



Biogeographic and bathymetric patterns of benthic molluscs in the Gulf of Mexico

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ABSTRACT

The Biodiversity of the Gulf of Mexico (BioGoMx) database, which contains occurrence information of extant species in the Gulf of Mexico (GOM), allows for the analysis of benthic mollusc diversity and distribution across the entire basin. For analyses, the GOM was split in 4 geographic sectors (NE, NW, SE, and SW) and 6 depth classes (inshore, upper shelf, lower shelf, upper slope, lower slope, and abyssal plain) for a total of 24 geographic-depth polygons. The northern GOM contained higher species richness than the south, the east more than the west. Species richness decreased with depth with maxima occurring on the upper shelf. Bivalves and gastropods dominated each geographic sector and depth class, together comprising >90% of the molluscan species richness. Assemblages were structured by depth more than by geographic sector. GOM molluscs fell into 3 broad depth-based assemblages: the inshore and continental shelf, the continental slope, and the abyssal plain species combined with the western lower slope. Geographically, taxonomic distinctness analysis indicated most NE depths fell below average distinctness and by depth polygons above and below the continental shelf break were frequently distinct. Cluster analysis based on taxonomic dissimilarity agreed with the analyses based on the species occurrence data. Mollusc feeding strategies largely followed estimated proportions for the larger Atlantic. Carnivory and suspension feeding were the most common with grazing, herbivory, and parasitism following behind. Chemosymbiotic species were also prevalent due to the widespread occurrence of cold seep habitats. Further taxonomic research and more sampling are needed to determine patterns at finer scales.

1. Introduction

Molluscs have served as a model for observing benthic diversity patterns for decades (Fischer, 1960; Stehli et al., 1967; Schopf, 1970), due in part to Mollusca being one of the largest of the marine animal phyla. At around 113,600 extant species and eight major lineages, molluscs comprise about 23% of all named marine organisms (Rosenberg, 2014; Vinther, 2015). Not only are they taxonomically rich, but they also exhibit a wide variety of functional strategies. Molluscs can be sessile, motile, infaunal, nektonic, and planktonic; they can be carnivores, scavengers, herbivores, grazers, photosymbiotic, chemosymbiotic, and suspension feeders (Skelton, 1978). Ecologically, molluscs act as biofoulers and ecosystem invaders, but also serve important roles in ecosystem function and as sentinels of ecosystem integrity. Moreover, they have long been employed as model taxon for characterizing large diversity patterns across global geographic and bathymetric gradients (Rex, 1977; Rex et al., 1993, 2005a).

Recently, it has become clear that there are more spatial gradients

than previously expected for molluscs (Roy et al., 1994, 1998; Flessa and Jablonski, 1995; Crame 2000a,b; Oliverio, 2003; Valdovinos et al., 2003; Rex et al., 2005a), particularly notable is the inter-regional variation on multiple spatial scales (Rex et al., 2005a). One regional basin that may have finer-scale variation in molluscan assemblages is the Gulf of Mexico (GOM). Early work largely focused on the biogeographic placement of the GOM relative to larger ocean basins. Two contemporaneous early studies (Johnston, 1856; Woodward, 1856) were the first to divide the western tropical Atlantic using molluscan faunal composition, largely using qualitative data. Johnston (1856), largely considered the first comprehensive treatise of global marine biogeography, split the world into nine, latitudinally-organized homeozoic belts with little sub-regionalization, with the GOM placed in the Central belt along with the southern Pacific, most of the southern Mid-Atlantic and central Indian ocean. Woodward (1856), the first to apply the term “provinces” as a biogeographic unit, assigned the GOM to the Caribbean province.

Later work began to suggest some intra-basin differences in the GOM mollusc fauna. For example, Ekman (1967), who was the first to

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overturn the notion of faunal provinces in favor of “regions” and “sub-regions”, divided the GOM into two subregions, the Atlanto-East Pacific, and Tropical and Subtropical American. Warmke and Abbott (1961), embracing the concept of a large tropical region in the western Atlantic, erected a Caribbean province that encompassed the southern GOM, the Caribbean basin, the Antilles, and the entire coast of Brazil south to Cabo Frio, but excluding the northern GOM. The schemes outlined by Ekman (1967) and Warmke and Abbott (1961) are now regarded as over-generalized, lacking the nuance of finer scale resolution (Petuch, 2013). Valentine (1973), who would be the first to define provinces and sub-provinces based on the cluster analysis of molluscan faunal composition, largely affirmed the demarcations of Woodward (1856), but placed the GOM back into a single province of its own. Later work, integrating over several pelagic and benthic taxa, would corroborate the stand-alone GOM province designation (Briggs, 1974; Costello et al., 2017).

Subsequent studies of benthic fauna in the GOM were limited by the geographic area sampled (e.g., Parker, 1960; Pequegnat et al., 1983, 1990; Pérez-Mendoza et al., 2003; Escobar-Briones et al., 1999; Baguley et al., 2006a, Baguley et al., 2006b; Escobar-Briones et al., 2008; Wei et al., 2010), or by depth (e.g., Engle and Summers, 2000; Sharma et al., 2012) or both. Most of these were investigations of α -diversity, almost none considering each taxon's functional role in the ecosystem. Only three previous studies have investigated system-wide GOM benthic diversity (Spivey, 1981; Wicksten and Packard, 2005; Reuscher and Shirley, 2014) and only one has considered GOM benthic biological and functional diversity simultaneously (Reuscher and Shirley, 2014), but was limited to polychaetous annelids. Thus, finer-scale mollusc assemblage patterns within the GOM province, in terms of both species distributions and functional aspects, remain underinvestigated.

The development of relational databases based on species occurrence records available in museums, universities, and private collections, allows for testing hypotheses of biogeographical distributions within large regional basins like the GOM (e.g., Rosenberg, 1993/cross-ref>; Linse et al., 2006; Clarke et al., 2007; Fortes and Absalão, 2011; Belanger et al., 2012). Further investigation of biogeographic patterns within the GOM are enabled by the development of the Biodiversity of the Gulf of Mexico database (BioGoMx), which represents one of the most comprehensive compilations of GOM fauna. Utilizing this database, the purpose of this study was to investigate species richness and trophic diversity of six major classes of benthic molluscs in the Gulf of Mexico. Assemblage distributions were also compared among geographic region and depth class by characterizing species turnover rates. Specific questions addressed are (1) what are the geographic and bathymetric distributions of benthic mollusc diversity in the GOM? (2) Are the same trends observed true for all major classes? (3) Are some regional sectors and depths more taxonomically distinct than others? (4) What are the trends in the functional diversity of GOM molluscs? (5) How do different regional sectors and depths compare in terms of assemblage structure?

2. Materials and methods

2.1. Biological data

Species records for molluscs in the Gulf of Mexico were retrieved from occurrence data archived in the BioGoMx database (Moretzsohn et al., 2011), which includes species depth and geographic distributions based on the data and expertise of the 140 taxonomists that assembled the database (Moretzsohn et al., 2011). From the available data, we could not distinguish which records were based on live vs. dead shells for shelled-gastropods (Rosenberg et al., 2009) and bivalves (Turgeon et al., 2009) and so all location data were included for these taxa. We also could not distinguish if records were for singleton occurrences based on the database literature.

Pelagic and benthic species tend to have incongruent ranges owing to their disparate dispersal strategies, which has led researchers to consider their respective biogeographic patterns separately (Spalding et al., 2007,

2012). Thus, to focus on benthic molluscs, from the downloaded dataset, pelagic, bathypelagic, oceanic, and neritic molluscs and non-native species were excluded from analysis. Species names were updated to the latest nomenclature using the World Registry of Marine Species (WoRMS) database (Appeltans et al., 2012) (Table A1). Three aplousobranchs in the dataset could not be identified past family. A few species were also listed with the addition of “cf.” for uncertain species identification; these were treated as operational taxonomic units, and included in subsequent analyses. Feeding strategies were assigned to each species following the original designations determined by taxonomists involved in the original compilation of the database (Ivanov and Scheltema, 2009; Judkins et al., 2009; Kraeuter, 2009; Lyons and Moretzsohn, 2009; Rosenberg et al., 2009; Turgeon et al., 2009). Those species without a designation in the database were assigned one using WoRMS or by referencing the primary literature (Table A1). Categories used for feeding strategy include: carnivores, parasites, molluscs with chemosynthetic symbionts, detritivores, grazers, herbivores, and suspension feeders. Carnivores are those organisms that consume prey items but may also consume large amounts, intentionally or not, of non-living materials (i.e., scavengers). Parasites refer to species that form relationships with other species where one benefits at the cost of the other, the host. Chemosymbiotic species include organisms living with symbiotic chemosynthetic bacteria. Detritivores are heterotrophs that exclusively consume detritus. Grazers are species whose primary feeding mode involves consuming sedentary organisms such as plants, bacteria or other epibiotic species. Herbivores are organisms that only derive nutrients from plant materials. Suspension feeders represent those species that draw plankton, detritus, and other materials from the water column.

2.2. Polygon designations

Geographic and bathymetric divisions for the GOM as well boundaries relative to the Atlantic Ocean follow Moretzsohn et al. (2011). A straight line from the general area of Key Largo, Florida 25°06'N, 80°26'W to Punta Hicacos, Cuba (23°12'N, 81°08'W) demarcated the border between the GOM and the Atlantic. To separate the Caribbean Sea from the GOM, a line was run from Cabo Catoche, Quintana Roo, Mexico (21°33'N, 87°00'W) to Cabo de San Antonio, Cuba (21°51'N, 84°57'W) (Fig. 1). Felder et al. (2009), originally divided the GOM into eight octants (A and B; northeast, C and D; southeast, E and F; southwest, G and H; northwest), we followed this division for consistency and to facilitate biogeographic and bathymetric designations of the taxa covered in the BioGoMx census.

The assignment of species to sectors in the development of the BioGoMx was intentionally broad (Felder et al., 2009). The generalized nature of the sector designations obscures the biogeographic significance of certain habitat types such as the abundant coral reefs and hydrocarbon seeps of the GOM. Since there is not a comprehensive map of these habitat types across the Gulf to be able to parse out the data records by habitat type, the sector designation instead provide a systematic, first-order analysis of benthic mollusc diversity and assemblage structure. Further, it provides a baseline of comparison for future study as benthic habitat mapping in the GOM becomes more sophisticated.

Using this octant data set, we found that presence data from the mollusc database for octants within each geographic sector were identical (e.g. A had virtually all the same species present as B in the northeast, C was the same as D, etc.), and therefore for analyses these were combined into four major units, referred to as Northeast (A and B), Northwest (C and D), Southwest (E and F), and Southeast (G and H) sectors. The arbitrary border between sectors was placed at 25°N latitude and 90°W longitude following Moretzsohn et al. (2011). Each sector was then divided into depth classes, defined by bathymetric isobaths. Depth classes were set with Class 1 including inshore areas of bays and estuaries in depths 0–20 m; class 2 ranging from 20 – 60 m for the upper continental shelf; class 3 representing the lower continental shelf

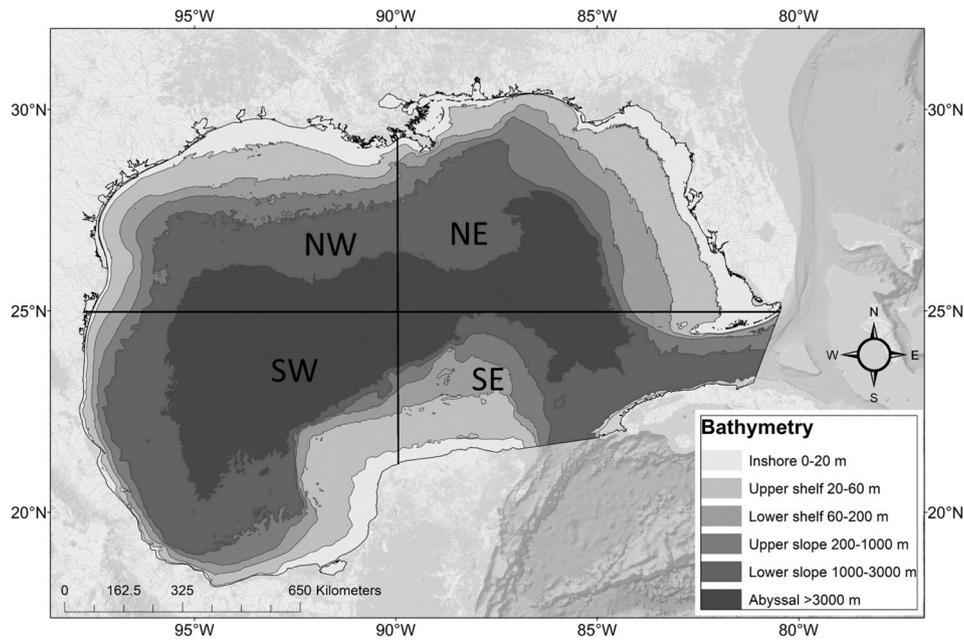


Fig. 1. Map of Gulf of Mexico with BioGoMx geographic sectors and color-coded depth classes. NE = northeast, SE = southeast, SW = southwest, NW = northwest.

at 60–200 m; class 4 the upper continental slope for depths 200–1000 m; class 5 including the lower continental slope at 1000–3000 m; and class 6 comprising the abyssal plain at depths more than 3000 m. Using these guidelines, 24 geographic-depth polygons were demarcated for analyses.

2.3. Species richness and assemblage structure analyses

Species richness was calculated for all benthic molluscs for each geographic sector and depth. The frequency of occurrence of each feeding strategy was also calculated for each geographic-depth polygon.

The highly disparate methodologies of the studies behind the database preclude analysis of faunal abundances, thus presence/absence was used for multivariate comparison of assemblage structure among polygons. Pairwise similarities were calculated using the Sørensen index (Sørensen, 1948), a measure of β -diversity (Chao et al., 2012). Similar to the more common Jaccard coefficient, it doubly weights joint occurrences which is more suitable for scenarios where joint species occurrence happens infrequently and the number of species at each site is highly variable (see Jackson et al., 1989). It also produces more informative cluster topologies (Murguía and Villaseñor, 2003). Modified by Clarke and Gorley (2006), the similarity between 2 polygons is computed with the formula

$$\beta = 100[2a / (2a + b + c)] \quad (1)$$

where a represents the number of species occurring in both polygons; b is the species found solely in the first of the compared polygons; and c is the number of species occurring only in the second of the two polygons. Similarities were visualized using ordination via non-metric multidimensional scaling (NMDS) and cluster analysis through group-average linking. To examine assemblage structure for individual classes, the rank correlation between all pairs of similarity matrices for each mollusc class was computed and arranged in a new similarity matrix, then ordinated via 2Stage NMDS. Further, the fauna that contribute the most to a *a priori* geographic sector and depth classes were identified through analysis of similarity percentages (SIMPER).

To further test the uniqueness of each geographic region and depth class we computed the taxonomic distinctness metric developed by Clarke and Warwick (1998) to capture community structure as well as the distribution of occurrence among species while simultaneously

considering taxonomic relatedness. Modified to accommodate presence/absence data, average taxonomic distinctness (Δ^+) (1) takes the average length between 2 randomly chosen species present in the sample:

$$\Delta^+ = \left[\sum_{i < j} \omega_{ij} \right] / [s(s-1) / 2] \quad (2)$$

where s is the number of species in the study and ω_{ij} is the weight of distinctness such that $\omega = 1$ (for congeners i and j), $\omega = 2$ (confamilials with different genera), $\omega = 3$ (same order but different families), $\omega = 4$ (species with different orders but same class), $\omega = 5$ (species fall into same phyla but different classes). Δ^+ significance for each polygon was determined by a two-tailed comparison with the 95% upper and lower confidence limits of a range of Δ^+ of increasing sample size. Values falling outside the bounds are significantly different from expected variation. Taxonomic distinctness analysis has previously been able to distinguish spatial differences at multiple taxonomic levels for benthic molluscs (Terlizzi et al., 2009).

To complement the taxonomic distinctness analysis, clustering of the incidence data was also conducted using the taxonomic dissimilarity index (Γ^+) (Izsak and Price, 2001), an extension of the Sørensen index. Γ^+ is defined as:

$$\Gamma^+ = \frac{\left(\sum_{i=1}^{s_1} \min_j \{ \omega_{ij} \} + \sum_{j=1}^{s_2} \min_i \{ \omega_{ij} \} \right)}{(s_1 + s_2)} \quad (3)$$

where there are s_1 species in the first polygon and s_2 species in the second polygon, ω_{ij} is the distance through the classification tree from species i of polygon 1 to species j of polygon 2. All analyses were conducted in PRIMER 6.1.18 (Clarke and Gorley, 2006).

3. Results

3.1. Species richness

Representatives from every extant class of Mollusca except for monoplacophorans were present in the final dataset. After nomenclature updates, a total of 2298 species were left for analysis. Gastropods and bivalves were the most diverse with 1674 (73%) and 520 (23%) species

respectively. Scaphopods and polyplacophorans were represented at 41 (2%) and 42 species (2%). Cephalopods and aplacophorans were the least diverse with 10 (0.4%) and 11 (0.5%) species each (Table 1). Geographically, the northeast and southeast had similar numbers of species (1371 and 1310, respectively), followed by the northwest (836) and the southwest (519) (Table 1). The richest mollusc classes overall were also the richest in each individual sector. Gastropod proportions ranged from 56–67%, and bivalves 29–41%, with the remaining classes at proportions of 3% or less in each sector (Table 1).

Mollusc richness peaked at the upper shelf (Fig. 2A) and then decreased. By class, gastropods and bivalves showed a smoother decrease with depth (Fig. 2B). Scaphopods and cephalopods reached species richness maxima in the lower shelf and upper slope depths. Polyplacophorans were the only group to decrease with depth. Aplacophorans only occurred on the upper shelf and deeper and showed an increase with depth (Fig. 2B). Aplacophorans, cephalopods, and polyplacophorans were not recorded in the abyssal depths of the GOM.

3.2. Trophic diversity

Trophically, carnivory was the dominant feeding strategy in the Gulf among molluscs at 1066 species (46%), followed by suspension feeders with 503 species (22%). Grazers, herbivores, and parasitic molluscs followed with 311 (14%), 182 (8%), and 117 (5%) respectively (Table 2). The least common feeding strategies were detritivory and chemosymbiosis with 69 (3%) and 50 (2%) species (Table 2). Trophic group proportions were largely similar to the overall GOM, but in the western geographic sectors, the richness of suspension feeders was slightly greater than the richness of carnivores. Grazing was the third most common feeding strategy in each geographic region, followed by herbivory and then parasitism (Table 2).

Bathymetric trends for each trophic group reflected the overall geographic pattern with carnivores dominating most depths followed by suspension feeders. However, in the abyssal depths, parasites made up a comparatively high proportion of the feeding strategies with 19% of the relative representation. Most feeding groups reached a maximum species richness on the upper shelf, but detritivores, grazers and herbivores displayed maximum species richness in inshore areas (Table 2).

3.3. Taxonomic distinctness

The comparison of $\Delta+$ values to mean expected taxonomic distinctness for the GOM for each polygon is illustrated in Fig. 3. Most of the NE polygons fell below average $\Delta+$ for GOM benthic molluscs ($p < 0.05$; Table 3). The NW lower shelf and upper slope regions were significantly greater than expectation ($p < 0.05$; Table 3). In the SE, the inshore, upper shelf, and the lower slope region also demonstrated higher than expected distinctness. The SW had the largest spread around mean distinctness but almost all fell within expectations except for the upper slope ($p < 0.05$; Table 3) with points above and below average $\Delta+$ for the GOM.

Table 1

Species richness and relative abundance of major mollusc classes by geographic sector and depth class.

	NE	SE	SW	NW	Inshore	Upper shelf	Lower shelf	Upper slope	Lower slope	Abyssal	GOM TOTALS
Aplacophora	7 (1%)	0 (0%)	0 (0%)	11 (1%)	0 (0%)	1 (0.07%)	4 (0.34%)	7 (1%)	7 (3%)	0 (0%)	11 (0.5%)
Bivalvia	403 (29%)	407 (31%)	186 (36%)	342 (41%)	300 (23%)	379 (25%)	276 (24%)	145 (21%)	70 (26%)	20 (34%)	520 (23%)
Cephalopoda	8 (1%)	9 (1%)	6 (1%)	5 (1%)	1 (0.08%)	2 (0.13%)	8 (1%)	7 (1%)	1 (0.37%)	0 (0%)	10 (0.4%)
Gastropoda	916 (67%)	829 (63%)	315 (61%)	468 (56%)	957 (73%)	1111 (72%)	850 (73%)	519 (74%)	180 (66%)	35 (59%)	1674 (73%)
Polyplacophora	15 (1%)	35 (3%)	12 (2%)	6 (1%)	36 (2.76%)	20 (1%)	3 (0.26%)	4 (0.57%)	1 (0.37%)	0 (0%)	42 (2%)
Scaphopoda	22 (2%)	30 (2%)	0 (0%)	4 (0.48%)	10 (0.76%)	20 (1%)	26 (2%)	24 (3%)	13 (5%)	4 (7%)	41 (2%)
TOTALS	1371	1310	519	836	1304	1533	1167	706	272	59	2298

3.4. Assemblage structure

The NMDS plots based on Sørensen and $\Gamma+$ indices show assemblage structure for all molluscs falls into 3 main groups at 20% similarity that correspond to depth groups across geographic sectors (Fig. 4A and B). Inshore and the shelf regions clustered into the left group in the ordination plot, continental slope regions the central group, and the abyssal and southwest lower slope regions as the right-most group. There is also a slight north-south separation of the geographic sectors from the top to the bottom of the NMDS. When ordinated by 2 stage NMDS; bivalves, gastropods, and cephalopods were the most similar in terms of structure within the larger GOM mollusc assemblage, but little similarity was observed among scaphopods, aplacophorans, and polyplacophorans (Fig. 4C). Cluster analysis of the assemblage structure largely affirms the NMDS (Fig. 5A and B).

SIMPER analysis of the species contributing to structure within each geographic sector indicate gastropods contributed the most to within-sector assemblage similarity ($\geq 50\%$) and bivalves are the second-highest with contributions ranging from 22 to 39% (Fig A1A). The remaining classes made individual contributions at $< 3\%$. Aplacophorans only contributed in the northern sectors of the GOM while polyplacophorans and scaphopods made minor additions to within-sector similarity and made none in the SW sector (Fig A1A).

By depth, gastropods had the strongest contribution to within-sector similarity, usually more than 40%. Contributions peaked around the upper continental slope (Fig A1B). Contributions made by bivalves were also high and varied between 21–30%, with contributions increasing and exceeding that of gastropods towards the lower continental slope and abyssal regions (Fig A1B). The remaining mollusc classes made contributions of less than 3% to within-class similarity by depth. Contributions from polyplacophorans ceased below upper shelf regions and aplacophorans made no contribution at all. Scaphopod contributions peaked around mid-depth regions spanning the upper shelf to the upper slope (Fig A1B).

4. Discussion

4.1. Broad-scale patterns

Previously, the GOM has been described as a single biogeographic region, or part of a larger one that connects to the greater Atlantic. However, some studies have hinted that there may be variation within the basin itself, placing one portion of the GOM into a biogeographic region with the Atlantic, and the other portion with the Caribbean or Pacific (Ekman, 1967; Warmke and Abbott, 1961). Potential for variation within the GOM is corroborated by studies that have considered a subset of the dominant benthic taxonomic groups (e.g., polychaetes (Reuscher and Shirley, 2014), barnacles (Spivey, 1981), and decapod crustaceans (Wicksten and Packard, 2005)).

For a temperate, semi-enclosed basin, the GOM exhibits a high degree of benthic molluscan species richness with 2298 species

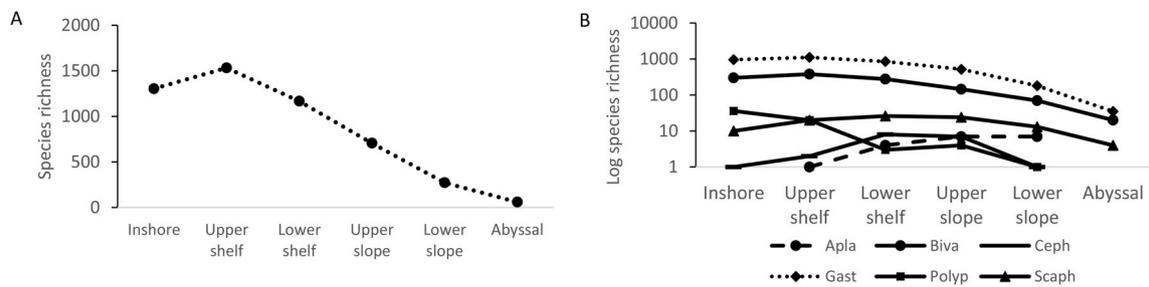


Fig. 2. A) Total species richness by depth. B) Species richness by depth for each major mollusc class. Inshore ranges from 0–20 m, upper continental shelf 20–60 m, lower continental shelf 60–200 m, upper continental slope 20–1000 m, the lower slope 1000–3000 m, and the abyssal region >3000 m.

Table 2
Species richness and relative abundance by trophic class for GOM molluscs by geographic sector and depth class.

	NE	SE	SW	NW	Inshore	Upper shelf	Lower shelf	Upper slope	Lower slope	Abyssal	GOM TOTALS
Carnivore	577 (42%)	539 (41%)	175 (34%)	270 (32%)	502 (38%)	689 (45%)	600 (51%)	384 (54%)	126 (46%)	22 (37%)	1066 (46%)
Detritivore	41 (3%)	29 (2%)	11 (2%)	16 (2%)	43 (3%)	24 (2%)	19 (2%)	27 (4%)	14 (5%)	2 (3%)	69 (3%)
Grazer	148 (11%)	180 (14%)	64 (12%)	94 (11%)	211 (16%)	210 (14%)	110 (9%)	67 (9%)	33 (12%)	3 (5%)	311 (14%)
Herbivore	104 (8%)	101 (8%)	44 (8%)	51 (6%)	136 (10%)	110 (7%)	74 (6%)	42 (6%)	11 (4%)	1 (2%)	182 (8%)
Parasite	73 (5%)	37 (3%)	25 (5%)	48 (6%)	88 (7%)	97 (6%)	68 (6%)	32 (5%)	14 (5%)	11 (19%)	117 (5%)
Suspension feeder	394 (29%)	391 (30%)	193 (37%)	333 (40%)	300 (23%)	370 (24%)	272 (23%)	134 (19%)	65 (24%)	14 (24%)	503 (22%)
Chemosymbiotic	34 (2%)	34 (3%)	7 (1%)	24 (3%)	24 (2%)	33 (2%)	24 (2%)	20 (3%)	9 (3%)	6 (10%)	50 (2%)
TOTALS	1371	1310	519	836	1304	1533	1167	706	272	59	2298

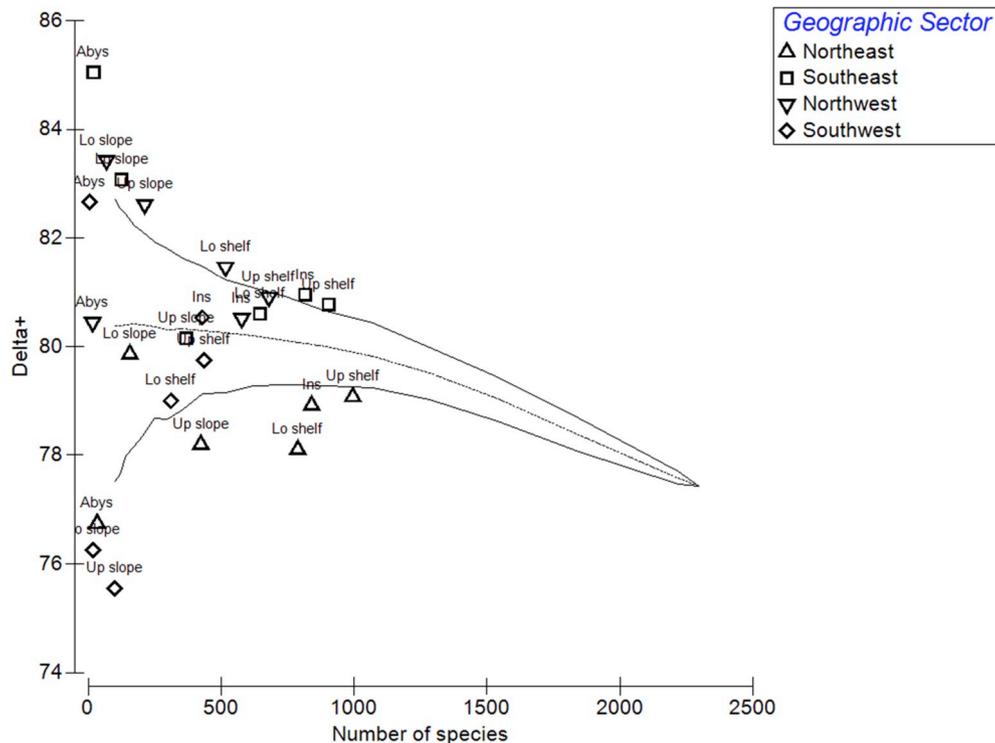


Fig. 3. Confidence funnel (mean and 95% confidence interval) of average taxonomic distinctness ($\Delta+$). Depth categories are abbreviated as inshore (Ins), upper shelf (Up shelf), lower shelf (Lo shelf), upper slope (Up slope), lower slope (Lo slope), and the abyssal regions (Abys).

documented. Previous regional studies across the northern GOM, spanning roughly the same depth range, have also noted a high abundance of molluscs, especially megafaunal and macrofaunal bivalves, and macrofaunal aplousobranchs, but distributed among a smaller number of

taxa than reported here (Pequegnat et al., 1990; Wei et al., 2010). Pequegnat et al. (1990), for instance, only noted 55 bivalve taxa (species-level or higher), 53 gastropod taxa, and 1 aplousobranch taxon. Wei et al. (2010) reported 94 named and operational bivalve species.

Table 3

Taxonomic distinctness of GOM polygons. Polygons significantly different from expectation are indicated in bold ($p < 0.05$). Values of 1–6 after the sector designation indicate depth zone from shallowest to deepest.

Polygon	No. species	$\Delta+$ Value	p-value
NE1	841	78.92	0.004
NE2	996	79.07	0.018
NE3	789	78.10	0.002
NE4	424	78.20	0.004
NE5	157	79.86	0.607
NE6	34	76.74	0.176
NW1	578	80.51	0.593
NW2	680	80.91	0.09
NW3	517	81.47	0.026
NW4	213	82.62	0.004
NW5	69	83.43	0.052
NW6	17	80.44	0.819
SE1	816	80.95	0.016
SE2	905	80.77	0.02
SE3	646	80.6	0.38
SE4	369	80.15	0.809
SE5	125	83.08	0.018
SE6	20	85.05	0.12
SW1	429	80.53	0.661
SW2	435	79.75	0.358
SW3	312	79.00	0.088
SW4	99	75.55	0.008
SW5	19	76.26	0.23
SW6	6	82.67	1

The overall molluscan species richness for the GOM is comparable to other large basins such as the Mediterranean, where [Oliverio \(2003\)](#) reported 2308 mollusc species. The proportional distribution of species richness among molluscan classes in the GOM also strongly matches Mediterranean malacofauna, where [Oliverio \(2003\)](#) found bivalves and gastropods to be 20% and 73% of molluscs respectively. Remaining molluscan classes in their study, including monoplacophorans, also had proportions of 3% or less. The absence of monoplacophorans in the GOM and low percentage in the Mediterranean, are consistent with their global rarity with only 30 known species, occupying depths greater than 3500 m ([Schwabe, 2008](#); [Lindberg, 2009](#); [Sigwart and Sumner-Rooney, 2015](#)).

Other areas have lower molluscan richness, for example in a study with a similar geographic distance and depth range on the Brazilian continental shelf and slope, [Benkendorfer and Soares-Gomes \(2009\)](#) documented 404 gastropod species and morphotypes. [Linse et al. \(2006\)](#) identified 1274 gastropod and bivalve species for the Southern Ocean. However, species richness at sites more centered in tropical latitudes may exceed the levels found in the GOM. For example, in the tropical southwest Pacific, [Bouchet et al. \(2002\)](#), documented 2738 gastropod species alone in a 295 km² site in New Caledonia.

Despite a large portion of the southern GOM falling into tropical latitudes, our analysis shows more species in the northern GOM (2207 species) compared to the southern half (1829), likely reflecting the greater sampling intensity that has occurred in the north. Within the larger N–S differences, the NE and SE sectors were particularly speciose. The taxonomic and species richness of the two eastern sectors may be boosted by proximity to the larger Atlantic and tropical Caribbean. Exchange with the tropical Caribbean and West Indian regions has been documented with various benthic crustacean taxa ([Spivey, 1981](#); [Wicksten and Packard, 2005](#)) and polychaetes ([Reuscher and Shirley, 2014](#)). The high species richness in the NE is corroborated by a regional study of the northern GOM by [Wei and Rowe \(2019\)](#), who attribute it to the higher particulate organic carbon (POC) flux related to associated mesoscale eddies and lateral transport of organics from the Mississippi River as well as the Mississippi and DeSoto Canyons. The low richness in the NW Gulf may be caused by lower surface productivity ([Biggs et al., 2008](#)). The low richness of the SW GOM could be an undersampling bias as this sector had a much larger area compared to the other sectors and is

also likely the least sampled sector in the dataset.

Although the NE had the highest species richness, taxonomic distinctness indicated that this quadrant, particularly inshore to the lower shelf, was less taxonomically rich than the average for the GOM. The inconsistency between taxonomic distinctness and species richness metrics has been documented before in faunistic surveys of the benthos and has been attributed to the generally stronger relationship species richness has with environmental gradients ([Somerfield et al., 1997](#); [Ellingsen et al., 2005](#); [Salas et al., 2006](#); [Bevilacqua et al., 2009](#)), or with the differential taxonomic ranking faunal groups can have ([Ellingsen et al., 2005](#)). In a multi-phylum, analysis of taxonomic distinctness, [Ellingsen et al. \(2005\)](#) point out that there is a tradeoff between taxonomic breadth and the likelihood that taxonomic ranks of an assemblage under consideration are similar. This implies that the amount of attention a group has received from taxonomists and the challenges of unresolved taxonomies can influence distinctness, which may contribute to the mismatch of species richness and taxonomic distinctness observed in the NE sector as several molluscan groups are poorly resolved at the species level. One molluscan group for which this may be particularly relevant are the aplousobranchs, which are often reported as highly abundant molluscs in the GOM (e.g., [Pequegnat et al., 1990](#)), yet remain rather obscure compared to bivalves, gastropods, and even chitons ([Todt et al., 2008](#); [Todt, 2013](#)) and their taxonomy remains a topic of debated revision ([Mikkelsen et al., 2019](#)).

Species richness for GOM molluscs peaked in the upper shelf (20–60 m) with some groups (cephalopods and scaphopods) reaching a maximum on the lower shelf (60–200 m). This corresponded with the finding that GOM molluscs, above and below the shelf break, are taxonomically distinct for most of the GOM. It is not uncommon for mollusc diversity to peak at intermediate levels of chemical energy availability (i.e., POC flux) ([Tittensor et al., 2011](#); [McClain et al., 2012](#)) and high productivity is observable in GOM shelf waters ([Lohrenz et al., 1997](#); [Gonzalez-Rodas, 2000](#); [Hernández-Arana et al., 2003](#); [Biggs et al., 2008](#)). Other large-scale studies found similar results in terms of richness for polychaetes and barnacles at roughly similar depths in the GOM. [Reuscher and Shirley \(2014\)](#), whose polychaete distribution data also originated from the BioGoMx database, similarly reported a species richness maximum on the upper shelf. [Spivey \(1981\)](#) also observed peak richness across most cirriped superorders in the “sublittoral” (0–180 m).

However, subregional studies indicate peak richness may vary by GOM taxon. [Pequegnat et al. \(1990\)](#) found northern GOM polychaetes maintained a relatively similar species richness through most of the depth range (355–2600) and most macrofaunal crustaceans reached species richness maxima between 600–1000 m, similar to later studies on northern GOM deep-sea isopods ([Wilson, 2008](#)) where species richness peaked between 800 and 1200 m. Globally, benthic diversity tends to peak at depths 1500–2500 m ([Rex, 1983](#); [Grassle and Maciolek, 1992](#); [Levin et al., 2001](#); [Rex and Etter, 2010](#)) but can vary with continental margin setting ([Menot et al., 2010](#)). The deep-sea below 200 m is critically underexplored and further sampling below 200 m in the GOM may reveal a different pattern of richness with depth than the one documented here.

4.2. Trophic diversity

Regions of high primary productivity such as coastal and shelf continental margins are expected to support a prevalence of suspension feeding ([Prins and Escaravage, 2005](#)). Carnivorous molluscs can also dominate over other feeding modes in shallow ocean regions ([Valentine et al., 2002](#)). In deeper waters, [Clarke \(1962\)](#) estimated Atlantic deep-sea mollusc proportions at 54% for carnivores (including scavengers) 24% for detritivores, 15% for suspension feeders, and commensals and parasites at 4%. While [Allen \(1983\)](#) contends these proportions no longer hold given the predominance of deposit feeders among more recently discovered species, our data tends to match [Clarke \(1962\)](#) estimates. Carnivory (including scavengers) was consistently the

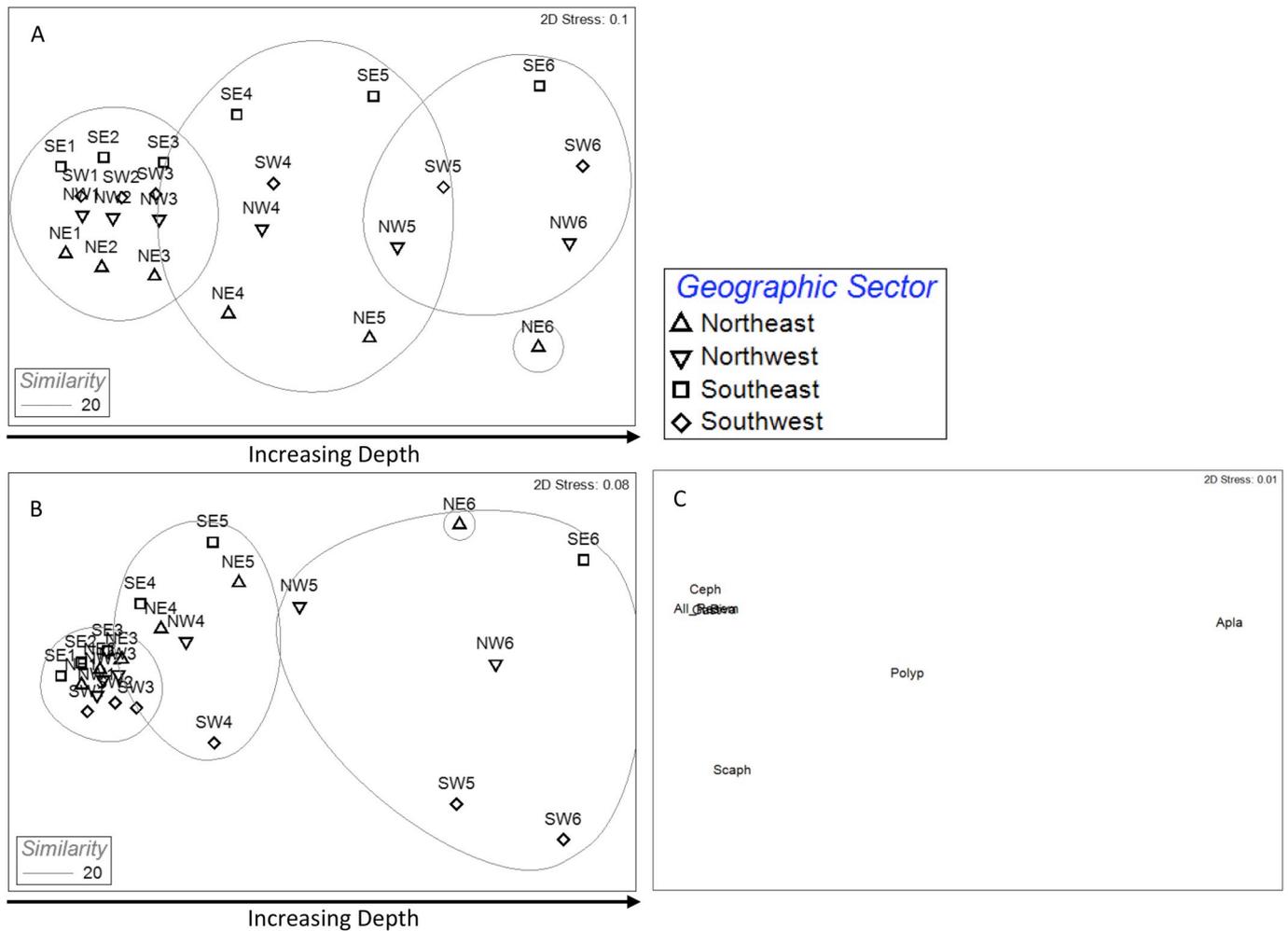


Fig. 4. A) Non-metric multidimensional scaling for GOM mollusc assemblage polygons using Sørensen similarities. Ovals represents 20% similarity level. B) 2Stage MDS for mollusc class resemblance matrices. C) Non-metric multidimensional scaling of Γ^+ dissimilarities. Clustering represents 20% similarity clustering. In the 2Stage MDS “Apla” = Aplacophorans, “Biv” = Bivalvia, “Ceph” = Cephalopoda, “Gast” = Gastropoda, “Polyp” = Polyplacophora, “Scaph” = Scaphopoda.

dominant trophic strategy across geographic sectors and depths (32–51% of species), followed by suspension feeding (19–40%), with chemosymbiotic and parasites at 1–10%. Only detritivores failed to match Clarke (1962) estimates, holding proportions of 2–5%. Proportions of carnivores were similar to what has been found with GOM polychaetes where more than half of species are carnivores or omnivores, though suspension feeding polychaetes held proportions of 11% or less (Reuscher and Shirley, 2014).

The dominance of carnivory in the GOM molluscs can be attributed to the high proportion of gastropods. Snail-like gastropods with coiled shells are generally considered to be motile carnivores (Gage and Tyler, 1991). In most areas of the world, at least half of the gastropods can be classified as predators (Taylor et al., 1980), the wide proliferation of which indicates its large success as a trophic strategy. Suspension feeders, largely bivalves, stayed at relatively similar proportions with depth in the current study. Their persistence with depth might be reflective of the large amounts of detrital material that is exported to the continental slope and beyond in the GOM (Rowe et al., 2008).

Herbivory and grazing were the next most common feeding strategies and persisted in high proportions until abyssal depths where their numbers dropped precipitously. Herbivores had large depth ranges that spanned the photic zone through to the deeper lower slope. Any herbivores observed in aphotic regions likely originated from source populations in photic zones and probably do not form sustaining populations given the dearth of photosynthetic biomass (Rex et al.,

2005b). Known regions of large phytodetritus accumulation are generally thought to be limited to notable bathymetric depressions such as marine canyons and trenches (e.g., Wolff, 1979; Josselyn et al., 1983; Vetter and Dayton, 1998, 1999; Harrold et al., 2003; Wei et al., 2012; Hunter et al., 2013). However, herbivore distribution may be more widespread than previously considered as deposits of ocean-derived macrophyte detritus can be found rather evenly throughout the northern GOM (Wei et al., 2012). Grazers likely share some distributional patterns with herbivores given they can also consume phytodetritus but they can also subsist by feeding on bacterial mats, general detrital deposits, or on sedentary animals such as sponges, ascidians, and coelenterates (Taylor et al., 1980).

Strict detritivores, parasites, and chemosymbiotic molluscs exhibited similarly low species richness within the GOM. Most parasites identified in our dataset were pyramidellid gastropods with smaller representation from eulimids and acclid snails. Pyramidellids have long been known to be parasitic gastropods (Fretter and Graham, 1949) whose hosts include polychaetes and other molluscs (Høisæter, 2014) and can range from inshore to considerable depths (Warren, 1966) and as deep as the abyssal floor in the GOM. Chemosynthetic cold seep habitats are especially abundant in the GOM and host an abundance of limpets, and symbiont-bearing bivalves (Kennicutt, 2017). Endosymbiont-bearing mussels in the GOM may also inhabit wood falls (Lyons and Moritzsohn, 2009; Turgeon et al., 2009).

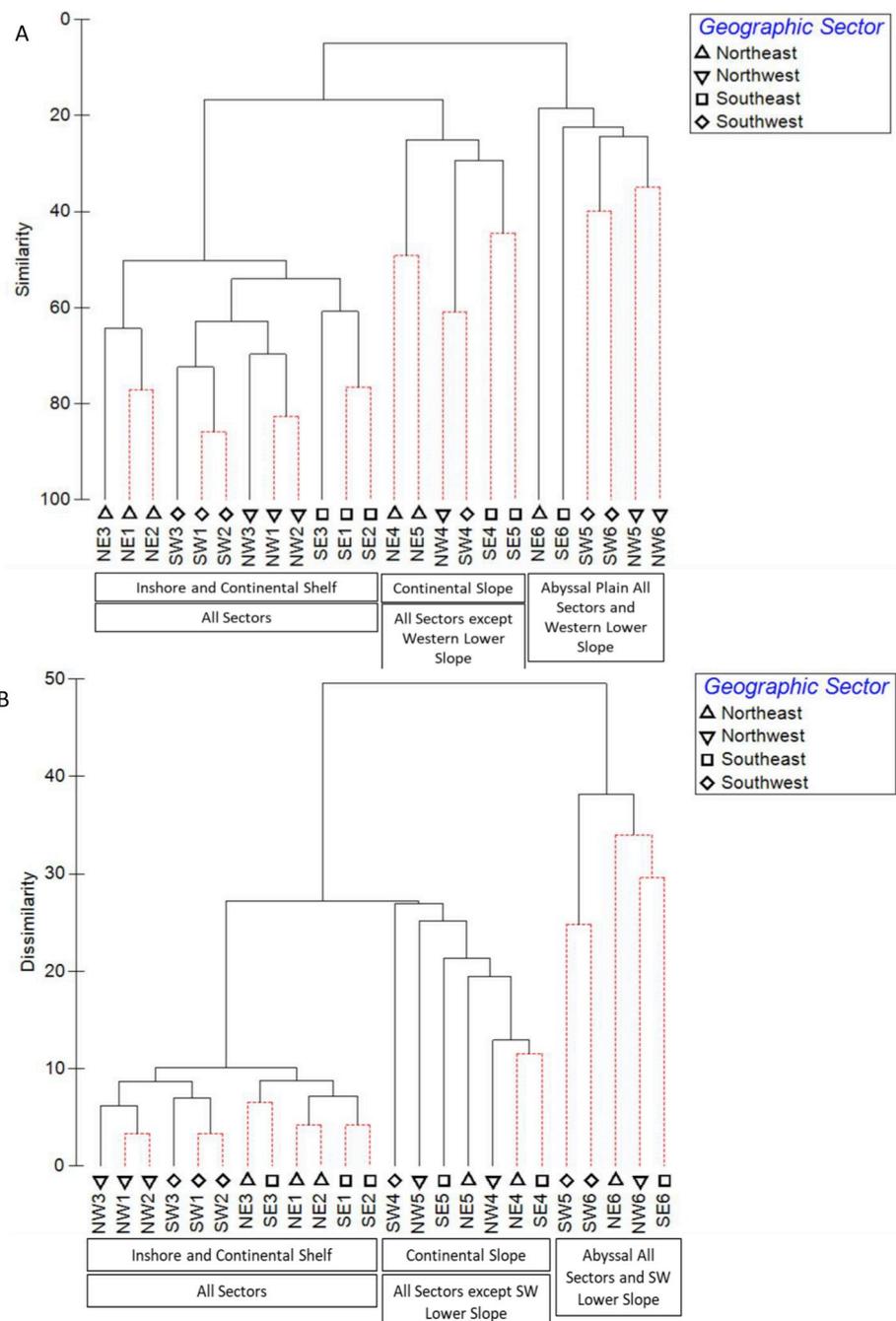


Fig. 5. A) Cluster diagram of GOM mollusc assemblage structure based on Sørensen similarities. B) Cluster diagram of $\Gamma+$ dissimilarity for GOM mollusc assemblages. NE is the northeastern sector, NW northwestern sector, SE southeastern sector, SW southwestern sector. Numbers 1–6 represent the 6 depth classes from inshore to the abyssal plain.

4.3. Assemblage structure

Two separate multivariate analyses of assemblage structure were in strong agreement, one based on the Sørensen index and one on taxonomic similarity ($\Gamma+$), with the cluster and ordination of both indices indicating three depth groups at the inshore-continental shelf (0–200 m), continental slope (200–3000), and abyssal (>3000 m) bathymetric zones; along with a weak north-south pattern apparent in the MDS. As demonstrated by the high overlap in the inter-class ordination of the 2Stage MDS and SIMPER plots, bivalves and gastropods drove within-class similarity for geographic sectors and depth class, as expected given their high dominance.

Depth has been noted as a strong structuring or highly correlated

factor for other GOM-wide studies of benthic invertebrate assemblages such as crustaceans (Wicksten and Packard, 2005), polychaetes (Reuscher and Shirley, 2014), and mesophotic reefs (Semmler et al., 2017). It even strongly structures high productivity, mollusc-dominated GOM cold seep communities (Cordes et al., 2007; Olu et al., 2010). Regional studies in both the northern GOM (Pequegnat et al., 1983, 1990; Baguley et al., 2006a, 2006b; Wei et al., 2010), and southern GOM (Escobar-Briones et al., 1999, 2008) note the importance of depth as well. Generally, the shelf break is a common ecotone (Forbes, 1856; Hedgpeth, 1957; Briggs, 1974) with high species turnover rates for molluscs (Rex, 1977) and a documented point of high faunal turnover for benthic molluscs in the larger Atlantic (Olabarria 2005, 2006; Rex et al., 2005a). The GOM continental shelf break is a clear boundary for

benthic assemblage structure in these analyses and has been noted in Gulf-wide studies for polychaetes (Reuscher and Shirley, 2014), and also for smaller regional mollusc studies (Bieler and Mikkelsen, 2004), and regional cross-phyla studies (Blake and Doyle, 1983; Pequegnat et al., 1990) in the northern GOM. It may be concomitant with and energy availability observed in shelf-break regions. Indeed, high productivity can be observed in shelf waters of the GOM (Lohrenz et al., 1997; Gonzalez-Rodas, 2000; Hernández-Arana et al., 2003; Biggs et al., 2008).

The faunal changeover around 3000 m we observed is not unprecedented in the Gulf of Mexico (Pequegnat et al., 1990; Escobar-Briones et al., 1999; Wicksten and Packard, 2005; Baguley et al., 2006b) and largely thought to be POC-driven (Baguley et al., 2006a; Wei et al., 2010). Some studies, however, indicate this delineation is more variable depending on taxon and subregion, as with isopods and polychaetes in the northern GOM (Pérez-Mendoza et al., 2003; Wilson, 2008; Stuart et al., 2016). Isopods exhibit strong overlap in species composition between slope and abyssal communities, thought to be produced from recolonization after recent geological extinction (Wilson, 2008). Polychaetes similarly show high nestedness due to subregional environmental heterogeneity such as the low POC in the oligotrophic NW GOM (Stuart et al., 2016). Our results show a merging of the 1000–3000 depth sector on the western slope with the abyssal region. In fact, the shared similarity of slope and abyssal polygons seems to be found across the entire basin for GOM polychaetes (Reuscher and Shirley, 2014). These patterns may be representative of benthic assemblage structure in the larger western Atlantic. Western Atlantic mollusc population differentiation has been shown to diminish with depth and abyssal assemblages exhibit a high degree of nestedness with bathyal neighbors (Etter et al., 2005; Brault et al., 2012, 2013) while higher turnover tends to dominate the eastern Atlantic (Olabarria, 2005, 2006; Brault et al., 2013). Ultimately the patterns of faunal change may depend on the taxon and geographic location (Rex, 1981; Billett, 1991; Gage and Tyler, 1991; Grassle and Maciolek, 1992; Cartes et al., 2002).

Latitudinally, a marginal north-south trend in assemblage structure was also observed in the MDS that did not hold up as strongly in the cluster analyses. Other Gulf-wide benthic studies noted a weak north-south separation among decapod crustaceans (Wicksten and Packard (2005) and Reuscher and Shirley (2014) observed a latitudinal separation for benthic polychaetes. The coarse resolution of this dataset and other GOM-encompassing datasets may obscure the trend as it has been more pronounced in sub-regional studies, e.g., Bieler and Mikkelsen (2004) observed a marked northeast-to-southwest gradient with bivalves in the Florida Keys on the Florida Bay-side. The N–S trend observed may be a product of the strong effect the latitudinal gradient has on mollusc diversity, which is evident at the genus and family level (Roy et al., 1998; Crame, 2000a).

5. Conclusions

Molluscs are particularly species-rich within the GOM and depth proved to be the stronger factor compared to geographic distance for patterns in GOM molluscan species richness and assemblage structure, with a strong break at the continental shelf and at 3000 m depth. This was largely driven by the bivalves and gastropods whose dominance led to the prevalence of the carnivore and suspension feeding strategies. The patterns described here should be regarded as preliminary considering that sampling of the deep ocean continues to prove sparse, especially in the southern GOM compared to the north. More research would not only offset biases from our dataset's coarse resolution but resolve undue influence from taxonomic uncertainty. Clearer taxonomic boundaries, through more morphological and genetic analyses, would better delineate species geographical ranges and help overcome false conclusions about group distributions. This research underlines how large species databases can provide insight into species diversity and assemblage structure over large spatial scales. Continual curation of such databases

and characterizing trends is critical for the ongoing effort of understanding and preserving marine global diversity.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2019.103167>.

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