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Orientation of migrating leatherback turtles in relation to ocean currents

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During their offshore movements, leatherback turtles, *Dermochelys coriacea*, associate frequently with ocean currents and mesoscale oceanographic features such as eddies, and their movements are often in accordance with the current flow. To investigate how individual turtles oriented their ground- and water-related movements in relation to the currents encountered on their journeys, we used oceanographic techniques to estimate the direction and intensity of ocean currents along the course of 15 leatherbacks tracked by satellite during their long-distance movements in the Indian and Atlantic Oceans. For all individuals a non-negligible component of active swimming was evident throughout the journeys, even when their routes closely followed the currents, but overall the turtle water-related orientation was random with respect to current directions. For turtles in the North Atlantic, the ground-related movements largely derived from the turtles' active swimming, while in the Indian Ocean currents contributed substantially to the observed movements. The same pattern was shown when distinct parts of the routes corresponding to foraging bouts and travelling segments were considered separately. These findings substantiate previous qualitative observations of leatherback movements, by revealing that turtles were not simply drifting passively but rather swam actively during most of their journeys, although with a random orientation with respect to currents. Our analysis did not provide any indication that leatherbacks were able to detect the current drift they were exposed to, further highlighting the navigational challenges they face in their oceanic wanderings.

For animals living in the open sea, ocean currents represent a key environmental factor that greatly affects their movements and overall behaviour (Chapman et al. 2011). Currents can influence the distribution and movements of pelagic animals in a variety of ways, for instance determining the distribution of food resources (Olson et al. 1994; Bost et al. 2009; Kai et al. 2009) or physically influencing their displacement (Girard et al. 2006, 2009; Cotté et al. 2007). Indeed, the observed velocity of marine animals is the vector sum of their swimming velocity and the water velocity (i.e. the current velocity) so that the resulting ground-based path may differ, sometimes substantially, from the animal's water-related route (Green & Alerstam 2002; Gaspar et al. 2006; Girard et al. 2006). Such a current drift is expected to play a strong role in the long-distance oceanic movements of many marine animals, possibly leading to special navigational performances (Sale & Luschi 2009; Chapman et al. 2011).

Leatherback sea turtles, *Dermochelys coriacea*, are ideal subjects for studying the role that oceanographic features play in the movements of marine animals. Leatherbacks spend a lot of their time in the open sea (Eckert et al. 2012), foraging for gelatinous plankton associated with ocean currents (Olson et al. 1994; Lutcavage 1996). In recent years, satellite telemetry has provided a wealth of data documenting the migratory movements of adult sea turtles (Godley et al. 2008), and studies that have integrated tracking data with oceanographic information have shown how the turtles' movements are often influenced by the oceanic circulation of the areas frequented (Luschi et al. 2003a). Leatherbacks, in particular, have been found to associate frequently with mesoscale features such as eddies, following circuitous courses in accordance with the rotation of the water masses (Luschi et al. 2003b; Doyle et al. 2008; Lambardi et al. 2008). Movements in general agreement with the current flow have also been revealed outside eddies, for instance in the presence of stable, strong currents (Luschi et al. 2003b; Lambardi et al. 2008; Shillinger et al. 2008). Quantitative assessments of the currents along the leatherback routes have further revealed that the geographical displacements of ocean-moving turtles are largely determined by currents (Gaspar et al.

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2006; Shillinger et al. 2008; Fossette et al. 2010a) and that the water-related motor paths of individuals often differ from the ground-related courses as recorded by satellite (Gaspar et al. 2006).

However, no experimental data are currently available on how individual leatherbacks actually deal with the currents they encounter, and to what degree they take them into account in their long-distance journeys. For instance, it is unclear whether the often observed pattern of leatherback movements that are in accord with prevailing currents derives from a simple drift of the turtle with little or no active swimming in the horizontal plane, or whether individuals contribute actively to the observed movements in these cases. This issue can be profitably addressed by relying on existing methods to evaluate the direction and intensity of the currents at a given time in oceanic locations. These methods are based upon estimations of the currents' geostrophic component deduced from satellite altimetry data and of the wind-driven component derived from satellite scatterometer measurements and have proven to provide reliable quantitative estimates of the currents encountered by satellite-tracked turtles at various points along their paths (Gaspar et al. 2006; Girard et al. 2006; Shillinger et al. 2008; Fossette et al. 2010a, 2012). In the present study, we applied this approach to the extended and prolonged routes of 15 leatherbacks tracked in the Indian and Atlantic Oceans (1) to study how individual turtles oriented their movements in relation to the currents encountered during their open-sea journeys, (2) to quantify to what extent the currents actually contributed to the reconstructed turtle movements, and (3) to establish whether the leatherbacks' responses to currents were indicative of their detection of the current flow or of their being unaware of the current drift they were subjected to. While previous studies on green sea turtles, *Chelonia mydas*, employing these methods have provided no indications that these turtles were able to detect currents during offshore movements (Girard et al. 2006; Luschi et al. 2007), it is not possible to extend these findings readily to leatherbacks, which belong to a different family and broadly differ from green turtles in their ecology and spatial behaviour. For instance, because of their marked pelagic habits, leatherbacks may have evolved special skills to detect currents that are not available to the green turtles, which spend far less time in the oceanic environment.

METHODS

Analysed Movement Data

We have analysed a large set of tracking data on leatherbacks tracked in the Atlantic ($N = 11$) and the Indian ($N = 4$) Oceans. Details of the duration and length of tracks can be found in Table 1 and in previously published papers (Hughes et al. 1998; Luschi et al. 2003b; Hays et al. 2004a, 2006; James et al. 2006; Doyle et al. 2008; Lambardi et al. 2008; Fossette et al. 2010a). In all cases, turtles were tracked by means of satellite-linked radiotransmitters localized by the Argos System, which provided locations unevenly spaced in time and space and differing in spatial accuracy (see www.argos-system.org for details). In 13 turtles, transmitters were attached using custom-fitted harnesses, while in turtles A6 and A7 the units were directly attached to the carapace (Fossette et al. 2008). The turtles were tracked for long periods (mean: 6.3 months; range 2–11 months, Table 1) while moving in the oceanic environment (see Figs S1, S2 in the Supplementary Material) during different periods of their migratory cycle, including the postnesting migrations towards high-latitude foraging areas, the successive migrations towards tropical and subtropical waters, as well as the residence periods in relatively limited areas for feeding purposes (Table 1). During their journeys, they encountered a variety of oceanographic conditions, such as strong currents like the Gulf Stream or the Agulhas Current, eddies and gyres (Luschi et al. 2003b; Hays et al. 2006; Doyle et al. 2008; Lambardi et al. 2008). The reconstructed routes displayed a large degree of variation, probably deriving from the different migratory strategies adopted by the turtles (Fossette et al. 2010a). Most journeys extended over huge distances (2023–8994 km; Table 1) and led the turtles to visit well-known leatherback foraging areas such as the North American continental shelf (James et al. 2005a, b; Eckert et al. 2006), the offshore convergence zones of North and central Atlantic (Ferraroli et al. 2004; Eckert 2006) and the southwestern Indian Ocean (Luschi et al. 2006). Most routes included both straight and circuitous segments, but some only consisted of straight or convoluted parts (Figs S1, S2 in the Supplementary Material).

Table 1
Main statistics of the analysed turtle tracks

Turtle ID	Starting location	Tracking duration (months)	Track length (km)	Type of movement
A1	Grenada	11.4	2831	Postnesting migration (equatorial)
A2	Grenada	7.5	7564	Postnesting migration (round trip)
A3	Grenada	6.7	4608	Postnesting migration (northbound)
A4	Grenada	7.0	8994	Postnesting migration (northbound)
A5	Grenada	6.0	6913	Postnesting migration (northbound)
A6	French Guiana	3.3	5271	Postnesting migration (northbound)
A7	Ireland	5.3	8276	Southbound migration
A8	Nova Scotia	4.3	8923	Feeding grounds residence+southbound migration
A9	Nova Scotia	2.2	2023	Feeding grounds residence
A10	Ireland	9.3	7479	Southbound migration
A11	Grenada	7.5	8494	Postnesting migration (round trip)
I1	South Africa	7.4	7683	Postnesting migration (southbound)
I2	South Africa	5.6	5766	Postnesting migration (round trip)
I3	South Africa	4.1	5416	Postnesting migration (southbound)
I4	South Africa	7.4	8806	Postnesting migration (southbound)

All tracked turtles were females except turtle A7. Values of tracking duration and length refer to the parts of the routes considered for the analysis (i.e. excluding the parts for which current estimation or a proper interpolation was not possible).

Data Processing

Each track was processed by using the same protocol applied previously (Gaspar et al. 2006) to reconstruct the turtles' routes. Argos locations of any accuracy were used, but those implying a ground speed above 10 km/h (278 cm/s) were discarded, and the resulting track was resampled with a fixed sampling period $\Delta t = 8$ h. Locations for which a proper interpolation was not possible because of large temporal gaps in the original satellite fixes were discarded. As a result, some segments of the turtles' routes were not considered for the analysis (Figs S1, S2 in the Supplementary Material). When successive resampled positions $[\mathrm{X}(t), \mathrm{X}(t+\Delta t)]$ were available, a track vector (T) was systematically computed:

$$\mathrm{T}(t) = [\mathrm{X}(t+\Delta t) - \mathrm{X}(t)]/\Delta t \quad (1)$$

This vector is the actual velocity on the ground of the tracked animal averaged over the whole time interval $[t, t+\Delta t]$.