



# Epibionts Reflect Spatial and Foraging Ecology of Gulf of Mexico Loggerhead Turtles (*Caretta caretta*)

Ian Silver-Gorges<sup>1\*</sup>, Jeroen Ingels<sup>2</sup>, Giovanni A. P. dos Santos<sup>3</sup>, Yirina Valdes<sup>4</sup>, Leticia P. Pontes<sup>3</sup>, Alexandra C. Silva<sup>3</sup>, Patricia F. Neres<sup>3</sup>, Arvind Shantharam<sup>1</sup>, Destin Perry<sup>2</sup>, Andrew Richterkessing<sup>2</sup>, Sofia Sanchez-Zarate<sup>5</sup>, Laura Acevedo<sup>6</sup>, Anthony J. Gillis<sup>1</sup>, Simona A. Ceriani<sup>7</sup> and Mariana M. P. B. Fuentes<sup>1</sup>

<sup>1</sup> Department of Earth, Ocean, and Atmospheric Science, Florida State University, Tallahassee, FL, United States, <sup>2</sup> Coastal and Marine Laboratory, Florida State University, St. Teresa, FL, United States, <sup>3</sup> Zoology Department, Federal University of Pernambuco, Recife, Brazil, <sup>4</sup> Department of Biosciences, Federal University of Paraíba, Areia, Brazil, <sup>5</sup> Department of Computer Science and Engineering, Columbia University, New York, NY, United States, <sup>6</sup> Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark, <sup>7</sup> Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Saint Petersburg, FL, United States

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### \*Correspondence:

Ian Silver-Gorges  
ims19c@my.fsu.edu

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Sea turtles are exposed to numerous threats during migrations to their foraging grounds and at those locations. Therefore, information on sea turtle foraging and spatial ecology can guide conservation initiatives, yet it is difficult to directly observe migrating or foraging turtles. To gain insights into the foraging and spatial ecology of turtles, studies have increasingly analyzed epibionts of nesting turtles, as epibionts must overlap spatially and ecologically with their hosts to colonize successfully. Epibiont analysis may be integrated with stable isotope information to identify taxa that can serve as indicators of sea turtle foraging and spatial ecology, but few studies have pursued this. To determine if epibionts can serve as indicators of foraging and spatial ecology of loggerhead turtles nesting in the northern Gulf of Mexico we combined turtle stable isotope and taxonomic epibiont analysis. We sampled 22 individual turtles and identified over 120,000 epibiont individuals, belonging to 34 macrofauna taxa (>1 mm) and 22 meiofauna taxa (63  $\mu\text{m}$ –1 mm), including 111 nematode genera. We quantified epidermis  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , and used these to assign loggerhead turtles to broad foraging regions. The abundance and presence of macrofauna and nematodes did not differ between inferred foraging regions, but the presence of select meiofauna taxa differentiated between three inferred foraging regions. Further, dissimilarities in macrofauna, meiofauna, and nematode assemblages corresponded to dissimilarities in individual stable isotope values within inferred foraging regions. This suggests that certain epibiont taxa may be indicative of foraging regions used by loggerhead turtles in the Gulf of Mexico, and of individual turtle foraging and habitat use specialization within foraging regions. Continued sampling of epibionts at nesting beaches and foraging grounds in the Gulf of Mexico and globally, coupled with satellite telemetry and/or dietary studies, can expand upon our findings to develop epibionts as efficient indicators of sea turtle foraging and spatial ecology.

**Keywords:** epibiont, foraging, Gulf of Mexico, isotopes, macrofauna, meiofauna, nematode, loggerhead sea turtle

## INTRODUCTION

Sea turtles are highly migratory animals: hatchling turtles may circumnavigate entire ocean basins before maturation (Carr, 1987; Mansfield et al., 2014), and individual mature turtles migrate thousands of kilometers between specific foraging and breeding grounds each year (Plotkin et al., 2002; Broderick et al., 2007; Shillinger et al., 2008). Sea turtles spend much of their lives at foraging grounds (Bolten, 2003; Hawkes et al., 2006), and may be exposed to various threats at these locations (Hart et al., 2018; Fuentes et al., 2020) or while migrating between foraging and breeding regions (Hart et al., 2014).

Knowledge of sea turtle foraging and spatial ecology is critical to identify areas of high/potential use, assess their exposure to threats, and inform management and conservation of sea turtles (Hawkes et al., 2006; Gredzens et al., 2014; Mazor et al., 2016; Rees et al., 2016; Fuentes et al., 2019). However, sea turtle research overwhelmingly relies upon data collected from nesting sea turtles, as they are easier to encounter and sample than foraging, in-water turtles (Hamann et al., 2010; Rees et al., 2016). Satellite telemetry and stable isotope analysis (SIA) are two techniques commonly employed at nesting beaches that provide insight into sea turtle behavior away from nesting beaches (Ceriani et al., 2012; Jeffers and Godley, 2016). Satellite telemetry can be used to track turtles between nesting beaches and foraging grounds and to understand the spatial ecology of sea turtles at foraging grounds (Jeffers and Godley, 2016; Hays and Hawkes, 2018). However, the cost of satellite transmitters is often prohibitive to their use, and many studies only track a small percentage of any nesting assemblage (Rees et al., 2016). Analysis of carbon and nitrogen stable isotopes is less expensive than satellite telemetry and can be used to approximate where sea turtles forage and at what trophic level (DeNiro and Epstein, 1978; Rubenstein and Hobson, 2004; Reich et al., 2007; Vander Zanden et al., 2010). Such inferences depend upon the available baseline stable isotope data in a region, and on isotopic differences between turtles from different foraging grounds, however, baseline data is not always available for a region nor do turtles from different foraging grounds always have different isotopic signatures (Vander Zanden et al., 2015; Ceriani et al., 2017). Therefore, novel, cost-effective and informative tools to explore turtle foraging and spatial ecology would prove useful additions to satellite telemetry and SIA (Rees et al., 2016; Hays and Hawkes, 2018).

Recent attention has turned to sea turtle epibionts as potential natural data loggers of sea turtle migratory and foraging behaviors (Frick and Pfaller, 2013; Pearson et al., 2019; Ten et al., 2019). Epibionts are organisms that colonize other organisms, and are commonly found on the carapaces of all seven sea turtle species (Frick and Pfaller, 2013; Robinson et al., 2016). Epibiotic colonization typically begins after chemical alteration of submerged substrates, followed by the establishment of (1) unicellular bacteria; (2) diatoms and protozoans, and (3) meiofauna and macrofauna (Wahl, 2009; dos Santos et al., 2018). Colonization requires ecological and spatial overlap of epibionts and living substrate (such as sea turtle carapaces), and it is thought that colonization of sea turtle carapaces occurs

primarily at foraging grounds, with some colonization occurring at breeding areas (see Figure 15.1 in Frick and Pfaller, 2013; Reeves et al., 2018; Hart et al., 2021).

Few studies have sought to characterize the relationships between epibiont colonization and turtle foraging ecology (Reich et al., 2010; Ten et al., 2019). This is a difficult endeavor, as most epibiont studies report on assemblages sampled from nesting sea turtles, which may share epibiont taxa from recent colonization (Reeves et al., 2018; Hart et al., 2021), and do not pair epibiont sampling with satellite telemetry or stable isotope analysis of turtle tissues to relate epibiosis to foraging or spatial ecology (Frick and Pfaller, 2013; except see Reich et al., 2010; Nolte et al., 2020). Additionally, most studies of sea turtle epibionts focus on large, easily observable species and do not characterize microscopic organisms such as meiofauna that may colonize sea turtle carapaces in large numbers, establishing diverse epibiotic communities (Frick and Pfaller, 2013; notable exceptions include Corrêa et al., 2014; Robinson et al., 2016; dos Santos et al., 2018; Ingels et al., 2020).

Diverse epibiont assemblages, cumulating in over 200 taxa, have been documented on loggerhead sea turtles (*Caretta caretta*; Frick and Pfaller, 2013). A recent study of loggerheads nesting at St. George Island (SGI), Florida, characterized the abundance of 20 meiofauna taxa including 111 nematode genera, and reported discrete groups of epibiont assemblages (Ingels et al., 2020). This implies that some sampled loggerheads underwent similar colonization processes and as such may display similar foraging and spatial ecology. We investigated if and how epibiont assemblages can be informative toward understanding sea turtle foraging and spatial ecology, both alone and when integrated with SIA data. To do so, we analyzed the meiofauna epibiont data from Ingels et al. (2020), along with new data from macrofauna epibiont and stable isotope analyses from the same turtles. We tested to see if and how epibiont assemblages differed between turtles from different inferred foraging regions, and if stable isotope data predicted variation in epibiont assemblages. Our work tests fundamental theories on epibiont colonization and explores the extent to which epibionts can provide information on sea turtle foraging and spatial ecology.

## MATERIALS AND METHODS

We encountered nesting loggerhead sea turtles during nightly surveys at SGI (Figure 1). St. George Island hosts the largest loggerhead assemblage in the Northern Gulf of Mexico Recovery Unit (NGMRU) for loggerhead sea turtles (FFWCC, 2020). The NGMRU spans beaches from the United States-Mexico border in Texas to Franklin Co., FL, and is a small (Ceriani et al., 2019), genetically discrete subpopulation (Shamblin et al., 2012) of the Northwest Atlantic Ocean Regional Management Unit (RMU) of loggerhead turtles (Wallace et al., 2010), the largest loggerhead RMU globally (Casale and Tucker, 2017; Ceriani et al., 2019). Surveys took place over 2 weeks during the peak of the 2018 nesting season at St. George Island, from June 16th to July 1st (Ingels et al., 2020). We sampled encountered turtles after they had begun covering their egg chambers. We checked all turtles



for pre-existing Inconel flipper or PIT tags, and applied these whenever necessary following protocols in the Florida Fish and Wildlife Conservation Commission Marine Turtle Conservation Handbook (FFWCC, 2016). We sampled the entire carapace of each turtle for epibionts following Ingels et al. (2020). Briefly, we scraped off large fauna such as barnacles with a putty knife, and collected small fauna such as nematodes with a sponge by wiping down the entire surface until visibly clean. We stored all epibionts in DESS or a formalin solution until they could be sorted and identified (see below). We collected epidermal tissue samples for SIA from the shoulder of each turtle using 5 mm biopsy punches and stored samples in salt.

We washed and sorted epibiont samples into macrofauna (>1 mm) and meiofauna (63  $\mu\text{m}$ –1 mm) at the Florida State University Coastal and Marine Laboratory. We stored macrofauna and meiofauna separately in a solution of dimethyl sulfoxide, ethylenediaminetetraacetic acid, and saturated sodium chloride (DESS). We identified meiofauna to higher taxa (Higgins

and Thiel, 1988; Giere, 2009, following quantitative subsampling procedures from Ingels et al., 2020), and macrofauna to the lowest taxonomic level possible, usually family or a lower level using stereoscopic microscopes and taxa-specific keys to Gulf of Mexico invertebrates (Fauchald, 1977; Culter, 1986). We picked out nematodes *ad hoc* from meiofauna samples (120 individuals per sample), which we then desiccated, and mounted on slides for identification to genera using available nematode keys (Platt and Warwick, 1983; Bezerra et al., 2019).

We prepared turtle tissue samples for SIA at Florida State University Department of Earth, Ocean, and Atmospheric Science. Samples were brushed and then rinsed with deionized water to remove particulate matter and salt, dried in an oven for 2 h at 60°C to remove all moisture, and homogenized using a sterile scalpel (following Lemons et al., 2011; Levin and Currin, 2012; Gillis et al., 2018). We sent homogenized samples to the Paleoclimatology, Paleoceanography, and Biogeochemistry Laboratory at the University of South Florida College of Marine

Science for lipid extraction and SIA. Lipids were extracted from samples using an accelerated solvent extractor (Model 200, Dionex) with petroleum ether (3 cycles of 5 min heating followed by 5 min static purging). Samples were then weighed to 0.5–0.7 mg using a Mettler Toledo micro balance, placed into Costech tin cups, and converted to N<sub>2</sub> and CO<sub>2</sub> using a Carlo-Erba NA2500 Series 2 Elemental Analyzer (Thermoquest Italia). Isotope ratios were measured in a continuous flow mass spectrometer (Delta Plus XP, Thermofinnigan). Sample ratios are expressed as parts per mille (‰) and calculated using the equation:

$$\delta X = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] * 1000$$

where  $X$  is <sup>15</sup>N or <sup>13</sup>C, and  $R$  is the ratio of <sup>15</sup>N:<sup>14</sup>N or <sup>13</sup>C:<sup>12</sup>C. Standards for <sup>15</sup>N and <sup>13</sup>C were atmospheric nitrogen and Pee Dee Belemnite, respectively.

SIA values were incorporated into continuous probability surfaces (CPSs) and discriminant functions (DFs) to assign turtles to broad foraging regions within the Gulf of Mexico [as designated by Vander Zanden et al., 2015: Northern Gulf of Mexico (NGOM), Eastern Gulf of Mexico (EGOM), Southern Gulf of Mexico (SGOM), Subtropical Northwest Atlantic (SNWA) and South Atlantic Bight (SAB); **Figure 1**]. We retrieved previously published scute SIA values, foraging locations, and isoscapes from tracked Gulf of Mexico loggerheads from Vander Zanden et al. (2015). We converted SIA values for sampled turtles from epidermis to scute using equations in Vander Zanden et al. (2014), and generated continuous probability rasters for each individual turtle following Ceriani et al. (2017). Individuals were assigned to the foraging region containing the highest probability raster cell. We constructed DFs to assign individuals to foraging regions with the same published SIA data from turtles with known foraging locations in SPSS 27 (IBM; i.e., Ceriani et al., 2014). The first two DFs were constructed based on 39 training individuals and tested with 19 individuals, both groups with known foraging locations. Assignments were made using unequal priors and a leave-one-out cross-validation method (Ceriani et al., 2014; Vander Zanden et al., 2014). Wilks' Lambda was used to assess if the first two DFs adequately explained group membership. Assignment probabilities and odds ratios (Wunder, 2012) were used to assess foraging region assignments for turtles sampled at SGI.

We imported epibiont abundance, SIA, and foraging data into Primer-e V7 (Clarke and Gorley, 2015) with the PERMANOVA+ add on (Anderson et al., 2008) to characterize epibiont assemblages (i.e., diversity indices) and explore relationships between epibiont assemblages, foraging regions, and SIA data. We analyzed macrofauna, meiofauna, and nematodes independently to determine whether and which taxa might relate to the foraging ecology of individual turtles. We square root (sqrt) transformed abundance data to reduce the influence of particularly abundant taxa on multivariate statistics, and presence-absence (p-a) transformed abundance data to determine if the presence or absence of certain taxa related to turtle foraging ecology (Clarke and Gorley, 2015). Square-root transformed data were duplicated and standardized (sqrt-stan) to

minimize the influence of variable abundances between samples. Bray-Curtis and Euclidean distance were used as the resemblance measures for epibiont and SIA data, respectively. We used non-metric Multi-Dimensional Scaling (nMDS) plots to visualize data and qualitatively assay for dissimilarities in epibiont assemblages between turtles assigned to different foraging grounds. CLUSTER and SIMPROF (with 5% significance tests) were used to identify similar groups of epibiont assemblages and determine if these groups corresponded to turtles assigned to the same foraging grounds. ANOSIM and PERMANOVA were used to determine if epibiont assemblages differed between turtles assigned to different foraging regions, and SIMPER was used to identify taxa contributing to these differences. RELATE and BEST were used to determine if individual foraging ecology related to epibiont assemblages, and which sample epibiont assemblage dissimilarities correlated significantly (significance level = 5%) to SIA sample dissimilarities. We ran all tests over 10,000 iterations (Clarke and Gorley, 2015).

## RESULTS

We sampled 23 individuals for epibionts and 22 individuals for stable isotopes (summary statistics are presented in **Table 1**). The first two foraging region assignment DFs constructed using

**TABLE 1** | Epibiont and stable isotope summary statistics and foraging assignment frequencies.

### Epibiont summary statistics

Epibionts ( $n = 23$ )	Total taxa (Range, Mean $\pm$ SD)	Abundance Range (Mean $\pm$ SD)
Macrofauna	34 (7–19, 12 $\pm$ 3)	24–11,569 (3,420 $\pm$ 3,172)
Meiofauna (+ Nematodes)	22 (7–16, 12 $\pm$ 2)	6,590–146,190 (35,235 $\pm$ 29,756)
Meiofauna (– Nematodes)	21 (6–15, 11 $\pm$ 2)	4,840–132,530 (26,739 $\pm$ 26,220)
Nematodes	111 (8–50, 27 $\pm$ 10)	427–20,200 (6,434 $\pm$ 4,638)

### Stable isotope summary statistics (‰, $n = 22$ )

Isotope	Range	Mean $\pm$ SD
$\delta^{13}\text{C}$	–17.1–10.25	–14.64 $\pm$ 1.45
$\delta^{15}\text{N}$	6.18–15.74	10.96 $\pm$ 2.06

### Foraging assignment frequencies

Assignment method	NGoM	EGoM	SGoM	SNWA
CPS	3	8	10	1
DF	6	7	8	1

*Meiofauna statistics are presented with all nematode genera grouped together (+ Nematodes) and without nematodes (– Nematodes). Stable isotope values are presented as parts per mille (‰). Foraging assignment frequencies are presented for both continuous probability surface (CPS) and discriminant function (DF) assignments. NGOM, Northern Gulf of Mexico; EGoM, Eastern Gulf of Mexico; SGoM, Southern Gulf of Mexico; SNWA, Subtropical Northwest Atlantic. Foraging regions are delineated in **Figure 1**.*

the training data were significant ( $p > \text{Wilks' Lambda} < 0.000$ ). The first two DFs had a combined  $\chi^2(6) = 98.954$ , ( $p < 0.000$ ). Alone, the second DF had a  $\chi^2(2) = 9.74$ , ( $p = 0.008$ ). The first DF explained 97.4% of the between-group variability, and the second DF explained 2.6% of the between-group variability. 30/39 (76.9%) loggerheads in the training data and 14/19 (73.7%) loggerheads in the testing data were assigned correctly to their known foraging regions. Assignment probabilities ranged from 0.41 to 1 (mean =  $0.66 \pm 0.18$  SD). Odds ratios that described how much more informative the DFs were for assigning individual turtles to foraging regions than a random assignment procedure ranged from 2.04:1 to 6,040,365:1 (mean =  $13.6:1 \pm 27.4$  SD). We have chosen to retain all DF assignments in subsequent analyses (following Kelly et al., 2005; Szymanski et al., 2007; López-Castro et al., 2014). The DF assignments made here had higher probability than if turtles were assigned at random (all turtles had  $> 0.25$  probability of being assigned to their most likely foraging region), and we acknowledge the potential for erroneous assignments when not using a probability threshold (i.e.,  $> 0.6$ ; see discussion). The CPS and DF foraging ground assignments produced similar results: most turtles were assigned to SGOM (CPS,  $n = 10$ ; DF,  $n = 8$ ), followed by EGOM (CPS,  $n = 8$ ; DF,  $n = 7$ ), NGOM (CPS,  $n = 3$ ; DF,  $n = 6$ ), and finally SNWA (CPS,  $n = 1$ ; DF,  $n = 1$ ; **Table 1**). No turtles were assigned to SAB. Fewer turtles were assigned to NGOM using CPS ( $n = 3$ ) than DF ( $n = 6$ ), and more turtles were assigned to EGOM and SGOM using CPS ( $n = 8$  and  $10$ , respectively) than using DF ( $n = 7$  and  $8$ , respectively, **Table 1**).

CLUSTER and SIMPROF identified distinct, significant ( $p < 0.05$ ) groups (k) of similar epibiont assemblages within the meiofauna ( $k_{\text{sqr}} - \text{stan} = 2$ ; **Supplementary Figure 1**) and nematodes ( $k_{\text{sqr}} - \text{stan} = 3$ ,  $k_{p-a} = 2$ ,  $k_{\text{sqr}} = 4$ ; **Supplementary Figure 2**), but not within macrofauna. SIMPROF groups did not appear to correspond to CPS or DF foraging ground assignments in visual examinations of two dimensional nMDS plots (**Supplementary Figures 1, 2**), but presence-absence transformed meiofauna and square-root transformed nematode assemblages did group visibly according to foraging assignment categories (**Figure 2**). The presence and absence of certain meiofauna contributed to assemblage differences below or near statistical significance (ANOSIM:  $\text{Rho} = 0.158$ ,  $p = 0.032$ ) between turtles assigned to the NGOM and SGOM by DF (ANOSIM:  $\text{Rho} = 0.278$ ,  $p = 0.015$ ; PERMANOVA: pseudo-F = 78.005,  $t_{13} = 1.75$ ,  $p = 0.019$ ), and EGOM and SGOM (ANOSIM:  $\text{Rho} = 0.156$ ,  $p = 0.052\%$ ). SIMPER identified Sarcomastigophorans, Bivalves, Polychaetes, Turbellarians, Limulids, Tanaidaceans, Nauplii, and Acari as contributing to a cumulative 77.18% of the differences between NGOM and SGOM assemblages (**Figure 3A** and **Supplementary Table 1**). Many of the same taxa contributed to differences between EGOM and SGOM assemblages (72.16%) with a few modifications: Nauplii and Tanaidaceans did not contribute to differences, while Hydroids did (**Figure 3A** and **Supplementary Table 2**). The abundance of nematode genera also contributed significantly to differences (ANOSIM:  $\text{Rho} = 0.183$ ,  $p = 0.034\%$ ) between turtles assigned to the EGOM and SGOM by CPS (ANOSIM:  $\text{Rho} = 0.2$ ,  $p = 0.013\%$ ; PERMANOVA: pseudo-F = 37.374,

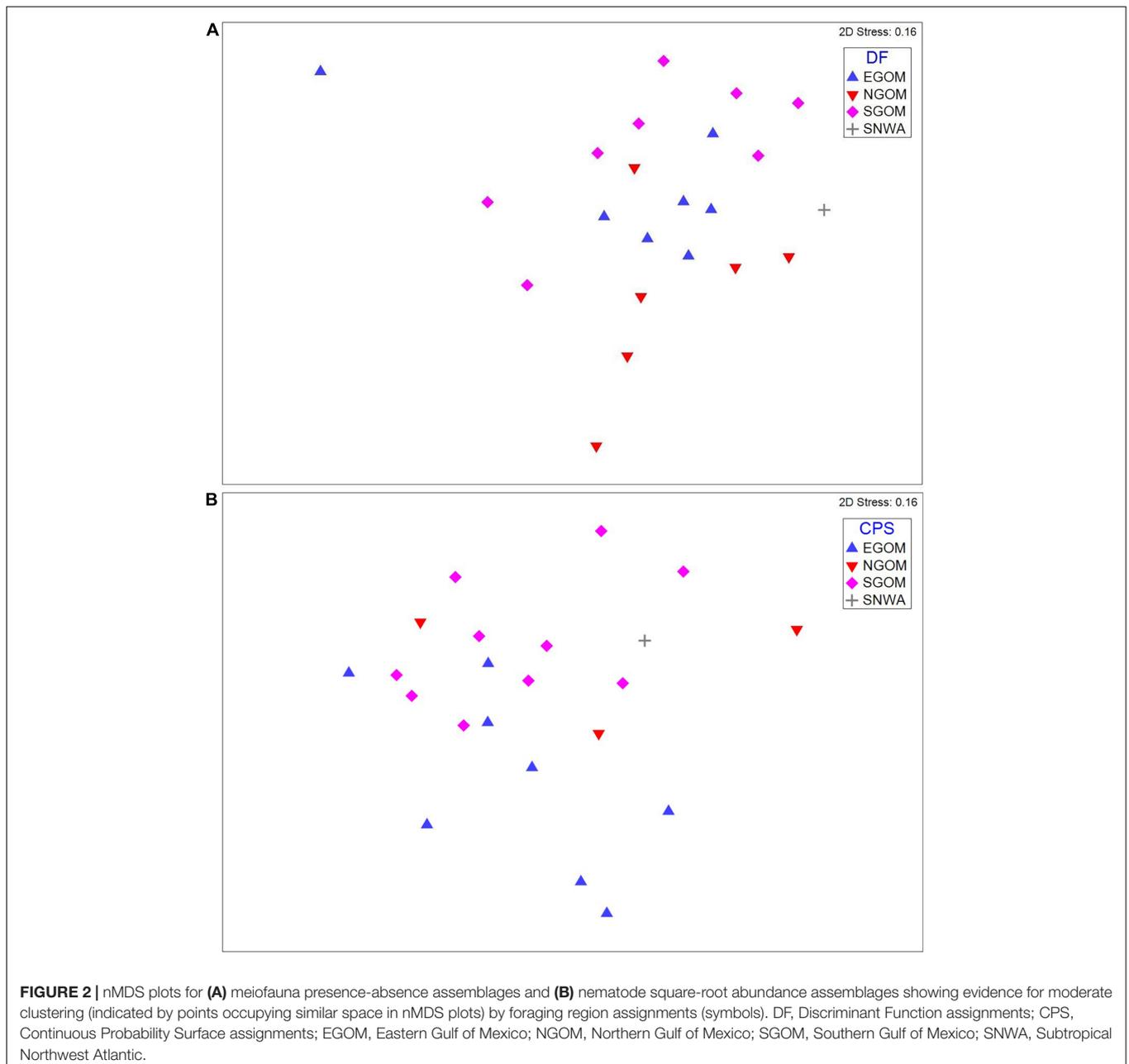
$t_{16} = 1.38$ ,  $p = 0.022$ ). SIMPER identified 27 nematode genera that contributed to 70.96% dissimilarity between EGOM and SGOM assemblages (**Figure 3B** and **Supplementary Table 3**). Nematode abundance in SGOM assemblages was higher than in EGOM assemblages for nearly all genera that contributed most to dissimilarities between assemblages from these foraging regions (**Figure 3B** and **Supplementary Table 3**).

Dissimilarities in SIA data related to dissimilarities in epibiont assemblages consistently within DF-assigned foraging regions. Dissimilarities in  $\delta^{15}\text{N}$  correlated moderately with dissimilarities in macrofauna abundances within DF-assigned foraging regions (BEST:  $\text{Rho} = 0.49$ ,  $p = 0.01$ ). Dissimilarities in SIA data between individual turtles correlated significantly with dissimilarities between individual assemblage meiofauna abundance (RELATE:  $\text{Rho} = 0.22$ ,  $p = 0.05$ ) and presence or absence of certain taxa (RELATE:  $\text{Rho} = 0.246$ ,  $p = 0.046$ ) within DF-assigned foraging regions. Dissimilarities in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  correlated also significantly with dissimilarities in nematode genera abundances (BEST:  $\text{Rho} = 0.409$ ,  $p = 0.045$ ) between samples within DF-assigned foraging groups.

## DISCUSSION

Epibionts may serve as useful indicators of sea turtle spatial and foraging ecology between and within broad foraging regions. In our study, meiofauna higher taxa and nematode genera proved more discriminative and informative toward broad foraging locations and foraging ecology than macrofauna higher taxa. Previous studies of loggerhead turtle epibiont assemblages elsewhere have suggested that differences in assemblages correspond to a foraging dichotomy between pelagic and neritic habitats (Reich et al., 2010; Nolte et al., 2020). Mature loggerhead turtles in the Atlantic Ocean, particularly in the Gulf of Mexico, restrict foraging to the shallow ( $< 200$  m), continental shelf (Hart et al., 2012, 2020; Hardy et al., 2014). Further, individuals exhibit specialized foraging behaviors across their entire foraging range (Vander Zanden et al., 2010, 2016). Variation in epibiont assemblages from adult loggerheads in the Gulf of Mexico therefore likely corresponds to habitat and habitat-use variation between and within foraging regions, rather than pelagic-neritic foraging dichotomies (Reich et al., 2010). Our findings lend support to these paradigms, as we found that some epibiont taxa differed between turtles from different foraging regions, and that epibiont assemblages differed between turtles from within the same foraging region. As colonization depends upon spatial and ecological overlap of epibionts and hosts (Frick and Pfaller, 2013), our analysis of epibionts is informative to the distribution of epibionts among turtle foraging regions and to the behaviors of turtles within those foraging regions.

Many taxa were commonly found on turtle carapaces, regardless of foraging region or SIA data. This may be due to recent colonization, epibiont taxa life-histories, and/or baseline abundance across foraging regions. Turtles that breed and nest in the same region are likely to be colonized in the short-term by the same taxa in similar abundances, particularly if individual turtles are behaving similarly (i.e., reserving resources for generating

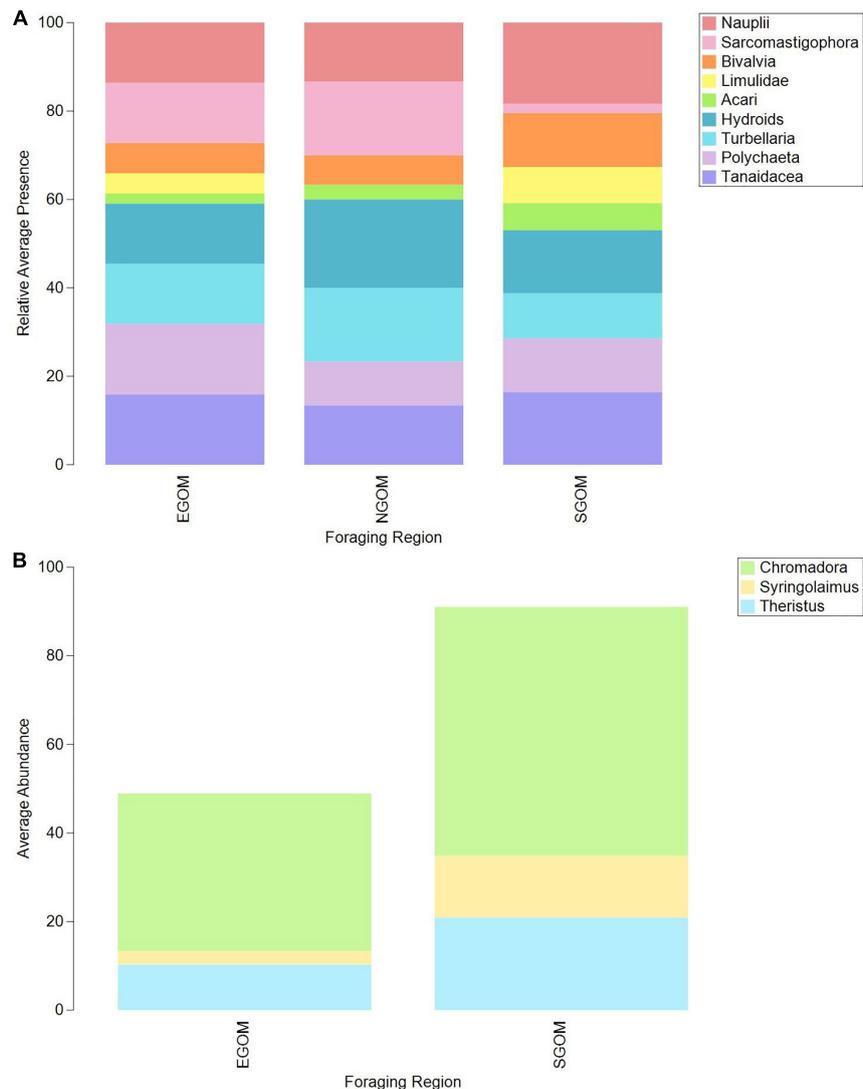


multiple clutches of eggs; Houghton et al., 2002). Organisms such as barnacles settle quite quickly, especially in the northern Gulf of Mexico (Reeves et al., 2018; Hart et al., 2021). It is possible that some ubiquitous epibionts such as turtle barnacles (*Chelonibia testudinaria*) and skeleton shrimp (*Caprella andreae*) settled on sampled turtles as they rested in-between nesting events. Organisms that colonize from a planktonic larval stage may disperse relatively far distances from their original substrate (Thiel, 2003), and therefore be found more commonly on turtles regardless of foraging region, prey-item preferences, or habitat use. This may be one reason why the macrofauna identified here did not differ between turtles from different foraging regions. Twenty-one of the 34 macrofauna taxa identified here have a

largely pelagic larval stage before settling, including the highly abundant turtle barnacle and juvenile *Cirripedia* sp. Some taxa without larval dispersal (i.e., skeleton shrimp) were still the most abundant macrofaunal taxa on all turtles. These are abundant benthic species globally (Cabezas et al., 2013), and as such may be abundant turtle epibionts.

The presence and absence of select meiofauna taxa and the differential abundance of nematode genera drove differences between epibiont assemblages of turtles that forage in the NGOM, EGOM, and SGOM. This may have been driven by three factors.

First, colonization frequency may correspond to baseline abundances of these taxa within foraging regions. The presence or absence, or abundance, of taxa in epibiont assemblages can



**FIGURE 3 |** Bar plots of average relative presence of **(A)** meiofauna and **(B)** nematode taxa contributing to dissimilarities between Eastern Gulf of Mexico (EGOM), Southern Gulf of Mexico (SGOM), and Northern Gulf of Mexico (NGOM) DF-assigned turtles, identified via SIMPER. See **Supplementary Tables 1, 2** for specific taxa contributions to dissimilarities between groups (full SIMPER results).

depend upon whether or not those taxa are found commonly within broad foraging regions. If turtles do not frequently encounter certain epibiont species within a foraging region, it is likely that those species will not be present (or will be present in reduced numbers) as epibionts of turtles from that foraging region (Frick and Pfaller, 2013).

Second, the life-histories of specific taxa may vary between foraging regions. For example, larval horseshoe crabs (family *Limulidae*) were not found on turtles that forage in the NGOM, but were present on SGOM and EGOM foragers. In the northwest Atlantic Ocean, horseshoe crabs begin breeding with the onset of warm temperatures (Rudloe, 1980; Cohen and Brockmann, 1983). It is possible that breeding had not begun in the NGOM by the time females migrated to SGI to breed. While it is also possible that turtles and horseshoe crabs do not interact

in the NGOM, loggerheads are known to prey on horseshoe crabs (Seney and Musick, 2007; Botton, 2009) and would provide substrate for planktonic larvae in their vicinity (as evidenced here). If potential epibionts are not ready to settle on substrate when they encounter a turtle, they will not colonize.

Third, individual turtle habitat use within foraging regions may influence colonization (Reich et al., 2010; Vander Zanden et al., 2010; Frick and Pfaller, 2013). Turtles forage on specific prey items (or a specific set of prey items) at foraging grounds (Vander Zanden et al., 2010; Nolte et al., 2020). Epibiosis likely occurs in part as a byproduct of foraging; epibionts may colonize from the water column or benthos as turtles search and maneuver for prey items (Frick and Pfaller, 2013). Both potential epibionts and prey items may be found in association with certain habitat types (i.e., mangroves, sea grass beds) in some regions, but

not in others. This could be due to interspecific variation or habitat degradation (and associated declines in diversity; Reed and Hovel, 2006), among other reasons. Colonization cannot occur in certain foraging regions if potential epibionts and prey items are not sympatric where turtles seek out prey items. We cannot determine which of the above factors contributed to differences in meiofauna colonization between NGOM, EGOM, and SGOM foraging turtles with our available data. Nevertheless, our results indicate that epibionts can be informative to turtle spatial ecology, and vice-a-versa.

Differences between epibiont assemblages from turtles assigned to the same foraging region corresponded to differences in SIA values from those turtles (as per RELATE and BEST results). SIA values vary with location and foraging item preference (DeNiro and Epstein, 1978; Rubenstein and Hobson, 2004). Thus, differences in epibiont assemblages within foraging regions may reflect individual specialization in specific prey items or a specific combination of prey items (Vander Zanden et al., 2010; Nolte et al., 2020). Specializing in certain prey may require that turtles utilize specific foraging mechanisms, or frequent certain habitats, that then allow for differential colonization of epibionts. For example, loggerhead turtles that feed on benthic mollusks may dig for their prey, which can suspend benthic organisms that may colonize carapaces (Lazar et al., 2011). Loggerheads that graze on suspended fauna such as gastropods and chondrophores (Hatase et al., 2007) do not perturb sediment, and are colonized by a different suite of organisms. These turtles could exhibit different SIA values and epibiont assemblages, yet be present at the same foraging region. Further, turtles with preferences for specific prey items may have to frequent different habitat types to consume those items (Cardona et al., 2009; Williams et al., 2017). These habitats have their own invertebrate communities, which could contribute to unique colonization of loggerhead carapaces. Epibionts may provide insight into loggerhead turtle foraging preferences and habitat use within foraging regions, and future studies that explicitly relate foraging preferences and habitat use to epibiosis (as discussed below) will allow researchers to garner more information from the epibionts of nesting sea turtles.

Studies such as ours can be most informative by sampling a high proportion of nesting turtles from nesting assemblages, integrating epibiont analysis and SIA with satellite telemetry, and using molecular techniques to identify taxa. Our turtle sample size was representative for the 2018 nesting season at SGI (~35–40% of nesting turtles; S.C. personal communication, Ceriani et al., 2019), but low relative to the average annual number of nesting turtles at SGI (I.S. unpublished data, Ceriani et al., 2019). Further, this low sample size mitigates the power of inferences that can be made using foraging region assignments. CPS and DF performed slightly differently, and subsequent analyses identified different relationships between epibionts and turtles assigned to foraging regions using the two techniques. It would be unreasonable to expect these methods to perform identically, but increasing sample size could mitigate the bias that slight differences in assignments between CPS and DF have on downstream analyses. Increasing sample size might also allow us to implement assignment probability thresholds for DF assignments (as per Wunder, 2012;

Ceriani et al., 2014; Vander Zanden et al., 2014) if future samples have higher probabilities, which would increase certainty in assignments and in the relationships identified here between epibionts, inferred foraging regions, and SIA. Sampling additional turtles for epibionts and SIA would therefore allow us to be more confident in differences between and within inferred foraging regions, and integrating satellite telemetry with our epibiont analysis and SIA would reduce error in foraging ground assignments. However, these efforts would be costly and labor intensive and were beyond the scope of this study.

Molecular techniques such as sequencing of COI barcodes (Hebert et al., 2003) or 16s rRNA (Goetze, 2010) could help further identify epibiont taxa to species, populations, or operational taxonomic units. This could improve taxonomic resolution to demonstrate differences in the presence or abundance of certain common taxa between turtles between and within different foraging regions. This is particularly true for higher taxa identified to phyla or classes and for abundant taxa identified to species (i.e., skeleton shrimp). Certain families, genera, or species within the higher taxa identified here could differ between or within foraging regions, and skeleton shrimp and other common species may exhibit genetic population differences between foraging regions that are not apparent from morphological identification alone. Further, taxa such as diatoms are found ubiquitously on sea turtle carapaces (Robinson et al., 2016), and differ between loggerhead turtles sampled across broad geographic scales (van de Vijver et al., 2020). Diatoms might therefore discriminate between sea turtles at smaller scales, such as in this study. Improving taxonomic resolution and breadth in similar, future studies could render common epibiont taxa more informative toward sea turtle spatial and foraging ecology.

Sampling and identifying epibionts, especially small meiofauna, from nesting turtles provides promising insights into sea turtle foraging and spatial ecology, but our understanding of carapace colonization should be refined to develop and streamline these techniques. Sampling epibionts from mature turtles in-water at foraging grounds, although difficult, is necessary to establish baseline data for epibionts of turtles within foraging regions (Nolte et al., 2020). Observations of turtle foraging ecology, spatial ecology, and habitat use at foraging grounds (via isotopic mixing models, satellite transmitters and/or animal borne cameras, e.g., Thomson and Heithaus, 2014; Gillis et al., 2018; Hays and Hawkes, 2018) can be paired with epibiont identification to relate epibiosis to specific prey item selection, foraging mechanisms, and habitat use within foraging regions. This would allow studies of epibionts from nesting turtles to draw more specific inferences on the spatial and foraging ecology of individual turtles. Finally, sampling the benthos and water column for invertebrates at known turtle foraging locations at different times throughout the year can establish a baseline for potential colonizers and provide insight into the phenology of potential colonizers within foraging regions. These baseline data may be crucial to identifying epibiont species for future studies of nesting turtles that focus on determining the spatial and foraging ecology of individuals, without necessarily having to rely upon expensive techniques such as satellite telemetry. Nevertheless, our

study has provided new foundations for studies to further explore the relationships between epibionts and sea turtle spatial and foraging ecology in the Gulf of Mexico and elsewhere.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors as **Supplementary Material**, without undue reservation.

## ETHICS STATEMENT

The animal study was reviewed and approved by the Florida State University Animal Care and Use Committee.

## AUTHOR CONTRIBUTIONS

IS-G, JI, MF, GS, YV, and SC conceived the project and designed methodology. IS-G, JI, GS, YV, LP, ACS, PFN, AS, DP, AR, SS-Z, LA, and AG contributed to epibiont collection, sorting, and identification. IS-G and JI analyzed epibiont data and led the writing of the manuscript. SC and AG generated stable isotope data. IS-G, SC, and MF analyzed stable isotope data. All authors contributed critically to the drafts and gave final approval for publication.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.696412/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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