

# **Spatial comparison of the Maputaland leatherback, *Dermochelys coriacea* and loggerhead, *Caretta caretta*, turtles' interesting movements, and implications for management**

By:

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## Abstract:

Sea turtles globally are under great threat, and their population numbers are decreasing. Loggerheads and leatherbacks, which both make use of iSimangaliso Wetland Park (iSimangaliso) as a nesting ground, are considered endangered and critically endangered respectively. Beach protection of nests and individuals has been implemented in the region in order to protect the turtles during the vulnerable nesting period. Despite the efforts being made the leatherback population has remained stable, whereas the loggerhead population has shown an increase in the population trend. It is therefore necessary to determine if the protection supplied by the protected area is sufficient for both species, by determining the distribution, home ranges and habitat and depth selection. It was found that loggerhead home ranges are 100% within the MPA, while leatherback home ranges are 8 % within the MPA, showing a significant difference from parity ( $\chi^2 = 86.00$ ,  $df = 1$ ,  $p < 2.2 \times 10^{-16}$ ). Leatherback distribution is found to occur 25 % within the MPA during the internesting period, while loggerheads are found 99 % within the MPA, showing a significant difference from parity ( $\chi^2 = 42.8173$ ,  $df = 1$ ,  $p = 6.01 \times 10^{-11}$ ). Distances travelled by leatherbacks are significantly further than the distance travelled by loggerheads during the internesting period ( $F = 16.45$ ,  $p < 0.5$ ) with a distance travelled of  $187.90 \pm 52.68$  km (mean  $\pm$  S.E) per nesting event while loggerheads travel a distance of  $19.20 \pm 4.06$  km (mean  $\pm$  S.E). Time intervals of nesting events were significant different between loggerheads and leatherbacks ( $F = 10.07$ ,  $p < 0.5$ ). Loggerhead individual nesting events last a greater time  $16.89 \pm 1.79$  days, compared to leatherback nesting events which last  $9.49 \pm 0.67$  days. Loggerheads select for habitat, with Natal Delagoa Reflective Sandy Coast being the greatest preferred habitat in home and core ranges ( $PI = 0.63$ ). Leatherbacks having a wide range show no selection for habitat. Loggerheads remain in shallow waters close to shore, within 0-15 m in core and 0-20 m in home range, while leatherbacks show no preference for depth range. Protection offered by the MPA is insufficient to protect leatherbacks during the nesting period, but shows adequate protection for loggerheads. The MPAs and monitoring should be extended further south to offer adequate protection for leatherbacks, even if it is only during the internesting period.

## Introduction:

Sea turtles were once ubiquitous in coastal waters (Hughes 1989, Hughes *et al.* 1998, Seminoff *et al.* 2008) however, world turtle populations are declining and this has led to turtles being classified as endangered according to the IUCN red listings (Finkbeiner *et al.* 2011, Seminoff & Shanker 2008). Turtles are particularly vulnerable to threats, and this is exaggerated during the nesting period where turtles form high density aggregations in near shore waters (Schofield *et al.* 2010). The threats are from natural sources such as predation (Hughes 1991), but the most significant are anthropogenic threats (Dutton *et al.* 2005, Seminoff *et al.* 2008), including poaching of nests, hatchlings and adults, bycatch in fisheries (Mast *et al.* 2006, Mortimer 2000) and ship strikes (Luschi *et al.* 2006). These trends have led turtle populations to be heavily dependent on some form of protection (Seminoff 2008) and implementation of conservation during this period will have maximum conservation rewards due to high density aggregations (Schofield *et al.* 2010). However, we would expect different turtle species to have different conservation needs due to their different life histories and ecology (Nel *et al.* 2011). The spatial and temporal behaviour during the internesting period is largely unknown (Georges *et al.* 2006), and because the effectiveness of any conservation attempt is closely linked with the correct placement of protection, the distribution and behaviour of turtles during the nesting period need to be identified to infer necessary conservation actions (Hooker & Gerber 2004).

Turtles migrate annually from foraging grounds, thousands of kilometres away (Pelletier *et al.* 2003) to the natal nesting grounds for the nesting period (Pike 2008). During this period a female turtle will mate with numerous males (Moore & Ball 2002) and store sperm within her oviduct to fertilize the eggs (Branch *et al.* 2007). These eggs mature within the female, and once the eggs have reached maturity, the female will haul out onto the beach to lay her clutch, and then return back to the sea (Branch *et al.* 2007). This is referred to as a nesting event (Branch *et al.* 2007). The number of nesting events in a single season varies among species (Hughes 1980). Female loggerheads, for example, repeat this process on average four times per season (Schofield *et al.* 2010), while leatherbacks will have up to seven nesting events (Rafferty *et al.* 2011). The periods between the consecutive nesting events within a season are termed the internesting periods and last on average 15 days in loggerheads and between 9 and 10 days in leatherbacks (Rafferty *et al.* 2011), this is linked to the time taken for eggs to mature (Hughes 1980).

The behaviour during the internesting period is vastly different to that of their migratory cycles because the internesting period corresponds with high energy demands and physiological changes within the female turtle (Houghton *et al.* 2002). These changes are attributed to metabolic and physiological changes in relation to ovulation, fertilization, albumin deposition and calcification of eggs (Houghton *et al.* 2002, Wallace & Jones 2008). However the greatest energy usage is due to the haul out onto and crawl up

the beaches, because turtles are not well equipped for land movement (Wallace *et al.* 2006, Wallace & Jones 2008). It would make sense that turtles, like other egg-laying species, would modify their behaviour, physiology and ecology to reduce their metabolic needs and energy usage during this period (Houghton *et al.* 2002). Female turtles do not forage during the internesting period and therefore rely on reserves built up while in the foraging areas prior to the breeding season (Houghton *et al.* 2002). The internesting period is so highly energetically costly that females rarely breed in successive years (Wallace & Jones 2008, Hatase & Tsukamoto 2008); quiescence varies, but on average is between two and three years in loggerheads (Miller *et al.* 2003) and one to five in leatherbacks (Hughes 1980). In order to maintain body and regulatory functioning (Wallace & Jones 2008), the activities of the turtles are greatly reduced and they rely on the biotic and abiotic conditions to aid them (Wallace *et al.* 2006, Wallace & Jones 2008).

These marked differences can be seen in the plasticity of their behaviour to suit the environmental conditions in the region (James *et al.* 2009, Wallace & Jones, 2008). In a bid to reduce energy usage, turtles will locate and remain in warmer water pockets that dominate the tropical and subtropical regions during the internesting period (Pike 2008). The increased water temperature aids in egg maturation and development (Schofield *et al.* 2010), and therefore decreases energy expenditure. If turtles are able to adapt to locating warm water pockets, perhaps they also select for other abiotic features, such as depth, habitat or currents to reduce their energy expenditure. It is noted that during the internesting period neritic loggerheads tend to aggregate in shallow water between 3 m and 32 m (Houghton *et al.* 2002), close to the coast line (< 2 km) (Schofield *et al.* 2010). They predominantly rest on the sea bed and make use of the benthic habitat in the region, often utilising reefs or rocky outcrops (Hays *et al.* 1991). Pelagic leatherbacks however, utilise neutral buoyancy to rest in mid water (Hays *et al.* 2003, Minamikawa *et al.* 2000) and are often found in deeper waters over the continental shelf (Georges *et al.* 2007). These behavioural adaptations vastly reduce the energy demands associated with swimming and actively feeding, related with the migratory cycle (Wallace *et al.* 2006, Wallace & Jones 2008).

South Africa provides an interesting case study because both leatherbacks and loggerheads nest in Maputaland, northern KwaZulu-Natal, between October and November (Mortimer 2000). The populations were at risk of extinction, when formal protection was put in place in 1916, and a marine protected area (MPA) was later established in 1986 aimed at conserving the populations (Nel *et al.* 2011). Despite the implementation of the conservation areas on the nesting beaches, recovery of the populations has not had expected results (Nel *et al.* 2011). From the research in iSimangaliso Wetland Park (iSimangaliso), long-term nesting data (1965-2010) have shown loggerhead population numbers to have increased, while leatherback numbers have remained stable. The recovery of loggerheads has been far greater and more rapid than that of the leatherbacks (Nel *et al.* 2011). The nest density at the start of the protection (1965) was a 5:1

loggerhead to leatherback ratio, however currently there are over 10 loggerhead nests to every leatherback nest (Nel *et al.* 2011). A possible reason for the difference in response could be due to the critical areas of their interesting regions are not adequately protected (Georges *et al.* 2007).

To determine why the two species are responding differently to the conservation in place, the spatial behaviour of both leatherbacks and loggerheads need to be determined and compared (Byrne *et al.* 2009). This will allow a comparison of spatial and temporal metrics and utilisation and distribution of turtles within the region (Georges *et al.* 2007). These spatial patterns can be utilised to identify critical oceanographic features, such as depth and habitats (Schofield *et al.* 2010), and high vulnerability regions between species. Inferences can then be made into the behaviour during this period and adequate management plans can be implemented (Shillinger *et al.* 2011).

## Methods:

### *Study Site*

iSimangaliso Wetland Park is a RAMSAR and World Heritage site (Sunde & Isaacs 2008) which extends from Ponto do Ouro in the north to Mapelane in the south, spanning a distance of 200 km. The region has had formal, yet poorly enforced protection since 1916, and in 1963 became a turtle sanctuary (Nel *et al.* 2011). The St. Lucia Marine Reserve was established in 1979, and the Maputaland Marine Reserve was later established in 1986 these two adjacent MPAs now form the part of the iSimangaliso Wetland Park (Nel *et al.* 2011). They run along 150 km of the coast line and extend 3 nm seaward. Of the most northern portion of this coastline, 56 km is utilized as a turtle monitoring region, with the main research centre being Bhanga Nek (Nel *et al.* 2011). This is important region as it is a shared nesting ground to endangered turtle loggerhead, *Caretta caretta*, and critically endangered leatherback, *Dermochelys coriacea*, turtles (Mast *et al.* 2006).

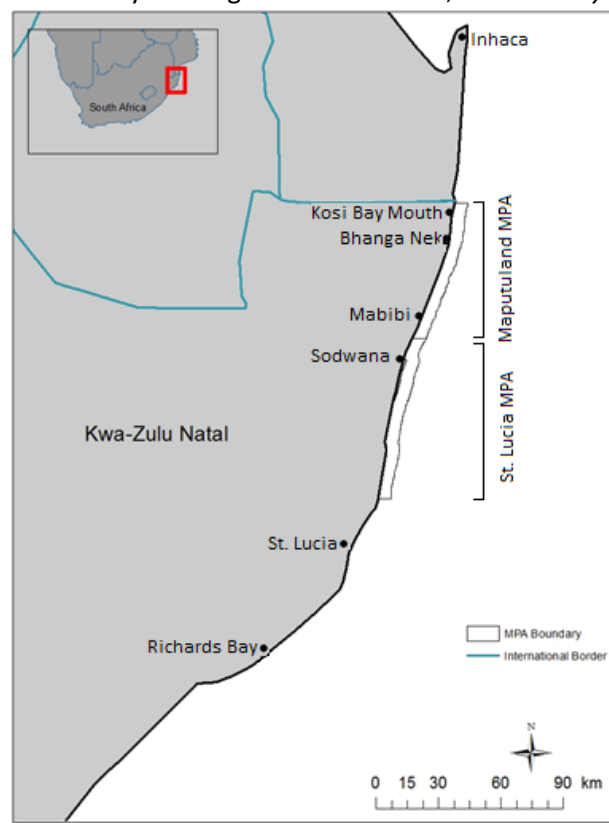


Figure 1 Indication of the study area and the iSimangaliso Wetland Park, located in northern KwaZulu-Natal. The extent of the two adjacent MPAs, Maputaland and St. Lucia MPAs are also indicated.

### ***Satellite Tag Deployment***

SPOT 5 transmitters from Wildlife Computers were attached to six leatherback and fifteen loggerhead females. Loggerheads were fitted with tracking devices in December of 2010 off Bhanga Nek, known to be the hotspot for the nesting (Ezemvelo Unpublished Data). Satellite tags were fitted directly onto the turtles' hardened keratinised shell, on their return to the sea, irrespective of a successful nesting event. The loggerhead females were restrained by building a small wooden box around the individual, allowing movement but preventing escape the shell was prepared by washing and sanding the carapace to clear it of sand and fouling organisms such as barnacles and algae that had grown on the shell. Acetone was applied to completely dry the shell. The tag was then placed on the shell with epoxy and left to dry. The tag was placed on the highest point to ensure that the antenna will break the water surface when the turtle breathes. Antifouling paint was applied over and around the tag to prevent biofouling.

Leatherbacks tend to nest to the south, between Sodwana Bay and Mabibi, and hence the transmitters were attached to the leatherback turtles nesting in this area. This took place between the 5<sup>th</sup> and 8<sup>th</sup> of December 2006, during the approximate 15 minutes of nest laying, because it is difficult to restrain leatherbacks on their return to the water. Leatherback turtles, with a softer, compressible cartilage shell, that is covered in live skin makes it unsuited for the method used to satellite tag loggerheads. A number of methods of applying satellite tags to leatherbacks have been tested previously and the method

used in this project (which is now no longer applied) was to use a custom build backpack with a corrodible link that would disintegrate over time and the backpack shed, as described by Eckert and Eckert (1986). The tag, as well as the straps of the harness were treated with antifouling paint.

Satellite tags were linked to the Argos system, where time, date, GPS position and the integrity (LC value) of the signal received were recorded. The GPS points were categorised according to their integrity, and the low reliability points (LC = 0, A, B, Z) were excluded. These low integrity points are often a result of cloud cover, or a turtle not completely surfacing, which could compromise the strength of the signal between the transmitter and the satellite. The GPS points remaining for analysis thus represent the more accurate positions (LC = 1, 2, 3), which had an accuracy of 1500m, 500m and 250m respectively. Furthermore, in order to ensure that each GPS point was an independent observation, any points recorded within 3 hours of the previous point were excluded. Data for each individual turtle were added into ArcGIS 10 (ESRI), and projected into Universal Transverse Mercator (UTM) using the WGS84 projection (used for all spatial analyses in this study). Points that corresponded to land positions further than the beach extent, whereby turtles would not logically be able to move, were removed. Movement tracks of individual turtle's tracks were created using ArcGIS Tracking Analyst extension based on a date and time field. The post nesting migration routes (consistent movement away from the nesting ground without return) were identified from these tracks, and removed. The remaining GPS points comprising the tracks thus represented the interesting period for each turtle, and were used as the base layers for further analyses. These layers (shapefiles) were overlaid onto Quickbird satellite imagery of the study site.

### ***Data analysis***

An interesting period was defined as an apparent haul out by the turtle onto shore followed by a period at sea longer than 10 days for leatherbacks and 15 days for loggerheads, followed by a second haul out. A haul out was identified if the buffer zone (with a radius equivalent to the spatial accuracy of the GPS point, based on its respective LC value) around a GPS point intersected the beach by the LC value, to the beach. Tracking layers only displaying the interesting periods were created, using ArcGIS Tracking Analyst Extension (ESRI). Only turtles having at least one complete interesting period were further analysed; turtles with no complete interesting periods were excluded. The tracking layer shapefiles were added into ArcView 3.2a (ESRI), where the total distance travelled per interesting period was calculated using the Consecutive Distance tool in the Movement extension. Times taken per interesting period were calculated in Microsoft Excel 2010 by comparing the date attribute at the start to that at the end of each nesting event. Loggerheads' and leatherbacks' total distance travelled and time duration of interesting periods were compared, using a one way ANOVA in Statistica 10.

Adaptive kernel home ranges of the modified leatherback and loggerhead data sets were constructed in ArcView 3.2a (ESRI) using the Animal Movement Extension (Hooge & Eichenlaub 2000). A 95%-utilisation density (UD) for home ranges and 50 %-UD for core ranges were selected, with the smoothing factor (H) determined by least square cross validation (LSCV) method, to ensure the best fit of the kernel (Worton 1989, Gitzen 2003). The kernel home ranges were added into ArcGIS 10, where they were clipped according to the African continent shape file, using the clip function in the Geoprocessing Extension. This was done to exclude area of the kernels that overlapped with land, to allow for a more accurate core-range and home-range, size estimation and comparison.

The core and home ranges were overlaid onto the following layers in ArcGIS 10. The St. Lucia and Maputaland MPAs, depth contours, displaying 15 m (obtained from Ezemvelo), 20 m, 30 m, 50 m, 100 m, 200 m, 500 m and 1000 m isobaths (SANHO 2011), and the marine and coastal benthic habitats (Sink *et al.* 2011). These layers were clipped respectively by the core and home range of the leatherbacks and loggerheads. Area of the home and core ranges, the MPAs and the different habitat areas were calculated using the Basic Statistics tool in ArcGIS. The preference index (PI), described by Mills and Gorman (1997), was used to determine preferred habitat of the species. PI value greater than 0.3 is considered a preferred habitat, while a value less than 0.3 show no preference (Mills & Gorman 1997). The small portion of the leatherback range that extended into Mozambique had to be excluded from the habitat usage and depth selection analysis because no suitable data were available for this region.

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Area use of the MPA and the ratio of the area range in the MPA were calculated. Significant difference from parity was tested using  $\chi^2$  function in R version 2.12.1 (R Development Core Team 2010) between species' home and core ranges, for both the area utilisation and the area ratio ranges falling within the MPA. Use of the MPA was determined by calculating the number of observations in and out of the MPA boundaries of both species. Using  $\chi^2$  in R version 2.12.1 (R Development Core Team 2010) significant difference of parity was established between the species. Using PI (Mills & Gorman 1997), preferred depth was determined for each species using the kernel range clips of the depth contours, as in the habitat selection.



## Results:

From the original data set of six leatherbacks and fifteen loggerheads, the size was reduced to four leatherbacks and eight loggerheads, which all contained at least one complete internesting period. Table 1 displays the summary data per turtle during the internesting period.

Leatherbacks are pelagic drifters and are capable of travelling great distances both during the migratory cycles and during internesting, whereas loggerheads generally travel short distances during internesting. This was observed in the study where leatherbacks were recorded to travel significantly greater distances compared to loggerheads ( $F = 16.45$ ,  $p < 0.5$ ) during the internesting events. Leatherbacks travelled as much as  $187.9 \pm 52.7$  km (mean  $\pm$  S.E) on a single internesting event (Fig. 2). The greatest distance recorded (Turtle 72589) was as far as 376km, and the shortest distance (27 km) travelled was by Turtle 56100 (Table 1). Loggerheads however, travel shorter distances during the internesting period, on average  $19.2 \pm 4.0$  km per internesting event (Fig. 2). Loggerhead 66293 has the shortest distance of all the tagged individuals, with a distance of 3 km recorded during the first internesting event. Whereas loggerhead 66347 recorded the furthest distance travelled of 50 km (Table 1).

The duration of a single internesting period is significantly longer in loggerheads compared to leatherbacks ( $F = 10.07$ ,  $p < 0.5$ ). Loggerhead individual nesting events last  $16.9 \pm 1.8$  days (mean  $\pm$  S.E), while average leatherback nesting events last  $9.5 \pm 0.7$  days (Table 1; Fig. 3). Loggerhead internesting period durations were highly variable, which ranged from 11.3 days (Turtle 6631) and 29 days (Turtle 66309). Leatherback 56100 recorded the longest internesting period durations during both her internesting periods, 11.5 and 11.4 days respectively (Table 1). It is interesting that longest internesting durations corresponded with the shortest distances travelled by all tagged leatherbacks (Table 1). Leatherback 56104 had the shortest recorded internesting period of all tracked leatherbacks, which lasted 6.5 days.

Table 1 Summary data of loggerheads and leatherbacks per individual turtle, indicating spatial and temporal data per turtles' individual interesting periods.

Species	Turtle ID Tag	Number of Internesting Periods	Internesting Period Distance (km)	Internesting Event Duration (days)	Number of GPS co-ordinates in the MPA	GPS co-ordinates in the MPA (%)	Number of GPS co-ordinates out the MPA	GPS co-ordinates out the MPA (%)
Leatherback	56100	1	26	11.5	27	17	128	83
		2	47	11.4				
	56104	1	292	9.9	28	32	59	68
		2	103	6.5				
	72589	1	376	9.9	8	27	22	73
		2	155	8.2				
	72590	1	315	9.0	18	46	21	54
	Total	10	1314		81		230	
	Average	1.4	187.7	9.5		17		73
Loggerhead	66229	1	10	22.2	10	100	0	0
	66289	1	7	13.0	9	100	0	0
	66293	1	3	13.8	9	100	0	0
		2	9	12.0				
	66309	1	28	29.0	7	88	1	12
	66312	1	12	23.7	14	93	1	7
		2	18	11.3				
	66347	1	50	20.2	10	100	0	0
	66362	1	26	15.2	39	100	0	0
		2	27	11.8				
	66385	1	22	13.7	21	100	0	0
	Total	14	212		119		2	
	Average	1.3	19.3	16.9		98		2

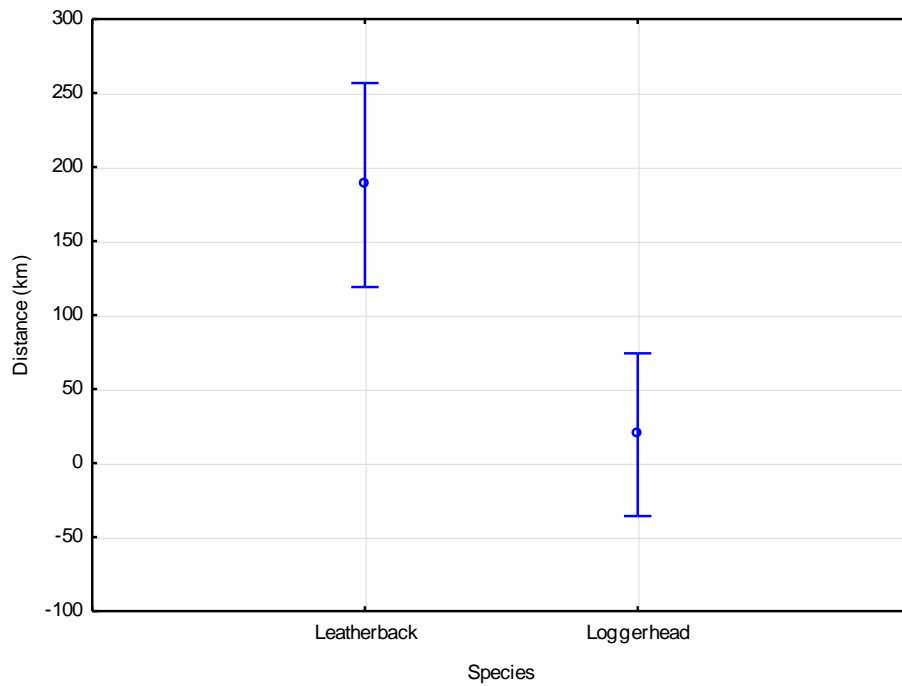


Figure 2 Comparison of distances travelled in individual nesting events between leatherback and loggerhead turtles. Data presented as mean  $\pm$  95 % confidence interval.

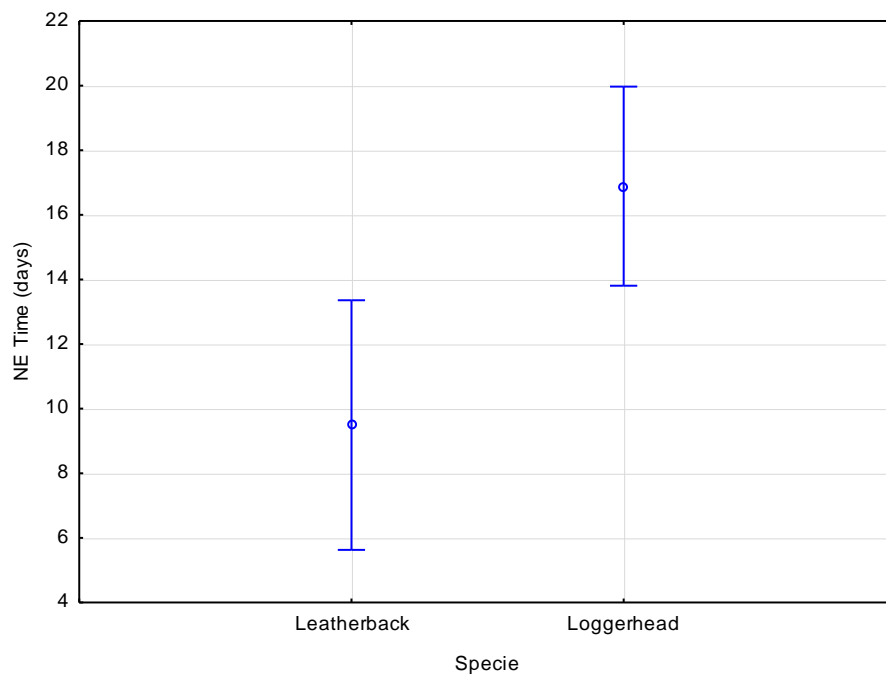


Figure 3 Comparison of time taken to complete of individual nesting events between loggerhead and leatherback turtles. Data presented as mean  $\pm$  95 % confidence interval.

The distributions of the two species were dramatically different. Loggerheads were distributed in the northern extent of the region, extending from Kosi Bay Mouth to south of Bhanga Nek. The majority of the

distribution remained close to shore, within the 3nm MPA, with only two incidence of turtles moving past the MPA boundary (Fig. 4B). Leatherbacks however, had a variable distribution, covering the entire St. Lucia and Maputaland marine reserves. Their extents not only had vast offshore movements but also consisted of movement records ranging from Inhaca, Mozambique, well into Durban (Fig. 3A). It is important to note the difference in extents of loggerheads and leatherbacks.

The distribution is mirrored in the kernel range. The home range of leatherbacks was located between Maputo (southern Mozambique) and Richards Bay (north-eastern South Africa) and a small range clump was located around Inhaca (southern Mozambique). The core range was located at St. Lucia, with a small portion of the core range extending into the St. Lucia MPA (Fig. 6A). The loggerhead home range is located within the Maputaland MPA, ranging from Bhanga Nek to south of Kosi Bay Mouth (Fig. 6B). The kernel range of leatherbacks are considerably larger than that of loggerheads. The core range of leatherback distribution comprises a 1325 km<sup>2</sup> area, compared to loggerhead core distribution of 4 km<sup>2</sup>. The home ranges have the same trends, the leatherback home range comprises of a 15166 km<sup>2</sup> area, compared to the loggerheads 28 km<sup>2</sup> home range.

Table 2. Comparison of the different kernel ranges of loggerheads and leatherbacks indicating the area of the range falling within the MPA and the area of the MPA that is utilised by the corresponding range.

Species	Kernel (% UD)	Area of Range in MPA (%)	Area Utilisation of MPA (%)
Loggerhead	Home Range (95 %)	100	4
	Core Range (50 %)	100	1
Leatherback	Home Range (95 %)	5	100
	Core Range (50 %)	8	14

To test the significance of the MPA in the conservation of both species, it was hypothesized that MPA utilisation and the area of the home range within the MPA of loggerheads would equal that of leatherbacks. However, usage of the MPA was significantly different between the species' home ranges ( $\chi^2 = 86.00$ ,  $df = 1$ ,  $p < 2.2 \times 10^{-16}$ ) and core ranges ( $\chi^2 = 77.81$ ,  $df = 1$ ,  $p < 2.2 \times 10^{-16}$ ). Loggerhead home and core ranges fell completely (100 %) within the MPA boundaries (Table 2). Leatherbacks, however, have only a small portion of their kernels within the protected region of the MPA; 5 % of their home range and 8 % of their core range. Loggerheads range is selective as they utilise a relatively small portion of the MPA; 4 % of the MPA overlapped with their home range and 1 % of the core range overlapped with the MPA. In contrast, leatherbacks utilised the entire park, with 100% of the MPA overlapping with their home range, and 14 % with their core range (Table 2). There is therefore, a significant difference in the area utilisation by the home range ( $\chi^2 = 89.40$ ,  $df = 1$ ,  $p < 2.2 \times 10^{-16}$ ), and core ranges ( $\chi^2 = 12.96$ ,  $df=1$ ,  $p = 3.19 \times 10^{-4}$ ) between the species.

By comparing the number of individual GPS coordinates that fall inside and outside the MPA it is clear that a large proportion of the leatherback internesting period is located outside the MPA (Fig. 4A; Table 1). It was predicted that the protection awarded to both species to be the same, having equal spatial extents within the MPA however, this was not the case. All four of the leatherback turtles tended to be outside of the MPA boundary more frequently (78 %) during the internesting period (Table 1). Turtle 56100 showed the greatest percentage observations outside of the MPA region (83 %) while the Turtle 72590 had 54 % of her observations outside of the MPA. Loggerheads however, remain within the MPA almost exclusively (98 %). Comparison among the individual loggerheads showed that six of the eight turtles remained completely within the MPA boundary during the internesting period. Turtles 66309 and 66312, were the only individuals that ventured out the MPA, both recording only one satellite point outside of the MPA boundary (Fig. 4B; Table 1). These data show a significant difference from the hypothesised equality of points inside ( $X^2 = 42.82$ ,  $df = 1$ ,  $p = 6.01 \times 10^{-11}$ ) and outside ( $X^2 = 70.56$ ,  $df=1$ ,  $p < 2.2 \times 10^{-16}$ ) the MPA between species.

Table 3. Comparison of bathymetric selection between the core and home ranges of loggerheads and leatherbacks. (\* indicates preferred depth range and – indicates an isobath not falling within the kernel range)

Depth (m)	Loggerhead PI		Leatherback PI	
	Core Range	Home Range	Core Range	Home Range
0-15	<b>0.32*</b>	<b>0.42*</b>	<b>0.83*</b>	<b>1.05*</b>
15-20	0.28	<b>0.37*</b>	<b>0.55*</b>	<b>0.78*</b>
20-30	0.24	0.24	<b>0.69*</b>	<b>0.75*</b>
30-50	-	0.20	0.10	<b>0.38*</b>
50-100	-	-	0.08	0.28
100-200	-	-	0.12	<b>0.48*</b>
200-500	-	-	-0.51	-0.06
500-1000	-	-	-1.35	-0.68
>1000	-	-	-	-0.58

Loggerhead kernel range was selectively within the shallow waters, with the core range extending to the 30 m isobath while the home range was between the 30- and 50-m isobaths (Fig. 7). The greatest depth preference (Table 3) was the 0-15 m depth range, utilised most for both the core (PI = 0.32) and home ranges (PI = 0.42). Loggerheads utilise this narrow stretch of depth region specifically so it could be assumed that they are selectively utilising the depth or some other abiotic feature within the region. Leatherbacks cover a wider expanse of the depth regions (Fig. 6). The core range extends to the 1000 m isobath, while the home range extends past the 1000 m isobath (the greatest resolution bathymetry data available) as seen in Figure 6. The greatest preference within the core and the home ranges is the 0-15 m depth range, PI = 0.83 and 1.05 respectively (Table 3). The 0-30 m range was the preferred depth range corresponding with the high density core range. Leatherbacks within the home range also show preference for the 30-50 m and the 100-200 m depth ranges. It is important to note that they strongly avoid regions past the 200 m isobath,

indicated by the negative PI values, even though their range extends into these regions. There is a patchy selectivity among the leatherback preferences, as seen in the home range (Table 3). It can therefore be assumed that leatherbacks are not selecting for a specific depth.

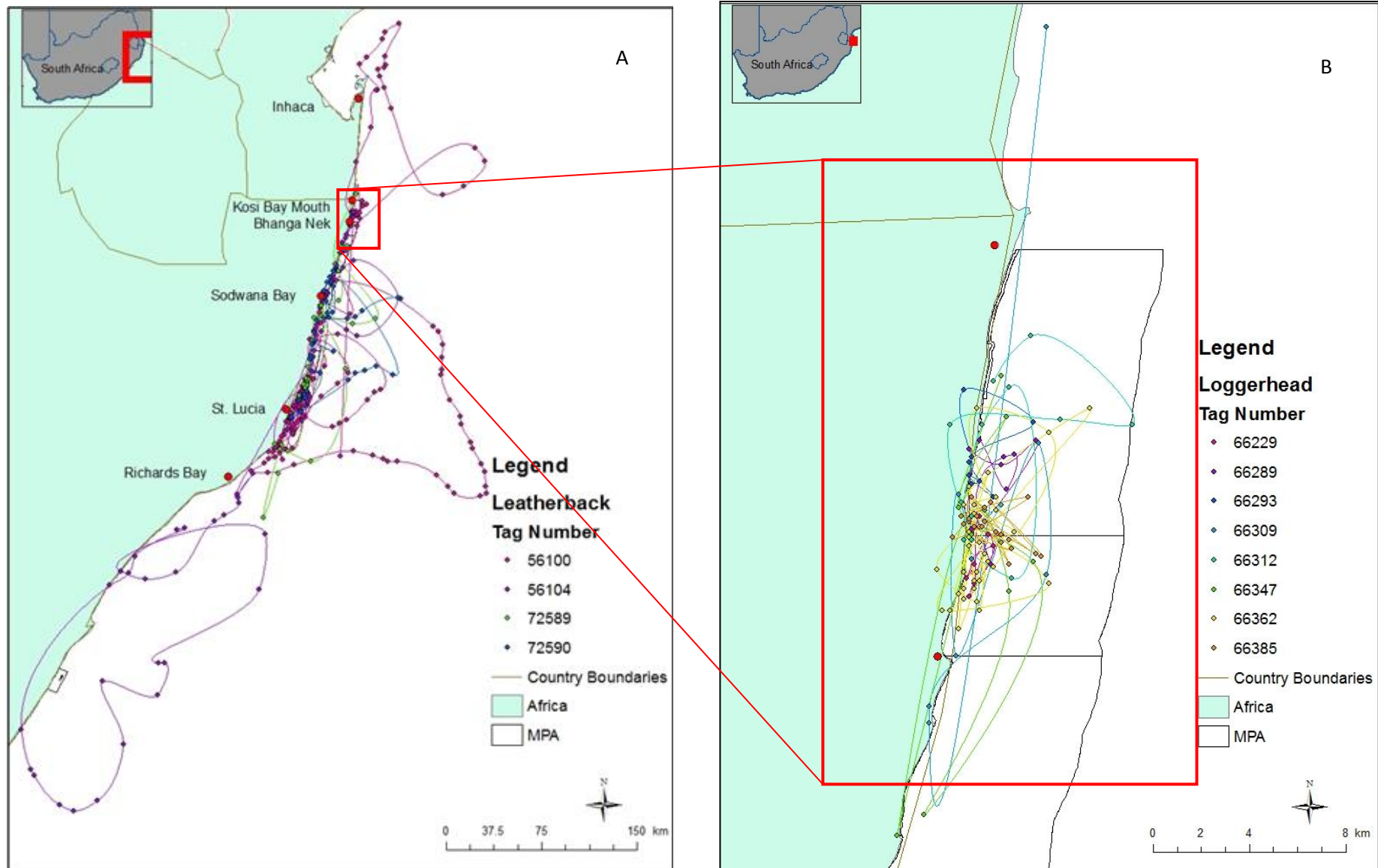


Figure 4 Tracking layers of individual turtles, leatherbacks (A) and loggerhead (B), during the internesting period. Included is the MPA boundary.

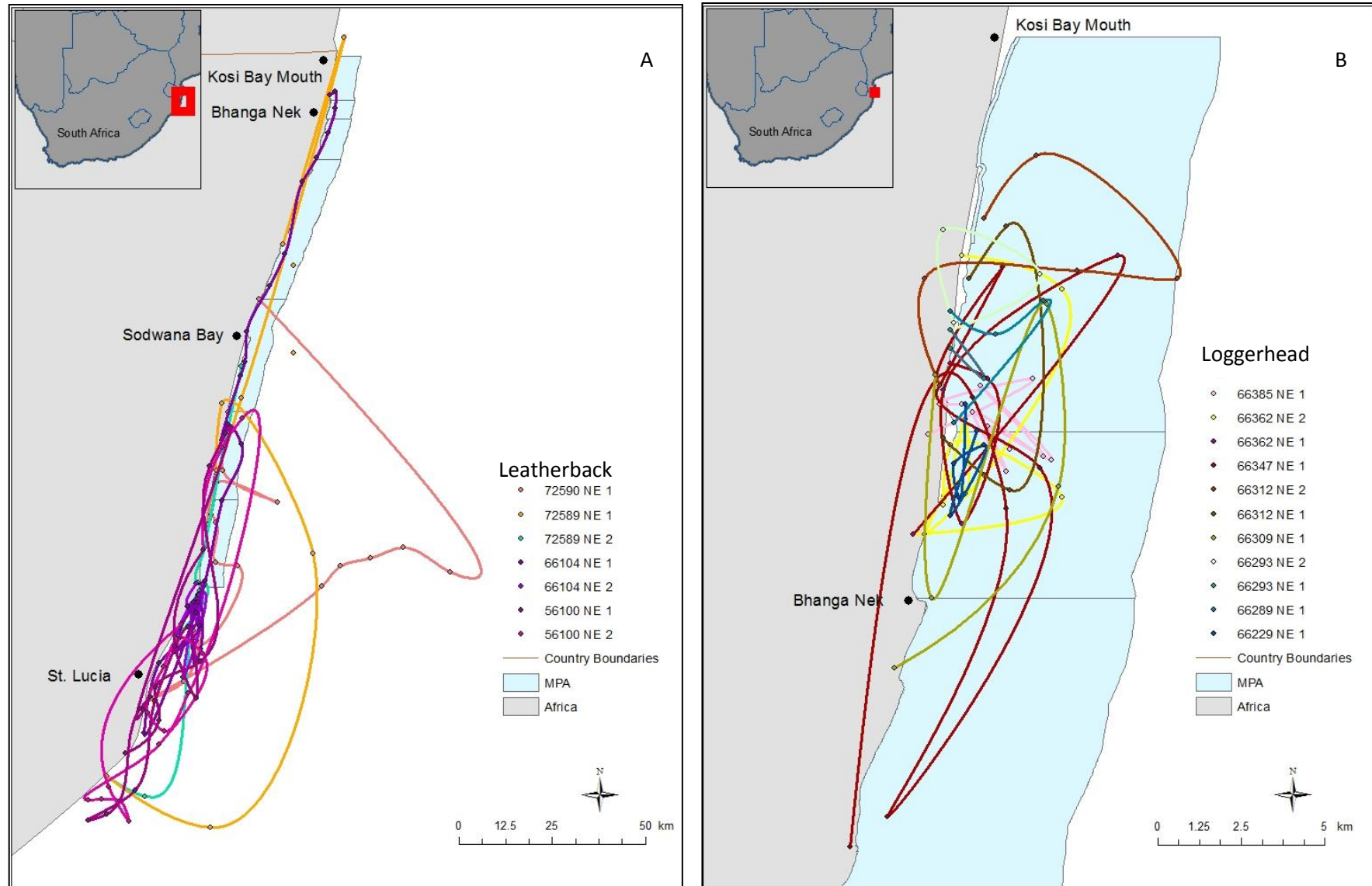


Figure 5 MPA overlaid with the interesting period tracks (NE) of individual leatherback (A) and loggerhead (B) turtles during the interesting period, overlaid on the MPA.



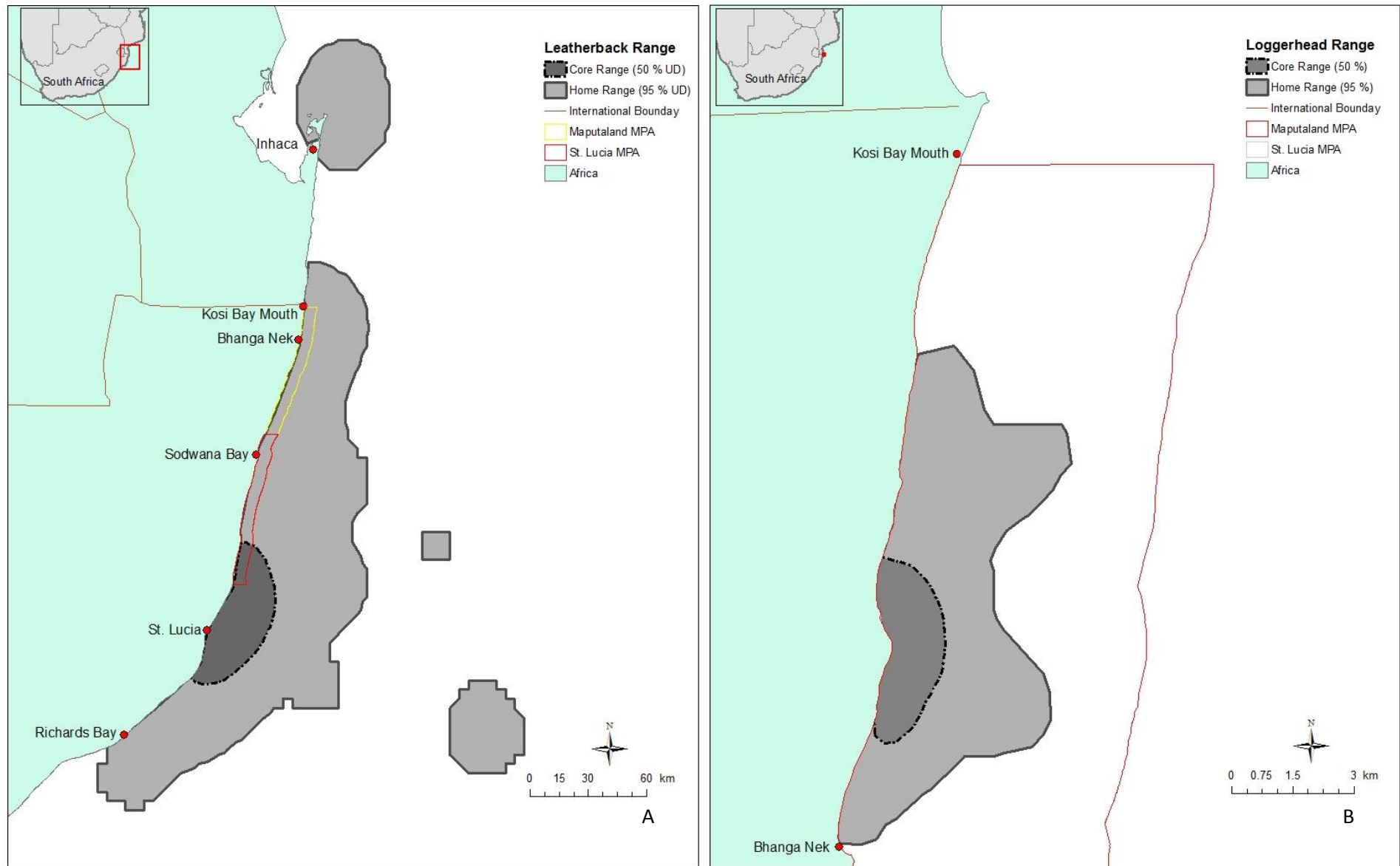


Figure 6 Ranges of the leatherback,  $H=0.19$  (A), and loggerhead,  $H=0.01$  (B), turtles. Indicating the home (95 % UD) and core (50 % UD) ranges of their distributions and the MPA.

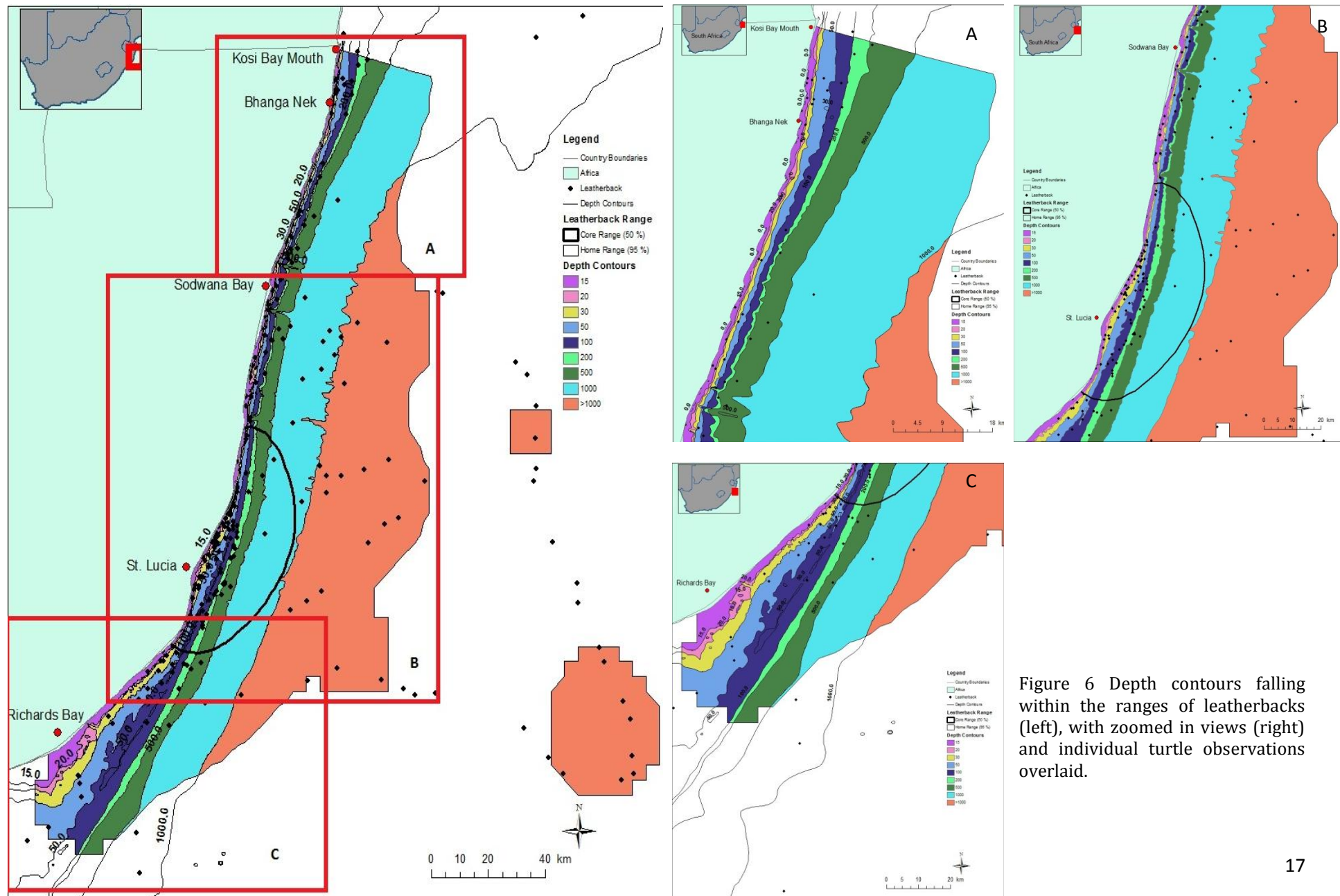


Figure 6 Depth contours falling within the ranges of leatherbacks (left), with zoomed in views (right) and individual turtle observations overlaid.

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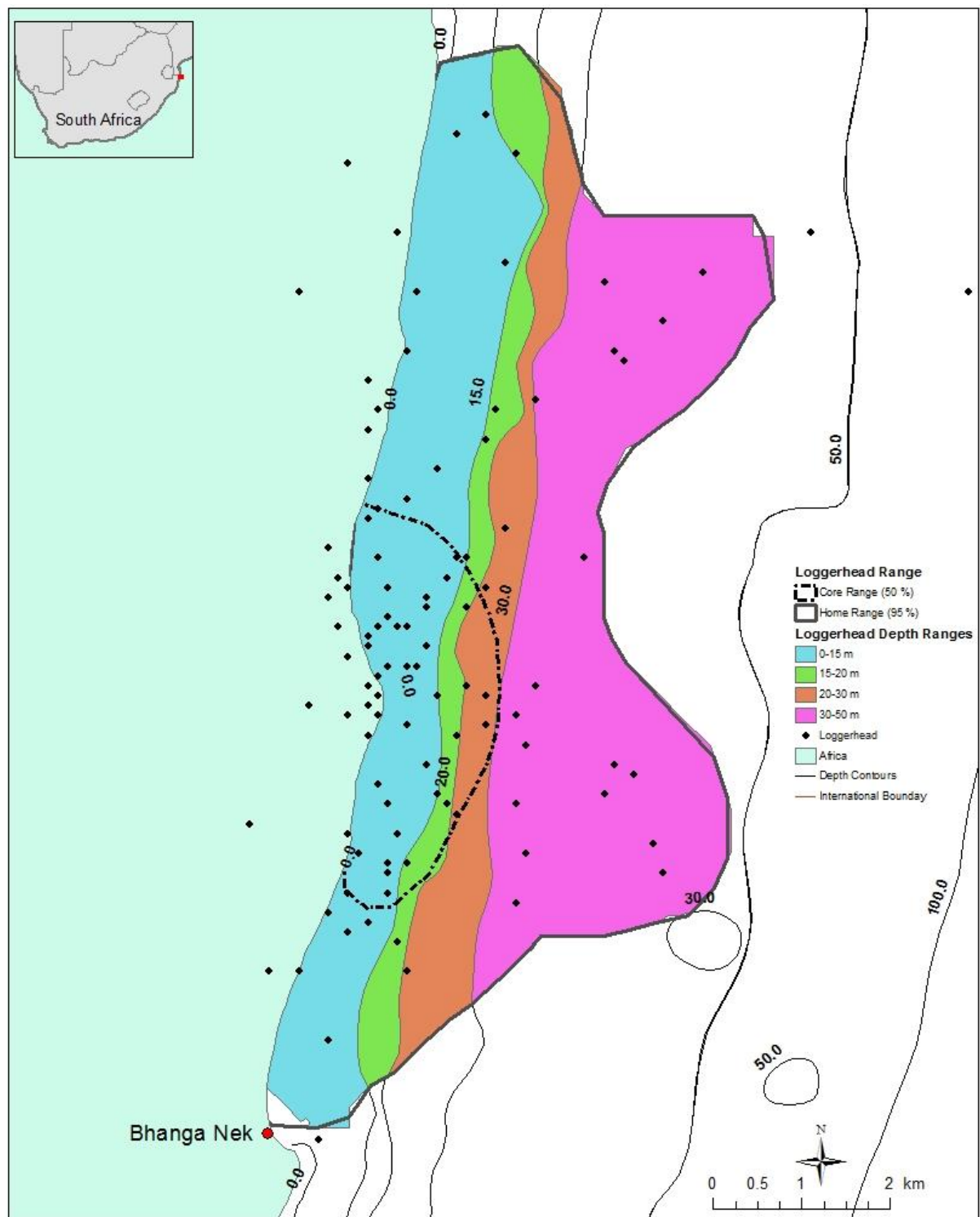


Figure 7. Depth contours within the loggerhead range, with the individual turtle observations overlaid.





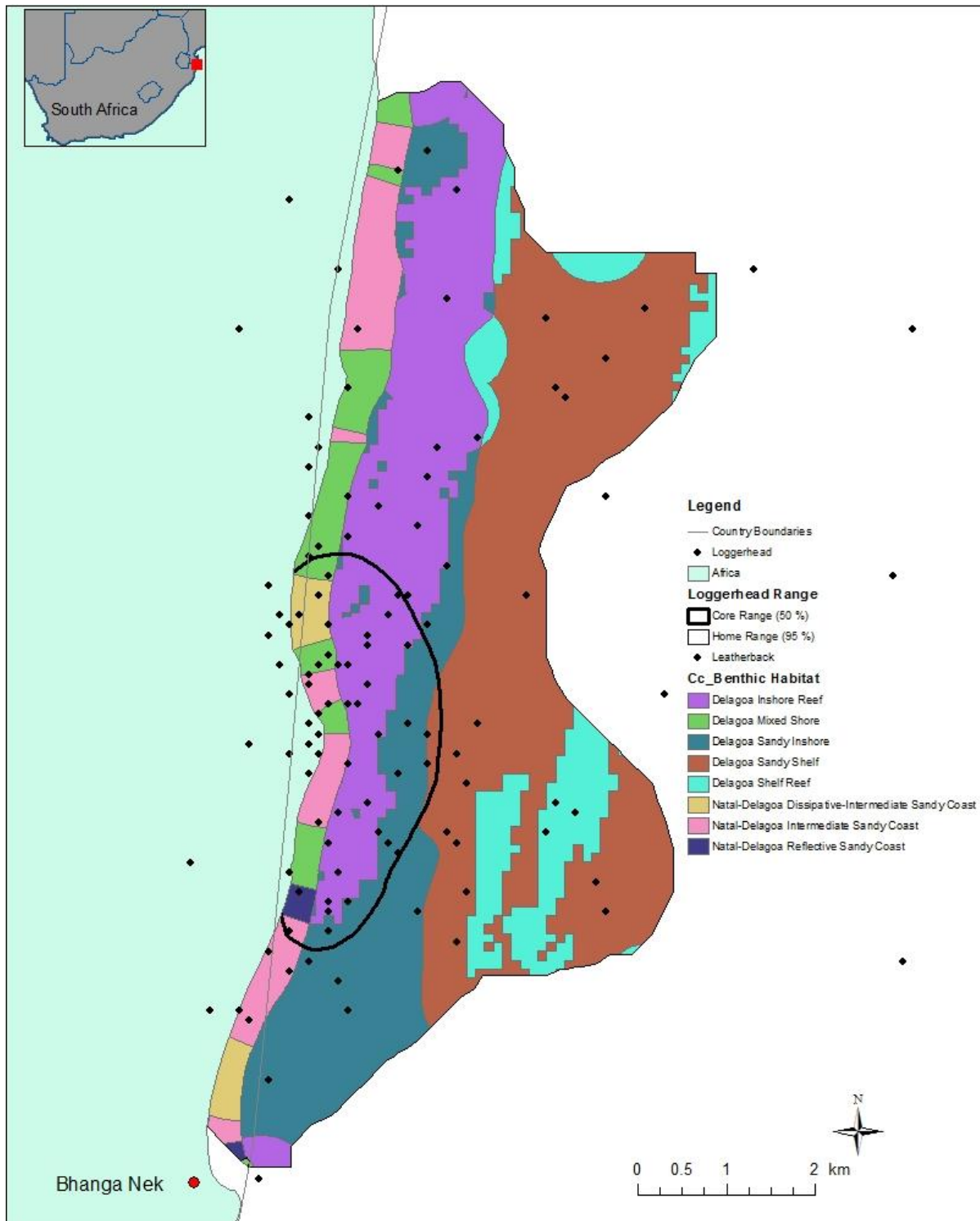


Figure 9 Loggerhead habitat use within the range.

Table 3 Habitat selection, identified by PI, showing core and home range selection of leatherbacks and loggerheads (\* indicates preferred habitat,  $PI \geq 0.3$  and - indicates a habitat not falling within the range)

Habitat	Loggerhead PI		Leatherback PI	
	Core Range	Home Range	Core Range	Home Range
Delagoa Sandy Shelf Edge	-	-	0.12	<b>0.40*</b>
Delagoa Canyon	-	-	-	<b>0.38*</b>
Delagoa Inshore Reef	<b>0.30*</b>	<b>0.41*</b>	0.00	<b>0.99*</b>
Delagoa Mixed Shore	0.25	<b>0.37*</b>	<b>0.62*</b>	<b>1.34*</b>
Delagoa Sandy Inshore	0.24	<b>0.30*</b>	<b>0.43*</b>	<b>0.95*</b>
Delagoa Sandy Shelf	<b>0.46*</b>	0.21	0.16	<b>0.61*</b>
Delagoa Shelf Edge Reef	-	-	0.00	0.00
Delagoa Shelf Reef	-	0.15	<b>0.38*</b>	<b>0.64*</b>
Delagoa Very Exposed Rocky Coast	-	-	-	0.00
Harbor	-	-	-	0.00
Natal Exposed Rocky Coast	-	-	0.00	<b>1.78*</b>
Natal Gravel Shelf	-	-	-	0.00
Natal Inshore Reef	-	-	<b>0.80*</b>	0.00
Natal Mixed Shore	-	-	<b>1.09*</b>	<b>1.47*</b>
Natal Sandy Inshore	-	-	<b>0.86*</b>	0.00
Natal Sandy Shelf	-	-	<b>0.38*</b>	0.00
Natal Sandy Shelf Edge	-	-	<b>0.30*</b>	0.00
Natal Shelf Edge Reef	-	-	<b>1.23*</b>	<b>1.60*</b>
Natal Shelf Reef	-	-	<b>0.49*</b>	<b>0.68*</b>
Natal-Delagoa Dissipative Sandy Coast	-	-	0.00	<b>3.87*</b>
Natal-Delagoa Dissipative-Intermediate Sandy Coast	0.00	<b>0.37*</b>	0.00	<b>1.76*</b>
Natal-Delagoa Estuarine Shore	-	-	0.00	<b>2.53*</b>
Natal-Delagoa Intermediate Sandy Coast	0.29	<b>0.40*</b>	<b>0.97*</b>	<b>0.37*</b>
Natal-Delagoa Reflective Sandy Coast	<b>0.63*</b>	<b>0.63*</b>	0.00	<b>1.01*</b>
Southwest Indian Lower Bathyal	-	-	-	0.15
Southwest Indian Upper Bathyal	-	-	0.02	0.09

Loggerheads and leatherbacks have significantly different utilisation of both the number and the types of habitats they prefer (Fig. 9 & 10). The highest habitat preference within the loggerhead core and home range was Natal-Delagoa Reflective Sandy Coast ( $PI=0.63$ ), followed by Delagoa Sandy Shelf ( $PI=0.46$ ) in the core range and Delagoa Inshore Reef ( $PI=0.41$ ) in the home range (Table 4). Loggerheads have a limited use of different habitats, only utilising 7 and 8 habitat types in the home and core ranges respectively. Noting that the loggerheads have a much smaller kernel range, this may suggest they are specifically selecting for these habitats. Leatherbacks on the other hand have a vast number of habitats that they show preference for, 21 habitats in the core range and 26 in the home range (Table 4). Leatherbacks have the greatest preference for Natal Shelf Edge Reef ( $PI=1.24$ ) and Natal Mixed Shore ( $PI=1.09$ ) within the

core and home range. However, leatherbacks utilise the expanse of ocean rather than depth or habitat type, because they are pelagic they are not actively 'selecting' a habitat as loggerheads do.

## Discussion

Both loggerheads and leatherbacks from the studied population make use of the Maputaland nesting grounds during the internesting period, however the spatial extents of the satellite tagged turtles had significant differences during the internesting period, in regards to range extents, abiotic feature selection and the utilisation of the area. These clear differences are presumed to be an adaptation to conserve as much energy as possible during the highly energy costly internesting period (Wallace & Jones 2008).

The loggerhead internesting event duration lasted on average 16.9 days. This is slightly longer than the conventional 15 days (Hughes 1980). The variation in the data may be due to the turtles not having a successful nesting, in this case she would return to the ocean and re-emerge the next day. By inferring these 'false nests' to be a nesting event (by the definition), would cause deviations in the results. For future studies it may be advantageous to correlate the assumed nesting events with the nesting database of all encountered nesting turtles on the beaches. Leatherbacks had an internesting period lasting 9.5 days, which falls within the predicted range of 9 to 10 days (Branch *et al.* 2007, Hughes 1980).

Loggerheads have a tiny home range ( $28 \text{ km}^2$ ) and core range ( $4 \text{ km}^2$ ) this is similarly found in the Zakynthos, where loggerheads have  $20 \text{ km}^2$  home range and a  $5 \text{ km}^2$  core range (Schofield *et al.* 2010). It is important to note that loggerheads are neritic species (Hatase *et al.* 2007, Mortimer 2000), which make use of benthic sea floor during internesting periods (Hatase *et al.* 2007). The results obtained supported this, because they travel on average 19.3 km per internesting period this could indicate that they disperse in a near shore region where they remain relatively inactive, with low energy expenditure. Loggerhead turtles have a small range utilisation which corresponds with the high density nesting region (Botha 2010). It can therefore be assumed that the turtles are selecting for this region, possibly for abiotic features such as depth or habitat.

Loggerheads tend to have a preference for shallow depths ( $< 30 \text{ m}$ ), close to shore, which minimises the distances needed to travel for a nesting event. This is in accordance with Houghton *et al.* (2002), who found that loggerheads aggregate within the depth range of 3 to 32 m. Loggerheads utilise habitat areas that contain reefs or rocky outcrops (Miller *et al.* 2003), this was evident in the habitat selection where loggerheads had a high preference for Delagoa Inshore Reef. However, there was a high preference for

Delagoa Sandy Shelf which was not expected. This habitat and inshore reef both have high productivity levels (Hallegraeff & Jeffery 1984), which may suggest that the turtles are in fact feeding, as few populations have been noted to do (Houghton *et al.* 2002, Georges *et al.* 2007, Schofield *et al.* 2010). High preference for Natal Delagoa reflective sandy coast, which is a habitat that extends into the intertidal zone, would imply loggerheads are selecting this morphodynamic beach type for emergence. iSimangaliso predominantly consists of intermediate beaches, with less reflective beaches (Harris 2008), this further supports the assumption that they are selecting for this region. This coincided with other studies that have found high nest densities on beaches with reflective and intermediate morphodynamics which are dominated by coarse grain size and steep beaches (Witherington *et al.* 2009).

Leatherbacks travelled great distances, up to 376 km, which contradicts the hypothesis of reducing energy-demanding activities during this period. However, leatherbacks are pelagic drifters (Luschi *et al.* 2003), which make use of neutral buoyancy in mid waters (Brando & Sakamoto 2000) and the currents to aid their distributions (Lambardi *et al.* 2008). It is therefore hypothesised that the long distances travelled are an effect of the turtles entering the currents and eddies, where they are transported with minimal energy expenditure. To prove this theory it is necessary to do further study, where the turtle internesting distribution is overlaid onto currents to determine a correlation. Leatherbacks were located predominantly in shallower waters, up to 200 m. These results are different to those in other studies where depths up to 1000 m (Muir 2004) have been recorded during the internesting period (Houghton *et al.* 2008). The leatherbacks showed strong avoidance for the increasing depth, greater than the 200 m isobath. This may be a predator avoidance adaptation because in open mid water they will be clearly silhouetted to possible predators below (Houghton *et al.* 2008).

The leatherbacks encompassed a vast range during the internesting period, the home range covered an area of 15166 km<sup>2</sup>, which was much greater than the Atlantic leatherback population which have a home range of up to 6000 km<sup>2</sup> (Schofield *et al.* 2010). The differences in the ranges may correspond to the sizes of the available adjacent nesting beaches (Schofield *et al.* 2010). The wide home range is mirrored in their nesting distribution, having a haphazard nesting style which lacks philopatry (Nel *et al.* 2011). However, the core range does correspond with the high density nesting region (Botha 2010). The possible reason behind the wide distribution in their range may be accredited to the low emergence success of leatherback nests, with approximately 50 % success rate (Nordmoe, *et al.* 2004), compared to other turtles with a rate of approximately 80 % (Rafferty *et al.* 2011). They therefore nest haphazardly in an attempt to maximise the survival rates in a sporadic environment (Maison 2010), because the placement of a clutch will determine the nesting success (Nordmoe *et al.* 2004). Leatherbacks seem to nest in regions that lack fringing reefs as



manoeuvring over the rocks would pose a major threat to their soft carapace (Eckert 1987), it would seem that the home range then relates to a region lacking rocky regions and reefs, with a great proportion of the successful nestings in Maputaland being in regions lacking reefs. Natal Delagoa Intermediate Sandy Coast was the highest preferred intertidal habitat within the core range, which has highest density nesting frequency. This would imply that the leatherbacks are selecting this habitat for nesting emergence, Botha (2010) also found that high leatherback emergence was on intermediate beaches.

From the distribution patterns and the protection offered by the MPA protection, loggerheads receive maximum benefit from the current conservation measures, with their kernel range overlapping completely with the MPA. However, leatherbacks do not receive the same level of protection, although their home range overlaps with the MPA, the high density core only marginally intersects the MPA. In order for the leatherbacks to receive adequate protection from conservation, the MPA would need to offer additional protection to the high density core region (Schofield *et al.* 2010). Therefore it is suggested that the MPA extent should be lengthened in a southern direction along the coast to at least St. Lucia, which will ensure at least half of the core density is protected. For the best conservation returns however, it would be beneficial to extend the MPA southerly to overlap with the entire core zone. Additionally it may be best to implement the additional protection seasonally, to coincide with the internesting period, October to March. Turtle monitoring is only enforced for the initial 56 km northern extent of the park (Nel *et al.* 2011), which does not correspond with the high density range. For adequate population estimates it would also be necessary to extend the monitoring to the high density region.

## **Conclusion:**

Loggerheads and leatherbacks have significantly different distribution, area utilisation and oceanographic preferences during the internesting period. From the study it is assumed that the differences in behaviour are adaptations to reduce energy expenditure during the highly energetically costly internesting period. The spatial extents that the turtles utilise awards the two species different levels of protection. Loggerheads receive maximum gain from the protection, however leatherbacks are not adequately protected. It is suggested that the MPA be seasonally extended southwards along the coast, to overlap with the high density core of the leatherback distribution. Additionally it would be necessary to include turtle monitoring in this region for most accurate leatherback population data.

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## References

- BOTHA, M. 2010. Nest site fidelity and nest selection of loggerhead, *Caretta caretta* and leatherback *Dermochelys coriacea*, turtles in KwaZulu-Natal, South Africa. In: Department of Zoology, p. 115. Nelson Mandela Metropolitan University, Unpublished Thesis.
- BRANCH, G.M., GRIFFITHS, C.L., BRANCH, M.L. & BECKLEY, L.E. 2007. *Two Oceans: A guide to the marine life of southern Africa* 4<sup>th</sup> ed. Edited by David Phillip. Cape Town: Struik Publishers
- BYRNE, R., FISH, J., DOYLE, T., HOUGHTON, J. D. R. 2009. Tracking leatherback turtles (*Dermochelys coriacea*) during consecutive inter-nesting intervals: Further support for direct transmitter attachment. *Journal of Experimental Marine Biology and Ecology* **377**: 68-75.
- CRIM, J. L., SPOTILA, L. D., SPOTILA, J. R., O'CONNOR, M., REINA, R., WILLIAMS, C. J., PALADINOS, F. V. 2002. The leatherback turtle, *Dermochelys coriacea*, exhibits both polyandry and polygyny. *Molecular Ecology* **11**: 2097-2106.
- DUTTON, D. L., DUTTON, P. H., CHALOUPIKA, M., BOULON, R. H. 2005. Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biological Conservation* **126**: 186-194.
- ECKERT, S., NELLIS, D., ECKERT, K., KOOYMAN, G. 1986. Diving Patterns of Two Leatherback Sea Turtles (*Dermochelys coriacea*) during Internesting Intervals at Sandy Point, St. Croix, U.S. Virgin Islands. *Herpetologica* **42 (3)**: 381-388.
- ECKERT, K. L. 1987. Environmental Unpredictability and Leatherback Sea Turtle (*Dermochelys coriacea*) Nest Loss. *Herpetologica* **43(3)**: 315-323.

- GEORGES, J., FOSSETTE, S., BILLES, A., FERRAROLI, S., FRETEY, J., GRÉMILLET, D., LE MAHO, Y., MYERS, A., TANAKA, H., HAYS, G. 2007. Meta-analysis of movements in Atlantic leatherback turtles during the nesting season: conservation implications. *Marine Ecology Progress Series* **338**: 225-232.
- GITZEN, R. A., MILLSPAUGH, J. J. 2003. Comparison of Least-Squares Cross-Validation Bandwidth Options for Kernel Home-Range Estimation. *Wildlife Society Bulletin* **31(3)**: 823-831.
- HALLEGRAEFF, G. M., JEFFERY, S. W. 1984. Tropical phytoplankton species and pigments of continental shelf waters of North and North-West Australia. *Marine Ecology Progress Series* **20**: 59-74.
- HATASE, H., OMUTA, K., TSUKAMOTO, K. 2007. Bottom or midwater: alternative foraging behaviours in adult female loggerhead sea turtles. *Journal of Zoology* **273**: 46-55.
- HAYS, G, C. WEBB, P. I., HAYES, J. P., PRIEDE, I. G., FRENCH, J. 1991. Satellite tracking of a loggerhead turtle (*Caretta caretta*) in the Mediterranean. *Journal of Marine Biology Association*, **71**: 743-746.
- HAYS, GRAEME C., BRODERICK, ANNETTE C., GODLEY, BRENDAN J., LUSCHI, PAOLO, NICHOLS, WALLACE J. 2003. Satellite telemetry suggests high levels of fishing-induced mortality in marine turtles. *Marine Ecology Progress Series* **262**: 305-309.
- HOOGE, P. N. & EICHENLAUB, B. 2000. Animal movement extension to Arcview. ver. 2.0. Alaska Science Center - Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.
- HOOKE, S.K, GERBER, L.R. 2004. Marine reserves used as a tool for ecosystem-based management: the potential importance on megafauna. *Bioscience* **54(1)**: 27-39.
- HOUGHTON, J. D. R., BRODERICK, A. C., GODLEY, B. J., METCALFE, J. D., HAYS, G. C. 2002. Diving behaviour during the internesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Marine Ecology Progress Series* **227**: 63-70.
- HOUGHTON, J. D. R., CEDRAS, A., MYERS, A. C., LIEBSCH, N., METCALFE, J. D., MORTIMER, J. A., HAYS, G. C. 2008. Measuring the state of consciousness in a free-living diving sea turtle. *Journal of Experimental Marine Biology and Ecology* **356**: 115-120.
- HUGHES, G. R., LUSCHI, P., MENCACCI, R., PAPI, F. 1998. The 7000-km oceanic journey of a leatherback turtle tracked by satellite. *Journal of Experimental Marine Biology and Ecology* **229(2)**: 209-217.

- HUGHES, GEORGE R. 1989. Sea turtles. In *Oceans of Life off Southern Africa*, by R. Crawford & A. Payne. Vlaeberg, Cape Town: Vlaeburg Publishers. 230- 243p.
- FINKBEINER, E. M., WALLACE, B. P., MOORE, J. E., LEWISON, R. L, CROWDER, L. B., READ, A. J. 2011. Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. *Biological Conservation* **144**: 2719-2727.
- JAMES, M. C., MYERS, R. A., OTTENSMEYER, C. A. 2005. Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proceedings of the Royal Society of Biological Sciences* **272**: 1547-1555.
- LUSCHI, P., LUTJEHARMS, J. R. E., LAMBARDIA, P., MENCACCI, R., HUGHES, G. R., HAYS, G C. 2006. A review of migratory behaviour of sea turtles off southeastern Africa. *South African Journal Of Science* **102**: 51-58.
- LUSCHI, P., SALE, A. & MENCACCI, R. 2003. Current transport of leatherback sea turtles (*Dermochelys coriacea*). *The Royal Society* **270**: 129-132.
- MAISON., K. A., KING, R., LLOYD, C., ECKERT, S. 2010. Leatherback Nest Distribution and Beach Erosion Pattern at Levera Beach, Grenada, West Indies. *Marine Turtle Newsletter* **127**: 9-12.
- MAST, R., HUTCHINSON, B. & PILCHER, N.J. 2006. The burning issues for global sea turtle conservation 2006: The Hazzards and urgent prioritie in Sea Turtle Conservation. *Indian Ocean Turtle Newsletter* **3**: 29-31.
- MILLER, JEFFREY D, COLIN J LIMPUS, AND MATTHEW H GODFREY. 2003. Nest Site Selection, Oviposition, Eggs, Development, Hatching, and Emergence of Loggerhead Turtles. In *Loggerhead Sea Turtle*, by Blair E. Witherington Alan B. Bolten. Washington D.C: Smithsonian Istitution Press. 125-143p.
- MILLS, M. G. L., & GORMAN, M. L. 1997. Factors Affecting the Density and Distribution of Wild Dogs in the Kruger National Park. *Conservation Biology* **11(6)**: 1397-1406.
- MINAMIKAWA, S., NAITO, Y., SATO, K., MATSUZAWA, Y., BANDO, T., SAKAMOTO, W. 2000. Maintainance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *The Journal of Experimental Biology* **203**: 2967-2975.
- MOORE, M. K., BALL, R. M. 2002. Multiple paternity in loggerhead turtle (*Caretta caretta*) nests on Melborne Beach, Florida: a microsatellite analysis. *Molecular Ecology* **11**: 281-288.

- MORTIMER, J. A. 2000. A Strategy to Conserve and Manage the Sea Turtle Resources of the Western Indian Ocean Region. IUCN, WWF, and The Ocean Conservancy. 17pp
- MUIR, C. E. 2004. An Assessment of the Status of Turtles, Dugongs and Cetaceans in Mnazi Bay Ruvuma Estuary Marine Park & Recommendations for a Conservation Strategy. *Conservation Assessment, Tanzania: UNDP*. 75pp.
- NEL, R., PUNT, A. E., HUGHES, G. 2011. Does beach conservation benefit different species of migratory sea turtles equally? South Africa's 45-year program as an example. Submitted to Conservation Biology.
- NORDMOE, E. D., SIEG, A. E., SOTHERLAND, P. R., SPOTILA, J. R., PALADINO, F. V., REINA, R. D. 2004. Nest site fidelity of leatherback turtles at Playa Grande, Costa Rica." *Animal Behaviour* 68: 387-394.
- PELLETIER, D., ROOS, D., CICCIONE, S. 2003. Oceanic survival and movements of wild and captive-reared immature green turtles (*Chelonia mydas*) in the Indian Ocean. *Aquatic Living Resources* 16: 35-41.
- PIKE, D. A. 2008. Environmental correlates of nesting in loggerhead turtles, *Caretta caretta*. *Animal Behaviour* 76: 603-610.
- R DEVELOPMENT CORE TEAM, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. <http://www.R-project.org>.
- RAFFERTY, A. R., TOMILLO, P. S., SPOTILA, J. R., PALADINO, F. V., REINA, R. D. 2011. Embryonic Death Is Linked to Maternal Identity in the Leatherback Turtle (*Dermochelys coriacea*). *PLoS One* 6(6): 1-7.
- SCHOFIELD, GAIL, HOBSON, VICTORIA J., LILLEY, MARTIN K. S., KATSELIDIS, KOSTAS A., BISHOP, CHARLES M., BROWN, PETER, HAYS, GRAEME C. 2010. Inter-annual variability in the home range of breeding turtles : Implications for current and future conservation management. *Biological Conservation* 143(3): 722-730.
- SEMINOFF, J., SHANKER, K. 2008. Marine turtles and IUCN Red Listing: A review of the process, the pitfalls, and novel assessment approaches. *Journal of Experimental Marine Biology and Ecology* 356: 52-68.
- SINK, K., STEPHEN HOLNESS, S., HARRIS, L., MAJIEDT, P., ATKINSON, L., ROBINSON, T., KIRKMAN, S., HUTCHINGS, L., LESLIE, R., LAMBERTH, S., KERWATH, S., VON DER HEYDEN, S., LOMBARD, A., TALJAARD, S., WEERTS, S., COWLEY, P., AWAD, A., HALPERN, B., GRANTHAM, A., WOLF, T. 2011. Volume 4: Coastal and Marine Technical Report. National Biodiversity Assessment 2011. South African National Biodiversity Assessment, Cape Town.

- SUNDE, J., ISAACS, M. 2008. *Marine Conservation and Coastal Communities: Who Carries the Costs? A Study of Marine Protected Areas and Their Impact on Traditional Small-scale Fishing Communities in South Africa*. Chennai: India: International Collective in Support of Fishworkers.
- WALLACE, B. P., JONES, T. T. 2008. What make marine turtles go: A review of metabolic rates and their consequences. *Journal of Experimental Biology and Ecology* **356**: 8-24.
- WITHERINGTON, B., KUBILIS, P., BROST, B., MEYLAN, A. 2009. Decreasing annual nest counts in a globally important loggerhead sea turtle populatio. *Ecological applications* **19(1)**: 30-54.
- WORTON, B. J. 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology* **70(1)**: 164-168.