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Regional Variation in Kemp's Ridley Sea Turtle Diet Composition and Its Potential Relationship With Somatic Growth

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Reptile growth is influenced by many ecological processes that can cumulatively give rise to divergent somatic growth rates within spatially structured populations. As somatic growth variation can strongly influence a species' population dynamics, identifying proximate drivers can be critical to the conservation and management of protected species. Kemp's ridley sea turtles (*Lepidochelys kempii*) exhibit spatial variation in both diet composition and growth, but whether components of this variation are linked has not been evaluated. Through an integration of skeletochronological and stable isotope analyses of stranded turtle humerus bones we characterized regional variation in Kemp's ridley diet composition and potential relationships with somatic growth rates. Turtles were divided among five regions within the United States Gulf of Mexico (GoM) and Atlantic Coast based on location of stranding, and humerus bones were sampled for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios. These data were combined with region-specific prey stable isotope data sourced from the primary literature into Bayesian stable isotope mixing models (MixSIAR) to estimate the proportional contribution of five prey groups (crustaceans, bivalves, gastropods, fish, and macroalgae/seagrass) to Kemp's ridley diets. Our analysis revealed strong regional differences in mixing model-derived diet composition estimates that closely tracked published records of Kemp's ridley diet. Invertebrates generally comprised the largest proportion (43.5–97.7%) of turtle diets. However, we also observed high proportional contributions of fish (42.6–43.1%) to western GoM turtle diets and macroalgae/seagrass (42.4–47.8%), or isotopically similar prey resources (e.g., tunicates), to eastern GoM turtle diets. Growth rates were poorly correlated with $\delta^{15}N$ values—a proxy for trophic level—and diet composition estimates, suggesting that diet composition alone may not explain the regional differences in somatic growth observed in this species. This study highlights the value of complementary skeletal and isotopic analyses to understanding regional

diet variation in sea turtles as well as the importance of continued collection of isotopic data for both sea turtles and their prey. These results also help fill critical knowledge gaps pertaining to the relationship between sea turtle foraging ecology and somatic growth dynamics, a topic of high importance to sea turtle conservation and management.

Keywords: stable isotope analysis, skeletochronology, mixing model, growth rates, diet analysis, foraging ecology

INTRODUCTION

Somatic growth variation manifests from the cumulative effect of multiple biological, ecological, and environmental processes (Congdon, 1989; Stearns, 1992). Environmental effects on growth rates are particularly strong in ectothermic reptiles, such as sea turtles, where resource use, quality, and availability interact with temperature to determine how much of an individuals' total energy budget is devoted to growth, maintenance, storage, and reproduction (Gibbons, 1967; Dunham et al., 1989). Spatiotemporal variation in energy allocation to growth within and among individuals can have profound effects on individual fitness and species population dynamics through influences on key life history features such as time to maturity (Frazer et al., 1993; Bjorndal et al., 2013), size-dependent mortality (Werner and Gilliam, 1984; O'Brien et al., 2005), and fecundity (Berry and Shine, 1980; Frazer and Richardson, 1986). Sea turtle somatic growth rates are highly variable within and among species and life stages, and a suite of environmental factors are thought to contribute to this variability (e.g., temperature, density-dependence, prey dynamics, diet quality, and individual behavior; Balazs, 1982; Bjorndal et al., 2003; Balazs and Chaloupka, 2004; Hatase et al., 2010; Peckham et al., 2011). Disentangling the myriad potential drivers of sea turtle somatic growth variation is challenging given the logistical limitations associated with studying highly migratory species (Omeyer et al., 2017). Nevertheless, identifying factors influential to sea turtle growth rates is of high importance to their conservation and management given that their population dynamics are sensitive to changes in demographic rates (Crouse et al., 1987; Gerber and Heppell, 2004).

Variation in resource use and availability is a primary driver of somatic growth variation within animal populations. For example, it is well-established that fish growth and population dynamics are strongly influenced by zooplankton composition, abundance, and distribution (Cushing, 1990; Brodeur and Ware, 1992; Durant et al., 2007). Similarly, variation in multiple seabird demographic rates, including growth, have been linked to differences in prey availability, composition, and energy density (Cairns, 1988; Abraham and Sydeman, 2004; Hennicke and Culik, 2005; Piatt et al., 2007). For loggerhead sea turtles (*Caretta caretta*), geographic variation in resource availability is thought to contribute to differences in somatic growth rates among life stages and breeding populations (Bjorndal et al., 2003; Piovano et al., 2011). These differences may relate to divergent prey energy densities or geographic differences in primary productivity (Bosc et al., 2004; Peckham et al., 2011). Observations of compensatory and density-dependent growth in loggerhead and green sea turtles (*Chelonia mydas*) provide further support for the importance of resource use in shaping sea turtle growth rates (Bjorndal et al., 2000, 2003). Within the Gulf of Mexico, factors that affect foraging resources for sea turtles include fisheries (Robinson et al., 2015), seasonal hypoxic zones (Craig et al., 2001), oil spills (Wallace et al., 2017), red tides (Dupont et al., 2010), hurricane activity (Engle et al., 2009), and climate change (Sanchez-Rubio et al., 2011), among others.

Kemp's ridley sea turtles (*Lepidochelys kempii*) display distinct regional differences in somatic growth rates that may be linked to differences in diet composition. During neritic life stages, this species occupies nearshore marine habitats throughout the Gulf of Mexico (GoM) and United States Atlantic (NMFS and USFWS, 2015). Comparative studies prior to the year 2000 suggest juvenile Atlantic Kemp's ridley sea turtles exhibit slower grow rates than conspecifics in the GoM (Caillouet et al., 1995; Zug et al., 1997; NMFS and USFWS, 2015; Avens et al., 2017), though causal mechanisms remain unknown. In contrast, juvenile Kemp's ridley growth rates do not appear to vary substantially within the United States GoM and Atlantic (Ramirez, 2019). Although crabs are generally thought to constitute the bulk of their diet across their range, regional differences in Kemp's ridley foraging patterns have been observed that may influence their somatic growth rates (Shaver, 1991; Burke et al., 1993, 1994; Seney and Musick, 2005; Schmid and Tucker, 2018). Diets are particularly variable among Kemp's ridleys that inhabit the GoM. For example, tunicates are a common prey item for turtles in southwest Florida (Witzell and Schmid, 2005), whereas fish—likely sourced as discards from shrimp fisheries—are often consumed by turtles in the northern and western GoM (Werner, 1994; Cannon, 1998; Stacy, 2015). Shrimp fisheries are the overwhelmingly dominant source of fish discards throughout the Kemp's ridleys' range but the availability of this potential resource is an order of magnitude higher in the western and northern GoM than in the eastern GoM and United States Atlantic (Diamond, 2004; Harrington et al., 2005; Scott-Denton et al., 2012). In contrast to their GoM counterparts, Atlantic Kemp's ridleys appear less likely to deviate from the traditional diet of crabs and molluscs (Burke et al., 1993, 1994; Frick and Mason, 1998; Seney and Musick, 2005). Ultimately, whether this spatial variability in diet composition correlates with regional differences in growth rates has yet to be evaluated.

As the isotopic composition of consumer tissues closely tracks that of their assimilated diet, stable isotope analyses provide a means of characterizing intra-population variation in diet composition over space and time (Newsome et al., 2007; Katzenberg, 2008). Importantly, the proportional contribution of different resources to a consumer's diet can be quantified using

mass-balance stable isotope mixing models when isotopic data are available for both consumers and potential prey (Phillips, 2001). While many environmental and physiological processes can influence stable isotope deposition rates into consumer tissues, the latest generation of mixing models allows for incorporation of various sources of uncertainty through Bayesian inference to improve estimations of diet composition (Phillips and Koch, 2002; Semmens et al., 2009; Parnell et al., 2010; Stock and Semmens, 2016). This approach in turn yields source contribution estimates that are accompanied by probability distributions that more accurately reflect model uncertainties. Kemp's ridley humerus bones contain annual records of somatic growth that can be revealed through histological processing and analysis (Snover and Hohn, 2004; Avens et al., 2017). Combining skeletochronological and stable isotope analyses within a mixing model framework may thus provide a means of investigating the influence of diet composition on sea turtle growth rates across multiple spatiotemporal scales. The integration of these tools has already shed valuable insight into sea turtle ontogenetic growth dynamics and resource shifts (Snover et al., 2010; Avens et al., 2013; Ramirez et al., 2017, 2019; Turner Tomaszewicz et al., 2017a).

In this study we integrated skeletochronological and stable isotope analyses of Kemp's ridley humerus bones to (1) characterize regional variation in diet composition and (2) quantify the relationship between diet composition and somatic growth rates. To reduce biases associated with translating isotopic data to diet composition estimates for a highly mobile species, our analysis assesses diet composition at a broad taxonomic level (e.g., % fish, % invertebrate, and % macroalgae/seagrass). We specifically investigated if turtles inhabiting areas where fish discards are prevalent (western and northern GoM) showed evidence of consuming greater proportions of fish relative to turtles from other regions (eastern GoM and United States Atlantic). Because the energy density of fish is generally higher than that of crustaceans (Doyle et al., 2007; Peckham et al., 2011; Schaafsma et al., 2018), we also investigated whether fish subsidies to turtle diets enhance somatic growth rates, thereby contributing to regional differences in somatic growth. This investigation presents one of the first studies explicitly linking sea turtle foraging ecology to their somatic growth dynamics.

MATERIALS AND METHODS

Geographic Breakpoints

Variation in Kemp's ridley diet composition and growth was evaluated by dividing turtle and prey data among five geographic regions within the species' range (**Figure 1**): (1) western Gulf of Mexico (wGoM, n = 44 turtles; Texas/Mexico border to Vermilion Bay, LA), (2) northern Gulf of Mexico (nGoM, n = 28 turtles; Vermilion Bay, LA, to Mobile Bay, AL), (3) eastern Gulf of Mexico (eGoM, n = 24 turtles; Apalachicola Bay to Florida Bay, FL), (4) North Carolina (NC, n = 32 turtles; Long Bay to Albemarle Sound, NC), and (5) Virginia (VA, n = 25 turtles; North Carolina/Virginia border to lower Chesapeake Bay). These breakpoints were primarily determined based on known or presumed spatial variation in ocean chemistry. We explored using smaller geographic areas to more closely link turtle and prey stable isotope data in space. However, there was generally insufficient prey data for one or more prey groups to use smaller regional units for this analysis (see below).

Within the GoM, the West Florida Shelf is characterized by relatively low stable nitrogen isotope ratios ($\delta^{15}N$) due to the presence of *Trichodesmium* (Lenes et al., 2001; Mulholland et al., 2006; Vander Zanden et al., 2015), a N_2-fixing cyanobacteria; N_2-fixation reduces $\delta^{15}N$ values (Montoya et al., 2002). Marine organisms occupying the West Florida Shelf thereby may have lower $\delta^{15}N$ values than conspecifics elsewhere due to chemical differences at the base of the food web. In contrast, the nGoM and Virginia regions may have relatively high $\delta^{15}N$ values and low stable carbon isotope ($\delta^{13}C$) values than adjacent regions due to high nitrogen loading from agricultural runoff (i.e., high nitrogen content; Black et al., 2017; Fritts et al., 2017) and freshwater influences, respectively—freshwater systems have distinctly lower $\delta^{13}C$ values than marine systems (Fry and Sherr, 1989).

Prey Stable Isotope Ratios

Kemp's ridley sea turtles are generalist carnivores, consuming primarily invertebrates (crustaceans, gastropods, bivalves, and tunicates) but also variable amounts of fish, macroalgae, and seagrasses (Shaver, 1991; Seney and Musick, 2005; Witzell and Schmid, 2005). Although regional differences in foraging patterns have been observed for this species, such as increased consumption of fish in turtles from Louisiana and Texas (Werner, 1994; Cannon, 1998; Stacy, 2015) and tunicates in turtles from Southwest Florida (Witzell and Schmid, 2005), crabs have generally constituted >75% of their observed diet by weight (Shaver, 1991; Burke et al., 1993, 1994; Seney and Musick, 2005; Schmid and Tucker, 2018). Given the spatiotemporal extent and retrospective nature of this study, we relied on the primary literature to source stable isotope data of representative prey species for our mixing model.

We first performed a structured literature search in Web of Science and Google Scholar using the following Boolean search terms: stable isotope, crustacean, crab, shrimp, mollusc, arthropod, gastropod, sea snail, bivalve, clam, oyster, mussel, fish, tunicate, seagrass, and macroalgae. We then performed an unstructured literature search using the reference lists of relevant publications found in the structured search. Following exclusion of studies performed outside the focal geographic areas, the literature search yielded 86 studies from which stable carbon and nitrogen isotope ratios were collated. If studies reported multiple stable isotope values for a single prey species, a weighted mean and pooled standard deviation (SD) were calculated to collapse the reported data into one estimate per species per study. Tunicates, though potentially an important Kemp's ridley prey group, were excluded from our analysis given their poor representation in the literature (n = 2 studies) and overlap in isotopic values with macroalgae and seagrass. The final prey stable isotope dataset comprised 552 isotopic records (see **Table 1** for summary and **Supplementary Table S1** for full dataset). Original collection dates spanned 1975 to 2016, but primarily encompassed the years 1990 to 2016—pre-1990

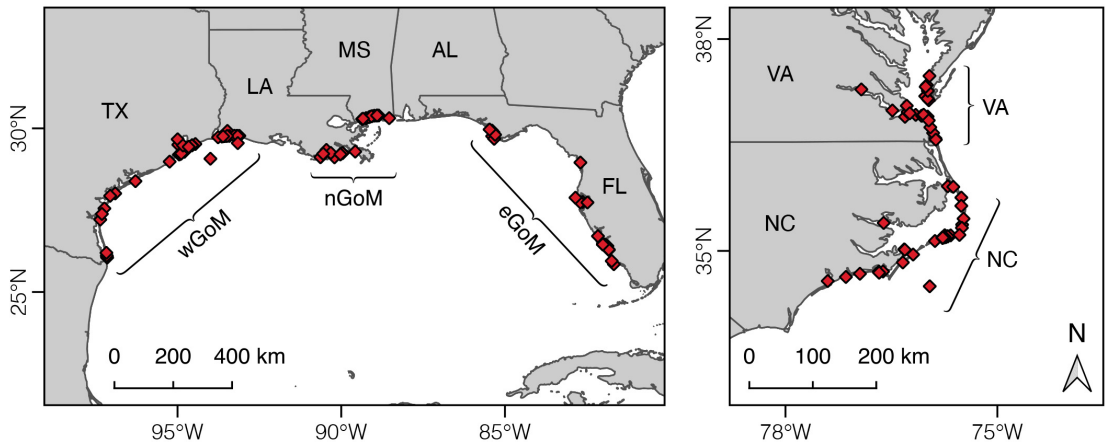

FIGURE 1 | Map of Kemp's ridley sea turtle stranding locations for the humerus bones used in this study and geographic breakpoints used to cluster turtles and prey groups. wGoM, western Gulf of Mexico; nGoM, northern Gulf of Mexico; eGoM, eastern Gulf of Mexico; NC, North Carolina; VA, Virginia.

TABLE 1 | Taxonomic and geographic summaries of Kemp's ridley sea turtle prey stable isotope data collated from the published literature.

Prey groups	Taxonomic family (Common name, *n**)	Counts* by region				
		Gulf of Mexico			Atlantic	
		W	N	E	S	N
Crustacean/Chelicerate		28	48	26	15	10
Horseshoe crab	Limulidae (horseshoe crabs, 4)	0	1	0	2	1
Crab	Portunidae (swimming crabs, 43), Panopeidae (mud crabs, 14), Epialtidae (spider crabs, 5), Menippidae (stone crabs, 4), Diogenidae (hermit crabs, 3), Aethridae (box crabs, 1), Paguridae (hermit crabs, 1), Multiple** (1)	13	26	17	9	7
Shrimp	Penaeidae (Penaeid shrimp, 48), Squillidae (Mantis shrimp, 3)	15	21	9	4	2
Bivalve	Ostreidae (Eastern oyster, 29), Mytilidae (mussels, 23), Veneridae (venus clams, 7), Mactridae (Atlantic rangia, 5), Tellinidae (tellin clams, 4), Arcidae (ark clam, 2), Pectinidae (scallops, 2)	15	27	12	13	5
Gastropod	Littorinidae (periwinkles, 18), Melongenidae (Crown conch, 3), Muricidae (murix snails, 3), Nassariidae (Nass mud snails, 3), Naticidae (Atlantic moon snail, 3), Busyconidae (whelks, 2), Calyptraeidae (slipper snail, 2), Cerithiidae (ceriths, 2), Columbellidae (dove snails, 2), Buccinidae (Tinted cantharus, 1), Neritidae (Olive nerite, 1), Potamididae (Ladder horn snail, 1), Turbinidae (West Indian starsnail, 1)	3	19	6	12	2
Fish	Sciaenidae (croaker and weakfish, 75), Sparidae (porgy and pinfish, 29), Engraulidae (anchovy, 23), Mugilidae (mullet, 20), Clupeidae (menhaden and herring, 18), Ariidae (sea catfish, 17), Paralichthyidae (flounder, 17), Haemulidae (grunt, 4), Phycidae (spotted hake, 3), Synodontidae (inshore lizardfish, 3), Achiridae (sole, 2), Pomatomidae (bluefish, 2), Triglidae (searobins, 2), Carangidae (round scad, 1)	42	52	86	20	16
Macroalgae/Seagrass		25	11	35	11	13
Seagrass	Cymodoceaceae (shoal and manatee grass, 20), Hydrocharitaceae (turtlegrass, 18), Zosteraceae (Common eelgrass, 5), Multiple** (4), Unidentified (1)	14	3	25	3	3
Macroalgae	Ulvaceae (Sea lettuce, 13), Unidentified (8), Gracilariaceae (red algae, 6), Multiple** (5), Cladophoraceae (green algae, 2), Codiaceae (Green sea fingers, 2), Dictyotaceae (brown algae, 2), Gelidiaceae (red algae, 2), Solieriaceae (red algae, 2), Ceramiaceae (red algae, 1), Ectocarpaceae (brown algae, 1), Fucaceae (bladder wrack, 1), Halymeniaceae (red algae, 1), Wrangeliaceae (red algae, 1)	11	8	10	8	10

Number of species-specific isotopic values identified in the primary literature. **Mean composite of samples from multiple families. See* ***Supplementary Table S1* *for full dataset.*

data were included in some instances to fill important data gaps for poorly represented taxa within each region, namely bivalves and gastropods.

Prey stable isotope data were grouped into five primary prey groups (crustaceans, bivalves, gastropods, fish, and macroalgae/seagrass) within each of the five geographic regions (**Supplementary Figures S1, S2**). For all animal prey groups, a simple mean and pooled SD were calculated for each region using the 552 isotopic values from the published literature. Although isotopically distinct, macroalgae and seagrass were grouped to

reduce the number of sources in the mixing model. As with the other prey groups, we first calculated a simple mean and pooled SD for macroalgae and seagrass separately and then calculated a simple mean of these estimates to yield final estimates for the macroalgae/seagrass prey group, thereby weighting each prey type equally in the models. Final means and SDs for all prey groups used in the mixing model are presented in **Table 2**. We assume that isotopic data collated from the published literature accurately reflect the means and variances of these prey groups.

TABLE 2 | Mean ± SD stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios collated from the primary literature for Kemp's ridley sea turtle prey groups by geographic region.

Prey group	$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)		
	n_{means}	n_{total}	Mean ± SD	n_{means}	n_{total}	Mean ± SD
Western GoM						
Crustacean	28	318	−18.37 ± 1.32	27	317	9.68 ± 1.33
Bivalve	14	165	−22.74 ± 1.70	15	262	9.65 ± 1.13
Gastropod	3	11	−14.81 ± 0.78	2	6	8.95 ± 0.35
Fish	42	311	−17.40 ± 1.44	33	274	12.64 ± 1.42
Macroalgae/ seagrass	25	153	−14.56 ± 2.11	24	93	6.43 ± 1.84
Northern GoM						
Crustacean	48	1545	−18.67 ± 1.59	44	1517	10.89 ± 1.14
Bivalve	25	247	−23.63 ± 0.92	18	242	7.75 ± 0.66
Gastropod	19	478	−18.00 ± 0.74	15	461	9.36 ± 0.26
Fish	52	1334	−19.84 ± 1.13	52	1295	11.93 ± 0.79
Macroalgae/ seagrass	11	57	−15.31 ± 1.18	11	57	6.94 ± 0.94
Eastern GoM						
Crustacean	26	570	−19.58 ± 1.92	22	544	6.88 ± 0.97
Bivalve	12	301	−22.40 ± 0.75	7	258	6.51 ± 0.36
Gastropod	6	30	−19.24 ± 1.94	5	29	6.49 ± 0.83
Fish	86	1679	−17.91 ± 1.22	65	1571	10.64 ± 1.09
Macroalgae/ seagrass	29	243	−14.57 ± 2.18	30	779	4.44 ± 1.37
North Carolina						
Crustacean	15	141	−17.68 ± 0.96	15	141	10.00 ± 0.85
Bivalve	13	45	−19.98 ± 0.35	6	35	7.62 ± 0.25
Gastropod	12	40	−16.81 ± 1.25	6	23	6.32 ± 0.61
Fish	17	206	−18.33 ± 0.98	17	208	11.98 ± 0.91
Macroalgae/ seagrass	11	35	−14.70 ± 0.61	5	14	4.81 ± 1.32
Virginia						
Crustacean	10	62	−16.43 ± 0.63	8	50	11.34 ± 0.98
Bivalve	5	97	−19.59 ± 0.98	5	97	9.84 ± 0.78
Gastropod	2	6	−16.21 ± 0.64	2	6	9.83 ± 0.54
Fish	16	318	−18.42 ± 1.33	11	258	14.63 ± 0.89
Macroalgae/ seagrass	13	94	−13.59 ± 1.51	13	94	7.86 ± 1.13

Mean ± SD is the simple mean and pooled SD of species-specific isotopic values collated from referenced studies. n_{means} is the number of mean values included in each $\delta^{13}C$ and $\delta^{15}N$ estimate. n_{total} is total number of prey items sampled in referenced studies. Values are uncorrected for trophic discrimination factors. See ***Supplementary Table S1*** *for source list and complete prey stable isotope dataset resulting from the literature review.*

Given uncertainties in the types of fish consumed by sea turtles, potential fish prey for our analysis included species previously observed in Kemp's ridley gut and fecal contents (e.g., mullet, croaker, weakfish, menhaden, sea catfish, flatfish, and lizardfish; see Shaver, 1991; Werner, 1994; Cannon, 1998; Witzell and Schmid, 2005; Stacy, 2015; Seney, 2016) as well as ecologically similar species abundant in shrimp fishery discards (e.g., porgy, pinfish, herring, and searobin; Harrington et al., 2005; Benaka et al., 2019). When possible, fish isotopic data were restricted to specimens <30 cm in length to align with those likely to be consumed by Kemp's ridleys. However, only 45% of studies reported fish lengths, so this was not always possible. Fish stable isotope data were initially grouped based on feeding mode (e.g., piscivorous, benthophagous, and planktivorous) to evaluate trophic differences. However, isotopic data for these three fish groups tended to overlap extensively in isospace within each region and were thus collapsed to reduce the number of sources in the mixing model.

Sea Turtle Stable Isotope Ratios

Kemp's ridley humerus bones utilized in this study were originally collected as whole front flippers from 153 turtles stranded dead along the United States Gulf and Atlantic Coasts between 1993 and 2015 by participants of the Sea Turtle Stranding and Salvage Network. At time of stranding, carapace length (notch to tip), calendar date, and stranding location (state, latitude, and longitude) were recorded for each turtle. Body size was typically measured as straightline carapace length (SCL), but in cases where only curved carapace length was recorded measurements were converted to SCL following Avens et al. (2017). Sea turtle diets and growth rates vary throughout their lifetime (Bjorndal, 1997; Chaloupka and Musick, 1997). To reduce the potential for ontogenetic effects to bias our results we only sampled bone growth layers from juvenile Kemp's ridleys corresponding to their benthic life stage (i.e., age $\geq$ 0.75 and $\delta^{15}N$ values $\geq$ 10.7‰; Ramirez, 2019; Ramirez et al., 2019).

Prior to sampling, each humerus bone was cleaned of soft tissue using a knife and then boiled. To perform complementary growth and stable isotope analyses, two sequential 2–3 mm thick cross-sections were cut from each humerus bone distal to the site of the deltopectoral muscle insertion scar using a low-speed isomet saw (Buehler). One section was histologically processed using standard methods to reveal the annual growth layers contained within each bone and estimate sea turtle growth rates (see below), whereas the second was reserved for complementary stable isotope analysis. Methods for histologically processing sea turtle bones are detailed in Avens and Snover (2013) but are briefly outlined here. First, humerus bone sections were decalcified over multiple days using a fixative/decalcifier (Cal-Ex II or RDO). Then, bone sections were thin sectioned using a freezing-stage microtome or cryostat, stained using Ehrlich's hematoxylin, and finally mounted onto microscope slides and digitally imaged. Two or three independent readers (among L. Avens, L. Goshe, M. Ramirez, and M. Snover) then analyzed the bone images to determine the number and placement of lines of arrested growth (LAGs), which delimit the outer edges of each skeletal growth mark.

To characterize resource use, ∼1.5 mg of bone dust was milled from the most recently deposited growth layer of each sea turtle bone cross-section reserved for stable isotope analysis (ESI New Wave Research MicroMill). This time period represents the geochemical history within 1 year of death, dependent on individual stranding date. A 0.3 mm diameter carbide drill bit (Brasseler) was used in conjunction with transparencies of the digital skeletochronology images to guide precision drilling to a depth of ≤1.0 mm for each sample. Bulk bone dust samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ values via continuous-flow isotope-ratio mass spectrometry at the Oregon State University Stable Isotope Lab (Corvallis, OR, United States). The system consists of a Carlo Erba NA1500 elemental analyzer interfaced with a DeltaPlusXL isotope-ratio mass spectrometer (Finnigan MAT, Bremen, Germany). The standards used for $\delta^{13}C$ and $\delta^{15}N$ were Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2, respectively. The internal standard IAEA-600 (Caffeine; isotopic composition of $\delta^{15}N$ = 1.00‰) was calibrated at regular intervals and used to correct for instrument drift and linearity. Analytical precision was 0.08‰ for $\delta^{13}C$ values and 0.05‰ for $\delta^{15}N$ values. In addition to stable isotope ratios, %N and %C were calculated using mass 28 and mass 44 peak areas, respectively, with a precision of 0.55% for %N and 0.28% for %C. C:N ratios (%C divided by %N) for all samples were below 3.5, characteristic of unaltered protein with low lipid content (Post et al., 2007). Following stable isotope analysis, bulk bone $\delta^{13}C$ values were mathematically corrected to account for carbonate-derived carbon as recommended by Turner Tomaszewicz et al. (2015). Using their approach, we developed a $\delta^{13}C$ conversion equation ($\delta^{13}C_{collagen}$ = 0.975 * $\delta^{13}C_{bulk}$ − 1.126, $F_{1,42}$ = 550.1, $P < 0.001$, adjusted R^2 = 0.93) that was used to mathematically correct bulk bone $\delta^{13}C$ values (see **Supplementary Mateiral** for details).

We assumed that stranding location was reflective of recent foraging location based on two lines of evidence. First, while we did not know precise locations of death in the ocean for turtles herein, it is likely that most turtles included in this study died relatively close to their stranding locations as ocean conditions were likely favorable for short carcass drift distances. The majority of turtles included in our study stranded in the spring, summer, and fall when sea surface temperatures, and thereby decomposition rates, would have been relatively high (Higgins et al., 2007). Therefore, in order for stranding to occur before carcasses dissociated due to decomposition, drift times and distances would have needed to be low (∼2–5 days, 15–30 km; Nero et al., 2013; Santos et al., 2018). Second, Kemp's ridleys display relatively high intra- and inter-annual site fidelity to nearshore, shallow (<50 m depth) foraging areas (generally <1,000 km^2) that are well constrained spatially within our defined geographic regions (Renaud and Williams, 2005; Schmid and Witzell, 2006; Shaver and Rubio, 2008; Seney and Landry, 2011; Coleman et al., 2017). Therefore, turtles that stranded within each geographic area are likely to have been foraging within their stranding location-assigned geographic area prior to death. As Kemp's ridleys have been occasionally documented migrating >1,000 km in a single year (Renaud and Williams, 2005), we acknowledge that some of our turtles may be misclassified geographically, particularly those that stranded near the edges of our pre-defined geographic areas.

Stable Isotope Mixing Model

We implemented multiple Bayesian hierarchical mixing models using the *MixSIAR* package (v 3.1.10, Stock et al., 2018) in R (v 3.5.3, R Core Team, 2019) to estimate the proportional contribution of five prey groups (crustaceans, bivalves, gastropods, fish, and macroalgae/seagrass) to Kemp's ridley diets. MixSIAR uses Markov chain Monte Carlo (MCMC) procedures to estimate posterior probability distributions of plausible proportional contributions of prey groups to consumer diets (Moore and Semmens, 2008), while accounting for uncertainty associated with trophic discrimination factors (TDFs; Parnell et al., 2010), concentration dependence (Phillips and Koch, 2002), fixed and random effects (Semmens et al., 2009), and variability in the predation process (i.e., error structure) (Parnell et al., 2010; Stock and Semmens, 2016). Initial investigations using a hierarchical structure that nested *individuals* within *regions* in a single modeling framework failed to converge after running for multiple days due to model complexity and size. Therefore, we implemented separate mixing models for each region.

To characterize inter- and intra-regional differences in diet composition, we implemented four mixing models for each region in a 2 × 2 factorial design that included one of two prior distributions (uninformative vs. informative prior; **Supplementary Figure S3**) for each prey group and one of two model configurations (null model vs. individual random effect model). We first ran the models using uninformative priors that assumed a generalist diet and weighted prey groups equally (α = 1, 1, 1, 1, 1). We then ran the model using an informative/specialist prior that weighted the prey group prior distributions using published diet composition data. Taking a weighted average of taxon-specific diet composition estimates from six Kemp's ridley diet studies (**Supplementary Table S2**), we constructed the informative priors assuming diet compositions (by dry mass) of 76.74% for crustaceans, 2.12% for bivalves, 2.12% for gastropods, 5.97% for fish, and 2.13% for macroalgae/seagrass—10.92% of diet contents were categorized as Other/Unidentified, which was excluded from this analysis. As recommended by Stock et al. (2018), the hyperparameters (α) for the informative priors were scaled to have a total weight equal to the number of sources (α = 4.31, 0.12, 0.12, 0.34, 0.12). Between region diet variation was assessed using null models, whereas within region diet variation was assessed using models that included *individual* as a random effect. In all models, the invertebrate prey groups were aggregated *a posteriori* (Phillips et al., 2005). All models included multiplicative error (process × residual error) and were run using the "extreme" MCMC settings (chain length = 3,000,000 iterations; burn-in = 1,500,000; posterior thinning = 500; 3 chains). Convergence was assessed using Gelman–Rubin (R_c < 1.01) and Geweke diagnostics (Gelman and Rubin, 1992; Geweke, 1992). Most models that included an informative prior and individual random effects failed to converge with these settings. Convergence was achieved after

re-running them using a chain length of 6,000,000 and burn-in of 3,000,000.

Prior to model implementation all source and consumer $\delta^{13}C$ values were corrected for the Suess Effect, the global decrease in atmospheric $\delta^{13}C$ values driven by the combustion of fossil fuels over the past 150 years (Keeling et al., 1979; Francey et al., 1999). We followed Chamberlain et al. (2005) and Fox-Dobbs et al. (2007) in applying a linear correction to standardize our data. To develop a $\delta^{13}C$ correction factor we analyzed the atmospheric $\delta^{13}C$ data for Maua Loa and La Jolla available on the Scripps CO_2 Program website[1] (Keeling et al., 2001), which indicated that atmospheric $\delta^{13}C$ values declined by ∼0.025 ‰ per year since 1978. We used this rate of $\delta^{13}C$ change to correct turtle and prey $\delta^{13}C$ values to modern values (modern = 2016; i.e., $\delta^{13}C$ values were reduced by 0.025‰ in 2015, 0.050‰ in 2014, and so on). Concentrations of carbon and nitrogen for each prey group, derived from the literature (**Supplementary Table S3**), were also included in the models to account for taxon-specific differences in digestibility (Phillips and Koch, 2002).

Stable isotope mixing models require estimates of diet-tissue trophic discrimination factors (TDFs; Δ)—the difference in isotopic ratios between consumers and their diet—to estimate the proportional contribution of different prey groups to consumer diets. As diet-bone TDFs have not been quantified for Kemp's ridleys or other primarily carnivorous sea turtles, we used diet-bone TDFs estimated from dead, captive, juvenile green sea turtles (*Chelonia mydas*) ($\Delta^{13}C = 2.1 \pm 0.6$, $\Delta^{15}N = 5.1 \pm 1.1$) (Turner Tomaszewicz et al., 2017b). Although these turtles were maintained on omnivorous diets composed of ∼56% animal matter (squid, shrimp, and fish) and ∼43% plant matter (lettuce) by weight, percent digestible N and C from animal protein was estimated to be 96.8 and 81.9%, respectively. Even though Bayesian stable isotope mixing models account for uncertainty in TDFs, their outputs are still highly sensitive to variation in TDFs (Bond and Diamond, 2011). Given uncertainty in the diet-bone TDFs for sea turtles, we used a sensitivity analysis to characterize the influence of varying TDFs on diet composition estimates that encompass the range of diet-bone TDFs reported for sea turtles and other animal species maintained on carnivorous diets (∼2–6‰; e.g., Ambrose and DeNiro, 1986; Hobson and Clark, 1992; Fox-Dobbs et al., 2007; Borrell et al., 2012; Kim et al., 2012; Cloyed et al., 2015; Webb et al., 2016; Matsubayashi et al., 2017).

Somatic Growth Rates

To examine the influence of sea turtle trophic ecology on somatic growth rates, we compared complementary diet composition data generated from the stable isotope mixed models with annual somatic growth rate data generated through skeletochronology for each stranded turtle. The somatic growth rate data presented herein are a combination of newly collected (n = 58 turtles stranded 2010–2015) and previously collected data (n = 95 turtles stranded 1993–2009) originally presented in Snover et al. (2007) and Avens et al. (2017). We followed Avens et al. (2017) to calculate growth rates for the newly processed turtles.

[1]http://scrippsco2.ucsd.edu

First, LAG diameter and humerus section diameter (HSD) were measured using image analysis software (Olympus Microsuite and cellSens) for each histologically prepared bone cross-section. The body proportional hypothesis back-calculation technique (BPH; Francis, 1990) was then used to estimate SCL for every measurable LAG, adjusted for turtle–specific SCL and HSD at death (Snover and Hohn, 2004; Avens et al., 2017). Annual somatic growth rates were calculated by taking the difference between SCL estimates of successive LAGs. However, given that LAGs are deposited in the spring and we sampled turtles that died throughout the year, only 73/153 turtles had true annual growth rate estimates.

To extend the growth dataset we calculated marginal growth rates for the 36 turtles that stranded between November and March by taking the difference between SCL at stranding and the SCL estimate of the most external LAG. While these marginal growth rates are considered minimum estimates of annual somatic growth, Kemp's ridleys likely grow little during the boreal winter when temperatures are cooler and sea turtle metabolic rates and activity patterns are reduced (Balazs and Chaloupka, 2004; Hochscheid et al., 2007; McMichael et al., 2008). Indeed, skeletal growth appears to asymptote in November (Snover and Hohn, 2004). The 44 turtles that stranded between June and October were excluded from the growth analysis, highlighting a potential disconnect in data availability for linking sea turtle growth and diet that could be overcome in future analyses through targeted sampling of only turtles that stranded in the spring.

To examine the influence of sea turtle trophic ecology on somatic growth rates, we implemented a series of Generalized Linear Models (GLMs) that included somatic growth as the response variable, age as a fixed effect, and either $\delta^{15}N$ value or estimated diet composition as a fixed effect. Separate GLMs that included $\delta^{15}N$ values as a fixed effect were implemented for each region, whereas GLMs that included estimated diet composition as a fixed effect were only implemented for regions with considerable intra-population variation in diet composition. As sea turtle growth rates change throughout their ontogeny, age was included in the model to account for ontogenetic effects on growth and diet. Age was chosen over body size to account for ontogenetic effects as models that included age had consistently lower AIC values than models that included body size. All GLMs included a Gamma distribution and were implemented in R (version 3.5.3) using the *mgcv* package (Wood, 2006; R Core Team, 2019).

RESULTS

Prey and Sea Turtle Stable Isotope Ratios

Prey $\delta^{13}C$ and $\delta^{15}N$ values were significantly different both within and among regions (Kruskal–Wallis rank sum tests, $P < 0.05$; see **Supplementary Table S4**). *Gastropod* was the only prey group that did not exhibit significant regional differences for both stable isotopes examined, although differences in $\delta^{13}C$ were sometimes evident. Despite this regional variation in isotopic composition

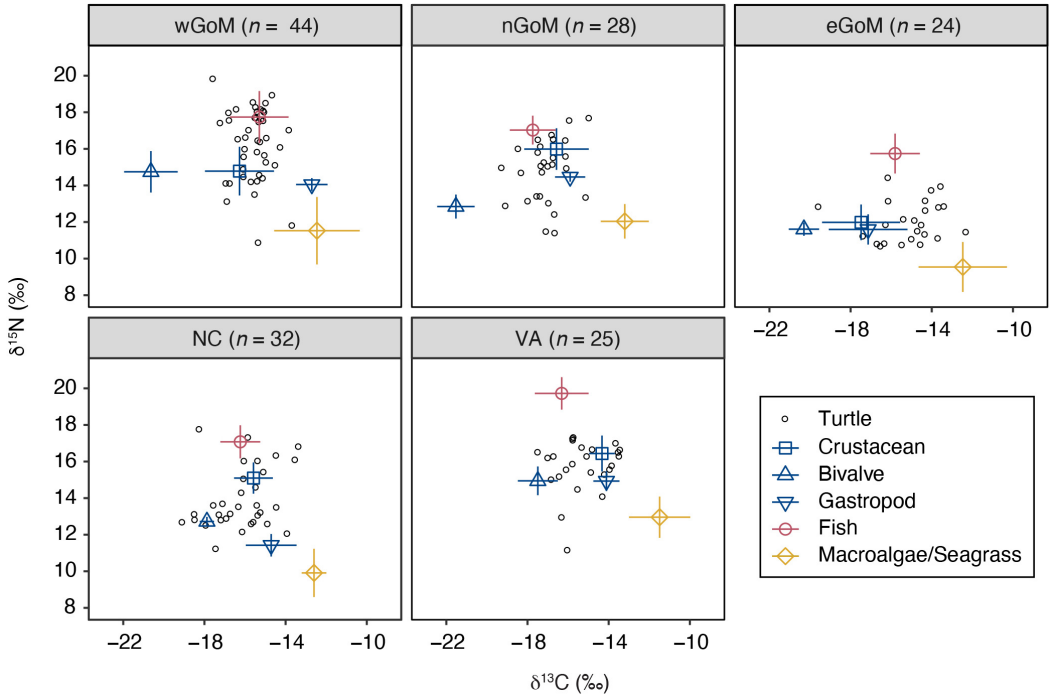

FIGURE 2 | Biplots of $\delta^{13}C$ and $\delta^{15}N$ values for Kemp's ridley sea turtles (*open circles*) and their potential prey groups (mean ± SD) by geographic region. Turtle sample sizes are presented at the top of each plot. Data are for the most recently deposited growth layer prior to death only. Prey values are corrected for trophic discrimination factors ($\Delta^{13}C$ = 2.1 ‰, $\Delta^{15}N$ = 5.1 ‰; see **Table 2** for uncorrected values). $\delta^{13}C$ values are corrected for carbonate carbon and the Suess effect.

within prey groups, the relative positioning of prey groups in bivariate isospace was similar across regions (**Figure 2**). As expected, fish $\delta^{15}N$ values were greater than the other prey groups in all cases, with mean values ranging between 10.64 and 14.63‰ (**Table 2**). Similarly, the macroalgae/seagrass group exhibited the lowest $\delta^{15}N$ values (mean range 4.44–7.86 ‰) and highest $\delta^{13}C$ values of all prey groups (mean range −15.31 to −13.59‰), reflective of their position at the base of coastal benthic food webs. Bivalves, which tended to be sampled in closest proximity to coastlines and freshwater inputs, had the lowest $\delta^{13}C$ values (mean range −23.63 to −19.59‰). Crabs and gastropods displayed the greatest variability in isospace positioning of the five prey groups but generally fell within the polygon formed by macroalgae/seagrass, bivalves, and fish (**Figure 2**). Within regions, fish, crustaceans, bivalves, and macroalgae/seagrass differed statistically for at least one stable isotope (Wilcoxon rank sum tests, $P < 0.05$; see **Supplementary Table S5**). However, gastropods tended to share isospace with at least one other prey group in each region, likely due in part to small sample sizes—gastropod stable isotope values are poorly represented in the primary literature (see **Supplementary Figure S1**).

Kemp's ridley bone stable isotope values were generally constrained by the prey stable isotope data (**Figure 2**). Summary characteristics of bone growth layers sampled for stable isotope ratios are presented in **Table 3**. An analysis of variance on these data showed there was significant variation among regions for both $\delta^{13}C$ ($F_{4,148} = 11.68$, $P < 0.001$) and $\delta^{15}N$ ($F_{4,148} = 129.19$, $P < 0.001$) values. A *post hoc* Tukey test determined that turtle bone $\delta^{13}C$ values were significantly lower in turtles stranded in the nGoM relative to all other regions ($P < 0.05$; **Supplementary Table S6**), possibly a result of influences of the Mississippi River, as freshwater systems generally have distinctly lower $\delta^{13}C$ values than marine systems (Fry and Sherr, 1989). In addition, $\delta^{15}N$ values were significantly higher in turtles from the wGoM and lower in turtles from the eGoM relative to all other regions ($P < 0.05$). Differences in $\delta^{15}N$ values between turtles in the eGoM and other regions may be driven by regional differences in nitrogen cycling or trophic ecology. The West Florida Shelf is an area of high N_2-fixation due to the presence of the cyanobacteria *Trichodesmium* (Lenes et al., 2001; Mulholland et al., 2006; Vander Zanden et al., 2015), which reduces $\delta^{15}N$ values (Montoya et al., 2002). Similarly, Kemp's ridleys in southwest Florida are known to eat tunicates, a low trophic level marine species with characteristically low $\delta^{15}N$ values (Williams et al., 2014). Along the United States Atlantic Coast, $\delta^{15}N$ values were significantly higher and less variable in turtles from Virginia relative to turtles in North Carolina, tracking differences in prey isotopic composition, which is possibly due to nutrient loading by anthropogenic activities in the Chesapeake Bay.

Regional Variation in Diet Composition

We observed distinct regional differences in diet composition (% fish vs. % invertebrate vs. % macroalgae/seagrass) for Kemp's ridleys (**Figure 3** and **Table 4**). Diet proportion estimates derived from mixing models that included both uninformative and informative priors indicated that Kemp's ridley diets were

TABLE 3 | Summary characteristics for Kemp's ridley sea turtle bone growth layers sampled for stable isotope values.

	Stranding and isotopic data								Somatic growth data	
Geographic region	***n***	**SCL (cm)**	**Age (year)**	**Year range**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**%C**	**%N**	***n***	**Growth rate (cm year^{-1})**
Western GoM	44	41.5 ± 8.1 (27.8, 58.9)	3.55 ± 2.62 (0.75, 12.75)	1999, 2012	−15.6 ± 0.8 (−17.6, −13.7)	16.3 ± 2.0 (10.9, 19.8)	13.8 ± 0.8	4.5 ± 0.3	38	6.5 ± 2.9 (0.8, 11.6)
Northern GoM	28	42.7 ± 8.6 (25.7, 61.8)	3.25 ± 1.84 (0.75, 7.75)	1992, 2014	−17.1 ± 1.0 (−19.3, −15.0)	14.8 ± 1.7 (11.4, 17.7)			20	6.3 ± 2.6 (3.0, 12.2)
Eastern GoM	24	43.3 ± 8.0 (26.5, 56.3)	3.38 ± 1.50 (0.75, 5.75)	1999, 2013	−15.1 ± 1.6 (−19.6, −12.3)	12.0 ± 1.1 (10.7, 14.4)			16	6.1 ± 3.0 (2.2, 13.0)
North Carolina	32	40.0 ± 7.7 (27.5, 59.6)	4.41 ± 2.50 (0.75, 12.75)	1997, 2012	−16.2 ± 1.5 (−19.1, −13.4)	13.9 ± 1.7 (11.2, 17.8)			18	5.9 ± 1.9 (1.8, 9.8)
Virginia	25	43.7 ± 5.9 (29.9, 53.1)	5.23 ± 2.10 (1.75, 10.75)	1998, 2012	−15.3 ± 1.2 (−17.5, −13.5)	15.7 ± 1.4 (11.2, 17.3)			17	5.5 ± 1.2 (2.4, 7.6)

Values reported are mean ± SD (min, max). SCL is straightline carapace length (notch to tip) at stranding. Year and age are calendar year and estimated age at start of growth layer sampled. δ^{13}C values are corrected for carbonate carbon and the Suess effect. Reported %C and %N are for all sampled growth layers. Growth rate is annual growth rate and includes both true and marginal growth rates. Only the most external, recently deposited growth layer was sampled for each turtle bone.

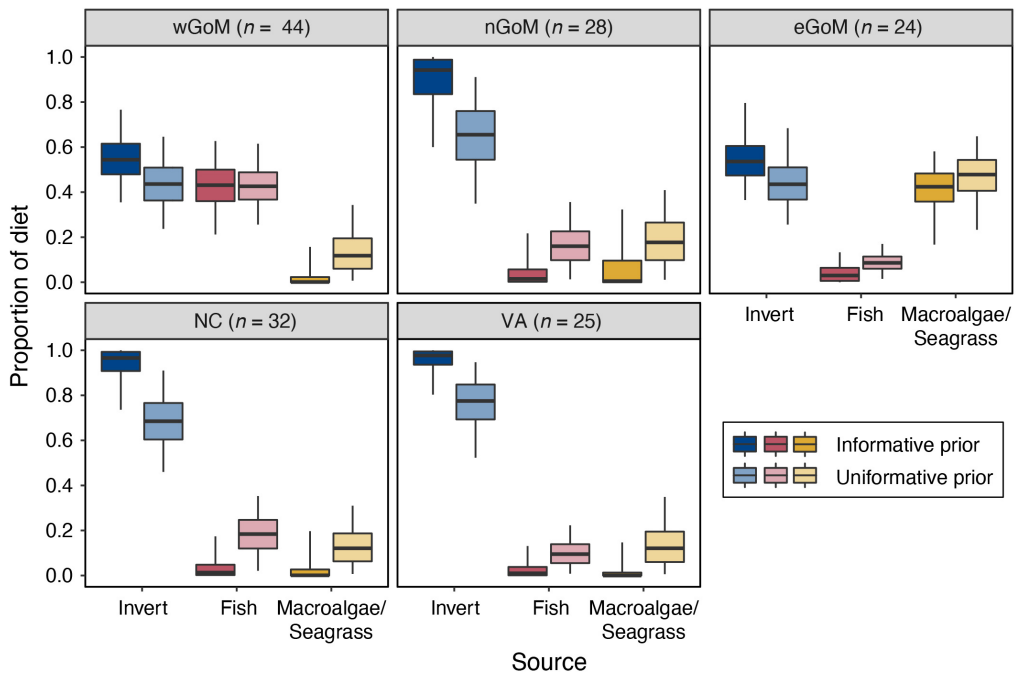

FIGURE 3 | Proportional contribution of each prey group to Kemp's ridley sea turtle diets by geographic region based on MixSIAR models that included an informative prior constructed from published diet proportion data and an uninformative prior that assigned equal probability to all prey groups. Turtle sample sizes are presented at the top of each plot. Data for invertebrate prey groups (crustacean, bivalve, and gastropod) were aggregated *a posteriori*. Lines in boxes are medians, boxes are 50% credible intervals, error bars are 95% credible intervals. See **Table 4** for samples sizes, medians, and credible interval values.

dominated by invertebrates in the nGoM, North Carolina, and Virginia (65.6–97.7%). In contrast, diets in the wGoM and eGoM were more evenly divided between invertebrates (43.6–54.5%) and fish (42.6–43.1%) or invertebrates (43.5–53.6%) and macroalgae/seagrass (42.4–47.8%), respectively. As it is unlikely that Kemp's ridleys would consume such high proportions of macroalgae/seagrass, the eGoM results likely reflect consumption of an isotopically similar benthic resource, such as tunicates (∼5.5‰; Williams et al., 2014), or incorrect parameterization of the model. Within the wGoM and eGoM regions, individual variation in turtle diets was high for wGoM turtles but low for eGoM turtles. The proportional contribution of fish and invertebrates to individual wGoM turtle diets ranged between 12 and 60% and 36 and 85%, respectively, whereas the proportional contribution of macroalgae/seagrass and invertebrates to individual eGoM turtle diets ranged between 32 and 48% and 49 and 63%.

In most cases, models that included uninformative priors estimated slightly greater contribution of fish and macroalgae/seagrass prey groups to Kemp's ridley diets

TABLE 4 | Median (95% CI) posterior Bayesian mixing model estimates of diet proportion by geographic region for Kemp's ridley sea turtles (n = 153).

Geographic region	Informative prior			Uninformative prior		
	Invert (%)	Fish (%)	Macroalgae/ seagrass (%)	Invert (%)	Fish (%)	Macroalgae/ seagrass (%)
Western GoM (n = 44)	54.5 (35.5, 76.6)	43.1 (21.2, 62.7)	0.1 (0.0, 15.7)	43.6 (23.7, 64.6)	42.6 (25.6, 61.5)	11.8 (0.7, 34.3)
Northern GoM (n = 28)	94.2 (60.0, 100.0)	1.5 (0.0, 21.7)	0.5 (0.0, 32.3)	65.6 (34.9, 91.1)	16.0 (1.3, 35.6)	17.7 (1.1, 40.9)
Eastern GoM (n = 24)	53.6 (36.5, 79.6)	3.0 (0.0, 13.3)	42.4 (16.7, 58.1)	43.5 (25.6, 68.4)	8.6 (1.5, 17.0)	47.8 (23.3, 64.8)
North Carolina (n = 32)	96.6 (73.6, 100.0)	1.3 (0.0, 17.4)	0.1 (0.0, 19.7)	68.5 (46.0, 91.0)	18.4 (2.1, 35.3)	12.1 (0.7, 31.0)
Virginia (n = 25)	97.7 (80.3, 100.0)	1.0 (0.0, 13.1)	0.0 (0.0, 14.7)	77.5 (52.3, 94.7)	9.5 (0.8, 22.3)	12.1 (0.6, 34.9)

*The uninformative prior is constructed from the Dirichlet Bayesian prior whereas the informative prior is constructed from diet proportions published in the primary literature (see **Supplementary Table S2**).*

relative to models with informative priors. However, posterior distributions and 95% credible intervals overlapped extensively between each set of models (**Figure 3** and **Supplementary Figure S5**). Larger differences between these model sets were evident in the pre-aggregated invertebrate data, where mixing models with uninformative priors estimated more even contribution of crustaceans, bivalves, and gastropods to Kemp's ridley diets relative to models with the informative priors (**Supplementary Figure S6**).

As expected for Bayesian stable isotope mixing models (Bond and Diamond, 2011), sensitivity analyses performed on the null mixing model with informative priors for wGoM turtles showed that changes in diet-bone TDFs affected estimated proportional contribution of prey groups to Kemp's ridley diets (**Supplementary Figure S6**). Specifically, the median estimated proportional contribution of fish and invertebrate prey to wGoM turtle diets was highly sensitive to changes in Δ^{15}N but less sensitive to changes in Δ^{13}C, unsurprising given that these prey groups primarily differ in δ^{15}N values (**Figure 2**). Diet estimates within one standard deviation of the Δ^{15}N mean ranged between 7.9 and 66.9% for fish and 30.7 and 79.2% for invertebrates, whereas estimates within one standard deviation of the Δ^{13}C mean ranged between 35.7.and 45.4% for fish and 41.7 and 62.6% for invertebrates. Mixing model estimates for proportional contribution of individual invertebrate groups to turtle diets displayed greater sensitivity to changes in Δ^{13}C values. Bivalve and gastropod diet composition estimates were more sensitive to changes in Δ^{13}C than Δ^{15}N, although their relative contribution to turtle diets remained low within one standard deviation of the mean Δ^{13}C value (0–7.4% for bivalve, 0–11.9% for gastropod). Crustacean estimates were equally sensitive to both changes in Δ^{13}C and Δ^{15}N values, with bivariate changes in both TDFs resulting in estimates ranging from 19.5 to 90.7%.

Diet Composition and Somatic Growth Rates

After controlling for the influence of age on somatic growth rates, our GLMs revealed no significant relationships between δ^{15}N values and somatic growth rates across most regions (**Table 5** and **Figure 4**). The only exception was for nGoM turtles, where there was a weakly negative relationship between δ^{15}N values and somatic growth rates (P = 0.07). This negative trend was still evident when marginal growth rates were excluded from the analysis, but the relationship became non-significant (P = 0.11). When marginal growth rates were excluded, trends across the other regions remained the same, exhibiting a shallow, non-significant decline in somatic growth rates with increasing δ^{15}N values. These patterns ran counter to our expectation of higher growth rates with increasing δ^{15}N values (i.e., foraging higher in food web), and could indicate that turtles consuming proportionally higher amounts of fish bycatch might be growing slower than conspecifics feeding primarily on invertebrates, or that physiological processes related to changes in size/age are

TABLE 5 | Summary of statistical output for Generalized Linear Models used to evaluate the influence of diet (composition and δ^{15}N values) on Kemp's ridley sea turtle annual growth rates.

Model	n	AIC	Var	Est	SE	t	Pr > |t|
(A) Growth ~ δ^{15}N + Age							
wGoM	38	186.11	δ^{15}N	−0.03	0.03	−0.741	0.463
			Age	−0.11	0.03	−4.234	**<0.001**
nGoM	20	83.93	δ^{15}N	−0.10	0.05	−1.902	0.074
			Age	−0.07	0.04	−1.753	0.098
eGoM	16	83.23	δ^{15}N	0.00	0.12	0.038	0.971
			Age	−0.11	0.08	−1.397	0.186
NC	18	65.90	δ^{15}N	−0.04	0.03	−1.273	0.222
			Age	−0.09	0.02	−4.410	**<0.001**
VA	17	59.31	δ^{15}N	−0.06	0.04	−1.465	0.165
			Age	−0.04	0.04	−1.196	0.252
(B) Growth ~ *p*Fish + Age							
wGoM	38	185.04	*p*Fish	−0.68	0.53	−1.295	0.204
			Age	−0.11	0.03	−4.364	**<0.001**

(A) Comparison of δ^{15}N values and growth rates across all regions. (B) Comparison of median percent of fish in diet (pFish) on growth rates for western GoM turtles only. Bold signifies statistically significant relationships.

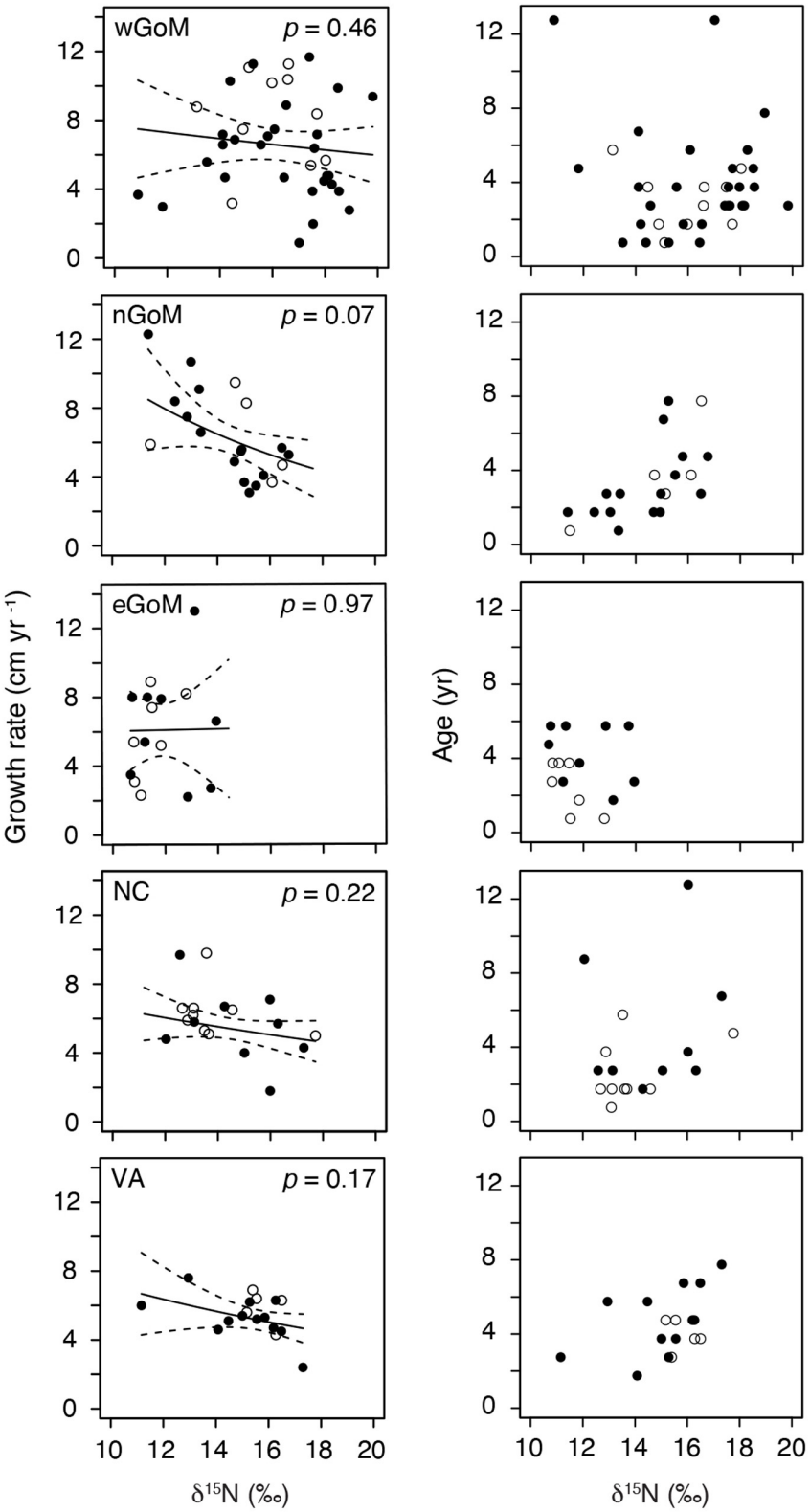

FIGURE 4 | Generalized Linear Model results examining the relationships between annual Kemp's ridley sea turtle growth rates and $\delta^{15}N$ values, and age and $\delta^{15}N$ values, for individual turtles by geographic region. Data are for the most recently deposited growth layer prior to death only. Closed circles are true annual growth rates (i.e., turtle stranded in spring, yielding a complete growth interval). Open circles are estimated annual growth rates for turtles that stranded during the winter (November–March); we assumed that annual skeletal growth asymptotes in November (see section "Somatic Growth Rates in Materials and Methods").

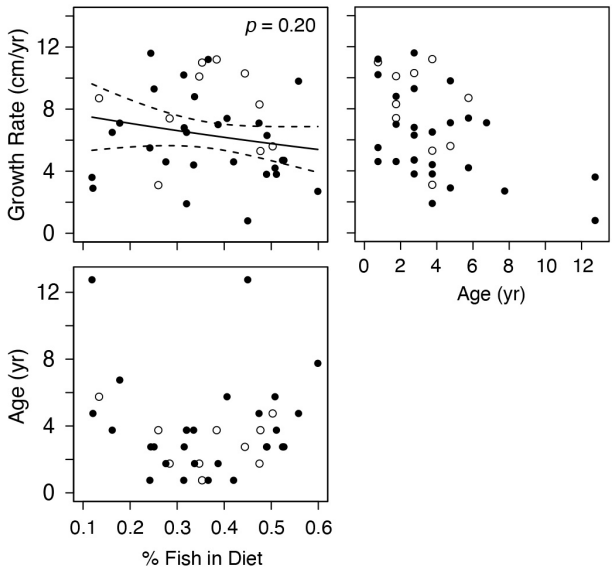

FIGURE 5 | Generalized Linear Model results examining the relationship between annual Kemp's ridley sea turtle growth rates and proportional contribution of fish to western Gulf of Mexico turtle diets. Diet estimates are derived from a stable isotope mixing model that included informative priors. Data are for the most recently deposited growth layer prior to death only. Closed circles are true annual growth rates (i.e., turtle stranded in spring, yielding a complete growth interval). Open circles are estimated annual growth rates for turtles that stranded during the winter (November–March); we assumed that annual skeletal growth asymptotes in November (see section "Somatic Growth Rates in Materials and Methods").

influencing δ^{15}N values. In nGoM and VA turtles, δ^{15}N values and age exhibited a weakly positive relationship (**Figure 4**). However, across all regions, turtles with the highest δ^{15}N values tended to span a wide range of ages, suggesting that larger/older turtles are generally not any more likely than smaller/younger turtles to feed higher in the food web.

Given the low intra-regional variation in diet composition for most regions, we only examined relationships between estimated diet composition and growth rates for turtles from the wGoM (**Figure 5**). For these turtles, growth rates were not strongly related to the proportion of fish in turtle diets ($P = 0.20$). Again, a shallow, non-significant, negative trend was evident in this relationship that did not change following exclusion of marginal growth rates from the analysis. Similar to covariate relationships with δ^{15}N values, the proportional contribution of fish was not strongly related to age (**Figure 5**).

DISCUSSION

Through an integration of multiple skeletal analyses, we provide the first population-level evaluation of Kemp's ridley diet composition and investigation into the relationship between individual foraging ecology and somatic growth. Our stable isotope mixing models revealed strong regional differences in the proportional contribution of different prey groups to turtle diets that generally followed findings of published gut and fecal content studies. We specifically observed greater contribution of fish to turtle diets in the western GoM and greater contribution of macroalgae/seagrass—or other isotopically similar benthic resources—to turtle diets in the eastern GoM, whereas invertebrates dominated turtle diets in other regions. Through comparative analyses of somatic growth rates, stable isotope values, and mixing model-derived diet composition estimates, we found that individual Kemp's ridley somatic growth rates were generally poorly correlated with stable isotope-based evidence of turtle trophic ecology within regions. Turtles that foraged higher in the food web (i.e., more fish in diet, higher δ^{15}N values) grew at the same rate as or slower than conspecifics foraging lower in the food web, even after accounting for ontogenetic effects on growth rates. Our results suggest that diet composition alone is not a primary determinant of Kemp's ridley growth rates, which may be more strongly influenced by other factors such as prey availability, foraging rate and efficiency, and nutritional condition.

Regional Diet Variation

Kemp's ridleys are opportunistic foragers, naturally feeding on a wide range of invertebrate species (Shaver, 1991). Various crab species generally constitute >75% of total dietary dry mass, whereas molluscs and vegetation generally make up <5–10% (Shaver, 1991; Burke et al., 1993, 1994; Seney and Musick, 2005; Servis et al., 2015; Schmid and Tucker, 2018). In the western and northern GoM, Kemp's ridleys also consume a significant amount of fish and shrimp. Fish can comprise up to 13.7% of total dietary dry mass and have been reported in 40.1–76.1% of stranded turtle gastrointestinal tracts in these regions (Werner, 1994; Cannon, 1998; Stacy, 2015). Fish prey are most likely obtained as discarded bycatch or bait from fisheries given that Kemp's ridleys are thought to lack the speed necessary to catch them live (Shoop and Ruckdeschel, 1982; National Research Council, 1990). This conclusion has been supported by the co-occurrence of *Nassarius* species—molluscs that scavenge dead animal tissues—in turtle stomachs that also contain fish (Shaver, 1991; Bjorndal, 1997). In contrast, fish are an uncommon prey item for Kemp's ridleys along the United States Atlantic Coast, occurring in a maximum of 16.7% of sampled turtles (Burke et al., 1993, 1994; Seney and Musick, 2005).

Results of our Bayesian isotope mixing models largely follow these patterns, with invertebrates comprising 68.5–97.7% of turtle diets along the United States Atlantic Coast but smaller and more variable proportions within the GoM. In the western GoM, where shrimp fishing effort is relatively high (Scott-Denton et al., 2012), we estimated the region-level contribution of fish to turtle diets was 42.6–43.1%. The similarity in posterior distribution estimates for models with informative and uninformative priors suggests our stable isotope data were highly informative and that these estimates are relatively robust (Moore and Semmens, 2008). Kemp's ridleys display remarkable plasticity in diet that appears largely driven by local availability rather than preferences for specific prey species (Bjorndal, 1997). Importantly, even with the implementation of bycatch reduction devices, shrimp fishery discard rates are high in the GoM, accounting for ∼50% of total

United States fishery discards (Diamond, 2004; Harrington et al., 2005; Scott et al., 2012). It is thus probable that consumption of fish bycatch discarded by shrimp trawlers is a facultative response to local availability in addition to ease of acquisition.

Diet composition estimates for turtles in the northern GoM were similar to those for turtles along the United States Atlantic Coast, with estimated contributions of invertebrates to diets ranging between 65.6 and 94.2%. These results were unexpected given our hypothesis regarding the spatial relationship between shrimp trawl activity and fish consumption, and contrast with recent necropsy results for the region which suggest higher contributions of fish to turtle diets (Stacy, 2015). Even though fishery discard rates are high in the northern GoM, natural prey availability is also high in this region and may be sufficient to support the Kemp's ridley population. Indeed, blue crab landings in Louisiana represent > 75% of all landings in the Gulf of Mexico, whereas those in Texas comprise only 7% (GSMFC, 2015). The negligible estimated contribution of fish to northern GoM turtle diets may also be due to the close proximity of fish and crustaceans in isospace (**Figure 2**). Mixing models require sources to be sufficiently separated in order for the model to be able to differentiate them (Parnell et al., 2013). It is thus possible that fish contribute more to Kemp's ridley diets in this region than our mixing models indicate. Further refinement of the prey stable isotope data to more accurately reflect fish (species and size) and invertebrate species consumed by Kemp's ridleys may improve mixing model-derived diet estimations for this and other regions.

Within the eastern GoM, we estimated Kemp's ridley diets primarily comprise invertebrates (43.5–53.6%) and macroalgae/seagrass (42.4–47.8%). These results do not align with the current understanding of Kemp's ridley diet composition and are likely due to two factors. First, the invertebrate prey groups in the eastern GoM are the most clustered in isospace relative to other regions, with $\delta^{13}C$ values for crustaceans and gastropods being particularly low (**Figure 2**). Such a $\delta^{13}C$ mismatch could arise if the eastern GoM crustaceans and gastropods included in our study derived a greater proportion of their carbon from terrestrial vs. marine sources relative to the other regions (Michener and Schell, 1994). This, combined with slightly higher turtle $\delta^{13}C$ values in this region, resulted in the largest isotopic mismatch between invertebrates and turtles of all regions after accounting for trophic enrichment. It is thus possible that the prey data included in our mixing model did not accurately reflect those prey groups or turtle diets in this region. Second, it is also possible that our mixing model is missing a key prey source. Notably, tunicates are thought to be an important prey source for Kemp's ridleys in southwest Florida, occurring in 83.3% of fecal samples and constituting 38.6% of fecal dry mass (n = 64 turtles; Witzell and Schmid, 2005). A dearth of tunicate stable isotope data prevented their inclusion in our mixing models. However, two tunicates sampled in Saint Joseph's Bay, Florida, had $\delta^{15}N$ values of 5.51 and 5.56‰ and $\delta^{13}C$ values of −12.72 and −12.78‰ (Williams et al., 2014), which fall within the range of seagrass and macroalgae stable isotope values included in our study. Therefore, our results may in fact reflect consumption of this or another similar benthic resource rather than macroalgae/seagrass.

While isotopic mixing models have greatly advanced our ability to discern diets from isotopic data, their utility and accuracy still rely on substantial ecological knowledge for proper parameterization—these models will always attempt to fit the data, even if the consumers fall outside the mixing space (Phillips and Koch, 2002; Parnell et al., 2010). Given the spatiotemporal scale of this study it was necessary to rely on prey isotopic data from the primary literature, which may have inserted certain biases into the analysis. We ameliorated temporal effects to the best of our abilities by using time-corrected $\delta^{13}C$ values. However, it was not possible to overcome spatial biases in sample collection and as a result this may represent the greatest source of bias in our analysis. Kemp's ridley sea turtles forage in a wide range of shallow, benthic marine habitats, including a substantial part of the continental shelf (Shaver et al., 2013; Hart et al., 2018). Unfortunately, few studies have characterized invertebrate stable isotope values for continental shelf habitats resulting in greater prevalence of estuarine and coastal organisms in our prey isotopic dataset. Given the growing application of stable isotopes to the study of sea turtle foraging and spatial ecology (Pearson et al., 2017; Figgener et al., 2019), quantifying means and variances in known prey stable isotope values across sea turtle ranges should be a high-priority research area. Future analyses using compound-specific isotope analysis of amino acids, which can more accurately estimate consumer trophic position, may also greatly aid in understanding diet variation in sea turtles (Evershed et al., 2007; McMahon and Newsome, 2018).

Trophic Ecology and Somatic Growth Dynamics

The lack of strong relationships among bone $\delta^{15}N$ values, mixing model-derived diet composition estimates, and somatic growth rates suggests that within-population variation in diet composition may not be a primary determinant of Kemp's ridley somatic growth variation, and that diet composition may not be a strong driver of the regional (Atlantic vs. GoM) somatic growth differences observed in this species. However, we measured only one component of a sea turtles' diet—composition—and foraging rate, nutrient assimilation rate, and nutritional status can also strongly influence animal growth rates. Unfortunately, these factors are difficult to study in sea turtles due to their high mobility and conservation status, which has thus far limited investigations into relationships between sea turtle trophic ecology and growth. Wallace et al. (2009) provides the only other comparison of sea turtle trophic ecology and somatic growth where they compared blood plasma $\delta^{15}N$ and $\delta^{13}C$ values with growth rates of recaptured loggerhead turtles from North Carolina, United States. They found no strong relationships between these covariates and hypothesized that intra-population growth variation may instead be driven by alternative habitat use (coastal vs. oceanic habitat; McClellan and Read, 2007). However, recent research suggests that loggerhead growth dynamics are similar between coastal and oceanic life stages and foragers (Ramirez et al., 2017), indicating that perhaps other factors underlie the observed variability in growth.

Surprisingly, our results suggest that turtles foraging at higher trophic levels may in fact exhibit lower growth rates than conspecifics foraging at lower trophic levels. Our study does not shed light on underlying mechanisms for this pattern, but these findings suggest that foraging strategies that rely on higher trophic level prey may not be energetically optimal for sea turtles. For example, that this energy rich (Williams et al., 2014; Schaafsma et al., 2018), yet presumably similarly digestible (Tibbetts et al., 2006; Peckham et al., 2011), prey does not infer a growth advantage may indicate that the energetic costs associated with searching for and consuming fish (discards) outweigh energetic gains. Similarly, Kemp's ridleys may not be well adapted to consume fish given that fish are considered an unnatural prey item. Our understanding of sea turtle nutritional ecology is poor for omnivorous species (Bjorndal, 1997), but it is plausible that sea turtles may less efficiently assimilate nutrients from fish relative to invertebrates due to evolutionary constraints.

However, it is also possible that the conditions that lead Kemp's ridleys to consume fish also contribute to reduced growth rates. If Kemp's ridleys consume fish due to low natural prey availability or poor condition, turtles may consume fewer resources overall or be nutritionally stressed which would lead to reduced growth rates. Additionally, the tissues of nutritionally stressed animals tend to have higher $\delta^{15}N$ values because they catabolize their own tissues for energy (Hobson et al., 1993; Fuller et al., 2005). Given the retrospective nature of our study, we were not able to evaluate the nutritional condition at stranding for sampled turtles. However, necropsies of Kemp's ridleys stranded in the northern GoM (Louisiana, Mississippi, and Alabama) between 2010 and 2014 suggest there was a decline in stranded turtle nutritional condition during this period (Stacy, 2015). As all but one of the northern GoM humerus bones we sampled were from turtles stranded between 2010 and 2014, the apparent decline in growth rates with increasing $\delta^{15}N$ values for this region may be attributed in part to this general decline in turtle nutritional condition in the region. Future studies combining stranded turtle nutritional assays, skeletochronology, and stable isotope analyses would greatly aid in identifying factors underpinning the observed growth patterns.

An important source of uncertainty in our growth analysis is the potential influence of growth rates on isotopic signatures and trophic discrimination factors (TDFs). For neonate loggerhead sea turtles (*Caretta caretta*), somatic growth can explain up to half of the total rate of isotopic incorporation into blood, skin, and scute tissues, and likely explains age-related differences in nitrogen TDFs (Reich et al., 2008). Indeed, multiple studies have demonstrated that faster growth can reduce $\Delta^{15}N$ values because nitrogen input greatly exceeds nitrogen loss—more ^{14}N is retained in the body which lowers $\delta^{15}N$ values and reduces isotopic differences between consumers and their prey (Fuller et al., 2004; Martinez del Rio and Wolf, 2005; Reich et al., 2008; Kurle et al., 2014). Such physiological effects, if not accounted for in stable isotope-based studies, can lead to spurious conclusions, particularly in species with distinct ontogenetic changes in size and growth (Villamarín et al., 2018). For our study, a growth-induced decline in $\Delta^{15}N$ values may have caused us to underestimate the proportional contribution of fish to turtle diets for faster growing individuals. In contrast, animals that consume large amounts of animal-derived proteins typically have higher $\Delta^{15}N$ values (Vander Zanden et al., 2012; Kurle et al., 2014; Turner Tomaszewicz et al., 2017b). A diet-induced increase in $\Delta^{15}N$ would therefore potentially have the opposite effect as growth on TDFs, causing an overestimation of the proportional contribution of fish to turtle diets for individuals that forage higher in the food web. Given the sensitivity of our results to changes in $\Delta^{15}N$ values, more studies are needed that characterize isotopic routing within sea turtle tissues and effects of diet type and physiology on TDFs, particularly for bone tissue (e.g., Turner Tomaszewicz et al., 2017b).

CONCLUSION

The integration of skeletal growth and stable isotope analysis provides a powerful tool to reconstruct sea turtle trophic ecology while simultaneously investigating relationships between diet composition and somatic growth rates. Using this approach, we elucidated substantial regional variation in Kemp's ridley diet composition that aligns with results of site-specific studies of their foraging ecology. This study also provides one of the few quantitative assessments of the relationship between sea turtle trophic ecology and somatic growth. While we present a promising new approach for studying drivers of somatic growth variation in sea turtles, our analysis was limited due to critical data and knowledge gaps. Greater characterization of sea turtle prey stable isotope values throughout the western North Atlantic Ocean, and diet-tissue isotopic discrimination factors, would substantially improve the stable isotope mixing models herein and allow for more robust isotope-based investigations into sea turtle foraging ecology (Pearson et al., 2017; Figgener et al., 2019). Additionally, applications of stable isotope mixing models to Kemp's ridleys at narrower spatiotemporal scales (e.g., specific foraging grounds, ages, and years) and using greater taxonomic specificity for prey groupings may help reduce sources of uncertainty, improve model estimates, and clarify relationships between diet composition and growth rates (e.g., Wallace et al., 2009; Lemons et al., 2011; Goodman Hall et al., 2015). Integrating additional data gleaned from dead stranded turtles (e.g., gut contents, nutritional condition, and parasite load) into these analyses may also be informative. Ultimately, our analysis further highlights the unique importance of stranded and salvaged turtles to investigating otherwise intractable questions in sea turtle ecology.

DATA AVAILABILITY STATEMENT

All prey isotope datasets, and turtle isotope and growth metadata, generated for this study are included in the article/**Supplementary Material**. Full turtle isotope and growth datasets are available upon request to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this study only utilized samples opportunistically collected from animals that died naturally and washed up on beaches.

AUTHOR CONTRIBUTIONS

MR, LA, and SH contributed to the conception and design of the study. LA and MC provided samples for analysis. MR, LA, LG, and MS performed skeletochrological analyses. MR performed stable isotope and statistical analyses and wrote the first draft of the manuscript. All authors contributed to manuscript revision and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00253/full#supplementary-material

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