



Fine scale daily movements and habitat use of East Pacific green turtles at a shallow coastal lagoon in Baja California Sur, Mexico

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ABSTRACT

Green turtles spend most of their lives in coastal foraging areas where they face multiple anthropogenic impacts. Therefore, understanding their spatial use in this environment is a priority for conservation efforts. We studied the fine scale daily movements and habitat use of East Pacific green turtles (*Chelonia mydas*) at Laguna San Ignacio, a shallow coastal lagoon in Baja California Sur, Mexico where sea turtles are subject to high levels of gillnet bycatch and directed hunting. Six turtles ranging from 44.6 to 83.5 cm in straight carapace length were tracked for short deployments (1 to 6 d) with GPS-VHF telemetry. Turtles were active throughout diurnal, nocturnal, and crepuscular periods. Although they moved greater total distances during daytime, their speed of travel and net displacement remained consistent throughout 24-h periods. A positive selection for areas of seagrass and moderate water depth (5 to 10 m) was determined using Ivlev's electivity index, with neutral selection for shallow water (<5 m) and avoidance of deep water (>10 m). Turtles exhibited two distinct behavioral movement patterns: circular movements with high fidelity to the capture–release location and meandering movements with low fidelity to the capture–release location. Our results indicate that green turtles were active throughout the diel cycle while traveling large distances and traversing multiple habitats over short temporal scales.

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1. Introduction

Many large marine vertebrates (e.g. marine mammals, sharks, seabirds, and sea turtles) are vulnerable to overexploitation due to their life history characteristics, such as long lifespans, late maturity, slow reproductive rates, and extended migrations (Baum et al., 2003; Fujiwara and Caswell, 2001; Lewison et al., 2004a,b). These animals are important for maintaining ecosystem function and their removal can lead to cascading ecological changes (Fujiwara and Caswell, 2001; Lewison et al., 2004b). Like other large marine vertebrates, when abundant, sea turtles play key ecological roles as consumers, prey and competitors, hosts for parasites and pathogens, substrates for epibionts, seascape and marine substrate engineers, and nutrient transporters (Bouchard and Bjorndal, 2000; Bjorndal, 2003; Bjorndal and Bolten, 2003; Bjorndal and Jackson, 2003). Green turtles (*Chelonia mydas*) are especially important in coastal areas because their grazing

behavior significantly reduces nutrient cycling times in seagrass pastures (Moran and Bjorndal, 2005, 2007).

Although once one of the most abundant large vertebrates in the Pacific Ocean, East Pacific green turtles have declined precipitously since the 1950s due to intense commercial fisheries (Marquez et al., 1982; Marquez 1990) and egg harvesting (Clifton et al., 1982; Nichols, 2003). Mexico implemented a management and recovery program in 1978 (Garcia-Martinez and Nichols, 2000), but populations continued to crash and in 1990 the government issued a complete moratorium on the use of sea turtles (Aridjis, 1990). However, despite widespread protection on central nesting beaches and the complete moratorium, current populations remain well below historical levels mainly due to directed hunting and incidental fisheries bycatch (Seminoff, 2004; Koch et al., 2006, 2007). During the past decade sea turtle harvest and bycatch mortality along the Baja California peninsula has been estimated to be as high as 35,000 turtles per year, including at least 7,500 green turtles killed per year (Nichols et al., 2002, 2003; Nichols, 2003), representing a region with one of the highest known sea turtle mortality rates in the world (Gardner and Nichols, 2001; Hays et al., 2003; Nichols and Safina, 2004; Koch et al., 2006; Peckham et al., 2007, 2008; Mancini and Koch, 2009; Mancini, 2009).

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The majority of East Pacific green turtles that are killed in northwestern Mexico consist of juveniles or sub-adults occupying coastal foraging areas (Koch et al., 2006, 2007). East Pacific green turtles may spend up to 20 years or more in these near-shore habitats before reaching maturity (Seminoff et al., 2002; Seminoff, 2004; Koch et al., 2007) and the removal of only a small number of individual turtles from this environment could substantially limit or impede population recovery (Crouse et al., 1987; Crowder et al., 1994; Crouse, 1999). Therefore, understanding green turtle spatial use in these areas is a priority for conservation efforts. Nevertheless, the movements and habitat use of sea turtles that inhabit coastal foraging environments is poorly understood in contrast to migrating adult females (Seminoff et al., 2002; Seminoff and Jones, 2006; Schofield et al., 2007; Godley et al., 2008; Hazel, 2009).

Tracking the movements of free living animals, such as sea turtles, is fundamental to understanding their feeding ecology, migratory behavior, habitat use, general life history parameters, and conservation needs (Cooke et al., 2004; Cooke, 2008; Costa et al., 2010). Since the late 1970s satellite telemetry has been used to track the movements of adult sea turtles, most of which have been nesting females (Godley et al., 2008). Despite progressive size reductions, the costs to purchase and operate satellite telemetry remain high (Fuller et al., 2008). Most of these broad scale studies employ Platform Terminal Transmitters (PTTs) with the Argos data service (www.argos-system.org). A major limitation of this method is the spatial precision of locations, which lack the high resolution accuracy needed for fine scale tracking (Hazel, 2009; Costa et al., 2010).

In contrast to Argos, Global Positioning System (GPS) technology provides much more accurate spatial precision, but this method was historically ineffective for tracking marine vertebrates because they do not spend sufficient time at the surface to allow complete acquisition of satellite information (Schofield et al., 2007; Hazel, 2009; Kuhn et al., 2009; Costa et al., 2010). However, the advent of fast acquisition of GPS ephemeris (e.g. Yasuda and Arai, 2005; Schofield et al., 2007) means that high resolution and long-term tracking of marine species is now possible (Hazel, 2009; Schofield et al., 2009; Costa et al., 2010). In some cases GPS receivers have been linked to Argos transmitters allowing long-term remote relay of GPS data (Schofield et al., 2010).

To date, the majority of fine scale sea turtle movement studies have used sonic and radio tracking techniques or traditional mark and recapture methods (Seminoff et al., 2002; Godley et al., 2008). Continuous high resolution movement data overlaid with seascape features are particularly scarce for green turtles inhabiting neritic environments (Mendonca, 1983; Brooks et al., 2009; Hazel, 2009), but these data are important for defining core areas for conservation. Thus, we used GPS-VHF telemetry to link the fine scale movements of green turtles with direct assessments of habitat type at a coastal foraging area where both incidental fisheries bycatch and directed hunting are relevant conservation issues.

2. Methods

2.1. Study area

The study was conducted in June 2008 at Laguna San Ignacio, a shallow coastal lagoon located along the Pacific coast of Baja California Sur (BCS), Mexico (Fig. 1). The lagoon is part of the El Vizcaino Biosphere Reserve and provides important foraging and developmental habitat for East Pacific green turtles (Lopez-Castro et al., 2010). Tidal currents are strong due to tidal amplitudes that commonly exceed 2 m at spring tides. Average water depth is less than 5 m with large shallow/intertidal areas and extensive mangrove swamps along the shoreline (Nichols, 2003). The substrate consists primarily of sand and mud (Kurth, 2007). Seagrass and algae are abundant but patchily distributed (Kurth et al., 2008). The community of Laguna San Ignacio

is comprised of a small village and several fishing camps. There are approximately 200 residents and the local economy is based mostly on small-scale fisheries and, during the winter months, gray whale ecotourism.

2.2. Habitat survey

Water depth in the lagoon was measured using a portable depth sounder (Humminbird 500 Series, Eufaula, AL) mounted on the transom of a 6 m fiberglass boat. The location of the boat was determined using a handheld GPS device (Garmin GPS7, Olathe, KS). Depth measurements were corrected for tidal height using the nearest known station (Puerto San Carlos, BCS, Mexico) via the online tidal height prediction program published by the University of South Carolina (<http://tbone.biol.sc.edu/tide>) and merged in ArcGIS 9.3 Geographic Information System (GIS) software (Environmental Systems Research Institute, Redlands, CA). Depth data were partitioned into three classes: shallow (<5 m), moderate (5 to 10 m), and deep (>10 m). Seagrass coverage was determined using an underwater video camera (Aqua-Vu Scout II, Brainerd, MN) suspended from the boat and connected to a handheld VCR (Canon ZR-10, Lake Success, NY). One-minute recordings were made as the boat drifted in the wind and current at locations throughout the lagoon spaced out on a regular 1 km grid. Snorkel surveys were conducted in areas where turtles were sighted or captured to determine the presence or absence of seagrass. Using this information, maps with polygons of seagrass and depth classes (see supplementary material) were constructed in ArcGIS 9.3 to determine green turtle habitat selection.

2.3. Turtle capture and morphometric measurements

Turtles were captured using nylon and cotton entanglement nets (100 m long, 50 cm stretched mesh) specifically designed to catch sea turtles. Captured turtles were able to surface and breathe because the nets have very little weight on the lead line. The nets soaked for approximately two to four hours and were monitored at regular intervals (≤ 0.5 h) for entangled turtles. The nets were set during slack tide at various sites in the lagoon with most capture effort conducted at night. After capture, turtles were landed on the nearest beach and standard measurements (straight carapace length and width, curved carapace length and width, head width, total and partial tail length, mass, and body condition) were conducted. No turtles were kept for longer than two hours. All measurements were recorded on standardized sea turtle data sheets modified from Koch et al. (2007). After measurements were completed, turtles were tagged using metal inconel tags (National Band and Tag Company, Newport, KY), applied proximal and adjacent to the first large scale on each rear flipper following Balazs (1999). We defined sexual maturity as 77.3 cm SCL, the mean size of nesting female green turtles at the closest major nesting beach (Michoacán, Mexico) following Seminoff et al. (2003).

2.4. Turtle tracking and analysis

We tracked green turtles using a custom-made floating buoy attached to the turtle via a 10 m monofilament tether that housed a GPS data logger/receiver (20 Channel EM-408 SiRF III Receiver with Antenna/MMCX, Sparkfun Electronics, Boulder, CO) and VHF transmitter (148.103–148.146 MHz). The GPS device had a positional accuracy of 10 m. The design of the tracking system was an evolution of the apparatus used by Brooks et al. (2009). The effects of the tethered buoys on free living green turtles appear to be minimal in the short-term (Senko, 2009; Brooks et al., 2009). Turtles were released at the capture location once measurements were completed and the tracking device was affixed. The VHF signal was tracked from the shore and from boats using a handheld directional 5-element Yagi antenna (Advanced Telemetry Systems, Isanti, MN). Tracking was

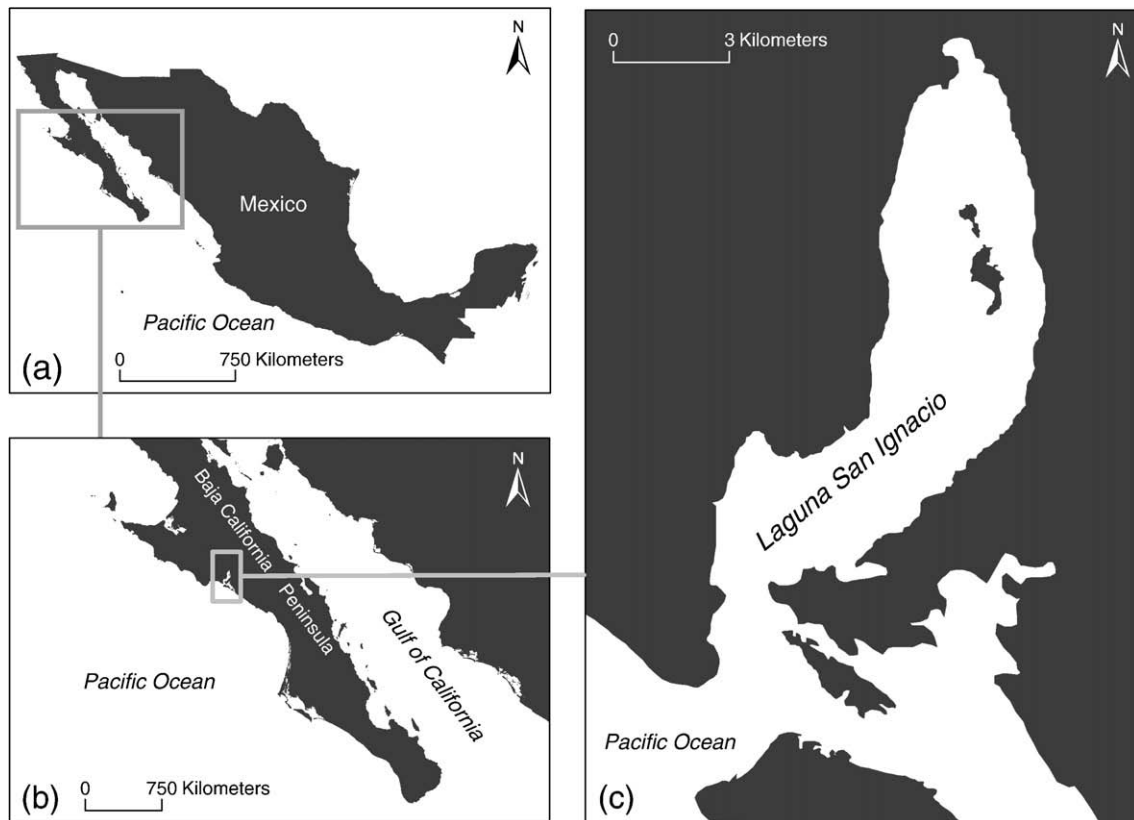


Fig. 1. Map of the Laguna San Ignacio region, Baja California Sur, Mexico.

terminated when the tether broke naturally from the turtle. After detachment from the turtle, the buoys drifted to shore and were usually recovered at low tide.

GPS units were configured to receive and record locations every five minutes. Data were downloaded on site from the GPS devices after the termination of each tracking period. The GPS units recorded latitude, longitude, time, and date of each location. Data were screened to remove locations demonstrating abrupt changes in direction and biologically unrealistic speeds (see Hays et al., 2001), defined as rates of movement greater than those achieved during the first two GPS fixes post-release when animals exhibited initial bursts of speed. To account for behavioral responses to capture and handling, data from the first six hours post-release were not used in the analysis. Rates of movement and GIS animations of each track suggested that turtles resumed evidently normal behavior when their initial bursts of speed were followed by subsequent resting periods indicated by little movement. This was always observed in less than three hours, but six hours was used as a conservative estimate. To determine when the buoy became detached from the turtle, we recorded the last time we observed the tether attached to the turtle from daily supervision of the animal and created GIS animations of each track in ArcGIS 9.3. Using this information, we conservatively estimated the first possible point at which the tether could have become detached and removed all subsequent points from the analysis.

2.5. Fine scale daily movement analysis

Distance calculations were determined by connecting successive GPS fixes with straight lines using Hawth's Tools (Beyer, 2004) in ArcGIS 9.3. These calculations assumed that turtles followed a straight line between successive GPS fixes. Although GPS loggers recorded a location every five minutes, these calculations should be considered minimum estimates (Tremblay et al., 2006). Tracks were partitioned into diurnal (0500–1859 h) and nocturnal (1900–0459 h) periods of

activity following Seminoff et al. (2002) and Seminoff and Jones (2006) to determine variability in daily movements. These times also approximated local daylight and nighttime conditions observed at the study site during June 2008. Vagility was determined by calculating the total distance traveled for diurnal, nocturnal, and daily (24-h) time periods. Net displacement was calculated by measuring the straight-line distance from the start and finish of each track for diurnal, nocturnal, and daily (24-h) time periods. Daily (24-h) activity ranges were calculated with the 100% Minimum Convex Polygon method (Burt, 1943) using Hawth's Tools. All measurements were calculated in ArcGIS 9.3 using X Tools Pro (www.xtoolspro.com).

2.6. 24-h activity pattern analysis

Tracks were partitioned into three equal activity periods to determine whether turtles exhibited greater vagility during nocturnal (2200–0559 h), crepuscular (0600–0959 h and 1800–1959 h), or diurnal (1000–1759 h) periods. To determine if turtles were more active at spring tides, we designated tides as “spring” if they fell within one day of a spring tide. All other tides were designated as “normal”, unless they fell within one day of a neap tide.

2.7. Water depth and seagrass versus turtle distribution

We calculated the proportion of time turtles spent in each habitat type (seagrass, shallow water, moderate water, and deep water). Ivlev's electivity index (Ivlev, 1961; Jacobs, 1974) was used to determine green turtle habitat selection by comparing the proportion of area used to the proportion of area available. For each habitat type, the Ivlev's index E_i for habitat i was calculated with the formula: $E_i = (o_i - a_i) / (o_i + a_i)$, where o_i is the proportion of time observed in habitat i (habitat utilized) and a_i is the proportion of habitat i available in the overall study area. The index has a range from -1 to $+1$; negative values suggest avoidance (or lower concentration than

chance alone would be expected to produce), positive values suggest preference (or higher concentration than chance alone would be expected to produce), and 0 indicates a neutral response (or a proportion equal to availability) (Manly et al., 2002).

2.8. Statistical analysis

Values were averaged for each turtle with more than one diel cycle to avoid pseudo replication. A paired t-test was used to compare: (1) diurnal and nocturnal vagility, net displacement, and travel speed; (2) daily vagility at spring and normal tides; and (3) the SCL (log) of turtles captured and tracked during the study period. The relationship between movement parameters (daily vagility, daily net displacement, and daily activity ranges) and turtle size (log SCL) were analyzed using a linear mixed-effects model because tracking durations (number of diel cycles) were not always equal among turtles. In this model, turtle ID was considered a random effect to acknowledge correlated measures within individual turtles. A one-way analysis of variance was used to test for differences in vagility between crepuscular, diurnal, and nocturnal activity periods. Statistical analyses were performed in R 2.9.2. Mean values are followed by standard errors (\pm SE). Statistical significance was inferred at a probability of 0.05 or less.

3. Results

3.1. Study animals and tracking effort

Study animals measured from 44.6 to 83.5 cm SCL and 10.9 to 75.6 kg in mass (Table 1). Sediment at capture sites included sand, shell, and pebble. There was no significant difference between the SCL (log) of turtles we captured during June 2008 and the SCL (log) of turtles we tracked during June 2008 ($t = -0.8498$, $df = 6.968$, $p = 0.4237$). All telemetry buoys were successfully recovered at the termination of tracking. Total tracking time ranged from 41.5 to 184.0 h. Turtle movements encompassed the entire lagoon but no turtles ventured outside the mouth (Fig. 2). Of the six turtles tracked, five provided data for two or more diel cycles (48-h). Movements of individual turtles varied temporally (Table 2). Data highlighted two distinct behavioral movement patterns: four turtles exhibited circular movements with high fidelity to the capture–release location and two turtles exhibited meandering movements with low fidelity to the capture–release location (Table 3).

3.2. Fine scale daily movements

Daily vagility (24-h) ranged from 2.0 to 29.6 km (mean = 12.92 ± 467 km) and daily activity ranges (24-h) were from 1 to 1575 ha (mean = 404 ± 386 ha) with travel speeds of $0.1\text{--}1.2$ km h⁻¹ (mean = 0.54 ± 0.19 km h⁻¹). Daily net displacement (24-h) ranged from 0.18 to 19.10 km (mean = 4.67 ± 4.17 km) with diurnal net

displacement covering 1% to 99% (mean = $27 \pm 24\%$) of diurnal vagility, nocturnal net displacement covering 2% to 85% (mean = $42 \pm 26\%$) of nocturnal vagility, and daily net displacement (24-h) covering 4% to 77% of daily (24-h) vagility (mean = $34 \pm 21\%$). Turtles moved significantly farther during the diurnal period versus the nocturnal period ($t = -2.3822$, $df = 9.518$, $p = 0.03965$), but exhibited no significant differences in nocturnal–diurnal net displacement ($t = -0.2359$, $df = 5$, $p = 0.8229$) and travel speeds ($t = -0.816$, $df = 9.896$, $p = 0.4337$). The linear mixed-effects model indicated that daily vagility, daily net displacement, and daily activity ranges were not significantly correlated with turtle size (log SCL) (Table 4).

3.3. 24-h activity patterns

There were no significant differences in vagility during the three equal activity periods ($df = 2$, $f = 0.58$, $p = 0.5695$), although the greatest proportion of movement occurred during the nocturnal period (37.8%), followed by the crepuscular period (31.6%), and diurnal period (30.6%) (Fig. 3). There was no significant difference between daily vagility during spring or normal tides ($t = 0.6421$, $df = 1$, $p = 0.6366$), but these results should be interpreted cautiously because of the small sample size (see Table 2).

3.4. Water depth and seagrass versus turtle distribution

Turtles spent most (59%) of their tracking duration in the <5 m depth class, followed by the 5 to 10 m depth class (34%), and the >10 m depth class (7%), with 69% of their tracking duration occurring over areas of seagrass. When we examined habitat selection by comparing the proportion of each habitat used to the proportion of each habitat available, the Ivlev's electivity index showed positive selection for areas of seagrass and moderate water depth (5 to 10 m), neutral selection for shallow water (<5 m), and avoidance of deep water (>10 m). Turtles showed stronger selection for shallow water at night, stronger selection for moderate water during the day, stronger avoidance for deep water at night, and slightly stronger selection for areas of seagrass during the day (Fig. 4).

4. Discussion

While direct long-term tracking of sea turtles is now possible with Fastloc GPS-Argos tags which allow GPS tracking of individuals for one year or more (Costa et al., 2010; Schofield et al., 2010), attaching standard GPS loggers via tethers provides a reliable alternative method for less expensive short-term tracking (Brooks et al., 2008; Senko, 2009). Despite our small sample size, we believe this study gives a good preliminary assessment of green turtle daily movements and habitat use in a region where both incidental fisheries bycatch and directed hunting are relevant conservation issues.

The temporal differences in daily vagility, daily net displacement, and daily activity ranges within and between turtles (Table 2) may be a result of our small sample size and short tracking duration, although variability in daily movements of green turtles has been reported elsewhere (Mendonca, 1983; Brill et al., 1995; Whiting and Miller, 1998; Seminoff and Jones, 2006; Hazel, 2009; Brooks et al., 2009). To our knowledge, the mean daily vagility found in this study is the second largest mean value recorded for green turtles at a coastal foraging area. Rather than crop and maintain distinct seagrass pastures (Bjorndal, 1980), turtles at our study site may have moved large distances to exploit patchily distributed food resources and possibly select foods with higher nutritional quality or areas with higher food biomass (Whiting and Miller, 1998). Strong tidal currents likely facilitated the large distances turtles traveled over short temporal scales (e.g. Brooks et al., 2009). Although we were unable to quantitatively measure tidal flows, it frequently appeared that turtles were swimming with the tide rather than against it.

Table 1

Summary of morphological and tracking data of six *Chelonia mydas* tracked in Laguna San Ignacio, Baja California Sur, Mexico.

Turtle ID	SCL (cm)	CCL (cm)	Mass (kg)	TTL (cm)	Sex	Tracking interval		Total duration (h)
						Begin	End	
CM 1	59.2	62.0	26.9	10.0	U	6/20/08	6/24/08	98.5
CM 2	69.9	74.5	43.5	13.4	U	6/20/08	6/21/08	41.5
CM 3	62.4	67.5	31.2	7.3	U	6/19/08	6/22/08	75.5
CM 4	83.5	88.5	75.6	16.5	F	6/25/08	6/27/08	56.1
CM 5	44.6	46.0	10.9	9.1	U	6/18/08	6/21/08	86.0
CM 6	56.2	59.0	24.1	10.3	U	6/11/08	6/19/08	184.0

SCL = straight carapace length; CCL = curved carapace length; TTL = total tail length; U = undetermined; F = probable female.

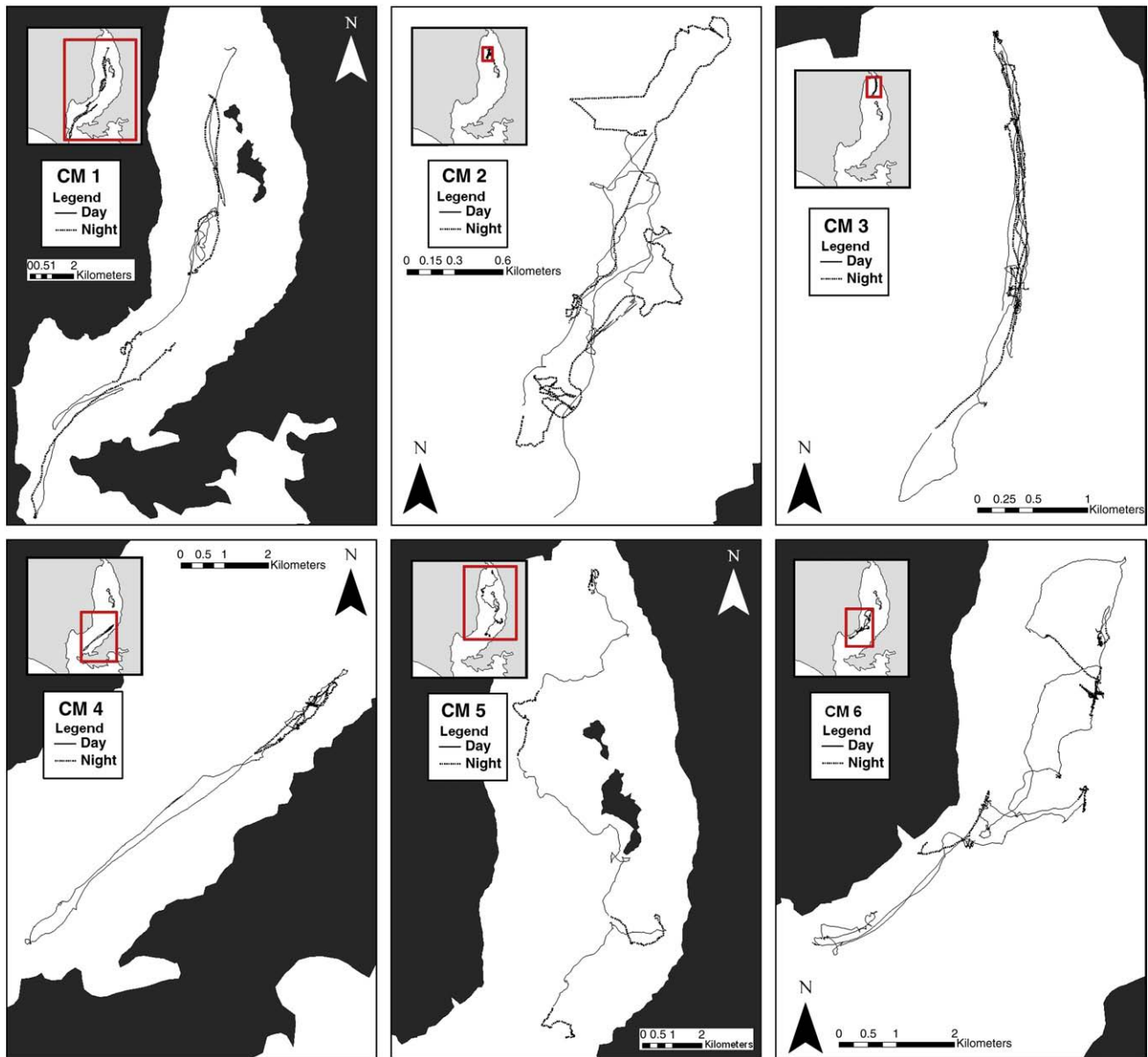


Fig. 2. Movements of six *Chelonia mydas* tracked in Laguna San Ignacio, Baja California Sur, Mexico. Tracks are partitioned into day (0500–1859 h) and night (1900–0459 h) periods of activity and exclude the first 6 h.

Turtles moved significantly farther total distances during the diurnal period versus the nocturnal period, but this was because daytime was 40% longer than nighttime during the summer when turtles were tracked. We found no significant differences in diurnal–nocturnal speeds and net displacement, suggesting that turtles were active throughout day and night. There were also no significant differences in vagility when tracks were partitioned into three equal activity periods (diurnal, nocturnal, and crepuscular), again indicating that turtles were active throughout the diel cycle. These results contrast with other studies (Bjorndal, 1980; Mendonca, 1983; Ogden et al., 1983; Williams, 1988; Makowski et al., 2006; Taquet et al., 2006; Hazel, 2009; Hazel et al., 2009), which have suggested that green turtles prefer to travel and feed by day and rest at night. However, turtles that occur in areas with strong tides, such as our study site, may lack predictable diurnal–nocturnal movement and habitat use patterns (like the tides), especially if they forage on intertidal food resources (Whiting and Miller, 1998). If turtles actively or passively use the tides to conserve energy and exploit the patchy distribution of seagrass and algae at our study site, they may do so regardless of time

of day. Brooks et al. (2009) found that East Pacific green turtles from a nearby coastal foraging area (~250 km away) with strong tides displayed no differences between day and night travel speeds, suggesting that these turtles were also active throughout the diel cycle.

All turtles remained in the lagoon throughout their tracking duration. While temporally limited, our data suggest that green turtles may demonstrate at least some degree of fidelity to the lagoon. Senko et al. (2010) reported that only two out of 154 East Pacific green turtles recaptured at least once over a five-year period along the Baja California peninsula were found in a different foraging area, indicating a high site fidelity. However, spatial use of green turtles at coastal foraging areas is highly variable. Not all animals appear to stay in these areas as permanent residents and many turtles may commence extensive developmental migrations (Bjorndal and Bolten, 1997; Musick and Limpus, 1997). Immature green turtles tagged on foraging grounds in the southern Bahamas remain in these coastal habitats for varying lengths of time before emigrating to other foraging areas throughout the Greater Caribbean (Bjorndal et al., 2003). Juvenile

Table 2

Summary of daily movement parameters and travel speeds of six *Chelonia mydas* tracked in Laguna San Ignacio, Baja California Sur, Mexico.

Turtle ID	Diel cycle	Distance moved (km)						Travel speed (km h ⁻¹)			Daily activity range (ha)
		Day vagility	Day net	Night vagility	Night net	24-h vagility	24-h net	Day	Night	24-h ^a	
CM 1	1 ^b	15.55	7.10	14.07	12.0	29.62	19.10	1.11	1.41	1.23	1575.0
	2	12.44	5.26	4.29	1.30	16.73	6.56	0.89	0.43	0.70	682.0
	3	6.81	3.89	8.24	6.0	15.05	9.89	0.49	0.82	0.63	452.0
CM 2	1 ^b	7.97	1.51	4.82	1.46	12.79	2.97	0.57	0.48	0.53	125.0
CM 3	1 ^b	4.96	0.15	3.50	2.48	8.46	2.63	0.35	0.35	0.35	51.0
	2 ^b	4.87	0.07	4.46	2.80	9.33	2.87	0.35	0.45	0.39	193.0
CM 4	1 ^c	4.43	1.0	3.02	0.81	7.45	1.81	0.32	0.30	0.31	45.0
	2	16.65	0.73	5.55	0.10	22.20	0.83	1.19	0.56	0.93	398.0
CM 5	1 ^b	7.09	7.0	3.90	1.50	10.99	8.50	0.51	0.39	0.46	715.0
	2 ^b	10.40	6.12	4.28	3.10	14.68	9.22	0.74	0.43	0.61	1174.0
	3 ^b	8.94	3.72	2.40	1.20	11.34	4.92	0.64	0.24	0.47	811.0
	1 ^b	8.20	1.25	5.90	0.17	14.10	1.42	0.59	0.59	0.59	140.41
	2 ^b	2.59	0.30	0.69	0.16	3.28	0.46	0.19	0.07	0.14	23.29
CM 6	3 ^b	0.82	0.16	1.21	0.02	2.03	0.18	0.06	0.12	0.08	0.98
	4	7.60	2.45	2.46	0.66	10.07	3.11	0.54	0.25	0.42	368.79
	5	7.80	0.29	1.85	0.08	9.65	0.37	0.56	0.19	0.40	179.63
	6	5.33	1.76	3.90	1.60	9.23	3.36	0.38	0.39	0.38	206.87
	7	6.66	1.39	2.25	0.85	8.91	2.24	0.48	0.22	0.37	156.00
	Mean	8.23	2.43	4.68	2.24	12.92	4.67	0.59	0.47	0.54	404.20
	SD	2.65	2.43	2.18	2.22	4.46	4.17	0.19	0.22	0.19	386.87

Each diel cycle represents one 24-h period and tracks are partitioned into day (0500–1859 h) and night (1900–0459 h) periods of activity. Vagility was determined by calculating the total distance traveled during each time period. Net displacement (day net, night net, and 24-h net) was calculated by measuring the straight-line distance from the start and finish of each track. Daily activity range (24-h) was calculated with the Minimum Convex Polygon method (Burt, 1943). Mean and SD values are represented as an overall mean of the mean value per turtle to prevent skewing data to turtles with longer tracking durations. Tides were designated as “spring” or “neap” if they fell within 1 d of spring or neap tides.

^a Adjusted for actual proportion of the 14-h day and 10-h night where the 24-h travel speed = day speed (14/24) + night speed (10/24).

^b Spring tide.

^c Neap tide.

Brazilian green turtles tracked on their foraging areas via satellite telemetry (Godley et al., 2003) exhibited three main patterns of behavior: extended residency with high site fidelity, moderate range movements (<100 km), and long range movements (>100 km).

Turtles demonstrated two distinct behavioral movement patterns: circular movements with high fidelity to the capture–release location and meandering movements with low fidelity to the capture–release location (Table 3). Although turtles showed high fidelity to their capture–release sites over the entire tracking duration, fidelity was sometimes observed over a time period greater than one diel cycle. This suggests that green turtles may require multiple days to access all of their preferred locations within the foraging area (Seminoff and Jones, 2006; Hazel, 2009). Whereas four turtles exhibited circular movements with high fidelity to their capture–release site, two turtles demonstrated meandering movements with low fidelity to their capture–release site. The reason for this apparent dichotomy in movement behavior is unclear, although it may have to do with the dietary preferences of individual turtles (Megill et al., 2009). Both turtles that displayed meandering movements were tracked for three days, suggesting that their movements were probably not the result of

Table 3

Summary of behavioral movement patterns of six *Chelonia mydas* tracked in Laguna San Ignacio, Baja California Sur, Mexico; where Type 1 = circular movements with high fidelity to the capture–release site and Type 2 = meandering movements with low fidelity to the capture–release site.

Turtle ID	Type	Fidelity ^a (km)
CM 1	2	Low (10.3)
CM 2	1	High (0.3)
CM 3	1	High (0.7)
CM 4	1	High (0.6)
CM 5	2	Low (12.5)
CM 6	1	High (1.2)

^a Fidelity = straight-line distance (km) between final GPS location of tracked turtle and capture–release location of tracked turtle.

a short tracking duration (e.g. a flee response due to the stress of capture and handling). Both meandering turtles were among the smallest we tracked and were below the mean SCL of turtles captured at Laguna San Ignacio during a five-year period (Lopez-Castro et al., 2010). At least one of these turtles (CM 5) may have been a new recruit to the lagoon, possibly reflecting a lack of familiarity with a new environment.

Turtles showed positive selection for areas of seagrass and moderate water depth (5 to 10 m), neutral selection for shallow water (<5 m), and avoidance of deep water (>10 m). Although green turtles exhibited neutral selection for shallow water, we assumed that each habitat was equally available to turtles at all times. In reality, this may not have been true if some shallow water sites in the lagoon were unavailable to turtles during low tides. Even so, the occurrence of green turtles at our study site reveals that they have already made a

Table 4

Summary of linear mixed-effects model of turtle size (SCL) fitted to daily movement parameters of six *Chelonia mydas* tracked in Laguna San Ignacio, Baja California Sur, Mexico; SCL = straight carapace length.

Parameter	Value	SE	t-value	p-value
<i>Vagility</i>				
(Constant)	18.572745	94.92414	0.19565882	0.8482
SCL (log)	−1.06068	21.79702	−0.04866172	0.9642
<i>Net displacement</i>				
(Constant)	29.605431	60.3068	0.4909136	0.6323
SCL (log)	−6.341271	13.85271	−0.4577641	0.6782
<i>Activity range</i>				
(Constant)	5746.36	6260.746	0.9178395	0.3768
SCL (log)	−1281.425	1439.064	−0.890457	0.4388

Vagility was determined by calculating the total distance traveled by each turtle for one diel cycle (24-h). Net displacement was calculated by measuring the straight-line distance from the start and finish of each track for one diel cycle (24-h). Activity range was calculated with the 100% Minimum Convex Polygon method (Burt, 1943) for one diel cycle (24-h).

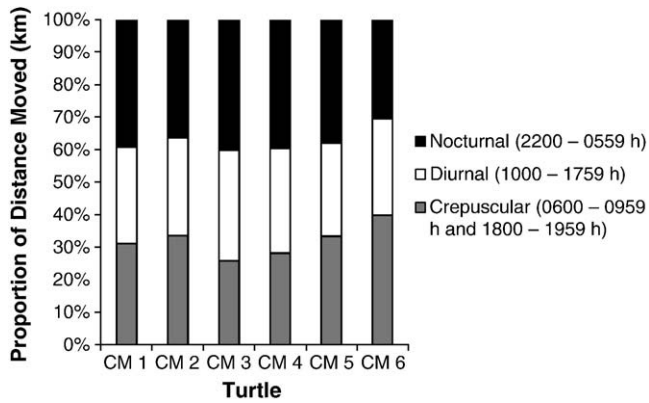


Fig. 3. Proportion of total distance moved (km) in three equal activity periods of six *Chelonia mydas* tracked in Laguna San Ignacio, Baja California Sur, Mexico.

selection for the area (see Johnson, 1980). This is likely due to the abundance of shallow water and corresponding food resources, which may explain why the area has the second highest green turtle catch per unit effort along the Baja California peninsula (Lopez-Castro et al., 2010).

The relatively small positive selection for areas of seagrass should be interpreted with caution because we were only able to collect data on seagrass presence or absence. Ideally, future studies should record species specific data on seagrass biomass, distribution, and nutrition. Seagrass dynamics could have played a role in the depth selection we observed if abundance, distribution, or nutritional quality was lower in shallow water and higher at moderate water depths. During periods of low tide at our study site, some shallow water areas containing seagrass may be exposed, which could affect nutritional quality and biomass (Stapel et al., 1997). Nevertheless, it is unclear whether turtles selected moderate water depths for feeding, whether they foraged opportunistically at these depths, or whether they used these areas because they contain tidal channels that transport them to nearby shallow water foraging pastures.

The strong avoidance for deep water is likely due to a lack of available food resources and structured resting sites in these areas. Extensive substrate observations via underwater remote video revealed a poorly structured hard sand/clay seafloor lacking seagrass or algae in depths > 10 m. Predation risk also may have played a role in turtles avoiding deep water. Heithaus et al. (2007) found that predation risks from tiger sharks influenced green turtle distribution in a condition dependent manner.

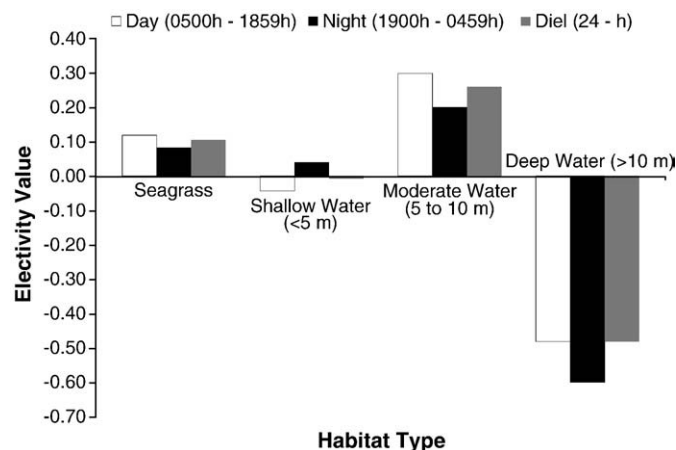


Fig. 4. Habitat selection of six *Chelonia mydas* tracked in Laguna San Ignacio, Baja California Sur, Mexico represented by Ivlev's electivity index. The index has a range from -1 to $+1$, with negative values suggesting avoidance (or lower concentration than chance alone would be expected to produce), positive values suggesting preference (or higher concentration than chance alone would be expected to produce), and 0 indicating a neutral response (or a proportion equal to availability).

Large sharks were historically plentiful throughout the region (Pachico Mayoral, pers. comm.) and in spring 2010 a small longline fishery targeted bull sharks for several weeks inside the lagoon (Ranulfo Mayoral, pers. comm.).

Turtles showed stronger selection for shallow water at night, stronger selection for moderate water depths during the day, and stronger avoidance for deep water at night. Use of shallower water during the night has been documented before (Brill et al., 1995; Seminoff et al., 2002; Southwood et al., 2003), but other studies (Bjorndal, 1980; Ogden et al., 1983; Makowski et al., 2006; Taquet et al., 2006; Hazel et al., 2009) have reported that green turtles were more active in shallower water by day and rested in deeper water at night. Whereas green turtles showed positive selection for shallow and moderate water depths at night, they clearly avoided deep water during this period. Selection of deeper water at night would have allowed turtles to dive with greater oxygen stores and remain submerged for longer time periods due to greater lung inflation (Hays et al., 2000, 2004a; Hazel et al., 2009). Why then did turtles strongly avoid deeper water at night? One possible explanation is that our study area lacks structured resting sites (confirmed via extensive substrate observations using an underwater remote video) that appear to favor selection of deeper water at night (Hazel et al., 2009). In addition, turtles were active throughout the diel cycle and consequently may lack predictable diurnal–nocturnal activity and feeding patterns, especially if they forage in intertidal areas. While green turtles showed slightly stronger selection for areas of seagrass during the day, the difference was negligible, suggesting that turtles may have been foraging throughout the diel cycle.

Temporal patterns in behavior have been widely recorded in sea turtles, with distinct overwintering behaviors observed in coastal environments (Hochscheid et al., 2005). Thus, future studies extending tracks from a few days to a few months or even years would be useful and could readily be accomplished with state-of-the-art biotelemetry equipment. In addition to recording the fine scale movements of turtles via GPS tracking, future studies could also employ patterns of depth utilization (e.g. Hazel et al., 2009), if/when turtles are asleep (e.g. Houghton et al., 2008), and patterns of flipper stroking as a measure of swimming effort (e.g. Hays et al., 2004b).

This study revealed that green turtles were active throughout the diel cycle while traveling large distances and traversing multiple habitats over short temporal scales. Therefore, conservation efforts intended to benefit green turtles may need to include the entire lagoon rather than target a few high use areas. These efforts should be broad based and focus on ways to mitigate the impacts of incidental fisheries bycatch which currently pose the greatest threat to green turtles at this coastal foraging area. Given that large numbers of green turtles continue to drown in gillnets at Laguna San Ignacio despite existing conservation efforts (Koch and Mancini, 2009; Mancini, 2009), novel and multidisciplinary approaches to address this problem are urgently needed.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2010.06.017.

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