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Surficial Hydrocarbon Seep Infauna from the Blake Ridge (Atlantic Ocean, 2150 m) and the Gulf of Mexico (690–2240 m)

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With 4 figures and 7 tables

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Abstract. Infauna, including foraminifera and metazoans, were enumerated and identified from five types of seep habitats and two adjacent non-seep habitats. Collections were made with the deep submergence research vessel 'Alvin' from three areas of active seepage in the Gulf of Mexico (Alaminos Canyon [2220 m], Atwater Canyon [1930 m], and Green Canyon lease block 272 [700 m]) and on the Blake Ridge Diapir [2250 m], which is located off the southeastern coast of the United States. The seep habitats sampled included four types of microbial mats (*Beggiatoa*, *Thioploca*, thin and thick *Arcobacter*) and the periphery of a large mussel bed. Sediments under large rhizopod protists, xenophyophores, were sampled adjacent to the mussel bed periphery. A non-seep site, which was >1 km away from active seeps, was also sampled for comparison. Densities of most taxa were higher in the Gulf of Mexico seeps than in Blake Ridge samples, largely because densities in the thick microbial mats of Blake Ridge were significantly lower. Diversity was higher in the *Thioploca* mats compared to other microbial-mat types. Within an ocean basin (*i.e.*, Atlantic, Gulf of Mexico) we did not observe significant differences in meiofaunal or macrofaunal composition in *Beggiatoa* versus *Thioploca* mats or thin versus thick *Arcobacter* mats. Foraminifera represented up to 16% of the seep community, a proportion that is comparable to their contribution at adjacent non-seep communities. In general, the observed densities and taxonomic composition of seep sites at the genus level was consistent with previous

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*Author to whom correspondence should be addressed. Department of Geology and Geophysics, Woods Hole Oceanographic Institution, MS 22, Woods Hole, MA 02543, USA. E-mail: jbernhard@whoi.edu observations from seeps (*e.g.*, the foraminifers *Bolivina* and *Fursenkoina*, the dorvilleid polychaete *Ophryotrocha*).

Problem

Descriptions of deep-water hydrocarbon seep communities are based primarily on underwater still photographs, video recording, and megafaunal sampling obtained from submersibles (Sibuet & Olu, 1998). Less work has been done on the smaller eukaryotic organisms inhabiting seep sediments. A review of previous investigations regarding seep infauna (foraminifera, metazoan meiofauna and macrofauna) can be found in Levin (2004). Most studies documenting metazoan seep communities describe a fauna comprised largely of annelids and nematodes, with reduced species richness and elevated dominance compared to more typical deep-sea environments. The few studies of seep foraminifera indicate relatively low diversity and density at seeps and a lack of indigenous foraminiferal fauna (*e.g.*, Sen Gupta & Aharon, 1994; Rathburn *et al.*, 2000; Bernhard *et al.*, 2001). While a few studies have considered both metazoan meiofauna and macrofauna at seeps (Powell *et al.*, 1986; Dando *et al.*, 1991; Jensen *et al.*, 1992; Olu *et al.*, 1997), none have considered foraminifera in their meiofaunal counts.

This paper examines the densities and composition of foraminifera, metazoan meiofauna, and polychaetes within different environments from active seep areas and non-seep areas located on the slope of passive continental margins in the Gulf of Mexico (Alaminos Canyon, Atwater Canyon, and Green Canyon) and in the mid-North Atlantic (Blake Ridge). Using material collected from seep (microbial mats, mussel beds) and non-seep sediments (under xenophyophores, off active seeps), the following questions were addressed: (1) Do microbial-mat covered seep sediments support different infaunal communities compared to non-seep sediments? (2) Do communities of varied microbial mats differ within basins? (3) Do individual faunal constituents (*e.g.*, foraminifera, metazoan meiofauna, macrofauna) show similar responses in seep environments (*i.e.*, are densities positively correlated?) and (4) Are community dominants in the Gulf of Mexico and Blake Ridge hydrocarbon seeps similar to those in other seep sediments? To address these questions, we documented the density and composition of benthic foraminifers and metazoans in the surficial sediments of microbial mat habitats (*i.e.*, *Beggiatoa* and *Thioploca* in the Gulf of Mexico and thin and thick *Arcobacter* mats at Blake Ridge), a mussel-bed seep habitat, and adjacent non-seep sites (distant from active seeps and under xenophyophores). This description of infaunal densities, general taxonomic composition and a detailed examination of diversity and species composition in foraminifera and polychaetes from these four seeps augments the existing database on smaller seep infauna, and provides material for biogeographical comparisons.

Gas hydrates of the western North Atlantic are exposed at the Blake Ridge methane seep, which is located off South Carolina (Fig. 1; Van Dover *et al.*, 2003). Megafaunal constituents of the Blake Ridge seep include the chemoautotrophic mussel *Bathymodiolus heckerae*, vesicomyid clams, cake urchins, and, possibly, xenophyophores (Paull *et al.*, 1996; Van Dover *et al.*, 2003). The dominant feature at the Blake Ridge site is a large *B. heckerae* bed, which has a diameter of $\sim$20 m, consisting of live mussels near the center and dead mussels around the periphery.

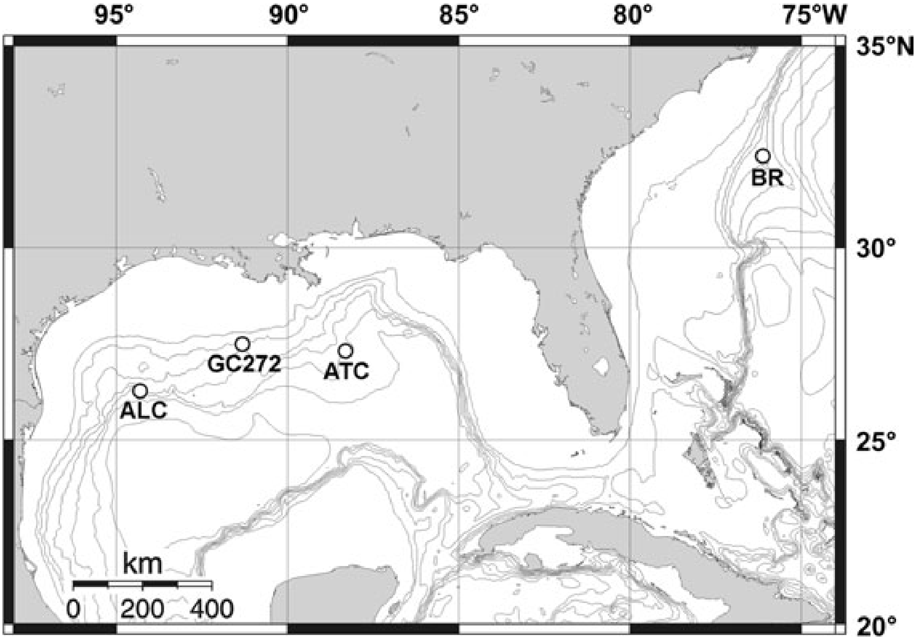

Fig. 1. Map showing locations of the sampling sites off the southeastern United States. ALC = Alaminos Canyon; GC272 = Green Canyon lease block 272; ATC = Atwater Canyon; BR = Blake Ridge. Contour interval = 500 m.

The Alaminos Canyon, which lies in the northwestern Gulf of Mexico (Fig. 1), was created by a combination of coalescing salt canopies along with erosional events such as turbidity and debris flows (Rowe & Kennicutt, 2001). Major megafaunal constituents of this seep include unidentified chemolithic mussels and vestimentiferan tubeworms (Carney, 1994). The Atwater Canyon site is a hydrocarbon seep atop a diapiric hill that has tubeworms, mussels, carbonate rubble, and possible gas hydrate mounds (MacDonald *et al.*, 2003). Green Canyon 272 is an oil seep located in lease block 272 of Green Canyon that supports vesicomyid clams (Sassen *et al.*, 1994).

Material and Methods

1. Sample collections

The deep submergence research vessel 'Alvin', supported by RV 'Atlantis', was used to obtain all samples, which were 6.9-cm inner-diameter pushcores. Nine cores were collected at Blake Ridge Diapir from water depths of 2154–2158 m during 'Alvin' dives 3709–3712, which centered on Ocean Drilling Program (ODP) site 996 (32°30.5′ N, 76°11.5′ W; Fig. 1, Table 1). Five cores were collected from Alaminos Canyon from water depths ranging from 2215 to 2238 m during 'Alvin' dives 3624 and 3625, which centered around 26°21.2′ N, 94°29.5′ W. Three additional Gulf of Mexico cores were examined: two from ∼700 m in Green Canyon 272 (27°41.151′ N, 91°32.293′ W; 'Alvin' dive 3627), and one from 1934 m in Atwater Canyon (27°34.748′ N, 88°30.625′ W; 'Alvin' dive 3633).

Pushcores were housed in a high-density polypropylene container to minimize thermal warming on ascent. As soon as possible after the submersible was secured on the fantail, this container was taken into the ship's cold room (5 °C). Pushcores with intact sediment-water interfaces were extruded; the top 1-cm

Table 1. Pushcore sample information.

habitat	site	collection date	water depth [m]	core
non-seep	Alaminos Canyon	17 Oct 2000	2238	17
non-seep	Alaminos Canyon	17 Oct 2000	2238	18
Beggiatoa mat	Alaminos Canyon	18 Oct 2000	2222	23
Beggiatoa mat	Alaminos Canyon	18 Oct 2000	2215	25
Beggiatoa mat	Alaminos Canyon	18 Oct 2000	2215	26
Thioploca mat	Green Canyon 272	20 Oct 2000	692	46
Thioploca mat	Green Canyon 272	20 Oct 2000	700	48
Thioploca mat	Atwater Canyon	26 Oct 2000	1934	81
thin *Arcobacter* mat	Blake Ridge Diapir	25 Sept 2001	2158	3
thin *Arcobacter* mat	Blake Ridge Diapir	28 Sept 2001	2154	14
thin *Arcobacter* mat	Blake Ridge Diapir	28 Sept 2001	2155	16
thick *Arcobacter* mat	Blake Ridge Diapir	26 Sept 2001	2156	5
thick *Arcobacter* mat	Blake Ridge Diapir	26 Sept 2001	2155	6
mussel-bed periphery	Blake Ridge Diapir	25 Sept 2002	2155	2
mussel-bed periphery	Blake Ridge Diapir	25 Sept 2001	2157	4
under xenophyophore	Blake Ridge Diapir	28 Sept 2001	2157	13
under xenophyophore	Blake Ridge Diapir	28 Sept 2001	2157	15

portion of each core was either divided into halves or equal thirds depending on sampling needs and preserved in 10% buffered formaldehyde or in 3% TEM-grade glutaraldehyde/0.1 M cacodylate buffer (pH 7.2) using standard procedures (Bernhard *et al.*, 2001). In pushcores containing a xenophyophore, the epifaunal xenophyophore was removed with as little disturbance to the sediment surface as possible and subsequent core sectioning proceeded as usual. Faunal counts do not include specimens associated with the xenophyophore test (shell). Pushcores that degassed hydrocarbons during ascent were too homogenized for our purposes and were therefore not analyzed for this study.

2. Specimen isolation and statistical analyses

Once in the shore-based laboratory, the formalin-preserved samples were stained with rose Bengal to facilitate sample sorting. After a >12 h incubation in rose Bengal, each sample was sieved over a 63 μm screen using artificial seawater; the coarser fraction (*i.e.*, all specimens retained on the 63 μm screen) was examined using a Nikon SMZ-2B stereo-dissecting microscope. Due to high densities in the Atwater Canyon material and one GC272 sample, only a (known) fraction of these samples was analyzed.

For convenience, we adopt the conventional size classes and major taxonomic groupings for meiofauna (63–300 μm; *i.e.*, nematodes, copepods, kinorhynchs, ostracods, foraminifers) and macrofauna (>300 μm; *e.g.*, polychaetes). All rose-Bengal-stained foraminifera and metazoans were isolated, enumerated and archived. Shelled foraminifera (*i.e.*, calcareous and agglutinated) were placed on micropaleontological slides; metazoans were sorted by major taxa. For foraminifera, only calcareous and agglutinated specimens were counted; data for the rarely occurring allogromid foraminiferans are pending. Foraminifera remain in the collection of the corresponding author. Polychaetes are archived at the Scripps Institution of Oceanography invertebrate collection. Nematodes are housed in the laboratory of P. J. D. Lambshead (Natural History Museum, London). Differences in taxon mean densities between basins (*i.e.*, Gulf of Mexico and Blake Ridge), among varied microbial mat types within the same basin, and among all seven habitats sampled were assessed by one-way analysis of variance (ANOVA) followed by a Tukey multiple comparison test. To meet the assumption of normal distributions required by the ANOVA, total densities of organisms were log transformed (with base 10). Results were considered significant at the $P < 0.05$ level. Group analyses were conducted for total taxa, total metazoan meiofaunal taxa, and macrofaunal taxa. Individual taxa with sufficient numbers of individuals were statistically analyzed separately (*i.e.*, foraminifera, polychaetes, nematodes, copepods, copepod nauplii).

Multivariate analyses of community structure were carried out on data for foraminifera and metazoan taxa (all those listed in Table 2). Analyses, including multivariate community analyses (Multidimensional Scaling, ANOSIM, SIMPER) and diversity indices, were conducted with Primer Software (Clarke & Warwick, 1994) on fourth-root transformed data. A Bonferoni corrected alpha ($\alpha = 0.05$/number of

Table 2. Densities [individuals·(10 cm^3)$^{-1}$] of meiofauna and macrofauna in Alaminos Canyon (ALC), Atwater Canyon (ATC), Green Canyon (GC272), and Blake Ridge (BR) pushcores.

core	ALC					ATC	GC272		BR								
	non-seep		*Beggiatoa*			*Thioploca*	*Thioploca*		thin *Arcobacter*			thick *Arcobacter*		mussel bed		xenophyophore	
	17	18	23	25	26	81	46	48	3	14	16	5	6	2	4	13	15
Foraminifera	7.4	10.7		16.0	16.8	17.1	97.9	12.8	10.4	4.0	6.4	1.6		4.3	8.6	0.5	0.5
Nematoda	44.9	58.3	611.9	107.5	139.1	4809	125.2	381.9	31.3	23.3	55.4	1.6	2.4	78.1	41.7	23.0	18.2
Kinorhyncha				1.6													
Polychaeta	0.5	0.5	13.9			36.4	266.4	112.3	0.8		0.8				2.1		
Copepoda	4.8	10.2	39.6	24.1	33.2	340.2	63.6	73.8	2.4	1.6				25.1	20.3	33.2	27.8
Copepoda nauplii	7.5	6.4	104.8	30.0	24.1	1254	67.9	41.7	62.6	3.2	1.6	5.6		29.4	5.9	32.6	4.3
Tanaidacea														0.5			
Acari														0.5			
Isopoda			2.1											1.1	0.5		
Cumacea	1.1			0.5	1.1			2.1									
Ostracoda								57.8	12.8	1.3	1.6	1.6		0.5	2.7		
Gastropoda	1.1		2.1		1.6		8.0	6.4			1.6				0.5		1.1
Bivalvia		1.6	0.5	1.6	4.3		2.7		0.8					4.3	0.5	0.5	0.5
total	67.4	87.7	774.9	181.3	220.3	6457	631.7	688.9	121.1	33.7	67.4	10.4	2.4	143.9	82.9	89.8	52.4

treatments) was applied to ANOSIM interpretations. Rarefaction curves were generated to assess foraminiferal diversity using Biodiversity Pro. Cores from each habitat were pooled for rarefaction analysis.

Results

1. Sediment and microbial-mat characteristics

All four sites had various habitats associated within and around active seep areas; seven habitats were sampled. All active seep sites had patches of white microbial mats that varied in appearance when observed from both the submersible as well as in the pushcore (Fig. 2). Samples from these mats were designated as belonging to four habitats. Sediments containing what appeared to be mats of the sulfide-oxidizing chemolithotrophic filamentous bacterium *Beggiatoa* were collected in three cores (Alaminos Canyon, cores 23, 25, 26; Table 1). Core 23 was taken from a mat that was not well developed or extensive (<20 cm diameter). Cores 25 and 26 contained long, filamentous bacterial strands, which, in contrast to other mats, extended into the overlying water (Fig. 2A). Core 25 was taken ∼1 m away from core 26. Distinctly black, anoxic sediments were not obviously present in either of these two cores. Cores from Green Canyon 272 (cores 46, 48) and Atwater Canyon (core 81) also contained filaments similar in appearance to *Beggiatoa*, but microscopic examination revealed that these filaments were typically bundled in organic sheaths. Thus, these mats were considered to be comprised of the sulfide-oxidizing bacterium *Thioploca* and are designated as *Thioploca* mats (Fig. 2G).

From the submersible, the Blake Ridge seafloor had white patches that appeared to be thin (∼1–3 mm) *Beggiatoa* mats (Fig. 2B–F). Microscopic examination, however, indicated that the filaments in cores 3, 14, and 16 were morphologically unlike *Beggiatoa*. Rather, this material represented inorganic fibers, perhaps of elemental sulfur, and cohesive organic matter as matrix, suggesting the 'mats' included the vibrioid sulfur-oxidizing *Arcobacter* (Taylor & Wirsen, 1997; Wirsen *et al.*, 2002). Regardless of their true nature, we refer to these white patches as *Arcobacter* and they differ from *Beggiatoa* and *Thioploca* mats. Although these mats have been briefly described from other Gulf of Mexico seeps (Nikolaus *et al.*, 2003), their eukaryotic faunal composition remains undocumented. During the retrieval of these three cores, a black cloud of sediment was discharged (Fig. 2D). Photographs of these pushcores show a layer of black, and presumably anoxic, mud beneath the thin film of white material at the sediment-water interface (Fig. 2E). These cores expelled a strong odor of hydrogen sulfide and hydrocarbons when uncapped in the cold room prior to subsampling.

The Blake Ridge also had areas of white material that were much thicker (up to ∼3 cm) than those noted above. The maximum dimension of these patches was ∼12 cm (Fig. 2F). Microscopically the composition of the white material in the respective pushcores (cores 5, 6) was similar to that of cores 3, 14, and 16. Thus, these thick mats are also preliminarily identified as *Arcobacter*. None of the microbial mats sampled were taken from locations that had visible 'blow-out' structures (*i.e.*, visibly removed surface sediments from vigorous fluid expulsion). Another seep habitat sampled was the periphery of the Blake Ridge mussel bed, which was cored twice (cores 2, 4) in sediments lacking large mussels.

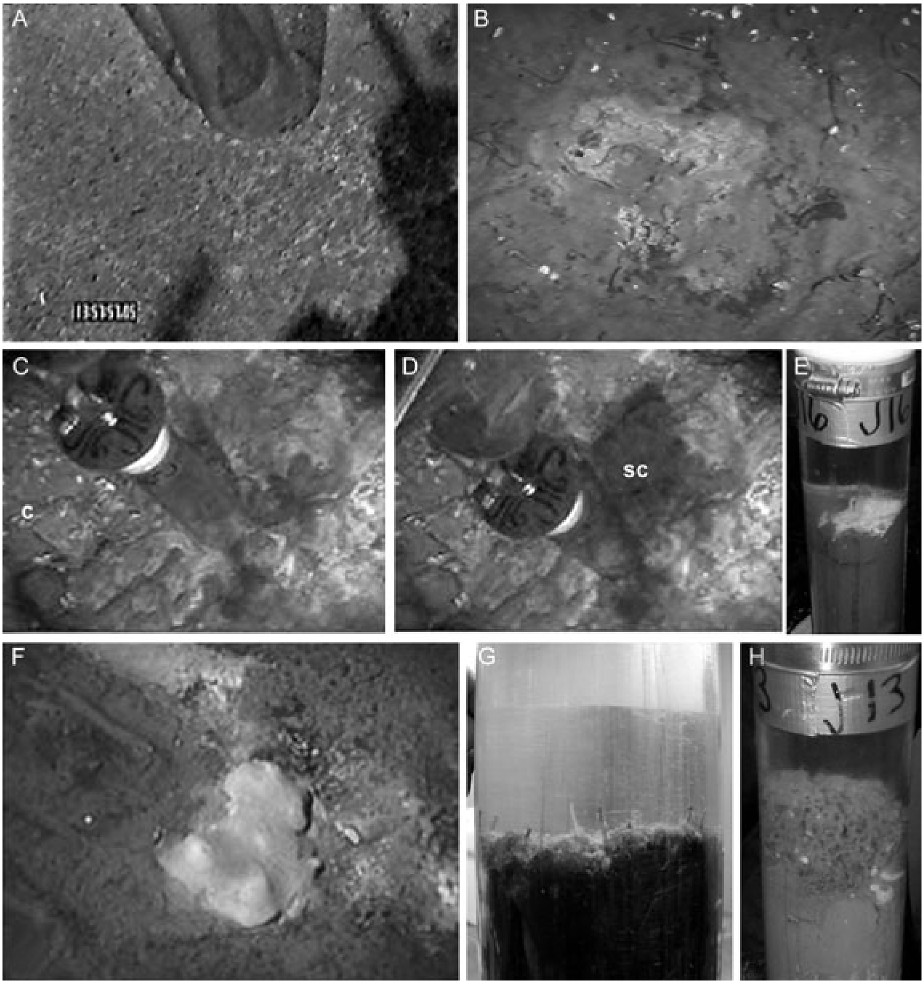

Fig. 2. Photographs showing some of the habitats sampled. A, B, C, D, F were taken at depth using 'Alvin' video cameras. A: *Beggiatoa* mat from Alaminos Canyon. B: Thin *Arcobacter* mat. Another thin *Arcobacter* mat before (C) and during (D) coring, plus resultant core as viewed before sectioning (E). Note cloud of black sediments (sc) caused by sampling. F: Thick *Arcobacter* mat. Distance between dots caused by laser beams is 20 cm. G: *Thioploca* mat also showing polychaete tubes. H: Core containing xenophyophore.

Two non-seep habitats were sampled for comparison. The xenophyophores at Blake Ridge live within a few centimeters of the mussel bed (Van Dover *et al.*, 2003). However, for our purposes, sediments from the xenophyophore cores were classified as a non-seep habitat because xenophyophores are not considered seep-endemic taxa and at Blake Ridge they were located adjacent to dead chemoautotrophic mussels. Xenophyophores are large rhizopods that usually construct tests of sedimentary material. Those at Blake Ridge probably belong to the genus *Syringammina* (A. J. Gooday, electronic comm.), congenerics of which have recently been identified as a foraminiferan (Pawlowski *et al.*, 2003). Two cores (cores 13, 15; Fig. 2H) were taken from this habitat, each containing one individual xenophyophore that had a diameter approaching that of the corer. The final non-seep habitat included samples taken about 1.2 km away from visible surface manifestations of seep activity in Alaminos Canyon (cores 17, 18).

2. Faunal densities and composition

The fauna of samples from all four sites consisted mainly of foraminifera, nematodes, harpacticoid copepods, and polychaetes, although bivalves, gastropods, kinorhynchs, isopods, cumaceans, ostracods, tanaids, and mites also occurred (Table 2).

2.1. Foraminifera

Foraminiferal densities varied considerably [0–98 individuals·$(10\ \mathrm{cm}^3)^{-1}$] and foraminifera comprised up to 16% of the total community. Combining all habitats and sites within a basin, foraminiferal densities at Gulf of Mexico sites were five fold higher than at Blake Ridge in the Atlantic (ANOVA, $P = 0.031$). There were significant between-basin differences in composition (ANOSIM, Global $R = 0.351$, $P = 0.002$), with 96.85% dissimilarity (SIMPER). Differences were due mainly to higher densities of *Epistominella exigua*, *Reophax nodulosus*, *Nodellum membranaceum*, *Hoeglundina elegans*, and *Cibicidoides* spp. in the Gulf of Mexico and higher densities of *Fursenkoina complanata* at Blake Ridge (Table 3). Although densities in microbial mat sediments in the Gulf of Mexico did not differ significantly from those in mats at Blake Ridge, the composition was distinct (Global $R = 0.30$, $P = 0.048$). Comparisons of densities by mat type within the Gulf of Mexico (*Thioploca* versus *Beggiatoa*) revealed no difference in density (ANOVA, $P = 0.208$) or composition (ANOSIM, $P = 0.300$). However, thin *Arcobacter* mats had higher foraminiferal densities than thick *Arcobacter* mats at Blake Ridge (ANOVA, $P = 0.047$), although the composition was similar (ANOSIM, $P = 0.750$).

When each habitat was treated individually, none of the foraminiferal assemblages had significantly different compositions from one another despite a significant overall ANOSIM (Global $R = 0.469$, $P = 0.003$; Fig. 3A, Table 4). This is because within-habitat heterogeneity of cores was relatively large (0–41% assemblage similarity, SIMPER, Table 4), suggesting that foraminiferal distributions reflect considerable small-scale patchiness. There were, however, notable density differences. Foraminifera were absent in two samples: one *Beggiatoa* mat and one *Arcobacter* mat (Tables 2 and 3). All samples from thick *Arcobacter* mats and xenophyophore cores had very few, if any, foraminifera. Densities at the Gulf of Mexico non-seep site were significantly higher than those from the Blake Ridge ‘non-seep’ xenophyophore pushcores (ANOVA, $P = 0.007$); they were not significantly different from any other habitat. Within the same basin at Blake Ridge, foraminiferal densities in xenophyophore samples were significantly lower than in thin *Arcobacter* mats (ANOVA, $P = 0.014$) and at the mussel-bed periphery (ANOVA, $P = 0.034$).

The foraminiferal assemblages were relatively diverse given their low densities (Table 5). Gulf of Mexico assemblages (average core H' log base $10 = 0.95$) are significantly more diverse (t-test for cores with >1 individual, $t_9 = 2.595$, $P = 0.029$) than those at Blake Ridge (average core H' log base $10 = 0.62$). On average (although not

Table 3. Densities [individuals·(10 cm^3)$^{-1}$] of rose-Bengal-stained foraminifera in Alaminos Canyon (ALC), Atwater Canyon (ATC), Green Canyon (GC272), and Blake Ridge (BR) pushcores.

core	ALC					ATC	GC272		BR								
	non-seep		*Beggiatoa*			*Thioploca*	*Thioploca*		thin *Arcobacter*			thick *Arcobacter*		mussel bed		xenophyophore	
	17	18	23	25	26	81	46	48	3	14	16	5	6	2	4	13	15
Ammodiscus tenuis		0.5															
Ammolagena clavata					0.5												
Bathysiphon sp.							0.5										
Bolivina sp.					0.5						0.8						
Brizalina earlandi		0.5		1.6			1.1		1.6	1.6					0.5		
Brizalina ordinaria							3.2	1.1									
Brizalina spathulata?							10.2	1.1		0.8							
Brizalina translucens								10.2									
Brizalina sp.															1.1		
Bulimina aculeata							3.2										
Bulimina marginata								1.1									
Cassidulina neocarinata					0.5												
Chilostomella oolina							0.5										
Cibicides sp.							0.5										
Cibicidoides robertsonianus				0.5													
Cibicidoides spp.							3.7	3.2									
Cyclogyra sp.							12.3										
Dentalina aphelis	0.5				0.5			1.1									
Epistominella exigua	2.7	0.5		8.6	2.7		5.9										
Fissurina annectens									0.8								
Fursenkoina complanata				1.1			5.3		4.0		3.2	0.8		1.1	1.6		
Fursenkoina rotundata								3.2									
Gavelinopsis translucens							9.1	2.1									

Table 3. Continued.

core	ALC					ATC	GC272		BR								
	non-seep		*Beggiatoa*			*Thioploca*	*Thioploca*		thin *Arcobacter*			thick *Arcobacter*		mussel bed		xenophyo-phore	
	17	18	23	25	26	81	46	48	3	14	16	5	6	2	4	13	15
Globobulimina pacifica							3.7										
Globocassidulina cf. *biora*							0.5	1.1									
Globocassidulina sp.							0.5										
Gyroidina sp.							1.1										
Hoeglundina elegans	1.1	2.7			2.7												
Hyperammina elongata		0.5															
Lagena multilatera?											0.8						
Lagena nebulosa											0.8						
Lagena sp.							1.1										
Lagenammina arenulata				0.5													
Lagenammina sp.				0.5													
Lenticulina gibba					0.5		0.5										
Melonis pompilioides																	0.5
Nodellum membranaceum	1.6	1.6			3.7												
Nodellum sp.	0.5																
Nonionella basiloba	0.5						4.3										
Oolina globosa				0.5													
Oridosalis umbonata								1.1									
Osangularia umbonifera					0.5												
Parafissurina felsinea				0.5													
Planispiroides bucculentus?		0.5															
Praeglobobulimina ovata				0.5					0.8			0.8		0.5	0.5		
Pullenia quinqueloba							1.1		1.6	0.8				0.5	0.5		
Pullenia sp.		0.5				0.5											
Pulleniatina obliquiloculata														0.5			
Pyrgo depressa														0.5			

Table 3. Continued.

core	ALC					ATC	GC272		BR								
	non-seep		*Beggiatoa*			*Thioploca*	*Thioploca*		thin *Arcobacter*			thick *Arcobacter*		mussel bed		xenophyo-phore	
	17	18	23	25	26	81	46	48	3	14	16	5	6	2	4	13	15
Pyrgo murrhina		0.5															
Pyrgo sp.									1.6						1.1		
Pyrulina angusta	0.5																
Quinqueloculina spp.		1.0					3.2										
Reophax dentaliniformis					0.5		1.6										
Reophax nodulosus						17.1	0.5										
Rhizammina algaeformis		0.5															
Robertina tasmanica						0.5											
Technitella sp.															1.1		
Textularia sp.							1.6			0.8	0.8			0.5	1.6		
Trifarina bradyi							3.2	1.1									
Triloculina sp.					3.2		1.1										
Trochammina sp.							1.1										
Uvigerina peregrina							0.5									0.5	
Vagulinopsis reniformis				0.5										0.5			
Veleroninoides wiesneri															0.5		
juvenile agglutinate spp.				0.5			1.6										
juvenile calcareous spp.	0.5	0.5			0.5		1.6										
total	7.4	10.7	0.0	16.0	16.8	17.1	97.9	12.8	10.4	4.0	6.4	1.6	0.0	4.3	8.6	0.5	0.5

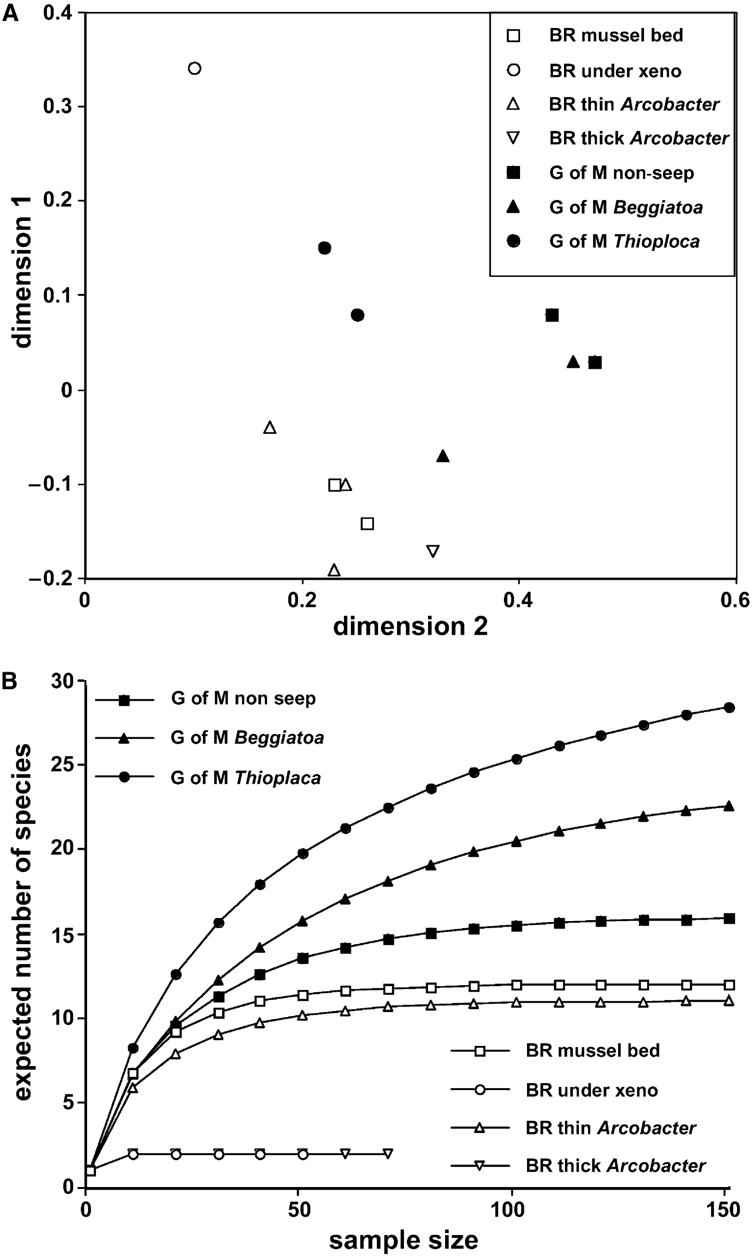

Fig. 3. A: MDS plot illustrating foraminiferal assemblages from the Gulf of Mexico (G of M) *Beggiatoa* mats, *Thioploca* mats, and non-seep sediments (filled symbols) and Blake Ridge (BR) thin *Arcobacter* and thick *Arcobacter* mats, mussel bed periphery, and under xenophyophores (xeno) (open symbols). Stress = 0.01. One xenophyophore core is off scale and one thick *Arcobacter* core with 0 individuals is not plotted. B: Rarefaction curves based on pooled rose-Bengal-stained foraminiferal counts from each habitat.

Table 4. Multivariate analyses of foraminifera. SIMPER within-habitat percent similarity is given on the diagonal (bold); SIMPER between-habitat dissimilarity is given below the diagonal. ANOSIM probabilities of between-habitat differences are given above the diagonal.

	Thioploca	*Beggiatoa*	thin *Arcobacter*	thick *Arcobacter*	mussel bed	xeno-phyophore	non-seep
Thioploca	**5.8**	0.30	0.10	0.50	0.20	0.20	0.20
Beggiatoa	95.4	**16.1**	0.10	0.67	0.33	0.33	1.00
thin *Arcobacter*	97.8	91.0	**28.9**	0.75	1.00	0.10	0.10
thick *Arcobacter*	96.0	92.9	84.4	**n.a.**	0.33	1.00	0.33
mussel bed	98.0	90.4	68.0	64.1	**41.7**	0.33	0.33
xenophyophore	99.8	100	100	100	100	**0**	0.33
non-seep	97.1	68.6	97.9	100	98.6	100	**41.2**

Global R = 0.469; P = 0.003.

significant, $P = 0.079$), evenness is higher at Blake Ridge ($J = 0.95$) than in the Gulf of Mexico ($J = 0.87$; Table 5). When only microbial-mat cores were analyzed for foraminiferan diversity, H′ was greater in the Gulf of Mexico ($t_6 = -3.051$, $P = 0.023$), but no between-basin difference in evenness (J) was detected (t-test, $P = 0.197$). Rarefaction analyses suggest that, within an ocean basin, foraminifera in seep habitats exhibited higher diversity than non-seep forms (thick *Arcobacter* mats were the one exception; Fig. 3B). *Fursenkoina complanata* was the most abundant species, occurring in seven of the 17 samples. Only one other species occurred in at least one sample from each of Alaminos Canyon, Green Canyon, and Blake Ridge: *Brizalina earlandi*. A total of 13 species occurred in more than one seep locality (Table 3).

Table 5. Diversity calculations for foraminifera in each core. BR = Blake Ridge, GoM = Gulf of Mexico.

site	habitat	species (n)	H′(log10)	J	rank 1 dominance	dominant species
BR	mussel bed	7	0.83	0.98	0.26	*Fursenkoina complanata*
BR	mussel bed	9	0.91	0.96	0.19	*Fursenkoina complanata*
BR	xenophyophore	1	0.00		1.00	*Uvigerina peregrina*
BR	xenophyophore	1	0.00		1.00	*Melonis pompilioides*
BR	thin *Arcobacter*	6	0.71	0.91	0.38	*Fursenkoina complanata*
BR	thin *Arcobacter*	4	0.58	0.96	0.40	*Brizalina earlandi*
BR	thin *Arcobacter*	5	0.60	0.86	0.50	*Fursenkoina complanata*
BR	thick *Arcobacter*	2	0.30	1.00	0.50	*Fursenkoina complanata*
GoM	non-seep	7	0.75	0.89	0.36	*Epistominella exigua*
GoM	non-seep	13	1.02	0.92	0.25	*Hoeglundina elegans*
GoM	*Beggiatoa*	12	0.77	0.71	0.54	*Epistominella exigua*
GoM	*Beggiatoa*	13	0.96	0.86	0.22	*Nodellum membranaceum*
GoM	*Thioploca*	32	1.31	0.87	0.13	*Cyclogyra* sp.
GoM	*Thioploca*	9	0.91	0.95	0.25	*Cibicidoides* spp.
GoM	*Thioploca*	1	0.00		1.00	*Reophax nodulosus*

2.2. Metazoa

Total metazoan meiofaunal densities were higher in the Gulf of Mexico than at Blake Ridge for both seep and non-seep habitats (ANOVA, $P = 0.007$) and for seep habitats alone ($P = 0.004$). Thick *Arcobacter* mats at Blake Ridge had significantly lower meiofaunal densities than *Beggiatoa* (P = 0.013), *Thioploca* (P = 0.030) and thin *Arcobacter* (P = 0.034) mats.

Nematodes were the only taxon that occurred in all samples. Densities ranged from 1.6 to 4809 nematodes·(10 cm^3)$^{-1}$ (Table 2). There were significantly more nematodes in the Gulf of Mexico than at Blake Ridge for all habitats combined (P = 0.002) and for microbial mat sediments only (P = 0.004). Thick *Arcobacter* mats contained fewer nematodes than all other habitats (P = 0.032 to 0.004). Also, densities in *Beggiatoa* mats were significantly higher than in thin *Arcobacter* mats (P = 0.040) and xenophyophore pushcores (P = 0.047), but were not significantly different from *Thioploca* mats (P = 0.424). There were significantly fewer nematodes in Blake Ridge xenophyophore cores compared to Gulf of Mexico non-seep samples (P = 0.035).

Copepods were the second most abundant taxon, but were absent from three of the 17 analyzed samples. Densities were greater in the Gulf of Mexico than Blake Ridge for all habitats combined (P = 0.015) and especially for microbial-mat sediments (P < 0.0001). This was because densities were much lower in thin and thick *Arcobacter* mats relative to all other habitats (P = 0.024 to <0.001), and much higher in *Thioploca* mats (P = 0.003 to 0.006) (Table 2). Copepodite nauplii exhibited similar between-basin differences.

Harpacticoid copepods were the dominant crustacean in all samples. Ostracods occurred in low diversity in the Blake Ridge samples and one Green Canyon 272 sample (core 48). Most of the specimens were juveniles and thus difficult to identify. Adults of *Xylocythere* sp. (C. Alvarez-Zarikian, written comm., 2002) occurred in samples from both the mussel-bed periphery and all but one Blake Ridge bacterial mat.

The harpacticoid copepods were only identifiable at the family level, if at all. Most of the collected copepods are likely new to science (B. C. Coull, pers. comm., 2002). At least seven to nine species of harpacticoid copepods were recovered from under xenophyophores (B. C. Coull, pers. comm., 2002) and at least four species were present in mussel-bed periphery samples. Harpacticoids were the only crustaceans recovered from the thin *Arcobacter* bacterial mat. Only two copepod genera were found in mussel samples and thin *Arcobacter* samples: *Metahuntemannia* and *Mesocletodes*.

Macrofaunal results were similar to those obtained for the meiofauna; densities were higher in the Gulf of Mexico than at Blake Ridge (P = 0.005 for all habitats and P = 0.005 for microbial mat sediments). *Thioploca* mats had significantly higher densities than all other habitat types (*Beggiatoa*, P = 0.029; thin *Arcobacter*, P = 0.005; thick *Arcobacter*, P = 0.008; mussel beds, P = 0.032; xenophyophore, P = 0.014; Gulf of Mexico non-seep, P = 0.019), due mainly to large numbers of polychaetes and gastropods (Table 2). Thick *Arcobacter* mats and one thin *Acrobacter* core yielded very few macrofauna.

Polychaete densities were one to two orders of magnitude higher in the Gulf of Mexico than at Blake Ridge for all habitats combined (P = 0.0245) and for microbial mat habitats alone (P = 0.042) (Table 6). Densities ranged from 1 to 498 individuals per sample, with higher densities in *Thioploca* mats than any other habitat (P = 0.0245 to 0.002) (Tables 2 and 6). Two shallower-water *Thioploca* mat samples from the Green Canyon 272 exhibited one to two orders of magnitude higher polychaete densities [~266,000·m^{-2} (498 per sample) and 112,000·m^{-2} (105 per sample), respectively] than any other sample. The density in the one *Beggiatoa*-mat sample from Alaminos Canyon that had polychaetes was ~14,000·m^{-2} [13.9 specimens·(10 cm^3)$^{-1}$] (Tables 2 and 6). In general, polychaetes were an order of magnitude less abundant than most meiofaunal taxa. A bacterial-mat sample collected from Atwater Canyon (core 81) yielded a higher density ($\sim$36,400 polychaetes$\cdot$m^{-2}, 17 individuals per sample) than the other deeper-water sites. Blake Ridge polychaete densities were exceptionally low [<3 polychaetes$\cdot$(10 cm^3)$^{-1}$; $\sim$2100 specimens$\cdot$m^{-2}].

Most polychaetes in the above cores were juveniles, including specimens from five families (Table 6). The polychaete population in the single *Beggiatoa* mat sample from Alaminos Canyon (core 23) and three *Thioploca* mat samples from Atwater Canyon and Green Canyon in the Gulf of Mexico were comprised mostly of dorvilleid, hesionid, and syllid polychaetes (Table 6). The lack of adult specimens hampered confident species-level identifications.

Nine polychaete families were present in our samples, mainly Dorvilleidae (54%), Cirratulidae (27%), Ampharetidae (11%), and Hesionidae (4%) (Table 6). Only two of these families, Hesionidae and Cirratulidae, were present at Blake Ridge. Blake Ridge polychaete densities were too low to evaluate species diversity. Among Gulf of Mexico microbial mats, the one *Beggiatoa* sample had lower diversity (H′ log base 10 = 0.63) but higher evenness (J = 0.91) than the three *Thioploca* cores (H′ log base 10 = 0.75 to 0.90; J = 0.81 to 0.83). These quite low values reflect the high dominance of cirratulids and dorvilleids. Most dorvilleid individuals belonged to three species in the genus *Ophryotrocha*. Many of these taxa are characteristic of enriched, sulfidic or hypoxic settings worldwide (Grassle & Morse-Porteous, 1987; Levin *et al.*, 2003). The Cossuridae, Spionidae, Syllidae, and Acrocirridae were represented by just a few individuals.

3. Analysis of all infauna

The overall infaunal assemblage composition (based on major taxon data in Table 2, and MDS in Fig. 4) strongly differed between Blake Ridge and the Gulf of Mexico (Global R = 0.191, P = 0.016; SIMPER assemblage dissimilarity = 71.1%), driven largely by higher faunal densities in the latter (ANOVA; all habitats: P = 0.005; mats: P = 0.003). This between-basin difference is also evident when comparing all seep sites (ANOSIM, Global R = 0.491, P = 0.002) and microbial mat habitats only (ANOSIM, Global R = 0.611, P = 0.002), but not for non-seep samples (ANOSIM, P = 0.333). There were no assemblage differences between *Thioploca* and *Beggiatoa* mats (ANOSIM, P = 0.30) nor between thin and thick *Arcobacter* mats (ANOSIM, P = 0.10) (Table 7).

4. Comparisons between taxa

If different taxonomic groups were responding similarly to environmental characteristics, then their densities should be correlated. Foraminiferal densities were not correlated with densities of metazoan meiofauna (P = 0.796), but were highly correlated with those of metazoan macrofauna ($r^2 = 0.836$, $P < 0.0011$) and polychaetes ($r^2 = 0.838$, $P < 0.0001$), which are the most abundant macrofaunal group. Macrofaunal and meiofaunal densities were uncorrelated (P = 0.758). Within the meiofauna, copepod and nematode values were strongly positively correlated ($r^2 = 0.951$, $P < 0.0001$).

Table 6. Densities [individuals·(10 cm^3)$^{-1}$] of Polychaeta in Gulf of Mexico and Blake Ridge samples.

core	ALC					ATC	GC272		BR								
	non-seep		*Beggiatoa*			*Thioploca*	*Thioploca*		thin *Arcobacter*			thick *Arcobacter*		mussel bed		xenophyo-phore	
	17	18	23	25	26	81	46	48	3	14	16	5	6	2	4	13	15
Dorvilleidae																	
Ophryotrocha sp. S-a							92.6	22.5									
Ophryotrocha sp. S-b							7.0										
Ophryotrocha sp. S-c						12.8											
Ophryotrocha juv.			3.2			2.1	29.4	2.1									
unidentif. *Ophryotrocha*							2.1	10.2	4.3								
Parougia spp.								4.3									
Cossuridae																	
Cossura sp.								1.1									
unidentif. cossurid								3.2									
Hesionidae																	
Keferstenia sp.							11.2	2.1									
hesionid juvenile			3.7						0.8						0.5		
Spionidae																	
Paraprionospio sp.	0.5		0.5														
spionid juvenile								1.1									
Syllidae																	
unidentif. juvenile			2.1			2.1		3.2									
Ampharetidae																	
Glyphanostomum sp. A							12.3	12.8									
Glyphanostomum sp. B							6.4										
ampharetid juvenile							7.5	1.1									
Capitellidae																	
Mediomastus sp. juvenile						2.1											

Table 6. Continued.

core	ALC					ATC	GC272		BR								
	non-seep		*Beggiatoa*			*Thioploca*	*Thioploca*		thin *Arcobacter*			thick *Arcobacter*		mussel bed		xenophyophore	
	17	18	23	25	26	81	46	48	3	14	16	5	6	2	4	13	15
Acrocirridae																	
Macrochaeta spp.								8.6									
Cirratulidae																	
Chaetozone sp.						2.1	46.5	20.3									
Aphelochaeta spp.							8.6										
cirratulid juvenile						2.1	13.9				0.8						
unidentified		0.5	4.3			10.7	20.9	25.7							1.6		
number counted	1	1	26			17	498	105	1		1				4		
total [indiv.·(10 cm^3)$^{-1}$]	0.5	0.5	13.9			36.4	266.4	112.3	0.8		0.8				2.1		
total [indiv.·m^{-2}]	535	535	13906			36371	266361	112321	802		802				2139		

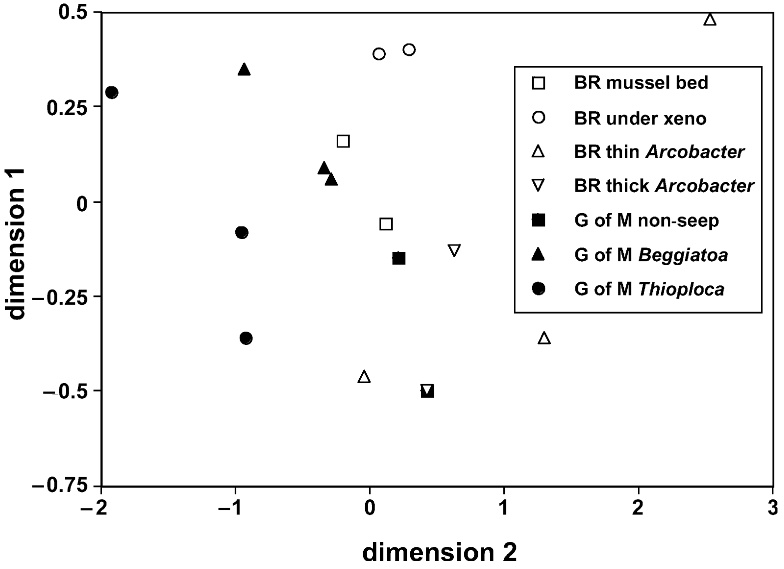

Fig. 4. MDS plot illustrating metazoan assemblages classified by major taxa from the Gulf of Mexico (G of M) *Beggiatoa* mats, *Thioploca* mats, and non-seep sediments (filled symbols) and Blake Ridge (BR) thin *Arcobacter* and thick *Arcobacter* mats, mussel bed periphery, and under xenophyophores (xeno) (open symbols). Stress = 0.04.

Table 7. Multivariate analyses of major taxa. SIMPER within-habitat percent similarity is given on the diagonal (bold); SIMPER between-habitat dissimilarity is given below the diagonal. ANOSIM probabilities of between-habitat differences are given above the diagonal.

	Thioploca	*Beggiatoa*	thin *Arcobacter*	thick *Arcobacter*	mussel bed	xeno-phyophore	non-seep
Thioploca	**26.3**	0.30	0.10	0.10	0.30	0.10	0.20
Beggiatoa	65.3	**53.4**	0.10	0.10	0.30	0.10	0.30
thin *Arcobacter*	87.2	68.4	**49.1**	0.10	0.30	0.10	0.60
thick *Arcobacter*	98.8	96.0	84.7	**25.0**	0.33	0.33	0.33
mussel bed	80.2	47.6	45.7	89.2	**65.1**	0.33	0.33
xenophyophore	86.4	62.9	57.6	87.6	39.9	**72.2**	0.33
non-seep	85.3	58.0	36.4	86.8	28.0	53.1	**82.7**

Global R = 0.461; P = 0.001.

Discussion

1. Density and taxonomic comparisons to other seep and non-seep sites

Although one of our seep samples had high infaunal densities (~6500 individuals·(10 cm^3)$^{-1}$; all taxa analyzed), most had moderate values (*e.g.*, <775 individuals·(10 cm^3)$^{-1}$; Table 2). Our densities were therefore far below those observed for some deep-water seeps (*e.g.*, Olu *et al.*, 1997). For most taxa we studied, seep and adjacent non-seep sites did not have significantly different densities. Exceptions were (1) the Blake Ridge thick *Arcobacter* mats, which had lower densities of total meiofauna, total macrofauna, nematodes, copepods and polychaetes compared to Gulf of Mexico non-seep sediments, and (2) the Gulf of Mexico *Thioploca* mats, which had higher densities of copepods, polychaetes and total macrofauna. An absence of seep versus non-seep density differences was reported for sites in Sagami Bay, Japan (1170 m water depth; Shirayama & Ohta, 1990) and on the northern California slope at 500 m (Levin *et al.*, 2003).

In the present study, foraminiferal density was positively correlated with macrofaunal density ($r^2 = 0.83$). A similar relationship was reported for these taxa at 800 m non-seep stations along the North Carolina margin (Gooday *et al.*, 2001) and at non-seep sites across depths on the Oman margin (Gooday *et al.*, 2000). Metazoan meiofauna and macrofauna were not correlated in this study, although they were correlated in a transect across the oxygen minimum zone off Peru (Levin *et al.*, 2002).

In general, our taxon-specific density results were similar to previous reports of seep meio- and macrofauna. Methodological differences (*i.e.*, sampling interval, sieve size, isolation technique) preclude direct comparisons for many cases, but trends can be discussed. In addition, localized conditions of seep habitats are not necessarily consistent from site to site, so comparisons are made with caution. Nematodes dominated the adult fauna in all our microbial mat samples, in Monterey Bay microbial mat samples (Buck & Barry, 1998), and in shallow-water (~15–20 m) bacterial mats associated with seeps off southern California (Montagna *et al.*, 1989) and New Zealand (Kamenev *et al.*, 1993). Nematodes are also known to dominate other seep areas (*e.g.*, Luth *et al.*, 1999), including seep clam beds (Shirayama & Ohta, 1990). Although we did not sample clam beds, the nematode-dominated mussel bed periphery samples may be comparable to the clam-bed habitat. The high ratio of nematodes to harpacticoid copepods may reflect low oxygen availability or elevated sulfide concentrations (Levin *et al.*, 1991). The dominance of nematodes at seeps contrasts with many non-seep, deep-water sediments where another meiofaunal taxon dominates (*e.g.*, foraminifera; Coull *et al.*, 1977; Snider *et al.*, 1984; Buck & Barry, 1998; Gooday *et al.*, 2000). Our samples lacked gnathostomulids and turbellarians, which dominate certain shallow Gulf of Mexico seeps (Powell *et al.*, 1983). Our samples also lacked rotifers, which were highly abundant in *Beggiatoa*-laden sediments from Hydrate Ridge, OR (USA; Sommer *et al.*, 2003).

Foraminiferal densities in shallower seep sites (543–587 m) in the Gulf of Mexico were comparable to densities at our deep-water sites (*e.g.*, ~3–11 foraminifers·$(10\ \mathrm{cm}^3)^{-1}$; Sen Gupta *et al.*, 1997). Conversely, foraminiferal densities at two California seep sites from ~500–1000 m were considerably higher than at our ~2-km sites, but comparable to the values observed in one of our ~700-m-deep samples (~98 foraminifers·$(10\ \mathrm{cm}^3)^{-1}$; core 46; Green Canyon 272). More specifically, densities of ~55–68 foraminifers·$(10\ \mathrm{cm}^3)^{-1}$ were noted at seep clam beds off Eel River (500–525 m water depth; Rathburn *et al.*, 2000) and 40–876 specimens·$(10\ \mathrm{cm}^3)^{-1}$ at seep bacterial mats in Monterey Bay (~900–1000 m; Bernhard *et al.*, 2001). Some of the foraminiferal genera from this study's seep samples are typical for seeps (*e.g.*, *Bolivina*, *Fursenkoina*, *Gavelinopsis*, *Praeglobobulimina;* Sen Gupta *et al.*, 1997; Rathburn *et al.*, 2000; Bernhard *et al.*, 2001); others, however, are atypical (*e.g.*, *Cibicidoides*, *Pyrgo*, *Quinqueloculina*).

The presence of a high-density, low-diversity polychaete assemblage in the *Thioploca* mats of Green Canyon 272 (~700 m) is consistent with observations from similar mats at upper slope seeps off Oregon (600 m; Sahling *et al.*, 2002) and northern California (500 m; Levin *et al.*, 2003). Half of the Gulf of Mexico cores contained abundant dorvilleid polychaetes. Consumption of mat-forming sulfur bacteria by some dorvilleid polychaetes is indicated by direct gut content observations and by stable isotopic signatures (Levin & Michener, 2002). The two cores (46 and 48) from Green Canyon 272 contained at least four dorvilleid species, including three within the genus *Ophyrotrocha* and one in the genus *Parougia*. Representatives of these genera are common in Pacific seep clam beds and microbial mats (Sahling *et al.*, 2002; Levin *et al.*, 2003; Mendoza *et al.*, 2003) as well as at whale falls (Smith *et al.*, 1998; Smith & Baco, 2003). Dorvilleid polychaetes are also common in sulfidic shallow-water settings such as pulp mills and polluted harbors (Paavo *et al.*, 2000). Most of the other abundant polychaetes exhibit affinities with other enriched or reduced settings. Hesionids occur at petroleum-infused sediments of the Guaymas hydrothermal mounds (Grassle *et al.*, 1985) and are rapid colonists in disturbed (Levin & DiBacco, 1995) or enriched sands (Menot *et al.*, unpublished data). Cirratulids, cossurids, and ampharetids are abundant on organic rich, hypoxic margins in the Arabian Sea and Eastern Pacific (reviewed in Levin, 2003).

The local polychaete densities we observed are either lower (Blake Ridge), average (Atwater Canyon, Alaminos Canyon) or higher (Green Canyon 272) than reported from other seep sites. Accurate global comparisons of macrofaunal communities will require additional quantitative samples from these and other seep sites. The lower polychaete densities in some of our samples remain unexplained, especially because at least some polychaetes are known to harbor ectobionts (*e.g.*, Gaill *et al.*, 1987; Müller *et al.*, 2001), presumably to help them survive in sulfidic environments.

2. Habitat effects

The considerable patchiness we observed among the seep cores is a common phenomenon in the deep sea (Gage & Tyler, 1991, pp. 396–399). Highly localized conditions may therefore regulate the distribution of seep infauna. One factor may be fluid flow, whose rates may differ fundamentally in the Gulf of Mexico and Blake Ridge sites: Alaminos, Atwater and Green Canyons have smaller aggregations of seep megafauna ($\sim 1\ m^{-2}$) than Blake Ridge ($\sim 400\ m^{-2}$; Van Dover *et al.*, 2003). Smaller megafaunal patches suggest more concentrated or localized fluid emanations compared to larger patches, which suggest regular diffuse fluid expulsion (Sibuet & Olu, 1998).

In our study, the only habitat not dominated by nematodes was the xenophyophore habitat, which was dominated by adult copepods. Enhanced harpacticoid copepod abundance has been observed in sediments beneath xenophyophores as well as within xenophyophore tests (Levin & Thomas, 1988; Levin & Gooday, 1992). The coarser sediments inhabited by xenophyophores may favor copepod survival. Interestingly, cores containing xenophyophores had low densities of smaller foraminifera, suggesting possible competition for food or available surface area between these two foraminiferal groups. Perhaps xenophyophores prey on smaller foraminifers, given that predation within this group is documented (Hallock & Talge, 1994).

A lack of significant differences in densities for any taxon between mussel-bed periphery cores and non-seep cores suggests that the mussels use most or all of the seep emanations, thereby keeping pore-water concentrations of methane and sulfide below the toxicity threshold of the meio- and macrofauna. This is supported by the eight major taxa present in both mussel-bed periphery cores, versus six or less major taxa in all other sampled habitats (Table 2). Levin *et al.* (2003) also noted enhanced macrofaunal species richness in other seep-associated molluscan-bed samples (clam bed samples) relative to non-seep and bacterial-mat habitats.

Regardless of the true identity of the microbial mats, the thick *Arcobacter* mats had significantly fewer specimens than other habitats, suggesting that the pore-water conditions were suboptimal for meio- and macrofauna or that the mat was too cohesive for settlement within or under the mat. Montagna *et al.* (1989) observed strong links between densities of nematodes and bacteria at seeps. Our thick *Arcobacter* mats, however, had very low nematode densities, suggesting that enhanced bacterial production does not necessarily boost nematode density.

Inclusion of the nanobiota (*i.e.*, ciliates and flagellates) and prokaryotic communities along with the meio- and macrofaunal analyses would further enhance our understanding of seep ecosystems. For example, biomass analyses of the small-sized benthic biota (*i.e.*, bacteria, fungi, protists, meiofauna) indicate differences between clam beds and bacterial mats at the Hydrate Ridge seep area (Sommer *et al.*, 2002), but the methods employed in that study (DNA and total adenylate concentrations) precluded determination of group-specific contributions.

3. Between-basin and between-microbial-mat contrasts

This study provides the first direct comparison of seep infauna in different types of microbial mat systems and in two oceans. We observed strong differences between seeps in the Gulf of Mexico and Atlantic Ocean for most taxa examined. The Gulf was characterized by higher densities and different species. Oil, which is common at Gulf of Mexico seeps (*e.g.*, Sassen *et al.*, 1994), is potentially responsible. Note that the differences were undoubtedly biased by the different habitats studied in each ocean. Future studies should compare identical habitats (*i.e.*, mussel beds, *Beggiatoa* mats, *Thioploca* mats) in both basins. Within-basin comparisons revealed few significant differences between the fauna of *Beggiatoa* and *Thioploca* mats, and between thick and thin *Arcobacter* mats, possibly because they are associated with similar geochemical conditions (Wirsen *et al.*, 2002). However, the Blake Ridge *Arcobacter* mats, and in particular the thick *Arcobacter* mats, appear to represent the most hostile setting studied for all taxa.

Conclusions

This study of seep fauna is unique in identifying foraminiferan protists *and* metazoans from both the meiofaunal and macrofaunal size classes. It thus provides the most comprehensive look at the microbial mat seep fauna from the Gulf of Mexico and western Atlantic region, and is the first direct comparison of meiofaunal, macrofaunal, and foraminiferal densities. This diversity of taxa and size classes serves as a valuable initial database for future comparison. The Gulf of Mexico microbial mats supported higher densities and diversity of most taxa than the Blake Ridge microbial mats. The assemblages described here, although derived from a limited number of samples, document some unifying features of seep habitats (*e.g.*, prevalence of nematodes and dorvilleid polychaetes), but reveal significant biotic heterogeneity in seep sediments both between ocean regions and among different seep habitats. Foraminifera contributed surprisingly little to the total seep fauna, and copepod densities beneath xenophyophores were very high. These differences probably reflect protistan-metazoan interactions with the geochemical environment. Further sedimentary geochemical characterization (*e.g.*, concentrations of sulfide, methane, oxygen; type of organics) may contribute to a mechanistic understanding of faunal distribution and diversity patterns at hydrocarbon seeps.

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