Biological Conservation 145 (2012) 185–194

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Common coastal foraging areas for loggerheads in the Gulf of Mexico: Opportunities for marine conservation

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ARTICLE INFO

Article history:
Received 29 May 2011
Received in revised form 8 October 2011
Accepted 20 October 2011
Available online 3 December 2011

Keywords:
Loggerhead
Satellite-tracking
Switching state-space modeling
Gulf of Mexico
Kernel density estimation
Foraging

ABSTRACT

Designing conservation strategies that protect wide-ranging marine species is a significant challenge, but integrating regional telemetry datasets and synthesizing modeled movements and behavior offer promise for uncovering distinct at-sea areas that are important habitats for imperiled marine species. Movement paths of 10 satellite-tracked female loggerheads (*Caretta caretta*) from three separate subpopulations in the Gulf of Mexico, USA, revealed migration to discrete foraging sites in two common areas at-sea in 2008, 2009, and 2010. Foraging sites were 102–904 km away from nesting and tagging sites, and located off southwest Florida and the northern Yucatan Peninsula, Mexico. Within 3–35 days, turtles migrated to foraging sites where they all displayed high site fidelity over time. Core-use foraging areas were 13.0–335.2 km^2 in size, in water <50 m deep, within a mean distance to nearest coastline of 58.5 km, and in areas of relatively high net primary productivity. The existence of shared regional foraging sites highlights an opportunity for marine conservation strategies to protect important at-sea habitats for these imperiled marine turtles, in both USA and international waters. Until now, knowledge of important at-sea foraging areas for adult loggerheads in the Gulf of Mexico has been limited. To better understand the spatial distribution of marine turtles that have complex life-histories, we propose further integration of disparate tracking data-sets at the oceanic scale along with modeling of movements to identify critical at-sea foraging habitats where individuals may be resident during non-nesting periods.

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1. Introduction

Marine turtles spend the majority of their lives at sea, yet little is known about their oceanic life compared to the biology of females and hatchlings on coastal nesting beaches. Sea turtles have complex life histories which involve often disparate developmental, foraging, and nesting habitats (McClellan and Read, 2007). As such, sea turtle conservation represents a significant management challenge because a single management unit, often defined as a breeding area, may be sourced from geographically scattered foraging habitats (Hamann et al., 2010). Satellite telemetry and molecular genetic methods in particular have helped to illuminate levels of connectivity between sea turtle nesting, coastal, and offshore habitats (Bjorndal and Bolten, 2008), yet this picture has only recently begun to emerge at the scale of oceanic basins (Wallace et al., 2010).

Whereas satellite tracking studies have grown in number and scope over the past several decades (Godley et al., 2008; Hart and Hyrenbach, 2009), synthesis of satellite tracking data across studies on a single subpopulation of a species are needed to elaborate trends in at-sea spatial use of the oceans and coastal areas (e.g., Hawkes et al., 2011). As Godley et al. (2008) highlighted, a growing body of studies can now boast tracking datasets with durations in the foraging sites approaching a year or more, thereby yielding significant insights into aspects such as variable levels of foraging site fidelity among populations. However, despite the publication of > 100 sea turtle satellite- and GPS-tracking studies (e.g., Schofield et al., 2009), few syntheses of data on sea turtles at foraging areas are available (Hamann et al., 2010). Several previous analyses have focused on identifying likely foraging habitat for pelagic loggerheads (*Caretta caretta*, Linneaus, 1758; Polovina et al., 2004; Kobayashi et al., 2008). However, connections that exist among rookeries and foraging grounds, in particular, and location of oceanic 'hotspots' that include key foraging habitats are poorly

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0006-3207/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.biocon.2011.10.030

defined. Further, mechanisms of foraging site selection remain poorly understood.

Globally, loggerhead numbers are today much reduced from historic estimates (NMFS and USFWS, 2008). Continued declines in loggerhead nest numbers in major rookeries in Florida (Witherington et al., 2009) along with consistent interactions with fisheries were both factors in a proposal for elevating the level of protection for loggerheads in the USA (USFWS and NOAA, 2010), and recent designation of nine distinct population segments of loggerheads as either endangered or threatened (USFWS and NOAA, 2011). In the USA, although loggerhead interactions with fisheries activities prompted proposed changes in Gulf reef fish bottom longline rules (i.e., Amendment 31; NMFS, 2010), another threat for loggerheads in the Gulf of Mexico presented itself in the spring and summer of 2010 as the Deepwater Horizon/Mississippi Canyon 252 blowout preventer failed, causing the historic Gulf oil spill. In addition to the immediate effects of oil exposure in 2010 on loggerheads in the vicinity of the oil spill (Bjorndal et al., 2011), risks to marine turtles in the Gulf of Mexico continue through effects to their habitat and food resources which consists primarily of benthic invertebrates (Plotkin et al., 1993).

To illuminate potential at-sea opportunities for conservation of loggerheads, we aimed to integrate different satellite-tracking datasets for loggerheads in the Gulf of Mexico. In this region, several distinct nesting subpopulations exist (Bowen et al., 2005; Shamblin et al., 2011). Girard et al. (2009) summarized post-nesting movements and selected foraging sites of Casey Key loggerheads in 2005, 2006, and 2007; results confirmed preliminary information on migratory patterns and foraging destinations obtained from flipper tag recovery (Schroeder et al., 2003). However, it was unclear whether foraging destinations identified by Girard et al. (2009) also served as important foraging grounds for loggerheads nesting in other parts of the Gulf of Mexico. Thus, our goal was to synthesize recent satellite-tracking results with respect to foraging areas for loggerheads from three Gulf subpopulations: St. Joseph Peninsula in northwest Florida (NW FL nesting subpopulation), Casey Key in southwest Florida (SW FL nesting subpopulation), and Dry Tortugas National Park west of the Florida Keys (Dry Tortugas nesting subpopulation) (NMFS and USFWS, 2008). We tested the hypothesis that loggerheads exhibit a preference for common foraging areas, despite their association with different nesting subpopulations. In addition, we aimed to characterize foraging sites selected by loggerheads with respect to depth, primary productivity, and proximity to shore. Finally, we examined the selection of discrete foraging sites according to turtle size, to explore phenotypic differences in migration and foraging habitat selection and use.

2. Material and methods

We used satellite telemetry to track the movements of 10 adult female nesting loggerheads intercepted on three different nesting beaches in the Gulf of Mexico in the summers of 2008, 2009, and 2010. Turtle interception and tagging followed methods similar to those in Girard et al. (2009) and Hart et al. (2010). Briefly, we intercepted nesting loggerhead females after they had finished nesting on the beach. We corralled each turtle to confine her for workup and followed established protocols for taking biological samples and marking each animal (NMFSSFSC, 2008). Immediately after marking each turtle with Inconel and PIT tags, we took standard carapace measurements, including curved (CCL) and straight (SCL) carapace lengths. After removing epibiota and cleaning the carapace, we adhered platform transmitter terminals (PTTs) using slow-curing epoxy. We used two types of PTTs: SPOT5s from Wildlife Computers (Redmond, WA, USA; $n = 8$) and Kiwisat 101s from Sirtrack (Havelock North, New Zealand; $n = 2$). We streamlined attachment materials to minimize any buoyancy or drag effects on the turtle's swimming ability and limited the epoxy footprint. Each tag was set to be active for 24 h d^{-1}. Once tagging was complete, we removed the corral, allowing the turtle to return to the sea.

2.1. Sea turtle tracking

We analyzed Argos location data using the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley, 2005) available on www.seaturtle.org, using location classes (LC) 3, 2, 1, 0, A, and B to reconstruct routes and calculate straight-line and total distances travelled by tracked turtles. We excluded LC Z (for which no error estimation was available) and those data that required swim speeds >5 km h^{-1} from the analysis. Previous studies have determined that post-nesting migrations for sea turtles were complete when movement was no longer directed for at least three consecutive days (Zbinden et al., 2008; Marcovaldi et al., 2010), or upon visual inspection of turtle tracks that showed restricted movements (e.g., multidirectional and backtracked over previous tracks). Troëng et al. (2005) defined a foraging area for green turtles (*Chelonia mydas*, Linneaus, 1758) as that area in which turtles remained within a 20 km diameter for more than 24 h, and Schofield et al. (2010b) defined foraging sites based on changes in turtle travel speed (i.e., 1 km h^{-1}) and an absence of overlap of 90% KDE for patches of GPS locations separated by less than 50 km. However, we used a switching state-space modeling approach to determine arrival date of each loggerhead at its respective foraging ground (see below).

2.2. Switching state-space modeling

We used a switching state-space modeling (SSM) approach (Jonsen et al., 2003; Patterson et al., 2008) to characterize the movements of adult nesting loggerhead females in the Gulf of Mexico. The model was described by Jonsen et al. (2005) and has previously been applied to model movement of marine animals including turtles (Jonsen et al., 2006, 2007; Bailey et al., 2008; Maxwell et al., 2011). Location data obtained through satellite transmitters are often received at irregular time intervals, and sometimes involve large gaps and positional errors. Ad hoc filtering of location data based on location quality is not sufficient to remove erroneous location and also results in loss of information (Jonsen et al., 2006). Switching SSM estimates location and behavioral mode at regular time intervals, accounting for satellite positional errors and dynamics of the animal movement pattern (Jonsen et al., 2005). The behavioral mode was binary, defined as 'foraging' and 'migration' as in earlier applications (Jonsen et al., 2005, 2007; Breed et al., 2009); however, since we tagged animals during nesting seasons, we defined behavioral mode as 'foraging and/or nesting' and 'migration'. We applied the model used by Breed et al. (2009), a modified version of Jonsen et al. (2005), that estimates model parameters by Markov Chain Monte Carlo (MCMC) using WinBUGS via R. We used all tracking data except for LC Z, and we fit the model to tracks of each individual turtle to estimate location and behavioral model every six hours from two independent and parallel chains of MCMC. Our samples from the posterior distribution were based on 10,000 iterations after a burn-in of 7000 and thinned by five.

Using a switching SSM allowed us to interpret fine-scale behavioral information within the tracks. We specifically used the model to determine the date of arrival for each satellite-tagged loggerhead at its foraging destination. We summarized data for the period of migration away from nesting beaches and then after arrival at the foraging area until the transmitters stopped sending information, or at the time of data synthesis.

2.3. Data analysis

After fitting the switching SSM to individual loggerhead tracks, we identified the first date when each animal entered foraging mode at its final destination area. Using satellite location data during the foraging period, we generated mean daily locations for each turtle from the filtered locations within the foraging area to minimize autocorrelation, following methods of Seney and Landry (2008). The resulting coordinates provided raw data for kernel density estimation (KDE) analysis across all individuals. Kernel density is a non-parametric method used to identify one or more areas of disproportionately heavy use (i.e. core areas) within a home-range boundary (Worton, 1987, 1989; White and Garrott, 1990), with appropriate weighting of outlying observations. We used the Home-Range Tools for ArcGIS extension (Rodgers et al., 2005) and fixed-kernel least-squares cross-validation smoothing factor (*hcv*) for each KDE (Worton, 1995; Seaman and Powell, 1996). When we observed unequal variance of the *x* and *y* coordinates, we followed Seaman and Powell (1996) and rescaled the data to select a single best bandwidth. We used ArcGIS 9.3 (ESRI, 2007) to calculate the in-water area (km^2) within each kernel density contour (50% and 95%) and to plot the data; we used 50% KDEs to represent core area of activity at foraging sites (Hooge et al., 2001).

We also tested location data for and quantified site fidelity using the Animal Movement Analysis Extension for ArcView 3.2. Using Monte Carlo Random Walk simulations (1000 replicates), we tested tracks during a turtle's time at the foraging ground for spatial randomness against randomly generated walks (Hooge et al., 2001). Coordinates were standardized due to unequal standard deviation of latitude and longitude for some animals. Tracks exhibiting site fidelity indicate that the turtles' movements were more spatially constrained rather than randomly distributed (Hooge et al., 2001).

To further characterize at-sea foraging areas selected by individual loggerheads, we summarized the spatial separation between the centroid of each turtle's 50% KDEs at each foraging ground, and characterized bathymetry, ocean Net Primary Production (NPP), and Sea Surface Temperature (SST) at each site. For bathymetry, we used the NOAA National Geophysical Data Center (GEODAS) ETOPO2 Global Bathymetry data, http://www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html (accessed 15 February 2011). We also used Oregon State University ocean productivity data (0.1°), http://www.science.oregonstate.edu/ocean.productivity/index.php (accessed 20 February 2011), in which monthly NPP was derived as a function of chlorophyll, light, and photosynthetic efficiency (Behrenfeld and Falkowski, 1997). For each animal, we identified months in the final foraging site and created a raster layer of mean NPP. We included all available data for months during which turtles were at their foraging grounds; November and December 2010 data were not available and thus were not included in the summary. We extracted bathymetry and mean NPP within each turtle's 50% KDE area. Moderate Resolution Imaging Spectroradiometer (MODIS) Terra Global Level 3 Mapped Mid-IR SST, ftp://podaac.jpl.nasa.gov/pub/documents/dataset_docs/modis_sst.html (accessed March 21, 2011), were used to characterize sea surface temperature in modeled migration passes and at foraging grounds.

2.4. Statistical comparisons

Results of several previous studies on nesting loggerheads elsewhere have suggested turtle body size could be a predictor of whether turtles selected neritic or oceanic foraging grounds (Hatase et al., 2004). Thus, we calculated the correlation between turtle body size (CCL) and maximum water depth at estimated locations during the tracking period of each turtle, as well as investigated the correlation between turtle body size and size of core-use areas. To further characterize the spatial separation of turtles at foraging grounds, we examined the distance between centroids of 50% KDEs within each foraging ground, and the distance from each 50% KDE to the nearest shoreline. For all statistical comparisons, we used an α level of 0.05.

3. Results

We intercepted turtles during the 2008, 2009, and 2010 nesting seasons in May, June, July, and August. Turtle size varied from 84.3 cm curved carapace length (CCL) (Turtle E) to 103.2 cm CCL (Turtle D), with a mean of 96.2 cm CCL (SD 5.73) (Table 1). In a total of 1124 turtle tracking days (mean 112.4, SD 46.3; range 48–188), we observed that turtles migrated to their foraging destinations during the months of July and August, within a 3–35 day window but on average in 13.2 days (SD 10.6) (Table 1). Turtles traveled between 102 and 904 km straight-line distances to selected foraging sites (mean 404.8, SD 291.7) (Table 1; Fig. 1).

Through satellite-tracking, we discovered consistent use of two important regional foraging areas in the Gulf by turtles corresponding to three different subpopulations. One common foraging area for loggerheads from all three subpopulations was off the coast of SW Florida (SWFL), and the second was off the northern tip of the Yucatan Peninsula, Mexico (MX) (Fig. 2a and b). Out of 10 turtles, seven selected foraging grounds off SWFL, whereas three selected foraging grounds off MX. Turtles that traveled to SWFL migrated a mean straight-line distance of 253 km (SD 153.8, range 102–495), whereas those that travelled to MX migrated a mean straight-line distance of 521 km (SD 207.7, range 521–904). Although turtles spent a range of 3–35 days migrating, there were variations across turtles from the different nesting subpopulations; SJP turtles (A–D) spent 11–15 days migrating, CK turtles (E, F) spent 3–5 days migrating, and DRTO (G-J) turtles spent 4–35 days migrating (Table 1). Mean water depth during migration varied across all turtles but ranged from 21.5 m (SD 9.0) for Turtle H to 1317.5 m (SD 1459.7) for Turtle A (Table 1). Pearson's correlation coefficient between carapace size and maximum depth was 0.213. However, the medium-sized turtles were the ones that migrated over the deepest waters (Fig. 3).

We observed that 5 of the 10 turtles arrived at foraging sites in July, 3 in August, and 2 in September. The time between earliest arrival (12 July) and latest arrival (9 September) was 59 days, or approximately 2 months. Turtles arrived at foraging sites off SWFL in July and August, whereas those that traveled to MX foraging sites arrived there later, in August and September. The size range of turtles using SWFL foraging sites ranged from 84.3 to 103.2 cm CCL, with a mean of 95.4 (SD 6.8). The size range of turtles, using MX foraging sites ranged from 97.2 to 99.5 cm CCL, with a mean of 98.0 (SD 1.3). At the time of data synthesis, the number of turtle-tracking-days at foraging sites ranged from 20 to 56 in MX, and 25–128 in SWFL, with an overall mean 61.1 days (SD 37.8), yet several turtles were still transmitting from their respective foraging sites.

The size of core-use areas (i.e., 50% KDEs) at both foraging grounds ranged from 13.0 to 335.2 km^2 (mean 91.8, SD 105.7; Table 2). We observed that turtle tracks and movements for each turtle during its time at its foraging site were more constrained than random movement paths; in all cases, *p* (the proportion of the randomly generated movement paths with higher mean squared distance (MSD) values than the observed path) was >97.2, indicating

Table 1
Turtle, tagging, and tracking details for 10 loggerhead females (*Caretta caretta*) satellite-tracked in the Gulf of Mexico, USA, in 2008, 2009, and 2010. Tagging locations are abbreviated as in text: SJP = St. Joseph Peninsula; CK = Casey Key; DRTO = Dry Tortugas National Park. CCL = curved carapace length.

Tagging site and date	Turtle	Turtle size (CCL-tip, cm)	Total no. tracking days	Migration period (no. days in migration)	Mean water depth during migration depth (N locations)	No. migration locations
SJP, 8/3/2010	A	97.2	93	8/13/2010–9/7/2010 (25)	1317.5 (1459.7)	78
SJP, 8/4/2010	B	90.0	92	8/4/2010–8/21/2010 (17)	24.2 (6.4)	51
SJP, 7/26/2010	C	99.5	48	7/27/2010–8/15/2010 (19)	972.3 (1354.2)	64
SJP, 7/27/2010	D	103.2	51	8/12/2010–8/23/2010 (11)	41.6 (3.7)	34
CK, 6/7/2010	E	84.3	150	7/16/2010–7/21/2010 (5)	24.5 (16.9)	48
CK, 5/27/2010	F	92.7	188	7/24/2010–7/27/2010 (3)	22.6 (15.1)	15
DRTO, 5/29/2010	G	97.3	159	8/5/2010–9/9/2010 (35)	943.2 (948.5)	98
DRTO, 5/29/2010	H	101.0	105	7/7/2010–7/12/2010 (5)	21.5 (9.0)	15
DRTO, 5/20/2008	I	100.5	95	7/17/2008–7/21/2008 (4)	39.2 (16.5)	23
DRTO, 6/6/2009	J	96.3	143	7/14/2009–7/22/2009 (8)	27.1 (6.4)	29

site fidelity in the satellite tracking data (Table 2). However, the Pearson's correlation coefficient between turtle body size (CCL) and size of 50% KDE area was −0.200, indicating no correlation between these 2 factors.

For loggerheads at foraging sites in SWFL, size of core use areas ranged from 13.0 to 335.2 km^2 (mean 85.7, $n = 7$, SD 112.9), and the number of activity centers that comprised individual core-use areas ranged from 1 to 5 (Table 2). For those turtles that selected foraging sites in MX, core-use areas were slightly larger in size and ranged from 29.6 to 229.4 km^2 (mean 106.1, $n = 3$, SD 107.9), with only one activity center present for each turtle (Table 2). Across all turtles, we observed little overlap in individual core use areas; mean distance between individual turtle core foraging areas at both sites was 49.0 km (SD 25.0, range 28.8 to 87.3). Additionally, depth of core use areas ranged from 2.4 to 57.8 m in SWFL, and 13.6–32.9 m in MX. All turtles selected foraging sites in relatively shallow water (<50 m) and nearshore (mean 58.5 km from the coast, SD 36.3, range 4.9–122.0 km). Net primary productivity (i.e., chlorophyll a values) at foraging sites ranged from 253.3 to 1180 mg C/m^2/day. For 6 of the 7 turtles off SWFL, NPP ranged from 253.3 to 1084 mg C/m^2/day; we observed a similar range of NPP values for those three turtles off MX (379 to 1180 mg C/m^2/day; Table 3). However, mean SST across all foraging sites ranged from 26.6 to 30.0 °C. Overall, mean NPP in foraging grounds (2720.8 C/m2/day; SD 762.4) was larger than that during migration, possibly because foraging sites were all near the coast; however, this difference was not significant, perhaps due to relatively low sample size ($n = 10$). Further, a *t*-test of means showed that among all 10 turtles, mean NPP during migration at locations predicted from SSM was 2263.4 mg C/m^2/day (SD 437.0) slightly lower than mean NPP at foraging locations predicted from SSM (2720.8 mg C/m^2/day, SD 762.4), but not significantly different ($t = 1.65$, $p = 0.12$). Similarly, mean SST during migration at locations predicted from SSM was 28.7 °C (SD 0.3) and mean SST at foraging locations predicted from SSM was 28.5 °C (SD 0.5), again not significantly different ($t = -0.9$, $p = 0.33$). Finally, results of a Wilcoxon test showed that 8 of 10 turtles occupied significantly different water depths at migration versus at their foraging areas, further indicating little evidence of foraging behavior during migration (Supplemental Information).

4. Discussion

Although turtles nesting in Florida have been identified as four genetically distinct subpopulations (NMFS and USFWS, 2008; Shamblin et al., 2011), we found that turtles from 3 of these groups selected common foraging areas in the Gulf of Mexico. Other studies have also tracked turtles to these same foraging sites (loggerheads, Girard et al., 2009; critically endangered Kemp's ridleys (*Leopidochelys kempii*, Garman, 1880), Shaver and Rubio, 2008), however, ours is the first study to consolidate tracking data from three different nesting subpopulations in the Gulf of Mexico. The common regional locations of selected foraging sites highlights the need for viewing these discrete nesting subpopulations in a more Gulf-wide perspective, which fits with the "regional management unit" concept recently defined by Wallace et al. (2010). As well, these results indicate a need to place greater emphasis on management of in-water threats at these sites, as protection of turtles at these sites could affect more than one loggerhead subpopulation and at least two marine turtle species (i.e., loggerheads and Kemp's ridleys).

Because nesting beaches are easily accessible, research is often focused on and management decisions based solely on this relatively small and isolated snap-shot of sea turtle life-history. However, sea turtles are highly migratory species that require geographically large areas. Loggerhead turtles are currently declining (NMFS and USFWS, 2008; Witherington et al., 2009), and most recently 9 distinct population segments (DPS) of loggerheads were classified by regulatory agencies in the USA as either threatened or endangered (USFWS and NOAA, 2011). Such designations underscore the need for effective protection of the species, both on land and in the water. In this study, we tracked several turtles from USA nesting beaches off the continental shelf and into Mexican waters; this result highlights the need for protection of turtles to go beyond individual nesting beaches, genetic subpopulations, and political boundaries (Blumenthal et al., 2006; Broderick et al., 2007; Girard et al., 2009).

Here we also described a new objective method for identifying arrival time of tracked turtles at foraging sites. Previous studies have defined arrival at foraging grounds through subjective visual inspection (Troëng et al., 2005; Marcovaldi et al., 2010; Rees et al., 2010) or use of travel speed and absence of overlap in home range estimates (Schofield et al., 2010b). Our approach using switching SSM provides a method for quantifying at-sea animal behavior and allowing statistical determination of not only arrival date at foraging grounds, but also most likely migration pathway. Knowing precisely where turtles travel while migration and when turtles arrive at discrete foraging sites could offer an opportunity for management of at-sea activities in these well-defined areas at specific times of year. In addition, our description of oceanographic characteristics for selected foraging sites contributes to the limited data describing adult loggerhead foraging areas and at-sea habitat needs for these imperiled species (but see Schofield et al., 2010b; Hawkes et al., 2011).

Whereas previous emphasis has focused on characterizing migration routes during tracking studies (Shaver and Rubio, 2008; Girard et al., 2009), less information is available describing characteristics of the foraging areas of adult turtles. Schroeder et al. (2003) generally described foraging areas for adult loggerheads as being 10's of square kilometers, a size that was supported

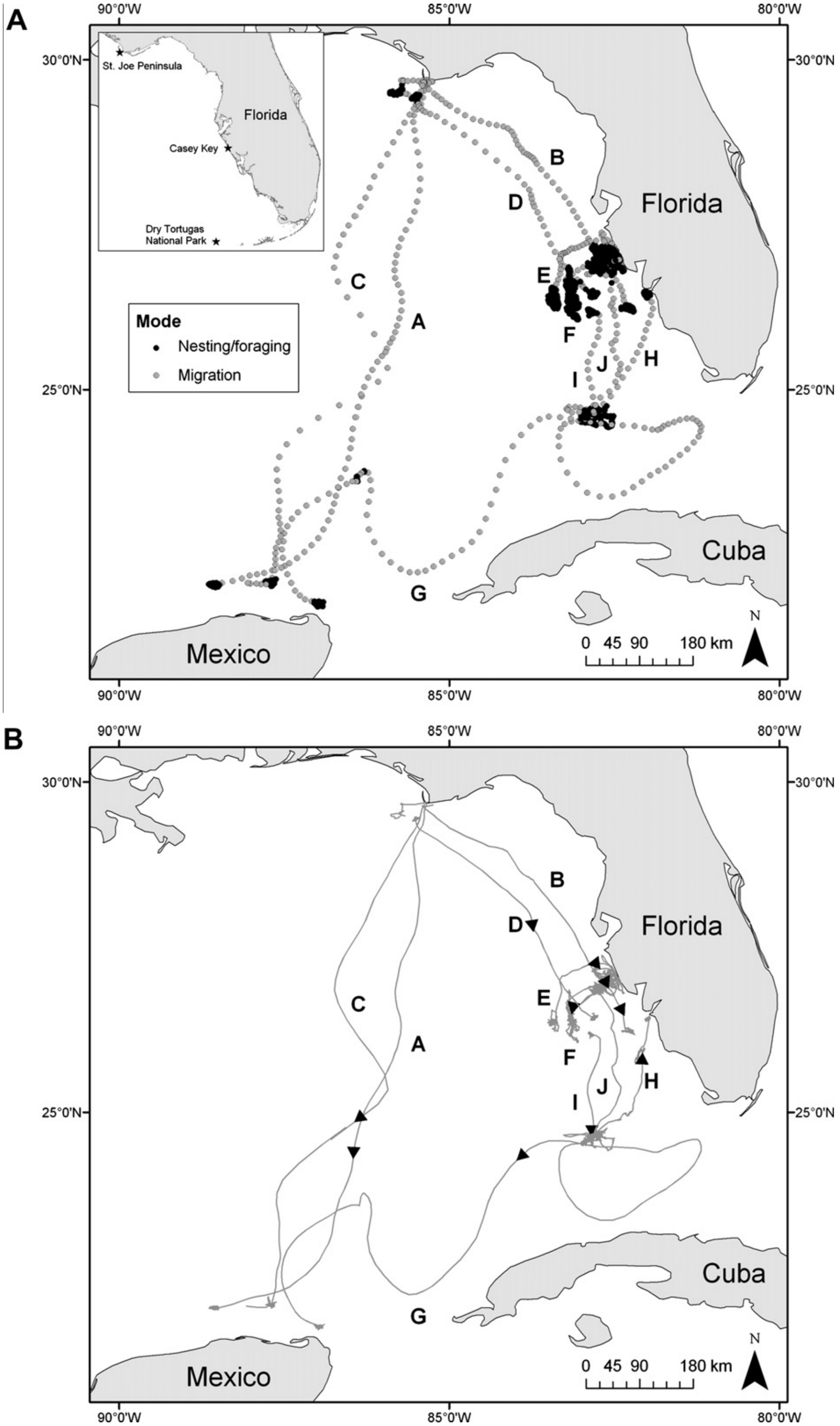

Fig. 1. Panel A: Switching state-space model (SSM) results for Gulf loggerheads tagged at St. Joe Peninsula (northwest Florida), Casey Key (southwest Florida), and Dry Tortugas National Park (south Florida). The inset box shows initial release locations. Panel B: SSM results showing direction of travel for each turtle (black arrows).

by Broderick et al. (2007) who found core-use areas for Mediterranean loggerheads ranged from 55 km^2 in summer to 331 km^2 in winter. Schofield et al. (2010b) also reported relatively small (mean 10.2 km^2) core-use areas for loggerheads in the Mediterranean. However, Hawkes et al. (2011) found that size of core-use areas for southeastern loggerheads ranged from 645.1 km^2 in summer to 339.0 km^2 in winter. Marcovaldi et al. (2010) recently described the size of the mean core foraging areas for loggerhead turtles tracked off the coast of Brazil as 889 km^2, and Zbinden et al. (2008) described foraging areas for Mediterranean loggerheads as large as 1198 km^2. In our study, mean size of foraging areas for loggerheads tracked in the Gulf of Mexico was most

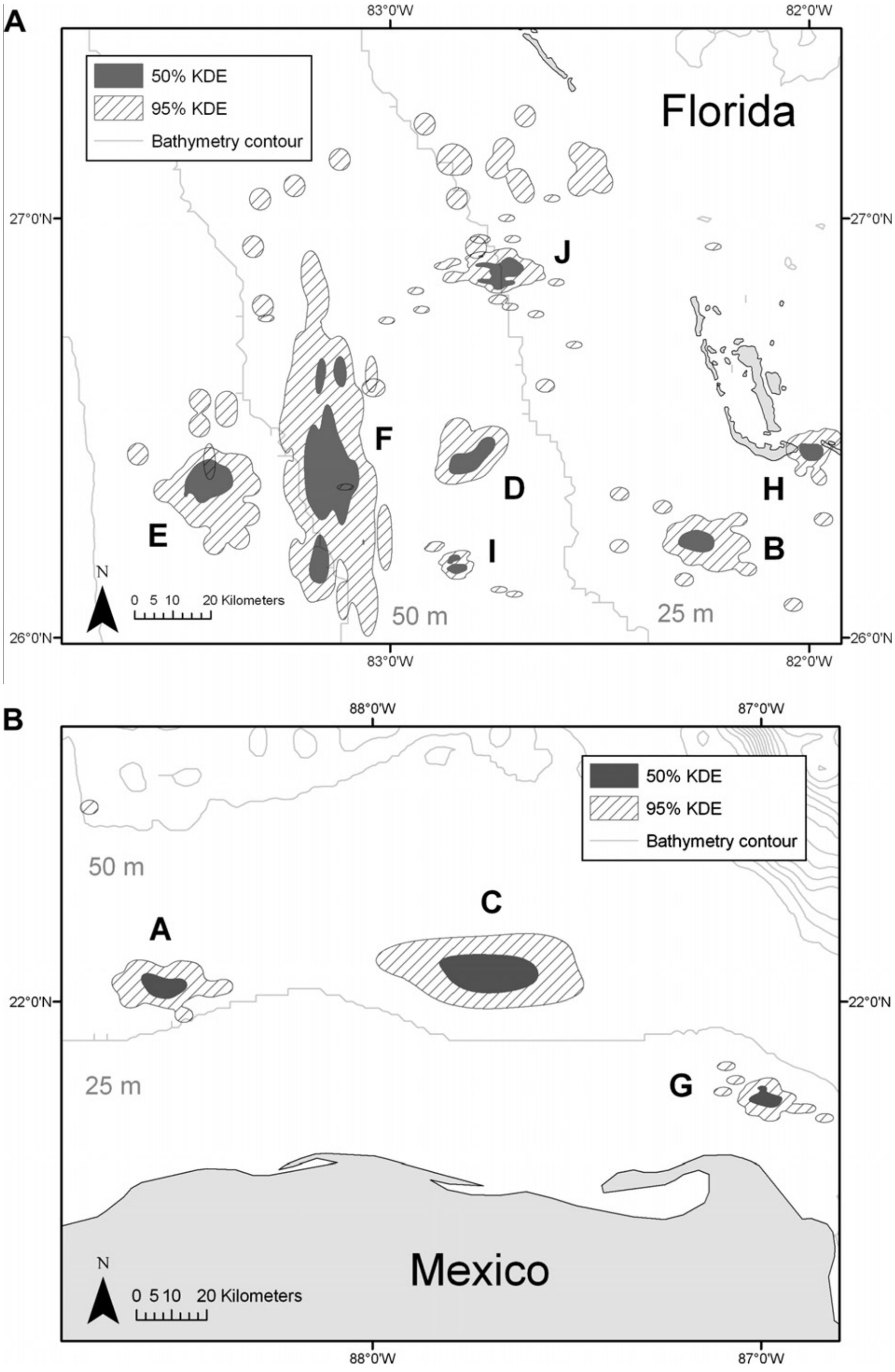

Fig. 2. Panel A: Core-use areas (i.e., 50% kernel density estimates (KDEs)) and 95% KDEs for 7 out of 10 adult female loggerheads (*Caretta caretta*) (turtles B, D, E, F, H, I, and J) satellite-tracked from nesting areas in the Gulf of Mexico to selected foraging sites off southwest Florida. Panel B: Core-use areas and 95% KDEs for 3 out of 10 adult female loggerheads (turtles A, C, and G) satellite-tracked from nesting areas in the Gulf of Mexico to selected foraging sites off the Yucatan Peninsula, Mexico.

similar to size of foraging areas described by Hawkes et al. (2011), Zbinden et al. (2008), and Marcovaldi et al. (2010), i.e., 100's of square kilometers rather than 10's of square kilometers. As in these other studies, turtles from our study exhibited significant fidelity to their core foraging area with little overlap in core use areas between individual turtles, suggesting the possibility that turtles establish individual foraging territories that they may return to year after year. In fact, Marcovaldi et al. (2010) presented repeated use of remarkably similar individual foraging sites for Brazilian loggerheads tracked >1200 days and Schofield et al. (2010b) found loggerhead males tracked in the Mediterranean returned to their previous foraging sites in subsequent years. However, future, long-term tracking of loggerheads tagged at nesting beaches and in-water sites is needed to improve certainty in foraging area fidelity. Regardless, evidence now exists that long-term residence of adult loggerheads at discrete foraging sites occurs not only off Brazil (Marcovaldi et al., 2010) and in the Mediterranean (Schofield et al., 2010b), but also in the Gulf of Mexico (*this study*); we argue that this predictability of foraging site selection presents a unique opportunity for conservation. Although marine turtles are

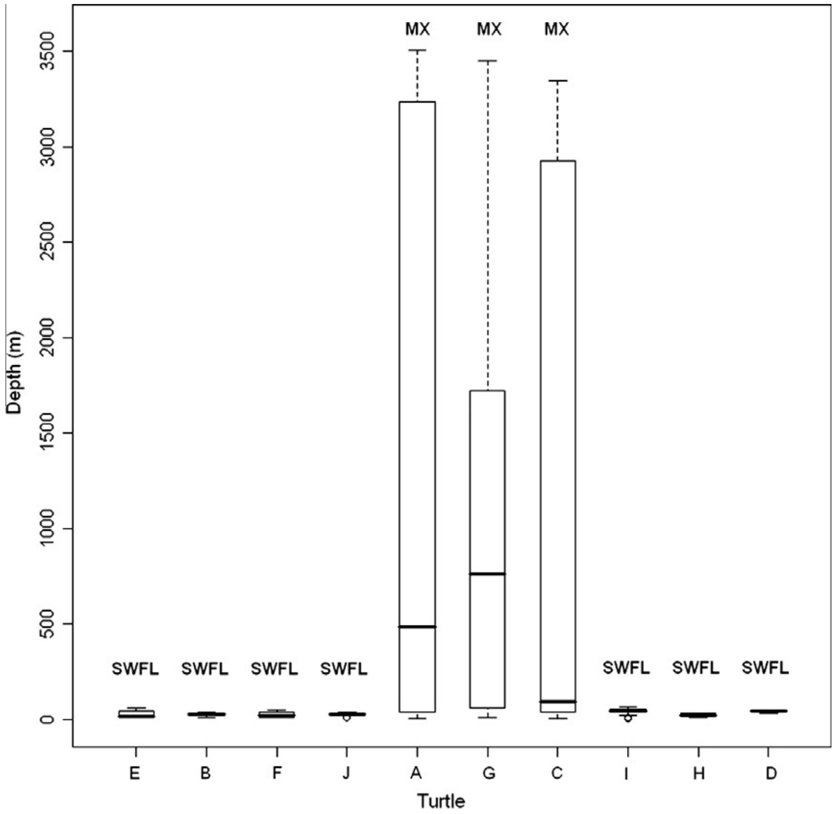

Fig. 3. Box plots of depth along migration route, showing five number summaries (i.e., sample minimum and maximum, lower and upper quartiles, and median), for individual turtles satellite-tracked from nesting beaches in the Gulf of Mexico to foraging sites in southwest Florida (SWFL) and off the Yucatan Peninsula, Mexico (MX). Turtles are individually identified as in Table 1, and ordered horizontally smallest (Turtle E) to largest (Turtle D), left to right.

wide-ranging vertebrates, their use of discrete foraging sites for long periods of time between breeding years offers resource managers direct locations for prioritization of protection.

Recent studies also described variability in foraging strategies of post-nesting loggerheads (Hatase et al., 2004; Hawkes et al., 2006; Girard et al., 2009; Rees et al., 2010; Hawkes et al., 2011). Hatase et al. (2004) and Hawkes et al. (2006) suggested a dichotomy in adult loggerhead turtles off Japan and Cape Verde, with larger individuals foraging in more productive neritic waters and smaller individuals foraging in oceanic waters. However, off Oman (Rees et al., 2010) and in the Gulf of Mexico (Girard et al., 2009; Hart et al., *this study*), there was little correlation between body size and location of selected foraging sites. In our study, all turtles selected foraging sites in shallow neritic waters ranging in depth from 6.7 to 42.2 m which is similar to results reported by Hawkes et al. (2011) for loggerheads in the North Atlantic (depth range of foraging sites in that study was 3.0–89.0 m). Thus far, our tracking results show that not all loggerheads exhibit strong phenotypic dichotomies in selection of foraging sites. Moreover, whereas all turtles traveled to neritic foraging grounds, those that went to SWFL remained over relatively shallow waters during migration and those that traveled to Mexico did so over deep oceanic waters. Continued tracking of additional Gulf loggerheads from each tagging site will allow determination of population-level foraging strategies as well as consistency of migration routes or corridors (e.g., Broderick et al., 2007; Marcovaldi et al., 2010).

Hatase et al. (2004) suggested the phenotypic dichotomy observed in Japanese loggerheads at adult foraging areas was part of a variable life-history strategy where food abundance encountered as post-hatchlings regulated growth rates, thereby influencing the juvenile ontogenetic shift from oceanic to neritic habitats. Their theory would indicate that turtles nesting at our sites in the Gulf of Mexico all recruited to neritic foraging grounds as juveniles. However, in the Atlantic, McClellan and Read (2007) found loggerheads did not undergo a discrete ontogenetic shift and instead frequently moved back and forth between neritic and oceanic habitats throughout their development. Our data further highlight the complexity of loggerhead life-history; as in McClellan and Read (2007), we observed no turtle size-related partitioning of the habitat. Yet in the Gulf of Mexico, our data indicate that turtle size may play a role in determining migratory pathways, with smallest and largest turtles remaining in neritic zones and larger turtles migrating oceanically. As with other marine animals, loggerheads most likely use a variety of strategies throughout their life to increase survival, fitness, and reproductive output; these strategies probably vary considerably depending on the suite of variables turtles experience in their specific range (i.e., currents, temperatures, productivity, prey distribution, and predator abundance form multiple combinations to create a distinct environment for each loggerhead group) (Broderick et al., 2007; Suryan et al., 2009; Schofield et al., 2009, 2010b; Hawkes et al., 2011). Turtle movement patterns are most likely formed in response to the unique environmental forces each turtle group must maximize for greatest survival and reproductive output which results in variability in strategies used among groups.

Many pelagic predators use biological and physical oceanographic features as cues to identify areas of high productivity, foraging in currents or along continental shelves (Suryan et al., 2006). This appears to be a common strategy for loggerhead turtles which have been found to migrate along major currents and forage in shallow nearshore areas with high primary or secondary productivity (Hawkes et al., 2007, 2011; Zbinden et al., 2008; Marcovaldi et al., 2010); turtles in the Gulf of Mexico also appear to use this strategy. Core foraging areas in our study were all relatively

Table 2
Characteristics of foraging sites selected by 10 satellite-tracked loggerhead females (*Caretta caretta*) in the Gulf of Mexico, USA. Details include area of home range (i.e., 95% kernel density estimate (KDE)) at foraging sites and core-use (i.e., 50% KDE) areas, including bathymetry and water depth (equivalent to bathymetry −1).

Turtle	Period at foraging site (No. days at foraging site)	Foraging site location	Straight-line distance to foraging site (km)	Mean bathymetry (m) of 50% KDE (core area) at foraging site (SD)	No. locations analyzed at foraging site	h_{cv}	Are of 95% KDE (km^2)	Area of 50% KDE (km^2)	No. activity centers at 50% KDE (km^2)	Mean water depth (m) at foraging site (SD)	No. locations analyzed at foraging site for water depth
A	9/7/2010–11/4/2010 (20)	MX	852	−30 (0.00)	16	0.845	351.9	59.2	1	30.73 (2.58)	196
B	8/21/2010–11/4/2010 (56)	SWFL	495	−16.27 (1.05)	37	0.455	323.1	37.2	1	16.24 (1.13)	225
C	8/15/2010–9/12/2010 (26)	MX	904	−32.86 (1.11)	76	0.19	911.7	229.4	1	32.41 (1.23)	85
D	8/23/2010–9/16/2010 (25)	SWFL	431	−31.32 (1.49)	25	0.337	236.8	53.8	1	28.76 (4.34)	115
E	7/21/2010–11/4/2010 (106)	SWFL	107	−57.77 (1.01)	107	0.05	1007.1	90.4	1	42.22 (19.94)	404
F	7/27/2010–12/1/2010 (128)	SWFL	102	−46.46 (2.65)	117	0.217	1503.3	335.2	5	35.77 (16.11)	548
G	9/9/2010–11/4/2010 (56)	MX	521	−13.56 (3.62)	55	0.186	200.9	29.6	1	38.6 (159.1)	375
H	7/12/2010–9/11/2010 (62)	SWFL	215	−2.43 (1.18)	37	0.455	112.7	20.9	1	6.69 (7.31)	328
I	7/21/2008–8/23/2008 (34)	SWFL	175	−37.8 (0.40)	33	0.08	73.3	13.0	2	22.21 (13.2)	261
J	7/22/2009–10/27/2009 (98)	SWFL	246	−25.18 (1.38)	97	0.11	261.9	49.5	2	23.15 (5.21)	397

Table 3
Oceanographic characteristics of foraging sites selected by 10 satellite-tracked loggerheads in the Gulf of Mexico, USA. NPP = net primary production; SST = sea surface temperature.

Turtle	Months, year at foraging site	Foraging ground	Mean NPP (mg C/m^2/day) (SD[a])	Mean SST (°C) (SD[a])
A	9–11, 2010	MX	395.0 (0.0)	27.0 (0.02)
B	8–11, 2010	SWFL	1084.0 (0.0)	27.6 (0.06)
C	8–9, 2010	MX	379.0 (19.6)	28.5 (0.07)
D	8–9, 2010	SWFL	325.5 (0.0)	30.0 (0.02)
E	7–12, 2010	SWFL	253.3 (0.0)	28.2 (0.04)
F	7–12, 2010	SWFL	289.8 (4.7)	28.2 (0.07)
G	9–11, 2010	MX	1180 (0.0)	26.6 (0.06)
H[b]	7–9, 2008	SWFL	–	29.5 (0.00)
I	7–8, 2008	SWFL	352.5 (0.0)	29.4 (0.00)
J	7–10, 2009	SWFL	532.5 (0.0)	29.0 (0.11)

[a] SD = 0 when 50% KDE is within one grid; see text for grid spacing.

[b] Data for 50% KDE for Turtle H was not available because the area was extremely close to the shoreline.

nearshore in shallow water (<50 m deep), within a narrow temperature range (SST range 26.6–30.0 °C at foraging sites), and in areas of relatively high NPP. Because we found that environmental variables such as SST were relatively consistent in the Gulf of Mexico throughout the summer and into the fall, we suggest that perhaps turtles foraging in this body of water do not need to move as water temperatures change throughout the year as has been reported for turtles in the Atlantic (James et al., 2005); this may allow them to remain within their core foraging area year-round.

5. Conclusions

Marine populations and ecosystems exhibit complex system behaviors, and as such, marine spatial planners and managers must understand the heterogeneity of biological communities, their key components and the processes that maintain them (Crowder and Norse, 2008). Designing conservation strategies that protect wide-ranging marine turtles is a significant challenge (Hamann et al., 2010); however, our results pinpointing specific locations of and discrete measures for core foraging areas contribute key information that can be used in marine spatial planning efforts to protect several subpopulations of adult loggerheads (and perhaps several marine turtle species) in the Gulf of Mexico. For example, our results could be used in defining the spatial limits of potential area-based closures at foraging sites of satellite-tracked loggerhead sea turtles. We recognize that boundaries around each regional foraging area that we have defined would contain a large area (i.e., >40,000 km^2), but conserving marine species that make long-distance movements requires innovative management practices. Our results contribute towards defining areas for place-based management, a promising approach towards implementing ecosystem-based management in the marine ecosystem (Crowder et al., 2006; Crowder and Norse, 2008).

Until now knowledge of important at-sea foraging areas for adults loggerheads in the Gulf of Mexico has been limited (Girard et al., 2009). Our finding that different nesting aggregations of loggerheads use common foraging areas provides not only a starting point for marine spatial planning, but also an international opportunity for conservation and co-management of marine turtles with Mexico. Further, endangered Kemp's ridley sea turtles have also been shown to migrate to the same SWFL foraging ground (D. Shaver, pers comm.); this spatial similarity and overlap of selected foraging sites highlights distinct areas for prioritization of management strategies towards protection of important at-sea foraging areas for marine turtles. Moreover, at foraging sites, turtles may be resident for up to 2.5 years (Broderick et al., 2007; Marcovaldi et al., 2010; K. Hart, pers. observ). Thus, with additional marine turtle tracking datasets, we expect to see repeated use of these, and possibly other, common foraging areas. Such information would be valuable in the current effort to site a network of marine protected areas in the Gulf of Mexico (Ritchie and Keller, 2008). Finally, although loggerheads have complex population structure (Bowen et al., 2005) and complexity and variation in life history (McClellan and Read, 2007; Schofield et al., 2010a), the convergence of loggerheads from different subpopulations at common foraging sites should provide an opportunity to invest in protection of multiple "stocks" of these imperiled marine turtles. Conservation efforts for loggerheads, until now, have not included a focus on in-water foraging sites. Given the fragile status of loggerheads globally (USFWS and NOAA, 2011), we echo the suggestion of Hamann et al. (2010) that research and restoration attention should be focused on important in-water foraging sites. Satellite tracking in combination with switching SSM is an effective tool set to clearly define such distinct foraging sites, and further syntheses of marine turtle tracking datasets in the Gulf of Mexico is warranted.

Acknowledgements

All work was permitted by Florida Marine Turtle Permits 176 (K.H.), 094 (R.C., M.L.), and 155 (A.T.), as well as Dry Tortugas National Park permits DRTO-2008-SCI-0008 and DRTO-2010-SCI-0009 (K.H.). All turtle handling and sampling was performed according to Institutional Animal Care Protocols USGS-SESC-IACUC 2011-05, University of Florida IACUC-A621, and Mote IACUC 10-03-AT1. Funding for this work was provided by the National Park Service, USGS Priority Ecosystem Science Program, and USGS Coastal and Marine Geology Program. We acknowledge the use of www.seaturtle.org and the satellite-tracking and analysis tool (STAT), and the use of telemetry data generated as part of the ongoing Deepwater Horizon Natural Resource Damage Assessment which is publicly available on www.seaturtle.org. References to non-USGS products and services are provided for information only and do not constitute endorsement or warranty, expressed or implied, by the US Government, as to their suitability, content, usefulness, functioning, completeness, or accuracy.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.10.030.

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