



Community composition of mussel associates at deep-sea methane seeps in the Gulf of Mexico and the US Atlantic Margin

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ABSTRACT

Efforts to understand and preserve the methane seep communities of the Gulf of Mexico and the US western Atlantic margin begin with an understanding of biodiversity and community composition. In this study, 10,143 individuals representing 63 different taxa were sampled from mussel-beds surrounding methane seeps at various depths within two different ocean basins. Diversity in mussel beds was highest at Baltimore Canyon, the shallowest site sampled in the Atlantic. Although only four species were sampled at more than one site, species composition was most alike among sites found at similar depths; the two deepest sites sampled, Florida Escarpment and Blake Ridge, showed a 9.6% similarity. However, depth is not the only predictor of similarity: Baltimore Canyon and Chincoteague are both located in the Atlantic Ocean at different depths but had a 5.3% similarity in species composition. The high diversity of individuals sampled among these sites emphasizes the importance of preserving seep communities, which provide essential nursery habitats and primary production that establish a food source for many migratory species within the deep-sea ecosystem. Not only is the diversity of seep communities unique and important to the deep sea, but seeps may be beneficial to the overall health of our Earth's ecosystem through the support of commercial fisheries and the sequestering of methane.

1. INTRODUCTION

Cold seeps are defined by the upward convection of methane and other hydrocarbons from the subsurface seabed to the seafloor and are typically found on continental margins worldwide (Ruff et al., 2015). The exploration of cold-seep communities first began in 1984 at depths ranging from 500 to 1000 m (Kennicutt et al., 1985). With the growing expansion of deep-sea exploration by commercial interests such as oil drilling, sea-floor mining, and deep-water fisheries (Levin et al., 2016), it is imperative to understand the community compositions surrounding these seeps to determine how they

might be affected by anthropogenic factors. Much of the deep sea is food-limited, and methane seeps offer essential niches that provide habitat structure and primary production, supporting multi-trophic communities (Turner et al., 2020). In a largely barren ecosystem, methane seeps are biodiversity hotspots that provide an abundance of life. The invertebrates that settle among the foundation species of methane seeps contribute to food sources for migratory species and sequester a significant amount of the methane that sinks to the seafloor (Ruff et al, 2015).

Oxygen availability is often limited to the

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immediate surrounding area, resulting in a thin suboxic layer below the emitted hydrocarbon. It is here that partial pressure causes the methane to diffuse out of gas bubbles and into the water column, where microbial methane-oxidizing archaea (ANME) and sulfate-reducing bacteria (SRB) symbionts can use this resource to create a habitable environment. The primary production of communities of marine invertebrates within the deep sea is dependent on a process known as chemosynthesis—the conversion of inorganic energy sources to fuel. Chemosynthetic bacteria and archaea occur worldwide at cold seeps but are locally selected by the environment (Ruff et al., 2015).

Cold seeps are often characterized by one or more foundation species, often symbiont-bearing megafauna such as tubeworms or mussels (Turner et al., 2020). For instance, bathymodiolin mussels act as habitat engineers by modifying the physical and chemical environment, forming biogenic habitats that support a variety of additional species (Govenar 2010). Methane seeps are initially dominated by resident species, which use the foundation species for attachment, shelter, and access to food through grazing or currents (Cordes et al., 2010; Levin et al., 2016). The compositions of invertebrates living on the foundation species help characterize methane seeps' food chains and interspecies interactions. The ecological patterns surrounding seeps are typically influenced by bathymetric changes regarding interspecific interactions such as predation and competition (Cordes et al., 2010). Methane seeps with mussel beds as the foundation species are typically dominated by resident grazing gastropods, smaller decapod crustaceans, and worms of various phyla (MacAvoy et al., 2002). Many seep communities have been found to support both resident and vagrant species. The resident species are integrated into the phytoplankton detritus-based food web of the surrounding ecosystem. Conversely, vagrant species are characterized by a high degree of movement into and out of seep communities. This movement is essential for the export of seep

production into the vast ecosystem of the deep sea (MacAvoy et al., 2002).

This study aims to determine the differences in invertebrate species compositions between methane seeps in the Gulf of Mexico and the US western Atlantic margin and also among seeps at different depths. Variations in species compositions at seep communities may be attributed to abiotic variables such as depth, food availability, latitude, and substrate type (Rex et al., 2000). Biogenic habitats are also sensitive to changes in fluid flux and chemical composition, which determine the distribution of symbiont-bearing megafauna and community composition (MacDonald et al., 1989). As depth and distance from shore increase, fewer nutrients are transported by currents to seep communities (Turner et al., 2020). In the Atlantic Ocean, variation in seep community patterns has been attributed to the faunal boundary between the upper-bathyal (200-1500 m) and lower bathyal/abyssal (>1500 m) seeps (Bernardino et al., 2012). A similar transition zone is thought to exist at 1000 m in the Gulf of Mexico (Cordes et al., 2010). Therefore, it is hypothesized that sites located at similar depths will display greater similarity and species overlap due to the previously-described bathymetric boundaries.

2. METHODS

2.1. SAMPLE COLLECTION

Mussel-bed communities were sampled from a total of six methane seeps: three sites along the western Atlantic margin (WAM) and three sites in the Gulf of Mexico (GOM) (Fig. 1). Scoops of mussels and their associates were collected from the seafloor in February and March of 2019 using HOV Alvin deployed from RV *Atlantis*. Sampling was also done in May and June of 2021 using ROV Jason deployed from RV *Thomas G. Thompson*. Both vehicles recovered the samples inside closed bioboxes, and the invertebrates within were then sorted from the foundation species (*Gigantidas childressi* and *Bathymodiolus heckeriae*). Next, species were identified and

sorted based on morphology on board the ship. Samples were preserved in 10% buffered formalin and later transferred to 70% ethanol for storage. Preserved samples were further sorted by differences in morphology and identified to the lowest possible taxonomic level before being photographed in the laboratory. Samples were identified using the original published description of species. 70% ethanol deteriorates samples over time by bleaching them; therefore, some samples such as juvenile forms or fragments of an organism were more susceptible to degradation compared to fully developed adult samples. Those of these that were too degraded to photograph were still included in the statistical analysis.

2.2. DATA ANALYSIS

Samples collected in 2019 were organized into binary categories—presence or absence at each site—as there was no overlap in species. Diversity indices and the Bray-Curtis similarity index were not run on these data. This resulted in one site, Bush Hill, being excluded from the statistical analysis; it had been sampled only in 2019 and was not revisited in 2021. However, Bush Hill was still included in the tax-comparison portion of this study. Samples from 2021 were organized into counts of species present, as there was some overlap of species found at each site. Diversity among these sites was estimated using a combination of diversity indices, including Shannon-Weiner diversity (H'), Pielou's index of evenness (J'), Margalef's richness (D), and individual-based rarefaction curves calculated using Primer v6 (Clarke and Gorley 2006). A Bray-Curtis similarity index assessed similarity among sites following a fourth-root transformation of species densities. The data were transformed to balance species with high individual counts. The Bray-Curtis similarity matrix was then visualized using a non-metric multi-dimensional scaling plot.

3. RESULTS

A total of 10,143 individuals representing 63

different taxa across six phyla were sampled from the mussel beds surrounding the studied methane seeps (Fig. 2). The six phyla present were Cnidaria, Nemertea, Annelida, Arthropoda, Mollusca, and Echinodermata. The majority of the samples represented morphologically-distinct species; however, the taxonomy remains largely unresolved. Of the six different phyla represented in this study, not all groups were present at each site (Table 1). The three Atlantic sites: Blake Ridge (2167 m), Baltimore Canyon (388 m), and Chincoteague (1028 m) were the only sites that contained samples from the annelid subclass Oligochaeta. Brine Pool (651 m), sampled in the Gulf of Mexico, was the only site that provided samples from the molluscan class Polyplacophora. Baltimore Canyon (388 m), sampled in the Atlantic Ocean, was the only site that contained representatives from all six phyla present in this study. Bush Hill (562 m), the shallowest study site in the Gulf of Mexico, only contained species from two phyla: Annelida and Arthropoda. Brine Pool (651 m), sampled in the Gulf of Mexico, had Cnidaria, Annelida, Mollusca, and Echinodermata representatives. Chincoteague (1028 m), an Atlantic site, contained species from the phyla Annelida, Mollusca, Arthropoda, and Echinodermata. Blake Ridge (2167 m), the deepest site sampled in the Atlantic, contained five out of the six phyla, missing only Nemertea. Florida Escarpment (3287 m), sampled in the Atlantic Ocean, contained species from the same phyla as Brine Pool: Cnidaria, Annelida, Mollusca, and Echinodermata.

Despite the large number of individuals represented in this study, very few species were found across multiple sampling sites. A small brittle star, *Ophioctenella acies*, was found at both Blake Ridge and Florida Escarpment. These sites were located in different ocean basins but were the deepest sites sampled (Table 2). The Brine Pool and Bush Hill sites were located in close proximity to one another and at similar depths within the Gulf of Mexico, but only one species was found at both sites: the galatheid crab, *Munidopsis sp.1* (Table 3). Bush Hill and

Chincoteague were also located in different ocean basins, and Chincoteague was almost twice as deep, but the shrimp *Alvinocaris stactophila* was present at both sites (Table 3). The unidentified morphotype of “juvenile ophiuroid” was the only species present at more than two sites: Florida Escarpment, Blake Ridge, Baltimore Canyon, and Chincoteague (Table 2). These four sites represent both oceanic basins sampled in this study as well as the shallowest and deepest sites sampled.

Although Baltimore Canyon had the fewest number of individuals present, it had the highest species richness, evenness, and diversity (Table 4). Chincoteague had the second-greatest species richness, evenness, and diversity. Blake Ridge was the deepest site sampled in the Atlantic Ocean and was less diverse, even, and species-rich than the shallower sites. However, the opposite was true for the Gulf of Mexico sites: the deepest sites in this sample region displayed greater diversity, evenness, and species-richness than the shallower sites. Florida Escarpment had a greater species richness, evenness, and diversity than Brine Pool (Table 4). Florida Escarpment also had substantially more individuals present than any other sites sampled. The individual-based rarefaction curves indicate that the species sampled represent the population well because the curves all plateau (Fig. 3). As indicated by the multidimensional scaling plot of communities, the Florida Escarpment and Blake Ridge sites have the most similar species compositions (Fig. 4). The Bray-Curtis Resemblance matrix showed a 9.6% similarity between the two sites. They were both the deepest sites sampled in their respective oceanic basins. Baltimore Canyon and Chincoteague, both found in the Atlantic Ocean, varied greatly in depth but showed a 5.3% similarity in species present (Fig. 4).

4. DISCUSSION

In this study, Florida Escarpment (3287 m) and Blake Ridge (2167 m) were characterized by the same foundation species, *Bathymodiolus heckarae*, and were the two deepest sites

sampled. However, they were located in different ocean basins. Baltimore Canyon (388 m) and Chincoteague (1028 m) were found close together along the western Atlantic margin and were characterized by the same foundation species, *Gigantidas childressi*, but had a substantial difference in depth. This study found evidence that the site with the most species richness was Baltimore Canyon (388 m). I hypothesize that runoff from Chesapeake Bay may have been supporting increased productivity—and therefore, species richness—at this site. Throughout the Atlantic Equatorial belt, species richness is often highest at seeps of intermediate depth (between 1000-2000 m) where deep and shallow species overlap, supporting the previously-described bathymetric boundaries by Turner et al. (2020). The similarity found between Florida Escarpment and Blake Ridge only partially supports the hypothesis that sites at similar depths have species compositions that are more alike. Similarity was also found between Chincoteague and Baltimore Canyon, but the sites were located at different depths. Brine Pool and Bush Hill also had alike species compositions, though their similarity was not supported by statistical analysis. This study suggests that depth plays an important role in the composition of seep communities by influencing nutrient availability.

When considering the bathymetric boundaries responsible for community settlement, the larval dispersal of the invertebrates sampled in this paper must be considered as a potentially-important factor. How and when these immature species settle can be helpful in determining why species are found at some sites and not others. Variation in population connectivity can result from differences in the timing and location of spawning, hydrodynamic processes, larval behavior, and post-settlement processes such as emigration and mortality (VanDover et al., 2002). As there was a wide range of species found throughout the sites sampled, there were many different larval forms, lifespans, and factors

contributing to the differences in communities.

The potential of larval dispersal is dependent on biological factors such as vertical migration, buoyancy of embryos, predation, food availability, developmental rate, physical tolerances, and planktonic larval duration (Cordes et al., 2007; Young et al., 2012) and is assumed to influence the habitat range of adult conspecifics (Thorson, 1950). Due to the wide range of depths sampled in this study, there are several different filtering factors that determined which larvae are able to settle at these respective sites. Behaviors that determine larval depth may be especially key to deep sea community composition due to the increased variability of current speed and direction at different depths (McVeigh et al., 2017). As most invertebrate larval forms are incapable of mobility—with the exception of vertical migration in the water column—they are highly dependent on currents to deposit them in a habitable environment. Therefore, larval dispersal is highly dependent on which currents are present in the vicinity of spawning. Gulf of Mexico metapopulations are likely to be sources for larval dispersal, while western Atlantic margin populations are likely to be sinks, indicating a unidirectional exchange (Young et al., 2012). If further studies are conducted on the topic, larval dispersal may be able to explain why there are species overlaps at the sites within the Gulf of Mexico. However, planktonic larvae are still subject to barriers such as seamounts, oceanic ridge axes, and other topography that may present an impediment to dispersal between basins (McClain and Hardy, 2007). The shallow straits of Florida have been known to create a biogeographical barrier to larval dispersal (McVeigh et al., 2017), a phenomenon which is pertinent to the present study. This barrier, among other factors, may be responsible for the minimal overlap of invertebrates among the sites sampled in the Gulf of Mexico with those in the Atlantic Ocean.

Foundation species patterns may also account for variation among sites. The biogenic habitats of the two most similar sites in this

study—Blake Ridge and Florida Escarpment—are composed of *B. heckeræ*. Further study of the larval journeys of each respective foundation species may also help to determine why the sites are characterized by different species. *Bathymodiolus heckeræ* may rely on Gulf Stream meanders to be deposited into shallower depths. In the absence of Gulf Stream meanders, larvae likely remain in deeper waters and are transported south along the western boundary current, explaining why the deeper site mussel beds are comprised of *B. heckeræ* (Cordes et al., 2007). The biogenic habitats of the other sites included in this study are composed of *Gigantidas childressi*. Habitat-building differences between *B. heckeræ* and *G. childressi* may be responsible for the variability among sites' species compositions, though the impacts of foundation species composition are difficult to separate from those of depth. Variations in sites' chemical environments impact foundation species' growth rates and reproductive output. The environmental factors within the two ocean basins sampled favor *G. childressi*, which outcompetes *B. heckeræ* for space and resources (Turner et al., 2020). *G. childressi* contain only methanotrophic symbionts, possibly creating a different chemical habitat than that of mussel beds composed of *B. heckeræ*. *G. childressi* are also longer-lived and thrive closer to the surface, where faster currents may facilitate dispersal (Arellano et al., 2014). These environmental factors can help explain why the majority of the sites in this study are characterized by *G. childressi*.

Communities found at deep-sea methane seeps are essential for enhancing the productivity of deep-sea ecosystems, combating climate change, and boosting fishery yields. Therefore, understanding how anthropogenic actions affect these ecosystems is vital. Methane seeps provide habitat and food for various migratory deep-sea organisms by creating primary production and trophic levels that help structure the deep-sea food web (Turner et al., 2020). These ecosystems also furnish breeding and nursery sites that help maintain species

populations and bolster reproductive success (Beck et al., 2001). As such, seep communities may hold the key to maintaining a food and reproduction source for species often fished in commercial industries (Levin et al., 2016). Further, methane seeps are paramount to the ecological succession of the deep sea. Mussel taxonomy suggests that the decomposition of large bone and wood deposits may serve as successional steps for the introduction of mussel taxa to seeps, and, therefore, the support of chemoautotrophy-dependent invertebrates (Distel et al., 2000). Macro- and microorganisms at methane seeps and sulfate methane transition zones consume 75% of the methane that reaches the seafloor from subsurface zones (Ruff et al., 2015). This removal of methane from the seafloor allows for habitable environments to become established around these methane seeps where other invertebrates can then feed and settle. Furthermore, the rapidly-expanding deep-sea exploration movement enhances the urgency of understanding these interactions, especially as disturbances increase due to gas extraction, seabed mining, and bottom trawling (Levin et al., 2016).

5. CONCLUSION

The findings of this study only partially support the hypothesis. The two deepest sites, Florida Escarpment and Blake Ridge, had the greatest similarity. However, Baltimore Canyon and Chincoteague were found at different depths but still had a similar species composition. Although there were very few species found across multiple sites, the results of this study highlight the uniqueness of seep communities in the deep sea. The differences in seep community composition across the Gulf of Mexico and the western Atlantic margin include depth, foundation species, larval dispersal, and biogeographical barriers. Seep communities are relatively understudied due to the difficulties paired with accessing the deep sea, with the limitations of currently-available technology acting as a constraining factor on our overall understanding of these ecosystems. Methane

seeps are paramount to the ecological succession of the deep sea, providing a habitat for invertebrates as well as a food source for migratory species. Therefore, as our technological capabilities improve, it is recommended that further studies be conducted to better understand the succession of seep communities, how they may influence fisheries, and finally, how they interact with other deep-sea habitats, with the end goal of advancing conservation efforts and limiting anthropogenic effects.

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FIGURES

Table 1. Presence (1) and absence (0) of all species found at sites, from both 2019 and 2021.

Species	Brine Pool	Bush Hill	Fl. Escarpment	Blake Ridge	Baltimore Canyon	Chincoteague
Cnidaria						
Anemone sp.1	0	0	0	1	0	0
Anemone sp.2	0	0	1	0	0	0
Sponge cf. Sycon	0	0	0	0	1	0
Sponge sp.1	0	0	0	0	1	0
Sponge sp.2	0	0	0	0	1	0
Zoanthinaria	1	0	0	0	0	0
Nemertea						
Nemertean sp.1	0	0	0	0	1	0
Annelida						
Sipunculid						
Sipunculid sp.1	0	0	0	1	0	0

Sipunculid sp.2	0	0	0	0	1	0
Sipunculid sp.3	0	1	0	0	0	0
Polychaeta						
Cossura sp.1	0	0	0	1	0	0
<i>Laubierus mucronatus</i>	0	0	1	0	0	0
<i>M. dendrobranchiata</i>	1	0	0	0	0	0
<i>Nereis</i> sp.1	0	0	0	0	0	1
<i>Nicomache</i> sp.1	0	0	0	0	1	0
<i>Nicomache</i> sp.2	0	0	0	1	0	0
<i>Nicomache</i> sp.3	0	0	0	0	0	1
Polychaetae sp.1	0	0	0	0	1	0
Polychaetae sp.2	0	0	0	0	0	1
Polychaeta sp.3	0	0	0	1	0	0
Polychaeta sp.4	0	0	0	0	0	1
Oligochaete						
Oligochaete sp.1	0	0	0	0	1	0
Oligochaete sp.2	0	0	0	0	0	1
Tubeworm sp.1	0	0	0	1	0	0
Mollusca						
Bivalvia						
<i>Bathymodiolus</i> sp.1	1	0	0	0	0	0
<i>Ladella sublevis</i>	0	0	1	0	0	0
Gastropoda						
<i>Fucaria</i> sp.1	0	0	1	0	0	0
Snail sp.1B	0	0	0	0	1	0
Snail sp.2A	0	0	0	1	0	0
Snail sp.2B	0	0	0	1	0	0
Snail sp.3A	0	0	0	0	1	0
<i>Solariella</i> sp.1	0	0	0	0	0	1
<i>Provanna</i> sp.1	0	0	0	0	0	1
Snail sp.5B	0	0	0	0	0	1
Snail sp.6B	0	0	0	0	0	1
<i>Prosiphon</i> sp.1	0	0	1	0	0	0
<i>Provanna</i> sp.2	0	0	1	0	0	0
Snail sp.9B	0	0	0	0	0	1
Snail sp.10B	0	0	1	0	0	0
<i>Mohnia</i> sp.1	1	0	0	0	0	0
Whelk sp.1B	0	0	0	0	1	0
<i>Eosiphon</i> c.f. <i>canetae</i>	1	0	0	0	0	0
Whelk sp.2B	0	0	0	0	0	1
Whelk sp.3A	0	0	1	0	0	0
Whelk sp.3B	0	0	0	0	0	1
<i>Eulapetopsis</i> c.f. <i>vitrea</i>	0	0	1	0	0	0
Polyplacophora						
Chiton sp.1	2	0	0	0	0	0
<i>Leptochiton</i> sp.1	1	0	0	0	0	0
Arthropoda						
<i>Alvinocaris</i> <i>stactophila</i>	0	1	0	0	0	1
<i>Alvinocaris</i> sp.1	0	0	0	1	0	0
<i>Alvinocaris muricola</i>	0	0	0	1	0	0
<i>Alvinocaris williamsi</i>	1	0	0	0	0	0
Amphipod sp.1	0	0	0	1	0	0
Isopoda sp.1	0	0	0	0	1	0
<i>Munidopsis</i> sp.1	1	1	0	0	0	0
<i>Munidopsis</i> sp.2	0	0	0	1	0	0
Shrimp sp.1	1	0	0	0	0	0
Echinodermata						
Asteroidea						
Juvenile steroid sp.1	0	0	0	0	0	1
<i>Sclerasterias tanneri</i>	0	0	1	0	0	0
Ophiuroidea						
<i>Ophiactenella acies</i>	0	0	1	1	0	0
Juvenile ophiuroid sp.1	0	0	1	0	1	1
Holothuroidea						
<i>Chiridota</i> sp.	0	0	1	1	0	0
Sea cucumber sp.1	0	0	1	0	0	0

Table 2. Total species list and counts from 2021.

Species	Brine Pool	FL Escarpment	Blake Ridge	Baltimore Canyon	Chincoteague
Cnidaria					
Sponge cf. <i>Sycon</i>	0	0	0	0	1
Sponge sp.1	0	0	0	0	1
Sponge sp.2	0	0	0	0	5
Nemertea					
Nemertean sp.1	0	0	0	0	1
Annelid					
Sipunculid					
Sipunculid sp.2	0	0	0	0	1
Polychaeta					
<i>Laubierus mucronatus</i>	0	1	0	0	0
<i>M. dendrobranchiata</i>	10	0	0	0	0
Tubeworm sp.1	0	0	1	0	0
Mollusca					
Bivalvia					
<i>Ladella sublevis</i>	0	25	0	0	0
Gastropoda					
Snail sp.1B	0	0	0	0	2
Snail sp.2B	0	0	0	0	9
<i>Solariella</i> sp.1	0	0	0	0	300
<i>Provanna</i> sp.1	0	0	0	0	835
Snail sp.5B	0	0	0	0	346
Snail sp.6B	0	0	0	0	835
<i>Prosiphon</i> sp.1	0	20	0	0	0
<i>Provanna</i> sp.2	0	2000	0	0	0
Snail sp.9B	0	0	0	0	2
Snail sp.10B	0	0	3	0	0

Whelk sp.1B	0	0	0	0	15	0
Whelk sp.2B	0	0	0	0	0	4
Whelk sp.3B	0	0	0	0	0	4
<i>Eulapetopsis</i> c.f. <i>vitrea</i>	0	2603	0	0	0	0
Polyplacophora						
<i>Leptochiton</i> sp.1	4	0	0	0	0	0
Arthropoda						
Amphipod sp.1	0	0	0	80	0	0
<i>Munidopsis</i> sp.1	150	0	0	0	0	0
<i>Munidopsis</i> sp.2	0	0	2	0	0	0
Shrimp sp.1	8	0	0	0	0	0
Echinodermata						
Asteroidea						
Juvenile steroid sp.1	0	0	0	0	0	1
Ophiuroidea						
<i>Ophiactenella acies</i>	0	1268	11	0	0	0
Juvenile ophiuroid sp.1	0	20	0	1	1	3
Holothuroidea						
<i>Chiridota</i> sp.1	0	29	0	0	0	0

Table 3: Presence/absence of species from 2019.

Species	Brine Pool	Bush Hill	FL Escarpment	Blake Ridge	Baltimore Canyon	Chincoteague
Cnidaria						
Anemone sp.1	0	0	0	1	0	0
Anemone sp.2	0	0	1	0	0	0
Zoanthinaria	1	0	0	0	0	0
Annelida						
Sipunculid						
Sipunculid sp.1	0	0	0	1	0	0
Sipunculid sp.2	0	0	0	0	1	0
Sipunculid sp.3	0	1	0	0	0	0
Polychaeta						
<i>M. dendrobranchiata</i>	1	0	0	0	0	0
<i>Cossura</i> sp.1	0	0	0	1	0	0
<i>Macrachaeta clavicornis</i>	0	0	0	0	1	0
<i>Nereis</i> sp.1	0	0	0	0	0	1
<i>Nicomache</i> sp.1	0	0	0	0	1	0
<i>Nicomache</i> sp.2	0	0	0	1	0	0
<i>Nicomache</i> sp.3	0	0	0	0	0	1
Polychaetae sp.1	0	0	0	0	0	1
Polychaetae sp.2	0	0	0	0	0	1
Polychaetae sp.3	0	0	0	1	0	0
Polychaetae sp.4	0	0	0	0	0	1
Oligochaete						
Oligochaete sp.1	0	0	0	0	0	1
Oligochaete sp.2	0	0	0	0	0	1
Mollusca						
Bivalvia						
<i>Bathymodiolus</i> sp.1	1	0	0	0	0	0
Gastropoda						
<i>Fucaria</i> sp.1	0	0	1	0	0	0
Snail sp.2A	0	0	0	1	0	0
Snail sp.3A	0	0	0	0	0	1
<i>Mohnia</i> sp.1	1	0	0	0	0	0
<i>Eosiphon</i> c.f. <i>canetae</i>	1	0	0	0	0	0
Whelk sp.3A	0	0	1	0	0	0
Sea Slug sp.1	0	0	1	0	0	0
Polyplacophora						
Chiton sp.1	1	0	0	0	0	0
<i>Leptochiton</i> sp.1	1	0	0	0	0	0
Arthropoda						
<i>Alvinocaris stactophila</i>	0	1	0	0	0	1
<i>Alvinocaris</i> sp.1	0	0	0	1	0	0
<i>Alvinocaris muricola</i>	0	0	0	1	0	0
<i>Alvinocaris williamsi</i>	1	0	0	0	0	0
Isopoda sp.1	0	0	0	0	0	1
<i>Munidopsis</i> sp.1	1	1	0	0	0	0
Echinodermata						
Asteroidea						
<i>Sclerasterias tanneri</i>	0	0	1	0	0	0
Holothuroidea						
<i>Chiridota</i> sp.1	0	0	0	1	0	0
Sea cucumber sp.1	0	0	0	1	0	0

Table 4: Collection and diversity information for each site sampled in this study, for both 2019 and 2021. Species richness, abundance, and diversity indices do not include the mussel foundation species. The following abbreviations are used: S (species richness), N (number of individuals), d (Margalef's Richness), J' (Pielou's Evenness), and H' (Shannon Weiner Diversity).

Site	Longitude	Latitude	Depth(m)	Foundation species	S	N	d	J'	H'(loge)
Baltimore Canyon	-73.822	38.048	388	<i>G. childressi</i>	9	39	2.184	0.7878	1.731
Blake Ridge	-76.191	32.494	2167	<i>B. heckeriae</i>	4	94	0.6603	0.3741	0.5186
Brine Pool	-91.279	27.723	651	<i>G. childressi</i>	4	172	5828	0.3714	0.5149
Bush Hill	-91.504	27.776	562	<i>G. childressi</i>	-	-	-	-	-
Chincoteague	-74.102	37.541	1028	<i>G. childressi</i>	9	2330	1.032	0.6019	1.322
Florida Escarpment	-84.911	26.028	3287	<i>B. heckeriae</i>	9	5969	0.9201	0.5232	1.15

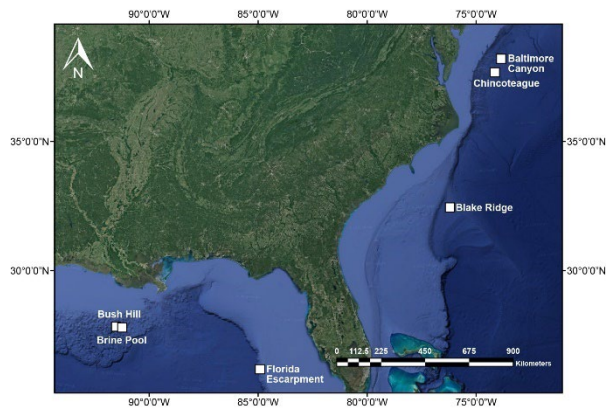


Figure 1: Map of the sites used in this study from both the 2019 and 2021 cruises. A green box indicates the site with the corresponding dive number.

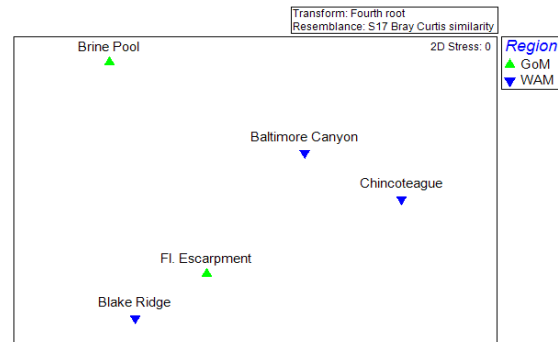


Figure 4: Multidimensional scaling plot of community similarity among mussel associated communities. Similarity is estimated by the Bray-Curtis similarity index based on fourth-root transformed species densities using 2021 data (GoM=Gulf of Mexico; WAM=Western Atlantic margin).

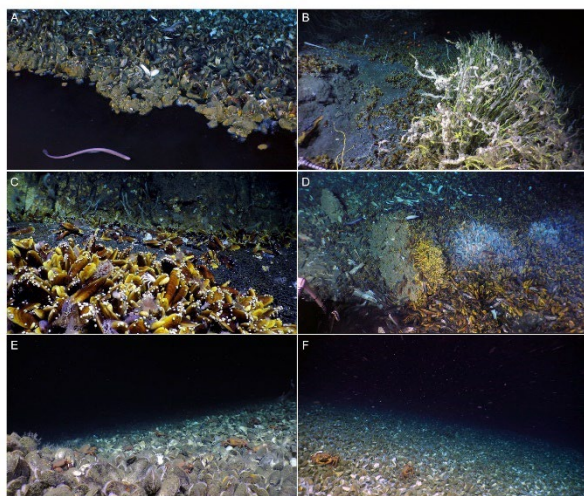


Figure 2: Photographs of each individual site. (A: Brine Pool; B: Bush Hill; C: Florida Escarpment; D: Blake Ridge; E: Chincoteague; F: Baltimore Canyon).

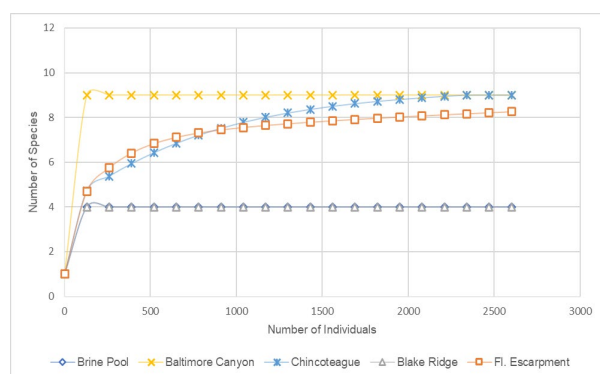


Figure 3: Species accumulation curves for mussel-associated fauna using 2021 data. Note: Brine Pool line is directly underneath Blake Ridge and thus not fully visible.

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