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Straight as an arrow: humpback whales swim constant course tracks during long-distance migration

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Humpback whale seasonal migrations, spanning greater than 6500 km of open ocean, demonstrate remarkable navigational precision despite following spatially and temporally distinct migration routes. Satellite-monitored radio tag-derived humpback whale migration tracks in both the South Atlantic and South Pacific include constant course segments of greater than 200 km, each spanning several days of continuous movement. The whales studied here maintain these directed movements, often with better than 1° precision, despite the effects of variable sea-surface currents. Such remarkable directional precision is difficult to explain by established models of directional orientation, suggesting that alternative compass mechanisms should be explored.

Keywords: humpback whales; navigation; constant course; migration; sea-surface currents

1. INTRODUCTION

With one-way lengths that can exceed 8000 km, the seasonal migrations of humpback whales (*Megaptera novaeangliae*) are the longest known for any mammal [1,2]. These movements, across vast areas of open ocean, occur despite a high degree of fidelity between winter calving and summer feeding grounds in many populations [3,4]. Widespread application of modern animal tracking technologies has expanded our knowledge of humpback whale migration routes, destinations and travelling speeds [5,6]. However, the mechanisms by which humpback whales navigate during these remarkable long-distance migrations remain unknown.

There are two main theoretical frameworks explaining orientation and navigation during migration, commonly referred to as 'map and compass' [7] and 'clock and compass' [8] models. Over the past 60 years, significant experimental research has identified two sources of directional (i.e. 'compass') information used by animals: the Earth's main magnetic field and the position of the Sun. However, most of these experiments were performed on birds, with limited investigation of directional orientation in obligate marine animals. The lack of knowledge largely reflects the difficulty of studying animals that make extensive ocean-basin scale movements. The situation is now partially remedied by the relatively new capacity to track whales with satellite-linked telemetry devices [5,6,9].

Animal tracking research demonstrates that diverse taxa can maintain constant courses, suggesting that precise directional orientation is a common feature of marine animal migration [10–12]. Here, we present satellite tag-derived location data for 16 humpback whales migrating away from low-latitude coastal habitats in the South Atlantic and South Pacific Oceans between 2003 and 2010. The only three whales tracked to high-latitude feeding grounds ended their migrations within approximately 100 km of 58° S, 23° W despite migrating in different months of different years along distinctly different migration routes.

All tracks included constant course segments of greater than 200 km distance spanning several days of continuous movement (table 1). The whales studied here maintained these directed movements, the majority with better than 1° precision, despite the effects of variable sea-surface currents, weather events, magnetic field parameters and positions of the Sun. Our results demonstrate that migrating humpback whales can affect precise, continually updated, directional orientation that is difficult to reconcile with known compass mechanisms.

2. MATERIAL AND METHODS

Whale locations were remotely sensed using polar-orbiting operational environmental satellites (POESs) between 2003 and 2010. Wildlife Computer SPOT3, SPOT4 and SPOT5 satellite transmitters were configured into deployable implantable tags attached to individual whales from inflatable boats using a fibreglass pole [5,9]. Whale position data were obtained using the Argos data collection system, and data quality was evaluated using published procedures [5,9]. Whale locations include both high accuracy (types 1, 2, 3) and undefined accuracy locations (types 0, A, B) [13]. We performed piecewise linear regression on both high accuracy locations and all locations to quantify the directionality of whale movements.

Astronomical algorithms [14] were used to calculate Greenwich Mean Sidereal Time, azimuth of the Sun at sunrise and sunset (i.e. Sun altitude $= -0.8333°$), and altitude of Sun transit, for all whale positions. Geomagnetic field properties were calculated using the 11th generation of the International Geomagnetic Reference Field model (IGRF-11) available through the National Geophysical Data Center (NGDC) of the US Department of Commerce's National Oceanographic and Atmospheric Administration (NOAA) website [15].

3. RESULTS AND DISCUSSION

The most salient spatial pattern common to each of these migration tracks is the presence of long-distance constant course track segments (figure 1). Piecewise linear regression, performed separately on both

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Table 1. Spatial and temporal data corresponding with the lettered migration track segments presented in figure 1. The square of Pearson's correlation coefficient r^2 is found by least-squares linear regression performed on Mercator easting versus northing values. 'All' and 'high' correspond with the satellite monitored location quality. Whale headings, and 95% confidence intervals, were calculated using all location data.

segment	tag	latitude (start/end)	longitude (start/end)	duration (days)	distance (km)	average velocity (km h^{-1})	no. locations (all/high)	r^2 (all/high)	heading (±95% CI)	per cent track distance (total)
A	21 810.03	−19.6/−23.3	−39.3/−41.8	7	600	3.1	19/7	0.988/0.989	211.5 (1.5)	13.9 (13.9)
B	24 642.03	−20.7/−26.7	−39.6/−37.3	8	709	3.7	22/8	0.991/0.992	161.2 (0.87)	18.2
C	24 642.03	−26.7/−31.8	−37.3/−39.1	8	766	4.0	18/12	0.989/0.992	197.3 (1.0)	19.6
D	24 642.03	−33.4/−52.5	−39.2/−30.6	28	2232	3.3	107/61	0.985/0.987	162.1 (0.40)	57.1 (94.9)
E	10 946.05	−35.0/−52.2	−33.0/−28.3	25	1898	3.2	44/12	0.960/0.964	172.1 (0.84)	40.8
F	10 946.05	−20.1/−28.1	−37.8/−35.6	10	919	3.8	23/1	0.985/n.d.	166.4 (0.84)	19.8 (60.6)
G	87 760.08	−34.0/−37.6	−38.2/−32.9	7	624	3.8	34/9	0.993/0.995	131.1 (0.79)	17.2 (17.2)
H	87 773.08	−30.1/−39.9	−40.6/−36.6	12	1151	4.0	85/16	0.994/0.998	162.9 (0.34)	40.5 (40.5)
I	87 771.09	−22.2/−29.0	−37.5/−35.9	6	773	5.7	35/10	0.981/0.983	167.1 (0.62)	17.6
J	87 771.09	−32.5/−41.6	−36.2/−32.0	8	1071	4.5	63/17	0.992/0.991	159.7 (0.39)	24.4
K	87 771.09	−43.3/−49.4	−31.0/−26.4	8	771	4.3	56/5	0.996/0.999	151.4 (0.43)	17.5 (59.5)
L	87 783.09	−15.3/−31.6	−36.2/−23.7	18	2205	5.2	92/20	0.996/0.998	144.4 (0.35)	33.8
M	87 783.09	−33.9/−39.8	−22.9/−16.8	13	844	2.8	46/9	0.990/0.997	137.7 (0.89)	12.9 (46.7)
N	27 259.07	−32.5/−34.4	168.1/172.4	5	496	3.8	19/2	0.981/1.0	112.4 (1.4)	15.7
O	27 259.07	−34.4/−37.4	173.0/176.8	8	545	3.0	25/5	0.989/0.946	127.4 (1.3)	17.3 (33.0)
P	33 001.07	−22.8/−24.7	167.7/168.7	3	239	3.5	9/5	0.978/0.984	151.8 (3.2)	25.6
Q	33 001.07	−24.8/−28.1	168.8/173.0	7	578	3.5	17/3	0.983/0.994	129.0 (2.0)	62.0 (87.6)
R	37 229.07	−24.0/−26.9	169.6/171.3	3	370	6.0	13/5	0.982/1.0	150.2 (2.2)	17.2

S	37 229.07	−27.3/−32.1	171.7/174.0	5	599	5.0	21/10	0.996/0.998	155.1 (0.62)	27.8
T	37 229.07	−33.0/−34.1	176.8/179.9	4	320	3.8	6/2	0.950/1.0	106.4 (5.0)	14.8 (59.8)
U	27 262.07	−21.2/−19.7	−160.1/−162.5	2	296	6.3	11/6	0.982/0.990	299.8 (2.7)	36.0
V	27 262.07	−19.4/−18.0	−163.6/−165.7	2	273	4.8	10/2	0.993/1.0	303.5 (2.2)	33.2 (69.2)
W	37 232.07	−21.2/−21.8	−159.8/−163.2	4	368	3.6	14/7	0.943/0.956	259.8 (1.7)	38.0 (38.0)
X	37 233.07	−21.4/−21	−164.9/−168.2	3	338	4.5	16/10	0.979/0.970	277.3 (0.67)	29.7 (29.7)
Y	37 234.07	−21.2/−17.6	−160.2/−169.6	7	1075	6.5	30/13	0.998/0.996	291.1 (0.30)	66.6 (66.6)
Z	37 277.07	−21.1/−19.7	−160.1/−162.5	2	294	6.2	8/5	0.984/0.987	300.8 (4.5)	79.6 (79.6)
a	37 282.07	−20.1/−17.7	−163.3/−165.0	3	365	4.7	17/4	0.982/0.989	325.2 (2.2)	18.9
b	37 282.07	−17.5/−14.9	−166.0/−170.6	7	676	4.2	22/10	0.998/0.996	296.7 (0.54)	35.0 (53.9)

high-accuracy locations and all locations, identified several track segments exhibiting strong correlations between Mercator easting and northing ($r^2 > 0.95$; table 1 and figure 1). All of these segments required maintenance of constant course movements with better than 5° directional precision at the 95% confidence level (CI), regardless of location quality, and better than 1° precision for 15 of the 28 segments identified in our analysis of all track locations (table 1). Our results indicate that humpback whales, tagged in three distinct areas, navigate with extreme directional precision across wide expanses of open ocean (240–2230 km range) over time periods of between 2 and 28 days. These constant course track segments constitute between 14 and 95 per cent of total individual track distances, and greater than 50 per cent of the distance travelled in nine of 16 tracks (table 1), indicating long-distance constant course movement is a typical feature of humpback whale migration.

To evaluate the effects of sea-surface currents on these highly directional track segments, we determined the sea-surface current direction and velocity, at the time and location of the whales studied, from Argo drifter-buoy coordinate data [16,17]. These currents deflected whale headings, but not their tracks, by as little as less than 1° and as much as 25°. Maintenance of constant courses, despite these highly variable sea-surface currents, indicates that humpback whales compensate for passive displacement, presumably by minimizing the period of path integration between sequential orientation steps. Constant course track segments also spanned diverse ocean bathymetries (figure 1) and weather events, including the rare occurrence of a tropical storm off the coast of Brazil (in January 2004).

The temporal and spatial variability between the whales' migrations provide crucial insight into how they navigated. The constant course track segments shown here spanned a wide range of latitudes and time periods (figure 1). Hence, the position of the Sun at sunrise, transit and sunset differed by several degrees azimuth (*ca* 1–10°) or altitude (*ca* 3–26°) within and between individual track segments. Our analysis further indicates that whales from each area can both follow similar headings, despite experiencing different Sun positions and follow different headings despite experiencing similar positions of the Sun (figure 2). Such variation suggests that, if the Sun was used for directional orientation purposes by these whales, its location must have been transduced relative to a moving reference datum. Thus, Sun–compass orientation, in isolation, cannot explain the directional precision exhibited by these whales.

The position of the magnetic field also varies widely across individual constant course segments. Magnetic inclination varies by as much as 22°, and as little as 1°, across individual segments (figures 1 and 2). Despite experiencing similar local magnetic inclinations at low-latitude tagging areas, whales depart from these coastal waters along highly variable constant course headings (figures 1 and 2). The lack of any systematic relationship between magnetic inclination and constant course whale headings suggests that these whales did not navigate by using only a simple magnetic inclination compass.

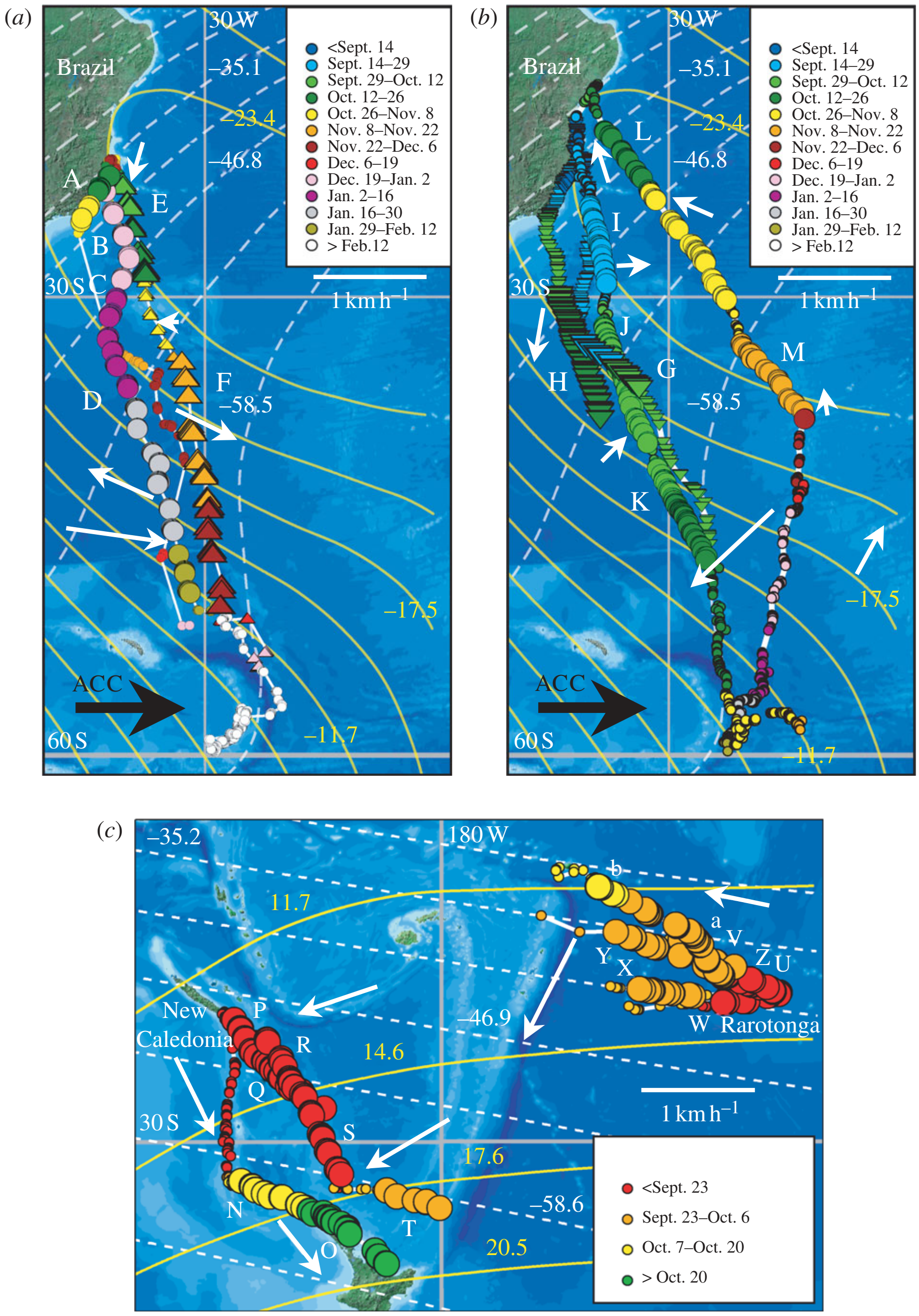

Figure 1. Satellite tag-derived southward migration track maps for seven South Atlantic humpback whales tagged off the coast of Brazil in (*a*) 2003 (circles) and 2005 (triangles), (*b*) 2008 (inverted triangles) and 2009 (circles) and nine South Pacific humpback whales and (*c*) tagged off the coasts of Rarotonga, Cook Islands and New Caledonia in 2007 (circles). Constant course track segments are indicated by the larger symbols. Segment labels (A–b) correspond with table 1. White arrows represent sea-surface current vectors with velocities proportional to the white 1 km h^{-1} scale bar shown. The generalized position and direction of the approximately 1 km h^{-1} Antarctic circum-polar current (ACC) are shown by the black arrow in (*a*) and (*b*). Magnetic declination isogonics (yellow lines) and magnetic inclination isoclinics (white dashed lines) as of 1 January 2005 are shown for reference.

Similarly, magnetic declination varies by as much as 12°, and as little as 0.5°, across individual constant course segments. As was the case for magnetic inclination, individual whales departed from low-latitude habitats along distinctly different headings despite experiencing similar magnetic declination values (figures 1 and 2). This difference is even more pronounced between areas. Whales migrating away from Rarotonga followed westerly to north-westerly headings, whereas whales migrating away from New Caledonia followed southerly to south-easterly headings despite the less than 1° difference in magnetic declination between the two areas (figure 2). Maintenance of constant courses despite the whales experiencing variable magnetic declination values, and individual movements along distinct course directions despite their experiencing similar magnetic declination values, suggest that magnetic declination was not the sole source of directional information used by these whales. Alternatively, individual whales could use spatial information derived from the magnetic field to inform their movements in different

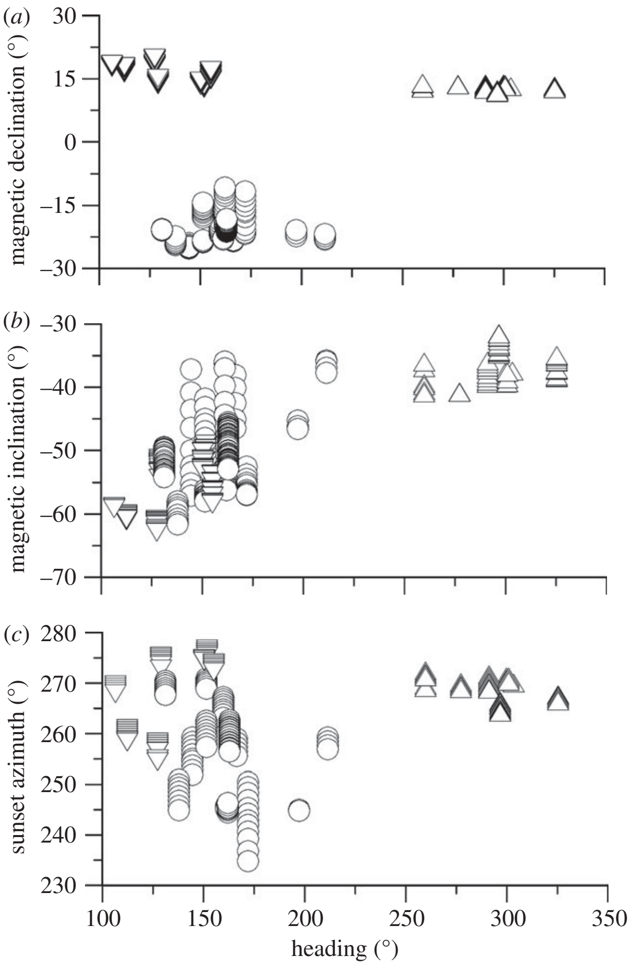

Figure 2. (*a*) Magnetic declination, (*b*) magnetic inclination, and (*c*) sunset azimuth plotted against constant course segment heading for each of the three low-latitude tagging areas studied. Magnetic coordinates and Sun azimuths were calculated at the time and location of individual whales using the methods described in the text. Circles, Brazil; triangles, Rarotonga; inverted triangles, New Caledonia.

ways; thus, the lack of any systematic relationship between whale headings and magnetic declination and inclination values does not conclusively indicate that humpback whale movements are not informed by spatial information derived from the magnetic field.

4. CONCLUSION

Here, we offer several insights into humpback whale migratory orientation. First, humpback whales commonly follow highly directional headings with extreme precision over large expanses of open ocean, despite the effects of sea-surface currents, bathymetry and weather. Second, constant course oceanic movements require correction for passive displacement using an exogenous spatial reference frame and orientation cues. Third, although our findings suggest that humpback whale navigation is compatible with 'goal orientation' using a map and compass system, it seems unlikely that individual magnetic and solar orientation cues can, in isolation, explain the extreme navigational precision achieved by humpback whales. The relatively slow movements of humpback whales, combined with their clear ability to navigate with extreme precision over long distances, present outstanding opportunities to explore alternative mechanisms of migratory orientation based on empirical analysis of track data.

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