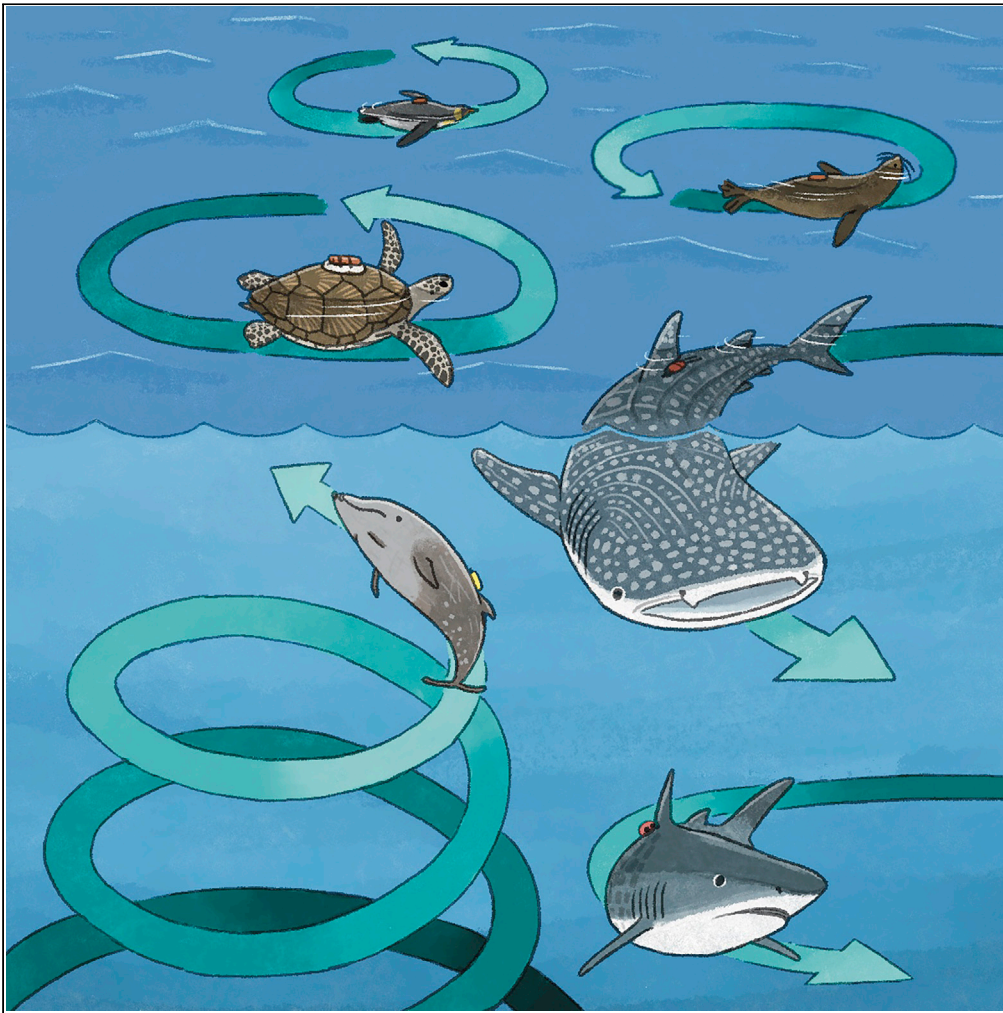**Article**

Similar circling movements observed across marine megafauna taxa

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HIGHLIGHTS

Biologging 3D movement data revealed circling behaviors in marine animals

Circling behaviors were observed in sharks, turtles, penguins, and marine mammals

Circlings might serve several purposes including foraging, navigation, etc.

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Article

Similar circling movements observed across marine megafauna taxa

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SUMMARY

Advances in biologging technology have enabled 3D dead-reckoning reconstruction of marine animal movements at spatiotemporal scales of meters and seconds. Examining high-resolution 3D movements of sharks (*Galeocerdo cuvier*, N = 4; *Rhincodon typus*, N = 1), sea turtles (*Chelonia mydas*, N = 3), penguins (*Aptenodytes patagonicus*, N = 6), and marine mammals (*Arctocephalus gazella*, N = 4; *Ziphius cavirostris*, N = 1), we report the discovery of circling events where animals consecutively circled more than twice at relatively constant angular speeds. Similar circling behaviors were observed across a wide variety of marine megafauna, suggesting these behaviors might serve several similar purposes across taxa including foraging, social interactions, and navigation.

INTRODUCTION

Analysis of animal tracks provides our understanding of navigation, moving capacity, and internal state of moving animals, as well as identifying the effect of external factors affecting their movements (Nathan et al., 2008). Marine animals move through an inherently 3D environment, yet their movements have been primarily examined in less dimensions (i.e., diving depth profiles from time-depth recorders and horizontal surface tracks from satellite tags) due to logistical and technical difficulties primarily derived from seawater's impermeability to radio waves. Recent advancements in multi-sensor data loggers have enabled simultaneous recording of various parameters (e.g., pitch, roll, heading, speed, etc.), opening up opportunities to examine 3D movements of free-ranging marine animals using dead reckoning (Wilson et al., 2007; Narazaki et al., 2009; Shiomi et al., 2010). Using this technique, high-resolution underwater 3D movements can be reconstructed by integrating locomotion vectors calculated from animal speed, heading, and change in depth, making it possible to examine fine-scale movements occurring at scales of meters and seconds that have been overlooked in previous studies.

In this study, we examined high-resolution 3D movements of various marine animals, including tiger sharks (*Galeocerdo cuvier*), a whale shark (*Rhincodon typus*), green turtles (*Chelonia mydas*), king penguins (*Aptenodytes patagonicus*), Antarctic fur seals (*Arctocephalus gazella*), and a Cuvier's beaked whale (*Ziphius cavirostris*). We report the discovery of circling behavior where animals move in a circular manner at relatively constant angular speed. Here, we document the context (i.e., foraging, homing trips) and the detailed behavior of the circling events observed in these different species and discuss possible explanations for this behavior.

RESULTS AND DISCUSSION

A circling event was defined as more than two consecutive circling movements detected using compass heading time series data (Table 1 for summary statistics for circling events). From an energetics perspective, swimming in a straight line is the most efficient and sinuous movements should only be favored if the higher cost of turning is outweighed by other benefits, such as enhancing the chance of achieving a given aim (e.g., foraging success; Wilson et al., 2013). Some circling events were recorded within animal's known foraging habitats, suggesting their possible relation to foraging. For example, a total of 272 circling events were observed in four tiger sharks tagged off Hawaii (Figures 1A and 2A). Sharks circled 2–30 times at wide-ranging depths (0.8–129.3 m) but maintained relatively constant depth during each circling event. The mean duration of circling events was 5.6 ± 4.8 min (±SD, range = 0.9–31.4 min), and the mean circle

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diameter was 9.4 ± 5.1 m. Circling events were recorded more during day (88%) than night (12%). An event was also observed in a whale shark that circled 17 times (diameter = 24.7 ± 2.0 m) during day (Figures 1B and 2B). In addition, circling behaviors previously reported in bottom-feeding sandbar sharks (*Carcharhinus plumbeus*) occurred primarily close to the sea floor, suggesting a role in foraging (Andrzejaczek et al., 2018). Some circling movements are integral to prey capture: humpback whales (*Megaptera novaeangliae*) are known to employ a unique "bubble-net" feeding behavior where they swim in a circular manner while expelling air underwater to form a vertical cylinder ring of bubbles around their prey (Wiley et al., 2011).

However, many circling events appear unrelated to foraging. For example, a shark-mounted video showed a male tiger shark circling to approach a female for courtship (Meyer et al., 2018). In our study, a Cuvier's beaked whale circled during ascent from foraging at mesopelagic depths (>700 m), typically circling 3–6 times during the final ascent phase of deep dives (N = 12, diameter = 72.3 ± 9.9 m; Figures 1F and 1H). The whale started circling when it returned to shallower depths of 644.3 ± 41.8 m and continued until it reached the sea surface (Figure 2C). Four out of six chick-rearing king penguins circled 2–26 times for a total of 267 circling events (Figure 1C) both at day (31%) and night (69%) during foraging trips. Eighty-five percent of these events occurred at the surface (<1 m) (no data for diameter due to technical constraints in measuring swim speed at sea surface). Similarly, all circling events recorded by four Antarctic fur seals (Figure 1D) occurred at the surface (<1m) between foraging dive bouts (N = 111). Penguin and fur seal circling events were typically clustered in time and space (Figures 2D and 2E). As both penguins and fur seals catch their prey during dives (Hanuise et al., 2010; Iwata et al., 2015), circling events recorded at sea surface are unlikely to be related to foraging. Moreover, fur seal circling events occurred predominantly during daytime (99%; Figure 2E), whereas they forage mainly during nighttime. Although circling behavior occurs primarily during active swimming, some circling might occur passively: northern elephant seals (*Mirounga angustirostris*) fall in a spiral manner during inactive drift phases of resting dives (Mitani et al., 2010). Seals constantly fall at low vertical speed of <0.4 m s^{-1} and descended for ca 100 m during circling drift phase lasting for several minutes (Mitani et al., 2010). Interestingly, seals appear to maintain directional sense during circling drift phases because their travel directions are consistent between drift phases (Matsumura et al., 2011).

Navigation could be another driver for circling behavior. Three-dimensional movements of three nesting green turtles displaced to oceanic release sites included a total of 29 circling events on returning to waters off their nesting beaches (Figures 2F and 3). Circling events occurred both day (66%) and night (34%), and all but two events occurred at the surface. One turtle circled repeatedly 76 times at a dominant cycle of 19.9 s (Figure 1E). Twenty hours later, this turtle circled intensively again for 37 rotations (dominant cycle = 16.0 s). It is noteworthy that circling behaviors were observed primarily at locations where turtles show significant navigational changes in relation to their destinations (e.g., just before the final approach to their goals; Figure 3). Turtles selected the correct direction after the intensive circling behaviors. Circling movements may be an effective strategy for collecting navigational cues, such as visual, olfactory and magnetic information, etc. Similar mechanical circling movement was also reported in a post-nesting loggerhead turtle (*Caretta caretta*) that circled 17 times in 3.75 min during the flat-bottom phase of a U-dive, although the geographic location of this circling behavior is unknown (Gunner et al., 2020).

We hypothesize that some circling movements are associated with examination of the geomagnetic field. Diverse taxa are known to detect and use the geomagnetic field as a source of directional information. Additionally, some animals, including sea turtles, are likely to be capable of deriving positional "map" information from the geomagnetic field (Lohman et al., 2007). Despite persuasive evidence supporting the existence of a magnetic sense, the mechanism of magnetoreception remains elusive and thus the behaviors directly involved in the process of magnetic sensing remain largely unknown. A few exceptions include head and body scanning behaviors in migratory garden warblers (*Sylvia borin*) and sandhoppers (*Talorchestia martensii*), respectively (Mouritsen et al., 2004; Ugolini 2006). Laboratory experiments strongly suggested that they detect magnetic field by turning their head/body because animals in natural geomagnetic fields found the correct direction after scanning behaviors, whereas animals in a zero magnetic field could not find their way despite increased scanning frequency. Similar scanning behaviors were observed in loggerhead turtles while adjusting their heading during straight-line travel (Narazaki et al., 2009). Interestingly, submarines also circle during geomagnetic observation because accurate measurement can be achieved by using values measured from all directions to cancel noises, such as hull magnetization (Figure 1G; Fujiwara 2009). Given that magnetization derived from the body would not be an issue for animals, circling

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Table 1. Summary of circling events reported in the present and previous studies.

Species	Status	N	Study site [magnetic inclination (°)]	Animal ID	Data duration (h)	Total time spent for circling events (%)	No. of circling events [clockwise, anticlockwise]	No. of circles	Circling cycles (s)	Duration (min)	Depth (m)	Pitch (°)	References
Galeocerdo cuvier	Foraging	4	Hawaii [38.2]		743.7	3.6	272 [145, 127]	5.9 ± 5.0 (2–30)	52.3 ± 24.7 (11.2–141.0)	5.6 ± 4.8 (0.9–31.4)	61.0 ± 31.5 (0.8–129.3)	−1.9 ± 10.5 (−45.9–23.6)	This study
				TS1301	252.8	3.4	59 [29, 30]	5.8 ± 4.3 (2–20)	82.3 ± 26.2 (14.0–141.0)	8.8 ± 6.9 (1.0–31.4)	38.5 ± 25.6 (1.3–120.1)	−2.6 ± 5.6 (−16.6–14.7)	
				TS1302	206.2	0.7	23 [11, 12]	3.5 ± 2.0 (2–11)	57.9 ± 24.9 (11.2–109.0)	3.9 ± 3.0 (0.9–15.7)	33.2 ± 20.5 (1.2–89.5)	2.3 ± 8.3 (−24.5–19.2)	
				TS1303	149.9	8.6	148 [77, 71]	6.8 ± 5.5 (2–27)	42.8 ± 10.1 (19.5–76.0)	5.2 ± 3.8 (1.2–23.9)	76.3 ± 22.6 (0.8–129.3)	−5.2 ± 11.2 (−45.9–7.1)	
				TS1304	134.8	1.7	42 [28, 14]	4.2 ± 4.4 (2–30)	40.8 ± 24.5 (16.7–139.0)	3.4 ± 2.9 (1.1–19.5)	54.2 ± 38.5 (0.8–111.0)	8.6 ± 5.9 (−6.3–23.6)	
Rhincodon typus	Foraging	1	Okinawa [38.5]		20.7	4.8	1 [0, 1]	17	200.6	60.2	1.0	4.5	This study
Chelonia mydas	Homing trip	3			195.8	0.8	29 [15, 14]	6.0 ± 10.2 (2–49)	36.9 ± 27.1 (8.0–117.0)	3.0 ± 3.0 (0.6–14.9)	1.3 ± 2.1 (0.2–8.7)	25.0 ± 9.5 (5.6–51.3)	This study
			Comoro [−44.0]	C900	118.0	1.2	26 [14, 12]	6.5 ± 10.7 (2–49)	36.7 ± 28.0 (8.0–117.0)	3.2 ± 3.1 (0.6–14.9)	1.2 ± 2.2 (0.2–8.7)	25.3 ± 9.7 (5.6–51.3)	
			Ogasawara [36.8]	O3	39.5	0.07	1 [1, 0]	2	31.3	1.6	3.2	20.1	
				O4	38.3	0.2	2 [0, 2]	2.0 ± 0.0 (2 -2)	42.8 ± 28.6 (22.5–63.0)	1.8 ± 0.4 (1.5–2.1)	1.4 ± 0.2 (1.2–1.6)	23.6 ± 12.1 (15.0–32.1)	
Aptenodytes patagonicus	Foraging	6	Possession Is. [−63.1]		1304.1	0.7	267 [101, 166]	3.0 ± 2.1 (2–26)	30.8 ± 17.7 (10.0–114.0)	2.1 ± 2.4 (0.7–29.9)	13.4 ± 43.1 (0.0–264.0)	−4.7 ± 10.1 (−89.4–41.7)	This study
				K1	171.0	0	0	–	–	–	–	–	
				K3	178.1	0.1	10 [7,3]	2.0 ± 0.0 (2–2)	24.7 ± 12.0 (13.0–52.0)	1.3 ± 0.3 (0.9–1.7)	49.9 ± 60.3 (0.0–158.2)	3.2 ± 24.3 (−50.7–41.7)	
				K4	176.4	3.9	197 [62, 135]	3.1 ± 2.4 (2–26)	27.8 ± 11.8 (10.0–80.8)	2.1 ± 2.6 (0.7–29.9)	6.9 ± 30.8 (0.0–211.9)	−5.1 ± 8.5 (−89.4–39.5)	
				K5	170.8	0	0	–	–	–	–	–	

Table 1. Continued

Species	Status	N	Study site [magnetic inclination (°)]	Animal ID	Data duration (h)	Total time spent for circling events (%)	No. of circling events [clockwise, anticlockwise]	No. of circles	Circling cycles (s)	Duration (min)	Depth (m)	Pitch (°)	References
				K6	297.8	0.05	6 [1, 5]	2.3 ± 0.5 (2–3)	27.8 ± 9.4 (15–41)	1.6 ± 0.6 (1.0–2.8)	26.4 ± 64.3 (0.0–157.6)	−0.1 ± 5.4 (−4.3–9.7)	
				K9	310.0	0.7	54 [31, 23]	2.7 ± 1.3 (2–8)	42.9 ± 28.9 (12.4–114.0)	2.5 ± 2.0 (0.9–13.0)	28.8 ± 64.5 (0.0–264.0)	−5.3 ± 11.3 (−41.1–29.7)	
Arctocephalus gazella	Foraging	4	Bird Is. [-54.8]		689.9	1.8	111 [52, 59]	4.2 ± 4.1 (2–25)	92.2 ± 24.5 (15.1–157.3)	6.7 ± 4.9 (2.2–35.1)	0.3 ± 0.06 (0.1–0.4)	0.9 ± 5.8 (−10.2–10.5)	This study
				908	162.9	0.6	9 [4, 5]	3.1 ± 2.3 (2–9)	107.5 ± 17.8 (84.0–141.0)	6.1 ± 4.1 (3.0–16.4)	0.3 ± 0.06 (0.2–0.3)	1.2 ± 7.5 (−6.1–10.5)	
				911	163.3	1.5	28 [10, 18]	2.7 ± 1.4 (2–7)	93.9 ± 26.9 (52.0–157.3)	5.1 ± 2.5 (2.7–12.3)	0.3 ± 0.04 (0.2–0.4)	4.3 ± 3.3 (−1.1–8.5)	
				919	185.0	3.6	43 [22, 21]	6.4 ± 5.7 (2–25)	85.9 ± 22.6 (49.8–147.0)	9.3 ± 6.6 (2.6–35.1)	0.3 ± 0.05 (0.1–0.4)	1.2 ± 6.5 (−6.8–9.4)	
				920	178.7	1.4	31 [16, 15]	2.7 ± 1.3 (2–8)	95.0 ± 24.9 (15.1–142.0)	4.8 ± 2.2 (2.2–11.3)	0.3 ± 0.08 (0.1–0.4)	−2.6 ± 3.8 (−10.2–5.6)	
Ziphius cavirostris	Foraging	1	Ogasawara [36.7]		23.0	9.3	18 [6, 12]	3.8 ± 1.4 (2–6)	105.8 ± 47.0 (48.7–272.7)	7.1 ± 3.3 (1.7–13.7)	258.0 ± 105.8 (4.0–402.5)	12.0 ± 42.0 (−60.3–46.4)	This study
Carcharhinus plumbeus	Foraging	4	Western Australia [-56.2]		73.7	NA	NA	NA	NA	max. 55	43.8 ± 23.2 (14.6–67)	NA	Andrzejaczek et al. (2018)
Caretta caretta	Post-nesting	1	Cape Verde Is. [12.9]		NA	NA	NA	17	NA	3.8	approx. 3	NA	Gunner et al. (2020)
Mirounga angustirostris	Homing trip	6	California [60.6]		NA	NA	NA	11.7 (8–32)	NA	8.1 ± 1.2 (1.2–16.4)	[a]266.6 ± 10.2 (137.5–394.75)	NA	Mitani et al. (2010)
	Homing trip	2	California [60.6]		NA	NA	NA	NA	NA	NA	NA	NA	Matsumura et al. (2011)
Megaptera novaeangliae	Foraging	6	Gulf of Maine [68.0]		NA	NA	[b]118 [118, 0]	2.1 ± 0.3	NA	70.6 ± 15.2	(4.4–41.1)	NA	Wiley et al. (2011)

Mean ± standard deviations with ranges in parenthesis were shown for number of circles, dominant cycles, duration, and depth of circling events.

[a]Depth of drift phase.
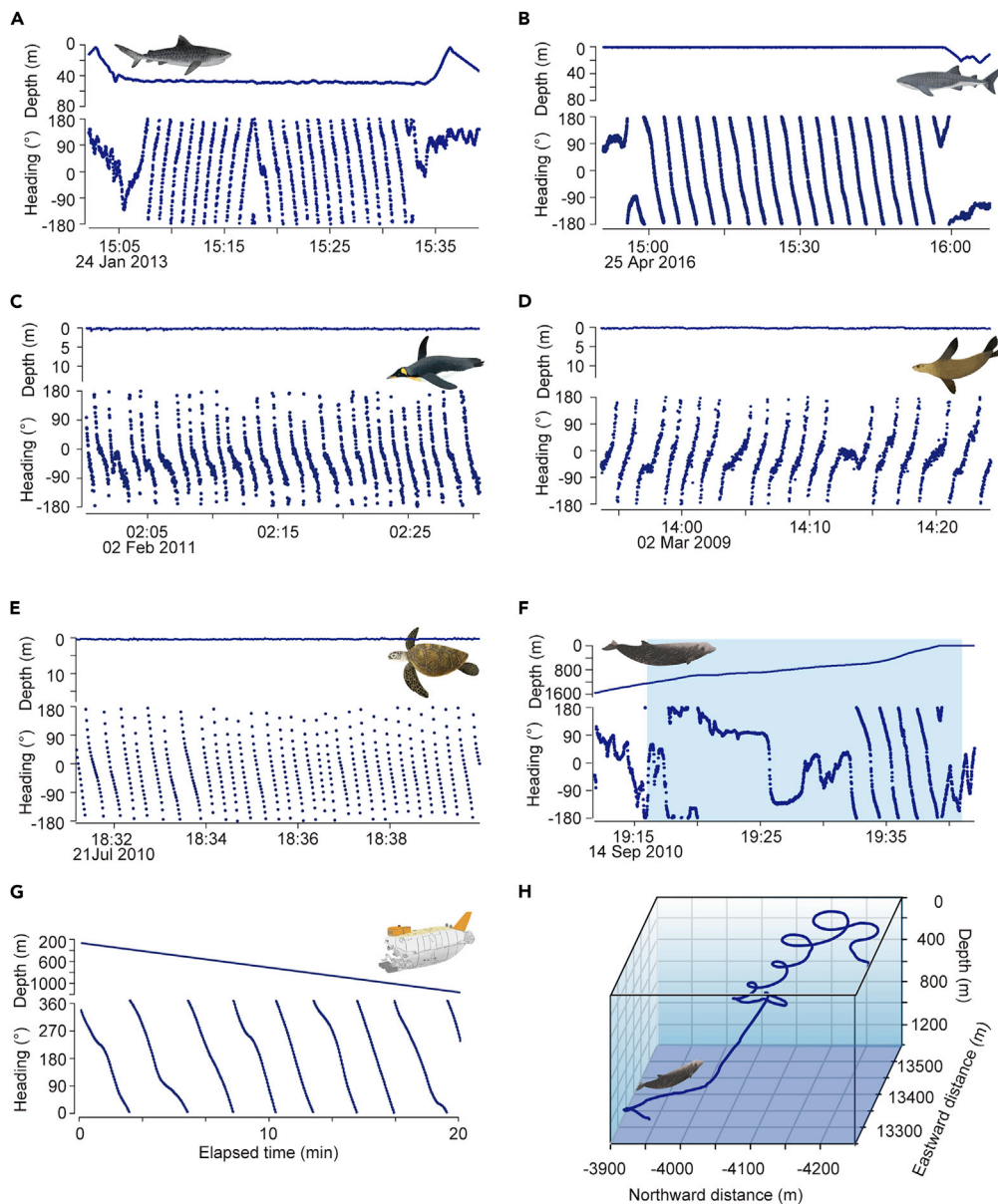
[b]Upward spiral bubble-net feeding event.

Figure 1. Examples of circling movements recorded in each species

(A) A tiger shark, (B) a whale shark, (C) a king penguin, (D) an Antarctic fur seal, (E) a green turtle, (F) a Cuvier's beaked whale.

Movement of a submarine during geomagnetic measurements (modified from Fujiwara 2009) is also shown in (G).

The shaded area in (F) is displayed three-dimensionally in (H) showing how a Cuvier's beaked whale circled during final ascent phase of a deep dive.

movements seem to be well suited for examination of the geomagnetic field by scanning the maximum and minimum magnetic field strength direction and/or detecting the magnetic symmetry plane in visually mediated magnetoreception (Ritz et al., 2000). Animals might also be able to improve measurement accuracy by taking multiple samples by circling several times. Animals might circle to derive directional/positional cues from the geomagnetic field, especially in navigationally challenging situations (e.g., homing trips in sea turtles, foraging trips of central place foragers such as penguins and seals).

Similar circling movements were observed across marine megafauna taxa, suggesting that this could be convergent behavior with common functions. Potential explanations for circling behavior discussed here
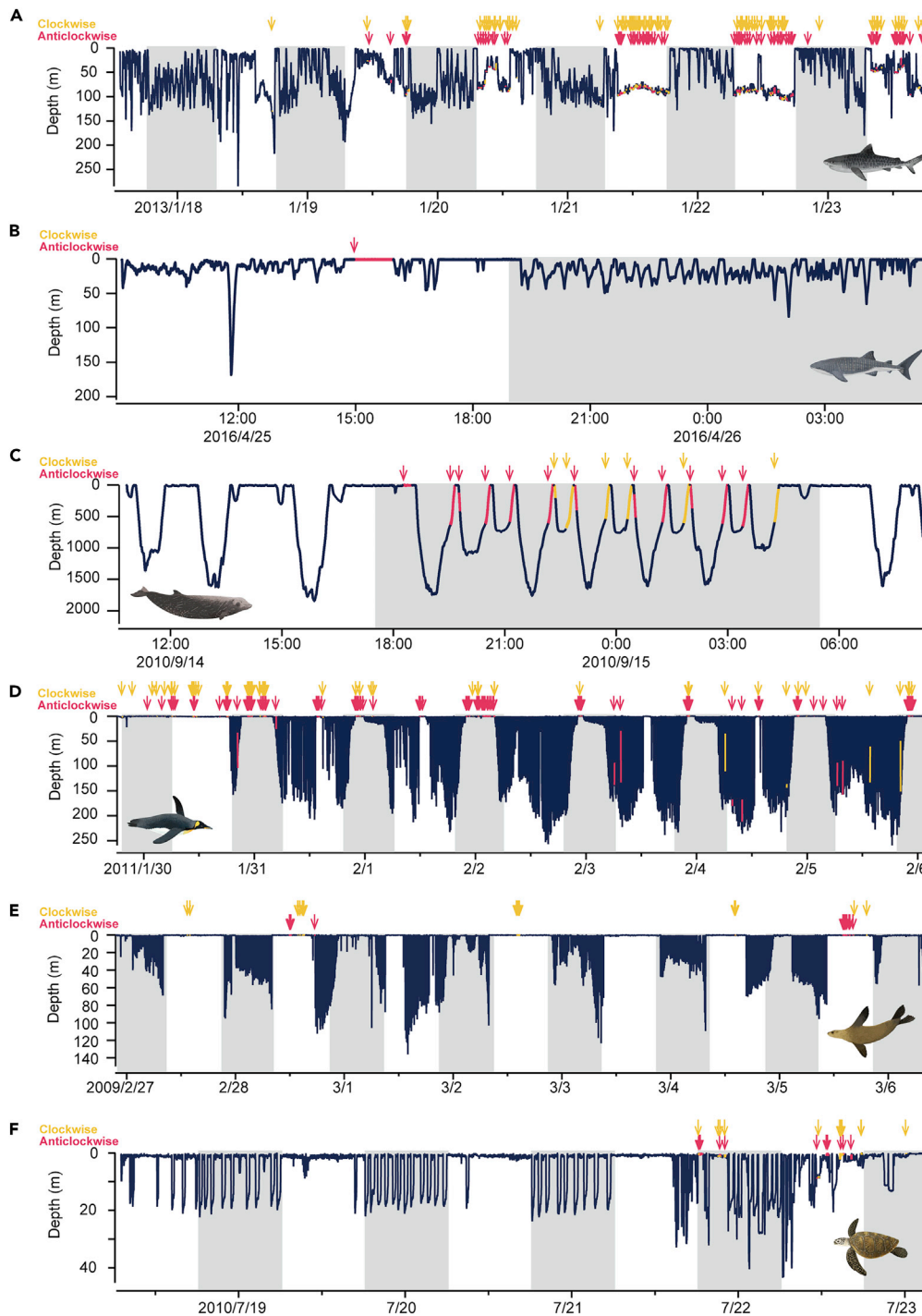
Figure 2. Example of time series depth recordings of each species

(A) A tiger shark, (B) a whale shark, (C) a Cuvier's beaked whale, (D) a king penguin, (E) an Antarctic fur seal, (F) a green turtle.

The data of penguins and fur seals were recorded during foraging trips, although they only covered from the beginning to the middle of trip due to shortage of memory size/battery. The green turtle data covered an entire homing trip during a displacement experiment. Gray shades indicate nighttime. Clockwise and anticlockwise circling events are indicated in yellow and magenta, respectively, with the arrow of corresponding color indicating the start of each event.

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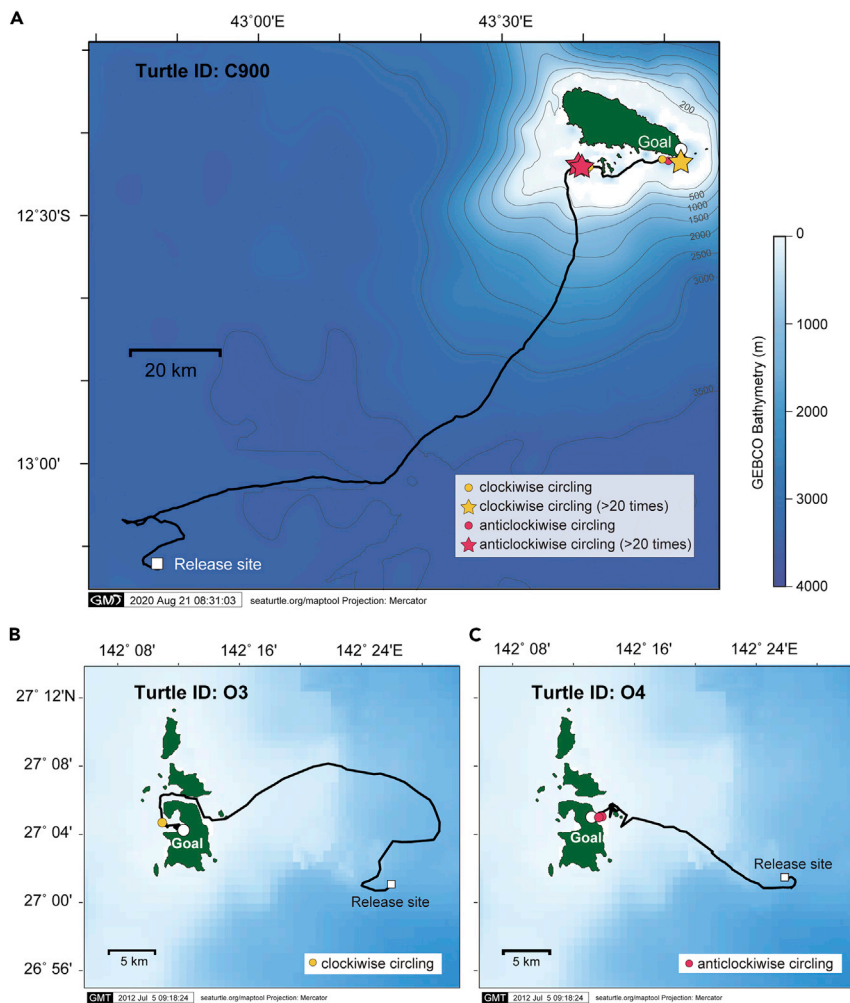
Figure 3. GPS tracks of homing green turtles

(A) Homing routes during displacement experiments conducted at Moheli Island, Comoro (12°22′S, 43°52′E) in 2010 and (B and C) Chichijima Island, Ogasawara, Japan (27°04′N, 142°12′E) in 2012.

are not mutually exclusive. For example, some animals might move in circles to enhance prey search while simultaneously collecting geomagnetic information. Others, such as elephant seals drifting down like falling leaves, might maintain directional sense by geomagnetic scanning while resting in seemingly featureless mesopelagic depths. Enhancing studies scrutinizing fine-scale movements would reveal circlings in more species that have otherwise been overlooked. Further examinations in relation to animals' internal state and environmental conditions would provide new insights into the function and mechanism underlying the movements.

Limitations of the study

This is an observational study based on the examination of high-resolution 3D movements of tagged animals. As such, our study lacks information about the surrounding environment such as landscapes, landmarks, and presence of other individuals of the same and/or other species. Simultaneous analysis of high-resolution 3D movements and animal-borne video recordings would be useful to examine circling movements in the context of social interactions and/or prey capture. Further investigations including some hypothesis testing experiments (e.g., magnet on/off experiments) are necessary to draw clear conclusions on the reasons of the circling movements.

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Resource availability

Lead contact

Further information and questions should be directed to and will be fulfilled by the lead contact, Tomoko Narazaki (naratomoz@gmail.com)

Material availability

No new materials were generated in this study.

Data and code availability

The original/source data are available from the lead contact on request.

METHODS

All methods can be found in the accompanying Transparent methods supplemental file.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2021.102221.

AUTHOR CONTRIBUTIONS

Conceptualization, T.N. and K. Sato; Investigation, T.N., I.N., K.A., T.I., K. Shiomi, P.L., H.S., C.G.M., R.M., C.A.B., H.Y., M.A., R.O., K.M., S.C., and J.B.; Writing – Original Draft, T.N.; Writing – Review & Editing, T.N., I.N., K.A., T.I., K. Shiomi, P.L., C.G.M., C.A.B., J.B., and K. Sato; Funding Acquisition, T.N. and K.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Supplemental information

Similar circling movements observed

across marine megafauna taxa

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Supplemental Information

Transparent Methods

Sampling behavioural Data

Fine-scale 3D movements data of tiger sharks (*Galeocerdo cuvier,* N = 4), a whale shark (*Rhincodon typus,* N = 1), green turtles (*Chelonia mydas,* N = 3), king penguins (*Aptenodytes patagonicus*, N = 6), Antarctic fur seals (*Arctocephalus gazella,* N = 4) and a Cuvier's beaked whale (*Ziphius cavirostris,* N = 1) were obtained by deploying multi-channel data loggers (3MPD3GT, Little Leonardo, Japan) that recorded depth, temperature, swim speed and 3-axis magnetism at 1 Hz and 3-axis acceleration at 8 - 16 Hz.

Two male and two female tiger sharks were captured using demersal longline set off the north-east coast of Oahu Island, HI, USA (21° 26' N, 157° 58' W) in 2013. Captured sharks were tail-roped alongside of a research boat and inverted to induce tonic immobility. Data loggers were attached to each shark following Nakamura et al. (2011). A male whale shark incidentally captured by a set-net in Yomitan (Okinawa Island, Japan, 26° 28' N, 127° 55' E) was equipped with a data logger package and released (see Nakamura et al. 2020 for the details).

For green turtles, displacement experiments were conducted for adult females nesting at oceanic islands: one nesting female at Moheli Island, Comoro (12°22'S, 43°52'E) in 2010 and two nesting females in Chichijima Island, Japan (27°04'N, 142°12'E) in 2012. The turtles were captured before laying eggs and individually confined in wooden crates at their nesting beach. On the following day, the turtles were transferred to oceanic release sites that were 150 km southwest and 20 km east from their nesting beaches in 2010 and 2012, respectively. Turtles were equipped with 3MPD3GT data loggers and Argos-linked Fastloc GPS tags (MK10, Wildlife Computers, USA in 2010 and F4G 371A, Sirtrack Ltd., New Zealand in 2012). All instruments were retrieved from the turtles when they returned to their nesting beaches 2 – 5 days after the release.

For king penguins, data were collected from chick-rearing penguins (sex unknown) at Possession Island (46° 25' S, 51° 45' E), Crozet Archipelago, South Indian Ocean, from late January to early March in 2011. For field procedures, see Shiomi et al. (2016) for the details.

For Antarctic fur seals, the fieldwork was conducted at Bird Island (54° 00' S, 38° 03' W), South Georgia during breeding season in 2009. All data was collected from females. For details, see Iwata et al. (2012).

A Cuvier's beaked whale was equipped with data loggers off the Ogasawara Islands (27°04'N, 142°12'E) in the western North Pacific Ocean during September in 2010. The whale was estimated as adult-size, but its sex was unknown. We approached the whale with a 20-m long fishing boat and deployed a suction-cup-attached tag using a 6 m pole. The weight of the whole tag was 410 g (see Type B tag in Aoki et al. 2012). After deploying the tag, we tried to follow the

37 tagged whale to observe its behaviour while maintaining >300 m distance from the whale to avoid
38 any disturbances.

39

40 *Data analysis and extraction of circling events*

41 Time-series data obtained from 3MPD3GT were analysed using IGOR Pro. ver. 6.37
42 (WaveMatrics, Lake Oswego, OR, USA) and 3D movements of each tagged animal was
43 reconstructed using data on swim speed, acceleration and magnetism, as described in Narazaki et
44 al. (2009). In this study, we defined a circling event as a consecutive same-direction circling
45 movement lasting for more than two times. To extract circling events, angular speed (deg s^{-1}) was
46 calculated from heading data and smoothed by 3 – 20 s to remove the effect of instantaneous noises.
47 Clockwise/anticlockwise circling events began when accumulated angular speed for 30s exceeded
48 mean angular speed plus/minus standard deviation multiplied by 1.5 – 2.0. Circling events ended
49 when the sign of angular speed changed (e.g., positive angular speed turn to negative in clockwise
50 event) and when mean angular speed for next 30 s reached zero (i.e., no constant turning occurred
51 in next 30s). All detected circling events were visually inspected to remove any false events. For
52 each circling event, cross-spectral density of sine of smoothed heading was computed using
53 DSPPeriodogram function in IGOR Pro to obtain dominant circling cycle of each event.

54

55 *Ethics statement*

56 This study was performed in accordance with the guidelines of the Animal Ethic Committee of the
57 University of Tokyo, and the protocol of the study was approved by this committee (Permit No.10-
58 26 for king penguin, No. P12-5 for green turtles in Ogasawara, No. P16-8 for sharks, No. P12-6
59 for beaked whales). The study of green turtles in Comoro was conducted as a part of the project
60 ESTVOI (ANR-07-BLAN-0220). The study of whales was carried out under a permit from the
61 Ogasawara Whale Watching Association (No.10-07). The studies of Antarctic fur seals were
62 approved by the British Antarctic Survey and the University of Cambridge Animal Welfare Review
63 Committee. Tiger shark handling and tagging activities were carried out in accordance with the
64 animal use protocols of the University of Hawaii Institutional Animal Care and Use Committee
65 (IACUC) and were approved under IACUC protocol #05-053.

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