). In the SWIO, green and hawksbill turtles are the most abundant and widely distributed species, while loggerhead and leatherback turtles are the most common in South African waters but otherwise rare in the SWIO region (Bourjea 2015). All 5 species are found in South Africa: two nesting species, loggerhead and leatherback turtles; two “resident” foraging species, green and hawksbill turtles (Chapter 2); and one vagrant species, the olive ridley turtle. With the exception of leatherback turtles, the distribution of the other species all falls within their southern-most ranges (Wallace et al. 2010). To date, only one study has focussed on the diets of sea turtles present in South Africa (Hughes 1974), with no further feeding ecology investigations.

Hughes (1974) described the diet of loggerheads at different life stages; the stomach content of stranded hatchlings appeared to be dominated by bluebottle fragments, *Physalia sp.*, with *Janthina janthina* shells also present as well as plastic beads, bird feathers and tree bark, suggesting that they are opportunistic or indiscriminate foragers. The diet of sub-adult and adult loggerheads were described in three size class categories (50 - >80 cm) with pelagic prey items still dominating the diet of smaller sized individuals with a switch over to benthic prey items in the larger individuals. These stomach contents were dominated by benthic molluscs *Bufonaria crumenoides*, and *Ficus subintermedius*. Hermit crabs were also frequently present, but it was uncertain if these were consumed purposely or mistaken for molluscs. However, it is commonly part of the diet. Bivalves like *Perna perna* were also found to be commonly ingested species. One large individual also contained the scutes of a hatchling loggerhead. It was recorded as the only incidence of (accidental or intended) cannibalism. The diet of hawksbills was only generically described as being dominated by sponges (Hughes 1974), whereas shark net-caught green turtles had stomachs dominated by *Gelidium*, *Codium* and *Caulerpa* spp. A single individual stranded to the north in Mozambique had a different complement of species in the stomach (Hughes 1974).

Stomach content analysis is a common method used in dietary studies and can provide valuable insight into (short-term) foraging ecology (Boyle and Limpus 2008, Polito et al. 2011). Stomach content analysis is a direct approach, through removing and identifying prey items from the gut of turtles by dissection of dead turtles or through gastric lavages of live individuals. Stomach content analysis, however, provides a snapshot of the animal’s last meal, frequently identified from hard, indigestible parts such as bones, shells, scales, and is thus likely to underestimate the presence of soft-bodied prey (Polito et al. 2011), or full dietary spectrum of prey items.

With technological advances, stable isotope analysis, has become a popular, widely used tool in ecology and is also used in trophic ecology. Unlike stomach content analysis it provides a long-term signal (weeks to months) on the trophic level and allows to infer trophic interactions. It is therefore complementary to the information obtained from stomach content analysis (Burkholder et al. 2011). Stable isotope ratios of nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) and carbon ($^{13}C/^{12}C$; $\delta^{13}C$) are commonly used elements for dietary investigations and to infer trophic position. Through the digestion of organic matter, isotopic fractionation of these two elements occur, resulting in the enrichment of the heavier isotope in the consumer (Boyle and Limpus 2008). The enrichment factor between trophic levels for carbon is ~1% and ~3–5% for nitrogen. The carbon isotopes ($\delta^{13}C$) is typically used to trace an animal's food source or habitat where a higher $\delta^{13}C$ is more representative of oceanic regions, and lower $\delta^{13}C$ of neritic regions (Ferreira et al. 2018). $\delta^{15}N$ is used to infer trophic position, as consumers at a higher trophic level typically display a higher $\delta^{15}N$ value (Godley et al. 1998). By plotting $\delta^{13}C$ vs. $\delta^{15}N$ of turtles and their respective prey species, ecosystem trophic levels can be elucidated and prey that was previously underestimated in stomach content analysis can be accounted for.

The aim of this study is to determine and quantify the i) diet and ii) isotopic niche of loggerhead, green and hawksbill sea turtles along the eastern seaboard of SA. This will be done by combining the use of stomach content and stable isotope analysis. Prey items found in the stomach content will be identified and quantified to their relative abundance, and the combined diet per species described and contrasted with that of other species. Stable isotope analysis of sea turtle epidermal tissue will help elucidate the contribution of these and other potentially underestimated or undetected prey items in the diets of these animals. This will provide an indication of each species' longer-term isotopic niche. It is hypothesised that respective sea turtle species from iSimangaliso and in the central and south of KZN will comply with their conventional diets, but with species-specific prey distributed along the east African seaboard. It is thus also predicted that green, hawksbill and loggerhead turtles will occupy different isotopic niches across different trophic levels, and fulfil different ecological roles.

3.3 Materials and Methods

Ethics Statement & Permits

Ethics clearance for the capture and collection of skin biopsies from loggerhead, green and hawksbill turtles from along the east coast of South Africa (inclusive of those animals sampled within the iSimangaliso Wetland Park) were obtained from the Nelson Mandela University Animal Ethics Committee: A13-SCI-ZOO-012. Permits to work on and/or to collect samples from within the iSimangaliso Wetland Park were issued by the Department of Environmental Affairs (DEA), Republic of South Africa

(RES2014/64). Ethics approval for the retrieval of stomach contents was not required as these samples were obtained from study specimens which were fatally captured bycatch in the KwaZulu-Natal Sharks Board's bather protection nets.

Study Area & Sample Collection

The iSimangaliso Wetland Park, a UNESCO world heritage site, is a known hotspot for nesting loggerhead and leatherback turtles, as well as foraging green and hawksbill turtles (Hughes 1974, Nel et al. 2013, Bourjea 2015). These turtles are now protected within the newly established iSimangaliso Marine Protected Area (MPA), which extends from the South Africa-Mozambique border in the north, to Cape St Lucia Lighthouse in the south, extending offshore for ± 90 kms and to a maximum depth of almost 2000 m (Government Gazette 42478).

The KwaZulu-Natal (KZN) Sharks Board currently implements the combined use of nets and drumlines at 37 beaches along the east coast of South Africa, as part of the KZN bather protection programme (see Dicken et al. (2017) and www.shark.co.za for operation specifications). The sea turtle catches from these nets seem to have minimal impact on turtle populations from the Western Indian Ocean and is thus considered negligible and sustainable (Brazier et al. 2012). Sea turtle stomach contents were retrieved from incidental fatally captured animals from the KZN bather protection nets which range from Zinkwazi to Port Edward (Figure 3.1) during the period 2007-2016. Turtles will be distinguished as North, when sampled from iSimangaliso and Central-South, when sampled from the bather protection nets

Skin biopsies for stable isotope analysis were opportunistically collected from all animals along the eastern seaboard of South Africa; this included active captures on SCUBA, nesting female loggerheads, and fatally stranded individuals from the shark nets. Nesting turtles as well as those caught on SCUBA were specifically captured in the north from within the iSimangaliso Wetland Park. Nesting loggerheads were specifically targeted at their main nesting beach aggregation, 10-16 km south of the Kosi Bay estuary mouth (Nel et al. 2013). Turtles were caught on SCUBA off the coast of Sodwana, along a network of reefs

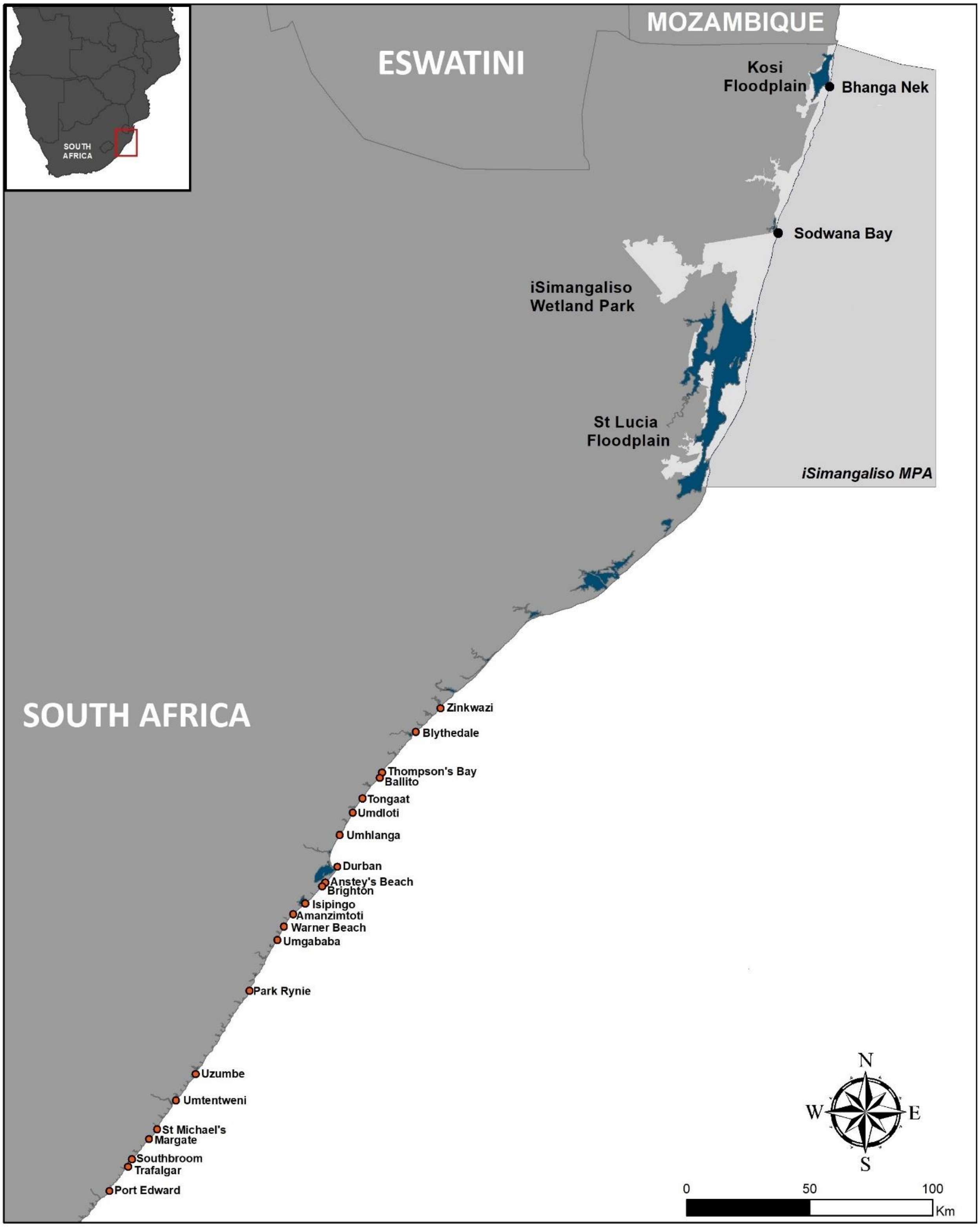

Figure 3.1 Study map indicating regions of sampling sites of both stable isotope and stomach content collection. Orange dots show locations at which turtles were fatally captured in the KZN Sharks Board bather protection nets, from which stomach contents were subsequently collected. Skin biopsies for stable isotope analysis were collected from those fatally captured turtles, as well as from nesting loggerheads (Bhanga Nek) and turtles caught on SCUBA (Sodwana Bay). Bhanga Nek and Sodwana Bay fall within the iSimangaliso MPA. Terrestrial reserves of the park are also displayed (light grey).

– a popular ecotourist dive site that sea turtles have been known to frequent.

All sea turtles used in this study were subjected to standard morphometric measurements; these included either or in combination: 1) minimum curved carapace length (CCL) and width (CCW), and 2) minimum straight carapace length (SCL) and width (SCW) as described by Wyneken and Witherington (2001).

Laboratory Processing & Data Analyses

Stomach content analysis

Stomachs were collected from loggerhead (n=27), green (n=13) and hawksbill turtles (n=2) and were initially stored frozen and later thawed out prior to processing. Stomachs were emptied of their content and rinsed through a 2 mm mesh sieve and stored in 70 % ethanol, where it was later processed for identification to the lowest possible taxonomic level using dissecting and compound microscopy.

Prey items were quantified using Frequency of Occurrence (%FO) and Volume (Vi). Volume was measured using the water displacement method in a graduated cylinder (Williams et al. 2013). An Index of Relative Importance (IRI, and %IRI) based on the combination of volume and frequency of occurrence was calculated to give a better indication of prey contribution to the diet in terms of importance (Williams et al. 2013). IRI and %IRI were calculated both at a wider categorical taxon level and at a species level. Therefore, it is possible to determine both the most important larger grouping taxon prey group, and the most important/preyed upon species within that taxon (Appendix 1, 2, 3 and Figure 3.3).

$$\%FO = \left(\frac{Number\ of\ stomachs\ prey\ item\ found\ in}{Total\ number\ of\ stomachs}\right) \times 100$$

$$IRI = \frac{100(\%FOVi)}{\sum_{i=1}^{n}(\%FOVi)}$$

$$\%IRI = \left(\frac{IRI}{\sum_{n=1}^{n} IRI}\right) \times 100$$

Cumulative prey curves were plotted to determine if a sufficient sample size of stomach contents was examined. These curves cumulatively build on the number of new prey items found as the number of samples (whole stomachs) increase. If a sufficient number of stomachs have been sampled, then the curve should approach an asymptote, where the number of new prey items remain constant (Ferry and Cailliet 1996). The order in which the stomachs were analysed was randomized five times and the mean number of those five randomizations were plotted with standard deviations.

Cluster and non-metric Multidimensional Scaling (nMDS) ordination plots were constructed in PRIMER (PRIMER-E Ltd., Ivybridge, UK) using all prey items from the three turtle species. Cluster analysis aims to group together samples that are more similar to each other using a dendrogram, while nMDS constructs a two-dimensional "map", placing similar samples more proximate to each other (Clark and Warwick 1994). Data were pre-treated used fourth root transformations and similarity matrices were constructed using the Bray-Curtis similarity coefficient. Individuals which contained no stomach content or only a single dietary item in their gut were excluded from analyses to depict a clearer plot (loggerhead turtles, n=13; green turtles, n=13; hawksbill turtles, n=2).

Stable isotope analysis

Epidermal tissue was collected from the anterior flippers (between the scales) of sea turtles using a 6 mm biopsy punch. Samples were stored in 70 % ethanol as recommended for sea turtles (Barrow et al. 2008) and were later processed by wiping down each sample with an alcohol swap and separating the epidermis from the underlying dermis, where possible. These samples were subsequently rinsed in distilled water and dried at 60 °C for 24-48 hours. Samples were then ground to a homogeneous powder and loaded (0.5±0.05 mg) in 6 x 4 mm tin capsules which were rolled and processed for mass spectrometry of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures. Samples were processed at the Stable Isotope Analysis Laboratory of the Mammal Research Institute in Pretoria, South Africa. Samples were analysed by continuous-flow isotope ratio mass spectrometry using a Flash EA 1112 Series elemental analyser connected via an interface (Conflo III) to a Thermo Fisher Scientific Delta V Plus isotope ratio mass spectrometer. Calibrated laboratory standard (Merck Gel; 0.2±0.02 mg) and blank samples were run after every 12 unknowns. Isotopic ratios for carbon ($^{13}C/^{12}C$; $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) are expressed in delta notation (δ) in parts per thousand (‰) as:

$$\delta\, R\, ‰ = \left(\left[\frac{R_{\text{sample}}}{R_{\text{standard}}}\right] - 1\right) \times 1000$$

where R is the heavy to light isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). The standard material is Vienna Pee Dee Belemnite (PDB) limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$.

Lipid and tissue-type testing

Paired-sample t-tests were performed to determine if lipid extractions for epidermal tissue samples were necessary. Lipid extraction was done using a chloroform/methanol (2:1) solution (Revelles et al. 2007, Bergamo et al. 2016). Hawksbills were excluded from this analysis as sample size was insufficient, however graphic representation for available data are still presented (Appendix 5). The difference between the control and treatment for all species were normally distributed ($p > 0.05$).

In most cases the amount of epidermal tissue present from the biopsy sample was insufficient to process for stable isotope analysis. These samples were then treated as "whole" samples with both epidermal and the underlying dermal tissue present. Lipid extraction was done for all whole tissue samples. Independent sample t-tests, or in cases where assumptions were not met, Mann-Whitney U tests were performed to establish any significant differences in carbon and nitrogen between epidermal and whole tissue samples. These tests were performed at multiple spatial scales; both across the entire study region, as well as within specific proximate grouped regions (iSimangaliso Wetland Park in the north and the KZN Shark-net samples from central and southern KZN) to accommodate for spatial signature variation, for each species. The results concluded that there were no significant differences in carbon and nitrogen between epidermal and whole tissue samples at all spatial levels within the study region ($p > 0.05$) for all species. All skin biopsy samples can therefore be considered comparable regardless of tissue type.

Geographic intra- and interspecies comparisons

MANCOVAs were run to test for statistically intraspecific significant differences in carbon and nitrogen stable isotope signatures, while controlling for size (CCL) between iSimangaliso and shark-net samples. This was done to determine if each species could, in fact, be considered as a single unit consisting of individuals from both locations, spanning along the length of KwaZulu-Natal. A further split in the sharks-net captures between central and southern areas was also considered but was not possible due to limited sample sizes. Hawksbill turtles were also excluded from this analysis due to low sample size ($n=2$ in the shark-net catches). All assumptions were satisfied for MANCOVAs ($p > 0.05$).

MANOVAs were subsequently conducted to determine if there were interspecific differences in carbon and nitrogen signatures within each site. Hawksbill turtles were excluded from the shark-net MANOVA due to low sample size ($n=2$ in the shark nets). Pillai's trace was interpreted for both MANOVAs at each site as assumptions for equality of covariance (Box's test; $p=0.005$) and multicollinearity

(Pearson correlation = -0.369) were violated for the shark-net and iSimangaliso sites respectively. Scheffe post-hoc tests for unequal sample size were interpreted where Pillai's trace was found to be significant ($p<0.05$). MANCOVAs and MANOVAs were conducted in IBM SPSS Statistics (Version 25).

Isotopic niche

The isotope data were then expressed in the context of isotopic niche width for all species in the iSimangaliso and shark-nets using metrics based in a Bayesian framework (Stable Isotope Bayesian Ellipses in R, ie. SIBER; Jackson et al. 2011). Hawksbill turtles from the shark-nets were excluded from this analysis because of insufficient samples size (n=2). Standard Ellipse Area adjusted for small sample size (SEA_C; $n < 10$), were performed to ascertain the niche area occupied for each species from respective sites (Jackson et al. 2011). Each ellipse is obtained through Bayesian inference and is by default, set to encompass 40% of the data and is insensitive to sample size (Jackson et al. 2011, Ferreira et al. 2018). SIBER analyses were performed in R 3.4.3 (R Core Team 2017) using the "SIBER" package.

3.4 Results

Stomach content analyses

A total of 27 loggerhead turtle stomachs were analysed (CCL range: 69-89 cm), of which 11 (41%) were empty. Species diversity of 58 prey items were identified (Appendix 1), of which 50 could be attributed to an identifiable taxon. Loggerhead diet mainly constituted crustaceans (41%) and molluscs (39%). The species that ranked the highest in terms of relative importance (%IRI) within the crustacean and molluscan taxa was *Planes minutus* (24%) and *Bufonaria cf. crumena* (6%). Other taxa that contributed to loggerhead diet were tunicates (7%), tube worms (3%), perciformes (2%) and echinoderms (1%). Trace amounts of cnidarians, algae and poriferans were also found (< 0.1 %IRI). Pollutants including plastic fragments occurred in 19% of loggerhead turtle stomachs. The broad diet retrieved from the 16 stomachs were not sufficient to describe a comprehensive loggerhead diet as the prey diversity curve did not reach an asymptote (Figure 3.2). Interestingly, from the hierarchical cluster analysis and nMDS ordination, all loggerhead turtles apart from four individuals clustered together, suggesting strong overlap in the prey items which are different from those found in other turtle species. Two of the four individuals both contained the highest displacement volume (Vi) for *Planes minutus* (the Columbus crab symbiont) while the other two contained the highest volume for the gastropod, *Bufonaria cf. crumena*.

Table 3.1 Metadata of individuals of the respective species sampled for stomach content analysis. An indication of the two most common prey items are given for individuals based on volume.

Species	No	Turtle ID	Location	CCL	SCL	Sex	Most abundant prey item (by volume)	
							Group taxon	Species
Loggerhead turtle (*Caretta caretta*)	1	Unknown 1	-	-	-	U	Cnidaria, Tunicata	?Physalia sp. 1, ?Aplousobranchia or ?Phlebobranchia
	2	Unknown 2	-	-	-	U	Crustacea, Mollusca	*Planes major, Janthina janthina*
	3	ST 14009	St Michaels	-	70.0	U	Perciformes, Crustacea	*Liza richardsonii, Ovalipes trimaculatus*
	4	UMG 32	Umgababa	85.1	-	U	Mollusca, Echinodermata	*Bufonaria cf. crumena,* Unidentified Asterozoan ossicles
	5	BAL 69	Ballito	-	-	U	Crustacea, Tunicata	*Planes major, ?Polyandrocarpa* sp.
	6	BAL 130005	Ballito	-	77.6	F	Mollusca, Tube worm	Unidentified Pteriidae sp. 3, Unidentifed tube worm casing
	7	TB 151	Thompson's Bay	-	86.0	M	Mollusca	*Bufonaria cf. crumena*, Unidentified Gastropoda tissue
	8	AMA 13001	Amanzimtoti	-	80.0	M	Tube worm, Echinodermata	Unidentifed tube worm casing, *?Marthasterias glacialis*
	9	TON 13004	Tongaat	-	80.0	F	Crustacea	Unidentified Dromiidae sp. 1, Unidentified Mojoidea sp. 1
	10	BRI 13005	Brighton Beach	-	70.0	M	Tube worm, Pollutant	Unidentified tube worm casing, Synthethic fiber
	11	PAR 136	Park Rynie	89.9	83.0	F	Tunicata	*Polycarpa aff. Insulsa*
	12	UMD 16001	Umdloti	84.4	79.3	F	Mollusca	Unidentified Gastropoda shell fragments, Unidentified Bivalvia sp. 8
	13	UMD 85	Umdloti	69.4	68.0	F	Mollusca	Unidentified Pteriidae sp. 4
	14	UMH 138	Umhlanga	-	72.0	F	Mollusca	Unidentified Bivalvia sp. 9*
	15	DUR 738	Durban	-	-	U	Other, Mollusca	Unidentifed animal matter, Unidentified Bivalvia sp. 6
	16	DUR 14085	Durban	-	83.0	M	Other	Stones, Unidentified animal matter
	17	DUR 684	Durban	89.4	-	F	Empty	Empty
	18	UMT 13004	Umtentweni	-	72.4	M	Empty	Empty
	19	ISP 13001	Isipingo	-	84.0	F	Empty	Empty
	20	BAL 13008	Ballito	-	76.2	F	Empty	Empty
	21	MG 13014	Margate	-	75.0	M	Empty	Empty
	22	DUR 864	Durban	75.6	78.0	F	Empty	Empty
	23	AMA 174	Amanzimtoti	81.2	-	F	Empty	Empty

	24	BAL 74	Ballito	77.2	74.0	F	Empty	Empty
	25	AMA 137	Amanzimtoti	72.9	70.7	M	Empty	Empty
	26	DUR 899	Durban	78.2	73.2	F	Empty	Empty
	27	DUR 732	Durban	-	-	U	Empty	Empty
Green turtle (*Chelonia mydas*)	1	ZIN 13020	Zinkwazi	-	66.5	F	Chlorophyta, Rhodaphyta	*Caulerpa filiformis*, *Rhodymenia natalensis*
	2	ST 133	St Michaels	48.4	45.1	F	Rhodaphyta, Chlorophyta	*Gelidium Pteridifolium*, *Codium* sp. 1
	3	ISP 17	Isipingo	107.2	84.0	M	Chlorophyta	*Caulerpa filiformis*, *Codium* sp. 3
	4	TRA 39	Trafalgar	57.2	57.0	F	Chlorophyta	*Codium* sp. 3, *Caulerpa filiformis*
	5	UMZ 37	uMzumbe	48.0	47.0	F	Rhodaphyta	*Gelidium pteridifolium*, *Hypnea* sp. 1
	6	TRA 40	Trafalgar	57.8	57.0	M	Chlorophyta	*Caulerpa filiformis*, *Codium* sp. 1
	7	MG 119	Margate	66.6	65.2	M	Chlorophyta, Rhodaphyta	*Codium* sp. 1, *Gelidium pteridifolium*
	8	ZIN 101	Zinkwazi	72.2	71.2	F	Chlorophyta	*Codium* sp. 1, *Caulerpa filiformis*
	9	SOB 14003	Southbroom	-	72.0	U	Chlorophyta	*Codium platylobium*, *Codium* sp. 1
	10	MG 13004	Margate	-	60.0	F	Chloropyhta	*Caulerpa filiformis*, *Codium* sp. 1
	11	ANS 15010	Anstey's Beach	66.5	66.3	F	Chlorophyta, Rhodaphyta	*Codium* sp. 1, *Gelidium pteridifolium*
	12	BLY 14001	Blythedale	-	81.0	U	Chlorophyta, Tunicata	*Caulerpa filiformis*, ?*Appendicularia* sp.
	13	BAL 12006	Ballito	39.7	33.9	M	Chlorophyta	*Caulerpa filiformis, Codium* sp. 1
Hawksbill turtle (*Eretmochelys imbricata*)	1	WAR 1302	Warner Beach	37.2	32.1	F	Porifera	Order: Astrophorida, Hadromerida
	2	PE 68	Port Edward	48.0	46.2	F	Other, Crustacea	Unidentified animal matter, Unidentified Brachyura sp.

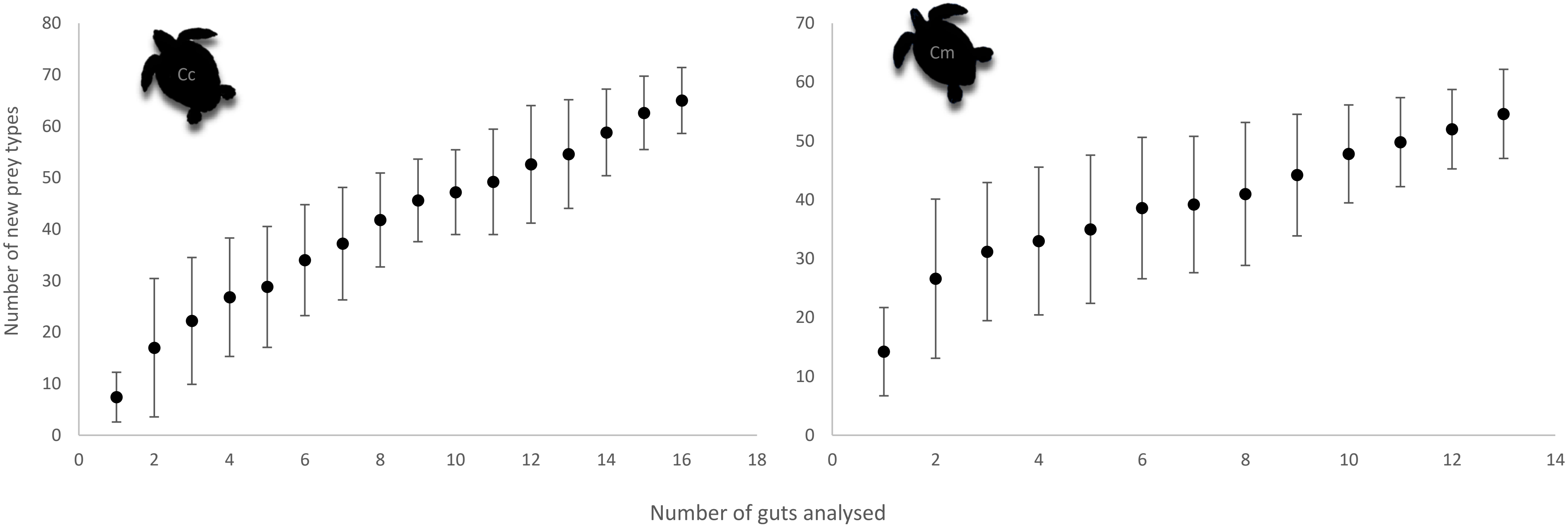

Figure 3.2 Randomized cumulative prey curves of fatally captured loggerhead (n=16) and green (n=13) turtles in the KZN bather protection nets. Hawksbill turtles were excluded from this analysis due to small sample size (n=2).

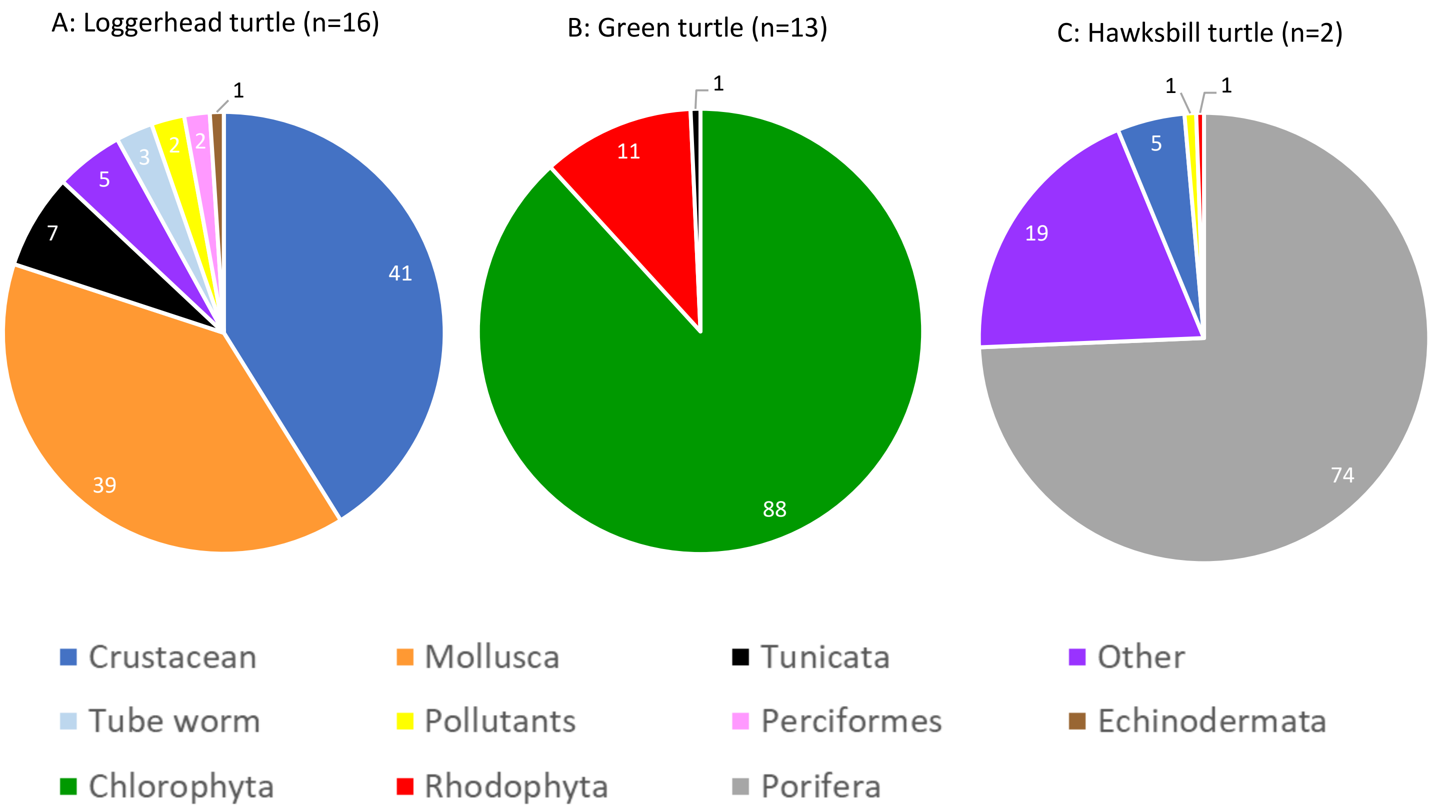

Figure 3.3 Summary data indicating the dietary composition of loggerhead (A), green (B) and hawksbill (C) turtles along the eastern seaboard of South Africa. Numbers indicate percentage contribution in terms of relative importance to the overall diet (%IRI).

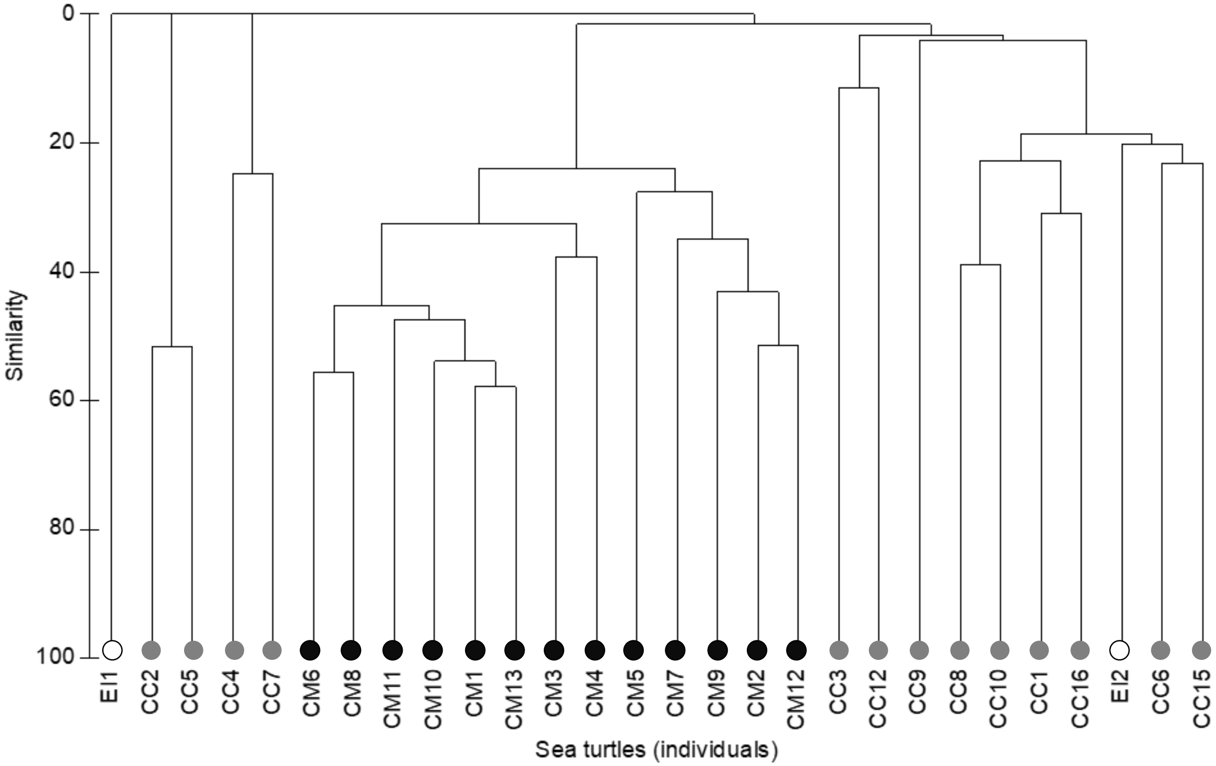

Figure 3.4 Dendrogram for hierarchical clustering of loggerhead (Cc), green (Cm) and hawksbill (Ei) sea turtles using group-average linking of Bray-Curtis similarities calculated from fourth square rooted diet volume data. Numbers next to species code are representative of each individual (Table 3.1)

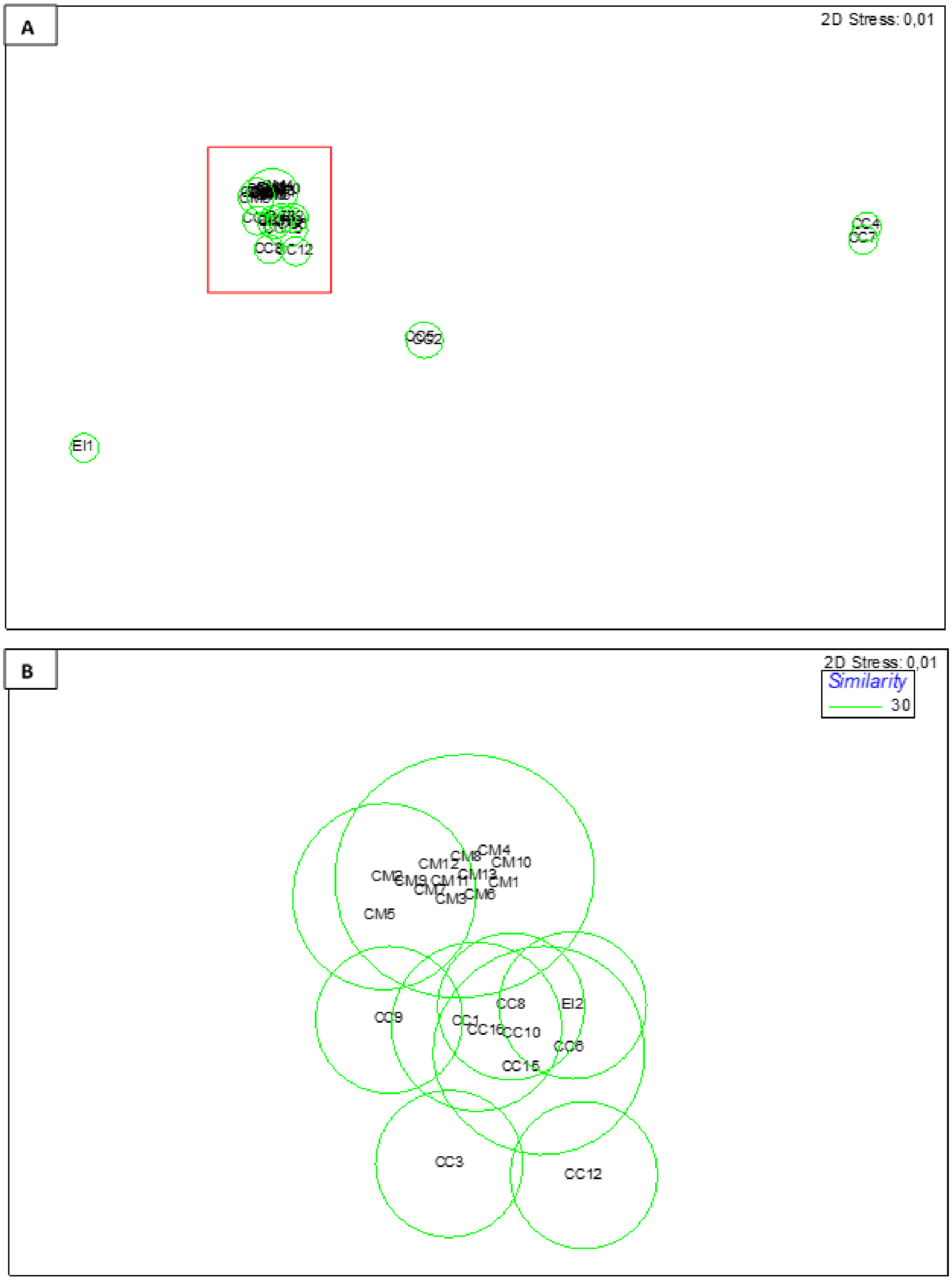

Figure 3.5 MDS ordinations of loggerhead (Cc), green (Cm) and hawksbill (Ei) sea turtles based on fourth squared root transformed diet volume data and Bray-Curtis similarities. **(A)** Overall ordination map **(B)** Focused ordination of bulk similarity cluster.

The stomach contents of 13 green turtles were analysed (CCL range: 39-107 cm), all of which contained a substantial amount of prey items in the gut. A species diversity of 58 prey items was found (Appendix 2), of which 54 could be categorized into an identifiable taxon. Green turtle diet comprised mainly of chlorophyta (88%) and rhodophyta (11%) (Figure 3.3). Within these taxa *Caulerpa filiformis* (49%) and *Codium* sp. 1 (20%) had the highest chlorophyta %IRI, while *Gelidium pteridifolium* (7%) had the highest rhodophyta %IRI. Tunicates, cnidarians and plant material were present in trace amounts (< 1 %IRI). Although total pollutant displacement volume (Vi) was low (2.10 ml), plastics and other inorganic pollutants were found in 46% of green turtle stomachs. The nMDS ordination and hierarchical cluster analysis does not indicate much dissimilarity amongst green turtle diet, indicating quite a homogenous diet across individuals. However, the cumulative prey curve did not reach a horizontal asymptote, indicating a diverse diet relative to the number of green turtles sampled, and that a higher number of green turtle stomachs will give a better indication of the diet.

Only two individuals of hawksbill turtles (CCLs: 37 and 48 cm) were available for diet analysis. Hawksbill turtles had a species diversity of 7 prey items in their diet (Appendix 3), of which 5 could be categorized into an identifiable taxon. Poriferans (74%) had the greatest %IRI for hawksbill turtle diets. Astrophorida (52%) and Hadromerida (19%) had the highest %IRI within the poriferan taxon. The hierarchical cluster analysis and nMDS ordination plots completely separated these two individuals based on their diet, indicating a high level of dissimilarity.

Stable isotope analyses

A total of 25 loggerhead turtle skin samples (CCL range: 57-99 cm) was analysed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes signatures. In iSimangaliso (n=17), loggerhead turtles had a $\delta^{13}C$ range of -17.9 – -9.3‰ (-14.5±2.3‰) and a $\delta^{15}N$ range of 6.9 – 13.0‰ (9.5±1.5‰). Loggerhead turtles from the shark nets (n=8) had a $\delta^{13}C$ range of -16.4 – -14.5‰ (-15.3± 0.6‰) and a $\delta^{15}N$ range of 7.8 – 12.9‰ (10.4±1.8‰).

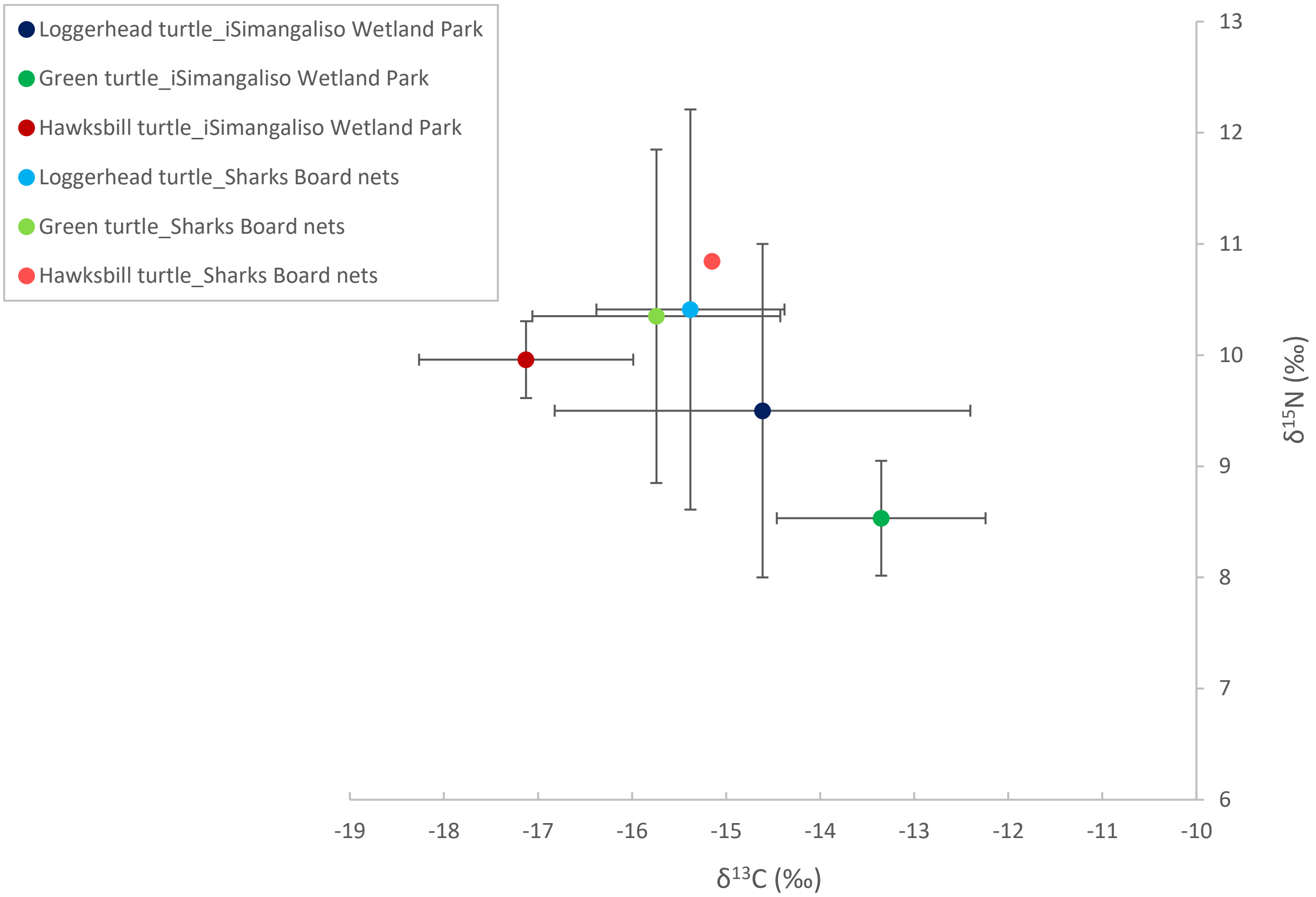

Figure 3.6 Trophic position of different species of sea turtles sampled from within the iSimangaliso Wetland Park and animals caught in the KZN Sharks Board nets. Points are plotted as mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) for the respective species from each site.

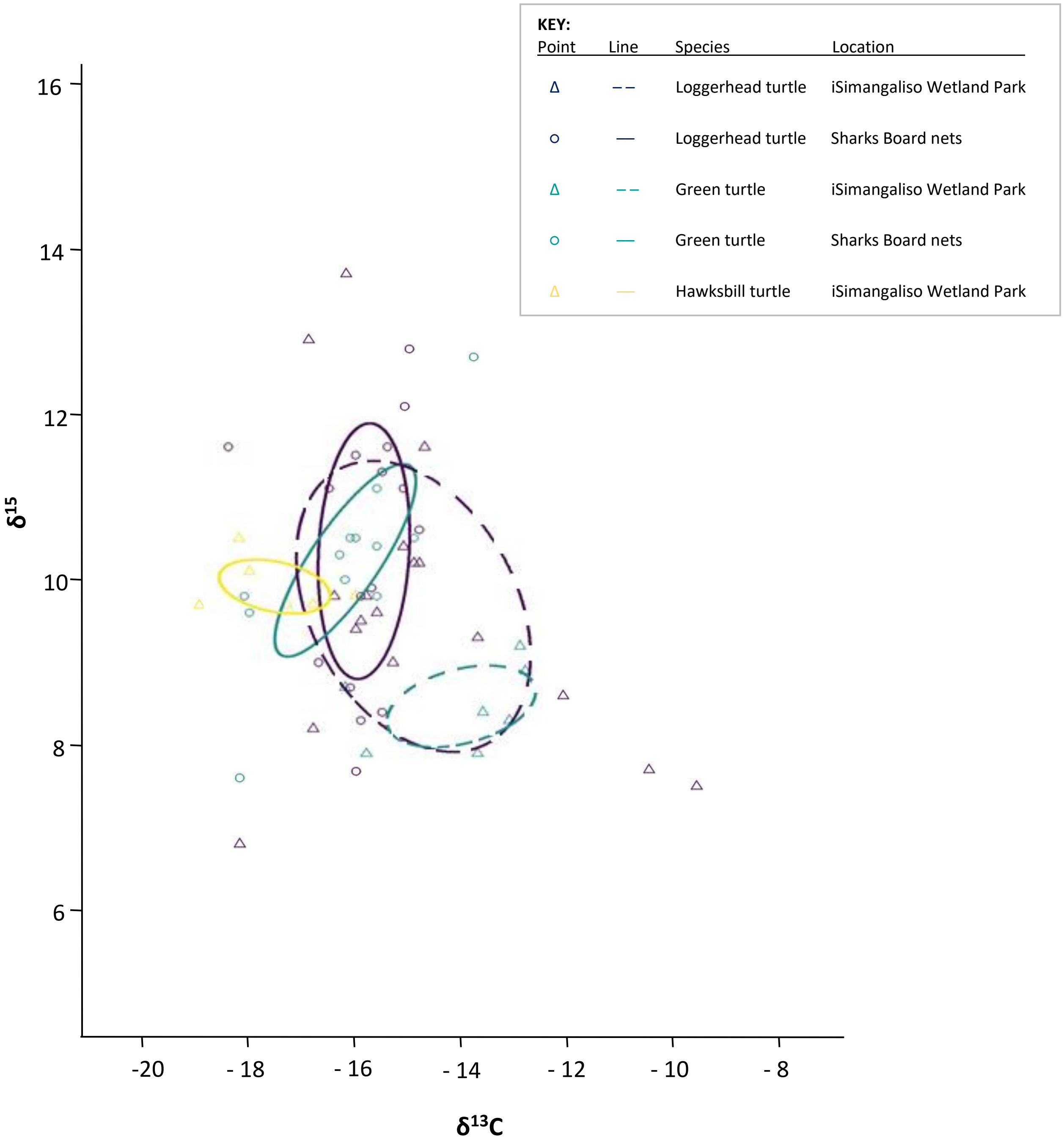

Figure 3.7 Isotopic niches of loggerhead, green and hawksbill turtles from individuals within the iSimangaliso Wetland Park and stranded individuals caught in the KZN Sharks Board bather protection nets. Isotopic niches are plotted as a biplot of carbon and nitrogen stable isotopes using Bayesian ellipses (set at maximum likelihood and encompassing 40% of the data, see Jackson et al. (2011))

Table 3.2 Standard Ellipsis Area with correction factor for small sample size (SEA$_c$; $n < 10$) for study species within respective study sites.

	Shark nets		**iSimangaliso**		
	Loggerhead	Green	Loggerhead	Green	Hawksbill
SEAc	4.44	3.06	12.18	2.43	1.26

Stable isotope signatures were obtained for 13 green turtles (CCL range: 39-107 cm). In iSimangaliso (n=6), green turtles had a δ^{13}C range of -15.5 – -12.5‰ (-13.4±1.1‰) and a δ^{15}N range of 8.0 – 9.3‰ (8.5±0.5‰), whereas green turtles from the Sharks board nets (n=7) had a δ^{13}C range of -17.9 – -13.5‰ (-15.6±1.3‰) and a δ^{15}N range of 7.7 – 12.8‰ (10.4±1.5‰).

Hawksbill turtles from iSimangaliso (n=5) had a δ^{13}C range of -18.6 – -15.7‰ (-17.1±1.1‰) and a δ^{15}N range of 9.8 – 10.6‰ (10±0.3‰), while hawksbill turtles from the Sharks board (n=2) had a δ^{13}C range of -15.4 – -14.9‰ (-15.1±0.4‰) and a δ^{15}N range of 9.9 – 11.8‰ (10.8±1.3‰) (Figure 3.7, Appendix. 4).

Loggerhead turtles, when controlled for size (CCL), did not show any statistically significant differences in carbon and nitrogen between the iSimangaliso and Sharks board sites (Wilk's Lambda, $p>0.05$). However green turtles, when controlled for size (CCL), did show significant differences in both carbon ($p=0.028$) and nitrogen ($p=0.003$) between iSimangaliso and the shark nets (Wilk's Lambda, $p<0.05$). Due to these signature differences in carbon and nitrogen for green turtles, iSimangaliso and the shark nets will be considered as separate units, as they are isotopically distinct.

In iSimangaliso, there were significant differences (Pillai's trace, $p=0.026$) found in carbon ($p=0.010$) but not in nitrogen ($p=0.165$) among loggerhead, green and hawksbill turtles. These significant differences in carbon were found to be between loggerhead and hawksbill turtles ($p=0.048$), and green and hawksbill turtles ($p=0.011$). There were no significant differences found in carbon and nitrogen between loggerhead and green turtles at the Sharks board (Pillai's trace, $p=0.535$).

Loggerhead turtles from iSimangaliso had a three times larger isotopic niche area than loggerhead turtles from the shark nets (Table 3.2), and thus a more extensive carbon and nitrogen range in their isotopic niche. The shark nets loggerhead turtles utilised a more restricted carbon range but had higher nitrogen values in their isotopic niche, although the niches overlapped. Green turtles from the central and southern KZN (from the shark nets) had a greater niche area (3.06) than those from iSimangaliso (2.43). These shark-net caught green turtles had a broader, and higher nitrogen range in their isotopic niche. Although the isotopic niche width for carbon in green turtles were similar, shark net captured green turtles had lower carbon values (Figure 3.7). There appears to be no overlap in isotopic niches between green turtles from the shark nets and iSimangaliso.

In iSimangaliso, the largest isotopic niche area (Table 3.2) was associated with loggerhead turtles (12.18), followed by green turtles (2.43) and hawksbill turtles (1.26). No isotopic niche overlap is apparent between green and hawksbill turtles in iSimangaliso, however there appears to be substantial overlap between loggerhead and green turtles, and partial overlap between loggerhead and hawksbill turtles (Figure 3.7). Green turtles have a larger nitrogen range than hawksbill turtles in their isotopic niche. Loggerhead turtles have a more expansive range in their isotopic niche for both carbon and nitrogen than green and hawksbill turtles. Hawksbill turtles have the lowest range values for carbon in their isotopic niche. Loggerhead turtles from the shark nets have a larger isotope niche area (4.44) than green turtles (3.06) and there appears to be a substantial amount of overlap between the two species. Loggerhead turtles have a more extensive isotopic niche range for nitrogen than green turtles, but a less extensive isotopic niche range for carbon in central and southern KZN from the shark nets.

3.5 Discussion

The key objectives of this study were to investigate the foraging ecology of three hard-shelled turtle species by describing the diet and isotopic niche along the subtropical coast of South Africa. Hughes (1974) previously described the stomach content of some loggerhead and green turtle individuals, although it was not the primary focus of the study which was centered around the nesting species in (now) the iSimangaliso Wetland Park. The present study, even though it addresses a very basic question, is the most comprehensive study to date on the foraging ecology for the nesting and non-nesting component of loggerhead turtles, and the non-nesting green and hawksbill turtle species in South Africa.

The diet from 16 loggerhead turtle stomachs constituted mainly crustaceans and molluscs, making up a combined index of relative importance (%IRI, based on frequency of occurrence and volume) of 80%. This is consistent with the sub-adult to adult stage loggerhead turtle conventional diet of benthic invertebrates described by various studies (Hughes 1974, Plotkin et al. 1993, Bjorndal 1997, Godley et al. 1997, Casale et al. 2008). Interestingly, the most predominant crustacean, *Planes minutus*, and molluscan, *Bufonaria cf. crumena*, were only present in a few individuals but accounted for most of the dietary content in those individuals. This was also the case for the presence of tunicates in the current study. Hughes (1974) also noted the marked presence of the mollusc, *B. crumena* in loggerhead turtle diet from 26 individuals in South Africa, however no records of tunicates were reported. The presence of hermit crabs and bivalve fragments in loggerhead turtle diet should also be interpreted with some caution as these may be the result of incidental ingestion, while foraging for more targeted prey such as gastropods and tube worms (Hughes 1974, Plotkin et al. 1993). The single fish species, *L. richardsonii*, found in one individual is also considered as incidental or opportunistic foraging, as loggerhead turtles are not known to actively forage and/or rarely target fish species as prey (Tomas et al. 2001, Parker et al. 2005). The 11 empty stomachs found in the nesting loggerhead turtle species can be attributed to known periods of fasting or reduced feeding during the breeding season (Hays et al. 2002).

Green turtle diet from the stomachs of 13 individuals revealed that algae, specifically chlorophyta and rhodophyta, were the predominant prey items making up 99% IRI of the total diet. This is consistent with the conventional diet of green turtles, which is known to have a herbivorous diet of algae or seagrass (Bjorndal 1985). Hughes (1974) also noted the high presence of two rhodophyta species (Gelidium spp.) and two chlorophyta species (*Caulerpa filiformis* and *Codium duthieae*) from the diet of 12 green turtles in South Africa. Other regions in the SWIO that host green turtles such as the Republic of the Seychelles also reported a primarily plant-based diet, with 95% mean gut content biomass constituting seagrass (predominately *Thalassodendron ciliatum*) in males and non-breeding females (Stokes et al. 2019). Macroalgae made up only 13% of the mean gut content biomass in breeding females (Stokes et al. 2019). Both chlorophyta and rhodophyta were present in all individuals in the present study, while seagrass (*Zostera capensis*) was only found in 2 individuals and in trace amounts (%IRI=0.01). Differences in composition of intestinal microflora are thought to occur between green turtles that feed on algae versus seagrasses (Bjorndal et al. 1991), but evidence of mixed diets have also been reported (Stokes et al. 2019). It is interesting to note in the current study the dominance of either only chlorophyta or rhodophyta as the main bulk prey item for each individual. Tunicates and cnidarians were also quite ubiquitous in the diet in terms of frequency, but these items accounted for less volume and thus their contribution in terms of overall importance (%IRI) was lower. However, it has now been established that the presence of soft-bodied prey items have long been underestimated from the stomach content due to a faster turnover rate, and contribute much more to the overall diet of green turtles (Burkholder et al. 2011, Carman et al. 2013, Williams et al. 2013).

Hawksbill turtle diet was only represented from two individuals with contrasting diets. One individual contained stomach content dominated by poriferans, while the stomach content of the other constituted a range of crustacean, rhodophyta and unidentified animal matter (Appendix 3). These contrasting diets, however, still align with conventional hawksbill turtle diets. Hawksbill turtles have been known to portray indiscriminate benthic feeding behaviour which incorporates amongst sponges, other substantial quantities of non-sponge invertebrates from their environment (Meylan 1988, León and Bjorndal 2002, Ferreira et al. 2018). Foraging stocks in the Seychelles revealed that hawksbill turtles fed predominantly on demosponges and anthozoans, consistent with that of other foraging stocks from the Atlantic and Pacific oceans (Von Brandis et al.2014). Rhodophyta was also found in the diet of one individual from the current study, but this was found in trace amounts and can be attributed to the benthic foraging nature of hawksbill turtles, incidentally ingesting surrounding algae along with the targeted prey item. Von Brandis et al. (2014) also noted the presence of seaweeds (particularly Rhodophyta and Phaeophyta), but also usually in trace amounts and attributed to incidental ingestion. However, in one individual where a Rhodophyta species, *Hypnea cornuta*, was found to have been ingested abundantly, it was suggested that hawksbills may occasionally gorge themselves on seaweed to facilitate digestion of their primarily sponge diet (Von Brandis et al. 2014). The small number of hawksbill samples is an effect of the species' distribution range. Hawksbill turtles are more equatorial and tend not to have a high presence along the more southern regions of the eastern seaboard of South Africa, and thus their interactions with the shark nets are minimal. Brazier et al. (2012) reported a hawksbill turtle mean annual mortality of 1.5 individuals per year for the study period 1981-2008 from the KZN shark nets.

Overall diets of loggerhead, green and hawksbill turtles indicate that there are distinct differences among the three species. Although there are some regions of overlap for certain prey items, these do not constitute the primary diet of the three species. This is also evident from the hierarchical cluster analysis and nMDS ordination plots which clearly show the separation amongst species based on diet. The four individuals of loggerhead turtles which separated from their respective intraspecific group contained very specific diets, with two individuals showing a particular affinity to *Planes minutus*, and the other two individuals favouring *Bufonaria cf. crumena*. Variations in foraging behaviour have previously been recorded among individuals in a population, with a marked increase in specialization noted for adult turtles (Vander Zanden et al. 2013, Figgener et al. 2019). The loggerhead turtles that foraged on *B. crumena* can be both classified as adults as their straight carapace length exceeds the size at sexual maturity (83.7 ± 4.15 cm) (Tucek et al. 2014). Unfortunately, size data for the loggerheads foraging on *P. minutus* were unavailable. The stark contrast in hawksbill turtle diet from the two individuals displayed a high level of dissimilarity and ranked the hawksbill turtle with crustacean in the diet closer to loggerhead turtles. However, the low sample size for hawksbill turtle diet content limits further investigations of shared diet with loggerhead turtles. It should also be noted that this hawksbill turtle was found at Port Edward (the southern-most shark net), which is uncharacteristic of its usual distribution range.

The stable isotope data revealed regional differences between green turtles from iSimangaliso and the shark nets in terms of habitat use ($\delta^{15}C$) and trophic level ($\delta^{13}C$). The SIBER plot indicates green turtles from the shark nets utilized regions closer inshore and feeding at a higher trophic level. It could be that green turtles from the shark nets have a mixed diet, incorporating both algae and animal matter. This is evident from the dietary analysis, as it did show frequent ingestion of tunicate and cnidarian species, as well as the larger isotopic niche area associated with green turtles from the shark nets. Gillis et al. (2018) also found foraging regional differences in green turtles from Bimini in the Bahamas, where turtles from one site had a generalist omnivorous diet and the other site contained turtles with a more specialist herbivorous diet. It is less likely that the differences are due to isotopic baseline differences between the two sites because loggerhead turtles from the same regions showed no significant differences in either carbon or nitrogen signatures. Although there were no significant isotopic differences for loggerhead turtles between iSimangaliso and the shark nets, loggerhead turtles from iSimangaliso had a three times larger isotopic niche. This could be attributed to an effect of location, based on loggerhead turtle migration pathways between nesting and foraging grounds. Harris et al. (2018) described three migration corridors for loggerheads between nesting sites and foraging grounds in South Africa: 1.) Mozambique Corridor – closely following the coast northwards into Mozambique; 2.) Malagasy Corridor – north-east across the Mozambique Channel into northern Madagascar; 3.) Agulhas Corridor – southwards in the Agulhas current along the coast to the Agulhas Banks. Epidermal tissue achieves equilibrium with turtle diet (turnover rate) between 6-12 months, indicating that turtle isotopic signatures should reflect past locations and the food ingested there from that time period (Ferreira et al. 2018). Therefore, the larger isotopic niche seen from the nesting site in iSimangaliso could be an accumulation from multiple stocks' signatures from various sites, while signatures from the more southern regions are more representative of a single stock (Agulhas Corridor). Interestingly, there were no statistical differences between carbon and nitrogen between these two sites. This indicates that despite the large variation for carbon and nitrogen at iSimangaliso, loggerhead turtles from potentially different stocks in the region usually tend to utilize similar resources in terms of habitat and diet.

Loggerhead, green and hawksbill turtles from iSimangaliso, and loggerhead and green turtles from central and south KZN appear to all forage in similar trophic levels within their respective sites. The stomach content from loggerhead and green turtles from the shark nets reveals that the diet of these two species, although there is some overlap, are predominantly distinct. This suggests that all species within their respective sites fulfill their different ecological roles within the same trophic level. Thus, these species offer a level of complexity within the ecosystem at a similar trophic level. Further, this occurs in a similar habitat for loggerheads and green turtles from both iSimangaliso and the shark nets. Goatley et al. (2012) observed the differential removal of two algal types off a coral reef by respective green and hawksbill turtles, noting the importance of each role as significant in maintaining coral reef health. The hawksbill turtles at iSimangaliso, however, appear to carry out their role in a more inshore region. Hawksbill turtles have been shown to differentially use habitats, with larger individuals using deeper regions and smaller individuals occurring more inshore (Ferreira et al. 2018). Therefore, the lower carbon range, and thus more inshore presence, could potentially be attributed to sampling effect based on size, as all hawksbill turtles for the study were caught on SCUBA from inshore reefs. Immature life stages of hawksbill turtles were also shown to have smaller isotopic niches (Ferreira et al. 2018), which is also evident from iSimangaliso as these turtles had the smallest isotopic niche.

3.6 Conclusion

Loggerhead, green and hawksbill turtles followed their conventional distinct diets ascribed from the literature. A total of 16 loggerhead turtles possessed stomach content which mainly comprised of crustaceans and molluscs, while 11 stomachs were found to be empty. Individual specialization was noted for 4 loggerhead individuals. Green turtles (n=13) diet mainly compromised of algae, specially rhodophyta and chlorophyta. Tunicates and cnidarians also had a high frequency in the green turtle diet. Only two individuals for hawksbill turtles were sampled, with contrasting diets but still indicative of the conventional benthic invertebrate diet. Habitat and trophic level isotopic differences were found between the north (iSimangaliso) and central and south KwaZulu-Natal (shark nets). Central and south KZN green turtles used closer inshore areas and foraged at a higher trophic level, suggesting the presence of a mixed animal-based diet. Loggerhead, green and hawksbill turtles from the north (iSimangaliso), and loggerhead and green turtles from central and south KwaZulu-Natal appear to all forage in similar trophic levels within their respective sites.

Further studies require higher sample sizes for both diet and stable isotope analyses. The central and south region of KwaZulu-Natal (shark nets) covers a large geographic area and further isotopic variations may occur along this gradient. The region should also be surveyed at known foraging sites to determine if the dietary content is a function of availability or preference.

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3.8 Supplementary Material

APPENDIX 1 Diet of loggerhead turtles (*Caretta caretta*) along the eastern seaboard of South Africa (n=27). FO, Frequency of occurrence; Vi, Volume; IRI, Index of Relative Importance; %IRI, IRI presented as a percent of the whole both at a wider taxon (shaded) and at a species level within each taxon.

Prey Item	FO	Vi	IRI	%IRI
Crustacea	**25.93**	**163.70**	**5.90**	**41.09**
Planes minutus	7.41	93.00	0.51	24.40
Unidentified Dromiidae sp. 1	3.70	31.80	0.09	4.17
Diogenes sp.	11.11	10.30	0.09	4.05
Unidentified Majoidea sp. 1	3.70	11.90	0.03	1.56
Ovalipes trimaculatus	3.70	9.00	0.02	1.18
Unidentified Brachyura fragments	3.70	3.80	0.01	0.50
Unidentified Calappidae sp. 1	3.70	1.80	0.00	0.24
Unidentified Decapoda fragments	3.70	0.70	0.00	0.09
Paguristes sp.	3.70	0.60	0.00	0.08
Unidentified Xanthidae sp. 1	3.70	0.60	0.00	0.08
Unidentified Paguroidea sp. 1	3.70	0.20	0.00	0.03
Mollusca	**40.74**	**98.55**	**5.58**	**38.87**
Gastropoda (Class)				
Bufonaria cf. crumena	7.41	23.80	0.13	6.24
Unidentified Gastropoda tissue	3.70	6.20	0.02	0.81
Unidentified Gastropoda shell sp. 3	3.70	3.80	0.01	0.50
Mitra sp.	3.70	1.80	0.00	0.24
Unidentified Gastropoda shell fragments	3.70	1.50	0.00	0.20
Unidentified Gastropoda shell sp. 2	3.70	1.20	0.00	0.16
Unidentified Gastropoda shell sp. 1	3.70	0.80	0.00	0.10
Bullia cf. rhodostoma	3.70	0.80	0.00	0.10
Unidentified Gastropoda shell sp. 4	3.70	0.40	0.00	0.05
Bullia sp. 1	3.70	0.30	0.00	0.04
Bullia similis	3.70	0.26	0.00	0.03
Janthina janthina	3.70	0.10	0.00	0.01
Unidentified Nassariidae sp. 1	3.70	0.10	0.00	0.01
Unidentified Gastropoda operculum	3.70	0.10	0.00	0.01
Bivalvia (Class)				
Unidentified Pteriidae sp. 3	3.70	52.00	0.14	6.82
Unidentified Pteriidae sp. 2	3.70	3.00	0.01	0.39
Unidentified Bivalvia shell fragments	14.81	0.60	0.01	0.31
Unidentified Pteriidae sp. 4	3.70	1.60	0.00	0.21
Unidentified Bivalvia sp. 9	3.70	1.00	0.00	0.13
Unidentified Bivalvia sp. 8	3.70	0.80	0.00	0.10
Unidentified Pteriidae sp. 1	3.70	0.80	0.00	0.10

Unidentified Bivalvia sp. 6	3.70	0.24	0.00	0.03
Unidentified Bivalvia sp. 1	3.70	0.10	0.00	0.01
Unidentified Bivalvia sp. 2	3.70	0.10	0.00	0.01
Unidentified Bivalvia sp. 7	3.70	0.10	0.00	0.01
Unidentified Bivalvia sp. 3	3.70	0.01	0.00	0.00
Unidentified Bivalvia sp. 4	3.70	0.01	0.00	0.00
Unidentified Bivalvia sp. 5	3.70	0.01	0.00	0.00
Tunicata	**11.11**	**64.60**	**1.00**	**6.95**
Polycarpa aff. insulsa	3.70	50.00	0.14	6.56
?Polyandrocarpa sp.	3.70	13.00	0.04	1.71
?Aplousobranchia or ?Phlebobranchia	3.70	1.60	0.00	0.21
Other	**29.63**	**17.40**	**0.72**	**4.99**
Unidentified animal matter	22.22	13.98	0.23	11.00
Stones	18.52	7.81	0.11	5.12
Unidentified shell fragments	7.41	1.22	0.01	0.32
Unidentified plant matter	7.41	1.10	0.01	0.29
Bird feather	3.70	0.10	0.00	0.01
Tube worm	**11.11**	**25.08**	**0.39**	**2.70**
Unidentified tube worm casing	11.11	25.08	0.21	9.87
Pollutants	**18.52**	**13.50**	**0.35**	**2.42**
Hard plastics	7.41	5.40	0.03	1.42
Synthetic fabric	3.70	5.50	0.02	0.72
Soft plastics	7.41	2.61	0.01	0.68
Perciformes	**3.70**	**52.00**	**0.27**	**1.86**
Liza richardsonii	3.70	52.00	0.14	6.82
Echinodermata	**7.41**	**14.20**	**0.15**	**1.02**
Unidentified Asterozoan ossicles	3.70	1.20	0.00	0.16
?Marthasterias glacialis	3.70	13.00	0.04	1.71
Cnidaria	**3.70**	**2.50**	**0.01**	**0.09**
?*Physalia* sp. 1	3.70	1.80	0.00	0.24
Unidentified Cnidaria sp. 1	3.70	0.70	0.00	0.09
Chlorophyta	**3.70**	**0.20**	**0.00**	**0.01**
Caulerpa filiformis	3.70	0.20	0.00	0.03
Porifera	**3.70**	**0.01**	**0.00**	**0.00**
Unidentified Porifera sp. spines	3.70	0.01	0.00	0.00

APPENDIX 2 Diet of green turtles (*Chelonia mydas*) along the eastern seaboard of South Africa (n=13). FO, Frequency of occurrence; Vi, Volume; IRI, Index of Relative Importance; %IRI, IRI presented as a percent of the whole both at a wider taxon (shaded) and at a species level within each taxon.

Prey Item	**FO**	**Vi**	**IRI**	**%IRI**
Chlorophyta	**100.00**	**2858.12**	**19.41**	**87.67**
Caulerpa filiformis (thallus only)	84.62	1082.90	2.07	49.73
Codium sp. 1	69.23	539.40	0.85	20.27
Caulerpa filiformis (with stolon)	76.92	209.64	0.37	8.75
Codium platylobium	15.38	834.00	0.29	6.96
Codium sp. 3	30.77	122.20	0.09	2.04
Caulerpa filiformis (with bryozoan *E. pilosa* attached)	61.54	41.80	0.06	1.40
Halimeda cuneate	53.85	6.78	0.01	0.20
Codium sp. 1 (with bryozoan *E. pilosa* attached)	7.69	13.00	0.00	0.05
Codium sp. 2	23.08	1.20	0.00	0.02
Caulerpa filiformis (with hydroid *A. operculata* attached)	15.38	1.50	0.00	0.01
Caulerpa filiformis (with hydroid *A. pluma* attached)	7.69	2.70	0.00	0.01
Codium sp. 4	7.69	2.80	0.00	0.01
Caulerpa serrulata var. hummii	7.69	0.20	0.00	0.00
Rhodophyta	**100.00**	**358.30**	**2.43**	**10.99**
Gelidium pteridifolium	53.85	269.60	0.33	7.88
Inkyuleea beckeri	53.85	29.20	0.04	0.85
Rhodymenia natalensis	61.54	19.40	0.03	0.65
Osmundaria serrata	30.77	10.90	0.01	0.18
Phacelocarpus oligocanthus	7.69	16.00	0.00	0.07
Portieria hornemanii	15.38	3.30	0.00	0.03
Hypnea rosea	15.38	3.60	0.00	0.03
Polyzonia elegans	46.15	0.50	0.00	0.01
Hypnea sp. 1	15.38	1.60	0.00	0.01
Hypnea cf. musciformis	7.69	1.20	0.00	0.01
Placophora binderi	15.38	0.80	0.00	0.01
Prionitis filiformis	7.69	1.10	0.00	0.00
Hypnea cf. rosea	15.38	0.30	0.00	0.00
Hypnea sp. 2	7.69	0.30	0.00	0.00
Hypnea tenuis	7.69	0.20	0.00	0.00
Nienburgia serrata	7.69	0.20	0.00	0.00
Rhodymenia natalensis (with bryozoan *E. pilosa* attached)	7.69	0.10	0.00	0.00
Rhodymenia natalensis (with hydroid *A. operculata* attached)	7.69	0.00	0.00	0.00
Cheliosporum proliferum	7.69	0.00	0.00	0.00
Tunicata	**46.15**	**54.20**	**0.17**	**0.77**
Appendicularia (Class)				
?Appendicularia sp.	7.69	8.00	0.00	0.03

Ascidiacea (Class)				
?Aplousobranchia or ?Phlebobranchia sp.	7.69	0.60	0.00	0.00
?Stolidobranchia or ?Phlebobranchia sp.	7.69	5.80	0.00	0.02
Ascidiacea: Aplousobranchia (Order)				
?Rhopalaea or ?Clavelina sp.	15.38	24.80	0.01	0.21
Eudistoma sp.	7.69	15.00	0.00	0.06
Cnidaria	**76.92**	**13.52**	**0.07**	**0.32**
Hydrozoa: Leptothecata				
Lytocarpia Formosa	61.54	2.70	0.00	0.09
Amphisbetia operculata	38.46	3.12	0.00	0.07
Symplectoscyphus sp.	46.15	2.30	0.00	0.06
Aglaophenia pluma	53.85	0.80	0.00	0.02
Sertularella sp.	7.69	0.10	0.00	0.00
Macrorhynchia cf. phillippina	7.69	0.10	0.00	0.00
Sertularella arbuscula	7.69	0.00	0.00	0.00
Hydrozoa: Siphonophorae				
Physalia sp.	15.38	4.40	0.00	0.04
Plant material	**53.85**	**13.38**	**0.05**	**0.22**
Unidentified plant matter	23.08	11.10	0.01	0.14
Zostera capensis	15.38	1.68	0.00	0.01
Prionium serratum	38.46	0.60	0.00	0.01
Pollutants	**46.15**	**2.10**	**0.01**	**0.03**
Plastic	30.77	1.90	0.00	0.03
Fishing line	7.69	0.10	0.00	0.00
String	30.77	0.10	0.00	0.00
Phaeophyceae	**15.38**	**0.20**	**0.00**	**0.00**
Dictyota sp.	7.69	0.00	0.00	0.00
Dictyoteris sp.	7.69	0.20	0.00	0.00
Arthropoda	**7.69**	**0.00**	**0.00**	**0.00**
Hexapoda: Insecta (Class)				
Apidae sp.	7.69	0.00	0.00	0.00
Helodidae sp.	7.69	0.00	0.00	0.00
Mollusca	**7.69**	**0.00**	**0.00**	**0.00**
Gastropoda (Class)				
Unidentified gastropod shell sp. 5	7.69	0.00	0.00	0.00
Crustacea	**7.69**	**0.00**	**0.00**	**0.00**
Hexanauplia: Cirripedia				
Unidentified Balanomorpha sp. 1	7.69	0.00	0.00	0.00
Other	**7.69**	**0.20**	**0.00**	**0.00**
Unidentified animal matter	7.69	0.20	0.00	0.00

APPENDIX 3 Diet of hawksbill turtles (*Eretmochelys imbricata*) along the eastern seaboard of South Africa (n=2). FO, Frequency of occurrence; Vi, Volume; IRI, Index of Relative Importance; %IRI, IRI presented as a percent of the whole both at a wider taxon (shaded) and at a species level within each taxon.

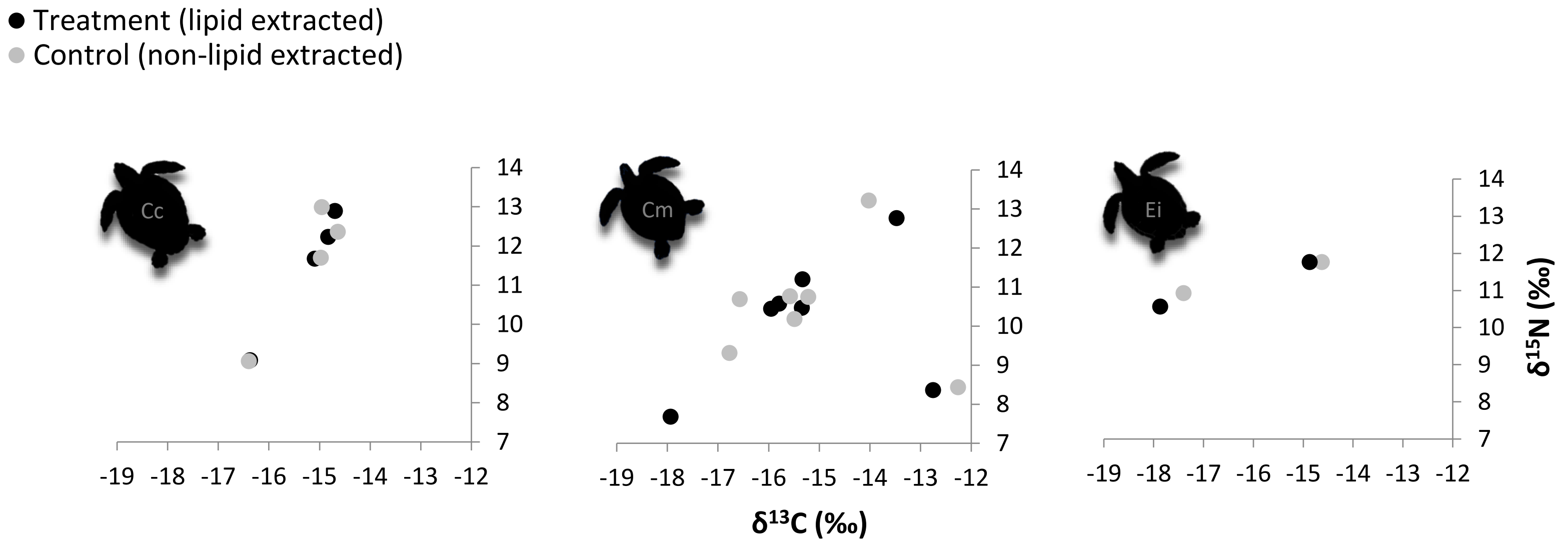
Prey Item	**FO**	**Vi**	**IRI**	**%IRI**
Porifera	**50.00**	**53.60**	**14.87**	**74.34**
Order: Chondrosida	50.00	1.20	0.24	1.66
Order: Astrophorida	50.00	38.10	7.55	52.84
Order: Hadromerida	50.00	14.30	2.83	19.83
Crustacean	**50.00**	**3.50**	**0.97**	**4.85**
Unidentified brachyuran sp. 1	50.00	3.50	0.69	4.85
Rhodophyta	**50.00**	**0.40**	**0.11**	**0.55**
?Gelidium pteridifoilum	50.00	0.40	0.08	0.55
Other	**50.00**	**14.00**	**3.88**	**19.42**
Unidentified animal matter	50.00	14.00	2.77	19.42
Pollutants	**50.00**	**0.60**	**0.17**	**0.83**
Paper	50.00	0.60	0.12	0.83

APPENDIX 4 Stable isotope metadata for loggerhead, green and hawksbills turtles

Species	Site	Sex	Size (CCL)cm	N	C
Loggerhead	iSimangaliso	Female	86.9	6.9	-17.9
Loggerhead	iSimangaliso	Female	97.3	9.9	-16.1
Loggerhead	iSimangaliso	Female	89.3	11.7	-14.4
Loggerhead	iSimangaliso	Female	90.7	8.7	-11.8
Loggerhead	iSimangaliso	Female	90.9	8.3	-16.5
Loggerhead	iSimangaliso	Female	89.4	7.6	-9.3
Loggerhead	iSimangaliso	Female	89.5	9.1	-15.0
Loggerhead	iSimangaliso	Female	99.4	9.4	-13.4
Loggerhead	iSimangaliso	Female	94.4	9.7	-15.3
Loggerhead	iSimangaliso	Female	93.2	10.5	-14.8
Loggerhead	iSimangaliso	Female	88.7	9.5	-15.7
Loggerhead	iSimangaliso	Female	82.9	10.3	-14.5
Loggerhead	iSimangaliso	Female	92.5	9.6	-15.6
Loggerhead	iSimangaliso	Female	82.1	13.0	-16.6
Loggerhead	iSimangaliso	Female	88.2	7.8	-10.2
Loggerhead	iSimangaliso	Female	91.6	9.9	-15.5
Loggerhead	iSimangaliso	Female	86.7	10.3	-14.6
Loggerhead	KZN Sharks Board	Male	81.2	10.7	-14.5
Loggerhead	KZN Sharks Board	Male	72.9	8.8	-15.8
Loggerhead	KZN Sharks Board	Female	78.2	7.8	-15.7
Loggerhead	KZN Sharks Board	Female	69.4	12.9	-14.7
Loggerhead	KZN Sharks Board	Male	75.6	9.9	-15.6
Loggerhead	KZN Sharks Board	Female	77.2	12.2	-14.8
Loggerhead	KZN Sharks Board	Female	89.8	11.7	-15.1
Loggerhead	KZN Sharks Board	Female	57.2	9.1	-16.4
Green	iSimangaliso	Immature	81.6	9.0	-12.5
Green	iSimangaliso	Immature	62	8.0	-13.4
Green	iSimangaliso	Female	98.4	8.4	-12.8
Green	iSimangaliso	Immature	95	9.3	-12.6
Green	iSimangaliso	Female	81.3	8.5	-13.3
Green	iSimangaliso	Immature	60.9	8.0	-15.5
Green	KZN Sharks Board	Male	107.2	12.8	-13.5
Green	KZN Sharks Board	Female	72.2	10.4	-16.0
Green	KZN Sharks Board	Female	39.7	10.6	-15.8
Green	KZN Sharks Board	Male	57.8	7.7	-17.9
Green	KZN Sharks Board	Female	66.6	10.5	-15.3
Green	KZN Sharks Board	Female	48.4	9.9	-15.3
Green	KZN Sharks Board	Female	48	11.2	-15.3
Hawksbill	iSimangaliso	Immature	76.5	9.8	-17.0
Hawksbill	iSimangaliso	Female	80.6	9.8	-18.6

Hawksbill	iSimangaliso	Immature	79	10.6	-17.9
Hawksbill	iSimangaliso	Immature	44.6	9.9	-15.7
Hawksbill	iSimangaliso	Immature	53.7	9.8	-16.5
Hawksbill	KZN Sharks Board	Female	37.2	9.9	-15.4
Hawksbill	KZN Sharks Board	Female	48	11.8	-14.9

APPENDIX 5 Epidermal tissue testing for lipid (treatment) and non-lipid (control) extracted samples for green (Cm), loggerhead (Cc) and hawksbill (Ei) turtles.



Chapter 4: General Conclusion

Historical populations of sea turtles were considered to be robust, but over time have declined globally (Bjorndal and Bolten 2003). Therefore, turtle populations have been effectively reduced without fully realising their ecological roles. One of the global research priorities for sea turtle management and conservation is defining the past and present ecological roles of sea turtles (Hamann et al. 2010, Lazar et al. 2011). With the advent of new technologies, exploring these ecological roles today depict a level of variability that suggest that sea turtles are still key species and play an important role in driving ecosystem functions and processes.

This study aimed to assess the potential ecological roles of loggerhead, green and hawksbill turtles along the eastern seaboard of South Africa. This was done by looking at key ecological traits such as distribution, habitat use, diet and isotopic niche through the multi-technique use of satellite tracking, stomach content analysis and stable isotope analysis. The combination of these techniques is complementary and can give us a better understanding of sea turtle ecology.

Sea turtles have a circum-global distribution, yet regional populations are genetically distinct and warrant unique conservation status (Wallace et al. 2010). These populations or Regional Management Units (RMUs) are usually shared between regions of the animal's migration route from foraging ground to nesting site. Therefore, location information throughout the distribution, as well as a relative measure of proportional habitat use such as home ranges and habitat preference, can help better inform the RMU framework (Wallace et al. 2010). Our study tracked the movements of nesting loggerhead and non-nesting foraging green and hawksbill turtles. In addition to their distribution, each species home and core range as well as their habitat preference were analysed. Internesting loggerhead turtles displayed relatively small home and core range and had a high affinity to the coast, with preference shown to any habitat proximate to their nesting beach at Bhanga Nek. Green and hawksbills turtles displayed a high affinity to the coast and had small home and core ranges with overlap present, even at an individual level. Both species also showed extreme site fidelity to Sodwana for the duration of the tracking, indicating that green and hawksbill turtles are coastal resident foragers in the iSimangaliso MPA. Although these species home and core ranges were quite similar, they displayed differential habitat preference with green turtles more present at sandy and reef habitats, and hawksbills on inshore and shelf edge reefs.

Since the spatial distribution, movement and habitat preference of these species have been described, further investigation into what these turtles do (i.e. ecological role) can be explored. The closest interaction between an organism and its environment is the ingestion of a subset of that environment (Bjorndal 1997). Understanding the diet of sea turtles, as well as their trophic ecology is not only a fundamental goal of basic biology, but is also essential for effective population management (Tomas et al. 2001). Our study described the diet and isotopic niche of nesting loggerhead and non-nesting foraging green and hawksbill turtles along the eastern seaboard of South Africa. Diet (through stomach content) of all species from the south and central of KwaZulu-Natal (shark nets) revealed feeding within their respective conventional diet spectrums; loggerhead turtles contained a diet predominantly with crustaceans and molluscs, green turtles had a diet almost entirely composed of red and green algae, whereas hawksbill turtles contained benthic invertebrates. Habitat and trophic level differences (through stable isotope analysis) occurred between sampling sites from north (iSimangaliso) and the central and south (shark nets) of KwaZulu-Natal for green turtles. Loggerhead, green and hawksbill turtles from the north (iSimangaliso), and loggerhead and green turtles from central and south KwaZulu-Natal appear to all forage in similar trophic levels within their respective sites.

The combination of complementary multi-technique approach also allowed for strengthening of certain arguments. The compact distribution of loggerhead turtles described from satellite tracking data was used to provide evidence that this population of loggerheads does not forage during the internesting period. This can be further substantiated by the lack of stomach content found from at least 40% of all loggerhead shark net captures (n=27). The high intraspecific overlap in distribution displayed by hawksbill turtles in their home and core ranges can also been seen through their very limited isotopic niche. Green turtles from central and south KwaZulu-Natal (shark nets) were found to forage at a higher trophic level than green turtles from the north (iSimangaliso). It was suggested that green turtles from central and south KwaZulu-Natal had a more mixed diet, or omnivorous diet. This can be supported from green turtle diets from shark nets which indicated the high frequency at which tunicates and cnidarians were ingested. Finally, loggerhead, green and hawksbill turtles from the north (iSimangaliso), and loggerhead and green turtles from central and south KwaZulu-Natal were all shown to forage in similar trophic levels within their respective sites. By comparing the diet of all these species from the shark nets, we can see that their diets are distinct. While there are some overlap in minor prey species that contribute to the diet, there is no overlap in the dominant prey. Sea turtle species thus fulfil different ecological roles within the same ecosystem at similar trophic levels. This has direct implications for conservation and management.

South Africa has recently declared 20 new and/or extended Marine Protected Areas (MPAs), some explicitly for the protection of turtles. However, there is very limited ecological knowledge, especially for the non-nesting green and hawksbill turtles and therefore we are protecting species without truly understanding their basic biology. Further, this limited ecological knowledge gap is not only applicable to South Africa, but to the SWIO region (Von Brandis et al. 2014). This study has found that the current iSimangaliso MPA provides sufficient protection in terms of covering the distribution range and habitat use associated with nesting loggerhead turtles and resident foraging green and hawksbill turtles. It has also demonstrated that these turtles have different ecological roles which occur at small spatial scales within similar trophic levels. Therefore, sea turtles in turn play a pivotal role in maintaining healthy reef dynamics within the MPA, eg. nesting loggerhead turtles introduce nutrients into beach systems, while resident green and hawksbill turtles differentially manage the control of reef competitors. Future studies should pursue the methods outlined in this study to obtain greater sample sizes. This would help elucidate the shortcomings of the current study and will allow for more robust data and hypothesis testing. Additional genetic studies, especially of the resident foraging green and hawksbill turtles, would be interesting to assess to determine the natal origin of these animals as it has been shown that foraging stocks can consist of individuals from various proximate nesting grounds (Vásquez-Carrillo et al. 2020). It is also suggested to sample other regions with known turtle sighted frequencies, such as the Aliwal Shoal MPA. Non-nesting species were found to be resident foragers within the iSimangaliso MPA with different ecological roles. Therefore resources should be invested in exploring other ecosystems and determining their ecological processes towards an increased management and conservation goal.

4.1 References

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