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

Travis W. Horton, Richard N. Holdaway, Alexandre N. Zerbini, Nan Hauser, Claire Garrigue, Artur Andriolo and Phillip J. Clapham

Biol. Lett., published online 20 April 2011

References

This article cites 13 articles, 3 of which can be accessed free
http://rsbl.royalsocietypublishing.org/content/early/2011/04/14/rsbl.2011.0279.full.html
#ref-list-1

P<sup>P</sup>

Articles online 20 April 2011 in advance of the print journal.

Subject collections

Articles on similar topics can be found in the following collections

- behaviour (1967 articles)
- ecology (2332 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click here

Advance online articles have been peer reviewed and accepted for publication but have not yet appeared in the paper journal (edited, typeset versions may be posted when available prior to final publication). Advance online articles are citable and establish publication priority; they are indexed by PubMed from initial publication. Citations to Advance online articles must include the digital object identifier (DOIs) and date of initial publication.

To subscribe to Biol. Lett. go to: http://rsbl.royalsocietypublishing.org/subscriptions

This journal is © 2011 The Royal Society
Straight as an arrow: humpback whales swim constant course tracks during long-distance migration

Travis W. Horton1,*, Richard N. Holdaway1,2,3, Alexandre N. Zerbini1,4,5,6, Nan Hauser7,8,9, Claire Garrigue7,9, Artur Andriolo7,10 and Phillip J. Clapham6

1Geological Sciences, and 2Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand
2Palaeoloc Research Ltd., 167 Springs Road, Christchurch 8042, New Zealand
3US National Marine Mammal Laboratory, Alaska Fisheries Science Center, Seattle, WA 98115, USA
4Instituto Aquatico, Proyecto Monitoreo de Baleia por Satelite, Río de Janiero, Brazil
5Cascadia Research Collective, Olympia, WA 98501, USA
6South Pacific Whale Research Consortium, PO Box 3069, Avarua, Rarotonga, Cook Islands
7Cook Islands Whale Research Centre, Rarotonga, Cook Islands
8Operation Cetaceas, BP 12827, 98802 Noumea, New Caledonia
9Departamento de Zoologia, ICB Universidade Federal de Juiz de Fora, Juiz de Fora, Minas Gerais, Brazil
10Author for correspondence (travis.horton@canterbury.ac.nz).

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 maintained 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 $s = -0.8333$), 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
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.

<table>
<thead>
<tr>
<th>segment</th>
<th>tag</th>
<th>latitude (start/end)</th>
<th>longitude (start/end)</th>
<th>duration (days)</th>
<th>distance (km)</th>
<th>average velocity (km h(^{-1}))</th>
<th>no. locations (all/high)</th>
<th>( r^2 ) (all/high)</th>
<th>heading (±95% CI)</th>
<th>per cent track distance (total)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>21810.03</td>
<td>-19.6/-23.3</td>
<td>-39.3/-41.8</td>
<td>7</td>
<td>600</td>
<td>3.1</td>
<td>19/7</td>
<td>0.988/0.989</td>
<td>211.5 (1.5)</td>
<td>13.9 (13.9)</td>
</tr>
<tr>
<td>B</td>
<td>24642.03</td>
<td>-20.7/-26.7</td>
<td>-39.6/-37.3</td>
<td>8</td>
<td>709</td>
<td>3.7</td>
<td>22/8</td>
<td>0.991/0.992</td>
<td>161.2 (0.87)</td>
<td>18.2</td>
</tr>
<tr>
<td>C</td>
<td>24642.03</td>
<td>-26.7/-31.8</td>
<td>-37.3/-39.1</td>
<td>8</td>
<td>766</td>
<td>4.0</td>
<td>18/12</td>
<td>0.989/0.992</td>
<td>197.3 (1.0)</td>
<td>19.6</td>
</tr>
<tr>
<td>D</td>
<td>24642.03</td>
<td>-33.4/-52.5</td>
<td>-39.2/-30.6</td>
<td>28</td>
<td>2232</td>
<td>3.3</td>
<td>107/61</td>
<td>0.985/0.987</td>
<td>162.1 (0.40)</td>
<td>57.1 (94.9)</td>
</tr>
<tr>
<td>E</td>
<td>10946.05</td>
<td>-35.0/-52.2</td>
<td>-33.0/-28.3</td>
<td>25</td>
<td>1898</td>
<td>3.2</td>
<td>44/12</td>
<td>0.960/0.964</td>
<td>172.1 (0.84)</td>
<td>40.8</td>
</tr>
<tr>
<td>F</td>
<td>10946.05</td>
<td>-20.1/-28.1</td>
<td>-37.8/-35.6</td>
<td>10</td>
<td>919</td>
<td>3.8</td>
<td>23/1</td>
<td>0.985/0.985</td>
<td>166.4 (0.84)</td>
<td>19.8 (60.6)</td>
</tr>
<tr>
<td>G</td>
<td>87760.08</td>
<td>-34.0/-37.6</td>
<td>-38.2/-32.9</td>
<td>7</td>
<td>624</td>
<td>3.8</td>
<td>34/9</td>
<td>0.993/0.995</td>
<td>131.1 (0.79)</td>
<td>17.2 (17.2)</td>
</tr>
<tr>
<td>H</td>
<td>87773.08</td>
<td>-30.1/-39.9</td>
<td>-40.6/-36.6</td>
<td>12</td>
<td>1151</td>
<td>4.0</td>
<td>85/16</td>
<td>0.994/0.998</td>
<td>162.9 (0.34)</td>
<td>40.5 (40.5)</td>
</tr>
<tr>
<td>I</td>
<td>87771.09</td>
<td>-22.2/-29.0</td>
<td>-37.5/-35.9</td>
<td>6</td>
<td>773</td>
<td>5.7</td>
<td>35/10</td>
<td>0.981/0.983</td>
<td>167.1 (0.62)</td>
<td>17.6</td>
</tr>
<tr>
<td>J</td>
<td>87771.09</td>
<td>-32.5/-41.6</td>
<td>-36.2/-32.0</td>
<td>8</td>
<td>1071</td>
<td>4.5</td>
<td>63/17</td>
<td>0.992/0.991</td>
<td>159.7 (0.39)</td>
<td>24.4</td>
</tr>
<tr>
<td>K</td>
<td>87771.09</td>
<td>-43.3/-49.4</td>
<td>-31.0/-26.4</td>
<td>8</td>
<td>771</td>
<td>4.3</td>
<td>56/5</td>
<td>0.996/0.999</td>
<td>151.4 (0.43)</td>
<td>17.5 (59.5)</td>
</tr>
<tr>
<td>L</td>
<td>87783.09</td>
<td>-15.3/-31.6</td>
<td>-36.2/-23.7</td>
<td>18</td>
<td>2205</td>
<td>5.2</td>
<td>92/20</td>
<td>0.996/0.998</td>
<td>144.4 (0.35)</td>
<td>33.8</td>
</tr>
<tr>
<td>M</td>
<td>87783.09</td>
<td>-33.9/-39.8</td>
<td>-22.9/-16.8</td>
<td>13</td>
<td>844</td>
<td>2.8</td>
<td>46/9</td>
<td>0.990/0.997</td>
<td>137.7 (0.89)</td>
<td>12.9 (46.7)</td>
</tr>
<tr>
<td>N</td>
<td>27259.07</td>
<td>-32.5/-34.4</td>
<td>168.1/172.4</td>
<td>5</td>
<td>496</td>
<td>3.8</td>
<td>19/2</td>
<td>0.981/1.0</td>
<td>112.4 (1.4)</td>
<td>15.7</td>
</tr>
<tr>
<td>O</td>
<td>27259.07</td>
<td>-34.4/-37.4</td>
<td>173.0/176.8</td>
<td>8</td>
<td>545</td>
<td>3.0</td>
<td>25/5</td>
<td>0.989/0.946</td>
<td>127.4 (1.3)</td>
<td>17.3 (33.0)</td>
</tr>
<tr>
<td>P</td>
<td>33001.07</td>
<td>-22.8/-24.7</td>
<td>167.7/168.7</td>
<td>3</td>
<td>239</td>
<td>3.5</td>
<td>9/5</td>
<td>0.978/0.984</td>
<td>151.8 (3.2)</td>
<td>25.6</td>
</tr>
<tr>
<td>Q</td>
<td>33001.07</td>
<td>-24.8/-28.1</td>
<td>168.8/173.0</td>
<td>7</td>
<td>578</td>
<td>3.5</td>
<td>17/3</td>
<td>0.983/0.994</td>
<td>129.0 (2.0)</td>
<td>62.0 (87.6)</td>
</tr>
<tr>
<td>R</td>
<td>37229.07</td>
<td>-24.0/-26.9</td>
<td>169.6/171.3</td>
<td>3</td>
<td>370</td>
<td>6.0</td>
<td>13/5</td>
<td>0.982/1.0</td>
<td>150.2 (2.2)</td>
<td>17.2</td>
</tr>
</tbody>
</table>
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 \( (ca \pm 10°) \) or altitude \( (ca \pm 3°–26°) \) 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.
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 areas.
Constant course navigation by whales  T. W. Horton et al.  5

Humpback whale tagging in Brazil was funded and supported by: Exploration and Production Division of Shell Brazil SA; Biodynamica Engenharia e Meto Ambientes (Brazil); National Marine Mammal Laboratory (USA); Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington (USA). Tagging was conducted under permits issued by the Brazilian Council for Scientific and Technological Development (CNPq permit CMC 026/02, 028/03) and the Brazilian Environmental Agency (IBAMA permit 009/02/CMA/IBAMA, process no. 02001.000085/02-27). Sea-surface current data were collected and made freely available by the International Argo Project and the national programmes that contribute to it. Tagging in the Cook Islands and in New Caledonia was supported in part by Greenpeace International, as part of a programme of non-lethal research on Southern Ocean whales. Tagging was conducted under permit delivered by Province Sud of New Caledonia (1146-07/PSS).

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.


16 Argo. Available from http://www.argo.ucsd.edu