Comparing Diets of Kemp's Ridley Sea Turtles (*Lepidochelys kempii*) in Mangrove Estuaries of Southwest Florida

Jeffrey R. Schmid^{1,2} and Anton D. Tucker^{3,4}

¹Conservancy of Southwest Florida, 1495 Smith Preserve Way, Naples, Florida USA ³Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida USA

ABSTRACT.—We quantified diets of Kemp's Ridley Sea Turtles (*Lepidochelys kempii*) in Charlotte Harbor National Estuary, Florida, to identify possible ontogenetic variation in prey consumption, to examine the use of local prey, and to contrast the diets of conspecifics at other foraging areas. Dietary analysis was conducted by identifying prey remains recovered in 58 fecal samples from 53 turtles (24.2–63.7 cm midline straight carapace length). Turtles consumed seven prey categories: crustaceans, chelicerates, fish, sessile invertebrates, molluscs, plants/algae, and unidentified items. Spider crabs (*Libinia* sp.) are the dominant prey consumed in the mangrove estuary, occurring in 94.8% of fecal samples, accounting for 71.4% of dry mass, and as 76.3% in the Index of Relative Importance. We found no significant ontogenetic differences in prey composition between small (<40 cm) and large (≥40 cm) turtles, although crustaceans were more prevalent in diets of the larger turtles. The prey consumed in Charlotte Harbor differed significantly from a similar study of a nearby mangrove estuary in the Ten Thousand Islands. Sandy-Skinned Tunicates (*Molgula occidentalis*) were the predominant food item in the latter locale, and there were no significant ontogenetic differences in prey composition. A comparison of prey availability and use suggests that Kemp's Ridley Sea Turtles ingested the most abundant prey in the Charlotte Harbor estuary. Geographic differences in diet may reflect localized differences in use of foraging habitat and available prey, but more studies are needed on the availability, use, and selection of both habitat and prey.

Ontogenetic shifts in resource use are common in reptiles with patterns of diet change predicted to occur with increasing body size (Werner and Gilliam, 1984). Marine turtles increase in size by several orders of magnitude during their life time and most species have complex life cycles involving developmental shifts in habitat and diet (Bjorndal, 1996; Snover, 2008). For Kemp's Ridley Sea Turtles (Lepidochelys kempii), epipelagic juveniles (<20 cm straight carapace length [SCL]) primarily feed omnivorously on the invertebrates associated with the Sargassum surface drift community (Shaver, 1991; Witherington et al., 2012). Post-pelagic turtles (20-25 cm; Ogren, 1989) begin feeding mainly on demersal crabs after recruiting to coastal habitats and cancrivory continues through adulthood (>60 cm). Gonadal development is estimated to begin at ~40 cm SCL, leading some researchers to suggest the Kemp's Ridley Sea Turtle life cycle includes a prematurational juvenile stage (20–39 cm) and a maturational subadult stage (40–59 cm; Coyne, 2000). Size-specific shifts in habitat use and associated prey for immature coastal-benthic turtles may coincide with the proposed physiological changes (Schmid et al., 2003; Schmid and Barichivich, 2005, 2006). Body size-based differences in feeding habits have been demonstrated among immature Green Sea Turtles (Chelonia mydas) inhabiting U.S. coastal waters (Redfoot and Ehrhart, 2013; Howell et al., 2016).

Potential influences on marine turtle diet include resource availability, growth and energetic requirements, and resource use abilities or limitations (Werner and Gilliam, 1984; Snover, 2008). Kemp's Ridley Sea Turtles are opportunistic consumers of a variety of crab species (Shaver, 1991), feeding on the most abundant species (Werner, 1994) or exhibiting selectivity for less abundant species (Morreale and Standora, 1998). For selective feeding, size-specific prey use may occur in which smaller

²Corresponding Author. E-mail: jeffs@conservancy.org

DOI: 10.1670/16-164

turtles consume easily captured walking crabs (e.g., spider crabs, *Libinia* sp.) and then transition to the consumption of more elusive swimming crabs (e.g., Blue Crabs, *Callinectes sapidus*) as they grow and forage more extensively in coastal-benthic habitats (Morreale and Standora, 1998, 2005). Additional diet selection studies are needed to relate availability of potential food items to those that are ingested by turtles at different foraging areas.

Most information on regional variation in Kemp's Ridley Sea Turtle diet are derived from turtles collected along temperate saltmarsh coastlines, but inferences derived from these studies may not apply to foraging areas in the southern portion of the species' range. Turtles inhabiting a subtropical estuary in the Ten Thousand Islands, Florida, fed primarily on the benthic tunicate Molgula occidentalis despite indications of crabs available as prey (Witzell and Schmid, 2005). A Kemp's Ridley Sea Turtle in Charlotte Harbor was observed feeding on a horseshoe crab (Limulus polyphemus; Barleycorn and Tucker, 2005), a relatively rare food item in other studies, but there is no other information on turtle diet or availability of prey within this subtropical estuary. Charlotte Harbor is a large open-water estuary with a mangrove fringe coastline, three major rivers contributing freshwater from the urbanized mainland and a series of barrier islands separating the marine waters of the Gulf of Mexico. Approximately 90 km to the south, the Ten Thousand Islands estuary is comprised of numerous small mangrove islands and backwater embayments with many small tributaries and undeveloped mangrove forest extending inland. Pine Island Sound has the highest seagrass coverage in the Charlotte Harbor complex (Corbett, 2006), whereas seagrass is discontinuous and patchy in the Ten Thousand Islands (Iverson and Bittaker, 1986). The proximity of these subtropical foraging areas allows for investigation as to whether prey compositions may differ given the characteristics of each estuary. Improved biological understanding of Kemp's Ridley Sea Turtle foraging ecology coupled with protection of habitats rich in prey species is essential to the management of conservation areas in each estuarine complex.

⁴Present address: Western Australia Department of Parks and Wildlife, 17 Dick Perry Avenue, Kensington, Western Australia, Australia.

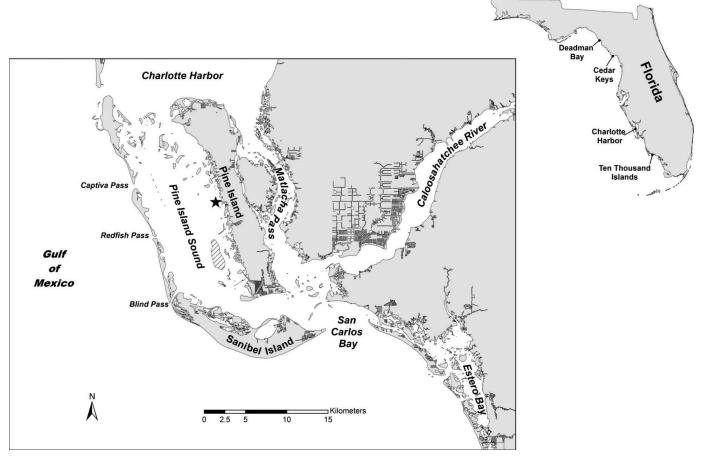


Fig. 1. Map of southwest Florida showing the lower region of the Charlotte Harbor National Estuary. The black star indicates the location of Mote Marine Laboratory's field station on Demere Key, and the cross-hatched polygon denotes our study area.

This study addresses questions regarding ontogenetic and regional differences in the dietary composition of Kemp's Ridley Sea Turtles in mangrove estuaries of southwest Florida. We chose to examine whether patterns of prey consumption for turtles in Charlotte Harbor differ from that of an earlier study in the Ten Thousand Islands, whether there was ontogenetic variation in prey composition in these subtropical estuaries, how prey use may differ from the availability of common prey found at the Charlotte Harbor study site, and how the diet of conspecifics may vary from different regions of the geographic range.

Materials and Methods

Turtle Capture.—We focused turtle collections in the Pine Island Sound portion of Charlotte Harbor estuary and based operations from the Mote Marine Laboratory (MML) field station on Demere Key (Fig. 1). Five-day surveys were conducted monthly between March and May and August and November from 2009 to 2013. We used a 7-m tunnel hull boat to deploy a 200-m strike net with 35.5 cm stretch-mesh nylon webbing, 4 m deep, braided polyfoam float line, and braided leadcore line per protocols established by previous studies (Witzell and Schmid, 2004). The net was deployed only when a turtle was visible at the surface and retrieved within 20 min of the sighting. Minimum straightline carapace length (MSCL, midline of nuchal scute to the posterior notch of supracaudals) of captured turtles was measured to the nearest 0.1 cm with Vernier calipers. We recorded the physical condition of the turtle as to injuries

(carapace and flipper wounds, etc.) or other abnormalities and examined each turtle for tag scars and previously applied external and internal tags. Inconel flipper tags (National Band and Tag Co., Newport, KY) were applied to the trailing edge of the front flippers and a GPT 12 passive integrated transponder (PIT) tag (Biomark Inc., Boise, ID) inserted into the left front flipper of previously untagged turtles.

Diet Samples.—Upon capture, we transported turtles to the field station and transferred individuals into shaded holding tanks at dockside with ambient temperature seawater (FFWCC, 2007). The water in holding tanks was changed twice daily with seawater pumped from Pine Island Sound. Turtles usually passed a fecal bolus within 24–48 h of capture and all excreta were collected into individually marked plastic bags, which were frozen for later analysis. Each turtle was returned to its original capture site following the collection of fecal samples.

We thawed and washed the fecal samples through U.S. standard #4 (4.75 mm) and #200 (0.075 mm) sieves. The items retained by a #4 sieve were identified to the lowest possible taxon, and items retained by the #200 sieve were unidentified given the small size of components. Sorted prey items were placed in aluminum weighing dishes and dried in an oven at 80°C for 24 h. Dry mass (to the nearest 0.01 g) of each prey item in each sample was measured on an electronic balance.

Local Prey Availability.—Concurrent with turtle sampling, we conducted a sample of decapod prey species during trips from August 2011 to April 2013. We deployed three baited wire mesh crab traps in areas of turtle capture and checked traps at least

once each day. Trapped items were identified to the lowest taxonomic level, enumerated, and released near the collection site. Our passive sampling method allowed for an inventory of the local decapod fauna despite potential bias for catchability with baited traps and prioritization of effort to turtle capture. The trap survey provided an index of decapod availability relative to those occurring in turtle fecal samples and added a temporal context for putative prey in the study area.

Data Analyses.—We determined percent frequency of occurrence (% FO) and percent dry mass (% DM) of prey items in each fecal sample by:

% FO =
$$\left(\frac{\text{number of samples containing prey item}}{\text{total number of samples}}\right) \times 100$$

% DM =
$$\left(\frac{\text{dry mass of prey item}}{\text{total mass of all prey items}}\right) \times 100$$

Prey items were not enumerated owing to mastication of the food and resultant difficulties with identifying prey fragments as discrete units (Hyslop, 1980). Analyzing diet based on feces may omit or underestimate more digestible components (Burke et al., 1993; Bjorndal, 1996), but such bias was assumed minimal given the durophagous habits of Kemp's Ridley Sea Turtles (Pritchard, 2007). We used the index of relative importance (IRI) modified from Bjorndal et al. (1997) for mass and calculated for each prey group *i* with the equation:

$$\%IRI = \frac{100(FO_iDM_i)}{\sum_{i=0}^{n}(FO_iDM_i)}$$

The prey data were grouped by turtle size class (<40 cm MSCL and ≥40 cm MSCL) corresponding to the possible onset of gonadal maturation in larger immature turtles (Coyne, 2000). We used PRIMER v6 software (Clark and Gorley, 2006) to examine ontogenetic differences in prey compositions. The fecal mass of the prey items was converted to percent compositions using the total mass of each sample. Mass measurements provide a more accurate representation of diet than do frequency of occurrence data as the latter may overrepresent small quantities of prey (Deagle et al., 2007). Furthermore, calculating the percent composition for each sample standardizes for differences in fecal mass and size of the turtle (Lindeman, 2006). We generated a Bray-Curtis similarity matrix for the prey mass proportions of captured turtles and compared the prey compositions of the size classes with one-way analysis of similarity (ANOSIM; 9,999 permutations).

The prey data in Charlotte Harbor (CH) estuary were contrasted with a published diet study in the Ten Thousand Islands (TTI; Witzell and Schmid, 2005). Both studies used the same methods for turtle capture and data collection. Carapace length distributions for turtles used in each study were compared with the Mann-Whitney *U*-test. As described above for CH, we converted fecal mass of prey items for turtles in TTI to percent compositions and compared the prey mass proportions of size classes. Fecal sample data for CH and TTI were combined and the prey mass proportions were compared by locality. Prey items contributing to any significant differences in diet composition were identified for the localities. Nonmetric multidimensional scaling (NMDS) was applied to the combined similarity matrix to plot the relationships of prey compositions by locality.

We summed the trapped collections of decapod crustaceans for comparison to the occurrence of prey in fecal samples of each concurrent trip. A Bray-Curtis similarity matrix was calculated for the decapod frequency proportions of each trip and one-way ANOSIM was used to compare the composition of prey availability, as measured by trap-caught decapods, with prey consumption, as measured by turtle fecal composition. The SIMPER routine was used to identify decapods contributing to any differences in prey availability and use. The annual differences in the frequencies of the predominant crab species in turtle fecal samples were compared with Chi-square tests. All means are followed by \pm SD.

RESULTS

Most Kemp's Ridley Sea Turtles we captured in Pine Island Sound were immature with relatively low recapture rates and consequently very few repetitive fecal samplings. Fifty-eight fecal samples were collected from 53 turtles, 5 of which were recaptured after multiple months at liberty and yielded two independent samples. Turtle sizes ranged from 24.2 to 63.7 cm MSCL with a mean size of 40.7 ± 8.5 cm MSCL. Two turtles were adult-size (\geq 60 cm). Dry mass of the fecal samples ranged from 3.10 to 116.54 g.

Crustaceans were the dominant prey category in fecal samples although turtles also consumed plants/algae, molluscs, chelicerates, fish, live bottom (i.e., sessile non-crustacean invertebrates attached to hard substrate), and unidentified prey items (Table 1). All turtles consumed crustaceans (100% FO), and this category had the highest percent dry mass (80.5% DM) and index of relative importance (80.9% IRI). Libinia sp. was the dominant prey item (94.8% FO, 71.4% DM, and 76.3% IRI). Balanus sp. had the second highest frequency of occurrence (36.2% F) for crustaceans, followed by Persephona mediterranea (32.8% FO); however, these items contributed only 0.7% and 7.2%, respectively, to the total fecal mass with correspondingly low relative importance. Plants/algae, primarily Halodule wrightii, were also a common food item (51.7% FO), but their negligible dry mass contribution (0.1% DM) and relative importance (<0.1% IRI) suggest plant/algal material was consumed incidentally with animal prey. Molluscs occurred in 15.5% of the samples but contributed only 0.3% to the total dry mass with a very low relative importance. The chelicerate L. polyphemus was a very minor component of the samples (5.2%) FO, 0.1% DM, and <0.1% IRI). Fish and live bottom were the least common categories (3.4% FO), and both had very low mass contributions and negligible relative importance. Two turtles had each consumed a single sea horse Hippocampus sp., and two others had limited quantities of the tunicates M. occidentalis or Styela plicata in the feces. All the samples contained unidentified components, primarily crab fragments passing through a #4 sieve, that represented the second highest mass contribution (19.0% DM) and second highest relative importance (19.1% IRI).

Ontogenetic Contrasts.—There were no significant differences in prey composition between the size classes although there were notable size-specific differences in the frequencies of some prey items (Table 1). The mass proportions of prey items were not significantly different (Global R=0.029, P=0.11) between turtles <40 cm (mean = 33.8 ± 5.0 cm MSCL, N=26) and those ≥40 cm (mean = 46.8 ± 5.9 cm MSCL, N=32). Libinia sp., P. mediterranea, and Balanus sp., particularly the latter, occurred more frequently in turtles ≥40 cm. Menippe mercenaria was found only in the samples of larger turtles as was the fish Hippocampus. Mollusc components occurred more frequently in turtles <40 cm, although Crassostrea virginica was more frequent for turtles ≥40

Table 1. Percent frequency of occurrence (% FO), dry mass (% DM), and index of relative importance (% IRI) for food items of Kemp's Ridley Sea Turtles captured in Charlotte Harbor National Estuary and size classes of captured turtles (<40 cm [N=26] and ≥40 cm [N=32]).

	% FO	% DM	% IRI	Turtles <40 cm			Turtles ≥40 cm		
Category/Taxa				% FO	% DM	% IRI	% FO	% DM	% IRI
Crustaceans	100.0	80.5	80.9	100.0	81.3	81.9	100.0	80.1	80.4
Libinia sp.	94.8	71.4	76.3	88.5	68.3	74.6	100.0	73.0	77.4
Persephona mediterranea	32.8	7.2	2.7	26.9	9.7	3.2	37.5	5.9	2.4
Hepatus epheliticus	6.9	0.6	< 0.1	7.7	1.4	0.1	6.3	0.1	< 0.1
Hexapanopeus angustifrons	3.4	0.2	< 0.1	7.7	0.6	0.1	0	0	0
Menippe mercenaria	5.2	0.3	< 0.1	0	0	0	9.4	0.4	< 0.1
Callinectes sapidus	1.7	0.1	0	3.8	0.4	< 0.1	0	0	0
Portunus gibbesii	1.7	< 0.1	Ö	0	0	0	3.1	< 0.1	ő
Calappa sp.	1.7	< 0.1	ő	3.8	< 0.1	ŏ	0	0.1	ő
Farfantepenaeus sp.	1.7	< 0.1	ő	0	0.1	ŏ	3.1	< 0.1	ő
Balanus sp.	36.2	0.7	0.3	23.1	0.9	0.3	46.9	0.6	0.3
Chelicerates	5.2	0.1	< 0.1	7.7	0.3	< 0.1	3.1	< 0.1	0.5
Limulus polyphemus	5.2	0.1	< 0.1	7.7	0.3	< 0.1	3.1	< 0.1	0
Fish	3.4	0.1	0.1	0	0.3	0.1	6.3	0.1	< 0.1
Hippocampus	3.4	0.1	ő	ő	ő	ő	6.3	0.1	< 0.1
Live Bottom	3.4	0.1	0	3.8	0.2	< 0.1	3.1	< 0.1	0.1
Molgula occidentalis	1.7	< 0.1	Ő	0	0.2	0.1	3.1	< 0.1	0
Styela plicata	1.7	0.1	0	3.8	0.2	< 0.1	0	0.1	0
Molluscs	15.5	0.3	< 0.1	23.1	0.3	0.1	9.4	0.2	< 0.1
Nassarius sp.	3.4	< 0.1	0.1	7.7	< 0.1	0.1	0	0.2	0.1
Cerithium sp.	1.7	0.1	0	3.8	< 0.1	0	0	0	0
Costoanachis sparsa	1.7	< 0.1	0	3.8	< 0.1	0	0	0	0
Costounuchis spursu Crepidula fornicata	1.7	< 0.1	0	3.8	< 0.1	0	0	0	0
	1.7	< 0.1	0	3.8	0.1	0	0	0	0
Busycon egg case	5.2	0.1	< 0.1	3.8	0.1	< 0.1	6.3	0.2	< 0.1
Crassostrea virginica	1.7	< 0.1	0.1	3.8	< 0.2	0.1	0.3	0.2	0.1
Modiolus sp.	1.7	< 0.1	0	0	0.1	0	3.1		0
Tagelus sp.			-	46.2				$< 0.1 \\ 0.1$	
Plants/Algae	51.7	0.1	< 0.1		< 0.1	< 0.1	56.3		< 0.1
Halodule wrightii	41.4	< 0.1	< 0.1	34.6	< 0.1	< 0.1	46.9	< 0.1	< 0.1
Thalassia testudinum	12.1	< 0.1	0	7.7	< 0.1	0	15.6	< 0.1	0
Syringodium filiforme	8.6	< 0.1	0	3.8	< 0.1	0	12.5	< 0.1	0
Acanthophora spicifera	3.4	< 0.1	0	3.8	< 0.1	0	3.1	< 0.1	0
Unidentified red algae	3.4	< 0.1	0	3.8	< 0.1	0	3.1	< 0.1	0
Unidentified green algae	1.7	< 0.1	0	3.8	< 0.1	0	0	0	0
Unidentified	100.0	19.0	19.1	100.0	17.9	18.0	100.0	19.5	19.6
Unidentified invertebrate	3.4	< 0.1	0	0	0	0	6.3	< 0.1	0
#200 unidentified	100.0	18.3	20.6	100.0	17.5	21.6	100.0	18.7	19.8
#4 unidentified	5.2	0.7	< 0.1	3.8	0.4	< 0.1	6.3	0.8	< 0.1

cm. Seagrasses *H. wrightii, Thalassia testudinum,* and *Syringodium filiforme* had higher frequencies in the samples of turtles \geq 40 cm.

Regional Contrasts in Diet.—Turtles inhabiting subtropical mangrove estuaries were similar sizes, but there were differences in major prey items for each foraging area. There was no difference in distributions of carapace length (Mann Whitney U =1694, Z = 0.49, P = 0.624) for turtles captured from CH (N = 58) and from TTI (N = 65), although the range of carapace lengths was less in TTI (28.2-52.5 cm MSCL). There was no significant difference of mass proportions of prey (Global R = -0.004, P =0.489) between size classes of turtles captured within TTI (<40 cm N = 28 and ≥ 40 cm N = 37). The prey mass proportions for turtles captured in CH were significantly different from those of turtles captured in TTI (Global R = 0.405, P = 0.0001) but the intermediate R-value indicates some overlap in prey compositions between these localities. The similarity percentages (SIM-PER) routine indicated a high average dissimilarity (78.3%) in prey composition between localities with a high proportion of Libinia sp. in the CH diets and a high proportion of M. occidentalis in the TTI diets (Table 2). Some turtle diets in TTI had relatively high contributions of Libinia sp. or P. mediterranea, which resulted in greater dietary variation for this locale and overlap with the prey composition of CH turtles (Fig. 2).

Local Prey Index.—There was a significant difference between the availability of crab species and their use by turtles, but the analysis was confounded by a crab species consumed by turtles that was missing from the trap survey. The trap collection of locally available prey yielded 160 Libinia sp., 20 Hepatus epheliticus, 5 Callinectes/Portunus, and 3 M. mercenaria. The decapod crustacean composition in the fecal samples (prey use) was significantly different (Global R = 0.137; P = 0.036) from the composition collected in traps (prey availability) during concurrent sampling trips (N = 9). The very low R-value, however, indicated the compositions were strongly overlapping and barely

TABLE 2. Prey items contributing the most (>10% dissimilarity) to differences in diet compositions for Kemp's Ridley Sea Turtles captured in Charlotte Harbor (CH) and captured in the Ten Thousand Islands (TTI) by Witzell and Schmid (2005).

	Averag prop	Percent contribution	
Prey items	CH captures	TTI captures	to dissimilarity
Libinia sp.	67.9	15.2	36.6
Molgula occidentalis	0.0	34.5	22.0
#200 unidentified	19.3	13.1	11.9
Persephona mediterranea	8.7	10.7	10.1

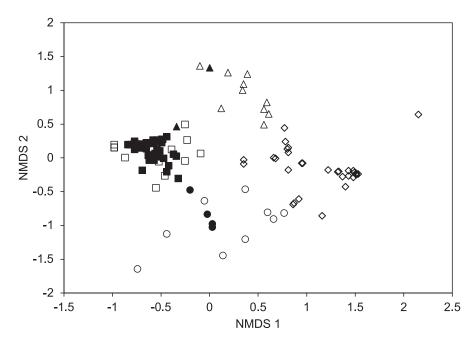


Fig. 2. Nonmetric multidimensional scaling (NMDS) of prey mass compositions showing dietary overlap and variation for Kemp's Ridley Sea Turtles captured in Charlotte Harbor (closed symbols) and Ten Thousand Islands (open symbols). Polygons denote groupings of the prey items contributing the most (>10% dissimilarity) to differences in diet compositions: square, *Libinia* sp.; circle, *Persephona mediterranea*; diamond, *Molgula occidentalis*; and triangle, #200 unidentified.

differed in terms of resource availability and usage. The similarity percentages (SIMPER) routine also indicated a low average dissimilarity (30.8%) for the compositions with *Libinia* sp. and *P*. mediterranea contributing the most to the differences (Table 3). Libinia sp. was the most abundant decapod available in Pine Island Sound and a primary food item for captured turtles, but the average proportion of use (72.5%) was lower than that of availability (91.2%). Persephona mediterranea was not captured in crab traps and, therefore, perceived as unavailable as prey, but this decapod had the second highest average proportion of use (16.9%) in diets of captured turtles. There also appeared to be annual variation in the use of P. mediterranea as a prev item during the duration of the study. Persephona mediterranea had a higher frequency of occurrence in 2011 fecal samples (Fig. 3), and there was significant variation in its annual occurrence during 2010–2012 ($\chi^2 = 14.800$, df = 2, P = 0.0006) but not for *Libinia* sp. $(\chi^2 = 0.125, df = 2, P = 0.939)$. Sampling in 2013 was performed during only the first half of the year (March to May) but P. mediterranea exhibited a higher frequency of occurrence compared to fecal samples collected in 2010 and 2012.

DISCUSSION

Kemp's Ridley Sea Turtles from Pine Island Sound in the Charlotte Harbor estuary were cancrivorous and *Libinia* (spider crabs) was the major dietary component. All large immature (40–59 cm) and adult-size (≥60 cm) turtles consumed these slow, bottom-walking crabs rather than evasive prey such as swimming, portunid crabs. Kemp's Ridley Sea Turtles of similar size on the Texas and western Louisiana coasts consumed mostly swimming crab species (Shaver, 1991; Werner, 1994), suggesting that larger turtles forage primarily on portunid crabs (NMFS, 2011; Shaver et al., 2013). Contrary to the perception that smaller-size turtles select easily captured walking crabs (Burke et al., 1994; Morreale and Standora, 1998, 2005), the smallest Kemp's Ridley Sea Turtle (24 cm) captured in Charlotte

Harbor was the only turtle that consumed *Callinectes sapidus* (Blue Crabs). The same individual was recaptured 675 days later, measured 43.3 cm, and had a diet of spider crabs. The second smallest turtle (26 cm) had consumed only *P. mediterranea* (Mottled Purse Crabs) as the crustacean component. Blue Crabs are fast-moving swimming crabs and Mottled Purse Crabs are sedentary crabs that bury in sediments (Rothschild, 2004), either of which would be elusive prey for new recruits inexperienced to foraging in benthic habitats. These observations should be viewed cautiously, however, given our small sample size for both post-pelagic (20–25 cm) and adult turtles. Additional diet studies are needed regarding the ontogenetic shift from oceanic to nearshore habitats and the food habits of mature turtles throughout their range.

The data from adult-size (≥60 cm) Kemp's Ridley Sea Turtles in nearshore estuarine foraging grounds of west Florida represents a notable addition to earlier studies that were comprised of free-ranging immature turtles (Schmid and Barichivich, 2005, 2006). Both adult fecal samples collected in Charlotte Harbor contained spider crabs and undigested traces

Table 3. Differences in decapod composition for trap sampling (prey availability) and fecal samples of captured Kemp's Ridley Sea Turtles (prey use) in the Pine Island Sound region of the Charlotte Harbor National Estuary.

	Average free proporti	Percent contribution to		
Decapods	Availability	Use	dissimilarity	
Libinia sp.	91.2	72.5	41.5	
Persephona mediterranea	0.0	16.9	27.5	
Hepatus epheliticus	5.8	0.0	9.4	
Hepatus epheliticus Hexapanopeus angustifrons	0.0	5.6	9.0	
Menippe mercenaria	1.3	3.2	6.9	
Calappa sp.	0.0	1.9	3.0	
Callinectes/Portunus	1.7	0.0	2.7	

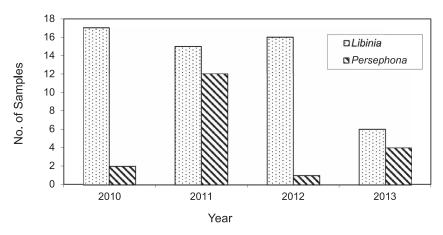


Fig. 3. Annual frequency of occurrence for *Libinia* sp. and *Persephona mediterranea* in fecal samples of Kemp's Ridley Sea Turtles captured in Charlotte Harbor National Estuary.

of seagrass, likely consumed when these turtles were feeding in a nearshore habitat several days prior to capture if we can assume similar digestive turnover rates to that of immature Kemp's Ridley Sea Turtles from Long Island Sound (Burke et al., 1994). Historical accounts suggest a more offshore habitat for adult turtles, although a gravid female was reportedly taken in shallow waters of a river mouth (Carr and Caldwell, 1958) and satellite telemetry indicates some post-nesting females may establish foraging areas off the southwest Florida coast (Shaver and Rubio, 2008; Shaver et al., 2013). Prey consumed in these offshore habitats likely differs from that in nearshore foraging areas. The exponential increase in females on the western Gulf nesting beaches (1985-2009; Gallaway et al., 2016) would result in increased abundance at these offshore foraging grounds and a greater likelihood for detecting adult turtles that venture inshore to feed in estuarine waters.

Spider crabs were the most abundant decapod crustacean trapped in Pine Island Sound, suggesting that Kemp's Ridley Sea Turtles might have been consuming the most readily available prey. Mottled Purse Crabs were a secondary prey item but were not collected in crab traps, presumably a result of bias in our sampling method. As such, their absence overestimated the availability of spider crabs and the use of Mottled Purse Crabs in our analyses, resulting in disproportionate use of both prey items. Mottled Purse Crabs are typically collected with trawls or dredges (Williams, 1984; J. Rudloe, Gulf Specimen Marine Laboratories, pers. comm.), but these gear types may not capture crabs that burrow and/or associate with hardbottom structures such as Stone Crabs (M. mercenaria). Despite the fact that data from our trap sampling were useful, a more comprehensive sampling protocol is needed to characterize prey availability in Kemp's Ridley foraging grounds.

Regionally, variations in diet composition of Kemp's Ridley Sea Turtles likely reflect localized differences in use of foraging habitat and availability of prey. Spider crabs constitute the greatest proportion of the diet for turtles captured in western Florida seagrass habitat either bisected by narrow, sandy channels (e.g., Deadman Bay; Barichivich et al., 1998) or a soft-substrate basin interdigitated with sponge beds (e.g., Pine Island Sound; current study). For live bottom habitats, turtles tend to consume Stone Crabs (*Menippe* sp.) and Blue Crabs with rock outcroppings as substrate (e.g., Cedar Keys; Schmid et al., 2003) or benthic tunicates with tube-building polychaetes as substrate (e.g., Ten Thousand Islands; Witzell and Schmid, 2005). In addition, spider crabs may also constitute a substantial

portion of Kemp's Ridley Sea Turtle diets in the tubicolous live bottom habitat. The prevalence of spider crabs in western Florida diets is in contrast to the consumption of swimming crabs by turtles in other regions such as seagrass meadows in Chesapeake Bay (Lutcavage and Musick, 1985; Seney and Musick, 2005) and along the Texas coast (Shaver, 1991; Werner, 1994). The ingestion of polychaete worm tubes in Texas may indicate the importance of live bottom as foraging habitat, similar to the Ten Thousand Islands (Seney, 2016). Stable isotope studies have revealed complex trophic relationships of other marine turtle species, their prey, and habitat components (McClellan et al., 2010; Lemons et al., 2011; Howell et al., 2016) and similar studies would help to elucidate such patterns in Kemp's Ridley Sea Turtles.

We demonstrated the importance of benthic invertebrates as a food source for Kemp's Ridley Sea turtles across a range of body sizes in southwestern Florida. There were no clear indications for size-specific shifts in diet but discernible differences in prey consumed at adjacent subtropical foraging areas. Differences in estuarine characteristics (freshwater inflow patterns, geomorphological processes, benthic habitat types, etc.) certainly seem to influence diet composition throughout the species' range, information that will be important for resource management. Location-specific knowledge of dietary habits will be essential for the effective conservation of foraging habitats (Burke et al., 1993). Furthermore, understanding regional dietary habits may be useful for predicting catastrophic events such as harmful algae blooms that may affect turtles consuming filter-feeding tunicates (Perrault et al., 2014) or potential effects of oil spills on benthic crustaceans and other prey. Given the recent uncertain trend at nesting beaches (Bevan et al., 2016; Galloway et al, 2016), protected estuaries throughout the Gulf of Mexico and U.S. Atlantic seaboard will remain essential for sustaining the viability of the Kemp's Ridley Sea Turtle population.

Acknowledgments.—This project received support from research grants awarded by the Sea Turtle Grants Program, funded from the sale of the Florida Sea Turtle License Plate (www.helpingseaturtles.org). The National Save the Sea Turtle Foundation provided funding to offset trips compromised by foul weather. The Gulnacs graciously allowed docking in the Demere Key boat basin, and A. Adams facilitated access to the field station. E. Seney and five reviewers added many helpful comments to the manuscript. We conducted fieldwork under NMFS permit 13544 and FFWCC permit 136.

LITERATURE CITED

- Barichivich, W. J., K. J. Sulak, and R. R. Carthy. 1998. Final Report: Characterization of Kemp's ridley sea turtles in the Florida Big Bend Area. Research Work Order 177. Available from: http://ufdc.ufl.edu/UF00072284/00001. Archived by WebCite at http://www.webcitation.org/6aXEfDF5R on 4 August 2015.
- Barleycorn, A. A., and A. D. Tucker. 2005. *Lepidochelys kempii* diet. Herpetological Review 36:58–59.
- Bevan, E., T. Wibbels, B. M. Z. Najera, L. Sarti, F. I. Martinez, J. M. Cuevas, B. J. Gallaway, L. J. Pena, and P. M. Burchfield. 2016. Estimating the historic size and current status of the Kemp's ridley sea turtle (*Lepidochelys kempii*) population. Ecosphere 7:1–15.
- BJORNDAL, K. A. 1996. Foraging ecology and nutrition of sea turtles. Pp. 199–231 in P. L. Lutz and J. A. Musick (eds.), The Biology of Sea Turtles. CRC Press, USA.
- BJORNDAL, K. A., A. B. BOLTEN, C. J. LAGUEUX, AND D. R. JACKSON. 1997. Dietary overlap in three sympatric congeneric freshwater turtles (*Pseudemys*) in Florida. Chelonian Conservation and Biology 2:430–433.
- Burke, V. J., E. A. Standora, and S. J. Morreale. 1993. Diet of juvenile Kemp's ridley and loggerhead sea turtles from Long Island Sound. Copeia 1993:1176–1180.
- Carr, Â. F., and D. K. Caldwell. 1958. The problem of the Atlantic ridley turtle (*Lepidochelys kempi*) in 1958. Revista de Biologia Tropical 6:245–262.
- CLARKE, K. R., AND R. N. GORLEY. 2006. PRIMER v6: User Manual/ Tutorial. PRIMER-E Ltd. Plymouth, U.K.
- CORBETT, C. A. 2006. Seagrass coverage changes in Charlotte Harbor, Florida. Florida Scientist 69:7–23.
- COYNE, M. S. 2000. Population Sex Ratio of the Kemp's Ridley Sea Turtle (*Lepidochelys kempii*): Problems in Population Modeling. Unpubl. PhD diss., Texas A&M University, USA.
- Deagle, B. E., N. J. Gales, K. Evans, S. N. Jarman, S. Robinson, R. Trebilco, and M. A. Hindell. 2007. Studying seabird diet through genetic analysis of faeces: a case study on Macaroni Penguins (*Eudyptes chrysolophus*). PLoS One 2:1–10.
- FFWCC (FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION). 2007. Marine Turtle Conservation Guidelines. Available from http://myfwc.com/media/418106/Seaturtle_Guidelines.pdf. Archived by WebCite at http://www.webcitation.org/6aXGgjX9C on 4 August 2015.
- Gallaway, B. J., W. J. Gazey, C. W. Caillouet Jr., P. T. Plotkin, D. J. Shaver, F. A. Abreu Grobois, A. F. Amos, P. M. Burchfield, R. R. Carthy, M. A. Castro Martínez, et al. 2016. Development of a Kemp's ridley sea turtle stock assessment model. Gulf of Mexico Science 33:138–157.
- HOWELL, L. N., K. J. REICH, D. J. SHAVER, A. M. LANDRY JR., AND C. C. GORGA. 2016. Ontogenetic shifts in diet and habitat of juvenile green turtles in the northwestern Gulf of Mexico. Marine Ecology Progress Series 559:217–229.
- HYSLOP, E. J. 1980. Stomach content analysis—review of methods and their application. Journal of Fish Biology 17:411–429.
- IVERSON, R. L., AND H. F. BITTAKER. 1986. Seagrass distribution and abundance in eastern Gulf of Mexico coastal waters. Estuarine, Coastal, and Shelf Science 22:577–602.
- Lemons, G., R. Lewison, L. Komoroske, A. Gaos, C. T. Lai, P. Dutton, T. Eguchi, R. Leroux, and J. A. Seminoff. 2011. Trophic ecology of green sea turtles in a highly urbanized bay: insights from stable isotopes and mixing models. Journal of Experimental Marine Biology and Ecology 405:25–32.
- LINDEMAN, P. V. 2006. Diet of the Texas map turtle (*Graptemys versa*): relationship to sexually dimorphic trophic morphology and changes over five decades as influenced by an invasive mollusk. Chelonian Conservation and Biology 5:25–31.
- Lutcavage, M., and J. A. Musick. 1985. Aspects of the biology of sea turtles in Virginia. Copeia 1985:449–456.
- McClellan, C. M., J. Braun-McNeill, L. Avens, B. P. Wallace, and A. J. Read. 2010. Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtles. Journal of Experimental Marine Biology and Ecology 387:44–51.
- MORREALE, S. J., AND E. A. STANDORA. 1998. Early life stage ecology of sea turtles in northeastern U.S. waters. NOAA Technical Memorandum NMFS-SEFSC-413.
- 2005. Western North Atlantic waters: crucial developmental habitat for Kemp's ridley and loggerhead turtles. Chelonian Conservation and Biology 4:872–882.
- NMFS (NATIONAL MARINE FISHERIES SERVICE, U.S. FISH AND WILDLIFE SERVICE, AND SEMARNAT). 2011. Bi-National Recovery Plan for the Kemp's

- Ridley Sea Turtle (*Lepidochelys kempii*). 2nd rev. National Marine Fisheries Service, USA.
- Ogren, L. H. 1989. Distribution of juvenile and subadult Kemp's ridley turtles: preliminary results from the 1984–1987 surveys. Pp. 116–123 in C. W. Caillouet Jr., and A. M. Landry Jr. (eds.), Proceedings of the First International Symposium on Kemp's Ridley Sea Turtle Biology, Conservation, and Management. Texas A&M University Sea Grant College Program, USA.
- Perrault, J. R., J. R. Schmid, C. J. Walsh, J. E. Yordy, and A. D. Tucker. 2014. Brevetoxin exposure, superoxide dismutase activity and plasma protein electrophoretic profiles in wild-caught Kemp's ridley sea turtles (*Lepidochelys kempii*) in southwest Florida. Harmful Algae 37:194–202.
- PRITCHARD, P. C. H. 2007. Evolutionary relationships, osteology, morphology, and zoogeography of ridley sea turtles. Pp. 45–57 in P. T. Plotkin (ed.), Biology and Conservation of Ridley Sea Turtles. John Hopkins University Press, USA.
- Redfoot, W., and L. Ehrhart. 2013. Trends in size class distribution, recaptures, and abundance of juvenile green turtles (*Chelonia mydas*) utilizing a rock riprap lined embayment at Port Canaveral, Florida, USA, as developmental habitat. Chelonian Conservation and Biology 12:252–261.
- ROTHSCHILD, S. B. 2004. Beachcomber's Guide to Gulf Coast Marine Life: Texas, Louisiana, Mississippi, Alabama, and Florida. 3rd ed. Taylor Trade Publishing, USA.
- SCHMID, J. R., AND W. J. BARICHIVICH. 2005. Developmental biology and ecology of Kemp's ridley turtles in the eastern Gulf of Mexico. Chelonian Conservation and Biology 4:828–834.
- ——. 2006. Lepidochelys kempii—Kemp's ridley turtle. Pp. 128–141 in P. A. Meylan (ed.), Biology and Conservation of Florida Turtles. Chelonian Research Foundation, USA.
- SCHMID, J. R., A. B. BOLTEN, K. A. BJORNDAL, W. J. LINDBERG, H. F. PERCIVAL, AND P. D. ZWICK. 2003. Home range and habitat use by Kemp's ridley turtles in west-central Florida. Journal of Wildlife Management 67: 196–206.
- SENEY, E. E. 2016. Diet of Kemp's ridley sea turtles incidentally caught on recreational fishing gear in the northwestern Gulf of Mexico. Chelonian Conservation and Biology 15:132–137.
- SENEY, E. E., AND J. A. MUSICK. 2005. Diet analysis of Kemp's ridley sea turtles (*Lepidochelys kempii*) in Virginia. Chelonian Conservation and Biology 4:864–871.
- SHAVER, D. 1991. Feeding ecology of wild and head-started Kemp's ridley sea turtles in south Texas waters. Journal of Herpetology 25: 327–334.
- SHAVER, D. J., AND C. RUBIO. 2008. Post-nesting movement of wild and head-started Kemp's ridley sea turtles (*Lepidochelys kempii*) in the Gulf of Mexico. Endangered Species Research 4:43–55.
- SHAVER D. J., K. M. HART, I. FUJISAKI, C. RUBIO, A. R. SARTAIN, J. PEÑA, P. M. BURCHFIELD, D. G. GAMEZ, AND J. ORTIZ. 2013. Foraging area fidelity for Kemp's ridleys in the Gulf of Mexico. Ecology and Evolution 3:2002–2012.
- SNOVER, M. L. 2008. Ontogenetic habitat shifts in marine organisms: influencing factors and the impacts of climate variability. Bulletin of Marine Science 83:53–67.
- Werner, S. A. 1994. Feeding ecology of wild and head started Kemp's ridley sea turtles. Unpubl. master's thesis, Texas A&M University, USA.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393–425.
- WILLIAMS, A. B. 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, USA.
- WITHERINGTON, B., H. HIRAMA, AND R. HARDY. 2012. Young sea turtles of the pelagic *Sargassum*-dominated drift community: habitat use, population density, and threats. Marine Ecology Progress Series 463:1–22.
- WITZELL, W. N., AND J. R. SCHMID. 2004. Immature sea turtles in Gullivan Bay, Ten Thousand Islands, southwest Florida. Gulf of Mexico Science 22:54–61.
- ——. 2005. Diet of Immature Kemp's ridley turtles (*Lepidochelys kempii*) from Gullivan Bay, Ten Thousand Islands, southwest Florida. Bulletin of Marine Science 77:191–199.

Accepted: 3 February 2018. Published online: 14 June 2018.