# SPATIAL REOUIREMENTS OF DIFFERENT LIFE-STAGES OF THE LOGGERHEAD TURTLE (CARETTA CARETTA) FROM A DISTINCT **POPULATION SEGMENT IN THE NORTHERN GULF OF MEXICO**

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Abstract.—Many marine species have complex life histories that involve disparate developmental, foraging and reproductive habitats and a holistic assessment of the spatial requirements for different life stages is a challenge that greatly complicates their management. Here, we combined data from oceanographic modeling, nesting surveys, and satellite tracking to examine the spatial requirements of different life stages of Loggerhead Turtles (Caretta caretta) from a distinct population segment in the northern Gulf of Mexico. Our findings indicate that after emerging from nesting beaches in Alabama and Northwest Florida, hatchlings disperse widely and the proportion of turtles following a given route varies substantially through time, with the majority (mean of 74.4%) projected to leave the Gulf of Mexico. Adult females use neritic habitat throughout the northern and eastern Gulf of Mexico both during the inter-nesting phase and as post-nesting foraging areas. Movements and habitat use of juveniles and adult males represent a large gap in our knowledge, but given the hatchling dispersal predictions and tracks of post-nesting females it is likely that some Loggerhead Turtles remain in the Gulf of Mexico throughout their life. More than two-thirds of the Gulf provides potential habitat for at least one life-stage of Loggerhead Turtles. These results demonstrate the importance of the Gulf of Mexico to this Distinct Population Segment of Loggerhead Turtles. It also highlights the benefits of undertaking comprehensive studies of multiple life stages simultaneously: loss of individual habitats have the potential to affect several life stages thereby having long-term consequences to population recovery.

Key Words.—connectivity; dispersal; Loop Current; marine vertebrate; ocean circulation model; sea turtle

## INTRODUCTION

Numerous marine species are highly itinerant with life histories characterized by ontogenetic shifts in habitat use (Snover 2008). There are often substantial gaps in knowledge of the ecology of these species due to poorly-defined linkages between life stages or because they possess life stages that preclude direct observation (Bolten 2003; Rooker et al. 2007). This prob- age and reproduce at discrete but widely sepa-

lem is observed across diverse taxa, including species harvested by fisheries such as salmon (Snover et al. 2006), lobsters (Childress and Herrnkind 2001), tuna (Rooker et al. 2007), and reef fishes (Dahlgren and Eggleston 2000), as well as those of conservation concern such as sea turtles (Snover et al. 2010; Stewart et al. 2013) and marine mammals (Mendes et al. 2007; Drago et al. 2009). Adults of these groups often forrated locations (Pike 1962; Kenney et al. 2001; For example, molecular genetic studies have been Snover et al. 2006; Stewart et al. 2013). Environmental and anthropogenic factors occurring at each location, and along the oceanic corridors that link them, presumably play a substantial role in the growth, reproductive output, and survival of these species (Rooker et al. 2007; Saba et al. 2008). The deficiencies in basic information on the spatial ecology of such species across life stages impede the development of scientifically sound management recommendations and put the species and the fisheries that depend upon them at risk of collapse (Block et al. 2005; Hamann et al. 2010). Here, we provide a preliminary assessment of the spatial ecology across different life stages of a wide-ranging marine species from one distinct nesting group: Loggerhead Turtles (Caretta caretta) in the northern Gulf of Mexico (GoM).

Globally, Loggerhead Turtle populations today are much reduced from historic estimates (NMFS and USFWS 2008). Reasons for the decline of this species include interactions with commercial fisheries (Witherington et al. 2009), impacts on their habitat and food resources (which consist primarily of benthic invertebrates; Plotkin et al. 1993), pollution (Witherington 2002), and global warming (Hawkes et al. 2009). Loggerhead Turtles exhibit a life history that involves often disparate developmental, foraging, and nesting habitats (Bolten 2003; McClellan and Read 2007) which increases potential exposure to these activities throughout their life history. Hatchlings leave their natal beach, swim offshore and remain in oceanic habitats for several years (Bolten 2003; Godley et al. 2008, 2010). Many juveniles then recruit to neritic foraging areas, which may be offshore of their natal beach and may represent the same foraging habitat they will return to as adults (Limpus and Limpus 2001; Casale et al. 2007). Alternately an unknown proportion of juveniles remain in the open sea (McClellan et al. 2010; Arendt et al. 2012). New techniques and technologies have provided insights into movements and habitat use of different life-history stages. hatchling dispersal in this study. To determine

used to define distinct nesting groups (Shamblin et al. 2012), and satellite tracking technology combined with stable isotope analyses have broadly identified at-sea foraging areas (Marcovaldi et al. 2010; Zbinden et al. 2011; Pajuelo et al. 2012). However, relatively few efforts have been made to combine these analyses and technologies to derive an integrated understanding of the life history of this endangered species.

Connections between marine turtle nesting and foraging grounds are only recently being uncovered in the Gulf of Mexico. For example, genetic studies (Shamblin et al. 2012) have indicated that turtles nesting in the northern GoM represent one of ten recently defined Distinct Population Segments, and satellite telemetry has suggested female fidelity to the GoM by identifying foraging areas restricted to the southeastern and southern GoM for Loggerhead Turtles nesting in this region (Hart et al. 2012; Foley et al. 2014). Taken alone, these studies provide important information for each life-history stage. However when integrated with additional tracking data and information on hatchling dispersal, they have the potential to provide a more comprehensive view of the life history of this species. Using oceanographic models simulating hatchling dispersal, published information on juvenile Loggerhead Turtle habitat use, and satellite tracking data for adult female Loggerhead Turtles tagged on nesting beaches in the Northern Gulf of Mexico (Hart et al. 2014), we estimated the potential extent of each life stage in the Gulf of Mexico and calculated potential overlap among life stages.

### **MATERIALS AND METHODS**

Hatchling dispersal.—We used surveys for turtle nesting and hatching activity conducted from 1994 to 2011 every morning from 1 May to 30 November along 5 km of beach on Cape San Blas, in Northwest Florida (Fig. 1) to generate timing of the hatching season used to model



**FIGURE 1.** Cape San Blas represents the southern tip of the St. Joseph Peninsula in Northwest Florida, USA and is an important nesting beach for Loggerhead Turtles (*Caretta caretta*). The Peninsula forms the western boundary of St. Joseph Bay which supports a large number of juvenile turtles including Loggerhead Turtles.

likely dispersal routes for hatchling Loggerhead Turtles, we tracked the dispersal of virtual particles within hindcast output from the Gulf of Mexico Hybrid Coordinate Ocean Model (GOM HYCOM). The GOM HYCOM output has a spatial resolution of 0.04° (about 4.5 km grid spacing) and a daily snapshot of current velocity at midnight. The model is forced using wind stress, wind speed, heat flux, precipitation, and assimilates satellite altimetry data, sea surface temperature, and in situ measurements from expendable bathythermographs (XBTs), Argo floats, and moored buoys to produce realistic hindcast model output (http://hycom.org). Thus, GOM HYCOM hindcasts accurately resolve mesoscale processes such as meandering currents, fronts, filaments,

and oceanic eddies (Bleck 2002; Chassignet et al. 2007; Mariano et al. 2011). We performed numerical experiments with ICHTHYOP (v.2) particle-tracking software (Lett et al. 2008). For advection of particles, ICHTHYOP implemented a Runge-Kutta 4th order time-stepping method whereby particle position was calculated each half hour (Lett et al. 2008). To simulate sub-grid scale turbulent processes, we also included horizontal dispersion in the advection process (Lett et al. 2008). The HYCOM-ICHTHYOP system accurately predicts the movement of surfacedrifting buoys (Fossette et al. 2012; Putman and He 2013) and is well established for studying sea turtle dispersal (Lohmann et al. 2012; Putman and He 2013; Putman and Naro-Maciel 2013;



0.00 0.15 0.30 0.45 0.60 0.75 0.90 1.05 1.20 1.35 1.50

**FIGURE 2.** (a) Gulf of Mexico HYCOM domain in which simulations were performed. Boxes indicate regions in analyses (NW = northwest region, NE = northeast region, SW = southwest region, SE = southeast region). Dark grey shading indicates release locations of virtual particles. The thin black line closest to coast indicates the 20 m isobath, the thin line further from the coast indicates 200 m isobaths, i.e., the outer edge of the continental shelf. (b, c) Composite predicted distribution of 80,000 virtual particles released along Alabama and Florida panhandle from 2003–2010 and tracked over the course of 1.5 y. (b) Shading indicates the number of particles at a particular location throughout the 1.5-y simulation (counted at daily intervals). Note that the shading is scaled logarithmically (i.e,  $\log 10[n+1]$ , where n is the total number of particles at a particular location.

Naro-Maciel et al. 2014).

Every four days, we released 500 virtual particles in the coastal waters (5-20 m depth) between Baldwin County, Alabama (30.2°N, 88.0°W) and Franklin County, Florida (29.85°N, 84.35°W) from 1 August to 15 October in 2003–2010 (Fig. 2a). We programmed particles to swim offshore for the first 48 h at 0.25 m/s in accordance with the several day frenzy period known in Loggerhead Turtles (Wyneken and Salmon 1992). The particles then drifted passively the remainder of the 1.5-y simulation. Although even weak swimming can influence the distribution of marine organisms at sea (Putman et al. 2012a, 2014), we make no attempt to simulate turtle behavior beyond the initial frenzy period because such assumptions would introduce additional uncertainty that, without a priori information on orientation behavior of this population (e.g., Lohmann et al. 2012), would be impossible to parameterize. Instead, we present a strictly physical model of turtle dispersal based on circulation at the ocean surface. At half-year intervals (0.5, 1.0, 1.5 y), we recorded the percentage of particles that were in the northwest, northeast, southwest, and southeastern GoM (Fig 2a). Additionally, we recorded the percentage of particles that crossed east of longitude 80.5°W (into the Atlantic Ocean) within 0.5, 1.0, and 1.5 y.

**Overall distribution and overlap of life stages.**—We delineated areas in the GoM that are likely used by each life stage of Loggerhead Turtles. We defined hatchling dispersal extent as 0.04° grid cells in which at least one simulated particle crossed. We also defined hatchling high density areas, which are the grid cells with larger numbers of particles than the lower 95% confidence interval around the mean.

We delineated the juvenile extent by the 200m isobaths (Bolten 2003) using NOAA National Geophysical Data Center (GEODAS) ETOPO1, one arc-minute global relief model of Earth's surface (Available at http://www.ngdc.noaa.gov/ mgg/global/global.html Accessed 26 January 2012). Once hatchlings reach the juvenile stage, an unknown proportion remains in the oceanic environment (Casale et al. 2007; Arendt et al. 2012). Other juveniles move into neritic foraging grounds where they consume primarily hardshelled invertebrates in shallow habitats (Dodd 1988; Bolten 2003; Dalleau et al. 2014) with occasional foraging on mid-water prey (Narazaki et al. 2013). There is a great deal of evidence that these foraging areas can be near their natal beaches (Avens et al. 2003; Bolten 2003; Bowen et al. 2004; Casale et al. 2012; Clusa et al. 2014); however, few studies have examined abundance, distribution, or origin of juvenile Loggerhead Turtles in the GoM (Carr 1962; Renaud and Carpenter 1994; Bowen et al. 2004; Witherington et al. 2012). The Neritic stage of juvenile Loggerhead Turtles are generally thought to occupy the coastal waters, broadly in the vicinity of their natal site (Bowen et al. 2004, 2005) or where smaller turtles are initially carried by ocean currents (Clusa et al. 2014). Therefore, to determine the likely spatial extent of neritic stage juveniles, we selected waters in the GoM that were shallower than 200 m (i.e., the continental shelf) that received inputs of juveniles from the dispersal simulations described above.

Given that some individual juvenile Loggerhead Turtles of some populations make use of both nearshore and oceanic waters for foraging (McClellan and Read 2007; Mansfield et al. 2009; McClellan et al. 2010; Mansfield and Putman 2013; Dalleau et al. 2014), our assumptions here may underestimate of the extent of oceanic habitat used by juvenile Loggerhead Turtles. Of course, by including the entire continental shelf as potential habitat for juvenile turtles, we might overestimate the extent of juvenile habitat range in the GoM. Without tracking studies and genetic analyses, the movement patterns, habitat use, and connectivity of Loggerhead Turtles in the GoM remain unknown and force managers to broadly estimate potential juvenile extent, as was necessary for this study.

We estimated extent of the area used by adults based on satellite tracked locations of 47 nesting Loggerhead Turtles in northern GoM between Gulf Shores, Alabama, and the St. Joseph Peninsula, Florida, which were used in Hart et al. (2014). We filtered the satellite data without location quality (CL) Z by 5-km track speed and removed erroneous locations, such as locations on land. Using the remaining data, we created a minimum convex polygon as a proxy to the in-water area used by adults during inter-nesting, migration, and foraging periods. We calculated the area used by each size class as well as the area overlapped by different life stages using ArcGIS 10.3.

### RESULTS

Simulations based on GOM HYCOM surface currents indicate that young Loggerhead Turtles from Alabama and the Florida panhandle experience a wide range of dispersal possibilities (Fig. 2). Two dispersal trajectories are most prominent; one is southward via the Loop Current, the other is westward via eddies pinched off of the Loop Current. Particles entrained in the Loop Current are quickly advected out of the GoM and into the western Atlantic. In contrast, particles transported westward remain in the GoM for much longer, though eventually some of these will circulate out also. Predicted patterns of distribution within the GoM indicated that at 0.5 y, on average, 20.6% of particles were in northwest region, 17.2% were in the southeast region, 17.0% were in the northeast region, and 8.5% were in the southwest region. At 1.0 y, most particles were within the northwest region (15.3%), followed by the northeast region (13.0%), the southeast region (9.0%) and the southwest region (4.0%). After 1.5 y, most particles were within the northwest region (14.2%), followed by the southwest region (4.6%), the northeast region (3.5%), and the southeast region (3.4%). Within the first half year, on average, 36.7% of particles were advected out of the GoM, by 1.0 y this increased to

58.6%, and by 1.5 y this increased to 74.4% of particles (Table 1).

Given results from our dispersal modeling, in which the entire GoM continental shelf was predicted to receive inputs of northern Gulf posthatchlings (Fig. 2B), we defined the juvenile habitat as all areas within 200 m bathymetry contour in the GoM (i.e., the continental shelf). For our analysis of overall distribution and overlap of life stages, we found that at least 83% of the GoM was used by one life stage of Loggerhead Turtles (Table 2; Fig. 3). When examined by individual life stage, the potential extent for adult Loggerhead Turtles encompassed 83%, followed by the juvenile extent at 37% and the hatchling high-density area at 23%. Hatchlings and juveniles potentially overlap in 12% of the Gulf while hatchlings and adults overlap in 22%, and juveniles and adults in 31% (Table 2). In our estimates, areas that potentially support all three life stages of Northern Gulf Loggerhead Turtles cover 11% of the GoM.

### DISCUSSION

The problem of addressing ecological phenomena across scales is a central issue in biology (Levin 1992). Cross-scale studies are critical to complement more traditional investigations conducted on the single scales of space, time and organizational complexity (Levin 1992). Most studies use one method to provide information on one life stage at a time (Finstad et al. 2008; Druon et al. 2011; Hart et al. 2012; Putman et al. 2013; Casale and Mariani 2014). However, recent studies with marine turtles suggest linkages between life stages: dispersal routes of juveniles might determine the locations where adults will eventually forage (Hays et al. 2010; Scott et al. 2014) and spatial patterns of nest abundance appear to be determined by the proximity of beaches to ocean currents that facilitate hatchling offshore migration (Putman et al. 2010a, 2010b). Given these and other linkages between life stages, a holistic perspective is necessary to understand

Release Year	NW Region	SW Region	NE Region	SE Region	Outside Gulf
2003 - 0.5 y	38.3	14.6	15.9	14.3	25.8
2004 - 0.5 y	23.4	9.9	20.1	18.1	28.5
2005 - 0.5 y	18.3	8.6	14.1	13.2	45.7
2006 - 0.5 y	20.5	9.8	14.6	21.7	33.4
2007 - 0.5 y	21.1	5.7	29.5	17.5	26.2
2008 - 0.5 y	24.7	4.8	25.8	11.9	32.9
2009 - 0.5 y	17.9	14.5	16.3	20.1	31.2
2010 - 0.5 y	0.2	0.0	8.7	20.8	70.3
Mean - 0.5 y	20.6	8.5	7.0	17.2	36.7
2003 - 1.0 y	28.2	4.6	9.2	6.4	51.6
2004 - 1.0 y	13.0	7.1	12.5	3.8	63.6
2005 - 1.0 y	12.9	3.2	16.6	9.2	58.2
2006 - 1.0 y	14.0	5.6	8.7	9.1	62.6
2007 - 1.0 y	21.5	3.2	24.0	5.8	45.5
2008 - 1.0 y	22.1	4.8	16.0	16.2	40.9
2009 - 1.0 y	10.7	3.9	14.2	6.8	64.4
2010 - 1.0 y	0.3	0.0	2.6	15.3	81.8
Mean - 1.0 y	15.3	4.0	13.0	9.1	58.6
2003 - 1.5 y	28.1	4.2	3.2	4.1	60.4
2004 - 1.5 y	11.8	8.7	2.4	2.6	74.5
2005 - 1.5 y	12.6	3.3	4.2	5.9	74.0
2006 - 1.5 y	11.7	5.6	4.0	4.4	74.3
2007 - 1.5 y	19.9	4.0	2.8	2.9	70.4
2008 - 1.5 y	18.3	6.7	2.1	6.0	66.9
2009 - 1.5 y	10.6	4.0	3.0	0.4	81.9
2010 - 1.5 y	0.5	0.1	5.9	0.9	92.6
Mean - 1.5 y	14.2	4.6	3.5	3.4	74.4

**TABLE 1.** Percentage of particles in each region of the Gulf of Mexico at half-year intervals (see Fig. 2A for location of regions). Each particle represents one Loggerhead Turtle (*Caretta caretta*) hatchling emerging from a nesting beach in the northern Gulf of Mexico.

the ecology of these wide-ranging species. Our primary objective was to provide an integrated understanding of Loggerhead Turtle life history in the GoM. Our data highlight the importance of the GoM to Loggerhead Turtles and indicate that some Loggerhead Turtles that emerge from nesting beaches in the northern GoM may remain in this basin (Bird et al. 2005) throughout their entire lives. It also demonstrates that examining the spatial links between life stages is crucial for understanding the ecology of species that undertake ontogenetic shifts in habitat use.

Hatchling dispersal models indicate that, on tion of different hatchling cohorts) are most likely average, approximately 25% of particles that left regulated by dominant current patterns (Revelles

nesting beaches in the northern GoM did not enter the Atlantic but remained in the GoM for the duration of the 1.5-y simulation. Although the movements of oceanic juvenile turtles are unlikely to be completely passive, given their relatively weak swimming abilities, oceanic currents play a fundamental role in the movement (and thus habitat occupancy) of this life stage (Putman et al. 2012a, 2012b; Scott et al. 2012; Mansfield and Putman 2013). Therefore, dispersal of Loggerhead Turtles away from nesting beaches and distribution of oceanic juveniles (and variation in the distribution of different hatchling cohorts) are most likely regulated by dominant current patterns (Revelles



**FIGURE 3.** Distribution in the Gulf of Mexico for different life stages of Loggerhead Turtles (*Caretta caretta*) from the Northern Gulf of Mexico subpopulation including the simulated post-hatchling dispersal extent, high post-hatchling density areas (grid cells with greater than lower 95% CI in number of virtual particles), juvenile extent (within 200 m isobaths in the entire GoM), and adult extent estimated by minimum convex polygon (MCP) of 47 satellite-tracked nesting Loggerhead Turtles in Northern Gulf of Mexico. The satellite tracks of all 47 adult females are also shown. The insets show individual layers for each life stage and an image (all overlap) that highlights only those areas where life stages potentially overlap.

et al. 2007; Mansfield and Putman 2013). There are two dominant semi-permanent features of the circulation in the GoM: the Loop Current system in the eastern Gulf and an anti-cyclonic cell of circulation along the western boundary (Nowlin and McLellan 1967; Elliott 1982). Variation in the position of the Loop Current and the formation of eddies can be great however (Oey 1995) which helps explain the considerable annual variation among the eight hatchling cohorts we modeled, with as many as 39.6% of the 2003 hatchling cohort remaining in the GoM and as few as 7.4% of the 2010 cohort remaining. The predicted abundance of hatchlings in open waters (> 200 m water depth) was greatest to the north and gradually decreased to the south. Abundance was also relatively high along the coastline, as

well as extending along the east coast of Florida. Exceptions to high abundance in coastal waters included the Campeche Bank, Mexico, western Louisiana waters, and the waters around Cuba. This predicted distribution of post-hatchling Loggerhead Turtles reflects dynamic surface currents; high-energy processes such as eddies and tropical cyclones likely result in substantial dispersion and mixing of turtles.

High-energy currents also impact the age distribution (mean age of particles at a given location) of post-hatchlings. Our results suggest that younger turtles would be found within the deeper waters and older ones are more likely to be found in the vicinity of coastal regions. Smaller juveniles have been found to be strongly associated with *Sargassum* (Witherington et al.

	Area (km <sup>2</sup> )	Coverage (%)
Total area in the Gulf of Mexico	1,545,090	
Hatchling high density area (> lower 95% CL)	354,051	23
Juvenile extent	565,707	37
Adult extent	1,275,684	83
Hatchling-juvenile overlap	191,619	12
Hatchling-adult overlap	332,649	22
Juvenile-adult overlap	477,735	31
Hatchling-juvenile-adult overlap	173,020	11

**TABLE 2.** Estimated potential extent in  $km^2$  and by proportion of the entire Gulf of Mexico for three life stages of Loggerhead Turtles (*Caretta caretta*) from the Northern Gulf of Mexico subpopulation.

2012), which may explain the difference in distribution among sizes. Kemp's Ridley Turtles (Lepidochelys kempii) dispersing from beaches in northern Mexico also appear to be segregated by age with smaller (presumably younger) turtles found more in the western Gulf near the rookeries and larger (presumably older) juveniles found near areas known to be important juvenile foraging habitat (Collard and Ogren 1990; Witherington et al. 2012). Dispersal simulations of oceanic-stage Kemp's Ridley Turtles are generally consistent with this hypothesis (Putman et al. 2013). However, those recent modeling studies (Putman et al. 2013) and our present results also indicate that turtles of different, and of the same ages, potentially mix extensively. For instance, in less than half a year, turtles could disperse across the latitudinal and longitudinal extent of the GoM. These six-month old turtles would share the same space with turtles 1.5-y old, and indeed, even adults (see Fig. 1 in Hart et al. 2012). These analyses highlight the importance of this entire basin to the oceanic life stage of this Loggerhead Turtle population.

Also of note is the percentage of particles that are predicted to leave the GoM (74.4%, on average). Given the strength of the Loop Current (> 1.5 m/s) and the swimming ability of young Loggerhead Turtles (about 0.3 m/s; Scott et al. 2012), it is unlikely that swimming behaviors could keep all turtles within the basin even if they actively attempted to remain. Although the model domain

used in these simulations does not allow us to say much about the fate of the turtles that left, it suggests that this population has likely experienced significant evolutionary pressure to successfully navigate within the larger North Atlantic basin (Merrill and Salmon 2011; Putman et al. 2012b).

Our results suggest that it is plausible that much of the continental shelf across the GoM could be used as juvenile habitat (Dodd 1988; Bolten 2003; Cardona et al. 2009; Arendt et al. 2012; Dalleau et al. 2014). Within this broad developmental habitat, some observations suggest that individual turtles may show fidelity to fairly restricted areas (Revelles et al. 2008; Casale et al. 2012). Three juvenile Loggerhead Turtles have been recaptured in St. Joseph Bay (Margaret Lamont, unpubl. data), a coastal bay that borders one of the largest Loggerhead Turtle nesting beaches in the northern Gulf (Lamont et al. 2012; Fig. 4.). Two of these juveniles had originally been released in the bay after being held at the National Marine Fisheries Service laboratory in Galveston, Texas, USA: XXT304 was released on 28 May 2002 and recaptured on 12 June 2002 (15 d); XXT039 was originally released on 29 September 2001 and was recaptured on 28 July 2003 (667 d). The third turtle (RRX928) was originally captured and tagged in St. Joseph Bay on 27 June 2003 and was recaptured on 15 May 2005 (687 d) approximately 0.45 km from its original capture location. These long-term recaptures suggest these juveniles may exhibit fidelity



FIGURE 4. Release and recapture locations for juvenile Loggerhead Turtles (Caretta caretta) in St. Joseph Bay, Florida. Recaptures for two of the turtles (XXT304 and RRF293) occurred more than 600 d after initial capture suggesting these turtles exhibit long-term fidelity to this foraging location.

to developmental habitat (Revelles et al. 2008; Casale et al. 2012). In the context of these recaptures and published data on genetic analyses of juvenile Loggerhead Turtles in the northern GoM (Bowen et al. 2004), we can offer a hypothesis that some post-hatchling Loggerhead Turtles from northern GoM beaches return to shallow water habitats near their natal rookery and that these areas may serve as long-term developmental habitats. However, the lack of data on juvenile Loggerhead Turtles in this region must be addressed before a comprehensive understanding of juvenile habitat use in the GoM is possible.

hibit site fidelity both to nesting beaches and foraging grounds (Miller 1997; Marcovaldi et al. 2010). These foraging areas may also be the same ones they recruited to as juveniles (Limpus and Limpus 2001; Casale et al. 2007; Clusa et al. 2014). Recent analysis of 47 satellite tracks of post-nesting females from northern Gulf beaches by Hart et al. (2014) showed none of these females left the GoM: all migrated and established foraging areas within the GoM. This might be a conservative estimate of the adult female extent in the GoM as we used tracks from only 47 individuals to define this range. Given that there As adults, female Loggerhead Turtles often ex- are an estimated 141–1,012 females in the subpopulation (Lamont et al. 2014), this represents anywhere from 6-42% of the total population. A caveat to our findings, however, is that we include no data on the distribution of adult male Loggerhead Turtles in this study. To our knowledge, there are no data available on adult male Loggerhead Turtles from the northern GoM subpopulation. However, recent studies elsewhere suggest that distribution and movement patterns of male sea turtles is similar to that of females (Schofield et al. 2010; Arendt et al. 2012, Varo-Cruz et al. 2013). Arendt et al. (2012) tracked four adult male Loggerhead Turtles captured off the east coast of Florida into the Gulf of Mexico where they foraged in areas that overlap with reported foraging sites for females that had nested in the northern GoM (Foley et al. 2014; Hart et al. 2014) as well as females from additional subpopulations (Girard et al. 2009; Foley et al. 2014). The overlap in adult male and female foraging sites suggests our study may account for some adult male habitat use. Current sample sizes are small however and more tracking of adult males in the GoM is needed to fully understand habitat use of these turtles.

By integrating data sets among multiple life stages of Loggerhead Turtles, we suggest that at least some individuals in this population may complete their life cycle entirely within this relatively small ocean basin. The results of this study also demonstrate the importance of individual habitats within the GoM to multiple life stages (Fig. 3). Our overlap analysis suggests greater than two-thirds of the GoM is used by at least one life stage of Loggerhead Turtle. The assumptions made in this analysis must be acknowledged, however. For example, the assumptions involved in deriving juvenile extent (see Methods) and the use of 47 adult females to define the entire adult extent. The only way to improve these estimates and provide a better understanding of areas used by Loggerhead Turtles in the GoM is to fill these knowledge gaps with empirical data such as tracking and genetic analyses. While we recognize the limitations of our results, we believe

the analysis provides a useful starting point for understanding the spatial ecology of Loggerhead Turtles in the GoM and highlights areas that need additional attention. As our results demonstrate, understanding the relationships among life stages is crucial; management actions undertaken in one habitat not only affect the target life stage but may impact additional life stages as well. We believe this is particularly important considering recent critical habitat designations for Northwest Atlantic Loggerhead Turtles (NMFS and USFWS 2014).

Efforts have been made among taxa to synthesize data sets to examine connections among individual foraging or reproductive habitats (Block et al. 2005; Godley et al. 2010; Stewart et al. 2013); however, even these integrative studies are typically limited to one life stage. By demonstrating that some Loggerhead Turtles may remain in the Gulf their entire lives, we have highlighted the importance of considering the spatial requirements for multiple life stages simultaneously. Disasters, such as the Deepwater Horizon oil spill, may impact not only one life stage of Loggerhead Turtles from this declining population (Lamont et al. 2012, 2014), but multiple life stages. By identifying linkages in habitat use among different life stages of a wide-ranging species, we have provided information that allows critical habitats to be managed comprehensively rather than as individual areas supporting one specific life history parameter or one life stage.

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