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Loggerhead turtle (*Caretta caretta*) movement off the coast of Taiwan: characterization of a hotspot in the East China Sea and investigation of mesoscale eddies

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Satellite tags were attached to 34 non-reproductive loggerhead turtles (*Caretta caretta*) caught as bycatch in the Taiwanese coastal poundnet fishery from 2002 to 2008. Transmission durations ranged from 6 to 503 d (median 172 d), with 5860 d tracked in total. Horizontal track data were processed using the Bayesian state-space modelling to extract the most likely daily positions, taking into account ARGOS data quality and other forms of statistical error. A region of high occupancy in the East China Sea, covering 433 549 km^2 of coastal and pelagic area next to Taiwan, China, Japan, and South Korea, was characterized from the tracking data. Various attributes of this hotspot are described using satellite tracks and remotely sensed data. The tracks were merged with oceanographic data, emphasizing a new global dataset characterizing mesoscale eddies from satellite altimetry data. A proximity-probability approach coupled with odds ratio testing was used to infer orientation to eddy features. Comparisons against random points, simulated particle tracks, and drifter buoys were used to demonstrate turtle differential responses to eddies inside and outside the hotspot, depending on eddy features (i.e. cyclonic vs. anticyclonic, edges vs. centres). Turtles inside the hotspot utilize fewer strong cyclonic eddy edges than those outside.

Keywords: *Caretta caretta*, East China Sea, habitat, loggerhead turtle, mesoscale eddies, movement, pelagic behaviour, satellite tags.

Introduction

The open ocean contains a large portion of global habitat, but it remains difficult to survey and sample effectively. Remotely sensed satellite data products offer the unique opportunity to observe large expanses of ocean efficiently over short periods. Remotely sensed data have been used for many applications, including studies related to the management of pelagic marine species. These applications have assisted in improving the efficiency of catching harvested species (Zainuddin *et al.*, 2006), as well as improving the efficiency of protection for species of concern taken incidentally (Howell *et al.*, 2008). There is much potential for remotely sensed data products to assist in the management and recovery of marine species that are protected, endangered, or threatened, because such indirect approaches are non-extractive and non-invasive and can address processes at the requisite spatio-temporal domains of long-lived, wide-ranging species (Druon, 2009). Increased knowledge of their pelagic habitat requirements can be used to minimize harmful anthropogenic interactions that could jeopardize populations.

Loggerhead turtles (*Caretta caretta*) are one such species of concern whose management could benefit from remotely sensed data. Satellite tags have yielded many insights into their pelagic behaviour and habitat use worldwide. In the Mediterranean Sea, loggerheads in certain areas exhibit a combination of passive drift and site fidelity (Cardona *et al.*, 2005; Revelles *et al.*, 2007), which may be a function of age and/or size (Eckert *et al.*, 2008). In the North Pacific, satellite tags have revealed that many pelagic juvenile loggerheads, after hatching in Japan, have a protracted residence in the Kuroshio Extension Bifurcation Region (KEBR) and eastward adjacent areas of the central North Pacific (Polovina *et al.*, 2000, 2006; Kobayashi *et al.*, 2008), where they forage and interact with pelagic fisheries (Polovina *et al.*, 2004; Kobayashi and Polovina, 2005; Parker *et al.*, 2005). A prominent number of pelagic juveniles is similarly quasi-resident in the productive waters off Baja California, where they feed extensively on pelagic red crabs (*Pleuroncodes planipes*) and interact with coastal fisheries (Nichols *et al.*, 1999; Koch *et al.*, 2006; Peckham *et al.*, 2007). Both the KEBR and the Baja region are thought to be physical and biological hotspots, where marine predators accumulate

(Palacios *et al.*, 2006). Eastward and westward transpacific movements of loggerhead turtles have been documented using conventional and satellite tags (Uchida and Teruya, 1988; Nichols *et al.*, 2000), but the prevalence of this type of directed migration remains unknown. Despite these widespread movements and complex patterns of spatial occupancy, the North Pacific population of loggerhead turtles appears to be a single stock originating from nesting sites in Japan (Bowen *et al.*, 1995; Kamezaki *et al.*, 2003). Loggerhead turtles in the North Pacific are often found in areas not directly in the pathway between these nesting sites and the above-mentioned foraging sites. The reasons for this remain unclear.

In the western Pacific, loggerhead turtles are commonly caught as bycatch in poundnets off the coast of Taiwan (Cheng and Chen, 1997), far southwest of nesting sites in Japan. The Taiwanese poundnet fishery utilizes >100 individual nets moored in shallow water (<20 m deep) along the coastline (Gilman *et al.*, 2010). This type of fishery can exert a significant impact on loggerhead turtle stocks via incidental catch, yet mortality remains low in the Taiwanese fishery (Cheng and Chen, 1997). This appears to result from frequent tending (2–3 times per day) of the gear by fishers, and the shallow depth, coupled with air-accessible catch chambers that allow turtles to breathe (Ishihara, 2007). Taiwan is not known to have any loggerhead nesting sites, and genetic analysis indicates that these individuals are likely from the Japanese nesting stock (P. Dutton, Southwest Fisheries Science Center, pers. comm.). That stock is currently thought to be in a healthy condition (Kamezaki *et al.*, in press), and it is an important component of the worldwide loggerhead population. Any additional sources of mortality require careful examination and mitigation. The purpose of this study was to analyse the movement patterns of satellite-tagged loggerhead turtles taken as bycatch in the Taiwanese coastal poundnet fishery. Remotely sensed satellite data were used to infer patterns of habitat use with respect to regional oceanographic features.

Material and methods

In all, 34 non-reproductive loggerhead turtles were tagged with satellite transmitters after being caught as bycatch in the coastal poundnet fishery off the Pacific coast of Taiwan (Table 1). Catches were made from 2002 to 2008, and animals ranged in size from 64 to 92 cm straight-line carapace length (SCL; 69–95 cm curved carapace length). Several different types of tag were used during the study: Telonics ST-18 ($n = 10$), ST-14 ($n = 2$), ST-20 ($n = 14$), ST-24 ($n = 2$), and Wildlife Computers SPLASH tags ($n = 6$). The duty cycle of the tags varied between 12:48 (12 h on, 48 h off) and 6:48 for the Telonics tags, and variable 6:42 for the Wildlife

Table 1. Summary of tracking information for 34 loggerhead turtles (*Caretta caretta*) caught as poundnet bycatch in the Taiwanese fishery, equipped with electronic tags, and tracked by satellite.

Turtle number	SCL (cm)	Date deployed	Start latitude (°N)	Start longitude (°E)	Date terminated	End latitude (°N)	End longitude (°E)	Days tracked	Integrated distance (km)	Endpoint distance (km)
T01	71.8	25 January 2007	24.50	121.80	13 July 2007	33.31	123.57	170	5 603.27	992.65
T02	64.0	2 April 2003	24.49	121.90	16 August 2004	28.32	123.58	503	7 997.52	456.62
T03	74.5	16 January 2004	24.46	121.94	28 August 2004	32.28	126.98	226	5 809.04	997.47
T04	67.7	19 February 2003	24.45	122.00	10 August 2003	22.46	117.98	173	4 130.11	465.84
T05	74.0	22 March 2004	24.47	121.89	27 August 2004	35.11	161.06	158	8 642.19	3 966.55
T06	72.0	30 November 2004	24.47	121.84	23 May 2005	34.66	145.11	175	5 980.64	2 522.40
T07	68.7	8 March 2004	24.49	121.81	20 March 2005	22.52	117.86	377	3 905.98	459.12
T08	72.1	19 April 2004	24.50	121.80	25 June 2004	35.79	151.68	68	4 666.79	3 138.90
T09	76.5	5 May 2002	24.56	122.00	9 October 2002	32.97	128.22	158	3 453.35	1 112.86
T10	71.3	21 December 2003	24.50	121.80	31 January 2005	29.32	149.72	408	14 285.62	2 824.89
T11	74.5	23 December 2008	25.59	122.20	16 February 2009	21.42	115.46	52	1 225.34	829.64
T12	66.5	4 December 2007	25.38	122.66	1 July 2008	32.46	132.56	210	2 483.99	1 244.03
T13	74.5	17 October 2006	24.50	121.80	20 January 2007	28.17	130.27	96	3 814.74	938.55
T14	92.0	19 October 2007	24.51	122.03	5 April 2008	14.47	111.16	169	3 707.65	1 593.81
T15	82.5	14 January 2008	26.37	125.20	2 August 2008	26.45	127.64	90	2 151.86	243.85
T16	70.0	18 May 2008	25.94	122.80	9 November 2008	27.32	126.04	174	2 254.59	357.92
T17	78.0	10 June 2008	25.49	123.30	28 June 2009	29.21	126.53	382	4 929.34	521.97
T18	69.5	9 February 2007	24.33	122.10	20 April 2007	21.52	116.90	70	2 009.11	617.56
T19	72.0	14 January 2005	25.51	123.00	8 July 2005	23.09	118.10	173	3 258.40	565.38
T20	70.0	19 May 2005	24.58	121.90	11 March 2006	30.08	153.28	295	10 960.24	3 164.93
T21	69.7	2 June 2003	24.50	121.80	7 June 2003	25.80	123.13	6	205.43	195.97
T22	74.5	26 June 2005	24.49	121.87	22 August 2006	30.23	125.61	387	5 017.65	736.52
T23	79.0	21 November 2005	24.49	121.86	16 January 2006	28.59	125.73	57	1 115.18	595.71
T24	83.0	14 April 2005	24.49	121.81	7 November 2005	27.77	123.66	208	4 674.89	407.11
T25	67.3	15 March 2005	24.50	121.80	21 November 2005	28.28	122.03	251	5 957.75	419.13
T26	74.5	21 December 2005	25.23	122.70	7 March 2006	22.46	117.88	77	1 755.23	579.00
T27	76.0	4 April 2005	24.91	123.70	30 June 2005	28.34	121.83	87	2 214.29	423.35
T28	80.5	1 February 2005	24.44	121.90	29 May 2005	5.61	114.89	118	5 199.59	2 216.07
T29	72.5	28 April 2006	24.44	122.59	24 September 2006	37.02	141.75	82	4 139.80	2 304.64
T30	73.0	10 March 2006	22.41	118.83	4 June 2006	26.38	120.71	73	661.39	478.52
T31	78.5	17 January 2006	24.56	121.89	17 May 2006	29.68	124.83	62	1 666.05	637.86
T32	76.0	10 February 2006	24.59	121.50	14 July 2006	2.36	104.41	154	4 968.15	3 079.59
T33	73.0	13 May 2006	24.64	122.00	8 September 2006	25.13	121.76	60	1 547.36	58.75
T34	77.0	4 January 2007	25.47	122.40	29 April 2007	27.00	124.50	111	1 459.65	270.37

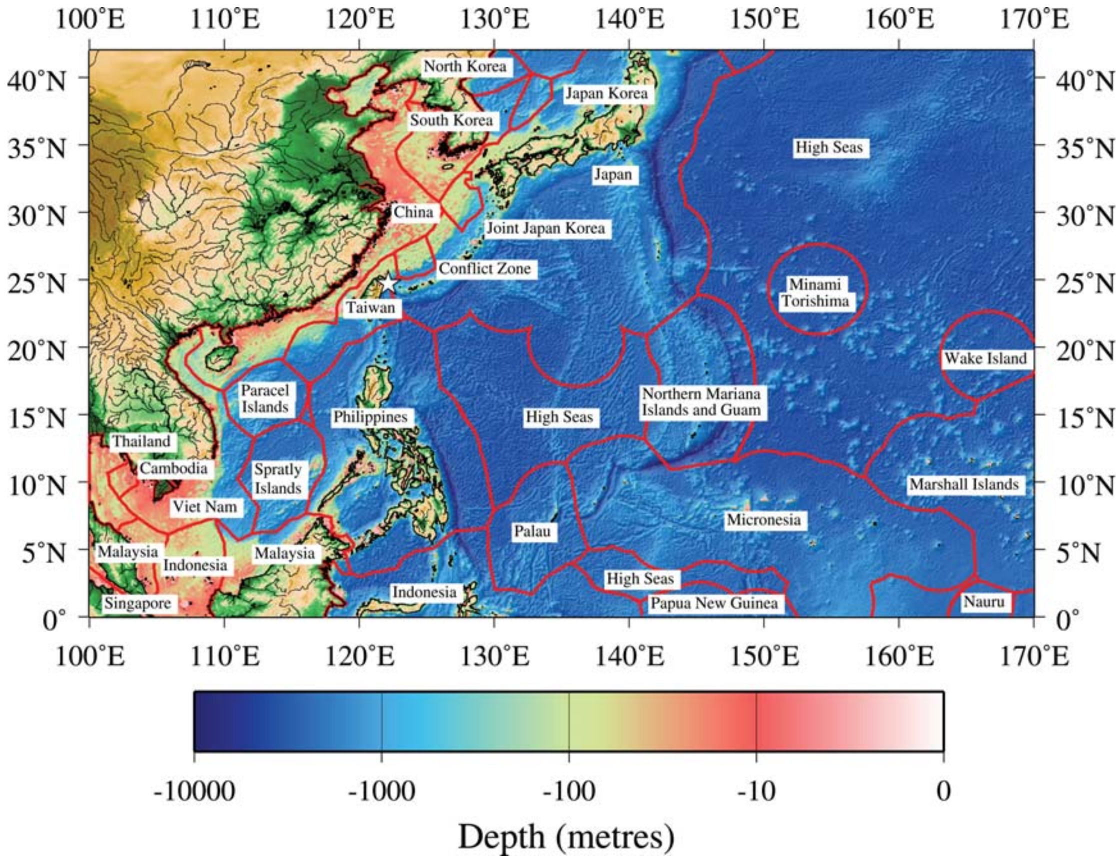

Figure 1. Reference map of the study area in the western North Pacific. EEZs are delineated by solid red lines. The white star at the northeast corner of Taiwan indicates the average release location for the 34 tagged loggerhead turtles.

Table 2. Summary of distance measures evaluated in this study, with distance measures 1–12 reflecting a nested ordering based on the eddy type (any type, cyclonic, or anticyclonic), eddy strength (any strength or strong only), and the feature of interest (eddy edge or eddy centre), respectively.

Distance measure	Eddy type	Eddy strength	Feature of interest
1	Any type	Any strength	Eddy edge
2	Cyclonic	Any strength	Eddy edge
3	Anticyclonic	Any strength	Eddy edge
4	Any type	Strong	Eddy edge
5	Cyclonic	Strong	Eddy edge
6	Anticyclonic	Strong	Eddy edge
7	Any type	Any strength	Eddy centre
8	Cyclonic	Any strength	Eddy centre
9	Anticyclonic	Any strength	Eddy centre
10	Any type	Strong	Eddy centre
11	Cyclonic	Strong	Eddy centre
12	Anticyclonic	Strong	Eddy centre

Computers tags. Inconsistencies in the datastreams attributable to this variable duty cycle, i.e. irregular temporal spacing/clumping of data, were resolved using a Bayesian model approach, as described below. Tags were affixed to turtle carapaces using polyester resin and fibreglass cloth (Balazs *et al.*, 1996), and the animals were then released. Positional data were downloaded from ARGOS (http://www.argos-system.org/) and archived locally for processing. The study concluded when all 34 tags ceased transmitting. The study region and adjoining areas are illustrated in Figure 1.

Raw ARGOS positional data from the satellite tags were processed using a Bayesian state-space model (SSM; Jonsen *et al.*, 2005). The SSM produced the most likely trajectory through the datapoints, taking into account ARGOS data-quality codes and temporally adjacent positions. The SSM also recast the tracks into daily streams of points, so removing the effects of variable duty cycles and/or intermittent tag-transmission behaviour. These new daily datastreams were archived and plotted using the mapping software Generic Mapping Tools (GMT; Wessel and Smith, 1991). Kernel density was also calculated with the R language subroutine *kde2d* using the SSM tracks and a smoothing bandwidth (*h*) of 2.5° longitude and latitude. As a kernel density estimate of habitat utilization can be influenced unduly by potentially arbitrary release locations and possible post-release effects on behaviour, an additional kernel density was performed for a subset of track data after 30 d at liberty (∼17% reduction in the track database, omitting 996 early track days across all 34 individuals). A polygon representing a high-occupancy area was extracted by contouring the output of *kde2d* with the GMT subroutine *grdcontour*. The surface area of this polygon (in a spherical context and for marine areas only) was calculated with the R language subroutine *areaPolygon*, coupled with a high-resolution bathymetric database (Smith and Sandwell, 1997). Daily track locations and all marine regions of the kernel density polygon were tabulated to exclusive economic zones (EEZs) using the EEZ boundary database available from the Flanders Marine Institute at http://www.vliz.be/vmdcdata/marbound/download.php. The track and kernel density locations were assigned to closed polygon regions using a ray-casting algorithm written as a QuickBASIC v4.5 subroutine.

Tracks were first merged to a suite of available oceanographic, bathymetric, and magnetic data products. These included NOAA Pathfinder sea surface temperature (SST), AVISO altimetry products (sea surface height, SSH; geostrophic *u*-component; geostrophic *v*-component), SeaWiFS ocean colour, Smith and Sandwell (1997) bathymetry, and earth magnetic-field data from the IGRF-10 model (total force, declination, inclination). Data were examined daily and integrated over the entire track duration by averaging across the daily exposures per individual. These oceanographic data were extracted from weekly (SST, AVISO) or monthly (SeaWiFS, earth magnetic field) grids by interpolation of corresponding trackline values using the GMT subroutine of *grdtrack* (Wessel and Smith, 1991). Most grids were 0.1° resolution, except for the Smith and Sandwell (1997) bathymetry, which was 0.033° resolution. Trackline aggregated values were examined for evidence of multimodality in an attempt to distinguish significant groupings of turtle behaviour. Some variables of interest (e.g. SST, SeaWiFS) were tabulated over the trackline to compare average conditions inside and outside a region of high occupancy.

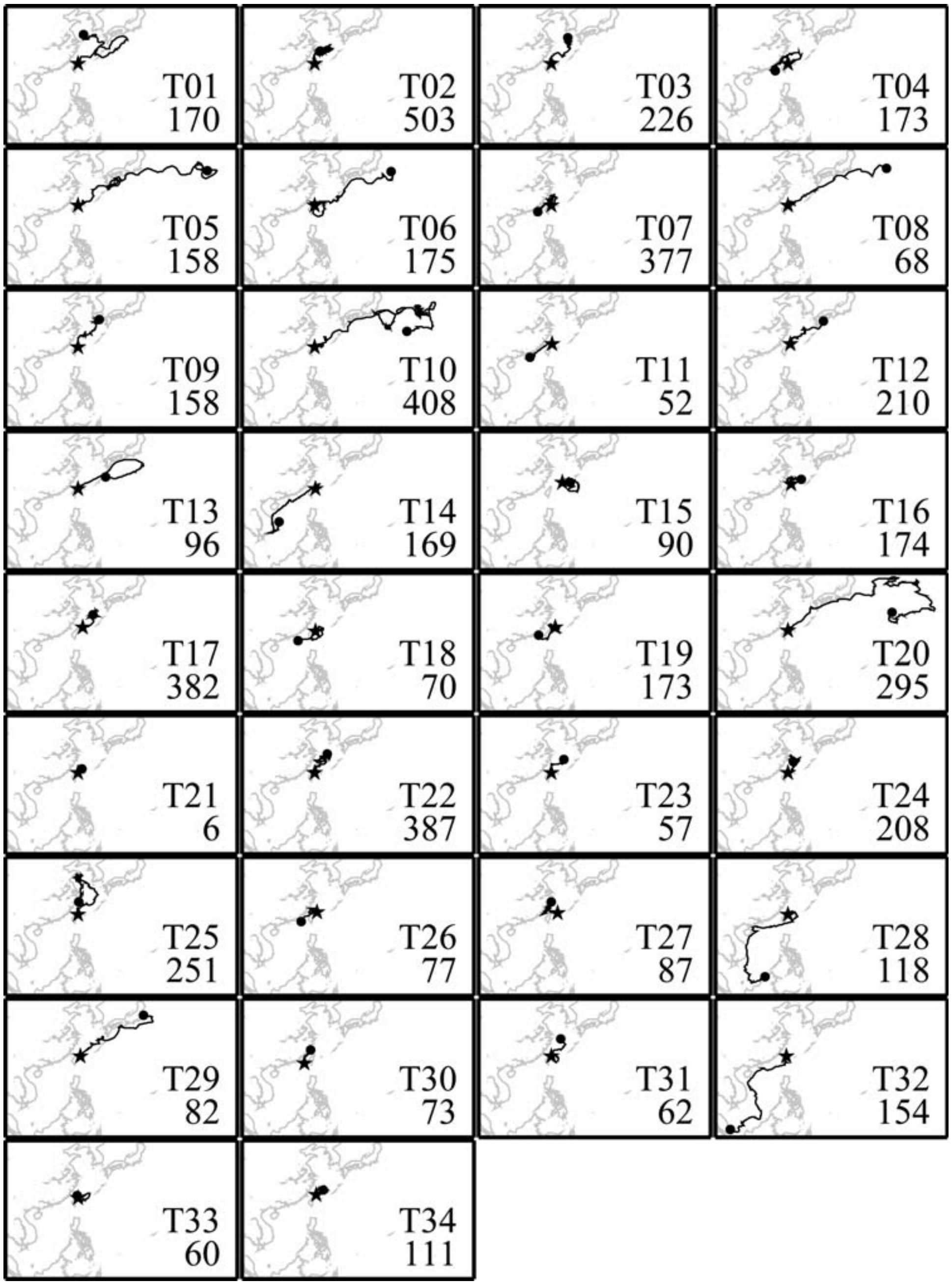

Figure 2. Individual loggerhead turtle tracks using the same map coordinates as in Figure 1. Refer to Table 1 for summary information corresponding to individual tags T01–T34. The number below the tag designation is the number of days at liberty with successful tag transmission. Continents and other landmasses are outlined in grey. Black star, starting location; black circle, last transmission location.

The SSM tracks were also merged to a new oceanographic data product that quantifies individual eddies from a time-series of remotely sensed altimetry fields (Chelton *et al.*, 2007, in press). These energetic mesoscale features have scales of tens to hundreds of kilometres and tens to hundreds of days, and account for most of the variability in the ocean; they are one of the primary dynamic features in the ocean, along with large oceanic currents and gyres (Klein and Lapeyre, 2009). The dataset was created with a procedure that automatically processes SSH data from satellite altimeters and tracks eddy trajectories over time and space, using the SSH fields in the AVISO Reference Series, which are constructed from pairs of simultaneously operating altimeters, one in a 10-d repeat orbit (TOPEX/Poseidon followed by Jason-1 then by Jason-2) and the other in a 35-d repeat (ERS-1, followed by ERS-2, then by ENVISAT; Ducet *et al.*, 2000). Eddies were identified with this procedure from closed SSH contours, as described in detail by Chelton *et al.* (in press) in their eddy documentation. During the period 1992–2008, 176 614 eddy tracks (89 704 cyclonic, 86 910 anticyclonic) with lifetimes of 4 weeks or longer were identified in the global database. Over the domain of the current study (2002–2008, 100–180°E 0–45°N), there were 61 273 eddy tracks (31 292 cyclonic, 29 981 anticyclonic).

In addition to their identification in time and space, eddies can be characterized by attributes such as effective radius, amplitude, edge SSH, and geostrophic rotational speed. The median effective radius of the eddies in the study domain was 95 km (14–378 km). Eddy shapes were approximated as circles using the effective radius, and the daily SSM turtle positions were compared with points along the circumference. Radii at 5° intervals of arc originating in the central locations of the eddies were used for circle construction, and these radii-endpoint locations were used for comparison with the SSM data. The central locations of all eddies were also compared with the SSM data. Eddies were classified as either cyclonic or anticyclonic by the nature of their SSH anomaly (negative SSH anomaly = cyclonic; positive SSH anomaly = anticyclonic) and further classified by eddy strength, as indicated by the ratio of vertical amplitude and the effective eddy radius, which is highly correlated with the maximum rotational geostrophic speed within the eddy. Amplitude values in the dataset were defined as the absolute difference between the SSH contour along the edge of the eddy and the most extreme value within the eddy interior. For the purposes of this study, ratios >0.065 were classified as strong eddies. This value represents the median eddy strength over the entire domain of eddies in this analysis (range 0.0054–1.2913; $n = 61\ 273$). Using this merging of datasets, 12 distance-measure metrics were calculated, as summarized in Table 2, reflecting a nested ordering based on eddy type (cyclonic or anticyclonic), strength (any strength or strong), and the feature of interest (eddy edge or centre), respectively.

Some discussion of data resolution is appropriate here, because we are attempting to resolve differences of the order of tens of kilometres to determine whether turtles prefer edges or centres of eddies. Most satellite-altimetry data products have an approximately weekly sampling cycle and tracklines ~100–300 km apart. Trackline data are then processed with sophisticated algorithms to resolve mesoscale processes with wavelength scales of ~200 km, which corresponds to an eddy radius of ~40 km (Chelton *et al.*, in press). The SSM daily positions include the Bayesian credible intervals in both latitudinal and longitudinal directions. The average 95% interval was 0.64° (~71 km) around latitude and 0.73° (~70 km) around longitude. If an actual turtle position was in maximal error, it would still likely be closer to the edge or centre of the eddy as originally measured. Therefore, loggerhead turtle positions were known with reasonable certainty with respect to mesoscale eddy dimensions and feature locations.

Distance measurements were calculated for all daily positions along the SSM tracks. All daily positions within 1° latitude/longitude were tabulated as being in proximity to the eddy feature of interest. These tabulations were converted to proximity probabilities, and comparisons were made using odds ratio tests. Two subsets of the SSM track data were examined separately for those daily positions found within a high-occupancy region and those found outside it.

Proximity probabilities to eddy features were calculated for three sources of spatial data in addition to the SSM daily turtle positions. First, a set of random-walk tracks was examined. These were essentially a sequence of random points in space constrained to span the study domain. A sample of 100 tracks was examined. Second, a set of simulated passive-particle tracks was

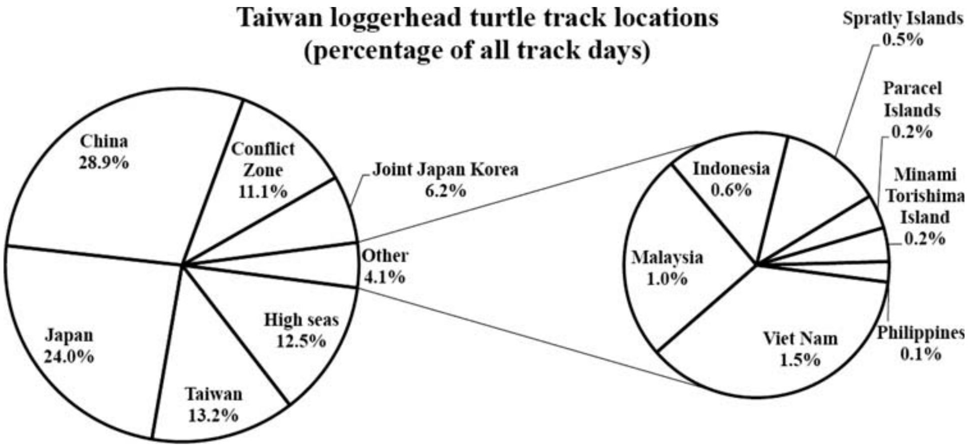

Figure 3. Loggerhead turtle percentage occupancy of different EEZs, all loggerhead turtle tracks combined (2002–2008). The secondary chart on the right is a further breakdown of the "other" category on the primary chart, representing an aggregate 4.1% of the total days.

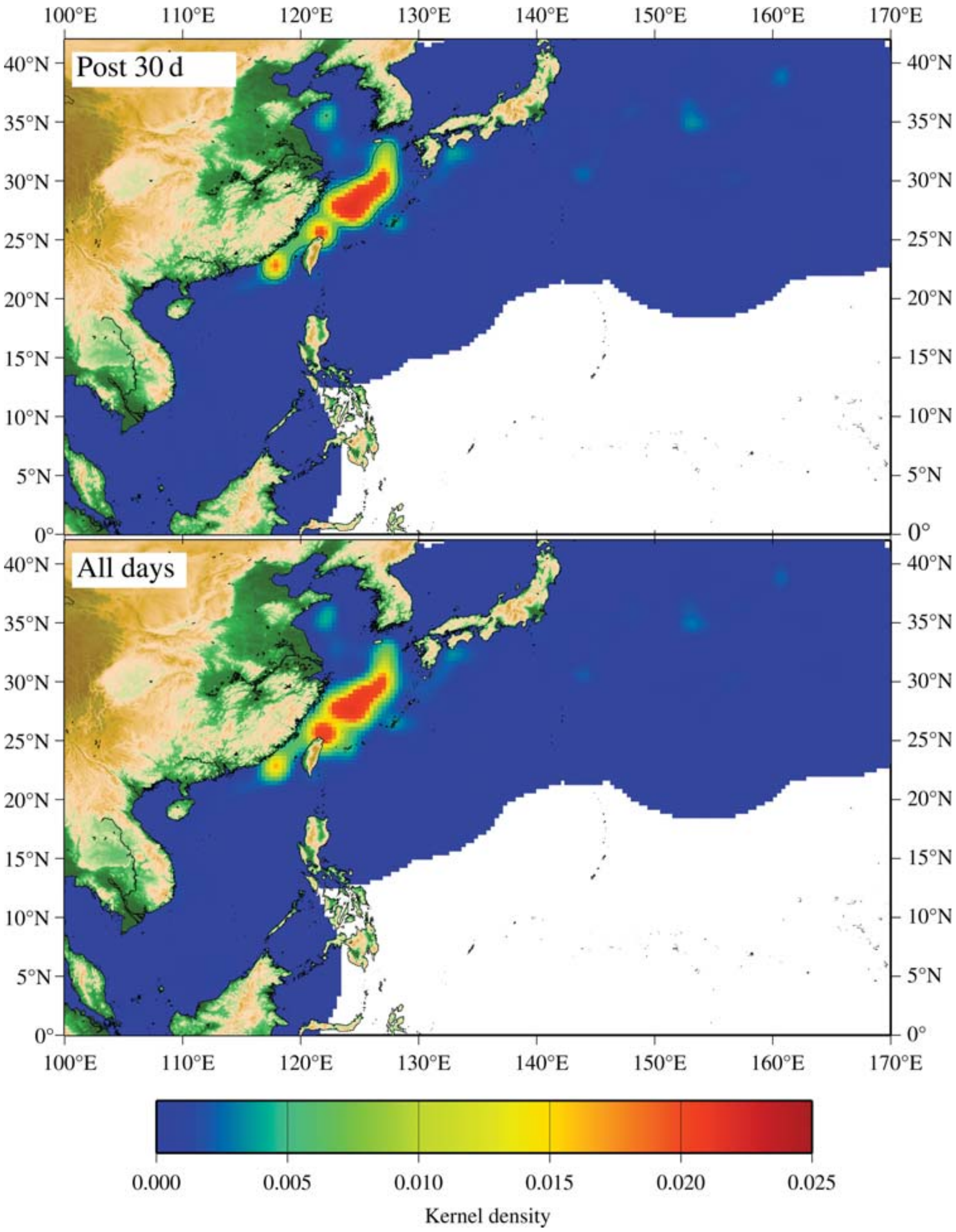

Figure 4. Kernel density distribution for all loggerhead turtle tracks combined (2002–2008), using a smoothing bandwidth (h) of 2.5° longitude and latitude. (Upper panel) Kernel density distribution using only track data after the initial 30 d of each of the tagged individuals; (lower panel) kernel density distribution for all days.

generated and analysed. These particles were driven by NOAA OSCAR (Ocean Surface Current Analyses-Real Time) current fields, estimated using data from satellite altimeters and scatterometers. The movement of particles was simulated using a Lagrangian advection-diffusion model (Polovina *et al.*, 1999). Currents were matched spatially and temporally to that of the domain of this analysis, with releases from the same average release location of the bycatch turtles. Time at liberty was set at 1 year, with 50 replicates released at the beginning of each of the study years 2002–2008. Third, data from drifting buoys deployed 15 m deep (referred to as surface drifters) that were encountered in the spatial and temporal domain of this analysis ($n = 1291$ buoys with 32 963 individual locations) were examined. Surface drifters are routinely deployed by research vessels and vessels of opportunity as part of a programme studying global circulation patterns (Lumpkin and Pazos, 2006). The surface drifter dataset used in this analysis is administered by the Global Drifter Program at NOAA (http://www.aoml.noaa.gov/phod/dac/index.php).

As these three additional sources of spatial data were non-sentient, the *a priori* hypothesis was that none of the three tests would detect patterns resulting from active orientation and swimming behaviour. However, if there were passive accumulation or dispersal processes within the eddy features (e.g. convergence or divergence), such processes may manifest themselves as significant test results in the examinations of proximity probabilities. Comparison of the SSM test results and these additional applications might also yield insights into the underlying mechanism of eddy utilization patterns by loggerhead turtles and the role of passive vs. active orientation. A matrix of odds ratio tests was applied, using the reduced-degrees-of-freedom approach (Kobayashi *et al.*, 2008) to alleviate concerns of pseudoreplication (Hurlbert, 1984). Pseudoreplication is a potential issue, because of the lack of independence among the many days of track data.

The array of proximity probabilities for the two subsets of turtle tracks, the random points, the simulated particles, and the surface drifters were used to characterize patterns of track behaviour using non-metric multidimensional scaling (NMDS) ordination. This attempted to distinguish significant groupings of turtles based on their utilization of the high-occupancy area and the other types of spatial track. The NMDS was done with the software package PC-ORD (McCune and Grace, 2002).

Results

The 34 tags transmitted for an average of 172 d (range 6–503 d), providing 5860 individual days tracked before transmissions ceased. The Bayesian SSM was successfully applied to the 34 tracks and the data are plotted in Figure 2. Some turtles moved northeast into the KEBR; others moved southwest. However, the dominant pattern was a quasi-resident behaviour in a region between Taiwan, China, Japan, and South Korea. Loggerhead turtles spent portions of their track time in 12 EEZs (Figure 3). The primary EEZ was China (28.9%), with Japan, Taiwan, and the Conflict Zone being the only other EEZs with at least 10% occupancy. High seas locations represented 12.5% of the total track time.

The kernel density distribution for all tracks combined is displayed in the lower panel of Figure 4. This distribution suggests a localized pattern of occupancy in the East China Sea around Taiwan, China, Japan, and South Korea. However, that distribution (i.e. Figure 4, lower panel) also assimilates release locations, which were all similar and located in proximity to the area of occupancy. Post-release behaviour, e.g. lethargy or flight, may have an undesirable effect on the analysis. The upper panel of Figure 4 displays the kernel density distribution using track data after only 30 d of liberty. This suggests that the observed pattern is not heavily influenced by the similarity and/or proximity of release locations to the area of occupancy. It is also likely, although not quantified, that turtle behaviour was not significantly altered because of the tagging and release process. A polygon enclosing the kernel density distribution at values >0.005 encompasses 433 549 km^2 of ocean, after correcting for intersections with land features (Figure 4, upper panel). The area spans diagonally along the Taiwan Strait between Taiwan and China and extends northeast into the East China Sea, starting at 116°43'E 21°35'N and ending at 128°17'E 33°19'N. The depth there ranges from 0 to 3117 m, with an average of 195 m. Similar to the tracking breakdown, the bulk of the East China Sea kernel density distribution is situated in the Chinese EEZ (40.73%), with the Joint Japan Korea Area (15.73%), Taiwan (14.48%), Japan (13.29%), Conflict Zone (11.81%), and South Korea (3.97%) also represented (Figure 5).

Individual mesoscale eddy tracks identified over the domain of this study are displayed in Figure 6, including a snapshot of eddy activity at the time when the maximum number of tagged turtles were at liberty ($n = 7$; 25 May 2005). Eddy activity was evident over the entire spatial and temporal domain.

Proximity probabilities are presented in Figure 7, and the results of the individual odds ratio tests in Table 3. An odds ratio test value is an indication of the odds differential between the two categories being compared for a particular attribute; hence, the test indicated that the odds of being in proximity to a strong cyclonic eddy edge were approximately ninefold greater for turtle tracks outside, than for those inside, the hotspot. There were also significant results for strong eddy edges, centres, and cyclonic centres. Turtle tracks outside the hotspot did not have significantly higher odds of being in proximity to eddy features than the three non-sentient spatial data sources. Tracks inside the hotspot differed from the three non-sentient spatial data sources with respect to proximity to strong eddy edges and strong cyclonic edges, revealing much lower odds of proximity.

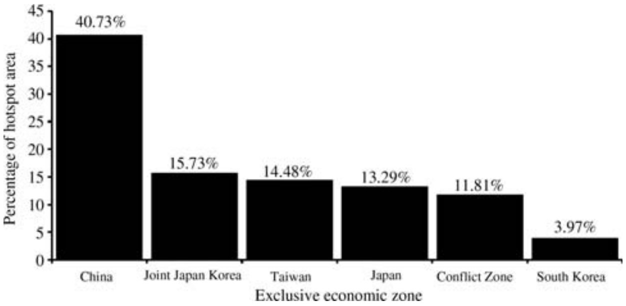

Figure 5. Kernel density distribution for different EEZs, excluding land and only considering the breakdown of the marine portion of the hotspot.

The NMDS-ordination results are summarized in Figure 8. The loggerhead turtle tracks inside the hotspot were clearly responding differently from those of turtles outside the hotspot or the three other sources of spatial data. Interestingly, the turtles outside the hotspot were most closely associated with the simulated particle tracks, whereas the random points and the surface drifters formed another clustering in the NMDS.

Discussion

Differential utilization of certain portions of mesoscale eddies by loggerhead turtles is intuitively easy to understand from an ecological perspective. There may be mechanisms that result in apparent attraction or repulsion from such features passively, cues that lead the turtles to orientate to them actively, or a combination of these factors. Conventional eddy pumping theory (McGillicuddy *et al.*, 1998) suggests that primary dynamics are in the centre of the eddy, where vertical velocities and biological responses may be greatest. Many studies have documented strong primary production patterns related to eddy dynamics (Vaillancourt *et al.*, 2003). Some empirical research has indicated that cyclonic eddy centres and anticyclonic eddy edges have more biological productivity (Mizobata *et al.*, 2002). Some of these findings are consistent with application of the standard omega equation (Hoskins *et al.*, 1978) to estimate vertical velocities when the three-dimensional density field and horizontal velocities are known (Klein and Lapeyre, 2009). Doming of the pycnocline or thermocline would be most pronounced at the centre and could reflect a different thermo-saline habitat. The eddy perimeter, where the geostrophic rotational velocities peak, likely functions as an ecotone between distinctly different water masses/habitats and may have an ecological function not easily delineated by its measurable attributes.

There could be passive accumulation in regions of convergence or downwelling. A floating object entrained in such a flowfield would be retained over regions of downwelling, because it

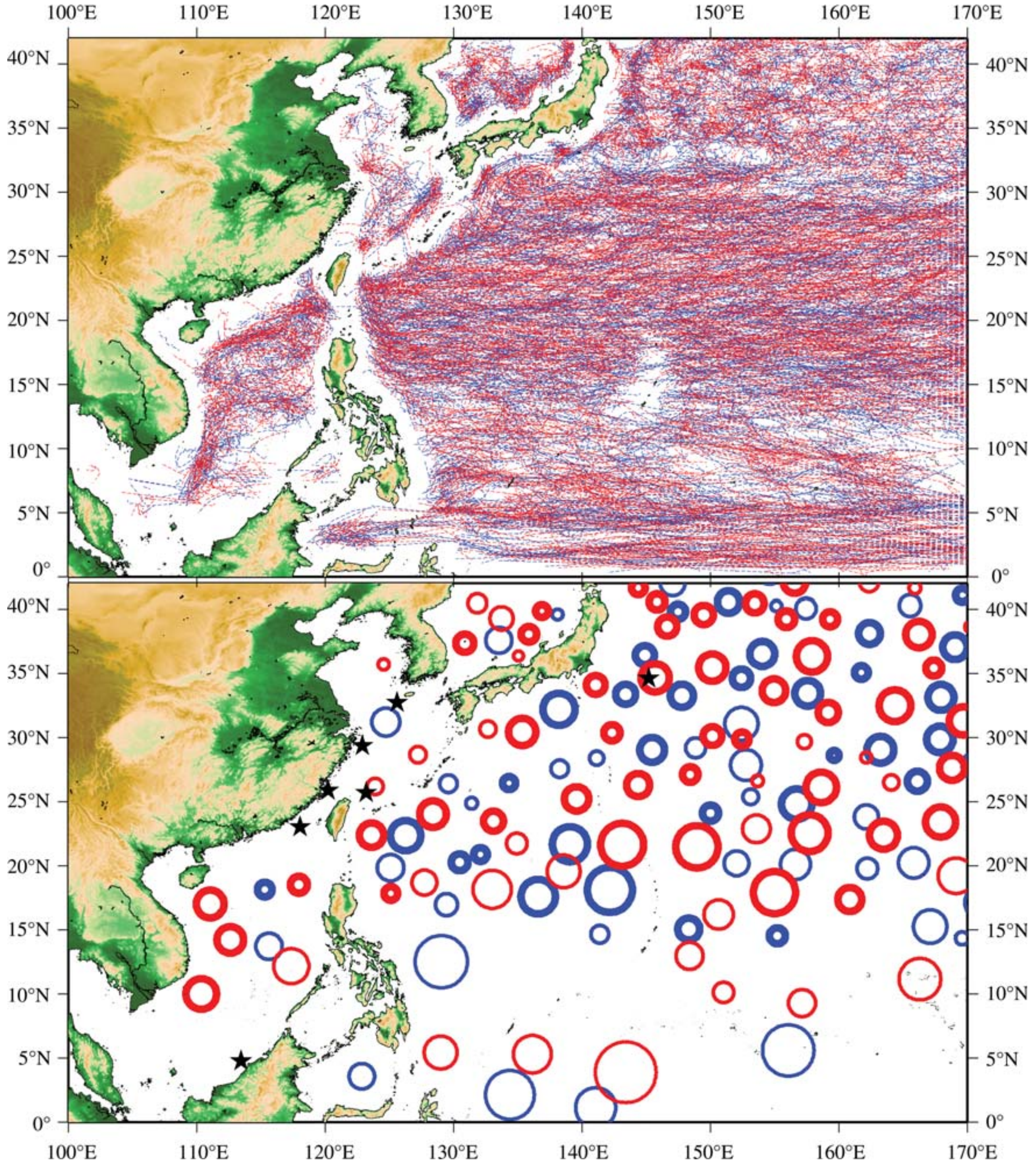

Figure 6. Altimetric eddy tracks over the entire study domain (upper) and a specific example of eddy size (circle size) and location on 25 May 2005 (lower). For both panels, blue represents cyclonic eddies, and red shows anticyclonic eddies. In the lower panel, thicker circles distinguish strong (the ratio of amplitude and radius $>$0.065) from weaker eddies. Black stars indicate the location of seven loggerhead turtles at liberty as this manuscript was being prepared.

cannot be advected downwards, though further horizontal movement would be dampened by the converging flowfields. This mechanism is known to accumulate floating debris in Langmuir cells and surface slicks generated by internal waves and other subsurface phenomena (Shanks and Wright, 1987). A turtle in a passive floating mode of transport or basking (Bentivegna *et al*., 2007; Hochscheid *et al*., 2010) could become entrained in eddy regions of convergence, most likely located near the centre. This would then likely keep the turtle near the centre, although also transporting it horizontally in synchrony with the typically westward eddy propagation. Such rafting could be an energy-efficient means of moving in any direction across an ocean basin.

Active orientation to eddy features could be linked to many types of behaviour, such as targeting locations for foraging, social/reproductive opportunities, and thermal habitat. Alternatively, there may be no proximate cause beyond the innate curiosity common in animals (Pisula, 2009); a turtle may simply be exploring a perceived discontinuity in an otherwise homogenous pelagic environment. Mesoscale eddies are more physically and biologically dynamic than regions without such features. Their potential use as waypoints for navigation or "meeting

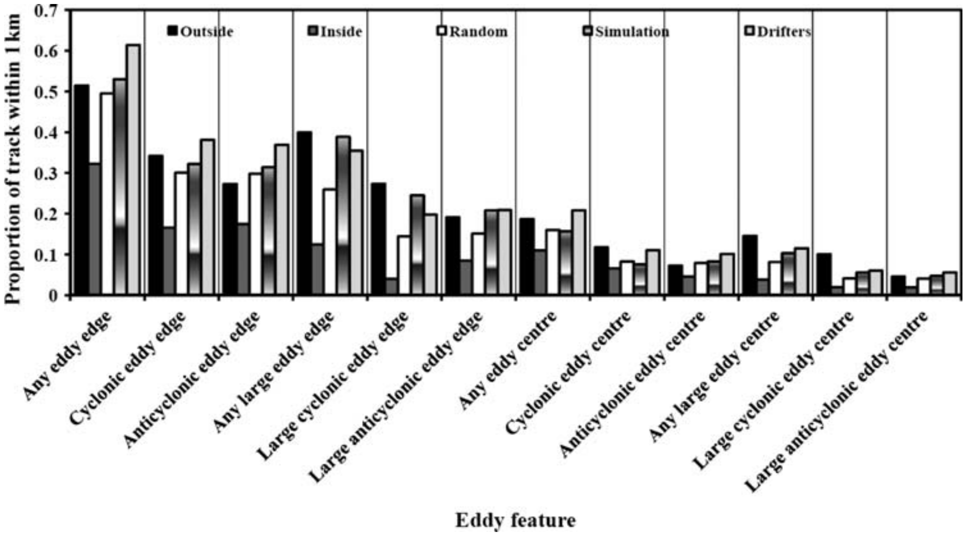

Figure 7. Proximity probabilities for two subsets (outside and inside the East China Sea hotspot) of loggerhead turtle tracks, random points, simulated particles, and surface drifters. Each bar represents the proportion of days where the position of the object was within 1° of the latitude/longitude of a particular eddy feature.

Table 3. Summary of odds ratio tests of turtle track proximity probabilities comparing two subsets (outside and inside the hotspot) and with the three non-sentient spatial data sources (random points, simulated particles, and surface drifters), with the statistical test showing either not significant (n.s.) or significant at $p = 0.05$ (*).

	Odds ratio test result and significance						
Proximity	**Outside: Inside**	**Outside: Random**	**Outside: Simulation**	**Outside: Drifters**	**Inside: Random**	**Inside: Simulation**	**Inside: Drifters**
Any eddy edge	2.23 n.s.	1.08 n.s.	0.94 n.s.	0.67 n.s.	0.48 n.s.	0.42 n.s.	0.30 n.s.
Cyclonic eddy edge	2.61 n.s.	1.21 n.s.	1.09 n.s.	0.84 n.s.	0.46 n.s.	0.42 n.s.	0.32 n.s.
Anticyclonic eddy edge	1.77 n.s.	0.88 n.s.	0.82 n.s.	0.64 n.s.	0.50 n.s.	0.46 n.s.	0.36 n.s.
Any strong eddy edge	4.68*	1.90 n.s.	1.05 n.s.	1.21 n.s.	0.41 n.s.	0.22*	0.26*
Strong cyclonic eddy edge	9.05*	2.24 n.s.	1.16 n.s.	1.53 n.s.	0.25*	0.13*	0.17*
Strong anticyclonic eddy edge	2.54 n.s.	1.32 n.s.	0.90 n.s.	0.89 n.s.	0.52 n.s.	0.35 n.s.	0.35 n.s.
Any eddy centre	1.86 n.s.	1.20 n.s.	1.23 n.s.	0.87 n.s.	0.65 n.s.	0.66 n.s.	0.47 n.s.
Cyclonic eddy centre	1.89 n.s.	1.47 n.s.	1.62 n.s.	1.07 n.s.	0.78 n.s.	0.86 n.s.	0.56 n.s.
Anticyclonic eddy centre	1.62 n.s.	0.91 n.s.	0.87 n.s.	0.69 n.s.	0.56 n.s.	0.54 n.s.	0.43 n.s.
Any strong eddy centre	4.28*	1.93 n.s.	1.47 n.s.	1.31 n.s.	0.45 n.s.	0.34 n.s.	0.31 n.s.
Strong cyclonic eddy centre	5.67*	2.62 n.s.	1.89 n.s.	1.75 n.s.	0.46 n.s.	0.33 n.s.	0.31 n.s.
Strong anticyclonic eddy centre	2.50 n.s.	1.14 n.s.	0.96 n.s.	0.81 n.s.	0.45 n.s.	0.38 n.s.	0.33 n.s.

places" for social facilitation should also not be discounted; similar to how fish aggregating devices influence pelagic fish species (Fréon and Dagorn, 2000; Castro *et al.*, 2001).

The differential response by loggerhead turtles based on their time tracks inside the hotspot is perplexing, but suggestive of aversion behaviour. There might be preferred areas >1 km from the eddy edge or quasi-stationary eddy features correlated with other important ecological considerations. Such a differential response warrants further investigation. As indicated above, eddies were present throughout the spatial and temporal domain of the study area, but the spatial patterning of eddy fields may need further attention. Eddy density is obviously lower in the coastal and shallow regions of the domain (Figure 6), and there may be other eddy-size-related or eddy-type-related distributional patterns which relate to this finding. An alternative approach to examining orientation to eddy features is being developed and will involve temporal randomization (eddy field randomization). This should preserve spatial patterns of the eddy field distribution and abundance, but still allowing quantitative investigation of orientation behaviour to specific parts of eddies based on temporal match–mismatch. This and partitioning or constraining of the non-sentient spatial datasets to regions inside and outside the hotspot are also topics for future investigation.

Enhanced foraging opportunity appears to be a likely mechanism for the prolonged residence in waters north of Hawaii (Polovina *et al.*, 2004; Parker *et al.*, 2005). These productive waters of the Subtropical Frontal Zone (Roden, 1980) and the Transition Zone Chlorophyll Front (Polovina *et al.*, 2001)

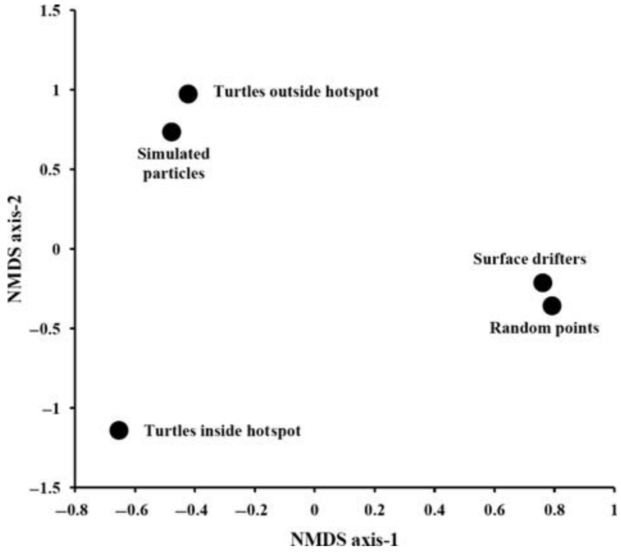

Figure 8. NMDS ordination of proximity probabilities for two subsets of loggerhead turtle tracks and three non-sentient spatial data sources.

contain many frontal features that may aggregate forage items. Mesoscale eddy activity in these areas is correlated with diving behaviour, suggesting that subsurface foraging may be important (Howell *et al.*, 2010). Most pelagic diet studies have indicated that loggerhead turtles forage on gelatinous zooplankton or other slow-swimming or sessile pelagic invertebrates. Benthic foraging is also common in coastal areas or when the bottom depth is within diving range (Plotkin *et al.*, 1993). Opportunistic foraging on fishery discards has also been documented (Seney and Musick, 2007; Wallace *et al.*, 2009). Pelagic forage could accumulate in regions of oceanographic convergence; if these regions were heavily fished or quasi-resident over shallow continental shelf areas, there could be local enhancement of other types of forage (benthic organisms or fishery discards). Extended residence by loggerhead turtles off the coast of Baja California appears to be related to the patterns of abundance of pelagic red crab (*P. planipes*), a forage species (Nichols *et al.*, 1999; Peckham *et al.*, 2007). The distribution and abundance of appropriate forage items in and around these mesoscale eddies and eddy location in time and space are important topics for future work. Particular attention needs to be paid to quasi-stationary eddy features over shallow continental shelves. Gelatinous zooplankton and biota inhabiting floating objects are often overlooked in ecosystem surveys, because of sampling difficulties or a focus on detrimental effects of floating objects, such as marine debris.

The area of high residence in the East China Sea continental shelf appears to be a localized region of biological activity similar to hotspots seen in the KEBR (Polovina *et al.*, 2000, 2006) and off the Baja California coastline of Mexico (Nichols *et al.*, 1999; Koch *et al.*, 2006; Peckham *et al.*, 2007). This region is of great interest because of its large size and proximity to the shore. The hotspot also straddles several EEZs, with the principal area in Chinese waters (Figure 5). There are also jurisdictional issues to resolve in the area, considering that two prominent locations within this hotspot lie in contested waters of the Conflict Zone or the Joint Japan Korea Area under joint sovereignty. Notably, 15 of the 34 turtles spent at least 90% of their time in the hotspot, accounting for 51% of the total track days (Figure 9). This behaviour was most clearly displayed by loggerhead T02 (Figure 1), which spent more than 500 d and all its time there. Clearly, this underscores the need to examine behaviour on an individual level, because it is difficult to characterize an average behaviour with this dataset.

Some sections of the hotspot area are on the continental shelf next to the Yangtze River, which could be an important foraging area. The dynamics of the region where the Yangtze River plume meets the Kuroshio Current intrusion are complex (Du *et al.*, 2000); these intersecting water masses are likely a primary factor for the region's high productivity (Liu *et al.*, 2003; Tseng and Shen, 2003). The seabed there is shallow enough for benthic foraging, yet also contains much eddy activity (Figure 6). Comparison of chlorophyll *a* data with SSM tracks inside the hotspot indicated that productivity there was nearly twice as high as in waters encountered by turtles outside the hotspot (Figure 10). The area is also intensively fished, primarily by boats from China. The incidental or targeted take of loggerhead turtles by these and other fisheries over the continental shelf is largely unknown and requires additional investigation. Loggerhead turtle diet and community structure of both the benthic and pelagic habitat are not well understood in this hotspot and require more study. It seems likely that a wide spectrum of marine predators converge in the

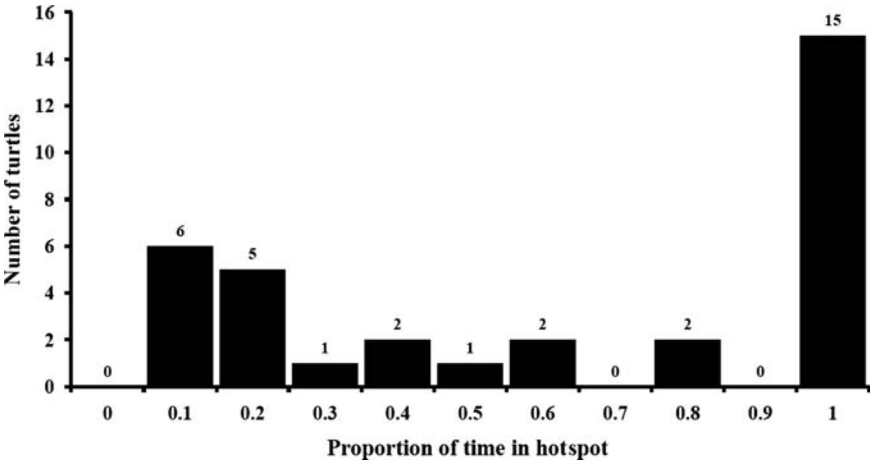

Figure 9. Individual turtle hotspot occupancy patterns, each bar corresponding to a tabulation of the 34 tracks into bins of 10%.

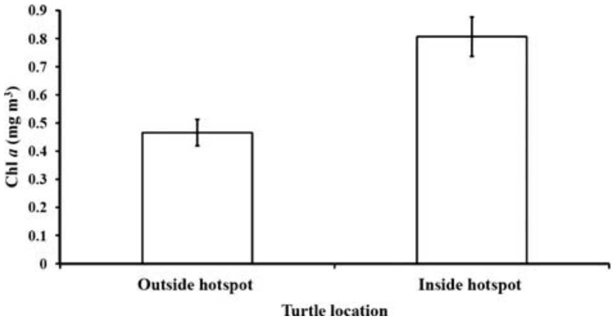

Figure 10. Average chlorophyll *a* concentration encountered by loggerhead turtles inside and outside the East China Sea hotspot. Error bars represent 95% confidence intervals.

region where the Yangtze River plume meets the Kuroshio Current intrusion, so future studies should concentrate on a wide array of species in its ecosystem.

To conclude, a hotspot region of high occupancy by loggerhead turtles was characterized in the East China Sea between Taiwan, China, Japan, and South Korea. Oceanographic investigations provided new insights using a global ocean-eddy dataset. The statistical analysis of eddy association was extended to three other sources of spatial data: random tracks, simulated particles, and surface drifters. Turtles inhabiting the hotspot appear to use eddy features differently from turtles outside the region and when compared with other types of spatial data. Specifically, turtles within the hotspot appear to associate less with strong cyclonic eddy edges than those located elsewhere, or compared with the non-sentient spatial datasets. Further regional oceanographic work, studies of fine-scale horizontal and vertical distributions of loggerhead turtle forage, and quantification of fishery bycatch in the presumed foraging region within the hotspot are key areas for future research.

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