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## Comparisons of Community Structure between Seep and Vent Mussel-Beds

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COMPARISONS OF COMMUNITY STRUCTURE  
BETWEEN SEEP AND VENT MUSSEL-BEDS

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A Thesis  
Presented to  
The Faculty of the Department of Biology  
The College of William and Mary in Virginia

In Partial Fulfillment  
Of the Requirements for the Degree of  
Masters of Arts

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by  
Mary Turnipseed  
2002


APPROVAL SHEET


This thesis is submitted in partial fulfillment of  
the requirements for the degree of

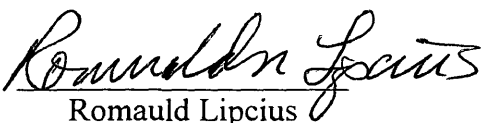
Master of Arts

  
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## ABSTRACT

Measures of community structure (e.g. species composition, richness, and evenness) are fundamental to studies of underlying processes that govern natural communities. These descriptors are poorly known for deep-sea seep and vent communities. Florida Escarpment cold-seep and Snake Pit hydrothermal-vent mussel beds support highly endemic communities of gastropods, polychaetes, crustaceans, and echinoderms, but the two chemosynthetic habitats share only one species. It has been hypothesized that diversity is higher at seeps than at vents, which is attributed to the stability of seep habitats enabling greater species accumulation over time. We sought to validate the claim of higher diversity at seeps by comparing diversity indices generated from Florida Escarpment seep mussel beds and 6 vent mussel beds. The seep mussel-bed fauna was significantly more diverse ( $H'$ ,  $J'$ ,  $\Delta$ ) than the vent mussel-bed faunas. Metal toxicity is proposed to promote 'weedy species' at vents and limit vent diversity, and geological isolation and disparate adaptations of seep and vent organisms may limit species-level similarities between seep and vent communities.



COMPARISONS OF COMMUNITY STRUCTURE  
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## INTRODUCTION

Discovery of a deep-sea, cold-seep ecosystem at the base of the Florida Escarpment in 1984 (Paull et al. 1984) revealed striking taxonomic similarities at the generic level between its community and eastern Pacific hydrothermal-vent communities (Hecker 1985). Since then, vent and seep communities throughout the world's oceans have been explored and found to share many higher taxa, though overlap is restricted at the species level (~20 shared species out of > 650 known species; Sibuet and Olu 1998; Tunnicliffe et al. 1998; *this manuscript*). Shared genera in vent and seep invertebrates point to evolutionary links between the faunas (Tunnicliffe et al. 1998; Craddock et al. 1995; Hecker 1985), though dispersal limitations or different habitat preferences may limit overlap between vent and seep species.

Vent and seep ecosystems share the attribute of a ready availability of redox couples (e.g. hydrogen sulfide and oxygen) that fuel microbial primary production. Vents are always associated with volcanic systems and typically occur along mid-ocean ridges and back-arc spreading centers, where seawater percolates through cracked basalt into the earth's crust. The water becomes heated, infused with metals and reduced compounds, and flows back into the sea through chimneys or fissures in newly formed basalt (Edmond et al. 1982). Seeps are associated with passive and active continental margins within a variety of geological contexts. At seeps, seawater enriched with reduced compounds derived from biogenic and/or thermogenic processes emanates from organic-rich sediments (Sibuet and Olu 1998). Elevated temperatures characterize active vent

habitats, ranging from ~5-10 °C in diffuse flow zones to 400 °C at the openings of black smoker chimneys (Von Damm 1995), whereas minimal temperature anomalies, 0.01 °C to 0.5 °C above ambient seawater temperature, generally mark cold-seep habitats (e.g. Paull et al. 1984; Boulègue et al. 1987; Kulm et al. 1986; Suess et al. 1998).

Habitat stability may also distinguish vents from seeps. Vent sites last only 5 to 10+ years on fast-spreading centers (e.g., southern East Pacific Rise; Van Dover 2000) and for intermittent, multi-decadal periods on slow-spreading centers (e.g., Mid-Atlantic Ridge; Lalou et al. 1993). Vent life-spans are restricted by tectonism and the clogging of subsurface conduits by mineralization. Seep habitats are generally considered to be more stable than vent habitats, persisting for 100's to 1000's of years (Sibuet and Olu 1998).

Geological and geochemical processes and the temperature and stability of the habitats differentiate vents from seeps, yet, at both habitats, chemosynthesis by free-living and symbiotic bacteria supports dense communities of symbiotrophs (organisms that depend on endo- and epi- symbionts for their nutrition), deposit-feeders, grazers, and carnivores/scavengers (reviewed in Van Dover 2000 and Sibuet and Olu 1998). Visually, vent and seep communities can appear remarkably similar, because they share many congeneric or confamilial megafaunal species of tubeworms, mussels, and clams. These habitat-generating foundation species (organisms that affect community structure by altering environmental conditions, species interactions, and resource availability: Dayton 1972; Bruno and Bertness 2001) support analogous communities of invertebrates at vents and seeps. Comparisons between communities hosted by similar foundation species enable us to explore the abiotic and biotic processes that govern patterns in community structure (e.g., Tsuchiya and Nishihira 1985, 1986; Lintas and Seed 1994; Iwasaki 1995;

Seed 1996; Svane and Setyobudiandi 1996; McKindsey and Bourget 2000; Van Dover and Trask 2000; Van Dover 2002, *in review*).

Mussels in the genus *Bathymodiolus* occur at many deep-sea vents and seeps and provide a protective, 3-dimensional habitat to a host of invertebrates in the same way that *Mytilus* species do in rocky-intertidal habitats (e.g. Menge and Branch 2001). Studies of vent *Bathymodiolus* spp. mussel-bed communities have enabled biogeographic and community structure comparisons among vent ecosystems spanning 30° of latitude on the East Pacific Rise (Van Dover *in review*) and vent ecosystems located in different ocean basins (Van Dover 2002). Comparisons of vent mussel-beds with intertidal mussel-beds have addressed how fundamental differences between chemosynthetic and photosynthetic habitats may influence community structure and diversity (Van Dover and Trask 2000).

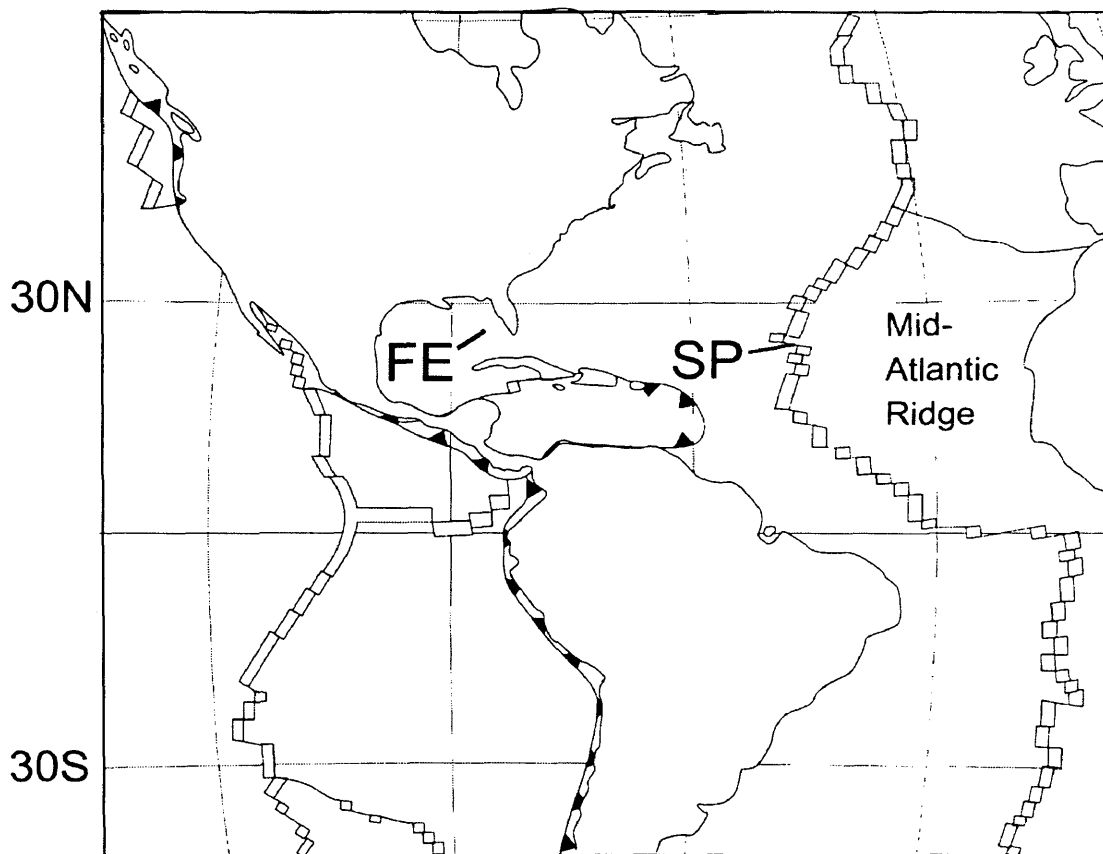
What has not been addressed, though, is a comparison of seep and vent mussel-bed communities. I present an ecological comparison of mussel-bed communities at the Florida Escarpment seep and the Snake Pit vent on the Mid-Atlantic Ridge, which are located at approximately the same depth in the same ocean basin and display faunal alliances at the specific, generic, and familial levels. It has been hypothesized that species diversity at seeps is greater than species diversity at vents, which is attributed to the stability of seep habitats fostering greater radiation and persistence of fauna than vent ecosystems (Sibuet and Olu 1998; Craddock et al. 1995). I sought to validate the claim of higher diversity at seeps by comparing diversity indices generated from the Florida Escarpment seep species-abundance data and an extensive database of species-abundance data for 6 vent mussel-beds.

### *Site descriptions*

The Florida Escarpment is the steep, eroded edge of a Lower Cretaceous carbonate platform that rims southeastern United States (Figure 1; Paull et al. 1984). The chemosynthetic ecosystem at its base (26° 01.8' N, 84° 54.9' W; 3288 m) is fueled by the seepage of cold sulfide-, methane-, and ammonia-rich brine in localized channels from the sediments at the sharp juncture between the limestone escarpment and the abyssal plain (Figures 1, 2a; Paull et al. 1984; Chanton et al. 1991; Martens et al. 1991). Biomass at the cold seep is dominated by symbiotrophic *Bathymodiolus heckeriae* mussels and vestimentiferan tubeworms (*Escarpia laminata* and *Lamellibrachia* sp.), which provide structural habitats for communities of associated fauna (Hecker 1985), shrimp (*Alvinocaris muricola*), galatheid squat lobsters (*Munidopsis* cf. *subsquamosa*), and zoarcid fish (*Pachycara sulaki*). The age of the Florida Escarpment seep community is unknown, but seepage from the base of the escarpment has occurred since the Holocene or Pleistocene (0.01 to 1.64 million years; Paull 1991).

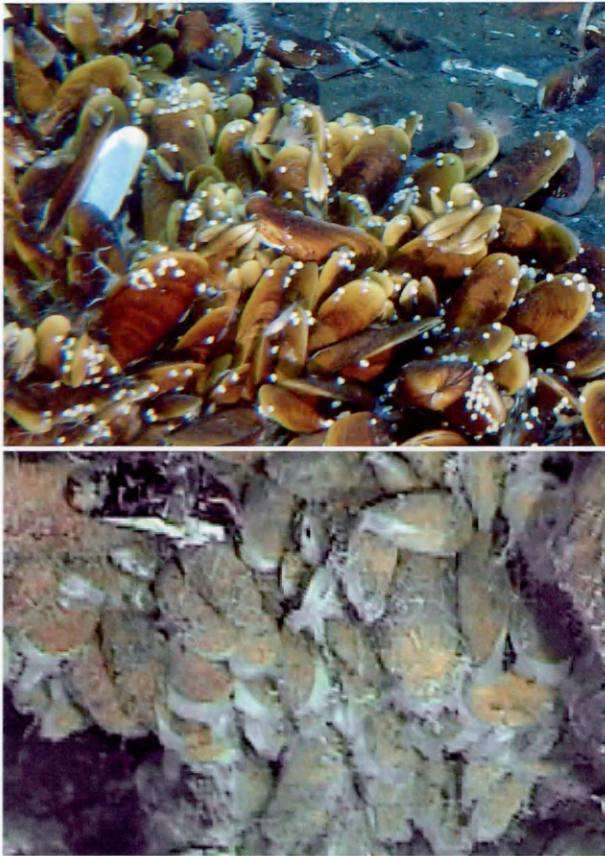
The Snake Pit hydrothermal vent lies just south of the Kane transform fault, in the middle of the Mid-Atlantic Ridge (MAR) axial valley (23° 22.1' N, 44° 56.9' W; 3490 m) (Figures 1, 2b; Kong et al. 1985; Karson and Brown 1988). Snake Pit is an old hydrothermal site, with sulfides dated to 4000 years ago (Lalou et al. 1993). Since then, venting has been intermittent and is thought to persist for multi-decadal pulses (Lalou et al. 1993). Active venting of sulfide- and methane-enriched fluid is from black smokers (325-330 °C), beehive-like diffuser vents (> 70 °C; Fouquet et al. 1993; Van Dover 1995), and diffuse flow zones at 4 deposits (Moose, Beehive, Fir Tree, and Nail) that sit on a ~40 m mound of massive sulfide blocks (Karson and Brown 1988). Mussels

FIGURE 1



Location of the Florida Escarpment cold seep and the Snake Pit hydrothermal vent.

FIGURE 2



A. Florida Escarpment seep mussel-bed community  
(image reproduced with permission of Ian MacDonald).  
B. Snake Pit vent mussel-bed community.

(*Bathymodiolus puteoserpentis*), shrimp (*Chorocaris chacei*, *Mirocaris keldyshi*, *Rimicaris exoculata*, and *Alvinocaris markensis*), bythograeid crabs (*Segonzacia mesatlantica*), galatheid squat lobsters (*Munidopsis crassa*), and zoarcid, synphobranchid, and bythitid fish (*Ilyophis saldanhai*, *Pachycara thermophilum*, and Bythitidae gen. sp.) dominate the Snake Pit biomass (Mével et al. 1989; Segonzac 1992; Fouquet et al. 1993; Williams 1987; Segonzac et al. 1993; Sudarikov and Galkin 1995; Van Dover 1995; Desbruyères et al. 2000; Biscoito et al. *in press*).

#### *Mussel-bed habitats*

Florida Escarpment seep mussel-bed communities are restricted to patches of dark-brown, sulfide-enriched sediment that dot a 20 to 30 m band along the base of the escarpment (Hecker 1985). Snake Pit vent mussel-beds are found in diffuse-flow zones (~5 °C: Jenkins and Van Dover *unpubl. data*), usually beneath sulfide outcrops and in crevices. Both seep and vent mussel beds occur at the mixing zone of anoxic and oxic water, but the thermal buoyancy of vent water pushes this zone above the seafloor, with the result that the mussels are stacked higher at the vent than at the seep (Figure 2). *B. heckerae* and *B. puteoserpentis* rely on symbiotic thiotrophic and methanotrophic bacteria (Cavanaugh et al. 1987; Cavanaugh et al. 1992).



## METHODS

Eleven quantitative samples plus 1 qualitative sample of the mussel-bed community at the Florida Escarpment cold seep were collected during three *Alvin* dives in October 2000. Two *Alvin* dives were conducted at the Snake Pit hydrothermal vent in July 2001 to collect mussel-bed community data (Jenkins and Van Dover *unpubl. data*). Sampling methods and effort at the Florida Escarpment seep and Snake Pit vent mussel beds provide species-abundance data comparable with that from previous studies at Southern and Northern East Pacific Rise (EPR) vents (see Van Dover 2002, Van Dover *in review*).

Quantitative samples were haphazardly collected from the seep and vent mussel beds using pot sampling gear (described in detail in Van Dover 2002) that collects mussels and the organisms associated with them. Qualitative samples were collected with a kevlar-lined scoop and stored in bio-boxes. Data from quantitative samples, standardized to number of individuals per liter of mussel volume collected (henceforth, referred to as standardized abundance data), were used in all abundance-based measures of community structure and diversity of the seep and vent. Data from qualitative box samples were used to supplement the species lists and species richness measures, including species-effort curves.

On deck, mussels were washed three times with filtered seawater, and washings were sieved at 263  $\mu\text{m}$ . Retained organisms, byssal threads, and sediment were fixed in 10% buffered formalin in seawater for 24 h and stored in 70% ethanol. Mussel volumes ( $\pm 0.1$  L) were measured by displacement of water and were used as a measure of

sampling effort.

Sieved samples were sorted twice under a dissecting microscope, the second time after staining with Rose Bengal. Individuals were sorted to morphospecies (except anemones, nematodes, nemerteans, halacarid mites, and copepods) and identified to the lowest possible taxonomic classification. Florida Escarpment and Snake Pit samples were compared to archived specimens collected at East Pacific Rise and Lucky Strike vent mussel beds; identification of polychaetes was confirmed by K. Fauchald (USNM).

Large taxa and highly motile organisms, which were not adequately sampled, are excluded from the species-abundance matrix and community structure analyses but are included in the biogeographic analyses. They were the squat lobsters (*Munidopsis* cf. *subsquamosa*) at the Florida Escarpment seep and the bythograeid crabs > 25 mm (*Segonzacia mesatlantica*) at the Snake Pit vent. Colonial hydroids, found attached to dead mussel shells in one qualitative sample at the Florida Escarpment seep, were also omitted from diversity analyses. Individuals of the commensal polychaetes, *Brachiopolynoe seepensis* (Florida Escarpment), *B. aff. seepensis* (Snake Pit), and *Laubierus mucronatus* (Florida Escarpment), which live in the mantle cavity of bathymodiolid mussels, were not included, as they are not members of the community living among the mussel beds. Postlarval and juvenile mussels < 5 mm were deemed not to have a structural role in the mussel-bed communities and are thus included in analyses of the associated fauna.

To compare the habitat structure of *Bathymodiolus heckerae* mussels at the Florida Escarpment seep and *Bathymodiolus puteoserpentis* mussels at the Snake Pit vent, size-frequency distributions were determined from length measurements of mussels.

A chi-square test was used to distinguish the population size-structure of seep and vent mussels > 5mm.

Biogeographic comparisons between the fauna of the Florida Escarpment seep and Snake Pit vent were made using the presence/absence data and the Bray-Curtis percent dissimilarity coefficient (C) to attain the percent similarity coefficient (100-C). The Bray-Curtis percent dissimilarity coefficient was calculated using  $C = 100 * (T_{a1} + T_{a2}) / (2T_s + T_{a1} + T_{a2})$  where  $T_{a1}$  = the number of species present at site 1 but not at site 2,  $T_{a2}$  = the number of species present at site 2 but not at site 1, and  $T_s$  = the total number of shared species between the 2 sites. Values of the Bray-Curtis percent similarity coefficient (100-C) range from 0 (sites share no species) to 100 (identical species lists).

Species-effort curves were computed from quantitative and qualitative species-abundance data for each site using EstimateS (Colwell 1997; randomization operations = 200 without replacement). Regression analysis of semi-log plots of randomized species-effort curves (Hayak and Buzas 1997) was used to calculate the number of species represented by 10,000 individuals ( $S_{10,000}$ ) at the seep and vent mussel beds.

For computation of diversity indices and multivariate measures of community structure, standardized abundance data were used. The Shannon-Weiner diversity index ( $H'$ ) and Pielou's evenness ( $J'$ ) index were calculated for each site from cumulative standardized abundance data using the DIVERSE subroutine in PRIMER v5 (Clarke and Gorley 2001). Evenness in the mussel-bed communities was also evaluated with species-rank curves of standardized abundance data from the seep and vent.

Taxonomic diversity and distinctness ( $\Delta$  and  $\Delta+$ ), which describe the taxonomic breadth of a community as a proxy measure of phylogenetic diversity, were also

calculated using the DIVERSE subroutine in PRIMER v5 (reviewed in Warwick and Clarke 2001). Taxonomic diversity ( $\Delta$ ) describes the average taxonomic distance through the taxonomic tree of a community between two randomly chosen individuals. It, thus, is influenced by species with the greatest abundances and provides a measure of the taxonomic breadth of the numerically dominant species in a community. Taxonomic distinctness ( $\Delta^+$ ) is a measure of the average taxonomic distance between two species chosen at random from a community and is generated from species presence/absence data. Taxonomy of the Florida Escarpment seep anemones, nemertean, and crustaceans is poorly resolved; therefore, measures of  $\Delta$  and  $\Delta^+$  of the seep and vent communities were generated from polychaete, molluscan, and echinoderm data.

For comparison of trophic structure between the seep and the vent, standardized abundance data for symbiotrophs, deposit-feeders, grazers, secondary consumers, copepods and taxa with unknown trophic strategies were converted into percent abundances per sample. Copepods were not grouped with other taxa because they may include both parasitic siphonostomes and free-living species (Humes 1987-1989, 1996).

Cluster analysis was used to evaluate heterogeneity in community structure within the vent and seep mussel beds, employing Bray-Curtis similarities calculated from square-root transformed, standardized species-abundance data (PRIMER v5; Clarke and Gorley 2001). Analysis of similarity (subroutine ANOSIM in PRIMER v5) was used to quantify the average similarity of samples from each site. The percentage contributions of species to the similarity between cluster groups were determined by the SIMPER subroutine in PRIMER v5.

To compare diversity at vents and seeps, I calculated univariate diversity measures

[species richness (S), species diversity (H'), evenness (J'), taxonomic diversity ( $\Delta$ ), and taxonomic distinctness ( $\Delta+$ )] for several hydrothermal vents (species-abundance data for East Pacific Rise vents in Van Dover 2002, *in review*). Sampling at all sites was limited to invertebrates associated with *Bathymodiolus* spp. mussel beds. The data were analyzed by percentile, non-parametric bootstrap (Efron and Tibshirani 1998) to test the one-tailed, null hypothesis that diversity measures did not differ between the vents and seep ( $\alpha = 0.05$ ). The alternative hypothesis was that diversity measures were higher at the seep than at the vents. In the bootstrap analysis, I was able to assume that the sampled vents comprised a representative subset of all vents because the vents were distributed across different ridge systems and ocean basins.

The test statistic was the difference between the mean of the 6 vent values and that of the seep ( $\theta_{obs}$ ), which would not differ significantly from 0 if the null hypothesis were true. The 7 observed vent and seep values for a particular diversity measure were combined and resampled with replacement to generate a bootstrap sample of 6 vent values and 1 seep value under the null hypothesis. From this data set, the difference between the mean of the 6 resampled vent values and that of the resampled seep value was recalculated as a bootstrap replicate ( $\theta_{boot}$ ). This bootstrap simulation was repeated 10,000 times to generate the frequency distribution of the difference ( $\theta_{boot}$ ), from which the probability value (P) of the observed difference ( $\theta_{obs}$ ) was acquired directly.

## RESULTS

### *Comparison of species lists between Florida Escarpment seep and Snake Pit vent faunas*

Florida Escarpment seep and Snake Pit vent mussel-bed faunas share one morphospecies, the ophiuroid, *Ophioctenella acies*. The seep and vent mussel beds are 2.4% similar, as distinguished by the Bray-Curtis coefficient of similarity. At higher taxonomic levels, mussel-bed communities at the seep and the vent are more similar. Seep and vent genera are 21% similar, and similarity at the familial level was even higher (49%).

### *Comparisons of habitat and community structure between Florida Escarpment seep and Snake Pit vent mussel beds*

Size distributions for mussels > 5 mm significantly differed between the seep and vent (Figure 3;  $\chi^2$ ,  $p < 0.001$ ). Median length of mussels > 5 mm at the vent (69 mm) was almost twice that of the seep mussels (36 mm), even though the largest mussel (232 mm) was collected from the seep.

Fifty-seven species were distinguished from 10,229 individuals collected from Florida Escarpment seep mussel beds (Table 1). Twenty-seven species were represented in 9403 individuals collected from Snake Pit vent mussel beds (Jenkins and Van Dover *unpubl. data*).

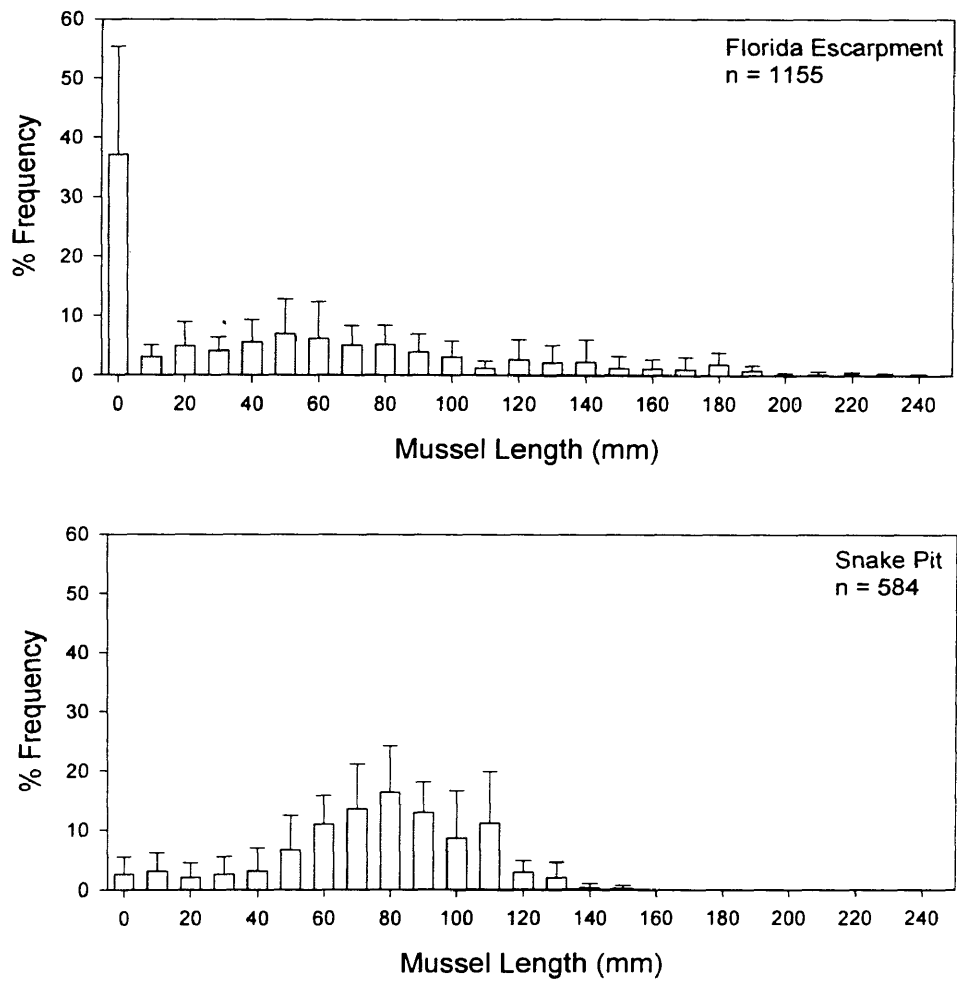
Nematodes accounted for ~43% of the individuals collected in the Florida Escarpment seep samples and >90% of the individuals from samples containing sediment. Nematode abundance was found to be positively correlated with sediment volume (Spearman's rank-order correlation,  $r_s = 0.82$ ). Thus, I omitted nematodes from community structure analyses to avoid confounding the results with data from the infaunal sediment community underlying the seep mussel-bed community. The relative abundances of the dominant species in the samples containing sediment (marked with \* in Table 1) were approximately equivalent to those of the other samples.

The communities associated with mussel beds at the Florida Escarpment seep and Snake Pit vent were numerically and taxonomically dominated by crustaceans, molluscs, echinoderms, and polychaetes (Tables 1, 2). A small number of species comprised a large percentage of the total abundance of individuals at the Florida Escarpment seep and Snake Pit vent (Table 2; Figure 4). Seventy percent of the individuals belonged to 6 species at the seep and to only 2 species at the vent (Table 2; Figure 4). Florida Escarpment seep mussel-bed communities were numerically dominated by copepod species, trochid gastropods, limpets, ophiuroids, and ampharetid polychaetes (Table 2). Snake Pit vent mussel-bed communities were dominated by copepod species and *Ophioctenella acies* (Table 2).

Postlarval and juvenile mussels accounted for 37% of the *Bathymodiolus heckerae* mussels collected at the Florida Escarpment seep (Figure 3). No postlarval *B. puteoserpentis* mussels were found at the Snake Pit vent, and juveniles (< 5mm) comprised only 3% of the mussel population (Figure 3).

Additional samples collected at the seep and the vent would contribute few new

FIGURE 3



Mussel size-frequency distributions (mean and standard deviations for each size class) for A. *Bathymodiolus heckeriae* at the Florida Escarpment seep and B. *Bathymodiolus puteoserpentis* at the Snake Pit vent. X-axis labels indicate lower boundary of size class.



TABLE 1

Phylum Class	Family	Taxon	1	2	3	4	5	Sample #				11*	12	Box*		
			6*	7	8	9*	10*	11*	12	Box*						
Cnidaria	Family Indet.	anemone	5	8	9	1	1	3	3	3	1	10	5	1	2	10
Nemertea	Families Indet.	nemertean	28	12	44	8	8	4	-	1	28	4	7	7	-	14
Platyhelminthes			-	4	-	-	-	1	-	-	15	3	-	-	-	7
Class Indet.																
Annelida																
Polychaeta	Capitellidae	<i>Capitella</i> sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	6
		<i>Dasybranchus</i> sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-
		<i>Dasybranchus</i> sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	1
		<i>Notomastus</i> sp.	-	-	-	-	-	12	-	-	-	-	-	-	-	2
		capitellid A	29	26	30	-	1	95	2	1	17	11	6	-	-	36
		polynoid A	1	5	6	2	10	11	3	18	6	2	3	5	4	4
		polynoid B	-	4	5	2	3	5	4	8	9	1	4	1	4	4
		polynoid C	-	-	-	-	-	-	-	-	-	-	-	-	-	1
		<i>Nicomache</i> sp.	4	2	-	-	-	12	-	-	-	-	-	-	-	9
		hesionid	22	25	35	-	1	51	20	2	8	1	4	-	-	-
		nereid	3	2	9	2	12	9	1	-	6	2	4	-	-	5
		<i>Ancistrosyllis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	5
		syllid	-	-	-	-	-	-	-	-	-	-	-	-	-	50
		<i>Ophrotrocha</i> sp.	3	1	9	-	-	16	-	-	5	1	-	-	-	23
		<i>Aphelochaeta</i> sp.	21	-	19	-	-	3	-	-	2	-	-	-	-	114
		cirratulid A	-	-	-	-	-	-	-	-	-	-	-	-	-	2
		flabelligerid	17	4	13	-	-	9	-	1	5	2	1	-	-	27
		<i>Amythasides</i> sp.	172	73	284	3	1	238	5	1	54	18	11	-	-	32
		<i>Glyphanostomum</i> sp.	108	177	176	5	1	34	3	5	156	174	86	-	-	7



Phylum Class	Family	Taxon	Sample #													
			1	2	3	4	5	6*	7	8	9*	10*	11*	12	Box*	
		isopod B	4	-	2	-	-	-	-	-	-	-	-	1	-	11
		^isopod C	-	-	-	-	-	-	-	-	-	-	1	-	-	-
		^isopod D	-	-	-	-	-	-	-	-	-	-	-	1	-	-
	Alvinocarididae	<i>Alvinocaris muricola</i>	2	2	1	16	3	4	-	2	-	-	-	1	-	-
Echinodermata																
Stelleroidea	Ophiuridae	<i>Ophioctenella acies</i>	134	331	56	37	123	134	210	15	163	51	4	13	159	
Holothuroidea	Synaptidae	<i>Chirodota</i> sp.	5	1	2	-	2	13	1	2	2	5	1	2	1	
Total number of individuals			993	1063	1028	293	519	1483	774	876	967	456	462	204	1111	
Total number of species			33	27	31	18	18	31	18	24	25	26	24	16	40	
Mussel volume sampled (l)			1.2	2.9	1.55	1.8	2.9	1.95	3.1	1.95	2.5	2.7	2.25	1.0	N/A	
Sediment volume sampled (l)					-		-	0.325		-	0.055	0.075	0.015	-	0.465	

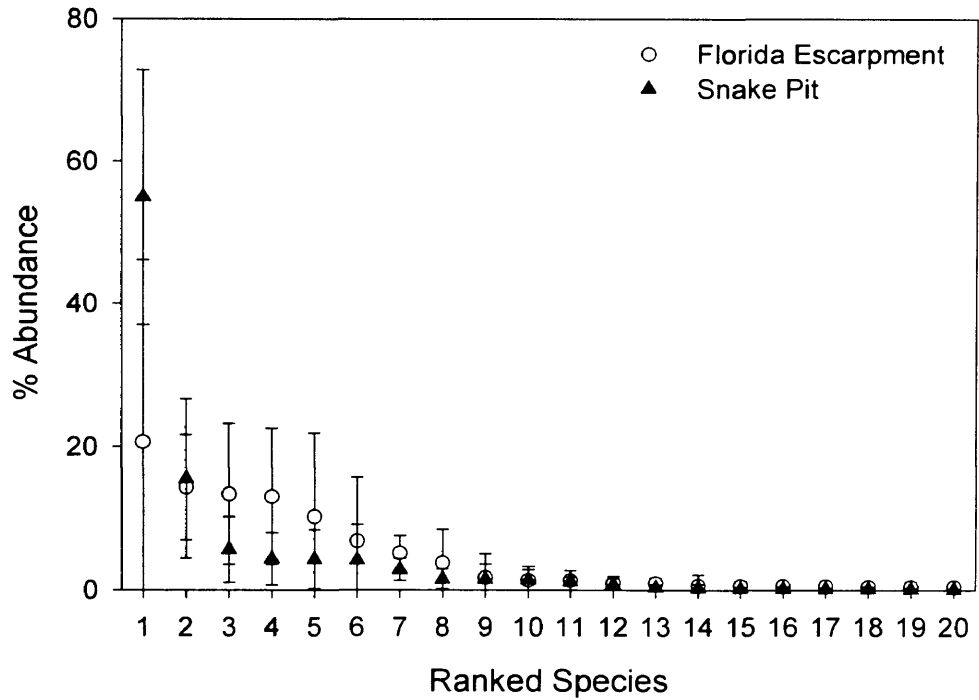
Raw Florida Escarpment seep species-abundance matrix and mussel volume data. Indet.: indeterminate. -: Samples in which the species were not found. \*: Samples that included sediment; ^species only found in samples that included sediment.

TABLE 2

Florida Escarpment	%	Snake Pit	%
copepod spp.	16.4	copepod spp.	51.5
<i>Fucaria</i> n. sp.	14.2	<i>Ophioctenella acies</i>	18.0
<i>Ophioctenella acies</i>	12.4	<i>Opisthotrochopodus</i> sp.	6.4
<i>Amythasides</i> sp.	11.1	spionid	5.8
<i>Glyphanostomum</i> sp.	9.9	<i>Chorocaris chacei</i>	3.8
<i>Paralepetopsis floridensis</i>	9.8	<i>Rimicaris exoculata</i>	3.6
amphipod A	5.7	<i>Amathys lutzi</i>	2.9
<i>Bathymodiolus heckerae</i> < 5 mm	5.4	<i>Levensteiniella</i> sp.	1.8
capitellid A	2.5	<i>Archinome rosacea</i>	1.4
hesionid A	1.9	hesionid B	1.4
Total percentage	89.2		96.7

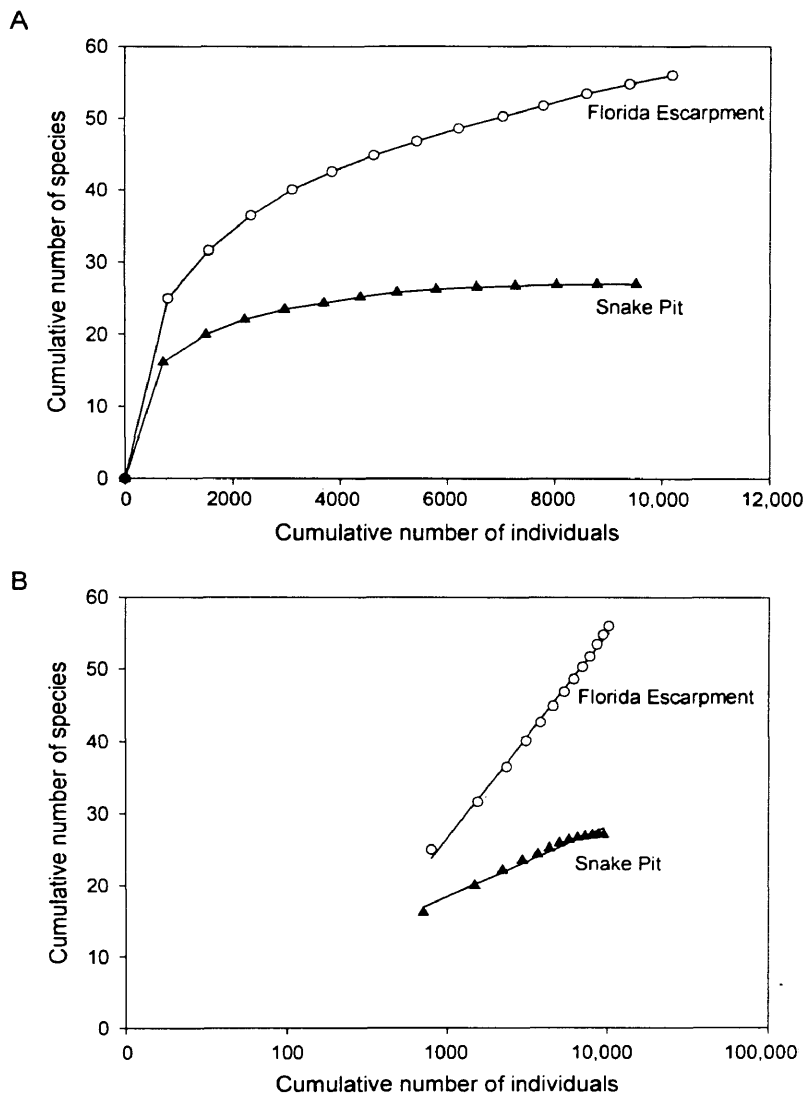
Ten most abundant taxa at the Florida Escarpment cold seep and the Snake Pit hydrothermal vent (Mid-Atlantic Ridge). Percentages are calculated from total species abundances standardized to sampled mussel volume. Snake Pit species-abundance data will be presented in Jenkins and Van Dover (*unpubl. data*).

FIGURE 4



Comparison of species rank order abundance for Florida Escarpment seep and Snake Pit vent mussel-bed communities, calculated from all quantitative samples from both sites (mean  $\pm$  standard deviation). Snake Pit species-abundance data will be presented in Jenkins and Van Dover (*unpubl. data*).

FIGURE 5



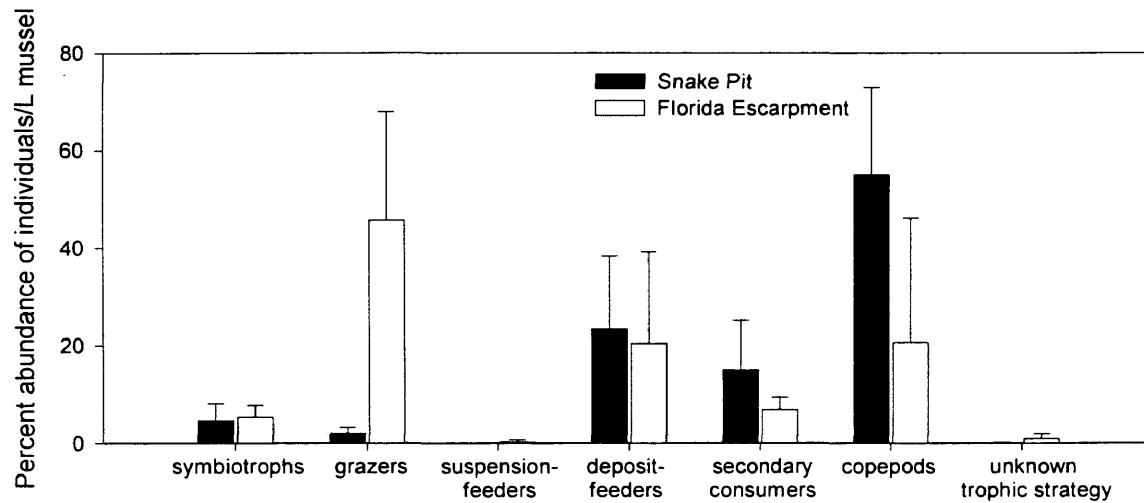
A. Species-effort curves for the Florida Escarpment seep and Snake Pit vent with effort based on cumulative number of individuals. B. Semi-log plots of species-effort curves. Snake Pit species-abundance data will be presented in Jenkins and Van Dover (*unpubl. data*).

species to the total species diversity of either site (Figure 5a). Species richness standardized to 10,000 individuals ( $S_{10,000}$ ) is 55 for the seep mussel beds and 28 for the vent mussel beds (Figure 5b).

Other diversity indices distinguished the communities associated with the seep and vent mussel beds. The Florida Escarpment seep fauna had a higher species diversity ( $H' = 2.58$ ) and evenness ( $J' = 0.66$ ) than the Snake Pit vent fauna ( $H' = 1.71$ ;  $J' = 0.52$ ). Taxonomic diversity of the seep fauna was also greater ( $\Delta = 77.67$ ) than that of the vent fauna ( $\Delta = 67.49$ ). Taxonomic distinctness did not distinguish between the seep ( $\Delta+ = 83.55$ ) and vent ( $\Delta+ = 84.56$ ) mussel beds.

Seep mussel beds were dominated by grazers (Figure 6; ~46%). In contrast, vent mussel beds supported few grazers (~2%) and were dominated by copepods (Figure 6; ~55%). Symbiotrophs made up ~5% of both mussel-bed communities (Figure 6). Suspension-feeders were not numerically important to either mussel-bed fauna (Figure 6). Within-site heterogeneity in community structure was high at small spatial scales (< 1 m) at the Florida Escarpment seep and Snake Pit vent. Two samples collected next to each other at the Florida Escarpment seep (samples A4, A5) were no more similar, 80 to 85%, than samples collected from different mussel beds (Figure 7: samples A1, A2). Two adjoining Snake Pit vent samples, B3 and B7, were only 66% similar (Figure 7), but other samples collected next to each other (B1, B2; B5, B6; B9, B10) were 85% similar. Species composition and abundances were only 59% similar among seep samples and 71% similar among vent samples, as determined by average Bray-Curtis similarities calculated from species-abundance data (Figure 7). Ampharetid polychaetes, capitellid polychaete A, the gastropod *Fucaria* n. sp., juvenile mussels, copepods, amphipod A, and

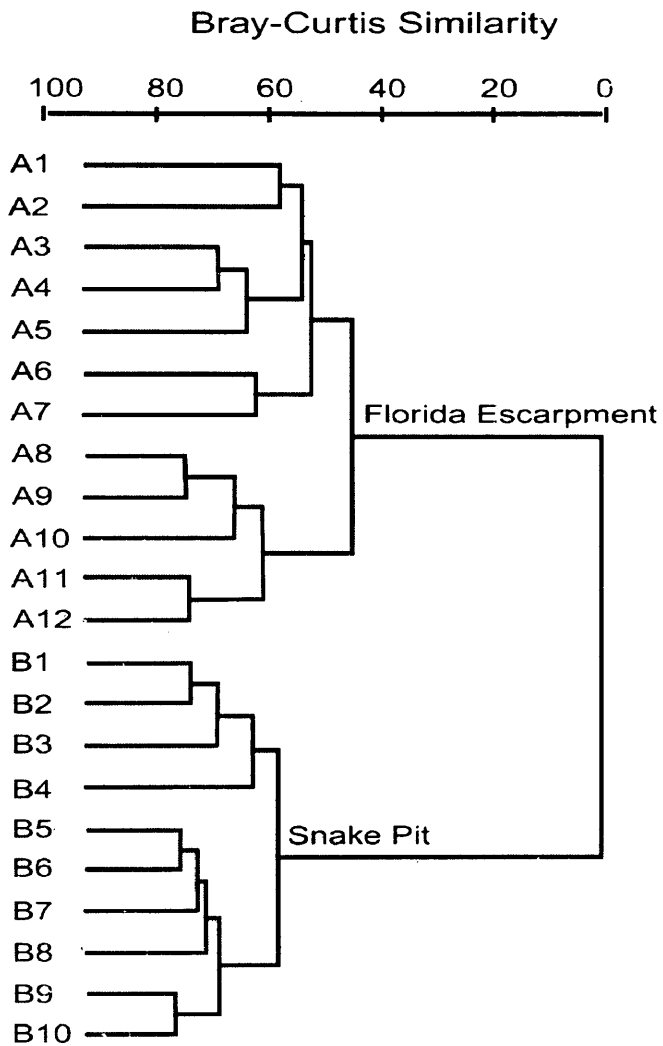
FIGURE 6



Comparison of the distribution of individuals for major trophic groups at Florida Escarpment seep and Snake Pit vent mussel beds, calculated from all quantitative samples from both sites (mean  $\pm$  standard deviation). Snake Pit species-abundance data will be presented in Jenkins and Van Dover (*unpubl. data*).



FIGURE 7



Cluster analysis using Bray-Curtis similarity coefficients of the invertebrate communities associated with Florida Escarpment seep and Snake Pit vent mussel beds.

the ophiuroid *Ophioctenella acies* accounted for ~50% of the variability in community structure at the seep (SIMPER). At the vent, variations in the abundances of polychaetes (*Archinome rosacea*, *Opisthotrochopodus* sp., *Levensteiniella* sp., and spionid sp.), shrimp (*Rimicaris exoculata* and *Chorocaris chacei*), copepods, and *O. acies*, accounted for almost 70% of the heterogeneity in community composition (SIMPER). No significant difference in habitat structure, as assessed by median mussel lengths averaged across samples, accompanied the differences in community structure expressed by the cluster groups within the Florida Escarpment samples (t-test, df = 8,  $p > 0.05$ ) or the Snake Pit samples (t-test, df = 5,  $p > 0.05$ ).

#### *Comparisons of diversity at seep and vent mussel beds*

Relative to the 6 vent mussel-bed communities, the invertebrate fauna associated with the seep mussel bed had significantly higher  $H'$ ,  $J'$ , and  $\Delta$  values (Table 3). Species richness (S) was higher at the seep (S = 55) than at any of the vents (S = 23 to 51); this difference was marginally non-significant ( $P = 0.065$ , Table 3).  $\Delta+$  of the seep fauna, which is based on species presence/absence data, did not differ significantly from the vent values (Table 3).

TABLE 3

Seep	MAR Vent		Southern EPR Vents			Northern EPR Vents			
	Florida Escarpment	Snake Pit	Oasis	Rehu Marka	Train Station	East Wall	Biovent		
S <sub>10,000</sub>	55	28	51	51	23	36	38		
H'	2.58	1.71	1.97	2.42	1.59	1.83	1.73		
J'	0.66	0.52	0.50	0.63	0.46	0.50	0.46		
Δ	77.67	67.49	62.65	66.74	39.12	42.32	58.66		
(Δ+)	83.55	84.56	82.78	84.63	78.85	77.42	77.71		

Species richness, total abundance, S<sub>10,000</sub>, H', J', Δ, Δ+, VarΔ+, Snake Pit data will be presented in Jenkins and Van Dover (*unpubl. data*); Oasis, Rehu Marka, Train Station, East Wall, and Biovent data are from Van Dover (*submitted*).

## DISCUSSION

The invertebrate fauna of Florida Escarpment seep mussel beds (55) is nearly twice as speciose as Snake Pit vent mussel beds (28). Evenness is also higher at the seep than at the vent. Florida Escarpment seep mussel beds are numerically dominated by polychaetes, gastropods, crustaceans, and echinoderms. The vent mussel beds are dominated by crustaceans and polychaetes. Although gastropods comprise one third of the species associated with Snake Pit vent mussel beds, they are numerically unimportant to the community (~2% of total individuals). Copepods are abundant at the vent (~50% of total individuals), and they may be outcompeting gastropods for grazed detritus and bacteria.

Four genera and 10 families are shared between the Florida Escarpment seep and Snake Pit vent mussel-bed communities. At the familial level, the seep mussel-bed fauna are as different from Snake Pit mussel-bed fauna as they are from East Pacific Rise mussel-bed fauna (Van Dover et al. *submitted*). Though the seep and vent faunas are well differentiated, similarities between the Florida Escarpment, Snake Pit, and East Pacific Rise faunas indicate that there are evolutionary ties between global chemosynthetic ecosystems (Tunnicliffe et al. 1998).

Despite similarities at higher taxonomic levels between the seep and vent, similarity at the species level is restricted. According to biogeographic divisions for chemosynthetic habitats, faunas with a Bray-Curtis similarity coefficient between 0 and

5%, belong to separate biogeographic regions (Van Dover et al. *submitted*). With only one shared species, the Florida Escarpment cold seep and Snake Pit hydrothermal vent belong to separate biogeographic regions. Geographic isolation due to the Florida Peninsula and/or different habitat preferences of seep and vent organisms may serve as barriers to species' dispersal and recruitment among Gulf of Mexico seeps and Mid-Atlantic Ridge vents. Dispersing larvae of vent species may not be able to locate seeps, which do not emit as large a chemical signal into the water column as vents do. Conversely, metal toxicity of vent habitats may prevent successful recruitment of seep-derived larvae to vent ecosystems.

There is evidence, though, for limited species exchange on an ecological scale among the Florida Escarpment seep and other seep and vent habitats in the Atlantic. The Florida Escarpment seep shares its ophiuroid, *Ophioctenella acies*, with Snake Pit and Logatchev hydrothermal vents (Tyler et al. 1995; Gebruk et al. 2000), and its clam, *Calyplogena* aff. *kaikoi*, with the Logatchev vent and with seeps on the Barbados accretionary prism (Peek et al. 2000). The Florida Escarpment mussel, *Bathymodiolus heckerae*, was recently discovered at the Blake Ridge methane hydrate seep off of North Carolina (Van Dover et al. *accepted pending revision*), a potential stepping-stone habitat between the Florida Escarpment seep and Mid-Atlantic Ridge vents. Circulation of deep-ocean water in the Atlantic Ocean may enable the exchange of animals between populations of some species between Florida Escarpment and Blake Ridge seeps and Mid-Atlantic Ridge vents (Van Dover et al. 2002). Deep-water circulation has also been implicated in possibly maintaining the faunal similarities between the Mimani-Ensei Knoll vent and Sagami Bay seep communities in the Western Pacific, which, despite

being separated by >1000 km, share 4 species (Hashimoto et al. 1995).

A cryptic sister species of *Branchiopolynoe seepensis*, the commensal polychaete worm found inside the mantle cavities of *B. heckerae* at the Florida Escarpment seep, dwells within the mantle cavities of *B. puteoserpentis* at the Snake Pit vent (Chevaldonné et al. 1998); neither species is found within *B. heckerae* mussels at the Blake Ridge methane hydrate seep off of North Carolina (Van Dover et al. *accepted pending revision*).

Future molecular work may reveal that the populations of *Ophioctenella acies* at the Florida Escarpment seep and the Snake Pit vent are also morphologically indistinguishable sister species.

No mussel postlarvae and few juveniles were collected from Snake Pit mussel-beds; the only other mussel-bed community without mussel recruitment that I have studied is Animal Farm, a waning hydrothermal vent site on the Southern EPR (Van Dover 2002). At active vent sites, mussel postlarvae and juveniles generally comprise 60-80% of mussel populations (Van Dover et al. 2001). Neither abiotic factors nor biotic interactions that I indirectly assessed reveal why mussels were not recruiting to Snake Pit mussel beds. Elevated temperatures and shimmering water indicated that diffuse hydrothermal flow in the mussel beds was still active. The lack of recruitment to the Snake Pit mussel population is not explained by relative proportions of trophic groups presumed to prey on or disturb newly settled mussels. Secondary consumers, which may prey on young mussels (Micheli et al. 2002), comprised a slightly higher percent abundance at Snake Pit than at the Florida Escarpment, though the difference was not statistically significant. Grazers, which are presumed to “bulldoze” postlarvae as they graze free-living bacteria (Micheli et al. 2002), comprised one-tenth the percentage of

individuals at the vent as they did at the seep.

A positive relationship between species richness and habitat stability over ecological and evolutionary time scales was invoked to explain the hypothesized higher species richness at seeps than at vents (Sibuet and Olu 1998; Craddock et al. 1995). This ‘stability-time’ hypothesis was used to explain high diversity in the deep sea (Sanders 1968), and has since been largely supplanted by non-equilibrial explanations involving habitat heterogeneity (Etter and Mullineaux 2001). The idea that seeps are more stable than vents is itself controversial. Seepage at the base of the Florida Escarpment has occurred since the Holocene or Pleistocene (Paull et al. 1991), but signs of recent cessation of seepage (empty mollusk shells, decomposing vestimentiferan tubes) pepper the Florida Escarpment and other seep sites (Van Dover et al. *accepted pending revision*; Jollivet et al. 1990). Although differences in diversity between seep and vent habitats have been attributed to stability, other factors such as metal toxicity of vent fluids may limit the ease with which some invertebrate groups can invade vent sites (Hessler and Smithey 1983) and promote the dominance of ‘weedy’ species. That the fauna at the seep have a more even distribution than the vent faunas may indicate a fundamental difference between seep and vent communities.

Taxonomic diversity ( $\Delta$ ) and taxonomic distinctness ( $\Delta+$ ) have been negatively correlated with environmental stress due to heavy metal and hydrocarbon pollution (Clarke and Warwick 2001; Warwick and Clarke 1995). Lower  $\Delta$  at vents may reflect the effect of environmental stress (habitat instability, toxicity) on community structure. Where seeps are associated with noxious chemicals (e.g., where hosted by hydrocarbon-rich sediments), or where they are unstable on short timescales relative to the life histories

of their pool of potential colonists, I expect that taxonomic and other diversity measures of seep communities will be indistinguishable from those of vents. Given the large number of shared taxa at levels higher than species (Sibuet and Ulu 1998; Tunnicliffe et al. 1998; Hecker 1985) it is not surprising that taxonomic distinctness ( $\Delta+$ ) did not differ significantly between vents and the seep.

## CONCLUSIONS

Despite similarities in community structure with hydrothermal vents, the Florida Escarpment mussel-bed community does not belong to any of the hydrothermal-vent biogeographic provinces or regions defined in Van Dover et al. (*in review*). Present-day dispersal limitations or disparate adaptations of vent and seep organisms to their particular geological and geochemical settings must dictate the low level of species overlap between cold seep and hydrothermal vent communities.

Diverse chemosynthetic mussel-bed communities have low species diversity and low community evenness. Mussel-bed communities in intertidal zones also host communities with variable species richness and relatively low levels of species diversity (generally,  $1.2 \leq H' \leq 3.2$ ; Van Dover 2000) and evenness ( $0.51 \leq J' \leq 0.79$ ; Tsuchiya and Nishihira 1985). Low diversity in both chemosynthetic and intertidal mussel-beds may promote a mussel-bed community paradigm in which habitat characteristics associated with mussel beds may fundamentally restrict diversity in shallow-water and deep-sea ecosystems.



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## VITA

### Mary Parker Turnipseed

Mary Parker Turnipseed was born in Atlanta, Georgia on 19 January 1978. In 1996 she enrolled at Haverford College, and, during the first half of 1999, studied at Melbourne University in Australia. At Haverford College, she studied sperm ultrastructure of a cold-seep vestimentiferan with Dr. Stephen L. Gardiner at Bryn Mawr College. In July 2000, she entered the lab of Dr. Cindy Lee Van Dover at the College of William and Mary and, before it was all over, had dived in ALVIN two times and enjoyed immeasurable research opportunities. She defended the work presented in this thesis on 26 July 2002.