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The Sea Turtles of South-East Africa

II. The biology of the Tongaland Loggerhead Turtle *Caretta caretta L.* with comments on the Leatherback Turtle *Dermochelys coriacea L.* and the Green Turtle *Chelonia mydas L.* in the study region

by

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Introduction

This report constitutes the second in a two-part series on the sea turtles of South-East Africa and should be regarded as a contribution to the knowledge of the biology of the loggerhead sea turtle *Caretta caretta* Linnaeus.

As virtually all the data pertaining to the loggerhead were collected from a single nesting assemblage in Tongaland conclusions reached in this report need not necessarily apply to loggerhead assemblages elsewhere in the world. Where possible, however, attempts have been made to compare local data with those from foreign sources.

Further, during the present study a considerable quantity of data was collected on various biological aspects of the leatherback turtle *Dermochelys coriacea* Linnaeus and the green turtle *Chelonia mydas* Linnaeus. Unfortunately, data pertaining to either species were insufficient to justify inclusion as discrete sections and have been incorporated within the loggerhead section.

Briefly the background to the Tongaland loggerhead work is as follows:

During 1963, the Department of Bantu Administration and Development and the Natal Parks Board became aware of the need to protect the turtle populations nesting on the isolated portion of the Natal coast known as Tongaland. Motivated by Mr. Peter Potter, Assistant Director Administration, the Natal Parks Board sent two students Mr. H. J. McAllister and Mr. A. J. Bass (now Dr. Bass) to work with Mr. H. J. van Schoor the Ranger-in-Charge of the area in which the nesting grounds were found. Since the pioneering efforts of these four men, the Tongaland conservation programme has continued unbroken for ten years and it is the results of their work and the contributions of subsequent investigators that is summarized here.

Once again no claim is made of completeness but the report has been compiled and presented in the hope that it may contribute to a better understanding of the life history of the loggerhead turtle. This may, in time, lead to a more rational exploitation of a natural resource in those parts of the world where the loggerhead is utilized.

Major stages in the life cycle of the loggerhead turtle with comments on other species

Introduction

Research into the life cycles of sea turtles necessitates considerable speculation because from the time newly emerged hatchlings enter the sea from the nesting beaches, very limited quantities of material are available and it is from this limited material that major stages of growth and behaviour must be deduced.

Firstly the mortality rate of hatchlings in the first few weeks, or months, is apparently enormous and their almost complete disappearance for varying periods makes study difficult, forcing the use of negative evidence.

An added problem lies in the ageing of the material that does become available. Attempts find growth rings in bone, nail, cartilage and shields have all proved futile and, further, it will be seen that growth rate is highly variable so size is an unsatisfactory guide except in very general terms. It must be added that growth rates in mature females are almost untraceable after the first nesting season which makes ageing by size even less justified.

In this section, therefore, some meagre facts are presented, spiced with speculation and an awareness of many shortcomings. It is felt, however, that there are sufficient facts on which to base these speculations and although a great deal remains to be learnt and more detailed evidence is required for confirmation, the life cycle of the loggerhead is presented with some conviction. The fragmental information on other species is included for record purposes.

Methods

In this sub-section only the methods are to be discussed, the results are all incorporated in later sub-sections.

HATCHLINGS — TAGGING

As in all localities, hatchling tagging has proved an almost insurmountable problem. Carr (1967: 108-110) describes the difficulties encountered in trying to tag green turtle hatchlings. Several methods have been tried in Tongaland.

During the 1967-68 season 623 loggerhead hatchlings were tagged with a small plastic tag normally used for trout. This tag was attached to the edge of the carapace immediately adjacent to the inframarginal bridge and held in place by pieces of nylon monofilament fishing line. There were no recoveries (Hughes, 1970: 8-9).

The 1969-70 season saw a new attempt using small lengths (2 to 3mm) of stainless steel wire which were implemented under a selected vertebral scale by means of a hypodermic syringe. Although in turtles of 50cm carapace length and less the tags stood out clearly under X-ray, the limitations of the method were obvious and it would be useful only in the early stages. 3 141 loggerhead and 22 leatherbacks were tagged and released. There were no recoveries (Hughes, 1971b: 7).

Dr. H. R. Bustard (*pers. comm.*) reported that mutilation tagging, or notching of the carapace, had proved successful in experiments in Australia, and that after 4½ years the excision was still clearly visible and appeared to be permanent. During the 1971-72 season a programme of notching was initiated and continued during 1972-73. An ordinary leather punching tool was used, its advantage being that it has six punch sizes, all but one of which are sufficiently small to use on loggerhead hatchlings. The site chosen for notching during the 1971-72 season was the first marginal scale immediately left of the left supracaudal scale; in the 1972-73 season the scale notched was the first marginal immediately right of the right supracaudal (Plate 1). After notching, the wound was immediately coated with Gentian Violet (1%) and left to dry.

Some hatchlings came from the experimental hatchery but most were gathered at night on the beaches. 5 000 were dealt with in 1971-72 and 5 250 in 1972-73. All were notched, a sample weighed and measured the morning following capture, and released the next evening. Mass and size samples were between 100 and 400 hatchlings per season.

The method proved to be quick, neat and although there was an initial reaction to the notching, the hatchling's behaviour returned to normal within a few minutes and no further signs of discomfort were observed. Notched hatchlings kept in captivity were harrassed by other hatchlings biting the notched area but it is felt that this is unlikely to occur in the sea (Hughes and Brent, 1972: 42).

Recoveries of notched hatchlings will be discussed later.

GROWTH STUDIES

In March, 1972, 200 loggerhead hatchlings were brought to Durban from Tongaland and installed in a plastic swimming pool measuring 3 x 3 x 0.5m. A strong flow of water, pumped directly from the sea, passed through the tank maintaining a slight circular current. For two months there were no casualties then in May problems developed, including fouling of the tank, which led to a heavy fungal infection and this resulted in very heavy mortalities. If caught early, the affected areas; mainly the eyes and divisions between carapace scales, responded to treatments with Gentian Violet (1%). Weekly dips in Gentian Violet would be practised during any future mass growth experiments.

A further reason for mortalities was attributed to a drop in temperature in May and that the tank received no sun after the end of April. In June this situation was realised and the tank moved to the roof of the aquarium where it was exposed to the sun. It was too late, however, and mortalities continued. Thus in the long term the experiment was a failure but growth results from the early stages are useful as an indication of what might be expected from wild hatchlings at similar temperatures and some are included below.

TEMPERATURE TOLERANCES

During April, 1972 an experiment was devised to test the response of loggerhead hatchlings to sharp changes in water temperatures.

4 perspex tanks measuring 55 x 40 x 40cm, each containing 66 litres of water, were suspended to the water line in a large temperature controlled behaviour tank (6 x 2 x 1.7m) in a basement experimental room at the Oceanographic Research Institute. Water temperature in the behaviour tank was set at 12°C but by situating the perspex tanks at different points in the tank it was possible to obtain temperature differences that held steady for three days prior to the start, and showed few variations throughout the duration of the experiment. Four temperature regimes were established; 18°C, 17°C, 15°C and 14°C and these were checked three times daily.

30 hatchlings were randomly selected from the yard tank, sponge-dried and weighed to the nearest 0.1g on an Ohaus triple-beam balance.

Ten hatchlings, chosen as controls, were marked with Indian ink so as to be individually identifiable and returned to the yard tanks which had a temperature of approximately 24°C throughout the experiment.

The remaining 20 were divided into 4 groups of 5, and, using a different colour paint on each group, were marked individually. Each group was then placed directly into a perspex tank representing temperature changes of 6°, 7°, 9° and 10°C.

The experiment ran for two weeks during which time the hatchlings were fed three times daily at 0900, 1200 and 1500 hours. Pieces of sardine or hake were weighed to the nearest 0.01g and suspended at the surface of the water. A fifth piece was placed in a separate tank to ascertain water absorption, if any. Food mass intake of hatchlings was adjusted in accordance with the mass deviations of the control food sample.

Hatchlings were weighed after 7 and 14 days. The results of the experiment are discussed later.

STRANDED AND NET-CAUGHT MATERIAL

During the course of each hatchling marking season appeals were made, through the news media of Natal and the Cape, for the return of stranded hatchlings to Durban. The public response was gratifying.

Sub-adult and adult material came mainly from the Natal coast, having been caught in the Anti-Shark nets set by meshers under contract to the Natal Anti-Shark Measures Board. The meshers were requested to submit a monthly report on turtle catches but this proved tedious as a result of a low incidence of turtle catches so they agreed to submit a report only when a turtle was caught. The response from individual meshers varied from enthusiastic to indifferent.

Dead specimens were brought to the Institute where their statistics were recorded and the stomach contents examined. As the majority of specimens had been dead for some time few reproductive data were collected. The carapace, skull and gut contents were retained and the remainder discarded.

The first year (the 'lost' year)

HATCHLING AND ORIENTATION TO THE SEA

These aspects of turtle behaviour have been thoroughly investigated by many workers; Carr and Ogren (1959: 14-15) described the emergence of leatherbacks in Costa Rica and Carr and Hirth (1962: 68-70) described the mechanism of social facilitation in green turtles. Hughes

(1969: 9) described the emergence of loggerheads in Tongaland and the means of ascent through the sand appears identical in all these species.

Bustard (1967: 317) described the incidence of emergence arrest at the beach surface, if green turtle hatchlings approached it during the heat of the day. He also mentioned hatchlings lying dormant, with a few showing their heads above the sand, in a small depression caused by sand filtering down amongst the hatchlings. During the present field study this was found to be a common sight on Europa Island.

Mrosovsky (1968: 1 338) investigated this behaviour and found that the critical temperature in Surinam beaches was 28.5°C above which green turtle hatchlings were inhibited from movement. This temperature limit is similar on Europa Island where no hatchlings were observed to emerge until the beach temperature dropped to 29°C which normally occurred between 1600 and 1730 hours. Daylight emergence occurred daily on Europa Island which would suggest that it is not light which is the inhibiting mechanism.

This temperature inhibition applies also in loggerheads and leatherbacks in Tongaland where daylight emergences are a rarity; only 3 instances having been recorded in 10 seasons. Two emergences (1 loggerhead and 1 leatherback) were observed on overcast days and another loggerhead about noon on a hot clear day. In the latter case all hatchlings died within 15 metres of the nest. During hatchling tagging in Tongaland it has been noticed that throughout the night of capture the level of activity in the retaining boxes has been high. With the coming of daylight the hatchlings became quiet, not moving again until evening.

There are indications that the critical inhibitory temperature is lower in Tongaland. Figure 1 shows the mean daily sea and beach temperatures during the 1966-67 season, together with the 1800 hours beach surface temperature from the 8th January when hatchling emergences were first recorded. It can be seen that beach surface temperatures rarely reach 29°C.

Beach surface temperature at 1800 hours:		*nights*	%
	29°C	4	12.9
	28°C	5	16.1
	27°C	10	32.3
	26°C	4	12.9
	25°C	5	16.1
	24°C	2	6.5
	23°C	1	3.2
		31	100.0

Hatchlings in Tongaland, either leatherbacks or loggerheads, emerge from 1900 hours and have been observed to emerge throughout the night. As the above temperatures were recorded at 1800 hours one could expect a further drop of 0.5°C by 1900 hours. Thus it would seem that the inhibiting temperature is in the region of 26.5°C to 27.0°C. It is perhaps of interest to note that the offshore sea surface range is remarkably similar.

Sea finding orientation has been exhaustively investigated (Ehrenveld, 1966; Limpus, 1971; Mrosovsky and Carr, 1967; Mrosovsky and Shettleworth, 1968 and Mrosovsky, 1970). No investigations have been undertaken in Tongaland as hatchling behaviour does not differ from that described for other areas. Mrosovsky (1970: 650) summarizes by stating that any kind of visual stimulus has some effect on the seafinding orientation of hatchlings and that the orientation depends on a relatively uncomplicated type of tropotactic reaction.

INITIAL ACTIVITY

It is common knowledge that once hatchlings have emerged there is frenzied activity and if placed in water there is continuous swimming. In the initial stages this behaviour has high survival value for it removes the hatchlings from the predator infested littoral zone. Dr. D. Hughes (*pers. comm.*) suggested that a green turtle hatchling may cover up to 7km during the first night and this is likely to be somewhat more than the smaller, less vigorous loggerhead. Local currents assist the Tongaland loggerhead in its removal. Harris (1964: 237) has shown that mass movement of water in the surf zone is northward and there are cells terminated by powerful rip currents sweeping up to a kilometre offshore. These cells are between 500 and 700 metres in length so hatchlings, although swimming, would have little distance to drift before being carried out beyond the surf zone. The larger, more powerful leatherback probably needs no assistance from the rip currents.

Captive loggerhead and leatherback hatchlings refuse food for at least two days after emerging on the beach so it is assumed that this is the minimum length of time spent swimming out to sea. As the Agulhas Current flows within 10 kilometres of the Tongaland coast all hatchlings should be well within its flow before commencing feeding.

Green turtle hatchlings from Europa and Tromelin Islands are carried rapidly away from the shore by strong currents. As frigate birds are efficient predators of green turtle hatchlings and can remain a threat within 100km of the islands, a longer and faster swim by green turtle hatchlings would have high survival value.

THE ROLE OF OCEAN CURRENTS IN DISPERSON: THE AGULHAS CURRENT

It has long been assumed that the ocean currents play an important role in the movements of sea turtles at all stages of their lifetime. Deraniyagala (1938: 540) and Parker (1939a: 121; 1939b: 156) linked the stranding in Europe of loggerhead and Kemp's ridley turtles with the Gulf Stream and North Atlantic Drift.

Other workers have accepted the role as fact and based dispersal hypotheses thereon (Brongersma, 1968: 118; Carr, 1957: 54; Deraniyagala, 1943: 89; Pritchard, 1967: 30).

Proof that ocean currents act as distributing agents has not been forthcoming until recently. It would now appear that in the case of Tongaland loggerhead and leatherback hatchlings the Agulhas Current plays a significant role in their distribution. During 1967, Mr. Peter Dreyer of Cape Town reported that hatchlings were occasionally washed ashore at Cape Agulhas, 1 650km south of the Tongaland nesting beaches. A serious effort was made to gather more information and stranded hatchlings, with encouraging results which led to a preliminary report summarizing the data collected (Hughes, 1970: 16-21). It appeared that at Cape Agulhas in particular, strandings were occasionally substantial, up to several hundred hatchlings coming ashore at a time. Further, there appeared to be a modal increase in size with increasing distance from Tongaland. It was assumed that the hatchlings came from Tongaland but it was not proven. Sufficient recoveries of loggerhead hatchlings, marked in Tongaland during the 1971-72 and 1972-73 seasons, have now been recorded to remove all doubts as regards the origin of *some* of the stranded hatchlings.

Data from six marked hatchlings recovered away from Tongaland are presented in Table 1. Figure 2 shows the size distribution (carapace length) of all recorded strandings of loggerheads and leatherbacks during the period February — June over the past 6 years. Localities are shown on Figure 3 which shows also the release and recovery points of drift cards released during the present survey; the lines connecting the points are not meant to indicate the lines of drift.

Figure 4 shows the size distribution of loggerhead hatchlings stranded during 1973. Table 2 presents data collected from unseasonal and unusual strandings of hatchling and early juvenile sea turtles in South Africa.

Discussion of the data presented will be deferred until the end of this section.

THE TOLERANCE OF LOGGERHEAD HATCHLINGS TO TEMPERATURE CHANGES

Figure 5 illustrates the results of the experiment on temperature tolerance carried out on loggerhead hatchlings during April 1972. Each line in the graph illustrates the mean response of each group to the different temperature regimes expressed in terms of mass loss and mass gain. The first 14 days represent the period in which the groups were in the experimental tanks, the remaining 14 days the response to the warmer conditions in the control tanks at 24°C.

Differences in mass between each group were apparent within the initial 7 days of the experiment. Compared to the control group mass increase was reduced in those hatchlings at 17° and 18°C; the 15°C turtles remained almost static and the 14°C turtles lost mass steadily. During the 2nd week the lower temperature groups had continued to lose mass, the mass gains of the 17° and 18°C groups were reduced, whilst control hatchlings continued to gain mass steadily. The experiment was terminated at 14 days because it was obvious that continuation would result in mortalities; two hatchlings from the 14°C group died within 3 days of being returned to the control tank.

The immediate response to the 24°C water was surprising and it is noteworthy that within a week the rate of mass gain was almost identical for all five groups.

It was thought that the quantity of food ingested per day by each group would be indicative of their activity. The results are illustrated in Figure 6. The 18° and 17°C groups reflected an almost rhythmic feeding pattern; takng food in increasing quantities for 2 or 3 days then reducing intake sharply, followed by a gradual increase again. The lowest temperature groups were far less active and fed more erratically but with a weak pattern still apparent in the early stages. The pattern broke down in the latter half of the experiment.

DISCUSSION

In summary the experiment showed that loggerhead hatchlings can:

(i) Survive sharp drops in sea temperature.
(ii) Continue to feed and grow in temperatures as low as 17°C.
(iii) Survive for at least 14 days in waters having temperatures of 14°C.
(iv) Recover immediately if returned to warmer waters and gain mass at the same rate as they had previously been doing in warmer water.

Thus hatchlings entering cold water will experience growth arrest which will result in their being markedly smaller than their siblings that have not been subjected to cold temperatures.

The tolerance of loggerhead hatchlings to adverse temperature conditions has high survival value in the study region. Hatchlings are carried south along the east and south coasts of South Africa in the Agulhas Current (see sub-section above). Large eddies and counter-currents are features of the circulatory system and wind variations often result in localised upwelling, particularly along the south coast, with sea temperatures dropping suddenly to 14°C. Should wind, eddy currents or upwelling result in hatchlings being situated in cold water they have up to 14 days in which to be blown or drifted into warmer water. The effects of local upwelling would not persist for as long as 14 days (F. P. Anderson, *pers. comm.*) thus posing no long-term threat to the loggerhead hatchling unless in its period of relative inactivity it is blown ashore by onshore winds.

Further comments will be made in the general discussion below.

GROWTH RATES

Figure 7 shows the mean and range of growth rate, expressed in terms of carapace length, in a sample of 200 loggerhead hatchlings over a period of 10 weeks. The weekly mean sea temperature of the tank for the same period is also shown.

Mean growth rate was steady throughout most of the period of study but declined with the temperature during the final fortnight. Variations in growth rate was marked after one week and became increasingly so. At 12 weeks when mortalities showed a sharp increase, the carapace length variation in 168 hatchlings was from 55mm to 85mm (Insert; Fig. 7).

Despite the limitations of captive growth studies in general and this study in particular it is felt that the data presented in Figure 7 is useful for comparison with wild growth rates because temperatures were similar to, if not slightly higher than, the sea temperature to which wild hatchlings would be subject.

Further, from the stranding records of hatchlings during 1973 (Fig. 4) where considerable size variation is apparent, there seems little reason to believe that loggerhead hatchlings in the wild state are not subject to growth variation such as has been shown for the captive group in Figure 7.

Further evidence to support these suggestions is derived from the recovery of notched hatchlings. The carapace lengths of notched hatchlings recovered during 1972 and 1973, and identified by the letters A, B, C, D, E and F (Table 1), have been entered on Figure 7 at their minimum possible age, i.e. in 4 out of 6 cases the time between their possible release (the termination of the notching programme) and the date of their recovery (Table 1).

Specimen B has been awarded a minimum age of 8 days on the grounds that; it had to travel a distance of 400km; the speed of the Agulhas Current reaches 60cm/sec. in the autumn and thus would take at least 7 days to cover the distance at 50-60km/day; and it is assumed that a half day was required to enter the current and a half day to drift ashore.

For similar reasons Specimen C, with a distance of 1 100km to travel, has been awarded a minimum age of 21 days.

Specimen D is recorded at the minimum possible age. With Specimen B, these two hatchlings show a growth rate apparently more rapid than the experimental animals. It is suggested that this is unlikely because the remaining specimens are well below the size of captive hatchlings of similar ages.

PREDATION

LOGGERHEADS AND LEATHERBACKS

In Tongaland hatchlings are preyed upon mainly by the ghost crabs *Ocypode ceratopthalmus* and *O. kuhlii.* Table 3 gives an indication of the percentage loss to ghost crabs from emerging loggerhead clutches. There are numerous factors affecting the predation rate; size of clutch; the fewer hatchlings the higher the percentage kill, state of tides, e.g. low spring tides result in the hatchlings being exposed for longer periods, etc. Although the crabs constitute the biggest single threat, their victims are often stragglers, or those with poor orientation facility and it is thus advantageous to have these hatchlings removed from the population gene pool.

Other predators in Tongaland are feral dogs, which can cause chaos within a single hatching but are more a danger to eggs than hatchlings; rusty spotted genets (*Genetta rubiginosa*) water mongoose (*Atilax paludinosus*) and occasionally during the day the yellowbill kite (*Milvus aegyptius*) has been seen to take hatchlings.

Ants (*Dorylus* spp.) can also destroy hatchlings en route to the surface. It would appear that the ants attack the hatchlings which then dissipate their energy trying to dislodge the ants rather than continuing to climb towards the surface. These ant attacks are restricted to nests laid hard against the dune forest margins and are of negligible importance.

GREEN TURTLE HATCHLINGS

On the islands of Europa and Tromelin the two major terrestrial predators are hermit crabs (2 species: *Caenobita rugosus* and *C. cavipes*) and the frigate bird *Fregata minor*. Ghost crabs on the islands are small and scarce posing a negligible threat to hatchlings.

No detailed figures are available on hermit crab predation. Unlike the ghost crab which takes a hatchling down its burrow, the hermit crab consumes the hatchling on the surface of the beach, leaving a cleaned carapace. A morning count over 50 metres of beach on Europa Island revealed 124 cleaned carapaces. The hermit crabs (Plate 2) pursue a hatchling with agility lifting their shells high above the sand. On catching the hatchling the shell is dropped onto the beach as a dead weight which the hatchling cannot pull. Immediately a hatchling has been stopped hermit crabs descend upon the victim from metres around and form a pile over the hatchling. Hatchlings following in the track of the victim have a much higher chance of survival.

The frigate bird decimates all daylight emergences both on the beach and in the sea. A typical example of their effect on a daylight emergence:

1630 hours — hatchlings start to emerge onto beach.
1631 hours — frigates attack in increasing numbers.
1642 hours — 133 hatchlings have emerged.
1645 hours — all hatchlings have been eaten.
Distance of nest from sea — 45 metres.
Estimated numbers of frigates — 40.

Two frigate birds were collected and both had 6 hatchlings in their crops: 2 hatchlings were still alive and released only to be taken immediately by other frigate birds.

Other predators on the islands are the pied crow (*Corvus albus;* Europa Island), rock crabs (*Grapsus* spp.) and moray eels (*Echidnae*). The black rat (*Rattus rattus*) previously introduced to all the islands visited, have been seen on the beaches and would probably take hatchlings as would the numerous small sharks, particularly the reef blackfin shark (*Carcharhinus melanopterus*), in the lagoon on Europa.

Paulian (1950) claimed that on Europa the pink-footed booby (*Sula sula*) preyed on hatchlings. No suggestion of this was seen during two visits to Europa.

Near Europa Island green turtle hatchlings were found in the stomachs of the red devilfish or red snapper (*Lutianus argentimaculatus*) and the yellowfin tunny (*Germo albacora*) (Mr. D. Willans, *pers. comm.*).

A juvenile green turtle (straight carapace length 25.7cm) was removed from the stomach of an oceanic white-tip shark (*Carcharhinus longimanus*), caught some 107km off Durban.

FEEDING

Table 4 summarizes the stomach contents of 37 loggerhead hatchlings collected on the beaches of Cape Agulhas. Unfortunately much of the material examined was fragmentary and the only food organism clearly identifiable was *Physalia.* The nature of the other identifiable matter; feathers, plastic beads, bark, etc. suggests that loggerhead hatchlings will eat anything that is floating and small enough to swallow. Captive hatchlings feed voraciously on *Physalia*, *Porpita*, *Velella* and *Janthina janthina.* The grit found in the stomach and intestines of some of the hatchlings examined might be fragments of *Janthina* shell.

No identifiable material has been found in stranded leatherback hatchlings.

The juvenile green turtle taken from the stomach of a shark 107km off Durban had its stomach filled with *Janthina janthina.*

PARASITES, EPIZOITES AND INJURIES

Hatchling leatherbacks and loggerheads, on stranding at Cape Agulhas, have been found to harbour internal parasites (roundworms, *sp.* ?) and numerous external epizotic organisms such as goose-neck barnacles (*Lepas spp.* and *Conchoderma virgatum*), acorn barnacles (*Balanus sp.*) (Plates 3 and 4), and the bryozoan *Membranipora membranacea.*

The occasional loggerhead hatchling has been found with fine strands of green algae on the plastron but it is not common to all.

Injuries are uncommon and restricted to the hind flippers from which crescent shaped pieces are missing (Plate 5). Such wounds, if persisting to adulthood, could be misidentified as shark bites.

GENERAL DISCUSSION

From the data presented above it is concluded that loggerhead and leatherback hatchlings spend at least three months under the direct influence of the Agulhas circulation; feed on pelagic organisms and, as they collect numerous surface epizotic organisms, it appears that they are relatively inactive.

The wide variation in the sizes of hatchlings stranded on the South African coast requires comment (Fig. 2). At 60cm/sec. the Agulhas Current could carry a drifting hatchling from Tongaland to Cape Agulhas in 32 days. The notched hatchlings found at Cape Agulhas (Table 1) took at least 48 days which would suggest that the turtles do not remain in the main stream of the current but are probably delayed by eddy circulations or possibly winds. If this is assumed, then the wide range of hatchling sizes can be explained. If caught in an eddy of high water temperature and optimal growth conditions, a larger hatchling will result. In the same period of time, siblings caught in an inshore eddy coming into contact with upwelled water will be smaller (*cf.* Fig. 5).

Stranded hatchlings are a direct result of inshore eddies coming into contact with water of low temperature associated with the south-east wind. At Cape Agulhas, Mr. P. van As (*pers. comm.*) reported two loggerhead hatchlings walking out of the sea shortly after the termination of a south-easterly gale which resulted in a strong northerly current with a water temperature of 15°C.

Strandings during 1973 show a clear association with the south-east wind. Between the 4th and 27th April there were substantial strandings of hatchlings along the shores of Cape Agulhas. Hundreds came ashore over the weekend of the 6th, 7th and 8th at Waenhuiskrantz (Dr. R. van der Westhuizen, *pers. comm.*).

At the Heunignes Research Station weather records showed that the south-easter started on the 3rd April (Dr. N. Fairall, *pers. comm.*) and blew almost continuously until the 26th April. The last hatchlings reported were on the 27th April.

The numbing effect of cold water is illustrated by the behaviour of a loggerhead observed during the present study on Cape Agulhas during April, 1970 when the water temperature dropped from 21°C to 17°C. The hatchling had been washed ashore at high tide and left in the debris line as the tide fell. It is thought that with exposure to the sun the hatchling had recovered sufficiently to walk back towards the sea. After maintaining a direct line for 20m it suddenly lost orientation and circled and wandered for about a metre and then stopped. It was found at 1630 hours alive but weak and it died within an hour.

The possibility that stranded hatchlings have been subjected to varying periods in cold water, and thus growth arrest, must be taken into consideration when viewing the sizes of recovered notched hatchlings. From Figure 7 it would appear that the wild growth rate is markedly slower than the captive specimens. It is almost certain that the notching does not affect the hatchling adversely as, with specimens E and F (Table 1) was a third unmarked hatchling measuring 52.2mm, suggesting that the three were in a group (resulting from water mass movement, not conscious adhesion). The size distributions in Figure 2 would seem to indicate group arrivals in different size classes but in the 1973 recoveries (Fig. 4), only the Cape Agulhas strandings during April suggest a size group.

Table 2 shows some extreme cases: firstly, some hatchlings collected at Port Elizabeth in late March measuring over 100mm carapace length. No hatchlings have ever been seen to emerge in Tongaland during December so if the stranded specimens did originate there they are less than 12 weeks old. They might, however, have come from Mozambique, the stranding of a 60.0mm loggerhead in northern Tongaland during early March (Table 2) suggests that this might be possible as loggerheads are known to nest as far north as 23°S.

The stranding of a 112mm loggerhead 4½ months after those mentioned above show the wide range of sizes emanating from a single season. The largest and only juvenile specimen found in South Africa was the 219.0mm specimen from George (Table 2). Assumed to be approximately one year old this turtle showed a faster rate of growth than ever recorded in the Durban Aquarium.

With the exception of this single specimen no juvenile loggerheads have been recorded from the entire South African coast and no more hatchlings after early June (again with the exception of the 112mm specimen in August). This would suggest that the currents bear the hatchlings away from the coasts either into the Agulhas gyral via the Agulhas return current or around the Cape of Good Hope into the South Atlantic. It is suggested that hatchlings travel in both directions but with the majority recycling in the gyral. Unless hatchlings passing around the Cape are blown close inshore on the west coast there are no temperatures low enough to form a barrier preventing their entrance into the South Atlantic. Whether or not these hatchlings make their way back to the Indian Ocean is a matter of great interest.

It is assumed that the leatherback turtle is subject to the same influences as the loggerhead but is possibly less hardy (see Hughes, in press).

Accepting the role of ocean currents it would appear that green turtles from Europa Island are kept within the Mozambique Channel gyral with the occasional stray being carried southwards by the Agulhas current (Table 2 and the specimen from the stomach of an oceanic whitetip shark).

Tromelin green turtle hatchlings should be carried to the coast of Madagascar and possibly recirculated in the gyral between the Mascarene ridge and Madagascar.

With both nesting areas the gyrals are small and would ensure that turtles are brought within reach of suitable feeding grounds within a few months.

Green turtles can change to the adult vegetarian diet at about 6 months of age.

Loggerheads on the other hand are swept into larger gyrals (Fig. 3) which would necessitate long periods at sea, e.g. the Tongaland loggerheads enter the Agulhas gyral or even the South Indian Ocean gyral. Loggerheads from South-East Madagascar are probably carried into the south Indian Ocean gyral and some may find their way into the Agulhas gyral; in either direction a long sea voyage is obligatory (Fig. 3). Evidence presented in the following sub-sections will show that this is a plausible hypothesis.

In summary, the ocean currents play an important, if not the dominating, role in the initial year of life in sea turtles. After the first year the influence of the currents declines according to the requirements of the species.

Growth rate to maturity and beyond

Having discussed growth rates in the hatchling stages it is pertinent, and convenient at this point, to establish an approximate time scale for the stages which will be dealt with later in this section. These stages are expressed in terms of straight carapace length as follows:

Juvenile stage: 15.0 - 60.0cm
Sub-adult stage: 61.0 - 80.0cm
Adult stage: 81.0cm upwards

In the preceding sub-section it was noted that loggerhead growth rates in the first year are variable both in captive specimens and those recovered from the tagging programme. Further, early hatchlings and late hatchlings will be subject to different sea temperature regimes and will also show variation in growth rates. These combined factors should eventually lead to a stage where no age class would be discernible in terms of size or time. In support of this suggestion Table 5 is presented showing, in 2cm classes, the size range of loggerheads stranded or caught along the Natal coast during the past 5 years. There is no indication of any size class being associated with a particular time of the year. Thus any growth curve related to time, based on carapace length or mass, must be regarded as an approximation only.

This being accepted, Figure 8 is presented showing an approximate growth curve relating time and straight carapace length. The data were collected from captive loggerheads in the Durban Aquarium. The oldest two loggerheads have been reared from hatchlings to 9½ years of age, always at ambient sea temperatures and all specimens are fed twice daily on either pilchard or hake. In presenting this curve it must be stated that the tanks through which the turtles have passed are variable in size, are often unsuitable and can have considerable effect on the growth rates of the turtles.

For example, another specimen, now 5 years old, was kept in a basement tank containing 7 200 litres of water and reached a mass of 10.5kg and remained at the same mass for eight months.

Transferred to the main fish tank containing 800 000 litres of water, its mass increased by 3.6kg in 23 days, and doubled in another 73 days to 20.0kg. In the same time the carapace length increased from 41.0 to 49.0cm.

As a result of these variables and the obvious shortcomings of using captive material as a source of data, errors of up to two years in the suggestions as to the duration of the various stages in the life cycles discussed later must be tolerated until an accurate ageing method becomes available. The possible future recovery of some turtles, notched as hatchlings in Tongaland, might also provide a guideline as regards age at maturity.

Included on Figure 8 are growth data from other sources. Data from foreign sources are summarized in Brongersma (1972: Table 11) whilst data from East London and Port Elizabeth were provided by Messrs. A. Parkins and T. Dalton respectively. Uchida (1967: 500) and Parker (1926; 1929, in Brongersma, *ibid.*) recorded growth rates consistently more rapid than those observed in Durban and it would be of value to know whether the hatchlings were kept in heated aquaria during the first winter after hatching.

Temperature, as has been shown, is critical during the first year after which the main factor governing growth rate is probably availability of food. This is exemplified by comparing the the growth rates recorded in Durban, where no heating facilities are available, and those recorded in Port Elizabeth where hatchlings are kept at 21.1°C throughout the first winter. At the end of the first year Port Elizabeth turtles are larger than those in Durban (Fig. 8) and are then transferred to unheated external ponds in which they thrive. Thus the age at maturity might be dependant on what environmental conditions the hatchling finds itself during its first winter; if in the southern part of a gyral growth rate will be reduced and vice versa if it is the northern part where temperatures are more amenable.

If the the data collected from recovered wild hatchlings, notched in Tongaland, are valid then it would appear that all of the growth rates reported, with the exception of the East London data, are too rapid in the early stages. As far as the Durban data are concerned, unsuitable tanks may have reduced the growth in the juvenile stages.

Commenting on the reported ages of loggerheads at maturity it seems likely that Uchida's (*op. cit.*: 497) suggestion of 6-7 years is slightly previous and Hughes' (1972: 21) suggestion of 10-12 years is certainly too long. During the past two years the oldest loggerheads in the Durban Aquarium have shown a sharp decline in growth rate possibly prompted by the limitations of the tank.

It is therefore suggested that under optimal conditions loggerheads can reach sexual maturity in 6 years (Uchida, *ibid.*) but in the more hostile conditions likely to be encountered by the Tongaland loggerhead the age of maturity is probably nearer eight. From this suggestion it can be assumed that the juvenile stage can terminate between four and five years and the subadult stage would last two or three years, with the size of the turtle at sexual maturity being variable.

Although there is obviously a minimum size at which loggerheads are capable of nesting there are few data to support the suggestion that a nesting turtle of 85cm curved carapace length is a neophyte nester or that a large female of 98.0cm curved carapace length is an old turtle. The Tongaland programme has been underway for 10 years and during the 1972-73 season 47% of the females handled had nested at least once, twice and occasionally three times before. If there was substantial growth after a female had nested for the first time it would be expected that those that were known to be older, i.e. those that bore tags implanted in previous seasons, should be significantly larger than the untagged group which must contain a certain proportion of neophyte nesters.

Figure 9 shows the size frequency, in 1cm classes, of tagged and untagged loggerheads encountered during the 1972-73 season. The mean curved carapace lengths of tagged and untagged turtles were 94.34cm (S.D. 3.92; n = 119) and 93.6cm (S.D. 4.39; n = 138) respectively. The apparent difference in length was not statistically significant ($P > .1$) although larger samples in future might show that a difference does exist.

It had been thought that carapace length measurements would show differences as the turtles aged. Unfortunately since the inception of the Tongaland programme standard field measurements have been taken over-the-curve using flexible steel tapes (Hughes, *et al.*, 1967: 10) and the substantial loss of plastic tags has masked the inaccuracies of the method until the 1972-73 season.

Figure 10 shows measurement differences in loggerheads after intervals of one, two, three and five years, and in leatherbacks after intervals of two, three and six years. Allowances of up to 1cm had been made for measurement error but differences exceeding 5cm are obviously intolerable, and cast doubt on all the more acceptable measurements. Thus as far as mass data are concerned over-the-curve measurements are acceptable but at the individual level they must be regarded as useless.

It can be concluded, however, that in considering the lack of significance between the sizes of tagged (older) and untagged loggerheads (including younger animals) growth rate might be present but less than 0.5cm/year as most of the tagged turtles (91.0%) had been absent for at least two years. From the highly unsatisfactory data in Figure 10 only one dubious conclusion can be reached viz. if growth is continuous it is small, because after 5 years one loggerhead showed a 4cm decrease in length and even with an error of 5cm it is still remarkably similar to its original measurement.

There are no indications of remarkable growth rates in the leatherback data either.

No data are available on growth rates for green turtles in the study region but in Tortuguero, Costa Rica, Carr and Goodman (1970: 783), on analysing 15 years of measurement data taken with calipers, suggest that green turtles mature at various sizes, there being no tendency for a large green turtle to be an old animal.

Carr (1971: 32) maintains, however, that growth does occur in mature green turtle females and suggests that is in the order of 2.54mm per year which, as he claimed, is difficult to detect on an animal reaching a carapace length of 1200mm.

Carr's data on the green turtle does, however, lend some support to the apprehensive suggestion made above that a similar, barely traceable, rate of growth may be exhibited by the Tongaland loggerhead after it has reached nesting maturity.

The longevity of the loggerhead turtle is therefore impossible to judge from size. Flower (1937: 14) gives the longevity record of an Atlantic loggerhead as 33 years based on a captive specimen in the Lisbon Aquarium. In the study region the longest lived loggerhead was one which lived for 26 years in the East London Aquarium.

If one accepts eight years as a minimum age for sexual maturity then the oldest known female loggerhead nesting in Tongaland is a female (No. C207) which was first tagged in 1964 and was recorded in 1972-73, a total spread of 9 years. Added to the suggested minimal age at sexual maturity she is at least 17 years old and measures approximately 101.0cm over-the-curve of the carapace.

Although great ages are popularly attributed to sea turtles there is no scientific justification to this belief and only tagging programmes of long duration will provide an answer to the question of longevity.

Juvenile stage

LOGGERHEADS AND LEATHERBACKS

Hughes (in press) demonstrated that there is a total absence of juvenile loggerheads along the coast of the study region and only one juvenile leatherback has been caught off Cape Town.

Surveys of material in fishing villages where the hunting pressure on littoral sea turtle populations is intense, have shown that up to 60cm carapace length, these species are not present. Fishing is undertaken by net and harpoon and there is no selection, neither by size nor species. It would appear, therefore, that the juvenile stage of these two species is spent in the open ocean as was suggested in the previous section.

Added justification for this conclusion may be adduced from reports from skin divers in Reunion Island who claim that juvenile loggerheads are periodically found on the eastern littoral of the island but seldom remain for long periods. Individual size appears to be in the range 40-50cm carapace length and are sufficiently frequent to have a local name *La tortue blonde.* Adults are very rare around Reunion and are known as *Gros tête.*

Current configurations would suggest that these juveniles originate in South-East Madagascar but they could be from the African nesting grounds as their size would indicate that they are between 3 and 4 years of age (Fig. 8) or roughly a year younger than the size at which loggerheads return to the littoral.

In the total absence of evidence to the contrary, and, considering the data presented above, it would appear that loggerheads in the study region spend at least 4 or 5 years well away from the littoral zone and thus the situation is similar to that suggested by Brongersma (1972: 144) for loggerhead movements in the North Atlantic and by Uchida (1973: 15) for the North Pacific.

It is assumed that the drifting juvenile loggerheads feed on pelagic organisms such as *Janthina janthina*, *J. prolongata* and *Physalia.* Pouchet and de Geurne (1886, in Brongersma, *op. cit.:* 158) found pteropods, goose-necked barnacles, fragments of medusae, pieces of bark, etc. in the stomachs of juvenile loggerheads caught in deep water near the Azores, suggesting that, like the hatchlings, juveniles will feed on anything that is floating (see also section on feeding in sub-adults, below).

In the light of the above, juvenile leatherbacks are probably in the open ocean as well but it is doubtful whether they drift as does the loggerhead.

GREEN TURTLES

Juvenile green turtles are found along the littoral throughout the study region, even as far south as Cape Agulhas. Brongersma (1972: 228) suggests that green turtle juveniles move over long distances and the presence of green turtle juveniles at the Cape would support his views. The nearest green turtle nesting ground is Europa Island, 2 800km away, and it is possible that they come from even further afield. On Europa Island the lagoon has numerous juveniles greens from 20.0cm carapace length upwards. From Hirth's (1971: 3: 17) review on growth data of the green, these Europa specimens would be at least one year old.

It would appear, therefore, that the pelagic stage in greens lasts for little more than a year and they return to the littoral, changing to the diets typical of the species viz. algaes and seagrasses (Table 8).

Some green turtle juveniles would appear to remain for extended periods in suitable feeding areas. On the 16th December, 1969 a juvenile green turtle (carapace length 36.7cm) was tagged (A201) and released at Inhassoro, Mozambique. 33 days later it was recaught at the same locality.

During January, 1967, 2 juvenile green turtles were caught in rock pools 4.8km north of the Bhanga Nek camp in Tongaland. They were tagged with conspicuous yellow plastic tags (4 970, 4 841) and released. 10 months later a tagged juvenile was seen at the same place. Unfortunately it avoided 3 members of staff trying to catch it so the number was not ascertained but there was no doubt as to the presence of the tag.

This apparent tenacity to a general locality was reported by Schmidt (1916: 16) who tagged and released juvenile greens in the West Indies.

Sub-adult to adult stage

RETURN TO THE LITTORAL

The smallest loggerhead recorded in the study region is 60.5cm straight carapace length. This suggests an age of between 4 and 5 years (Fig. 8).

As only one sub-adult leatherback has been taken in Natal no suggestions are made concerning their age.

Sub-adult greens have been dealt with above.

FEEDING CHANGES

LOGGERHEADS

Table 6 summarizes the stomach contents of 26 loggerhead turtles from the Natal coast. These data have been grouped into 3 size categories: 60-70, 71-80 and 80cm plus straight carapace length.

55.6% of the smallest size group are still feeding on floating material as was recorded for the hatchlings. The remainder contained littoral and benthic organisms.

60.0% of the 70-80cm group had the remains of benthic organisms in their stomachs but the remainder had floating material, the one specimen having the carapace shields of a hatchling loggerhead; the only incidence of cannibalism recorded in this area.

The larger size groups contained only benthic organisms comprising mainly molluscs. Table 7 gives a species list of identifiable molluscs. The most frequently eaten species are *Bufonaria crumenoides* and *Ficus subintermedius* and these are illustrated in Plate 6.

Hermit crabs appear frequently in stomach contents but whether they are deliberately eaten or are mistaken for Mollusca is difficult to assess. The more active hermit would make it easy prey for the loggerhead as its movement might render it more noticeable.

There is no doubt that molluscs are favoured because bivalves are commonly ingested. One turtle (Table 7) had 6kg of crushed black mussel *Perna perna* shells in the stomach and gut. The shell in the rectum showed no damage from digestive juices.

The crushing power in loggerhead jaws is illustrated by the rarity of whole shells in stomach contents.

During the past ten nesting seasons in Tongaland only 3 dead female loggerheads have been washed ashore. Two had empty stomachs but the third contained fragments of crab, spiny rock lobster, spiny sea urchin and in the oesophagus was jammed a porcupine fish *Diodon* sp. which is assumed to have caused the death of the turtle.

The only other report of a turtle eating fish was described by Mileham (1965: 20) who saw "a huge turtle" swimming in a shoal of pilchards *Sardinops ocellata* near Durban. The turtle was in the centre of the shoal with a circle of fish around it. Mileham reported that it took mouthfuls of fish at leisure.

GREEN TURTLES

Table 8 summarizes the stomach contents of 12 green turtles, juvenile, sub-adult and adult, from the Natal coast. The main algaes eaten by the green turtle in this region are two *Gelidium* spp., *Codium duthieae* and *Caulerpa filiformis*.

In Mozambique one green turtle stomach examined contained *Cymodocea ciliata*, *Halodule univervis* and *Zostera* sp., all of which are listed by Hirth (1971: 3: 16).

PARASITES AND EPIZOITES

LOGGERHEADS

In considering the presence of epizotic organisms on loggerheads of different sizes it is suggested that further evidence is provided to show a marked change in behaviour by the host animal.

Table 9 shows, in grouped size classes as in Table 6, the epizoites on the carapace of loggerheads from the Natal coast. It can be seen that in the smallest turtles the goose-neck barnacle *Lepas* sp. is still present on two animals (Plate 7). The typical acorn barnacle *Chelonibia* sp. of adult loggerheads is found on only 18% of the turtles whilst 64% have no adherents.

As the size of the turtle increases so does the frequency of *Chelonibia*; 18% to 21.4% to 47.4%. In a sample of 30 loggerhead females from Tongaland 73% carried *Chelonibia*.

Thus it would appear that in the 60-70cm size class there is a change in life patterns resulting in conditions unsuitable for *Lepas* but favourable for *Chelonibia*.

In mature females the carapace occasionally has burrowing barnacles *Stephanolepas* sp. (?), small skin barnacles *Platylepas* sp., red and green algaes and the leech *Ozobranchus maggoi*. Although uncommon, up to 49 leeches have been found around the cloaca of a single turtle (Hughes, *et al.* 1967: 27).

OTHER SPECIES

Nesting female leatherbacks normally carry small acorn barnacles *Platylepas* sp. on the skin. At sea leatherbacks have been photographed accompanied by sucker fish *Echeneis naucrates* and pilot fish *Naucrates ductor* (Condon, (1971): 117).

Juvenile green turtles in Mozambique have been found with heavy infestations of *Chelonibia* (see Hughes, 1971a: Fig. 10) but these epizoites are rare in adult females. Of 343 nesting females on Europa Island 92.7% had no adherents; 7.1% had either *Chelonibia* (only 1 each on three cases) or the burrowing barnacle *Stephanolepas* sp., three were so heavily infested with this parasite that half of the carapace was one continuous tumour (see Hendrickson, 1958: 524).

94% of laying females on Tromelin Island had no adherents, the remainder only *Chelonibia*.

Europa Island harbours an unusual parasite; the mosquito *Eretmapodites plioleucas* (Viette, 1966: 202). It is no exaggeration to state that there are millions of mosquitoes and they descend on nesting females, piling up to 2cm thick on the eyelids, and over the joints between the carapace shields.

Onset of sexual maturity and general movements

LOGGERHEADS

Hughes (in press) demonstrated that in the 60-70cm carapace length class the first signs of sexual maturity become apparent. At the same time there is a change in feeding emphasis from floating to benthic food organisms. These changes are accompanied by changes in the epizotic organisms adhering to the carapace. Hughes (*op. cit.*) further showed that at least 64.0% of the loggerheads recorded from the Natal coast are clearly immature, if the 80cm carapace length class is taken as the mature size and indications are that is an underestimation.

Figure 11 shows the catches of loggerhead, and other turtles, in the anti-shark network since 1965. A histogram showing unidentified turtles caught between 1965 and 1968, when shark-meshers had no means of identifying species, is included. In all 85 loggerheads have been caught since 1968 as compared to 49 greens, and it can be assumed that a large porportion of the unidentified turtles, 176 in all, also consisted of loggerheads. Of this substantial catch only one has borne a tag from the Tongaland programme (Table 10, No. A49). It was taken at Warner Beach, south of Durban, during late January, 1970 having just completed a nesting season.

Figure 11 shows also that the turtle catches correlate well with the sea temperature and these data suggest that either turtles are moving along the coast following the advances and retreat of warm water, or that they are moving away from the coast during the cold winter months. For example, at Durban the coolest temperature is recorded in August (20.5°C) whilst offshore temperatures are 21.1°C. In September the situation is reversed with cooler temperatures offshore (20.3°C) and Durban temperatures rising (20.8°C).

That there is movement, however, is clear and the data, applying as it does to all species except the leatherback, would favour the coastal movements.

Accepting that movement is characteristic of loggerheads the question arises why more adults are not caught in the nets. There is no doubt that some specimens are not brought to the Institute because of their size but as many animals were inspected as they were brought ashore this cannot be taken as a serious reason for the paucity of adults. Of all the females caught only one has been fully mature (i.e. nested, No. A49) and the largest female measured had a carapace length of 87.0cm which is just above the mean size recorded in Tongaland (86.4cm).

The most obvious answer, and valid up to a point, is the fact that 97.0% of extra-nesting area recoveries of females tagged in Tongaland have come from Mozambique, Tanzania and Zanzibar. There would appear to be almost complete segregation between adults and young stock.

However, the fact that one female has been found south of Tongaland suggests that the answer is more complex and may involve territories.

Table 10 summarizes the known recapture data on extra-nesting area tag recoveries of loggerheads (many other recovery records lack dates or tag numbers). With one possible exception all these turtles have been captured at dates suggesting movement associated with the nesting season.

Those turtles taken immediately after the completion of a nesting season have travelled long distances at substantial speed. It must be pointed out that speeds recorded in Table 10 must be regarded as minimal for the time interval is calculated from the last sighting in Tongaland although the turtle may have nested again and been missed by the staff.

The Zanzibar and Tanzanian recoveries showed that a loggerhead turtle, after a season of laying, can maintain a speed of 40km/day for 66 days. The purpose of this swift and lengthy migration would suggest that the turtle has a goal, possibly a feeding range or territory.

There are suggestions that sea turtles, with the exception of the olive ridley and leatherback, do have feeding territories. Carr (1952: 387-388) describes a large loggerhead which was seen over a period of many years in a creek in Georgia. Some 9.6km up the Kromme River, Cape Province, there is, apparently, a large sea turtle (loggerhead?) well known to local residents.

Carr (1955: 206-236) described several convincing stories showing the ability of green turtles to return to a home territory and the same coral head near which they had been previously caught. The speed of the return was comparable to the speeds exhibited by migrating loggerheads.

To summarize the above; tagged loggerhead females are taken mainly north of Tongaland in months associated only with the nesting season; they move with deliberation suggesting a goal to which the turtle returns after the nesting season.

Thus the apparent lack of mature females from the Natal coast might be explained simply as segregation or, that in regaining their territories, they swim directly down the coast, thus avoiding the shark nets which are normally within 200 metres of the shore and often situated in bays. Once in the home territory their movements are very limited thus reducing the chances of getting caught.

If turtle territories do exist the lack of tagged turtle catches during months not associated with the nesting season might also be explained.

To this must also be added the possibility that the larger loggerheads may prefer deeper water would which remove them from nets restricted to the littoral zone. However, in Madagascar, the balance between immature and mature size loggerheads taken on the littoral is very even (Hughes, in press) suggesting that in more tropical waters adults show no preference for deeper water.

ESTABLISHMENT OF A TERRITORY — THE MECHANISM OF DISPERSION

If the concept of a territory or home feeding range is accepted it is possible to provide another reason for the higher catch of immature turtles in the shark nets. The sub-adult stage is a period of change and movement and the turtles have not yet established a territory and are possibly driven away from suitable areas by resident adults.

From these movements the widespread nature of the loggerhead population might also be explained. Turtles tagged in Tongaland have been caught 2 800km north and 430km south of the tagging sites, a total spread of 3 310km. The speed of travel suggests that this is not merely random wandering, nor does the renesting recovery rates in Tongaland (see below) which have shown a consistent increase every year.

Therefore it is suggested that most, if not all, adult female loggerheads have home ranges or feeding territories as do most carnivores. Immature animals are therefore forced, on their return to the littoral and contact with the adults, to move constantly as they mature, until they find a suitable vacant niche. Movements can be southwards, although this is possibly not favoured by adults because of the cold winter temperatures, or north which might necessitate a long voyage before an unoccupied niche is found. Large populations would mean longer voyages and a wider dispersal of the species.

PREDATORS AND INJURIES

The main predator of sea turtles from the juvenile stage through adulthood is the shark, two species of which, in the study region, have been found to contain portions of larger sea turtles in their stomachs. These are the tiger shark *Galeocerdo cuvieri* and the Zambezi shark *Carcharhinus leucas* (Bass, 1972: Table 37).

A sub-adult hawksbill was found in the stomach of a brindle bass or garrupa *Promicrops lanceolatus* shot by skin-divers in Mozambique (Condon (1971): 253).

It is perhaps noteworthy that of 44 mainly sub-adult loggerheads examined along the Natal coast only 1 (2.2%) had any obvious natural injury.

In Tongaland, mature nesting females show a higher incidence of injuries. During the 1965-1966 season, of 204 adults 21% had notable injuries; 67.5% were on the flipper, 20.9% on the carapace, and the remainder deformations (lumps, etc.) for which no ready explanation is available.

This marked difference in injuries particularly on the flippers would suggest that adults survive more shark attacks than younger turtles.

As females tend to nest near rocky areas in Tongaland, they are exposed to carapace damage arising from collisons with rocks. Some carapace injuries appear to have been caused by sharks because the large crescent-shaped gaps could hardly be caused by anything else.

As was mentioned in hatchling predation (Plate 5) some flipper injuries if they persist to adulthood, might be mistaken for shark bites but in the light of sub-adult data presented above it would be a rare occurrence.

Few data are available on other species. One juvenile green brought into the Durban Aquarium had the last marginal of the left side of the carapace neatly excised. All other juveniles had no injuries.

On Europa Island only 35 green turtle females (9.1%) out of 383 had external injuries, 48.6% of which were flipper injuries and the remainder on the carapace. Hendrickson (1958: 522) estimated that 4% of the green turtles nesting on the Talang Islands off Sarawak had injuries attributable to sharks.

It might be concluded that the higher incidence of injuries on loggerheads as compared to greens is merely a result of there being so many more green turtles. However, the differences in feeding areas might have some effect as the loggerhead feeds on deeper reefs than the green, which, because of its vegetarian diet, is normally found in shallow water. Loggerheads rising for air from a 10 or 20 metre deep reef must be exposed to attack for longer periods than, for example, a green turtle rising from 2 or 3 metres.

General discussion

It has been shown that the loggerhead turtle is a hardy species surviving in temperatures not favoured by the green turtle. Almost all of its early life is spent in the temperate latitudes seldom penetrating sub-tropical waters. This would add credence to the suggestion made by Nishimura (1967: 32) that the loggerhead could be regarded as an antitropical species.

With regard to the study region this statement requires qualification because many adult females are found in sub-tropical waters reaching as far north as 6°S. It would appear that many adults come into temperate waters during the nesting season only.

Thus, in the first year of life, it has been shown that warm water is important to maintain a rapid rate of growth and it seems that after maturity females prefer warmer water. It would appear that there might be a link between the two stages.

Hatchlings carry no fat but sub-adults are almost always extremely well insulated, layers of fat around the inner surface of the carapace reaching thicknesses of 2cm. This fat would ameliorate the effects of cold temperatures and enable the sub-adults to survive the cooler winter temperatures of the South African east coast. There are suggestions that they can live in the cold waters of the west coast as a healthy sub-adult loggerhead was taken off Saldanha Bay during October, 1962 (Dr. P. Best, *pers. comm.*).

During a nesting season a female can lose a quarter of her body-weight and much of her fat reserves would be used up in egg production. She would be, therefore, ill prepared to face the low winter temperatures of the temperate waters and would probably retreat to warmer waters as has been suggested by tag recoveries and the lack of captures in the anti-shark network.

The presence of a feeding territory to which the effete female could return and recover in relative peace would be an advantage, particularly if the younger loggerheads were geographically separated from the adult stock and thus not competing for food. This situation protects the female in her vulnerable stage when she requires adequate food supplies.

With the green turtle such spatial separation of sub-adult and adult stocks is not necessary because of the unlimited quantities of vegetable matter at their disposal.

As far as the other species in the study region is concerned insufficient data have been collected on which to base conclusions other than the fact that there is no inter-specific competition for food except in the hatchling and juvenile stages when they are in the open ocean.

Migration, re-migration, orientation and recruitment in sea turtle populations with particular reference to the loggerhead turtle in Tongaland

Introduction

Intensive and continuous tagging programmes on sea turtle populations have been undertaken in Sarawak, Costa Rica, Australia and Tongaland. As the first three regions have mainly green turtles much of the general sea turtle biology available in literature is based on the behaviour of the green turtle.

Harrison (1956: 513) was the first to show that the green turtle did not nest every season and he confirmed the findings of Moorhouse (1933: 3) that green turtles nested several times within a season. The size of the Talang Islands on which he worked ensured that virtually every emerging turtle was checked and it was not until the third season after the year of initial tagging that 14 turtles returned to nest out of 1 514 turtles originally tagged.

From Costa Rica, Carr and Giovannoli (1957: 18) showed that long-range migrations were a proven feature in the life-cycle of green turtles but, as Harrison found in Sarawak, the recovery rates in turtles returning to Costa Rica were strikingly small (Carr and Ogren, 1960: 4) and after 15 years are still small, there having been only 447 recoveries from some 7 000 turtles tagged (Carr and Carr, 1970a: 336). Apparently recovery rates in the Australian programme on Heron Island are similarly small and it has been suggested that the re-nesting behaviour of the green turtle is inefficient (Bustard, *pers. comm.*).

In the study region the tagging programmes currently underway on the green turtles of Europa Island, the Glorious Islands and Tromelin Island have not been going long enough to add much to the knowledge of green turtle biology other than the fact that long range migrations are normal in this region.

The Tongaland programme, however, was the first to concentrate on the loggerhead turtle with a lesser emphasis on the leatherback of which there are very few in this area. From the data presented below it will be seen that the loggerhead would appear a more efficient nester than either the green or the leatherback; that it has a fairly well developed orientation ability and is the equal of the green turtle in its migratory ability.

Materials and Methods

PATROLS

The Tongaland research area originally covered some 32km and was fully described by McAllister, Bass and Van Schoor (1965). Since 1969 and aided by the arrival of a beach buggy in 1970 tagging has been extended to cover 56km and, beach state permitting. this area is patrolled at least once per day by vehicle.

Intensive foot patrols are now carried out 8km north and south of Bhanga Nek camp with the assistance of 2 university students and 2 trained African staff members ensuring double nightly coverage of the most heavily utilized stretch of beach (see Fig. 20).

During the 1971-72 season although record tagging figures were obtained for both the loggerhead and leatherback there were clear indications that the patrol methods were inefficient, i.e. the contact success between the staff and emerging loggerhead turtles was unsatisfactory. It was shown by Hughes and Brent (1972: 41) that at the single contact level the results were satisfactory, i.e. up to 84.79% of the emerging turtles were handled at least once during the course of the season. At the multiple contact level, however, results were unsatisfactory, the most successful year being 1968-69 in which 47.38% of all emergences were encountered, but the season was the one in which the fewest turtles were recorded. It appeared clear that the more turtles present the less one handled in a relative sense (see Fig. 12). Thus during the 1972-73 season the double patrol on foot was instigated along with more intensive buggy patrols and the results were gratifying: for the entire protected area the single contact success was 87.29% and the multiple contact success 48.31%. In the intensive patrol area the multiple contact success was 57.26%. It would appear, therefore, that although there is room for further improvements the patrol methods in Tongaland are now relatively efficient, although it is noted that 1972-73 was not a particularly successful year for loggerheads.

Leatherback handling has been consistently more erratic because of their smaller numbers and the fact that they are less concentrated than the loggerhead. Single contact handling is normally in the region of 60.0% and multiple contact 20%.

TAGGING

During the first two seasons in Tongaland small plastic tags bearing only a number were applied to nesting turtles (McAllister, *et. al.*: 1965: 14).

In the 1965-66 season a larger plastic "Rototag" was used bearing a number and a return address (Hughes, *et al.* 1967: 8) and the following 3 seasons saw the use of a round yellow plastic tag normally used by the Oceanographic Research Institute, Durban for tagging sharks (Hughes and Mentis, 1967: 57).

All plastic tags proved useless in the long run as virtually every tag has been lost. Few have persisted as long as two seasons and consequently a very substantial body of data has been lost. Fortunately, because most of the plastic tags necessitated punching a hole in the flipper, it has been possible to recognise a returning turtle because of a callous, or even two, in the site where tags are normally implanted viz. between the two innermost scales on the distal edge of the foreflipper.

With leatherbacks, identification of animals having lost tags is not as easy and they are now tagged twice; once in the distal edge of the foreflipper and again on the inner margin of the hindflipper, an insurance that has paid off on at least one occasion.

Since the latter half of the 1969-70 season only monel metal clinch tags supplied by the National Band and Tag Company have been used with excellent results.

Only monel metal tags have been used on green turtles during the past three years and the tags are implanted in the same site as used on loggerheads.

Results

Migration, from extra-nesting area recoveries

LOGGERHEADS

Table 10 gives details of recovered loggerhead females away from the nesting beaches. In addition to these recoveries, there have been other tagged turtles taken but no details recorded; the tag being thrown away or the turtle released alive. These details came to light during the questioning of fishermen in Mozambique. All recoveries are shown on Figure 13.

It is of interest to note that only two loggerhead turtles have been recovered away from the tagging beaches in Mon Repos, Australia. Both turtles had travelled north over extensive distances, 2 160km and 1 760km, one at a speed of 31km per day and immediately after a nesting season (Bustard and Limpus, 1970: 358; 1971: 230), thus showing migratory behaviour similar to that exhibited by Tongaland loggerheads.

As mentioned in the previous section only 1 of 34 recoveries of Tongaland females has been taken south of the nesting ground and the possible reasons for this have been discussed.

There seems little reason to believe that the migration exhibited by loggerheads is merely random wandering for in both Australia and South-East Africa, turtles have covered long distances at relatively high speeds.

OTHER SPECIES

Table 11 summarizes details of the only extra-nesting area recovery of a tagged leatherback female from Tongaland. One recovery is insufficient data on which to base conclusions.

Details of four recoveries of green turtles tagged on Europa Island are also summarized in Table 11 and the possible routes are illustrated in Figure 13. One turtle (A246) showed some determination by swimming 1 200km in 48 days; a mean daily speed of 25.0km/day.

From these tag recoveries it would appear that most, if not all, of Europa's breeding stock is drawn from the waters of Madagascar.

The recruitment source of green turtles nesting on Tromelin is as yet unknown but it is expected that they feed on the east coast of Madagascar. The general situation of Tromelin in relation to Madagascar is a miniature parallel to the Ascension Island — Brazil relationship as described by Carr (1965: 79).

Remigration from season to season tag recoveries

LOGGERHEADS

To date, 1 791 individual loggerhead females have been tagged in the Tongaland protected area (Fig. 12). At the end of the 1971-72 season 1 652 females had been tagged and over a nine-year period (1964/65 - 1972/73) 514 remigrating animals have been logged back in the protected area. Unfortunately only 183 of these returns have borne whole tags, the remainder having either broken tags or callouses.

Table 12 summarizes all remigration returns in terms of intervals between their initial tagging or previous encounter and they are also expressed as a percentage of all turtles *handled* during the particular season.

Figure 12 illustrates the increasing percentage of remigrations recorded in Tongaland over the past 10 seasons. In conjunction with this is shown the increasing numbers of turtles handled each year (Line A), and the increasing numbers of turtles utilizing the Tongaland protected area (Lines B and C). Line C shows the trend since the 1967-68 season when a more accurate method of estimating total nesting population was put into practice.

In both handling success and in the estimated total nesting populations, fluctuations are clearly recorded and similar fluctuations have been observed in green turtle populations in the study area.

Table 13 summarizes details of 10 loggerhead females that have returned in 3 or 4 separate seasons.

Although tag losses have been substantial and some remigrants have undoubtedly been missed in subsequent years it is thought that these missed turtles are relatively few in number. Therefore the most striking feature of the data is not the number of turtles that have returned but rather the number that have not. Some 1 138 turtles have been tagged, released and have not been seen again.

Either they are nesting on some other beaches and, apart from the odd female who moves along the Tongaland coast, there is no indication that this is occurring on a sufficiently large scale to explain the absence of such a large number of females, or these turtles are not nesting anywhere. Until data becomes available suggesting alternate nesting grounds it must be accepted that these non-returning turtles are not nesting.

At this point it is perhaps pertinent to examine the concept of reproductive periodicity or the remigration cycle as has been postulated for the green turtle and other species.

Harrisson (1956: 515) on recording the returns of 14 green turtles (out of 1 514 tagged) on the Talang Islands stated that green turtles do not breed more than once in three years. On the basis of Harrisson's data, Hendrickson (1958: 503) introduced the term cycle suggesting that "the Sarawak *Chelonia mydas* probably follow a triennial cycle of breeding". Carr and Ogren (1960: 14) postulated for Tortugueran greens a . . . "strong three year cycle" on the recovery of 16 turtles out of 495 tagged three years previously, and a weaker two-year cycle with 7 returns out of 114 originally tagged.

Carr and Carr (1970a: 335) summarized the remigration data of the then 15-year-old tagging programme in Tortuguero, Costa Rica and noted that 447 returns had been recorded, 48 of which were multiple returns, so the actual number of individual turtles was 399. As the total number of green turtles tagged during this period was in the region of 7 000, it is difficult to understand how these authors could postulate reproductive cycles for a population on the basis of a 5.7% remigration rate, particularly in view of the fact that in the same paper (p. 336) it is stated that site-fixity is strong in Tortugueran green turtles. Carr and Carr (1972: 426) show that the green turtle has a remarkable guidance ability and can return to the same stretch of beach in subsequent years. Thus, if the population as a whole has this ability to orientate accurately it would seem highly unlikely that 95% of the turtles would be missed year after year.

Results are perhaps more striking from the Sarawak Islands where every turtle was individually logged and there was no possibility of tagged turtles nesting unseen. A similar situation exists on Heron Island, Australia where every turtle is logged and low recovery rates are normal (Bustard, *pers. comm.*).

It will be shown below that site-fixity in the Tongaland loggerhead is well developed and thus in spite of the fragmentary data in Table 12 an attempt must be made to explain the low recovery rates of remigrating turtles.

The Oxford Concise Dictionary (5th Edition, 1972) defines the term 'cycle' as "a recurrent period of events". As only 514 (31.1%) out of 1 652 loggerhead females have returned to Tongaland after their year of initial tagging the term cyclic can be applied to the behaviour of the entire population only with some hesitation.

In Table 13 six out of ten individual remigrant loggerheads have shown a shift in their remigration intervals which negates the possibility of turtles showing regular remigration patterns. Thus if individual turtles exhibit irregular remigrations it is improbable that the population as a whole would have regular patterns and the data in Table 12 would suggest that irregularity is characteristic of reproduction by Tongaland loggerheads. For example, the 1972-73 season was preceded by three seasons in which monel tags were used yet only 56 monel-tagged turtles returned; 6 having nested in the previous season, 41 two seasons previously and 9 three seasons before. Besides these, 67 calloused turtles were logged back suggesting intervals of four or more seasons.

Thus there is a certain proportion of the Tongaland loggerheads exhibiting irregular cyclic nesting behaviour and the following explanations might be considered:

(i) That these irregular intervals are possibly related to the environmental conditions in which the turtle finds itself after a nesting season. The poorer the conditions the longer the interval before the turtle returns to nest again.

(ii) More simply, it might also be that there is considerable genetic variation in the reproductive capability of each individual. Some females are capable of annual reproduction e.g. Nos. 42, 47, A129, and A946 (Table 13), all of which have nested for three consecutive seasons, whilst considerably more require at least one season's absence to prepare for another laying season, the remainder requiring two or more seasons to re-attain reproductive preparedness.

(iii) A loggerhead female may become more irregular in her remigration absences as she ages. It should be remembered that the killing of females was stopped only in 1963 and the mortalities up to that date must have had some effect on the apparent behaviour of the turtles. Nest-robbing was intense prior to 1963 and this too must have had an effect on recruitment rates, reducing the numbers of young turtles in the population.

Unfortunately, as far as age being related to irregular nesting behaviour, there is as yet no data for or against this suggestion, and this is expected as nesting behaviour would be confusing until a more natural balance between old and young turtles was re-established. That this balance is re-establishing itself might be evidenced by the change in the upward slope of percentage recoveries shown in Figure 12 during the 1969-70 season. Unfortunately, it is thought more likely that calloused animals were missed in the preceding seasons. More convincing evidence may be found in the marked increase, during the 1972-73 season, of two-year nesters from 5.6% to 15.7%.

Thus it can be seen that the reproductive behaviour of the Tongaland loggerheads is both confusing and unusual. It is confusing in that irregularity appears to characterise the behaviour, and unusual in that so many females appear to nest only once in their life-time. Virtually every living creature has some form of cyclical reproduction, often regular but which is susceptible to environmental influences resulting in an apparent irregularity and referred to as fortuitous breeding. To interpret the limited returns of multiple nesters as suggesting that only *some* loggerheads have nesting cycles whilst the majority have the ability to nest once only appears to be plain bad science but the facts insist that the possibility be stated because loggerheads are site-tenacious in that they remain in the protected area for most of the nesting season, patrol methods are relatively efficient, and as far as is known they do not nest on any other beaches. (In support of this point it should be remembered that the Tortugueran green turtles show an even lower remigration rate). However, only many more years of research will confirm or deny this possibility which, it must be confessed, seems to be applying a rather drastic cut with Occam's Razor.

LEATHERBACKS

Table 14 summarizes all the remigration returns of leatherback turtles to Tongaland over the past nine seasons. Table 15 gives details of 15 multiple remigrations and it can be seen that shifts in migration intervals occur and there is no regular cyclic phenomenon because recoveries have been recorded in consecutive seasons, and after absences of one and two seasons.

The leatherback population in Tongaland is really too small on which to base conclusions but there does not appear to be any marked difference between their remigration behaviour and that exhibited by the loggerhead. The discussions concerning loggerhead can be taken to apply equally to the leatherback.

Orientation, from within season recoveries

LOGGERHEADS

It has been shown above that the loggerhead population in the study region is spread over some 3 200km of the East African coast. The fact that during the 1972-73 season in Tongaland 47% of the nesting females had nested at least once before, indicates that loggerheads possess a well developed navigation ability enabling them to orientate with considerable accuracy to a relatively small stretch of beach.

However, before considering the accuracy of remigrating females it is pertinent to examine first the adherence of nesting females to a particular stretch of beach throughout a nesting season.

Hughes *et al.* (1967: 22) and Hughes and Mentis (1967: 60) suggested that there was no significant tendency for turtles to emerge at the same site on consecutive emergences throughout a nesting season. These authors suggested that as there were no obvious pressures that would necessitate a turtle, with at least 160km of nesting beaches at their disposal, having a highly developed orientation mechanism, and that such a lack of precision was to be expected.

The conclusions of Hughes *et al.* (*op. cit.*) were not entirely in error because there is no significant tendency for turtles to return to the exact site on each emergence but there are indications that the stretch of beach used by the nesting turtles is very small in comparison with the overall distribution and thus their directional ability is highly developed but not perfect.

During the 1971-72 and 1972-73 seasons records of loggerhead movements were arranged in 4 phases:

Phase 1	The spatial interval between emergences in early November and late November.
Phase 2	The spatial interval between emergences in late November and early December.
Phase 3	The spatial interval between emergences in early December and late December.
Phase 4	The spatial interval between emergences in late December and January (including all January — January recoveries).

If an animal was recorded in early November and recovered only in early January the spatial interval between the first emergence and last emergence was entered on the early January record.

Figure 14 illustrates the spatial intervals of all recorded loggerhead turtle emergences in Tongaland at 4 separate phases of the 1971-72 and 1972-73 seasons in 800m (½ mile) classes. It should be noted that this does not infer that any individual turtle is included in the same column through each phase. An individual may emerge within 400m of its previous emergence in Phase 1 and move 3 200m in Phase 2 and remain in that position through Phases 3 and 4. From the figure it is clearly seen that there is a fair degree of accuracy but a somewhat higher degree of movement. Hughes *et al.* (*ibid.*) stated that there did not appear to be any tendency for successive nests of individual turtles to be sited consistently either northward or southward of the preceding nests. This conclusion must now be reassessed because more data than those previously extracted in random fashion, are now available.

Examination of Figure 14 reveals a degree of skewness in Phase 4 where there are more northward movements than southward movements. This is clear from Figure 15 (A) which shows all the data from Figure 14 expressed as percentages. It can be seen that the numbers of animals emerging within an 800 metre zone from emergence to emergence is between 20% and 30% throughout the season; a northward moving component is present which increases at the end of the season, similarly a southward moving component is also present which declines steadily from Phase 2.

In an attempt to assess just how important and extensive these movements are it was decided to extend the width of the zone of stability from 800 metres to 1 600 (Fig. 15 (B)); 3 200 (15 (C)); 6 400 (15 (D)) and 9 600 metres (15 (E)); this last figure representing less than a fifth of the total protected area in Tongaland.

From the series of graphs it can be seen that most (i.e. up to 90%) of the movements of loggerheads are contained within 9 600 metres of coast and those turtles moving either northwards or southwards, i.e. more than 4 800 metres away from their previous emergence, are relatively rare and the northward movements are only just more numerous than the southward movements.

From the data presented above three conclusions can be reached:

(i) Although it might be possible to accept the mode of each graph and say that each turtle has a target area of 800 metres width for which it aims with some 20-30% success, the considerable movement exhibited by each female renders this unlikely. It seems more acceptable to suggest that each turtle navigates to a particular stretch of coastline up to 9 600m in total width within which it nests consistently.

(ii) There is a tendency for there to be more southward moving animals in the early part of the season which might be interpreted as turtles arriving from the north.

(iii) There is also a tendency for there to be more northward moving animals at the end of the season which might be interpreted as the return of turtles starting northwards again.

However, all movements might be explained as responses to current drift and/or weather and surf conditions. For example towards the end of the season the Agulhas Current increases in velocity and the inshore, northward flowing counter-current presumably also increases in velocity. This might result in tendency for females to shift northwards between their penultimate and ultimate clutches. On the other hand the investigators may be the cause of these movements because of the interference factor. This factor certainly applies in certain cases; for example, one female was disturbed and renested the same night 12km from the original emergence site. This point can never be resolved because a degree of interference is necessary in order to tag or check the number of an existing tag. During the past 3 seasons interference has been kept to a minimum and few turtles are turned over for tagging purposes. Only when the turtle's imminent return to the water necessitates it being temporarily halted is the turtle turned.

BETWEEN SEASON ORIENTATION

Having established that the Tongaland loggerhead does not adhere to a specific site but rather to a relatively narrow zone during the course of a nesting season, it is now possible to assess the remigration orientation of turtles that have been away from the beaches for a year or more.

During the 1972-73 season 56 loggerhead females remigrated to the Tongaland beaches. The spatial differences between their original tagging site and that of their first encounter in the 1972-73 season is expressed in Figure 16 at 400 metre intervals. A table containing the remigration data from the 1971-72 season is to be found in Hughes and Brent (1972: 56) and these data have also been illustrated in Figure 16.

Of the 56 remigrants no single turtle adhered strictly to the same site and some showed wide deviations. Thus, if the turtles were orienting to a zone rather than a spot and, if some lateral movement is characteristic, it is likely that a recovery at the exact site of a previous emergence would be by chance. Out of 85 remigrants only 5 (5.9%) were recovered at the same site. Of four multiple remigrants Nos. A124, A923, A939, and A963 only the last turtle, A963, showed no deviations but it was only encountered once in each season. In the other 3 cases their zone of adherence was remarkably small:

A124:	maximum deviation 800m
A923:	maximum deviation 1 200m
A939:	maximum deviation 1 200m

From these three it is possible to suggest that some turtles can orient with great accuracy but most turtles have a less perfect mechanism.

The modal deviations in Figure 16 were 400 metres (1972-73) and 800 metres (1971-72) and the mean distance moved, was 4 536 metres (1972-73) and 3 352 metres (1971-72). The similarity at different zonal levels links the within season behaviour with that of the between season. No less than 93.1% of the remigrants logged back during 1971-72 were within 9 600 metres of their initial encounter site and 91.1% during 1972-73.

Thus, these remigration returns would add support to the conclusion of the preceding section that loggerhead turtles can orient with considerable accuracy to a definite stretch of beach when one considers the 3 200km-plus distribution of the population. This zone varies with the individual turtle from being as narrow as 400 metres but seldom wider than 9 600 metres.

It is confidently expected that with the replacement of lost plastic tags by monel tags and the increasing returns from year to year that further confirmation of these conclusions will be forthcoming in future seasons in Tongaland.

THE LEATHERBACK

Table 16 summarizes every leatherback within-season recovery since the Tongaland programme started in 1963. These data are illustrated in Figure 17 as deviations from the site of original encounter. As 7.1% of the turtles have re-emerged at the same site, and there have been some remigrations to the Tongaland beaches (Table 15) there is obviously some directional ability in the Tongaland leatherback population.

However, as shown in Figure 17 deviations of up to 40km have been recorded which would suggest that this orientation mechanism is either imperfect or unnecessary. It is felt that in considering the small numbers of leatherbacks utilizing the area and the widely scattered suitable beaches available to, and favoured by, leatherbacks further comment on the orientation ability of leatherbacks is simply not justified on the data presented.

Pritchard (1971: 21) made mention that in South America, leatherbacks tagged in Surinam moved up to 100km eastwards between nestings in as short a time as 17 days. It is obvious that this is a negligible distance for a leatherback to swim and taking Pritchard's data into consideration it would appear that the local leatherback population may be southward moving through the Tongaland protected zone. If it is a moving population this might explain the low within-season recoveries recorded in Tongaland. It might be assumed that the leatherbacks are moving southwards with the warm water in the spring and it is perhaps noteworthy that in the 1971-72 season the season was very cold in the early stages which might have temporarily halted the southward movement and resulted in the record tagging figure of 39 turtles. These are, however, merely speculations and confirmatory studies must be carried out on more substantial populations of leatherbacks.

GREEN TURTLES

No migrations of green turtle females to Europa or Tromelin Islands have so far been recorded but from a five-week stay on Europa sufficient data were collected from within-season recoveries to lend support to the suggestions of Carr and Carr (1972: 426) that the green turtle has a highly developed direction finding ability.

On Europa Island the tagging effort was restricted to a 500 metre beach immediately in front of the weather station. The beach was divided into 50 metre sections and a note made of the emergence site of each turtle. Of 382 turtles tagged on the beach, 111 (29%) were not seen again. 575 re-emergences were made on the study and adjacent beaches by the remaining 272 turtles.

It should be noted that only some 44.27% of these emergences were known to be successful nesting emergences having an interval of approximately 14 days between them. The remainder had intervals varying between 1 and 13 days. Few turtles emerged at exactly the same site more than twice but in terms of deviations from their previous emergence the turtles would appear highly selective in their nesting sites. Figure 18 illustrates the deviation data from the 575 emergences.

It is unfortunate that more regular patrols could not be carried out on the remaining beaches on Europa because this would have given a better idea of the spread of turtles from the study beach.

Indications are that the turtles tended to return to their original beach; firstly in the high recovery rate (71%) and also in the relatively few tagged turtles observed away from the study beach. For example the night patrol of the 18th November, 1970:

> The Patrol started at 2100 hours and work on the study beach was completed first:
> Results: 55 turtles: 30 (55%) untagged; 25 (45%) tagged.
>
> Then a check patrol was carried out between the study beach and the lagoon covering beaches Lagoon II, Reef and Lagoon III and minor beach IV (refer Hughes, in press: Table 11).
> Results: 418 turtles: 406 (97.1%) untagged: 12 (2.9%) tagged.
> Grand Total for evening: 473.

As there were turtles coming and going throughout the period of the patrol these figures must be regarded as minimal and there were the remaining beaches which were not checked that night. At this stage of work, 382 turtles had been tagged.

As some tagged turtles were recovered away from the study beach it is obvious that there is some movement between emergences, but the high recovery rates, from what must be regarded as a small tagging sample, can be interpreted as a general adherence to a nesting beach and show that in their emergence behaviour, green turtles in the study region do not differ from Caribbean green turtles.

Recruitment, from general tag returns

LOGGERHEADS

In Figure 12 it was shown that during the 1972-73 season the percentage remigrants to the Tongaland protected beaches had reached 47%. Within a few seasons this steady climb should level off and it should prove possible to assess with a high degree of accuracy the recruitment rates in the Tongaland loggerhead population.

In an attempt to assess the reasons for the present recruitment, which is also shown in Figure 12 as increasing trends in new animals, handling success and estimated total population, each seasonal sample of measured females was divided into 5 size classes and their numbers expressed as a percentage of the total sample.

These data from 7 seasons are summarized in Table 17 and the size class percentages are illustrated in Figure 19 with trend lines fitted using Bartlett's regression formula.

The smallest and largest females tend to contribute a steady proportion of each annual population but their combined contribution is small and not of particular importance.

In the early stages of the programme the 86-90cm curved carapace length class contributed over 20% of the total but has shown a steady decline over the following six seasons whilst the modal size class has shown a corresponding increase. The 96-100cm class has also shown an increase.

A possible explanation lies in the killing that went on prior to 1963. If turtles were killed on a reasonable scale and it has proved difficult to ascertain the exact extent of the persecution, there should have been a reduction in the number of larger (older?) turtles which would not have been made up by new recruits by 1965. Thus younger turtles, i.e. new recruits, would have contributed more substantially to the population as a whole.

With the progressing seasons there has been an increasing remigration of older animals and presumably in the larger size groups these are reinforcing the new recruits and giving the modal size class the tendency to increase.

The 1968-69 season is unusual because of the fact that so few animals arrived in Tongaland, it was the poorest season in ten and showed a preponderance of larger females. It is possible that some years previously there had been an almost total failure of eggs or an unduly high mortality of hatchlings and the number of new recruits was thus reduced resulting in the emphasis being placed on larger turtles.

The fluctuations in annual nesting populations as shown in Figure 12 might be traced back to "good" seasons or "bad" seasons but this will become apparent only after future seasons of accurate monitoring.

It has been suggested in a previous section that loggerhead turtles mature at various sizes and it is suggested that from the figures in Table 17 for the 1972-73 season there is no particular emphasis on the smaller size classes which would suggest that these are the principal source of recruits. It seems likely that the modal size class in which loggerhead females reach maturity is in the 91-96cm curved carapace length class and thus new recruits to a population of loggerheads will be found in all size classes.

If remigrants to Tongaland continue to increase at the rate recorded in the past three seasons then within the near future, it should prove possible to allocate the percentage new recruits within each size class and the true variation in size of turtles at their first season of nesting will be ascertained.

Finally it is suggested that the annual recruitment rate will be found to be relatively high, between 20% and 30%. The reason for this sugggestion is linked to the previous section in that many tagged turtles have not been recovered in Tongaland. Despite the large numbers of non-returning animals the overall population trends continue to move upwards and it is thus reasonable to assume that there must be many new recruits. This should be expected because of the total protection afforded the nesting colony since 1963. It will be of interest to see whether there is a sharp increase in total numbers within the next few years.

The success of the conservation programme will be judged on the recruitment of neophyte nesters and so far the results are promising.

LEATHERBACKS

As mentioned in a previous section there is a possibility that the leatherback population is drifting and not static; i.e. they do not adhere to a particular nesting zone unless it be a very wide zone. This reduces the chances of encounter and makes any assessment of recruitment extremely difficult.

Table 18 summarizes the size class composition of the seasonal measurement samples of leatherback females in Tongaland. The seasonal numbers are small and it is not possible to determine whether there has been any change in the size class composition since 1965.

Discussion

From the data presented above it is clear that the loggerhead turtle has a well developed direction finding ability which enables them to return periodically with great accuracy to the Tongaland beaches.

The guidance mechanism employed by these turtles would appear to be complex and it is pertinent to examine the most feasible theory on turtle orientation in the light of the data collected on the loggerhead.

CHEMORECEPTION

Koch, Carr and Ehrenfeld (1969: 167) postulated the possibility of green turtles finding Ascension Island by following an olfactory gradient of increasing strength between the feeding ground and the nesting ground. Carr (in press: 3) added to this and suggested that use may be made of sub-surface equatorial counter currents.

Considering that nearly all of the Tongaland loggerheads have been taken north and hence up-current, of the nesting grounds, it seems unlikely that chemoreception can be seriously considered as a long range guide because the possibility that counter currents and eddies could carry an olfactory cue for 3 600km is difficult to imagine.

Chemoreception might, however, play an important role in the final choice of a nesting site. Richard and Hughes (1972: 306) showed that green turtle nesting along the east coast of Costa Rica was clearly correlated with the outflow points of large rivers, being situated immediately down-current of each river mouth, the Tortuguero River being, apparently, particularly attractive to green turtles.

In Tongaland nesting is clearly associated with the Kosi Bay Estuary which has an outflow point immediately up-current of the main nesting areas. Figure 20 shows the nesting activity concentration points over eight seasons in Tongaland.

To suggest that this association is a direct result of outflow from the estuary mouth is, however, not necessarily justified.

Firstly, outflow is limited to low tides, as during high tides sea water enters into the lake system thus the net outflow of possible olfactory cues is limited.

Secondly, the longshore drift is normally northward although it does change if a northerly wind blows steadily for more than two days. Thus, what little outflow there is would be carried northward and not southward where the turtles nest.

A third reason for the nesting orientation not being linked to outflow through the estuary mouth is the distinct break in nesting distribution along the favoured 24km of coast. It would be expected that if orientation was directly linked to outflow there would be an even distribution of nests over the area of most powerful olfactory cue. Variations in current directions should be evened out over eight seasons but in fact each season has emphasized the site selection.

Finally, it is perhaps noteworthy that during 1965 the estuary mouth was closed for five months (Breen and Hill, 1969: 285) so there was no outflow at all and this did not markedly affect the homing accuracy of the nesting turtles (Hughes, *et al.*, 1967: 14).

It was noted by Hughes (in press) that loggerheads in Tongaland showed site selection in that they always emerged near intertidal reefs and where there were no rocks nesting was either minimal or non-existent. It was suggested that inter-specific competition for nesting sites between the leatherback and loggerhead might have led to spatial separation and the preference by loggerheads for rocky areas. This may have some effect but the site selection exhibited by loggerheads does not justify this as the sole reason. The cumulative data in Figure 20 shows firstly the preference for rocky areas and then the greater concentration in the northern section of the protected area, and herein may lie the link between site selection and olfactory cues.

If there is a link between the Kosi Bay Lake system and the orientation of nesting sea turtles, and the link is not directly associated with outflow through the estuary mouth, then it must be an underground link.

Tinley (1971: Appendix 6) discusses at length the presence of impermeable hardpan layers which act as highly efficient aquifers in the Tongaland region, and cites, as a good example of such an aquifer, dune rock along the coastal zone. Evidence of freshwater seepage may be adduced from the dune rock itself which is formed through the cementing of sand under the influence of fresh water and a strong calcareous component. Therefore there is a possibility that there is drainage from the Kosi Bay Lake system via hardpan horizons to the shore line. If the hardpan continues out onto the beach, a relatively stronger flow would be present at that point as compared to a section of beach where the hardpan layer either dips or has been eroded away resulting in the water flow diffusing through a thick layer of sand and being further diffused by wave action as it enters the sea.

One could assume that the water draining over hardpan layers might itself provide the olfactory cue towards which turtles home if it had distinct properties.

For example, in Figure 20 there are two modal points in the peak nesting areas in the north of the protected area. Immediately south of each point there is a dramatic drop in nesting activity, whereas north of the modal points there is a very much less drastic fall in activity. In other words the nesting distribution is skewed to the north.

It has been mentioned above that coastal longshore drift is predominantly northward and this would carry the olfactory cue in a northerly direction away from the point of entry into the sea. The skewed distribution shown in Figure 20 would lend support to this suggestion. Figure 21 illustrates the relationship between the Kosi lakes and the main turtle nesting areas and shows the possible sources of the cue medium.

It is possible, however, that the association between the lakes and the nesting beaches may be less direct and may involve the turtles providing their own olfactory cue. Loggerhead nests have a distinct smell which would appear to be a strong disadvantage in areas with large numbers of terrestrial predators. In Tongaland feral dogs find turtle nests from which all surface traces have long been obliterated by wind action. On the Hutchinson Island rookery in Florida, raccoons cause extensive damage by digging up loggerhead nests (see Gallagher, Hollinger, Ingle and Futch, 1972: 6; Routa, 1967: 291). It would seem that the selective disadvantage of having a powerful odour attached to the eggs must be outweighed by a selective advantage or the colony would have been wiped out. It would appear feasible that the advantage derived from having large numbers of turtles nesting in one area, would be by producing more eggs than could be dealt with by the predators and thus reduce, to a tolerable level, the harmful effects of predation.

These predators can find the nest when it is freshly laid which would suggest that the smell is associated with the mucus exuded by the female in the process of laying but this might be later reinforced by the breakdown of unhatched eggs which, as is well known by workers dealing with turtles, has an extremely pungent odour.

Therefore if the turtles leave an olfactory cue in the sand it is logical to assume that the more turtles utilizing an area the stronger the olfactory cue and in turn the more attractive will be the area to nesting turtles.

As it is unlikely that the cue will be carried by winds it must be carried by dissolving in interstitial water and draining down towards the sea by gravity. If one considers the rainfall regime in Tongaland, one finds that in September or October there is always a period of rain preceding the beginning of the turtle nesting season (see Tinley, 1958: Fig. 2). This could be sufficient to initiate the percolation of olfactory cues down to the water table, or more simply, there is possibly a continuous leaching downwards to the water table.

The link with the lakes might be as a result of their maintaining a high water table which would flow, albeit slowly, even in times of drought which may have a marked effect on seepage points further south.

Further the drainage lines on the hardpan layer (dune rock) may cause the olfactory cues to be channeled to a particular outlet where it would enter the sea in relatively high concentration, being distributed by the longshore drift as was mentioned above.

Thus longshore drift, local winds and variations in wave patterns would shift or dilute the cue medium over limited areas before mixture with the sea rendered it untraceable. Further if the cue was gradually seeping over the rock layer it would tend to concentrate in rock pools and the lower beach during low tide periods and be at its strongest at the turn of the tide.

If the cue was either direct seepage from the Kosi lakes or the turtle-originating cue carried in this seepage, two separate outlets situated some 10km apart would explain the apparent zone target postulated above, rather than a specific point target, for the Tongaland loggerhead.

Similarities in the properties of the two cue sources either as a result of their being from the same original source (the Lakes), or from their being simply a "loggerhead" cue, would explain the periodic shifts by nesting turtles from the northern concentration to the southern and vice versa. Variations in sensitivity on the part of individual turtles would easily explain the ability of some turtles to orientate with remarkable accuracy whilst others are less precise.

Boteler Point is a good example, situated between two high nesting density areas, to show that the presence of rocks alone is not the attraction. It probably lacks a seepage point or a nesting density sufficiently high to create a cue.

The presence of nesting turtles in the southern part of the protected area is a little enigmatic. Either there are smaller seepage areas with a unique character making them attractive to turtles and into which is channelled turtle-cue, or these seepage outlets are not perennial because of the lack of a major water course inland and in times of drought they stop, lose their guidance role, and hence their nesting turtles, and have to be built up again. There is no other obvious reason why these southerly beaches are not more heavily utilized by the nesting turtles. If cues were weak or even non-existent in some seasons new recruits would probably nest in the strong cue areas further north and further reinforce these zones.

Thus the presence of a water table containing either identifiable water or acting as a carrier appears to be of value to loggerhead rookeries. In Madagascar the most important stretch of loggerhead nesting beach is separated from a long string of brackish and fresh water lakes by a set of high dunes.

In the United States there are three documented loggerhead rookeries on the east coast separated by large areas of apparently suitable beach (Caldwell, Carr and Ogren, 1959: 296). Baldwin and Lofton (1959: 320) show that the Cape Romain nesting beaches are backed by hectares of salt marsh which would maintain a high water table.

In Georgia, Jekyll Island and Little Cumberland are closely associated with mainland marsh areas whilst Hutchinson Island in Florida is backed completely by the Indian River Lagoon (see Caldwell, Carr and Ogren, 1959: 298; Routa, 1967: 288; and Gallagher, Hollinger, Ingle and Futch, 1972: 3).

Gallagher, *et al.* (*op. cit.:* 7) note a series of internesting intervals recorded from tagged loggerheads and the Hutchinson Island turtles seem somewhat less accurate than Tongaland turtles and this would be expected with such a wide area (22 miles, 35.2km) having an identical lagoon backing.

It will be of interest to see if future work in these areas shows a nest distribution that can be correlated with particular sites and longshore current direction.

From this hypothesis several other behavioural traits of the loggerhead are brought to mind.

Firstly the sand-smelling behaviour observed not only in Tongaland loggerheads but in other species as well (see for example Carr, 1967: 21). With the Tongaland loggerhead sand-smelling occurs immediately after stranding when the beak is thrust into the wet sand. Some females walk up the beach thrusting the beak in front of them like a ploughshare.

This behaviour, previously thought of as tactile testing of sand consistency, might now be described as it was originally named, i.e. "sand-smelling". If the cue is seeping to the shore line in drainage lines and then being carried northwards along the immediate shoreline the sand from the high tide mark down should be impregnated with the cue medium. The turtle stranding after low tide has a broad guide path which it can follow up the beach.

The strength of the cue distributed over the beach between high and low tide mark might also inform the female when she is above the high tide mark. There is possibly a sharp drop in the cue strength when the female passes the high tide mark which would trigger a new set of responses resulting in the turtle being susceptible to external stimuli. The presence of a bank, log or vegetation is then sufficient to trigger nest building behaviour.

It has been noted in Tongaland that the presence of a large log or bank below the high water mark does not generally stimulate nesting behaviour. On the contrary females take vigorous avoidance actions and if unsuccessful in bypassing or climbing the obstacle will return to the sea without nesting. Higher up the beach a relatively minor bank or patch of vegetation will immediately prompt nesting.

If no obstacle is encountered some turtles in Tongaland have been observed to walk for hundreds of metres before laying.

Baldwin and Lofton (*op. cit.:* 322) were the first to note that loggerheads execute exploratory crawls. These "half-moon" tracks, often observed in Tongaland, might be explained as the tracks left by an emerging turtle which not having found the correct cue, has immediately returned to the water.

Finally, the presence of a distinct smell in the egg chamber must be the first sense imprint experienced by the hatchling loggerhead. It hatches within an enclosed chamber permeated with the smell and ascends for three or four days in company with its identically tainted siblings and only thereafter is it exposed to foreign stimuli through vision and surface odours. It is suggested that visual stimuli are dominated, during the night emergence, by the seaward orientation drive based on a single light source.

In conclusion it is suggested that chemoreception of a water-borne guidance cue, either as a property of the water itself, or in traces left by heavy nesting of the species in previous seasons, is of importance in the within season and remigration finding of a specific nesting site. A chemoreceptive agent and its distribution along and coast agrees with the data collected and explains various, as yet poorly understood, aspects of nesting behaviour in the Tongaland loggerhead.

Nordeng (1971: 412) and Solomon (1973: 232) have provided convincing evidence that char and salmon utilize a chemical cue or pheromone, derived from their own relatives or group, as a guide to their home stream rather than the cue being provided by the stream water itself. In other words the pheromone is species specific or even group specific. A similar pheromone-guidance mechanism may be employed by sea turtles.

It is not suggested that chemoreception is acceptable as a long range navigation system because all migrations should require a reversible mechanism if the turtle is going to return to a favoured feeding ground or sleeping rock. Further a chemical trace carried by a surface current would be uni-directional and could not apply to turtles coming from both north and south of the nesting area.

Not having undertaken any specific work on long range navigation it is not intended to enter into a detailed review of navigational possibilities to explain how loggerheads get to Tongaland, but it is felt that Hirth (1971: 3: 23) is right in suggesting the answer may lie in non-visual theories.

In concluding one can only acknowledge that the Tongaland loggerhead, and Europa and Tromelin green turtles, are fine navigators but it seems likely that human understanding of their feats may never be realized.

The reproductive behaviour and potential of sea turtle populations in south-east Africa with especial reference to the Tongaland loggerhead *Caretta caretta*, the Tongaland leatherback *Dermochelys coriacea* and the green turtle *Chelonia mydas*

Introduction

The following section deals with the activity and behaviour associated with the nesting season excluding orientation and site selection which has been dealt with.

In Tongaland, it is unfortunate that patrol methods are not as efficient as desired. The records are seldom sufficiently complete and recourse must be made to interpretive treatment of data that could be perfectly straight forward if every turtle was handled. Observations on green turtles on Europa and Tromelin Islands are even more scantily recorded and details are reported below for completeness and in the full knowledge that the data are drawn from minimal samples.

The problem of too short a working time must be faced once more with regards to the reproductive lifetime of the loggerhead turtle and the conclusions contained within some of the subsections must be accepted as tentative. Definite, conclusive results can only be forthcoming from long term tagging studies.

Methods

Many of the data contained below have resulted from direct observation or are derived from the recovery of tagged females.

Fertility and hatching success in turtle clutches are based on nests excavated after the departure of the hatchlings. On Europa and Tromelin Islands nests were inspected as found and the results are therefore fortuitous. In Tongaland natural nests were marked immediately after laying and excavated after the hatchlings had gone but were not interfered with in any way which could have affected the hatching success. The eggshells, hatchlings and eggs remaining in the nest were then counted. The fertility of unhatched eggs was adjudged on the presence or absence of blood spots. If the embryo was microscopic then the egg would be regarded as infertile. Bustard (1972: 99) discusses the possibility of numerous microscopic embryos being killed during laying and indeed, this is thought to be possible. Development of the embryo must commence immediately after fertilization and before the shell is laid down. If a turtle is disturbed by bad weather or research workers and laying is delayed for some days the embryos would be well advanced when the eggs are eventually laid and be susceptible to damage from the fall into the nest. It is felt, however, that any errors contained in the fertile-infertile data is of limited importance when compared to the emergence success.

Although small pilot hatcheries, into which have been moved clutches of loggerhead and leatherback eggs, are operated annually in Tongaland, few of the data collected therefrom are included in this section. Details concerning the hatchery programme are to be found in the Lammergeyer reports (see for example Hughes, 1972: 15-16). It is sufficient to say that barring natural disasters, the mean hatching success has been as high as 68.7%.

All egg measurements have been taken with Vernier Calipers and the mass recorded on an Ohaus triple-beam balance.

Results

FACTORS INFLUENCING THE NESTING SEASON

During 1971, three turtle nesting grounds in the south-western Indian Ocean viz. Europa Island, Tromelin Island and St. Brandon, were found to have a lower nesting activity than expected during November. This phenomenon was also observed in Tongaland where all loggerhead activities were markedly lower during November than those recorded during the two previous seasons (Hughes and Brent, 1972: 44).

Table 19 summarizes loggerhead and leatherback nesting and tagging records, expressed as a monthly percentage of the season's totals, and sea surface temperatures for the months of November, December and January during the 1969-70, 1970-71, 1971-72 and 1972-73 seasons.

Figure 22 illustrates the sea surface temperatures for the four seasons and compares them with the loggerhead nest records. It can be seen that during the 1971-72 season the sea temperature was lower in October and November and appeared to result in the season having a slower start. As it was a record season, with January nest records abnormally high it is assumed that the lower temperatures off Tongaland did not result in loggerheads nesting in Mozambique where warmer temperatures must have prevailed. Thus the lower temperatures retarded the start of the season but did not restrict eventual nesting intensity. A χ^2 test between the four seasons showed no significant difference between three of them but between the 1970-71 and

1971-72 seasons, which are the most divergent, there was a significant difference at the 5% level. Therefore, sea temperatures are almost certainly linked with nesting activity, although other environmental factors may be involved.

As it is considered unlikely that the female loggerhead is sensible to temperature differences of 2°C it is probable that these differences are brought about by the resultant efficiency of the body functions of the animal, i.e. by advancing or retarding egg development.

Table 20 summarizes the mean inter-nesting intervals of individual loggerhead turtles during the 1969-70, 1970-71, 1971-72 and 1972-73 seasons. Each season is divided into five phases and the mean inter-nesting interval is compared with the mean sea temperature during each phase. A statistical comparison between the two sets of data showed a highly significant negative correlation ($r = -0.861$; $p. < 0.001$) which suggests that the influence of low temperature is expressed by the retardation of egg development. Hence the lower the sea temperatures in October and November the later the season.

McAllister, *et al.* (1965: 30) expressed the nesting season in terms of air temperatures extracted from the records at St. Lucia Meteorological Station, and inferred that the season was influenced by air temperature. Although there is a great similarity between sea and air temperatures in oceanic regimes this is not necessarily so along the coastal areas of large landmasses, take for example the development of sea advection fogs. It is felt therefore that it is better to express the turtle nesting season in terms of sea temperature. It is also more logical when considering the activity of an animal that spends almost all of its lifetime immersed in the sea. As sea turtles are to a greater or lesser degree poikilothermic it would be expected that ambient sea temperatures would affect their activity.

Table 19 includes the leatherback data from the same four seasons and there is no significant difference between any of the nesting activities recorded. This would be expected in the light of the findings of Mrosovsky and Pritchard (1971: 630) and Frair, Ackman and Mrosovsky (1972: 792) all of whom have shown that the leatherback can maintain its body temperature up to 18°C above the ambient sea temperature and the findings of Greer, Lazell and Wright (1973: 181) showing that the leatherback has a countercurrent heat exchanger.

Sea temperatures also influence the nesting of green turtles in the St. Brandon Islands. Figure 23 shows the sea surface temperatures over 15 years in St. Brandon and compares them with the monthly exploitation figures recorded from the islands over the same period.

Although the peak nesting activity is almost invariably associated with the highest sea temperatures there is nothing to suggest that sea temperatures have any influence on the numbers of turtles nesting. The fluctuations in numbers are clearly wide and the seasons for these fluctuations remains a mystery.

It is concluded, therefore, that sea temperatures are linked with the nesting season and can advance or retard nesting activity.

MODE OF ARRIVAL

LOGGERHEADS

Caldwell, Berry, Carr and Ragotskie (1959: 309) suggested on the basis of limited tag returns, that there were indications of group adherence and nesting in Atlantic loggerheads and further that gravid animals arrived off the nesting beaches in small groups.

As in America, clumped tag returns have been recorded in Tongaland, because of a number of turtles tagged on any single evening, a certain proportion of them will be recovered some 14-16 days later. These results depend to a large degree on the handling success of the patrols. Whether these observations can be interpreted as cohesive group nesting, however, is open to doubt for several reasons:

(i) The "group" may be extended over an area of 56km and can be hardly considered cohesive. Similarly, the loggerhead has a reasonably well developed site fixity and the chances are high that they will emerge in proximity to the site of their initial emergence, thus suggesting group behaviour.

(ii) The Tongaland loggerheads exhibit a surprisingly consistent renesting interval which appears to be linked to the ambient sea temperature (see above), so any two or more females tagged on a specific evening, irrespective of their mode of arrival, are likely to be recovered within a day or two of one another at their next emergence. Therefore they can be regarded as a fortuitous group only.

(iii) Even if a number of turtles did arrive as a group off Tongaland it is unlikely that all would have identical stages of egg development and thus the group would soon lose its identity as individuals responded to the nesting urge.

(iv) Figure 24 represents the cumulative nesting records for the 1972-3 season based on the internesting periods recorded during the season (see Table 20). The number of days contained in each interval is shown on the figure. It is assumed that all nests contained within any single period were laid by separate individuals. The periods become shorter as the season progresses as was shown in the previous sub-section. For example:

Period 1: all nests laid from the 16th October to the 2nd November inclusive.
Period 2: all nests laid from the 17th October to the 3rd November inclusive, etc.

From the figure there appears to be a steady accumulation of females arriving to nest on the Tongaland beaches followed by a more abrupt but still smooth withdrawal.

Figure 24 has an unexpected peculiarity and that is the trough between the two peaks. The first peak is the expected trend viz. there should be an accumulation of new arrivals and then the numbers should remain more or less static until turtles begin to depart, having completed their nesting.

There are two possible reasons for the apparent drop in nesting activity; the first is that the turtles were nesting elsewhere but there are no data suggesting this, or, that during this period, which was characterised by severe south westerlies, a very substantial number of nests were not recorded. This can very easily occur because if a strong wind develops halfway through the evening all traces of nests are obliterated within minutes and it is possible to ‘lose’ up to forty nests in a night. This point does, however, illustrate the value of the method used to estimate nesting populations in Tongaland; there is little possibility of an overestimation and all estimates must be regarded as minimal.

From the above data it is concluded that:

(i) The recording of fortuitous groups of tagged turtles on the nesting beaches cannot be interpreted as being indicative of group arrivals off the nesting beaches.

(ii) There are no indications of substantial group arrivals, neither by direct observation nor in the accumulative nesting records. Thus, if there are groups, they appear so small at present as to be indistinguishable from a steady stream of individual arrivals. However, group arrivals may take place but this will only be proven through direct observation and not through tag recoveries.

OTHER SPECIES

Clumped recoveries of tagged leatherbacks have also been recorded in Tongaland, two animals have been recovered twice in subsequent seasons, but it is felt that this need not be indicative of conscious group adhesion.

No data have been collected on the three other species in the study area but there are records of mass movements of sea turtles in other areas (see, for example Carr, 1955: 237 on).

COURTSHIP BEHAVIOUR

LOGGERHEADS

Off the Tongaland beaches copulation and courtship is seldom seen as all mating seems to take place some one to two kilometres offshore in 15 to 20 metres of water. Mating couples seem to spend most of their time underwater.

No courtship behaviour has been seen off Tongaland but in the main tank in the Durban Aquarium mating took place on the 6th October, 1970. It is of interest to note that both the male and female loggerheads involved had been in the main tank for 8 years or more and no copulatory behaviour had been previously recorded. Having had no contact with the open sea for 8 years this pair commenced courtship behaviour at the same time as turtles were starting to gather off the Tongaland beaches. Loggerhead nests have been recorded as early as the 20th August and occasionally in September but nesting normally starts at the end of October or early November depending on the water temperature.

In the main tank, copulation between the two loggerheads was preceded by several days of courtship activity with the male pursuing the female around the tank, normally slightly above her. No pattern was observed, but this may have been due to the confines of the tank, and the animals periodically touched their beaks together. Occasionally the male would break away from the female to pursue a young loggerhead male that had not yet begun to exhibit his secondary sexual characteristics. The older male bit pieces out of the rear end of the younger turtle's carapace.

Off Tongaland a pair of males were observed fighting for five minutes before being disturbed by the presence of a diver. Apparently the fight consisted of slow motion biting and thrusting at one another with no serious damage resulting from the encounter (Mr. M. Schleyer, *pers. comm.*).

Copulation in the Aquarium lasted up to an hour on the one occasion that it was observed in full. No eggs were observed to be subsequently laid by the female but they may have been laid at night and consumed by the other occupants of the tank.

GREEN TURTLES

Around Europa Island and Tromelin Island copulating and mating behaviour was observed daily. It would appear to be an arduous ordeal for the female because females were observed to come ashore on Tromelin Island to escape the attentions of males. On one occasion a female was observed to beach herself on numerous occasions to avoid two small males which tried to mount her the moment she left the shallows. Bustard (1972: 143) reported similar beaching behaviour on Bountiful Island, Australia.

Numerous authors have reported mating behaviour in green turtles because unlike the loggerhead, mating takes place close inshore (see for example Hendrickson 1958: 482; Carr and Giovannoli, 1957: 30; Frazier, 1971: 377). Only Bustard (*op. cit.*: 144) has described the actual courtship actions. Off Europa Island during this study a pair of green turtles were observed to exhibit a repetitive series of movements which are assumed to be courtship behaviour because the patterns agree in parts with the description reported by Bustard.

On Europa Island the turtles were in some three metres of clear water below a high reef point from which obstruction-free observations could be made.

There were five basic movements and these are illustrated in Figure 25. Briefly these were:

(i) A circling pattern lasting for about a minute followed by:

(ii) The turtles stopping and facing one another underwater and maintaining their positions with gentle movements of the flippers, then;

(iii) closing in on one another with the flippers seeming to embrace as their bodies swing downwards to a vertical position, then;

(iv) a close embrace plastron to plastron and nuzzling of the neck and shoulder region.

(v) Finally the female sliding over the male's back. This latter movement was remarkable because males are normally the ones that mount but one had the decided impression that the female was doing the courting!

The entire pattern took some 3-4 minutes to complete after which there would be some random swimming around, as they both rose to breathe, and after a minute the circling started the pattern again. Three full cycles were observed in 20 minutes after which the male swam away.

It is not suggested that this is the normal behaviour of Europa's green turtles as this activity was seen only once, and it was unusual in that the female was so active.

STRANDING AND THE CHOICE OF NEST SITE

LOGGERHEADS

Baldwin and Lofton (1959: 324) found no correlation between the tidal phase and the strandings of loggerhead females on the Cape Romain beaches of the eastern United States. However, Hughes *et al.* (1967: 24) commented that in Tongaland there were indications of a response to the tidal state and this has been further investigated during the 1971-72 and 1972-73 seasons. Records were kept of turtles emerging prior to and after midnight over a full tidal cycle.

Hughes and Brent (1972: 51-53) discussed the results obtained during 1971-72 and concluded that there was a definite link between tidal state and nesting activity. It was shown that during neap tides there was more nesting activity prior to midnight when the high tide takes place during the first half of the night and vice versa during spring tides when activity was higher in the second half of the night.

Figure 26 shows the distribution of loggerhead nesting activity on the peak spring and full neap tide periods during December, 1972 and January, 1973. Unfortunately emergences after midnight on some nights could not be allocated a specific time and consequently have been lumped.

The data are more specific than the 1971-72 season and although the general trend is similar to that found during the previous season, reversals show that the association is not exclusive. Furthermore, a comparison between loggerhead emergences during a rising tide and a falling tide showed no significant differences ($p>0.10$) neither on the peaks of tidal phases nor throughout the month of December.

It is thus concluded that loggerhead females strand at any time of the night but show a preference for higher tidal periods probably in response to the numerous outcrops of rock that precludes nesting at the lowest tides. Furthermore Figure 26 shows clearly that there is no tendency for loggerheads to emerge immediately after dark, which is normally around 1900 hours.

The occasional loggerhead female has been observed to emerge during the daylight hours but this is rare.

Bustard (1972: 68) has described the stranding behaviour of the loggerheads in eastern Australia and in no way does his description differ from the behaviour of Tongaland loggerheads.

The possible factors governing the choice of nest site in Tongaland loggerheads have been discussed above.

LEATHERBACKS

Figure 27 shows the recorded encounters with emerging leatherback females during two full seasons in Tongaland. As they emerge on beaches having no obstructions there is no reason for leatherbacks to respond to tidal state. In Tongaland one might expect to encounter a leatherback any time after 2100 hours irrespective of tides.

Pritchard (1971: 18) has described the stranding behaviour of the leatherback turtle in French Guiana and there is no notable difference in the behaviour of the Tongaland leatherbacks even in stranding time as Guianan leatherbacks emerge in the middle hours of the night.

The choice of nest site seems to be dictated by the nature of the offshore sea bed (see Hughes, in press).

GREEN TURTLES

On Europa and Tromelin Islands there is a response to the tidal state by nesting green turtles. At dead low tides the turtles cannot get over the extensive wave platform and the animals must wait until there is sufficient water over the reef. Thereafter turtles come in as long as it is possible, whether the tide is rising or falling.

Carr and Giovannoli (1957: 28-29) have described in detail the stranding of green turtle females and there appear to be no behavioural differences between Tortugueran turtles and those in the study region.

DIGGING OF NEST AND GENERAL BEHAVIOUR

LOGGERHEADS AND LEATHERBACKS

McAllister, *et al.* (1965: 22-27) described in detail the nest digging behaviour of the Tongaland turtles. Hughes *et al.* (1967: 24 and 42) gave the duration of the various phases of the process. There is considerable variation but a loggerhead seldom spends less than 45 minutes on the beach and leatherbacks less than an hour.

Neither species is aggressive although there is an occasional reaction to tagging involving the opening of the beak. No investigator has ever been deliberately bitten in Tongaland.

GREEN TURTLES

Although it is thought that the time involved in nesting depends to a large extent on the consistency and dryness of the beach, particularly in the case of the green turtles of Europa where the nesting density is very high and the upper surfaces of the beach dry due to turning by nesting females, some examples of the duration of nesting activity from three localities are given in Table 21.

Green turtles seldom show any aggression towards investigators and during the present survey only one incident was recorded. On Europa Island one female (No. A365) exhibited what appeared to be threat behaviour by thrusting its head at the investigator and flapping its fore-flippers vigorously. These actions were repeated three times and there was no suggestion of the head being withdrawn or a return to the sea as is normal with green turtle females.

RETURN TO THE SEA

LOGGERHEADS AND LEATHERBACKS

Loggerheads in Tongaland return directly to the sea and make no attempt to avoid reef exposed by a falling tide. McAllister *et al.* (1965: 29) have described the return to the sea by leatherbacks in which they mentioned the occasional circles, some three metres in diameter, executed by females. No ready explanation is available for this behaviour as it is not a common feature.

GREEN TURTLES

On Tromelin Island and the Primeiras there is no great expanse of reef exposed at low tide so turtles can attain the sea with no problem.

On Europa, however, falling tides often expose the turtles to lengthy hauls of several hundred metres over exposed reef or sandbanks. Further, the turtles penetrate through small gaps in the raised coral reef and on returning to the sea cannot find the gap and crawl over the top of the reef, occasionally falling into holes from which they cannot extricate themselves. During a six week stay on Europa some 50 females perished in this way.

If faced with a long crawl over the reef females will enter shallow pools and remain there splashing themselves occasionally until the tide comes in.

In the lagoon at Europa, green turtle females, if caught on the exposed sandbank, were observed to dig body cavities in the sand, exactly as the nesting body cavity is dug, and once water had percolated into the hole splashed themselves in the same way as those observed in rock pools. This is a daily occurrence on Europa.

FACTORS AFFECTING THE INTERNESTING INTERVALS

LOGGERHEADS AND LEATHERBACKS

It has been shown in the sub-section on factors influencing the nesting season that there is a strong correlation between sea temperature and the internesting interval in Tongaland loggerheads.

Hughes and Brent (1972: 49) showed that during the 1971-72 season leatherbacks responded only slightly to the cooler temperatures by having internesting intervals of ten days whereas the more normal period is nine days. During the 1972-73 season the interval was 9.7 days (n = 22, range: 8-12).

No basking behaviour by loggerheads has been observed off the Tongaland beaches but one leatherback was seen from the air floating on the surface about one kilometre offshore.

GREEN TURTLES

Insufficient time was spent on any of the green turtle nesting areas to record whether there was a response to sea temperatures by nesting females but it is assumed that temperatures are important because basking behaviour took place throughout all days with calm seas. This may, however, be a warming process after the turtle has spent an hour or so sleeping on the bottom. The reasons for this being that no individual turtle was observed to spend more than nine minutes floating at the surface. During this time breathing varied between three intakes to 18. At the surface about two thirds of the carapace was exposed and after a few moments the exposed portion would be dry. Movement was restricted to lifting the head and the occasional stroke by the hind-flippers. As, on Europa Island, there are between 200 and 400 turtles on the surface at all times of the day it is difficult to watch an individual because the slightest distraction results in confusion.

NUMBER OF NESTS AND EGGS PER SEASON

LOGGERHEADS

Table 22 shows the number of nests recorded in the Tongaland protected area during the past four seasons and the estimated total nesting population of females during each season. Although not entirely justified a simple division suggests that the mean number of nests laid per season is four.

Table 22 shows also the observed number of nests laid by individual females and it can be seen that numerous females lay up to five times in one season which would, at roughly 15 day intervals between each nesting, span the two-month nesting season.

If, however, every female lays five times, then either winds wipe out the traces of more nests than is expected or there is some movement on the extremities of the protected area resulting in nests being laid outside and thus not recorded.

It is likely that nests are missed for both reasons and it is suggested that the Tongaland loggerhead lays either four or five times during a season. Thus the total egg production of an individual female is estimated at between 450 and 570 eggs per season at a mean clutch size of 114 eggs (Table 22).

In Tongaland the policy has been not to kill females under any circumstances so only one turtle has been examined in detail. Table 23 summarizes the number of ova in each ovary (ova smaller than 5.0mm estimated by mass) and there is nothing to suggest the total reproductive lifetime of the female. Apart from the mass of minute ova there were 169 developing ova of various sizes which did not suggest any particular size grouping. However, as the animal was killed near the end of the season it may be that these were merely remnants which would be reabsorbed in due course. Caldwell *et. al.* (1959: 316) found some evidence of grouping of ovarian eggs in Atlantic loggerheads killed early in the nesting season and similar quantities of minute ova.

LEATHERBACKS

Table 22 shows also that leatherback turtles in Tongaland lay up to 8 clutches per season giving the total egg production of normal yolked eggs as 800 or more. With the substantial movements of leatherbacks between layings it is likely that many nests are laid outside of the protected area and hence unrecorded.

One female killed outside of the protected area on the 29th December, 1971 was found to contain 902 well developed ova measuring approximately 35.0mm in diameter with 113 shelled yolked eggs ready to lay. This made a total of 1 015 eggs which, if spread over 8 nestings, would be 127 eggs per clutch which is well within the observed range of leatherback clutch sizes in Tongaland (Table 22). At nine layings this would mean the clutch size would be 113 the size of the one clutch that was ready for laying.

GREEN TURTLES

Insufficient time was spent on any green turtle nesting ground to ascertain the number of eggs or nests made by green turtle females in the study region. Details of egg sizes and numbers may be found in Hughes (in press; Table 19).

THE REPRODUCTIVE LIFETIME

LOGGERHEADS

The Tongaland programme is still too young to have produced conclusive results on the reproductive lifetime of the loggerhead. In a previous section it was shown that reproduction by individual animals was irregular so time is not a suitable indicator and it is not yet possible to assess the duration of the reproductive lifetime.

Although two and three recorded nesting seasons per individual are common, only two females have been logged in four separate seasons out of nine (Table 13). It is reasonable to assume that if this was a frequent occurrence, more data would have been collected even with the loss of tags. However, as these tag losses have been heavy, it is tentatively suggested that the reproductive potential of a loggerhead female is spread over four nesting seasons spanning a highly variable length of time. As each female has a massive reserve of ova it would appear that preparation for a nesting season is heavily dependant on the environmental conditions surrounding the female during non-nesting periods.

Thus, accepting four seasons nesting at approximately 513 eggs per season, the total number of eggs laid during a reproductive lifetime is around 2 000.

LEATHERBACKS

As the same time-drawbacks as was outlined above for loggerhead turtles apply to leatherback results and there are fewer data it is not intended to make any quantitative suggestions concerning the reproductive lifetime.

It can be said only that leatherbacks lay up to 1 000 eggs per season for at least three nesting seasons giving a possible maximum number of eggs as 3 000 per reproductive lifetime. Many more data are required before these figures can be confirmed or added to.

FACTORS AFFECTING THE HATCHING SUCCESS OF EGGS

Bustard and Greenham (1968: 275) showed that, in Australia, the chloride concentration in the sand is not a limiting factor in the hatching success of eggs except below high spring tide levels where the chloride concentrations can reach lethal levels. At 365mg Cl-/Kg dried sand they reported 65% egg mortality in green turtle clutches.

Loggerheads in Tongaland rarely lay near the high water mark but leatherback nests are often situated close to, either above or below, the high water mark. Hughes (1970: 33) reported the results of a survey of leatherback nests in Tongaland, showing that 17 (30%) out of 56 nests were laid in this marginal zone. Sand samples from eleven sites had a mean chlorinity value of 180mg Cl-/Kg dried sand (range 66-499, S.D.111).

Thus, variation in chlorinity values is wide in this narrow zone and the highest values might endanger some of the clutches laid there. If mortalities do occur this might be another partial explanation for the moderate extent of the leatherback population in Tongaland.

Other factors observed in Tongaland are:

(i) Waterlogging through continual emergence in water either through being buried too deeply above a shallow rock layer (observed only in hatchery nests) or as a result of beach erosion and waves washing continuously over the nest.

(ii) Predation through feral dogs (the most serious threat), ants (*Dorylus* spp.) (in those nests laid close to the natural bush), and monitor lizards (*Varanus* spp.).

Hill and Green (1971: 11-13) suggest that in Surinam some 11.8% of each clutch is destroyed by ghost crabs but they did not explain how they distinguished between eggs burst by the prodding stick used to find the nest originally and those eaten by crabs. They showed also that they had burst some five eggs per clutch. It is thought likely that the contents of the burst eggs would have attracted the crabs and thus give the impression that they were predators. In Tongaland neither species of ghost crab has been observed, either directly or indirectly, to inflict damage on turtle eggs. On numerous occasions crab tunnels have been found leading into nests after the hatchlings have departed but there has been no evidence to suggest that the crabs had been there prior to hatching and attacked eggs or hatchlings.

On Europa Island considerable damage is inflicted by nesting females digging up prepreviously laid eggs (see Bustard and Tognetti, 1969: 939-941).

REPRODUCTIVE SUCCESS

Table 24 summarizes the fertility, hatching and emergence success of clutches laid by loggerhead and leatherbacks in Tongaland, and by green turtles on the islands of Europa and Tromelin.

As the loggerhead data included in Table 24 was based on marked nests not interfered with in any way until after the expected incubation period had elapsed, they are more realistic than those reported by Hughes *et. al.* (1967: 32) who dealt with emerged nests only.

The hatching success of leatherbacks in Tongaland is similar to that reported by Schulz (1968: 72) for leatherbacks in Surinam and by Pritchard (1971b: 24) for Mexico. The markedly lower emergence success suggests that the metre, or more, climb to the surface of the beach is a laborious undertaking for hatchling leatherbacks.

No obvious reason is available to explain the differences between the hatching and emergence successes of the green turtle samples as both are from oceanic islands with similar sand beaches.

Perhaps larger samples taken at the same time of the year would show less difference because the Europa sample was collected in early December and the Tromelin sample in October after a cold winter season.

SURVIVAL RATE TO MATURITY

LOGGERHEADS

Despite the premature stage of research in Tongaland some tentative suggestions concerning the survival rate to maturity are pertinent here.

Taking the past four seasons as being the most thoroughly recorded and averaging the data one has:

(1) Mean number clutches/season: 1 660 (Table 24).
Mean number eggs/clutch: 114 (Table 24).
Therefore total number eggs/season: 189 240.

As mean hatching success is 78.6% the total number of hatchings is 148 743 and the mean emergence success 147 229. However ghost crab predation is 3.7% (Table 3). Therefore the number of hatchlings entering the sea is 141 782.

(2) The percentage remigrants, both with tags and those that had lost tags, recorded during the 1972-73 season was 47% therefore the recruitment rate is at most 53%. It is likely, however, there are some remigrants that have never been tagged before so the recruitment rate could be any percentage between 53% and 0. It would seem unlikely to be less than 10%.

(3) The mean number of females utilizing the Tongaland beaches during the past four seasons is 420 (Table 24).

(4) The sex ratio between males and females is thought to be one male for every two females (see Hughes, in press).

(5) Therefore if the recruitment rate is considered at the 50%, 40%, 30%, 20%, and 10% levels we have the following possibilities:

(i) The 50% recruitment rate
No. of females: 210
+Males (1 : 2) 105
Total: 315
Survival rate from 141 782 hatchlings entering the sea: 0.22%

(ii) 40% recruitment rate
No. of females: 168
+Males: 84
Total: 252
Survival rate: 0.178%

(iii) 30% recruitment rate
No. of females: 126
+Males: 63
Total: 189
Survival rate: 0.133%

(iv) 20% recruitment rate
No. of females: 84
+Males: 42
Total: 126
Survival rate: 0.089%

(v) 10% recruitment rate
No. of females: 42
+Males: 21
Total: 63
Survival rate: 0.044%

Therefore, as far as the present data permits it would appear that the survival rate to maturity is between 0.2% and 0.044%. In whole figures this means that only one or two hatchlings per thousand reach maturity after entering the sea.

That these figures have some value may be derived from the suggested total production of an individual female. So far the Tongaland data suggests that an average female lays 4.5 times per season for four seasons. At 114 eggs per clutch her total egg production is 2 052 eggs.

From these eggs 1 537 hatchlings might be expected to reach the sea having lost 3.7% to ghost crabs. In order that the population remains stable at least one female must survive to maturity but as there is thought to be one male for every two females it is easier to consider the production of two females as follows:

Total hatchling production: 3 074
Two female and one male survivors: 3
Percentage survival rate: 0.098%

At this survival rate the annual recruitment rate in Tongaland would be 139 turtles. consisting of 93 females and 46 males.

At 93 females the nesting recruitment rate would be 22.0% which is thought to be a plausible figure. Within the next five years it will be possible to ascertain the accuracy of these suggestions.

It is to be hoped that for a time the recruitment rate will be higher than this hypothetical calculation as the population recovers from the artificial mortality imposed prior to the protection efforts instigated in 1963.

Discussion

In general the nesting behaviour of all three species dealt with in the study region is identical to reported accounts from other regions. There seems to be little doubt that the sea temperature has considerable influence on the nesting season and fluctuations in sea temperature can be linked with internesting intervals and incubation periods (Hughes and Brent, 1972: 47). Responses to tidal phases are negligible in leatherbacks, slight in loggerheads, and direct in green turtles from Europa Island. There is no relationship at all between moon phase and nesting activity within a season (see Fig. 28) as was first reported by Baldwin and Lofton (1959: 324).

One unexplained aspect of turtle nesting activity is the fluctuation in numbers of females coming to the beaches each season. In Tongaland, loggerhead numbers have varied between 217 (1968-69) and 502 (1971-72) and leatherbacks from five (1966-67) to 55 (1971-72). These fluctuations have been observed in green turtle nesting areas as well, e.g. Tortuguero (Carr and Carr, 1970b: 283), Sarawak (Banks, 1937: 529), and the St. Brandon Islands (see Fig. 23).

No obvious reason for these fluctuations is available. Banks (*ibid.*) suggested that one season of high rainfall resulted in the following season being poorly attended by turtles but he presented limited data and the actual link between rainfall on the nesting ground and a potential nester which may be a long distance (1 600km) away is not clear. Of course, referring back to Section 1, it is possible that heavy rainfall leaches out or diffuses the olfactory turtle cue resulting in the following season's nesters being unable to find the nesting ground, depending on whether such a cue does exist and if it is used as a long range guide. This immediately raises the question as to where the turtle does lay her eggs if she cannot find the home nesting ground, or if she reabsorbs the eggs.

Further, it seems unlikely that temperature would have any influence on the numbers of turtles nesting considering the wide distribution of the loggerhead population in the study region. At the individual turtle level there is no suggestion of differences in egg production or general behaviour, and the percentage contributions of remigrants and new animals continues to rise at a consistent rate every season, irrespective of overall numbers (see Fig. 12).

Exploitation of the adult stocks away from Tongaland might be an explanation but there are no data to support this and it is considered unlikely.

Finally, there is the possibility that a poor nesting season is the result of a previous nesting season experiencing a natural disaster with excessively high egg and/or hatchling mortality, and a subsequent loss of recruits. This too seems unlikely in that it would be expected that in such a season the percentage remigrants would appear markedly higher which is not the case.

The present evidence suggests that whatever the cause of these fluctuations it affects both recruits and remigrants. It must be assumed therefore that it is an environmental factor, not variation within individual females, and must be far-reaching to cover the spread of the whole population. Temperature, rainfall and food could all be considered local phenomena as values vary from area to area and perhaps it is a combination of all three or might simply be the availability of food.

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Tables

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Season	Duration of tagging programme	Number tagged	Mean measurements of sample in Tongaland c.l. (mm)	c.w. (mm)	Mass (g)	Spec. No.	Locality Recovered	Date	Distance (km)	Age in days Min. - Max.	Measurements c.l. (mm)	c.w. (mm)	mass (g)
1972	27 Jan.-1 Mar. (33 days)	5 000	45.1	36.9	20.0	A	Pt. Elizabeth	1 May	1 100	61 - 92	57.0	54.2	45.3
1973	15 Jan.-10 Mar. (54 days)	5 250	44.3	36.3	19.1	B	Durban	13 Feb.	400	4 - 28	49.0	39.0	22.6
						C	Pt. Elizabeth	20 Feb.	1 100	7 - 36	52.0	47.0	29.0
						D	Pt. Elizabeth	7 Apr.	1 100	28 - 75	65.0	60.5	49.9
						E	Cape Agulhas	27 Apr.	1 650	48 - 102	52.5	51.5	32.0
						F	Cape Agulhas	27 Apr.	1 650	48 - 102	52.8	49.5	32.7

Table 1. Details of 6 notched loggerhead hatchlings recovered at various localities along the east and south coasts of South Africa.

Species	Localities	Date	Measurements Carapace length (mm)	 Carapace width (mm)
Loggerhead	Bhanga Nek, Tongaland	5 Mar. 1971	60.0	54.9
	Port Elizabeth	28 Mar. 1968	101.6	—
	Port Elizabeth	28 Mar. 1968	110.0	—
	Port Elizabeth	11 Aug. 1968	112.0	102.0
	George, Cape	28 Dec. 1968	219.0	202.0
Leatherback	Cape Agulhas	2 Apr. 1968	100.0	74.8
Green	Port Elizabeth	12 Sept. 1969	190.0	156.0

Table 2. Unseasonal and unusual strandings of juvenile sea turtles in the study region.

Date	Time	Total Number hatchlings	Number taken by crabs	% Kill
24 January 1973	0020	25	4	16.0
15 February 1973	2200	91	2	2.2
16 February 1973	2300	61	2	3.3
16 February 1973	2315	92	3	3.3
16 February 1973	2340	135	2	1.5
17 February 1973	2100	94	0	0
17 February 1973	2150	90	0	0
18 February 1973	0015	130	1	0.7
18 February 1973	2115	84	3	3.6
18 February 1973	2215	75	5	6.7
			Mean:	3.7

Table 3. The incidence of ghost crab (*Ocypode* spp.) predation on loggerhead hatchlings in Tongaland.

Number of hatchlings	Stomach contents
5 . . .	Nothing
8 . . .	Fine grit only
8 . . .	Grit; feathers (1 x 36mm; 1 x 18mm and 15mm; 1 x 10mm; 1 x 21mm; 1 x 9mm)
2 . . .	Fragments of algae (sp. ?); piece of bark 5mm x 3mm
2 . . .	Grit; spherical 1mm plastic beads
2 . . .	Pieces of fine plastic sheet (both pieces about 30mm long and 20mm at widest point)
9 . . .	Gelatinous material — *Physalia* (?)
1 . . .	Clearly *Physalia physalis*

Table 4. Stomach contents of 37 loggerhead hatchlings stranded on Cape Agulhas.

	Months											
Size class (cm)	J	F	M	A	M	J	J	A	S	O	N	D
60·–61.9	—	X	—	—	—	—	X	—	—	—	—	—
62·–63.9	—	—	—	—	—	—	—	X	—	—	X	—
64·–65.9	—	—	X	—	—	—	—	X	—	X	X	—
66·–67.9	—	X	—	—	—	—	X	—	—	—	—	—
68·–69.9	—	—	—	—	—	—	—	—	—	—	—	—
70·–71.9	—	—	—	—	—	—	—	—	—	—	—	—
72·–73.9	—	—	—	—	—	—	—	—	—	—	X	—
74·–75.9	—	—	X	—	2	—	X	—	—	—	—	—
76·–77.9	—	—	X	—	—	X	—	—	—	X	X	—
78·–79.9	—	—	—	X	X	—	X	X	—	X	—	X
80·–81.9	3	—	X	X	—	—	X	—	—	—	X	—
82·–83.9	X	—	2	X	—	—	X	—	2	—	—	—
84·–85.9	—	—	—	—	—	—	—	—	—	X	—	2
86·–87.9	X	—	—	—	—	—	X	—	—	—	—	—

Table 5. Size classes (straight carapace length) of loggerhead turtles found along the Natal coast during various months of the year.

Carapace length	Mollusca (%)	Echinoderma (%)	Porifera (%)	Crustacea (%)	Ascidiacae (%j	Coelenterata (%)	Miscellaneous (%)	Sample Mass (g)	Remarks and principal articles
60.5	3.0	—	—	—	—	—	97.0	25.0	Sugar cane; bark; plastic strip; *Janthina.*
62.0	37.8	—	—	—	—	62.2	—	18.7	*Porpita* spp.
62.2	21.0	68.9	—	—	—	—	10.0	14.7	*Prionocidaris baculosa* (the slate-pencil urchin); plastic bag.
63.9	—	—	—	61.6	—	38.4	—	61.5	*Paguristes* spp.
64.0	69.4	—	—	—	—	—	30.6	12.4	*Janthina*; *Spirula* skeletons; Pteropoda shells.
64.7	7.9	—	—	47.0	41.6	—	3.7	267.0	*Pagurus* spp.; *Pyura stolonifera* (?); pieces of glass.
65.0	0.2	—	—	—	—	—	99.8	15.5	Bark, plastic bag; *Janthina.*
66.0	11.6	—	—	14.6	—	63.3	11.0	42.4	*Physalia* (?); *Janthina*
67.0	76.0	—	—	7.1	—	—	16.9	22.6	See table 7.
72.9	—	—	—	6.0	—	—	94.0	16.6	Fragments of Pagurids; grit.
77.0	36.5	—	—	55.3	—	—	8.2	151.6	*Pagurus arresor* (?); see table 7.
78.5	100.0	—	—	—	—	—	—	9.7	See table 7.
78.5	8.8	—	—	57.0	—	—	34.2	33.9	*Janthina*; *Lepas* spp.; bark; carapace shields of hatchling loggerhead
79.6	59.8	—	—	40.2	—	—	—	71.7	*Janthina*; *Spirula* shells
80.6	68.7	—	—	4.1	—	—	27.4	87.5	See table 7.
81.0	26.6	—	22.9	22.2	—	—	28.4	1 114.0	See table 7; Pagurids.
81.3	100.0	—	—	—	—	—	—	6 000.0	*Perna perna*
83.3	70.8	9.0	—	18.5	—	—	1.8	85.0	See table 7.
84.0	29.0	20.0	—	8.4	—	—	42.6	389.9	See table 7.
84.2	26.7	38.8	—	1.0	—	—	33.4	825.0	See table 7.
85.0	90.0	—	—	10.0	—	—	—	320.0	See table 7.
86.0	—	—	—	76.8	—	—	23.2	398.0	*Pagurus arresor*
86.7	—	—	—	100.0	—	—	—	2.0	Fragments.
87.0	57.2	0.4	—	13.4	—	—	29.0	898.8	See table 7.
87.2	52.8	—	—	35.1	—	—	12.1	93.3	See table 7.
89.0	15.5	51.1	—	7.7	—	—	25.7	585.2	See table 7; *Prionocidaris baculosa.*
Means:	38.5	7.5	0.8	23.3	1.7	6.6	21.6	—	

Table 6. The stomach contents of 26 loggerhead turtles from the South African coast. The percentage contributions of each phylum expressed in terms of mass.

1	*Bufonaria crumenoides* (Plate 6) *Ficus subintermedius* (Plate 6)
2	*Babylonia pintado* *Tonna variegata* *Lyria ponsonbyii* *Bullia similus*
3	*Limaria fragilis* *Ficus ficus* *Harpa major* *Astrea andersoni*
4	*Nassarius kraussianus* *Harpa davidus*
5	*Rapana rapiformis* *Perna perna* *Charonia lampas pustulata* *Latirus abnormis* *Pintada radiata* *Pecten* spp. *Conus* spp.
6	*Cymatium labiosum* *Bursa granularis* *Harpa amouretta* *Mayena australasia gemmifera* *Anitica* spp. *Marginella pipenata* *Murex falax* *Action* spp. *Dupliclaria* spp. *Polinices didyma* *Glycimeris queketti* *Vepricardium asiaticum* *Pinna* spp.

Table 7. Species list of littoral and benthic Mollusca taken from the stomachs of loggerhead turtles. Listed in order of frequency.

Specimen 1 - 12												
Article	1	2	3	4	5	6	7	8	9	10	11	12
Gelidium cartilagineum	49.2	60.4	95.2	50.5	94.6	—	25.4	—	—	—	73.0	8.8
Gelidium amanzii	—	30.0	—	—	—	91.2	—	—	—	100.0	—	—
Codium duthieae	31.1	1.9	4.8	28.3	—	7.8	70.0	—	2.2	—	26.0	—
Codium platylobium	—	—	—	—	—	—	2.3	—	—	—	—	—
Caulerpa filiformis	18.4	7.7	—	5.5	5.3	0.9	2.4	96.5	76.5	—	—	90.1
Halimeda cuneata	1.4	—	—	—	—	—	1.0	0.1	0.3	—	—	—
Ulva spp.	—	—	—	—	—	—	—	—	—	—	—	0.1
Cladophora capensis	—	—	—	—	—	—	—	3.0	—	—	—	—
Kirchenpaneria pinnata	—	—	—	—	—	—	—	0.4	—	—	—	—
Unidentifiable	—	—	—	15.7	—	—	—	—	21.0	—	1.0	1.0

Table 8. Stomach contents of 12 green turtles from the coast of Natal. Percentages expressed in terms of mass.

Carapace L.	Detail	
60.5	Nothing	18% *Lepas* sp. 18% *Chelonibia* sp. 64% No epizoites
62.0	*Lepas* sp. (Pl. 7)	
62.2	Nothing	
63.9	Nothing	
64.0	*Lepas* sp.	
64.0	Nothing	
64.2	Nothing	
64.7	Nothing	
65.0	*Chelonibia* sp.	
66.0	Nothing	
67.0	*Chelonibia* sp.	
72.9	Nothing	21.4% *Chelonibia* sp. 78.6% No epizoites
75.5	Nothing	
76.1	Nothing	
76.4	Nothing	
76.5	Nothing	
77.0	*Chelonibia* sp.	
77.9	Nothing	
78.5	Nothing	
78.5	Nothing	
78.5	*Chelonibia* sp.	
78.5	*Chelonibia* sp.	
78.5	Nothing	
79.0	Nothing	
79.6	Nothing	
80.0	Nothing	47.4% *Chelonibia* sp. 52.6% No epizoites
80.6	*Chelonibia* sp.	
80.7	*Chelonibia* sp.	
81.0	Nothing	
81.0	Nothing	
81.0	*Chelonibia* sp.	
81.1	Nothing	
81.3	Nothing	
82.0	Nothing	
83.0	*Chelonibia* sp.	
83.3	*Chelonibia* sp.	
83.8	Nothing	
84.0	*Chelonibia* sp.	
86.0	Nothing	
86.7	*Chelonibia* sp.	
87.0	*Chelonibia* sp.	
87.1	Nothing	
87.2	*Chelonibia* sp.	
89.0	Nothing	

N.B. Tongaland females: 73% *Chelonibia* sp.
27% No epizoites

Table 9. Epizoites on the carapaces of 44 loggerhead turtles from Natal.

Tag No.	Date last seen in Tongaland	Date recovered	Time interval (days)	Locality recovered	Distance (km)	Minimum distance per day (km)
T81	30 Dec. 1965	16 March 1966 (?)	76	Kilwa Masoka, Tanzania	2 640	35
T59	11 Jan. 1966	3 April 1967	82	Mikindani, Tanzania	2 400	29
A49	28 Dec. 1969	27 Jan. 1970	30	Warner Beach, Natal	430	14
A165	5 Dec. 1970	9 Feb. 1971	66	Kilwa Masoka, Tanzania	2 640	40
A868	8 Jan. 1971	17 Nov. 1971	313	Lourenco Marques, Moz.	120	0.4
B72	2 Dec. 1971	9 Aug. 1972	251	Lourenco Marques, Moz.	120	0.5
A30	17 Dec. 1969	19 Feb. 1973	1 060	Zanzibar Channel	2 880	2.7

Table 10. Some extra-nesting area recoveries of loggerhead turtles tagged in Tongaland.

Tag No.	Locality tagged	Date last seen	Date recovered	Time interval	Locality recovered	Distance (km)	Minimum distance travelled per day
(a) Green turtles							
A246	Europa Island	6 Nov. 1970	25 Dec. 1970	48	Farafangana, Madag.	1 200	25 km
A421	Europa Island	12 Nov. 1970	3 Jul. 1971	234	Ambaro Bay, Madag.	1 400	6 km
A521	Europa Island	29 Nov. 1970	15 Oct. 1972	685	Morembe, Madag.	320	—
A443	Europa Island	8 Dec. 1970	18 Sept. 1973	965	Tulear, Madag.	400	—
(b) Leatherback							
B235 B236	Tongaland	7 Dec. 1971	10 Dec. 1972	369	Beira, Mozam.	1 000	—

Table 11. Details of recoveries of tagged green turtles and a tagged leatherback turtle from Tongaland.

Season	Number of turtles encountered	Period of absence												Calloused	%	Percentage remigrations of turtles handled
		1 yr.	%	2 yr.	%	3 yr.	%	4 yr.	%	5 yr.	%	6 yr.	%			
1964-65	223	3	1.4	—	—	—	—	—	—	—	—	—	—	—	—	1.3
1965-66	200	5	2.5	9	4.5	—	—	—	—	—	—	—	—	—	—	7.0
1966-67	221	3	1.4	16	7.2	3	1.4	—	—	—	—	—	—	—	—	9.9
1967-68	293	5	1.7	12	4.1	4	1.4	9	3.1	—	—	—	—	11	3.8	14.0
1968-69	184	—	—	3	1.6	3	1.6	5	2.7	1	0.5	—	—	16	8.7	15.2
1969-70	285	—	—	—	—	—	—	1	0.4	1	0.4	4	1.4	68	23.9	26.0
1970-71	241	8	3.3	—	—	—	—	—	—	1	0.4	2	0.8	70	29.1	33.6
1971-72	321	10	3.1	18	5.6	—	—	—	—	—	—	1	0.3	101	31.5	40.5
1972-73	262	6	2.3	41	15.7	9	3.4	—	—	—	—	—	—	67	25.6	47.0
Totals		**40**	**21.9**	**99**	**54.1**	**19**	**10.4**	**15**	**8.2**	**3**	**1.6**	**7**	**3.8**			

Table 12. Details of loggerhead remigrations to the Tongaland beaches.

Tag No.	Original Season		Interval (years)	Recovery 1		Interval (years)	Recovery 2		Interval (years)	Recovery 3		Number of Seasons Nested
	Date	Loc.†		Date	Loc.		Date	Loc.		Date	Loc.	
S/Yellow 42	17 Dec. '63	2.4 S	1	10 Dec. '64	4.0 S	1	10 Dec. '65	4.0 S	—	—	—	3
S/Black 38	17 Nov. '64	2.8 S	1	21 Dec. '65	8.0 S	2	11 Nov. '67	11.2 S	—	—	—	3
S/Black 47	23 Nov. '64	3.2 N	1	8 Dec. '65	4.8 N	1	2 Nov. '66	6.8 N	2	21 Nov. '68	2.4 N	4
S/Black 71	24 Nov. '64	6.4 S	2	12 Dec. '66	7.2 S	2	13 Dec. '68	4.8 S	—	—	—	3
S/Black 90	29 Nov. '64	1.6 N	2	21 Dec. '66	8.4 S	5	19 Dec. '71	2.4 S	—	—	—	3
L/Red T72*	—	—	1	28 Dec. '65	5.2 N	2	7 Dec. '67	3.6 N	—	—	—	3
A25*	—	—	?	19 Dec. '69	5.6 N	1	16 Dec. '70	5.2 N	2	5 Dec. '72	8.8 N	4
A129	1 Nov. '69	6.4 S	1	13 Nov. '70	6.4 S	1	7 Dec. '71	5.6 S	—	—	—	3
A946	23 Dec. '70	6.0 S	1	8 Dec. '71	7.2 S	1	24 Nov. '72	10.0 S	—	—	—	3
A963*	had a broken tag 1964-65		6?	5 Jan. '71	4.8 S	2	6 Dec. '72	4.8 S	—	—	—	3

Table 13. Details of 10 loggerhead turtle multiple remigrations to Tongaland.

*Denotes that turtle had been tagged previously but had lost original tag.

†Denotes distance (km) north or south of Bhanga Nek camp.

In addition to the above at least 29 females have nested in 3 separate seasons in Tongaland.

Season	Number of turtles encountered	Period of absence								Calloused	%	% remigrations of turtles handled
		1 yr.	%	2 yr.	%	3 yr.	%	4 yr.	%			
1964-65	13	1	7.7	—	—	—	—	—	—	—	—	7.7
1965-66	26	—	—	2	7.7	—	—	—	—	—	—	7.7
1966-67	5	—	—	2	40.0	—	—	—	—	—	—	40.0
1967-68	18	—	—	—	—	—	—	—	—	—	—	—
1968-69	19	—	—	—	—	4	21.0	1	5.3	—	—	26.3
1969-70	28	—	—	3	10.7	—	—	2	7.1	5	17.9	35.7
1970-71	17	—	—	3	17.7	—	—	—	—	2	11.8	29.4
1971-72	39	—	—	2	5.1	—	—	—	—	3	7.7	12.8
1972-73	21	—	—	1	4.7	—	—	—	—	3	14.3	19.1
	Totals	1	2.9	13	38.2	4	11.8	3	8.8	13	38.2	

Table 14. Details of leatherback remigrations to the Tongaland beaches.

Tag No.	Original Season Date	Original Season Locality	Interval (years)	Recovery 1 Date	Recovery 1 Locality	Interval (years)	Recovery 2 Date	Recovery 2 Locality	Number of seasons nested
S/Blue 16	19 Jan. 1964	27.2 S	1	3 Dec. 1964	0.8 N	2	3 Jan. 1967	10.00 S	3
S/Yellow 19	10 Dec. 1963	1.2 N	2	30 Dec. 1965	1.6 N				2
S/Green 24	23 Dec. 1963	27.2 S	2	25 Jan. 1966	19.6 S				2
L/Blue T36	19 Dec. 1964	2.0 N	2	3 Dec. 1966	19.6 S				2
L/Green T22	31 Jan. 1966	5.6 S	3	13 Jan. 1969	20.8 S	2	18 Nov. 1970	9.6 S	3
L/Yellow T65	3 Jan. 1966	19.1 S	3	12 Jan. 1969	10.0 S	2	3 Jan. 1971	6.4 N	3
L/Yellow T79	8 Feb. 1966	13.6 S	3	8 Jan. 1969	12.8 S				2
L/Red T87	29 Dec. 1965	5.2 N	4	21 Jan. 1970	0.4 S	2	22 Dec. 1971	1.6 N	3
L/Red T93	30 Dec. 1965	2.8 N	4	28 Dec. 1969	3.6 S	2	19 Dec. 1971	7.2 N	3
R/Yellow 5085	26 Dec. 1967	4.0 N	2	9 Jan. 1970	10.4 S				2
R/Yellow 4627	11 Jan. 1968	6.0 N	2	4 Dec. 1969	4.8 N				2
R/Yellow 4652	13 Dec. 1967	20.8 S	2	12 Nov. 1969	10.4 S				2
R/Yellow 4415	8 Jan. 1969	6.4 N	2	21 Nov. 1970	8.8 N				2
A951	28 Dec. 1970	35.2 S	2	6 Jan. 1973	36.8 S				2

Table 15. Details of 15 leatherback turtle multiple remigrations to Tongaland. (Distances as in Table 13).

Season	Tag Nos.	Locality of original encounter	Recoveries 1	2	3
1964-65	T7gr.	0.8N*	0.4N	0.8N	—
	S/blu.28	14.4S	13.6S	—	—
	S/bla.32	4.8S	0.4N	0.4N	—
1965-66	T57Y	18.4S	18.4S	—	—
	T64Y	19.2S	20.0S	—	—
	T65Y	19.6S	9.6S	—	—
	T71R	1.2N	12.0S	1.2S	1.2S
	T93R	2.8N	4.8S	—	—
	T70W	1.2S	0.4N	9.2S	—
1967-68	T5G	19.6S	5.6S	—	—
	4652/72	20.8S	19.2S	21.6S	—
1968-69	4360/61	9.6S	9.6S	—	—
	4384/85	10.8S	10.4S	—	—
	4387/88	12.8S	5.6S	2.4N	1.2N
	4407/09	1.2N	17.6S	—	—
	4432/33	8.4S	15.2S	13.2S	—
	4469/71	12.8S	18.0S	—	—
	4472/74	21.6S	21.6S	—	—
	4475/76	18.0S	17.6S	—	—
	4481/83	10.4S	20.4S	—	—
	4563/65	14.4S	21.6S	—	—
	4584/86	14.4S	20.0S	—	—
1969-70	4670/71	30.0S	39.2S	—	—
	6225/26	4.8N	5.2S	14.4S	—
	2280/2810	8.0N	1.2N	—	—
	2556/59	9.6S	6.4S	—	—
1970/71	A152/153	9.6S	24.0S	—	—
	A706/707	26.4S	26.0S	32.0S	—
	A709/712	31.2S	0.8N	—	—
	A952/953	28.8S	22.4S	—	—
	A954/955	27.2S	6.0S	—	—
1971/72	B3	6.0S	19.6S	—	—
	B20/21	13.2S	18.4S	—	—
	B77/78	30.4S	30.0S	—	—
	B84/85	17.6S	20.0S	28.0S	—
	B104/105	28.8S	13.2S	—	—
	B174/175	1.2N	7.6N	—	—
	B313/314	23.6S	31.2S	—	—
	B328/331	16.4S	8.0N	—	—
	B351/352	32.0S	26.0S	—	—
	A45/47	7.2N	6.8N	—	—
	A102/103	1.6N	1.2N	—	—
1972-73	C10/11	4.4S	10.4N	8.4S	—
	C52/53	2.0N	1.2N	2.4N	—
	C71/72	21.6S	18.4S	—	—
	C73/74	36.8S	2.4N	1.6N	—
	C81/82	17.6S	3.6S	—	—
	C112/113	6.4S	5.6N	—	—
	C182/183	2.0N	5.6S	1.2N	—
	C202/—	4.4N	13.6S	—	—
	C228/229	0.4N	5.2N	5.6S	1.2S
	C232/233	1.6N	18.4S	—	—

Table 16. Details of all within season recovery records of leatherback females in Tongaland 1963-73.
*Distances in km north or south of the Bhanga Nek camp.

Curv. carap. 1. size class	New turtles	%	Remigrant turtles	%	Size class %	Curv. carap. 1. size class	New turtles	%	Remigrant turtles	%	Size class %
1965-66 Season						**1970-71 Season**					
Up to 85cm	3	100.0	0	—	2.6	Up to 85cm	4	80.0	1	20.0	3.3
86 - 90	24	96.0	1	4.0	21.4	86 - 90	19	68.0	9	32,0	18.3
91 - 95	47	92.0	4	8.0	43.6	91 - 95	44	71.0	18	29.0	40.5
96 - 100	31	97.0	1	3.0	27.4	96 - 100	38	76.0	12	24.0	32.7
101 + cm	6	100.0	0	—	5.0	101 + cm	6	75.0	2	25.0	5.2
	111		6				111		42		
1966-67 Season						**1971-72 Season**					
Up to 85cm	4	100.0	0	—	2.5	Up to 85cm	6	100.0	0	—	1.9
86 - 90	29	88.0	4	12.0	20.5	86 - 90	32	71.0	13	29.0	14.0
91 - 95	57	92.0	5	8.0	38.5	91 - 95	87	57.0	65	43.0	47.4
96 - 100	42	79.0	11	21.0	32.9	96 - 100	50	48.0	53	52.0	32.1
101 + cm	9	100.0	0	—	5.6	101 + cm	10	72.0	4	28.0	4.6
	141		20				185		135		
1967-68 Season						**1972-73 Season**					
Up to 85cm	5	100.0	0	—	1.9	Up to 85cm	4	67.0	2	33.0	2.4
86 - 90	47	87.0	7	13.0	20.1	86 - 90	26	63.0	15	37.0	16.5
91 - 95	100	92.0	9	8.0	40.7	91 - 95	50	47.0	57	53.0	43.2
96 - 100	84	93.0	6	17.0	33.6	96 - 100	44	54.0	37	46.0	32.7
101 + cm	8	80.0	2	20.0	3.7	101 + cm	7	54.0	6	46.0	5.2
	244		24				131		117		
1968-69 Season						**Overall size class percentages**			n		
Up to 85cm	4	100.0	0	—	3.1	Up to 85cm	—	2.4%	33		
86 - 90	20	100.0	0	—	15.3	86 - 90	—	17.6%	246		
91 - 95	40	91.0	4	9.0	33.6	91 - 95	—	42.0%	587		
96 - 100	41	72.0	16	28.0	43.5	96 - 100	—	33.3%	466		
101 + cm	2	33.0	4	67.0	4.6	101 + cm	—	4.7%	66		
	107		24						1 398		

Table 17. Size class composition of 7 seasonal nesting populations of loggerhead females in Tongaland.

Curved carapace l. size class	1965-66 n	1965-66 %	1966-67 n	1966-67 %	1967-68 n	1967-68 %	1968-69 n	1968-69 %	1970-71 n	1970-71 %	1971-72 n	1971-72 %	1972-73 n	1972-73 %	Totals n	Totals %
Up to 140cm. . . .	—	—	—	—	—	—	—	—	—	—	1	2.6	—	—	1	0.8
141 - 150	1	4.4	—	—	1	6.7	1	5.6	1	10.0	3	7.7	1	4.8	8	6.3
151 - 160	7	30.4	2	100.0	7	46.7	7	38.9	3	30.0	17	43.6	12	57.1	55	43.0
161 - 170	10	43.5	—	—	7	46.7	7	38.9	6	60.0	15	38.5	8	38.1	53	41.4
171 +.	5	21.7	—	—	—	—	3	16.7	0	—	3	7.7	0	—	11	8.6
Totals	23	100.0	2	100.0	15	100.1	18	100.1	10	100.0	39	100.1	21	100.0	128	100.1

Table 18. Composition in size classes of 7 seasonal nesting populations of leatherbacks in Tongaland.

		Loggerheads					Leatherbacks			
Month	Season	Nests recorded	Per cent of season total	Taggings	Per cent of season total	Mean sea Temp. °C	Nests recorded	Per cent of season total	Taggings	Per cent of season total
November	1969-70	500	26.91	111	38.20	24.3	94	27.49	7	25.93
	1970-71	529	30.74	94	39.00	24.3	49	23.90	3	16.67
	1971-72	381	21.03	60	18.70	21.7	71	20.17	6	15.39
	1972-73	367	29.96	93	35.63	24.0	59	28.37	6	28.57
December	1969-70	807	43.43	135	47.40	26.0	123	35.49	10	37.05
	1970-71	805	46.78	117	48.60	26.0	76	37.07	11	61.11
	1971-72	775	42.77	160	49.80	24.3	132	37.50	13	33.33
	1972-73	462	37.71	140	53.64	25.3	80	38.46	12	57.14
January	1969-70	551	29.66	39	14.40	26.0	125	36.55	10	37.04
	1970-71	387	22.48	30	12.50	26.3	80	39.03	4	22.22
	1971-72	656	36.20	101	31.50	27.0	149	42.33	20	51.28
	1972-73	396	32.33	28	10.73	25.7	69	33.17	3	14.29

Table 19. Monthly tagging, nesting and sea surface temperature records in Tongaland for the seasons 1969-70, 1970-71, 1971-72 and 1972-73.

Phase	Season	Sea surface temperature (°C)	Mean internesting interval (days)	Number observations
1 November-November	1969-70	24.0	15.8	38
	1970-71	24.5	16.1	14
	1971-72	21.5	17.7	7
	1972-73	24.0	17.1	13
2 November-December	1969-70	24.5	15.5	66
	1970-71	24.5	15.1	46
	1971-72	22.0	16.6	37
	1972-73	24.4	16.0	49
3 December-December	1969-70	26.0	14.7	78
	1970-71	26.0	15.1	62
	1971-72	23.5	15.2	69
	1972-73	25.3	14.8	92
4 December-January	1969-70	26.5	14.2	66
	1970-71	25.5	15.0	38
	1971-72	24.5	15.1	99
	1972-73	25.7	14.0	65
5 January-January	1969-70	26.0	13.6	32
	1970-71	26.3	14.3	12
	1971-72	27.0	13.9	48
	1972-73	25.8	13.8	29

Mean internesting intervals	1969-70	14.8 days	Mean sea surface temperatures	1969-70	25.4°C
	1970-71	15.1 days		1970-71	25.4°C
	1971-72	15.7 days		1971-72	23.7°C
	1972-73	15.1 days		1972-73	25.0°C

Table 20. Mean inter-nesting intervals of loggerhead females during four seasons in Tongaland; compared with the corresponding sea surface temperatures.

Locality	Tag No.	Outward crawl	Excavation of nest cavity	Laying time	No. eggs	Covering time	Return crawl	Total time
Europa Island	A327	10	45	28	153	51	10	144
Tromelin Island	B416	?	38	22	81	72	11	143
Primeiras Islands	A506	5	48	31	130	31	6	121

Table 21. Details of the duration (minutes) of green turtle nesting activity from three localities in the study region.

	Loggerheads			Leatherbacks		
	Total No. nests	Estimated total No. females	Mean No. nests/turtle	Total No. nests	Estimated total No. females	Mean No. nests/turtle
(a) Bulk nest records						
1969-70	1 860	466	3.99	364	47	7.75
1970-71	1 725	410	4.21	216	26	8.31
1971-72	1 831	502	3.65	373	55	6.78
1972-73	1 225	301	4.07	218	35	6.23

	No. nests per female					Total females encountered	No. nests per female							Total females encountered
	5	4	3	2	1		7	6	5	4	3	2	1	
(b) Individual nest records														
1969-70	20	35	38	30	162	285	—	1	—	—	1	2	22	26
1970-71	4	26	35	32	144	241	1	—	1	3	—	—	12	17
1971-72	17	32	57	53	162	321	—	2	1	1	5	2	28	39
1972-73	15	45	49	46	107	262	—	1	1	1	3	2	13	21

	Mean	Range	$\hat{\sigma}$	No. clutches	Mean	Range	$\hat{\sigma}$	No. clutches
(c) No. eggs/clutch	113.6	69 - 173	25	290	104	60 - 160	25.6	59

	Mean	$\hat{\sigma}$	No. eggs	Mean	$\hat{\sigma}$	No. eggs
(d) Size	40.9	1.7	260	53.07	1.49	165

(e) Incubation period	46.0 - 67.0 days	62.5 - 72.0 days

Table 22. A summary of nest and egg data from loggerhead and leatherback turtles from Tongaland during the 1969-70, 1970-71, 1971-72 and 1972-73 seasons.

Size of ova		Left ovary	Right ovary
0.0 — 5.0mm	. . . . .	44 653	98 404
6.0 — 10.0mm	. . . . .	11	7
11.0 — 15.0mm	. . . . .	17	15
16.0 — 20.0mm	. . . . .	10	10
21.0 — 25.0mm	. . . . .	19	23
26.0 — 30.0mm	. . . . .	8	21
31.0 — 35.0mm	. . . . .	6	9
36.0 — 40.0mm	. . . . .	7	6

Table 23. Ova counts from an adult female loggerhead from Tongaland.

	No. eggs/ clutch	Infertile eggs	Fertile/ unhatched	Hatchlings in nest		Hatchlings emerged	Total No. hatchlings	Fertility %	Hatching success %	Emergence success %
				Live	Dead					
(1) Loggerheads — Tongaland (n = 72 clutches)										
Mean	105.3	18.8*	4.53*	0.5*	0.33*	81.21	82.0	82.7	78.6	77.8
Range	39-154	0-113	0-63	0-7	0-4	0-130	0-132	0-100	0-98.7	0-98.7
S.D.	21.7	27.0*	8.71*	1.31*	0.82*	32.1	32.4	22.9	26.0	25.9
(2) Leatherbacks — Tongaland (n = 39 clutches)										
Mean	103.7	20.1*	3.7*	4.41*	2.85*	71.9	79.3	79.6	76.2	68.9
Range	55-142	4-70	0-31	0-24	0-23	5-114	18-121	21.4-96.2	20.2-96.2	5.6-93.2
S.D.	20.8	17.2*	5.8*	5.45*	5.6*	24.0	22.9	16.4	15.7	18.6
(3) Green turtles — Europa Island (n = 27 clutches)										
Mean	142	8.7*	14.2*	7.78*	0.89*	110.2	118.7	93.9	84.3	77.6
Range	75-238	0-30	0-98	0-20	0-8	50-196	67-197	82.3-100.0	41.1-98.9	30.9-98.9
S.D.	35.1	8.2*	20.02*	6.9*	1.8*	37.7	34.12	5.0	13.08	15.62
(4) Green turtles — Tromelin Island (n = 30 clutches)										
Mean	124.6	9.13*	19.2*	3.3*	4.5*	88.7	96.3	92.2	76.34	69.84
Range	79-230	1-37	0-71	0-19	0-50	32-196	38-196	57.5-99.4	34.1-98.8	28.7-97.7
S.D.	31.5	8.55*	20.5*	5.17*	10.66*	40.75	39.05	8.38	20.64	22.05

Table 24. The fertility and hatching success of loggerhead, leatherback and green turtle clutches in the study area.
(*) N.B. The distribution of these data is strongly skewed but the data does not fit a Poisson distribution.

Figures

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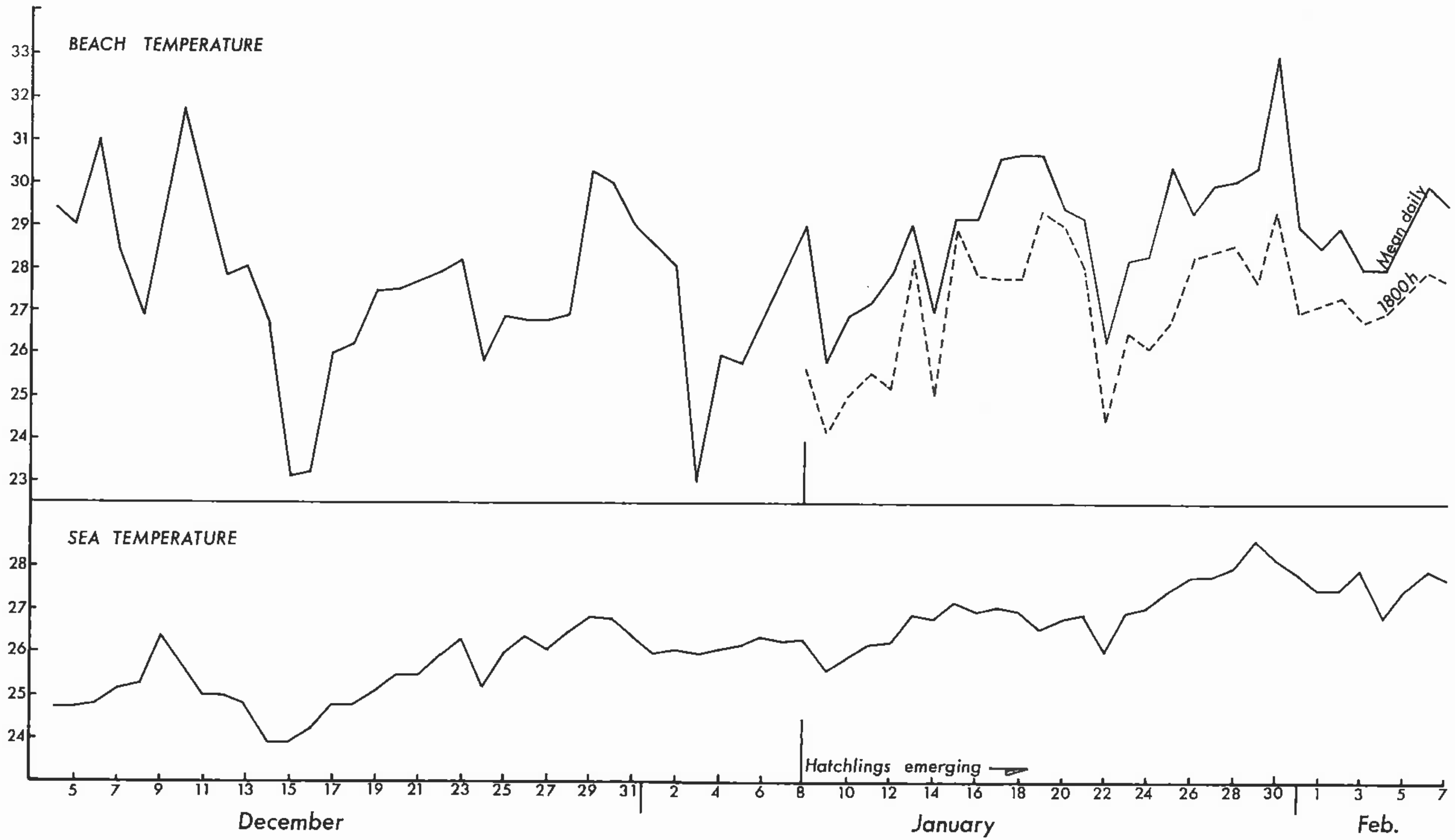

Fig. 1. Mean daily sea surface and beach surface temperatures at Bhanga Nek (Boteler Point), Tongaland during part of the 1966-67 season (December 4th - February 7th). The beach surface temperature at 1800 hrs. from the 8th January is shown as a broken line.

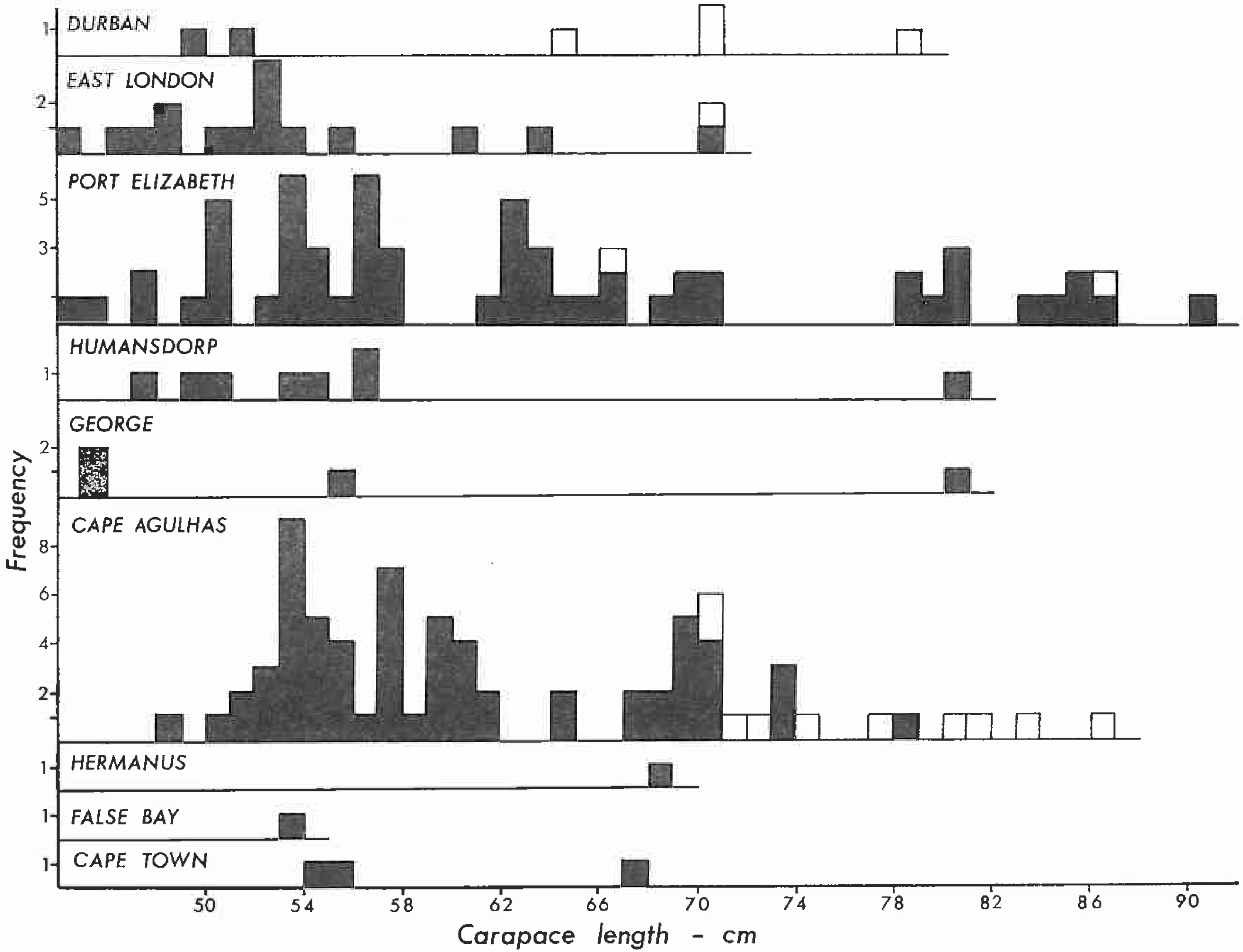

Fig. 2. Size distribution of loggerhead (solid blocks) and leatherback (open blocks) hatchlings stranded at various localities in South Africa.

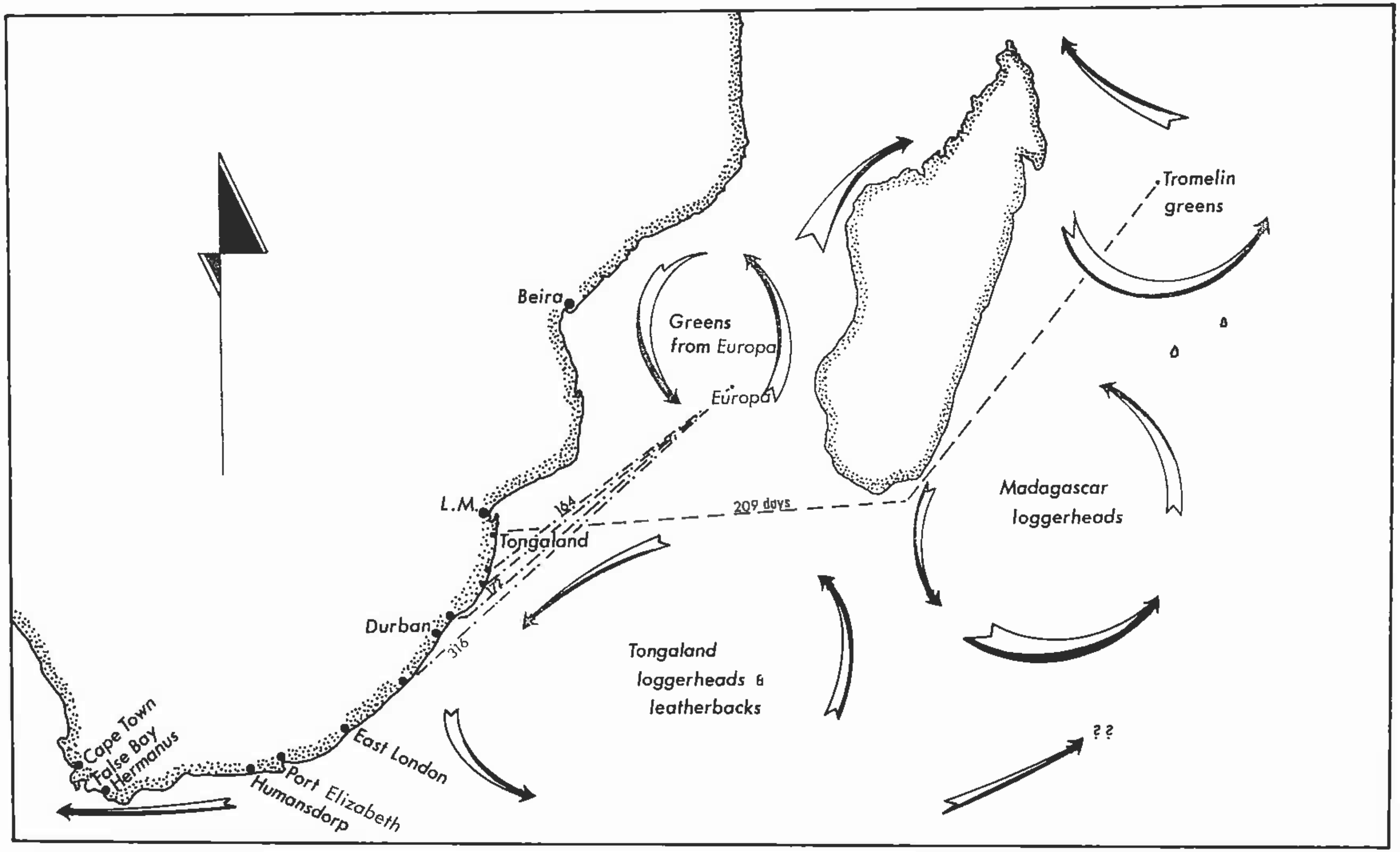

Fig. 3. The study region showing localities of hatchling strandings in South Africa; release and recovery points of drift cards released during the present study; and the hypothetical distribution of turtle hatchlings from known nesting areas.

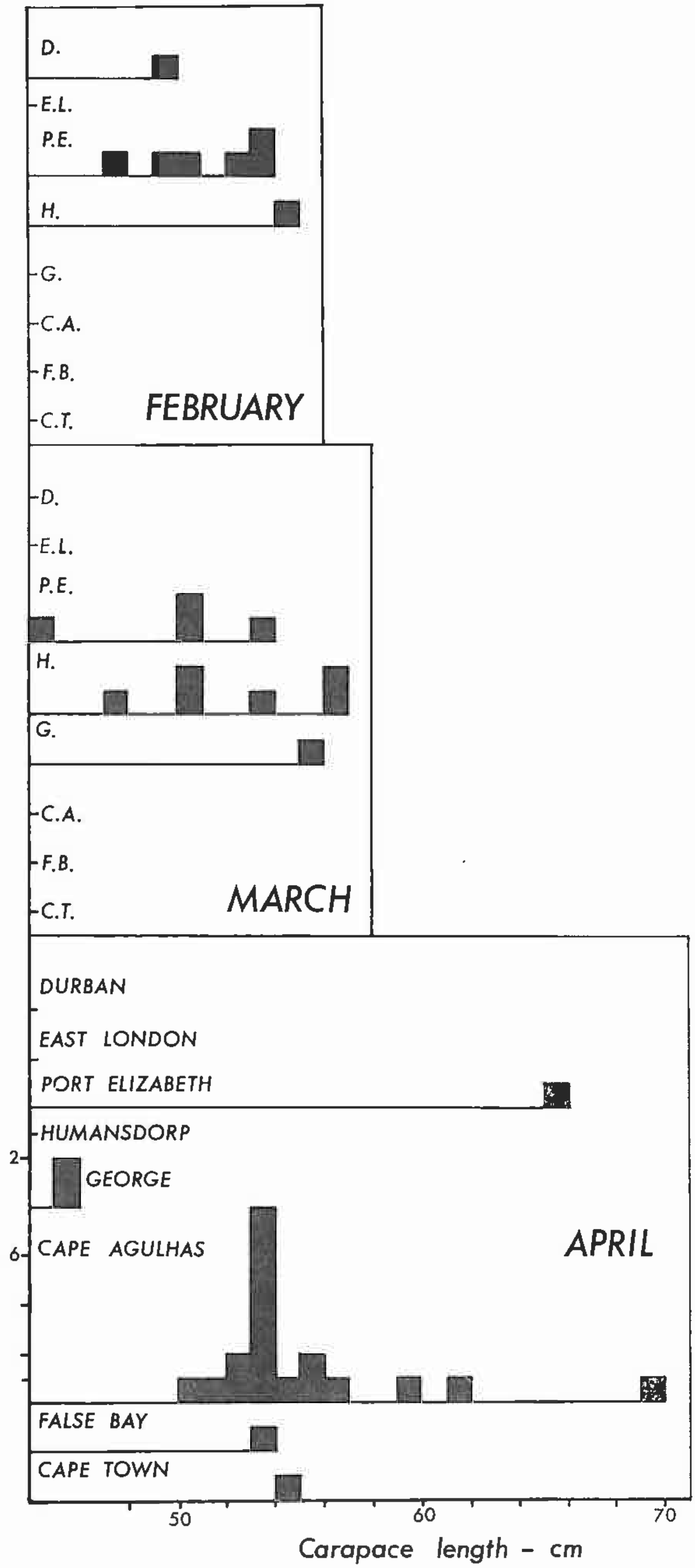

Fig. 4. The size distribution of loggerhead hatchlings stranded in South Africa during February, March and April, 1973.

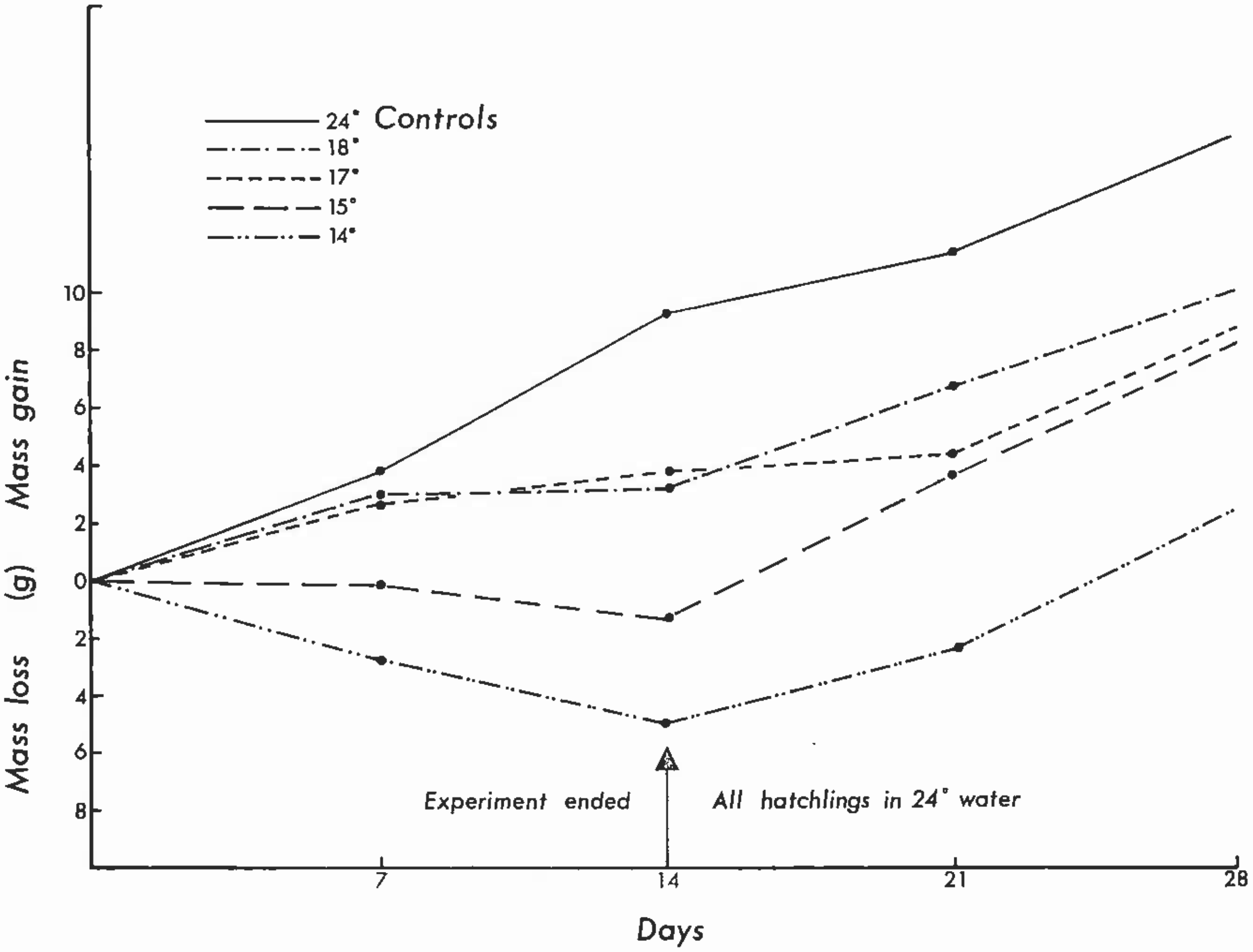

Fig. 5. The response, expressed as mass changes, of 5 groups of loggerhead hatchlings to different temperature regimes.

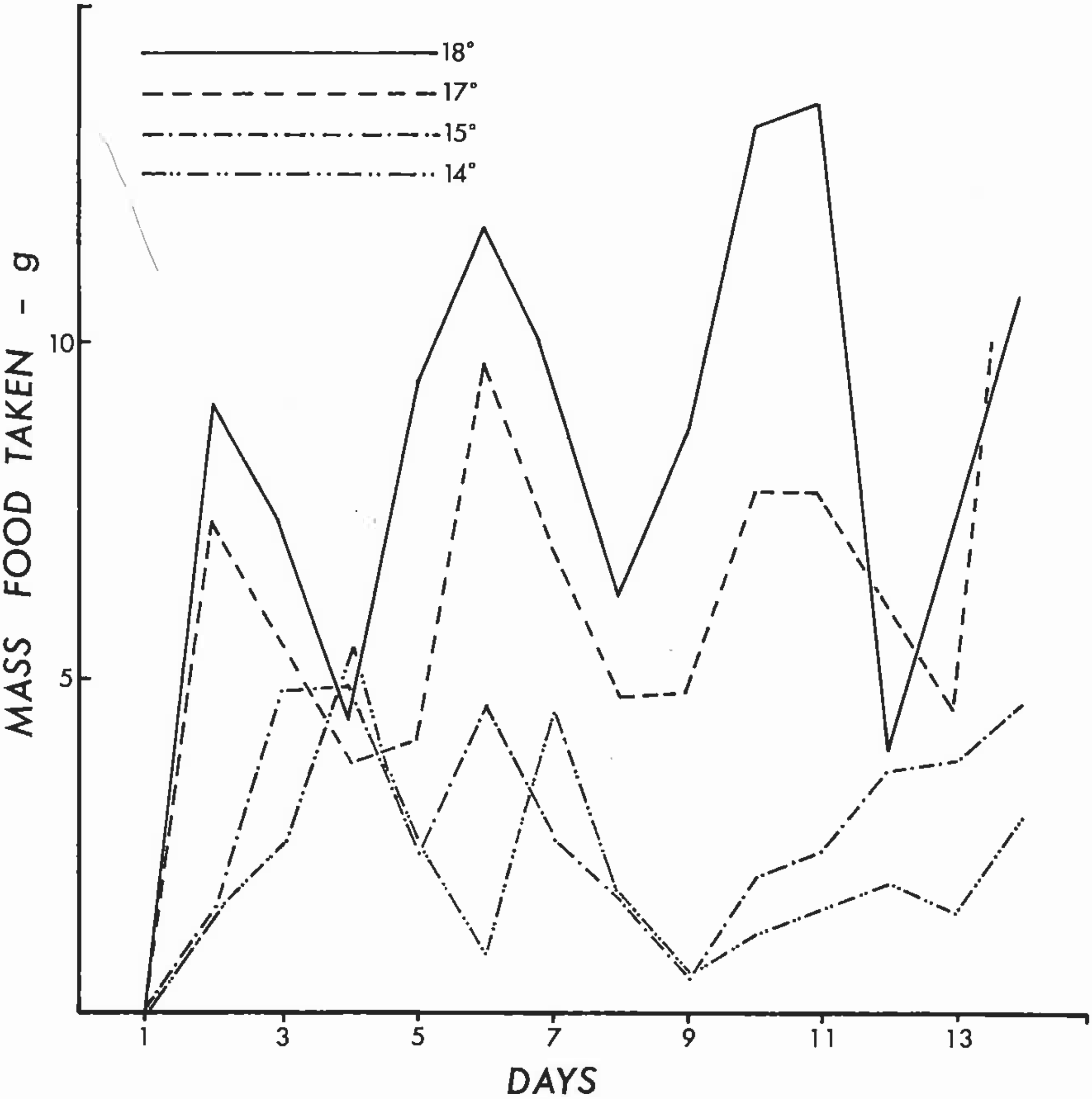

Fig. 6. Daily food intake of experimental loggerhead hatchlings in different temperature regimes.

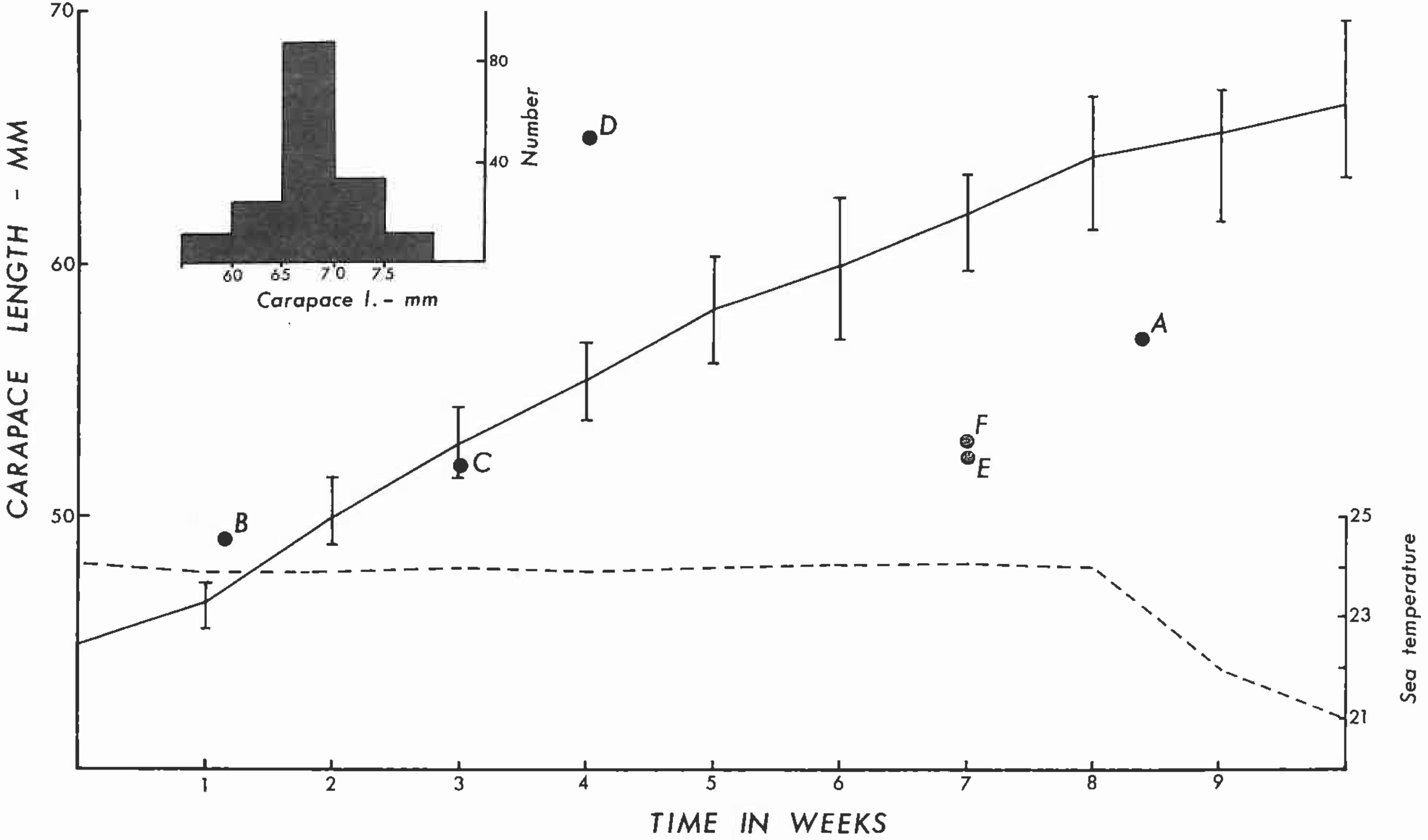

Fig. 7. The mean growth rate of a sample of 200 loggerhead hatchlings kept at the Durban Aquarium. Vertical bars indicate ranges. The mean weekly sea temperature is shown as a broken line. Inset is the range of sizes in 168 hatchlings at 12 weeks. Recovered notched hatchlings labelled A-F are shown at their minimum possible age.

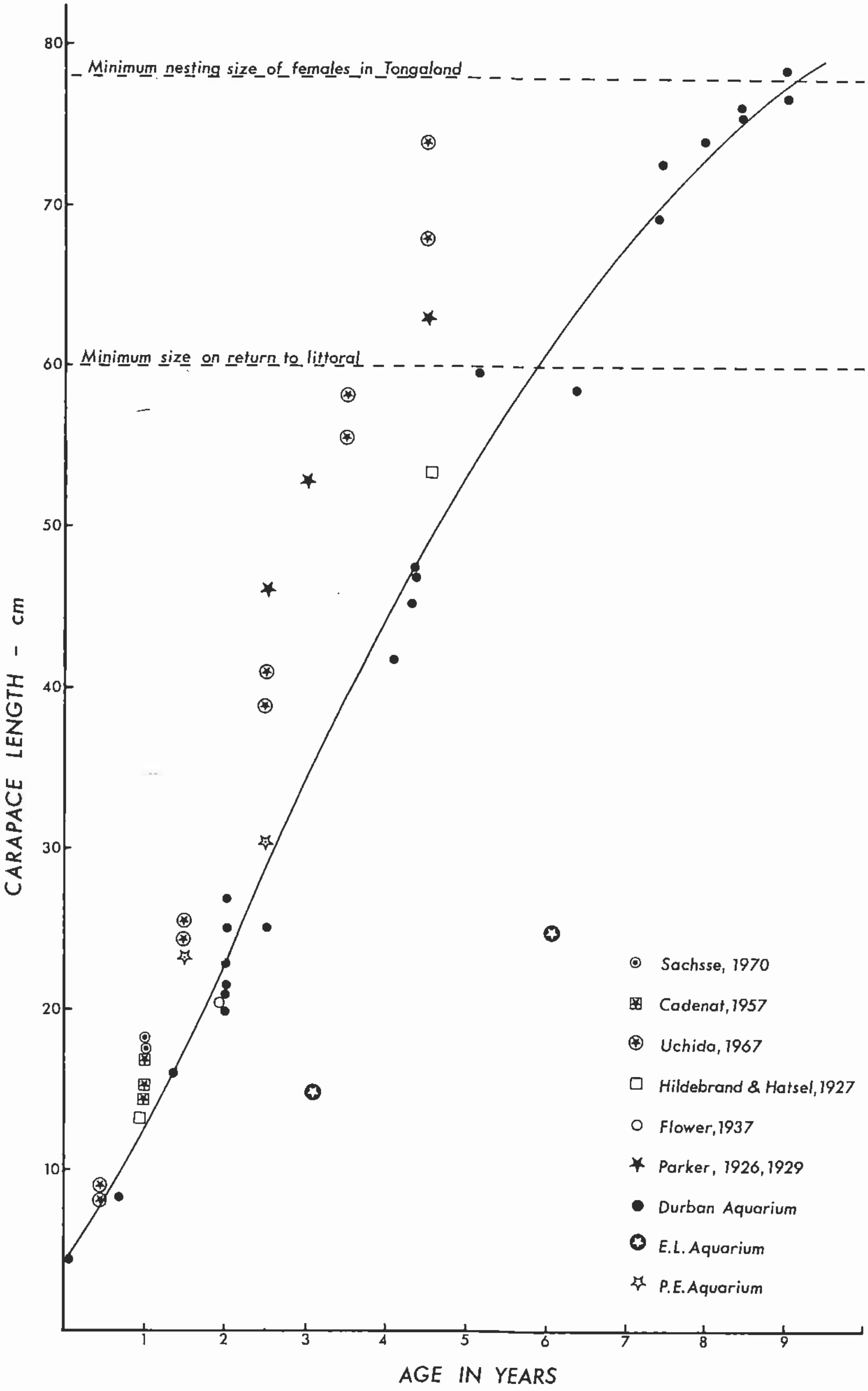

Fig. 8. An approximate growth curve for the loggerhead turtle based on data from captive turtles from the Durban Aquarium. Growth rates reported by other investigators are included for comparison.

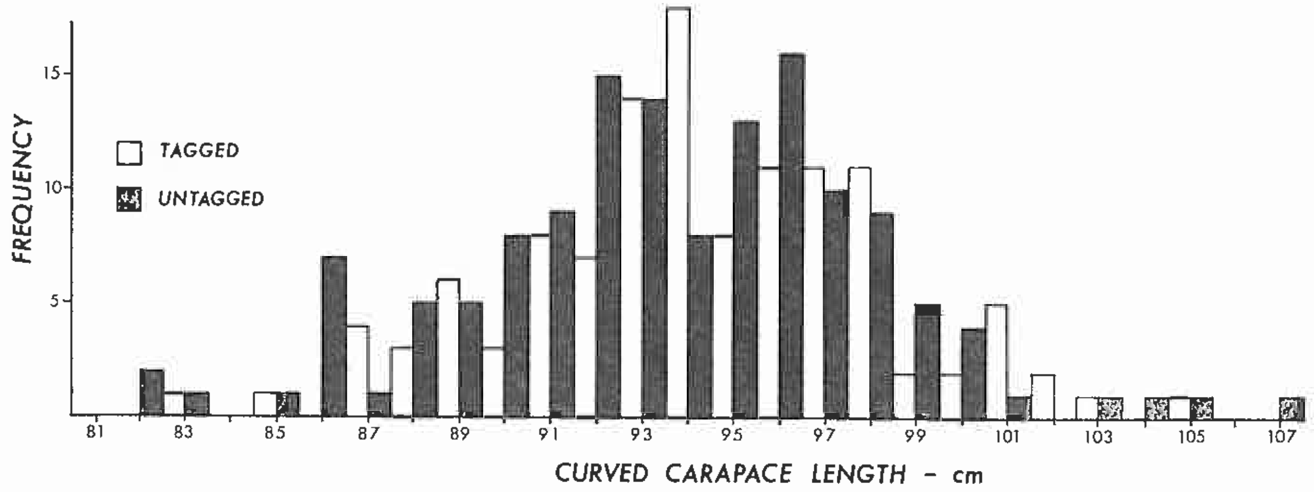

Fig. 9. The size distribution of tagged and untagged loggerhead females in Tongaland during the 1972/73 season.

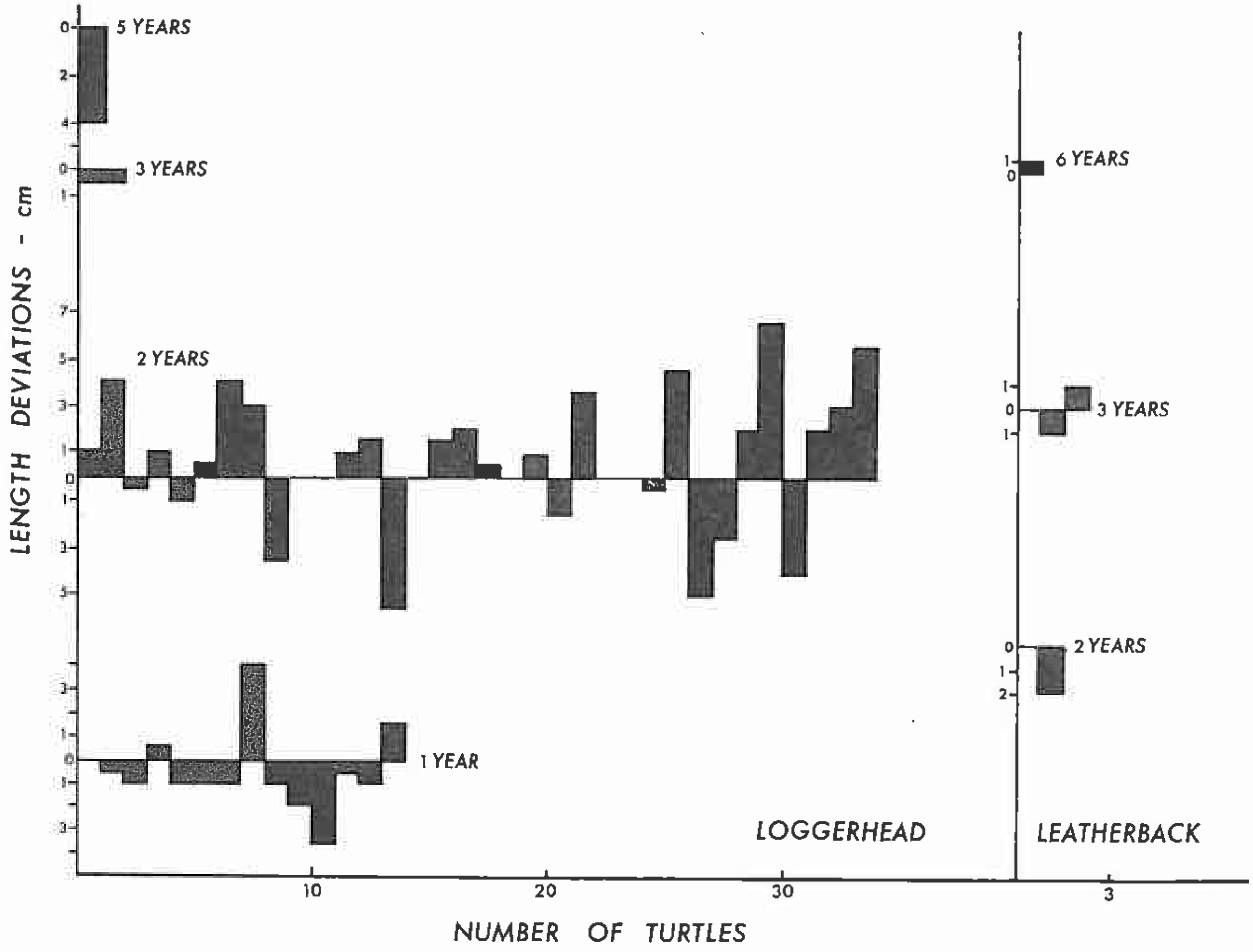

Fig. 10. Measurements differences in loggerhead and leatherback females after varying periods of absence from Tongaland.

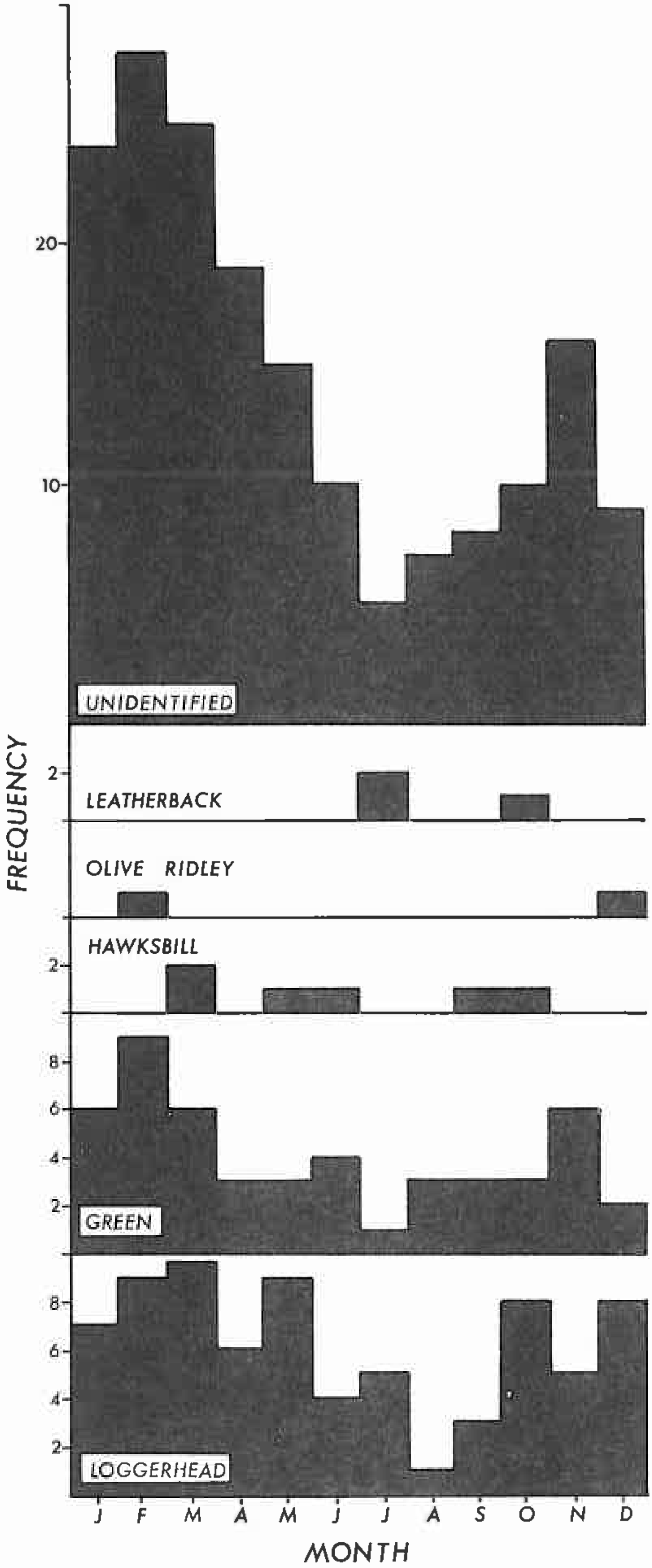

Fig. 11. The catches of loggerhead turtles, and other species, in the anti-shark network along the Natal coast: 1965-1973.

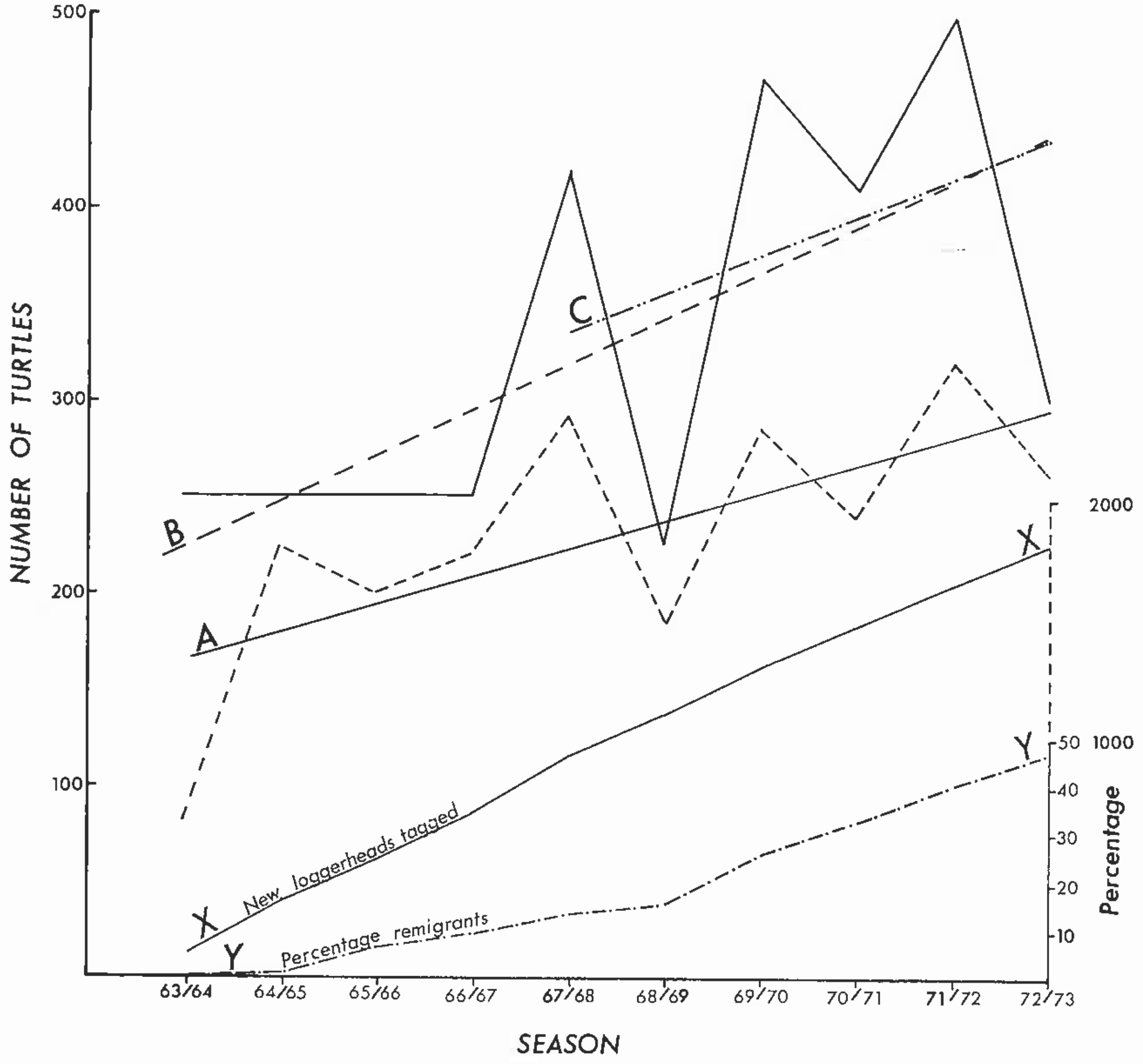

Fig. 12

(i) The estimated total annual nesting populations of female loggerhead turtles in the Tongaland protected area; 1963-1972 (solid line) with trend lines B and C (see text).

(ii) The seasonal totals of loggerhead females encountered since 1963 (broken line) with trend line A.

(iii) The cumulative number of new females tagged since 1963 (line X).

(iv) The increasing percentage of remigrant loggerhead females found each season since 1964 (line Y).

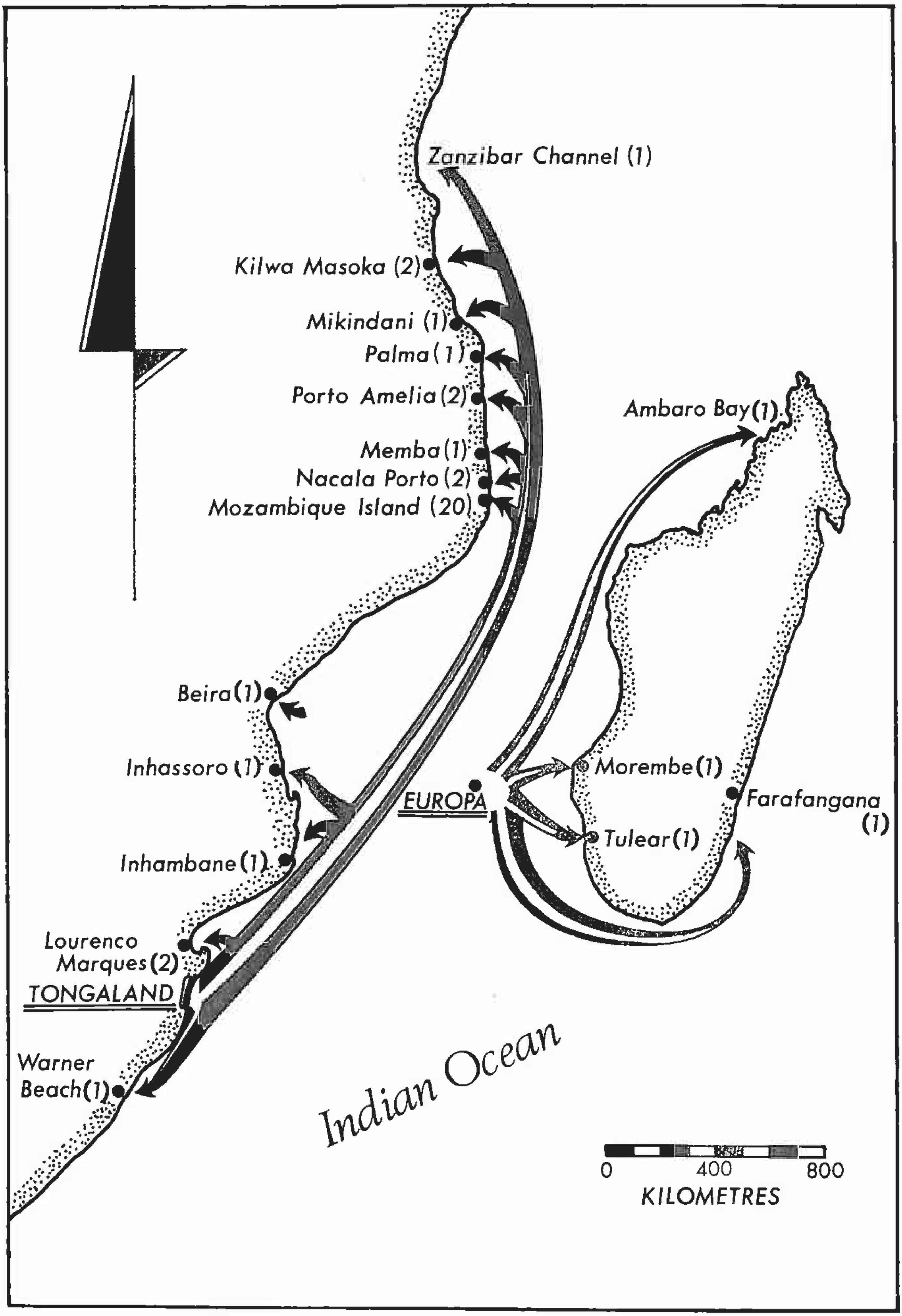

Fig. 13. Extra-nesting area recoveries of loggerhead turtles tagged in Tongaland and of green turtles tagged on Europa Island. One leatherback turtle, tagged in Tongaland, has been recovered near Beira.

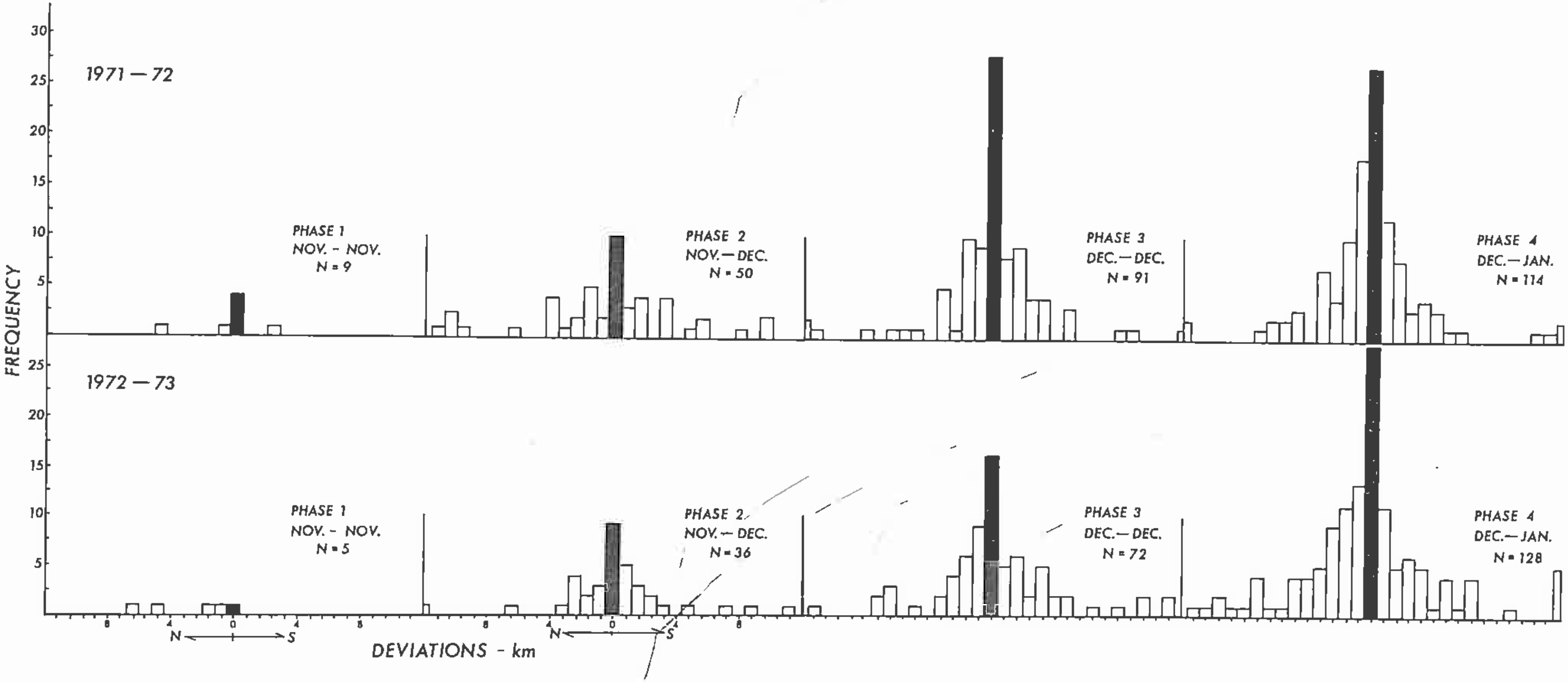

Fig. 14. The spatial intervals between emergences of loggerhead turtles during two seasons in Tongaland.

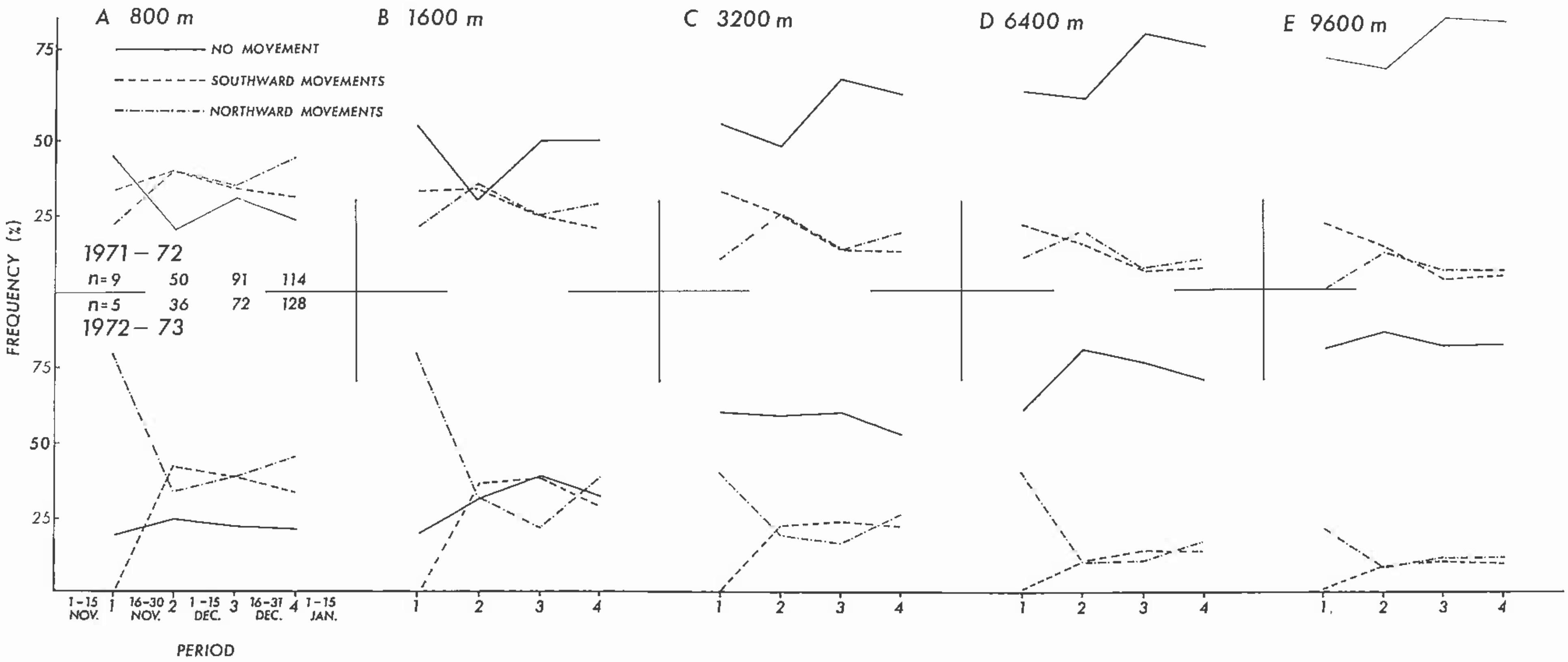

Fig. 15. The movement and site tenacity of loggerhead females during the 1971-72 seasons and 1972-73 seasons expressed as percentages at four phases of each season (see test) and at five zonal widths.

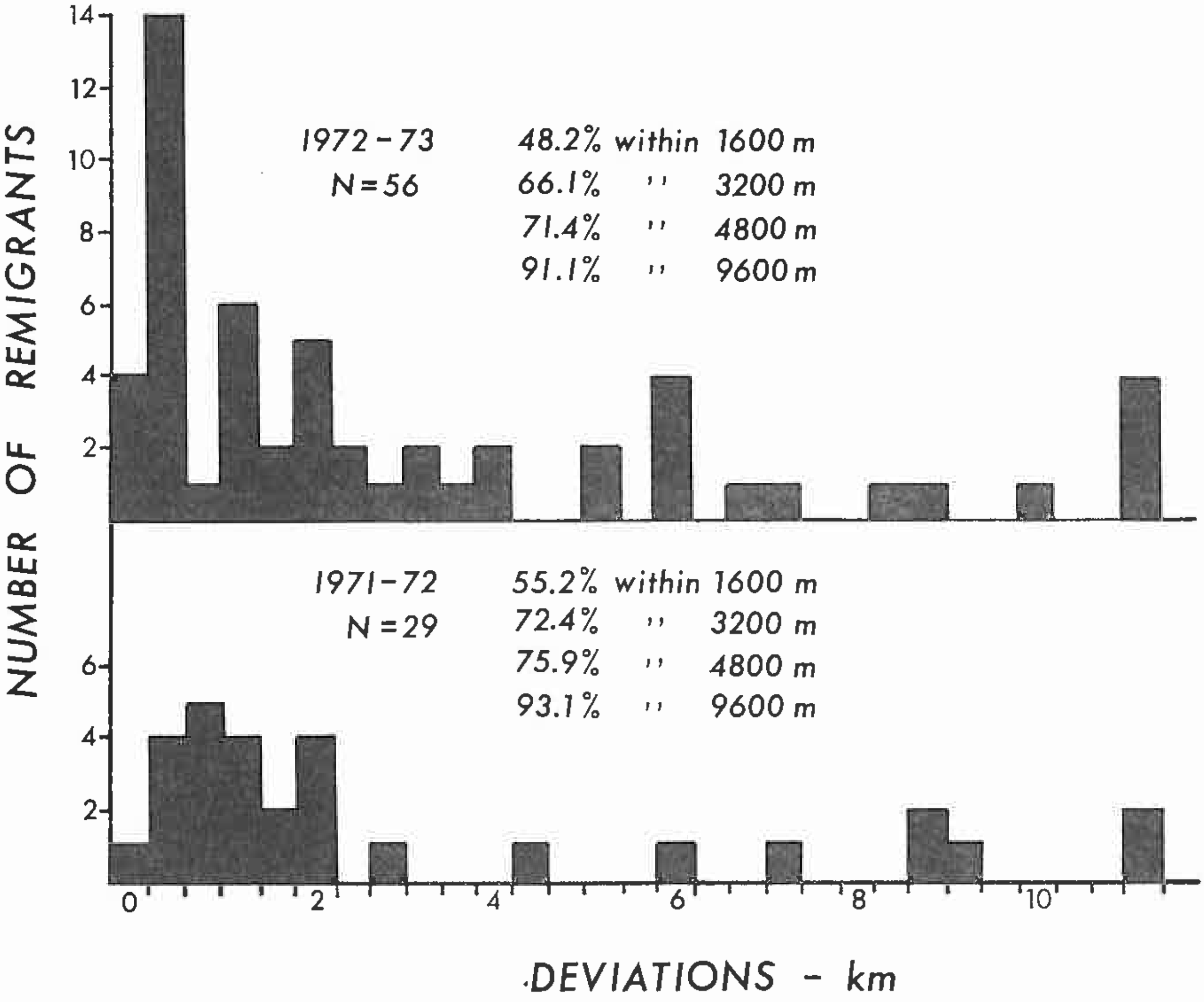

Fig. 16. Deviations in km from the site of original encounter of remigrant loggerhead females from the 1971-72 and 1972-73 seasons.

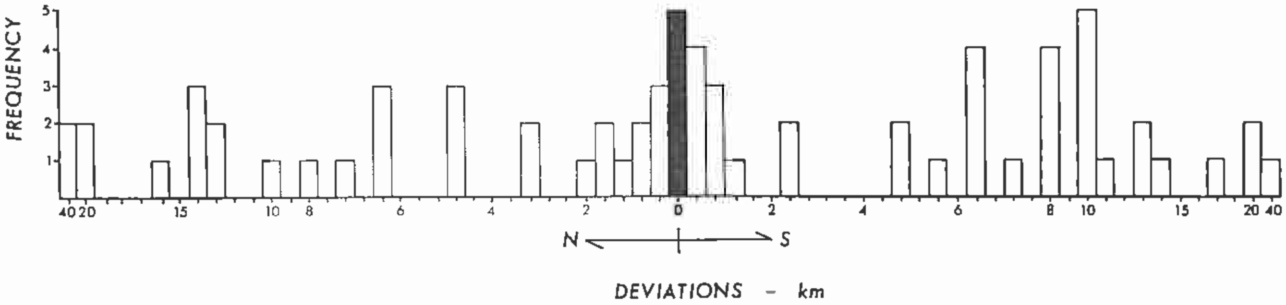

Fig. 17. Deviations in km between the emergences of leatherback turtles in Tongaland; 1963-1973.

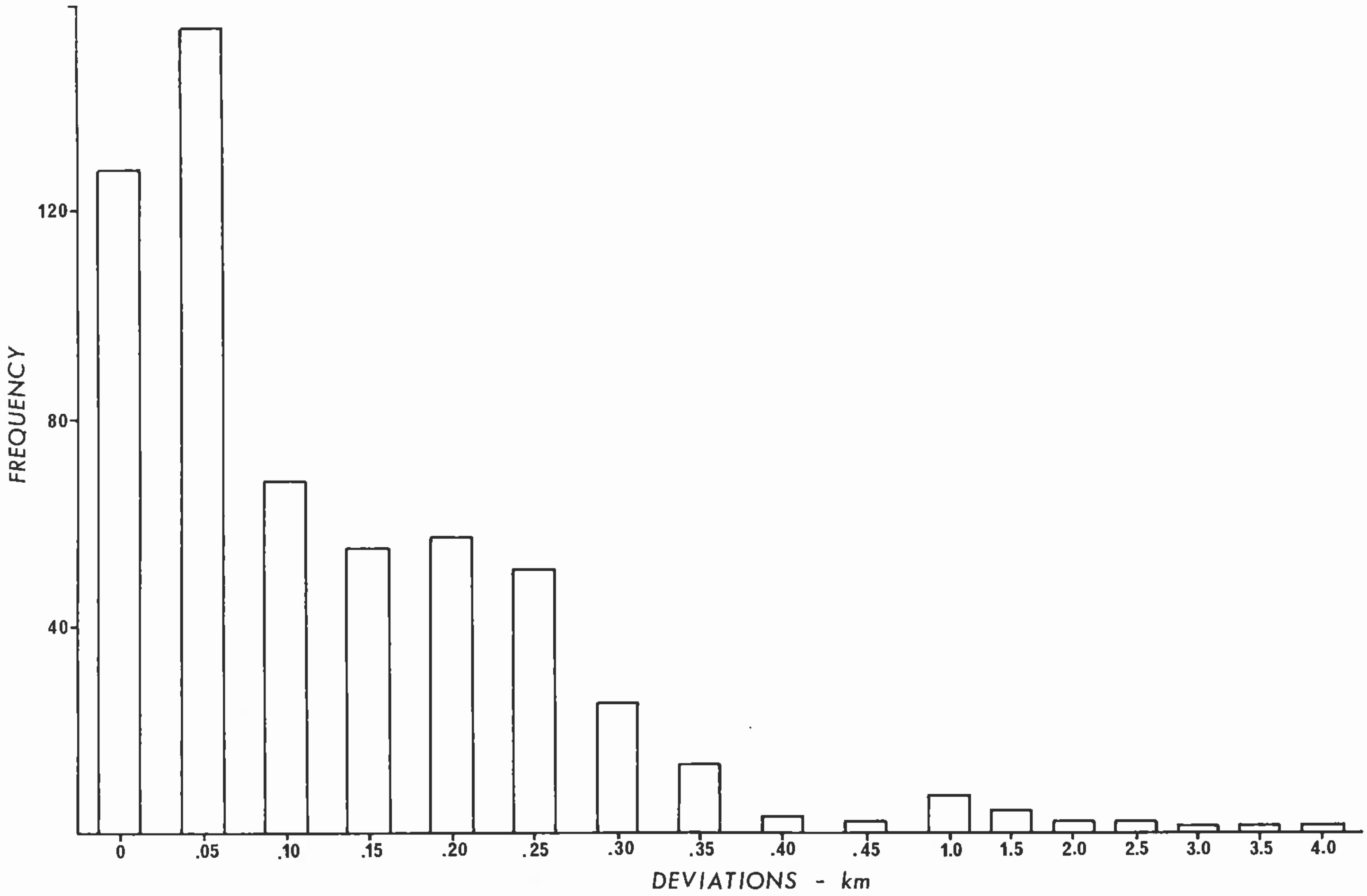

Fig. 18. Observed deviations (in km) of green turtle females from the site of their previous emergence on Europa Island, November to December, 1970.

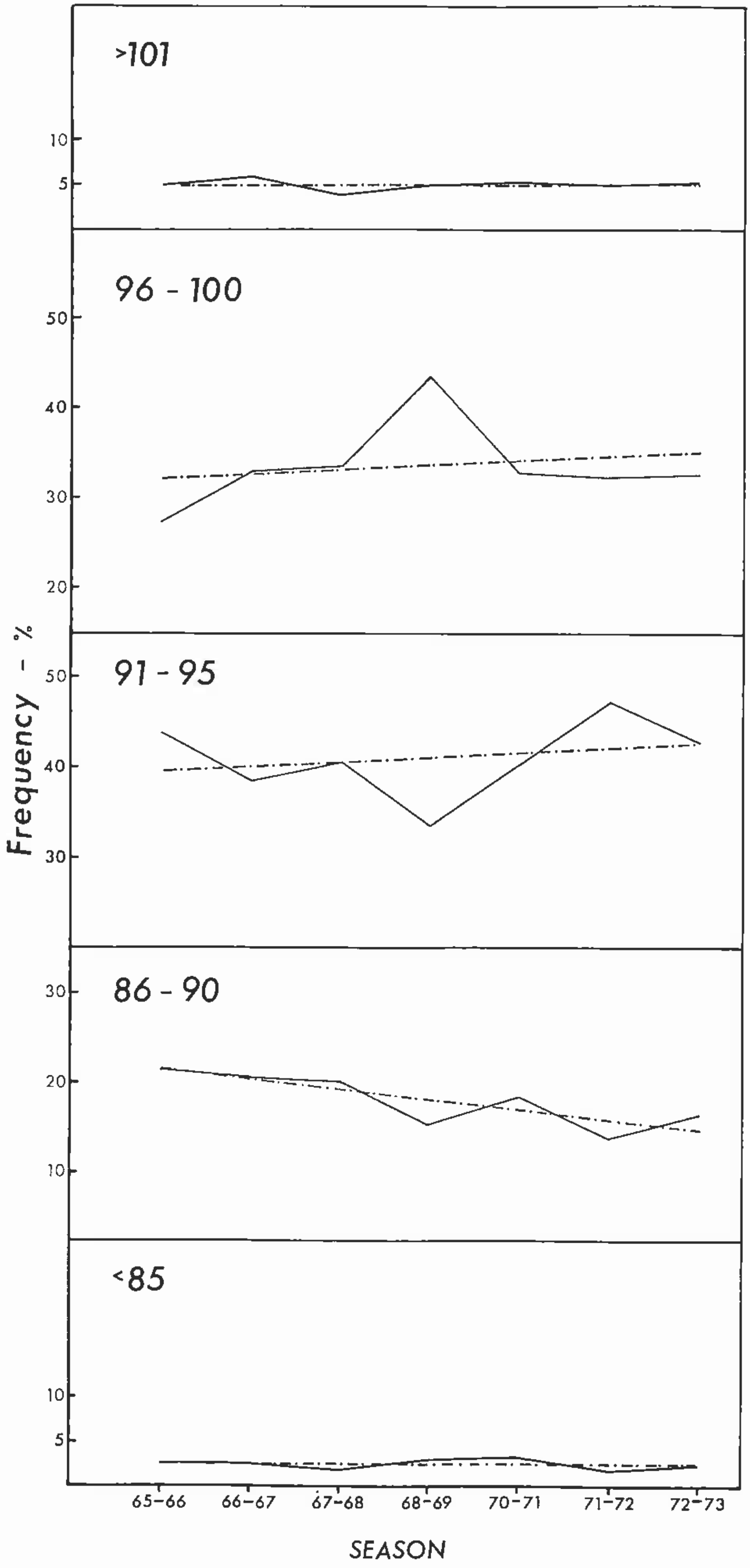

Fig. 19. Size class compositions, with trendlines, of seven seasonal nesting populations of loggerhead females in Tongaland.

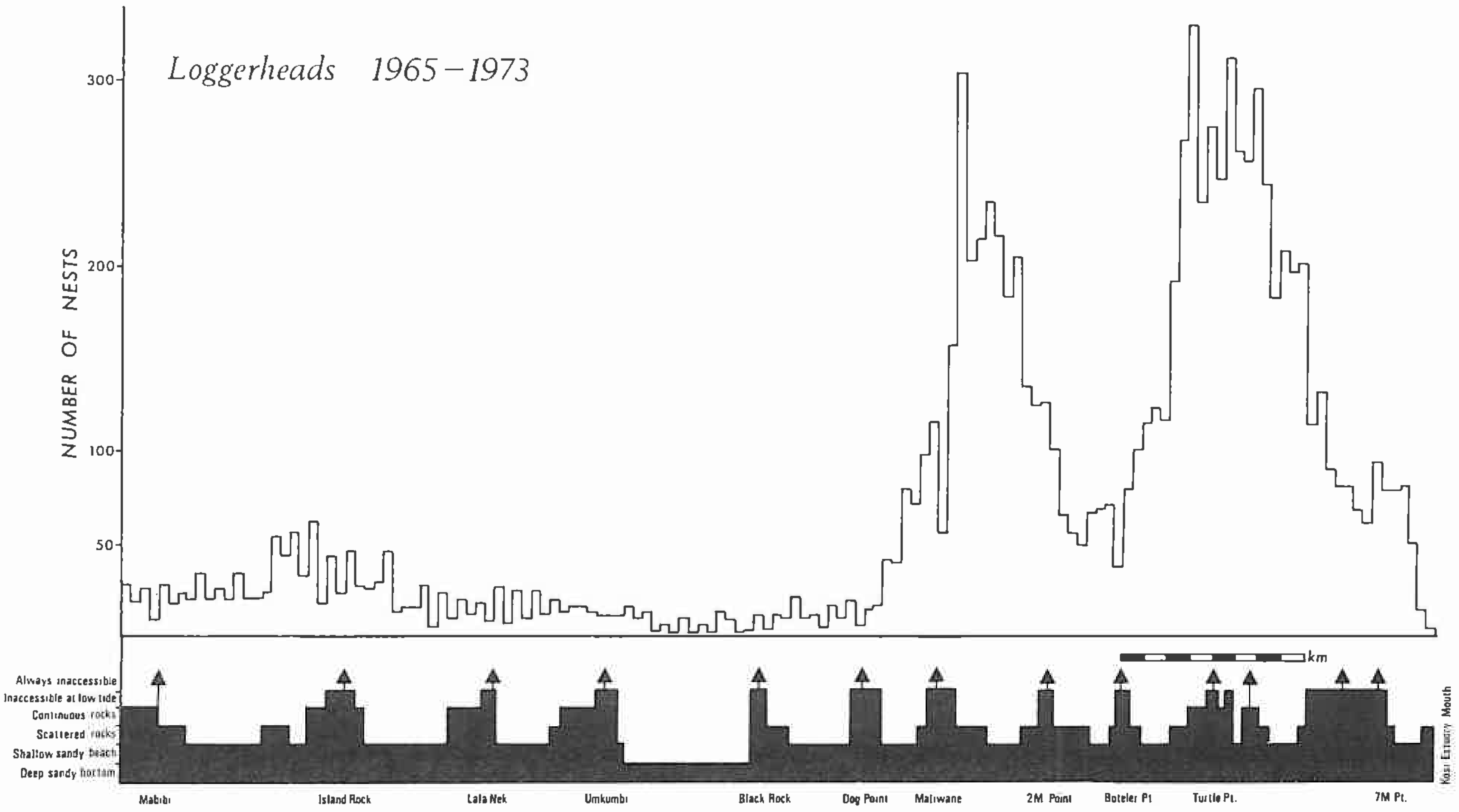

Fig. 20. Loggerhead nesting activity in 8 seasons from 1965-66 to 1972-73. Distances in 400m intervals.

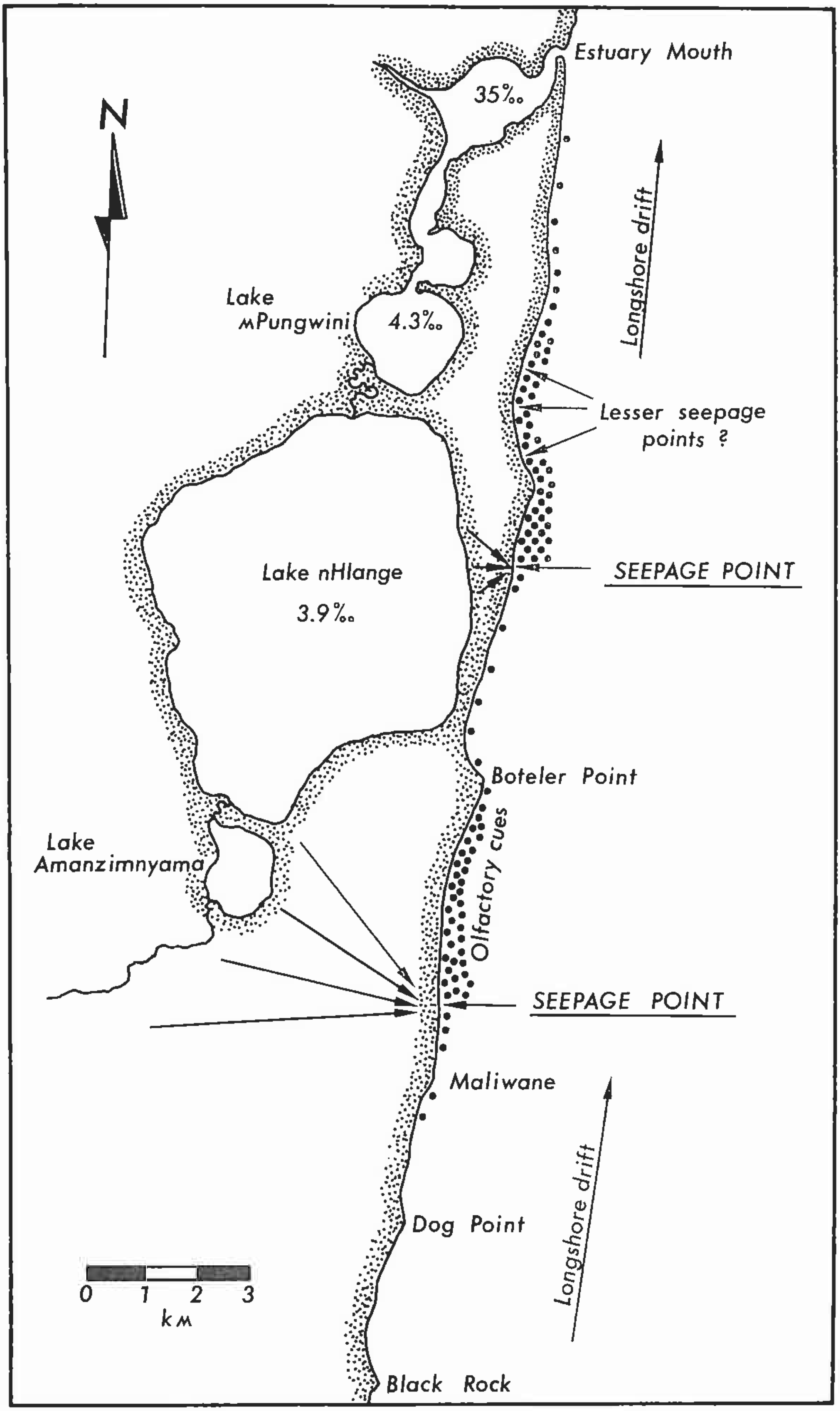

Fig. 21. The high density loggerhead nesting areas in Tongaland showing their position in relation to the Kosi Bay lake system with the hypothetical seepage points and northward distribution of the olfactory cue (see text for details).

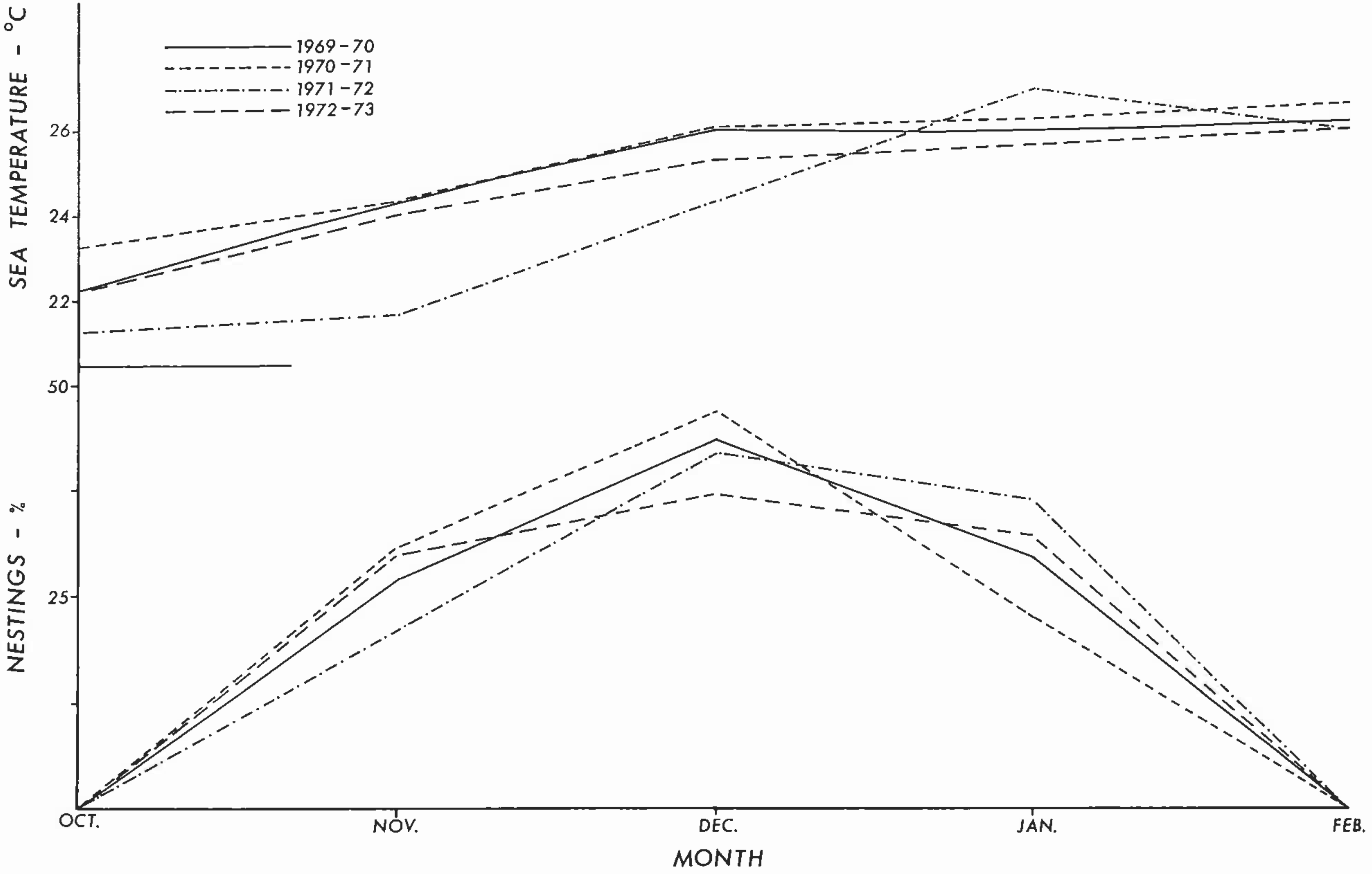

Fig. 22. Monthly loggerhead nesting records, expressed as percentages, for the seasons 1969-70, 1970-71, 1971-72 and 1972-73 compared with the corresponding mean monthly sea surface temperature records.

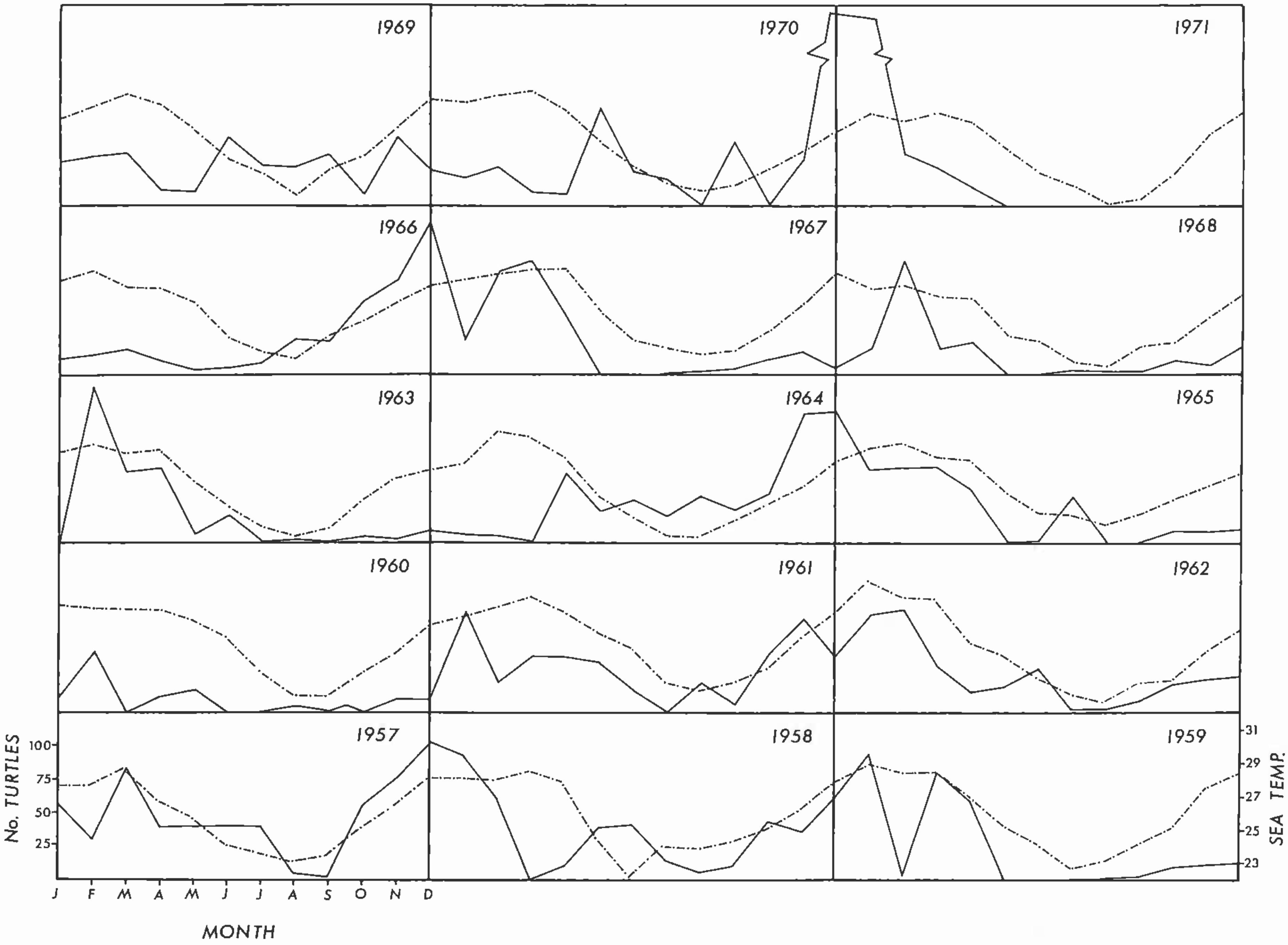

Fig. 23. The monthly distribution of sea surface temperatures over 15 years (broken line) with the monthly

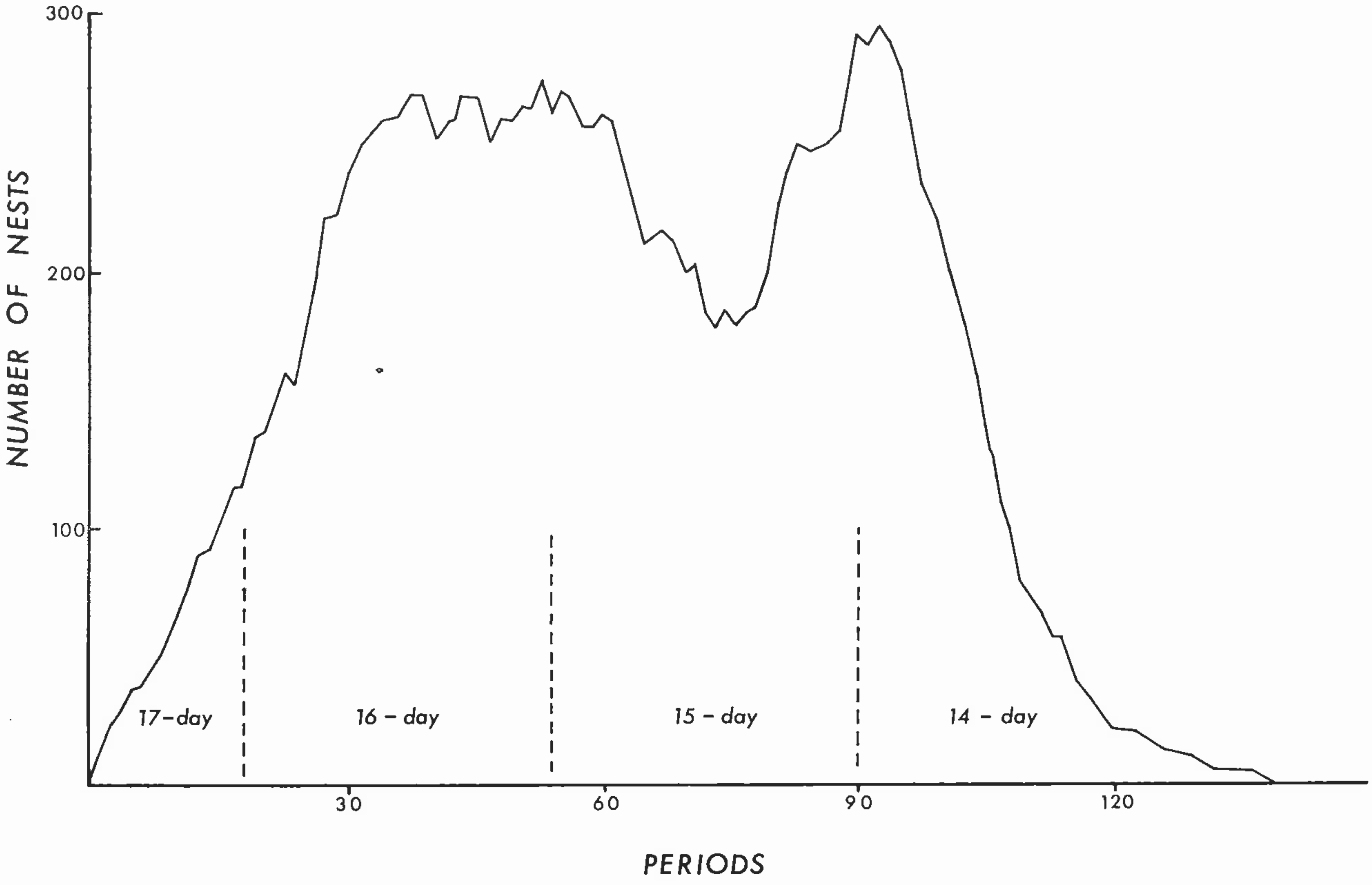

Fig. 24. The cumulative nesting records of loggerhead females for the 1972-73 season. See text for details.

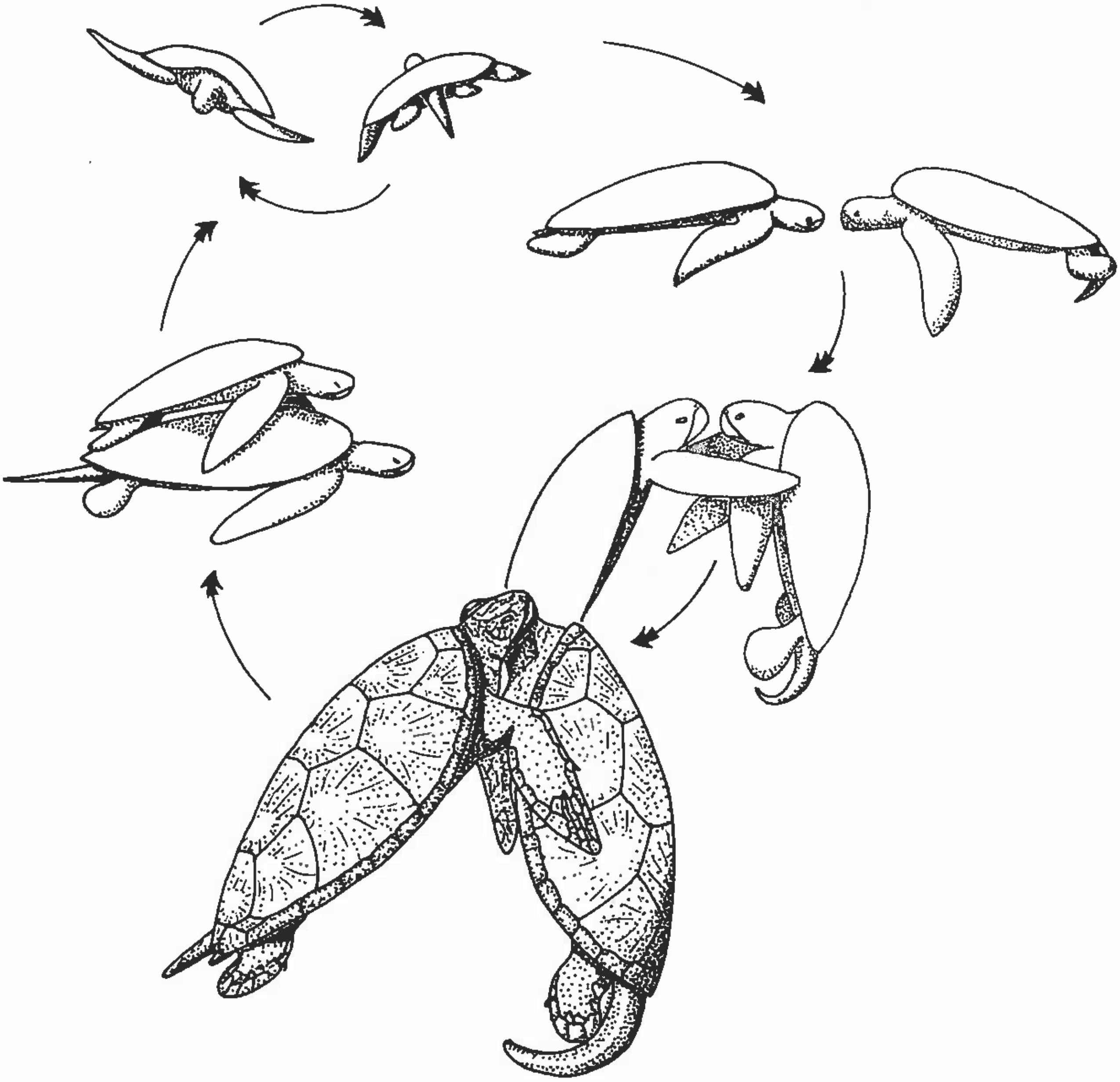

Fig. 25. Five stages in the possible courtship behaviour of green turtles at Europa Island.

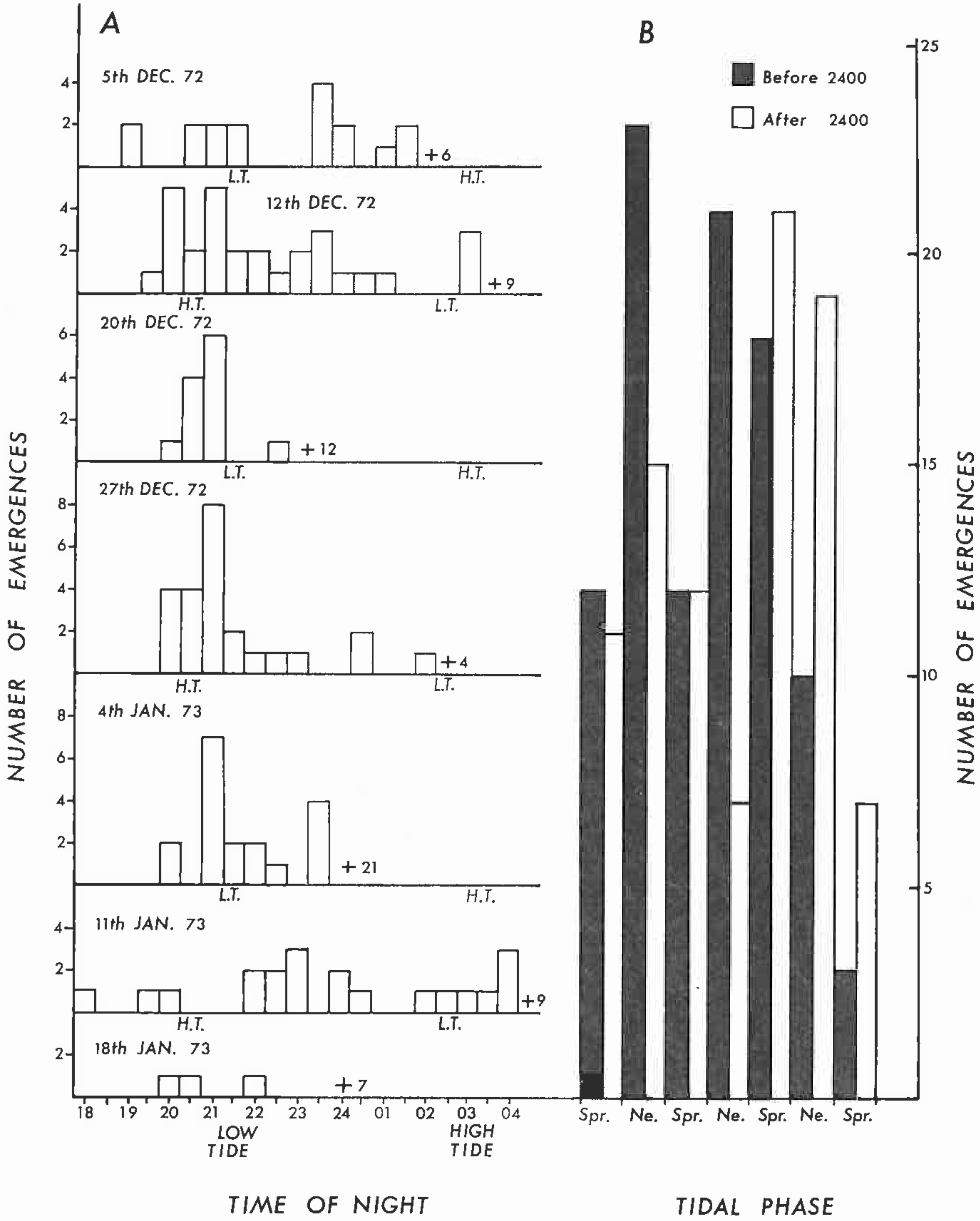

Fig. 26. The distribution of loggerhead nesting activity on the peak spring and full neap tide periods during December, 1972 and January, 1973. A, the exact time of emergence; B, expressed as before and after midnight.

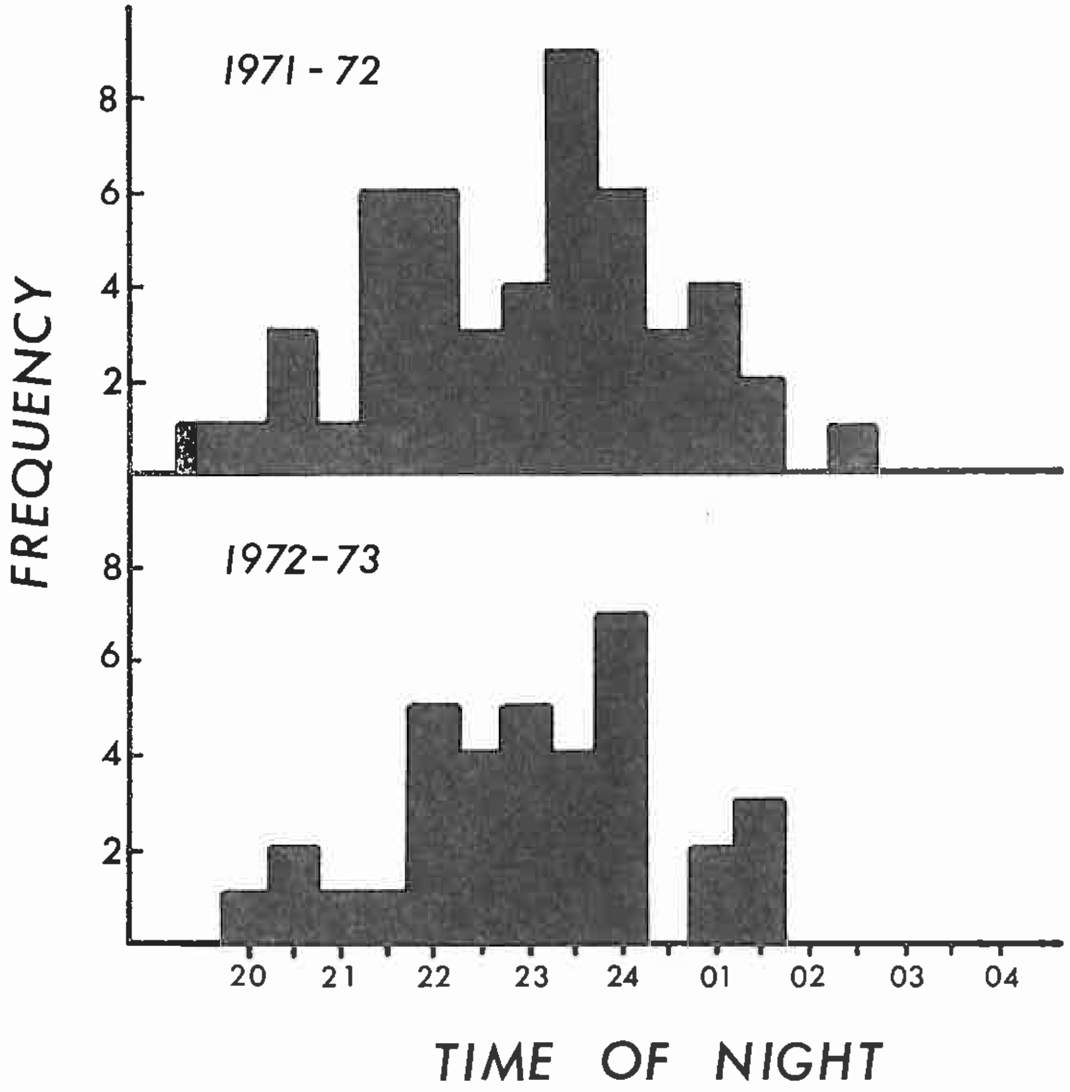

Fig. 27. The frequency of leatherback nesting emergences in Tongaland during the 1971-72 and 1972-73 seasons.

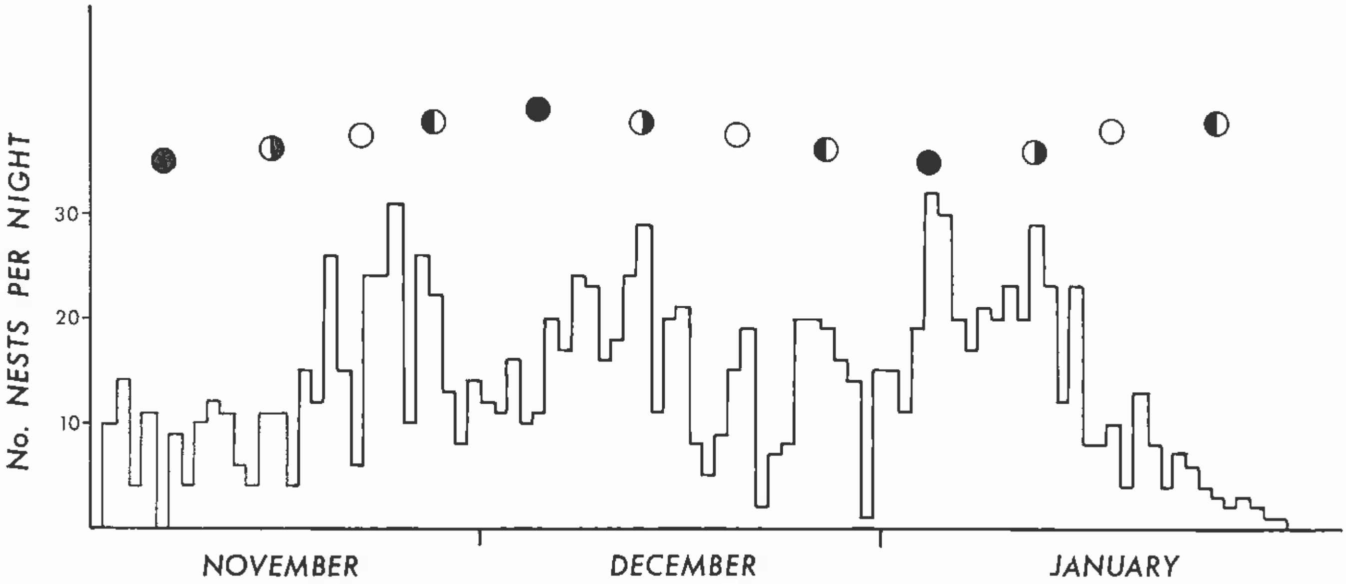

Fig. 28. The nightly nesting activity of loggerheads during the 1972-73 season, with the moon phases in November, December and January.

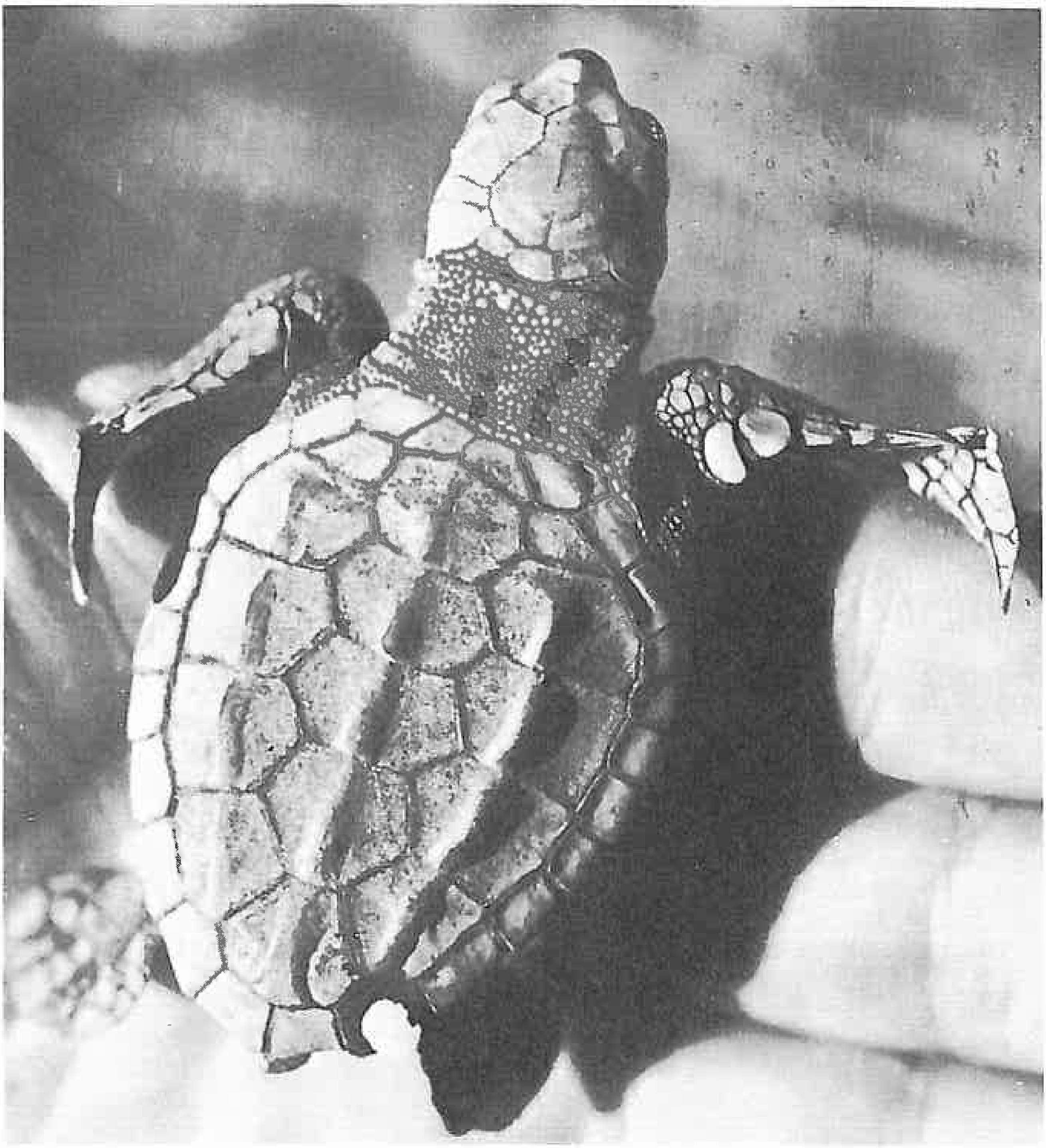

Plate 1. A typical loggerhead hatchling from Tongaland showing the notching site during the 1972-3 season.

Plate 2. Hermit crabs *Caenobites* sp. on the beach at Europa Island, November, 1970.

Plate 3. The goose-necked barnacle *Conchoderma virgatum* on the hind flipper of a leatherback hatchling stranded at Cape Agulhas.

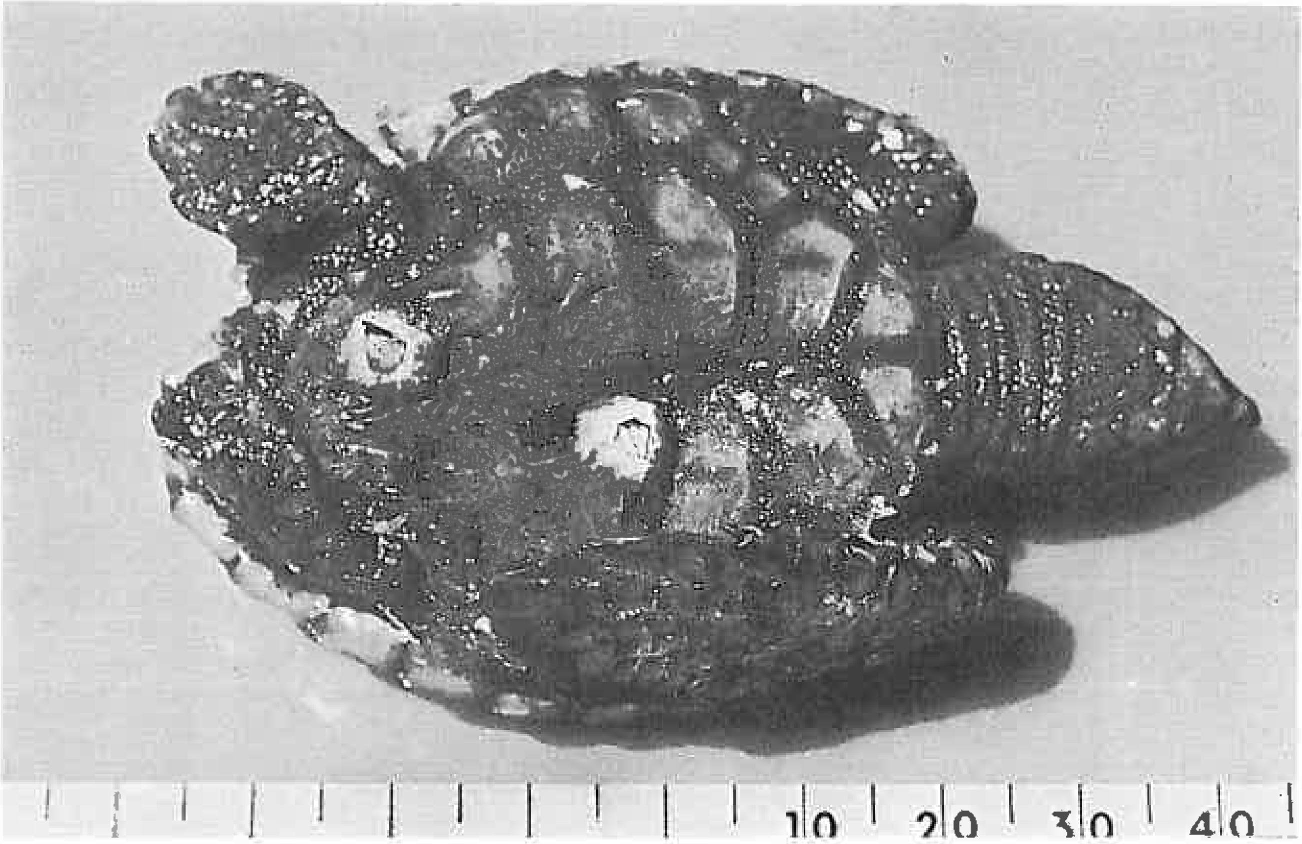

Plate 4. Acorn barnacles *Balanus* sp. on the plastron of a loggerhead hatchling stranded at Cape Agulhas.

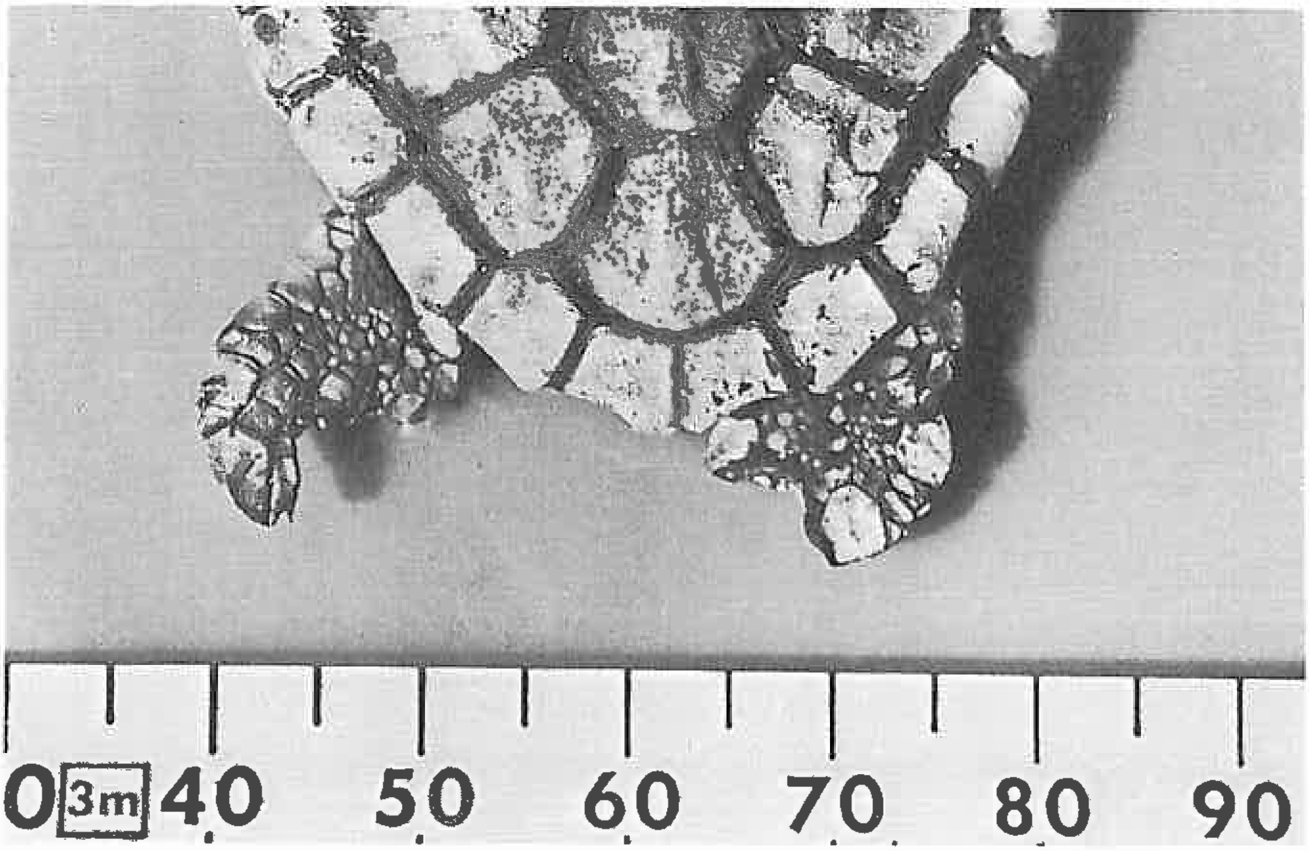

Plate 5. Crescent shaped injuries to the hindflippers of a loggerhead hatchling stranded at Cape Agulhas.

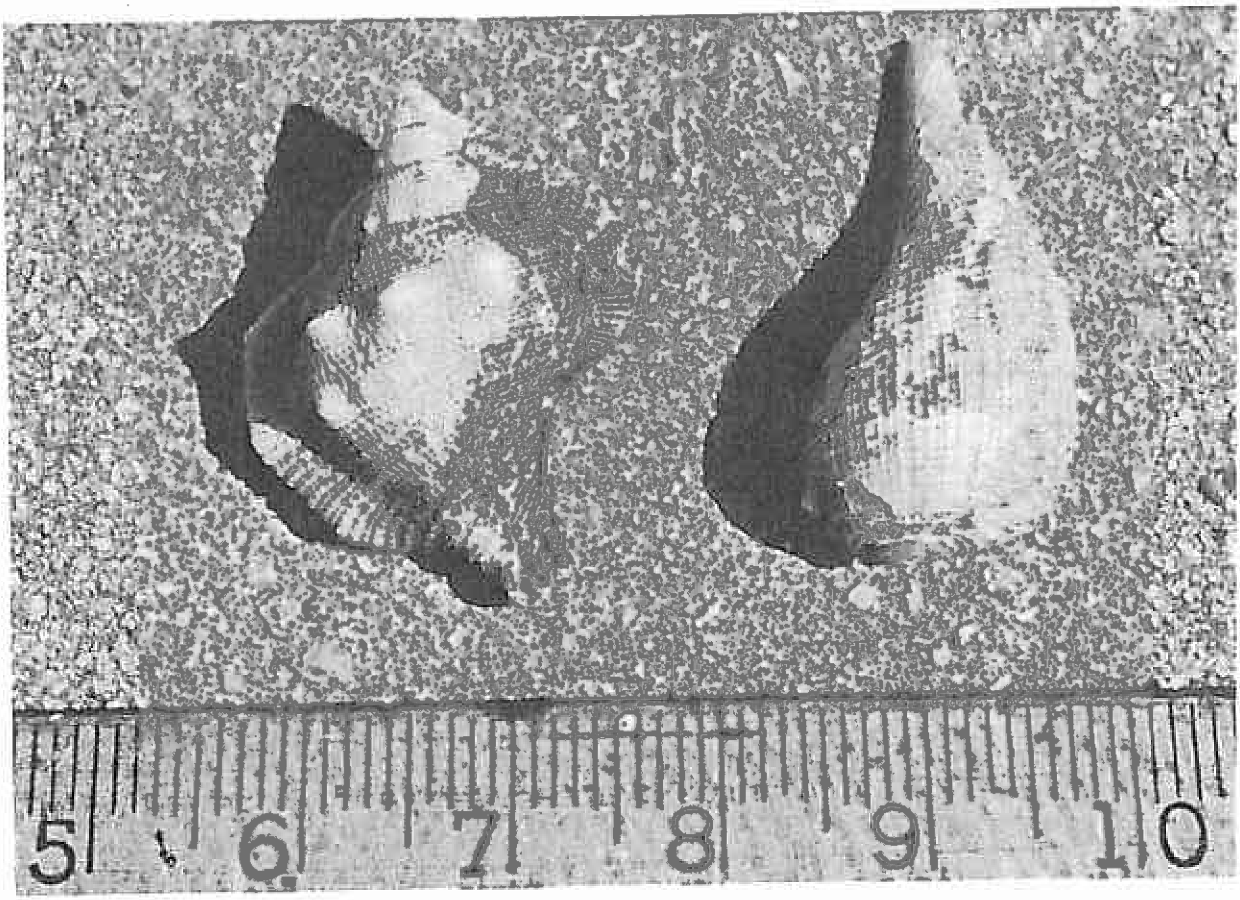

Plate 6. The most common species of Mollusca from the stomachs of loggerhead turtles along the Natal
Left, *Bufonaria crumenoides;* right, *Ficus subintermedius.*

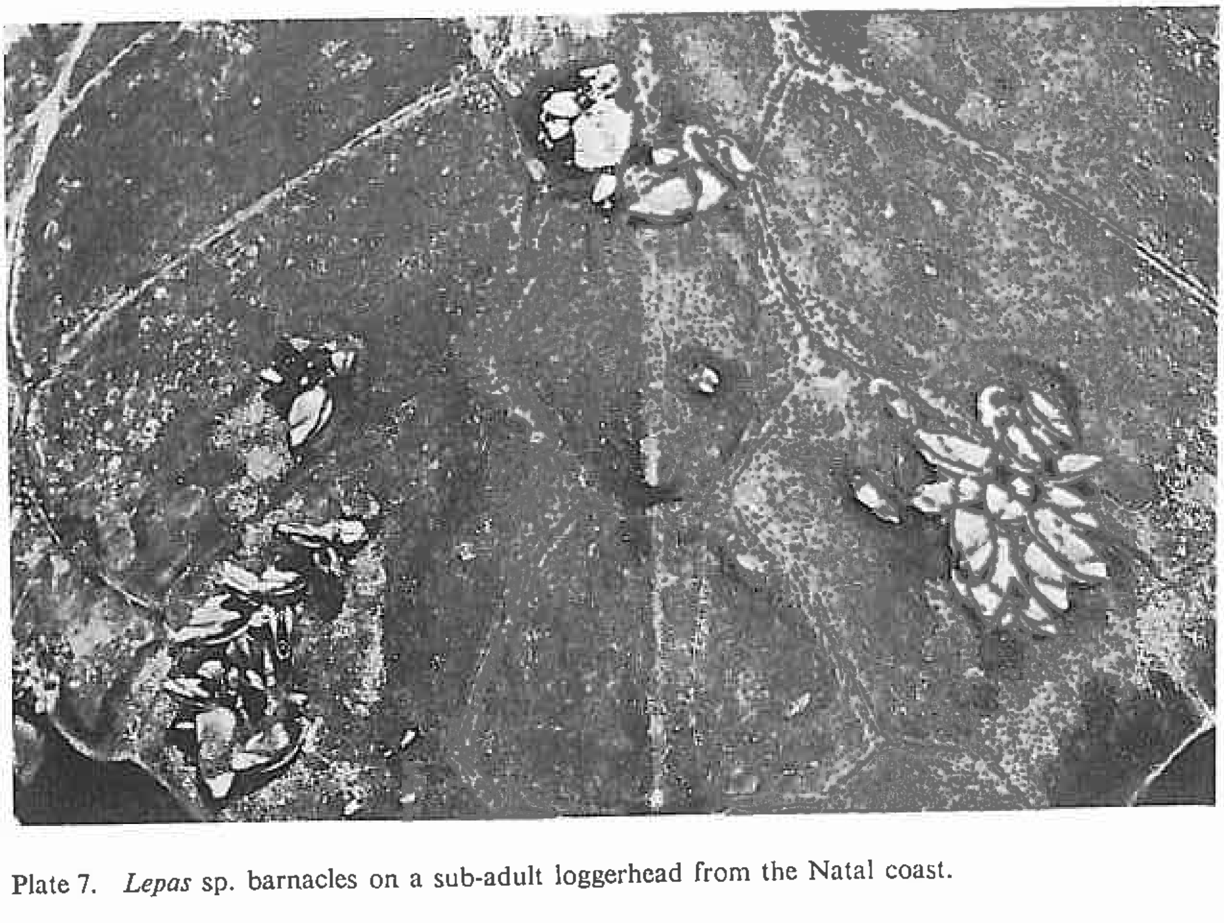

Plate 7. *Lepas* sp. barnacles on a sub-adult loggerhead from the Natal coast.