



# Identification of high-use internesting habitats for eastern Pacific leatherback turtles: role of the environment and implications for conservation

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**ABSTRACT:** The numbers of leatherback turtles *Dermochelys coriacea* in the eastern Pacific Ocean have declined by up to 90% in the past 2 decades. Initially, egg harvesting was determined to be the largest causative factor, but now that this has been eliminated, high estimated adult mortality from fisheries bycatch poses the single greatest threat to this population. During the nesting season, adult female leatherback turtles nest multiple times and occupy coastal marine habitats near their nesting beaches. In this study, we characterize the interannual variability of high-use internesting habitats used by 44 (out of 46 total) female leatherback turtles that were satellite-tagged at Playa Grande, Costa Rica, from 2004 to 2007. A total of 1135 d of internesting movements were recorded across 3 tracking years. The core 25% utilization distribution (UD) remained predominantly centered within the marine protected area, Parque Nacional Marino Las Baulas (PNMB). The turtles generally dispersed in a northward or southward direction over the shallow continental shelf framing Costa Rica's Nicoya Peninsula. However, there was considerable interannual variation in the shape and area of the larger UD polygons, which was driven by variability in the thermal environment. The maximum swimming speeds and distance traveled from the nesting beach occurred during 2007. Significantly deeper and longer dive durations to cooler temperatures also occurred in this year, which may have been in response to the warming trend from the south driven by the strong Costa Rica Coastal Current. Our findings, therefore, validate the importance of PNMB as a critical habitat for internesting leatherback turtles, but also suggest that a latitudinal expansion of the park is warranted.

**KEY WORDS:** Conservation · Costa Rica · *Dermochelys coriacea* · Diving behavior · Marine Spatial Planning · Marine turtles · Satellite tracking

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## INTRODUCTION

Eastern Pacific (EP) leatherback turtles *Dermochelys coriacea* have declined by up to 90% during the past 2 decades and are currently classified as Critically Endangered (Spotila et al. 2000). These declines have been driven by many factors operating synergistically, including environmental variation in foraging areas,

habitat loss, poaching and fisheries bycatch (Spotila et al. 2000, Santidrián-Tomillo et al. 2008, Wallace & Saba 2009). Life history theory implies that populations of these leatherback turtles, because they are long-lived and slow to mature, are particularly vulnerable to the effects of adult mortality (Stearns 1992). A population modeling study (Santidrián-Tomillo et al. 2008) determined that egg harvesting was the largest causative

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factor of the leatherback turtle population decline at Parque Nacional Marino Las Baulas (PNMB), Costa Rica, and substantiated the importance of ongoing nesting-beach conservation efforts to enhance turtle recruitment. However, because poaching has been eliminated by the existence of beach patrols and strong enforcement by the Costa Rican Ministerio del Ambiente, Energia y Telecomunicaciones (MINAET), estimated high adult mortality (~22%), presumably from bycatch, presents the single greatest threat to the EP population (Santidrián-Tomillo et al. 2008). An integrated approach addressing threats to early and late stages is therefore necessary for effective leatherback turtle conservation (Congdon et al. 1993, Heppell et al. 1996).

Leatherback turtles nesting within PNMB along the Pacific coast of Costa Rica show strong nest site

fidelity to 3 specific beaches (Playa Grande, Playa Langosta and Playa Flamingo; 10° 20' N, 85° 51' W; Fig. 1) (Reina et al. 2002, Nordmoe et al. 2004, Santidrián-Tomillo et al. 2007). These 3 beaches support the highest density nesting colony of leatherback turtles in the eastern Pacific Ocean (Spotila et al. 2000). Leatherback turtles at PNMB nest multiple times within a single season at approximately 8 to 10 d intervals (Steyermark et al. 1996); these intervals are also referred to as interesting periods.

Although the postnesting movements of adult female leatherback turtles within the tropical eastern Pacific have been well described (Morreale et al. 1996, Shillinger et al. 2008), little is known about the fine-scale use of critical interesting habitats, an area essential to the conservation of this population, during the reproduc-

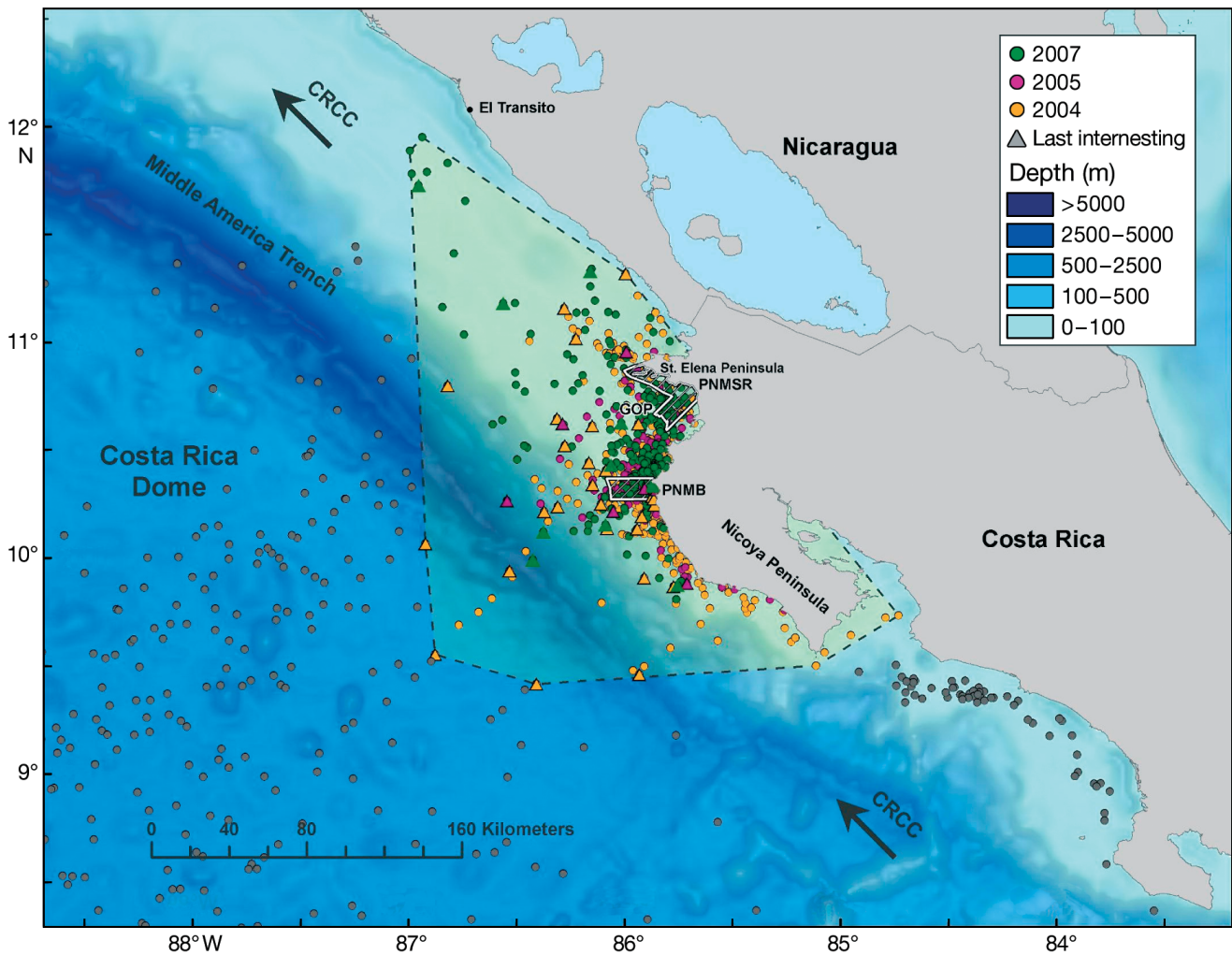


Fig. 1. *Dermochelys coriacea*. Interesting positions for leatherback turtles during 2004 (○), 2005 (●) and 2007 (●) overlaid on bathymetry. Triangles demarcate the last interesting position per platform transmitter terminal (PTT) within each of the tracking seasons (▲, 2004; ▲, 2005; ▲, 2007). Dashed black line represents 95% minimum convex polygon (MCP) for combined tracking seasons. Polygons bordered in white are Playa Grande National Marine Park (PNMB) and Santa Rosa National Marine Park (PNMSR). Circles outside of the MCP illustrate how turtle movements continued post-interesting but have been greyed out as they are not considered in the analysis. GOP: Gulf of Papagayo. Costa Rica Coastal Current (CRCC) is denoted with directionality arrows

tive period (October to March). This is a time when turtles are concentrated within nearshore habitats and can be at risk from fisheries interactions and other anthropogenic pressures. PNMB's marine boundaries extend 22.2 km (12 nautical miles, n miles) from the nesting beaches, and the marine sector of the park is managed as a no-take zone for all fishing activity, although the adjacent marine areas are not managed under any type of protected status. In this study, we identify and characterize the interannual variability of high-use interesting habitats of leatherback turtles satellite-tagged at Playa Grande, Costa Rica. The identification of high-use interesting habitats through electronic tracking studies will help to refine measures aimed at mitigating human impacts on leatherback turtles and will provide insights into the degree to which the current marine protected area, PNMB, encompasses critical interesting habitats for this endangered species.

## MATERIALS AND METHODS

**Tagging and data processing.** Sea Mammal Research Unit (SMRU) satellite relay data logger (SRDL) tags were attached to 36 female leatherback turtles during 2004 ( $n = 17$ ), 2005 ( $n = 8$ ) and 2007 ( $n = 11$ ). The SRDL tags were programmed to collect and transmit position, temperature, dive data and tag diagnostic information. An additional 10 turtles were tagged during 2004 with wildlife computer smart position only tags (SPOTs), which were programmed to provide position data. The satellite transmitters were mounted on the turtles during oviposition by means of a harness (Eckert 2002). Data from the tags were transmitted via the Argos satellite system. A state-space model (SSM), which can account for different location class errors, was applied to all of these raw Argos-acquired locations to produce final position estimates at regular 6 h intervals to improve position accuracy and to align with SMRU summary dive data (Jonsen et al. 2003, Bailey et al. 2008, Shillinger et al. 2008) (Fig. 1). The application of a switching SSM provided the capacity to discern between 2 behavioral modes based on a first-difference correlated random walk. The location of the switch between these 2 behavioral modes was used to objectively define the transition from interesting ('mode 2') to the postnesting migration ('mode 1') (Bailey et al. 2008). In the few cases where a clear switch was not present, a sudden increase in the travel speed was used to determine the cut-off point. Travel speeds were calculated by first-differencing consecutive 6-h SSM mean position estimates. To align with environmental data that were only available on a daily basis, the median of the four 6-h SSM mean positions was calculated for each day.

Dive data were obtained from a pressure sensor on the SRDL tags (to accuracy of 0.33 m). Dive initiation and termination were determined by the tag's conductivity sensor. Profiles were recorded for all dives deeper than 10 m. Bespoke software onboard the tag was used to examine dive profiles and identify 5 significant inflection points within the dive (Fedak et al. 2002). Information about the geolocation of dive profiles, dive start and end times and dive profile inflection points was provided, along with maximum dive depth attained on individual dives, summary dive data (e.g. proportion of time spent diving below 10 m, mean dive depths and durations for dives below 10 m) in 6 h bins and tag diagnostic information (Fedak et al. 2002, Hays et al. 2004). The tag summary and diagnostic information was used to filter inaccurate dive profiles from the dive tables within SMRU-developed database queries. Dives that occurred from 06:00 to 18:00 h local time were considered day dives and those after 18:00 h to before 06:00 h local time were considered night dives. Differences in dive behavior between day and night were tested with a 2 sample *t*-test.

Sea surface temperature (SST) measurements were extracted from the temperature-at-depth data transmitted by the SRDL tags (resolution to 0.1°C). Surface was considered to be the first depth bin (mean = 5.1 m, SD = 0.7 m). A total of 917 temperature measurements were available after we discarded 105 records because the first depth was missing, had a negative value or had spurious position values. The 1 m interval temperature-at-depth data were obtained by Loess filtering the 12 temperature-at-depth points provided by the tag. These data were used to produce log frequency temperature-depth plots. For each 1 m depth interval the temperature at peak use was identified and fit with a third order polynomial.

The turtle morphological and life history information was obtained from field data recorded by research teams coordinated through the Goldring Marine Biology Field Station, including Drexel University, Indiana Purdue-Fort Wayne University, and MINEAT, Costa Rica. The tagged turtles had a mean curved carapace length (CCL) of 145.5 cm, mean estimated clutch frequency (Steyermark et al. 1996, Reina et al. 2002) of 8 clutches and mean clutch size of 60 eggs (Table 1). All interesting periods defined within this paper were recorded by observers on beach patrols at PNMB.

**Environmental data.** Monthly SST (°C) composites were obtained from the NOAA GOES Imager (0.05° spatial resolution) for the months of December (2003, 2004 and 2006) and January to March (2004, 2005 and 2007), the main nesting period for our tagged turtles. Monthly composites for net primary productivity (NPP) were obtained from Aqua Modis at 0.05° spatial resolution (available at <http://coastwatch.pfeg.noaa.gov/data.html>)

Table 1. *Dermochelys coriacea*. Biological data for leatherback turtles satellite tagged at Playa Grande, Costa Rica, during 2004 (n = 27), 2005 (n = 8) and 2007 (n = 11). Mean values for each year and all years combined are in **bold** text. PTT ID: tag identification number; CCL: caudal carapace length; CCW: caudal carapace width; ECF: estimated clutch frequency; na: data not available

PTT ID	CCL (cm)	CCW (cm)	No. of clutches	ECF	Clutch size (no. of eggs)	Date		First season observed	Years observed
						First nest	Last nest		
<b>2004</b>									
37595	144.6	104.5	3	9.8	53.0	13 Nov	4 Feb	2003/04	1
37596	148.4	104.2	10	10.0	59.0	21 Nov	15 Feb	1994/95	5
40672	149.2	105.5	8	8.0	57.3	8 Dec	18 Feb	2000/01	2
40673	146.5	105.4	4	5.8	78.0	29 Dec	12 Feb	1998/99	3
40675	142.8	102.3	5	5.0	na	10 Jan	18 Feb	2000/01	2
41687	143.9	103.1	5	7.3	na	9 Dec	6 Feb	2003/04	1
41688	148.9	106.3	7	7.0	79.3	7 Dec	31 Jan	2003/04	1
41689	145.8	107.3	11	11.0	61.0	6 Nov	9 Feb	2000/01	2
41690	140.0	103.2	8	8.0	74.5	29 Nov	7 Feb	2000/01	2
41691	157.4	106.9	9	9.0	43.3	13 Nov	30 Nov	1994/95	3
41692	141.1	97.3	4	6.1	71.0	12 Dec	1 Feb	2003/04	1
41693	140.6	99.8	5	4.1	80.0	18 Jan	16 Feb	2003/04	1
41694	148.0	103.4	5	5.0	82.0	8 Jan	18 Feb	2003/04	1
41695	151.3	105.4	7	7.0	59.3	17 Nov	19 Jan	1995/96	3
41696	148.2	107.4	9	9.0	65.5	7 Nov	19 Jan	1997/98	3
41697	139.4	101.2	8	8.0	73.0	6 Dec	13 Feb	2000/01	2
41698	151.3	108.4	9	9.0	79.5	27 Nov	12 Feb	1999/00	2
41699	133.5	96.7	9	9.0	67.0	25 Nov	2 Feb	2003/04	1
41700	142.1	103.1	8	7.1	na	14 Dec	6 Feb	2000/01	2
41701	154.8	112.5	11	11.2	63.3	6 Nov	6 Feb	1999/00	2
41702	148.1	108.8	14	13.9	62.0	15 Oct	13 Feb	2000/01	2
41703	138.2	98.1	7	7.0	na	14 Dec	11 Feb	2003/04	1
41704	144.6	106.8	5	6.0	61.0	28 Dec	11 Feb	1994/95	3
41705	139.0	100.8	6	5.8	57.7	11 Dec	28 Jan	2003/04	1
41706	143.4	103.2	8	9.1	55.2	19 Nov	3 Feb	2001/02	2
41707	126.9	96.5	5	5.0	48.7	17 Dec	24 Jan	2003/04	1
41708	136.8	104.7	11	11.0	57.0	12 Nov	12 Feb	2000/01	2
41709	137.8	99.6	11	11.2	56.0	23 Oct	21 Jan	2003/04	1
41710	146.5	100.6	8	6.0	63.0	11 Dec	16 Feb	2000/01	2
41711	145.3	105.6	4	8.9	na	16 Dec	28 Feb	2003/04	1
<b>Mean</b>	<b>144.1</b>	<b>103.6</b>	<b>7.5</b>	<b>8.0</b>	<b>64.3</b>				<b>1.9</b>
SD	6.3	3.8	2.7	2.3	10.5				0.9
<b>2005</b>									
56268	151.3	106.5	5	8.4	39.3	29 Nov	7 Feb	1994/95	3
56272	140.4	97.8	2	3.7	53.5	4 Jan	29 Jan	2004/05	1
56274	149.7	102.7	9	10.7	43.5	30 Oct	28 Jan	2000/01	2
56276	145.2	109.4	10	9.9	58.8	11 Nov	3 Feb	1999/00	3
56279	133.1	101.5	9	9.1	64.2	7 Dec	21 Feb	2000/01	2
56280	154.5	109.6	4	5.6	64.7	17 Jan	1 Mar	1994/95	4
56282	141.4	100.7	9	9.3	61.4	2 Dec	18 Feb	1994/95	3
56283	150.2	106.5	5	5.6	71.0	7 Jan	19 Feb	2004/05	1
<b>Mean</b>	<b>145.7</b>	<b>104.3</b>	<b>6.6</b>	<b>7.8</b>	<b>57.1</b>				<b>2.4</b>
SD	7.1	4.3	3.0	2.5	10.9				1.1
<b>2007</b>									
72474	139.0	107.0	7		51.0	15 Dec	18 Feb	1995/96	4
72475	143.9	106.7	7	8.9	77.0	15 Nov	28 Jan	2000/01	2
72476	153.1	111.7	11	11.6	50.0	11 Nov	19 Feb	2000/01	3
72477	156.9	107.9	11	12.0	48.5	3 Nov	14 Feb	2003/04	1
72478	142.7	103.9	8	10.5	55.3	26 Nov	23 Feb	1995/96	3
72479	165.6	115.2	9	9.3	87.7	20 Nov	6 Feb	1995/96	3
72480	155.8	109.6	10	12.5	63.5	2 Nov	18 Feb	1994/95	4
72481	149.1	99.1	4	5.7	51.0	6 Jan	19 Feb	1997/98	4
72482	146.2	103.6	8	10.8	68.4	10 Nov	10 Feb	1995/96	3
72483	142.5	102.7	2	2.1	na	3 Feb	13 Feb	2006/07	1
72485	146.3	104.4	4.0	5.3	50.0	5 Jan	14 Feb	2006/07	1
<b>Mean</b>	<b>149.2</b>	<b>106.5</b>	<b>7.4</b>	<b>8.9</b>	<b>60.2</b>				<b>2.6</b>
SD	7.9	4.5	3.0	3.4	13.6				1.2
<b>Mean for all years</b>	<b>145.5</b>	<b>104.4</b>	<b>7.3</b>	<b>8.2</b>	<b>62.0</b>				<b>2.1</b>
SD	7.0	4.2	2.7	2.6	11.4				1.1

for the months of December (2003, 2004 and 2006) and January to March (2004, 2005 and 2007). Bathymetry was extracted from the global sea-floor topography of Smith & Sandwell (1997; v. 8.2, November 2000; available at [http://topex.ucsd.edu/WWW\\_html/mar\\_topo.html](http://topex.ucsd.edu/WWW_html/mar_topo.html)). This dataset combines all available depth soundings with high-resolution marine gravity information provided by the Geosat, ERS-1/2 and TOPEX/Poseidon satellite altimeters, and has a nominal resolution of 2 arc-minutes (~4 km).

**Utilization distribution and minimum convex polygon (MCP) analysis.** Geographic information systems software (ArcGIS 9.3 and ArcView 3.3) was used to map turtle movements and delineate high use interesting habitats. High-use habitats were defined by calculating fixed kernel home ranges for all turtles using the median daily SSM-generated positions for each animal. This process involved creating seasonal utilization distribution (UD) maps (Worton 1989) of the data using the Home Range Extension in ArcView. A fixed kernel approach was selected because it provided a better estimate of home-range size than adaptive kernel approaches (Seaman & Powell 1996), and the least-squares-cross-validation method was used to calculate the smoothing parameter (Worton 1989). The 25, 50, 75 and 95% UD polygons were created for all turtles for individual years and for all years combined (Fig. 2). The core region was assigned to be the 25% UD (Hyrenbach et al. 2006), and everything outside of the 25% UD but contained within the 95% UD was considered as noncore. We extracted vertical and horizontal turtle movement from the core and noncore regions for our analyses. Kruskal-Wallis tests compared vertical behaviors within the UD polygon core and noncore regions and also between tracking years. A multiple comparison ANOVA was subsequently applied to conduct post hoc pairwise comparisons between the mean ranks. MCPs were created with Hawth's Tools in ArcGIS using a fixed mean selection at 100% coverage to delineate total interesting habitat use for each turtle within each tracking season, and for all turtles across all 3 tracking seasons.

## RESULTS

### Track durations and observed interesting periods

A total of 1135 d of interesting movements were recorded (2004: 690 d, 2005: 188 d, 2007: 257 d; Table 2). Across the entire dataset, the tracking period per turtle during the interesting period ranged to 88 d (mean = 25.8 d, SD = 18.1 d). One turtle (tag identification no. 56272) that initiated migration immediately after tagging was eliminated from the interesting

dataset. Analyses of interesting durations were potentially reduced by our tag deployment approach, which targeted turtles during the latter part of the nesting season so as to minimize possible stress or interference during the nesting process from the tracking device.

Specific interesting periods were determined by visual observations of nesting events. An analysis of the initial subset of validated interesting intervals ( $n = 27$ ) revealed that these intervals ranged from 9 to 12 d (mean = 10.1 d, SD = 0.9 d). Since turtles occasionally nested on beaches without observer coverage and remained within interesting habitats after the end of the field research period (March), it is possible that some nesting events were not recorded. We did not attempt to derive nesting events from satellite tracking location data alone, due to uncertainty associated with possible false crawls or aborted nesting attempts, and the possibility that shallow water dive behavior and surface behavior within near-shore habitats could create a false positive result. Haul-out data, based on the length of time the saltwater switch on the satellite tag was dry, provides another method of recording nesting events that deserves attention in future studies (Georges et al. 2007).

### Environmental data

We used a suite of remote sensing data to characterize variability within the interesting habitat. Analysis of SST (Fig. 3) and NPP imagery (Fig. 4), revealed consistent annual surface patterns in SST and productivity within the tracking region as well as in the area ranging to 20°N. Strong transitions in SST and NPP occurred during the peak of interesting (between December and January) and during the end of interesting (between February and March). The imagery implied strengthening of the Papagayo and Tehautepec jets (Palacios & Bograd 2005, Kessler 2006), which forced local upwelling near the Gulf of Papagayo (GOP) and Gulf of Tehautepec (GOT) and within the interesting MCP (Fig. 2). These jets also contributed to the formation of large and long-lived anti-cyclonic eddies that entrained and exported biogenic material offshore and enhanced productivity throughout the tracking region. The seasonal development of the locally productive Costa Rica Dome (CRD; Kessler 2006) was apparent in both the SST and NPP imagery. During January and February of each tracking year a cold nutrient-rich region located to the north and west and extending into the MCP was apparent. This region remained through March 2007. Along with the overall warmer temperatures during 2007, this cold region contributed to the wider range of temperatures within the MCP during 2007. The thermal signal from the Costa Rica Coastal Current (CRCC) within the SST

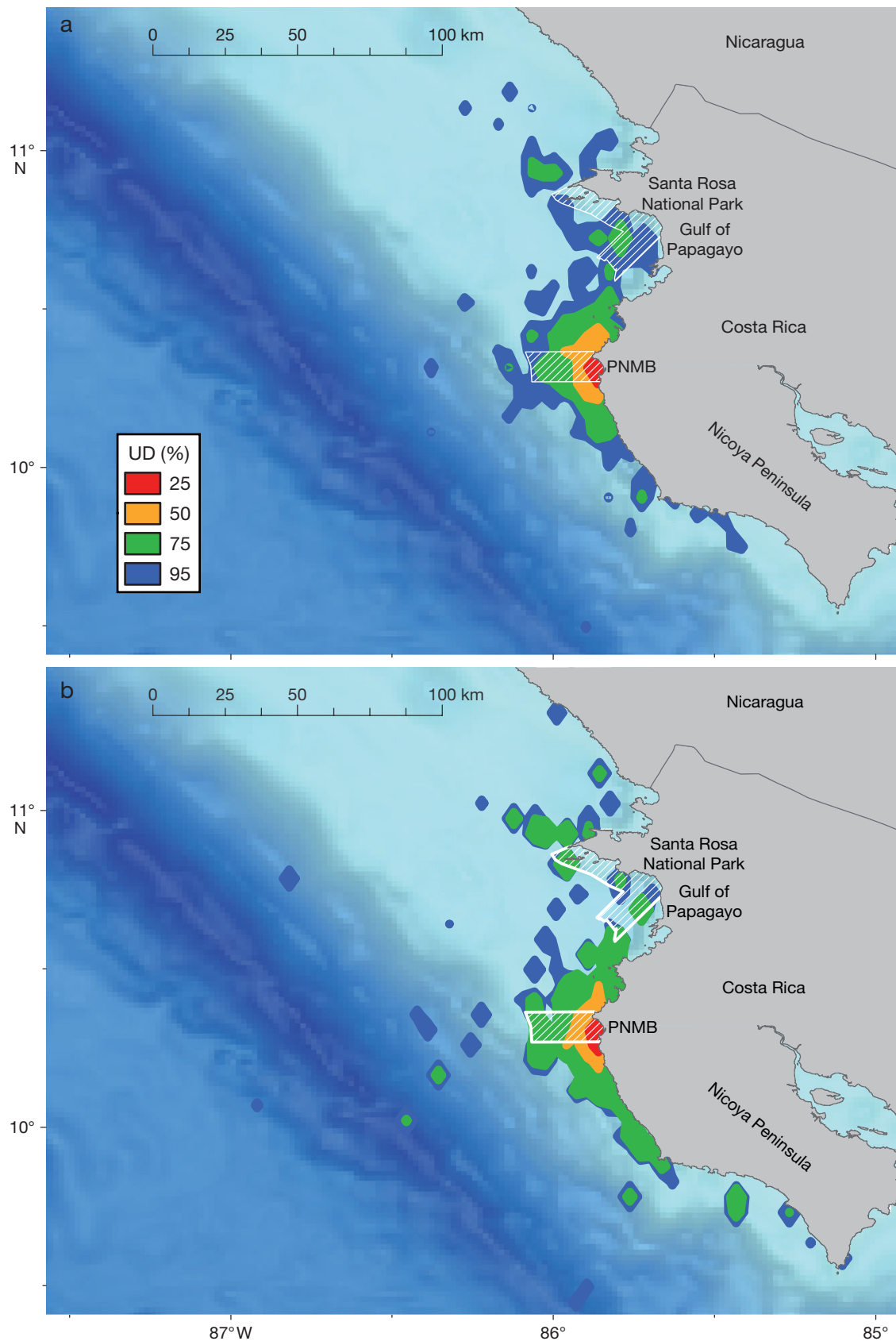


Fig. 2. *Dermochelys coriacea*. Utilization distribution (UD) of interesting region occupied by 46 leatherback turtles during (a) all years combined, (b) 2004 ( $n = 27$ ), (c) 2005 ( $n = 8$ ) and (d) 2007 ( $n = 11$ ). Polygons bordered and cross-hatched in white are Playa Grande National Marine Park (PNMB) and Santa Rosa National Marine Park (PNMSR). See Fig. 1 for bathymetry details

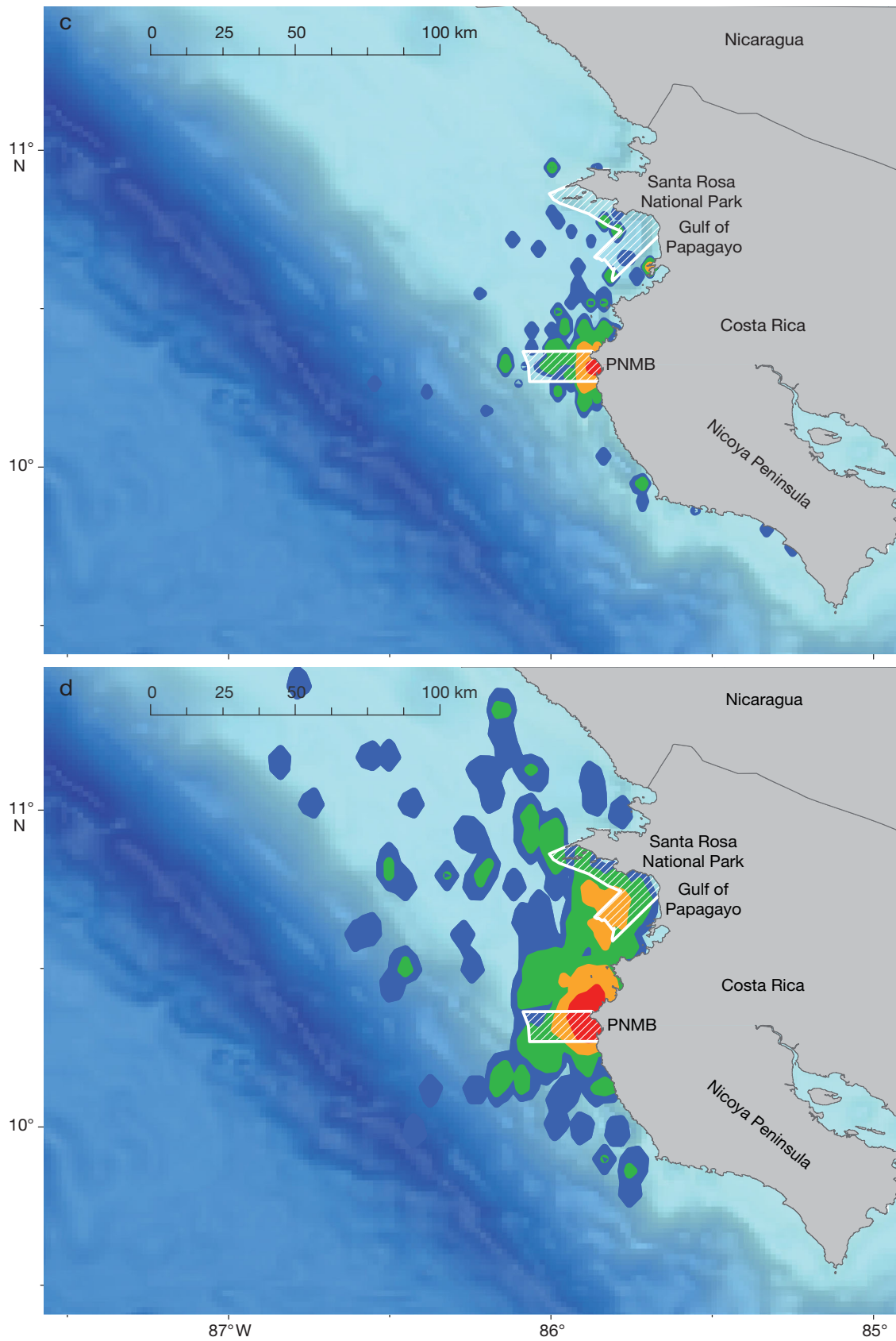


Fig. 2 (continued)

Table 2. *Dermochelys coriacea*. Horizontal movement data for leatherback turtles satellite tagged at Playa Grande, Costa Rica, during 2004 (n = 27), 2005 (n = 8) and 2007 (n = 11). A single location (85.82° W, 10.31° N) on the nesting beach was used as a reference point for calculating the minimum convex hull polygons (MCP), the convex hulls and maximum distance range calculations, and the maximum and minimum latitudinal and longitudinal range calculations. Sea surface temperature (SST, °C) was extracted from the SMRU SRDL tag-derived data for the 1 m depth bin. Mean values for each year are in **bold** text. PTT ID: tag identification no.; Total rec. days: total no. of days recorded; na: data not available

PTT ID	Tagging date	Interinteresting end date	Total rec. days	Observed interinteresting periods	Total distance travelled (km)	Mean speed (km d <sup>-1</sup> )	95% MCP (km <sup>2</sup> )	Max. range (km)	Lat. range (°N)		Long. range (°W)		Mean SST (°C)
									Max.	Min.	Max.	Min.	
<b>2004</b>													
37595	26 Jan	24 Feb	30	1	130.20	4.34	958.07	47.38	10.4760	10.0061	85.9928	85.7569	27.69
37596	26 Jan	28 Feb	33	2	61.50	1.86	194.78	11.40	10.3339	10.2799	85.9349	85.8438	27.60
41687	27 Jan	20 Feb	23	1	81.57	3.55	5957.11	97.35	10.1752	10.1752	86.2265	85.8832	na
41688	20 Jan	4 Feb	14	1	75.04	5.36	4727.67	66.45	10.7285	10.3933	85.9137	85.7588	na
41689	30 Jan	15 Feb	16	1	42.50	2.66	724.89	30.52	10.5582	10.2030	85.9640	85.8312	na
41690	28 Jan	4 Mar	36	1	120.11	3.34	1400.13	49.23	10.5582	10.2334	86.0202	85.8492	na
41691	30 Jan	25 Feb	25	0	127.62	5.11	1728.62	59.84	10.4094	10.2395	86.3613	85.8636	na
41692	1 Feb	12 Feb	11	0	83.33	7.58	2020.07	66.30	10.7128	10.3404	85.9888	85.8092	na
41693	16 Jan	23 Mar	35 <sup>a</sup>	0	119.96	3.43	1390.85	31.33	10.5910	10.2094	86.0019	85.8344	na
41694	18 Jan	29 Feb	10 <sup>a</sup>	0	38.06	3.81	2373.32	89.55	11.1219	10.8708	85.9977	85.8431	na
41695	19 Jan	23 Feb	33	0	137.44	4.16	3830.69	121.58	10.5018	9.8628	86.5656	85.7593	na
41696	19 Jan	30 Jan	10	0	47.94	4.79	1389.88	102.02	10.9844	10.7164	86.0562	85.9638	na
41697	27 Jan	15 Mar	48	2	153.54	3.20	975.33	46.15	10.7267	10.1854	85.9009	85.7345	27.65
41698	23 Jan	16 Feb	24	2	103.12	4.30	754.38	49.36	10.7091	10.2993	85.9036	85.6932	27.04
41699	24 Jan	15 Feb	22	2	74.47	3.34	431.85	34.65	10.3483	10.2247	85.9990	85.8522	27.03
41700	29 Jan	16 Mar	49	1	150.98	3.08	556.44	42.67	10.4167	10.0360	86.0065	85.7361	27.19
41701	29 Jan	10 Feb	12	1	30.83	2.57	150.97	14.37	10.4148	10.2546	85.9217	85.8367	27.55
41702	24 Jan	6 Feb	13	1	85.34	6.56	4156.83	56.24	10.7135	10.3129	85.8973	85.7425	27.30
41703	23 Jan	20 Mar	58	2	196.46	3.39	739.76	46.03	10.3212	10.0404	85.9009	85.8127	27.41
41704	23 Jan	20 Feb	28	2	163.78	5.85	2522.19	163.78	11.1297	10.1222	86.0234	85.7887	27.03
41705	29 Jan	11 Feb	13	0	122.85	9.45	5366.04	141.16	10.3126	9.5315	85.8528	85.8161	28.33
41706	25 Jan	17 Feb	22	1	105.82	4.81	964.13	49.32	10.3880	10.1388	85.9356	85.8161	27.52
41707	25 Jan	31 Jan	6	0	107.74	17.96	3018.43	117.77	10.0254	9.8892	85.7597	85.3876	27.97
41708	25 Jan	25 Feb	31	2	171.11	5.52	1057.65	106.54	10.3751	9.6880	85.9123	85.3193	27.76
41709	22 Jan	3 Feb	12	0	57.16	4.76	2150.50	76.61	10.9864	10.6040	86.0839	85.9437	26.44
41710	27 Jan	29 Feb	34	2	261.87	7.70	2006.53	78.48	10.5691	9.8037	86.1323	85.4788	26.82
41711	27 Jan	23 Apr	88	2	495.07	5.63	3922.42	106.37	10.5153	9.6387	85.9025	85.2329	26.72
<b>Mean</b>			<b>27.6</b>	<b>1.00</b>	<b>123.90</b>	<b>5.11</b>	<b>2054.43</b>	<b>70.46</b>					<b>27.36</b>
SD			18.3	0.83	91.00	3.10	1626.47	38.51					0.48
<b>2005</b>													
56268	8 Feb	26 Mar	46	0	213.82	4.65	3492.52	74.10	10.8531	10.2915	86.0926	85.7291	27.73
56272	29 Jan	29 Jan	0	0	na	na	na	na	na	na	na	na	na
56274	28 Jan	8 Feb	11	0	12.03	1.09	81.92	14.19	10.3636	10.2786	85.9894	85.8580	27.83
56276	4 Feb	5 Mar	29	0	200.52	6.91	1162.75	69.12	10.8074	10.3211	85.9418	85.8245	27.05
56279	11 Feb	23 Feb	12	1	26.18	2.18	363.32	26.18	10.5518	10.3188	85.9918	85.8684	26.80
56280	8 Feb	23 Mar	43	2	129.60	3.01	581.94	50.18	10.4166	9.9909	85.9711	85.7818	27.95
56282	30 Jan	18 Feb	19	2	64.48	3.39	181.82	15.53	10.2628	10.2628	85.9453	85.8615	27.19
56283	9 Feb	9 Mar	28	2	269.65	9.63	4417.45	92.35	10.7424	9.8058	86.2213	85.3738	27.86
<b>Mean</b>			<b>23.5</b>	<b>0.88</b>	<b>130.90</b>	<b>4.41</b>	<b>1468.82</b>	<b>48.81</b>					<b>27.49</b>
SD			16.0	0.99	100.40	2.96	1754.61	31.01					0.46
<b>2007</b>													
72474	29 Jan	8 Feb	10	0	84.70	8.47	676.18	52.72	10.7364	10.4505	85.9156	85.7481	28.04
72475	29 Jan	29 Jan	1	0	na	na	na	na	na	na	na	na	31.26
72476	31 Jan	3 Mar	31	2	247.63	7.99	3095.47	87.41	10.9591	10.2535	86.2514	85.7679	27.11
72477	3 Feb	20 Feb	17	1	143.96	8.47	3848.25	117.26	11.1386	10.3140	86.1476	85.8862	28.07
72478	3 Feb	3 Apr	59	2	315.64	5.35	3169.82	116.09	11.1658	10.2856	86.2141	85.7627	26.88
72479	7 Feb	1 Mar	22	0	92.48	4.20	600.76	52.54	10.0717	10.0717	85.9879	85.8136	28.07
72480	8 Feb	2 Mar	22	1	232.57	10.57	11038.96	214.91	11.8906	10.5324	86.9532	85.8002	27.89
72481	9 Feb	13 Apr	62	1	273.91	4.42	1203.23	36.21	10.5785	10.3215	86.0267	85.8030	28.91
72482	10 Feb	14 Feb	4	0	7.84	1.95	878.22	23.71	10.2519	10.2519	86.0025	86.0025	28.83
72483	14 Feb	2 Mar	16	0	167.19	10.45	6327.43	90.91	10.8311	10.1914	86.5341	85.8567	29.02
72485	15 Feb	28 Feb	13	0	62.65	4.82	1320.97	46.19	10.2702	10.0579	86.1254	85.8973	28.48
<b>Mean</b>			<b>23.4</b>	<b>0.64</b>	<b>162.86</b>	<b>6.67</b>	<b>3215.93</b>	<b>83.79</b>					<b>28.41</b>
SD			20.2	0.81	101.78	2.91	3294.67	56.42					1.17

<sup>a</sup>The state-space model (SSM) interinteresting positions for turtles with tag identification nos. 41693 and 41694 were interpolated across land for this track. These movement positions were eliminated by a land mask. Mean speed and distance travelled were based on movement data from position estimates that were not eliminated by the land mask



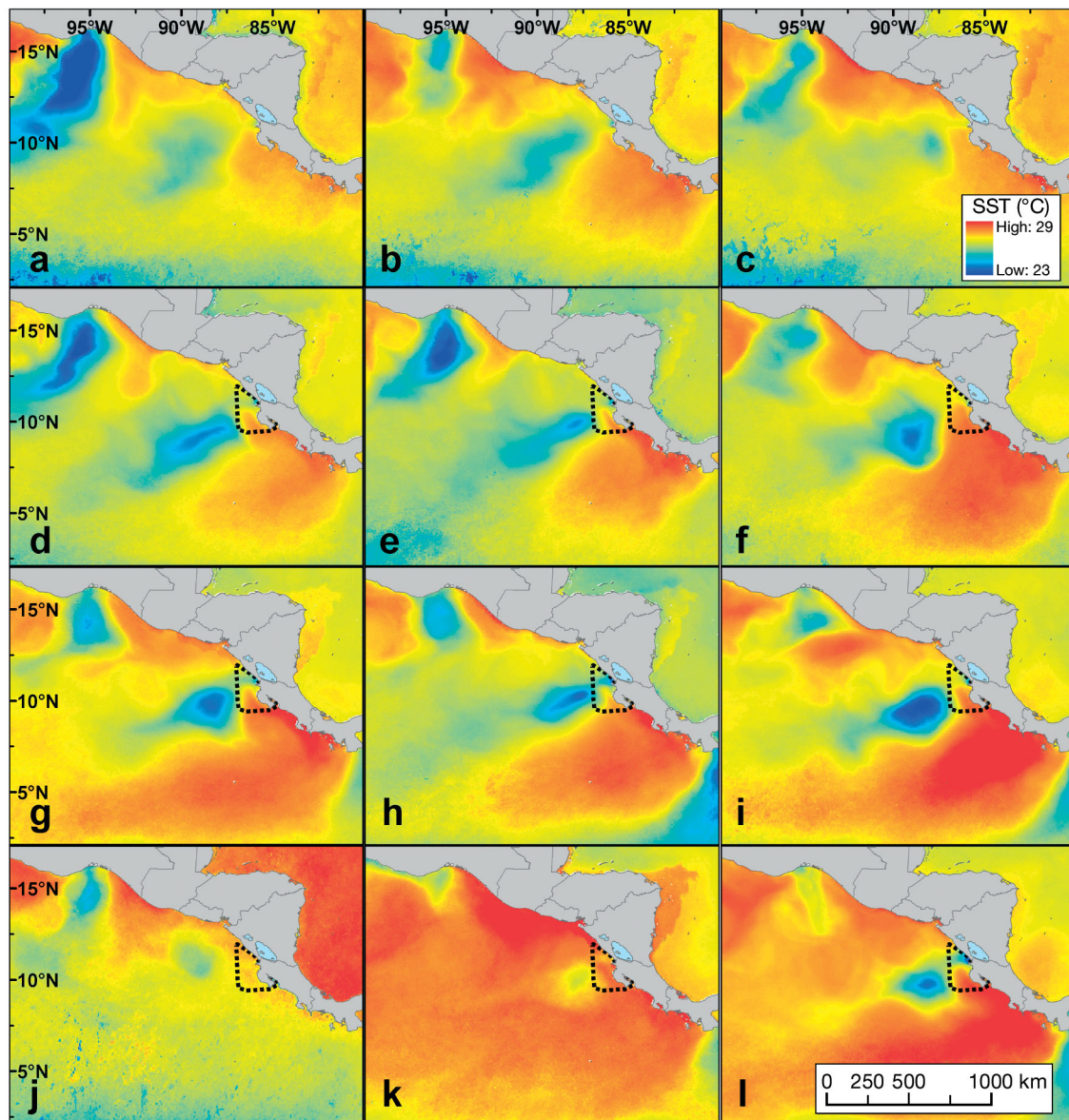


Fig. 3. *Dermochelys coriacea*. Monthly composite of mean sea surface temperatures (SST, °C) within the eastern Pacific region surrounding and encompassing the interesting region delineated by the minimum convex polygon (MCP) in Fig. 1, during (a) December 2004, (b) December 2005, (c) December 2007, (d) January 2004, (e) January 2005, (f) January 2007, (g) February 2004, (h) February 2005, (i) February 2007, (j) March 2004, (k) March 2005 and (l) March 2007. Dotted black line represents the MCP for turtle interesting habitat during 3 combined seasons. Images from NOAA GOES Imager, day and night, 0.05°, western hemisphere

imagery implied that this current's influence was stronger during 2007 than during 2004 and 2005.

### Horizontal movements

The MCP derived from the turtle interesting geolocation data for all seasons covered 33 542 km<sup>2</sup> and spanned from 11.95° N to 9.42° N and from 84.73° W to 86.99° W (Fig. 2). Interesting turtles ranged as far

south as the southernmost point of the Nicoya Peninsula (Cabo Blanco National Park), east into the Gulf of Nicoya (approximately 28 km south of Puntarenas) and north to coastal habitats within 30 km offshore from the beachfront town of El Transito, Nicaragua. Although latitudinal movements did not vary significantly across years (Kruskal-Wallis  $H = 1.7$ ,  $p = 0.40$ ), longitudinal movements during 2007 were significantly different (farther offshore) from those of 2004 and 2005 (Kruskal-Wallis  $H = 10.6$ ,  $p < 0.01$ ). Across all 3 track-

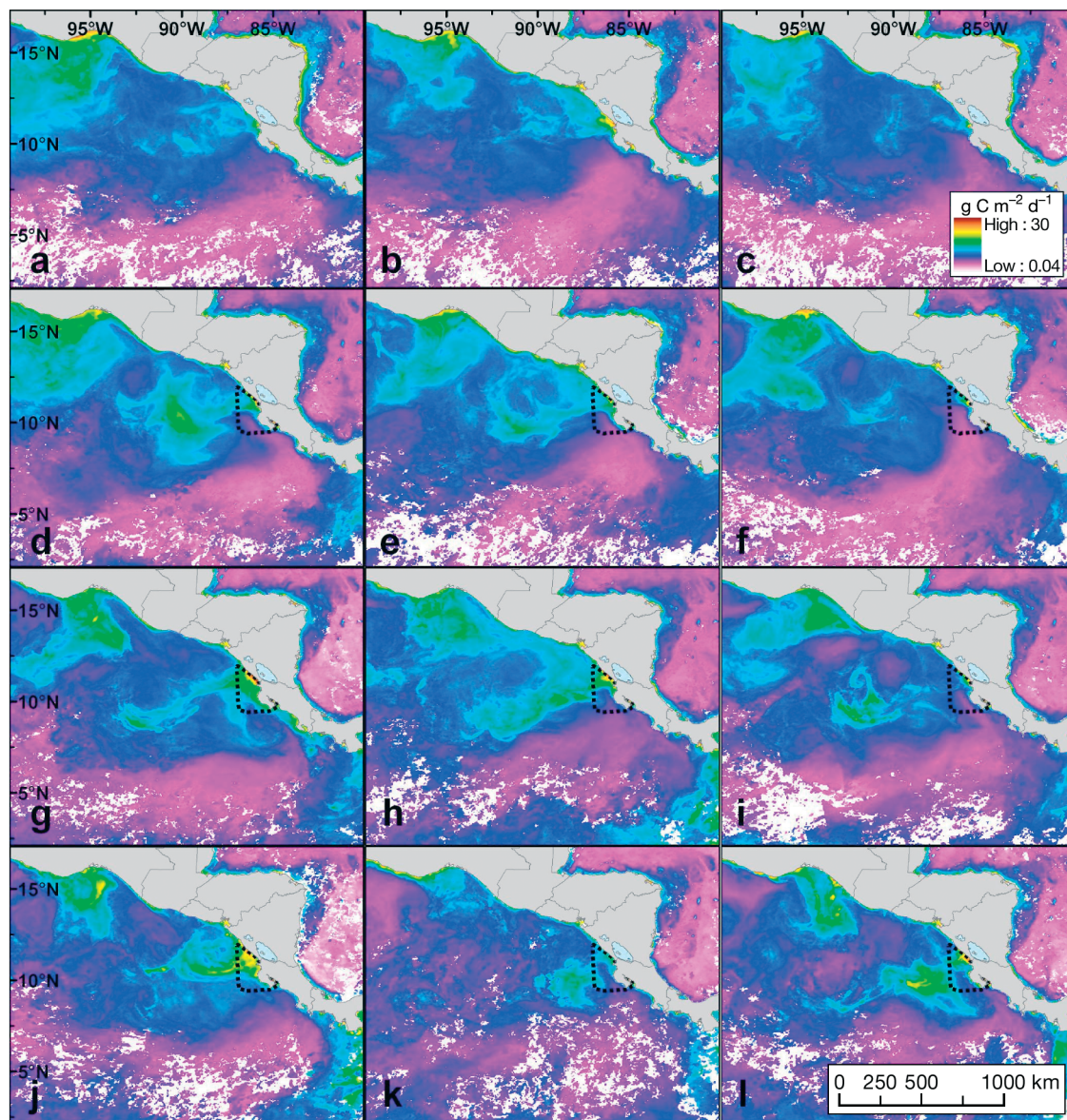


Fig. 4. *Dermochelys coriacea*. Monthly composite of mean net primary productivity (NPP,  $\text{g C m}^{-2} \text{d}^{-1}$ ) within interesting region during (a) December 2004, (b) December 2005, (c) December 2007, (d) January 2004, (e) January 2005, (f) January 2007, (g) February 2004, (h) February 2005, (i) February 2007, (j) March 2004, (k) March 2005 and (l) March 2007. Dotted black line represents minimum convex polygon (MCP) for turtle interesting habitat during 3 combined seasons. Images from Aqua Modis at  $0.05^\circ$  spatial resolution (available at <http://coastwatch.pfeg.noaa.gov/data.html>)

ing seasons, the mean maximum distance that interesting turtles traveled from their tag deployment location was 70.1 km (SD = 42.6 km) and mean daily speeds ranged from 1.1 to 18.0  $\text{km d}^{-1}$  (mean = 5.4, SD = 3.1  $\text{km d}^{-1}$ ) (Table 2). Turtle speeds were not significantly different between tracking years (Kruskal-Wallis  $H = 4.5$ ,  $p = 0.10$ ). The maximum distance traveled from the tagging location (214.2 km) and the greatest area covered (11 039.96  $\text{km}^2$ ) occurred during 2007 when the majority of turtles tended to move north

into the Gulf of Papagayo and near the Santa Elena Peninsula (Fig. 2). However, the distances traveled and total area covered were not significantly different (Kruskal-Wallis  $H = 1.9$  and 2.9,  $p = 0.40$  and 0.23, respectively) across years.

The UD analysis of the interesting data revealed that the 25, 50, 75 and 95% UD polygons for all years encompassed 27.4, 187.9, 685.0 and 2092.2  $\text{km}^2$ , respectively (Fig. 2). Although there was considerable interannual variation in shape and area of the UD poly-

gons, the core 25 % UD remained predominantly centered within PNMB during each tracking year. During every tracking season waters within and immediately adjacent to the PNMB were high-occupancy areas for all turtles. Across all years, approximately 0.02% (0.01 km<sup>2</sup>) of the 25 % UD extended south of PNMB. For 2004 approximately 14% (4.7 of 33.4 total km<sup>2</sup>) extended south of PNMB, for 2005 100% (10.7 km<sup>2</sup>) was contained within PNMB and for 2007 approximately 34% (44.4 of 128.5 km<sup>2</sup>) extended north of PNMB (Fig. 3). The highest use habitats within PNMB occurred within a 6 n mile (~11.1 km) range from the shore. Turtles occupied habitats across the entire 12 n miles (~22.2 km) longitudinal extent of the PNMB, throughout the Gulf of Papagayo around the Santa Elena Peninsula and across the entirety of Santa Rosa National Marine Park (37 117 ha land, 78 000 ha marine area) (Fig. 2).

Tag-derived SST experienced by the turtles within the core 25 % UD polygon for all years averaged 27.6°C (SD = 0.82°C, range = 25.9 to 29.2°C), which was similar to that within the noncore 25 to 95 % UD (mean = 27.5 °C, SD = 1.6°C, range = 20.1 to 31.1°C). Satellite-derived SST data (Fig. 3) across the entire interesting MCP averaged 27.2°C during January of all years (SD = 0.5°C, range = 24.2 to 29.6°C), 27.0°C during February (SD = 0.4°C, range = 23.1 to 30.8°C) and 27.5°C during March (SD = 0.4°C, range = 22.7 to 30.5°C).

Turtles that remained within the interesting habitats for more than 1 d (n = 45) tended to disperse in close proximity to the coast, within a mean distance of 10 km from the shore, and to occupy continental shelf habitats, although offshore movements beyond the edge of the shelf (in waters exceeding 1500 m depth) did occur during each tracking season. Turtles nesting at PNMB had easy access to deep waters due to the narrow continental shelf off the Nicoya Peninsula, which quickly sloped to depths in excess of 6000 m within the Middle American Trench (Fig. 1). Bottom depths across the entire interesting MCP ranged to 5034 m (mean = 1327.8, SD = 1545.3 m).

## Vertical movements

After filtering, a total of 20 848 interesting dives were obtained via Argos. The total number of dives observed per turtle (including 35 SMRU SRDL-tagged turtles and excluding turtle no. 56272 for which no vertical interesting behavior was recorded) across all tracking years ranged from 21 to 1918 dives (mean = 595.7, SD = 463.1 dives), with mean depth of 23.4 m (SD = 6.5, range = 13.4 to 42.4 m) and mean maximum depth of 108.2 (SD = 53.3 m, range = 39 to 314 m) (Table 3). Mean dive durations across all tracking

years ranged from 6.1 to 20.3 min with a mean dive duration of 11.6 min (SD = 3.7 min), and a mean maximum dive duration of 27.2 min (SD = 7.3, range = 17.5 to 51.2 min). Turtles spent approximately 65.4 % (SD = 16.1%) of their time diving (depth ≥ 10 m) during the interesting period (Table 3). Turtle dive depths and dive durations were significantly deeper within both the 25 % UD and 25 to 95 % UD (25 % UD: Kruskal-Wallis  $H = 166.0$ ,  $p < 0.01$ ; 25 to 95 % UD: Kruskal-Wallis  $H = 131.0$ ,  $p < 0.01$ ) and longer (25 % UD: Kruskal-Wallis  $H = 166.8$ ,  $p < 0.01$ ; 25 to 95 % UD: Kruskal-Wallis  $H = 328.7$ ,  $p < 0.01$ ) during 2007 than during 2004 and 2005 (Fig. 5).

During the day, turtles dove, on average, approximately 5 m deeper and reached mean maximum depths approximately 41% greater than at night (mean = 107.7 and 76.6 m during day and night, respectively;  $t$ -test:  $t = -3.2$  and  $-2.9$ ,  $df = 68$ ,  $p < 0.01$  and  $p < 0.01$ , respectively). Turtle mean dive durations did not differ significantly between day and night ( $t = -0.2$ ,  $df = 68$ ,  $p = 0.83$ ).

Tag-derived SST (depth = 1 m) did not vary significantly among years (Kruskal-Wallis  $H = 0.2$ ,  $p = 0.90$ ) within the core area 25 % UD polygons. However, the temperatures at mean dive depths within the 2004 and 2005 25 % UD polygons were significantly cooler than those within the 2007 25 % UD polygon (Kruskal-Wallis  $H = 22.6$ ,  $p < 0.01$ ) (Fig. 5).

The temperature-depth use pattern for 2007 was different than for 2004 and 2005, showing a bimodal trend that was not apparent in the previous 2 tracking years (Fig. 6). Our analysis revealed that interesting turtles spent most of their time in shallow depths in 2007 (depth < 15 m) within warmer temperatures ranging from 28 to 29°C. It also showed nearly as high usage within the 27 to 28°C range at depths to approximately 35 m. The highest use region extended over a temperature range of approximately 15 to 30°C to a depth of approximately 80 m. The depths and temperature ranges occupied during 2007 were greater than those for the previous 2 tracking years (Fig. 6).

## DISCUSSION

Recent studies have examined the influence of environmental factors on leatherback turtle foraging and migration behavior in the eastern Pacific at the ocean basin scale (Saba et al. 2008, Shillinger et al. 2008, Reina et al. 2009). Currently, little information exists regarding the influence of oceanographic conditions within their interesting habitats. Short-term behavioral studies of interesting leatherback turtles using time-depth recorders (Reina et al. 2005, Wallace et al. 2005), heart rate monitors (Southwood et al. 1999) and

Table 3. *Dermochelys coriacea*. Vertical movement data for leatherback turtles satellite tagged at Playa Grande, Costa Rica, during 2004 (n = 27), 2005 (n = 8) and 2007 (n = 11). Mean values for each year are in **bold** text. PTT ID: tag identification no.; na: data not available

PTT ID	No. of dives	Dive depth (m)			Dive duration (min)			Dive frequency (% time)
		Max.	Mean	SD	Max.	Mean	SD	
<b>2004</b>								
37595	797	124.00	25.27	19.19	37.8	12.58	8.57	78.98
37596	779	39.00	13.38	6.71	39	13.38	7.49	78.65
41687	na	na	na	na	na	na	na	na
41688	na	na	na	na	na	na	na	na
41689	na	na	na	na	na	na	na	na
41690	na	na	na	na	na	na	na	na
41691	na	na	na	na	na	na	na	na
41692	na	na	na	na	na	na	na	na
41693	na	na	na	na	na	na	na	na
41694	na	na	na	na	na	na	na	na
41695	na	na	na	na	na	na	na	na
41696	na	na	na	na	na	na	na	na
41697	873	120.00	19.40	15.02	17.5	7.28	4.27	70.11
41698	430	68.00	20.06	12.60	25.5	9.42	5.33	73.92
41699	349	104.00	17.92	12.74	26.17	8.55	5.33	70.91
41700	733	100.00	15.25	11.88	20.17	6.07	3.81	74.01
41701	175	55.00	21.46	12.77	24.17	11.64	5.56	78.53
41702	270	128.00	23.83	19.69	21.5	9.52	5.68	66.1
41703	1314	84.00	15.60	10.13	21.5	8.54	10.13	74.8
41704	856	88.00	22.84	14.82	33.83	9.64	6.84	78.24
41705	233	104.00	24.31	14.54	30.83	15.93	8.23	80.67
41706	474	88.00	22.07	15.67	24.83	9.3	5.74	72.97
41707	79	68.00	29.12	14.39	24.17	15.31	6.48	70.25
41708	470	112.00	20.11	14.81	26.83	9.45	5.94	79.06
41709	206	100.00	24.94	18.18	22.17	9.8	5.83	80.2
41710	612	80.00	20.30	12.75	18.17	20.3	12.75	66.78
41711	1918	72.00	16.48	9.38	22.83	8.67	4.19	72.33
<b>Mean</b>	<b>622</b>	<b>90.24</b>	<b>20.73</b>	<b>13.84</b>	<b>25.71</b>	<b>10.90</b>	<b>6.60</b>	<b>74.50</b>
SD	464	24.80	4.16		6.29	3.59		4.66
<b>2005</b>								
56268	486	142.00	20.39	17.42	29.5	10.21	6.56	80.72
56272	na	na	na	na	na	na	na	na
56274	130	72.00	28.41	13.22	30.17	14.84	7.01	61.88
56276	629	68.00	15.75	9.87	17.50	8.41	3.69	55.97
56279	349	88.00	19.04	15.86	20.17	8.91	5.04	68.42
56280	1102	100.00	14.76	11.44	25.50	7.50	5.62	51.71
56282	368	55.00	18.43	9.96	19.50	8.87	4.63	64.69
56283	603	120.00	18.16	14.96	32.50	11.13	7.29	79.18
<b>Mean</b>	<b>524</b>	<b>92.14</b>	<b>19.28</b>	<b>13.25</b>	<b>24.98</b>	<b>9.98</b>	<b>5.69</b>	<b>66.08</b>
SD	306.32	30.85	4.46		5.96	2.45		10.95
<b>2007</b>								
72474	338	80.00	27.41	17.09	26.17	10.97	6.29	51.51
72475	21	96.00	31.97	22.69	17.5	9.38	5.06	4.93
72476	749	112.00	27.43	18.63	32.5	13.37	7.08	62.79
72477	370	116.00	33.04	23.11	36.5	17.47	8.70	57.63
72478	1622	100.00	23.78	18.69	27.5	10.19	5.75	72.19
72479	504	100.00	28.13	16.20	29.5	13.98	6.70	61.05
72480	483	246.00	32.28	27.99	51.17	19.15	12.98	54.03
72481	1785	120.00	21.61	15.57	28.17	9.69	5.98	65.61
72482	131	158.00	42.38	27.70	31.5	17.54	7.96	30.81
72483	364	166.00	28.57	24.17	24.83	10.43	6.26	32.89
72485	246	314.00	33.65	26.79	35.17	18.25	7.56	67.03
<b>Mean</b>	<b>601.18</b>	<b>146.18</b>	<b>30.02</b>	<b>21.69</b>	<b>30.96</b>	<b>13.67</b>	<b>7.30</b>	<b>50.95</b>
SD	578.93	72.52	5.59		8.50	3.80		20.18

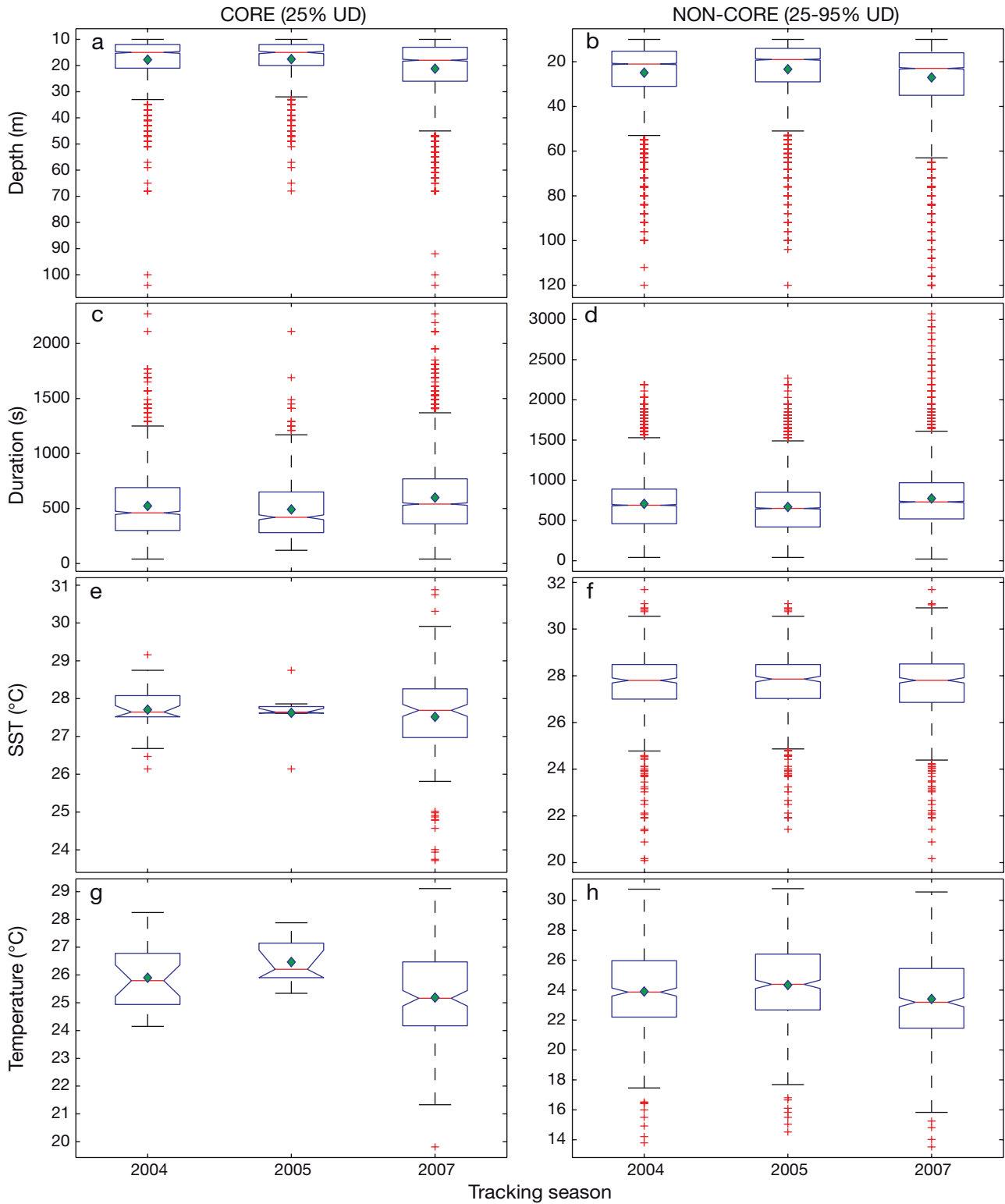
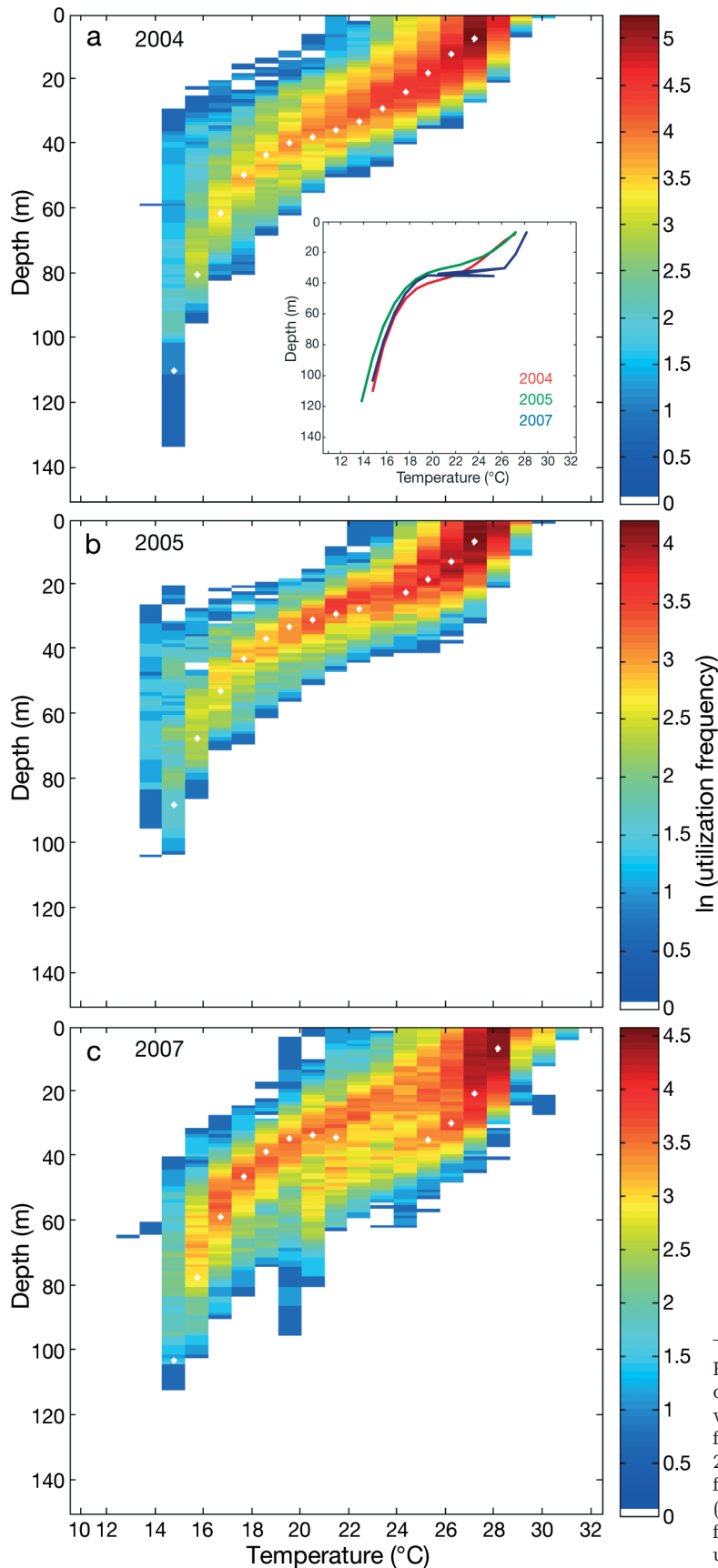


Fig. 5. *Dermochelys coriacea*. Environmental influences on turtle behavior and temperatures ( $^{\circ}\text{C}$ ) experienced by turtles at surface (SST) and at mean dive depths during 2004, 2005 and 2007 within interesting 25% utilization distribution (UD, core) and 25 to 95% UD (noncore) regions. Box plots for (a) median dive depth within 25% UD, (b) median dive depth within 25 to 95% UD, (c) median dive duration within 25% UD, (d) median dive duration within 25 to 95% UD, (e) median tag-derived SST ( $^{\circ}\text{C}$ ) within 25% UD, (f) median tag-derived SST ( $^{\circ}\text{C}$ ) within 25 to 95% UD, (g) median temperature ( $^{\circ}\text{C}$ ) at mean dive depth within 25% UD and (h) median temperature ( $^{\circ}\text{C}$ ) at mean dive depth within 25 to 95% UD. Boxes show the first and third quartiles; red lines show the median; whiskers encompass all non-outlier data points; red cross-hatches denote outliers, and green diamonds the means



body temperature probes (Southwood et al. 2005) have provided valuable insights into the vertical behaviors, physiology, foraging ecology and metabolic rates of turtles nesting at Playa Grande. Our study complements these efforts by providing an integrated horizontal and vertical context of habitat use and examining these movements in relation to the interannual variability in oceanographic features. The capacity to combine satellite tagging data with oceanographic data provided an unparalleled opportunity to define the critical habitat.

The leatherback turtle nesting season at Playa Grande coincides with a series of predictable environmental transitions in the eastern Pacific Ocean, many of which are driven by topographically influenced wind forcing from the American continents (Kessler 2006). Leatherback turtles nesting at Playa Grande arrive during September to October from putative foraging grounds in the South Pacific (Shillinger et al. 2008). This interesting region is flanked from the west by the cool nutrient-rich waters of the CRD, characterized by a productive region of elevated thermocline centered at 9° N, 90° W. To the north, seasonal winter winds that form the Papagayo jet push through Central American mountain passes and move out over the Gulf of Papagayo, thereby enriching the waters of the Nicoya Peninsula. From the south, the deep (subthermocline) northwestward flowing CRCC, bathes the coast of Costa Rica in a strong jet of warm water that flows ( $\sim 20 \text{ cm s}^{-1}$ ) from the eastern edge of the CRD and continues into the Gulf of Tehuantepec (GOT) off the coast of Mexico (Kessler 2006). The Playa Grande interesting region is subject to interannual fluctuations in SST, sea surface height (SSH) and chlorophyll *a* (chl *a*) concentrations associated with the waxing

Fig. 6. *Dermochelys coriacea*. Frequency of turtle occupancy, expressed as  $\ln$  (utilization frequency), within a temperature and depth ( $T$ - $Z$ ) space defined as  $T = 1^\circ\text{C}$  by  $Z = 1 \text{ m}$  boxes for (a) 2004, (b) 2005 and (c) 2007.  $\ln$  (utilization frequency) ranges from  $<1$  (blue) through the spectral range to  $>5$  (dark red). The white diamonds refer to a 3rd-order fit (inset in panel a) through the peak temperature utilization points within each 1 m depth interval

(El Niño) or waning (La Niña) of the North Equatorial Countercurrent (NECC) in the Central Pacific. The impact of these phenomena on the availability of prey resources for foraging leatherback turtles in other regions of the eastern Pacific has recently been linked to timing of leatherback remigration intervals and changes in their reproductive ecology in the eastern Pacific (Saba et al. 2007, Reina et al. 2009). Although the precise mechanism is unclear, we suggest that interannual changes in oceanographic conditions, even at small scales (interesting region), can also influence the behavior and distribution of interesting leatherback turtles.

During the 3 interesting seasons at Playa Grande, we observed strong transitions in SST and NPP (Figs. 3 & 4) that coincided with the peak of nesting (between December and January) and with the end of interesting (between February and March). Although mean monthly SST for January, February and March within the interesting MCP did not vary considerably for each of the tracking years (26.5 to 28.0°C), during all years the range of SST available to the turtles (within this same region) increased from January to February as wind-forced upwelling (note the coastal upwelling cool SST signal in Fig. 3d–l) drove colder water into the northern part of the interesting region. During 2004 and 2005, the range of satellite-observed SST available to the turtles peaked during February and declined in March. During 2007, a warming trend from the south driven by a strong CRCC was countered by cooling from the north and a strong CRD signal (Fig. 3l), which dramatically increased the SST range from February through March within the MCP (Fig. 3f,i,l).

We also examined tag-derived SST within core and noncore interesting habitats to obtain a direct measure of turtle temperature preferences. Our findings demonstrated no significant differences in turtle SST preference among tracking years (Fig. 5), and revealed that interesting turtles during all years occupied a mean SST range of approximately 27.5 to 27.7°C within both the interesting core and noncore regions. However, during 2007, the turtles dispersed more widely, ranged farther north and swam at higher maximum speeds than during the other 2 yr. Additionally, turtles targeted a mean temperature range of 25.2 to 26.5°C while diving across tracking seasons, and when the range of available temperatures was greatest in 2007, they seemed to adjust their dive behavior to target cooler waters at slightly deeper depths during the warmer period of 2007 (Figs. 5 & 6). These results corroborate findings of Wallace et al. (2005) that leatherback turtles might behaviorally thermoregulate by selecting particular ranges of water temperatures available to them in

interesting habitats. Thus, the occupation of specific SSTs appears to be critical for the biology of the leatherback turtle and the interesting period, because temperatures may in fact be optimal for physiological performance (e.g. egg production) in the warm waters associated with the interesting period (Wallace et al. 2005, Schofield et al. 2009). Selection of the temporal and spatial habitat associated with breeding may be driven by the seasonality and be related to a critical thermal window that opens at the time of year when breeding occurs.

We attribute the distinct vertical and horizontal behaviors of the turtles in this year to the effects of the warm CRCC (Fig. 3). The GOP emerged as a high-use area during 2007, where turtles could access cooler upwelled waters and seek refuge from the warm waters and strong CRCC in the lee of the Santa Elena Peninsula (Fig. 3). Turtle swim speeds may have been affected by the increased strength of the CRCC during this year. A positive relationship between increased turtle swim speeds versus increased current strengths was observed within the same population of turtles during their postnesting migrations as they traversed high energy equatorial zonal currents (Shillinger et al. 2008). The 2004 and 2005 tracking years were oceanographically more similar to each other than they were to 2007. The coldest year in the tracking dataset, 2005, was characterized by strong Papagayo upwelling and the weakest CRCC in the tracking dataset. During this period turtles remained close to the nesting beach and exhibited the lowest mean swim speeds and shallowest mean dive behavior (although not significantly so), which may have been a direct result of the cooler water. However, it is difficult to discern the turtles' thermal limits without further investigation of their internal body temperatures during diving.

Synthesizing the relationships between variation in vertical and horizontal movements and environmental drivers, we suggest that the observed turtle movements may have reflected a compensatory thermoregulatory response. Thus, turtles move horizontally or vertically to exploit preferred water temperatures, thereby maintaining a physiologically optimal thermal range (Paladino et al. 1990, Wallace et al. 2005).

Turtle movements might also have been related to foraging activity, with turtles dispersing into productive habitats within the GOP to find prey (Myers & Hays 2006, Fossette et al. 2008b). Their nocturnal (shallower) dive behavior also implied that turtles may have been following vertically migrating prey (Eckert et al. 1989). The hypothesis of leatherback turtles foraging during the nesting season has been supported by active swimming behaviors, diving patterns and beak movements (Fossette et al. 2008b). Potential prey items are known to occur in the vicinity of nesting

beaches, although direct observations of feeding have not yet been made (Reina et al. 2005, Fossette et al. 2009).

Turtle vertical movements were constrained by bathymetry, with shallower dives occurring in shallower waters immediately adjacent to the nesting beach and increasing in depth (to 314 m, Table 3) as turtles moved westward towards the edge of the continental shelf. The shallow dive behavior within shelf waters has been reported previously for Playa Grande leatherback turtles (Southwood et al. 1999, Wallace et al. 2005) and observed within other populations of internesting leatherback turtles, including in French Guiana (Fossette et al. 2007, Georges et al. 2007), Malaysia (Eckert et al. 1996) and Gabon (Georges et al. 2007). Although offshore excursions were relatively infrequent, turtles nesting at PNMB had access to deep waters (exceeding 1500 m) offshore in the nearby Middle America Trench (Fig. 1).

The results in this study only reflect the behavior of female turtles, since tagging occurred on the nesting beach. It is much more difficult logistically to tag males as they do not come on land. However, there are increasing efforts to tag male turtles (James et al. 2005, Schofield et al. 2009). As temperatures increase as a result of climate change, male offspring will become rarer and they will play an increasingly important role (Hawkes et al. 2007).

While the use of harnesses for tag attachment on leatherback turtles has been the standard technique since its development more than 20 yr ago (Eckert & Eckert 1986), studies now indicate that there may be a hydrodynamic effect of the harness on the turtle's swimming and diving capabilities (Fossette et al. 2008a, Byrne et al. 2009). There have also been observed effects of tagging and handling on the turtles (Sherrill-Mix & James 2008), suggesting the need for less invasive and less time-consuming attachment methods. A recent new development has been the use of direct attachment devices, for which preliminary assessments have been made (Doyle et al. 2008, Fossette et al. 2008a, Byrne et al. 2009). However, it is clear that the effects of any tagging technique should be carefully considered and weighed against the potential conservation benefits to make it justifiable. Particularly when involving endangered species, the fitness costs of tagging should be minimized as much as possible to ensure we are not contributing to their decline (Sherrill-Mix & James 2008).

Our study revealed that the current delineation of the marine sector of PNMB and related conservation measures (e.g. fishing inside the park is prohibited) for internesting leatherback turtles from the Playa Grande population are well-targeted and effective, but these efforts should be augmented because turtles fre-

quently move well beyond the boundaries of PNMB (Fig. 2; Shillinger et al. 2008), and because the fisheries that might have important impacts on leatherback turtles typically occur outside of the park boundaries. Park rangers perform patrols to enforce the prohibition on fishing activities within PNMB, but these activities are predominantly small-scale hand-line operations that probably would not have deleterious effects on the turtles. However, trawl vessels are also spotted close to or within PNMB boundaries and could interact with leatherback and other sea turtles within the park. In addition to trawls, other fishing gears (e.g. longlines and coastal gill nets) are known to affect sea turtles in Costa Rica's exclusive economic zone (Arauz 2001, Arauz et al. 1998), and potential interactions between these gear types and internesting leatherback turtles from PNMB merit attention.

The entire internesting habitat region (internesting MCP, Fig. 2) over the 3 yr tracking period was encompassed within an area of approximately 33 542 km<sup>2</sup>, ranging as far south as the tip of the Nicoya Peninsula and north into waters offshore from southern Nicaragua (Fig. 2). High Argos location errors could lead to artifacts in the size of the home range (e.g. see Bradshaw et al. 2007), but as Argos location classes were broadly similar across individuals and different years our inferences about temporal changes in home ranges are likely to be robust. Recently developed high resolution GPS tracking might lead to more refined estimates of home range (Schofield et al. 2007). Although there was significant interannual variation in turtle dispersal and habitat use, the internesting core region (25% UD) consistently occurred within or around PNMB during every tracking year (Fig. 2). Given the high degree of nesting-site fidelity displayed by the Playa Grande turtles, it was expected that waters in the immediate vicinity of the nesting beach would comprise core habitats.

Our findings validated the importance of PNMB as critical habitat necessary for leatherback turtle conservation and substantiated the efficacy of current governmental and nongovernmental collaborative efforts to address leatherback turtle conservation within PNMB, especially within the marine sector. For example, we observed no indication of possible mortality of turtles during the internesting periods (i.e. all turtles performed postnesting migrations, Shillinger et al. 2008), which might suggest that bycatch effects in the internesting areas that leatherback turtles occupied across multiple years were minimal. Thus, at least within the marine sector of PNMB, no-take regulations appear to be effective in reducing leatherback turtle bycatch. However, because internesting leatherback turtles also occupy areas outside of the current PNMB boundaries, expanded protection of this species in



marine areas outside of the park, particularly during the breeding season in October to March (Fig. 2), should be considered. We propose that the ongoing conservation efforts at PNMB be integrated with other marine protected areas within the identified leatherback turtle interesting region along the Nicoya Peninsula, including Santa Rosa National Park, and Caletas and Camaronal refuges (Fig. 3). In addition, we recommend programs to raise awareness and engage local communities along the Guanacaste coast about the existence of the no-take PNMB and about the seasonal presence of leatherback turtles to bolster any official management actions to protect the species in Costa Rican waters.

Our findings also demonstrated that interannual environmental variation influences the distribution and behavior of interesting leatherback turtles. The transboundary movements of these turtles into Nicaraguan waters and their wide dispersal along the Nicoya Peninsula require the development of cooperative regional and international strategies for their management and conservation. Moreover, the near-shore, continental shelf-based movements of interesting leatherback turtles probably expose the turtles to anthropogenic threats, such as coastal fisheries and possible pollution from development zones. Our study has improved the understanding of environmental influences upon leatherback turtle behavior and distribution, particularly during the interesting period when reproductively active turtles are concentrated, and will be very useful to conservation initiatives designed to protect this population.

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