Marine Biology (2004) 145: 121–132
DOI 10.1007/s00227-004-1304-z

RESEARCH ARTICLE

M. Turnipseed · C. D. Jenkins · C. L. Van Dover

Community structure in Florida Escarpment seep and Snake Pit (Mid-Atlantic Ridge) vent mussel beds

Received: 6 May 2003 / Accepted: 17 December 2003 / Published online: 10 February 2004

Abstract Comparisons between invertebrate communities hosted by similar foundation species under different environmental conditions permit identification of patterns of species distributions that might be characteristic of the different ecosystems. Similarities and differences in community structure between two major types of chemosynthetic ecosystems were assessed by analyzing samples of invertebrates associated with *Bathymodiolus heckerae* Gustafson et al. mussel beds at the Florida Escarpment seep (Gulf of Mexico, 26°01.8′N; 84°54.9′W; October 2000) and *B. puteoserpentis* von Cosel et al. mussel beds at the Snake Pit vent (Mid-Atlantic Ridge, 23°22.1′N; 44°56.9′W; July 2001). Macrofaunal species richness was nearly twice as high in the seep mussel bed compared to the vent mussel bed, and only a single morphospecies, the ophiuroid *Ophioctenella acies* Tyler et al., was shared between the sites. Similarities between the two faunas at higher taxonomic levels (genus and family) were evident for only a small percentage of the total number of taxa, suggesting that evolutionary histories of many of these seep and vent macrofaunal taxa are not shared. The taxonomic distinctiveness of the seep and vent mussel-bed macrofaunal communities supports the hypothesis that environmental and oceanographic barriers prevent most taxa from occupying both types of habitats. Macrofaunal community heterogeneity among samples was similar in seep and vent mussel beds, indicating that spatial scales of processes regulating community variability may be similar in the two types of ecosystems. Suspension feeders were not represented in the macrofauna of seep or vent mussel beds. Primary consumers (deposit feeders and grazers) contributed more to the total abundance of macrofauna of seep mussel beds than vent mussel beds; secondary consumers (polychaetes and shrimp) were more abundant in the vent mussel beds.
Electronic Supplementary Material Supplementary material is available in the online version of this article at http://dx.doi.org/10.1007/s00227-004-1304-z.

Communicated by J.P. Grassle, New Brunswick

M. Turnipseed · C. D. Jenkins · C. L. Van Dover (✉)
Biology Department, The College of William and Mary,
Williamsburg, VA 23187, USA
E-mail: clvand@wm.edu
Tel.: +1-757-2212229
Fax: +1-757-2216483

Introduction

Characteristics of seeps and vents

Cold seeps and hydrothermal vents were discovered more than 15 years ago, yet little is known about quantitative distinctions between the faunas of these two major types of chemosynthetic ecosystems. Seep and vent habitats are characterized by a ready availability of redox couples (e.g. hydrogen sulfide and oxygen, methane and oxygen) that fuel microbial primary production by free-living and symbiotic bacteria. A diversity of symbiotrophs (organisms that depend on endo- and epi-symbionts for their nutrition), deposit feeders, grazers, predators, and scavengers have overcome invasion barriers imposed by physiological stress (e.g. sulfide toxicity) to take advantage of chemosynthetic primary production in an otherwise food-limited deep sea (reviewed by Sibuet and Olu 1998; Van Dover 2000).

In the present study, we compare community structure in mussel beds at the Florida Escarpment (FE) seep site in the Gulf of Mexico and the Snake Pit (SP) vent site on the Mid-Atlantic Ridge. These sites were chosen for comparison because they occur at similar depths (3,300–3,500 m) and because the Gulf of Mexico is a marginal basin connected to the Atlantic Ocean, with which it shares at least some deep-water taxa (Carney 1994). Deeper waters of the Gulf of Mexico are separated by sills in the straits of Yucatan (1,650 m) and the straits of Florida (800 m), providing the potential for

isolation and differentiation of species between the two regions (Carney 1994).

Seep and vent ecosystems often look similar, because they share congeneric or confamilial megafaunal species of habitat-generating tubeworms, mussels, and clams. Mussel beds, which are globally distributed at seeps, vents, and in shallow water, have proven to be a convenient habitat for quantitative studies of community structure within chemosynthetic ecosystems and between chemosynthetic and photosynthetic ecosystems (Van Dover and Trask 2000; Van Dover 2002, 2003; Turnipseed et al. 2003).

Is community structure (species diversity, abundance, evenness, taxonomic composition, trophic structure) likely to be the same in seep and vent environments? Diversity, expressed as species richness or as univariate indices that take into account the number of species or taxonomic distinctness of species and the relative abundance of individuals among species, is a fundamental metric of community structure. Sibuet and Olu (1998) suggested that diversity was greater at seeps than at vents, and they pointed to the greater duration of seeps on passive and tectonically active continental margins compared to vents on volcanically active mid-ocean ridges as one factor promoting greater diversity at seeps. When tested using quantitative samples of invertebrates associated with mussel-bed habitats at two seep and six vent sites, diversity measures (species richness, $H'_{(\log e)}$, J', and Δ) were indeed greater at seeps, but the degree of difference in diversity between seep and vent pairs was strongly dependent on the location of the vent mussel bed (East Pacific Rise vs. Mid-Atlantic Ridge; Turnipseed et al. 2003). The datasets used in Turnipseed et al. (2003) include diversity measures calculated from original data reported here. Because we restrict our analyses to macrofaunal taxa only, diversity measures reported herein differ from those of Turnipseed et al. (2003).

Taxonomic composition is also an important attribute of community structure. In the current global species list for seep and vent communities, taxonomic overlap between seep and vent faunas is restricted at the species level ($\sim$20 shared species out of >650 known; Sibuet and Olu 1998; Tunnicliffe et al. 1998). This led us to expect that the number of shared species between any seep and vent mussel bed would be low, perhaps $<5\%$ of the total number of species found in both habitats. At higher taxonomic levels (genus and family), there are shared evolutionary lineages of taxa endemic to chemosynthetic environments (Tunnicliffe and Fowler 1996). For example, Craddock et al. (1995) documented evolutionary alliances between mytilids from seeps and vents using molecular phylogenetic techniques. Before discovery of Atlantic vent communities, Hecker (1985) reported five species at the Florida Escarpment seep that were congeneric with eastern Pacific vent species. We expected Gulf of Mexico seeps and Atlantic vents to show even stronger faunal alliances at the generic and familial levels, reflecting a shared evolutionary heritage of their faunas (Sibuet and Olu 1998; Tunnicliffe et al. 1998).

There are differences in the style of delivery of reduced compounds to mussel beds at seeps and vents. At seeps, seawater enriched with reduced compounds derived from biogenic and/or thermogenic processes emanates from organic-rich sediments (Sibuet and Olu 1998). Minimal temperature anomalies (0.01–0.5°C above ambient seawater temperature) are characteristic of seep habitats (e.g. Paull et al. 1984; Kulm et al. 1986; Boulègue et al. 1987; Suess et al. 1998), and seep fluids deliver sulfide to seep organisms at lower flux rates than vent fluids (Scott and Fisher 1995). Elevated temperatures (up to 400°C; Von Damm 1995) characterize vent environments, but vent mussel beds are in diffuse-flow zones at low temperatures (2–10°C; Van Dover 2000). Both seep and vent mussel beds occur at the mixing zone of anoxic and oxic water. Thermal buoyancy of hydrothermal fluids extends the zone of mixing above the seafloor at vents, with the result that mussels are typically stacked higher at vents (up to 50 cm or more vertical relief) than at seeps. More extreme thermal and chemical gradients at vents led us to expect that Snake Pit mussel beds would exhibit greater within-site heterogeneity in community structure than Florida Escarpment seep mussel beds.

Several authors have suggested that secondary consumers are scarce in chemosynthetic ecosystems, at least in part because of the toxicity of these habitats (Tunnicliffe 1991; Carney 1994; Voight 2000). In addition to greater sulfide fluxes over larger zones of mixing at vents than at seeps, vent fluids are enriched in heavy metals (Von Damm 1995) and seep fluids are not. We thus expected that Florida Escarpment seep mussel beds would support a greater density of secondary consumers than Snake Pit vent mussel beds. Our sampling methods did not permit us to estimate densities of larger, mobile consumers such as crabs, squat lobsters, octopus, and fish within the mussel beds, but we could quantify the number of putative secondary consumers in the macrofauna. The potential for differences in the relative importance of top-down versus bottom-up control (Menge and Branch 2001) at seeps and vents led us to anticipate differences in the relative abundance of primary consumers between the sites. The conflicting interactions between these two regulatory processes make it impossible to predict the direction of these differences in seeps versus vents at this time. Even our ability to distinguish primary and secondary consumers within the macrofaunal taxa is limited, given our lack of knowledge about species-specific diets, especially among the polychaete taxa. Our goal in considering trophic structure was thus primarily one of descriptive comparison.

Site descriptions

The Florida Escarpment is the steep, eroded edge of a Lower Cretaceous carbonate platform that rims the southeastern United States (Fig. 1; Paull et al. 1984).

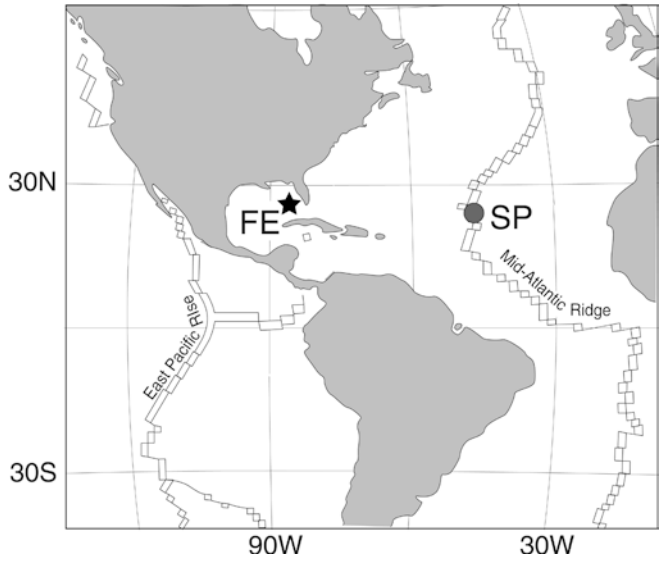

Fig. 1 Location of the Florida Escarpment seep (*FE*) and the Snake Pit vent (*SP*)

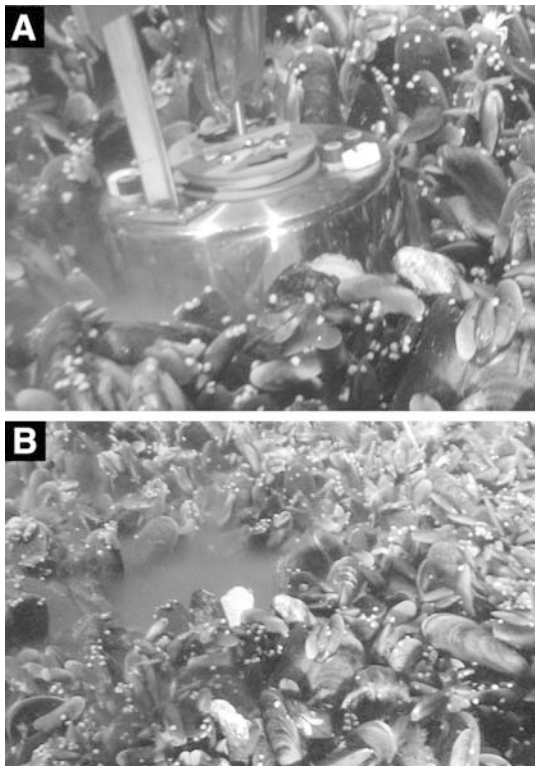

Fig. 2A, B *Bathymodiolus heckerae*. Mussel beds at the Florida Escarpment seep site. **A** Mussel pot sampling gear in mussel bed. **B** Divot produced in the mussel bed after removal of sample. Small white dots on mussels are trochid gastropods (*Fucaria* n. sp.)

The chemosynthetic ecosystem at its base (26°01.8′N; 84°54.9′W; 3,288 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 (Paull et al. 1984; Martens et al. 1991; Chanton et al. 1993). Biomass at the FE seep was dominated by symbiotrophic mussels (*Bathymodiolus heckerae*; Fig. 2) and vestimentiferan tubeworms (*Escarpia laminata* and *Lamellibrachia* sp.) that provide structural habitats for communities of associated invertebrates (Hecker 1985). More than 95% of the total mussel length is above the surface of the sediment at this site; we consider these mussels to be epifaunal rather than infaunal organisms. Other, non-habitat-generating megafauna included shrimp (*Alvinocaris muricola*), galatheid squat lobsters (*Munidopsis* cf. *subsquamosa*), and zoarcid fish (*Pachycara sulaki*). The age of the FE seep community is unknown, but seepage from the base of the escarpment has occurred since the Holocene or Pleistocene (0.01–1.64 million years ago; Paull et al. 1991). *B. heckerae* mussels rely on thiotrophic and methanotrophic symbionts (Cavanaugh et al. 1987) and were generally restricted to patches of dark-brown, sulfide-rich sediment on the order of 2–5 m in maximum dimension that dotted a 20- to 30-m band along the base of the escarpment.

The Snake Pit hydrothermal vent (Fig. 1) lies just south of the Kane transform fault, in the middle of the Mid-Atlantic Ridge axial valley (23°22.1′N; 44°56.9′W; 3,490 m; Karson and Brown 1988). Active venting of sulfide- and methane-enriched fluid is from black smokers (325–330°C), beehive-like diffuser vents (> 70°C), and diffuse-flow zones at four deposits (Moose, Beehive, Fir Tree, and Nail) on ca. 40-m-high mounds of massive sulfide blocks (Karson and Brown 1988; Fouquet et al. 1993; Van Dover 1995). Shrimp (*Rimicaris exoculata*) dominated the biomass on the black smokers, but, on the substratum at the base of the smokers at the Moose site, mussels (*Bathymodiolus puteoserpentis*) were biomass dominants and were the only habitat-generating megafauna in the system. Other, non-habitat-generating megafauna included shrimp (*Chorocaris chacei*, *Mirocaris fortunata*, *Rimicaris exoculata*, and *Alvinocaris markensis*), bythograeid crabs (*Segonzacia mesatlantica*), galatheid squat lobsters (*Munidopsis crassa*), and zoarcid (*Pachycara thermophilum*), synaphobranchid (*Ilyophis saldanhai*), and bythitid (Bythitidae gen. sp.) fish (Williams 1988; Mevel et al. 1989; Segonzac 1992; Fouquet et al. 1993; Segonzac et al. 1993; Sudarikov and Galkin 1995; Van Dover 1995; Desbruyères et al. 2000; Biscoito et al. 2002). Snake Pit is a relatively old hydrothermal site, with sulfides dated to 4,000 years ago (Lalou et al. 1993). Since then, high-temperature venting has been intermittent and is thought to occur in multi-decadal pulses (Lalou et al. 1993). *B. puteoserpentis* mussels contain thiotrophic and methanotrophic bacteria (Cavanaugh et al. 1992; Robinson et al. 1998) and were sampled from two adjacent linear (~3 m) patches over hairline fissures from which emanated warm, diffuse vent water (~5°C). Smaller patches (< 1 m max. dimension) were observed beneath sulfide outcrops and in crevices, or, more rarely, on the vertical surfaces of the sulfide chimneys. The areal

extent of SP mussel beds was less than that of the FE mussel beds, but not by more than an order of magnitude (qualitative estimate).

Materials and methods

A total of 12 quantitative samples (plus 1 qualitative sample) of the *Bathymodiolus heckerae* Gustafson et al. community at the FE seep were collected from two mussel beds during three "Alvin" dives in October 2000. Nine of the quantitative samples (FE 4–12) came from the historical FE seep site, marked by abandoned gear. The other three quantitative samples (FE 1–3) and one qualitative sample (FE B1) were collected from a mussel bed south of the historic site (SoHi). The historic and SoHi beds were separated by ~20 m, and, within a bed, samples were separated from one another by no more than 2–3 m. Another 11 quantitative samples (plus 2 qualitative samples) of the mussel-bed community (*B. puteoserpentis* von Cosel et al.) at the Moose site in the SP vent field were collected during two "Alvin" dives in July 2001. One of the SP vent quantitative samples (SP3) and the two qualitative samples (SPB1, SPB2) were collected from a small patch (1-m diameter) of mussels located on the vertical surface of a sulfide deposit. All other SP vent samples were collected from two adjacent mussel beds located about 5 m from the sulfide deposit. Samples from these mussel beds were separated from one another by no more than 2–3 m. Sampling methods and effort at the FE seep and SP vent mussel beds provided species-abundance data comparable with data from previous studies at southern and northern East Pacific Rise vents (see Van Dover 2002, 2003).

Quantitative samples were haphazardly collected from the seep and vent mussel beds using "pot" sampling gear (described in detail in Van Dover 2002; Fig. 2). Each pot is lined by a kevlar bag that, when cinched closed, retains all mussels and the organisms associated with them. The pots sample a maximum volume of 11.35 l over a sample area of 531 cm^2. When used on hard substrata, the pots sample a volume of mussels, but do not remove all of the mussels down to the basalt. For sedimentary settings, as at the FE mussel beds, the intent was to sample only the epifaunal mussel bed and its associated community, but some samples penetrated into the mud beneath the mussels. Qualitative samples were collected with a kevlar-lined scoop and stored in boxes with closed lids. Data from quantitative samples, standardized to number of individuals per liter of mussel volume collected (henceforth referred to as standardized abundance data), were used for mussel size-frequency calculations and in all abundance-based measures of community structure and diversity in seep and vent mussel beds. We used volume rather than area as our standard dimension, because mussel beds at most vents (including SP vents) are three-dimensional habitats with up to 50 cm or more vertical relief. Data from qualitative box samples were used to supplement the species lists, species-richness measures (including the species-effort curves), and the biogeographic analyses (Bray–Curtis presence/absence coefficients) at species, genus, and family levels.

On deck, mussels were washed three times with filtered seawater; washings were collected onto 250-μm and 63-μm sieves. Mussel volumes (±0.1 l) were measured by displacement of water and were used as a measure of sampling effort. Retained organisms, byssal threads, and sediment were fixed in 10% buffered formalin in seawater for 24 h and stored in 70% ethanol.

Coarse-sieve samples were sorted twice under a dissecting microscope, the second time after staining with Rose Bengal, to ensure that all invertebrates in the samples were identified and counted. Individuals were sorted to morphospecies (except anemones, nematodes, nemerteans, halacarid mites, and copepods) and identified to the lowest possible taxonomic classification. Specimens are archived in the Biology Department at the College of William and Mary (as are the unsorted 63-μm sieve samples). Florida Escarpment and Snake Pit samples were compared to archival specimens (also at William and Mary) collected at East Pacific Rise and Lucky Strike vent mussel beds. A. Warén (Swedish Museum of Natural History) assisted with gastropod identifications and retains a selection of this material; K. Fauchauld (US National Museum of Natural History) assisted with polychaete identifications.

Large taxa and highly motile organisms, which were not adequately sampled, were excluded from the quantitative analyses, but were included in our biogeographic comparisons. These taxa include squat lobsters (*Munidopsis* spp.) at the FE seep and SP vent and bythograeid crabs >25 mm (*Segonzacia mesatlantica*) at the Snake Pit vent. Commensal polychaetes living in the mantle cavities of bathymodiolin mussels [*Branchipolynoe seepensis* (Florida Escarpment), *B.* aff. *seepensis* (Snake Pit), and *Laubierus mucronatus* (Florida Escarpment)] were not included in the analysis, since we do not consider them to be members of the community living among the mussels. We limit our analyses to macrofaunal species and exclude meiofaunal taxa (prolecithophoran platyhelminthes, nemerteans, nematodes, mites, copepods, ostracods, mysids, and cumaceans). This procedure differs from that of our previous studies of mussel-bed faunas in chemosynthetic ecosystems (Van Dover and Trask 2000; Van Dover 2002, 2003; Turnipseed et al. 2003). On-going studies of fine sample fractions collected on the 63-μm sieve indicate that a large number of diverse nematodes, copepods, plus a small number of other meiofaunal elements are contained in these fractions (J. Zekely, personal communication). We thus conclude that this meiofaunal fraction is not quantitatively sampled by the coarse-sieve samples. Mussels <5 mm were included as macrofauna because they were deemed not to have a structural role in the mussel-bed communities. The 5 mm cut-off is arbitrary (Van Dover 2002). To facilitate comparisons across mussel beds, we have retained this arbitrary size cut-off in all subsequent species-abundance matrices (e.g. Van Dover 2003).

To compare the physical structure of *B. heckerae* mussels at the FE seep and *B. puteoserpentis* mussels at the SP vent, size-frequency distributions (10-mm intervals) were determined from length measurements of mussels and were compared using a chi-squared test. We excluded the <10-mm size class from this analysis, because there was a statistically significant difference in mean percent frequency of this size class between sites (*t*-test, $P < 0.001$) that would have a strong influence on the goodness-of-fit test.

Macrofaunal species-accumulation curves were sample based and were generated from quantitative and qualitative samples using EstimateS (Colwell 1997; randomization operations = 200, without replacement). Regression analysis of semi-log plots of randomized species-effort curves (Hayek and Buzas 1997) was used to calculate the number of species represented by 5,000 individuals (S_{5000}) at the seep and vent mussel beds. The choice of a standard sample size of 5,000 individuals reflects the lowest maximum level of sampling effort in the site pairs and permits us to use the regression approach without concern about errors introduced by extrapolation. The Shannon diversity index ($H'_{(\log e)}$), evenness index (J'), and taxonomic diversity (Δ) for macrofaunal invertebrates in samples from the mussel-bed communities were calculated using PRIMER v5 (Clarke and Gorley 2001). H' is a measure of the uncertainty with which one can predict the species of an individual chosen at random. Maximum uncertainty will occur when each of the species is equally represented. H' increases as diversity increases, but can never be greater than $\ln S$, where S is the total number of species (Hayek and Buzas 1997). J' provides a measure of the degree to which individuals are evenly distributed among species. Taxonomic diversity is the average taxonomic distance (Linnaean classification scheme) between pairs of individuals in a sample (Clarke and Warwick 2001). Taxonomic distance between species pairs is scaled according to path lengths (ω_{ij}) of 0 (same species), 20 (different species, same genus), 40 (different genera, same family), etc. Formally,

$$\Delta = \left[\Sigma\Sigma_{i<j}\omega_{ij}X_iX_j\right]/[N(N-1)/2], \quad (1)$$

where the double summation is over all pairs of species i and j, and N is the total number of individuals in the sample (Warwick and Clarke 1995). We restricted our Δ-analysis to species within the Polychaeta and the Gastropoda, where we could assign generic and higher taxonomic identifications. Rank-abundance curves were generated using mean percent abundances by species rank within samples for each site.

Within-site and biogeographic comparisons at species, genus, and family levels between the fauna of the FE seep and SP vent were made using presence/absence data and the asymmetric Bray–Curtis similarity coefficient $\{C = 100[2a/(2a+b+c)]$, where a is the number of species present in both samples, b is the number of species present in sample j but absent in sample k, and c is the number of species present in sample k but absent in sample $j\}$. The asymmetric character of the Bray–Curtis coefficient means that it is not affected by joint absences (Legendre and Legendre 1998; Clarke and Warwick 2001). Cluster analyses used the hierarchical agglomerative, group-averaging method in PRIMER v5 (Clarke and Gorley 2001). For cluster analyses at higher taxonomic levels, we included only those species for which we knew the genus or family. Unlike in the quantitative analyses, we did include large and motile taxa observed at the sites in the biogeographic comparisons.

Cluster analysis and multidimensional scaling (MDS) techniques were used to evaluate heterogeneity in macrofaunal community structure within the seep and vent mussel beds. Cluster analysis and MDS are complementary techniques; where stress values are low (<0.1), MDS provides a good representation of inter-sample relationships (Warwick and Clarke 1995). The similarity matrices for cluster and MDS analysis of quantitative data were generated using Bray–Curtis coefficients calculated from square-root-transformed, standardized abundance data (PRIMER v5; Clarke and Gorley 2001). Square-root transformation allows species with mid-range abundances to contribute to the similarity between sample pairs. Non-parametric analysis of similarity (subroutine ANOSIM in PRIMER v5) was used to test for significant differences between sample groups identified in MDS plots. The percentage contributions of species to the dissimilarity between sample groups were determined using the SIMPER subroutine in PRIMER v5 with square-root transformation.

To compare trophic structure between seeps and vents, macrofaunal species were assigned to trophic guilds (symbiotrophs, grazers, deposit feeders, and secondary consumers), and mean percent abundance ($\pm$SE) per liter of mussel volume for each guild was determined. Assignment of a species to a trophic guild was accomplished by either reference to published accounts of dietary resources for the species or by analogy with closely related shallow-water species (S1). Assignment of polychaete species to trophic guilds was particularly problematic since there have been no targeted studies of diets on the species we collected in our samples or from chemosynthetic communities elsewhere, with the exception of the ampharetid polychaetes. It is likely that at least some of the polychaete species we list as secondary consumers are best described as omnivores. *T*-tests were used to test for between-site differences in the relative abundance of different trophic guilds.

Results

Size-frequency distributions for mussels ≥10 mm differed between the seep and vent (S2; χ^2, $P<0.001$). Median length of mussels ≥10 mm in the FE seep samples (58 mm) was less than that of mussels in the SP vent mussels (70 mm), even though the largest mussel (232 mm) was collected from the seep. Recruitment of mussels, measured as the percent of individuals with shell lengths <5 mm, was an order of magnitude greater at FE seep mussel beds (37% of the total number of mussels) than at SP vent mussel beds (3%).

Excluding meiofaunal taxa, 46 species were identified in 8,171 individuals collected from FE seep mussel beds (Table 1), and 23 taxa were identified in 5,244 individuals collected from SP vent mussel beds (Table 2). Macrofaunal communities associated with mussel beds at the FE seep were numerically dominated by gastropods (*Fucaria* n. sp., *Paraleptopsis floridensis*), ophiuroids (*Ophioctenella acies*), and polychaetes (especially the ampharetid polychaetes *Glyphanostomum* sp. and *Amythasides* sp.) (Table 3). Gastropods were relatively sparse at Snake Pit, although the limpet *Pseudorimula midatlantica* was collected in every sample. Ophiuroids (*Ophioctenella acies*), alvinocarid shrimp (*Rimicaris exoculata* and *Chorocaris chacei*), and polychaetes (especially *Opisthotrochopodus* sp. and an unidentified spionid species) were abundant in SP vent mussel beds (Table 3). A small number of taxa comprised a large percentage of the total abundance of macrofaunal individuals at the FE seep and SP vent (Table 3; S3). More than 70% of the individuals belonged to five species at the seep and to five species at the vent (Table 3; S3). Rank-order mean abundances (%) for the FE seep and SP vent samples overlapped, indicating little difference in the degree of dominance between the sites (S3). Singletons (taxa represented by a single individual in the entire sampling effort) made up $>20\%$ of the macrofaunal species list in FE seep mussel beds (11 of 46 species) and $<10\%$ of the species list in SP vent mussel beds (2 of 23 species).

The rate of accumulation of species with sampling effort was greater at the FE seep site than at the SP vent site (Fig. 3). Although the effort curve for seep species did not reach an asymptote, each additional unit of sampling effort at the FE seep would contribute on average only one additional species to the observed species richness. The species-effort curve for the Snake Pit mussel bed was more asymptotic (Fig. 3), suggesting that the species composition of Snake Pit mussel beds was complete. Macrofaunal species richness (Table 4), standardized to a sample size of 5,000 individuals (S_{5000}), was 41 species for the FE seep mussel bed and 23 species for the SP vent mussel bed (r^2 values for semi-log regressions, FE: 0.995; SP: 0.998). There was no significant difference in mean H', J', and Δ

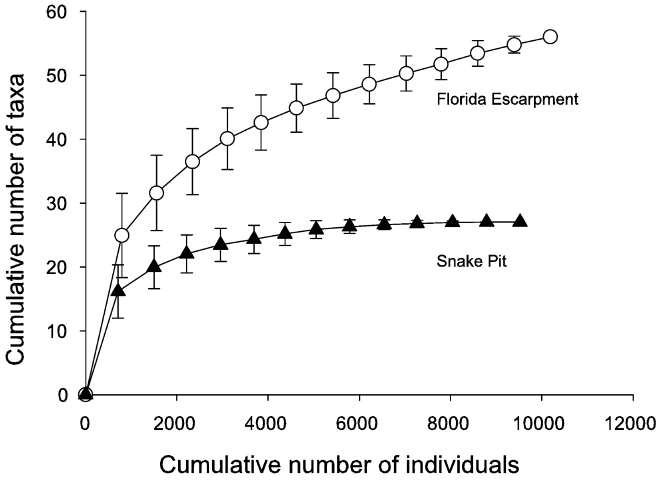

Fig. 3 Sample-based, macrofaunal species-effort curves for the Florida Escarpment seep and Snake Pit vent, calculated from quantitative and qualitative samples. Points represent cumulative mean ($\pm$SD) number of species per cumulative mean number of individuals in samples after 200 randomizations

Table 1 Florida Escarpment seep taxon-abundance matrix (not standardized to sample volume) and sample volumes. Samples 1, 2, 3, and B1 are from the SoHi mussel bed. The rest of the samples are from the "historical" FE seep site (*B1* qualitative sample;*indet*. indeterminate; *n.a*. data not available)

Phylum			Sample Number												
Class	Family	Taxon	1	2	3	4	5	6*	7	8	9*	10*	11*	12	B1*
Cnidaria															
	Family Indet.	anemone	5	8	9	1	1	3	3	1	10	5	1	2	10
Annelida															
Polychaeta	Capitellidae	*Capitella* sp. 1	1	0	0	0	0	0	0	0	0	0	0	0	6
	Capitellidae	*Dasybranchus* sp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0
	Capitellidae	*Dasybranchus* sp. 2†	0	0	0	0	0	0	0	0	0	0	0	0	1
	Capitellidae	*Notomastus* sp.†	0	0	0	0	0	12	0	0	0	0	0	0	2
	Capitellidae	capitellid A	29	26	30	0	1	95	2	1	17	11	6	0	36
	Polynoidae	polynoid A	1	5	6	2	10	11	3	18	6	2	3	5	4
	Polynoidae	polynoid B	0	4	5	2	3	5	4	8	9	1	4	1	4
	Polynoidae	polynoid C†	0	0	0	0	0	0	0	0	0	0	1	0	1
	Maldanidae	*Nicomache* sp. 1	4	2	0	0	0	12	0	0	0	0	0	0	9
	Hesionidae	hesionid A	22	25	35	0	1	51	20	2	8	1	4	0	0
	Nereididae	nereid A	3	2	9	2	12	9	1	0	6	2	4	0	5
	Pilargidae	*Ancistrosyllis* sp. 1†	0	0	0	0	0	0	0	0	0	0	0	0	5
	Syllidae	syllid A	0	0	0	0	0	0	1	0	0	0	0	1	50
	Dorvilleidae	*Ophyrotrocha* sp. 1	3	1	9	0	0	16	0	0	5	1	0	0	23
	Cirratulidae	*Aphelochaeta* sp. 1	21	0	19	0	0	3	0	0	2	0	0	0	114
	Cirratulidae	cirratulid A†	0	0	0	0	0	0	0	0	0	0	0	0	2
	Flabelligeridae	flabelligerid A	17	4	13	0	0	9	0	1	5	2	1	0	27
	Ampharetidae	*Amythasides* sp. 1	172	73	284	3	1	238	5	1	54	18	11	0	32
	Ampharetidae	*Glyphanostomum* sp. 1	108	177	176	5	1	34	3	5	156	174	86	0	7
	Ampharetidae	ampharetid A†	0	0	0	0	0	0	0	0	0	0	0	0	1
	Terebellidae	*Terebellides* sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	1
	Spionidae	spionid A	1	0	0	0	0	2	0	0	0	5	0	0	7
Mollusca															
Gastropoda	Neolepetopsidae	*Paralepetopsis floridensis*	58	99	54	88	144	109	195	39	87	29	46	29	88
	Trochidae	*Fucaria* n. sp.	103	166	70	47	57	318	224	65	234	53	25	24	145
	Pyropeltidae	*Pyropelta* sp. 1	0	1	0	0	0	2	0	0	0	0	0	0	0
	Turridae	turrid A	1	0	0	0	0	0	0	0	0	1	0	0	0
	Turridae	*Phymorhynchus* n. sp.	1	0	0	0	0	1	0	0	0	0	0	0	1
	Turridae	*Phymorhynchus* aff. *carinatus*	1	0	1	0	0	0	0	0	1	0	0	0	2
	Turridae	*Phymorhynchus* aff. *alberti*	1	1	0	0	0	0	0	0	0	3	0	0	0
	Xylodisculidae	*Xylodiscula* n. sp.†	0	0	0	0	0	1	0	0	0	0	0	0	0
	Cimidae	*Cima* n. sp.†	0	0	0	0	0	0	0	0	0	0	1	0	0
Bivalvia	Mytilidae	*Bathymodiolus heckerae* < 5mm	77	81	66	21	21	57	63	6	59	15	11	8	89
	Vesicomyidae	*Calyptogena* cf. *kaikoi*	1	0	5	0	0	0	0	0	3	1	0	0	22
Arthropoda															
Crustacea	Family Indet.	amphipod A	82	15	42	12	7	253	21	1	20	6	8	2	4
	Family Indet.	amphipod B	0	2	3	3	1	0	0	1	0	2	3	1	8
	Family Indet.	amphipod C	0	0	0	0	0	0	0	0	0	0	0	1	0
	Family Indet.	amphipod D	0	0	1	0	0	0	0	0	0	0	0	0	0
	Family Indet.	amphipod E	0	0	1	0	0	0	0	0	0	0	0	0	0
	Family Indet.	isopod A	1	0	5	0	0	0	0	0	0	0	0	3	11
	Family Indet.	isopod B	4	0	2	0	0	0	0	0	0	0	1	0	11
	Family Indet.	isopod C†	0	0	0	0	0	0	0	0	1	0	0	0	0
	Family Indet.	isopod D†	0	0	0	0	0	0	0	0	0	0	1	0	0
	Alvinocarididae	*Alvinocaris muricola*	2	2	1	16	3	4	0	2	0	0	1	0	0
Echinodermata															
Stelleroidea	Ophiuridae	*Ophioctenella acies*	134	331	56	37	123	134	210	15	163	51	4	13	159
Holothuroidea	Synaptidae	*Chiridota* sp. 1	5	1	2	0	2	13	1	2	2	5	1	2	1
Total number of individuals			858	1027	904	239	388	1392	756	168	848	388	223	92	888
Total number of taxa			27	22	24	13	16	24	15	16	19	21	20	13	31
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	na
Sediment volume sampled (l)			0.0	0.0	0.0	0.0	0.0	0.32	0.0	0.0	0.05	0.07	0.01	0.0	0.46

*Samples with sediment
†Species only found in samples with sediment

for macrofauna in FE seep and SP vent samples ($P > 0.05$, *t*-tests; Table 4).

FE seep and SP vent mussel-bed faunas shared only a single morphospecies, the ophiuroid *O. acies*. Macrofaunal species composition of seep and vent mussel beds was thus < 5% similar (Bray–Curtis coefficient of similarity based on species presence/absence data; S4). Similarity between the taxonomic composition of FE seep and SP vent mussel-bed macrofaunas increased to ~20% when genera were compared and to ~30% at the familial level (S4). Similarities in species composition among samples within the seep and vent sites was

Table 2 Snake Pit vent taxon-abundance matrix (not standardized to sample volume) and sample volumes (*B1*,*B2* qualitative samples; *indet*. indeterminate)

Phylum			Sample Number												
Class	Family	Taxon	1	2	3*	4	5	6	7	8	9	10	11	B1*	B2*
Cnidaria															
	Family Indet.	anemone	0	0	0	1	0	0	0	0	1	0	0	0	0
Annelida															
Polychaeta	Ampharetidae	*Amathys lutzi*	15	54	2	30	66	30	17	11	10	6	5	7	13
	Amphinomidae	*Archinome rosacea*	0	1	0	2	18	65	3	0	4	2	0	0	6
	Capitellidae	*Capitella* sp. 2	13	6	0	11	3	16	5	6	0	0	1	0	0
	Polynoidae	*Opisthotrochopodus* sp. 1	9	237	5	97	69	79	45	6	15	8	3	5	3
	Polynoidae	*Levensteiniella* sp. 1	2	86	0	10	42	9	7	2	12	1	2	6	0
	Hesionidae	hesionid B	10	17	0	8	23	37	6	0	1	3	2	0	7
	Spionidae	spionid B	13	421	7	38	31	27	12	18	11	3	8	4	17
Mollusca															
Gastropoda	Clypeosectidae	*Pseudorimula midatlantica*	12	6	206	8	20	6	6	9	5	7	3	187	140
	Scissurellidae	*Sutilizona pterodon*	0	0	0	0	1	0	0	5	0	0	5	0	0
	Skeneidae	*Protolira thorvaldssoni*	4	0	1	4	0	0	3	3	2	0	4	1	0
	Peltospiridae	*Peltospira smaragdina*	0	0	0	0	0	0	0	1	0	0	0	0	0
	Phenacolepadidae	*Shinkailepas briandi*	0	0	0	0	0	0	2	0	0	3	0	0	0
	Turridae	turrid B	0	2	0	0	0	0	0	0	0	0	0	0	0
	Turridae	*Phymorhyncus ovatus*.	1	3	0	0	1	1	0	1	0	0	3	0	0
	Turridae	*Phymnorhynchus moskalevi*	0	0	0	0	0	1	0	0	0	0	0	0	0
Bivalvia	Mytilidae	*Bathymodiolus puteoserpentis* < 5mm	1	6	2	4	4	4	0	1	0	0	0	0	0
Arthropoda															
Crustacea	Alvinocarididae	*Alvinocaris markensis*	0	0	0	0	4	0	0	0	0	0	0	0	0
	Alvinocarididae	*Chorocaris chacei*	125	14	106	4	5	40	53	21	17	8	8	42	3
	Alvinocarididae	*Rimicaris exoculata*	33	7	247	0	4	29	40	38	19	18	33	22	8
	Alvinocarididae	*Mirocaris fortunata*	0	0	0	1	1	0	0	0	0	0	0	0	0
	Bythograeidae	*Segonzacia mesatlantica* < 25 mm	0	10	0	2	1	0	1	0	1	1	0	0	1
Echinodermata															
Stelleroidea	Ophiuridae	*Ophioctenella acies*	190	733	6	308	176	102	7	33	81	36	2	0	0
Total number of individuals			428	1603	582	528	469	446	207	155	179	96	79	274	198
Total number of species			13	15	9	15	17	14	14	14	13	12	13	8	8
Mussel volume sampled (l)			3.9	4.7	1.45	3.5	4.0	2.5	3.1	3.55	2.8	1.3	1.45	4.45	8.3

*Sample from sulfide chimney

Table 3 Relative abundance (mean %, SD) of the ten numerically dominant macrofaunal species in quantitative samples from the Florida Escarpment seep and the Snake Pit hydrothermal vent (outlier sample SP03 excluded) (*n* number of samples)

Florida Escarpment N = 12	Mean %	S.D.	Snake Pit N = 10	Mean %	S.D.
Fucaria n. sp.	20	9.1	*Ophioctenella acies*	32	18.7
Ophioctenella acies	16	9.8	*Rimicaris exoculata*	13	13.3
Paralepetopsis floridensis	19	12.1	*Opisthotrochopodus* sp.	11	7.0
Glyphanostomum sp.	13	15.3	*Chorocaris chacei*	11	9.8
Amythasides sp.	8	9.8	spionid B	9	6.8
amphipod A	4	4.9	*Amathys lutzi*	7	3.0
Bathymodiolus heckerae < 5 mm	7	2.1	*Levensteiniella* sp.	3	2.8
capitellid A	2	2.0	*Pseudorimula midatlantica*	3	2.1
hesionid A	2	1.4	hesionid B	3	2.4
polynoid A	2	3.1	*Archinome rosacea*	2	4.5
TOTAL	93			94	

generally high (70–90%). An exception was a single sample (FE12) from the Florida Escarpment site that was species poor and was just under 60% similar in species composition to the other samples.

Mean (±SD) abundance of macrofaunal invertebrates in quantitative samples did not differ between FE seep (303 ± 241 ind. l^{-1}) and SP vent samples (146 ± 120 ind. l^{-1}; $P > 0.05$, *t*-test). There was also no

Table 4 Species richness ($S_{(5000)}$), Shannon's diversity index (H'), evenness (J'), and taxonomic diversity (Δ) for macrofaunal invertebrates associated with Florida Escarpment seep and Snake Pit vent mussel beds. $S_{(5000)}$ is species richness standardized to a sample size of 5,000 individuals and is derived from regression analysis of semi-log species-effort plots. H', J', and Δ are mean values (SD) for quantitative samples within each site (Florida Escarpment seep, $n = 12$; Snake Pit vent, $n = 11$)

		Diversity Index		
	$S_{(5000)}$	$H'_{log(e)}$ (SD)	J' (SD)	Δ (SD)
Florida Escarpment seep	41	2.0 (0.24)	0.68 (0.05)	68.1 (5.5)
Snake Pit hydrothermal vent	23	1.8 (0.33)	0.70 (0.11)	60.1 (18.7)

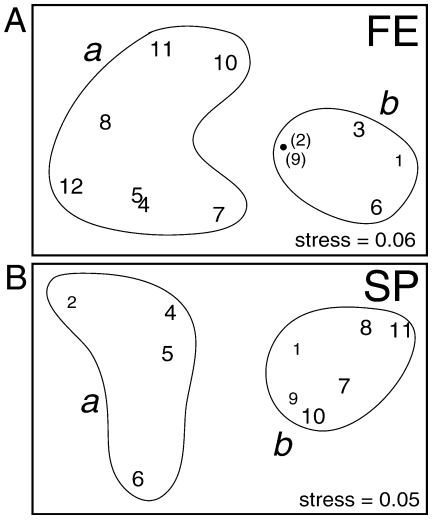

Fig. 4A, B Florida Escarpment (*FE*) and Snake Pit (*SP*) mussel-bed macrofaunal community structure. MDS plots for **A** FE seep samples and **B** SP vent samples; sample SP03 is not plotted because it falls so far from the other samples that a plot including it would show only two groups (i.e. SP03 and all other samples) (*a*, *b* a posteriori clusters of similar samples identified within each site)

difference ($P > 0.05$, *t*-test) in average within-site, pairwise Bray–Curtis similarity coefficients in community structure between FE seep samples (59 ± 11) and SP vent samples (62 ± 20). Two a posteriori sample groups (*a* and *b*) were evident within each study site in both cluster and MDS analyses (Fig. 4), but these groups do not correspond to sample proximities on the seafloor, and other explanations of the groupings are lacking. The SP vent sample from the sulfide chimney (SP03) is an outlier from the other groups. ANOSIM indicated that the groups were well separated in each case (FE seep: global $R = 0.724$, $P = 0.001$; SP vent: global $R = 0.905$, $P = 0.005$). Substructure within groups *a* and *b* at FE and SP mussel beds was not well defined. Because there was almost complete non-overlap of macrofaunal species composition, FE seep and SP vent mussel-bed faunas were well differentiated based on multivariate analyses. For the FE seep mussel beds, the difference between sample groups was largely driven by greater relative abundances of shared dominant taxa in the group *a* samples than in the group *b* samples (i.e. *Amythasides* sp., *Glyphanostomum* sp., *O. acies*, *Fucaria* n. sp., amphipod sp. A, capitellid sp. A, *B. heckerae* post-larvae and juveniles, and hesionid sp. A were from 3 to 50 times more abundant in group *a* samples than in group *b* samples). Almost 30% of the difference between sample groups from the SP vent mussel bed was attributable to the four to six times greater abundances of the ophiuroid *O. acies* and the polynoid polychaete *Opisthotrochopodus* sp. in the group *a* samples. Polychaetes in general were more abundant in the SP group *a* samples; shrimp were more abundant in the SP group *b* samples. Differences between the samples collected from the sulfide structure (SP03, SPB1, SPB2) and samples collected from mussel beds on basalt were striking when relative abundances were considered (Table 3). Taxonomic composition of the mussel-bed macrofauna from sulfide samples was not exceptionally different from that of the other Snake Pit mussel-bed fauna (S4). The mussels sampled from sulfide chimneys in SP03 contained large numbers of shrimp (*Chorocaris chacei*: 73 ind. l^{-1}, *Rimicaris exoculata*: 170 ind. l^{-1}) and limpets (*Pseudorimula midatlantica*: 142 ind. l^{-1}), and lacked high densities of ophiuroids that were abundant in most other Snake Pit samples.

The FE seep and SP vent mussel-bed macrofaunas differed in trophic structure (S5), with grazers significantly more abundant at the seep site (grazers: $P = 0.017$) and secondary consumers more prevalent at the vent site ($P < 0.001$). No significant difference between seep and vent mussel beds in the representation of symbiotrophs or deposit feeders was evident ($P > 0.05$). Suspension feeders were not represented in the macrofauna associated with mussel beds at either site.

Discussion

Recent studies of macrofaunal invertebrates associated with biogenic habitats in hydrothermal ecosystems (mussel beds and tubeworm aggregations) define spatial scales and environmental conditions that correlate with patterns of macrofaunal community structure (Van Dover and Trask 2000; Van Dover 2002, 2003; Tsurumi 2003; Tsurumi and Tunnicliffe 2003; Tsurumi et al. 2003). There have been few comparisons of community structure between seep and vent ecosystems, with the

exception of a qualitative review of seep and vent faunas (Sibuet and Olu 1998) and the quantitative study of diversity in seep and vent mussel beds (Turnipseed et al. 2003). Mussels in the genus *Bathymodiolus* occur at many deep-sea seeps and vents and provide a protective, three-dimensional habitat that supports other invertebrates in the same way that *Mytilus* species do in rocky intertidal habitats (e.g. Menge and Branch 2001). The invertebrate fauna of FE seep mussel beds is made up of more than twice as many species as SP vent mussel beds (Turnipseed et al. 2003; present study). More than 20% of the macrofaunal species richness within the seep mussel beds is attributable to extremely rare (singleton) taxa. We suspect that many of the seep singleton taxa may not be restricted to chemosynthetic habitats (e.g. *Dasybranchus* spp., ampharetid and terebellid polychaetes, turrid gastropods, and *Cima* sp.) and are widespread in shallow water and in the deep sea (e.g. Levin et al. 1991; Cosson-Sarradin et al. 1998; Rex et al. 2000; Frouin and Hutchings 2001); the gastropod *Xylodiscula* sp. may be an exception (Marshall 1994; Hoeisaeter and Johannessen 2001; Warén and Bouchet 2001). Singleton taxa made up $<10\%$ of the Snake Pit species list. There was no difference in the H' diversity indices between the sites, which contrasts with the significantly greater seep H' values reported by Turnipseed et al. (2003). The Turnipseed et al. (2003) dataset included copepods, which were numerical dominants in the SP vent mussel-bed samples and would thus lower the H' and J' diversity values in these samples. Numerical dominance by a small number of macrofaunal taxa at both the FE seep and SP vent is reflected in the rank-order plots at the two sites and by the lack of a significant difference in evenness values (J'). This dominance pattern matches similar observations in other vent systems and in intertidal mussel beds (e.g. Van Dover and Trask 2000; Van Dover 2002, 2003; Tsurumi and Tunnicliffe 2003) and differs from the more even distribution of individuals among species that is characteristic of the non-chemosynthetic deep sea (e.g. Grassle et al. 1985).

Representation of higher macrofaunal taxa was generally greater in FE seep mussel beds than in SP vent mussel beds (phyla: 5 seep vs. 5 vent, classes: 7 seep vs. 6 vent; families: ≥27 seep vs. ≥17 vent; genera: ≥30 seep vs. 21 vent). This difference in taxonomic diversity between the sites is not reflected in the Δ taxonomic diversity index based on polychaete and gastropod faunas only.

Greater species richness and greater representation of higher taxa at seeps versus vent habitats could indicate a number of non-exclusive conditions, including greater stability and ecological age of seep habitats (Rosenzweig 1995; Sibuet and Olu 1998), and fewer barriers to invasion (Tunnicliffe 1991; Carney 1994; Voight 2000). The FE seep site is inferred to have been active for ≥10,000 years (Paull et al. 1991), the SP vent site, for ≤ 100 years (Lalou et al. 1993). Seep fluids have relatively low sulfide fluxes and are devoid of heavy metals such as Fe, Cu, and Zn (Scott and Fisher 1995), which are elevated in low-temperature vent fluids (Luther et al. 2001). Given the maximum length of the FE mussels sampled (232 mm) compared to that of the SP mussels (148 mm) and the presumed slower growth rates of seep organisms (Fisher et al. 1997), we infer that the seep mussel bed is older. Carney (1994) argues that seep diversity might be enhanced by greater access to potential invaders (especially secondary consumers), given the proximity of seep environments to productive shallow waters.

As expected, $<5\%$ of the total number of macrofaunal invertebrate species identified were shared between the seep and vent mussel beds. Only one morphospecies (*Ophioctenella acies*) and one documented pair of cryptic polynoid polychaete species (*Branchipolynoe seepensis* and *B.* aff. *seepensis*; Chevaldonné et al. 1998) were shared between the seep and vent mussel beds. Molecular studies may reveal that populations of *O. acies* at the FE seep and the SP vent are also distinct species. Seven genera (*Branchipolynoe*, *Capitella*, *Bathymodiolus*, *Phymorhynchus*, *Alvinocaris*, *Munidopsis*, *Ophioctenella*) were shared between the FE seep and SP vent mussel-bed samples. Four of these genera (*Branchipolynoe*, *Bathymodiolus*, *Alvinocaris*, *Ophioctenella*) are so far known only from chemosynthetic habitats. Eleven families were shared between the seep and vent mussel bed samples (Ampharetidae, Capitellidae, Hesionidae, Spionidae, Polynoidae, Turridae, Mytilidae, Halacaridae, Alvinocarididae, Galatheidae, Ophiuridae). Only one of these families (Alvinocarididae) and the mussel subfamily Bathymodiolinae are so far known from chemosynthetic habitats. Thus, evidence exists of shared evolutionary links and shared taxa between the FE seep and the SP vent faunas (Tunnicliffe et al. 1998). At generic and familial levels, the assemblage of invertebrates associated with FE seep mussel beds was as different from the mussel-bed fauna at the SP vent on the Mid-Atlantic Ridge (present study) as it was from the mussel-bed faunas of the East Pacific Rise (Van Dover 2003). Taxonomic distinctiveness of seep and vent mussel-bed communities supports the hypothesis that environmental and oceanographic barriers prevent most taxa from occupying both types of habitats (Sibuet and Olu 1998).

If *O. acies* proves to be shared between FE seeps and SP vents, its presence in both locales suggests genetic exchange among populations, presumably through populations occupying suitable habitats between the two sites. *O. acies* was also reported from Logatchev vents on the Mid-Atlantic Ridge (Tyler et al. 1995; Gebruk et al. 2000) and from methane-hydrate seeps at the Blake Ridge on the continental margin of the eastern USA (Van Dover et al. 2003). The FE seeps share a clam species (*Calyptogena* aff. *kaikoi*) with the Logatchev vent site 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 South Carolina (Van Dover et al. 2003), and, although detailed molec-

ular and morphological comparisons remain to be conducted, it seems likely that *B. heckerae* may prove to be the same species as *B. boomerang* described from Barbados seeps (von Cosel and Olu 1998). The southward-flowing western boundary current of the deep Atlantic and the general east-to-west circulation of equatorial deep-ocean water in the Atlantic Ocean may enable the exchange of propagules between populations at seeps in the Gulf of Mexico, at seeps associated with continental margins of the western Atlantic, and at Mid-Atlantic Ridge vents, and perhaps even at seeps on the continental margin of the eastern Atlantic (Van Dover et al. 2002). Deep-water circulation has also been implicated in the maintenance of limited faunal similarities between the Sagami Bay seep and Minami-Ensei Knoll vent communities in the western Pacific, which, despite being separated by > 1,000 km, share four species (Hashimoto et al. 1995).

Sample pairs from the FE seep and SP vent mussel beds displayed the same degree of community heterogeneity when analyzed using multivariate techniques based on species abundance. This result suggests that abiotic and biotic processes regulating community heterogeneity operate on similar scales at both sites. Within each site, two sample groups were defined by relative abundances of a few dominant species. These sample groups were not spatially correlated. Biotic interactions may generate patchiness in community structure on scales observed here, but gradients in chemical and physical properties are also likely to be important in generating heterogeneity in chemosynthetic systems at local scales (Micheli et al. 2002). Geochemical variables (e.g. sulfide concentration and flux) that underlie community assemblages in either system will become apparent only with chemical analysis of sediment porewaters at seeps and of diffuse flows at vents at the same scale of spatial resolution as the biological sampling. Integrated sediment geochemistry (sulfide and methane flux) in core samples and community structure analysis proved useful in delimiting the different habitat characteristics between clam bed and bacterial mat habitats within seeps (Sahling et al. 2002). A similar approach applied to porewaters of the FE seep and diffuse flows of SP vent mussel beds would likely provide the resolution necessary to assess the role of environmental factors influencing within-habitat community heterogeneity at the Florida Escarpment and Snake Pit mussel beds.

Macrofaunal grazers and deposit feeders inferred to derive their nutrition from free-living bacteria were the abundant primary consumers in both FE seep and SP vent mussel beds; they made a greater contribution to total abundance at seep than at vent mussel beds. Macrofaunal suspension feeders were not present in samples from either system. Although secondary consumers were expected to be less abundant at vents than at seeps, there was a significantly greater contribution of secondary consumers (especially predatory or scavenging polychaetes and shrimp) to total abundance of macrofaunal invertebrates in the SP vent mussel beds than in the FE seep mussel beds. Macrofaunal secondary consumers may maintain the lower relative abundances of primary consumers in the SP mussel beds, but a test of this interpretation requires experimental manipulations. Megafaunal consumers were relatively scarce at FE seep mussel beds; zoarcid fish were abundant ($\sim$5 m^{-2}) in video images of the Snake Pit mussel beds (Van Dover, personal observations). Zoarcids of East Pacific Rise vents consume gastropods and amphipods (Micheli et al. 2002); the zoarcid at Snake Pit is likely to be an important influence on macrofaunal abundance and biomass in the mussel beds.

Although we consider mussel beds to be one of the most similar habitats shared among geographically remote chemosynthetic ecosystems, we emphasize that this similarity is only a first-order approximation. Differences in habitat structure (e.g. significant differences in size-frequency distributions between seep *B. heckerae* and vent *B. puteoserpentis* populations) can influence community structure in subtle ways (Tsuchiya and Nishihira 1986). Other physical and chemical differences among mussel-bed habitats (temperature, sulfide availability, metal concentrations, age of the mussel bed, etc.) influence community structure (Van Dover 2003), as do biological interactions (Micheli et al. 2002). We set out to explore how community structure in seep and vent mussel beds differs, given their markedly different geological settings. We found that, as expected, species richness was higher at seeps than at vents. Taxonomic composition in the two habitat types was distinctive, even at higher taxonomic levels. We found evidence for community heterogeneity on local spatial scales (< 10 m) at both seeps and vents, which argues for attention to environmental variation within mussel beds and to biotic interactions at these scales. Grazers were the dominant macrofaunal trophic guild at seeps and vents, and there was a greater abundance of macrofaunal secondary consumers at the vent site than at the seep site. While we can document differences in seep and vent community structure, it seems likely that some of these differences are idiosyncratic and that other seep–vent pairs might yield opposite results.

Acknowledgements We thank the captain and crew of the R.V. "Atlantis", the pilots and crew of the D.S.V. "Alvin", and the shipboard scientific parties for assistance in collecting and processing samples. We also thank M. Doerries, K. Knick, S. Rapaport, E. Raulfs, M. Ward, and C. Zoon for assistance in sorting samples and are grateful to A. Warén, P. Tyler, K. Fauchald, M. Hooge, and S. Tyler, who helped us with identifications. R. Lipcius and S. Ware contributed to the development of this manuscript. Two anonymous reviewers provided valuable critiques of the original manuscript. This work was supported by the National Science Foundation (Division of Biological Oceanography; OCE-988550, OCE-9982999), NOAA's National Undersea Research Program—University of North Carolina, Wilmington, and the College of William and Mary. Work completed in this study complied with the current laws of the country in which they were undertaken.

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