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MIGRATORY ECOLOGY OF SEA TURTLES

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With love for Joe, my hero and brother.

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LIST OF ABREVAITIONS

PG – Playa Grande

SP – Sandy Point

MND – Median Nesting Date

CTns – Central Tendency of the Nesting Season

SAO – South Atlantic Ocean

MC – Mozambique Channel

WIO – Western Indian Ocean

ENSO – El Niño-Southern Oscillation

MEI – Multivariate ENSO Index

AMO – Atlantic Multidecadal Oscillation Index

NAO – North Atlantic Oscillation Index

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ABSTRACT

Robinson, Nathan Jack. Ph.D., Purdue University, December 2014. Migratory ecology of sea turtles. Major Professor: Jeffrey Lucas.

Establishing the movement patterns of free-ranging animals is imperative to understanding their behavior and ecology, and is often necessary for designing effective conservation-strategies. This is especially true for migratory species, such as sea turtles, whose long-distance movements form a major component of their life history. In this thesis, I investigated which factors are driving the migratory behavior of the leatherback turtle *Dermochelys coriacea*. Firstly, I examined whether the timing of the nesting season (nesting phenology) is influenced by oceanographic conditions along the pre-nesting migratory route or by variation in population structure. The discovery that nesting phenology appears more influenced by population structure than environmental conditions has implications for the capacity of these animals to adapt to climate change. Leatherback turtle populations may not be expected to respond directly to increasing global temperatures by shifting their nesting phenology, and so nesting under cooler seasonal conditions; however, this could still occur in populations that are increasing in size or average age of the reproductively active individuals. Secondly, I outlined a novel method for identifying behavioral changes in satellite telemetry based on Change-Point Analysis (CPA). Subsequently, I applied it to analyze the post-nesting leatherback turtles tracked from the iSimangaliso Wetland Park, South Africa. Half (n = 8) of the turtles tracked migrated to foraging areas in the shallow coastal waters of the Sofala Banks, Mozambique. Such coastal behavior is very rare in leatherback turtles, which are otherwise often described as ‘pelagic specialists’. Overlaying the output of the CPA model with contemporaneous oceanographic data suggests that these coastal habitats are productive, all-year round foraging areas. In contrast, the foraging behavior of the turtles that migrated towards pelagic foraging areas in the Western Indian or South Atlantic Ocean appears to be more associated with ephemeral and dynamic oceanographic processes. Thirdly, I validated the use of stable isotope analysis as a tool for determining the foraging habitats of leatherback turtles. By comparing the stable isotope analysis data to the satellite tracking data, I was also able to infer the potential affects that satellite telemetry devices with high drag can have on migratory behavior. Stable isotope analysis confirmed the importance of the Sofala Banks as a critical foraging habitat for leatherback turtles, but it also previous satellite tracking studies employing high drag devices might have inadvertently been influencing migratory behavior. In essence, altering the very behaviors these devices are used to measure. The findings of this thesis highlight how migratory ecology is influenced

by a complex array of factors including population dynamics, individual variation, and environmental conditions. Unraveling these factors can provide surprising insights into the behavior of these animals and help guide the development for future conservation strategies.

CHAPTER 1. INTRODUCTION TO THE MIGRATORY ECOLOGY OF SEA TURTLES

Movement is among the most basic and conspicuous characteristics of life. Some of the most impressive movements in the animal kingdom are those undertaken by long-distance migrants such as sea turtles. Sea turtles are known to routinely swim distances that may span over 10,000 km – the distance between the eastern and western shores of the Pacific Ocean – when migrating from nesting to foraging areas (Nichols et al. 2000, Benson et al. 2011). These epic migrations are understandably a central feature of the life-history of long-distance migrants. Knowledge of the factors governing migratory behavior can provide wide-ranging insights into their ecology and is often invaluable for conservation management.

In this chapter, I will present an introductory overview of the migratory ecology of sea turtles, with an emphasis on the leatherback turtle *Dermochelys coriacea* – the species that will be the central focus of this thesis. I begin by discussing the evolutionary basis for why long-distance migrations are a common trait of almost all sea turtle populations. Subsequently, I will introduce the 3 topics that I will focus on in the following chapters and outline the major research gaps that I will address.

1.1 Evolution of migratory behavior in sea turtles

Migration is an adaptation to spatially- and temporally-heterogeneous environments (Alerstam et al. 2003, Fryxell and Holt, 2013). By migrating between habitats, animals are able to better exploit certain resources (e.g. food or nesting habitat) than they could if they remained at a fixed location (Cohen 1976). For migration to also become an evolutionarily stable strategy, the benefits provided by migrating must outweigh the potential costs (e.g. time and energy) of moving between these locations

(Simpson and Sword 2010). As the energetic costs of locomotion differ between animals that walk, swim, or fly (Schmidt-Nielsen 1972), the occurrence and distance of migration similarly differ between animals utilizing these separate modes of transport (Tucker 1975). Swimming appears to generally be the most energetically efficient method of moving long-distances (Schmidt-Nielsen 1972) and long-distance migrations are thus particularly common among marine species (Dingle 2006).

Of the seven extant species of sea turtle, each has been recorded conducting routine long-distance migrations (Godley et al. 2008). The prevalence of migratory behavior in sea turtles stems partially from their evolutionary heritage. Sea turtles, like many reptiles, lay hard-shelled amniotic eggs. The capacity to lay such eggs evolved when the earliest reptiles diverged from primitive amphibians about 300 million years ago (Reisz 1997). The membrane-lined amniotic egg protected the embryo from desiccation, freeing reptiles from the need to return to water for reproduction (Packard and Seymour 1997) – as is still the case for all modern amphibians. With this novel adaptation, reptiles were able to rapidly spread across terrestrial environments (Carroll 2001). However, about 110 million years ago the ancestors of all sea turtles returned to the sea and readapted to life in marine habitats (Kear and Lee 2006). Extant sea turtles now have a range of adaptation specifically suiting them to a life at sea, such as flipper-shaped limbs (Davenport et al. 1984), lungs that can survive the intense pressures experienced while diving down the water column (Berkson 1967), and specialized glands for removing the excess salt intake that is a consequence of inhabiting marine environments (Reina et al. 2002). One trait for terrestrial living that has been retained is the requirement to lay their eggs on dry land. Even though sea turtles are now able to feed, breed, and even mate in the water, adult females still emerge on sandy beaches worldwide to nest in the dry sand away from the water’s edge. Nevertheless, the environmental conditions that create a suitable nesting beach do not necessitate that a productive foraging area will be available in nearby waters. As a result, sea turtles evolved the capacity to conduct routine migrations to-and-from their distant foraging areas and nesting rookeries (James et al. 2005; Benson et al. 2011).

1.2 Threats and conservation status of the leatherback turtle

Leatherback turtles are listed on the IUCN as globally vulnerable and populations in the Pacific Ocean, Indian Ocean, and Southern Atlantic Ocean are of special concern (Wallace et al. 2013). During the latter half of the 20th century, egg poaching was the primary factor leading to the rapid decline of many leatherback turtle populations (Spotila et al. 2000). Although in many cases this issue has now been addressed (Santidrián Tomillo et al. 2008, Nel et al. 2013), many populations have continued to decline and this has been largely attributed to mortality associated with fisheries by-catch (Spotila et al. 2000). Leatherback turtles are often caught or entangled in nets or on hooks intended for commercial species, such as tuna or swordfish. Many of these individuals die as a result of not being able to return to the water's surface to breathe, are injured as they try to free themselves, ingest fishing gear that many potential suffocate them or form a blockage in their digestive system, or are injured when they are brought onboard the fishing vessel. Global estimates predict that over 50,000 leatherback turtles a year are caught as bycatch (Lewison et al. 2004).

To protect sea turtles from incidental fisheries bycatch, the first step is to identify interaction hot-spots between fisheries and turtles. This can be achieved by comparing data on the spatio-temporal distribution of both sea turtles and fisheries. In turn, this information can be used to determine the most effective methods for minimizing sea turtle by-catch. In some instances this may involve spatially- or temporally-explicit fisheries closures, restrictions or modifications to fishing gear, or changes in the depth as which fishing gear is set. A program called TurtleWatch even devised a program, founded on knowledge of the environmental habitat preferences of loggerhead sea turtles *Caretta caretta*, which provides fisheries with daily recommendations on to fish to minimize sea turtle bycatch based on remotely-sensed oceanographic conditions (Howell et al. 2008).

The substantial conservation benefits that may be gained from understanding the factors driving the oceanic distribution of leatherback turtles provided the main impetus for this thesis. In the next three sections, I will outline the three aspects of the migratory ecology of these species that I will investigate in the subsequent three chapters.

1.3 Chapter 2: Nesting phenology - being in the right place at the right time

The ultimate goal of migration – to maximize (life-time) reproductive output – is achieved through optimally managing the time spent in discrete habitats (Cohen 1976). In other words, arrival at each location of the migratory cycle should be coordinated with periods of favorable conditions, while departure ought to occur before the environment becomes too deleterious. The importance of timing in migratory behavior is particularly evident in sea turtle nesting phenology.

Sea turtles nest on sandy tropical and sub-tropical beaches worldwide. Nesting is typically seasonal, lasting between 2 to 6 months of each year; however, strong variation exists in both the onset and duration of the nesting season between populations (Mazaris et al. 2012, Robinson et al. 2014). These differences are probably driven by spatial variation in the climatic and oceanographic phenomena that influence the success of incubating sea turtle nests.

Nesting sea turtles bury their eggs at depths between 30 and 80 cm, depending on the species. After this, the eggs receive no parental care and so conditions within the nest are largely governed by ambient environmental conditions (Hays et al. 2003). Arguably, the most important environmental parameter is temperature, and the eggs must remain between 24 and 36 °C to hatch successfully (Ackerman 1997, Santidrián Tomillo et al. 2009). Temperature also dictates the gender of the developing embryos with males being produced at lower temperatures and females at higher temperatures (Morreale et al. 1982). For most species, the pivotal temperate at which 50 % females are produced occurs between 27 and 31 °C (Ackerman 1997). Consequently, there are only a small range of climatic conditions that can successfully support populations of nesting sea turtles (Pike 2013). These generally only occur in the warmest months at temperate or sub-tropical latitudes and the coldest-months in equatorial latitudes (Mazaris et al. 2012, Robinson et al. 2014).

Nest temperatures are understandably tied to local air temperatures, but they are also linked to precipitation patterns (Valverde et al. 2010). In fact, local precipitation patterns can be a better predictor of hatching success than air temperatures (Santidrián Tomillo et al. 2012). This is probably because the rainfall influences sand temperature and moisture levels, with the latter having additional impacts on hatching success (McGehee 1990). Moisture levels could even alter hatchling fitness, as seen in other Testudines (Finkler 1999).

Despite the effect that the timing of the nesting season has on the success of the incubating eggs, little is known about the mechanisms that turtles use to coordinate the timing of the nesting season or their pre-nesting migrations. Some studies have found correlations between the onset of the nesting season in loggerhead and green turtles *Chelonia mydas* and sea surface temperature of the waters both near the nesting ground and in the foraging areas (Weishampel et al. 2004; Pike et al. 2006; Mazaris et al. 2008; Mazaris et al. 2009; Weishampel et al. 2010; Dalleau et al. 2012). However, leatherback turtles are uniquely able, among sea turtles, to maintain body temperatures significantly elevated above ambient conditions through a series of adaptations termed gigantothermy (Paladino et al. 1990, Southwood et al. 2005, Bostrom & Jones 2007). The effect of temperature on the nesting phenology of leatherback turtles may therefore be less distinct. Moreover, the only published study investigating migratory phenology in leatherback turtles identified that the onset of their pre-nesting migrations were more closely correlated with surface chl-α concentrations (used as a proxy for food availability) at their foraging areas than sea surface temperature (Sherrill-Mix et al. 2008). These authors concluded that in leatherback turtles the timing of the pre-nesting migrations, which in turn dictate the timing of the nesting season, is influenced by foraging success. Simply put, animals with higher foraging success are able to acquire the necessary resources to nest earlier than animals with lower foraging success.

Additional factors that may play an important role in controlling the migratory phenology of leatherback turtles, although their effects have not been previously studied, are population size or demography. Turtles that have nested previously are known to nest earlier than neophyte nesters (Santidrián Tomillo et al. 2009; Rafferty et al. 2011). The ratio of experienced to neophyte nesters in a population could therefore influence the timing of the nesting season. Alternatively, many bird species are known to have higher mating success when populations are larger and, in turn, this also lead to earlier nesting seasons (Ezard et al. 2008, Votier et al. 2009, Doxa et al. 2012). If population size also influences nesting phenology in sea turtles the effects could be substantial, especially considering that many sea turtle populations world-wide have experienced large declines or impressive recoveries in recent years (Spotila et al. 2000; Dutton et al. 2005). Interestingly, increases were observed in the population size of many sea turtle populations were recent advances have been observed in the timing of the nesting season (Weishampel et al 2004; Pike et al. 2006).

The mechanisms that govern the timing of the nesting season in sea turtles are not currently well understood; however, understanding how sea turtle nesting phenology is likely to change in the future can play an important role in predicting how sea turtles will adapt to climate change. As global temperatures increase, this is likely to lead to increasingly female-biased sex ratios in sea turtles (Laloë et al. 2014) and overall decreases in hatching success (Santidrián Tomillo et al. 2012), unless sea turtles are able to shift the timing of the nesting season towards cooler seasonal conditions. If food availability controls the timing of the nesting season, then global shifts may be seen in nesting seasons depending on how climate change impacts food supplies. Alternatively, if population size or demography is more important than the potential for adaptation may be more dependent on other conservation strategies, such as nest shading.

In Chapter 2, I will investigate the role of food availability and population size on the nesting phenology of two major leatherback turtle nesting populations.

1.4 Chapter 3: Behavioral changes during the migratory cycle

Most turtles spend the majority of their time in the upper 200 m of the water column (Polovina et al. 2003, Sale et al. 2006, Rice and Balazs 2008), but leatherback turtles have been recorded diving to depths of up to 1280 m (Doyle et al. 2008). One of the main reasons that leatherback turtles dive to such extreme depths is to search the water-column for diel-migrating gelatinous zooplankton (Houghton et al. 2008). Gelatinous zooplankton are the predominant food source for leatherback turtles and due to their low-energy content it is estimated leatherback turtles must consume about 100 kg per day to survive (Jones et al. 2012). The movement patterns of leatherback turtles are therefore intrinsically linked to the distribution of gelatinous zooplankton in the world's oceans (Houghton et al. 2006, Witt et al. 2007). Considering that gelatinous zooplankton form a major component of most marine ecosystems (Pauly et al. 2009), often prey on or compete with commercially important fish species (Lynam et al. 2006, Kawahara et al. 2006, Quiñones et al. 2013), and pose risks to human health for beach-goers and swimmers (Gershwin et al. 2009), leatherback turtles can function as relevant indicators of broad-scale ecosystem functioning and health (Wallace et al. 2006; Fossette et al. 2010).

Leatherback turtles are often found associated with dynamic oceanographic features, such as fronts or seasonal upwelling sites that promote the formation of mass aggregations, or blooms, of gelatinous zooplankton (Shillinger et al. 2011, Dodge et al. 2014). However, these blooms are largely ephemeral in nature and the exact oceanographic conditions required for a bloom to form are not completely understood (Graham et al. 2001). In response to such dynamic prey-scapes, leatherback turtles conduct flexible foraging migrations that can encompass entire ocean basins (Hays et al. 2006). These migrations are very different to the common 'shuttling' migrations observed in loggerhead or green turtles *Chelonia mydas*, where animals migrate between specific locations along a relatively-straight and generally consistent route (Blanco et al. 2012, Schofield et al. 2013) and instead have been described as being more akin to a 'prolonged sojourn in a vast feeding area' (Luschi et al. 2006).

When analyzing the broad-scale movements of leatherback turtles, many studies have employed a range of statistical tools to determine when a switch has occurred from migrating to foraging (Eckert 2006, Jonsen et al. 2006; Jonsen et al. 2007; Bailey et al. 2008). In recent years, this has been most commonly achieved using a Bayesian State-Space Switching Models (Shillinger et al. 2011, Benson et al. 2011, Dodge et al. 2014). These models have the capacity to define a 'switch' in an individual's behavior based on its horizontal movement patterns. Specifically, if an animal has slow horizontal movement speeds and large turn angles between subsequent locations it is considered to be foraging, while if movement speeds are high and turn angles between subsequent locations are low then it considered that the animal is migrating (Jonsen et al. 2007). Although this rule is generally true for terrestrial animals (Turchin 1991, Moreales et al. 1991), it needs to be remembered that diving marine species move in a fully 3D environment. Furthermore, it has been demonstrated that changes in diving behavior can occur independently of horizontal movement patterns (James et al. 2005, Schick et al. 2013) and may even provide better indicators of foraging behavior (Sale et al. 2006). As a result, there is a need for new statistical tools to be developed that are able to identify behavioral shifts in migratory marine species from both their horizontal movement patterns and their diving behavior.

In Chapter 3, I will outline a novel statistical method to achieve this and then apply this model to analyze data from satellite-transmitters deployed on nesting leatherback turtles within the iSimangaliso Wetland Park, South Africa.

1.5 Chapter 4: Tracking animal movement through multiple methods

It is almost impossible to visually track movements of marine species over long periods of time. As such, the migratory patterns of most marine species were largely unknown until the development of animal-borne satellite telemetry devices in the early 1980s. These devices were able to relay the location of an animal anywhere in the globe, but only if the transmitter’s antenna was above the surface of the water. They were particularly suited to tracking the movements of air-breathing marine animals as they must periodically return to the surface, and the first marine animal to be successfully satellite tracked was a loggerhead turtle (Stoneburner 1982, Timko and Kolz 1982). Since these early beginnings the use of satellite telemetry to study the movement of marine megafauna has expanded exponentially and the variety of species that have been tracked in this manner is continually increasing (Hart and Hyrenbach 2009, Graham et al. 2012).

Satellite transmitters have now been deployed on all seven species of sea turtle and the insights these devices have provided into the ecology of these species has been invaluable (Morreale et al. 1996, Seminoff et al. 2008, Godley et al. 2008, Hawkes et al. 2012). Yet concurrently a wide range of chemical and isotopic tools have been developed that also have the capacity to provide information on the migratory patterns of marine megafauna (Burton 2009). Of these, perhaps the most widely used technique is stable isotope analysis. The use of stable isotope analysis for animal tracking relies on the principle that animals foraging in different locations will incorporate the unique stable isotopic signatures of the areas in which they are foraging (Hobson 1999, Rubenstein and Hobson 2004). Stable isotope analysis might not be able to currently provide as fine-scale tracking information as can be achieved by satellite telemetry, but it does have some alternative benefits. Firstly, C and N stable isotope analysis is far cheaper (approx. $10 per sample) than satellite transmitters (between $1000-5000 per unit). As a result, stable isotope analysis is far more suited, than satellite telemetry, for studies that require large sample sizes. A second benefit of stable isotope analysis is that they inform you where an animal was previously. Consequently, the inferences gained from stable isotope analysis should be affected by the sample collection. Lastly, stable isotope analysis can provide additional insights into not only the movements of the sampled animal but also its diet (Post et al. 2002).

Although the vast potential utility of stable isotope analysis in animal tracking, the foraging locations of an animal can only be determined by stable isotope analysis if the isotopic signatures of different foraging locations are known. In addition, spatial patterns in stable isotopic signatures – or isoscapes – of marine megafauna are currently only known for a few species in a few regional locations (Graham et al. 2011). To this extent, stable isotope analysis often must be validated by combining it with other tracking methods, such as satellite telemetry (Seminoff et al. 2012, Ceriani et al. 2013). Once the isoscape has been established, it can then help provide information for tracking a wide range of animals (Graham et al. 2011) and even provide information on broad-scale oceanographic patterns (Wallace et al. 2006).

In Chapter 4, I will validate the use of stable isotope analysis to track leatherback turtle movements in the waters around southern Africa. I will also use the insights provided by stable isotope telemetry to infer the potential impacts that high-drag satellite telemetry devices have on the migratory behavior of leatherback turtles.

1.6 Summary

In the following chapters of this thesis, I hope to address a number of knowledge gaps concerning the migratory ecology of the leatherback turtle. In Chapter 2, I will investigate the effects of food availability and population size on the nesting phenology of nesting populations of leatherback turtles in the Atlantic and Pacific Oceans. In Chapter 3, I will employ a novel statistical tool for analyzing the movement patterns of diving animals to investigate the migratory patterns of post-nesting leatherback turtles from the iSimangaliso Wetland Park, South Africa. In Chapter 4, I will validate the use of stable isotope analysis for tracking the movement of leatherback turtles around the waters of southern Africa and also investigate the potential impacts of high-drag biologging devices on the migratory behavior of these animals.

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CHAPTER 2. MULTIDECADAL TRENDS IN THE NESTING PHENOLOGY OF PACIFIC AND ATLANTIC LEATHERBACK TURTLES ARE ASSOCIATED WITH POPULATION DEMOGRAPHY

2.1 Abstract

Knowledge of the mechanisms influencing phenology can provide insights into the adaptability of species to climate change. Here, I investigated the factors influencing multidecadal trends in the nesting phenology of the leatherback turtle *Dermochelys coriacea* at Playa Grande, Costa Rica, in the eastern Pacific Ocean and at Sandy Point, US Virgin Islands, in the western Atlantic Ocean. Between 1993 and 2013, the median nesting date (MND) at Playa Grande occurred later, at a rate of ~0.3 d yr^{-1}. In contrast, between 1982 and 2010, the MND at Sandy Point occurred earlier, at a rate of ~0.17 d yr^{-1}. The opposing trends in the MND of each population were not explained by variation in the multivariate El Niño-Southern Oscillation index, North Atlantic Oscillation index, or Atlantic Multidecadal Oscillation index; however, the MND at Playa Grande was significantly correlated with nesting population size. I propose that changes in the ratio of earlier-nesting ‘experienced’ turtles to later-nesting neophyte nesters, which are linked to the population decline at Playa Grande, and the population recovery at Sandy Point may explain the contrasting trends in MNDs. If the observed trends in MND continue into the future, the nesting season at Playa Grande will coincide with increasingly adverse conditions for hatching success, exacerbating the already detrimental effects of climate change. Alternatively, shifts in the nesting phenology may make the Atlantic populations more resilient to climate change. Our findings highlight the increasing need for conservation efforts for eastern Pacific leatherback turtles to consider climate change mitigation practices.

2.2 Introduction

As global temperatures continue to rise, there is increasing concern over the ability of organisms to adapt to these changes (Hoffmann & Sgrò 2011, Doney et al. 2012, Pike 2014). A potential plastic response to climate change is a shift in the timing of seasonal biological phenomena, termed phenology (Parmesan 2006). By migrating and reproducing when seasonal weather patterns are cooler, many migratory species have mitigated some of the detrimental effects of a warming climate on reproductive success (Møller et al. 2008). Yet such adaptive trends are not universal among species (Both et al. 2009) or even populations (Gordo 2007). Understanding why different populations express divergent responses to climate change requires an understanding of the factors governing the phenology of a species (Gienapp et al. 2007). Moreover, such knowledge is necessary for developing bioclimatic envelope models with the capacity to accurately predict the response of a species to climate change at regional, or even global, scales (Guisan & Thuiller 2005).

Sea turtles nest on tropical and sub-tropical beaches during distinct nesting seasons that generally last between 3 and 6 mo. The timing of the nesting season must, at least partially, coincide with seasonal temperature and precipitation patterns that create suitable conditions for incubating eggs on the beach (Pike 2013). As climate change progresses, however, shifts in phenology may be required to maintain the nesting season within optimal beach conditions. Indeed, a recent climate-forced population model for the eastern Pacific leatherback turtle *Dermochelys coriacea* predicted that the anticipated reduction in hatching success resulting from a warming climate could be partially offset if the nesting season shifts to earlier in the year when conditions are cooler and wetter (Saba et al. 2012). Incubation temperatures also govern the gender of the developing hatchlings, with females being produced at higher temperatures (Binckley et al. 1998). Shifts in nesting phenology could therefore have the additional benefit of counteracting female-biases in hatchling production (Doody et al. 2006). However, no previous studies have investigated whether leatherback turtles are likely to respond to climate change though adaptive shifts in nesting phenology.

The factors governing nesting phenology have only been investigated for 2 sea turtle species: loggerhead turtles *Caretta caretta* (Weishampel et al. 2004, Pike et al. 2006, Mazaris et al. 2013) and green turtles *Chelonia mydas* (Pike 2009, Weishampel et al. 2010, Dalleau et al. 2012). For both species, it has been repeatedly shown that the timing of the nesting season is influenced by the sea surface temperature of the waters near the nesting grounds (e.g. Weishampel et al. 2004, 2010, Mazaris et al. 2008, Dalleau et al. 2012). However, leatherback turtles are uniquely able among sea turtles to maintain elevated and constant body temperatures through a series of adaptations termed gigantothermy (Paladino et al. 1990, Southwood et al. 2005, Bostrom & Jones 2007). The effect of temperature on the nesting phenology of leatherback turtles may therefore be less distinct. Consequently, determining the factors influencing leatherback nesting phenology likely requires the investigation of a broader range of oceanographic variables. Furthermore, even though local climate conditions directly affect hatching success (Santidrián Tomillo et al. 2009, 2012), environmental conditions at the nesting beach are unlikely to govern when a turtle will arrive at the nesting beach, although they may do so over long time scales through natural selection (Berteaux et al. 2004). This is because leatherback turtles conduct extensive reproductive migrations, and the distance between nesting grounds and foraging areas can extend across entire ocean basins (Benson et al. 2011, Witt et al. 2011). As a result, the nesting grounds are often physically disconnected from the climate of the foraging area.

Leatherback turtles forage exclusively on gelatinous zooplankton, a polyphyletic taxon whose distribution is strongly tied to physical oceanographic conditions (Graham et al. 2001). As a result, the broad-scale distribution and abundance of gelatinous zooplankton are often tied to large oceanographic phenomena, such as the El Niño-Southern Oscillation (ENSO; Raskoff 2001), North Atlantic Oscillation (NAO; Lynam et al. 2004), and the Atlantic Multidecadal Oscillation (AMO; Edwards et al. 2013). In turn, such oceanographic phenomena are also inherently linked to foraging success in leatherback turtles (Saba et al. 2007, Reina et al. 2009). Moreover, the relationships observed between oceanographic conditions and the onset of migration towards the nesting grounds has led to the hypothesis that turtles foraging in more productive areas are able to acquire resources more rapidly, allowing them to migrate to their nesting grounds earlier (Saba et al. 2007, Sherrill-Mix et al. 2008). In addition, leatherback turtles are expected to forage while migrating (Lambardi et al. 2008). Consequently, a decrease in food availability en route could result in increased time spent searching for food and a longer migration duration. Better foraging conditions could even increase the number of clutches that each female lays in the upcoming nesting season. This would extend the length of time that each turtle spends at the nesting grounds and may even extend the length of the nesting season.

Beyond the impacts of foraging success, nesting phenology may also be related to factors such as population size or structure (Votier et al. 2009, Shirai 2013). In another marine migrant, the dalmatian pelican *Pelecanus crispus, larger populations* nest earlier than smaller populations (Doxa et al. 2012). Although the exact mechanism driving this phenomena is not well understood, it could be linked to population demographics. In many birds, older individuals also tend to nest earlier in the year than younger individuals (Hipfner et al. 2010). Similar trends have been observed in leatherback turtles, as older and/or more experienced individuals tend to arrive earlier to nest and lay more clutches (Santidrián Tomillo et al. 2009, Rafferty et al. 2011). As a result, populations with an older mean age may have both earlier and longer lasting nesting seasons (Ezard et al. 2007).

In the present study, I investigated the nesting phenology of 2 leatherback turtle populations over multiple decades. Firstly, I determined whether there had been a change in the timing or length of the nesting season over the study period. Secondly, I investigated whether interannual patterns in nesting phenology were influenced by oceanographic conditions experienced prior to departing the foraging area, while departing the foraging area, during migration, or after arriving at the nesting grounds. Thirdly, I investigated whether nesting phenology was affected by population size. Lastly, to discern how any shifts in nesting phenology may be influencing the conditions experienced by the developing nests, I compared historic trends in nesting phenology to local air temperatures and precipitation levels.

I obtained data from 2 of the longest tagging programs for nesting leatherback turtles: Playa Grande, Costa Rica (10° 20’ N, 85° 51’ W), in the eastern Pacific Ocean and Sandy Point, US Virgin Islands (17° 40’ N, 64° 52’ W), in the western Atlantic Ocean. I chose these sites because both support long-term (≥ 20 yr) tagging programs, are located in separate ocean basins, and have contrasting population trends, with the population decreasing at Playa Grande (Santidrián Tomillo et al. 2007, F. V. Paladino unpubl. data) and increasing at Sandy Point (Dutton et al. 2005, USFWS unpublished data). By investigating 2 distinct populations, I aimed to investigate differences in the capacity of leatherback turtles from either the Pacific or Atlantic Ocean to respond to climate change via adaptive shifts in nesting phenology.

2.3 Methods

2.3.1 Study sites

Playa Grande is a sandy beach, 3.6 km long, on the Pacific coast of Costa Rica. Playa Grande is part of a 3-beach complex, along with nearby Playa Ventanas (1 km long) and Playa Langosta (1.3 km), all of which are used by substantial numbers of nesting leatherback turtles (Reina et al. 2002). Together, these beaches host an estimated 70% of the entire leatherback population nesting on the eastern Pacific shores of Costa Rica and have the highest density of nesting leatherback turtles in the eastern Pacific Ocean. Of these 3 beaches, Playa Grande has supported the longest running monitoring program for leatherback turtles (since 1993/94) and has the majority of the nesting activity (70 to 90%; Reina et al. 2002). In the present study, I thus exclusively used data collected on Playa Grande.

Sandy Point is a dynamic sandy beach (3.0 km long) on the coast of St. Croix, US Virgin Islands, in the Atlantic Ocean. A tagging program for nesting leatherback turtles at Sandy Point has been in place since 1978. Even though consistent saturation tagging (the concept of identifying every turtle on a specified nesting beach) has only been achieved since 1982, this still remains one of the longest running saturation tagging programs for leatherback turtles worldwide.

2.3.2 Nesting dates

At both locations, the nesting season began in the coolest month of the year and lasted for approximately 6 mo; at Playa Grande, the nesting season was between October and March, while at Sandy Point it was between March and August. Over the nesting season, the beaches were patrolled nightly to encounter nesting females as well as to count and identify tracks of missed turtles. In this manner, a track was recorded for every sea turtle emergence even if the turtle itself was not encountered.

For logistical reasons, the start and end dates of the monitoring programs differed between years. I accounted for this sampling bias by cropping the available datasets to include only the longest consistently patrolled sampling period for all of the years in the study. For Playa Grande, this was between 1 November and 10 February (a total of 132 d) from 1994/95 until 2011/12, and for Sandy Point, this was between 1 April and 5 July (95 d) from 1982 until 2010.

Differences in the monitoring methodologies between Playa Grande and Sandy Point affected our ability to calculate nightly nesting activity. At Playa Grande, observers recorded whether or not a track contained a body-pit, i.e. a large disturbance in the sand that is formed during the initial stages of the nesting process. At Playa Grande, around 10% of the turtles were missed and only a body-pit was seen. Although it is difficult to confirm whether a leatherback turtle nested from visual inspection of only its tracks, body-pits were readily identifiable from the tracks, and 90% of body pits were shown to result in a nest (Reina et al. 2002). Consequently, I used body-pit counts as our measure of nesting activity at Playa Grande. At Sandy Point, it was not the practice to record from a track whether a body-pit was made or not. Therefore, I used confirmed nest counts (where the turtle was witnessed laying) as our measure of nesting activity at Sandy Point. At this location, less than 5% of turtles were missed each year.

Using the daily body-pit counts at Playa Grande and daily nest counts at Sandy Point, I calculated the median nesting date (MND). One day was added to the median nesting date during each leap year. I also calculated the standard deviation of the mean nesting date. I termed this measure the central tendency of the nesting season (CTns). As the distribution of nesting activity in sea turtle nesting seasons can be roughly fit to a normal distribution (Girondot et al. 2007), the CTns could be used as a proxy for the length of the nesting season.

2.3.3 Ocean conditions

I compared the MND and CTns to the multivariate ENSO index (MEI) for turtles nesting at Playa Grande, and to the NAO and AMO indices for turtles nesting at Sandy Point. These oceanographic indices provide a univariate representation of oceanographic conditions within the Pacific or Atlantic Oceans. Values for the MEI, NAO, and AMO were accessed from www.esrl.noaa.gov/psd/enso/mei/, www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao_index.html, and www.esrl.noaa.gov/psd/data/correlation/amon.us.data, respectively.

To determine whether oceanographic conditions influence the MND and CTns, we chose to average the MEI or NAO over discrete periods of time that would best coincide with different parts of the migratory cycle. To this extent, I averaged the MEI and NAO over 4 discrete 3 mo periods that encompassed the year preceding the month of peak nesting, which was December for Playa Grande and May for Sandy Point. From earliest to latest, the 3 mo periods represented the conditions (1) before departure from the foraging areas, (2) during departure from the foraging areas, (3) during migration from foraging to nesting grounds, and (4) upon arrival at the nesting grounds. These 3 mo time periods were chosen because post-nesting leatherback turtles require between 2 and 6 mo to reach their foraging areas (James et al. 2005, Shillinger et al. 2008). Thus I assumed that the pre-nesting migrations would take a similar length of time and individuals would remain in their foraging grounds for many months before returning to their nesting areas. Furthermore, the nesting seasons at Playa Grande and Sandy Point last around 6 mo, with the majority of turtles arriving in the first 3 mo.

2.3.4 Population size

At Playa Grande and Sandy Point, passive integrated transponder (PIT) tags with unique ID numbers were implanted into every turtle encountered over the nesting season. As leatherback turtles nest an average of 7 times per nesting season (Reina et al. 2002) and there was a ~90 to 95% encounter rate for nesting turtles at Playa Grande and Sandy Point, respectively, there is only a nominal probability that a turtle would be missed in a given season. Thus, these tagging data provide an accurate representation of the number of nesting individuals each year.

2.3.5 Local air temperature and rainfall

Monthly air temperatures and rainfall for Playa Grande and Sandy Point were obtained from the Daniel Oduber Quiros International Airport (44 km from the nesting site) via the National Meteorological Institute of Costa Rica. For Sandy Point, these data were obtained from the Christiansted Hamilton Field Airport (10 km from the nesting site) via www. ncdc.noaa.gov/cdo-web/datasets/GHCNDMS/stations/GHCND:VQW00011624/detail. I calculated the mean monthly air temperature and total precipitation over the 6 mo nesting season.

2.3.6 Statistical analyses

I tested whether there had been a change in the MND, CTns, local air temperature, or local precipitation over the study period using least-squares linear regression. To compare the effects of ocean conditions before departure from foraging areas, ocean conditions during departure from foraging areas, ocean conditions during migration to nesting grounds, ocean condition on arrival at nesting grounds, and nesting population size on the MND and CTns, I used a generalized linear model with a Gaussian variance function and an identity link function. I compared these models using Akaike's information criterion (AIC). Data were analysed using program R (R Development Core Team). For all statistical tests, $\alpha = 0.05$.

2.4 Results

At Playa Grande between 1993–94 and 2012–13, the MND shifted to later in the season at a rate of approximately 0.31 d yr^{-1}, totaling a shift of 6 d (Fig. 1a). This shift was close to statistical significance ($r^2 = 0.17$; $p = 0.07$). The MND was highly variable with a range of 17 d. Much of this range was attributed to atypically late MNDs that occurred in 1993–94, 2002–03, and 2008–09. At Sandy Point, the MND shifted to earlier in the season at a rate of approximately 0.17 d yr^{-1}, totaling a shift of 5 d over 29 yr (Fig. 1c). While this shift was smaller than that at Playa Grande, it was statistically significant ($r^2 = 0.14$, $p < 0.01$). The total range of MNDs at Sandy Point was 14 d.

I found no significant correlations between the MND at Playa Grande and the MEI, yet there was a significant negative correlation between population size and the MND at Playa Grande ($p < 0.01$; Table 1; Fig. 2a). Furthermore, the AIC indicated that the best model for predicting MND included population size as the only variable (Table 2). No significant correlations were found between the MND at Sandy Point and the NAO, AMO, or population size (Table 1).

At both locations, the CTns showed no significant change over time (Playa Grande: $r^2 = 0.02$, $p = 0.53$; Sandy Point: $r^2 = 0.04$, $p = 0.32$; Fig. 1d). However, significant negative correlations were observed between the CTns at Playa Grande and the MEI during migration ($p = 0.03$) and the CTns at Sandy Point and the NAO during departure ($p < 0.01$; Table 1, Fig. 3a,b).

At Playa Grande, neither local air temperatures ($r^2 < 0.01$, $p = 0.77$) nor precipitation levels ($r^2 < 0.01$, $p = 0.97$) showed any significant changes over the study period (see Fig. 4). The local air temperatures at Sandy Point decreased significantly ($r^2 =$

0.28, $p < 0.01$), but the observed decrease in precipitation levels was not significant ($r^2 = 0.04$, $p = 0.22$).

At both sites, there was a large change in the size of the nesting population over the study period, which was evident beyond the substantial interannual fluctuations. The number of turtles nesting per year at Playa Grande decreased from ~300 at the beginning of this study to ~30 at the end. In contrast, the number of turtles nesting per year at Sandy Point increased from ~20 to ~150.

2.5 Discussion

Here, I examined multidecadal trends in the nesting phenology of 2 populations of leatherback turtles inhabiting different ocean basins. To determine which factors govern nesting phenology for each population, I compared the observed trends in MND and CTns to ocean conditions experienced at different phases of migration as well as nesting population size. I also compared past trends in the MND to conditions at the nesting beach, to determine how such phenological changes may affect conditions for incubating nests. This information provided insights into the capacity of different leatherback turtle populations to adapt to future climate change through shifts in the timing of the nesting season.

Over the study period, the MND at Playa Grande occurred later, at a rate of 0.31 d yr^{-1}. In contrast, the MND at Sandy Point occurred earlier, at a rate of 0.17 d yr^{-1}. Such shifts in nesting phenology are relatively slow compared to other sea turtle species at higher-latitude nesting beaches (e.g. Weishampel et al. 2004, Pike et al. 2006, Mazaris et al. 2013). Moreover, the shift observed at Playa Grande is the first time a shift for nesting late in the year has been reported for any sea turtle population.

The strongest correlation with MND was observed between nesting population size and MND at Playa Grande. Although the shift in the nesting phenology at Playa Grande over time was not significant, this trend is likely to continue if the nesting population size is indeed affecting nesting phenology and population size continues to decline. However, no significant correlation was observed between nesting population size and the MND at Sandy Point. I therefore hypothesize that the changes in nesting phenology may not be driven specifically by nesting population size, but by changes in nesting population demography. Specifically, the trends may be caused by changes in the ratio of younger and later nesting turtles to more experienced, and earlier nesting, turtles. Between the mid-1970s and early 1990s, approximately 90% of all the eggs laid at Playa Grande were poached (Santidrián Tomillo et al. 2008). As leatherback turtles are estimated to reach sexual maturity between 9 and 16 yr (Zug & Parham 1996, Jones et al. 2011), the resulting 'missing' generation should have begun nesting between the mid-1980s and early 2000s. Consequently, in 1993 at Playa Grande, the beginning of our study period, a large portion of the younger and later nesting individuals were absent. Yet over time, as the hatchlings from nests protected from poaching became reproductively mature, this younger generation of nesting turtles should again reappear in the population and this should shift the MND to later in the year. This shift in the average age of the population at Playa Grande may even be compounded by the increasingly high levels of adult mortality suffered by this population due to incidental take by fisheries (Spotila et al. 2000, Lewison et al. 2004), which would also reduce the average age of the population. In contrast, at Sandy Point, there has been a marked increase in the population of nesting leatherback turtles since the early 1980s (Dutton et al. 2005). As this increase was largely a product of increased recruitment into the population, the average age of the nesting population has probably remained low or only increased slightly, thus potentially explaining the lack of a correlation between nesting population size and MND at Sandy Point.

At both Playa Grande and Sandy Point, I found no correlation between the MND and any of the chosen oceanographic indices. Such results are surprising considering that oceanographic conditions have previously been linked to the departure date of prenesting leatherback turtles from their foraging areas in the waters of eastern Canada (Sherrill-Mix et al. 2008). However, that study investigated satellite-tracked individuals and thus was able to examine the oceanographic conditions directly at the animal's location. In our study, I did not know the exact location of the turtles prior to nesting so I chose to use indices that provide a coarse representation of ocean conditions over entire ocean basins, specifically the MEI, NAO, and AMO. Our decision to use such broad-scale oceanographic factors may have masked the actual effect of ocean conditions on the MND. Thus, I recommend that future studies attempt to focus their investigation onto areas within known high-use leatherback turtle habitats, such as the eastern portion of the South Pacific Gyre for turtles from Playa Grande (Shillinger et al. 2011) or the waters of eastern Canada for the turtles from Sandy Point (Fossette et al. 2010).

The only correlations I found between oceanographic conditions and nesting phenology were between the MEI and NAO with the CTns of nesting season at Playa Grande and Sandy Point, respectively. Specifically, CTns at Playa Grande was negatively correlated with the MEI during the migration period, and CTns at Sandy Point was negatively correlated with the NAO during the departure period. Positive values of the MEI are generally associated with lower food availability for leatherback turtles in the Pacific Ocean (Saba et al. 2007, Reina et al. 2009), and similar patterns might also be true for the NAO in the Atlantic Ocean (Attrill et al. 2007). When less food is available to pre-nesting turtles, they might not be able to brood as many eggs and thus lay fewer clutches on arrival at the nesting grounds, leading to a shorter nesting season. Alternatively, if food is more patchily distributed then this could also lead to greater variation in departure dates and, in turn, also arrival dates.

2.5.1 Conservation implications

At both Playa Grande and Sandy Point, beach temperatures increase over the season (Santidrián Tomillo et al. 2009; see Fig. 5). Consequently, nests laid later in the season are exposed to hotter and drier conditions and this leads to female-skewed sex ratios, lower hatching success, and reduced emergence rates (Santidrián Tomillo et al. 2009). At Playa Grande, where the nesting season is shifting to later in the year, this means that an increasing portion of the population will experience fatally hot and dry conditions, and hatchling output will decrease. Furthermore, those hatchlings that are produced will be increasingly female. Even though no increase in local temperature has been recorded over the past 20 yr, female-skewed sex ratios and declines in hatchling output are likely to be further exacerbated by future climate change (Santidrián Tomillo et al. 2012) as global temperatures are expected to increase by approximately 2°C before the end of this century (Stocker et al. 2013).

In contrast to the leatherback turtles nesting in Playa Grande, those nesting at Sandy Point may be able to better persist under conditions of climate change due to the observed shifts in nesting phenology. Indeed, so far the MND at Sandy Point is shifting towards cooler conditions at the beginning of the nesting season. Local air temperatures have even decreased over the past 29 yr. However, this does not mean that populations at Sandy Point are safe from the effect of climate change over long time scales. Shifts in nesting phenology may not continue indefinitely if they are ultimately controlled by demography, and even the lowest seasonal temperatures will eventually rise if current trends persist with climate change.

If population demography does have a significant influence on nesting phenology, a method to facilitate beneficial shifts in nesting phenology may be possible. Specifically, conservation efforts that focus on reducing adult mortality may have the additional benefit of increasing the average age of the nesting population. More experienced, older individuals also tend to nest earlier and so this could shift the MND to earlier in the year. Yet it must be noted that the shifts observed in our study are small and, thus, shifts in nesting phenology may not be rapid enough to offset the future impacts of rapid climate change. Instead, the conservation of leatherback turtles, especially in the Pacific Ocean where populations are already severely depleted (Spotila et al. 2000, Tapilatu et al. 2013), may have to rely on additional proactive measures to reduce incubation temperatures for eggs through direct manipulation of environmental conditions, e.g. watering or shading nests (Patino-Martinez et al. 2012).

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2.7 Tables

Table 2.7.1 Comparison of median nesting date (MND) and central tendency of the nesting season (CTns; see ‘Materials and methods: Nesting dates’) for leatherback turtles *Dermochelys coriacea* at Playa Grande, Costa Rica (Pacific Ocean), and Sandy Point, US Virgin Islands (Atlantic Ocean), to oceanographic conditions and population size using a generalized linear model with a Gaussian variance function and an identity link function. MEI: Multivariate El Niño-Southern Oscillation index; NAO: North Atlantic Oscillation index; AMO: Atlantic Multidecadal Oscillation index. Each index was averaged over periods that represented the time before departure from the foraging area, during departure from the foraging area, during migration between foraging and nesting areas, and upon arrival at the nesting areas. Asterisks (*) denote a significant correlation (p < 0.05).

Variable	Playa Grande		Sandy Point			
	MEI		NAO		AMO	
	t	p	*t*	p	*t*	p
MND						
Before departure	- 0.07	0.95	0.71	0.72	< 0.01	0.93
Departure	0.50	0.63	0.06	0.06	0.02	0.45
Migrating	- 0.29	0.78	0.39	0.39	0.03	0.38
Arrival	- 0.32	0.75	0.60	0.60	0.08	0.14
Combined	- 0.30	0.77	0.94	0.94	0.07	0.15
Population size	- 3.39	< 0.01*	0.67	0.57		
CTns						
Before departure	- 0.51	0.64	0.94	0.17	0.18	0.74
Departure	- 1.03	0.32	0.43	< 0.01*	0.12	0.93
Migrating	- 2.35	0.03*	0.37	0.10	0.21	0.62
Arrival	- 1.96	0.07	0.14	0.99	0.12	0.94
Combined	- 1.59	0.13	0.14	0.21	0.12	0.87
Population size	- 1.93	0.07	1.05	0.41		

Table 2.7.2 Akaike's Information Criterion (AIC) for each model comparing oceanographic conditions or population size of leatherback sea turtles *Dermochelys coriacea* to median nesting date (MND) or to the central tendency of the nesting season (CTns). AIC values are presented for models including only a single parameter (oceanographic conditions: before departure from the foraging area, during departure from the foraging area, during migration between foraging and nesting areas, and upon arrival at the nesting areas; or population size) and for models with 2 parameters (oceanographic conditions and population size). Lowest values for AIC denote the best model and are indicated with an asterisk (*). Nesting locations are Playa Grande, Costa Rica (Pacific Ocean), and Sandy Point, US Virgin Islands (Atlantic Ocean). MEI: Multivariate El Niño-Southern Oscillation index; NAO: North Atlantic Oscillation index; AMO: Atlantic Multidecadal Oscillation index.

	Playa Grande		Sandy Point			
	MEI		NAO		AMO	
Model	AIC (Single parameter model)	AIC (Model w/ population size)	AIC (Single parameter model)	AIC (Model w/ population size)	AIC (Single parameter model)	AIC (Model w/ population size)
MND						
Before Departure	121.47	111.04	160.44	162.18	160.58	162.17
Departure	121.20	109.92	156.69*	157.55	159.92	161.91
Migrating	121.39	111.03	159.78	161.54	159.72	161.69
Arrival	121.36	111.01	160.29	162.01	158.14*	160.13
Combined	121.38	111.08	160.58	162.20	158.14*	160.21
Population Size	109.08*		160.22	160.95	159.61	
CTns						
Before Departure	48.47	46.45	82.24	83.45	85.64	84.98
Departure	47.62	45.99	79.54*	82.86	85.24	85.21
Migrating	43.41*	43.45	83.54	84.28	85.14*	84.75
Arrival	44.91	43.76	84.25	83.65	85.78	85.69
Combined	46.13	44.62	83.55	82.41	85.69	84.59
Population Size	44.99		84.21		84.58	

2.8 Figures

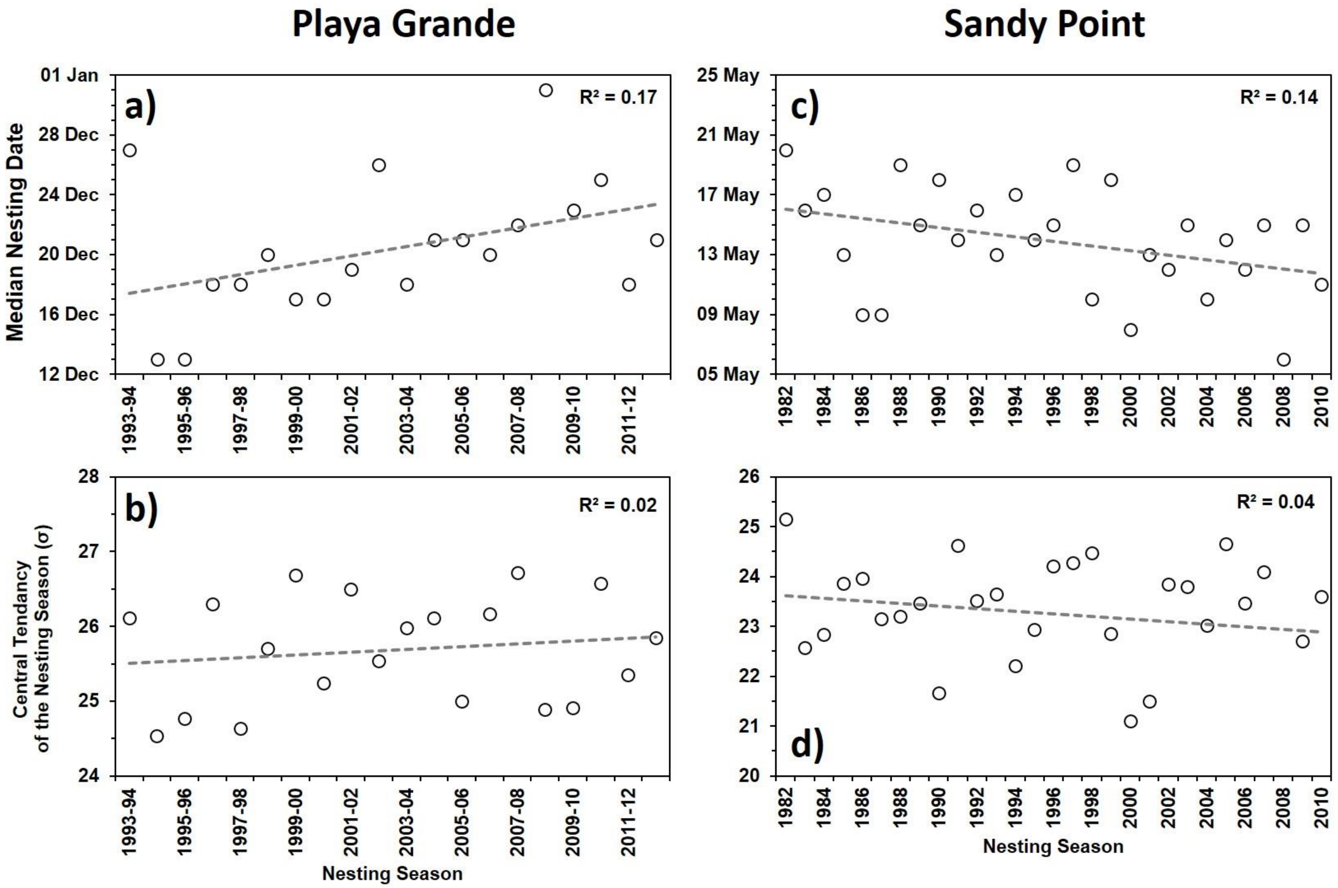
Playa Grande
Sandy Point
a)
R² = 0.17
Median Nesting Date
01 Jan
28 Dec
24 Dec
20 Dec
16 Dec
12 Dec
1993-94
1995-96
1997-98
1999-00
2001-02
2003-04
2005-06
2007-08
2009-10
2011-12
c)
R² = 0.14
25 May
21 May
17 May
13 May
09 May
05 May
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
b)
R² = 0.02
Central Tendancy of the Nesting Season (σ)
28
27
26
25
24
Nesting Season
d)
R² = 0.04
26
25
24
23
22
21
20
Nesting Season

Fig. 2.8.1 Interannual trends in (a,c) the median nesting date (MND) and (b,d) the central tendency of the nesting season (CTns; see ‘Materials and methods: Nesting dates’) for leatherback turtles *Dermochelys coriacea* at (a,b) Playa Grande (Pacific Ocean) and (c,d) Sandy Point (Atlantic Ocean). Dashed lines represent linear least-squares trendlines.

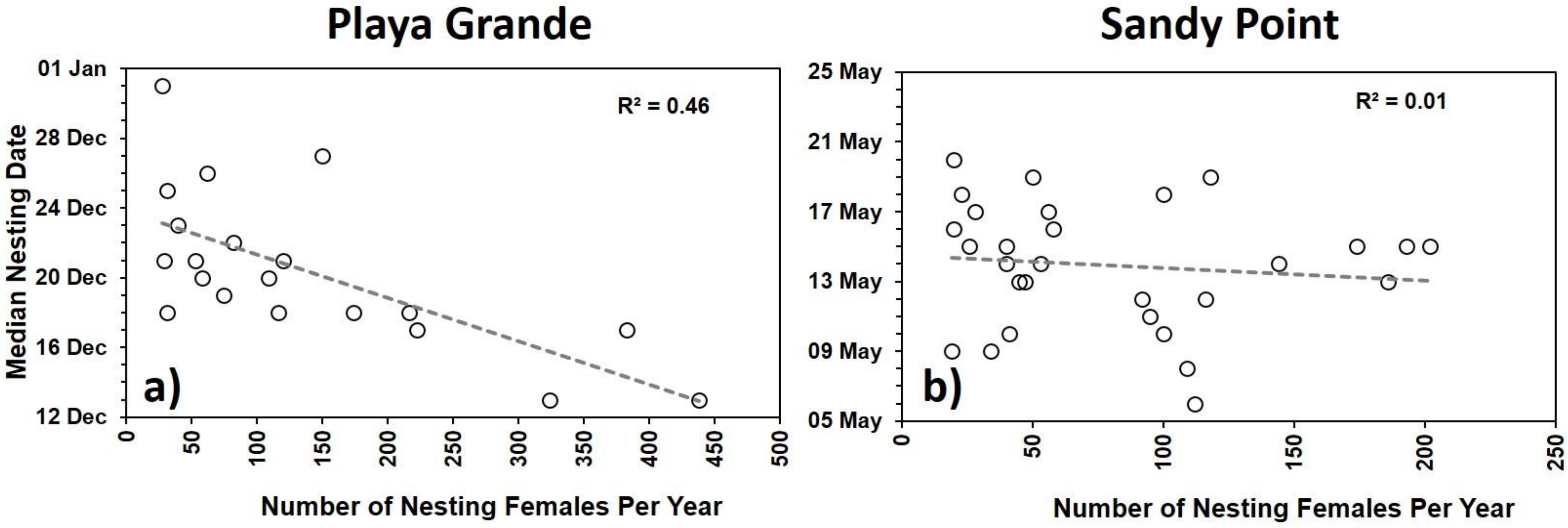

Fig. 2.8.2 Comparison of the median nesting date (MND) of leatherback turtles *Dermochelys coriacea* to nesting population size at (a) Playa Grande (Pacific Ocean) and (b) Sandy Point (Atlantic Ocean). Dashed lines represent linear least-squares trendlines.

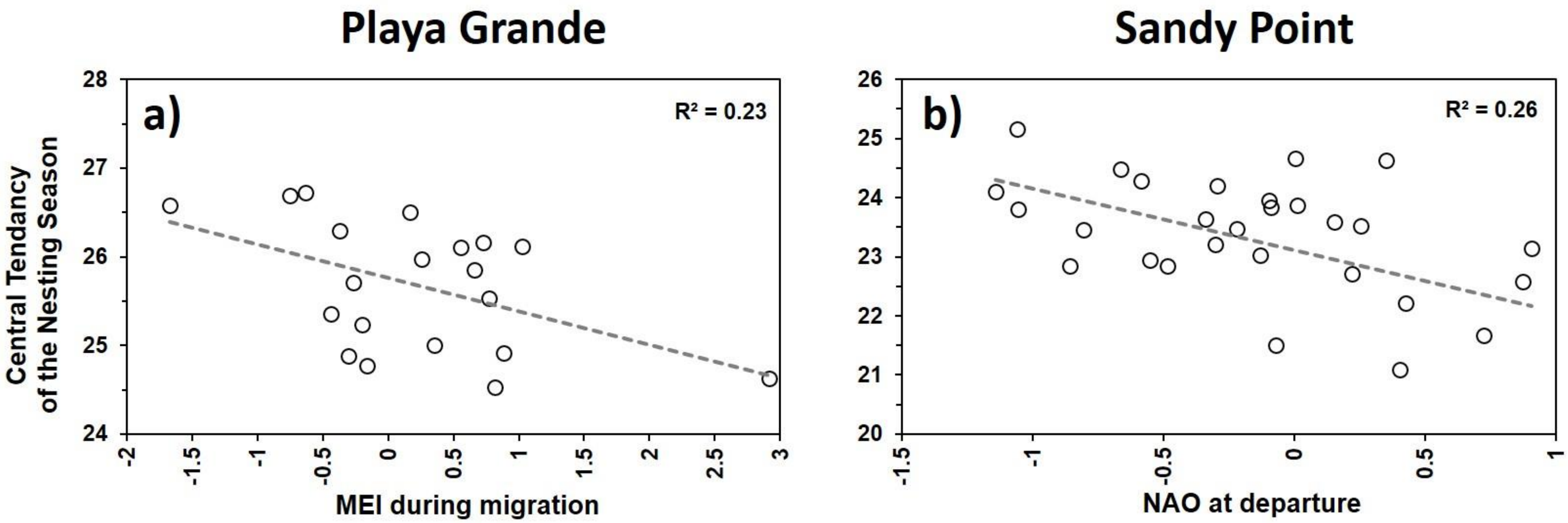

Fig. 2.8.3 Comparison of the central tendency of the nesting season CTns for leatherback turtles *Dermochelys coriacea* and oceanographic conditions during specific sections of their post-nesting migrations. (a) At Playa Grande, the comparison between the contrary tendency of the nesting season and the multivariate El Niño-Southern Oscillation index (MEI) during the migration between foraging areas and nesting grounds is shown. (b) At Sandy Point, the comparison between the contrary tendency of the nesting season and the North Atlantic Oscillation (NAO) index during departure from the foraging areas is shown. Dashed lines represent linear least-squares trendlines.

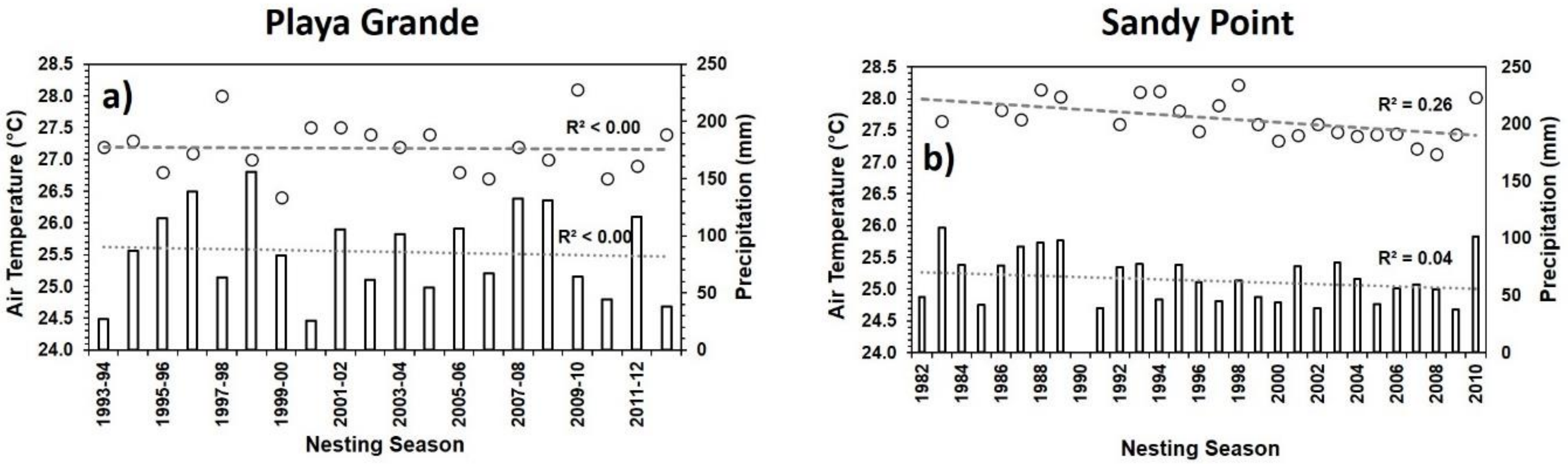

Fig. 2.8.4 Mean air temperature (dots) and total precipitation (bars) over the leatherback sea turtle *Dermochelys coriacea* nesting seasons at Playa Grande (October to March) and Sandy Point (March to August). Data for Playa Grande were obtained from the Daniel Oduber Quiros International Airport, 44 km from the nesting beach. Data for Sandy Point were obtained from the Christiansted Hamilton Field Airport, 10 km from the nesting beach. Dashed lines represent linear least-squares trendlines.

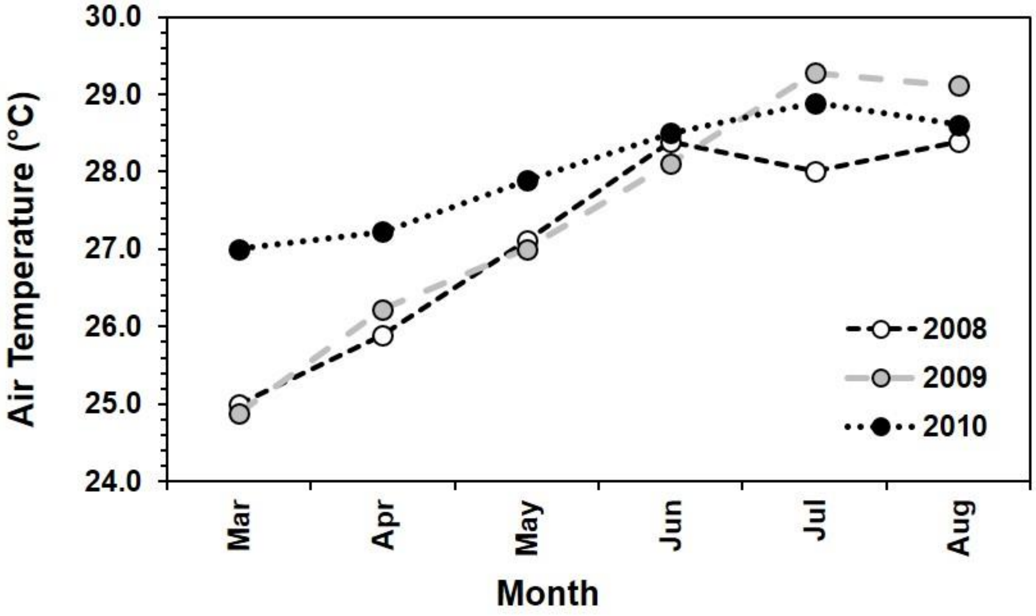

Fig. 2.8.5 Average monthly air temperatures from the Christiansted Hamilton Field Airport, 10 km from Sandy Point, during the leatherback sea turtle *Dermochelys coriacea* nesting season. Data are from 2008 until 2010.

CHAPTER 3. MIGRATORY MOVEMENTS AND DIVING BEHAVIOR OF LEATHERBACK TURTLES AROUND SOUTHERN AFRICA: EMPLOYING A NOVEL CHANGEPOINT ANALYSIS MODEL TO IDENTIFY BEHAVIORAL CHANGES IN BIOTELEMETRY DATA

3.1 Abstract

Maximising the insights that we can gain from the use of novel telemetry devices requires the simultaneous development of novel methods for analyzing the resulting data. Here, I describe a model based around Changepoint Analysis that has the capacity to identify behavioral shifts in migrating marine animals by simultaneously analyzing patterns in both horizontal and vertical (diving) movement patterns. I apply this model to investigate the movement patterns of 16 leatherback turtles *Dermochelys coriacea* tracked from their nesting beaches in the iSimangaliso Wetland Park, South Africa. Post-nesting leatherback turtles migrated to either pelagic foraging areas in the Western Indian or South Atlantic Ocean or, previously undescribed, coastal foraging areas in the Mozambique Channel. The foraging patterns of pelagic individuals were strongly associated with ephemeral mesoscale eddies, while those of ‘coastal’ individual were strongly associated with net primary productivity. Nevertheless, all individuals made comparable changes in dive behavior when reaching a foraging area, which suggests that diving behavior is an important metric when identifying foraging behaviour. Unlike the pelagic individuals, the coastal cohort remained with the Exclusive Economic Zones of South Africa and Mozambique. Furthermore, on reaching their foraging areas they remained resident within areas generally less than 50 km^2 for the remainder of the tracking duration. Thus, these coastal individuals could provide a unique opportunity for focused conservation measures.

3.2 Introduction

Establishing the movement patterns of free-ranging animals is imperative to understanding their behavior and ecology, and is often necessary for designing conservation strategies (Liedvogel et al. 2014). Today, the movements of almost any animal can be tracked as long as they are large enough to carry a satellite transmitter (Hart and Hyrenbach 2009, Bridge et al. 2011). In addition, telemetry devices are increasingly being fitted with arrays of sensors able to record and relay auxiliary biological information, such as body temperature or heart-beat rate (Cooke et al. 2004, Evans et al. 2012). The scope of the data that can be gathered from modern biotelemetry devices is extensive (Payne et al. 2014); however, maximizing the ecological insights that can be gained from the use of such devices often requires the development of equally novel methods for analyzing the resulting data (Jonsen et al. 2003, Shepard et al. 2008).

As animals move through heterogeneous landscapes, their movement patterns change depending on local conditions (Lima and Zollner 1996, Firle et al. 1998). To understand an animal's long-term movement patterns therefore requires statistical techniques for delineating between behavioral states, such as transiting or foraging (Morales et al. 2004, Gurarie et al. 2009, Jonsen et al. 2012). This can be achieved using a Switching State-Space Model (SSSM) and the use of these tools has rapidly proliferated in recent years, especially when analyzing the movement of marine megafauna (Patterson et al. 2008, Hart and Hyrenbach 2009, Jonsen et al. 2012). SSSMs are statistically robust tools for identifying transitions between discrete behavioral-states, while also accounting for the measurement error and opportunistic data recovery inherent in satellite telemetry (Jonsen et al. 2005, Jonsen et al. 2007).

Most SSSM analyses of animal tracking data use movement speed and turn angle to discriminate between Area Restricted Search (ARS) behavior – often considered a proxy for foraging – and transiting behavior (e.g. Benson et al. 2011, Shillinger et al. 2011, Bailey et al. 2012a, Dodge et al. 2014). ARS is characterized as a decrease in movement speed and an increase in track sinuosity and for transiting it is vice versa (Bovet and Benhamou 1988). Yet such assumptions about the underlying movement processes may not be valid, especially for pelagic megafauna, which often forage along thermal fronts and do not necessarily begin ARS upon encountering prey patches (Sims and Quayle 1998, Polovina et al 2004, Lambardi et al. 2008). In addition, most SSSMs do not include vertical (diving) movement patterns even though the diving behavior of marine megafauna can provide valuable insights into foraging behavior (Austin et al. 2006, Robinson et al. 2007) and diving behavior can change independently of horizontal movement patterns (Sale et al. 2006).

The leatherback turtle *Dermochelys coriacea* conducts some of the deepest dives of any air-breathing animal and has been recorded descending to depths of up to 1280 m (Doyle et al. 2008). Leatherback turtles are thought to undertake such extreme dives in search of diel-migrating gelatinous zooplankton (Houghton et al. 2008). Gelatinous zooplankton are the predominant food source for leatherback turtles and due to their low-energy content it is estimated leatherback turtles must consume about 100 kg per day to survive (Jones et al. 2012). As a result, the movement patterns of leatherback turtles are tightly linked to the horizontal and vertical distribution of gelatinous zooplankton throughout the world’s oceans (Houghton et al. 2006, Fossette et al. 2010a, Schick et al. 2013).

As gelatinous zooplankton form a major component of most marine ecosystems (Pauly et al. 2009), often prey on or compete with commercially important fish species (Lynam et al. 2006, Kawahara et al. 2006, Quiñones et al. 2013), and pose risks to human health (Gershwin et al. 2009), the movement patterns of leatherback turtles can function as broad-scale indicators of ecosystem functioning and health (Fossette et al. 2010a; Bailey et al. 2012b). In addition, many leatherback turtle populations are currently of conservation concern due to recent declines and/or low population sizes (Nel et al. 2013, Tapilatu et al. 2013). As much of the threat posed to these populations is from mortality due to fisheries bycatch (Spotila et al. 2000, Lewison et al. 2004), knowledge of the habitat preferences and oceanic distribution of this species can help us design strategies for minimizing interactions between fisheries and leatherback turtles (Roe et al. 2014, Fossette et al. 2014).

Here, I aim to improve our understanding of the behavioral patterns of post-nesting leatherback turtles in waters around southern Africa. This will be achieved in three major steps. (1) I will describe the horizontal and vertical movement patterns of leatherback turtles tagged using satellite transmitters within the iSimangaliso Wetland Park, South Africa. This location was chosen for this study as leatherback turtles previously tagged at this site exhibited highly dynamic movement patterns immediately upon leaving the nesting area that have been associated with foraging events (Luschi et al. 2003, Luschi et al. 2006, Lambardi et al. 2008). (2) I will outline a method for identifying behavioral transitions using a changepoint analysis. Changepoint analysis is a statistical tool capable of identifying step-changes in the mean and/or variation of time-series data. Changepoint analysis is far less processor intensive than other more commonly used methods for identifying changes in an animal's behavioral state, such as SSSM, and as such is suited to analyzing multiple metrics simultaneously. Also, as changepoint analysis does not require any prior specification of the movement process, unlike SSSM, it is not reliant on prior assumptions on movement patterns and thus can be run on any selected behavioral metric. (3) I will overlay the identified behavioral changes onto remotely-sensed oceanographic data that influence the distribution and abundance of gelatinous zooplankton prey ((Lilley et al. 2011, Lucas et al. 2014) and thus also predicted to influence leatherback turtles movements.

3.3 Methods

3.3.1 Study site

The iSimangaliso Wetland Park is located in the north-east corner of South Africa (28°0' S, 32°30' E). The coastal portion of the Park is approximately 280 km long and is characterized by a series of sandy beaches separated by rocky headlands 5 to 15 km apart. To encounter nesting turtles, I patrolled the northern 56 km of the Park – a stretch of beach along which leatherback turtles nest with a roughly uniform distribution (Thorson et al. 2012).

3.3.2 Tagging

To encounter nesting turtles, I patrolled the nesting beaches by vehicle every night during the peak nesting season (November to February) over two years: 2011/12 and 2012/13. Nesting turtles were only approached after egg laying had commenced. For every turtle encountered, I checked for and applied metal and passive integrated transponder (PIT) tags; recorded a GPS location, and scanned the ovaries of each turtle using a Sonosite 180 Plus real-time portable ultrasound (Sonosite, Washington, USA). The purpose of the ultrasound scan was to determine whether or not a turtle would continue to lay nests during the remaining nesting season (Rostal et al., 1996; Blanco et al., 2011). We preferentially deployed satellite transmitters onto turtles that had finished nesting for this season and were about to begin its post-nesting migrations; however, this was not always possible. A number of transmitters were also deployed on turtles that were still inter-nesting. If an inter-nesting turtle with a transmitter was re-encountered on a subsequent nesting event, the original transmitter was removed and replaced with a new device. In total, I deployed 20 Mk10-PAT satellite transmitters (Wildlife Computers, Washington, USA).

3.3.3 Attachment and recovery of transmitters

Transmitters were anchored to the pygal process (caudal peduncle) using a tethering method adapted from Morreale (1999), Blanco et al. (2012), and Patel (2013).

Prior to deployment, transmitters were fitted with an additional ring of high-density foam around the pre-existing float to improve their buoyancy (Figure 1). This was to ensure the transmitter would float to the surface, and remain upright, when the turtle was at the water’s surface. The additional floatation was fixed to each transmitter using two-part epoxy (Loctite® Epoxy Heavy Duty). The transmitters were also spray-painted black (Rust-Oleum) and then coated with an anti-fouling spray paint (Silpar TK). Care was taken not to cover any sensors with the additional foam, paint or anti-fouling. The mean buoyancy of the transmitters with the additional foam was 41.36 g ± 3.65 SD.

To attach the transmitter, a cordless drill with a sterilized 5 mm drill bit was used to create an incision 20 to 30 mm from the posterior edge of the pygal process. The incision was immediately treated with spray antiseptic (oxytetracycline). Sterile surgical tubing was threaded through the hole and then cut flush with the carapace. Delrin buttons were placed above and below the hole through which was threaded a monofilament fishing line (180 kg test). The fishing line and buttons were fastened in place using a corrodible crimp. To one of the over-hanging ends of the fishing line a swivel, which was connected to the transmitter, was fastened using another corrodible crimp. The entire tether, from the anchor to the transmitter, was kept between 30 and 35 cm in length to minimize the potential for entanglement with the hind flippers. The transmitters also come pre-fitted with an emergency release pin that breaks under 40 kg of force. The emergency release pin was also set to automatically release after 1 year to prohibit long-term encumbrance of the study animal.

It required less than 10 mins for the transmitter to be attached and did not require the animal to be restrained. Transmitters were only deployed on nesting turtles that appeared to be in good health and were without visible injuries. When recovering a transmitter, the fishing line beneath the lower button was cut and the tether was pulled free. A new transmitter was then anchored through the same hole that was created on the original deployment.

3.3.4 Setup of satellite telemetry devices

The transmitters were programmed to record depth every 10 seconds, although due to band-width limitations not all these data could be dependably relayed remotely. Instead, on-board software identified the maximum depth and total duration of individual dives, defined as each time the transmitter descended below a depth of 3 m until the transmitter returned to a depth shallower than 3 m. The dive data were assigned to bins (dive depth bins were set at 0, 6, 10, 30, 50, 100, 150, 200, 300, 400, 500, 600, 800, 1000, and > 1000 m. The dive duration bins were set at 0, 2, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 60, 90, and

> 90 mins) and then relayed a frequency histograms of the number of dives, dive duration, and maximum dive depth in successive 4 h time intervals.

The transmitters relayed their dive data along with their location via the Argos Satellite System (Maryland, USA). The transmitters were not duty-cycled but were programmed to relay a maximum of 52 messages day^{-1} – enough to relay all of the frequency histograms collected that day twice over. If any fewer than 52 messages were sent in a given day, the unused messages would be added to the message limit for the subsequent day. The transmitters were programmed to prioritize relay data collected within the past 10 days over older data.

3.3.5 Processing horizontal movement data

The Argos Satellite System gives each location a value of 3, 2, 1, 0, A, or B depending on the confidence of the locations accuracy, with 3 being the most accurate and B being the least. To remove erroneous data, the data were filtered using an algorithm modified from Freitas et al. (2008). First, all locations were excluded that were located over 5 km from the previous location and required a movement speed over 240 km d^{-1}. Location less than 5 km apart were retained as otherwise many good-quality locations, for which the implausible swim speeds are an artefact resulting for the locations being recorded close to each other in time, could be removed. In addition, maximum movement speed was chosen by as prior inspection of the data suggested that animals could reliably reach speeds up to 200 km d^{-1} when swimming with the prevailing flow of the Agulhas Current. Next in the filtering process, all the locations were removed that required turn angles greater than 165° if the track leading to them was longer than 5 km. This was chosen to remove conspicuous and abrupt movement patterns that are more likely to be a product of measurement error than animal behavior. For later analysis I required daily position estimates (see section 3.3.6), so as a final filtering step all but the highest LC for each day was deleted. When there were multiple equivalently high LC locations for a given day, I chose the earliest received location.

Due to filtering and haphazard data transmission, daily locations were not always available. This issue was address using a State-Space Model, as defined in Jonsen et al. 2007, on the speed and turn angle filtered data (not the best-daily location). The output of this model was used to ‘fill-in’ the locations between the filtered daily locations. The output of the SSM was only used for interpolation if the gap between subsequent locations was shorter than 15 days. In total, 8% of the tracking data was derived from the SSM model.

As the transmitters also relayed dive data, I could use this information to verify that the transmitter was still attached to the animal. When a transmitter stopped diving to depths lower than 10 m for a period of over 10 days, it was assumed the transmitter had broken off the animal. Consequently, all data from when diving ceased were ignored.

3.3.6 Changepoint Analysis Model (CAM)

From the satellite telemetry data, I generated an array of both horizontal and vertical movement metrics that would be indicative of a behavioral shift. Specifically, metrics were chosen that might be indicative of foraging behavior based on previous studies that have identified shifts in the diving behavior of leatherback turtles, and other marine animals, upon reaching putative foraging areas. The 4 metrics I chose were:

Locations within 75 km – I calculated the number of daily locations within a 75 km radius of each individual location along the entire track of each turtle. This provided us a metric to identify decreases in movement speed or increases in track sinuosity that are commonly associated with ARS behavior. I used a 75 km radius as this is close to maximum swimming speed per day that has been observed in other studies tracking leatherback turtles (Shillinger et al. 2011, Bailey et al. 2012b).

Number of Dives – I calculated the number of dives that occurred per 4 h period from both the dive duration and dive depth histograms. Field data for leatherback turtles have shown that animals reduce both dive durations and surface intervals when in putative foraging areas (James et al. 2005, James et al. 2006a, Fossette et al. 2010b), which should lead to a large increase in the number of dives per time-period. The number of dives can therefore provide a proxy for activity levels.

Variation in Dive Duration – I calculated the standard deviation for dive duration per 4 h period from the dive duration histogram (using the conservative limit of the dive duration bins). We chose this metrics as previous models of optimal diving theory have suggests that animals could improve their encounter rate with diffuse prey by varying their dive duration (Thompson and Fedak 2001). Conversely, I therefore predict that animals that have encountered large prey assemblages, such as gelatinous zooplankton blooms, would show minimal variation in dive duration as they optimize their diving strategy to maximize food intake in a super-abundant foraging area.

Maximum Dive Depth – I calculated the maximum dive depth per 4 h period using the max-min-depth function of the Mk10-PAT transmitters. At putative foraging areas, leatherback turtles tend to dive to much shallower depths (James et al. 2006a, Fossette et al. 2010b). This could be because food is present closer to the surface at prey aggregations or that deep diving during transit is associated with exploring the water-column for food (Houghton et al. 2008) or are a more efficient mechanism for travelling long-distances (Weihs 1973).

After calculating each of these 4 metrics for each turtle, I conducted changepoint Analysis on each of these metrics using the package '*changepoint*' in R (R Development Core Team, Killick and Eckley 2014). I used the binary segmentation method to identify a changepoint in the mean and variance of the time-series data using the Cumulative Sum of Squares Method (as it has no distributional assumptions), a penalty value of 5, and identified a maximum of 5 changepoints for each metrics. When changepoints occurred in at least 3 separate metrics within a period of 3 days, it was considered to constitute a single behavioral change. I was able to identify the initial behavioral state of each individual by consulting the ultrasound data. If an animal was identified to still have more clutches to lay that season, its behavior was classified as inter-nesting. Conversely, if the turtle had no more nests to lay and thus was about to begin its post-nesting migrations, its behavior was classified as transiting. The first behavioral change observed in inter-nesting intervals was considered a switch to transiting behavior, while the next change observed in transiting individuals was considered a switch to foraging behavior. Behavioral shifts that occurred in foraging individuals were considered as either a reversion back to transiting behavior or a continuation of foraging behavior depending on how similar the new movement metrics are to the previously identified behavioral states. Transiting and foraging behaviors as defined as either coastal, if the animal was within 50 km of the coastline, or pelagic, if the animal was over 100 km from the coastline. The changepoint analysis model (CAM) was only run on turtles that were tracked into their post-nesting migrations.

3.3.7 Oceanographic data

The tracks of each turtle, incorporating the identified behavioral changes, were superimposed onto contemporaneous maps reflecting oceanographic conditions. These included maps of bathymetry, sea surface temperature (SST), net primary productivity (NPP), and ocean currents. Bathymetry data at a spatial resolution of 0.017 ° were provided by the global relief model, ETOPO1, available at the National Geophysical Data Center, USA (http://www.ngdc.noaa.gov/mgg/global/). SST at daily intervals and a spatial resolution of 0.054 ° were provided by The Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) from the UK Met Office and were available at (http://podaac-www.jpl.nasa.gov/dataset/, UKMO-L4HRfnd-GLOB-OSTIA). NPP at 8-day intervals and a spatial resolution of 0.083 ° were provided by the Epperly-VPGM model available at the Oregon State University Ocean Productivity Page (http://www.science.oregonstate.edu/ocean.productivity/index.php). Ocean currents were available at 5-day intervals and a spatial resolution of and a resolution of 0.333 ° by Ocean Surface Current Analysis Real-time (OSCAR) and were available at (http://podaac-www.jpl.nasa.gov/dataset/, OSCAR_L4_OC_third-deg).

3.4 Results

A total of 20 leatherback turtles were tracked via satellite telemetry from their nesting beaches in the iSimangaliso Wetland Park. Of these, 16 were tracked into their post-nesting migrations (Figure 2) and 3 of these (G, J, and O), I encountered at least twice during their inter-nesting periods allowing for recovery and redeployment of their transmitters. The mean tracking duration of the turtles that were tracked into their post-nesting migrations was 111.5 ± 41.32 SD days and the maximum tracking duration was 208 days (Table 1). The CAM model was run on each of the turtles tracked into their post-nesting migrations (Figures 3 - 19).

For each of the turtles tracked into their post-nesting migrations it was possible to assign putative foraging areas in one of three major oceanic regions: the (1) South Atlantic Ocean (SAO) (n = 3), (2) Western Indian Ocean (WIO) (n = 5), and (3) Mozambique Channel (MC) (n = 8).

3.4.1 South Atlantic Ocean (SAO)

The turtles that migrated towards the SAO initially headed south-west of the nesting area. Turtles A and C moved rapidly along a roughly straight-path heading southwest from the nesting area at speeds that periodically exceeded 200 km d^{-1}. The relatively straight path taken by these animals roughly reflects the east South African coastline and the prevailing flow of the Agulhas Current (Figure 20, see Video 1 on the Supplmentary CD). Turtle B followed a more meandering path southwest of the nesting area following the edges of the eddies of the Agulhas Retroflection. At approximately 18 °E, all of these turtles began heading north. Turtles B and C exhibited slower movement speeds and started conducting looping movements just west of the highly productive waters of the Beguela Upwelling System (Figure 21, see Video 2 on the Supplmentary CD). Turtle A continued north on a roughly straight course, but began to slow down in the open-waters off the coast Angola at approximately 22 °S.

The diving behavior of turtles A and C stayed relatively consistent as they remained within the Agulhas Current and the diving patterns of turtle A even stayed consistent as it migrated north (Figure 4). Conversely, the CAM model identified a behavioral shift, categorized by an increase in the number of dives, a reduction in the variation in dive duration, and an increase in locations within 75 km, as soon as turtle C moved north of the Agulhas Current. The switch to foraging behavior lasted 17 days before the turtle switched back to a transiting behavior even though it remained within the pelagic waters of western South Africa (Figure 6).

For turtle B, the CAM identified a single behavioral change, categorized by an increase in the number of dives, decrease in the variation of dive duration, and a decrease in maximum dive depth. This change was observed upon reaching the seamount at 36 °S that peaks around 2,000 m depth (Figure 5). No further behavioral changes were observed for the remainder of this animal’s movements even though distinct fluctuations were evident in the number of dives as the turtle migrated north towards the Benguela Upwelling System

3.4.2 Western Indian Ocean (WIO)

The turtles that migrated towards the WIO generally moved away from the nesting areas in a south-easterly direction. Turtles E, G, H, and F all conducted tightly circuitous paths for up to 30 days between 36 and 38 °S (Figure 8, 9, 10, and 11, respectively). Each of these circuitous paths began when individuals moved into the center of eddies. The turtle then left these areas as soon as the eddy began to dissipate (Figure 22, 23, 24; see Video 1 on the Supplmentary CD). Afterwards, all of these turtles except E, began moving east again and the movements of turtles H and F tightly followed the easterly flow of the Agulhas Retroflection. None of these turtles, or those that migrated to the SAO, were observed moving further south than 43 °S and always remained in water with a SST above 14 °C (see Video 3 on the Supplmentary CD).

While migrating these turtles had relatively low numbers of dives and high variation in dive duration, but while conducting the circuitous paths, the number of dives were notably higher and variation in dive duration lower. As such, the CAM identified behavioral changes for each of these animals as they moved into the center of each of the eddies and another as the animals left these eddies. Another behavioral change was identified in turtle H, 3 days before the end of its tracking duration (Figure 11). Once again this change was associated with an increase in the number of dives, a decrease in the variation of dive duration, and an increase in the locations within 75 km.

3.4.3 Mozambique Channel (MC)

Half of the turtles tracked during their post-nesting migrations headed north of the nesting area towards the MC (Figure 25). All of the turtles that migrated to the Sofala Banks generally remained within 100 km of the coastline as they migrated north; however, 4 individuals conducted looping movements that extended up to 250 km out to sea before returning to the coastline. While migrating north, movement speeds of up to 50 km d^{-1} were observed, although upon reaching the Sofala Banks, where these turtles appeared to take up residence, the movement speeds generally dropped to less than 10 km d^{-1}. The areas of the Sofala Banks utilized by leatherback turtles are largely contained within the 50 m isobaths (Figure 25) and is an area where NPP exceeds 2000 mg C m^{-2} day^{-1} throughout the year (Figure 26).

The turtles that migrated to the MC showed very similar diving patterns while migrating north of the nest area: these turtles all demonstrated low numbers of dives, with notable high variation in dive duration and maximum dive depth. Upon reaching the Sofala Banks, the numbers of dives rose rapidly, the variation in dive duration decreased, and the maximum dive depth decreased. These very clear patterns meant that the CAM identified behavioral changes in all individuals as soon as they reached the Sofala Banks. In individuals J and P, a second behavioral change occurred while the turtles where foraging in the Sofala Banks (Figure 13 and 19). For turtle J, this corresponded with a 100 km move from the southern to northern Sofala banks, while turtle P was already in the northern Sofala Banks and just moved slightly inshore. Turtle P, which had the longest transmitter duration at 209 days, remained in the Sofala Banks for 146 days after which the transmitter stopped functioning.

Turtle H was the only turtle that migrated north but did not head to the Sofala Banks. Instead, this turtle began to head east just after passing Maputo Bay, Mozambique and swam within 50 km of Europa Island, France before continuing towards the west coast of Madagascar (Figure 11). Upon reaching the Madagascan coastline the CAM identified a behavioural change, coinciding with an increase in the number of dives, a decrease in the variation in dive duration, and low maximum dive depth. A second behavioral change was identified as the animal approached northern Madagascar.

3.4.4 Inter-nesting

Using ultrasonography I was able to confirm that some turtles were still nesting when the transmitters were deployed. In the turtles from which I was able to recovery transmitters: Q, J, T, G, O, there were clear repeating patterns over every 9 to 14 days. The general trend was for a decrease in both the number of dives and variation in dive duration, although the pattern was generally clearer in variation in dive duration.

3.5 Discussion

I employed satellite transmitters to determine the post-nesting movements and diving behavior of leatherback turtles from the iSimangaliso Wetland Park. To achieve this I employed a novel tethering technique for attaching satellite transmitters that has not be used before at this location. This technique is predicted to increase the hydrodynamic drag of a swimming leatherback turtle by less than 5 % (Jones et al. 2014), while the backpack method used in previous satellite tracking studies at this location can increase hydrodynamic drag by over 100 % (Jones et al. 2014). Furthermore, turtles tracked using backpacks swam slower and conduct shorter dives than those tracked using other low-drag attachment techniques (Fossette et al. 2007, Witt et al. 2011). The lower drag-attachments used in this study are likely to demonstrate the most accurate portrayal of leatherback turtles behavior in the waters of southern Africa to date, and indeed this is the first study to satellite track leatherback turtles migrating towards the coastal waters of the Sofala Banks. Furthermore, this is the first study to CAM, or indeed any other technique apart from SSSM (e.g. Jonsen et al. 2007, Shillinger et al. 2011, Benson et al. 2011, Dodge et al. 2014) to statistically identify behavioral shifts in migrating leatherback turtles. This technique provided unique insights into how migrating leatherback turtles respond to dynamic oceanographic features in both their horizontal and vertical behavior. The insights into leatherback turtle behavior provided in this study provides an important step forward in understanding the habitat preferences of this species.

3.5.1 Pelagic or coastal specialists

The turtles tracked in this study fell into two major groups: those that migrated to pelagic foraging grounds in either the SAO or the WIO, and those that migrated to coastal foraging areas in the Mozambique Channel. Migrating to pelagic foraging areas is similar to the behavior observed in leatherback turtles previously tracked from the iSimangaliso Wetland Park (Hughes et al. 1998, Luschi et al. 2003, Lambardi et al. 2008) and is common in leatherback turtles foraging in all ocean basins (Shillinger et al. 2011, Witt et al. 2011, Benson et al. 2011). However, only post-nesting turtles from Pacific coast of Costa Rica and Indonesia have been recorded remaining in shallow (< 200 m) coastal waters en route to equally shallow foraging areas, and in both cases this constituted less than 10 % of the individuals tracked from this location (Benson et al. 2011). As such, the prevalence of coastal behavior in the leatherback turtles tracked in this study suggests that leatherback turtles might have more flexible habitat preferences than previous considered. The relatively small percent of coastal turtles identified in other studies could indeed be due to the coastal turtles being largely eradicated by fisheries, as suggested by Saba et al. (2007).

Many studies have highlighted the importance of ocean currents in defining the movement patterns of leatherback turtles worldwide (Gaspar et al. 2006, Gall et al. 2013) and the post-nesting movements of the leatherback turtles from South Africa are a prime example (Luschi et al. 2003). Earlier tagging studies observed that many leatherback turtles migrating from South Africa followed the main flow of the Agulhas Current down the east coast of Africa. Similar patterns were observed in turtles A and C; however, a greater percentage of individuals actually migrated east or southeast from the nesting area. These individuals did not follow the Agulhas Current, although they regularly followed the path of mesoscale eddies en route to the Agulhas Retroflection. Following major current patterns may not take individuals in the most direct route to a potential foraging area, but the benefits of passive advection may make it an efficient mechanism for traversing long distances (Luschi et al. 2003) or could provide evidence that these organisms are only migrating towards broad-scale oceanic areas (Lambardi et al. 2008). Indeed, it has been previously postulated that the movement patterns of leatherback turtles are more akin to prolonged sojourns in vast foraging areas than conventional migrations (Luschi et al. 2006).

Many of turtles tracked to pelagic foraging areas initially headed towards the frontal region where the Southern Ocean converges with the Atlantic and Indian Oceans. Like most frontal-zones, this often exhibits high-levels of NPP where cold-nutrient rich waters mix with warmer-nutrient poor waters (Strass 1991). However, the movement of leatherback turtles in this study generally bypassed the areas of highest NPP in this frontal-zone. Even those leatherback turtles that migrated to the SAO did not migrate towards the high NPP zone of the Benguela Upwelling System, but remained in the lower NPP regions off-shore. Instead, the movements of leatherback turtles in both the SAO and WIO showed regular behavioral changes when in the centre of mesoscale eddies. Mesoscale eddies are thought to often create large confluences of food (Nel et al. 2001, Ream et al. 2005, Polovina et al. 2006) and could provide a better predictor of gelatinous zooplankton distribution than NPP. Indeed, many marine predators including penguins (Cotté et al. 2007), tuna (Fiedler and Bernard 1987), and whales (Doniol-Valcroze et al. 2007) often focus foraging efforts at the centers of mesoscale eddies.

The leatherback turtles tracked in this study never moved into waters with SST colder than 14 °C, and so never moved into the Southern Ocean. Similar patterns are observed in the North Atlantic where leatherback turtles are only rarely observed in water less than 12 °C (Witt et al. 2007), although it should be noted that leatherback turtles have been observed repeatedly diving into waters as cold as 0.4 °C (James et al. 2006b). This suggests that temperatures between 12 and 14 °C may represent the minimal temperature at which leatherback turtles can remain in for prolonged periods of time, although brief forays into colder waters are possible.

The turtles that migrated towards pelagic foraging areas generally showed multiple behavioral shifts over the tracking duration (range 0 to 3). In contrast, the CAM identified only one behavioral shift in each individual migrating towards the MC as soon as it reached the Sofala Banks. Moreover, after reaching the Sofala Banks most individuals remained resident within areas less than 50 km^2 for the remainder of their tracking duration. This suggests that pelagic individuals experience more sporadic foraging conditions than in the Sofala Banks. Moreover, NPP appeared to be a good indicator of foraging behavior for these coastal individuals. A promising avenue for future research could be the effects of differing foraging conditions on individual variation in reproductive output. Indeed, turtles from a single nesting area, but foraging in different locations, have been observed to significantly differ in a wide range of factors influencing reproductive fitness, including body-size, clutch size (Zbinden et al. 2011), or remigration interval (Caut et al. 2008).

Many recent publications have highlighted the difficulty in protecting leatherback turtles due to their extensive migratory behavior (Fossette et al. 2014, Roe et al. 2014). Yet as this coastal cohort remained with the Exclusive Economic Zones of South Africa and Mozambique during the tracking period this could represent a unique chance for an otherwise complex multinational conservation plan. Protecting these animals could also be achieved by prohibiting fishing activities over a relatively small and spatially-explicit area. However, the Sofala Banks also hosts a prawn-trawl fishery than is one of the major industries in Mozambique (Palha de Sousa et al. 2006) and is known to have leatherback turtle bycatch (Gove et al. 2001). The most productive avenue might therefore be to promote the use of bycatch mitigation tools, such as Turtle Excluder Devices, without the need for fisheries closures (Brewer et al. 2006).

3.5.2 Assessment and limitations of the CAM

Many of the shifts in horizontal movement patterns, as identified by the CAM, were mirrored by shifts in the diving behavior metrics. In addition, the same patterns were observed in all diving behavior metrics upon switching from transiting to foraging behavior. Specifically, upon beginning foraging behavior there was an increase in the number of dives, a decrease in the variation of dive duration, and a reduction of maximum dive depth. Interestingly, these patterns were the same regardless of whether an individual was foraging along a front (e.g. turtle B and H), within mesoscale eddies (e.g. see turtles E, G, H, and F), on in a coastal upwelling zone (e.g. turtles I, J, K, L, N, O, and P). This indicates that diving behavior patterns are indeed useful indicators of foraging behavior in leatherback turtles. Furthermore, changes in diving behavior indicative of foraging behavior often occurred when no such change was observed in the horizontal movement patterns (e.g. turtle B). To this extent, vertical movement patterns alone even could even better indicators of foraging than horizontal movement patterns.

However, it is important to note that the validity of the CAM model depends on whether distinct shifts in vertical or horizontal movement patterns do reflect switches from transiting to foraging behavior. To confirm this is the case, future studies are needed that track the horizontal movements and diving behavior of free-diving leatherback turtles, while also collecting data that can be used to confirm foraging behavior. This could be achieved through the use of stomach temperature sensors that are able to identify when a turtle has swallowed a prey item (Casey et al. 2010) or animal-borne video cameras that can visually confirm prey ingestion (Heaslip et al. 2012). From these studies, it would be possible to determine those metrics are the most appropriate for identifying the onset of particular behaviors.

Nevertheless, a major strength of the CAM model is its adaptability. As Changepoint Analysis does not require prior specification of the movement process to be identified, it can identify shifts in the mean and/or variance of any given variable. As such, CAMs could theoretically incorporate any number of behavioral metrics, such as heartbeat rate or body temperature, to help identify any shifts in behavior or physiology.

3.6 Literature cited

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3.7 Tables

Table 3.7.1 Details of all the satellite transmitters deployed in this study.

Turtle ID	Date Deployed	Last Location	Final Destination	Data days	SSSM days
A	27/2/2012	24/5/2012	South Atlantic Ocean	84	4
B	09/1/2012	05/6/2012	South Atlantic Ocean	142	7
C	13/1/2013	06/4/2013	South Atlantic Ocean	83	4
D	14/11/2011	30/12/2011	Western Indian Ocean	40	7
E	09/1/2012	01/5/2012	Western Indian Ocean	91	13
F	22/1/2013	15/4/2013	Western Indian Ocean	56	4
G	25/1/2012	08/6/2012	Western Indian Ocean	128	8
H	01/2/2013	06/4/2013	Western Indian Ocean	56	9
I	11/2/2013	29/5/2013	Mozambique Chanel	103	5
J	16/1/2013	05/6/2013	Mozambique Chanel	139	2
K	13/2/2012	09/6/2012	Mozambique Chanel	115	3
L	24/1/2013	15/5/2013	Mozambique Chanel	101	10
M	15/2/2013	17/4/2013	Mozambique Chanel	62	0
N	20/1/2012	23/5/2012	Mozambique Chanel	111	14
O	28/12/2012	03/6/2013	Mozambique Chanel	138	20
P	27/2/2012	22/9/2012	Mozambique Chanel	119	10
Q	10/11/2011	14/12/2011	Nesting area	33	2
R	11/12/2011	30/12/2011	Nesting area	18	2
S	04/1/2013	21/2/2013	Nesting area	31	20
T	13/1/2013	20/2/2013	Nesting area	10	0

3.8 Figures

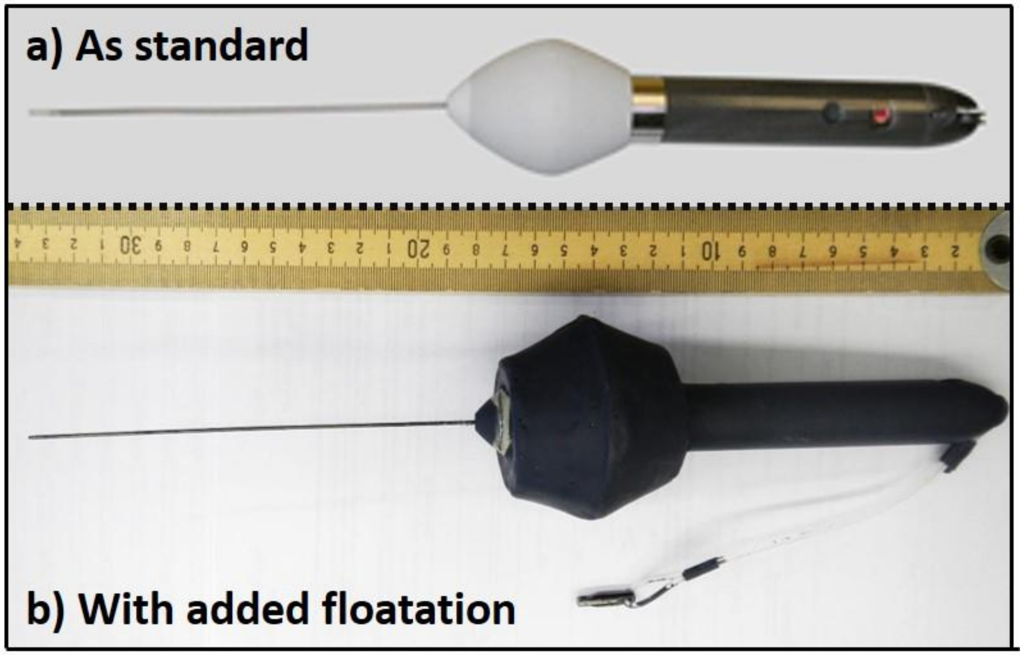

Figure 3.8.1 PAT Mk10 transmitters as (a) standard from Wildlife Computers (Washington, USA) and (b) custom-built floatation.

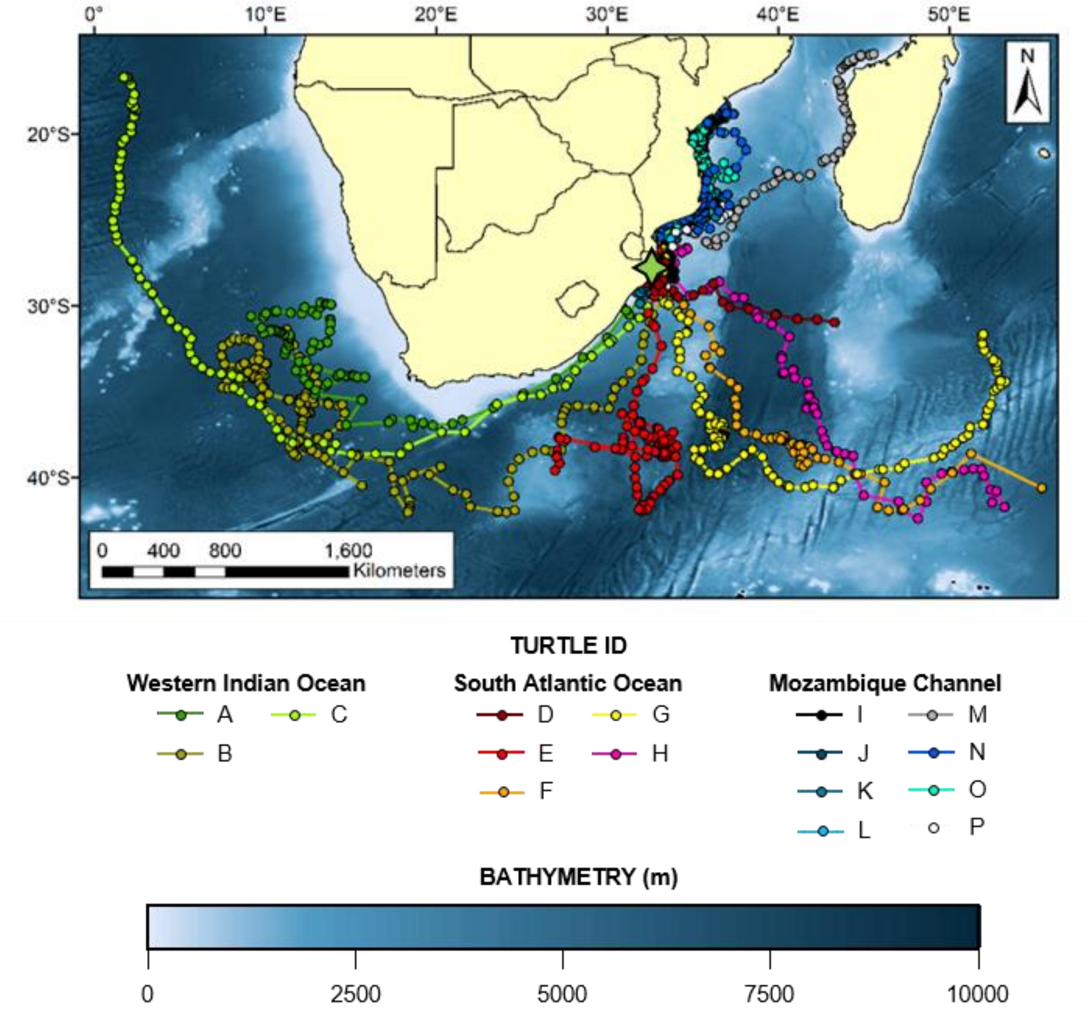

Figure 3.8.2 Movements of 16 leatherback turtles tracked by satellite telemetry from their nesting grounds in the iSimangaliso Wetland Park. Tracks are overlaid onto a bathymetric map.

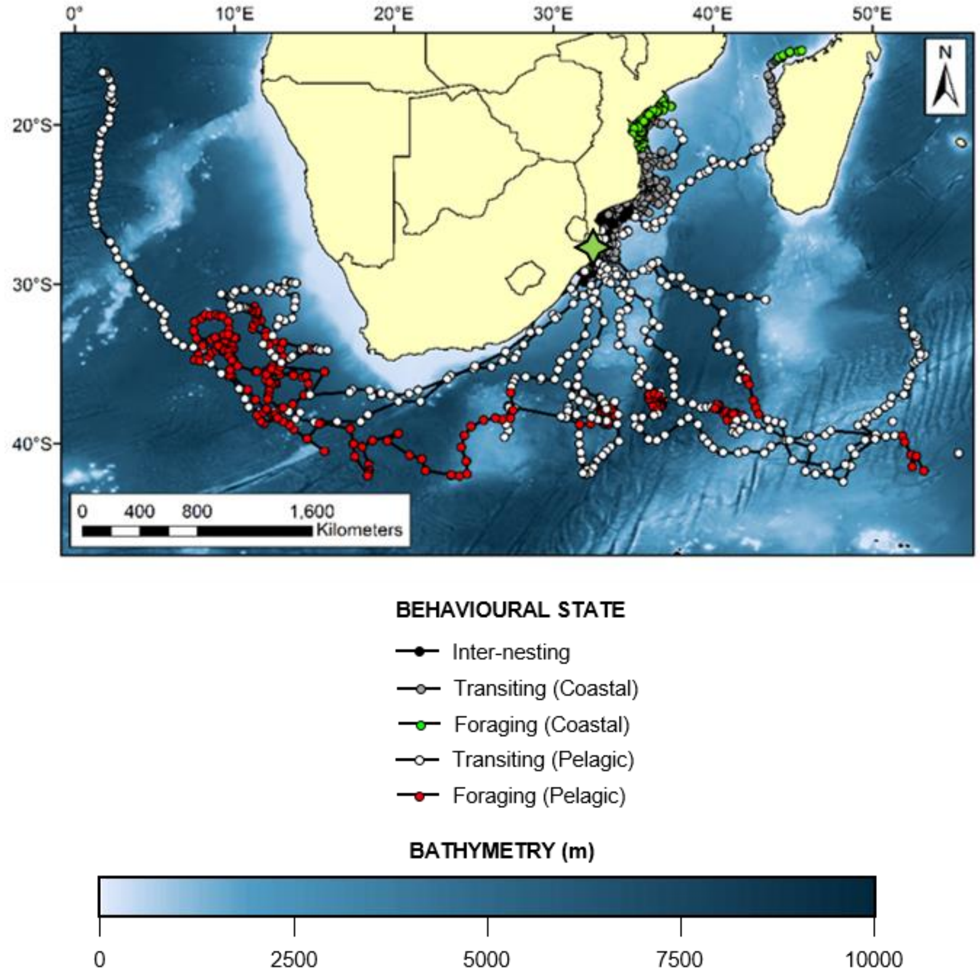

Figure 3.8.3 Movements of 16 leatherback turtles tracked by satellite telemetry from their nesting grounds in the iSimangaliso Wetland Park. Each track has been analyzed by a changepoint analysis model to determine its behavioral state. Tracks are overlaid onto a bathymetric map.

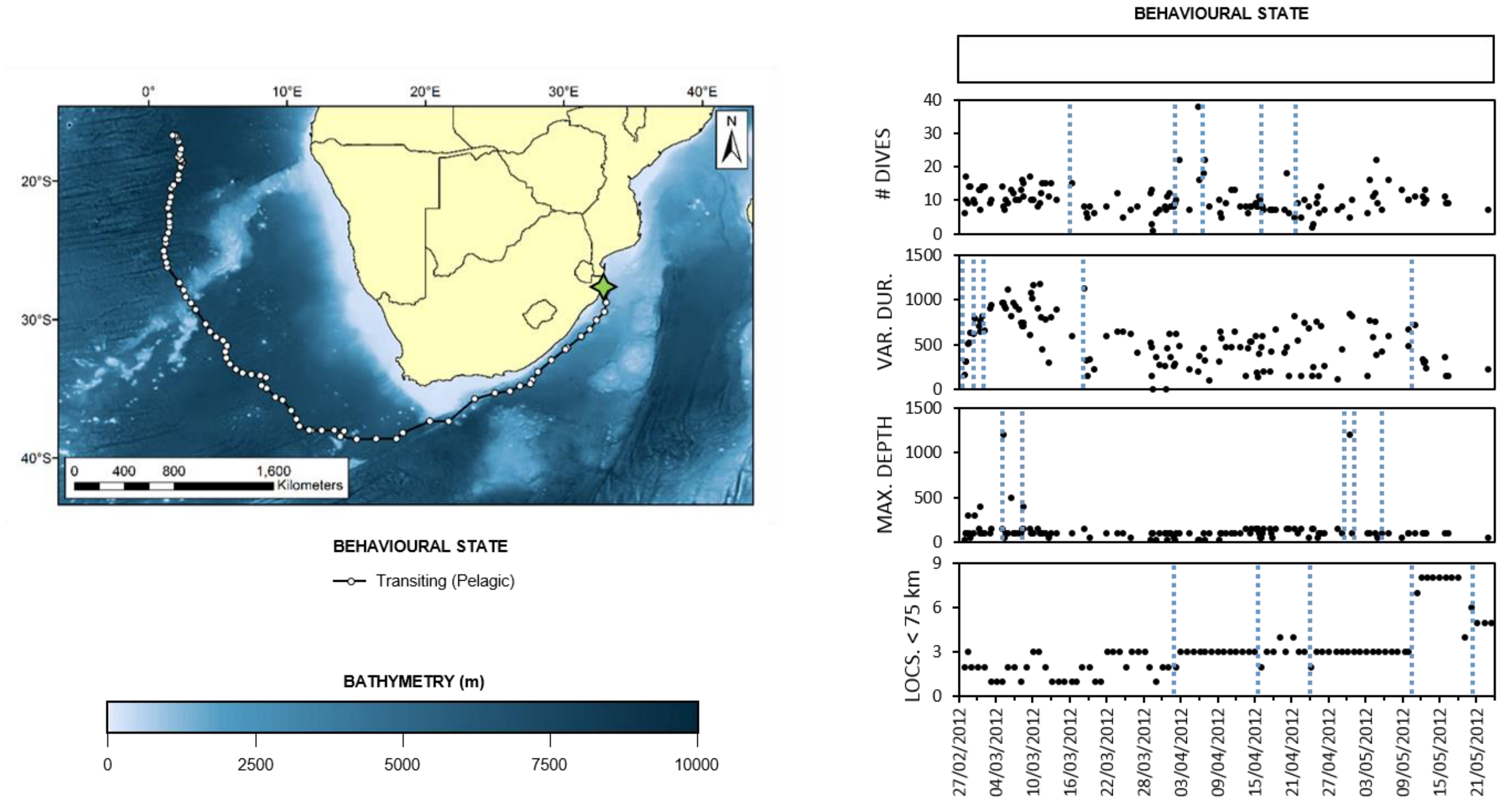

Figure 3.8.4 Movements and dive behavior of Turtle A tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

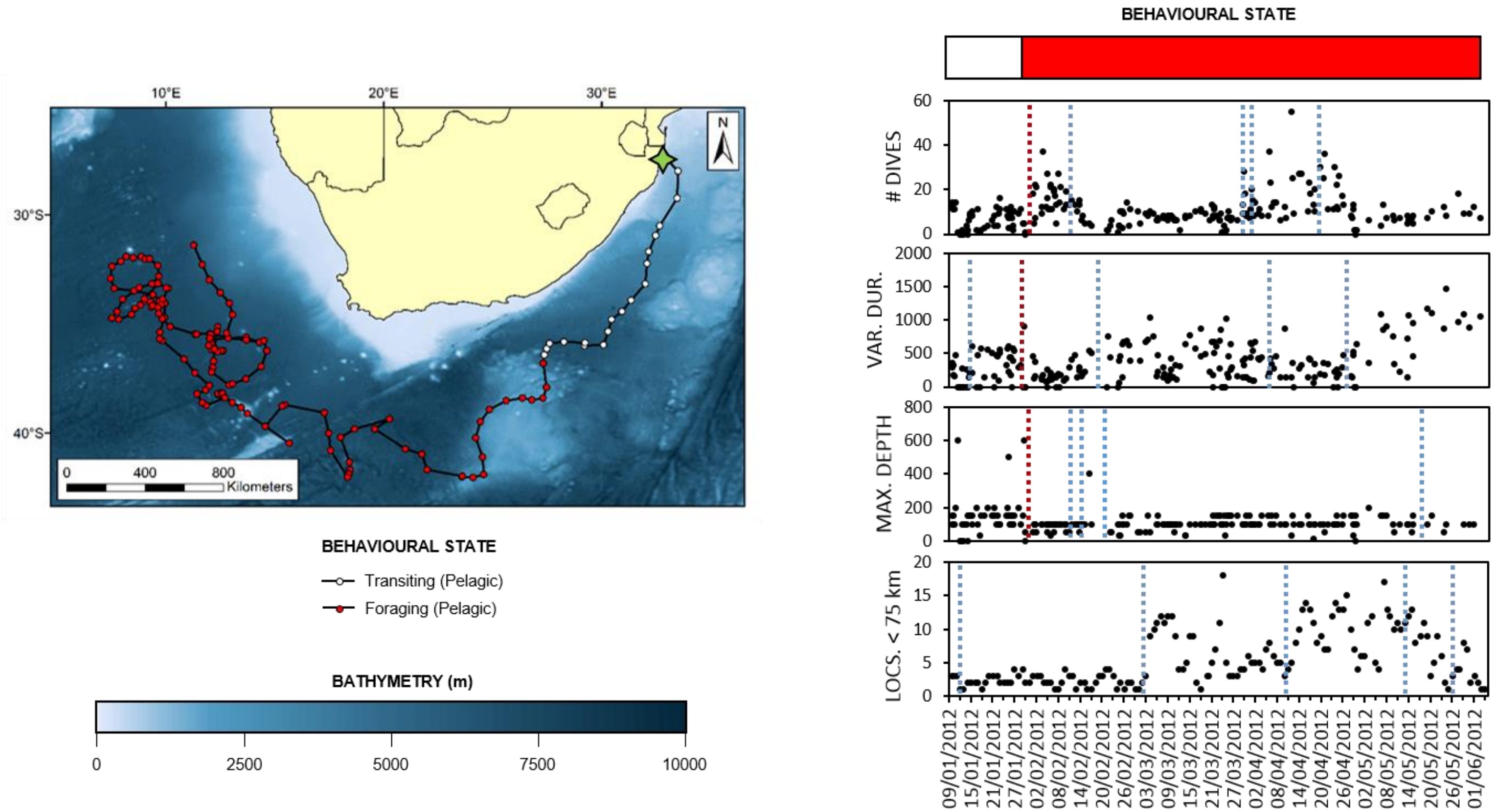

Figure 3.8.5 Movements and dive behavior of Turtle B tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

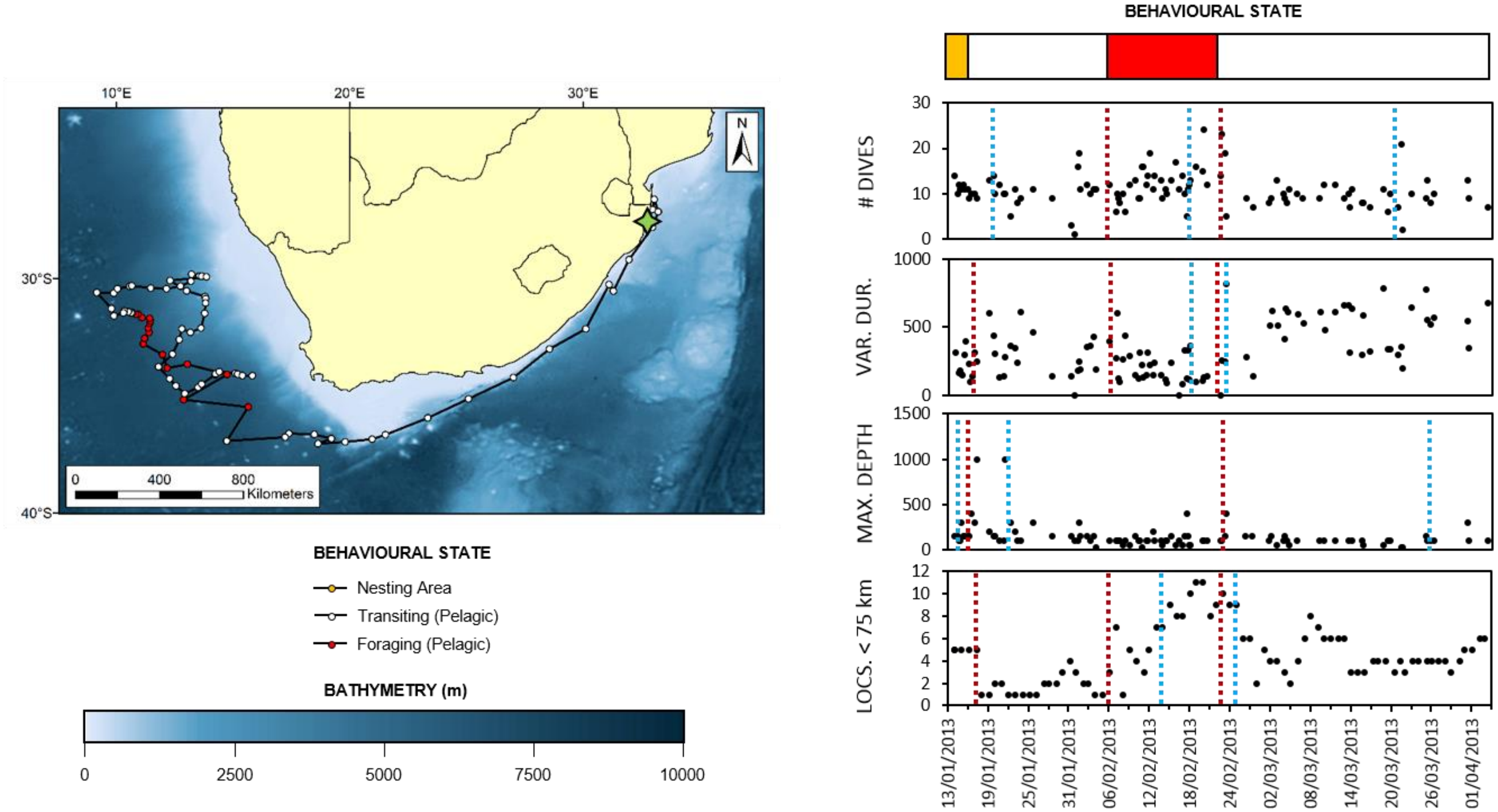

Figure 3.8.6 Movements and dive behavior of Turtle C tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

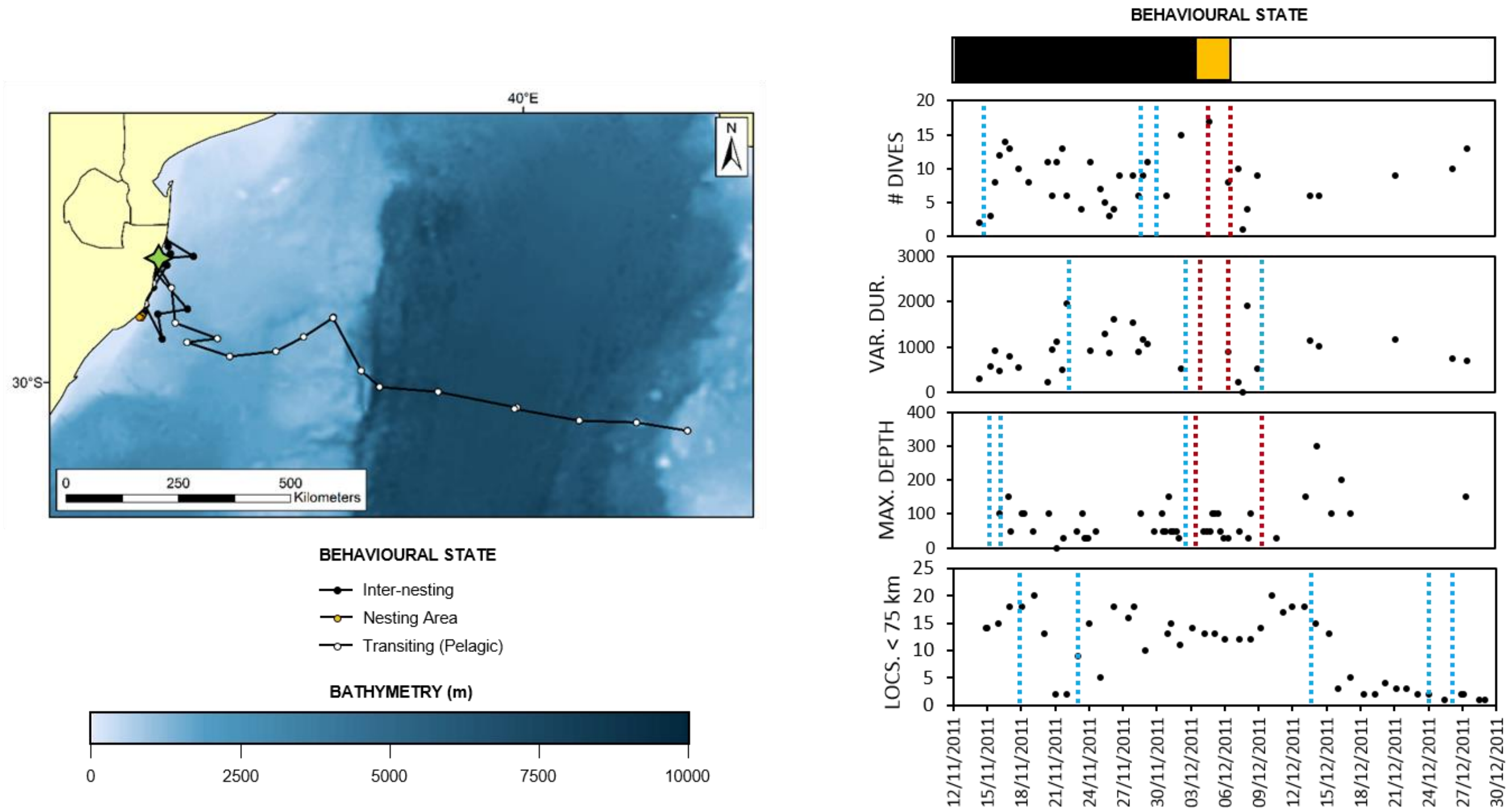

Figure 3.8.7 Movements and dive behavior of Turtle D tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

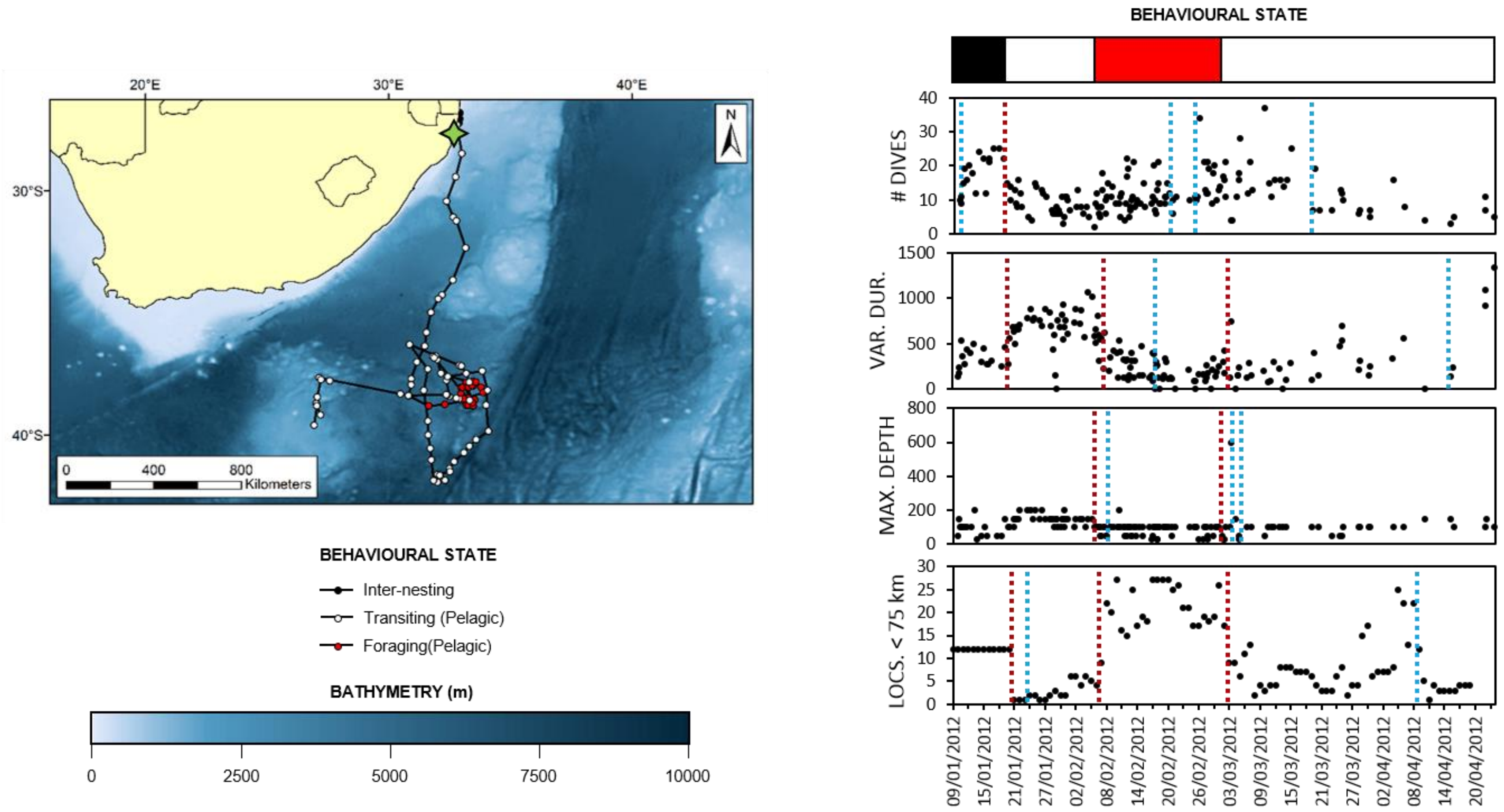

Figure 3.8.8 Movements and dive behavior of Turtle E tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

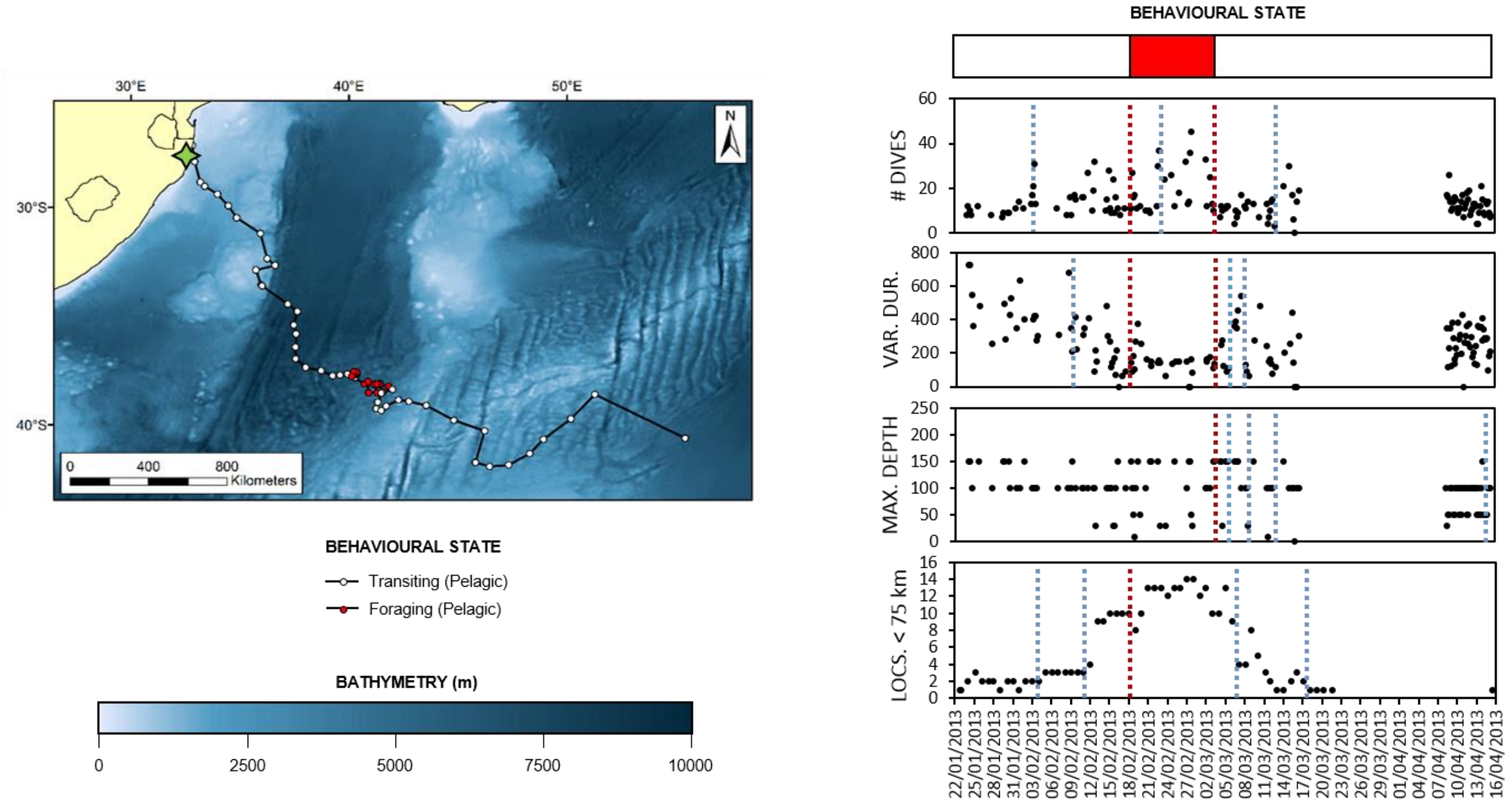

Figure 3.8.9 Movements and dive behavior of Turtle F tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

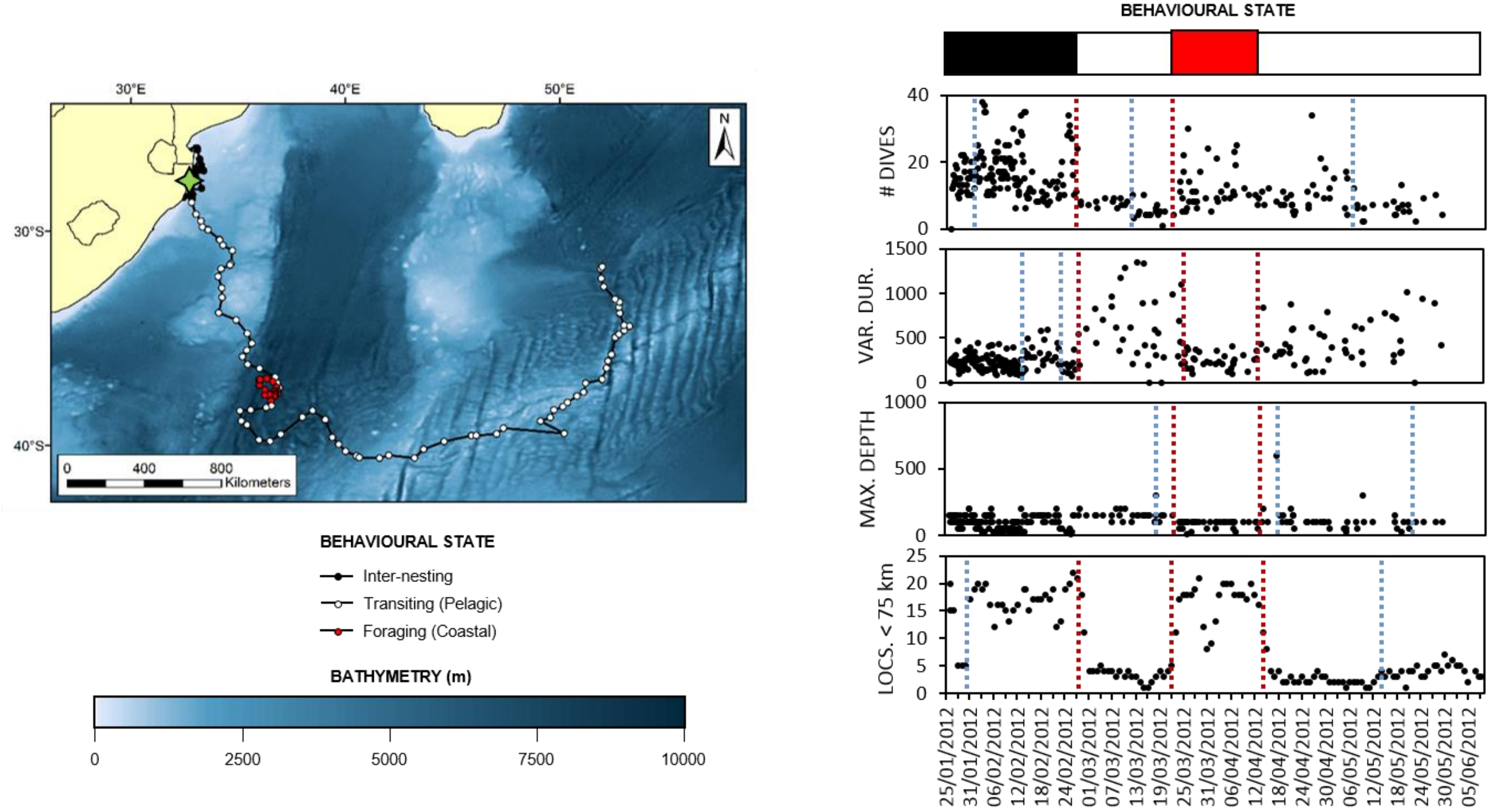

Figure 3.8.10 Movements and dive behavior of Turtle G tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

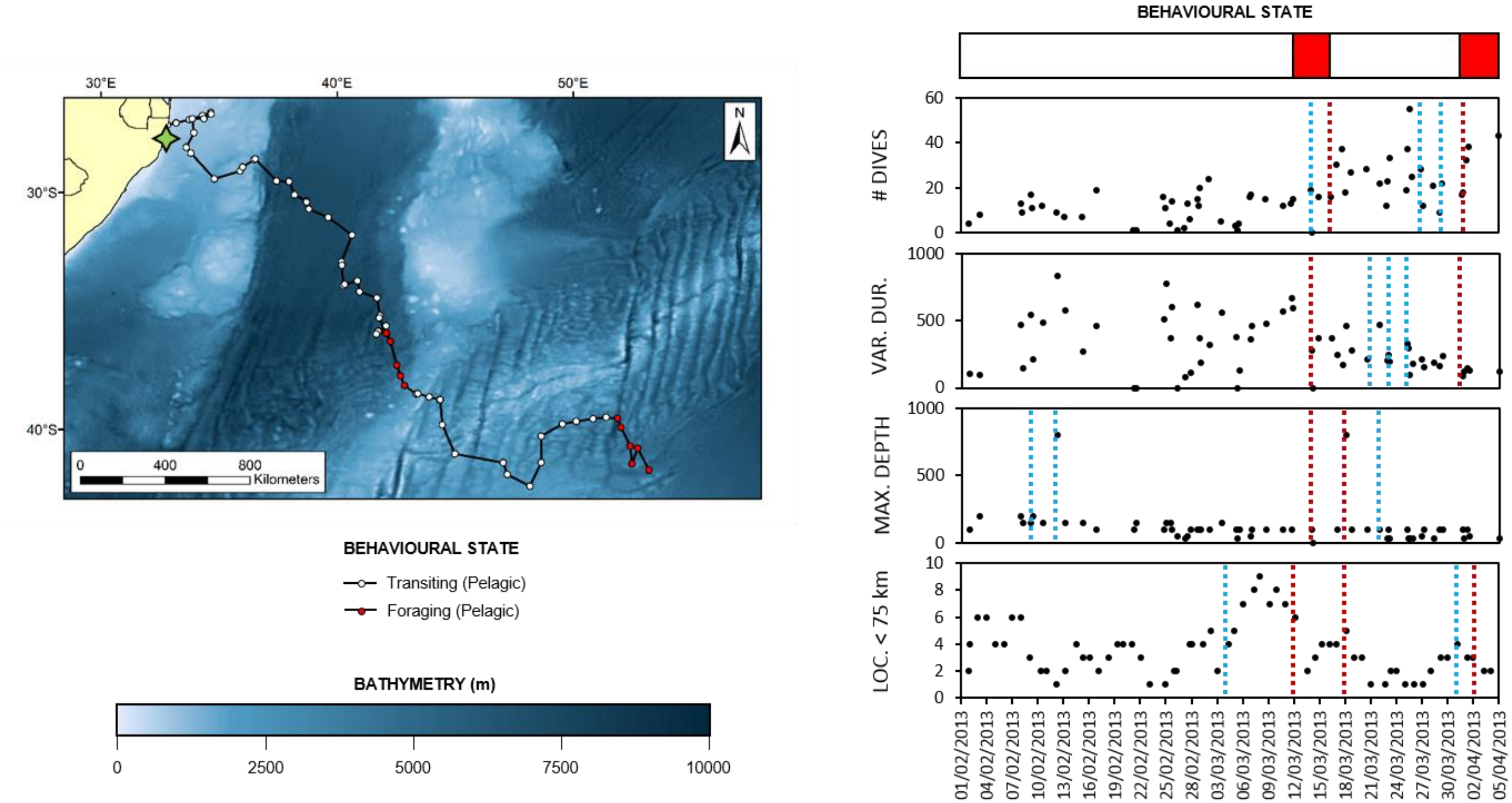

Figure 3.8.11 Movements and dive behavior of Turtle H tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

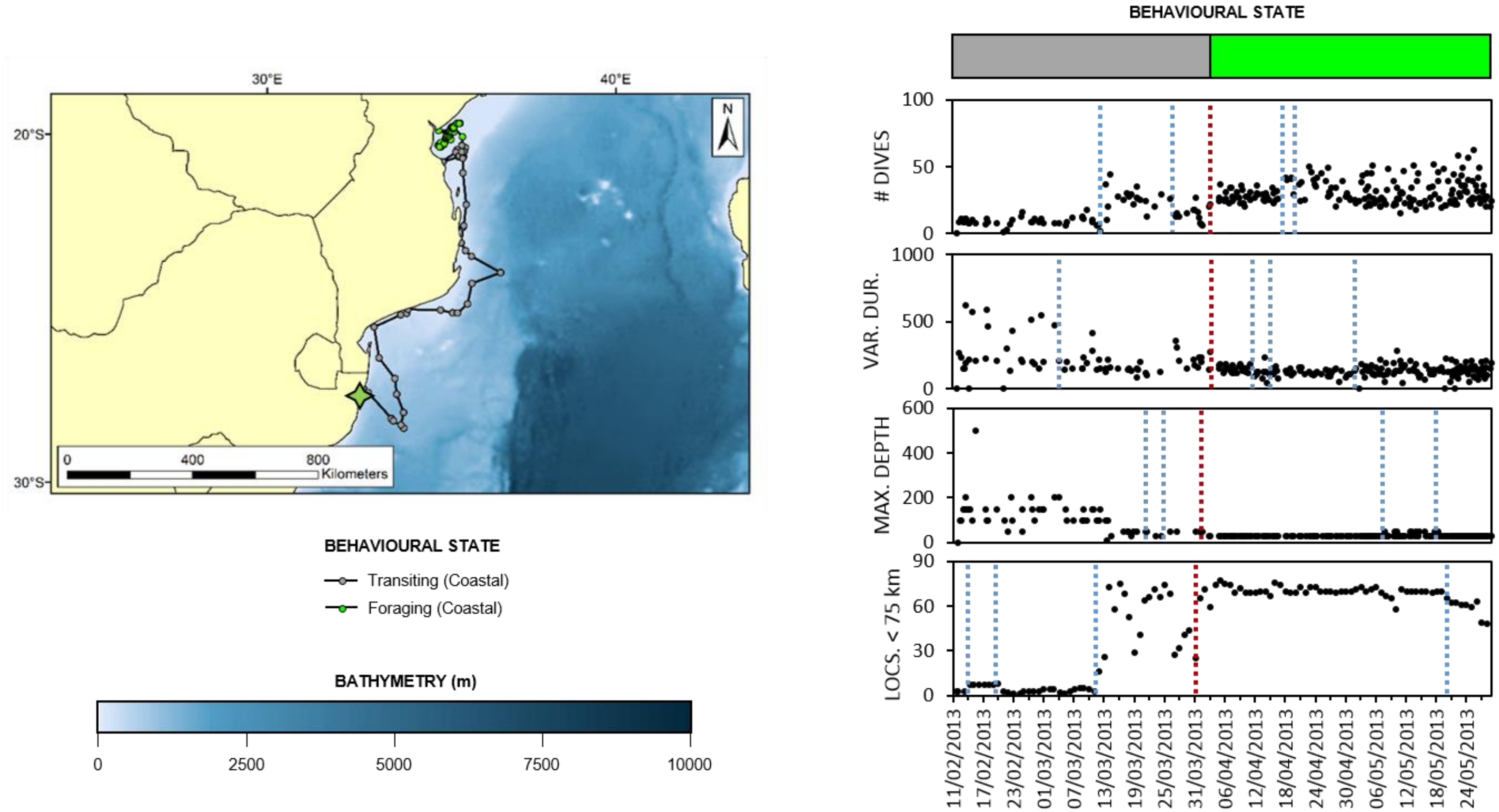

Figure 3.8.12 Movements and dive behavior of Turtle I tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoint occurred in different metrics within a period of 3 days, otherwise dots are in blue.

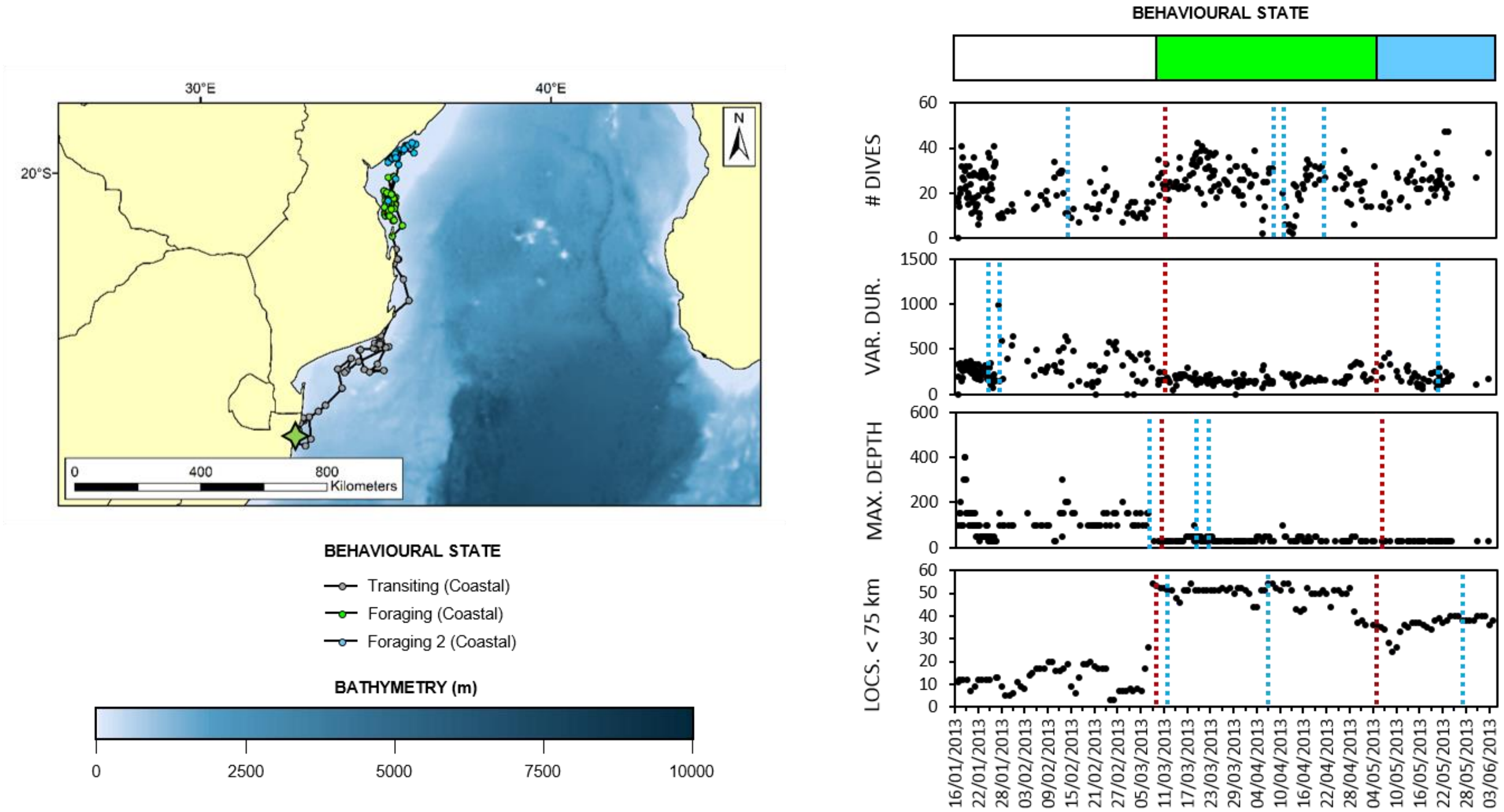

Figure 4.8.13 Movements and dive behavior of Turtle J tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoint occurred in different metrics within a period of 3 days, otherwise dots are in blue.

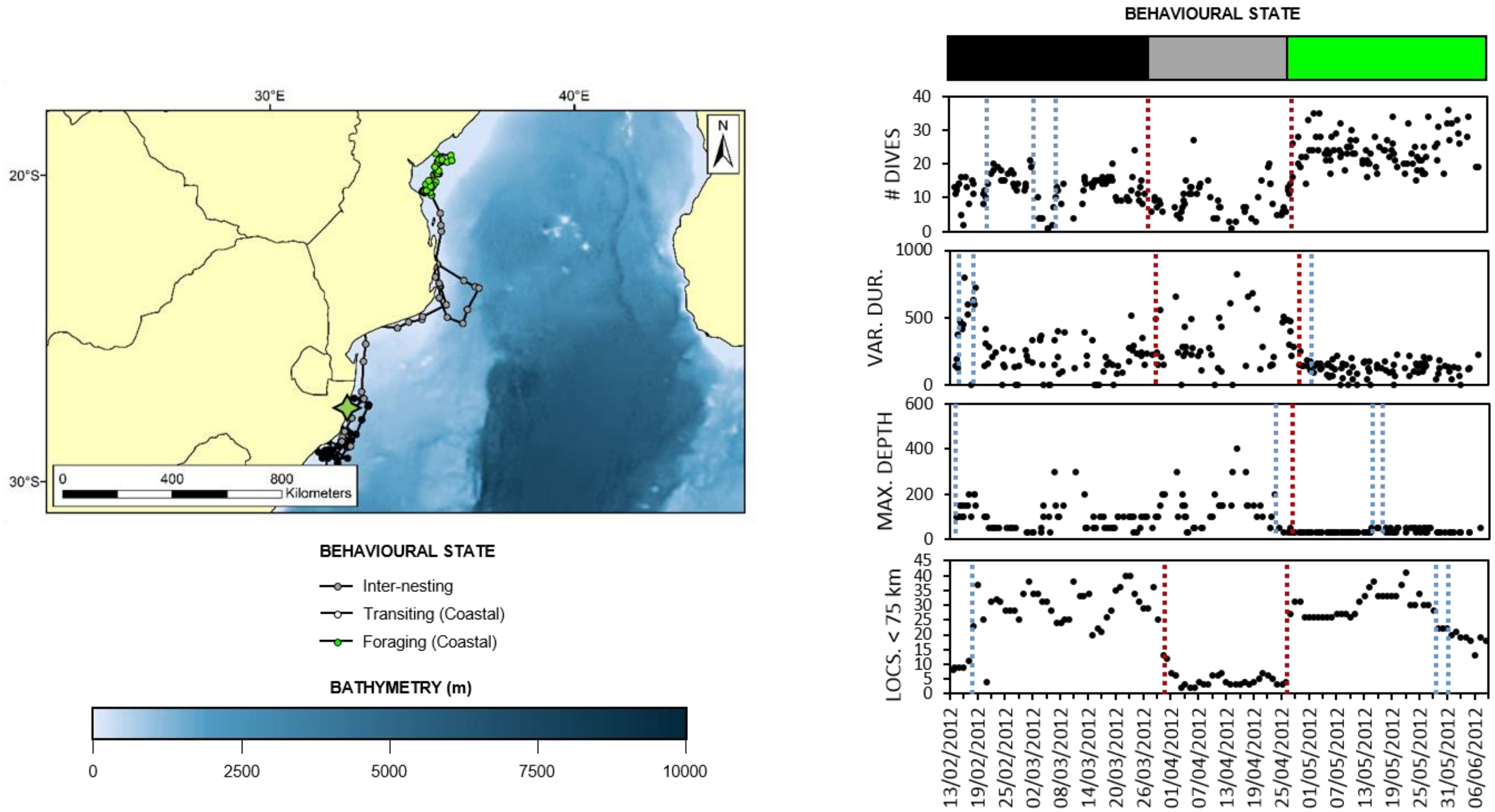

Figure 4.8.14 Movements and dive behavior of Turtle K tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

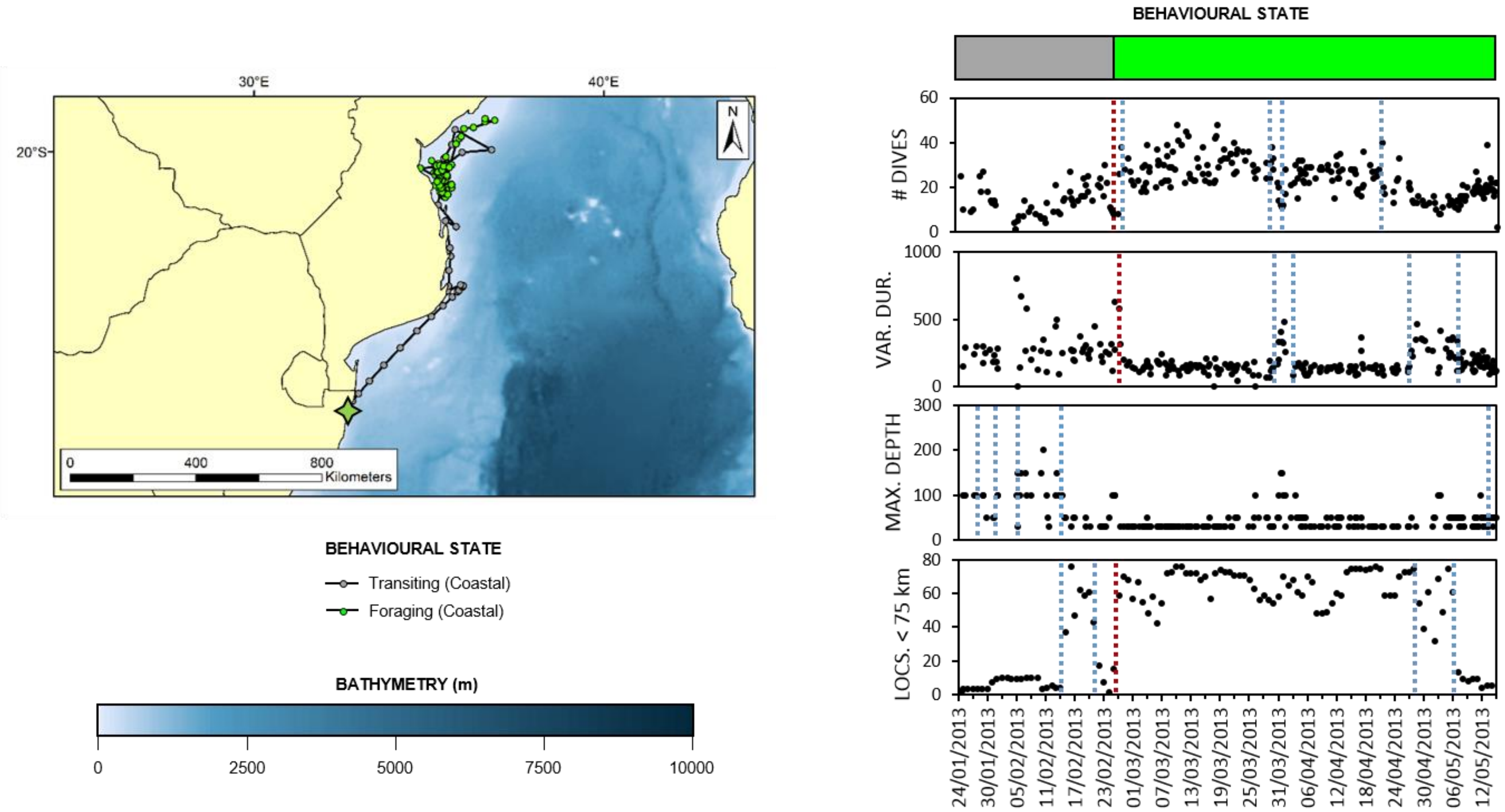

Figure 4.8.15 Movements and dive behavior of Turtle L tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

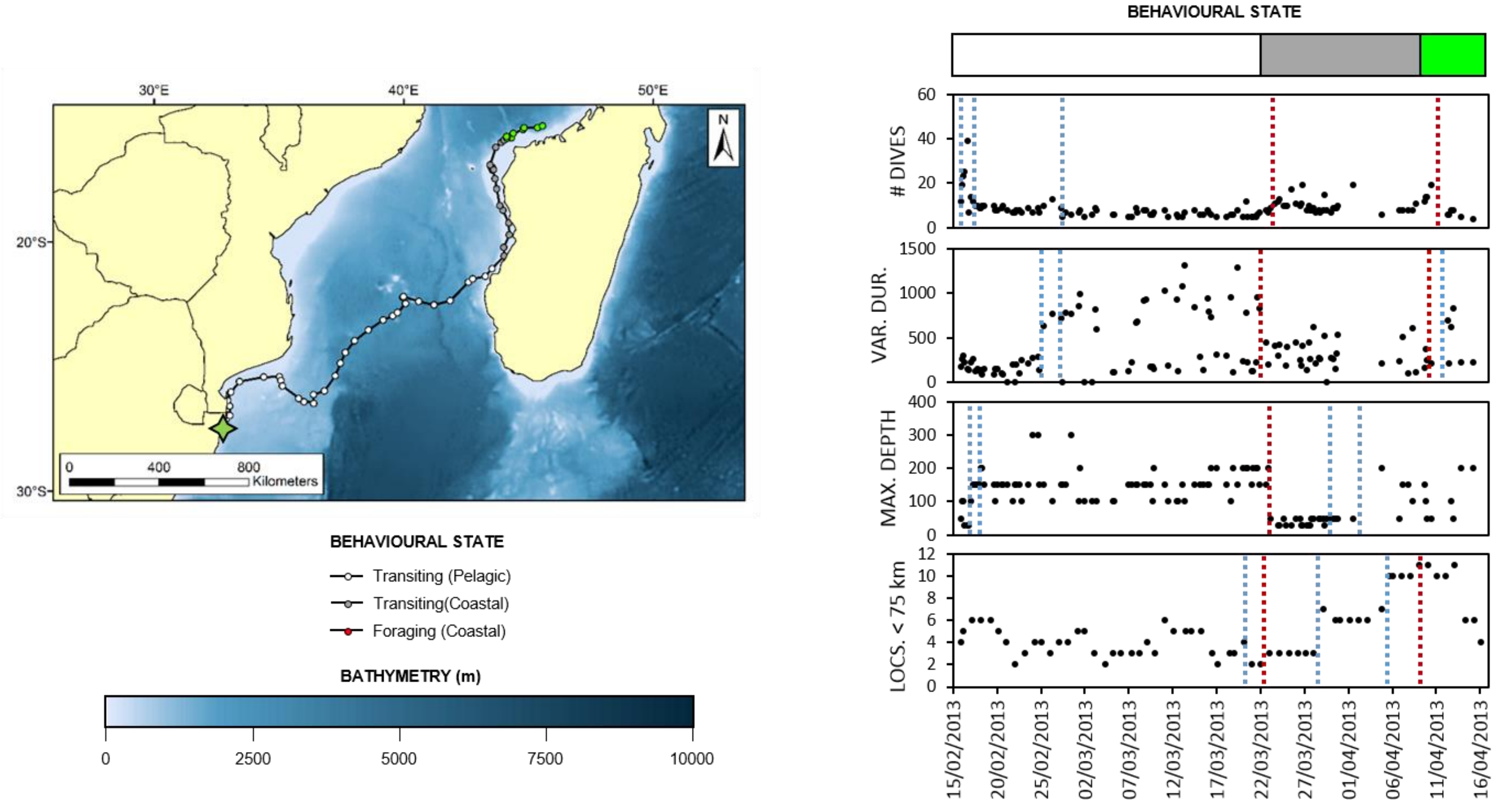

Figure 4.8.16 Movements and dive behavior of Turtle M tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

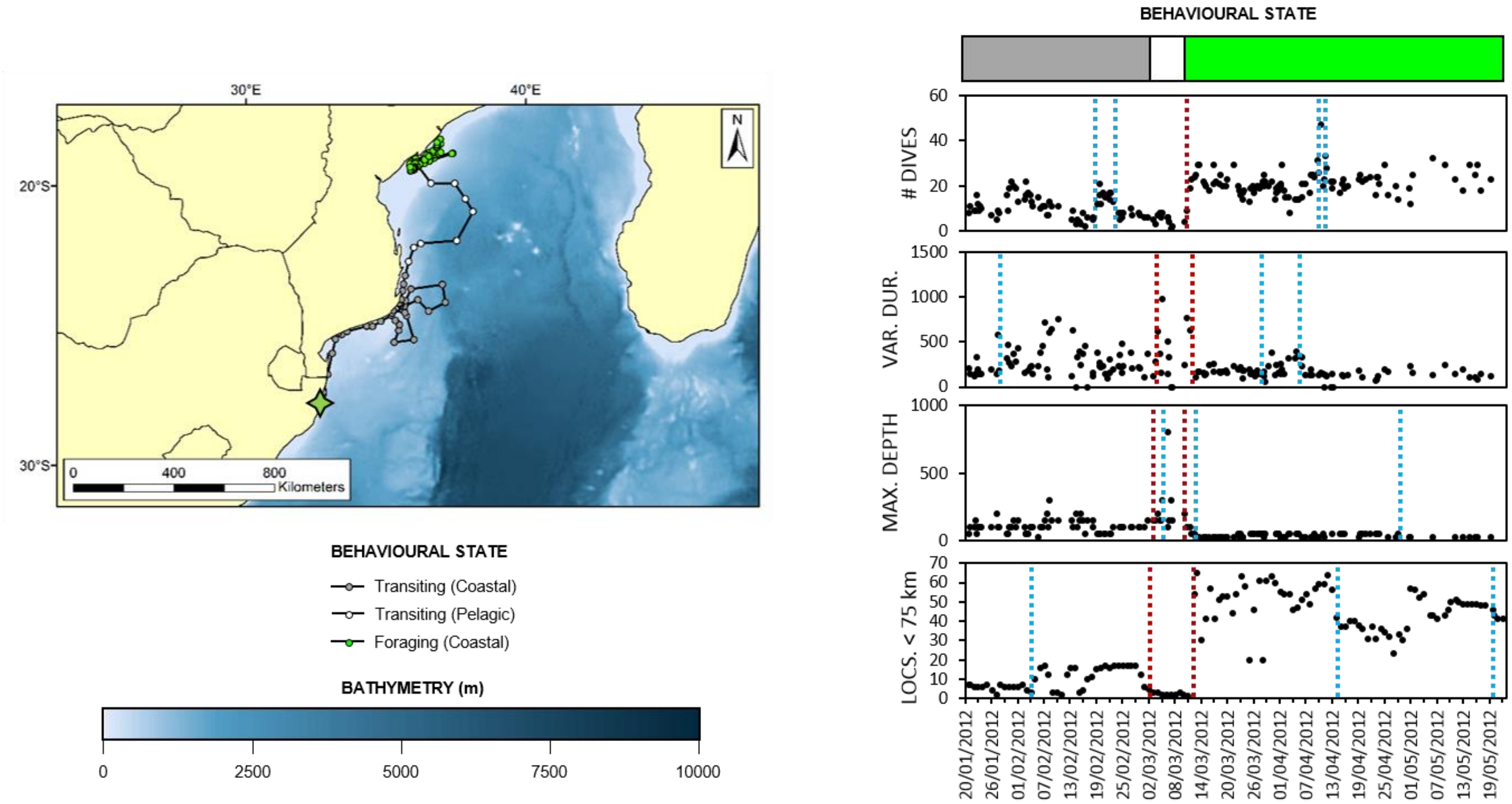

Figure 4.8.17 Movements and dive behavior of Turtle N tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

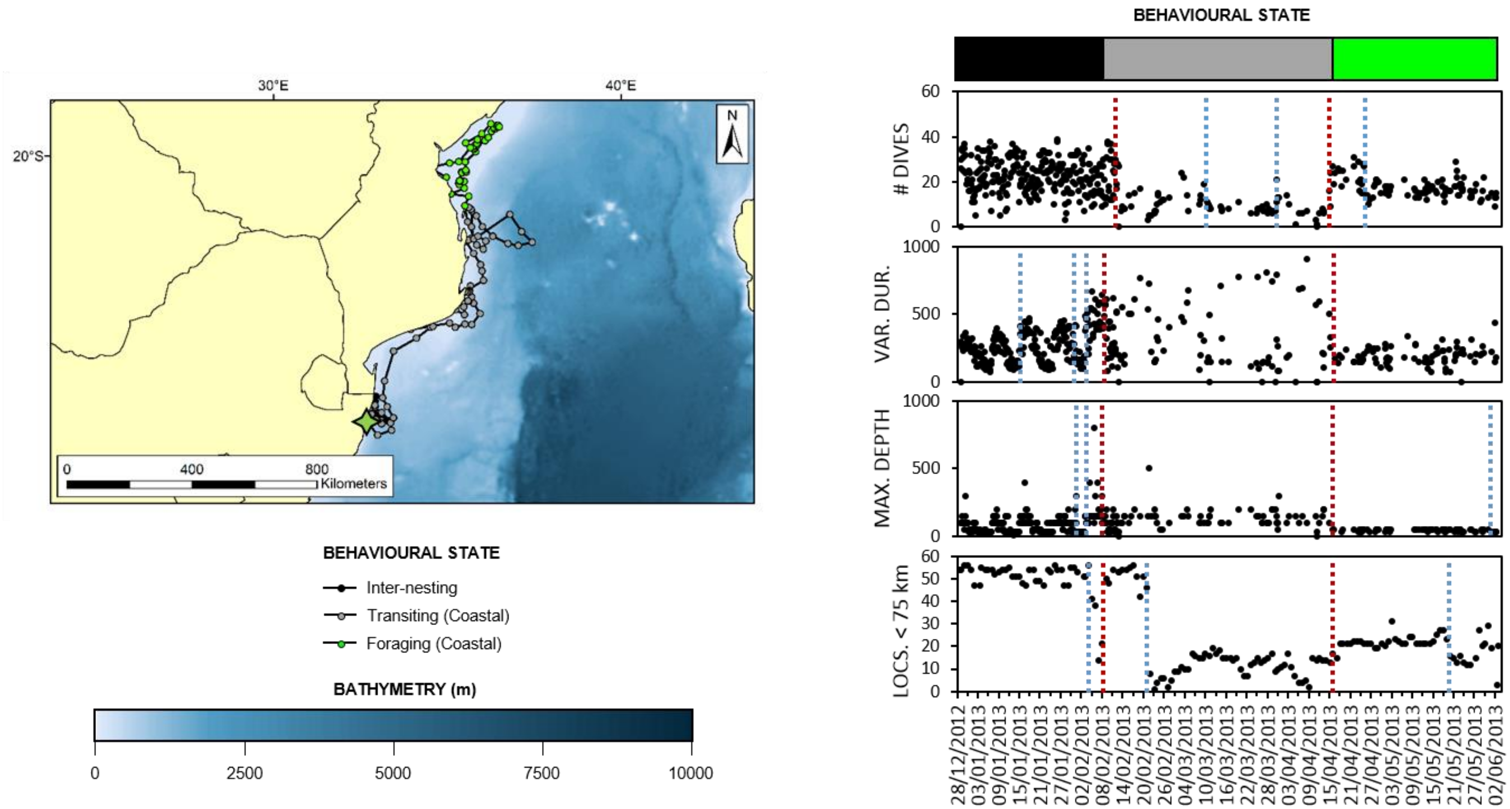

Figure 4.8.18 Movements and dive behavior of Turtle O tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoint occurred in different metrics within a period of 3 days, otherwise dots are in blue.

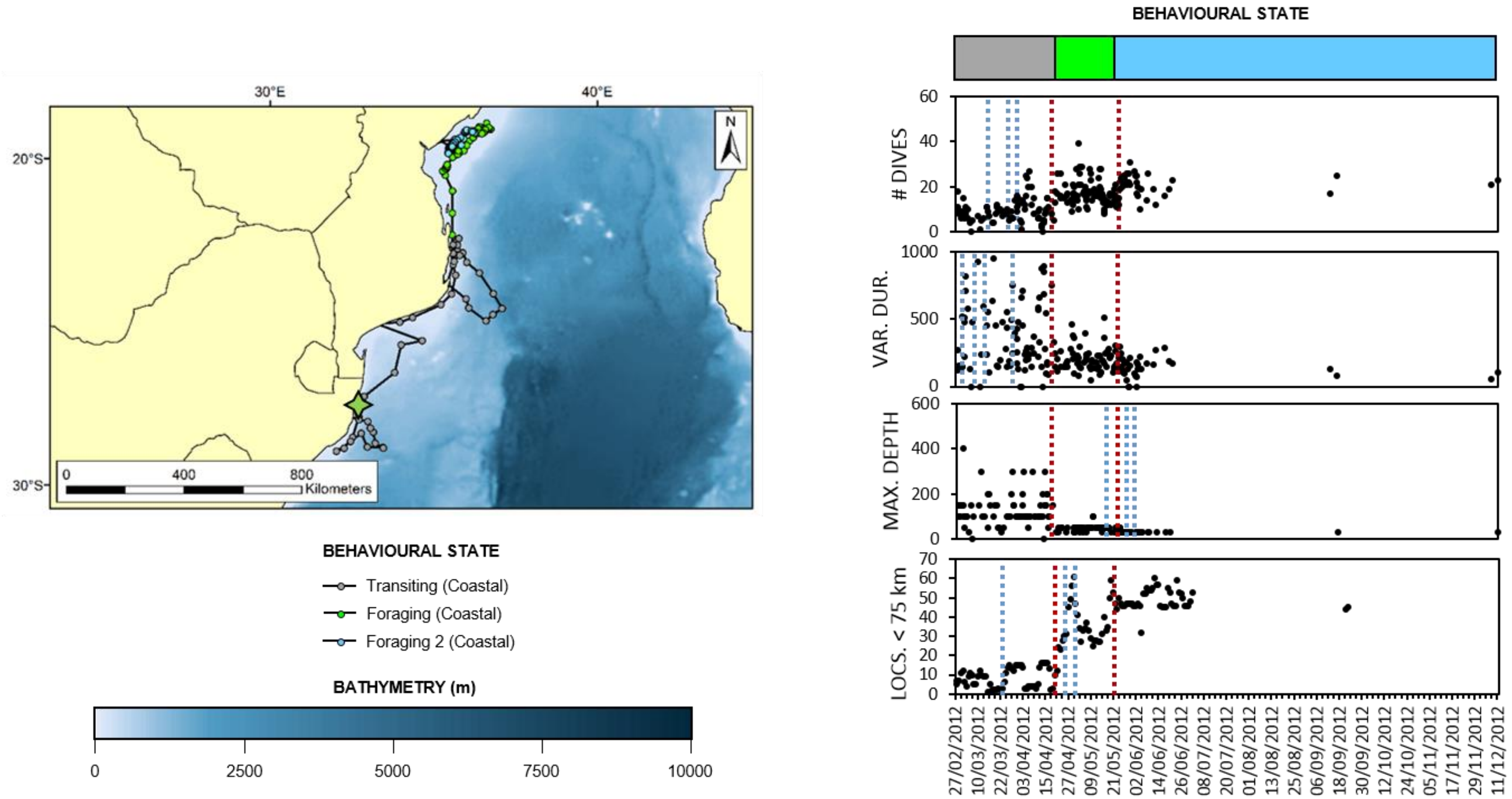

Figure 4.8.19 Movements and dive behavior of Turtle P tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. Dive metrics are the number of dives per 4 h period (# DIVES), variation in dive duration per 4 h period (VAR. DUR.), the maximum dive depth per 4 h period (MAX. DEPTH), and daily locations within 75 km of each individual location (LOCS. < 75 km). Dotted lines represent the presence of a changepoint. Dot in red are when 3 or more changepoints occurred in different metrics within a period of 3 days, otherwise dots are in blue.

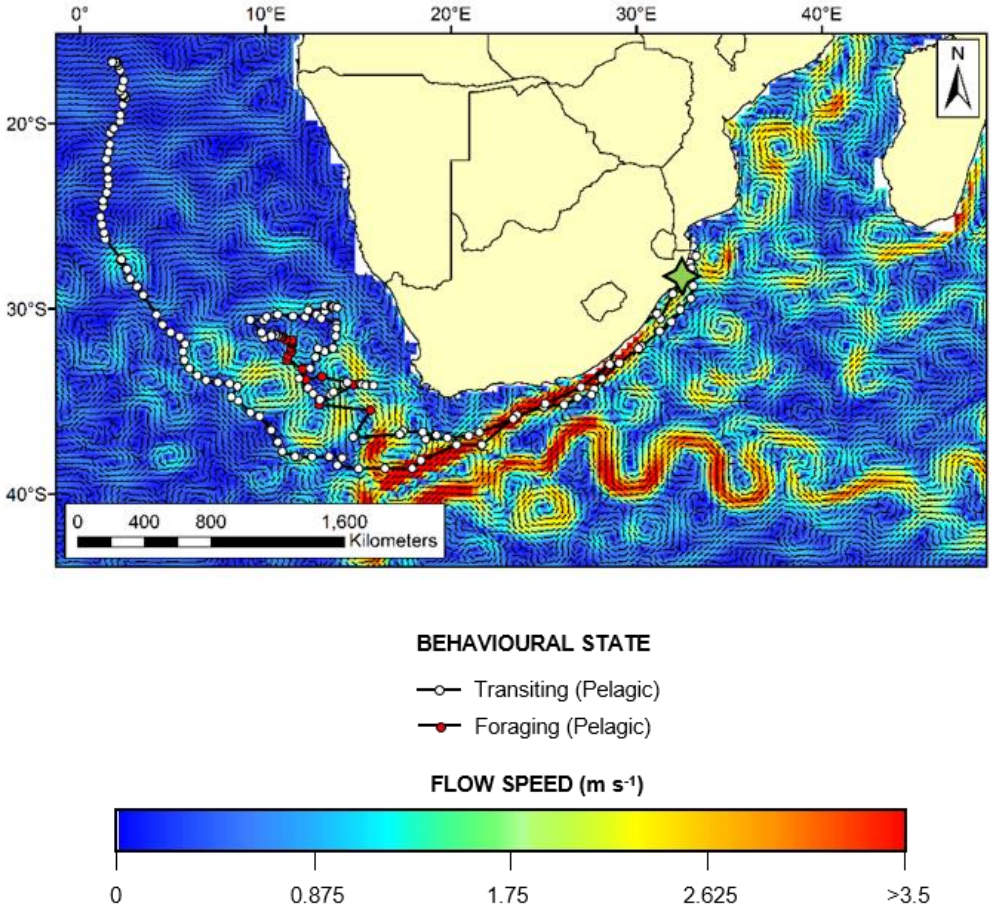

Figure 4.8.20 Movements of turtle A and C tracked by satellite telemetry from their nesting grounds in the iSimangaliso Wetland Park. Each track has been analyzed by a changepoint Analysis Model to determine its behavioral state. Tracks are overlaid onto a map of ocean currents for the 5-day period between 9/3/12 and 13/3/12.

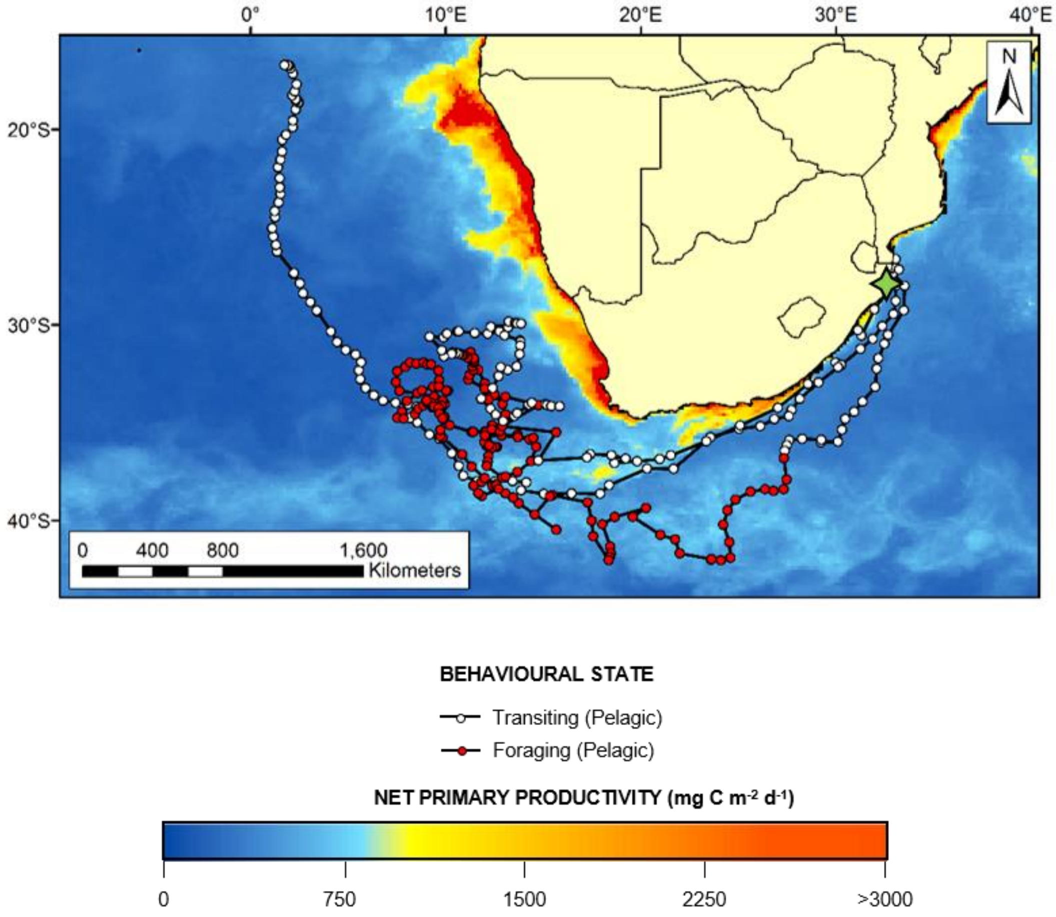

Figure 4.8.21 Movements of turtle A, B and C tracked by satellite telemetry from their nesting grounds in the iSimangaliso Wetland Park. Each track has been analyzed by a changepoint Analysis Model to determine its behavioral state. Tracks are overlaid onto a map of Net Primary Productivity for a monthly period between 1/4/12 and 1/5/12.

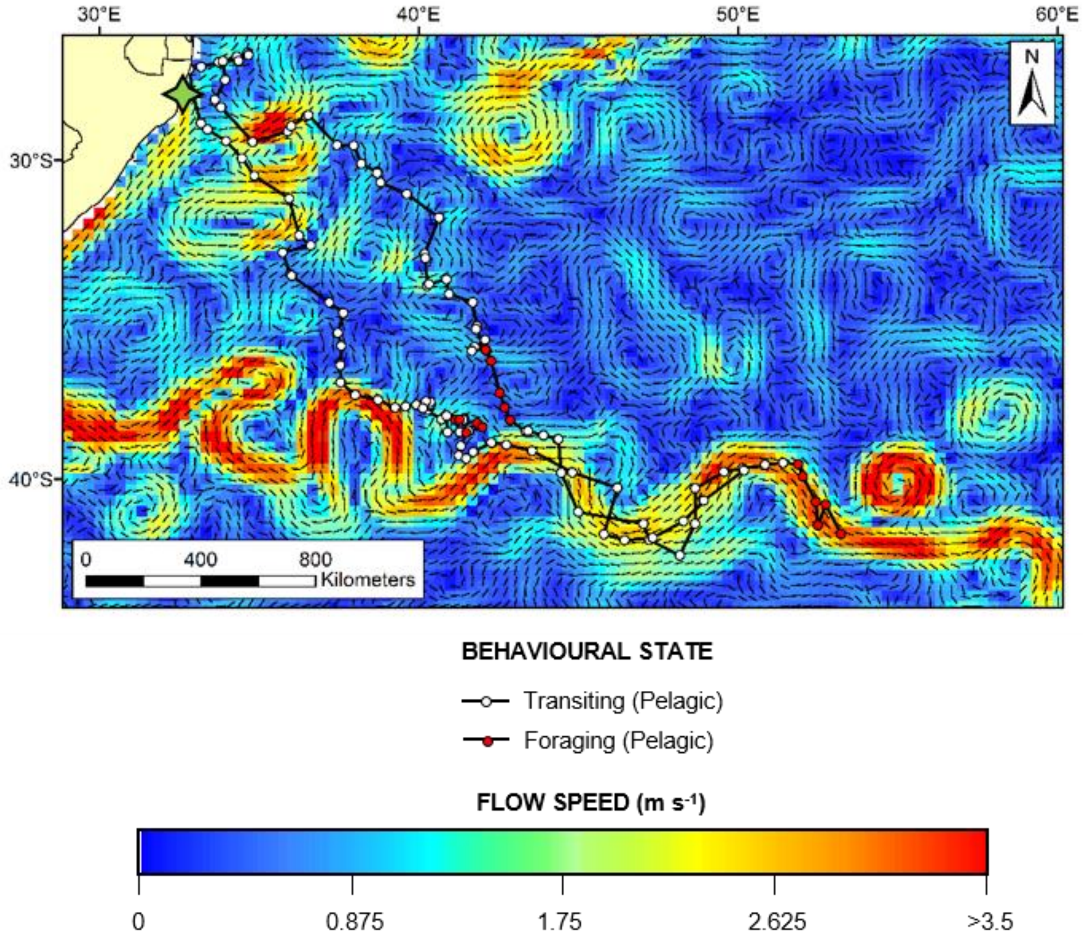

Figure 4.8.22 Movements of turtle F and H tracked by satellite telemetry from their nesting grounds in the iSimangaliso Wetland Park. Each track has been analyzed by a changepoint Analysis Model to determine its behavioral state. Tracks are overlaid onto a map of ocean currents for the 5-day period between 27/2/13 and 3/3/13.

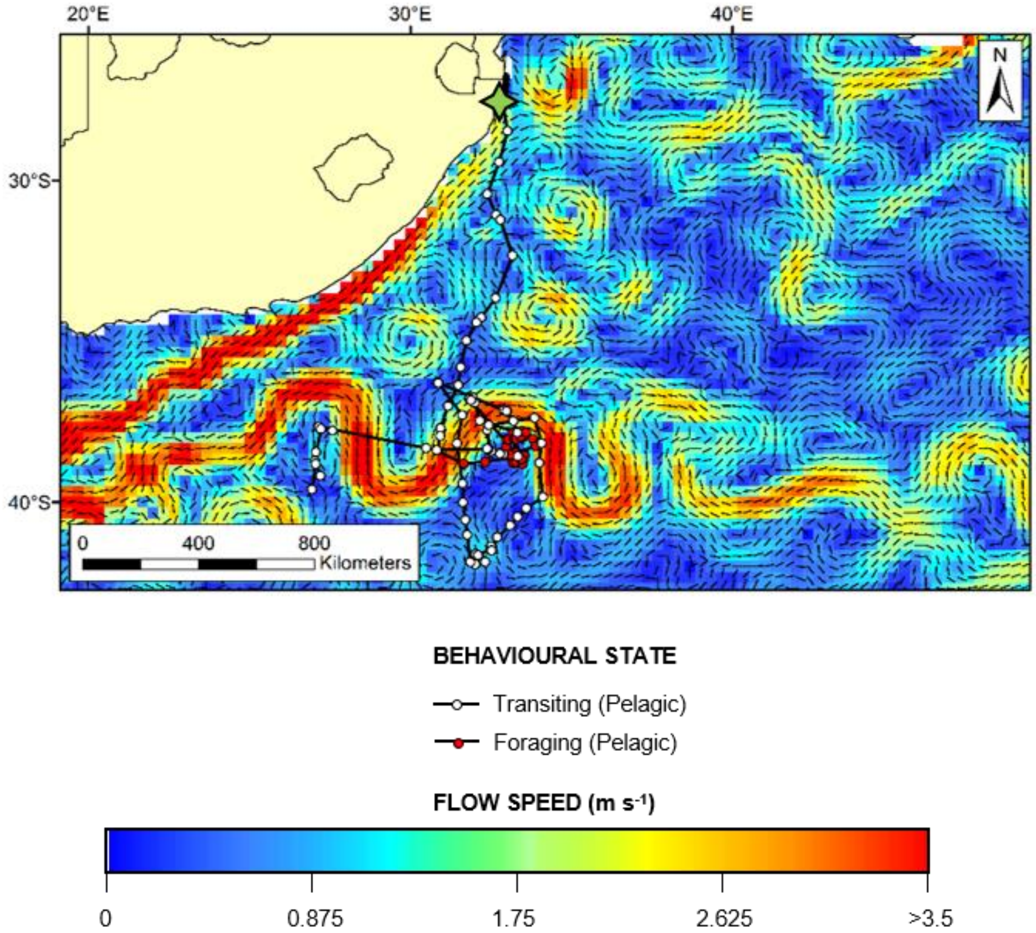

Figure 4.8.23 Movements of turtle E tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. This track has been analyzed by a changepoint Analysis Model to determine its behavioral state. This track are overlaid onto a map of ocean currents for the 5-day period between 3/3/12 and 8/3/12.

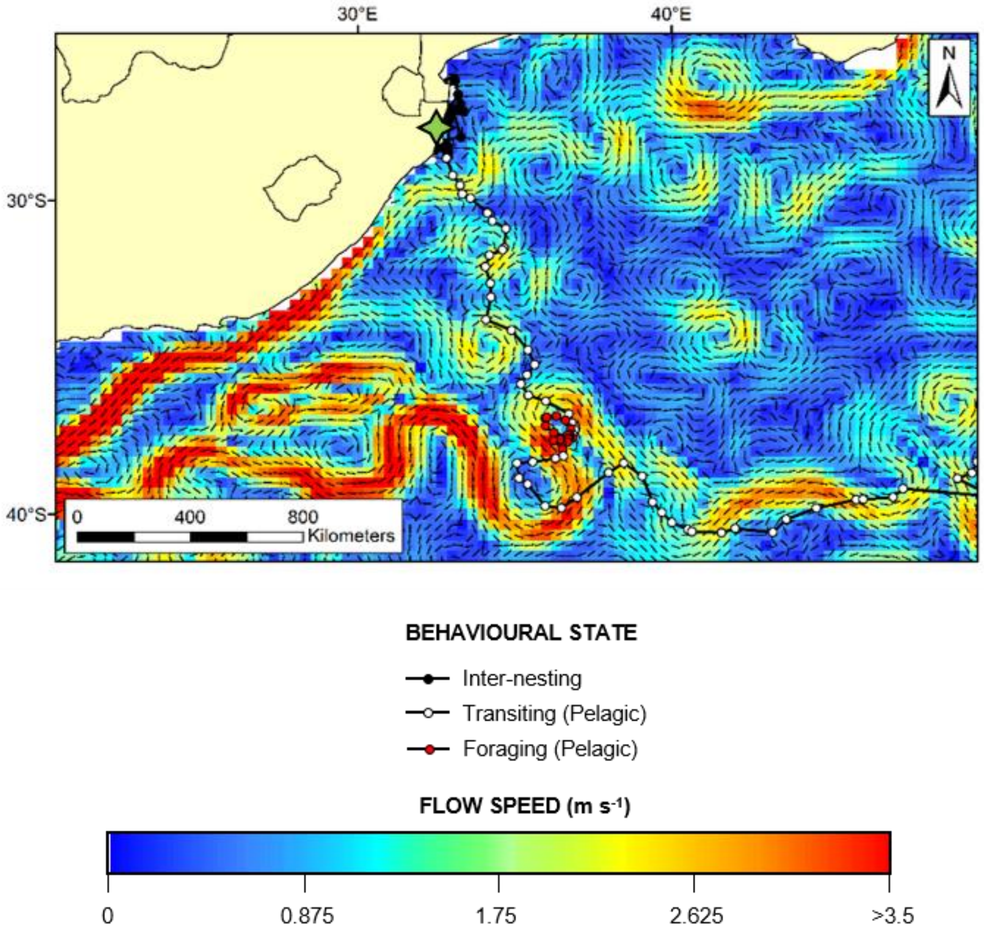

Figure 4.8.24 Movements of turtle G tracked by satellite telemetry from its nesting grounds in the iSimangaliso Wetland Park. This track has been analyzed by a changepoint Analysis Model to determine its behavioral state. This track are overlaid onto a map of ocean currents for the 5-day period between 1/4/12 and 6/4/12.

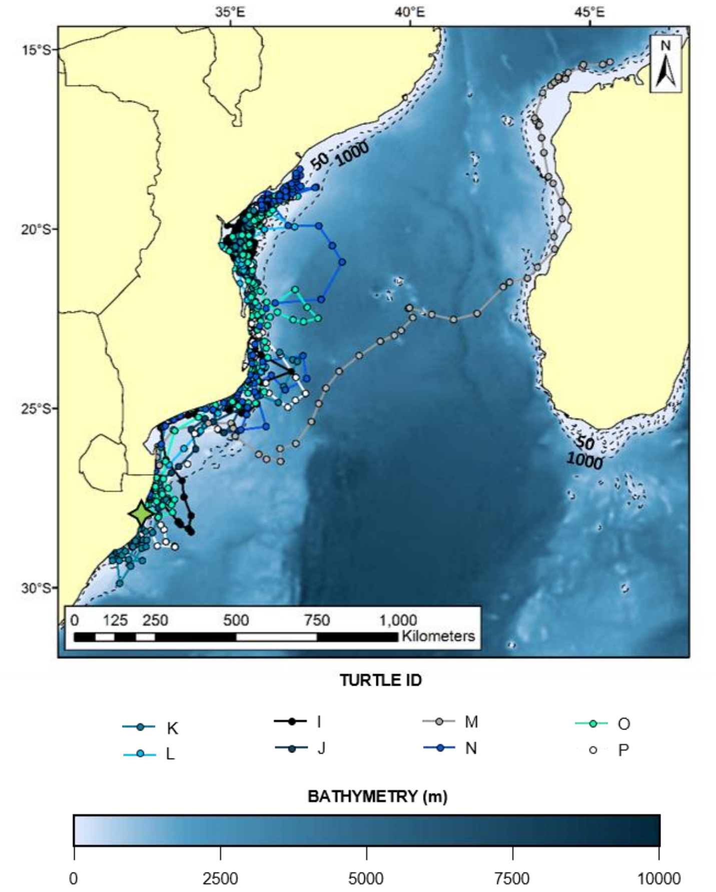

Figure 4.8.25 Movements of 8 leatherback turtles tracked by satellite telemetry from their nesting grounds in the iSimangaliso Wetland Park that migrated to the Mozambique Channel. Tracks are overlaid onto a bathymetric map. Dotted black lines represent 50 and 1000 m isobars.

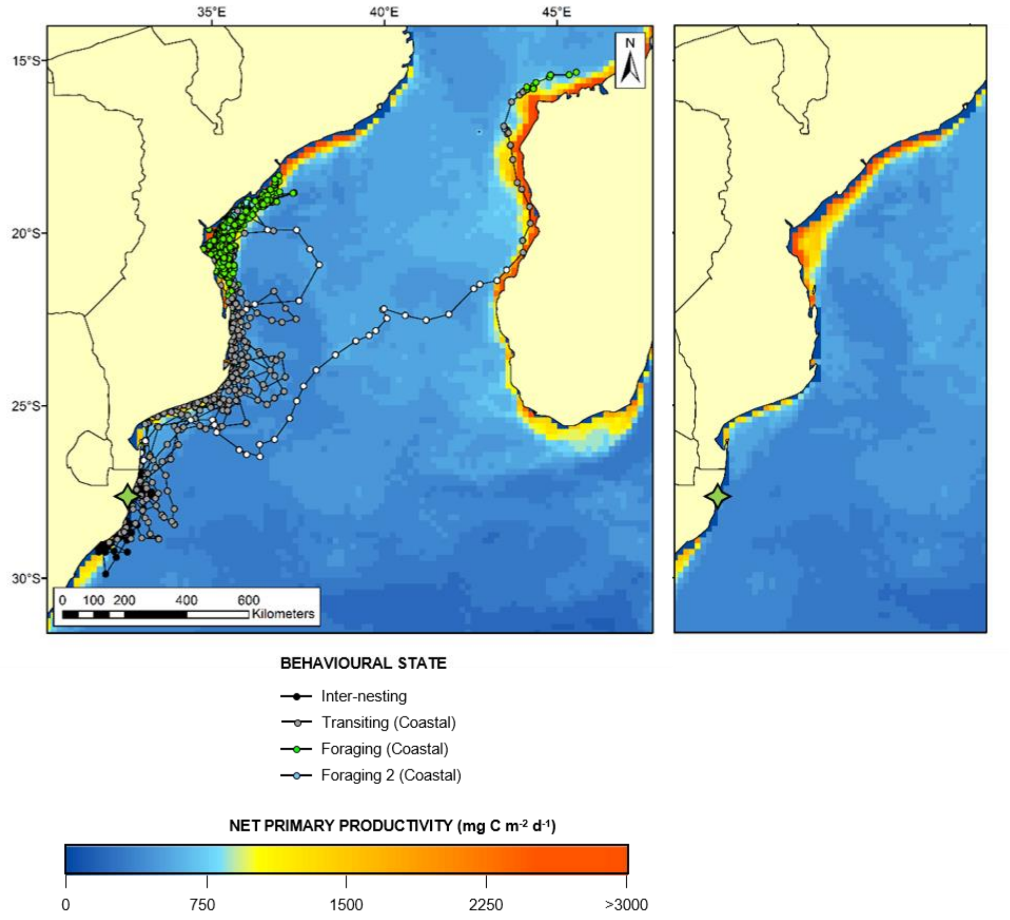

Figure 4.8.26 Left - Movements of turtle I, J, K, L, M, N, O, and P tracked by satellite telemetry from their nesting grounds in the iSimangaliso Wetland Park. Each track has been analyzed by a changepoint Analysis Model to determine its behavioral state. Tracks are overlaid onto a map of Net Primary Productivity for a monthly period between 1/4/12 and 1/5/12. Right – The Net Primary Productivity map with the turtle locations removed.

CHAPTER 4. STABLE ISOTOPE ANALYSIS AND SATELLITE TELEMETRY REVEAL THE MIGRATORY BEHAVIOR OF LEATHERBACK AND LOGGERHEAD TURTLES AROUND SOUTHERN AFRICA AND THE CONSEQUENCES OF HIGH-DRAG BIOLOGGING DEVICES

4.1 Abstract

Combining satellite telemetry and stable isotope analysis can provide deep ecological insights into the habitat preferences of migratory species. In this study, we employed both techniques to investigate the at-sea behavior of leatherback *Dermochelys coriacea* and loggerhead *Caretta caretta* turtles nesting in the iSimangaliso Wetland Park. Specifically, we aimed to (1) use satellite telemetry to validate whether carbon and nitrogen stable isotope analysis of skin tissue could be used to identify pre-nesting foraging habitats, (2) use both techniques to determine the relative importance of different foraging areas for these nesting populations, and (3) compare the migratory behavior of leatherback turtles tracked using either high- or low-drag satellite-transmitter attachments (harness or tethers, respectively). Overall, stable isotope analysis mirrored the migratory patterns that were recorded by tethered satellite transmitters and both techniques confirmed that the Mozambique Channel is the most common foraging area for leatherback and loggerhead turtles nesting in South Africa. Conversely, stable isotope analysis did not reflect the migratory patterns of leatherback turtles tracked using harness satellite transmitters. Furthermore, the movements of those animals tracked using harnessed transmitter animal appear move influenced by the prevailing currents than those tracked using tethered transmitters. We conclude that stable C and N isotope analysis of sea turtle skin tissue is a practical tool for scaling-up the inferences that can be gained from satellite telemetry to be more applicable on a population-scale. We also

conclude that low-drag transmitters are necessary to accurately assess ‘natural’ migratory behaviors of marine animals, especially when individuals may be interacting with strong currents.

4.2 Introduction

In recent decades, there has been a rapid proliferation in the use of animal-borne satellite telemetry devices to study the movements of free-roaming animals (Hart and Hyrenbach 2009). The use of such devices has become particularly widespread when investigating species that are challenging to track visually, such as marine organisms and long-distance migrants (Godley et al. 2008; Robinson et al. 2010; Hammerschlag et al. 2011). Yet the rise in the use of satellite telemetry in ecological studies has not been matched by an equivalent increase in the number of studies assessing the limitations of these devices (Hebblewhite and Haydon 2010; McMahon et al. 2011; Vandenabeele et al. 2011). One such limitation is that satellite transmitters are currently very expensive (up to $5,000 per device). This constrains their utility in studies requiring large sample sizes, such as those aiming to discern the spatial distribution of a migratory species at a population-scale (Börger et al. 2006; Lindberg and Walker 2007). Another issue is that the attachment and retention of the device may alter an animal’s behavior and even lower its fitness (Walker and Boveng 1995; Gauthier-Clerc et al. 2004; Thomson and Heithaus 2014). This raises ethical concerns, especially when working with endangered species, and has implications for the applicability of the collected data (Wilson and McMahon, 2006). The issues of small sample sizes or device-induced atypical behavior can be circumvented, however, by complimenting satellite telemetry with the use of elemental or stable isotope analysis as a tool for identifying animals’ foraging habitat preferences.

Stable isotopes are non-radioactive atoms with the same number of protons (atomic number) but differing numbers of neutrons (atomic weight). Through stable isotope analysis, it is possible to determine the ratios of ‘lighter’ (neutron depleted) to ‘heavier’ (neutron enriched) isotopes of a given element (e.g. carbon or nitrogen). Early ecological studies employing stable isotope analysis discovered that the stable isotope ratios of primary producers often varied along environmental gradients (Goericke and Fry 1994; Altabet and Francois 1994; Montoya 2007). In addition, stable isotope ratios are transferred up the food-web in a roughly predictable manner (Peterson and Fry 1987). For example, consumers tend to be enhanced in $\delta^{15}N$ by 3 – 4 ‰ relative to their prey, while $\delta^{13}C$ is only enhanced by 0 – 1 ‰ (Post 2002). As a result, animals foraging in different habitats or at different trophic levels tend to have distinct isotopic ratios (Cherel and Hobson 2007; Rooker et al. 2008; Hückstädt et al. 2012). With knowledge of how stable isotope ratios vary between foraging grounds it is thus possible to infer an animal's previous foraging location through stable isotope analysis of superficial tissue samples (Hobson, 1999; Rubenstein and Hobson, 2004).

Currently, spatial patterns in isotopic ratios have only been established for some species in a narrow range of locations (Graham et al., 2010). However, this can be addressed by conducting stable isotope analysis on individuals with known foraging areas, such as those tracked by satellite telemetry. Once the isotopic signature of each foraging areas has been identified then stable isotope analysis can be used alone to infer the foraging areas of non-satellite tracked individuals. The benefits of using stable isotope analysis in this manner are that it is a relatively inexpensive ($5 to 20 per sample). As such, this technique is often suitable for inferring the movements of large numbers of individuals at a low cost (Zbinden et al. 2011; Ceriani et al. 2013). In addition, stable isotope analysis can provide information about an animal's *previous* foraging location (if a tissue is sampled that has an appropriate isotopic turnover rate). As such, the collection of a tissue sample, unlike the attachment of a transmitter, has no influence on the behavioral patterns discerned in the analysis.

For several reasons, sea turtles are prime taxonomic candidates for spatial tracking via stable isotope analysis. First, tissue samples can be readily collected when adult females emerge on their nesting beaches. Second, each female from a single nesting beach generally forages in one of a number of spatially distinct areas that are often located vast distances from the nesting area (Witt et al. 2011; Benson et al. 2011; Foley et al. 2013; Schofield et al. 2013). Third, sea turtles are usually capital breeders and accumulate all energy for reproduction in the foraging grounds many weeks or months before they reach their breeding grounds (Plot et al., 2013). Finally, the time required for the superficial tissues (e.g. skin or blood) of large reptiles to reflect the isotopic composition of their food is in the scale of months to years (Seminoff et al. 2007; Rosenblatt and Heithaus 2013). All these factors together mean that superficial tissue samples taken from nesting sea turtles should not reflect the isotopic signature of their migratory or nesting areas but be broadly reflective of their foraging areas.

Stable isotope analysis has already been used to discern the foraging areas of leatherback turtles *Dermochelys coriacea* in both the Pacific and North Atlantic Ocean (Caut et al. 2008; Seminoff et al. 2012). Yet no such studies have focused on the population in the Indian Ocean or specifically those nesting in the iSimangaliso Wetland Park, South Africa. Initial tracking studies conducted at this location demonstrated that the movements of post-nesting leatherback turtles are strongly influenced by ocean currents (Luschi et al. 2003a). Specifically, most individuals are advected with the prevailing Agulhas Current down the east coast of South Africa into pelagic foraging areas, in either the South Atlantic or Western Indian Ocean (Hughes et al. 1998; Lambardi et al. 2008). However, the transmitters used in these studies were attached using a harness – a technique that is now known to increase hydrodynamic drag on these species by over 100 % (Jones et al. 2013). Alternatively, by using transmitters attached by a hydrodynamic tether that only increased drag by < 5 % (Jones et al. 2014), we observed that most individuals from this nesting population actually swim against the Agulhas current and into coastal habitats in the Mozambique Channel (see Chapter 3). Here, we further investigated the importance of the Mozambique Channel as a foraging ground for the leatherback turtles nesting in the iSimangaliso Wetland Park through stable isotope analysis. Such analysis could be conducted on sample sizes far beyond those currently available from satellite telemetry studies. In addition, the determination of foraging area by stable isotope analysis would provide an *unbiased* benchmark to assess whether migratory behaviors are influenced by using tracking methods with differing levels of drag.

This study has three major objectives. (1) To use satellite telemetry to validate whether stable isotope analysis can be used to infer the foraging areas of the leatherback turtles nesting in the iSimangaliso Wetland Park. To achieve this, we investigated whether satellite-tracked leatherback turtles that migrate to different foraging areas have distinct stable isotopic signatures. We will also compare these results to the stable isotope values of sympatrically nesting loggerhead turtles *Caretta caretta* that are known to forage in the Mozambique Channel (R Nel, unpublished data). (2) To use both satellite telemetry and stable isotope analysis to determine the relative importance of different foraging areas for the leatherback and loggerhead turtles nesting in the iSimangaliso Wetland Park. (3) To determine if satellite tracking influences migratory behavior. To achieve this, we tested if the number of turtles migrating to each foraging area is similar regardless of whether they were tracked by a transmitter attached by a high-drag harness or low-drag tether. Furthermore, these results were compared to the foraging area assignments as determined by stable isotope analysis.

4.3 Methods

4.3.1 Study site

The iSimangaliso Wetland Park is located in the north-east corner of South Africa (28°0’ S, 32°30’ E). The coastal portion of the Park is approximately 280 km long and is characterized by a series of rocky headlands separated by sandy beaches of 5 to 15 km in length. These beaches host sympatrically nesting populations of loggerhead and leatherback turtles. We patrolled the northern-most 56 km of the Park’s coastline to encounter nesting turtles.

When a nesting turtle was encountered we applied metal and passive integrated transponder (PIT) tags; collected a skin sample; and, if appropriate, attached a satellite transmitter. Nesting turtles were not approached until egg laying had commenced to minimize the potential of interrupting the nesting process.

4.3.2 Satellite telemetry

Satellite transmitters were deployed on 42 nesting leatherback turtles between 1995 and 2013 (for a full summary see Figure 1). The first 9 of these transmitters, which were deployed between 1996 and 2003, were attached using a harness method as described in Eckert and Eckert (1986). These tracks have been published previously (Hughes et al. 1998; Luschi et al. 2003a; Luschi et al. 2006). The next 13 transmitters, which were deployed between 2006 and 2009, were also attached using a harness method. These transmitters were deployed by the organization Oceans and Coasts (Cape Town, South Africa). The remaining 20 transmitters, which were deployed between 2011 and 2013, were attached using a low-drag tethering technique as described in Chapter 3 and Appendix A. This technique was originally adapted from Morreale et al. (1999). Satellite transmitters were only deployed on turtles that appeared to be in good health and with no evident injuries.

To maximize the tracking duration during post-nesting migrations, the transmitters were typically deployed in the last 2 months of the nesting season (January and February). In addition, between 2011 and 2013, we employed the use of a Sonosite 180 Plus real-time portable ultrasound (Sonosite) to determine whether a turtle would continue to lay nests during the remaining nesting season (Rostal et al., 1996; Blanco et al., 2012). Using this method, we were able to mainly deploy transmitters onto turtles that had laid their final clutch for that season and were about to begin their post-nesting migrations.

In addition to location data, the tethered transmitters provided data on dive behavior. When a transmitter stopped recording dives to depths lower than 10 m for a period of over 10 days, it was assumed the transmitter had broken off the animal. Consequently, subsequent location data were ignored, starting from when diving activity was no longer recorded. In contrast, the harness transmitters from this study either did not collect dive data, or we did not have access to these data, and so we could not use diving behavior to confirm if the transmitter had prematurely detached from the animal.

4.3.3 Tissue sampling and preparation

Skin samples were collected from a total of 96 leatherback turtles and 120 loggerhead turtles between 2011 and 2013. In some cases, individuals were sampled during separate nesting events in a single nesting season (for a full summary see Figure 2). Skin samples were collected from every individual with a tethered satellite transmitter.

Skin samples were collected using a sterile 6 mm biopsy punch from the medial rim of the front or rear flipper, avoiding any previous scar tissue. After the skin sample was removed, the area was sterilized using antiseptic spray (oxytetracycline). The skin sample was immediately stored in 95 % non-denatured ethyl ethanol and kept at room temperature until transport to the lab. The upper layer of the skin (stratum corneum; subsequently referred to only as skin) was separated from the underlying tissue using a scalpel. The remaining skin was rinsed with deionized water and diced into 10 to 20 pieces. The diced samples were dried for a minimum of 6 h using a rotary evaporator. Between 0.3 and 1.0 mg of the dried samples were weighed using a microbalance and packed into tin capsules for stable isotope analysis.

4.3.4 Stable isotope analysis

Stable isotope analyses were conducted at the Purdue Stable Isotope Facility, housed in the Department of Earth, Atmospheric, and Planetary Sciences at Purdue University, USA. The ratio of ^{13}C to ^{12}C and ^{15}N to ^{14}N in each sample was determined using a Carlo Erba 1108 Elemental Analyser coupled with a Sercon 20-22 Continuous Flow Isotope Ratio Mass Spectrometer. Stable isotope values were expressed in delta (δ) notation relative to universal standards in parts per thousand (‰) using the following equation:

$$\delta X = \left(\left[\frac{R_{sample}}{R_{standard}}\right] - 1\right) * 1000$$

where X is ^{13}C or ^{15}N and R_{sample} and $R_{standard}$ is the ratio of heavier to lighter isotopes of the appropriate element in the sample and the standard, respectively. δ^{13}C is expressed relative to the standard Pee Dee Belemnite and δ^{15}N is expressed relative to atmospheric nitrogen. Analyses are calibrated, to ensure reproducibility, using replicates of Peach Leaf standards (NIST1547) with standard deviations (σ) of δ^{13}C being ≤ 0.2 ‰ and δ^{15}N being ≤ 0.35 ‰. We did not use a post-hoc correction factor to account for lipids in the samples because Post et al. (2007) recommends against lipid normalization for samples preserved in ethanol. To assess stable isotope variation between skin samples, 27 samples were chosen at random and run in duplicate. The standard deviation (σ) between duplicate samples in δ^{13}C was 0.37 ‰ and δ^{15}N was 0.55 ‰.

For turtles that were sampled on more than one occasion, we calculated the mean δ^{13}C and δ^{15}N values for that individual. We used mean values as previous studies have confirmed that δ^{13}C and δ^{15}N values in blood plasma do not vary over the nesting season (Caut et al. 2008). Moreover, in reptiles the isotopic turnover rates for blood plasma are far more rapid than those for skin (Seminoff et al. 2007; Rosenblatt and Heithaus 2013).

4.3.5 Analysis of movement data

The locations of the transmitters were reported via the Argos Satellite System (Maryland, USA). The Argos Satellite System assigns each location a class (LC) of 3, 2, 1, 0, A, or B depending on the confidence of the locations accuracy, 3 being the most accurate and B being the least. Using all locations regardless of LC, we filtered all data where the movement rate exceeded 240 km d^{-1}. The filtered data was smoothed using a state-space model as outlined by Jonsen et al. (2007). For each of the turtles, putative foraging grounds were assigned depending on the ocean basins each track was recorded heading towards.

4.3.6 Statistical analyses

To determine whether stable isotope analysis could be used to determine foraging areas for leatherback turtles, we separated the tracked telemetry into groups based on their final relayed location. We tested to see if animals tracked to different foraging areas had different values for $\delta^{13}C$ and $\delta^{15}N$ using a Multivariate Analysis of Variance (MANOVA) with a Pillai's trace test. Data were tested for normality and homogeneity using Kolmogorov-Smirnov and Levene's test, respectively.

If the stable isotope value of turtles tracked to discrete foraging areas were statistically different this would not only provide evidence that stable isotope analysis can be used to track sea turtle movements but also that turtles post- and pre-nesting foraging areas are similar (foraging site fidelity).

To assign non-satellite tracked individuals to a specific foraging area based on their stable isotope ratios, we used Linear Discriminant Function Analysis (DFA). We used the $\delta^{13}C$ and $\delta^{15}N$ ratios of the 16 satellite-tracked leatherback turtles with known foraging areas as a training data set (using equal weighted priors) to define the discriminant functions. The derived discriminant functions were used to determine the probability that each non-satellite tracked individual belonged to a specific foraging area. If the probability was > 80 %, individuals were assigned to that foraging area. To test the accuracy of the assignment by the DFA, we utilized a Jackknife (leave-one-out) cross-validation to the training dataset. In this method, each turtle is removed in turn from the training dataset and then classified to a foraging area using the discriminant functions derived from the remaining turtles in the training dataset. Data were analyzed using the program R (R Development Core Team 2011) with an α level of 0.05.

4.4 Results

4.4.1 Satellite telemetry

Although 42 satellite transmitters were deployed on leatherback turtles in the iSimangaliso Wetland Park between 1996 and 2013, only 32 continued to function during these animals' post-nesting migrations (Figure 3). Of these, 16 were from transmitters attached by harness and 16 were from transmitters attached by tether.

Considering the movements of both harnessed and tethered turtles collectively, we identified three basic migratory behaviors. We separated these behaviors by the ocean region each individual headed towards (Figure 4), which were: the South Atlantic Ocean (SAO), Western Indian Ocean (WIO), and Mozambique Channel (MC). (1) SAO: Over half of the tracked individual immediately headed south of the nesting area after the completion of nesting. These individuals tended to move within eddies formed by the prevailing Agulhas Current that flows down the east coast of South Africa. After reaching approximately 36 ° to 40 °S, a total of 9 individuals began heading west into the South Atlantic Ocean. These individuals eventually travelled north towards either the Benguela Upwelling System or to open waters off the coast of Angola. (2) WIO: Similar to the previous behavior, turtles initially followed a route south of the nesting beach. On reaching between 36 and 40° S, a total of 10 individuals headed east and remained in the Western Indian Ocean. Two of these individuals also eventually began moving north into either the open-waters west of Madagascar or into the Mozambique Channel. (3) MC – Contrary to the other behaviors, 8 individuals travelled immediately north from the nesting area until they reached the Sofala Banks or western Madagascar. While migrating, these individuals generally remained within 50 km of the coastline and only occasionally ventured out into deeper waters.

Considering the movements of both harnessed and tethered turtles separately, there are notable differences in behavior between the two tracking methods. All the turtles tracked by harnessed transmitters initially travelled south of the nesting beach with the exception of two individuals that conducted large loops near to the nesting ground and one individual that headed predominantly east. Those individuals that travelled south also tended to remain within 300 km of the South African shoreline and made multiple curves or revolutions. In contrast, when the tethered turtles migrated south it was less common for individuals to remain within 300 km of the South African shoreline and the tracks were straighter, showing far fewer revolutions. Moreover, only tethered turtles were observed ever immediately migrating north of nesting area and into the coastal habitats of the MC.

For the harnessed transmitters, the mean tracking duration was 143.3 ± 117.6 SD days and the maximum tracking duration was 463 days. For the tethered transmitters, the mean tracking duration was 111.5 ± 41.32 days and the maximum tracking duration was 209 days.

4.4.2 Stable isotope analysis

The δ^{13}C of leatherback turtle skin samples ranged from -19.14 to -15.21 ‰ (Figure 5). The values for δ^{13}C have a bi-modal distribution with an apparent distinction between the two groups at approximately -17.50 ‰. The δ^{15}N of leatherback turtle skin samples ranged from 9.45 to 15.09 ‰, although the second highest value was only 12.80 ‰. Values for δ^{15}N were uni-modally distributed.

The stable isotope values of satellite tracked leatherback turtles revealed that individuals migrating to the SAO had a wide-range of δ^{13}C and δ^{15}N values, almost spanning the entire range of these values observed for leatherback turtles in this study. The stable isotope values of leatherback turtles with foraging areas in the WIO were all in the lower δ^{13}C cluster, although they had a wide-range of δ^{15}N values. The stable isotope values of those leatherback turtles with foraging areas in the MC were all in the higher δ^{13}C cluster and also had similarly high δ^{15}N values. The stable isotopic values of individuals tracked to the WIO and MC were significantly different (MANOVA: F = 18.30, $p < 0.001$), but no significant difference was identified between the WIO and SAO (MANOVA: F = 0.47, $p = 0.649$) or the SAO and MC (MANOVA: F = 2.66, $p = 0.130$). As the WIO and SAO were more similar than the MC and SAO, we decided to combine the SAO and WIO individuals into a single grouping that would represent individuals predominantly occupying pelagic foraging areas. This would contrast with the individuals from the MC that exclusively occupied coastal foraging areas. The isotopic values of these newly defined ‘pelagic’ and ‘coastal’ groups were significantly different (MANOVA: $F = 9.51$, $p = 0.003$).

Using the stable isotope values of the satellite tracked individuals foraging in either pelagic or coastal environments as a training data set, we calculated a linear discriminant function that could be used to assign foraging areas for those individuals that were not tracked by satellite telemetry. Discriminant function analysis of the training data set correctly assigned foraging areas for all but two of the satellite tracked individuals (87.5 % assigned correctly) with an > 80 % probability of group membership. The individuals that were incorrectly assigned consisted of one individual from the SAO that was assigned to the coast cohort and one individual from the MC that could not be assigned with > 80 % probability of group membership. The robustness of the discriminant function analysis was tested using a Jackknife cross-validation method that performed just as well as the original model (87.5 % assigned correctly). When the discriminant function analysis was applied to non-satellite tracked individuals, it assigned 61 out of 81 untracked turtles (75.3 %) to either pelagic or coastal foraging habitats. Specifically, 29 individuals were assigned to pelagic foraging areas (35.8 %), 33 were assigned to coastal foraging areas (40.7 %), and 19 were left unassigned (23.5 %). Applying the discriminant function analysis to all turtles, satellite tracked and non-satellite tracked, 36 individuals were assigned to pelagic foraging areas (37.1 %), 41 were assigned to coastal foraging areas (42.3 %), and 20 were left unassigned (20.6 %).

The $\delta^{13}C$ of loggerhead turtle skin samples ranged from -18.98 to -9.35 ‰, a much greater range than the leatherback turtles (Figure 6). The $\delta^{15}N$ of loggerhead turtle skin samples ranged from 7.03 to 14.88 ‰. Both $\delta^{15}N$ and $\delta^{13}C$ were normally distributed, but the $\delta^{15}N$ values were slightly positively skewed. At lower $\delta^{15}N$ values, there was a notable increase in $\delta^{13}C$. There was a large overlap between the $\delta^{13}C$ of the loggerhead turtles and the leatherback turtles that were assigned as coastal foragers.

4.4.3 Comparison of tracking methods

To compare how tracking method may influence migratory behavior we determined how often ‘coastal’ or ‘pelagic’ behaviors were recorded using harnessed transmitters, tethered transmitters, or stable isotope analysis (Figure 7). From the 16 harness leatherback turtles that were tracked long enough to identify post-nesting behaviors, all migrated into pelagic habitats in the SAO and WIO with the exception of one individual that after initially heading south, eventually looped north into the MC. From the 16 harness leatherback turtles that were tracked long enough to identify post-nesting behaviors, only 8 migrated into the pelagic foraging areas in the SAO and WIO. The other 8 migrated directly to coastal habitats in the MC. A similar pattern to the tethered transmitters was observed in the stable isotope analysis with 47 % being assigned to pelagic foraging areas and 53 % being assigned to coastal foraging areas (this calculation does not include unassigned individuals).

4.5 Discussion

Through a combination of satellite telemetry and stable isotope analysis, we were able to gain novel insights into the at-sea behavior of the leatherback and loggerhead turtles. Specifically, by validating the use of stable isotope analysis for tracking the foraging movements of this population, we were able to confirm the Mozambique Channel as the most common foraging areas for the nesting populations of leatherback and loggerhead turtles nesting in the iSimangaliso Wetland Park. We also identified that stable isotope analysis mirrored the migratory patterns that were recorded by the low-drag tethered satellite transmitters, although this was not also the case for turtle tracked using high-drag harness transmitters.

4.5.1 Isotopic characterization of leatherback turtle foraging behavior

The data generated by the satellite transmitters identified that the leatherback turtles from the iSimangaliso Wetland Park foraged in three different ocean regions: the pelagic waters of the SAO and WIO, as well as coastal waters of the MC. Although there appears no stable isotopic discrimination between either pelagic foraging location (SAO or WIO), individuals foraging in pelagic areas had significantly different C and N stable isotope values to those foraging in the MC. To this extent, we propose that C and N stable isotope analysis can function as a practical alternative to satellite telemetry for gaining information on broad-scale foraging habitats of leatherback turtles using samples sizes more apt for drawing population-scale conclusions. A productive avenue for future research could consequently combine the use of stable isotope analysis with measurements of fitness correlates, such as clutch size or carapace length, to provide insights into the difference of coastal and pelagic foraging habitats for resource acquisition. In turn, this could provide an understanding of the mechanisms that maintain, and the demographic consequences of, such divergent foraging habitats (Hatase et al. 2013). An additional avenue for future research could also investigate whether increasingly fine-scale patterns of habitat selection could be determined by combining bulk stable isotope analysis with the additional analysis of alternative biomarkers including amino-acid specific stable isotopes or trace metals (e.g. Herbert et al. 2009; Szép et al. 2009).

This stable isotopic distinction between coastal and pelagic leatherback turtles observed in this study was primarily due to individuals from coastal habitats having elevated $\delta^{13}C$ relative to their pelagic counterparts. Higher levels of $\delta^{13}C$ have also been observed in coastal individuals, relative to pelagic individuals, in both loggerhead (Hatase et al. 2002) and green turtles *Chelonia mydas* (Reich et al. 2007), as well as many other taxa including marine mammals (Cherel and Hobson 2007), seabirds (Jaeger et al. 2013), and invertebrates (Hill et al. 2006). In contrast, very little distinction was observed between coastal and pelagic leatherback turtles in $\delta^{15}N$. The relative lack of discrimination in $\delta^{15}N$ between different leatherback foraging areas suggests leatherback turtles tend to forage at the same trophic level, a pattern that has been confirmed in the Pacific (Seminoff et al. 2012). Indeed, the total range in $\delta^{15}N$ values (3.35 ‰ when excluding a single individual of 15.09 ‰) is comparable to the 3 – 4 ‰ enrichment generally seen in $\delta^{15}N$ per trophic level (Post 2002).

4.5.2 Isotopic characterization of loggerhead turtle foraging behavior

Almost all the loggerhead turtle samples in this study overlapped in $\delta^{13}C$ values with the leatherback turtles foraging in the MC, as identified by discriminant function analysis. Furthermore, $\delta^{13}C$ is commonly used to identify species foraging in similar locations, even for species foraging on different prey, as only nominal enrichment of $\delta^{13}C$ occurs along trophic interactions (Post 2002; Jaeger et al. 2013). Thus, the stable isotope data suggests that loggerhead turtles predominantly feed in coastal habitats in the Mozambique Channel. This corroborates findings from external tag recoveries (Luschi et al. 2003b; R Nel, unpublished data) and satellite telemetry (Papi et al. 1997; Luschi et al. 2003b; R Nel, unpublished data).

Unlike the leatherback turtles, loggerheads had a wide range of $\delta^{15}N$ values (total range = -7.53 ‰). This indicates that individuals within this population forage on a range of trophic levels and also on a range of different prey items. Indeed, loggerhead turtles are often considered opportunistic omnivores due to the wide-range of species on which they feed and the varied environments in which they forage (Tomas et al. 2001; Thomson et al. 2012).

A particularly interesting pattern observed in this study from the stable isotope data from loggerhead turtles is that at low $\delta^{15}N$, $\delta^{13}C$ also increases. As $\delta^{15}N$ is often a good indicator of trophic level, as predators are predictably enriched relatively to their prey (Post 2002), and $\delta^{13}C$ is often a good indicator of foraging location, due to its lack of trophic enrichment, (Cherel and Hobson), this suggests that the loggerhead turtles nesting in the iSimangaliso Wetland Park might be foraging in two geographic distinct locations and at different trophic level. Thus, we hypothesize that this lower $\delta^{15}N$ and higher $\delta^{13}C$ grouping is a product of some individuals foraging in particularly shallow coastal environments, where their diets may even have an increased prevalence of seagrass (Macia et al. 2004, Lugendo et al. 2006). Evidence for this hypothesis is provided by the stable isotope values of seagrasses and decapods (common prey of loggerhead turtles, Tomas et al. 2001) within the region. Seagrasses and benthic decapods in collected in the coastal waters of Tanzania had δ^{15}N values between 2 and 5 and δ^{13}C values between -13 and -16 (Lugendo et al. 2006), which if we accept δ^{15}N and δ^{13}C should be enriched by 1 and 4 ‰ respectively, fits with the low δ^{15}N and high δ^{13}C loggerhead turtles grouping (Figure 8). Conversely, pelagic decapod samples collected from the Benguela Upwelling System had δ^{15}N values between 6 and 9 and δ^{13}C values between -15 and -17 (Schukat et al. 2014) and this fits with the high δ^{15}N and low δ^{13}C loggerhead grouping. Nevertheless, confirming whether the loggerhead turtles in the iSimangaliso Wetland Park also forage in either coastal and pelagic environments, and have differing diets depending on their foraging location, would require further satellite tracking, gut-content analyses and/or in-water observations.

4.5.3 Does satellite tracking affect migratory patterns?

Data from both stable isotope analysis and the tethered transmitters confirmed the MC as a critical habitat for leatherback and loggerhead turtles. This is promising evidence that low-drag transmitters can accurately record the ‘natural’ migratory behavior of free-swimming animals. In contrast, previously published movements of leatherback turtles tracked from the iSimangaliso Wetland Park using harness transmitters (Luschi et al. 2006) were very similar to those from the additional harness transmitters deployed in this study by Oceans and Coast. In the majority of these cases, post-nesting turtles headed south of the nesting grounds and conducted loops or revolutions in the presence of, and often in accordance with, rotating water masses associated with the Agulhas Current (Luschi et al. 2003a). Upon reaching the southern extent of the Agulhas Current, these turtles either migrated into the SAO or followed the Agulhas Retroflection and remained in the WIO (Lambardi et al. 2008). Similar terminal foraging areas were also seen in the leatherback turtles that were tracked using low-drag tethered transmitters; however, the migratory pathways to reach these locations tended to differ. Tethered individuals tended to follow straighter routes away from the nesting location. In particular, no looping behavior was observed associated with the Agulhas Current until individuals reached eddies formed by the Agulhas Retroflection close to 38 °S. Moreover, half of the tethered turtles did not migrate with the Agulhas Current and instead followed near-shore pathways into coastal waters in the MC.

Inter-annual variation in the oceanographic conditions near the nesting grounds during the years when the transmitters were deployed could explain the behavioral differences observed in turtles tracked by harnessed or tethered transmitters. However, the prevailing oceanographic features near the nesting beach are fairly consistent between years (Gründlingh 1983; De Ruijter et al. 1999). The iSimangaliso Wetland Park is found at the landward origin of the southward flowing Agulhas Current, which is fed in part by eddies from the Mozambique Channel. The Agulhas Current is one of the strongest western boundaries currents in the world and is often considered the southern hemisphere's equivalent to the Gulf Stream (Durgadoo et al. 2013). While the southerly reaches of the Agulhas Current are typified by dynamic meandering (Dencausse et al. 2010), it shows minimal inter-annual meandering from its average position in its northern range (Gründlingh 1983; De Ruijter et al. 1999). The anticyclonic mesoscale eddies that flow from the Mozambique Channel occasionally extend into the Agulhas Current, but the paths of these eddies are also rather uniform and follow the coastal bathymetry of east South Africa (Schouten et al. 2003). Furthermore, it should be noted that tethered transmitters were deployed over 2 separate years and each year multiple individuals (3 in 2011/12 and 5 in 2012/13) migrated into the MC, yet this behavior was never observed in any of these harnessed turtles tracked between 1996 and 2006. To this extent, it is unlikely that the inter-annual variation in oceanographic conditions explains the different migratory behaviors observed between turtles tracked using harnessed or tethered transmitters.

An alternative explanation is that the differences in migratory behavior are a result of the impacts of attaching or retaining either type of transmitter. While attaching bio-logging devices the handling of an organism can often dramatically impact its behavior (Sherrill-Mix and James 2008). However, these effects are generally on the scale of days and not months as seen in this study (James et al. 2006; Thomson and Heithaus 2014). Instead, it could be that retention of the device may affect behavior due to the effects of increased drag. The design and placement of a bio-logging device can significantly alter the amount of additional drag these device incur (Hazekamp et al. 2010; Shorter et al. 2014) and it has been estimated that harnessed transmitters may increase the drag experienced by swimming leatherback turtles by over 100 % (Jones et al. 2013). In contrast, tethered transmitters are only estimated to increase drag by < 5 % (Jones et al. 2014). The differences in drag might therefore lead to the differences in behavior between transmitter attachments. Changes in movement speed have already been observed between turtles tracked using different tracking methods, with turtles with low-drag ridge-mount attachments swimming 10 to 30 % faster than individuals tracked using harness attachments (Fossette et al., 2008; Byrne et al. 2009). However, no previous studies have indicated that high-drag attachments may alter even migratory pathways.

Leatherback turtles with harnessed transmitters are evidently able to actively swim against currents that might flow at a similar rate to their average movement speed (Galli et al. 2012). However, the increased energetic expenditure due to the increased drag may affect the inclination of an individual to immediately swim against the particularly strong currents, especially for species like the leatherback turtles that tend to demonstrate flexible foraging migrations (Fossette et al. 2010; Shillinger et al. 2011). This effect may be particularly apparent for the turtles nesting in the iSimangaliso Wetland Park considering the strength of the Agulhas Current that flows just offshore. As such harnessed individual may not head to their typical foraging areas in the MC and instead follow the prevailing flow of the Agulhas Current south, opportunistically foraging when possible. This could also explain why looping within eddies of the Agulhas Current was particularly common in harnessed turtles, but not tethered animals that showed more directed movements.

4.5.4 Conclusions and conservation implications

Our study validates that stable isotope analysis can be used to identify foraging habitats for leatherback and loggerhead turtles in the waters of southern Africa. Through this method we confirmed the importance of the MC and especially the Sofala Banks as a critical foraging habitat for the leatherback and loggerhead turtles nesting in the iSimangaliso Wetland Park. Worryingly, the Sofala Banks also hosts a profitable shrimp-trawling fishery (Palha de Sousa et al. 2006) and this fisheries incur substantial sea turtle by-catch for both leatherback and loggerhead turtles (Gove et al. 2001). In fact, by-catch of leatherback turtles in the Sofala Banks could explain why the leatherback turtle populations have remained low even after the protection of their nesting beaches (Nel et al. 2013). However, by-catch rates could be reduced by the implementation of turtle-excluder devices throughout the shrimp-trawl fishery. Considering the importance of this coastal foraging area for leatherback turtles, we recommend the use of such conservation measures to ensure the long-term survival of leatherback turtles in the MC.

While the importance of this habitat had been suggested by the deployment of low-drag tethered transmitters deployed on leatherback turtles (Chapter 3), such behavior was notably rare in turtles tracked using high-drag harnessed transmitters. To gain an accurate depiction of animal movement patterns, we thus recommend using transmitters with nominal increases in drag, especially when animals are interacting with strong currents, such as the Agulhas Current. Future efforts should therefore be made to minimize the drag associated with bio-logging devices if they are to collect an accurate representation of an animal’s ‘natural’ movement patterns. This is particularly important when considering that spatial management plans are increasingly being developed around satellite tracking data (Roe et al. 2014; Fossette et al. 2014). Finally, the coastal foraging pattern observed in leatherback turtles in this study is relatively uncommon for this species. In fact, leatherback turtles are often considered paradigmatic examples of pelagic specialists (Luschi et al. 2006; Shillinger et al. 2011). Our findings suggest that in contrary the habitat preferences of leatherback turtles appears to far more flexible than previously thought.

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4.7 Tables

Table 4.7.1 Details of all the satellite transmitters deployed onto leatherback turtles *Dermochelys coriacea* nesting in the iSimangaliso Wetland Park, South Africa between 1996 and 2013. Transmitter 1079011 was purposefully removed from an inter-nesting turtle that was encountered on a subsequent nesting event.

Turtle ID	Transmitter Model	Attachment Method	Date Deployed	Last Location	Final Destination	First Published
1	ST-14	Harness	16/1/1996	18/5/1996	Western Indian Ocean	Hughes et al. (1998)
2	ST-6	Harness	31/1/1999	11/9/1999	South Atlantic Ocean	Luschi et al. (2003)
3	ST-6	Harness	31/1/1999	30/9/1999	South Atlantic Ocean	Luschi et al. (2003)
4	ST-6	Harness	30/1/2000	16/6/2000	Agulhas Current	Luschi et al. (2003)
5	ST-6	Harness	2/2/2000	2/4/2000	Nesting area	Luschi et al. (2006)
6	ST-6	Harness	13/2/2001	20/5/2001	Agulhas Current	Luschi et al. (2006)
7	ST-6	Harness	13/2/2001	8/7/2001	Nesting area	Luschi et al. (2006)
8	SRDL	Harness	13/1/2002	30/1/2002	Western Indian Ocean	Luschi et al. (2006)
9	SRDL	Harness	29/1/2003	16/7/2003	South Atlantic Ocean	Luschi et al. (2006)
10	SPOT	Harness	07/12/2006	22/12/2006	Nesting area	This study
11	SPOT	Harness	04/12/2006	27/3/2007	Western Indian Ocean	This study
12	SPOT	Harness	05/12/2006	26/1/2007	Agulhas Current	This study
13	SPOT	Harness	06/12/2006	13/4/2007	South Atlantic Ocean	This study
14	SPOT	Harness	05/12/2006	10/3/2007	Western Indian Ocean	This study
15	SPOT	Harness	06/12/2006	23/12/2006	Nesting area	This study
16	SPOT	Harness	20/01/2008	29/8/2008	South Atlantic Ocean	This study
17	SPOT	Harness	24/01/2008	17/8/2008	Mozambique Chanel	This study
18	SPOT	Harness	25/01/2008	02/5/2009	South Atlantic Ocean	This study
19	SPOT	Harness	NO DATA			This study
20	Splash	Harness	15/1/2009	20/2/2009	Nesting area	This study

21	Splash	Harness	14/1/2009	29/8/2009	Agulhas Current	This study
22	Splash	Harness	14/1/2009	20/1/2009	Western Indian Ocean	This study
23	MK10-PAT	Tether	10/11/2011	14/12/2011	Nesting area	This study
24	MK10-PAT	Tether	14/11/2011	30/12/2011	Western Indian Ocean	This study
25	MK10-PAT	Tether	11/12/2011	30/12/2011	Nesting area	This study
26	MK10-PAT	Tether	09/1/2012	01/5/2012	Western Indian Ocean	This study
27	MK10-PAT	Tether	09/1/2012	05/6/2012	South Atlantic Ocean	This study
28	MK10-PAT	Tether	20/1/2012	23/5/2012	Mozambique Chanel	This study
29	MK10-PAT	Tether	25/1/2012	08/6/2012	Western Indian Ocean	This study
30	MK10-PAT	Tether	13/2/2012	09/6/2012	Mozambique Chanel	This study
31	MK10-PAT	Tether	27/2/2012	24/5/2012	South Atlantic Ocean	This study
32	MK10-PAT	Tether	27/2/2012	22/9/2012	Mozambique Chanel	This study
33	MK10-PAT	Tether	28/12/2012	03/6/2013	Mozambique Chanel	This study
34	MK10-PAT	Tether	04/1/2013	21/2/2013	Nesting area	This study
35	MK10-PAT	Tether	13/1/2013	20/2/2013	Nesting area	This study
36	MK10-PAT	Tether	13/1/2013	06/4/2013	South Atlantic Ocean	This study
37	MK10-PAT	Tether	16/1/2013	05/6/2013	Mozambique Chanel	This study
38	MK10-PAT	Tether	22/1/2013	15/4/2013	Western Indian Ocean	This study
39	MK10-PAT	Tether	24/1/2013	15/5/2013	Mozambique Chanel	This study
40	MK10-PAT	Tether	01/2/2013	06/4/2013	Western Indian Ocean	This study
41	MK10-PAT	Tether	11/2/2013	29/5/2013	Mozambique Chanel	This study
42	MK10-PAT	Tether	15/2/2013	17/4/2013	Mozambique Chanel	This study

Table 4.7.2 Number of skin samples collected from nesting leatherback *Dermochelys coriacea* and loggerhead *Caretta caretta* turtles in the iSimangaliso Wetland Park between 2011/12 and 2012/13.

	Leatherback					**Loggerhead**				
	# of times an individual was sampled					**# of times an individual was sampled**				
Year	**1**	**2**	**3**	**4**	**Total**	**1**	**2**	**3**	**4**	**Total**
2011/12	46	11	4	0	61	43	0	0	0	43
2012/13	24	8	2	2	36	76	1	0	0	77
Total	70	19	6	2	134 samples from 97 individuals	119	1	0	0	121 samples from 120 individuals

4.8 Figures

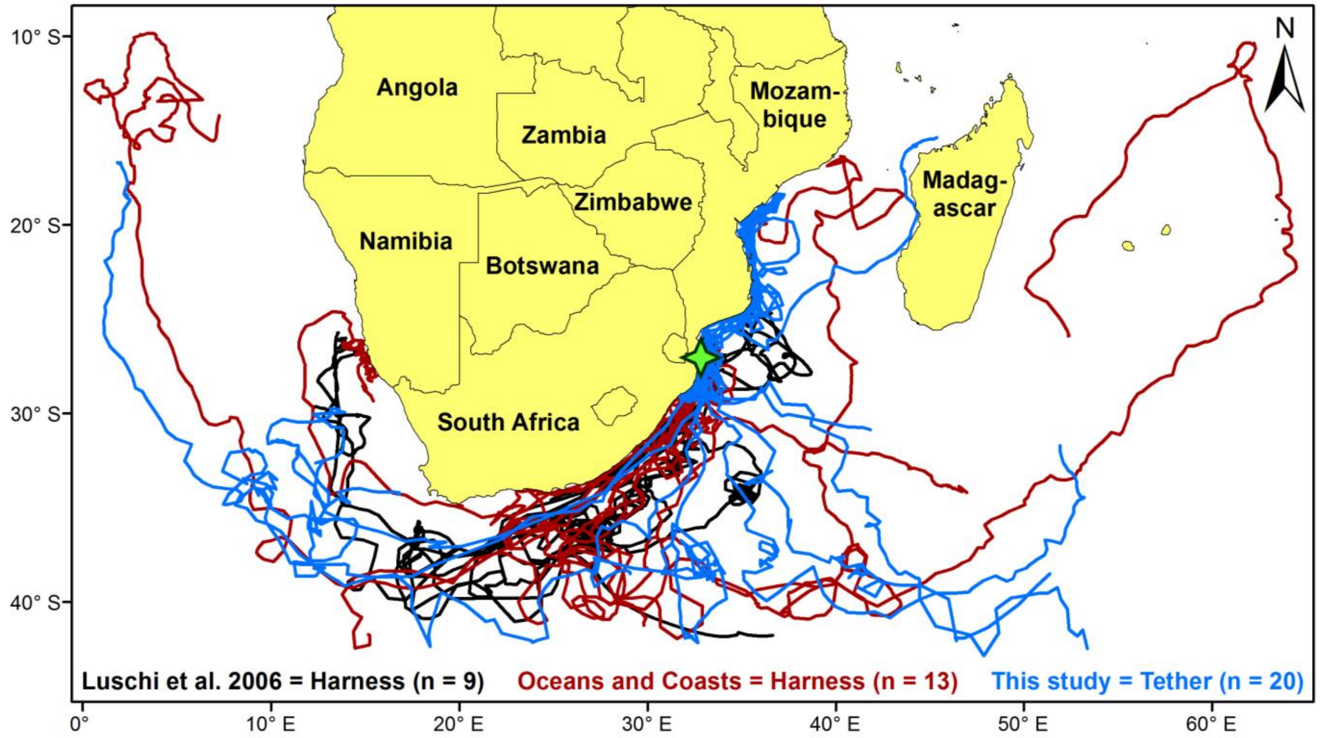

Figure 4.1 Movements of 42 leatherback turtles *Dermochelys coriacea* tracked from their nesting beach in the iSimangaliso Wetland Park (green star) between 1996 and 2013. Black lines represent the movements of 9 turtles that were tracked using satellite transmitters attached using a harness. These tracks have been previously published in Luschi et al. (2006). The dark-red lines represent the movements of 13 turtles that were tracked using satellite transmitters attached using a harness and deployed by the organization Oceans and Coasts, South Africa. The blue lines represent the movements of 20 turtles that were tracked using satellite transmitters attached using a tethered and deployed as part of this study.

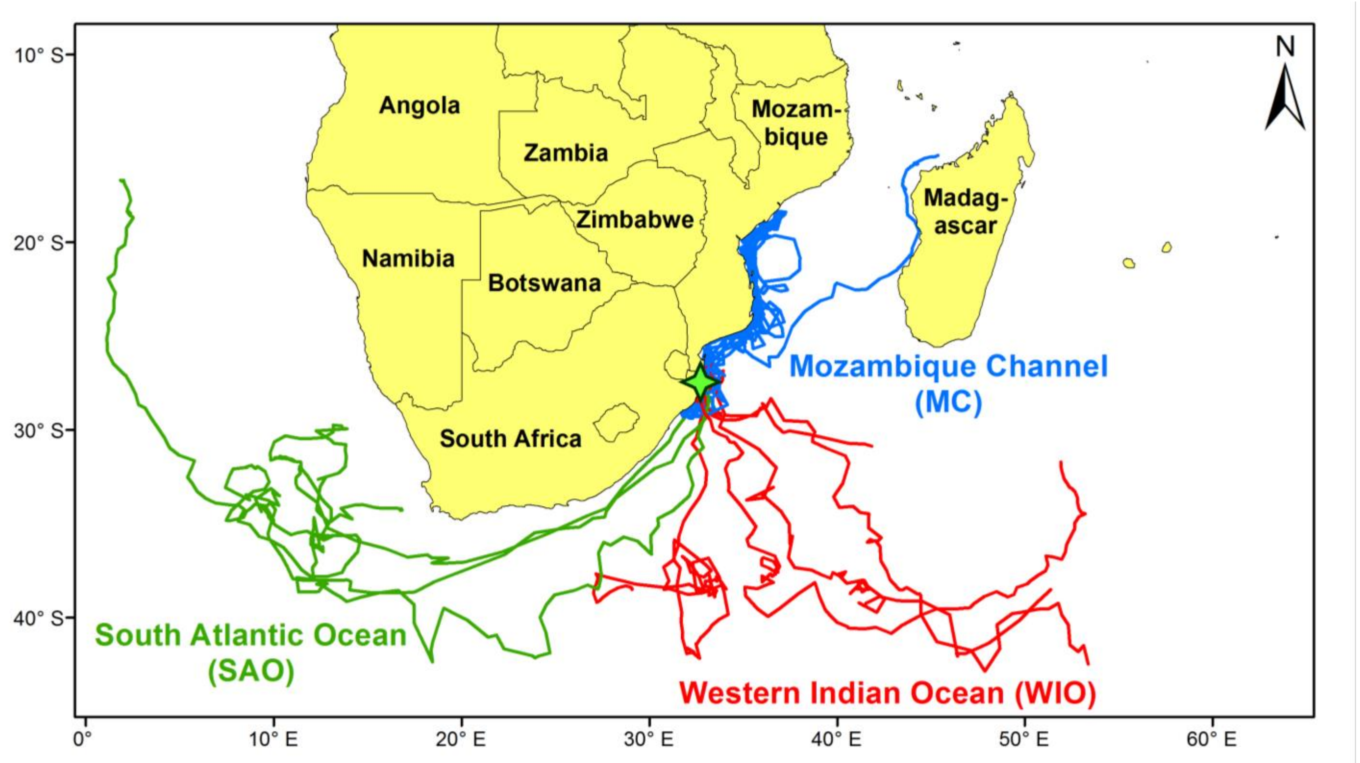

Figure 4.2 Movements of 20 leatherback turtles *Dermochelys coriacea* tracked from their nesting beach in the iSimangaliso Wetland Park (green star) between 2011 and 2013. All turtles were tracked using satellite transmitters attached using a tethering method. The tracks are color coded depending their terminus: green represents the South Atlantic Ocean, red represents the Western Indian Ocean, and blue represents the Mozambique Channel.

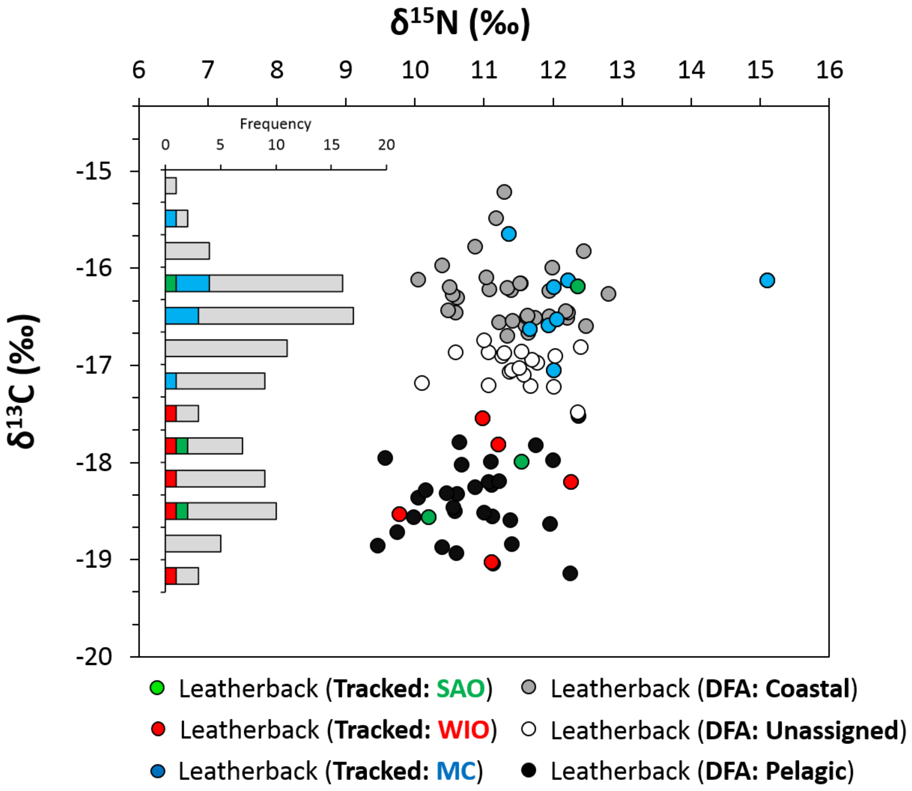

Figure 4.3 Stable isotope values of skin (stratum corneum) samples collected from nesting leatherback turtles *Dermochelys coriacea* within the iSimangaliso Wetland Park between 2011 and 2013. Colored circles represent individuals that were tracked using satellite telemetry: red circles represent individuals that migrated into the Western Indian Ocean (WIO), green circles represent individuals that migrated into the South Atlantic Ocean (SAO), and blue circles represent individuals that migrated into the Mozambique Channel (MC). Individuals migrating to the WIO and SAO were separated from the MC to represent pelagic and coastal foragers, respectively. Discriminant function analyses were used to assign foraging areas for non-satellite tracked individuals as either coastal (grey) or pelagic individuals (black). Individuals that could not be assigned to either group with > 80 % certainty were left unassigned (white).

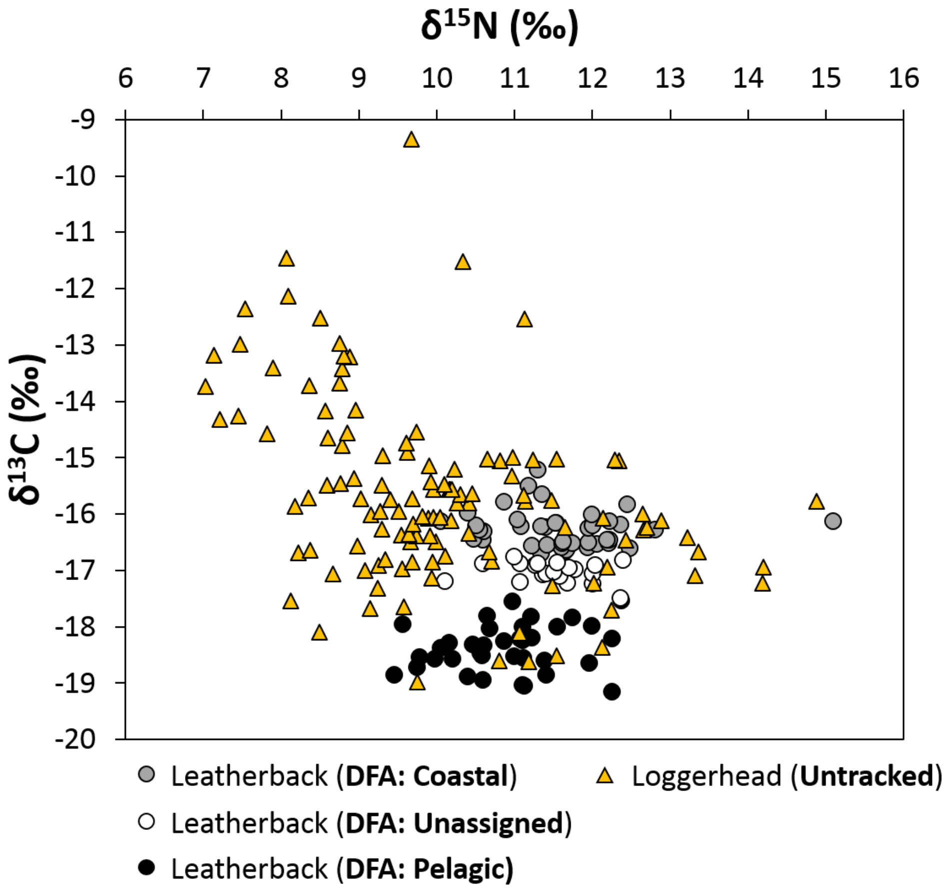

Figure 4.4 Stable isotope values of skin (stratum corneum) samples collected from nesting loggerhead *Caretta caretta* and leatherback *Dermochelys coriacea* turtles within the iSimangaliso Wetland Park between 2011 and 2013. Loggerhead turtles are represented by yellow triangles and leatherback turtles are represented by circles. For the leatherback turtles, discriminant function analyses were used to assign foraging areas for non-satellite tracked individuals as either coastal (grey) or pelagic individuals (black). Individuals that could not be assigned to either group with > 80 % certainty were left unassigned (white).

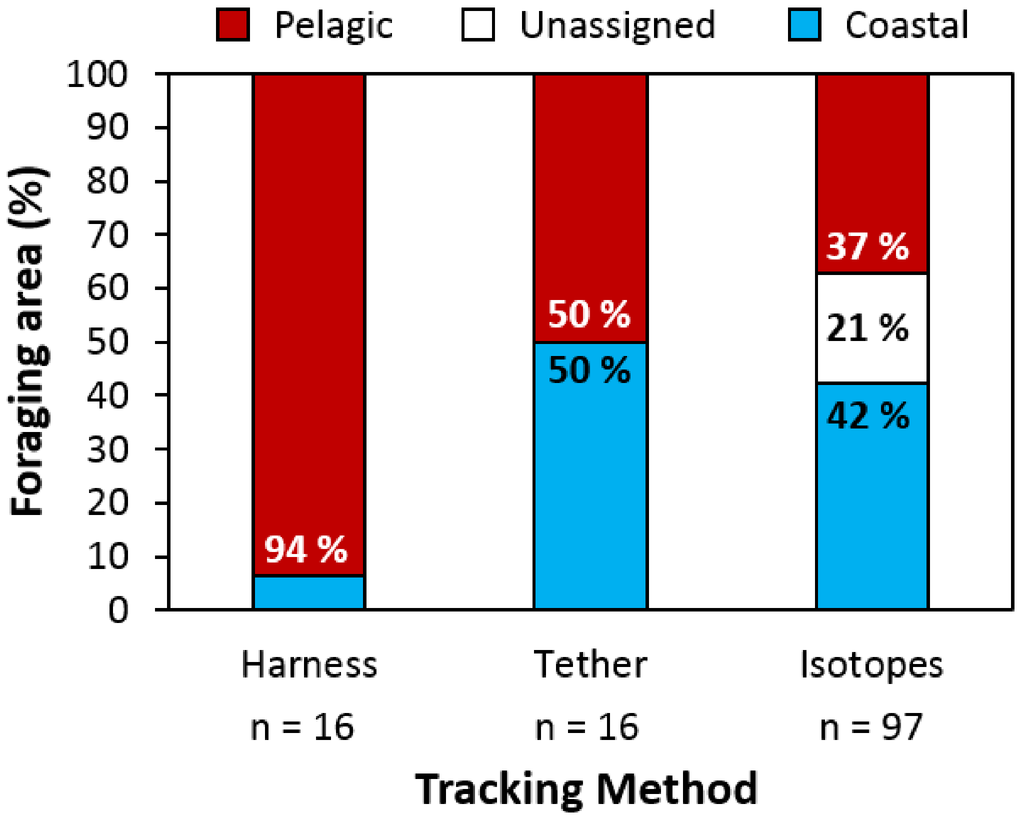

Figure 4.5 Comparison to whether different tracked methods: harnessed or tethered transmitters, or stable isotope analysis; recorded differential importance of pelagic or coastal foraging areas for the leatherback turtles *Dermochelys coriacea* nesting in the iSimangaliso Wetland Park.

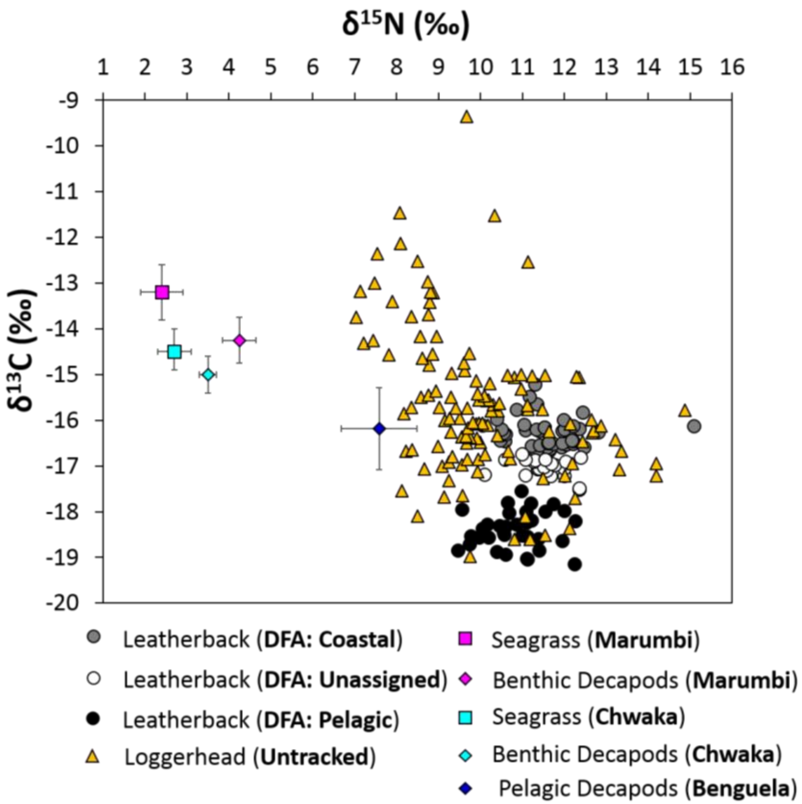

Figure 4.6 Stable isotope values of skin (stratum corneum) samples collected from nesting loggerhead *Caretta caretta* and leatherback *Dermochelys coriacea* turtles within the iSimangaliso Wetland Park between 2011 and 2013. Also displayed are potential food items. Loggerhead turtles are represented by yellow triangles and leatherback turtles are represented by circles. For the leatherback turtles, discriminant function analyses were used to assign foraging areas for non-satellite tracked individuals as either coastal (grey) or pelagic individuals (black). Individuals that could not be assigned to either group with > 80 % certainty were left unassigned (white). Seagrass are represented by squares and decapods are represented by diamonds. Samples in pink and turquoise were collected from the benthos from Marumbi, Tanzania and Chwaka, Tanzania, respectively, and were both previously published in Lugendo et al. (2006). Dark blue diamonds represent the mean stable isotope values from 6 different decapod species collected in pelagic waters of the Benguela Upwelling System and were previously published in Schukat et al. (2014). Error bars represent ± 1 SD.

APPENDICES

APPENDIX A

Methodology for attaching towable devices to sea turtles

The tethering method used to attach the transmitter was similar to that used in Morreale (1999), Blanco et al. (2012), and Patel (2013). The attachment method can be divided into a six major steps (Figure 1).

(*Step 1*) An electric drill with a sterilized drill bit was used to create a 5 mm diameter incision 20 to 30 mm from posterior edge of the pygal process. The incision was immediately treated with spray antiseptic.

(*Step 2*) The ‘needle’ – a pre-made length of surgical tubing of 5 mm diameter and walls of 1 mm thickness attached to 45 kg (100 lb) fishing line using an equivalent strength crimp – was pulled through the incision, leaving some surgical tubing protruding both above and below the carapace.

(*Step 3*) The protruding surgical tubing was cut flush with the carapace.

(*Step 4*) A length of 180 kg (400 lb) flexible fishing line approximately 1.25 m long was threaded halfway through the incision. To reduce friction between the surgical tubing and the fishing line, the fishing line was coated with a water-based lubricant. The fishing line extending below the carapace was looped through the ‘lower button’ – a delrin cyclinder 40 mm in diameter and 15 mm in height with an upside-down Y-shaped hole in the centre. The fishing line was then re-thread back through the surgical tubing, reapplying lubricant if needed.

(*Step 5*) On the dorsal-side of the carapace, both ends of the fishing line were passed through the ‘upper button’ – a delrin cylinder 20 mm in diameter and 10 mm in height with a straight hole in the middle. Both ends of the fishing line were pulled taught and crimped directly above the upper button using 180 kg (400 lb) crimps.

(*Step 6*) The longest free-length of fishing line was fastened using a crimp to the swivel on the transmitter's 'lanyard' at a length of between 25 and 30 cm. The 'lanyard' was formed of a length of fishing line approximately 15 cm long that was attached at opposing ends to a 180 kg (400 lb) swivel and the Mk10 PAT with 180 kg (400 lb) crimps. As a result, the total length of the tether was between 40 and 55 cm from the upper button to the base of the transmitter. The exact length was decided in the field, ensuring that the Mk10 PAT could not be reached by the front flippers but would be able to reach the surface when the turtles emerged to breathe. When it was confirmed that the transmitter was securely attached to the turtle, all the excess fishing line was trimmed to the base of the crimps using wire cutters.

Recovering and reattaching a new transmitter

If a turtle with an attached satellite transmitter was encounter during a subsequent nesting event the transmitter was recovered and a new device was deployed. To remove a transmitter the fishing line beneath the lower button was cut and the tether was pulled free. To deploy a new transmitter required only *steps 4* to *6*.

Literature cited

Blanco GS (2010) Movements and Behavior of the East Pacific Green Turtle (*Chelonia mydas*) from Costa Rica. Ph.D Dissertation, Drexel University.

Patel SH (2013) Movements, behaviors and threats to loggerhead turtles, *Caretta caretta,* in the Mediterranean Sea. Ph.D Dissertation, Drexel University.

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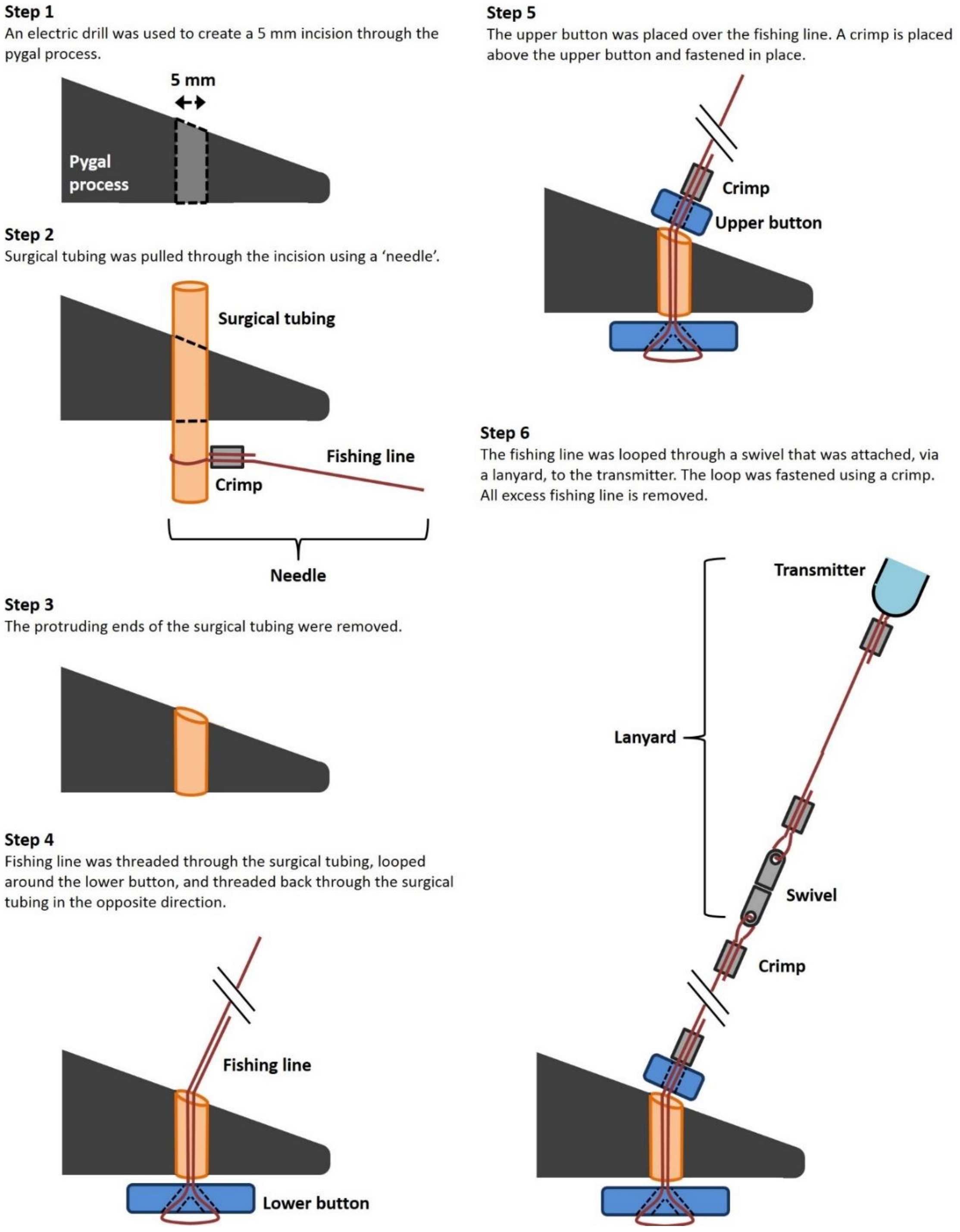
Figures



Step 1
An electric drill was used to create a 5 mm incision through the pygal process.

Step 2
Surgical tubing was pulled through the incision using a 'needle'.

Step 3
The protruding ends of the surgical tubing were removed.

Step 4
Fishing line was threaded through the surgical tubing, looped around the lower button, and threaded back through the surgical tubing in the opposite direction.

Step 5
The upper button was placed over the fishing line. A crimp is placed above the upper button and fastened in place.

Step 6
The fishing line was looped through a swivel that was attached, via a lanyard, to the transmitter. The loop was fastened using a crimp. All excess fishing line is removed.

Fig. A.1. Method for attaching an Mk10-PAT transmitter onto a sea turtles carapace

APPENDIX B

Risks associated with tethered transmitters

Two major concerns are often raised when proposing the use of tethered transmitters on sea turtles: (1) entanglement with the tether and (2) creating a hole in the carapace to provide an anchoring site for the tether. Here, I will discuss these issues and present evidence provided while completing this thesis that impact the validity of these concerns.

Entanglement

One often-raised concern with tethered transmitters is that the tether could become entangled in the turtle's hind-flippers or snagged on a rock or fishing net. While the probability of this occurring is low, the consequences could be fatal. To minimize this risk, each transmitter was fitted with a release pin that would break upon receiving 45 kg (100 lb) of tension. This is low enough that a leatherback turtles should be able to break the release pin with ease and thus, free itself if entangled. Evidence that leatherback turtles are indeed able to break the release pin was provided during a reencounter with a nesting leatherback turtle that previously had a transmitter (107903) attached. When the turtle was re-encountered, the transmitter was missed but the anchor mechanism for holding the tether to the carapace of the turtle was undamaged. Moreover, later that month I started to received signal from the missing satellite transmitter. I only received signals during spring-low tides and their location was 100 m offshore from the nesting beach. I conclude that while the turtle was returning to the ocean from a previous nesting event that transmitter had become snagged on a rock that was only exposed at spring-low tides. The transmitter had then broken off the turtle but remained snagged on the rock. This would explain the location of the transmitter and that is only transmitted data at spring-low tides.

The attachment site

Another concern associated with tethered attachments is potential for harm when creating a hole in the carapace, into which the tethered will be anchored. In this study, the hole was 5 mm in diameter and made through the pygal process. To minimize the risk of infection, the hole was created using a drill bit that had been sterilized with alcohol and a new drill bit was used for each attachment. In addition, after the hole had been created it was immediately sterilized using an antiseptic spray (oxytetracycline).

Making the hole extruded a white pithy substance. In only 2 out the 20 attachments was blood seen. In both instances the bleeding was not severe and stopped immediately after the surgical tubing was put in place.

As 8 of the turtle with transmitters were re-encountered multiple times, it was possible to reinspect the attachment sites multiple weeks after their creation. In none of the cases was there any evidence of infection or that the hole had enlarged (Figure 1).

Conclusion

Bio-logging devices often have non-intentional impacts on the behaviour of the study animals (Chapter 4). Serious consideration must therefore be given to the style of bio-logging device, and the attachment mechanism, before such devices are deployed. After careful deliberation, we chose to employ pop-up archival transmitters attached using a tethering techinique (Appendix A). While concerns are often raised about the potential risk associated with the use of such transmitters, during this study we found no evidence supporting these claims.

Figures

Figure B.1 An incision in the pygal process of the carapace of a leatherback turtle *Dermochelys coracea*. The incision was initially made for the attachment of a tethered transmitters. The picture was taken 30 days after the original attachment and after the tether had been removed.

APPENDIX C

Why towable transmitters stop transmitting?

Satellite transmitters have finite life-spans, but the reasons they stop functioning can be highly varied. These may include: (1) premature release from or death of the study animal, (2) bioaccumulation of epibiota blocking important sensors, or (3) battery constraints. Here, I will discuss these three potential reasons that transmitters stop functioning and investigate which may have played the most important role in defining life-span of the transmitters used in this study.

Premature release

When a transmitter stopped diving to depths lower than 10 m for a period of over 10 days, it was assumed the transmitter had broken off the animal or the animal had died (Table 1). This occurred in 6 cases. In 3 of these instances it occurred while the turtle was still inter-nesting and the transmitter probably snapped off while the turtle was nesting. In the other 3 instances it occurred when the turtle was far out to sea. It could also be that the transmitters remained attached but the animal had died; however, it is impossible with the available data to determine if a transmitter had detached or the animal had died.

Bio-fouling

Tethered transmitters must float the surface in order to make a successful satellite connection. To this extent, the transmitters must remain positively buoyant to continue relaying data. However, epibiota attaching to the transmitter (bio-fouling) can gradually reduce its buoyancy. We predict that biofouling rates would be highest on these animals that migrated to the Mozambique Channel because turtles swam slower and occupied warmer temperature than those that migrated into more pelagic waters. Yet this was not the case (Figure 1). Thus, we conclude that bio-fouling is not a majorly limiting factors in the life-span of the transmitters used in this study.

Battery life

With the setup described in section 3.3.4, the Mk10-Host software (v1.26.2003; Wildlife Computers) predicted transmitters, which were fitted with two AA batteries, should be able to continually function to 150 to 300 days. This is far shorter than the 123.8 days mean transmitter life-span observed in this study and only 6 transmitters relayed data for longer than 150 days (Table 1). However, it is important to note that this calculation includes data from transmitters that are suspected to have detached from the animal before the transmitter stopped functioning.

These transmitters that are no longer attached to an animal may be expected to continue to transmitter data continually until the battery fails. As the transmitters occasional relay data on the remaining voltage of the battery pack, we can use this information to infer the minimum voltage that must remain in the battery pack for the satellite transmitter to remain functioning. Looking at the battery voltage over time for all the deployed transmitters indicated that all transmitter start with approximately 3.6 V and this remains rather consistent until the transmitters has been deployed for approximately 100 days (Figure 2). After this point, the voltage begins to decline. This decline continues until below 3.0 V at which all the transmitters stop functioning. I hypothesis this is the point at which the battery voltage is too low to continue functioning.

7.5. Conclusions

It appears that a combination of premature release and battery-life are the major factors determining the life-span of each transmitter, while biofouling is of relatively minor importance.

To determine which factors cause transmitters to release prematurely could be achieved by observing tethered turtles during active swimming. This information could provide valuable insights into why transmitters prematurely release and what can be done to avoid this. It would be possible to increase the battery-life by increasing the number of batteries within each transmitters (MK10-PAT contain 2 AA batteries as standard); however, this would increase the weight of the transmitter. Offsetting the increased weight would increase require additional float for buoyancy and increase the overall size and drag of the transmitter. More promising would be the use of solar-power transmitters, or those that are powered by the animal movements, as they can function indefinitely.

Tables

Figure C.1 Life-span of transmitters accounting for recovery and redeployement. Values in brackets are the final transmission from the transmitter, while values not in brackets are those when diving data were no longer recorded and it was assumed the transmitter had broken off the animal. Final destinations are: Mozambique Channel (MC), Western Indian Ocean (WIO), and South Atlantic Ocean (SAO).

Transmitter #	1st Deployed	Recovered	2nd Deployed	Recovered	3rd Deployed	Final Transmission	Duration (d)	Final Location	Fate
37795	4/1/2013	25/01/2013	03/02/2013	12/02/2013	15/02/2013	17/04/2013 (17/04/2013)	91 (91)	MC	Battery
37801	1/2/2013					06/04/2013 (06/04/2013)	64 (64)	WIO	?
107887	16/1/2013	26/01/2013	12/02/2013			03/06/2013 (03/06/2013)	121 (121)	MC	Battery
107889	13/1/2013					06/04/2013 (04/07/2013)	83 (172)	SAO	Release
107892	13/1/2013					20/02/2013 (02/03/2013)	38 (48)	NB	Release
107901	10/11/2011	14/12/2011	09/01/2012			05/06/2012 (05/06/2012)	182 (182)	SAO	?
107902	14/11/2011					30/12/2011 (30/12/2011)	46 (46)	WIO	?
107903	11/12/2011					30/12/2011 (20/06/2012)	19 (192)	NB	Release
107904	9/1/2012					01/05/2012 (01/05/2012)	113 (113)	WIO	?
107905	20/1/2012					23/05/2012 (23/05/2012)	124 (124)	MC	?
107906	25/1/2012	13/2/2012	28/12/2012	03/02/2013	15/02/2013	21/02/2013 (17/04/2013)	62 (117)	NB	Release

107907	13/2/2012					08/06/2012 (08/06/2012)	116 (116)	WIO	?
107908	13/2/2012					09/06/2012 (09/06/2012)	117 (117)	MC	?
107909	27/2/2012					24/05/2012 (24/05/2012)	87 (87)	SAO	?
107910	27/2/2012					22/09/2012 (22/09/2012)	208 (208)	MC	Battery
107911	26/1/2013					05/06/2013 (05/06/2013)	130 (130)	MC	?
107912	25/1/2013	5/2/2013				05/02/2013 (27/06/2013)	11 (11)	NB	Release
107913	11/2/2013					29/05/2013 (27/08/2013)	107 (107)	MC	Release
107914	24/1/2013					15/05/2013 (24/06/2013)	111 (151)	MC	Release
107915	22/1/2013					15/04/2013 (30/07/2013)	83 (189)	WIO	Release
							Total 95.7 (123.8)		

Figures

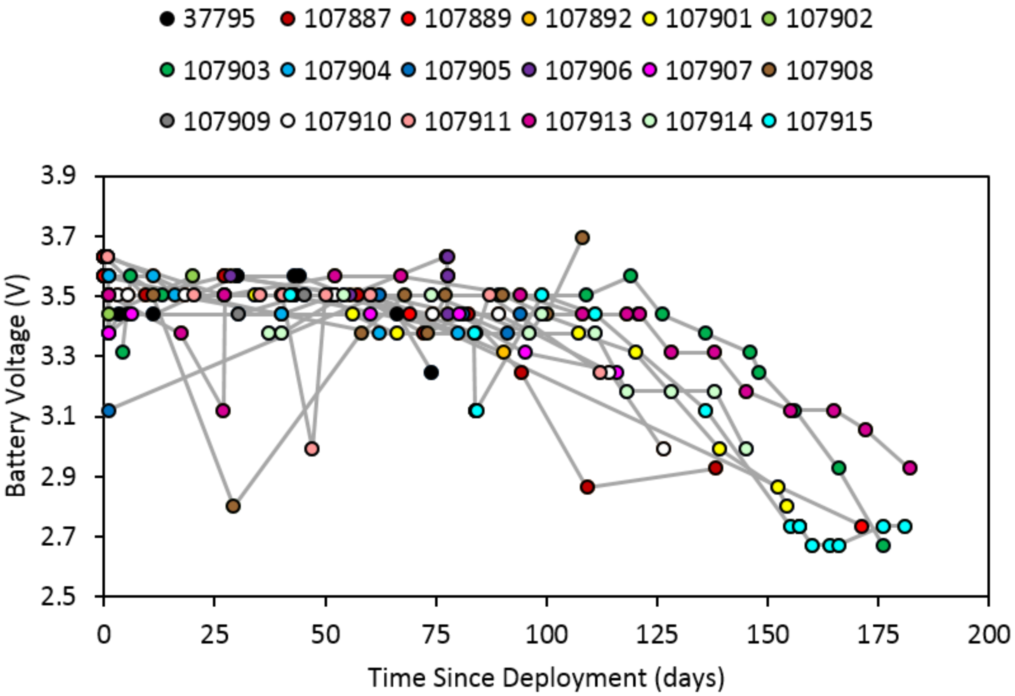


Figure C.1 Decrease in the battery power of a PAT Mk10 transmitter over its lifespan. Transmitter duration includes both when attached to leatherback turtles, broken off but still transmitting, and when used in a previous study.

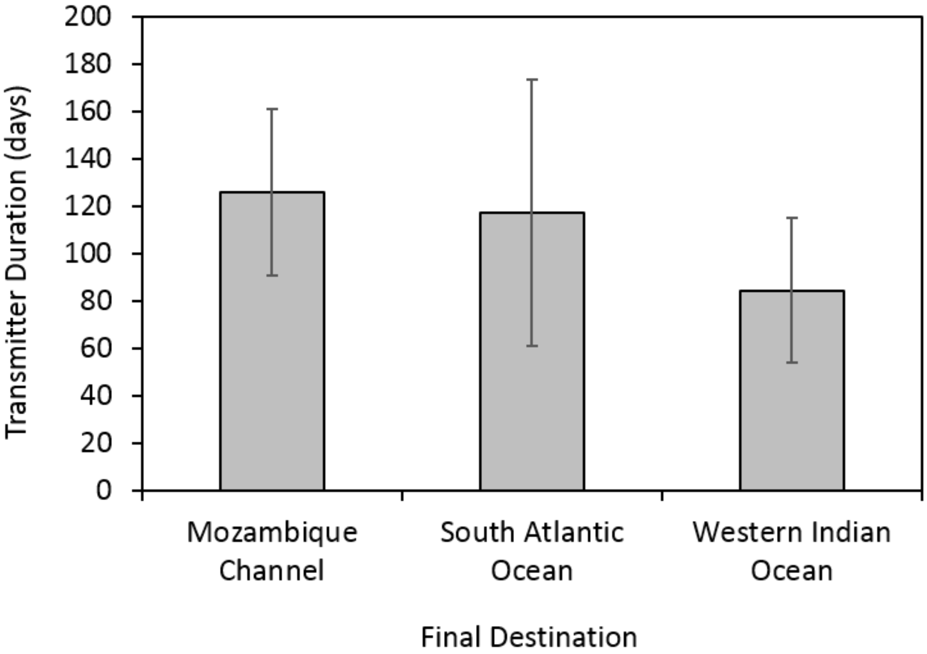


Figure C.2 Average trasmitter durations for turtles that migrated towards different ocean basins.

VITA

VITA

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EDUCATION

Aug '10 – Present **PhD candidate in Biological Sciences**
Purdue University, USA.
Co-advised by Frank V. Paladino, Ph.D. and Jeffrey R. Lucas, Ph.D.
Thesis: Migratory ecology of sea turtles. Graduating in Dec '14.

Sep '05– Jun '09 **MMarBiol, Masters of Marine Biology**
University of Southampton, UK.
Advised by Sven Thatje, Ph.D.
Thesis: The role of specific dynamic action in the hydrostatic pressure tolerance of the shallow water spider crab *Maja brachydactyla*
Awards: First-class Honours

PROFESSIONAL EXPERIENCE

Oct '13 – Present **Field and Research Manager: The Leatherback Trust, Costa Rica**

- Managing all research activities conducted from the Goldring-Gund Marine Station, including the sea turtle monitoring project at Las Baulas National Marine Park.
- Coordinating a team of biologists and an EarthWatch volunteer program.
- Advising and overseeing graduate students’ research projects.

Oct '11 – Mar '13 **Field Manager: Maputaland Conservation & Management, South Africa**

- Managing the sea turtle monitoring project at iSimangaliso Wetland Park for Nelson Mandela Metropolitan University.
- Coordinating a Work Travel SA volunteer program.
- Consultant for a governmental initiative to track sea turtles using satellite transmitters.

Jun '08 – Jun '09 **Field Leader: ARCHELON – The Sea Turtle Protection Society, Greece**

- Managing the sea turtle monitoring projects at Kyparissia Bay (2008) and Rethymno (2009).
- Coordinating groups of over 40 volunteers.
- Directing public outreach programs.

May '09 – Jun '09 **Research Assistant: Surveying the Whittard Submarine Canyon aboard the RRS James Cook**

- Identifying species during ROV transects of the abyssal plain.
- Examining the effects of temperature and pressure on deep-sea crustaceans.
- Processing deep-sea sediment cores.

RESEARCH INTERESTS

My research interests are the ecology and conservation of marine mega-fauna, with special consideration for how animals are able to adapt, either behavioural or physiologically, to variations in environmental conditions.

TEACHING EXPERIENCE

Aug '12 – Sep '12 **Human Anatomy and Physiology. BIOL20300.**
Lecturer. Indiana University-Purdue University Fort Wayne, USA.

Aug '12 – Dec '12 **Medical Terminology. BIOL10500.**
Lecturer. Indiana University-Purdue University Fort Wayne, USA.

Jan '10 – Jun '11 **Environmental and Conservation Biology. BIOL48300.**
Teaching assistant. Purdue University, USA.

Aug '10 – Dec '10 **Human Anatomy and Physiology. BIOL20300.**
Teaching assistant. Purdue University, USA.

PUBLICATIONS IN PEER-REVIEWED LITERATURE

Robinson NJ, Valentine SE, Santidrián Tomillo P, Saba VS, Spotila JR, Paladino FV (2014) Multidecadal trends in the nesting phenology of Pacific and Atlantic leatherback turtles are associated with population demography. Endangered Species Research 24(3):197-206. doi:10.3354/esr00604

Robinson NJ, Paladino FV (In press) Diving behavior and physiology. In: *The Leatherback Turtle: Biology and Conservation*. Spotila JR, Santidrián Tomillo P (eds). Johns Hopkins Press, Baltimore, MD, USA.

Thatje S, **Robinson N** (2011) Specific dynamic action affects the hydrostatic pressure tolerance of the shallow-water spider crab *Maja brachydactyla*. Naturwissenschaften 98:299-313. doi:10.1007/s00114-011-0768-1

Robinson NJ, Thatje S, Osseforth C (2009) Heartbeat sensors under pressure: a new method for hyperbaric physiology. High Pressure Research 29:422-430. doi:10.1080/08957950903076398

PUBLICATIONS IN PREPARATION

Neeman N, **Robinson NJ**, Paladino FV, Spotila JR, O'Connor MP (In review) Phenology shifts in leatherback turtles (*Dermochelys coriacea*) due to changes in sea surface temperature. Journal of Experimental Marine Biology and Ecology.

Dornfeld TC, **Robinson NJ**, Santidrián Tomillo P, Paladino FV (In review) Nesting Ecology of Olive Ridley Sea Turtles, *Lepidochelys olivacea*, at Playa Grande, Costa Rica: A Solitary Nesting Beach In Between Two Arribada Beaches. Marine Biology.

Robinson NJ, Morreale SJ, Kotze D, McCue S, Meyer M, Oosthuizen H, Nel R, Paladino FV (In prep) Stable isotope analysis and satellite telemetry reveal the migratory behaviour of leatherback and loggerhead turtles in southern Africa and the consequences of using high-drag biologging devices.

PUBLICATIONS IN NON PEER-REVIEWED LITERATURE

Robinson NJ, Paladino FV (2013) Sea turtles. In: *Reference Module in Earth Systems and Environmental Sciences*. Elsevier, Amsterdam. doi:10.1016/B978-0-12-409548-9.04352-9

SYMPOSIUM PRESENTATIONS

Robinson NJ, Morreale SJ, Batchoo S, Kotze D, McCue S, Meyer M, Oosthuizen H, Nel R, Paladino FV (2014) Revealing the migratory behaviour of nesting leatherback and loggerhead turtles from South Africa using satellite telemetry and stable isotope analysis. 34th Annual Symposium on Sea Turtle Biology and Conservation. New Orleans, USA. Oral presentation.

Robinson NJ, Morreale SJ, Nel R, Paladino FV (2014) Identifying behavioural changes in migrating leatherback turtles using a Change-Point Analysis Model. 34th Annual Symposium on Sea Turtle Biology and Conservation. New Orleans, USA. Poster presentation.

Robinson NJ, Nel R., Morreale SJ, Paladino FV (2013) Coastal or pelagic: updating the leatherback paradigm. 33rd Annual Symposium on Sea Turtle Biology and Conservation. Baltimore, USA. Oral presentation.

Robinson, NJ, Valentine S, Garner J, Santidrián Tomillo P, Saba VS, Spotila JR, Paladino FV (2012) Factors influencing the timing of the nesting season for Pacific and Atlantic leatherback turtles. 32st Annual Symposium on Sea Turtle Biology and Conservation. Oaxaca, Mexico. Oral presentation.

Robinson NJ, Valentine S, Santidrián Tomillo P, Spotila JR, Paladino FV (2011) Effect of population demographics on the nesting phenology of the leatherback turtle (*Dermochelys coriacea*) at Playa Grande, Costa Rica. Joint Meeting of Ichthyologists and Herpetologists. Minneapolis, USA. Oral presentation.

Robinson, NJ, Santidrián Tomillo P (2010) Cheer for the turtles: bridging the gap between monitoring and public outreach. 31st Annual Symposium on Sea Turtle Biology and Conservation. San Diego, U.S.A. Poster presentation.

Valentine S, **Robinson NJ,** Santidrián Tomillo P, Spotila JR, Paladino FV (2010) Climate change impacts on nesting leatherback turtles in the Eastern Pacific. 31st Annual Symposium on Sea Turtle Biology and Conservation. San Diego, U.S.A. Oral presentation.

GRANTS

Aug '12	$9,000 – Bilsland Dissertation Fellowship. From Purdue University, USA.
Mar '12	$1,000 – Purdue Student Travel Award. For the 32st Annual Symposium on Sea Turtle Biology and Conservation. Oaxaca, Mexico.
Mar '12	$300 – International Sea Turtle Society Travel Grant. For the 32st Annual Symposium on Sea Turtle Biology and Conservation. Oaxaca, Mexico.
Mar '11	$200 – International Sea Turtle Society Travel Grant. For the 31st Annual Symposium on Sea Turtle Biology and Conservation. San Diego, USA.
Jan '11	$50,000 – The Leatherback Trust Grant for Ph.D. research.

AWARDS

Apr '14	Archie Carr Award for Runner-Up Best Oral Presentation in Biology at the 34th Annual Symposium on Sea Turtle Biology and Conservation. New Orleans, USA.
Jun '09	National Oceanography Centre’s Award for the Highest Achieving Graduating Student in Oceanography

INVITED REVIEWER FOR PEER-REVIEWED JOURNALS

- Marine Turtle Newsletter
- Herpetologica

PROFESSIONAL SKILLS

- Handling of large marine species.
- Attachment of animal-borne sensors.
- Experienced on oceanic research vessels.
- Qualified SCUBA diver (PADI – Open Water).
- European driving licenses.
- First Aid certified.
- Proficiency with: Microsoft Office, ArcGIS, SPSS, SigmaPlot, Dbase, and R
- Website design (goldringmarinestation.org).
- Conversational Spanish and French.

PHOTOGRAPHY CREDITS

Feb ’13	**Cornell University Homepage (**www.cornell.edu**)** **News Sentinel (**http://www.news-sentinel.com) **Fondriest – Environmental Monitor (**http://www.fondriest.com)

MEDIA APPEARANCES

Oct '13	**Tico Times: A Turtle’s Paradise Still**
Mar '10	**Green Living Project: The Leatherback Trust**

REFERENCES

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