Benthic foraminifera living in Gulf of Mexico bathyal and abyssal sediments:

Community analysis and comparison to metazoan meiofaunal biomass and density

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ABSTRACT

Benthic foraminiferal biomass, density, and species composition were determined at ten sites in the Gulf of Mexico. During June 2001 and June 2002, sediment samples were collected with a GoMex boxcorer. A 7.5-cm diameter subcore was taken from a box core collected at each site and sliced into 1-cm or 2-cm sections to a depth of 2 or 3 cm; the >63-μm fraction was examined shipboard for benthic foraminifera. Individual foraminifers were extracted for adenosine triphosphate (ATP) using a luciferin-luciferase assay, which indicated the total ATP content per specimen; that data was converted to organic carbon. Foraminiferal biomass and density varied substantially (~2-53 mg C m^{-2}; ~3,600-44,500 individuals m^{-2}, respectively) and inconsistently with water depth. For example, although two ~1000-m deep sites were geographically separated by only ~75 km, the foraminiferal biomass at one site was relatively low (~9 mg C m^{-2}) while the other site had the highest foraminiferal biomass (~53 mg C m^{-2}). Although most samples from Sigsbee Plain (>3000 m) had low biomass, one Sigsbee site had >20 mg foraminiferal C m^{-2}. The foraminiferal community from all sites (i.e., bathyal and abyssal locales) was dominated by agglutinated, rather than calcareous or tectinous, species. Foraminiferal density never exceeded that of metazoan meiofauna at any site. Foraminiferal biomass, however, exceeded metazoan meiofaunal biomass at five of the ten sites, indicating that foraminifera constitute a major component of the Gulf's deep-water meiofaunal biomass.

Keywords: foraminifera, meiofauna, biomass, deep sea; USA, Gulf of Mexico

1. INTRODUCTION

Foraminifera are commonly occurring constituents of deep-sea benthic communities (e.g., Gooday 1986; Gooday et al 2000). In some cases, benthic foraminifera are known to be very abundant in the bathyal to abyssal zones (e.g., Sen Gupta et al., 1981; Bernhard et al., 2000; Gooday 2002). Numerous publications exist regarding the benthic foraminiferal fauna of the Gulf of Mexico slope, but many reports are on total assemblages in which live and dead specimens were not distinguished from each other. Publications with information on living (or recently living) populations (utilizing the rose Bengal or copper sulfate stains) include Phleger and Parker (1951), Parker (1954), Reynolds (1982), Sen Gupta and Aharon (1994), Sen Gupta *et al*. (1997) and Robinson *et al*. (2004). Of these studies, the first two were regional in scope, covering much of the northern Gulf, but mainly targeting the total assemblage. The others, although focused on cytoplasm-containing populations, covered only small portions of the northwestern Gulf, including cold seeps. Here we present a report on unequivocally live benthic foraminifera, including agglutinated and tectinous species, from the Gulf of Mexico slope and abyss.

Few studies have compared foraminiferal biomass and density to those of metazoan meiobenthos in the deep sea. In those that directly compare foraminifera and metazoan meiofauna, results commonly show (1) dominance of foraminifera in terms of biomass in bathyal and abyssal areas (e.g., Coull *et al*., 1977), and (2) foraminiferal densities exceeding those of other meiofauna and macrofauna (e.g., Snider *et al*., 1984; Gooday, 1986; Smith, 1992; Gooday *et al*., 2000; Cornelius and Gooday, 2004). In addition, deep-water areas with depleted oxygen concentrations or sulfidic conditions are also known to have communities where foraminiferal biovolume exceeds that of metazoan meiofauna (Buck and Barry, 1998; Bernhard *et al*., 2000).

As regards the Gulf of Mexico, however, the only published comparison of foraminiferal and metazoan meiofaunal densities and biomass is just for a few hydrocarbon seeps (Robinson et al., 2004). Here, we present another comparison, but for a much larger area.

2. METHODS

Foraminifera were obtained from ten sites using the RV *Gyre* in June 2001 and June 2002 (Fig. 1). Site locations included a variety of water depths (range ~550-3700 m) and physiographic settings, as well as considerable coverage in latitude and longitude across the Gulf (Table 1). Sites included two from the Mississippi Trough (MT3; MT6), two from the salt diapir basinal complex (Bush Hill; C7), two from the Florida Escarpment region (S36; S42), and four from the Sigsbee Abyssal Plain (JSSD1; JSSD2; JSSD4; JSSD5). Samples were collected as part of the Deep Gulf of Mexico Benthos (DGoMB) Project (e.g., Rowe and Kennicutt, 2001; Baguley, 2004).

Samples were obtained from subcores of GoMex boxcores (Boland and Rowe, 1991). Although multiple corers (e.g., SMBA multiple corer, Ocean Instruments MC800) are generally considered superior to most types of corers, including boxcorers (Barnett et al., 1984), a multicorer was not available for this project. In addition, a box core was necessary due to the different sample types required by the entire DGoMB project as well as for studying the replicate box cores for macro- and megafaunal analyses. Prior to box core deployment, subcores were mounted in the corer, away from its side walls. Although mounting subcorers in the boxcore barrel prior to deployment may have increased the bow wave, thereby negatively affecting core quality, this effect was minimized by stopping the boxcorer ~10-20 m above the seafloor and then slowly lowering it during penetration.

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After box core recovery on deck, a 7.5-cm inner diameter subcore for foraminiferal analysis was removed as quickly as possible into a refrigerated van (~5°C), and sectioned into 1 or 2 cm intervals. In general, the 0-1 and 1-3 cm intervals were analyzed, but some cores were sectioned in 1-cm intervals to only 2 cm core depth. In one case (i.e., JSSD4), the 0-2 cm section was processed as one sample due to the box core's steeply inclined surface. Sections were split into 8 pie-shaped aliquots; two aliquots, each representing 12.5% of the core slice, were kept in separate containers. The remaining 75% of the core was fixed in formalin and archived.   One 12.5% aliquot of each sample was sieved gently and briefly over a 63-µm screen with chilled seawater; the coarser fraction was kept on ice and examined for benthic foraminifera with a stereo-dissecting microscope. In cases when foraminifers were not abundant, a second aliquot was also sieved and examined. From each sample, at least fifty specimens were selected for ATP analysis. Specimens were selected on the basis of their appearance: empty tests (shells) were ignored, as these could not have been living. Specimens that appeared to have cytoplasm or sedimentary infilling were analyzed. In all cases, all potentially live foraminifers were picked from the sediment aliquot, so the results represent total estimates of foraminiferal biomass and abundance per sample. On the June 2002 cruise, prior to specimen extraction, photographs were taken of individual foraminifers with a Nikon CoolPix 995 digital camera (with an ocular attachment; Optem Avimo Precision Instruments, Fairport, NY) through the ocular of the stereo-dissecting microscope.

Because conventional methods involving weight or volume measurements to determine biomass can not be used for foraminifera due to their biomineralized or agglutinated shell, benthic foraminiferal biomass was determined using an adenosine triphosphate (ATP) assay. Within ~6 hours of box core collection, specimens were individually extracted for ATP in a

boiling phosphate-citrate buffer (DeLaca, 1986) after their lengths and widths were recorded.

Extracts were frozen until further analysis. Replication of multiple cores per site was not

possible due to the necessity of timely ATP extractions to avoid collection and sampling artifacts

(i.e., cell death prior to extraction) in combination with limited person power aboard the vessel

for foraminiferal extractions.

In the shore-based laboratory, frozen ATP extracts were thawed and analyzed with

luciferin-luciferase reaction using a Berthold Lumat LB9507 luminometer. Standard curves of

known ATP concentrations ([ATP]) were also run for each reagent batch as appropriate.

Luminometer counts were converted to ATP content and, subsequently, organic carbon content

(i.e., biomass) was calculated from ATP data using the established conversion factor for

foraminifera (i.e., C:ATP = 300; DeLaca, 1986). Because our objective for the DGoMB project

was to determine total foraminiferal biomass rather than distinguish live from dead specimens,

the [ATP] from all specimens with positive readings was summed, rather than using only data

above a live-dead threshold (e.g., Bernhard and Reimers, 1991). Foraminiferal density too was

determined from ATP results, because conventional rose Bengal staining can be inaccurate (see

Bernhard, 2000 and references therein); those specimens with ATP were considered to be living

at the time of extraction, thus the number of living foraminifers could be calculated given that

the aliquot volume was known. Length and width measurements recorded prior to ATP

extraction were used to determine the volume of each individual by considering each

species/morphotype as having an idealized geometric shape (e.g., cylinder, oblate spheroid,

prolate spheroid, hemisphere). A 95% significance level was used to determine significance in

our linear regressions. Foraminiferal community composition was analyzed with non-parametric

multivariate multidimensional scaling (MDS) analyses, based on Bray-Curtis similarity. Data

was double square root transformed prior to analysis to down-weight the effect of dominant species. Grouping of stations in the MDS plot was based on Bray-Curtis similarities of 20 and 40%. Diversity indices and non-parametric multivariate community analyses (cluster analysis and multidimensional scaling) of foraminiferal data were calculated with PRIMER 5.0 (Clarke and Warwick, 2001). Foraminiferal biomass differences with depth were tested by comparing stations shallower and deeper than 2000 meters with an unpaired t-test.

Metazoan meiofaunal data were collected from 5.5-cm inner diameter subcores taken from five replicate box cores at each site. To conform to other studies of deep-sea meiofauna (see Thistle *et al*., 1991), a 45-μm mesh sieve was used to retain meiofauna. Meiofauna were extracted from the 0-3 cm sediment interval using the Ludox centrifugation technique (deJonge and Bouwman, 1977; Burgess, 2001).   Samples were then sorted and counted to a major metazoan taxonomic category (for more detailed information see Baguley, 2004).

Meiofaunal counts comprise two categories: temporary meiofauna (i.e., those juveniles of the macrofauna that will eventually grow into larger organisms) and permanent meiofauna (i.e., those groups where adults are <300 μm in length; e.g., Nematoda, Harpacticoida, Gastrotricha, Turbellaria, Acari, Gnathostomulida, Kinorhyncha, Tardigrada, Ostracoda, and some Nemertinea, Oligochaeta, Polychaeta; Higgins and Thiel, 1988; Giere, 1993). Biomass was calculated for nematodes and harpacticoid copepods, the two dominant components of Gulf of Mexico deep-sea meiofauna community biomass, using a newly-developed digital microphotographic approach (Baguley *et al.* 2004, Baguley, 2004). Foraminiferal and metazoan biomass differences were compared using a paired t-test. All parametric statistical analyses were conducted using SAS statistical software (SAS Institute Inc., 1989).

3. RESULTS

3.1 Density and Biomass

In the surface centimeter, benthic foraminiferal densities ranged over an order of magnitude ($\sim$3,600-45,500 individuals m^{-2}) and foraminiferal biomass ranged from $\sim$2 to 53 mg C m^{-2} (Table 1). When data from the top three centimeters were integrated, foraminiferal densities ranged from $\sim$9,100 to 82,000 m^{-2} and biomass ranged from 3.4 to 98.1 mgC m^{-2} (Table 1). In six cases, the biomass and density in the subsurface interval (1-2 cm or 1-3 cm) equaled or exceeded that of the surface cm (Fig. 2). Integrated foraminiferal biomass was significantly greater at stations shallower than 2000 m, in comparison to stations deeper than 2000 m (P = 0.0486). However, foraminiferal biomass at stations S42 and MT3 (<1000 m) was comparable to the deeper JSSD stations (>3000 m). There is a significant trend of decreased biomass per individual with increasing water depth (Fig. 3A; y=1.48-0.0003x; r^2_{adj}=0.529), even though the variability in many sample populations was considerable. The average volume per live foraminifer was not significantly correlated to increasing water depth (Fig. 3B), with a maximum specimen size at $\sim$1000 m (sta. C7).

3.2 Taxonomic Composition

Agglutinated foraminifera were more abundant than calcareous forms (Table 2; Fig. 4). Nine of the ten most abundant species were agglutinated taxa (Table 3). *Saccorhiza ramosa* was the most common species observed, living at eight of the ten sites.   Species of *Reophax* were also relatively common, occurring at seven sites. *Ammolagena clavata* and *Bathysiphon* spp. occurred in six of the subcores; *Eratidus foliaceus* and *Karrerulina conversa* occurred at half the sites. *Usbekistania charoides* lived at four of the ten sites.   Komokiacean foraminifers were also observed in a variety of forms (e.g., *Lana* sp., *Edgertonia argillispherula*, *Septuma* sp.). The

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most common calcareous taxa were *Bolivina* spp. and *Cibicides wuellerstorfi*, which occurred at only a few sites (≤3) but occasionally in relatively high abundance. Other calcareous taxa that lived at three sites were *Bulimina* spp., *Pyrgo* sp. and *Quinqueloculina* sp. Allogromid foraminifers were found living at two sites. *Nodellum membranaceum*, which has a tectinous shell similar to that of allogromids, occurred at two sites, in some instances in relatively high abundances (site JSSD4; 3410 m). Also, one specimen of the rhizopod *Gromia*, which is a closely related taxon to foraminifera, was found living at a depth of 1838 m (site S36).

Numerous large (up to 5 cm long) "tree-like" agglutinated foraminifers occurred at site S36 (1848 m), with densities up to ~130 m^{-2}. These are tentatively identified as *Pelosina* sp. (Fig. 5). Although no specimens were present in the subcore used for foraminiferal analyses, these dendritic foraminifers were observed in most boxcores collected from this site. *Pelosina* sp. biomass, determined from ATP analysis of six individuals, ranged from ~2.8 to 13 µg C $specimen^{-1}$, thus comprising a monospecific biomass of up to ~1.7 mg C m^{-2}. A few additional *Pelosina* sp. specimens were also observed at site C7 (1076 m).

Diversity measurements indicate that no significant trends existed with respect to water depth (Table 4). Multidimensional scaling analysis indicates, however, that there are four distinct groups that are approximately 25% similar (Fig. 6), including two singlets (one each from the Florida Escarpment and Sigsbee Abyssal Plain). The maximum similarity between any two stations was 46% (C7 and S36). Both Mississippi Trough samples grouped together, but were only 27% similar. The remainder comprised the largest group with an overall similarity of approximately 30%.

3.3 Comparison to Metazoan Meiofauna

In the surface 3 cm, foraminiferal density never exceeded metazoan meiofaunal density (Table 5; Fig. 7A). For the same 3-cm interval, foraminiferal biomass did, however, exceed the metazoan meiofaunal biomass at five of the ten sites (Table 5; Fig. 7B). At stations shallower than 2000 m, foraminiferal biomass exceeded metazoan meiofaunal biomass only at one station (Bush Hill). Conversely, foraminiferal biomass exceeded metazoan meiofaunal biomass at four of the five stations deeper than 2000 m (Table 5; Fig 7B). Foraminiferal biomass was not significantly different, however, than metazoan meiofaunal biomass at stations shallower ($P = 0.2184$) or deeper ($P = 0.3076$) than 2000 m ($\alpha = 0.05$).

4. DISCUSSION

4.1 Foraminiferal Density and Biomass

The foraminiferal densities obtained from the Gulf of Mexico slope and abyss were lower than those determined in a previous study (using ATP analysis) across a similar water-depth range in the eastern Pacific (624-3728 m, ~3,000-408,000 foraminifers m^{-2}; Bernhard, 1992). In general, Gulf of Mexico foraminiferal densities determined in this study were comparable to the density of foraminifers estimated using rose Bengal at one site in the Arabian Sea (3350 m, ~58,000 foraminifers m^{-2}; Gooday *et al.*, 2000). The foraminiferal densities determined here were comparable to or slightly higher than those determined using rose Bengal at another Gulf of Mexico non-seep site. More specifically, foraminiferal densities at a non-seep site in the Alaminos Canyon (western Gulf; 2238 m) ranged from ~0.7 to 1.1 foraminifers cm^{-3} (Robinson *et al.*, 2004), vs. ~0.4 to 4.5 foraminifers cm^{-3}, as observed in this study.

It is important to note that at the time of box core recovery, the temperature of the water overlying the cored sediments was often elevated (>18°C) due to the high surface-water and air temperatures during collection (June). Given that ambient bottom-water temperatures at the collection sites are all < 10°C, this thermal difference could have been detrimental to foraminiferal survival during box-core recovery. We still found it necessary to sample these cores, because of the time constraints of the multi-tasked DGoMB project, especially in the context of the depths of the abyssal sites which prolonged the core-recovery periods (e.g., collection of a core from a 3000-m site required >2.0 hours). In some box cores, the overlying water was murky, indicating that the core had been disturbed and/or that the sediment surface had been lost. Thus, in some cases, foraminiferal biomass and density data were possibly underestimated. On the other hand, foraminiferal density could be overestimated for some agglutinated forms given the tubular dendritic morphology of those taxa. Estimates of biomass for these forms are not an overestimate, however, due to the normalization of this parameter to test (shell) volume.

The maximum foraminiferal density occurred in the subsurface (i.e., >1 cm) at two sites; two others had subsurface values that equaled those of the surface cm. Subsurface maxima of foraminiferal density have been noted in other slope settings (eastern Pacific, Bernhard, 1992). Down-core (i.e., 1-3 cm) maxima in foraminiferal biomass occurred at the three shallowest sites, suggesting that refractive organic matter is utilized by these benthic communities.

Foraminiferal density did not consistently vary with water depth or longitude (Table 1; Fig. 8). Foraminiferal biomass did vary somewhat with depth (Table 1, Fig. 2B). This difference in biomass was not strongly significant (i.e., $P = 0.0486$), however, primarily due to high variability within stations shallower than and greater than 2000 m. For example, in the

surface centimeter at one ~1000-m site (Site MT3; 985 m), foraminiferal biomass was relatively

low (~9 mg C m-2) while another ~1000-m site (Site C7; 1076 m) had the highest foraminiferal

biomass (~53 mg C m-2); and for stations deeper than 2000 m, JSSD5 (3316 m) had

foraminiferal biomass 2-7 times higher than the other four stations in this group. Note that, MT3

and C7 were geographically separated by only ~75 km (Fig. 1).

The highest estimates of foraminiferal biomass were from the two salt-diapir basin sites,

which were near hydrocarbon seeps (Bush Hill, C7); these foraminiferal biomasses may be

linked to chemosynthetic productivity at the seeps, given an increase in foraminiferal density was

noted at other Gulf of Mexico seeps compared to an adjacent non-seep site (Robinson *et al.*,

2004). The site with the lowest foraminiferal biomass is on the Mississippi Fan (MT6; 2742 m),

where a high sedimentation rate may negatively affect foraminiferal standing stocks. The other

Mississippi Trough site (MT3), which is located in the shallower part of the Trough (985 m),

also had relatively low foraminiferal density and biomass. Particulate organic matter flux at

MT3 is high compared to stations of similar depth in the northern Gulf of Mexico (Baguley

2004). Thus, high sedimentation rates may be responsible for the relatively low foraminiferal

abundances.

Although most samples from Sigsbee Abyssal Plain had low foraminiferal biomass (i.e.,

<9 mg C m^{-2}), one had >20 mg foraminiferal C m^{-2} (JSSD5). This site is located at the base of

the Sigsbee Escarpment and lies slightly off the Loop Current axis, suggesting that deep-water

currents and sedimentation rates may have been favorable at this site compared to other parts of

the Sigsbee Plain, supporting a relatively high foraminiferal biomass. In comparison, the other

three Sigsbee Plain sites (JSSD1, JSSD2, JSSD4), which have typical abyssal clay sediments,

had low foraminiferal biomass but relatively high foraminiferal densities. Although the average

volume per specimen in Sigsbee Plain samples was not significantly lower than those from shallower sites, the average biomass per specimen was low. Sigsbee Plain foraminifers were small but populations were dense for the Gulf of Mexico in general. Given the lack of replication and the typical box core disturbance, however, the density and biomass results presented here should be considered with caution. In addition, patchiness of foraminifera is noted to occur in the deep sea (e.g., Bernstein *et al.*, 1978; Bernstein and Meador, 1979), so conclusions about the forces driving foraminiferal distributional and diversity patterns are tentative (also see below).

4.2 Foraminiferal Taxonomic Composition

A comparison of foraminiferal species identified in this study with those reported at and near Gulf of Mexico seeps (Alaminos Canyon, Atwater Canyon, Green Canyon; Robinson *et al.*, 2004) shows limited similarity: of the 57 taxa noted here, 24 were conspecifics or congenerics of those listed in Robinson *et al.* (2004). The dominant species in this study, *Saccorhiza ramosa*, was not observed, however, in either the non-seep or seep samples of Robinson *et al.* (2004). Foraminiferal diversity, which is not significantly correlated to water depth in our samples, could correlate to physiography but the lack of replication in our study and the patchiness in deep-sea foraminiferal populations (Bernstein and Meador, 1979) prevent confident assessments here regarding the controlling factors of diversity. The observed foraminiferal community evenness (J') was comparable to that of an Alaminos Canyon non-seep site (Robinson *et al.*, 2004). While agglutinated foraminifers are expected to dominate over calcareous forms at water depths greater than the calcite compensation depth, they also dominated in Gulf of Mexico bathyal depths, which are not below the calcite compensation depth. The predominance of dendritic

agglutinated foraminifers on the slope (e.g., S36, *Pelosina*) suggests that bottom-current activity is sufficient to support large populations of suspension feeders (e.g., Cedhagen, 1993).

We note that the relative abundance of the agglutinated group is much higher in our data than in earlier data on living foraminifera from deeper bathyal or abyssal Gulf of Mexico (Phleger and Parker, 1951; Parker, 1954; Reynolds, 1982; Sen Gupta and Aharon, 1994; Sen Gupta *et al.*, 1997). We argue that this discrepancy is due to a substantial difference in sample handling. In contrast to the cited studies, the sediment treatment in our investigation did not include (1) ethanol or formaldehyde fixation (which makes relatively ductile agglutinated tests more brittle, and thus prone to damage or destruction during wet sieving); (2) sieving under a faucet; and (3) oven drying, as in some earlier studies. Thus, soft- and thin-shelled foraminifera were much better preserved in our >63-μm sediment fraction. Four such genera (*Catena, Edgertonia, Lana, Septuma;* Figs. 4, 5), have never before been reported from the Gulf of Mexico (Sen Gupta et al., in press).

Multidimensional scaling analysis indicated (1) a similarity between the two sampling sites of 975 m and 2742 m water depths in the Mississippi Trough, and (2) a grouping of most Sigsbee Abyssal Plain and the deeper Florida Escarpment sites (all >1840 m) with the much shallower salt-diapir basin sites (548 and 1076 m). Four different water masses cover these physiographic realms: Oxygen Minimum Water (250-650 m); Subantarctic Intermediate Water (650-1000 m), Caribbean Midwater (1000-1500 m), and Gulf Basin Water (>1500 m) (Nowlin, 1971, 1972; Morrison *et al.*, 1983). Thus, our present data from the deeper seafloor of the Gulf do not show a linkage of discrete benthic foraminiferal communities with particular water masses. In contrast, however, analyses of large data sets based mainly on counts of individuals that were dead when collected (empty tests from surface sediment) have shown conspicuous

matches of species groups or associations with water masses (Denne and Sen Gupta, 1991, 1993; Jones and Sen Gupta, 1995).   For example, the dominant taxon Poag (1981) ascribes to the Mississippi Fan (i.e., *Cibicides*) is not the dominant one in our sample collected from the Fan (MT6). We emphasize that for all depth regimes, species distributions reported in these earlier studies, showing dominance of calcareous taxa, are very different from our findings; the discrepancy is possibly related to a procedural difference in sample collection and treatment (discussed earlier), and to in-situ, post-mortem test destruction of delicate agglutinated tests. In any case, any firm conclusion on the relationship between boundaries of water masses and those of living foraminiferal communities in the bathyal-abyssal Gulf of Mexico must await more extensive sampling than was possible in the current project.

4.3 Foraminiferal-Metazoan Comparison

Although two different methods were used to calculated foraminiferal and metazoan meiofaunal data, metazoan meiofauna outnumbered foraminifers at all sites, but metazoan meiofauna biomass was not significantly different than foraminiferal biomass.   Although biomass values were not statistically different for foraminiferal and metazoan meiofauna, a general trend was observed. That is, foraminiferal biomass exceeded metazoan biomass at deeper stations (>2000 m), while metazoan meiofaunal biomass exceeded foraminiferal biomass at shallower stations (<2000 m). In particular, foraminifers dominated the biomass at stations BH and C7, which is near known seeps. This may suggest preferential survival by foraminifers relative to metazoans in the proximity of seeps. Conversely, metazoan meiofauna dominated the biomass at stations S42 and MT3, which had particularly high particulate organic matter flux (Baguley 2004), perhaps suggesting preferential survival by metazoans in areas of organic enrichment.

Overall, these comparisons reveal that foraminifers and metazoan meiofauna contribute approximately equally to the deep-sea benthic community, and constitute a major component of the Gulf's deep-water meiofaunal biomass. Therefore, the total meiofauna likely contribute significantly to whole community metabolism, although this group has been largely ignored in previous studies of deep-sea benthic community function.

5. CONCLUSIONS

The Gulf of Mexico bathyal and abyssal foraminiferal fauna is dominated by agglutinated forms. Foraminiferal abundance and diversity do not simply vary with water depth in the Gulf of Mexico, but there appears to be a weak relationship of biomass with depth. Additional phenomena responsible for the observed patterns could be associations with geographic features, each with particular forces that affect the faunal distributions (e.g., proximity to seeps, proximity to the Mississippi River Delta, proximity to the Sigsbee Escarpment, and to the Loop Current). Comparable biomass of foraminifers and metazoan meiofauna suggests that both groups may play an important role in deep-sea benthic community function and therefore carbon cycling.

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Figure Captions

Figure 1. Map showing site locations (*) in the Gulf of Mexico. Other symbols represent additional collections of the DGoMB project (Rowe and Kennicutt, 2001).

Figure 2. A. Benthic foraminiferal density (individuals m^{-2}; A) and biomass (mg C m^{-2}; B) with respect to water depth (m). Plus symbols, 0-1 cm; open squares, 1-2 or 1-3 cm; filled triangles, integrated over 0-3 cm. See Table 1 to determine exact sampling intervals in a core.

Figure 3. Average amount of biomass estimated from ATP per live specimen (A) and average volume per live specimen (B) related to water depth.

Figure 4. Light micrographs of representative Gulf of Mexico bathyal and abyssal benthic foraminifers. **A**. *Ammolagena clavata,* dead (JSSD1); **B**. *Ammoscalaria tenuimargo*, live (JSSD5); **C.** *Aschemonella ramuliformis*, live (JSSD2); **D.** *Catena piriformis*, live (JSSD5); **E.** *Cibicides wuellerstorfi*, live (JSSD4); **F.** *Edgertonia argillispherula*, live (JSSD2); **G.** *Eratidus foliaceus* (JSSD2); **H.** *Hormosinella distans*, dead (JSSD5); **I.** *Jaculella obtusa*, live (JSSD4); **J.** *Karrerulina conversa* (JSSD2); **K.** *Lana* sp., dead (JSSD1); **L.** *Marsipella cylindrica*, dead (JSSD4); **M.** *Nodellum membranaceum*, dead (JSSD5); **N.** *Nodellum* sp., dead (JSSD5); **O.** *Praeglobobulimina ovata*, live (JSSD4); **P.** *Psammosphaera* sp., live (JSSD1); **Q.** *Reophax agglutinatus*, live (JSSD1); **R.** *Reophax dentaliniformis*, live (JSSD4); **S.** *Reophax spiculifer*, live (JSSD1); **T.** *Rhabdammina cornuta*, dead (JSSD5); **U.** *Rhizammina* sp., dead (JSSD1); **V.** *Saccorhiza ramosa*, live (JSSD2); **W.** *Saccorhiza ramosa*, dead (JSSD2); **X.** *Septuma* sp., live

(JSSD2); **Y.** *Usbekistania charoides* (JSSD2). Scale bars = 200 µm, except M, N, Y bars = 100 µm.

Figure 5. Light micrographs of *Pelosina* sp., large agglutinated arborescent foraminifer. **A.** Specimen *in situ*. **B.** Specimen removed from sediment to show sub-surface "root" structure. **C.** Two additional specimens, one broken. Approximate location of the sediment-water interface when in life position is indicated by the arrows. All scale bars ~ 1 cm.

Figure 6. Multidimensional scaling analysis based on foraminiferal species composition. Species abundance was double square root transformed prior to analysis to deemphasize the influence of dominant species. Distance between stations is proportional to the similarity of species composition. Circled groups are greater than 25% (solid line) and 30% (dashed line) similar in species composition.

Figure 7. Paired comparison of metazoan meiofaunal (black bars) and benthic foraminiferal (grey bars) density (A) and biomass (B) in the top 3 cm of sediment. Stations are listed in order of increasing water depth. Stations BH, S42, MT3, C7, and S36 are all shallower than 2000 m depth. Stations MT6, JSSD5, JSSD4, JSSD1 and JSSD2 are all greater than 2000 m.

Figure 8. Benthic foraminiferal density (A) and biomass (B) in the top 1 cm at each sampling site. Unit for density values is number per square meter; unit for biomass is mg C m^{-2}.

Table 1. Site designations, dates of collection, water depths, site coordinates, and benthic foraminiferal abundances (# m^{-2}) and biomass (mgCm^{-2}) for the surface cm (0-1 cm) and integrated over the top 3 cm (0-3 cm). * data from 0-2 cm only (no data for 2-3 cm); + data from 0-2 cm instead of 0-1 cm.

Site	Date	Water Depth (m)	^{o}N, ^{o}W	0-1 cm Density (#×10^4 m^{-2})	0-1 cm Biomass (mgC m^{-2})	0-3 cm Density (#×10^4 m^{-2})	0-3 cm Biomass (mgC m^{-2})
Bush Hill	18 June 01	548	27°47.8, 91°28.2	4.5	47.1	8.2*	98.1*
S42	7 June 01	768	28°15.3, 86°25.6	0.4	2.9	0.7	6.0
MT3	16 June 01	985	28°13.3, 89°30.6	1.3	8.8	2.4	18.9
C7	16 June 01	1076	27°43.7, 89°58.7	2.5	53.4	4.2*	74.9*
S36	9 June 01	1848	28°55.4, 87°39.0	2.9	52.5	4.5	62.1
MT6	13 June 01	2742	27°00.2, 88°00.9	0.5	1.8	0.9	3.4
JSSD5	13 June 02	3316	25°29.5, 88°16.2	1.1	20.9	2.7*	23.8*
JSSD4	10 June 02	3410	24°14.5, 85°29.1	4.5+	8.4+	5.0	9.8
JSSD1	3 June 02	3520	25°00.6, 92°00.7	2.7	3.7	3.1	6.4
JSSD2	6 June 02	3732	23°30.0, 92°00.2	3.5	8.0	7.5*	11.9*

Table 2. Number of benthic foraminifera determined by ATP assay to be live, from all analyzed core intervals per site (0-2 cm cores denoted with *; others are 0-3 cm) BH = Bush Hill, JS = JSSD series.

	BH*	S42	MT3	C7*	S36	MT6	JS5*	JS4	JS1	JS2*
Allogromid				1	1					
Ammodiscus sp.			1							
Ammolagena clavata	1	3		2	4		1			5
Ammoscalaria tenuimargo							1			
Aschemonella ramuliformis	2					1				4
Bathysiphon spp.	1		2	3	7	1		1		
Bolivina spp.	8									
Bulimina marginata			1	1						
Bulimina mexicana	1									
Catena piriformis							3			
Chilostomella sp.	1									
Cibicides wuellerstorfi				1			1	6		
Cibicidoides sp.	2	1								
Edgertonia argillispherula										4
Edgertonia sp.									1	
Epistominella sp.	2									
Eratidus foliaceus				1			1	1	1	2
Globobulimina sp.	1									
Hoeglundina elegans					2		1			

Species										
Hormosinella distans									2	
Hormosinella guttifera							1			
Jaculella obtusa								3		
Karrerulina conversa	2			1	1			3	4	
Lagenammina difflugiformis										2
Lana sp.	1		2							2
Marsipella cylindrica										1
Miliammina sp.				2						
Miliolinella subrotunda				1						
Nodellum membranaceum				1				4		
Nodellum sp.	1				1					
Oridosalis sp.			1							
Oryctoderma sp.					1					
Pelosina sp. 2								1		
Praeglobobulimina ovata								3		
Psammosphaera sp.				1	1				1	
Pyrgo spp.		1			1					1
Quinqueloculina sp.		1	1					1		
Recurvoides sp.	2					1		1		
Reophax agglutinatus								2	1	
Reophax dentaliniformis							1	2	2	1
Reophax gaussicus								1		
Reophax spiculifer							2		1	

Species										
Reophax spp.	6		3		2		1		1	1
Rhabdammina cornuta							1			
Rhabdammina sp.						1	1			
Rhizammina sp.				1						
Saccamminid	1									
Saccorhiza ramosa	6		4	7	6	5		19	5	12
Septuma sp.										1
Storthosphaera albida			1							
Textularia sp.	1									
Trifarina sp.	1									
Triloculina sp.			2							
Usbekistania charoides	2				2			2		4
Uvigerina hispida			1							
Veleroninoides sp.	1							1		
Calcareous juvenile										1
Unidentified calcareous sp.					1					
Gromia sp.					1					
Total number live	43	6	19	23	31	9	15	51	19	41
Number extracted (0-3 cm)	100	100	100	100	120	100	107	125	100	110
Number of species	20	4	11	13	14	5	12	16	10	14

Table 3. Dominant foraminiferal species found in this study of the deep Gulf of Mexico.

Species	% Contribution	Cumulative %
Saccorhiza ramosa	51.7	51.7
Ammolagena clavata	10.1	61.8
Bathysiphon spp.	7.0	68.7
Reophax spp.	6.7	75.5
Karrerulina conversa	4.1	79.5
Eratidus foliaceus	3.5	83.0
Usbekistania charoides	2.8	85.8
Reophax dentaliniformis	2.3	88.0
Quinqueloculina sp.	1.4	89.4
Aschemonella ramuliformis	1.2	90.6

Table 4. Diversity calculations for live foraminiferal community (all those with ATP), listed by site. J' = Pielou's evenness; ES = Hurlbert's rarefaction; H' = Shannon Weiner information index.

Site	Water Depth (m)	J'	ES(6)	H'$_{(log 10)}$
Bush Hill	548	0.895	5.081	1.164
S42	763	0.896	4.000	0.540
MT3	990	0.943	5.047	0.982
C7	1066	0.889	4.809	0.989
S36	1826	0.885	4.788	1.014
MT6	2743	0.810	3.667	0.566
JSSD5	3350	0.964	5.473	1.041
JSSD4	3400	0.808	4.351	0.973
JSSD1	3545	0.905	4.687	0.905
JSSD2	3725	0.865	4.611	0.991

Table 5. Foraminiferal density and biomass compared to metazoan density and biomass (0-3 cm).

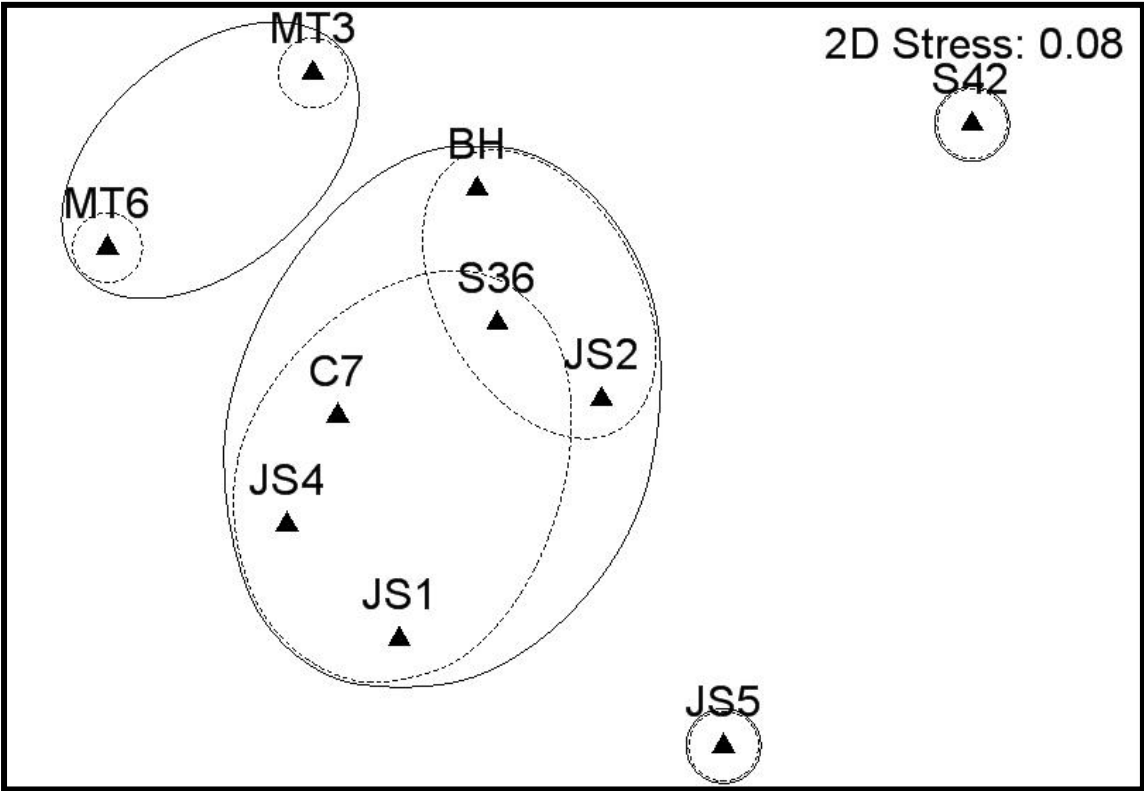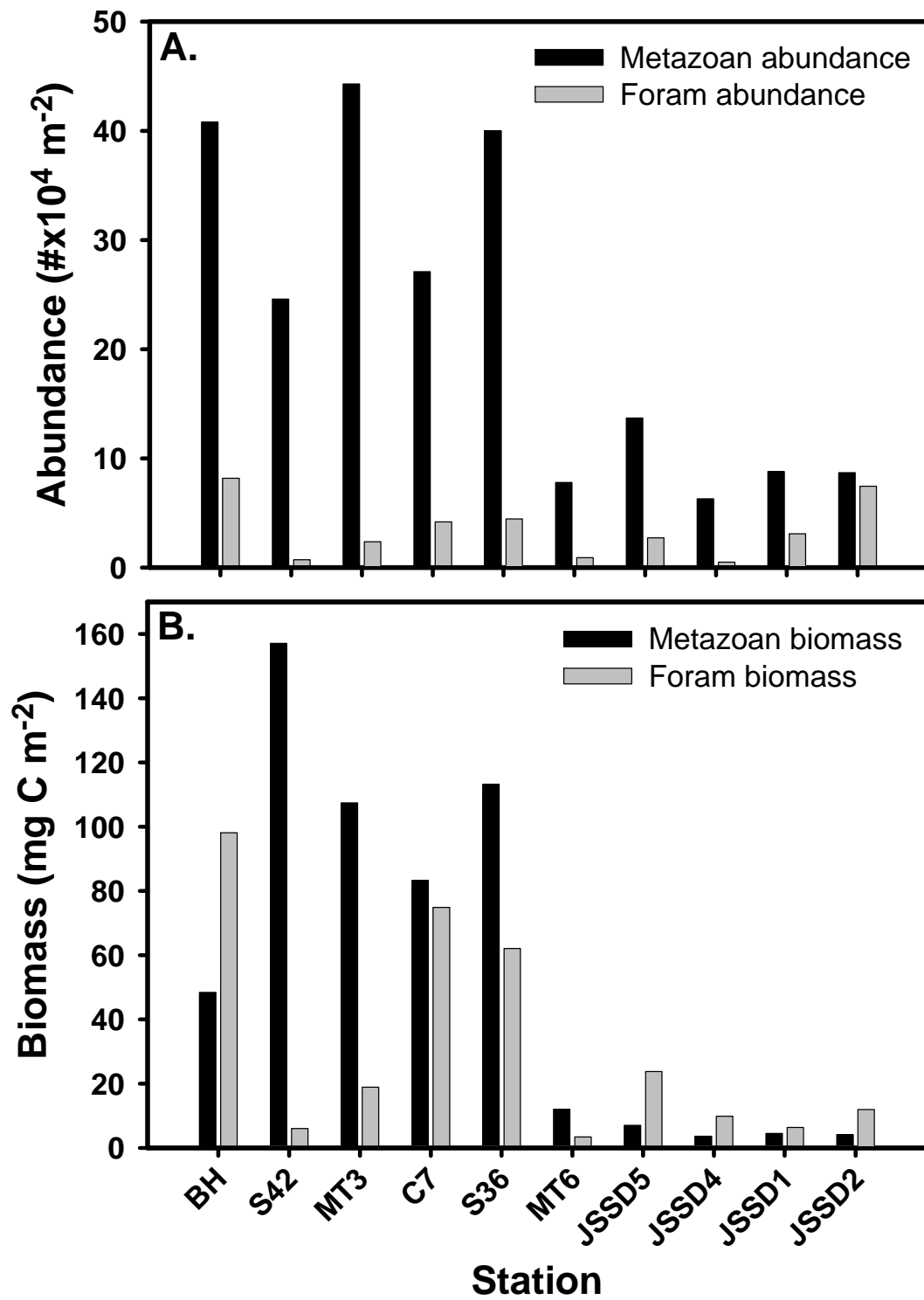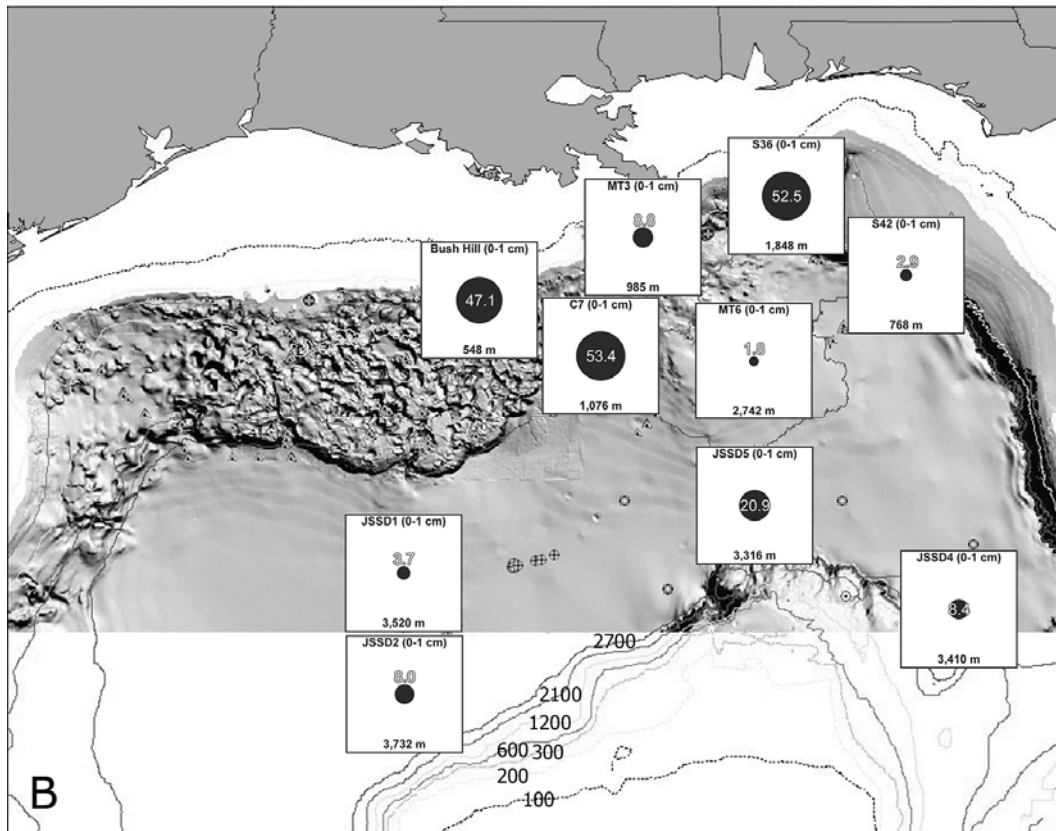| Site	Water	Foraminifera		Metazoa	
	Depth	Density	Biomass	Density	Biomass
	(m)	($\#\times10^4$ m^{-2})	(mgC m^{-2})	($\#\times10^4$ m^{-2})	(mgC m^{-2})
Bush Hill	548	8.2*	98.1*	40.8	48.4
S42	768	0.7	6.0	24.6	157.1
MT3	985	2.4	18.9	44.3	107.4
C7	1076	4.2*	74.9*	27.1	83.3
S36	1848	4.5	62.1	40.0	113.2
MT6	2742	0.9	3.4	7.8	12.0
JSSD5	3316	2.7*	23.8*	13.7	7.0
JSSD4	3410	5.0	9.8	6.3	3.6
JSSD1	3520	3.1	6.4	8.8	4.5
JSSD2	3732	7.5*	11.9*	8.7	4.1
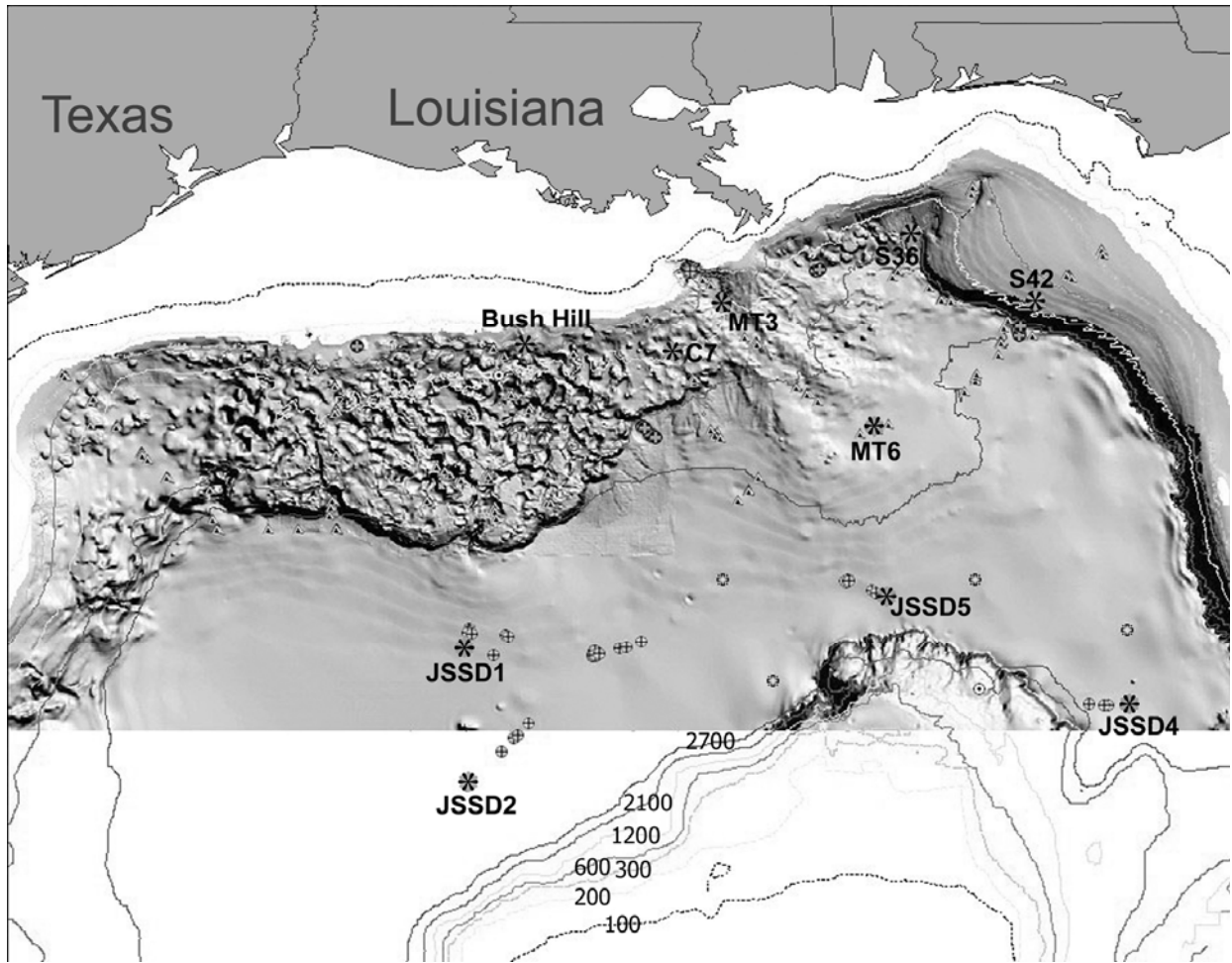
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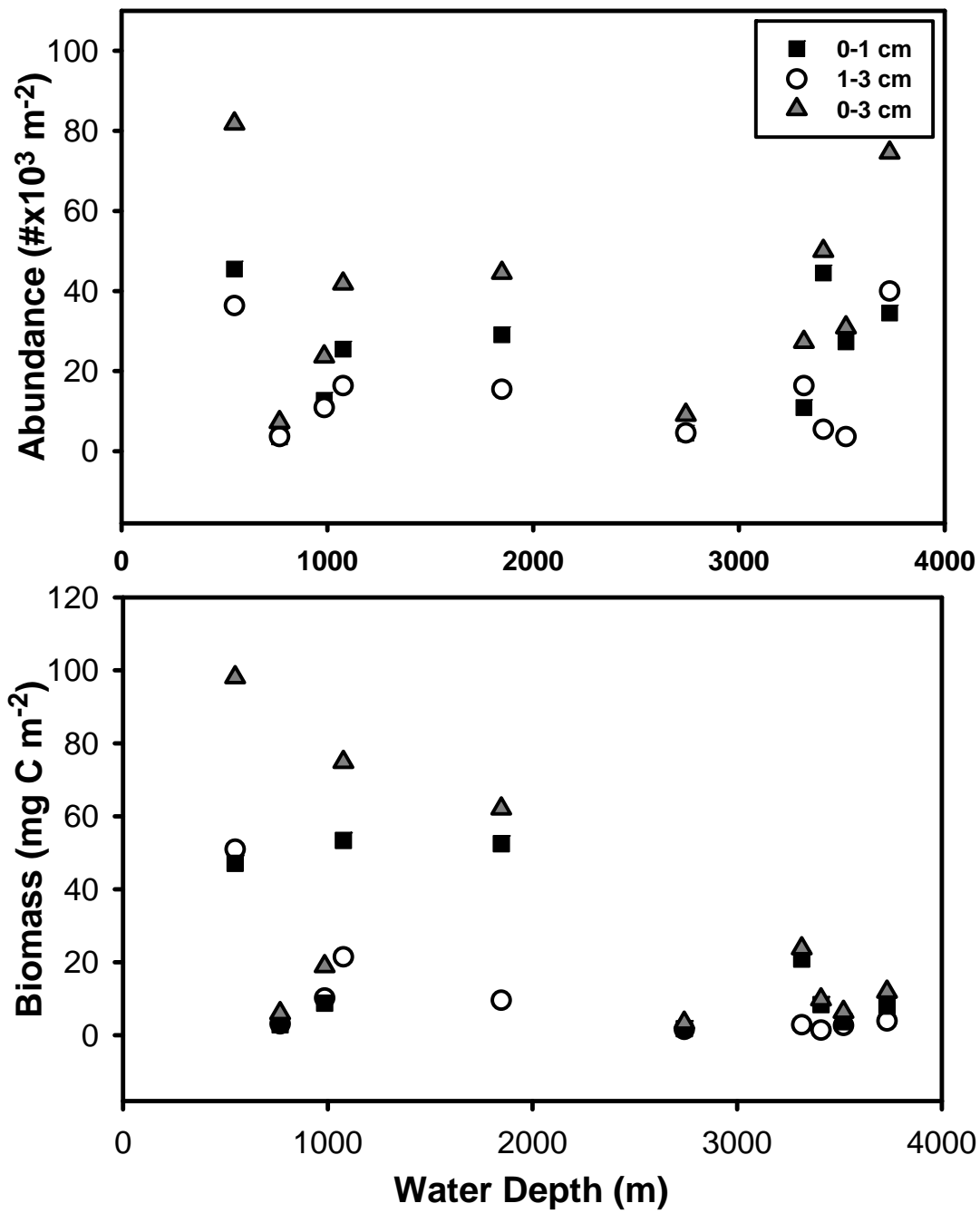
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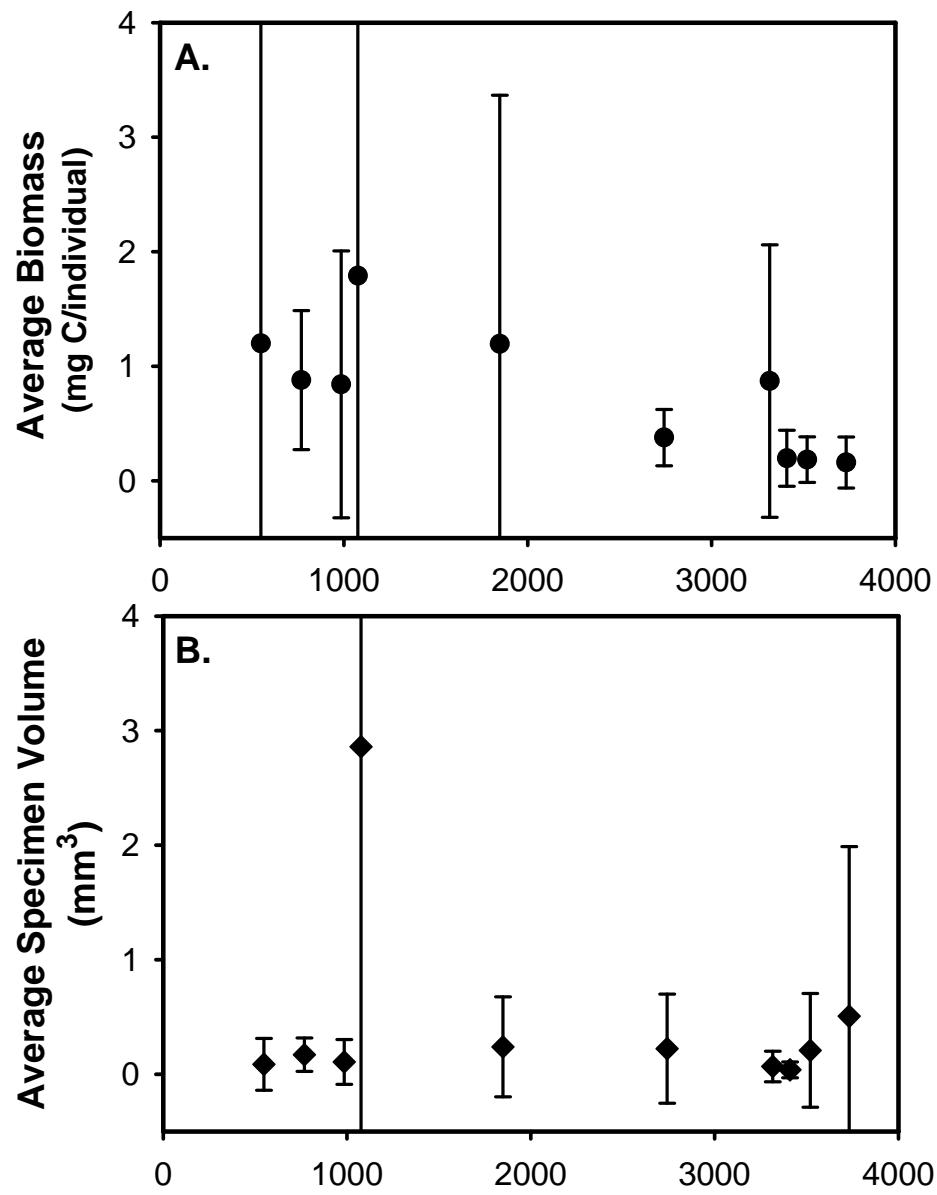
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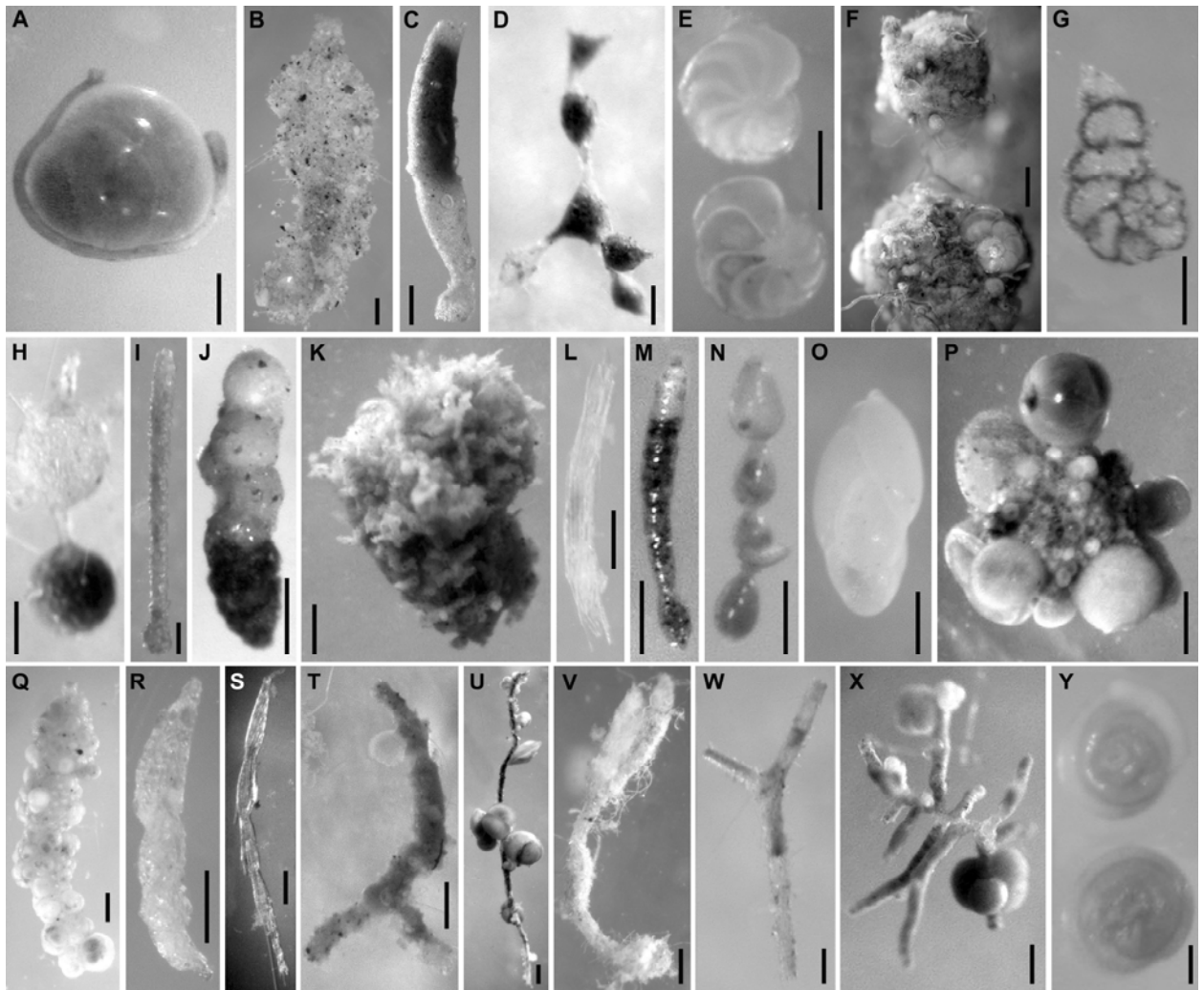
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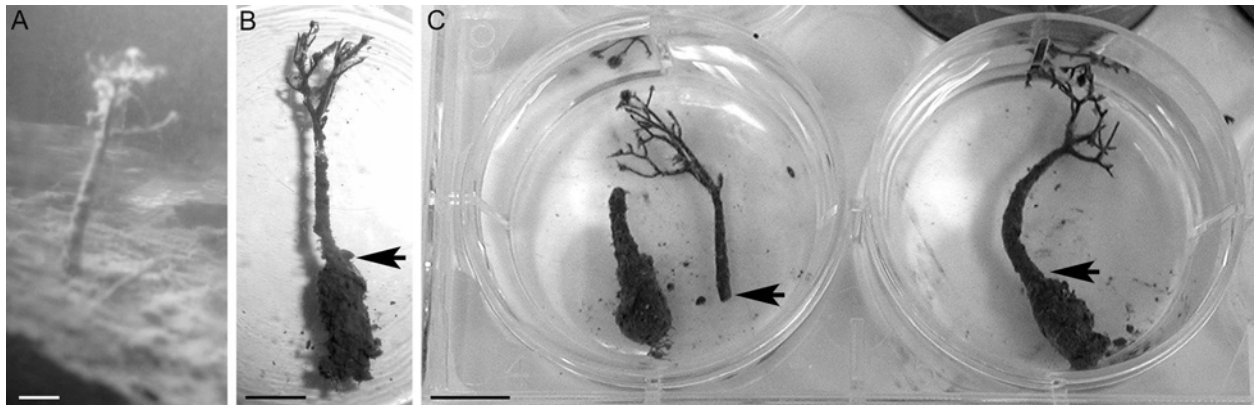
Figure 5.

Fig. 6.

Figure 7.

Figure 8.