



Foraging Habits of Green Sea Turtles (*Chelonia mydas*) in the Northwestern Gulf of Mexico

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Knowledge of green turtle (*Chelonia mydas*) foraging ecology in the northwestern Gulf of Mexico (GOM) is critical as populations begin to recover from heavy harvesting in prior centuries. We present a comprehensive long-term assessment of green turtle diets from carcasses salvaged from 1987 to 2014 along the Texas coast. Digestive tract contents were examined from 420 green turtles, ranging in size from 7.3 to 86.0 cm in straight carapace length (SCL_{max}). Green turtles as small as 16.2 cm SCL_{max} recruit from the oceanic environment to nearshore foraging habitat in the northwestern GOM and consume macroalgae principally. A successive shift in diet and habitat to inshore seagrasses was evident by the seagrass-dominated diet of turtles larger than 30 cm SCL_{max}. Animal matter remained a frequently ingested diet item suggesting these immature green turtles are better classified as omnivores. The overall evidence indicates that Texas' recovering green turtle assemblage is exhibiting foraging plasticity within seagrass meadows changing species composition and density.

Keywords: sea turtle, *Chelonia mydas*, gut content analysis, foraging ecology, Texas

INTRODUCTION

Green turtles (*Chelonia mydas*) were once so abundant in Texas waters that they supported a commercial fishery, with a peak annual landing of approximately 265,350 kg of turtles in 1890 (Hildebrand, 1982). Pressures on this marine turtle assemblage were inexorable. By 1903 the green turtle fishery had virtually collapsed due to the commercial harvest and severe hypothermic stunning events in the winters of 1894–1895 and 1899, which decimated the turtle population (Hildebrand, 1982; Doughty, 1984). Since green turtles were listed under the protection of the U.S. Endangered Species Act in 1978 and Mexico banned the commercial harvest of all sea turtles in 1990, Texas waters once again support a rapidly growing immature green turtle aggregation (Shaver et al., 2013). In-water research indicates increased green turtle population growth, with a catch per unit of effort on the lower Texas coast at 10 times greater in 2002–2010 than in 1991–1994 (Metz and Landry, 2013). Furthermore, the Sea Turtle Stranding and Salvage Network (STSSN) provides evidence of an increased Texas green turtle population. The STSSN reports increasingly high stranding numbers of immature green turtles (Stacy et al., 2020) and record-breaking stranding events from cold weather. From 1980 through 2015, the largest totals (>450 turtles) of turtles cold-stunned were during the winters of 2009–2010, 2010–2011, 2013–2014, and 2014–2015 (Shaver et al., 2017).

Immature green turtles in Texas primarily originate from Mexican rookeries in the western Gulf of Mexico (GOM) (Shamblin et al., 2016). They disperse from their nesting beaches as hatchlings and occupy an oceanic stage in the offshore waters of the GOM (Bolten, 2003). During this life-history stage, young green turtles reside and feed within the large *Sargassum* mats floating in the GOM (Witherington et al., 2012). The aforementioned algae mats break away in massive segments and wash ashore in the spring and summer seasons in massive wracks along the Texas gulf coast (Gherskiere et al., 2006; Gower et al., 2006; Webster and Linton, 2013). Large recruitment pulses of immature oceanic green turtles frequently accompany these *Sargassum* mats (Shaver et al., 2017; Stacy et al., 2020). Post-oceanic recruits often reside at neritic granite rock jetties designed to stabilize channels that connect to inshore bays and lagoons (Manzella et al., 1990; Renaud et al., 1992; Williams and Manzella, 1992; Coyne, 1994; Renaud et al., 1994; Shaver, 1994; Renaud and Williams, 1997; Williams and Renaud, 1998). These structures provide protection and abundant invertebrate and macroalgae food sources, with over 80 macroalgae species reported at the Port Mansfield jetty in south Texas (Edwards and Kapraun, 1973; Kaldy et al., 1995). Green turtles have been documented to inhabit jetty channels for up to 1,100 days (Shaver, 2000), where they consume macroalgae (Coyne, 1994). Some of the smallest daily movements recorded for juvenile green turtles were at a jettied pass in South Texas (Renaud et al., 1995), further evidence of the green turtles' dependency on this habitat.

Texas green turtles exhibit a size-based transition, typically at 25–45 cm SCL, from jetty inhabitation to residency in inshore seagrass beds (Gorga, 2010; Howell, 2012). Among these beds, there are macroalgal communities (Breuer, 1962; Hildebrand and King, 1978). Data on the green turtle foraging habits in the northern GOM are historically limited. While Atlantic green turtles are known to maintain and selectively feed within seagrass plots (Bjorndal, 1985), only recently was this identified for the first time in the northern GOM (Rodriguez and Heck, 2020). Research suggests seagrasses are the dominant diet item for turtles captured in Texas' lagoon and bay systems (Landry et al., 1992; Coyne, 1994). The three most common species of seagrass in Texas waters are shoal (*Halodule beaudettei*), Gulf manatee (*Cymodocea filiformis*), and turtle (*Thalassia testudinum*) grass (Quammen and Onuf, 1993; Withers, 2002). The 209-km long Laguna Madre accounts for 81% of the Texas coast's entire seagrass coverage (Mendelssohn et al., 2017). Consequentially, the Laguna Madre supports the greatest abundance of inshore green turtles in the state (Doughty, 1984; Metz and Landry, 2013).

Ecological succession in seagrass beds typically starts with the colonization of shoal grass in disturbed or barren areas and climaxes with turtle grass (Patriquin, 1975). Historically, shoal grass dominated Texas' estuaries. However, from the mid-1960s to 1998, bare regions increased, and shoal grass acreage declined by 36%, with partial replacement by turtle and manatee grass (Quammen and Onuf, 1993; Onuf, 1996; Pulich and Onuf, 2007; Gutierrez et al., 2010; Hobson and Whisenant, 2018). The changes in seagrass coverage and composition are attributed to maintenance dredging, propeller

scarring, brown tide algae blooms, and natural processes (Onuf, 1994; Pulich and Calnan, 1999; Dunton et al., 2002). With the drafting of a Seagrass Conservation Plan for Texas in 1999, efforts to protect and enhance Texas seagrass beds' health and quality were implemented. They were expected to be effective at seagrass restoration within 2 years once high-priority actions were accomplished (Pulich and Calnan, 1999). Although seagrass distribution and density are essential to Texas's green turtle occurrence (Shaver et al., 2017), the impact of changes in seagrass composition and coverage on turtles' foraging habits is unknown.

The Texas coast is temperate to a subtropical system, with long hot summers and short, mild winters. Temperature frequently drives the macroalgal seasonality in warm-water regions like Texas (Mathieson and Penniman, 1986). Seagrass beds in Texas have displayed similar growth and biomass changes from the seasons' light and temperature-dependent fluctuations (Kowalski et al., 2009). Variability in resource availability can bring about variation in turtle foraging habits (López-Mendilaharsu et al., 2008; Guebert-Bartholo et al., 2011). For these reasons, it is critical to understand Texas green turtle foraging habits within their year-round range and how the diet might change with seasonal environmental fluctuations.

Describing the diet of green turtles found stranded in Texas for nearly three decades may discern any food-related changes due to seagrass composition and abundance variations. Further, examining the diet of multiple life-history stages in this rapidly increasing assemblage will provide a baseline for future diet studies. The significance of conventional gut contents analyses (GCA) to improve nutrition interpretation is highlighted in the sea turtle literature (Parker et al., 2005; Hatase et al., 2006; Revelles et al., 2007; Casale et al., 2008; Hoarau et al., 2014; Behera et al., 2015). We used GCA to examine the dietary composition of all size ranges of green turtles stranding on the Texas coast and to explore ontogenetic, temporal, and seasonal diet trends.

MATERIALS AND METHODS

Study Area

Seven major estuaries are covering 2.6 million acres along the Texas coast (Figure 1). Across the 350 miles long Texas coast, nine federally maintained jettied ship channels (Army Corps of Engineers, 2021) provide access to the bays and the Laguna Madre. Red algae species are most numerous in the jetty habitat, followed by brown and green algae (Fikes and Lehman, 2010). There are five species of seagrass in Texas, including widgeon (*Ruppia maritima*), star (*Halophila engelmannii*), shoal (*Halodule beaudettei*), Gulf manatee (*Cymodocea filiformis*), and turtle (*Thalassia testudinum*) grass. Amongst the seagrass beds, there are macroalgal communities dominated by *Cladophora* sp., *Digenea simplex*, *Gracilaria* spp., *Hypnea musciformis*, *Ulva lactuca*, and *Yuzurua poiteaui* (Breuer, 1962; Hildebrand and King, 1978).

Sample collection. We collected diet samples from 306 green turtles stranded from 1987 to 2014 from the Texas coast's inshore and offshore waters, and we incorporated the unpublished weight data from 114 Texas green turtles (Howell et al., 2016); for

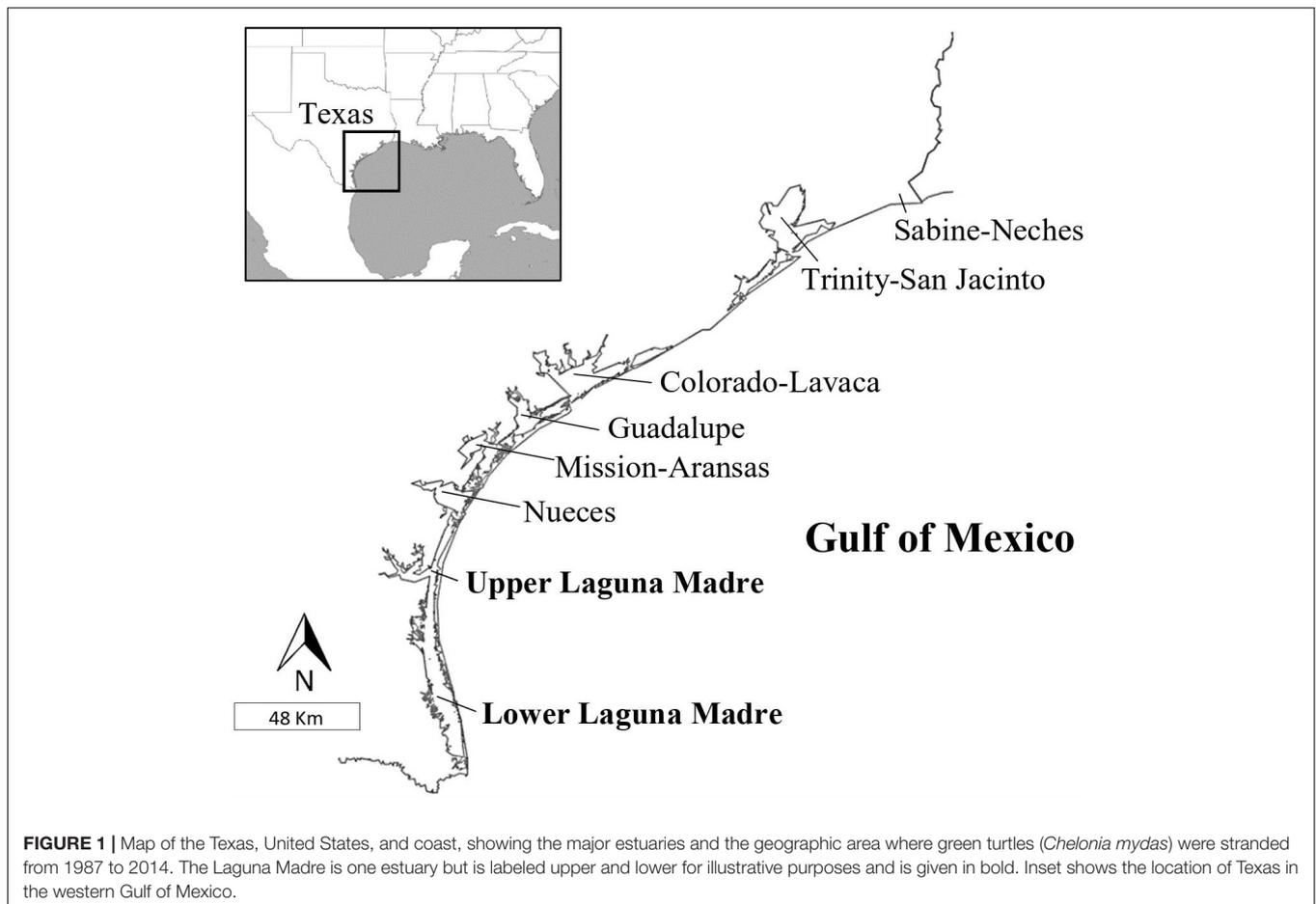


TABLE 1 | The number of stranded green sea turtles (*Chelonia mydas*) analyzed temporally and seasonally in this study ($n = 306$) and from previously unreported data from Howell et al. (2016) ($n = 114$), within each size class.

Size class, straight carapace length (cm)	Samples		Temporal		Seasonal			
	Present study (dry gravimetric)	Howell et al., 2016 (wet gravimetric)	1987–2000	2001–2014	Spring	Summer	Fall	Winter
Oceanic (≤ 20.0 cm)	10	5	6	9	8	6	1	0
Recruit (20.1–30.0 cm)	88	42	67	63	50	29	28	23
Transitional (30.1–40.0 cm)	139	43	93	89	31	28	34	89
Inshore (≥ 40.1 cm)	69	24	46	47	16	15	10	52
Total	306	114	212	208	105	78	73	164

a total of 420 samples from individual turtles (**Table 1**.) All measurements presented are maximum straight carapace length (SCL_{max}); ± 0.1 cm, measured from carapace notch to the posterior-most tip. Turtles sampled for this study ranged in size from 7.3 to 86.0 cm SCL_{max} , and their body condition suggested normal behaviors (i.e., actively foraging) prior to death. Data were grouped into four size classes, based on previous size-based distribution studies in Texas, to improve our assessments of size-based diet and habitat differences (Coynes, 1994; Shaver, 2000; Shaver et al., 2013; Howell et al., 2016). These size classes are referred to herein as oceanic (≤ 20.0 cm), recruit (20.1–30.0 cm), transitional (30.1–40.0 cm), and inshore (≥ 40.1 cm).

Necropsies were performed on carcasses following standard sampling procedures (Wyneken, 2001), and the entire digestive tracts were extracted and frozen for subsequent analysis. Diet items were removed from the whole gastrointestinal tract and identified to the lowest taxon possible with a dissecting microscope. Diet items were quantified by dry ($n = 306$) and wet ($n = 114$) gravimetric analyses (Hyslop, 1980; Bigg and Perez, 1985; Forbes, 1999). Dry weights were obtained by drying identified taxa samples for 24–48 h at 60°C and measuring the cooled samples to the nearest hundredth of a gram. The wet mass of each identified taxa was weighed to the nearest hundredth of a gram.

Sample Analysis

Cumulative prey curves were employed to determine if an adequate number of samples had been collected to describe Texas's green turtle diet (Ferry and Cailliet, 1996). The order in which the samples were analyzed was randomized 10 times to reduce bias to construct the prey curve. The cumulative number of prey types was plotted against the cumulative number of guts analyzed. The number of samples analyzed is considered sufficient for describing dietary habits when the resulting curve reaches an asymptote.

The percent weight (W_i) by individual diet taxon was used as a more effective measure to reduce variance, minimize bias from the difference in individual sample weights, and standardize amongst quantification methods. The W_i calculated by dividing each diet taxon's weight in a given sample by the total weight of that turtle's foregut contents ($\times 100$). The gravimetric method may overestimate the relative importance of slowly digested hard-bodied items (George and Hadley, 1979); accordingly, additional metrics are useful to interpretations (Amundsen and Sánchez-Hernández, 2019). The frequency of occurrence (F_i) for each diet item was determined by dividing the number of samples containing each food item by the total number of samples examined ($\times 100$). The relative importance of each item in the diet was determined using an index of relative importance (IRI; Bjordal et al., 1997):

$$IRI (\%) = \frac{100 (F_i W_i)}{\sum_{n=1}^i (F_i W_i)}$$

where F is the frequency of occurrence of the target taxon i , and W is the mean percent taxon weight in all individual turtles (W_i) for the collective gravimetric methods.

The IRI is a compound index incorporating frequency of occurrence and weight into a single numerical measure to estimate dietary importance. While single metrics aid diet interpretations, compound indices can additionally provide a general picture of prey items' importance in predators' diets (Liao et al., 2001). Higher IRI values indicate a less diverse diet. Depending on the gravimetric method employed, hard-bodied prey can bias prey importance outcomes by contributing more to the W_i (Hyslop, 1980). The IRI values for each gravimetric method were calculated independently and collectively to explore differences between them. There were no differences detected amongst the principal diet groups' estimated dietary importance. Therefore, all gravimetric data were collectively combined and analyzed.

Food habits were analyzed in relation to the size class, the season of stranding (northern meteorological seasons of winter, spring, summer, fall), and two time periods (1987–2000, 2001–2014). The year divisions of 1987–2000 and 2001–2014 were used to compare general diet information after the 2-year implementation of the 1999 Texas Seagrass Conservation Plan. The frequency of occurrence approach provides a comprehensive and reliable account of diet composition, is unaffected by the diet item's condition, and can be used to make comparisons across studies (Baker et al., 2014). With a large sample size for

this study, the frequency of occurrence allows for population-wide assessments with minimal bias. The frequency of occurrence was the consistent metric used for statistical analyses. Chi-square tests were conducted using the software package IBM SPSS 25.0 to examine the relationship between size class and whether a particular diet taxon was consumed. The Cochran-Armitage test of trend was used to determine whether there was a linear trend in the primary diet group chosen within each life-history stage over the study period. The Cochran-Armitage test was additionally conducted to examine any linear trends in seagrass species selected by all combined size classes. The binomial logistic regression procedure in SPSS Statistics was used to generate the result of the Cochran-Armitage test of trend. The Goodman and Kruskal's lambda test was used to measure the strength of the association between the diet items selected by each size class within the stranding season. For all analyses, $\alpha = 0.05$.

RESULTS

The cumulative prey curve reached asymptote indicating most major prey items had been collected to describe green turtles' diet in Texas waters (Figure 2). Green turtles consumed 73 unique species, comprised of five seagrasses, 33 red algae, 12 green algae, eight brown algae, and 15 animals (Supplementary Table 1). Food items were classified as six major diet groups based on an overall $F \geq 25\%$: seagrasses, animal matter, anthropogenic debris, red, green, and brown macroalgae. All F values presented refer to the frequency of occurrence from all 420 turtles. Results were collectively presented on *Sargassum* species and *Gelidium* species, which intermix in their respective habitat.

Ontogenetic Shifts

Multiple size-based diet shifts were evident in the IRI values (Figure 3). There was a significant association between the ingestion of brown macroalgae and size class [$\chi^2(3) = 70.149$, $p < 0.0001$]. Brown macroalgae, specifically *Sargassum* spp., were the principal diet item of oceanic stage turtles ($F = 93.3\%$, $IRI = 73.9\%$). Red macroalgae and the size class feeding on them were significantly associated [$\chi^2(3) = 21.538$, $p < 0.0001$]. The highest IRI values for recruits demonstrated red and brown macroalgae were the most important diet groups ($IRI = 24.2\%$, $IRI = 27.4\%$, respectively). The relationship between the frequency of green algae consumption and size class was significant [$\chi^2(3) = 9.563$, $p = 0.022$]. The food items with the highest frequency of occurrence in the recruits were *Sargassum* spp. (63.0%), turtle grass (38.5%), mollusks (36.9%), shoal grass (33.1%), red algae *Gelidium* spp. (29.2%), and green algae *Ulva* spp. (23.1%). A secondary size-based diet shift was apparent with significant differences in seagrass consumption among the size classes [$\chi^2(3) = 46.0047$, $p < 0.0001$]. Seagrass was the principal diet item for the transitional class ($IRI = 51.2\%$) and inshore class ($IRI = 83.6\%$). The highest frequency of occurrence among food items in the transitional turtles was shoal grass (44.5%), turtle grass (43.9%), *Gelidium* spp. (41.7%), mollusks (38.4%), manatee seagrass (24.2%), and *Ulva* spp. (21.3%). Turtles of the

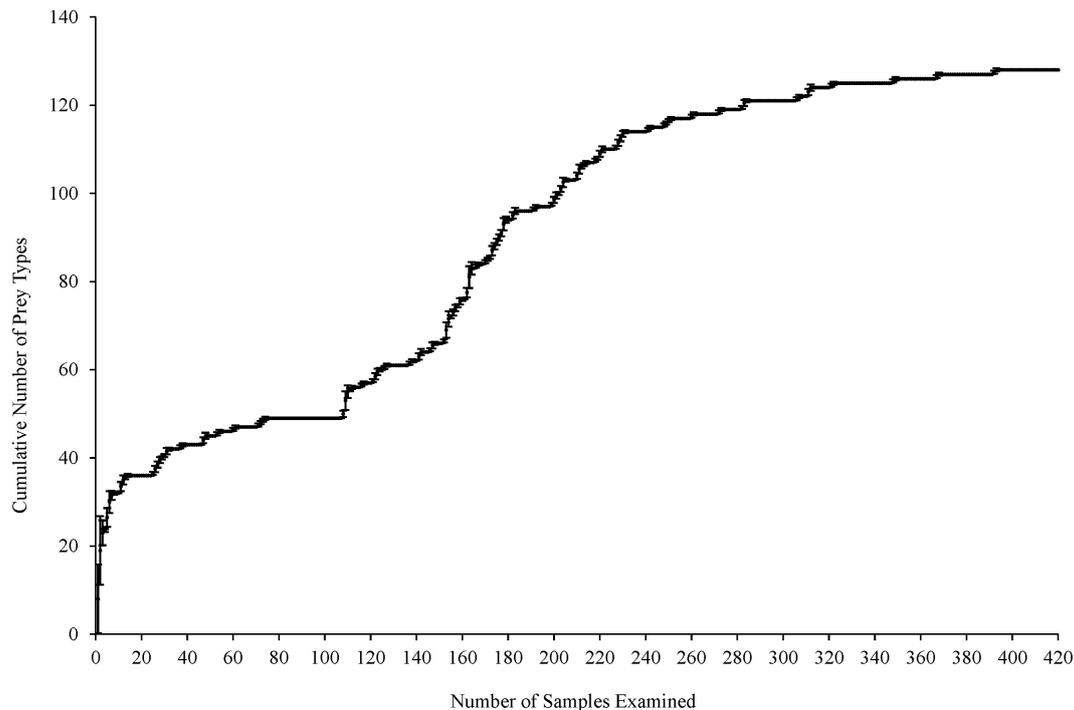


FIGURE 2 | Cumulative prey curve (prey taxa per gastrointestinal tract) for green turtles (*Chelonia mydas*) ($n = 420$) collected along the Texas coast. Error bars represent one standard deviation.

inshore class most frequently consumed turtle grass (62.4%), shoal grass (51.6%), mollusks (36.56%), manatee grass (33.3%), and star grass (*Halophila englemannii*) (33.3%). Foraging on anthropogenic debris occurred most frequently ($F = 60.0\%$) in oceanic class turtles with significant variation amongst all size classes [$\chi^2(3) = 19.521, p = 0.0002$]. In all collective size classes, $\geq 53.3\%$ of individuals ingested animal matter. There was not a significant association between animal matter consumption and the size class feeding on it [$\chi^2(3) = 2.965, p = 0.397$].

Temporal Trends

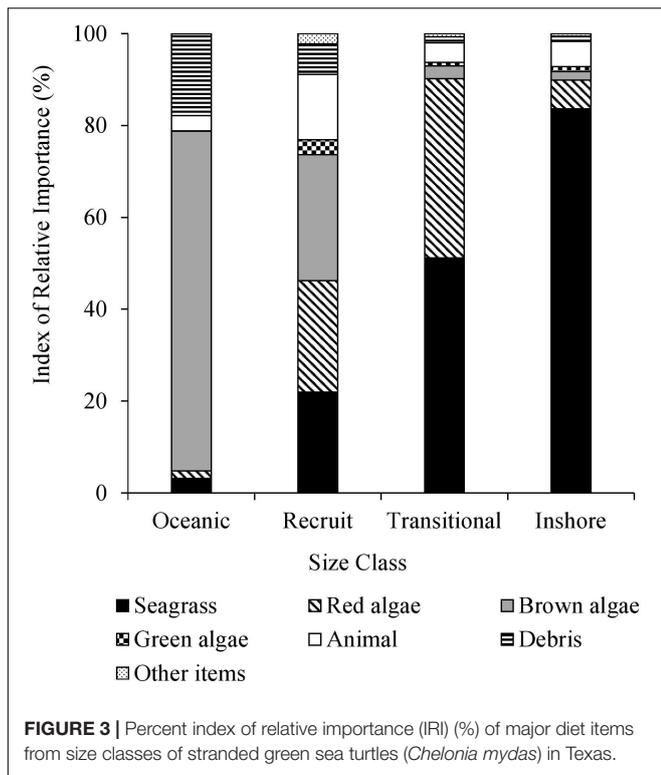
There was a significant decrease in the frequency of seagrass consumption in recruits ($p < 0.0001$) and transitional turtles ($p = 0.031$) between the two study periods (**Figures 4B,C**). Ingestion of red macroalgae by recruits increased significantly ($p = 0.028$) over time while there was no significant change in transitional turtles ($p = 0.131$). The presence of anthropogenic debris in gastrointestinal tracts decreased significantly between the two time periods for oceanic and recruits ($p < 0.05$) (**Figures 4A,B**). Inshore class turtles consumed red algae ($p = 0.045$) and brown algae ($p < 0.0001$) less frequently over time (**Figure 4D**). Among all size classes combined, turtle grass consumption decreased significantly over time, from $F = 50.0\%$ to 40.0% ($p = 0.023$). The ingestion of shoal grass decreased across the collective size classes, from $F = 50.9\%$ to 31.8% between the two periods ($p < 0.0001$). Manatee grass consumption did not change over time ($F = 21.6\text{--}22.2\%$, $p = 0.989$).

Seasonal Differences

The interseasonal differences in oceanic turtles' diet were not statistically analyzed as samples were unavailable for all seasons (**Figure 5A**). The proportion of recruits consuming red algae was significantly associated with the time of year of stranding ($\lambda = 0.022, p = 0.037$), with red algae consumption documented the least in the spring months (**Figure 5B**). The proportion of brown algae recorded in recruits was predicted by the season ($\lambda = 0.150, p = 0.006$), present in 92% of the spring turtles. In the winter and spring months, recruits ingested animal matter proportionally more than the other seasons ($\lambda = 0.020, p = 0.050$). There was a significant association between seagrass consumption and season of stranding in transitional turtles ($\lambda = 0.060, p = 0.0005$), wherein seagrass was documented more frequently in the winter months (**Figure 5C**). The presence of red algae in the diet was significantly associated with the season in which transitional turtles were stranded ($\lambda = 0.026, p = 0.003$). It was documented less frequently in the winter months than any other season. The consumption of green algae by the inshore class was significantly associated with the time of year ($\lambda = 0.039, p = 0.014$). Inshore size class turtles ingested green macroalgae most frequently in the spring (**Figure 5D**).

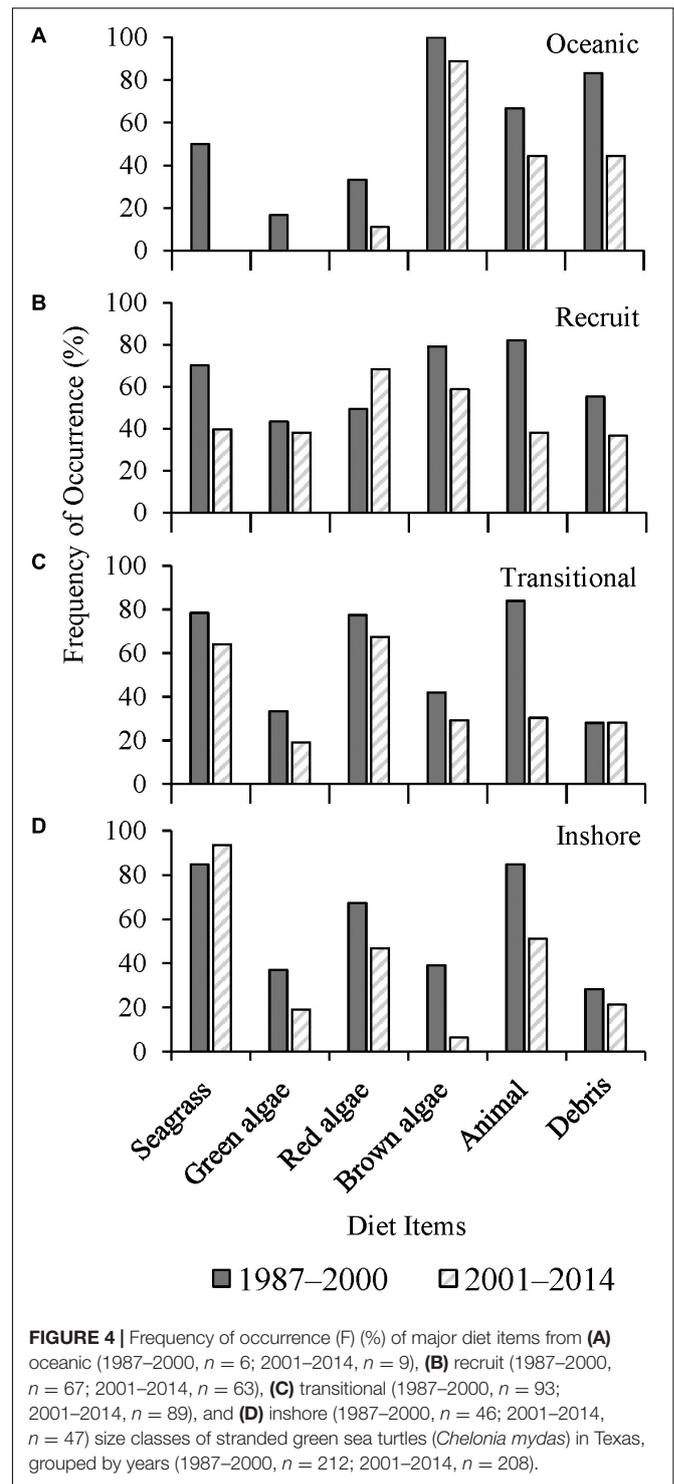
DISCUSSION

The green turtle population in Texas is increasing rapidly, and, as such, understanding the diet of this growing assemblage is critical

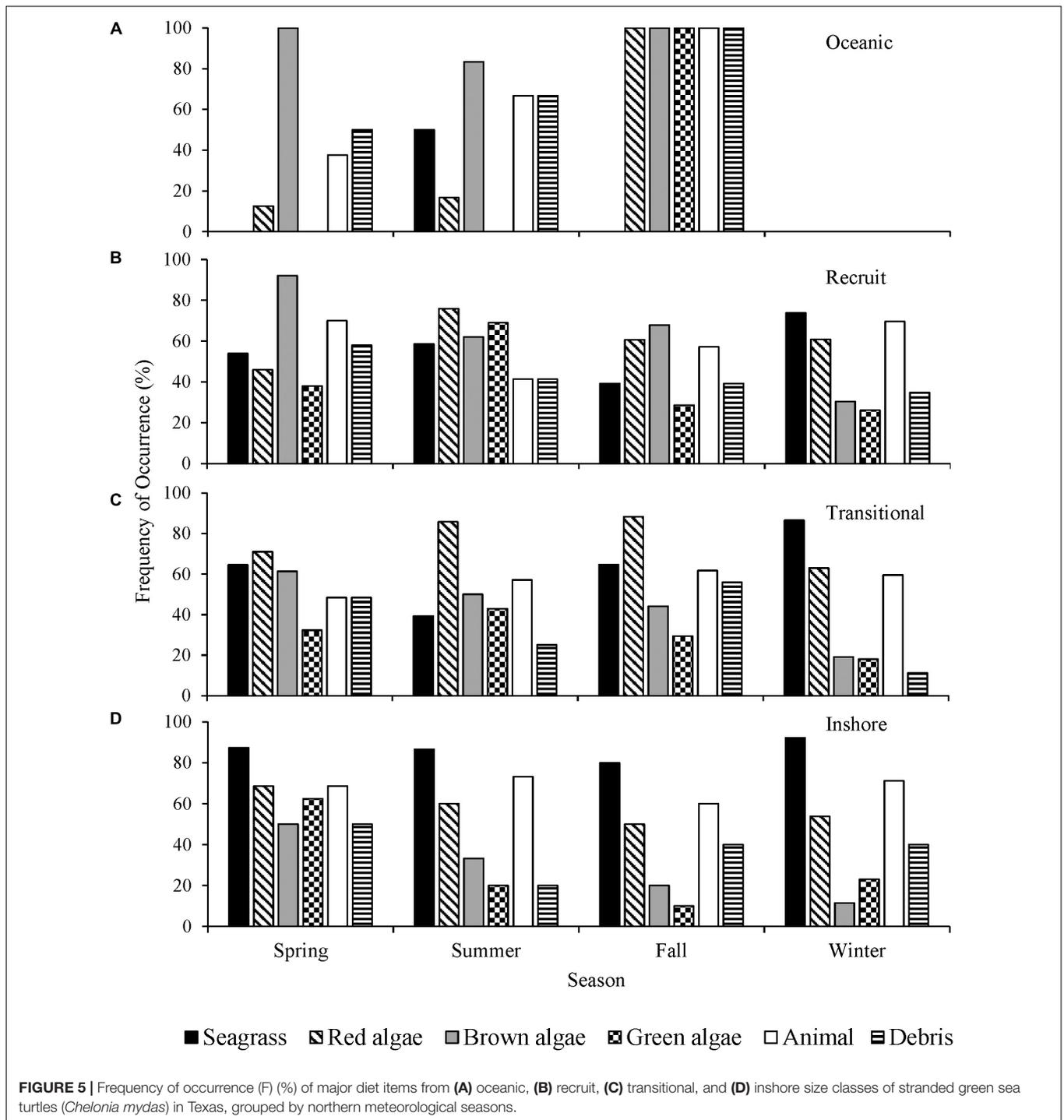


to endangered species management. Conservation managers can then prioritize preservation areas and policies designed to protect these essential green sea turtle foraging grounds. We characterized the diet of green turtles stranding along the Texas coast for 28 years to evaluate changes over time. This first long-term diet study of Texas green turtles demonstrated turtles ingest a diversity of food items across size classes with foraging differences observed seasonally and temporally.

Diet of the smallest size class suggested this group was mostly representative of the oceanic life-history stage. The frequency of brown macroalgae ($F = 93.3\%$), specifically the *Sargassum* spp., in oceanic turtles diet, was similar to the esophageal and fecal samples ($F = 86, 87\%$, respectively) from oceanic size green turtles captured in pelagic *Sargassum* habitat off Florida, United States (Witherington et al., 2012). The authors suggested the ingestion of *Sargassum* was incidental to foraging on sessile, epiphytic animals on the brown algae. Furthermore, the high occurrence of *Sargassum* in the oceanic size class is similar to studies that have reported turtles foraging at the surface (Carr, 1987b; Morais et al., 2014). Stable isotope results ($\delta^{15}\text{N}$ values) from the scutes of some of our oceanic-sized green turtles indicate they are not assimilating the *Sargassum*-dominated diet. Instead, they had tissue isotope values reflective of the animals that frequent the floating algae mats (Howell et al., 2016). Primarily the animals ingested by this size class are organisms known to be closely associated with the *Sargassum* community (e.g., Cnidarians, Schyphozoans, Teleosts) (Witherington, 2006; Boyle and Limpus, 2008; Jones and Seminoff, 2013).



Convergence zones are oceanographic features that collect *Sargassum* and marine debris (Carr, 1987a), and as such, anthropogenic debris consumption was highest in oceanic turtles ($F = 60\%$). Anthropogenic rubbish ingestion by marine turtles has been linked to numerous health issues, including blockage and compaction of the digestive tract, ultimately with lethal



effects (Bjorndal et al., 1994; Tourinho et al., 2010; Gonzalez Carman et al., 2014; Wilcox et al., 2016). Our findings were similar to a study on oceanic green turtles captured in the *Sargassum* habitat, where synthetic material was the third most frequently ingested diet item (Witherington et al., 2012). Reduction of marine debris is identified as a recovery action in the Atlantic green turtle’s ESA Recovery Plan (NMFS, 1991), and prioritization should continue.

Previous diet studies in Texas showed seagrass was not present in turtles ≤ 20 cm SCL_{max} in Texas (Howell, 2012); therefore, our finding of seagrass in the diet of ≥ 16.2 cm–20 cm SCL_{max} turtles ($F = 20.0\%$) was unexpected. These oceanic size class turtles also consumed macroalgae frequently found along the Texas coast (Kaldy et al., 1995; Agan and Lehman, 2002; Fikes and Lehman, 2008, 2010), suggesting nearshore occupancy for them. Young green turtles inhabiting jetty channels feed on

flotsam, including seagrass blades detached from nearby inshore grass beds (L. N. Howell, D. J. Shaver, per. obs.). Our diet data suggest these individuals were likely foraging on benthic algae and floating seagrass blades in the nearshore environment before death. There are inherent variabilities in obtaining these smallest turtles, and our interpretations are based on a limited sample size. Nonetheless, the presence of multiple benthic species of neritic diet items in the oceanic class demonstrates recruitment at ≤ 20 cm SCL_{max} to Texas' nearshore waters. Marine turtles are vulnerable to being taken as bycatch in coastal fishery operations and other anthropogenic threats (Magnuson et al., 1990). An explicit understanding of size ranges occupying Texas nearshore waters is critical to protected species management, as threats vary depending on the size class.

While green turtles in neritic foraging grounds typically consume benthic items (Redfoot, 1997; Holloway-Adkins, 2001; Gilbert, 2005; Makowski et al., 2006; Foley et al., 2007), floating *Sargassum* spp. were the most frequently ingested item in recruits and dominated the diet of turtles found in spring months. The mean digestive passage time for a food item consumed by immature green turtles was determined to be 23.3 ± 6.6 days (Amarocho and Reina, 2008). The size at recruitment to the neritic zone varies for oceanic stage green turtles (summarized in Avens and Snover, 2013). Consequently, the *Sargassum*-dominated diet of oceanic stage turtles could still be present in newly recruited turtles' gastrointestinal tracts. Alternatively, it is equally plausible that Texas recruits are resourcefully foraging inside the massive wracks of *Sargassum* that enter the channel passes in the spring months (Breuer, 1962) while continuing to feed benthically within the jetty environment. Immature neritic Atlantic green turtles foraging amongst artificial structures in Florida, United States, were noted to opportunistically consume flotsam in addition to their benthic macroalgae-dominated diet (Holloway-Adkins and Hanisak, 2017). The stomach contents of multiple recruits contained jetty algae (e.g., *Gelidium* spp. and *Ulva* spp.) and *Sargassum* spp., indicating this size class inhabits the jetty habitat. Dedicated surveys of turtle feeding behavior within the channel environment when *Sargassum* mats are present would help elucidate the foraging activity of turtles resident in these channels. Collectively, benthic macroalgae found on the Texas coast (Wynne, 2008) dominated the recruits' diet indicating this size group is in the jetty habitat.

Several recruits ($F = 23.3\%$) ingested all three primary species of seagrasses, suggestive of foraging in seagrass beds and not on the floating matter in the jetty channels. Tracking data revealed that turtles occupying the jetty environment made brief expeditions into the nearby inshore habitat but returned to jettied-channels (Shaver, 2000). Recruitment may not represent a distinct unidirectional shift from one habitat to the next. As an alternative, younger turtles may display an intermediate stage sampling on macroalgae and seagrasses in diverse environments (Arthur et al., 2008). Considerably, the fluctuation in density and concentration of macroalgae on jetty structures (Kaldy et al., 1995; Renaud et al., 1995; Fikes and Lehman, 2008) could force turtles to feed at alternative sites. Studies incorporating fecal analysis and esophageal lavage may provide a more precise understanding of recruitment size and principal diet.

Green turtles in the western Atlantic are frequently considered obligate seagrass consumers (Mendonca and Ehrhart, 1982; Bjorndal, 1997), with omnivory reported in the Atlantic southwest (Bugoni et al., 2003) and the Pacific (Bjorndal, 1997; Seminoff et al., 2006; Fukuoka et al., 2019). More than half the individuals in all collective size classes ingested animal matter, indicating that Texas's immature green turtles are omnivores in these developmental foraging grounds. This finding is similar to other studies that have demonstrated animal consumption persisting through ontogeny (Amarocho and Reina, 2008; Cardona et al., 2010; Carrión-Cortez et al., 2010; Morais et al., 2014). The relative importance of animal matter varied across the size classes, with the highest collective IRI value noted in recruits, primarily due to mollusk consumption. Mollusc ingestion may occur incidentally to foraging on macroalgae in the jetty habitat or represent a selective effort. The more frequent ingestion of animals in the winter and spring months by the recruit size class could be proportional to the seasonal variation in the macroalgal abundance documented in the Texas jetty habitat (Fikes et al., 2010). In a previous study in the northern GOM, immature green turtles consumed animal matter more in the winter months due to the seasonal fluctuations in seagrass and algae biomass (Williams et al., 2014). Furthermore, green turtle digestive efficiency decreases when water temperatures drop (Bjorndal, 1980); and animal matter is easier to digest than plant material for green turtles (Bjorndal, 1985). Conceivably, the recruit class selects easier to digest animal matter more frequently during the cooler months when jetty algae composition changes. Regardless of seasonal environmental variations, we recommend that juvenile green turtles foraging in Texas be described as omnivores. Multisource stable isotope mixing models have highlighted invertebrate consumption and assimilation among omnivorous green turtles (Lemons et al., 2011). Therefore, future diet studies in Texas should incorporate isotope mixing models to gain supplemental information on the nutritional contribution and importance of animal matter to all size classes' diets.

The recent seagrass conservation efforts in Texas have achieved some success. Seagrass acreage was reported to have increased to cover a mean area of $87.7 \pm 25.5\%$ in the upper and $50.0 \pm 38.4\%$ in the Lower Laguna Madre (Dunton et al., 2013). However, transitional turtles consumed seagrass less frequently over time, indicating that this size class utilizes different habitat niches. Any beneficial effects of recovering seagrass meadows may be negated by an exponentially growing turtle population (Shaver et al., 2017). Plausibly driven by resource competition from turtles in the seagrass beds, transitional turtles incorporate a varied diet of seagrasses and algae. Satellite tracking data revealed green turtles (mean SCL 37.9 ± 5.2 cm) migrate in and out of the Laguna Madre seagrass beds via the jetty habitats (Shaver et al., 2013). The high frequency of ingestion of the typical jetty red algae, *Gelidium* spp. by transitional turtles indicates turtles supplement their seagrass diet with benthic macroalgae as they transit from inshore waters to the GOM. The concept above is further supported by analyzing digesta boluses throughout the gastrointestinal tract, which indicate separate feeding sessions. Some transitional turtles alternated their diets between seagrass (e.g., *Cymodocea* sp.) and jetty algae (e.g., *Gelidium* spp.).

In contrast to transitional turtles, the more frequent consumption of seagrasses by the inshore size class indicates these larger turtles have become highly reliant on the seagrasses with time. Immature green turtles are more susceptible to cold stunning in Texas as they overwinter and show strong site fidelity for inshore habitats (Arms, 1996). Cold stunning is the most significant cause of stranding events in Texas (Shaver et al., 2017) and cold-stunned turtles comprised most winter samples for transitional and inshore size classes. The high frequency of seagrasses in the diet of the two largest classes of turtles stranded in the winter months most certainly reflects this strong seagrass bed dependency.

Shoal grass in the lower Laguna Madre has declined in abundance and increased in bed fragmentation, while the upper Laguna Madre has indicated some expansion in coverage (Onuf, 2007; Wilson and Dunton, 2017). Previous research revealed green turtles in the Laguna Madre selected shoal grass over the other seagrasses (Coyne, 1994). Interestingly, we documented a significant decrease of shoal grass in all size classes' diet over time with no parallel increase in the frequency of other seagrass species consumed. Turtle grass was still frequently consumed and dominated the diet of our inshore size classes. Conceivably, immature turtles are exhibiting foraging plasticity within their changing seagrass meadows by consuming a variety of macroalgae and animal matter species. Overall, seagrass collectively dominated the diet of turtles larger than 30 cm SCL_{max} , illustrating the necessity of conserving and monitoring seagrass habitats along the northwestern GOM coast. Potential impacts of changes in seagrass composition and distribution on this green turtle assemblage's diet should be rigorously monitored through future diet studies.

Management and Conservation Implications

Marine turtles inhabiting the Texas coast face a variety of threats, both human-related and natural. As this green turtle population continues to increase rapidly, it is critical to incorporate foraging ecology studies into conservation management decisions that strengthen the species and habitat protection. Size-related variation in sea turtle foraging habits necessitates integrated management strategies that reduce impacts to immature turtles in Texas jetty and seagrass habitats. Gear modifications in commercial fisheries could be implemented to reduce the incidental take in our nearshore waters, hence providing increased protection of this threatened species. Additionally, it is essential to manage the seagrass beds fundamental to the survival

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of this exponentially growing green turtle assemblage that will eventually recruit to the breeding population.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the animals used in this study were deceased upon discovery.

AUTHOR CONTRIBUTIONS

DS and LH conceived and designed the study. LH performed the statistical analysis, created the figures, and wrote the manuscript's first draft. Both authors contributed to manuscript revision, read 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.2021.658368/full#supplementary-material>

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