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**Loggerhead (*Caretta caretta*) and Leatherback
(*Dermochelys coriacea*) nesting activity along
the Maputaland coast (South Africa):**

1965 – 2002

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Submitted in partial fulfillment of the Masters Degree in Zoology
at the University of Cape Town

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University of Cape Town

1. ABSTRACT

From 1963 until the present, loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) female turtles nesting on a 56-km stretch of beach in Maputaland, on the northeast coast of KwaZulu-Natal, South Africa have been tagged and monitored. In this study, population trends, size, preference for timing of nesting and nesting sites, and seasonality in nesting activity and nesting area were analysed and the effectiveness and efficiency of the monitoring programme assessed. Since the programme's inception, approximately 46893 loggerhead and 11509 leatherback females have nested on the Maputaland beaches. A non-linear relationship was found between the numbers of nesting females of both species over time, with three distinct phases. Large interannual variations in nesting numbers were evident for both species, as were synchronized seasons of elevated or depressed nesting activity. While Maputaland leatherbacks appear to be approximately the same size as in populations elsewhere, the loggerhead females were significantly smaller compared to other populations. Peak nesting activity occurred from November to January and was associated with warmer sea temperatures, as was the subsequent emergence of hatchlings. Marginal temporal shifts in the nesting numbers of both species were evident during peak nesting-activity seasons, with the peak nesting period beginning slightly earlier than usual. Peak nesting-activity seasons appeared to follow El Niño events with a lag period of between 0 and 2 years. Separate 'preferred' nesting areas were found for each species, largely associated with the offshore seabed topography. The loggerheads exhibited a fairly narrow nesting-area distribution in the north, while the leatherbacks utilised a far wider area in the southern region. The length of the 'preferred' nesting area (km) was strongly correlated with the total number of nesting loggerhead and leatherback females. No major nesting-area shifts were evident over the programme's duration. However, distinct spatial shifts, with increases in the length of the 'preferred' nesting area, were evident for both species during peak nesting-activity seasons, and was possibly related to the increased influx of nesting females. Interspecific competition appeared to be of little importance in Maputaland, as both populations displayed strong synchrony in nesting declines and increases over time, and while both populations have increased, no major shifts in the 'preferred' nesting area of either species have occurred. No correlations were found between the Southern Oscillation Index (SOI) values and nesting activity or changes in nesting area. However, a negative correlation was found between the average curved carapace lengths (CCL) of both species and the SOI values, most likely related to sea surface temperatures and the resultant changes in food availability that occur during El Niño events. Disturbance incurred during monitoring caused, at most, only a 5% reduction in the nesting rates of both species. To date, the conservation efforts of the monitoring programme appear to have come to fruition, with both the loggerhead and leatherback nesting populations healthy and in a more-or-less stable state. The importance and value of continuing the current monitoring programme was emphasized, and several management and sampling strategies proposed for future seasons.

2. INTRODUCTION

On an evolutionary scale, sea turtles have existed since the Mesozoic period (Campbell, 1990), however in recent years there have been significant declines reported in both localised nesting populations of various countries, and in the global populations of almost all seven turtle species (Spotila et al., 1996, Clarke et al., 2000, IUCN Species Survival Committee, 2003). In 1996, the IUCN assessed and listed the loggerhead (*Caretta caretta* Linnaeus), green (*Chelonia mydas* Linnaeus) and olive ridley turtles (*Lepidochelys olivacea* Eschscholtz) as “endangered” throughout their global distributions, while the hawksbill (*Eretmochelys imbricata* Linnaeus), Kemp’s ridley (*Lepidochelys kempii* Garman) and leatherback turtles (*Dermochelys coriacea* Linnaeus) were listed as “critically endangered” (IUCN Species Survival Committee, 2003).

The estimation of population size is an important conservation and management tool (Hays, 2000, Shanker & Pilcher, 2003). In recent years, numerous studies have been conducted on sea turtle populations to determine nesting trends and nesting behaviour, approximate growth rates and conservation status of nesting populations on beaches throughout the world (Margaritoulis, 1982, Bjorndal & Meylan, 1983, Settle, 1995, Boulon Jr. et al., 1996, Chan & Liew, 1996, Girondot & Fretey, 1996, Hughes, 1996, Leslie et al., 1996, Clarke et al., 2000, Chaloupka & Limpus, 2001, Amorocho, 2003).

Sea turtles are highly migratory (Salm & Humphrey, 1996, Bjorndal et al., 1999) and generally display large interannual variations in nesting numbers (Hughes, 1989, Bjorndal et al., 1999, Hays, 2000, Broderick et al., 2001). Both factors have made sampling programmes and the estimation of sea turtle population sizes very complicated (Limpus, 1995, Bjorndal et al., 1999, Hays, 2000, Broderick et al., 2001). In recent years, there has been a growing body of research on the causes of this interannual variation. A relationship between turtle behaviour, nesting activity (particularly interannual variation in nesting numbers) and El Niño Southern Oscillation

(ENSO) events has been established (Limpus & Nicholls, 1988, Limpus & Chaloupka, 1997, Chaloupka, 2001, Polovina et al., 2001), and is particularly obvious for green turtles in both northern Australia (Limpus & Nicholls, 1988) and Southeast Asia (Chaloupka, 2001).

Chaloupka and Limpus (2001: 244) listed five different methods commonly used (together with modelling) to assess the size of sea turtle populations:

1. Trawl net bycatch reports (CPUE estimates)
2. Beach strandings
3. Aerial surveys of nesting beaches and/or feeding grounds
4. Tagging studies
5. Continuous, long-term monitoring programmes of nesting activity on beaches.

Several problems are associated with the use of long-term monitoring of nesting activity to assess population size, particularly the fact that such estimates do not include the entire population, merely the sexually mature, breeding females (Bjorndal et al., 1999, Chaloupka & Limpus, 2001) and large interannual fluctuations in nesting numbers can confound broad population trends (Limpus, 1995, Hays, 2000, Broderick et al., 2001, Chaloupka & Limpus, 2001). Nonetheless, this method has been widely used by many researchers throughout the world to track population trends (Margaritoulis, 1982, Bjorndal & Meylan, 1983, Boulon Jr. et al., 1996, Girondot & Fretey, 1996, Hughes, 1996, Steyermark et al., 1996, Clarke et al., 2000, Godley et al., 2001). Population trends are complex and often prove difficult to resolve (Hays, 2000), and thus the success of this type of study depends largely on whether these monitoring programmes are of sufficient duration, with a large enough sampling effort and tag-returns, that reliable population size estimates can be made over adequate time periods (Hughes, 1989, National Research Council, 1990, Sarti et al., 1996, Broderick et al., 2001).

Of the five species of sea turtles that occur in South African waters, the three most commonly observed are the green, loggerhead and leatherback (Hughes, 1989, Lubke & de Moor, 1998).

However, only the loggerhead and leatherback females nest along these shores (Hughes, 1989, Lubke & de Moor, 1998). Loggerheads occur off the east coast of southern Africa, from Tanzania down to the southern Cape waters, and also around the entire coastline of Madagascar (Hughes, 1974a). Leatherbacks occur from Mozambique down the east coast of southern Africa into the south Atlantic, along the south and south-western coasts of Madagascar (Hughes, 1974a) and also utilize feeding grounds in the Southern Ocean, as discovered by Hughes et al. (1998) with the aid of satellite tracking. Green turtles are found down the east coast of Africa to the southern Cape, around the coast of Madagascar, and can also be found feeding in estuaries (Hughes, 1974a, Lubke & de Moor, 1998).

Marine turtles are highly migratory and spend the majority of their lives in the open ocean (Branch et al., 1994, Salm & Humphrey, 1996, Hays, 2000, Hays et al., 2002). Nesting generally occurs in clearly discrete seasons on temperate, subtropical and tropical beaches throughout the world (Hughes, 1989, Hays & Speakman, 1991, Davenport, 1997, Hays, 2000, Godley et al., 2001, Hays et al., 2002). Maputaland is in a subtropical region (Hughes, 1974a) and nesting occurs between October and February (Hughes 1989, Branch et al., 1994). Turtles are extremely long-lived animals (Spotila et al., 1996, Davenport, 1997) and iteroparous breeders (Hays & Speakman, 1991, Broderick et al., 2001), loggerhead females attain sexual maturity after 12 – 15 years (Hughes, 1989), while leatherback females breed from approximately 13 – 14 years of age (Davenport, 1997). Copulation generally occurs close inshore near the nesting beaches, and the sperm stored by the breeding females (Hughes, 1989, Davenport, 1997). Although females can emerge and nest many times in a single season (Hughes, 1989, Hays & Speakman, 1991), they do not return every year to nest and may only return to breed again, several years later (Carr & Carr, 1978, Davenport, 1997, Hays, 2000, Broderick et al., 2001).

The eggs undergo a two-month incubation period (Hughes, 1989, Branch et al., 1994, Davenport, 1997). During incubation a process referred to as temperature-dependent sex

determination occurs (Hughes, 1989). Davenport (1997) and Godley et al. (2001) describe this process as the determination of the gender of the hatchlings due to the nest or incubation temperature experienced during the middle third period of development. In Maputaland, temperatures between 20 and 24°C produce males, while higher temperatures (> 29.2 °C) produce females (Hughes, 1989). Once the turtles have hatched and left the surf zone they enter the Agulhas Current itself or the Agulhas gyral (Hughes, 1974b) and remain in the open ocean for a long period of time, in the order of 5 – 10 years (Hughes, 1989, Davenport, 1997).

In the past, the first year that elapsed after the hatchlings left the nesting beaches, was often referred to as the “lost year” due to the uncertainty associated with the habits, distribution and movement of hatchlings and juveniles during this time (Carr, 1987). Carr (1987: 111) found that turtles adopt a “pelagic developmental” phase, and feed on floating organisms often present in abundance at convergence zones or frontal driftlines in the open ocean. This too appears to be the case for Maputaland hatchlings (Hughes, 1989).

Once the turtles have reached sexual maturity they migrate to the nesting beaches (Davenport, 1997). After the breeding season ends adults migrate back to the feeding grounds often located at convergence zones (Hughes, 1974b, Hughes et al., 1998, Polovina et al., 2001) to rebuild their energy and fat reserves that were depleted by the reproductive migration and egg-production and egg-laying processes (Hughes, 1974b, Kwan, 1994, Hays, 2000). It takes approximately 9 months for the process of vitellogenesis or egg production (Limpus & Nicholls, 1988). Therefore if the breeding females have sufficient fat and energy reserves, by January the Maputaland females will begin to undergo vitellogenesis and produce eggs for the upcoming nesting season.

Juvenile loggerheads and both juvenile and adult leatherbacks feed on buoyant pelagic prey which consists mostly of scyphozoa and hydrazoa e.g. bluebottles (*Physalia* sp.), various

species of bubble raft shells (*Janthina* sp.), by-the-wind-sailors (*Velella* sp.) and raft hydroids (*Porpita* sp.) (Hughes, 1974b, Branch et al., 1994), while juvenile green turtles consume molluscs and fish until they are approximately 6 months to a year old (Hughes, 1974b, Branch et al., 1994). Both loggerheads and green turtles undergo a change in diet as they develop from a juvenile to an adult (Hughes, 1974b, Branch et al., 1994). At approximately 60 – 70 cm carapace length, the diet of loggerheads changes to include molluscs, echinoderms, crustaceans, sponges, cuttlefish and prawns (Hughes, 1974b, Branch et al., 1994, Lubke & de Moor, 1998). Green turtles older than 1 year undergo a dietary change whereby they consume only plant matter i.e. sea grasses and various species of seaweed (Hughes, 1974b, Lubke & de Moor, 1998, Broderick et al., 2001).

In 1916, all harvesting of sea turtles was banned in South Africa, and from the early 1960s, concerted efforts were made to enforce legislation banning egg collection and the harvesting of adults (Hughes, 1989), aided by effective continuous and high-intensity monitoring. In 1963, under the auspices of the then Natal Parks Board, a turtle conservation and monitoring program was initiated along the northeastern coast of KwaZulu-Natal in the St. Lucia Marine Reserve and the Maputaland Marine Reserve, which have since been amalgamated into the Greater St Lucia Wetland Park (Hughes, 1993). Nesting loggerhead and leatherback females were observed and tagged during consecutive nesting seasons and the beaches regularly patrolled to gather information, and to protect the nesting females, nests and emerging hatchlings (Hughes, 1993).

This programme, currently under the supervision of Ezemvelo KwaZulu-Natal (EKZN) Wildlife, is still in existence today and is one of the longest quantitative loggerhead-leatherback turtle-monitoring programmes in the world (Hughes, 1993). Four turtle drive-concessions have been granted to independent ecotourism operators in the Greater St Lucia Wetland Park: three operators conduct beach drives between Jesser Point and Gobey Point; and one operator based at Rocktail Bay, patrols the beaches between Mabibi and Manzengwenya. Of these operators,

only the Rocktail Bay operator tags nesting females and collects data for the monitoring programme and relays the data to the EKZN Wildlife authorities. In addition to the drive-concessions, there is one turtle walk-concession at Kosi Bay/Bhanga Nek whereby local guides take small groups along the beach to watch turtles nesting. Since the programme's inception, a number of studies have been conducted on these nesting populations, including satellite tagging experiments (Hughes et al., 1998), and assessments of the state and size of these populations at various stages (Hughes et al., 1967, Hughes, 1970, 1972, 1974, 1974a, b, 1989, 1995, 1996).

This study is a joint-project that was undertaken by the University of Cape Town in conjunction with EKZN Wildlife. The main objective was two-fold: firstly to provide a comprehensive overview of the biological and behavioural data collected on the Maputaland loggerhead and leatherback nesting populations from 1965 until 2002/2003, and secondly to evaluate the effectiveness of the monitoring programme in terms of conservation and management. Prior to 1965 data were recorded, but these are currently not available on the database. Thus only data from 1965 onwards were analysed for the purposes of this study.

The biological and behavioural aspects included an assessment of:

- Population status and long-term trends
- Size distribution of nesting females, and long-term trends in size
- Preferences in timing of nesting within a season, nesting site selection and habitat type
- Seasonality of nesting activity and nesting area
- Relationship between environmental factors (sea surface temperature, ENSO events and to a lesser extent food availability) and the population trends, nesting activity, 'preferred' nesting areas and average size of nesting females.

The effectiveness of the monitoring programme was evaluated via a series of management-related questions:

- To date has the protection afforded by the programme and the conservation efforts been effective?
- Is the dataset consistent and useful for long-term comparisons among years?
- Is the sampling protocol detrimental to the nesting females in the light of the highly endangered status of marine turtles?
- Are the concession areas adequately sampled, or are they a cause for concern?
- Is there a potential to downscale the monitoring seasons (reduce costs and patrol effort) without loss of important data and information?

3. METHODS

The Maputaland monitoring programme encompasses a 56-km stretch of beach, from the Kosi Estuary mouth (26°53' 48.7"S, 32° 53' 12.7"E) to Mabibi (27° 19' 54.7"S: 32° 45' 03.9"E) in the Greater St. Lucia Wetland Park, northern KwaZulu-Natal on the northeast coast of South Africa (Figure 1). Within the study site, there are permanent numbered beacons located at either 400m or 1600m intervals, which serve as reference points for turtle nesting sites. These include beacons from 32N to 0N (north) and from 0S to 100S (south). From beacons 32N to 28S, the nesting counts were made at 400-m intervals, but south of beacon 28S, nesting counts were made at 1600-m intervals (or every fourth beacon). Therefore, to avoid confusion with regards to nesting counts, 1600-m areas were used as the units of study throughout the entire area and the data presented as the number of turtles nested per 4-beacon area, for example 32N–28N, 27N–24N etc.

The study site was divided into several patrol areas approximately 8-km in length, and beach patrols were undertaken every night during the nesting season (mid October to mid March of the following year) by EKZN Wildlife rangers, and more recently, community monitors. Each patrol area was covered twice on foot every night. In addition, frequent vehicle patrols were undertaken

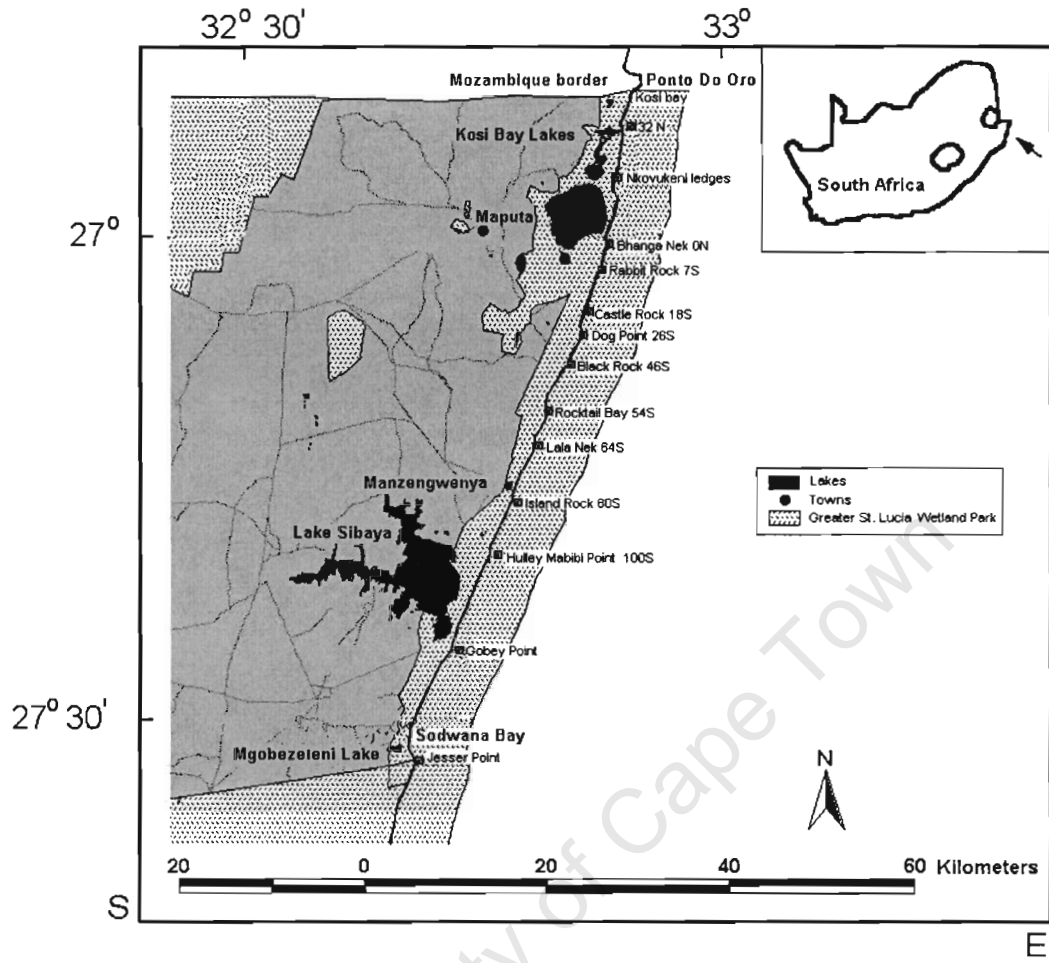


FIGURE 1: The Maputaland study site in northern KwaZulu-Natal on the northeast coast of South Africa (see arrow in inset picture). Included are several beacon numbers and site names.

that encompassed the entire study area in a single night. Once a turtle emerged and moved from the wet swash zone, the field rangers checked the animal for tags. The beach location, date and time of the emergence was recorded and various environmental factors (presence of clouds, lightening, thunder, rain and the wind strength and direction) were subjectively noted. Turtles were recorded as 'nested' when they were actively observed nesting or when a nest was located. In the latter case when a nest was found but the female had already returned to the sea, the species identity of the nested female was determined by assessing or 'reading' the tracks. Turtles were recorded as 'not nested' when they were seen to emerge but returned to the sea without nesting, or when tracks were present on the beach but no nest, or evidence of nesting, was found. There was no simple method of estimating whether individuals that were classed as 'not nested', but which had not been tagged, returned later in the season to nest.

If an animal was a neophyte (first-time or new nester), or had not been recorded in that specific season, it was checked for calluses or scars (as an indication of tag loss), identified to species level (*Caretta caretta* or *Dermochelys coriacea*), and the curved carapace length (CCL) and width (CCW) measured using giant callipers (accurate to $\pm 0.5\text{cm}$) for loggerhead females, and flexible measuring tape (accurate to $\pm 0.5\text{cm}$) for leatherback females. After the individual had nested, a numbered titanium tag was attached on the distal edge of the foreflipper of loggerhead females, or on the inside trailing edge of the hindflipper under the carapace in the case of leatherback females. Over the duration of the programme various tags have been used, namely plastic cattle tags from 1963 until 1969/70, then metal monel tags until the 1983/84 season, and from then until the present, titanium tags. When females that had been tagged in a previous season emerged to nest, the tag number and colour was noted, the emergence data recorded and the CCL and CCW measured. For those turtles that emerged and nested more than once during a single season, the tag number and colour, time, location and environmental factors were noted at each emergence, but the carapace length and width were not re-measured within that season.

Sites with 'elevated nesting' were defined as those with 50 or more loggerheads, or 10 or more leatherbacks, nesting within a 4-beacon site during a single season. The substrate composition of the nesting beacon sites (Figure 2) throughout the study area was determined by means of habitat mapping (from EKZN Wildlife ARCVIEW GIS database, unpublished data). This encompasses the entire coastline of the study from the subtidal zone to the forest dunes, in 100-m block-transects, and describes the substrate composition as high rock ledges, low rock ledges, scattered rocks, or sand.

Monthly mean sea surface temperatures (SST) off the KwaZulu-Natal coast (after Greenwood & Taunton-Clark, 1992) were compared with the average monthly nesting numbers of both species over the programme's duration. Mean sea surface temperature data were calculated using extracted SSTs from 5-day Meteosat images, using a processing method described by Demarcq & Citeau (1995). An area 31.98km wide by 36.06km long, offshore of Sodwana Bay (27.42°S to 27.527°S) was used in the current analysis (after Agenbag, unpublished data). Only SST data from 1987 to 2003 were used, as prior to this period no comprehensive Meteosat data were available. Average annual (April to March) and nesting-season (October to March) sea surface temperatures (1987 to 2002/03), taken from Meteosat images offshore Sodwana Bay (K. Agenbag, unpublished data), were compared with the seasonal nesting activity of the loggerheads and leatherbacks nesting on the Maputaland shores.

3.1 Data analysis

Several nesting variables and trends were examined, which included the population trends and nesting activity of both species over the duration of the programme, average curved carapace lengths (CCL) of nesting females, the timing of nesting and the nesting areas and habitat types of both species. Reasons for any changes observed in the above nesting variables (nesting activity, nesting area distribution and average size) were investigated, particularly with regards

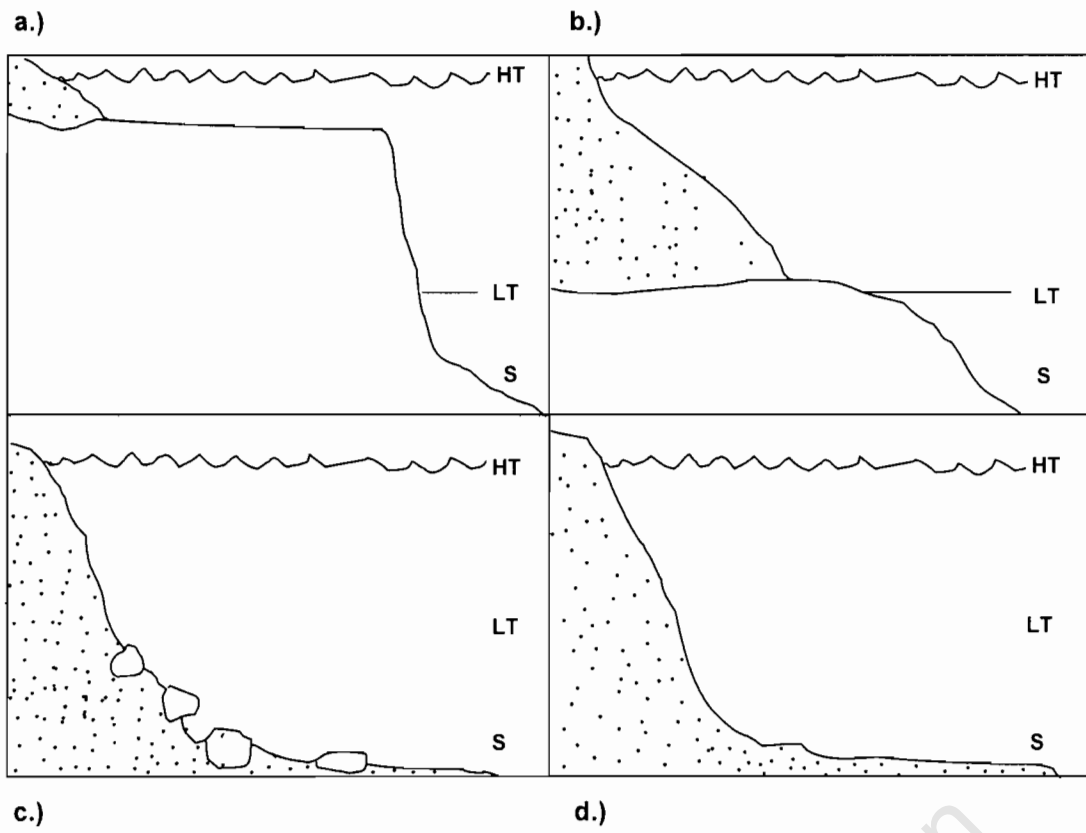


FIGURE 2: Illustration of the substrate composition types identified, namely (a) high rock ledges, (b) low rock ledges, (c) scattered rocks and (d) sand. Note HT refers to the high tide water mark, LT to the low tide water mark and S to the subtidal zone.

to:

- Sampling effort
- Seasonal variation (monthly and annually)
- Environmental factors (sea surface temperatures)
- ENSO events (regression analyses of annual Southern Oscillation Index (SOI) values and nesting number, length of the 'preferred' nesting area and average size, CCL).

Annual SOI values, which reflect changes in air pressure between Tahiti and Darwin, were used as indices of El Niño and La Niña events (after the Commonwealth Bureau of Meteorology, 2004). Lag periods of 0, 1 and 2 years following an El Niño event were used in the regression analyses, the lag period with the best correlation being chosen for presentation. For the purposes of the current analyses, only post-1979/80 CCL size data were used because of inaccuracies in the database and the availability of earlier size-measurement data. Lastly, tagging disturbance and its effects on the number of nesting females of both species was assessed using one-way Chi-square tests (Zar, 1984).

4. RESULTS

4.1 Biological and behavioural aspects

4.1.1 Population Trends

Over the programme's existence approximately 46893 loggerhead and 11509 leatherback females were recorded nesting on the Maputaland beaches. While the number of nesting turtles of both species has increased since the programme's inception (Figure 3a and b), there was no significant linear trend for either species over time (loggerhead: $y = 6.93x + 1142.6$; $r = + 0.209$, $p = 0.08$, $n = 37$; leatherback: $y = 3.01x + 256.7$; $r = + 0.224$, $p = 0.07$, $n = 37$) when considered over the entire period. An average of 1267 loggerhead females (S.D. = 359, $n = 37$) nested each breeding season, while 1097 females (S.D. = 360, $n = 37$) emerged, but failed to nest. In

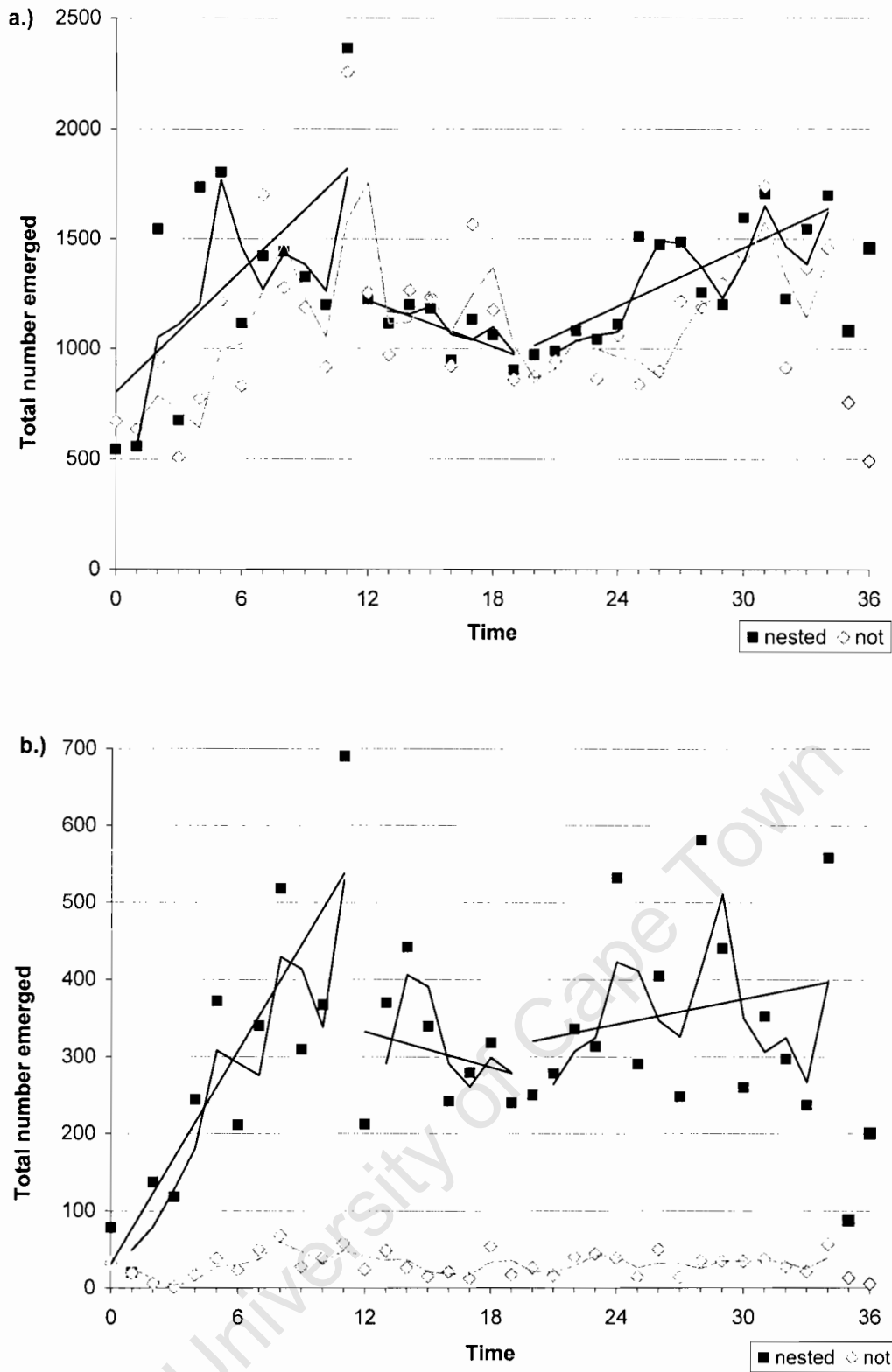


FIGURE 3: Total number of (a) loggerhead and (b) leatherback females emerging each season for the duration of the programme. Included on the graph are the number nested and not nested, their respective moving averages of 2 time periods and the regression lines of the three phases identified for the nested data. Time 0 refers to the 1965/66 season.

comparison, an average of 311 leatherback females (S.D. = 144, n = 37) nested each season, while 30 females (S.D. = 16, n = 37) emerged, but failed to nest. During this period, large interannual variations in the numbers of nesting females were apparent for both species.

In the history of the programme, the largest number of females of both species nested in the 1977/78 season (time 11), while the smallest numbers nesting were in 1965/66 (time 0) and 1966/67 (time 1) for the loggerheads and leatherbacks, respectively (Figures 3a and 3b).

A rapid increase in the number of nesting females was apparent from 1965/66 (time 0) to 1977/78 (time 11) (loggerheads: $y = 92.5x + 801.0$; $r = + 0.616$, $p = 0.01$, $n = 12$; leatherbacks: $y = 46.1x + 30.09$; $r = + 0.865$, $p = 0.005$, $n = 12$). This increase was significantly greater for the loggerhead population ($t = - 5.05$; d.f. = 20; $p = 0.01$).

Between 1978/79 (time 12) and 1985/86 (time 19) there was a decrease in the number of nesting females, although this relationship was only significant for the loggerhead population (loggerheads: $y = -34.94x + 1637.2$; $r = - 0.730$, $p = 0.025$, $n = 8$; leatherbacks: $y = -7.74x + 425.2$; $r = - 0.245$, $p = 0.13$, $n = 8$). From 1986/87 (time 20) to 2000/01 (time 34), there was an increase in the number of nesting females that was again only significant for the loggerhead population (loggerheads: $y = 44.36x + 127.4$; $r = + 0.765$, $p = 0.005$, $n = 15$; leatherbacks: $y = 5.47x + 210.7$; $r = + 0.208$, $p = 0.09$, $n = 15$).

Clearly a non-linear relationship existed between the total numbers of nesting females of both species over time, with three phases evident. The overall pattern was clear-cut increases in nesting numbers in the recovery phase (1965/66 to 1977/78), followed by oscillations. These phases (of significantly increasing or decreasing nesting numbers over several seasons) were more distinct for the loggerhead, whereas the leatherback displayed a greater amount of interannual variation (coefficient of variation, C.V. = 46.32%) than the loggerhead population

(C.V. = 28.32%).

4.1.2 Correlation between the nesting activities of both species

Although the interannual trends in nesting numbers (i.e. the three distinct phases) were far more pronounced for the loggerhead than the leatherbacks, and the interannual variation was far greater for the leatherback population, the total numbers of loggerhead and leatherback females nesting each year, were positively correlated with one another ($y = 1.376x + 839.5$; $r = + 0.552$; $p = 0.005$; $n = 37$). Thus distinct seasons of elevated or depressed nesting activity were synchronized for both species (Figure 4).

4.1.3 Sizes of nesting females

Sizes were only analysed subsequent to the 1979/80 season due to inaccuracies in the database and the availability of earlier size measurement data. From 1980 to 2003, Maputaland loggerhead females ranged between 52.0 and 116.0 cm curved carapace length (CCL), with a modal class between 82.0 and 87.0 cm for both the nested and the not-nested individuals (Figure 5a). In addition, a large number of females fell in the 87.0 to 92.0-cm CCL size class. The average CCL of nesting loggerhead females was 86.7 cm (S.D. = 6.56, $n = 3725$), with relatively few individuals falling outside the 72.0 – 102.0-cm size range.

Over the same period, the leatherback females displayed a far wider size range than the loggerhead population (Figure 5b), of between 83.5 and 207.5 cm, with a modal class of 155.0 to 160.0 cm for the nested females. The average curved carapace length of nesting leatherback females was 159.9 cm (S.D. = 128.36, $n = 1503$).

Very little overlap existed in the sizes of loggerheads and leatherbacks with the loggerhead females being considerably smaller than the leatherbacks. A gradual decline in the average CCL of loggerhead nesting females was evident over the decades (1980s: 87.2 ± 7.88 cm; 1990s:

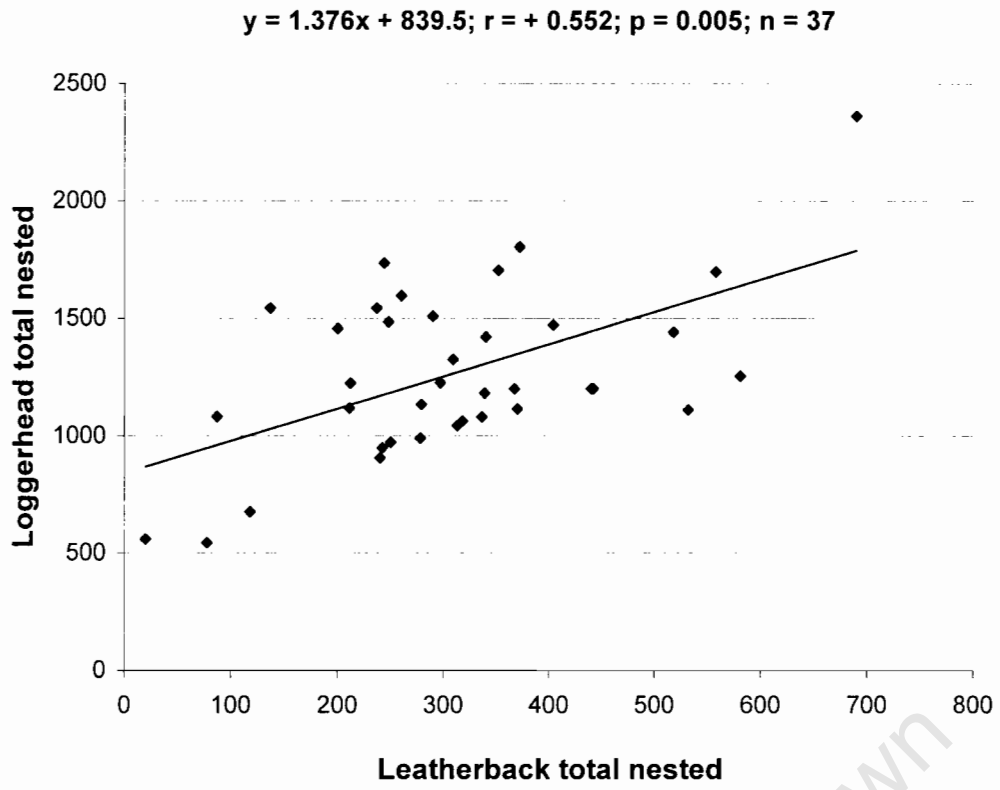


FIGURE 4: Regression of the total number of loggerhead and leatherback females nesting each breeding season. The solid line is a linear fit and the regression equation is included on the graph.

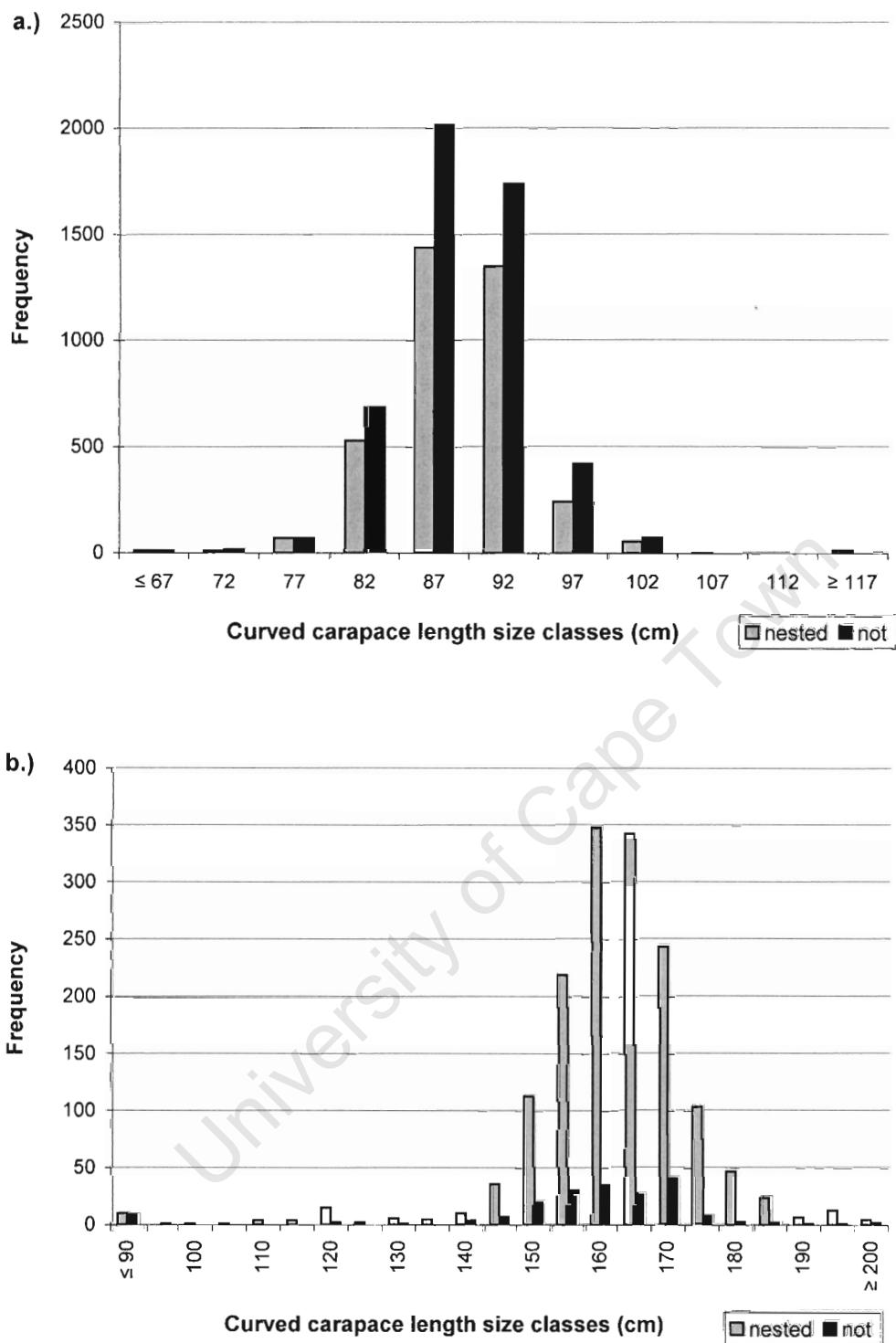


FIGURE 5: Size distribution of the curved carapace length (cm) of (a) loggerhead and (b) leatherback females that emerged on the Maputaland shores since the 1980/81 season. The light bars indicate nesting females while the darker bars indicate those that emerged but did not nest.

86.7 ± 5.90 cm; 2000s: 85.4 ± 4.79 cm), and the average size (CCL) of nesting loggerhead females decreased significantly from the 1980/81 season onwards ($r = -0.495$; $p = 0.01$; $n = 23$) (Figure 6a). However, there was no trend in the leatherback population (1980s: 160.1 ± 13.62 cm; 1990s: 159.4 ± 13.0 cm; 2000s: 160.2 ± 14.4 cm), with no significant change in the average size (CCL) since the 1980/81 season ($r = -0.207$; $p = 0.10$; $n = 23$) (Figure 6b).

4.1.4 Timing of nesting season

There were significant differences in the number of females nesting during various months within the nesting season, i.e. between October and March (loggerheads: $\chi^2 = 46188.7$, d.f. = 5, $p = 0.001$; leatherbacks: $\chi^2 = 10116.9$, d.f. = 5, $p = 0.001$). Both species thus displayed a clear penchant regarding the months in which they nested, with the majority nesting during November, December and January (Figures 7a and 7b). The average monthly sea surface temperature (SST) is lowest during August (19.95°C) and increases sharply to a maximum of 24.75°C in February. During the peak nesting months (November to January) the average monthly SSTs varied between 21.6°C and 24.0°C.

On average, December had the highest nesting activity for both species, whereas October, February and March were months with very low nesting activity. Although there was a large amount of variation around the mean number of females that nested at the start of the season in October (loggerheads: C.V. = 74.5%; leatherbacks: C.V. = 83.1%) and near the end of the season in February (loggerheads: C.V. = 77.1%; leatherbacks: C.V. = 81.9%), the average number of nesting females was far lower in these months than in November, December and January. Therefore, although minor interannual shifts in the start or end of the season may be possible, the peak nesting period fell consistently over November to January for both species.

4.1.5 Timing of nesting activity

The timing (month) and intensity of nesting activity (total number nested) are shown for both loggerhead and leatherbacks in Figures 8 and 9 respectively, together with the average annual

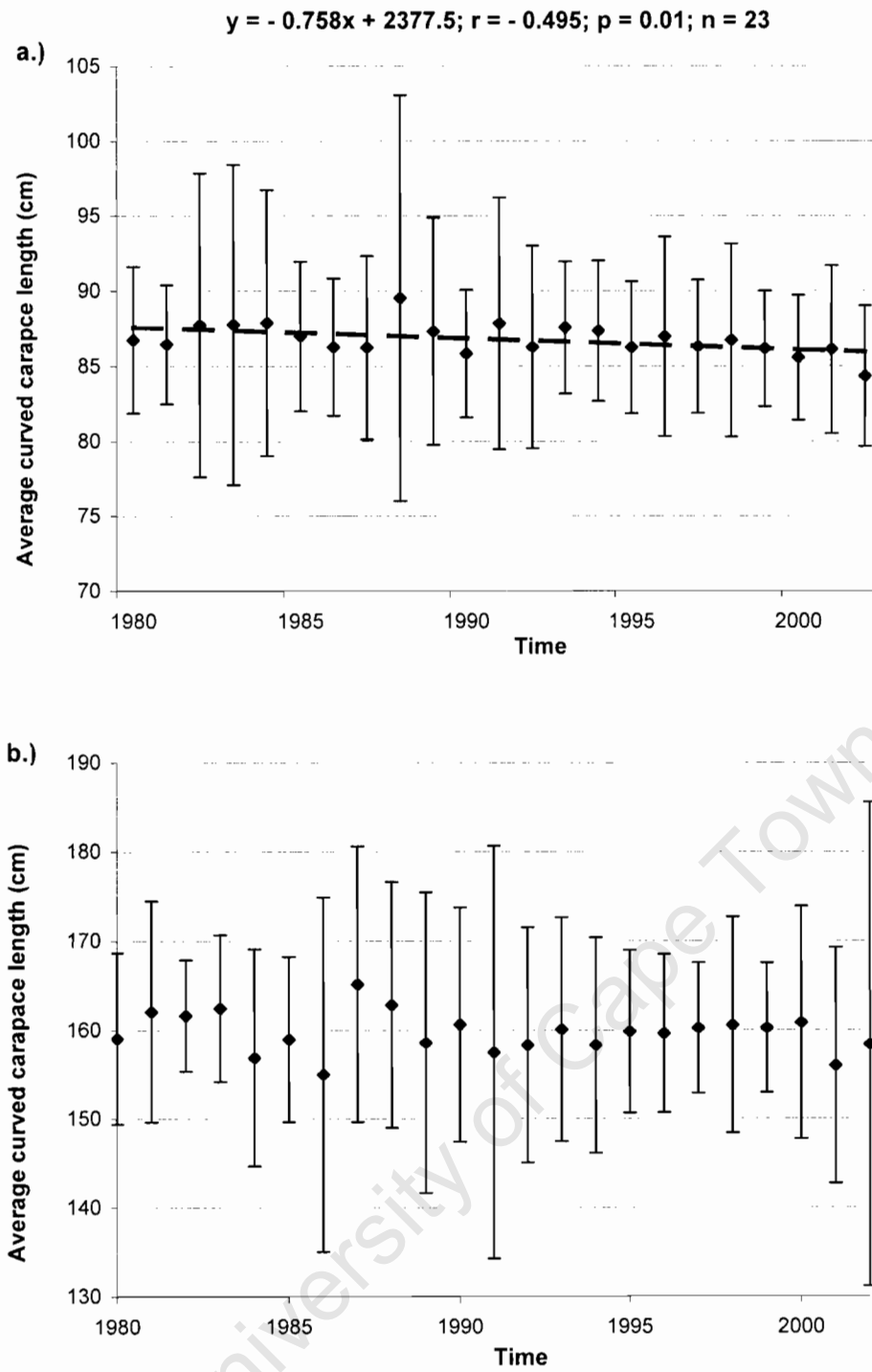


FIGURE 6: The average CCL (cm) \pm 1 S.D. of nesting (a) loggerhead and (b) leatherback females since the 1980/81 season. The dashed line is a linear fit for the loggerhead, and the regression equation is included on the graph.

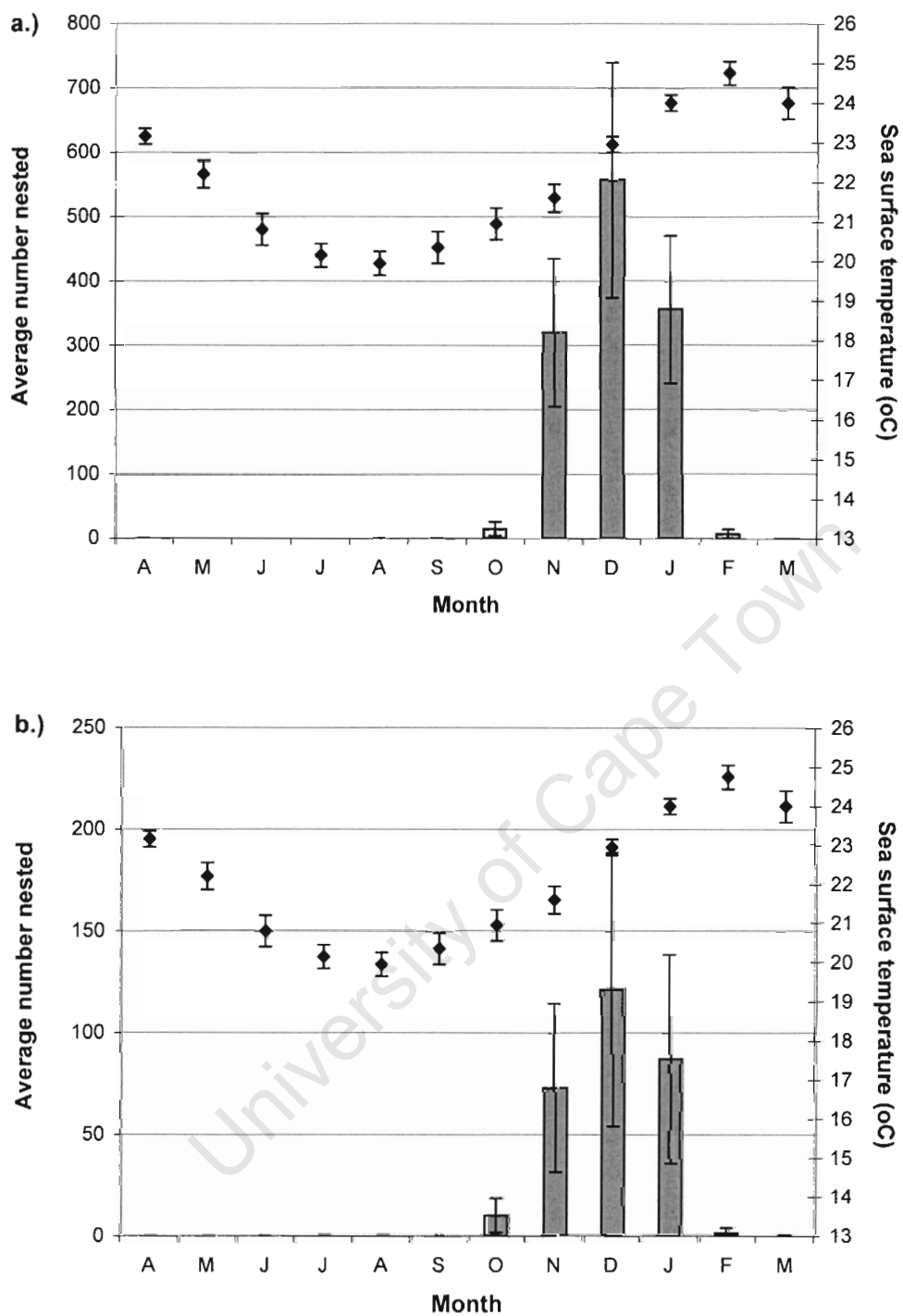


FIGURE 7: Bar graph of the average number of (a) loggerhead and (b) leatherback females nesting each month over the duration of the programme. Error bars indicate one standard deviation. Included on the graph are the average monthly sea surface temperatures ($^{\circ}\text{C}$) and the 95% confidence intervals (after Greenwood & Taunton-Clark, 1992).

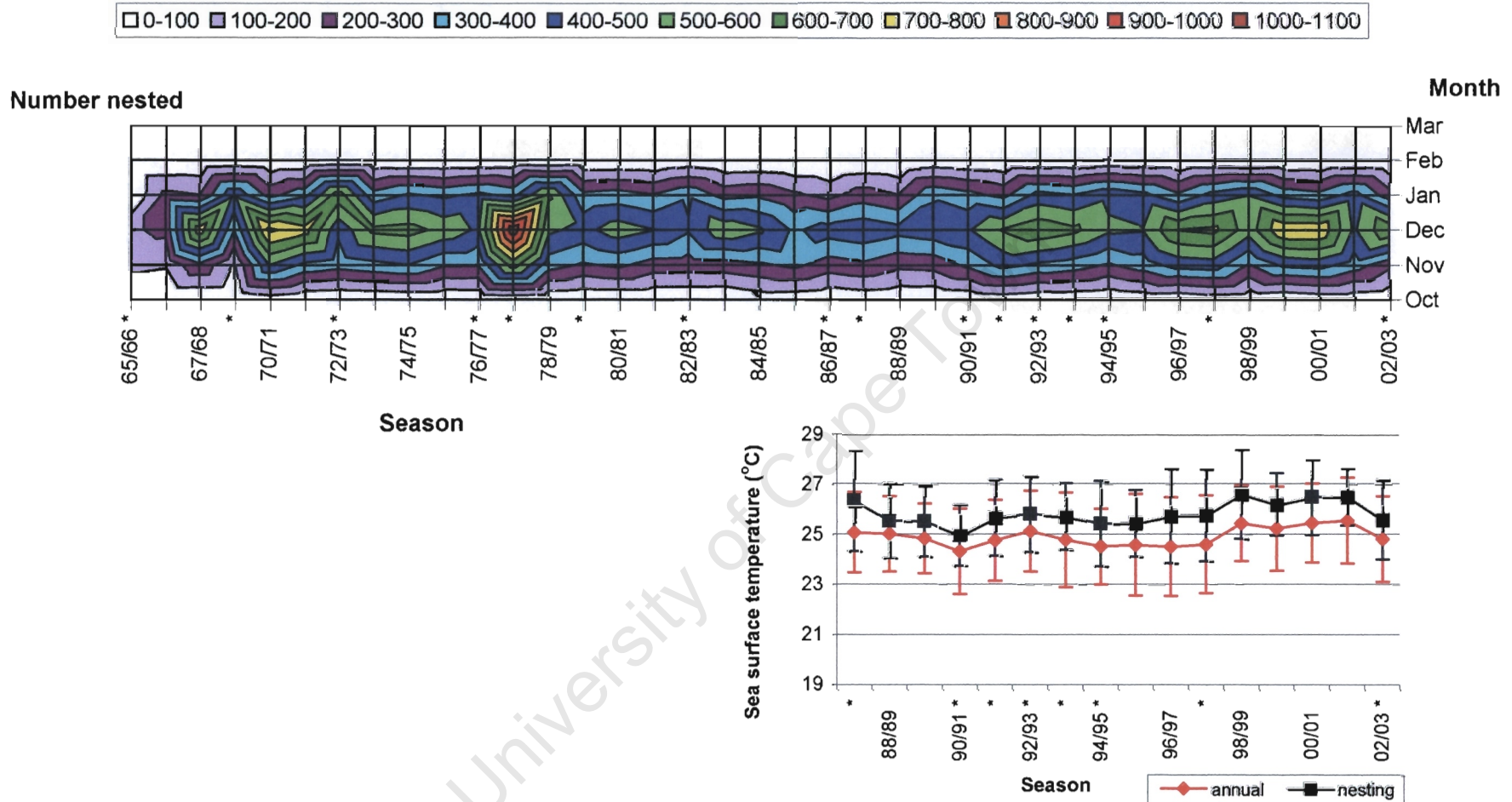


FIGURE 8: Three-dimensional surface plot of the total number of loggerhead females nested each month over the duration of the programme. Included on the graph are asterisks denoting El Niño events. The average annual (April to March) and nesting-season (October to March) sea surface temperatures (°C) (\pm one standard deviation) offshore Sodwana Bay are shown from 1987/88 to 2002/03.

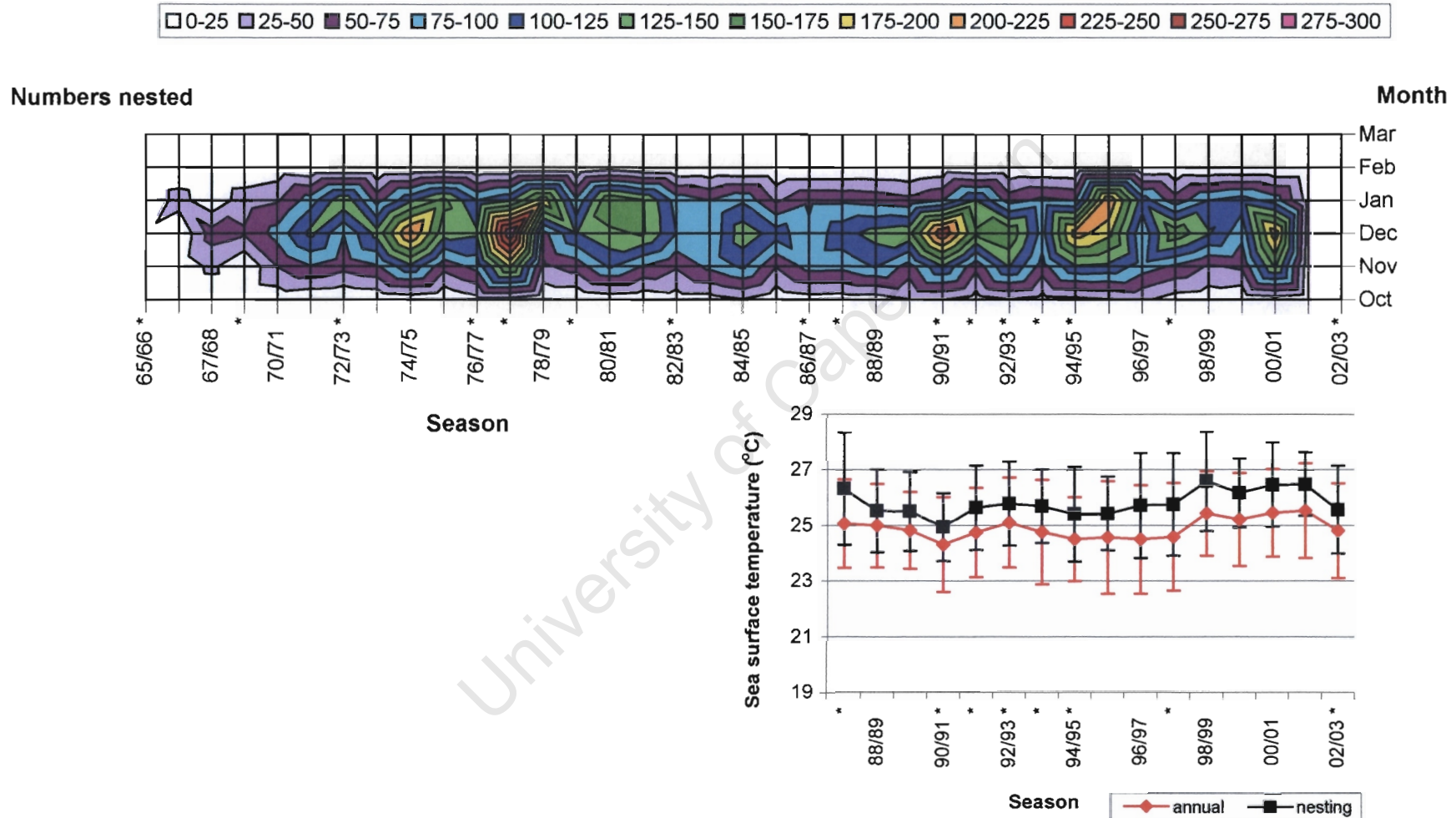


FIGURE 9: Three-dimensional surface plot of the total number of leatherback females nested each month over the duration of the programme. Included on the graph are asterisks denoting El Niño events. The average annual (April to March) and nesting-season (October to March) sea surface temperatures (°C) (\pm one standard deviation) offshore of Sodwana Bay are shown from 1987/88 to 2002/03.

(April to March) and nesting-season (October to March) sea surface temperatures (SSTs), from 1987/88 to 2002/03 (SST data are not available prior to this period). Certain patterns are apparent. In general, for those years when El Niño events were reported, the nesting activity period began marginally later than normal, i.e. during mid to late November and ceased significantly later than usual in late January. In short, the nesting period was relatively compressed, as depicted by the narrow waist-like features in Figures 8 and 9. However, following an El Niño year, with lag periods that varied between 0 – 2 years, distinct periods of high nesting activity were often evident for both species (Figure 10). This pattern was most obvious over the period 1965/66 to 1988/89.

Fairly high nesting activity was observed in both the loggerhead and leatherback populations during the 1970s and again in the 1990s. However, during the 1960s and 1980s relatively low levels of nesting activity were recorded for both species. During the 1990s and early 2000s, the majority of intense nesting seasons for both species coincided with El Niño years, including the 1992/93, 1994/95, 1997/98 and 2002/03 seasons, as well as 1991/92 for the loggerheads alone, and 1990/91 for the leatherbacks alone. The majority of these peak-nesting seasons were years when El Niño events occurred in successive years (Figure 10).

The mean annual SSTs off Sodwana Bay varied between 24.3°C to 25.5°C from 1987/88 to 2002/03 (Figures 8 and 9). No relationship was found between the loggerhead nesting activity (total number nested per season) and the average annual ($y = -26.7x + 2005.5$; $r = -0.04$; $p > 0.10$; $n = 15$) or nesting-season SSTs ($y = 61.7x - 252.2$; $r = +0.118$; $p > 0.10$; $n = 15$), whereas a weak negative relationship existed in the case of the leatherback and the average annual SSTs ($y = -130x + 3575.7$; $r = -0.36$; $p = 0.07$; $n = 15$) or average nesting-season SSTs ($y = -112.3x + 3238.1$; $r = -0.387$; $p = 0.06$; $n = 15$).

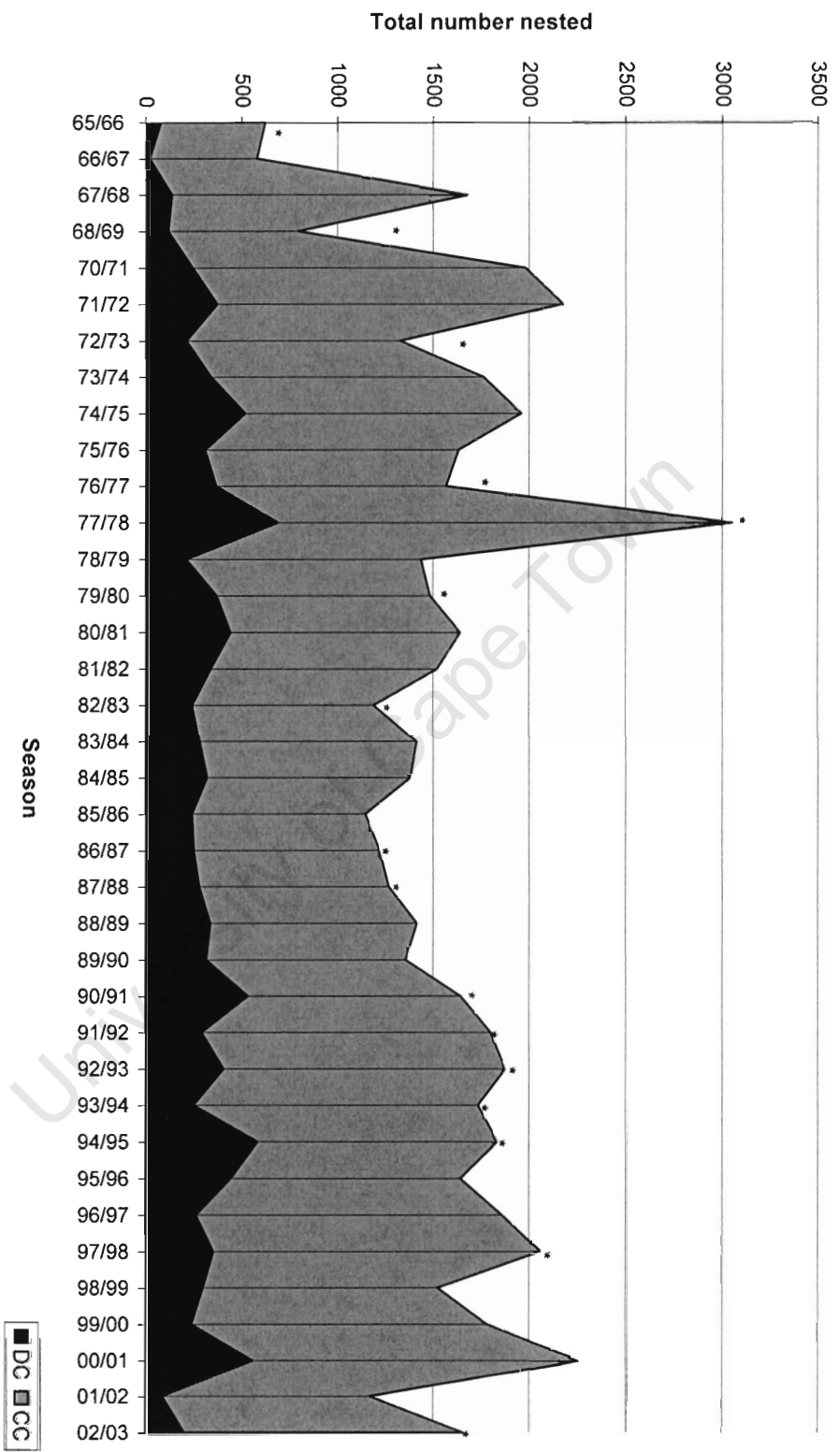


FIGURE 10: Area plot of the total number of loggerhead (CC) and leatherback (DC) turtles nested over the programme's duration. The asterisks denote El Niño events.

4.1.6 Location of nesting sites

The distribution of nesting activity (total number nested) is shown in Figures 11 and 12 respectively for loggerheads and leatherbacks. Between 1965/66 and 1972/73, the nesting activity of both species appeared to be concentrated in a narrow area covering 17.6 km of coastline, between beacons 12N–9N and 30S–27S. This was, however, an artefact of the sampling method employed during this time, whereby only this area was intensively surveyed. From 1972/73 onwards, the entire study area was sampled with equal intensity and thus for the purposes of the current analysis, the period prior to this was omitted from further analyses.

With respect to the loggerhead population, sites that displayed 'elevated nesting' for 75% or more of the seasons analysed, were classified as 'preferred' nesting sites. Two clearly defined and consistent areas of elevated loggerhead nesting activity existed in the northern region of the study site, namely a 3.2-km stretch from 11S–14S to 15S–18S, and an 8.0-km stretch from 20N–17N to 4N–1N. Nesting activity south of the 23S–26S beacons was minimal (Figure 11).

Five leatherback 'preferred' nesting sites existed, namely two less consistent 1.6-km stretches, 4N–1N and 11S–14S, and three consistent stretches that included a 4.8-km area from 39S–50S; a 3.2-km area from 71S–78S; and a 4.8-km area from 83S–94S. The leatherbacks had a far more extensive 'preferred' nesting distribution than the loggerheads, and nesting activity was generally higher, and more consistent, south of the 31S–34S beacons. Much less leatherback nesting activity was recorded in the northern region of the study site, between 16N–32N (Figure 12).

Numbers nested

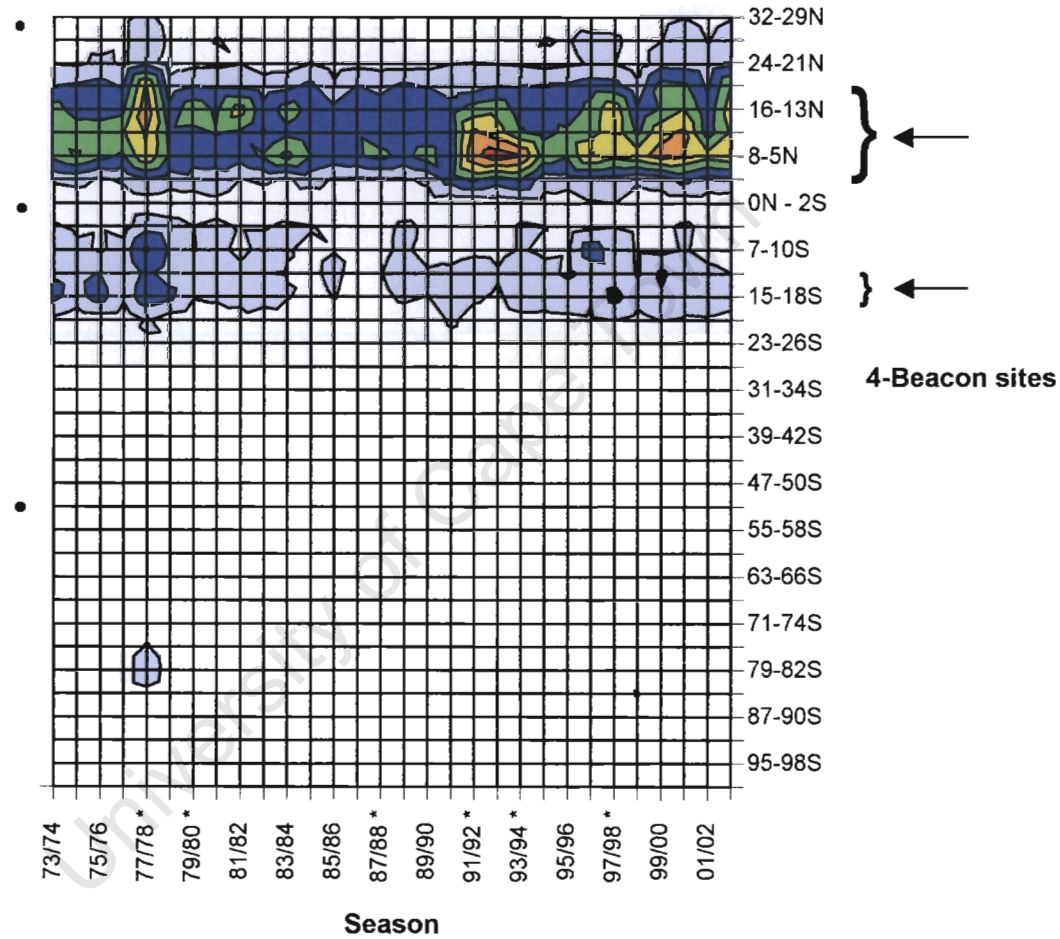


FIGURE 11: Three-dimensional surface plot of the total number of loggerhead females nesting each season within the study site. Note that the study site is subdivided into 1600-m (or 4-beacon) areas. The asterisks at the bottom denote El Niño events, arrows on the right indicate 'preferred' nesting areas (> 50 nesting females) and black dots on the left show areas of human activity.

Numbers nested

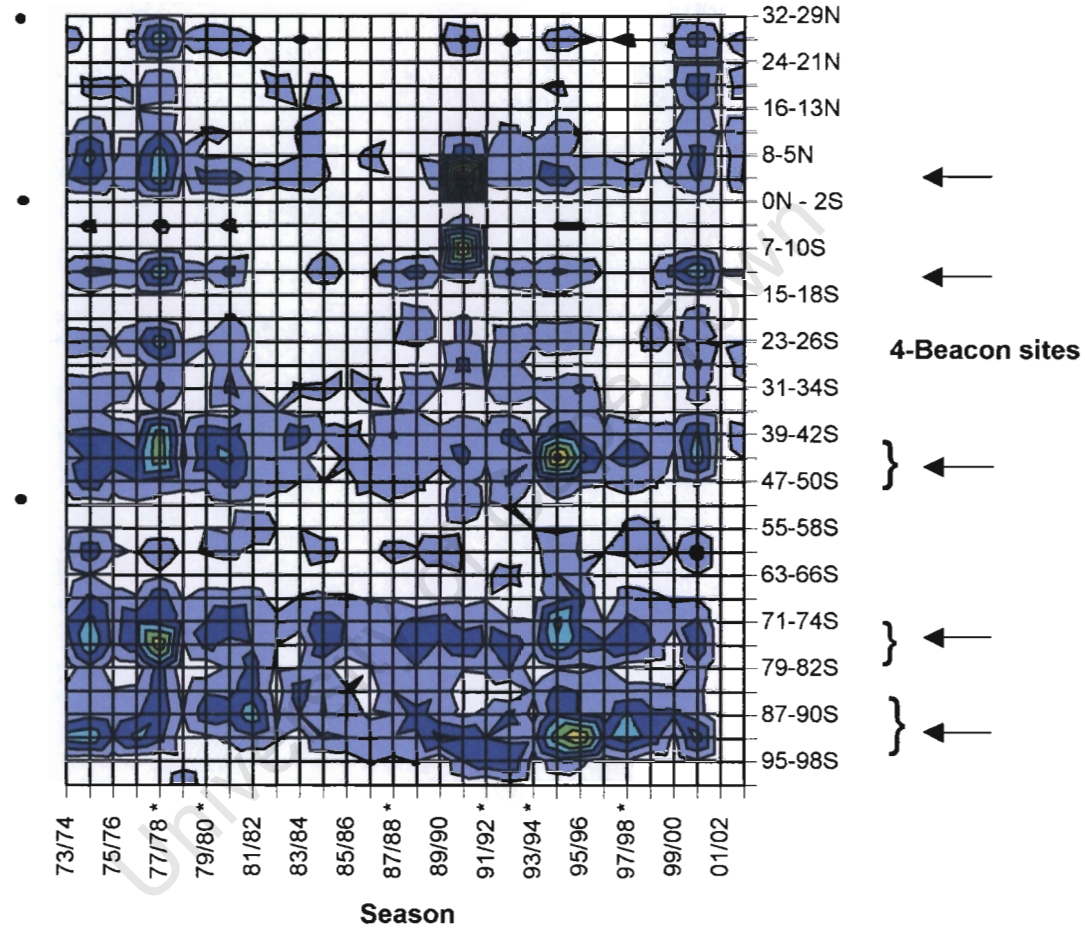


FIGURE 12: Three-dimensional surface plot of the total number of leatherback females nesting each season within the study site. Note that the study site is subdivided into 1600-m (or 4-beacon) areas. The asterisks on the bottom denote El Niño events, arrows on the right indicate 'preferred' nesting areas (> 10 nesting females) and black dots on the left show areas of human activity.

4.1.7 'Preferred' habitat type

In general, the loggerhead 'preferred' nesting areas included a higher concentration of scattered rocks and high and low rock ledges than that of the 'preferred' leatherback sites (Figure 13). Most of the 'preferred' leatherback nesting areas had subtidal and low shore zones that were primarily sandy (i.e. clear of any obstructions). There were a few 'preferred' areas where isolated ledges and rocks were present in the low shore, but these were generally instances where one of the beacons within the 4-beacon site area was in close proximity to a rocky point and/or reef, for example Bhangha Nek (0N) and Miempie's Reef (83S–86S). In most cases, nesting areas that were little used by loggerheads were either 'preferred' leatherback nesting sites, or in close proximity to 'preferred' leatherback sites. Conversely, low-frequency leatherback-areas were 'preferred' loggerhead nesting areas.

4.1.8 Changes in nesting area

No long-term shifts were evident in the loggerhead and leatherback nesting distribution from the 1973/74 season onwards. In general, the northern region was more important for loggerheads, while the southern region proved to be more important for leatherbacks.

Although the nesting distribution of the two species was markedly different, a number of similarities existed with regards to seasonal changes in the length of the total 'preferred' nesting areas. For both loggerheads and leatherbacks, 'preferred' areas were maintained consistently throughout the programme, irrespective of whether or not there was elevated nesting activity. However, the length of the total 'preferred' nesting areas of both species appeared to increase considerably during peak nesting seasons, with several areas being utilized during those peak nesting activity periods only (Figures 11 and 12).

For both species, the length of the 'preferred' nesting area and the total number of nesting females displayed similar trends over the duration of the programme (Figures 14a and 14b) and

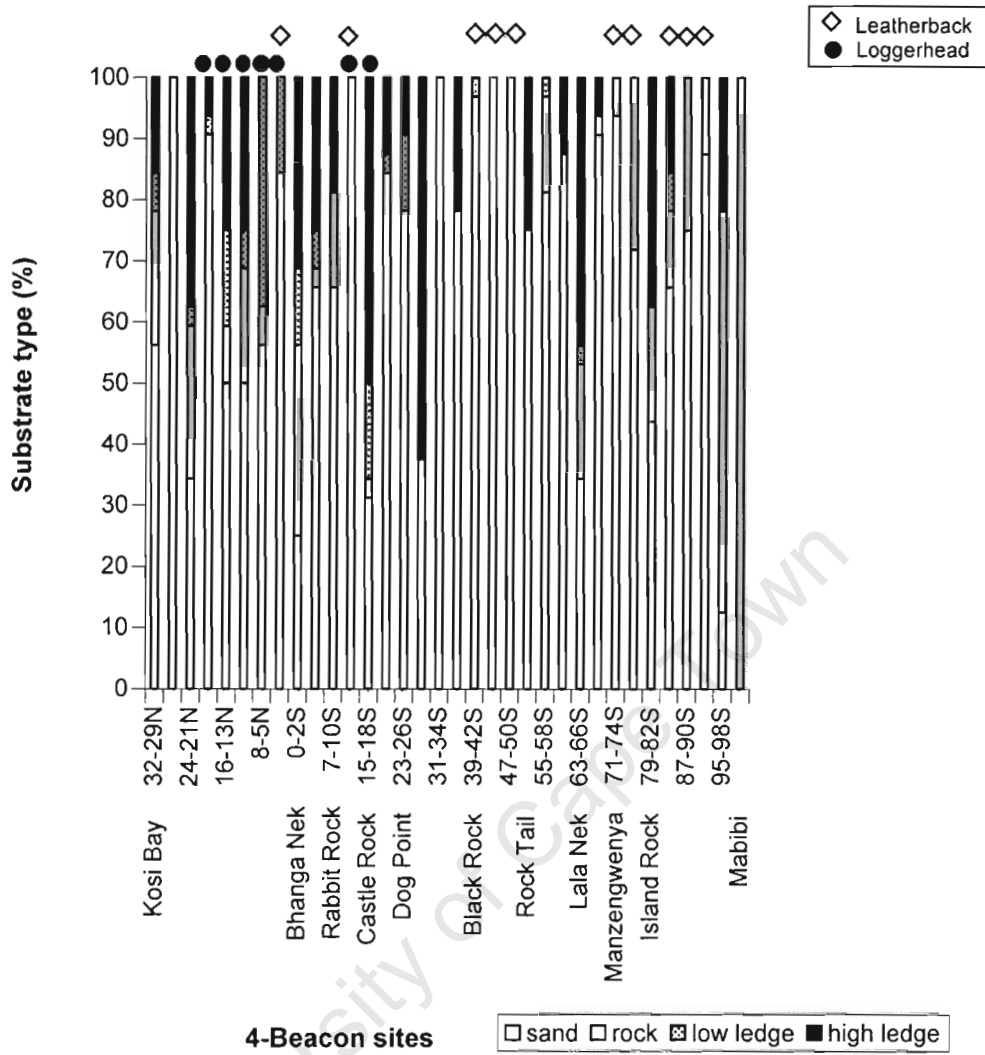


FIGURE 13: Substrate composition of the subtidal and low shore zone of the 4-beacon sites within the study site adapted from the EKZN Wildlife ARCVIEW data. Loggerhead and leatherback refer to the 'preferred' nesting sites of both species.

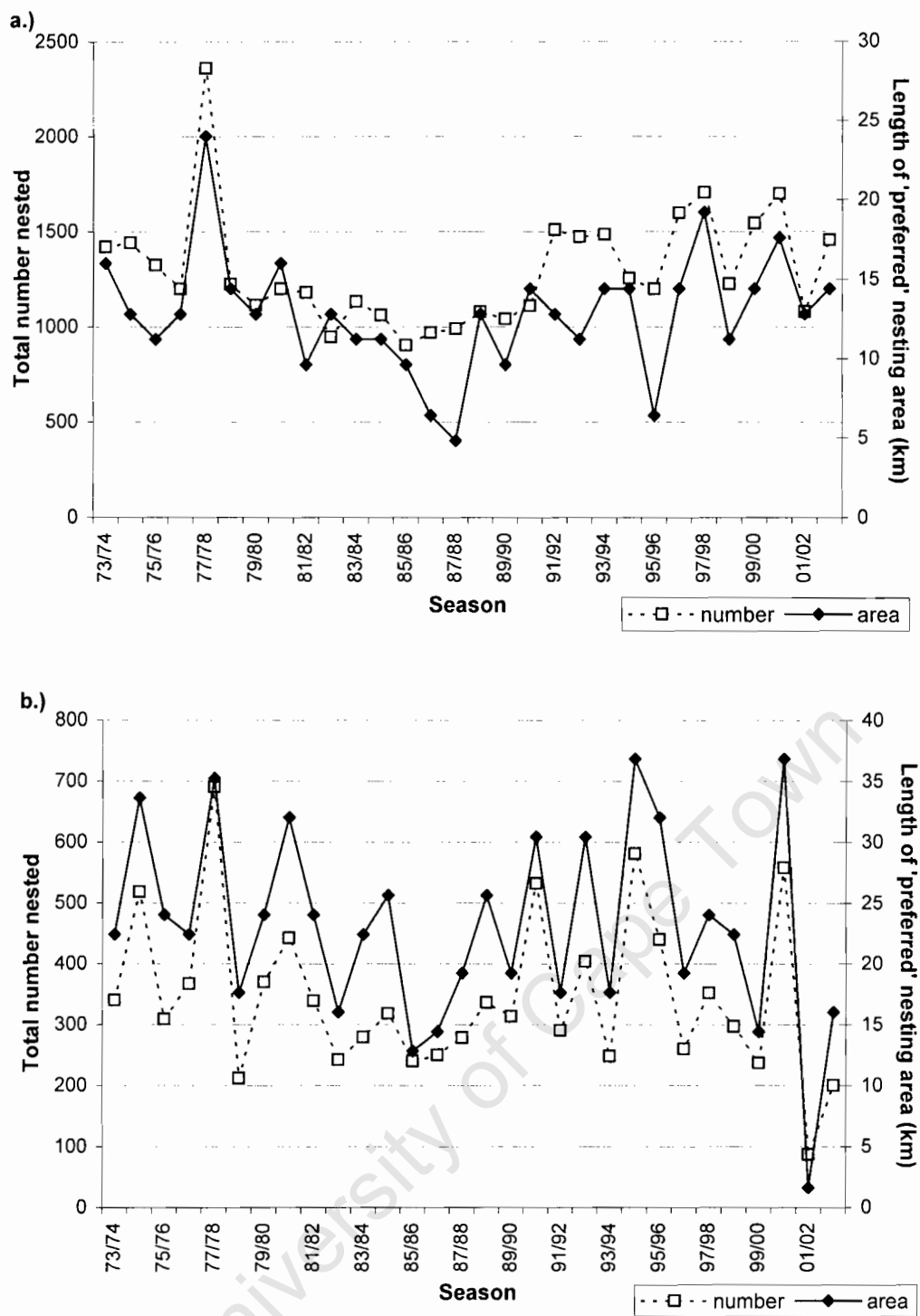


FIGURE 14: Relationship between the total number of nesting (a) loggerhead and (b) leatherback females and the length of the 'preferred' nesting area (km) since the 1973/74 season. The 'preferred' nesting area included those areas where more than 50 loggerheads or more than 10 leatherbacks nested during a single season.

there was a strong positive correlation between the two, for both loggerheads ($r = + 0.77$; $p < 0.005$; $n = 30$) and leatherbacks ($r = + 0.93$; $p < 0.005$; $n = 30$) (Figures 15a and 15b, respectively). Although the start and end of the nesting period was scarcely influenced by elevated nesting activity, the length of the 'preferred' nesting area increased significantly to incorporate the larger number of nesters. Thus a spatial and not temporal shift was evident.

4.1.9 El Niño Southern Oscillation (ENSO) regressions

There appeared to be a relationship between nesting activity and El Niño events (Figures 8, 9 and 10). But even taking into account various lag periods of between 0 to 2 years, no correlations were found between the annual Southern Oscillation Index (SOI) values and the total number of loggerhead and leatherback females nesting over time (loggerhead - lag 2: $r = + 0.134$; $p = 0.10$; $n = 34$; leatherbacks - lag 2: $r = + 0.165$; $p = 0.10$; $n = 34$).

It was hypothesized that a relationship existed between the increase in the length of the 'preferred' nesting area and El Niño events, as seen by the widening in the 'preferred' nesting area following an event of this nature (Figures 11 and 12). However, again no significant correlations with the SOI values were found, (loggerhead – lag 2: $r = + 0.167$; $p = 0.13$; $n = 29$; leatherbacks – lag 2: $r = - 0.001$; $p > 0.13$; $n = 29$).

Taking into account various lag periods, strong negative correlations were found between the annual Southern Oscillation Index (SOI) values and the average CCL (cm) of nesting loggerhead and leatherback females (Figures 16a and 16b) since the 1980/81 season (loggerhead - lag 2: $r = - 0.561$; $p < 0.005$; $n = 21$; leatherbacks – lag 1: $r = - 0.325$; $p = 0.06$; $n = 22$). Of interest is the fact that the lag period yielding the greatest correlation for loggerhead females was 2 years, while that for leatherbacks was only 1 year following an El Niño event.

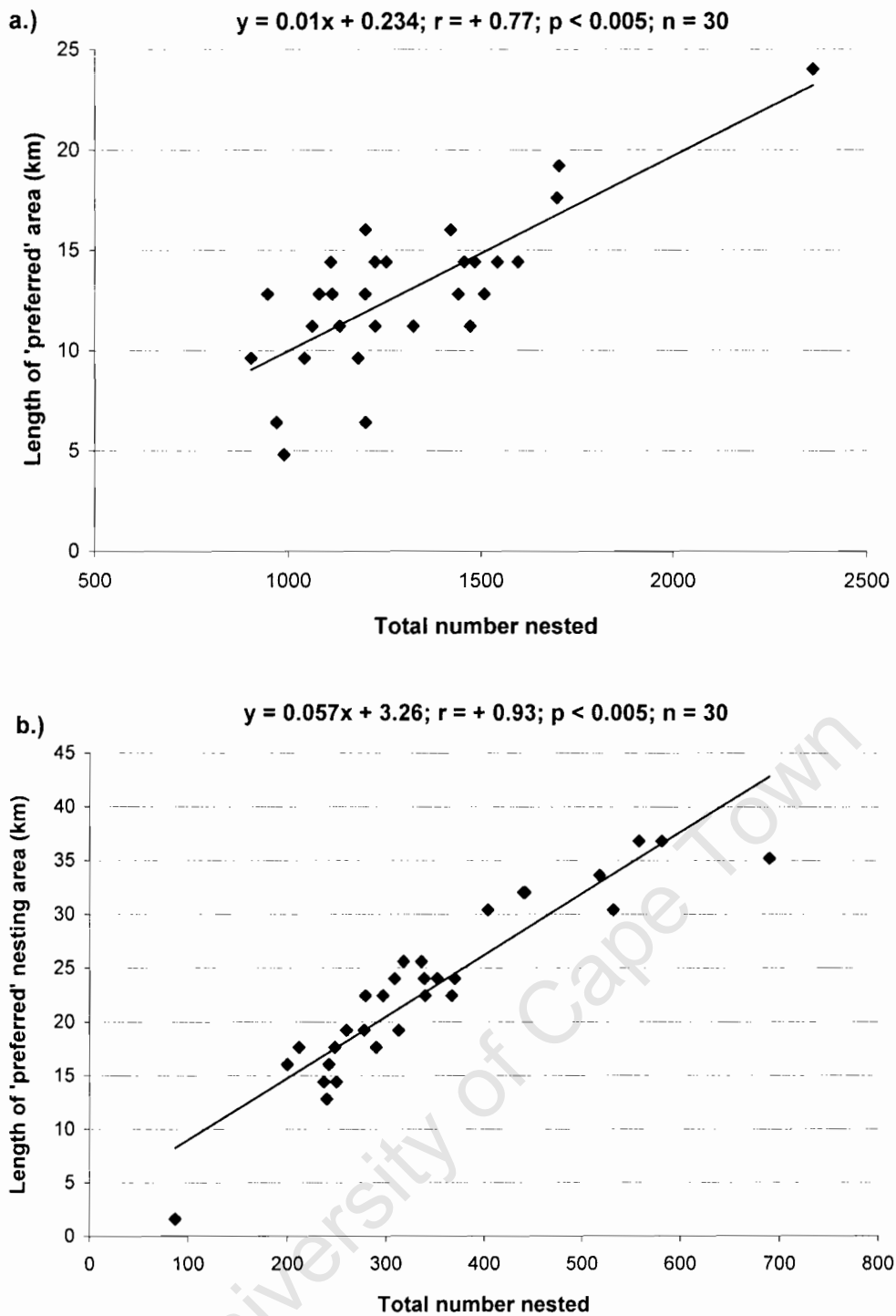


FIGURE 15: Relationship between the total number of (a) loggerhead and (b) leatherback females that nested during a season and the respective length of the 'preferred' nesting area (km). The nesting area included those areas where more than 50 loggerheads, or more than 10 leatherbacks nested during a single season. The regression equations of the linear trend lines are included on the graphs.

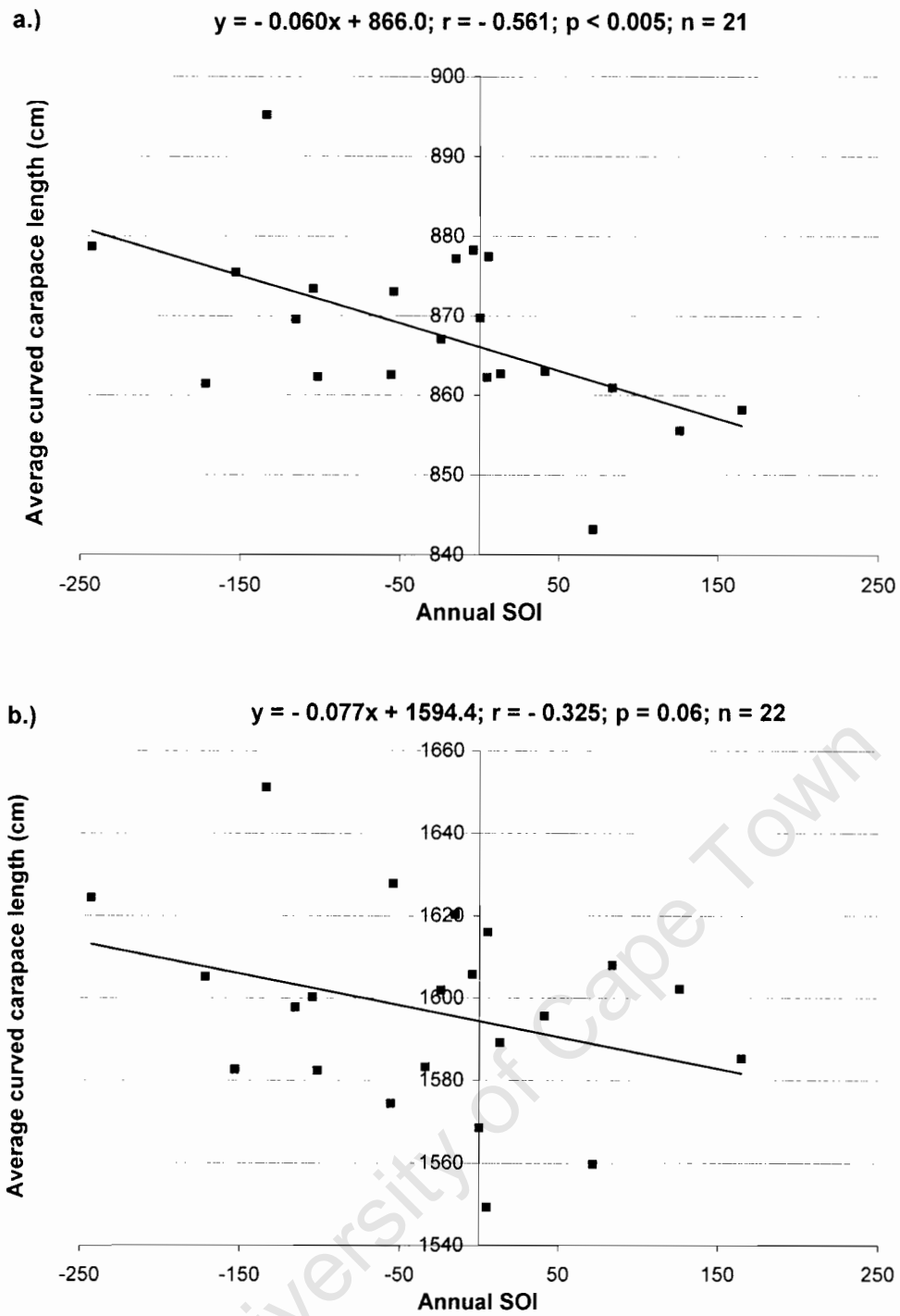


FIGURE 16: The relationship between the annual Southern Oscillation Index (SOI) values and the average (a) loggerhead and (b) leatherback curved carapace length (cm) since the 1980/81 season, based on a two-year lag period for the loggerheads and a one-year lag period for the leatherbacks. The regression equations of the linear trend lines are included on the graph.

4.2 Conservation and management

4.2.1 Human disturbance and its effect on nesting

During sampling, there were two distinct situations: a presumably high-disturbance situation where turtles were observed and actively tagged, and a low-disturbance situation where there was minimal, if any, human interaction with the turtles (for example, evidence of nesting was found, but the turtle was not seen and thus no interaction occurred).

Of the emerging loggerhead females, for both the high-disturbance (50.1% nest; 49.9% not) and low-disturbance situations (55.8% nest; 44.2% not) approximately half of the emerging females nested (Figure 3a). Conversely for emerging leatherback females, whether in the high-disturbance (88.2% nest; 11.8% not) or low-disturbance situations (93.4% nest; 6.7% not), a very high proportion of individuals nested (Figure 3b). However for both species, it appears that a significantly greater proportion of individuals failed to nest in the high-disturbance situation (loggerhead: $\chi^2 = 111.92$; d.f. = 1; $p < 0.005$; leatherback: $\chi^2 = 29.26$; d.f. = 1; $p < 0.005$).

In addition, there were three sites where very little nesting activity was recorded for either species, namely 32N–29N, 51S–54S and 0N–2S (Figures 11 and 12). The first two sites include tourist lodges (Kozi Lodge and Rocktail Bay Lodge) and the last includes a boat-launch site (Bhanga Nek). Consequently, all have regular human activity associated with them.

5. DISCUSSION

5.1 Biological and behavioural aspects

5.1.1 Population trends

Both loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) populations have shown huge global declines in recent years, with more than an 80% decline recorded in the global leatherback population over the past three generations or ten years (IUCN Species

Survival Committee, 2003). This has consequently led to the leatherback being defined as “critically endangered” and the loggerhead as “endangered” (IUCN Species Survival Committee, 2003).

Between 1985 and 1998, the southern Great Barrier Reef loggerhead nesting population exhibited an 8% p.a. decline (Chaloupka & Limpus, 2001), while for the central Caribbean coast of Colombia; the decline was 96–97% (Amorocho, 2003). Thailand’s loggerhead nesting population appears to have been completely destroyed (Settle, 1995). Catastrophic leatherback declines were reported from Terengganu, Malaysia with an approximately 99% decline between the 1950s and the 1990s (Chan & Liew, 1996), while the Mexiquillo population declined at an estimated 23% p.a. between 1986 and 1994 (Sarti et al., 1996). From the early 1960s, conservation measures were applied in Maputaland: prohibitions on egg collection and the harvesting of adults, coupled with beach patrols and law enforcement efforts associated with the monitoring programme (Hughes, 1989). These measures appear to have paid dividend because, in contrast to trends in most other turtle populations, the Maputaland loggerhead and leatherback populations actually increased markedly over the initial phase from 1965/66 to 1976/77, and have remained more-or-less stable or have oscillated slightly since then, and appear to be fairly healthy.

Of interest is the fact that the loggerhead population appeared to recover or respond far quicker to the conservation measures taken than the leatherback population, as evidenced by the significantly steeper increase in the loggerhead population at the start of the programme, between 1965/66 and 1977/78.

With regards to the three clear phases displayed by the loggerhead population, and to a lesser extent the leatherback population (Figures 3a and 3b), a number of turtle populations in different countries have also displayed marked increases and declines over time. Declines were reported

for the southern Great Barrier Reef loggerhead nesting population between 1985 and 1998 (Chaloupka & Limpus, 2001), and for the leatherback population in Mexiquillo between 1986 and 1994 (Sarti et al., 1996). However, green turtles (*Chelonia mydas*) in Tortuguero, Costa Rica, reportedly increased from the early 1970s to the mid 1980s, then decreased slightly during the late 1980s, and once again increased in the 1990s (Bjorndal et al., 1999). It is remarkable that both the loggerhead and leatherback populations in Maputaland displayed trends that were fairly similar to those of the green turtles of Costa Rica. In addition to this, the increase in the Maputaland loggerhead (and perhaps also leatherback) numbers between 1986/87 (time 20) and 1997/98 (time 31) (Figures 3a and 3b) appear to correspond with increases in green turtle populations in the Sabah and Baguan Island Marine Turtle Sanctuary in Southeast Asia, over this same period (Chaloupka, 2001).

In most cases, assessing the conservation status and population trends of turtles is complicated by the fact that numerous interacting factors can influence turtle nesting populations (Limpus, 1995, Hayward, 1997, Hays, 2000, Broderick et al., 2001), for example human harvesting (Spotila et al., 1996, Hayward, 1997), incidental by-catch in commercial fisheries (Settle, 1995), coastal pollution and development (Chan & Liew, 1996, Steyermark et al., 1996, Amorocho, 2003), both marine and terrestrial predation (Hughes, 1989, Burger & Garber, 1995) and stochastic environmental factors, namely the El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO), with associated changes in sea surface temperature and food availability (Sarti et al., 1996, Davenport, 1997, Hays, 2000, Broderick et al., 2001, Chaloupka, 2001).

5.1.2 Correlation between the nesting activities of both species

There were distinct years of elevated or depressed nesting activity evident, in which the two species were synchronized (Figure 4). There are two possible reasons for this. First, both species increased in numbers during the early phases of monitoring (1965/66 to 1976/77)

subsequent to the implementation of conservation measures. And second, throughout the monitoring period, the interannual fluctuations observed might have reflected environmental factors that had similar effects on both species (for example, food availability, sea surface temperatures or other ENSO-related factors). It is unlikely that the synchronized fluctuations are an artefact of sampling effort, because the most intensive sampling period occurred during the first 10 years of the programme, yet the numbers of nesting females recorded over this period were consistently lower than those recorded during the years that followed. Although the reasons for the trends are unclear, it seems more probable that these distinct elevated and depressed nesting activity seasons are related to environmental factors rather than being an artefact of sampling effort.

5.1.3 Sizes of nesting females

The minimum (52.0 cm) and maximum (116.0 cm) loggerhead curved carapace lengths (CCL) in Maputaland were far greater than the range of 75.0 – 107.0 cm reported by Hughes (1974). Very few 'extreme-sized' animals were recorded. The average CCL of 86.7 cm found in the current analysis was similar to the 86.4 cm documented by Hughes (1974b). However, the modal class of 82.0 – 87.0 cm was less than that previously reported by Hughes (1974), namely 92.0 - 97.0 cm, a fact reinforced by the significant decrease observed in the average CCL since the 1980/81 season (Figure 6a).

In comparison, the Zakynthos loggerhead population in Greece had a far smaller average CCL of 80.4 ± 6.2 cm (Margaritoulis, 1982), whereas Hughes (1974a) found that the loggerheads in Japan and especially North America were significantly larger than those in Maputaland. Hughes (1974a) concluded that the smaller sizes of the Maputaland females must have occurred during the juvenile and sub-adult stages and could either be the result of:

- Longer migration periods for Atlantic neophytes (which could allow for greater growth and consequently larger females), or

- Non-ideal feeding and environmental conditions in the Agulhas gyres and southwest Indian Ocean as opposed to those of Atlantic loggerheads.

Further support for the feeding-condition viewpoint is the fact that sub-adult oceanic-stage loggerheads in the North Atlantic have been found to display compensatory growth (Bjorndal et al., 2003). Bjorndal et al. (2003) described this concept as the opportunistic responses in both plants and animals to highly unpredictable and variable environments (especially with regards to food and temperature), whereby highly elevated growth rates are exhibited during favourable conditions. Negative aspects of the compensatory growth strategy can include reduced survival, lower reproductive success and smaller body size (Bjorndal et al., 2003). Thus it is possible that Maputaland loggerheads employ this strategy during early stages in their life histories.

As previously mentioned, juvenile and hatchling Maputaland loggerheads and leatherbacks spend several years in the Agulhas Current and gyres before they reach sexual maturity and undergo reproductive migration to the nesting beaches (Hughes, 1974b). This environment is highly variable particularly with regards to temperature e.g. reaching 14°C at times (Hughes, 1974b). In addition, the feeding conditions in the Agulhas gyres are thought to be less favourable than in the Atlantic (Hughes, 1974a), thus Maputaland individuals may not remain in favourable conditions as long as the Atlantic loggerheads, which could provide an possible explanation for their comparatively small body sizes.

A decline in the average CCL of Maputaland loggerheads was observed during the early 1970s (Hughes, 1974a), and was again recorded in the present analysis, with a downward shift in the modal class and a decrease in the average CCL since the 1980/81 season (Figure 6a). Turtles are known to return to their natal beaches (Hughes, 1989, Davenport, 1997), thus the decrease in size (CCL) observed over time, could be an indication that recruitment has increased over time and that more mature recruits are returning to the natal beaches to nest.

Conversely, the decrease in average CCL of nesting loggerheads since the 1980/81 season could be an indication that adverse circumstances, for example illegal harvesting and incidental by-catch in trawl and gill nets, have resulted in a decrease in the average size of individuals that nest. However, further work is required on hatchling and remigration rates, to ascertain whether these size shifts and reductions are due to the recruitment of greater numbers of smaller neophytes into the nesting population, or a loss of returning larger and older females.

With respect to the leatherback nesting population, the CCL size range of between 83.5 and 207.5cm has widened substantially from the range of 133.5 – 177.5 cm reported by Hughes (1974a). Boulon Jr. et al. (1996) found a CCL size range of between 131.0 and 177.4cm for the populations at St. Croix, U.S. Virgin Islands. Hughes (1996) reported an average CCL of 159.6cm in the 1994/95 season at Maputaland, a value very close to the current nesting average of 159.9cm. He also reported a decrease in the average CCL of leatherbacks between the 1964/65 and 1994/95 seasons. However, we could not detect any significant changes in the average CCL over time since the 1980/81 season (Figure 6b). The widening of the CCL size range of nesting leatherbacks to include smaller individuals could reflect the entry of new recruits into the nesting population. If so, this was insufficient to result in an overall, significant reduction in the average CCL.

5.1.4 Timing of nesting season

Clear seasons of elevated nesting activity are evident for the majority of turtle species and populations (Miller, 1996). However, in different countries around the world, the timing of these seasons and 'preferred' nesting months varies (Figure 17). Green turtles also display periodicity in nesting activity with heightened activity between January and May at Ascension Island (Godley et al., 2001), from October to April in northern Australia (Limpus & Nicholls, 1988) and from July to September in Southeast Asia (Chaloupka, 2001). The high nesting-activity months do not appear to be species-specific (e.g. all green turtles nest in January), but more the result of

Species	Locality	Major nesting activity months												Source
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Loggerheads	Colombia, Caribbean ^N					■	■	■	■	■				Amorocho, 2003 Clarke et al., 2000 Marcovaldi & Marcovaldi, 1999 This study
	Egypt, Mediterranean ^N						■	■	■	■				
	Brazil, S. America ^S	■	■	■						■	■	■	■	
	Tongaland ^S	■	■								■	■	■	
Leatherbacks	St.Croix, U.S. Virgin. Isl. ^N		■	■	■	■	■	■	■					Boulon et al., 1996 Leslie et al., 1996 This study
	Tortuguero, Costa Rica ^N			■	■	■	■	■						
	Tongaland ^S	■	■								■	■	■	
Greens	Southeast Asia ^N							■	■	■				Chaloupka, 2001 Godley et al., 2001 Limpus & Nicholls, 1988 Marcovaldi & Marcovaldi, 1999
	Ascension Island ^S	■	■	■	■	■								
	Northern Australia ^S	■	■	■	■						■	■	■	
	Fernando de Noronha, Brazil ^S	■	■	■	■	■							■	

FIGURE 17: Comparison of the most important nesting activity months of turtle populations from various localities. Note: N and S refer to whether the locality falls within the Northern or Southern Hemisphere respectively.

the hemisphere in which the females nest. Turtles from all the localities shown in Figure 17 appear to nest from late spring, through summer and into early autumn, a fact previously reported by Limpus & Nicholls (1988) for green turtles in northern Australia. Hughes (1989), and Miller (1996) attributed this nesting periodicity ('preferred' months within defined nesting seasons) to warmer sea temperatures. Support for this theory was based on previous work by Hughes (1974) on the Maputaland populations, and was again evident in the current study. The timing of the nesting seasons of both Maputaland loggerheads and leatherbacks, from October to March (Figures 7a and 7b), corresponds largely to those months when the average sea surface temperatures (SSTs) were warm along the Maputaland coast.

Turtles are poikilotherms (Hughes, 1974) and thus sea temperature is of great influence (Davenport, 1997). Although adult leatherbacks are able to regulate their body temperatures (Hughes, 1974, Davenport, 1997), it is thought that leatherback hatchlings (and certainly loggerhead hatchlings) cannot maintain their core body temperature and are therefore more reliant on warmer, more favourable sea temperatures for survival and optimal growth rates (Hughes, 1974).

The only form of parental care exhibited by turtles appears to be the nesting-site choice and the timing of nesting (Hays & Speakman, 1991, Davenport, 1997). The incubation period for eggs is in the order of 60 days or 2 months, but this is largely temperature-dependant (Hughes, 1989, Davenport, 1997, Hays et al., 2002). In Maputaland, the majority of hatchlings emerge from January to March (Hughes, 1989, Lubke & de Moor, 1998), which corresponds with the warmest average SSTs off the KwaZulu-Natal coast (Figures 7a and 7b). Hughes (1989: 240) noted that over these months, the Agulhas Current was "strongest", most likely due to the fact that the current moves closer inshore over this period (Branch & Branch, 1988). Hatchlings are largely at the mercy of the currents (Hughes, 1974b, Hughes, 1989, Lubke & de Moor, 1998). Thus, the timing of hatchling emergence takes full advantage of the position and strength of the Agulhas Current, and the presence of warmer water close inshore, all of which have the potential to

increase survival and growth rates, and possibly improve the feeding regime of the hatchlings (Hughes, 1974b). Therefore, although the adults do not emerge and nest during the warmest months, it may be geared to ensuring optimal timing of hatchling emergence i.e. during favourable temperatures, a distinct selective advantage for largely poikilothermic animals (Hughes, 1974, Davenport, 1997).

5.1.5 Timing of nesting activity

Marginal shifts in the timing of peak nesting activity periods were observed from year to year (Figures 8 and 9), i.e., slightly later peak nesting was observed during El Niño years and slightly earlier peak nesting periods were found in those seasons following El Niño years. Hughes (1974) stated that sea surface temperatures off Maputaland during October and November could affect the start/timing of a nesting season, with colder waters reducing the rate of egg development and resulting in a later start to the season, whereas warmer waters would increase the rate of egg development and result in an earlier start to the season. A study on the internesting intervals (time between repeated nestings within a single season) of green and loggerhead turtles at Cyprus and Ascension Island conducted by Hays et al. (2002) provided strong support for this theory. Of interest is the fact that in the southern Benguela region off the Namibian coast, anchovy (*Engraulis encrasicolus*) stocks spawned marginally later than normal during the El Niño events in 1972/73 and 1982/83 (Shannon et al., 1984).

Breeding is an energetically expensive process for turtles (Jackson & Prange, 1979, Hughes, 1989, Hays & Speakman, 1991) and is often reliant on females achieving a minimum or 'threshold' body condition (Hays, 2000, Broderick et al., 2001), most likely related to the build up of energy and fat reserves (Kwan, 1994). Fat reserves and energy are not only required for egg production, but also needed for migration to the nesting beaches (Kwan, 1994). For Maputaland females to be able to nest during the following breeding season (October onwards), they must have achieved 'threshold' body condition by January in order to induce vitellogenesis, as found

by Limpus & Nicholls (1988) for green turtles in northern Australia.

Distinct years of elevated (comparatively high) nesting activity were found for both species in Maputaland (Figures 8 and 9). Similar elevation of breeding has been observed not only in several turtle populations around the world, but also in other marine organisms, and has been linked to El Niño events. For leatherback turtles in Las Baulas National Park, Costa Rica increases and declines in the nesting activity during the mid 1990s were directly related to sea surface temperatures (and El Niño events) (Steyermark et al., 1996), while Ainley et al. (1995) observed positive and negative reproductive anomalies in seabird colonies off the Californian coast which also appeared to be related to ENSO events. Ainley et al. (1995) stated that poor breeding periods were observed during El Niño years, but prior to and following these, elevated breeding periods were observed. Chaloupka (2001) reported that for several populations of green turtles in Southeast Asia, when an El Niño event resulted in a peak in nesting activity this would be followed by a period of low reproductive activity as individuals required time to recover and to re-attain the minimum or 'threshold' body condition necessary for reproduction. A similar trend was observed in the current analysis whereby relatively high nesting seasons were generally followed by comparatively low nesting activity periods (Figure 10).

Although changes in nesting activity have been directly attributed to El Niño events, time series analyses (Chaloupka, 2001) and laparoscopic examinations of female green turtles in Australian waters (Limpus & Nicholls, 1994 cited by Chaloupka, 2001) indicate lag periods of duration between 1 and 2 years following an El Niño event (Chaloupka, 2001). In the current analysis, the lag period appeared to be between 0 and 2 years following a Pacific El Niño event (Figure 10). Similarities have been found with respect to the timing of Pacific warm-water events and southern Benguela warm-water events (Walker et al., 1984), and the Southern Oscillation Index (SOI) is a common measure of the ENSO (El Niño Southern Oscillation) cycle. However in the current analysis no correlation was found between the number of nesting females of either

species and the SOI values. Reasons for this are discussed below.

In the Maputaland context, it is possible that an ENSO-related factor, and not the actual ENSO event itself, may be responsible for any apparent relationship. The effects of El Niño events on nesting activity have largely been attributed to food availability (Bjorndal, 1997, Hays, 2000, Broderick et al., 2001). Barber & Chavez (1983) explained the reduction in biological productivity observed during El Niño events, whereby abnormally warm and nutrient-poor water present during El Niño events is brought to the surface through the process of upwelling, but due to the reduced nutrient levels present cannot support high levels of biological productivity. As a result of this reduced biological productivity, predators and animals at higher trophic levels are negatively affected through ecosystem effects (Barber & Chavez, 1983). Examples include seabirds (Duffy et al., 1984, Ainley et al., 1995) and even intertidal and near-shore organisms (Branch, 1984).

Polovina et al. (2001) found a relationship between the movements of the transition zone chlorophyll front (an important feeding zone that supports a large variety of organisms, including jellyfish, a preferred prey item of juvenile loggerheads and adult leatherbacks), and that of migrating loggerheads in the North Pacific. The movement of the chlorophyll front was related to the 1998 El Niño and 1999 La Niña events (Polovina et al., 2001). In addition to this, during the 1982/83 warm-water event Branch (1984) recorded mass mussel mortalities (*Choromytilus meridionalis*) and crab strandings (*Charybdis smithii*) on the South African coast (preferred food items of adult loggerheads – Hughes, 1974b), and large abundances and strandings of *Physalia*, bluebottles (preferred food of juvenile loggerheads and adult leatherbacks – Branch et al., 1994, Lubke & de Moor, 1998). Thus it appears that several of the preferred food items of both juvenile and adult loggerheads and leatherbacks can be affected by warm-water events off the South African coast, although this information is based on an isolated study of a single warm-water episode. Further work is required to determine whether preferred prey species undergo changes in abundance, and hence availability, in response to ENSO events and sea surface temperature

changes in the southeast Atlantic and southwest Indian Oceans. In future studies, it would be valuable to incorporate an index of preferred prey abundance or food availability.

It is possible that other factors were responsible for the elevated and depressed nesting activity seasons, for example changes in ocean currents (Davenport, 1997), which were not accounted for in the present analysis.

5.1.6 Interannual variation

A large amount of interannual variation is a typical feature of marine turtle population estimates (Hughes, 1989, Limpus, 1995, Bjorndal et al., 1999, Hays, 2000), most notably for green turtles (Broderick et al., 2001) and to a lesser extent for loggerheads and leatherbacks (Hughes, 1989). The current study was no exception.

Interannual variations have been attributed to a potentially inherent, non-consecutive-year nesting behaviour in marine turtles (Carr & Carr, 1970), and also to food availability and the attainment of a minimum 'threshold' body condition (Carr & Carr, 1970, Hughes, 1989, Broderick et al., 2001), an idea that has received support through the use of theoretical models of variable remigration intervals (Hays, 2000). In northern Australia, Limpus and Nicholls (1988) found a correlation between the large interannual variation in the number of nesting green turtles and El Niño Southern Oscillation (ENSO) events. Hays (2000) stated that this correlation could be due to changes in food availability (Ainley et al., 1995, Bjorndal, 1997, Broderick et al., 2001), with prey species being affected by changes in sea surface temperatures (Barber & Chavez, 1983, Broderick et al., 2001). Alternatively, the changes in sea temperatures could directly affect the turtles themselves (Davenport, 1997, Hays, 2000, Hays et al., 2002). Sea temperature changes could be a very influential factor as most turtle species are poikilotherms (Hughes, 1974, Davenport, 1997).

In the Maputaland context, a strong positive correlation was found between the numbers of turtles caught in shark nets off the southeast African coast in the mid 1960s to early 1970s, and the sea surface temperatures over that period, whereby turtles appeared to migrate along the coast in response to the movement of warm water (Hughes, 1974b).

In the current analysis, no correlation was found between the annual and nesting-season SSTs offshore Sodwana Bay (Figures 8 and 9) and loggerhead nesting activity, contrary to the positive relationship found by Hughes (1974b). The (admittedly weak) negative correlation between the leatherback nesting activity and the annual and nesting-season SSTs is surprising and reasons for this are not known. Further investigation is required to ascertain the causes. Sea surface temperature data sets of longer duration than the 15-year period currently available would be an important contribution.

The annual and nesting-season SSTs reported were recorded close offshore of KwaZulu-Natal, and very little interannual variation was evident even during the ENSO events (Figures 8 and 9). It may be of value for future studies to measure the SSTs in the foraging grounds of these two populations i.e. off the east coast of southern Africa and around Madagascar for the loggerheads and in the southern Ocean and South Atlantic for the leatherbacks, as the turtles will spend the majority of the year in these foraging areas and not near the nesting beaches.

With regards to the Maputaland populations' interannual variation and the three distinct phases evident in the strong long-term trends (Figures 3a and 3b), it is unclear which of the above hypotheses (ENSO events, sea surface temperature changes, food availability or a combination thereof) is applicable. Most probably a number of interacting factors are responsible.

5.1.7 Location of nesting sites and 'preferred' habitat type

The Maputaland leatherback nesting distribution was far more extensive than that of the loggerhead population, as previously noted by Hughes (1974). Pritchard (1973) and Eckert et al.

(1989) argued that the nesting-site fidelity of oceanic leatherbacks is low on unprotected, exposed beaches, and attributed this to the unstable nature of these beaches (Davenport, 1997). The Maputaland nesting beaches have been described as fairly exposed (Hughes, 1974a), and it is possible that lower levels of site fidelity are the reason for the wider nesting distribution of leatherbacks as opposed to loggerheads in Maputaland (Hughes, 1989).

'Preferred' loggerhead nesting areas clearly had more scattered rocks and ledges in the subtidal and low shore zones (Figure 13), while the leatherback 'preferred' areas included those with predominantly sandy subtidal and low shore zones, and thus "unobstructed approaches" (Hughes, 1974a: 40). Mortimer (1982) emphasized the importance of offshore seabed topography as an influential factor in the site choice of green turtles nesting on Ascension Island. In Maputaland, this too appears to be an important factor, particularly for leatherback females, as boulders and rocky ledges have the potential to severely damage their leathery carapaces (Hughes, 1974a). However with regards to the loggerheads, although they appear to be capable of nesting in rocky areas, the choice of nesting site may also be governed, not only by the offshore seabed topography, but also by olfactory cues and gradients that may exist offshore the 'preferred' areas as hypothesized by Hughes (1974). In summary, Hughes (1974, 1989) attributed the nesting distribution of both Maputaland populations largely to:

- Offshore seabed topography (reefs and rocky points – loggerheads; sandy and 'obstruction-free approaches' – leatherbacks)
- Southern limit of the 25°C summer sea isotherm
- Presence of olfactory cues, in the northern region (in the case of loggerheads)

The current analysis provides strong support for the first of these suggestions, but is impartial with respect to the other two.

As observed by Hughes (1974a), the 'preferred' nesting sites of the loggerhead and leatherback populations were largely separate, but a fair amount of geographic overlap in nesting areas has

existed ever since observations started in the 1960s. Hughes (1974a) postulated that a greater separation between the two populations might occur in the event of the leatherback population increasing in size. There was however no evidence of this in our study. Whether interspecific competition for nesting sites occurs between the two species, is an unresolved question. The two species exhibit different 'preferred' nesting areas, which may reflect niche partitioning as a result of competition, but could also be the result of different requirements (offshore seabed topography, chemoreception) of the two species. Synchrony in the increases and decreases in nesting activity of the two species (Figure 4) argues against there being any competition. In addition, there is no suggestion that either species has shifted its nesting areas as nesting numbers have increased. Competition therefore seems unlikely, and any temporal changes of spatial distribution are more likely linked to environmental factors.

Increased human activity and interaction has affected nesting activity in various populations around the world through the destruction of nesting beaches, largely due to increased coastal development and erosion (Clarke et al., 2000, Amorochó, 2003), artificial beachfront lighting (Hughes, 1989), shading of nesting beaches by beachfront condominiums (Mrosovsky et al., 1995) and marine pollution (Chan & Liew, 1996). It is possible that the limited nesting activity near the launch site (0N–2S) and tourist lodges (32–29N; 51–54S) in the study area (Figures 11 and 12) is attributable to increased human activity. In addition, the launch site and tourist lodge developments were all built close to rocky points (Figure 13), and thus it is possible that the reduced nesting in these areas may be the result of increased beach erosion (reduced beach stability) due to the presence of man-made structures near the rocky points. Reasons for this correlation, and the implications thereof, are discussed under the conservation and management section below.

5.1.8 Changes in nesting area

No major shifts in nesting area have been detected for either species since comprehensive monitoring began in the 1970s (Figures 11 and 12), a fact previously evident in Hughes' (1989)

findings. In the current study, an increase in the length of the 'preferred' nesting areas of both species was observed during certain years, when the incidence of nesting rose (Figures 14a and 14b). Godley et al. (2001) also reported that variations in the nesting density of green turtles nesting at Ascension Island could be affected by seasonal changes and interannual variations in nesting activity.

While temporal shifts of nesting seasons were fairly marginal (all fell between the months of November and January) (Figures 8 and 9), spatial shifts in the 'preferred' nesting areas were more pronounced. Strong positive correlations were found between the number of nesting females and the length of the 'preferred' nesting area of both species (Figures 15a and 15b), probably reflecting the need to accommodate the greater influx of nesting females.

5.1.9 El Niño Southern Oscillation (ENSO) Regressions

Reasons for the lack of correlation between nesting activity and the Southern Oscillation Index (SOI) values are uncertain, but probable explanations are discussed below.

Interannual variation in nesting activity is far greater for green turtles than for either loggerhead or leatherback turtles and this has largely been related to the different species' dietary requirements and changes in food availability (Broderick et al., 2001). The most obvious examples of ENSO-event effects on nesting turtle populations are based on green turtle populations in northern Australia (Limpus & Nicholls, 1988) and Southeast Asia (Chaloupka, 2001). As previously mentioned, adult green turtles feed only on plant matter, while loggerheads and leatherbacks are carnivores (Branch et al., 1994), and thus green turtles are potentially more susceptible to ENSO-related factors through the direct effects of ENSO events on primary production, for example macroalgae (Barber & Chavez, 1986, Broderick et al., 2001). As mentioned above, ENSO events do affect higher trophic level predators (carnivores) through

ecosystem effects, however all the above examples were of relatively short-lived animals that reach sexual maturity at a comparatively young age (Branch & Branch, 1988).

In the case of marine turtles, these animals are long-lived and slow-growing, reach sexual maturity after several years (Hughes, 1989, Spotila et al, 1996, Davenport, 1997, Godley et al., 2001) and require a 'threshold' body condition approximately 9 months prior to nesting in order to undergo vitellogenesis (Limpus & Nicholls, 1988). Hence the effects of ENSO events may be far less obvious and only become evident after many seasons or, they may be masked by other factors, for example interannual variation in nesting numbers (Limpus, 1995, Bjorndal et al., 1999, Hays, 2000, Broderick et al., 2001), thus explaining the lack of correlation between the SOI values and the nesting activity of both species.

Many complications arise when attempting to describe variation in species abundance solely using climate change e.g. ENSO events, largely due to the numerous complicating and interacting factors present (Hayward, 1997). Thus the lack of correlation between the SOI values and the Maputaland nesting activity in the current analysis could be the result of other confounding, and possibly ENSO-related factors, for example the link between sea surface temperature changes and food availability. In addition, it is also possible that the lag period following an ENSO event may not remain constant, and thus the use of a fixed lag period in the SOI regression analyses may not be ideal. Finally, it is possible that the SOI is not an appropriate index for the consequences of ENSO-related effects on the east coast of southern Africa.

During the initial recovery phase (Figures 3a and 3b) nesting-activity levels were low, irrespective of the recurrence of ENSO events. After that initial period, the nesting numbers oscillated (decreasing and then increasing phases between 1978/79 – time 12 and 2000/01 – time 34) again potentially masking any influence or effects of ENSO events. Authors have commented on the fact that when attempting to determine population trends other variables

(particularly interannual variation) may mask broad trends through confounding effects (Limpus, 1995, Bjorndal et al., 1999, Hays, 2000, Broderick et al., 2001). In the Maputaland context, it is possible that long-term changes in abundance may also have masked any potential correlations between nesting activity and ENSO events.

Sarti et al. (1996) discussed the possibility of a relationship between nesting distribution shifts in the Mexiquillo leatherback population and the ENSO events that occurred between the late 1980s and early 1990s. However, in the current analysis, again no correlations were found for either species between the length of the 'preferred' nesting area and the SOI values.

The relationship between the SOI values and the average CCL of nesting females was the only correlation found between the Maputaland nesting females and an index of the ENSO cycle. The negative correlations between the SOI values and the average CCL of both loggerhead and leatherback females (Figures 16a and 16b) may be a growth response related to ENSO events. ENSO and North Atlantic Oscillation events have been associated with changes in food availability in many areas worldwide and for many different species (Barber & Chavez, 1983, Duffy et al., 1984, Ainley et al., 1995, Hayward, 1997, Broderick et al., 2001) and therefore have the potential to influence growth rates (Broderick et al., 2001).

As previously mentioned, there is a widely-held opinion that ENSO events have a nutritional influence on nesting activity and behaviour (Bjorndal, 1997) and this may be an important factor in the Maputaland context. Further support for this is the fact that Branch (1984) observed changes in the behaviour, abundance, body condition and survival of a number of subtidal and nearshore organisms (several of which are the preferred prey items of loggerhead and leatherback turtles), that were associated with a warm-water anomaly off the south and west coasts of South Africa. This provides a link between Pacific El Niño events and the availability of potential prey items in the southwest Indian Ocean.

Sea turtles are long-lived animals that are characterised by slow growth rates (Spotila et al., 1996, Davenport, 1997). Through the use of theoretical nonparametric regression models, a relationship was detected between ENSO events in the 1980s, and temporary elevated growth rates of immature female green turtles in the southern Great Barrier Reef waters, possibly the result of food availability (Limpus & Chaloupka, 1997). However, Limpus & Chaloupka (1997) also emphasized that ENSO events involve changes in sea surface temperatures. Thus the direct effects of temperature changes cannot be discounted. Hughes (1974b) reported that growth and size variations in loggerhead hatchlings were closely related to sea temperatures. Thus while there could be a nutritional link between ENSO events and the Maputaland turtle populations which may explain the correlation between the average size of nesting females and the SOI values, sea surface temperature changes in the foraging grounds could per se also be an important influential factor.

In summary, strong pointers indicate that ENSO-related factors could affect the nesting activity and behaviour of Maputaland populations, although long-term changes in the overall abundance, namely the early recovery phase (1965/66 to 1976/77) and the high intrinsic variability thereafter, may have masked any potential relationship between ENSO events and interannual nesting-activity.

Further work, together with the use of theoretical models in the Maputaland context, is needed to determine whether food availability and/or sea surface temperature changes are responsible for the apparent link between ENSO events and the population trends (changes in nesting activity and nesting area, seasonal increases and declines, interannual variation, and reductions in size).

5.2 Conservation and management

5.2.1 Effectiveness of protection

Since the legislation prohibiting harvesting of eggs and adults was introduced in 1916 and the conservation and monitoring programme ensured enforcement from 1963 onward (Hughes, 1989), both loggerheads and leatherbacks exhibited an increase in nesting numbers over time. This trend was statistically significant over the first 11 years of monitoring, after which numbers stabilized or fluctuated slightly (Figures 3a and 3b). This is an encouraging result especially in light of the status of other populations elsewhere, and on a global scale (IUCN Species Survival Committee, 2003). The Maputaland populations now appear to have reached a relatively healthy and more-or-less stable state. This success can largely be attributed not only to the above legislation, but also to the monitoring programme and the associated conservation and enforcement efforts (Hughes, 1993). Monitoring programmes not only serve to collect valuable data that can be used to estimate population trends, but also help to reduce illegal harvesting of eggs and adults, and protect nesting females, nests and hatchlings from physical damage (Spotila et al., 1996, Garcia et al., 2003, Hasting, 2003). In addition to the above, the 2003 legislation banning off-road vehicles on South African beaches may further contribute to protecting nesting turtles.

The practice of beach protection has been widely accepted as an important management and conservation tool (Settle, 1995, Spotila et al., 1996, Garcia et al., 2003). Many beach protection programmes have resulted in the stabilization or increase of turtle nesting populations (Spotila et al., 1996). Examples include the St. Croix leatherback population (Boulon Jr. et al., 1996, Spotila et al., 1996), the olive ridley (*Lepidochelys olivacea*) populations on small protected nesting beaches in Mexico, which have exhibited increased nest productivity (Garcia et al., 2003), and the British Virgin Island leatherback population, which has gradually increased through a combination of increased public awareness, legislation, law enforcement and beach patrols (Hasting, 2003). Spotila et al. (1996: 216) quoted the Maputaland leatherback population as

having grown largely as a result of successful beach protection and management.

5.2.2 Duration and consistency of monitoring

a.) *Duration*: Due to the long-lived nature of marine turtles, their delayed reproductive maturity and slow growth rates (Spotila et al., 1996, Davenport, 1997), the response of marine turtle populations to various human activities (including both harvesting and management and conservation actions) is normally only obvious after a number of years of monitoring (Settle, 1995, Aikanathan & Watling, 1996, Bjorndal et al., 1999). Thus, the need for ongoing, long-term programmes has become increasingly important. Hughes (1989), the National Research Council (1990), Limpus (1995), Hays (2000) and Shanker & Pilcher (2003) emphasized the importance of continuous long-term monitoring programmes to allow adequate, reliable population estimates in the face of huge interannual variability. The current dataset has provided a valuable opportunity to record the nesting behaviour of these turtle populations over several decades, from the inception of the programme, which included increased protection and conservation efforts leading to a recovery phase (Hughes, 1993), through numerous ENSO events and shifts and changes in the populations. Monitoring of nesting turtles needs to be maintained, but added value would be gained if monitoring of relevant physical and biological variables could be implemented in parallel.

b.) *Consistency*: Some confusion existed with regards to beacon nesting counts, i.e. whether counts were undertaken every 400m-interval (per beacon) or for 1600m-intervals (every fourth beacon). These nesting beacons however, are not only reference points but imply a specific area which can lead to uncertainty regarding the nesting concentration, density and distribution per area. ARCVIEW mapping of the coastline currently provides information on 100m-blocks of habitat type along the coast, which is a suitable level of accuracy when taking 400m-interval counts. However, as the total number of nested turtles in the current study had to be calculated over 1600m-blocks (4-beacon area) to standardize the study area, the added detail of ARCVIEW

becomes lost as it is never clear in which specific part of a 1600m-area the turtles in fact nested. Thus if the ARCVIEW data is to be used for future analyses, nesting counts should be made at 400m intervals throughout the study area so as to standardize the nesting counts and make all counts comparable to those in the northern region.

5.2.3 Human disturbance and its effect on nesting

Roughly half of the loggerhead females that emerged on the shore succeeded in nesting, while the majority of emerging leatherback females nested. Even in the case of low-disturbance monitoring, the loggerhead non-nesting rate was very high; suggesting that this may be an inherent characteristic of loggerhead turtles. Chemical olfactory cues are thought to trigger final nesting-site orientation and nesting in loggerhead females (Hughes, 1989), thus Hughes (1974) theorized that the low nesting rate of loggerheads could be related to the strength and detection of these chemical olfactory cues on nesting beaches.

Significantly more individuals of both species failed to nest if they were subject to high-disturbance monitoring. Thus, it appears that the low loggerhead-nesting rate was exacerbated by human disturbance and interference. Hughes (1989) concluded that emerging loggerheads are deterred from nesting by light, human proximity and other visual stimuli, whereas emerging leatherbacks are seldom affected by external stimuli and outside disturbance. However, in the current analysis not only loggerheads, but also leatherbacks, had a higher proportion of individuals that failed to nest on a given night in the high-disturbance situation. To put this into perspective, the magnitude of the effects of disturbance were, at most, a 5% reduction in the nesting rates of both species. Moreover, although the numbers of turtles nesting on a given night may be reduced through high-disturbance monitoring, experience has shown that individuals will generally return to nest later in the season in the event of a failed nesting emergence (Hughes, G.R. *pers. comm.*, Broderick & Godley, 1999). In addition, Broderick and Godley (1999) found that tagging did not appear to significantly and/or negatively affect the nesting duration,

behaviour or hatching success of both loggerhead and green turtles in Cyprus.

Thus, it is our belief that the sampling protocol is not overly detrimental to nesting females and should continue unchanged, as the data the programme provides are invaluable for the continued protection and ongoing management of these populations.

5.2.4 Concession areas

As previously mentioned, the only ecotourism concessionaire collecting data for the monitoring programme operates between Manzengwenya (71S-74S) and Mabibi (99S-100S). This area included two of the five 'preferred' leatherback-nesting sites found in the study area and was comparable with the 'preferred' sites found further north (Figure 12 and 13). Therefore it appears that the concessionaire is collecting data that are consistent with the remainder of the study area and the EKZN Wildlife monitors.

However, the limited nesting activity found near the launch site (0N–2S) and tourist lodges (51–54S; 32–29N), may either be attributable to increased human activity not associated with the monitoring programme, reduced beach stability (erosion) due to man-made structures, or a combination thereof. Further work is needed to ascertain whether these apparent reductions in nesting activity are real or an artefact of reduced sampling effort, whether the reductions are due to increased human activity and the associated developments, and whether these effects are a cause for concern in terms of the loss of potentially favourable nesting habitat for Maputaland females.

5.2.5 Future seasons

With regards to potentially reducing the cost and effort associated with the monitoring programme, several factors need to be emphasized. Firstly a reduction in sampling effort would reduce costs and could be achieved either by a reduction in the frequency of monitoring between different seasons (every 2nd or 5th nesting season is monitored) or within a season (the length of

the monitoring season or the length of the area monitored). It would not be prudent to reduce the 'between-seasons' monitoring for two reasons. Firstly, due to the large interannual variation exhibited by both the loggerhead and leatherback nesting populations (Figures 3a and b), by only monitoring every other season, nesting numbers may either be abnormally high or low due to environmental factors, food availability or other ENSO-related factors thus giving a distorted view of the state of the nesting populations. And secondly, not only do the rangers measure the turtles and record data, but also by their physical presence on the beaches they have the potential to reduce or even eradicate illegal harvesting of both nesting females and eggs (Spotila et al., 1996, Garcia et al., 2003, Hasting, 2003).

A "within-season" reduction in effort would be a far better choice. Very limited nesting was recorded in October. On average in a given season, only $1.2\% \pm 0.86$ of loggerheads and $3.4\% \pm 2.4$ of leatherbacks nested in October. Thus, the start of the monitoring season could be delayed until the beginning of November without significant loss of information. It is our belief that this would reduce costs but should not negatively affect the integrity of the dataset. Curtailment of monitoring in March should not be contemplated even though very little nesting takes place, as the main emergence of hatchlings spans December to March (Hughes, 1989). While a reduction in the area sampled could be introduced for loggerheads (restrict monitoring to the area north of Dog Point, 23S – 26S), an area reduction would not be advisable for leatherbacks at this stage. Leatherbacks have a far wider nesting distribution with 'preferred' nesting areas from Bhanga Nek (0N – 2S) to Manzengwenya (71S – 74S).

While it will incur further costs, it would be of value to estimate the number of hatchlings emerging each season. From hatchling data, the relative hatchling success in Maputaland and any changes in hatchling success could be determined and assessments made of whether these can be attributed to human activity (e.g. trampling of nests and hatchlings) or to natural factors (predation, erosion, sand and air temperatures etc.). Given the uncertainties about whether or

not the turtles are responding to ENSO events, the inclusion of some measure of sea surface temperature would also be of value.

In summary, the Maputaland monitoring programme is one of the longest quantitative loggerhead-leatherback turtle-monitoring programmes in the world (Hughes, 1993), and it would be of great value to continue this dataset into the future. Long-term monitoring programmes of this type not only serve to broaden our understanding of the biology and behaviour of turtles and assist in determining population sizes, but ultimately help in the ongoing conservation and protection of these unique marine vertebrates.

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