# The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry

**P. Luschi**[1], **G. C. Hays**[2], **C. Del Seppia**[3], **R. Marsh**[4], **and F. Papi**[1*]

[1]*Dipartimento di Etologia, Ecologia, Evoluzione, University of Pisa, Via A. Volta 6, I-56126 Pisa, Italy*
[2]*School of Biological Sciences, University of Wales—Swansea, Singleton Park, Swansea SA2 8PP, UK*
[3]*Centro di Studio per la Faunistica ed Ecologia Tropicali del CNR, Via Romana 17, I-50125 Firenze, Italy*
[4]*James Rennel Division, Southampton Oceanography Centre, Empress Dock, Southampton SO14 3ZH, UK*

Previous tagging studies of the movements of green turtles (*Chelonia mydas*) nesting at Ascension Island have shown that they shuttle between this remote target in the Atlantic Ocean and their feeding grounds on the Brazilian coast, a distance of 2300 km or more. Since a knowledge of sea turtle migration routes might allow inferences on the still unknown navigational mechanisms of marine animals, we tracked the postnesting migration of six green turtle females from Ascension Island to Brazil. Five of them reached the proximity of the easternmost stretch of the Brazilian coast, covering 1777–2342 km in 33–47 days. Their courses were impressively similar for the first 1000 km, with three turtles tracked over different dates following indistinguishable paths for the first 300 km. Only the sixth turtle made some relatively short trips in different directions around Ascension. The tracks show that turtles (i) are able to maintain straight courses over long distances in the open sea; (ii) may perform exploratory movements in different directions; (iii) appropriately correct their course during the journey according to external information; and (iv) initially keep the same direction as the west-south-westerly flowing current, possibly guided by chemical cues.

**Keywords:** green turtles; migration; orientation; Ascension Island; sea currents

## 1. INTRODUCTION

Sea turtles, like other marine animals, face formidable navigational challenges when they undertake long journeys for distant breeding or foraging towards areas that may be tiny oceanic islands or specific spots of continental shores (Carr 1984). So far, the guidance mechanisms used by adult turtles have only been matter of speculation (see Papi & Luschi 1996). Green turtles (*Chelonia mydas*) nesting at Ascension Island (7°57′ S, 14°22′ W) are often cited as a paradigm since the recovery of 66 females tagged at the island with numbered flipper tags showed that they migrate to feeding grounds located on the Brazilian coast, a distance of 2300 km or more (Koch *et al.* 1969; Carr 1975; Mortimer & Carr 1987).

As emphasized by the pioneer of sea turtle research, Archie Carr (Carr 1972, 1984), a first step in understanding the underlying navigational mechanisms would be to identify the courses followed by these migrating turtles. This is now made possible by satellite telemetry, which has proved to be a reliable tool for tracking long-distance journeys of marine animals (Taillade 1993; McConnell & Fedak 1996; Morreale *et al.* 1996; Papi & Luschi 1996). In our case, tracking the journey from Brazil to Ascension would have been the best approach to study the turtles' ability to pinpoint a small target, but this approach is hard to achieve due to the difficulty in capturing females when they are just about to leave Brazil. However, tracking the reverse journey could also be helpful to study turtle navigational skills, since green turtles are also known to undertake postnesting migrations directed towards specific targets (see, for instance, Balazs 1994, Balazs *et al.* 1994, Luschi *et al.* 1996). In the case of Ascension turtles, it might be expected that the first target of migrating turtles would be the coastal waters of the easternmost part of the Brazilian bulge into the Atlantic (i.e. the coast between *ca.* 5° and 10° S). It is in fact reasonable that turtles leaving Ascension Island should move towards this area to reduce the length of their journey in the open sea, even when their coastal feeding grounds are located to the north or south. Indeed, most of the recovered females tagged at Ascension were from this area (Carr 1975, 1984; Mortimer & Carr 1987). Even if such a target is not as small as Ascension is for turtles migrating from Brazil, the reconstruction of the routes followed by postnesting turtles may still allow an evaluation of their navigational performance. This would then allow a re-examination of the hypotheses so far proposed about the navigational system used by these turtles to pinpoint Ascension, assuming that the same mechanisms guide the postnesting migration as well.
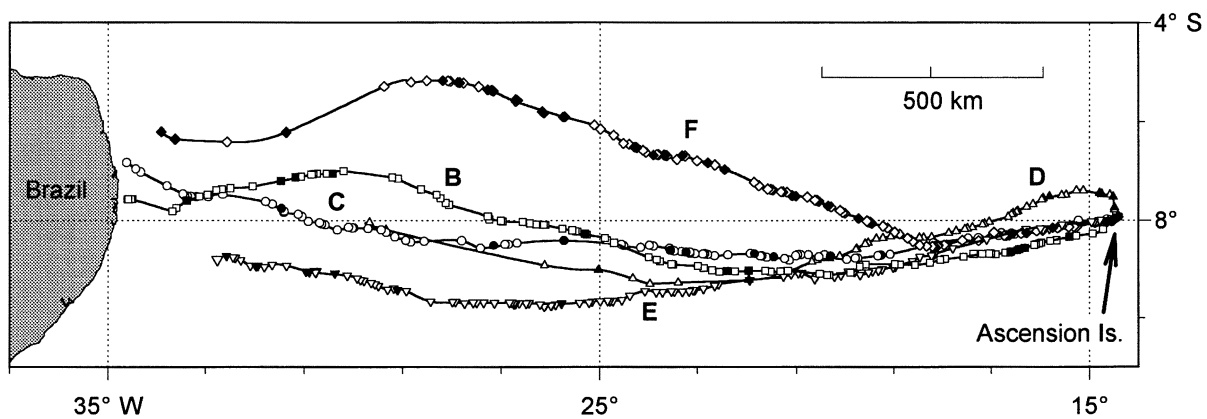
Figure 1. Migratory routes of the turtles B–F as they left Ascension Island for their postnesting migration towards Brazil. Filled symbols represent fixes of the three most accurate classes (typically within 1 km of the true location), while open symbols represent the less accurate fixes. Only fixes considered valid are plotted in the figure (see text for details). The chart is constructed on equatorial Mercator's projection.

## 2. MATERIALS AND METHODS

During April–July 1997, six female green turtles were located while nesting on Long Beach near Georgetown, Ascension Island (table 1). Immediately after egg laying, Telonics ST-14 satellite transmitters were attached to their carapace using standard methods (Balazs *et al*. 1996; Papi *et al*. 1997).

The turtles were then localized through the Argos satellite system (Taillade 1993; French 1994), which classified their locations into six classes of decreasing accuracy (less than 1 km for the first three classes). The routes followed by the turtles have been reconstructed disregarding those fixes of the lower three classes which were considered to be erroneous (33 out of 585) because they inferred either a swimming speed exceeding $5 \, \mathrm{km} \, \mathrm{h}^{-1}$ ($n = 25$ fixes; this threshold value was derived from speed values calculated from high-accuracy localizations only), or a swimming direction which differed for more than $90°$ from those recorded in the preceding and following three days ($n = 8$ fixes). These disregarded fixes were thought to be due to inaccuracies in the locations provided by the Argos system. For each turtle, total distance covered was computed by adding the distances between successive valid fixes. The straightness index was calculated as the ratio between the beeline distance from Long Beach to the last fix of a turtle's route and the total length of the route (Batschelet 1981).

To compare turtle performances in periods which had a different availability of orientating cues, we distinguished four types of segment between successive valid fixes: those which had been travelled mostly ($>90\%$) during the day, or mostly during the night; those covered at night when the moon was above the horizon (moon segments); and those when the moon was not above the horizon (moonless segments). Turtles' speed and direction recorded in the different segments were compared by means of $t$- or $U^2$-test (Batschelet 1981). Data from segments covered in less than 120 min were excluded.

To assess the prevailing ocean currents in the study area, we used a primitive equation general circulation model called the global isopycnic model (GIM, Marsh *et al*. 1998). GIM is essentially a $1.25°$ resolution global version of the Atlantic model used in a previous study of juvenile loggerhead turtles (Hays & Marsh 1997). This mathematical model provided information on the direction and relative strength of the currents (see Marsh *et al*. (1998) and Hays & Marsh (1997) for fuller technical descriptions of the model).

Table 1. *Details of the six turtles for which postnesting migrations were tracked by satellite for 19–47 days*

(CCL, curved carapace length.)

| turtle | release date | CCL (cm) | tracking duration (d) | distance covered (km) | straightness index |
|---|---|---|---|---|---|
| A | 27 April | 115.5 | 19 | 969.0 | 0.13 |
| B | 12 May | 120.0 | 35 | 2320.7 | 0.96 |
| C | 22 June | 112.0 | 39 | 2346.6 | 0.95 |
| D | 25 June | 110.0 | 33 | 1792.9 | 0.95 |
| E | 28 June | 107.0 | 47 | 2095.0 | 0.97 |
| F | 2 July | 117.0 | 36 | 2284.8 | 0.95 |

## 3. RESULTS

Five of the tracked turtles (B–F) directly headed towards Brazil (figure 1), whereas turtle A moved around in different directions until the transmitter stopped emissions after 19 days (figure 2). The routes clearly show that the turtles are able to maintain straight courses in the open sea and to move towards a common target. Turtle D, which left Ascension in a north-westerly direction, soon corrected her course in line with the others. A striking feature of tracks B–F is their coincidence, which is particularly marked in the first 500 km that were covered in a west-south-western direction (figures 1, 2). Turtles B–E continued in the same direction for a further 500 km, whereas turtle F turned and headed north-west. It is particularly impressive that turtles C, E and F followed indistinguishable paths for the first 300 km even though they were tracked over different dates. Sooner or later, all of the turtles corrected their initial west-south-western course and headed west-north-west. Turtles B and F later compensated again for the excess of the first correction with the result that all five tracks converged on the easternmost part of the Brazilian bulge (figures 1, 3). The straightness index of the five courses ranges between 0.95 and 0.97 (table 1), thus indicating similar navigational performances. The five turtles were tracked for a large part of their journey to the bulge of Brazil (1770–2342 km), but the early cessation of the emissions of all
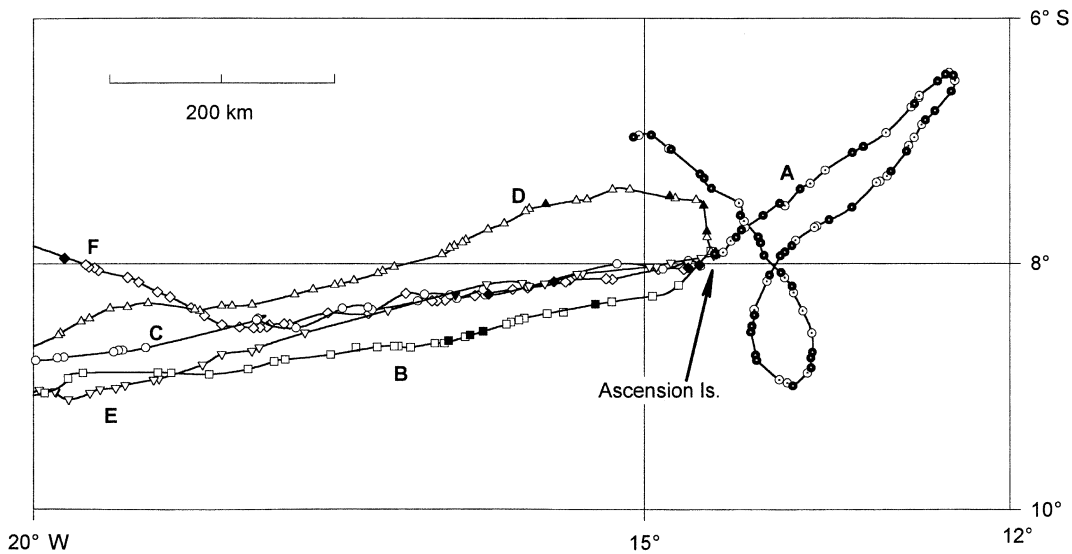
Figure 2. The first part of the migratory journey of turtles B–F and the reconstructed route of turtle A. Other explanations are as in figure 1.



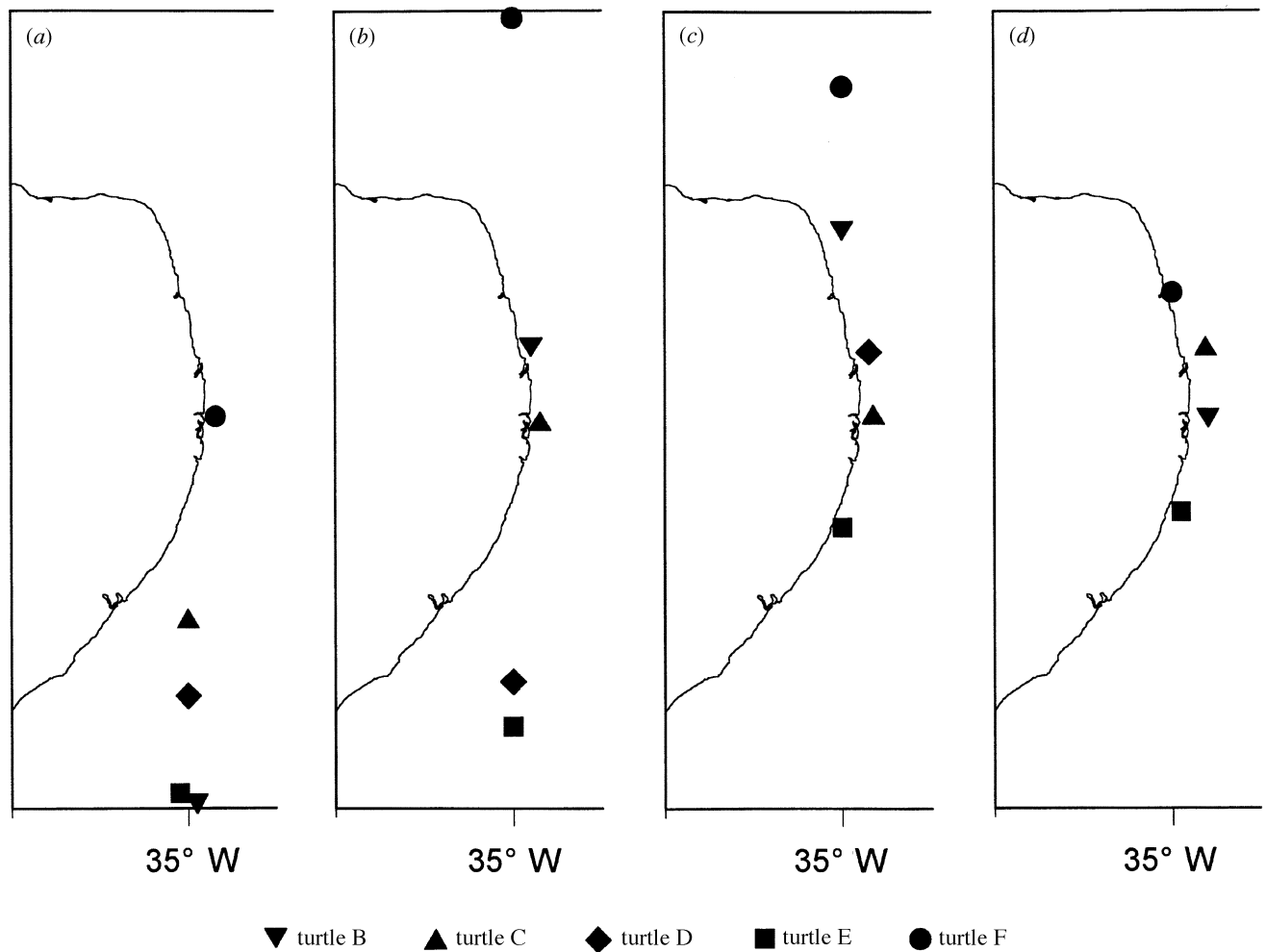▼ turtle B      ▲ turtle C      ◆ turtle D      ■ turtle E      ● turtle F

Figure 3. Progressive adjustment of course of the turtles as they migrate towards Brazil. Symbols on the charts represent the site where the single turtles were expected to cross the 35° W meridian or to reach the coast if they maintained the mean direction held (*a*) before 20° W, (*b*) between 20–25° W, (*c*) between 25–30° W and (*d*) after 30° W (excluding turtle D, which did not cross the 30° W meridian). For turtles B and C, which were tracked up to the coast, the symbols in chart (*d*) show their last fix. All the turtles progressively corrected their course while approaching Brazil to orientate towards the easternmost part of the bulge.

transmitters prevented us from unveiling where the turtles' feeding grounds were located. The emissions lasted for much less than expected according to the specifications of the transmitters and to our previous

experience with transmitters of the same model (Luschi *et al*. 1996; Papi *et al*. 1997; Hughes *et al*. 1998).

With the exception of turtle D, all the turtles maintained a slightly slower swimming speed during the night,

Table 2. *Turtle performances in terms of speed and direction in segments between successive valid fixes*

(For each turtle, mean±s.e. speed and mean vector direction and length in four different types of segments are reported. Mean heading calculations were not done for turtle A, who repeatedly changed her direction of movement. Other explanations are in the text. Vector length, which varies from zero to one, is inversely proportional to the extent of scatter of the segment directions (Batschelet 1981). (*a*) Shows data for turtles travelling >90% during the day or the night. (*b*) Compares migrations on nights where the moon was above the horizon (moon segments) or not (moonless segments). In (*a*) and (*b*), *n* day, *n* night, *n* moon and *n* moonless represent the number of different segments recorded.)

| (*a*) | mean±s.e. speed (km h$^{-1}$) | | | mean vector direction and length | | |
|---|---|---|---|---|---|---|
| turtle (*n* day, *n* night) | daytime segments | night-time segments | *t*-test | daytime segments | night-time segments | $U^2$-test |
| A (20, 18) | 3.13±0.11 | 2.85±0.15 | $p = 0.143$ | — | — | — |
| B (28, 22) | 3.16±0.08 | 2.83±0.08 | $p = 0.006$ | 267°, 0.96 | 273°, 0.95 | $p > 0.05$ |
| C (24, 25) | 2.86±0.16 | 2.27±0.15 | $p = 0.010$ | 279°, 0.94 | 278°, 0.95 | $p > 0.05$ |
| D (15, 10) | 2.82±0.15 | 2.91±0.14 | $p = 0.693$ | 260°, 0.91 | 252°, 0.99 | $p > 0.05$ |
| E (39, 9) | 2.51±0.12 | 1.65±0.27 | $p = 0.004$ | 265°, 0.96 | 265°, 0.90 | $p > 0.05$ |
| F (30, 28) | 2.85±0.13 | 2.45±0.11 | $p = 0.027$ | 280°, 0.97 | 282°, 0.97 | $p > 0.05$ |

| (*b*) | mean±s.e. speed (km h$^{-1}$) | | | mean vector direction and length | | |
|---|---|---|---|---|---|---|
| turtle (*n* moon, *n* moonless) | moon segments | moonless segments | *t*-test | moon segments | moonless segments | $U^2$-test |
| A (6, 12) | 3.22±0.21 | 2.67±0.18 | $p = 0.087$ | — | — | — |
| B (14, 8) | 2.74±0.07 | 3.00±0.19 | $p = 0.138$ | 270°, 0.96 | 278°, 0.94 | $p > 0.05$ |
| C (17, 8) | 2.40±0.20 | 1.99±0.15 | $p = 0.214$ | 277°, 0.93 | 278°, 0.98 | $p > 0.05$ |
| D (4, 6) | 3.23±0.15 | 2.69±0.16 | $p = 0.049$ | 249°, 0.99 | 254°, 0.99 | $p > 0.05$ |
| E (5, 4) | 2.03±0.37 | 1.19±0.24 | $p = 0.117$ | 270°, 0.97 | 258°, 0.84 | $p > 0.05$ |
| F (18, 10) | 2.21±0.13 | 2.89±0.12 | $p = 0.001$ | 284°, 0.97 | 278°, 0.97 | $p > 0.05$ |

the difference being significant in turtles B, C, E, and F (table 2). In none of the cases were significant differences found between nocturnal and diurnal directions (table 2*a*). When the moon was absent, turtles carried on with apparently unchanged speed and heading (table 2*b*).

## 4. DISCUSSION

The behaviour of turtle A is difficult to understand (figure 2). It seems to be improbable that her 280–150 km-long trips in different directions represent wrong attempts to move towards Brazil. Unlike the other turtles we tracked, turtle A was afflicted with a fibropapilloma, but these tumours do not seem to produce the major anomaly in migratory behaviour that we observed (Balazs 1994). It may be possible that the turtle was exploring the waters around Ascension in search of new feeding grounds. The only safe conclusion about the navigational skills of this turtle is that she showed the ability of course reversal since she returned to the Ascension area after the trips she made.

All the other turtles directly migrated towards the Brazilian bulge (figure 1). It is impossible to know whether this was their final target or just a stop-over area in the journey to more distant feeding grounds (see also Mortimer & Carr 1987). However, the reconstructed tracks allow some inferences to be drawn regarding the navigational mechanisms. The trips occurred over deep oceanic waters and thus in the absence of landmarks or detectable bathymetric features. In such conditions, covering long, straight journeys at least requires the usage

of compass mechanism(s). It is very probable that marine turtles rely on a time-compensated sun-compass, which is widespread in animals and has also been demonstrated in freshwater turtles (De Rosa & Taylor 1980). As found in previous studies (Luschi *et al.* 1996; Hughes *et al.* 1998), the turtles were also able to keep their course at night when the moon was absent. Since they are too myopic in the air to see stars (Ehrenfeld & Koch 1967), it seems likely that they can orientate using non-visual cues. Indeed experimental studies, which have so far been limited to hatchlings, have shown that turtles have the ability to direct their movements in relation to both the earth's magnetic field and wave direction (Lohmann & Lohmann 1996*a*).

As described above, the turtles appropriately adjusted their course while migrating to orientate towards their target (figure 3). This shows that Ascension turtles, besides one or more compasses, also rely on additional navigational tools based on external information picked up en route. This had already been suspected, considering that compass mechanisms alone could hardly allow turtles arriving from Brazil to find their target in the middle of the Ocean (Koch *et al.* 1969; Carr 1984). In connection with this, two hypotheses have been put forward. According to Lohmann & Lohmann (1996*b*), adult turtles might retain the capacity they have as hatchlings of detecting differences in magnetic field intensity and inclination. If so, Ascension turtles could determine their position from the isoclinics and isodynamics that intersect at a great angle in the equatorial Atlantic Ocean, thus making up a bicoordinate grid. This could

theoretically allow turtles to determine their position over the entire journey, and to select the most appropriate route to orientate themselves towards their target. Reliance on such a mechanism of magnetic navigation, however, hardly explains the initial deflection of all our turtles towards the west-south-west, which leads them away from the shortest course towards Brazil. However, this deflection might be due to a drift produced by the South Atlantic equatorial current (SAEC, see later), for which turtles are initially unable to compensate.

The second hypothesis was advanced by Carr and co-workers (Koch *et al.* 1969; Carr 1972, 1984) specifically to address the question of how Ascension Island was pinpointed by the incoming turtles from Brazil. Chemical substances originating from the target island would be transported westwards by the SAEC at a speed of up to $1.8 \, \mathrm{km \, h^{-1}}$, giving rise to an odour plume that might be detected by migrating turtles. Turtles would leave Brazil and head eastwards by means of a compass mechanism and, once they intersected the plume, they would remain within it until reaching the Ascension area. As shown by theoretical calculations, the features of the SAEC limit the dilution of the dissolved chemicals, thus maintaining their concentration high enough to be detected by a biological chemosensor, even at a large distance from the Island (Koch *et al.* 1969). The females on their first reproductive migration would recognize the Ascension-derived chemical stimuli as the same one they had been imprinted with as hatchlings (Owens *et al.* 1986).

Although it has been suggested that the SAEC may temporarily reverse its direction during the austral summer (i.e. while the pre-nesting migration to Ascension occurs; Brown 1990), we think that the existence of a chemical link between Ascension and Brazil needs to be considered at least in relation to the postnesting migration. Since the current flow during the rest of the year is known to be westerly, turtles might use the chemical cues from the plume to orientate even during the return trip to Brazil. At the time of year that we tracked the turtles, two buoy tracking studies (Reverdin & McPhaden 1986; Schäfer & Krauss 1995) have shown that the surface current from Ascension flows in a direction of 255–260°, i.e. between west and west-south-west. Near-surface (model mixed layer) currents in the equatorial South Atlantic of the GIM are very similar in May, June and July (figure 4). In common with the buoy studies, in these three months the model also showed a west-south-western current flow from Ascension towards South America, with this current tending to weaken with distance west and south (figure 4). These empirical and modelling studies therefore suggest that during May and July the west-south-western current is a constant feature of the area close to Ascension. The directions followed by the turtles in the first part of their trip show an impressive coincidence with the current, both being *ca.* 260°.

To remain within the SAEC, turtles might rely on several cues which certainly characterize the current (e.g. temperature, salinity, etc.), but the fact that the courses, in the first part of the journey, were confined within a narrow corridor starting from Ascension, indicates that the turtles referred to cues derived directly from the island itself, such as the chemical substances borne by the current. The coincidence of the first part of the routes can
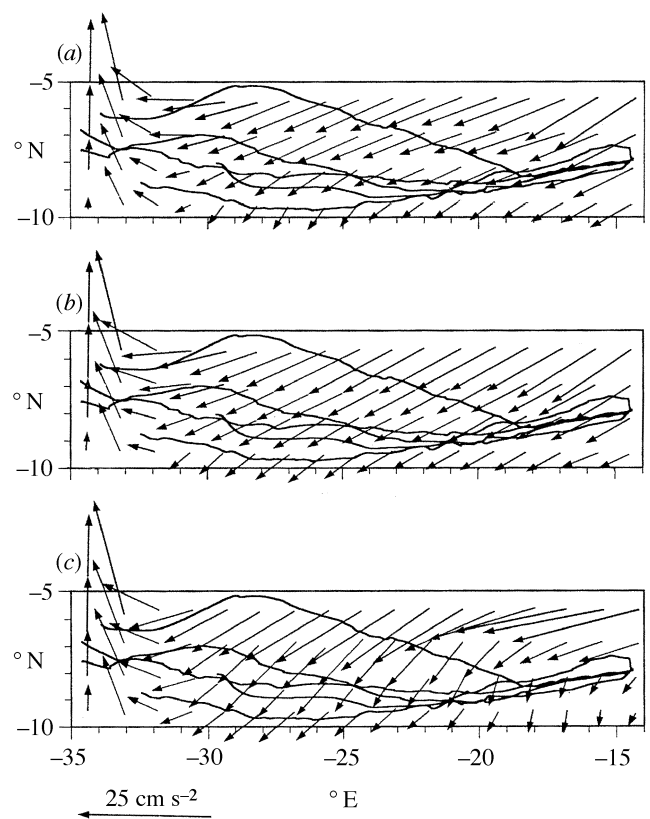


Figure 4. Tracks of turtles B–F superimposed to mixed layer currents in the equatorial South Atlantic of GIM after 30 years spin-up, during the middle of (*a*) May, (*b*) June, (*c*) July. Charts are equatorial Mercator's projections.

thus be interpreted as evolving from the turtles' tendency to swim in the axis of the plume of Ascension-derived chemicals, by correcting their course when perceiving a decrease in the concentration of the current-borne substances. On average, turtles spent >90% of the time submerged with dive durations generally between about 4 and 16 min (G. C. Hays, P. Luschi, C. Del Seppia and F. Papi, unpublished data). These dives may potentially be important in exploring the depth profile of the odour plume from Ascension. The occurrence of migratory corridors in sea turtles has also been observed in other areas (Balazs 1994; Balazs *et al.* 1994; Morreale *et al.* 1996; Balazs & Ellis 1998), but their relationship with currents has not been investigated in detail. As well as possibly providing navigational cues to aid migration, swimming with the prevailing current will also increase the turtles' speed of travel and so may help to minimize the energetic cost of the postnesting migration.

As the distance from the source increases the canalization effect of the plume will become less effective since the steepness of the north–south gradient will decrease. This may explain why the turtle tracks began to diverge hundreds of kilometres downstream from Ascension. Moreover, in the second part of the journey, the turtles tended to abandon the stream of the current, which, if followed, would have led them too far south. It is uncertain whether these course changes might be due to a modification in the pattern of current-borne chemical cues or to a switching to orientational cues of a different nature. For

instance, an approximate evaluation of the latitude, possibly based on magnetic cues (Lohmann & Lohmann 1996a), might account for these course corrections.

In conclusion, the present results show that Ascension turtles use information picked up en route to adjust their migratory course, and suggest that current-borne cues, probably of a chemical nature, may be involved in this process for at least part of the journey. Swimming within the plume provided the turtles with a reliable and efficient guidance mechanism towards Brazil, even though the current direction diverged slightly from the shortest straight-line course to Brazil. Clearly, reliance on such a mechanism of navigation would only be possible in the particular case in which currents set up a sensory link between the rookery and the feeding grounds. In the other cases, turtles may rely on different navigational strategies, of unknown nature, to find their way through the oceans.

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