Factors affecting survivorship of loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles of South Africa

By

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Declaration

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DECLARATION:

In accordance with Rule G4.6.3, I hereby declare that the above-mentioned treatise/ dissertation/ thesis is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

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Abstract

Loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles as well as their eggs and hatchlings have been protected on their nesting beach in South Africa since 1963. Both nesting populations were expected to show similar trends in recovery following the application of identical protection and conservation measures. The loggerhead nesting population has responded favourably to these protection efforts. In contrast, the leatherback nesting population showed an initial increase but is currently stable. The reason for this difference in response is thought to be due to differential offshore mortality of these two species. This prompted an investigation into the different sources of sea turtle mortality in the South Western Indian Ocean (SWIO). Specific aims were to identify and quantify sources of loggerhead and leatherback mortality on nesting beaches as well as in the oceans.

Reasonable survivorship at all age classes is important to ensure recruitment of new nesting individuals into sea turtle populations. Mortality of nests, eggs per nest and hatchlings were quantified over two seasons for the loggerheads and leatherbacks nesting in SA. The beach was patrolled on foot to encounter and record females emerging from the ocean and later, hatchlings from their nests. The nests were then monitored during the incubation period and excavated once hatched. The fates of 925 nests were determined during these two nesting seasons (2009/2010 and 2010/2011). The main source of loggerhead and leatherback nest destruction was predation (8.6 % and 15.7 % respectively) followed by nest erosion (2.2 % and 6.3 % respectively). Overall nest success was high but higher for loggerheads (89 %) than for leatherbacks (78 %). The main cause of egg mortality for both species was early developmental arrest, followed by predation by ants and ghost crabs. Hatchlings *en route* to the sea were almost exclusively predated by ghost crabs (4.2 % of emerged loggerhead hatchlings and 3.2 % of emerged leatherback hatchlings). It appears that both species benefit from the coastal conservation efforts.

When sea turtles leave the nesting beach, either as hatchlings or adults, conservation and monitoring becomes more difficult and sea turtles are exposed to a multitude of threats, including anthropogenic threats. Age classes tend to be spatially separated due to different habitat and dietary requirements. The type of threat sea turtles are exposed to thus depends on the current age class. Offshore sources of mortality in the SWIO were identified and where possible loggerhead and leatherback mortality was quantified and mapped spatially. Loggerheads were mostly exposed to and had the highest mortality in the artisanal fisheries in the SWIO (> 1000 per annum), inshore trawling (ca. 41 per annum), shark nets (protective gill nets) (21.6 ± 6.7) per annum) and the pelagic longline fishery $(5.0 \pm 4.4$ per annum). In contrast, leatherbacks with a pelagic lifestyle were mostly exposed to pelagic longline fisheries (7.8 ± 7.8) per annum). A spatial analysis of fishing activities indicated that leatherback home ranges overlapped 41 % with pelagic longline fishing activity in the SA EEZ, whereas the overlap between pelagic longliners and loggerhead home ranges was only 29 %. The quantified sources of mortality provide some explanation for the trend in the loggerhead nesting population but not the trend in the leatherback nesting population.

Hatchling survivorship to adulthood was estimated to determine the viability of the two nesting populations as well as to determine whether offshore mortality was responsible for the difference in recovery of the two populations. Loggerhead hatchling survivorship to adulthood was estimated at between 2 and 10 per 1000 hatchlings, the minimum requirement for an increasing population. The adopted sophisticated model shows that leatherbacks have a survival rate of 5 to 10 per 1 000 hatchlings. However, this suggests that the population is increasing, but the leatherback population is stable. Perhaps the age to maturity of SA leatherbacks is greater than 12 years, or fisheries-related mortality affects younger age classes than initially thought.

It is therefore recommended that the turtle monitoring area is extended to include other potential nesting grounds. In addition, observer or monitoring programs for commercial as well as artisanal fisheries needs to be extended throughout the SWIO to quantify sea turtle mortality. Ultimately a comprehensive multi-regional approach is required for the conservation of these highly migratory species.

Key words: Loggerhead, *Caretta caretta*, leatherback, *Dermochelys coriacea*, mortality estimate, survivorship, threats; predation, bycatch

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Summary

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Introduction

The pattern of survivorship from offspring to adulthood varies greatly among species (Begon et al., 1990, Molles, 2008). This variation is due to differing life history traits among species, including natality, growth rate and age to maturity (Begon et al., 1990). The key to understanding the pattern of survival from offspring to adulthood of a species is thus to investigate life history characteristics. Among these characteristics, natality (birth rate or reproductive output) has been documented most frequently because these events tend to be predictable (by being seasonally synchronised) or animals occur in high concentrations (at breeding or spawning sites) (Domeier and Colin, 1997, Crawford et al., 1999). However, estimating mortality is often more complicated because individuals of populations disperse and occupy habitats that are not easily accessible, particularly in the marine environment. It is especially important to understand this pattern of survival (or conversely mortality) of endangered species by specifically identifying and quantifying the threats they face (Kappel, 2005, Bolten et al., 2010), to enact conservation and management programmes and so prevent population extinctions (Martin et al., 2007).

Two broad groups of life history strategies are recognised, namely r-selection and Kselection strategies (MacArthur and Wilson, 1967). Species with a small body size typically display an r-selected life history strategy. These species invest heavily in reproduction and thus they grow and mature rapidly and produce small offspring in large numbers (Pianka, 1972, Begon et al., 1990), often in a single reproductive event (semelparity). Mortality of offspring is high due to the absence of parental care. Marine species adopting this strategy include zebra mussels (*Dreissena polymorpha*) (McMahon, 2002) and fish such as sardines (*Sardinops* spp.). In contrast, K-selected species tend to have a large body size and produce fewer, large offspring that are protected and nourished by the parent (e.g. African elephants, *Loxodonta africana*). These species tend to live longer than r-strategists. Due to their

larger size juvenile and adult survival is higher and reproduction, often in multiple events (iteroparity), occurs later in life. Nevertheless, most species have adopted a life history strategy that combines characteristics of both strategy types (Pianka, 1972), including various fish species (King and McFarlane, 2003), bird species (Western and Ssemakula, 1982) as well as all species of sea turtles. However, before we can review the life history strategy of sea turtles, we need to review the life cycle of sea turtles in some detail.

Life history of sea turtles

Female sea turtles come ashore seasonally, predominantly at night, to excavate a nest and deposit a clutch of eggs. The number of eggs per clutch varies among species (Broderick et al., 2003) and individuals (Bjorndal and Carr, 1989). The eggs incubate for two months during which time they are vulnerable to predation and tidal inundation. Once hatched, hatchlings typically emerge together as a clutch to share the workload of "digging" to the surface (social facilitation digging) (Carr and Hirth, 1961). A drop in the sand temperature is suggested to be a cue for the hatchlings to emerge from the nest (Miller et al., 1999). Once they clear the egg chamber, they then cross the beach crawling towards the ocean. However, during this sprint, hatchlings are under severe predation pressure from ghost crabs and birds such as frigate birds (*Fregata* spp.) (Lagarde et al., 2001). Successful hatchlings enter the surf and swim for several days before reaching the currents that move them away from the coast (Hughes, 1974b). For the first year they are classed as posthatchlings that drift in pelagic waters feeding on planktonic prey items (Hughes, 1974b, Luschi et al., 2003). They return to neritic habitats after approximately 10 years as developed juveniles and remain there as sub-adults and ultimately mature adults. Age to sexual maturity (age to first nesting) differs among individuals, populations and species. Interestingly, green turtles in Australia"s Great Barrier Reef take between 25 and 50 years to become sexually mature, depending on the metapopulation (Chaloupka et al., 2004). Age to sexual maturity for Pacific leatherbacks ranges between 5 and 14 years (Zug and Parham, 1996) whereas Hawaiian green turtles take approximately 30 years to become sexually mature (Zug et al., 2002). Once mature, these adult males and females seasonally return to their

natal beach to breed (Limpus, 1993). However, adult females do not breed every year and the remigration interval varies also among individuals, populations and species. For example hawksbill turtles from Antigua, West Indies, have a mean remigration interval of three years (Richardson et al., 1999) whereas those from Australia"s Great Barrier Reef have a mean remigration interval of 3.4 years (Dobbs et al., 1999). Although females display skipped nesting behaviour, most males seem to breed every year (Limpus, 1993, James et al., 2005a).

Of all reptiles, sea turtles thus probably have the most complex life history strategy; they have both terrestrial and marine phases and they display a combination of rand K-selection life history strategies. This particular combination can be referred to as a "Periodic" life history strategy (Winemiller and Rose, 1992). Periodic life history strategies are characterised by four attributes; high offspring production and subsequent high juvenile mortality, followed by late maturation and no parental care (Winemiller and Rose, 1992). Other species that display similar life history traits include ocean sunfish (*Mola mola*) and crocodiles (*Crocodilus* spp.) (Molles, 2008). Sea turtles specifically, have a large body size, typical of K-strategists, but produce many small offspring (in multiple clutches) which is a trait typically displayed by rstrategists. Furthermore, typical of K-strategists, survivorship of sub-adults and adults is significantly higher than post-hatchlings and juveniles (Heppell et al., 2003) because predation pressure decreases with increasing body size (Molles, 2008).

Considering all these life history characteristics it is easy to understand why the majority of sea turtle research has focussed on the life history stages that occur on land. Monitoring the pattern of survival (or conversely mortality) of sea turtle populations offshore is particularly complicated. However, identifying and quantifying threats or sources of mortality is an essential component in the understanding of the dynamics of these species that have a high risk of extinction (Bolten et al., 2010).

Sources of mortality on nesting beaches

The life history age classes that are seasonally present on beaches include adult females, eggs, and hatchlings. Adult females are vulnerable to terrestrial predators once they come ashore to nest because they move very slowly on land. In Kenya, hyenas and even lions have been reported to prey on nesting female turtles (Church and Palin, 2003). Because eggs and hatchlings are nutrient rich relative to other protein sources on the beach they are sought after by predators. Furthermore, because these age classes are defenceless, natural mortality in the form of predation of eggs and hatchlings is relatively high (Heppell et al., 2003, Molles, 2008). For two to three months of the year opportunistic predators can destroy thousands of eggs (Church and Palin, 2003, Engeman et al., 2003, Barton and Roth, 2008, Engeman et al., 2010). Raccoons (*Procyon lotor*) destroy significant numbers of sea turtle eggs in the United States. Prior to implementing predator control measures, up to 95 % of the nests on Florida nesting beaches were destroyed (Engeman et al., 2003). Other vertebrate predators include pigs (Mortimer, 1984), honey badgers (*Melivora capensis)* (Hughes and Bartholomew, 1998) and foxes (Mendonça et al., 2010). Green turtle hatchlings are frequently predated by frigate birds in the Western Indian Ocean (WIO) islands (Lagarde et al., 2001) either as they emerge, cross the beach or enter the surf. On Raine Island in Australia, 71 % of observed emerging nests were completely predated by seabirds, mainly the Rufous night heron (*Nycticorax caledonicus*) (Limpus et al., 2003). Sea turtle egg predation by invertebrates such as ghost crabs and ants can also be substantial (Fowler, 1979, Brown, 2009). Ghost crabs also predate on hatchlings, especially once hatchlings move across the beach towards the ocean (Diamond, 1976, Alexander, 1979, Brown, 2009, Tomillo et al., 2010). Ants have been documented to consume entire clutches and they attack hatchlings, weakening them and making them more vulnerable to secondary predation (Hughes, 1974b). Nevertheless the life history strategy employed by sea turtles is adapted to cope with high levels of egg and hatchling predation by producing large quantities of eggs in multiple clutches.

Some populations of olive ridley turtles (*Lepidochelys olivacea*) seem to have developed a particular strategy to deal with high levels of nest and hatchling

predation. Arribada nesting (synchronous mass nesting) in places such as Costa Rica occurs to induce predator satiation and so increase hatchling survival (Eckrich and Owens, 1995). During the nesting season at arribada sites, thousands of females emerge together once a month to lay their eggs over a period of three to four days (Hughes and Richard, 1974, Bernardo and Plotkin, 2007). When the eggs hatch after incubation, the beach is flooded with hatchlings and nest raiders become overwhelmed and quickly satiated. The majority of the hatchlings thus make it safely to the ocean (Bernardo and Plotkin, 2007). Most other sea turtle populations as well as other reptiles such as crocodiles are solitary nesters and avoid nest predation by nesting at night, making it more difficult for diurnal predators to locate nests. They also deposit hundreds of eggs in separate clutches to improve the probability of survival with an extended ritual to disguise the egg chamber.

In addition to predation on nesting beaches, various non-natural human impacts have been identified as major threats to sea turtles and their nesting beaches (Arianoutsou, 1998, Halpern et al., 2007, Fish et al., 2008). Beach erosion due to coastal development and sea level rise is one of the biggest threats to sea turtle habitat globally (Fish et al., 2008, Bolten et al., 2010). In the context of climate change, an increase in the intensity and frequency of storms could increase beach and nest erosion (Van Houtan and Bass, 2007). In addition, sea level rise will cause beaches to become inundated and reduced area available for nesting could result in increased nest density in refuge areas with lowered hatching success (Garcıa et al., 2003, Fish et al., 2008). Leatherback nests are particularly vulnerable because they nest closer to the high tide mark (Eckert, 1987) with a subsequent increased risk of nest erosion and inundation.

Sources of mortality in the oceans

Predation

In contrast to our relatively good understanding of the causes of sea turtle mortality on beaches, identifying and quantifying offshore threats are more challenging due to

the dispersed nature and limited knowledge regarding sea turtle movements (Godley et al., 2007). Hatchlings and post-hatchlings are particularly vulnerable to predation in the neritic environment (above the continental shelf) due to their small size (Witherington and Salmon, 1992) as well as the high density of predators. Large teleosts, octopus and elasmobranchs are concentrated on coastal reefs and prey on these individual turtles swimming past *en route* to the dispersal currents that carry them away from the coast. These predators can consume hatchlings in large quantities. For example, a kingfish (*Caranx ignobilis*) caught off the South African (SA) east coast contained 17 loggerhead hatchlings in its stomach (Hughes, 1993). Further, because hatchlings and post-hatchlings rarely dive deeper than 2 m (Davenport and Clough, 1986), they are still vulnerable to bird predation once in the ocean. Sub-adult and adult sea turtles are less susceptible to predation due to their larger size but large sharks (Heithaus et al., 2007) and even killer whales (Pitman and Dutton, 2004, Elwen and Leeney, 2011) have been documented as predators of these size classes, either killing or injuring them, or amputating limbs.

Pollution

Pollution, in all forms, is globally regarded as one of the most significant anthropogenic threats to all marine life (Bolten et al., 2010, Donlan et al., 2010). These include oil, plastics or other materials that do not decompose quickly, as well as heavy metals. Sea turtles are particularly vulnerable to each of these forms of pollution because they are exposed to those pollutants within their food as well as those that are spread across the ocean's surface.

The impacts of oil spills on sea birds are well represented in the literature (King and Lefever, 1979, Ford et al., 1987, Crawford et al., 2000). Their feathers become impregnated with oil and they are unable to fly (Burger and Fry, 1993). Furthermore oiled and cleaned birds are incapable of maintaining their body temperature and many die of hypothermia (Erasmus et al., 1981). Sea turtles of all age classes are also vulnerable to oil spills but for different reasons. Because sea turtles have to break the surface of the water to breathe, they have to surface through the oil slick.

During this process they get covered in oil, which could irritate the skin and the mucous membranes of the eyes and mouth. Accidental ingestion of oil affects physiological processes such as digestion and excretion (Milton et al., 2003) which would lead to slow starvation. One of the more recent oil spills, the Deep Horizon oil spill in the Gulf of Mexico, would have resulted in thousands of sea turtle deaths without well-organised rescue operations (Gaskill, 2010). Furthermore oil on beaches covering sea turtle nests, could inhibit gaseous exchange in eggs as is the case with birds (King and Lefever, 1979). Hatchlings drenched in oil will be unable to move across the beach or swim. If oil is swallowed, digestion will also be inhibited. Nevertheless, the long term impacts of oil pollution on sea turtle biology are still largely unknown.

Solid wastes such as plastics, fishing nets, floating nylon material that takes a long time to decompose or other floating debris are a major problem for marine mammals, sea birds and sea turtles (Derraik, 2002). Especially leatherbacks mistake these floating plastic fragments for food (Tomás et al., 2002, Mrosovsky et al., 2009) or become entangled. Intake of indigestible material, even in small amounts, obstructs the digestive tract which through starvation or infection will result in death (Bugoni et al., 2001). A complication from fishing that has received much attention in the last decade is ghost fishing (Brown and Macfadyen, 2007). Ghost fishing is used to describe any discarded fishing gear that still has the capacity to entangle target or non-target species (Brown and Macfadyen, 2007). The discarded or snagged fishing gear includes nets and line. Entangled sea turtles would be unable to swim properly and either starve or drown. Discarded fishing gear detection and removal strategies have been developed recently to prevent incidental mortality of endangered species such as seals and sea turtles (McElwee et al., 2010). These methods include using models to predict probable locations of discarded fishing gear (using currents for example) as well as remote sensing technology.

Bioaccumulation of toxic organic compounds (such as DDT) and heavy metals (such as mercury) is becoming an increasing concern (Caurant et al., 1999). Physiological processes as well as systems, such as the digestive and nervous systems, are affected (Storelli and Marcotrigiano, 2002, Tanabe, 2002). Organochlorine

compounds (such as DDT) are highly toxic endocrine disrupters that take a long time to break down and are thus persistent in the environment. The potential for bioaccumulation through the trophic levels and in tissues is high (Tanabe, 2002). Because sea turtles have such variable diets, they are vulnerable to ingestion of these toxic compounds. These compounds and other pollutants are thought to be responsible for many stranding events of cetaceans and mortalities of sea birds (Tanabe, 2002) and is expected to also be the case for sea turtles.

Mortality directly related to fisheries

High offshore mortality owing to targeted catch and bycatch in fisheries is suggested to be a major cause of diminishing sea turtle populations globally (Bourjea et al., 2008, Donlan et al., 2010, Spotila et al., 1996). Incidental capture of sea birds, marine mammals and sea turtles in commercial fisheries has received much attention in the last two decades (Barnes et al., 1997, Lewison et al., 2004a). All species of sea turtles interact with longline fisheries (Caminas et al., 2006, Carranza et al., 2006, McClellan et al., 2010) in all ocean basins (Kotas et al., 2004, Peterson, 2008, Bartram et al., 2010). Lewison et al (2004b) estimated that 200 000 loggerheads and 50 000 leatherbacks were caught in Atlantic and Pacific pelagic longline fisheries during the year 2000. Loggerheads are attracted to the bait, frequently hooked in the mouth and consequently drown. In contrast, leatherbacks most often are entangled in the fishing gear or foul-hooked on the flipper or body (Carranza et al., 2006). Shallow-water trawl nets are particularly non-selective and consequently bycatch (including sea turtle bycatch) rates are high (Hall et al., 2000). In the Mediterranean it is estimated that more than 4 000 individual turtles are caught annually in this fishery (Casale et al., 2004). The use of gill nets, especially anchored driftnet fishing has been banned in many countries specifically because of the high bycatch of juvenile fish and non-target species associated with this gear type. Despite this and various other management measures, several studies have indicated that globally the current rate of sea turtle bycatch is unsustainable (Gilman et al., 2006, Lewison et al., 2004b). Unless bycatch mitigation methods are implemented and enforced in fisheries sea turtle population declines are unavoidable.

In addition to the incidental bycatch of sea turtles in commercial fisheries, sea turtles have been and still are frequently targeted in artisanal fisheries throughout the poorer regions of the world such as the South West Indian Ocean (SWIO) (Bourjea et al., 2008) the Caribbean (Witzell, 1994) and South East Asia (Hamann et al., 2006). Sea turtles are either captured in the near shore using spears or gillnets, or are speared while nesting. They are captured and killed for their meat, oil and hawksbills (*Eretmochelys imbricata*) particularly for their shells (Church and Palin, 2003). Regardless of legislation to protect turtles throughout the world, thousands of turtles are captured and killed annually (Hughes, 1974a, Humber et al., 2010). Legal trade of turtle products has been reduced and legal international trade has ceased since the inception of international agreements such as CITES (Convention on International Trade in Endangered Species). Nevertheless, in Costa Rica there is a sustainable and well managed community-based conservation program allowing the legal harvest of olive ridley (*Lepidochelys olivacea*) eggs (Campbell et al., 2007). Because hundreds of eggs are damaged by other nesting females during arribada events, the already "doomed" eggs are allowed to be collected by members of the local community. The overall hatching success of the population is also improved (Campbell et al., 2007). This programme is a good example of balancing the consumptive need of humans and the need to conserve an endangered species.

Accidental deaths of sea turtles have also been documented. Propeller or boat strikes cause severe injury and even mortality of endangered marine animals including whales, dugongs and sea turtles. Mitigation of collisions can be achieved by avoiding areas where these animals congregate or by reducing the speed of the vessels (Hazel et al., 2007). Sea turtle migration routes overlap with or cross major shipping lanes and fishing areas (James et al., 2005b) and thus the probability of injury is high. Even though these interactions have been documented, they are very difficult to quantify especially if the incidents take place offshore. Further, the rookery of origin is not always obvious. It is only possible to identify the rookery the individual belongs to if the stranded turtle is an adult female that has been tagged in a monitoring programme or when a detailed genetic study is in place.

Population trends for SA nesting sea turtles

The SA nesting populations of loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles have been protected since 1963 (Hughes, 1996). This protection was initiated through the implementation of the Maputaland turtle conservation and monitoring programme. This programme, managed by Ezemvelo KZN Wildlife (Ezemvelo), is centered on community monitors patrolling the nesting beach on foot to count the number of females and nests while also providing physical protection. Due to the recognised value and vulnerability of these nesting populations and the importance of long term quantitative monitoring, plans for the development of a deep water harbour in Kosi Lake in 1982 were discarded (Hughes, 2009). Two marine protected areas (MPAs) were proclaimed off the KwaZulu-Natal (KZN) nesting beach; St. Lucia Marine Reserve declared in 1979 and the Maputaland Marine Reserve declared in 1986 (Hughes, 2009) (Fig. 1.1). In 1999 both these MPAs and the St. Lucia lake area were declared a UNESCO (United Nations Educational, Scientific and Cultural Organisation) world heritage site, now named the iSimangaliso Wetland Park (iSimangaliso). Because of the ongoing conservation presence and intensive beach monitoring during the nesting and hatching season, poaching of eggs, hatchlings and nesting females have effectively been eliminated.

Loggerhead and leatherback turtles nesting in SA have received identical protection effort for 50 years and are therefore expected to show similar trends in recovery (relative to the biology and relative reproductive output of the species). Nevertheless, the leatherback population, with a higher relative reproductive output per individual female (Nel, 2010), has failed to recover to the same extent as the loggerhead population (Fig. 1.2). The number of loggerhead females has increased from approximately 80 to approximately 600 nesting per annum while leatherback nesting females showed an initial increase from about 20 individuals to 80 females per annum, but has remained stable at this number for the last three decades (see Chapter 5). Because most human-induced sources of beach mortality have been eliminated, the dissimilarity in the recovery rate suggests that the incubation environment of these two species differ with a difference in sex ratios or hatching

and emergence success, or these two species are differentially vulnerable to offshore threats and causes of mortality (Lewison et al., 2004a).

The annual SA turtle conservation and monitoring programme has focussed on track and nest counts and on tagging (using PIT and flipper tags and notching) and measuring carapace length and width of nesting females. The data from the programme therefore provide an estimate of the number of neophytes and remigrant (experienced) females that nest each year. Age to maturity has also been estimated for loggerheads (Tucek et al, in prep) using mutilation tagging (i.e. notching, described in Chapter 5). Since sea turtles display natal philopatry, combining hatchling production with the number of neophyte nesters, survival (rate) to adulthood can be estimated. Currently, the understanding of "one per thousand hatchlings" is used as a general expression to indicate survival of hatchlings to adulthood across all species or across all populations (Hughes, 1974b). However, to date there is no quantitative estimate for SA. Even though there is quantitative monitoring on nesting effort, there is no up to date data available on the number of successful nests, the number of hatchlings produced or that make it to the sea or any other estimate of survival to justify this number, on the beach or offshore for the SA programme. This study aims to estimate mortality (or conversely survival) at various age classes for loggerhead and leatherback turtles of SA.

Figure 1.1: The protected sea turtle nesting beaches fall within the iSimangaliso Wetland Park in KZN, SA. The Maputaland Marine Reserve borders the park in the north while the St. Lucia Marine Reserve borders the park in the south (data obtained from Ezemvelo and iSimangaliso).

Figure 1.2: The trends in the number of loggerhead (Cc) and leatherback nests (Dc) between 1965 and 2010 for the monitoring area from Nel (2010).

Aims and Objectives

In an attempt to estimate mortality for the SA loggerhead and leatherback sea turtles the most important sources of mortality at various age categories needed to be identified and quantified. To achieve this, the sources of mortality will be separated between sources of mortality impacting turtles on nesting beaches and those offshore. Specifically the fates of nests, eggs, hatchlings and adult females will be determined on nesting beaches. Offshore sources of loggerhead and leatherback mortality will be identified without separating neritic and oceanic threats. Instead, data on specific fisheries such as pelagic longlining, shallow-water prawn trawling and the shark nets, known to have an impact on loggerheads and leatherbacks, will be collated and quantified. In addition, the spatial distribution of both loggerheads and leatherbacks will be overlaid with fishing efforts. These results will further be augmented and interpreted by collating strandings information and tag return data. A basic survivorship estimate of hatchlings to adulthood will be calculated for both species by combining the long-term monitoring database and superimposing the calculated estimates of mortality per life history phase. This will provide insight into the observed population trends (based on nesting females) for both species. Finally, the data will be compared between the species and size classes and with existing estimates for other populations to provide some indication of where future conservation efforts should be focussed.

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Chapter 2: Mortality on nesting beaches

Introduction

Estimating demographic parameters such as the number and size of offspring, age to sexual maturity and growth rate are essential for the management of populations (Begon et al., 1990). This is particularly true for those populations that have a high extinction probability (Dennis et al., 1991) such as sea turtles. Because sea turtles nesting on land are easily accessible, research on developmental biology, physiology and ecology of eggs, hatchlings and adult females is abundant in the literature (Fowler, 1979, Erk'akan, 1993, Leslie, 1993, Wallace et al., 2006). These data also provide the opportunity to model population size or demographics (Troëng et al., 2004, Witherington et al., 2009). Despite the research emphasis on natality, eggs and hatchlings are particularly exposed to a variety of threats. These include natural predators as well as human-induced threats that impact directly on sea turtles, e.g. poaching and harvesting of both females and eggs, as well as indirectly through for example habitat destruction. Nevertheless, sea turtle population dynamics cannot be adequately studied without incorporating both natality and mortality estimates on the nesting beaches into population models.

Sea turtles are extremely susceptible to predators on land because they have impaired mobility and no obvious defence mechanisms. Beached turtles are particularly vulnerable to large carnivores; for example, hyenas and lions have been documented to attack nesting females in Kenya (Church and Palin, 2003). Sea turtle eggs and hatchlings serve as an easy source of protein to a variety of desperate predators foraging on otherwise nutrient poor sandy beaches. Turtle nests are opportunistically raided by raccoons (*Procyon lotor*), foxes, honey badgers (*Mellivora capensis*) and a variety of bird species (Fowler, 1979, Hughes and Bartholomew, 1998a, Engeman et al., 2003). Most of the predators are site- or region-specific; for example, raccoons destroy sea turtle eggs and consume hatchlings on beaches in
Florida (Barton and Roth, 2008, Engeman et al., 2010) whereas foxes and wolves pursue green turtle eggs and hatchlings in Oman (Mendonça et al., 2010).

Invertebrate nest predators tend to be limited to ghost crabs and ants. Documented ghost crab (*Ocypode* spp.) consumption of sea turtle eggs is generally high, ranging between 17 % egg loss per clutch in Florida (Brown, 2009) to 35 % egg loss per clutch in the Seychelles (Hitchins et al., 2004). Ants, specifically invasive fire ants (*Solenopsis invicta*) (Allen et al., 2001, Parris et al., 2002) devour both eggs and hatchlings. Emerging hatchlings attacked by ants are physically weakened and may subsequently be more vulnerable to other opportunistic foragers (Hughes, 1974b). Hatchlings emerge at night as a predator avoidance strategy (Drake and Spotila, 2002). However, nocturnal predators such as ghost crabs, Rufous night herons (*Nycticorax caledonicus*) and frigate birds (*Frigata* spp.) target hatchlings on their way to the ocean (Lagarde et al., 2001, Limpus et al., 2003, Barton and Roth, 2008).

Several human-induced factors have been implicated in the decline of a number of sea turtle nesting populations (Arianoutsou, 1998, Bugoni et al., 2001, Bourgeois et al., 2009). Beaches are under increased pressure from human use and coastal developments that destroys the habitat or alters the functioning of these ecosystems (Halpern et al., 2007, Defeo et al., 2008). The construction of hotels, harbours as well as groynes on sandy shorelines disrupts sand budgets, causing beach erosion. The intertidal and dune habitat is destroyed, therefore reducing the area for nesting. Furthermore, developments in coastal areas are invariably associated with increased light pollution and human traffic (foot and/or vehicle) on beaches. Lights on beaches deter female turtles from nesting, displacing them to marginal beaches (Salmon, 2003). Human and vehicle traffic disturbs females to the point of aborting the nesting attempt, even if she has started laying (pers. obs). Hatchlings become disorientated when stuck in vehicle tracks. Consequently they remain on the beach for longer, increasing the risks of both predation and dehydration (Lamont et al., 2002). Furthermore, the effects of climate change, such as sea level rise and the increased intensity and frequency of storms (Van Houtan and Bass, 2007), could result in a major loss of nesting habitat for sea turtles (Fish et al., 2008). Where setback line regulations are not adhered to, beaches cannot naturally retreat when storms occur,

resulting in greater damage and beach loss (Feagin et al., 2005). Consequently the size of the available nesting area could be dramatically reduced. This could also result in increased nest density where habitat is still intact (Mazaris et al., 2009) and possible decreased nest and hatching success. Pristine beaches are more resilient to changes in sea level, and the associated impacts and consequences are less severe (Harris, 2008).

All species of sea turtles are still exploited by humans for their eggs, meat and shells (Bourjea et al., 2008), despite global conservation efforts. In poorer, developing countries like Madagascar (Rakotonirina and Cooke, 1994), sea turtles and their eggs are targeted as an easy (and predictable) protein source (Koch et al., 2006, Buitrago et al., 2008). Females are easily captured when emerging onto the beach. Eggs are collected during the laying process or excavated soon after the female turtle has covered up the nest with sand. Harvesting turtles and fishing are synonymous for the Veso culture in Madagascar (Lilette, 2006). In addition to consumption, sea turtles have important cultural meaning in some nations. For example, green turtles play an important part in the poetry, mythology and clothing culture of Seri Indians in Baja California (Garcia-Martinez and Nichols, 2000). Nevertheless, sea turtles are now protected by law in most countries (Hughes, 1971, Garcia-Martinez and Nichols, 2000) but because law enforcement can be poor (Lombard, 2009), direct harvesting of females and eggs continues at alarming rates.

In South Africa (SA) major anthropogenic threats to sea turtles, such as coastal development and harvesting, have been eliminated due to the proclamation of marine reserves and a world heritage site protecting both turtles and their habitat. Illegal developments are prevented by strong management presence and the beaches and reefs are protected from poaching and harvesting up to three nautical miles offshore. The iSimangaliso Wetland Park thus provides a unique opportunity to quantify natural mortality of loggerhead and leatherback sea turtles in near-pristine beach conditions. This estimate can be used as a benchmark for natural mortality and can be compared to nesting beaches that experience high levels of anthropogenic threats. Most monitoring programmes use the increase or decrease in the number of nests per unit time per index area as a measure of conservation

success (Schroeder and Murphy, 1999, Witherington et al., 2009). However, using this metric in isolation is biased as it assumes that all nests produce hatchlings and that the hatching success is constant over time. This assumption may be to the detriment of sea turtle conservation because changes in habitat quality, impacting on hatching success, may only be detected when females fail to return two to three decades later. Monitoring nest success and hatchling production is thus important because it provides a more realistic representation of the successful reproductive effort from a particular rookery.

The aim of this chapter is to estimate survivorship (or conversely mortality) of loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles from the egg stage to the stage when the hatchlings enter the sea. The specific objectives are to identify and quantify the causes of nest, egg and hatchling mortality of loggerheads and leatherbacks on nesting beaches in SA. This will be done by firstly estimating reproductive output i.e. the number of nests deposited, eggs laid and hatchlings emerging. The fate of nests will be monitored to evaluate the proportion that produces eggs successfully. Subsequently, nests will be excavated to assess hatching and emergence success and finally, the fate of hatchlings crossing the beach to the ocean will be monitored. These data will be used to estimate beach mortality per age class per species.

Materials and Methods

Study Site

Loggerhead and leatherback female turtles nest along the north-east coast of KwaZulu-Natal (KZN), SA (Fig. 2.1). This nesting area has been protected since 1963, when an annual turtle conservation and monitoring programme was initiated (McAllister et al., 1965). As mentioned, the nesting beaches fall within the iSimangaliso Wetland Park, a UNESCO (United Nations Educational Scientific and Cultural Organisation) world heritage site since 1999. The majority of sea turtle nesting occurs in the Maputaland reserve, a 90 km stretch of beach (nesting beach) of which 56 km is intensively monitored (monitoring area) for sea turtle nesting during the nesting season (mid- October to mid-March) (McAllister et al., 1965). The entire coastal strip, between Kosi Bay and Cape Vidal (~ 170 km) has been marked with marker poles (i.e., beacons). The monitoring area between beacons 32N and 33S is divided into 400 m sections while the remainder of the nesting beach is divided into 1600 m (i.e. 1 mile) sections. Each beacon is numbered according to distance and direction from the Bhanga Nek research station (-27. 0098°S; 32 8651°E; 0N). Beacons north of Bhanga Nek are indicated by (N) and south indicated by (S) (Fig. 2.1). A 5 km stretch between beacons 0N and 12N is the high density nesting section for loggerheads (Fig. 2.1; Nel, 2010). This strip of beach is located adjacent to the Kosi lake system separated from the sea by a dune barrier (Hughes, 1989). The dunes between beacons 0N and 5N are vegetated, with primary dunes covered by *Ipomoea* spp. and *Scaevola plumier*, while coastal dune forest dominates the secondary dunes. The dunes between beacons 6N and 10N have no fore dunes. None of the dunes at beacons 11N and 12N are covered by vegetation and are thus characteristically mobile dunes (pers. obs).

Estimation of nesting female mortality

Females come ashore to nest from mid-October onwards each year. The monitors in the monitoring programme patrol the beach on foot at night in search of nesting turtles. Once an individual is encountered she is tagged (with metal flipper tags) and her carapace measured (straight carapace length, SCL (mm) and width, SCW (mm)). The long-shore position of each nest relative to the nearest beacon is also noted. The monitors re-walk the beach in the morning to score all nesting that took place after midnight (or when they completed their shift). The data per season are pooled, and appended to the long-term Ezemvelo KZN Wildlife (Ezemvelo) monitoring programme database. This nesting database was used to calculate the total number of nesting loggerhead and leatherback females along the entire monitoring area during the 2009/2010 and 2010/2011 nesting seasons. Furthermore, evidence of adult female turtle predation and poaching (although extremely rare) was noted. These data were also included to estimate adult female mortality.

Figure 2.1: (a) The position of the turtle monitoring area, beacons 32N to 100S, in northern KZN, SA indicating the location and distribution of the beacons (data obtained from Ezemvelo and iSimangaliso). (b) A photograph of the typical conditions of the loggerhead nesting hotspot (0N to 12N) (photo: A de Wet).

Estimation of nest, egg and hatchling mortality

In order to estimate the mortality of nests, eggs and hatchlings, the total reproductive output (i.e. the number of nests deposited, eggs laid and hatchlings emerging) was quantified first. This was conducted for both loggerhead and leatherback females by marking several nests as they were being laid and observing them over time to monitor their fate. The experiment was concentrated over a 5 km stretch of beach in the high density nesting area for loggerhead turtles, with additional vehicle patrols carried out throughout the monitoring area. This stretch of beach was patrolled on foot every night during the nesting season from mid-November to mid-January for two consecutive seasons (2009/2010 and 2010/2011). When an emerging female was encountered on the low shore, she was allowed to cross the beach, dig and start to lay eggs undisturbed. Headlamps equipped with red bulbs were used when working with nesting females to avoid disturbance. The clutch size was obtained by counting eggs as they were laid. In the case of leatherbacks, the shelled albumen eggs (SAGs) were excluded from the counts and calculations. The latitude and longitude co-ordinates of each nest were recorded on a handheld Garmin GPS (model 60Cx with \pm 5 m accuracy). The nests were marked in a standardised way; two ping pong balls, joined with a section of weathering resistant nylon, one meter in length. One end with one ball tied down, was placed within the nest (to make it difficult to pull the nylon out). The other ball was placed above the nest on the surface of the sand. Nest location was also recorded in relation to the nearest beacon (as per the standard monitoring protocol). The nests were checked for signs of predation, inundation (nest flooding) or erosion (nest partially or completely washed away) daily when possible, but at least once per week. The fate of every marked nest was scored to estimate nest mortality (Fig. 2.2a). The low density nesting beach was patrolled by vehicle and a similar procedure was followed. However due to vehicle constraints (and beach driving restrictions) effort along this stretch of beach was inconsistent and intermittent but still extremely valuable because a greater distance of beach could be covered. The proportion nests of each fate were calculated out of the total number of nests encountered.

In order to estimate nest success (*NS*), monitored nests were categorised as follows: hatched (more than 50 % of the eggs hatched); partially predated (more than 50 % eggs predated); undeveloped (nests contained more than 50 % whole, yolky eggs); inundated (positioned below the high water mark with mostly unhatched eggs); predated completely (completely destroyed by a predator and assumed to have zero hatching success, Fig. 2.2a); and eroded (washed away). Predated nests were typically surrounded by animal tracks and occasionally eggs were scattered on the surface of the sand. The data were recorded as a frequency per category and finally expressed as a percentage.

At the onset of the hatching season (mid-January), the beach was patrolled on foot in the early evenings in search of emerging hatchlings. Emerging hatchlings were quantified and observed with a red-bulb headlamp, to minimise disturbance, while they were moving down the beach until the last hatchling made it to the sea. The number of hatchlings captured by ghost crabs or any other visible predator was scored (Fig. 2.2c). The hatchling tracks were followed up the beach to locate the hatched nests that were then marked with a stake and the GPS position to relocate the nest later for excavation. The number of hatchlings preyed on (per predator) per nest was expressed as a ratio of the number of hatchlings emerged. The later excavation and fate of straggler hatchlings does introduce a bias into the data; any late emerging hatchlings preyed on would not have been observed and thus discounted in the hatchling predation estimates. However it is also assumed that the proportion of hatchlings emerging on their own, that are predated, will be low (< 1 %) (Glen et al., 2006).

Nests were excavated by hand four days after hatching to allow straggler hatchlings to emerge naturally. During excavations, the number of hatched shells, unhatched eggs, dead and live hatchlings still in the nest, was recorded to determine both the hatching and emergence success (Miller, 1999). Egg infestation by ants (*Dorylus helvolus*) and predation by ghost crabs (*Ocypode* spp.) were quantified; eggs preyed on by ants were characterized by small holes on the egg shell surface (Fig. 2.2b), while those raided by ghost crabs were mostly shredded but contained traces of yolk (Bouchard and Bjorndal, 2000). Once the nest was excavated, the distance from the

nest to the dune base, the distance from the nest to the high water mark and nest depth were measured with measuring tape. Unmarked nests that showed signs of vertebrate predator activity were noted, the position marked with the GPS and if possible the predator was identified by the paw prints.

Figure 2.2: Photographic examples of the fate of nests, eggs and hatchlings encountered; (a) a nest completely destroyed and eggs predated on by a vertebrate predator; (b) loggerhead eggs predated on by ants; (c) a loggerhead hatchling captured by a ghost crab (*O. ryderi*) (photographs: A de Wet).

To score the fate of eggs, only nests that were categorised as hatched, partially predated, undeveloped and inundated were used. Thus, nests that were destroyed completely (through either predation or erosion) were excluded from this analysis. The following parameters were calculated: hatching success (*HS)* as the number of eggs that hatched out of the total number of eggs in the clutch, expressed as a proportion; emergence success (*ES*) as the number of hatchlings that emerged from the nest out of the total number of eggs in the clutch, expressed as a proportion and clutch predation (*CP*) as the number of eggs that were preyed on out of the total number of eggs in the clutch, also expressed as a proportion.

Statistical analyses were performed using the statistical software package R version 2.13.2. The proportions of hatching success, clutch predation and undeveloped eggs out of the total number of eggs per clutch were determined. Because all nest metrics were expressed as proportions, arcsine transformations were performed to normalise the distributions (Zar, 1999). The data were first analysed for differences between seasons for each of the categories (*HS*, *ES* and *CP*). If there was no significant difference (Two-sample t-test, $p > 0.05$) between the two seasons the data for the seasons were pooled. A Two-sample t-test (Zar, 1999) was then performed to test the null hypothesis of no difference in the metrics between species i.e. that hatching success, clutch predation and undeveloped eggs between loggerhead and leatherback turtles were the same. Clutch size as the number of eggs per nest was also compared between the two species using a Two-sample ttest (Zar, 1999). The fate of hatchlings within the nest, emergence success, as a proportion of total clutch size, was arcsine transformed before using a Two-sample ttest to test whether there was a significant difference in *ES* between loggerheads and leatherbacks (Zar, 1999).

Extrapolating ghost crab predation pressure

Ghost crabs (*O. ryderi*, *O. madagascariensis* and *O. ceratophthalmus)* were predicted to be the most significant predator of hatchlings as they are mostly nocturnal, overlapping with hatchling emergence which occurs mainly at night. It was also expected that the rate at which hatchlings were caught would be a function of the ghost crab densities where higher ghost crab numbers relative to hatchling numbers will result in higher predation pressure. Two additional experiments were therefore conducted to i) quantify predation pressure (ghost crab burrow density per unit area) between the high density and low density area and ii) to assess if ghost crabs change their abundance or distribution by moving between locations (i.e. the beacons) between the nesting season and the hatching season. This was conducted by estimating ghost crab densities using pitfall traps during the nesting and again during the hatching seasons on the high density nesting beach.

Crab burrow density

Ghost crab predation pressure (as the probability of hatchlings being captured) may be different between the high density and low density nesting areas (Begon et al., 1997). An experiment was therefore conducted in an attempt to quantify potential predation pressure in these areas. Ghost crab burrow density (no.m⁻²) was used as a proxy for estimating actual ghost crab density (Strachan et al., 1999). Four locations (beacons) were selected at random along the beach and sampled on different but consecutive days. Sampling took place in the early morning or late afternoon on the low, incoming tide. The number of crab burrows was counted in 1 $m²$ quadrats along 50 m transects parallel to the shore. Three transects were conducted per tidal zone namely, low shore, mid shore and high shore. The mean ghost crab density was calculated per area and compared to the number of nests and hatchlings produced in the same area.

Pitfall traps

The response in the ghost crab density to hatchlings available was evaluated in the high density nesting area by comparing the ghost crab density and sizes of individuals between the peak nesting and peak hatching seasons, between beacons. Pitfall traps (5 *litre* buckets) were buried in the sand every 400 m (i.e. at each beacon) at dusk and baited with a 2 cm piece of fish (mackerel). Three traps were placed at the dune base while another three were placed at the drift line (Schlacher et al., 2007). After four hours the traps were excavated and the species composition and the catch was quantified (Fig. 2.3a). The carapace width of 10 randomly selected individuals per trap was measured with metal vernier callipers (accuracy ±

0.1 mm). Due to the extent of the sampling area (and the constraint of sampling on foot), the study beach was halved, thus six beacons were sampled per night. A total of 36 traps were used per night (Fig. 2.3b). The full 5 km stretch of beach was thus sampled over two consecutive nights with a total of 72 traps collecting ghost crabs. The experiment was repeated three times during the peak nesting season in December 2010 and again in the peak hatching season in February 2011. Since Schlacher et al (2007) indicated that ghost crabs tend to be more active on darker evenings, all these experiments were conducted on the new moon phase.

Figure 2.3: Photographic example of buckets baited with mackerel (a), were buried in the sand at both the dune base and drift line (b) as pitfall traps to collect ghost crabs (photographs: A de Wet).

Ghost crab density was expressed as the mean number per square meter (no. m^{-2}). The data per zone were tested for normality (Shapiro-Wilk normality test) but because the data were non-normal a non-parametric Kruskal Wallis test was performed. The mean ghost crab burrow density (no.m⁻²) within the three beach zones (i. e. low shore, mid shore, high shore) on the high density nesting beach was compared with the three beach zones on the low density nesting beaches (Zar, 1999).

The extent of ghost crab predation on eggs and hatchlings was tested using Pearson"s product-moment correlation analysis. This test was used to determine if egg predation increased with an increase in mean burrow density (no.m⁻²). This was repeated for hatchling predation. Hatchling predation by ghost crabs was calculated as a proportion of the total clutch size. A chi-square test was used to test whether the number of hatchlings predated by ghost crabs was different between the two nesting turtle species (Zar, 1999). Larger ghost crabs are more likely to catch, kill and consume hatchlings. Ghost crab size frequency histograms were created to compare the number and sizes of individuals sampled during December 2010 and February 2011. In addition, a Kruskal Wallis test was performed (as the assumption of normality was violated to perform an ANOVA). This statistic was calculated to determine whether there was a significant difference in the size of ghost crabs sampled between these two seasons. The mean size of loggerhead and leatherback hatchlings was compared to the sizes of ghost crabs sampled, predicting that smaller loggerhead hatchlings would be "preferred" over leatherback hatchlings.

Hatchling production

In order to estimate the number of individuals that survive to enter the next size class, the total reproductive output was calculated as the number of hatchlings entering the ocean. Hatchling success (*HLS*, the number of hatchlings that made it to the sea) was estimated using Equation 2.1 modified from Hitchins et al (2004):

Equation 2.1:

Hatchling success (HLS) = $N \times NS \times CS \times ES \times (1 - HP)$

Where hatchling success (*HLS*) is calculated as: the number of nests (*N)* multiplied by the nest success (*NS, as a fraction)* multiplied by the mean clutch size (*CS, as a number*) multiplied by the mean emergence success (*ES, as a fraction)* multiplied by one minus mean hatchling predation (*HP, as a fraction of the total number of hatchlings that emerged from each nest*).

Results

Fate of nesting females

Nesting females are skittish when they have just emerged, but once egg laying has started they are in a "trance" and vulnerable to predators and poachers. During the 2009/2010 nesting season, a total of 521 loggerhead and 61 leatherback females were recorded whereas during the 2010/2011 season 614 loggerhead and 68 leatherback females were recorded. The majority of the loggerhead females nested in the area between beacon 0N and 12N, whereas leatherback nests were spread evenly along the nesting beach. Even though large predators are occasionally seen on shore e.g. leopards, there are no recorded incidences of any interactions between adult turtles and terrestrial predators. Further, the area is well protected and thus poaching is minimal. There was one reported case of poaching of a loggerhead female during the 2009/2010 season (Nel, 2010). The poacher indicated that it was not the first, but the fourth sea turtle taken that season. Therefore, adult mortality does occur, but is incidental. Poaching on SA nesting beaches is not considered a major source of mortality and thus adult mortality is concluded to be << 1 % which is too low for analysis.

Fate of nests

During the 2009/2010 nesting season, the fates of 316 (292 *C. caretta* and 12 *D. coriacea*) of 3 229 nests were determined. The following season (2010/2011) was a particularly good season for both loggerheads and leatherbacks and the fates of 609 (485 *C. caretta* and 155 *D. coriacea*) of 3 835 nests were determined. In total the fates of 925 nests were thus determined in this study (Table 2.1). The data were pooled for this analysis because the numbers per category were small. Loggerhead nest survival was higher than that of leatherbacks (89 % and 78 % respectively). Thus 89 % of loggerhead nests produced some hatchlings and over 70 % of these nests had > 50 % hatching success. In terms of natural mortality, tidal inundation had the smallest effect: none of the leatherback nests were inundated by tides and very few (< 1 %) loggerhead nests were inundated. However, more leatherback nests were eroded than loggerhead nests (6.3 % vs 2.2 %). Overall, more loggerhead nests suffered developmental arrest (contained mostly whole, yolky eggs) than leatherback nests (7.3 % and 4.7 % respectively, Table 2.1). Seven loggerhead nests were destroyed by other nesting loggerheads. Of these nests, three were predated completely soon afterwards and four later eroded. Thus, these nests were categorised as predated and eroded respectively. No leatherback nests were observed to be destroyed by other nesting females.

Nest predation mainly occurred during the month of February, which coincides with the peak hatching month (Fig. 2.4). Predation was the greatest single source of nest mortality (11.6 %, including loggerhead, leatherback and unidentified species) with the following recorded predators: ants, honey badgers, monitor lizards, mongooses and domestic dogs (Table 2.1). A greater proportion of leatherback nests (15.7 %) were completely predated compared to that of loggerhead nests (8.6 %). Partial predation of nests was limited to ghost crabs and ants and accounted for 6.8 % of monitored loggerhead and leatherback nests (Table 2.1).

Over the two sampled seasons, loggerhead nests were concentrated in the strip between beacons 0N and 12N whereas leatherback nests that were predated were distributed evenly along the monitoring area. Most of the loggerhead nests destroyed completely by predators were located in the high density nesting area (0N to 12N; Fig. 2.5) whereas leatherback nests predated completely were mainly located towards the south, outside the main sampling area (33S to 100S, Fig. 2.6). Eroded nests of both species were also distributed evenly along the beach with no particular stretch of beach affected more.

Table 2.1: The fate of loggerhead (*C. caretta*) and leatherback (*D. coriacea*) sea turtle nests along the monitored area of the Maputaland coast (32N to 100S) for the 2009/2010 and 2010/ 2011 seasons. The frequency is given per category with the percentage in brackets ($n = 925$).

Figure 2.4: Temporal change in predation pressure on both loggerhead (Cc) and leatherback (Dc) nests. Bars represent the total number of nests that were predated completely in each month of the nesting season on the Maputaland coast summed for the 2009/2010 and 2010/2011 seasons ($n = 87$).

Loggerhead nests were destroyed by a variety of animals but not all predators could be identified. The animal"s tracks in the sand lost detail quickly due to variability in the environment (e.g. wind and waves) which made it difficult to distinguish between species. However these nests were destroyed by vertebrate predators like dogs, honey badgers, monitor lizards and mongooses. Further invertebrate predators such as ants and ghost crabs tended to remain in the nest. Of the identified predators, dogs from nearby villages destroyed most of the depredated loggerhead nests (19.4 %) followed by ants (14.9 %; Fig. 2.7a). Dogs had no effect on leatherback nests though (Fig. 2.7b). Ants destroyed more loggerhead nests than leatherback nests (Fig. 2.7a and 2.7b). Ant predation was also only recorded in the high density loggerhead nesting area whereas honey badger predation was only recorded in the southern part of the monitoring area. Honey badgers were the main predators of leatherback nests (55.0 %; Fig 2.7b). Nests that were partially predated still produced hatchlings, irrespective of the predator. No anthropogenic sources of nest mortality were recorded during the 2009/2010 and 2010/2011 nesting seasons although there were a few attempted nest raids.

Figure 2.5: Spatial distribution of monitored loggerhead nests (hatched) and mortality (eroded and nests predated completely) along the Maputaland coast during the 2009/2010 and 2010/ 2011 seasons (n = 777) (Image: Google Earth ©).

Number of leatherback nests

Figure 2.6: Spatial distribution of monitored leatherback nests (hatched) and mortality (eroded and nests predated completely) along the Maputaland coast during the 2009/2010 and 2010/2011 seasons (n = 127) (Image: Google Earth ©).

Figure 2.7: The relative contribution (%) by different predators to the number of predated loggerhead (a; $n = 67$) and leatherback (b; $n = 20$) nests along the Maputaland coast during the 2009/2010 and 2010/2011 nesting seasons.

Fate of eggs

Hatching success, clutch size and clutch predation were not statistically significant between the two seasons sampled and data were pooled for further analysis. The fate of eggs was determined from nests that were categorised as hatched, partially predated, inundated or undeveloped. Loggerheads had a significantly larger mean (\pm SE) clutch size (106.6 \pm 0.9) than leatherbacks (84.1 \pm 2.6) (t_{0.05/2)} $_{790}$ = 7.97, p < 0.05), but not significantly different (although marginally lower) hatching success than leatherbacks (73.4 % and 76.8 % respectively; $t_{0.05(2), 790} = -1.20$, $p = 0.23$; Table 2.2). Developmental arrest (undeveloped eggs) $(t_{0.05(2), 790} = 1.52, p = 0.13)$ and egg predation was similar between the two species $(t_{0.05(2) 790} = -0.72, p = 0.47)$. Emergence success was also similar between loggerhead and leatherback hatchlings $(t_{0.05(2)790} = -0.61, p = 0.54;$ Table 2.2).

During nest excavations, ghost crab tunnels as well as individual ghost crabs were observed in several nests. Nests between beacons 8N and 9N were located near dune vegetation because the beach is narrow, and the back-beach absent along this stretch. This section is also where most ant predation occurred. Egg predation by ants seemed to decrease with increasing distance from the dune vegetation, while egg predation by ghost crabs displayed the opposite trend, although these trends were weak, insignificant correlations $(r = -0.2, p = 0.2$ and $r = 0.1, p = 0.3$ respectively).

Ocypode ryderi was the most abundant ghost crab species found in the study area as per pitfall trap catches ($n = 2031$). Other ghost crab species were encountered in lower numbers i.e. *O. madagascariensis* (n = 30) and *O. ceratophthalmus* (n = 3). The overall mean ghost crab burrow density was significantly higher on the high density nesting beach than on the low density nesting beach for the total density $(\chi^2$ _{0.05, 1} = 997.86, p << 0.001; Figure 2.8). In addition, ghost crab density per zone was significantly higher on the high density nesting beach than on the low density nesting beach (Low Shore χ^2 _{0.05,1} = 836.71, p << 0.001; Mid Shore χ^2 _{0.05,1} = 628.34, p << 0.001; High Shore χ^2 _{0.05,1} = 39.48, p < 0.001; Fig. 2.8). The significantly higher

ghost crab burrow density on the high density nesting beach could be increased food availability in the form of turtle eggs and hatchlings. Ghost crabs were more abundant on the low shore on both beach stretches, because this is their usual feeding zone. There was a significant positive correlation between mean ghost crab burrow density and egg predation ($r = 0.5$, $p = 0.001$; Fig. 2.9).

Table 2.2: The fate of loggerhead (*C. caretta*) and leatherback (*D. coriacea*) eggs on the Maputaland coast with data combined for two nesting seasons, 2009/2010 and 2010/2011 (mean \pm standard error; n = 792 nests).

Figure 2.8: The mean density of ghost crab burrows (no.m⁻² \pm SE) on the high density (HD) and low density (LD) nesting beach stretch based on burrow counts $(n = 2000$ quadrats).

Figure 2.9: Correlation of egg predation (with mean loggerhead and leatherback eggs combined) per nest ($n = 19$) per beacon against mean ghost crab burrow density (no.m⁻².beacon⁻¹).

Fate of hatchlings

A total of 57 hatched nests were observed, 52 were loggerhead and five were leatherback nests. Thus 4 338 loggerhead and 350 leatherback hatchlings were observed during their race to the ocean (Table 2.3). There was a significant difference in the number of loggerhead hatchlings caught by ghost crabs when compared to leatherback hatchlings $(\chi^2$ _{0.05, 1} = 116.12, p < 0.05; Table 2.3). In terms of temporal trends, significantly larger ghost crabs were collected in the hatching peak (February 2011; 36.47 mm \pm 4.0 mm) compared to the nesting peak (December 2010; 32.37 mm \pm 6.1 mm and χ^2 _{0.05, 1} = 222.92, p < 0.01; Fig. 2.10a and Fig. 2.10b). Ghost crab breeding occurs in summer months between November and March (Jackson et al., 1991) and thus crabs are more active, explaining the high crab abundance. However, the higher abundance during February could be attributed to crabs moving into an area with greater food availability in the form of eggs. Smaller ghost crabs (< 20 mm) were probably not attracted to the bait or they were consumed by larger ghost crabs in the trap before they were checked. Some of the ghost crabs sampled in February were larger than the mean size of loggerhead hatchlings (44.7 mm) but no ghost crabs were larger than the mean size of leatherback hatchlings, 58.7 mm, (Hughes, 1974b) (Fig. 2.10).

Table 2.3: The number of loggerhead (*C. caretta*, n = 52) and leatherback (*D. coriacea*, n = 5) hatchlings killed by ghost crabs during the 2009/2010 and 2010/2011 nesting seasons.

Figure 2.10: Size frequency histogram of *O. ryderi* along the high density nesting beach during December 2010 (a; $n = 797$) and February 2011 (b; $n = 1007$). The black dotted line indicates the mean carapace length of loggerhead hatchlings (44.7 mm).

Correlation analysis did not show hatchling mortality to significantly increase with increasing mean ghost crab burrow density $(r = 0.43, p = 0.16;$ Fig. 2.11). Other predators observed to feed on hatchlings that emerged at dawn or dusk includes the palm nut vulture (*Gypohierax angolensis*), yellow billed kite (*Milvus aegyptius*) and the African fish eagle (*Haliaeetus vocifer*). These predators were opportunistic when hatchlings emerged during twilight but as interactions were incidental, it was not quantified.

Figure 2.11: Correlation of hatchling mortality (mean % of total emerging hatchlings.nest⁻¹.beacon⁻¹) and mean ghost crab burrow density (no. m⁻²) along the Maputaland coast $(n = 12)$.

Hatchling production

The total number of nests (*N)* was used together with mean annual estimates of nest success (*NS*), clutch size (*CS*), hatching success (*HS*), emergence success (*ES*) and hatchling predation (*HP*) to estimate the number of hatchlings that made it to the sea per species per season. It was estimated that between 192 573 and 199 319 loggerhead hatchlings and between 10 075 and 11 070 leatherback hatchlings made it to the sea during the 2009/2010 season (Table 2.4). The following season had a higher yield for both species (loggerheads ranged between 222 026 and 229 805 hatchlings and leatherbacks ranged between 16 571 and 18 207 hatchlings). This increase is largely due to the greater number of nests deposited during the 2010/2011 season.

Table 2.4: A summary of the estimated number of loggerhead (*C. caretta*) and leatherback (*D. coriacea*) hatchlings that made it to the sea during the 2009/2010 and 2010/2011 seasons using Equation 2.1 (mean ± standard error).

Discussion

Some charismatic taxa use backshores of sandy beaches to breed. Examples are shorebirds like oystercatchers (*Haematopus* spp.), plovers (*Charadrius* spp.) and sanderlings (*Calidris* spp.) as well as all species of sea turtles. Many of the shorebird species migrate across hemispheres to nest (Myers, 1983), but unlike shorebirds which stay ashore to incubate their eggs and protect their nests (parental care) (Oro et al., 1999, Engeman et al., 2010), sea turtles come ashore, nest and depart without any idea of the success of their effort. As an aid to prevent predation, they bury their eggs and disguise the nest before departing. The nocturnal nesting behaviour of turtles presumably makes it less likely for diurnal predators to encounter females or their nests. Despite these measures, sea turtle eggs are nutrient rich morsels (Bouchard and Bjorndal, 2000) and are frequently and opportunistically consumed by predators that come across an incubating or emerging turtle nest.

This study compared the reproductive success of two species of sea turtles, loggerheads and leatherbacks, nesting in SA. Nest success (i.e. nests that produced hatchlings) was proportionately higher for loggerheads (89 %) than for leatherbacks (78 %). Even though loggerhead and leatherback nests were exposed to similar threats, the relative impact of each threat differed between the two species. Predation was the most significant cause of nest destruction for both loggerheads (8.6 %) and leatherbacks (15.7 %). Honey badgers, the most significant predator of leatherback nests, are generalist foragers and "switch" between prey species depending on availability (Begg et al., 2003). This contributes to the seasonal shift in predation pressure on sea turtle eggs. Dogs from local villages destroyed mainly loggerhead nests and were concentrated around beach access points such as beacons 15N and 10S. These non-natural predators only arrived with the settlement of humans and considering the conservation status of sea turtles as well as their SA nesting beaches, their numbers should be better managed. Dogs and other nonnatural predators, such as pigs, are known to cause major problems in other rookeries such as green turtles in the Seychelles (Hitchins et al., 2004) and Costa Rica (Fowler, 1979) due to their destructive impact on turtle nests.

Excessive nest predation is a recognised problem across the world, particularly for declining sea turtle populations. For example, 27 % of the annual green turtle and loggerhead nests in northern Cyprus are completely destroyed by predators (Broderick and Godley, 1996). In Turkey, approximately 75 % of monitored green turtle nests were destroyed by foxes and jackal in a single season (Brown and Macdonald, 1994). These estimates are higher than the impact of all predators combined in the present study (11.6 %). In Florida, predator numbers have increased dramatically because supplementary food sources from humans are readily available. Specifically the numbers of raccoons and foxes have had to be controlled due to their excessive predatory impact on sea turtle nests (Brown and Macdonald, 1994, Engeman et al., 2010, Turkozan, 2000). Fortunately such drastic measures are not required in SA because beach predation is predominantly from natural sources.

Even though the proportion of loggerhead nests that were partially predated was higher (7.6 %) than for leatherback nests (3.1 %), ant and ghost crab predation, and developmental arrest within these nests (i.e. eggs) was similar for both species. Approximately 75 % of the eggs deposited by both loggerhead and leatherback females survived and developed into hatchlings. Of the natural predators in the area, ants were the most significant predators of loggerhead nests (14.9 %). Ant predation was particularly high between beacons 8N and 11N, the preferred loggerhead nesting site during the previous two seasons. The predatory and aggressive ant, *D. helvolus* (Picker et al., 2004), destroyed entire clutches, equivalent to results found in several other studies (Allen et al., 2001, Hughes and Bartholomew, 1998b). Nevertheless, these invertebrates are likely to play an important role in the decomposition of undeveloped eggs, thus recycling nutrients to the sandy beach ecosystem (Bouchard and Bjorndal, 2000).

One factor that affects both shorebird and sea turtle nests is extreme weather. Exceptionally high tides and sea level changes cause erosion and inundation (Galbraith et al., 2002, Kappel, 2005). Nests that are located too close to the high water mark, like leatherback nests, are more vulnerable. Birds have a high parental investment to care for few offspring but turtles have overcome this challenge by producing large numbers of eggs and nesting over a range of locations within the same season. This strategy has proven successful for turtles until recently, due to the increasing number of threats to sandy beach ecosystems (Defeo et al., 2008). With the current spatial overlap of interests between sea turtles and human activities, sea turtles have no escape, not even on the high seas.

In this study a greater proportion of leatherback nests were eroded (6.3 %) than loggerhead nests (2.2 %). Leatherbacks generally nested closer to the high water mark (Pritchard, 1971) and therefore their nests were more susceptible to erosion and tidal inundation than those of loggerheads. Nest erosion may simply occur because the back-beach (i.e. the zone between the drift line and the dune base) is relatively narrow in some areas (e.g. at beacon 9N). In other areas the intertidal beach gradient is gentler, with a narrow back-beach and the swash zone overtops all the way to the dunes during spring high tide, particularly at beacons 1N and 2N, where many loggerheads prefer to nest. Interestingly, no monitored leatherback nests were (observed to be) inundated in this study. Egg mortality due to inundation depends on the frequency and extent of overwash as well as the developmental stage of the embryos when overwash events occur (Caut et al., 2010). The shallower nests of loggerheads are further from the high water mark and raised from the ground water table and thus seldom become flooded. Embryonic development thus continued in a fraction of the eggs even after inundation. Increased levels of beach erosion and nest inundation are predicted to affect coasts across the world (Baker et al., 2006). Beaches with a narrow back-beach or those "boxed in" by development will be particularly vulnerable. The loss of sea turtle nesting habitat could increase the density of nests in other areas and indirectly cause a decrease in the hatching success (Mazaris et al., 2009). Approximately 20 % of the nesting sites in the Caribbean have already been lost due to human interference (McClenachan et al., 2006). Nevertheless, erosion is a relatively small threat to the nesting beaches in KZN because the beaches are well protected in a world heritage site. Development on the coast is essentially banned and dunes provide a buffer against the rising seas. Impacts should thus be restricted to a few seasons before beaches reestablish themselves (Harris, 2008).

Ghost crabs (*O. ryderi*) were the main predator of hatchlings scrambling to the ocean. Leatherback hatchlings were much larger than most of the ghost crabs sampled (Hughes, 1974b) and this suggests that smaller loggerhead hatchlings may be more vulnerable to ghost crab predation. Hatchling predation (of observed nests) by ghost crabs was estimated to be 4.1 % per clutch ($n = 58$). The results correspond well to Hughes (1974b), which used a similar estimating method and obtained a mean of 3.7 % hatchlings predated per clutch ($n = 10$). This suggests that hatchling predation by ghost crabs has been relatively constant over time. These estimates are considerably lower than in Playa Grande where hatchling predation by ghost crabs is as much as 12 % per clutch (Tomillo et al., 2010). Predatory attack by ghost crabs is often directed at the weaker hatchlings (pers. obs) and therefore the loss of these weaker hatchlings would not ultimately influence the reproductive potential of the population as a whole. Emergence of hatchlings at night is likely to be a predator avoidance strategy and also prevents dehydration (Drake and Spotila, 2002). Furthermore hatchlings emerging as a clutch, induces predator satiation and thus lowers the overall predation rate (Hirth, 1980).

This study on the SA nesting beach showed that survivorship from the egg to hatchling stage that makes it to the sea is greater than 70 % for both loggerhead and leatherback turtles. This estimate is considerably higher than that of hawksbill turtles in Seychelles (61 %) (Hitchins et al., 2004). Thirty percent mortality within the first two months of life is considerably high. Nevertheless, this estimate was based on fairly pristine conditions and representative of natural mortality. The number of loggerhead hatchlings that survived to the next stage was approximately 200 000 per season for the seasons studied. There was a large difference in the number of leatherback hatchlings that survived to the next age class between the two seasons that were studied. This is mainly due to the greater number of females that deposited more nests during the 2010/2011 season than the 2009/2010 season. Once through the shore break, these hatchlings are vulnerable to predation by a multitude of predatory fish, octopus and birds. Despite high predation rates of post-hatchlings and juveniles, it is assumed that such high rates of hatchling production and survival is important to boost survival of later age classes (Mazaris et al., 2005).

In conclusion, even though natural mortality is low in this rookery, the effects of climate change are not well documented. However these estimates, even though they correspond well with the results obtained by Hughes (1974b), should be monitored more frequently. The reason being that nest success is not very representative of emergence success especially as climate change could threaten the survival of nests (Hawkes et al., 2009). Therefore, continued monitoring and protection of nesting beaches is vital to enhance survival of hatchlings. Even though the life history strategy of sea turtles is adapted to handle high offspring mortality, declining populations cannot recover if these mortality levels are excessively high (Crouse et al., 1987). Improved knowledge of mortality levels at each life stage on the nesting beach is required to refine such estimates.

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Chapter 3: Spatial overlap of sea turtles and fisheries

Introduction

Marine fisheries are generally considered to be the most important human-induced threat to the world"s oceans today (Wallace et al., 2010). These threats are not evenly spread as fishery operations tend to focus on areas where target species aggregate (like spawning areas) or occur in high abundance (foraging areas) such as nutrient upwelling zones. These areas attract both target and unfortunately, nontarget species (Gardner et al., 2008, Lewison et al., 2009). There is growing concern regarding both overexploitation of fish stocks (FAO, 2010), and the magnitude of the incidentally caught non-target species (i.e. bycatch) in global fisheries (Hamann et al., 2010, Wallace et al., 2010). This combination has significant impacts on ecosystem production and functioning through the alteration of trophic levels and hence it has been realised that ecosystems based management of fisheries is required.

Marine mammals, sea birds, sharks and sea turtles are migratory marine vertebrates exposed to a variety of fisheries across the seascape (Lewison et al., 2004a). Sea turtles in particular migrate great distances between nesting and foraging grounds, overlapping with both commercial and artisanal fisheries throughout their geographic distribution (Ferraroli et al., 2004, Blumenthal et al., 2006). Because these species are long-lived and late maturing, it is paramount that mature individuals have a reasonably high survivorship to get the opportunity to breed and so maintain population numbers (Crouse et al., 1987). However, the size classes of sea turtles most vulnerable to fisheries are the larger individuals (sub-adults and adults) which are also the reproductively valuable turtles (Spotila et al., 1996). Further, these size classes have "out-grown" most natural predation pressures and should have high survival for this life history strategy to succeed. For this reason, fisheries bycatch has been implicated in the declines of several sea turtle populations (Lewison et al.,

2004a, Donlan et al., 2010, Wallace et al., 2010). Fisheries impact on those size classes that are naturally meant to have high rates of survival.

In order to understand the pressures imposed by fisheries, it is important to understand the relevant types of fishing. Fisheries can be classified into three broad types based on the objective of the activity; recreational, commercial and artisanal. Recreational fishers catch fish for the thrill and often employ a "catch and release" policy (Cooke and Cowx, 2004). However the impact on sea turtles is very small and largely absent from the literature. It will therefore not be considered further in this thesis. Commercial fisheries operate on a large scale in space and time, deploy expensive fishing gear, tend to use the best available fish-finding technology and operate exclusively to generate income. Most commercial operations are targetspecies driven with fishing gear designed to select and capture a particular species (or suite of species). For example, longliners target pelagic top predators like tuna, swordfish and sharks (Lewison et al., 2004a). Trawl nets would target mid- or bottom species like hake or prawns (Fairweather et al., 2006), and purse seiners target small pelagic species, such as sardines and anchovies (Lluch-Belda et al., 1989). Commercial fisheries do not change the target species in mid operation. In contrast, artisanal fishers carry and use a variety of gears (like gillnets, hand lines, spears or seine nets), often simultaneously to catch species opportunistically (Hughes, 1974a). The objective in artisanal fisheries is to provide sustenance for families. These fishers tend to use no or little technology and do not move far away from land. They also operate on comparatively short time scales (i.e. fishers going out daily, rather than weeks or months at a time, as is the case for many commercial fisheries).

The main commercial fisheries in South African (SA) waters likely to interact with sea turtles are pelagic longlining and shallow-water prawn trawling (Peterson, 2008). SA and Australia have another unique fishery type that interacts with sea turtles. These are anchored gillnets installed in coastal waters to protect bathers from dangerous sharks (Dudley, 1997). Driftnets have been banned in SA due to the unselective design and excessive bycatch of this fishery (Bourjea et al., 2008). Purse seining is probably the biggest fishery operating mostly off the west coast of SA, with

apparently little impact on sea turtle populations. Only fisheries with a known impact on SA sea turtles will be considered in this thesis.

Pelagic longline fisheries target swordfish (*Xiphias gladius*), tuna (*Thunnus* spp.) and a variety of shark species. These operations involve using hundreds of baited hooks that are attached to lines branching off a mainline, many kilometres in length being left overnight anchored or drifting at sea to catch fish (Peterson, 2008). In the years between 2006 and 2010, fifty vessels were licensed to fish in the SA Exclusive Economic Zone (EEZ; which extends to 200 nm) and the high seas. This fleet was split between SA and Asian vessels fishing under a bilateral agreement with SA. Asian vessels (~ 60 % of fleet) tend to target tuna, set their gear relatively deep (up to 300 m), mainly during the day. The SA fleet that targets swordfish sets gear much shallower (50 – 120 m), and tend to operate at night, often using light sticks. Compulsory independent observers that record bycatch incidents are placed on all Asian vessels with only \sim 5 % of the SA fleet was observed.

Longline fishing has globally been criticised for the high levels of sea bird, shark and sea turtle bycatch (Belda and Sanches, 2001, Ferraroli et al., 2004, Lewison et al., 2004b, Carranza et al., 2006). Several studies reporting on sea turtle bycatch in the Pacific and Atlantic Oceans all claim that the current rate of turtle bycatch is not sustainable (Carruthers et al., 2009, Donoso and Dutton, 2010). Lewison et al (2004b) estimated that 50 000 leatherbacks (*Dermochelys coriacea*) and 200 000 loggerheads (*Caretta caretta*) were caught during the year 2000 by the pelagic longline fishing fleets operating in the Pacific and Atlantic Oceans. Leatherbacks seem to be especially vulnerable to bycatch in this fishery because of the high degree of spatial overlap between foraging and fishing grounds and depths (Ferraroli et al., 2004). Loggerheads are also caught in significant numbers because they are carnivores attracted to the bait (such as mackerel, pilchards and squid) used in this fishery (Hall et al., 2000). Loggerheads are therefore most often hooked in the mouth or, when the bait is swallowed, in the digestive tract (Watson et al., 2005).

Trawl fisheries are classified according to their target species. Demersal trawling in SA for example targets hake in deep water off the south and west coasts (Fairweather et al., 2006) while shallow-water trawling off the east coast targets prawns (Fennessy et al., 1994). Due to the non-selective design of the trawl nets, bycatch in these fisheries can be high (Hall et al., 2000). Up to 70 % of the catch can be composed of non-target species (DEAT, 2005) such as unwanted (trash) fish species and elasmobranchs. Marine mammals, but sea turtles in particular, also get caught (Zeeberg et al., 2006, Fennessy et al., 2008). Not all trawling will impact on sea turtles though; sea turtles are unlikely to interact with deeper bottom (300 - 500 m) and mid-water (50 - 300 m) trawls. Bottom trawling may disturb turtle feeding habitat and so have an indirect effect. The depth columns targeted by shallow-water prawn trawling in SA coincides with the feeding zones of most juvenile and adult sea turtle species (Fennessy and Isaksen, 2007). It was estimated that as many as 11 000 sea turtles were caught per annum in the northern and eastern Australian prawn trawl fishery (Poiner and Harris, 1996). These catches were reported before the introduction of Turtle Excluder Devices (TEDs) which have substantially reduced turtle bycatch in prawn trawl fisheries (Wamukoya et al., 1997, Hall et al., 2000,).

The third fishery impacting on sea turtles in SA is the bather protection program. In 1952 a shark control program using anchored gillnets, was implemented on the east coast of SA after a series of shark attacks on a number of bathers (Cliff and Dudley, 2011). The beaches along the lower KwaZulu-Natal (KZN) coast are a popular tourist destination due to the warm ocean temperatures and subtropical climate. The shark gillnets are designed to reduce the number of large sharks in the area and to create an obstacle for sharks, preventing their interaction with bathers (Dudley and Cliff, 1993, Krogh and Reid, 1996). However, gillnets are notorious for high levels of bycatch due to non-selectivity (Hall et al., 2000). Globally driftnets, which are unanchored gillnets, have been banned for this reason. Numerous non-target species are also accidentally caught. Loggerheads comprise the bulk of the turtle bycatch from shark nets, followed by green turtles (*Chelonia mydas*) and leatherbacks (Young, 2001, Brazier et al., 2012). In an attempt to limit ecosystems impacts, total netting effort has been reduced considerably over the last 10 years.

Experimental drumlines have also recently been deployed to replace a number of the gillnets (Cliff and Dudley, 2011). The drumlines (baited hooks on a line attached to a drum float) are more selective than nets and hence reduce bycatch. Nevertheless, previous studies on bycatch in the shark nets suggested that catches in the shark nets (in isolation) were not a threat to the stability of the nesting populations of loggerhead and leatherback sea turtles in SA (Dudley, 1997, Young, 2001, Brazier et al., 2012)

Loggerhead and leatherback sea turtles nesting in SA migrate throughout the western Indian and eastern Atlantic Ocean basins (Hughes et al., 1998, Luschi et al., 2006). They are therefore not only exposed to the fisheries in the SA EEZ, but also to commercial fisheries operating off the coast of Namibia and the high seas, and to artisanal fisheries along the Mozambique Channel. Flipper tag returns of postnesting females have been collected throughout the South Western Indian Ocean (SWIO) for both loggerhead and leatherback turtles providing an indication of their foraging distribution as well as artisanal fishery mortality. Very few studies have actually quantified mortality caused by either commercial or artisanal fisheries in this region. The literature does however suggest that targeted catch and bycatch of turtles in artisanal fisheries may be on par or exceed catches by commercial fisheries (Bourjea et al., 2008, Alfaro-Shigueto et al., 2010, Humber et al., 2010).

Human-related impact on sea turtles (and marine life in general) is not limited to fisheries or direct take. Indirect impacts of fishing are also a problem; this includes ghost fishing (Brown and Macfadyen, 2007) and boat strikes (Hazel et al., 2007). The effects of pollution (marine debris, oil and chemicals) on sea turtles and other marine organisms in general is also a growing concern (Mrosovsky et al., 2009). Strandings data provide some indication of the relative importance of these indirect causes of mortality. The exact cause of mortality is often difficult to identify because carcasses often arrive ashore in a badly decomposed state, masking the primary cause of death (Epperly et al., 1996). Alternatively turtles wash ashore without any obvious signs of trauma (like swallowed hooks or plastic entanglements), or obtained internal injuries which cannot be determined without a proper necropsy. Furthermore, the number of stranded sea turtles only provides the minimum estimate

of mortality and the actual extent is unknown (Hart et al., 2006). It should be noted that not all turtle stranding events are as a result of human activity. Disease, such as fibropapillomatosis, or parasite infestations may also be a reason for turtle stranding events (Work et al., 2004). Diseases may be as difficult to identify.

The combined spatial footprint of threats to sea turtles in the SWIO is largely unknown. It is thus necessary to identify the threats, map the spatial distribution of the threats (of which fisheries pressures are considered the most important) and then map the spatial overlap of sea turtle distribution. To achieve this, both commercial and artisanal fisheries will be mapped (based on effort and impact) to identify areas of high risk and highlight data gaps. This is also an important step towards the development of offshore monitoring programs and eventually bycatch mitigation measures.

The aim of this chapter was to describe the fisheries around the country and along the migratory corridors, which could pose a threat to loggerhead and leatherback turtles nesting in SA. This will be conducted with the specific objectives of i) mapping the distribution of post-nesting females, tag return and stranding data indicating their nesting and foraging distribution and ii) the spatial distribution of relevant fisheries (pelagic longlining, shallow-water trawling and shark nets) with some indication of effort iii) to identify the high-risk areas where turtles and fisheries are likely to overlap in space (and less so in time as the data resolution is not available). (A more detailed analysis, quantifying bycatch and the impacts on the turtle populations will be conducted in Chapter 4).

Materials and Methods

Spatial distribution of sea turtles

Satellite tracking

Nine leatherbacks were fitted with a back pack containing Platform Transponder Terminals (PTT) that were attached to a harness between 1996 and 2006 using standard methods (Hughes et al., 1998). Thirteen loggerhead females were detained after nesting during the 2010/2011 nesting season and were equipped with SPOT 5 transmitters (Wildlife Computers) attached to the shell using a quickset epoxy adhesive. A similar procedure was followed during the 2011/2012 nesting season when six loggerheads were satellite tagged. All transmitters were followed on the Argos tracking system.

The tracking data were first filtered to remove inaccurate (Location Class Z locations) and erroneous locations. Then a single, best quality location point was plotted per day. If there was more than one good location point per day, the earliest point was used. Geographic Information Systems (GIS) spatial software ArcGIS 10 (ESRI, 2010) and ArcView 3.3 (ESRI, 2002) were used to plot the location points as well as to calculate the 50 % and 95 % kernel home ranges (KHR) of both species (Worton, 1989), using least squares cross validation as a smoothing parameter (Seaman et al., 1998).

Sea turtle flipper tag returns and stranding events

Nesting loggerhead and leatherback females are marked at their SA nesting beach using Oceanographic Research Institute (ORI), monel and since 1996, titanium flipper tags (Hughes, 1996). Each of the flipper tags is coded with a unique number to trace the nesting history and ultimately the fate of the female turtle. Each tag contains the return address as well as a message of a reward. International tag returns are indicative of sea turtle mortality by artisanal fishers. In addition, these tag returns as well as reported cases of stranded individuals can give an indication of the

foraging destinations of loggerhead and leatherback turtles. The locations of international tag returns were mapped using (GIS) spatial software ArcView 10.0 (ESRI, 2010). The annual sea turtle nesting season reports were consulted to evaluate strandings of loggerheads and leatherbacks. Turtles were categorised by age class (hatchling, juvenile, or adult) in these reports. Stranding events were often reported with only an approximate location as to where the turtle was found. Thus stranding events (mean no.yr⁻¹) were grouped per species, per age class according to the section of the SA coastline in which they occurred; east (Mozambique border to East London), south (East London to Cape Town) or west coast (Cape Town to Namibia border). However, because leatherbacks rarely stranded, these data could not be analysed.

Spatial distribution of fisheries

Pelagic longline fishing effort (no. of hooks deployed per set per year) and fleet distribution data (latitude and longitude co-ordinates) were obtained from catch reports submitted to Oceans and Coasts (Department of Environmental Affairs) for the period of 2006 to 2009. In addition, the Indian Ocean Tuna Commission (IOTC) database was consulted to obtain longline fishing effort (mean no. hooks.yr⁻¹) in the SWIO for the period of 1995 to 2010 (IOTC, 2010). The data were filtered to remove distribution data coarser than one-degree cells. These filtered data include fishing effort and distribution data for the following countries that have fishing rights in the area: Seychelles, India, Reunion, Mauritius, Thailand and SA. The distribution of fishing effort was mapped within the SA EEZ as well as in the SWIO using ArcGIS 10.0 (ESRI, 2010). Grids were created and joined to the fishing effort shape files using the Spatial Join function in ArcGIS 10.0. The distribution of SA EEZ fishing effort was plotted in five minute grid cells whereas the distribution of fishing effort in the SWIO was plotted in one degree grid cells depending on the amount of detail avaialble.

The shallow-water prawn trawl fishery operated between 1988 and 2010 on the Tugela Bank located along the east coast of SA and targeted three main prawn

species: *Penaeus indicus*, *Metapanaeus monoceros* and *Penaeus monodon*. The spatial distribution of inshore and offshore trawling fishing effort was obtained from the ORI. Shark net locations and netting effort per beach was obtained from the KZN Sharks Board for the period of 1981 to 2010 (km -net⁻¹.yr⁻¹). Drumlines (baited hooks attached to a line and floated by buoyed drums) were deployed at 18 beaches to replace some of the nets between 2005 and 2010. The beaches were numbered on the maps with the beach names in Appendix A. All spatial data were mapped using the spatial software ArcGIS 10.0 (ESRI, 2010) and ArcView 3.3 (ESRI, 2002).

Spatial overlap of sea turtles and fisheries

Overlap of sea turtle activity with SA pelagic longline fishery activity

The overlap between the kernel home range (KHR) of longline fishing activity and the KHR of both loggerhead and leatherback turtles was calculated as a percentage of the area (km^2) (Peterson, 2008). Observers on the SA and Asian pelagic longline fleets recorded the location (latitude and longitude co-ordinates) and the species of sea turtle if and when caught. These positions were mapped using ArcGIS 10.0 (ESRI, 2010) to determine the spatial extent of turtle bycatch in this fishery.

Sea turtle mortality in the SWIO

The IOSEA (Indian Ocean-South East Asia Marine Turtle Memorandum of Understanding) threats database was used to construct a spatial representation of offshore sources of sea turtle mortality in the SWIO, including the following; incidental bycatch in commercial fisheries in general, boat strikes and direct offshore harvest. These mortality causes were scored by local experts in each nation as high (3), medium (2) or low (1) impact, thus the values are relative to each country. The spatial extent of these values was mapped per mortality source using ArcGIS 10.0 to evaluate the intensities.

Results

Spatial distribution of sea turtles

Satellite tracking of nesting females

All post-nesting loggerhead females that were equipped with satellite transmitters during the 2010/2011 nesting season migrated northwards, away from the nesting beach. During the entire journey, the females hugged the coastline sticking to water shallower than 700 m (Fig. 3.1a). The northern-most point reached by an individual during this season was Beira, Mozambique, approximately 1000 km north of the rookery, after 69 days of tracking. Clustering of location points indicates that individuals have reached the foraging grounds. These foraging zones are in areas of known inshore reefs (Vilanculos). Of the six females equipped with satellite tags in 2011/2012 all migrated northwards after nesting but one. This female travelled south with the Agulhas Current (tracked for 181 days). Two other females migrated northwards (pink and orange) then crossed the Mozambique Channel and continued northwards, hugging the west coast of Madagascar (Fig. 3.1b). They were tracked for 180 and 183 days respectively. The remaining three females followed a near identical route to those tagged in the previous season; they migrated north until they reached the Bazaruto Archipelago where they stopped for the remainder of the satellite tracking time.

In contrast to the tendency of loggerhead females to migrate northwards against the Agulhas Current after nesting, most post-nesting leatherback females travelled south along the southern Cape coast continental shelf using the Current (Fig. 3.2). From here, one individual (purple) moved east before migrating back north into the subtropical waters of the Mozambique Channel. Three other individuals (light green, red and pink) subsequently moved northwards with the cold Benguela Current along the Namibian coastline. These individuals were tracked for 195, 184 and 192 days respectively. Transmission of one individual ended off the Angolan coast. Leatherback females from the SA population thus migrate throughout both the southeast Atlantic and western Indian Ocean basins (Fig. 3.2).

Figure 3.1a: The spatial distribution of 13 post-nesting loggerhead females satellite tracked during the 2010/2011 nesting season (minimum 25 and maximum 79 tracking days).

Figure 3.1b: The spatial distribution of six post-nesting loggerhead females satellite tracked during the 2011/2012 nesting season (minimum 80 and maximum 183 tracking days).

Figure 3.2: The spatial distribution of nine post-nesting satellite tagged leatherback females between 1996 and 2006 (minimum 21 and maximum 303 tracking days).

Sea turtle flipper tag returns

Tag return data give an indication of sea turtle interactions with artisanal fishers. Tag returns were highest from Kenya, Tanzania and Mozambique ranging 1 – 5 tags in total. The northern-most loggerhead tag return was received from southern Somalia. Tagged leatherbacks were also caught in Mozambique and Madagascar. Three tagged leatherback females were caught in the shark nets in KZN, SA (Fig 3.3). Most people that found tagged loggerheads and leatherbacks refused to give details regarding the fate of the tagged turtle. The turtles were probably caught by artisanal fishermen incidentally or intentionally for food or sale.

Figure 3.3: The distribution of the locations of international and national tag returns for loggerhead ($n = 102$) and leatherback ($n = 5$) females that were flipper tagged in Maputaland (SA and Mozambique coastal border; 1972 – 2010) that were caught or killed elsewhere.

Stranding events

Loggerhead turtles stranded more frequently than leatherback turtles (Fig. 3.4). This is mainly because of a difference in habitat preference. Leatherbacks are pelagic drifters frequently moving off the coast (Fig. 3.2) and thus are more likely to decompose out at sea before stranding on the shore. Frequent stranding events of hatchlings (> 10 indiv.yr⁻¹) along both the east and south coasts indicate that the Agulhas Current plays a vital role in hatchling dispersion (Hughes, 1974a, Hart et al.,

2006). The Current carries hatchlings south, away from the nesting beach. Leatherback hatchlings were rarely reported. The few that made it to shore stranded along the south coast $(n = 5)$ whereas loggerhead hatchlings were reported along the entire SA coastline. No juvenile leatherbacks were reported stranded. The bulk of leatherback adults stranded on the west coast of the country $(n = 22, 88\%)$, suggesting a preferred foraging habitat in this area. Loggerhead adults stranded most frequently along the south coast (Fig. 3.4).

Figure 3.4: The mean annual number of loggerhead strandings (no.yr⁻¹ ± SE) per age class along the east (Mozambique border to East London), south (East London to Cape Town) and west (Cape Town to Namibia border) coasts of SA (n = 232) (1972-2010).

Spatial distribution of fisheries

Pelagic longline fishing effort

The SA pelagic longline fishery that operated between 2006 and 2009 concentrated their efforts within the SA EEZ with some effort extended into the high seas. Fishing effort was however focused along the edge of the continental shelf as well as the Agulhas Bank. Maximum effort was 5 000 hooks deployed per 5 "x 5" grid cell per annum in these regions (Fig. 3.5). Fishing effort was considerably lower in the extreme east of the SA EEZ as well as the extreme south-west (Fig. 3.5).

Pelagic longline fishing vessels from Seychelles, India, Reunion, Mauritius and Thailand were also spread throughout the SWIO (Fig. 3.6). Fishing effort ranged from 2 000 to 22 000 hooks per 1° x 1° grid cell per annum. The IOTC data identified south-eastern Madagascar and the Seychelles islands as longlining hotspots (Fig 3.6). Fishing effort appears to be low in the Mozambique Channel however, there are no data for country specific EEZs and the IOTC data for some countries such as Korea, China or Japan were too coarse to include.

Figure 3.5: The spatial distribution of the fishing effort (mean annual no. of hooks per 5" x 5" cell) of the SA pelagic longline fishery (SA and Asian vessels, 2006 to 2009; data obtained from DEA).

Figure 3.6: The spatial distribution of pelagic longline fishing effort (mean annual no. of hooks per 1° x 1° cell) in the SWIO 1995 to 2010 (Data obtained from IOTC).

Shallow-water prawn trawling

Shallow, inshore prawn trawling was limited to the sub-tropical east coast of SA. Five vessels operated between the St. Lucia Estuary (iSimangaliso) and Durban on the Tugela Bank with the largest area trawled being east of Durban (Fig. 3.7). The maximum trawling depth was 50 m. Inshore trawling was seasonal and operated between September and February each year with a mean annual effort of 980.4 \pm 800.8 sets.yr⁻¹ (mean \pm SD). Effort ranged from a maximum number of trawls in 1988 of 2 478 sets to a minimum of only 5 in 2010.

Figure 3.7: The location of the offshore and inshore prawn trawl fishing activity along the east coast of SA as well as the bathymetry of the area (Data obtained from ORI).

Shark nets

Shark netting effort along the south east coast of KZN, SA, varied according to the number of bathers that frequent a particular beach. The majority of the nets are deployed all year round; however some of the nets are lifted during the annual "sardine run" during the winter months. Of the 45 beaches where nets were deployed, Durban, a very popular bathing and surfing beach (net no.7, Fig. 3.8), had the highest mean annual netting effort (5.97 km-net 1 -yr 1) while Marina Beach (net no. 17, Fig. 3.8) had the lowest mean annual netting effort $(0.2 \text{ km-net}^{-1} \text{ yr}^{-1})$. Drumlines were located at 18 out of the 45 beaches with Margate (line no. 16, Fig. 3.9) having the highest mean annual number deployed (11.5 drumlines per annum).

Figure 3.8: The spatial distribution of the shark nets as well as the mean netting effort (km-net⁻¹.yr⁻¹) at each location along the middle and southern sections of the KZN coastline, SA (1981 – 2010; data obtained from KZN Sharks Board).

Figure 3.9: The spatial distribution of drumlines and drumline effort (mean annual number of lines per beach) along the middle and southern section of the KZN coastline, SA (2005 – 2010; data obtained from KZN Sharks Board).

Spatial overlap of sea turtle activity and fisheries operation

Pelagic longline bycatch

Four species of sea turtles (loggerheads, leatherbacks, olive ridley and green turtles) were recorded in the SA pelagic longline fishery catches between 2006 and 2009. In total, 65 turtles were caught of which loggerheads and leatherbacks made up the bulk of the catch and were caught in equal numbers ($n = 19$; see Chapter 4). No hawksbills were reported during this time. All these catches were recorded within the SA EEZ or the high seas of Namibia, Angola and towards Gabon (Fig. 3.10). The majority of the turtles were caught within the SA EEZ ($n = 46$).

Figure 3.10: The spatial distribution of sea turtle bycatch (relative to the EEZ of each country) of the observed vessels of the SA pelagic longline fishery (2006 – 2009; $n = 65$).

Loggerhead bycatch in the SA EEZ was concentrated along the east and south coasts of the country (Fig. 3.11). Most captures occurred along the Agulhas Bank. The KHR of loggerheads (based on post-breeding migration data) covers an area of 2 705 200 km^2 . The 50 % home range shows where loggerheads spent most of their time. There was marginal overlap (29.3 %) between loggerhead home ranges and SA pelagic longline fishing activity (Fig. 3.11).

Leatherback bycatch in the SA EEZ occurred predominantly on the Agulhas Bank off the southern Cape coast (Fig. 3.12). Fishing effort was highest both in effort (no. hooks per annum) and spatial extent in this area (Fig. 3.4). Leatherbacks had a larger KHR (3 326 100 km²) than loggerheads (1.3 x), which overlapped substantially (40.6 %) with pelagic longline fishing activity (Fig. 3.12).

Sea turtle mortality in the SWIO

From the available data, incidental capture of sea turtles in both commercial and artisanal fisheries was rated by local experts as high along the coasts of Kenya, Tanzania and south-west Madagascar (Fig. 3.13). The majority of the mortalities along the Madagascan coast are probably due to artisanal bycatch and intentional turtle fisheries. Fisheries bycatch was rated as medium in southern Mozambique and the Comoros islands. Direct harvest of sea turtles is still a major problem in all countries in the SWIO except SA and the French Scattered Islands (Fig. 3.13). Boat strikes were reported in the coastal waters along the coasts of Tanzania and Kenya as well as Madagascar. It was however unclear whether these estimates were based on turtle fatalities or injuries.

Figure 3.11: The 50 % and 95 % KHR of loggerheads (n = 12) overlapping with the SA pelagic longline fishery (2006 - 2009) as well as loggerhead bycatch events within the SA EEZ ($n = 14$).

Figure 3.12: The 50 % and 95 % KHR of leatherbacks (n = 7) overlapping with the pelagic longline fishery (2006 – 2009) as well as leatherback bycatch events within the SA EEZ ($n = 13$).

Figure 3.13: Spatial representation of three categories of threats to sea turtles in the SWIO including bycatch in fisheries, direct harvest and boat strikes (data obtained from IOSEA). The respective nations as well as their EEZs are indicated.

Discussion

Sea turtles migrate over large distances and cross multiple international boundaries during their lifetime (Luschi et al., 2003a, Blumenthal et al., 2006). They are therefore vulnerable to a myriad of threats in the territorial waters of different nations as well as on the high seas (Polovina et al., 2000, Hays et al., 2003, James et al., 2005). The main aim of this chapter was to identify the spatial overlap between sea turtles and fishing activities or other (unidentified) causes of mortality. From the data obtained, there appears to be substantial spatial overlap between sea turtle distribution and fisheries operations. It is therefore expected that the fisheries investigated will make a significant contribution to sea turtle mortality. The true impacts of fisheries on turtles however also depends on the temporal overlap (Grantham et al., 2008, Wallace et al., 2010) the species and their biology (Lewison et al., 2004a), relative population size as well as the life stage of the individuals caught (Largacha et al., 2005, Lewison and Crowder, 2006). Therefore, substantial amounts of data are required to properly analyse sea turtle-fisheries interactions.

Hatchlings of both nesting species (loggerhead and leatherback) that enter the ocean are carried south along the east coast of SA by the Agulhas Current (Hughes, 1974b). While traversing the surf, moving away from the coast or travelling in this dispersal current, they are at risk of predation by sea birds and predatory fishes (Witherington and Salmon, 1992). During these hatchling or post-hatchling stages they are not easily caught in fisheries because of their small size or the short distance they travel off shore. Hatchlings do however get caught inshore of the major currents and they wash ashore when they are tired or weak (due to disease or deformation) (see Fig. 3.4). Nevertheless, as turtles grow or increase in size they become less vulnerable to natural predation but increasingly vulnerable to bycatch in fisheries and direct harvest.

Post-nesting loggerhead females primarily migrated northwards in the Mozambique Channel, staying mostly in inshore waters where they foraged. This neritic foraging behaviour of sub-adult and adult loggerheads and other neritic sea turtle species places them at risk of capture in coastal fisheries, particularly artisanal fisheries. Thousands of sea turtles are reportedly caught annually by these artisanal fishers, incidentally and purposefully (Muir, 2005). In south-west Madagascar, local artisanal fishermen from a single village harvest up to 300 turtles (including greens, loggerheads, hawksbills, olive ridleys and leatherbacks) per month (Walker and Robberts, 2005). A unique fishing operation exists at Inhambane in Mozambique whereby seine nets are pulled ashore using tractors on the beach (Louro et al., 2006). This fishing method, although indirectly, is also responsible for hundreds of turtle deaths because they drown while trapped in the nets. Dynamite fishing is a recurring problem in Tanzania, but the impact on turtles has not yet been quantified. (West, L. pers. comm.) The distribution of tag returns show that SA loggerheads (and to a lesser extent leatherbacks) are vulnerable to these threats in the SWIO.

Although the majority of post-nesting loggerhead females migrated north, there is evidence that they also migrate south. Loggerheads of both sexes and almost all age classes are caught in the shark nets, spatially operating inshore and south (along the same coastline) of the nesting grounds. The bulk of the loggerhead catch in the shark nets is comprised of sub-adult and adult individuals (Brazier et al., 2012). The foraging preferences of these age classes coincide with the location of this fishery. The KZN Sharks Board, the organisation that manages the shark nets, is attempting to reduce bycatch in this fishery by replacing nets with baited drumlines. By reducing the netting effort incidental bycatch of sea turtles may be reduced (Cliff and Dudley, 2011).

Further evidence of loggerhead presence south of the nesting grounds comes from loggerhead bycatch in the shallow-water prawn trawl fishery. No indication of the sex or sizes of the captured turtles were recorded. However, the operation of this fishery depends on the status of the St. Lucia estuary mouth. At present the mouth is closed and thus poses no threat to turtles. However, the post-nesting migratory patterns of loggerheads suggest that they could encounter the shallow-water prawn trawl fishery on the Sofala Banks in Mozambique (de Sousa et al., 2006). Although use of turtle excluder devices (TEDs) are compulsory in Mozambique, enforcement of these regulations is poor (Fennessy and Isaksen, 2007). Fishers are reluctant to use TEDs and other bycatch reduction devices (BRDs) because of the alleged lowered target catch rate (Hall et al., 2000, Fennessy et al., 2008) and increased fuel consumption of the vessel.

Leatherbacks feed on gelatinous organisms throughout their entire life cycle and follow their prey (Houghton et al., 2006, Witt et al., 2011) mainly to regions of upwelling areas. They generally use currents to travel (Luschi et al., 2003a, Luschi et al., 2003b) and remain in pelagic habitats or on continental shelves. Regions of high phytoplankton productivity such as the Tugela Bank, Agulhas Bank and Walvis Ridge attract a wide range of predatory fish and foraging sea turtles (Grantham et al., 2008, Nelson and Hutchings, 1983). These regions are extensively fished and are suggested to be important pre- and post-breeding foraging regions for SA leatherbacks (Nelson and Hutchings, 1983, Luschi et al., 2006, Lambardi et al., 2008). Consequently, there is geographic overlap of activity between foraging leatherbacks and longline fishing operators (40.6 % in this study) within these regions (James et al., 2005). Interestingly, jellyfish biomass has exceeded fish biomass off the coast of Namibia owing to intensive fishing pressure in the area (Lynam et al., 2006). Aggregations of jellyfish in the Walvis Ridge area could attract more leatherbacks, making them vulnerable to capture in the Namibian and Angolan longline, gillnet or trawl fisheries. Extrapolation techniques suggest that as many as 4 200 sea turtles are caught here, in the central and southern Benguela Current region annually (Honig et al., 2007).

Once leatherbacks reach sexual maturity (at approximately 12 to 14 years of age (Zug and Parham, 1996) they initiate a seasonal migration, moving periodically closer inshore to breed. Once leatherbacks approach the coast they become equally vulnerable to capture in coastal fisheries such as the shark control programme and trawl nets. This explains why the majority of the leatherbacks caught in the shark nets were adults and that they were mostly caught during summer months (Brazier et al., 2012). Nevertheless, because leatherbacks feed primarily on cnidarians they are not attracted to the fish-baited drumlines. The probability of capture is thus low. Therefore, replacement of nets with drumlines should reduce leatherback bycatch in the shark control programme considerably. Up until 2010, only a single leatherback has been fowl hooked on a drumline and was released alive (see Chapter 4).

This chapter confirms that the post-nesting migration patterns of SA loggerhead and leatherback turtles are very different and overlap substantially with various fishing activities. The southern, wide ranging expansion of leatherbacks make them vulnerable to commercial fisheries, particularly longlining. In contrast, the northern, coastal migration of loggerheads overlaps with trawl and artisanal fisheries. Further, the post-nesting migration of these populations is quite unique because they extend into two ocean basins; the south western Indian and south east Atlantic Ocean basins. Protection of sea turtles during migrations and at foraging grounds is just as important as protecting them at their nesting beaches, although more difficult. Marine protected areas provide some form of spatial protection from fisheries; however, migratory species spend comparably little time in these areas and thus receive minimal benefits (Kerwath et al., 2008). Protecting migratory corridors (through spatial-temporal closures) and connecting breeding and foraging grounds may be a more effective conservation strategy for highly migratory marine species. Systematic conservation planning is a tool that could be used to identify high use areas as well as areas of high risk (Sarkar et al., 2006) and thus sites and corridors can be prioritised for conservation of sea turtles.

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Chapter 4: Quantifying offshore mortality

Introduction

Offshore factors that could affect survival (or conversely mortality) of sea turtles include both natural causes (like disease or predation) and human impacts (including fisheries related mortality, boat strikes or pollution). Each of these causes needs to be identified and quantified to estimate total mortality (*Z*), an important metric in population demographic studies. To identify causes of mortality is straightforward but to quantify mortality of sea turtles (and marine species in general) is particularly difficult because of the extent of their distribution and their highly migratory behaviour (Lewison et al., 2004a). For example, leatherbacks (*Dermochelys coriacea*) migrate thousands of kilometres and spend most of their time on the high seas but their distribution and interaction with fisheries and predators remains complex (Ferraroli et al., 2004, Kotas et al., 2004). Globally, spatial analyses of the distribution of marine megafauna have helped to identify areas of high risk with regards to fisheries (Grech et al., 2008, Lewison et al., 2009). However identifying only the spatial extent of threats without actually quantifying mortality is insufficient to explain demographic trends in large marine fauna populations.

The three main fisheries that interact with sea turtles in South African (SA) waters were described in Chapter 3; these are pelagic longlining, shallow-water prawn trawling and the KwaZulu-Natal (KZN) shark nets. The operations of these fisheries and sea turtle distribution overlap horizontally (geographically) as well as vertically (depth). These commercial fisheries operate in a manner to optimise profit and maximise the number of fish caught for minimal effort and cost. In addition to commercial fisheries in SA and Namibia, SA loggerhead (*Caretta caretta*) and leatherback sea turtles are also exposed to artisanal fisheries throughout the South Western Indian Ocean (SWIO) where they are caught both intentionally and incidentally.

Globally, the best studied fishery regarding bycatch of sea turtles is the pelagic longline fishery (Pinedo and Polacheck, 2004, Carranza et al., 2006, Lewison and Crowder, 2006, Bartram et al., 2010). Pelagic leatherback catch rates tend to be higher than neritic turtle species such as loggerheads because their offshore foraging habitat overlaps with longlining hotspots operating in deeper waters (Ferraroli et al., 2004). In addition leatherbacks mistake the fish-attracting light sticks used in swordfish fisheries for jellyfish (Crognale et al., 2008). Consequently they become entangled in the fishing lines (Lewison et al., 2004a). In contrast, loggerheads are attracted to squid or mackerel bait and are frequently hooked in the mouth or digestive tract if they swallow the hook (Watson et al., 2005). Circle hooks have been shown to significantly reduce sea turtle bycatch (Caminas et al., 2006), but in some cases the catch of the target species is also reduced (Read, 2007). Circle hooks are therefore not widely implemented, especially without extensive field trials. There seems to be no straightforward solution to mitigate longline-related bycatch (Hall et al., 2000), because mitigation measures appear to be species- and region-specific. The first assessment of sea turtle bycatch in the SA pelagic longline fishery showed that leatherbacks (in proportion to their abundance) were more vulnerable to capture in this fishery than other sea turtle species (Peterson, 2008).

Trawl fisheries that operate in the Atlantic and Indian Oceans vary with regards to the depth in which they operate as well as the species they target (Fairweather et al., 2006). Examples include the mid-water and bottom demersal trawling fisheries targeting hake (*Merluccius* spp*.*) that operate at depths of 300 m and greater than 500 m respectively (Walmsley et al., 2007). There is no indication though that these fisheries interact with sea turtles in SA waters. This is because the depth ranges of these fisheries do not overlap with sea turtle activity. Although leatherbacks can dive up to 1 km deep (Hays et al., 2004a), most turtles spend their time at shallower depths (maximum depth of 100 m) (Polovina et al., 2003). Nevertheless, the Italian mid-water and bottom trawl fisheries caught between 2 000 and 8 000 turtles per annum in the north Adriatic Sea (Casale et al., 2004). The shallow-water prawn trawl fishery in SA is more likely to interact with sea turtles than the offshore trawl fishery because of vertical (depth) and horizontal (geographical) overlapping areas of activity. This fishery operates up to 50 m deep on the Tugela Bank off the east coast of SA (Fennessey, pers comm. see Chapter 3), which is in close proximity to the loggerhead and leatherback turtle nesting grounds.

In addition to trawl and pelagic longlining, sea turtles are exposed to shark nets when in SA waters. The bather protection nets incidentally catch a variety of shark species, cetaceans and sea turtles (Young, 2001). Loggerheads are caught most frequently (67.4 %), followed by green turtles (19.6 %) and leatherbacks (8.8 %) (Brazier et al., 2012). Fortunately this fishery is well managed and monitored, and any live animals found in the nets are released (Cliff and Dudley, 2011). Previous studies on bycatch in the shark nets suggested that catches of sea turtles were not a threat to the stability of the nesting populations for both loggerheads and leatherbacks (Dudley, 1997, Young, 2001, Brazier et al., 2012).

Although there are numerous ways to estimate offshore sea turtle mortality, including fisheries observer programmes and strandings reports, there are biases associated with these methods (Hall et al., 2000). Not all vessels of all fishery types have independent observers to collect bycatch data. Further, when a trawl or line arrives on board there is fish and bycatch to be processed simultaneously and often valuable, detailed species-specific data such as size and sex of the captured animal is omitted. Furthermore, the location and body condition of a stranded sea turtle can give an indication of the threats faced offshore. However, determining the cause of death of stranded marine megafauna is difficult in the absence of obvious external scars. Carcasses may show no evidence of the primary cause of death or the sequence of events (e.g. boat strike leading to infection) that resulted in strandings (Epperly et al., 1996). Similarly if carcasses are heavily decomposed all external clues are destroyed (Hart et al., 2006). The range of causes resulting in sea turtle strandings can be diverse; including cold stunning (Morreale et al., 1992), ingestion of pollutants (Mrosovsky et al., 2009), boat strikes (Hazel et al., 2007), ghost fishing and other fishery-related injuries (Bugoni et al., 2001, Tomás et al., 2002). Dynamite fishing impact on sea turtles in Tanzania is of increasing concern, not only because turtles are killed but their habitat is also destroyed (Guard and Masaiganah, 1997). Further, natural mortality from diseases such as fibropapillomatosis (Work et al., 2004) and predation (Elwen and Leeney, 2011) can be very difficult to identify and to quantify.

Regardless of all these shortcomings and constraints, there is a substantial amount of literature (including grey literature) available that provide some insight into the magnitude and relative importance of some of the causes of sea turtle mortality. However, it is not equally-well documented per source or per country. Furthermore, a single fishery in isolation may not have a significant impact on turtle populations, but the impacts of multiple fisheries can result in population declines. All the available data will be collated here for a semi-quantitative analysis of different sources of mortality which will also highlight data gaps that should be addressed.

The aim of this chapter is to attempt to quantify offshore sources of mortality of loggerhead and leatherback sea turtles that nest in SA. Specifically, the objectives are to estimate offshore mortality using fishery bycatch data from the three most important fisheries interacting with sea turtles; the pelagic longline fishery, shallowwater prawn trawl fishery and shark nets. We will also collate data from other sources (such as strandings data, tag returns or conservation reports) to estimate the relative importance of artisanal catches to investigate temporal trends in sea turtle mortality.

Materials and Methods

Quantifying mortality

Pelagic longline fishery in the SA Exclusive Economic Zone (EEZ)

Sea turtle bycatch data were provided by DEA (Directorate: Oceans and Coast) through their observer programme managed by CAPFISH. Thirty SA and Asian vessels had fishing rights in the SA EEZ as well as the high seas. All Asian vessels and 5 % of the SA fleet had independent observers onboard monitoring (sea turtle) bycatch. These data together with the fishery logbook data were used to investigate turtle bycatch in this fishery (2006 - 2010). The mean annual catch per species was estimated (no. caught.yr⁻¹). Sea turtle catch rates in the pelagic longline fishery were calculated as the number of turtles caught per 1 000 hooks (no. caught. $1\,000^{-1}$ hooks). The total catch was calculated by extrapolating the catch rate to the total fishing effort (total number of hooks) of the fleet using the Equation 4.1 modified from Peterson (2008):

Equation 4.1:

$$
Cb = \left(\frac{Co}{H_0}\right) * Hd
$$

The estimated total bycatch (*Cb*) is equal to the observed bycatch (*Co*) divided by the number of hooks observed (H*o*) all multiplied by the total number of hooks deployed (H*d*). Bycatch is reported in terms of numbers of turtles per 1 000 hooks.

Generalised Linear Models explaining sea turtle bycatch events per set were constructed from observer and fishery logbook data (2006 – 2009). Typically, if more than one sea turtle is caught on a set and, the response variable would assume a Poisson distribution (a discrete number or event occurring in a specific set or unit time) (Gardner et al., 2008, Peterson, 2008). In this study, the response variable, bycatch, is a binary event because either a turtle was caught on a set, or not caught, thus a maximum of one turtle was caught on a set. Most sets did not catch any turtles. Bycatch events were modelled using a generalised linear model (GLM) with a Binomial distribution and a logit link function, using a forward-stepwise α-enter approach using the statistical software package R version 2.13.2 (R Development Core Team, 2011). The following explanatory variables were modelled: year, season, vessel, area (regions divided into a 5° x 5° grid, see Appendix B) and target species (swordfish or tuna). The number of hooks was used as an offset variable (Peterson, 2008). A chi-square goodness-of-fit analysis was used to test the significance of each model. Hierarchical partitioning was then used to calculate the individual contribution of each variable to the fit of the final model using the hier.part package for R (Walsh, 2008). Total bycatch as well as loggerhead and leatherback bycatch was analysed separately in this manner. Additionally, to account for potential

misidentification of species, bycatch of all hard-shelled turtles were analysed separately.

Sea turtle bycatch varies in both space and time (Lewison et al., 2009). Catch rates (no. caught. $1000⁻¹$ hooks.yr⁻¹) in the pelagic longline fishery were tested for normality (Shapiro-Wilk test for normality) and homogeneity of variance (*F* ratio test). Thereafter simple linear regression models were performed to determine the trends in the catch rate (no. caught. $1\,000^{-1}$ hooks.yr⁻¹) of the pelagic longline fishery between 2006 and 2010. All statistical analyses were conducted with the statistical software package R version 2.13.2 (R Development Core Team, 2011).

SA shallow-water prawn trawl fishery

The SA shallow-water prawn trawl fishery operated off the coast of the KZN province on the Tugela Bank. Total trawling effort data per annum was obtained from the Department of Agriculture, Forestry and Fisheries (DAFF). Information regarding the observed number of sea turtles caught in the shallow-water prawn trawl fishery was obtained from the Oceanographic Research Institute (ORI) for 2003 to 2006. These observed trawls were not distributed evenly throughout this time period. No indication was given regarding the fate or size of turtles caught and correct species identification was possibly difficult. Sea turtle bycatch in the prawn trawl fishery was reported as total number caught per observed trawl (set) per year (no.set $^{-1}$.yr $^{-1}$). The estimated total number caught was calculated by extrapolating turtle bycatch in observed sets to the total fishing effort using Equation 4.2 modified from Peterson (2008):

Equation 4.2:

$$
\mathit{Cb} = \left(\frac{\mathit{Co}}{\mathit{To}} \right) * \mathit{Td}
$$

The estimated total bycatch *(Cb)* is given by the observed bycatch (*Co*) divided by the number of trawls observed (*To*) all multiplied by the total number of trawls deployed (*Td*). Bycatch is reported in terms of total number of turtles caught.

To test whether the shallow-water prawn trawl fishery had an impact on the loggerhead nesting population, the trends in total fishing effort was correlated with the estimated total number of nesting loggerhead females per annum (1988 – 2010). This test was performed using Pearson"s product-moment correlation using the software package R. version 2.13.2.

Bather protection installations

Nets are installed parallel to the beach, 300 m to 500 m offshore and vary in length (Dudley, 1997). The KZN Sharks Board checks the nets once a day on weekdays and releases any live animals (Young, 2001). Some of the nets are removed during the annual "sardine run" when shoals of sardines (*Sardinops sagax*) enter inshore waters in June and July (Cliff and Dudley, 2011). Total netting effort has gradually been reduced by half from 44.4 km in 1988, to 23.0 km in 2010. In addition, 76 baited drumlines (baited hooks attached to a buoyed drum) replaced 19 nets between 2005 and 2010 (Cliff and Dudley, 2011). Data recorded for sea turtles includes; species, size (field length, straight carapace length and curved carapace length), sex and fate of the animal as well as the capture location. In this study data from 1981 to 2010 were analysed.

Size frequency histograms were constructed for both loggerheads and leatherbacks that were caught in the nets. In this study the field length (mm) was used. According to Marquez (1990), the maximum size of loggerheads at maturity along the KZN coast is 985 mm while the maximum for the leatherback is 1 700 mm (CCL).

To standardise the shark net catches and mortality over time (years), the catch per unit effort (CPUE; the number of turtles caught) and mortality per unit effort (MPUE; the number of turtles that die in the nets) was calculated as the number of individuals per km-net⁻¹.yr⁻¹. All mean values are given with standard deviations. The CPUE and MPUE per beach were mapped using GIS spatial software ArcGIS 10.0 (ESRI, 2010).

Turtle catch and mortality rates in the shark nets were tested for normality (Shapiro-Wilk test for normality) and homogeneity of variance (*F* ratio test). Simple linear regression models were then performed to determine the trends in the numbers caught, numbers dead, CPUE and MPUE in the shark nets between 1981 and 2010 (Zar, 1999) for both loggerheads and leatherbacks. All statistical analyses were conducted with the statistical software package R version 2.13.2 (R Development Core Team, 2011).

Other sources of mortality in the SWIO

The Ezemvelo KZN Wildlife annual turtle monitoring programme season reports (1965 – 2010) were consulted to estimate the mean number of loggerhead and leatherback strandings per annum (no. indiv. yr^{-1}). All means are shown with the standard error (SE). Individuals were categorised according to age class; hatchlings, juveniles or adults.

Because the loggerhead and leatherback sea turtles nesting in SA migrate into the SWIO and to the west coast of Southern Africa (see Chapter 3), causes of mortality and mean annual mortality estimates in Southern Africa (including SA) were summarised from available publications and reports (see Appendix C for summary of data acquired). Sources of offshore mortality were categorised as follows: longline and trawl bycatch, shark nets bycatch, artisanal fisheries-related mortality and beach seine netting.

Results

Estimating mortality

Pelagic longline fishery: Quantifying bycatch

A total of 19 378 758 hooks were deployed in the SA pelagic longline fishery between 2006 and 2010, of which 58.3 % of the sets were monitored by onboard observers. Sea turtles were mainly caught on Asian vessels targeting tuna rather than swordfish (83.0 % and 17.0 % respectively). Most leatherbacks were caught by vessels targeting tuna (84.0 %) that set their hooks in deeper zones. Most turtles were caught during 2007 (42.3 %) while only three (reported) individuals were caught in 2006. A total of 97 sea turtles were observed to be caught in this fishery between 2006 and 2010 (see Chapter 3 for spatial distribution) with a catch rate of 0.008 turtles.1 000 $^{-1}$ hooks (Table 4.1). The extrapolated total catch over this time period was 148 individuals. Leatherbacks were caught in higher numbers ($n = 39$, 7.8 \pm 7.8, mean \pm SD per annum) than loggerheads (n = 25, 5.0 \pm 4.4, mean \pm SD per annum) whereas only two green turtles were caught (Table 4.1). Extrapolated total catch of leatherbacks was 60 individuals in five years while the extrapolated total catch of loggerheads was 38 individuals over this time period. Olive ridleys had a catch rate of 0.0007.1 000⁻¹ hooks. Unidentified individuals were likely hard-shelled turtles, loggerhead, olive ridley or green turtles. No hawksbill turtles were identified.

The most parsimonious generalised linear model explaining total sea turtle bycatch (2006 – 2009) includes the parameters "area" (region) (88.2 %), "target species" (3.7 %) and "year" (8.1 %) (Table 4.2). Leatherback bycatch was best explained by the parameters "season" (81.9 %) and "year" (18.4 %). The majority of leatherbacks were caught during summer months (79.0 %). Loggerhead bycatch was mainly explained by the parameters "vessel" (97.4 %) followed by "target species" (2.6 %). This suggests that only a few vessels are responsible for loggerhead bycatch. Most loggerheads were caught on Asian vessels, with gear set relatively deeply. To account for misidentification of species, bycatch of hard-shelled species were analysed separately. In this instance, the factors "vessel" (81.6 %) and "area" (18.4 %) accounted for most of the variance.

Table 4.1: A summary of sea turtle bycatch in the SA pelagic longline fishery (2006 - 2010).

Table 4.2: Summary of the percentage variance explained by each factor in the most parsimonious Generalized Linear Model for Total, Leatherback (*D. coriacea)*, Loggerhead (*C. caretta*) and all hard-shelled species bycatch (2006 – 2009; n = 65).

Pelagic longline fishery: Temporal trends in sea turtle bycatch

The loggerhead catch rate in the pelagic longline fishery has declined significantly since 2006 (F_{1, 4} = 13.9, R² = 0.83, p = 0.03). Leatherback catches showed an initial decline but then a sharp increase in 2010 ($F_{1,4}$ = 2.5, R^2 = 0.45, p = 0.21; Fig. 4.1). This sharp increase could be due to increased fishing intensity, particularly on the Agulhas Bank along the continental shelf of the south coast (Chapter 3).

Figure 4.1: The trends in the catch rate (no. caught .1 000^{-1} hooks.yr⁻¹) of loggerhead (Cc) and leatherback (Dc) turtles in the SA pelagic longline fishery (2006 -2010).

SA shallow-water trawl bycatch

Twenty eight loggerhead turtles were caught on observed sets in the inshore prawn trawl fishery off the Tugela Bank between 2003 and 2006. Extrapolating loggerhead bycatch to total fishing effort (1 241 trawls) estimates that 164 individuals were caught during this time. The mean annual catch was 41 loggerheads.yr⁻¹. The catch rate was thus 0.13 turtles.set.⁻¹.yr⁻¹. If we apply this catch rate to the total fishing effort over time, an estimated maximum of 2 978 loggerheads were possibly caught between 1988 and 2011. A single leatherback was caught during 2003.

The inshore trawling fishing effort has reduced dramatically over the last 20 years. The high variability in the fishing effort (980 \pm 800 sets.yr⁻¹, mean \pm SD) is due to the fluctuating availability of prawns. Between 1988 and 1993 the number of trawls was > 1 000 per annum. However, this was followed by many years of fluctuating effort in trawling. From 2003 until present there has been a steady decline in the number of trawls deployed per year. The continuous decline in fishing effort appears to be because shallow-water trawling was not economically viable to operate due to the importation of farmed prawns. If there is no impact of trawling on SA loggerhead turtles, there will be no relationship between fishing effort and nesting abundance, or that more turtles are caught with an increase in effort (due to availability). However there was a significant negative correlation between trawling effort (total no. of trawls per year) and the number of loggerhead females that nest in close proximity to the trawling grounds ($r = 0.5$ and $p = 0.02$; Fig. 4.2) suggesting that this fishery has had a negative impact on the loggerhead nesting population.

Figure 4.2: The significant negative correlation between the annual shallow-water prawn trawling fishing effort (no.trawls.yr⁻¹) and the annual number of nesting loggerhead females (1988 – 2010).

Bather protection installations: Shark nets

Loggerheads dominated the turtle catch (66.6 %, Table 4.3) in the shark nets with a mean (\pm SD) annual catch of 41.4 \pm 9.8 individuals per year. Nevertheless they also had the lowest proportional mortality (52.2 %) with a mean $(\pm SD)$ annual mortality of 21.6 ± 6.7 individuals per year. Green turtles made up the second largest component of the total catch (19.3 %). Leatherbacks were caught in low numbers with a catch rate of 5.2 ± 2.7 (mean \pm SD) per annum but had high mortality (62.4 %). Olive ridley and hawksbill turtles were rarely caught because they are not resident species and occur in low abundance in this area. Hawksbill turtles had the highest mortality percentage of all turtle species caught (71.2 %).

The highest loggerhead CPUE was off Blythedale beach $(2.65.$ km-net⁻¹.yr⁻¹). This was followed by Park Rynie (2.57.km-net¹.yr⁻¹) and Karridene (2.63.km-net⁻¹.yr⁻¹), which are located in close proximity to the Aliwal Shoal, a reef habitat frequented by loggerheads (Fig. 4.3). There is a reef located off the coast of Hibberdene (1.92.km-

net⁻¹.yr⁻¹) as well, explaining the high loggerhead catch rates in this area. Leatherbacks were caught in higher numbers at Zinkwazi (0.51.km-net⁻¹.yr⁻¹) and Glenmore $(0.44 \text{ km-net}^1 \text{ yr}^1)$ beaches (Fig. 4.4). Even though Durban (net no. 7) had the highest mean annual netting effort (5.97 km-net⁻¹.yr⁻¹, Chapter 3), both the loggerhead and leatherback CPUE was relatively low at this particular beach $(1.24.$ km-net. 1 yr $^{-1}$ and 0.17.km-net $^{-1}$.yr $^{-1}$ respectively).

Bather protection installations: Drumlines

Seven sea turtles were caught in the baited drumlines between 2007 and 2010. Loggerheads were caught most frequently $(n = 5)$, one of which was dead. Only a single leatherback was caught and released alive. One green turtle was caught which was dead upon checking. No olive ridley or hawksbill turtles were caught. The bycatch rate (1.75 per annum) is considerably lower than that of the shark nets.

Table 4.3: Sea turtle bycatch and mortality in the shark nets (including drumlines) between 1981 and 2010 (mean ± standard deviation; $n = 1864$).

Figure 4.3: The spatial distribution of the shark nets and the loggerhead (Cc) CPUE (no.km-net⁻¹.yr⁻¹) at each net installation $(1981 - 2010; n = 1241)$. The numbers represent the beaches where nets are located (Appendix A).

Figure 4.4: The spatial distribution of the shark nets and the leatherback (Dc) CPUE (no.km-net⁻¹.yr⁻¹) at each net installation $(1981 - 2010; n = 157)$. The numbers represent the beaches where nets are located (Appendix A).

Out of the > 1 100 loggerhead turtles caught, the individual sizes (SCL) ranged 400 mm to 1 100 mm (SCL; Fig. 4.5 top). The mean size was 812.6 ± 116.6 mm (mean \pm SD) with a median size and mode of 800 mm. The distribution is thus skewed towards the larger size classes. If size at maturity is > 800 mm (Tucek, 2008) the majority of loggerheads caught in the shark nets were classed as subadults and adults. A size frequency histogram of leatherbacks ($n = 122$) shows a normal distribution and sizes ranged from 780 mm to 1 800 mm. No juveniles were caught but the majority of leatherbacks caught were adults (≥ 1300 mm (Hughes, 1974), Fig. 4.5 bottom). The mean size was 1 401.2 \pm 207.4 mm (mean \pm SD) with a median size class of 1 420 mm.

Figure 4.5: The size frequency distribution of loggerheads (top, SCL) and leatherbacks (bottom, CCL) caught in the shark nets between 1981 and 2010 (n = 122). The dotted line indicates approximate size at maturity.

Bather protection installations: Temporal trends in sea turtle bycatch

Simple linear regression indicated that both the total number of loggerheads caught in the shark nets and the CPUE had increased over time, however only the CPUE increased significantly (F_{1, 29} = 0.86, p = 0.36, R² = 0.03 and F_{1, 29} = 11.5, p = 0.002, R^2 = 0.3 respectively; Fig. 4.6) although there is high variability between years. The number of leatherbacks caught and the CPUE showed decreasing trends, although not significantly $(F_{1, 29} = 3.1, p = 0.09, R^2 = 0.09$ and $F_{1, 29} = 0.06, p = 0.81$, R^2 = 0.002 respectively; Fig. 4.7). The number of loggerheads that died in the shark nets has decreased since 1981 ($F_{1, 29} = 3.7$, $p = 0.07$, $R^2 = 0.12$; Fig. 4.8). Nevertheless, even though the netting effort has been substantially reduced along the coast over the last 25 years, the trend in MPUE of loggerheads was not significant (F_{1, 29} = 2.8, p = 0.1, R² = 0.1). This is due to high variability in turtle mortality. Fewer leatherbacks were caught annually than loggerheads. There was a decreasing trend in both total leatherback mortality and MPUE ($F_{1, 29} = 3.6$, $p = 0.06$, $R^2 = 0.11$ and $F_{1, 29} = 0.07$, p = 0.78, $R^2 = 0.003$, respectively; Fig. 4.9).

There was a significant, positive correlation between the annual number of loggerhead females nesting in northern KZN and the CPUE of loggerheads in the shark nets ($r = 0.35$, $p = 0.003$; Fig. 4.10 top). This suggests that loggerheads are frequently caught because they occur in high abundance. There was no correlation between the number of leatherback females nesting in KZN and the CPUE of the shark nets $(r = -0.02, p = 0.6; Fig. 4.10 bottom)$.

Figure 4.6: The significant declining trend in CPUE (no. caught.km-net⁻¹.yr⁻¹) and total number of loggerheads caught in the shark nets (1981- 2010).

Figure 4.7: The decreasing trends in both CPUE (no. caught.km-net⁻¹.yr⁻¹) and total number of leatherbacks caught in the shark nets (1981- 2010).

Figure 4.8: Loggerhead mortality and MPUE (no. dead.km-net⁻¹.yr⁻¹) in the shark nets (1981 – 2010). The trend line indicates the significant decreasing trend in loggerhead mortality over time.

Figure 4.9: Leatherback mortality and MPUE (no. dead.km-net⁻¹.yr⁻¹) in the shark nets (1981 – 2010).

Estimating mortality from strandings

Six stranded leatherback hatchlings and 24 adults have been reported over the last 40 years. Twenty of these adults were found on the shore in the Walvis Bay region in 2006, however the cause of death was unknown (Papillon, 2007). This may have been because of fishery-related injuries. One leatherback was reportedly struck by a boat propeller (Nel, 2008). Loggerhead strandings occurred more frequently than leatherback strandings (Fig. 4.11). Loggerhead hatchlings were reported in higher numbers (n = 179) than adults (n = 39) and juveniles (n = 14) in the last 40 years. Hatchlings are carried south in the Agulhas Current and if they get too close to shore they are washed up on the beach. The cause of death was not identified for any of these stranded turtles. Ghost fishing, other fishery-related injuries, disease or pollution may be responsible for these fatalities.

Figure 4.11: Mean annual number of loggerhead (Cc, n = 232) and leatherback (Dc, $n = 30$) strandings (\pm SE) along the SA coastline (1972 – 2010).

Other Causes of Mortality in the SWIO and Namibia

Data on sea turtle mortality bycatch collected on all the fisheries in the SWIO allows for a comparison to assess the relative contribution per fishery to sea turtle catches (Table 4.4; references in Appendix C). The availability and quantity of data varied widely per country. Mozambique for example had only a few recent reports, whereas South Africa, France, and Madagascar had a number of publications related to fisheries, if not directly applicable to turtle bycatch. Few of the reports or publications discriminated between catch and mortality, and none (other than shark net data) reported the state or fate of the turtles. The species composition caught across these fisheries include all five species of turtles present in the SWIO (Bourjea et al., 2008) namely loggerheads (*Cc*), green turtles (*Cm*), olive ridleys (*Lo*) and hawksbills (*Ei*) and leatherbacks (*Dc*) across all life history stages (if hatchling strandings are taken into account). Because SA loggerheads and leatherbacks migrate to the West Coast (Luschi et al., 2006), data for Namibia were included.

The biggest apparent threat to sea turtles in the SWIO is the artisanal fishery, both those targeting turtles and those that do not. The artisanal fishery in north-west-and south-west Madagascar is the largest contributor to this mortality estimate $(12 030.yr⁻¹)$. The pelagic longline fishery in Namibia does not have an observer programme; this estimate (670.0 yr^{-1}) was derived by extrapolating the bycatch rate of sea turtles in the SA fishery to the total fishing effort off Namibia (1995 – 2005). Both trawling and gillnetting are banned in La Reunion (France) and bycatch in these fisheries was thus zero. Sea turtle habitat is also threatened by dynamite fishing in Tanzania however these impacts are difficult to quantify and the impact on sea turtle numbers is unknown.

Table 4.4: Summary of the sources and mean annual estimates of offshore sea turtle mortality in the SWIO (no. indiv.yr⁻¹).

**Cc, Caretta caretta; Cm, Chelonia mydas; Lo, Lepidochelys olivacea, Ei, Eretmochelys imbricata; Dc, Dermochelys coriacea*

Discussion

The life history strategy of sea turtles requires that the high mortality of eggs, hatchlings and juveniles is compensated by high survival of sub-adults and adults. However, human-induced mortality of these reproductively valuable age classes compromises this strategy and fisheries bycatch of adults in particular has been implicated in the decline of sea turtle populations globally (Spotila et al., 1996, Lewison et al., 2004a, Wallace et al., 2010). Due to the large spatial and vertical overlap of sea turtle and fisheries activities, incidental turtle catch in fishing gear is inevitable.

Of all the fisheries investigated, the shallow-water prawn trawl fishery had the greatest proportionate impact on loggerheads. The strong correlation between the change in trawling effort and the trends in the loggerhead nesting population suggests that this fishery has had a significant impact on the recovery of the loggerhead population in the past. This is because of the vertical and horizontal overlap of this fishing operation with loggerhead feeding and breeding activity. This shallow-water prawn trawl fishery operates in similar depth columns that loggerheads inhabit, up to 50 m (Fennessey, pers. comm). In addition, the location and season of operation overlaps with the locality and season of loggerhead breeding. Since 2007, the yield of the SA prawn trawl fishery has declined significantly and operations have substantially reduced (Fennessy, pers.comm). However, if the St. Lucia estuary had to open again and provide habitat for prawns, the trawling effort may increase in the future. The iSimangaliso Authority is currently implementing a GEF-funded habitat restoration programme to facilitate this vision of a naturally functioning St. Lucia Estuary, as it was in the 1960"s. The estuary mouth should be open more permanently, and prawn habitat restored. This may be good news for prawns and the prawn fishery, but poses a looming risk for migrating and foraging loggerheads.

Besides the SA shallow-water prawn trawl fishery, post-nesting loggerhead and leatherback females are exposed to numerous other trawl vessels operating in the Mozambique Channel (de Sousa et al., 2006). Bycatch of loggerheads, green turtles and hawksbill turtles has been recorded in this fishery on the Sofala Bank (de Sousa et al., 2006). Despite the legal requirement of TEDs in this fishery, very few vessels comply with this regulation and do not implement TEDs (Fennessy and Isaksen, 2007, Bourjea et al., 2008). One of the main reasons is the perceived reduction in the catch rate of the target species (Wamukoya et al., 1997). Therefore, loggerhead and leatherback bycatch in Mozambican operated and other nation"s trawl vessels remains a threat.

Comparatively, the annual turtle bycatch in the SA shallow-water prawn trawl fishery is lower than elsewhere. For example, it was estimated that 4 273 sea turtles were captured annually by 19 vessels operating in the Adriatic Sea (Casale et al., 2004). In northern Australia (128 vessels), 47 % of the sea turtles caught in trawl vessels were either injured, comatose or had drowned (Poiner and Harris, 1996). Turtle excluder devices (TEDs) have reduced turtle bycatch in many trawl fisheries (Hall et al., 2000, Brewer et al., 2006). Further, use of TEDs has reduced the number of trawl-related loggerhead strandings in South Carolina, USA (Crowder et al., 1995). Therefore TEDs are a promising innovation to mitigate turtle bycatch, but requires active implementation and enforcement of these regulations remains a challenge (Hall et al., 2000, Lewison et al., 2002).

The SA pelagic longline fishery had the most significant impact on leatherbacks $(n = 39, 7.8 \pm 7.8 \text{ yr}^1, \text{ mean } \pm \text{ SD})$ followed by loggerheads $(n = 25, 5.0 \pm 4.4 \text{ yr}^1,$ mean \pm SD). Leatherbacks were caught at a higher rate (0.003.1 000⁻¹ hooks) than loggerheads (0.002.1 000 $⁻¹$ hooks) because they are pelagic species and forage in</sup> the same areas where longline vessels operate (Ferraroli et al., 2004, Hays et al., 2004b). Consequently they are more vulnerable to bycatch in this fishery than any other sea turtle species. In addition, leatherback bycatch in the pelagic longline fishery was best explained by the factor "season", with most individuals being caught during summer on the Agulhas Bank. Adult leatherbacks were caught (entangled) during pre-and post-nesting migrations during these same summer months (Luschi et al., 2006). In contrast, loggerhead bycatch events were best explained by the

factor "vessel". This suggests that a small number of vessels, fishing in specific areas, are responsible for most loggerhead bycatch (Peterson, 2008).

Most loggerheads and leatherbacks were caught by pelagic longline vessels that target tuna ($n = 19$). The bait used on these vessels was mainly squid (55 %) with the gear set at depths that range from 6 m on the margins to 216 m in the middle of the main fishing line (Petersen and Honig, 2006). Because loggerheads restrict their dives to approximately 100 m (Polovina et al., 2003), individuals were likely caught on the hooks set in the shallower zones of the main fishing line. Although leatherbacks spend most of their time at depths of less than 50 m (Hays et al., 2009), they can dive to depths greater than 1 km (Eckert et al., 1986, Hays et al., 2004a). This ability makes them more likely to come into contact with deep set pelagic longlines than loggerheads that occupy shallower depths.

The leatherback and loggerhead catch rates in the SA pelagic longline fishery are substantially lower than those reported globally. Leatherback catch rates range from $0.0268.1$ 000⁻¹ hooks off the coast of Chile (Donoso and Dutton, 2010) to as high as $0.64.1 000⁻¹$ hooks in the Gulf of Guinea (Carranza et al., 2006). Loggerhead bycatch estimates range from $0.0056.1~000^{-1}$ hooks off the Chilean coast (Donoso and Dutton, 2010) to 0.91.1 000⁻¹ hooks in the Mediterranean (Caminas et al., 2006) to 4.31.1 000⁻¹ hooks in Brazil (Kotas et al., 2004). The lower catch rates of both loggerheads and leatherbacks in the SA EEZ may be because the SA populations are smaller in comparison and the fishing effort in this region is lower than other regions. Even though fishing effort and the turtle catch rate for the period between 2006 and 2010 is known, sea turtle mortality is unknown. Peterson (2008) reported that 84 % of the individuals captured in the SA pelagic longline fishery were released alive. Globally, although catch rates are high (Lewison et al., 2004b) it appears that mortality of sea turtles caught in pelagic longline fisheries is low, probably less than 50 % (Donoso and Dutton, 2010, Lewison et al., 2004b, Sales et al., 2008). Loggerheads appear to be particularly resilient to longline bycatch mortality (Pinedo and Polacheck, 2004). However many individuals are released with the hooks still attached (Peterson, 2008) and post-release mortality is unknown (Chaloupka et al., 2004).

Loggerheads were the most frequently caught species in the shark nets at 66.6 % $(41.4 \pm 9.8, \text{ mean } \pm \text{ SD})$ with moderate mortality rates $(-50\%, 21.6 \pm 6.7, \text{ N})$ mean \pm SD). This is because loggerheads are highly abundant in SA waters and share the neritic habitat where the shark nets are located along the coast. Leatherbacks were caught in much lower numbers $(3.3 \pm 1.8, \text{ mean } \pm \text{ SD})$ but larger, adult leatherbacks were caught most frequently, during summer (Brazier et al., 2012). This is because adults move closer inshore to breed during these months. The increasing trend in both the number of loggerheads caught in the shark nets and the CPUE can be attributed to the increasing size of the nesting population (Brazier et al., 2012). The declining trends in both mortality and MPUE for both loggerheads and leatherbacks is likely due to a gradual increase in the frequency of net checking and more efficient release of live animals (Cliff and Dudley, 2011).

Sea turtles are air-breathing reptiles and can only hold their breath for about 20 minutes when doing shallow dives. Deeper dives require that they respire anaerobically, which can increase their breath-hold time to three hours (Lutz and Bentley, 1985). However, capture stress reduces their breath-hold capacity substantially (Lutcavage and Lutz 1991). Individuals that get caught in fishing gear (longline hooks or trawl nets for example) probably do so during a planned shallow dive, become stressed while entangled and drown. Even though there was no data regarding mortality rates of turtles captured in the SA pelagic longline or trawl fisheries, there were estimates for mortality in the shark nets. In this fishery, green turtles had higher mortality (67.8 %) than both loggerheads (52.0 %) and leatherbacks (61.9 %). This may be indicative of a lower stress tolerance of green turtles (Hoopes et al., 2000). Individuals that are released soon after becoming entangled, recover faster from capture stress than individuals that spend many hours entangled in the nets (Lutcavage and Lutz 1991). The baited drumlines that have replaced a number of shark nets, are buoyed and thus when sea turtles become hooked, they are still able to reach the surface to breathe. Even though both loggerheads and leatherbacks were caught in the drumlines, the numbers were much lower (only one leatherback and seven loggerheads in four years). Therefore continued replacement of nets with drumlines should reduce sea turtle bycatch and mortality substantially.
Tag returns throughout the SWIO as well as the available fishery-related mortality data obtained, suggest that loggerheads are at greater risk of being caught in artisanal fisheries and directly harvested in this region than leatherbacks. Mozambican waters appear to be particularly hazardous for SA loggerheads because there are numerous fisheries in this region including artisanal fisheries and commercial trawling (Bourjea et al., 2008). Beach seine netting using tractors is responsible for capturing specifically green turtles (Hughes, 1971). However, literature suggests that in Mozambique, sea turtle eggs are a more popular food source than the adults because it is more difficult to capture them in the near shore using gill nets or spears (Hughes, 1971). Adult females however, are an easy target while nesting but it appears that direct harvesting is declining, particularly on southern beaches (Lombard, 2005). Across the Mozambique Channel however, along the south-west coast of Madagascar, artisanal fishers deliberately harvest between 10 000 and 16 000 sea turtles each year (Humber et al., 2010). These fishers provide food for their families but many sell their goods at local markets as well (Humber et al., 2010). Various conservation programs have been initiated throughout SWIO countries to create awareness regarding the vulnerability of turtle populations and to obtain more realistic data regarding the impact of artisanal fishers on turtle populations (Slade, 2000, Muir, 2005, Lilette, 2006). However there is still much uncertainty in terms of the exact numbers killed per species due to difficulties in correct species identification.

Both loggerheads and leatherbacks are vulnerable to bycatch in the various fishery types operating in SA waters. However, the results from this chapter suggest that commercial trawling and artisanal fisheries in the SWIO are significant threats to loggerheads whereas the pelagic longline fishery is the most significant threat to leatherbacks. Nevertheless, more quantification of sea turtle bycatch in artisanal fisheries is required, particularly in the light of the socio-cultural value that sea turtles have in the countries in the SWIO. Furthermore, this study has highlighted the importance of independent observers aboard commercial vessels to record bycatch, especially the details such as species, size and sex. This information will greatly improve our understanding of sea turtle-fishery interactions.

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Introduction

Mortality and survivorship are challenging demographic parameters to estimate in any natural population, but particularly for those inhabiting the marine environment (Bjorndal 1980). Historically, mortality of marine mammals was estimated as a constant rate over the entire lifespan of an animal (Barlow and Boveng, 1991). However, long-lived organisms including sea turtles have different mortality rates across different age classes. Each age class, of each sea turtle species, occupies a different habitat type owing to variations in their dietary requirements resulting in different growth rates and exposure to threats (Heppell et al., 2003). Thus, juvenile loggerheads for example will be exposed to a large number of natural predators (Bjorndal et al., 2003) but are able to escape medium or large mesh nets. Subadults and adults on the other extreme have lower natural mortality but these size classes are more vulnerable to fisheries bycatch and direct harvesting, especially nesting females. Offshore sea turtle mortality is particularly difficult to estimate because of a paucity of data across size classes especially for the oceanic part of their life cycle (Bjorndal 1980, Lewison et al., 2004a).

To better understand population biology, the underlying dynamics (specifically birth rates, death rates, immigration and emigration) of a population need to be explored (Lebreton et al., 1993). Because of the complexity of this field of biology, population models have been developed as tools to assess population viability and to predict survivorship (*S*) (Heppell, 1998, Molles, 2008). Basic population models are linear in approach with few parameters. Specifically for sea turtles, the most commonly reported survivorship metrics are i) an estimate of survival (or survivorship) from hatchling to adulthood (Hirth and Schaffer, 1974, Parmenter and Limpus, 1995) and ii) adult female survivorship (Frazer, 1983, Dutton et al., 2005, Tomillo, 2007). Sea turtles display natal philopatry (Hughes, 1974a, Lohmann et al., 2008). Hence most conservation programmes determine adult survivorship indirectly by tagging nesting females and monitoring their return (Campbell and Lagueux, 2005). This mark-

capture-recapture technique to model survivorship has proved quite effective (Cormack, 1972) if one can account for skipped nesting behaviour (Chaloupka and Limpus, 2002, Thorson et al., 2012). These are relatively simple methods to model survival (Hughes, 1974b, Frazer, 1896) but more complex models have been developed involving multiple parameters that incorporate age-class specific survival (Pistorius et al., 1999). The equation $l(x) = \binom{Nx}{N0}$ is used in the construction of life tables, where *lx* is the survival rate from one age or stage to the next, *N^x* is the population size at time (*x*) and *N⁰* is the population size at time (0) (*x* = 0, 1, 2…*x*) (Frazer, 1983, Molles, 2008). These models require substantial amounts of quantitative data, including age- or stage-specific survival, fertility, growth rates and migration patterns (Chaloupka, 2002), for which the data are difficult to obtain. Nevertheless, in the absence of detailed data and models, simpler models still prove useful to describe population patterns. Further, satellite telemetry has enabled the spatial monitoring of individuals across age classes (Polovina et al., 2006) allowing us to better estimate age-class specific survival. Survival estimates of some sea turtle populations have also been published based on distribution and interactions with fisheries (Bjorndal et al., 2003, Campbell and Lagueux, 2005).

Although survivorship has been estimated for other sea turtle populations across the globe, very little is known about survivorship of sea turtle populations in the South Western Indian Ocean (SWIO). The loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) nesting populations in South Africa (SA) are the southernmost in the world and are thus populations of global importance, especially in the light of climate change. Additionally, these populations span two ocean basins which is unique but more difficult to track in terms of life histories, growth rates, threats and hence mortality. Further, both these populations have been monitored for \sim 50 years thus long-term data are available for nesting females. Leatherbacks are IUCN redlisted as critically endangered worldwide and any nesting population, however small, should be protected. Wallace *et al.*, (2010) listed the SWIO population as vulnerable due its small size (< 100 nesting females per annum) despite its stability and protection status.

The aim of this chapter is to integrate the results of the previous three chapters to estimate survivorship (or conversely mortality) of both loggerheads and leatherbacks nesting in SA. This may aid our understanding of the difference in recovery of these two populations. The first objective is to establish the trends in the nesting populations by quantifying the number of neophytes (first time nesters), nests and hatchlings produced over time. The second objective is to construct a basic model of hatchling survival to adulthood using basic recruitment values and then to compare these survival or mortality estimates with existing, more sophisticated models. The third objective is to compare the "best" modelled mortality estimate (basic or sophisticated) with offshore mortality estimates obtained in Chapter 4.

Materials and methods

Population trends: Annual number of adult female nesters, nests and hatchling production

The annual Maputaland conservation and monitoring programme was initiated in 1963 with the explicit intent of protecting nesting sea turtles and their eggs while collecting population data. The sampling has been more or less consistent over time but with an expansion of the monitoring area in 1972/1973. Sampling consisted of counting tracks or nests of emerged females, flipper tagging and obtaining the straight or curved carapace length and width of all turtles handled. Each track not resulting in a nest was recorded as "not nested". The number of nests per species was thus obtained over time. Furthermore, because each nesting female has a unique tag number it was possible to quantify the number of nesting individuals per species. Additionally, it was possible to determine the number of neophyte nesters each season. Neophyte nesters are females that nest for the first time, thus the first year a particular tag number appeared in the database would be the first year of nesting for that particular individual (if not calloused). Simple linear regressions were performed to establish trends in the number of nests and the number of neophyte nesters over time for both loggerheads and leatherbacks using R version 2.13.2 (Zar, 1999).

The nest success (*NS*), mean clutch size (*CS*), mean emergence success (*ES*) and mean hatchling predation (*HP*) were estimated from the 2009/2010 and 2010/2011 seasons (Chapter 2) and applied to all previous seasons (1965 – 2010) (Table 5.1). Estimates of emergence success and hatchling predation in this study were similar to those estimated by Hughes (1974b) for both species, thus we can assume that these parameters have remained relatively constant over time. The mean annual number of hatchlings that entered the sea each year (Hatchling success, *HLS*) was estimated using the equation 5.1 modified from Hitchins (2004):

Equation 5.1:

$$
Hatching success = N \times NS \times CS \times ES \times (1 - HP)
$$

Hatchling success (*HLS*) is equal to the number of nests (*N*) multiplied by the nest success (*NS*) multiplied by the mean clutch size (*CS*) multiplied by the mean emergence success (*ES*) multiplied by one 1 minus mean hatchling predation (*HP*).

Table 5.1: Summary of the parameters used to determine *HLS* (± SE) for loggerheads (*C. caretta*) and leatherbacks (*D. coriacea*) 1965 – 2010, estimated during the 2009/2010 and 2010/2011 seasons (from Chapter 2).

Basic survivorship models: Using hatchling recruitment to estimate mean annual mortality

Hatchling survival to adulthood was estimated using two methods. Firstly, recruitment into the population was measured by the number of neophytes nesting each season. Thus to estimate the number of female hatchlings that were recruited into the SA nesting population, the relationship between the number of hatchlings that made it to the sea each season and the number of neophyte nesters with a time lag was tested. Loggerheads nest for the first time at approximately 24 years thus this was the time lag for loggerheads (Tucek et al*.*, in review), whereas the age of first nesting for leatherbacks is at approximately 12 years (Zug and Parham, 1996, Dutton et al., 2005) and thus was the time lag for leatherbacks. Hence the slope \mathcal{A} $\bar{\gamma}_{\Delta y}$) of the correlation between hatchling production and neophyte nesters is an

estimate of survival or mortality $1 - (\Delta)$ $\left(\mathcal{V}_{\Delta\mathbf{y}}\right)$. Pearson's product-moment correlation analysis was performed to test the significance of this relationship for both species using R version 2.13.2. Secondly, the loggerhead notching program provides a unique method to estimate hatchling survival to adulthood. Between 1972 and 2002, approximately 300 000 loggerhead hatchlings had one or two lateral scutes removed with a leather punch. Each season had a specific "scute code". Notched individuals that return to nest after approximately 24 years can thus be identified by this code. The return of these females that were notched as hatchlings can provide an estimate of survivorship from hatchling to adulthood. The sex ratio of loggerhead hatchlings produced in SA during the peak incubation season appears to be female biased (80:20) (Boonzaaier, 2010), however Maxwell et al (1988) suggested that the sex ratio is male-biased at the beginning of the nesting season. Therefore, because this study considers the entire nesting season over a long time period, it will assume a 70:30 female biased sex ratio. The sex ratio for leatherback hatchings produced was assumed to be 50:50 because there is a paucity of data for this population. Thus the number of individuals in the above models was adjusted to compare female hatchlings with female adults.

Sophisticated survivorship models: Using age-specific mortality estimates to estimate mean annual mortality

To estimate mean annual mortality for SA loggerheads and leatherbacks, the above recruitment estimates (i.e. a basic mortality model) were compared to more sophisticated models that incorporate stage-specific mortality rates (*lx*) from existing models (Crouse, 1999). Hatchling survivorship (*HLS*) was modelled until they reached sexual maturity where sexual maturity was taken to be at the age of 24 years for loggerheads and 12 years for leatherbacks using the following equation:

$$
l(x) = \left(\frac{Nx}{N0}\right)
$$

Thus the starting point (*T0*) was the mean annual number of female hatchlings that made it to the sea. The model was based on stage-specific survival estimates derived by Chaloupka (2002) for Australian loggerheads, and Tomillo (2007) for east Pacific leatherbacks. Performing these models however relies on the following assumptions: i.) the respective populations are stable; ii.) all females become sexually mature at the ages described above; iii.) survivorship of the different age classes for the loggerhead population in Australia and the leatherback population in the eastern Pacific are equivalent to those in SA; iv.) no tag loss has occurred and that all tagged females and first time nesters are detected. There is also a high degree of variability in the reproductive output of both species from year to year and thus an assumption had to be made that nest success, the mean clutch size, emergence success and hatchling predation from two seasons was sufficient to describe this inter-annual variability. To test whether the sophisticated mortality models could be used to describe the mortality trends of the SA populations a chi-square test was performed to determine whether there was a significant difference between the mean number of observed neophytes (mean number of newly tagged females) according to the Ezemvelo nesting database and the predicted number of neophytes according to the sophisticated models (Zar, 1999). This was performed using the statistical software program R version 2.13.2.

Comparing models: Which best corresponds to estimates of offshore mortality?

The model (basic or sophisticated) that best described the trends (mortality) in SA loggerhead and leatherback nesting populations, was used to evaluate the offshore mortality estimates obtained in Chapter 4. Because both loggerheads and leatherbacks nesting in SA undergo extensive migrations into the South Western Indian Ocean (SWIO) and towards the west coast of Southern Africa (Chapter 3), estimates of mortality in these regions were summarised from available publications and reports. Mortality estimates in the SWIO and Namibia (from Chapter 4) were adjusted according to the relative abundance of each species per region, because species were not always identified in the published documents (original estimates in Appendix C). In Madagascar, Tanzania and Kenya, green turtles are most abundant (-90%) , while loggerhead abundance is only \sim 10 % (Humber et al., 2010, St John and Muir, 2006). Very few leatherbacks are sighted in this region thus abundance was assumed to be zero. Abundance in SA and Mozambique were adjusted according to the relative proportions of species caught in the shark nets (loggerheads \sim 66 %, leatherbacks \sim 8 %, Chapter 3). In Namibia, the relative abundance of loggerhead and leatherbacks is largely unknown, but proportional estimates from longline bycatch along the west coast of SA were used as an alternative (loggerheads ~ 60 % and leatherbacks ~ 16 %) (Honig et al., 2007). An assumption was made that all reported mortalities referred to adult males and females because no indication of size was given in reports and this size class is most likely to be caught in these fisheries (Kotas et al., 2004, Lewison et al., 2004a). The mean annual mortality estimates derived from fisheries bycatch sources was then compared to the mean annual mortality estimates obtained from the sophisticated models, to determine whether these estimates could explain the trends in the loggerhead and leatherback populations.

Results

Population trends: Annual number of adult female nesters, nests and hatchling production

The number of both loggerhead and leatherback nests showed an increase over time, however only the number of loggerhead nests increased significantly $(F_{1,45} = 72.47$ on 44 df; $p < 0.001$; $R^2 = 0.62$ and $F_{1,45} = 1.27$; $p = 0.27$; $R^2 = 0.03$; Fig. 5.1). The number of leatherback nests deposited showed large inter-annual variation. The number of neophyte nesters of both loggerheads and leatherbacks has increased significantly since 1965 ($F_{1,45} = 21.49$; p < 0.001; R² = 0.33 and $F_{1,45}$ = 10.54; p = 0.002; R² = 0.19; Fig. 5.1 respectively) but declined between 2001 and 2004. Since then numbers have increased again.

Assuming that *NS*, *CS*, *ES* and *HP* have remained more or less constant over time the number of loggerhead hatchlings thus produced per annum will also be significantly positive $(F_{1,45} = 72.47$ on 44 df; $p < 0.001$; $R^2 = 6.2$; Fig. 5.2). Leatherback production, in contrast, remained constant over time despite the high inter-annual variability in the number of leatherback nesting females ($F_{1,45} = 1.27$; $p = 0.27$; $R^2 = 0.03$; Fig. 5.2). Particular seasons had extremely high numbers of females, and hence hatchlings, but this was frequently followed by a dramatic fall in the numbers (e.g. 2000/2001 peaked at $>$ 500 nests but in 2001/2002 the number of nests were < 100, and one of the poorest nesting seasons to date).

Figure 5.1: Regressions of the number of loggerhead (top) and leatherback (bottom) neophytes and nests in the monitored area of the Maputaland coast (1965 – 2010).

Figure 5.2: The mean annual number of loggerhead (top) and leatherback (bottom) hatchlings produced including the upper and lower estimates (only showing 1995 – 2010).

Basic survivorship models: Using hatchling recruitment to estimate mean annual mortality

There was no correlation between the number of hatchlings produced and the number of neophyte nesters for both loggerheads (time-lagged 24 years) and leatherbacks (time-lagged 12 years) ($r = -0.1$, $p = 0.66$ and $r = 0.02$, $p = 0.9$; Fig. 5.3). Therefore these slopes could not be used to estimate survival of hatchlings to adulthood.

There was a significant correlation between the number of notched hatchlings and the number of notched neophyte adult females that returned to nest after 24 years $(r = 0.54, p = 0.02; Fig. 5.5)$. The slope of the relationship between notched loggerhead hatchlings and notched adult females ($^{\Delta}$ $\mathcal{V}_{\Delta \mathcal{Y}}$) (after an estimated 24 years) suggests that 1 per 1 000 loggerhead female hatchlings survive to adulthood. The same data are not available for leatherbacks so no such estimate is available.

Figure 5.3: Correlation between the estimated number of loggerhead (top) and leatherback (bottom) hatchlings that made it to the sea and the number of neophyte nesters that returned at maturity after 24 and 12 years respectively.

Figure 5.4: Correlation between the number of notched female loggerhead hatchlings and the number of notched adult females.

Sophisticated survivorship models: Using age-specific mortality estimates to estimate mean annual mortality

The estimated mean number of female loggerhead hatchlings produced is 63 972 individuals (using Equation 5.1). The mean annual mortality estimate for the SA loggerhead population based on the Chaloupka model is 19.5 % (Table 5.2). The number of loggerhead neophyte nesters predicted by the Chaloupka (2002) model was not significantly different from the actual number of observed neophyte loggerheads $(\chi^2_{0.05,1} = 0.569, p = 0.45;$ Table 5.4). Thus these mortality estimates can be used to describe the trends in the SA loggerhead population. Loggerhead survivorship varies between age classes; post-hatchlings and juveniles have high natural mortality, whereas sub-adults and adults are more vulnerable to fisheries bycatch and thus have higher non-natural mortality (Table 5.2, Fig. 5.5). The model suggests that post-hatchling loggerheads have the highest mean annual mortality (35.5 %) whereas adults have the lowest mean annual mortality $($ \sim 10 %). The model also suggests that 5 out of 1 000 female hatchlings survive to adulthood.

Using Equation 5.1, and the estimated mean annual number of leatherback hatchlings produced is 7 569 individuals. The leatherback mean annual mortality estimate based on the Tomillo (2007) model is 34.3 %. This model suggests that 5 out of 1000 leatherback female hatchlings survive to adulthood. However, the model predicts that post-hatchlings, juveniles and sub-adults have identical survivorship (Table 5.3, Fig. 5.6), yet this is very unlikely. However, no other survival estimates fitted the model so that the number of predicted neophyte leatherbacks was not significantly different from the observed number of leatherback neophytes (Table 5.4). Thus the stage-specific survival estimates of eastern Pacific leatherbacks by Tomillo (2007) can be used to describe the mortality pattern of the population of SA leatherbacks $(\chi^2_{0.05,1} = 1.124, p = 0.29;$ Table 5.4).

Table 5.2: Life table for SA loggerheads based on stage-specific survival estimates by Chaloupka (2002) showing the mean annual number of females.

Table 5.4: A comparison between the mean annual number of neophytes predicted by the sophisticated life table models and the mean annual number of actual, observed neophyte nesters for both loggerheads and leatherbacks.

Figure 5.5: An estimated survivorship curve for SA loggerhead females showing the mean as well as the upper and lower survival estimates based on stage-specific survival estimates of Australian loggerheads by Chaloupka (2002) using the mean values calculated in Table $5.2 \pm SE$ (NM: Natural mortality; NNM: Non-natural mortality).

Figure 5.6: An estimated survivorship curve for SA leatherback females based on stage-specific survival estimates of eastern Pacific leatherbacks by Tomillo (2007), using the mean values calculated in Table $5.3 \pm SE$ (NM: Natural mortality; NNM: Non-natural mortality).

Estimates of offshore mortality

The adjusted mean annual mortality estimates for loggerheads in the SWIO sums up to 2 060 adult males and females (Table 5.5). The artisanal fishery in Madagascar is mostly responsible for this large estimate. Of the commercial fisheries, trawl bycatch in SA and Mozambique as well as pelagic longline bycatch in Namibian waters make the largest contributions to loggerhead mortality. The shark nets are only installed in SA and account for 22 loggerhead and three leatherback deaths per annum. The summed estimate for leatherback mortality is substantially lower at approximately 109 adult males and females per annum (Table 5.5). The most significant offshore source of leatherback mortality seems to be the pelagic longline fishery.

Table 5.5: The mean annual mortality estimates for loggerheads (*Cc*) and leatherbacks (*Dc*) (males and females combined) in the SWIO and off Namibia adjusted according to the relative abundance of each species per region (Summarised from Chapter 4).

To summarise the above findings; a mean number of 1 400.0 \pm 641.9 (mean \pm SD) loggerhead nests are deposited in the monitoring area each year (1965 – 2010) (Table 5.6). Most loggerheads nest four to five times per season, but only once every three years (Nel et al., submitted). The average number of nesting females per season is thus ~ 350 individuals and the total female population is composed of approximately 1050 individuals. If we assume a female biased 70:30 sex ratio, the total breeding population size is approximately 1 500 individuals. The annual offshore mortality estimate of 2 060 (Table 5.4), would have caused this population to go extinct already thus loggerhead mortality is over-estimated.

A mean number of 325.7 \pm 139.4 (mean \pm SD) leatherback nests are deposited in the monitoring area each year (1965 – 2010) (Table 5.6). Leatherback females nest an average of six times per season (Nel et al., submitted) and the average number of nesting leatherbacks is 54 individuals. A remigration interval of three years (Hughes, 1996), means that the female population is composed of \sim 162 individuals. Therefore assuming a 50:50 sex ratio, the total breeding population is approximately 324 individuals. The mean annual mortality estimate of 109 loggerhead adults (Table 5.4), 30 % of the size of the nesting population, does not explain the trend in the nesting population.

Table 5.6: Summary of the population parameters used to test the validity of the estimated mortality of loggerheads (*C. caretta*) and leatherbacks (*D. coriacea*).

Discussion

The SA sea turtle conservation and monitoring programme is one of the longest, continuous running programmes of its kind globally. Similar programs have enhanced hatchling success by protecting nests and facilitated the recovery of leatherbacks in the Caribbean (Dutton et al., 2005), green turtles in Hawaii (Balazs and Chaloupka, 2004) and hawksbills in Barbados (Beggs et al., 2007). However, increasing the production of hatchlings does not necessarily counterbalance high (non-natural) mortality of sub-adults and adults (Crouse et al., 1987, Spotila et al., 1996). This is expected to be the case for the SA leatherback population. Sea turtle population declines have been attributed to a number of factors, however high offshore mortality in fisheries (Witherington et al., 2009, Wallace et al., 2010), pollution (Bolten et al., 2010) and climate change, affecting the sex ratio of hatchlings produced (Schwanz and Janzen, 2008), are among the major contributors to these population declines.

In SA, the number of neophyte nesters of both loggerheads and leatherbacks increased significantly over time. This suggests that the overall sizes of the nesting populations increased as well. The loggerhead population showed an impressive and significant increasing trend. Although the number of nests deposited and hatchlings produced increased significantly, the leatherback population does not show the same increasing trend but is stable. Loggerheads have a higher degree of nest site fidelity than leatherbacks (Botha, 2010) and their nests are generally concentrated in a smaller area (Beacons 1N to 12N). Because the monitoring protocol has been relatively consistent over many years there is a high probability of detecting and recording nesting females of both species within the monitored area (Nel, 2010). Perhaps the discrepancy between the increasing number of leatherback neophytes and the declining total population is because a large proportion of leatherback females may be nesting outside the monitored area, in Mozambique (Hughes, 1996). Hence, the number of leatherback nesters in the SA population may be under-estimated.

Using notched individuals, survival from hatchling to adulthood was estimated as 2 per 1 000 hatchlings. This is a similar estimate to the findings by Hughes (1974b) for the same population. It has been suggested that between 2 and 10 hatchlings per 1 000 must survive to adulthood for a population to be stable (Hirth and Schaffer, 1974). Thus the loggerhead population is relatively stable, but according to the trends in the number of nesting females and the number of nests deposited, this population is increasing. Furthermore, the more sophisticated models based on agespecific mortality estimates suggest that up to 10 hatchlings per 1 000 (mean annual mortality of 19.5 %) survive to adulthood, which would better explain the increasing trend of the loggerhead nesting population. Using these age-specific mortality estimates is a more realistic approach (Cochran and Ellner, 1982) because age classes are differentially vulnerable to offshore threats (Chaloupka, 2002), therefore

this is a good indication of the fate of SA loggerheads at different stages in their life history.

In contrast to loggerheads, the basic survivorship model for leatherbacks could not be estimated as there was no relationship between hatchling production and adults with a 12 year lag. In contrast, the more sophisticated model using age-specific mortality estimates (mean annual mortality of \sim 34 %) suggests that 5 per 1 000 female hatchlings survive to adulthood, similarly to loggerheads. However, this is only valid if the sex ratio is even and if SA leatherbacks become sexually mature at 12 years of age, as was estimated for Caribbean leatherbacks (Dutton et al., 2005). However, a recent study on leatherbacks in the north-Atlantic, using a skeletochronological approach, found that age to maturity was between 24 and 29 years of age (Avens et al., 2009). Therefore age at maturity shows great variability between leatherback populations and the estimate for the SA population may be much higher than used here. Delayed age at maturity would mean that leatherbacks have lower reproductive potential and recovery of a declining population would be near-impossible (Avens et al., 2009, Jones et al., 2011). Delayed age at maturity combined with high fisheries-related mortality may be what is contributing to the slower recovery of the SA leatherback population. Thus SA leatherbacks may be exposed to a multitude of threats for a longer time period before reproducing and thus the recovery of the population is slower than expected. Currently both the sex ratio and age to maturity of SA leatherbacks are being investigated (Tucek, unpublished data). Consequently the mean annual mortality estimate of SA leatherbacks can be re-visited in the near future.

The loggerhead breeding population is estimated to comprise of 1 500 individuals. According to the offshore mortality estimate, 2 060 adult loggerheads die of nonnatural causes each year. If this were the case, the loggerhead population has a high probability of extinction in the near future. This is because reduction in the reproductively valuable adults results in a subsequent decline in hatchling production (Crouse et al., 1987). Additionally, non-natural mortality of sub-adults and adults will remain high. However, quantities of incidental and intentional catch of loggerheads in

artisanal fisheries in the SWIO is unreliable regarding the species identification. Therefore the mortality estimate of loggerheads by artisanal fishers is likely overestimated in this study. Nevertheless, artisanal fishers around the globe are responsible for the capture of thousands of sea turtles annually (Mortimer, 1984, Seminoff et al., 2003, Humber et al., 2010). However, of all the data obtained, the fishery with the biggest apparent impact on SA loggerheads was the shallow-water prawn trawl fishery (Chapter 4). As previously discussed, this fishery is no longer operating at its maximum due to the importation of farmed prawns (Fennessey, pers. comm.). Fortunately, this reduces the morality risk of SA loggerheads in the western Indian Ocean.

The leatherback population is estimated to be composed of approximately 324 individuals. The adult mortality estimate $($ \sim 100 per annum), may explain the trend in the leatherback nesting population. Because leatherback density is low in the SWIO, the largest contributors to offshore leatherback mortality occur in SA and Namibian waters. Pelagic longlining and the shark nets are the most reliable data sources regarding leatherback mortality. Consequently, this highlights the paucity of leatherback bycatch data that is available in this region. Pelagic longlining has been implicated in the decline of leatherback populations worldwide (Spotila et al., 1996, Ferraroli et al., 2004, Lewison et al., 2004b). Although adults are more prone to capture in these fisheries, Jones *et al* (2011) have shown that leatherbacks are vulnerable to bycatch and entanglement in fisheries at only three years of age. Perhaps the SA leatherback population experiences similar pressures with higher mortality at the juvenile and sub-adult stages than expected. No natural population can maintain a stable state with continuously high levels of sub-adult and adult mortality (Bjorndal 1980) thus methods of mitigating sea turtle bycatch in pelagic longline fisheries require urgent attention. Use of circle hooks has been shown to reduce bycatch of sea turtles considerably (Watson et al., 2005). Additionally, experimenting with the gear to develop bait and lines that consider the behaviour and visual capabilities of target and non-target species may also be required to reduce bycatch (Southwood et al., 2008).

The models used in this study are very simple, but the results do however highlight the need for more species- and age-class-specific mortality data. The models suggest that there are two probable reasons for the difference in the recovery of the loggerhead and leatherback nesting populations. Firstly, it appears as though many leatherbacks do not nest within the monitored area. Leatherback females may also be nesting northwards in Mozambique or to the south of the monitored area where they are not detected by monitors (Thorson et al., 2012). This can only be confirmed if monitoring activities are extended to include the southern component of the Maputaland MPA and the St. Lucia MPA. In addition, data from monitoring programmes in Mozambique needs to be collated with the SA dataset to identify remigrant (experienced) leatherback nesters. The second explanation for the difference in the recovery of the two nesting populations may be due to a differential response in offshore mortality. High offshore mortality particularly due to fisheries has been implicated in the decline of sea turtle populations worldwide (Lewison et al., 2004b, Spotila et al., 1996). Beach-based conservation efforts cannot act in isolation to protect loggerhead and leatherback populations. Additional conservation and monitoring actions have to be extended into the oceans to reduce mortality of reproductively valuable adults. Fisheries bycatch observer or monitoring programmes need to be implemented in particularly coastal areas, because this is where some form of control and enforcement can be applied.

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Chapter 6: Conclusions

The nesting populations of loggerheads (*Caretta caretta*) and leatherbacks (*Dermochelys coriacea*) have both been conserved and protected for 50 years in South Africa (SA). Similar conservation programmes have facilitated the recovery of nesting populations in other nations (Balazs and Chaloupka, 2004, Dutton et al., 2005). However, of the two SA rookeries, only the loggerhead population has responded favourably to conservation efforts. The leatherback population increased initially but has remained stable for the last three decades. This prompted an investigation into the potential sources of sea turtle mortality in the South Western Indian Ocean (SWIO). The key objectives for this dissertation were to identify and quantify sources of loggerhead and leatherback mortality on nesting beaches as well as in the oceans. Better understanding of the magnitude of mortality may provide insight into the reasons for the difference in the recovery trends between the two species.

This study showed that nest, egg and hatchling mortality on the SA nesting beach for both loggerheads and leatherbacks was lower in comparison to those of sea turtle populations globally (Bell et al., 2003, Engeman et al., 2006, Fowler, 1979). The most significant causes of mortality on SA nesting beaches were natural. Both loggerhead and leatherback nests were affected by predation, particularly loggerhead nests located near the dune vegetation. Unlike many nesting beaches that have many predators like raccoons that can destroy up to 95% of nests (Engeman et al., 2003), nest predation in SA was minimal. Within those nests that produced hatchlings, developmental arrest was the most significant source of egg mortality. Nocturnal emergence of hatchlings at the study site is likely to be a predator avoidance strategy (Hays et al., 1992). Hatchlings crawling from the nest to the ocean were almost exclusively predated on by ghost crabs. Overall, both species had amongst the highest hatchling success (*HLS*) in the world (Bell et al., 2003, Margaritoulis, 2005). This suggests that both species receive maximal benefit from conservation efforts on these beaches. Furthermore, the nesting beaches in SA are in near-pristine condition and will thus be more resilient to the effects of climate Chapter 6 Chapter 6 Conclusions

change (increased sea level rise specifically) compared to developed beaches. This makes these two rookeries in the SWIO RMU (Regional Management Unit) globally important for the conservation of these sea turtle species (Wallace et al., 2010). Therefore, current conservation efforts should continue into the future.

Offshore mortality was assessed using both a spatial and quantitative approach. The horizontal and vertical overlap of sea turtles with fisheries places them at great risk of incidental mortality. Commercial fisheries bycatch in SA is comparably lower than bycatch rates globally for all fisheries investigated (Bolten et al., 2010, Carranza et al., 2006, Koch et al., 2006, Lewison et al., 2004, Zeeberg et al., 2006), however the combined impact on the small loggerhead (-600 p.a.) and leatherback (-100 p.a.) nesting populations was shown to be large.

The fishery in the SA EEZ that had the greatest impact on loggerheads in terms of spatial location and effort was the inshore shallow-water prawn trawl fishery (41 indiv. p.a.). Further, there was a strong negative correlation between the annual fishing effort and the trends in the loggerhead population (1988 – 2010). Due to the closure of the St. Lucia estuary, the fishing effort has been dramatically reduced for the last 10 years. However, if prawn trawling were to become viable again in the future, this fishery will once again be a threat to foraging and migrating turtles. Therefore, future experimentation with and implementation of Turtle Excluder Devices (TEDs) in this fishery is vital. In addition to the trawl fishery, the shark nets, a coastal fishery, also had a large impact on loggerheads because of their overlapping habitat preference with the location of this fishery. However, baited drumlines caught fewer sea turtles and thus continued replacement of nets with drumlines should reduce sea turtle bycatch considerably. Therefore, there are means to reduce fisheries-related morality of SA loggerheads, however this requires careful planning and co-operation among the organisations involved.

The SA fishery that seemed to pose the greatest threat to leatherbacks was the pelagic longline fishery. This is mainly because of the large overlap between leatherback home ranges and distribution of this fishery. Because leatherbacks are

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vulnerable to longline capture from as young as three years (Jones et al., 2011), mitigation of sea turtle bycatch is critical, especially if fishing effort should increase in future. Because loggerheads are attracted to the bait (Gilman et al., 2006) and die from damage caused by hook ingestion, replacement of J hooks with circle hooks may reduce bycatch and mortality of this species. Use of these hooks as well as offset hooks have been shown to reduce foul hooking of leatherbacks (Gilman et al., 2006, Watson et al., 2005). By setting hooks deeper in the water column encounters with sea turtles can be avoided because they prefer shallower areas (Shiode et al., 2005). Mid-water floats can be attached to the mainline to lift it. Consequently all the hooks can be set at a similar depth, deeper than the preferred depth of sea turtle activity (> 100 m) (Shiode et al., 2005). Temporary spatial closures were suggested by Grantham *et al* (2008) to be the most effective approach to reduce bycatch of sea turtles, sea birds as well as sharks in SA. Because the factor "season" was the main explanatory variable for leatherback bycatch using the GLMs, seasonal fishery closures may be the best leatherback bycatch mitigation measure. However the extensive migrations and differing routes among individual leatherbacks suggest that this will only be a partial solution. Experimentation with these and other bycatch mitigation measures need to be conducted in SA to reduce bycatch of sea turtles in general. Additionally, bycatch observer programs should be extended into the Namibian as well as the SWIO pelagic longline fisheries to obtain more robust estimates of sea turtle bycatch, and subsequent mortality of released turtles.

This study confirms that SA loggerheads and to a lesser extent, leatherbacks, migrate and forage throughout the SWIO. It also showed that artisanal and commercial fisheries in Mozambique, Madagascar, Tanzania and Kenya are significant threats to these species. The preferred foraging grounds of loggerheads are easily accessible to artisanal fishers. Nevertheless, the exact impact of incidental and intentional artisanal fishers is largely unknown (but see Humber et al., 2010). International cooperation is required to quantify the magnitude of sea turtle mortality in all SWIO fisheries using a standardised and consistent method by observers, and scientists using standardised metrics.

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For a sea turtle population to be stable, a female must reproduce enough times to replace herself and a male (Hirth and Schaffer, 1974). This study showed that the number of neophyte nesters of both loggerheads and leatherbacks increased significantly since the start of the conservation programme. But because the total number of leatherback nesters remained stable, it suggests that previously tagged nesters were not being recorded in the monitoring area or their offshore mortality is higher than expected. To test this, beach conservation and monitoring should be extended to include the southern section of the MPAs. Leatherback nesting data from Mozambique should also be collated with the SA database to identify and quantify remigrants. Furthermore, we suspect that longliners may have a greater impact on the leatherback population and suggest that trained, independent observers be placed aboard a larger number of vessels.

This study has shown that the loggerheads and leatherbacks that nest in SA both have high hatchling success (*HLS*) owing to conservation actions on these nesting beaches. The Maputaland nesting grounds are the southern-most nesting grounds for loggerheads globally, and is the only significant nesting area for leatherbacks in the western Indian Ocean (Luschi et al., 2006). Conservation of these two populations is thus of global importance. However, sub-adult and adult age classes of both species are reproductively valuable (Bolten et al., 2010) and continuous high non-natural mortality of these age classes may result in further population declines (Crouse et al., 1987, Heppell, 1998). Regardless of conservation strategies on nesting beaches, unless adults and sub-adults are protected at both foraging and developmental grounds, as well as along migratory corridors, population decline is inevitable (Spotila et al., 1996). Although there are numerous challenges, effective future conservation of loggerhead and leatherback turtles can only be achieved if conservation measures are extended into the oceans and a regional, integrated approach is adopted to assess the combined impact of threats (Bolten et al., 2010, Rhodes et al., 2011). Particularly the leatherback population will benefit from improved offshore monitoring and initiation of comprehensive bycatch reduction programmes.

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Appendix A

Table 1: Summary table of the names of the beaches where shark nets are located along the KZN coast, SA.

Appendix B

Figure 1: The grid showing the different regions used in the GLM to model turtle bycatch.

Appendix C

Table 1: Summary of the sources of sea turtle mortality, the species affected and the mean annual mortality estimates per country in the SWIO and Namibia.

Table 1 cont.

Table 1 cont.

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