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## STABLE ISOTOPE ANALYSIS OF ANTIPATHARIAN DIETS FROM THE NORTHWESTERN GULF OF MEXICO

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**AbsTRACT:** Antipatharians, or black corals, form a key component of the benthic fauna found throughout the Gulf of Mexico (GOM). In the northwestern GOM, they are a common member of the communities found on the natural relic coral-algal banks known as the South Texas Banks as well as on artificial reefs. They are known to provide important habitat for many ecologically and economically important species in the area but are relatively understudied. Here we present a study on their trophic ecology using stable isotope analysis of carbon and nitrogen from 2 species, Antipathes atlantica and Stichopathes luetkeni from a mesophotic artificial reef in close proximity to the South Texas Banks. We observed that a large proportion of the 2 coral's diets was composed of detrital matter, likely driven by the continuous disturbance of the benthos by high velocity benthic currents common to the region that support a persistent nepheloid layer below 30 m. Both species also show a reliance on different members of the planktonic community, with A. atlantica consuming more micro and mesozooplankton compared to S. *luetkeni*. Comparative analysis between soft tissue and skeletal material also indicates that A. atlantica may change its diet on a seasonal basis, while S. *luetkeni* appears to rely on detrital matter consistently. This study represents the first assessment of the diets of these organisms and provides valuable insight on the trophic ecology of 2 common antipatharian corals in the GOM on natural and artificial reef ecosystems.

**KEY WORDS:** black coral, particulate organic matter, soft coral, trophic ecology, detritus

#### INTRODUCTION

Antipatharians, or black corals, are colonial, passive suspension feeding cnidarians that produce a proteinaceous skeleton that lacks calcium carbonate (Wagner et al. 2012). This results in a flexible but strong skeletal morphology that is typically observed as a branched "bushy" form or a single stranded "wire" type morphology (Wagner et al. 2012). While antipatharians have a cosmopolitan distribution throughout the world's oceans, they are typically associated with mesophotic or deepsea habitats. Within these habitats, their flexible skeleton allows them to take advantage of areas where surrounding topography accelerates currents, thus enhancing their passive suspension feeding. However, due to their poorly developed musculature (Daly et al. 2003), their polyps are unable to retract into skeletal groves, which can leave them vulnerable to abrasive sediments or high energy environments (e.g., shallow fringing reefs). Additionally, they require hard substrate for larvae to adhere to and produce a holdfast (Wagner et al. 2012). As a result, they are typically unable to exist in areas with high sediment cover and low availability of hard substrates. It is these 2 factors that restrict them to hardcover banks within the Gulf of Mexico (GOM) (Rodriguez et al. 2018, Bollinger et al. 2022), such as the South Texas Banks or Flower Garden Banks.

Such aggregations are commonly referred to as coral forests, which provide structural complexity to an otherwise homogenous environment in the GOM (Nuttall et al. 2022). Coral forests can sustain high levels of biodiversity by serving as habitat for a variety of ecologically and economically important species in the GOM (e.g., Red Snapper, *Lutjanus campechenus*). The dense aggregations of both passive and active suspension feeders are also a core component of benthic—pelagic coupling in the region, resulting in carbon and nitrogen retention on the seafloor (Rodriguez et al. 2018, Bollinger et al. 2022). On the South Texas Banks, antipatharians can be found in densities of up to 5.4 ind/m<sup>2</sup> (Bollinger et al. 2022) and can often be the primary component of coral forests on the banks. Antipatharians and other soft corals are also found on artificial reef structures throughout the GOM (Johnston et al. 2022). A wide diversity of artificial reefs exists in the GOM and also provide important habitat for a variety of benthic and pelagic fauna (Johnston et al. 2022). Given that antipatharians are important and abundant members of the mesophotic, deep benthic and artificial reef communities, understanding their trophic ecology is crucial to gaining an overall understanding of their effect on benthic-pelagic coupling in the region. This information will provide valuable data for restoration efforts as many of these corals exist in areas where fishing and hydrocarbon industries are active (Clark et al. 2016, Etnoyer et al. 2016). While many natural and artificial reefs that support antipatharians are protected via habitat areas of particular concern ordinances, antipatharians have no formal protections of their own (Bollinger et al. 2022), which increases their susceptibility to anthropogenic disturbances.

Most antipatharians lack an association with symbiotic dinoflagellates of the family Symbiodiniaceae and are entirely heterotrophic in their feeding strategy (Wagner et al. 2012). Typically, antipatharians utilize direct interception of particles as the primary method of food capture, but the use of mucus nets has also been noted (Lewis 1978). Previous studies based on gut content analysis have observed various zooplankton items (Carlier et al. 2009) and stable isotopic analyses show that different species rely on different size fractions of the plankton, which can vary seasonally (Coppari et al. 2020). However, few studies have assessed the role of detrital matter in antipatharian diets. This may be an important contributor to the diets of antipatharians relative to live particulate organic matter in the GOM, particularly on the continental shelf in the northern GOM, where a persistent nepheloid layer and strong currents can deposit both inorganic and organic matter onto the banks regularly (Rezak 1985, Rezak et al. 1990, Nash et al. 2013). In this study, we present a stable isotopic analysis of antipatharian tissue and skeleton from species commonly associated with mesophotic banks in the GOM, Antipathes atlantica and Stichopathes luetkeni. The 2 target species differ in their skeletal and polyp morphology, with S. luetkeni displaying a wire-like skeletal structure and larger polyps (0.7-1.8 mm diameter) while A. atlantica has a branching morphology with smaller polyps (0.5–1.1 mm diameter; Opresko et al. 2016, Wagner and Shuler 2017). Such morphological differences may play a role in their ability to feed and distribution patterns. The data presented here will enhance our understanding of the biology and ecology of antipatharians in the GOM and the role they play in benthic-pelagic coupling on GOM mesophotic communities.

#### MATERIALS AND METHODS

#### Sample collection and processing

During 2 sampling trips on 26 August 2021 and 21 September 2021, clippings from 2 target antipatharians, *Antipathes atlantica* (Figure 1A) and *Stichopathes luetkeni* (Figure 1B), were collected at the Texas Clipper (PS–1122) Artificial Reef (hereafter Clipper Artificial Reef; 26°11′21" N, 96°51′33" W) at depths between 27–35 m using open circuit SCUBA diving. The Clipper Artificial Reef provides a good analog to the nearby South Texas Banks, as its deck typically extends above the nepheloid layer, allowing for invertebrates to avoid smothering and to persist. While it is not a natural system in the GOM, the wreck

provides habitat for many of the major groups found on the natural GOM banks, such as gorgonians, antipatharians and sponges, similar to the multitude of other artificial reef structures in the GOM (Johnston et al. 2022, Macartney and Hicks, pers. observ.). For A. *atlantica*, about 10 cm long "branchlets" were clipped from the main apical branches (n = 10). For S. *luetkeni*, the first 15 cm were clipped from the apical end of the coral (n = 17). Clippings were placed in resealable plastic bags and transported on ice to the laboratory at the University of Texas Rio Grande Valley (UTRGV) Port Isabel campus and frozen at  $-20^{\circ}$ C. Samples of both species were also preserved in 95% ethanol for polyp diameter measurements using a dissection scope to verify that S. *luetkeni* had larger polyps than A. *atlantica*, as described in the literature (Opresko et al. 2016; Supplemental Figure S1).

Plankton samples were collected during both collection trips and represent the mean of the stable isotopic composition of the food sources between the 2 sampling trips. Three 5L nisken bottles were carried to 30 m depth by divers, "shaken" to force any remaining surface water from the chamber and then capped at both ends. One bottle opened on ascent during the September sampling resulting in only 2 samples. The bottles were transported in a cooler to the laboratory at UTRGV and immediately filtered through a series of filters representing different size fractions of plankton (sensu Coppari et al. 2020). About 5L of water was first poured through a 200 µm stainless steel mesh to capture the mesozooplankton fraction (>200 µm) and then through a 20 µm stainless steel mesh for the microplankton fraction (20 - 200 µm). To capture the pico and nanoplankton fraction the water was then filtered onto pre-combusted 0.7 µm glass fiber filters (Whatman GF/F 47mm). The microplankton and mesozooplankton were carefully rinsed from the mesh filters into acid washed glass beakers using 0.22 µm filtered seawater and ultimately captured on pre-combust-

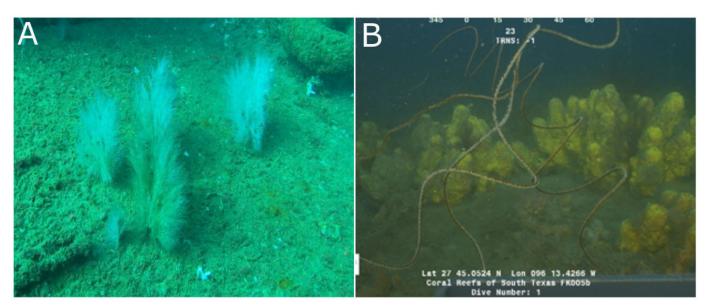


Figure 1. Photographs of black coral species on the South Texas Banks. A. Antipathes atlantica in-situ at the Clipper Artificial Reef site. B. Stichopathes luetkeni from ROV Global Explorer (R.V. Falkor, Schmidt Ocean Institute).

ed 0.7  $\mu$ m GF/F filters. The mesozooplankton filters were examined under a dissection microscope at 10X magnification to remove any large particles such as detrital matter (e.g., pieces of macroalgae) or anthropogenic waste (e.g., plastic).

Detritus was collected during the September sampling trip by brushing loose organic matter from the deck of the wreck into 50 ml collection tubes. The deck of the Clipper Artificial Reef is consistently covered by resuspended organic and inorganic particulate matter due to the high velocity currents and nepheloid layers present in the area (Macartney, pers. observ.), so detrital organic matter from the deck originates from both pelagic and benthic sources. The collection areas were located 1–2 m away from where antipatharians were collected and care was taken to avoid scraping living algae or invertebrates into the tubes. The tubes were transported on ice to the laboratory and excess seawater was immediately drained off. Samples were examined under a dissection microscope at 10X magnification to remove any living organisms, large pieces of macroalgae, plastic or metal flakes.

#### Sample preparation for stable isotope analysis

Tissue samples were rinsed with DI water to remove any residual debris or CaCO<sub>3</sub> from collection and then tissue was removed from each sample using sterile razor blades and dried at 60°C for 24 hours. Dried antipatharian tissue destined for  $\delta^{15}$ N analysis was then ground to a fine powder and 0.4–0.6 mg was weighed into 9x5 mm tin capsules for bulk stable isotope analysis (SIA). An entire piece of skeleton was selected from the midpoint of the largest branching sections in A. atlantica and cut at both ends. In S. luetkeni, a 1-2 cm piece was clipped from the middle of the coral. As antipatharians skeletons are produced by concentrically layered Antipathin (a chitinous compound) around a central canal, these samples represent a stable isotopic record of skeletal deposition from the time that each section was first growing as the apical end of the coral. Based on growth rates reported in Salinas (2022), skeletal fragments represented about 5-6 months of growth, whereas tissue turnover is typically in the order of days to weeks for invertebrates (Vander Zanden et al. 2015, Quinby et al. 2020). The samples of skeleton were scraped to remove all tissue under a dissection microscope. The skeleton samples were then dried, pulverized, and 0.4–0.6 mg was weighed into 9x5 mm tin capsules for bulk SIA (A. atlantica n = 5, S. luetkeni n = 5). Tissue and skeleton samples for antipatharians were not acidified as their skeletons do not contain CaCO<sub>3</sub>.

Plankton fraction filters were dried at 60°C for 24 hours and the 47 mm filters were then cut in half. One half was acidified using 1M HCL fumigation to remove CaCO<sub>3</sub> for  $\delta^{13}$ C analysis. The other half remained unacidified and was used for  $\delta^{15}$ N analysis. The filter halves were cut again for packing into 9x5 mm tin capsules for SIA.

Detrital matter was dried at 60°C for 24 hours. Subsamples were taken and acidified in 1M HCL for 12 hours for  $\delta^{13}$ C analysis and 1mg was weighed into 9x5 mm tin capsules for bulk SIA. For detrital  $\delta^{15}$ N, 10 mg was weighed into the capsules due to the presence of inorganic matter in these samples.

#### Stable isotope analysis

Samples were analyzed at the University of Texas at Austin – Marine Science Institute, Core Isotope Facility in Port Aransas, TX. An automated system for coupled nitrogen– and carbon–isotope measurements using a Thermo Fisher Scientific Flash EA–Isolink CNSOH elemental analyzer connected to a Thermo Fisher Scientific Delta V Plus isotope–ratio–mass– spectrometer was used to perform the analysis. The isotope results are presented using the conventional  $\delta$ –notation:

 $δ^{13}$ C (or  $δ^{15}$ N) = [(R<sub>sample</sub>/R<sub>standard</sub>)–1] (in ‰) Equation 1 where R<sub>sample</sub> and R<sub>standard</sub> = <sup>13</sup>C/<sup>12</sup>C (or <sup>15</sup>N/<sup>14</sup>N). All δ–values are reported relative to VPDB (Vienna Pee Dee Belemnite) for carbon and AIR (atmospheric nitrogen standard) for nitrogen, unless otherwise stated (Coplen 1996). A 2–point calibration of  $δ^{13}$ C to VPDB and to  $\delta^{15}$ N to AIR was achieved using USGS–40 (–26.39‰, –4.52‰) and USGS–41a (+36.55‰, +47.55‰) reference standards, respectively. Internal laboratory standards, casein protein and glycine were used to evaluate the carbon and nitrogen isotope precision and accuracy. Overall, the accuracy and precision of the carbon and nitrogen isotope results had a standard deviation of less than 0.2‰.

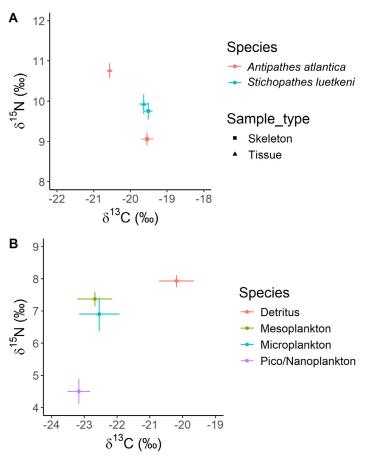
#### Statistical analysis

Statistical analyses for differences between species, tissue type and food sources for all SIA variables were conducted with ANOVA in JMP statistical software (version 16.2). Any variables not meeting the assumptions of normality, based on Shapiro-Wilkes tests, were log<sub>10</sub> transformed before analysis to meet assumptions of normality and back transformed for graphical purposes. To assess stable isotopically derived trophic niche overlaps for both species, the R package Stable Isotope Bayesian Ellipses in R (SIBER) was run using default settings (Jackson et al. 2011). This package produces ellipses of SIA values plotted on a biplot and estimates the standard ellipse area corrected for sample size (SEA<sub>c</sub>), which contain 40% of the variation of a group. The SEA<sub>c</sub> is a robust metric for assessing isotopic niche spaces for groups with different sample sizes which is useful for quantifying overlaps in dietary patterns (Jackson et al. 2011). The relative dietary contribution of different planktonic or detrital food sources was assessed using the R package "MixSIAR" (Stock et al. 2018), which uses a Bayesian mixed modelling framework to assess dietary contributions from source SIA values (e.g., different particulate organic matter (POM) fractions collected in this study). As very little feeding information exists for antipatharians, no prior assumptions were added to the mixed model. Tissue and skeletal samples were used to reconstruct the diets in order to present a shortterm and long-term estimation of diet, respectively. Source endmember values for food sources were taken from averaged data collected in this study (Supplemental Table S1). Trophic discrimination factors for both  $\delta^{13}$ C and  $\delta^{15}$ N (1‰ in  $\delta^{13}$ C and by 3‰ in  $\delta^{15}$ N) were based on data collected in Coppari et al. (2020) and represent the approximate isotope fractionation occurring during incorporation of sources into consumer tissue (Peterson and Fry 1987).

#### RESULTS

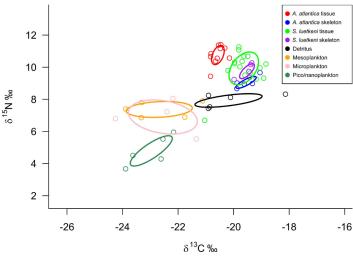
#### $\delta^{13}C$ and $\delta^{15}N$ of antipatharian tissue and skeleton

There were significant differences between A. atlantica and S. luetkeni tissue  $\delta^{13}$ C ( $t_{25} = 5.291$ , p = <0.0001) and  $\delta^{15}$ N ( $t_{25} = -2.374$ , p = 0.026). Mean tissue  $\delta^{13}$ C was higher in S. luet keni while mean tissue  $\delta^{15}$ N was higher in A. atlantica (Figure 2A). There was also a significant difference between the skeletal  $\delta^{15}$ N ( $t_{25} = 2.662$ , p = 0.028) between both species, with S. luetkeni higher than A. atlantica (Figure 2A). There was no significant difference between the 2 species skeletal  $\delta^{13}$ C ( $t_{25} = 0.16$ , p = 0.873).



**Figure 2.** Stable isotope analyses of black coral species and food sources from the South Texas Banks. A. Biplot of  $\delta^{15}N$  and  $\delta^{13}C$  (± se) values from the tissue and skeleton of A. atlantica and S. luetkeni. B. Biplot of  $\delta^{15}N$  and  $\delta^{13}C$  (± se) values of the food sources collected in this study.

Differences between the 2 sample types (tissue and skeleton) were also tested within each species. In *A. atlantica*, the  $\delta^{13}$ C of the skeleton samples was significantly higher than the tissues ( $t_{13} = -6.738$ , p = <0.0001) but the  $\delta^{15}$ N of the skeleton samples was significantly lower than the tissue ( $t_{13} = 5.846$ , p = <0.0001; Figure 2A). In *S. luetkeni*, there were no significant differences between the skeleton and tissue samples for both  $\delta^{13}$ C ( $t_{21} = -0.481$ , p = 0.682) and  $\delta^{15}$ N ( $t_{21} = 0.359$ , p = 0.723; Figure 2A). The SIBER analysis showed SIA niche overlap between *S. luetkeni* tissue and skeleton as well as *A. atlantica* skeleton samples (Figure 3, Supplemental Figures S2 and S3).



**Figure 3.** Ellipse plot of all target species, tissue types and food types generated in SIBER. Ellipses represent 40% of the variation seen within the stable isotope values.

#### $\delta^{13}C$ and $\delta^{15}N$ of planktonic and detrital food sources

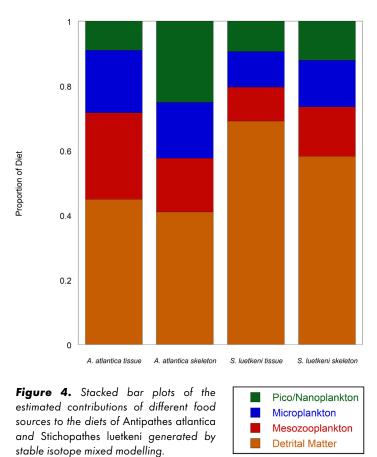
There were significant differences between the food sources sampled in this study. For  $\delta^{13}$ C (ANOVA:  $F_{3,15} = 6.809$ , p = 0.004), detritus was significantly higher than the living food sources (Tukey's HSD = <0.05; Figure 2B). For  $\delta^{15}$ N (ANOVA:  $F_{3,15} = 16.673$ , p = <0.0001), the pico/nanoplankton fraction was significantly lower than the other food sources (Tukey's HSD = <0.05; Figure 2B). There was SIA niche overlap within the SIBER analysis between the mesozooplankton and microplankton fractions of the food sources (Figure 3).

#### Diet reconstruction

For A. *atlantica*, the short-term diet (based on tissue samples) consisted of about 45% detrital matter, 9% pico/nanoplankton, 19% microplankton and 27% mesozooplankton (Figure 4). The long-term diet (based on skeletal samples) consisted of about 41% detrital matter, 25% pico/nanoplankton, 17% microplankton and 17% mesozooplankton (Figure 4). For S. *luetkeni*, the short-term diet consisted of about 69% detrital matter, 9% pico/nanoplankton, 11% microplankton and 11% mesozooplankton (Figure 4). The long-term diet consisted of about 58% detrital matter, 12% pico/nanoplankton, 14% microplankton and 15% mesozooplankton (Figure 4).

#### DISCUSSION

The significant differences between soft tissue  $\delta^{13}$ C and  $\delta^{15}$ N and skeletal  $\delta^{13}$ C and  $\delta^{15}$ N in A. *atlantica* indicates that diet likely varies on a seasonal basis, as observed previously in antipatharians and gorgonians (Cocito et al. 2013, Coppari et al. 2020). The skeletons of antipatharians contain no CaCO<sub>3</sub>, instead they are formed by a collagen—protein matrix that is deposited continually and can be used to estimate environmental conditions or diet over time (Williams et al. 2007). As stable isotope turn over in soft tissues typically occurs over a period of weeks in soft bodied invertebrates (Vander Zanden et al. 2015), the skeletal samples provide a longer—term view of diet. Stud-



ies on other heterotrophic corals have shown their diets are dictated primarily by the food available to them within their particular habitat (Ribes et al. 1999, Cocito et al. 2013, Coppari et al. 2020, Rakka et al. 2020) and this appears to occur in the corals from this study. During the summer, when this study was conducted, A. *atlantica* tissues had a higher  $\delta^{15}$ N and a lower  $\delta^{13}$ C compared to skeletal samples and suggests this species consumes more mesozooplankton when they are abundant during the summer, reverting to pico and nanoplankton when blooms subside in the winter months (Shropshire et al. 2020). Such a pattern has been observed previously in the Mediterranean coral, Antipathes subpinnanta (Coppari et al. 2020). While seasonal changes in zooplankton abundance throughout the GOM are generally driven by fluvial input, upwelling or current patterns (Ortner et al. 1989), global patterns such as El Niño events can influence food availability for antipatharians in the GOM on a more broad scale (Daly et al. 2021). The pattern was also observed in S. luetkeni, and while not significant, it suggests that it also opportunistically feeds on zooplankton when they are abundant. Changes in mesozooplankton community composition overtime (Ortner et al. 1989, Yebra et al. 2022) might also account for the difference in long term diets between the 2 species as their polyp structure and density may dictate the prey items available to them.

The  $\delta^{13}$ C and  $\delta^{15}$ N values of the planktonic food sources are similar to those collected in the GOM previously (McClain– Counts et al. 2017) and can provide a representative value for the diets of antipatharians in the GOM. The results of diet reconstructions show that despite its smaller polyp size, A. atlantica consistently consumes more zooplankton compared to S. luetkeni. Previous studies in the Red Sea on a similar set of corals with similar morphological characteristics, Antipathes griggi and Stichopathes spp. found that A. griggi had a higher trophic position compared to the Stichopathes spp. (Morgulis et al. 2022). The higher rate of feeding on zooplankton by members of the Antipathes could be a result of its morphology as its fan like shape and high polyp density may aid in capture and immobilization of larger zooplankton compared to singular polyps found on the wire-like Stichopathes. Remarkably, we observed a large contribution of detritus to the diets of both species, likely a mix of both pelagic and benthic derived matter due to the high velocity benthic currents and fluvial input found in this area of the GOM (Rezak 1985, Nash et al. 2013). Detrital matter contributed about one half or two thirds to the diets of A. atlantica and S. luetkeni respectively.

The incorporation of detrital matter into antipatharian or gorgonian diets is well described. Research conducted on deep water corals (Sherwood et al. 2008, Carlier et al. 2009) and shallow water gorgonians (Ribes et al. 1999, Cocito et al. 2013) show that members of these groups often rely on resuspended POM. As detrital matter in the water column may be the most abundant particle available at times when benthic currents are present, detritus would be the particle that is captured most frequently as particle ingestion rate is expected to follow a linear pattern with particle concentration (Ribes et al. 2003). Both tissue and skeleton SIA values were higher than those from Antipathes subpinnata, which relies primarily on live plankton as a food source in mesophotic Mediterranean reefs (Coppari et al. 2020). Instead, the values from this study are closer to those found in Bathypathes artica (Sherwood et al. 2008) and Leiopathes glaberrima (Carlier et al. 2009), both of which inhabit deep water reefs and rely heavily on resuspended POM as a food source.

Differences in the proportion of detrital matter used by A. atlantica and S. luetkeni could be driven by 2 potential factors. Their morphology is distinct, with a fan-like structure seen in A. atlantica and a wire-like structure seen in S. luetkeni, which could have the potential to affect both micro and macro scale currents surrounding their polyps (Wagner et al. 2012). The higher surface area and increased polyp density of A. atlantica could increase the capture rate of live prey. The larger but less densely grouped polyps of S. luetkeni may result in a less effective capture rate of live prey but enhance their ability to collect larger detrital particles. An alternative explanation of these differences might be a result of the locations these corals are found on the artificial reef itself. Antipathes atlantica is often found on the outer decks of the Clipper Artificial Reef which could allow for higher exposure to live prey compared to S. luetkeni, which is typically found within hold compartments or under structures (Macartney and Salinas, pers. observ.). As currents move through the wreck, matter found inside these more enclosed spaces would be resuspended and trapped, therefore leading to increased detritus exposure for corals inside such a space.

This distribution is similar to the natural distributions of these 2 corals on the nearby South Texas Banks, where A. atlantica is most common on high relief banks that are raised above the nepheloid layer and S. luetkeni is found throughout the banks regardless of the relief of the bank (Bollinger et al. 2021). Stichopathes luetkeni's resistance to sediment deposition and their use of resuspended detrital matter common in such areas could explain this apparent habitat partitioning. It is also possible that the nepheloid layer could influence where antipatharians reside on other GOM artificial reef structures. Antipatharians may have a competitive advantage on deeper structures due to increased food availability and reduced light penetration as photoautotrophic fauna would be negatively impacted by increased turbidity. As the nepheloid layer persistence or general turbidity can be highly variable by depth throughout the GOM, this will impact local distributions of antipatharians coincidentally and should be considered in studies of the ecology of both natural and artificial reefs.

#### CONCLUSIONS

Here we have shown that antipatharians in the northwestern GOM are able to utilize both live and detrital POM as a food source, with an increased reliance on detrital matter

as a food source compared to previous studies on mesophotic antipatharians. Additionally, we observed potential seasonal changes in their diet by analyzing both tissue and skeleton as short- and long-term diet metrics. These results will be of use for the management of antipatharians in the GOM as they can be threatened by both climatic and anthropogenic disturbance events, such as the Deep Water Horizon oil spill (Etnoyer et al. 2016). Furthering our understanding of the trophic interactions of these organisms will be crucial in studies relating to their general ecology and their restoration potential, such as their ability to survive in aquaculture and subsequent out planting efforts after large scale disturbance events. While the organisms from this study were taken from an artificial reef, the location and structure of the reef provides a crucial firstlook into the trophic ecology of predominant members of the mesophotic benthic community that occur across natural and artificial habitats in the northern GOM with a persistent nepheloid layer. However, future studies on the trophic ecology of these organisms should include feeding assays and prey capture measurements along with the inclusion of isotopic tracer studies to fully understand how these organisms react to changes in available prey items in the water column.

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