



## Research

**Cite this article:** Dodge KL, Galuardi B, Lutcavage ME. 2015 Orientation behaviour of leatherback sea turtles within the North Atlantic subtropical gyre. *Proc. R. Soc. B* **282**: 20143129.  
<http://dx.doi.org/10.1098/rspb.2014.3129>

Received: 27 December 2014

Accepted: 5 February 2015

**Subject Areas:**

behaviour, ecology

**Keywords:**

leatherback turtles, migration, North Atlantic subtropical gyre, satellite tracking, current drift, compass orientation

**Author for correspondence:**

Kara L. Dodge

e-mail: [kara.dodge@post.harvard.edu](mailto:kara.dodge@post.harvard.edu)

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2014.3129> or via <http://rspb.royalsocietypublishing.org>.

# Orientation behaviour of leatherback sea turtles within the North Atlantic subtropical gyre

Kara L. Dodge<sup>1,2,3</sup>, Benjamin Galuardi<sup>2</sup> and Molly E. Lutcavage<sup>2</sup><sup>1</sup>Department of Biological Sciences, University of New Hampshire, Durham, NH 03824, USA<sup>2</sup>Large Pelagics Research Centre, UMass-Amherst, Gloucester, MA 01930, USA<sup>3</sup>Integrated Statistics, 16 Sumner Street, Woods Hole, MA 02543, USA

Leatherback sea turtles (*Dermochelys coriacea*) travel thousands of kilometres between temperate feeding and tropical breeding/over-wintering grounds, with adult turtles able to pinpoint specific nesting beaches after multi-year absences. Their extensive migrations often occur in oceanic habitat where limited known sensory information is available to aid in orientation. Here, we examined the migratory orientation of adult male, adult female and subadult leatherbacks during their open-ocean movements within the North Atlantic subtropical gyre by analysing satellite-derived tracks from fifteen individuals over a 2-year period. To determine the turtles' true headings, we corrected the reconstructed tracks for current drift and found negligible differences between current-corrected and observed tracks within the gyre. Individual leatherback headings were remarkably consistent throughout the subtropical gyre, with turtles significantly oriented to the south-southeast. Adult leatherbacks of both sexes maintained similar mean headings and showed greater orientation precision overall. The consistent headings maintained by adult and subadult leatherbacks within the gyre suggest use of a common compass sense.

## 1. Introduction

Sea turtles show remarkable orientation and navigation abilities, locating their natal nesting beaches, for example, over long tracts of open ocean, but how they accomplish these feats is still not well understood [1–4]. Studies have revealed a myriad of cues that turtles may use to orient and navigate in their coastal and oceanic environments. Extensive research on sea turtle hatchlings' ocean-finding abilities demonstrates the importance of visible light [5,6] and beach slope elevation [7], whereas hatchling orientation in coastal waters relies primarily on wave direction [8–11]. In deep water beyond the reach of shoreward-propagating waves, hatchlings switch to other cues that may include the Earth's magnetic field [12–15].

Magnetic orientation has been demonstrated in many long-distance migrants including monarch butterflies (*Danaus plexippus*) [16], yellowfin tuna (*Thunnus albacares*) [17], birds [18], sockeye salmon (*Oncorhynchus nerka*) [19] and sea turtles [14]. Loggerhead sea turtle (*Caretta caretta*) hatchlings are capable of detecting magnetic inclination angle [13] and magnetic field intensity [20], and they appear to use these features during migration [21]. Juvenile green sea turtles (*Chelonia mydas*) subjected to magnetic conditions found north and south of their capture location demonstrated orientation back to the capture site, further supporting a magnetic map sense [22]. Although laboratory experiments on orientation in adult sea turtles are lacking, field studies demonstrated the potential role of geomagnetic cues during open-sea homing of adult green turtles [23]. Adult female loggerhead turtles appear to use geomagnetic cues to find their natal beaches along continental coastlines through a combination of geomagnetic imprinting and magnetic navigation [24].

Although magnetic features are a promising source of global positional information for long-distance migrations, sea turtles are unlikely to rely on them exclusively. Experimental evidence suggests that, under some conditions,

green sea turtles can maintain headings and reach goals in the presence of distorted magnetic fields [25,26]. Pacific leatherback turtles (*Dermodochelys coriacea*) have been hypothesized to travel along 'persistent corridors' using topographic features [27,28], but in the Atlantic no evidence of migratory corridors has been found [29–32]. Travel adjacent to oceanic fronts has also been hypothesized [33,34]. Additional studies point to a 'multifactor navigation system' in turtles [35] that may include a combination of visual and magnetic cues [36], currents [37] and, possibly, olfactory cues over shorter distances [38,39]. Sea turtles may rely on a combination of orientation cues in different situations (i.e. navigation over long distances versus localized movements) [26,40]. Sea turtles' ability to identify and maintain appropriate headings will impact migration distance, duration and, for reproductively active adults, breeding schedules. Understanding migratory orientation and potential cues is an important step towards understanding how sea turtles optimize travel routes and minimize energetic costs of migration.

Here, we examined the migratory orientation of adult male, female and subadult leatherback sea turtles during their open-ocean travel in the western North Atlantic between 2008 and 2009 by analysing their satellite-derived tracks. In this region, leatherbacks make extensive migrations between temperate feeding and tropical breeding and (or) over-wintering grounds [29–32,41], often travelling through the subtropical gyre where there are few known sensory cues (e.g. visual, chemosensory) available to aid in their migration.

## 2. Material and methods

Twenty adult and subadult leatherback turtles were fitted with Wildlife Computers (Redmond, WA) model MK10-A ( $n = 8$ ) and MK10-AF ( $n = 12$ ) ARGOS-linked satellite time depth recorders (STDRs). Leatherbacks were located in their feeding grounds off the coast of Massachusetts, USA (approx.  $41^\circ\text{N}$ ,  $70^\circ\text{W}$ ) from August 2007 to September 2009, and captured with either a break-away hoopnet ( $n = 11$ ) or accessed through the Massachusetts sea turtle disentanglement network ( $n = 9$ ) [32]. We brought turtles on board commercial fishing or research vessels using a custom-built stern ramp. Leatherbacks were measured to the nearest cm (CCL, curved carapace length; CCW, curved carapace width) with a flexible fibreglass measuring tape. We used CCL to classify turtles as adults (CCL  $\geq 145$  cm) or subadults (CCL  $< 145$  cm), and determined gender based on tail length of adult turtles [42]. Five subadult turtles were sexed based on presence of a penis, subsequent necropsy or nesting.

The STDRs were attached directly to the leatherbacks' carapace medial ridge using biocompatible tethers and corrodible crimps [32], and tags transmitted Fastloc GPS locations (MK10-AF tags only) and ARGOS-derived locations (all tags) via Service ARGOS (Toulouse, France). Ninety-five per cent of Fastloc GPS locations are accurate to  $\pm 55$  m [43], whereas ARGOS-derived location error varies by location class (LC) as follows: LC3  $< 150$  m, LC2 = 150–350 m, LC1 = 350–1000 m and LC0  $> 1000$  m. ARGOS does not provide accuracy estimates for LCA and LCB locations, and LCZ are considered unreliable. We filtered 30 173 raw ARGOS and GPS locations using Kalman filter methods outlined by Royer & Lutcavage [44]. Because our analysis included GPS data, we extended the original error covariance structure to include this information. Data were interpolated to a 3 h time step and smoothed. As we were interested in the turtles' migratory orientation within the North Atlantic subtropical gyre, we limited our analysis to track segments that occurred in the North Atlantic Subtropical Gyral West province defined by

Longhurst [45], hereafter referred to as the subtropical gyre. Here, leatherback behaviour was characterized by rapid, highly directed travel consistent with migration [32]. The interpolated, reconstructed track segments within the subtropical gyre included 3904 filtered locations from fifteen turtles (table 1).

To determine the turtles' true headings at each time step, we corrected the reconstructed tracks for current drift. We subtracted an estimate of the surface current velocity from the observed turtle velocity at each location, following the methods described by Gaspar *et al.* [46] and Fossette *et al.* [47]. To calculate the surface current velocity, we extracted surface geostrophic and Ekman current data from the NOAA Environmental Research Division's Data Access Programme website. The geostrophic component was available as a  $0.25^\circ$  daily product inferred from sea surface height deviation, climatological dynamic height and basic fluid mechanics (<http://coastwatch.pfeg.noaa.gov/erddap/info/erdTAgeo1day/index.html>), and the Ekman component was available as a  $0.125^\circ$  weekly product inferred from surface wind velocity (<http://coastwatch.pfeg.noaa.gov/erddap/info/erdQSekm8day/index.html>). We calculated turtle orientation angle (e.g. heading) and great circle distance between successive locations for the observed and current-corrected tracks using the bearingTrack and distanceTrack functions in the 'argosfilter' package in R [48].

All statistical analyses were carried out using the program 'circular' in R [48] and ORIANA v. 4.0 (Kovach Computing). For the distribution of angles for each leatherback, we determined a mean vector that included the mean vector length ( $r$ ), ranging from 0 (uniformly scattered distribution) to 1 (fully concentrated distribution), and the mean vector angle ( $\theta$ ). Because adult leatherbacks might be expected to navigate more efficiently than subadults owing to greater experience or goal orientation (e.g. travel to specific breeding areas), we also grouped turtles by age class and used Watson's two-sample test of homogeneity to test for significant differences in orientation between adults and subadults [49,50]. We calculated the grand mean vector, including grand mean angle, vector length and 95% confidence limits, for all turtles and turtles grouped by age class for both observed and current-corrected tracks [50]. Hotelling's one-sample second-order test was used to determine whether the turtles had a significant mean direction during migration.

## 3. Results

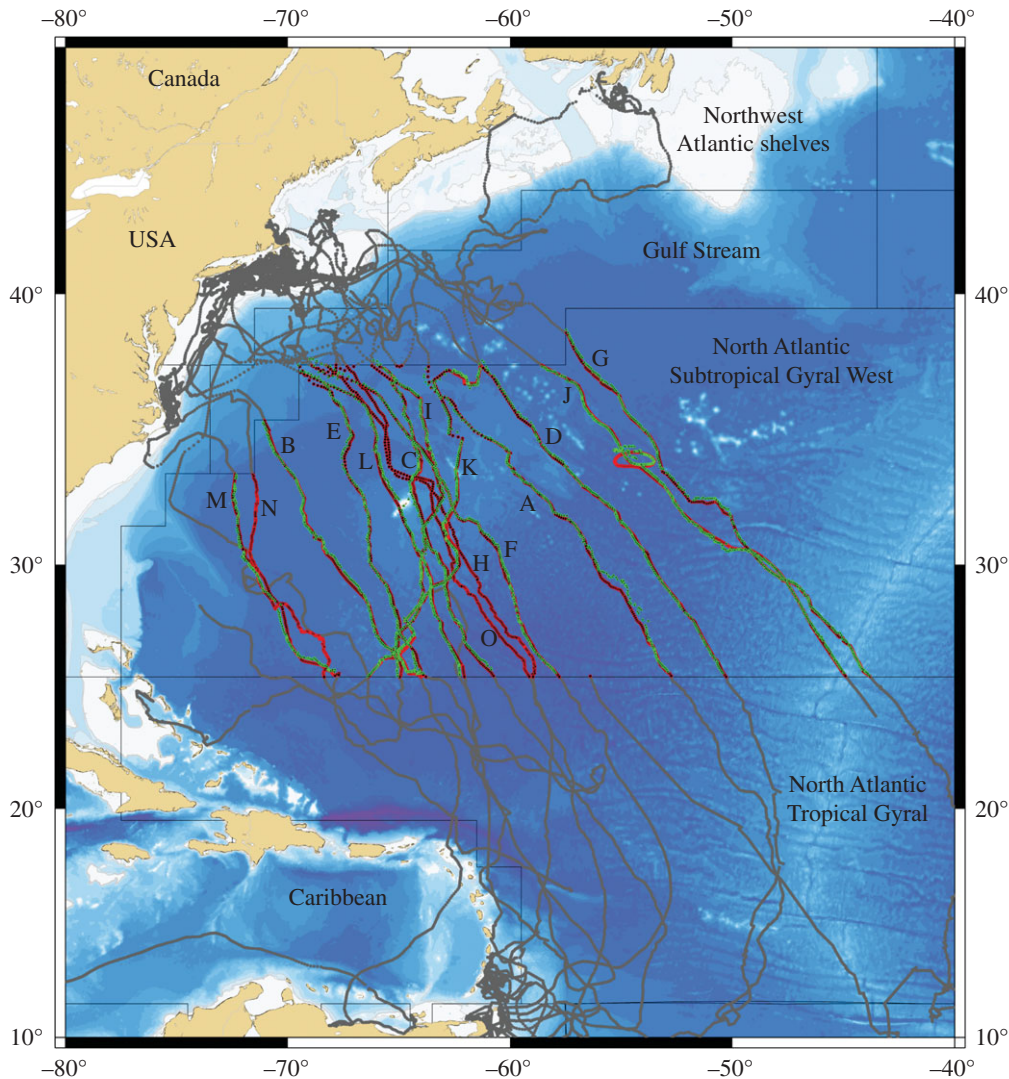
Fifteen turtles were tracked for sufficient duration to observe migration from temperate to tropical latitudes. Leatherback turtles travelled within the subtropical gyre for an average of 32 ( $\pm 11$ ) days, covering distances of 1105–2290 km (table 1). Adult leatherbacks had a higher average rate of travel (observed mean  $60 \text{ km d}^{-1}$ , s.d.  $8 \text{ km d}^{-1}$ ; current-corrected mean  $63 \text{ km d}^{-1}$ , s.d.  $9 \text{ km d}^{-1}$ ) than subadult leatherbacks (observed mean  $47 \text{ km d}^{-1}$ , s.d.  $10 \text{ km d}^{-1}$ ; current-corrected mean  $54 \text{ km d}^{-1}$ , s.d.  $8 \text{ km d}^{-1}$ ; table 1). Twelve track segments were successfully corrected for currents, whereas three track segments in 2009 could not be corrected owing to limited temporal coverage of the satellite-derived surface current products. There were negligible differences between the current-corrected and the observed turtle tracks in the subtropical gyre (figure 1), with most mean current-corrected turtle headings within  $1^\circ$  of observed mean turtle headings, but there was greater overall variability in current-corrected turtle headings (figure 2; electronic supplementary material, table S2).

Individual leatherback turtles were significantly oriented in the subtropical gyre with a grand mean heading of  $154^\circ$

**Table 1.** Summary data for 15 leatherback sea turtles equipped with satellite tags during the migratory period within the North Atlantic subtropical gyre. PTT, platform transmitter terminal; CCL, curved carapace length; S, subadult (<145 CCL); A, adult ( $\geq 145$  CCL); M, male; F, female; U, unknown sex; NASW, North Atlantic Subtropical Gyral West; n.a., not available.

turtle ID	PTT no.	latitude (start/end)	longitude (start/end)	CCL (cm)	age	sex	date entered NASW	time in NASW (days)	mean observed distance (km)	mean observed (corrected) travel rate (km d <sup>-1</sup> )
A	68364a	37.4/25.5	-63.7/-52.7	150	A	F	8 November 2008	26	1778	67 (74)
B	82052	35.5/25.5	-71.0/-63.8	162	A	F	4 November 2008	33	1480	45 (51)
C	76988	37.4/25.5	-65.9/-60.7	152	A	M	26 October 2008	29	1520	52 (55)
D	82051	37.5/25.5	-61.3/-50.3	153	A	M	21 October 2008	29	1718	60 (63)
E	76989	37.4/25.5	-69.5/-64.0	145	A	F	8 October 2008	23	1525	67 (70)
F	85538	37.4/25.5	-68.8/-57.8	154	A	M	8 November 2008	27	1778	67 (69)
G	82053	38.6/25.5	-57.5/-43.8	146	A	M	7 October 2008	37	2052	55 (57)
H	27579	37.5/25.5	-69.3/-59.0	155	A	M	17 November 2009	27	1728	64 (n.a.)
I	68370	37.5/25.5	-66.2/-65.0	138	S	U	6 January 2008	28	1540	55 (60)
J	76990	37.5/25.5	-58.6/-44.9	140	S	U	29 October 2008	64	2290	36 (43)
K	82055	37.5/25.5	-61.3/-66.4	134	S	U	16 October 2008	46	1911	42 (48)
L	85537	37.3/25.5	-69.4/-62.1	139	S	M	12 November 2008	28	1571	56 (62)
M	82054	33.5/25.5	-72.4/-67.7	140	S	U	2 December 2008	22	1105	50 (55)
N	82056	33.5/25.5	-71.6/-68.4	127	S	U	20 November 2009	36	1143	32 (n.a.)
O	82057	37.4/25.5	-67.3/-59.1	128	S	U	23 November 2009	30	1695	57 (n.a.)





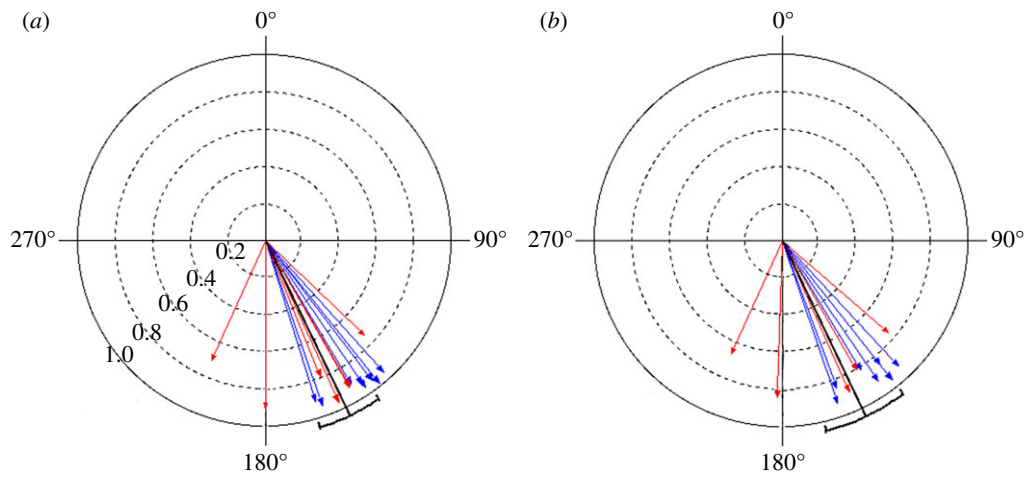
**Figure 1.** Locations from the reconstructed tracks of 15 satellite-tagged leatherback sea turtles in the western North Atlantic Ocean. Grey dots represent all track locations ( $n = 15$  turtles). Red dots represent observed locations ( $n = 15$  turtles) and green dots represent current-corrected locations ( $n = 12$  turtles) within the North Atlantic subtropical gyre during the southbound migration. The Longhurst [45] region boundaries are represented by thin black lines. Tags were deployed on adult females (A,B,E), adult males (C,D,F,G,H) and subadults (I,J,K,L,M,N,O).

(observed and current-corrected; figure 2; electronic supplementary material, table S3) for all turtles. When analysed by age class, adult and subadult leatherback groups were both significantly oriented, with a grand mean angle of  $148^\circ$  (adults, observed and current-corrected),  $161^\circ$  (subadults, observed) and  $163^\circ$  (subadults, current-corrected; figure 2; electronic supplementary material, table S3). Although adult leatherbacks maintained similar within-group headings and showed greater overall precision in orientation (figure 2; electronic supplementary material, table S2), adult and subadult distributions were not significantly different (Watson test,  $U^2 = 0.041$ ,  $p > 0.10$ ). The observed distributions of angles were highly concentrated for all turtles ( $r$ -values  $\geq 0.7$ ), with the highest concentrations in the adult group ( $r$ -values  $\geq 0.9$ ; figure 2; electronic supplementary material, table S2).

#### 4. Discussion

This study demonstrates that adult and subadult leatherback turtles can consistently maintain southward headings while travelling within the subtropical gyre. Migration between

feeding and breeding areas, over thousands of kilometres of open ocean, requires an ability to orient in the absence of topographic features, landmarks and other such cues that would be available in coastal regions. With the exception of the island platform of Bermuda, the western North Atlantic subtropical gyre is characterized by deep water where leatherbacks are unlikely to use topography to guide them. Weak ocean currents owing to light and variable winds, and lack of stationary reference points, make hydrodynamic cues improbable guidance mechanisms within the subtropical gyre interior (i.e. Sargasso Sea). Wind- or current-borne cues disperse rapidly over the long distances (more than 1000 km) recorded in our study and would be unlikely to keep leatherbacks on course (reviewed by Lohmann *et al.* [40]). Sea turtles' poor eyesight above water probably reduces the utility of celestial cues such as stars [40,51,52], although heightened visual acuity underwater may allow sea turtles to use visual cues subsurface [52–54]. Lacking bathymetric, hydrodynamic, celestial (star patterns) and chemosensory guidance, leatherbacks migrating through the subtropical gyre may orient to some aspect of the Earth's geomagnetic field (magnetic compass) and/or the position of the sun on the horizon (solar compass).



**Figure 2.** (a) Observed and (b) current-corrected headings of adult (blue) and subadult (red) leatherback turtles in the North Atlantic subtropical gyre. Each arrow indicates the mean vector length (ranging from 0 to 1) and mean vector angle of a single turtle. The thick black lines indicate the grand mean vectors and 95% CIs. Data are plotted relative to geographical north ( $0^\circ$  true). (a)  $n = 15$ ; (b)  $n = 12$ .

Sea turtles have been shown to use the Earth's magnetic field as a compass for holding a consistent heading [12–15]. In laboratory experiments, leatherback hatchlings were found to have a light-independent magnetic compass [55]. Existence of this compass in hatchlings suggests that subadult and adult leatherback turtles may also use a magnetic compass to maintain consistent headings while migrating within the subtropical gyre. Leatherback orientation in our study was consistent throughout the day and night, supporting the possibility of a light-independent magnetic compass like that found in hatchlings [55]. Evidence for a solar compass has also been found in sea turtles. For example, during controlled experiments where juvenile loggerheads were deprived of magnetic cues, the turtles were still able to orient with visual cues alone [36], and leatherbacks may also be able to interchangeably use magnetic and visual (e.g. solar) compasses. Other long-distance migrators, such as the sharp-tailed sand piper [56], may use both solar and magnetic orientation cues during their extensive migrations. Some birds [57,58] and bats [59] calibrate their magnetic compasses by the sun, specifically using sunrise/sunset for directional reference. It is feasible that leatherbacks also calibrate their magnetic compasses using sunrise/sunset cues to reduce orientation errors over their long-distance migration. James *et al.* [60] found that leatherbacks spent a greater proportion of time at and near the surface during the day during their southward migrations in the western North Atlantic, and we recorded the highest leatherback percentage surface (0–2 m) time (44%) during the day (12.00–18.00 GMT) in the subtropical gyre compared with other oceanographic regions [32]. Greater surface time during the day may be related to greater use of a solar compass for orientation [60,61].

It is surprising that adult leatherbacks failed to show greater precision in orientation than subadults since some adults presumably orient to specific beaches to breed and/or nest. Although not statistically different, the mean observed orientation angles of adult leatherbacks were more concentrated ( $r$ -value range: 0.89–0.98) than subadult leatherbacks ( $r$  value range: 0.70–0.95). Our statistical power would be improved by larger sample sizes for adults and subadults, and by verification of reproductive status that is inferred from age. Our age classification was based on curved carapace length, and leatherbacks show considerable variability in size

at first nesting [62], so it is possible that a proportion of the turtles classified as subadults were sexually mature.

Our tracks recorded the turtles' natural journeys through a dynamic ocean environment, so we can only speculate on the role of a magnetic and/or solar compass in helping leatherbacks maintain consistent headings in the gyre. We also cannot rule out the possibility of alternative perceptual cues that have yet to be discovered and were not considered in this study. Spatial memory (e.g. of geomagnetic field parameters) could be a potentially important influence on leatherback migratory movements, but memory-driven behaviours are difficult to distinguish from reactive sensory-driven movements during migration [63]. The remarkable consistency of individual leatherback headings over such a broad swath of ocean supports further investigation into the role of magnetic and/or solar orientation cues during open ocean migrations of leatherback sea turtles in the western North Atlantic Ocean.

**Ethics statement.** This work was conducted under the authority of the National Marine Fisheries Service Endangered Species Act Section 10 Permit no. 1557-03 and University of New Hampshire IACUC no. 060501 and no. 090402. Turtle disentanglement was conducted under the authority of NOAA 50 CFR Part 222.310.

**Data accessibility.** Data from this study are archived online using Satellite Tracking and Analysis Tool (STAT) from [www.seaturtle.org](http://www.seaturtle.org).

**Acknowledgements.** We thank A. Myers, C. Merigo, C. Innis, M. Dodge, G. Purmont, M. Leach, B. Sharp, S. Landry, M. Murphy, G. Tomasian, N. Frago, K. Sampson, R. Smolowitz, K. Hirokawa, J. Casey, S. Leach, J. Wilson and E. Eldredge for invaluable assistance in the field. We thank F. Royer for insightful discussions, advice and assistance with track reconstruction and current correction. We are grateful to B. Prescott and K. Dourdeville for timely leatherback sightings information in the southern New England region ([www.seaturtle-sightings.org](http://www.seaturtle-sightings.org)). Massachusetts Environmental Police, US Coast Guard and staff from Provincetown Centre for Coastal Studies and New England Aquarium provided logistical support. We thank M. Baumgartner, H. Haas and two anonymous reviewers for comments that greatly improved earlier drafts of this manuscript.

**Funding statement.** This work was supported by National Oceanic and Atmospheric Administration grant no. NA04NMF4550391 and National Fish and Wildlife Foundation grant no. 2008-0076-000 to M.E.L. Turtle disentanglement was supported by the Massachusetts Division of Marine Fisheries through the National Oceanic and Atmospheric Administration grant no. NA07NMF4720052. Additional funding was provided by the Cape Cod Commercial Hook Fishermen's Association. K.L.D. was supported by a UNH Marine Program Fellowship administered by the Large Pelagics Research Centre.

## References

- Carr AF. 1967 *So excellent a fish: a natural history of sea turtles*. Garden City, NY: The Natural History Press.
- Schmidt-Koenig K. 1975 *Migration and homing in animals*. Zoophysiology and ecology, vol. 6. New York, NY: Springer.
- Papi F, Liew HC, Luschi P, Chan EH. 1995 Long-range migratory travel of a green turtle tracked by satellite: evidence for navigational ability in the open ocean. *Mar. Biol.* **122**, 171–175. (doi:10.1007/BF00348929)
- Sale A, Luschi P. 2009 Navigational challenges in the oceanic migrations of leatherback sea turtles. *Proc. R. Soc. B* **276**, 3737–3745. (doi:10.1098/rspb.2009.0965)
- Carr AF, Ogren LH. 1959 The ecology and migrations of sea turtles, 3, *Dermodochelys* in Costa Rica. *Am. Mus. Novit.* **1958**, 1–29.
- Mrosovsky N, Shettleworth SJ. 1968 Wavelength preferences and brightness cues in the water finding behaviour of sea turtles. *Behaviour* **32**, 211–257. (doi:10.1163/156853968X00216)
- Salmon M, Wyneken J, Fritz E, Lucas M. 1992 Sea finding by hatchling sea turtles: role of brightness, silhouette, and beach slope as orientation cues. *Behaviour* **122**, 56–77. (doi:10.1163/156853992X00309)
- Salmon M, Lohmann KJ. 1989 Orientation cues used by hatchling loggerheads (*Caretta caretta*) during their offshore migration. *Ethology* **83**, 215–228. (doi:10.1111/j.1439-0310.1989.tb00530.x)
- Lohmann KJ, Salmon M, Wyneken J. 1990 Functional autonomy of land and sea orientation systems in sea turtle hatchlings. *Biol. Bull.* **179**, 214–218. (doi:10.2307/1541772)
- Lohmann KJ, Swartz AW, Lohmann CMF. 1995 Perception of wave direction by sea turtles. *J. Exp. Biol.* **198**, 1079–1085.
- Wyneken J, Salmon M, Lohmann KJ. 1990 Orientation by hatchling loggerhead sea turtles, *Caretta caretta*, in a wave tank. *J. Exp. Mar. Biol. Ecol.* **139**, 43–50. (doi:10.1016/0022-0981(90)90037-D)
- Light P, Salmon M, Lohmann KJ. 1993 Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. *J. Exp. Biol.* **182**, 1–10.
- Lohmann KJ, Lohmann CMF. 1994 Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *J. Exp. Biol.* **194**, 23–32.
- Lohmann KJ, Lohmann CMF. 1996 Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* **199**, 73–81.
- Goff M, Salmon M, Lohmann KJ. 1998 Hatchling sea turtles use surface waves to establish a magnetic compass direction. *Anim. Behav.* **55**, 69–77. (doi:10.1006/anbe.1997.0577)
- Guerra PA, Gegear RJ, Reppert SM. 2014 A magnetic compass aids monarch butterfly migration. *Nat. Commun.* **5**, 4164. (doi:10.1038/ncomms5164)
- Walker MM. 1984 Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*. *J. Comp. Physiol. A* **155**, 673–679. (doi:10.1007/BF00610853)
- Wiltschko W, Wiltschko R. 1996 Magnetic orientation in birds. *J. Exp. Biol.* **199**, 29–38. (doi:10.1016/0022-0981(95)00166-2)
- Quinn TP. 1980 Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *J. Comp. Physiol.* **137**, 243–248. (doi:10.1007/BF00657119)
- Lohmann KJ, Lohmann CMF. 1996 Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59–61. (doi:10.1038/380059a0)
- Lohmann KJ, Cain SD, Dodge SA, Lohmann CMF. 2001 Regional magnetic fields as navigational markers for sea turtles. *Science* **294**, 364–366. (doi:10.1126/science.1064557)
- Lohmann KJ, Lohmann CMF, Ehrhart LM, Bagley DA, Swing T. 2004 Animal behaviour: geomagnetic map used in sea-turtle navigation. *Nature* **428**, 909–910. (doi:10.1038/428909a)
- Luschi P, Benhamou S, Girard C, Ciccione S, Roos D, Sudre J, Benvenuti S. 2007 Marine turtles use geomagnetic cues during open-sea homing. *Curr. Biol.* **17**, 126–133. (doi:10.1016/j.cub.2006.11.062)
- Brothers JR, Lohmann KJ. 2015 Evidence for geomagnetic imprinting and magnetic navigation in the natal homing of sea turtles. *Curr. Biol.* **25**, 1–5. (doi:10.1016/j.cub.2014.12.035)
- Papi F, Luschi P, Akesson S, Capogrossi S, Hays GC. 2000 Open-sea migration of magnetically disturbed sea turtles. *J. Exp. Biol.* **203**, 3435–3443.
- Benhamou S, Sudre J, Bourjea J, Ciccione S, De Santis A, Luschi P. 2011 The role of geomagnetic cues in green sea turtle open sea navigation. *PLoS ONE* **6**, e26672. (doi:10.1371/journal.pone.0026672)
- Morreale SJ, Standora EA, Spotila JR, Paladino FV. 1996 Migration corridor for sea turtles. *Nature* **384**, 319–320. (doi:10.1038/384319a0)
- Shillinger GL *et al.* 2008 Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biol.* **6**, e171. (doi:10.1371/journal.pbio.0060171)
- Ferraro S, Georges JY, Gaspar P, Maho YL. 2004 Endangered species: where leatherback turtles meet fisheries. *Nature* **429**, 521–522. (doi:10.1038/429521a)
- Hays GC, Houghton JD, Myers AE. 2004 Pan-Atlantic leatherback turtle movements. *Nature* **429**, 522. (doi:10.1038/429522a)
- James MC, Ottensmeyer CA, Myers RA. 2005 Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol. Lett.* **8**, 195–201. (doi:10.1111/j.1461-0248.2004.00710.x)
- Dodge KL, Galuardi B, Miller TJ, Lutcavage ME. 2014 Leatherback turtle movements, dive behavior and habitat characteristics in ecoregions of the Northwest Atlantic Ocean. *PLoS ONE* **9**, e91726. (doi:10.1371/journal.pone.0091726)
- Olson DB, Hitchcock GL, Mariano AJ, Ashjian CJ, Peng G, Nero RW, Podesta GP. 1994 Life on the edge: marine life and fronts. *Oceanography* **7**, 52–59. (doi:10.5670/oceanog.1994.03)
- Lutcavage ME. 1996 Planning your next meal: leatherback travel routes and ocean fronts. In *Proc. 15th Ann. Symp. Sea Turtle Biology and Conservation* (eds JA Keinath, DE Barnard, JA Musick, BA Bell), p. 355. Washington, DC: National Oceanic and Atmospheric Administration.
- Rozhok AF. 2008 *Orientation and navigation in vertebrates*. Berlin, Germany: Springer.
- Avens L, Lohmann KJ. 2003 Use of multiple orientation cues by juvenile loggerhead sea turtles, *Caretta caretta*. *J. Exp. Biol.* **206**, 4317–4325. (doi:10.1242/jeb.00657)
- Luschi P, Sale A, Mencacci R, Hughes GR, Lutjeharms JRE, Papi F. 2003 Current transport of leatherback sea turtles (*Dermodochelys coriacea*) in the Ocean. *Proc. R. Soc. Lond. B* **270**, S129–S132. (doi:10.1098/rsbl.2003.0036)
- Hays GC, Åkesson S, Broderick AC, Glen F, Godley BJ, Papi F, Luschi P. 2003 Island-finding ability of marine turtles. *Proc. R. Soc. Lond. B* **270**, S5–S7. (doi:10.1098/rsbl.2003.0022)
- Endres CS, Lohmann KJ. 2013 Detection of coastal mud odors by loggerhead sea turtles: a possible mechanism for sensing nearby land. *Mar. Biol.* **160**, 2951–2956. (doi:10.1007/s00227-013-2285-6)
- Lohmann KJ, Lohmann CMF, Endres CS. 2008 The sensory ecology of ocean navigation. *J. Exp. Biol.* **211**, 1719–1728. (doi:10.1242/jeb.015792)
- Eckert SA. 2006 High-use oceanic areas for Atlantic leatherback sea turtles (*Dermodochelys coriacea*) as identified using satellite telemetered location and dive information. *Mar. Biol.* **149**, 1257–1267. (doi:10.1007/s00227-006-0262-z)
- James MC, Sherrill-Mix SA, Myers RA. 2007 Population characteristics and seasonal migrations of leatherback sea turtles at high latitudes. *Mar. Ecol. Prog. Ser.* **337**, 245–254. (doi:10.3354/meps337245)
- Bryant E. 2007 *2D location accuracy statistics for Fastloc® cores running firmware versions 2.2 and 2.3*. Technical Report TR01. Leeds, UK: Wildtrack Telemetry Systems. See [http://www.wildtracker.com/results\\_files/Technical%20Report%20TR01.pdf](http://www.wildtracker.com/results_files/Technical%20Report%20TR01.pdf).
- Royer F, Lutcavage M. 2008 Filtering and interpreting location errors in satellite telemetry of marine animals. *J. Exp. Mar. Biol. Ecol.* **359**, 1–10. (doi:10.1016/j.jembe.2008.01.026)
- Longhurst AR. 2007 *Ecological geography of the sea*, 2nd edn. Burlington, MA: Academic Press.
- Gaspar P, Georges J, Fossette S, Lenoble A, Ferraroli S, LeMaho Y. 2006 Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proc. R. Soc. B* **273**, 2697–2702. (doi:10.1098/rspb.2006.3623)



47. Fossette S, Putman NF, Lohmann KJ, Marsh R, Hays GC. 2012 A biologist's guide to assessing ocean currents: a review. *Mar. Ecol. Prog. Ser.* **457**, 285–301. (doi:10.3354/meps09581)
48. R Development Core Team. 2013 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
49. Mardia KV. 1972 *Statistics of directional data*. London, UK: Academic Press.
50. Batschelet E. 1981 *Circular statistics in biology*. New York, NY: Academic Press.
51. Ehrenfeld DW, Koch AL. 1967 Visual accommodation in the green turtle. *Science* **155**, 827–828. (doi:10.1126/science.155.3764.827)
52. Bartol SM, Musick JA, Ochs AL. 2002 Visual acuity thresholds of juvenile loggerhead sea turtles (*Caretta caretta*): an electrophysiological approach. *J. Comp. Phys. A* **187**, 953–960. (doi:10.1007/s00359-001-0262-x)
53. Bartol SM, Mellgren RL, Musick JA. 2003 Visual acuity of juvenile loggerhead sea turtles (*Caretta caretta*): a behavioral approach. *Int. J. Comp. Psychol.* **16**, 143–155.
54. Fritsches KE, Warrant EJ. 2013 Vision. In *The biology of sea turtles volume III* (eds J Wyneken, JA Musick, KJ Lohmann), pp. 31–58. Boca Raton, FL: CRC Press.
55. Lohmann KJ, Lohmann CMF. 1993 A light-independent magnetic compass in the leatherback sea turtle. *Biol. Bull.* **185**, 149–151. (doi:10.2307/1542138)
56. Grönroos J, Muheim R, Åkesson S. 2010 Orientation and autumn migration routes of juvenile sharp-tailed sandpipers at a staging site in Alaska. *J. Exp. Biol.* **213**, 1829–1835. (doi:10.1242/jeb.040121)
57. Cochran WW, Mouritsen H, Wikelsi M. 2004 Migratory songbirds recalibrate their magnetic compass daily from twilight cues. *Science* **304**, 405–408. (doi:10.1126/science.1095844)
58. Muheim R, Phillips JB, Åkesson S. 2006 Polarized light cues underlie compass calibration in migratory songbirds. *Science* **313**, 837–839. (doi:10.1126/science.1129709)
59. Holland RA, Borissov I, Siemers B. 2010 A nocturnal mammal, the greater mouse-eared bat, calibrates a magnetic compass by the sun. *Proc. Natl Acad. Sci. USA* **107**, 6941–6945. (doi:10.1073/pnas.0912477107)
60. James MC, Ottensmeyer CA, Eckert SA, Myers RA. 2006 Changes in diel diving patterns accompany shifts between northern foraging and southward migration in leatherback turtles. *Can. J. Zool.* **84**, 754–765. (doi:10.1139/z06-046)
61. Eckert SA. 2002 Swim speed and movement patterns of gravid leatherback sea turtles (*Dermochelys coriacea*) at St. Croix, US Virgin Islands. *J. Exp. Biol.* **205**, 3689–3697.
62. Stewart K, Johnson C, Godfrey MH. 2007 The minimum size of leatherbacks at reproductive maturity, with a review of sizes for nesting females from the Indian, Atlantic and Pacific Ocean basins. *Herp. J.* **17**, 123–128.
63. Fagan WF *et al.* 2013 Spatial memory and animal movement. *Ecol. Lett.* **16**, 1316–1329. (doi:10.1111/ele.12165)