

Biomarkers reveal sea turtles remained in oiled areas following the *Deepwater Horizon* oil spill

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Abstract. Assessments of large-scale disasters, such as the *Deepwater Horizon* oil spill, are problematic because while measurements of post-disturbance conditions are common, measurements of pre-disturbance baselines are only rarely available. Without adequate observations of pre-disaster organismal and environmental conditions, it is impossible to assess the impact of such catastrophes on animal populations and ecological communities. Here, we use long-term biological tissue records to provide pre-disaster data for a vulnerable marine organism. Keratin samples from the carapace of loggerhead sea turtles record the foraging history for up to 18 years, allowing us to evaluate the effect of the oil spill on sea turtle foraging patterns. Samples were collected from 76 satellite-tracked adult loggerheads in 2011 and 2012, approximately one to two years after the spill. Of the 10 individuals that foraged in areas exposed to surface oil, none demonstrated significant changes in foraging patterns post spill. The observed long-term fidelity to foraging sites indicates that loggerheads in the northern Gulf of Mexico likely remained in established foraging sites, regardless of the introduction of oil and chemical dispersants. More research is needed to address potential long-term health consequences to turtles in this region. Mobile marine organisms present challenges for researchers to monitor effects of environmental disasters, both spatially and temporally. We demonstrate that biological tissues can reveal long-term histories of animal behavior and provide critical pre-disaster baselines following an anthropogenic disturbance or natural disaster.

Key words: *Caretta caretta*; *Deepwater Horizon*; *Gulf of Mexico*; loggerhead; oil spill; petroleum hydrocarbons; resource use; stable isotopes.

INTRODUCTION

In 1989, the Exxon Valdez grounded in Prince William Sound, Alaska, USA, and released approximately 0.26 million barrels of crude oil into the surrounding ecosystem (Wolfe et al. 1994). At the time, it was the largest oil spill in U.S. history, and assessments of environmental recovery efforts after the event were stymied by inadequate pre-disaster baseline data (Paine et al. 1996). In their review of lessons from the Exxon Valdez oil spill, Paine et al. (1996) highlighted the need for better baseline data and suggested that future studies focus on long-lived species and organisms that preserve chronological records of growth. Yet over two decades later, when the *Deepwater Horizon* (DWH) explosion released 4.4–4.9

million barrels of oil into the Gulf of Mexico (GoM; Crone and Tolstoy 2010, Lubchenco et al. 2012), clearly a vulnerable area, efforts to assess the effects of the oil spill and to implement a plan for environmental recovery were obstructed by a similar scarcity of data (Bjorndal et al. 2011, Graham et al. 2011).

We use a novel application of biomarkers in inert tissue to provide a pre-disaster baseline dataset to evaluate the impacts of the DWH oil spill on a vulnerable marine organism. Long-lived sea turtles store chronological histories in scute, or the keratinized tissue that covers the bony plates of the carapace. A sequential long-term record can be obtained from this tissue, as biomarkers incorporated into the scute reflect resource use and foraging patterns at the time of synthesis. In previous studies, these inert records have been useful for examining diet and migration patterns for periods of up to a decade in healthy populations of sea turtles (Reich

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et al. 2007, Vander Zanden et al. 2010, 2013b), and we use stable isotope analysis of scute from adult loggerhead sea turtles (*Caretta caretta*) to evaluate responses to the oiling of their foraging grounds. More specifically, we examine whether loggerheads moved away from oiled areas after the DWH oil spill or if they remained, thus increasing their potential for exposure to negative effects. This approach could be applied to other marine species with inert tissues, such as whale baleen, pinniped whiskers, shark vertebrae, fish otoliths, squid gladii, and bivalve shells (Schell et al. 1989, Campana and Thorrold 2001, Cherel et al. 2009, Newsome et al. 2009, Lorrain et al. 2011, Carmichael et al. 2012, Kernaléguen et al. 2012, Kim et al. 2012, Nelson et al. 2015).

Following the DWH oil spill, approximately 75% of the oil released from the damaged well remained in the environment, while 25% was removed through burning, skimming, or recovered directly (Kerr 2010). Buoyant oil traveled up the water column and formed surface slicks covering over 112,000 km² cumulatively, with the maximum extent on a single day reaching nearly 40,000 km² (Environmental Response Management Application 2014). More than 1,600 km of the GoM shoreline was visibly oiled, particularly along the coasts of Louisiana, Mississippi, Alabama, and western Florida (Barron 2012). It is estimated that as much as half of all the hydrocarbons released remained in the water column (Barron 2012), and a continuous plume of subsurface oil stretching to the southwest of the well at least 35 km in length persisted for months without substantial biodegradation (Camilli et al. 2010). Oil-derived carbon was transferred into the planktonic food web and higher trophic level mesopelagic shrimp and fish (Graham et al. 2010b, Mitra et al. 2012, Quintana-Rizzo et al. 2015), and observations of wildlife with external oiling included birds, sea turtles, and mammals (Barron 2012).

Little is known about the toxicity of oil to sea turtles, as experimental exposure studies are restricted for all sea turtle species under the 1973 U.S. Endangered Species Act. Sea turtles are vulnerable to oil at all life stages, and there are a number of ways in which sea turtles can be exposed to chemicals in oil or dispersants. For example, sea turtles must continually come to the surface to breathe, which can cause physical exposure to surface oil, dispersants, and inhalation of vapors (Milton et al. 2003). Oil that remained in the water column or settled to the benthos may be ingested through contaminated water or prey. For juvenile sea turtles, floating *Sargassum* algae is an important habitat for both protection and food, and up to 23% of this habitat was estimated to have been lost as a result of oil exposure (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). Eggs and hatchlings are also vulnerable to oil exposure at nesting beaches where oil reached the shoreline.

The only laboratory trial investigating the direct impact of oil on sea turtles demonstrated a lack of oil avoidance behavior by juvenile loggerhead turtles (Lutcavage et al. 1995). Trials using freshwater turtles as a surrogate for

sea turtles found oxidative and DNA damage in addition to decreased digestive function and assimilation of nutrients when two freshwater turtle species were exposed to DWH oil (Mitchellmore and Rowe 2015). Among all exposure pathways observed, veterinarians and sea turtle biologists concluded that the most acute physical and physiological adverse effects to sea turtles following the DWH oil spill resulted from direct contact with surface oil, and the probability of death increased with degree of oiling (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). Of the 536 sea turtles recovered live from the slick following the DWH oil spill, 85% were visibly oiled (Natural Resource Damage Assessment 2012). Whereas the majority of these individuals was rehabilitated and released, it was estimated that between 4,900 and 7,600 large juveniles and adult loggerhead and Kemp's ridley (*Lepidochelys kempii*) sea turtles (including up to 3,600 loggerheads) using continental shelf waters and between 55,000 and 160,000 small juvenile loggerhead, Kemp's ridley, green (*Chelonia mydas*), and hawksbill (*Eretmochelys imbricata*) sea turtles using open ocean habitats were killed by the DWH oil spill in the GoM (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016).

Given the strong site fidelity to foraging areas that has been observed in large juveniles and adults (Broderick et al. 2007, Marcovaldi et al. 2010, Schofield et al. 2010, Hawkes et al. 2011), it is possible that sea turtles may have remained at polluted or degraded habitats despite potential sub-lethal effects. For example, green turtles have persisted at foraging grounds long after the quality and/or quantity of food resources decline instead of moving to available, higher quality foraging grounds nearby (Williams 1988, Fourqurean et al. 2010, Christianen et al. 2014). While nesting female loggerheads make regular migrations between nesting and foraging areas, site fidelity has been observed for both endpoints of these migratory movements. Within the GoM and Caribbean, loggerheads that were satellite tracked on multiple occasions from the same nesting beach in Florida returned to foraging sites within 13.2 km, on average, from their first tracking event (Tucker et al. 2014). Adult loggerheads have been documented to use waters less than 200 m depth across the GoM, and within a foraging site, core-use areas are generally limited, ranging from 5 to 852 km² in this region (Hart et al. 2012, 2014, Tucker et al. 2014, Lamont et al. 2015).

Loggerheads are known to feed on a diversity of benthic invertebrates at the population level (Dodd 1988, Bjorndal 1997). Despite site-specialization, loggerheads may be diet generalists at an individual level (Thomson et al. 2012), though high site affinity may limit prey available in spatially restricted core-use areas. Diet elasticity has been demonstrated in loggerheads when abrupt changes in prey abundance resulted in diet shifts (Seney and Musick 2007), and thus it is also possible that loggerheads may remain at foraging areas even when prey availability changes.

The Natural Resource Damage Assessment (NRDA) seeks to restore injured resources and services to baseline conditions, which is defined as the conditions that would have existed had the spill not occurred. The NRDA Status Update Report for the DWH oil spill outlined activities planned to assess the injury to the GoM ecosystem, including an assessment plan for sea turtles (Natural Resource Damage Assessment 2012). However, the plan only identified nesting survey data from Texas, Alabama, and Florida as a source of baseline data without including in-water habitats or other life stages (likely because the data would have been insufficient; Natural Resource Damage Assessment 2012). Given the vulnerability of sea turtles to oil at all life stages and limited baseline data regarding foraging populations in this region, we sought to examine whether the DWH oil spill affected loggerhead sea turtle foraging patterns.

To answer this question, we first examined the carbon and nitrogen stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values in scute records from 76 adult loggerheads foraging in the GoM to determine if they maintained consistent foraging patterns over time, similar to those of sea turtles in other regions outside the GoM that have been measured previously (Vander Zanden et al. 2010). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in consumer tissue are assimilated through the diet, and thus reflect the trophic ecology of organisms, as well as other baseline processes that vary with geographic location, making them useful indicators of geographic origin in the marine environment (Graham et al. 2010a, Hobson et al. 2010, McMahon et al. 2013, Vander Zanden et al. 2013a, 2015). Confirming the presence of these consistent isotopic patterns would allow us to interpret changes observed in turtles that were likely exposed to surface oil. Second, we examined the isotopic records in a subset of the loggerheads ($n = 10$) that used oiled areas in the northern GoM (NGoM) to detect whether sea turtles remained in their foraging locations with a consistent diet following the oil spill.

METHODS

Sample collection

Scute samples were collected from 76 nesting females at six nesting beaches along the Gulf Coast in 2011 and 2012: Gulf Shores, Alabama (GS), Eglin Air Force Base, Florida (EAFB), Saint Joseph Peninsula, Florida (SJP), Casey Key, Florida (CK), Keewaydin Island, Florida (KI), and Dry Tortugas, Florida (DRTO; Fig. 1, Table 1). Samples were taken from the posterior medial region of the third right lateral scute with a sterile 6-mm biopsy punch. Prior to sampling, the carapace was cleaned with isopropyl alcohol. The scute sampling process is non-invasive, and repeated scute sampling does not significantly affect the health or physiological condition of loggerheads (Bjorndal et al. 2010).

All of the individuals were satellite tracked and classified to one of five discrete foraging areas (Fig. 1).

Described in Appendix S1, these areas are consistent with regional divisions used previously (Vander Zanden et al. 2015) and included sites known to contain surface oil following the DWH oil spill (Environmental Response Management Application 2014). Satellite transmitters were attached to nesting females after oviposition and after scute sampling; the transmitter was not placed over the sampling site. The foraging location was determined as the centroid of the post-nesting home range based on satellite tracking data, though foraging centroids were not available for nine of the females because transmission ceased before the foraging area was reached. Fifty-nine of these centroids have been part of previous publications (Hart et al. 2014, 2015, Tucker et al. 2014, Vander Zanden et al. 2015). A complete list of the centroids (Appendix S1: Table S1) and additional details on sample preparation and foraging area determination are included in Appendix S1.

The majority of the samples ($n = 49$) was air dried prior to storage, while 22 were stored in 70% ethanol and five were frozen at -10°C prior to processing. The use of a frost-free freezer was avoided in storing frozen samples. These methods of preservation (70% ethanol and freezing) do not significantly alter the stable isotope values of loggerhead skin and therefore were not expected to alter the isotopic values of scute (Barrow et al. 2008).

Scute preparation and stable isotope analysis

All scute samples were rinsed with deionized water and dried at 60°C for 24 h in the laboratory prior to lipid extraction (see Appendix S1) and analysis. Each scute biopsy was glued ventral side down with the dorsal surface (oldest tissue) exposed, and 50- μm layers were obtained using a carbide end mill with digital readout (Sherline 5100, Vista, CA). This interval was selected as the smallest interval that would provide sufficient sample mass for stable isotope analysis and represents approximately 0.6 yr or 219 d of resource use in adult loggerhead turtles (Vander Zanden et al. 2010). We estimated dates associated with each layer by using this time interval to calculate backward from the collection date. In some cases, a single layer did not provide sufficient mass for stable isotope analysis, such that successive layers were combined. Sample collection dates spread across two summers and the occasional merging of successive layers resulted in incremental records that do not align across all individuals, but rather, represent the longest history possible from each individual. Complete isotopic records are available in Supplement Data S1.

Carbon and nitrogen isotope composition in each sample ($n = 1,202$ layers) was measured at the Department of Geological Sciences, University of Florida, Gainesville, Florida, USA, using a Carlo Erba NA 1500 CNS elemental analyzer (Thermo Scientific, Waltham, Massachusetts, USA) interfaced via a ConFlo II to a DeltaV Advantage isotope ratio mass spectrometer (Thermo Electron, Waltham, Massachusetts, USA).

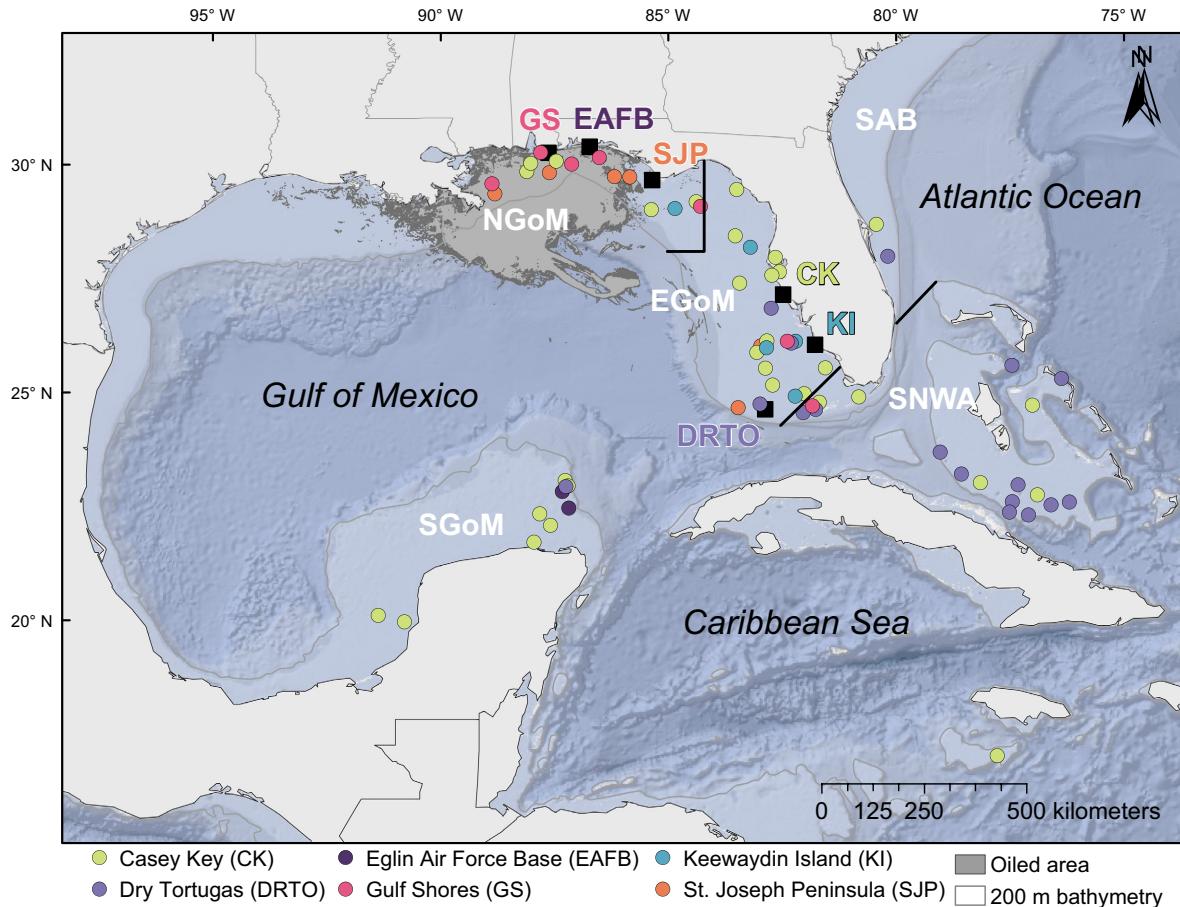


FIG. 1. Foraging locations were based on satellite tracking data for 67 of the 76 loggerheads included in this study and were classified to one of five discrete foraging areas. Foraging centroids were not available for nine of the females. Nesting beaches are indicated by black squares and foraging centroids are colored according to the nesting beach from which females were tracked. The gray area in the NGoM represents the oil footprint of surface oiling following the Deepwater Horizon oil spill (Environmental Response Management Application 2014). Abbreviations are NGoM, Northern Gulf of Mexico; EGoM, Eastern Gulf of Mexico; SGoM, Southern Gulf of Mexico; SNWA, Subtropical Northwest Atlantic; and SAB, South Atlantic Bight.

Sample stable isotope ratios relative to the isotope standard were expressed in the following conventional delta (δ) notation: $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$ with units per mil (‰) where R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) in the sample and international standard, respectively. Vienna Pee Dee Belemnite was used as the standard for ^{13}C and atmospheric N_2 for ^{15}N . The reference materials USGS40 (L-glutamic acid with isotopic compositions of $\delta^{13}\text{C} = -26.29\text{‰}$ and $\delta^{15}\text{N} = -4.52\text{‰}$) and USGS41 (L-glutamic acid enriched in ^{13}C and ^{15}N with isotopic compositions of $\delta^{13}\text{C} = 37.63\text{‰}$ and $\delta^{15}\text{N} = 47.57\text{‰}$) were used to calibrate all results. The standard deviation of USGS40 was 0.09‰ for $\delta^{13}\text{C}$ values and 0.14‰ for $\delta^{15}\text{N}$ values ($n = 188$), and the standard deviation of USGS41 was 0.25‰ for $\delta^{13}\text{C}$ values and 0.54‰ for $\delta^{15}\text{N}$ values ($n = 50$). Repeated measurements of a laboratory reference material, homogenized loggerhead scute collected from an individual at a different site, were used to examine consistency in a

sample with similar isotopic composition to samples in this study. The standard deviation of the laboratory reference material was 0.15‰ for $\delta^{13}\text{C}$ values and 0.22‰ for $\delta^{15}\text{N}$ values ($n = 57$).

Data analysis

Comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among the foraging areas were evaluated with MANOVA (Pillai's trace) and post hoc Tukey HSD methods. In the NGoM, only the turtles whose foraging centroids overlapped with the surface oil footprint were considered in these analyses ($n = 10$). In addition, the NGoM group was divided into pre- and post-oil-spill data points for the MANOVA, such that two data groups were evaluated from this region with one group for each of the remaining four regions. Repeated-measures ANOVA was used to examine $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values pre- and post-oil-spill in the ten loggerheads whose foraging centroids overlapped with the oiling footprint. Pre-oil-spill data was restricted

TABLE 1. Collection year, total number of samples, range in thickness, and time period represented in the scute samples collected from nesting loggerheads in the Gulf of Mexico during the sampling period.

Nesting beach	Year	Samples collected	Foraging centroid determined by satellite tracking	Scute thickness range (μm)	Time period (yr)
Gulf Shores, AL	2012	8	7†	350–850	4.2–10.2
Eglin Air Force Base, FL	2012	2	2‡	700–1,100	8.4–13.2
St. Joseph Peninsula, FL	2011	5	2§	750–800	9.0–9.6
	2012	8	4§	450–700	5.4–8.4
Casey Key, FL	2011	23	22¶	600–1,350	7.2–16.2
	2012	8	8¶	300–1,200	3.6–14.4
Keewaydin Island, FL	2012	5	5#	700–900	8.4–10.8
Dry Tortugas, FL	2012	17	17	700–1,500	8.4–18.0
All sites	2011–2012	76	67	300–1,500	3.6–18.0

Note: Not all individuals had satellite-tracking information that allowed a foraging centroid to be determined. Abbreviations are AL, Alabama and FL, Florida.

†Six centroids reported previously in Hart et al. (2014).

‡Two centroids reported previously in Hart et al. (2014).

§Five centroids reported previously in Hart et al. (2014).

¶Thirty centroids reported previously in Tucker et al. (2014).

#Five centroids reported previously in Vander Zanden et al. (2015).

||Eleven centroids reported previously in Hart et al. (2015).

to provide an equal number of layers to the post-oil-spill layers that were available for each individual. All layers from all females ($n = 76$) were used to evaluate consistency by comparing mean values within individuals to that of the whole population. All statistics were evaluated using R version 3.0.2 with $\alpha = 0.05$ (R Core Team 2013).

RESULTS

The thickness of the scute samples obtained from the 76 nesting loggerheads ranged from 300 to 1,500 μm , representing a total period of resource use history from 3.6 to 18.0 yr (Table 1). Foraging centroids were classified to one of five discrete foraging areas (Fig. 1), though sufficient data were not available to determine the foraging centroid of nine females. Tracking data indicated that the remaining 67 females used a range of foraging sites in waters <200 m depth, occupying all three of the foraging regions within the GoM, while 21 females migrated outside the GoM (Fig. 1). Ten females used foraging sites containing surface oil, and the pre- and post-oil-spill isotopic records from these individuals were used to examine how foraging patterns were affected by the spill.

The long-term scute isotopic records demonstrate a high degree of temporal consistency within all loggerheads in the study ($n = 76$ females) in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, irrespective of foraging area, indicating that loggerheads have high foraging site fidelity (Fig. 2). Substantially lower isotopic variation was observed within individuals (mean $\delta^{13}\text{C}$ range = 1.4‰, mean $\delta^{15}\text{N}$ range = 1.1‰) than across the population (total $\delta^{13}\text{C}$ range = 17.4‰, total $\delta^{15}\text{N}$ range = 14.0‰).

In order to conduct the following comparisons among foraging regions and within the surface oil footprint, we only included the satellite-tracked females with

foraging areas that overlapped the oil footprint within the NGoM group (Fig. 1). The isotopic data from the NGoM oil group was further subdivided into pre- and post-oil-spill points based on the time period represented in each layer. Differences in stable isotope values were related to the foraging area (Fig. 3), as MANOVA results indicated that there were significant differences among the six groups ($n = 62$ females) in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($F_{5,1006} = 340.4$, $P < 0.001$). However, post hoc tests demonstrated that pre- and post-oil isotopic data from turtles in the NGoM oiled area were not significantly different in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values. Repeated-measures ANOVA, restricted to equal sample sizes from each of the ten individuals pre- and post-oil-spill (1–3 points per turtle per time period), showed no significant changes in $\delta^{13}\text{C}$ values ($F_{1,9} = 3.58$, $P = 0.09$) or $\delta^{15}\text{N}$ values ($F_{1,9} = 2.455$, $P = 0.15$) after the oil spill (Fig. 4). We found no evidence of an isotopic change between the pre- and post-oil-spill scute records, which indicates that loggerhead foraging patterns did not change following the DWH oil spill.

DISCUSSION

Long-term site fidelity

The long-term isotopic records contained within loggerhead scute provided a pre-disaster baseline from which to assess potential effects of the DWH oil spill on sea turtle foraging patterns in the greater GoM. Across all individuals, the isotopic records were remarkably consistent pre- and post-oil-spill, indicating that loggerheads foraging in the GoM have high site fidelity to foraging sites, irrespective of the foraging area used. This pattern of consistency is similar to what has been observed in

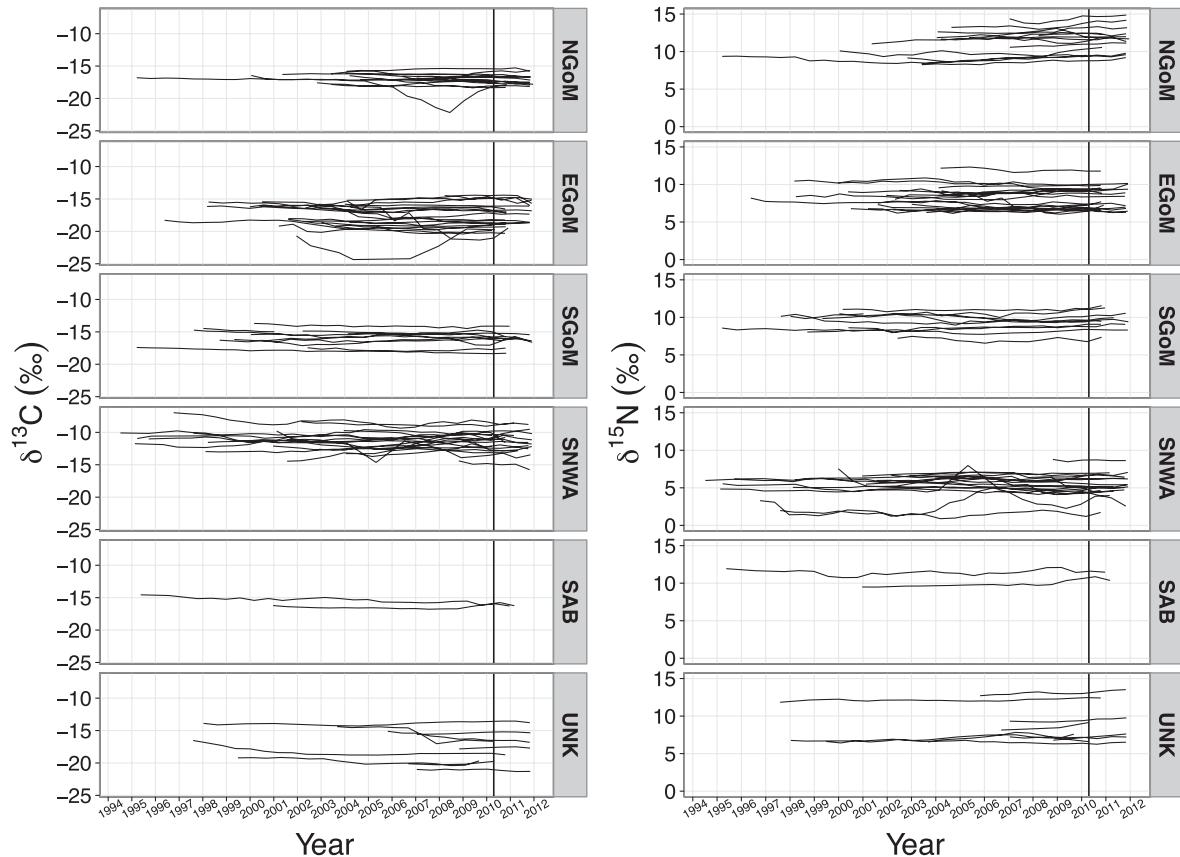


FIG. 2. Individual resource-use history for 76 loggerhead turtles indicated by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in sequential layers of scute, representing a period ~ 3.6 – 18.0 yr, depending on the original thickness of the scute sample (see *Methods* for estimations of time). Panels are divided by foraging area based on satellite tracking information. Samples were collected in 2011 and 2012; thus, the most recent layers do not all extend to 2012. The vertical line represents the date of the Deepwater Horizon oil spill on 20 April 2010. Abbreviations are NGoM, Northern Gulf of Mexico; EGoM, Eastern Gulf of Mexico; SGoM, Southern Gulf of Mexico; SNWA, Subtropical Northwest Atlantic; SAB, South Atlantic Bight; and UNK, no area was determined for nine individuals.

scute records obtained from loggerheads nesting on Florida's east coast (Vander Zanden et al. 2010) and for adult green turtles (*Chelonia mydas*) nesting in Costa Rica (Vander Zanden et al. 2013b).

The smaller isotopic range within individuals compared to the total isotopic range across the population is reflective of individuals partitioning the available resources or individual specialists in a generalized population (Vander Zanden et al. 2010). Whereas stable isotope values can reflect a combination of diet, habitat, and location, they appear to be a reliable indicator of loggerhead foraging area use in the GoM and greater Northwest Atlantic (Pajuelo et al. 2012, Ceriani et al. 2014, Tucker et al. 2014, Vander Zanden et al. 2015). Therefore, this partitioning of resources is a result of spatial patterns in the isotope values at the base of the food web, and each individual consistently uses a small portion of the potential suitable habitat. A high degree of foraging site fidelity in loggerhead turtles has previously been documented in the GoM and in other regions, mainly through satellite telemetry with repeated observations over seven years or less (Broderick et al. 2007,

Marcovaldi et al. 2010, Schofield et al. 2010, Hawkes et al. 2011, Tucker et al. 2014), and the isotopic data in this study demonstrate consistent foraging area use for nearly two decades.

Whereas the high degree of isotopic variability among individuals was mainly influenced by foraging site, we also observed smaller scale isotopic variation among individuals within the same foraging area (Fig. 2) that are likely related to inter-individual dietary differences. Investigations into the cause of variability in $\delta^{15}\text{N}$ values of loggerheads from various foraging aggregations in the Northwest Atlantic and Caribbean indicate that individuals within the same foraging area exhibit variability in diet and/or trophic level, which increases with greater resource diversity (Pajuelo M, Bjorndal KA, Arendt MD, Reich KJ, Schroeder B, Folley A, Witherington B, Lagueux CJ, Prescott R, Bolten AB, *unpublished data*). Therefore, individual loggerheads may partition the dietary niche within a foraging region, but the observed long-term isotopic consistency is likely a result of the combined effects of individuals maintaining consistency in dietary items and remaining at the same foraging site over time.

The individuals in the NGoM with foraging centroids overlapping the oil footprint did not demonstrate an isotopic shift after the oil spill and thus were likely exposed to any negative health consequences of the oil or chemical dispersants that were present. If an isotopic shift had been detected in loggerhead scute following the oil spill, it could have been a result of (1) dietary changes, including the consumption of different diet items, dietary shifts in lower trophic levels, or changes in isotopic composition of diet items as a result of incorporating of oil-derived carbon (Graham et al. 2010b, Quintana-Rizzo et al. 2015) or (2) locational changes if individuals moved out of the area to an isotopically distinct foraging area (Vander Zanden et al. 2015). A diet-related shift might be reflected in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values, while a locational shift would most likely be indicated by a change in the $\delta^{15}\text{N}$ values, which show greater isotopic separation among foraging areas (Fig. 3). For example, the mean difference between $\delta^{15}\text{N}$ values of turtles in the oiled area compared to the nearest foraging area in the eastern GoM is 4.1‰. In contrast to the turtles in this study, pre- and post-oil-spill $\delta^{13}\text{C}$ values of nesting female Kemp's ridleys (*Lepidochelys kempii*) were significantly different, perhaps because of indirect ingestion of oil via consumption of contaminated prey (Reich KJ, López-Castro MC, Shaver DJ, Iseton C, Hart KM, Hooper MJ, Schmitt CJ, unpublished data). Additionally, stranded juvenile Kemp's ridleys had decreased fat stores after 2010, indicating a decline in nutritional status, potentially due to reduced prey availability or quality (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). In this study, foraging patterns do not appear to have changed for loggerheads using foraging sites within the region of the surface oil slick.

Potential exposure and toxicity

The observed isotopic consistency among records of loggerheads using the NGoM pre- and post-oil-spill indicates that these individuals continued consuming a similar diet and remained at the same foraging sites. Therefore, loggerheads demonstrated a lack of avoidance behavior with respect to potential oil exposure, as has been observed in experimental trials of loggerheads exposed to surface oil (Lutcavage et al. 1995). In a separate study of loggerheads tracked from NGoM nesting beaches, all turtles displayed foraging site fidelity and a portion of the tracked turtles used oiled areas, such that 17% of the 44 tracked individuals had foraging centroids located within the DWH surface oiling footprint (Hart et al. 2014). In addition, it is possible that turtles found in the NGoM may never leave the GoM, as a portion of loggerheads that emerge from nests in the NGoM may remain in the GoM their entire lives (Lamont et al. 2015). Therefore, it is clear that sea turtles in this region were at risk for exposure to oil and dispersants following the DWH oil spill.

Exposure could have occurred through a variety of pathways, including direct contact; inhalation of oil, oil

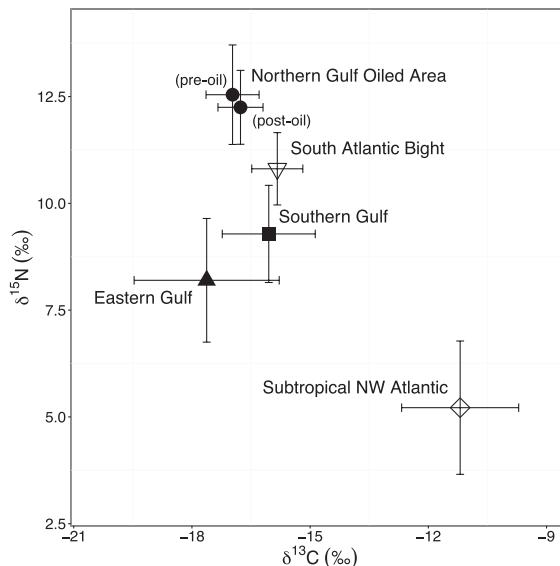


FIG. 3. Carbon and nitrogen stable isotope mean values (\pm SD) in loggerhead scute layers grouped by foraging area (see foraging area divisions in Fig. 1). Solid symbols designate regions within, and open symbols designate regions outside the Gulf of Mexico. The Northern Gulf Oiled Area points were limited to data from turtles with a foraging centroid that overlapped with the oiled footprint (10 of 15 loggerheads in the Northern Gulf of Mexico foraging area) and were divided into pre- and post-oil-spill groups. Foraging areas differed significantly in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, though post hoc tests demonstrated that pre- and post-oil groups in the Northern Gulf Oiled Area were not significantly different in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values.

vapors, and smoke; ingestion of oil-contaminated water and prey; transfer of oil compounds from females to their developing embryos; and contamination of habitats (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). The subsurface plume of oil extended to the southwest of the wellhead (Camilli et al. 2010), which was not an area used by turtles in this study. Therefore, the turtles in this study with foraging areas that overlapped the surface oil slick were likely to be at most risk, as the surface oil was determined to be the exposure pathway with the highest potential for adverse effects (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016).

The understanding of long-term effects of oil toxicity on sea turtles is limited (Milton et al. 2003). Prolonged exposure to oil may cause poor body condition and disrupt feeding activity, which could have contributed to the death of sea turtles after the Ixtoc I oil spill in the southern GoM three and a half decades ago (Hall et al. 1983). The sea turtles that were found dead in Texas following the Ixtoc I spill demonstrated visible external oil as well as characteristics of chronic petroleum hydrocarbon exposure (Hall et al. 1983). Juvenile loggerheads that experienced acute exposure to surface oil in laboratory trials exhibited elevated white blood cell counts, indicating a stress response,

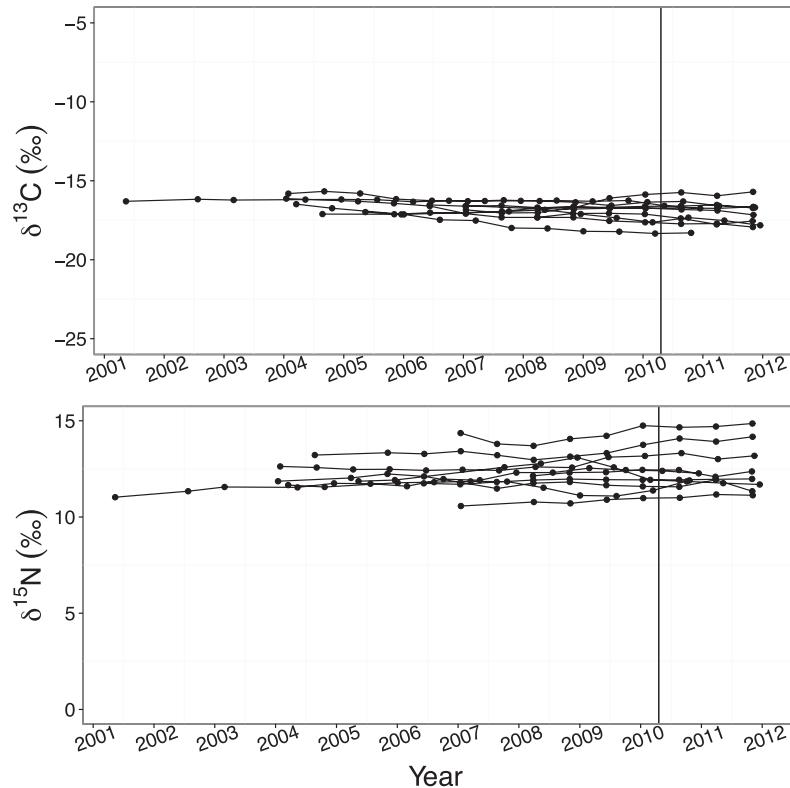


FIG. 4. Individual resource use history of 10 loggerhead females from the Northern Gulf of Mexico for which the foraging centroids overlapped the footprint of surface oiling. No significant changes in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values were observed after the oil spill (indicated by the vertical line). Note the use of the same y-axis scale as Fig. 2.

as well as peeling skin that did not return to normal for nearly a month after exposure (Lutcavage et al. 1995).

Following the DWH oil spill, boat-based rescue efforts of sea turtles in the GoM documented more than 900 turtles in the spill zone, and more than 80% of the captured turtles were visibly oiled (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). Oiled turtles had blood abnormalities attributable to stress, dehydration, and exertion caused by oiling, capture, and transport, while heavy oiling conditions were fatal without intervention (Stacy 2012). Nearly all heavily oiled turtles were found within 90 km of the wellhead; thus, exposure to oil was likely to have been more severe for small, oceanic turtles due to the dependence of these animals on habitats where the oil accumulated (Putman et al. 2015, Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). None of the females sampled were observed to have visible oil during their nesting events following the oil spill, and given the severe side effects of heavy oiling and distance, it is unlikely any heavily oiled adults would have survived to reproduce one to two years after the spill. Thus, any exposure to oil and dispersants of females in this study was likely to have been mild to moderate.

Isotopic shifts outside the oil spill region

In other areas of the GoM where oil was not present, the occurrence of isotopic shifts in the loggerhead records was limited, though six of the 76 females had $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges that exceeded 3‰ (Appendix S1: Fig. S1, Table S2). The observed isotopic shifts may represent either dietary or foraging location shifts, as it is difficult to parse the relative influence of diet and geographic location on the assimilated isotopic values. Some of these shifts were temporary, while others were unidirectional. These within-individual isotopic excursions are not likely to be a result of short-term reproductive migrations or seasonal isotopic variability for two reasons. First, female sea turtles are thought to fast during migration and reproduction (Plot et al. 2013, Perrault et al. 2014). Because the stable isotopes of carbon and nitrogen are assimilated through the diet, these fasting periods are not expected to be recorded in scute records. Second, the temporal resolution of the scute layers (0.6 year increments) would dampen most seasonal variability if it did exist. Isoscapes in widely distributed fish species in the eastern GoM were consistent between seasons and years, indicating that higher trophic level organisms in this region do not reflect seasonal variations that might exist at the base of the food web (Radabaugh

et al. 2013). Therefore, these turtles might have countered the site-fidelity trend and moved foraging sites temporarily or indefinitely, depending on the nature of the shift. As scute records become a more commonly used tissue to study foraging patterns, we may gain more information about how to interpret these shifts.

Conclusions

We demonstrate the advantages of using inert tissue samples to assess the ecological consequences of natural disasters on animal populations. These tissues can supply baseline data in the absence of pre-disaster studies or data availability. One advantage of using an inert tissue that can be sub-sampled sequentially is the ability to obtain a single sample that represents multiple time intervals, whereas the use of metabolically active tissues would require encountering the same individual on multiple occasions to provide sequential records. Consistent isotopic values in the long-term records of adult loggerheads in the NGoM indicate individuals did not move out of the area following the DWH oil spill, increasing their risk of chronic exposure to oil and dispersants. This method has wide applicability to other organisms with inert tissues to provide pre- and post-disturbance conditions and aid assessments of the biological impacts of such events.

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