

## RESEARCH ARTICLE

### Underwater and surface behavior of homing juvenile northern elephant seals

Moe Matsumura<sup>1,\*</sup>, Yuuki Y. Watanabe<sup>2</sup>, Patrick W. Robinson<sup>3</sup>, Patrick J. O. Miller<sup>4</sup>, Daniel P. Costa<sup>3</sup> and Nobuyuki Miyazaki<sup>5</sup>

<sup>1</sup>Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5, Kashiwanoha, Kashiwa-shi, Chiba, 277-8568 Japan, <sup>2</sup>National Institute of Polar Research, 10-3, Midoricho, Tachikawa Tokyo 190-8518 Japan, <sup>3</sup>Long Marine Laboratory, Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA, <sup>4</sup>Sea Mammal Research Unit, Scottish Oceans Institute, University of Saint Andrews, Saint Andrews, Fife, KY16 8LB, UK and <sup>5</sup>Ocean Policy Research Foundation, Kaiyosenpaku Building, 1-15-16, Toranomon, Minato-ku, Tokyo, 105-0001 Japan

\*Author for correspondence (mmmoee@hotmail.com)

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#### SUMMARY

Northern elephant seals, *Mirounga angustirostris*, travel between colonies along the west coast of North America and foraging areas in the North Pacific. They also have the ability to return to their home colony after being experimentally translocated. However, the mechanisms of this navigation are not known. Visual information could serve an important role in navigation, either primary or supplementary. We examined the role of visual cues in elephant seal navigation by translocating three seals and recording their heading direction continuously using GPS, and acceleration and geomagnetic data loggers while they returned to the colony. The seals first reached the coast and then proceeded to the colony by swimming along the coast. While underwater the animals exhibited a horizontally straight course (mean net-to-gross displacement ratio=0.94±0.02). In contrast, while at the surface they changed their headings up to 360 deg. These results are consistent with the use of visual cues for navigation to the colony. The seals may visually orient by using landmarks as they swim along the coast. We further assessed whether the seals could maintain a consistent heading while underwater during drift dives where one might expect that passive spiraling during drift dives could cause disorientation. However, seals were able to maintain the initial course heading even while underwater during drift dives where there was spiral motion (to within 20 deg). This behavior may imply the use of non-visual cues such as acoustic signals or magnetic fields for underwater orientation.

Key words: data logger, 3-D dive, orientation, navigation, migration.

#### INTRODUCTION

Northern elephant seals, *Mirounga angustirostris* Gill 1866, spend most of their time at sea, and come ashore to breed and molt (Le Boeuf and Laws, 1994). Adult female seals from colonies in California and Mexico swim to offshore foraging areas in the North Pacific and the Gulf of Alaska (typically >4500 km away) twice per year and exhibit strong philopatry (Le Boeuf, 1994; Le Boeuf et al., 2000; Simmons et al., 2007). There are 15 major colonies along the west coast of North America, requiring them to find the correct colony among these sites at the end of their long migration. Elephant seals also return to their own colony after being experimentally translocated about 100 km. The return rate is nearly 90%, and they often follow direct routes home (Le Boeuf, 1994; Oliver et al., 1998). However, it remains unknown how they guide themselves back to the colony.

Elephant seals dive nearly continuously during transit to the home colony and spend most of their time submerged well below the surface. Five to 10% of dives are 'drift dives', in which the seal flips over and sinks in a spiral manner. The period of spiraling motion is generally known as the drift phase ('falling-leaf' phase) (Crocker et al., 1997; Mitani et al., 2010). This behavior is important in a navigation context because if the seals are able to orient/navigate only at the surface, this spiraling would likely cause disorientation. We might expect errors in swimming direction during ascent following the drift phase and a re-orientation at the surface. However, if the seals are utilizing cues at depth, the seal should be

able to maintain the initial bearing even after the drift phase. Pinnipeds seem to have rather sharp aerial vision when light is not limiting (Hanke et al., 2009). Thus, visual information could play an important role for the spatial navigation of the elephant seals when in the vicinity of the coast. Visual cues could also supplement other navigational strategies such as path integration and geomagnetic-based navigation (Quinn and Brannon, 1982; Srinivasan et al., 1996; Wehner et al., 1996).

Body orientation (geographic heading) during homing could help narrow the list of potential cues. Davis et al. reported the 3-D underwater movement of northern elephant seals and demonstrated that they do tend to maintain a relatively consistent trajectory underwater, but the results were limited to several hours and were derived from a single subject (Davis et al., 2001). There has been no detailed study of heading directions both underwater and at the surface in a navigation context. In this study, we attached a tri-axial acceleration and magnetometry data logger and a GPS tag to translocated juvenile northern elephant seals from Año Nuevo State Reserve, CA, USA. By reconstructing 3-D movements, we examined the animals' return paths at the scale of the entire transit and individual dives. Focusing on their heading directions underwater and at the surface, we also examined whether they look around or keep still. If the elephant seals rely, at least in part, on visual information, we expect they should make some adjustments at the surface to maintain a consistent direction toward the colony.

## MATERIALS AND METHODS

### Field experiments

We captured three juvenile elephant seals (1.3 years of age, S1, S2 and S4) at Año Nuevo State Reserve, CA, USA, in April 2008 using standard procedures (Le Boeuf et al., 1988). We transported the seals to Long Marine Laboratory at the University of California at Santa Cruz and chemically immobilized them to attach data loggers (see below) (Le Boeuf et al., 1988; Le Boeuf et al., 2000). The devices used were: (1) a 3-D accelerometer/magnetometer and swim velocity data logger (W2000-3MPD3GT: 26 mm diameter, 175 mm in length, 140 g mass in air; Little Leonardo Co., Bunkyo-ku, Tokyo, Japan); (2) a GPS/ARGOS transmitter (MK10-AF, Wildlife Computer, Redmond, WA, USA); and (3) a VHF radio transmitter (MM160, ATS, Isanti, MN, USA). The 3-D data logger was attached to the back of the seal and recorded swimming speed, diving depth, 3-D (longitudinal, lateral and dorso-ventral) geomagnetism at 1 s intervals and 3-D acceleration at 1/16 s intervals with a memory of 512 Mb. The maximum range of the depth sensor was 2000 m with a resolution of 0.5 m. The GPS/ARGOS transmitter was attached to the head of the seal, and the VHF radio transmitter was attached to the back of the seal posterior to the accelerometer. As part of a separate experiment, we also attached a lead weight (3.63 kg) and a float of copolymer foam (2.28 kg), just behind the loggers on the seal's back, both on time released and controlled to maintain neutral buoyancy underwater. We assumed that the weight/float apparatus did not impact the navigation performance of the seal. The seals were held overnight at Long Marine Laboratory, transported by boat 60 km southwest of the Año Nuevo colony, and released over deep water above the Monterey Canyon (S1, 36°33.249'N, 122°29.758'W; S2, 36°34.048'N, 122°30.575'W; S4, 36°34.849'N, 122°31.660'W). The weather at the time of release was calm with a heavy fog, inhibiting the views of the coastline. The instruments were retrieved when the seals returned to the Año Nuevo colony. All procedures used were approved by the UCSC CARC (IACUC) committee and permitted under NMFS marine mammal permits #786-1463 and #87-143.

### 3-D dive data analysis

Data were analyzed using IGOR Pro (WaveMetrics Inc., Lake Oswego, OR, USA). The impeller rotation count was converted to actual swimming speed ( $\text{ms}^{-1}$ ) using the calibration line that was estimated for each seal (Sato et al., 2003). Briefly, a calibration line was created from a linear regression of revolutions  $\text{s}^{-1}$  against speed calculated as vertical speed (as determined from the depth recorder) divided by sine of the pitch angle (from an acceleration sensor along the longitudinal axis). Low-frequency acceleration components were extracted using a low-pass filter (0.4–0.6 Hz) (IFDL Version 4.0; Wave Metrics Inc.) (Tanaka et al., 2001). Low-frequency components of the surge acceleration were used to calculate the pitch angle of the seals (Sato et al., 2003). An ascending pitch angle is represented as a positive value. Headings were computed from 3-D geomagnetism and acceleration, and the 3-D dive paths were reconstructed from headings, pitch, depth and swimming speed data using dead-reckoning methods (Johnson and Tyack, 2003; Mitani et al., 2003; Shiomi et al., 2008). Horizontal migration paths were derived from headings and horizontal swimming speed every second using dead reckoning. Straightness of the horizontal homing route and path of each dive was quantified using net-to-gross displacement ratio (NGDR) (Davis et al., 2001). The NGDR is computed as the ratio of the linear distance between the starting and ending point of the track and the total path length swum. It varies from 0 to 1.0: a value of 1.0 when the path is completely

straight and a value of zero when the path is circular. NGDRs of dive paths were averaged within each section in the homing routes, and examined for each seal. For the analysis presented here, submergence was defined as periods deeper than 1.5 m based on the sensor's absolute accuracy, and dives with a maximum depth greater than 10 m were used for reconstructing 3-D dive paths and calculating NGDR. The GPS tracking data were used to correct the dead-reckoning paths by first calculating the distance between the GPS point and the corresponding point estimated by dead reckoning. Then, the net error was divided by the time elapsed between the subsequent GPS point, and the fraction was applied to each dead-reckoning point.

### Heading analysis

We classified each dive cycle into four phases (descent, bottom, ascent and surface). The submerged period consisted of a descent phase (D: from the beginning of a dive to the first ascent), an ascent phase (A: from the time of the last descent to the end of the dive), and a bottom phase (B: the time between the end of descent and the beginning of ascent). The surface phase (S) was defined as the period from the end of the dive to the start of the next dive. To examine the heading change, we quantified the changes using  $r$ , i.e. an index of angular dispersion of the circular data with values from zero to one [chapter 26 in Zar (Zar, 1998)]. The value of  $r$  varies inversely with the amount of dispersion in the data. It is unit-less and may vary from 0 (when there is so much dispersion that a mean angle cannot be described) to 1.0 (when all the data are concentrated at one direction). We used the  $r$  value derived from periods of at least 50 s.

We examined  $r$  values within a dive cycle (descent, bottom, ascent and surface) in each seal, and used only the surface headings for the following analysis. Homing routes of the seals were classified into three categories: (a) after-release period [AR: the period immediately following release until the mean heading direction of descent (first 60 s) changed more than 30 deg from the previous direction. This dramatic route change was seen within two hours from the release for all seals]; (b) deep-water period (DW: the period swimming over deep water); and (c) inshore period (IS: the period swimming over the continental shelf and along the coast). We examined the relationship between the magnitude of the heading change and the location of the seal in accordance with the homing route sections of each seal (AR, DW and IS). We also calculated the mean heading direction of each surface interval. These directions were grouped together by homing route section and examined for variations in relation to a direction of the nearby coast. For drift dives, heading directions both pre- and post-drift were examined in each seal. The pre-drift phase was defined as the period from 100 m depth to just before initiation of passive drifting; the post-drift phase was defined as the period from the end of the drift phase to 100 m in depth. The uniformity of the distribution of heading directions and a specified mean direction in the surface intervals were examined using the V-test, and that of mean angle was examined using the one-sample chi-squared test with a 95% confidence interval [chapter 27 in Zar (Zar 1998)]. Statistical analysis was performed using Excel-Toukei 2008 (SSRI Co. Ltd, Tokyo, Japan). Values for statistical analysis were set at  $P < 0.05$ . Means ( $\pm$ s.d.) are reported.

## RESULTS

The three seals returned with a mean transit time of  $2.2 \pm 0.6$  days. Total numbers of dives, mean dive depth, mean dive duration and mean surface intervals between dives are summarized in Table 1.

Table 1. Age, body mass, translocation date and summary of diving statistics for northern elephant seals (S1, S2 and S4)

Individual	Sex	Body mass (kg)	Release time* (PST)	Return latency (days)	No. of dives	Dives		No. of drift dives	Surface	
						Dive depth (m)	Dive duration (s)		Duration (s)	Pitch angle (deg)
S1	F	161.0	12:30 h	1.8	169	189.6±115.1	720.7±310.3	13	92.3±42.2	40.0±9.6
S2	M	162.0	12:00 h	2.9	296	157.7±122.5	726.4±290.2	2	100.2±36.2	29.1±15.4
S4	—	193.0	11:20 h	1.9	126	121.3±113.2	689.4±256.3	—	101.5±51.5	28.9±8.3

\*Release date was 17 April 2008.

Values are means ± s.d.

Dive depth is the maximum depth of the dives.

The seals maintained a positive pitch angle while at the surface (Table 1). Mean swimming speed while submerged was  $1.06 \pm 0.23 \text{ ms}^{-1}$ . The migration routes were not direct from the released point to the colony (Fig. 1 and Table 2). All seals departed in different directions right after the release; however, S1 and S4 showed a trajectory aligned with the Año Nuevo colony shortly after the release. Subsequently, the seals traveled indirectly toward the nearby coast, south of Año Nuevo. After reaching the coast, they headed north to the Año Nuevo colony. S4 made several north-south movements after arriving at the coast. S1 and S4 arrived to the coast within 3 km from the strand at night, and S2 arrived during the day.

#### Parallel between dead-reckoning paths and GPS paths

Net horizontal displacement based on the last GPS positional data and the endpoint of dead-reckoning paths at the same time was 14.5 km with a heading of 119.9 deg from the dead-reckoning point to the GPS point for S1, 14.8 km with a heading of 57.7 deg for S2, and 26.7 km with a heading of 84.0 deg for S4 (Fig. 1A–C). The dead-reckoning paths and the GPS paths were similar in shape; however, there were differences in either angle or scale depending on the individual. All the dead-reckoning paths were generally deflected in a westerly direction from the GPS paths. There are typically southward or southeastward coastal surface currents off Monterey Bay in spring (Lynn et al., 2003). The direction of the displacement from GPS paths to the dead-reckoning paths and the direction of surface current off Monterey Bay could explain the magnitude of the observed offsets.

#### Underwater behavior

3-D paths were calculated for 435 dives throughout the trips of the translocated seals. The horizontal dive paths were remarkably straight in each dive, despite the curved large-scale homing routes (Table 2 and Fig. 2A,B). Although the mean NGDR of individual dives was over 0.85 on the three homing sections, the value for the inshore period was significantly higher than the other two periods in S1 and S2 (Steel–Dwass test: AR vs DW,  $P=0.96$  and  $P=1.0$ ; AR vs IS,  $P<0.005$  and  $P<0.001$ ; DW vs IS,  $P<0.001$  and  $P<0.001$  for S1 and S2, respectively; Table 2). Drift dives (Crocker et al., 1997; LeBoeuf et al., 1996) were observed in two of the seals (13 dives by S1 and 2 dives by S2) with a mean maximum depth of  $343.7 \pm 63.3 \text{ m}$  and  $368 \pm 24 \text{ m}$ , respectively. During the drift phase, elephant seals have been observed to sink in a belly-up position and a spiral ‘falling-leaf’ manner (Mitani et al., 2010) (Fig. 2C–E). However, unlike the previous report, the pitch angles were positive with a mean angle of  $31.7 \pm 13.9 \text{ deg}$  for S1 and  $8.0 \pm 3.7 \text{ deg}$  for S2. Despite over 20 complete spirals during the drift phase, the seals maintained their initial direction at the end of the drift dives, with a mean absolute difference between pre-drift and post-drift directions of  $18.4 \pm 14.2 \text{ deg}$  for S1 and  $9.8 \pm 9.5 \text{ deg}$  for S2.

#### Surface behavior

The headings varied more at the surface than while submerged (Fig. 3). Comparing the surface phase with the other three phases (descent, bottom and ascent), the  $r$  values of the surface phase were significantly lower than the others within individuals (Steel–Dwass test: S vs D,  $P<0.001$ ; S vs A,  $P<0.001$ ; S vs B,  $P<0.001$  for S1, S2 and S4; Fig. 4). The surface  $r$  values immediately after the release and during the inshore period were significantly lower than during the deep-water period ( $\chi^2$  test: S1,  $z=2.30$ ,  $P<0.005$ ; S2,  $z=4.15$ ,  $P<0.001$ ; S4,  $z=0.86$ ,  $P=0.19$ ; Fig. 5). The surface  $r$  values did not vary between night and day in S2 and S4; however,  $r$  tended to be low at night in S1 (Fisher’s exact test: S1,  $P<0.05$ ; S2,  $P=1.0$ ; S4,  $P=0.85$ ). During surface intervals, mean heading direction of the three homing sections (AF, DW and IS) was biased for all seals (V-test:  $P<0.001$ ; Fig. 6), and the mean angle tended to point coastward within a 95% confidence interval as the seals entered the inshore

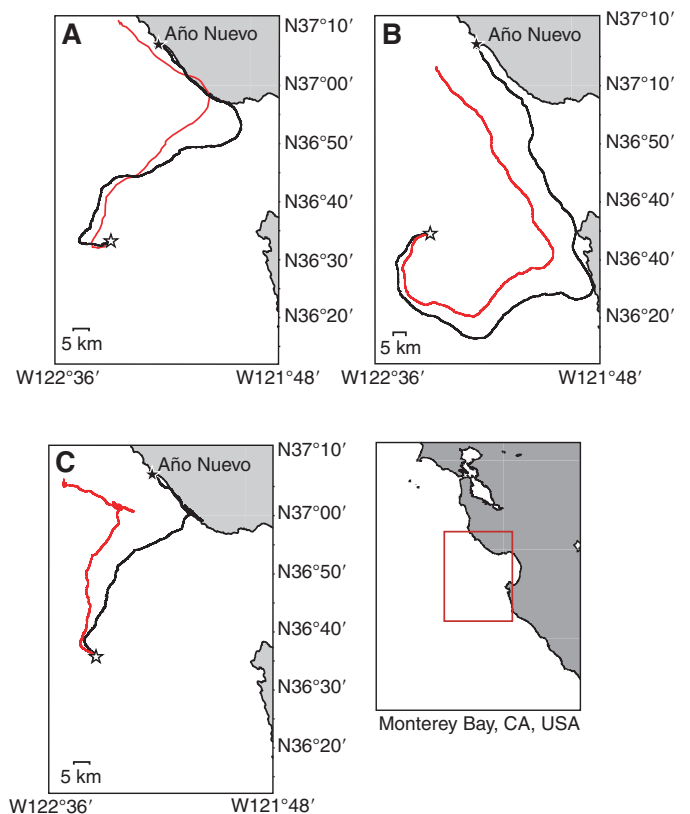


Fig. 1. Migration paths recorded with GPS (black) and accelerometry via dead reckoning (red) in each northern elephant seal (A, S1; B, S2; C, S4). White stars indicate release positions, and black stars indicate the end positions of trips. Inset, research location.

Table 2. Net-to-gross displacement ratio (NGDR) of the horizontal migration path and the horizontal dive path

Individual (No. of dives)	Migration path	All dives				Non-drift dives	Drift dives ( <i>N</i> )
		Total	After release	Deep water	Inshore		
S1 (173)	0.53	0.86±0.07	0.80±0.19*	0.84±0.13**	0.96±0.03	0.92±0.1	0.81±0.1 (13)
S2 (346)	0.33	0.94±0.06	0.96±0.03**	0.94±0.07**	0.97±0.05	0.95±0.05	0.92±0.07 (2)
S4 (180)	0.54	0.94±0.05	0.92±0.03	0.95±0.04	0.94±0.06	0.94±0.05	—

NGDR of all dives was also averaged by homing route sections in addition to total result.  
Steel–Dwass test was used, and the results are vs inshore period. \**P*<0.05, \*\**P*<0.01.

period (one-sample *t*-test: S1, 3.1±31.8 deg; S2, 12.6±16.2 deg; S4, 92.6±16.9 deg; Fig. 6). Subsequently, the heading directions shifted gradually to the direction of the Año Nuevo colony while the seals were swimming along the coast and getting closer to the colony (S1, 314.5±12.0 deg; S2, 333.4±10.5 deg; S4: 0.0±29.2 deg; Fig. 6).

DISCUSSION

Experimentally translocated seals showed different characteristics in headings when submerged vs at the surface. The seals changed their heading greatly at the surface; however, they maintained a consistent direction underwater indicated by a high NGDR within individual dives. This unidirectional swimming behavior while

submerged demonstrates the seals’ impressive orientation ability. Consistent with prior studies, the seals also sank in a spiral manner with a belly-up position during the drift phase of drift dives. Despite the possible disorientation of such spiraling, the seals maintained a consistent direction throughout a dive with <20 deg difference between pre- and post-drift phases. The seals appeared to maintain a directional sense while submerged, even during drift. This could be an important capability for their long-distance migration in the wild. Direct transits between the colony and foraging areas would be crucial for the seals to complete a long foraging trip. As drift dives make up about 5% of all dives (Le Boeuf et al., 2000), an ability to maintain directional sense in drift dives would save the

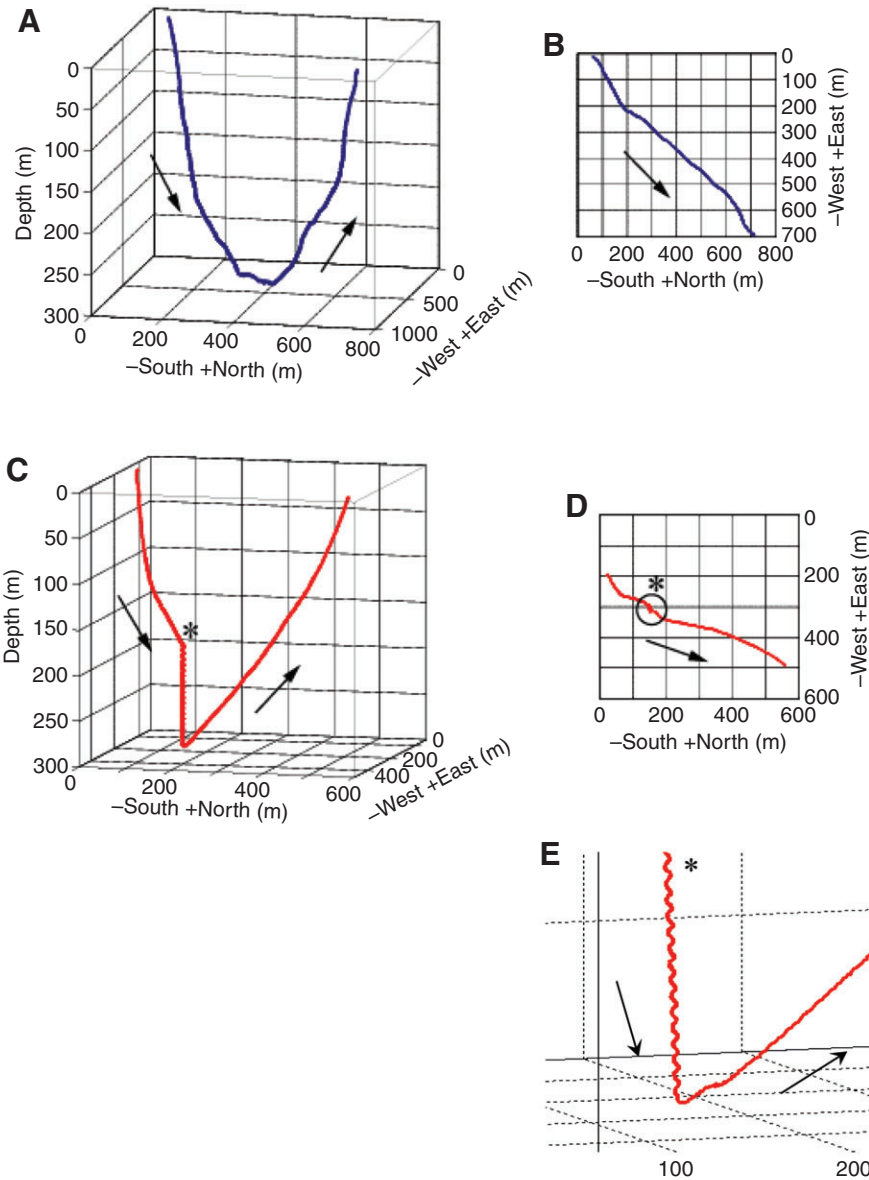


Fig. 2. Typical 3-D dive path of a non-drift dive (blue) and a drift dive (red) of the northern elephant seal (S1). Arrows indicate swimming directions, and an asterisk indicates the start of the drift phase. (A) Non-drift dive (solid figure); (B) non-drift dive (plane view); (C) drift dive (solid figure); (D) drift dive (plane view); (E) drift dive (close-up view).



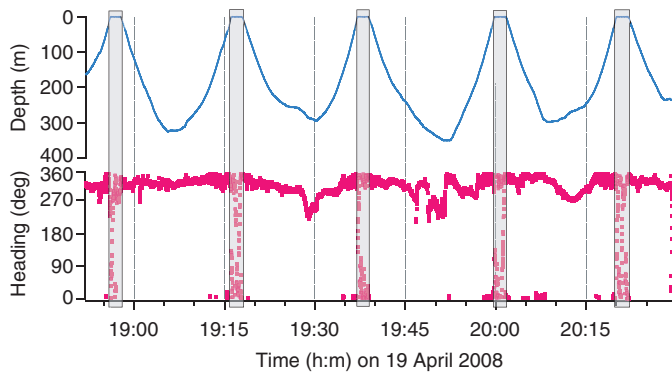


Fig. 3. Typical dives during the trip of a northern elephant seal (S2). The x-axis is time, and y-axis is dive depth (blue) and headings (red); shaded areas indicate surface intervals.

loss of traveling distance due to swimming in a different direction after a drift phase and possibly in subsequent dives. Moreover, the remarkable orientation ability after the complex circular motion in the dark implies the use of a navigational cue that is accessible and perceivable at relatively deep depths, away from surface cues. One candidate cue is the ambient acoustic sound field; elephant seals detect acoustic pressure better underwater than in air, while other phocid species have amphibiously adapted hearing (Kastak and Schusterman, 1999; Schusterman et al., 2000). The elephant seal's ear is better adapted for use underwater in terms of both energy efficiency in receiving and transducing the relevant mechanical stimulus, and is sensitive to lower frequencies. If the seals were able to detect and perceive the direction of underwater sound, they could orient in the dark by maintaining the directional relationship between the body orientation and the direction of the sound. Indeed, a swimming harbor seal can localize a sound source with the mean deviation from 2.8 to 4.5 deg (Bodson et al., 2006). If the elephant seals can localize underwater sounds with the same accuracy as a harbor seal, they would be able to maintain a consistent direction after a drift dive with an error of less than 20 deg.

In contrast, the seals in our study changed their headings up to 360 deg when at the surface between dives. The seals were apparently drifting in ocean currents during most of transit, as indicated by the difference between the dead-reckoning paths and the GPS paths. However, the seals kept swimming in consistent directions while under the influence of the currents. The NGDR of horizontal dive paths were significantly higher in the inshore period

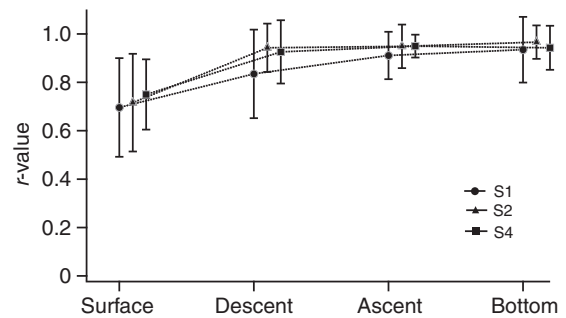


Fig. 4. Mean  $r$  values of each dive phase in each northern elephant seal (S1, S2 and S4). Error bars indicate  $\pm$ s.d.

than the other periods for S1 and S2 (Table 2). They might rely more on the initial direction when they are in the vicinity of the coast. Given the NGDR of dive paths and greater heading change at the surface, it could be implied that the seals swam with an intended direction that was based on visual scanning at the surface, especially near the coast.

The importance of visual landmarks has been suggested in far-ranging avian orientation (Burt et al., 1997). Vyssotski et al. showed the detection of visual landmarks in homing pigeons, which possess the flexibility of using different cues for successful homing (Vyssotski et al., 2009). The surface heading change of the seals in our study was greater after the release and while swimming inshore. Also, the mean heading directions in the surface intervals pointed coastward as the seals were getting closer to the coast (Fig. 6). This was not observed while traveling over deep water. Considering the visible distance while at sea and the rather sharp aerial vision of the seals, we assumed that the seals could see coastal landmarks when they were over the continental shelf, which stretches about 14 km from the coast. Intriguingly, surface heading directions started pointing coastward from the inshore period, and the NGDR of individual dives during that period was significantly higher than the other two periods, after release and deep water, in each seal (Table 2). Day and night variation did not seem to influence the surface heading change. S1 showed lower heading change at night; however, this could be confounded by S1 swimming in the inshore phase almost exclusively at night (which was not observed in the other seals). The magnitude of heading change was higher in the

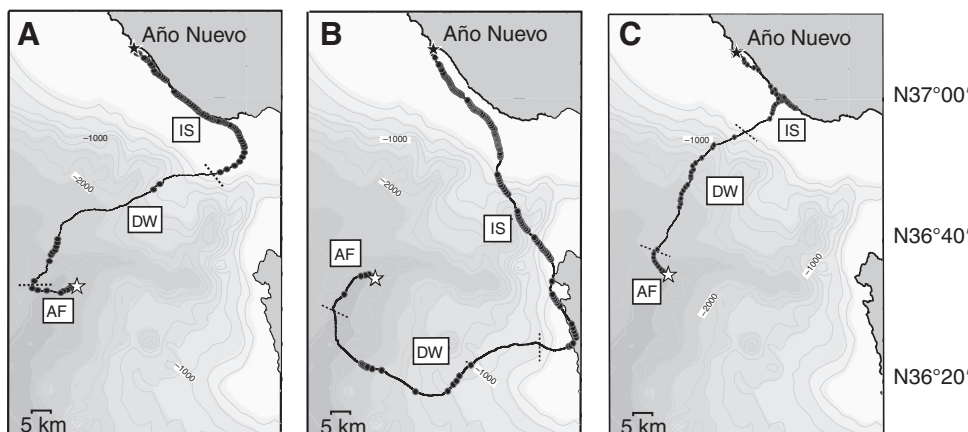


Fig. 5. Homing routes of northern elephant seals (A, S1; B, S2; and C, S4) and locations of surface intervals (filled circles), which have lower than average  $r$  values. White stars indicate the released points, and black stars indicate the end points of the homing routes. Homing routes are divided into three sections separated by broken lines (AF, after release; DW, deep water; IS, inshore).

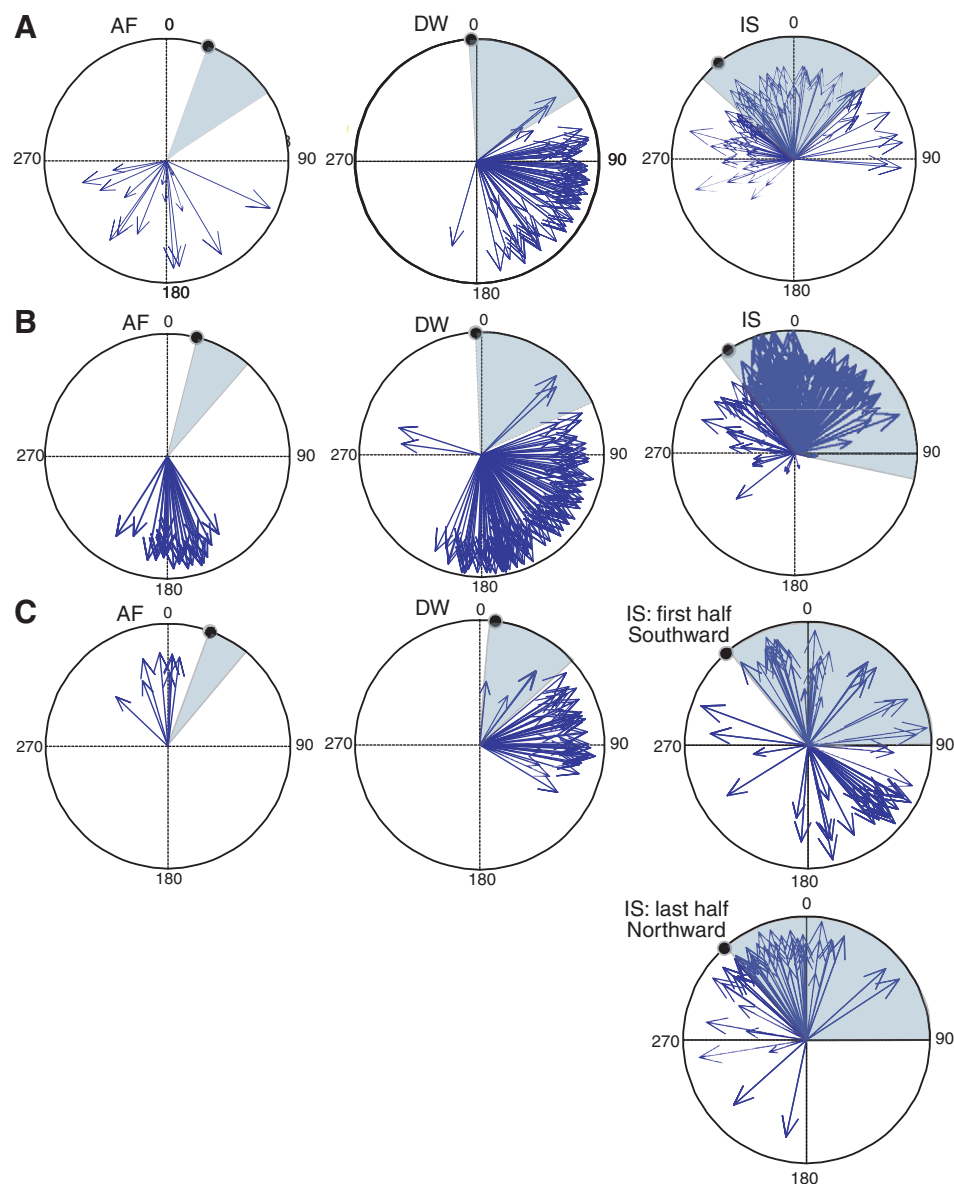


Fig. 6. Relationships among the directions of mean surface headings, the colony and the coastline for the homing route of each section. (A, S1; B, S2; C, S4). Black filled circles are the direction of the colony, and shaded areas are the direction of the coastline. The IS period from seal S4 was further divided in two sections due to the southward and northward movements along the coastline (Fig. 1C). The first half is southward movement, and the second half is northward movement. AF, after release; DW, deep water; IS, inshore.

inshore period than the other two periods. Therefore, the magnitude of surface heading change could be attributed to the proportion of time spent along the coast, not to the time of day. Low-light levels probably would not preclude navigation because elephant seals have remarkably sensitive vision (Levenson and Schusterman, 1999). Straight-line underwater swimming and adjusting traveling direction at the surface were observed in loggerhead turtles *Caretta caretta* (Narazaki et al., 2009), although the cue(s) used have not been determined. This behavior resembles our results. Acquiring directional information at the surface would be indispensable for both sea turtles and seals in addition to maintaining a consistent swimming direction underwater. Our result implies that the seals decided the swimming direction at the surface, at least in part, by using visual cues, possibly landmarks. Then, they swam toward the nearby coast, not directly to the Año Nuevo colony, when they were close enough to detect the direction of the land.

The seals tended to swim parallel to the coast upon reaching shallow water, and the trajectories were directed toward the Año Nuevo colony. The surface headings varied most while swimming along the coast with the mean heading directions of each surface

interval pointing coastward. The closer the seals were to the colony, the more directed the mean headings. If the seals rely on visual signals for their navigation, the seals could obtain more detailed information to find their colony by swimming along the coast because of the increase in availability of unique features of the coastline. The seals reached the nearby coast first instead of swimming directly to the Año Nuevo colony. Then, they swam along the coast even though their major predator (white sharks) occurs more frequently in coastal areas (Klimley et al., 1992; Klimley et al., 2001). This implies that reaching the nearby coast is an essential part of returning home for the seals, and by doing so they may be able to reliably orient and detect the location of their colony.

However, this also raises questions regarding how they guided themselves until they were close enough to detect the land, and from where they were able to recognize the direction of the land. Notably, two seals (S1 and S4) directly headed to the Año Nuevo colony for several hours in the early phase of their trips. A few studies have shown the possibility for marine mammals to exploit the patterns of skylight polarization and/or a sun compass (Quinn, 1980; Quinn and Brannon, 1982; Avens and Lohmann, 2003;

Waterman, 2006). If the primary source for the seals' navigation is visual information, they might use the celestial cues to guide themselves until being able to see the landmarks. Yet, due to a dense fog on the day of release, it would not have been possible to see any of these features until several hours after the release. Thus, it is unlikely that the seals used the celestial cues for navigation in the early phase of homing. Another potential cue is the geomagnetic field, which is thought to be used by many marine animals as well as land animals (Quinn, 1980; Quinn et al., 1981; Lohmann and Lohmann, 1994; Lohmann et al., 1995; Ugolini and Pezzani, 1995; Lohmann and Lohmann, 1996; Lohmann et al., 2004). Geomagnetic and acoustic cues are particularly appealing as navigation cues because they are available underwater. However, available information cannot explain what navigational cues were actually used to navigate during the migration, and why the seals deviated from the line trajectory in spite of the direct heading to their colony. Another potential cue could be olfactory. The importance of olfaction was suggested in gray seals for recognizing pups (Burton et al., 1975), and acute olfactory sensitivity was reported in harbor seals (Sylvia et al., 2006). The wind direction during the experimental day was from the north where the colony was located. The seals did not directly head to their colony. If seals relied on some olfactory cues from the colony, they would have changed their traveling direction to the north. However, there is not enough information to examine whether the seals used olfactory cues for orientation. Given the weather conditions on the experimental day, magnetic field or acoustic signals are the most plausible cues, but we did not collect any evidence in direct support of this. It is likely the seals are able to navigate using a variety of cues as suggested for other migratory species (Quinn and Brannon, 1982; Maaswinkel and Whishaw, 1999; Avens and Lohmann, 2003; Walcott, 2005).

Although other cues may be important for the long-distance navigation of seals, the results of this study suggest visual cues are particularly important for the final stage of homing, as evident by the greater heading changes exhibited during the middle of their homing route, or deep-water period. Bathymetric features could be a directional cue, but dive depths were too shallow to reach the ocean floor until the seals reached the continental shelf. To explain the linear trajectory over deep water without obvious visual cues at the surface, further study will need to focus on the use of additional cues available at sea.

In conclusion, our study showed the remarkable ability of the northern elephant seal to maintain a consistent horizontally straight course underwater even during drift dives. This orientation ability, especially during drift dives, may indicate the use of a cue available underwater, such as acoustic or geomagnetic. The seals first reached the nearby coast and they then headed directly to their colony and changed their headings most commonly at the surface. The result suggests that the seals might be orienting at the surface using visual cues, and possibly perceiving landmarks when they were vicinity of the coast, especially while swimming along the coast. For the translocated juvenile elephant seals, it is assumed that the features of the coastline would give them information to reliably find the location of their colony. In addition, our study implies use of multi-modal navigation cues for the elephant seals. Further research will be needed to reveal how visual cues are used and how seals are able to navigate efficiently in open-ocean habitat, away from coastal cues.

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