Variation in community structure within hydrothermal vent mussel beds of the East Pacific Rise

Cindy Lee Van Dover*

Biology Department, Millington Hall, PO Box 8795, College of William & Mary, Williamsburg, Virginia 23187, USA

ABSTRACT: Patterns in invertebrate community structure associated with mussel beds at 3 hydrothermal vents on the northern East Pacific Rise (NEPR) were explored using quantitative, replicate sampling methods and were compared to those of southern East Pacific Rise (SEPR) mussel beds (~3000 km apart). Univariate measures of diversity (H', J') did not differ among 3 NEPR mussel beds. Diversity by most estimates was lower at NEPR mussel beds than at SEPR mussel beds. Invertebrate faunas of NEPR and SEPR mussel beds belong to the same biogeographic province, and the numerically dominant species at NEPR mussel beds were also numerical dominants at SEPR mussel beds. Patterns of community structure within and among NEPR mussel beds, between NEPR and SEPR mussel beds, and between 'young' (<6 yr) and 'old' (>8 yr) mussel beds could be differentiated using multivariate techniques based on species-abundance matrices. Overall, these observations suggest that NEPR and SEPR mussel-bed communities are remarkably similar, differing primarily in the relative abundances of their shared, numerically dominant species and in the composition of the rare species.

KEY WORDS: Community structure · Hydrothermal vent · East Pacific Rise · Mussel beds · Diversity

INTRODUCTION

Perennial questions in marine ecology include how communities change over time and how they differ from one location to another (e.g. Ricklefs & Schluter 1993, Legendre et al. 1997, Menconi et al. 1999). Temporal change can be measured on a variety of scales, from geological and historical to seasonal time frames; spatial variation may be examined within communities on a local scale, between adjacent communities and between communities across many degrees of latitude. The ultimate goal is to understand the biotic and abiotic processes that influence community structure across time and space. Good examples of development of this understanding in shallow-water communities include those relating to intertidal mussel beds, where there are scale- and site-dependent patterns of recruitment (Archambault & Bourget 1996, Dudgeon & Petraitis 2001), biogenic neighborhood effects (Wahl 2001), predation effects (Navarrete 1996) and biogeographic effects (Broitman et al. 2001). To understand these processes, one must first understand the scope and pattern of variation within communities (Underwood et al. 2000, Menge & Branch 2001). This is a tractable problem in intertidal systems, but as one moves into deeper water, quantitative patterns are at best challenging to obtain. Despite the relative inaccessibility of the deep sea, a large body of literature developed over recent decades has made considerable progress in understanding local and regional diversity in soft-sediment habitats, where there can be geographic variation in local species diversity on spatial scales of 100 to 1000 km (reviewed in Levin et al. 2001). Landscape-level complexity in deep-sea soft sediments is influenced by large-scale processes in the upper ocean (Levin et al. 2001). In contrast, chemosynthetically based ecosystems in the deep sea (including hydrothermal vents, cold seeps, whale skeletons) represent a basic permutation of the carbon cycle (Levin et al. 2001) and can be relatively isolated from upper-ocean processes (Van Dover 2000). As such, patterns and processes in community structure at vents and

*Email: clvand@wm.edu

seeps have the potential to provide critical counterpoints to those observed in non-chemosynthetically based deep-sea communities.

Two attributes of deep-sea hydrothermal systems—their insularity and their gradient regimes of fluid flow and chemistry—suggested *a priori* that measures of community structure and similarity at vents would be especially sensitive to the degree of proximity between sites being compared, to the age of the sites and to within-site heterogeneity. These factors, however, might be counterbalanced by the transiency of hydrothermal vents, which places a premium on effective dispersal and recruitment. Hydrothermal vents on mid-ocean ridges are fragmented systems that occur as small islands of habitat along a narrow corridor of hard substratum; invertebrates colonizing these habitats have larval stages that are subject to dispersal in an open system, although mechanisms of larval retention must exist to account for the large settlement events observed (Mullineaux & France 1995, Marsh et al. 2001, Van Dover et al. 2001). Vent habitats, especially those of fast-spreading centers such as the East Pacific Rise (EPR), where there is a rich magma budget and extensive volcanism, undergo a relatively rapid hydrothermal cycle of waxing and waning (on the order of days to decades; Haymon et al. 1993, Delaney et al. 1998, Shank et al. 1998). At the start of a hydrothermal cycle, when new loci of diffuse flow are formed, the habitat is rich in the sulfide on which chemoauotrophic microorganisms depend. For the more stable sites, diffuse flow lasts for years, followed inevitably and ultimately by reduction in flow and cessation of venting (e.g. Hessler et al. 1985, 1988, Fustec et al. 1987). Community evolution tracks the hydrothermal cycle, with initial colonization, growth and development of the community, followed by its demise.

Geological, biological and chemical aspects of the hydrothermal cycle have been documented for sites on the Juan de Fuca Ridge (Butterfield et al. 1997, Sarrazin et al. 1997, Delaney et al. 1998, Tsurumi & Tunnicliffe 2001) and the northern EPR (NEPR; Haymon et al. 1993, Von Damm et al. 1995, Shank et al. 1998). These studies show that colonization at vents is rapid (Lutz et al. 1994, Tunnicliffe et al. 1997, Shank et al. 1998). Quantitative studies of changes in community structure in macrofaunal invertebrates in hydrothermal vents are scarce, however, in part due to the difficulty of obtaining replicate samples from hard substrata using submersible technology. An exception is recent work by Van Dover (2002), who described a quantitative approach to sampling mussel beds on basalt to document differences in species composition and abundance in mussel beds of active and waning vent fields on the southern EPR (SEPR), and who noted a shift toward depauperate populations and invasion by non-vent species at the waning site.

In terms of spatial distributions of open-ocean habitats, hydrothermal vents may best be compared to those of seamounts: both vents and seamounts occur in regional chains of closely spaced systems. Like seamounts, vents have been recognized as being of potential importance in understanding ocean biogeography due to their large proportions of endemic species (Tunnicliffe & Fowler 1996, Vrijenhoek 1997, Van Dover et al. 2002). Species overlap among seamounts in the southwest Pacific is low relative to that of vent sites separated by comparable distances, with differences in longevity between vent and seamount habitats (decades to centuries vs millions of years) postulated as responsible for the higher degree of endemism at seamounts (Richer de Forges et al. 2000).

Primary questions concerning community structure in vent ecosystems include the extent to which community attributes vary within a site, between sites within a single vent field and between vent fields separated by many degrees of latitude on a ridge system. The most common means of assessing these scales of variability has been by comparison of species' lists among sites on different ridge segments or ridge systems (e.g. Tunnicliffe 1988, Hashimoto et al. 1995, Tunnicliffe & Fowler 1996, Tunnicliffe et al. 1998, Desbruyères et al. 2000, Kojima 2002, Van Dover et al. 2002). In general, species lists do not discriminate faunas of adjacent ridge segments very well; there are overlapping occurrences of the majority of species within vents across approximately 5° of latitude along the northeast Pacific Ridges (Juan de Fuca, Explorer, Gorda Ridges) and across similar distances along the EPR (Tunnicliffe 1988, Tunnicliffe et al. 1998). Species-abundance matrices and multivariate statistics, however, may be useful in differentiating communities along a ridge segment.

In this study, I use replicate, quantitative samples to explore the scale and scope of variation in community structure (species richness, species composition, diversity, evenness, similarity) of the invertebrate fauna associated with mussel beds at hydrothermal vents on the EPR at 9° 50′ N, with attention to patchiness within mussel beds and to differences between mussel beds of different ages separated by <2.5 km. The null hypothesis is that community attributes are similar, regardless of position within a mussel bed, distance between mussel beds, or age of the mussel bed. Knowledge of this aspect of the community ecology of hydrothermal vent ecosystems is especially relevant as sampling, experimentation and instrumentation impacts of scientific research are slated to increase at a small number of well-studied sites, including the 9° 50′ N site on the EPR (Malakoff 2000, Allen 2001,

Dando & Juniper 2001, RIDGE Office 2002). I also compare diversity data from these sites with published data from mussel beds at 17° 30′ S on the EPR (Van Dover 2002) to determine the degree of similarity in their invertebrate faunas across more than 27° of latitude. Mussel beds at NEPR and SEPR vent sites are made up of *Bathymodiolus thermophilus*, which host sulfide-oxidizing, chemoautotrophic microorganisms in their gill tissues (Fiala-Médioni 1984).

MATERIALS AND METHODS

Study sites. The 9° 50′ N vent field on the NEPR (Fig. 1) includes hydrothermal habitat that was established prior to the 1991 volcanic eruption and that was unaffected by the lava flows. The 1991 eruption paved a large portion of the ridge axis between 9° 45′ N and 9° 52′ N with fresh basalt, with subsequent blanketing of the area by microbially derived, flocculent material (Haymon et al. 1993). Mobile vent fauna (e.g. amphipods, copepods, brachyuran crabs) proliferated in response to this increased biological production; tubeworms were evident within 1 yr of the eruption and by the 3rd year after the eruption, mussels were evident (Haymon et al. 1993, Shank et al. 1998). East Wall and Train Station mussel beds were established after the eruption and were 4 and 5 yr old, respectively, at the time of sampling; the Biovent mussel bed pre-dates the eruption and thus was at least 8 yr old at the time of sampling (T. Shank & R. Lutz pers. comm.). The hierarchy of median shell lengths for mussels >10 mm length matched that of the age of each site (author's unpubl. data): Biovent (103 mm) > Train Station (87 mm) > East Wall (73 mm). Train Station is the southern-most site, separated by 1715 m from East Wall, which in turn is 800 m south of Biovent. Other mussel beds occur in the 9° 50′ N region. Details of the SEPR mussel beds (Fig. 1A) are provided in Van Dover (2002) and are briefly summarized here: Two mussel beds at active vent sites on the SEPR (Oasis and Rehu Marka; 850 m apart) were sampled. At the time of sampling, the Oasis mussel bed was 6 yr old and the Rehu Marka mussel bed was between 10 and 16 yr, based on repetitive observations of the sites (Fouquet et al. 1994). Median shell lengths for mussels (>10 mm length) in quantitative samples from Oasis and Rehu Marka were 109 and 105 mm, respectively.

Sample collection and processing. Replicate samples of mussels and their associated invertebrates were collected using the submersible *Alvin* during November 1999 from the Train Station, East Wall and Biovent sites on the NEPR (Fig. 1B). Mussels occupied low-temperature (<10°C) flow zones associated with cracks in lobate basalt lavas and, at 2 of the sites (Train Sta-
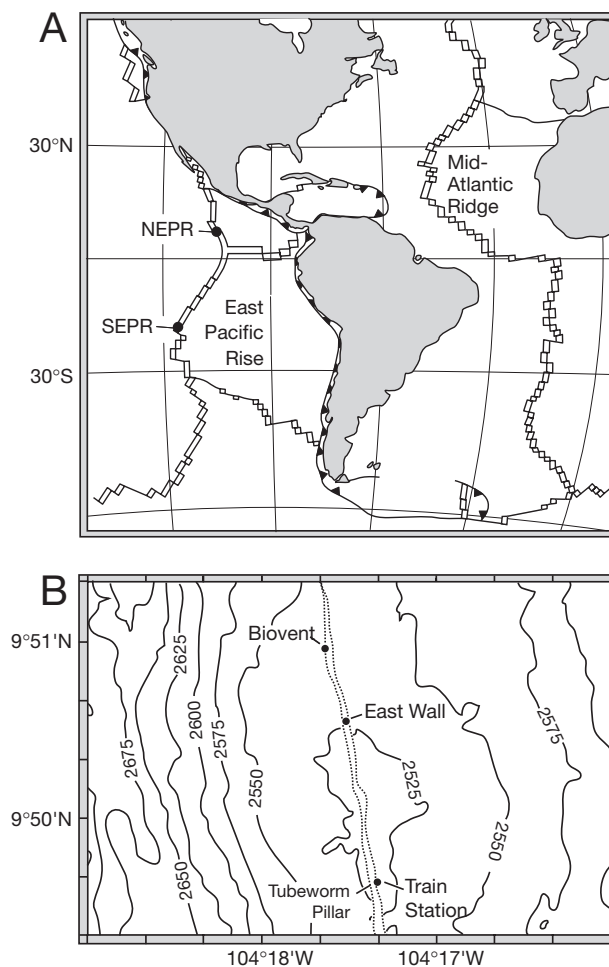

Fig. 1. (A) Location of the northern East Pacific Rise (NEPR; Train Station, East Wall, Biovent) and southern East Pacific Rise (SEPR; Oasis, Rehu Marka) vent sites. (B) Detail of NEPR mussel bed locations with bathymetric contours; dotted line marks the axial caldera that is the spreading center. Train Station: 9° 49.645′ N, 104° 17.357′ W (2491 m); East Wall: 9° 50.534′ N, 104° 17.520′ W (2499 m); Biovent: 9° 50.992′ N, 104° 17.592′ W (2494 m); Oasis: 17° 25.394′ S, 113° 12.323′ W (2582 m); Rehu Marka: 17° 24.940′ S, 113° 12.190′ W (2581 m)

tion and East Wall), were adjacent to clusters of vestimentiferan tubeworms *Riftia pachyptila*. The mussel beds ranged in maximum dimension from 20 to 50 m.

Discrete, quantitative samples were collected using pot samplers (Van Dover 2002). Each sampler was lined with a kevlar bag; the pot with its bag liner was positioned so as to engulf a clump of mussels, and the bag was then cinched closed. Each pot sampled a variable mussel volume over a constant area of 531 cm². Once the bag was closed, the pot was placed in a quiver on the submersible basket to prevent loss of animals. In addition, qualitative samples were collected using a kevlar-lined scoop and stored in indi-

vidual bio-boxes on the submarine. For univariate analysis of species richness (including species-effort curves), data from quantitative and qualitative samples were combined. Only quantitative samples were used (with abundances standardized to numbers of individuals per liter of mussel volume sampled) for calculation of numerically dominant taxa, diversity indices and for multivariate analyses. At the Train Station site on the NEPR, pot samples were collected along a 5 m transect from the periphery of the field to a central clump of tubeworms *Riftia pachyptila*. Samples collected from all other sites were haphazard.

Once on deck, mussels were washed 3 times in filtered (10 µm) seawater and the washings were passed through a 263 µm sieve. Retained material was preserved in buffered 10% formalin and stored in 70% EtOH. Sampling effort is expressed here both as numbers of individuals collected and, because mussel beds are 3-dimensional features, as volume of mussels collected per sample. Mussel volume in liters (±0.1 l) was determined after washing by displacement of plastic-bagged mussels immersed in seawater in a graduated container. Mussel shell length (±0.1 mm) and dry weight measures (±0.01 g) were determined for a representative subset of individuals from each site. Sieved samples were sorted twice under a dissecting microscope, the second time after staining with Rose Bengal. All individuals were identified to the lowest taxonomic level possible (i.e. morphological species, except for copepods, nematodes and nemerteans) and counted. Identifications were made with reference to collections at the US National Museum of Natural History and to voucher specimens of material examined by taxonomic specialists in the author's collections.

Large taxa observed but not collected in the samples (i.e. galatheid squat lobsters *Munidopsis subsquamosa*, bythograeid crabs *Bythograea thermydron*, and zoarcid fish *Thermarces cerberus*) were not included in the analysis, although juvenile stages of these species are included. The polychaete species that is a symbiont in the mantle cavities of mussels *Branchipolynoe symmytilida* was also not included in the diversity measures since it is not a part of the fauna that occupies the interstitial volume of the mussel bed. Mussels <5 mm were included in the analysis, as they are deemed to be part of the associated fauna rather than structural at this stage of their life history.

Statistical analysis. Cumulative species-effort curves were generated for each mussel bed using EstimateS (Colwell[1]; randomization operations = 100). Effort was

measured as numbers of individuals and as volume of mussel bed sampled. To facilitate comparisons among sites, ecologists often calculate the estimated number of species for a given number of individuals sampled. The stratified and replicated sampling design (3 sites, 5 to 6 quantitative and 2 qualitative samples per site) permitted sample-size standardization to 10 000 individuals using randomization and regression methods (Hayek & Buzas 1997). As noted by Levin et al. (2001), rarefying samples to a common number of individuals, regardless of the rarefaction method, does not eliminate the sensitivity of richness estimates to sampling effort; comparisons should be made at the asymptote of the species accumulation curve or by tests of the degree of separation of regressions generated by randomized plots of cumulative species versus cumulative log number of individuals. Asymptotic *S*-values were estimated from species accumulation curves using Chao 1 (Colwell & Coddington 1994); however, Chao 1 is influenced by the collection of rare species, which is a function of the number of individuals sampled. The Shannon diversity index ($H'_{\log e}$) and Pielou's evenness index (J') were calculated for standardized quantitative samples using PRIMER v5 (Clarke & Gorley 2001). Bray-Curtis dissimilarities (C) based on species' presence or absence were calculated using PRIMER v5 (Clarke & Gorley 2001).

Cluster and non-metric, multi-dimensional scaling (MDS) techniques were used to examine community structure within sites (each NEPR mussel bed), among sites within a region (all NEPR mussel beds) and between regions (NEPR and SEPR mussel beds), based on Bray-Curtis similarities calculated from square-root transformed, species-abundance data from standardized quantitative samples (PRIMER v5; Clarke & Gorley 2001). Square-root transformation downweights the importance of the highly abundant species; the result is that the calculated similarities reflect a contribution from both the most abundant and the less common ('mid-range') species (Clarke & Warwick 2001). Analysis of similarity tests (ANOSIM subroutine of PRIMER v5) were performed on standardized quantitative samples to determine significant differences between groups identified by cluster and MDS techniques. Dissimilarity percentages in square-root transformed, standardized quantitative data sets were calculated using the SIMPER subroutine of PRIMER v5.

Spearman rank-order correlation coefficients, regressions (using the dummy variable technique to test the significance of the separation of lines of similar slopes with differing intercepts), and analysis of variance of H' and J' were calculated using MiniTab software (v13.20, 2000). Comparisons of mean H' and J' values for NEPR and SEPR mussel beds were made

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[1]Colwell RK (1997) EstimateS v5: statistical estimation of species richness and shared species from samples. User's guide and application; available at viceroy.eeb.uconn.edu/estimates

using a percentile, non-parametric, bootstrap technique (Efron & Tibshirani 1998) to test the null hypothesis that these diversity measures did not differ. In this bootstrap analysis, the sampled mussel beds on the NEPR are assumed to be representative of NEPR mussel beds in general. The test statistic (θ_{obs}) was the difference between the mean of the 3 NEPR values and that of the Rehu Marka site for which sufficient quantitative replicates were collected, which would not differ significantly from 0 if the null hypothesis were true. The 4 observed NEPR and SEPR values for a particular diversity measure were combined and resampled with replacement to generate a bootstrap sample of 3 NEPR values and 1 SEPR value under the null hypothesis. From this data set, the difference between the mean of the 3 resampled NEPR values and that of the resampled SEPR value was recalculated as a bootstrap replicate (θ_{boot}). This bootstrap simulation was repeated 10 000 times to generate the frequency distribution of the difference, from which the probability value (p) of the observed difference was acquired directly.

RESULTS

Community structure in NEPR mussel beds

Sixty-one invertebrate taxa were represented in 74 397 individuals collected from the 3 NEPR mussel beds. Abundances and distribution of species and individuals within samples and sites are presented in Appendix 1 (www.int-res.com/journals/suppl/vandover_appendix.pdf). All quantitative samples were numerically dominated (>10% of all individuals) by limpets *Lepetodrilus elevatus*, copepods, lysianassid amphipods *Ventiella sulfuris*, and ampharetid polychaetes *Amphisamytha galapagensis*. Approximately 25% of the taxa within each mussel bed were represented by single individuals; 13 taxa (~20%) were represented by only 1 individual in the entire sampling effort. At least 8 of these 13 extremely rare mussel-bed taxa (*Tevnia jerichonana*, *Nicomache arwidssoni*, *Lepidonotopodium riftense*, serpulids, *Paralvinella grasslei*, *Neomphalus fretterae*, *Provanna ios*, and *Rhynchopelta concentrica*) occur in larger numbers within other microhabitats of the vent field (e.g. in warmer waters, on peripheral basalt, among tubeworms). There was no significant correlation between mussel-bed structure (indexed by median mussel length per sample) and abundance of individuals per liter of mussel volume for quantitative samples (Spearman = s rank-order correlation; $r_s = -0.178$, p = 0.494). There was also no significant separation of log-transformed shell length versus dry weight relationships among sites (Biovent = reference; p > 0.200).

Species-effort curves (Fig. 2) indicate that Biovent and East Wall have similar species richness, while Train Station supports fewer species. This applies regardless of whether the metric of effort was number of individuals (Fig. 2A) or volume of mussels sampled (Fig. 2B). Chao 1 estimates of total diversity at each site (Table 1) also suggested there was lower diversity at the Train Station site than at East Wall or Biovent, despite the greater number of individuals sampled at Train Station. Diversity (H') and evenness (J') indices within quantitative samples (Table 1) did not differ among the mussel beds (H': $F_{3,16} = 1.17$, p = 0.340; J': $F_{3,16} = 0.39$, p = 0.683).

For the Train Station mussel bed, where sampling was systematic from edge to center, differences in community structure were suggested by cluster analysis (Fig. 3), but the power of the test was too low to
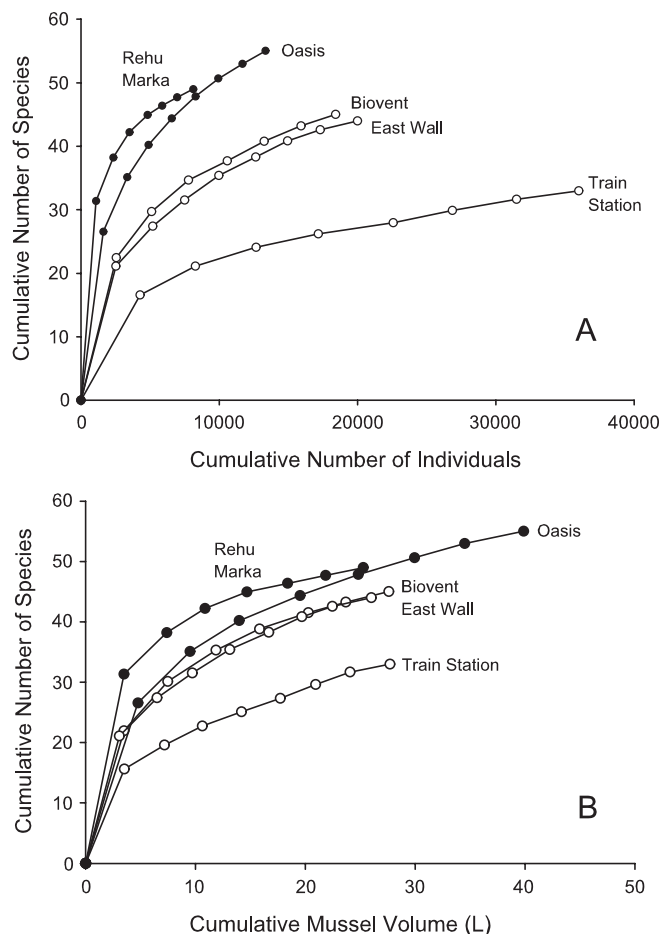

Fig. 2. Species-effort curves for Train Station, East Wall, Biovent mussel beds (northern East Pacific Rise [NEPR]: ○) and Oasis and Rehu Marka mussel beds (southern East Pacific Rise [SEPR]: ●). (A) Effort based on cumulative number of individuals. (B) Effort based on cumulative mussel volume sampled

Table 1. Species richness (S), Chao 1 (SD), total abundance (n), number of species in 10 000 individuals ($S_{10\,000}$) with r^2 values (derived from semi-log regressions), mean $H'_{\log e}$ (SE) and mean J' (SE). At the Oasis mussel bed, too few quantitative samples were collected to allow calculation of average H' and J' measures. NEPR = northern East Pacific Rise; southern East Pacific Rise = SEPR; nd = not determined

	S	Chao 1	n	$S_{10\,000}$	r^2	H'	J'
NEPR	61	75 (13.1)	74397	34	0.995	1.607 (0.054)	0.539 (0.0164)
Train Station	34	42 (10.7)	36000	23	0.992	1.497 (0.064)	0.534 (0.0241)
East Wall	44	57 (14.4)	19987	36	0.992	1.672 (0.103)	0.558 (0.0341)
Biovent	46	54 (10.7)	18410	38	0.998	1.661 (0.108)	0.521 (0.0292)
SEPR	57	62 (2.5)	21444	52	0.997	2.250 (0.056)	0.654 (0.0091)
Rehu Marka	48	50 (1.5)	8110	51	0.998	2.250 (0.056)	0.654 (0.0091)
Oasis	52	65 (7.8)	13333	51	0.997	nd	nd

Table 2. Species contributions (> 5%) to Bray-Curtis dissimilarities (standardized and square-root transformed) between invertebrates at outer edge and at center of mussel bed at Train Station, northern East Pacific Rise (NEPR)

Taxon	Average abundance		Contribution to dissimilarity	
	Outer edge	Center	Contribution (%)	Cumulative (%)
Copepods	585	85	31.9	31.9
Amphisamytha galapagensis	129	45	9.7	41.6
Bathymodiolus thermophilus (<5 mm)	9	48	7.6	49.2
Lepetodrilus ovalis	25	2	7.5	56.7
Ophryotrocha akessoni	49	19	6.4	63.1
Lepetodrilus elevatus	459	585	6.1	69.2

Table 3. Bray-Curtis dissimilarities (C) based on species presence/absence data. For northern East Pacific Rise (NEPR) versus southern East Pacific Rise (SEPR) comparisons, NEPR = combined species list for Train Station, East Wall, Biovent; SEPR = combined species list for Oasis, Rehu Marka

	Species shared	Total species	C
NEPR			
Train Station vs East Wall	28	47	28
Train Station vs Biovent	27	53	33
East Wall vs Biovent	30	58	29
NEPR vs SEPR	41	77	31

detect a significant difference even with perfectly separated groups. An abundance of post-larval and juvenile mussels (<5 mm) and of the limpet *Lepetodrilus elevatus*, together with a paucity of copepods, ampharetid *Amphisamytha galapagensis* and ophryotrochid *Ophryotrocha akessoni* polychaetes, and a congener to *L. elevatus* (*L. ovalis*) characterized samples from the center of the mussel bed relative to those from the outer edge (Table 2). Within-site differences at Train Station were generally less than between-site differences for Train Station, East Wall, and Biovent (Fig. 3).

Comparison of mussel bed communities between NEPR and SEPR vent fields

More than 50% of all species collected from NEPR and SEPR mussel beds were shared. Average Bray-Curtis dissimilarity (C; Table 3) between NEPR mussel beds ($C = 30$) was not different from the dissimilarity between NEPR and SEPR mussel beds ($C = 31$). Of the 8 numerically dominant taxa (comprising >1% of the total number of individuals in quantitative samples) at NEPR mussel beds, all occurred on the comparable list for SEPR mussel beds, although the rank order was different between these regions (Table 4). At SEPR mussel beds, the amphipod *Ventiella sulfuris* replaced the limpet *Lepetodrilus elevatus* as the numerical dominant. SEPR vents were also colonized by a large number of amphipods identified as *Syrrhoe* sp., a species that is so far not known from NEPR mussel beds, and by abundant leptostracans *Dahlella caldariensis*, which were collected from NEPR mussel beds, but only in low numbers.

Twenty species were only found at NEPR mussel beds (33% of the regional species list), while 16 species were unique to SEPR mussel beds (28% of the regional species list). Of these 36 regionally endemic species, only *Cyathermia naticoides* (NEPR) and
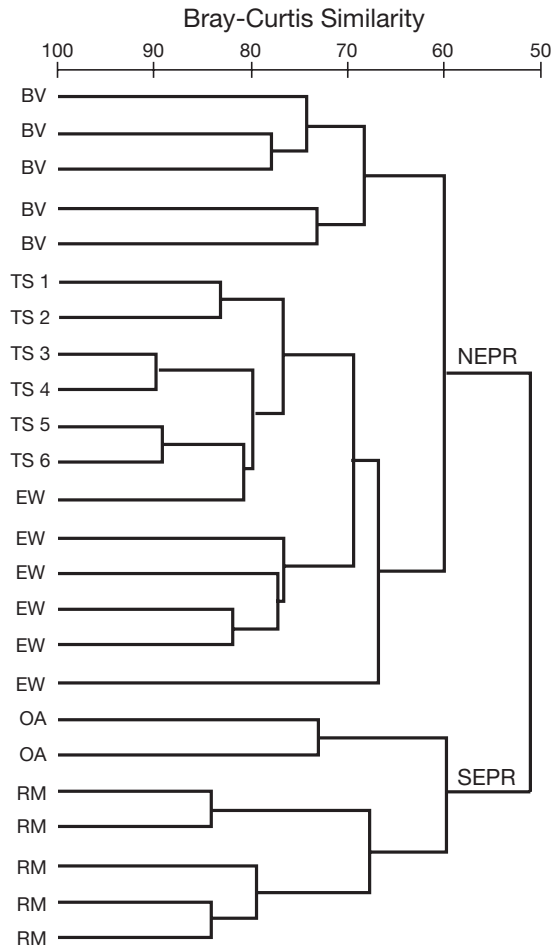
Bray-Curtis Similarity

Fig. 3. Cluster diagram using multivariate Bray-Curtis similarity coefficients for quantitative samples (abundance data standardized to numbers of individuals per liter of mussels sampled and square-root transformed) at northern East Pacific Rise (NEPR) and southern East Pacific Rise (SEPR) mussel beds. TS = Train Station, EW = East Wall, BV = Biovent, OA = Oasis, RM = Rehu Marka. Train Station Samples 1 through 6 correspond to locations along a transect from the edge (1) to the center (6) of the mussel bed

Table 4. Comparison of numerically dominant taxa (≥1% of total number of individuals) at northern (Train Station, East Wall, Biovent) and southern (Oasis, Rehu Marka) East Pacific Rise mussel beds (quantitative samples only). SEPR data are from Van Dover (2002)

| Taxon	% of total
NEPR	
Lepetodrilus elevatus	36.8
Copepods	21.1
Ventiella sulfuris	16.3
Amphisamytha galapagensis	11.7
Ophryotrocha akessoni	4.5
Bathymodiolus thermophilus <5 mm	3.8
Archinome rosacea	1.9
Lepetodrilus ovalis	1.7
SEPR	
Ventiella sulfuris	38.3
Amphisamytha galapagensis	18.5
Lepetodrilus elevatus	8.0
Bathymodiolus thermophilus <5 mm	6.9
Lepetodrilus ovalis	5.1
Copepods	4.2
Syrrhoe sp.	3.2
Dahlella caldariensis	3.0
Ophryotrocha akessoni	2.9
Eulepetopsis vitrea	2.3
Archinome rosacea	1.2
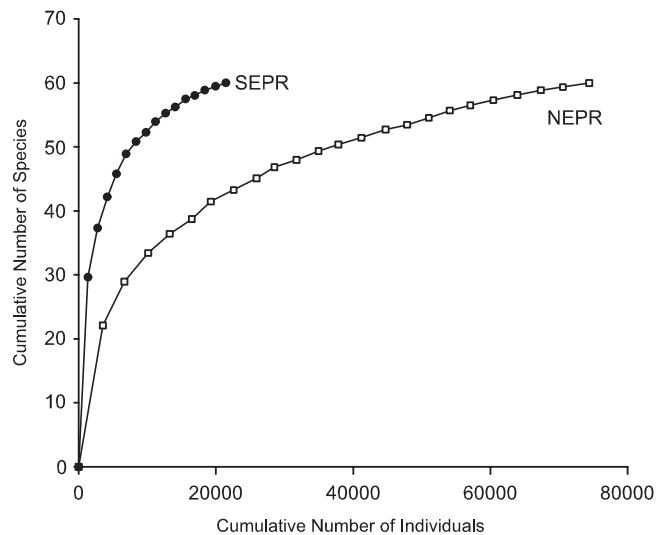
Fig. 4. Cumulative species-effort curves for northern East Pacific Rise (NEPR) and southern East Pacific Rise (SEPR) mussel beds

Syrrhoe sp. (SEPR) occurred at densities of more than a few individuals per sample.

Species richness was higher at the NEPR site compared to the SEPR site (61 vs 57 species; Table 1), as were Chao 1 estimates of total species richness (75 vs 62 species; Table 1). The projected asymptotes of the NEPR and SEPR species-effort curves when all samples are combined, however, are not consistent with greater diversity at NEPR mussel beds (Fig. 4). There was a significant separation of the regressions of cumulative species versus log cumulative individuals for SEPR versus NEPR mussel beds (p < 0.001). Mean H' and J' values for Train Station, East Wall and Biovent samples were also less than those of Rehu

Marka samples (Table 1; bootstrap analysis, H': p = 0.028; J': p = 0.040).

NEPR and SEPR samples separate into 2 well-defined clusters at a Bray-Curtis similarity level of just over
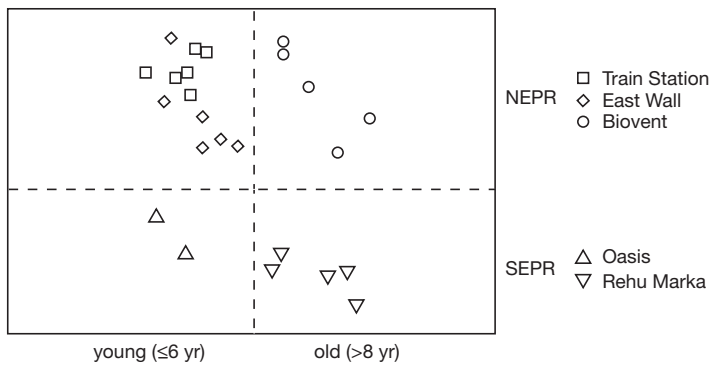
Fig. 5. Multi-dimensional scaling (MDS) plot of quantitative, standardized (number of individuals per liter of mussel volume sampled) northern East Pacific Rise (NEPR) and southern East Pacific Rise (SEPR) mussel bed samples (stress = 0.12). Superimposed on the plot are dashed grids and legends that identify the age and geographic relationships among the sites

50% (Fig. 3). The similarity between Oasis and Rehu Marka is ~60%; Biovent also separates from Train Station and East Wall at about the 60% similarity level. Clustering of samples is emphasized by MDS ordination of NEPR and SEPR samples (Fig. 5). East Wall and Train Station, which are of approximately the same age, are the only pair-wise comparisons that can not be differentiated (analysis of similarities [ANOSIM]; $R <$ 0.4; p > 0.15). Differences in community structure related to geographic location and age of the vent field are suggested by the MDS plot. Greater abundances of *Lepetodrilus elevatus*, copepods, and *Amphisamytha galapagensis*, and lesser abundances (or complete absence of) the crustaceans *Ventiella sulfuris*, *Syrrhoe* sp., and *Dahlella caldariensis* (Table 5) differentiate NEPR mussel beds from SEPR mussel beds. The multivariate difference between old (Biovent, Rehu Marka) and young (Train Station, East Wall, Oasis) sites is most strongly influenced by the lesser abundances of *Ventiella sulfuris* at the older sites, accounting for 5 to 13% of the dissimilarity.

DISCUSSION

The scale of variation in community structure at hydrothermal vents and the underlying structuring mechanisms have been the focus of many descriptive and experimental studies. Hessler & Smithey (1983) and Smith (1985) were the first to describe zonation patterns of megafaunal invertebrates at vents and to attribute these distributions to discrete physico-chemical regimes. Subsequent field programs suggested that recruitment processes and competitive interactions among tubeworm species and mussels can result in successional stages at vents in the eastern Pacific (Fustec et al. 1987, Hessler et al. 1988, Shank et al. 1998, Mullineaux et al. 2000). Small-scale variation and succession have also been well documented for invertebrate communities of northeast Pacific vents using qualitative methods (e.g. Sarrazin et al. 1997, Sarrazin & Juniper 1999). These studies addressed important aspects of spatial and temporal variation and led to an appreciation of some dramatic local population dynamics in response to changes in fluid flow and biological interactions among a relatively small number of species.

Within established mussel beds on the EPR, differentiation of community structure is subtle and, while aspects of community structure may be sensitive to the age of the mussel bed and to scales of spatial variation, the ability to resolve differences is dependent on the method of comparison used. Two of the most common univariate measures of community structure, H' and J', had low coefficients of variation within mussel beds (10 to 15%) and did not differentiate mussel beds of different ages (4, 5 and >8 yr) distributed along ~2.5 km of the ridge axis. Species richness ($S_{10\,000}$) at Train Station was 60% of that observed at East Wall or Biovent, but since the Train Station mussel bed is 1 yr older than the East Wall mussel bed, this result is not consistent with an age effect. Many other factors could influence species richness within a mussel bed, including differences in physico-chemical characteristics, in

Table 5. Species contributions (>3%) to Bray-Curtis dissimilarities (standardized and square-root transformed) between invertebrates of northern East Pacific Rise (NEPR) and southern East Pacific Rise (SEPR) regions

Taxon	Average abundance		Contribution to dissimilarity	
	NEPR	SEPR	Contribution (%)	Cumulative (%)
Lepetodrilus elevatus	388	43	15.7	15.7
Ventiella sulfuris	172	208	12.5	28.2
Copepods	222	23	12.1	40.3
Syrrhoe n. sp.	0	17	4.8	45.1
Amphisamytha galapagensis	123	100	4.5	49.6
Dahlella caldariensis	<1	16	3.5	57

biotic interactions as well as proximity to adjacent or nearby low-temperature habitats. Two factors— median mussel length and mussel condition as measured by tissue dry wt versus shell length—did not differ among sites and thus were not likely to have contributed substantively to differences in community structure in this study. In intertidal mussel beds, significant variations in H' and S correlated with variations in intertidal height and hydrodynamic regimes can be detected at the sub-meter and 10 m scales within mussel communities on subarctic, intertidal boulders (McKindsey & Bourget 2001). Although hydrothermal-vent mussel beds have been compared to intertidal mussel beds (Johnson et al. 1994), gradients of temperature and chemistry within vent mussel beds do not appear to influence community structure to the same extent that gradients of exposure may affect community structure in intertidal mussel beds (Underwood & Denley 1984).

When NEPR and SEPR mussel beds are compared, most of the diversity measures (H', J', S or $S_{10\,000}$) were lower within NEPR mussel beds. Chao 1 estimates of total diversity gave an opposite result, but this value is suspect, given the 3-fold greater number of individuals sampled at NEPR mussel beds. Diversity in mussel beds is higher at vent sites on the fast-spreading EPR than it is at 2 vent sites on the slow-spreading Mid-Atlantic Ridge (MAR), which were studied using comparable sampling efforts (Lucky Strike and Snake Pit; Van Dover & Trask 2000, author & C. D. Jenkins unpubl.); along the EPR, diversity is higher at the faster-spreading SEPR site than at the NEPR site (this study). This positive relationship between spreading rate and diversity matches the relationship between spreading rate and frequency of venting along ridge axes (Baker et al. 1995). Preliminary assessment of species richness in mussel beds at 11° N on the EPR and at Logatchev vents on the MAR are consistent with this diversity versus spreading-rate relationship (author unpubl.). Van Dover (1995) and Juniper & Tunnicliffe (1997) predicted this relationship, but for different, non-exclusive reasons: Van Dover (1995) suggested that while a higher probability of genetic isolation may promote speciation on the MAR, the probability of extinction is even greater, resulting in lower overall diversity where vents are far apart. Juniper & Tunnicliffe (1997) posited that where there is more habitat, more species can fit. Continued analysis of diversity within mussel beds from ridge axes that cover a range spreading rates and degrees of isolation, and from ridge axes in ocean basins of different ages will help to determine if diversity may be dependent on the spatial frequency of venting.

H', J' and S are summary statistics that do not describe or provide insight into similarities in species composition. All of the numerically dominant species at NEPR mussel beds were also numerical dominants at SEPR mussel beds. It is impossible to know at this point how many of the rare species not shared between regions are true regional endemics, or if their apparent distributions are artifacts of limited sampling. The Bray-Curtis dissimilarity coefficient (C) *between* NEPR and SEPR mussel beds (separated by 3000 km) was 31, essentially the same value as observed *within* NEPR mussel beds (separated by at most 2.5 km; $C = 28$ to 33). Earlier work based on submersible observations and opportunistic collections suggested that the SEPR vent fields had the same zoological composition of the megafauna as NEPR vent fields (i.e. tubeworms *Riftia pachyptila*, *Tevnia jerichonana*, clams *Calyptogena magnifica*, squat lobsters *Munidopsis subsquamosa*, etc.; Geistdoerfer et al. 1994). Even with the more detailed sampling reported here, the extent of species differentiation between NEPR and SEPR mussel bed faunas is not sufficient to distinguish them even as sub-provinces.

The relatively high level of similarity in vent mussel-bed species lists over large latitudinal distances should not be considered a general attribute of vent faunas. For vent communities on the MAR, there is sufficient differentiation among species lists of several sites distributed across 15° of latitude (~23° to 38° N) for these sites to be posited as 'faunal islands' by Desbruyères et al. (2000). At Snake Pit and Lucky Strike vents on the MAR (separated by ~2000 km), the Bray-Curtis dissimilarity coefficient was 60 for the vent species (i.e. not including 'penetrating', non-vent species); for Lucky Strike and Menez Gwen vents (separated by ~50 km), $C = 47$ (Desbruyères et al. 2000). The greater degree of endemicity among vent faunas of MAR vents is thought to be due at least in part to the greater range in depths among MAR vent sites (MAR: 850 to 3500 m; EPR: 2500 to 2600 m), which influences both the chemical character of the venting fluids and the physiological attributes of the organisms (Van Dover et al. 1996, Desbruyères et al. 2000).

Fish and invertebrate faunas of adjacent seamounts (median $C = 79$; Richer de Forges et al. 2001) are more dissimilar than invertebrates faunas of adjacent vent mussel beds ($C = 30$); seamounts separated by only 1000 km had no shared species ($C = 100$; Richer de Forges et al. 2001), while vents separated by 3000 km shared 38 species ($C = 31$). Vents are often described as being made up of endemic species (e.g. Tunnicliffe et al. 1998, Van Dover 2000, this study). This descriptor arises from comparisons of the vent faunal lists with those of the non-vent deep-sea or of other chemosynthetically based environments (seeps, whale skeletons). Many vent species are not geographically re-

stricted to the same extent as seamount species, and cannot be regarded as endemic when comparisons are made at geographic scales rather than among habitat types. Of the numerically abundant macrofaunal taxa, only 2 species (*Cyathermia naticoides*, NEPR; *Syrrhoe* sp., SEPR) appear to be regional endemics. An understanding of the reproductive attributes, dispersal capabilities and population genetics of these species in comparison to closely related species with more extensive ranges should be illuminating.

Multivariate statistics that take into account both species composition and relative abundance proved most useful in discriminating among mussel beds on the NEPR. Using cluster analysis, it was possible to recognize edge-to-center effects at the Train Station site, but the differences are subtle and are driven primarily by relative abundance rather than species composition. The extent to which the differences observed reflect biotic or abiotic influences is unknown. Further systematic sampling with corresponding temperature and chemistry measurements and experimental manipulations are needed before we understand how distributions of organisms reflect physicochemical gradients and the effects of biological interactions.

NEPR and SEPR mussel beds are readily distinguished by multivariate cluster analysis and, using MDS plots, differences in community structure that correlate with the age of a vent ('young' vs 'old') and latitude are suggested. Multivariate measures may be more sensitive than univariate statistics as means of documenting spatial or temporal variation in mussel-bed communities. Compared to seamounts or intertidal mussel beds, however, community structure in vent mussel beds on the EPR is relatively insensitive to spatial scale (or differences in age) along an extended length of ridge axis, at least for established mussel beds of active vents.

Results of this study reinforce the notion that many of the invertebrates associated with vent mussel beds on the EPR are likely to be resilient to habitat destruction. Most of the numerically dominant species in the community have extensive ranges and many of the rare species in mussel beds occur in large numbers within other microhabitats of a vent field. Habitat degradation generated by scientific sampling will almost certainly be of lesser impact than that of volcanic eruptions on the EPR and is not likely to threaten regional populations or the existence of the numerically dominant species. This stands in contrast to the situation on seamounts (Richer de Forges et al. 2001) and, perhaps, in cold-seep chemosynthetic communities, where there may be high levels of regional endemicity and corresponding susceptibility to habitat degradation (Sibuet & Olu 1998).

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