Shared habitat use by juveniles of three sea turtle species

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ABSTRACT: The first step in understanding how sympatric species share habitat is defining spatial boundaries. While home range data for juvenile sea turtles exists, few studies have examined spatial overlap of multiple species in foraging habitat. Using satellite tracking technology, we define home ranges for juveniles of 3 sea turtle species (loggerhead, Kemp's ridley, and green; n = 21) captured at 2 adjacent foraging sites in the northern Gulf of Mexico. In these areas, green turtles are known to be primarily herbivorous, whereas Kemp's ridley turtles forage predominately on crabs, and loggerhead turtles on various hard-shelled benthic invertebrates. No differences in home range size or characteristics, such as water depth and distance to shore, were observed among species, although fine-scale foraging patches were not examined in this study. A high degree of overlap in habitat-use among all 3 species was documented in summer at both sites. Seasonal movements, triggered by colder winter temperatures, were documented and appeared to differ among species, with Kemp's ridley and loggerhead turtles leaving bays, and green turtles overwintering inside bays. By identifying shared habitat-use by juvenile sea turtles, we have created a foundation for further fine-scale studies on resource partitioning that will aid in habitat management and conservation of these threatened and endangered species.

KEY WORDS: Gulf of Mexico · Loggerhead · Home range · Satellite tracking · Kemp's ridley · *Chelonia*

INTRODUCTION

How sympatric species share habitat is a primary question in ecology (Roughgarden 1976, Gowans & Whitehead 1995, Pendoley et al. 2014). Concepts such as niche partitioning have been developed to help us understand adaptations that allow shared habitat use by similar species. To avoid competition, species can divide resources through morphological adaptations, variations in diet, or life-history traits (Hayward & Kerley 2008, Owen-Smith & Mills 2008, Sousa et al. 2016) For example, herbivores grazing in the African savannah partition grasslands by body size, habitat (e.g. grass height), and digestive ability, to avoid competition (Cromsigt & Olff 2006). Species can also partition resources through behavior; for example lizards vary activity patterns in response to

light (Leal & Fleishman 2002). In sympatric shorebird species, foraging resources are partitioned by microhabitat, environmental conditions, and foraging behavior (Burger et al. 1977, Bocher et al. 2014).

In marine systems, resource partitioning has been documented for many species including elasmobranchs (Cartamil et al. 2003, Speed et al. 2012), marine mammals (Pinela et al. 2010, Kernaléguen et al. 2015), and fish (Linke et al. 2001). Sharks using coastal habitats segregate themselves in a variety of ways, including by life-stage (Simpfendorfer et al. 2005). For example, in southwest Florida, the smallest bull sharks *Carcharhinus leucas* use estuarine waters. As they mature, they move into more open water habitats (Simpfendorfer et al. 2005). This ontogenetic partitioning has also been reported for marine mammals (Kernaléguen et al. 2015) and sea turtles (Fer-

reira et al. 2018). Adult female sea turtles deposit clutches of eggs in sandy beaches. After emerging from the nest and traversing the beach, hatchlings spend their first few years in oceanic habitat (Miller et al. 1997). Many juveniles of the hard-shelled species (i.e. all sea turtle species except the leatherback *Dermochelys coriacea*) shift from oceanic to neritic habitat and some species, such as the green turtle *Chelonia mydas*, also transition from a primarily omnivorous to a primarily herbivorous diet (Bjorndal & Bolten 1988, Reich et al. 2007, Cardona et al. 2009a). While in neritic foraging habitats, juvenile sea turtles frequently utilize similar habitats, yet spatial overlap within these habitats has not been investigated (Shimada et al. 2016, Fernandes et al. 2017).

The first step in understanding relationships among sympatric species in shared habitat is defining the spatial boundaries for those species. Once the boundaries are delineated, understanding the ecological role can be furthered through knowledge on the trophic interactions and resource use that may exist within these species. Habitat use, movement patterns, and home range sizes for various juvenile sea turtle species have been reported at foraging sites throughout the world's coastal habitats (Van Dam & Diez 1998, Cardona et al. 2009b, Seney & Landry 2011, González Carman et al. 2012). Characteristics of habitat use have been described including home range size (Schmid & Witzell 2006), diurnal (Bechhofer & Henderson 2018) and seasonal (Fernandes et al. 2017) movement patterns, and relationships to environmental variables (Brooks et al. 2009, Hart & Fujisaki 2010). While our knowledge of habitat use by juvenile turtles has increased, the majority of work examines habitat use by one species at a time.

All species of sea turtles using US waters are listed as threatened or endangered under the (US) Endangered Species Act of 1973 (www.fws.gov/endangered/esa-library/pdf/ESAall.pdf). The northern Gulf of Mexico (GoM) supports loggerhead *Caretta caretta*, Kemp's ridley *Lepidochelys kempii* and green turtles (hereafter referred to as loggerheads, Kemp's ridleys and greens), yet few studies have been published on these assemblages. Much of the data originate from information gathered during mass stranding events due to extreme cold temperatures (i.e. cold stunning; Foley et al. 2007, Avens et al. 2012). Seasonal and diurnal movements have been documented for greens, which are generally considered a tropical species (Broderick et al. 2007, Christiansen et al. 2017), and for Kemp's ridleys (Shaver & Rubio 2008, Seney & Landry 2011), which are the smallest of the hard-shelled sea turtle species. On the other hand, logger-

heads, which are large-bodied and considered more temperate, exhibit a dichotomy in seasonal movement patterns (Broderick et al. 2007, Hawkes et al. 2007, Zbinden et al. 2008, Dujon et al. 2018). Juvenile green turtles that stranded in northwest Florida during a cold stunning event were found to originate from nesting beaches in Mexico and on Florida's east coast (Foley et al. 2007), and assemblages in south Texas originated primarily from nesting beaches in southern Florida and the Caribbean (Anderson et al. 2013). Little is known of juvenile loggerhead assemblages in the GoM, although Bowen et al. (2004) suggested juvenile loggerheads forage in nearshore waters off of their nesting beaches. Information on abundance, home range, and habitat use of juvenile turtles in this region is lacking (see Schmid & Witzell 2006, Seney & Landry 2011, Lamont et al. 2015). This data gap was highlighted during the *Deepwater Horizon* oil spill that occurred in April 2010 (Bjorndal et al. 2011). Without baseline information on the home ranges and movement patterns of juvenile turtles in the GoM, it was difficult to determine whether turtles were affected by the spill. To address this data gap and explore the potential for shared habitat use by juvenile turtles, we examined tracking data from satellite tags deployed on Kemp's ridleys, loggerheads and greens in 2 adjacent coastal bays in northwest Florida.

MATERIALS AND METHODS

Study site

St. Joseph (SJB) and St. Andrew (SAB) Bays are located in northwest Florida in the northern GoM (Fig. 1A). SJB covers approximately 26 000 ha in Gulf County, Florida. It has a mean depth of 7 m, the greatest depth being 13.3 m in the northern end and the shallowest being 1 m in the southern end (FL DEP 2008). Seagrass beds cover approximately one-sixth of the Bay (4000 ha) and are most abundant in the shallow southern end (FL DEP 2008). The most abundant seagrass species is *Thalassia testudinum.* SAB is similar in size to SJB, covering about 28 000 ha in Bay County, Florida (FL DEP 2004). It has a maximum depth of 12 m with shallower (<5 m) seagrass and mud flats fringing the deeper channels throughout the bay. SAB is divided into 5 segments: Main Bay, East Bay, North Bay, West Bay, and Crooked Island Sound. Seagrasses cover approximately 4300 ha, with *Thalassia testudinum* also dominating this system. SAB is surrounded by Panama City (population
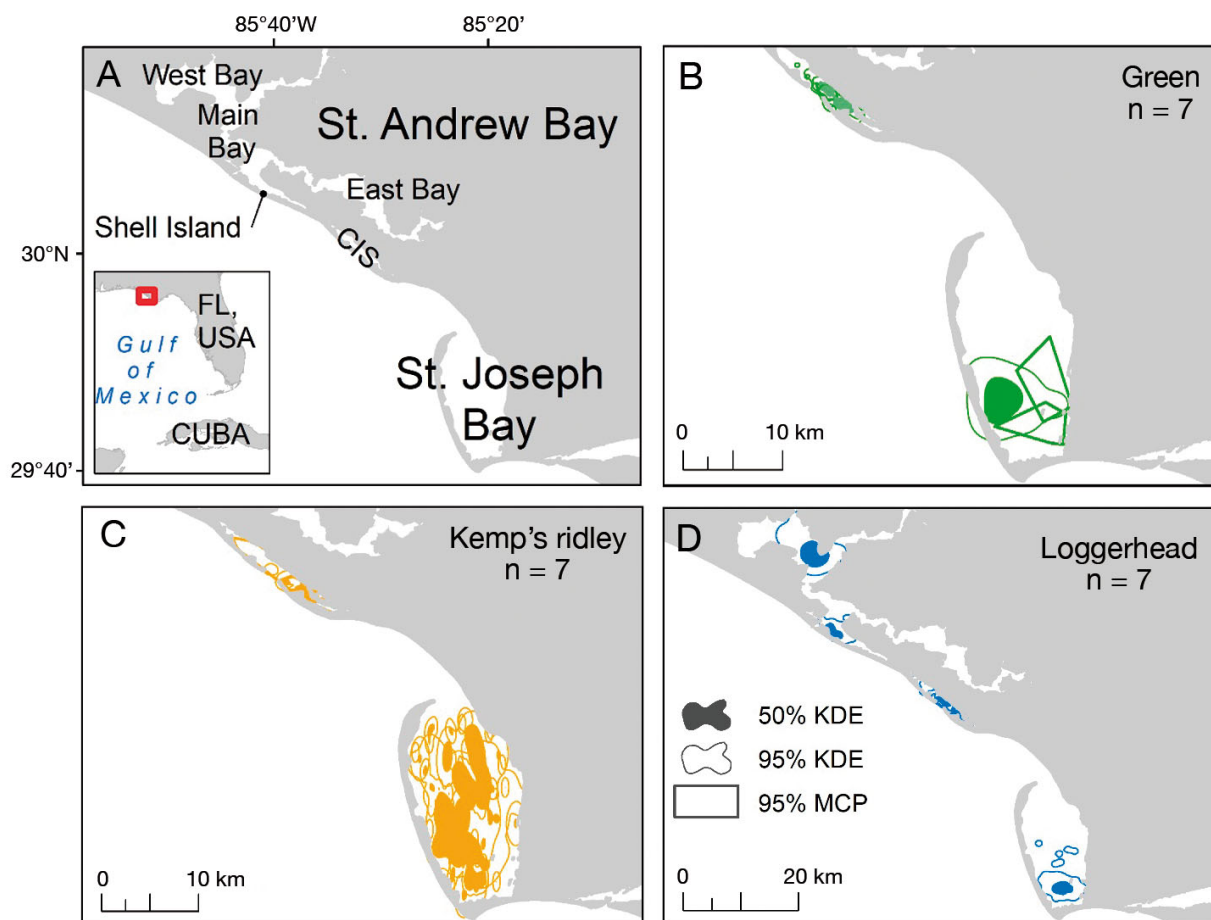
Fig. 1. (A) Location of St. Joseph and St. Andrew Bays in northwest Florida. (B–D) Juvenile green *Chelonia mydas*, Kemp's ridley *Lepidochelys kempii* and loggerhead *Caretta caretta* sea turtles were tracked. Shown are core-use areas (50% kernel density estimates [KDEs]) and home ranges (95% KDEs and 95% minimum convex polygons [MCPs]) for the 3 species (Kemp's ridley, loggerhead and green)

38 000) and Tyndall Air Force Base and is considered less pristine than SJB, which is bordered only by the small town of Port St. Joe (population 3500; FL DEP 2004, 2008).

Turtle capture

Turtles were captured in SAB (n = 42) and SJB (n = 254) from 2011–2017. These captures included greens (SJB = 60, SAB = 28), Kemp's ridleys (SJB = 171, SAB = 10), and loggerheads (SJB = 23; SAB = 7). All turtles were captured between March and November using a set net, dip net, or by hand. All captured turtles were individually marked with a metal Inconel tag placed along the trailing edge of each front flipper and a passive integrated transponder (PIT) tag placed subcutaneously in the left shoulder. Turtles were measured using 2 methodologies: (1) straight carapace length (SCL) and width using calipers, and (2) curved cara-

pace length (CCL) and width using a cloth tape measure. Weight was determined by placing the turtle in a harness and hanging the harness from a hand-held Pesola spring scale. A subset of healthy turtles, depending on their size (>30 cm CCL), was selected to carry a SPOT5 satellite tag (Wildlife Computers). Turtle size was compared among species using PROC GLM on SAS 9.4 software.

Satellite tag deployment

Satellite tags were fitted to the dorsal portion of the carapace using a cool-setting epoxy (Superbond™) and following established protocols (NMFS SEFSC 2008). We ensured that the total weight of the Platform Transmitting Terminal (PTT) and epoxy did not exceed 5% of the turtle's body weight. Prior to PTT attachment, we removed epibionts and cleaned and sanded the attachment site with isopropyl alcohol.

We streamlined the attachment materials to reduce drag on the turtle (Watson & Granger 1998). All tagged turtles were released at or near their capture location. Each tag was set to be active for 24 h d^{-1}.

Tracking and filtering

Locations were tracked with the Argos satellite system and downloaded using the Satellite Tracking and Analysis Tool (Coyne & Godley 2005) available on www.seaturtle.org. We summarized data when the transmissions ceased. We used all location classes (LC) except LC Z as these locations fail the Argos plausibility test (CLS 2011). We then filtered the remaining locations by speed (points requiring >5 km h^{-1} movement), land (locations on land or crossing land, e.g. into inland bays), and distance (>120 km from remaining locations). Finally, we separated out locations defined as 'forays' (see 'Forays' section below; see Dujon et al. 2018 for an alternative foray definition). Once 'true' forays were identified, the remaining locations outside the bay were removed as erroneous. Similarly, during times of extended forays, points inside the bay were removed as erroneous.

Overall home ranges

With filtered locations inside bays, we quantified site fidelity using the software program RStudio, version 1.0.143 (R Core Team 2017) and the package 'adehabitatLT' (Calenge 2006). We compared each animal's movement trajectory to 100 replicates of randomly generated trajectories (random walks). These were generated by randomizing the angles of the observed trajectories' steps. Then the R-squared and linearity values from the observed and random trajectories were compared. We constrained the random walks to represent realistic movements for turtles; we set the bounds from −200 m to 0 m, but smoothed this with a 750 m inland buffer to allow for random walks to be generated close to land. Movements exhibiting site fidelity are more spatially constrained than randomly dispersed (Hooge et al. 2001); we defined turtle tracks to have site fidelity if the observed track was more constrained than the random tracks using an alpha level of 0.05. Tracks that passed site fidelity were included in home range analyses.

To minimize autocorrelation and prepare for home range analyses, we generated mean daily locations (MDL) from filtered locations for each turtle using the software program R version 3.1.2 (R Core Team 2017). When a track had ≥20 MDLs, we used kernel density estimation (KDE) and when a track had <20 MDLs, we used filtered satellite locations and created 95% minimum convex polygons (MCPs).

We calculated KDEs and MCPs using R and the package 'adehabitatHR' (Calenge 2006). KDE appropriately weights outlying observations to identify areas of disproportionately heavy use within a home range (Worton 1987, 1989, White & Garrott 1990). For each KDE, we applied the fixed-kernel least-squares cross-validation smoothing factor (h_{cv}) (Worton 1995, Seaman & Powell 1996). When the standard deviation of the x and y coordinates were unequal (<0.5 or >1.5), we re-scaled the data by dividing the coordinates by their standard deviation (following Seaman & Powell 1996). We classified 95% KDE contours as home ranges and 50% KDE contours as core-use areas (Hooge et al. 2001). We used ArcMap 10.4 (ESRI 2016) to calculate the area (km^2) within each KDE and MCP.

For each 50% KDE and 95% MCP, we obtained the centroid location; if a 50% KDE included multiple separated contours, we calculated the centroid for the largest contour area. For each centroid location we calculated the distance to the nearest shoreline and extracted the associated bathymetry value using the NOAA National Geophysical Data Center (GEODAS) ETOPO1, 1 arc-minute global relief model of Earth's surface (www.ngdc.noaa.gov/mgg/geodas/geodas.html; accessed 26 January 2012). However, due to poor resolution of this bathymetry layer in SAB (all values 0 m) we manually measured water depth at centroid locations using a Garmin 74SV. Because of the relatively large errors associated with location-only data, we were unable to determine diurnal movement patterns or associate movements with environmental variables such as tides. Use of GPS tags or acoustic tracking would be necessary to address these issues (Dujon et al. 2018).

Lastly, we combined all 95% KDEs for each species separately and incorporated these data into a 0.5 km grid to depict the number of species (1 to 3) using each grid cell across all grid cells with 95% KDEs. Home range characteristics among species was assessed using PROC GLM on SAS 9.4 software.

Forays

Due to satellite location error estimates and the relatively small geographic area of the bays, we defined forays outside the bays based on a set of criteria. A foray must include: (1) consecutive points outside the

bay for >30 h, (2) at least one high-quality LC (1, 2, 3, or 0), and (3) at least 4 consecutive locations. To describe forays, we measured the length of foray tracks (summed straight-line distance between filtered locations) and the furthest distance between foray locations and the turtle's home range centroid. We also extracted the minimum and maximum bathymetry values along the track and the minimum/ maximum distance from the nearest shoreline.

A logistic regression using PROC LOGISTIC on SAS 9.4 was used to analyze the response of forays (1 = no foray, 2 = foray) on the independent variables of season (fall, spring and winter; small sample sizes prohibited inclusion of summer), species, temperature, and speed of the turtle. We used ordinal season (fall = September–November; winter = December– February; spring = March–May) temperatures because of the sample size requirements to run a logistic regression with class variables.

Temperature

Sea surface temperature (SST) was obtained from University of Southern Florida buoy data (http:// optics.marine.usf.edu, accessed 1 June 2017). To match locations to temperature data in SAB we used data from station SAB 01, and for SJB we used data from SJB 03. For foray data we matched locations to stations OSJ 01 and OAP 01. Data from buoys included weekly mean SST and we matched these values to locations using the R package 'plyr' (Wickham 2011). Locations with 'NA' values were removed (n = 30) and the remaining were incorporated into a 0.5 km grid showing the overall average from all locations in each grid cell of weekly mean SST values.

RESULTS

Tracking and filtering

We tracked 21 juveniles from 2 different bays (SAB and SJB; Fig. S1 in the Supplement at www.int-res. com/articles/suppl/m606p187_supp.pdf) and 3 species: Kemp's ridleys (7), loggerheads (7) and greens (7). Mean (±SD) CCL size of greens was 42.3 ± 7.4 cm, Kemp's ridleys 42.4 ± 7.6 cm, and loggerheads 74.7 ± 8.9 cm (Table S1 in the Supplement). Loggerheads were significantly larger than Kemp's ridleys and greens (p < 0.001). To help describe the overall scope of the study, we combined tracking times for all individuals which resulted in a total tracking time of

2084 d with a mean (±SD) tracking time of 99.2 ± 106.0 d. Species-specific averages were 45.9 ± 44.6 d for greens, 57.4 ± 40.9 d for Kemp's ridleys, and 194.4 ± 133.5 d for loggerheads. During this time, we obtained 4071 filtered locations: 699 for greens, 1218 for Kemp's ridleys, and 2154 for loggerheads (Table S1).

Home ranges

Home range size and characteristics did not differ among the 3 species (Fig. 1B–D). We ran 4 ANOVA designs. The response variables with model p-values were log of the 50 % KDE (p = 0.2739), log of the 95 % KDE (p = 0.1631), centroid water depth (p = 0.6291), and centroid distance from land (p = 0.2944). We also ran the log of the 50 % KDE and log of the 95 % KDE with tracking days as a covariable, but they were also not significant with p-values of 0.1413 and 0.1193, respectively. The grid with home ranges (95 % KDEs) shows overlap for all 3 species in the Crooked Island Sound section of SAB and in the southern portion of SJB (Fig. 2). The area for the in-water portions of grid cells used by 1 species was 186.4 km^2, for 2 species 37.7 km^2, and for 3 species 37.4 km^2.

Greens

Four of 7 greens had enough MDLs for KDE analysis. These KDEs represented 252 tracking days and 161 MDLs (Fig. 1D). Mean (±SD) core-use areas and home ranges were 4.2 ± 5.2 km^2 and 15.8 ± 19.4 km^2, respectively. Centroids were close to shore (mean 0.9 km) and in shallow water (mean 4.3 m deep; Fig. S2 in the Supplement). Three turtles had MCPs covering 44 tracking days (Fig. 1) with a mean size of 12.0 ± 9.6 km^2; Table 1).

Kemp's ridleys

Of the 7 Kemp's ridleys, 6 had enough MDLs for KDEs (Fig. 1B); however, one of these did not pass the site fidelity test (ID 120862) and was not used in KDE analysis. The 5 KDEs represented 253 tracking days and 216 MDLs. Mean (±SD) core-use areas and home ranges were 13.5 ± 13.2 km^2 and 53.1 ± 48.4 km^2, respectively. Centroids were close to shore (mean 1.5 km) and in shallow water (mean 3.6 m deep; Fig. S2, Table 1). Two turtles had MCPs covering 36 tracking days (Fig. 1) with a mean size of 7.6 km^2 (Table 1).

Loggerheads

All 7 loggerheads had enough MDLs for KDE analysis (Fig. 1C). These KDEs covered 1106 tracking days and 432 MDLs. Mean (±SD) core-use and home range areas were 4.3 ± 4.7 km^2 and 17.7 ± 19.2 km^2 respectively. Centroids of 50% KDEs were a mean 0.7 km from shore and in water an average of 3.1 m deep (Fig. S2, Table 1).

Forays

Ten turtles took forays outside the bays in which they had home ranges (Table 2). Two turtles (1 Kemp's ridley and 1 loggerhead) had 2 different forays each. For all species, mean weekly SST was about 22°C at the first foray locations. Length of forays ranged from 5.1 km (greens) to 444.3 km (Kemp's ridleys). Seasonal temperature had a positive effect on whether a turtle undertook a foray, with forays occurring more often in winter than in fall (p < 0.0001). In addition, Kemp's ridleys were more likely to undertake a foray than loggerheads (p < 0.0001).

DISCUSSION

Three primary dimensions describe the ecological niche of a species: habitat, time and diet (Kiszka et al. 2011). Our study involved only 2 of those dimensions (habitat and time) and only during a snapshot in time (e.g. while the individuals were tracked). Although we did not examine diet in this project, studies have described separation in diet between herbivorous green turtles and carnivorous Kemp's ridleys and loggerheads (Witzell & Schmid 2005, Brooks et al. 2009, Williams et al. 2014). Potential exists however for overlap in diet between these species (Marshall et al. 2014). Wallace et al. (2009) demonstrated high frequency of blue crabs (*Callinectes sapidus*) in juvenile loggerhead diets in North Carolina; blue crabs also comprise the majority of the diet for juvenile Kemp's ridleys in Southern Florida (Witzell & Schmid 2005) and Texas (Shaver 1991). Flexibility in diet has been demonstrated for both species, and for juvenile green turtles, depending on foraging location (Burke et al. 1994, Seney & Musick 2005, Peckham et al. 2011, Williams et al. 2014). For example, Kemp's ridleys at a foraging location in southwest Florida foraged primarily on tunicates (Witzell & Schmid 2005).

Although this study included a relatively small sample size of 7 individuals from each species at only 2 foraging sites in the GoM, significant overlap in habitat use by all 3 species was observed in summer in both bays (Fig. 2). Home range characteristics among species, such as size and water depth, were not statistically different although this may reflect the small sample sizes available for analyses. It may also reflect the lack of fine-scale data available from the
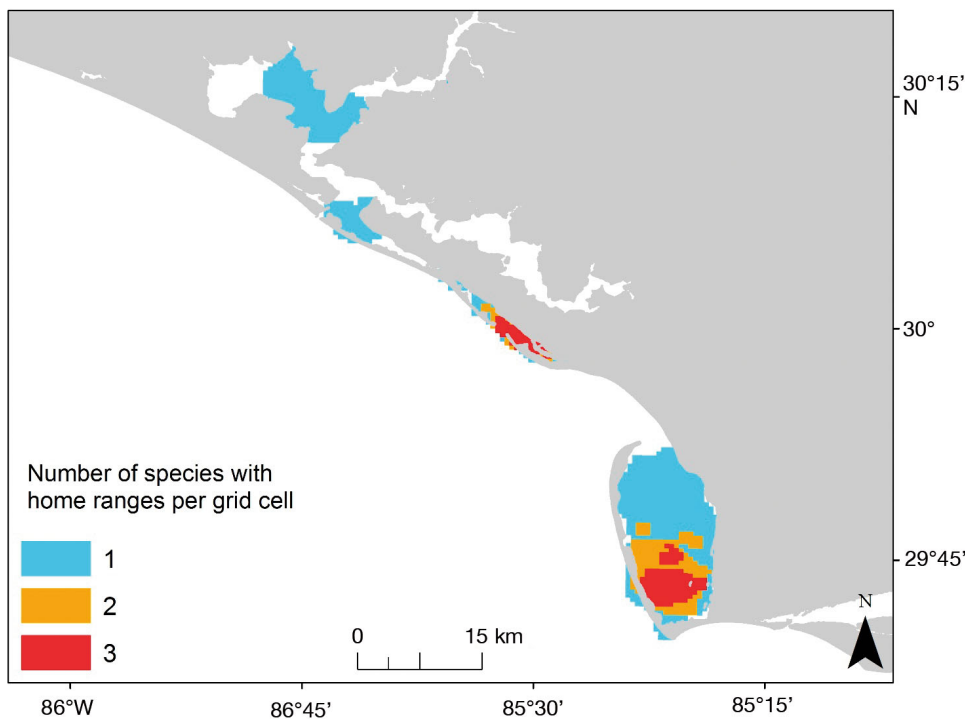

Fig. 2. Grid (0.5 km squares) depicting the number of species that have their home range (95% kernel density estimate) in each cell. Species comprise green *Chelonia mydas*, Kemp's ridley *Lepidochelys kempii*, and loggerhead *Caretta caretta* sea turtles

location-only satellite tags used in this study (see Dujon et al. 2018). Loggerheads reportedly forage in deeper waters than Kemp's ridleys (Keinath et al. 1987, Byles 1988) but that was not evident in our study. In fact, loggerhead home ranges were slightly shallower (−3.1 m) than Kemp's ridleys (−3.6 m) although this comparison was not statistically significant. Partitioning of resources in this habitat may occur through variations in body size or diet. Dietary overlap tends to be greatest between species of similar body size (Kartzinel et al. 2015); adult Kemp's ridleys are the smallest sea turtle species whereas adult greens are the largest of the hard-shelled turtles

(NMFS & USFWS 1991, NMFS et al. 2011). Turtle size in this study differed among species with greens (42.3 cm) and Kemp's ridleys (42.4 cm) significantly smaller than loggerheads (74.7 cm). Although adult Kemp's ridleys and loggerheads use neritic waters in the GoM, Hart et al. (in press) identified minimal overlap in foraging locations for these species. With fine-scale information available from acoustic tracking (Fujisaki et al. 2016) or GPS tags (Dujon et al. 2018), partitioning of resources within species' home ranges in these coastal bays may be evident.

For many sympatric species, there is clear interspecific differentiation in resource use. For example,

Table 1. Kernel density estimate (KDE) and minimum convex polygon (MCP) values for 3 species of juvenile sea turtles (green *Chelonia mydas*, Kemp's ridley *Lepidochelys kempii*, and loggerhead *Caretta caretta*) satellite-tagged in the northern Gulf of Mexico. S.F. = site fidelity; MDL = mean daily location; C. bathy = centroid bathymetry; C. dist = centroid distance to shore. Land was removed from KDE and MCP layers prior to area calculation. For centroid bathymetry, those marked with asterisk were measured manually (see 'Materials and methods: Overall home ranges') and rounded to the nearest integer. Dates are mm/dd/yy; '−' = no data

ID	Type	Home range dates (d)	S.F. p-value	MDL	50% KDE (km²)	95% KDE (km²)	95% MCP (km²)	C. bathy (m)	C. dist. (km)
Green									
104832	MCP	10/6−10/12/2011 (7)	0.0099	7	−	−	20.43	−6	2.06
104833	KDE	10/22−11/21/2011 (31)	0.0099	23	11.92	44.89	−	−5	2.05
104831	MCP	10/27−11/12/2011 (17)	0.0495	10	−	−	13.85	−1	0.98
120864	KDE	5/15−6/25/2013 (42)	0.0099	35	1.88	7.02	−	−3*	0.40
141028	KDE	10/2−11/9/2014 (39)	0.0099	29	1.90	6.50	−	−4*	0.59
141021	KDE	7/16−12/2/2016 (140)	0.0099	74	1.01	4.77	−	−5*	0.59
141030	MCP	9/28−10/17/2016 (20)	0.0099	10	−	−	1.58	−5*	0.53
	KDE mean	63.0	−	40.3	4.2	15.8	−	−4.3	0.9
	KDE SD	51.5	−	23.0	5.2	19.4	−	1.0	0.8
	MCP mean	14.7	−	−	−	−	12.0	−3.7	1.2
	MCP SD	6.8	−	−	−	−	9.6	2.5	0.8
Kemp's ridley									
120862	MCP	5/10−5/29/2013 (20)	0.2277	20	−	−	12.64	−4*	0.52
141029	KDE	9/24−10/22/2014 (29)	0.0099	26	2.79	9.28	−	−1*	0.14
141020	KDE	9/3−10/6/2015 (34)	0.0099	32	0.94	3.88	−	0*	0.00
141023	MCP	9/5−9/20/2015 (16)	0.0099	14	−	−	2.57	−4*	0.61
141033	KDE	10/27/2016−1/17/2017 (83)	0.0099	73	9.07	48.17	−	−1	2.20
141034	KDE	10/27/2016−1/10/2017 (76)	0.0099	63	30.46	111.9	−	−7	2.26
141032	KDE	11/16−12/16/2016 (31)	0.0396	22	24.45	92.14	−	−9	2.96
	KDE mean	50.6	−	43.2	13.5	53.1	−	−3.6	1.5
	KDE SD	26.6	−	23.2	13.2	48.4	−	4.1	1.4
	MCP mean	18.0	−	−	−	−	7.6	−4.0	0.6
	MCP SD	2.8	−	−	−	−	7.1	0.0	0.1
Loggerhead									
120863	KDE	3/25/2013−6/19/2014 (452)	0.0099	93	6.00	32.50	−	−2	1.62
141025	KDE	8/28−11/13/2014 (78)	0.0099	44	1.33	5.14	−	−3*	0.35
141026	KDE	8/30/2014−5/19/2015 (263)	0.0099	39	13.91	54.72	−	−5	0.79
141027	KDE	9/12−12/19/2014 (99)	0.0099	78	4.06	13.72	−	−4	0.83
141022	KDE	7/29−11/21/2016 (116)	0.0099	98	0.98	4.13	−	−3*	0.47
141024	KDE	8/23−10/3/2016 (42)	0.0099	28	3.41	11.55	−	−4*	0.52
141031	KDE	10/27−12/21/2016 (56)	0.0099	52	0.42	2.37	−	−1*	0.01
	KDE mean	158.0	−	61.7	4.3	17.7	−	−3.1	0.7
	KDE SD	148.9	−	27.8	4.7	19.2	−	1.3	0.5

Table 2. Trips taken outside of bays where home ranges occurred (forays) for 3 species of juvenile sea turtles (green *Chelonia mydas*, Kemp's ridley *Lepidochelys kempi*, and loggerhead *Caretta caretta*) satellite-tagged in the northern Gulf of Mexico. Two turtles took 2 forays each (marked with 'a' and 'b' after ID number). Foray start = the local date and time for the first foray location; Days = the number of days turtles were tracked on a foray; SST = mean weekly SST for week containing the foray start date; Length of track = successive distances between foray points, summed together; Furthest dist. from C. = the largest straight-line distance between any foray location and the turtle's home range centroid; Min./Max. bathy = the smallest and largest bathymetry values for foray locations; Min./Max. dist. to shore = smallest and largest straight-line distances between any foray location and the nearest shoreline

ID	Foray start	Days	SST (°C)	Length of track (km)	Furthest dist. from C. (km)	Min. bathy	Max. bathy	Min. dist. to shore (km)	Max. dist. to shore (km)
Green									
104833	11/12/2011 9:24	5.5	20.0	47.5	25.5	−27	−4	0.1	20.5
141028	10/22/2014 21:18	1.4	24.3	5.1	2.6	−5	0	0.0	1.3
	Mean:	3.4	22.2	26.3	14.0	−16.0	−2.0	0.1	10.9
	SD:	2.9	3.0	30.0	16.2	15.6	2.8	0.1	13.6
Kemp's ridley									
141020a	9/14/2015 12:11	1.5	28.0	13.6	9.0	−20	0	1.0	7.3
141020b	10/13/2015 23:32	22.6	25.6	273.2	20.7	−23	0	0.02	9.5
141032	12/16/2016 16:07	6.0	17.5	60.4	28.6	−17	−2	0.02	12.9
141033	1/18/2017 14:21	44.2	17.7	444.3	73.4	−27	0	0.01	30.1
141034	11/21/2016 4:04	2.5	21.4	10.5	14.1	−20	−11	3.6	7.9
	Mean:	15.4	22.0	160.4	29.2	−21.4	−2.6	0.9	13.5
	SD:	18.2	4.7	191.9	25.8	3.8	4.8	1.5	9.5
Loggerhead									
141024	9/12/2016 19:27	3.4	29.2	104.2	19.4	−24	−4	0.0	15.4
141025	12/2/2014 13:13	65.3	17.8	295.5	134.7	−44	−12	15.2	71.4
141026	12/10/2014 20:10	36.3	17.3	27.5	72.0	−26	−14	0.7	6.7
141027a	10/19/2014 20:38	1.4	26.2	64.6	33.1	−13	−3	0.0	1.9
141027b	11/6/2014 10:28	1.4	21.5	7.6	3.1	−13	−2	0.1	1.6
	Mean:	21.6	22.4	99.9	52.5	−24.0	−7.0	3.2	19.4
	SD:	28.6	5.2	115.4	52.6	12.7	5.6	6.7	29.6

small odontocetes forage at different trophic levels or on different prey items (Pinela et al. 2010, Kiszka et al. 2011). In sea turtles, greens are known to be primarily herbivorous which would appear to naturally segregate them from carnivorous species such as Kemp's ridleys and loggerheads. However, recent studies have reported omnivorous behavior in juvenile greens (Lemons et al. 2011, Williams et al. 2014) and greens appear capable of crushing small invertebrates such as crabs (Marshall et al. 2014). Although diet studies show greens forage on soft-bodied invertebrates (i.e tunicates) and typically not on species utilized by Kemp's ridleys and loggerheads these physiological studies suggest limited potential for overlap in diet between greens, Kemp's ridleys and loggerheads. A more in-depth examination of trophic levels used by these 3 species through stable isotope analyses is necessary at our study site to better understand the role of diet in resource partitioning among juvenile sea turtles (Gross et al. 2009, Kiszka et al. 2011).

Temporal partitioning of habitat has also been described for some marine species (Speed et al. 2012). Diurnal variations in habitat use have been documented for juvenile turtles (Seminoff et al. 2002, Senko et al. 2010); however, due to methods used (i.e. location-only tags versus GPS tags or acoustic tracking; Senko et al. 2010, Dujon et al. 2018) these comparisons were not possible in our study. There is the potential that the juvenile turtles in our study partitioned the resource seasonally. Substantial overlap in home ranges occurred in summer in the southern end of SJB and the eastern end of CIS (see Fig. 2), however, more Kemp's ridleys and loggerheads made seasonal movements out of the bays during winter than greens. This is supported by stranding data that show large numbers of greens documented during mass stranding events due to extreme cold during winter in SJB (Foley et al. 2007, Avens et al. 2012). Four of the 7 (57%) Kemp's ridleys and 4 of 7 (57%) loggerheads left the bays in winter whereas only 2 of 7 (29%) greens appeared to leave the bays
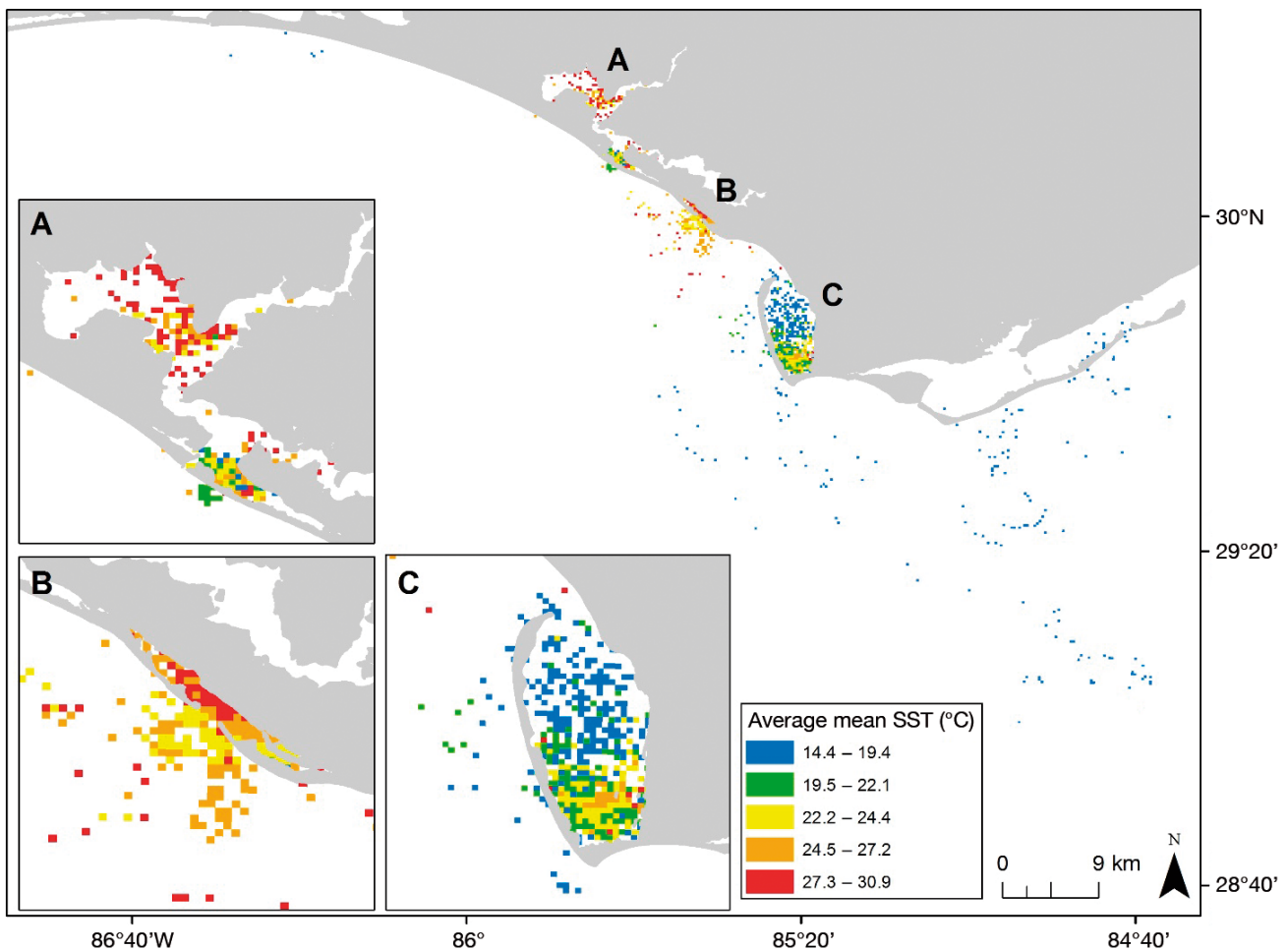
Fig. 3. Grid (0.5 km squares) depicting the weekly mean sea surface temperature (SST). For each cell, filtered locations across all turtles were matched with weekly mean SST, and then these values were averaged for 1 value per grid cell. Species comprise green *Chelonia mydas*, Kemp's ridley *Lepidochelys kempii*, and loggerhead *Caretta caretta* sea turtles

(but see below regarding green forays). Some of this individual variation may reflect tracking times: the 4 Kemp's ridleys that left the bays were tracked into at least mid-November whereas the 3 that did not leave were not tracked past October 23.

Movements undertaken by individuals in this study appeared to be driven by water temperatures (Fig. 3). As poikilothermic species, sea turtles are negatively impacted by extremely cold temperatures (Avens et al. 2012). Water temperatures below 10°C can affect sea turtle physiology and mortality can occur at temperatures below 5−6°C (Schwartz 1978, Anderson et al. 2011). Turtles have been shown to move into deeper waters when SST falls below 20°C (Mendonça 1983). In this study, the mean temperature at which forays out of the bays were initiated was 22.0°C (Table 2). Individual variation within species was observed with temperatures at foray initiation ranging from 17.5−28.0°C for Kemp's ridleys, 17.3−29.0°C for

loggerheads and 20.0−24.4°C for greens (but see below regarding green turtle forays). The minimum SST documented in this study was 14.4°C which falls within the range reported at Kemp's ridley winter foraging grounds elsewhere in the GoM (Schmid & Witzell 2006, Coleman et al. 2016).

We observed seasonal movements out of the bays for a few loggerheads and Kemp's ridleys. Seasonal movements of juvenile Kemp's ridleys have been documented for turtles in Texas (Shaver & Rubio 2008, Seney & Landry 2011), Mississippi (Coleman et al. 2016) and northeastern GoM (Schmid & Witzell 2006) waters and these seasonal migrations were initiated primarily in mid to late November (Schmid & Witzell 2006). Seasonal movements by juvenile loggerheads appear less consistent than those reported for juvenile Kemp's ridleys and this was also evident in our study. For example, the loggerhead that we tracked for the longest time (462 d) remained in SJB

for the entire tracking period. Researchers have documented a dichotomy in seasonal movements by loggerheads with some individuals making seasonal movements south in winter and others remaining at latitude but moving from summer neritic foraging grounds into oceanic waters in winter (McClellan & Read 2007, Cardona et al. 2009b, Hawkes et al. 2011, Arendt et al. 2012, González Carman et al. 2016). In addition, loggerheads may move out of foraging patches for several weeks in winter to allow for resource recovery before returning to their original foraging site (Dujon et al. 2018). In the northern GoM, loggerheads are individual specialists: they exhibit variation in diet across the species but specialization within individuals (Vander Zanden et al. 2010). Availability of prey items may vary among years or seasons. If an individual's primary prey item becomes over-foraged, that individual may undertake a foray to utilize another location while the primary foraging area recovers (Dujon et al. 2018). Although coastal bays in the northern GoM are considered temperate and shallow (e.g. maximum depth of SJB = 10 m) at least some loggerheads remained in these bays through the winter. To our knowledge, this nonmigratory over-wintering behavior has not been reported elsewhere.

It would be expected that tropical green turtles would move out of temperate foraging grounds during winter while loggerheads, which in this study were also larger bodied individuals than greens, would have a greater tendency to remain (see Broderick et al. 2007), however, this was not what we observed. Two green turtles fit our criteria of exhibiting foray movements outside of the coastal bays, however, it is possible that these individuals did not actually leave the bays. Both SJB and Crooked Island Sound are separated from the GoM by narrow sandy spits of land (St. Joseph Peninsula = 500–750 m wide; Shell Island = 100–250 m wide). The most accurate Argos location classes (LC) available for non-GPS capable tags (LC 3) have an error of <250 m and LC 0 has an error of >1500 m. Because of this potential error, a relatively high-quality location such as LC 0 (the minimum LC class we used for our foray criteria; see 'Materials and methods') for a turtle that is inside the bay may actually be outside of the bay and in the GoM. These 2 green turtles established home ranges immediately adjacent to the sandy spits separating the bays from the GoM. They showed no track leading out of the mouth of either bay and both supposed forays were relatively short (1–5 d). Because of these reasons, we suspect these individuals remained inside of the bays throughout the duration of their

tracking periods. Regardless, a majority of greens tracked during this study did not leave the bays during their tracking periods.

Juvenile greens overwinter in many areas (Felger et al. 1976, Mendonça 1983, Southwood et al. 2003, Hart & Fujisaki 2010, MacDonald et al. 2013, Shimada et al. 2016) but also exhibit seasonal movements in others (González Carman et al. 2012, Vélez-Rubio et al. 2018). Stranding (Foley et al. 2007, Avens et al. 2012) and previous acoustic tracking (Lamont et al. 2015) data support our findings of over-wintering by green turtles in SJB. These seasonal movements are most likely related to prey availability. Stomach contents of stranded greens from this foraging site suggest these individuals forage throughout the winter but not necessarily on seagrass. Diet of some individuals included invertebrates, such as tunicates, and stable isotope analyses supported low consistency in winter diet for greens in St. Joseph Bay (Williams et al. 2014). This flexibility in diet may allow greens to remain in this productive system year-round. St. Joseph Bay has some of the most extensive and healthy seagrass meadows in Florida (Yarbro & Carlson 2013) and this habitat supports an extremely productive invertebrate community (Valentine & Heck 1993). Some invertebrate species appear at greater densities in SJB than at other sites in the northern GoM (Valentine & Heck 1993). Although we did not document green turtles leaving the bays in winter, there is evidence (Lamont et al. 2015, Lamont et al. 2018) that green turtles in SJB move to deeper waters in response to falling temperatures, as was reported by Broderick et al. (2007). The availability of resources and proximity to deep water within SJB may allow greens to over-winter in this temperate habitat (Lamont et al. 2018).

In general, home range sizes for turtles tracked in Northwest Florida were smaller for the carnivorous species and larger for herbivorous greens than home range sizes documented elsewhere using similar methods as we used here. Kemp's ridley home range sizes were similar to those reported in the northeastern GoM (Schmid & Witzell 2006) but smaller than other areas such as Texas (Seney & Landry 2011) and Mississippi (Coleman et al. 2016). Loggerhead home ranges were smaller than those reported in the Mediterranean (Casale & Simone 2017), southern Atlantic (Barcelo et al. 2013) and mid-Atlantic (Hawkes et al. 2011, Arendt et al. 2012). Green home ranges were larger than those reported in SJB using acoustic technology (Lamont et al. 2015), which may reflect differences in tracking methodology rather than behavior. McClellan & Read (2007) tracked greens using both

satellite tracking and manual acoustic tracking and reported maximum MCPs were less than a third of the size when gathered using acoustic technology than with satellite tags. Many factors can influence home range size calculations (Thomson et al. 2017) and these should be considered when making comparisons among studies. Interspecific variation in home range size is predominately driven by body-size dependent metabolic requirements (Harestad & Bunnel 1979, Lindstedt et al. 1986, van Beest et al. 2011), however, intraspecific variations have been shown to be driven by a variety of intrinsic and extrinsic characteristics including age, reproductive status, rainfall and temperature (van Beest et al. 2011). For sea turtles, home range size differs greatly between neritic (~10 km^2) and oceanic habitats (1000 km^2; Schofield et al. 2010) which most likely reflects differences in density of prey. Our home range estimates only considered time spent inside the bays; forays outside the bays were not included in these analyses, therefore, our home range estimates were more similar to those calculated for neritic habitat than oceanic habitat.

Resource partitioning promotes biodiversity (Hutchinson 1959, Chase & Leibold 2003, Bowen et al. 2013). Understanding how species use available resources is therefore critical in conserving both the species and the habitat. First, however, we must define how species are using the habitat by identifying home ranges and their associated environmental characteristics. Here, we present the first home range estimates for a multi-species assemblage of juvenile sea turtles sharing habitat in the northern GoM. This study identifies a multi-species 'hot spot' in the northern GoM and highlights the need for further studies on resource partitioning by juvenile turtle species particularly concerning diet and fine-scale movement patterns.

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