

Cold seeps of the deep Gulf of Mexico: Community structure and biogeographic comparisons to Atlantic equatorial belt seep communities

Erik E. Cordes^{a,*}, Susan L. Carney^{a,1}, Stephane Hourdez^b, Robert S. Carney^c, James M. Brooks^d, Charles R. Fisher^a

^aBiology Department, Pennsylvania State University, 208 Mueller Lab, University Park, PA, USA

^bEquipe Ecophysiologie, CNRS-UPMC UMR 7127, Station Biologique, BP74, 29682 Roscoff, France

^cCoastal Ecology Institute, Louisiana State University, South Stadium Road, Baton Rouge, LA, USA

^dTDI-Brooks International, 1902 Pinon, College Station, TX, USA

Received 4 May 2006; received in revised form 3 January 2007; accepted 5 January 2007

Available online 25 January 2007

Abstract

Quantitative collections of tubeworm- and mussel-associated communities were obtained from 3 cold seep sites in the deep Gulf of Mexico: in Atwater Valley at 1890 m depth, in Alaminos Canyon at 2200 m depth, and from the Florida Escarpment at 3300 m depth. A total of 50 taxa of macro- and megafauna were collected including 2 species of siboglinid tubeworms and 3 species of bathymodioline mussels. In general, the highest degree of similarity was between communities collected from the same site. Most of the dominant families at the well-characterized upper Louisiana slope seep sites of the Gulf of Mexico were present at the deep sites as well; however, there was little overlap at the species level between the upper and lower slope communities. One major difference in community structure between the upper and lower slope seeps was the dominance of the ophiuroid *Ophioctenella acies* in the deeper communities. The transition between upper and lower slope communities appears to occur between 1300 and 1700 m based on the number of shared species with the Barbados seeps at either end of this depth range. Seep communities of the deep Gulf of Mexico were more similar to the Barbados Accretionary Prism seep communities than they were to either the upper slope Gulf of Mexico or Blake Ridge communities based on numbers of shared species and Bray–Curtis similarity values among sites. The presence of shared species among these sites suggests that there is ongoing or recent exchange among these areas. An analysis of bathymodioline mussel phylogeography that includes new collections from the west coast of Africa is presented. This analysis also suggests recent exchange across the Atlantic equatorial belt from the Gulf of Mexico to the seeps of the West Nigerian margin.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: *Bathymodiolus*; Benthos; Biodiversity; Multivariate analysis; Phylogenetics; Vestimentiferans; *Lamellibrachia*; *Escarpia*; USA; Gulf of Mexico; Africa; Nigeria

*Corresponding author. Current address: Organismic and Evolutionary Biology, Harvard University, 16 Divinity Ave., Cambridge, MA 01238, USA.

E-mail address: ecordes@oeb.harvard.edu (E.E. Cordes).

¹Current address: Mote Marine Laboratories, 1600 Ken Thompson Parkway, Sarasota, FL, USA.

1. Introduction

Cold seeps inhabited by dense macrofaunal communities are known from over 30 locations on active and passive continental margins throughout the world's oceans (Sibuet and Olu, 1998; Tyler et al., 2003). Additional studies continue to add to the list of known seep sites with discoveries on the Sunda Arc (Wiedicke et al., 2002) and Makran accretionary prism (von Rad et al., 2000) in the Indian Ocean, as well as on the Gorda Escarpment (Stakes et al., 2002), in the Sea of Okhotsk (Sahling et al., 2003), and near Lihir Island Papua New Guinea (Schmidt et al., 2002; Southward et al., 2002) in the Pacific. Seeps supporting siboglinid tubeworms with symbiotic sulfide-oxidizing bacteria (vestimentiferans and pogonophorans) range in depth from the shallow waters (80 m) of Kagoshima Bay (Miura et al., 2002) to hadal depths in the Kurile Trench (9345 m, Mironov, 2000). Lush cold seep communities were first discovered in the Gulf of Mexico in the 1980s (Paull et al., 1984; Kennicutt et al., 1985) and are perhaps the most intensively studied of any cold seeps in the world. New sites continue to be found even in this well-explored region, with recent discoveries in Atwater Valley in the northern Gulf of Mexico (Milkov and Sassen, 2003; MacDonald et al., 2003) and the Campeche Knolls in the southern Gulf of Mexico (MacDonald et al., 2004).

The vast majority of cold-seep communities are dominated by the same families of symbiotic organisms, primarily the siboglinid polychaetes, bathymodioline mussels, and vesicomid bivalves (Sibuet and Olu, 1998). The similarity among these communities extends to the organisms inhabiting the physical structure produced by the tubeworms, mussels, and clams; including the polynoid polychaetes, trochid gastropods, alvinocarid shrimp, and galatheid crabs among others (Sibuet and Olu, 1998). One of the persistent questions in the biogeography of chemosynthetic ecosystems is the degree to which the species are capable of dispersing among relatively isolated cold-seep and hydrothermal vent sites. To begin to address this question in the seep setting, an adequate description of seep communities in well-defined areas is required. The Atlantic Equatorial Belt, extending from the Gulf of Mexico through the Caribbean Sea and Equatorial Atlantic to the Nigerian Margin has been suggested as a one of the target areas for these studies (Tyler et al., 2003).

The Gulf of Mexico includes one of the most geologically active of the passive continental margins of the world's oceans. The geology of the northern Gulf is dominated by an underlying salt layer formed during the successive opening and closing of the connection between the Gulf and the Atlantic Ocean in the Jurassic, and potentially during the Paleocene and Eocene as the Caribbean plate moved to the east across the region (Rosenfeld and Pindell, 2003). Differential loading from terrigenous sediment deposition on the continental shelf over the incompressible salt sheet has caused the formation of vertically mobile salt pillars and domes (Humphris, 1979). As these structures impact the sedimentary overburden, they compress oil-bearing reservoir sands and cause faulting in overlying shale layers (Brooks et al., 1987; Aharon et al., 1992), resulting in the upward migration of hydrocarbons and brines (Kennicutt et al., 1988). Where the faults reach the sediment surface, they often form fluid and gas expulsion features: the seeps and mud volcanoes of the Gulf of Mexico.

Most of the previous investigations of cold seep community ecology in the Gulf of Mexico have focused on sites in less than 1000 m water depth on the upper Louisiana slope (i.e. Kennicutt et al., 1988; MacDonald et al., 1990; Carney, 1994; Bergquist et al., 2003; Cordes et al., 2005; Cordes et al., 2006). This depth coincides with the maximum operating depth of the commonly used Johnson Sea-Link submersibles. In deeper waters, there are published records from 5 cruises with the DSV Alvin at 7 sites in the Gulf of Mexico, with a total of 58 submersible dives made to depths below 1000 m. Four of these sites contained vestimentiferan tubeworms and/or bathymodioline mussels: Mississippi Canyon (MC 853, MacDonald et al., 2003), Atwater Valley (AT 425, MacDonald et al., 2003; Milkov and Sassen, 2003), Alaminos Canyon (AC 645, Bryant et al., 1990; Brooks et al., 1990; Carney, 1994), and Florida Escarpment (VN 945, Paull et al., 1984; Cary et al., 1989; Van Dover et al., 2003; Turnipseed et al., 2004).

Here, we present the first data from quantitative collections of the communities associated with tubeworm aggregations from greater than 1000 m depth in the Gulf of Mexico and new data from collections of mussels and associated fauna from these depths. We compare the tubeworm- and mussel-associated communities from 3 of the most well-developed seep sites known at water depths greater than 1000 m in the Gulf: Atwater Valley,

Alaminos Canyon, and Florida Escarpment. The distribution of the tubeworms and mussels forming the foundation of this community along with the biogeography of their associated communities are compared among the cold seeps of the upper and lower slope of the Gulf of Mexico, Blake Ridge, and Barbados accretionary prism in the Atlantic Equatorial Belt, a key area of interest in the exploration and documentation of the diversity and biogeography of chemosynthetic ecosystems (Tyler et al., 2003). To complement and augment these biogeographic comparisons, an analysis of the phylogeography of bathymodioline mussels from collections in the Gulf of Mexico and from the Nigerian seeps off the coast of Africa is presented.

2. Methods

Intact vestimentiferan aggregations were obtained with the DSV Alvin using the Bushmaster Jr. collection device (Urcuyo et al., 2003; Bergquist et al., 2003) in October 2003. This device has an open diameter of approximately 70 cm and is lined with a 63 μm mesh net. The contents of each Bushmaster collection were sieved through a 2 mm mesh (the size fraction of macrofauna considered in this study) and sorted to the lowest possible taxonomic level on board the ship. Smaller size fractions were retained for complementary investigations by collaborators and will be presented elsewhere. Mussel bed samples were obtained with the hydraulically actuated Harbor Branch Oceanographic Institution (HBOI) “clam shell” sampler manipulated by the Alvin. This sampler is identical to the sampler used on the HBOI Johnson Sea Link submersible and similar to the “Pac Man” sampler used by the Canadian ROV ROPOS. It consists of two halves of a cylinder split lengthwise, enclosed in an aluminum frame. The two halves rotate to form a cylinder that encloses the sample. Each mussel bed was sampled with 3–4 successive grabs of 342 cm^2 surface area using this sampling device. Samples were processed similarly to tubeworm samples. All associated fauna were fixed in 10% buffered formalin and preserved in 70% ethanol for transport back to The Pennsylvania State University and final determination of taxonomic status. E.E.C. and S.H. identified all polychaetes. Primary identification of other groups was carried out and specimens sent to experts for further identification or verification. Colonial or encrusting organisms contributed to species richness, but these were not enumerated

and, therefore, were not included in quantitative analyses.

Tubeworms and mussels were counted and measured on board, time permitting. The remainder of each collection was preserved in formalin and transported to the laboratory for processing. Tubeworm length was measured to a standardized posterior outer tube diameter of 2 mm. This diameter was the common point where the tubeworms entered a dense, tangled mass at the base of the aggregation. Surface area of tubeworms was calculated as for a cone frustrum (Bergquist et al., 2002). Mussel length and height were measured at their greatest points. A function relating length and height to surface area was determined using a subsample of mussel shells. Eighteen shells were covered with a single layer of aluminum foil. The foil was weighed and the surface area of the foil was calculated based on the mass of a 1 cm^2 piece of foil. This empirically determined surface area (sa) was related to the surface area calculated as a cone including the base in a regression function:

$$sa = 1.053(\pi r^2 + \pi r\sqrt{r^2 + l^2}) + 14.38,$$

where r is one half of the height of the shell and l is the length ($p < 0.0001$, $r^2 = 0.987$). This function was used to determine the surface area of the rest of the mussels from their lengths and heights. A number of different functions relating height and length to mussel volume (including treating them as rectangular and cylindrical) were tested, but the conical function provided the best fit to the data.

Species abundances were standardized to tubeworm or mussel surface area to provide a measure of species density irrespective of collection size. Community diversity of each collection was assessed using the Shannon–Wiener diversity index (H'):

$$H' = - \sum_i p_i \ln(p_i),$$

where p_i is the relative abundance (%) of the i th species. Pairwise similarity in community structure between aggregations was examined using the Bray–Curtis (BC) similarity index based on density of fauna. BC similarity was determined using the following function:

$$S_{jk} = 100 \left(1 - \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p (y_{ij} + y_{ik})} \right),$$

where y_{ij} is the abundance of the i th species in the j th sample and p is the total number of species. Tubeworms and mussels were not included in this analysis when they were the primary foundation species, although *Bathymodiolus brooksi* is listed when it occurred within a tubeworm aggregation. Sub-samples of mussels from the Florida Escarpment were dissected to confirm the presence of the commensal polychaete *Branchipolynoe seepensis*, but because not all mussel individuals were dissected in this study, *B. seepensis* is not included in the quantitative analyses. Pairwise similarity between sites (upper Louisiana slope, deep Gulf of Mexico, Barbados accretionary prism, Blake Ridge) was based on presence/absence of species in the samples presented here and as reported in Olu et al. (1996), Sibuet and Olu (1998), Bergquist et al. (2003), Van Dover et al. (2003), Turnipseed et al. (2004), Cordes et al. (2005), and Cordes et al. (2006). Because the Barbados species inventories were primarily from grab samples and video and photographic records (Olu et al., 1996; Olu et al., 1997), only megafaunal taxa (those easily observed in video records or likely to be retained by grabs) and mussel commensals were included in these comparisons (Table 3). Potential shared taxa that were not identified to species level in previous studies were included in this analysis but are indicated by a question mark in Table 3. The number of shared species was determined twice, once including these species and once excluding them. Therefore, ranges in number of shared species between pairs of sites are presented based on these differences in taxonomic resolution. In the statistical analyses, all potentially synonymous species were included; therefore, the results are not conservative, but rather are based on the maximum number of shared taxa between any two sites. Cluster analysis of pairwise BC similarity values was based on group average linkage in PRIMER software (Clarke and Warwick, 2001).

Mussel tissue samples were obtained from the clam shell collections at the Florida Escarpment and Alaminos Canyon, and from Atwater Valley collections in 2000 (dive 3633). Mussel mantle tissue was dissected from the organism and frozen at -80°C until processing back in the laboratory. Samples of the “long” (*Bathymodiolus* sp. A) and “short” (*Bathymodiolus* sp. B) mussel types from the Nigerian seeps were obtained in 50×50 -cm stainless steel box core samples ($4^{\circ}59'N$, $4^{\circ}08'E$, 1700 and 2200m depth). Mussels were frozen whole and shipped to the Pennsylvania State University for

analyses. DNA extractions were performed by a standard phenol-chloroform method (Ausubel et al., 1989). The mitochondrial cytochrome oxidase subunit I (COI) gene was amplified using the primers of Folmer et al. (1994) and sequenced by dye terminator cycle sequencing according to the manufacturer's protocol (Beckman Coulter). GenBank accession numbers for previously published sequences are as follows: *B. brooksi*—AY649797; *B. heckerae*—AY649794; *Tamu fisheri*—AY649803; *Idas macdonaldi*—AY649804; *Bathymodiolus childressi*—AY649800; *Benthomodiolus lignola*—AY275545. Sequences for the new Nigerian mussel sequences in this study, as well as those for newly identified haplotypes of *B. brooksi* and *B. childressi*, have been submitted to GenBank (accession numbers EF051241–EF051246). Phylogenies were determined by the maximum parsimony and neighbor-joining methods of MEGA3 (Kumar et al., 2004) using Tajima-Nei distances.

3. Results and discussion

3.1. Site descriptions and communities

Atwater Valley lies to the south of Mississippi Canyon and represents a continuation of this geological structure extending from approximately 1800m depth out to the abyssal plain (Fig. 1). Within the Atwater Valley (AT) 425 lease block (Table 1) is a large knoll representing a fluid release site on top of a shallow salt ridge (Milkov and Sassen, 2003). Along the flanks of the knoll, at approximately 1890 m, are a series of ridges with extensive areas of seepage (MacDonald et al., 2003; Sassen et al., 2003). On the northwest slope, there were mussels lining the channels between ridges (MacDonald et al., 2003). Approximately 1 km to the south, along the western slope, carbonate outcrops occur on the crests of the ridges with small mounds similar to gas hydrate mounds and bubbling sediments indicating active seepage. Small tubeworm aggregations and mussel beds were present in dark (presumably brine-stained) sediments in depressions in this area.

The community associated with one of the mussel beds was sampled at the AT 425 site. The bed was composed of *B. brooksi*, identified based on morphological characters and mitochondrial COI gene sequences, which were identical to other reported Gulf of Mexico *B. brooksi* sequences (Fig. 2). This extends the known upper depth limit

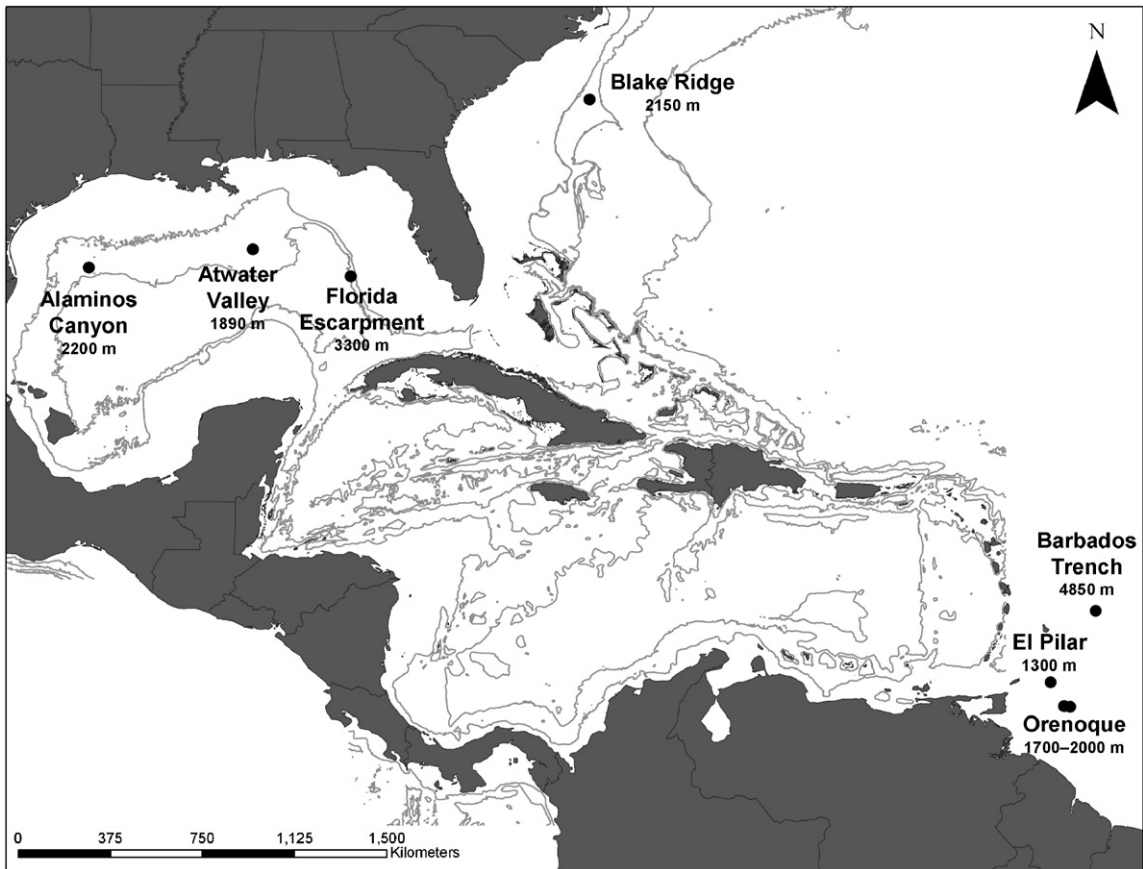


Fig. 1. Collection sites in Gulf of Mexico and locations of Blake Ridge and Barbados seeps. Contour lines are 1000, 3000, and 5000 m bathymetry. Bushmaster and mussel bed samples were collected at Atwater Valley (1890 m), Alaminos Canyon (2200 m), and Florida Escarpment (3300 m). The other seeps of the western side of the Atlantic Equatorial Belt that have been sampled previously are also shown: Blake Ridge (2150 m, Van Dover et al., 2003), and the seeps near Barbados including El Pilar (1300 m, Olu et al., 1997), Orenoque A (1700 m, Olu et al., 1997), Orenoque B (2000 m, Olu et al., 1997), and the Barbados Trench sites (4850 m, Olu et al., 1996). The upper slope sites of the Gulf of Mexico (ULS) lie just north of the Atwater Valley and Alaminos Canyon sites in water depths between 500 and 800 m.

of *B. brooksi* from 2200 to 1890 m. There were only 2 species of macrofauna associated with this mussel bed collection, the brittle star *Ophioctenella acies* and the shrimp *Alvinocaris muricola* (Table 2). In addition to mussel beds, a few *Escarpia laminata* aggregations were noted and an undescribed species of lamellibrachid tubeworm was collected during the same submersible dive (DSV Alvin dive 3918). This lamellibrachid may be the same *Lamellibrachia* sp. nov. reported from the Alaminos Canyon site (Nelson and Fisher, 2000), though additional collections coupled with morphological and genetic investigations are required to resolve the taxonomy of lamellibrachids at these sites.

Alaminos Canyon cuts through the continental slope off the coast of Texas between approximately 1500 and 3000 m, exposing alternating salt and

carbonate layers (Bryant et al., 1990). The seep sites in Alaminos Canyon (AC 645; Table 1) are located at 2200 m depth on the eastern side of the canyon in an area of relatively flat bathymetry (Fig. 1). Throughout the area is a thin authigenic carbonate veneer and scattered outcrops (Aharon et al., 1997) with isolated tubeworms and small to moderate-sized (less than 1 m in diameter) aggregations. The most well-developed area is characterized by massive uplifted carbonate blocks (Roberts and Aharon, 1994) associated with larger vestimentiferan aggregations, mussel beds and areas covered in disarticulated mussel shells (Brooks et al., 1990). The undersides of some of the overhangs were covered in a white crust (resembling methane hydrate) where methane bubble streams became trapped.

Table 1
Community collections examined in this study

Site	Lease Block	Name	Latitude	Longitude	Depth (m)	Surface Area (m ²)	Abundance	Density (ind/m ²)	Biomass (g AFDW)	Biomass/m ²	Diversity	Evenness
Atwater Valley	AT425	atm1	27°34.1'N	88°29.8'W	1893	0.27	606	2236.2	1.6	5.9	0.02	0.032
Alaminos Canyon	AC645	acm1	26°21.3'N	94°29.9'W	2221	0.01	37	4457.8	1.7	201.4	0.25	0.226
Alaminos Canyon	AC645	acm2	26°20.7'N	94°29.9'W	2208	0.74	118	160.1	3.8	5.1	0.93	0.404
Alaminos Canyon	AC645	ac1	26°21.3'N	94°29.9'W	2210	1.19	160	134.3	2.6	2.2	0.44	0.315
Alaminos Canyon	AC645	ac2	26°21.3'N	94°29.9'W	2223	0.73	133	181.4	4.2	5.7	2.11	0.705
Florida Escarpment	VB944	fem1	26°01.7'N	84°54.7'W	3291	0.36	1363	3807.3	9.4	26.3	1.03	0.401
Florida Escarpment	VB944	fem2	26°01.8'N	84°54.7'W	3288	0.15	535	3639.5	28.8	196.1	1.47	0.558
Florida Escarpment	VB944	fel	26°01.8'N	84°54.7'W	3286	0.42	256	606.6	15.9	37.7	1.86	0.687

Listed are collection site, minerals management service lease block designation, names used in Table 2 and Fig. 3, latitude and longitude, depth of collection, surface area of foundation species (tubeworm tubes or mussel shells), and descriptors of the associated community: abundance, density (abundance per m² foundation species surface area), biomass (ash-free dry weight in grams), biomass per m² surface area, diversity (Shannon–Weaver diversity index, H'), and evenness (Pielou's J').

The only species of siboglinid in tubeworm aggregations collected from Alaminos Canyon in 2003 was *E. laminata*. The majority of the tubeworms collected harbored a small mass on the top of their obturaculum containing 2–3 individuals of *Protomystides* sp., a phyllodocid polychaete. The digestive cavities of all of the phyllodocids examined were full of blood, possibly from their tubeworm hosts. A hydrothermal vent phyllodocid, *Galapagomystides aristata*, is also thought to feed on the blood of the siboglinid *Riftia pachyptila* (Jenkins et al., 2002). Further investigations of this relationship are underway. The rest of the community associated with *E. laminata* aggregations at Alaminos Canyon was dominated by *O. acies*, *A. muricola*, and *Phascolosoma turnerae* (Table 2). Beds of the mussels “*B.*” *childressi* (sensu Jones et al., 2006) and *B. brooksi* contained fewer taxa of associates (12) than the tubeworm aggregations (20). Mussel bed samples were dominated to a greater extent by *A. muricola* (78% of individuals) than tubeworm aggregations (9% of individuals) and contained a spionid polychaete (*Prionospio* sp.) not collected with the tubeworms. This site contained 3 taxa with distributions that extended to the shallower upper slope sites: “*B.*” *childressi*, the polychaete *Eurythoe* sp. and the sipunculan *P. turnerae*. Although “*B.*” *childressi* is found along the upper slope and at Alaminos Canyon, allozyme differences between the ULS and AC populations suggested a degree of reproductive isolation (Cradock et al., 1995), though they are currently considered to be conspecific (Gustafson et al., 1998; Carney et al., 2006). Data from specimens collected during this study support the designation of “*B.*” *childressi* as one continuous population throughout this depth range in the Gulf of Mexico (Fig. 2). Specimens of *Eurythoe* sp. and *P. turnerae* were morphologically indistinguishable from those collected at the upper slope sites (Bergquist et al., 2003; Cordes et al., 2005), but their exact taxonomic status awaits additional morphological and genetic investigations by experts in their respective groups.

The Florida Escarpment site is at the base of a massive carbonate wall on the edge of the continental slope off the western coast of Florida at approximately 3300 m (Fig. 1, Table 1). Where the base of this wall meets the abyssal plain, extensive areas of hypersaline brine seepage containing high concentrations of hydrogen sulfide and methane are present (Paull et al., 1984). While West Florida Escarpment seepage has been attributed to

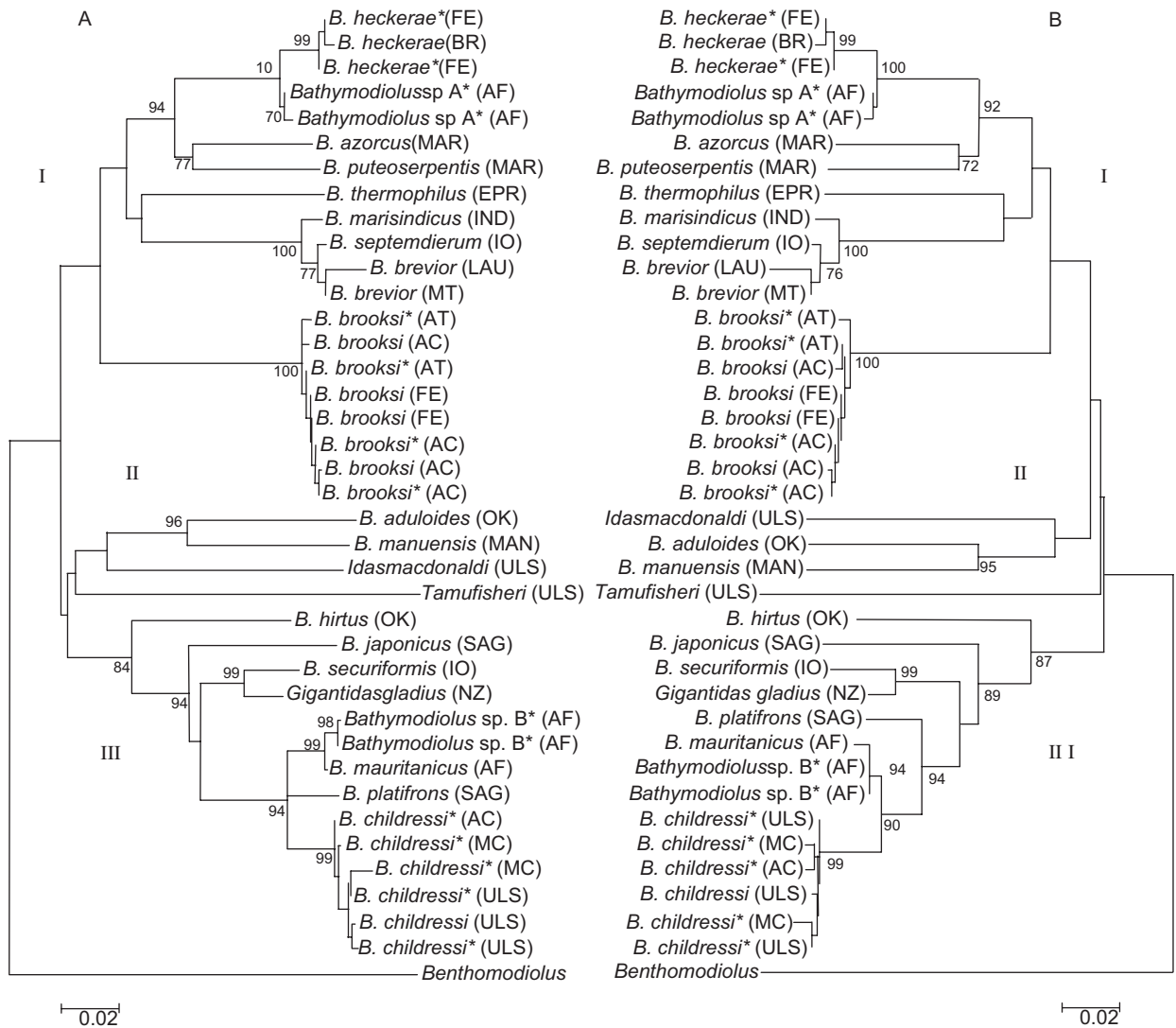


Fig. 2. Phylogenetic relationships of seep mussels in this study, with *B. lignola* as the outgroup, based on 510 base pairs of mitochondrial COI nucleotide sequence. Phylogenies determined using the maximum parsimony (A) and neighbor-joining (B) methods of MEGA3 (Kumar et al., 2004) based on Tajima-Nei distances. Bootstrap values less than 70% are not shown. Scale bar indicates nucleotide differences between branches. Site names are as follows: AC (Alaminos Canyon, 2200 m), AF (African seeps including the Nigerian Margin, 1000–1700 m), AT (Atwater Valley, 1890 m), BR (Blake Ridge, 2000 m), EPR (East Pacific Rise, 2500 m), FE (Florida Escarpment, 3300 m), IND (Central Indian Ridge, 2800 m), IO (Izu-Ogasawara Island Arc, 1300 m), LAU (Lau Basin, 1800 m), MAN (Manus Basin, 1700 m), MAR (Mid-Atlantic Ridge, 900–3500 m), MS (Mississippi Canyon, northern Gulf of Mexico, 630 m), MT (Mariana Trough, 1500 m), NZ (New Zealand, 200 m), OK (Mid-Okinawa Trough and Back-arc Basin, 700–1600 m), SAG (Sagami Bay, Japan, 1200 m), ULS (upper Louisiana Slope, 530 m).

continental discharge (Paull et al., 1984; Chanton et al., 1991), reevaluation may be needed as the eastward extent of hydrocarbon and salt sheet provinces become better known. Detectable concentrations of sulfide and methane are largely restricted to areas influenced by actively seeping fluids (Cary et al., 1989). On the outer edges of the

area visited for this study, there are thin carbonate crusts, scattered tubeworms and bacterial mats, and bivalve shell hash. Closer to the escarpment, these become more numerous and small mussel beds in darkly stained depressions are present. Near the escarpment wall, large areas of sediments are darkly stained and small rivulets of brine appear. There are

Table 2
Total abundance of tubeworm and mussel associated fauna in Gulf of Mexico quantitative collections

	ac1	ac2	acm1	acm2	atm1	fe1	fem1	fem2
Cnidaria								
actiniaria sp1						P		
actiniaria sp2			P			P	P	
actiniaria sp3						P		
hydroid spp.	P					P		
stolonifera spp.						P		
Platyhelminthes								
platyhelminthes spp.		2						
Nemertea								
nemertean spp.				1				
Sipuncula								
<i>Phascolosoma turnerae</i>		13		2				
Annelida								
Polychaeta								
Ampharetidae								14
<i>Branchinotogluma</i> sp. nov.				2			4	15
Capitellidae sp.	10	3						
Chaetopteridae		3						
<i>Cirriiformia</i> sp.				1				
<i>Eurythoe</i> sp. nov.		3						
<i>Flabelligera</i> sp.		2					22	
Maldanidae		3		1				
Nautilinelid								5
<i>Nereis</i> sp. nov.								4
<i>Nicomache</i> sp.							10	
Orbiniid							9	
Pogonophoran						7	7	
<i>Prionospio</i> sp.				22				
<i>Protomystides</i> sp.	143	61				112		
Sabellidae		1						
<i>Scoloplos</i> sp.								3
<i>Synelmis</i> sp.							2	
Mollusca								
Aplacophora								
Aplacophora sp.						3		
Polyplacophora								
Gastropoda								
<i>Fucaria</i> sp.						24	609	170
<i>Lepetodrilus</i> sp.	2	1						
Nudibranch								1
<i>Paraleptopsis</i> sp.				1		27	30	83
<i>Phymorhyncus</i> sp.							1	3
Provannidae						1		
Bivalvia								
<i>Bathymodiolus brooksi</i>		1						
Lucinidae		2		1				
<i>Cuspidaria</i> sp.		2					5	
Arthropoda								
Crustacea								
<i>Alvinocaris muricola</i>	5	23	35	85	2	4	3	1
Amphipod sp. 1						2		
Amphipod sp. 2						2		
Amphipod sp. 3		1				31		2
Isopod sp. 1		4				3		

Table 2 (continued)

	ac1	ac2	acm1	acm2	atm1	fe1	fem1	fem2
<i>Munidopsis</i> sp. 3		1				3		
<i>Phippsia</i> sp. 3						8		2
Chelicerata								
Pycnogonida								
<i>Colloseideis</i> sp.						1		
Echinodermata								
Holothuroidea								
Holothuroidea sp. 1		4		1				
Ophiuroidea								
<i>Ophienigma spinilimbatum</i>		5	1				1	7
<i>Ophioctenella acies</i>		23	1		604	25	660	225
Total abundance	160	158	37	117	606	253	1363	535
Total number of species	5	20	4	10	2	20	14	14

ac = Alaminos Canyon, at = Atwater Valley, fe = Florida Escarpment. Mussel collections are indicated with the letter m in the name, other collections are tubeworm aggregations. P = species was present but not enumerated.

also more extensive *E. laminata* aggregations, beds of *B. brooksi* and *B. heckerae*, and vesicomylid clams in upright positions within the sediments near the wall.

The communities associated with tubeworms and mussels at the Florida Escarpment site were numerically dominated by *O. acies*, the gastropod *Fucaria* sp., and the limpet *Paraleptopsis floridensis* (Table 2). Mussel beds generally contained greater relative abundances of associated fauna than tubeworm aggregations on the Florida Escarpment. The only tubeworm aggregation collected at this site contained the same number of taxa as the two mussel beds (20 taxa). There were 4 taxa of crustaceans present in the tubeworm aggregation but not in the mussel beds, and 9 taxa of polychaetes in the mussel beds but not in the tubeworm aggregation. The majority of the *E. laminata* collected had one or more *Protomystides* sp. on the top of their obturaculum.

The associated community collected in the three Florida Escarpment samples was similar to the community found in the 13 mussel bed collections in another recent study of this site (Turnipseed et al., 2004) (Table 3). These other collections were also dominated by the gastropods *Fucaria* sp. and *P. floridensis*. Differences between these studies, such as the much higher abundance of ampharetid polychaetes in the Turnipseed et al. (2004) samples, likely reflect the superior mussel bed sampling methodology in that study. A more detailed comparison of community structure and species density is not appropriate because of the low sample

size in our study, differences in sampling protocol and sieve sizes used (2 mm vs. 250 µm), as well as different methods of density calculation (mussel and tubeworm surface area vs. mussel biovolume).

3.2. Comparisons among seep communities in the Gulf of Mexico

Community similarity was higher among collections within a site than it was among sites in the Gulf of Mexico (Fig. 3). The 3 collections from the Florida Escarpment seeps grouped together, mainly because of the abundance of *Fucaria* sp., a species that was absent from the other sites (Table 2). The Alaminos Canyon collections clustered together largely as a result of the greater degree of dominance by *A. muricola*. The composition of the Atwater Valley mussel bed and one of the Alaminos Canyon mussel bed communities were similar in that they both contained *O. acies* and *A. muricola*. However, the dominance of *O. acies* (604 individuals) in the Atwater Valley collection is similar to the Florida Escarpment mussel beds. It is possible that this is due to an inherent difference in the communities harbored by the different foundation species. At the ULS seeps, mussel beds constitute an early successional stage and contain a subset of the species found in tubeworm aggregations (Bergquist et al., 2003; Cordes et al., 2005, 2006). More subtle differences in the communities may be attributed to either depth or distance. Some of the associated fauna could possess either more limited bathymetric

Table 3

Presence of shared species between upper Louisiana slope (ULS), Atwater Valley (AT), Alaminos Canyon (AC), Florida Escarpment (FE), Barbados Accretionary Prism sites El Pilar (EP), Orenoque A (OA), Orenoque B (OB), Barbados Trench (BT), and Blake Ridge (BR)

Average depth	Gulf of Mexico				Barbados				Blake ridge
	600 ULS	1890 AT	2200 AC	3300 FE	1300 EP	1700 OA	2000 OB	4850 BT	2150 BR
<i>Symbiotic fauna</i>									
Annelida									
Polychaeta									
Siboglinidae									
<i>Escarpia laminata</i>		x	x	x	x	x	x		
<i>Escarpia</i> sp.	x								
<i>Lamellibrachia luymesii</i>	x				?				
<i>Lamellibrachia</i> sp.		x	?			?			
<i>Seepiophila jonesi</i>	x				?		?		
Mollusca									
Bivalvia									
<i>Bathymodiolus boomerang</i>						x	x		
<i>Bathymodiolus brooksi</i>		x	x	x					
<i>Bathymodiolus childressi</i>	x		x		?	?			
<i>Bathymodiolus heckerae</i>				x		?	?		x
<i>Bathymodiolus</i> sp. nov.					x	x			
<i>Calyptogena ponderosa</i>	x								
<i>Calyptogena</i> sp.				x				?	
Lucinid spp.	x		?						
Solemyidae sp.						x		x	
<i>Tamu fisheri</i>	x								
<i>Thyasira oleophila</i>	x				?				
<i>Vesicomya chordata</i>	x								
<i>Vesicomya</i> cf. <i>chuni</i>						x	x		
<i>Vesicomya</i> cf. <i>venusta</i>									x
Associated Fauna									
Sipuncula									
<i>Phascolosoma turnerae</i>	x		x				x		
Annelida									
Polychaeta									
Ampharetid sp.				x				?	
<i>Branchinotogluma</i> sp. nov.			x	x					
<i>Branchipolynoe seepensis</i>	x	x	x	x		x	x		
Capitellidae sp.	?		?						x
Chaetopteridae			?					?	x
<i>Eurythoe</i> sp. nov.	x		x						
<i>Flabelligera</i> sp.			x	x					
Maldanidae			?					?	x
Nautilinelid				x	x	x	x	x	x
<i>Nereis</i> sp. nov.	x			x					
<i>Nicomache</i> sp.	?			?			x	?	?
Polynoidae	?		?	?		x	x		
<i>Protomystides</i> sp.			x	x					
Serpulidae	?					x			
Mollusca									
Polyplacophora									
<i>Leptochiton</i> spp.	?				x				
Gastropoda									
<i>Bathynnerita naticoidea</i>	x				x	x			
<i>Cataegis meroglypta</i>	x				x				
<i>Paraleptopsis</i> sp.			x	x					
<i>Phymorhyncus</i> sp.				x			x	x	
Turridae	?					x			

Table 3 (continued)

Average depth	Gulf of Mexico				Barbados				Blake ridge
	600 ULS	1890 AT	2200 AC	3300 FE	1300 EP	1700 OA	2000 OB	4850 BT	2150 BR
Site									
Trophoninae					x		x		
Bivalvia									
<i>Cuspidaria</i>			x	x					
Arthropoda									
Crustacea									
<i>Alvinocaris muricola</i>		x	x	x	?	x	?	?	
<i>Alvinocaris stactophila</i>	x								
<i>Munidopsis</i> sp.			x	x		x	x		x
Echinodermata									
Asterozoa									
<i>Ceremaster</i>					x	x			
<i>Plinthaster</i>					x	x			
Holothuroidea									
<i>Chiridota heheda</i>			x	x					x
Synallactidae sp.	x					x			
Ophiuroidea									
<i>Ophienigma spinilimbatum</i>		x	x	x					x
<i>Ophioctenella acies</i>			x	x			x		x
Chordata									
Osteichthyes									
Zoarcid						x	x		

Only species that could be observed in video records or commensal with symbiotic species are included in the analysis. Question marks indicate species identified to the genus or family level only for which conclusions about shared species are premature. Data compiled from Olu et al. (1996), Olu et al. (1997), Sibuet and Olu (1998), Bergquist et al. (2003), Van Dover et al. (2003), Cordes et al. (2005), and Cordes et al. (2006).

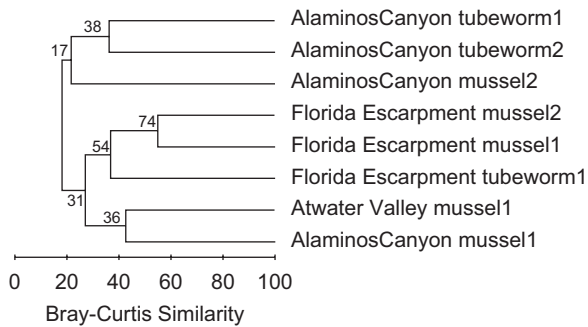


Fig. 3. Cluster diagram for tubeworm- and mussel-associated communities from Atwater Valley (1890 m), Alaminos Canyon (2200 m), and Florida Escarpment (3300 m). Clustering based on group average linkage of associated fauna density scaled to surface area of mussels or tubeworms in collection with bootstrap values based on 100 iterations.

distributions, or be limited in their capacity to disperse across the 960 km that separate Alaminos Canyon and Florida Escarpment.

The most striking difference between the seeps sampled here and the upper slope communities was

the dominance of the first-level consumer trophic position by *O. acies* in the deeper communities. At the shallower seeps, this trophic level is dominated by grazing gastropods (primarily *Bathynnerita naticoidea* and *Provanna sculpta*) and bresilid shrimp (*Alvinocaris stactophila*), while ophiuroids are almost entirely absent (Carney, 1994; Bergquist et al., 2003; Cordes et al., 2005) (Table 3). Though gastropods were present at the Florida Escarpment site (*P. floridensis* and *Fucaria* sp.) and *A. muricola* was present at all 3 sites, these species were far less abundant than *O. acies*. There is a general trend of increasing echinoderm dominance with depth in soft-sediment communities in the Gulf of Mexico (Pequegnat et al., 1990). This trend appears to be consistent at the seeps at least with regards to the ophiuroid populations, since no ophiuroid-dominated seep communities have been documented at the well-sampled upper slope seeps. This shift in species composition may reflect replacement within the primary-consumer trophic level, or it may be caused by differences in food sources. The gastropods of the upper slope seeps are mainly radular

grazers, likely feeding on epibiotic microbes and meiofauna or mucus produced by mussels. Ophiuroids are assumed to be micro-detritus feeders, carrying small particles to the mouth with tubefeet. This shift in relative dominance of feeding modes may reflect changes in the quantity and quality of food sources with depth, but these bathymetric gradients in nutrient input have yet to be established within seep habitats.

A preliminary evaluation of the change in nutrient input with depth can be gleaned from comparisons of the diversity, abundance, and biomass of the seep communities among the shallow (<700 m) and deep (>1800 m) sites in the Gulf of Mexico that have been sampled with the same methodology. The Shannon–Wiener diversity index of the associated community appears to decline with depth from a range of 1.37–3.12 at the shallow sites (Bergquist et al., 2003; Cordes et al., 2005) to a range of 0.02–2.11 at the deeper sites examined here (Table 1). In the background (non-seep) fauna, a mid-slope diversity maximum at approximately 1400 m was observed with diversity declining precipitously at greater depths (Pequegnat et al., 1990). The lower diversity index of the deep seeps found in this study could reflect the lower abundance and diversity of background colonists entering the seep habitat (Carney, 1994). The density of associated fauna in these collections (134–4457 ind/m²) (Table 1) was within the range of those reported from the shallow sites (11–5633 ind/m²) (Bergquist et al., 2003; Cordes et al., 2005). The biomass of the associated communities in this study (2–201 gAFDW/m²) was also similar to that found at the shallower seeps (1–206 gAFDW/m²) (Cordes et al., 2005; Cordes et al., 2006). The lack of a decline in density and biomass of fauna stands in contrast to the patterns seen in the background communities where density and biomass of fauna steadily declined with depth (Pequegnat et al., 1990). This suggests that the relative quantity and quality of the food supply to the localized seep communities does not decrease with depth in the same manner as the food source for the background fauna. Although these findings suggest some general patterns in seep communities, these are preliminary comparisons between 8 samples from the deep seeps and 29 samples from the upper slope seeps. Additional sampling effort at the deep seep sites, and exploration of potential seep sites at mid-slope depths in the Gulf of Mexico are required to fully evaluate these hypotheses.

3.3. Similarity among seep communities in the Atlantic equatorial belt

The similarities between the fauna of the Gulf of Mexico seeps and the communities at the Barbados accretionary prism seep sites suggest a depth range within which the change in community composition occurs between upper slope and deeper-water communities in the Gulf of Mexico. The dominant fauna at the 1300 m El Pilar site (Olu et al., 1997) appears similar to that of the upper slope seeps of the Gulf of Mexico (Bergquist et al., 2003; Cordes et al., 2005, 2006). Seep communities sampled at El Pilar consisted of aggregations of *Lamellibrachia* sp. (listed as the same “*Lamellibrachia* sp.” as the upper Louisiana slope, now known to be *Lamellibrachia luymsi*) and beds of “*Bathymodiolus* sp. B”, potentially “*B.*” *childressi* (indicated by question marks in Table 3). These foundation species supported populations of *B. naticoidea*, *Cataegis meroglypta*, and *Alvinocaris* cf. *stactophila*, all common species at the upper slope seeps in the Gulf of Mexico (Table 3). The Barbados sites at 1700 m (Orenoque A) and 2080 m (Orenoque B) depth were dominated by *E. laminata* and *Bathymodiolus boomerang* (reported as *Bathymodiolus* sp. A and likely synonymous with *B. heckerae*, Van Dover et al., 2003) and contained high abundances of *Alvinocaris* cf. *muricola* (Olu et al., 1997), suggesting a greater affinity to the deeper (1890–3300 m) sites of the Gulf of Mexico. These data suggest a region of rapid species replacement between 1300 and 1700 m, though caution must be used when extending faunal zonation from one basin to another (Haedrich et al., 1980). However, *B. naticoidea* and a number of species of uncertain taxonomy including a species of *Munidopsis* and a number of shared polychaete families were also found at 1700 m (Table 3). More intensive quantitative sampling is required within the 1300–1700 m depth range within the Gulf of Mexico, Barbados, and potential sites in the Caribbean Sea to resolve the location of this apparent zone of transition.

Depth appears to be a more important factor affecting seep community structure than distance. In order of similarity in presence/absence of large macrofauna and megafauna (Fig. 4, Table 4), the sites are clustered: (1) within site and depth range, (2) among Gulf of Mexico and Barbados sites between 1700 and 3300 m, (3) among intermediate depth (1700–3300 m) sites in the Gulf, Barbados, and Blake Ridge, (4) between the shallower

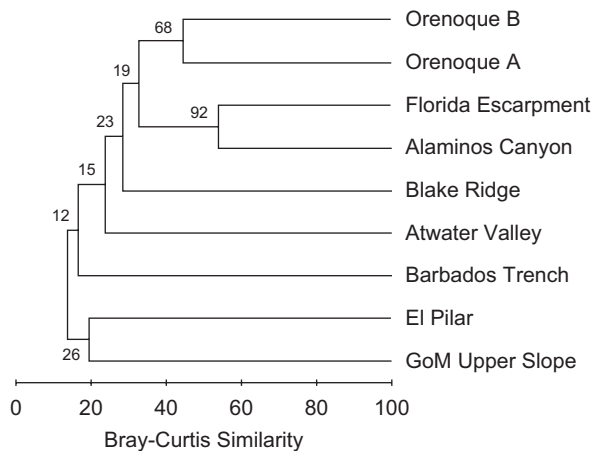


Fig. 4. Cluster of community similarity based on species presence/absence at western Atlantic seep sites including Gulf of Mexico (GoM) upper slope between 500 and 700 m, Atwater Valley at 1890 m, Alaminos Canyon at 2200 m, Florida Escarpment at 3300 m, Barbados Accretionary Prism sites El Pilar at 1300 m, Orenoque A at 1700 m, Orenoque B at 2000 m, Barbados Trench at approximately 4850 m, and Blake Ridge at 2200 m. Clustering based on group average linkage of associated fauna with bootstrap values based on 100 iterations.

Table 4
Matrix of numbers of shared species and Bray-Curtis similarity values in pairwise comparisons between seeps sites in this study

	ULS	AT	AC	FE	EP	OA	OB	BT	BR
ULS	23	1	4–10	2–6	2–8	3–10	2–5	0	0–2
AT	2.8	6	6	5	1–2	3–4	2–3	0–1	1
AC	20.8	33.3	22	15–17	1–3	3–8	4–8	0–3	3–8
FE	12.1	25.6	54.0	21	2–3	4–9	5–10	1–4	5–7
EP	19.5	18.2	13.0	12.2	13	6–7	3–5	0–1	1
OA	21.5	24.2	28.1	30.0	32.6	18	8–10	1–2	1–4
OB	11.9	25.0	33.3	39.2	29.4	44.4	15	1–2	2–5
BT	0.0	13.3	15.4	19.0	8.0	11.1	14.8	9	0–3
BR	4.9	9.5	35.6	29.2	6.5	19.0	30.3	25.0	11

Only large macrofauna and megafauna are included in this analysis as these were the most likely to have been sampled in all studies compared here. Numbers of shared species presented range from well-identified species shared between sites (indicated with an “x” in Table 3) to all potentially shared species of unresolved taxonomic affinity (indicated with a “?” in Table 3). Bray-Curtis similarity values are based on presence/absence of species listed in Table 3. On the diagonal are total numbers of species considered in this analysis for each site. ULS = Upper Louisiana slope, AT = Atwater Valley, AC = Alaminos Canyon, FE = Florida Escarpment, EP = El Pilar, OA = Orenoque A, OB = Orenoque B, BT = Barbados Trench, BR = Blake Ridge.

(500–1300 m) sites in the Gulf and Barbados, and finally (5) all sites deeper than 1700 m. The first group comprises the communities inhabiting the

deep seeps of the Gulf of Mexico (2200–3300 m) and the intermediate-depth sites of the Barbados accretionary prism (1700–2000 m). The foundation species are primarily *E. laminata* and *B. heckeriae* (or *B. boomerang*) and shared associates include *A. muricola*, *Munidopsis* sp., *O. acies*, *Brachipolynoe seepensis*, a nautilinellid polychaete, *Chiridota* sp., and *Phymorhynchus* sp. (Table 3). Taken together, these Gulf of Mexico and Barbados sites are all more similar to the 2150 m Blake Ridge site than they are to the sites in the same basin at other depths. Although the levels of similarity are quite low ($BC < 30$), the ordering emphasizes the relative importance of bathymetry over distance.

The upper slope sites of the Gulf of Mexico clustered with the El Pilar Barbados site (Fig. 4), but BC similarities between the upper slope and El Pilar (19.5), Orenoque A (21.5) and Alaminos Canyon (20.8) were all similar (Table 3). The sites of the upper slope of the Gulf of Mexico (ULS) shared a maximum of 12 taxa with the sites below 1700 m when sites in both the Gulf of Mexico and Barbados are considered together. Those taxa with resolved taxonomy that are shared include *B. naticoidea*, *P. turnerae* and *B. seepensis*. Although definitive conclusions await higher degrees of taxonomic resolution, these results also suggest that the greater boundary to dispersal is depth rather than distance since taxa that cross this bathymetric barrier are common to both geographic regions.

3.4. Patterns in bathymodioline mussel divergence

Biogeographic patterns in the distribution of the bathymodioline mussel species are congruent with these general patterns in community similarity. The two versions of the phylogenetic trees (Fig. 2A, maximum parsimony, Fig. 2B, neighbor-joining) agree on the divisions within the Subfamily Bathymodiolinae, but are not congruent in the placement of a few species within these groups. Three main groups are identified: (I) *B. heckeriae*, *Bathymodiolus* sp. A, and *B. brooksi* along with the vent species, (II) *I. macdonaldi*, *B. aduloides*, *B. manuenensis*, and (in one analysis) *T. fisheri*, and (III) *B. childressi*, *Bathymodiolus* sp. B, *Bathymodiolus mauritanicus*, and a number of Pacific species including *Gigantidas gladius*.

In group I, *B. brooksi* forms a distinct clade separated from the rest of the species in the group. *B. brooksi* distribution is restricted to the Gulf of Mexico from 1890 to 3300 m, suggesting that it has

a more limited dispersal capability than the species that occur in multiple basins. *B. heckerae* occurs from 2150 m on the Blake Ridge in the Atlantic to 3300 m in the Gulf of Mexico. It is possible that this is the same species as *B. boomerang* described from the 1700 to 2000 m Barbados sites based on morphology, but this determination awaits molecular data. *Bathymodiolus heckerae* is closely related to the recently collected *Bathymodiolus* sp. A from the Nigerian seeps. The most similar species to the seep species *B. heckerae* and *Bathymodiolus* sp. A are the mussels of the Mid-Atlantic Ridge hydrothermal vents, *B. azoricus* and *B. puteoserpentis*. The structure of this portion of the phylogeny suggests that *B. heckerae* and *Bathymodiolus* sp. A represent a colonization of the seep habitats from vent ancestors. This was previously suggested for *B. heckerae* (Jones et al., 2006), and can now be extended to both sides of the Atlantic. These data contribute to the growing body of evidence that bathymodioline mussels have a remarkable range and capacity for dispersal worldwide (Craddock et al., 1995; Won et al., 2003; Carney et al., 2006).

Group II is a loose collection of 3 or 4 species including *B. aduloides* from near Japan, *B. manusensis* from the Manus Basin, *I. macdonaldi* from the Gulf of Mexico, and possibly *T. fisheri* from the Gulf of Mexico. In one analysis, this group (excluding *T. fisheri*) is aligned with group I, and in the other it is aligned with group III. The placement of COI sequences from *Idas* and *Tamu* species among *Bathymodiolus* species indicates that a revision of the genera of the bathymodioline mussels as suggested by Jones et al. (2006) is warranted.

Group III contains species from the Indo-Pacific, Africa, and the Gulf of Mexico. The base of this group comprises *Bathymodiolus* sp. from near Japan and *G. gladius* from near New Zealand, suggesting this group originated in the Indo-Pacific. The COI sequence from *Bathymodiolus* sp. A from the recent Nigerian margin samples is highly similar to the previously published *B. mauritanicus*. This group of sequences will be referred to as *B. cf. mauritanicus*, although an evaluation of the taxonomic status of *Bathymodiolus* sp. A awaits expert morphological examination. The “*B.*” *childressi* group consists of individuals collected at 530 m (Green Canyon 234 and Bush Hill sites on the upper Louisiana Slope), 630 m (Mississippi Canyon), and 2200 m (Alaminos Canyon). This wide bathymetric range suggests that “*B.*” *childressi* possesses wide thermal and pressure

tolerances and that there is no absolute barrier to dispersal between the upper and lower slope of the Gulf of Mexico. The closest relatives to “*B.*” *childressi* based on mitochondrial COI and 16S nucleotide sequences are *B. cf. mauritanicus* from Africa and *Bathymodiolus platifrons* from the seeps near Japan (Fig. 2). In this analysis, the “*B.*” *childressi* sequences examined appear more similar to other species of *Bathymodiolus* than they are to *T. fisheri*. These data suggest that the removal of “*B.*” *childressi* from the genus *Bathymodiolus*, as recommended by Jones et al. (2006), may not be warranted. Additional data on these species, *T. fisheri* in particular, are required to resolve this open question.

3.5. Potential for dispersal within the equatorial Atlantic belt

The commonality of fauna at these widely disparate sites suggests that, while the frequency of dispersal or migration may be low, they are not entirely isolated. Within the 1700–3300 m depth range, the greatest degree of exchange appears to occur between the deep Gulf of Mexico sites and the Barbados Prism, followed by the Gulf and Blake Ridge, and finally between the Barbados and Blake Ridge sites. This suggests that the current structure of the western Atlantic, Caribbean, and Gulf of Mexico provides a mechanism for dispersal among all of these seeps (Fig. 1). The connection through the 1850 m deep Yucatan Strait could provide both northerly and southerly transport between the deep Gulf of Mexico and the Caribbean Sea (Ochoa et al., 2001; Sheinbaum et al., 2002). In conjunction with deep easterly flow through the St. Vincent (980 m) and Dominica (980 m) passages in the southern Caribbean (Wilson and Johns, 1997), this could provide a connection between the Gulf of Mexico and Barbados.

Water entering the Gulf of Mexico may also exit through the Florida Straits, through which flow at all depths from the surface to the 700 m sill depth is primarily to the east and north (Winkel et al., 2002). Propagules remaining shallower than 1000 m would be transported to the north with the Gulf Stream to the seeps of the Blake Ridge and possibly further to the north. If they sink below 1000 m, larvae could be transported along with the deep western boundary current of the Atlantic. This countercurrent runs beneath the Gulf Stream between approximately 1100 and 5000 m depth and delivers North Atlantic

Deep Water to the equatorial Atlantic (Lavin et al., 2003). This water mass passes over the Blake Ridge and may pass into the Caribbean through the Anagada Pass (1915 m sill) or the Windward Pass (1700 m sill) (MacCreedy et al., 1999), or continue along to the east of the Lesser Antilles to Barbados and the equatorial Atlantic. The further connection to the seeps off the coast of Africa is provided by the equatorial deep jets (Ponte et al., 1990) that alternate in direction from easterly to westerly on short vertical scales throughout the water column (Gouriou et al., 2001; Bourles et al., 2003), with mean flow at depth to the east south of the equator and to the west at the equator (Boning and Kroger, 2005). These currents could transport propagules in both directions across the Atlantic, and provide a connection between the Nigerian seeps and Barbados in particular.

The potential for dispersal among all of these sites is dependent on the depth range within which the larvae of various species travel and the duration of larval life span. Larvae of siboglinid polychaetes (vestmentiferan tubeworms) can persist for weeks in the water column, while preliminary evidence suggests that larvae of bathymodioline mussels could live far longer (Tyler and Young, 1999). Additional investigations using similar sampling equipment and sampling efforts at known sites will help to resolve some of the biogeographic questions addressed here. In addition, further exploration of the Gulf of Mexico slope for new sites, particularly between 1000 and 2000 m, and additional sites in the Caribbean (i.e. the Cayman Trench, Jamaica, Venezuela) and Atlantic (i.e. Brazil, Congo, Nigeria, Angola), including whale falls (Feldman et al., 1998; Goffredi et al., 2004) and decomposing biomass (Dando et al., 1992) are required to resolve the relationships between the Gulf of Mexico, Caribbean, and Atlantic seeps. It is our hope that this study will provide testable hypotheses regarding these links and help to focus future biogeographic studies in this region.

Acknowledgments

We would like to thank all of the participants on the Atlantis cruise 11-01, also known as the “Rabbit Cruise.” Guy Telesnicki, Julia Zekely, Erin McMullin, Bill Gilhooly, Lisa Levin, and Roger Sassen all provided assistance and thoughtful discussions at sea. The expedition was funded by the NOAA Ocean Exploration Program. Ian MacDonald

supplied the mussel specimens from Alvin dive #3633. We are indebted to Anders Waren, Sabine Stohr, and Julia Sigwart for their taxonomic expertise. Some of the ideas for future work and exploration of seep sites were drawn from discussions with and presentations by numerous colleagues at the Chemosynthetic Ecosystems (ChEss) biodiversity workshops held in Southampton, UK in 2002 and Barcelona, Spain in 2006, and we are thankful to the ChEss steering committee and Eva Ramirez-Llodra and Maria Baker for organizing the workshops.

References

- Aharon, P., Roberts, H.H., Sneling, R., 1992. Submarine venting of brines in the deep Gulf of Mexico: Observations and geochemistry. *Geology* 20, 483–486.
- Aharon, P., Schwarcz, H.P., Roberts, H.H., 1997. Radiometric dating of submarine hydrocarbon seeps in the Gulf of Mexico. *GSA Bulletin* 109, 568–579.
- Ausubel, F.M., Brent, R., Kingston, R.E., Moore, D.D., Seidman, J.G., Smith, J.A., Struhl, K., 1989. *Current Protocols in Molecular Biology*, vol. 1.
- Bergquist, D.C., Urcuyo, I.A., Fisher, C.R., 2002. Establishment and persistence of seep vestimentiferan aggregations from the upper Louisiana slope of the Gulf of Mexico. *Marine Ecology Progress Series* 241, 89–98.
- Bergquist, D.C., Ward, T., Cordes, E.E., McNelis, T., Howlett, S., Kosoff, R., Hourdez, S., Carney, R., Fisher, C.R., 2003. Community structure of vestimentiferan-generated habitat islands from upper Louisiana slope cold seeps. *Journal of Experimental Marine Biology and Ecology* 289, 197–222.
- Boning, C.W., Kroger, J., 2005. Seasonal variability of deep currents in the equatorial Atlantic: a model study. *Deep-Sea Research I* 52, 99–121.
- Bourles, B., Andrie, C., Gouriou, Y., Eldin, G., du Penhoat, Y., Freudenthal, S., Dewitte, B., Gallois, F., Chuchla, R., Baurand, F., Aman, A., Kouadio, G., 2003. The deep currents in the Eastern Equatorial Atlantic Ocean. *Geophysical Research Letters* 30, 1–4.
- Brooks, J.M., Kennicutt, M.C., Fisher, C.R., Macko, S.A., Cole, K., Childress, J.J., Bidigare, R.R., Vetter, R.D., 1987. Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources. *Science* 238, 1138–1142.
- Brooks, J.M., Wiesenburg, D.A., Roberts, H.H., Carney, R.S., MacDonald, I.R., Fisher, C.R., Guinasso, N.L., Sager, W.W., McDonald, S.J., Burke, R.A., Aharon, P., Bright, T.J., 1990. Salt, seeps and symbiosis in the Gulf of Mexico. *Eos* 71, 1772–1773.
- Bryant, W.R., Bryant, J.R., Feeley, M.H., Simmons, G.R., 1990. Physiographic and bathymetric characteristics of the continental slope, northwest Gulf of Mexico. *Geo-Marine Letters* 10, 182–199.
- Carney, R.S., 1994. Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. *Geo-Marine Letters* 14, 149–159.
- Carney, S.L., Formica, M.I., Divatia, H., Nelson, K., Fisher, C.R., Schaeffer, S.W., 2006. Population structure of the

- mussel "*Bathymodiolus*" *childressi* from Gulf of Mexico hydrocarbon seeps. *Deep-Sea Research I* 53, 1061–1072.
- Cary, C., Fry, B., Felbeck, H., Vetter, R.D., 1989. Multiple trophic resources for a chemoautotrophic community at a cold water brine seep at the base of the Florida Escarpment. *Marine Biology* 100, 411–418.
- Chanton, J.P., Martens, C.S., Paull, C.K., 1991. Control of pore-water chemistry at the base of the Florida escarpment by processes within the platform. *Nature* 349, 229–231.
- Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis*. Primer-E, Plymouth, UK, 170pp.
- Cordes, E.E., Hourdez, S., Predmore, B.L., Redding, M.L., Fisher, C.R., 2005. Succession of hydrocarbon seep communities associated with the long-lived foundation species *Lamellibrachia luymesii*. *Marine Ecology Progress Series* 305, 17–29.
- Cordes, E.E., Bergquist, D.C., Predmore, B.L., Jones, C., Deines, P., Telesnicki, G., Fisher, C.R., 2006. Alternate unstable states: Convergent paths of succession in hydrocarbon-seep tubeworm-associated communities. *Journal of Experimental Marine Biology and Ecology* 339, 159–176.
- Craddock, C., Hoeh, W.R., Gustafson, R.G., Lutz, R.A., Hashimoto, J., Vrijenhoek, R.J., 1995. Evolutionary relationships among deep-sea mytilids (Bivalvia: Mytilidae) from hydrothermal vents and cold-water methane/sulfide seeps. *Marine Biology* 121, 477–485.
- Dando, P.R., Southward, A.J., Southward, E.C., Dixon, D.R., Crawford, A., Crawford, M., 1992. Shipwrecked tube worms. *Nature* 356, 667.
- Feldman, R.A., Shank, T.M., Black, M.B., Baco, A.R., Smaith, C.R., Vrijenhoek, R.C., 1998. Vestimentiferan on a whale fall. *Biological Bulletin* 194, 116–119.
- Folmer, O., Black, M., Hoeh, W., Lutz, R.A., Vrijenhoek, R.C., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3, 294–299.
- Goffredi, S.K., Paull, C.K., Fulton-Bennett, K., Hurtado, L.A., Vrijenhoek, R.C., 2004. Unusual benthic fauna associated with a whale fall in Monterey Canyon, California. *Deep-Sea Research I* 51, 1295–1306.
- Gouriou, Y., Andrie, C., Bourles, B., Freudenthal, S., Arnault, S., Aman, A., Eldin, G., du Penhoat, Y., Baurand, F., Gallois, F., Chuchla, R., 2001. Deep Circulation in the Equatorial Atlantic Ocean. *Geophysical Research Letters* 28, 819–822.
- Gustafson, R.G., Turner, R.D., Lutz, R.A., Vrijenhoek, R.C., 1998. A new genus and five new species of mussels (Bivalvia, Mytilidae) from deep-sea sulfide/hydrocarbon seeps in the Gulf of Mexico. *Malacologia* 40, 63–112.
- Haedrich, R.L., Rowe, G.T., Polloni, P.T., 1980. The megabenthic fauna in the deep sea south of New England, USA. *Marine Biology* 57, 165–179.
- Humphris, C.C., 1979. Salt movement on continental slope, northern Gulf of Mexico. *American Association of Petroleum Geologists Bulletin* 63, 782–798.
- Jenkins, C.D., Ward, M.E., Turnipseed, M., Osterberg, J., Van Dover, C.L., 2002. The digestive system of the hydrothermal vent polychaete *Galapagomystides aristata* (Phyllodoceidae): evidence for hematophagy? *Invertebrate Biology* 121, 243–254.
- Jones, W.J., Won, Y.-J., Maas, P.A.Y., Smith, P.J., Lutz, R.A., Vrijenhoek, R.C., 2006. Evolution of habitat use by deep-sea mussels. *Marine Biology* 148, 841–851.
- Kennicutt, M.C., Brooks, J.M., Bidigare, R.R., Fay, R.R., Wade, T.L., McDonald, T.J., 1985. Vent-type taxa in a hydrocarbon seep region on the Louisiana slope. *Nature* 317, 351–353.
- Kennicutt, M.C., Brooks, J.M., Bidigare, R.R., Denoux, G.J., 1988. Gulf of Mexico hydrocarbon seep communities I. Regional distribution of hydrocarbon seepage and associated fauna. *Deep-Sea Research A* 35, 1639–1651.
- Kumar, S., Tamura, K., Nei, M., 2004. MEGA3: integrated software for molecular evolutionary genetics analysis and sequence alignment. *Briefings in Bioinformatics* 5, 150–163.
- Lavin, A.M., Bryden, H.L., Parrilla, G., 2003. Mechanisms of heat, freshwater, oxygen and nutrient transports and budgets at 24.5°N in the subtropical North Atlantic. *Deep-Sea Research I* 50, 1099–1128.
- MacCready, P., Johns, W.E., Rooth, C.G., Frattoni, D.M., Watlington, R.A., 1999. Overflow into the deep Caribbean: effects of plume variability. *Geophysical Research* 104, 25913–25935.
- MacDonald, I.R., Guinasso, N.L., Reilly, J.F., Brooks, J.M., Callender, W.R., Gabrielle, S.G., 1990. Gulf of Mexico seep communities: VI. Patterns in community structure and habitat. *Geo-Marine Letters* 10, 244–252.
- MacDonald, I.R., Sager, W.W., Peccini, M.B., 2003. Gas hydrate and chemosynthetic biota in mounded bathymetry at mid-slope hydrocarbon seeps: Northern Gulf of Mexico. *Marine Geology* 198, 133–158.
- MacDonald, I.R., Bohrmann, G., Escobar, E., Abegg, F., Blanchon, P., Blinova, V., Brückmann, W., Drews, M., Eisenhauer, A., Han, X., Heeschen, K., Meier, F., Mortera, C., Naehr, T., Orcutt, B., Bernard, B., Brooks, J., de Farago, M., 2004. Asphalt volcanism and chemosynthetic life in the Campeche Knolls, Gulf of Mexico. *Science* 304, 999–1002.
- Milkov, A.V., Sassen, R., 2003. Preliminary assessment of resources and economic potential of individual gas hydrate accumulations in the Gulf of Mexico continental slope. *Marine Petroleum Geology* 20, 111–128.
- Mironov, A.N., 2000. New taxa of stalked crinoids from the suborder Bourgueticrinina (Echinodermata, Crinoidea). *Zoological Zhurnal* 79, 712–728.
- Miura, T., Nedachi, M., Hashimoto, J., 2002. Sulphur sources for chemoautotrophic nutrition of shallow water vestimentiferan tube worms in Kagoshima Bay. *Journal of the Marine Biological Society UK* 82, 537–540.
- Nelson, K., Fisher, C.R., 2000. Absence of cospeciation in deep-sea vestimentiferan tube worms and their bacterial endosymbionts. *Symbiosis* 28, 1–15.
- Ochoa, J., Sheinbaum, J., Badan, A., Candela, J., Wilson, D., 2001. Geostrophy via potential vorticity inversion in the Yucatan Channel. *Journal of Marine Research* 59, 725–747.
- Olu, K., Sibuet, M., Harmegnies, F., Foucher, J.P., Fiala-Medioni, A., 1996. Spatial distribution of diverse cold seep communities living on various diapiric structures of the southern Barbados prism. *Progress in Oceanography* 38, 347–376.
- Olu, K., Lance, S., Sibuet, M., Henry, P., Fiala-Medioni, A., Dinet, A., 1997. Cold seep communities as indicators of fluid expression patterns through mud volcanoes seaward of the Barbados accretionary prism. *Deep-Sea Research I* 44, 811–841.

- Paull, C.K., Hecker, B., Commeau, R., Freeman-Lynde, R.P., Neumann, C., Corso, W.P., Golubic, S., Hook, J.E., Sikes, E., Curry, J., 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science* 226, 964–967.
- Pequegnat, W.E., Gallaway, B.J., Pequegnat, L.H., 1990. Aspects of the ecology of the deep-water fauna of the Gulf of Mexico. *American Zoologist* 30, 45–64.
- Ponte, R.M., Luyten, J., Richardson, P.L., 1990. Equatorial deep jets in the Atlantic Ocean. *Deep-Sea Research A* 37, 711–713.
- Roberts, H.H., Aharon, P., 1994. Hydrocarbon-derived carbonate buildups of the northern Gulf of Mexico continental slope: a review of submersible investigations. *Geo-Marine Letters* 14, 135–148.
- Rosenfeld, J., Pindell, J., 2003. Early Paleogene isolation of the Gulf of Mexico from the world's oceans? Implications for hydrocarbon exploration and eustasy. *Bulletin of the Houston Geological Society* 46, 15–17.
- Sahling, H., Galkin, S.V., Salyuk, A., Greinert, J., Foerstel, H., Piepenburg, D., Suess, E., 2003. Depth-related structure and ecological significance of cold-seep communities—a case study from the Sea of Okhotsk. *Deep-Sea Research I* 50, 1391–1409.
- Sassen, R., Milkov, A.V., Ozgul, E., Roberts, H.H., Hunt, J.L., Beeunas, M.A., Chanton, J.P., DeFeitas, D.A., Sweet, S.T., 2003. Gas venting and subsurface charge in the Green Canyon area, Gulf of Mexico continental slope: evidence of a deep bacterial methane source? *Organic Geochemistry* 34, 1455–1464.
- Schmidt, M., Botz, R., Winn, K., Stoffers, P., Thiessen, O., Herzig, P., 2002. Seeping hydrocarbons and related carbonate mineralisations in sediments south of Lihir Island (New Ireland fore arc basin, Papua New Guinea). *Chemical Geology* 186, 249–264.
- Sheinbaum, J., Candela, J., Badan, A., Ochoa, J., 2002. Flow structure and transport in the Yucatan Channel. *Geophysical Research Letters* 29, 1–4.
- Sibuet, M., Olu, K., 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Research II* 45, 517–567.
- Southward, E.C., Schulze, A., Tunnicliffe, V., 2002. Vestimentiferans (Pogonophora) in the Pacific and Indian Oceans: a new genus from Lihir Island (Papua New Guinea) and the Java Trench, with the first report of *Arcovestia ivanovi* from the North Fiji Basin. *Journal of Natural History* 36, 1179–1197.
- Stakes, D.S., Trehu, A.M., Goffredi, S.K., Naehr, T.H., Duncan, R.A., 2002. Mass wasting, methane venting, and biological communities on the Mendocino transform fault. *Geology* 30, 407–410.
- Turnipseed, M., Jenkins, C.D., Van Dover, C.L., 2004. Community structure in Florida Escarpment seep and Snake Pit (Mid-Atlantic Ridge) vent mussel beds. *Marine Biology* 145, 121–132.
- Tyler, P.A., Young, C.M., 1999. Reproduction and dispersal at vents and cold seeps. *Journal of the Marine Biological Association of the UK* 79, 193–208.
- Tyler, P.A., German, C.R., Ramirez-Llodra, E., Van Dover, C.L., 2003. Understanding the biogeography of chemosynthetic ecosystems. *Oceanologica Acta* 25, 227–241.
- Urcuyo, I.A., Massoth, G.J., Julian, D., Fisher, C.R., 2003. Habitat, growth and physiological ecology of a basaltic community of *Ridgeia piscesae* from the Juan de Fuca Ridge. *Deep-Sea Research I* 50, 763–780.
- Van Dover, C.L., Aharon, P., Bernhard, J.M., Caylor, E., Doerries, M., Flickinger, W., Gilhooly, W., Goffredi, S.K., Knick, K.E., Macko, S.A., Rapoport, S., Raulfs, E.C., Ruppel, C., Salerno, J.L., Seitz, R.D., Sen Gupta, B.K., Shank, T., Turnipseed, M., Vrijenhoek, R., 2003. Blake Ridge methane seeps: characterization of a soft-sediment, chemosynthetically based ecosystem. *Deep-sea Research I* 50, 281–300.
- von Rad, U., Berner, U., Delisle, G., Dose Rolinski, H., Fechner, N., Linke, P., Lueckge, A., Roeser, H.A., Schmaljohann, R., Wiedicke, M., Block, M., Damm, V., Erbacher, J., Fritsch, J., Harazim, B., Poggenburg, J., Scheeder, G., Schreckenberger, B., von Mirbach, N., Drews, M., Walter, S., Ali Khan, A., Inam, A., Tahir, M., Tabrez, A.R., Cheema, A.H., Pervaz, M., Ashraf, M., 2000. Gas and fluid venting at the Makran accretionary wedge off Pakistan. *Geo-Marine Letters* 20, 10–19.
- Wiedicke, M., Sahling, H., Delisle, G., Faber, E., Neben, S., Beiersdorf, H., Marchig, V., Weiss, W., von Mirbach, N., Afiat, A., 2002. Characteristics of an active vent in the fore-arc basin of the Sunda Arc, Indonesia. *Marine Geology* 184, 121–141.
- Wilson, W.D., Johns, W.E., 1997. Velocity structure and transport in the Windward Islands Passages. *Deep-Sea Research I* 44, 487–520.
- Winkel, D.P., Gregg, M.C., Sanford, T.B., 2002. Patterns of shear and turbulence across the Florida Current. *Journal of Physical Oceanography* 32, 3269–3285.
- Won, Y., Young, C.R., Lutz, R.A., Vrijenhoek, R.C., 2003. Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae: Bathymodiolus) from eastern Pacific hydrothermal vents. *Molecular Ecology* 12, 169–184.