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Long-distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study

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Abstract Four green turtle females were tracked by satellite during their post-reproductive migration in the South China Sea. Three of them reached their feeding grounds 923-1551 km distant. During nesting activity, a female was displaced twice, and her return trips to the nesting beach from 11 and 284 km were tracked by a direction-recording data-logger and by satellite, respectively. Part of the journeys occurred coastwise, indicating that leading geographical features had been utilised. The straightness of the turtles' tracks in open seas, both over shallow and deep waters, and their ability to pinpoint distant targets and home after displacement off their usual routes, provides circumstantial evidence for a true navigation mechanism.

Key words Green sea turtle · Migration · Homing · Satellite tracking

Abbreviation *PTT* platform transmitter terminal

Introduction

Like many bird species, migrating sea turtles are able to reach very distant, specific targets which may even be small isolated oceanic islands (Carr 1972, 1984). In spite of its interest, the unsettled question about the guidance mechanism(s) through the apparently cueless uniformity of the ocean has hardly been investigated. A possible first step in tackling the problem is reconstruction of the routes followed by the turtles in open seas, which is facilitated by the satellite tracking technique (see Renaud et al. 1993; Balazs et al. 1994 for references). Successive steps might consist in displacement experiments and manipulation of sensory information, two approaches which remain in their preliminary stages (Baldwin 1972; Carr 1972). An important contribution may also be derived from orientation experiments on hatchlings, which are available in large numbers and can be easily subjected to laboratory tests (e.g. Lohmann and Lohmann 1993).

The green turtle is the best known species as far as migratory travels and ability to pinpoint small isolated targets are concerned (Carr 1972, 1984; Balazs 1994; Balazs et al. 1994). A recent satellite tracking of a female migrating in the South China Sea has permitted some inferences on turtle mechanisms of navigation (Papi et al. 1995), and paved the way for further experiments on the same nesting community. Our study is a part of a research program on the biology and migration of West Malaysian green turtles. The present paper reports results of interest for an understanding of the navigational mechanisms of sea turtles. Liew et al. (1995) have reported elsewhere the original data from the Argos satellite-based system on the locations obtained from the four turtles considered in the present paper.

Materials and methods

The females we tracked were caught in the summer of the 1994 while nesting on the Chagar Hutang beach (5°49′N, 103°00′E) of Pulau Redang, an island located 45 km off the coast of Terengganu, Peninsular Malaysia. The egg laying of the turtles on this beach has been regularly monitored since 1993; the internesting activity has been object of a recent study (Liew and Chan 1993).

The transmitters linked to the Argos system (Taillade 1993) were Telonics ST-3. The method used to attach them to turtles is described in detail by Liew et al. (1995). An improved model of the

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route recording device developed by Bramanti et al. (1988, see also Dall'Antonia et al. 1993) and previously used on birds (Ioalè et al. 1994; Dall'Antonia et al. 1995), was implemented in one of the two homing experiments by inserting it in a waterproof case attached to the turtle carapace. The device records the angle between the turtle body axis and magnetic North every 4 s. Following recovery of the device, the stored data permits route reconstruction.

The turtles were chosen among those which, on the basis of their previous nesting activity in the season, were expected to be about to leave for the feeding grounds. Turtles B, C, and D were equipped with the PTT immediately after nesting and let free to start migration. Conversely, turtle A was caught when it landed to nest, was prevented from nesting, and soon after was equipped with the route recorder and displaced by boat to be released in the open sea 11.1 km N. After her return to the beach, she was allowed to nest and was used later in a second displacement experiment. The turtle was first transported to the mainland by boat and then southwards by van. She was finally equipped with a PTT and released at a site on the Malay east Coast (3°17'N, 103°25'E) 284 km South of Redang after a trip lasting 15 h.

The locations (or fixes) calculated by the satellites were assigned by Argos to six classes on the basis of their estimated accuracy. In Figs. 1–3, the locations of the four best classes are indicated by filled or open dots, those of the two worst classes by asterisks or X. In reconstructing the tracks those fixes which were clearly erroneous (indicated in the figures by a Y, upright or overturned) were disregarded, and the broken line joining the valid fixes was smoothed to compensate for the approximation of the fixes. The plotted tracks have been used to roughly calculate the length A of the turtle's course; another method employed was that of calculating the length B by adding the segments of the broken line. Usually, the former method produces underestimated values (especially when the fixes are widely spaced), while the latter gives an overestimated length (especially in the opposite case). The values obtained with the two methods are given as distance A and B, respectively. The trip was assumed to start from the first fix followed by a consistent movement towards the feeding grounds. As arrival point we considered the first fix inside the area where the turtle then remained wandering around. The distance (bee-line) between starting and arrival points is derived from the loxodromic route, the orthodromic route being – for the distances and latitudes considered – virtually coincident. The ratio between distance and length of the route provided the straightness index (Batschelet 1981), which varies between 0 and 1.

For the turtles which navigated in the open sea we have compared diurnal vs nocturnal performance in terms of speed and directedness. To achieve this, we have considered the segments between successive fixes travelled completely or mostly (> 90%) during the night or day. Data from segments covered in less than 120 min were excluded because of their lower reliability. Velocity comparison was carried out using the Mann-Whitney U-test (Siegel 1956).

As regards the homing course tracked with the route recorder, the data stored in the memory were processed by software running on PC, assuming a constant speed of the turtle. This method, along with any effect of current drift, produced an error in the calculation of the end-point of the homing trip, which turned out to be 1.9 km E of the nesting beach. The track given in Fig. 3 has been corrected for this error.

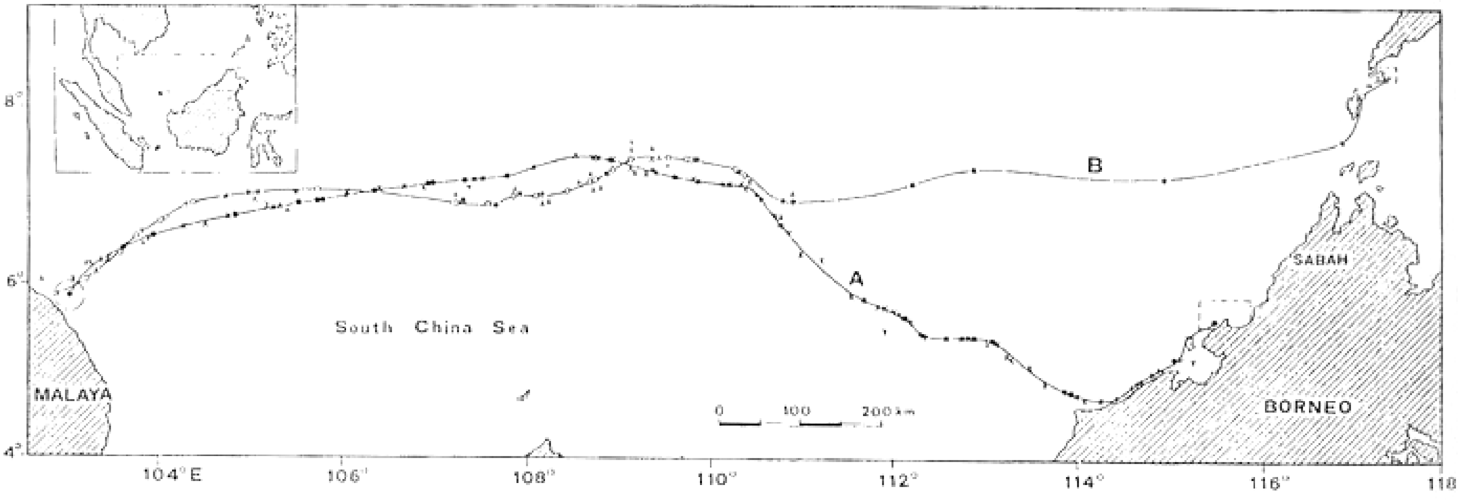
Results

Migratory trips to the feeding grounds

The tracking of the turtles migrating to the feeding grounds was successful, as the four PTTs applied allowed the reconstruction of three complete migratory trips and a large part of a fourth one (Figs. 1 and 2). The main features of the four trips can be summarised as follows.

Turtle A. After having come back to the Redang area from the second displacement (see later), this turtle nested on Chagar Hutang beach on Sept. 8 and was recorded in migration on Sept. 9. The trip (Fig. 1) consisted of three legs: the first in open seas steering eastward, the second with a south-east bearing until the Brunei coast in Borneo was reached, and the third coastwise, north-east up to the feeding grounds in Sabah. The distance (bee-line) between starting and arrival points is 1376 km, and the length of the track 1615(A)–1606(B) km. The value of the straightness index is 0.85(A)–0.86(B). The trip lasted 29 d 20 h, with a mean speed of 2.25 (A)–2.24(B) km/h. Emissions from the resident grounds were recorded for 60 more days, after which we asked Argos to stop supplying data.

Fig. 1 Tracks of turtles *A* and *B*. Departures occurred from Redang Island, located at the centre of the large open circle on the far left. Symbols on or close to the tracks indicate satellite locations: *filled dots*, *X* and *Y* refer to turtle *A*; *open dots*, *asterisks* and *overturned Y* to turtle *B*. The *rectangular areas* with *dashed borders* at the right ends of the tracks show the areas where the turtles were located after migration was completed. Other explanations in the text



Turtle B. This turtle performed the longest migratory journey, her feeding grounds being located around the small Bugsuk island, close to the southern end of the Palawan Island in the Philippines (Fig. 1). Navigation occurred in open seas, following a straight course with only minor oscillations. The distance between starting and arrival points is 1616 km, and the length of the track 1737(A)–1719(B) km. The value of the straightness index is 0.93(A)–0.94(B). The trip, which began on 21 Sept., lasted 28 d 07 h, with a mean speed of 2.56(A)–2.53(B) km/h. Emissions from the feeding ground area stopped 39 days after arrival.

Turtle C. This turtle left Redang in a southward direction, moving along the coast of the Malay Peninsula, crossed the Singapore Strait and then coasted along Bintang Island and the Linga Archipelago (Fig. 2). After that, the turtle swam for about 150 km in open seas to attain Bangka Island, where her feeding grounds were located. The distance between starting and arrival points is 923 km, and the length of the track is 1080(A)–1153(B) km. The straightness index is 0.85(A)–0.80(B). The trip, which began on Sept. 11, lasted 27 d 22 h, with an average speed of 1.61(A)–1.72(B) km/h. Emissions from the feeding grounds were recorded for 61 more days, after which we asked Argos to stop supplying further data.

Turtle D. After the turtle left Redang, it kept a gently winding SE course, so gradually moving away from the coast (Fig. 2). The track passed west of the Anambas Archipelago; thereafter the emissions were no longer received for about two and half days. The two last fixes indicated that the turtle was heading for the Tambelan Islands. The distance between the starting point and the last fix is 623 km, and the length of the track 627(A)–714(B) km. The value of the straightness index is 0.99(A)–0.87(B). The recorded trip began on 28 Sept. and lasted 16 d 09 h, with a mean speed of 1.55(A)–1.77(B) km/h.

As regards the during day- or night-time performance of the three turtles which travelled in open seas, it turns out that the night speed was slightly lower in all the turtles, but the significance was only reached in turtle D ($P < 0.05$). No consistent differences were found between nocturnal and diurnal courses. Turtles B and D navigated in open seas during the new moon with apparently unaltered nocturnal performance.

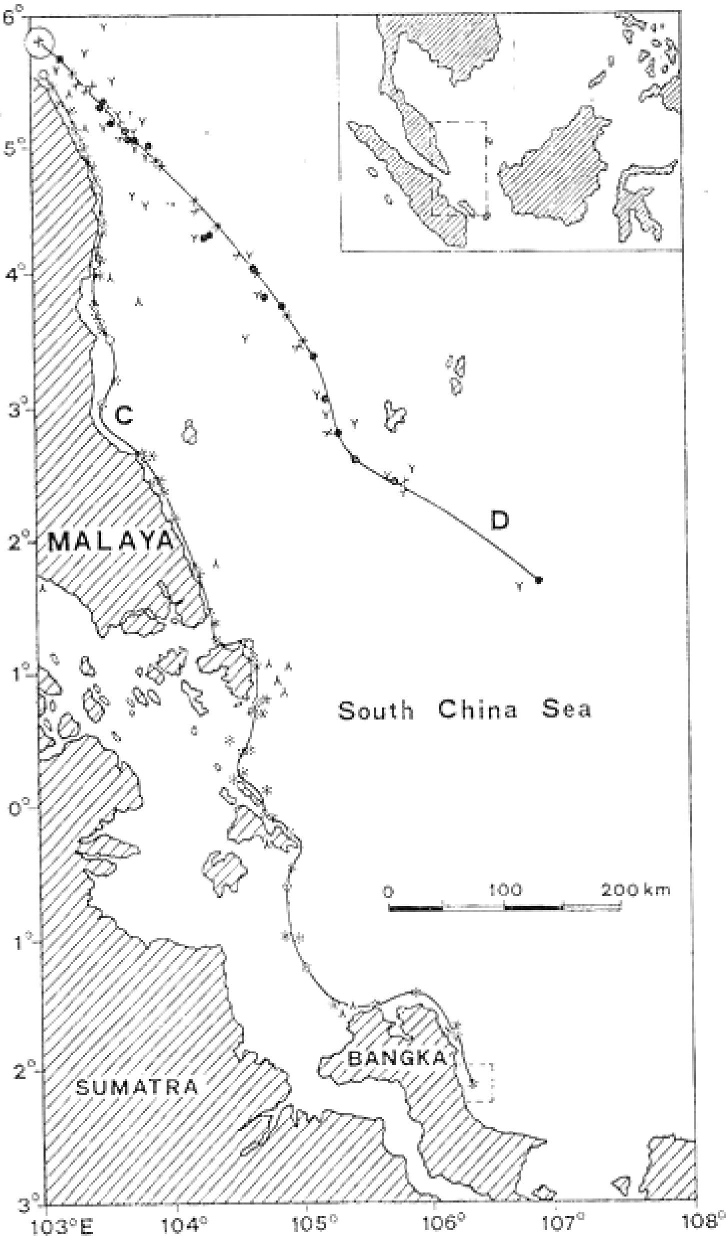


Fig. 2 Tracks of turtles *C* and *D*. Redang Island is located at the centre of the *large open circle* at the top left. *Open dots, asterisks* and *overturned Y* refer to turtle *C*; *filled dots, X* and *Y* to turtle *D*. Other explanations as in Fig. 1

Displacement experiments

The two experiments were performed on turtle A. This female was caught for the first time when she landed for her seventh nesting at the Chagar Hutang Beach on 25 Aug. at the beginning of the night. She was equipped with the route recorder, transported by boat 11.1 km North and there lowered into the sea at 2220 h. She was caught again while nesting on the same beach at 2020 h of the 26 Aug. The data stored in the route recorder made it possible to reconstruct the path given in Fig. 3, which was swum with an average speed of 2.4 km/h. As the path was reconstructed on the assumption that the turtle kept a constant speed, the track plotted in the figure is only indicative of the route actually followed. In any case, there is evidence for an initial series of segments in different directions followed by a leg heading straight for the beach. The data stored in the recorder show that the turtle arrived just off the beach at 0543 h. Thereafter, she wandered nearby all day long and landed to nest after dusk, as turtles usually do. These wandering movements are not reported in the picture.

After nesting, the female was transported to the release site on the peninsular coast, about 284 km South

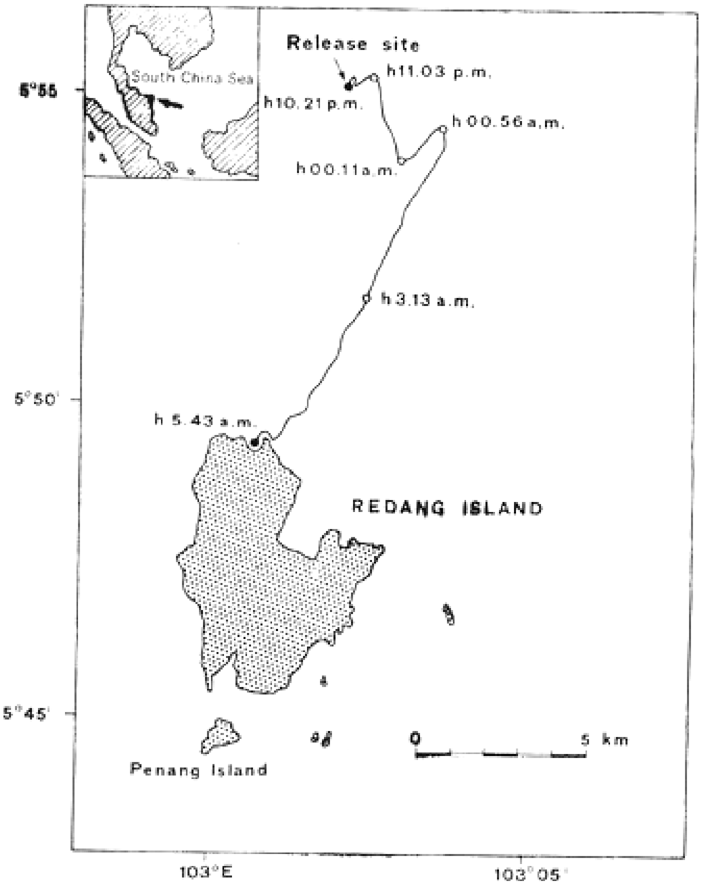


Fig. 3 Homing journey of turtle *A* displaced 11.1 km North of the nesting beach, as reconstructed according to the data stored in the direction-recording data-logger

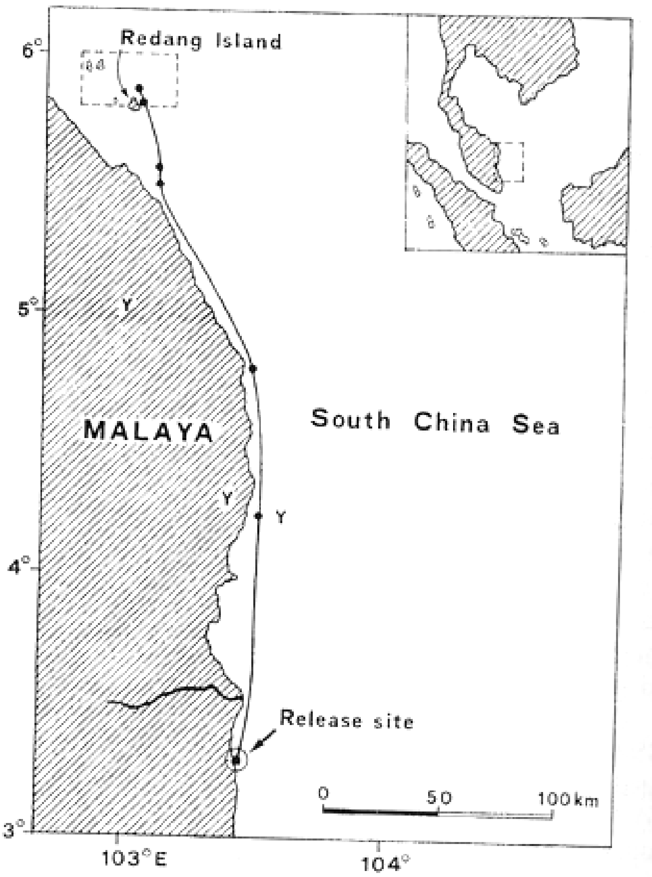


Fig. 4 Journey of the displaced turtle *A* from the release site on the Malayan east coast to Redang Island. The *rectangle* around Redang indicates the area in which the turtle was located before her later nesting. Other explanations as in Fig. 1

of Redang (see 'Methods'). There she was equipped with a PTT and let free on 27 Aug. at 1500 h. The first fix after release was obtained 3 d 13 h later, the turtle being 104 km north of the release site (Fig. 4). After that, she continued to move northwards, following a coastwise route; on 3 Sept. she reached the waters surrounding Redang with a straight course. We consider that the trip back to the nesting area ended 7 d 01 h after release. The length of the track is 298(A)–304(B) km and the average speed 1.77(A)–1.81(B) km/h. The value of the straightness index is 0.95(A)–0.93(B). After returning, the turtle wandered for five days in the waters north of Redang and landed to nest again on the Chagar Hutang Beach on 8 Sept.

Discussion

The pattern of the four migratory routes and the return journeys of the displaced turtle allow some inferences about the navigational mechanisms of sea turtles. The green turtle is known to be a migrant regularly shuttling between specific nesting and feeding grounds (Meylan 1982; Limpus et al. 1992; Balazs 1994). We may therefore assume that our turtles A, B, and C were successful in reaching the intended goal with their migratory trips, while turtle D was heading home when PTT emissions stopped. Turtle A was similarly successful in returning to the nesting beach after passive displacement, not only from a short distance, but also from a quite distant site (280 km) off her usual migestory route.

Considering the tracked routes, some features are immediately striking. Turtle C was able to use the coastline as a guide for most of the migratory journey, in a way similar to turtle A after her second displacement. Turtles A, B, and D migrated on open seas, keeping an almost direct course towards their feeding grounds (Figs. 1 and 2). This is confirmed by the high values of the straightness index and by the amazing fact that turtle B pinpointed the Strait of Balabac, the main way to her feeding grounds, at the end of a very long leg in the open sea (Fig. 2). Another intriguing finding is that the first leg of the journeys of turtles A and B, though made separately, coincided almost perfectly.

Considering now the mechanisms which permitted the navigational performance of our turtles, our starting point is the assumption that the migratory journeys are homing events, just like the trips back after displacement, as they all involve a return to a familiar site. Therefore, in the following discussion we can use the concepts and terms on which a recent classification of homing phenomena is based (Papi 1992). Beginning with turtle C, we note that her trip is different from the others, as it almost completely runs along continental and insular coasts. In theory, a mechanism of route reversal based on a landmark series might be sufficient to explain her orientation, although pilotage based on an acquired topographical map cannot be excluded. In any case, the leg of her journey in open seas from Linga Archipelago to Bangka Island (about 150 km, see Fig. 2) seems to have required, at least, the use of a compass mechanism.

Further cases of coasting are shown by turtle A, in the leg of her migration along the Borneo coast and the trip back after the second displacement. In the latter case, map-based pilotage can be excluded if we assume that the turtle was in an unfamiliar area. We do think it possible that the turtle established her southern position with respect to the nesting beach and then kept a northern bearing with a compass mechanism. As the selected direction was close to that of the straight coast she might have switched to a landmark-based orientation, keeping the coast as a guiding line. Similar behaviour, which does not necessarily imply a familiarity with landmarks, is known in birds (Geyr von Schweppenburg 1963), which can rely for that on their excellent visual sense. For turtles, the nature of the leading cues deriving from the coast is not known with certainty, but Timko and Kolz (1982), on the basis of their satellite tracking of a coastal trip of a loggerhead turtle (*Caretta caretta*), have proposed the role of a specific depth contour in guiding the journey.

The trips in open seas are noteworthy for their straightness and seem to involve the use of complex mechanisms. As in the case of the green turtle reported by Papi et al. (1995), long legs of the trips recorded in open seas are straight, with a roughly constant heading and speed during both night and day. One explanation that springs to mind is that a piloting mechanism could be effective in directing the turtles even in open seas. This idea seems to be supported by the fact that part of the trips of turtles A and B coincided very closely, as if there were a 'turtle highway' in the open sea (Fig. 1). In our case, this coincidence occurs over shallow waters where the shoal features might provide guiding seamarks, but Balazs (1994) and Balazs et al. (1994) have reported similar cases over the deep waters between Fiji and Samoa and round the Hawaiian Archipelago. Moreover, straight courses are also held by turtles A and B in the last part of their trips when, having crossed the escarpment of the continental shelf at about 110°E, they swam in deep waters.

Another mechanism to be considered is vectorial navigation. Turtles might rely on a spatio-temporal programme of migration based on their previous experience. It is however doubtful whether information on the target's direction and distance alone might be effective in leading turtles home. This would involve the use of a compass mechanism (see later) and expose long-distance navigators to harmful deflections from the right course, due both to inaccuracy of the biological steering mechanism and current drift. While the first factor is not assessable, we have tried to estimate the influence of the local currents on the turtles' courses by relying on ship drift data (Richardson 1989) on the mean monthly parameters of the currents. However, the currents in the area vary substantially both in time – as shown by the monthly means – and in space, as they largely depend on wind patterns. It therefore appears to be improbable that the current drift can be compensated by programmed deflection of the heading from the target's bee-line direction, as migratory birds successfully do when facing constant winds (Williams and Williams 1990).

Considering the weakness of the hypotheses discussed above, we can conclude that green turtles probably rely on a mechanism of true navigation, i.e. that they use local cues to calculate goal direction, which is then selected by means of a compass-like physiological mechanism. This idea, which is in agreement with the findings of Papi et al. (1995), is also supported by the results of our displacement experiments. The quick return home of turtle A after the second displacement is very impressive, although perhaps facilitated by the direction of the coast. Displacement experiments, made with animals caught at home or during migration are crucial in testing the idea of a true navigation ability. So far, however, only a few other attempts on this line have been made with sea turtles (Baldwin 1972; Carr 1972; Ireland 1980), and the results have been quite inconclusive, either because of the short displacement distance or the incompleteness of the tracking. Our second experiment is the first that has demonstrated homing ability with a straight course home in a turtle displaced over a long distance.

Some considerations have to be devoted to the nature of the compass and of the local cues that permit position fixing. Satellite tracking at night shows that the course is held with unchanged accuracy with respect to daytime even on moonless nights. Since sea turtle eyes are very myopic out of the water and are therefore unable to see the stars (Ehrenfeld and Koch 1967), a physiological mechanism based on sensitivity to the earth's magnetic field is the only compass – among those known in animals – which could then be utilised in the absence of moon or sun. This is consistent with the recent results obtained in laboratory experiments with hatchlings of two sea turtle species (Lohmann 1991; Lohmann and Lohmann 1993).

True navigation can be based either on a mosaic of local cues or on a grid of physical or chemical gradients, but we are unable to solve even this first dilemma. The ability to pinpoint a distant target through a long trip in deep, open seas seems to support the grid rather than the mosaic hypothesis. It is worth recalling here that in the case of the green turtles migrating from the Brazilian coasts to Ascension Island it has been suggested that an odorous gradient originating from the target can act as a guide (Koch et al. 1969; Carr 1972). Contrary evidence, however, is provided by a study of the relevant features of the South Atlantic equatorial current (Brown 1990) and also the straightness of the green turtle migratory routes reconstructed by satellite (Balazs 1994; Balazs et al. 1994; Papi et al. 1995; present study) hardly agrees with a chemical mechanism for long-distance orientation.

Lastly, it is worth mentioning the possibility that turtles use low-frequency sounds to orientate, as has been proposed for birds (Yodlowski et al. 1977). Such sounds also originate from waves breaking on rocky shores and propagate through the water for very long distances, so that islands and headlands may act as beacons. So far there are no indications about which parameters of such acoustic stimuli could actually be perceived by turtles, so providing them with useful navigational information. Experimental research on turtle navigation is only just beginning, and detailed testing of this idea can now be considered a further important objective.

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