

COMMUNITY STRUCTURE AND BIOGEOGRAPHY
OF MUSSEL BED COMMUNITIES AT PACIFIC HYDROTHERMAL VENTS

Lau and North-Fiji Back-Arc Basins, 32° S – East Pacific Rise,
and 38° S – Pacific Antarctic Ridge

A Thesis

Presented to

The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of

Master of Science

by

Elizabeth Anne Blake

2006

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

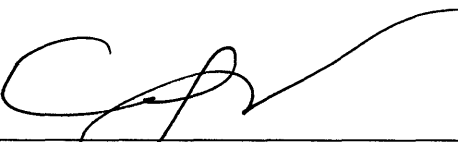
The requirement for the degree of

Master of Science

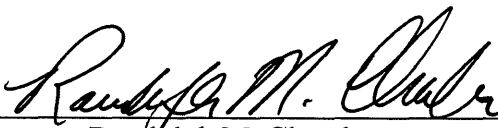


Elizabeth Anne Blake


Approved by the Committee, May 2006




Cindy L. Van Dover, Chair



Randolph M. Chambers



Stewart A. Ware



Rochelle D. Seitz
Virginia Institute of Marine Sciences

To my parents for all their support for my education and happiness

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	v
LIST OF TABLES	vi
LIST OF FIGURES	vii
ABSTRACT	viii
INTRODUCTION	2
METHODS	13
RESULTS	21
DISCUSSION	61
REFERENCES	74
VITA	81

ACKNOWLEDGMENTS

I wish to show appreciation to Dr. Cindy Van Dover, under whose guidance this investigation was achieved, for her valuable direction and advice throughout the investigation. I am indebted to Professors Randolph Chambers, Rochelle Seitz, and Stewart Ware for their assistance evaluating my approaches to this study and their helpful criticism of the manuscript. I thank my friends and colleagues, Anne Condon, Kristin Erickson, Megan Evans, Heather Heiser, Elise Larsen, Carol Logan, Jessica Wallace Ng, Jamie Underdown, Megan Ward, who provided valuable insight, advice, and entertainment throughout my research. I wish to thank the Captains and crews of the R/V Atlantis and Melville and the pilots and technicians of the DSV Alvin and ROV Jason, and the members of the scientific party for their assistance in obtaining biological specimens at sea. I am grateful to A. Waren and M. Segonzac who helped with the identifications of specimens. I am also thankful to A. Burton, C. Gustafson, and J. Underdown for their assistance in sorting samples. This work was supported in part by research and travel grants from The College of William & Mary.

LIST OF TABLES

Table	Page
1. Lau Basin species-abundance matrix	25
2. Top five abundance dominants at Lau and N. Fiji Basin	27
3. North Fiji Basin species-abundance matrix	29
4. 32° S – EPR species-abundance matrix	32
5. Top five abundance dominants at 32° S – EPR and 38° S – PAR	33
6. 38° S – PAR species-abundance matrix	34
7. Western Pacific species diversity	40
8. Back-arc basin species contribution to dissimilarity	43
9. Eastern Pacific species diversity	44
10. Mid-ocean ridge species contribution to dissimilarity	48
11. Mussel bed species diversity	53

LIST OF FIGURES

Figure	Page
1. Site map	6
2. Mussel size frequency	22
3. Mussel condition	23
4. Back-arc basin MDS plot	28
5. Rank-abundance plot	36
6. Taxon abundance	37
7. Species-effort curve	38
8. Back-arc basin cluster plot	41
9. Mid-ocean ridge MDS plot	46
10. Mid-ocean ridge cluster plot	47
11. Map of deep-sea chemosynthetic mussel-bed macrofauna sites	51
12. Species-effort curve for all chemosynthetic mussel-beds	52
13. Mussel bed diversity and evenness	54
14. MDS plots of all chemosynthetic mussel-beds	56
15. Cluster plots of all chemosynthetic mussel-beds	57
16. Changes in community similarity over distance	59
17. Species-effort curve of different marine communities	72

ABSTRACT

Comparisons of macrofaunal community structure (species composition, abundance, rank order, species richness, diversity) in hydrothermal vent mussel beds were made between paired sites in the eastern and western Pacific Ocean to address the degree of biogeographical isolation of vent sites. Also, evaluations were made of the biogeography of previously described chemosynthetic mussel beds. Vent communities on the same ridge segment include many shared species. As the linear distance between vent communities along a ridge axis increases, differences in species composition become evident because gene flow between vents decreases as successful dispersal over long distances decreases. Deep-ocean current systems and geo-morphological features (such as microplates and transform faults) can also be dispersal barriers.

In the eastern Pacific two vent locations [32° S on the East Pacific Rise (EPR) and 38° S on the Pacific Antarctic Ridge (PAR)] are separated by 650 km on the ridge axis and the Juan Fernandez microplate. In the western Pacific the two back arc basin vent locations (Lau and North Fiji basins) are separated by 1100 km of ocean, with presumably limited dispersal between basins. The two eastern Pacific locations shared 63% of their species and the western Pacific locations shared 57% of their species. Only two morphospecies were found at all four vent locations (*Amphisamytha galapagensis* and *Archinome rosacea*). Species richness (S_{5000}) was highest for Lau (37) and lowest for N. Fiji (23). Both eastern Pacific locations had roughly the same species richness (32° S: 25; 38° S: 26).

Similarity between hydrothermal vents decreased over distance on a ridge axis. Sites less than 1000 km apart shared more species than sites over 1000 km apart. There was no difference in the decrease in similarity over distance between the EPR and the Mid-Atlantic Ridge. Cold seep mussel-bed populations were more isolated than hydrothermal vent populations. But at the familial level, hydrothermal vent and cold seep mussel beds were at least 35% similar.

COMMUNITY STRUCTURE AND BIOGEOGRAPHY
OF MUSSEL BED COMMUNITIES AT PACIFIC HYDROTHERMAL VENTS

INTRODUCTION

Ever since the discovery of hydrothermal vents along the Galapagos Rift in 1977, the distinct fauna found at vent sites have fascinated researchers. Since then, hydrothermal vents have been reported from mid-ocean ridges (Van Dover 2000), as well as at back-arc basin spreading centers (Hessler et al. 1988) and seamounts (Karl et al. 1988). Six biogeographical provinces of hydrothermal vent ecosystems are described from mid-ocean ridge and back-arc spreading centers: western Pacific, northeast Pacific, East Pacific Rise, Azores, Mid-Atlantic Ridge, and Indian Ocean (Van Dover et al. 2002). These provinces coincide with ocean basins and non-vent biogeographical provinces (Mironov et al. 1998). All hydrothermal vent communities have a similar trophic structure that includes: primary producers (free-living bacteria, or animals hosting epi- or endosymbiotic bacteria), primary consumers (grazers and suspension feeders), and secondary consumers (carnivores and scavengers; Grassle 1986). The most visible faunistic difference among vent communities often corresponds to variation in the megafauna species that host symbiotic bacteria (Jollivet 1996). In the eastern Pacific, tubeworms and mussels are the dominant megafauna; in the Atlantic, shrimp and mussels dominate; and in the western Pacific and Indian Ocean, gastropods and mussels are the dominant megafaunal species that host symbiotic bacteria. Symbiotic hosts are important as foundation species in chemosynthetic environments because they create or alter habitat for many of the other species in the ecosystem (Bruno & Bertness 2001). The communities of macrofaunal invertebrates (organisms between 250 μm and 1-2 cm) rely on the mussels,

gastropods, or tubeworms to generate habitat (surface area they can attach to), provide refuge to hide from predation, and enhance the supply and retention of propagules by increasing the spatial complexity of the environment (Bruno & Bertness 2001). Changes in temperature, chemistry, and stability of vent ecosystems affect the structure of both the foundation and macrofaunal populations.

Vent communities vary with distance along ridge axes and between ocean basins. Vent communities differ in population genetics (Vrijenhoek 1997), species composition (Tunnicliffe et al. 1998), and community structure (Van Dover 2002, Van Dover 2003). Rift valley walls may constrain currents containing vent larvae along ridge axes, but transform faults and horizontal offsets of mid-ocean ridges are barriers to this linear connection (Vrijenhoek 1997). Vent communities on the same ridge segment include many shared species, but as the linear distance between vent communities along a ridge axis increases to thousands of kilometers, differences in species composition become evident. As the distance between vents increases, the amount of gene flow between the vents decreases due to increased barriers to dispersal and results in greater isolation and more opportunities for speciation (Vrijenhoek 1997, Van Dover et al. 2002). Over large distances, species composition at vent sites change and new species make up the vent community. Species and genetic level similarities between vent fields on different ridges or back-arc basins can also reveal clues to the evolution of vents and history of tectonic plate movement.

By comparing vent fauna among vent fields and among ridge segments, Van Dover and Hessler (1990) suggested that along any given ridge segment there is a pool of shared species where vent sites draw their fauna. The species present and their relative abundances depend on the physical and chemical characteristics of the vent field (Luther et al. 2001).

This shared pool of species is evident in the remarkable similarity of megafauna at the familial level among 13° N – 11° N East Pacific Rise (EPR) and the Galapagos Spreading Center (Van Dover & Hessler 1990). The composition of vent fauna on the southern EPR (17° S to 19° S) is also very similar to the vent community on the northern EPR and on Galapagos Spreading Center (Fig. 1: Geistdoerfer et al. 1995). The range of a species on a mid-ocean ridge relies, at least partly, on the dispersal ability of the species. Some organisms have lower dispersal capabilities than others. The lysianassid amphipod *Ventiella sulfuris* has no specialized dispersal phase in its life cycle; adults brood their eggs and release juveniles in the form of miniature adults (France et al. 1992). The Hess Deep, a 50-km depression and the Galapagos microplate isolate the EPR and Galapagos populations of *V. sulfuris*. The genetic differentiation of their populations is great enough to consider the two populations of *V. sulfuris* two different species (France et al. 1992).

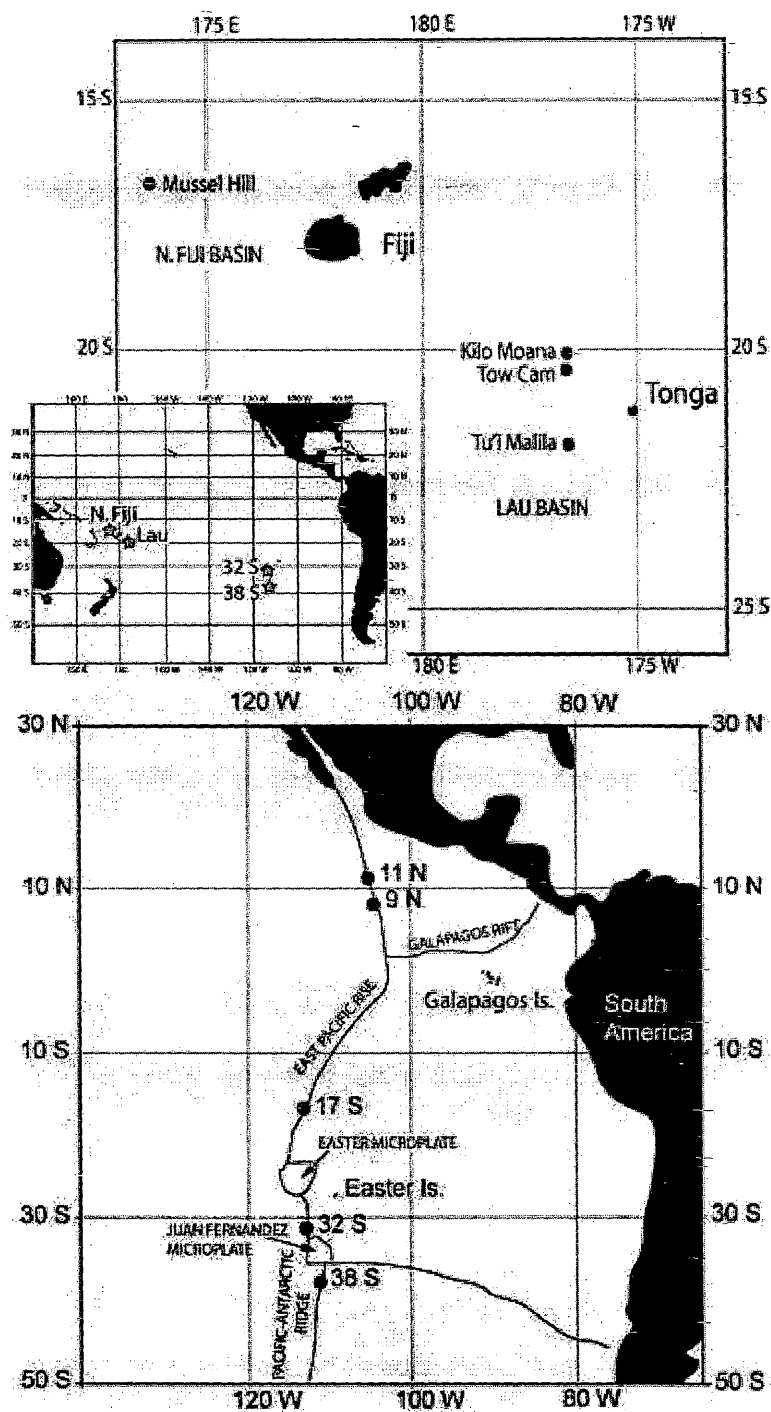
Along the EPR and the Galapagos Spreading Center, the mussel (*Bathymodiolus thermophilus*) population is genetically homogeneous from 13° N to 11° S; indicating that gene flow is continuous in this region (Won et al. 2003). Farther south on the ridge, the Easter Microplate is associated with a great divergence in mussel populations to the north and south. Bythograeid crabs also show a north-south Easter Microplate differentiation. *Allograea tomentosa* and *Bythograea vrijenhoeki* have only been collected south of the microplate, while their sister-species, *Cyanograea praedator* and *Bythograea laubieri* are found to the north (Guinot & Hurtado 2003). However, gene flow of two polychaete species, *Alvinella pompejana* and *Branchiopolynoe symmytilida*, is not obstructed across the Easter Microplate (Hurtado et al. 2004). The impressive dispersal of *A. pompejana* may be due to its large negatively buoyant eggs that drift with bottom currents and its ability to arrest

embryonic development (Pradillon et al. 2001). Thus, the Easter Microplate region may form a discrete boundary between the southern EPR and the Pacific Antarctic Ridge (PAR) or the region may serve as a diffuse boundary that affects species differently based on dispersal methods.

The Easter Microplate region is comprised of two microplates, the Easter and Juan Fernandez Microplates. This region lies at the boundary between the Indo-Pacific and Antarctic marine biogeographic provinces (Vinogradov 1979) and the distribution of vent faunas may be controlled by the same factors that control the distribution of non-vent deep-sea faunas. These factors include major current systems and large geomorphological features (Mironov et al. 1998, Van Dover et al. 2002). The 32° S – EPR vent site is separated from sites to the north by the Easter Microplate and from sites to the south by the Juan Fernandez Microplate (Fig. 1). This inter-microplate ridge section is believed to be the Earth's fastest active seafloor, with spreading rates of 14.9 cm/yr (Hey et al. 1995). South of the Juan Fernandez Microplate, the PAR connects the Pacific and the Antarctic plates (Fig. 1). The spreading rate here is slower than to the north, only 9.5 cm/yr (Hey et al. 1995). The microplates interrupt the ridge axis gene flow along the mid-ocean ridge for approximately 1600 km, potentially disrupting the larval dispersal from the north (Pardee et al. 1998). The PAR is hypothesized to be the source of gene flow between the eastern and western Pacific hydrothermal vents (Hessler and Lonsdale 1991). The PAR connects the eastern Pacific mid-ocean ridge with the subducting zones in the western Pacific and the Southeastern Indian Ridge. Preliminary observations from south of the Juan Fernandez

FIGURE 1

SITE MAP



Map of eastern (lower map) and western (upper map) Pacific vent sites. Starred sites on inset map show locations newly sampled in 2005.

Microplate (37° S – PAR) show that the vent fauna is similar to fauna seen at sites on the southern EPR, except for the lack of *Riftia pachyptila* tubeworms (Stecher et al. 2002). *Bathymodiolus*-spp. mussels and *Lepetodrilus* spp. limpets dominate the sites (Stecher et al. 2002).

Compared to the western Pacific back-arc basins, the connectivity along mid-ocean ridges is high (Tunnicliffe et al. 1998). In the western Pacific, hydrothermal vents are found along isolated back-arc spreading centers instead of mid-ocean ridges. Back-arc spreading centers form along active plate margins where the old ocean crust is subducting beneath a continental plate moving the same direction (Hessler & Lonsdale 1991). Unlike mid-ocean ridges, the back-arc basins of the western Pacific are relatively recent and spreading centers in back-arc basins are only active for a short time, 5-10 my (Desbruyères et al., in press). Back-arc basin vent sites are also more geographically isolated than sites along a mid-ocean ridge where vent sites are connected by a ridge axes. Despite their isolation, western Pacific back-arc basin vents show evidence of genetic dispersal between spreading centers (Hessler & Lonsdale 1991). Back-arc basin vents may be 'stepping stones' for biodiversity, allowing genes to disperse great distances between the isolated sites.

Ancestral ties link the eastern Pacific vent faunas with those of the back-arc basins of the western Pacific. Prior to 55 mya, the Kula-Pacific Ridge provided an east-west connection across the Northern Pacific (Hessler and Lonsdale 1991). After the closing of this connection, the only link between the eastern and western Pacific was provided by the PAR to the south. Comparisons of taxa among known back-arc basin vent sites showed that Lau and N. Fiji Basins shared the most taxa with the nearby Marianas back-arc basin sites, but

also shared genera and some species with vents in the eastern Pacific (Tunnicliffe & Fowler 1996).

Active hydrothermal venting has been reported from two back-arc basins – North Fiji and Lau basins – approximately 1100 km apart in the southwestern Pacific (Desbruyères et al. 1994). The two basins are situated at the boundary between the Pacific and Indo-Australian plates. The N. Fiji Basin is split down the middle by an active ridge (approximately 3 million years old) that spreads at the rate of 5 cm/yr (Auzende et al. 1988, Desbruyères et al. 1994). The ridge morphology of the Lau Basin is more complex than that of the N. Fiji Basin, with many segments, secondary ridges and volcanoes (Nautilau Group 1990). The Lau Basin is bordered by the fossil Lau Ridge to the west, the Tofua Volcanic Arc to the east. The Valu Fu Ridge spreading center is found in the southern half of the Lau basin. The Lau Basin is believed to be younger and have a slightly faster spreading rate (7.4 cm/yr) than the North Fiji Basin (Auzende et al. 1988).

Community structure can also be useful in comparing regional and global variation between vents. Descriptions of the community structure of invertebrate assemblages can provide insight into the underlying physiological, ecological and evolutionary processes of vent sites. Differences in community structure between sites could be due to vent field size, habitat stability, depth, temperature, substrate, variation in vent chemistry, vent age, barriers in dispersal and biological interactions (Mullineaux et al. 1998, Luther et al. 2001, Micheli et al. 2002, Van Dover 2002, 2003, Tsurumi & Tunnicliffe 2003, Dryer et al. 2005). Mussel-bed habitats are used for such studies because they are more structurally similar to each other across ocean basins than other

vent habitats (Van Dover 2002). Beds of *Bathymodiolus* spp. have been reported from all six hydrothermal vent biogeographic provinces, except the northeast Pacific. However, single *Bathymodiolus* spp. have been collected from the northeast Pacific, and mussel beds may yet to be found in the region (McKiness et al. 2005). *Bathymodiolus* spp. mussel beds occupy similar settings in the diffuse flow of hydrothermal vents where temperatures rarely exceed 10 to 15° C (Van Dover 2002). Mussels stack up on top of each other and create a three-dimensional habitat providing homes for many macrofaunal invertebrates. Slight differences in the chemical and physical characteristics of the mussel beds could affect which invertebrates colonize the habitat.

Previous community structure studies have focused on mussel beds and tubeworm assemblages on the East Pacific Rise (Van Dover 2002, 2003, Dreyer et al. 2005, Govenar et al. 2005), Juan de Fuca Ridge (Tsurumi & Tunnicliffe 2003), and the Mid-Atlantic Ridge (Desbruyères et al. 2000, 2001, Van Dover & Trask 2000, Turnipseed et al. 2004, Van Dover & Doerries 2005). Studies have focused on how community structure varies within a vent site, within a vent field, with age of vent sites, with vents in different ocean basins, and between vent and intertidal mussel beds. Community structure varies at a vent over the course of its lifetime. At vent habitats along the fast-spreading EPR, the hydrothermal cycle of waxing and waning is comparatively fast, occurring in years or decades (Van Dover 2003). At the start of the hydrothermal cycle the habitat is rich in sulfide and the flow becomes more diffuse as the vent ages (Van Dover 2003). First- and second-year assemblages of fauna at Juan de Fuca ridge were distinct from the older assemblages (Tsurumi & Tunnicliffe 2003). After these first few years, the community becomes stabilized until the hydrothermal flow begins to wane (Van Dover 2002, Tsurumi & Tunnicliffe 2003, Dreyer et al. 2005). As

hydrothermal flow begins to cease at a vent site, its community structure begins to transition to a background community as recruitment of tubeworms and mussels ceases (Van Dover 2002, Tsurumi & Tunnicliffe 2003, Dreyer et al. 2005), and non-vent deep-sea organisms invade, taking advantage of the newly opened, non-toxic habitat. The last remaining animals at the vent sites subsist on decaying organic matter, heterotrophic bacterial mats or each other (Tsurumi & Tunnicliffe 2003).

Differences in spreading rate between the Mid-Atlantic Ridge (MAR; 2-4 cm/yr) and the EPR (12-16 cm/yr) correlate with many of the differences in community structure between Atlantic and Pacific vent communities (Tunnicliffe et al. 1998, Van Dover & Doerries 2005). Species richness is greater in samples from faster-spreading ridge axes, where vents are closely spaced but shorter lived than on slow-spreading ridge axes, where vents are farther apart but longer-lived (Van Dover & Doerries 2005). Models based on dispersion in a linear fragmented habitat cannot be applied easily to slow spreading ridges. The biogeographic model for the MAR is more complex because local conditions are affected by changing source rocks and variation in depth at vent sites (Desbruyères et al. 2000). The faunal organization found at Atlantic vent sites differs from that in the Pacific. Alvinocarid shrimps and bathymodiolin mussels are the dominant species along the MAR; tubeworms and alvinellid polychaetes are absent (Tunnicliffe et al. 1998). Vent fields along the MAR vary in depth from relatively shallow – Menez Gwen (850 m) and Lucky Strike (1700 m) – to deep – Snake Pit (3500 m) and TAG (3650 m). Shallower vent sites are dominated by the mussel *Bathymodiolus azoricus*, and have been penetrated by bathyal species (organisms that live between 800 – 2,000 m deep), while deeper vent sites are dominated by the bresiliid shrimp and have more endemic hydrothermal species

(Desbruyères et al. 2000). Invasion of shallower vents by non-vent fauna is due to phase separation of vent fluid caused by the decrease of hydrostatic pressure. This produces vent fluid that lacks the toxic metals normally dissolved in the vent fluids, allowing non-vent fauna to invade the sites (Desbruyères et al. 2000).

Bathymodiolus spp. mussel beds also occur in cold seep communities. Macrofaunal species richness is higher at cold seep samples from Blake Ridge (Atlantic) and Florida Escarpment (Gulf of Mexico) locations than from hydrothermal vents in the Atlantic (Turnipseed et al. 2003, 2004). More deep-sea species may be able to invade the mussel beds at seeps due to stability and lack of toxic chemicals. High species richness and diversity were also seen in tubeworm assemblages from hydrocarbon seeps on the upper Louisiana slope of the Gulf of Mexico (Bergquist et al. 2003). However, relatively shallow seep mussel beds on the upper Louisiana slope (depth = 500-700 m) had lower species richness and diversity than what was reported from Blake Ridge and Florida Escarpment (Bergquist et al. 2005). Species richness and diversity at the upper Louisiana slope seep mussel beds were comparable to the low diversity seen at MAR mussel beds (Bergquist et al. 2005, Van Dover & Doerries 2005).

The primary objective of this study was to determine how hydrothermal vent communities differ with separation distance. This study aimed to determine whether the back-arc basin vent locations, Lau and N. Fiji, are as biogeographically isolated as generally believed. Another goal was to determine to what degree species compositions are shared throughout the Easter Microplate Region and how the microplates affect community structure at the 32° S – EPR and 38° S – PAR locations. Descriptions of community structure will be constructed of fauna associated with mussel beds at vents on

adjacent, but isolated back-arc spreading systems (Lau and N. Fiji), as well as two sites on the Eastern-Pacific mid-ocean ridge vent locations, 32° S – EPR and 38° S – PAR. Finally, results of mussel-bed community structure from these four Pacific sites will be compared to results of previously published reports on chemosynthetic mussel-bed community structure to determine global patterns in biogeography at chemosynthetic environments.

METHODS

Study sites

In this study, mussel-bed communities were sampled from four hydrothermal vent fields in the southern Pacific Ocean. Samples were collected from two mid-ocean ridge locations and two back-arc basin locations. The two mid-ocean ridge locations were in the southeastern Pacific at 32° S on the East Pacific Rise (EPR) and 38° S on the Pacific-Antarctic Ridge (PAR); the back-arc basin locations were the North Fiji and Lau Basins in the southwestern Pacific (Fig. 1).

For the mid-ocean ridge locations, one mussel-bed site was sampled from 32° S EPR and two mussel-bed sites were sampled from 38° S PAR. The two mid-ocean ridge locations were located ~660 km apart. The 32° S EPR site was the Saguaro vent field (31°51'S, 112°2'W; 2335 m). The 38° S PAR sites were Pale Etoile vent field (37°47'S, 110°55'W; 2215 m) and Annie's Anthill vent field (37°46'S, 110°55'W; 2228 m). The two 38° S PAR sites are located ~2 km apart. For the back-arc basin locations, one mussel-bed site was sampled from the North Fiji Basin and three mussel-bed sites were sampled from the Lau Basin. The two basins are ~1100 km apart. The North Fiji Basin site was Mussel Hill vent field (16°59'S, 173°55'E; 1990 m). The Lau Basin sites were Kilo Moana vent field (20°3'S, 176°8'W; 2622 m), Tow Cam vent field (20°19'S, 176°8'W; 2714 m), and Tu'i Malila vent field (21°22'S, 176°34'W; 1900 m). Tow Cam is located 30 km to the south of Kilo Moana and Tu'i Malila is located 125 km south of

Kilo Moana.

Sample collection and processing

Replicate samples of mussels and their associated invertebrate community were collected using submersibles during two research cruises in Spring 2005. Samples were collected using the Deep Submergence Vehicle Alvin during March 2005 from 32° S on the EPR and 38° S PAR. The Remotely Operated Vehicle Jason II collected samples in May 2005 from the Lau and North Fiji Basin.

Discrete, quantitative samples were collected haphazardly using pot samplers (see Van Dover 2002). The pot sampler, lined with a kevlar bag, was positioned over a mussel bed, and then adjusted over the mussels until reaching the basalt underneath. A drawstring tightened to close the kevlar bag around the mussels. After the bag was closed, the mussel pot was replaced into its quiver on the submersible basket to prevent the loss of sampled animals. Each pot sampled a variable volume over a constant area of 531 cm². Qualitative samples were collected by scooping mussels and associated fauna into individual bio-boxes with closeable lids. Data from the qualitative samples were used with the quantitative samples to build species-effort curves. All other analyses used only the quantitative samples.

Once on deck, mussels and their associated organisms were washed 3 times with filtered seawater (10 µm) over a 250 µm sieve. Retained material was preserved in buffered 10% formalin and stored in 70% ethyl alcohol. Sample volume (±0.1 L), was determined by displacement of plastic-bagged mussels in seawater using a graduated cylinder. Lengths were measured (± 0.1 mm) for all of the mussels > 5 mm. Dry tissue

weights of mussels (± 0.01 g) were obtained from a systematic sub-sample of individuals that represented the range of sizes sampled. Mussel dry weight versus shell length was used as mussel condition index and comparisons were made between mussels of the paired sites. Mussel washings were sorted twice under a dissecting microscope, the second sort was after staining with Rose Bengal to enhance visibility of small organisms. Individuals were separated to morphological species – taxa easily separable by morphological differences that are noticeable to individuals without extensive taxonomic training (Oliver & Beattie 1996), – identified to the lowest taxonomic level possible, and enumerated. Identifications were made using published descriptions, comparisons to voucher specimens in the collections of C.L. Van Dover, and consultation with taxonomic experts. Taxa considered to be meiofauna (copepods, ostracods, mites, and nematodes) were not included in this study. Post-larval and juvenile mussels < 5 mm were included in the community analyses because they do not yet function as structural elements in the system, but they do interact with other mussel-associated invertebrates. Commensal polychaetes (*Branchipolynoe* spp.) that live in the mantle cavities of *Bathymodiolus* spp. mussels were not included in the analyses because they are not considered to be members of the community living among the mussel beds.

Statistical analysis

The habitat structure of *Bathymodiolus* spp. mussel beds within the locations and between paired locations was compared using size-frequency histograms calculated from length measurements of sampled mussels. The Kruskal-Wallis Test was used to detect site/location differences in the median of size-frequency distributions (Minitab v. 13.30).

Mussel condition indices were compared between paired locations using an analysis of co-variance (ANCOVA) of log-transformed mussel shell length and log-transformed tissue-dry weight data that tested the significance differences between regression lines with similar slopes, but different intercepts.

Rank abundance plots were created from the sample-based percent contribution of individuals within species to total abundance. Data from both quantitative and qualitative samples were used to calculate species richness using cumulative species-effort curves. Cumulative species-effort curves were produced for each vent field using EstimatesS (Colwell 1997; randomization operations = 100, without replacement). Effort was shown as the cumulative number of individuals sampled. To compare among sites, effort was standardized to the level of the smallest number of individuals in any one collection (5,000 individuals).

For the rest of the analyses, only quantitative samples were used, except from the 38° S location, where all qualitative samples were also used due to an insufficient number of quantitative samples. One Lau-quantitative sample (Kilo Moana 140-2) and one N. Fiji quantitative sample (Mussel Hill 151-2) were excluded from the analysis due to problems in sample collection. The Shannon diversity index ($H'_{\log e}$; the measure of uncertainty by measuring the rarity and commonness of species in a community), Pielou's evenness index (J' ; the extent to which species are evenly distributed) and Fisher's α (the expected number of individuals represented by a single individual) were calculated for standardized (1-l mussel volume sampled) data using the DIVERSE subroutine in PRIMER v5 (Clarke & Gorley 2001). These univariate diversity indices were calculated with and without the numerically dominant limpet, *Lepetodrilus schrolli*

for the two Western Pacific sites. T-tests (Minitab v. 13.30) were used to compare means of diversity indices among paired locations. Jaccard similarity coefficients were computed ($\frac{\text{\# of species shared between site A \& B}}{\text{\# of species only at site A} + \text{\# of species only at site B} + \text{\# of species shared between site A \& B}}$) to show species similarity between paired sites and reported percent similarity.

Multidimensional scaling (MDS) and cluster analysis techniques were used to compare community structure among mussel beds. Bray-Curtis (BC) similarity was used to show community similarities among the samples. $BC_{sp. abd.}$ is used in the results to indicate where Bray-Curtis similarity was based on species abundances. Bray-Curtis similarity matrices were constructed from square-root transformed standardized (1-1 mussel volume sampled) abundance data from all four vent locations using PRIMER v5 (Clarke & Gorley 2001). Square-root transformation reduces the importance of highly abundant species and allows taxa with mid-range abundances to contribute to the Bray-Curtis similarity between sample pairs (Clarke & Warwick 2001). Data from mid-ocean ridge samples collected for this study from 32° S and 38° S were combined with previously collected data from 17° S EPR (Van Dover 2002) to generate Bray-Curtis similarity coefficients of the mid-ocean ridge sites. Clustering techniques were used to determine the similarity in species composition among the four locations sampled. MDS plots were generated from Bray-Curtis similarity coefficients. Analysis of similarity (ANOSIM; PRIMER v5) was determined from standardized samples to determine significant differences (indicated by the Global R value) between groupings of mussel beds detected in MDS plots. We used Clarke & Gorley's (2001) interpretation of the R statistic for pair-wise groups: $R > 0.75$, groups well separated; $R > 0.5$ groups

overlapping but clearly different; $R < 0.25$ groups barely separable. Contributions of species to the Bray-Curtis (community) dissimilarity between paired sites were calculated using the SIMPER subroutine of PRIMER v5.

Global comparisons of invertebrate fauna from chemosynthetic mussel beds

Comparisons of invertebrate fauna from 12 chemosynthetic mussel beds (5 East Pacific vents, 3 Mid-Atlantic vents, 2 West Pacific vents, 2 cold seeps) were made using species-abundances matrices from: 11° N – EPR (Dreyer et al. 2005), 9° N – EPR (2001, Dreyer et al. 2005; 1999 Van Dover 2003), 17° S – EPR (Van Dover 2002), 32° S – EPR (this paper), 38° S – PAR (this paper), Lucky Strike – MAR (Van Dover & Trask 2000), Snake Pit – MAR (Turnipseed et al. 2004), Logatchev – MAR (Van Dover & Doerries 2005), North Fiji Basin (this paper), Lau Basin (this paper), Florida Escarpment seep site (Turnipseed et al. 2004), and Blake Ridge seep site (Knick 2003). Meiofauna (i.e., nematodes, copepods, ostracocods, mites) were excluded from all data sets. New species-effort curves were generated where necessary using EstimatesS (Colwell 1997; randomization operations = 100, without replacement) where effort was expressed as the cumulative number of individuals sampled. Separate species-effort curves were calculated for each of the collections from 9°N – EPR (1999 & 2001). To compare among sites, effort was standardized to the smallest number of individuals in any one collection (4,500 individuals).

Univariate species diversity indices – species richness, Shannon diversity index ($H'_{\log e}$), Pielou's evenness index (J') – were calculated for each of the 12 sites using the DIVERSE subroutine in PRIMER v5 (Clarke & Gorley 2001). Diversity indices were

calculated separately for both collections from 9°N – EPR in 1999 & 2001. For all locations except Lucky Strike and 38° S – PAR, only quantitative mussel pot samples were used. For Lucky Strike and 38° S – PAR, all samples were used because there were not enough quantitative samples collected.

To determine community similarity among all the chemosynthetic mussel beds, the presence/absence of bivalves, gastropods, and decapods at each of the 12 locations were ascertained using the published species-abundance matrices and data collected in this study. Bivalves, gastropods, and decapods were used because they are the easiest classes of chemosynthetic fauna to identify to the species level; thus the data will be the most reliable. Species lists were combined for the two 9°N – EPR reports (1999 & 2001). For all locations, both quantitative and qualitative mussel pot samples were used. Bray-Curtis similarity coefficients were calculated three times based on the presence/absence of bivalves, gastropods, and decapods, at the species-, genus- and family-level, from each of the 12 locations using PRIMER v5 (Clarke & Gorley 2001). $BC_{+/-}$ is used in the results to indicate where Bray-Curtis similarity was based presence/absence of bivalves, gastropods, and decapods. For comparison purposes, the 12 locations were divided into four regions based on geographic location and type of chemosynthetic location: East Pacific Vents, Atlantic Vents, Back-Arc Basins, and Cold Seeps. Multidimensional scaling (MDS) and cluster analysis techniques based on Bray-Curtis coefficients ($BC_{+/-}$) were used to compare community structure among mussel beds at the species-, genus- and family-level. Differences in faunal assemblages among regions were tested using the ANOSIM randomization test procedure (Clarke & Gorley 2001).

The Bray-Curtis coefficients based on the presence/absence of bivalves, gastropods, and decapods were also used to compare pairs of sites different distances apart on the same ridge axis. Similarity of sites over distance was analyzed for sites in each region mentioned above. This comparison was carried out at the species-, genus- and family-level. Regression lines of the relationships between pair-wise distance and $BC_{+/-}$ were generated for sites along the EPR and MAR to compare the two mid-ocean ridges.

RESULTS

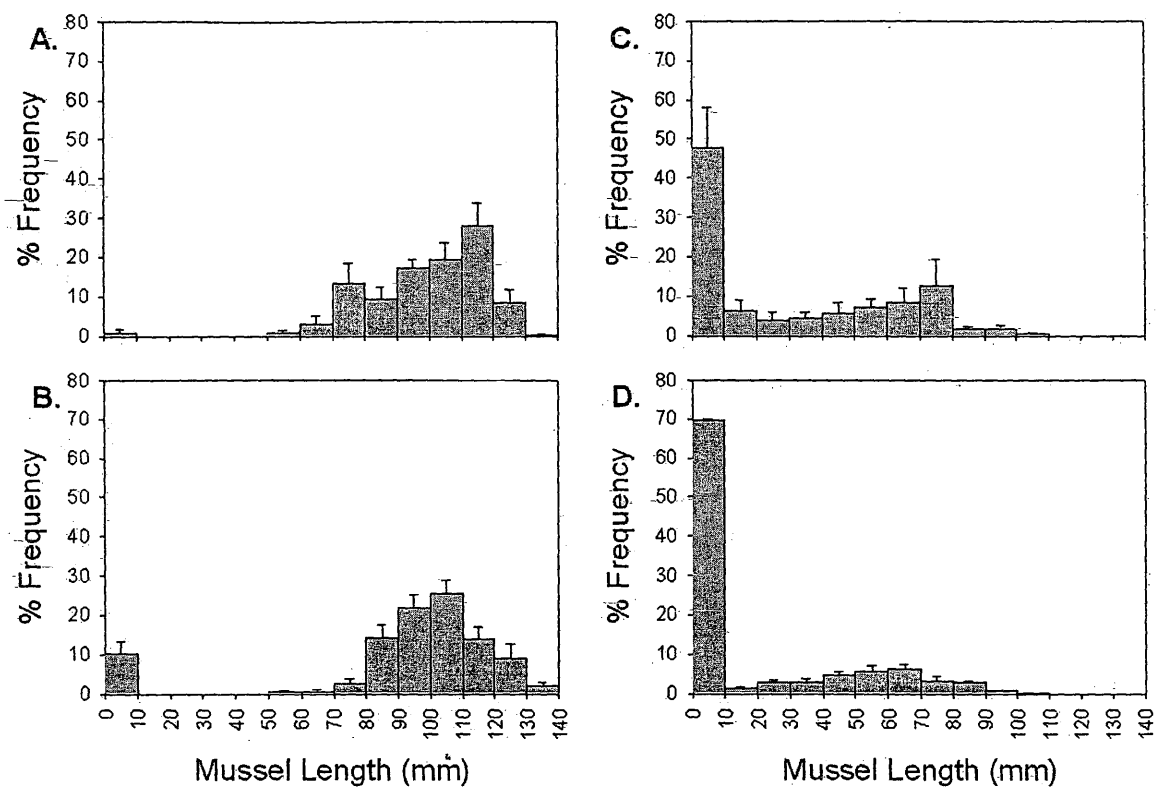
Comparison of mussel populations

Size-frequency distributions of mussels (> 5 mm) were significantly different between Lau Basin and North Fiji Basin mussel beds (Figs. 2A & 2B; Kruskal-Wallis, $p < 0.001$). There was no significant difference between the size-frequency distributions of mussels sampled from 38° S and 32° S (Figs. 2C & 2D; Kruskal-Wallis, $p = 0.079$). Median mussel length (mussels > 5mm) was greater in *Bathymodiolus cf. brevior* from western Pacific sites (99 mm) than in *B. cf. thermophilus* from eastern Pacific sites (50 mm). Median mussel length was greatest (101 mm) in N. Fiji samples and smallest (48 mm) in 38° S samples. Postlarval (< 5 mm) and juvenile mussels (5 to 10 mm) were found at all four mussel-bed locations (Fig. 2). The greatest abundance of postlarval and juvenile mussels was found at 32° S, accounting for 70% of the *B. cf. thermophilus* mussels collected. Postlarval and juvenile mussels accounted for 48% of the mussels collected at 38° S. Recent recruitment of mussels was much lower at the back-arc basin sites, where postlarval and juvenile mussels accounted for only 1% (Lau) and 10% (Fiji) of the total *B. cf. brevior* collected.

There was no difference in mussel condition in *Bathymodiolus cf. brevior* samples from Lau and N. Fiji back-arc basin vents (Fig. 3A; ANCOVA, $p = 0.167$). Mussel condition was better in *B. cf. thermophilus* samples from 32° S compared to those from 38° S (Fig. 3B; Comparison of Slopes test, $p < 0.001$).

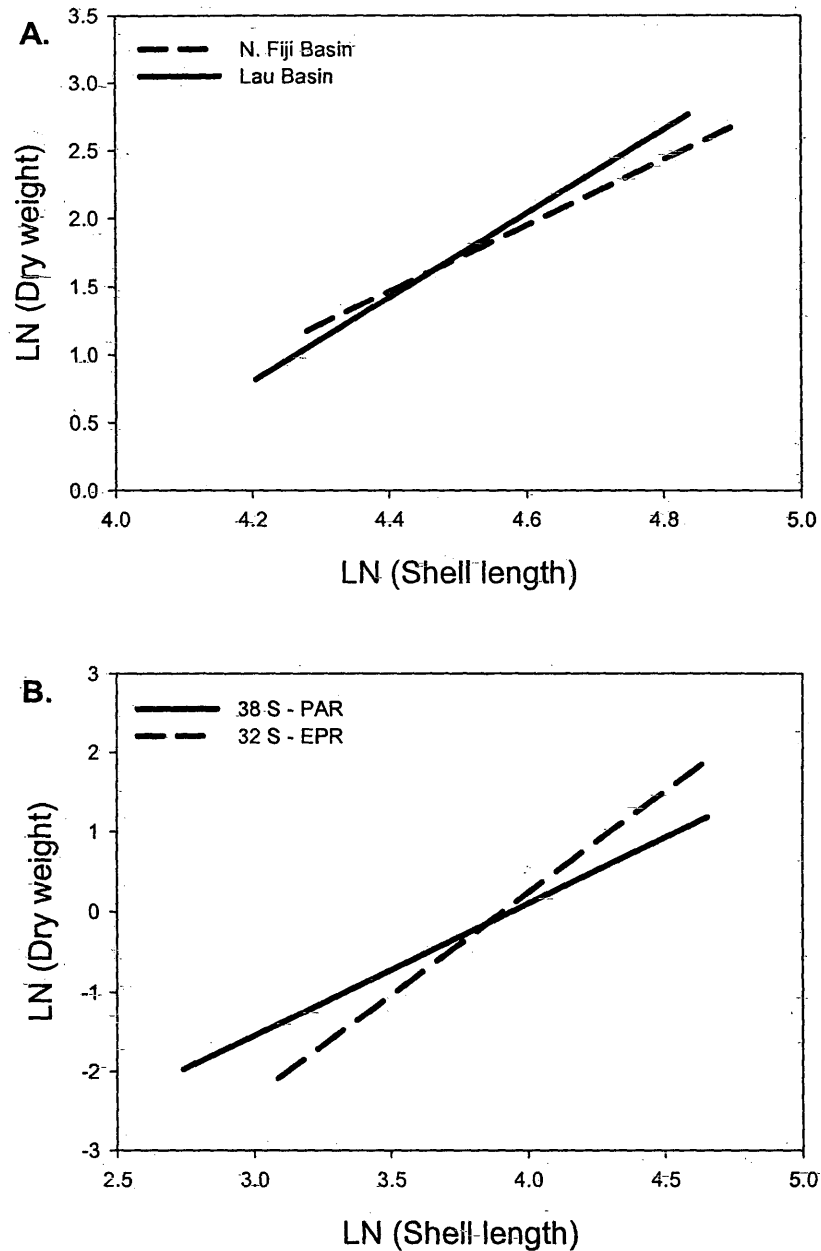
FIGURE 2

MUSSEL SIZE FREQUENCY



Mussel size frequency distributions (mean \pm s.e. for each-size class) for *Bathymodiolus* spp. from hydrothermal vents. **A.** Lau Basin (number of samples = 9; number of individuals = 241). **B.** North Fiji Basin (number of samples = 11; number of individuals = 232). **C.** 38° S PAR (number of samples = 5; number of individuals = 829). **D.** 32° S EPR (number of samples = 6; number of individuals = 1166).

FIGURE 3
MUSSEL CONDITION INDEX



Comparison of condition index in *Bathymodiolus* spp.: ln dry weight (g) vs. ln shell length (mm) showing linear regression for each site. **A.** Back-arc basin vent sites, Lau and North Fiji. **B.** Mid-ocean ridge vent sites, 38° S – PAR and 32° S – EPR.

Community structure in mussel beds

Lau Basin

Thirty-three morphospecies of macrofaunal invertebrates (11 mollusks, 11 polychaetes, 9 crustaceans, 1 anthozoan, 1 pycnogonid) were represented in 4,522 individuals collected from 3 mussel-bed sites (Kilo-Moana, Tow Cam, Tu'i Malila) within Lau Basin (Table 1). The most abundant species at Lau was the limpet *Lepetodrilus schrolli* (76% of the total individuals collected; Table 2). *L. schrolli* was the numerical dominant in all samples except Tu'i Malila 144-1, where the limpet, *Olgasolaris tullmani* was more abundant. Other abundant taxa in Lau mussel bed samples included limpets (*O. tullmani*, Peltospiridae n. gen. n. sp.), polychaetes (*Amphisamytha* cf. *galapagensis*), and a sessile barnacle (sp. 1) (Table 2). The remaining 28 species comprised less than 5% of the total individuals collected. Six species were singletons (i.e., species represented by a single individual in the entire sampling effort). Differences in community structure among Lau mussel-bed sites are evident in the MDS plot based on species-abundance matrices (Fig. 4). Each sampling location in the Lau Basin plots distinctly separate from each other. The average pair-wise similarity ($BC_{sp. abd.}$) between all samples within the Lau Basin was 52%.

North-Fiji Basin

Thirty-four morphospecies of macrofaunal invertebrates (14 mollusks, 11 polychaetes, 9 crustaceans) were represented in 18,004 individuals collected from the Mussel Hill site within N. Fiji Basin (Table 3). As at Lau, the most abundant species was the limpet *Lepetodrilus schrolli* (92% of the total individuals collected; Table 2). Other

TABLE 1 (CONTINUED)

Site	Kilo		Moana		Tow Cam		Tow Cam		Tow Cam		Tul Malia		Tul Malia		Tul Malia		Total Lau
	140	141	142	142	142	142	142	142	144	144	144	144	144	*BB			
Lowering #																	
Pot #	*2	4	1	2	3	4	1	2	1	2	1	2	2				
Species																	
Polychaetes (continued)																	
Hesionid sp. 2	0	1	0	1	0	0	0	0	1	0	0	0	1	0	1	4	
Sponiid sp. 1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	
Sponiid sp. 2	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	
Phylodocid sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Juvenile Polynoids	0	0	3	1	0	0	0	0	0	0	0	1	0	0	0	5	
Crustaceans																	
<i>Choriocaris vandoverae</i>	1	0	3	1	2	5	5	5	5	5	5	5	0	0	0	22	
<i>Nautilocaris staintlaurentiae</i>	0	0	0	0	0	0	0	0	0	0	0	2	6	6	8		
<i>Alvinocaris</i> sp. 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1		
Decapod sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Barnacle sp. 1	0	0	2	0	0	9	1	0	1	0	1	21	34	34	0		
Barnacle sp. 2	0	0	0	0	0	0	0	0	0	0	0	3	3	3	0		
Barnacle sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Amphipod sp. 1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2		
Leptognathid sp. 1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1		
<i>Munidopsis laevis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Munidopsis starmer</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Austlograea alyseae</i>	0	0	0	0	0	0	0	0	3	1	3	1	3	7	7		
Unknown Crustacean sp. 1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2		
Miscellaneous																	
Anemone sp. 1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
Pyrosomid sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
Total # of Individuals	216	456	1141	104	414	274	1285	98	567	4522							
Sample Volume (mL)	1200	2000	2400	2200	2200	2600	3300	1900	8400	26200							
Total # of Species	4	12	14	10	9	9	18	9	14	33							

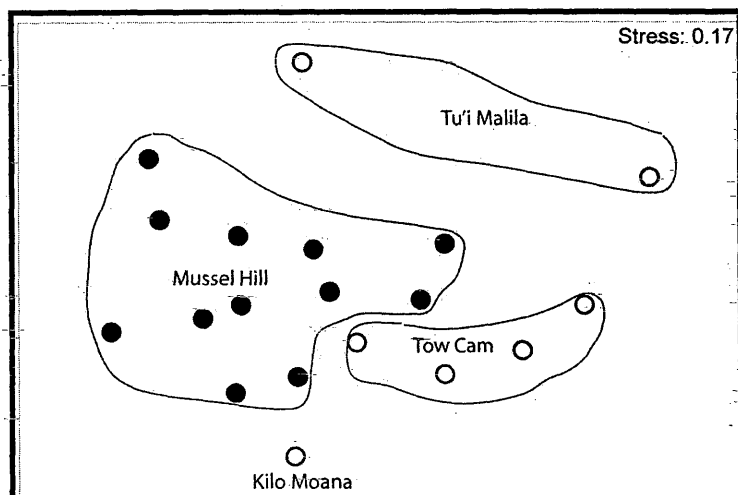
TABLE.2

Top 5 abundance dominants at Lau (from 7 samples) and North Fiji basin (from 12 samples).

Lau Basin		North Fiji Basin	
Species	Abundance (%)	Species	Abundance (%)
<i>Lepetodrilus schrolli</i> (limpet)	75.65	<i>Lepetodrilus schrolli</i> (limpet)	92.47
<i>Olgasolaris tullmani</i> (limpet)	15.96	<i>Symmetromphalus</i> aff. <i>hageni</i> (limpet)	1.44
<i>Amphisamytha</i> cf. <i>galapagensis</i> (polychaete)	1.36	<i>Amphisamytha</i> cf. <i>galapagensis</i> (polychaete)	0.94
Peltospiridae n. gen. n. sp. (limpet)	1.32	Polynoid sp. 1 (polychaete)	0.82
Barnacle sp. 1	0.75	<i>Olgasolaris tullmani</i> (limpet)	0.76
Percent Contribution	95.04		96.43
Total number of individuals collected	4,522		18,032

FIGURE 4

-BACK-ARC BASIN MDS PLOT



Multidimensional scaling (MDS) plots of macrofauna community structure in quantitative samples from mussel bed sites in the Lau and N. Fiji basins. Outlined circles represent samples from the Lau Basin and filled circles represent samples from the N. Fiji Basin.

abundant taxa included limpets (*Olgasolaris tullmani*, *Symmetrophalus* aff. *hageni*), and polychaetes (*Amphisamytha* cf. *galapagensis*, polynoid sp. 1). The remaining 29 species comprised less than 4% of the total individuals collected. Five species were singletons. The average pair-wise similarity ($BC_{sp-abd.}$) between all samples within the N. Fiji Basin was 60%.

32° S – EPR

Thirty-three morphospecies of macrofaunal invertebrates (12 mollusks, 15 polychaetes, 3 crustaceans, 2 anthozoans, 1 ophiuroid) were represented in 18,089 individuals collected from the Saguaro mussel-bed site at 32° S EPR (Table 4). The most abundant species at 32° S was the amphipod, Iphemidiidae sp. 1 (60% of the total individuals collected; Table 5). Other abundant taxa in 32° S mussel-bed samples included polychaetes (*Ophryotrocha akessoni*, *Archinome* cf. *rosacea*), *Bathymodiolus* cf. *thermophilus* juveniles, and an amphipod (*Syrrhoe* sp. 1; Table 5). The remaining 28 species comprised less than 14% of the total number of individuals collected. Only one singleton species was collected from 32° S EPR. The average pair-wise similarity ($BC_{sp-abd.}$) between all samples within the 32° S location was 68%.

38° S – PAR

Thirty-two morphospecies of macrofaunal invertebrates (13 mollusks, 11 polychaetes, 5 crustaceans, 2 anthozoans, 1 ophiuroid) were represented in 10,351 individuals collected from two mussel-bed sites (Annie's Anthill, Pale Etoile) at 38° S (Table 6). The most abundant species at 38° S was the limpet, *Lepetodrilus* aff. *elevatus*,

TABLE 4

32° - EPR species-abundance matrix (not standardized to sample volume) and sample volume data.

Site	Saguaro	Saguaro	Saguaro	Saguaro	Saguaro	Saguaro	Total
Dive #	4092	4092	4093	4093	4093	4093	325
Pot #	3	4	1	2	3	4	
Species							
Mollusks							
<i>Eulepetopsis</i> aff. <i>vitrea</i>	4	23	4	150	7	6	194
<i>Gorgoleptis</i> aff. <i>spiralis</i>	5	19	8	18	10	3	63
<i>Lepetodrilus</i> aff. <i>tevinanus</i>	0	0	93	1	9	41	144
<i>Lepetodrilus</i> aff. <i>ovalis</i>	1	2	20	76	21	18	138
<i>Lepetodrilus</i> aff. <i>galriftensis</i>	5	20	14	92	5	16	152
<i>Lepetodrilus</i> aff. <i>elevatus</i>	5	8	25	7	7	83	135
<i>Clypeosectus</i> aff. <i>delectus</i>	0	0	0	7	0	0	7
<i>Gorgoleptis</i> aff. <i>emarginatus</i>	0	0	0	0	0	0	0
<i>Fachydermia</i> aff. <i>laevis</i>	14	15	8	15	13	25	90
Peltospiridae n. sp.	133	49	7	45	14	354	602
<i>Bathymargarites</i> aff. <i>aymplector</i>	1	4	0	1	0	0	6
<i>Phymorhynchus</i> sp.	0	0	0	0	0	0	0
<i>Provanna</i> aff. <i>ios</i>	0	0	0	0	0	0	0
<i>Eosipho</i> <i>auzendei</i>	1	0	5	2	1	0	9
<i>Bathymodiolus</i> cf. <i>thermophilus</i>	44	224	123	75	168	158	792
Polychaetes							
<i>Amphisamytha</i> cf. <i>galapagensis</i>	10	13	23	27	27	34	134
<i>Archinome</i> cf. <i>rosacea</i>	33	65	71	492	214	84	959
<i>Ophryotrocha</i> <i>akessoni</i>	20	128	421	406	401	833	2209
<i>Hesiospina</i> <i>vestmentifera</i>	4	50	33	92	9	32	220
<i>Orseis</i> sp. 1	2	0	0	13	6	7	28
Spionid sp.3	0	0	4	0	2	2	8
Maldanid sp. 1	0	0	4	0	4	0	8
Phyllodocid.sp. 1	0	0	0	0	0	0	0
Phyllodocid sp. 2	0	3	0	2	0	0	5
Nereidid sp. 1	0	0	0	0	0	1	1
<i>Iphionella</i> <i>risensis</i>	24	40	21	107	41	94	327
<i>Opisthotrochopodus</i> sp. 2	4	2	4	8	8	10	36
Polynoid sp. 2	1	6	3	12	12	4	38
Polynoid sp. 3	0	0	1	0	12	0	13
<i>Tevnia</i> cf. <i>jerichonana</i>	0	0	0	0	1	0	1
<i>Oasisia</i> cf. <i>alvinae</i>	0	0	0	0	3	0	3
Crustaceans							
Iphemiidae sp-1	65	71	5295	106	3220	2103	10860
<i>Syrrohoe</i> sp. 1	82	90	117	319	139	35	782
<i>Eochionelasmus</i> sp. 1	0	0	0	0	0	0	0
<i>Neolepas</i> <i>rapanui</i>	0	0	0	0	0	0	0
Isopod sp. 1	0	0	0	0	0	0	0
<i>Bythograea</i> <i>vrijenhoeki</i>	0	1	1	0	2	0	4
Miscellaneous							
Anemone sp. 2	0	3	5	5	9	2	24
Anemone sp. 3	0	5	1	1	2	2	11
Ophiuroid sp. 1	13	16	20	30	2	5	86
Total # of Individuals	471	857	6331	2109	4369	3952	18089
Sample-Volume (mL)	400	1000	2000	2750	1500	2000	9650
Total # of Species	21	23	26	26	29	24	33

TABLE 5

Top five-abundance dominants at 32° S EPR (from 6 samples) and 38° S PAR (from 5 samples)

32° S		38° S	
Species	Abundance (%)	Species	Abundance (%)
<i>Iphemidiidae</i> sp. 1 (amphipod)	60.04	<i>Lepetodrilus</i> aff. <i>elevatus</i> (limpet)	66.54
<i>Ophryotrocha akessoni</i> (polychaete)	12.21	<i>Ophryotrocha akessoni</i> (polychaete)	6.86
<i>Archinome</i> cf. <i>rosacea</i> (polychaete)	5.30	<i>Gorgoleptis</i> aff. <i>spiralis</i> (limpet)	6.25
<i>Bathymodiolus</i> cf. <i>thermophilus</i> (bivalve)	4.38	<i>Amphisamytha</i> cf. <i>galapagensis</i> (polychaete)	4.59
<i>Syrrhoe</i> sp. 1 (amphipod)	4.32	<i>Bathymodiolus</i> cf. <i>thermophilus</i> (bivalve)	4.08
Percent Contribution	86.25		88.32
Total number of individuals collected	18,089		10,351

TABLE 6

38° S – PAR species-abundance matrix (not standardized to sample volume) and sample volume data.

Site	Annie's Anthill	Pale Etoile	Pale Etoile	Pale Etoile	Annie's Anthill	Total
Dive #	4088	4090	4090	4090	4090	38S
Pot #	2	A	B	C	E	
Species	<hr/>					
Mollusks						
<i>Eulepetopsis</i> aff. <i>vitrea</i>	2	4	3	1	0	10
<i>Gorgoleptis</i> aff. <i>spiralis</i>	1	240	327	76	3	647
<i>Lepetodrilus</i> aff. <i>tevinanus</i>	3	0	0	22	128	153
<i>Lepetodrilus</i> aff. <i>ovalis</i>	1	15	50	11	0	77
<i>Lepetodrilus</i> aff. <i>galriflensis</i>	0	36	49	37	0	122
<i>Lepetodrilus</i> aff. <i>elevatus</i>	300	912	2422	2324	930	6888
<i>Clypeosectus</i> aff. <i>delectus</i>	0	13	13	12	0	38
<i>Gorgoleptis</i> aff. <i>emarginatus</i>	0	0	0	0	4	4
<i>Pachydermia</i> aff. <i>laevis</i>	0	0	3	0	1	4
Peltospiridae n. sp.	3	94	76	84	16	273
<i>Bathymargarites</i> aff. <i>aymplector</i>	0	0	0	0	0	0
<i>Phymorhynchus</i> sp. 1	0	1	0	1	0	2
<i>Provanna</i> aff. <i>ios</i>	0	3	0	2	0	5
<i>Eosipho auzendei</i>	0	0	0	0	0	0
<i>Bathymodiolus</i> cf. <i>thermophilus</i>	6	125	172	117	2	422
Polychaetes						
<i>Amphisamytha</i> cf. <i>galapagensis</i>	0	33	50	87	305	475
<i>Archinome</i> cf. <i>rosacea</i>	0	0	9	0	0	9
<i>Ophryotrocha</i> <i>akessoni</i>	30	34	36	163	447	710
<i>Hesiospina vestimentifera</i>	3	19	33	84	4	143
<i>Orseis</i> sp. 1	0	0	0	0	0	0
Spionid sp. 3	0	2	0	2	0	4
Maldanid sp. 1	0	0	5	2	0	7
Phyllodocid sp. 1	0	0	10	5	3	18
Phyllodocid sp. 2	0	3	10	9	0	22
Nereidid sp. 1	0	0	0	0	0	0
<i>Iphionella risensis</i>	0	6	2	15	2	25
<i>Opishotrochopodus</i> sp. 2	0	6	14	14	4	38
Polynoid sp. 2	3	13	12	3	0	31
Polynoid sp. 3	0	0	0	0	0	0
<i>Tevnia</i> cf. <i>jerichonana</i>	0	0	0	0	0	0
<i>Oasisia</i> cf. <i>alvinae</i>	0	0	0	0	0	0
Crustaceans						
Amphipod sp. 2	25	2	13	4	33	77
Amphipod sp. 3	0	0	0	0	0	0
<i>Eochionelasmus</i> sp. 1	0	30	1	0	49	80
<i>Neolepas rapanui</i>	0	12	11	14	0	37
Isopod sp. 1	1	1	20	0	0	22
<i>Bythograea vrijenhoeki</i>	0	0	0	0	1	1
Miscellaneous						
Unidentified Anemone sp. 2	0	0	0	0	1	1
Unidentified Anemone sp. 3	0	0	1	0	0	1
Unidentified Ophiroid sp. 1	4	0	1	0	0	5
Total # of Individuals	382	1604	3343	3089	1933	10351
Sample Volume (mL)	600	2100	3500	3200	1600	11000
Total # of Species	13	22	26	23	17	32

(67% of the total individuals collected; Table 5). Other abundant taxa at 38° S included polychaetes (*Ophryotrocha akessoni*, *Amphisamytha* cf. *galapagensis*), a limpet (*Gorgoleptis* aff. *spiralis*), and *Bathymodiolus* cf. *thermophilus* juveniles. The remaining 27 species comprised less than 12% of the total individuals collected. Three singleton species were collected. The average pair-wise similarity ($BC_{sp. abd.}$) between samples within the 38° S location was 64%.

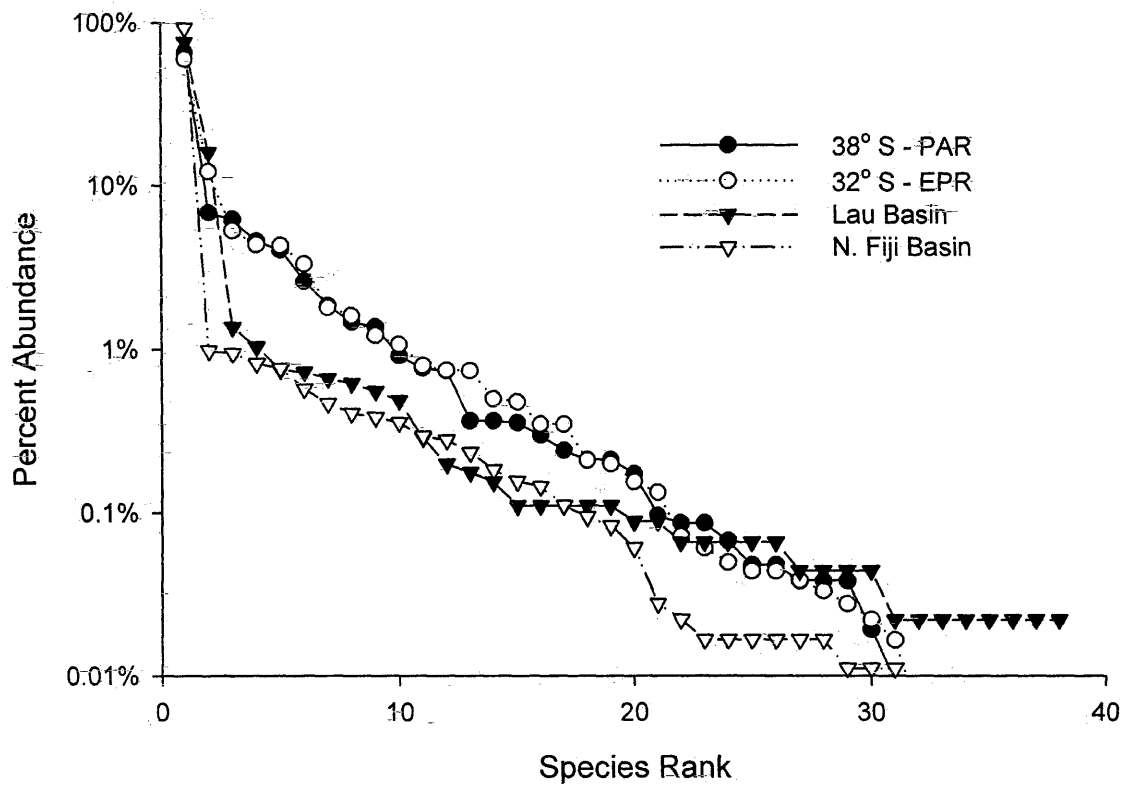
Comparison of community structure (species-abundance matrices) at Lau and Fiji back-arc basin mussel beds

Macrofaunal invertebrate abundance was significantly greater in N. Fiji mussel-bed samples (mean \pm s.e. = 768 ± 134 individuals/L) than in mussel-bed samples from Lau Basin (mean \pm s.e. = 212 ± 63 individuals/L; t-test, $p = 0.002$). Lau and N. Fiji mussel-bed samples shared 26 species (67% of species shared, Jaccard similarity coefficient), including 10 mollusks, 11 polychaetes, and 5 crustaceans. None of the singleton species was shared between basins (Tables 1, 3). The most abundant species was shared between basins (Tables 1, 3). The most abundant species was *Lepetodrilus schrolli* (Lau: 76%, Fiji 93%); *Olgasolaris tullmani* was the 2nd-ranked dominant species at Lau (16%; Table 2). All other species contributed <2% to the total abundance (Fig. 5). Nearly all of the individuals collected from both basins were mollusks (94%, Lau; 95%, N. Fiji; Fig. 6); polychaetes were the next most abundant group (4%, Lau and N. Fiji; Fig. 6).

Species richness of macrofaunal invertebrates for a given sampling effort was greater in Lau mussel-beds ($S_{4,500} = 37$; Fig. 7) than in N. Fiji mussel beds ($S_{4,500} = 24$; Fig. 7): The species-effort curve for Lau Basin is not asymptotic, while the curve for N.

FIGURE 5

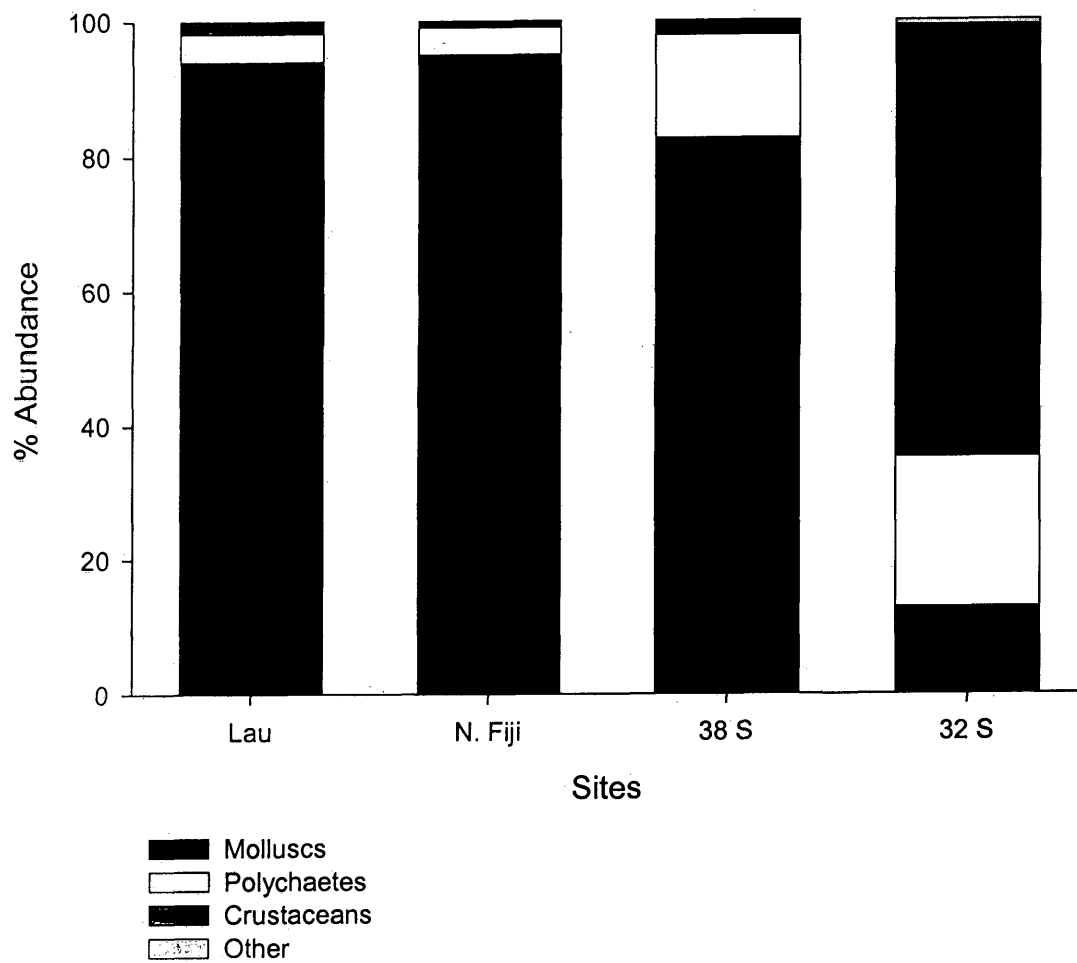
RANK-ABUNDANCE PLOT



Rank-abundance plot of hydrothermal vent mussel-bed communities in the eastern and western Pacific. Symbol indicates the percent abundance of a morphospecies for each location.

FIGURE 6

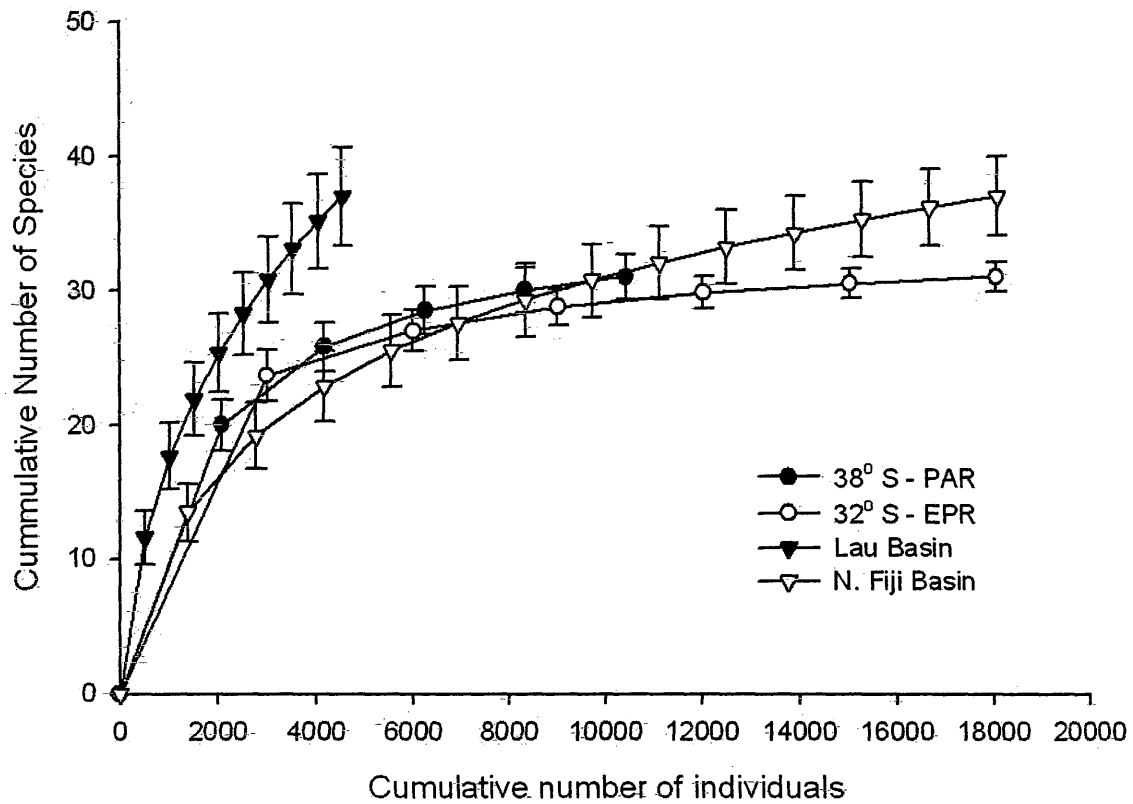
TAXON ABUNDANCE



Percent abundance of taxa that comprise the macrofauna in hydrothermal vent mussel beds from each location.

FIGURE 7

SPECIES-EFFORT CURVE



Comparison of species-effort curves for back-arc basin and mid-ocean ridge sites. Effort based on cumulative number of individuals. Points are means \pm s.d.

Fiji mussel beds approaches an asymptote; this provides further evidence that species richness is greater in Lau mussel beds.

Shannon-Wiener species diversity ($H'_{\log e}$) was not significantly different between the N. Fiji and Lau Basin samples when the numerically dominant *Lepetodrilus schrolli* was included (t-test, $p = 0.916$; Table 7). When *L. schrolli* was excluded from the calculations, species diversity was significantly greater in N. Fiji samples (t-test, $p = 0.043$). Fisher's α , another measure of species diversity, was not significantly different between basins, with or without *L. schrolli* (t-test; with *L. schrolli*: $p = 0.434$; without *L. schrolli*: $p = 0.492$; Table 7). Evenness (J') was not significantly different in the mussel-bed macrofaunal communities of the two back-arc basins, with or without *L. schrolli* (t-test, with *L. schrolli*: $p = 0.855$, without *L. schrolli*: $p = 0.807$; Table 7).

Community structure in Tow Cam (Lau) and Mussel Hill (N. Fiji) mussel beds was not distinguishable based on multivariate analysis of their species-abundance matrices (ANOSIM, global $R = 0.446$, $p = 0.008$; Figs. 4, 8). The low global R value indicates that the two communities are overlapping (Clarke & Warwick 2001). The average pair-wise similarity ($BC_{sp. abd.}$) of samples between Tow Cam and Mussel Hill sites was 49%. Kilo Moana and Tu'i Malila samples did not group with Tow Cam samples (Figs. 4, 8). Average pair-wise similarity ($BC_{sp. abd.}$) of samples was higher within basins (Lau: 52%; N. Fiji: 60%) than average pair-wise similarity of samples between basins (46%). When all 3 Lau mussel-bed sites were included in the multivariate analysis, community structure in Lau mussel beds was different from that of N. Fiji (ANOSIM; global $R = 0.412$, $p = 0.002$; average dissimilarity ($BC_{sp. abd.}$) = 54%, SIMPER analysis). Much of this difference (43%) was due to the greater abundance of

TABLE 7

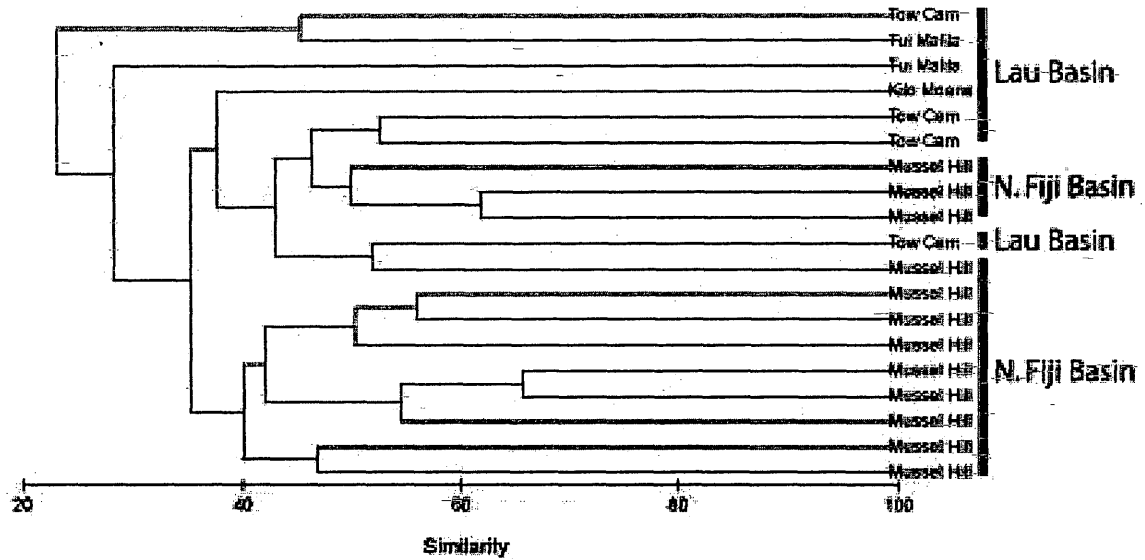
WESTERN-PACIFIC SPECIES DIVERSITY

Location	N	n	S	H' (log e)	J'	Fisher's α
Lau Basin						
w/ <i>Lepetodrilus schrolli</i>	7	3739	33	0.52 (0.13)	0.22 (0.05)	1.93 (0.28)
w/o <i>Lepetodrilus schrolli</i>	7	1012	32	1.49 (0.18)*	0.77 (0.08)	4.64 (0.41)
N. Fiji Basin						
w/ <i>Lepetodrilus schrolli</i>	12	18004	34	0.53 (0.10)	0.21 (0.04)	2.21 (0.18)
w/o <i>Lepetodrilus schrolli</i>	12	1297	33	1.94 (0.08)*	0.79 (0.03)	4.24 (0.39)

Number of samples (N), number of individuals (n), Species richness (S) and univariate diversity indices (with and without *Lepetodrilus schrolli*) for Lau and N. Fiji basin mussel-bed macrofauna. Diversity values are shown as mean (s.e.). * indicates a significant difference at $\alpha = 0.05$ between Lau and N. Fiji Basin.

FIGURE 8

BACK-ARC BASIN CLUSTER PLOT



Cluster plot using Bray-Curtis similarity coefficients based on species-abundance matrices of the mussel-bed communities associated with Lau and North Fiji basin hydrothermal vents.

Lepetodrilus schrolli and lower abundance of *Olgasolaris tullmani* in N. Fiji samples (Table 8).

Comparison of community structure (species-abundance matrices) at mid-ocean ridge sites

There was a marginally non-significant difference in macrofaunal invertebrate abundance between 32° S EPR (mean \pm s.e. = 1,809 \pm 427 individuals/L) and 38° S PAR (mean \pm s.e. = 906 \pm 97 individuals/L; t-test, $p = 0.094$). 32° S EPR and 38° S PAR mussel-bed samples shared 25 species (62.5% of total species), including 10 mollusks, 10 polychaetes, 2 crustaceans, 2 anemones and an ophiuroid. None of the singleton species were shared between 32° S and 38° S (Tables 4, 6). At both locations, the most abundant species comprised $\sim 60\%$ of individuals collected. At 32° S, amphipods were numerically dominant and at 38° S limpets dominated. *Ophryotrocha akessoni* was the 2nd-ranked dominant species in both locations. All other species contributed $<6\%$ to the total abundance (Fig. 5). Most of the individuals collected from 38° S were mollusks (84%), but at 32° S mollusks comprised only 13% of the macrofauna. Most of the individuals collected from 32° S were crustaceans (64%; Fig. 6).

Species richness of macrofaunal invertebrates for a given sampling effort was about the same in 32° S mussel beds ($S_{4,500} = 26$; Fig. 7) and in 38° S mussel beds ($S_{4,500} = 25$; Fig. 7). The species-effort curves for both locations closely approach their asymptote, suggesting that an adequate number of samples were collected and increased sampling effort would add only a few additional rare species (Fig. 7).

Species diversity ($H'_{\log e}$) was not significantly different between 32° S sites and 38° S sites (t-test, $p = 0.157$; Table 9). Evenness (J') was also not significantly different

TABLE 8

BACK-ARC BASIN SPECIES CONTRIBUTION TO DISSIMILARITY

Species	Average Abundance		Contribution to dissimilarity	
	Lau	North Fiji	% Contribution	% Cumulative
<i>Lepetodrilus schrolli</i>	162.88	699.35	36.41	36.41
<i>Olgasolaris tullmani</i>	31.75	8.05	7.01	43.42
<i>Symmetromphalus</i> aff. <i>regularis</i>	0.00	9.36	5.06	48.48
Polynoid sp. 1	1.10	2.64	4.93	53.40
<i>Amphisamytha</i> cf. <i>galapagensis</i>	3.51	7.63	4.00	57.40

TABLE 9

EASTERN PACIFIC SPECIES DIVERSITY

Location	N	n	S	H' (log e)	J'	Fisher's α
38° S PAR	5	10,351	32	1.25 (0.12)	0.43 (0.04)	3.06 (0.20)*
32° S EPR	6	18,089	33	1.75 (0.28)	0.56 (0.09)	3.81 (0.18)*

Number of samples (N), number of individuals (n), species richness (S) and univariate diversity indices for 38° S PAR and 32° S EPR mussel-bed macrofauna. Diversity values are shown as mean (s.e). * indicates a significant difference at $\alpha = 0.05$ between 38° S and 32° S.

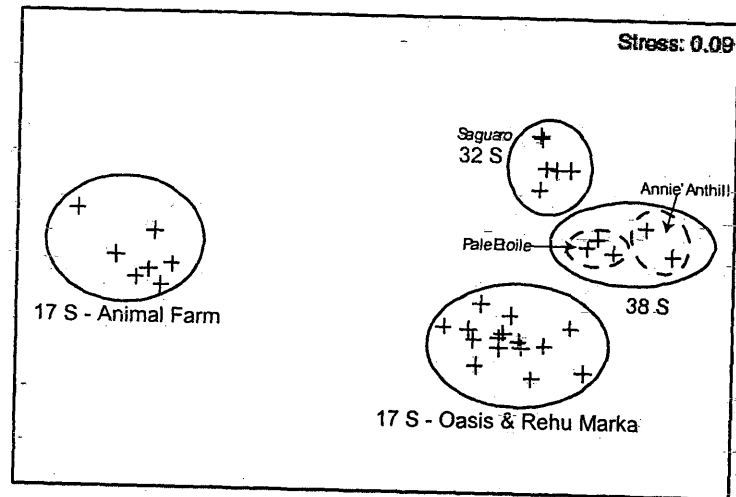
between 32° S and 38° S (t-test, $p = 0.240$; Table 9). Fisher's α was significantly greater at 32° S sites compared to 38° S sites (t-test, $p = 0.021$; Table 9).

Based on multivariate analysis of their species-abundance matrices, community structure at Annie's Anthill and Pale Etoile (38° S) were not distinguishable (ANOSIM, global $R = 0.75$, $p = 0.10$; Fig. 9, 10), but sample sizes were small (Pale Etoile, $n = 3$; Annie's Anthill, $n = 2$). The average pair-wise similarity ($BC_{sp. abd.}$) between samples from Annie's Anthill and Pale Etoile was 67%, which is greater than the pair-wise similarity ($BC_{sp. abd.}$) within the Annie's Anthill samples (58%). Samples from the two 38° S sites grouped together and were distinct from samples collected at the 32° S Saguaro mussel bed (ANOSIM, global $R = 1.00$, $p = 0.002$; Fig. 9, 10). Much of the difference (49%) between 32° S and 38° S samples is accounted for by the greater abundances at 32° S of two amphipod species and the polychaete *Archinome cf. rosacea* and the lower abundances of *Lepetodrilus aff. elevatus* in samples from 32° S (Table 10). Average pair-wise similarities ($BC_{sp. abd.}$) within 32° S (68%) and 38° S (64%) samples were higher than the average pair-wise similarity ($BC_{sp. abd.}$) in between 32° S and 38° S samples (39%).

Data from the 32° S and 38° S sites were also compared with mussel-bed data previously collected from three hydrothermal-vent mussel beds at 17° S on the EPR [Oasis, Rehu Marka, Animal Farm; Van Dover (2002)]. The 32° S and 38° S samples grouped most closely with the Oasis and Rehu Marka samples ($BC_{sp. abd.} = 42\%$; Fig. 9, 10). Animal Farm samples were distinct from all others ($BC_{sp. abd.} = 15\%$), consistent with the waning hydrothermal activity at Animal Farm and the colonization of the Animal Farm mussel beds by non-vent species.

FIGURE 9

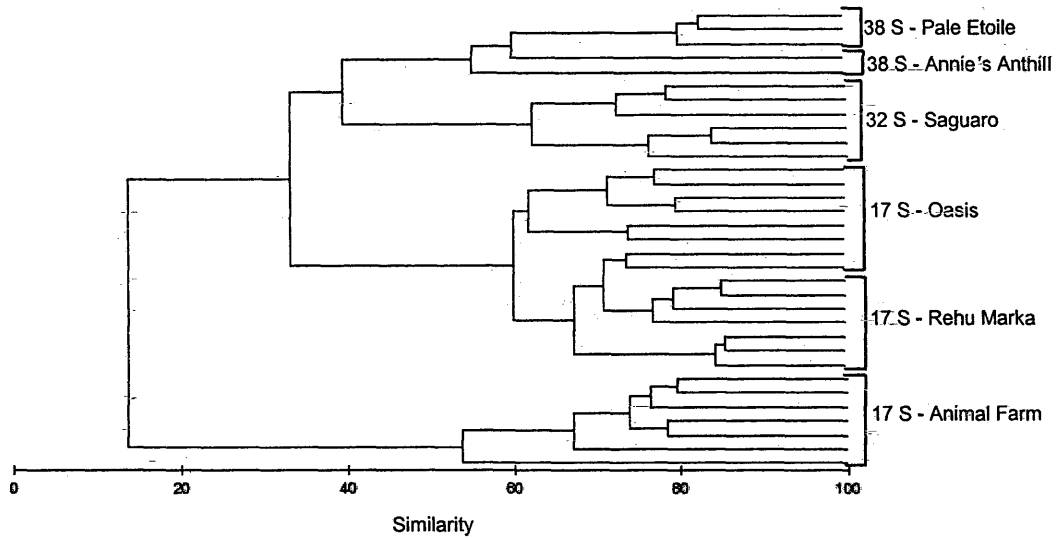
MID-OCEAN RIDGE MDS PLOT



Multidimensional scaling (MDS) plots of macrofauna community structure in samples from mussel-bed sites on the southern East Pacific Rise (17° S and 32° S) and Pacific Antarctic Ridge (38° S).

FIGURE 10

MID-OCEAN RIDGE CLUSTER PLOT



Cluster plot using Bray-Curtis similarity coefficients of the mussel-bed communities associated with mussel bed sites on the southern East Pacific Rise and Pacific Antarctic Ridge.

TABLE 10

MID-OCEAN RIDGE SPECIES CONTRIBUTION TO DISSIMILARITY

Species	Average Abundance		Contribution to dissimilarity	
	32° S EPR	38° S PAR	% Contribution	% Cumulative
<i>Iphemidiidae</i> sp. 1	1019.62	13.64	17.80	17.80
<i>Lepetodrilus</i> aff. <i>elevatus</i>	13.62	586.76	16.74	34.54
<i>Syrrhoë</i> sp. 1	96.61	0.00	7.60	42.14
<i>Archinome</i> cf. <i>rosacea</i>	91.10	0.51	7.18	49.32
<i>Ophryotrocha</i> <i>akessoni</i>	203.33	81.36	5.94	55.27
<i>Peltospiridae</i> n. sp.	97.95	21.55	4.16	59.42
<i>Bathymodiolus</i> cf. <i>thermophilus</i>	102.30	31.30	4.06	63.48

Contrasts in community structure at back-arc basin and mid-ocean ridge sites

Only two morphospecies (2.5% of the total species sampled) were shared between the back-arc basin and mid-ocean ridge samples: *Amphisamytha* cf. *galapagensis* and *Archinome* cf. *rosacea*. It is likely that each of these morphospecies will prove to be genetically distinct sister taxa. Back-arc basin mussel beds supported significantly lower abundances of invertebrates (mean \pm s.e. = 563 ± 446 individuals/L) than mussel beds on the mid-ocean ridge sites (mean \pm s.e. = $1,399 \pm 888$ individuals/L; t-test, $p = 0.012$). Back-arc basin sites were dominated by fewer species (~ 2) than mid-ocean ridge sites (~ 5 ; Tables 2, 5; Fig. 5) and there were more singleton species collected from back-arc basin mussel beds (Tables 1, 3) than from the mid-ocean ridge mussel beds (Tables 4, 6; Fig. 5).

Lau basin supported more species than the other three locations. There was no difference in species richness among the other three locations (Fig. 7). Species diversity ($H'_{\log e}$ and Fisher's α) in mussel beds was significantly lower at the back-arc basin sites than at the mid-ocean ridge sites when the numerically dominant limpet from back-arc basin sites, *Lepetodrilus schrolli*, was included (t-test, $H' p < 0.001$, Fisher's $\alpha p < 0.001$). When *L. schrolli* was excluded, there was no significant difference in H' species diversity between back-arc basin and mid-ocean ridge sites (t-test, $p = 0.205$), but Fisher's α was greater at the back-arc basin sites (t-test, $p = 0.039$). Species evenness (J') was significantly greater at the mid-ocean ridge sites when *L. schrolli* was included (t-test, $p = 0.001$), but when it was excluded from the calculations, back-arc basin sites have greater species evenness (t-test, $p = 0.001$).

Global comparisons of macrofaunal diversity in deep-sea chemosynthetic mussel beds

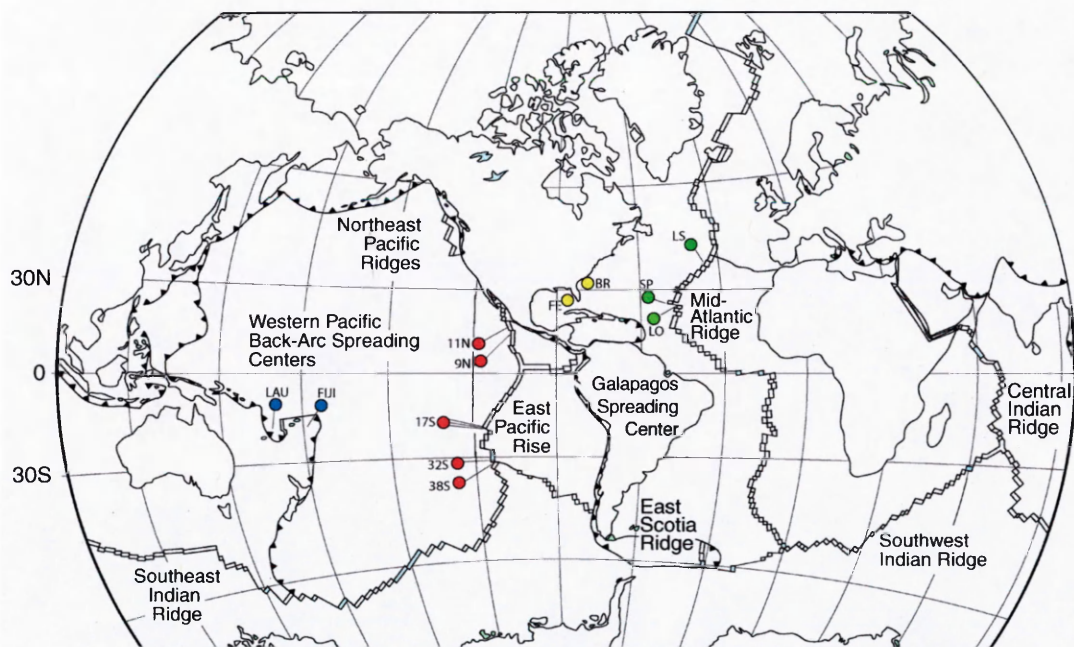
Macrofaunal communities of chemosynthetic mussel beds have been investigated at 10 hydrothermal vent locations and 2 cold seep locations (Fig. 11). When standardized to 4,500 individuals collected, 17° S –EPR had the highest species richness ($S_{4,500} = 43$) of all locations (Fig. 12). Lucky Strike – MAR had the lowest species richness ($S_{4,500} = 15$). Both cold seep locations – Blake Ridge and Florida Escarpment – had a high species richness compared to most hydrothermal vent sites ($S_{4,500} = 40$; Fig. 12). Diversity ($H'_{\log e}$) and evenness (J') were significantly greater at cold seep locations compared to hydrothermal vent locations ($H'_{\log e}$ $p < 0.001$, J' $p < 0.001$). Diversity ($H'_{\log e}$) was highest at Florida Escarpment cold seep (2.05) and at 17° S –EPR vent sites (1.91; Table 11; Fig. 13). Diversity ($H'_{\log e}$) was lowest at the back-arc basin locations (Lau: 0.52, N. Fiji: 0.53) and the Logatchev (0.88) and Lucky Strike (0.74) sites on the MAR (Table 11; Fig. 13), mainly due to the dominance by a single species (but not the same species) at each location. Evenness (J') was highest at the Snake Pit site on the MAR (0.71) and Florida Escarpment (0.68; Table 11; Fig. 13). One of the most diverse sites ($H'_{\log e}$), 17° S – EPR, also had high species evenness (Table 11; Fig. 13). The lowest evenness was reported from the back-arc basin sites (Lau: 0.22, N. Fiji: 0.21; Table 11; Fig. 13).

Biogeographic comparisons of deep-sea chemosynthetic mussel-bed communities

Taxonomic composition at the species, genus, and family level differed significantly (bivalves, gastropod, decapods only) among 12 globally distributed mussel-bed communities. The greatest differences were at the genus (ANOSIM, global $R = 0.997$, $p = 0.001$) and family level (ANISOM, global $R = 0.923$, $p = 0.001$). At the

FIGURE 11

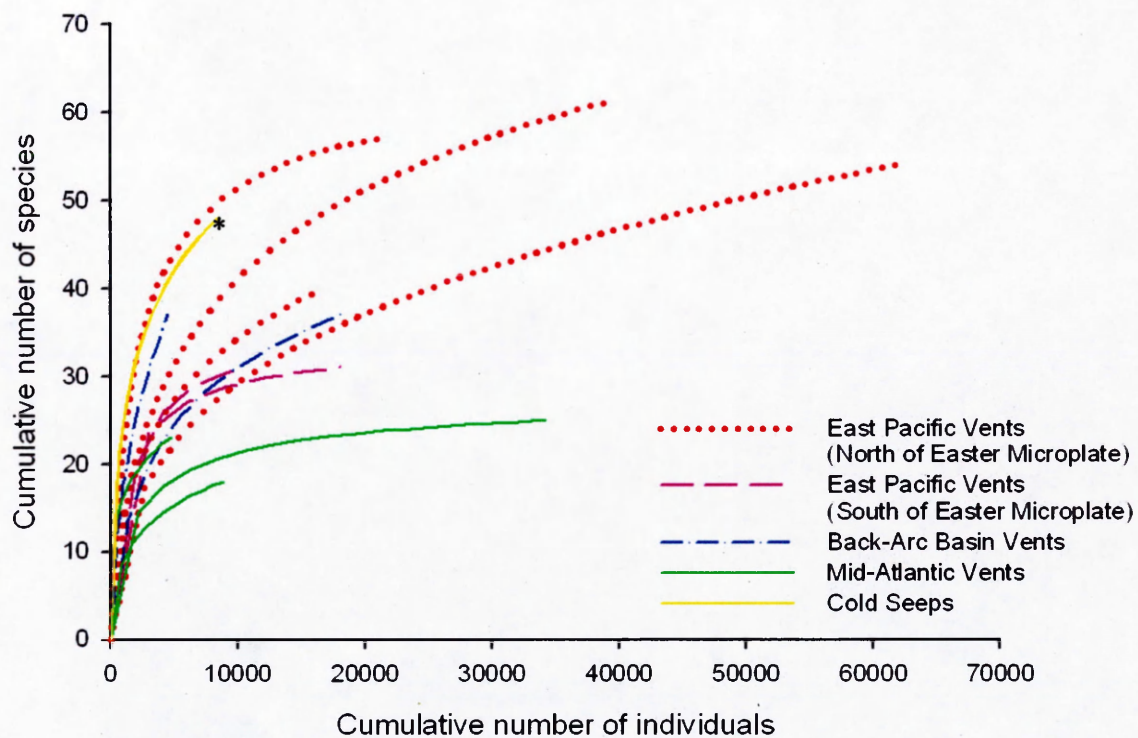
MAP OF DEEP-SEA CHEMOSYNTHETIC MUSSEL-BED MACROFAUNA SITES



Map showing the locations of the 10 hydrothermal vent and 2 cold seep mussel-bed locations. East Pacific sites are shown in red, back-arc basin sites are shown in blue, Mid-Atlantic sites are shown in green and cold seep sites are shown in yellow. BR = Blake Ridge, FE = Florida Escarpment, LO = Logatchev, LS = Lucky Strike, SP = Snake Pit.

FIGURE 12

SPECIES-EFFORT CURVE FOR ALL CHEMOSYNTHETIC MUSSEL-BEDS



Sample-based cumulative species effort curves for chemosynthetic mussel bed sites (10 hydrothermal vents and 2 cold seeps). * = x 2; the two cold seep sites plot on top of each other.

TABLE 11

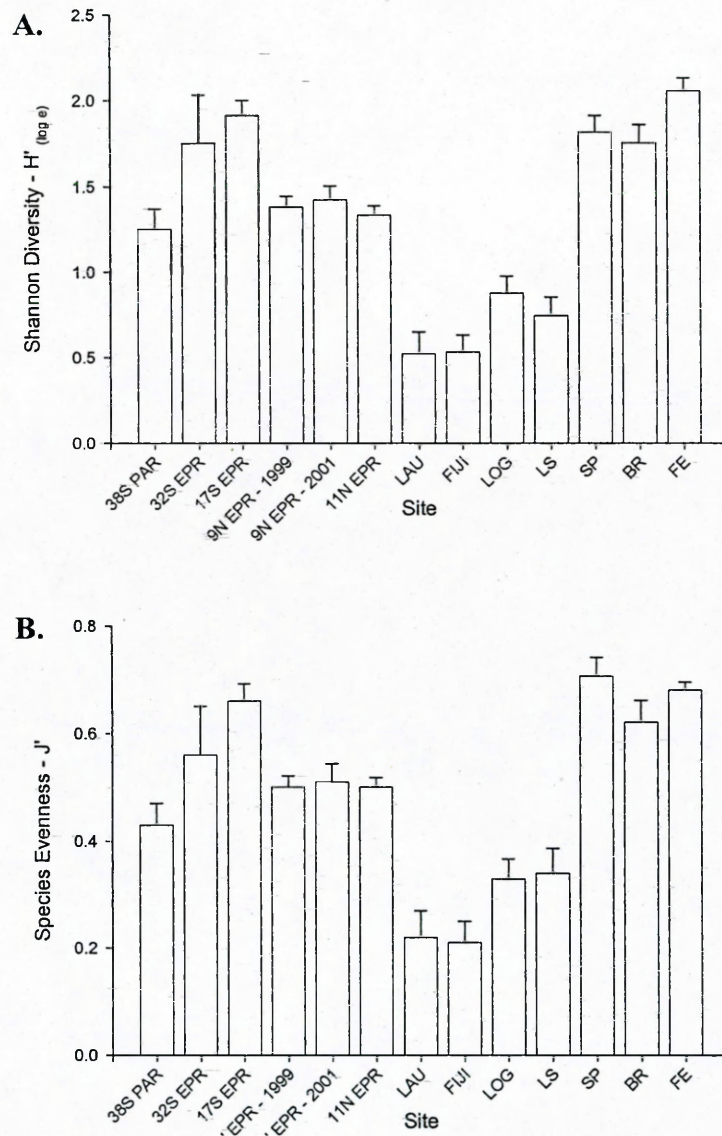
MUSSEL BED SPECIES DIVERSITY

Location	N	n	S	S _{4,500}	H' _(log e)	J'
Hydrothermal Vents						
<i>East Pacific</i>						
38° S – PAR	5	10,351	32	26	1.25 (0.12)	0.43 (0.04)
32° S – EPR	6	18,089	33	25	1.75 (0.28)	0.56 (0.09)
17° S – EPR	15	11,737	54	43	1.91 (0.09)	0.66 (0.03)
9° N - EPR – 1999	17	36,570	50	30	1.38 (0.06)	0.50 (0.02)
9° N - EPR – 2001	22	28,153	54	20	1.42 (0.08)	0.51 (0.03)
11° N – EPR	12	12,519	40	26	1.33 (0.06)	0.50 (0.02)
<i>West Pacific</i>						
Lau Basin	8	3,739	33	37	0.52 (0.13)	0.22 (0.05)
N. Fiji Basin	12	18,004	32	24	0.53 (0.10)	0.21 (0.04)
<i>Atlantic</i>						
Logatchev	16	34,243	25	18	0.88 (0.10)	0.33 (0.04)
Lucky Strike	10	8,902	18	15	0.74 (0.11)	0.34 (0.05)
Snake Pit	11	4,757	23	23	1.81 (0.10)	0.71 (0.04)
Cold Seeps						
Blake Ridge	10	4,747	44	40	1.75 (0.11)	0.62 (0.04)
Florida Escarpment	12	7,466	43	40	2.05 (0.08)	0.68 (0.02)

Number of samples (N), numbers of individuals (n), species richness of all individuals at site (S), species richness at 4,500 individuals (S_{4,500}), Shannon diversity (H'_{log e}), and species evenness (J') for macrofaunal communities at deep-sea chemosynthetic mussel beds. Diversity values are shown as mean (s.e.).

FIGURE 13

MUSSEL BED SPECIES DIVERSITY AND EVENNESS



Comparison of species diversity and evenness among chemosynthetic mussel-bed communities. **A.** Shannon diversity ($H'_{\log e}$). **B.** Species evenness (J'). BR = Blake Ridge, FE = Florida Escarpment, LOG = Logatchev, LS = Lucky Strike, SP = Snake Pit.

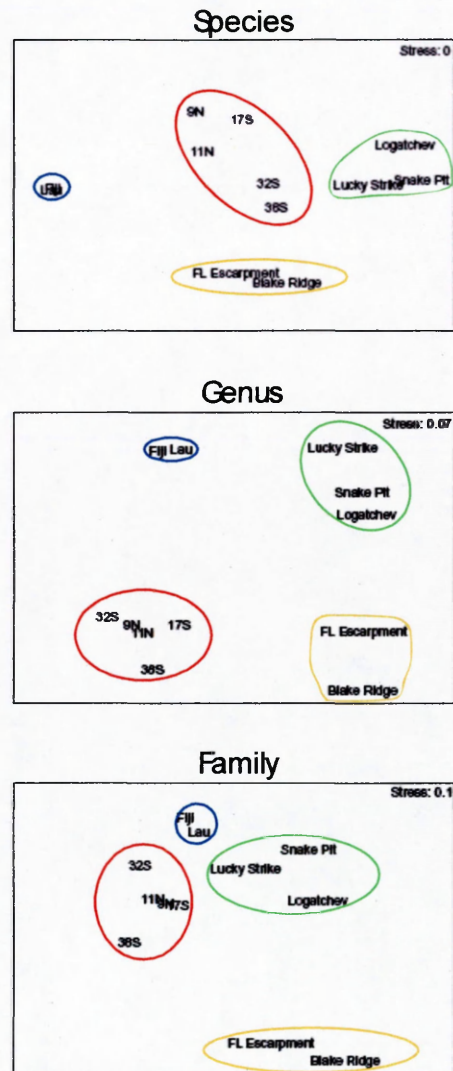
species level, each region was discernable, but to lesser degree (ANISOM, global $R = 0.667$, $p = 0.001$). The bivalve, gastropod, and decapod faunas of the 12 sites cluster into 4 groups corresponding to geographic regions: namely eastern Pacific mid-ocean ridge vents, western Pacific back-arc basin vents, Mid-Atlantic Ridge vents, and western Atlantic and Gulf of Mexico cold seeps (Fig. 14, 15). There were no shared bivalve, gastropod, or decapod species among these 4 regions. The distinction between regions was most evident at the genus level, where the relative differences among the groups are greatest (Fig. 14).

Within the eastern Pacific region, there was only a 5% species similarity ($BC_{+/-}$ of bivalves, gastropods, and decapods) between locations north (9° N, 11° N, and 17° S) and south (32° S and 38° S) of the Easter microplate (Fig. 15). The two cold seep locations also had a relatively low species similarity ($BC_{+/-} = \sim 20\%$). Highest Bray-Curtis species similarities ($\sim 80\%$) were between N. Fiji and Lau Basins, and between 32° S – EPR and 38° S – PAR.

At the genus level, all 12 locations were at least 20% similar ($BC_{+/-}$ of bivalves, gastropods, and decapods; Fig. 15), and there was a slightly greater alliance between vent and seep locations in the Atlantic and Gulf of Mexico than between Atlantic/GoM and eastern and western Pacific vents (Fig. 15). Within the eastern Pacific region, there was $\sim 60\%$ generic similarity ($BC_{+/-}$) between locations north and south of the Easter microplate (Fig. 15). The cold seeps locations have the lowest generic similarity ($BC_{+/-}$) of locations within the same region (43%). N. Fiji and Lau had the greatest generic similarity ($BC_{+/-}$) between locations (87%).

FIGURE 14

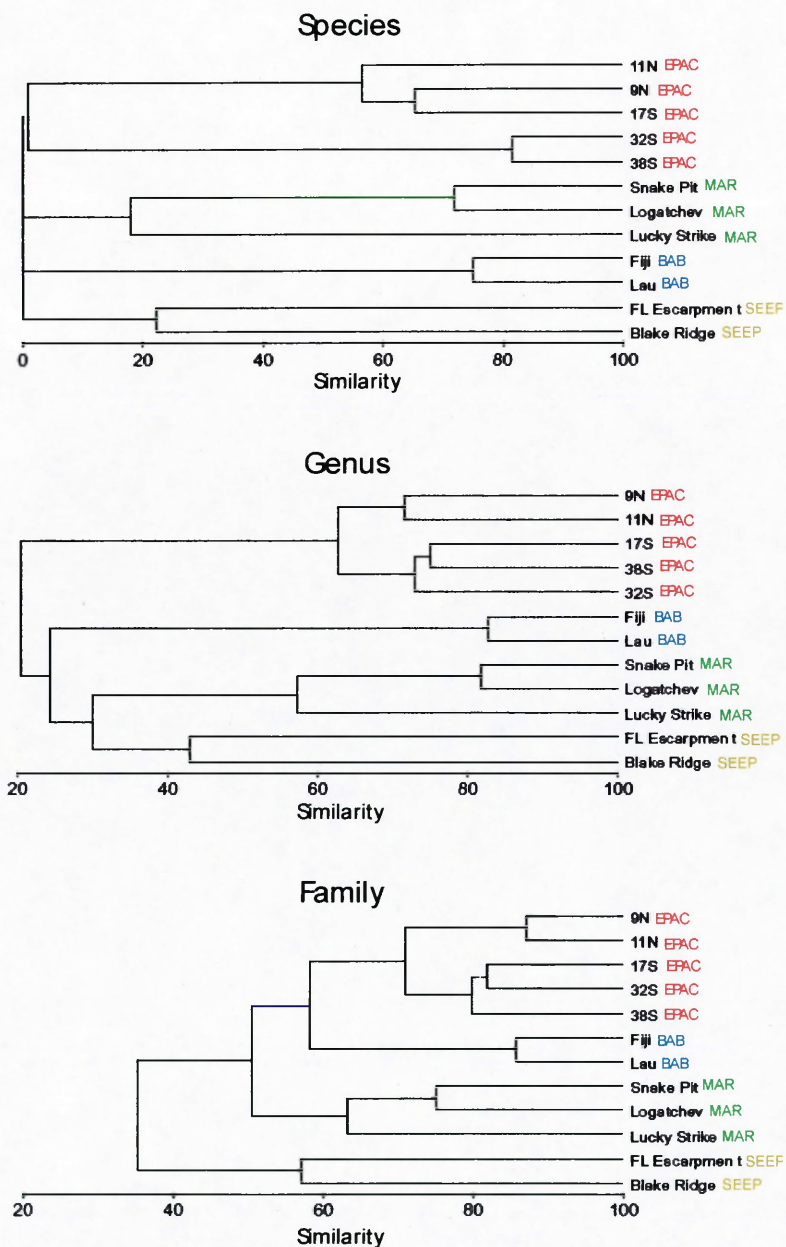
MDS PLOT



Presence/absence based multidimensional scaling (MDS) plots of decapod, gastropod, and bivalve populations at chemosynthetic mussel beds shown at the species, genus and family level. Red = East Pacific Vents, Blue = Western Pacific Back-Arc Basin Vents, Green = Mid-Atlantic Vents, and Yellow = Cold Seeps.

FIGURE 15

CLUSTER PLOT



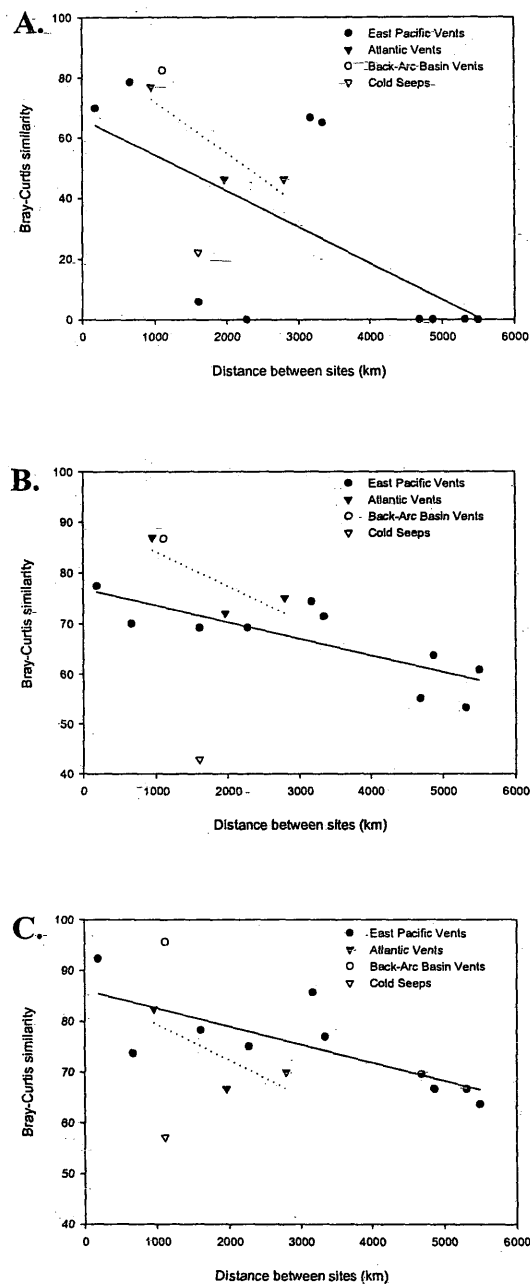
Cluster plot using Bray-Curtis similarity coefficients based on the presence and absence of bivalves, gastropod, and decapod species, genera and family. Red = East Pacific Vents, Blue = Western Pacific Back-Arc Basin Vents, Green = Mid-Atlantic Vents, and Yellow = Cold Seeps.

At the family level, all locations were at least 35% similar to each other ($BC_{+/-}$ of bivalves, gastropods, and decapods; Fig. 15). Vent and seep faunas grouped separately with 55% similarity ($BC_{+/-}$) within each group, indicating that some families were found only at seeps, others occurred at vents only. Within the east Pacific, there was ~70% ($BC_{+/-}$) similarity at the family level between locations north and south of the Easter microplate (Fig. 15). There was low family level similarity ($BC_{+/-} = 57\%$) between the two cold seep locations. N. Fiji and Lau had the greatest generic similarity ($BC_{+/-}$) between locations (96%).

Pair-wise species similarity ($BC_{+/-}$ of bivalves, gastropods, and decapods) between eastern Pacific mussel-bed locations and between the Mid-Atlantic Ridge decreased with increasing distance between pairs (Fig. 16). In the eastern Pacific, vent locations near each other (< 1000 km apart) had $BC_{+/-}$ values of 70 to 79%. Vent pairs > 4000 km apart (i.e. 9° N and 11° N pairs with 32° S and 38° S) in the eastern Pacific shared no bivalve, gastropod, or decapod species. Pair-wise species similarity ($BC_{+/-}$) was also high (77%) between vent locations on the Mid-Atlantic Ridge that were < 1000 km apart. Species similarity ($BC_{+/-}$) was lower (~45%) for sites > 1500 km apart on the Mid-Atlantic Ridge. For locations not connected by a ridge axis (i.e., back arc basins, cold seeps), species similarity ($BC_{+/-}$) was high (82%) for two back-arc basin locations located ~1000 km apart, but low (22%) for two cold seep locations located ~1500 km apart (following the shelf contour).

Pair-wise generic similarity ($BC_{+/-}$ of bivalves, gastropods, and decapods) between mussel-bed locations also decreased with increasing distance, but the drop was not as dramatic as in species similarity (Fig. 16). Generic similarity ($BC_{+/-}$) was greater

FIGURE 16.
CHANGES IN SIMILARITY OVER DISTANCE



Comparison of Bray-Curtis similarity based on the presence and absence of bivalves, gastropod, and decapod at the species (A), genus (B), and family (C) level and distance between locations. Linear regression lines for East Pacific locations (solid) and Mid-Atlantic Ridge locations (dotted) are also included.

between pairs of Mid-Atlantic Ridge locations than for pairs of eastern-Pacific locations the same distance apart. Generic similarity ($BC_{+/-}$) was > 50% on mid-ocean ridges, even for locations greater than 4000 km apart. For locations not connected by a ridge axis, generic similarity ($BC_{+/-}$) was high (87%) for two back-arc basin locations located ~1000 km apart, but low (43%) for two cold seep locations located ~1500 km apart.

The greatest pair-wise similarities ($BC_{+/-}$ of bivalves, gastropods, and decapods) at chemosynthetic mussel-bed communities were observed at the family level. Family similarities ($BC_{+/-}$) decreased with increasing distance, but were > 60%, even for locations more than 4000 km apart (Fig. 16). In contrast to the pattern for genera, family similarity ($BC_{+/-}$) was greater for eastern Pacific locations than for Mid-Atlantic Ridge locations the same distance apart. For locations not connected by a ridge axis, family similarity ($BC_{+/-}$) was greater (96%) for the two back-arc basin locations located ~1000 km apart and lower (57%) for two cold seep locations located ~1500 km apart.

DISCUSSION

Biogeography of south-Pacific hydrothermal vents

Faunal similarity at hydrothermal vents decreases with distance on a ridge axis (Hessler & Lonsdale 1991, Tunnicliffe & Fowler 1996), leading to the prediction that more isolated vent locations would be taxonomically and genetically more distinct (Vrijenhoek 1997). Hydrothermal vent sites within back-arc basins were believed to be isolated from other vents because they are unconnected in space and because they have relatively short geological life spans compared to mid-ocean ridges. Back-arc basins originate when the Earth's crust weakens enough to cause it to split forming spreading centers that are not connected to other areas of seafloor spreading and are only active for a relatively short period of time (5-10 million years; Hessler et al. 1988, Hessler & Lonsdale 1991). Back-arc basins are also considered isolated because their shallow rims prevent deep-water transfer from the surrounding deep-sea (Hessler et al. 1988).

Contrary to preconceptions of the isolation of back-arc basins, mussel-beds at Lau and N. Fiji Basins supported associations of macrofaunal invertebrates that were fairly similar in community structure. The two back-arc basin locations separated by ~1100 km shared more species (67% of species shared) than two mid-ocean ridge locations separated by ~600 km and the Juan Fernandez microplate (32° S – EPR and 38° S – PAR; 62.5% species shared). The average pair-wise Bray-Curtis similarity coefficient (based on species-abundance matrices) was greater between Lau and N. Fiji Basins (46%) than

they were between 32° S – EPR and 38° S – PAR (39%). The resemblance of the two back-arc basin vent communities indicates that interchange has occurred or is currently occurring between the basins. Geological hypotheses support a historical connection between the two basins. Auzende et al. (1988) proposed that prior to 10 mya there was a single island arc located between the Indo-Australian and Pacific plates and the Lau and N. Fiji Basins were created from the disruption of this arc. As recently as 3 – 0.7 mya, the Lau Spreading Center was connected to the North Fiji Triple Junction by an east-west ridge north of the Fiji Islands (Auzende et al 1988). This connecting ridge may have allowed communication between the vent populations in both basins.

The similarity between hydrothermal vent mussel-bed communities in the Lau and N. Fiji Basins reported here may be over-estimated due to the presence of cryptic species. The invertebrate macrofauna in this study were only identified to morphospecies based on physical appearance. Some of the morphospecies shared between the Lau and N. Fiji back-arc basins may be genetically distinct species within each basin. For example, gastropods in the genus *Alviniconcha* have been reported from four back-arc basins in the western Pacific, including the Lau and N. Fiji Basins, and a mid-ocean ridge location in the Indian Ocean. All of the *Alviniconcha* species collected are morphologically and anatomically similar, but genetic analysis identified two distinct species of *Alviniconcha* (sp. type 1 and 2) within the N. Fiji Basin (Kojima et al. 2001). The two species had a non-overlapping distribution and were collected from sites ~120 m apart (Suzuki et al. 2006). Both *Alviniconcha* sp. type 1 and 2 were also collected from sites in the Manus Basin (2800 km to the northwest of N. Fiji Basin; Kojima et al. 2001). Molecular studies by Suzuki et al. (2006) found that the *Alviniconcha* gastropods

collected from Vai Lili site in Lau Basin (130 km south of Tu'i Malila) were a third undescribed species. Each of the three *Alviniconcha* spp. has their own distinct endosymbionts. *Alviniconcha* sp. type 1 and the *Alviniconcha* sp. from Lau had γ -proteobacterial endosymbionts and *Alviniconcha* sp. type 2 had ϵ -proteobacterial endosymbionts (Suzuki et al. 2006). Preliminary study of the enzyme affinities of the other large provannid gastropod *Ifremeria nautilei* did not show a significant genetic differentiation between the Lau and N. Fiji back-arc basins (Desbruyères et al. 1994). However, *I. nautilei* populations from the N. Fiji and Manus back-arc basins did appear to be isolated from each other (Kojima et al. 2000).

Genetically distinct sister species in the western Pacific tend to remain morphologically similar after gene flow between the two populations has been interrupted. The isolation of vent populations of the Lau and N. Fiji Basin was a relatively recent event (< 0.7 mya; Auzende et al. 1988). The lack of detectable morphological variation between the cryptic sister-species may indicate that environmental or biological differences between the two locations are not strong enough to select for novel morphological features.

Previous exploration of N. Fiji hydrothermal vent sites reported the presence of two mussel species distinguishable based on differences in shell length/height ratios, *Bathymodiolus brevior* and *B. elongatus* (Cosel et al. 1994). The two species lack distinguishing characteristics in their soft anatomy and may belong to the same morphologically plastic species (R. C. Vrijenhoek, pers. comm.). Only *B. brevior* has been reported from the Lau Basin (Desbruyères et al. 1994). This investigation only found one morphospecies of *Bathymodiolus* at both of the back-arc basins. An

investigation of enzyme polymorphism analysis of populations of *B. brevior* from the Lau and N. Fiji back-arc basins showed that gene flow has been maintained between the two basins (Moraga et al. 1994). A more exact genetic analysis based on DNA sequencing of more samples of *Bathymodiolus* spp. mussels are needed in order to be confident about the species distribution and the amount of gene flow between basins.

In the eastern Pacific, the Easter Microplate acts as a dispersal barrier for *Bathymodiolus* spp. mussel on the EPR (Won et al. 2003). Levels of mitochondrial and allozyme divergence from mussels north and south of the Easter Microplate indicate that the mussels may be a distinct species (Won et al. 2003). Although *Bathymodiolus thermophilus* has planktotrophic larvae capable of long distance dispersal, it is unable to disperse south of the Easter Microplate. Populations of siboglinid tubeworms (*Oasisia* spp., *Riftia pachyptila*, and *Tevnia jerichonana*) were also subdivided across the Easter Microplate (Hurtado et al. 2002, Hurtado et al. 2004). However, the Easter Microplate is not a dispersal barrier for two polychaete species, *Branchiopolynoe symmytilida* and *Alvinella pompejana*, which may be due to how high up in the water column their larvae disperse (Hurtado et al. 2004). The polychaete, *A. pompejana*, has large negatively buoyant eggs that drift with the bottom currents, instead of becoming caught in the cross-axial current and swept away from the ridge axes (Pradillon et al. 2001).

Comparisons of community structure of hydrothermal-vent mussel beds north of the Easter Microplate (17° S – EPR), between the Easter Microplate and Juan Fernandez Microplate (32° S – EPR), and south of the Juan Fernandez Microplate (38° S – PAR) show that the distribution of vent locations with microplates are correlated with relatively high levels of dissimilarity among the mussel-bed locations. Bray-Curtis similarities

based on the presence/absence of species of bivalves, gastropods, decapods were extremely low (5%) between sites north and south of the Easter Microplate. Bray-Curtis similarities based on the presence/absence between sites to the north and the south of the Easter Microplate were higher when genus level was considered (~60%). The incongruity of species lists can be explained by a distinct southeastern Pacific vent gastropod fauna that is different from the classical EPR gastropod fauna from north of the Easter Microplate. Many of the gastropods collected at 32° S – EPR and 38° S – PAR show minor morphological differences from their sister-species collected to the north (A. Warén, pers. comm.), for example, *Eulepetopsis* aff. *vitrea*, *Lepetodrilus* aff. *elevatus*, *L.* aff. *tevinanus*, and *Gorgolepyis* aff. *spiralis*. Limpets from Northeast Pacific hydrothermal vent locations show the same trend of isolation and speciation with interruptions in the ridge axis (Johnson et al. 2006).

Transform faults on the north and south flanks of the Easter Microplate may cause the larvae of vent fauna to be entrained in the strong cross-axis current and swept away from ridge axes (Fujio & Imasato 1991). The Pacific-Nazca-Antarctic triple junction on the southern flank of the Juan Fernandez Microplate may cause the loss of additional larvae by cross-axis currents (Pardee et al. 1998). However, the molecular divergence of *Oasisia* spp. (Hurtado et al. 2002) and bythograeid crabs (Guinet et al. 2002 and Guinet & Hurtado 2003) indicate that divergence between sister species began before the formation of the microplates (~5 mya; Pardee et al. 1998). Other factors may contribute to the dispersal barrier of vent larvae in addition to the microplates.

Large-scale patterns of hydrothermal vent biogeography correspond to patterns for non-vent fauna. The distribution of both faunas on a global scale may be controlled

by the same factors [i.e., zonal distributions (longitudinal, circumcontinental, and vertical), physical and chemical factors, and large geomorphological barriers, Mironov et al. 1998]. Vinogradova (1997) divided the Pacific Ocean into six zones: northwestern and northeastern (north of 35° N), western tropical and eastern tropical (35° N to 40° S), and southwestern and southeastern (south of 40° S). The deep-sea fauna of the southern Pacific (south of 40° S) shows an increasing taxonomic isolation with depth from the fauna to the north. Abyssal fauna south of 40° S belongs to a separate biogeographic province from the abyssal fauna north of 40° S in the Pacific (Vinogradova 1997). The Antarctic Circumpolar Current (ACC) separates the Indo-Pacific region and the Antarctic region of deep-sea faunas at ~40° S (Vinogradova 1979). The ACC has linked the southern Pacific, Atlantic and Indian Oceans ever since the opening of the Drake Passage (20 – 30 mya; Barker & Thomas 2004) and the Tasmanian Gateway (33 – 34 mya; Stickley et al. 2004). Another study suggests an earlier starting point for the ACC during the late Eocene (37-33.7 mya) and that the Drake Passage opened before the Tasmanian Gateway (Scher & Martin 2006).

The ACC may also contribute to the dispersal barrier north and south of the Easter Microplate Region. According to computer simulations of deep-ocean circulations, a westward circulation, caused by the inflated bottom topography, exists along the northern part of the Easter Microplate (Fujio & Imasato 1991). The cross-axial bottom current may transport propagules of vent organisms away from hydrothermal vent locations, preventing their southward dispersal. The start of the ACC may have initiated the isolation of vent communities in the eastern Pacific. The estimate of the time of divergence for the southern lineage of *Oasisia* tubeworms from the northern lineages (at

least 18-21.6 mya) based on a siboglinid molecular clock (Chevaldonné et al. 2002) overlaps with the later time (~20 mya) of the start of the ACC crossing the EPR (Hurtado et al. 2004).

Global patterns of biogeography at chemosynthetic mussel beds

Chemosynthetic mussel-bed communities globally tend to decrease in community similarity with increasing distance between locations. Hydrothermal vents on mid-ocean ridges located <1000 km are more similar to each other than vents located >1000 km apart. A similar trend is seen in benthic seamount communities, but the similarity of even closely related sites is lower at seamounts. For distances <1000 km, paired hydrothermal vent sites have community similarity coefficients (0.6 – 0.8, BC_± of bivalves, gastropods, and decapods) and seamount benthic communities have community similarity coefficients (0.08 – 0.49; de Forges et al. 2000). Hydrothermal vents are relatively unstable environments; dispersal to new vent locations is essential to prevent extinction when the hydrothermal venting ceases to flow. Many vent species have adapted to this ephemeral environment by adopting long distance dispersal traits (reviewed in Tyler & Young 1999, Tyler & Young 2003).

Cold seep mussel-bed communities are more isolated than hydrothermal vent mussel bed communities. Even at the family level, Blake Ridge and Florida Escarpment, two seeps in the Atlantic basin located ~1500 km apart on the continental shelf, only have a 57% similarity (BC_± of bivalves, gastropods, and decapods) while hydrothermal vents in the Western Pacific back-arc basins have a 63% similarity to vents on the EPR (~6500 km across the Pacific Basin). The composition of seeps at the family level is almost as

dissimilar as vent location on the MAR and the EPR (BC+/- of bivalves, gastropods, and decapods = 54%), suggesting the long-term isolation and independent speciation of individual seep locations. The isolation of seep fauna may be caused by the lack of long distance dispersal and recruitment mechanisms for seep-endemic fauna or because cold seeps do not emit strong chemical signals as hydrothermal vents do (Sibuet & Olu 1998). Competition with non-seep specific opportunistic species could also lead to the distinctiveness of endemic seep fauna (Sibuet & Olu 1998, Levin et al. 2000). Similarly isolated benthic communities are also reported from seamounts in the southwestern Pacific (de Forges et al. 2000). There is little overlap in community composition between similar sites located <1000 km apart and seamount benthic fauna appear to endemic to seamount groups/chain (de Forges et al. 2000). Many seamount species have adapted to their environments by limiting their dispersal mechanisms (favoring direct development or short larval periods) to maintain their populations on the small area of favorable conditions around the seamount instead of sending their propagules in to the unknown conditions of the open sea (Parker & Tunnicliffe 1994). Similar dispersal adaptations may also occur in seep endemic organisms to maintain their populations in the stable seep environment.

Variation in the spreading rate of the mid-ocean ridge leads to differences in the timing and spacing of hydrothermal vents. The MAR has a slow-spreading rate of only 2-4 cm/yr (Tunnicliffe et al. 1998) and has a low-spatial frequency of hydrothermal venting (Van Dover 2000). The EPR has a fast-spreading rate of 12-16 cm/yr (Tunnicliffe et al. 1998) and has a higher spatial frequency of hydrothermal venting (Van Dover 2000). When sites are closer together there is a greater chance that larvae can be

dispersed between sites and populations can be well mixed. Local endemism should be higher where vent locations are further apart and exchange among sites is limited (Van Dover 1995). Accordingly, one would expect pair-wise similarities between sites on the EPR to be greater than pair-wise similarities between sites on the MAR. However, this was not the case and there was no significant difference between the two mid-ocean ridges. Pair-wise similarities between sites over distance on a ridge were slightly greater on the MAR compared to the EPR at the species and generic level. Pair-wise similarities between sites over distance on a ridge were only slightly greater on the EPR for the familial level. Despite the distance between sites on the MAR, some species are still able to disperse between sites. Mussel-bed communities at Lucky Strike had the most distinct community of the three mussel beds sampled in the MAR (Snake Pit, 3480 m, Logatchev 3050 m, Lucky Strike, 1700 m; Van Dover & Doerries 2005). Species turnover on the MAR appears to have more to do with changes in depth than it had to do with distances between sites. More sampling of vent communities on the MAR is needed to determine if this true.

Global patterns in species richness and diversity at mussel beds

Over many different environments, intertidal, subtidal, and even at hydrothermal vents and cold seeps, mussel beds tend to share many characteristics. Mussels and the other associated fauna generally densely populate mussel beds, and exhibit high levels of secondary production (Leigh et al. 1987). The structure created by mussels piling atop one another provides refuge from predation and harsh physical conditions, and suitable habitat to many macrofaunal invertebrates (Seed 1996). As foundation species, mussels

can have positive effects on their community by creating habitat, providing refuge from predation, enhancing the retention of the propagule supply, and increasing food availability (Bruno and Bertness 1998). In both shallow-water and chemosynthetic environments, associated macrofauna can easily be divided into three major groups: (1) epibiotic organisms, like barnacles, algae at shallow-water mussel beds, and bacteria at hydrothermal vents, that grow directly on the mussel shells; (2) mobile taxa that live in the matrix of the shells and byssal threads, such as limpets and polychaetes; (3) infaunal taxa that live in the enriched organic sediments and shell debris beneath the mussels (Seed 1996). In some ways, one can say, a mussel bed is a mussel bed no matter where it is located.

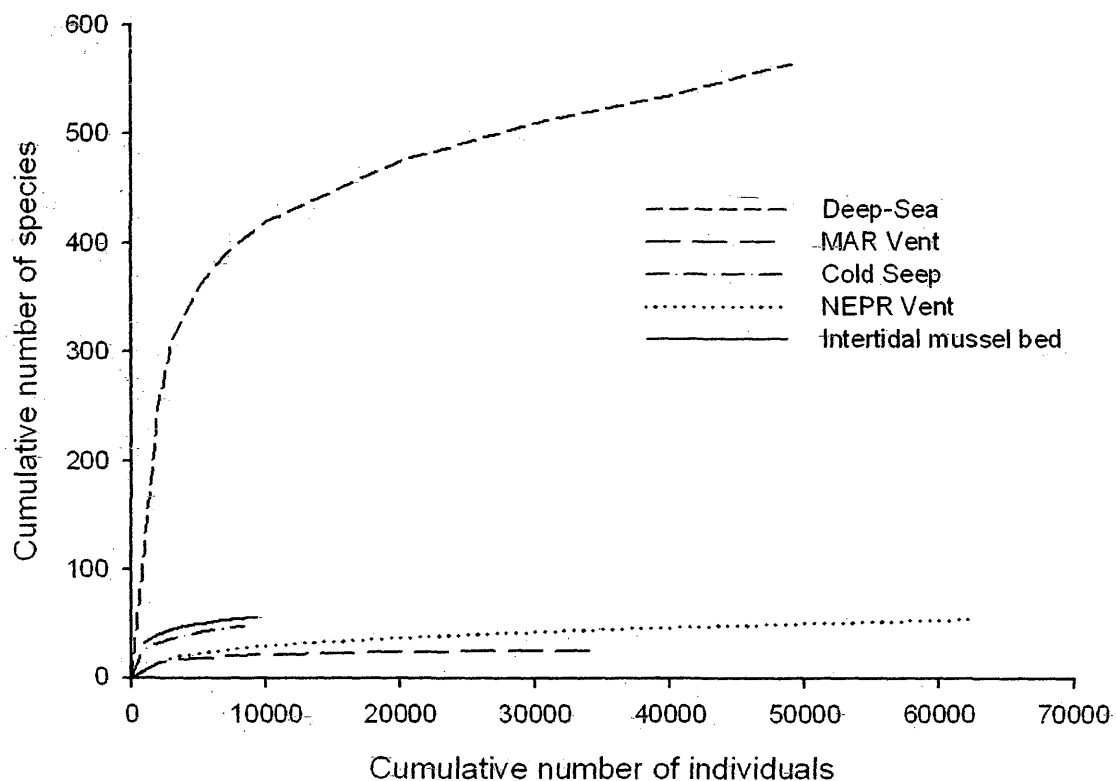
In shallow-water mussel beds, functionally analogous species, usually within the same genus, are recurrently found worldwide (Seed 1996). Members from the genera *Lasaea* (a bivalve), *Hyale* (an amphipod), and *Typosyllis* (a syllid polychaete), have been reported from mytilid communities across the globe. Even though genera or families generally are not shared between shallow-water and chemosynthetic mussel beds, many of the same functional groups are present in both systems. For example, molluscan and crustacean grazers feed on the enriched particulate organic material found in the interstitial spaces of the mussel bed. Mobile predators crawl on top of the mussels looking for prey taking refuge in the mussel bed. Chemosynthetic mussel beds share high degrees of generic and familial level similarity with each other. At the familial level, there is at least 35% (BC+/- of bivalves, gastropods, and decapods) similarity among hydrothermal vent and seep mussel beds.

Species richness at most hydrothermal-vent and cold-seep mussel beds reported here (Table 11) is within the reported range of macrofauna invertebrate species richness from rocky shore mytilid beds (32 to 100 taxa; Seed 1996). Species richness was higher at *Mytilus californianus* beds (~270 taxa) on the Pacific coast because *M. californianus* is a much larger-bodied mussel that forms thicker, multilayered beds (Suchanek 1979). Species richness at hydrothermal-vent mussel beds ranged from 18 to 54 taxa, with the lowest species richness (18-32 taxa) observed at MAR mussel beds. Species richness at cold-seep mussel beds was ~44 taxa. Although shallow water mussel-bed communities have relatively high species richness, they tend to be dominated by a few very abundant species (Seed 1996). Greater than 90% of the molluscan fauna associated with *Septifer virgatus* mussel beds was comprised of three small bivalve species (Seed 1996). This is also true for chemosynthetic mussel beds. As reported here, at N. Fiji back-arc basin mussel beds, one limpet species comprised over 90% of the total number of individuals collected. On the EPR, the most numerically dominant taxa collected usually accounts for 40-60% of the total number of individuals collected (Van Dover 2003, Dreyer et al. 2005).

Both intertidal and chemosynthetic mussel beds exhibit extremely low diversity when compared to the benthic diversity of the deep-sea (Grassle & Maciolek 1992). Approximately 800 macrofaunal species were represented in nearly 91,000 individuals collected from continental slope regions off the coast of New Jersey and Delaware. The number of macrofaunal species continued to increase as more samples were collected and did not approach an asymptote, unlike at the chemosynthetic mussel beds (Grassle & Maciolek 1992; Fig. 17). This dwarfs the highest species richness reported from

FIGURE 17

SPECIES-EFFORT CURVES OF DIFFERENT MARINE COMMUNITIES



Comparison of species effort curves from different marine communities. Deep-sea sediments – off New Jersey and Delaware (Grassle & Maciolek 1992); MAR hydrothermal vent mussel bed – Logatchev (Van Dover & Doerries 2005); cold seep mussel bed – Florida Escarpement (Turnipseed et al. 2004); NEPR hydrothermal vent mussel bed – 9° N (1999 and 2001 data combined, Dreyer et al. 2005); Intertidal mussel bed – Kasitsna Bay (Van Dover & Trask 2000).

hydrothermal vent mussel bed (54 species from ~12,000 individuals at 17° S – EPR) and from a cold seep mussel bed (44 species from ~5,000 individuals at Blake Ridge; Fig. 17). Deep-sea benthic species richness is even greater than that reported from the Pacific *Mytilus californianus*-beds (~270 taxa; Suchanek 1979). Shannon diversity (H') values are also much greater for deep-sea sediments (5.82 ± 0.13 ; Grassle & Maciolek 1992) than for hydrothermal-vent mussel beds (1.91 ± 0.09 at 17° S – EPR), cold-seep mussel beds (2.05 ± 0.08 at Florida Escarpment), and intertidal mussel beds (1.2 to 3.2; Iwasaki 1995, Seed 1996).

Lower species diversity at hydrothermal vents may be due to high disturbance rates. Vent communities and intertidal mussel-beds have higher disturbance rates and more harsh abiotic conditions than non-vent deep-sea communities do (Huston 1994; Tsurumi 2003). Low species diversity has also been reported from many other ecosystems with high disturbance rates, such as terrestrial areas after volcanic activity (del Moral & Bliss 1993), and areas after forest fires (Turner et al. 1997). The inhospitable conditions found at hydrothermal vents and cold seeps limits the species found there to organisms specifically adapted to the particular chemical environment. The larger number of species at the deep-sea floor may be caused by constant conditions and niche fragmentation in the physically unvarying seafloor environment (Gage 1996).

REFERENCES

- Auzende, J.-M., Y. Lafoy & B. Marsset B. 1988. Recent geodynamic evolution of the north-Fiji basin (southwest-Pacific). *Geology* 16: 925-929.
- Barker, P.F. & E. Thomas. 2004. Origin, signature and palaeoclimatic influences of the Antarctic Circumpolar Current. *Earth-Science Reviews* 66: 143-162.
- Bergquist, D.C., T. Ward, E.E. Cordes, T. McNelis, S. Howlett, R. Kosoff, S. Hourdez, R. Carney & C.R. Fisher. 2003. Community structure of vestimentiferan-generated habitat islands from Gulf of Mexico-cold seeps. *J. Exp. Mar. Biol. Ecol.* 289: 197-222.
- Bergquist, D.C., C. Fleckenstein, J. Knisel, B. Begley, I.R. MacDonald & C.R. Fisher. 2005. Variation in seep mussel bed communities along physical and chemical environmental gradients. *Mar. Ecol. Prog. Ser.* 293: 99-108.
- Bruno, J.F. & M.D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. In: Bertness M.D., S.D. Gaines & M.E. Hay, eds. *Marine Community Ecology*. Sinauer Associates, Inc., Sunderland, MA, pp. 201-218.
- Chevaldonné, P., D. Jollivet, D. Desbruyères, R.A. Lutz & R.C. Vrijmhoek. 2002. Sister-species of eastern Pacific hydrothermal vent worms (Ampharetidae, Alvinellidae, Vestimentifera) provide new mitochondrial COI clock calibration. *Cah. Biol. Mar.* 43: 367-370.
- Clarke, K.R. & R.N. Gorley. 2001. *PRIMER v5: User Manual/Tutorial*. PRIMER-E Ltd., Plymouth.
- Clarke, K.R. & R.M. Warwick. 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. PRIMER-E Ltd., Plymouth.
- Colwell, R.K. 1997. *EstimatesS: Statistical estimation of species richness and shared species from samples*. Version X. User's Guide and application published at: <http://viceroy.eeb.uconn.edu/estimates>

- von Cosel, R., B. Metivier, & J. Hashimoto. 1994. Three new species of *Bathymodiolus* (Bivalvia: Mytilidae) from hydrothermal vents in the Lau Basin and the North Fiji Basin, Western Pacific, and the Snake Pit area, Mid-Atlantic Ridge. *The Veliger* 37: 374-392.
- Desbruyères, D., A.-M. Alayse-Danet & S. Ohta. 1994. Deep-sea hydrothermal communities in Southwestern Pacific back-arc basins (the North Fiji and Lau Basins): composition, microdistribution and food web. *Mar. Geol.* 116: 227-242.
- Desbruyères, D., A. Almeida, M. Biscoito, T. Comtet, A. Khripounoff, N. Le Bris, P.M. Sarradin & M. Segonzac. 2000. A review of the distribution of hydrothermal vent communities along the northern Mid-Atlantic Ridge: dispersal vs. environmental controls. *Hydrobiologia* 440: 201-216.
- Desbruyères, D., M. Biscoito, J.-C. Caprais, A. Colaço, T. Comtet, P. Crassous, Y. Fouquet, A. Khripounoff, N. Le Bris, K. Olu, R. Riso, P.-M. Sarradin, M. Segonzac & A. Vangriesheim. Variation in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge near the Azores plateau. *Deep-Sea Res. I* 48: 1325-1346.
- Desbruyères, D., J. Hashimoto & M.-C. Fabri. In press. Composition and biogeography of hydrothermal vent communities in western Pacific back-arc basins.
- Dryer, J.C., K.E. Knick, W.B. Flickinger & C.L. Van Dover. 2005. Development of Macrofaunal community structure in mussel beds on the northern East Pacific Rise. *Mar. Ecol. Prog. Ser.* 302: 121-134.
- de Forges, B.R., J.A. Koslow & G.C.B. Poore. 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* 405: 944-947.
- France, S.C., R.R. Hessler & R.C. Vrijenhoek. 1992. Genetic differentiation between spatially-disjunct populations of the deep-sea, hydrothermal vent-endemic amphipod, *Ventiella sulfuris*. *Mar. Biol.* 114: 551-559.
- Fujio, S. & N. Imsato. 1991. Diagnostic calculation for circulation and water mass movement in the deep Pacific. *J. Geophys. Res.* 96: 759-774.
- Gage, J.D. 1996. Why are there so many species in deep-sea sediments? *J. Exp. Mar. Biol. Ecol.* 200: 257-286.
- Geistdoerfer, P., J.-M. Auzende, R. Batiza, D. Bideau, M.H. Cormier, Y. Fouquet, Y. Lagabrielle, J. Sinton & P. Spadea. 1995. Hydrothermalisme et communautés animales associées sur la dorsale du pacifique oriental entre 17°S et 19°S (Campagne-NAUDUR, Décembre 1993). *Comptes Rendus* 320 (Série II), 47-54.

- Govenar, B., N. Le Bris, S. Gollner, J. Glanville, A.B. Aperghis, S. Hourdez & C.R. Fisher. 2005. Epifaunal community structure associated with *Riftia pachyptila* aggregations in-chemically different hydrothermal vent habitats. *Mar. Ecol. Prog. Ser.* 305: 67-77.
- Grassle, J.F. 1986. The ecology of deep-sea hydrothermal vent communities. *Adv. Mar. Biol.* 23: 301-362.
- Grassle, J.F. & N.J. Maciolek. 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am. Nat.* 139: 313-341.
- Guinot D. & L.A. Hurtado. 2003. Two new species of hydrothermal vent crabs of the genus *Bythograea* from the southern East Pacific Rise and from the Galapagos Rift (Crustacea Decapoda Brachyura Bythograeidae). *Comptes Rendus Biologies* 326: 423-439.
- Guinot D., L.A. Hurtado & R.C. Vrijenhoek. 2002. New genus and species of brachyuran crab from the southern East Pacific Rise (Crustacea Decapoda Brachyura-Bythograeidae). *Comptes Rendus Biologies* 325: 1119-1128.
- Hessler, R.R., P. Lonsdale & J. Hawkins. 1988. Patterns on the ocean floor. *New Scientist* 117: 47-51.
- Hessler, R.R., & P.F. Lonsdale. 1991. Biogeography of Mariana Trough hydrothermal vent communities. *Deep-Sea Res. Part A.* 38: 185-199.
- Hey, R.N., P.D. Johnson, F. Martinez, J. Korenaga, M.L. Somers, Q.J. Huggett, T.P. LeBas, R.I. Rusby & D.F. Naar. 1995. Plate boundary reorganization at a large-offset, rapidly propagating rift. *Nature* 378: 167-170.
- Hurtado, L.A., M. Mateos, R.A. Lutz & R.C. Vrijenhoek. 2002. Molecular evidence for multiple species of *Oasisia* (Annelida: Siboglinidae) at eastern Pacific hydrothermal vents. *Cah. Biol. Mar.* 43: 377-380.
- Hurtado, L.A., R.A. Lutz & R.C. Vrijenhoek. 2004. Distinct patterns of genetic differentiation among annelids of eastern Pacific hydrothermal vents. *Mol. Ecol.* 13: 2603-2615.
- Huston, M.A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge.
- Jollivet, D. 1996. Specific and genetic diversity at deep-sea hydrothermal vents: an overview. *Biodiversity and Conservation* 5: 1619-1653.

- Johnson, S.B., C.R. Young, W.J. Jones, A. Waren & R.C. Vrijenhoek. 2006. Migration, isolation, and speciation of hydrothermal vent limpets (Gastropoda; Lepetodrilidae) across the Blanco Transform Fault. *Biol. Bull.* 210:
- Karl, D.M., G.M. McMurtry, A. Malahoff & M.O. Garcia. 1988. Loihi Seamount, Hawaii: a mid-plate volcano with a distinctive hydrothermal system. *Nature* 335: 532-535.
- Knick, K.E. 2003. Comparison of mussel-bed faunas at Blake Ridge and Florida Escarpment seeps. Masters Thesis, College of William and Mary, Williamsburg, Virginia.
- Kojima, S., R. Segawa, Y. Fujiwara, J. Hashimoto & S. Ohta. 2000. Genetic differentiation of populations of a hydrothermal vent-endemic gastropod, *Ifremeria nautilei*, between the North Fiji Basin and the Manus Basin revealed by nucleotide sequences of mitochondrial DNA. *Zool. Sci.* 17: 1167-1174.
- Kojima, S., R. Segawa, Y. Fujiwara, K. Fijikura, S. Ohta & J. Hashimoto. 2001. Phylogeny of hydrothermal-vent-endemic gastropods *Alviniconcha* spp. from the Western Pacific revealed by mitochondrial DNA sequences. *Biol. Bull.* 200: 298-304.
- Leigh, E.G., P.T. Paine, J.F. Quinn & T.H. Suchanek. 1987. Wave energy and intertidal productivity. *Proc. Natl. Acad. Sci.* 84: 1314-1318.
- Levin L.A., D.W. James, C.M. Martin, A.E. Rathburn, L.H. Harris & R.H. Michener. 2000. Do methane seeps support distinct macrofaunal assemblages? Observations on community structure and nutrition from the northern California slope and shelf. *Mar. Ecol. Prog. Ser.* 208: 21-39.
- Luther, G.W., III, T.F. Rozan, M. Tallefert, D.B. Nuzzio, C. DiMeo, T.M. Shank, R.A. Lutz and S.C. Cary. 2001. Chemical speciation drives hydrothermal vent ecology. *Nature* 410 813-816.
- McKiness, Z.P., E.R. McMullin, C.R. Fisher & C.M. Cavanaugh. 2005. A new bathymodioline mussel symbiosis at the Juan de Fuca hydrothermal vents. *Mar. Biol.* 148: 109-116.
- Micheli, F., C.H. Peterson, L.S. Mullineaux, C.R. Fisher, S.W. Mills, G. Sancho, G.A. Johnson & H.S. Lenihan. 2002. Predation structures communities at deep-sea hydrothermal vents. *Ecological Monographs* 72: 365-382.
- Mironov, A.N., A.V. Gebruk & L.I. Moskalev. 1998. Biogeographical patterns of the hydrothermal vent fauna: a comparison with 'non-vent biogeography'. *Cah. Biol. Mar.* 39: 367-368.

- del Moral, & L.C. Bliss. 1993. Mechanisms of primary succession: insights resulting from the eruption of Mt. St. Helens. *Advances in Ecological Research* 24: 1-66.
- Moraga, D., D. Jollivet & F. Denis. 1994. Genetic differentiation across the Western Pacific populations of the hydrothermal vent bivalve *Bathymodiolus* spp. and the Eastern Pacific (13° N) population of *Bathymodiolus thermophilus*. *Deep-Sea Res.* I 41: 1551-1567.
- Mullineaux, L.S., S.W. Mills & E. Goldman. 1998. Recruitment variation during a pilot colonization study of hydrothermal vents (9°50'N, East Pacific Rise). *Deep-Sea Res.* II 45: 441-464.
- NAUTILAU Group. 1990. Hydrothermal activity in the Lau Basin: first results from the NAUTILAU cruise. *EOS* 71(18).
- Oliver, I. & A.J. Beattie. 1996. Invertebrate morphospecies as surrogates for species: A case study. *Conservation Biology* 10: 99-109.
- Pardee, D.R., R.N. Hey & F. Martinez. 1998. Cross-sectional areas of mid-ocean ridge axes bounding the Easter and Juan Fernandez microplates. *Mar. Geophys. Res.* 20: 517-531.
- Parker, T. & V. Tunnicliffe. 1994. Dispersal strategies of the biota on an oceanic seamount: implications for ecology and biogeography. *Biol. Bull.* 187: 336-345.
- Pradillon, F., B. Shillito, C.M. Young & F. Gaill. 2001. Developmental arrest in vent worm embryos. *Nature* 413: 698-699.
- Scher, H.D. & E.E. Martin. 2006. Timing and climatic consequences of the opening of the Drake Passage. *Science* 312: 428-430.
- Seed, R. 1996. Pattern of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *J. Mar. Biol. Ass. U.K.* 76: 203-210.
- Sibuet, M. & Olu, K. 1998. Biogeography, biodiversity, and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Res.* II 45: 517-567.
- Stecher, J., M. Turkay & C. Borowski. 2002. Faunal assemblages on the Pacific-Antarctic Ridge near the Foundation Seamount chain (37°30'S, 110°30'W). *Cah. Biol. Mar.* 43:271-274
- Stickley, C.E., H. Brinkhuis, S.A. Schellenberg, A. Sluijs, U. Rohl, M. Fuller, M. Grauert, M. Huber, J. Warnaar & G.L. Williams. 2004. Timing and nature of the deepening of the Tasmanian Gateway. *Paleoceanography* 19: PA4027.

- Suchanek, T.H. 1979. The *Mytilus californianus* community: studies on the composition, structure, organization and dynamics of a mussel bed. PhD thesis, University of Washington, Seattle.
- Suzuki, Y., S. Kojima, T. Sasaki, M. Suzuki, T. Utsumi, H. Wantanabe, H. Urakawa, S. Tsuchida, T. Nunoura, H. Hirayama, K. Takai, K.H. Nealson & K. Horikoshi. 2006. Host-symbiont relationships in hydrothermal vent gastropods from the genus *Alviniconcha* from the southwest Pacific. *Appl. Environ. Microbio.* 72: 1388-1393.
- Tsurumi, M. 2003. Diversity at hydrothermal vents. *Global Ecology and Biogeography* 12: 181-190.
- Tsurumi, M. & V. Tunnicliffe. 2003. Tubeworm-associated communities at hydrothermal vents on the Juan de Fuca Ridge, northeast Pacific. *Deep-Sea Res. I.* 50: 611-629.
- Tunnicliffe, V. & C.M.R. Fowler. 1996. Influence of sea-floor spreading on the global hydrothermal vent fauna. *Nature* 379: 531-533.
- Tunnicliffe, V., A.G. McArthur & D. McHugh. 1998. A biogeographical perspective of the deep-sea hydrothermal vent fauna. *Adv. Mar. Biol.* 44: 353-442.
- Turner, M.G., W.F. Romme, R.H. Gardner & W.W. Hardgrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67: 411-433.
- Turnipseed, M., K.E. Knick, R.N. Lipcius, J. Dreyer & C.L. Van Dover. 2003. Diversity in mussel beds at deep-sea hydrothermal vents and cold seeps. *Ecology Letters* 6: 518-523.
- Turnipseed, M., C.D. Jenkins & C.L. Van Dover. 2004. Community structure in Florida Escarpment seep and Snake Pit (Mid-Atlantic Ridge) vent mussel beds. *Mar. Biol.* 145: 121-132.
- Tyler, P.A. & Young, C.M. 1999. Reproduction and dispersal at vents and cold seeps. *J. Mar. Biol. Ass. U.K.* 79: 193-208.
- Tyler, P.A. & Young, C.M. 2003. Dispersal at hydrothermal vents: a summary of recent progress. *Hydrobiologia* 503: 9-19.
- Van Dover, C.L. 1995. Ecology of Mid-Atlantic Ridge hydrothermal vents. In, L.M. Parson, C.L. Walker & D.R. Dixon (eds.). *Hydrothermal Vents and Processes*. *Geol. Soc. Spec. Publ.* 87: 257-294.
- Van Dover, C.L. 2000. *The ecology of deep-sea hydrothermal vents*. Princeton Univ. Press, Princeton, NJ, USA.

- Van Dover, C.L. 2002. Community structure at mussel beds at deep-sea hydrothermal vents. *Mar. Ecol. Prog. Ser.* 230: 137-158.
- Van Dover, C.L. 2003. Variation in community structure within hydrothermal vent mussel beds of the East Pacific Rise. *Mar. Ecol. Prog. Ser.* 253: 55-66.
- Van Dover, C.L. & R.R. Hessler. 1990. Spatial variation in faunal composition of hydrothermal vent communities on the East Pacific Rise and Galapagos Spreading Center. In: McMurray, GR (ed); *Gorda Ridge: a seafloor spreading center in the United States Exclusive Economic Zone*. Springer-Verlag, New York, pp. 253-264.
- Van Dover, C.L. & J.L. Trask. 2000. Diversity at deep-sea hydrothermal vent and intertidal mussel beds. *Marine Ecology Progress Series* 195: 169-178.
- Van Dover, C.L., C.R. German, K.G. Speer, L.M. Parson & R.C. Vrijenhoek. 2002. Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295: 1253-1257.
- Van Dover, C.L. & M.B. Doerries. 2005. Community structure in mussel beds at Logatchev hydrothermal vents and a comparison of macrofaunal species richness on slow- and fast-spreading mid-ocean ridges. *Marine Ecology* 26: 110-120.
- Vinogradova, N. 1979. The geographical distribution of the abyssal and hadal (ultra-abyssal) fauna in relation to vertical zonation of the ocean. *Sarsia* 64: 41-50.
- Vinogradova, N. 1997. Zoogeography of the Abyssal and Hadal Zones. *Adv. Mar. Biol.* 32: 325-387.
- Vrijenhoek, R.C. 1997. Gene flow and genetic diversity in naturally fragmented metapopulations of deep-sea hydrothermal vent animals. *Journal of Heredity* 88: 285-293.
- Won, Y., C.R. Young, R.A. Lutz & R.C. Vrijenhoek. 2003. Dispersal barriers and isolation among deep-sea mussel populations (*Mytilidae: Bathymodiolus*) from eastern Pacific hydrothermal vents. *Molecular Ecology* 12: 169-184.

VITA

Elizabeth Anne Blake

Elizabeth Anne Blake was born in Fairfax, Virginia on March 29th 1982. She graduated from George Mason High School in Falls Church, Virginia in 2000. In the fall of 2000, she entered the College of William and Mary. In the spring of 2002, Elizabeth began working in the lab of Dr. Cindy Lee Van Dover researching the reproduction of *Amathys lutzi*, a polychaete from hydrothermal vents. During the spring of 2003, she studied abroad at University of Adelaide in Australia. In the fall of 2003, she returned to her studies at William and Mary and received a B.S. in Biology and History in May 2004.

In August 2004, Elizabeth entered the graduate program in Biology at The College of William & Mary and continued doing research in the lab of Dr. Cindy Lee Van Dover. During her masters studies she had the opportunity to be on a research cruise in the Lau and North Fiji Basins on the R/V Melville. Elizabeth Blake defended the work presented in this thesis in May 2006. She is currently working to become a high school Biology teacher.