2003

Comparison of Mussel-Bed Faunas at Blake Ridge and Florida Escarpment Seeps

Kathleen Elizabeth Knick
College of William & Mary - Arts & Sciences

COMPARISON OF MUSSEL-BED FAUNAS AT BLAKE RIGE AND FLORIDA ESCARPMENT SEEPS

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

---

by

Kathleen E. Knick

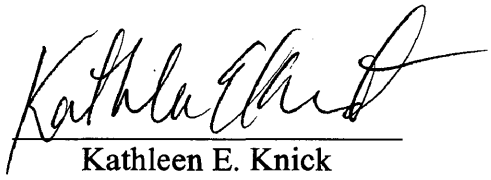
2003

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

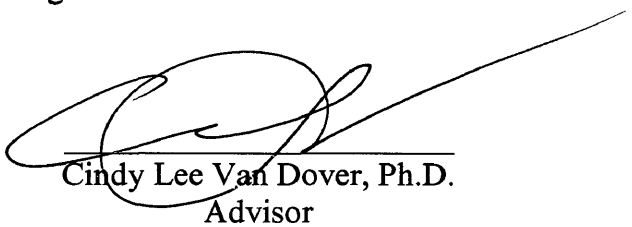
the requirements for the degree of

Master of Arts

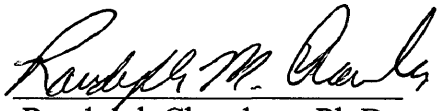


Kathleen E. Knick

Approved, August 2003



Cindy Lee Van Dover, Ph.D.
Advisor



Randolph Chambers, Ph.D.

Rochelle D. Seitz, Ph.D.
Biological Oceanography

TABLE OF CONTENTS

ACKKNOWLEDGEMENTS

I wish to express my appreciation to Professor Cindy Lee Van Dover, under whose guidance this investigation was achieved, for her valuable guidance and criticism throughout the investigation. I am indebted to Professors Randolph Chambers and Rochelle Seitz for their helpful criticism of the manuscript. My colleagues and friends, Mark Doerries, Jennifer Dreyer, Julie Kruse, Josh Leclair, Ryan Mroz, Shana Rapoport, Callie Raulfs, Jennifer Salerno, Conor Sipe, Mary Turnipseed, provided valuable insight, entertainment, and laughter throughout my investigation. I thank the Captain and crew of the R/V *Atlantis*, the pilots and technicians of the DSV *Alvin*, and members of the scientific party for their assistance in obtaining biological specimens at sea. I am grateful to J. Dreyer, A. Waren, P. Tyler, K. Fauchald, X. Komai, and S. Tyler who helped with identifications. This work was supported by the NOAA's National Undersea Research Program – University of North Carolina, Wilmington, and the College of William & Mary.

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

In September of 2001, four DSV *Alvin* dives were conducted at the Blake Ridge methane hydrate seep located off the coast of the Carolinas (32 29.623' N, 76 11.467' W; 2155 m depth). We used quantitative samples from mussel-bed habitats to explore the macrofaunal species composition and community structure within *Bathymodiolus heckerae* mussel beds at Blake Ridge seeps. Over 7,500 individuals representing 52 morphospecies were collected in the samples from Blake Ridge. Oligochaetes were the numerical dominant while *Alvinocaris* spp. shrimp dominated the biovolume of macrofaunal invertebrates in the mussel beds. Multivariate analyses revealed differences in community structure between juvenile and mature mussel beds. Comparisons of univariate diversity indices (species richness, $H_{\log(e)}$, and J') could not distinguish Blake Ridge mussel beds from Florida Escarpment mussel beds. Our analyses suggest that invertebrates associated with Blake Ridge mussel beds are located in a different biogeographic province than either Florida Escarpment cold seep (4 species shared species) or Mid-Atlantic Ridge vent (1 shared species) mussel-bed invertebrates. At generic and familial levels, the two seep faunas were almost as dissimilar from each other as hydrothermal vents on the East Pacific Rise and Mid-Atlantic Ridge.

MUSSEL-BED FAUNAS OF BLAKE RIDGE AND FLORIDA ESCARPMENT

INTRODUCTION

Discovery of seeps at the Florida Escarpment in the Gulf of Mexico (Paull et al. 1984) revealed megafaunal communities similar to those of hydrothermal vents (Hecker 1985). Seeps support dense communities often dominated by vestimentiferan tubeworms, vesicomyid clams, and bathymodiolin mussels. These biomass dominants provide habitats for large populations of macrofaunal invertebrates (Olu et al. 1997; Sibuet and Olu 1998; Sahling 2002; Turnipseed et al. in prep). Like the megafauna invertebrates at hydrothermal vents, most megafauna invertebrates at seeps have specialized, symbiotic relationships with thiotrophic and/or methanotrophic bacteria from which they obtain most of their nutrition (Kennicutt et al. 1985; Childress et al. 1986; Brooks et al. 1987; Distel and Cavanaugh 1994; Fujiwara et al. 2001; Barry et al. 2002). Seeps occur in a variety of settings, including active and passive continental margins, trenches, and mudslides, and are fueled by the oxidation of reduced compounds that seep from hydrocarbon reservoirs, methane hydrates, pore waters, and/or brines (reviewed by Sibuet and Olu 1998).

Initial studies of seep environments focused primarily on site descriptions and distributions of megafauna (e.g. Hecker 1985; Kennicutt et al. 1985; MacDonald et al. 1989; MacDonald et al. 1990; Sibuet et al. 1988; Olu et al. 1997, Sibuet and Olu 1998; Van Dover et al. 2003). Sulfide and methane availability was shown to influence the abundance and composition of megafaunal communities. For example, at mud volcanoes in the Barbados Trench, dense *Calyptogena* sp. beds were associated with relatively high

in the Barbados Trench, dense *Calyptogena* sp. beds were associated with relatively high fluid discharge velocities and high permeability conduits, whereas dispersed clams were likely sustained only by low, diffuse seepage of sulfide (Olu et al. 1997). In three seeps in Monterey Bay, the distribution of *Calyptogena pacifica* and *Calyptogena kilmeri* clam were linked to sulfide concentrations: *C. kilmeri* accounted for 85-99% of all vesicomyids in seeps with high sulfide content, *C. pacifica* accounted for 73% of all vesciomyids in seeps with low sulfide levels (Barry et al. 1997). Recent quantitative studies of faunal distributions at seeps document and interpret community structure, including patterns of taxonomic composition, diversity, and trophic dynamics in relation to physical and chemical environmental regimes (Sahling et al 2002, Levin in review, Turnipseed et al. in prep). Comparisons of patterns of community structure include between seep and non-seep environments, among habitats within seeps, and between seeps and vents. Invertebrates in clam beds at Eel River seeps, for example, were similar to assemblages of non-seep invertebrates of California margin environments (Levin et al. 2000). Studies of Eel River seeps showed that macrofaunal densities did not differ among the *Vesicomya* (*Calypotogena*) *pacifica* beds, microbial mats, and non-seep sediments, but biomass and diversity were lower and composition differed in the highly sulfidic microbial mat sediments relative to clam bed and non-seep sediments (Levin in review). Levin (in review) concluded that horizontal and vertical patterns of fluid flow and sulfide availability had a strong influence on fine-scale distribution, structure and composition of macrofaunal assemblages inhabiting methane seeps. At Hydrate Ridge, a methane seep off the coast of Oregon, species density, diversity, and composition were

linked to gradients in sulfide flux and concentrations in *Calyptogena (Vesicomya)* spp., *Acharax,* and bacterial-mat-dominated sediments (Sahling et al 2002). Foraminiferal abundance at Monterey Bay seeps was lower than at non-seep sites and foram diversity at the seeps was comparable to that of non-seep sites (Bernhard et al 2001). Although similarities were found in types of taxa shared in mussel bed fauna at seeps and vents, diversity of macrofaunal mussel bed fauna was found to be higher at 2 seeps than at 6 vents (Turnipseed et al in press).

In a review of 24 cold-seep communities, Sibuet and Olu (1998) proposed that seep faunas are more endemic than vent faunas due to the greater stability and age of seep habitats. Cold seeps share few taxa at the species level and out of 90 non-symbiont containing species identified, almost all were endemic to a single seep (Sibuet and Olu 1998). Symbiont-containing species were typically restricted to only one or two geographically close seeps (Sibuet and Olu 1998). At generic and familial levels, there was greater similarity between seeps than at the species level. Temporal stability of fluid flux in seep habitats might create more opportunity for local diversification and speciation at seeps (Craddock et al 1995). Low generic endemism of consumers at Gulf of Mexico sites was thought to be due to colonization from the surrounding benthos (Carney 1994). In Monterey Bay, foraminiferal species composition was not the same between two seep sites and many species occurred in both seep and non-seep sediments (Bernhard et al 2001). Quantitative studies are required to appreciate patterns of endemism and biogeography by compiling species compositions of similar seep habitats.

Site description, distribution of megafauna, and food web relationships of conspicuous macrofaunal have been documented for *Bathymodiolus heckerae* mussel beds at the Blake Ridge methane seep (Van Dover et al. 2003). Blake Ridge shared a small number of megafaunal morphospecies with the Florida Escarpment and Barbados Prism, (e.g. *B. heckerae, A. muricula, Chiridota* sp.) suggesting that a more detailed analysis was needed to clarify biogeographical and compositional relationships between these seeps. Community structure patterns such as abundance, biomass, and diversity indices of Blake Ridge mussel beds were evaluated with univariate and multivariate analyses. We tested whether there was within site heterogeneity at Blake Ridge in mussel beds. We also compared our analysis of community structure in Blake Ridge mussel-beds to community structure Florida Escarpment seeps mussel beds (Turnipseed et al in review) to determine the degree of similarity between these two seep faunas at the species, generic, and familial levels.

Study Sites

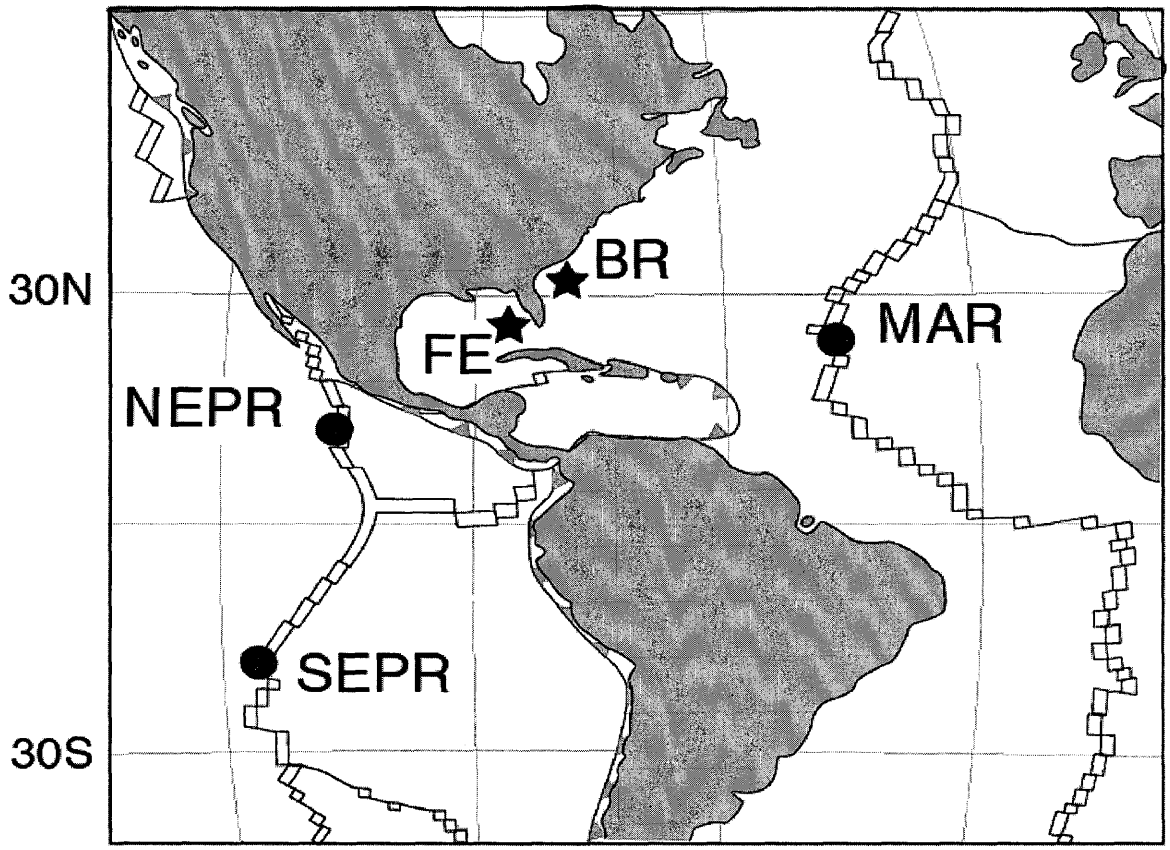
This study focused on mussel beds located on the crest of the Blake Ridge Diapir (Fig. 1) at ODP Site (32° 29.623' N, 76° 11.467' W; 2155 m). The Blake Ridge Diapir is the most southern diapir of a series of ~20 diapirs that begin near the intersection of the Blake Ridge with the Carolina Rise and extends northward on the eastern side of the Carolina Trough (Dillon et al., 1982). This area of South Atlantic Bight has been documented as a major gas hydrate province (26,000 km^2) within the US Exclusive Economic Zone (e.g., Markl et al, 1970; Tucholke et al, 1977; Paull and Dillon 1981).

Methane hydrates generally lie at depths greater than 100 m below seafloor (mbsf; Paull et al 1996). Focused seeps occur along the diapir due to the high thermal conductivity that alters the stability of methane hydrates. Faults act as conduits for the transfer of free gas and waters rich in dissolved gas (methane) to the seafloor (Paull et al. 1995). Invertebrate biomass at Blake Ridge was dominated by disjunct populations of bathymodiolin mussels (*Bathymodiolus heckerae*) and vesicomyid clams (*Vesicomya* cf. *venusta*) (Van Dover et al 2003). Mussel beds occurred in discrete patches generally 20-25 m in diameter. Methane and hydrogen sulfide occur in sediments directly below the mussel beds (Paull et al., 1996).

Chemosynthetic communities at the Florida Escarpment (26° 01.8' N, 84° 54.9' W; 3280 m) are supported by the seepage of cold sulfide-, methane-, and ammonia-rich brine from localized channels in the sediments at the sharp juncture between the limestone escarpment and the abyssal plain (Paull et al. 1984; Chanton et al. 1991; Martens et al. 1991). Biomass at the Florida Escarpment seep is dominated by bathymodiolin mussels (*Bathymodiolus heckerae*) and vestimentiferan tubeworms (*Escarpia laminata, Lamellibrachia* sp.). Mussel-bed communities are restricted to 20 to 30 m band along the base of the escarpment (Hecker 1985). Details of mussel-bed community structure at the Florida Escarpment brine seep are presented in Turnipseed et al. (submitted).

Bathymodiolus heckerae at both Blake Ridge and Florida Escarpment seeps host methanotrophic and thiotrophic symbiotic bacteria and the mussel tissues have isotopic compositions that indicate a nutritional dependence on both symbiont types (Cavanaugh et al. 1987; Cary et al. 1989; Vetter and Fry 1998; Van Dover 2003).

FIGURE 1



Site locations. Seeps (stars): Blake Ridge (BR) and Florida Escarpment (FE); vents (circles): northern East Pacific Rise (NEPR – Train Station, East Wall, Biovent), southern East Pacific Rise (SEPR – Oasis, Rehu Marka); Mid-Atlantic Ridge (MAR): Lucky Strike (LS), Snake Pit (SP).

METHODS

Processing of Samples

Multiple samples from two mussel beds at the Blake Ridge methane seep were collected using the submersible *Alvin* in September 2001. Plastic markers were deployed at these mussel beds; locations of the markers can be found on Fig. 5 of Van Dover et al. (2003). Size-frequency distributions of mussels within the beds were different. Mussels collected near Marker E were characterized by numerous juvenile mussels (10-30 mm length) attached to larger individuals (150-300 mm). Mussels collected at Marker B, approximately ~20 meters northeast of Marker E, were relatively uniform in size (120-220 mm). These mussel beds are herein referred to as the 'juvenile" and "mature" sites. A single quantitative sample was collected at the periphery of a mussel bed at Marker C. Quantitative samples were collected using a 26-cm-diameter pot sampler (Van Dover 2002). The pot sampler was lined with a kevlar drawstring bag. Each pot was inserted into the mussel bed to enclose a clump of mussels, and the bag was cinched closed as the T-handle of the *Alvin* manipulator was rotated. Pots were then inserted into quivers on the science basket of the submersible to prevent loss of organisms during the remainder of the dive. Qualitative samples were haphazardly scooped from mussel beds using a kevler-lined scoop and stored in bio-boxes. Clams and associated fauna were collected using a suction sampler (0.635 cm mesh; Van Dover et al. 2003).

On deck, bivalves were washed 3X with filtered-seawater (10 μm) and washings were collected on 250-μm sieve. Retained material was preserved in 10% buffered formalin in seawater for 48 hr and transferred to 70% ethanol. Mussel volume in liters (±0.1 L) was determined by displacement of plastic-bagged mussels in seawater in a graduated cylinder. Length measurements (± 0.1 mm) of all mussels > 5 mm and dry weights (± 0.01 g) of a representative size-series of mussels were determined.

Sieved samples were sorted twice under a dissecting scope, with the second sort stained with Rose Bengal. Organisms were sorted to morphospecies (except anemones, oligochaetes nematodes, nemerteans, mites, and copepods), identified to the lowest taxonomic level possible, and enumerated. Blake Ridge specimens were compared to archived specimens from the Florida Escarpment cold seep and Mid-Atlantic Ridge vents. Taxonomic specialists were consulted to confirm identifications [mollusks: A. Waren (Swedish Museum of Natural History); polychaetes: K. Fauchald (US National Museum of Natural History); ophiuroids: P. Tyler (Southampton Oceanography Centre); shrimp: X. Komai (Japanese Natural History Museum and Institute)].

Displacement in ethanol was used as a non-destructive method for determining biovolume (Knick et al., in review). Species biovolumes (ml ± 0.1) were standardized per liter of mussel volume (L) collected and are expressed here in units of ml L^{-1}. Only species making up >0.1 ml L^{-1} were included in this analysis.

Galatheid squat lobsters and zoarcid fish were not sampled quantitatively and thus were not included in the analyses of community structure. Juvenile mussels (<5 mm)

were included in the community analysis because they do not have a structural role in the mussel-bed habitat.

Statistical Analysis

To compare habitat structure of *Bathymodiolus heckerae* mussel beds within Blake Ridge and between Blake Ridge and Florida Escarpment mussel beds, size-frequency histograms were calculated from length measurements of sampled mussels. Chi-square tests were used to discern whether the size-frequency distributions of mussels were different among sites.

Quantitative and qualitative samples were used to compute sample-based species-effort curves and species-richness estimators with EstimateS (Colwell 1997; randomization operations = 200 without replacement). Sampling effort was measured as numbers of individuals collected and sampled mussel volume. To make comparisons with the Florida Escarpment, regression analysis of semi-log, randomized, sample-based species-effort curves (Hayak and Buzas 1997) was used to calculate the number of species represented by 10,000 individuals ($S_{10,000}$).

Multi-dimensional scaling (MDS) and cluster analyses were performed to examine community structure within the Blake Ridge mussel bed. Bray-Curtis similarities were calculated using square-root transformed, species-abundance matrices (PRIMER v5; Clarke and Gorley 2001), where abundance was standardized to number of individuals per liter of mussel volume sampled. The square-root transform allows both

the most abundant and the mid-range species to contribute to the similarity matrix (Clarke and Gorley 2001). Analysis of similarity (ANOSIM; Clarke and Gorley 2001) was used to determine if there were significant differences in community structure between the juvenile and mature mussel beds at Blake Ridge. The percentage contributions of species to the dissimilarity between the mussel beds were determined by the SIMPER subroutine in PRIMER v5.

T-tests and regressions (using the dummy variable technique to test the significance of the line of similar slopes with differing intercepts) were calculated using MiniTab software (Version 13.20, 2000). Mussel condition indices were calculated as the ratio of tissue dry weight to shell length. For computation of diversity measures and multivariate analysis, only quantitative species-abundance data, standardized per liter of mussel volume, were used. The Shannon-Weiner diversity index ($H'_{\log (e)}$) and Pielou's evenness index (J') were calculated from sample-based standardized abundance data using the DIVERSE subroutine in PRIMER v5 (Clarke and Gorley 2001).

Biogeography

Bray-Curtis dissimilarity measures were calculated from presence/absence matrices at species-, genera-, and family-levels for mussel beds at Blake Ridge and Florida Escarpment seeps. We also compared Bray-Curtis dissimilarities for presence/absence matrices at species-, genera-, and family-levels for mussel beds at hydrothermal vents on the Mid-Atlantic Ridge [MAR: Lucky Strike (Eiffel Tower, Sintra) and Snake Pit], the northern East Pacific Rise (NEPR: Train Station, East Wall,

Biovent), and the southern East Pacfic Rise (SEPR: Oasis, Rehu Marka). Species lists used in these analyses were from Van Dover and Trask (2000), Van Dover (2002), Van Dover (in press), Turnipseed et al. (submitted) and this study. Taxa not identified to morphospecies (e.g., nemerteans, nematodes, copepods) were not included in these biogeographic analyses. Where we could recognize morphospecies but lacked the expertise to assign generic or familial names (e.g., crustaceans, some polychaetes), these taxa were retained for species-level comparisons, but were excluded from higher-level comparisons. Although we did not sample large decapods (galatheid squat lobsters and bythograeid crabs) and did not include them in our analyses of community structure, large decapods were observed and were included in species lists for biogeographic comparisons.

RESULTS

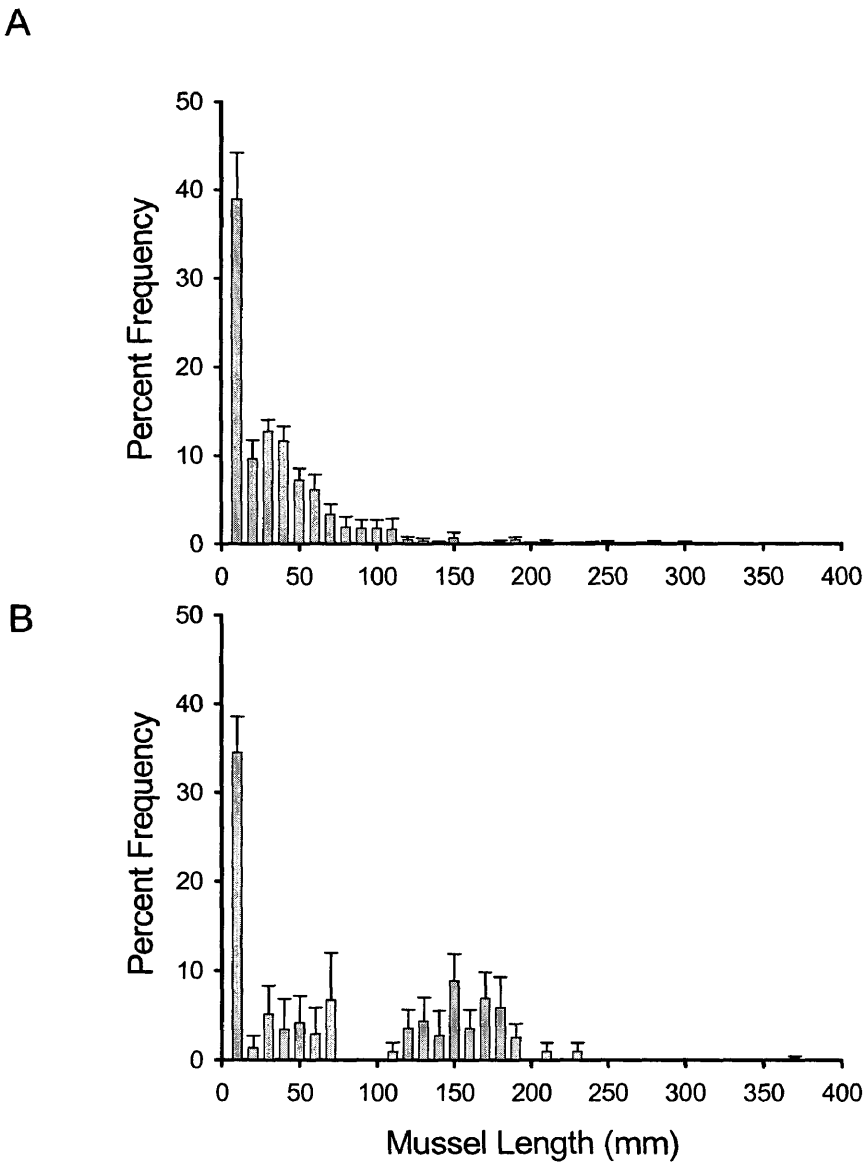
Community Structure in Blake Ridge Mussel Beds

Size-frequency distributions of mussels (> 10 mm) were significantly different between the juvenile and mature mussel beds (Fig. 2; χ^2, $p < 0.001$). Median mussel length (mussels >10 mm) in the juvenile bed was 32.5 mm; median mussel length in the mature bed was 47.7 mm. There was no difference in the percent contribution of post-larval and juvenile mussels (< 10 mm) to the total number of mussels in the juvenile and mature mussel beds (t-test: $p = 0.538$).

Nematodes accounted for 5702 individuals and 42 % of the total number of individuals collected in Blake Ridge seep samples. Nematode abundance was positively correlated with sediment volume (Pearson's product-moment: $p = 0.012$). Because we were interested in the invertebrates associated with the mussel-bed habitat and not the underlying sediment, we chose to omit nematodes from analyses of community structure.

Excluding nematodes, 52 species of macroinvertebrates, representing 8 phyla and 7858 individuals, were collected from Blake Ridge mussel beds (Table 1). Crustaceans (20 species) and polychaetes (16 species) were the best-represented taxonomic groups. Combined, they accounted for about 70% of the total number of species sampled (Table 1).

FIGURE 2



Mussel size-frequency distributions [mean ± (s.e.) for each size class] for *Bathymodiolus heckerae* from the Blake Ridge seep. A. Juvenile mussel bed (number of samples = 5; number of individuals = 1017). B. Mature mussel bed (number of samples = 4; number of individuals = 160).

Oligochaetes were the numerically dominant macroinvertebrate in the community, accounting for 22% of the mean number of individuals per sample (Table 2). Other abundant taxa include amphipod A, *Ophioctenella acies*, *Capitella* sp., copepods, *Bathymodiolus heckerae* (<5 mm), amphipod sp. B, amphipod sp. C, ostracod sp. A, and maldanid sp. A (Table 2). The remaining 42 species accounted for less than 10% of the mean number of individuals per sample. Nine (17%) of the taxa were singletons, i.e., species represented by only one individual in the entire sampling effort.

Alvinocaris sp. A was the biomass-dominant macroinvertebrate, representing 24% of the mean biovolume per sample (Table 2). Amphiurid sp. A, *Chiridota* sp. A, sipunculid sp. A, *Ophioctenella acies*, chaetopterid sp. A, *Phymorhynchus* sp. A, amphipod sp. A., amphipod sp. C, and oligochaete spp. accounted for 62% of the mean biovolume per sample; the remaining 42 species accounted for less than 10% of the mean biovolume per sample (Table 2; Table 3).

MDS ordination based on the species-abundance matrix showed that samples from juvenile and mature mussel beds group by site (Fig. 3a). Pair-wise comparisons indicated that the samples from the two mussel beds were well separated (ANOSIM; $R = 0.897$; $p = 0.008$). The juvenile and mature mussel beds were 57% dissimilar based on abundance. The juvenile mussel bed had greater abundances of oligochaetes, *Capitella* sp., amphipod B, *Bathymodiolus heckerae* and lower abundances of amphipods A and C compared to the mature mussel bed (Table 4). The number of individuals per liter of mussels sampled was higher in the juvenile mussel bed [482 ± 98 individuals L^{-1} (s.e.)] than in the mature mussel bed [214 ± 91 individuals L^{-1} (s.e.)], but this difference was not significant (t-test: $df = 6$; $p = 0.09$).

MDS ordination based on the species-biovolume matrix also showed that samples from juvenile and mature mussel beds group by site (Fig. 3b). Pair-wise comparisons indicated that the samples from the two mussel beds were well separated (ANOSIM; $R = 0.833$; $p = 0.008$). The juvenile and mature mussel beds were 65% dissimilar based on biomass. The juvenile mussel bed had greater biomass of *Chiridota* sp., sipunculids, chaetopterids, and oligochaetes, and reduced amounts of *Alvinocaris* sp. A, amphipod C, and *Alvinocaris* sp. B compared to the mature mussel bed (Table 5). Biovolume of macroinvertebrates per liter of mussel volume sampled did not differ significantly (t-test: df: 6; $p = 0.092$) between the juvenile mussel bed [7.99 ± 1.3 ml L^{-1} (s.e.)] and the mature mussel bed [4.62 ± 0.92 ml L^{-1} (s.e.)].

The single mussel-bed sample collected from the periphery of the mussel bed near marker C was dominated by oligochaetes and *Ophioctenella acies.* This sample was 43% dissimilar to the juvenile bed and 53% dissimilar to the mature bed. The clam slurp was numerically dominated by *Vesicomya* cf. *venusta* < 5mm (~80% individuals). The fauna of the clam slurp was largely a subset of the mussel-bed fauna, with 9 of 52 shared taxa. There were also 3 morphospecies unique to the clam bed (lumbrinerid sp. A, polynoid sp. C, aplacophoran sp. A).

TABLE 1

Phylum / Class	Family	Species	Sample A	B	C	D	E	F	G	H	I	J	Box1	Box2	Clam
Porifera															
	Family Indet.	sponge	0	0	0	0	0	0	0	0	1	0	0	1	0
Cnidaria															
	Family Indet.	anemones	0	0	2	0	0	0	0	0	0	0	2	0	0
Nematoda															
	Family Indet.	nematodes	398	642	610	52	326	153	22	1925	72	1133	238	52	4
Sipuncula															
	Family Indet.	sipunculid sp. A	0	1	6	0	0	0	0	1	0	3	0	0	0
Annelida															
Oligochaeta	Family Indet.	oligochaetes	592	121	188	69	2	6	14	279	13	540	48	9	21
Polychaeta	Aberrantidae	*Aberrenta* sp. *A*	0	0	0	1	0	0	0	0	0	0	0	0	0
	Lumbrineridae	lumbrinerid sp. A*	0	0	0	0	0	0	0	0	0	0	0	0	1
	Polynoidae	polynoid sp. A	0	0	0	0	0	0	0	0	0	1	0	0	1
		polynoid sp. B	0	0	0	0	0	2	0	0	0	0	0	0	0
		polynoid sp. C*	0	0	0	0	0	0	0	0	0	0	0	0	1
	Hesionidae	hesionid sp. A	2	0	0	2	1	0	0	4	5	1	0	2	0
		hesionid sp. B	2	0	0	0	0	0	0	2	0	0	0	0	0
	Spionidae	spionid sp. A	8	11	3	4	0	0	1	44	1	9	0	3	0
		spionid sp. B	3	0	0	0	0	0	0	0	0	1	0	0	0
	Chaetoperidae	chaetoperid sp.A	12	0	21	0	1	0	0	39	0	63	34	82	0
	Capitellidae	*Capitella* sp. A	79	100	198	5	3	5	1	398	13	129	5	2	2
		Dasybranchus sp. A	0	0	0	0	0	0	0	1	0	0	0	0	0
	Maldanidae	maldanid sp. A	5	15	25	0	0	4	0	33	2	81	29	51	0
	Orbiniidae	orbinid sp. A	0	0	0	1	0	0	0	0	0	0	0	0	0

Phylum Class	Family	Species	Sample A	B	C	D	E	F	G	H	I	J	Box1	Box2	Clam
Porifera															
	Family Indet.	sponge	0	0	0	0	0	0	0	0	1	0	0	1	0
Cnidaria															
	Family Indet.	anemones	0	0	2	0	0	0	0	0	0	0	2	0	0
Nematoda															
	Family Indet.	nematodes	398	642	610	52	326	153	22	1925	72	1133	238	52	4
Sipuncula															
	Family Indet.	sipunculid sp. A	0	1	6	0	0	0	0	1	0	3	0	0	0
Annelida															
Oligochaeta	Family Indet.	oligochaetes	592	121	188	69	2	6	14	279	13	540	48	9	21
Polychaeta	Aberrantidae	*Aberrenta* sp. *A*	0	0	0	1	0	0	0	0	0	0	0	0	0
	Lumbrineridae	lumbrinerid sp. A*	0	0	0	0	0	0	0	0	0	0	0	0	1
	Polynoidae	polynoid sp. A	0	0	0	0	0	0	0	0	0	1	0	0	1
		polynoid sp. B	0	0	0	0	0	2	0	0	0	0	0	0	0
		polynoid sp. C*	0	0	0	0	0	0	0	0	0	0	0	0	1
	Hesionidae	hesionid sp. A	2	0	0	2	1	0	0	4	5	1	0	2	0
		hesionid sp. B	2	0	0	0	0	0	0	2	0	0	0	0	0
	Spionidae	spionid sp. A	8	11	3	4	0	0	1	44	1	9	0	3	0
		spionid sp. B	3	0	0	0	0	0	0	0	0	1	0	0	0
	Chaetoperidae	chaetoperid sp.A	12	0	21	0	1	0	0	39	0	63	34	82	0
	Capitellidae	*Capitella* sp. A	79	100	198	5	3	5	1	398	13	129	5	2	2
		Dasybranchus sp. A	0	0	0	0	0	0	0	1	0	0	0	0	0
	Maldanidae	maldanid sp. A	5	15	25	0	0	4	0	33	2	81	29	51	0
	Orbiniidae	orbinid sp. A	0	0	0	1	0	0	0	0	0	0	0	0	0

Phylum			Sample												
Class	Family	Species	A	B	C	D	E	F	G	H	I	J	Box1	Box2	Clam
	Families Indet.	tanaid sp. A	0	0	0	0	1	0	0	2	0	0	3	0	0
		tanaid sp. B	1	0	0	0	0	0	0	0	0	0	1	0	0
Crustacea Isopoda	Families Indet.	isopod sp. A	3	3	7	8	0	1	0	4	19	6	15	13	0
		isopod sp. B	0	0	0	3	0	0	0	1	2	2	5	3	0
		isopod sp. C	2	3	0	0	1	0	0	3	2	14	5	1	0
		isopod sp. D	0	0	0	1	1	0	0	1	0	1	1	0	0
		isopod sp. E	0	0	0	0	0	0	0	0	0	0	1	1	0
Crustacea Decapoda	Alvinocarididae	*Alvinocaris muricola*	1	0	0	0	0	0	0	0	0	0	0	0	0
		Alvinocaris sp. A	0	1	1	3	7	7	5	0	8	0	0	0	0
		Alvinocaris sp. B	0	0	0	0	0	0	1	0	1	0	0	0	0
		unidentifiable juveniles	0	7	0	1	4	0	0	0	0	0	0	0	0
Echinodermata															
Holothuroidea	Chiridotidae	*Chiridota* sp. A	0	1	3	0	0	0	0	2	0	1	0	1	0
Stelleroidea	Ophiuridae	*Ophioctenella acies*	59	196	82	65	39	12	18	133	95	32	100	67	1
	Ophiuridae	amphiophiurid sp. A	2	12	17	2	1	1	0	6	1	6	1	0	0
Echinoidea	Clypeasteridae	*Sarsiaster griegi*	0	0	0	0	0	0	0	1	0	0	0	0	0
Total number of individuals			1357	1265	1333	273	794	330	105	3304	638	2503	822	544	244
Total number of individuals excluding nematodes			959	623	723	221	468	177	83	1379	565	1370	584	491	240
Total number of species			26	22	27	24	20	14	13	34	22	29	25	23	14
Mussel volume (L) sampled			1.25	2.50	2.55	0.55	2.15	2.30	0.90	2.68	1.20	2.28	4.48	3.48	
Sediment volume (ml) sampled			150	350	130	70	30	20	20	250	10	210	140	70	

Blake Ridge species-abundance matrix. A-J = quantitative samples. Box 1, 2 = qualitative samples. Clam = clam slurp. Indet.: indeterminate. * Species found only in the clam slurp

TABLE 2

Taxon	mean abundance (%)	± s.e.		mean biovolume (%)	± s.e.
oligochaetes	22.1	1.8	*Alvinocaris* sp.A	22.2	8.1
amphipod sp. A	16.3	5.7	amphiuroid sp. A	15.6	3.7
Ophioctenella acies	14.5	6.4	*Chiridota* sp. A	11.5	5.2
Capitella sp. A	9.9	3.1	sipunculid sp. A	9.2	1.7
copepods	9.4	3.2	*Ophioctenella acies*	8.1	3.9
Bathymodiolus heckerae < *5* mm	5.2	2.5	chaetoperid	7.3	5.7
amphipod sp. B	4.6	1.2	*Phymorhychnus* sp. A	7.0	3.5
amphipod sp. C	4.4	1.6	amphipod sp. A	3.6	1.4
ostracod sp. A	2.7	2.8	amphipod sp. C	3.5	2.5
maldanid sp. A	1.7	0.6	oligochaetes	2.1	1.3
Percent Contribution	90.9			90.1	

Top ten abundance and biovolume dominants at Blake Ridge.

TABLE 3

Phylum / Class	Family	Species	Sample A	B	C	D	E	F	G	H	I	J
Porifera												
	Family Indet.	sponge	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00
Cnidaria												
	Family Indet.	anemones	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sipuncula												
	Family Indet.	sipunculid sp. A	0.00	3.50	7.50	0.00	0.00	0.00	0.00	1.00	0.00	2.80
Annelida												
Oligochaeta	Family Indet.	oligochaetes	1.00	0.20	0.05	0.05	+	+	+	0.05	+	0.70
Polychaeta	Aberrantidae	*Aberrenta* sp. *A*	0.00	0.00	0.00	+	0.00	0.00	0.00	0.00	0.00	0.00
	Spionidae	spionid sp. A	0.10	0.15	0.10	0.10	0.00	0.00	0.03	1.00	0.05	1.00
	Chaetoperidae	chaetoperid sp. A	0.40	0.00	2.00	0.00	0.05	0.00	0.00	7.00	0.00	6.00
	Capitellidae	*Capitella* sp. A	0.10	0.15	0.40	0.02	0.02	0.02	1.30	1.30	0.02	0.45
	Maldanidae	maldanid sp. A	0.20	0.30	0.20	0.00	0.00	0.15	0.00	0.40	0.10	0.80
Mollusca												
Gastropoda	Conidae	*Phymorychanus* sp. A	1.00	0.00	0.00	5.50	0.00	0.00	0.00	0.00	0.00	0.00
	Marginellidae	Marginellidae sp. A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00
Bivalvia	Mytillidae	*Bathymodiolus heckerae* < *5mm*	0.07	0.10	0.07	+	+	+	+	0.05	0.10	0.10
	Vesicomyidae	*Vesicomya* cf. *venusta*	0.00	0.00	0.00	1.00	1.00	0.00	0.00	1.00	0.00	0.00
Arthropoda												
Crustacea Amphipoda	Families Indet.	amphipod sp. A	0.15	0.20	0.05	0.05	1.20	0.60	0.05	0.10	0.40	0.30
		amphipod sp. B	0.10	0.05	0.10	+	+	+	0.00	0.30	0.05	0.40
		amphipod sp. C	0.00	0.00	0.00	0.00	2.10	0.10	0.05	0.10	0.40	0.10
		amphipod sp. D	+	+	+	0.00	0.00	0.00	0.00	0.05	0.10	0.10
		amphipod sp. E	0.10	0.00	+	0.00	0.05	0.00	0.00	0.05	0.00	0.15
Crustacea Isopoda	Families Indet.	isopod sp. A	0.05	0.05	0.10	0.15	0.00	0.05	0.00	0.05	0.10	0.10
Crustacea Decapoda	Alvinocarididae	*Alvinocaris muricola*	1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Alvinocaris sp. A	0.00	0.40	0.30	2.10	1.95	2.50	3.20	0.00	5.00	0.00
		Alvinocaris sp. B	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.40	0.00
Echinodermata												
Holothuroidea	Chiridotidae	*Chiridota* sp. A	0.00	1.00	10.00	0.00	0.00	0.00	0.00	13.80	0.00	4.10
Stelleroidea	Ophiuridae	*Ophioctenella acies*	1.10	1.60	1.10	0.30	1.50	0.50	0.40	2.00	0.90	0.30
	Ophiuridae	amphiophiurid sp. A	1.80	2.50	4.50	0.90	1.00	3.00	0.00	1.50	1.00	1.40
Echinoidea	Clypeasteridae	*Sarsiaster griegi*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00

Blake Ridge species-biovolume matrix. Indet.: indeterminate.(+) Present but <0.01ml/L

TABLE 4

	Average Abundance		Contribution to Dissimilarity	
Taxon	Juvenile Bed	Mature Bed	Contribution %	Cumulative %
oligochaetes	188	7	14.8	14.8
Capitella sp. A	77	4	10.5	25.3
Amphipod sp. B	40	5	6.8	32.1
Amphipod sp. A	13	75	6.6	38.7
Amphipod sp. C	<1	25	5.5	44.2
Bathymodoilus heckerae < 5 mm	34	10	5.1	49.3
Ophioctenella acies	44	31	4.6	53.9
chaetoperid sp. A	12	<1	4.2	58.1
maldanid sp. A	14	<1	4.2	62.3
copepods	18	36	3.9	66.2

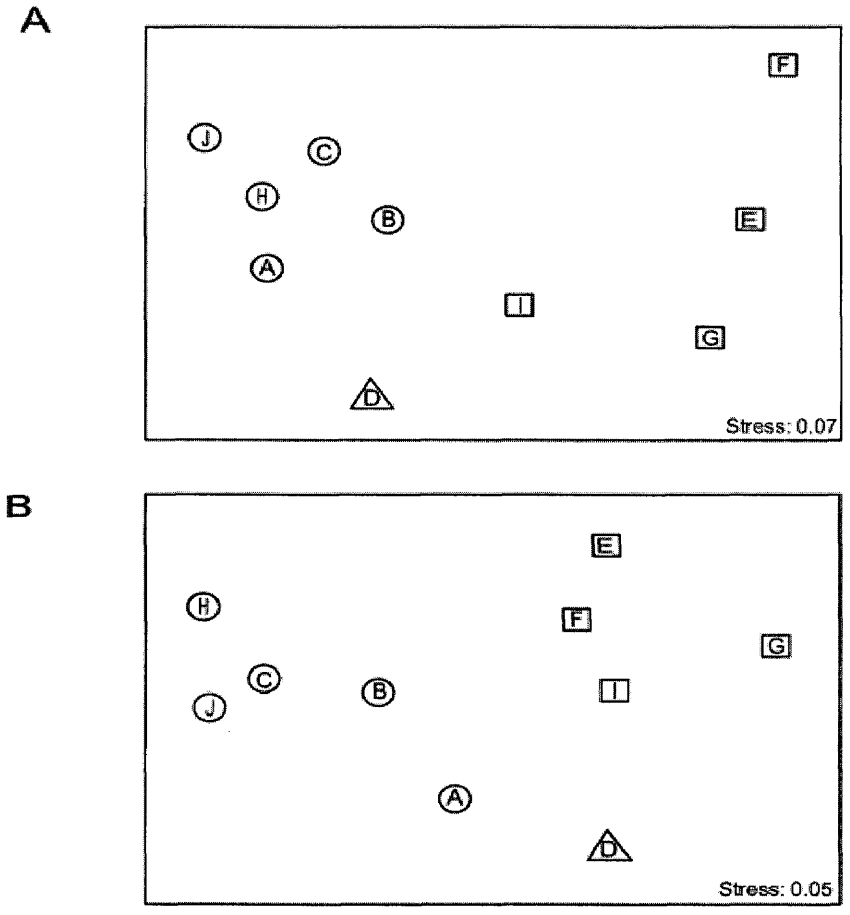
Species contributions (> 3%) to Bray-Curtis dissimilarities (standardized to number of individuals per liter of mussel volume sampled and square-root transformed) between invertebrates of Blake Ridge juvenile and mature mussel beds.

TABLE 5

	Average Biovolume		Contribution to Dissimilarity	
Taxon	Juvenile	Mature	Contribution %	Cumulative %
Alivnocaris sp. 1	0.06	2.43	15.19	15.19
Chiridota sp. A	2.26	0.00	13.79	28.98
sipunclulid sp. A	1.19	0.00	10.87	39.85
chaetoperid sp. A	1.27	0.01	10.03	49.88
amphiurid sp. A	1.08	0.65	5.38	55.26
amphipod sp. C	0.02	0.35	4.93	60.19
oligochaetes	0.25	0.00	4.82	65.01
Alvinocaris sp. B	0.00	0.22	3.75	68.76
Capitella sp. A	0.20	0.02	3.29	72.05
amphipod sp. A	0.08	0.30	3.19	75.24
maldanid sp. A	0.17	0.04	3.16	75.24

Bivolume contributions (> 3%) to Bray-Curtis dissimilarities (standardized per ml biovolume per liter of mussel volume sampled and square-root transformed) between invertebrates at Blake Ridge juvenile and mature mussel beds.

FIGURE 3



Multi-dimensional scaling analyses for Blake Ridge mussel bed samples. A. Abundance-based MDS plot of quantitative, standardized (number of individuals L^{-1} mussel volume sampled), square-root-transformed, species-abundance matrix. B. Biovolume-based MDS plot of quantitative, standardized (ml L^{-1} mussel volume sampled), square-root-transformed, species-biovolume matrix. Circles: samples from the juvenile mussel bed; squares: samples from the mature mussel bed; triangle: sample from the periphery of the Marker C mussel bed. Letters correspond to sample designations in Table 1.

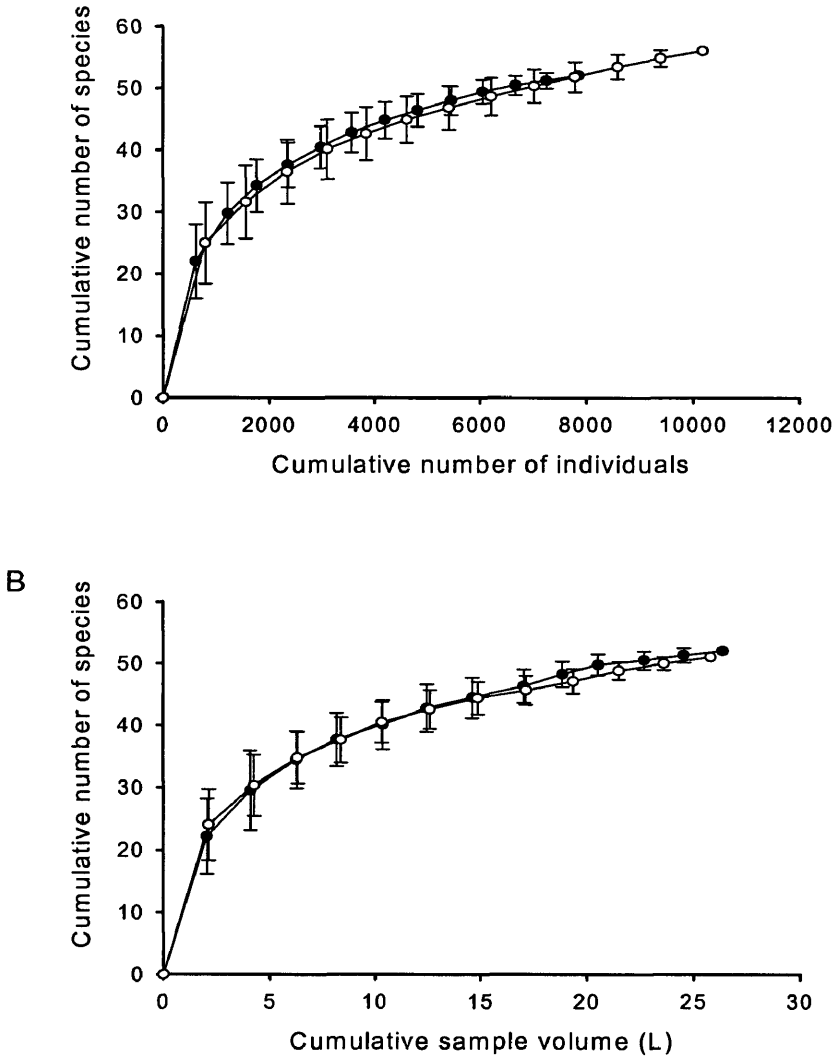
Comparison of Mussel-bed Communities between Blake Ridge and Florida Escarpment Seeps

Species-effort curves based on cumulative number of individuals or cumulative mussel volume for Blake Ridge and Florida Escarpment mussel-bed communities were similar (Fig 4). Species richness, standardized to a sampling effort of 10,000 individuals, was 55 species for both sites (Turnipseed et al. in press, this manuscript). Species-richness estimates were lower for Blake Ridge mussel beds (57 to 65 species) than for Florida Escarpment mussel beds (59 to 82 species). MMmeans was the lowest species-richness estimator for both sites while Jack2 (Blake Ridge) and Ace (Florida Escarpment) were the highest species-richness estimators. Mean H' and J' values for Blake Ridge and Florida Escarpment mussel bed samples were indistinguishable from one another other (Table 6; t-test, H': $p = 0.587$; J': $p = 0.962$).

Eight species comprised ~85% of the total abundance of individuals in Blake Ridge and Florida Escarpment samples (Fig. 5). At Blake Ridge mussel beds, invertebrates abundance was dominated by amphipod crustaceans (44%); biovolume was dominated by echinoderms (26%). At Florida Escarpment, mussel-bed abundance and biovolume of invertebrates with mussel beds were dominated by trochid gastropod molluscs (41%) (Fig. 6).

There was no significant separation of the y-intercepts in log-log transformed shell-length vs. dry weight relationships of mussels collected at Blake Ridge and Florida Escarpment (Fig. 7; $p < 0.001$), indicating that mussel condition was similar between the seep sites.

FIGURE 4



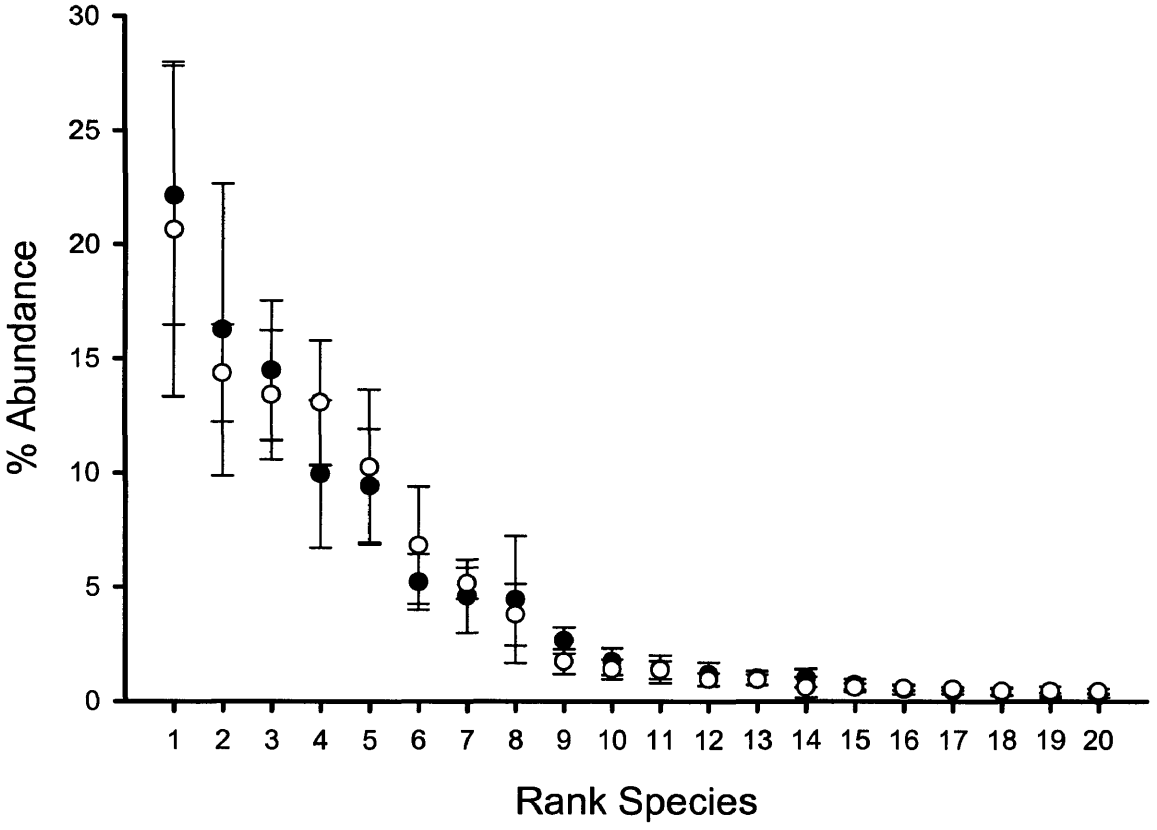
Sample-based species-effort curves for Blake Ridge (filled circles) and Florida Escarpment mussel beds (open circles). Points represent the mean (± s.d.) of 200 randomizations. A Effort based on cumulative number of individuals. B. Effort based on cumulative mussel volume sampled.

TABLE 6

	S	n	$S_{10,000}$	H'	J'
Blake Ridge	52	7858	55	1.941 (0.082)	0.637 (0.026)
Florida Escarpment	57	10229	55	2.028 (0.130)	0.639 (0.035)

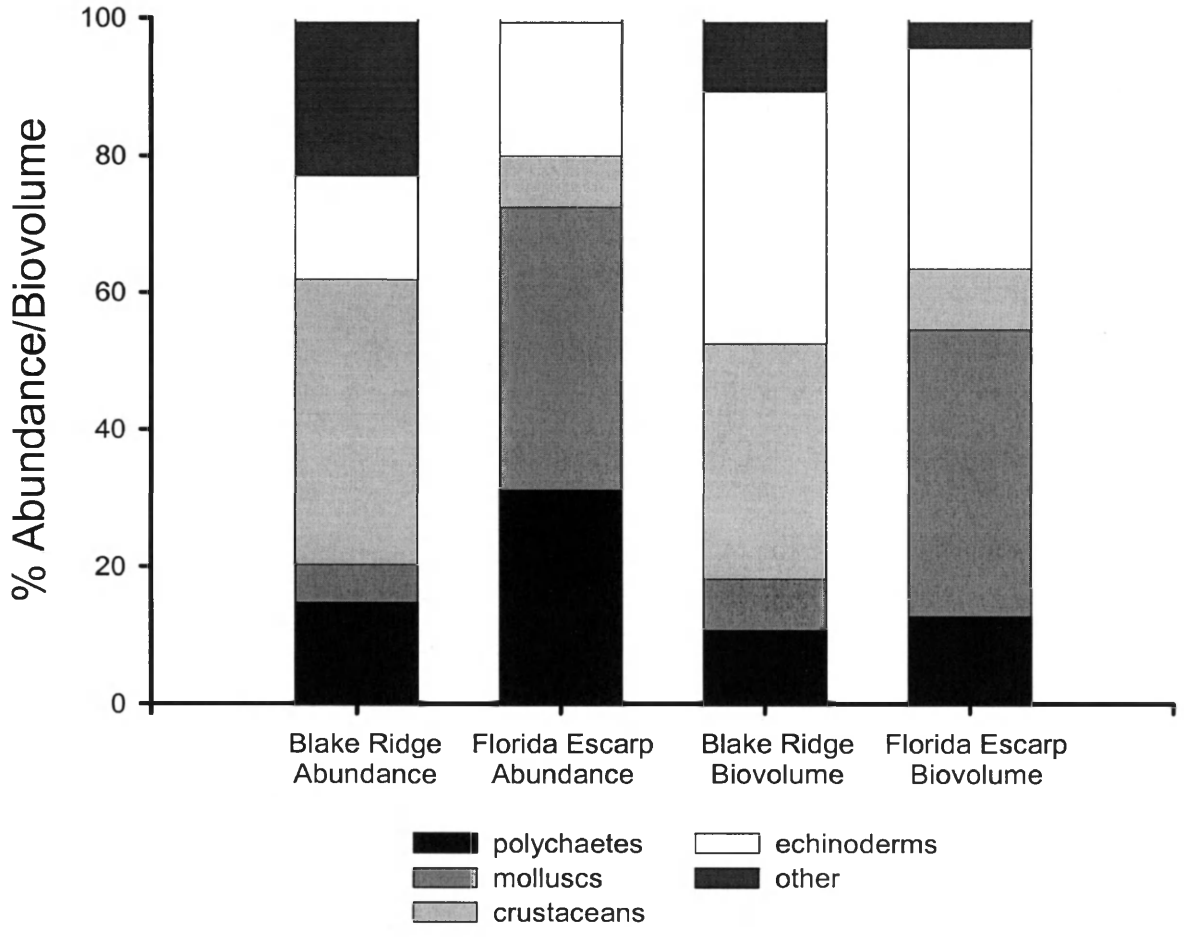
Species richness (S), total abundance (n), number of species in 10,000 individuals ($S_{10,000}$), mean $H'_{\log e}$ (std. error), and mean J' (std. error).

FIGURE 5



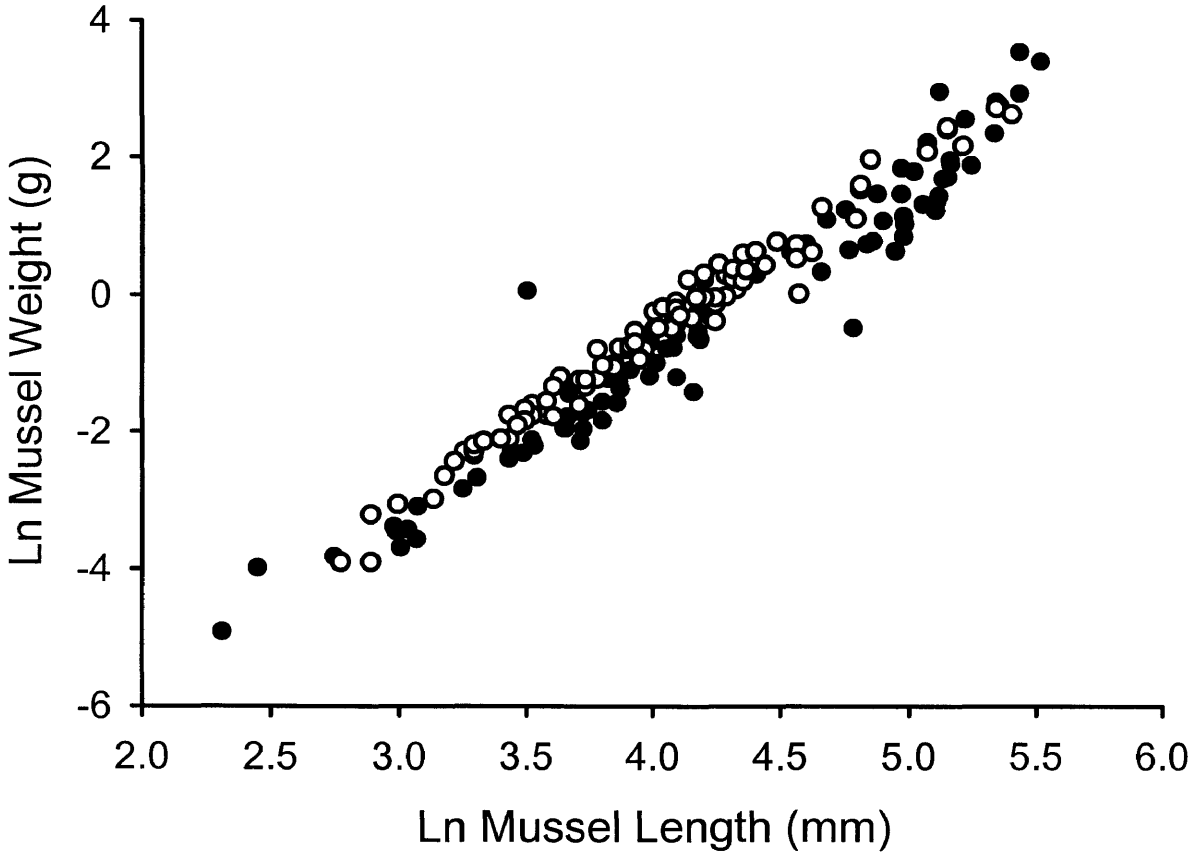
Rank abundance of the 20 numerically dominant taxa at Blake Ridge (n = 10 samples; total number of individuals = 6490; filled circles) and Florida Escarpment (n = 12; total number of individuals = 9118; open circles) of mussel-bed faunas. Points represent mean percent abundance (± s.e.).

FIGURE 6



Distribution of abundance and biovolume among major taxonomic groups at Blake Ridge and Florida Escarpment.

FIGURE 7



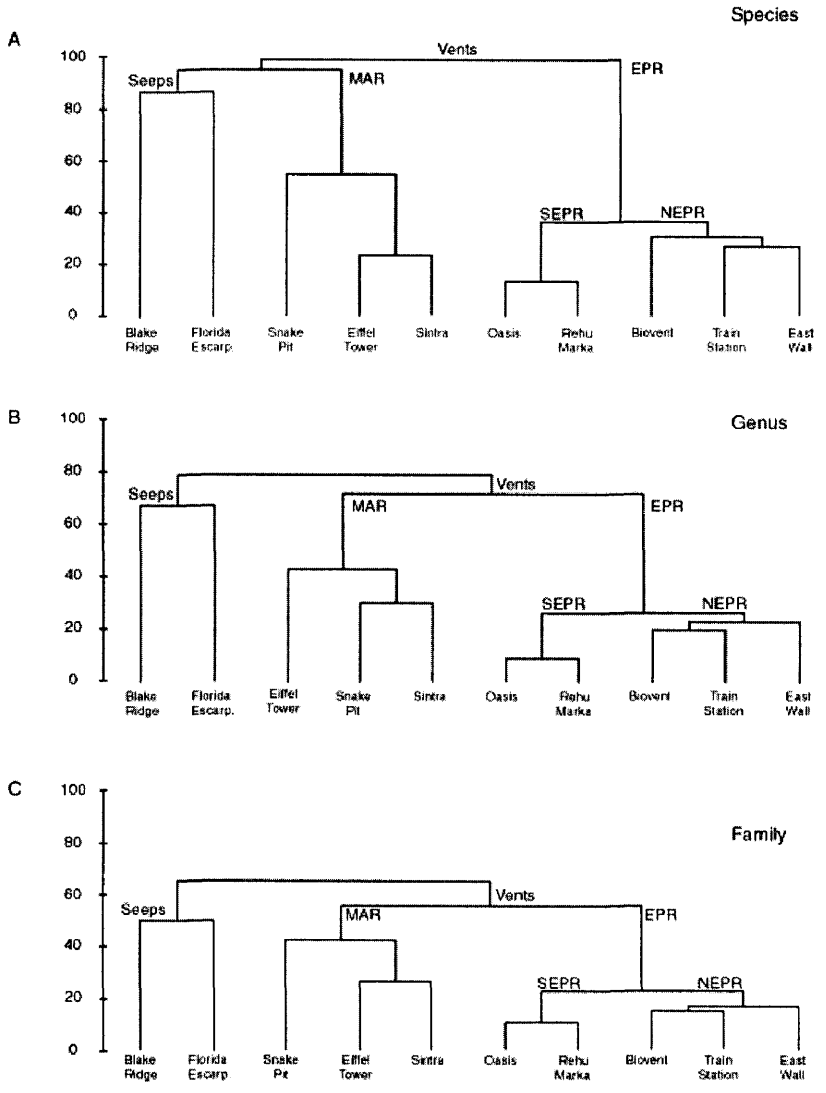
Bathymodiolus heckerae. Log tissue dry weight (g) vs. log shell length (mm). Filled circles: Blake Ridge; open circles: Florida Escarpment.

Species composition was different in mussel beds at Blake Ridge and Florida Escarpment, with 90% dissimilarity based on average Bray-Curtis coefficients using species presence/absence matrices (Fig. 8a). Blake Ridge mussel beds share only 4 species with the Florida Escarpment: *Bathymodiolus heckerae*, *Ophioctenella acies*, *Alvinocaris muricola, Chiridota* sp. A.

Comparisons of Genera and Families of Invertebrates associated with Chemosynthetic Mussel Beds

At the levels of genus and family, the mussel-bed fauna of the Blake Ridge were different from that of hydrothermal vents on the northern East Pacific Rise, southern East Pacific Rise, Mid-Atlantic Ridge and Florida Escarpment brine-seep mussel beds (Fig. 8b, c). At the generic level, seeps are 78% dissimilar from vents, and 60% dissimilar from each other. At the family level, the seep sites are almost as dissimilar to each other (52%) as vents on different ridge axe and in different ocean basins (58%). Blake Ridge and Florida Escarpment mussel beds share only one species (*Ophioctenella acies*) with Mid-Atlantic Ridge vent mussel beds, and no species with Eastern Pacific Rise vents.

FIGURE 8



Cluster diagrams of Bray-Curtis presence/absence dissimilarities using group-averaglinking. A. Species. B. Genus. C. Family.

DISCUSSION

Variation in Mussel Bed Communities at Blake Ridge

Size-frequency distributions of mussel at Blake Ridge differed between the juvenile and mature mussel beds, though both beds had similar levels of recruits (~20%). Ward et al. (in prep) found mussels with shell lengths greater than 100 mm at the juvenile Blake Ridge mussel beds were either lightly infected or uninfected with a possibly lethal viral infection. These mussels could represent a subset of the population that was immune to infection or was strong enough to fight off the infection before it became fatal. This viral infection could explain the reduction in the percent of larger mussel size classes (100-360 mm) at the juvenile bed in comparison to the mature bed. Alternatively, changes in loci of seepage (Van Dover et al. 2003) or spatial variability in biological processes (e.g. recruitment, settlement, predation) could also result in differences in size frequency patterns.

Within site variation of species composition, abundance, and biovolume was evident based on cluster of samples by mussel-bed type (juvenile vs. mature) based on multivariate analyses. Mean abundance and biovolume of invertebrates associated with mussel beds were generally higher in samples collected from the juvenile bed, but not significantly higher. Higher numbers of deposit-feeding oligochaetes, sipunculids, echinoderms, and capitellid polychaetes were present in juvenile mussel beds while higher numbers of grazing amphipods and shrimp were present in mature beds, which indicated that there were differences in nutritional sources in the beds. The single sample collected from the periphery of mussel beds at marker C appeared to be near a "dying"

bed of mussels, but it nevertheless contained large numbers of post-larval recruits of *Bathymodiolus heckerae* and *Ophioctenella acies.*

Spatial variation in mussel-bed communities at Blake Ridge may be attributed to a number of factors, including mussel size and spatial and/or temporal variation in fluid flux. In shallow-water mussel beds, spatial variation in communities has been correlated with a number of physical factors, including mussel-bed structure, shell surface area, abundance of byssal threads (Iwasaki 1994), amount and size of sediments (Iwasaki 1995), biodeposition (Tsuchiya 1980), and patch size of mussel bed (Tsuchiya and Nishihira 1985; 1986). Spatial and temporal variability of assemblages of organisms in shallow-water marine ecosystems is common (Underwood and Champan 1996) and has also been documented in chemosynthetic ecosystems (e.g. Hessler et al. 1985; Copley 1999; Sarrazin and Juniper 1999; Van Dover 2003). Changes in 3-dimensional habitat created by structuring species can force differences in the community that inhabits the area. For example, at hydrothermal vents on the Juan de Fuca Ridge, increased surface area of tubeworms was correlated with greater species diversity of invertebrates (Sarrazin and Juniper 1999). Within-mussel-bed variation is common in ecological studies and variation at cm- to m-scales often becomes residual, unexplained or random in analyses (Lawrie and McQuaid 2001), which is indicative of the patchiness of natural communities.

Comparison of Blake Ridge and Florida Escarpment Mussel Beds

Neither the Blake Ridge nor Florida Escarpment species accumulation curves reach a true asymptote, and curves cannot be differentiated from each other, regardless of

whether species richness or species density is the metric. Species richness measured as S_{10000} was the same for both Blake Ridge and Florida Escarpment mussel-bed faunas (55 taxa) (Turnipseed et al. submitted), but species richness measured as total species collected or as species richness estimators were lower for Blake Ridge mussel beds than at Florida Escarpment mussel beds. The difference between Blake Ridge and Florida Escarpment mussel bed diversity was especially evident using species-richness estimators, which take into account rare species (Colwell 1997). Florida Escarpment has more singletons (FE:14, BR:10) and uniques (FE:16, BR:11), but fewer doubletons (FE:4, BR:7), and duplicates (FE:6, BR:9) compared to Blake Ridge. Sample-based measures of diversity (H' $\log_{(e)}$) and evenness (J') at Blake Ridge and the Florida Escarpment were not different. In a comparison of mussel-bed faunas at vent and seep chemosynthetic ecosystems, Blake Ridge and Florida Escarpment mussel-bed faunas were more specious, and had higher diversity values (species richness (S_{10000}), Shannon-Weiner (H' $\log_{(e)}$), evenness (J'), and taxonomic diversity (Δ))than three NEPR, two SEPR , and one MAR vent mussel-bed faunas (Turnipseed et al. in press). Levin et al (in review) found species richness in clam beds was higher for a much small sampling effort (Es_{100}=36) compared to mussel bed fauna at Blake Ridge species richness for 100 individuals is one based on sampled based rarefaction curves.

Univariate values (S_{10000}, H' $_{\log (e)}$, J') of community structure did not differentiate Blake Ridge and Florida Escarpment mussel beds from each other, but species composition and dominant taxa were distinctive at each site. Deposit-feeding oligochaetes were numerical dominants at Blake Ridge, but no oligochaetes were found in Florida Escarpment mussel-bed samples. The grazing trochid gastropod *Fucaria* n. sp.

was numerical dominant at the Florida Escarpment, but no trochid gastropods were found in Blake Ridge samples. Grazers were both the biovolume dominants in mussel beds at both seeps with the shrimp *Alvinocaris* sp. A at Blake Ridge mussels bed and *Fucaria* n. sp at Florida Escarpment. Crustaceans were the numerically dominant phyla at Blake Ridge, which included amphipods, isopods, and *Alvinocaris* shrimp. Molluscs in general were numerically dominant phyla (~43% of the total individuals excluding mussels) at the Florida Escarpment mussel beds, which included trochid gastropods and the limpet *Paraleptopsis floridensis*; molluscs were rare at Blake Ridge mussel beds (< 1% of the total number of individuals excluding mussels). Deposit-feeding echinoderms (amphiuroid sp. A, *Chiridota* sp. A, and *Ophioctenella acies*) were biovolume dominant phyla at Blake Ridge while grazing trochid gastropod *Fucaria* sp. and the limpet *Paraleptopsis floridensis* were biovolume dominants at Florida Escarpment. Grazers and deposit-feeders are inferred to derive most of their nutrition from free-living bacteria and important primary consumers in chemosynthetic mussel-bed communities. In a comparison of trophic modes of macrofauna at the Florida Escarpment seep and the Snake Pit hydrothermal mussel beds, there was a significantly greater contribution of grazers and deposit feeders to total abundance at seeps compared to vents (Turnipseed et al. in review).

There were no differences in the condition indices of mussels at Blake Ridge and Florida Escarpment, which indicate the health of mussels at both sites was comparable. Mean biovolume of macrofauna at Blake Ridge (6.5 ml L^{-1}) was lower than reported values of the mean biovolume at the Florida Escarpment (11.2 ml L^{-1}) and within the

range of active EPR vent sites (Knick et al. in review). Knick et al (in review) found biovolume at EPR vents and the Florida Escarpment seep was characterized by a high degree of within- and between-site variability mean biovolume among sites and concluded within-site variability in biovolume is consistent with the patent spatial heterogeneity of vent and seep environments. Blake Ridge biovolume data was consistent with the spatial heterogeneity of invertebrates at chemosynthetic environments.

Biogeography

Van Dover et al. (2002) suggested deep-ocean water circulates in the Atlantic Ocean may population interaction between Florida Escarpment and Blake Ridge seep fauan and Mid-Atlantic Ridge vent fauna. Despite sharing the same species of mussel (Van Dover et al. 2003), the taxonomic comparison between Blake Ridge and Florida Escarpment mussel-bed fauna were 90% dissimilar, with only 4 shared species (*Bathymodiolus heckerae, Alvinocaris muricola, Ophioctenella acies, Chiridota* sp. A). The shrimp, *A. muricola,* is also present at other seeps in the Gulf of Mexico and the Barbados Prism (Sibuet and Olu 1998). The ophiuroid, *O. acies,* occurs at both Blake Ridge and Florida Escarpment seeps and is shared with Snake Pit, Logatchev, TAG, and Rainbow hydrothermal vents (Tyler et al. 1997, Gebruk et al. 2000, Turnipseed et al. 2003).

Mussel-bed faunas at the Blake Ridge and Florida Escarpment seeps, separated by ~1100 km (across the panhandle of Florida) or ~1320 km (around the panhandle) deployed greater dissimilarity (90%) than hydrothermal vents separated by ~ 3000 km on the Eastern Pacific Rise (50%) (Van Dover in press). The paucity of species between the

Blake Ridge and Florida Escarpment mussel-bed faunas supports the hypothesis that seep faunas are more isolated and share less species than hydrothermal vents (Sibuet and Olu 1998). This dissimilarity of fauna between Blake Ridge and Florida Escarpment could be attributed to lack of dispersal and recruitment mechanisms at seeps since seeps do not emit a large chemical signal as vents, geographic isolation, and/or competition with large populations of non-seep opportunistic species (Sibuet and Olu 1998; Levin 2000). Surface current patterns used to map dispersal routes of pelagic larvae from the Gulf of Mexico upstream to the southeastern United States (Roberts 1997) suggest there could be dispersal from the Florida Escarpment to Blake Ridge. The plankotrophic style of larval life of *B. heckerae* and *O. acies* could facilitate by-distance dispersal of tissue larvae from the Florida Escarpment to Blake Ridge. Low species overlap between Blake Ridge and Florida Escarpment suggests that the degree of biogeography resolution at seeps may be similar to that observed for invertebrates and fish associated with seamount clusters, which isolated and have highly localized species (de Forges et al. 2000).

The Blake Ridge and Florida Escarpment mussel-bed faunas shared few species. It is unknown how much of the Blake Ridge mussel-bed fauna which occur in the adjacent surrounding non-seep area. Some genera found at the Blake Ridge are commonly found in the deep-sea (*Benthonella, Phymorhynchus, Sarsiaster*) (Rex and Vetter 1990) and in shallow water (*Capitella, Dasybranchus*) (Stoner and Acevedo 1990; Levin 2000; Frouin and Hutchings 2001; Tsuchiya 2002). In shallow-water seep sites, seeps support some "specialty" species with chemosynthetic symbionts, but overall, the northern California shelf and slope faunas for example did not appear different from nearby non-seep faunas (Levin 2000). Levin (2000) also found a greater similarity

between seep and non-seep communities than among seep faunas at different sites. Conversely, megafauna and macrofauna associated with a chemosynthetic community at a whale-skeleton at 1240 m in the Santa Catalina Basin off California were taxonomically distinct from that of the surrounding area, with >97% of its morphospecies rare or absent in ambient sediments (Bennett et al. 1994). The whale-skeleton assemblage had strong taxonomic affinities to hydrothermal vents and cold seeps, with a megafauna dominated by vesicomyid clams and mytilid mussels hosting sulfide-oxidizing, chemoautotrophic bacterial endosymbionts (Bennett et al. 1994).

Blake Ridge and Florida Escarpment mussel-bed communities were ~70 % dissimilar from each other at the generic level and nearly 50 % dissimilar at the familial level. Despite Blake Ridge and Florida Escarpment being in the same ocean basin, at the generic and familial level, the seep mussel-bed faunas were almost as different from each other as Mid-Atlantic Ridge and East Pacific Rise mussel-faunas were from each other, suggesting long-term isolation and independent speciation. The seep and hydrothermal vent faunas were dissimilar from each other, but some shared genera *(Bathymodiolus, Phymorhynchus, Alvinocaris, Ophioctenella)* indicate there are evolutionary links between chemosynthetic ecosystems, especially for symbiont containing species (Tunnicliffe et al. 1998).

LITERATURE CITED

Barry, J.P., Kochevar, R.E., Baxter, C.H., 1997. The influence of pore-water chemistry and physiology on the distribution of vesicomyid clams at cold seeps in Monterey Bay: Implications for patterns of chemosynthetic community organization. Limnol Oceanogr 42: 318-328.

Barry, J.P., Buck, K.R., Kochevar, R.K., Nelson, D.C., Fujiwara Y., Goffredi, S., Hashimoto, J., 2002. Methane-based symbiosis in a mussel, *Bathymodiolus platifrons*, from cold seeps in Sagami Bay. Invertebr Biol 121: 47-54.

Bennett, B.A., Smith, C.R., Glaser, B., and Maybaum, H.L., 1994. Faunal community structure of a chemoautotrophic assemblage on whale bones in the deep northeast Pacific Ocean. Mar Ecol Prog Ser 108: 205-223.

Bernhard, J.M., Buck, K.R., Barry, J.P., 2001. Monterey Bay cold-seep biota: Assemblages, abundance, and ultrastructure of living foraminifera. Deep-Sea Res Part I, 48: 2233-2249.

Brooks, J.M., Kennicutt, M.C. II, 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.

Carney, R.S., 1994. Consideration of the oasis analogy for chemosynthetic communities of Gulf of Mexico hydrocarbon vents. Geo-Mar Lett 14: 149-159.

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. Mar Biol 100: 411-418.

Cavanaugh, C.M., Levering, P.R., Maki, J.S., Mitchell, R., Lidstrom, M., 1987. Symbiosis of methylotrophic bacteria and deep-sea mussels. Nature 325: 346-348.

Chanton, J.P., Martens, C.S., Paull, C.K., Coston, J.A., 1991. Sulfur isotope and porewater geochemistry of Florida Escarpment seep sediments. Geochim Cosmochim Acta 57: 1253-1266.

Chapman, M.G., 1994. Small- and broadscale patterns of distribution of the upper-shore littorinid *Nodilittorina pyramidalis* in New South Wales. Aust J Ecol 19: 83-95.

Childress, J.J., Fisher, C.R., Brooks, J.M., Kennicutt, M.C. II, Bidigare, R., Anderson, A.E., 1986. A methanotrophic marine molluscan (Bivalvia, Mytilidae) symbiosis: Mussels fueled by gas. Science 233:1306.

Clarke, K.R., Gorley, R.N., 2001. PRIMER v5: User Manual/Tutorial, PRIMER-E Ltd., Plymouth, UK.

Colwell, R.K., 1997. EstimateS: statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Copley, J.T.P., Tyler, P.A., Van Dover, C.L., Schultz, A., Dickson, P., Singh, S., Sulanowska, M., 1999. Subannual temporal variation in faunal distributions at the TAG hydrothermal mound (26 degree N, Mid-Atlantic Ridge). Mar Ecol 20: 291-306.

Craddock, C., Hoch, W.R., Gustafson, R.G., Lutz, R.A., Hashimoto, J., Vrijenhoek, R.C., 1995. Evolutionary relationships among deep-sea mytilids (Bivalvia: Mytilidae) from hydrothermal vents and cold-water methane/sulfide seeps. Mar Biol 121: 477-485.

de Forges, B.R., Koslow, J.A., Poore, G.C.B., 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405: 944-947.

Dillon, W.P., Popenoe, P., Grow, J.A., Klitgord, K.D., Swift, B.A., Paull, C.K., Cashman, K., 1982. Growth faulting and salt diapirism; their relationship and control in the Carolina Trough, eastern North America. In: Watkins, J.S., Drake, C.L. (Eds.), Studies in Continental Margin Geology, AAPG Memoir 34, pp. 21-46.

Distel, D.L., Cavanaugh, C.M., 1994. Independent phylogenetic origins of methanotrophic and chemoautotrophic bacterial endosymbioses in marine bivalves. J. Bacteriol. 176: 1932-1938.

Frouin, P., Hutchings, P., 2001. Macrobenthic communities in a tropical lagoon (Tahiti, French Polynesia, Central Pacific). Coral Reefs 19: 277-285.

Fujiwara, Y., Kato, C., Masui, N., Fujikura, K., Kojima, S., 2001. Dual symbiosis in the cold-seep thyasirid clam *Maorithyas hadalis* from the hadal zone in the Japan Trench, western Pacific. Mar Ecol Prog Ser 214: 151-159.

Gebruk, A.V., Chevaldonne, P., Shank, T., Lutz, R.A., Vrijenhoek, R.C., 2000. Deep-sea hydrothermal vent communities of the Logatchev area (14°45'N, Mid-Atlantic Ridge): diverse biotopes and high biomass. J Mar Biol Ass U K 80: 383-393.

Hayak, L.C., Buzas, M.A., 1997. Surveying natural populations. Columbia University Press, New York.

Hecker, B., 1985. Fauna from a cold sulfur-seep in the Gulf of Mexico: Comparison with hydrothermal vent communities and evolutionary implications. Bull Biol Soc Wash 6: 465-473.

Hessler, R.R., Smithey, W.M., Keller, C.H., 1985. Spatial and temporal variation of giant clams, tubeworms and mussels at deep-sea hydrothermal vents. Bull Biol Soc Wash 6: 465-474.

Iwasaki, K., 1994. Distribution and bed structure of the two intertidal mussels, *Septifer virgatus* (Wiegmann) and *Hormomya mutabilis* (Gould). Publ Seto Mar Biol Lab 36: 223-247.

Iwasaki, K., 1995. Comparison of mussel bed community between two intertidal mytilids *Septifer virgatus* and *Hormomya mutabilis*. Mar Biol 123: 109-119.

Kennicut, M.C. II, 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.

Lawrie, S.M., McQuaid, C.D., 2001. Scales of mussel bed complexity: structure, associated biota and recruitment. J Exp Mar Biol Ecol 257: 135-161.

Levin, L.A., 2000. Polychaetes as environmental indicators: response to low oxygen and organic enrichment. Bull Mar Sci 67: 668.

Levin, L.A., James, D.W., Martin, C.M., Rathburn, A.E., Harris, L.H., Michener, R.H., 2000. Do methane seeps support distinct macrofaunal assemblages? Observations on community structure and nutrition from the northern California slope and shelf. Mar Ecol Prog Ser 208: 21-39.

MacDonald, I.R., Boland, G.S., Baker, J.S., Brooks, J.M., Kennicutt, M.C. II, Bidigare, R.R., 1989 Gulf of Mexico hydrocarbon seep communities. Mar Biol 101: 235-247.

Markl, R.G., Bryan, G.M., Ewing, J.I., 1970. Structure of the Blake-Bahama Outer Ridge. J Geophys Res 75: 4539-4555.

Martens, C.S., Chanton, J.P., Paull, C.K., 1991. Biogenic methane in the Florida Escarpment brine seeps. Geol 19: 851-857.

MacDonald, I.R., Guinasso, N.L., Reilly, J.F., Brooks, J.M., Callender, W.R., Gabrielle, S.G., 1990. Gulf of Mexico hydrocarbon seep communities: VI. patterns in community structure and habitat. Geo-Mar Lett 10: 244-252.

Olu, K., Lance, S., Sibuet, M., Henry, P., Fiala-Medioni, A., Dinet, A., 1997. Cold seep communities as indicators of fluid expulsion patterns through mud volcanoes seaward of the Barbados accretionary prism. Deep-Sea Res I 44: 811-841.

Parker, J.D., Duffy, J.E., Orth, R.J., 2001. Plant species diversity and composition: Experimental effects on marine epifaunal assemblages. Mar Ecol Prog Ser 224: 55-67.

Paull, C.K., Dillon, W.P., 1981. Appearance and distribution of the gas hydrate reflection in the Blake Ridge region, offshore southeastern United States. Miscellaneous Field Studies Map - U. S. Geological Survey, Report: MF- 1252, 1 sheet.

Paull, C.K., Hecker, B., Commeau, R., Freeman-Lynde, R.P., Newmann, C., Corso, W.P., Golubie, S., Hook, J.E., Sikes, E., Curray, J. 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. Science 226: 965-967.

Paull, C.K., Ussler, W., Borowski, W., Spiess, F., 1995. Methane-rich plumes on the Carolina continental rise: associations with gas hydrates. Geol 23: 89-92.

Paull, C.K., Matsumoto, R., Wallace, P.J., 1996. Site 996. Proceedings of the ocean drilling program, Initial Reports 164: 241-275.

Rex, M.A., Vetter, R.J., 1990. Geographic variation in two deep-sea gastropods, *Benthonella tenella* (Jeffreys) and *Benthomangelia antonia* (Dall). Deep-Sea Res 37:1229-1249.

Roberts, C.M., 1997. Connectivity and management of Caribbean coral reefs. Science 278: 21.

Sahling, H., Rickert, D., Lee, R.W., Linke, P., Suess, E., 2002. Macrofaunal community structure and sulfide gas flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. Mar Ecol Prog Ser 231: 121-138.

Sarrazin, J., Juniper, S.K., 1999. Biological characteristics hydrothermal edifice mosaic community. Mar Ecol Prog Ser 185: 1-19.

Seed, R., Suchanek, T.H., 1992. The mussel Mytilus: Ecology, physiology, genetics and culture. Dev Aquacult Fish Sci 25: 87-170.

Sibuet, M., Juniper, S.K., Pautot, G., 1988. Cold-seep benthic communities in the Japan subduction zones: Geological control of community development. J Mar Res 46: 333-348.

Sibuet, M., Olu, K., 1998. Biogeography, biodiversity, and fluid dependence of deep-sea cold-seep communities at active and passive margins. Deep-Sea Res II 45:517-567.

Stoner, A.W., Acevedo, C., 1990. The macroinfaunal community of a tropical estuarine lagoon. Estuaries 13:174-181.

Tsuchiya., M., 1980. Biodeposit production by the mussel *Mytilus edulis* on rocky shores J Exp Mar Biol Ecol 47: 203-222.

Tsuchiya, M., 2002. Faunal structures associated with patches of mussels on East Asian coasts. Helgol Mar Res 56:31-36.

Tsuchiya, M., Nishihira, M., 1985. Islands of *Mytilus* as a habitat for small intertidal animals; effect of island size on community structure. Mar Ecol Prog Ser 25: 71-81.

Tsuchiya, M., Nishihira, M., 1986 Islands of *Mytilus edulis* as a habitat for small intertidal animals; effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. Mar Ecol Prog Ser 31: 171-178.

Tucholke, B.E., Bryan, G.M., Ewing, J.I., 1977. Gas-hydrate horizons detected in seismic-profiler data from the western North Atlantic. AAPG Bulletin 61: 698-707.

Tunnicliffe, V., McArthur, A.G., McHugh, D., 1998. A biogeographical perspective of the deep-sea hydrothermal vent fauna. Adv Mar Biol 34:353- 442.

Turnipseed, M., Knick, K.E., Lipcius, R.N., Dreyer, J., Van Dover, C.L., 2003. Diversity in mussel beds at deep-sea hydrothermal vents and cold seeps. Ecol Lett (in press).

Tyler, P.A., Paterson, G.J.L., Siguet, M., Guille, A., Murton, B.J., and Segonzac, M., 1997. A new genus of ophiuroid (Echinodermata: Ophiuroidea) from hydrothermal mounds along the mid-Atlantic ridge J Mar Biol Ass U K 75: 977-986.

Vetter, R.D., Fry, B., 1998. Sulfur contents and sulfur-isotope compositions of thiotrophic symbioses in bivalve molluscs and vestimentiferan worms. Mar Biol 132: 453-460.

Underwood, A.J., Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates Oecologia 107: 212-224.

Van Dover, C.L., 2000. The ecology of deep-sea hydrothermal vents. Princeton University Press, Princeton, NJ.

Van Dover, C.L., 2002. Community structure of mussel beds at deep-sea hydrothermal vents. Mar Ecol Prog Ser 230: 137-158.

Van Dover, C.L., 2003. Local, regional, and biogeographic variation in community structure within hydrothermal-vent mussel beds of the East Pacific Rise. Mar Ecol Prog Ser (in press).

Van Dover, C.L., Trask, J.L., 2000. Diversity at deep-sea hydrothermal vent and intertidal mussel beds. Mar Ecol Prog Ser 195: 169-178.

Van Dover, C.L., German, C.R., Speer, K.G., Parson, L.M., Vrijenhoek, R.C., 2002. Evolution and biogeography of deep-sea vent and seep invertebrates. Science 295: 1253-1257.

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., 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 Res I 50: 281-300.

Warwick, R.M., Clarke, K.R., 2001. Practical measures of marine biodiversity based on relatedness of species. Ocean and Mar Biol: Ann Rev 39: 207-231.

VITA

Kathleen Elizabeth Knick

Kathleen Elizabeth Knick was born in Richmond, Virginia, April 14, 1979. Graduated from Evans High School, Evans, Georgia in 1997. Fall of 1997 she entered the University of Georgia where she received a B.S.A. in Biological Sciences in May 2001. In June 2001, 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 May 9, 2003.