Received: 7 March 2023 | Revised: 15 August 2023 | Accepted: 5 September 2023

DOI: 10.1002/ecs2.4699

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Coastal and Marine Ecology

Deep octopod habitat in the western North Atlantic characterized by Standard Ecological Classification from videos

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Handling Editor: Rochelle D. Seitz

Abstract

Habitat characterization is important to assess fully the niches of different organisms. There is a large knowledge gap regarding habitat use by deep-sea benthic incirrate octopods, partly due to their assumed preference for hard-to-sample rocky substrata. This study uses observations from in situ videos recorded by remotely operated vehicles (ROVs) deployed from the NOAA Ship Okeanos Explorer and implements the Coastal and Marine Ecological Classification Standard (CMECS) to describe the habitat of three common species of bathyal incirrate octopods living in the western North Atlantic Ocean: *Bathypolypus bairdii* (Verrill 1873), *Graneledone verrucosa* (Verrill 1881), and *Muusoctopus johnsonianus* (Allcock, Strugnell, Ruggiero, & Collins 2006). Significant differences in species' preferences for geoform setting, depth, and substrate type were found. All three species are most likely to be observed by ROV in a submarine canyon and least likely to be seen on a seamount. *B. bairdii* was found shallower than *G. verrucosa* and *M. johnsonianus.* This is the first study of its kind using CMECS to classify the habitat of specific organisms as opposed to the habitat types in a specific area.

KEYWORDS

Coastal and Marine Ecological Classification Standard (CMECS), deep sea, habitat characterization, octopus, remotely operated vehicles

INTRODUCTION

The recent advances in remotely operated vehicle (ROV) and other submersible technologies have increased in situ observations of deep-sea organisms (Macreadie et al., 2018). The primary method of studying these deep-dwelling organisms has been collection by trawling, which does not allow detailed observations in their natural environment, and that can damage the specimens in the net. The use of ROVs provides opportunities to make observations on the ecology and life history of deep-sea organisms that were previously impossible.

One such program utilizing ROVs to explore otherwise inaccessible areas is NOAA Ocean Exploration (formerly Office of Ocean Exploration and Research; oceanexplorer.noaa.gov/about/welcome.html). Videos recorded by the ROVs deployed from NOAA Ship Okeanos Explorer have provided information on bathyal incirrate octopods, allowing researchers to compile in situ observations of these understudied organisms. Since 2009, approximately

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90,000 video files recorded by the Deep Discoverer ROV, comprising >2500 h, have been added to a publicly available database. Many of these videos photo-capture organisms in the deep sea (the rest record videos of the environment without any visible organisms present), allowing for detailed observations about habitat and use of resources by the animals. ROV videos have been used to characterize ocean habitats for industrial use, resource use by a particular species, or to investigate the general habitat types in a specific area (e.g., Grabowski et al., 2012; Greene, 2015; Greene et al., 1995).

Deep-sea incirrate octopods comprise a group of organisms that have remained understudied due to their inaccessibility through traditional sampling methods. Incirrate octopods have representatives in both the shallow and deep ocean: many are thought to prefer rocky habitat, based on information from shallow species, which makes them inaccessible to trawls (e.g., Bouth et al., 2011). This has left much to be learned about the deep-sea species beyond the reach of scuba.

Understanding species' habitat preferences can be useful for inferring information about their biology and feeding ecology, designing conservation plans, or planning field studies (e.g., different habitat types require different collection methods). Studies on the preferred habitat of shallow incirrates focus on a few well-studied species (Anderson, 1992; Guerra et al., 2015; Leite et al., 2009). In general, most studies of habitat in the deep sea focus broadly on the habitat available in an area, and not specifically on the requirements of a particular organism. A few studies have focused on habitat use by particular groups, for example, in fishes (Cailliet et al., 1999), nekton (Felley & Vecchione, 1995), cetaceans (Azzellino et al., 2008), and corals (Sanchez et al., 2014).

When characterizing habitat, it is useful to implement a standardized approach to allow comparisons among different studies and geographic areas using the same units of classification. The Coastal and Marine Ecological Classification Standard (CMECS) is a multifaceted hierarchical habitat classification tool created as a universal method for habitat characterization so that different areas can be compared (Federal Geographic Data Committee, 2012). The CMECS has been implemented in intertidal zones of Iran, in the Gulf of Mexico to analyze ecosystem services, and across the entire globe using environmental data from the World Ocean Atlas (Ansari et al., 2014; Carollo et al., 2013; Sayre et al., 2017). The CMECS combines four components to form biotopes, which are habitats determined using both abiotic and biotic factors. The components are Water Column, which considers the characteristics and structure of the water column; Geoform, or the geomorphic structure of the sea floor; Substrate, which is the composition of seabed substrate; and Biotic, which consists of the pelagic or benthic flora and fauna.

In a survey of bathyal incirrate octopods in the western North Atlantic using videos taken by ROVs deployed from NOAA Ship Okeanos Explorer, as well as museum records, *Bathypolypus bairdii* (Verrill 1873), *Graneledone verrucosa* (Verrill 1881), and *Muusoctopus johnsonianus* (Allcock, Strugnell, Ruggiero, & Collins 2006) were the most common species found (Pratt et al., 2021). However, no investigation into the species' biology or ecology was completed. Previous research has illuminated very little about the life history of these octopods. *B. bairdii*, included in past research as *Bathypolypus arcticus* (Muus, 2002), is the only species with documented life history information; growth rates, reproduction, and diet have been investigated in lab studies (Wood, 2000). It showed preferences for crustaceans in laboratory studies, but in a study of wild-caught individuals, 58% of adults had brittle stars in their stomachs (O'Dor & Macalaster, 1983; Wood, 2000). The other two species do not have any habitat information recorded other than that they are deep-sea species. The objective of this study was to assess and compare the habitat preferences of the three most common species of deep-sea incirrate octopods in the western North Atlantic: *B. bairdii*, *G. verrucosa*, and *M. johnsonianus*. For the remainder of the manuscript, reference to octopod refers to the three target species of this study. Using the same videos analyzed by Pratt et al. (2021), CMECS was applied to all observations of these three species.

MATERIALS AND METHODS

The study area for this project was the western North Atlantic Ocean, between 7.5–55° N and 50–98° W and depths >200 m, which were observed during ROV dives. There were 197 ROV dives from NOAA Ship Okeanos Explorer in the study area between 2011 and 2020, with 13 dives on seamounts and the remainder on the continental slope and canyons, comprising >1900 h of seafloor video: these are stored by NOAA as 22,861 video clips of approximately 5 min each.

The NOAA Ship Okeanos Explorer deploys the ROV *Deep Discoverer* in tandem with the camera sled *Seirios* to record HD video and environmental measurements in the deep sea (Kennedy et al., 2019). Video files are publicly available (https://oceanexplorer.noaa.gov/data/access/access.html; Eakins et al., 2019) and can be searched using keywords. Annotated video from expeditions since 2015 can also be viewed and searched using the web-based annotation interface SeaTube hosted by Ocean Networks Canada (https://data.oceannetworks.ca/ExpeditionManagement).

The video portal and SeaTube were searched for keywords and annotations (respectively) containing "octop," which would allow for spelling variants, for example, Octopoda, octopod, and octopus (see Pratt et al., 2021, for more details).

For each ROV video observation of a target octopod, the visible habitat in the vicinity of the octopod was categorized. The CMECS was used to classify different habitat types (Federal Geographic Data Committee, 2012); CMECS components (Water Column, Geoform, Biotic, and Substrate) are further described below. Assignment in each CMECS component varied in specificity because not all levels can be equally determined from ROV video data, for example, the exact grain size of the sediment cannot be determined without a physical sample.

CMECS components

Water Column includes five subcomponents: Layer (which includes depth), Salinity, Temperature, Hydroform, and Biogeochemical feature. Values for the Layer (with a benthic modification provided in CMECS since the default layer classification describes the pelagic layer), Salinity, and Temperature subcomponents were recorded. These data were derived from the ROV CTD sensor files for each expedition, downloaded from the NOAA Digital Atlas (https://oceanexplorer.noaa.gov/data/access/digital-atlas/digital-atlas.html). The CTD files were converted into a readable format using the program SBEDataProcessing-Win32 and the data matched to each video. For the Layer subcomponent, the depth categories provided by CMECS that are applicable in this study include Mesobenthic (200–1000 m) and Bathybenthic (1000–4000 m). This was further subdivided using classifiers from UNESCO (2009) consisting of mesobenthic (200–300 m), upper bathyal (300–800 m), and lower bathyal (800–3000 m). To test for a significant relationship between depth and observations of octopod species, a Kruskal–Wallis test (data did not meet normality assumption for ANOVA testing) compared the mean depth of occurrence across *G. verrucosa*, *B. bairdii*, and *M. johnsonianus*; Dunn's test with a Bonferroni correction was conducted for pairwise comparisons. To assign a zone for each species, the CMECS terms for benthic depth zones were applied to the mean depth of observation. Similar analyses were conducted to determine preferences in temperature and salinity.

The Geoform component consists of four subcomponents: Tectonic Setting, Physiographic Setting, and Level 1 and Level 2 Geoform (features at a scale of meters, such as sandbars, boulder fields, or caves). When possible, all these subcomponents were used, except Level 2 (which characterizes small-scale features such as pockmarks or caves), plus the Geoform modifiers rugosity and slope. Because the Geoform component has a hierarchical structure, habitats were grouped together based on uniqueness at the lowest level of classification present. For example, "Passive Continental Margin: Continental Slope" is referred to as continental slope, "Passive Continental Margin: Submarine Canyon" as submarine canyon, and "Abyssal Plain: Marine Basin Floor with a Level 1 Seamount" as seamount. The number of individuals that were found in each habitat type was counted. In addition, the Geoform settings of all ROV dives deployed from the Okeanos Explorer in the study area were characterized. To test for a significant relationship between octopod species and Geoform setting, Mann–Whitney *U* tests (normality assumptions were not met for *t* tests) on the mean number of individuals seen per dive on each setting were run. In addition, Kruskal–Wallis tests and Dunn's tests with a Bonferroni correction were used to test differences within Geoform setting among species. In addition, rugosity and slope were characterized in each video. Rugosity values are defined as the ratio of total surface area to flat planar area: very low is 1–<1.25, low is 1.25–<1.5, moderate is 1.5–<1.75, high is 1.75–<2.0, and very high is ≥2.0 (Federal Geographic Data Committee, 2012). Values for slope were defined as flat (0–<5°), sloping (5–<30°), steeply sloping (30–<60°), vertical (60–<90°), and overhang (≥90°). Although both rugosity and slope for each observation were characterized, the sample sizes in each category were too low for statistical testing.

Within the Biotic component, a hierarchy of classification was used for each habitat: Setting, Class, Subclass (these are not equivalent to the biological taxonomic categories Class and Subclass), and Group. For example, an area's Biotic component could consist of Setting: Benthic/Attached; Class: Faunal Bed; Subclass: Attached Fauna; and Group: Attached Corals. The most abundant slow-moving or sessile organisms in the area determine the classification assigned to that video frame; slow-moving is defined as not possessing the ability to move out of the area in 24 h. Any other organisms present that may be of importance but are either not the most abundant taxon or are motile, such as a fish, can be recorded as co-occurring elements in the component. No statistical testing was done on this component as the ability to characterize the other biota in the videos was inconsistent, due to lack of other organisms visible in the video.

For characterizing the Substrate component, the CMECS substrate component induration modifier (hard, mixed, soft) was applied as it was difficult to assess the origin of the substrate (Biogenic, Geologic, Anthropogenic), except in one case of obvious anthropogenic origin, a shipwreck; the origin of the substrate is the first level of the substrate hierarchy, and the inability to classify that renders it useless for our analyses. Substrate type was determined by a visual assessment of the kind of substrate that was present in the frame of the video clip in which the octopod was observed (Figure 1). The mixed label was used in cases where there was more than one type of substrate in the video frame. A χ^2 test was conducted to determine significant association between substrate type and species (all assumptions were met).

To test whether all habitat types were considered equally, a χ^2 test was conducted comparing the number of dives on the continental slope and in submarine canyons.

All statistics and graphs were completed in R (R Core Team, 2019). Mosaic plots were built using the "vcd" package and box plots, histograms, and bar graphs were made using "ggplot2" (Meyer et al., 2020; Wickham, 2016). χ^2 tests, Kruskal–Wallis, and Mann–Whitney *U* tests were conducted with the base packages in R. Dunn's tests were conducted with the "FSA" package.

Independently of any CMECS component, the proximity of the three different species to one another was assessed. For example, when one or more *B. bairdii* were seen, the presence of any other species was also noted. Each ROV dive was used as a transect (a typical ROV Deep Discoverer dive transits 600–1000 m distance) and the presence of more than one species observed during a single dive was noted.

RESULTS

ROV dives encompassed most of the study area latitudinally but were mostly aggregated along the continental slope (Figure 2); among the 197 ROV dives, only 13 were focused on seamounts. One hundred and eight *G. verrucosa*, 25 *B. bairdii*, and 19 *M. johnsonianus* were observed across the study area. Due to some environmental data not being recorded for certain observations, fewer observations than the total found were included in the statistical analyses (Table 1). While the study area encompassed the entire western North Atlantic, including the Gulf of Mexico and Caribbean, octopods of the three species of interest were only found off the eastern coast of the United States, in the northern half of the study area (Figure 3).

All observed incirrate octopod individuals were seen in waters classified under CMECS as euhaline. A Kruskal–Wallis test for significant difference in the mean salinity across species yielded significant results ($p < 0.001$). The Dunn's test with a Bonferroni correction indicated that there were significant differences between the mean salinity of *M. johnsonianus* and both other species (*B. bairdii*: $p < 0.001$; *G. verrucosa*: $p = 0.0062$), but not between *G. verrucosa* and *B. bairdii* ($p = 0.1098$).

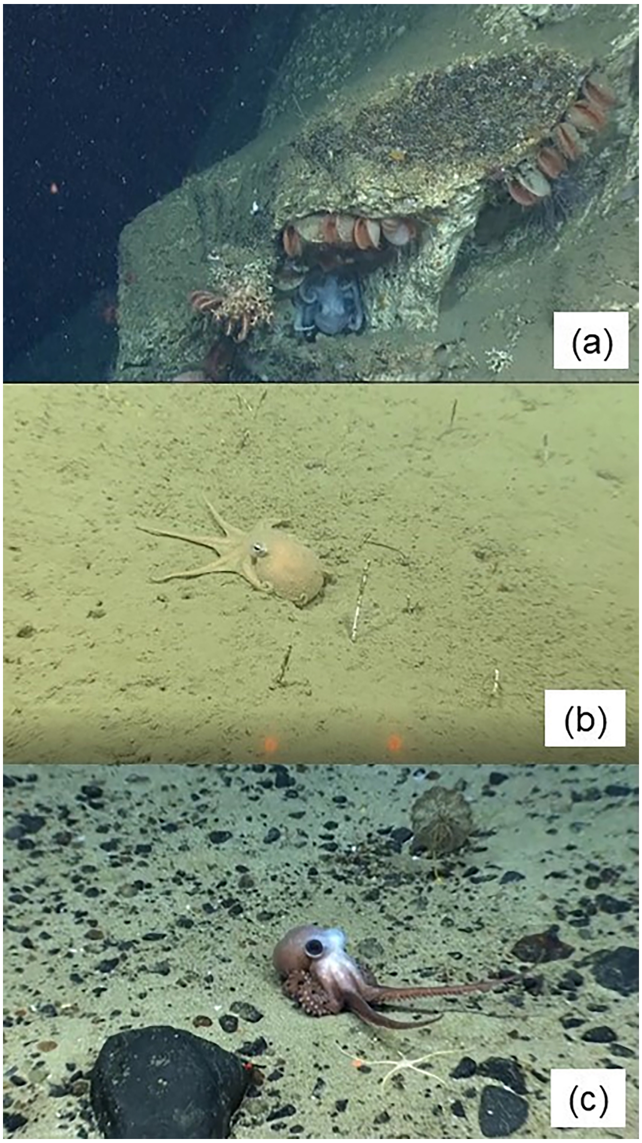

FIGURE 1 Screengrabs from remotely operated vehicle (ROV) videos showing the three octopod species on different substrate types. (a) *Graneledone verrucosa* on hard substrate. Recorded in a submarine canyon off the coast of Massachusetts, USA. Video by NOAA Ocean Exploration from Okeanos Explorer cruise EX1304L2, Northeast U.S. Canyons Expedition 2013; (b) *Bathypolypus bairdii* on soft sediment. Video by NOAA Ocean Exploration from Okeanos Explorer cruise EX1302, 2013 ROV Shakedown and Field Trials in the U.S. Atlantic Canyons; (c) *Muusoctopus johnsonianus* on mixed substrate. Recorded on Physalia Seamount off the coast of Massachusetts, USA. Video by NOAA Ocean Exploration from Okeanos Explorer cruise EX1404L3, Atlantic Canyons and Seamounts Expedition 2014.

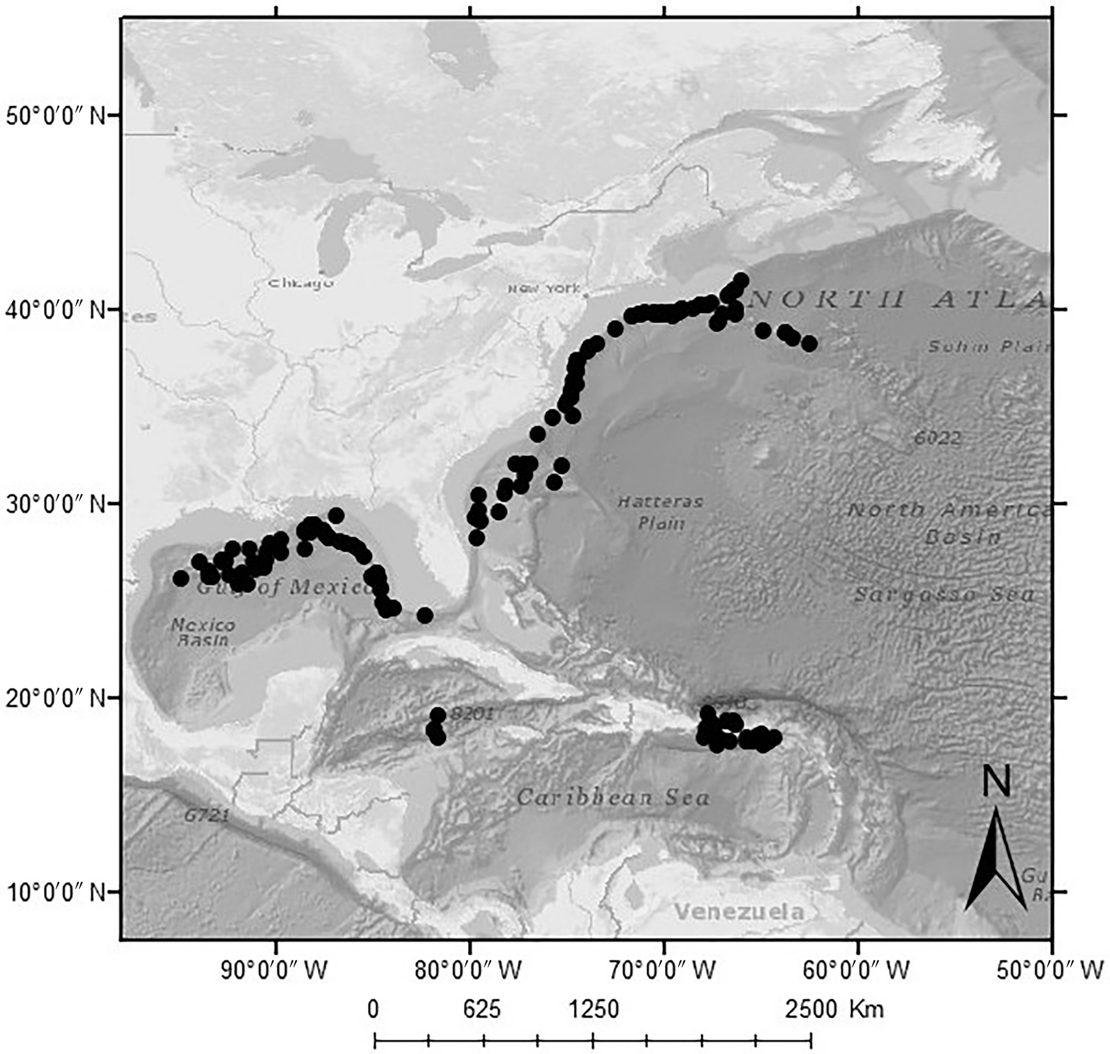

FIGURE 2 Distribution of remotely operated vehicle dives (with and without octopod observations) in the study area.

TABLE 1 Numbers of octopod observations from remotely operated vehicle (ROV) videos used for the different statistical analyses.

	CMECS component		
Species	**Water column**	**Geoform**	**Substrate**
Bathypolypus bairdii	21	22	21
Graneledone verrucosa	77	97	88
Muusoctopus johnsonianus	19	19	19

Note: Due to a lack of environmental data associated with certain observations, not all individuals seen were included in statistical analyses; this affected mostly *G. verrucosa*, for which there were 108 total observations.

Abbreviation: CMECS, Coastal and Marine Ecological Classification Standard.

Most *G. verrucosa* and all *M. johnsonianus* individuals were found in the lower bathyal, whereas most *B. bairdii* were seen in the upper bathyal (Figure 4a). Kruskal–Wallis testing of the relationship between species and depth yielded significant results ($p < 0.001$). The Dunn's test with a Bonferroni correction indicated that the differences within all species pairs were statistically significant (all $p < 0.001$). The temperature subcomponent correlated with the layer subcomponent, as expected, with most *G. verrucosa* and all *M. johnsonianus* found in deeper, "very cold" waters (0–<5°C), and most *B. bairdii* found in shallower, "cold" (5–<10°C) waters (Figure 3b). Kruskal–Wallis testing of the differences in mean temperature across species yielded significant results ($p < 0.001$). The Dunn's test with Bonferroni correction indicated significant differences among all species pairs ($p < 0.001$).

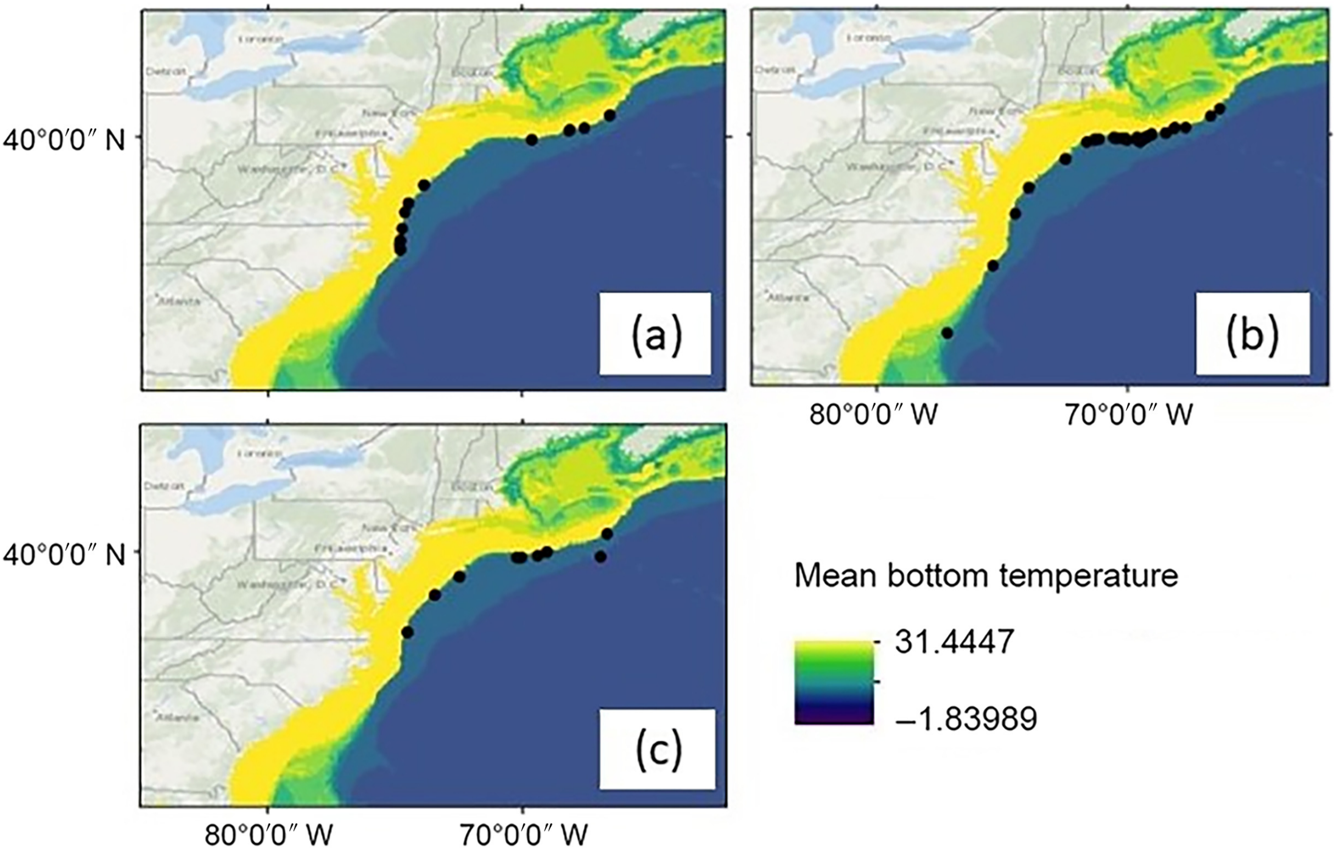

FIGURE 3 Distribution of octopods included in statistical analyses. (a) *Bathypolypus bairdii*, (b) *Graneledone verrucosa*, and (c) *Muusoctopus johnsonianus*.

Across the three species tested, the most frequent Geoform setting in which individuals were observed was submarine canyons, followed by the non-canyon continental slope (henceforth referred to as continental slope), despite there being significantly ($p = 0.002$) fewer dives in submarine canyons (60) than on the continental slope (100). Incirrate octopods were observed in 44.8% of canyon dives, but only 14.0% of dives on continental slopes, suggesting one is more likely to see an octopod of any species when the ROV is diving in a submarine canyon. The Kruskal–Wallis tests within Geoform component found significant differences between the mean number of individuals of all species per dive within submarine canyon dives versus continental slope dives ($p < 0.001$ and $p = 0.38$, respectively). At the species level, *G. verrucosa* and *M. johnsonianus* were observed significantly more often on dives in submarine canyons than on the continental slope (Mann–Whitney U: $p < 0.001$ and $p = 0.0289$), whereas *B. bairdii* did not show a significant difference ($p = 0.2512$) (Figure 5). Considering only submarine canyon dives, the Dunn test showed significantly higher mean numbers of individuals observed of *G. verrucosa* versus either *B. bairdii* ($p < 0.001$) or *M. johnsonianus* ($p < 0.001$), and no difference between *B. bairdii* and *M. johnsonianus* ($p = 1.0$). Only a single individual octopod of any species, a *M. johnsonianus*, was observed on a seamount, out of 13 dives on seamounts. Nonseamount dives deeper than 550 m (there is no habitat shallower than this in the New England Seamounts, where these dives occurred) have an average of 0.636 octopods per dive, while dives on seamounts have an average of 0.0769 observations per dive. As for rugosity, most individuals in all species were seen in low rugosity habitat. For slope, most individuals were seen in steep slope or overhang environments.

A Pearson's χ^2 test of substrate preference indicated significant differences between the numbers of each species seen on each substrate type ($p < 0.001$). *G. verrucosa* were found evenly across hard and mixed substrates, but rarely on soft sediment; *M. johnsonianus* on a fairly even mix of hard, mixed, and soft substrates; and *B. bairdii* were most often found on soft sediment, never on hard, and only three times on mixed substrates (Figure 6).

We were only able to classify a Biotic component for 89 of the videos (53%). The other videos had no other visible organisms present in the frame; this occurred most often in soft-sediment areas. The most common organisms seen regardless of the octopod

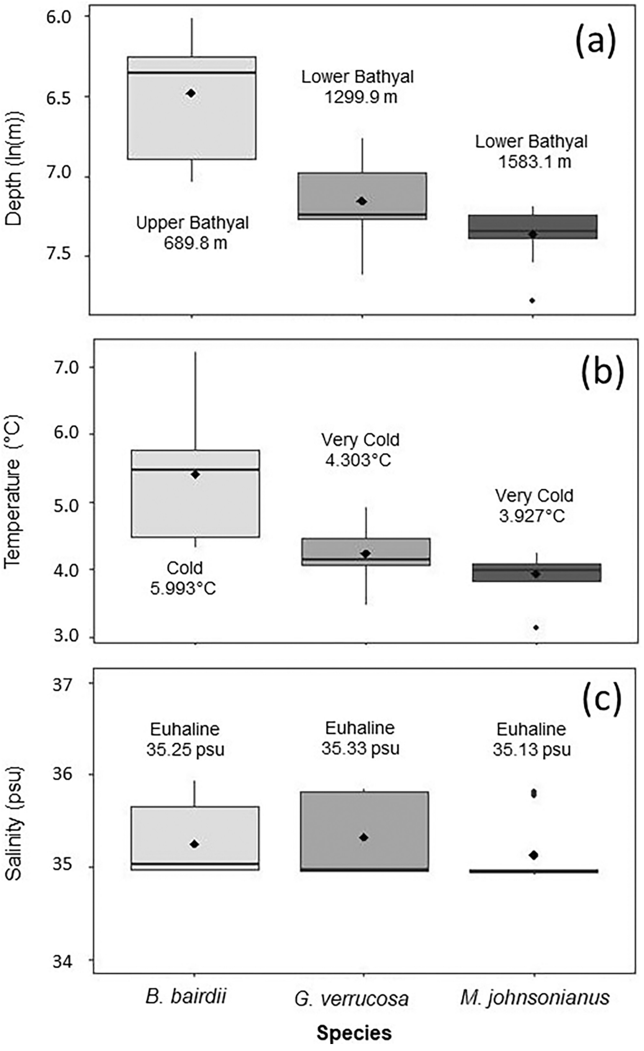

FIGURE 4 Boxplots depicting the association of specific species with different aspects of the Water Column component. (a) Depth showing mean depth of *G. verrucosa* and *M. johnsonianus* in the lower bathyal and *B. bairdii* in the upper bathyal. (b) Temperature, showing *G. verrucosa* and *M. johnsonianus* inhabit water considered "Very Cold" and *B. bairdii* in water considered "Cold." (c) Salinity, in which all species live in euhaline waters. The *M. johnsonianus* outliers for both depth and temperature are from the same observation, recorded on a seamount. The black diamond in the boxplot represents the mean of each sample. The box limits represent the first and third quartiles with the median as the midline. The whiskers are the minimum and maximum values that do not exceed 1.5 times the interquartile range. The outliers in the *M. johnsonianus* represent two single observations.

species observed were mussels, which were seen in hydrocarbon-seep areas, or brittle stars on soft sediment and attached corals and/or bivalves (distinct from the mussel species on soft sediment, typically *Acesta* sp.) on hard substrate.

In addition to the CMECS components, many brooding individuals of both *G. verrucosa* and *M. johnsonianus* were noted. Out of 119 *G. verrucosa* individuals, 20 were brooding females, 24 were unconfirmed, and 75 were not brooding. All brooding individuals of both *G. verrucosa* and *M. johnsonianus* were seen on hard substrate, and on some dives, both species inhabited dens near each other (e.g., seen in the same 5-min video clip) (Figure 7). In one video, at least six total individuals of *G. verrucosa* and *M. johnsonianus* were seen next to each other, each in its own den, on a vertical wall.

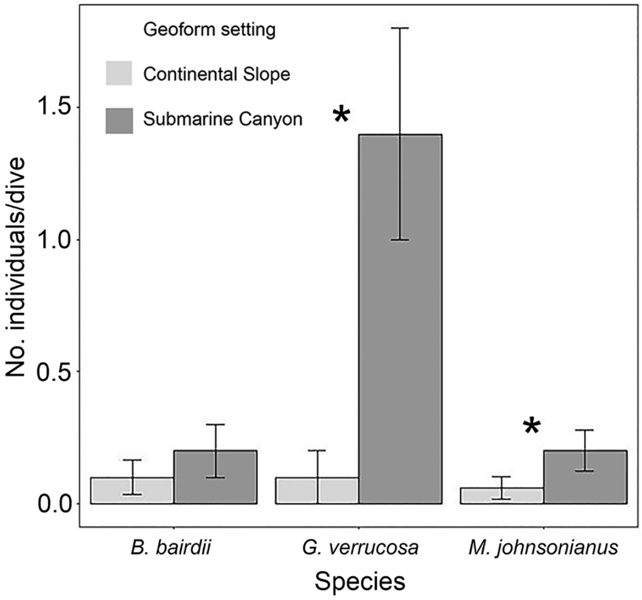

FIGURE 5 Results of the Mann–Whitney *U* test of Geoform preference for three octopod species (within species between habitat type). The bars represent the mean numbers of individuals per species seen on a remotely operated vehicle dive in general continental slope habitat or in a submarine canyon, with error bars indicating SE. Seamount habitat has not been included because only a single octopod was observed. Asterisks indicate significant differences between Geoform components within species.

There were some differences in the octopod species observed in each dive, independent of the CMECS components. When *B. bairdii* was observed, a different species was seen (*G. verrucosa*) during only one dive. During dives where *G. verrucosa* was observed, typically no other octopod species were seen. However, in five of the seven dives where *M. johnsonianus* was seen, *G. verrucosa* was also present.

DISCUSSION

We examined the habitat preferences of three common species of deep-sea incirrate octopods in the western North Atlantic by applying standardized habitat classifications to ROV videos showing octopods in situ. The

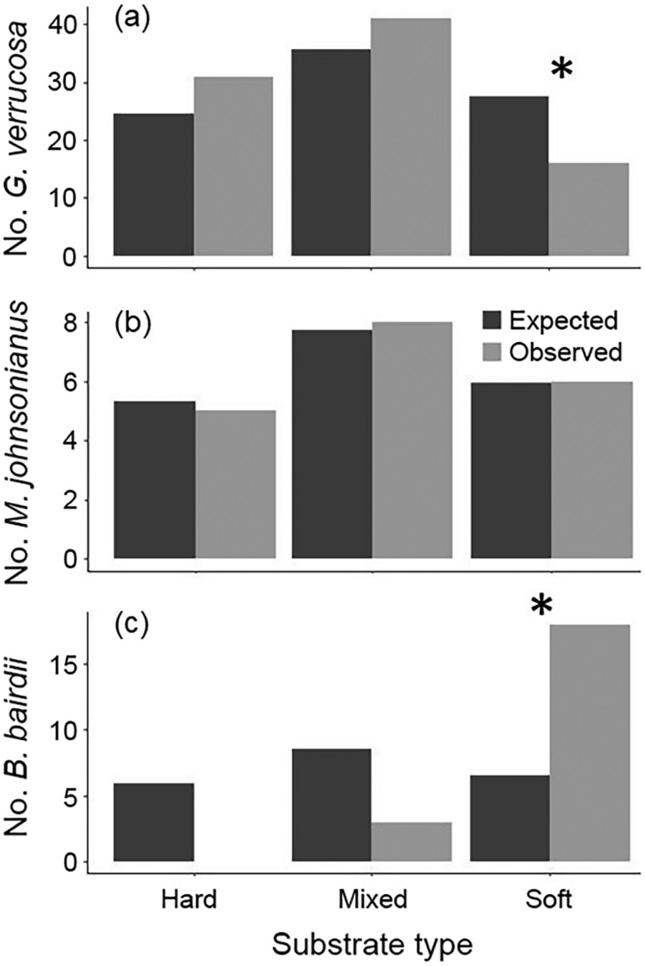

FIGURE 6 The relationship between substrate and species, with dark gray representing expected species counts and light gray representing observed values. Expected values are based on a contingency table. Asterisks represent a significant departure from expected values. (a) *Graneledone verrucosa* was found significantly less than expected on soft sediment. (b) *Muusoctopus johnsonianus* species counts were no different than expected. (c) *Bathypolypus bairdii* was found significantly more than expected on soft sediment.

most important characteristics differentiating species' habitat were depth (and the related variable, temperature), geoform setting (e.g., canyon vs. non-canyon), and substrate type. *G. verrucosa* prefers very cold, lower bathyal waters and hard or mixed substrate located in submarine canyons. Likewise, *M. johnsonianus* prefers very cold, lower bathyal waters in submarine canyons, but is as likely to be seen on one substrate or the other. *B. bairdii* has a shallower average depth in the upper bathyal, with a preference for soft sediment and no preference for Geoform setting. A deeper look into the ROV videos is needed to determine whether this is a true preference or there is simply more soft sediment available in shallower waters. It was not within the scope of this study to assess bottom type in all videos where an octopod was not observed as substrate has not been annotated on a regular and consistent basis, for example, it would require watching all 1905 h of video rather than a search of the metadata. However, the lack of any observations of *B. bairdii* on hard substrate, whereas hard substrate was encountered within its documented depth range, argues for a distributional preference for soft substrate. One caveat to our results is the effect on species observations of local disturbance caused by the ROV, which could potentially startle individuals to move to habitats outside of their preferred realm.

Differences in habitat preference affected the co-occurrence of the species. On dives where *B. bairdii* was seen, in only a single instance was a second species of octopod also observed (*G. verrucosa*), which reflects the difference in temperature, substrate, and depth preference of the species analyzed in this study. In contrast, on five of the seven dives where *M. johnsonianus* was seen, *G. verrucosa* was also present. One possible reason for this may be a shared brooding habitat. *Graneledone* and *Muusoctopus* (at the time of the publication of the cited research, referred to as *Benthoctopus*) have been recorded brooding adjacent to each other, possibly due to the restricted availability of hard substrate to attach their eggs (Voight & Grehan, 2000). In addition, the depth ranges of *M. johnsonianus* and *G. verrucosa* overlap more with each other than either one does with *B. bairdii*, allowing for a higher chance of co-occurrence.

We observed many brooding females in the ROV videos, which may affect the interpretation of habitat preference as females may seek a different type of habitat for brooding than they do for the earlier portion of their life. Brooding and nonbrooding individuals were observed somewhat close in proximity geographically, with the same type of habitat available to both groups. This behavior—sitting in one location protecting their eggs—makes them more likely to be seen by the ROV because they are less willing to move out of the ROV's path. Aggregations of brooding bathyal octopods have recently been documented off the coast of California, likely associated with seeping hydrothermal fluids (Drazen et al., 2003; King & Brown, 2019). While the numbers of brooding individuals reported here were not as high as those in the Pacific, nor were there any indication of hydrothermal fluids, these observations show that clusters of brooding female octopods are not uncommon in the deep sea and are likely driven by the availability of suitable habitat. Moreover, the Pacific brooding aggregations were of single species (*Graneledone* sp. in 2003 and *Muusoctopus* sp. in 2018), while our Atlantic video aggregations show both *G. verrucosa* and *M. johnsonianus* brooding near to each other. No brooding *B. bairdii* was observed.

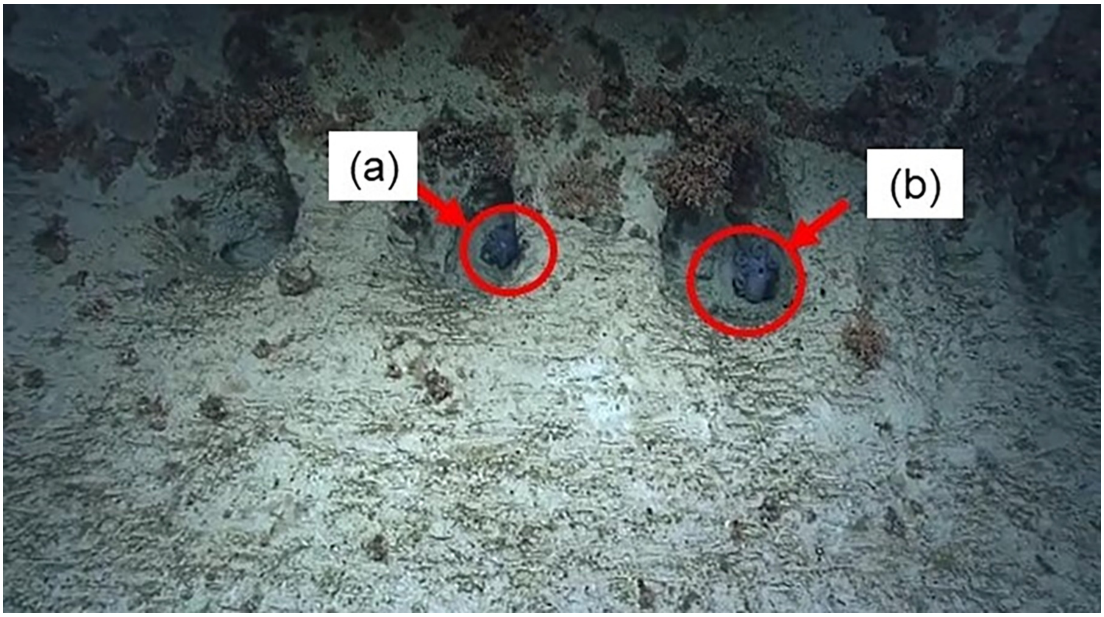

FIGURE 7 Screengrab from a remotely operated vehicle video showing a *Muusoctopus johnsonianus* and a *Graneledone verrucosa* brooding eggs in dens directly adjacent to one another. Recorded on the continental slope off the coast of New York, USA. Video by NOAA Ocean Exploration from Okeanos Explorer cruise EX1404L3, Atlantic Canyons, and Seamounts Expedition 2014.

Our statistical analysis of Geoform preference was restricted to comparing submarine canyon and continental slope dives as only a single individual among the three target species, *M. johnsonianus*, was seen on a seamount. If the frequency of octopod observations on seamounts was similar to that of nonseamount dives, approximately eight observations from seamounts would be expected. Octopods may be more prevalent in submarine canyons because canyons exhibit high habitat heterogeneity, which has been hypothesized to increase biodiversity and biomass (De Leo et al., 2012, 2014; Levin et al., 2010). Canyons have both hard and soft substrates, can act as a sink for organic particulates, and have enhanced current flow-through (De Leo et al., 2012, 2014; Levin et al., 2010). Submarine canyons have been identified as potential vulnerable marine ecosystems by the United Nations Food and Agricultural Organization (FAO) (Auster et al., 2011). In addition to higher levels of sediment and organic particulates, increased amounts of marine litter have been found in canyons (Figure 8) (Pham et al., 2014). Further anthropogenic sources of exploitation include fishing, mining, and oil extraction (Fernandez-Arcaya et al., 2017). The preference of *G. verrucosa* for canyons, particularly as nursery sites, could lead to vulnerability in their populations.

The observations for this study were biased toward continental slope and canyon habitats: of the 197 ROV dives from Okeanos Explorer in the study area from 2011 to 2019, only 13 dives were focused on seamounts. However, additional ROV dives in the western North Atlantic, conducted after our data collection and analyses were completed, reinforce the paucity of octopod observations in ROV video on seamounts. A brief survey of SeaTube video annotations from 19 ROV dives at seamounts during the 2021 North Atlantic Stepping Stones: New England and Corner Rise Seamounts expedition (EX2104) revealed only a single octopod (the cirrate, *Cirrothauma magna*). Similarly, across 14 ROV dives during the 2022 Voyage to the Ridge expedition (EX2205 and EX2206) to the Mid-Atlantic Ridge, there was only a single octopod observation (the incirrate, *Muusoctopus januarii*).

The depths explored during ROV dives on seamounts likely played a strong role in observations of our target species. The average maximum depth of dives on seamounts was 2761 m and ranged from 1303 to 4689 m. With respect to *B. bairdii*, the seamount dives explored depths deeper than their preferred depth range (Figure 3). The observed depth ranges of the other two species do overlap with the maximum-depth range of seamount dives, although most dives were deeper than the depth range of these species. The paucity of observations on seamounts may also reflect dispersal constraints across the very deep seafloor connecting the seamounts. With limited swimming ability, the physiological depth range of our species may preclude crawling between seamounts. They all have “crawl-away” hatchlings, rather than pelagic paralarvae, so the journey to a seamount would be impossible if they needed to cross seafloor deeper than the species’ physiological limit. Studies on

FIGURE 8 Screengrab from a remotely operated vehicle (ROV) video showing an octopod on a seafloor of low rugosity. In this case, a *Graneledone verrucosa* is using the only available shelter in the frame. Recorded at 1425 m on the continental slope off the coast of New York, USA. Video by NOAA Ocean Exploration from Okeanos Explorer cruise EX1304L1, Northeast U.S. Canyons Expedition 2013.

seamounts using different sampling methods show octopods are there. Shea et al. (2017) used trawling to explore cephalopod diversity on Bear Seamount and collected individuals of *G. verrucosa*, *Pteroctopus tetracirrhus*, and *Muusoctopus* spp. As the number of ROV dives on seamounts throughout the North Atlantic increases, exploring the full range of depths, we expect that an increased number of benthic incirrate octopod observations will be recorded, allowing for a more diverse sampling of geoform types and a more reliable comparison of geoform preference across species in offshore areas.

While the biotic component was not characterized consistently enough to conduct any statistical analyses, many of the species seen near octopod observations were simply common deep-sea species. A possible reason for seep mussels as one of the dominant soft-sediment organisms is that in many videos of soft-sediment habitat, no biotic component was visible, leading to heavily weighting seep habitats where mussels dominated. We hypothesized that the biotic component is related to the habitat type and has no direct control on octopod distributions.

All three species examined here have been shown to exhibit preferences in at least some CMECS components. Further observations are needed to test whether the habitat preferences for each species are consistent throughout their ranges, or whether each species prefers different habitat types in different parts of their ranges. Two of these species, *G. verrucosa* and *M. johnsonianus*, have geographic ranges that span the western and eastern Atlantic (Norman et al., 2016), and one of us (MV) has collected *B. bairdii* from the Barents Sea off Norway. This is perhaps surprising for *G. verrucosa* and *M. johnsonianus* as these species have large eggs suggestive of the lack of a planktonic larval stage, which usually correlates with a smaller geographic range (Villanueva et al., 2016). Published observations of these species in the few eastern Atlantic canyon biodiversity studies available do not exist (e.g., Appah et al., 2020; Davies et al., 2014). The previously discussed lack of observations from seamounts is important to note because if these species are indeed living across the entire North Atlantic, it would make sense that they would utilize the rare available hard substrates that these seamounts provide at bathyal depths across the central North Atlantic basin, at least for *G. verrucosa*, which prefers the hard substrate. Seamounts could provide habitat islands that individuals could use as stepping-stones across the Atlantic. One individual of *G. verrucosa* was observed on Bear Seamount, collected via trawling (Shea et al., 2017), but whether this represents the use of seamounts as stepping-stones across the Atlantic remains to be seen, as Bear Seamount is the most nearshore seamount in the New England Seamount chain and located on the continental slope. *M. johnsonianus* shows the most promise of using the seamounts, as there are two reported observations of this species from the Mid-Atlantic Ridge, the seamount observation from the present study, and two potential seamount observations identified only as *Muusoctopus* sp. from Bear Seamount (Richards & Vecchione, 2020; Shea et al., 2017; Vecchione et al., 2010).

Many octopod observations came from areas where seafloor rugosity was very low or low. Nonetheless, usually there were still places present to provide protection for the octopod. In 61.5% of observations in areas of very low or low rugosity, at least one feature provided, or could potentially provide, shelter. In many cases, the octopod seen in the video clip was associated with the only shelter within the entire video frame; therefore, the availability of structure for shelter could be a controlling factor for the distribution and abundance of the target octopod species (Figure 8). One explanation for the higher number of observations in less rugose habitats is that in areas with high rugosity, which would have more places to hide, octopods may be harder to see.

Although salinity preference showed statistical differences among species, all values were close to 35 psu and these differences may not be biologically meaningful. Instead, the differences more likely reflect the narrow depth range and associated narrow salinity range, where *M. johnsonianus* was observed. The relatively few observations of *M. johnsonianus* were mostly restricted to its narrowest depth range among these species (except for a single deep outlier), which in turn results in low variability in temperature and salinity (Figure 3).

Habitat preference may affect our knowledge of these species via its impact on sampling. In the ROV videos, *G. verrucosa* was more common than *B. bairdii* (85 and 15 individuals, respectively), but Pratt et al. (2021) found the opposite pattern in an examination of museum collections from the same area (38 *G. verrucosa* and 229 *B. bairdii*). Note that many of the *B. bairdii* museum specimens are cataloged as *Bathypolypus arcticus* due to a long-term taxonomic confusion; Muus (2002) determined that *B. arcticus* has a true arctic distribution and, therefore, all individuals in our study area should be considered *B. bairdii*. It is likely that greater numbers of *B. bairdii* in museum collections reflect their preference for soft sediment and shallower depth distribution, which makes them more susceptible to trawl collection; trawling for deep-sea fauna on hard substrates is quite challenging and therefore done less frequently. Depth preference may also affect collections; trawling deeper costs more, and so is less frequently conducted. Among the museum collections reviewed by Pratt et al. (2021), the deepest recorded specimen from the study area came from 1079-m depth. In our analysis of the ROV video data, *M. johnsonianus* preferred greater depths than this and thus would be (and probably was) missed or under-sampled in these museum collections.

This study has increased our knowledge of deep-sea incirrate octopods and their habitat preferences and may be the first use of CMECS for the characterization of habitat use by specific species, certainly in the deep sea. Past studies have mainly been focused on investigating different habitat types available in a specific area, including classifying coastal habitats in the Caspian Sea (Hoseinzadeh et al., 2016) and connecting habitat types with ecosystem services in the Gulf of Mexico (Carollo et al., 2013). Without studies such as these, the potential vulnerability of *G. verrucosa* due to its preference for canyon habitat would not have been identified. While the increase in baseline knowledge and potential vulnerabilities of these octopods is important, we believe that the highlighting of a new application of the CMECS scheme could have more important ramifications. CMECS is increasingly being used in the live annotations of ROV videos from the Okeanos Explorer program. This will benefit researchers by providing a standard classification associated with the videos in which the species observations are made.

ACKNOWLEDGMENTS

The first author would like to thank the other members of the France laboratory at UL Lafayette: L. Walling, J. Awbrey, and U. Ganguly for ideas and troubleshooting, and Dr. Mark Genung for his assistance with statistical analyses. The Invertebrate Zoology Department at the Smithsonian Institution's National Museum of Natural History and Nancy Voss (recently deceased) at the University of Miami Marine Invertebrate Museum allowed access to their respective collections. This study would not have been possible without the NOAA Ocean Exploration Program and the National Centers for Environmental Information, particularly Mashkoor Malik for help downloading and converting ROV CTD files, and the crew of the NOAA Ship Okeanos Explorer and ROV team from the Global Foundation for Ocean Exploration (GFOE).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available as follows: Video Portal: https://oceanexplorer.noaa.gov/data/access/access.html, search for "octop" in the keywords field and filter area to within 7.5–55° N and 50–98° W. SeaTube: https://data.oceannetworks.ca/ExpeditionManagement, under the Expeditions tab on the left-hand side, select expeditions of choice (by year), and search for "octop" in the annotations. CTD Data: https://oceanexplorer.noaa.gov/data/access/digital-atlas/digital-atlas.html, download files for each cruise/dive applicable.

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How to cite this article: Pratt, Abigail, Scott C. France, and Michael Vecchione. 2023. "Deep Octopod Habitat in the Western North Atlantic Characterized by Standard Ecological Classification from Videos." *Ecosphere* 14(12): e4699. https://doi.org/10.1002/ecs2.4699