



# Nomadic behaviour of the highly migratory olive ridley sea turtle *Lepidochelys olivacea* in the eastern tropical Pacific Ocean

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**ABSTRACT:** I studied the post-reproductive migrations of 30 male and female olive ridley sea turtles *Lepidochelys olivacea* in the eastern tropical Pacific Ocean (ETP) using satellite telemetry. Long-term data revealed that turtles were widely distributed in the pelagic zone from Mexico to Peru and lacked migratory corridors. Turtles migrated long distances, swam continuously, displayed no fidelity to specific feeding habitats, and were nomadic. An El Niño occurred in the middle of the study, and turtle migration patterns changed in response. ETP olive ridleys likely evolved migratory flexibility to adapt to the frequent and unpredictable environmental change characteristic of their large dynamic marine ecosystem. This suggests that ETP olive ridleys may be less vulnerable to the impacts of climate change than other sea turtle species.

**KEY WORDS:** *Lepidochelys olivacea* · Eastern tropical Pacific · Satellite telemetry · Nomadic · Highly migratory · El Niño

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## INTRODUCTION

Long-distance animal migrations are generally resource-driven, with migrants travelling between or among established locations at regular or seasonal intervals. When resources are predictable in time and space, migratory patterns are relatively static, whereas when resource distribution and abundance are variable and unpredictable, animals tend to have movement patterns that parallel their dynamic environment (Roshier & Reid 2003). Compensating for fluctuations in dynamic environments requires migratory adaptability, a trait that has evolved across multiple taxa (Alerstam et al. 2003) and has led to a rich diversity of migratory behaviours. The most flexible migratory behaviour is nomadism, broadly defined as the purposeful movement from a changing and unsuitable environment to other locations with no predetermined endpoint. Nomadism likely evolved to maximise fitness in unpredictable environments and is well-represented across diverse taxa, including invertebrates (Franks & Fletcher 1983), fish (Klimley et al. 2003), rep-

tiles (Plotkin 2003), birds (Dean 1997) and mammals (McCullough 1985).

Sea turtles are long-distance migrants that inhabit dynamic ocean environments and predictably should display migratory flexibility. Most species undertake seasonal return migrations, broadly defined as migrations between established breeding grounds and feeding areas at regular and somewhat predictable intervals (Plotkin 2003). For many years this generalisable model was advanced to characterise all sea turtle migrations. However, research conducted during the past decade has led to a paradigm shift, and the one general sea turtle migration model is now obsolete. Several key studies have revealed migratory flexibility, interspecific and intraspecific variation (Luschi et al. 2003, Plotkin 2003, Hays et al. 2004, Godley et al. 2008) and a strong relationship between patterns of movement and the distribution of key resources (e.g. Craig et al. 2004, Troëng et al. 2005a,b, Broderick et al. 2007, Morreale et al. 2007, Witt et al. 2007, Seminoff et al. 2008).

I studied the migratory behaviour of adult olive ridleys in the eastern tropical Pacific Ocean (ETP)

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from 1990 to 1994. Colleagues and I previously reported that the migrations of females are not socially facilitated, but often appear to be so because of a high degree of spatio-temporal overlap of individuals responding to the same environmental cues (Plotkin et al. 1995). We also previously described the reproductive and developmental synchrony of females during the internesting period (Plotkin et al. 1997) and the breeding ground behaviour and movements of males (Plotkin et al. 1996). Here I characterise the post-reproductive migrations of all turtles tracked, and the relationship between their migration routes and oceanographic features that characterise the ETP.

## MATERIALS AND METHODS

I attached satellite transmitters to 21 female and 9 male olive ridleys between 1990 and 1993. Most females were captured on Nancite Beach, Costa Rica (10.806° N, 85.699° W) during an 'arribada', the synchronous nesting of large numbers of turtles unique to the genus *Lepidochelys* (Bernardo & Plotkin 2007). When arribada turtles were unavailable, I attached transmitters to solitary nesting turtles, or to females captured in the Gulf of Papagayo, adjacent to Nancite Beach. Male ridleys were captured in these same waters. One male was captured during a research cruise in the ETP, several hundred km southwest of Panama (Owens 1993). Details of transmitter attachment methods used in this study are provided in Plotkin (1998). I used 2 different models of transmitters during this study: Telonics models ST-3 and ST-6. Turtle movements were monitored by the Argos Data Collection and Location System onboard 2 NOAA Tiros-N satellites that passed over the study area approximately 3 to 4 times daily (Argos 1984). Satellites received transmissions every 54 to 63 s only when a transmitter was turned on, a satellite was overhead and a turtle was at the ocean's surface. To increase the probability of long-term data collection, transmitters were programmed to transmit every second or third day (transmitter duty cycles were: 10 h on, 50 h off; 10 h on, 74 h off; or 8 h on, 52 h off). A description of the data received and the method used to filter data (i.e. reject incorrect or questionable data) is detailed in Plotkin (1998).

I calculated the minimum distance travelled for each turtle based on the sum of the straight line distances between consecutive locations, using a program written in Basic by T. Amos, University of Texas Marine Science Institute. I also calculated the rate of movement (ROM; km h<sup>-1</sup>) between consecutive locations and the mean ROM for each turtle. Statistical

analysis was conducted using JMP (SAS Institute, www.jmp.com). Maps were created using the Map-tool program, a product of www.seaturtle.org.

## RESULTS

Individual turtles were tracked for periods ranging from 6 to 779 d (Table 1). Data for 3 turtles are not included beyond that presented in Table 1 because transmissions ceased before their post-reproductive migration (7672b and 7676), or because I removed the transmitter intentionally when the turtle was recaptured nesting (7672a). Some of the data from an additional pair of turtles (7670b and 7671b) are not included in the analyses of transmitter duration, distance travelled and ROM because they are believed to have been captured and brought on board a vessel during their migration. For both turtles, transmitter pressure sensors no longer recorded changes in pressure (i.e. turtles were not diving) and their ROM increased significantly at and beyond their suspected point of capture. Excluding transmitter duration data for these 5 turtles, the mean  $\pm$  SD tracking duration for the remaining 25 turtles was 236  $\pm$  142 d, nearly 8 mo. Three turtles were tracked for more than 1 yr, and one of the 3 was tracked for more than 2 yr using 2 different transmitters.

### Migration routes and patterns

The migration routes of turtles from their breeding grounds in Costa Rica spanned nearly the entire ETP. The most distant points of the migratory range included the Gulf of Tehuantepec, Mexico, in the north, south across the Equator into Peruvian waters, and over 4000 km due west of Costa Rica. Turtles migrated within the territorial and/or international waters of Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador and Peru. Most turtles migrated in deep pelagic waters, from several hundred km to several thousand km from land. A few turtles migrated closer to shore (within tens of km from land), but were still swimming in deep water. There were no apparent migratory corridors and no common feeding grounds observed. In fact, there were no specific feeding grounds identified for any individual turtle. Turtles were wide-ranging and on the move almost all the time, with the exception of brief stops that lasted several days to a few weeks. Most turtles never returned to a location visited previously. Only 1 turtle was not wide-ranging (7674a; see Figs. S1 to S3 in the Supplement at [www.int-res.com/articles/suppl/n013p033\\_supp.pdf](http://www.int-res.com/articles/suppl/n013p033_supp.pdf)).

Table 1. *Lepidochelys olivacea*. Olive ridley turtle transmitter ID and model, gender, capture location, behaviour at time of capture, date of deployment and last transmission and number of days between deployment and last transmission. GP: Gulf of Papagayo; Arribada: nesting during 'arribada'; Mounted: captured while mounted to a female; Solitary: solitary nester; Swimming: captured while swimming

ID no.	Transmitter model	Gender	Capture location	Behaviour	Date deployed	Date last transmission	No. of days
7667	ST-3	F	GP	Swimming	13 Sep 90	6 Apr 91	205
7668	ST-3	F	Nancite	Arribada	18 Sep 90	8 Mar 91	171
7669	ST-3	F	Nancite	Arribada	18 Sep 90	25 Dec 90	98
7670a	ST-3	F	Nancite	Arribada	18 Sep 90	22 Apr 91	216
7670b <sup>a</sup>	ST-6	F	Nancite	Solitary	21 Nov 92	22 Apr 93	152
7671a	ST-3	F	Nancite	Arribada	18 Sep 90	25 Dec 90	98
7671b <sup>a</sup>	ST-6	M	GP	Mounted	12 Jul 93	18 Aug 93	37
7672a	ST-3	F	Nancite	Arribada	18 Sep 90	25 Nov 90	68
7672b	ST-3	M	GP	Mounted	12 Aug 91	7 Sep 91	26
7672c	ST-6	M	GP	Mounted	14 Jul 93	16 Mar 94	245
7673a	ST-3	F	Nancite	Arribada	18 Sep 90	6 Feb 91	141
7673b	ST-6	M	GP	Mounted	14 Jul 93	6 Dec 93	145
7674a	ST-3	F	GP	Swimming	20 Nov 90	11 Mar 91	111
7674b	ST-6	M	GP	Mounted	14 Jul 93	5 May 94	295
7675a <sup>b</sup>	ST-3	F	GP	Swimming	16 Nov 90	1 Nov 91	350
7675b	ST-3	M	ETP	Swimming	25 Mar 93	22 Sep 93	181
7676	ST-6	M	GP	Mounted	15 Jul 93	21 Jul 93	6
7677	ST-3	F	Nancite	Solitary	15 Nov 90	2 Mar 92	473
7678a	ST-3	F	Nancite	Arribada	31 Oct 91	1 Mar 92	122
7678b	ST-6	M	GP	Mounted	15 Jul 93	7 May 94	296
7679	ST-3	F	Nancite	Arribada	1 Nov 91	25 Apr 92	176
7680a	ST-3	F	Nancite	Arribada	5 Sep 91	7 May 92	245
7680b	ST-6	M	GP	Mounted	18 Jul 93	16 Feb 94	213
7681 <sup>b</sup>	ST-3	F	Nancite	Arribada	1 Nov 91	3 Jan 93	429
7682	ST-3	F	Nancite	Arribada	1 Nov 91	16 Apr 92	167
7683	ST-3	F	Nancite	Arribada	5 Sep 91	22 May 92	260
7685	ST-3	F	Nancite	Arribada	1 Nov 91	9 Nov 92	374
7686	ST-3	F	Nancite	Arribada	4 Sep 91	15 May 92	254
7687	ST-3	F	Nancite	Arribada	5 Sep 91	8 Mar 92	185
7688	ST-3	F	Nancite	Arribada	5 Sep 91	21 Mar 92	198
7689	ST-3	F	Nancite	Arribada	5 Sep 91	7 May 92	245

<sup>a</sup>Transmitters are believed to have been brought onboard a vessel during the study  
<sup>b</sup>These 2 transmitters were attached to the same turtle, during 2 different years

No apparent gender-specific differences were observed. The migratory patterns of female and male olive ridleys were strikingly similar. Both females and males swam more or less continuously, occupied oceanic waters and displayed no fidelity to any particular area. There was a clear distinction between the migratory patterns of females tracked during the first year (1990–1991) and females tracked during the second year (1991–1992; Fig. 1). Females tracked during the first year ( $n = 9$ ) were more widely dispersed throughout the ETP during their migrations, swimming north, west and south of Costa Rica. Females tracked during the second year ( $n = 11$ ) migrated primarily north and west of Costa Rica, from the Gulf of Tehuantepec, Mexico, south to the Gulf of Papagayo, Costa Rica. Males tracked from Costa Rica in 1993 ( $n = 6$ ) migrated north, west, and south of Costa Rica

(see Fig. S4 in the supplement at [www.int-res.com/articles/suppl/n013p033\\_supp.pdf](http://www.int-res.com/articles/suppl/n013p033_supp.pdf)). One additional male turtle captured at sea during a research cruise migrated northwest of his capture location, remaining in deep oceanic waters far from land (see Fig. S4).

### Distances travelled and rates of movement

The minimum distance travelled by females during both years ranged from 438 km in 98 d to 10 650 km in 779 d (mean  $\pm$  SD = 3669  $\pm$  2007 km,  $n = 20$ ; Table 2). The minimum distance travelled by males ranged from 1173 km in 245 d to 3914 km in 296 d (mean  $\pm$  SD = 2379  $\pm$  931 km,  $n = 6$ ; Table 2). The minimum distance travelled by females during the first year (1990–1991; mean  $\pm$  SD = 2751  $\pm$  2217 km,  $n = 9$ ) was significantly

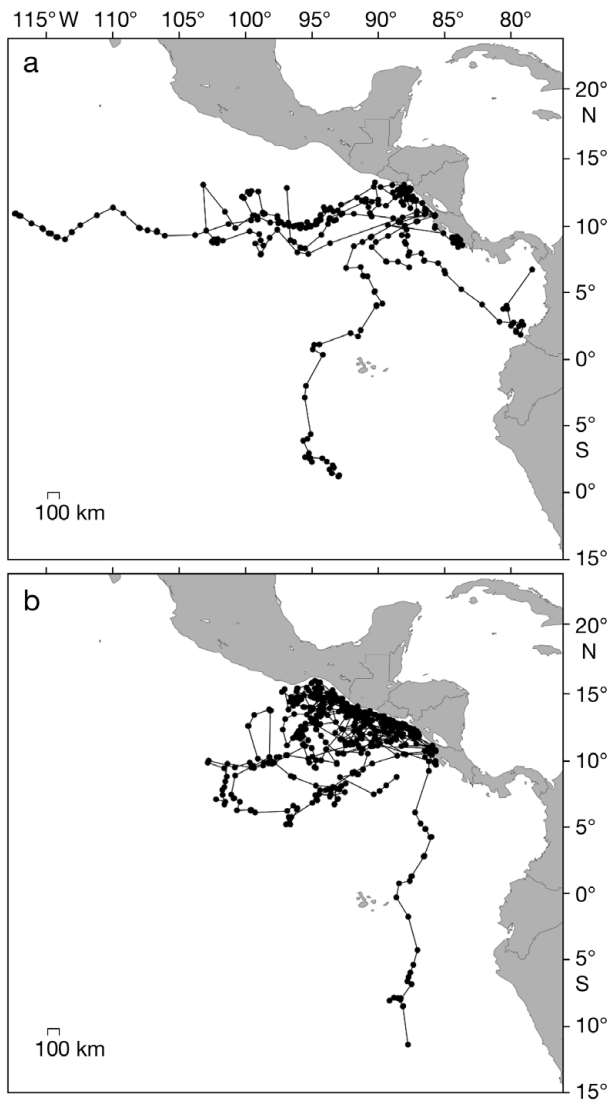


Fig. 1. *Lepidochelys olivacea*. Post-nesting migrations of 20 female olive ridleys during (a) 1990–1991 and (b) 1991–1992

less than during the second year (1991–1992; mean  $\pm$  SD =  $4422 \pm 1534$  km,  $n = 11$ ;  $t = 2.06866$ ,  $p = 0.05$ ), and this difference was unrelated to transmitter duration (mean  $\pm$  SD, 1990:  $207 \pm 127$  d,  $n = 9$ ; 1991:  $241 \pm 91$  d,  $n = 11$ ;  $t = 2.10092$ ,  $p = 0.05$ ). The minimum distance travelled by males was not significantly different than the distance travelled by females during the first year, but was significantly less than the distance travelled by females during the second year ( $t = 2.06866$ ,  $p = 0.05$ ). The mean ROM of females ranged from 0.41 to 1.69 km  $h^{-1}$  (mean  $\pm$  SE =  $1.18 \pm 0.04$  km  $h^{-1}$ ,  $n = 20$ ) and was not significantly different between years nor significantly different than the mean ROM of males, which ranged from 0.33 to 1.33 km  $h^{-1}$  (mean  $\pm$  SE =  $0.92 \pm 0.10$  km  $h^{-1}$ ,  $n = 6$ ;  $t = 2.06390$ ;  $p = 0.05$ ).

### One turtle's multi-year journey

I tracked 1 female continuously for more than 2 yr, using 2 different transmitters (7675a and 7681; Fig. 2). This turtle was captured in the Gulf of Papagayo in November 1990, was later observed nesting on Nancite Beach during the November 1990 arribada and then migrated north to an area south of the Gulf of Fonseca. She remained offshore Nicaragua and travelled 2625 km in 350 d. She returned to the Gulf of Papagayo in October 1991, was recaptured nesting on Nancite Beach during the November 1991 arribada, and a new transmitter was attached. This turtle left the Gulf of Papagayo after nesting just once, and began her migration along the same route she had travelled previously. She returned to the same area offshore Nicaragua, but did not remain there.

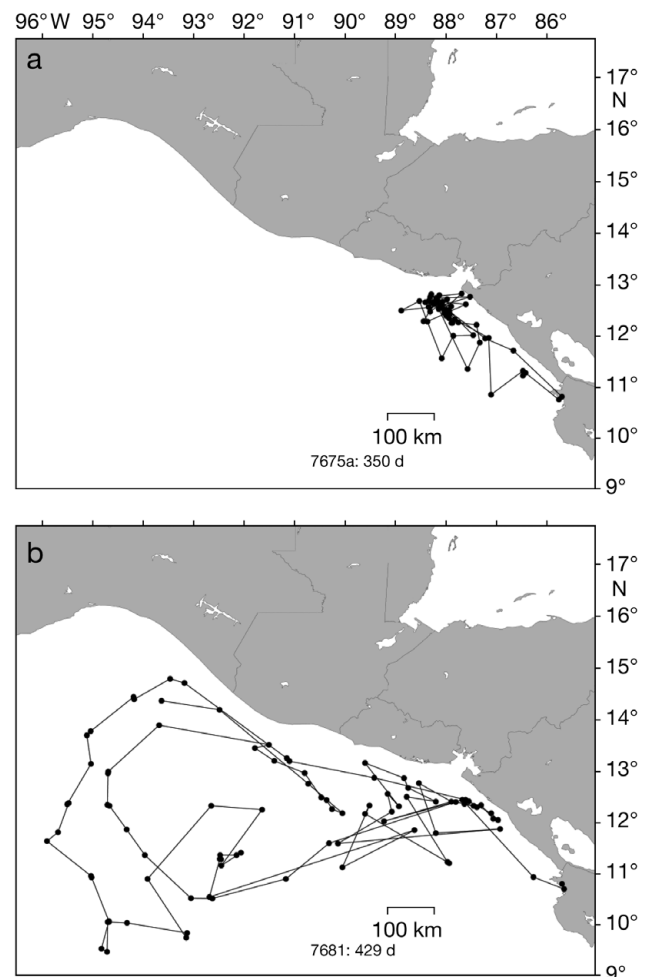


Fig. 2. *Lepidochelys olivacea*. Post-nesting migrations of 1 olive ridley during (a) 1990–1991 and (b) 1991–1992. Numbers below the scale bars indicate the transmitter ID and the number of days between transmitter deployment and last transmission

Table 2. *Lepidochelys olivacea*. Olive ridley turtle transmitter ID, location quality indices (LQ) for locations received, minimum distance travelled, mean rate of movement (ROM) and standard error (SE) of the mean. No LQ: no location quality assigned to a turtle's position; LQ0: precision of location unknown; LQ1: precision estimated to be within 1 km; LQ2: precision estimated to be within 350 m; LQ3: precision estimated to be within 150 m. For gender of turtles see Table 1. na: not available

ID no.	No LQ	LQ0	LQ1	LQ2	LQ3	Distance (km)	Mean ROM (km h <sup>-1</sup> )	SE
7667	25	66	28	6	1	4165	1.64	0.15
7668	16	46	7	1	0	3138	1.47	0.27
7669	4	23	1	0	0	438	0.41	0.14
7670a	19	73	15	0	0	3649	1.29	0.16
7670b <sup>a</sup>	4	51	28	40	14	5454	2.46	0.47
7671a	7	31	7	1	0	1032	1.32	0.22
7671b <sup>a</sup>	1	7	1	0	0	471	3.31	1.97
7672a	11	12	2	0	0	na	na	na
7672b	3	5	1	0	0	na	na	na
7672c	12	17	1	0	0	1173	0.33	0.06
7673a	11	27	5	0	0	1572	1.37	0.23
7673b	12	13	0	0	0	1977	1.06	0.27
7674a	8	27	6	0	0	662	0.41	0.11
7674b	18	31	1	0	0	2817	0.67	0.18
7675a <sup>b</sup>	11	63	7	2	0	2625	0.57	0.09
7675b	7	14	5	1	0	1973	1.16	0.24
7676	0	2	0	0	0	na	na	na
7677	31	91	10	1	0	7457	0.84	0.08
7678a	11	34	7	0	0	2510	1.30	0.25
7678b	13	18	3	0	0	3914	0.99	0.34
7679	10	40	10	3	0	3328	1.69	0.23
7680a	20	56	7	0	0	3758	0.99	0.13
7680b	20	19	4	0	0	2418	1.33	0.28
7681 <sup>b</sup>	28	112	24	8	0	8025	1.25	0.13
7682	20	31	12	1	0	3715	1.34	0.14
7683	22	85	6	2	0	4769	1.12	0.11
7685	20	67	23	1	0	4511	1.29	0.12
7686	22	65	7	0	0	3554	0.90	0.15
7687	27	59	12	0	0	5590	1.43	0.10
7688	28	54	12	1	0	3319	1.25	0.21
7689	35	100	27	2	0	5561	1.17	0.09

<sup>a</sup>The transmitters are believed to have been brought onboard a vessel during the study

<sup>b</sup>These 2 transmitters were attached to the same turtle, during 2 different years

Instead, she migrated farther north towards the Gulf of Tehuantepec, swam farther offshore than before and travelled a minimum distance of 8025 km in 429 d, nearly 3 times the distance travelled in the previous year. Her mean rate of movement increased from 0.57 km h<sup>-1</sup> in Year 1 to 1.25 km h<sup>-1</sup> in Year 2. During the nesting season of the second year (June to December 1992), she did not return to nest on Nancite Beach, nor is there any indication from the data that she nested on any other beach. The last location received for this turtle was on 3 January 1993 from offshore southwest Mexico.

## DISCUSSION

These data represent one of the largest long-term data sets of internesting movements (Plotkin et al. 1995, 1996, 1997) and post-reproductive migrations collected for olive ridleys. Tracking studies of other sea turtle species have documented long-distance post-reproductive movements to foraging habitats occurring within a few weeks post-breeding/nesting, and lasting as long as 3 to 4 mo (Plotkin et al. 1996, Luschi et al. 1998, Godley et al. 2002, Hays et al. 2002, McMahon et al. 2007, Cuevas et al. 2008, Seminoff et al. 2008). Therefore, the data reported in the present study represent turtles that had completed their post-reproductive migrations to foraging habitats.

Unlike many sea turtles that migrate from their breeding ground to a single foraging area, where they remain more or less resident until the next breeding season (Broderick et al. 2007), ETP olive ridleys are highly migratory, swimming more or less continuously and feeding as they travel throughout the ETP. Although feeding was not observed during this study, I presume the turtles were feeding during migrations, and that brief stops along the route were positive indications of resource availability. The slow swimming speeds, continual movements, tendency to spend short periods of time in an area before moving elsewhere, lack of migratory corridors leading towards common feeding grounds and migratory flexibility in response to changing environmental conditions characterise the olive ridley as a nomadic migrant.

The nomadic behaviour of ETP olive ridleys, and their distribution reported in this and other studies (Swimmer et al. 2006, Eguchi et al. 2007), parallels the large-scale variability and unpredictability of the ETP. This dynamic ecosystem is dominated by seasonal and inter-annual variability (Reilly & Fiedler 1994). Periodic El Niño-Southern Oscillation events occur regularly and cause significant shifts in oceanographic patterns and spatio-temporal distribution of resources (Fiedler 1992). During an El Niño, the winds that drive ocean circulation patterns and create upwelling are less intense and allow warmer water from the western Pacific

to move towards the eastern Pacific and displace highly productive cold upwelled water. Areas frequented by turtles overlapped with areas of upwelling. More specifically, these areas included the Middle American Trench from the Gulf of Tehuantepec (Mexico), south to the Gulf of Papagayo (Costa Rica); the Costa Rica Dome, a semi-permanent cyclonic eddy along 10° N; and the divergent current present between the westward flowing North Equatorial Current and eastward flowing North Equatorial Countercurrent.

An El Niño occurred in the ETP in 1991 (Monaster-sky 1993) in the midst of this study, and differences in the turtles' migration patterns were apparent, as predicted by Swimmer et al. (2006). The striking variation in the migration pattern of the female that was tracked for 1 yr prior to El Niño and 1 yr during El Niño, illustrates well the turtle's response to warming in the ETP. Collectively, the females were distributed primarily north of Costa Rica, from the Gulf of Tehuantepec to the Gulf of Fonseca during El Niño. One explanation for this distribution pattern lies in the unique topography of this region and its impact on air and ocean circulation. When surface waters of the ETP warm during El Niño and upwelling is less prevalent, seasonal wind-induced upwelling continues to occur from the Gulf of Tehuantepec in the north, south to the Gulfs of Papagayo (Costa Rica) and Panama (Stumpf & Legeckis 1977, McCreary et al. 1989). These seasonal wind events occur annually between November and April (the number and intensities vary) when high pressure systems develop in the Gulf of Mexico and continue south towards Central America. As these fronts move south, their associated winds are obstructed from the Pacific by the mountain chain that extends from Mexico into Central America, with the exception of 3 breaks in the chain located adjacent to the Gulfs of Tehuantepec, Papagayo and Panama. The winds funnel through these mountain passes, strengthen in intensity as they blow offshore and create an ageostrophic current which forces coastal upwelling and large cyclonic and anticyclonic gyres (Stumpf & Legeckis 1977, McCreary et al. 1989). These strong winds, often referred to as 'Tehuantepecers' in Mexico and 'Papagayos' in Costa Rica, produce meso-scale surface circulation features, or gyres. Satellite images have documented the offshore movements of these gyres up to several hundred km from the coast, and have shown that they persist for several weeks to months (Stumpf & Legeckis 1977). These patches of cold, nutrient-rich upwelled water provide important resources that likely attract and concentrate olive ridleys and other marine pelagics.

The migration patterns of turtles tracked in the present study affirm past speculation (Cornelius & Robinson 1986) that ETP olive ridleys spend their adult life in

oceanic waters. For many years, life in the pelagic zone was believed to be an adaptation unique only to leatherback sea turtles *Dermochelys coriacea* (Hendrickson 1980). The results of the present study also dismiss past speculation that post-nesting solitary nesting olive ridleys are not highly migratory and may reside near the breeding grounds (Cornelius & Robinson 1986). I tracked 2 solitary nesting olive ridleys, and both travelled to oceanic waters, far from land. It is important to note that not all olive ridleys are nomadic, highly migratory oceanic migrants. In other oceans, olive ridleys occupy neritic waters (McMahon et al. 2007, Whiting et al. 2007) and do not undertake the extensive migrations documented in the present study. Thus, broad generalisations regarding the migratory behaviour of all olive ridleys should not be drawn from the results of my study. Interestingly, the migratory behaviour of ETP olive ridleys is also in stark contrast to a congener, the Kemp's ridley turtle *Lepidochelys kempii*, a coastal migrant with notable gender-specific differences: females migrate far distances from the nesting beach, whereas males reside offshore the nesting beach year-round (Shaver et al. 2005, Seney & Landry 2008, Shaver & Rubio 2008).

Recent speculation on the potential impacts of climate change suggests disadvantageous consequences for sea turtles at sea and on land where the gender of offspring is determined by the incubation temperature of the eggs (Fuentes et al. 2010, Witt et al. 2010). Results from the present study, coupled with the reproductive plasticity of olive ridleys in this region (Bernardo & Plotkin 2007), suggest that ETP olive ridleys will be resilient to shifts in food availability arising from fluctuating ocean temperatures and changes in nesting beach suitability arising from sea-level rise. The impacts of climate change on olive ridleys in the ETP are therefore predicted to be less severe than they may be for less behaviourally plastic sea turtles.

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