

Sea turtles compensate deflection of heading at the sea surface during directional travel

T. Narazaki^{1,2,*}, K. Sato³, K. J. Abernathy⁴, G. J. Marshall⁴ and N. Miyazaki²

¹Department of Natural Environmental Studies, Graduate School of Frontier Science, The University of Tokyo, 1-15-1 Minamidai, Nakano, Tokyo 164-8639, Japan, ²Ocean Research Institute, The University of Tokyo, 1-15-1 Minamidai, Nakano, Tokyo 164-8639, Japan, ³International Coastal Research Center, Ocean Research Institute, The University of Tokyo, 2-106-1 Akahama, Otsuchi, Iwate 028-1102, Japan and ⁴National Geographic – Remote Imaging, 1145 17th Street NW Washington DC, 20036, USA

*Author for correspondence (tnarazaki@nenv.k.u-tokyo.ac.jp)

Accepted 15 September 2009

SUMMARY

Air-breathing marine animals, including sea turtles, utilise two fundamentally different environments (i.e. sea surface and underwater) during migration. Many satellite telemetry studies have shown travel paths at relatively large spatio-temporal scales, discussing the orientation and navigation mechanisms that guide turtles. However, as travel paths obtained by satellite telemetry only reflect movements at the surface, little is known about movements and orientation ability underwater. In this study, to assess orientation ability both at the surface and underwater, fine-scale 3-D movements of free-ranging loggerhead turtles *Caretta caretta* were reconstructed by using multi-sensor data loggers. Video systems ('Critttercam') were also used to record the behaviour of the turtles and the visual information surrounding the turtles. During August and October in 2006 and 2007, eight turtles were released from Otsuchi Bay, Japan (39°20'30N, 141°56'00E), and a total of 118 h of 3-D movements were reconstructed. Turtles maintained highly straight-line courses (straightness index >0.95) during 41% of the total duration (i.e. 'travelling periods'). During travelling periods, turtles swam continuously, maintaining unidirectional heading throughout dives whereas turtles changed heading remarkably at the surface. Despite highly directional movements during dives, travel direction tended to shift by the end of dives lasting 10 minutes or more. Such deflections seemed to be compensated during subsequent surfacing periods because there was a negative relationship between changes in travel direction arising during dives and subsequent surfacing periods. Therefore, remarkable changes in heading at the surface could be interpreted as direction-searching behaviour. Our results suggested that turtles undertaking directional travel were more dependent on directional information that was reliable at the surface.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/212/24/4019/DC1>

Key words: 3-D movements, orientation, loggerhead turtles, *Caretta caretta*.

INTRODUCTION

Sea turtles, like many marine animals, migrate for hundreds or thousands of kilometres between foraging and breeding habitats (Musick and Limpus, 1997; Plotkin, 2003). Although an extensive number of studies on land-living birds and insects provided significant insights on the orientation and navigation mechanisms (e.g. Wehner et al., 1996; Wiltschko and Wiltschko, 2003), the mechanisms that guide marine animals remain unrevealed. Advances in satellite telemetry in recent decades have allowed diverse species of marine megafauna to be tracked during long-distance migration (e.g. Block et al., 2003; Godley et al., 2007). In some cases, animals travelled in highly straight-line courses (Hughes et al., 1998; Luschi et al., 1996; Morreale et al., 1996; Weng et al., 2008). An astonishing example was reported by Luschi et al. (Luschi et al., 1998): green turtles (*Chelonia mydas*) nested at Ascension Island showed highly directed travel, maintaining straight courses for >1000 km during oceanic migration towards feeding grounds at the Brazilian coast, inferring the ability of directional travel during oceanic migration.

However, due to technical limitation, satellite telemetry only provides geographical locations when animals spent a sufficiently long time at the surface. Therefore, travel paths obtained by satellite telemetry are reconstructed by bridging sporadic points, which usually

exist in a relatively large spatio-temporal scale (i.e. in kilometres and in hours to days). As a consequence, these estimated travel paths only reflect movements at the surface but not underwater movements. It has been reported that sea turtles undertaking oceanic migration spent most of their time underwater (Hays et al., 2001; Rice and Balazs, 2008) where the sensory environment is fundamentally different from that of the sea surface (Lohman et al., 2008). To assess orientation and navigation ability of sea turtles during migration, therefore, it is necessary to examine underwater movements.

Two methods have been employed to reconstruct 3-D movements of free-ranging aquatic animals, of which direct observations are virtually impossible: acoustic telemetry and dead reckoning (Wilson et al., 2007). Using such methods, an increasing number of studies examined the 3-D movements of marine animals, such as seals (Davis et al., 1999; Davis et al., 2001; Hindell et al., 2002; Mitani et al., 2003), whales (Johnson and Tyack, 2003) and penguins (Shiomi et al., 2008). In acoustic telemetry, underwater movements of animals are tracked by acoustic receivers at known locations, which receive signals emitted from the animals. Acoustic receivers must be within a few hundred metres of the animals; thus, this method is difficult to use with widely ranging species (Wilson et al., 2007). Dead reckoning, however, overcomes this limitation. 3-

D movements are reconstructed by use of locomotion vectors: heading, depth (or pitch angle) and swim speed. It has been reported that fixed locations estimated by dead reckoning become more inaccurate with time due to the effects of ocean currents (Shiomi et al., 2008), because 3-D movements calculated by dead reckoning do not reflect any passive transport by external forces. However, dead reckoning provides fine-scale 3-D movements, which are useful to study the orientation of free-ranging animals by directly examining changes in heading on a timescale of seconds.

Therefore, by using dead-reckoning methods, we first aimed to reconstruct fine-scale 3-D movements of loggerhead turtles (*Caretta caretta*) under natural conditions. Then, by examining temporal changes in heading while undertaking travelling dives, we aimed to assess the orientation ability of turtles both at the surface and underwater.

MATERIALS AND METHODS

Study site and animals

During August and September in 2006 and during August and October in 2007, we attached multi-sensor data loggers to eight loggerhead turtles [*Caretta caretta* (L.)] and released them from Otsuchi Bay, Iwate, Japan (39°20'30N, 141°56'00E; Fig. 1A,B). In our study site, loggerhead turtles were occasionally captured by local set nets during summer (T.N., unpublished). The major nesting grounds of loggerhead turtles in the Pacific exist in southern Japan (Kamezaki et al., 2003). However, our study site is located at least several hundred kilometres away from the nesting grounds (Fig. 1A). It is inferred that turtles migrate to our study site for foraging as there are no nesting grounds in the vicinity. When by-catch occurred, turtles were immediately transferred to the International Coastal Research Center, Ocean Research Institute, the University of Tokyo (39°21'05 N, 141°56'04 E; Fig. 1B), where they were kept in captivity for between one week and up to two months. All turtles appeared in fine health. Size of turtles selected for instrumentation ranged from 588 to 850 mm (mean \pm s.d.=753 \pm 85 mm) in standard carapace length (SCL), and from 32.8 to 94.5 kg (mean \pm s.d.=66.1 \pm 18.8 kg) in body mass (BM) (Table 1). Although it is difficult to determine the degree of maturity in sea turtles, turtles used in the present study were considered as immature and mature turtles, based on measurements made of mature females nesting in Japan, ranged from 692 to 1031 mm in SCL (Kamezaki et al., 1995). Sex was determined as male only when obvious extension of the tail (tail length >300 mm) was observed in large turtles (SCL >700 mm). Otherwise, sex was not determined.

Data loggers

We used a multi-sensor data logger (W1000-3MPD3GT; 26 mm in diameter, 175 mm in length, 140 g in air; Little Leonardo Co., Tokyo, Japan), which recorded depth, temperature, swim speed, geomagnetic intensity and acceleration. Sampling interval was 1 s for all parameters except for acceleration that was recorded at 1/32 s intervals. Geomagnetic intensities and acceleration were recorded along 3-axes: transverse (i.e. sway), longitudinal (i.e. surge) and dorso-ventral (i.e. heave) axes (Fig. 2). 3MPD3GT can record up to 64 MB of data with 12-bit resolution. The maximum range of a depth sensor is 1000 m with a resolution of 0.24 m. The range of geomagnetic intensities and acceleration sensors were $\pm 2.0 \times 10^5$ nT and ± 49.0 ms⁻², respectively. Swim speed was recorded as the rotation of an external impeller mounted on the anterior end of 3MPD3GT. As there was strong linear relationship between number of rotations and speed of water flow passing

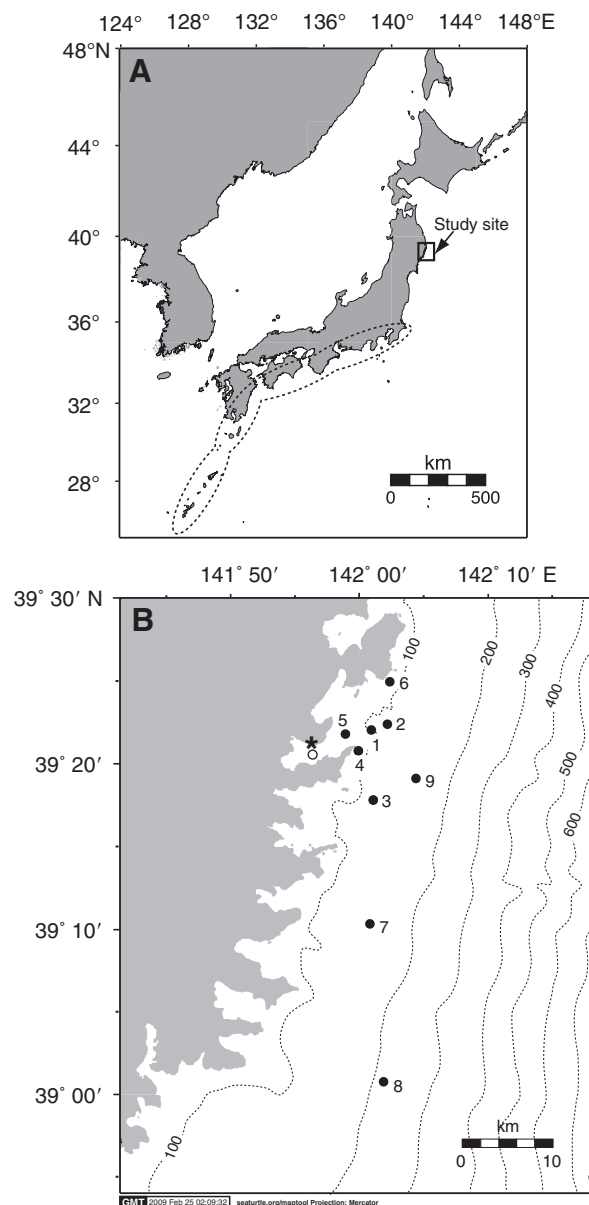


Fig. 1. (A) Japanese Archipelago showing the location of the study site. Coastal areas encircled by a broken line indicates locations of nesting sites of loggerhead turtles based on information by Kamezaki et al. (Kamezaki et al., 2003). (B) Map of the study site showing the locations where the instrumented turtles were released (open dot) and the instruments were retrieved (solid dots with deployment number) in relation to the bathymetry. In the case of deployment number 6, a dot indicates the location of set net in which the instrumented turtle was accidentally recaptured. An asterisk indicates the location of the International Coastal Research Center, Ocean Research Institute, the University of Tokyo, where turtles were kept until the time of release.

through the impeller (e.g. Akamatsu et al., 2002; Kawabe et al., 2004; Watanabe et al., 2008), rotation number of the impeller (number of rotations per second) was converted into swim speed (ms⁻¹) using a regression line obtained from a calibration experiment conducted for each logger. The coefficient of determination (R^2) was ≥ 0.95 for all loggers. The stall speed was 0.20 ms⁻¹, and speeds <0.20 ms⁻¹ were considered as indistinguishable from zero in this study.

Table 1. Summary of deployments on loggerhead turtles at Otsuchi Bay, Iwate, Japan, between August and October in 2006 and 2007

Deployment number	Turtle ID	Straight carapace length (mm)	Body mass (kg)	Sex	Time of deployment	Deployment duration (h)	Duration of travelling periods (h)
1	L0601	728	61.6	Male	Day	6.9	3.2
2*	L0711†	850	94.5	Unknown	Day	4.9	2.9
3	L0602	788	65.5	Male	Night	14.4	1.4
4	L0603	588	32.8	Unknown	Night	14.3	8.0
5	L0609	836	76.0	Male	Night	15.6	2.6
6*	L0711†	850	94.5	Unknown	Night	13.5	2.0
7*	L0708	730	54.5	Unknown	Night	16.5	11.5
8*	L0705	800	83.0	Unknown	Night	15.8	7.8
9*	L0704	700	60.5	Unknown	Night	16.9	9.0

*Cittercam was deployed in the experiment.

†L0711 was used for the study twice because it was recaptured by a set net after the first experiment.

In addition to 3MPD3GT, animal-borne imaging systems ('Cittercam', 76 mm in diameter, 350 mm in length, 1.5 kg in air; National Geographic – Remote Imaging, Washington DC, USA) were used in the five deployments conducted in 2007. Cittercam consists of a microprocessor-controlled video recorder (8-h maximum video recording time), batteries, lights, VHF transmitter, microphone and pressure transducer in the water- and pressure-proof housing. We programmed the Cittercam to record video during daytime (i.e. start recording shortly before dawn, and stop recording just before dusk) so that there is sufficient ambient light to avoid using the built-in lights. 3MPD3GT, however, recorded throughout the deployment.

Our data loggers must be retrieved to obtain the data. Because it is difficult to recapture instrumented turtles, we adopted an automatic time-scheduled release system modified from Watanabe et al. (Watanabe et al., 2004). In deployments conducted in 2006, a 3MPD3GT was attached to a float of copolymer foam (Nichiyu Giken Kogyo, Saitama, Japan), in which a VHF transmitter (Advanced Telemetry Systems, Isanti, MN, USA) and a time-scheduled release mechanism (Little Leonardo Co.) were embedded. In 2007, the 3MPD3GT was attached to a Cittercam, which was equipped with a VHF transmitter. 3MPD3GT and Cittercam package was positively buoyant by itself. On each turtle's carapace, we glued a plastic mesh with 5-min quick-set epoxy (Konishi Co., Osaka, Japan). Then, the logger package was attached onto the plastic mesh by a plastic cable-tie connected to a time-scheduled release mechanism. The release mechanisms were programmed to activate 5–17 h after deployments, at which time an electric charge incised the plastic cable, releasing the logger packages from the turtles. The logger package was located *via* VHF radio signals using a three-element Yagi antenna and a receiver (Ham Center, Sapporo, Hokkaido, Japan), and recovered by R/V 'Yayoi' from the International Coastal Research Center.

Data analysis

Time-series data obtained from 3MPD3GT were analysed using IGOR Pro (WaveMetrics, Lake Oswego, OR, USA). A dive was defined as any submergence to a depth of >1 m. In the present study, however, we only focused on deep dives, defined as those with a maximum depth >4 m, to exclude short subsurface dives. A surfacing was defined as a period between deep dives.

Acceleration sensors of 3MPD3GT recorded both dynamic (e.g. flipper movement) and static acceleration (i.e. gravity), allowing it to be used for a tilt sensor. Changes in static accelerations as a result of posture changes were extracted by using a 0.25 Hz low path filter (IFDL ver 4; WaveMetrics) (Sato et al., 2003). Due to variation in the shapes of the carapaces, 3MPD3GT was not always attached exactly parallel to the longitudinal axis of the turtle. To correct such deviance from the longitudinal axis *post hoc*, we measured the deviance by letting the instrumented turtles sit motionless for at least 30 s before release.

At the study site, the total geomagnetic intensity was 47812.8 nT at a vector defined as declining 7°55' to the west and inclining 53°24' downward using IGRF 2000 (Geophysical Data Center, NOAA Satellite and Information Service, <http://www.ngdc.noaa.gov/geomagmodels/IGRFWMM.jsp>). Geomagnetic intensity recorded by 3MPD3GT became maximum when the logger was directed to the vector of total geomagnetic intensity, and varied depending on the bearing and tilt of the logger. Thus, the heading of an instrumented turtle was deduced from 3-axis geomagnetic intensities and acceleration information (Johnson and Tyack, 2003; Shiomi et al., 2008). Headings were expressed in degrees following compass convention. Thereafter, 3-D movements were reconstructed from depth, heading, pitch and swim speed using the dead-reckoning method (Mitani et al., 2003; Shiomi et al., 2008; Wilson et al., 2007).

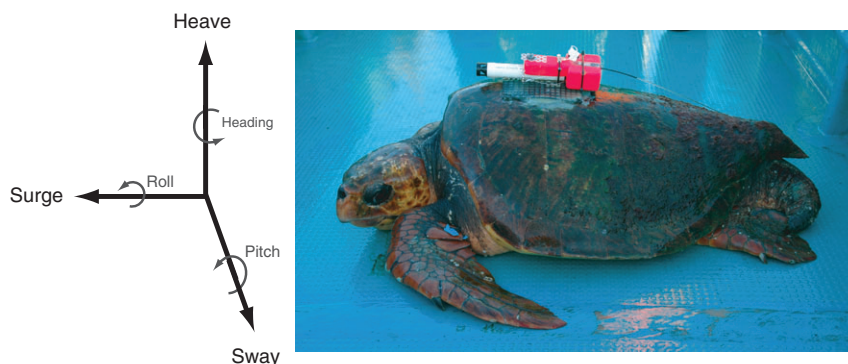


Fig. 2. A loggerhead turtle equipped with a 3MPD3GT and time-scheduled releasing mechanism. Arrows indicate direction of axes (surge, heave and sway) at which acceleration and geomagnetic intensity were recorded.

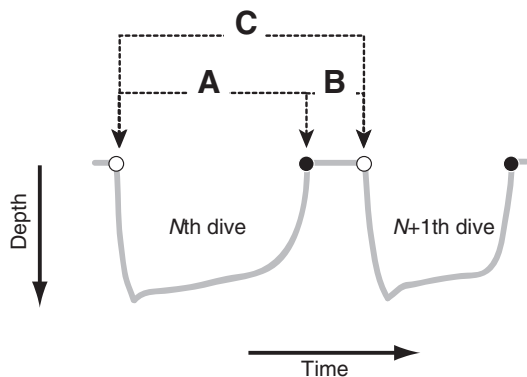


Fig. 3. A schematic diagram of consecutive dives that occurred during travelling periods. Open and solid dots indicate positions of the start and the end of dive, respectively. Mean headings of first and final 10 s of dives were compared using Moore test for second-order data (Zar, 1998) to test whether travel directions were the same at the start and the end of Mth dive (A); at the end of Mth dive and at the start of N+1th dive (B); and at the start of Mth dive and N+1th dive (C) (see Table 2 for results).

Crittercam recorded video data as MPEG4-DivX video format. Video data were analysed using DivX player for Macintosh-2.2 (DivX, San Diego, CA, USA), and linked with dive data recorded by 3MPD3GT.

Analysis of headings

In this study, we were interested in the orientation of turtles undertaking directional movements. A straightness index, calculated as the minimum horizontal distance between the start and end points divided by horizontal distance actually travelled (Benhamou, 2004), was computed on an hourly basis. A period of directional movements (hereafter called ‘travelling period’) was defined as a 1-h period of which a straightness index was greater than 0.95. During travelling periods, directionality, *r*, was calculated at each minute to examine temporal variation in directionalities of heading. Directionality, *r*, ranged from 0 when heading was uniformly oriented to 1 when heading was unidirectional (Zar, 1998).

To examine whether heading was consistent at the start and the end of each dive during travelling periods, mean headings of the first and the final 10 s of each dive were compared (see Fig. 3A). Furthermore, inter-dive changes in heading were compared in two ways: the end of a dive and the start of the subsequent dive (see Fig. 3B), and the start of two consecutive dives (see Fig. 3C). Inconsistency of heading was tested by Moore test, a non-parametric paired-sample test for circular data (Zar, 1998), at significant level of 0.05.

In addition, heading changes during post-dive surfacing periods were compared in relation with heading changes that arose during dives using generalised linear mixed model (GLMM) in R package (The R Project for Statistical Computing, <http://www.r-project.org/>). We used the mixed model because data obtained from the same individual as well as from the same deployment were not independent. Therefore, deployments and individuals were treated as random variables. Dependent variable was angular difference between heading at the end of a dive and the start of a subsequent dive (Fig. 3B). Explanatory variables were angular difference between at the start and the end of each dive (Fig. 3A), and time of day (i.e. daytime or night-time). We used the normal error and identity link function. The most parsimonious model was selected on the basis of Akaike Information Criterion (AIC). χ^2 analysis of deviance was used to determine the effect of term in selected model.

RESULTS

Deployment summary

A total of 118 h of 3MPD3GT data was obtained from eight turtles over nine deployments, and a total of 17 h of video data was recorded from four turtles (see Table 1 for deployment summary). Deployments were made either during daytime or night-time. Seven out of nine deployments were night-time deployments, in which data were recorded from dusk to the following morning (17:00 h to 10:30 h). In the other deployments, data were recorded during daytime (05:30 h to 12:30 h). The weather during deployments was either fair or cloudy. At the end of deployments, sets of instruments were successfully retrieved either at the mouth or outside of Otsuchi Bay (Fig. 1B) shortly after time-scheduled release mechanisms were activated. One exception was deployment number 6, in which the instrumented turtle was accidentally recaptured in a local set net in the middle of the experiment. Therefore, in this case, only data collected before entering the set net were used for analysis.

Diving behaviour during travelling period

3-D movement was reconstructed for each deployment (Fig. 4). To examine oriented movements, we focused on ‘travelling periods’, which accounted for 41% of the total duration. A total of 125 dives were recorded during travelling periods. Mean duration and depth of the dives were 17.7±12.6 min and 22.7±17.3 m (±s.d.), respectively. Dives usually occurred consecutively, which were interrupted by a few minutes of surfacing. Most of the dives (101 out of 125 dives) shared a common feature having a gradual ascent phase in between the initial descent and final ascent phase (see Fig. 5A). Such gradual ascent dives were observed during both daytime (42 dives) and night-time (59 dives). During gradual ascent dives, turtles swam continuously with a mean swim speed of 0.6±0.2 m s⁻¹ (±s.d., N=101).

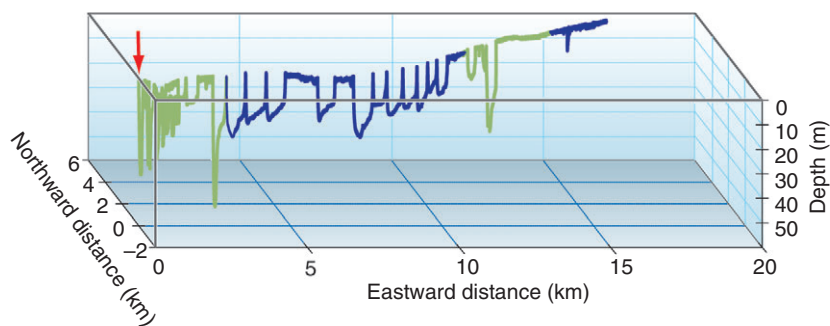


Fig. 4. An example of 3-D movements for 15 h. Release site is pointed by a red arrow. Periods of ‘travelling’ and ‘non-travelling (sinuous)’ were indicated with blue and green, respectively.

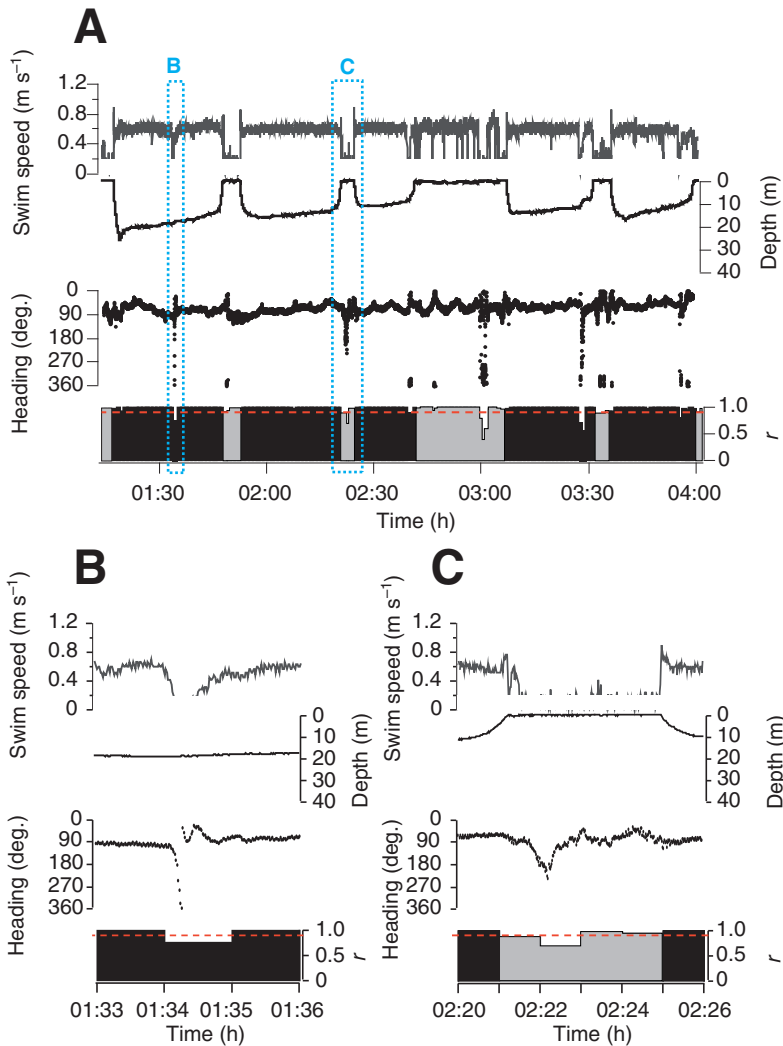


Fig. 5. (A) Time-series graph showing changes in swim speed, depth and heading. Additionally, directionality, r , computed for each minute was showed at the undermost axis, of which colour denoted the turtle was either diving (black) or surfacing (grey). The red broken line indicated $r=0.9$. (B) An example of heading fluctuation during a travelling dive. (C) An example of changes in heading during a surfacing between dives.

Orientation of travelling turtles

Directionality, r , computed at 1-min intervals during travelling periods, was plotted against mean depth in Fig. 6, which shows clear dichotomy between at surface and during dives. Directionality at the surface was significantly lower than that at depths of >1 m (Wilcoxon rank test, $P < 0.05$). Some remarkable changes in heading were occasionally recorded during surfacing in between travelling dives (Fig. 5C). Such changes in heading were also confirmed by video recorded by Crittercam while the turtles were taking breaths at the surface (see Movie 1 in supplementary material). By contrast, turtles tended to maintain unidirectional heading during dives (mean $r \pm$ s.d. = 0.99 ± 0.04 , $N = 2216$). In some cases, however, directionality drastically dropped below 0.90 during dives. Twenty such fluctuations in heading during dives (hereafter called 'fluctuation') were recorded from six turtles. Ranges of fluctuation sometimes reached >360 deg. (Fig. 5B). However, mean heading of post-fluctuation (i.e. 1-min after the fluctuation) was not significantly different from that of pre-fluctuation (i.e. 1-min before the fluctuation) (Moore test for second-order data, $N = 20$, $R' = 0.79$, $P > 0.10$). We successfully obtained video data for three fluctuation events: two were associated with mid-water foraging on gelatinous prey, and the other was associated with face scratching by flippers to get rid of food particles (see Movie 2 in supplementary material).

During travelling periods, most dives were performed consecutively interrupted by a few minutes of surfacing. For such consecutive dives (38 daytime and 65 night-time dives), headings at the start and the end of each dive (i.e. Fig. 3A) were significantly different in four turtles (see Table 2A for significant levels). Likewise, headings at the end of a dive and the start of a subsequent dive (i.e. Fig. 3B) were significantly different in five turtles (see Table 2B for significant levels), implying that travelling direction tended to shift both during each dive and surfacing. However, there were no significant differences in heading at the start of two consecutive dives (i.e. Fig. 3C) in any of the instrumented turtles (see Table 2C).

The GLMM for angular difference in heading arising during surfacing (i.e. Fig. 3B) revealed that it was related to angular difference in heading at the start and the end of the previous dive (i.e. Fig. 3A; $\chi^2 = 6.1941$, $P = 0.013$), time of day ($\chi^2 = 6.3089$, $P = 0.012$) and interaction between these two variables ($\chi^2 = 6.7284$, $P = 0.009$). Because the model showed that there was a significant interaction effect of heading change during dive and time of day, we used GLMM for daytime and night-time data separately to examine the relationship between heading changes arising during dives and during surfacings. The GLMM for night-time data revealed that angular differences in heading arising during surfacings were negatively related to those during the preceding dives (Fig. 7; $\chi^2 = 10.026$, $P = 0.002$). However, the model selected for daytime data

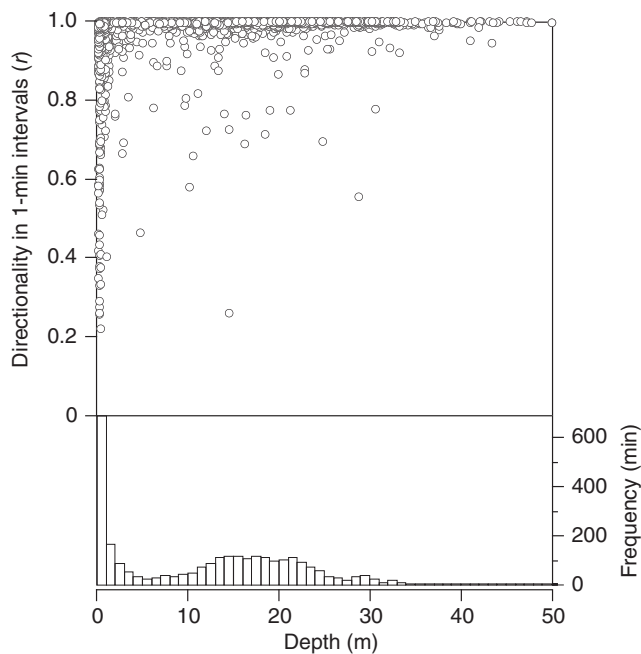


Fig. 6. Directionality of heading was plotted against mean depths for each 1-min interval during travelling periods in the upper figure. Histogram of mean depth for each interval was showed in the lower figure, revealing a bimodal pattern of depth utilisation with peaks near the surface and at approximately 18 m.

showed no significant relationship between angular differences in heading changes arising during dives and subsequent surfacing ($\chi^2=0.059$, $P=0.808$).

Angular difference in heading direction at the start and the end of daytime dives (mean absolute angular difference \pm s.d.= 17 ± 13 deg., $N=38$) was significantly smaller than that of night-time dives (mean absolute angular difference \pm s.d.= 24 ± 17 deg., $N=65$; Wilcoxon rank test, $P<0.05$). There was no significant difference in dive depth during daytime and night-time (Wilcoxon rank test, $P=0.18$).

DISCUSSION

To date, a number of laboratory experiments (for a review, see Lohmann and Lohmann, 1996) and satellite tracking studies (e.g. Akesson et al., 2003; Hays et al., 2003; Papi et al., 2000) have been conducted to examine potential cues used for orientation and navigation of sea turtles. However, little information about how turtles maintain their heading while swimming in the open sea was

presented. In the present study, we reconstruct 3-D movements using sophisticated multi-sensor data loggers to examine temporal changes in heading of turtles under natural conditions on a timescale of seconds. In addition, animal-borne video cameras were used simultaneously in some deployments, and orientation behaviours were examined in relation to the visual information around turtles. This is the first report of fine-scale 3-D movements of sea turtles, although 3-D movements have been described in some seals (Davis et al., 2001; Hindell et al., 2002; Mitani et al., 2003; Simpkins et al., 2001), whales (Johnson and Tyack, 2003) and penguins (Shiomi et al., 2008).

This study was conducted far beyond the northern limit of nesting sites of loggerhead turtles where some loggerhead and green turtles (*C. mydas*) were occasionally sighted during summer. Blessed with the nutrient rich, cold Oyashio current and the warm Kuroshio current, the study site may be a favourable foraging site for turtles. However, mean surface temperature falls to below 4°C in March (Sato et al., 2007), which seems to be below the lethal temperature for loggerhead turtles as cold-stunning events of loggerhead turtles were widely reported when surface temperature dropped below 8°C (e.g. Witherington and Ehrhart, 1989). Therefore, the study site only provides a seasonal habitat for loggerhead turtles. In fact, according to an ongoing study of demographics around the study site, occurrences of loggerhead turtles were limited to the period July through to October (T.N., unpublished). Turtles presumably migrate to warmer latitudes outside this period, evidenced from a recapture of a tagged turtle at approximately 1000 km south, seven months after being released from the study site (T.N., unpublished). Therefore, turtles in the present study were considered to be motivated to migrate to warmer habitats by the beginning of autumn. Unfortunately, however, we lack information about the exact destination of the instrumented turtles. Hence, we focused on the orientation of turtles while following straight paths on an hourly basis (i.e. 'travelling period'), which could be interpreted as highly directional movements (Benhamou, 2004).

During travelling periods, turtles repeatedly performed dives with a distinctive profile characterised by a prolonged phase of gradual ascending during the middle of dives, which have been widely reported in marine reptiles, such as sea snakes (Rubinoff et al., 1986), green turtles (e.g. Hochscheid et al., 1999), loggerhead turtles (e.g. Minamikawa et al., 1997) and flatback turtles (Sperling, 2008). In the present study, turtles swam continuously throughout the dives, including gradual ascent dives, maintaining unidirectional heading. Unidirectional travel could be achieved by simply repeating regular motions (i.e. keep a constant posture and flipper motions), which were regulated by internal sensory information. However, this strategy was insufficient because errors derived from motor and sensory systems would accumulate with passing time, suggesting

Table 2. Summary of statistical analysis (R' of Moore test for second-order circular data)

Deployment number	N	A		B		C	
1	25	0.8301	n.s.	1.2145	*	0.1710	n.s.
2	13	0.5000	n.s.	0.2913	n.s.	0.2989	n.s.
3	10	1.6274	***	1.7031	***	0.2081	n.s.
4	3	0.3833	n.s.	0.1314	n.s.	0.0756	n.s.
5	2	0.3541	n.s.	0.3559	n.s.	1.0441	n.s.
6	24	2.1380	***	2.0238	***	0.3234	n.s.
7	11	1.6989	***	1.7705	***	0.4410	n.s.
8	10	1.5610	***	1.5347	***	0.2773	n.s.
9	5	0.0828	n.s.	0.4451	n.s.	0.4628	n.s.

See Fig. 3 for three positions at which heading was compared (* $P<0.05$, ** $P<0.01$, *** $P<0.001$, n.s.: non-significant).

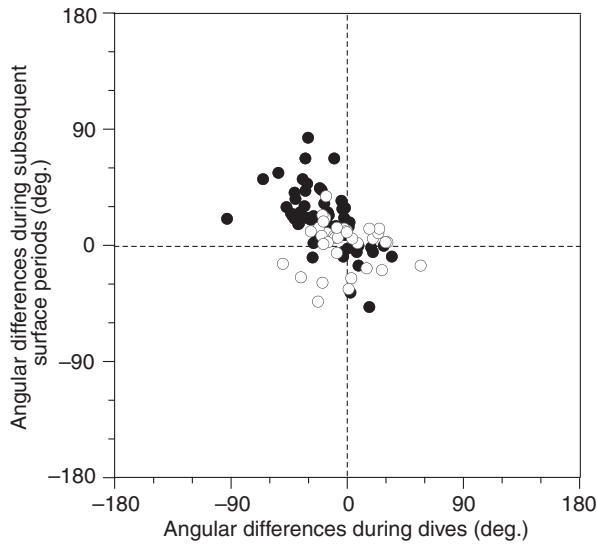


Fig. 7. A figure showing a relationship between angular differences in heading during post-dive surfacing (Fig. 3B) and that during dives (Fig. 3A). Positive value signifies that heading shifted in a clockwise direction. Open and solid dots indicate daytime and night-time dives, respectively. The GLMM for night-time dive revealed a negative relationship between angular difference in heading during dives and during post-dive surfacing periods.

the importance of aid *via* external directional references in oriented travel (Cheung et al., 2007). In the present study, fluctuations in heading, associated with occasional non-travelling behaviours (i.e. mid-water foraging and self-cleaning behaviours), occurred suddenly in the course of travelling dives. It is noteworthy that travel direction did not significantly change after fluctuation events although turtles sometimes whirled around more than once (see Fig. 5B for example). Our result showed the ability of sea turtles to orient to prior direction, which would not be accomplished without the aid of directional references.

Depths utilised by travelling turtles were mostly between 10 and 25 m (Fig. 6). Turtles probably selected the depth where they can attain neutral buoyancy to minimise the energy required for overcoming upward and/or downward forces (Minamikawa et al., 2000). It has been estimated for adult green turtles that maximum depths at which they can attain neutral buoyancy after fully inspiring their lungs were 15–20 m (Hays et al., 2004). Although our turtles were relatively smaller, it was speculated that our turtles could attain neutral buoyancy at similar depths. However, at these depths, celestial cues such as the position of the sun and stars could not be perceived because light was reflected, absorbed and scattered at the sea surface. Additionally, turtles were unable to use sea bottom topography as landmarks because regional depths of the study site were far greater than 25 m (Fig. 1B). Hence, geomagnetic information would be practically the only directional reference available in mid-water. Under laboratory conditions, a magnetic compass has been demonstrated to exist in various aquatic animals, such as sea turtles (for a review, see Lohmann and Lohmann, 1996), salmonid fishes (Quinn, 1980) and spiny lobsters (Boles and Lohmann, 2003). It is possible for loggerhead turtles that geomagnetic cues were being used for maintaining direction at depth.

Travel direction, however, did veer by the end of dives (i.e. mean dive duration = 17.7 ± 12.6 min) in some turtles, probably due to insufficient accuracy of directional compass (i.e. geomagnetic compass) and/or the gradual errors that accumulated over time.

Interestingly, our results showed that if the travel direction shifted during dives, then it also shifted during the subsequent surfacing periods (see Table 2A,B). In contrast to highly directional movements during dives, changes in heading were remarkable during surfacing (see Fig. 5C and Movie 1 in supplementary material). The result from the GLMM for night-time data indicated that there was a negative relationship between the directions of heading changes during dives and during subsequent surfacing periods (Fig. 7), i.e. turtles shifted their heading during post-dive surfacing to the direction to compensate for the deflection that occurred during dives in night-time. For example, when heading shifted in a clockwise direction during a dive, heading tended to shift in an anti-clockwise direction during post-dive surfacing, and *vice versa*. As a consequence, travel directions at the start of consecutive dives were retained (Table 2C). Therefore, remarkable changes in heading during surfacing could be considered as direction searching behaviour to orient itself toward the desired direction. In the present study, the result from GLMM for daytime data showed no obvious relationship between direction changes during dives and during subsequent surfacing periods. Unfortunately, we have limited duration of daytime data compared with night-time data. Therefore, our result did not refute the turtles' ability to direction search at the surface during daytime but, rather, more importantly, showed that turtles were capable of orienting themselves at the surface during night-time in the absence of sunlight.

It has been reported that sea turtles undertaking oceanic migration showed diel difference in their dive behaviour (Hays et al., 2001). Although there was no significant difference in dive depth during daytime and night-time, our result showed that the changes in direction with daytime dives were smaller than that with night-time dives (Fig. 7). As there would still be some visible light at depth (i.e. mean dive depth \pm s.d. = 22.7 ± 17.3 m) during the day, turtles might be able to maintain their heading during daytime dives. It is possible that turtles used different strategies for orientation during daytime and night-time.

It is suggested that turtles have limited access to directional references in seemingly featureless mid-water. However, once turtles came up to the sea surface, there were more potential orientation cues. For example, coastal topographical features could be used as a reference indicating the direction of the opening of Otsuchi Bay (see Movie 1 in supplementary material) or the current position in relation to the coast. Information derived from the sun (e.g. azimuth of the sun) could be also used at the surface. Use of a sun compass has been demonstrated in various taxa, including freshwater turtles (DeRosa and Taylor, 1980). However, in the present study, some travelling dives and direction searching at the surface were performed during night-time, indicating that turtles had the ability to orient and to undertake directional travel regardless of the time of day. Thus, it suggested that the sun was not essential for turtles' orientation, although use of the sun compass cannot be ruled out. In the absence of sunlight, coastal topographic features may also be invisible to turtles. Under such a situation, however, turtles might be able to orient in relation to the location of the coast using artificial light constantly emitted from local towns along the coast. Other potential visual cues available during night-time include celestial information (i.e. stars and moon). But previous studies using satellite telemetry reported that turtles were able to keep their course during moonless nights (Hughes et al., 1998; Luschi et al., 1998). Because ophthalmological and anatomical studies reported that sea turtles are too myopic in the air to see stars (Ehrenfeld and Koch, 1967), use of celestial compass seems to be unrealistic. Non-visual information, such as waves, was also potentially available at the sea surface. Given that

hatchlings have the ability to direct their movements in relation to wave direction (Lohmann and Lohmann, 1996), adult and immature turtles may utilise waves as a directional reference. It has been reported that many animals use multiple sources of directional references in orientation and navigation (reviewed in Able, 1991; Avens and Lohmann, 2003) (for juvenile loggerhead turtle), and some of these mechanisms seemed often to be related hierarchically (reviewed in Able, 1991). Time-series heading data showed that turtles have the ability to maintain unidirectional heading in featureless mid-water, with a certain degree of accuracy. Travel direction, however, tended to veer off by the end of travelling dives lasting 10 minutes or more, and such deflections were adjusted at the surface where more directional references were potentially available. Therefore, our results suggest that turtles undertaking directional travel were more dependent on directional information available at the surface, although the particular source(s) of information used by the turtles is yet to be determined.

Field experiments were conducted under permission from the Ethics Committee of the University of Tokyo. We are grateful to volunteers from Fisheries Cooperative Association of Funakoshi Bay, Kamaishi Bay, Kamaishi-Tobu, Miyako, Omoe, Otsuchi and Yamada for their assistance in collecting turtles. Special thanks goes to crews of R/V Yayoi: M. Kurosawa, K. Morita and J. Takada for assistance in the field. We also acknowledge use of the Maptool (<http://www.seaturtle.org/>) program for the map of study site. This study was financially supported by the Sasakawa Scientific Research Grant from The Japan Science Society (19-526), grants from the Japanese Society for the Promotion of Science (A19255001), JSPS Research Fellowship for Young Scientists (21-7432), and the program 'Bio-Logging Science of the University of Tokyo (UTBLS)' led by N. Miyazaki. We also thank to G. C. Hays for fruitful comments.

REFERENCES

- Able, K. P. (1991). Common themes and variations in animal orientation systems 1. *Integr. Comp. Biol.* **31**, 157-167.
- Akamatsu, T., Wang, D., Wang, K., Wei, Z., Zhao, Q. and Naito, Y. (2002). Diving behaviour of freshwater finless porpoises (*Neophocaena phocaenoides*) in an oxbow if the Yangtze River, China. *ICES J. Mar. Sci.* **59**, 438-443.
- Akesson, S., Broderick, A. C., Glen, F., Godley, B. J., Luschi, P., Papi, F. and Rays, G. C. (2003). Navigation by green turtles: which strategy do displaced adults use to find Ascension Island? *Oikos* **103**, 363-372.
- Avens, L. and Lohmann, K. J. (2003). Use of multiple orientation cues by juvenile loggerhead sea turtles *Caretta caretta*. *J. Exp. Biol.* **206**, 4317-4325.
- Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *J. Theor. Biol.* **229**, 209-220.
- Block, B. A., Costa, D. P., Boehlert, G. W. and Kochevar, R. E. (2003). Revealing pelagic habitat use: the tagging of Pacific pelagics program. *Oceanolog. Acta* **25**, 255-266.
- Boles, L. C. and Lohmann, K. J. (2003). True navigation and magnetic maps in spiny lobsters. *Nature* **421**, 60-63.
- Cheung, A., Zhang, S., Stricker, C. and Srinivasan, M. V. (2007). Animal navigation: the difficulty of moving in a straight line. *Biol. Cybern.* **97**, 47-61.
- Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., Kohin, S. and Horning, M. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* **283**, 993-996.
- Davis, R. W., Fuiman, L. A., Williams, T. M. and Le Boueuf, B. J. (2001). Three-dimensional movements and swimming activity of a northern elephant seal. *Comp. Biochem. Physiol. A* **129**, 759-770.
- Derosa, C. T. and Taylor, D. H. (1980). Homeward orientation mechanisms in 3 species of turtles (*Trionyx spinifer*, *Chrysemys picta* and *Terrapene carolina*). *Behav. Ecol. Sociobiol.* **7**, 15-23.
- Ehrenfel, D. W. and Koch, A. L. (1967). Visual accommodation in green turtle. *Science* **155**, 827-828.
- Godley, B. J., Blumenthal, J. M., Broderick, A. C., Coyne, M. C., Godfrey, M. H., Hawkes, L. A. and Witt, M. J. (2007). Satellite tracking of sea turtles: Where have we been and where do we go next? *Endang. Spec. Res.* **4**, 3-22.
- Hays, G. C., Akesson, S., Broderick, A. C., Glen, F., Godley, B. J., Luschi, P., Martin, C., Metcalfe, J. D. and Papi, F. (2001). The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive duration, dive profiles and depth distribution. *J. Exp. Biol.* **204**, 4093-4098.
- Hays, G. C., Akesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. and Luschi, P. (2003). Island-finding ability of marine turtles. *Proc. R. Soc. Lond. B.* **270**, S5-S7.
- Hays, G. C., Metcalfe, J. D. and Walne, A. W. (2004). The implications of lung-regulated buoyancy control for dive depth and duration. *Ecology* **85**, 1137-1145.
- Hindell, M. A., Harcourt, R., Waas, J. R. and Thompson, D. (2002). Fine-scale three-dimensional spatial use by diving lactating female Weddell seals *Leptonychotes weddellii*. *Mar. Ecol. Prog. Ser.* **242**, 275-284.
- Hochscheid, S., Godley, B. J., Broderick, A. C. and Wilson, R. P. (1999). Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Mar. Ecol. Prog. Ser.* **185**, 101-112.
- Hughes, G. R., Luschi, P., Mencacci, R. and Papi, F. (1998). The 7000-km oceanic journey of a leatherback turtle tracked by satellite. *J. Exp. Mar. Biol. Ecol.* **229**, 209-217.
- Johnson, M. P. and Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild mammals to sound. *IEEE J. Oceanic Eng.* **28**, 3-12.
- Kamezaki, N., Goto, K., Matsuzawa, Y., Nakajima, Y., Oomuta, K. and Sato, K. (1995). Carapace length and width of the loggerhead turtle, *Caretta caretta* nested in the coast of Japan. *Umigame Newsletter of Japan* **26**, 12-13. (in Japanese).
- Kamezaki, N., Matsuzawa, Y., Abe, O., Asakawa, H., Fujii, T., Goto, K., Hagino, S., Hayami, M., Ishii, M., Iwamoto, Y. et al. (2003). Loggerhead turtles nesting in Japan. In *Loggerhead Sea Turtles* (ed. A. B. Bolten and B. E. Witherington), pp. 210-217. Washington: Smithsonian Institution.
- Kawabe, R., Naito, Y., Sato, K., Miyashita, K. and Yamashita, N. (2004). Direct measurement of the swimming speed, tailbeat, and body angle of Japanese flounder (*Paralichthys olivaceus*). *ICES J. Mar. Sci.* **61**, 1080-1087.
- Lohmann, K. J. and Lohmann, C. M. F. (1996). Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* **199**, 73-81.
- Lohmann, K. J., Lohmann, C. M. F. and Endres, C. S. (2008). The sensory ecology of ocean navigation. *J. Exp. Biol.* **211**, 1719-1728.
- Luschi, P., Papi, F., Liew, H. C., Chan, E. H. and Bonadonna, F. (1996). Long-distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study. *J. Comp. Physiol. A* **178**, 447-452.
- Luschi, P., Hays, G. C., Del Seppia, C., Marsh, R. and Papi, F. (1998). The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proc. R. Lond. B.* **265**, 2279-2284.
- Minamikawa, S., Naito, Y. and Uchida, I. (1997). Buoyancy control in diving behavior of the loggerhead turtle, *Caretta caretta*. *J. Ethol.* **15**, 109-118.
- Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T. and Sakamoto, W. (2000). Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *J. Exp. Biol.* **203**, 2967-2975.
- Mitani, Y., Sato, K., Ito, S., Cameron, M. F., Siniiff, D. B. and Naito, Y. (2003). A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. *Polar Biol.* **26**, 311-317.
- Morreale, S. J., Standora, E. A., Spotila, J. R. and Paladino, F. V. (1996). Migration corridor for sea turtles. *Nature* **384**, 319-320.
- Musick, J. A. and Limpus, C. J. (1997). Habitat utilization and migration in juvenile sea turtles. In *The Biology of Sea Turtles* (ed. P. L. Lutz and J. A. Musick), pp. 137-164. Florida: CRC Press.
- Papi, F., Luschi, P., Akesson, S., Capogrossi, S. and Hays, G. C. (2000). Open-sea migration of magnetically disturbed sea turtles. *J. Exp. Biol.* **203**, 3435-3443.
- Plotkin, P. (2003). Adult Migrations and Habitat Use. In *The Biology of Sea Turtles volume II* (ed. P. L. Lutz, J. A. Musick and J. Wyneken), pp. 225-242. Florida: CRC Press.
- Quinn, T. P. (1980). Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *J. Comp. Physiol. A* **137**, 243-248.
- Rice, M. R. and Balazs, G. H. (2008). Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations. *J. Exp. Mar. Biol. Ecol.* **356**, 121-127.
- Rubinoff, I., Graham, J. B. and Motta, J. (1986). Diving of the sea snake *Pelamis platurus* in the Gulf of Panamá. *Mar. Biol.* **91**, 181-191.
- Sato, K., Mitani, Y., Cameron, M. F., Siniiff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J. Exp. Biol.* **206**, 1461-1470.
- Sato, K., Otsuki, M., Morita, K., Kurosawa, M. and Takada, J. (2007). Result of hydrographic and meteorologic observation in 2006. *Annual report of International Coastal Research Center, the University of Tokyo*, **32**, 37-47. (in Japanese).
- Shiomi, K., Sato, K., Mitamura, H., Arai, N., Naito, Y. and Ponganis, P. J. (2008). Effect of ocean current on the dead-reckoning estimation of 3-D dive paths of emperor penguins. *Aquat. Biol.* **3**, 265-270.
- Simpkins, M. A., Kelly, B. P. and Wartzok, D. (2001). Three-dimensional analysis of search behaviour by ringed seals. *Anim. Behav.* **62**, 67-72.
- Sperling, J. B. (2008). Two new dive types with a gradual ascent phase in flatback turtles (*Natator depressus*). *Marine Turtle Newsletter*. **120**, 9-11.
- Watanabe, Y., Baranov, E. A., Sato, K., Naito, Y. and Miyazaki, N. (2004). Foraging tactics of Baikal seals differ between day and night. *Mar. Ecol. Prog. Ser.* **279**, 283-289.
- Watanabe, Y., Wei, Q., Yang, D., Chen, X., Du, H., Yang, J., Sato, K., Naito, Y. and Miyazaki, N. (2008). Swimming behavior in relation to buoyancy in an open swimbladder fish, the Chinese sturgeon. *J. Zool.* **275**, 1-10.
- Wehrer, R., Michel, B. and Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. Exp. Biol.* **199**, 129-140.
- Weng, K. C., Foley, D. G., Ganong, J. E., Perle, C., Shillinger, G. L. and Block, B. A. (2008). Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Mar. Ecol. Prog. Ser.* **372**, 253-264.
- Wilson, R. P., Liebsch, N., Davies, I. M., Quintana, F., Weimerskirch, H., Storch, S., Lucke, K., Siebert, U., Zankl, S., Mueller, G. et al. (2007). All at sea with animal tracks: methodological and analytical solutions for the resolution of movement. *Deep Sea Res. Part II* **54**, 193-210.
- Wiltshcko, R. and Wiltshcko, W. (2003). Avian navigation: from historical to modern concepts. *Anim. Behav.* **65**, 257-272.
- Witherington, B. E. and Ehrhart, L. M. (1989). Hypothermic stunning and mortality of marine turtles in the Indian River lagoon system, Florida. *Copeia* **3**, 696-703.
- Zar, J. H. (1998). *Biostatistical Analysis*. 4th ed. New Jersey: Prentice Hall.