Investigating the fitness of sea turtles nesting in South Africa

By:

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Big things often have small beginnings…

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DECLARATION:

In accordance with Rule G5.6.3, I hereby declare that the above-mentioned thesis is my own work and that it has not previously been submitted for assessment to another University or for other qualification.

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Abstract

Sea turtles are particularly vulnerable to direct threats and changing environmental conditions because they are long-lived, slow maturing, and have low survival rates at early life stages, making them conservation-dependent. These characteristics also render them difficult to conserve due to their wide geographic distributions, spanning multiple jurisdictions and legislative systems with different conservation targets, and a complex life cycle with changes in habitats and diets at different life stages. Sea turtle populations have been severely depleted as a result of historical over-exploitation and current threats including fisheries bycatch, direct harvest, habitat loss, pollution and pathogens, and climate change. In many cases however, population declines have been reversed as a result of a variety of effective conservation measures such as beach protection programs, and marine protected areas, enabling successful population recovery around the world. Despite protection and apparent increase in abundance, indirect pressures can still affect turtle populations and it is thus fundamental to evaluate the effectiveness of conservation measures (fitness traits such as female and hatchling sizes) and examine underlying trends.

The South African rookeries of the South Western Indian Ocean (SWIO) loggerhead and leatherback regional management units have been continuously monitored for more than 5 decades, representing one of the longest-running sea turtle beach protection and monitoring programmes in the world. Although such conservation has been successful in protecting adults on land when they come to nest, it might not be enough to ensure population recovery if survival is not ensured across all life stages. The aim of this thesis was thus to evaluate the fitness of loggerhead and leatherback sea turtles nesting in South Africa. Long-term female size trends over time were evaluated and the populations were split between first-time nesters and experienced nesters. As sea turtle reproductive output (clutch size and egg size) is correlated with female size and evidence is showing that in some populations individual female size is decreasing, the effects of maternal body size on reproductive output and hatchling fitness were investigated for both species. Crawling and swimming speeds were used as proxies of hatchling fitness, as these two traits positively influence their survival. An oceanic model was further used in combination with a particle tracking framework to estimate, for the first time, post-hatchling dispersal of loggerhead and leatherback turtles in the SWIO. I also investigated whether the trend in female size for loggerhead

turtles nesting in South Africa is due to their foraging strategy and tested if there is a foraging dichotomy (neritic and oceanic).

Despite an apparent increasing population, loggerhead female size was found to be declining (4.2 cm) while leatherbacks are increasing slightly (3.3 cm) with a stable population. I hypothesise that these contradictory effects are attributable to the very distinct foraging ecologies of the two turtle species and speculate that these variation in carapace length may be driven by environmental change. The reproductive strategy of both loggerhead and leatherback turtles nesting in South Africa was found to support the optimal egg size theory with larger turtles produce larger clutches but not larger eggs. Egg size was thus constant irrespective of maternal length. Hatchlings with longer carapace and flippers had higher swimming speed, suggesting that larger hatchlings are fitter than smaller ones because they spend less time in high predation risk areas (i.e. beach and nearshore). The model revealed that dispersal trajectories of both loggerhead and leatherback sea turtle hatchlings were very similar and simulations indicated that initial active swimming (frenzy) as well as variability in oceanic conditions strongly influenced dispersal of virtual hatchlings.

The trends observed in this study emphasize the importance of long-term monitoring, examining not only abundance but also individual size, to understand population dynamics, support recovery planning and prioritize future conservation practices. Furthermore, the findings of this study have important implications for overall population growth if smaller hatchlings of lower fitness are produced due to climate change and thus have decreased dispersal abilities and likelihood of survival.

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Preface

The present thesis consists of six chapters, of which the four data chapters are written as scientific papers. These articles are submitted for publication or intended for submission. This manuscript is thus written as a series of discrete, stand-alone chapters but collectively, and coherently address a similar aim – factors affecting sea turtle fitness. Note that although every effort is made to minimise repetition in content among chapters, this was unavoidable in some places (like the repeated Study Site). In addition, the use of "we" rather than "I" within the text is noticeable and necessary as the chapters are formatted as articles. Ronel Nel, as academic promoter contributed to all chapters/articles and is thus recognised as a co-author on all the papers. Several collaborators contributed to different chapters. Linda Harris analysed the GPS data and Stephan Woodborne analysed the isotopic data and both reviewed the stable isotope chapter (Chapter 5). Bjorn Backberg provided the oceanographic model and Mike Hart-Davis created the particle tracking model. Both collaborators also reviewed the manuscript to the hatchling modelling chapter (Chapter 4).

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Chapter 1: General Introduction: sea turtle fitness and biology – a review

Chapter 1: General Introduction

Introduction

Historical over-exploitation has severely depleted species or populations globally. In many cases however population declines have been reversed as a result of a variety of effective conservation measures, enabling successful population recovery around the world (Hays, 2004; Mazaris et al., 2017). Although these conservation successes have frequently been evaluated solely based on changes in abundance, other population demographic metrics (e.g. size, nesting success, performance) provide resolution to the ecological resilience of these populations. The number of individuals in a population is thus not the only relevant metric to assess population recovery and new pressures require thorough and continuous monitoring of population dynamics. Assessing the fitness of a population might help inform on the ability of a species to maintain key functions and adapt to change (Fuentes et al., 2013).

Despite protection and an apparent increase in abundance, indirect pressures can suppress populations if species/individuals exposed to stochastic environments are protected in suboptimal habitats. Even large populations can decline (Caughley, 1994). Long-term time-series data provide both abundance data and size-class-specific demographic information (Balazs and Chaloupka, 2004; Stokes et al., 2014; Derville et al., 2015), which could inform on operational sex ratios, abundance per size class, nesting and hatching success, female health, which are indicators of current and future breeding success. All these aspects need to be inspected periodically and population trends assessed to inform on recovery potential and the long-term success of conservation measures (Bjorndal et al., 1999, 2010; Limpus, 2008).

Five of the 11 regional management units (RMUs) in the Indian Ocean are listed as endangered and thus of conservation concern (Wallace et al., 2011), with all of them receiving some form of protection. There is thus an imperative need to enhance our understanding of conservation success and failure. Of these 11 RMUs, the South Western Indian Ocean (SWIO) loggerhead is listed as vulnerable and leatherback turtles as critically endangered. South Africa is the stronghold for these two SWIO regional management units shared with Mozambique. The South African rookery is also one of the few sea turtle nesting locations in the world that have been continuously

protected and quantitatively monitored for more than 5 decades. This program represents a unique opportunity for assessing population trends, associated long-term indicators of population resilience and the effects of individual fitness traits, like size.

This thesis examines the life history and fitness of two species of sea turtles nesting in South Africa by measuring fitness traits to evaluate current conservation successes and inform on the value of conservation efforts, locally and globally. The key research focus is to investigate if individual females are getting smaller and the potential impacts of this on offspring fitness. This question will be evaluated by assessing if smaller females are producing smaller, less fit offspring, investigate the effects of hatchling size on dispersal abilities, and identify neonate dispersal pathways. Conversely, are larger hatchlings fitter with a higher chance of survival? Which morphological traits enhance hatchling performance, dispersal abilities and ultimately fitness potential?

To answer these questions, we start with a brief review of the relationship between animal fitness and fitness traits, and how these relate to the complex life history of sea turtles. We will also review the current knowledge on fitness traits for specific size classes/phases of sea turtles and how these associate to sea turtles nesting in South Africa.

Animal fitness

Fitness is perhaps one of the most challenging concepts in biology, but what is fitness and how do we define and measure it? Stearns (1976) stated it is "something everyone understands but no one can define precisely". Fitness according to Darwin, is the capacity to survive and reproduce (Darwin, 1859; De Jong, 1994). Although most agree that fitness includes some measure of success in contributing to future generations, no consensus has been reached on a single coherent working definition (Ariew and Lewontin, 2004; Hunt and Hodgson, 2010). This gap is partly because no single measure can reliably predict future success/fitness in all biological contexts. Fitness can be described as "a measurable feature of alleles, genotypes or traits of individuals that predicts their numerical representation in future generations" (Hunt & Hodgson, 2010).

Fitness studies thus attempt to explain how organisms survive and reproduce (Stearns, 2000). The main objective of this thesis is therefore not to understand survival *per se*, but the design/mechanisms for survival (Williams, 1966). It reflects how organisms evolved to solve ecological problems and how well an organism is adapted to its environment (Stearns, 1976; Kokko et al., 2017). Fitness is, therefore, a measure of survival and reproductive success which is driven by natural selection in response to environmental stressors (Stearns 1976, 2000). Thus "survival of the fittest" (Spencer, 1864) means: survival of the (genotypic or phenotypic) form that will leave the most copies of itself in future generations.

Survival is said to be size-dependent (Schmidt-Nielsen, 1984; Hunt & Hodgson, 2010), and natural selection should favour larger offspring. However, if selection favours large offspring, why do we not observe a trend towards larger organisms? The answer might lie in the fact that optimality theory assumes a stable environment which does not accurately represent natural systems, which are fluctuating environments (Irschick, 2003; Sæther and Engen, 2015). Consequently, it appears that fitness describes how organisms evolved to face ecological problems posed by a changing environment and achieve reproductive success to pass their genes onto the next generations (Stearns, 2000). This variability may indicate that in a stochastic environment, natural selection favours organisms which are able to exhibit a range of phenotypes in response to variation in the environment (Fordyce, 2006; Rollinson and Hutchings, 2013).

Simply put, fitness is an organism's entire lifetime reproductive success, but to measure this success is difficult; it is rarely possible to obtain such data, especially for long-lived species in large populations. Alternatively, researchers use fitness proxies, variables and traits presumed to be correlated with, or have significant effects on fitness components such as body size, growth rate, mating success, number of offspring reaching adulthood (McGraw and Caswell, 1996; Ariew & Lewontin, 2004). There is thus a need to investigate the fitness consequences for parents that deviate from optimality, which in turn will provide a better understanding of evolutionary processes by providing knowledge of the fitness traits that will maximise individual fitness (Rollinson and Hutchings, 2013). For sea turtles, finding fitness proxies is particularly challenging given their multifaceted life history, with ontogenetic shifts in behaviour and habitats at different life stages (Davenport, 1997). For sea turtle hatchlings, it appears that 'fitness' is linked to their locomotor performance and

survival. Although, hatchling fitness can be described as an individual's potential for contributing offspring to future generations or its future reproductive value (Botlen et al., 2010), fitness is evaluated by measuring traits such as self-righting time, and crawling and swimming speeds (Ischer et al., 2009; Mickelson and Downie, 2010; Booth et al., 2013; Sim et al., 2015). Slower locomotor responses are associated with a higher probability of injury or mortality.

Sea turtle life history

All marine turtles share a similar, yet complex life cycle (Fig. 1.1). In short, sea turtles mate in near-shore coastal waters adjacent to the tropical or subtropical nesting beaches. Polyandrous females mate with multiple males and store sperm to be used throughout the nesting season (Owen, 1980; Galbraith, 1993; Pearse & Avise, 2001). While males return to their foraging grounds (Ehrhart, 1982; Bolten et al., 1992; Miller 1997), female turtles stay behind to lay multiple clutches of eggs throughout the nesting season. After a female has deposited all her clutches, she will migrate hundreds to thousands of kilometres back to her foraging ground, leaving her nests without any parental care. Incubation periods of nests vary depending on local conditions and the species, but generally range 2-3 months. Days after hatching from the eggs, hatchlings usually emerge at night to avoid predation and desiccation, crawl down the beach and swim rapidly out to sea (Salmon & Wyneken, 1987; Hughes, 1974). This two-day swim is called the "swimming frenzy" to carry them offshore. Much of their subsequent life is enigmatic but they appear to disperse and migrate offshore in pelagic waters and spend several years drifting with ocean currents (Carr, 1986; 1987; Witherington, 2002; Reich et al., 2007; Mansfield et al., 2012, Putman et al., 2012a, b; Putman & Mansfield, 2015; Putman & Naro-Maciel, 2016). This drift is called the " lost years". Juveniles/subadults then finally recruit back to shallow coastal waters and join the adult neritic foraging grounds. Sea turtles life cycle is thus characterized by changes in habitats and diet at different stages and typically consists of four ontogenetic stages: 1) neonate post-hatch pelagic/oceanic phase (of poorly known duration); followed by 2) a juvenile and sub-adult phase commonly encountered in neritic shallow waters; 3) an adult foraging phase in coastal habitats; and 4) an adult breeding phase where sexually mature individuals migrate periodically to distant nesting grounds ff natal sandy beaches (Musik & Limpus, 1997; Davenport, 1997).
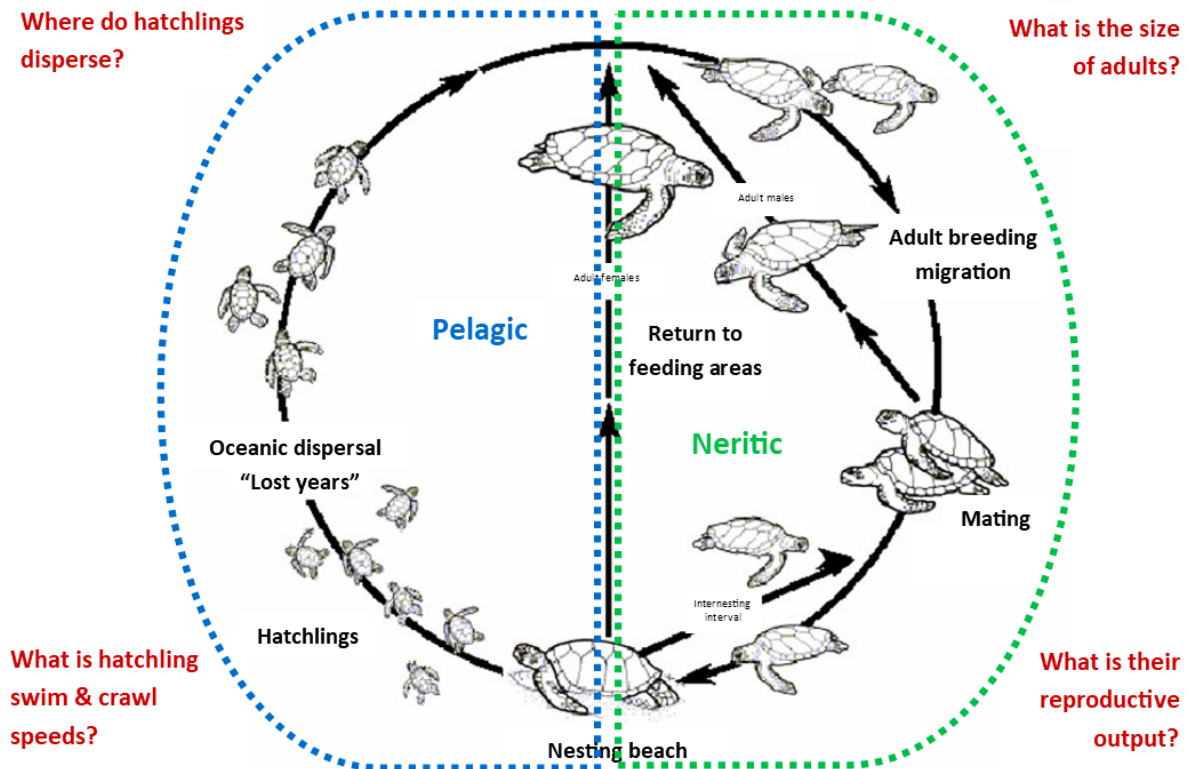
Figure 1.1: Illustration of a generalized sea turtle life cycle (modified from Lanyon et al., 1989) showing the life history phases and key fitness traits investigated in this thesis, at different life history stages.

Reproductive strategy

An essential aspect of life history research is understanding how energy is allocated throughout an organism's life cycle, which generally shifts between the growing phase, and maturing and reproductive phases. Reproductive effort is defined as the portion of an organism's total resources allocated to reproduction (Hirshfield & Tinkle, 1975). As the energy available to an organism is finite, fecundity might be set at some optimum level that would maximise lifetime reproductive output (Williams, 1966; Charnov and Krebs, 1974). Optimal egg size theory (OES) predicts that an increase in maternal investment per individual offspring would result in a decrease in the number of offspring that can be produced. And as the energy allocated per individual offspring increases, the fitness of individual increases (Smith & Fretwell, 1974). Therefore, there is a trade-off between offspring size and number. The size of individual offspring should thus be under strong normalizing selection reducing variation in egg and offspring size. Hence, for species that produce several offspring

per reproductive event, the OES predicts that variation in total reproductive investment should be determined (in stable environments) by offspring number rather than offspring size (Smith & Fretwell, 1974; Congdon & Gibbons, 1987).

The reproductive strategy of sea turtles is one of both high fecundity and high offspring mortality (Davenport, 1997). Marine turtles exhibit the highest reproductive output among oviparous reptiles, laying two to five clutches of 50 -150 eggs every two to four years (Miller, 1997). As marine turtles have very minimal parental care (restricted to site selection and nest digging), maternal investment in offspring is thus closely represented by the total energy content contained by the quality and quantity of yolk in each egg (Shine, 1988). Thus, due to the energetic cost of reproduction, sea turtles are non-annual breeders, and likely evolved this reproductive strategy of laying many small eggs in several clutches in response to high mortality during the egg and hatchling stages (Van Buskirk & Crowder, 1994; Wallace et al., 2007). By spreading risk, females avoid allocating high quantities of resources to any single, or only a few offspring.

Sea turtle migration & foraging

Understanding migration is crucial in understanding the ecology, demography, life history and conservation needs of populations. The regular seasonal movement of individuals, i.e., migration, is used by a range of taxa such as insects, birds, mammals (caribou, wales) and reptiles such as sea turtles; with individuals travelling thousands of kilometres, mostly between breeding and foraging locations and back (Webster et al., 2002). This form of long-distance movement is particularly true for sea turtles who spend most of their life at sea, undertake long migrations, use a variety of habitats at different life stages, and return to their natal beach to reproduce (Davenport, 1997; Bolten, 2003a, b). Furthermore, knowledge of where organisms forage is essential because it can affect their fitness depending on the resource available in each habitat (Hatase et al., 2004). Intraspecific variation in foraging strategies (habitat) and resource use within populations may contribute to differences in performance and fitness traits such as reproductive output and survival, leading to alternative life histories (Hatase et al., 2002; 2013). Consequently, differences in habitat and resource use may contribute to variation in fitness among individuals.

Recent studies have revealed a size-related dichotomy in foraging strategies of marine turtles that has important implications for individual fitness traits. Large neritic-foragers from different locations have been found to have higher fitness; with larger clutches (Zbinden et al., 2011), shorter remigration intervals (Hatase et al., 2004; Vander Zanden et al., 2014), and greater cumulative reproductive outputs, compared to small oceanic foragers (Hatase et al., 2013). It is, therefore, useful to have knowledge of the spatial distribution and foraging strategy of sea turtles as well as identify foraging areas to be able to predict the growth potential of populations and inform future conservation measures.

Conserving migratory species is challenging due to the extensive distances they travel, utilizing areas beyond national jurisdictions (Harris et al., 2017), the inaccessibility of their habitats, the technological difficulty of observing organisms at sea (Hobson, 1999; Ceriani et al., 2012), and their often-elusive nature (Schofield et al., 2006). Despite difficulties, our understanding of animal migrations and the links between foraging and breeding areas have considerably improved due to *inter alia* advances in genetics, satellite tracking technology, and stable isotope analysis. However, multi-technique approaches have proven to be the most powerful at elucidating trophic and spatial ecology of migratory species (Clegg et al., 2003; Chabot et al., 2012).

Satellite tracking provides high-resolution spatial and behavioural information for relatively short periods on a small number of individuals (due to logistical and financial costs involved), whereas stable isotope analysis is relatively inexpensive and can be applied more broadly (Rubenstein and Robson, 2004). A variety of isotope markers are increasingly being used to trace foraging behaviour/diet and general movement patterns of marine organisms (Hobson et al., 2010; Zbinden et al.,2011). Individuals that exploit geochemically distinct habitats or feed on different resources can be differentiated using stable isotope measurements, as the isotopic profile of consumers reflects that of their prey in a predictable manner (Peterson & Fry, 1987). Thus, as organisms move, they absorb the isotopic signature of local prey, enabling us to track their movement and ecology. This relationship is illustrated by the prevailing paradigm of stable isotopes of "you are what you eat" (DeNiro & Epstein, 1978), in addition to the novel approach of tracking movement that relies on "you are what you swim in" principle (Killingley & Lutcavage, 1983). Specifically, stable isotope analysis has

proven to be particularly useful and well suited to study marine turtles as they aggregate and come to shore during the breeding season, migrate between isotopically distinct foraging grounds and breeding areas, appear to show fidelity to both nesting and feeding areas throughout adult life, and are capital breeders that usually fast during reproduction using energy stores accumulated at the foraging grounds (Hatase et al., 2002a; Broderick et al., 2007; Zbinden et al., 2011; Plot et al., 2013; Vander Zanden et al., 214).

Growth rate

Growth rate is a fundamental parameter along with other life history aspects such as age at maturity, the duration of various life history stages, generation time and longevity, parental investment, number of offspring. These metrics are used to create demographic models (Crouse et al., 1987; Braun-McNeill et al., 2008; Casale et al., 2009, 2011; Jones et al., 2011; Scott et al., 2012). Demographic models, in turn, are used to model population trends, recovery potential, or likelihood of decline and extinction, and so determining the conservation status of endangered species. Ultimately it is also necessary for devising effective conservation and management strategies (Bjorndal et al., 2000; Berner & Blanckenhorn, 2007; Avens et al., 2015).

Sea turtles are slow-growing and take between 15 to 50 years to reach reproductive maturity, depending on the species (Davenport, 1994). It appears that wild leatherback turtles growth faster than smaller, hard-shelled turtles, with predicted maturity reached around 15 years of age (Zug and Parham, 1996), while it is estimated to be around 25 to 36 years for wild loggerheads to reach maturity (Limpus, 1979; Casale et al., 2011; Tucek et al., 2014; Avens et al., 2015). Although growth rates decay with age in sea turtles, they are believed to have indeterminate growth, with growth persisting throughout life (Omeyer et al., 2017, 2018).

Growth rates of wild and captive turtles differ considerably, with captive turtles growing up to four times faster than wild turtles (Mendonca, 1981), due to high-quality diets, and well-regulated temperatures, and presumably limited activity (Jones et al., 2011). However, growth rates studies in captivity have reported high levels of variation among individuals in the same population despite being raised under similar conditions (Stokes et al., 2006; Reich et al., 2008). However, even wild sea turtles in the first

years of life are capable of extremely fast, but variable, growth rates. Studies on wild turtles have reported growth rates during the first six months ranging from 10.1 cm per year for green turtles from Ascension Island, Surinam, and Costa Rica (Bjorndal et al., 2012), to 11.8 cm per year for loggerhead turtles in the Mediterranean (Casale et al., 2009), 12 cm per year for loggerhead turtles in the North Atlantic, and Azores (Bjorndal et al., 2000), to an extreme 34 cm per year for North Atlantic loggerhead turtles in Virginia (Swingle et al., 1993). However, growth decreases with an increase in size and age. Casale et al., (2009) reported 3.6 cm per year at the age of 2.5-3.5 years.

Stokes et al., (2006) found that larger hatchlings from northern subpopulations (from different nests) had higher growth rates than did hatchlings from southern subpopulations. However, this raises the question if larger hatchlings maintain higher growth rates over time or if it levels out at a specific age/size, and they have higher fitness? Bjorndal et al., (2003) demonstrated that oceanic staged loggerhead turtles exhibit compensatory growth ("catch up" growth) as a result of limited food sources, and when exposed to an improved nutritional environment grow at a more rapid rate. Compensatory growth has also been found for soft-shelled turtles (Ji et al., 2003). Additionally, differential growth has also been reported in other ectothermic species as a function of latitude, in King Salmon, and Arctic Char (although results should be interpreted with caution (Leggett and Carscadden, 1978). Thus, it appears that growth is affected by fitness traits such as size and larger hatchlings may have higher growth rates.

Estimating growth rates for sea turtles, however, is challenging as they can exhibit high variability in growth rates even among individuals within the same population. Consequently, age and size at maturity range broadly. Variation in growth rates may be caused by genetic variability, resource availability, habitat characteristics, competition, and/or other environmental factors (Heppell et al., 2003; Casale et al., 2011). Further, mapping early life history patterns during the first years of life, and the difficulty in observing them at sea (Bjorndal, 2003), results in early life estimates already being tenuous.

In sea turtles, most estimates of growth rates are generated from growth models based on capture-mark-recapture, some attempts of skeletochronology, or length-frequency analyses (Zug et al., 1995; Casale et al., 2009, 2011; Snover et al., 2007; Avens et

al., 2015). However, these approaches have limitations in that the baseline estimate must be known to be able to accurately age individuals, whether it is the year of hatching or age/length at sexual maturity (Bjorndal et al., 2012). However, capture-mark-recapture technique using saturation tagging (of adult females) has been successful in estimating age and size at first reproduction (Limpus and Chaloupka, 1997; Casale et al., 2009). Despite limitations, long-term data on some populations have successfully modelled age at maturity of green (Goshe et al., 2010), loggerhead (Heppel et al., 1996), and hawksbill turtles (Chaloupka and Limpus, 1997). Additionally, a 30 year mutilation tagging experiments have allowed to reliably predict age at maturation of loggerhead turtles to be an average age of 36.2 years in South Africa (Hughes and Brent, 1972; Tuček et al., 2014) and 29 years in Australia (Limpus, 2008). Furthermore, while estimates of growth rates of adult female sea turtles are possible in their nesting habitat (where they are easily accessible), there is a paucity of growth rate estimates of wild early pelagic life stage of hatchlings as a result of their small size, and low survival probabilities (Lutz & Musick, 1997).

Hatchling morphology & locomotor performance

Hatchling phenotype can be influenced by both biotic and abiotic factors; abiotic factors that influence the morphological traits of hatchlings are associated to nest or incubation environment, specifically, nest temperature, and hydric conditions (water availability to the developing embryo), which influence the metabolic rate of the embryo and thus determines incubation time (Miller, 1997; Glen et al., 2003). Increased incubation temperatures decrease incubation time and produce smaller hatchlings with a larger residual yolk compared to low incubation temperatures (Reece et al., 2002; Glen et al., 2003; Booth et al., 2004, 2013; Sim et al., 2015). Hatchling morphology and size will affect their survival by influencing predation rates and performance.

Hatchlings are vulnerable to a high abundance of predators when they crawl down the beach (crabs and birds) and swim over the fringing reef (Limpus et al., 1984; Janzen et al., 2000). On the beach, hatchlings are at risk to predators such as crabs and birds as they crawl down to the water (Janzen et al., 2000; Salmon et al., 2009; Tomillo et al., 2010). Predation rates seem to decrease with increased distance from the natal

beach (Gyuris, 1994; Pitcher et al., 2000). Predation risk decreases when hatchlings reach deeper oceanic waters (Salmon & Wyneken, 1987; Gyuris, 1994). However, predation may be site-specific and vary at each rookery. Pilcher et al., (2000) found that green turtle hatchlings in Malaysia suffered 40-60% mortality within the first two hours at sea before crossing the 10 m depth contour. Additionally, hatchlings do not actively avoid or defend themselves against predators and their survival appears to be directly related to crawling and swimming speed: the faster they craw or swim, the less time they are exposed to predators (Gyuris, 2000). Hatchling survival is, therefore, a trade-off between maximising morphological performance and minimising mortality risks. Locomotor/swimming performance is thus a significant factor in determining hatchling survival during their post-emergence migration success.

Locomotor performance of hatchlings seems to be affected by their size and shape, as longer limbs have greater stride, and larger hatchlings are thus faster, and presumably have higher fitness traits (Janzen, 1993; Ischer et al., 2009; Sim et al., 2015). Bigger hatchlings are also less vulnerable to predation, specially gape-limited predatory fish like dolphinfish, *Coryphaena hippurus* (Gyuris, 2000; Salmon & Scholl, 2014). Leatherback hatchlings are not easily taken by ghost crabs, *Ocypode ryderi* (De Wet, 2012). These findings are in accordance with the "bigger is better" hypothesis (Packard & Packard, 1988), which suggests that larger hatchlings (within or between species) may be less susceptible to predation, are better crawlers and swimmers, and thus have higher survivorship. Direct measurements of hatchling individual fitness traits are made difficult due to the long life span in sea turtles and crawling and swimming speeds can be used as fitness traits or fitness-related attributes to approximate future reproductive success or fitness (Booth et al., 2004).

Post-hatchling dispersal

The neonate stage is a perilous life history phase for sea turtles because it is characterized by high mortality and remains the least understood stage in sea turtle life history, with most information mainly been inferred rather than directly observed (Witherington, 2002; Reich et al., 2007; Mansfield et al., 2014). Upon entering the water, hatchlings swim continuously offshore to reach oceanic currents. This initial swimming phase, called the "swimming frenzy", is crucial to their survival because it

displaces them from shallow water habitats, and lasts from hours to days (Salmon & Wyneken, 1987, Hughes, 1979). During this continuous offshore migration, hatchlings orientate themselves using visual cues, ocean waves, and the Earth's magnetic field (Lohmann & Lohmann, 1996a, b; Luschi et al., 2007). Neonate hatchlings have limited swimming and diving abilities and are positively buoyant during the first year of dispersal (Hays et al., 2010). Studies have shown that juveniles loggerhead turtles spend 90% of their time within the first 5 m of the water column (Howell et al., 2010), while leatherback hatchlings have increased diving capacities as they growth during their first weeks and are able to dive to 20 m depth (Salmon et al., 2004).

Post-hatchlings then disperse into the open ocean and remain largely unobserved during a pelagic phase known as "the lost years" (Carr, 1986, 1987). Long-standing hypotheses suggests that neonate turtles remain offshore in oceanic waters, are passive drifters, and occupy sea surface habitats (Carr, 1986, 1987; Witherington, 2002; Mansfield et al., 2014). However, recent studies suggest that hatchlings actively disperse and exhibit oriented swimming behaviour (Wyneken et al., 2008; Putman et al., 2012a, b, 2016; Putman & Mansfield, 2015). These results indicate that ocean currents may not be the only factor influencing their dispersal but that hatchling morphology and physiology might also impact their distribution and performance.

Sea turtles are cold-blooded reptiles that rely on external sources of heat to determine their body temperature and are commonly constrained by the 20° C surface isotherm (Davenport, 1997). The distribution of adult sea turtle is thus essentially tropical, subtropical, and warm temperate waters for most cheloniid species except leatherback turtles that have thermoregulatory abilities and are found in high latitudes cold waters (5-15° C; Greer et al., 1973; Davenport et al., 1990; James & Mrosovsky, 2004; Bostrom et al., 2010; Davenport et al., 2016). Thermal tolerance in ectothermic animals generally increases with temperature rise and then falls when a critical temperature level is exceeded (O'Hara, 1980). Prolonged exposure to low temperatures (less than 10° C) can lead to growth arrest, and hypothermic stunning, and high temperatures (above 30° C) can result in decreased swimming activity and loss of locomotor coordination in sea turtle hatchlings (Schwartz, 1978; Morreale et al., 1992). In the South African turtle rookery, it is assumed that hatchlings are carried out south along the east and south coasts in the Agulhas Current where localised upwelling (14° C) occur and sea surface temperatures gradually decrease from about

28° C to 18° C (Hughes, 1974). Thus, hatchling swimming ability, growth and dispersal can be influenced by sea surface temperature which in turn may reduce their survival if exposure times were longer.

Hughes (1974) hypothesised that hatchlings from the Maputaland nesting beaches in the northeast coast of South Africa are carried south and enter the fast-flowing (1.5 m.s^{-1}; Lutjeharms, 2006) Agulhas Current (AC). It is suggested that South African loggerhead and leatherback hatchlings spend at least three months under the direct influence of the Agulhas circulation, however evidence from notched hatchlings indicate that neonates do not remain in the main stream of the current and are possibly delayed by eddy circulations (Lutjeharms et al., 1989, 2010; Casal et al., 2009). Recoveries of small, notched post-hatchlings from the South African rookery revealed that most travel southwards within the AC, with some rounding the Cape and entering the Atlantic Ocean (Baldwin et al., 2003). The AC flows southward along the edge of the continental shelf within 10 km of the coast and after that leaves the coast and follows the edge of the Agulhas Bank (near Port Elizabeth) (Lutjeharms, 2006). Upwelling and prolonged periods in cold water (decrease temperature from 23° C to < 20°; Lutjeharms et al., 2000; Rouault et al., 2010) may affect hatchling growth and survival. Thus, warmer water temperature optimal for growth would produce larger hatchlings while colder water will stunt hatchling growth. However, these assumptions have never been tested, and no studies have investigated the dispersal of neonate turtles from the South African nesting beaches and how different dispersal pathways (with varying water temperatures) may affect their fitness and survival.

Given their small size, positive buoyancy and limited locomotion, neonate turtles are assumed to be strongly affected by sea current circulation (Boyle et al., 2009; Luschi et al., 2003; Hays et al., 2010), and it is possible to assume that fitter hatchlings (larger and better swimmers) have survival advantages relative to smaller ones. However, incorporating hatchling "fitness" to predict dispersal pathways and survival probability has never been tested. Recently, oceanographic models have become a powerful tool to predict movements and dispersal patterns of sea turtle hatchlings (Hamann et al., 2011; Putman & Naro-Maciel, 2016).

High-resolution ocean circulation models can provide a useful first step towards understanding possible patterns of distribution. Advances in computing power and

remote-sensing over the last decade have greatly enhanced our ability to model movement of neonate sea turtles, especially where and how they disperse within ocean currents, which habitats they use and the duration in any specific habitat (Boyle et al., 2009; Monzon-Arguello et al., 2010; Okuyama et al., 2011; Briscoe et al., 2016; Christiansen et al., 2016). Although modelling hatchling dispersal can appear to simplify biological and ecological aspects, different scenarios/simulations can be generated and parameters (current speed, sea surface temperature, wind speed, swimming activity, duration, and direction, etc.) changed as our knowledge of hatchling behaviour increases (Hamann et al., 2011; Okuyama et al., 2011; Briscoe et al., 2016).

Thesis aims and structure

This thesis explores the intricacies of animal fitness especially for complex organisms such as sea turtles and attempts to determine the consequences of reduced fitness for sea turtles that are required to adapt to a changing environment to survive. Sea turtles have a very particular life cycle with limited parental care of the eggs, and offspring that do not have defences against predators leading to very high mortality during the early life stages. The post-hatchling phase is thus the most critical life stage where they are most vulnerable and when it is fundamental to understand what affects their fitness and survival. Furthermore, sea turtles are conservation-dependent and rely on protection measures to maintain viable populations. It is thus critical to evaluate the efficiency of management strategies and understand if the conservation measures being implemented are effective and succeeding in achieving population recoveries and growth. Therefore, the principal aim of this thesis is to investigate the fitness of both loggerhead and leatherback sea turtles nesting in South Africa. The South African turtle rookery is a very well-suited place to test this aim as it represents one of the longest-running sea turtle monitoring programs in the world. The thesis starts with a brief literature review to outline the state of knowledge on nesting sea turtle life histories and biology (Chapter 1).

Chapter 2 investigates long-term trends in individual loggerhead and leatherback female size over time. It has been shown that the two populations have responded differently to conservation measures although they have received similar protection, with loggerheads increasing exponentially, while leatherbacks initially increased but then stabilised. Furthermore, although the loggerhead population has been growing,

there might be evidence that individual female size has decreased. This chapter thus intends to assess if overall female size has decreased over time by using the long-term monitoring data and investigating trends for both neophyte and experienced nesters.

Since smaller turtles have lower reproductive output and so potential fitness, I question whether South African turtles produce fewer smaller eggs, resulting in smaller hatchlings with weaker fitness traits. Chapter 3 examines the effects of maternal body size on reproductive output and hatchling fitness traits for both loggerhead and leatherback turtles. Sea turtles are the most vulnerable and experience the highest mortality during the early life stages, and we thus attempt to explore fitness during this critical hatchling phase. As hatchling locomotor performance directly affects their survival, by minimising the time spend in predator-rich zones, we use crawling and swimming speeds as proxies of fitness and test these two traits with *in situ* trials. I thus hypothesise that there is a positive correlation between maternal body size and clutch size, but not egg size and larger females will produce larger clutches, and that larger hatchlings will have faster locomotor performance and thus have increased fitness than smaller ones.

Chapter 4 investigates if SWIO hatchlings capitalise on the two ocean basins available, and how behavioural and environmental factors can affect the outcome of their dispersal. In the South African rookery, such models have never been created yet, and it was assumed that hatchlings are directly influenced and transported in the Agulhas Current, with some potentially entrained into the South-East Atlantic, where lethal temperatures might affect their survival. This chapter is thus the first estimate of dispersal trajectories for both loggerhead and leatherback hatchlings from the South African component of the South Western Indian Ocean turtle rookeries. This chapter, thus, combines a high-resolution ocean model with a particle tracking framework and *in situ* observations of hatchling behaviour to identify potential dispersal pathways. Hypotheses are that (1) dispersal is controlled by oceanic currents and will thus transport post-hatchlings in the two ocean basins, the South-West Indian Ocean and the South-East Atlantic Ocean basins, and (2) neonate dispersal is independent of swimming behaviour and species.

Following on the results from Chapter 2 and to further elucidate the causes of the variability in individual size, we tested whether a dichotomy in foraging strategy could be responsible for the size differences found in loggerhead females in Chapter 5. This was achieved by combining satellite tracking data and stable isotope analysis to infer foraging areas used by South African nesting loggerhead turtles. As discussed, recent studies showed that smaller females are associated with oceanic habitats while larger females inhabit neritic areas. As sea turtles do not feed during migration and reproductive events, their isotopic signature represents that of their prey consumed at their foraging grounds. Chapter 5 examines if foraging area correlates with a turtle's body size. The hypotheses to be tested are that (1) body size is correlated with foraging strategy and that this be reflected in the isotopic ratios of turtle tissues; (2) turtles foraging in more pelagic habitats will be smaller and have lower δ^{13}C and δ^{15}N values than those foraging in neritic areas; (3) stable isotope analysis is an adequate tool to assign large-scale foraging areas to migrating sea turtles.

Chapter 6 provides a synthesis and conclusion from all the chapters. This chapter summarises the main findings in each of the content chapters and reviews some of the ecological and conservation implications it has for the management of the species. Lastly, we make general recommendations for future studies in the region and globally.

Chapter 2: The good and bad news of long-term monitoring: an increase in abundance but decreased body size suggests reduced potential fitness in nesting sea turtles

Chapter 2. The good and bad news of long-term monitoring: an increase in abundance but decreased body size suggests reduced potential fitness in nesting sea turtles

Abstract

Beach protection and monitoring has been used for about half a century as an effective sea turtle conservation strategy applied to multiple rookeries globally with successful population recovery. Loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) turtles nesting in South Africa have been continuously protected and monitored since 1963, representing one of the longest running sea turtle beach monitoring programs in the world (> 54 years). Evidence suggests that these previously harvested populations are growing as illustrated by increased numbers of nesting females and proportion of new recruits in the nesting cohort. A 35-year time series of consistently conducted nesting beach survey was used to assess trends in female sizes over time for both species. Despite increased nesting numbers, linear models indicated a significant 4.2 cm decrease in the size of both recruit and remigrant female loggerhead turtles but a small increase 3.3 cm in mean size of leatherback recruits. We hypothesize that these contradictory effects are attributable to the very distinct foraging ecologies of the two turtle species and speculate that these variation in carapace length may be driven by environmental change. Further research is needed to examine the impacts of a decreased female turtle size on reproductive outputs and overall population growth. The trends observed in this study emphasize the importance of long-term monitoring, examining not only abundance but also individual size, to understand population dynamics and support recovery planning and future conservation practices.

Introduction

Historical over-exploitation has severely depleted the majority of sea turtle populations worldwide, some still exhibiting declines as high as 30-80%, with current threats including fisheries bycatch, direct harvest, habitat loss, pollution and pathogens, and climate change (Mast et al., 2005; Bolten et al., 2010; Wallace et al., 2011). In many cases however, population declines have been reversed as a result of a variety of effective conservation measures such as beach protection programs, and protected areas, enabling successful population recovery around the world (Bjorndal et al., 1999; Hays, 2004; for a review see Mazaris et al., 2017). Despite protection and apparent increase in abundance, indirect pressures can still affect turtle populations and it is thus fundamental to evaluate the effectiveness of conservation measures and examine underlying trends.

Conservation of marine turtles is made difficult due to their wide geographical distribution spanning multiple jurisdictions and legislative systems with different conservation targets (Harris et al., 2015); a complex life cycle with changes in habitats and diet at different life stages (Davenport, 1997; Bolten, 2003; McClellan & Read, 2007); and variable reproductive outputs showing inter- and intra-population variations in growth, maturation, and nesting abundance and activity (Bjorndal et al., 2000; Snover, 2002; Marn et al., 2017a-b). Since marine turtles are long-lived and late maturing, long-term data are crucial in evaluating recovery potential due to the time lag effect of 20 to 40 years to attain sexual maturity in hard-shelled turtles (Casale et al., 2011; Piovano et al., 2011; Ehrhart et al., 2014).

Long-term time series data are critical in improving our knowledge by providing detailed abundance and size-class-specific demographic information (Balazs and Chaloupka, 2004; Stokes et al., 2014; Derville et al., 2015) and assessing population trends to ensure recovery and successful conservation measures (Bjorndal et al., 1999, 2010; Limpus, 2008). The South African component of the South Western Indian Ocean (SWIO) loggerhead and leatherback turtle rookeries are one of the few sea turtle populations that have been continuously monitored for the past 5 decades and so is suitable for assessing population and individual size trends. Both species have been protected through a combination of land-sea conservation measures of their breeding grounds in South Africa in the iSimangaliso Wetland Park. Turtles were first protected in 1916 by the Natal Ordinance, but efficient protection was only achieved

when the conservation and monitoring program was established in 1963 (McAllister et al., 1965). A quantitative study reviewing (comparing the nesting biology, reproductive output and initial nesting numbers; Nel et al., 2013) the long-term response to conservation of nesting turtles in South Africa showed that the loggerhead population is increasing exponentially with more than 1000 females nesting annually, while the leatherback population initially increased but then stabilized with only about 50 individuals (Thorson et al., 2012; Nel et al., 2013). Although the population has been growing there might be evidence that the individual size of nesting females has decreased over time (Tuček et al, 2014). A decrease in mean carapace size could be attributed to increasing numbers of first-time nesters (neophytes of smaller size) into the adult reproductive population, which is an indication of population growth (Hatase et al., 2002b; Richardson et al., 2006).

The present study thus aimed to assess trends in loggerhead and leatherback female size nesting in the South Africa during the 35-year period 1980-2015. Furthermore, based on the assumption that smaller turtles have smaller reproductive output and fitness (Bjorndal & Carr, 1989; Broderick et al., 2003; for a review see Van Buskirk & Crowder, 1994), we question whether both neophyte and remigrant sizes are decreasing and if that could affect current and future reproductive output and ultimately population growth, despite an apparent increasing population.

Methods

Study site

The study took place on the north-eastern coast of South Africa in iSimangaliso Wetland Park, Kwa-Zulu-Natal (Fig. 2.1). iSimangaliso - a World Heritage Site, Ramsar Site, and Site of International Importance for Sea Turtles under the Indian Ocean South East Asia (IOSEA) sea turtle agreement - comprises contiguous terrestrial and marine protected areas (MPAs). The beaches form the southernmost nesting grounds of loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles in the world (~27°S). The rookery is approximately 200 km long and supports nesting by *ca.* 1000 loggerhead females and <100 leatherback females each year (Nel et al. 2013). The majority of nests are laid in the northern section of the park, particularly for 5 km north of Bhanga Nek in the loggerhead nesting hotspot.

From 1965 to 1972, the survey area was 12.8 km long (index area) and was extended to 52.8 km in 1973 (monitoring area; see Nel et al., 2013 for details). The nesting season typically takes place from October to March, with peak nesting occurring in December-January for both species.

Figure 2.1: Location of the study area in the iSimangaliso Wetland Park in north-eastern South Africa indicating contiguous terrestrial reserves (hatched grey) and marine protected area (filled light grey). Turtle nesting is predominantly along the Maputaland coast; nest density is high at Bhanga Nek, and decays to the south, with low nest density at Manzengwenya and southwards. Major lakes are shown in white.

Data collection

All nesting data were collected by the provincial conservation authority Ezemvelo KZN Wildlife in accordance with their legislated conservation mandate. Standard beach survey procedures were followed (see Nel et al., 2013 for detailed description and history). Daily night patrols were conducted on foot and trained observers recorded the date, species, carapace size (straight carapace length: SCL_{min}: from anterior nuchal notch to posterior notch and curved carapace length, CCL, straight carapace width, SCW: widest points) with metal tree callipers or soft measuring tape, across-shore location of the nest, and tag numbers. When encountered for the first time, a turtle was double tagged with titanium tags at the proximal end of the front flippers, while the back flippers were used for leatherbacks following oviposition. Newly tagged females without tag scars were considered as neophytes/recruits, whereas females with tag scars or tags were considered as remigrants/experienced nesters.

Statistical analysis

The 54-year dataset comprises observations from mark-recapture methods for which marked individuals are not observed with equal probability on an annual basis, often violating the assumption of independence. Median size values were used for individuals that were measured several times during a season. The annual numbers of neophytes (first-time nesters) and remigrants (repeat nesters) were used to display the relative proportion of each category in the nesting population. A student t-test or Welch's approximate test (for unequal variances) were used to test if the neophyte and remigrant sizes were significantly different from each other for both species. The data were separated into remigrant and neophyte categories, and analyses were conducted from 1980 only and not 1965 due to high variability in the first 15 years of reporting size information. There was a change in monitoring method and reporting for loggerhead measurements only from 2014 onward and we thus decided not to include the data for the 2014 and 2015 nesting season.

A linear model was fitted to both the neophyte and remigrant data for each species to determine if new recruits and experienced nesters are getting smaller over time, using the 35-year dataset. It should be noted that the aim of this study was to assess trends over time and not to make predictions in the future. All data were checked to comply with the assumptions of normality and homoscedasticity using Shapiro-Wilk and

Levene tests respectively. Statistical analyses were performed in RStudio, version 3.3.1 (R Core Team, 2015) and all statistical conclusions were drawn with a significance value of α ≤ 0.05.

Results

The nesting trends (from 1965 to 2015) showed that loggerhead nesting numbers are increasing (Fig. 2.2a), while the leatherback is stable (Fig. 2.2b) and that both populations are dominated by neophyte nesters (Figure 2.3). The 35-year time series from 1980 to 2015 revealed that there were significant differences in carapace length between neophytes and remigrants for both loggerheads (t-test, t = -10.17, df = 9179, p < 0.0000; Fig. 2.4a) and leatherbacks (t = -3.99, df = 1010, p < 0.0000; Fig. 4b). Remigrant individuals were significantly bigger than neophytes for both loggerhead (mean SCL 858.8 mm neophyte versus 866.4 mm remigrant) and leatherback turtles (mean CCL 1608.2 mm neophyte versus 1623.7 mm remigrant).
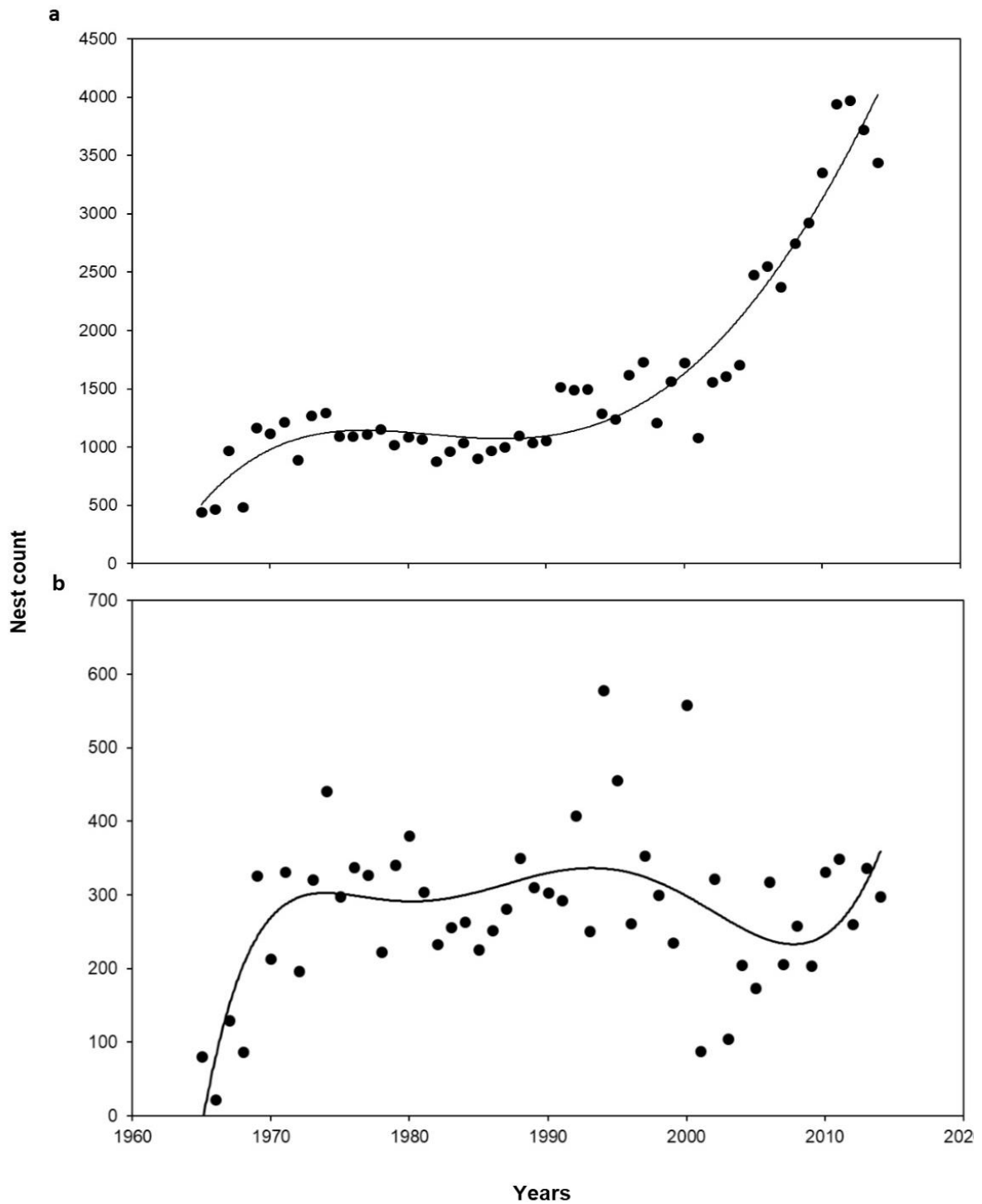
Figure 2.2: Nest counts of (a) loggerhead and (b) leatherback turtles nesting in South Africa for the monitoring area from 1965 to 2015. (Full and dotted lines represent 4th and 6th order polynomial fits respectively, for each population).
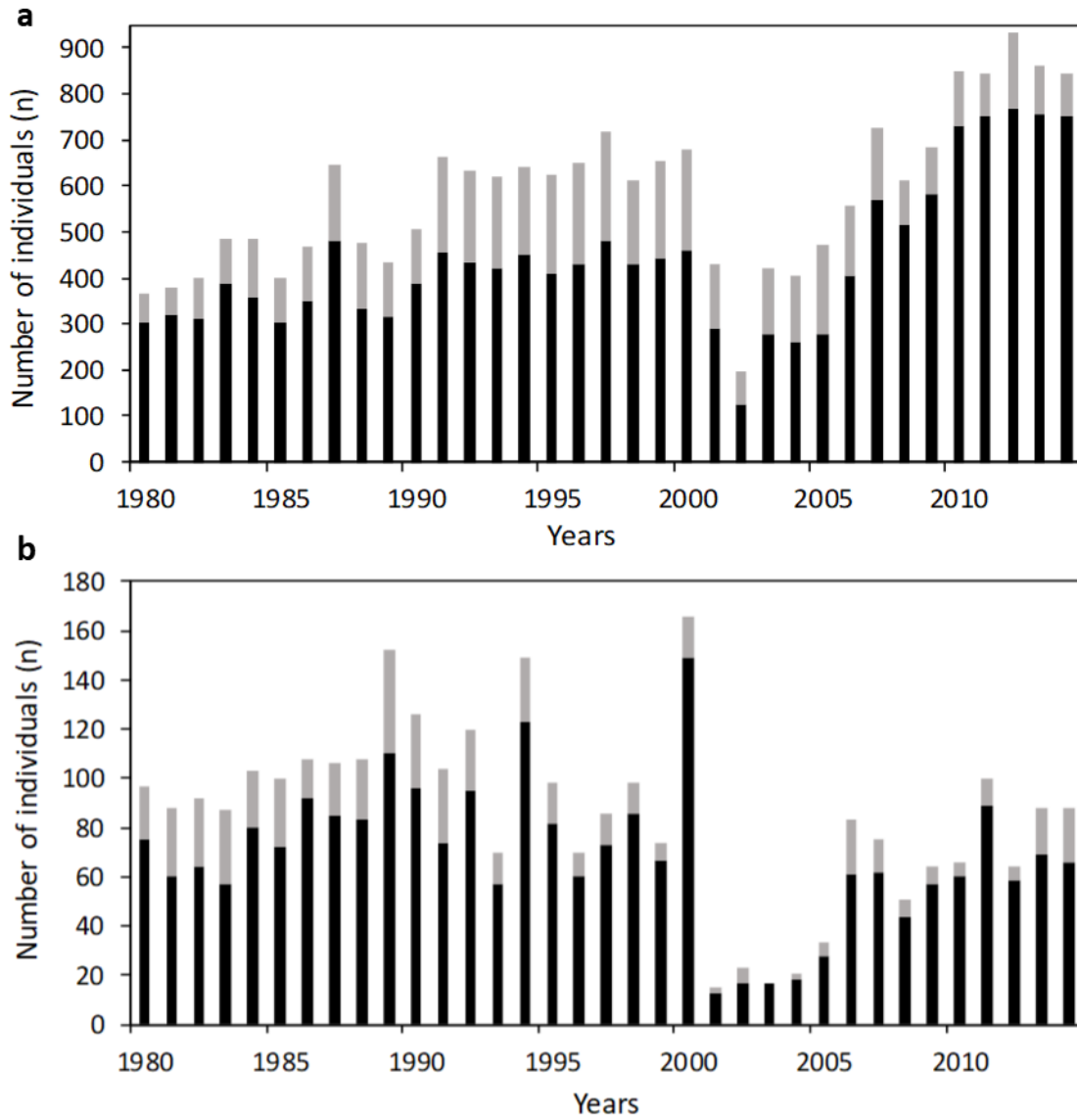
Figure 2.3: Abundance and composition of nesting (a) loggerhead and (b) leatherback turtles nesting in the South Africa and representing the proportion of neophyte (black) and remigrant (grey) nesters.
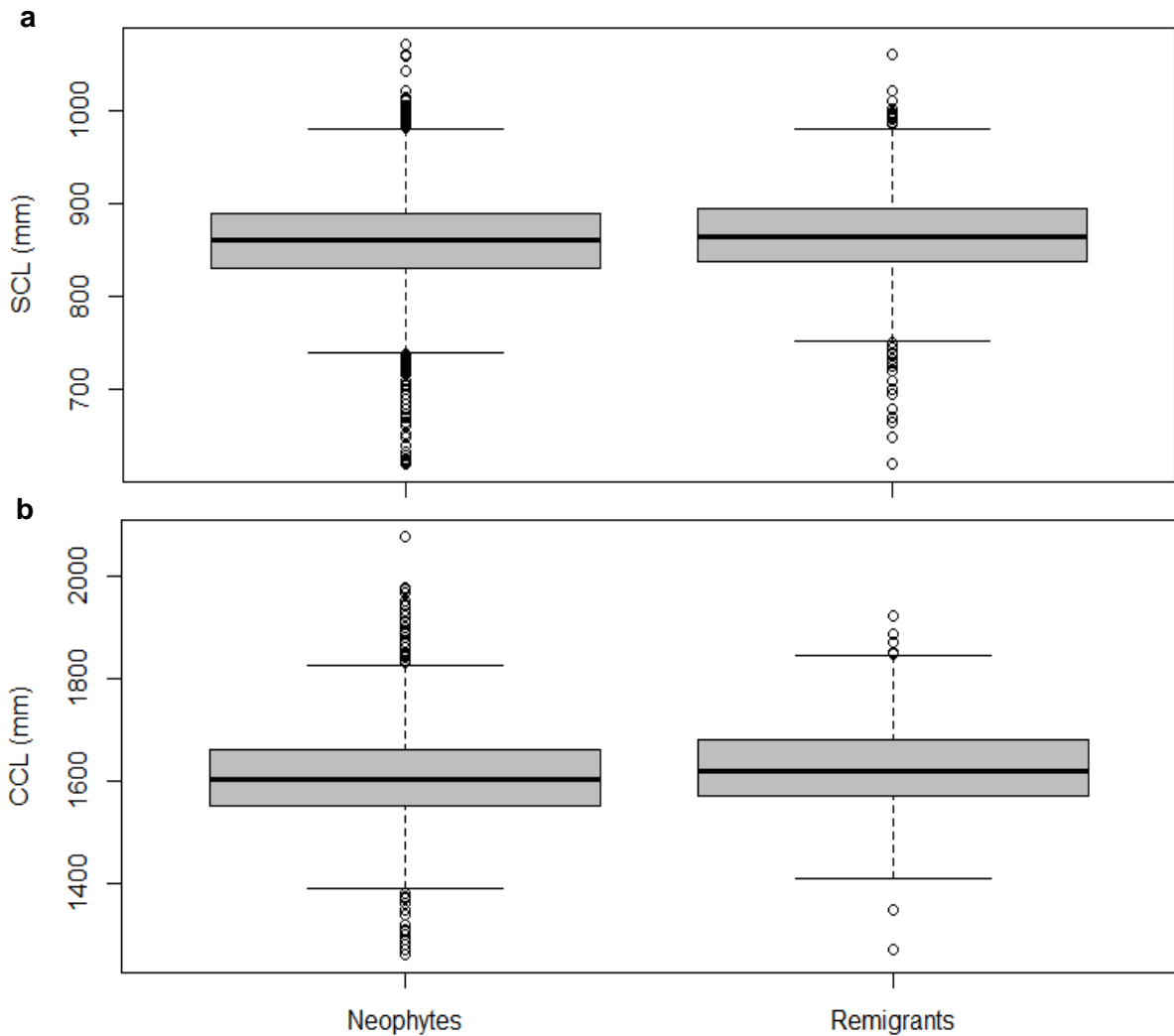
Figure 2.4: T-test of mean straight carapace length (SCL) of both neophytes and remigrants (a) loggerheads and (b) curved carapace length (CCL) of leatherbacks for the 1980-2015 period. Data are presented as medians (black lines), inter-quartile range (box), first and fourth quartiles (whiskers), and outliers (dots).

Loggerhead neophyte mean SCL ($\pm$ SD) varied from 871.0 $\pm$ 51.64 to 841.5 $\pm$ 47.60 mm (range 620-1070 mm, n = 13 966) from 1980 to 2013 (Fig. 5a), while remigrant size varied from 874.2 $\pm$ 54.11 to 849.3 $\pm$ 51.44 mm (range 620-1060 mm, n = 4 896; Fig. 2.5b). The linear model showed a significant -1.20 mm per year ($p < 0.0000$) decline in mean loggerhead neophyte, and a -1.19 mm ($p < 0.0000$) decline for remigrants, which equates to -42.0 mm and -41.65 mm respectively over the 35 years period (Fig. 2.6).

a

b
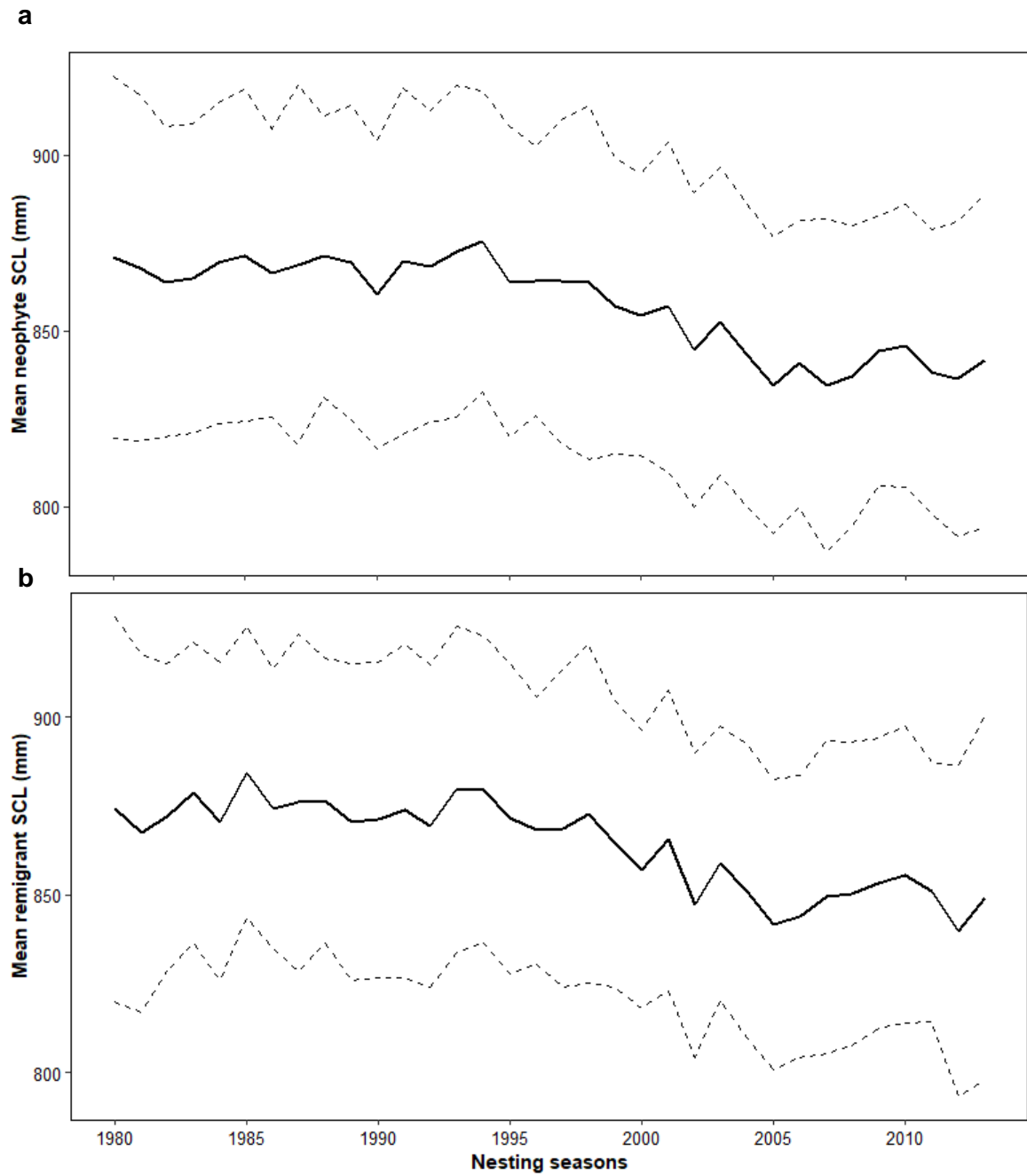
Figure 2.5: Mean straight carapace length (SCL; solid line, with SD; dashed lines) from 1980 to 2013 of (a) neophyte (n = 13966) and (b) remigrant (n = 4896) loggerhead females nesting in South Africa.
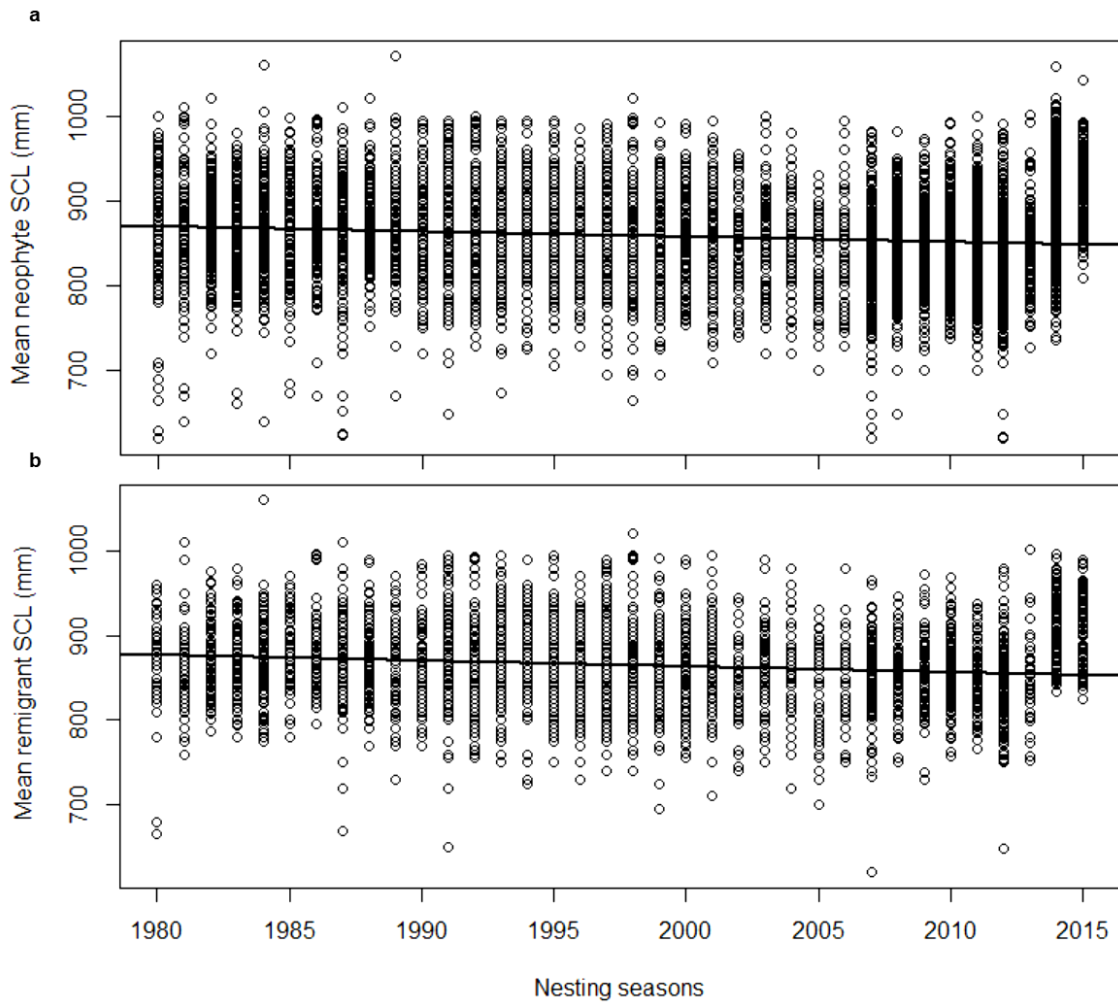
Figure 2.6: Linear regressions of both neophyte (a) and remigrant (b) loggerhead females nesting in South Africa from 1980 to 2013.

Mean curved carapace length (CCL ± SD) of leatherback neophyte varied from 1593.68 ± 75.01 to 1621.71 ± 84.02 mm (range 1260-2075 mm, n = 2428), while remigrant size varied from 1623.00 ± 67.54 to 1650.77 ± 96.12 (range 1270-1920 mm, n = 603), from 1980 to 2015 (Fig. 2.7). The linear model showed a small significant increase in mean CCL over time for both neophytes (0.48 mm per year, p = 0.0098), and remigrants (0.79 mm per year, p = 0.0152; Fig. 2.8).
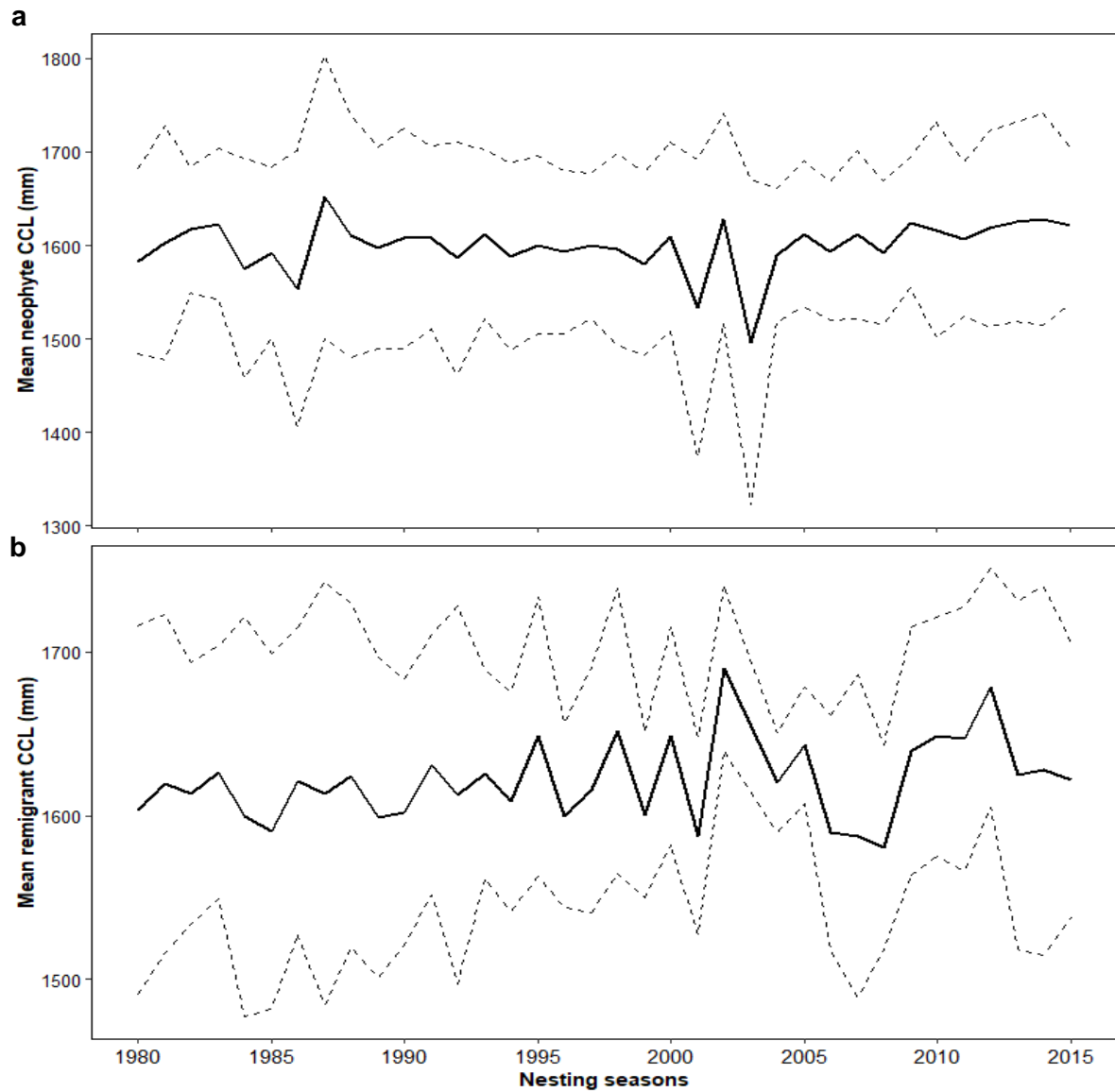
Figure 2.7: Mean curved carapace length (CCL; solid line, with SD; dashed lines) of (a) neophyte (n = 2466) and (b) remigrants (n = 723) leatherback females nesting in South Africa from 1980 to 2015.
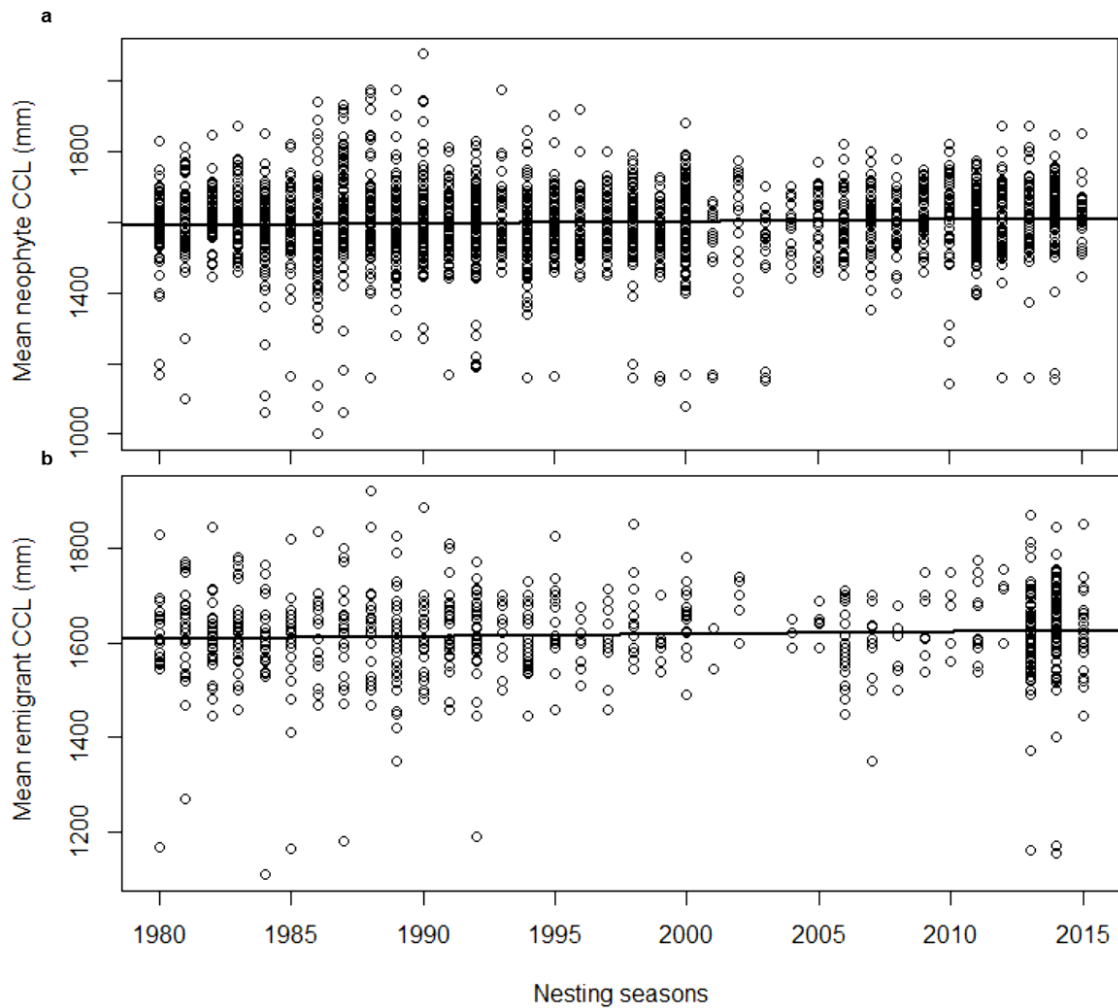
Figure 2.8: Linear model of both (a) neophyte and (b) remigrant leatherback females nesting in South Africa from 1980 to 2015.

Discussion

Female size over time

The study aimed to report on the relationships between sea turtle population size and individual size trends over time. The results showed that the South African component of the SWIO loggerhead nesting recruits have decreased in size by 4.2 cm over the past 35 year. Such a decline represents a significant change for a long-lived, slow-maturing species such as loggerhead turtles, especially considering growth rates declining with increased body size, and little or no growth following maturation (Witherington et al., 2006; Bjorndal et al., 2013; Avens et al., 2013). The opposite trend is however true for leatherback turtles with neophyte females increasing in size over time (3.3 cm). Theses contradictory trends observed for the two species might indicate

that the causes responsible for these changes in individual size are related to the different life histories of each species. Leatherback turtles are pelagic at all life stages, continuously swimming and foraging exclusively on gelatinous zooplankton in oceanic environments (James and Herman, 2001; Heaslip et al., 2012). Loggerheads on the other hand exhibit preference to foraging grounds in coastal areas (although evidence is showing that some individuals forage in pelagic areas), potentially indicating that the mechanisms responsible for the size decline in loggerheads operate in neritic habitats and may explain why leatherback turtles are not negatively affected.

Although the South African loggerhead nesting population is growing in numbers (Nel et al., 2013), a possible explanation for the decreasing trend in individual female body size could be partially supported by the recruitment of neophytes in the nesting cohort. A nesting population consists of recruits (neophytes) and remigrants (experienced nesters), and fluctuations in the percentages of each cohort may be used to infer potential causes for population or body size declines (Hatase et al., 2002b). Because sea turtles are long-lived, slow-growing and late-maturing, it is possible that the current exponential population growth is a direct result of the beach protection and monitoring program initiated in the early 1960s (Tuček, 2014). The higher abundance of neophytes compared to remigrants suggests that recruitment is taking place and that neophytes are entering the breeding cohort (Hatase et al., 2002b; Richardson et al., 2006; Piacenza et al., 2016). However, as both neophyte and remigrant loggerhead females are getting smaller, this explanation is not sufficient to elucidate the trends observed in this study. The same is true for leatherbacks since the population is dominated by neophytes that are increasing in size but not remigrants and that the population is stable and not increasing, indicating that pressures outside the nesting grounds and MPA are affecting experienced nesters.

High offshore mortality of breeding adults as a result of fisheries bycatch is recognized as a major threat to sea turtles worldwide (Limpus and Limpus, 2003; Bourjea et al., 2008; Alfaro Shigueto et a., 2008; Wallace et al., 2008; Bolten et al., 2010; Roe et al., 2014; Rees et al., 2016), and could be a another potential explanation to the decline in body size of loggerheads and the lack of population growth of leatherback turtles in South Africa. Incidental capture in fisheries has been suggested as the possible cause responsible for the decrease in loggerhead nesting numbers in Japan (Hatase et al., 2002b). Moreover, assessments are hindered by a lack of reliable information and

poor reporting (Finkbeiner et al., 2011). This is especially true in the Western Indian Ocean (WIO) where fishery-related sea turtle mortality data are limited due to the illegal, unreported, and unregulated fisheries and socio-economic complexities of the region (Bourjea et al., 2008; De Wet, 2012; Wallace et al., 2013). The lack of population expansion and increase in size of neophytes only for leatherbacks could be explained by fisheries effects but more data are needed to elucidate this potential mechanism. In the case of loggerheads however, our results do not support the potential explanation that the decline in individual size is due to fisheries impact as we would expect a similar decline in population size, but our nesting loggerhead numbers are increasing.

Similar declining trends in female sizes have been detected for loggerheads in Turkey (Ilgaz et al., 2007), olive ridleys in India (Shanker et al., 2003), green turtles in Hawaii (Piacenza et al., 2016), and hawksbill turtles in Mexico (Perez-Castaneda et al., 2007), and were potentially attributed to anthropogenic causes. Changing environmental conditions and anthropogenic threats have been proposed as the main driver of fluctuations in annual abundance of nesting sea turtles (Limpus & Nicholls, 2000; Chaloupka, 2001, et al., 2008; Van Houtan & Halley, 2011; Saba et al., 2012; Roe et al., 2014; Ascani et al., 2016). Recent research is showing that lower ocean productivity due to environmental change is negatively affecting green turtle growth rates and causing a regime shift in the western Atlantic (Piovano et al., 2011; Bjorndal et al., 2017).

Global climate change, in addition to strongly affecting nesting habitats, the timing of reproduction (Hawkes et al., 2009), incubation conditions and sex ratios (Witt et al., 2010; Laloë et al., 2017), and spatial distribution of marine turtles (Pike, 2013), will also affect temperature and food availability at foraging grounds (Chaloupka et al., 2008; Poloczanska et al., 2009; van Houtan & Halley, 2011). Our understanding of the impacts of climate change on the world's marine ecosystems is still rudimentary but there is strong evidence showing that the annual primary production of the world's oceans has decreased by at least 6% since the early 1980s, with large relative decrease occurring within Pacific and Indian ocean gyres (Gregg et al., 2003; Polovina et al., 2008; Boyce et al., 2010; Hoegh-Guldberg & Bruno, 2010; Currie et al., 2013). Furthermore, large-scale ocean-atmosphere anomalies such as El Nino-Southern Oscillation (ENSO) are important drivers of variation in climate and ecosystem

productivity in tropical regions, affecting primary and secondary production due to an increase in ocean temperature, increased stratification of the water column and changes in the intensity and timing of upwelling events (Rasmusson & Wallace, 1983).

Environmental conditions at the foraging grounds have been shown to affect sea turtle nesting numbers (although it might be more difficult to prove for carnivorous or pelagic species due to a potentially longer lag effect). For example, the number of green turtles nesting at two Australian rookeries has been significantly correlated with ENSO indices, with decreasing trends two years following ENSO events (Limpus & Nicholls, 1988; Limpus & Nicholls, 2000). Similarly, it has been suggested that annual nesting variability at Southeast Asian rookeries is due to a delayed female breeding response to El Niño events for green turtles (Allan, 1988; Lough, 1994; Chaloupka, 2001; Bjorndal et al., 2017), as well as leatherback turtles in the Eastern Pacific (Saba et al., 2007). Likewise, ecological regime shift due to the synergistic effect of a strong ENSO and the intensification of warming rate over the last two-three decades is resulting in decreased growth rates of green turtles in the West Atlantic (Bjorndal et al., 2017). Thus, as sea turtles are capital breeders and do not feed during reproduction and migration, the ecological conditions at the foraging areas will heavily influence turtle reproduction.

The contrasting results found in this study regarding the small increase in size of neophyte leatherback turtles is interesting and provides further support to our hypothesis of changing ocean conditions due to anthropogenic effects. However, in the case of leatherback turtles it appears to be a beneficial effect due to their diet consisting exclusively of gelatinous zooplankton (Heaslip et al., 2012). Evidence is showing that jellyfish populations are rising dramatically worldwide as a result of climate change and overfishing creating a regime shift in oceans (Lynam et al., 2006; Purcell et al., 2007; Richardson et al., 2009; Hays et al., 2018). This apparent explosion in jellyfish abundance could explain why neophyte leatherback turtles are getting bigger if young recruits are foraging in areas where their main food sources are plentiful and sustains higher growth.

Comparing population status and body size trends of several sea turtle species globally (Table 2.1), we can see that the decrease in individual size is not restricted to one oceanic region or species but is a global issue. Furthermore, it is concerning that

population that are decreasing as well as recovering/increasing are experiencing a decline in the size of nesting females. This suggests that the decline in size is not restricted to populations that are decreasing or under threat but also to growing populations that are similarly at risk of producing smaller individuals.

Even though conservation is successful in protecting adults and young adults, it might not be enough if individuals are impacted by lower ocean productivity that affects their growth and ultimately generates smaller adults. Are marine organisms getting smaller as a consequence of climate change and lower ocean productivity? Many taxa and species already exhibit smaller sizes as a result of climate change including invertebrates (Jokiel et al., 2008; Daufresne et al., 2009), plants (Barber et al., 2000), fish (Todd et al., 2008) terrestrial ectotherms (Reading, 2007), birds (Yom-Tov and Yom-Tov, 2006, Gardner et al., 2009), mammals (Post et al., 1997; Ozgul et al., 2009), and a continued decrease in organism size is expected to negatively affect ecological interactions and ecosystem services (Kuparinen and Merilä, 2007; Sheridan & Bickford, 2011).

Table 2.1: Comparison of population trends for several populations for which sea turtle species are decreasing in size. (Numbers in brackets for the time frame indicate the total number of years).

Species	Population trend	Carapace size	Time frame (yrs)	Country	Reference
Olive ridley	Declining	Decreasing	1978-2002 (24)	India	Shanker et al. 2003
Green	Increasing	Decreasing	1973-2010 (37)	USA	Piacenza et al. 2016
Hawksbill	Increasing	Decreasing	1995-2001 (6)	Mexico	Pérez-Casteñada et al. 2007
Loggerhead	Declining	Decreasing	1993-2004 (10)	Turkey	Ilgaz et al. 2007
Loggerhead	Increasing	Decreasing	1980-2013 (33)	South Africa	This study
Leatherback	Stable	Increasing	1980-2015 (35)	South Africa	This study

Potential implications for reproductive output

Growth rate is directly correlated with food availability for sea turtles, suggesting that a reduction in food in foraging areas (due to lower ocean productivity) will result in lower growth and body size (Tiwari & Bjorndal 2000; Marn et al., 2017b, 2018). However, since body size is also directly correlated to reproductive output in sea turtles, smaller females may have lower reproductive potential (Hays & Speakman, 1991; Hays et al., 1993; Van Buskirk & Crowder, 1994; Hawkes et al., 2005; Leblanc et al., 2014) and produce smaller offspring with lower fitness and survivorship.

Reproduction is energetically demanding for all species but more challenging for capital breeders; marine turtles do not feed during the breeding season and rely on energy acquired on the foraging grounds. Thus, a better fed mother may produce more or larger offspring (Kooijman, 2009). Evidence is showing that smaller hatchlings have lower fitness-related attributes, according to the "bigger is better" hypothesis, stating that being larger confers a survival advantage (Packard & Packard, 1988). Having shorter limbs, smaller hatchlings take longer to crawl down the beach and are more vulnerable to predation on land as well as in the shallow reef waters where predators are gape limited (Gyuris, 2000). Studies are demonstrating that larger hatchlings have higher crawling and swimming abilities and growth rates (Booth et al., 2004; Ischer et al., 2009; Sim et al., 2015), implying greater survival probability. Consequently, given that clutch size or egg size is positively correlated with female size in sea turtles, one could argue that smaller females may produce smaller hatchlings of lower fitness, which ultimately might have reduced survival probability during the post-hatchling migration. Alternatively, smaller females may produce fewer eggs which in turn might affect overall population growth.

As sea turtles do not exhibit parental care, maternal investment in an offspring is closely represented by the energy content (quality and quantity of yolk) in each egg (Shine, 1988), signifying that the amount of energy reserves left after embryonic development will determine how long a hatchling can survive before it needs to start feeding. Additionally, the energetic cost of escaping the nest decreases as the number of individuals in the cohort increases resulting in larger residual yolk reserve on emergence (Rusli et al., 2016). Hatchlings from larger clutches thus have higher survival. Consequently, smaller females may have smaller clutches of smaller eggs, producing hatchlings that will spend more energy escaping the nest which in turn will

result in decreased yolk reserve available to them and ultimately potentially lower survival.

Conservation Implications

The 35-year dataset demonstrated that long-term monitoring (with size and nesting number data) is critical for assessing population trends over time and investigating the effectiveness of conservation measures (Piovano et al., 2011; Bjorndal et al., 2017; Mazaris et al., 2017). The findings of the present study are interesting in that they represent two contrasting trends, with loggerhead turtles showing a decline in body size while leatherbacks are increasing. Although the South African component of the SWIO nesting loggerhead turtles are a conservation success story and the population is growing (Nel et al., 2013), the study revealed that both neophyte and remigrant females have decreased in size by 3 to 4 cm over the past 35 years, whereas leatherbacks have increased in size for neophytes by 3.3 cm and remained stable for remigrants. Thus, despite 54 years of conservation efforts the decline in mean individual size of both neophytes and remigrants indicates that only individuals in good condition, but also smaller, successfully reach the nesting grounds for loggerheads. This could suggest that South African loggerhead turtles may be responding to an environment with limited resources by maturing sooner and diverting energy from growth and maintenance to reproduction (Marn et al., 2017a, 2018). In the case of leatherbacks however, since only neophytes are increasing in individual size, we speculate that pressures on larger individuals outside the nesting grounds are responsible for the trends observed in this study. What is worrying is that to our knowledge, this is the first study to report that turtle female size is declining irrespective of whether the population is decreasing or increasing and shows that protecting females on nesting grounds is not enough to guarantee population growth if survival is not ensured at subsequent life stages at sea (Crouse et al., 1987; Crowder et al., 1994; Chaloupka & Limpus, 2001; Bjorndal et al., 2005; Margaritoulis, 2005; Mazaris et al., 2006). This has implications for management, since we do not yet know what the consequences of smaller individual size are on fitness and survival abilities of such long-lived organisms such as sea turtles. In the future, our results could be compared to other recovering populations of loggerhead turtles to determine if this size decline is a general trend. Further research is needed to understand the mechanisms

responsible for the decrease in loggerhead female size and determine if it can affect reproductive output and overall population growth. This research emphasizes the findings of Nel et al (2013) that coastal marine protected areas do work but do not guarantee the recovery of sea turtle population as pressures change over time highlighting the need for integrated management strategies and continued monitoring.

Chapter 3: Is bigger better? The influence of size on adult reproductive output and hatchling fitness traits in sea turtles

Chapter 3: Is bigger better? The influence of size on adult reproductive output and hatchling fitness traits in sea turtles

Abstract

Fitness theory attempts to explain how organisms survive by understanding not survival as such but the design that confers the highest survival. This study investigated the effects of phenotypic variation on the reproductive strategy (clutch and egg size) of loggerhead and leatherback sea turtles as well as the influence of size on hatchling fitness traits. We examined whether larger females produced larger hatchlings of higher fitness by testing two theories; the optimal egg size theory, and the bigger is better hypothesis. The study investigated how maternal length influences reproductive output (clutch size, egg size), and how hatchling morphology affects their performance. Hatchling performance was analysed by measuring two correlates of fitness, crawling and swimming speeds, as these two traits positively influence their survival by minimising the time of exposure in highly predated areas. The reproductive strategy of both loggerhead and leatherback turtles nesting in South Africa was found to support the optimal egg size theory whereby larger turtles produce larger clutches but not larger eggs. Egg size was constant irrespective of maternal length. Hatchling fitness assessment trials demonstrated that hatchlings with longer carapaces and flippers lengths swam faster. This adds to the growing body of evidence suggesting that larger hatchlings are more likely to survive because they spend less time in high predation risks areas (i.e. beach and nearshore) and thus assumed fitter than smaller ones. These findings have implications for overall population growth/recovery if smaller hatchlings of lower fitness are produced and have decreased dispersal abilities and thus likelihood of survival.

Keywords: reproductive strategy; maternal length; sea turtles; hatchling performance; fitness traits; crawling and swimming speed

Introduction

Life history theory attempts to explain how organisms survive and reproduce as well as how energy is allocated between growth, maintenance, and reproduction (Stearns, 2000). Life history theory is further based on the concept that fitness is a measurable feature (traits, genotypes) of individuals that predict their numerical representation in future generations (Hunt and Hodgson, 2010). As the energy available to an organism is finite, fecundity is set at some optimal (trade-off) level where the maternal investment per individual offspring is limited but the number of offspring produced maximised so that the lifetime reproductive output of the parent be maximal (Williams, 1966; Charnov and Krebs, 1974). The Optimal Egg Size theory (OES) states that as the energy expended on individual offspring increases, the fitness of individuals increases and that an increase in maternal investment per individual would result in a decreasing number of offspring that can be produced (Smith and Fretwell, 1974). The OES theory assumes that the probability of offspring survival increases with size and leading to a trade-off between offspring size and number. With selection acting to optimise offspring size, OES predicts that variation in reproductive investment should be determined by offspring number rather than size (Smith & Fretwell, 1974; Condon and Gibbons, 1987; Wilkinson and Gibbons, 2005). In the current context where organisms may be getting smaller due to global change (Sheridan and Brickford, 2011), research should investigate the consequences of smaller adult female size on reproductive outputs and offspring fitness.

Marine turtles have limited parental care of their eggs and maternal investment (other than digging a nest) in an offspring is thus closely represented by the number or size of eggs (Shine, 1988). Due to the energetic costs of reproduction (migration and laying several clutches per nesting season), sea turtles are non-annual breeders and exhibit the highest reproductive output among oviparous reptiles, laying 2 to 5 clutches of 50 to 150 eggs in most species, every 2 to 4 years (Miller, 1997), although it has been recognised that research efforts might underestimate female annual nest output (Tucker et al., 2018). Sea turtles evolved this reproductive strategy (laying many small eggs in several clutches) in response to high mortality during the egg and hatching phases, thus effectively avoiding allocating high quantity resources to any single offspring (Van Buskirk and Crowder, 1994). Numerous studies have found a positive relationship between female body size and clutch size in loggerheads (Frazer &

Richardson, 1986; Hays & Speakman, 1991; Broderick et al., 2003; LeBlanc et al., 2014), green turtles (Bjorndal & Carr, 1989; Hays et al., 1993; Johnson & Ehrhart, 1996), and leatherback turtles (Wallace et al., 2007; also see a review of all sea turtle species by Van Buskirk & Crowder, 1994), which adds support to the OES theory. Consequently, it appears that egg size is (more or less) constant within species, irrespective of maternal length/size, which suggests that female sea turtles optimise their fitness by producing larger clutches. Recent evidence also shows that there is benefit to hatchlings; energetic cost of emergence (escaping the nest) decreases as clutch size increases because of synchronous collective digging (Carr and Hirth, 1961; Gyuris, 1993; Rusli et al., 2016).

Sea turtle hatchlings do not have obvious predator avoidance or defence mechanisms and subsequently suffer high levels of mortality, both on land while crawling down the beach and at sea while swimming over shallow reefs (Gyuris, 1994; Salmon and Scholl, 2014). Hatchling survival probability is thus a direct function of the duration they spend in predator-rich habitats which in turn is dependent on hatchling's locomotor speed and growth rate. Further, many predators are gape-limited (Rice et al., 1993), so vulnerability to predators is therefore often size-dependent, suggesting that selection should favour larger individual and rapid early growth to reduce predation risks (Davenport and Scott, 1993; Urban, 2007). This has implications for offspring fitness and survival as "bigger is better" (Packard and Packard, 1988), and larger hatchlings should have superior locomotor abilities (longer limbs and greater stride) and escape high predator risks areas faster resulting in higher survival. Recent evidence supports this hypothesis and found that larger turtle hatchlings have higher swimming activity, speed (Janzen, 1993; Ischer et al., 2009; Sim et al., 2015), and growth rates (Stokes et al., 2006). We would thus expect intra- and interspecific differences to exist favouring larger animals. Locomotor performance in leatherback hatchlings, which are bigger, are expected to be faster than other species. However, a comparative study revealed that the larger leatherback hatchlings were slower than smaller green or loggerhead hatchlings (Wyneken et al., 1997). Also, smaller hatchlings have higher residual yolk reserves and could survive longer without feeding (Ischer et al., 2009). Consequently, hatchling fitness and survival is also a trade-off between size-specific predation pressure at the rookery and food availability in the post-hatch environment (Ischer et al., 2009; Kobayashi et al., 2018).

As sea turtle reproductive output is correlated with female size with evidence showing that in some populations individual female size is decreasing (Le Gouvello et al., in review), this study examined the relationship between maternal length and hatchling fitness. We investigated the effects of maternal body size on reproductive outputs and hatchling fitness for loggerhead and leatherback sea turtle hatchlings on South African nesting beaches. Since sea turtle hatchling locomotor performance directly affects their survival during the early life stages, crawling and swimming speed were used as proxies of hatchling fitness. We hypothesise that: (1) there is a positive correlation between maternal body size and clutch size but not egg size and larger female produce larger clutches; (2) larger hatchlings will have faster locomotor performance and thus have increased fitness than smaller ones.

Materials and Methods

Ethics Statement

Hatchling trials were undertaken with ethical clearance from the Nelson Mandela Metropolitan University Animal Ethics Committee: A16-SCI-ZOO-014, and hatchling collection was allowed with permission from the iSimangaliso Wetland Park Authority, Ezemvelo KwaZulu-Natal Wildlife, and Department of Environmental Affairs: Oceans and Coasts (permit numbers: RES2016/67, RES2017/73, & RES 2018/68).

Study Site

The study took place on the north-eastern coast of South Africa in iSimangaliso Wetland Park, Kwa-Zulu-Natal. iSimangaliso - a World Heritage Site, Ramsar Site, and Site of International Importance for Sea Turtles under the Indian Ocean South East Asia (IOSEA) sea turtle agreement - comprises contiguous terrestrial and marine protected areas (Fig. 3.1). The beaches form the southernmost nesting grounds of loggerhead (*Caretta caretta, Cc*) and leatherback (*Dermochelys coriacea, Dc*) sea turtles in the world (~27°S). The rookery is approximately 200 km long and supports nesting by ca. 1000 loggerhead females and <100 leatherback females each year (Nel et al. 2013). The majority of nests are laid in the northern section of the park, particularly for 5 km north of Bhanga Nek in the loggerhead nesting hotspot. From 1965 to 1972, the survey area was 12.8 km long (index area) and was extended to

52.8 km in 1973 (monitoring area; see Nel et al., 2013 for details). The nesting season typically takes place from October to March, with peak nesting occurring in December-January for both species.

Figure 3.1: Location of the study area in the iSimangaliso Wetland Park in north-eastern South Africa indicating contiguous terrestrial reserves (hatched grey) and marine protected areas (filled light grey). Turtle nesting is predominantly along the Maputaland coast; nest density is high at Bhanga Nek, and decays to the south, with low nest density at Manzengwenya and southwards. Major lakes are shown in white.

Data collection

Standard beach survey procedures were followed (see Nel et al., 2013 for a detailed description and history) during nine nesting seasons, between 2010 and 2018. Nightly patrols were conducted on foot and trained observers recorded the date, species, carapace size (to the nearest 1 mm), straight carapace length and width (SCL_{min}: straight carapace length from anterior nuchal notch to posterior notch, and SCW with metal tree callipers) and curved carapace length and width (CCL, curved carapace width, and CCW: widest points with a tape measure), clutch size (total number of eggs including deformed eggs but excluding spacers since they are not fertilized eggs) and frequency (during oviposition), and egg size (length and width, 10 eggs per clutch, measured with metal vernier callipers to the nearest 0.1 mm), across-shore location of the nest, and flipper tag numbers. When encountered for the first time/season, a turtle was double-tagged with titanium tags, at the proximal end of the front flippers, and leatherbacks on the back flippers, following oviposition. Newly-tagged females without tag scars, were considered first-time nesters or neophytes/recruits for that season, whereas females with tag scars or tags from a previous season were considered remigrants/experienced nesters. Clutch volume (CVol) was estimated as the product of egg size (eggs were assumed to be spherical) and clutch size (SAGs or shelled albumen gobs, which are albumen "production over-run" were not included in the total count; Wallace et al., 2004, 2007). In total 265 (2010 = 89, 2012 = 17, 2015 = 5, 2016 = 70, 2017 = 65, 2018 = 19) loggerhead and 24 leatherback (2010 = 4, 2012 = 4, 2014 = 1, 2016 = 5, 2017 = 10) sea turtles were sampled.

Hatchling crawling and swimming trials

In situ field experiments were conducted at night after monitoring marked nests throughout the incubation period. Hatchlings used for the experiments were collected from marked nests, to relate to female size, or selected opportunistically from random nests at Bhanga Nek (high loggerhead nest density beach; 26˚53'40.17"S; 32˚52'50.31"E) and Manzengwenya (high leatherback nest density beach; 27°26'72.6"S; 32°77'28.0"E). Following hatching, a subset of 25 hatchlings per nest (when possible) was randomly selected, brushed free of sand and used for swimming trials to investigate the effect of size on hatchling swimming ability. Hatchling crawling trials were conducted in a 2 m raceway made from PVC roof guttering partially filled

with beach sand, painted black (Fig. 3.2a), and oriented perpendicularly across the beach, towards the seas. Hatchling swimming trials were conducted in a 2 m raceway from modified PVC irrigation pipe (12 cm high, 15 cm wide; Fig. 3.2b), filled with fresh seawater (approximately 28°C), and also oriented perpendicularly across the beach. Each hatchling was placed at the landward end and a dim light was placed at the seaward end of the raceways to ensure directional movement. Each hatchling was timed crawling and swimming along the gutter with a stopwatch and the value converted to cm.s^{-1}. Immediately after the crawling trial, hatchlings started the swim test, simulating natural progression in the wild after hatchlings emerge from the nests and crawl down the beach to reach the sea. The swim test was repeated 3 times for 3 hatchlings per nests, to determine swimming performance. Standard morphometric measurements were taken for each hatchling (using metal vernier callipers, accurate to 0.1 mm) once all trials were terminated and included: the straight carapace length (SCL) and width (SCW), front flipper length (FFL) and width (FFW), back flipper length (BFL) and width (BFW; Fig. 3.3), and body mass (using a digital scale, accurate to the nearest 0.01 g). Shell height was measured as the length between the first ventral spine and the plastron. The size index (SCL x SCW, mm^2), as well as front flipper area (FFL x FFW, mm^2) and back flipper area (BFL x BFW, mm^2) were calculated. We sampled 287 hatchlings in 2016 (*Cc* = 263 from 11 nests, *Dc* = 24 from 1 nest), 425 in 2017 (*Cc* = 376 from 17 nests, *Dc* = 49 from 2 nests), and 33 in 2018 (*Cc* = 33 from 5 nests, *Dc* = 0). A total of 746 hatchlings were sampled over the three nesting seasons (*Cc* = 672, *Dc* = 73). The strong difference in the number of hatchlings sampled per species every year reflects the very low abundance and dispersed nature of leatherback turtles in the South African rookery.
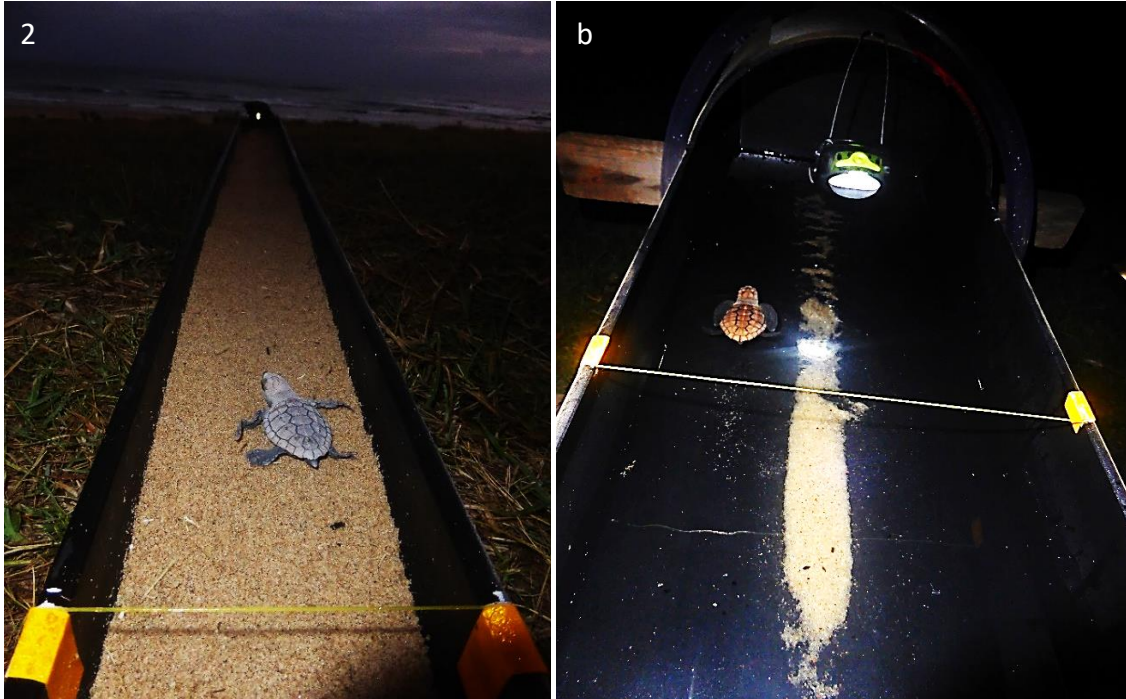
Figure 3.2: Illustration of the crawling (a) and swimming (b) raceways used to measure the locomotor performance of loggerhead and leatherback hatchlings in the field.

Hatchling growth rate

Fifty loggerhead hatchlings were collected from three different clutches on the beach at Bhanga Nek during the 2016 nesting season. All hatchlings were reared in captivity at the Bayworld Aquarium in Port Elizabeth for a period of 4 months. Hatchlings were kept in flow-through tanks supplied with inhouse filtered recirculated aquarium water) with water temperature maintained at 28°C using an aquarium heater and matched the seawater temperature in the study area during the hatching period. Hatchlings were divided into 8 tanks (90 cm length, 60 cm width, 40 cm height) and fed 9-11% of their body weight daily using a formulated diet that included a protein source (minced fish) imbedded in gelatine cubes and supplemented with reptile vitamins and minerals twice daily. Each hatchling was marked with non-toxic nail polish for identification and weighed using an electronic scale (to the nearest 0.1 g). Hatchling morphometric measurements and photographs were repeated every 10 days to assess the growth rate. No leatherback hatchlings were reared in captivity due to their critically endangered status in the region and their challenging survival in captivity.
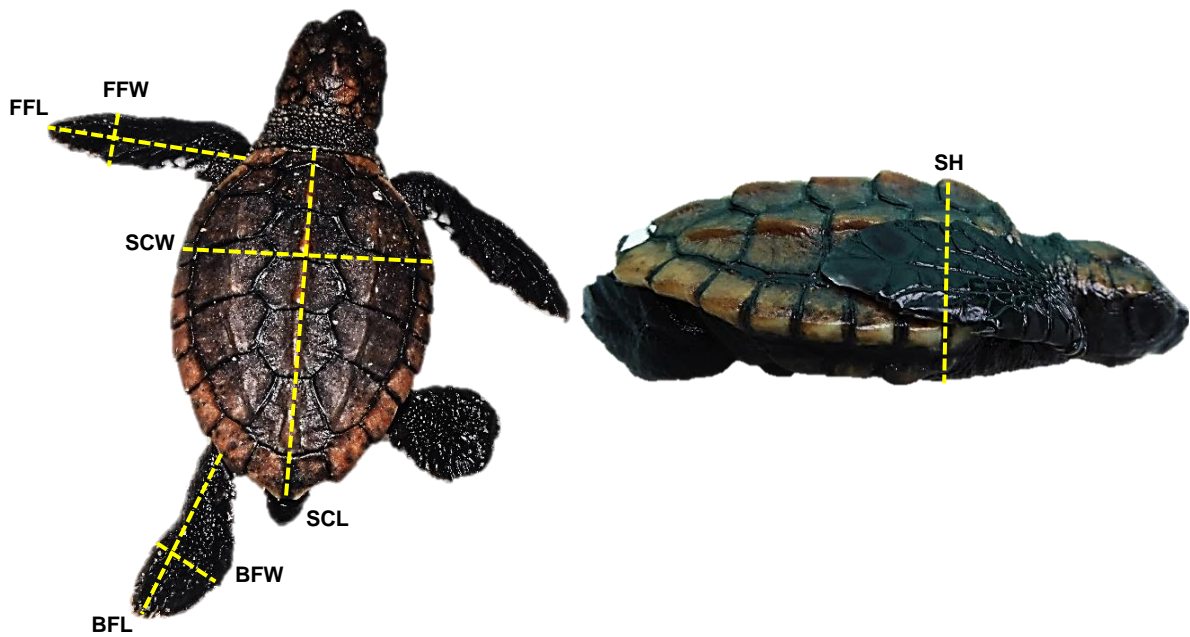
Figure 3.3: Photograph of a loggerhead hatchling illustrating standard morphometric measurements. Straight carapace length (SCL) and width (SCW), front flipper length (FFL) and width (FFW), back flipper length (BFL) and width (BFW), shell height (SH).

Statistical analysis

Linear regressions and generalized linear model (GLM) were used to investigate the relationships between maternal length and its effect on reproductive outputs (clutch size and egg size). The GLM evaluated the effects of maternal length on clutch size (1) and egg size (2). Analysis of variance (ANOVA) was used to test whether hatchling attributes have a significant effect on their locomotor performance. In the analysis hatchling attributes (body mass, carapace size, shell height, flipper size) were the factors and crawling and swimming speed the response variables. A linear mix effect model (LME, package lmer in R, Kuznetsova et al., 2017) was used to investigate if hatchling swimming speed improved with time. The use of LME has proven to be more robust than repeated measure ANOVA that may lead to erroneous results if assumptions are violated (Kristensen and Hansen, 2004; Jaeger, 2008). Linear regressions were used to assess hatchling growth rates and the relationships between hatchling morphometrics. All data were checked to comply with the assumptions of normality and homoscedasticity using Shapiro-Wilk and Levene's tests respectively. Statistical analyses were performed in RStudio, version 3.3.1 (R Core Team, 2017), and all statistical conclusions were drawn with a significance value of $\alpha \leq 0.05$.

Results

Female reproductive output

Loggerhead female straight carapace length (SCL ± SD) was on average 835.4 ± 39.31 mm (range 713 to 973 mm, n = 265), and were found to lay a mean clutch size of 110.0 ± 19.73 (range 47-171, n = 265), with a mean egg diameter of 39.9 ± 1.44 (range 33.6-43.3 mm, n = 265), and a mean clutch volume of 4529.9 ± 769.73 (range 2769.2-7661.1 cm^3, n = 265; Table 3.1, Fig. 3.4). The linear model indicated that larger loggerhead females laid larger clutches, with a significant relationship between clutch size and female size ($F_{1,263}$ = 60, R^2 = 0.18, p < 0.001; Fig. 3.5), whereas only 0.03% of the variation in egg size was explained by carapace length ($F_{1,263}$ = 10.4, R^2 = 0.034, p = 0.0014). The first GLM (Clutch size ~ SCL * Egg size) confirmed this result and indicated that 21.9% of the variability in clutch size was explained by maternal size only (significant positive relation, t = 2.34, p = 0.020) with egg size having a non-significant relation (t = 1.9, p = 0.055). The second model (egg size ~ SCL * Clutch size) showed that egg size is not affected by maternal length (0.67%, p = 0.055) or clutch size (p = 0.318).

Table 3.1: Summary data used in this study for loggerhead and leatherback turtles morphological and reproductive outputs parameters measured in South Africa. (SCL = straight carapace length: CCL = curved carapace length: CS = clutch size: ES = egg diameter: CVol = clutch volume: na = not applicable). For each parameter, the mean (± SD), sample size (*n*), and the range are provided.

Parameter	Loggerhead Mean ± SE (*n*), range	Leatherback Mean ± SE (*n*), range
SCL (mm)	835.4 ± 39.31 (265), 713 - 973	na
CCL (mm)	na	1633.6 ± 104.58 (24), 1404 - 1744
CS (Number of eggs)	113.5 ± 19.23 (265), 70 - 189	101.0 ± 26.24 (24), 41 - 140
ES (mm)	39.9 ± 1.44 (265), 33.7 - 43.3	50.8 ± 2.00 (24), 44.9 - 53.6
CVol (cm^3)	4529.9 ± 769.73 (265), 2769.2 - 7661.1	5142.9 ± 1334.16 (24), 1842.5 - 7000.7
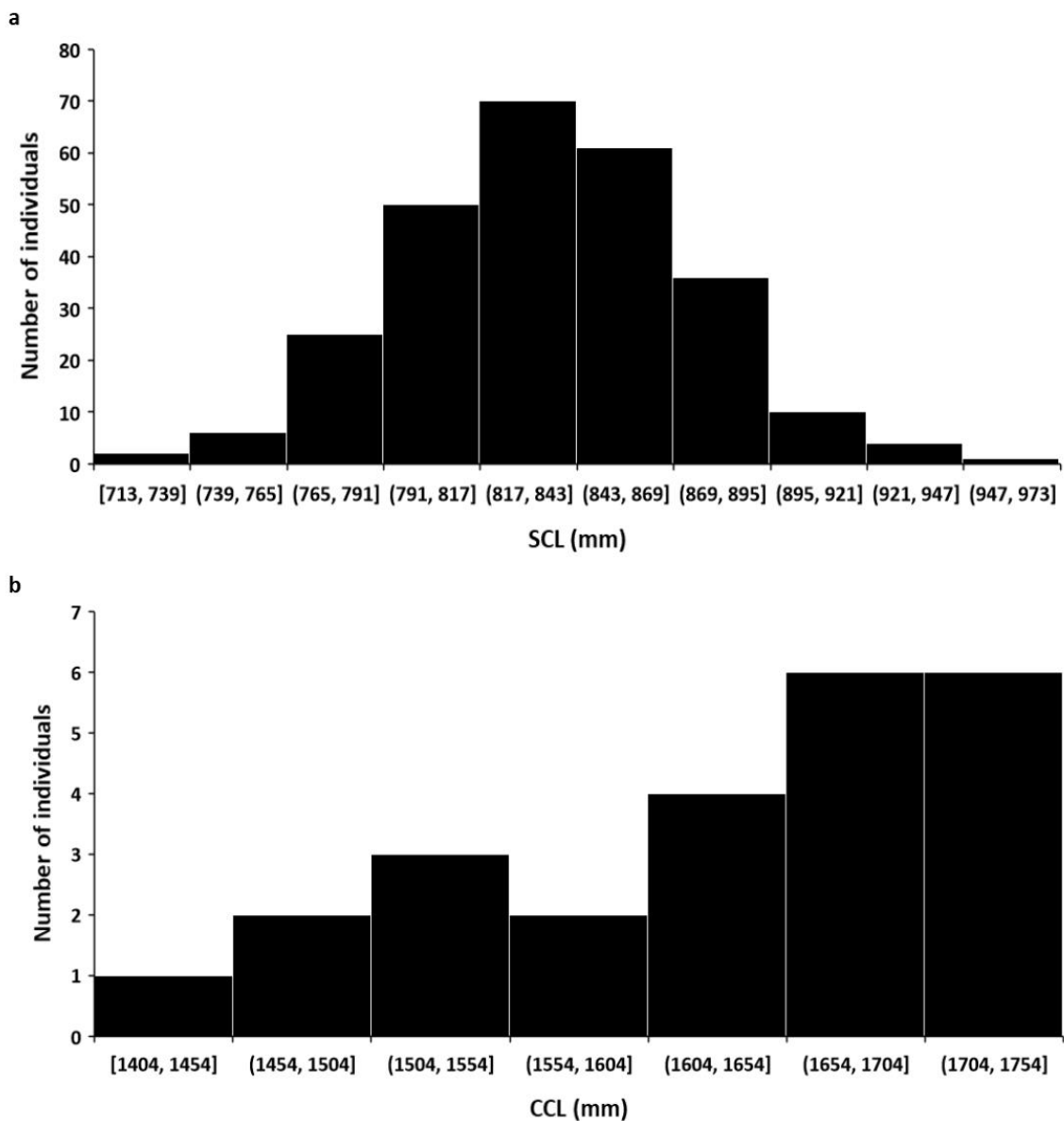
Figure 3.4: Frequency distribution of (a) loggerhead straight carapace length (SCL, n = 265), (b) and leatherback curved carapace length (CCL, n = 24) female turtles nesting in South Africa. (The leatherback size distribution is not normally distributed because it is a subset of the data and is not representative of the entire population.)

Mean curved carapace length (CCL ± SD) of leatherbacks was 1633.6 ± 104.58 mm (range 1404-1744 mm, n = 24), and females laid on average 101.0 eggs ± 26.24 (range 41-140, n = 24) per clutch, with a mean egg diameter of 50.8 ± 2.00 mm (range 44.9-53.6, n = 24), and a mean clutch volume of 5142.9 ± 1334.16 (range 1842.5-7000.7: Table 1, Fig. 3.4). Similar to loggerheads, larger leatherback females laid larger clutches ($F_{1,22}$ = 22.8, R^2 = 0.49, p < 0.001), while egg size was not correlated

with female size ($F_{1,22}$ = 0.63, R^2 = -0.02, p = 0.435; Fig. 3.6). In contrast to loggerheads, both GLMs had non-significant relationships between maternal length and clutch size (p = 0.160) and egg size (p = 0.721) for leatherback females.
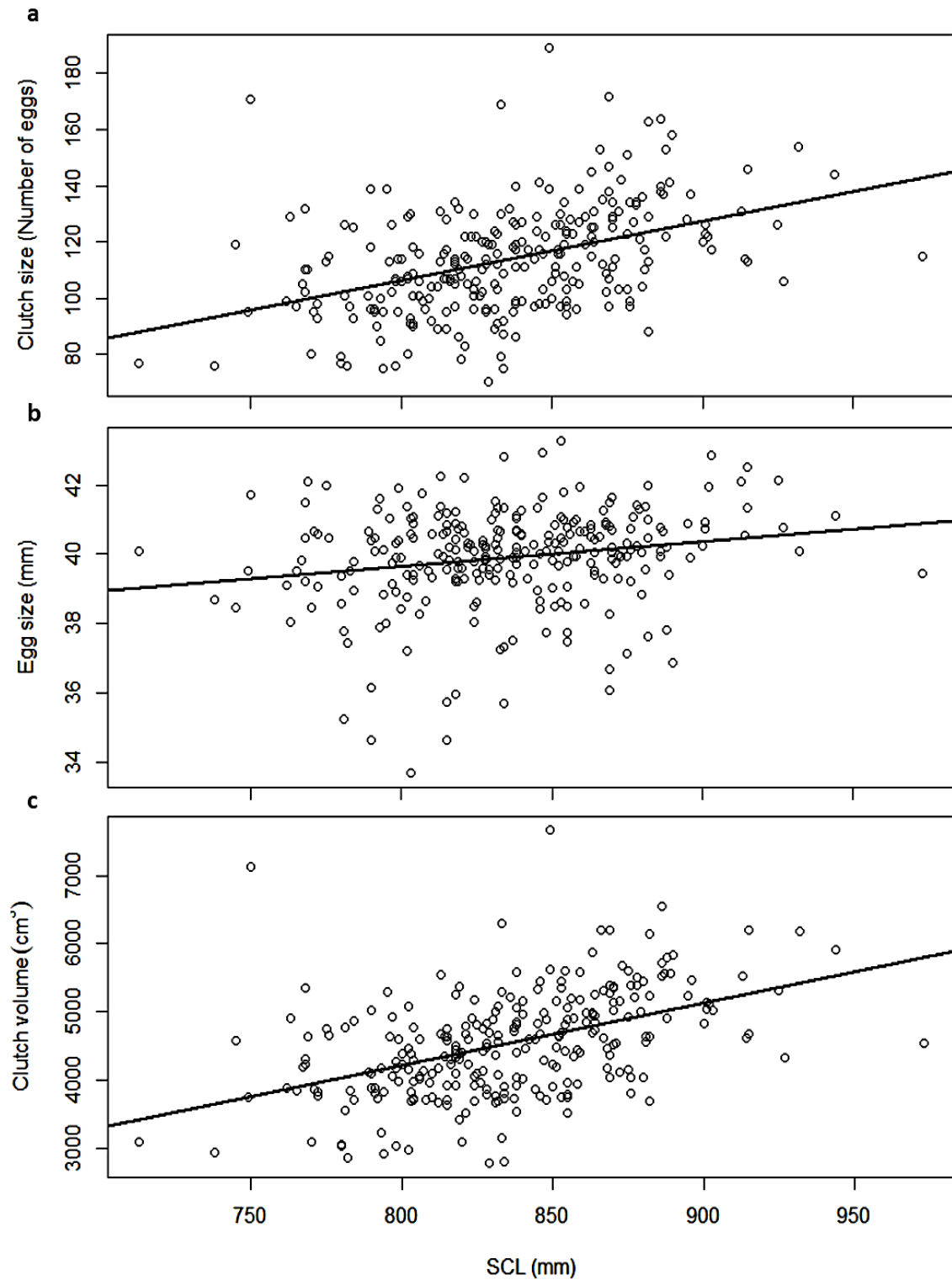
Figure 3.5: Relationship between female straight carapace length (SCL) and clutch size (a; r^2 = 0.183, p < 0.001, n = 265), egg size (b; r^2 = 0.034, p = 0.002, n = 265), and clutch volume (c; r^2 = 0.217 , p < 0.001, n = 265) for loggerhead turtles between 2010 and 2019 in South Africa.
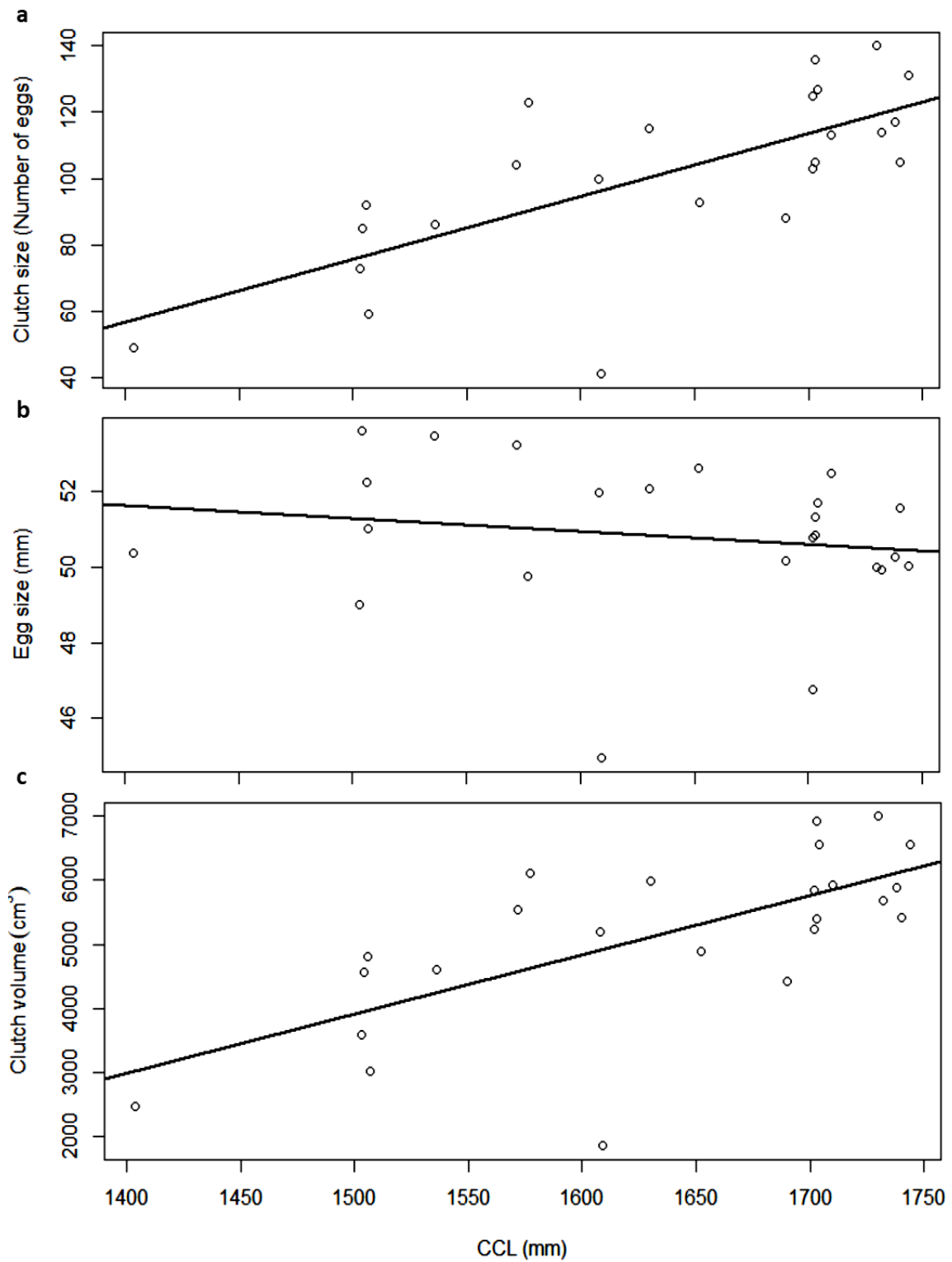
Figure 3.6: Relationship between female curved carapace length (CCL) and clutch size (a; r^2 = 0.486, p < 0.001, n = 24), egg size (b; r^2 = -0.016, p = 0.435, n = 24), and clutch volume(c; r^2 = 0.440, p < 0.001, n = 24) for leatherback turtles between 2010 and 2019 in South Africa.

Hatchling performance

The relationships between hatchling attributes and locomotor performance traits varied between species. Loggerhead hatchling swimming speed was only weakly positively correlated with hatchling front flipper width ($r^2 = 0.11$, $p < 0.001$) but none with crawling speed (Table 3.2). Swimming speed for leatherback hatchlings had a weak, positive correlations with back flipper width ($r^2 = 0,10$, $p = 0.029$) and front flipper area ($r^2 = 0.10$, $p = 0.032$), and none to crawling speed. The mixed effect model indicated that loggerhead hatchlings became faster swimmers with time (faster speed for swim 2 and 3; conditional $r^2 = 72.0\%$, $t = -4.16$, $p = < 0.001$, $n = 48$) but not leatherbacks (conditional $r^2 = 23.6\%$, $t = -0.71$, $p = 0.496$, $n = 6$).

Table 3.2: Results of the linear regression between hatchling performance traits and morphometric attributes. (SCL = straight carapace length; SCW = straight carapace width; Mass = body mass; Shell height = hatchling shell height; FFL = front flipper length; FFW = front flipper width; BFL = back flipper length; BFW = back flipper width; FFA = front flipper area; BFA = back flipper area; * represents significant results).

| | Performance traits | | | |
| | Crawling speed | | Swimming speed | |
Hatchling attributes	R^2	p-value	R^2	p-value
Loggerheads ($n = 412$)				
SCL	0.01	0.138	0.05	< 0.001[*]
SCW	0.01	0.330	0.02	0.003[*]
Body mass	0.01	0.158	0.07	< 0.001*
Height	0.01	0.143	0.02	0.003*
FFL	0.01	0.453	0.02	0.003*
FFW	0.01	0.574	0.11	< 0.001*
BFL	0.01	0.200	0.05	< 0.001*
BFW	0.01	0.439	0.04	< 0.001*
Size index	0.01	0.245	0.09	< 0.001*
FFA	0.01	0.476	0.06	< 0.001*
BFL	0.01	0.295	0.04	< 0.001*
Leatherbacks ($n = 49$)				
SCL	0.01	0.427	0.07	0.079
SCW	0.05	0.135	0.03	0.231
Body mass	0.05	0.120	0.08	0.046
Height	0.01	0.944	0.01	0.593
FFL	0.09	0.036*	0.08	0.046
FFW	0.06	0.101	0.06	0.084
BFL	0.01	0.485	0.00	0.798
BFW	0.07	0.081	0.10	0.029*
Size index	0.03	0.214	0.05	0.116
FFA	0.13	0.032*	0.10	0.032*
BFA	0.05	0.120	0.06	0.100

Loggerhead hatchling growth

Mean loggerhead hatchling straight carapace length (± SD) varied between 41.5 ± 0.94 mm to 82.5 ± 4.44 mm, straight carapace width from 353.5 ± 0.97 mm to 81.0 ± 4.35 mm, and body mass from 18.0 ± 0.98 g to 186.2 ± 23.82 g during the 15-week period of the captivity experiment. All morphometric measurements were strongly correlated with carapace length and body mass (Fig. 3.7 and 3.8), however five traits dominated the relationships (> 90% of the variation explained). Hatchling body mass was strongly correlated with straight carapace length (SCL, $r^2 = 0.94$, $p < 0.001$), while SCL ($r^2 = 0.91$, $p < 0.001$) and front flipper length (FFL; $r^2 = 0.92$. $p < 0.001$) correlate with time, and both front flipper length (FFL, $r^2 = 0.95$, $p < 0.001$) and back flipper length (BFL, $r^2 = 0.91$, $p < 0.001$) with SCL (Fig. 3.7, 3.8). Additionally, there was a significant difference in (absolute) growth between SCL and SCW mm (t-test, $t = 9.27$, $df = 868$, $p < 0.001$) with hatchlings growing longer than they grew wider throughout the experimental period.
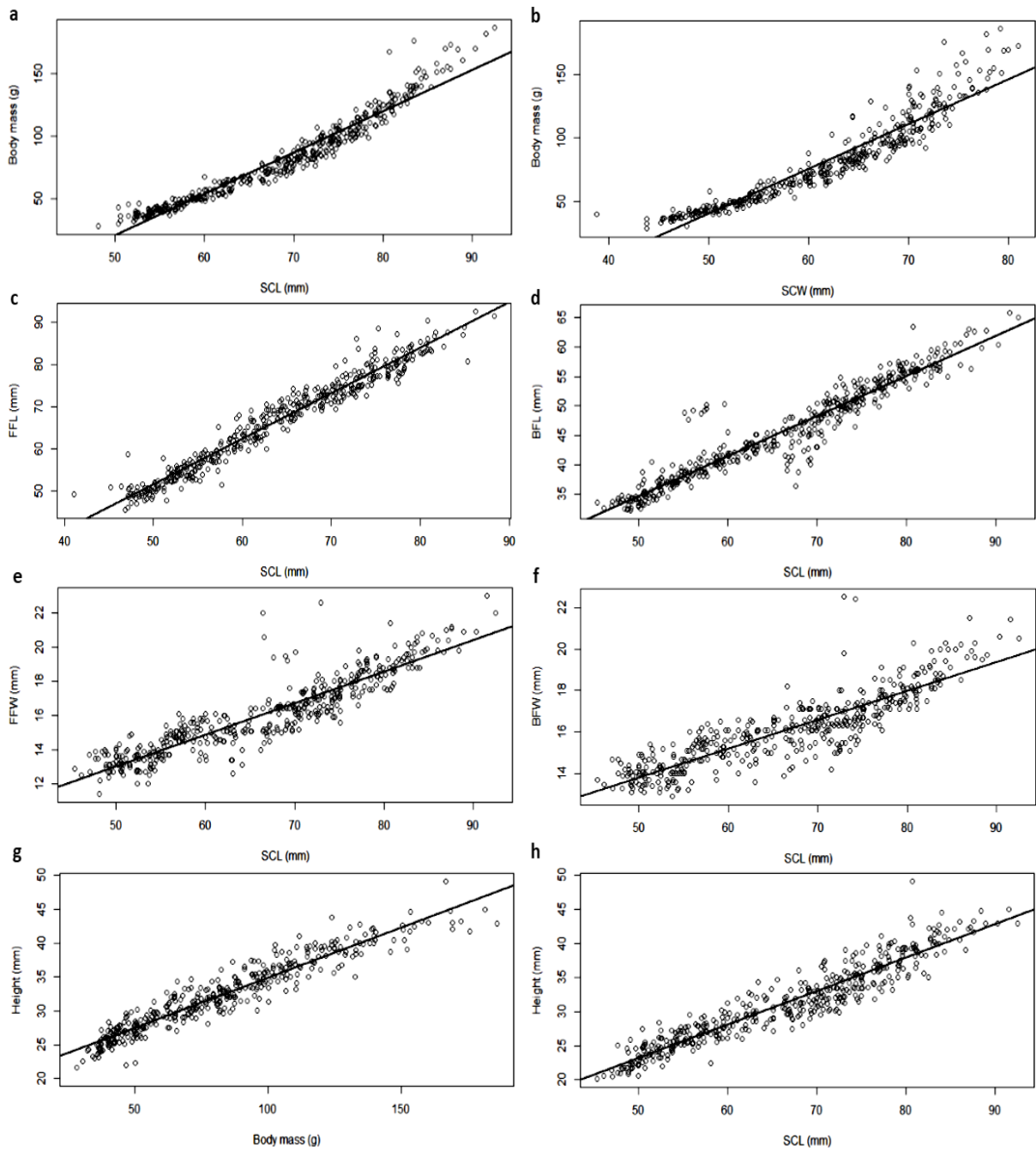
Figure 3.7: Relationships between loggerhead (a) straight carapace length (SCL) and body mass, (b) straight carapace width (SCW) and body mass, (c) front flipper length (FFL) and SCL, (d) back flipper length (BFL) and SCL, (e) front flipper width (FFW) and SCL, (f) back flipper width (BFW) and SCL, (g) height and body mass, and (h) height and SCL (n = 439 observations).
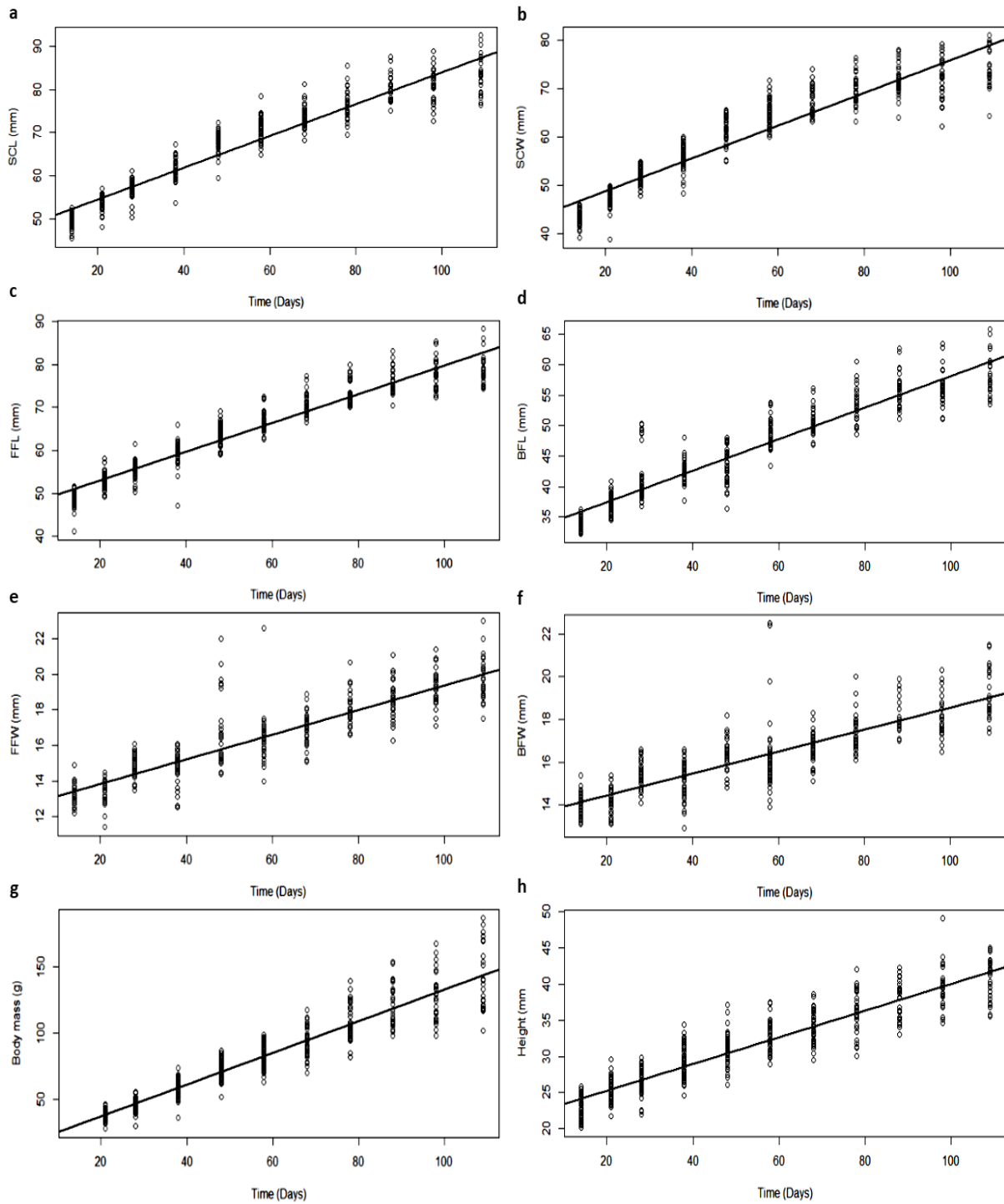
Figure 3.8: Relationships between (a) SCL, (b) SCW, (c) FFL, (d) BFL, (e) FFW, (f) BFW, (g) body mass, (h) height and time for loggerhead females nesting in South Africa *(n = 439 observations).*

Discussion

The ecological importance of body size for individual survival is apparent as most life-history traits are known to scale with size, including lifespan, metabolic rate, fecundity and numerous other morphological, physiological and behavioural factors (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). Sea turtles are endothermic reptiles with complex life history characteristics including early rapid growth, low juvenile survival, late maturity, high fecundity and a long lifespan (Van Buskirk & Crowder, 1994, Davenport, 1997). Gaining insight into the reproductive strategy that leads to the selective advantages of phenotypic variation in sea turtles at different life stages is fundamental in understanding the evolution of life-history traits (Sinervo and Doughty, 1996). In this study, it was hypothesised that there is a positive correlation between maternal length and clutch size but not egg size, in the context of the optimal egg size theory (EOS). Secondly, it was hypothesised that larger hatchlings will have better/faster locomotor performance thus conferring higher fitness compare to smaller hatchlings.

Female reproductive output

The results agree with our first hypothesis that larger females lay larger clutches in both loggerhead and leatherback turtles nesting in South Africa. This finding is in accordance with other studies that have shown that clutch size increases with female body size in sea turtles (Frazer & Richardson, 1986; Bjorndal & Carr, 1989; Hays & Speakman, 1991; Hays et al., 1993; Van Buskirk & Crowder, 1994; Johnson & Ehrhart, 1996; Broderick et al., 2003; LeBlanc et al., 2014; Wallace et al., 2007), and supports the EOS theory. However, larger females did not produce bigger eggs for either species, and this trait appears to be independent of maternal length. Indeed, many studies have found no relationship between egg size and maternal length (Hays & Speakman, 1991; Broderick et al., 2003), rather that seasonal fecundity and hatchling production increases with clutch frequency and size (Wallace et al., 2007).

Overall, the values of reproductive parameters measured in this study for both species overlap with the mean ranges found in other populations around the world except for leatherback egg diameter that is just below the mean minimum (Table 3.3). This is surprising as South African female leatherbacks tend to be larger than many other

populations globally, with only Western Pacific females exceeding their sizes (Van Buskirk & Crowder, 1994; Eckert et al., 2012). The small egg diameter but higher clutch size found in this study for leatherback turtles provides further support to the EOS theory where females maximise the number of eggs rather than egg size and indicates that changes in reproductive outputs are manifested primarily through changes in clutch size. Thus, in a stochastic environment with unpredictable and limited resources, offspring size should deviate from theoretical optimum and it is more advantageous to produce a range of offspring sizes (Wilkinson & Gibbons, 2005). Additionally, the South African leatherback population exhibits a high nesting frequency (nesting 6.7 times per season) and emergence success (73.8%), illustrating that the population has an overall high reproductive output (Nel et al., 2013). Thus, although they produce less eggs per clutch, reproductive success is achieved by producing many clutches and spreading the risks of nest failure. However, there might be an exception to this rule for flatback turtles that are smaller but lay few large eggs (CCL = 94 cm, clutch size = 52; Limpus, 2007) and are the only species where clutch size is not correlated with female size (Fig. 3.9; Van Buskirk & Crowder, 1994). This contrasting trend might be a result of their unique life-history, as flatback turtle hatchlings do not have an oceanic dispersal phase and are the only marine turtle species with an exclusive neritic development, and instead remain in coastal waters near the nesting beaches (Wildermann et al., 2017).

Table 3.3: Comparison of reproductive parameters between this study and other studies conducted around the world. (Egg diameter is expressed as a mean of 10 eggs measured per clutch, and hatchling sizes represent the mean of all hatchlings measured for the performance trials in this study. Worldwide measurements for loggerheads were extracted from LeBlanc et al., 2014 and from Eckert et al., 2012 for leatherbacks, where *n* = populations. Only mean samples with *n* ≥ 10 were used). For each dataset, the mean (± SE) and sample size (*n*) are provided for each variable.

	This study Mean ± SE (*n*)	Range of mean measurements worldwide (*n*)
Loggerhead		
Maternal length (SCL, mm)	835.4 ± 39.31 (265)	668.6 (11) – 970.9 (25)
Clutch size	113.5 ± 19.23 (265)	70.4 (128) – 149 (26)
Egg diameter (mm)	39.9 ± 1.44 (2 650)	37.6 (23) – 49.9 (260)
Hatchling length (SCL, mm)	43.9 ± 0.08 (412)	40.0 (221) – 45.8 (60)
Hatchling mass (g)	19.0 ± 0.09 (412)	18.7 (28) – 22.0 (58)
Leatherback		
Maternal length (CCL, mm)	1633.6 ± 104.58 (24)	1438.0 – 1695.0 (25)
Clutch size	101.0 ± 26.24 (24)	61.8 – 104.0 (34)
Egg diameter (mm)	**50.8 ± 2.00** (240)	51.0 – 55.4 (17)
Hatchling length (SCL, mm)	56.3 ± 0.29 (48)	53.5 – 65.0 (13)
Hatchling mass (g)	38.8 ± 0.26 (48)	37.3 – 52.6 (12)

Larger clutch size may also be beneficial as there is a minimum number of hatchlings required for successful emergence from a nest (Carr and Hirth, 1961; Frazer and Richardson, 1986; Warner et al., 2010). It has recently been found that the energetic cost of escaping the nest decreases as the number of individuals per clutch increases resulting in larger residual yolk reserve on emergence (Rusli et al., 2016).

Intrinsic and extrinsic factors that affect allocation of resources to reproductive parameters (clutch size and egg size) include age and maternal body condition, genetics, previous reproductive outputs, microhabitat selection, incubation environment (nest temperature and hydric conditions; Glen et al., 2003; Wilkinson & Gibbons, 2005). Consequently, it is likely a combination of factors that affect reproductive output in marine turtles, making it difficult to distinguish between maternal and environmental factors (Warner et al., 2010).
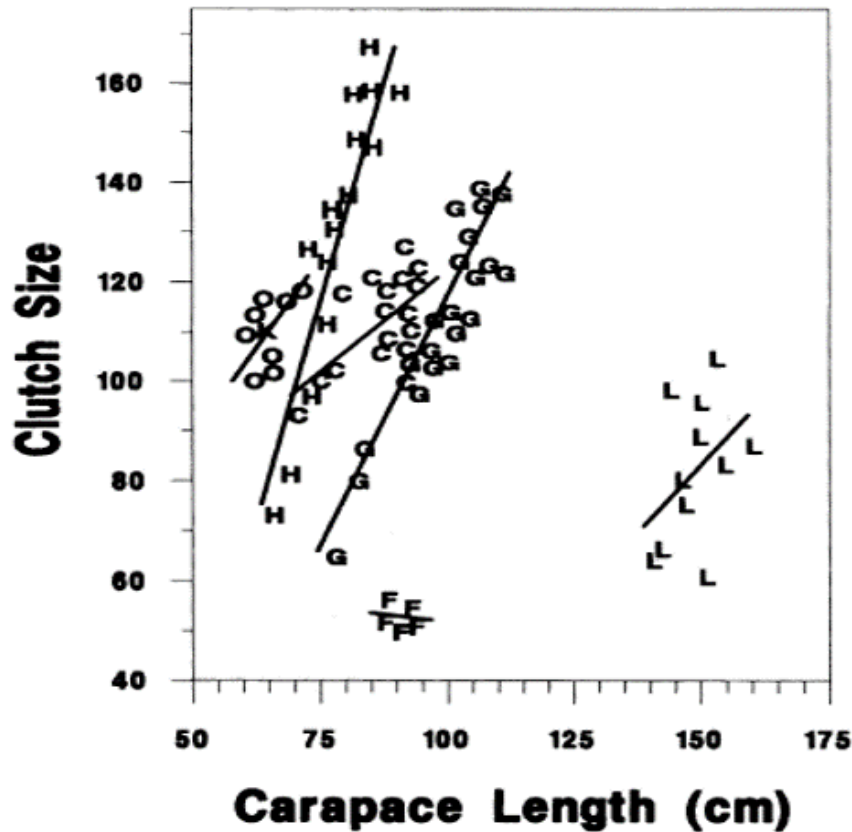
Figure 3.9: Species comparison of the relationship between clutch size and female carapace size for all seven species of sea turtles (mean values of a single population). Symbols represent: C = loggerhead, F = flatback, G = green, H = hawksbill, K = kemp's ridley, L = leatherback, and O = olive ridley turtle. (Figure from Van Buskirk and Crowder, 1994.)

Hatchling performance

This study further investigated the effects of phenotypic variation on the locomotor performance of loggerhead and leatherback sea turtle hatchlings that potentially affect their fitness and subsequent survival. Crawling and swimming speeds were used as proxies of hatchling fitness as these traits determine the duration that hatchlings will spend in predator-rich zones and the faster a hatchling can crawl on the beach and swim across the reef, the greater its chance of survival (Gyuris, 2000; Booth and Evans, 2011). Hence, with limited parental care in marine turtles, the only anti-predator strategy hatchlings have during the early life stage is to spend as little time as possible in the predator-rich zones to maximise survival, which should be directly correlated with crawling and swimming speeds (Gyuris, 1994). We hypothesised that larger

hatchlings will have increased locomotor performance with faster crawling and swimming speeds and therefore have enhanced fitness.

The results of this research differ from other studies and revealed that crawling speed was not significantly correlated with any of the hatchling attributes. Crawling speed was weakly correlated with carapace size index for green turtle hatchlings (Ischer et al., 2009), while loggerhead and leatherback hatchlings, that were larger (from cooler nests) performed better in crawling trials (Mickelson and Downie, 2010; Read et al., 2013; Sim et al., 2015). Further detail on leatherback hatchling dimensions revealed that those with a narrower carapace width and longer flipper reach had faster crawling speed (Mickelson & Downie, 2010). Thus, although we did not find any relationship between crawling speed and any hatchling attributes tested in our study, results from other studies suggest that locomotion of hatchling on land is maximised by being long and narrow. An elongated, streamlined body facilitate hydrodynamic movement, and so hatchlings with longer carapaces and limbs crawling faster which could enhance survival (Wyneken, 1997).

We would expect swimming speed in sea turtle hatchlings to increase with an increase in size since larger hatchlings would have longer limbs and larger flipper reach and so higher thrust and thus increased performance and speed. However, our results did not demonstrate such clear trends. Our study revealed that there are interspecies differences in swimming performance. A weak positive relationship between swimming speed and front flipper width was found for loggerhead hatchlings whereas leatherbacks hatchling swimming speed was weakly correlated with back flipper width and front flipper area. Most studies however, found that larger hatchlings had greater swimming performance, having greater thrust production and stroking rate (Ischer et al., 2009; Booth and Evans, 2011; Booth et al., 2013; Pereira et al., 2012; Sim et al., 2015; Kobayashi et al., 2018). Surprisingly, leatherback hatchlings were not faster crawlers nor swimmers than loggerhead hatchlings. Due to their large size we would expect leatherback hatchlings to have greater locomotor performance. However, comparison among loggerhead, green, and leatherback hatchlings revealed leatherbacks to be slower swimmers, with slower flipper movements than the other two smaller species (Wyneken, 1997; Salmon et al., 2004). This may be related to different swimming strategies characteristic of each species. Wyneken (1997) described the swimming stroke of leatherback hatchlings as a "marathon", with slow

swim speeds, driven by slow flipper movements, and long power stroke. This contrast distinctly with the "sprinter" strategy of loggerhead and green turtle hatchlings; they swim with rapid flipper movements, using a short power stroke. This further illustrates the differences in dispersal patterns observed between leatherback and loggerhead neonates. Leatherback post-hatchlings appear to swim continuously even after they have reached oceanic habitats, whereas cheloniids stop continuous swimming after reaching the offshore currents, displaying only intermittent swimming behaviour (Wyneken and Salmon, 1992; Scott et al., 2014).

Swimming speed/efficiency however is not static and increased with experience in loggerheads but not leatherback hatchlings. Other studies found obtained similar results for hard-shelled turtles with an initial increase in swimming efficiency during the frenzy period (Pereira et al, 2012; Scott et al., 2014). This is not surprising, as we would expect hatchlings to learn to stroke more efficiently, as they become stronger swimmers (Gyuris, 1994). The lack of trend for leatherbacks, might be explained by our small sample size for the repeated swimming trials ($n = 6$). The weak correlations found in this study between swim speed and hatchling attributes suggests that other factors (parental genotype, climate, nest microhabitat, predation; Warner et al., 2010) influence locomotor performance in sea turtle hatchlings that were not included in this study.

Hatchling fitness thus appear to be a trade-off between size and yolk reserves; larger hatchlings may have a greater chance to survive due to faster movement through the predator-rich beach and nearshore zones (Gyuris, 1994; Booth , 2006), but smaller hatchlings may travel further ashore before slowing down to forage or rest because of yolk reserves not used during development, emergence and offshore travel (Ischer et al., 2009). Hatchling survival and fitness is further complicated by food availability in the post-hatchling environment (Sim et al., 2015). Hatchlings that swim into food-poor habitats will be nutrient challenged, however, smaller hatchlings with leftover yolk reserves may be able to survive for longer without the need to feed. Conversely, larger hatchlings that swam through a gape-limited, predator-rich environment are more likely to survive (Gyuris, 1994), but will need to travel to favourable offshore habitats.

Hatchling growth

The growth curves for loggerhead hatchlings reared from emergence to four months old in captivity, showed that straight carapace length and front flipper length grew fastest. Furthermore, front and back flipper dimensions were strongly correlated with SCL, suggesting that these two body attributes (length of carapace and flippers) would be under strong selection and should confer survival advantages. These findings agree with results from performance studies indicating that larger hatchlings have faster locomotor abilities and therefore fitness. Our results also showed that width growth (absolute) was not linear and was initially fast then plateaued. This contrasts with the findings of Salmon and Scholl (2014), whereby hatchlings grew wider faster than they grew longer.

Ecological implications

Since small changes in hatchling's swimming speed can significantly affect its chances of survival, the negative effects of increased nest temperatures on swimming speed are expected to offset the benefits of an increase in sea surface temperature (expected to increase swimming speed; Booth & Evans, 2011; Kobayashi et al., 2018). It appears that intermediate incubation temperatures (28-30 °C) are optimal for hatchling emergence success, fitness (size and locomotor performance; Mueller et al., 2019) and dispersal and that even a non-lethal increase in global temperatures has the potential to detrimentally affect the fitness of marine turtle hatchlings by affecting their survival during their early life dispersal. The findings of this study suggest that the impacts of global warming on sea turtles may be more subtle than obvious threats such as loss of nesting habitat and skewed sex ratios (Hawkes et al., 2007; Hays, 2008; Saba et al., 2012; Monsinjon et al., 2019). As incubation temperature is thought to be negatively correlated with hatchling size (as less yolk is converted to hatchling tissue during shorter development time at higher temperatures; Glen et al., 2003), therefore climate change may affect locomotor performance and fitness of neonate turtles. Indeed, increased incubation temperatures are predicted to shorten incubation period and produce smaller hatchlings with decreased crawling and swimming speed (Ischer et al., 2009; Booth & Evans, 2011; Cavallo et al., 2015; Sim et al., 2015). Future research should investigate growth rates and recruitment rates of sea turtles under

different thermal regimes to accurately predicts the effect of climate change on marine turtles.

Conclusion

The present study showed that egg size did not increase with female size. This is consistent with the findings of other studies and supports the EOS theory which states that nesting turtles maximise clutch size rather than egg size in a heterogeneous environment. This evolutionary reproductive strategy of producing many small to normal eggs rather than fewer large ones may be a response to the high mortality at early life stages (Wallace et al., 2007; LeBlanc et al., 2014).

The finding that both carapace length and flipper size are the fastest growing hatchling attributes agrees with our locomotor performance trials that flipper size appears to be the main factor driving hatchling swimming speed. Although we do not have strong evidence for it, our study supports the "Bigger is better hypothesis" (Packard and Packard, 1988) in that hatchlings with longer and wider flippers had higher swimming speed. This suggests that flipper size is the most important factor driving locomotor performance of sea turtle hatchlings as it is the dominant morphological attribute influencing hatchling propulsion and thrust. In short, female turtles follow the OES theory to maximise their long-term reproductive fitness, whereas for hatchlings it is more advantageous to follow the "bigger is better" hypothesis as they only need to care for themselves and grow fast to outgrow predators and minimise time spent at vulnerable sizes.

Chapter 4: Effects of swimming behaviour and oceanography on sea turtle hatchling dispersal at the intersection of two ocean current systems

Chapter 4: Effects of swimming behaviour and oceanography on sea turtle hatchling dispersal at the intersection of two ocean current systems

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Abstract

The knowledge gap on the early life-history of sea turtles during the "lost years" continues to hinder research and conservation of this critical life stage when mortality rates are the highest. An oceanic model was used in combination with a Lagrangian particle tracking framework to simulate and identify potential post-hatchling dispersal trajectories of loggerhead and leatherback turtles in the South Western Indian Ocean. The study aimed to investigate the effect of hatchling swimming behaviour on hatchling dispersal and survival probability. To our knowledge, this study provides the first estimate of neonate sea turtle dispersal in the SWIO, by combining a particle tracking model with *in situ* hatchling behavioural data. The model revealed that most virtual hatchlings are transported south-westward in the Agulhas Current with three distinct final locations after a year-long simulation: the Agulhas Return, the SE Atlantic and the Southern Ocean zones. Dispersal trajectories of both loggerhead and leatherback sea turtle hatchlings were very similar and simulations revealed that initial active swimming (frenzy) as well as variability in oceanic conditions strongly influenced dispersal of virtual hatchlings. Furthermore, variability in oceanic conditions dispersed virtual hatchlings into different areas where threats, like fisheries bycatch, might also influence their survival. Lastly, the results of this study have potentially broad implications for climate change if turtles adapt by nesting earlier/later during the nesting season or further south which may influence hatchling locomotor performance and ultimately survival at early life stages.

Keywords: sea turtle hatchlings; oceanic dispersal; particle tracking; ocean currents; swimming behaviour; South Africa

Introduction

Sea turtles have complex life-cycles, with changes in habitat use and diet at different life stages (Bolten et al., 1992; Miller, 1997). After emerging from nests on sandy beaches, sea turtle hatchlings enter the ocean and spend several years in pelagic/oceanic habitats, a period known as the "lost years", before recruiting to neritic foraging grounds (Carr, 1980, 1986, 1987; Musick and Limpus, 1997; Bolten et al., 2003; Reich et al., 2007). This cryptic phase is the least understood life stage of sea turtles with a general paucity of information regarding their at-sea ecology and spatial distribution (Luschi et al., 2003; Godley et al., 2010). During this period, post-hatchlings are believed to swim offshore and remain in pelagic habitats, be passive drifters within oceanic currents, and occupying sea surface habitats, mostly feeding on neustonic prey items (Witherington, 2002, Boyle and Limpus, 2008; Mansfield et al., 2014). Furthermore, it has been assumed that neonate turtles have limited swimming and diving abilities due to their small size and positive buoyancy, remaining in the upper 5 m of the water column for the first few months depending on the species (Davenport and Clough, 1986; Salmon et al., 2004; Howell et al., 2010), and thus drift passively within ocean currents (Luschi et al., 2003; Hays et al., 2010).

Although ocean currents were thought to drive broad-scale post-hatchling dispersion into oceanic areas, recent evidence is showing that they actively swim and can influence their dispersal trajectories (Bolten et al., 2003; Hamann et al., 2011; Putman et al., 2012a). Research is revealing that neonate turtles engage in oriented swimming (using the earth's magnetic field; Lohman et al., 2012; Putman et al., 2012b; Putman & Mansfield, 2015), remain in productive waters (Scott et al., 2012; Putman and Naro-Maciel, 2016; Christiansen et al., 2016), and are driven by their physiological need to remain in suitable water temperatures (Okuyama et al., 2011; Gaspar et al., 2012; Varo-Cruz et al., 2016). Indeed, as ectotherms, sea turtles cannot regulate their own body temperature and sea surface temperature (SST) has been identified as one of the most important factors impacting post-hatchling habitat selection (Davenport, 1997; Gaspar and Lalire, 2017). As such sea turtles have an optimal temperature range at which fitness and growth are optimised, whereby swimming activity decreases in 30°C and locomotor coordination is lost above 33°C (O'Hara, 1980), while cold water temperature induces hypothermic stunning in water less than 10°C (Hughes; 1974; Morreale et al., 1992).

The movement and distribution of migratory marine species are generally poorly understood due to the challenges and logistical constraints of observing marine species in the open ocean (Schofield et al., 2013). Additionally, it is especially difficult to use animal tracking devices on very small animals such as sea turtle hatchlings, and their movement remains enigmatic, with knowledge inferred rather than empirically surveyed (Mansfield et al., 2012, 2014; Wyneken, 2008). Increased computational power and advances in numerical models of ocean circulation have facilitated the prediction of the distribution of the early life of marine organisms. Oceans models have thus become a valuable tool for predicting the movement of fish larvae (Vikebø et al., 2010), lobster larvae (Singh et al., 2018), and can also provide insights into the cryptic lost years of oceanic neonate turtles (Fossette et al., 2012; Scott et al., 2012, 2014; Haman et al., 2011). By combining high-resolution ocean models with particle tracking tools, it is possible to simulate their dispersal and estimate the spatio-temporal distribution of post-hatchling turtles during their oceanic phase (Putman et al., 2012a, 2014; Putman and Naro-Maciel, 2013). Furthermore, satellite-derived ocean products and numerical ocean models have been validated in a number of studies and have shown to reproduce ocean currents with a very high temporal and spatial resolution (Chassignet et al., 2007; Sudre and Morrow, 2008; Tonani et al., 2015; Hart-Davis et al., 2018; Cancet et al., 2019). While using oceanographic models to simulate hatchling dispersal can appear to simplify biological and ecological aspects, different scenarios/simulations can be generated and parameters (current speed, sea surface temperature, wind speed, swimming activity, duration, and direction, etc.) changed as our knowledge of hatchling behaviour increases (Hamann et al., 2011; Okuyama et al., 2011; Briscoe et al., 2016).

Despite conservation efforts that have contributed to the protection of sea turtles, there is a general lack of information regarding the dispersal and early life stage of sea turtles, with an urgent need to develop conservation strategies across all life stages (Godley et al., 2010; Boyle et al., 2009; Shillinger et al., 2012), especially for the critically endangered South Western Indian Ocean (SWIO) leatherback population. These SWIO turtle populations nest in one of the most complex and dynamic areas of the world's oceans, connecting two very contrasting ocean basins, the warm Indian Ocean on the east coast and the cold Atlantic Ocean on the west coast of Southern Africa, where strong and highly variable currents occur, potentially influencing post-

hatchling dispersal and survival (Lutjeharms et al., 2010). In South Africa, it is assumed that hatchlings are carried southwestward from the rookery along the east and south coasts in the Agulhas Current (Hughes, 1974), with some potentially entrained into the South East Atlantic where sea surface temperature gradually decreases below 15° C and localized upwelling are permanently present (Smit et al., 2010). Generating a high-resolution dispersion model for neonate turtles might help elucidate why the SWIO leatherback population is not increasing while having received the same protection as the SWIO loggerhead population that is growing exponentially (Nel et al., 2013). This study is thus the first attempt to identify potential dispersal pathways of loggerhead and leatherback turtles from the South African component of the SWIO populations by combining a high-resolution ocean model with a particle tracking framework and *in situ* observations of hatchling swimming behaviour. We hypothesised that (1) dispersal is controlled by oceanic currents and will thus transport post-hatchlings in the two ocean basins, the South-West Indian Ocean and the South-East Atlantic Ocean basins, and (2) neonate dispersal is independent of swimming behaviour and species.

Materials and Methods

Study site

The study took place on the north-eastern coast of South Africa in iSimangaliso Wetland Park, Kwa-Zulu-Natal. iSimangaliso is a UNESCO World Heritage Site, Ramsar Site, and comprises contiguous terrestrial and marine protected areas (MPAs). The shoreline is predominantly made up of intermediate beaches, with some coarse-grained, steep reflective beaches, interspersed with mixed shores and rocky outcrops (Harris et al. 2011). The beaches form the southernmost nesting grounds of loggerhead (*Caretta caretta*, Cc) and leatherback (*Dermochelys coriacea*, Dc) sea turtles in the world (~27°S). The rookery is approximately 200 km long and supports nesting of approximately 1000 loggerhead females and less than 100 leatherback females each year (Nel et al. 2013). The majority of nests are laid north of Sodwana, and particularly for 5 km north of Bhanga Nek in the loggerhead nesting hotspot while leatherback nests are distributed over the entire rookery.

South Africa is surrounded by two main boundary currents, the Agulhas Current (AC) and the Benguela Current (BC). The AC forms part of the South-west Indian Ocean sub-gyre and flows southwestward along the east coast of South Africa following the continental shelf edge, eventually retroflecting and flowing eastward back into the South Indian Ocean (Figure 1; Lutjeharms, 2006). The AC has been described as one the strongest western boundary currents in the world and is a highly dynamic current, with intense mesoscale (~ 100 km radius) variability (Hermes et al., 2007; Lutjeharms, 2006; Casal et al., 2009), and is characterized by warm tropical water (core temperature is 26.5°C ranging from 24 to 28°C; Lutjeharms et al., 2000). The total volume transport of the AC is the sum of the eddying flow through the Mozambique Channel, the poleward flowing East Madagascar Current, and recirculation from the South-West Indian Ocean sub-gyre (Lutjeharms and Ansorge, 2001; Lutjeharms et al., 2007; Hermes et al., 2007). The current is 60 to 100 km wide at the sea surface, and speeds in its core can exceed 7.2 km h^{-1} (Lambardi et al., 2008). The northern region of the AC is dominated by intermittent cyclonic and anticyclonic eddies flowing southward into the source region of the AC (Hermes et al., 2007, Braby et al., 2016) which in turn triggers the formation of cyclonic meanders known as Natal Pulses (forming between 29°S and 30°S) where the continental slope and wider shelf present favourable conditions for instabilities and upwellings (Lutjeharms et al., 2000). At the western end of the AC (between 39°S and 40°S), the current retroflects, turning eastward to the Indian Ocean along the Subtropical Convergence, creating the Agulhas Return Current. Where the shelf edge separates from the coast at the Agulhas Bank (near 33°S), the current is steered away, increasing its meandering nature and instability, and creating large ring shedding events at the retroflection, with warm, saline water drifting into the South Atlantic Ocean (Backeberg et al., 2008; Dencausse et al., Holton et al., 2017).

The Benguela Current, on the western coast of South Africa, has distinctly different characteristics compared to the AC. It is one of the world's four major eastern boundary upwelling systems that is strongly influenced by rings, eddies and filaments spawning from the Agulhas retroflection (Holton et al., 2017; Veitch and Penven, 2017). It is a weak eastern boundary current of the SE Atlantic Ocean with drift rate estimates of 5 to 15 km d^{-1} and characterized by an adjacent wind-driven coastal upwelling system, the Benguella Upwelling System, comprised of cold, nutrient-rich

water spreading offshore (Shannon and Nelson, 1996; Wedepohl et al., 2000). The near-shore (located 1° from the coast, ~13°C) permanently upwelled water (from the Namibian and west coast of South Africa, 18°S to 35°S) is cooler than the offshore boundary water (located 15° seaward, ~18°C; Santos et al., 2012). This complex assemblage of a warm intense and highly dynamic western boundary current, and a cold weak eastern boundary current represents the oceanic domain that neonate turtles are exposed to during the first few months of their cryptic oceanic life-stage (Fig. 4.1).
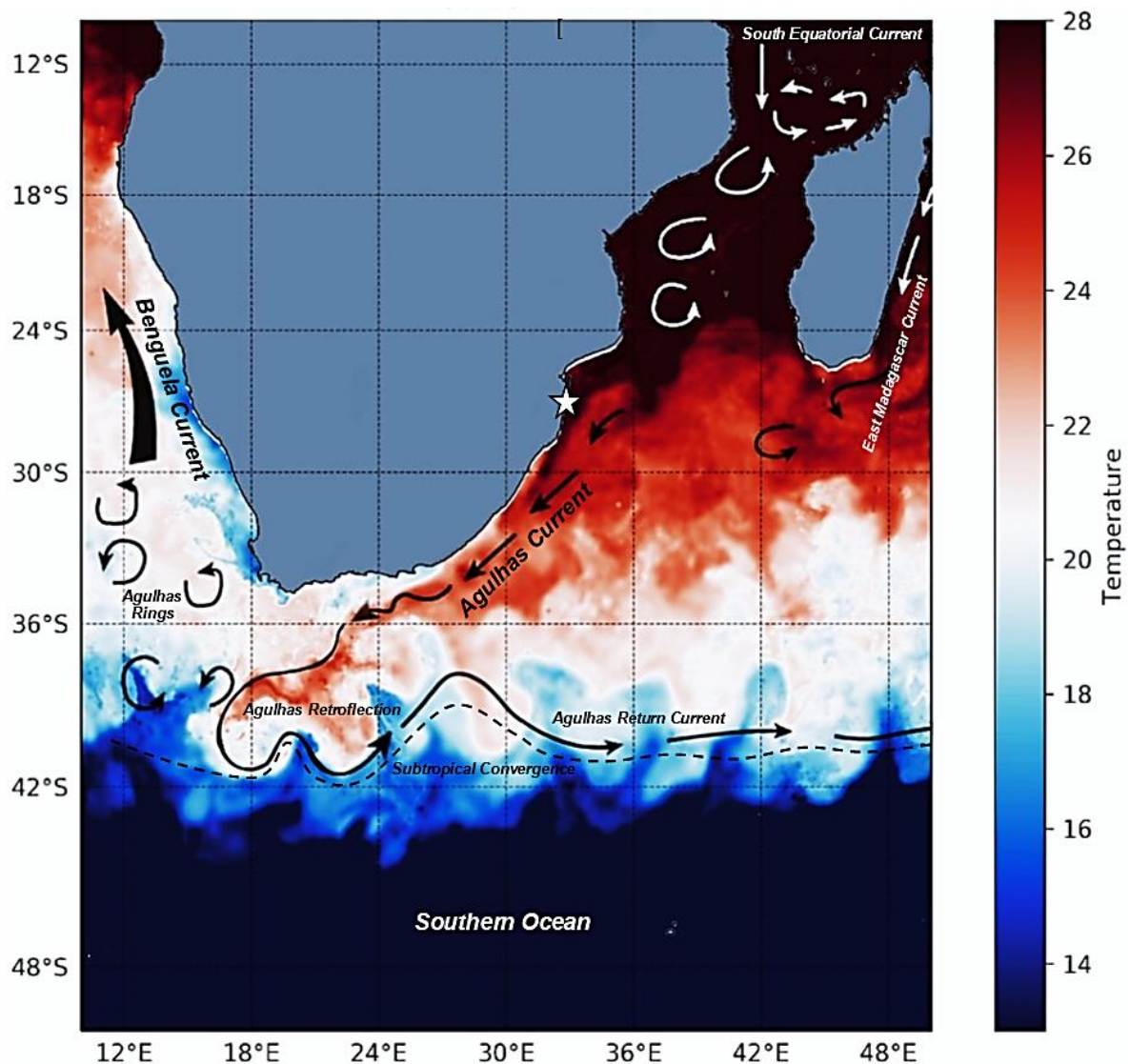
Figure 4.1: Schematic map of major surface currents and key features highlighting the complexity of the oceanography of the marine environment around southern Africa, and its associated sea surface temperature (snapshot from the 15th of February 2018 extracted from the GHRSST, available: http://podaac.jpl.nasa.gov) in the South East Atlantic and South West Indian Oceans. White star represents release location.

In situ hatchling data collection

Hatchling trials were undertaken with ethical clearance from the Nelson Mandela Metropolitan University Animal Ethics Committee: A16-SCI-ZOO-014, and hatchling collection was allowed with permission from the iSimangaliso Wetland Park Authority, Ezemvelo KwaZulu-Natal Wildlife, and Department of Environmental Affairs: Oceans and Coasts (permit numbers: RES2016/67, RES2017/73, & RES 2018/68).

In situ field experiments were conducted at night at the site of hatching. Hatchlings used for the experiments were collected from marked nests (that were monitored), to relate to female size, or selected opportunistically from random nests at Bhanga Nek (high loggerhead nest density beach; 26˚53'40.17''S; 32˚52'50.31''E) and Manzengwenya (high leatherback nest density beach; 27°26'72.6''S; 32°77'28.0''E). Following hatching, a subset of 25 hatchlings per nest (when possible) was randomly selected, brushed free of sand and used for swimming trials to investigate the effect of size on hatchling swimming ability. Each hatchling was placed at the landward end of a 2 m raceway made from plastic roof guttering (12 cm high, 15 cm wide, 2 m long, and painted black), and filled with fresh seawater (approximately 28°C). A dim light was placed at the end of the raceway to ensure directional movement. Each hatchling was timed swimming along the gutter with a stopwatch and the value converted to m/s (speed = distance/time ms^{-1}). After the trial, the straight carapace length (SCL) (from the nuchal notch to the supracaudal notch) and width (SCW) were measured for each hatchling using metal vernier callipers. In total 287 hatchlings were sampled in 2016 (Cc = 263 from 11 nests, Dc = 24 from 1 nest) and 425 (Cc = 376 from 17 nests, Dc = 49 from 2 nests) in 2017, and 33 in 2018 (Cc = 33 from 5 nests, Dc = 0).

Oceanographic model & particle tracking

We simulated the dispersal of virtual hatchling particles (referred to as virtual hatchlings onward) throughout the southwest Indian and southeast Atlantic Oceans within hindcast outputs from the Copernicus Marine Environment Monitoring Service (Copernicus, http://marine.copernicus.eu/). The Copernicus product is based on the modelling framework known as Nucleus for European Modelling of the Ocean (NEMO; Madec, 2008), used for oceanographic research, operational oceanography, seasonal forecast and climate studies created by a European consortium. The Copernicus

outputs used here (Global Analysis Forecast PHY_001_024) has a spatial resolution of 0.08° (approximately 6-9 km grid spacing), and the model is forced with atmospheric conditions that combine 6-hourly air temperature, humidity, and wind fields, from the ERA40 reanalysis with climatological radiation and freshwater fluxes from the CORE dataset (see Scott et al., 2012, 2017). Thus, NEMO hindcasts resolve mesoscale processes such as oceanic eddies and meanders and has successfully been used to track post-hatchling dispersal (Fossette et al., 2012; Putman et al., 2012; Scott et al., 2012, 2014, 2017).

Hatchling dispersal scenarios were simulated using the Lagrangian particle tracking framework Parcels (Probably A Really Computationally Efficient Lagrangian Simulator; Delandmeter, 2019). Parcels is a virtual particle tracking tool that computes the Lagrangian trajectories of virtual particles by using the following equation:

$$X(t + \Delta t) = X(t) + \int_{t}^{t+\Delta t} v(x, \tau) d\tau$$

where X is the three-dimensional position of a particle and $v(x, \tau)$ is the three-dimensional velocity field at that location from an ocean general circulation model.

Trajectories and final locations of virtual hatchling particles were plotted and divided into distinct geographical zones to identify hot spot areas and calculate the percentage of virtual hatchlings located in each zone. The oceanic regions (zones) for this study included the Mozambique Channel; the Agulhas Current together with the retroflection region; the Agulhas Return Current; the Benguela Current; SE Atlantic; and the Southern Ocean (Fig. 4.2). Once all the simulations were completed, the final positions of the virtual particles were determined. The final positions were then extracted to calculate the number of particles that ended up in each of the defined regions.
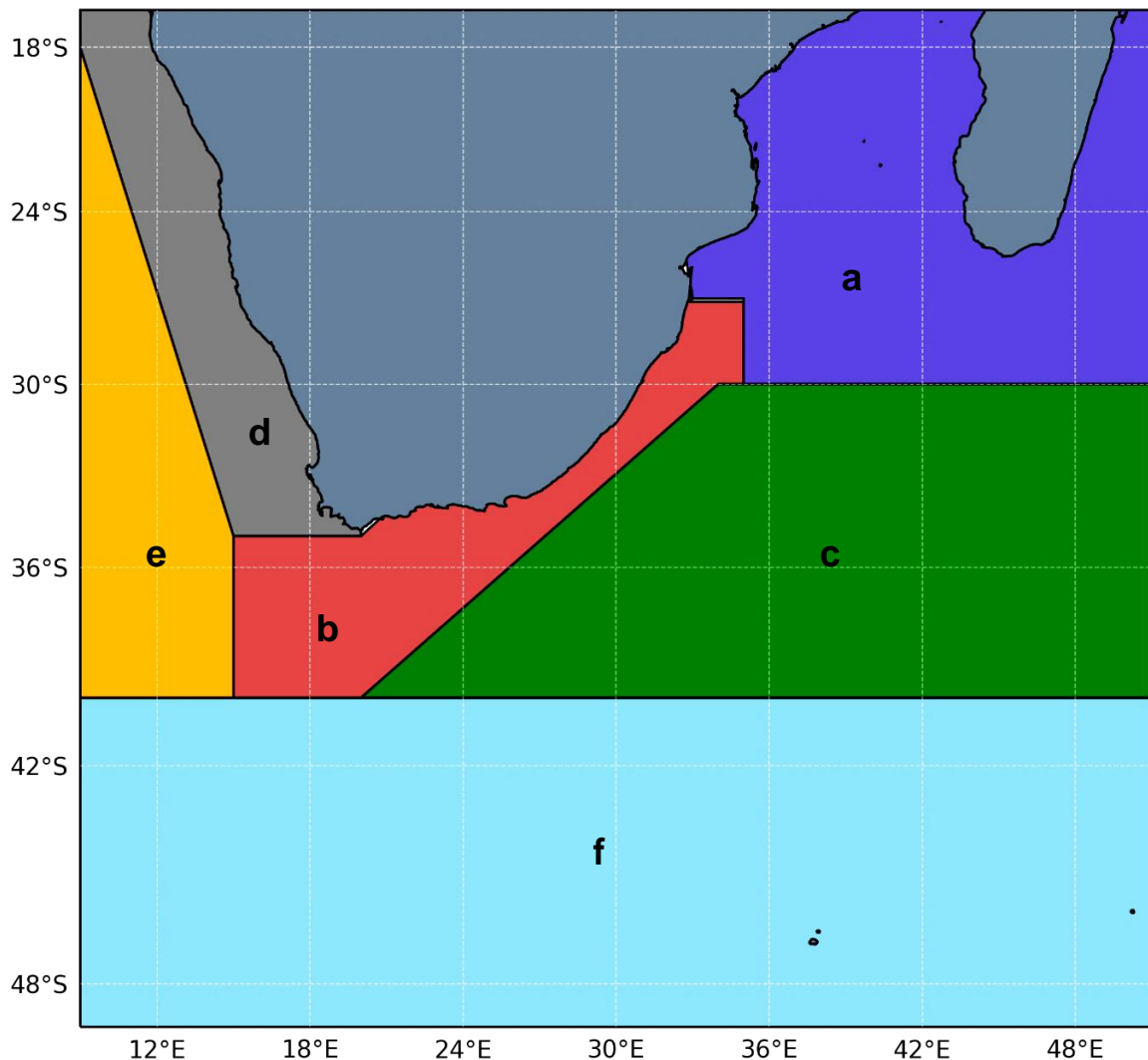
Figure 4.2: An illustration of the sub-regions of the study as the final locations of virtual hatchling trajectories that are defined as follows: a – Mozambique Channel, b – Agulhas Current and Retroflection, c – Agulhas Return Current, d – Benguela Current, e – SE Atlantic, f – Southern Ocean.

Oceanic variability

Virtual hatchling dispersal was simulated from two different beaches, representing the high and low loggerhead and leatherback turtle nest density beaches. Given the marked seasonal variability of the regional surface currents at the nesting grounds, the timing of hatchling release is important. Thus, to account for variability in oceanographic conditions, virtual hatchlings were released at two different times each coinciding with the peak hatching season for each species, 15th February for

loggerhead, and 15th March for leatherbacks. A total of 10 000 particles were released for each scenario in 2017 and 2018. These two years are a good representation of the oceanic conditions in the Agulhas Current. In 2017 a strong eddy was situated offshore of the nesting area, while in 2018 a weaker eddy was observed offshore of the nesting beaches. Hence the experiments provide a suitable example of different offshore oceanic conditions occurring at the nesting grounds. To identify if dispersal varies between species and with different swimming behaviours, outputs for each scenario included three simulations: the first 48 hrs, and 365 days trajectories as well as density plots after one year. Thus, for each year and species we have a total of 14 dispersal scenarios in which different locations, dates and swimming behaviours were simulated (Table 4.1). We further used a Pearson Chi-squared test with the function *chisq.test* (package stats, version 3.7.0 in R; Agresti, 2007) to determine if there were significant associations between scenarios and zones. A Cramer V test was then used to measure the strength of associations between groups (McHugh, 2013).

Hatchling swimming behaviour

Although post-hatchlings were believed to be passive drifters within oceanic currents, recent evidence shows that they are in fact active swimmers which influence their dispersal trajectories (Wyneken et al., 2008; Hamann et al., 2011; Gaspar et al., 2011; Putman et al., 2012a-b, 2014; Putman and Mansfield, 2015; Putman and Naro-Maciel, 2016). After entering the sea, post-hatchlings start to swim offshore continuously for about 24 to 48 hrs, called the frenzy period, to reach the main oceanic current (Salmon and Wyneken, 1987; Wyneken and Salmon, 1992). To replicate this frenzy period, we simulated dispersal for virtual hatchlings to either have or lack an initial swim at different velocities to assess if swimming behaviour influences their final dispersal trajectory. Particles (of virtual hatchlings) were programmed to swim offshore for the first 48 h of the simulations to replicate the frenzy behaviour and allow hatchlings to reach the offshore Agulhas Current. Swimming speeds that have been simulated for neonate turtles vary widely, ranging from 0.15 to 1.07 m/s depending on the species and age (Hamann et al., 2011; Putman et al., 2012a; Scott et al., 2012; Gaspar et al., 2012, 2017; Casale et al., 2014; Ascani et al., 2016). In this study, we used our hatchling swimming trial data with a mean (± SE) of 0.11 ± 0.06 m/s (range 0.07 to 0.40 m/s, *n* = 412) for loggerhead and 0.15 ± 0.07 m/s (range 0.06 to 0.33 m/s, *n* =

48) for leatherback turtle hatchlings (Fig. S4.1). We combined these with values from the literature and selected simulated swimming speed of 0.15 m/s (or 0.54 km/h) for loggerhead and 0.30 m/s (or 1.08 km/h) for leatherback hatchlings. These swimming speeds are in accordance with previous studies that found that average swimming velocities were under 1 km/h for juvenile loggerheads and around 1 km/h for leatherbacks (Polovina et al., 2006; Abecassis et al., 2013; Gaspar & Lalire, 2017). Conservative estimates of swimming speed were chosen as a precautionary approach to avoid overestimating the influence of post-hatchling behaviour on their dispersal (Putman et al., 2012a). Virtual hatchlings were simulated to swim offshore for the first 48 h of the simulation (initial swim), in accordance with the frenzy behaviour observed in hatchling sea turtles (Wyneken & Salmon, 1992), and then to swim with the current for 2 h of active swimming per day for 365 days.

Thermal environment and potential hatchling mortality

Additionally, as ectotherms, sea turtle survival and growth are strongly influenced by sea surface temperature (SST) and can only perform in a limited range of body temperature (Davenport, 1997; Gaspar & Lalire, 2017). To estimate potential mortality of post-hatchlings we assumed that their body temperature closely matches that of the sea temperature and thus use SST as a proxy of hatchling body temperature. Neonate turtles are known to decrease feeding rate in temperature lower than 20°C, have reduced swimming activity in temperature lower than 15°C, and die in temperature lower than 10°C for prolonged duration (Hughes, 1974; Schwartz, 1978; Davenport, 1997). We therefore assumed that post-hatchlings encountering a mean SST < 15°C for more than 14 days had a 50% chance of dying, and that post-hatchlings experiencing a mean SST ≤ 10°C for more than 3 days died of cold stunning. SST is thus assumed to have a strong influence on post-hatchling fitness and low survival rates are expected if they are transported into cold water, which might be the case in the SWIO if neonates are entrained in the cold Southeast Atlantic Ocean and Southern Ocean. SST data were obtained from the National Oceanic and Atmospheric Administration (NOAA, GHRSST), at a spatial resolution of 0.25° with daily values, covering the entire study area and tracking period.

Table 4.1: Dispersal parameters used in the fourteen simulations of loggerhead and leatherback hatchling dispersal scenarios for 2017 and 2018. All scenarios included a period of swimming except scenario 5 which was a passive drift dispersal. High: high nest density beach, Low: low nest density beach. (Bold text represents main differences between scenarios).

Scenario	Release location	Release date	Hatchling swimming behaviour
Loggerhead			
1	High	15Th February	Hatchlings swim offshore for 48 h at **0.3 m/s**, then with current direction at 0.15 m/s for 2 h/day for one year
2	High	15Th February	Hatchlings swim offshore for 48 h at **0.15 m/s**, then with current direction at 0.15 m/s for 2 h/day for one year
3	High	15Th February	Hatchlings swim offshore for 48 h at 0.15 m/s, **then no swimming**
4	High	15Th February	**No initial swim**, then with current direction at 0.15 m/s for 2 h/day for one year
5	High	15Th February	**Hatchlings do not swim** and are dispersed passively in the current
6	High	**15Th March**	Hatchlings swim offshore for 48 h at 0.15 m/s, then with current direction at 0.15 m/s for 2 h/day for one year
7	**Low**	15th February	Hatchlings swim offshore for 48 h at 0.15 m/s, then with current direction at 0.15 m/s for 2 h/day for one year
Leatherback			
1	High	15th March	Hatchlings swim offshore for 48 h at **0.4 m/s**, then with current direction at 0.2 m/s for 2 h/day for one year
2	High	15th March	Hatchlings swim offshore for 48 h at **0.3 m/s**, then with current direction at 0.2 m/s for 2 h/day for one year
3	High	15th March	Hatchlings swim offshore for 48 h at 0.3 m/s, **then no swimming**
4	High	15th March	**No initial swim**, then with current direction at 0.2 m/s for 2 h/day for one year
5	High	15th March	**Hatchlings do not swim** and are dispersed passively in the current
6	High	**15th February**	Hatchlings swim offshore for 48 h at 0.3 m/s, then with current direction at 0.2 m/s for 2 h/day for one year
7	**Low**	15Th March	Hatchlings swim offshore for 48 h at 0.3 m/s, then with current direction at 0.2 m/s for 2 h/day for one year

Results

Main dispersal pathways of virtual hatchlings in the SWIO

A total of 560 000 virtual hatchling particles were released in the simulations and the two species had very similar broad dispersal patterns. Most virtual hatchlings initiate their dispersal by being entrained south-westward with a core area of dispersal within the Agulhas Current (Fig. 4.3). Few virtual hatchlings however are advected north from the nesting beaches towards Mozambique, and this took place only in 2017 (Table 2). As virtual hatchlings move further offshore and initiate their oceanic journey three main dispersal pathways emerged with hatchlings reaching very different oceanic areas. The first two pathways continue in a south-westerly direction towards the southern edge of the continent and then split in two. Most virtual hatchlings remain under the influence of the AC and are carried eastwards via the Agulhas retroflection and Return Current to remain in the South West Indian Ocean (SWIO). This is referred to as the South Indian Ocean pathway. Virtual hatchlings following the second pathway are entrained into strong eddies and leaked into the South East Atlantic Ocean. This Atlantic pathway leads virtual hatchlings into two possible sub-trajectories. A northern route adjacent to the West African coast and the Benguela Current, and a southern route further West into the SE Atlantic. Lastly, the few virtual hatchlings that are advected north into Mozambique can be dispersed south of Madagascar or into the Mozambique Channel, and will be referred to as the Mozambique pathway. Particle counts after a year of simulated dispersal for each scenario also indicated that there were three main dispersal pathways (Table 4.2); the Agulhas Return zone, the Southern Ocean zone, and the SE Atlantic zone. Overall these three zones hosted the greatest proportion of virtual hatchlings across scenarios, years and for both species. The two zones with the least consistent amount of virtual hatchlings were the Mozambique Channel and the Benguela Current zones.
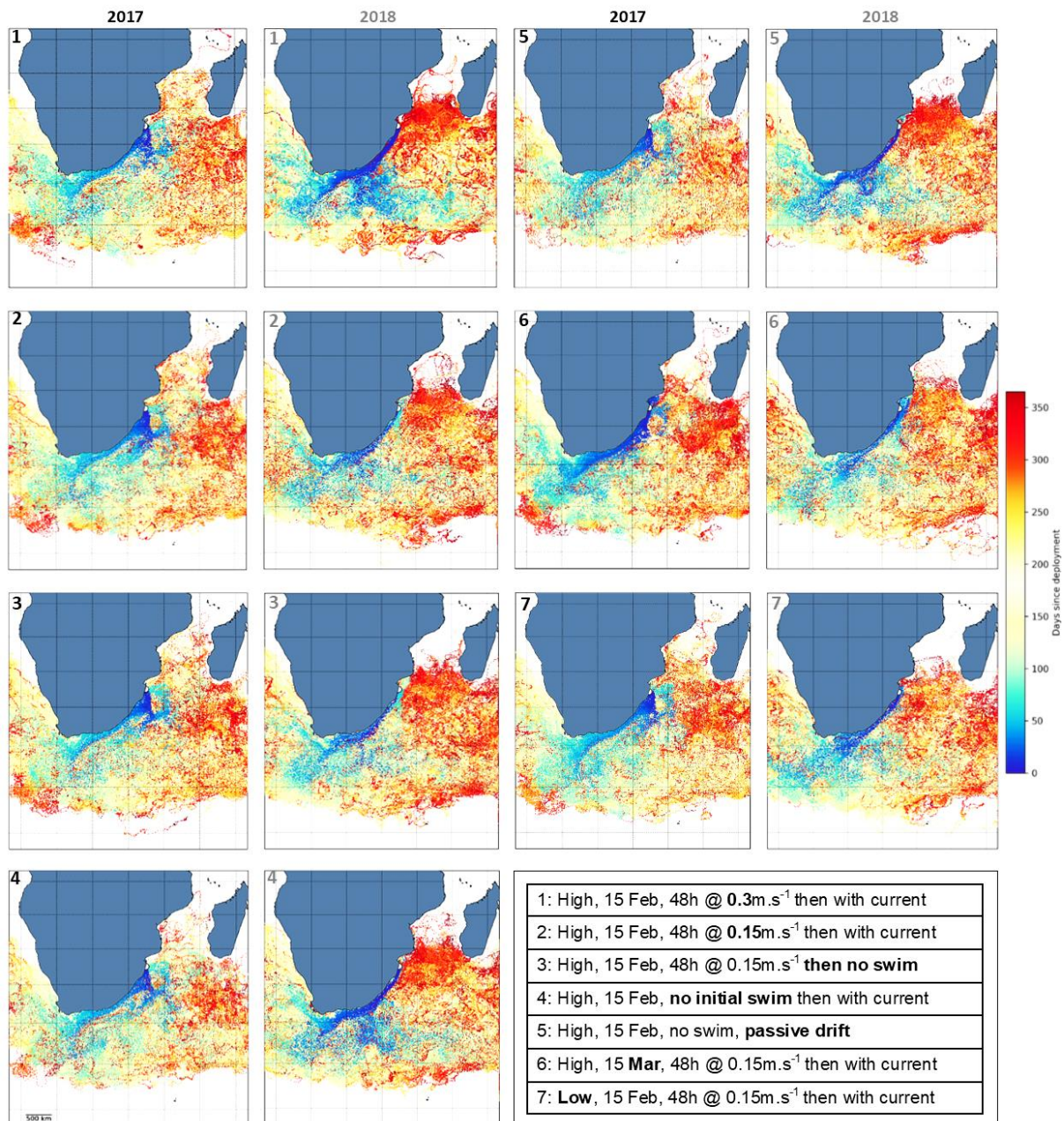
Figure 4.3: Comparison of virtual loggerhead hatchling trajectories after 365 days of modelled simulations in 2017 and 2018 under different scenarios during the peak breeding season. Each map represents a different dispersal scenario for 2017 (black numbers) and 2018 (grey numbers). The white circle represents the release location.

Oceanic variability

Although the long-term dispersal trajectories of virtual hatchlings under different scenarios follow similar broad patterns, the 48 hr zoom (Fig. 4.4) and particle counts indicated some differences between the seven scenarios. Dispersal scenarios differed

within and between years for both species, as was expected due to the dynamic nature of the Agulhas Current (Fig. 4.4, 4.5). In 2017 virtual hatchlings were retained in the vicinity of the nesting beach or pushed north due to the inshore current (Fig. S4.2), except for those that had stronger swimming speed during the frenzy or were released further south (Fig. 4.4,k). These were entrained in the current, flowing in a south-westerly direction. Virtual hatchling trajectories that lacked an initial swim or were completely passive had high retention rates at the release site in 2017 (scenario 3, Fig. 4.4m, c). The 2018 cohort experienced lower variability in oceanic conditions and the three dominant pathways remained the same for both species with more than 70% of loggerhead and 80% of leatherback particles accounted for in these three pathways (Table 4.2). However, the of virtual loggerhead hatchlings ended in the SE Atlantic and leatherbacks in the Southern Ocean.
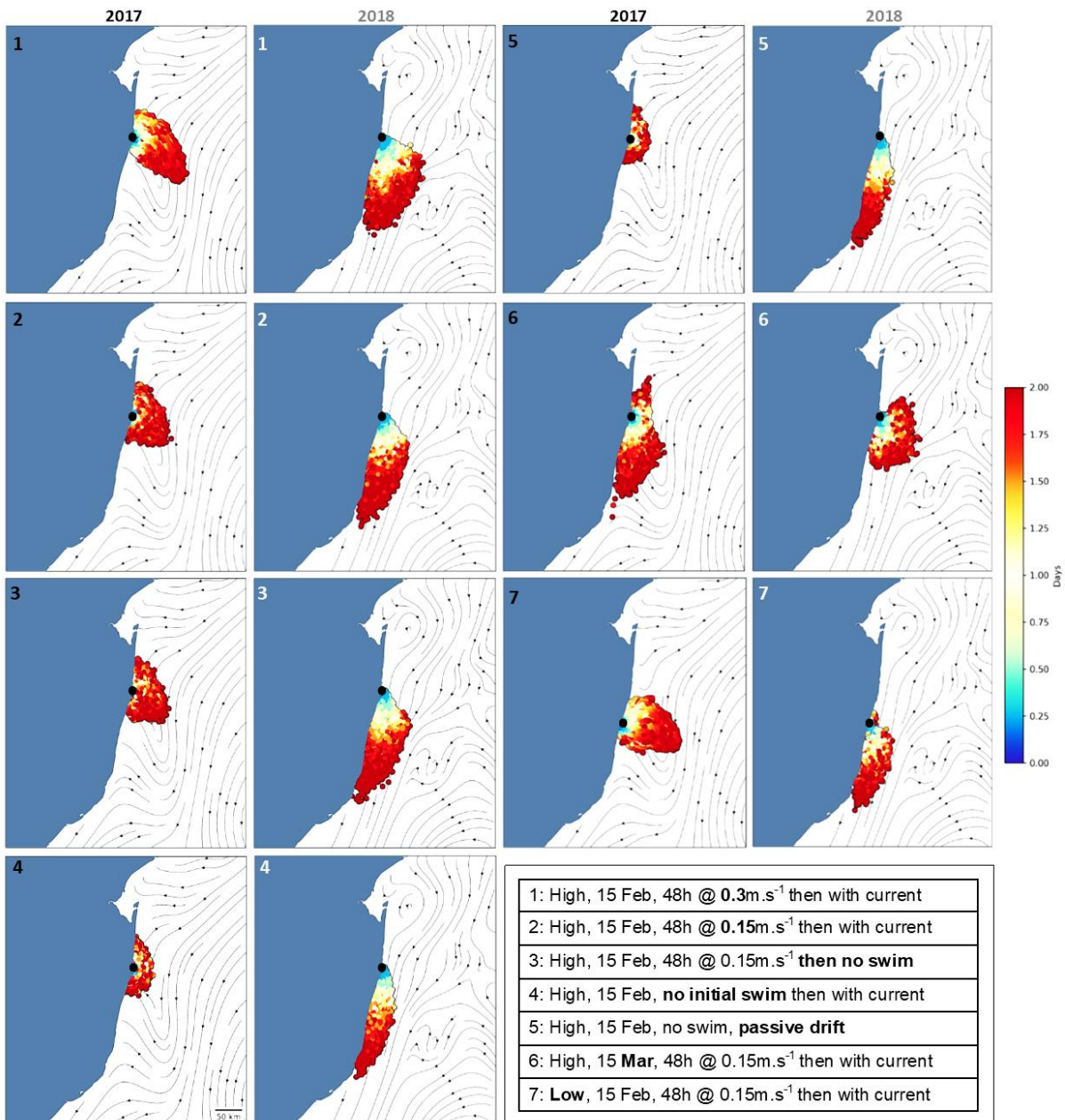
Figure 4.4: Comparison of virtual loggerhead hatchling trajectories after 2 days of modelled simulations in 2017 and 2018 overlaid onto streamlines of the surface current velocities for each scenario. Each map represents a different dispersal scenario for 2017 (black numbers) and 2018 (grey numbers). The black circle represents the release location.

Hatchling swimming behaviour

The particle counts revealed that the oceanographic conditions of 2017 resulted in disparate results among the scenarios with a high percentage of virtual hatchlings being advected north into the Mozambique Channel zone for scenarios with either no frenzy (scenario4) or no swimming at all (scenario 5) for both loggerhead (64.8% and 64.9%) and leatherback (76.4% and 76.2%) virtual hatchlings (Table 4.2, 4.3). Furthermore, higher variability was found in 2017 for loggerhead virtual hatchlings than leatherbacks with the highest number of particles having an end trajectory in the Agulhas Current (retained in the vicinity of the release site) for scenarios with slower swimming speed (scenarios 2 with 25.2% and 3 with 26.8% respectively) compared to leatherbacks with highest numbers in the Southern Ocean zone for the same scenarios (32.7% and 33.5%). The dominant end trajectory for loggerhead virtual hatchlings in 2018 was the SE Atlantic zone except for scenario 1 with a stronger swimming speed that took virtual hatchlings in the Agulhas Return zone (37.6%) and for scenario 6 with a change in release date that advected hatchlings in the Southern Ocean zone (33.5%). This variability was also noticeable for leatherbacks, but particles only deviated from the dominant zone (Southern Ocean) in scenario 6 with a change in release date (32.6%). Additionally, the scenario with the stronger swimming speed during the frenzy swim took loggerhead virtual hatchlings further offshore (Fig. 4.3a) compared to any other scenario but this was not observed in 2018 (Fig. 4.3b). These findings are supported by the correlation tests that indicated the strongest positive associations between scenarios 1, 6, and 7 (i.e. fastest initial offshore swim, March or low-density area release) with the majority of particles ending in the AR, SEA and SO (Fig. 4.6). However, the Cramer V Test indicated a moderate association among these scenarios in 2017 (Cramer V test = 0. 30) and a weak association in 2018 (Cramer V test = 0.11).
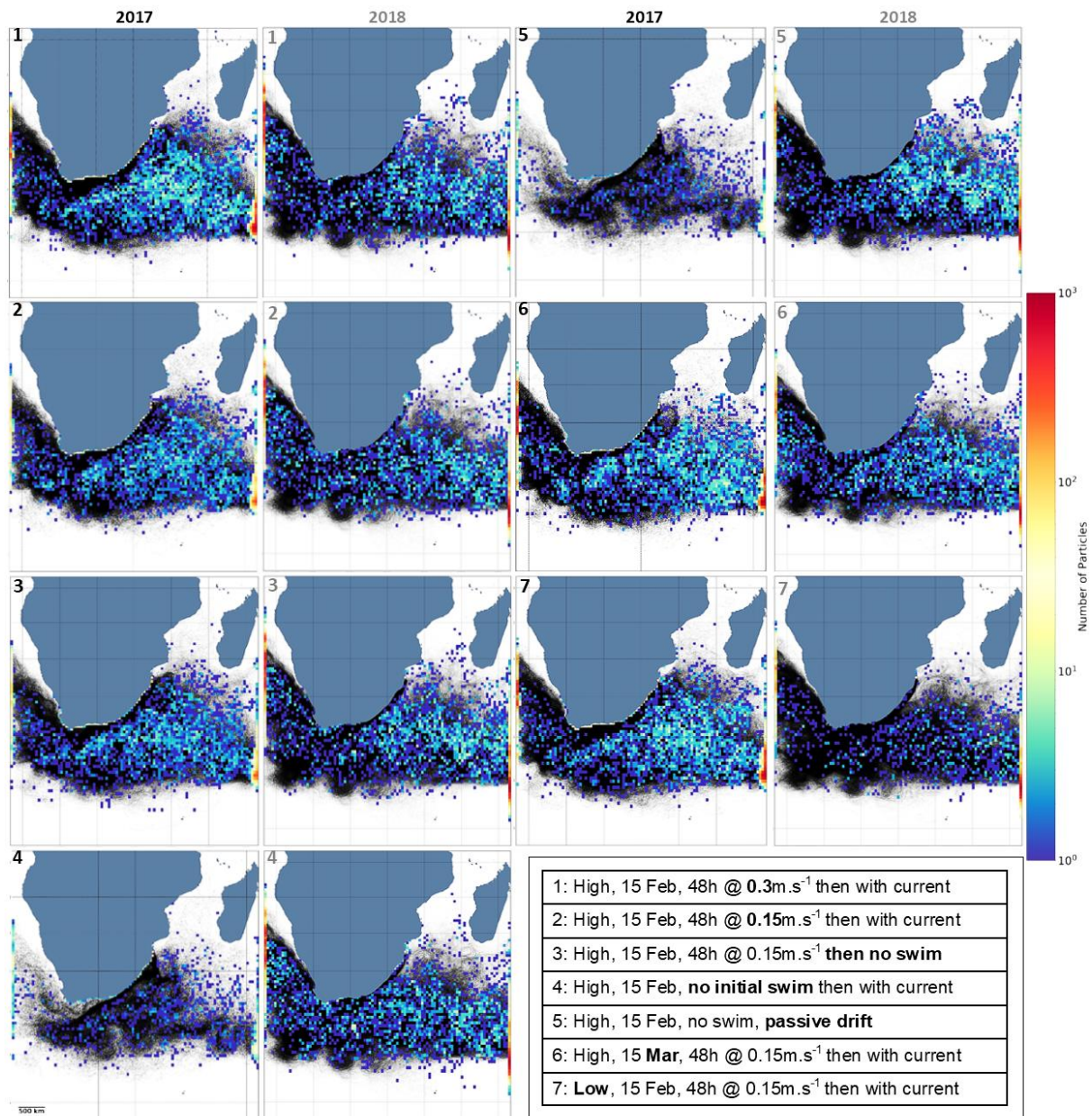
Figure 4.5: Particle density plots (log) of virtual loggerhead hatchling final position and full trajectories (black lines) after 365 days of modelled simulations in 2017 (black numbers) and 2018 (grey numbers) for each scenario. The white circle represents the release location.

Table 4.2: Proportions (%) of virtual loggerhead and leatherback hatchlings in each specific marine zones after one year of simulated dispersal for each scenario in 2017 and 2018. (MC = Mozambique Channel; AC = Agulhas Current; AR = Agulhas Return; BC = Benguela Current; SEA = SE Atlantic; SO = Southern Ocean; bold numbers indicate scenarios with the highest numbers for each zone).

Loggerhead						
	Marine zones					
Scenarios 2017	MC	AC	AR	BC	SEA	SO
1: High, 15 Feb, 48h @ **0.3**m.s^{-1} then with current	2.2	13.6	**29.5**	1.6	**22.9**	**30.1**
2: High, 15 Feb, 48h @ **0.15**m.s^{-1} then with current	18.9	**25.2**	20.5	0.9	14.9	**19.5**
3: High, 15 Feb, 48h @ 0.15m.s^{-1} **then no swim**	14.1	**26.8**	21.9	1.0	15.7	**20.5**
4: High, 15 Feb, **no initial swim** then with current	**64.8**	20.5	6.2	0.2	3.1	5.3
5: High, 15 Feb, no swim, **passive drift**	**64.9**	20.1	6.0	0.2	3.4	5.4
6: High, 15 **Mar**, 48h @ 0.15m.s^{-1} then with current	1.8	11.3	**25.8**	1.6	**31.1**	**28.4**
7: **Low**, 15 Feb, 48h @ 0.15m.s^{-1} then with current	1.9	17.2	**27.3**	1.3	**23.6**	**28.6**
Scenarios 2018						
1: High, 15 Feb, 48h @ **0.3**m.s^{-1} then with current	3.7	3.6	**37.6**	3.0	20.5	31.5
2: High, 15 Feb, 48h @ **0.15**m.s^{-1} then with current	2.3	6.0	**26.4**	6.0	34.9	24.4
3: High, 15 Feb, 48h @ 0.15m.s^{-1} **then no swim**	2.1	5.8	**27.5**	5.5	34.8	24.2
4: High, 15 Feb, **no initial swim** then with current	1.9	15.9	**23.2**	4.2	**29.5**	25.2
5: High, 15 Feb, no swim, **passive drift**	1.9	16.0	**22.1**	4.3	30.9	24.7
6: High, 15 **Mar**, 48h @ 0.15m.s^{-1} then with current	2.2	13.0	**27.2**	1.7	22.3	**33.5**
7: **Low**, 15 Feb, 48h @ 0.15m.s^{-1} then with current	2.3	5.8	**26.3**	5.9	34.7	25.0
Leatherback						
Scenarios 2017	MC	AC	AR	BC	SEA	SO
1: High, 15 Mar, 48h @ **0.4**m.s^{-1} then with current	1.5	2.7	28.6	**2.5**	**33.0**	31.7
2: High, 15 Mar, 48h @ **0.3**m.s^{-1} then with current	1.9	5.0	**32.3**	1.3	**26.8**	**32.7**
3: High, 15 Mar, 48h @ 0.3m.s^{-1} **then no swim**	**2.0**	5.2	31.6	**1.4**	26.3	33.5
4: High, 15 Mar, **no initial swim** then with current	0.3	**76.4**	6.4	0.5	8.6	7.8
5: High, 15 Mar, no swim, **passive drift**	0.4	**76.2**	6.6	0.6	8.7	7.6
6: High, 15 **Feb**, 48h @ 0.3m.s^{-1} then with current	**2.0**	17.5	27.8	**1.7**	22.2	28.8
7: **Low**, 15 Mar, 48h @ 0.3m.s^{-1} then with current	**2.2**	4.7	**34.5**	1.2	24.2	**33.1**
Scenarios 2018						
1: High, 15 Mar, 48h @ **0.4**m.s^{-1} then with current	1.1	4.2	24.7	**2.4**	29.9	37.7
2: High, 15 Mar, 48h @ **0.3**m.s^{-1} then with current	1.3	**5.8**	27.0	**3.1**	23.2	**39.7**
3: High, 15 Mar, 48h @ 0.3m.s^{-1} **then no swim**	1.0	4.0	26.5	2.0	24.6	**41.9**
4: High, 15 Mar, **no initial swim** then with current	**1.4**	15.7	27.1	2.0	22.7	31.0
5: High, 15 Mar, no swim, **passive drift**	**1.7**	15.6	26.5	2.1	22.7	31.4
6: High, 15 **Feb**, 48h @ 0.3m.s^{-1} then with current	**2.7**	3.9	**32.6**	**5.0**	28.1	27.6
7: **Low**, 15 Mar, 48h @ 0.3m.s^{-1} then with current	0.9	4.3	24.7	2.3	**27.7**	40.1

Thermal environment and potential hatchling mortality

We assumed that virtual hatchlings encountering a mean SST of less than 15°C for more than 14 days had a 50% chance of dying, and that those experiencing a mean SST equal or less than 10°C for more than 3 days died of cold stunning. By overlaying the SST encountered by virtual hatchlings throughout their first year of dispersal, we estimated the potential cold-induced mortality. The SST values indicated that only the Southern Ocean and Benguela Current zones had temperatures low enough to impact post-hatchling survival. Only a very small fraction of virtual hatchings ended in the Benguela Current (Table 4.2 and 4.3) and of these no loggerheads or leatherbacks encountered SST values to equal, or less than 10°C for three days or more, in 2017 or 2018, which could have induced hypothermia or mortality (Table 4.3). However, loggerhead virtual hatchlings encountered SST values equal or less to 15°C for more than 14 days (in decreasing order) for 15.1% of scenario 1, 12.2% of scenario 7, 11.7% for scenario 1, 7.8% for scenarios 2 and 3, and lowest percentage for scenarios 4 and 5 (1.9% and 1.8% respectively) had 50% chance of mortality in the Southern Ocean and overall very low numbers (equal or less than 2%) of encountering 10°C SST across all scenarios in 2017. The fraction of virtual hatchlings that encountered cold temperatures, 50% chance of hypothermia and experiencing 15°C SST for more than 14 days in the Southern Ocean were higher in 2018. The highest percentage for scenario 1 (25.5%), followed by scenario 6 (22.8%), scenario 4 (19.9%), scenario 5 (19.3%), with the lowest being scenario 7 (15.7%). Interestingly, the lowest mortalities for both temperatures in the Southern Ocean were found for the scenarios with no frenzy swim (scenario 4) or completely passive (scenario 5) but only in 2017.
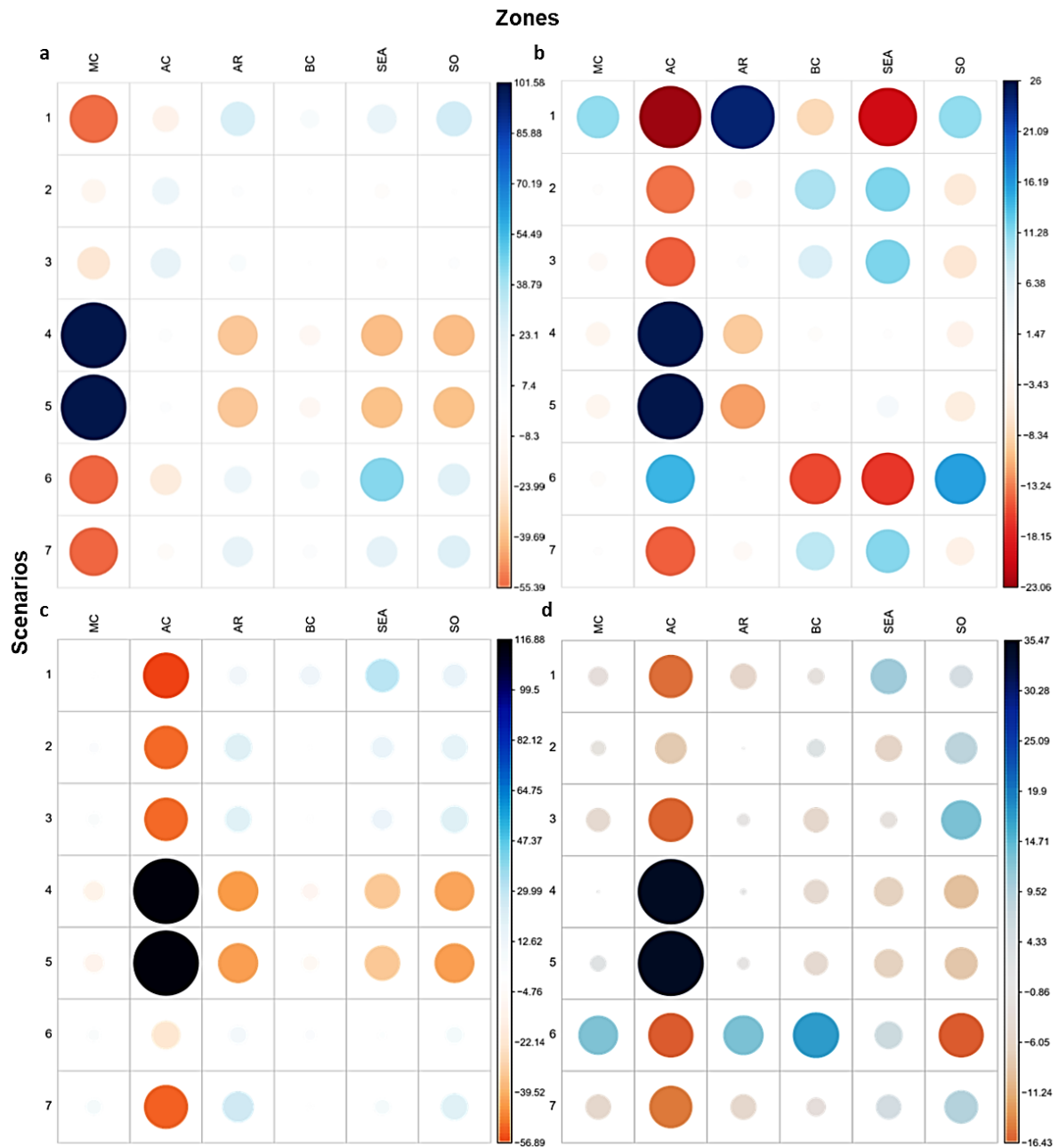
Figure 4.6: Correlation matrix representing the Pearson residuals from the Chi-squared test for loggerhead in 2017 (a) and 2018 (b) and leatherback (c, d) virtual hatchlings for each scenario. The size of the circle is proportional to the amount of the cell contribution. Positive residuals are in blue while negative ones are in red. Numbers represent scenarios.

Table 4.3: Cold-induced mortality (%) for virtual loggerhead and leatherback hatchlings for each scenario in 2017 and 2018. (Bold numbers indicate highest percentages).

Loggerhead							
15°C 2017	**Scenarios**						
Marine zone	1	2	3	4	5	6	7
Benguela Current	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Southern Ocean	11.7	7.8	7.8	1.9	1.8	15.1	12.2
15°C 2018							
Benguela Current	0.9	1.5	0	1.0	1.0	0.5	0.5
Southern Ocean	**25.5**	**18.1**	**18.0**	**19.9**	**19.3**	**22.8**	**15.7**
10°C 2017							
Benguela Current	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Southern Ocean	1.4	1.1	1.1	0.3	0.3	2.0	2.0
10°C 2018							
Benguela Current	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Southern Ocean	0.9	1.1	0.9	1.3	1.4	1.8	1.5
Leatherback							
15°C 2017	**Scenarios**						
Marine zone	1	2	3	4	5	6	7
Benguela Current	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Southern Ocean	13.5	**14.0**	**13.9**	4.2	4.0	**15.1**	12.2
15°C 2018							
Benguela Current	1.4	1.2	1.2	1.0	0.9	1.7	0.0
Southern Ocean	34.1	**49.8**	**52.4**	32.3	32.7	26.4	**52.2**
10°C 2017							
Benguela Current	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Southern Ocean	1.6	1.7	1.8	0.4	0.4	1.5	1.9
10°C 2018							
Benguela Current	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Southern Ocean	3.1	4.5	4.8	2.6	2.3	1.4	0.0

Comparison of loggerhead and leatherback dispersal patterns

Despite broad apparent similarities, a closer examination of our results revealed important differences in dispersal patterns of loggerhead and leatherback virtual hatchlings. Almost no virtual leatherback hatchlings were advected north into the Mozambique channel zone for the scenarios with no frenzy swim (scenario 4, 0.3%) or where they were completely passive (scenario 5, 0.4%) compared to >60% for loggerhead particles from the same scenarios (Table 4.2 and Fig. 4.3, 4.7). This is also evident on the 48 hrs maps ; Figs. 4.4e,I,c,g, 4.8). Additionally, the dominant end zone changed with a change in release location (scenario 6, 2017), being the Southern Ocean but the Agulhas Return Current with a change in date of release (scenario 7, 2018, Fig. 4.9), highlighting the impact of ocean variability near the nesting sites.

Similar to loggerheads, no virtual leatherback hatchlings encountered 10°C SST's in the Benguela Current zone in either years. However, some particles in the Southern Ocean zone encountered 10°C water for more than three days in both years. 2017 having lower mortalities (<2% for each scenario) and 2018 yielding higher potential mortalities for scenarios 3 with 4.8% and 4.5% for scenario 2 (Table 4.3). More leatherback particles had a 50% chance of mortality by experiencing 15°C SST's than loggerheads. Furthermore, percentages were more than double in the Southern Ocean in 2018 compared to 2017, with scenario 3 having the highest number (52.4%), followed by scenario 7 (52.2%), scenario 2 (49.8%), scenario 1 (34.1%), and scenarios 5, 4, 6 in descending order.
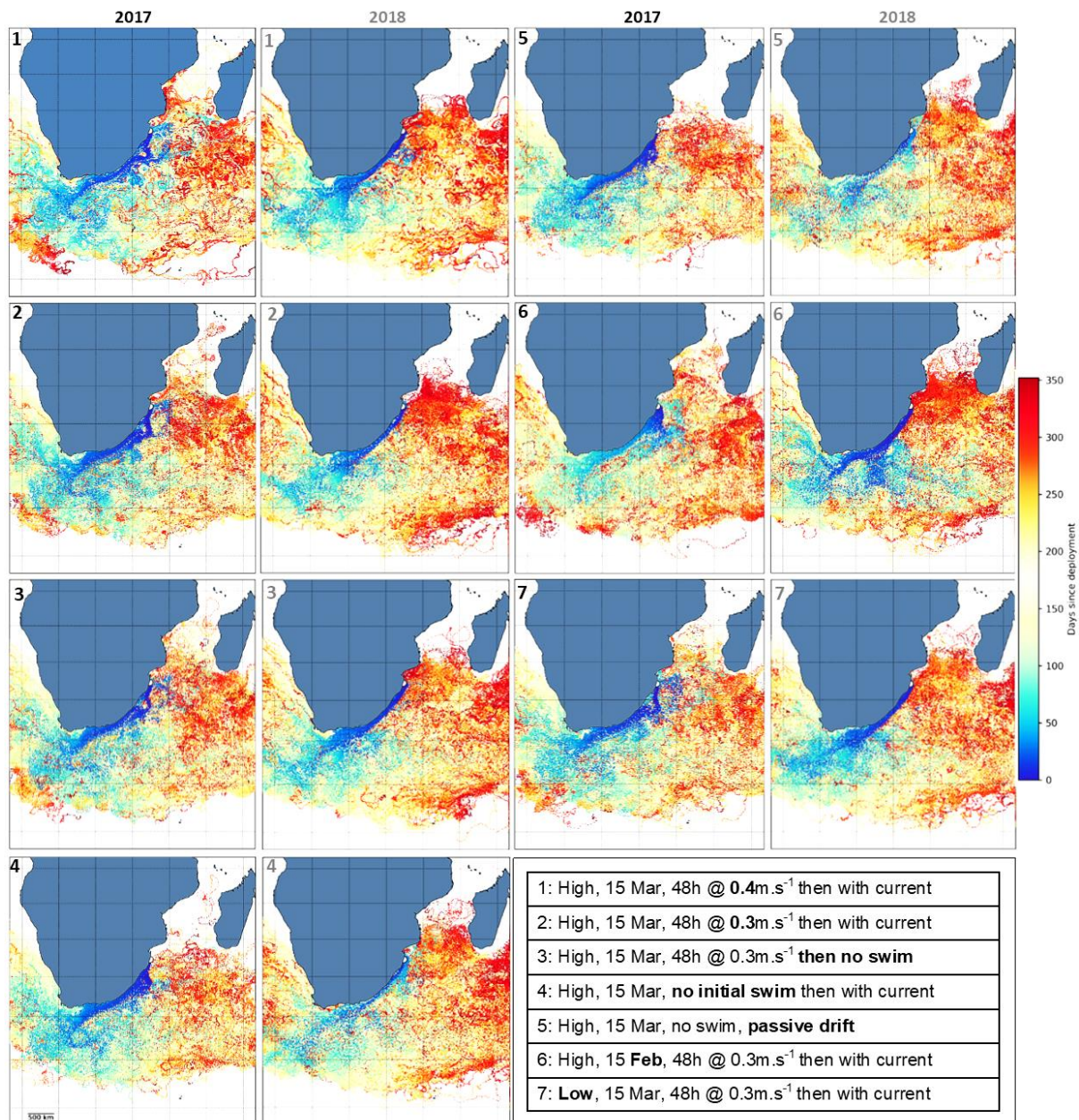
Figure 4.7: Comparison of leatherback virtual hatchling trajectories after 365 days of modelled simulations in 2017 and 2018 for each scenario. The white circle represents the release location.
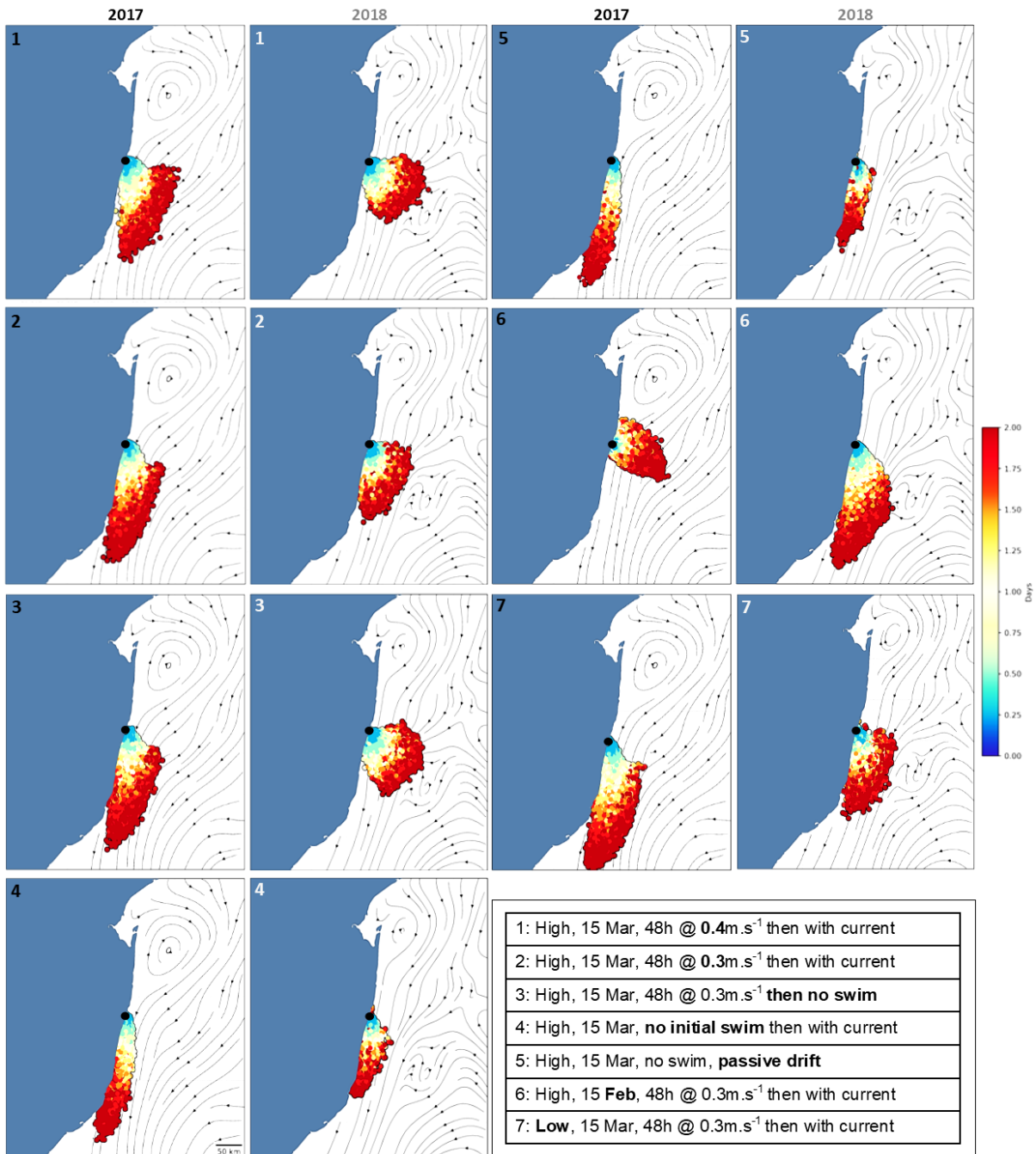
Figure 4.8: Comparison of leatherback virtual hatchling trajectories after 2 days of modelled simulations in 2017 and 2018 overlaid onto streamlines of the surface current velocities for each scenario. The black circle represents the release location.
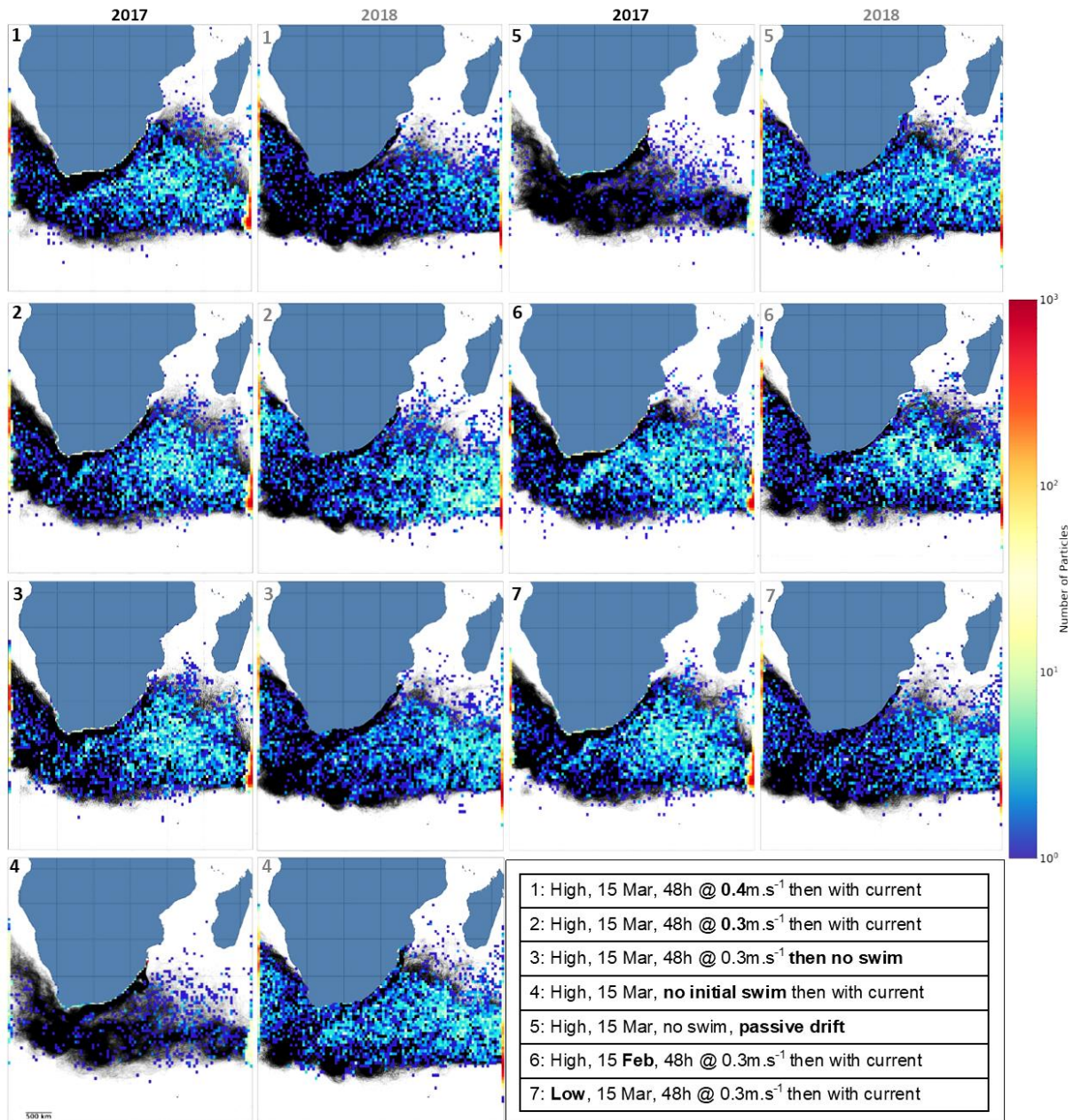
1: High, 15 Mar, 48h @ **0.4**m.s^{-1} then with current

2: High, 15 Mar, 48h @ **0.3**m.s^{-1} then with current

3: High, 15 Mar, 48h @ 0.3m.s^{-1} **then no swim**

4: High, 15 Mar, **no initial swim** then with current

5: High, 15 Mar, no swim, **passive drift**

6: High, 15 **Feb**, 48h @ 0.3m.s^{-1} then with current

7: **Low**, 15 Mar, 48h @ 0.3m.s^{-1} then with current

Figure 4.9: Particle density of virtual leatherback hatchling final position and full trajectories (black lines) after 365 days of modelled simulations in 2017 and 2018 for each scenario. The white circle represents the release location.

Discussion

Post-hatchling dispersal pathways in the SWIO

The simulations of the present study provided insight into a significant knowledge gap regarding the spatial distribution of post-hatchling sea turtles and presents the first estimate of neonate dispersal in the SWIO. The South African component of the SWIO turtle rookery is unique because hatchlings dispersing from these nesting beaches enter very complex and dynamic oceanic conditions, linking two extremely contrasting ocean basins. In this study we simulated the potential dispersal pathways of loggerhead and leatherback sea turtle hatchlings in the two ocean basins and assessed the effect of swimming behaviour on their dispersal trajectories, as well as compare the effect of varying coastal and oceanic conditions on these trajectories. Similar to other research, our model suggests that post-hatchling dispersal is influenced by a combination of oceanic variability and hatchling swimming behaviour (Gaspar et al., 2012; Putman and He, 2013; Putman and Mansfield, 2015; Gaspar and Lalire, 2017).

Virtual hatchling trajectories in the SWIO have a core dispersal area for both species under the direct influence of the AC during the first month of distribution (Fig. S4), moving rapidly south-eastward along the coast within the current. After reaching the southern tip of Africa, virtual hatchlings can then follow two main pathways. The first and main pathway remains under the influence of the AC and leads virtual hatchlings into the Agulhas Retroflection and then into the eastward flowing Agulhas Return Current, returning virtual hatchlings to the warm waters of the South Indian Ocean. The second pathway entrains virtual hatchlings into the Agulhas Rings and forces them to cross ocean basins to be transported into the SE Atlantic Ocean. This is in accordance with oceanographic and modelling research that found that 60% of modelled Agulhas Current flow follows the retroflection and 40% flows into the SE Atlantic (Hermes et al., 2007). From there trajectories can potentially subdivide into two minor pathways and exhibit a general north-westward direction: a Northern path that can interact with the South African continental slope and the cold Benguela Current Upwelling System, and a Southern route further south with substantial cooling of the water due to the adjacent Southern Ocean (Dencausse et al., 2010; Holton et al., 2017).

The results revealed that the simulated active and passive dispersal trajectories of virtual hatchlings are broadly similar and mostly influenced by ocean currents during their first year of dispersal, validating our first hypothesis that post-hatching dispersal would mainly be controlled by water circulation. This finding is in accordance with other studies for several sea turtle populations and species (Gaspar et al., 2012; Putman and He, 2013; Putman and Mansfield, 2015; Gaspar and Lalire, 2017). The similarity between the passive and active dispersal simulations in this study indicates that the simulated swimming speeds of virtual hatchlings are very weak compared to the current velocities of the study region. This is not surprising as the AC is a fast-flowing western boundary current and evidence suggests that even bigger juvenile turtles (under 30 cm) have average swimming speeds under 1 km/h (Abecassis et al., 2013) which is much less than the AC (mean surface velocity exceeding 3-4 km/h; Lutjeharms, 2006). This finding is similar to other dispersal studies where strong western boundary currents are present, such as the Kurushio Current in the Western Pacific, which controls leatherback and loggerhead hatchlings dispersal for the first two years of their lives (Ascani et al., 2016; Gaspar & Lalire, 2017). As hatchlings grow and reach 3 to 4 years, their swimming abilities improve, enabling them to actively target favourable habitats.

Oceanic variability

After a year of simulated dispersal in the two ocean basins, each scenario dispersed virtual hatchlings in highly variable oceanic areas, with a high variation between 2017 and 2018 in terms of the number of virtual hatchlings present in each oceanic zone. Indeed, local oceanic conditions varies considerably between years, with 2017 having landward current pushing particles onto land while in 2018 the dominant current is parallel to the coast with the presence of an eddy, taking particles away from the nesting beach southward (Fig. S5). Oceanic circulation at the nesting site is strongly influenced by eddies which develop in the Mozambique channel and move along the eastern coast of South Africa. Due to these strong mesoscale features, there is a high level of variability in oceanic conditions offshore of the nesting beaches but also along the entire length of the AC and South African coast (Lutjeharms et al., 2007; Braby et al., 2016). These eddies likely entrain hatchlings in south-westerly trajectories due to the influence of the fast flowing Agulhas Current, however some may be advected

north of the nesting site (Casal et al., 2009) if a strong eddy is present at the time of release (as in 2017). This finding is supported by evidence from several studies showing that variability in oceanic currents is the main driver of hatchling dispersal (Luschi et al., 2003; Hays et al., 2010; Okuyama et al., 2011; Putman et al., 2012; Shillinger et al., 2012; Scott et al., 2017). The high variability in ocean currents within or adjacent to the AC provide strong evidence that virtual hatchlings can become trapped and retained in eddies near or downstream of their release locations or entrained into the inshore northward current. This is supported by stranding data showing that most strandings of sea turtle hatchlings occur along the south coast of South Africa with very little on the east coast (close to the release site; De Wet, 2012).

Hatchling swimming behaviour

Our second hypothesis on the other hand, proposing that hatchling swimming behaviour will have little effect on their trajectory, was not entirely supported in this study. While our research highlights the importance of ocean currents when simulating sea turtle oceanic dispersal, we tested a variety of hypothetical swimming scenarios and conclude that the dispersal of post-hatchlings is affected by active swimming. This finding agrees with growing evidence showing that hatchling swimming behaviour can influence dispersal estimates (Hamann et al., 2011; Gaspar et al., 2012, 2017; Scott et al., 2012; Briscoe et al., 2017).

The active dispersal simulation involving the fastest swimming speed during the frenzy period (scenario 1) was the scenario with the lowest amount of stranded virtual hatchlings and is in accordance with stranding data and is thus hypothesised to be the closest to reality. Indeed, a detailed observation of the density plots and the particle counts of our passive and active simulations revealed that passive virtual hatchlings have higher retention rates at the nesting site than that of active swimming scenarios, which is not in accordance with stranding data (De Wet, 2012) and long-term field observations (R, Nel pers. Comm). Consequently, virtual hatchlings from scenarios with faster swimming speeds are less likely to be trapped in the inshore northward current or meanders off the AC and demonstrates that post-hatchlings do engage in active swimming even though the effects might not be as pronounced at first due to the strong current velocities of the AC.

Thermal environment and potential mortality

As ectotherms, the growth and survival of sea turtles is likely influenced by sea surface temperature (Mansfield & Putman, 2013; Christiansen et al., 2016; Gaspar & Lalire, 2017). Low temperatures are known to negatively affect sea turtles whose internal temperature follow that of the ambient temperature closely. A decline in SST can cause a similar decrease in circulation, oxygen uptake, and metabolic processes, causing marked physiological changes potentially leading to decreased growth and cold stunning (Hochscheid et al., 2004). The SST analysis in our study revealed that survival rates and thus fitness of virtual hatchlings varied depending on the location of the particles end trajectory in the different marine zones. Of the two zones where hypothermia could occur, the Southern Ocean zone had much higher potential mortality at 15°C for more than 14 days than the Benguela Current zone. Surprisingly, no virtual hatchlings encountered SST of 10°C or less for more than three days. However, due to the strong variability in oceanic conditions, validating this finding should be an important priority for future research and the model should be run for several years and for longer periods to assess if this finding represents real conditions and whether seasonal and interannual signals can be quantified. Additionally, the highest mortality at 15°C in the Southern Ocean for both species was with a change in the release date, suggesting that hatchlings that enter the ocean later their peak hatching time, they will potentially suffer higher mortality due to hypothermia, depending on the offshore oceanic conditions affecting their dispersion.

Furthermore, beyond apparent similarities between the active and passive dispersal pathways, cold-induced mortality changed with a change in swimming behaviour. There was higher potential mortality at 15°C when virtual hatchlings had higher swimming speed during the frenzy (scenario 1) and took more particles in the Southern Ocean, suggesting that it is not the SE Atlantic and BC that are a death trap for post-hatchlings dispersing in the SWIO, as was previously believed, but in fact the Southern Ocean zone. Furthermore, the strong variability in mortality of virtual hatchlings in the Southern Ocean zone illustrates how the SST in this oceanic region can vary between years and how it can affect post-hatchling fitness and survival. The higher potential mortality observed in 2018 might thus be a result of colder SST (below 15°C) for longer periods of time below the minimum tolerated temperature at which post-hatchlings will likely die. Abecassis et al., (2013) found that juvenile loggerheads in the north Pacific

occurred most frequently in temperatures of 15.6 to 17.1°C, which is cooler that what we anticipated to be the preferred thermal range but still within the thermal tolerance of both loggerhead and leatherback post-hatchlings. Consequently, it appears that the oceanic region where post-hatchling disperse can significantly affect their fitness and survival and that virtual hatchlings dispersing in the Southern Ocean south of 40°S have high probability (50%) of encountering lethal temperatures.

Favourable conditions of greater food availability are expected to be correlated with greater primary productivity and chlorophyll concentrations which are generally associated with features such as eddies and fronts (Polovina et al., 2000). This is because upwellings occur at the centre of eddies and convergence at the edge, where forage and preys concentrate (Polovina et al., 2006). This suggests that post-hatchling sea turtles would be able to reach more favourable developmental habitats through directional swimming and consequently increasing their fitness. Although feeding and growth rates of turtles generally decrease at colder temperatures (Hochscheid et al., 2004), the higher food availability might compensate for this and be beneficial to young turtles, as would be the case for virtual hatchling entering the SE Atlantic. This zone is highly productive (Shannon & Nelson, 1996; Hutchings et al., 2009), and might be favoured due to increased foraging opportunities. Thus, it appears that there is a trade-off between a suitable thermal environment and food availability (usually found in colder waters) and the survival of neonate turtles might depend on their ability to reach and remain in habitats offering both warm water and food resources (Gaspar & Lalire, 2017). The availability of thermally beneficial habitat (SST) and food resources are potentially the two most important factors affecting the fitness and survival of neonate sea turtles, as was found by other studies (Abecassis et al., 2013; Mansfield et al., 2014; Ascani et al., 2016; Christiansen et al., 2016; Varo-Cruz et al., 2016).

Dissimilarities between species

The subsequent part of the second hypothesis stating that post-hatchling dispersal is independent of species was supported in this paper. Both species follow very similar pathways and their dispersal was mostly driven by ocean currents. However, detailed observations revealed that there were interspecies differences. The simulation outputs of our one-year models show that virtual hatchling emerging from South African

beaches reach two main different oceanic areas that in turn affect their fitness and potential survival. The highly dynamic and complex oceanic conditions of the region present hatchlings with diverse marine habitats that confer varying levels of fitness to neonate turtles. Virtual loggerhead particles appear to follow ring shedding events off the Agulhas retroflection and then are transported into the SE Atlantic zone with on average less lethal temperatures than the Southern Ocean zone where more leatherbacks particles occur. This dominant loggerhead dispersal pathway might be a result of their weaker swimming speed that carry them on the inshore of the AC as oppose to leatherbacks that could be entrained further offshore on the outer edge of the AC leading them further south. This is supported by the annual stranding data with only occasional leatherback strandings around South Africa while dozens of loggerheads are stranded each year after the hatching season along the south and eastern coastline of South Africa (De Wet, 2012).

Consequently, it appears that of the two dominant zones, the SE Atlantic confers higher fitness benefits to neonate turtles compared to the Southern Ocean. The higher potential mortality of leatherback virtual hatchlings in the Southern Ocean is consistent with the lack of recovery of the species compare to loggerheads exponential increase in the South African rookery (Nel et al., 2013), although different threats might apply at different life stages (cold-induced mortality for post-hatchlings and fisheries bycatch for adults). This is surprising as leatherback turtles are able to maintain higher body temperatures than the surrounding water (James and Mrosovsky, 2004; Bostrom et al., 2010), and we assumed that they would have a survival advantage if dispersed into colder waters. However, their thermal ability might only be effective at older stages which could explain why they have higher mortality than loggerheads in this study.

Interestingly, our findings coupled with satellite data from South Africa demonstrate that adult female post-nesting migrations (Luschi et al., 2006; Lambardi et al., 2008; Harris et al., 2017; Robinson et al., 2018), may be similar to our virtual hatchling dispersal found in this study, and provides further support for the hypothesis that adult foraging migrations reflect their previous experiences as hatchlings (Fossette et al., 2010; Godley et al., 2010; Hays et al., 2010; Scott et al., 2014). However, more satellite data on both adults and juveniles are needed to verify this hypothesis.

Implications for sea turtle fitness and conservation

Although virtual hatchlings did not encounter lethal temperatures in the other 5 marine zones, besides the Benguela Current and Southern Ocean zones, it does not imply that they are not at risks from other pressures. Climate change can also potentially affect hatchling fitness and survival. As a result of increased global temperature, incubation temperature is also expected to increase leading to skewed sex ratio (Hawkes et al., 2009). Additionally, increased incubation temperatures are predicted to shorten incubation period and produce smaller hatchlings with decreased crawling and swimming speed (Ischer et al., 2009; Sim et al., 2015). Sea turtles have the potential to mitigate the negative effects of changing environmental conditions and adapt to climatic changes by altering their nesting phenology (nesting earlier or later) or by expanding their range (poleward expansion; Hawkes et al., 2009; Rees et al., 2016; Butler, 2019). A change in the timing of nesting as a result of increased temperatures affecting the incubation environment, has already been reported in some turtle populations, selecting for cooler portion of the nesting season to maintain favourable thermal conditions (Mazaris et al., 2008; Saba et al., 2012). Nesting range expansion could be another adaptation to climate change, whereby under warmer global temperatures, new habitat becomes suitable for turtles to colonise (Pike, 2013a; Butt et al., 2016, Carreras et al., 2019). However, it does not imply successful recruitment if the subsequent dispersal thermal environment does not ensure post-hatchling survival, that is if the water temperatures are too low and prevent hatchling growth and survival. Our simulation results suggest that nesting earlier in the season or further south would result in higher potential mortality of post-hatchlings during their oceanic dispersal due to hypothermia. Thus, even if they incubate and hatch successfully by nesting earlier, later or further south, the majority of hatchlings may not survive. Hence, although sea turtles have the ability to adapt to climate change, population viability is dependent on survival across all life stages. These adaptations may only partially offset the impacts of climate change and may lead sea turtles to nest in suboptimal habitats resulting in ecological traps (Pike, 2013b; Patel et al., 2016Monsinjon et al., 2019).

Additionally, as post-hatchling turtles grow and increase in size, they become more vulnerable to bycatch in fisheries. There is a general paucity of information on the spatial distribution of juvenile sea turtles at sea and it is critical information to identify

high use areas and evaluate risks of interactions with fisheries required for adequate management strategies (Huang, 2015; Gaspar & Lalire, 2017). Intense and persistent (shelf or wind driven) upwelling located on the inshore edge of the current and occurring along the full length of the AC are persistent features of this region contributing to higher levels of primary production (Lutjeharms et al., 2000, 2005; Roberts, 2005; Smit et al., 2010). Additionally, as the shelf widens at the southern end of the AC, large meanders are created at the shelf edge of the Agulhas Bank and the AC becomes more unstable (Lutjeharms et al., 2003). As the current meanders further east, the Agulhas Return Current is characterized by areas of high productivity including frontal areas such as the Agulhas Return Front and the Subtropical front (in the Indian Ocean sector of the Southern Ocean; Naik et al., 2015). These are all areas of high productivity, presenting post-hatchlings with high foraging opportunities and might drive them to actively engage in habitat driven movements (Putman et al., 2012; Christiansen et al., 2016; Mansfield et al., 2014; Gaspar & Lalire, 2017). This hot spot area (Agulhas Return Current zone) may represent a key area to support high survival rates of post-hatchling turtles. However, as a result of their high productivity these areas are also targeted by fisheries and might represent regions of high overlap with sea turtles. This is supported by evidence showing that there is geographic overlap between post-breeding foraging adult leatherbacks and longline fisheries in the Agulhas Bank (De Wet, 2012; Luschi et al., 2006; Grantam et al., 2008; Petersen et al2009). Similarly, virtual hatchlings that were entrained north into southern Mozambique likely represent a separate group and may be a less important pathway depending on the local oceanic condition at the time of hatching. However due to the high fishing pressures occurring in this area and the presence of a strong prawn fishery (De Sousa et al., 2006), virtual hatchlings might be at risk of interactions with these fisheries.

The validation of model outputs remains challenging due to the paucity of direct observations of hatchling spatial distribution at sea (Hamann et al., 2011; Gaspar et al., 2012). Despite these limitations Lagrangian analyses and oceanographic models provide a first estimate of post-hatchling dispersal which can be enhanced and simulations re-run as our understanding of hatchling behavioural ecology improves. A shortcoming of our post-hatchling dispersal simulations is that our model does not incorporate detailed information about the local inshore currents present in the coastal

waters adjacent to the nesting beaches and thus might not represent the oceanic conditions of the frenzy accurately (Godley et al., 2010). Future research could assess the inshore currents off the rookery and add the subsequent data into the simulations to enhance our model. Secondly, the model could be improved and validated by using nano satellite and acoustic tags on post-hatchlings leaving the nesting beaches to obtain information on their initial frenzy behaviour (direction, duration, etc.; Dalleau et al., 2014; Mansfield et al., 2014; Christiansen et al., 2016). It would also be beneficial to identify optimal habitat (temperature and abundance of prey) for neonate turtles by adding primary production data to the model as a proxy for optimal foraging areas and identify hot spots of higher probability of turtle presence (Abecassis et al., 2013). This could then be overlaid onto fisheries data to identify and predict areas of interactions and potential bycatch for juvenile turtles. It would be equally beneficial to also include growth data under different temperature regimes and run simulations for longer time period (Gaspar & Lalire, 2017). Lastly, high-resolution ocean velocity fields from NEMO are only available from 2007 to present and it could also be advantageous to run simulations further back in the past and for longer durations for different years and would allow identifying dispersal origin and connections from other rookeries such as Australia for loggerheads and Gabon for leatherbacks (Putman et al., 2014). Thus, further simulations incorporating the data mentioned above would be valuable to confirm the results described in this study and improve our knowledge of this cryptic stage of sea turtle life cycle.

Conclusion

Despite limitations and the general paucity of information regarding the spatial ecology of neonate turtles during the lost years, our simulations provide a first estimate of loggerhead and leatherback post-hatchling dispersal in the SWIO. The model combined an individual based particle tracking model with empirical data of hatchling swimming behaviour to identify dispersal pathways of two species of sea turtles nesting in South Africa. The post-hatchling dispersal of both loggerhead and leatherback turtle populations in the SWIO is unique because it encompasses two very contrasting ocean basins: the warm SWIO and the cold SE Atlantic Ocean basins. The AC is one of the strongest western boundary current in the world, which forms a conduit for inter-ocean exchange (Beal et al., 2011), and provides sea turtle hatchlings

in the Southwestern Indian Ocean with a unique habitat and suite of challenges. Although oceanic currents appear to be the main factor influencing the oceanic dispersal of neonate turtles, our results show that hatchling swimming behaviour also shape their dispersal pathway. Simulation outputs from this research provide a better understanding of the at-sea distribution of sea turtles during their early life stages by identifying developmental areas and thus could inform management and generate effective conservation measures for threatened species (Casale & Mariani, 2014; Gaspar & Lalire, 2017). Notwithstanding that we still do not know where South African juvenile turtles are distributed and only then could we conserve them effectively. Since static protected areas may be inadequate for highly migratory species such as sea turtles, dynamic protected areas as well as temporary spatial closures may be more suitable and allow connectivity between developmental, foraging, and reproductive areas (Grantham et al., 2008; Maxwell et al., 2015).

Supplementary Information
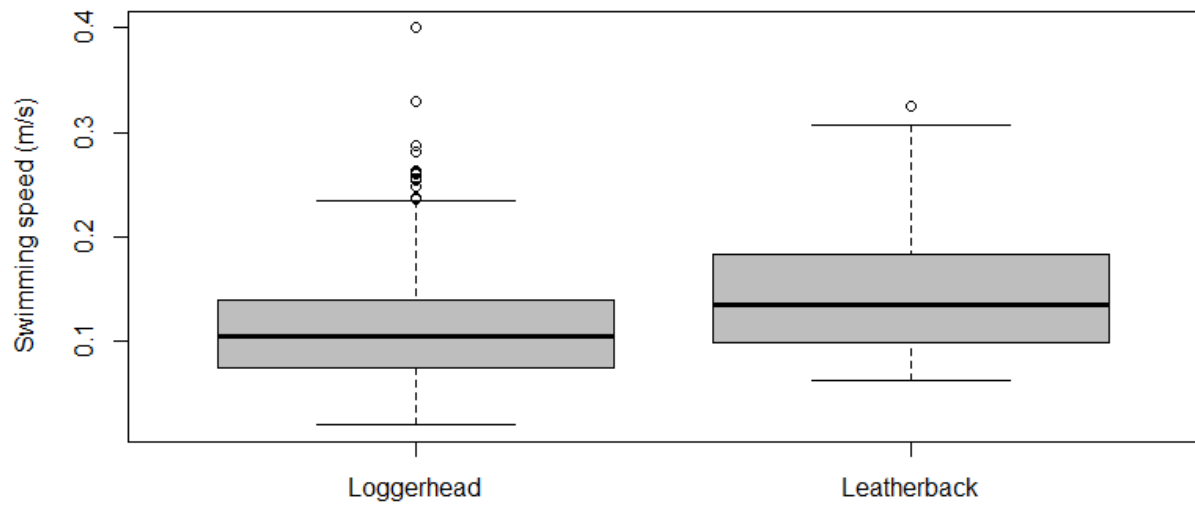
Figure S4.1: Swimming speeds of loggerhead and leatherback hatchlings that underwent locomotor trials in the field (Cc = 412, Dc = 48). Data are presented as median (black line), inter-quartile range (box), first and fourth quartiles (whiskers) and outliers (dots).
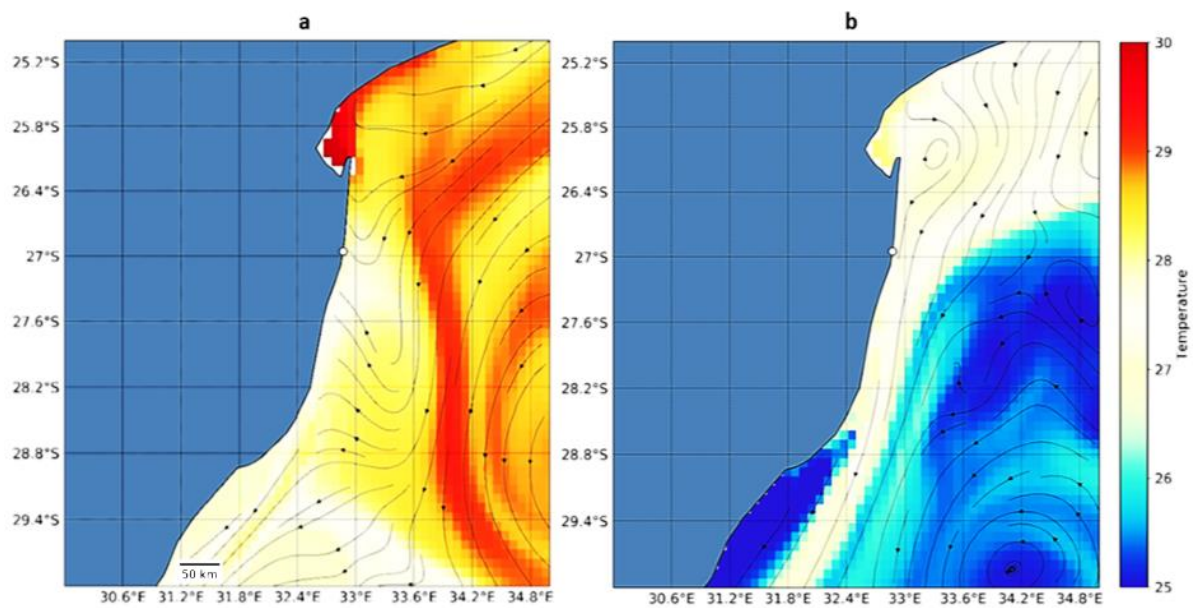
Figure S4.2: An illustration of the surface current velocities and SST around the high nest density beach (represented by the white dot) on the 15th of February (peak loggerhead hatching time) in 2017 (a) and 2018 (b).

Chapter 5. Intrapopulation variation in foraging strategy of nesting loggerhead turtles revealed by satellite tracking and stable isotope analysis

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Diane Z. M. Le Gouvello, Linda R. Harris, Ronel Nel, Stephan Woodborne

Abstract

Understanding and identifying foraging grounds and migratory connectivity is critical for adequate management and conservation of migratory species. Recently, a foraging dichotomy has been found for female sea turtles, with smaller females associated with oceanic habitats and larger females inhabiting neritic areas. We tested this for loggerhead turtles nesting in South Africa using a combination of satellite tracking and stable isotope analysis to infer their foraging areas and investigate the relationship between body size, and foraging strategy. We collected skin epidermis for stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope analysis from 11 nesting females equipped with satellite tags and an additional 307 samples from untracked females over three nesting seasons. We used k-means clustering to partition turtle isotope values and stable isotope Bayesian ellipses (SIBER) to identify isotopic niche areas. Two distinct clusters emerged based on δ^{13}C values (with a mean of δ^{13}-14.79‰ for the depleted cluster and δ^{13}-12.62‰ for the enriched one) and all size classes had a high degree of niche overlap. However, the SIBER analysis indicated that larger turtles have the smallest isotopic niche of all size classes, highlighting a diet-specialist foraging strategy. We could not conclusively identify distinct isotopic patterns to support variation in foraging strategies (neritic versus pelagic) for South African nesting loggerheads since all tracked turtles migrated to the same area. Additionally, our findings support the hypothesis that nesting beach location within 200-km long rookery may be responsible for a dichotomy in migratory routes and foraging area origins and provide insight for future research at this nesting ground. Combining stable isotope analysis with satellite tracking allowed to greatly increase the sample sizes permitting studies to answer population level questions.

Keywords: sea turtles; foraging strategy; body size; satellite tracking; stable isotope analysis

Introduction

Intraspecific variation in foraging strategies and resource use within populations may contribute to differences in performance and fitness traits such as reproductive output and survival, leading to alternative life histories (Hatase et al., 2002a; 2013). Consequently, differences in habitat and resource use may contribute to variation in fitness among individuals. It has been widely accepted that adult female sea turtles exhibit fidelity to foraging grounds and were believed to be obligate benthivores in neritic habitats (e.g., Bjorndal, 1997; Musick & Limpus, 1997; Broderick et al., 2007). However, recent studies have revealed that some individuals forage on planktonic prey in oceanic habitats, indicating a dichotomy in foraging strategies (e.g., Hatase et al., 2002a; Ceriani et al., 2012; Vander Zanden et al., 2014), contrasting with the commonly accepted model of sea turtle life history. Given this new information with evidence from the Atlantic and Pacific Oceans, it is not yet clear how widespread this dichotomy is and if it is also apparent for Indian Ocean loggerhead turtles.

Marine turtles have complex life histories, with changes in diet and habitat at different life stages. After emerging from nests on sandy beaches, sea turtle hatchlings swim offshore and are carried to oceanic habitats, feeding primarily on neustonic items indicative of a pelagic diet (Witherington, 2002; Boyle & Limpus, 2008). Juveniles then recruit to neritic areas, where they mature and forage mostly on benthic crustaceans (Bolten, 2003). This original hypothesis of an ontogenetic habitat shift from pelagic to neritic environments is thought to be triggered by increased food demand necessary to reach sexual maturity and maximise the amount of energy allocated to egg production (Bjorndal et al., 2000; Bolten, 2003; Avens et al., 2015; Ramirez et al., 2017).

Recent research has identified two distinct size-related foraging strategies in adult sea turtles, with small females foraging in pelagic habitats (> 200 m water depth) and feeding on nutrient-poor planktonic prey (e.g., jellyfish, salps, and other gelatinous items), whereas large females occur in neritic areas (< 200 m water depth) and feed primarily on nutrient-rich benthic prey (e.g., molluscs, crustaceans; Hatase et al., 2004, 2008, 2010; Hawkes et al., 2006; Eder et al.,2012; Vieira et al., 2014). This has important implications because fitness is positively correlated to body size in marine turtles (Frazer & Richardson, 1986; Hays & Speakman, 1991; Van Buskirk and Crowder, 1994; Broderick et al., 2003; LeBlanc et al., 2014). Large neritic-foragers

have higher fitness, with larger clutches (Zbinden et al., 2011), shorter remigration intervals (Hatase et al., 2004; Vander Zanden et al., 2014), and greater cumulative reproductive outputs, than small oceanic foragers (Hatase et al., 2013). Although the mechanisms responsible for maintaining intrapopulation variation in the use of foraging habitats by adult sea turtles are still unknown, they have the potential to influence turtles' reproductive output and ultimately affect population growth.

This size-related difference in foraging strategies by sea turtles has been highlighted using a combination of satellite telemetry and stable isotope analysis (Ceriani et al., 2012, 2014; Seminoff et al., 2012; Hatase et al., 2010, 2013). Acquiring knowledge on migratory behaviour and movement patterns is inherently challenging for highly migratory species such as sea turtles that are long-lived, exhibit late sexual maturity and spend the majority of their time in the marine environment (Schofield et al., 2006; Seminoff et al., 2012). Recent technological advances in genetic analyses, satellite tagging, and stable isotope analyses have greatly enhanced our knowledge of migratory connectivity (Ceriani et al., 2012, 2014). Stable Isotope Analysis (SIA) particularly has increasingly been used as a cost-effective and rapid tool for studying migratory behaviours (Rubenstein & Hobson, 2004; Hobson et al., 2010; Ramos & Gonzalez-Solis, 2012). Isotopic composition of consumer tissues integrates information from their foraging environment and provide evidence about their previous location (DeNiro & Eptstein, 1978, 1981). As sea turtles rarely feed during the nesting season and skin tissues have a slow turnover rate (from 4 to 8 months), their isotope signature reflects the prey consumed at the foraging grounds before migrating (Seminoff et al., 2006; Reich et al., 2008; Vander Zanden et al., 2010, 2013).

In the marine environment, both carbon and nitrogen stable isotope ratios can provide valuable information on foraging habitat and turtles generally have higher $\delta^{13}C$ and $\delta^{15}N$ values in neritic environments due to the differences in primary producers on which they feed (Michener and Schell, 1994; McCutchan et al., 2003). Additionally, natural isotopic latitudinal gradients for plankton $\delta^{13}C$ also exist resulting in predictable broad ocean-basin scale isotopic gradients (or isoscapes) such that warmer waters generally lead to enriched $\delta^{13}C$ values (Hofmann et al., 2000; Graham et al., 2010, McMahon et al., 2013). Similarly, nearshore and benthic systems have higher nutrients concentrations and productivity and are typically more $\delta^{13}C$ enriched than offshore, pelagic systems (France, 1995). Using a combination of satellite tracking and stable

isotope analysis has proven to be a powerful tool to infer migratory routes and foraging grounds of marine organisms including seabirds (Phillips et al., 2009; Jeager et al., 2010; Cruz-Flores et al., 2018), fin whales (Bentaleb et al., 2011), sea lions (Sepulveda et al., 2015), and sharks (Carlisle et al., 2015). Thus, it is possible to study the ecological connectivity (movement of individuals between spatially distinct locations; Harrison & Bjorndal 2006) of sea turtle migration from foraging areas to nesting grounds.

We aimed to test whether there is a dichotomy in foraging strategies (neritic/pelagic) in the loggerhead turtles nesting in South Africa, and if so, if it is correlated with their fitness (size). We did this by combing satellite tracking and stable isotope analysis to infer foraging areas used by South African loggerheads. Recognizing that sea turtle reproductive output increases with size (Van Buskirk & Crowder, 1994), we worked on the premise that larger turtles will have higher fitness and hypothesised that pelagic habitats associated with smaller females are less profitable and offer less nutritious prey than neritic foraging areas (Hatase et al., 2008). We hypothesised that: (1) body size is correlated with foraging strategy and that this be reflected in the isotopic ratios of turtle tissues; (2) turtles foraging in more pelagic habitats will be smaller and have lower δ^{13}C and δ^{15}N values than those foraging in neritic areas. We further hypothesized that stable isotope analysis is an adequate tool to assign large-scale foraging areas to migrating sea turtles and predict that turtle isotope values will reflect that of their foraging grounds.

Methods

Ethics statement

Satellite tagging was undertaken with ethical clearance from the Nelson Mandela University Animal Ethics Committee: A13-SCI-ZOO-012, and turtle tissue collection was allowed with permission from the iSimangaliso Wetland Park Authority, Ezemvelo KwaZulu-Natal Wildlife, and Department of Environmental Affairs: Oceans and Coasts (permit numbers: RES2013/10, RES2014/64, RES2015/69, RES2016/67, RES2017/73, & RES 2018/68).

Study site

The study took place on the north-eastern coast of South Africa in iSimangaliso Wetland Park, Kwa-Zulu-Natal (Fig. 5.1). iSimangaliso is a UNESCO World Heritage Site, Ramsar Site, and comprises contiguous terrestrial and marine protected areas (MPAs). The shoreline is predominantly made up of intermediate beaches, with some coarse-grained, steep reflective beaches, interspersed with mixed shores and rocky outcrops (Harris et al. 2011). The beaches form the southernmost nesting grounds of loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles in the world (~27°S). The rookery is approximately 200 km long and supports nesting by 1000 loggerhead females and <100 leatherback females each year (Nel et al. 2013). The majority of loggerhead nests are laid in the northern part of the rookery, and particularly for 5 km north of Bhanga Nek in the loggerhead nesting hotspot.
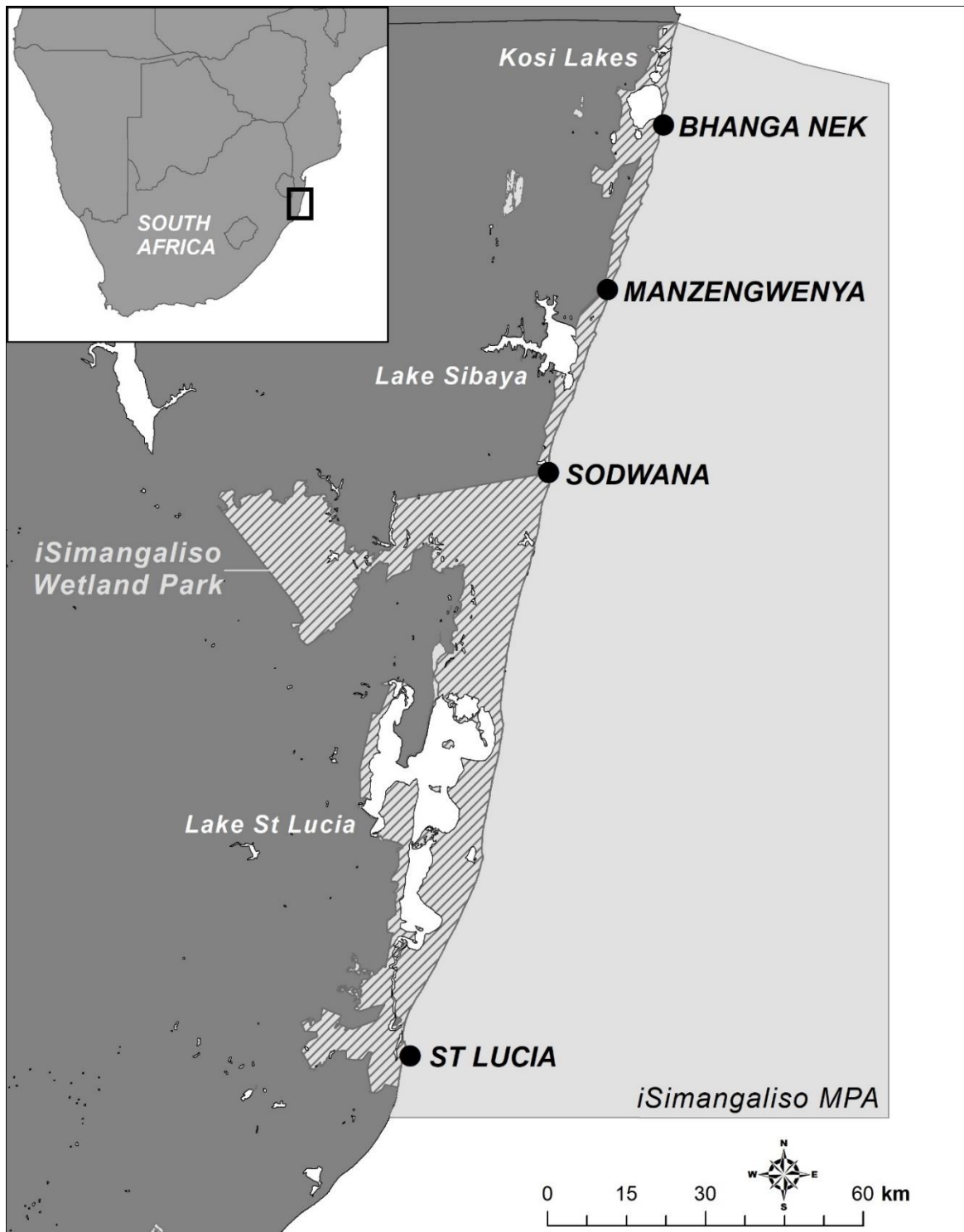
Figure 5.1: Location of the study area in the iSimangaliso Wetland Park in north-eastern South Africa indicating contiguous terrestrial reserves (hatched grey) and marine protected areas (filled light grey). Turtle nesting is predominantly along the Maputaland coast; nest density is high at Bhanga Nek, and decays to the south, with low nest density at Manzengwenya and southwards. Major lakes are shown in white.

Satellite tagging

Satellite tracking data come from previous studies by Harris et al. (2015, 2018). Satellite tags were attached after the females had nested and standard practices for transmitter attachments were followed (Harris et al., 2015). Twenty-four loggerhead turtles were each fitted with a SPOT 5 (Wildlife Computers) or Kiwisat (Sirtrack) tag in December 2010 and January 2011. In 2010 loggerheads were satellite tagged in the proximity of Bhanga Nek, and in 2011/2012 they were tagged near Manzengwenya (Fig. 5.1). Tags were attached directly to the loggerhead's hard shell using epoxy adhesive and epoxy cement and painted with anti-fouling paint. The females were tracked using the Argos system (CLS, 2015), running continuously. Previous findings from Harris et al. (2017) indicated that loggerheads use one of 3 migration corridors during their post-nesting migration: northwards into Southern Mozambique; across the Mozambique Channel to Northern Madagascar; and southwards to the Agulhas Bank. More than 80% of the population uses the first corridor travelling to southern Mozambique. Skin biopsies were collected for only 11 of the 24 turtles, and thus for this study, the data for those females only were used.

Stable isotope analysis

Skin biopsy samples were rinsed with distilled water, the surface epidermis (*stratum corneum*) was removed from the underlying tissue (*stratum germinativum*) and homogenized with a scalpel blade. The samples were then oven-dried at 60°C for a minimum of 48 h. Since it has been shown that it is not necessary to remove lipids for samples where surface epidermis was removed and that they do not affect the isotopic values (Tucker et al., 2014), lipids were not removed except for 10 samples that were too small to remove the epidermis (2 mm biopsy). Lipid extraction was carried out on the later samples using a modified Folch method (Folch et al., 1957). Samples were immersed in 2:1 chloroform: methanol solution for 50 min to remove free lipids, and then oven-dried at 60 ° C for 2 h. All skin (non-delipidated) samples were rinsed in distilled water and oven-dried at 60°C for 24 h ground to a fine powder using mortar and pestle. Protein aliquots of 0.5 mg were weighed into pre-cleaned tin capsules. Analyses of carbon and nitrogen isotope ratios followed the method described in Vander Zanden et al. (2012) and were undertaken at the Stable Isotope Analysis Laboratory of the Mammal Research Institute (Pretoria, South Africa). Samples were

analyzed by continuous-flow isotope ratio mass spectrometry using a Flash EA 1112 Series elemental analyzer connected via an interface (Conflo III) to a Thermo Fisher Scientific Delta V Plus isotope ratio mass spectrometer. A calibrated laboratory standard (Merck Gel, $\delta^{13}C$ = -20.6‰ and $\delta^{15}N$ = 6.8‰) and blank samples were run after every 12 unknowns. Stable isotope ratios are expressed in delta (δ) notation, defined as parts per thousand (‰) deviation from a standard material:

$$\delta R\ ‰ = ([R_{sample} / R_{standard}] - 1)\ x\ 1000$$

where R is the heavy-to-light isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). The standard material is Vienna Pee Dee Belemnite (PDB) limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. The precision of the standard analyses was 0. 06 ‰ for $\delta^{13}C$ and 0.07 ‰ for $\delta^{15}N$. All samples were run in duplicate producing a mean and standard deviation for each sample.

Statistical analysis

Statistical analyses were performed in R, version 3.0.2 (R Development Core Team, 2014), and all statistical conclusions were drawn with a significance value of $\alpha \leq 0.05$. We used a cluster analysis with the function k-means as the partitioning algorithm (package NbClust in R; Hartigan and Wong, 1979) to determine the number of clusters that best fit the distribution of the stable isotope signatures of individual turtles sampled (Kaufman and Rousseeuw, 1990). K-means clustering uses an algorithm to partition a dataset into multiple groups and assigns each data point to its closest centroid such that the sum of squares of each observation to their assigned cluster center is minimised (Kaufman & Rousseeuw, 1990). This method has been used previously on stable isotopes to classify birds and marine mammals into discrete isotopic groups (Pomerleau et al., 2014; Steenweg et al., 2017). We used the Euclidian distance algorithm to define the total-cluster variation as the sum of squared distances between items and the corresponding centroid. The silhouette method was used to validate and determine the optimal number of clusters required for each isotope, and the mean silhouette width was used to identify the best fit for numbers of clusters (Charrad et al., 2014). The silhouette approach measures the quality of a cluster by determining how well each observation lies within its cluster such that the silhouette width provides

an indication of the strength of cluster membership for each observation (value ranging from 0 to 1, with 1 being the strongest).

We used the Bayesian framework (SIBER package; Jackson et al., 2011) to analyze stable isotope data in the context of isotopic niche width and individual female size. This method is based on Bayesian inference techniques and allows for robust measures of isotopic niche width of both community members and entire communities. SIA provides information on both resource and habitat factors commonly used to define ecological niche space and thus, isotopic niche is likely to be closely correlated with the trophic or spatial niche of an organism (Mancini and Bugoni, 2014). In this context, an isotopic niche is defined as an area (in δ-space) with isotopic values (δ-values) as coordinates (Newsome et al., 2007).

We used SIBER to fit bivariate ellipses to stable isotope data using Bayesian inference to describe and compare their isotopic niches. Then, to compare individual groups with each other within a single community, we used the Standard Ellipse Area (SEA) (calculated on the posterior distribution of the covariance matrix for each group), yielding the Bayesian SEA and adding the maximum likelihood estimates of SEA to Bayesian estimates. To evaluate if turtle foraging in different areas differ in size, we compared SCL of the turtles from the two clusters with a t-test and then generated SIBER ellipses of niche width based on turtle size. Data were first tested for normality and homogeneity of variance using Shapiro-Wilk and Leven's test, respectively, to confirm t-test assumptions were met. To investigate if carbon and nitrogen isotope values differ with size, turtles were classified based on SCL values of: (a) < 800 = small (n = 62); 800 – 849 = medium-small (n = 120); 850 – 900 = medium-large (n = 66); > 900 mm = large (n = 11).

We then intended to separate the tracking data into groups based on their final location to determine if stable isotope analysis can be used to identify foraging areas for adult sea turtles. This was planned to be done using discriminant function analysis to assign non-satellite tracked individuals to a foraging area based on their stable isotope values, where the $\delta^{13}C$ and $\delta^{15}N$ ratios of the 11 satellite-tracked females with known foraging areas would be used as a training data set to define the discriminant functions. However, we could not use this method because all tracked turtles with associated stable isotope samples went to the same foraging area.

Results

Satellite telemetry and foraging grounds

The tracked turtles for which skin samples were collected were tracked for 4 to 490 days (two-thirds of the tags lasting 4-5 months or more; for further details on tracking data see Harris et al., 2017). These turtles moved across a narrow range of latitudes, closely following the coast northwards into southern Mozambique, ranging from 27.5°S at the nesting grounds to 18.5°S at the northernmost foraging ground. Female loggerhead turtles were tracked to only one trajectory endpoint foraging ground, remaining exclusively in Mozambique between the Bazaruto Archipelago and the Sofala Bank (off Beira) (Figure 5.2). Another two migration corridors were identified (for which no skin samples were available for these tracked turtles), and foraging grounds were grouped by proximity (and/or bioregion) of their final destinations: north-east across the Mozambique Channel to Northern Madagascar (Malagasy Corridor); and southwards in the Agulhas Current along the South Africa coast to the Agulhas Banks (Agulhas Corridor) (Harris et al., 2017).
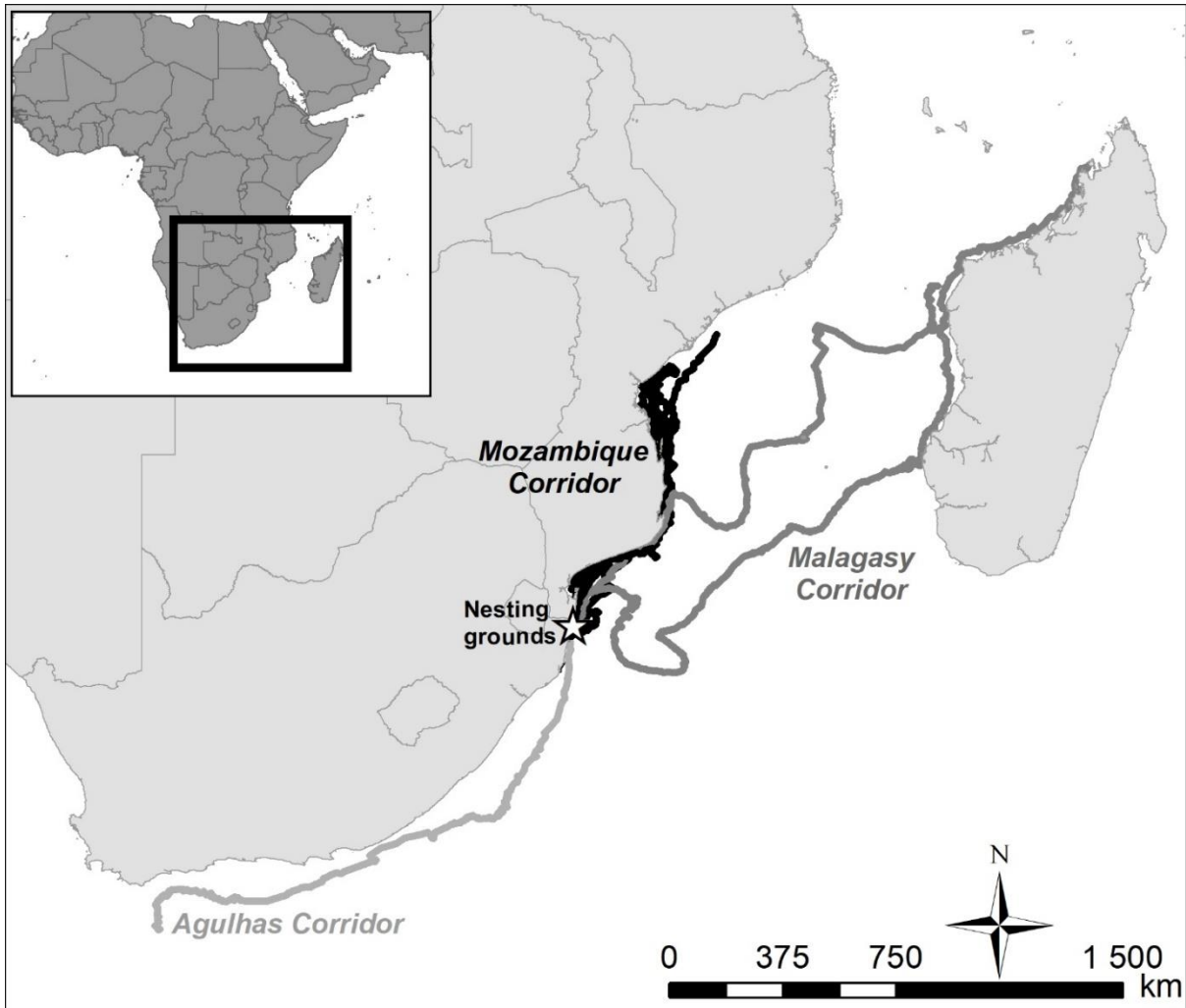
Figure 5.2: The migration corridors and end trajectory of loggerhead turtles nesting in South Africa (*n* = 11). The star represents the nesting grounds, black tracks represent the Mozambique corridor, dark grey Malagasy Corridor, and light grey Agulhas corridor. (Data from Harris et al., 2017).

Stable isotope analysis and partitioning

Two clusters, based on $\delta^{13}C$ only, best fitted the distribution of stable isotope values from the 319 nesting females (Table 5.1; Fig. 5.3a), with a silhouette width of 0.627 for the two clusters indicating strong cluster structure. The more depleted $\delta^{13}C$ cluster (*n* = 231, mean $\delta^{13}C$ = -14.79 ‰, range: -13.74 to -17.28 ‰, mean $\delta^{15}N$ = 11.51 ‰, range: 7.80 to 14.72 ‰) is separated at $\delta^{13}C$ = -13.75 ‰ from the more enriched $\delta^{13}C$ cluster (n = 88, mean $\delta^{13}C$ = -12.62 ‰, range: -9.85 to -13.73 ‰, mean $\delta^{15}N$ = 10.52 ‰, range: 7.74 to 13.60 ‰; Fig. 5.3a).

Table 5.1: Numbers of clusters based on average silhouette width using *k*-means partitioning algorithm. Clusters were evaluated for $\delta^{13}C$ values only, $\delta^{15}N$ values only, and for both $\delta^{13}C$ and $\delta^{15}N$ values. Bold value indicates best fit.

Numbers of clusters	$\delta^{13}C$ only	$\delta^{15}N$ only	$\delta^{13}C$ & $\delta^{15}N$
2	**0.627**	0.562	0.437
3	0.533	0.535	0.369
4	0.533	0.565	0.344
5	0.511	0.529	0.367

Figure 5.3: a) Distribution of carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios (‰) from nesting female loggerhead turtles in South Africa ($n = 307$) between 2016-2018. Two clusters, based on δ^{13}C only, best fit the distribution (Table 1) separated at δ^{13}C = -13.75 ‰ (dashed vertical index line). Open circles represent the depleted δ^{13}C cluster ($n = 231$); open triangles represent the enriched δ^{13}C cluster ($n = 88$), and filled stars represents individuals with satellite tags for which epidermis was sampled ($n = 11$). b) Loggerhead female carapace size in each cluster. Cluster 1 represents the more depleted δ^{13}C cluster while cluster 2 represents the more enriched δ^{13}C cluster. Data are presented as medians (black line), inter-quartile range (box), first and fourth quartiles (whiskers) and outliers (dots).

Stable isotope analysis and female size

The SCL of sampled females in the more depleted δ^{13}C cluster ranged 713 – 973 mm (mean: 825.9 mm) and for the more enriched δ^{13}C cluster ranged similarly 731 – 897 mm (mean: 828.97 mm). The t-test showed that there was no significant difference in size of individual females between the two clusters (t_{58} = -0.85, p = 0.396; Fig. 5.3b), however, large individuals (>900 mm) were found only in the depleted δ^{13}C cluster. The isotopic niche space of different sized turtles (four size classes) overlapped highly, however, the large size class (> 900 mm SCL) has a much smaller isotopic niche breadth than any other group, and mainly occurred in the more depleted δ^{13}C cluster (Fig. 5.4, 5.5a and Table 5.2). Similarly, there was no significant difference in isotope ratios of each turtle size class for δ^{13}C (Kruskal-Wallis $X^2{}_3$ = 7.759, p = 0.051) and δ^{15}N (Kruskal-Wallis $X^2{}_3$ = 6.4628, p = 0.091; Fig. 5.5b).

Figure 5.4: Core isotopic (δ^{13}C and δ^{15}N) niche space of loggerhead turtles nesting in South Africa plotted by size (n = 319), represented by standard ellipse (solid bold lines) using SIBER. The colour codes represent size classes: small < 800, green; medium-Small = 800 – 849, blue; medium-Large = 850 – 899, red; large > 900 mm, black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article). Dashed vertical index line represents the two clusters, based on δ^{13}C only, separated at δ^{13}C = -13.75 ‰.

Table 5.2: Standard ellipse area (SEA*c*) and convex hull area (TA) for nesting loggerhead stable isotopes ratios according to size classes, where small < 800 mm; mediumS = 800 – 849 mm; mediumL= 850 – 899; and large > 900 mm.

Size classes	SEA*c*	TA
small	17.397	4.392
mediumS	22.177	4.529
mediumL	26.376	5.824
large	3.963	2.361
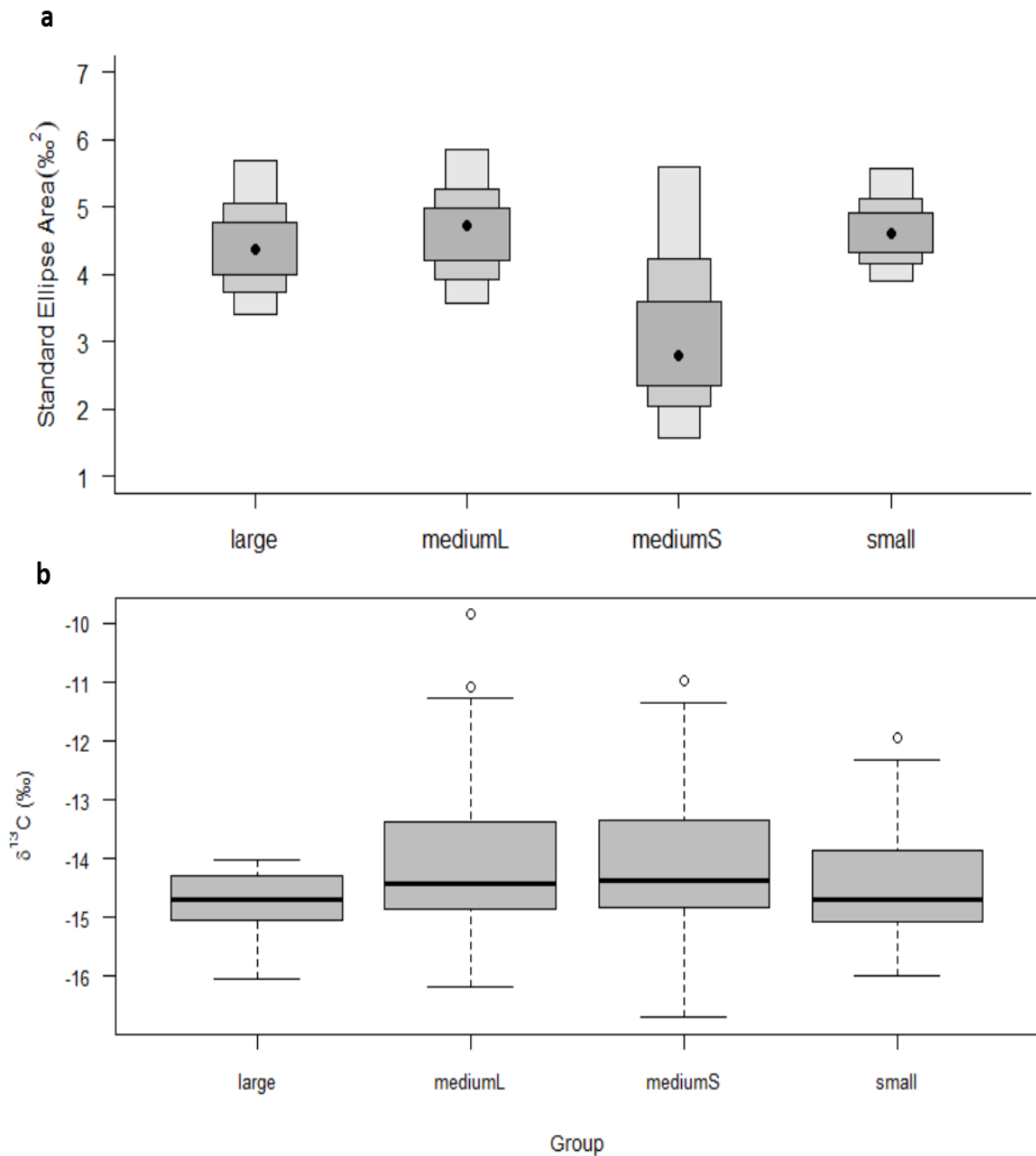
Figure 5.5: a) Bayesian standard ellipse areas (SEA) for each size class of loggerhead turtles nesting in South Africa calculated on the posterior distribution of the covariance matrix for each group. Data are presented as mean (black dot), middle 50th percentile (dark grey box), upper and lower 10-25th percentile (medium grey box), and upper and lower 10th percentile (light grey box). b) Distribution of loggerhead female carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios (‰) for each size class. Data are presented as medians (black line), inter-quartile range (box), first and fourth quartiles (whiskers) and outliers (dots). Where small < 800 (n = 62); mediumS = 800 – 849 (n = 120); mediumL = 850 – 900 (n = 66); large > 900 mm (n = 11).

Discussion

We aimed to test whether there is a dichotomy in foraging strategies (neritic/pelagic) in the loggerhead turtles nesting in South Africa, and if so, if it is correlated with their fitness (size). In addressing this aim, we proposed three hypotheses: (1) body size is correlated with foraging strategy and this will be reflected in the isotopic ratios of turtle tissues; (2) turtles foraging in more pelagic habitats will be smaller and have lower δ^{13}C and δ^{15}N values than those foraging in neritic areas; (3) stable isotope analysis is an adequate tool to assign large-scale foraging areas to migrating sea turtles. These hypotheses still hold because our results do not contain evidence that refutes them, with notable limitation in our study being that all sampled turtles seemed to come from a single foraging area. Although there was no significant trend in loggerhead isotopic values that would suggest different foraging strategies between neritic and pelagic foraging habitats, the present study did reveal important information about the migratory behaviour of South African loggerheads. We found two clusters (foraging groups) based on δ^{13}C ratios with no significant difference in turtle size between them. This is similar to other studies (Pajuelo et al., 2012; Bradshaw et al., 2017), who found no differences in body size related to isotopic values. Further, the SIBER analysis revealed that all size classes exhibited high niche overlap and were rather originating from one single community. This was confirmed by the satellite tracking data, which showed all tagged and biopsied turtles migrated to the same foraging area in southern Mozambique (Harris et al., 2017), which is also supported by previous studies that found that more than 80% of tracked loggerheads in South Africa migrated to identical areas in the neritic waters of southern Mozambique (Luschi et al., 2006; Robinson, 2014). Thus, although we could not test our original hypothesis explicitly because we did not have samples from known pelagic and neritic areas (from satellite-tracked individuals), none of the evidence presented here refutes the hypotheses. More importantly, our study revealed unexpected findings about the larger turtles, and raised other interesting questions about the nesting behaviour and migratory ecology of South African loggerheads.

Unexpectedly, we found that turtles from the large size class had more depleted δ^{13}C values and a smaller isotopic niche than any other size classes. We would expect larger turtles to have enriched isotopic values as δ^{13}C and δ^{15}N ratios commonly increase with body size due to a diet shift to higher trophic levels (Ceriani et al., 2014;

Blasi et al., 2018; Ferreira et al., 2018). A smaller isotopic niche space might indicate that larger turtles have a smaller trophic niche and are more specialized in their diet than juvenile or young adults that forage opportunistically (Vander Zanden et al., 2010). This selective behaviour is also found for turtle nest site fidelity, where older individuals (more experienced nesters) have a higher nest site fidelity (Botha, 2010; Harris et al., 2015; Schofield et al., 2009). Thus, it appears that as turtles become more experienced with age, they also become more specialized in both their nesting and foraging behaviour, having a higher nest site fidelity and a more specialized/selective diet. Depleted δ^{13}C ratios might suggests that larger females are foraging further south, as δ^{13}C is indicative of geographic area (primary carbon source) and generally decreases with latitude (Graham et al., 2010), while δ^{15}N illustrates trophic position (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Reich et al., 2010).

Several studies have reported that large turtles inhabit neritic foraging habitats (Parker et al., 2005; Zbinden et al., 2011; Eder et al., 2012), and differences in body size can be attributed to differences in prey quality and abundance between habitats. Nutrient-poor habitats in pelagic/oceanic systems generally have depleted δ^{13}C planktonic benthic prey items (e.g., gelatinous zooplankton) and nutrient-rich habitats in neritic/coastal areas have δ^{13}C-enriched prey items (e.g., molluscs and crustaceans; Bjorndal, 1997). South African female loggerheads had wide variations in both δ^{13}C (-17 to -9 ‰) and δ^{15}N (7 to 14 ‰) ratios, as was previously reported for South African loggerheads (Robinson, 2014). This potentially highlights the wide variety of prey consumed from different trophic levels and to primary producers shift in nitrogen values related to prevailing nitrogen cycling regimes transferred to higher trophic levels (McClellan et al., 2010, Graham et al., 2010). Loggerhead turtles are opportunistic consumers and the isotopic variability found likely relates to differences in foraging habitats, shifts in trophic status, and fluctuations in local food web baseline isotope values (Vander Zanden et al., 2010; Pajuelo et al., 2012; Tucker et al., 2014).

Even though we know South African loggerheads use three migratory corridors (Harris et al., 2017), 100% of our 318 sampled individuals (307 biopsy only; 11 biopsy and satellite tag) migrated to the same foraging area. Interestingly, all of these individuals were sampled in the northern section of the rookery. All the tracked turtles that migrated to different foraging areas (Northern Madagascar and Agulhas Bank), for which we unfortunately did not have isotope samples, were sampled from beaches in

the southern section of the rookery (Harris et al., 2017). Harris et al. (2015) hypothesised that ocean currents shape turtle movement ecology as hatchlings and that this persists through adulthood based on whether the hatchlings are dispersed in the north-flowing inshore current, or the south-flowing Agulhas Current. We take this hypothesis a step further and suggest that the local oceanography on the northern and southern parts of the rookery are different, with greater likelihood of turtles in the north being imprinted with a northward migration that they follow as adults. In turn, this might create a north-south dichotomy at the nesting beaches that not only influences subsequent migration but also their foraging behaviour and ultimately, fitness. Therefore, loggerheads nesting in the north of the rookery would migrate northward and get imprinted with neritic behaviour to reach feeding grounds in shallow shelf waters along the southern Mozambique coast. In contrast, loggerheads nesting in the southern section would be entrained southwards in the Agulhas Current, get imprinted with more pelagic behaviour and migrate to Cape Agulhas or northern Madagascar. By implication, we predict that the former turtles will have higher fitness because their foraging grounds have more nutritious prey compared to the pelagic habitat of the Agulhas Bank. This hypothesis is partly supported by a recent particle tracking model that simulates dispersal trajectories of neonate loggerheads in South Africa (Le Gouvello et al., unpublished manuscript). According to the model, South African loggerhead hatchlings can either disperse north into the longshore counter-current or south into the Agulhas Current retroflection and South East Atlantic, depending on the local oceanography at the time. The model also suggests that hatchlings dispersing into the South East Atlantic will have lower survival and fitness (due to the cold thermal environment of the Benguela Current of the West Coast of South Africa with potentially lower growth rates and developing into smaller adults).

Using a combination of satellite tracking and stable isotope analysis has proven to be a very useful tool to infer migratory connectivity of marine organisms. The method allowed a dramatic scale up in sample size that could not otherwise be achieved from satellite tracking and greatly increases our knowledge at the population scale (Zbinden et al., 2011). Although isoscapes will never achieve the fine-spatial scale details obtained with satellite tags and on-board instrumentation (e.g., time-depth recorders), they do provide a cost-effective approach and may be more suitable for answering population-level questions (i.e., stock discrimination) than tagging technologies or

even genetic markers (Graham et al 2010). Additionally, the relatively slow isotopic turnover rates (from 4 to 8 months) in turtle tissues make SIA a good indicator of pre- and post-nesting migrations from and to foraging grounds (Seminoff et al., 2008; 2010; 2012; Reich et al., 2008; Vander Zanden et al., 2013). Integrating SIA into sea turtle migration studies may not necessarily be applied to all breeding populations if certain prerequisites are not met (obtaining baseline data of the foraging grounds) but can hold great promise when successfully applied. To accurately infer movement and foraging behaviour of marine animals in oceanic ecosystems, there is a need to determine and improve our understanding of the temporal stability (seasonal fluctuations) of baseline isotope values, which are influenced by changes in in nutrient sources, species composition, biogeochemical cycling rates, and biological productivity (Graham et al., 2010).

The findings of the present study are very stimulating in that they challenge our traditional understanding of turtle ecology and illustrate the complexity (not just pelagic vs neritic) of sea turtle life histories (Haywood et al., 2019). Indeed, new evidence is revealing that sea turtles do not necessarily follow the accepted model of life history by exhibiting fidelity to neritic foraging grounds (Musick & Limpus, 1997), but rather can shift foraging strategy and feed in pelagic habitats (Hatase et al., 2002a; Ceriani et al., 2012; Vander Zanden et al., 2014). Further, we showed that turtle reproductive behaviour is not as simple as variability within a population but that the implications of that variability extend as far as nest placement, migration routes, movement ecology and fitness (Zbinden et al., 2011; Eder et al., 2012; Hatase et al., 2013, 2014). This study has revealed weaknesses in our sampling methodologies due to the north-south dichotomy in nesting behaviour and we would have needed more skin samples from the southern section of the rookery to be able to identify foraging grounds. Furthermore, the study was also lacking baseline isotope data to create isoscapes and accurately assign non-satellite tagged individuals to distinct foraging areas. Despite these shortcomings, the study provided valuable insights into South African loggerhead ecology and how to better sample and help prioritize future research. We suggest that the South African loggerhead population segregate into two distinct isotopic groupings and highlight the need to identify turtle foraging areas in the Western Indian Ocean. Future research at this rookery should use satellite tracking on more individuals from the southern and northern sections of the rookery, and compare

their remigration intervals, reproductive outputs, foraging areas and diet and link it to individual body size and fitness. Knowledge of migratory ecology and connectivity is essential to adequately conserve species throughout their life cycle, both during breeding on land as well as while migrating and foraging at sea (Luschi et al., 2006; Harris et al., 2015; Vander Zanden et al., 2015). Lastly, the present study did highlight the importance of southern Mozambique as a foraging area for loggerheads nesting in South Africa, which also hosts a prawn fishery in the Sofala Bank region and adequate conservation measures (space-time closures or zoning and international cooperation) should be implemented to decrease bycatch rates in the area (Palha de Sousa et al., 2006; Harris et al., 2015).

Chapter 6: General discussion

Chapter 6. General discussion

Despite recovery due to successful conservation measures, sea turtles are still at risks as a result of the numerous current anthropogenic threats affecting their survival (Mast et al., 2005; Bolten et al., 2010; Wallace et al., 2011). While loggerhead turtles have a global status of "Vulnerable", their regional status in the South West Indian Ocean (SWIO) has recently been down-listed in 2015 to "Near Threatened" on the IUCN Red List, leatherback turtles on the other hand have a global status of "Vulnerable" but are still "Critically Endangered" in the SWIO (IUCN, 2019). Thus, loggerheads in the study region are increasing while leatherbacks populations trends are decreasing, which is confirmed by studies done on the South African populations (Ronel et al., 2013; Harris et al., 2015). The long-term monitoring of the South African nesting loggerhead and leatherback rookeries offers a unique opportunity to assess population trends the efficiency of conservation measures in the region to inform future conservation measures.

While the long-term monitoring and protection of both turtle nesting species in South Africa represents a substantial conservation success, the stable (but not increasing) leatherback population suggests that underlying threats are presents are the nesting grounds and/or that threats are occurring outside protected areas. Thus, protecting sea turtles on land where they are easily accessible is not enough to ensure population growth if survival is not realised at subsequent life stages (Mazaris et al., 2017). Furthermore, this might indicate that the way conservation planning is conducted is not always appropriate for such long-lived and migratory species as sea turtles (Harris et al., 2015). Therefore, understanding what affects the fitness of marine turtles and how they respond to current protection measures is essential to understand if these populations are adapting to change and will persist in the future.

Key Findings

The overarching aim of this thesis was to assess long-term trends and fitness by measuring specific fitness traits in loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles nesting in South Africa, as well as their offspring. Firstly, I evaluated trends in individual size of nesting females of both species over a 33- and 35-year period. The study revealed that despite apparent increase in the

number of loggerheads and stable leatherback populations, loggerhead turtles have declined in individual size, with ~4.2 cm in 35 years, and leatherbacks have increased slightly with ~3.3 cm in 35 years (Chapter 2). While the loggerhead declining size trend is surprising because the population is increasing, it could be argued that it is a result of recruitment of new smaller individuals into the nesting cohort. However, this argument does not hold since both neophytes and remigrants are getting smaller and may indicate that habitat-related pressures outside the nesting grounds and MPA are affecting adult nesters. Although this chapter did not attempt to predict trends into the future nor identify the mechanisms responsible for the decline or increase in size, I hypothesised that the contradictory effects found in this research are attributable to the distinct foraging ecologies of the two species and speculate that these variations in carapace length may be driven by environmental change at the foraging grounds. This has been suggested in several rookeries around the world and has been shown to affect sea turtle nesting numbers (Limpus & Nicholls, 2000; Chaloupka, 2001; Saba et al., 2007; Bjorndal et al., 2017). This reduction in individual size as a result of lower food availability could lead to smaller size at maturation (Marn et al., 2018) and has consequences for the energy invested into reproduction, potentially producing smaller eggs, hatchlings and adults.

Secondly, I examined the effect of individual size on reproductive strategies for turtles nesting in South Africa, as well as their offspring (Chapter 3). Specifically, the chapter investigated the effects of maternal body size on reproductive outputs (clutch size, egg size) and hatchling size on fitness traits. Since hatchling locomotor performance directly affects their survival, crawling and swimming speeds were used as proxies of hatchling fitness. The results showed that clutch size increased with female size but egg size is independent of female size. Larger females (loggerhead SCL range 713-973 mm, leatherback CCL range 1404-1744 mm) produced larger clutches (loggerhead range 70-189, leatherback range 41-140) of varying egg sizes and thus supports the Optimal Egg Size Theory (Smith & Fretwell, 1974). This is possibly due to environmental stochasticity; it may be advantageous to produce a range of offspring sizes (Wilkinson & Gibbons, 2005), rather than fewer large offspring. Hatchling fitness, however, seems to be related to carapace and flipper length which affect their locomotor performance. Hatchlings with longer carapace lengths and flippers were faster swimmers than smaller ones and thus more likely to minimise time spent in

areas with high predation pressures, like the nearshore waters. These findings may have direct and indirect implications for long-term population growth/recovery and conservation. Hatching production may be high but survivorship through nearshore waters may be compromised with poorly adapted hatchlings (i.e. small in size). This pattern may become exacerbated by climate change as incubation temperature is negatively correlated with hatchling size (Glen et al., 2003). So, with climate change predicted to increase sand temperatures which would produce more smaller hatchlings of lower fitness, with decreased dispersal abilities and reduced survival (Ischer et al., 2009; Booth & Evans, 2011; Cavallo et al., 2015; Sim et al., 2015), populations may not recover at the expected rates.

The egg/early embryonic development, along with hatchling and post-hatchling phases are the most vulnerable stages in the life of a turtle (Carr, 1986; Witherington, 2002; Mansfield et al., 2014). Pivotal knowledge about these phases come from only a few research groups that have documented egg development (Miller et al., 2003; Miller et al., 2017), investigated the imprinting and homing behaviours (Lohman & Lohman, 1996a-b; Lohman et al., 2012), and documented early development and frenzy behaviour (Wyneken & Salmon, 1992; Wyneken et al., 1997, 2008). Most of these studies were done under controlled conditions or in laboratories. However, when hatchlings enter the open ocean they are incredibly difficult to study and to assess, and this is hence the least understood stage of a sea turtle's life cycle (along with knowledge about adult males) and has eluded sea turtle biologists for decades. There is thus a paucity of information on post-hatchling spatial distribution and what affects their dispersal and survival.

This study (Chapter 4), is the first attempt to estimate the potential dispersal pathways of loggerhead and leatherback hatchlings from northern KwaZulu-Natal, as well as the eventual fate of these hatchlings. Hatchlings emerging from these populations find themselves in a very complex and dynamic ocean area, with a "choice" of two contrasting ocean basins, the warm Indian Ocean on the east coast or the cold Atlantic Ocean on the west coast of Southern Africa. Strong and highly variable currents, may transport hatchlings south into the very cold Southern Ocean, potentially influencing post-hatchling dispersal and survival (Lutjeharms et al., 2010). Thus, I investigated the effect of hatchling swimming behaviour on their dispersal patterns and survival probability for the first year of their lives. This was achieved by *in situ* measuring of

hatchling swimming behaviour and in combination with a high-resolution ocean model with a particle tracking framework. I hypothesised that hatchling dispersal is entirely controlled by oceanic currents which will determine the transport routes of post-hatchlings into one of the two ocean basins. The alternative hypothesis is that neonate dispersal is determined by swimming behaviour (i.e. speed, duration, location, and date) which are species specific. Simulations revealed that (virtual particle) dispersal trajectories were dominated by oceanic conditions and currents, but initial swimming behaviour has an important impact on the spatial distribution; the faster (>0.15 m.s^{-1}) and longer (~48 hrs) the initial swim, the further hatchlings get into the Agulhas Current which results in dispersal ending further away from the release point. Moving (~30 km) south along the rookery or entering the sea a month later (February vs March) has the same effect. Conversely, slow or initial swim, early release or a northern entry, result in more localised or coastal distribution (and likely more strandings). Furthermore, the model revealed that most virtual hatchlings are transported south-westward in the Agulhas Current with three distinct final locations after a year-long simulation: the Agulhas Return, the SE Atlantic and the Southern Ocean zones. Despite broad similarities in dispersal pathways, the simulations demonstrated interspecies differences. Virtual loggerhead particles appear to follow ring shedding events off the Agulhas retroflection and then are transported into the SE Atlantic zone with on average less lethal temperatures than the Southern Ocean zone where more leatherbacks particles occur. This dominant leatherback dispersal trajectory might be a result of their stronger swimming speed that carry them on the offshore of the AC, leading them further south.

The model successfully identified important dispersal pathways and destinations for oceanic neonate turtles. The results of the simulations have broad implications for sea turtles under changing climatic conditions. Although marine turtles may have the ability to adapt to climate change and rising global temperature (by changing their nesting phenology and range expansion; Saba et al., 2012; Pike, 2013a; Monsinjon et al., 2019), the majority of hatchlings may suffer high mortality if the post-hatch thermal environment does not guarantee their survival. Additionally, the higher potential mortality of leatherback virtual hatchlings in the Southern Ocean is consistent with the lack of recovery of the species compare to loggerheads exponential increase in the South African rookery (Nel et al., 2013), although different threats might apply at

different life stages (cold-induced mortality for post-hatchlings and fisheries bycatch for adults). This highlights the need for integrated management strategies that incorporate all stages of the life cycle to adequately protect migratory species throughout their range (Casale & Mariani, 2014; Gaspar & Lalire, 2017).

Lastly, I aimed to test whether a dichotomy in foraging habitat (neritic/pelagic) could be responsible for the observed decreased in individual size of nesting loggerhead turtles (Chapter 5). The longer juveniles and sub-adult turtles spend in the oceanic environment, the smaller they may be at first nesting. This is because a recent partition has been found for female sea turtles, where smaller female size was associated with oceanic habitats and larger females assumed to inhabit neritic areas (Hatase et al., 2004; Hawkes et al., 2006; Ceriani et al., 2012). Additionally, research has shown that neritic-foragers may have higher fitness than smaller oceanic foragers (Zbinden et al., 2011; Hatase et al., 2013; Vander Zanden et al., 2014). I thus investigated if this size-related difference in foraging strategy was true for loggerhead turtles in South Africa using a combination of satellite tracking and stable isotope analyses to infer their foraging areas and investigate the relationship between body size, and foraging strategy. I hypothesised that foraging strategy (neritic vs pelagic) drives body size as reflected in the isotopic ratios of turtle tissues; so, turtles foraging in more pelagic habitats will be smaller and have lower δ^{13}C and δ ^{15}N values than those foraging in neritic areas. The stable isotope analysis partitioned the loggerhead population into two foraging clusters, but with all size classes having a high degree of niche overlap. However, interestingly larger turtles had a smaller isotopic niche, suggesting a diet-specialist foraging strategy. However, I could not conclusively identify distinct isotopic patterns to support variation in foraging strategies (neritic versus pelagic) for South African nesting loggerheads since all tracked turtles migrated to the same area, with possible opportunistic switching between these foraging strategies when necessary, like crossing the Mozambique Channel, for example. Further research, with much more extensive satellite tracking combined with other isotope techniques (e.g. oxygen isotopes), and *in situ* work the foraging grounds are needed to confirm/refute the hypothesis presented in this chapter. Additionally, research should focus on comparing the reproductive output of individuals with different foraging strategy to assess if habitat choice could affect turtle fitness.

Sea turtle fitness

This thesis attempted to address the challenging question on sea turtle fitness and the relationship with particular traits over time, however, the relationship is not straightforward nor definite. Fitness *per se* implies survival to achieve the highest lifetime reproductive output (Williams, 1966; Charnov & Krebs, 1974;), and is usually measured by the number of offspring that survive to reproductive age (McGraw & Casewell, 1996). This success is thus affected by a number of factors that drive survival (and so fitness) of sea turtles during each life stage. The complex life cycles of marine turtles, with changes in distribution, habitat requirements and diet at different life stages (Davenport, 1997), suggests that their fitness varies over time and that offspring and maternal fitness differ from each other (Rollinson & Hutchings, 2013). Thus, according to Bolten et al., (2010) the relative reproductive value (RRV), an individual's potential for contributing offspring to future generations adjusted by the summed annual mortality for each life stage and calculated by a staged-based demographic model, showed that as post-hatchling phase has the highest mortality and the smallest annual survival rate value (0.25), their RRV is hence also the lowest (0.004-0.029).

This is because different pressures apply at different life stages (Bolten et al., 2010). The hatchling phase is the one with the highest natural mortality rates due to the very small size and lack of predatory defences, whereas adult turtles are at risk to anthropogenic threats (like fishing). Hatchling survival is thus directly linked to the duration they spend in predator-rich areas which in turn is dependent on a hatchling's locomotor performance (Pereira et al., 2011). Hatchling fitness appears to be size-related since predation is size-dependent and predators are gape-limited (Guyris, 2000). Hatchling fitness is defined as an individual's potential for contributing offspring to future generations or its future reproductive value (Botlen et al., 2010). Thus, for hatchlings, size and outgrowing their predators is the most important factors during this phase (Salmon & Scholl, 2014).

As a result of the very high mortality during the early life stages, adult female turtles must produce large clutches to replace themselves (and their mate/s) in the next generations. Marine turtles are capital breeders, i.e., energy invested in reproduction is gathered prior to reproduction and usually fast during the migration and breeding season (Plot et al., 2013), thus needing to replenish their energy stores post-breeding

and reach a fixed body condition threshold in order to repoduce again (Lourdais et al., 2002). Sea turtles are resultantly (usually) non-annual breeders and skipping a reproductive cycle may be an advantageous breeding strategy to maximise lifetime reproductive success (Schaffer, 1974; Rivalan et al., 2005).

Fitness traits in adult sea turtles are less affected by predators than in hatchlings, since they have outgrown most natural predators (barring large sharks), and reproductive fitness may be more dependent on habitat quality or the (physiological) rate at which a female can replenish energy stores to prepare for the next breeding season. Larger individuals have larger energy reserves and will sustain prolonged period of unfavourable feeding conditions easier (Marn et al., 2017b). They will also be able to produce more clutches per season (Hatase et al., 2003), and have a larger morphological capacity to hold more eggs with a larger pelvic space (Congdon & Gibbons, 1987; Rasmussen and Litzgus, 2010). So, adult female turtle fitness appears to be dependent on the resources available in a given habitat, hatchling fitness on the other hand emerges to be dependent on the predation pressure at the rookery.

Future studies and way forward

Our long-term trend size analysis (of a decline in loggerhead female size) should heed caution to other rookeries of all other sea turtle species; we challenge researchers to follow suit and analyse long-term monitoring data for changes in individual size and not stop at recording only number of nests or nesters. It is also necessary to test whether our results are anomalous or if the results predict a more general issue affecting marine turtle populations from other ocean basins which may have major implications for conservation efforts if recovery strategies are undermined by rapid shifts in environmental conditions in marine ecosystems (Ingeman et al., 2019). Following on from this, studies testing the effects of sea surface temperatures on hatchling growth and performance should do so in captivity under controlled conditions but should also be validated with experiments on wild hatchlings. Climate change is expected to have negative impacts on the locomotor performance of sea turtle hatchlings by shortening incubation period and producing smaller, less fit individuals. Research should assess how this change in locomotor performance will influence their dispersal under a range of different sea surface temperatures. Phenological changes

and range shifts in adult nesting which are assumed as evolutionary adaptation may not be the solution/s we assume, as suggested by the particle tracking model (where southern turtles and later hatchlings were doomed).

Additionally, climate change is not the only major threat to sea turtle populations (Bolten et al., 2010). Future research should investigate if dispersal and developmental hot spots overlap with anthropogenic pressures like fisheries activities and evaluate potential negative interactions and bycatch, or with plastic pollution accumulation zones. The particle tracking model should be used to assess fisheries interactions with hatchling dispersal routes and inform national as well as international conservation strategies to ensure that each species have some form of protection at each life stages and throughout their range.

Sea turtle population models show that population growth rate is most sensitive to survival of the large juvenile and adult stages (Crouse et al., 1987; Crowder et al., 1994; Heppell et al., 1996) due to the lower reproductive value of eggs and hatchlings (Bolten et al., 2010). Thus, as long-lived and late-maturing organisms, survival of the early life stages will have a comparatively small impact. It is therefore fundamental to ensure adult and subadult survival while not overlooking the importance of hatchling production which is critical for recruitment to these later life stages (Heppell, 1997). This study used a variety of approaches to advance our understanding of sea turtle biology. Employing a combination of methods such as *in situ* experiments, numerical particle tracking models, and stable isotope analysis, as well as standard monitoring approaches, my work has advanced our knowledge of sea turtle reproductive strategy and life history, spatial distribution and foraging strategy at different life stages. Conservation is only as strong as the weakest link – it requires appropriate management measures across all life stages of a species. It is ineffective to protect female turtles on nesting grounds if their survival is not ensured at subsequent life stages. There is still considerable uncertainty about the juvenile phase of sea turtle life cycle that needs to be address and research should evaluate all aspects of population demography (sizes, sex ratios, hatchling production, etc.) to assess threats at each life stages and prioritize future conservation and management actions.

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