THEME SECTION

Post-nesting migrations of Galápagos green turtles *Chelonia mydas* in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data

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ABSTRACT: Post-nesting movements of 12 green turtles from the Galápagos Islands (Ecuador) were tracked with satellite telemetry during the 2003 and 2005 nesting seasons. To illuminate potential environmental influences on turtle movements we compared tracks with a variety of remotely sensed oceanographic variables including sea surface temperature (SST), SST front probability, surface height anomaly, surface current, and surface chlorophyll *a* concentration. Three distinct post-nesting migratory strategies were observed, including oceanic migration to Central America (Type A1 movements, n = 3), residency within the Galápagos (Type A2 movements, n = 2), and movement into oceanic waters southwest of the Galápagos (Type B movements, n = 7). Two turtles migrating to Central America reached neritic foraging areas in Nicaragua and Panama that were 1500 and 1542 km, respectively, from their nesting sites, and one resident turtle established a foraging home range 75 km from its final nesting site. Oceanic movements occurred in waters with a mean SST of 26.5°C and mean surface chlorophyll *a* concentration of 0.18 mg m^{-3}, whereas neritic movements were in waters with a mean SST of 24.3°C and mean surface chlorophyll *a* concentration of 0.47 mg m^{-3}. All turtles accessed SST frontal zones at a greater rate than their availability, and at least 2 turtles conducted movements in the oceanic zone that were indicative of foraging activity. This is the first report of migratory corridors for Galápagos green turtles, confirming prior flipper tagging data that show that the Galápagos is a source rookery for green turtles in coastal areas of Central America. The high proportion of green turtles departing the Galápagos (83%) indicates that marine fisheries bycatch and directed hunting on this stock outside the Galápagos may impact this population more than previously believed, and underscores the need for multi-national conservation efforts that combat these threats.

KEY WORDS: Black turtle · *Chelonia agassizii* · Cheloniidae · Chlorophyll *a* · Eastern Tropical Pacific Ocean · Frontal zones · Migration · Sea surface temperature · Sea surface height anomaly

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INTRODUCTION

Green turtles *Chelonia mydas* are highly migratory and undertake complex movements through geographically disparate habitats during their life cycle (Musick & Limpus 1997, Plotkin 2003). The periodic migration of hundreds to thousands of kilometers between breeding and foraging areas by adults is a prominent feature of their life history. The long-distance movements of green turtles were first resolved with flipper tagging (Carr et al. 1978, Alvarado & Figueroa 1992) and more recently with genetic analyses (Bass et al. 2006, Dethmers et al. 2006). The use of satellite telemetry has expanded this understanding, revealing foraging area destinations of migrating post-nesting turtles as well as providing information on migratory routes, travel speeds, and dive behavior (Cheng 2000, Godley et al. 2002, Hays et al. 2002, Craig et al. 2004, Kennett et al. 2004, Troëng et al. 2005, Blumenthal et al. 2006). Further, because satellite telemetry yields spatio-temporal patterns of turtle distribution, the resultant migratory tracks can be integrated with remotely sensed data to elucidate the underlying oceanographic conditions that may influence sea turtle habitat use.

Understanding such factors is critical for improving management and conservation initiatives for sea turtles. While basic environmental features such as bathymetry, sea surface temperature (SST), and surface currents have been linked to sea turtle movements (Morreale et al. 1996, Hays et al. 2001, Luschi et al. 2003, Pelletier et al. 2003, Etnoyer et al. 2006), the mechanisms underlying these relationships are inadequately understood. Dynamic mesoscale processes such as SST and chlorophyll fronts—areas of interface between 2 dissimilar water masses—are known to strongly affect water column primary and secondary productivity (Olson et al. 1994, Palacios et al. 2006), and their status as prey aggregation zones suggests that they too may influence sea turtle movements. For example, juvenile loggerhead turtles *Caretta caretta* in the North Pacific have been shown to forage in the Kuroshio Extension Bifurcation Region during periods of high surface chlorophyll (Polovina et al. 2006); when waters become vertically stratified and surface chlorophyll levels decrease, they move farther north to the Transition Zone Chlorophyll Front region—a well-described biological hotspot and an important oceanic foraging destination for a variety of marine taxa (e.g. Polovina et al. 2000, 2001). Frontal zones have also been described as important foraging zones for large whales (Doniol-Valcroze et al. 2007) and commercially targeted species such as tuna and swordfish (Fiedler & Bernard 1987, Podesta et al. 1993). Knowledge of the spatio-temporal persistence of these mesoscale fea-

tures can be highly informative for developing predictive models of sea turtle habitat use; however, there is an obvious need for additional data from a variety of marine species and ocean regions to determine the efficacy of such modeling efforts.

The Eastern Tropical Pacific Ocean (ETP) is an area with complex topography and substantial spatio-temporal variability in oceanographic characteristics (Chavez et al. 1999, Fieldler 2002a). Oceanic waters in this region contain several biological hotspots, including the nutrient-enriched Galápagos plume (Palacios 2002), the shoaling thermocline of the Costa Rica Dome (Fiedler 2002b), and the Peruvian coastal upwelling region (Strub et al. 1995, 1998). Such meso-scale features can be important areas of aggregation for a variety of marine organisms (Worm et al. 2005, Pennington et al. 2006), but their persistence is dramatically impacted by the El Niño Southern Oscillation (ENSO). This 3 to 6 yr cycle within the coupled ocean-atmosphere system of the tropical Pacific brings increased surface water temperatures and lower primary productivity, both of which have profound biological consequences (Chavez et al. 1999). This variability in oceanographic conditions coupled with the presence of numerous well-described biological hotspots provides an ideal opportunity to examine the effects of ocean climate on large, tractable marine species. As the ETP is a region of high use by sea turtles, this taxon is a prime candidate for commencing such studies. Satellite telemetry studies have described movements of olive ridley turtles *Lepidochelys olivacea* and leatherback turtles *Dermochelys coriacea* in relation to bathymetry in the area (Plotkin et al. 1995, Morreale et al. 1996), but so far no studies have examined turtle movements in relation to other oceanographic conditions in the ETP, although Saba et al. (2007) examined leatherback nesting biology relative to oceanography in the region.

Prominent in this area are the Galápagos Islands (hereafter referred to as the Galápagos), a 19-island archipelago located ~1000 km from coastal Ecuador (Fig. 1). The Galápagos are among the most important nesting areas for green turtles in the ETP, and turtles are afforded protection by the 138 000 km² Galápagos Biological Reserve of Marine Resources, which regulates fishing pressures and provides marine habitat and nesting beach protection (Heylings et al. 2002). Flipper tagging programs (Green & Ortiz-Crespo 1982, Green 1984, Zárate & Dutton 2002) and genetic data (P. H. Dutton unpubl. data) have shown that green turtles nesting in the Galápagos move to foraging areas both within the archipelago and along the continental shelf of Central and South America. However, although Galápagos green turtles evidently cross oceanic areas to reach mainland coastal habitats,

nothing is known about their migratory corridors, nor are there data on how these turtles are affected by oceanographic conditions. Further, with fewer than 30 long distance (>1000 km) tag returns of the ~14 000 green turtles that have been tagged (Green 1984, Zárate & Dutton 2002), there are sparse data on the relative importance of various coastal foraging sites for this nesting stock.

Knowledge about the oceanic movements and foraging area destinations of Galápagos green turtles can elucidate their susceptibility to human impacts such as fisheries bycatch and targeted capture and can also illuminate the areas of greatest need for conservation efforts. In the present study, we use satellite telemetry to track the post-nesting movements of green turtles from the Galápagos and compare these movement paths with a range of remotely sensed oceanic parameters. Our goals were to (1) quantify the proportion of green turtles that depart the Galápagos after nesting activity, (2) determine their migratory corridors and foraging area destinations, and (3) determine which, if any, oceanographic features influenced the movements of green turtles. Besides providing information on green turtles per se, our results will also have general relevance for the understanding of oceanographic influences on other sea turtle species in the ETP.

MATERIALS AND METHODS

Tracking data. Twelve adult female green turtles ranging from 71.6 to 96.5 cm curved carapace length (CCL, measured from nuchal notch to posterior-most tip of carapace; mean = 83.0 ± 2.0 cm) were fitted with satellite transmitters (Platform Transmitter Terminals; PTTs) during the 2003 (n = 4) and 2005 (n = 8) nesting seasons in the Galápagos Archipelago, Ecuador (Appendix 1). The turtles were equipped with PTTs prior to returning to the sea at 3 different nesting beaches: Las Salinas (Baltras Island; n = 3), Barahona (Isabela Island; n = 3), and Quinta Playa (Isabela Island; n = 6) (Fig. 1).

We used Telonics ST-18 (in 2003) and ST-20 (in 2005) transmitters (Mesa) that measured 6.0 × 12.3 × 2.8 cm in size and 276 g in weight (<1% of the approximate weight of each turtle). For the ST-18 transmitters, duty cycles (hours during

which transmissions are turned on/off to maximize battery life) were 12/48 for 3 of the PTTs and 24/24 for one of the PTTs. For the ST-20 transmitters, duty cycles were 24/0 for Days 1 to 45, 12/25 for Days 46 to 70, and 6/25 for Day 71 to end of tag life. Battery life was further prolonged by the presence of a salt-water-activated switch that prevented transmissions during immersion. Transmitters were affixed to the highest point of each turtle's carapace using fiberglass cloth and polyester resin (Balazs et al. 1996) after surfaces had been cleansed of grease and debris. Each unit was oriented with the antenna to the rear, with a roll of Kevlar® attached anterior to the antenna to protect its base.

Turtle positions were determined with the Argos system, which categorized each location message received into one of 6 location classes (LC): 3, 2, 1, 0, A, and B (Appendix 1). Argos assigns accuracy estimations of <150 m for LC 3, 150 to 350 m for LC 2, 351 to 1000 m for LC 1, and >1000 m for LC 0. No accuracy estimation is provided for LC A or LC B. However, rather than limiting our track construction to the use of LCs with optimal accuracy estimates (i.e. LC 3, 2, and 1), we instead used a series of filters that excluded biologically unreasonable results for travel speed (>5 km h^{-1}) or indicated turning angles that did not conform to a directional track line (<10°), as this approach has been shown to maximize the utility of Argos-derived positions for wildlife tracking (M. S. Coyne et al. unpubl.).
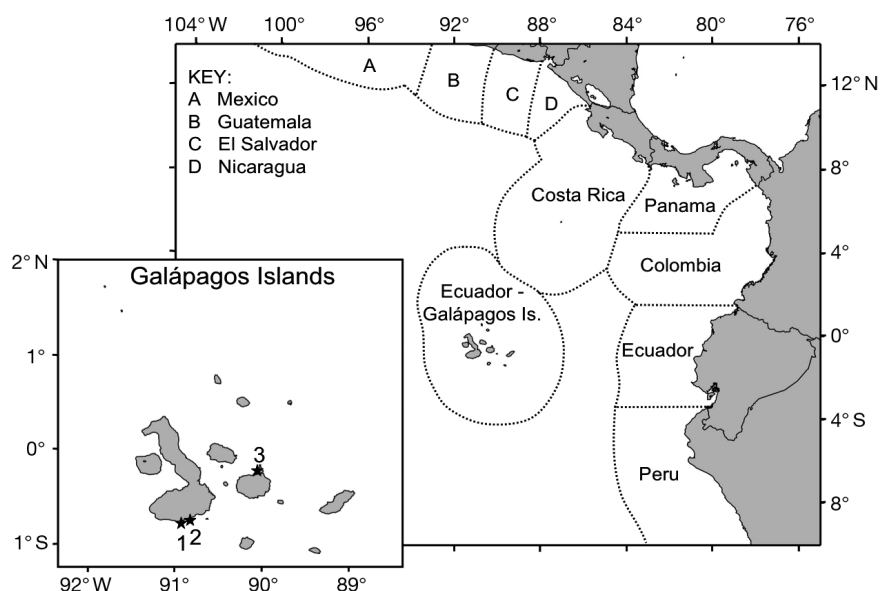

Fig. 1. Economic Exclusive Zones (EEZs) in the Eastern Tropical Pacific with inset map of the Galápagos Islands. Dashed lines indicate EEZ boundaries; ★: satellite tag deployment locations — 1, Quina Playa (Isabela Island); 2, Barahona (Isabela Island); 3, Las Salinas (Baltras Island)

The Argos locations were analyzed using Satellite Tracking and Analysis Tool (STAT) (Coyne & Godley 2005) and were mapped using MapTool and Generic Mapping Tools (Wessel & Smith 1991). The tracks from each turtle were partitioned based on the relationship between the time since deployment and distance from release point (i.e. displacement plot; Blumenthal et al. 2006; our Fig. 2). The curves of these displacement plots showed distinct inflections that corresponded with changes in travel speed as turtles commenced and/or completed migratory movements. Post-nesting migrations were considered to start on the day coinciding with the beginning of a positive slope lasting >25 d in the displacement curve and, for turtles moving to Central America, migration was considered to have been completed on the day that the positive slope reached asymptote. A migration straightness index (MSI) was calculated for each turtle's migratory movements, based on the ratio of straight line distance between first and last oceanic Argos locations to the total oceanic track length (Luschi et al. 1998, Godley et al. 2002). We determined mean travel speed (km d^{-1}) in each zone using the travel speeds of each successive track segment within the zone separated by ≥12 h. Mean ± SE are given unless otherwise noted.

Satellite data. We compared the tracks of each turtle with information on bathymetry, SST, SST front probability, geostrophic surface currents, sea surface height anomaly (SSHa), and surface chlorophyll *a* (chl *a*) concentration. Bathymetric values for the region were determined with the General Bathymetric Chart of the Oceans (GEBCO; www.ngdc.noaa.gov/mgg/gebco/; IOC, IHO, BODC 2003). SST data were obtained from 4 sources (Table 1), and were blended with weighted averages based on the nominal errors for each dataset. SST fronts were determined using a Frontal Probability Index (FPI; Breaker et al. 2005, Castelao et al. 2005), calculated as the fraction of days in a given 14 d period for which fronts are detected within each 0.05° × 0.05° (~5.5 × 5.5 km) cell in the study area

(delineated by 13° N, 13° S, 102° W, and the coast of Central and South America). The FPI used herein is derived through a combination of gradient threshold tests and along-front feature tracking algorithms (e.g.
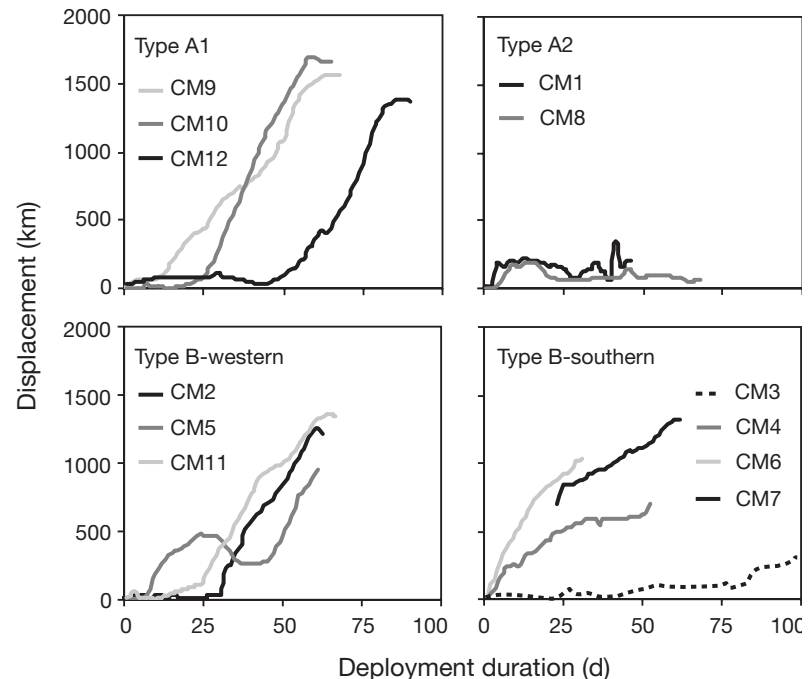

Fig. 2. *Chelonia mydas.* Displacement plots for green turtles tagged in the Galápagos Islands

Table 1. Satellite data extracted along the track of each turtle. These ocean satellite data products were extracted from the OceanWatch Thematic Real-time Environmental Distributed Data System (THREDDS). MODIS: Moderate Resolution Imaging Spectrometer; GOES: Geostationary Operational Environmental Spacecraft; POES: Polar-orbiting Operational Environmental Spacecraft; AMSR: Advanced Microwave Scanning Radimeter; AVHRR: Advanced Very-High Resolution Radiometer; GFO: Geosat Follow-On; OSCAR: Ocean Surface Currents Analyses; SST: Sea surface temperature; FPI: Frontal Probability Index; SSHa: sea surface height anomaly. When >1 sensor is used, the data format is a blended product. In addition, bathymetric data were collected via the General Bathymetric Chart of the Oceans (GEBCO), a global topographic dataset with one minute (1') spatial resolution

Parameter	Spacecraft	Environmental sensor	Spatial grid	Composite duration (d)
Surface chl *a*	Aqua	MODIS	0.05° × 0.05°	8
SST	Aqua	MODIS	0.1° × 0.1°	5
		AMSR-E	0.1° × 0.1°	5
	GOES	Imager	0.1° × 0.1°	5
	POES	AVHRR	0.1° × 0.1°	5
FPI	GOES	Imager	0.05° × 0.05°	14
SSHa	Jason-1	GFO	0.25° × 0.25°	~10
		Envisat	0.25° × 0.25°	~10
Ocean currents		OSCAR - real time	1.0° × 1.0°	10
Bathymetry		GEBCO	1'	–

Canny 1986, Cayula & Cornillon 1995) applied to the daily SST data obtained from the Imager (Table 1). The advantage of this dataset over other SST data sources is the high frequency of the images (48 d^{-1}), which greatly helps to mitigate the obscuring effects of clouds (Castelao et al. 2005). Sea surface current (geostrophic velocity vector) and SSHa data were obtained from the Centre National d'études Spatiales Aviso/Altimetry project (www.aviso.oceanobs.com; Ducet et al. 2000). Satellite-derived chl *a* pigment concentration data were collected by the Moderate Resolution Imaging Spectrometer (MODIS) and obtained from NASA Goddard Space Flight Center, Ocean Color Project (http://oceancolor.gsfc.nasa.gov). See Table 1 for a summary of the spacecrafts, environmental sensors, and spatial and temporal resolutions for each of the remotely sensed oceanographic datasets.

Statistical analysis. Argos-derived migration paths were compared to environmental conditions in 3 ways. To determine the water depth along each track line, satellite tracks were overlaid on bathymetric charts; locations in waters ≥200 m deep were considered 'oceanic', whereas those in water <200 m were considered neritic. To evaluate turtle movements in relation to surface currents and SSHa, we constructed animations in MapTool of the oceanic movements by turtles tagged in 2005, with each frame representing successive Argos turtle locations overlayed on the spatio-temporally coincident oceanographic data (see Figs. A1 to A7 in Appendix 2, available as Supplementary Material online at: www.int-res.com/articles/suppl/n004p057_app/). We determined the surface chl *a* concentration, SSHa, SST, and SST frontal probability at each Argos-derived turtle location and also calculated the mean for each oceanographic variable within a box (0.2° longitude × 0.2° latitude × 5 to 10 d) centered at the time and position of each satellite transmission and taken to represent the available habitat adjacent to each turtle location. The overall mean values in neritic and oceanic zones for each oceanographic variable were compared using 1-way analysis of variance (ANOVA). We also used ANOVA to compare FPI at Argos locations in the Galápagos neritic, oceanic, and mainland neritic zones with the mean FPI for each respective zone within the entire study area. A non-parametric Kruskal-Wallis test was used to confirm the results of the ANOVA for FPI, as this index occurs in a non-continuous, non-normal data distribution (Hollander & Wolfe 1999). Ocean satellite data products used for ANOVA were extracted from the OceanWatch Thematic Real-time Environmental Distributed Data System (THREDDS) hosted by the Environmental Research Division of the NOAA Fisheries' Southwest Fisheries Science Center using the program Open-source Project for a Network

Data Access Protocol (OPeNDAP) and analyzed using Matlab (Mathworks).

RESULTS

Three distinct post-nesting migratory strategies were observed, the patterns of which we classify following the nomenclature of Godley et al. (2008, this Theme Section [TS]). Three turtles conducted oceanic migrations to access neritic foraging areas along the Pacific coast of Central America (hereafter referred to as Type A1 movements), 2 turtles remained in the Galápagos (Type A2 movements), and 7 turtles moved into oceanic waters southwest of the Galápagos (Type B movements) (Table 2, Figs. 2 & 3). Among turtles conducting Type B movements, there was a tendency for their departures from the Galápagos to be largely west- or south-bound (Type B-western and Type B-southern, respectively; Table 2, Figs. 2 & 3); however, because we are unaware of the final destinations of these turtles, all movements are classified as Type B due to their mutual occurrence in oceanic waters. There was a significant difference in body size among groups (Kruskal-Wallis $H = 31.93$, $p < 0.0001$); turtles engaging in Type A1 movements were the largest, while those conducting Type A2 movements were the smallest.

Type A1 movements

The 3 turtles that migrated to neritic habitats of Central America (Turtles CM9, CM10, and CM12) conducted oceanic migrations that lasted from 31.3 to 53.7 d (Table 2). Turtle CM9, the largest tracked turtle (96.5 cm CCL), moved northeast along the Cocos Ridge for ~900 km and past the Nocoya Peninsula (Costa Rica) en route to a neritic site just south of the Gulf of Fonseca (Nicaragua). Turtle CM10 moved along a direct route (MSI = 0.95) past Malpelo Island (Colombia) and into neritic waters of the Gulf of Panama. Turtle CM12 traveled over the Cocos Ridge for ~1000 km, initially heading northwest away from the Galápagos then turning northeast en route to the ridge extending south of Panama, which it followed into the Gulf of Chiriquí (Panama). The mean travel speeds of turtles conducting Type A1 movements were significantly slower in neritic waters of Central America (20.6 ± 6.0 km d^{-1}) compared to oceanic waters (46.2 ± 5.5 km d^{-1}) ($t = 9.9$, $p = 0.03$, Table 2). This decrease was particularly evident for Turtles CM9 and CM10, both of which we believe reached their foraging area destinations based on the shorter daily travel distances at the end of their tracks (Fig. 4).

Table 2. Post-nesting movement summary. Turtles are grouped according to post-nesting migratory strategy, and movements are summarized as number of days (d), distance (km), and mean speed (km d^{-1}) in each zone. Migration straightness index (MSI) is provided for oceanic movements. CCL: curved carapace length (cm); (–): no data

Turtle	CCL (cm)	Galápagos neritic Duration	Distance	Speed (km d^{-1})	Oceanic Duration	Distance	Speed	MSI	Mainland neritic Duration	Distance	Speed (km d^{-1})	Overall Duration	Distance
Type A1													
CM9	96.5	11.1	192.3	17.3	53.7	1894.2	35.2	0.79	5.3	49.9	9.4	70.2	2136.3
CM10	93.0	27.2	361.7	13.3	31.0	1630.4	52.6	0.95	7.5	171.9	22.8	65.7	2164.0
CM12	81.0	45.1	390.0	8.6	37.3	1901.8	50.9	0.70	7.8	233.1	29.7	90.3	2524.9
Type A2													
CM1	74.7	47.9	1396.1	29.1	–	–	–	–	–	–	–	47.9	1396.1
CM8	71.6	69.0	691.9	10.3	–	–	–	–	–	–	–	69.0	691.9
Type B-western													
CM2	80.5	29.2	70	2.9	30.0	1231.7	41.0	0.95	–	–	–	59.1	1301.7
CM5	87.2	7.9	143.7	18.1	54.5	1912.1	35.1	0.50	–	–	–	62.5	2055.8
CM11	83.0	9.1	205.6	22.7	58.5	1534.8	26.2	0.87	–	–	–	67.6	1740.4
Type B-southern													
CM3	89.0	85.5	501.7	5.9	14.8	397.4	26.9	0.99	–	–	–	100.3	899.1
CM4	86.5	–	–	–	58.5	1662.5	32.4	0.60	–	–	–	58.5	1662.5
CM6	82.6	–	–	–	33.8	1404.5	44.7	0.75	–	–	–	33.8	1404.5
CM7[a]	78.0	–	–	–	40.1	1217.0	30.3	–	–	–	–	62.1	1903.5

[a]CM7 data based on partial track (Days 23 to 62); no MSI calculated

Type A2 movements

The 2 turtles remaining in the Galápagos (Turtles CM1 and CM8) were tracked for 49.1 to 69.0 d and visited coastal areas of at least 5 different islands, but did not nest again (Fig. 3). Turtle CM1 moved 1396.1 km after departing the Barahona nesting beach, and traveled at a mean speed of 29.1 km d^{-1} during the tracking period (Table 2). Upon the final Argos transmission, Turtle CM1 was moving along the outer edge of the Galápagos (water depth > 500 m) at a travel speed > 45 km d^{-1} and had not yet associated with a neritic foraging habitat. In contrast, Turtle CM8, the smallest turtle tracked (71.6 cm CCL), moved to a neritic foraging area along the north coast of Floreana Island that was 75 km from its nesting site on Isabela Island (Fig. 3). The mean travel speed for Turtle CM8 during its 49 d at this foraging area was 7.3 ± 1.2 km d^{-1}, compared to a mean travel speed of 17.7 ± 2.9 km d^{-1} during the 19 d prior to its arrival at this site.

Type B movements

The 7 turtles that departed the Galápagos to the southwest did so within 0 to 85.5 d of tagging and were tracked for 14.8 to 58.5 d in oceanic waters (Table 2). Turtles CM2 and CM11 moved to the west along a consistent trajectory (MSI = 0.95 and 0.87, respectively; Type B-western in Fig. 3). Turtle CM5 also followed this route after first moving in waters south of the Galápagos for the first 49 d of its deployment. At their final Argos-derived locations, these 3 turtles were at distances of 952 to 1331 km from the Galápagos and still moving west at travel speeds of 25 to 50 km d^{-1} (Fig. 4). The turtles conducting Type B-southern movements (Turtles CM2, CM4, CM6, and CM7) were last tracked at distances of 395 to 1247 km from the Galápagos (Type B-southern in Fig. 3). However, the track for Turtle CM3 was too short to provide useful information, while that of Turtle CM7 (the turtle tracked the farthest south) was missing the initial 23 d of track due to transmitter malfunction, thus preventing a full understanding of this turtle's oceanic movements. Nevertheless, Turtles CM4, CM6, and CM7 were not always moving away from the Galápagos while tracked and each maintained their location in the oceanic zone for at least 2 successive Argos transmissions on one or more occasions. This is particularly evident for Turtle CM4, which moved within a confined oceanographic area centered on 8° S, 92° W for 15 d at the end of its tracking duration (Figs. 2 & 3).

Oceanographic features

Integrating the oceanic movements of green turtles with geostrophic surface currents indicates that their movements oriented both with and against prevailing currents. Geostrophic current animations for Type A1
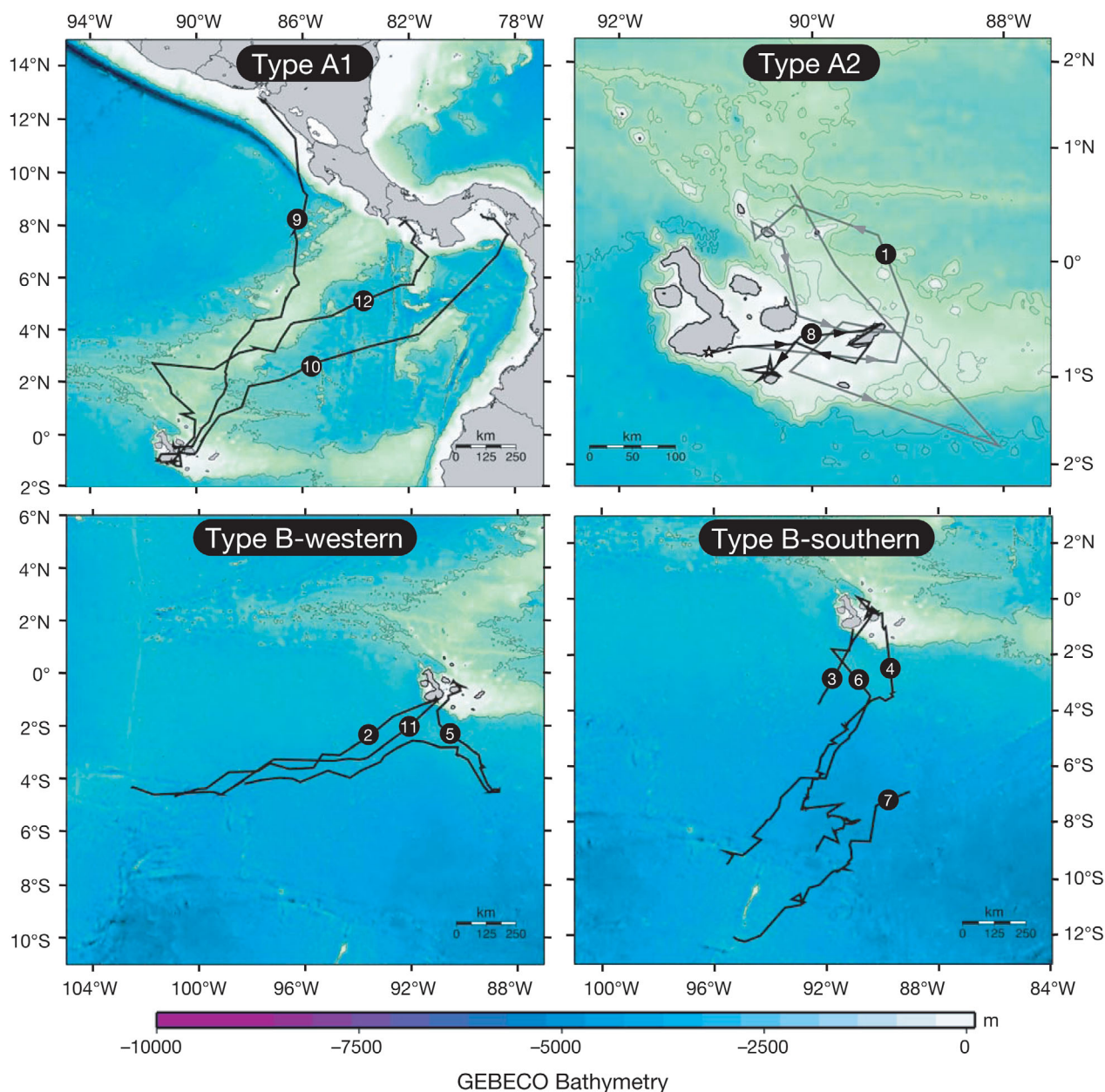
Fig. 3. *Chelonia mydas.* Satellite-tracked post-nesting movements of green turtles nesting in the Galápagos. Circular labels correspond to each of the 12 tracked turtles (i.e. 1 = CM1). Contour lines denote 2500 m water depth increments for Type A1 and Type B movements, and 500 m depth increments for Type A2 movements. Maps constructed with MapTool

movements depict the westward-flowing Northern Equatorial Current (NEC) extending from the Galápagos to ~4° N, as well as the eastward-flowing Northern Equatorial Countercurrent (NECC) south of the NEC (see Figs. A1 to A3 in Appendix 2). During the initial portions of northbound movements by Turtles CM9 (Fig. A1, Appendix 2) and CM10 (Fig. A2, Appendix 2), both turtles swam against NECC counter-clockwise rotating eddies (CM9 until 8° N and CM10 until 3.8° N) and thereafter moved in concordance with northward

flow along the edge of counter-clockwise rotating eddies. The initial movements of Turtle CM12 to the northwest were in concordance with the NEC and at ~3° N this turtle turned to the northeast and traveled largely in the same direction as surface currents, moving along the edges of a series of eddies as it progressed toward the coast of Central America (Fig. A3, Appendix 2). The movements by Turtles CM9, CM10 and CM12 to the northwest upon arriving in neritic waters may be reflective of compensatory navigation
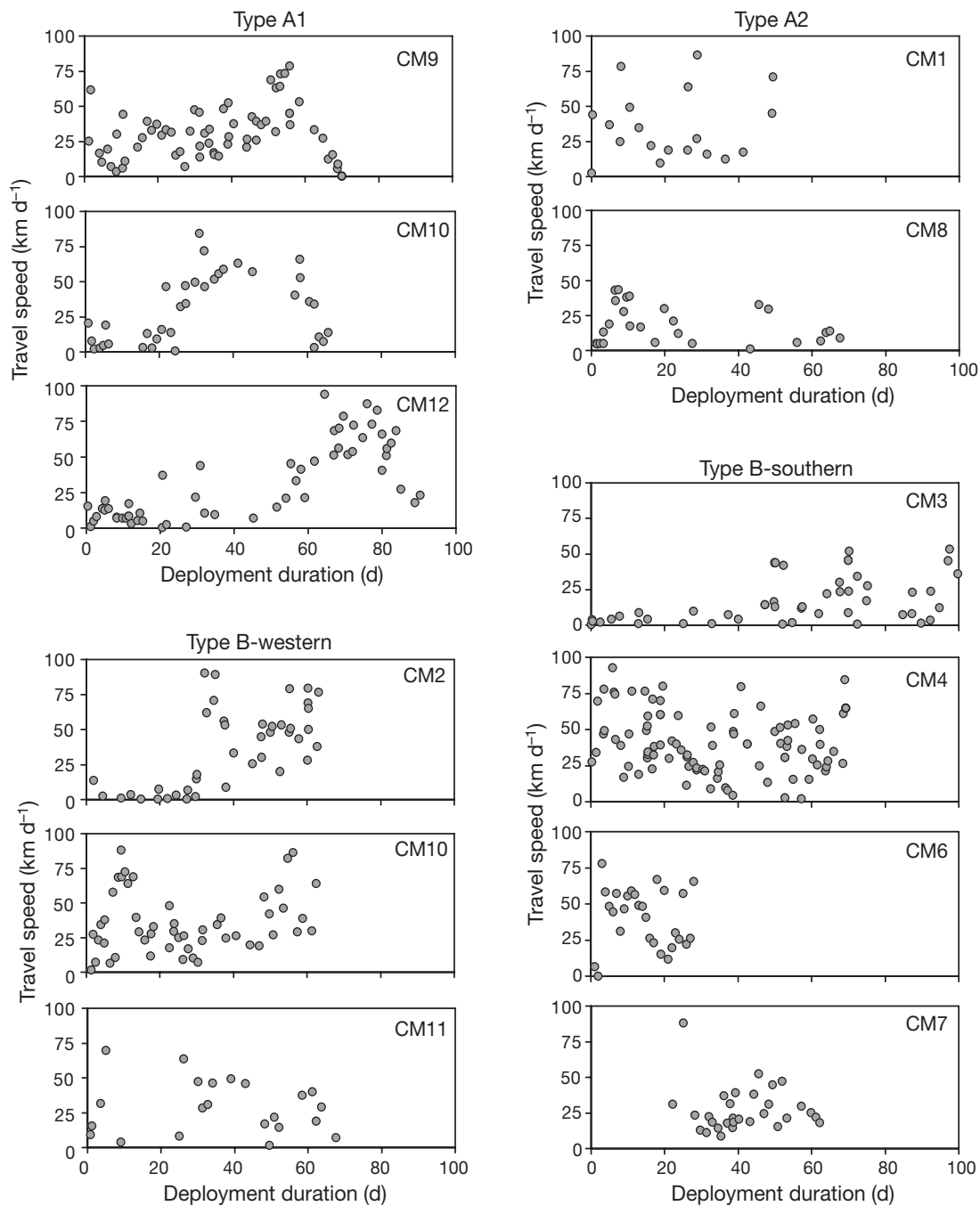
Fig. 4. *Chelonia mydas.* Swim speeds during satellite-tracked movement of green turtles in the Galápagos Islands

after being pushed to the east during migrations. If so, this suggests that the east-bound NECC and its various filaments were the most influential surface currents north of the Galápagos.

Type B movements were also variably oriented to prevailing surface currents. Turtles CM2 and CM11 (Fig. A4, Appendix 2) swam in concordance with the westward-flowing Southern Equatorial Current

(SEC) for the entirety of their respective tracking durations. Turtle CM5 also moved in parallel to the SEC for the final 13.5 d of its track, after becoming entrained in east-flowing surface waters and moving southeast for the first 21 d after leaving the Galápagos (Fig. A5, Appendix 2). At its southernmost location, Turtle CM5 meandered for 11 d in a very small area and its travel speed slowed to 34.3 ± 6.0 km d^{-1} com-

pared to 43.5 ± 6.1 km d^{-1} during earlier movements and 50.8 ± 6.2 km d^{-1} during later movements. The remaining Type B movements were more variable in relation to surface currents and there was no apparent major influence by the SEC or other surface currents. Instead, Turtles CM6 and CM7 (Figs. A6 & A7, respectively, Appendix 2) appeared to move substantial distances against the prevailing currents.

As turtles moved between neritic and oceanic zones, they encountered substantially different oceanographic conditions. A comparison of oceanographic variables in waters adjacent to Argos locations showed that these oceanic and neritic areas had significantly different values for SST, FPI, SSHa ($p < 0.0001$), but were not different in terms of surface chl *a* concentration, although we note that this latter relationship was only marginally insignificant ($p = 0.074$; Table 3). Likewise, the Argos-derived turtle locations in neritic and oceanic zones had significantly different values for SST, SSHa, and chl *a* concentration ($p < 0.05$),
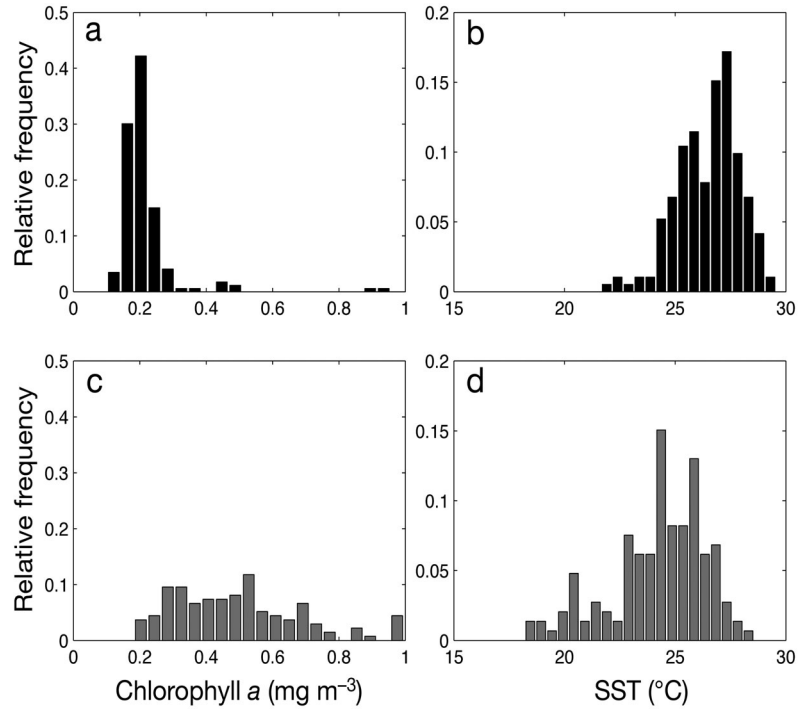

Fig. 5. Comparison of oceanographic variables at each Argos-derived green turtle location. (a,c) Surface chlorophyll *a* concentrations and (b,d) sea surface temperature (SST) in the (a,b) oceanic and (c,d) neritic zones

although there was no observed difference for SST front probability ($p = 0.76$; Table 3). The significant difference in mean surface chl *a* concentration at Argos locations in the neritic (0.47 ± 0.22 mg m^{-3}) and oceanic zones (0.18 ± 0.06 mg m^{-3}) despite the consistency in mean concentration in available waters of the neritic and oceanic zones (0.35 ± 0.007 and 0.34 ± 0.001 mg m^{-3}, respectively) suggests that chl *a* concentrations may have influenced turtles differently in these 2 zones (Table 3). In support, the range of chl *a* concentrations experienced by turtles was much broader in the neritic zone (Fig. 5a,c). With

respect to the thermal environment, green turtles rarely occupied areas with SST $\leq 24.0°$C, and mean SST along the oceanic portion of the turtles' movements was $>2°$C warmer than that for their neritic movements (Fig. 5b,d). Selectivity for thermal conditions was also indicated by the propensity of green turtles to access SST frontal zones at rates greater than their availability; i.e. FPI at Argos locations was higher than mean FPI in each respective zone (i.e. Galápagos neritic, oceanic, Central America neritic) within the study area (Table 4).

Table 3. Comparisons of oceanographic conditions in neritic and oceanic zones for all Argos-derived turtle locations as well as the means within a box ($0.2°$ longitude $\times 0.2°$ latitude $\times 5$ to 10 d) centered at the time and position of each satellite transmission and taken to represent the available habitat (i.e. background) adjacent to each turtle location

Oceanographic variable	Data set	Neritic			Oceanic			*F*-value	Significance (p)
		n	Mean	SE	n	Mean	SE		
Surface chl *a*	Argos locations	146	0.47	0.014	194	0.18	0.013	237	<0.0001
	Background	5.6×10^4	0.35	0.007	2.7×10^6	0.339	0.001	3.2	0.074
SST	Argos locations	146	24.27	0.146	194	26.51	0.128	133	<0.0001
	Background	1391	24.23	0.07	6.4×10^4	26.31	0.010	924	<0.0001
FPI	Argos locations	146	0.051	0.0078	194	0.0475	0.0067	0.1	0.7556
	Background	2642	0.0453	0.0019	1.1×10^5	0.0232	0.0003	129	<0.0001
SSHa	Argos locations	146	−0.0077	0.0038	194	0.0051	0.0033	6.47	0.01
	Background	784	−0.0319	0.0021	2.4×10^4	−0.009	0.0004	116	<0.0001

Table 4. SST Frontal Probability Index (FPI) for Argos locations and background values for neritic and oceanic habitats in the Eastern Tropical Pacific. FPI values were calculated as the fraction of days in a given 14 d period for which fronts are detected within each $0.05° \times 0.05°$ (~5.5×5.5 km) cell in the study area (delineated by 13° N, 13° S, 102° W, and the coast of Central and South America). All F values denote 95 % significance

FPI location	Data type	N	Mean ± SD	F	p
All regions	Argos locations	199	0.0925 ± 0.007		
	Background	1.12×10^5	0.0237 ± 0.0003		
	Comparison			96.3	<0.0001
Galápagos neritic	Argos locations	85	0.087 ± 0.0131		
	Background	2641	0.0453 ± 0.0023		
	Comparison			69.4	<0.0001
Oceanic	Argos locations	101	0.092 ± 0.01		
	Background	1.09×10^5	0.024 ± 0.003		
	Comparison			45.3	<0.0001
Mainland neritic	Argos locations	13	0.138 ± 0.011		
	Background	5400	0.004 ± 0.005		
	Comparison			123	<0.0001

DISCUSSION

Migratory strategies

The mosaic of post-nesting migration strategies for Galápagos green turtles, which included north-bound migration to Central America, residency in the Galápagos, and dispersal to oceanic waters southwest of the Galápagos, highlights the substantial flexibility in migratory routes and foraging area destinations for this nesting population. Variability of migratory strategies and foraging habitat affinities within nesting populations is an emerging theme among satellite telemetry studies of sea turtles (see review by Godley et al. 2008). For green turtles, such flexibility has previously been reported for nesting populations in Japan (Hatase et al. 2006) and the Mediterranean (Godley et al. 2003). Among other hard-shelled turtles this trait has been found in olive ridley turtles nesting in northern Australia, which migrate to coastal, continental shelf and continental slope feeding habitats (Whiting et al. 2007). The occupation of diverse foraging habitats after nesting is perhaps most common in loggerheads, as dedicated oceanic and neritic foragers have been documented among nesting populations in Japan (Hatase et al. 2002) and the Cape Verde Islands (Hawkes et al. 2006). Loggerheads nesting in North Carolina, USA, also show foraging area flexibility, with some females accessing temperate northern waters during summer months and others remaining in more southern, warm-water areas for the entirety of their tracking periods (Hawkes et al. 2007). Although the immense spatial scale of such movements may create challenges for conserving these nesting populations,

the range of habitat types occupied during non-reproductive periods may contribute to their stability over geologic time scales by buffering against catastrophic oceanographic events (e.g. ENSO, red tide) that affect nesting frequency and abundance.

The observed variation in post-nesting migratory strategy raises intriguing questions about the evolution of migration in sea turtles. Although little is known about how sea turtles choose foraging sites, at least some green turtles are philopatric to specific foraging habitats, returning to the same sites after nesting, year after year (Limpus et al. 1992, Godley et al. 2002, Broderick et al. 2007). If these are within the same ocean regions to which the turtles recruit during hatchling and pelagic juvenile dispersal, then explaining the migration routes and preferred foraging areas would benefit from focused examination of these dispersal mechanisms. Surface currents have been shown to play an important role in hatchling transport (Carr & Meylan 1980, Bass et al. 2006), and the flow of 4 major current systems (i.e. NEC, NECC, SEC, Peru Current) near the Galápagos may facilitate long-distance dispersal in multiple directions. The numerous current filaments and eddies generated by these convergences may also result in dispersal over only a very short distance from the nesting beach.

Upon recruitment to a foraging area, our results suggest that local conditions can profoundly affect the growth and size-at-maturity of sea turtles. It is interesting to note that the 2 resident turtles (Type A2 movement group) were the smallest turtles tracked during this study. Although we urge caution due to the small sample size, we suggest that their small body size may be due to the high green turtle density in Galápagos foraging habitats and the subsequent poor food availability (Zárate 2007) from which the effects on growth were perhaps enhanced as a result of foraging area philopatry. Adverse density-dependent effects on green turtle growth rate have been reported for green turtles in the Bahamas (Bjorndal et al. 2000) and the fact that juvenile growth rates in the Galápagos are among the slowest in green turtles studied to date ($\leq$0.5 cm yr^{-1}; Green 1993) suggests that density-dependent factors may be ongoing in this region. Phenotypically linked dichotomies in foraging areas, with larger turtles remaining in coastal habitats and smaller turtles occupying oceanic foraging zones, have been reported for loggerheads from the Cape Verde Islands (Hawkes et al. 2006) and Japan (Hatase et al. 2002). Consistent with our reasoning, the

smaller size of oceanic loggerheads from Japan is believed to be the result of poorer food availability (Hatase et al. 2002). Why smaller turtles would be present in Galápagos neritic versus oceanic waters as reported by Hatase et al. (2002) is unresolved. However, the smaller body size of resident turtles in our study, coupled with the prevalence of Type B movements (oceanic occupancy), suggests that oceanic foraging may be more energetically beneficial than neritic foraging for Galápagos green turtles. To further examine the energetic consequences of remaining in the Galápagos, it would be interesting to compare the reproductive periodicity of residents and migrants, since the rate of nutrient uptake is a major determinant of the interbreeding interval (Bjorndal 1985).

Although prior flipper tagging efforts have demonstrated the movement of green turtles from the Galápagos to the coast of Central America (Green 1984), this is the first study to reveal the specific migratory corridors that are used. The Cocos Ridge and, to a lesser extent, the ridge extending south of Panama appear to be important features associated with green turtle movements to Central America (Type A1 movement group). Although we do not know how these bathymetric features are detected, they may promote oceanographic conditions that are beneficial to migrating turtles. It is interesting that the Cocos Ridge also demarks the primary migratory corridor for leatherback turtles departing nesting beaches in Costa Rica (Morreale et al. 1996). However, it is also possible that these ridges do not directly or indirectly influence green turtle movements and are instead relevant only because of their presence along the most direct routes between the Galápagos and the preferred foraging areas for each turtle. In the absence of surface current influences on open-ocean migration, it is reasonable to expect a nutrient-depleted post-nesting turtle to access its foraging area by the most direct route possible in order to minimize the energetic cost of migration. Indeed, the Pacific coastal areas of Central America are highly productive and host numerous foraging hotspots for green turtles (Cornelius 1982, Amorocho & Reina 2007).

Whereas green turtles moving to the north were en route to neritic destinations along the coast of Central America, the functions of green turtle movements to the southwest of the Galápagos are less clear. We acknowledge that some of these turtles may have eventually returned to the Galápagos neritic, but because all were still moving away from the Galápagos at the last satellite transmission we believe this is unlikely. Based on geostrophic current plots, it is apparent that the westbound movements of turtles departing the Galápagos in 2003 and 2005 were assisted by the SEC, of which the surface layer from

~5° N to ~5° S is driven to the west by the prevailing easterly trade winds. The maximum speed of the SEC in this area reaches 25 cm s^{-1} (Kessler 2006) or 53 to 82% of the overall average speeds of Turtles CM2, CM5, and CM11. The nearly identical west-bound movements of these turtles may thus reflect surface current-facilitated and bearing-mediated movements towards known foraging areas outside the ETP. East Pacific green turtles (based on mitochondrial DNA data; Kuroyanagi et al. 1999) have been found in the western Pacific, and turtles with western Pacific mtDNA haplotypes are regularly sighted in the Galápagos (known locally as yellow turtles; Fritts 1981a, P. H. Dutton unpubl. data), indicating that transPacific movement of green turtles occurs in both directions. If Turtles CM2, CM5, and CM11 continued along the west–southwest trajectory, the nearest neritic habitats they would encounter are in French Polynesia, still ~2500 km from where the 3 turtles last transmitted. At the rate of travel measured when PTT transmissions ceased (26.2 to 41.0 km d^{-1}), these turtles would require an additional 70 to 95 d to reach this destination. This ~ 4000 km migration would represent one of the longest post-nesting migrations known for green turtles in terms of total distance and duration.

Linking satellite tracks with oceanography

Green turtles moving in oceanic zones as well as neritic zones in the Galápagos and Central America commonly associated with SST frontal zones. The affinity to these frontal areas is underscored by the fact that the ETP is a region of relatively low frontal activity (Eden & Timmerman 2004). However, this result should be viewed cautiously since there is a temporal discontinuity between the background FPI calculation (averaged over 14 d) and FPI at turtle locations (instantaneous for 1 d) in any one 0.05° × 0.05° cell. Nevertheless, although it is not certain that turtles associated with fronts per se, they at least maintained affinity to areas of more frequent front activity. The strategy used by green turtles to associate with these areas is unclear, although it is unlikely that they were able to detect the fronts at distances of 10s to 100s of km and actively navigate to them. Instead, we believe that turtles engaged with frontal zones opportunistically, and remained in such areas only if prey resources were adequate. Most fronts in this region result from current- or wind-induced upwellings, which increase biological productivity (Fiedler 2002a) and may result in greater food abundance in surface waters for sea turtles and other higher order consumers. Thus, by exploiting frontal areas, green turtles may decrease prey search times and increase their feeding effi-

ciency. To further elucidate green turtle use of frontal zones, it would be helpful to know more about their diving profiles during association with these areas to determine if their dives are shallower than when occupying waters away from thermal fronts.

Although SST frontal areas may constitute important oceanic foraging habitats for green turtles, the absence of east-bound movements toward the coast of South America — an area of substantial frontal activity (Fig. 6) — suggests that SST fronts may only be important if the associated temperatures are within an optimal range. Known as the Peruvian Coastal Upwelling Region (PCUR), the waters east of the Galápagos are among the coldest and most productive within the ETP (Pennington et al. 2006). Considering that this area was dominated by waters ≤25°C during the 2005 tracking season (Fig. 6), this temperature may represent the thermal threshold below which migrating green turtles actively avoid surface waters. We acknowledge that the lack of movements into the PCUR may be an artifact of small sample size or perhaps because accessing this area would require swimming against the prevailing SEC and Peru Current. However, we doubt that surface currents were a major factor in this lack of eastward movements since green turtles were found to swim countercurrent in other areas during this study. With respect to SST, Godley et al. (2002) reported a marked shift in diving behavior by migrating green turtles in the Mediterranean when mean sea temperatures dropped below 25°C, further supporting the likelihood that green turtles from the Galápagos avoided the PCUR due to its low surface temperatures. Interestingly, turtles in the Galápagos neritic appear willing to experience colder water, perhaps the result of a greater thermal tolerance during internesting behavior, but also possibly due to smaller-scale movements by turtles in these areas and the correspondingly lesser opportunity to choose specific water temperatures. It would be interesting to conduct telemetry studies of Galápagos green turtles during periods of elevated SST (i.e. ENSO) to determine if turtles are more likely to access waters east of the Galápagos during these periods. If so, these warming episodes may provide a mechanism for green turtles to access foraging habitats along the coast of South America.

In addition to thermal conditions, sea surface chl a concentration appears to be an oceanographic variable that influenced green turtle movements. Oceanic migrations occurred in waters with a mean sea surface chl a concentration of 0.18 mg m^{-3} and Argos locations were tightly grouped around the 0.2 mg m^{-3} surface chl a contour. This is consistent with satellite-tracked movements of loggerhead turtles foraging along the North Pacific transition zone chlorophyll front (TZCF) (Polovina et al. 2001). The 0.2 mg m^{-3} surface chl a contour is considered a proxy for identifying the convergence zone between the stratified low surface chl a (<0.15 mg m^{-3}) waters and the high surface chl a (>0.3 mg m^{-3}) vertically mixed waters (Polovina et al. 2000, 2001). This convergence zone is biologically important since the intersection of these 2 chlorophyll masses often results in the increased abundance of zooplankton and other buoyant organisms (Olson et al. 1994, Polovina et al. 2000, 2001, Graham et al. 2001) that constitute important food resources for marine predators. However, it should also be noted that the attenuation of light underwater increases exponentially with surface chl a (Smith & Baker 1978), the result being that waters with a surface chl a concentration of 0.2 mg m^{-3} are relatively clear, and likely beneficial to visual predators such as sea turtles. Thus, the affinity of green turtles to waters with a 0.2 mg
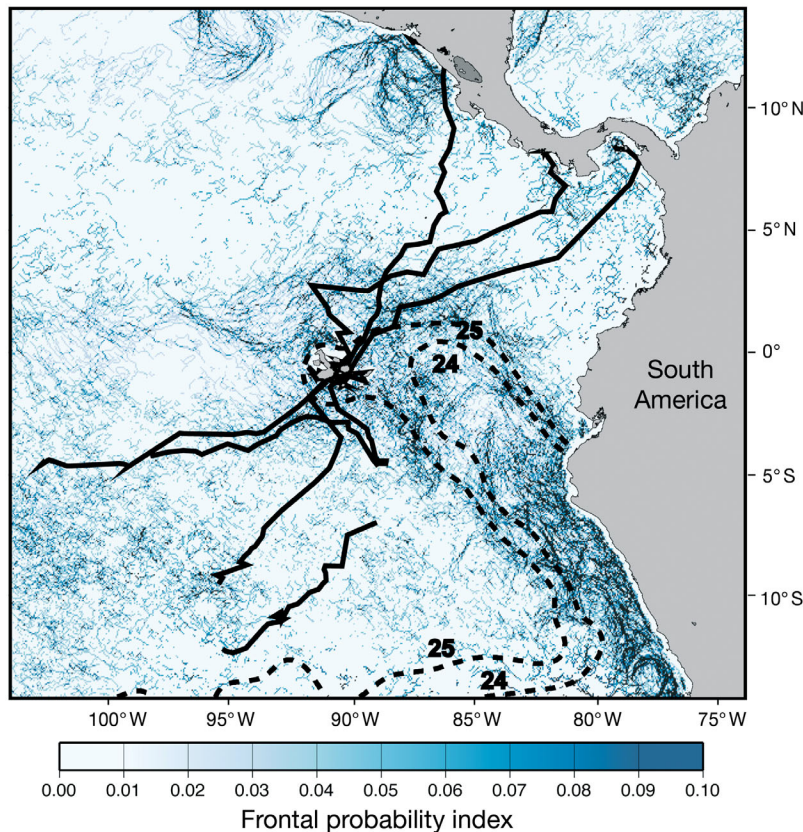

Fig. 6. *Chelonia mydas.* Green turtle post-nesting paths (continuous black lines) in 2005 in relation to frontal zones and SST contour locations (dashed lines)

m^{-3} surface chl *a* concentration may simply indicate their preference for clear water.

The localized movements of green turtles in areas south of the Galápagos, coupled with their association with prey-conducive surface chlorophyll levels and SST fronts, underscores the likelihood that at least some green turtles foraged in oceanic waters during tracking efforts. Oceanic foraging by green turtles has been demonstrated via stable isotope analyses by Hatase et al. (2006). Parker & Balazs (in press) analyzed stomachs of green turtles bycaught in oceanic zones of the central Pacific and found a variety of oceanic prey species such as sea jellies *Pyrosoma* sp., commonly found at the surface, gooseneck barnacles *Lepas* sp., which adhere to floating objects, and *Janthina* sp., a gastropod that occurs at the sea surface with the assistance of a gas-filled float, as well as >20 additional oceanic species. Green turtles captured in pelagic zones off mainland Ecuador and Peru have had stomachs filled with fish eggs (Fritts 1981b, Hays-Brown & Brown 1982). However, despite this evidence of oceanic foraging by green turtles, the strategies used to access oceanic prey resources remain poorly understood. To study this behavior we encourage additional satellite telemetry efforts that employ GPS and dive-profiling technology to reveal the exact locations of green turtles in relation to oceanographic features as well as depict the actual diving activity and surfacing intervals in these areas.

Conservation implications

Green turtles nesting within the Galápagos are protected by the Galápagos Biological Reserve of Marine Resources; however, after nesting, the majority of turtles swim to distant foraging areas that have less highly regulated and largely unmanaged exploitation of sea turtles (e.g. Chacón 2002). Turtles tracked during the present study traveled for substantial periods in international waters and entered jurisdictional waters of 5 Latin American nations (Fig. 7), all of which have been shown to have ongoing human impacts on sea turtles in neritic foraging areas (Cornelius 1982, Chacón 2002, Amorocho et al. 2005). Although not visited by green turtles during this study, coastal regions in Peru and mainland Ecuador also have high levels of directed take (de Paz et al. 2002, M. Helvey pers. comm.), further underscoring the widespread nature of green turtle hunting in the ETP. With regard to bycapture in fisheries gear, Arauz et al. (2000) describe a catch per unit effort of 0.85 green turtles per 100 hooks in Costa
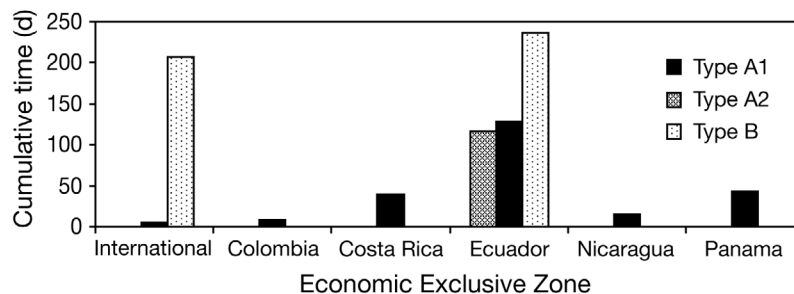

Fig. 7. Jurisdictional waters occupied by green turtles during post-nesting movements tracked with satellite telemetry

Rican longline fisheries operating east of the Galápagos. Green turtles are also the second most common sea turtle species bycaught in Peruvian artisanal shark longline fisheries (Kelez-Sara et al. 2006) and Colombian shrimp trawl fisheries (Amorocho et al. 2005), and have been killed as the result of bycatch in artisanal fisheries in Panama (P. Zarate unpubl. data) and Chile (M. Donoso pers. comm.). Together, these threats may have substantial negative effects on the Galápagos nesting population. A decline in the annual number of nesting females from 2000 to 2006 at the 4 primary beaches (Zárate 2007) suggests that the consequences of these effects are apparent at the nesting beaches.

Global conservation efforts have largely focused on nesting beaches, representing only a fraction of marine turtle life history, but it is now clear that safeguarding the migratory corridors and neritic foraging areas is essential. Fortunately, there are several sea turtle conservation initiatives ongoing in the ETP that may help protect sea turtles. Those turtles traveling north from the Galápagos to areas near Cocos Island (Costa Rica), Coiba Island (Panama), and Gorgona and Malpelo Islands (Colombia) are legally protected by the Marine Conservation and Sustainable Development Corridor, an initiative of the governments of Costa Rica, Panama, Colombia, and Ecuador which promotes sustainable management of marine resources within this part of the ETP. The Eastern Tropical Pacific Seascape Project is a complementary effort by non-governmental organizations which aims to protect a variety of marine vertebrate species within this same area (UNESCO 2006). Additional international instruments such as the Inter-American Tropical Tuna Commission (IATTC) and Inter-American Convention for the Protection and Conservation of Sea Turtles (IAC) are also designed to lessen the effects on sea turtles from fisheries and other human impacts. While clearly no single law or treaty can be 100% effective at minimizing anthropogenic impacts on sea turtles, these international agreements and laws provide a framework within which conservation advances can be made. However, there is also a need for a broad-based, cohesive sea

turtle conservation plan that targets all sea turtle species occurring in the ETP. The Permanent Commission of the South Pacific, under the Lima Convention, has developed an Action Plan for Sea Turtles in the Southeast Pacific (CPPS 2006), and is perhaps the most relevant of the international instruments in this region since all 5 nations from Panama to Chile are signatories. However, the successful implementation of this plan will require additional data on sea turtle biology and fisheries impacts as well as explicit discussion of the viable solutions to the ongoing problems. Clearly, such an effort would benefit from the participation and input of a diverse group including sea turtle biologists, wildlife managers, economists, fishers, and policy experts to address the growing challenges.

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Appendix 1. Satellite transmitter performance for 12 deployments on green turtles *Chelonia mydas*. Data for each individual includes date of deployment, start and end dates of satellite transmissions, days at large, and number of satellite uplinks summarized by location class (LC). BA: Barahona; LS: Las Salinas; QP: Quinta Playa; see Fig. 1 for tagging site locations

Turtle	Tagging site	Date of release	Date of first location	Date of final location	Track duration (d)	3	2	1	0	A	B	Z	Total uplinks
CM-1	BA	25 Feb 03	28 Feb 03	17 Apr 03	51	0	1	4	6	9	16	1	37
CM-2	BA	27 Feb 03	1 Mar 03	27 Apr 03	59	0	3	5	10	19	29	3	69
CM-3	LS	2 Mar 03	9 Mar 03	10 Jun 03	100	1	2	11	9	18	46	5	92
CM-4	LS	2 Mar 03	2 Mar 03	29 Apr 03	61	2	6	29	26	44	67	10	184
CM-5	LS	1 Apr 05	2 Apr 05	2 Jun 05	62	1	8	9	14	12	30	2	76
CM-6	QP	8 Apr 05	10 Apr 05	11 May 05	33	0	1	9	9	6	14	5	44
CM-7	QP	9 Apr 05	9 Apr 05	10 Jun 05	62	2	3	5	8	7	18	1	44
CM-8	QP	9 Apr 05	10 Apr 05	19 Jun 05	69	1	2	5	4	13	22	1	48
CM-9	QP	9 Apr 05	10 Apr 05	18 Jun 05	70	2	8	10	20	21	32	4	97
CM-10	QP	10 Apr 05	11 Apr 05	15 Jun 05	65	3	6	5	2	15	26	0	57
CM-11	QP	10 Apr 05	11 Apr 05	20 Jun 05	67	0	2	4	4	8	15	1	34
CM-12	BA	11 Apr 05	11 Apr 05	18 Jul 05	108	3	6	11	7	36	55	4	122
Total					807	15	48	107	119	208	370	37	904