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Riding on the fast lane: how sea turtles behave in post-nesting migration

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Abstract

Sea turtles are known as powerful swimmers. How do they behave when riding in strong currents during their migrations? In this study, three, satellite-tagged, post-nesting green turtles travelled from Lanyu Island, east of Taiwan, partly within the Kuroshio to their foraging sites approximately 1000 km away in the Ryukyu Archipelago. Their swimming behaviors were analyzed by comparing their migration velocities estimated from Argos tag data with ocean currents derived from a data simulation model and from AVISO advection estimates. Results suggest that the turtles take advantage of Kuroshio during the initial portion of their migration routes. They must then make a great effort to swim eastward, at speeds over 1 m s^{-1}, toward their foraging sites to avoid being carried off course by the strong current. The cues that might cause the change in swimming direction were evaluated with a Principle Component Analysis. The factors considered are ambient current velocity, wind, eddy activity (vorticity), magnetic field (latitude) and water temperature. The analysis shows that the ambient current and water temperature are negatively correlated with the eastward swimming velocity. This suggests that the changes in ocean current and a drop of water temperature, likely due to eddies impinging on the Kuroshio, may trigger the eastward swimming. Despite the differences among migratory routes of three Argos-tagged turtles after leaving the Kuroshio, they all reached foraging sites in the same general area. That suggests there may be more complex cues that guide the turtles to their foraging sites during their post-nesting migrations.

1 Introduction

It is fascinating to learn how sea turtles find their way to distant foraging sites after their nesting seasons. A pioneer sea-turtle researcher, Archie Carr (1967), suggested that sea turtles may migrate with the currents to save energy and to transit quickly to their foraging grounds (Hughes et al., 1998; Luchi et al., 2003). Reaching their for-

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aging grounds fast is important for post-nesting turtles that must replenish fat stores exhausted by their nesting activities (e.g. mating, chamber digging, laying eggs, etc.) and associated migrations (Miller and Limpus, 2003; Griffin et al., 2013). Since the late 1970s, satellite telemetry has provided a breakthrough technology for tracking sea turtle migrations (e.g. Balazs, 1994; Balazs et al., 1994; Byles and Keinath, 1990; Gillespie, 2001; Stonburner, 1982; Taillade, 1992). In recent years, the wide use of this technique has provided us detailed information on the distributions and migration behaviors of sea turtles in the ocean. Godley et al. (2008) reviewed more than 130 publications from over 20 years, proving that satellite telemetry is an effective tool for determining life history traits of sea turtles in detail. In another review paper, Cooke (2008) suggested that satellite telemetry could determine the behavior of marine animals in the ocean more readily than other instruments. The development of tags with both satellite telemetry and GPS functions allows us to study sea turtle behaviors on even finer scales, determining features such as home ranges and aggregations for mating during the nesting period (e.g. Schofield et al., 2009; Walcott et al., 2012).

Despite the physiological advantages to sea turtles and other marine animals, such as salmon, of swimming with the prevailing currents during long-distance migrations (e.g. Bolten et al., 1998; Sumich and Morrissey, 2004), the relationship between swimming capability and migration routes is not straightforward. Lambardi et al. (2008) showed that the migrations of leatherbacks are substantially influenced by ocean currents. However, as migratory distance increases, more active swimming is involved, apparently not all of it expended in efforts to head for specific foraging sites. Girard et al. (2009) tracked 28 female loggerheads and found that most long-distance migrants reached their specific foraging areas by compensating for deflections by ocean currents. Galli et al. (2012) tracked 15 leatherbacks with satellite tags during their long-distance migrations in the Indian and Atlantic Oceans and detected significant components of active swimming during their journeys. Although their routes closely followed the current streamlines, the orientation of turtles was random with respect to those, presumably related to feeding and predator avoidance. By combining solar-powered satellite tag results with oceanographic data, such as SST, current vectors and light intensity, Mansfield et al. (2014) suggested that hatchling loggerhead turtles released from the Atlantic side of Florida might not move with the Gulf Stream but actively selected habitats with relatively warm temperatures, presumably to promote development, growth and foraging.

In Taiwan, Cheng and Wang (2009) studied the post-nesting migrations of six female green turtles (*Chelonia mydas*) on the continental shelf east of Mainland China, finding three migration route patterns. The ambient currents were estimated from a combination of shipboard measurements with ADCP, a global tidal model and geostrophic flows derived from sea-surface height anomalies. All three patterns showed that the turtles had target destinations, and they knew how to use the currents by attending to cues available during the migration. For the first pattern, turtles that migrated northeastward rode the main surface currents at overall speeds less than $0.5\,\mathrm{m\,s^{-1}}$; however, they spent lots of energy adjusting their headings against the tidal currents. For the second pattern, turtles travelled south against the prevailing current required swimming speeds over $1\,\mathrm{m\,s^{-1}}$. Those turtles corrected their headings and increased swimming speeds when they encountered oceanic eddies that deflected them from their destinations. Turtles with the third migration pattern used coastal landmarks as migration guides; after crossing the Taiwan Straits they reached nearshore waters off Southern China. They swam at a constant speed of $0.7\,\mathrm{m\,s^{-1}}$ showing little influence from coastal currents.

Lanyu Island of Taitung County, off the east coast of Taiwan, is the second largest nesting site around Taiwan for green turtles (*Chelonia mydas*). This island is located in the main stream of the Kuroshio (Fig. 1) with strong northward flow at up to 3 knots or $1.5\,\mathrm{m\,s^{-1}}$. The main nesting season lasts from May to October each year (Cheng et al., 2009). Thus, it is interesting to see whether the post-nesting migrations of green turtles from Lanyu Island in the Kuroshio core are similar to those of turtles nesting on Wan-an Island near the Chinese coast in the Taiwan Strait (Cheng and Wang, 2009). There have been a few studies relating turtle migrations with strong currents like the Kuroshio and the Gulf Stream. For example, based on satellite telemetry from

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26 loggerhead turtles (*Caretta caretta*) caught as long-line by-catch and released after tagging in the Central North Pacific, Polovina et al. (2004) found that the turtles were carried along by the Kuroshio Extension after reaching it. They used forage sites on its southern edge. Griffin et al. (2013) tracked 68 post-nesting adult female loggerhead turtles from the Georgia coasts and found that 42 % migrated northward with the Gulf Stream to their foraging grounds on the continental shelf of the northeastern US.

In planning our study, we hypothesized that the Kuroshio plays an important role in the migration of green turtles after they nest on Lanyu Island. The migration routes of three post-nesting turtles were tracked by Argos tags to test that hypothesis. A Principle Component Analysis (PCA) was applied to evaluate the relationship between turtle swimming behavior and relevant environmental parameters, particularly the components of current transport.

2 Materials and methods

Three female green turtles were fitted with Satellite Relay Data Logger (SRDL; SMRU Instrumentation, Scottish Oceans Institute) tag during the nesting seasons on Lanyu Island in 2010 and 2012 (T2010-60718, T2012-60621, and T2012-60718). PowerFast© 2-part marine epoxy was used to attach the satellite tags on the second scute of the dorsal carapace. The size of the turtles, tag deployment date, starting date start of the post-nesting migration, date of arrival at a foraging site, post-nesting migration duration (d), and distance traveled (km) are listed in Table 1. The raw data are located in the Argos system (http://www.argos-system.org/). Each Argos location is provided with a location class (LC: accuracy of the location). Class LC 3 has a nominal standard deviation around the true position of < 150 m, LC2 has an accuracy of 150 to 350 m, LC1 has an accuracy of 350 to 1000 m, LC0 has an accuracy of > 1000 m, LCA and LCB have no accuracy estimates and LCZ is an invalid position (Argos Manual, 1996). All class 0, 1, 2 and 3 and LCA and LCB locations when they fit an apparent migration pattern were use.

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Ocean current data were then used to estimate the swimming ability of the turtles during the migration. The estimated swimming velocity of a turtle (u_s, v_s) is the vector difference between its migration velocity (u_m, v_m) and the ocean current (u_c, v_c). In this study, ocean current estimates came from a data-assimilating ocean model: the East Asian Seas Nowcast/Forecast System (EASNFS). EASNFS is an application of the US Naval Research Lab Ocean Nowcast/Forecast System (Ko et al., 2008, 2009) applied for ocean prediction. A statistical regression model, the Modular Ocean Data Assimilation System (MODAS; Carnes et al., 1996; Fox et al., 2002), was used to produce three-dimensional ocean temperature and salinity analyses from satellite altimetry along with Multi-Channel Sea Surface Temperature (MCSST, an AVHRR satellite sensor operated by the US Naval Oceanographic Office). The analyses were assimilated to produce realistic ocean features such as Kuroshio flow and eddy structures. Surface forcing was derived from the Navy Operational Global Atmospheric Prediction System (NOGAPS) (Rosmond, 1992). The full EASNFS model domain covers 17.3° S to 52.2° N and 99.2° E to 158.2° E. The horizontal resolution varies from ~ 9.8 km at the equator to ~ 6.5 km at the model's northern boundary. It is about 9 km in the study region. There are 41 sigma-z levels with thinner levels in the upper ocean to obtain better resolution. To better synchronize with Argos observations, and to compare currents with the turtle tracks, the currents from EASNFS at 5 m below the surface were used and model output was updated every 6 h.

After reviewing the ocean currents inferred from satellite data and simulated by the Global HYCOM model (spatial resolution of 1/8° and a daily time scale), Fossette et al. (2012) suggested that the error and uncertainty in spatial and temporal resolution of the surface current should be considered when data-assimilating model results are used in migration studies of large marine vertebrates such as sea turtles. Whenever possible, cross validation of different methods (e.g. indirect estimates vs. buoy trajectory) should be included. Thus, for further comparison and validation, we also applied the currents from the compiled data set of AVISO-MADT (Maps of Absolute Dynamic Topography and absolute geostrophic velocities). The resolution of AVISO-MADT is 7-

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days in temporal scale and a quarter degree (about 25 km) in spatial scale. The low resolution resulted in poor representation of the Kuroshio, but it provided constraints on the flow directions. AVISO-MADT current data with the closest time and location to the migration tracks of each tagged turtle were selected to calculate the advective component ("drift") of its tracks.

Principal component analysis is a common statistical procedure mostly used in exploratory data analysis. PCA can be done by singular value decomposition (SVD) of a data matrix. Let $\mathbf{X}$ be an $n \times m$ data matrix (n samples of m variables), where $\mathbf{X}$ is de-meaned. The matrix $\mathbf{X}$ can be factored into $\mathbf{X} = \mathbf{VYU}'$, where $\mathbf{U}$ and $\mathbf{V}$ are orthogonal, and $\mathbf{Y}$ is an ordered diagonal matrix with positive elements $r_1, r_2, \ldots, r_m$. The squares of r_i are the variances (eigenvalues) of $\mathbf{X}$, $\mathbf{V}$ is called the principal component, $\mathbf{U}$ the corresponding base (empirical orthogonal function). PCA can provide a projection of the first few principal components to reveal the internal structure of the data in a way that usually accounts for a large fraction of the data variance.

3 Results

3.1 Post-nesting migration of green turtles from Lanyu Island, 2010 and 2012

All three turtles started the migration northward following the Kuroshio. They then veered off from the Kuroshio and traveled in a northeasterly direction toward their foraging sites near islands in the southern Ryukyu Archipelago (Figs 2). Turtle T2010-60718 started its post-nesting migration on 26 September 2010, swam over 934 km in 9 days and reached Tarama Jima on 4 October (Table 1). Two outlier points far off the track were deleted from the analysis. The migration track is shown in Fig. 2a. The migration velocities (red arrows in Fig. 2a) were computed at the midpoints of consecutive locations from their coordinates and the time differences. The blue dots represent positions at 6 h intervals interpolated from the migration data. The turtle started its migration slowly, wondering around the nesting island for 3 days (26–29 September) before moving north in the Kuroshio and then northeast out of the strong current. She actually required only 2 days (29–30 September) to reach Ishigaki Island to the southwest of Tarama Jima after catching the Kuroshio. The average migration speed in the Kuroshio was $0.94\,m\,s^{-1}$ with a maximum value of $1.9\,m\,s^{-1}$. After reaching Ishigaki Island, she then slowed down and foraged among the islands.

Turtle T2012-60621 started its post-nesting migration on 1 September 2012, swam 606 km over 17 days and reached Miyakojima on 18 September (Table 1). Seven outlier points were deleted from the analysis. The migration track is shown in Fig. 2b. This turtle also wandered around to the north of Lanyu Island for the first two days (1–2 September). She then took 14 days (3–17 September) to reach Miyakojima in part (3–7 September) by the riding Kuroshio. The average migration speed was $0.5\,m\,s^{-1}$, with a maximum value of $1.7\,m\,s^{-1}$. Turtle T2012-60718 started post-nesting migration on 26 September 2012, swam over 704 km in 9 days and reached Iriomote with a more or less constant speed between 29 September and 3 October. Two outlier points were deleted from the analysis. The migration track is shown in Fig. 2c. The average migration speed was $0.78\,m\,s^{-1}$, with a maximum of $1.3\,m\,s^{-1}$. This turtle started migration slowly, heading northwest on the first day. On the 2 day, she was caught by the ocean current and moved to the northeast along the Kuroshio. This turtle made an obvious turn in the middle of her migration. The possible mechanisms that caused the direction change are discussed with the ocean currents in the following section.

3.2 Combination of migration tracks with ocean current drift tracks encountered by each turtle

The swimming velocities of the turtles were estimated as vector differences between migration velocity and ocean current velocity. Figure 3 shows the migration track of turtle T2010-60718 along with the drift tracks of ocean currents from EASNFS and AVISO-MADT. The swimming velocity is plotted as red arrows. This turtle wandered around the nesting island for 3 days in the first part of her migration. During that time, the turtle swam south and then southeast. It then swam with the Kuroshio in a north-

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west direction until reaching 23.5° N. The directions of current and the migration track were similar, suggesting that the turtle took advantage of the currents during this part of its migration. After traveling about 180 km from Lanyu Island, roughly at 23.5° N, she swam eastward, exited the Kuroshio and headed northeast toward Tarama Jima. A much greater maximum swimming speed of 1.20 $\mathrm{m\,s^{-1}}$ in the u direction compared to 0.28 $\mathrm{m\,s^{-1}}$ in the v direction at this time indicates that the turtle made a great effort to escape from the Kuroshio. Otherwise, she would have been transported to the northeast (but far to the west of her actual track) by the Kuroshio, as indicated by the drift tracks from both EASNFS and AVISO-MADT. She would have missed her foraging site altogether. The currents from AVISO-MADT, however, were slower than those from EASNFS, which is likely due to the inadequate sampling of the fast flowing Kuroshio current by the weekly altimetry maps of AVISO-MADT. Once she departed from the Kuroshio, the turtle swam very fast to reach her destination. After arriving at Tarama Jima, she slowed down and moved in the vicinity for over 10 months until 17 August 2011, indicating that this area is her foraging ground.

Turtle T2012-60621 took 12 days to migrate from Lanyu to Miyakojima (Fig. 4). The turtle drifted with currents briefly after she started her post-nesting migration. Before she reached 22.5° N, there was an obvious eastward turn, likely due to changes of the ambient flow. There was a distinct separation point between the migration track (black circles with red arrows in Fig. 4) and the drift trajectory of the current (blue squares in Fig. 4). The turtle persistently swam eastward during this period to avoid being pushed west by the current (due to an eddy, as indicated in Fig. 6). The turtle slowed down a bit after this event, drifting northward near 23° N. On reaching 24° N, she made another great effort to swim away from the strong current and reach Miyakojima. She then slowed down and stayed in her foraging ground until at least 14 February 2013, when the tag ceased to transmit. It is noted that the AVISO-MADT track (pale blue triangles in Fig. 4) followed the migration track more closely than EASNFS, possibly because its coarse temporal and spatial resolutions (7 days time interval and 25 km grids) could not resolve the eddy so clearly as the higher resolution of EASNFS (6 h time interval and 9 km grids).

Turtle 2012-60718 took 9 days to migrate from Lanyu to Iriomote (Fig. 5). She migrated west on 26 September heading into the Kuroshio and remained in that warm flow for 2 days, drifting northeast with the current. She started to swim east upon reaching 23.5° N, at the edge of an anti-cyclonic warm eddy (not shown) centered to the south of her migration route. The ambient currents changed direction several times relative to her eastward and northeastward course to the east of 122° E. During her 200 km migration route, she adjusted her swimming direction to compensate for the variation of currents caused by eddies. She reached the foraging ground in the nearshore waters of Irimote on 2 October 2012 and stayed there at least until 1 July 2013, when the tag ceased to transmit.

4 Discussion

The migrations of three green sea turtles that had nested on Lanyu Island, Taiwan, in 2010 and 2012 were analyzed from Argos satellite-tag data. Comparisons of their trajectories with ambient ocean currents confirm that all three turtles rode the Kuroshio current early in their migration routes and then swam eastward to destinations in the Ryukyu Islands. However, the relationship between the migrations and ocean currents was not straightforward. For example, the swimming velocity of Turtle T2012-60621 varied greatly (Fig. 4). The variations of ambient ocean currents and water temperature due to eddies during the migration period support the conjectures regarding the possible mechanisms (Fig. 6). Before T2012-60621 reached 23° N, at noon 2 September, she was caught by the northeast edge of a cyclonic eddy with strong northwestward flow (Fig. 6a). She apparently made a great effort to swim eastward (Fig. 4), separating her migration track from the ocean current drift. She sustained that migration course for 2 days until noon 4 September (Fig. 6b), when she encountered colder water and slowed a bit in both migration speed and swimming velocity. The turtle left the eddy and drifted northward away from her original course. On the morning of 5 September, she encountered the southwest edge of a cyclonic eddy (Fig. 6c) where the flow was northeastward. Turtle T2012-60621 then swam persistently eastward to maintain her migration course toward Ishigaki-shima. In the early morning of 6 September, she reached a strong current flowing northwest toward Taiwan (Fig. 6d). She made another great effort to swim east (as indicated in Fig. 4) against the current to avoid being pushed westward by the eddy. The shifting direction of strong currents in these two eddies forced the turtle to swim hard to maintain course and reach her foraging destination.

Despite the variation in the migratory trajectories caused by eddies and swimming efforts, all three turtles migrated with the Kuroshio for at least part of their post-nesting migrations. However, all of them swam eastward to escape the main ocean current and reached their foraging sites in the Southern Ryukyu Archipelago. Turtles can save energy by riding currents, reaching their destinations earlier and presumably increasing their fitness. However, this was not so strongly expressed by Turtle T2012-60621, which left the Kuroshio Current earlier than the other two turtles, and thus took longer to arrive at her destination (Table 1).

Another interesting question is what cues inform these turtles that they are at the right point to leave the Kursohio in order to reach their foraging grounds in the Southern Ryukyu Archipelago. Literature reviews suggest that sea turtles respond instinctively to environmental cues, such as shifts in magnetic declination, details of ocean currents, locations relative to celestial bodies, temperature, olfactory signals, etc., during their migrations (e.g., Äkesson et al., 2001; Avens and Lohmann, 2004; Hays et al., 2001; Cain et al., 2005; Endres et al., 2010; Lohmann, 2010). For example, Putman et al. (2012) suggested that loggerhead turtles possess a magnetic compass sense (i.e. detecting magnetic intensity and inclination) to guide them during their migrations. Lohmann et al. (2008) pointed out that sea turtles use one set of cues during their main ocean transits, and change to other cues when approaching their destinations. Southwood and Avens (2010), however, mentioned that open ocean migrants may also change the cues to which they adjust their trajectories.

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In this study, the possible cues resulting in the changes of migration toward the east are proposed as (1) ambient current, (2) eddy activity (vorticity of the current), (3) magnetic fields (related to latitude), (4) water temperature, and (5) surface wind. In order to verify which factor (*s*) is the most effective, 45 data sets from the original Argos observations were assembled into matrices for turtles T2010-60718, T2012-60621 and T2012-60718, with 7, 21 and 16 valid points, respectively. The time intervals between successive points range from a few hours to several days. In order to obtain an even distribution on the temporal scale, the data within the same day were averaged and resulted in 26 days of data with 6 variables (i.e. swimming velocity, ambient current, vorticity, latitude, water temperature, and wind velocity). The ambient current, vorticity, and water temperature were obtained from EASNFS. Data for wind velocity were obtained from an open ocean buoy (21°45′59″ N, 124°04′27″ E) of the Central Weather Bureau of Taiwan. Two outliers in which eastward swimming velocity exceeded $1\,\mathrm{m\,s^{-1}}$ were excluded from the analysis. The variables were then normalized by removing the mean of each variable and divided by the standard deviation of that variable. The cross correlation coefficients (Table 2) show that the swimming velocity in the u direction was negatively correlated with the ambient current in the u direction ($r = -0.68$) and with water temperature ($r = -0.45$). The cross correlation of swimming velocity in the u direction did not show significant correlation with other parameters, including vorticity ($r = 0.2$), latitude ($r = 0.1$), and eastward wind velocity ($r = -0.28$). These correlation coefficients merely indicate that the changes of migration route are related to the water temperature and ambient currents. To examine this, further statistical analyses were applied.

Our principle component analysis (PCA) followed the procedures of Forsyth and Uyeda (1975). We use the eastward swimming velocity as the dependent variable. The other 5 variables were included in the matrix analyzed by PCA. The first 3 modes accounted for 36 %, 25 % and 19 % of the total variance, respectively (Table 3). The results were not affected by the number of variables included in the PCA. We then examined the correlation of the swimming velocity (u) with each of the principle components. Principle component one (PC1) showed a strong correlation with the swimming velocity ($r = 0.63$), the 2nd and 3rd modes showed very weak correlations with the swimming velocity ($r = 0.01$ and 0.004 respectively). Figure 7 shows the significant negative correlation of swimming velocity with the first principle component. The base function (values) showed that the first principle component is correlated with ambient current (0.66) and water temperature (0.66), while weakly connected with vorticity (−0.3), latitude (−0.2) and wind-u (0.07). The PCA analyses show that the ambient current and water temperature are negatively correlated with the eastward swimming velocity. This means that when the ambient current changed its direction (away from the Ryukyus) and water became cooler, the turtles swam faster eastward. The Kuroshio is a warm and strong current and yet it is often impacted by eddies from the open ocean to the east (Lee et al., 2013). A cyclonic (counter-clockwise) cold eddy impinging on the Kuroshio can cause variation in the current and a drop in temperature, thus providing cues for turtles to swim eastward and escape the Kuroshio.

Also note that when the turtles encountered harsh environmental conditions, they may have used different strategies to overcome the impacts. For example, turtle T2012-60621 had to spend more effort to overcome the influence of strong eddies impinging on the Kuroshio and took longer to reach its foraging site than the other two turtles. Despite the difference in migration routes after the turtles left the Kuroshio, they all reached the same general area in the Southern Ryukyu Archipelago. Perhaps the turtles use more than one set of cues to reach their destinations. This result was similar to the arguments of Lohmann et al. (2008) that sea turtles use one set cues during their open-sea migrations, and then shift to other cues when approaching their destinations.

In this study, we only have a small data set covering a limited area for a relatively short time period. The turtles migrated in an area extending only three degrees in both latitude and longitude. With such short distances traveled, we would be unlikely to determine the influence of magnetic field variation on the migration trajectories. For the same reason, the vorticity shown in the PCA analysis was computed from the ambient current with resolution of about 9 km. The physical meaning of vorticity is the rotation of

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the currents. The typical size of an eddy in this region is on the order of 300 to 500 km. Thus, the resulting vorticity may not vary significantly at scales represented within the migration ranges of our turtles. The influence of ocean vorticity could be significant, when the migration distances are thousands of kilometers. In our analysis, the effects of eddies are actually indicated by the changes of current direction and speed and water temperature at the locations of the tagged turtles. In addition, we do not have proper data for chemical tracers and other parameters so as to include them in the PCA analyses. Despite these shortfalls, the migratory data in Kuroshio may serve as a "case in point" (Griffins et al., 2013) for the swimming behavior of adult female turtles searching for and moving toward their foraging habitats.

5 Conclusion

Argos data from three female turtles migrating to the northeast of Taiwan, along with refined model estimates of ocean currents, were applied to study the swimming behavior of green turtles in a strong current system. The EASNFS model was carefully verified (Lee at el., 2012) by comparing the mean eddy kinetic energy with AVISO altimeter results averaged over 8 years (2003–2010). Indeed, EASNFS provides reasonable estimates of ocean currents. The results show that post-nesting female turtles from the Lanyu Island take a short ride northward in the strong Kuroshio current. After that, in the middle of their migration route, they swim eastward strongly to escape from the main current. The three turtles took different routes after leaving the Kuroshio main current to reach their foraging sites in the same general area. The remarkable fact that these animals can take advantage of the ocean currents implies that they sense when their motion is in the right direction. They also initiated eastward swimming at appropriate latitudes relative to their goals. Possibly they sensed a change in ocean current direction or an eddy-related drop in water temperature.

Author contribution. I.-Jiunn Cheng conducted the entire satellite telemetries and contributed biological arguments of the manuscript. Yu-Huai Wang initiated the data analysis and contributed early draft of the manuscript. Luca Centurioni provided Argos drifters background current and reviewed the physical oceanographic arguments carefully. Both Cheng and Wang prepared the manuscript with contributions from all co-authors.

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Table 1. Body size, satellite tag deployment date, date of initial post-nesting migration, date of arrival at the foraging site, post-nesting migration duration (*d*), and distance traveled (km) for three female turtles that nested at Lanyu Island, Taitung County in 2010 and 2012.

Turtle ID	body size (cm) SCL	CCL	tag deployment date	*p* nesting migration date[a]	arrival date[b]	migration duration (*d*)	distance traveled (km)
T2010-60718	103.5	111	15 Aug 2010	26 Sep 2010	6 Oct 2010	11	934
T2012-60621	95	100	16 Jun 2012	1 Sep 2012	18 Sep 2012	17	606
T2012-60718	106	115	18 Jul 2012	26 Sep 2012	4 Oct 2012	9	704

[a] *p* nesting migration data: start date the post-nesting migration.
[b] Arrival date: date the turtle arrived at the foraging site.

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Table 2. The cross correlation coefficients of parameters applied in PCA, including swimming velocity-u, ambient velocity-u, vorticity, latitude, water temperature and wind velocity-u.

parameters	swimming velocity-u	ambient velocity-u	vorticity	latitude temperature	water velocity-u	wind
swimming velocity-u	1					
ambient velocity-u	−0.68	1				
vorticity	0.21	−0.08	1			
latitude	0.08	−0.17	0.08	1		
water temperature	−0.45	0.70	−0.23	−0.03	1	
wind velocity-u	−0.28	0.11	−0.22	−0.08	−0.15	1

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Table 3. The base function resulted from PCA analysis for 5 parameters including ambient velocity-u, vorticity, latitude, water temperature and wind velocity-u. The swimming velocity is the dependent variable which has good correlation with PC1.

	Mode 1(36 %)	Mode 2(25 %)	Mode 3(19 %)	Mode 4(16 %)	Mode 5(4 %)
ambient $_{\text{velocity-}u}$	0.66	−0.11	−0.09	−0.37	−0.64
vorticity	−0.29	−0.51	−0.42	−0.65	0.22
latitude	−0.19	−0.32	0.88	−0.27	−0.11
water temperature	0.66	−0.28	0.14	0.06	0.68
wind velocity-u	0.07	0.74	0.13	−0.60	0.27

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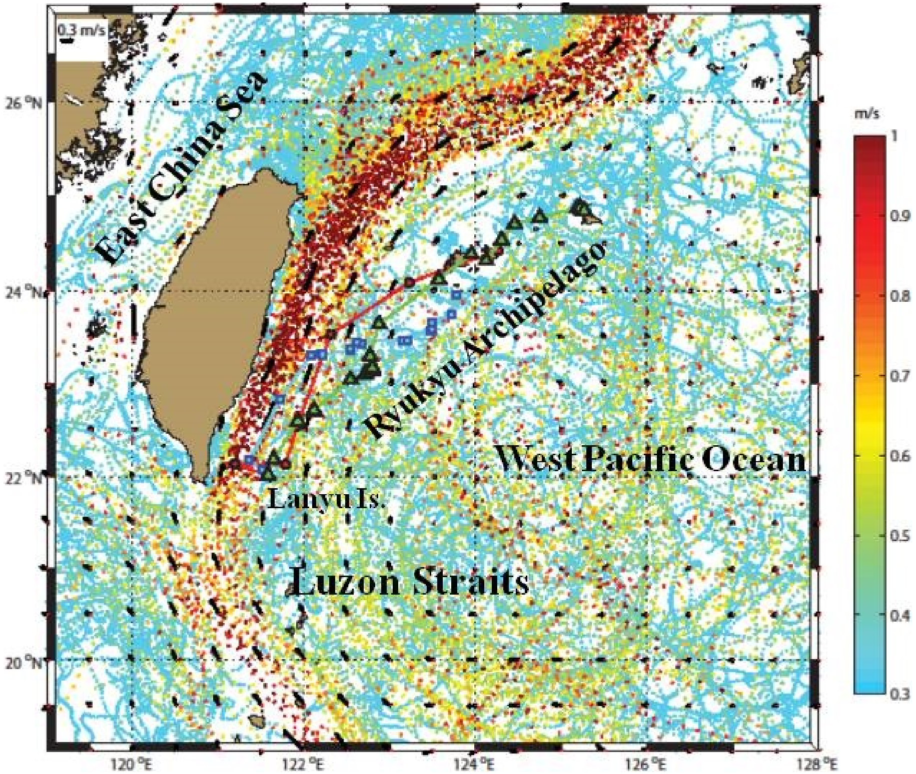

Figure 1. Migration tracks of 3 post-nesting green turtles from Lanyu Island. The markers represent positions obtained from Argos tags. Turtles were designated T2010-60718 (circles), T2012-60621 (triangles) and T2012-60718 (squares). The background lines are the tracks of Argos drifters at 15 m depth from 2001 to 2011 during August, September and October obtained from NOAA/AOML. The very dense drifter tracks east of Taiwan represent the main stream of Kuroshio. The tracks also show strong eddy activity east of the Kuroshio.

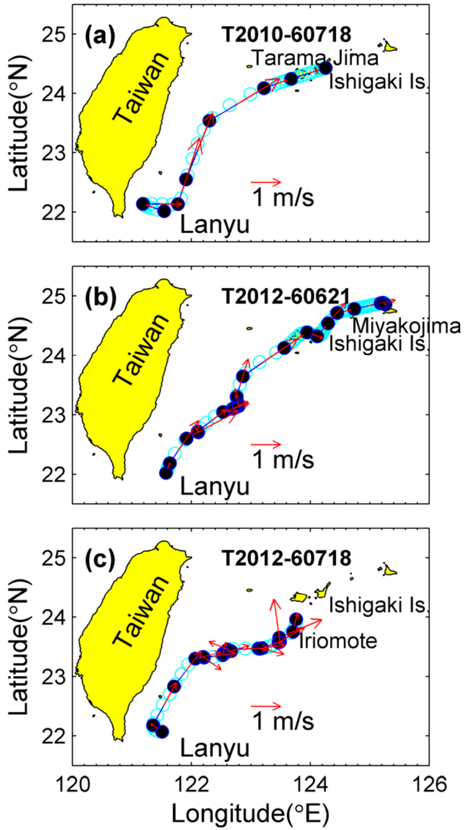

Figure 2. Migration tracks (solid dots) of turtles **(a)** T2010-60718, **(b)** T2012-60621 and **(c)** T2012-60718. The open circles are interpolated positions every 6 h. The arrows indicate the migration velocities derived from Argos positions.

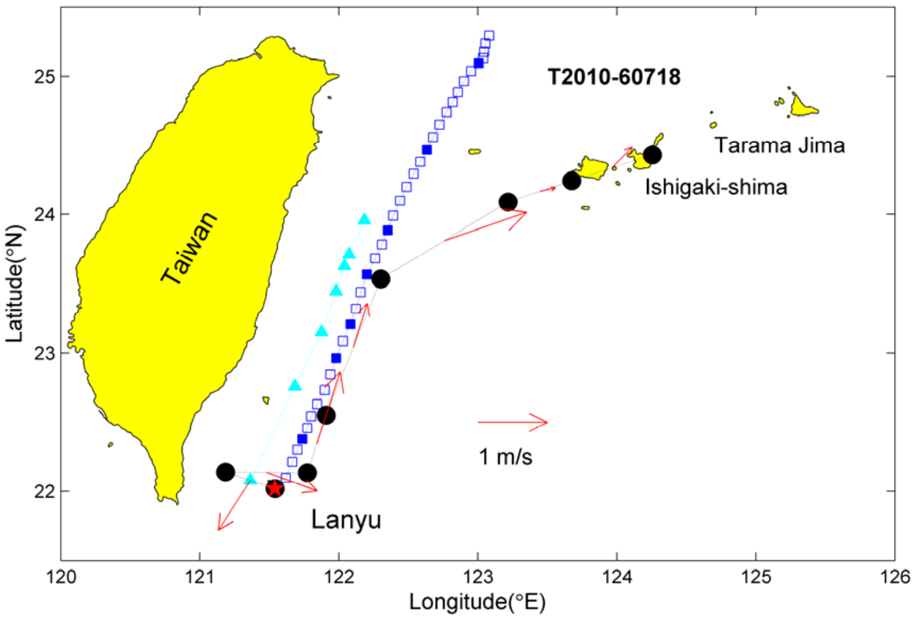

Figure 3. Migration track of turtle T2010-60718 (dots) along with her swimming velocity (arrows). The swimming velocity is computed as the migration speed minus the model current. The red star indicates the starting point. The drift tracks during the migration period, computed as EASNFS model currents (solid squares), and from AVISO-MADT data (triangles), are also plotted for comparison. The open squares in the model drift track are 6 h intervals.

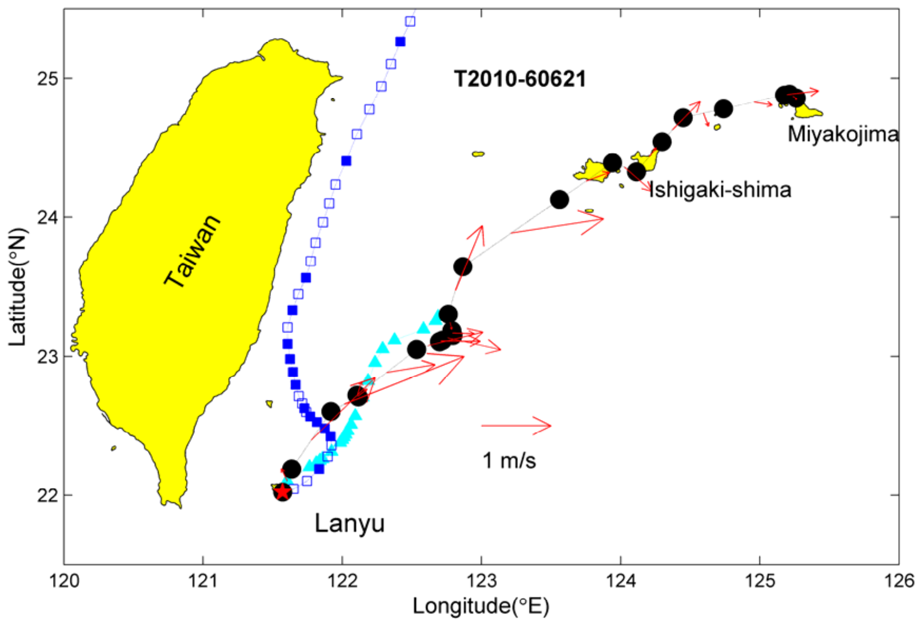

Figure 4. Migration track (black dots) of turtle T2012-60621 with swimming velocity (arrows). The red star indicates the starting point. The drift tracks due to the current during the same time period computed by the EASNFS model (solid squares) and AVISO-MADT (triangles) are also plotted for comparison. The square boxes in the modeled ambient current drift track represent 6 h time steps.

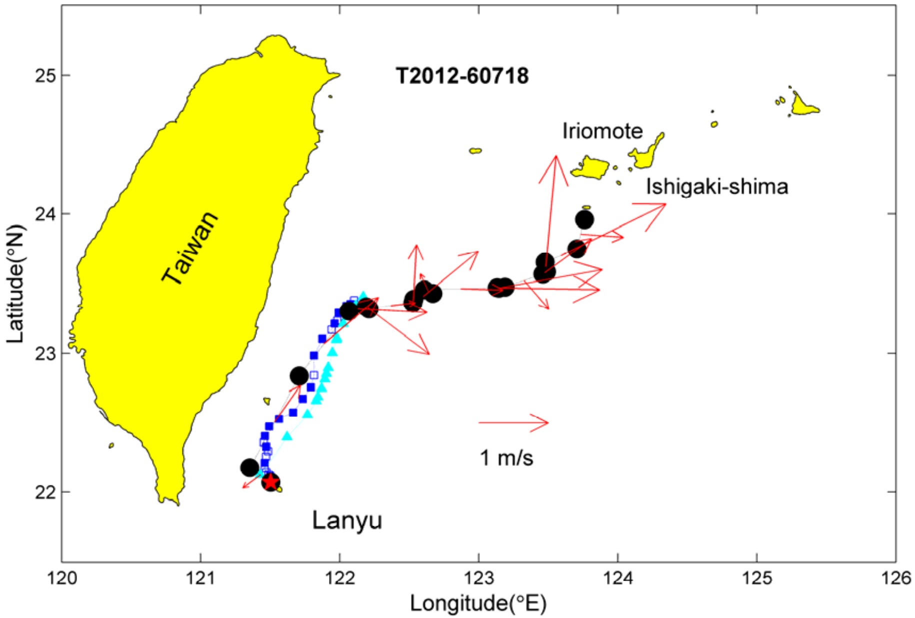

Figure 5. Migration track (dots) of turtle T2012-60718 along with her swimming velocity (arrows). The red star indicates the starting point. The drift tracks due to the current during the same time period computed by the EASNFS simulation model (solid squares) and AVISO observations (triangles) are also plotted for comparison. The square boxes in the modeled ambient current drift track represent 6 h time steps.

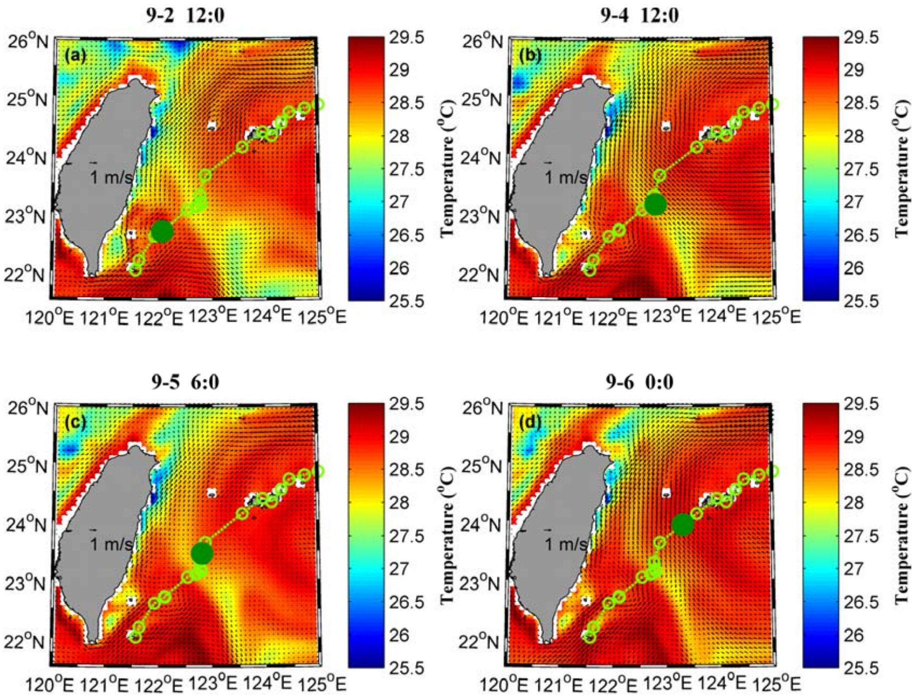

Figure 6. Predicted ocean current and water temperature at four selected dates and times showing the impact of oceanic eddies on the migration trajectory of a post-nesting turtle T2012-60621.

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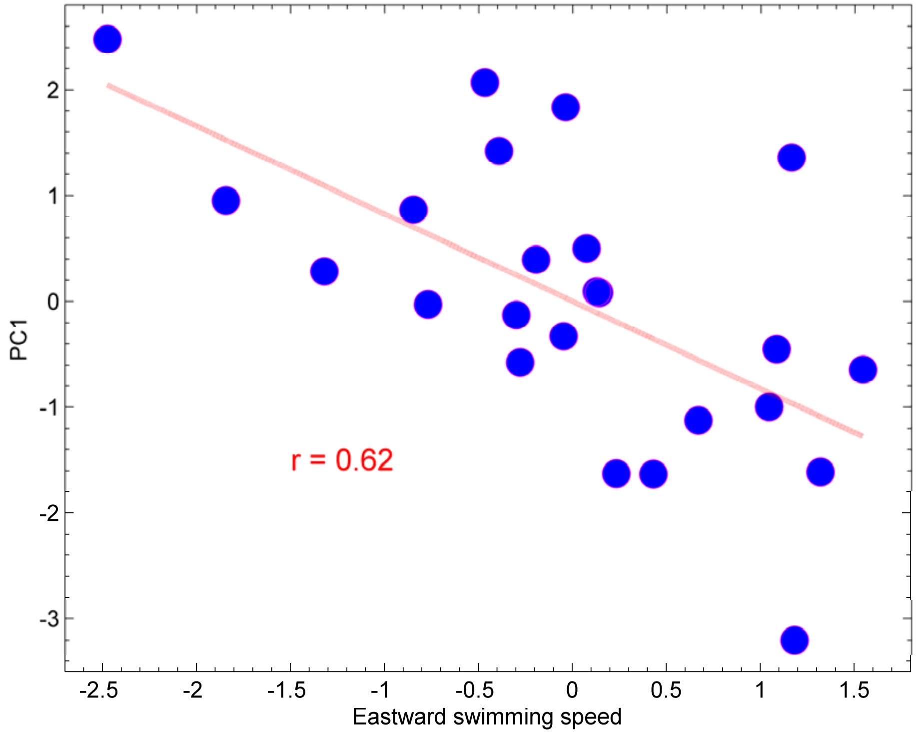

Figure 7. Correlation of eastward swimming speed with PC1 from the Principle Component Analysis. The base function of the PCA suggests that PC1 mainly characterizes the ambient current and water temperature.

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