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Foraging site fidelity and stable isotope values of loggerhead turtles tracked in the Gulf of Mexico and northwest Caribbean

Anton D. Tucker[1,3,*] Bradley D. MacDonald[2], Jeffrey A. Seminoff[2]

[1]Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida 34236, USA

[2]NOAA-National Marine Fisheries Service, Southwest Fisheries Science Center, 8901 La Jolla Shores Dr, La Jolla, California 92037, USA

[3]*Present address:* Department of Parks and Wildlife, Marine Science Program, 17 Dick Perry Ave, Kensington, WA 6151, Australia

ABSTRACT: We used stable isotope ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) analysis in combination with satellite telemetry to evaluate the foraging areas chosen by 88 loggerhead turtles *Caretta caretta* nesting in southwestern Florida. Nine turtles were tracked and skin-sampled in more than one nesting season to evaluate within-individual consistency in foraging sites and stable isotope values. Turtles migrated to 5 regions: Caribbean, Florida Keys, West Florida Shelf, northern Gulf of Mexico, and Yucatan Peninsula. The stable isotope ratios across these foraging grounds ranged from −21.16 to −7.69 ‰ for $\delta^{13}C$, 3.27 to 13.99 ‰ for $\delta^{15}N$, and 1.91 to 20.64 ‰ for $\delta^{34}S$. We compared bulk skin tissue stable isotope values for all turtles by bioregion, year, body size, depth of putative foraging area, and linear distance from the closest shore; among these factors, only bioregion showed a significant effect on isotope values. There were subtle regional differences in mean $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$, and an apparent north-south isotopic shift aligning strongly with ocean currents adjacent to the Florida Keys. The influence of coastal topography and shifting biogeographic boundaries such as the Loop Current may cause strong ocean water mixing that results in the observed similarities in stable isotope values among regions. These results indicate that stable isotopes alone may be an inadequate tool for identifying fine-scale (<100 km) residency of sea turtles within this ocean region.

KEY WORDS: Stable isotope · Carbon · Nitrogen · Sulfur · Premise testing · Satellite telemetry · Loggerhead turtle · *Caretta caretta* · $\delta^{13}C$ · $\delta^{15}N$ · $\delta^{34}S$

INTRODUCTION

Quantifying the prevailing stable isotope regimes and spatial structure within marine bioregions can help elucidate the oceanographic processes that characterize nearshore and open ocean ecosystems (Deutsch et al. 2007, McMahon et al. 2013). However, the lack of *in situ* data collection from many ocean regions has limited our understanding of marine stable isotope patterns. To fill these gaps, highly migratory large vertebrates can serve as 'ocean samplers' to collect oceanographic data over large spatio-temporal scales (Burton & Koch 1999, Wallace et al. 2006, Ramos et al. 2009, Pajuelo et al. 2010, Block et al. 2011). Their ability to reflect isotope patterns stems from their integration of the stable isotope characteristics of the marine habitats within which they forage into their own body tissues. Because of slow isotope turnover in low-metabolically active tissues such as epidermis, migrating consumers may retain this information long after departing these areas (e.g. after migration to breeding rookeries; Hobson &

*Corresponding author: tony.tucker@dpaw.wa.gov.au

Wassenaar 2008). It is also important to understand site fidelity and residency time in a particular habitat relative to isotope turnover rate to evaluate the efficacy of this approach for tracking animal movements among different habitats (Hatase et al. 2002, 2006, Rubenstein & Hobson 2004). However, without knowledge of the movement patterns of species, the use of stable isotopes for retrospective analysis is limited.

The application of satellite telemetry to tracking animal movement patterns has expanded in recent decades for animals within marine, aquatic, and terrestrial systems (Coyne & Godley 2005, Hart & Hyrenbach 2009, Godley et al. 2010, Zbinden et al. 2011). When stable isotope analyses (SIA) are combined with satellite telemetry, researchers are able to obtain information from dual time frames. Specifically, SIA provides information on the isotopic regime occupied prior to tissue sampling, whereas satellite telemetry documents the animal movements after they have been equipped with transmitters. Thus, the integration of SIA with satellite telemetry of marine organisms intended to serve as ocean samplers is limited to species that consistently use the same marine regions between migratory episodes (Godley et al. 2010, Zbinden et al. 2011).

Loggerhead turtles *Caretta caretta* are potential candidates to integrate SIA studies with satellite telemetry due to their broad ranging migrations, foraging associations that vary from pelagic to benthic foraging areas, and fidelity to natal nesting beaches where they can be easily sampled and equipped with tracking devices (Zbinden et al. 2011, Seminoff et al. 2012). Post-nesting migrations of loggerhead turtles are believed to be consistent across nesting seasons (Schroeder et al. 2003) such that individuals migrate back to the same foraging sites from which they originated prior to nesting (Broderick et al. 2007, Marcovaldi et al. 2010). Further, the post-nesting migrations of female loggerhead turtles are fueled with lipid reserves rather than en-route foraging; therefore, isotope values of slow-turnover tissues such as skin that are collected at the nesting beach are largely, if not exclusively, derived from nutrients acquired at foraging areas prior to nesting (Vander Zanden et al. 2010).

Inferences about oceanographic processes have been gained on numerous occasions via SIA of sea turtle tissues. For example, a nitrogen isotope dichotomy was established for the eastern Pacific versus western North Atlantic by studying body tissues of leatherback and loggerhead turtles in these 2 ocean regions (Wallace et al. 2006, Pajuelo et al. 2010). These differences were attributed to the influence of nitrogen cycling, whereby the stable isotope values for turtles in the eastern Pacific were influenced by the high levels of de-nitrification, which is known to substantially increase baseline $\delta^{15}N$ values in marine systems (Hood et al. 2004, Montoya et al. 2007). In contrast, turtles in the western North Atlantic resided in waters where N_2 fixation by *Trichodesmium* in the Sargasso Sea is the prevailing N cycling pattern, a process that is known to drive down the $\delta^{15}N$ values of surface waters (Montoya et al. 2007). A similar nitrogen isotope dichotomy was found in the eastern versus western Pacific, where Seminoff et al. (2012) linked satellite telemetry with bulk tissue and amino acid stable isotope values in skin tissue from widely migratory leatherback turtles nesting in the western Pacific. Also in the Pacific, Hatase et al. (2002) linked SIA with satellite telemetry and demonstrated comparably low stable carbon isotope values in the pelagic Pacific along the Kuroshio Current relative to higher $\delta^{13}C$ values in the neritic East China Sea. Taken together, such studies demonstrate the value of an integrative approach. However, isotopic data linking sea turtles in space and time remain sparse for many ocean regions (e.g. Graham et al. 2010, McMahon et al. 2013) and additional studies that combine the 2 technologies remain warranted.

Samples from nesting sea turtles can offer a reliable bio-indicator of marine isoscapes if (1) there is a clear isotopic signature in a tissue sample that is appropriately matched to the study time frame, (2) prey preferences remain stable in the months prior to nesting, (3) their habitats do not fluctuate in baseline isotopic values, and (4) the turtles do not feed across multiple regions that differ in baseline stable isotope characteristics. In this context, our goal was to determine if stable isotope values were reliable indicators of foraging habitat for loggerheads in the Gulf of Mexico and northwest Caribbean Sea. To do this, we investigated tendencies for site fidelity in serial tracking histories of individual loggerhead turtles and determined if individuals from the same habitats sampled in different years were consistent in their isotopic niches. In doing so, we were able to search for patterns of regional structure defined by stable carbon, nitrogen, and sulfur isotopes. Integration of SIA with satellite telemetry results may better delineate the regional management unit structure of western Atlantic loggerhead turtles (NMFS & USFWS 2007, Shamblin et al. 2012) and aid decisions affecting endangered species management and policy (Wallace et al. 2011).

MATERIALS AND METHODS

Field collections

Sarasota County, Florida, hosts ca. 50% of the loggerhead turtle nesting in the Gulf of Mexico (Witherington et al. 2009), and annual nesting densities on the barrier island of Casey Key (28.7° N, 82.3° W) range from 40 to 100 nests km^{-1}. We coordinated hourly tagging patrols on the southern 6 km of Casey Key with all-terrain vehicles to encounter nesting females for 8 to 11 wk during summer.

We approached females after oviposition to check for or apply Inconel® tags in both front flippers and a microchip (Biomark) in a rear flipper. We measured the carapace to the nearest 0.1 cm by standard protocols for straight-line morphometrics (with a tree caliper) and curved morphometrics (with a stretched and calibrated tape measure) and we report herein only midline curved carapace length (CCL; notch to tip). We collected a skin sample for SIA with a 5 mm biopsy punch from the trailing margin of a rear flipper. The biopsy tissue was stored in 70% ethanol. We obtained skin biopsies between 2006 and 2013, but the present study addresses only samples from 2006 to 2011.

As each turtle departed, we used standard practices for transmitter attachments at a nesting beach (cf. Tucker 2010). We enclosed each turtle in a portable wooden box, cleaned the carapace of epibiota, and wiped with fresh water and alcohol to ensure dryness. We affixed ARGOS transmitters (Sirtrack Kiwisat 101 or 202, Wildlife Computers SPOT5, ca. 200 to 400 g in air) to the carapace with construction adhesive (2 part slow curing epoxy from either Powers or Sika) smoothed into a hydrodynamic shape. The application process took 1 to 2 h to complete and all turtles returned to the water before daybreak. Satellite tags were applied between 2005 and 2013.

Tracking and analysis

We organized, evaluated, and archived data in Satellite Telemetry Analysis Tool (STAT; Coyne & Godley 2005). A tracking path of movements connected latitude and longitude fixes of ARGOS Location Classes 3, 2, 1, 0, and A. We filtered location data in STAT to exclude unlikely data for water depth <0.5 m, speeds >5 km h^{-1}, or for turn angles <15°. We calculated distance between successive fixes by a great circle route equation and plotted locations in ArcGIS 9.1.

Arrival at a foraging area at the end of post-nesting migratory movements was inferred by an asymptote in the relationship between deployment duration and cumulative distance (km) from the rookery (e.g. Seminoff et al. 2007; Fig. 1). For each of these foraging sites, we characterized the mean water depth (m) and distance from nearest shore (km) using STAT analytical subroutines.

We terminated Argos IDs after 3 criteria were met: a foraging ground was clearly indicated by an asymptotic distance from rookery, the individuals remained within a 10 km radius of the tracking terminus, and/or once tracking periods exceeded 12 mo. This decision created right-truncated data and perhaps a negative bias for tracking durations greater than a year.

Stable isotope analysis

We freeze-dried skin samples (VirTis Benchtop K-Manifold Liophilizer) at −55°C for 8 h and ground them to small size particles (0.05 mm diameter). We removed the lipids from samples using an accelerated solvent extractor (ASE 200; Dionex) with petroleum ether as the solvent for one 30 min ASE cycle. We completed sample preparation by freeze-drying for an additional 2 h to remove any residual solvent before isotopic analysis. Some studies have detected

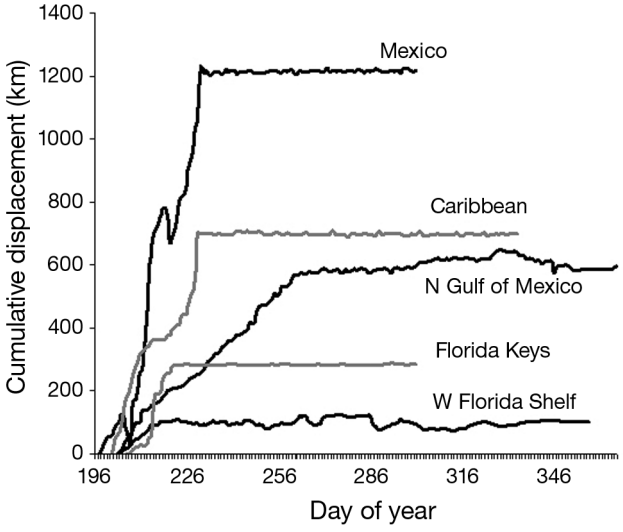

Fig. 1. Displacement plots (i.e. day of year vs. distance from deployment site) characteristic of the 5 bioregions in the wider Gulf of Mexico region that 88 loggerhead turtles were tracked to after nesting in Casey Key, Florida. A terminus of post-nesting migration at a foraging ground is illustrated by a characteristic plateau in cumulative distance traveled from rookery. Representative tracks are depicted for loggerheads from 5 biogeographic regions in this study

small changes in $\delta^{15}N$ of tissues as a result of lipid extraction (e.g. Sotiropoulos et al. 2004, Sweeting et al. 2006, Kojadinovic et al. 2008), but the changes have been extremely small (<1‰); slight changes were seen both ways, with slight enrichment and depletion in $\delta^{15}N$, and with virtually unchanged sample variances as a result. Whereas we consider changes for $\delta^{15}N$ to be significant when sample groups vary by upwards of 3 to 4‰, we suggest that the effects of lipid extraction in our study do not significantly impact the biological interpretations of our findings.

The Stable Isotope Laboratory at University of Florida conducted the stable carbon and nitrogen isotope analyses, with approximately 1.0 mg of tissue loaded into sterilized tin capsules and analyzed by continuous-flow isotope-ratio mass spectrometry using a Costech ECS 4010 elemental combustion system interfaced via a ConFlo III device (Finnigan MAT) to a Deltaplus gas isotope-ratio mass spectrometer (Finnigan MAT). Sample stable isotope ratios relative to the isotope standard were expressed in the following conventional delta (δ) notation in parts per mille (‰): $\delta = ([R_{sample}/R_{standard}] - 1) \times 1000$. R_{sample} and $R_{standard}$ were the corresponding ratios of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and standard, respectively. $R_{standard}$ for ^{13}C is Baker Acetanilide (C_8H_9NO; $\delta^{13}C = -10.4$‰) calibrated monthly against the Peedee Belemnite limestone formation international standard; $R_{standard}$ for ^{15}N is IAEA N1 Ammonium Sulfate ($[NH_4]_2SO_4$; $\delta^{15}N = +0.4$‰) calibrated against atmospheric N_2 and USGS Nitrogen standards. All analytical runs included samples of standard materials inserted every 6 samples to calibrate the system and compensate for any drift over time. Hundreds of replicate assays of standard materials indicated measurement errors of 0.05 and 0.095‰ for carbon and nitrogen, respectively. In addition to stable isotope ratios, we also interpreted the final isotope results with %C and %N measured for each tissue sample. Samples were combusted in pure oxygen in the elemental analyzer. Resultant CO_2 and N_2 gasses were passed through a series of thermal conductivity detectors and element traps to determine percent compositions. Acetanilide standards (71.09%C, 10.36%N) were used for calibration.

The Stable Isotope Laboratory at Washington State University conducted the stable sulfur isotope analyses, with approximately 3 mg of bulk tissue of each turtle loaded into sterilized tin capsules. Samples for sulfur isotopic analysis were combusted with an elemental analyzer (ECS 4010, Costech Analytical); SO_2 gases were separated with a 0.8 m GC column (100°C) and analyzed with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan) (Brenna et al. 1997). Reference material consisted of IAEA-S-1 silver sulfide (Coplen & Krouse 1998). Sulfur isotopic ratios were reported in per mille (‰) relative to VCDT (Vienna Cañon Diablo Troilite). The 2-sigma uncertainty of sulfur isotopic results was 0.5 ‰ unless otherwise indicated.

Statistical analysis

We incorporated satellite-tracked movements with stable isotope results for 88 female loggerhead turtles. We compared the track termini and respective $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values of each turtle with a suite of variables. Given the complexity in a study system spanning a wide range of latitudes and productivities, isotope values were evaluated in General Linear Models (GLMs) with bioregion, year, CCL, depth, and displacement distance as independent variables. We conducted Tukey's post hoc pairwise comparisons for variables that were statistically significant within the GLMs. For turtles that were satellite tracked and sampled for stable isotopes on multiple occasions (i.e. serially sampled), a paired *t*-test was used to evaluate the consistency of isotope values over time (years tracked). Statistical significance was evaluated at alpha = 0.05.

RESULTS

Satellite telemetry

Foraging grounds

The 88 female loggerhead turtles (from 80.3 to 116.0 cm CCL) were tracked to foraging areas across the Gulf of Mexico and neighboring regions (Fig. 2). The tracking termini of putative foraging areas extended from 54 to 1837 km from the Casey Key nesting beach. The tracked durations of foraging residencies ranged from 38 to 707 d (mean = 225 d). These foraging grounds were grouped by proximity and/or bioregion of their final destinations: 3 turtles migrated to the northern Gulf of Mexico, 44 migrated to the West Florida Shelf of the Gulf of Mexico, 15 migrated to regions offshore of the Yucatan Peninsula, 14 migrated to the Wider Caribbean and 12 migrated to the Florida Keys (Table 1).

Foraging grounds based on telemetry data spanned a tropical to temperate latitudinal range (17° to

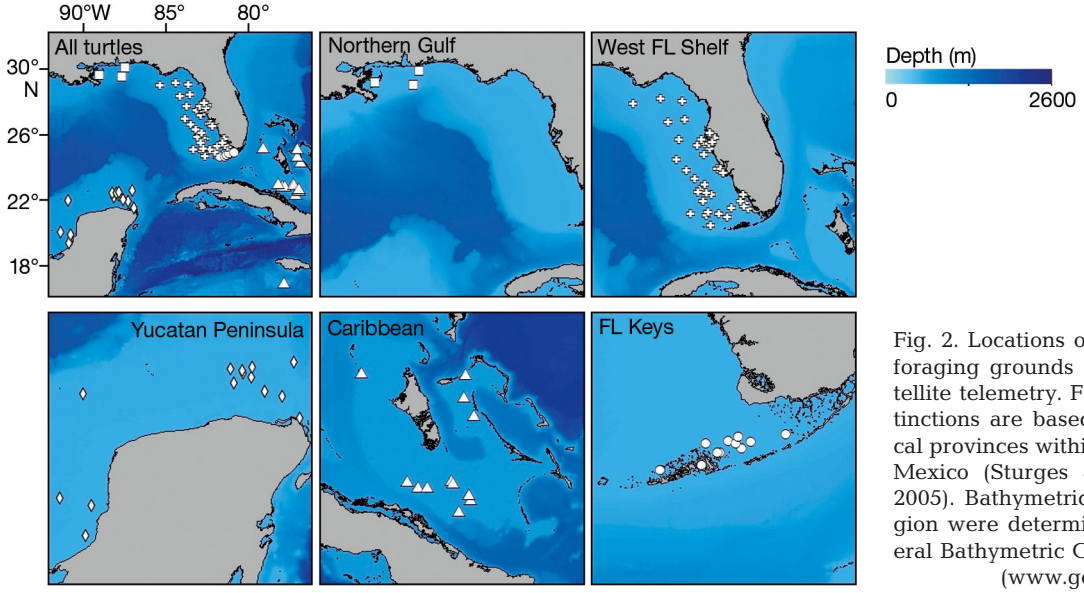

Fig. 2. Locations of loggerhead turtle foraging grounds determined via satellite telemetry. Foraging region distinctions are based on biogeographical provinces within the wider Gulf of Mexico (Sturges & Lugo-Fernandez 2005). Bathymetric values for the region were determined with the General Bathymetric Chart of the Oceans (www.gebco.net)

Table 1. Stable isotope values in ‰ ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) from skin of female loggerhead turtles from foraging grounds within and adjacent to the Gulf of Mexico

Region	n	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		$\delta^{34}S$ (‰)	
		Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
Northern Gulf of Mexico	3	−16.26 (0.53)	−16.76 to −15.71	12.89 (0.06)	12.82 to 12.94	18.86 (1.99)	16.78 to 20.64
West Florida Shelf	44	−16.05 (2.47)	−21.16 to −10.00	9.70 (2.23)	4.22 to 13.92	14.08 (3.24)	7.12 to 19.64
Yucatan Peninsula	15	−14.93 (2.41)	−18.71 to −11.18	11.04 (1.29)	9.08 to 13.51	13.53 (2.83)	6.56 to 17.52
Northern Caribbean	14	−11.38 (1.42)	−13.26 to −7.69	7.26 (1.21)	4.79 to 9.41	11.57 (2.50)	6.86 to 17.02
Florida Keys	12	−13.52 (2.80)	−19.52 to −10.07	8.43 (3.28)	3.27 to 13.99	8.81 (4.08)	1.91 to 16.29

30° N). The foraging grounds encompassed depths between 1 and 104 m, and were relatively close to shore (1 to 150 km). That is, loggerhead females of all sizes foraged in nearshore to offshore depths across a broad continental shelf but exhibited no foraging dichotomy of pelagic and neritic individuals.

Site fidelity

Nine individuals were tracked and tissue-sampled in 2 or more nesting seasons (Table 2). The transmitters of 7 females operated throughout post-nesting migrations to arrive at their respective foraging areas (Fig. 3). The foraging grounds of serially tracked turtles included Tampa Bay (Turtle WI, sampled and tracked 4 times to locations of 1 m depth at 1 km from shore), near or within Charlotte Harbor (Turtle LU, sampled and tracked twice, first to 4 m depth at 35 km from shore, and secondly to 1 m depth at 1 km from shore), Florida Keys (Turtles TU and CH, both sampled and tracked twice to depths of 1 m, 1 to 2 km from shore), Bahama Banks (Turtle G, sampled and tracked twice to 1 m depth at 70 km from shore; Turtle RA, sampled 3 times and tracked twice to a location at 1 m depth and 98 km from shore), and offshore West Florida Shelf (Turtle EL, sampled and tracked to 44 m depth at 102 km from shore and to 51 m depth at 104 km from shore) (Fig. 3).

The transmitters of 2 re-tracked turtles (West Florida Shelf: Turtle MI; Yucatan Peninsula: Turtle TH) ceased en route during their second satellite-tracked post-nesting migration. The last received signals indicated a steady progression toward their respective first tracking termini. Because of the equipment failure, the serial isotopic values of 2 turtles with incomplete second tracks were evaluated separately from isotopic patterns of 7 individuals that did reach their foraging area during the first and second tracking histories.

The isotopic study concluded in 2011, but the site fidelity analysis was extended temporally and spa-

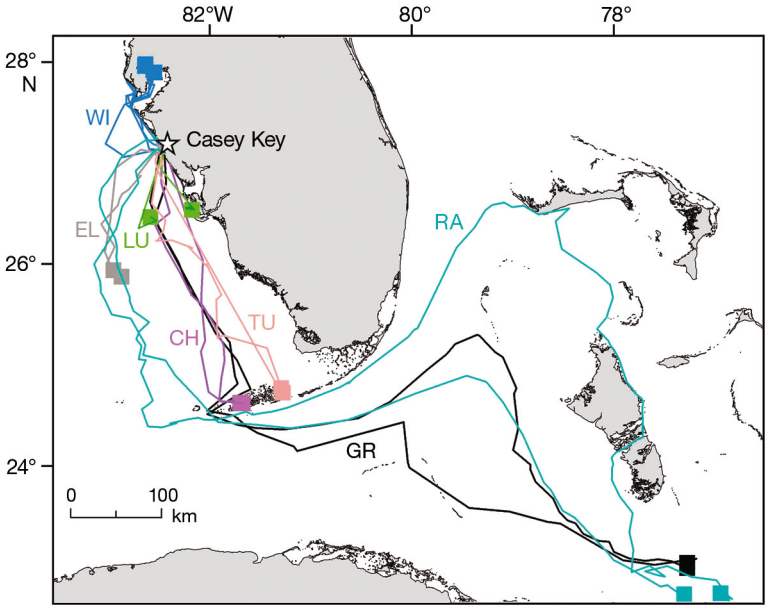

Fig. 3. Satellite-tracked post-nesting movements to foraging area termini of 7 loggerhead turtles that nested in Casey Key, Florida, and were tracked twice. Lines of the same color are tracks by the same turtle in different years

Table 2. Site fidelity of loggerhead turtles tracked on multiple occasions before, during, and after the isotope study (2006 to 2011). Distances between track termini (Dist.) were measured in GoogleEarth, and water depth was interpolated from GEBCO bathymetry in the program STAT

ID	Year	Latitude (°N)	Longitude (°W)	Dist. (km)	Depth (m)
CH	2007	24.650	81.719		1
CH	2009	24.646	81.725	0.61	1
EJ	2010	16.990	77.800		1
EJ	2012	17.025	77.775	4.76	1
EL	2009	25.954	82.988		44
EL	2011	25.879	83.056	10.45	51
GR	2007	23.037	77.249		1
GR	2010	22.975	77.214	7.79	1
LU	2007	26.467	82.588		23
LU	2010	26.553	82.170	42.57	1
MA	2010	25.318	81.857		14
MA	2013	25.324	81.857	29.14	15
RA	2006	22.643	76.866		1
RA	2009	22.752	76.897	12.5	1
TU	2006	24.775	81.294		1
TU	2010	24.775	81.311	1.73	1
VI	2005	29.923	88.012		31
VI	2012	30.032	88.017	12.12	20
WH	2009	24.260	77.057		1
WH	2011	24.726	77.004	54.74	1
WI	2007	27.934	82.609		1
WI	2008	27.971	82.640	5.14	1
WI	2009	27.972	82.652	1.18	1
WI	2011	27.966	82.647	0.83	1
SP	2004	24.900	80.817		1
SP	2011	24.907	80.823	0.98	1

tially by turtles retracked before or after the isotope study (Table 2). Turtle VI returned to a foraging residence in the northern Gulf of Mexico, Turtle EJ returned southward to Jamaica and Turtle MA on the West Florida Shelf completed a track spanning 1200 d of continuous tracking with 2 post-reproductive migrations to the same foraging grounds. Further support of foraging ground fidelity came from independent researchers (B. A. Schroeder & A. M. Foley unpubl. data) who documented Turtle SP in 2004 on its foraging ground in the Florida Keys (24.900° N, 80.817° W). In 2011, we tracked Turtle SP after nesting on Casey Key to a migration terminus at 24.907° N, 80.823° W located 1 km from the 2004 foraging site. The tracking history yielded additional data on foraging ground fidelity but added only one biopsy sample to the isotope study. Site fidelity averaged for all animals listed in Table 2 was 13.2 km (n = 14, range: 0.6 to 54.7 km).

Stable isotope analysis and regional differences

The stable isotope ratios at the foraging grounds for $\delta^{13}C$ ranged from –21.16 to –7.69‰, for $\delta^{15}N$ from 3.27 to 13.99‰, and for $\delta^{34}S$ from 1.91 to 20.64‰. When comparing bulk skin tissue stable isotope values for all turtles by bioregion, year, body size, depth of putative foraging area, and linear distance from the closest shore, only bioregion showed a significant effect (Table 3). Isotopes were normally distributed when examined at the regional scale (Fig. 4), with the exception of $\delta^{15}N$ values in the West Florida Shelf. However, GLMs have been shown to be robust to departures from normality (Jacqmin-Gadda et al. 2007). In addition, mean $\delta^{15}N$ values from the West Florida Shelf approached normality when random-

Table 3. General Linear Model output for testing variables of region, year, curved carapace length (CCL), foraging depth, and distance from shore

Factor	$\delta^{13}C$		$\delta^{14}N$		$\delta^{34}S$	
	F	p	*F*	p	*F*	p
Region	5.430	<0.001	4.340	0.003	4.021	0.005
Year	0.879	0.499	0.412	0.839	0.919	0.473
CCL	0.517	0.474	0.890	0.348	0.061	0.805
Depth	0.015	0.903	0.137	0.712	2.217	0.141
Distance	0.115	0.735	0.725	0.397	0.683	0.411

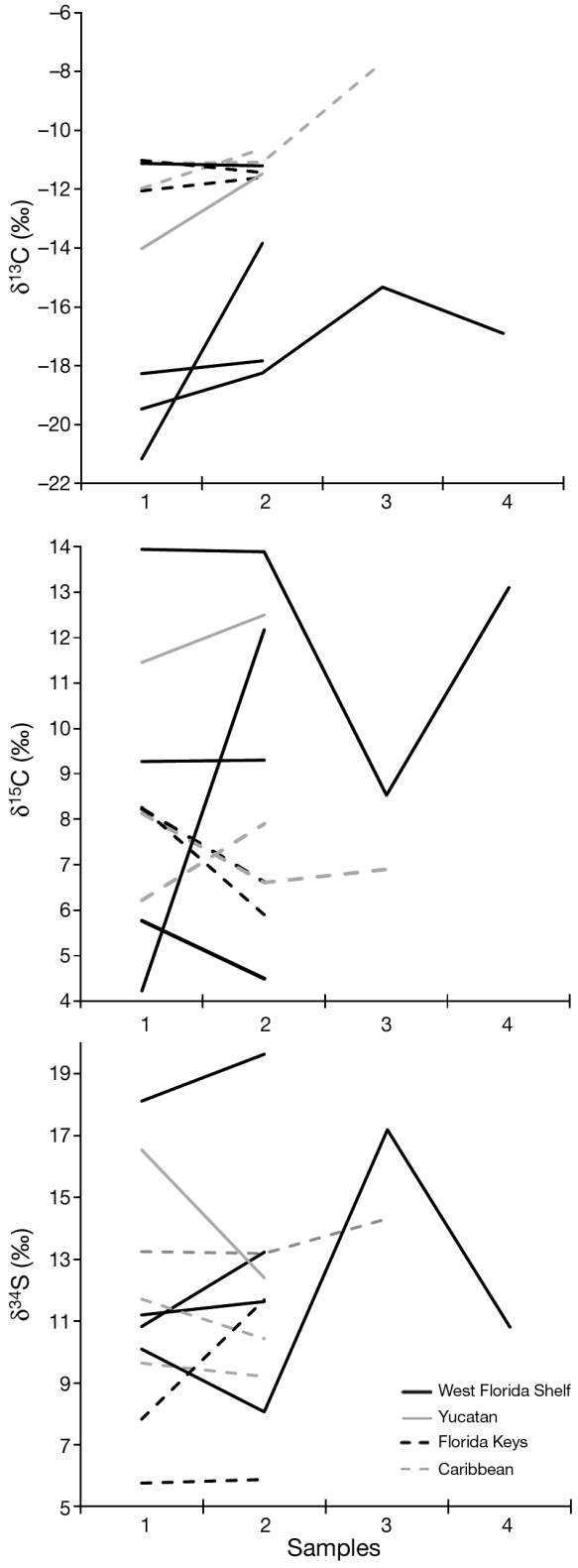

Fig. 4. Stable carbon, nitrogen, and sulfur isotopic ratios derived from up to 4 serial samples of 9 loggerhead turtles resident at bioregional foraging grounds in different years. No serial samples were available from the northern Gulf of Mexico bioregion

ization tests were conducted, as suggested by the Central Limit Theorem.

Regional differences were found for all 3 isotopes (Table 4). For $\delta^{13}C$, samples from the Caribbean were different from both the Yucatan Peninsula samples and the West Florida Shelf samples. The Caribbean samples were different (though not statistically significantly) from the northern Gulf of Mexico samples ($p = 0.077$) but not different from the Florida Keys samples, defining a $\delta^{13}C$ transitional isotopic boundary between the West Florida Shelf and the Florida Keys. For $\delta^{15}N$, the Florida Keys and the Caribbean together were different from the Yucatan Peninsula and very nearly different from the northern Gulf of Mexico ($p = 0.060$ and $p = 0.091$, respectively), again suggestive of a transitional isotopic gradient along the southern-most West Florida Shelf. For $\delta^{34}S$, the Florida Keys were different from the West Florida Shelf and the northern Gulf of Mexico; however, the Caribbean was similar to all study regions.

Loggerheads tracked on multiple occasions

Seven of the nine female loggerheads sampled and tracked in multiple years returned to the same foraging grounds on each tracking occasion (Fig. 3). These serially sampled turtles were tracked to all bioregions except the northern Gulf of Mexico. For 2 individuals with premature transmitter failures (Turtles MI and TH), the same foraging grounds were apparently targeted during sequential post-nesting migrations despite the turtles having to traverse shifting boundaries of the Loop Current or the Gulf Stream. All turtles that reached putative foraging areas in successive migrations showed a high degree of site fidelity (Fig. 3). However, 22% (2/9) of the turtles tracked on >1 occasion to the West Florida Shelf showed isotopic variation in their skin tissue across years (Fig. 5). Turtle LU shifted foraging grounds from 23 m depth at 35 km offshore to 1 m depth at 1 km offshore with a concomitant increase in $\delta^{13}C$, a decrease in $\delta^{15}N$, but negligible change in $\delta^{34}S$. Isotope variation was also seen for Turtle WI, tracked 4 times to Tampa Bay in 2007, 2008, 2009, and 2011, with all locations at 1 m depth and 1 to 4 km from shore. The stable isotope ratios of Turtle WI were consistent for all years but 2009, when skin tissue showed an increase in $\delta^{13}C$ and $\delta^{34}S$, and a decrease in $\delta^{15}N$. These changes coincided with intense harmful algal blooms of *Pyrodinium bahamense* in Tampa Bay during the summers of 2008 and 2009 (Karlen &

Table 4. Post hoc Tukey's pairwise comparisons of General Linear Model output structure for stable isotope values of 88 loggerhead turtles with foraging areas in 5 regions throughout the wider Gulf of Mexico: Caribbean (CAR), Florida Keys (FLK), West Florida Shelf (WFS), northern Gulf of Mexico (NGM), and Yucatan (YUC). *Statistically different at alpha = 0.05

	$\delta^{13}C$					$\delta^{15}N$					$\delta^{34}S$				
	YUC	NGM	WFS	FLK	CAR	YUC	NGM	WFS	FLK	CAR	YUC	NGM	WFS	FLK	CAR
YUC	–	0.824	0.673	0.832	0.037*	–	0.960	0.181	0.035*	0.010*	–	0.159	0.730	0.540	0.991
NGM	–	–	0.988	0.396	0.077	–	–	0.338	0.060	0.091	–	–	0.336	0.012*	0.156
WFS	–	–	–	0.103	0.001*	–	–	–	0.294	0.310	–	–	–	0.025*	0.593
FLK	–	–	–	–	0.573	–	–	–	–	0.999	–	–	–	–	0.810

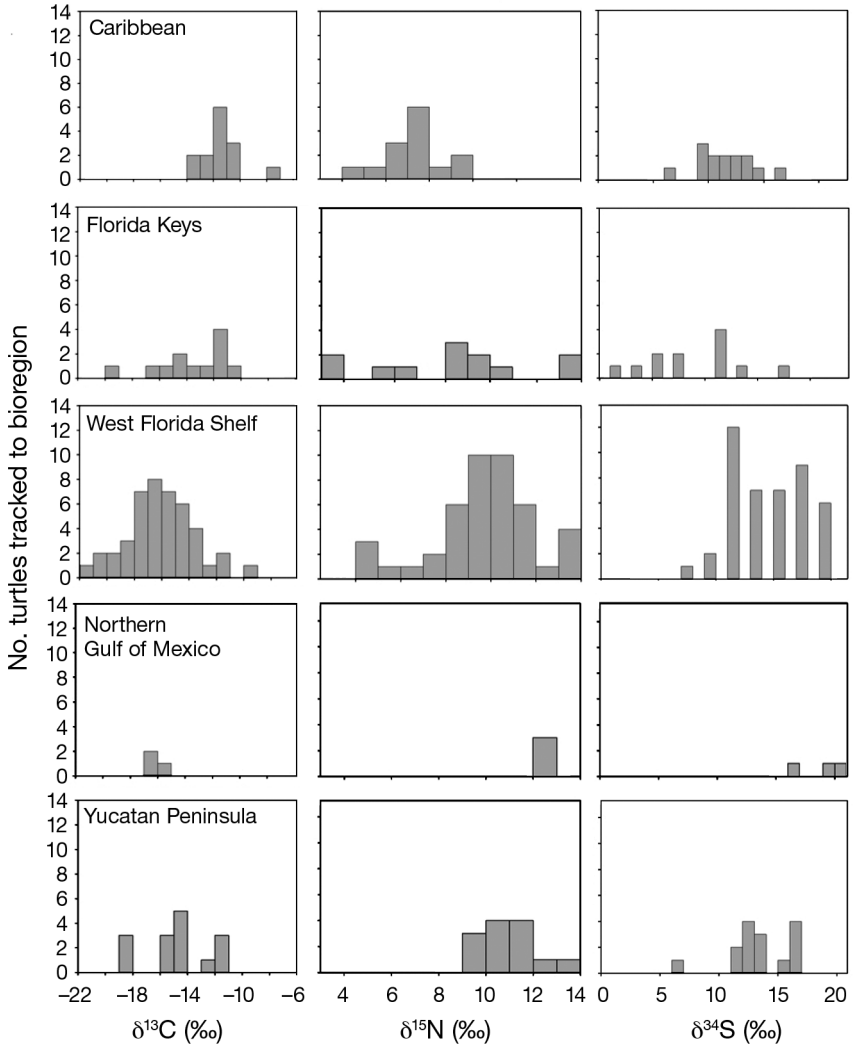

Fig. 5. Distributions of stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) among loggerhead turtles *Caretta caretta* tracked to 5 putative foraging regions throughout the wider Gulf of Mexico

Miller 2011). For both turtles, the sampling years that yielded anomalous isotope results were excluded from paired *t*-tests of the serial isotopic values. A paired *t*-test on serial isotope measurements of individuals indicated variation in $\delta^{13}C$ values ($t_8 = -2.33$, $p = 0.05$), but not for $\delta^{15}N$ ($t_9 = 1.13$, $p = 0.29$), or $\delta^{34}S$ ($t_{11} = -0.46$, $p = 0.65$).

DISCUSSION

The Gulf of Mexico is strongly influenced by the dynamics of the Loop Current (Girard et al. 2009) with variable upwelling that affects productivity in nearshore habitats throughout the region (Hu et al. 2011, Kourafalou & Kang 2012, Zheng & Weisberg 2012). While these factors challenge our ability to use sea turtles as indicators of isotopic profiles at multiple spatial scales, our results are fortified by the large sample size and multiple tracking of individual turtles over the course of 5 yr. The satellite tracking and tissue sampling of sea turtles in this study provide another example of the value of an integrated approach to study spatial patterns of stable isotope values in marine systems.

For highly migratory species to serve as reliable ocean samplers, tissue turnover rate should be understood in the context of the temporal scale of migration. For instance, if animals move through habitats faster than they can acquire signals, then those habitats will be underrepresented in SIA. The relatively slow isotopic turnover rates (from 4 to 8 mo; Seminoff et al. 2007, 2009, 2012, Reich et al. 2008, Vander Zanden et al. 2013) for sea turtle skin — the tissue used in this study — suggests that those foraging areas in which turtles resided for extended durations were reflected most prominently in isotope values presented here. It is also possible

that these values are the integration of stable isotope values from multiple foraging habitats resided within for shorter periods (i.e. weeks); however, current knowledge of loggerhead movements during non-reproductive periods offers little support for this possibility (Hart et al. 2012).

Our results reinforced that foraging area fidelity is exhibited by individual adult females over multiple nesting seasons (Broderick et al. 2005, Marcovaldi et al. 2010, Seminoff et al. 2012). The serial satellite tracks of individual turtles had similar tracking termini (Fig. 3), and the associated serial isotope values of these turtles were consistent between sampling events for a majority (78%, 7/9) of females.

The substantial shifts in isotope values (in 22% or 2/9 turtles) suggest that, at least for some animals, stable isotopes alone are not sufficient for assigning spatial associations in the Gulf of Mexico and Wider Caribbean region. The reasons for isotopic fluctuation for these 2 turtles are unclear, but likely relate to (1) differences in foraging habitat(s) occupied prior to each tracking season, (2) shifts in trophic status for the turtles during these years, and/or (3) changes to local baseline isotope values within a turtle's foraging habitat.

Lack of fidelity to the putative foraging areas inferred from satellite tracking is one possible reason for the inconsistencies in stable isotope values within serially tracked turtles. Perhaps some turtles transitioned among various foraging areas between the initially accessed site and the area resided in prior to commencing nesting migrations. For example, loggerhead turtles in temperate areas may move between seasonal foraging grounds or water depths prompted by changes in sea surface temperature (Hawkes et al. 2007, Ceriani et al. 2012). However, our study included turtles from tropical latitudes that had no abrupt sea surface temperature gradients that prompted seasonal movements. Interestingly, however, the turtles with the greatest differences in bulk skin isotope values across years were largely from the West Florida Shelf region, which is the northernmost region for which we have serial tracking and isotope information, and thus the most temperate region of the study area. Thus, isotope tracers may prove more reliable for loggerhead turtles residing year-round in the more southerly, thermally stable subtropical regions, rather than the temperate zones where seasonal shuttling exists (Hawkes et al. 2007, Pajuelo et al. 2012b).

The within-individual differences in stable isotope values may also result from changes in diet intake over the course of this study. Loggerhead turtles are opportunistic consumers (Parker et al. 2005, Reich et al. 2010), and the broad scope of foods they consume can encompass at least 2 full trophic levels (Wallace et al. 2009). Polymodal foraging has been inferred from previous stable isotope studies of loggerheads (McClellan et al. 2010, Reich et al. 2010, Vander Zanden et al. 2010). Thus, depending on the year and oceanographic conditions, turtles may consume largely different diets or perhaps the same foods but at different proportions. Nevertheless, isotopic studies examining keratin biopsies of loggerhead turtles nesting in eastern Florida have shown that a large proportion of individuals can maintain a consistent mixture of prey, habitat, and geographic location through time (Vander Zanden et al. 2010), suggesting that isotope shifts between subsequent years may not always be due to shifts in diet composition.

Inter-annual variability in the community composition and net primary productivity may also cause inter-annual variability in isotopic signatures in skin samples, even for turtles that reside within the same habitat over multiple foraging seasons. Fluctuations in isotope baseline values are found in coastal current systems such as the $\delta^{15}N$ in the California Current Large Marine Ecosystem along the US West Coast (Décima et al. 2013) or even adjacent current eddies of the Leeuwin Current of Western Australia (Waite et al. 2007). Indeed, inconsistency in N cycling in the Gulf of Mexico and Wider Caribbean region likely influences the $\delta^{15}N$ values in the skin of sea turtles occupying areas within different N cycling (Seminoff et al. 2012). Further, previous isotopic studies of loggerhead turtles, such as with western Atlantic males (Pajuelo et al. 2012a) and adult females in the Mid- and South Atlantic Bights (Ceriani et al. 2012), have documented large variations in $\delta^{13}C$ and $\delta^{15}N$. These variations were explained by differences in food web baselines, rather than by differences in the loggerhead trophic levels (Pajuelo et al. 2012a).

Spatial stable isotope patterns

Although the extent of regional differences varied among stable isotopes, the results implied that the Caribbean and Florida Keys regions appear to be similar to each other for $\delta^{13}C$ and $\delta^{15}N$ isotopes, but distinct from adjacent regions. The areas north of the Florida Keys and within the Gulf of Mexico were more homogenous in their stable isotope profiles. Some of these marginal differences may become better delineated after future samples are augmented

that might better characterize bioregional patterns of isotope variation.

A key finding in the present study was a difference in isotopic values across the Gulf of Mexico and into the eastern Caribbean. These bioregional isotopic signatures may be aligned in part by foraging grounds north (largely temperate) or south (largely tropical) of the Loop Current. Given this current's frequent changes of extent and direction, it would be inaccurate to categorize the isotopic variation as a simple latitudinal distribution (Sturges & Lugo-Fernandez 2005). The marine systems near Loop Current boundaries may be subjected to high isotopic variability and thereby pose a resolution limit for using isotopes to assign turtles to biogeographic regions at spatial scales finer than <100 km.

Aside from shifting boundaries of the Loop Current, there were minimal differences in stable isotope values among the sub-regions included in this study, a finding that is consistent with recent isoscape mapping efforts for the area (McMahon et al. 2013). To better understand the isotopic differences among bioregions, we encourage additional empirical diet studies and baseline isotopic sampling. In principle, compound specific stable isotope analysis (CSIA) of individual amino acids should determine why some individual turtles showed considerable isotopic variability between years and a large range of $\delta^{15}N$ values that spanned 3 trophic levels, or whether specific oceanographic areas within the Gulf of Mexico present a remarkable case of isotopic variation that needs to be more fully evaluated (Macko et al. 1984, Mulholland et al. 2006).

This study with loggerhead turtles is one of the first broad spatial scale surveys of stable sulfur isotopic patterns within the Gulf of Mexico. We found a surprisingly large range in $\delta^{34}S$ (1.91 to 20.64 ‰), perhaps owing to the gradient of near to offshore habitats that presumably varied in baseline $\delta^{34}S$. Given the long residence time of sulfur in the marine environment (2×10^7 yr), the marine sulfate isotope value is typically quite consistent at 21‰, as is marine phytoplankton given the minimum fractionation associated with sulfate assimilation. Marsh plants in anoxic environments, on the other hand, typically use sulfides with much lower $\delta^{34}S$ values (6 to 7‰). However, even this range did not fully encompass the nearly 20‰ range found in Gulf of Mexico loggerhead samples. We found higher $\delta^{34}S$ values in turtles whose satellite tracks ended in more offshore areas (Fig. 4), yet inshore habitats used by Gulf of Mexico dolphins are more sulfur isotope enriched than offshore habitats (Barros et al. 2010). We did not investigate if the high mixing and lack of deep-water habitat in the eastern Gulf of Mexico and Wider Caribbean region mask a sulfur isotope gradient evident in diets of coastal seabirds (Lott et al. 2003) and dolphins (Barros et al. 2010).

Future directions and conclusions

Results from isotopic studies of sea turtles have evolved beyond the early theme of 'you are what you eat' into a more contemporary view regarding site specialists and diet generalists (Reich et al. 2010, Thomson et al. 2012, Allen et al. 2013). Agglomerating separate studies such as those mentioned above will become increasingly vital to synthesize a more comprehensive framework of isoscapes when marine organisms are considered as sample devices (Hobson & Wassenaar 2008). Dietary isotope studies with migratory animals may present that subjects are unequally available and necessarily sampled at a time or place convenient to the researcher. A working assumption is that bulk isotope values determined from tissue are reflective of a previous foraging regime. However, an essential caveat is that actual baseline samples from a foraging area should be analyzed for comparison with animal tissues (Phillips et al. 2009). Otherwise, bulk isotopic values from skin tissue cannot accurately indicate foraging areas and the isoscape definition is called into question. Stable isotope values must be consistently different for sea turtles from oceanic versus neritic habitats (Reich et al. 2007, Snover et al. 2010) in order to offer credence to the use of bulk stable isotopes for inferring post-nesting migratory destinations. Our study found that isotope values (pre-nesting habitat) and satellite tracks (post-nesting habitats) did not always match. We determined that loggerhead turtles exhibited foraging site fidelity between subsequent nesting migrations, but also that there were limits to the applicability of isotopes for inferring habitat use. The present study presented novel insights on spatial limitations (i.e. fine spatial scale of <100 km) with isotopic applications in loggerhead turtles for the Gulf of Mexico through its empirical identification of foraging areas.

Two questions remain to be addressed in future studies: whether isotopic variability was influenced more by isotopic flux (an oceanographic effect on productivity and the baseline conditions; Saba et al. 2008a,b) or through flexibility of dietary choice (Seminoff et al. 2008, Reich et al. 2010, Vander Zanden et al. 2010). The present study identified bio-

regions within the Gulf of Mexico for future investigations of nutrient cycling gradients, productivity gradients, upwelling zones, hypoxic conditions, or other factors that may be affecting turtle isotope values (Macko et al. 1984). Future studies using compound specific stable isotope analysis (CSIA) should be able to discriminate more accurately between source or trophic amino acids to provide an internally indexed and normalized indicator of isotopic variability (Graham et al. 2010, McMahon et al. 2010). For example, comparisons by bulk SIA against CSIA showed that individuals in a nesting population of green turtles with different bulk $\delta^{15}N$ values fed at the same trophic position (Vander Zanden et al. 2013). Thus, the combined techniques should also be capable of evaluating if source and trophic isotopic variations within individuals are also operating in loggerhead turtles.

In coarse scale (>100 km) contrasts across regions of less oceanographic complexity (shallower depths and coastal proximity) and where the isotope-telemetry match is consistent among individuals, SIA may offer a complementary approach to satellite telemetry, even though the 2 methodologies address questions at different temporal and spatial scales. The possibility of reliable isotopic mapping may apply for temperate oceanographic realms such as the Mid- and South Atlantic Bights (Pajuelo et al. 2010, 2012a, Ceriani et al. 2012) or where a foraging dichotomy of pelagic and neritic individuals exists (Hawkes et al. 2006), but should be verified by concurrent satellite tracking of sampled individuals. Future studies based on tissue samples alone would offer isotopic values as a coarse scale predictor of spatial residence in lieu of the more expensive satellite tracking methods.

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