Ecology of hydrothermal vents on three segments of the Juan de Fuca Ridge, northeast Pacific

by

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B.Sc., McGill University, 1994

A Dissertation Submitted in Partial Fulfillment of the
Requirements for the Degree of

DOCTOR OF PHILOSOPHY

in the Department of Biology

We accept this dissertation as conforming
to the required standard

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Abstract

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This work seeks to explore current ecological theory through application to communities inhabiting hydrothermal vents. This thesis aims to: 1) add to and synthesise knowledge of species and their distributions at the intra- and intersegment scale; and 2) evaluate vent community patterns and speculate on processes. Samples used are submersible grabs of low temperature (<60^{o}C) tubeworm assemblages on basalt and sulphide surfaces.

Species abundances and distributions on three segments of the Juan de Fuca Ridge (Axial, Cleft, and CoAxial) are described. Community descriptors such as species density, Simpson's and the Shannon-Wiener diversity indices, evenness, species richness, species abundance-distribution models, species percent-average relative abundance and density are used. Vent community structure is compared among segments using these descriptors, visual descriptions, pairwise correlations, Friedman tests of distributions, cluster and correspondence analysis, rarefaction, complementarity, a test for saturation, and Whittaker's beta diversity.

Vent community composition on Axial, north Cleft, and CoAxial is similar at the segment and inter-segment scale. The limpet *Lepetodrilus fucensis* is the most abundant species at all sites. Differences among communities are best seen temporally, not spatially. Senescent communities can be distinguished from active vent assemblages. Pioneer communities, however, are statistically indistinguishable from intermediate communities when sampled two or more years post-eruption. Axial and Cleft species dispersion fits the core-satellite hypothesis. The exceptions are the polynoids *Branchinotogluma* sp., *Lepidonotopodium piscesae*, and *Levensteiniella kincaidi*, which are widespread and present in low local abundances. Both local and mesoscale regional mechanisms explain observed local diversity. Spatial isolation, not habitat differences, influences between-habitat diversity (beta diversity) on Axial, Cleft, and all three segments combined. Meiofauna are important for species richness estimates, identifying differences among structurally similar communities, and understanding input/output between vents and the deep-sea. Measurements such as species richness and diversity indices may be poor at distinguishing among vent communities because vents are species poor and uneven. The Michaelis-Menten, Jackknife 2, and Chao 2 nonparametric vent species richness estimators perform well with small samples. Vent communities should be compared to habitats of similar diversity and evenness as well as disturbance and productivity regimes. Candidate comparison communities include communities in early successional states, selected taxocenes such as carabid beetles on fungi, or high disturbance and/or low diversity systems like the rocky intertidal, organically polluted sediments and oxygen minimum zones below upwelling regions in the deep-sea.

Examiners:

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Acknowledgments

I am lucky to have had help from many people over the past five and a half years. I wish to thank all the people who were generous with their knowledge, time, reprints, cruise berths, data, materials, reference letters, emotional and monetary support, humour, friendship, floor space, and/or food over the course of my studies. It is impossible to name every individual.

Ed Baker, Gary Massoth, Bill Lavelle, and Dave Butterfield (NOAA), Stephen Gegg and Meg Tivey (WHOI), Dave Kadko (University of Miami), Jozee Sarrazin, Didier Jollivet (IFREMER), Tom Gore and Heather Down (UVic Advanced Imaging Lab), and the staff of the UVic Biology Office all provided answers to questions, reprints, technical support, and/or materials. I am grateful for their help during my time as a student. Frank Ferrari (USNM), Henry Reiswig (McGill University), Slava Ivanenko (State University of Moscow), Sophie Conroy-Dalton (Natural History Museum, London), Arthur Humes (Boston University), and Marian Pettibone (USNM) all provided taxonomic identifications. Dr. Humes is sorely missed. Keith Shepherd, Bob Holland and the ROPOS Guys, and ROPOS itself, were patient with my many questions, my endless tool-borrowing, and my sampling needs. Working their engineering magic, they made my research possible. Jim Illman (S.E.A) taught me long baseline navigation and helped make my cruise contributions possible by doing so. Thanks, Jim, for always talking to me as if I knew what data handshaking was.

Jon Kaye (University of Washington) was repeatedly my gracious Seattle host for meetings at NOAA or the University of Washington. Patrick von Aderkas (UVic Biology

Department) was graduate advisor for most of my time at UVic and was always a positive force and an interested participant in our hallway conversations. Janet Voight (Field Museum of Natural History) has given me much advice, help, and encouragement. There is much to thank her for, but I thank her most for being my friend. Jim Cowen (University of Hawaii) and Paul Johnson (University of Washington) gave me the most wonderful gift: a trip to the bottom of the ocean in Alvin. Paul Johnson, one of my favourite geophysicists, provided unflagging encouragement, support, cruise berths, and candy. Bob Embley and Bill Chadwick are my other two favourite geophysicists and are two reasons why I am addicted to going to sea. Special thanks to Bob for sharing his experience, knowledge, and rope tricks with me during a number of cruises. Kim Juniper (Universite de Quebec a Montreal) is what I would like to be when I grow up. Thank you Kim for all the reference letters past and future.

My mother and father were instrumental in getting me to this point. Both always offer unconditional support and love and both have an understanding of academics for which I am grateful. My friends are key to my life's enjoyment and two friends have sustained me the most: Jesse Schuhlein and Jennifer Canterbury.

I appreciate the time and commitment of my committee in helping and guiding me along my way. The Tunnicliffe Lab has been central to my existence for more than five years. The discussions, food, and support I have enjoyed there cannot be quantified. I have been lucky to have Andrew McArthur, Anja Schulze, Jacqueline O'Connell, Jean Marcus, Laura Genn, and Amanda Bates as labmates. Laurel Franklin has been my friend and succor. She has ungrudgingly spent countless hours of her work and leisure time to help me. I thank Verena Tunnicliffe, my supervisor. Five years are not enough to learn everything she has to teach, but I am grateful for what I have learned and the opportunities she has provided. She opened my eyes to the delights of the deep-sea.

Monetary support was provided by NSERC, the University of Victoria, the Maritimes Award Society of Canada, the Canadian Federation of University Women, the families of Maureen de Burgh and Gordon Fields, the Field Museum of Natural History, and the British Columbia Advanced Systems Institute.

Dedication

For Dr. H. M. Reiswig and Dr. A. G. Humes.

CHAPTER 1

Introduction

Hydrothermal vent ecology is in an early stage of development because of the relative novelty of vents to scientists and the inaccessibility of the habitat. Taxonomic efforts, crucial to any biological understanding of a system, were an early focus of biological efforts at vents due to the large number of new species and genera discovered in vent collections (Tunnicliffe 1991; Juniper and Tunnicliffe 1997). Vent systems have made important contributions to biology because of the unusual adaptations to extreme conditions and the insight given by vent animals into historical and phylogenetic relationships. The composition, setting, and biologic requirements of vent animals are unique: do ecological rules from other systems apply in this environment? Vent ecologists must detail the natural history, inter- and intraspecific interactions, life history strategies, diversity, and population level parameters such as density-dependent or independent growth to answer this question.

Most modern investigations of intertidal ecology search for general mechanisms and processes to explain observed patterns of distribution, abundance, and the intensity of interactions among component species (Underwood and Denley 1984). Early work on the intertidal began with detailed observations of distribution patterns of intertidal biota. This work laid the foundation for the modern era of manipulative experimentation in the intertidal that has resulted in generalisations and/or models about the nature and organisation of assemblages of species on rocky shores and elsewhere (Underwood and Denley 1984). Many of the fundamental theories we see in ecology texts were established in the intertidal and transferred to other ecosystems. Vent ecology is still moving from observations of patterns to detailed investigations of processes (Juniper and Tunnicliffe 1997). My dissertation involves identification of patterns of community organisation on the Juan de Fuca Ridge. Explanations for observed patterns draw on ecological theories of succession, diversity, rarity, and dispersion.

Goals

1) Describe community structure in terms of species composition, diversity, rank-abundance, density, and species associations on three segments of the Juan de Fuca Ridge (Axial, north Cleft, and CoAxial). Community organisation on each of the three segments as well all three segments is described (Chapters 2, 4, and 5).
2) Interpret descriptions of intrasegment and intersegment communities using theories of rarity, species abundance models, dispersion, distribution, diversity, local and regional diversity, and succession. This goal is achieved by examining rare species in the vent environment (Chapter 3), identifying non-vent communities to compare with vent assemblages (Chapters 4 and 6), evaluating species richness estimators for considerations of sample size (Chapters 5 and 6), and discussing community diversity and controls on local diversity (Chapters 2-6).
3) Contribute to general ecology. This goal is accomplished by assessing the utility of Geographical Information Systems applied to vent data (Chapter 2), describing senescence at vents (Chapters 2 and 3), discussing the vent interspecific abundance-distribution relationship (Chapters 4-6), testing species richness estimators (Chapter 5), using local versus regional diversity theory as a framework to discuss controls on

local vent diversity (Chapters 5 and 6), and evaluating the potential of metapopulation theory applied to vent populations (Chapter 6).

Geophysical setting

The accessibility of the Juan de Fuca Ridge has fostered several decades of research in many disciplines. The ridge lies about 400 km west of B.C., Washington, and Oregon (Figure 1.1). It is 525 km long, has an axis trending N020°E, and has seven principal segments (Baker and Hammond 1992): Middle Valley, Endeavour, Cobb, CoAxial, Axial, Vance, and Cleft. The Juan de Fuca Ridge has a spreading rate of 6 cm per year.

The major segments of a ridge are the "unit elements" of seafloor spreading and are usually characterised by along-strike changes in axis depth. The segments behave as distinct elements and along-strike changes are probably related to variations in magma supply under each segment. Shallow depth and broad axial volcanic ridge morphology occur at segment mid-points where magma supply is most robust and possibly centralised (Macdonald et al. 1988). The depth of each segment increases towards the ends. Shallow depths of most of the axial region on the Juan de Fuca suggest that magma is supplied regularly to most of the segments. Significant variations from segment to segment may be associated with variations in the phase of volcanic activity or with local, longer-lived variations in volcanic supply. For example, Axial Seamount is forming over a hotspot on the Juan de Fuca and appears to have a larger magmatic budget than the other segments (Davis and Currie 1993).

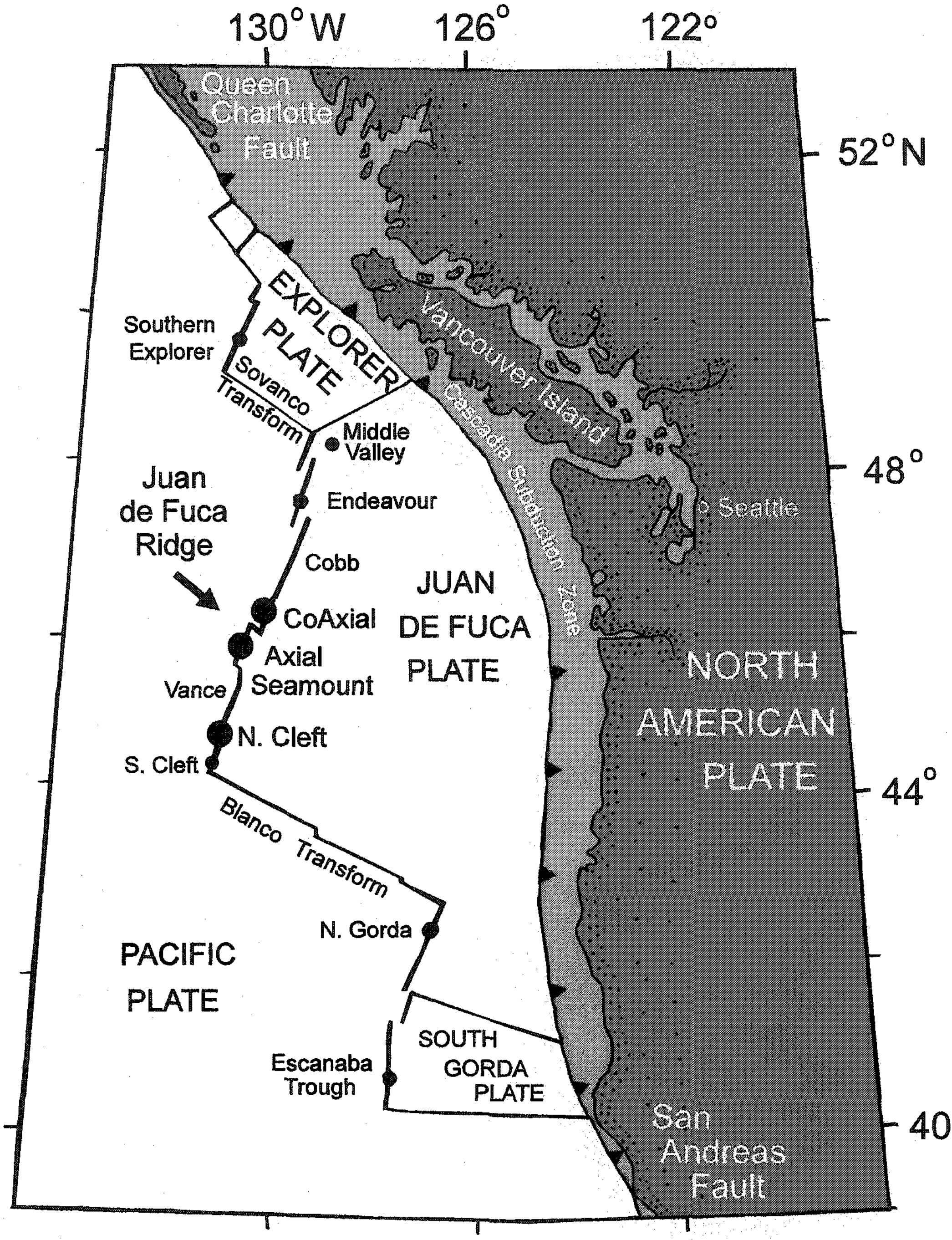


Figure 1.1. The Juan de Fuca Ridge in the northeast Pacific. Dots on the ridge represent segments with active vent sites. Large dots indicate segments discussed in the thesis: Axial, north Cleft, and CoAxial. The two closest mid-ocean ridges are also shown: Explorer to the north, and Gorda to the south. Adapted from Tunnicliffe et al. (1997).

Segments of the Juan de Fuca Ridge discussed in this thesis are: Axial (Chapters 4, and 5), Cleft (Chapters 2 and 5), and CoAxial (Chapters 3 and 5). The geophysical background of the segments considered in each chapter are provided in the chapters where appropriate. Vents are linearly distributed along a ridge axis, usually concentrated at the central topographic highs of each segment (Tunnicliffe 1991). Segments can be about 30 to 100 km-long and thus vents on any given segment are isolated from vents on neighbouring segments by at least 30 km or more. The distance from CoAxial, the most northern segment discussed in the thesis, to the southernmost vents on north Cleft is about 150 km. Axial lies between the two segments at a distance of about 37 km from the CoAxial vents and about 113 km from the north Cleft vents.

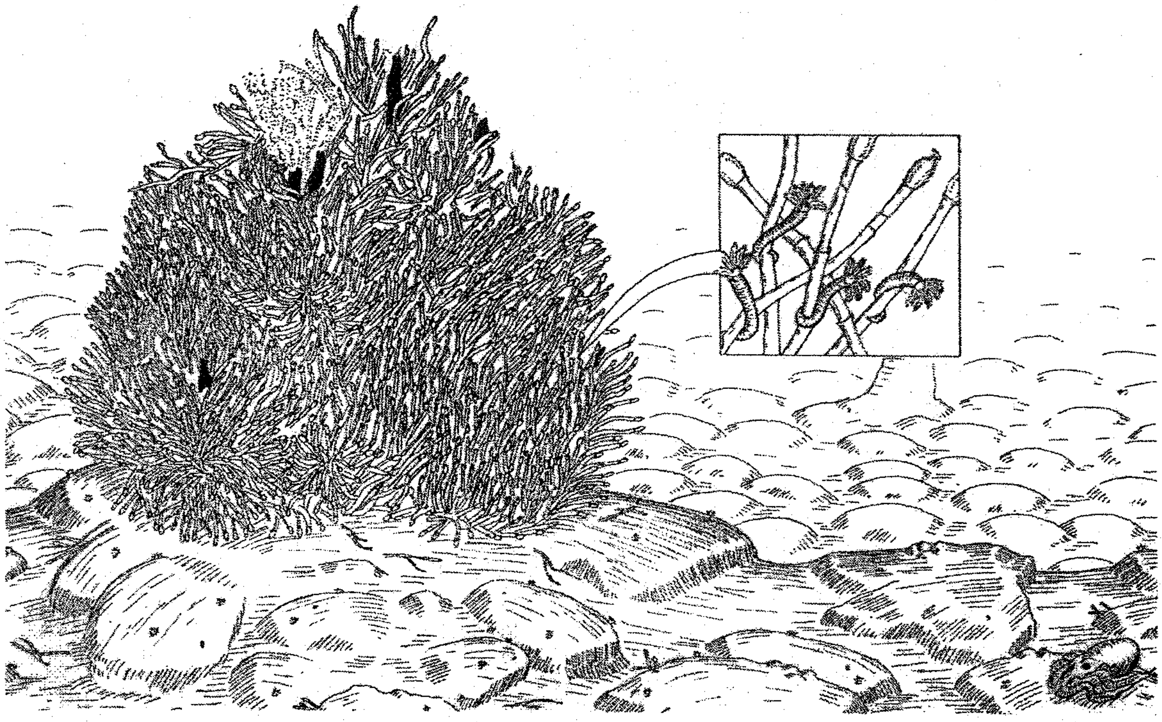
Vent characteristics

Hydrothermal venting is a product of deep-earth processes that drive plate tectonics and the genesis of ocean crust at spreading centres. At mid-ocean ridges, seawater circulating below the crust becomes heated and absorbs dissolved substances from the rock. Among these substances, dissolved sulphides in the vent fluids are important to the vent communities. Chemosynthetic microbes form the base of the trophic structure. These bacteria produce organic carbon by oxidising sulphide (predominantly) and are the basis for enhanced productivity at vents relative to the surrounding deep-sea. Vent macrofauna are mostly endemic and taxonomically distinct from that of the surrounding deep-sea community and relatively little is known about the biology of many of the vent species. Although phylum and class-level diversity is quite high for the Juan de Fuca Ridge (seven phyla and at least 11 classes), there are fewer than

100 species for the entire region (Tunnicliffe pers. comm.). Vent animals require vent conditions and most are not free to move between vent fields during their adult lifetime. For large mobile species such as gastropods and polynoid polychaetes, individual vents can probably be bridged within a vent field when the distance is on the scale of metres. At greater distances, however, migration between vent communities for all species (other than for non-endemic predators) is probably solely via larval dispersal. Because vent biota are dependent on the vent system, variations in vent outflow and fluid chemistry cause local heterogeneity (Luther et al. 2001). Heterogeneity of the vent habitat varies over time and space. Vents display extreme temperatures and temperature gradients and have high productivity. Vents can be ephemeral (lasting a few years) to long-term (lasting from decades to perhaps hundreds of years) (Grassle 1985; Campbell et al. 1988; Tunnicliffe 1991; Lalou et al. 1995). Individual vents can be separated by a few metres or kilometres within one vent field. Vent fields may be separated by tens to hundreds of kilometres on one segment. The vent environment is unpredictable and unstable for the individuals and species that inhabit it.

I call vent communities low temperature if the temperature is less than 60 °C, and high temperature if the temperature is greater than 60 °C. Low temperature assemblages on the Juan de Fuca are visually dominated by the tubeworm *Ridgeia piscesae* that forms much of the substratum for other vent fauna (Figure 1.2). Visible macrofauna on and around tubeworms include polynoid (crawling on tubes and rocks) and alvinellid (coiled around tubeworm tubes or attached to tubes in mucus sheaths) polychaetes and various gastropods. High temperature assemblages are visually dominated by a different morphotype of *Ridgeia piscesae* (discussed in Chapter 5), by the sulphide worm,

Figure 1.2. Low temperature vent assemblage. Line drawing of a tubeworm bush on basalt. Inset: the palm worm *Paralvinella palmiformis* on tubeworm tubes. The bush is about 1.2 m across at the base. A non-vent octopus is sitting to the right of the bush on the basalt. Courtesy of Verena Tunnicliffe, University of Victoria.



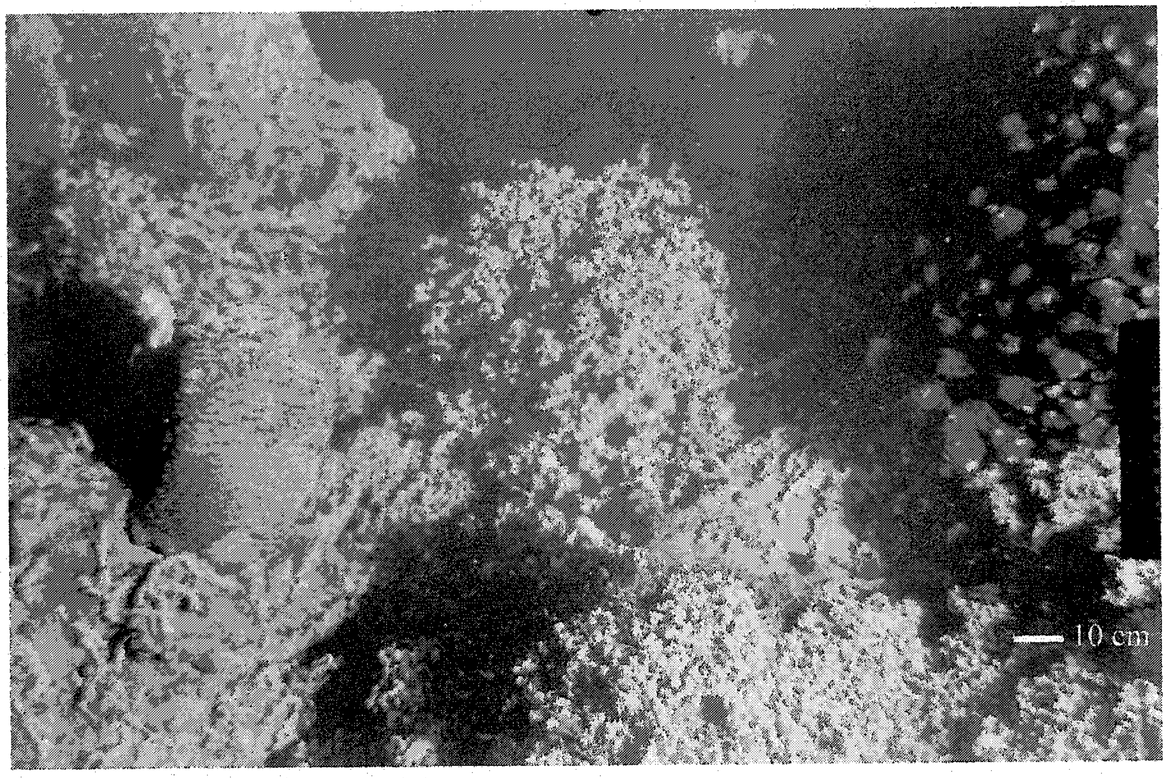
Paralvinella sulfincola, and/or by gastropods (Figure 1.3). High temperature communities surround orifices of focused fluid flow on sulphide chimneys. Low temperature communities are found on basalt or on sulphide structures away from areas of high temperature fluid flow.

Vents present practical limitations to research that impact any evaluation of the significance of ecological work in this system. Vents on the Juan de Fuca Ridge are found from approximately 1500-2400 m in depth. Because of weather, there is a short window of opportunity from late May to September within which fieldwork can be done. Fieldwork is very expensive (ship costs run from $20 000-30 000 per day) and the logistics of arranging ship and submersible time is daunting. With adequate funding, an available ship and submersible, good diving weather, and equipment and submersible running smoothly at sea, a maximum of eight to ten grab samples of tubeworm bushes can be obtained in one field season. Biologically useful data consist of animal and fluid samples, video, and still photographs. These data can only be taken once a year around the same time and often cannot be replicate sampled in the same or successive years.

Miscellany

During the course of writing this thesis, the polynoid polychaetes *Branchinotogluma grasslei* and *B. sandersi* were determined to be different sexes of the same species (Hourdez pers. comm.). A formal announcement of which name will be used has not been made, so I pool the abundance data for this species and call it "*Branchinotogluma* sp.". Appendix 1 is a master list of Juan de Fuca species discussed in the thesis. These species are present on Axial, north Cleft, and/or CoAxial. Also

Figure 1.3. High temperature vent assemblages on sulphide chimneys. High temperature communities are dominated by the tubeworm *Ridgeia piscesae* (fat morphotype), the sulphide worm *Paralvinella sulfincola*, and/or gastropods such as the limpet *Lepetodrilus fucensis* and the snail *Depressigyra globulus*. Red branchial plumes of *R. piscesae* are visible on the right-hand side of the figure. In the middle of the figure, *P. sulfincola* are attached to bare sulphide. Around the *P. sulfincola* are the gastropods. A high temperature orifice is on the left-hand side in the shape of a beehive.



10 cm

during the course of writing this thesis, there was an eruption on Axial Seamount (Embley and Baker 1999). Major earthquake activity on Axial in January 1998 was subsequently determined to be a volcanic eruption. I do not include any new vents formed by this eruption in my Axial data set. However, I do include samples from Axial taken in 1998 and 1999. These samples are communities believed to be established before the eruption but the communities may have been affected by the upheaval. For example, a change in vent fluid chemistry could have led to a shift in the species composition and abundances but this was not examined.

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CHAPTER 2

2.1 Prologue

This chapter investigates three levels of ecosystem properties:

- composition of the species pool;
- substratum differences and species associations; and
- community succession.

What is succession?

The term "succession" has many connotations for ecologists. Some vent ecologists avoid the term, choosing "temporal change" instead. The Concise Oxford Dictionary (1982) offers the biological definition: "an order of development of species or community". Succession in plant ecology is a pattern determined by life history traits and the availability of propagules whereby shifts in species dominance are caused by changes in the environment that affect the competitive balance. Interactions among speices modify the magnitude and or timing of change in the community, but the nature of that change follows a generally predictable pattern (for examples, see Brown and Southwood 1987; Chapin et al. 1994; Huston 1994; Halpern et al. 1997).

Is succession a useful concept in the vent environment? Succession is used in the vent literature (Sarrazin et al. 1997; Shank et al. 1998; Sarrazin and Juniper 1999; Sarrazin et al. 1999). Although Sarrazin et al. (1997) use succession to describe the process of community change on a single sulphide structure within an active vent field, Shank et al. (1998) use it in the more classical sense: new vent formation is a catastrophic phenomenon that opens up new habitat to be colonised in sequence by different species. Vent formation is similar to a lightning strike in a pine forest. It is catastrophic in the sense that the substratum is changed radically and most typical non-vent fauna are now excluded from this habitat. There is newly produced substratum that lacks all, or most, propagules and surviving organisms and this substratum is colonised in some kind of order (e.g. Horn 1974; Connell and Slatyer 1977; Tilman 1988; Del Moral and Bliss 1993). In the non-vent deepsea, succession is spatially and temporally variable (Rex et al. 1997). We do not know how predictable the sequence of vent colonisation may be. However, studies on the East Pacific Rise (Figure 2.1.1) (Hessler et al. 1988; Shank et al. 1998) and Juan de Fuca Ridge (Tunnicliffe et al. 1997) indicate a directional pattern of change in low temperature vent communities over time.

Vent successional studies

Describing spatial and temporal distributions of vent communities is a popular topic in hydrothermal ecology (Table 2.1.1). Succession is the focus of several studies (Hessler et al. 1985; Hessler et al. 1988; Desbruyeres 1995; Sarrazin et al. 1997; Shank and Lutz 1997; Tunnicliffe et al. 1997; Shank et al. 1998; Sarrazin and Juniper 1999; Sarrazin et al. 1999; Mullineaux et al. 2000). Early studies document change at vent fields on the East Pacific Rise and Galapagos Rift (Figure 2.1.1) without a pre-conceived plan to do so (Fustec 1985; Hessler et al. 1985; Fustec et al. 1987; Hessler et al. 1988). Community changes are linked to a decrease in overall vent emissions although this change and its cause are not quantified. Conclusions from these studies are the first step in the description of a pattern of vent succession.

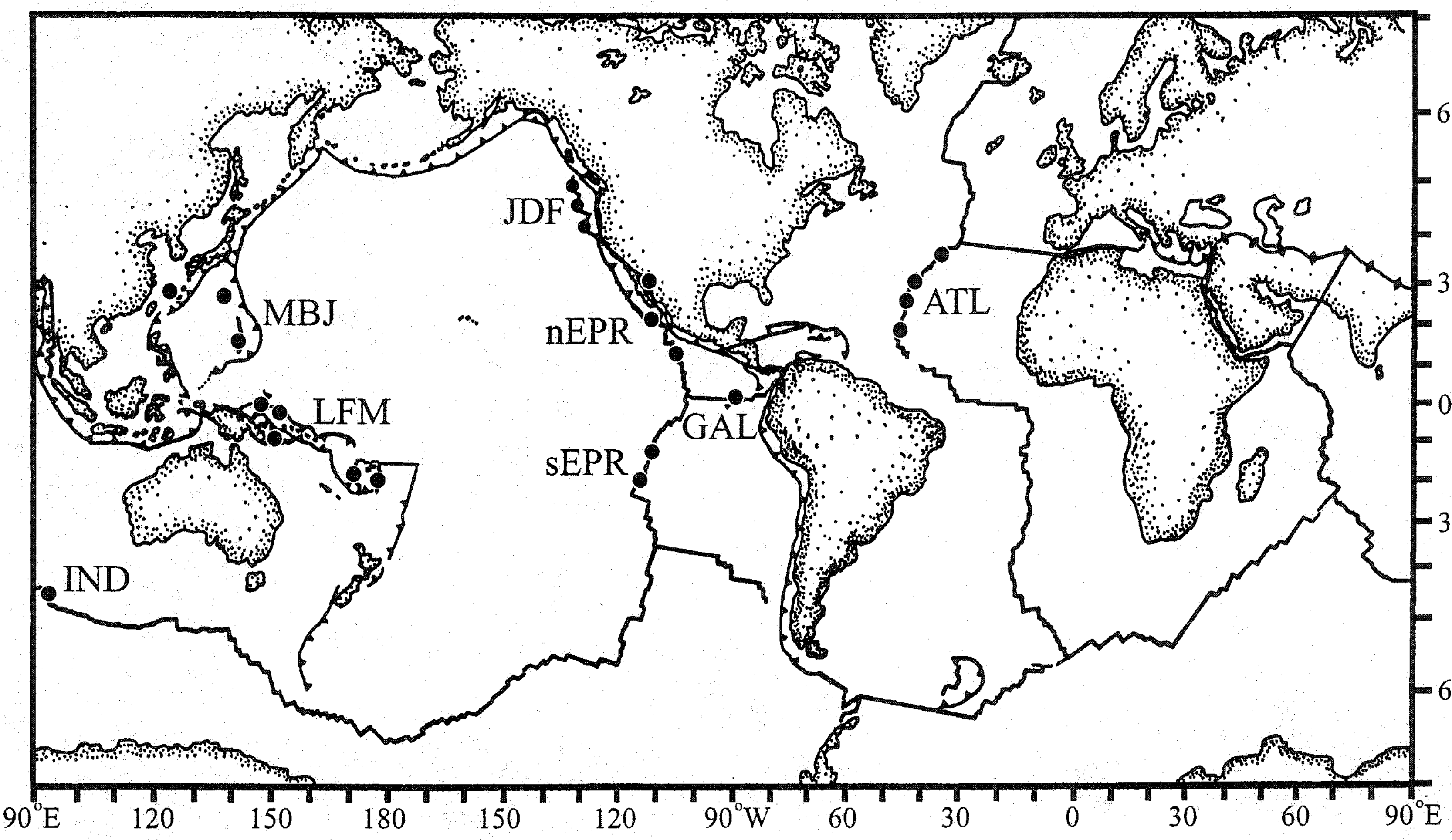

Figure 2.1.1. Distribution of major vent sites around the world. Each dot may represent several vent fields. JDF = Juan de Fuca Ridge; nEPR = north East Pacific Rise; sEPR = south East Pacific Rise; GAL = Galapagos Spreading Centre; ATL = Mid-Atlantic Ridge; MBJ = Marianas, Bonin, and Japan Trench; LFM = Lau, Fiji, and Manus back-arc basins; IND = Indian Ridge. Adapted from Tunnicliffe et al. (1998).

Table 2.1.1: Ecological studies at hydrothermal vents (see Figure 2.1.1 for location information).

Author	Location	Study interval	Successional stage	Time at initiation of study since major perturbation	Major conclusions	Spatial scale	Type of data
Desbruyères et al. 1982	11-13^{0}N EPR	Jan-Mar 1982	intermediate	none observed	biota comparable to 21^{0}N; fauna in concentric circles about vent opening	3 vent fields in a 148 km region	visual
Fustec 1985 and 1987	12^{0}N EPR	1982 and 1984	intermediate	none observed	vestimentiferans and serpulids grow and then decline; change related to fluctuations in fluid flow	6 sites in a 6 km region	visual
Grassle 1985	20^{0}S-46^{0}N Pacific & seeps in Gulf of Mexico	--	intermediate?	none observed	overview of other studies; vent comm. persist from several years to several decades	--	visual
Hessler et al. 1985	Clam Acres, 21^{0}N EPR	1982	intermediate and senescent?	none observed	bivalves dominate; cause of mortality is fluid related as think lack of H2S causes changes	1 vent field	visual
Hessler et al. 1988	Rose Garden, Galapagos	1979 and 1985	intermediate and early senescent?	none observed	vestimentiferans decrease as bivalves increase; suspension feeders decrease as scavengers increase	1 vent field	visual

Author	Location	Study interval	Successional stage	Time at initiation of study since major perturbation	Major conclusions	Spatial scale	Type of data
Arquit 1990	ASHES, Axial, JdFR	1985 and 1986	intermediate	none observed	3 ecological zones associated with the vent fluid, arranged in concentric circles around vent openings	vent field	visual
Tunnicliffe 1990	ASHES, Axial, JdFR	1 day, 1 month, and 11 months	intermediate	none observed	changes in vent composition due to submersible activity	1 vent	visual (TLC)
Tunnicliffe and Juniper 1990	Explorer Ridge and JdFR	1 day, 6 days, 1 month, and 1 year	early, intermediate and senescent?	none observed	control of biological distribution by physical factors; succession on chimneys	two vent fields, but chimneys only	visual (TLC) and samples
van Dover and Hessler 1990	Galapagos, 13^0N EPR, and 21^0N EPR	--	intermediate?	none observed	across 40^0 of latitude, megafauna of vent communities are remarkably consistent at familial level; along a segment there is a shared pool of species	within vent field, among vent fields within a cluster on a segment, and among segments	visual
Chevaldonné 1991	13^0N EPR, Lau, and North-Fiji	up to 47 hours	intermediate	none observed	tidal cycle observed	1 vent	temperature logger

Author	Location	Study interval	Successional stage	Time at initiation of study since major perturbation	Major conclusions	Spatial scale	Type of data
Chevaldonné and Jollivet 1993	13^{0}N EPR	1987	intermediate	none observed	visual biomass, density, and area estimation technique for alvinellids developed	1 vent	visual and samples
Lutz et al. 1994	9^{0}N EPR	1991-1993	initial and intermediate	< 1 year probably; maybe a few months	by 1993, have dramatic changes in community structure and *Riftia* are very large	14 km area in 1991 and then 1.37 km area in 1992 and 1993	visual
Desbruyères 1995	13^{0}N EPR	1982, 1984, 1990-1992, and 1994	intermediate	none observed	different sites at different stages of community development; emission instability affects population succession dynamics	4 vent fields within a 10 km region	visual and sampling
Grehan and Juniper 1996	Middle Valley	1 week	intermediate?	one observed	develop a methodology to do succession studies with video images	1 clam bed within a vent field	visual
Chevaldonné et al. 1997	22^{0}S—38^{0}N on EPR, Guaymas, and MAR	--	?	none observed	tidal cycles observed in vent environment	--	temperature loggers

Author	Location	Study interval	Successional stage	Time at initiation of study since major perturbation	Major conclusions	Spatial scale	Type of data
Sarrazin et al. 1997	Main Field, Endeavour, JdFR	1994 and 1995	early, intermediate and senescent	--	magnitude of small-scale heterogeneity can be very high; abiotic factors are the driving forces for observed change	2 chimneys	visual, chemical, and temperature
Shank and Lutz 1997	9^0N EPR	1992-1995	early and intermediate stages	1 year	sequence of colonisers; at 5-10 years post-eruption mytilid and vesicomyids replace vestimentiferans as dominant megafauna	1.37 km of axial summit caldera	visual, chemical, and temperature
Tunnicliffe et al. 1997	CoAxial, JdFR	1993-1995	initial colonisation and intermediate	3 months	constrain timing for tubeworm recruitment; document first colonisers	40 km segment, but most observations from one vent	visual, biological and chemical
Embley et al. 1998	17.5^0S EPR	Sept-Nov 1994	early and intermediate	within several years	use geological, chemical, and biological evidence to constrain the timing of the eruption	30 km along the segment	visual and chemical
Copley 1998	Broken Spur, MAR	1993 and 1994	intermediate	none observed	*R. exoculata* (shrimp) only; no differences	one vent field	visual

Author	Location	Study interval	Successional stage	Time at initiation of study since major perturbation	Major conclusions	Spatial scale	Type of data
					in population density between years		
Shank et al. 1998	9^0N EPR	1989, 1991-1995	early, intermediate, and early senescent?	~15 months pre-eruption and then starting at <11 months post-eruption	megafaunal dominance by vestimentiferan spp.1 first, then spp.2 and then bivalves; changes linked to changes in H2S	1.37 km biogeotransect area	visual, chemical, and temperature
Sarrazin and Juniper 1999	Main Field, Endeavour, JdFR	1994 and 1996	early, intermediate, and senescent	none observed	refine model of community succession for chimneys from Sarrazin et al. 1997	2 chimneys	visual and biological
Sarrazin et al. 1999	Main Field, Endeavour and N. Cleft, JdFR	1993 and 1995	early, intermediate, and senescent	none observed	significant influence of local physical and chemical conditions on species distributions; environmental factors most important in structuring community	2 chimneys	visual, chemical, and temperature
Mullineaux et al. 2000	9^0N EPR	1994 and 1995	early and intermediate	three years	*T. jerichonana* are pioneer colonisers	3 different vent sites over 2 km	biological (settling plates)

Author	Location	Study interval	Successional stage	Time at initiation of study since major perturbation	Major conclusions	Spatial scale	Type of data
					subsequently replaced by *R. pachyptila*; *T. jerichonana* may facilitate settlement of *Riftia* via excretion of a chemical		

The next generation of studies use two eruptions--one on 9°N East Pacific Rise and one on CoAxial segment of the Juan de Fuca Ridge--to document pioneer species at new vents and to confirm the successional pattern observed by earlier studies. Work on the submarine eruption at 9°45'-52'N on the East Pacific Rise (Lutz et al. 1994; Shank and Lutz 1997; Shank et al. 1998; Mullineaux et al. 2000) produced the following scenario of succession: 1) microbial debris from a subsurface source covers new vent areas in the form of thick, white mats within days of the eruption; 2) mobile vent fauna (e.g. amphipods, copepods, brachyuran and galatheid crabs) and some non-vent fauna proliferate in response to the increased microbial production; 3) within one year, the vestimentiferan *Tevnia jerichonana* colonises; 4) within two years, another species of vestimentiferan, *Riftia pachyptila,* dominates vent openings where *T. jerichonana* was at step 3); 5) within three years, mussels begin to colonise; 6) within four years, galatheids and serpulid polychaetes increase and approach active vent openings, and mussels begin to colonise *R. pachyptila* tubes; 7) from three to five years, there is a two- to three-fold increase in the number of species; and 8) at five years post-eruption, mussels and vesicomyid clams replace vestimentiferans as the dominant megafauna.

Work at 9°N extends knowledge of post-eruption community organisation to five plus years, and relates concomitant physico-chemical information to observed changes. Changes in fluid chemistry are thought responsible for the observed faunal succession. H_2S levels are very high (>1 mmol kg^{-1}) at initiation of venting and for at least a year afterwards; within two years H_2S levels appreciably decrease and continue to decline over the course of the study. Differences in fluid chemistry have been shown to be responsible for controlling the distribution of organisms at East Pacific Rise vents (Luther et al. 2001).

Tunnicliffe et al. (1997) use visual, biological (meiofauna included), and chemical data to document the sequence of community change from three months to two years post-eruption on the Juan de Fuca Ridge; the vent fauna here is distinct from that of the East Pacific Rise as it forms a separate biogeographic province (Tunnicliffe 1988). At CoAxial, initial colonisation and intermediate stages of the community are not that different from 9°N: 1) microbial communities in the form of thick, white mats are established three months after the eruption; 2) macrofauna arrive within one year (including the only vestimentiferan species on the ridge); 3) within two years, one-third of the regional vent species pool arrives; and 4) H_2S levels peak one year after the eruption and then drop off (Butterfield et al. 1997).

Recent vent succession studies document changes in assemblages inhabiting sulphide edifices (Sarrazin et al. 1997; Sarrazin and Juniper 1999; Sarrazin et al. 1999). On a single chimney, several distinct types of communities may be determined by abiotic factors such as substratum and fluid flow. Starting with a new vent opening and bare substratum, communities progress from Type I to Type VI as the animals modify their physical habitat and fluid flow through the chimney changes. Unpredictable changes in the sulphide edifice (e.g. pieces falling off or fluid conduits getting clogged) can cause assemblages to switch community type either forward or backward in the sequence.

Table 2.1.1 documents three features of study methodologies:

- almost all studies use visual data that cannot record many small species, in particular, meiofauna;

- the spatial scale of most studies encompasses a single vent or vent field; and
- all studies look at early and/or intermediate stages of succession.

Community structure of dying vents is not investigated. Lack of information on senescent communities is typical for successional studies in general, not just studies in the vent environment (Rosenzweig 1995). The lifetime of the system under study is often much longer than the research funds, career, interests and in some cases, life span of the scientist.

Geophysical background

In September 1986, investigators measuring the thermal and chemical properties overlying the southern Juan de Fuca (Figure 1.1) detected an event plume over Cleft segment (Baker et al. 1989). An event plume, or "megaplume" is a plume of hydrothermal effluent of extraordinary size and heat content compared to the lower chronic plumes found over continuously venting areas. This megaplume (Megaplume 1986, Figure 2.3.1), is estimated to have had heat flow of about one year's worth of discharge from a typical ridge crest vent field in a single month. The megaplume disappeared within one month. Another event plume was recorded in 1987 (Embley et al. 1994). Both plumes are thought to be the result of a sudden expulsion of fluids from a pre-existing hydrothermal system, probably from a fissure produced by an episode of seafloor extension (Baker et al. 1989; Embley et al. 1994). Sea Beam side scan sonar and deep-towed cameras subsequently confirmed that a basaltic fissure eruption occurred in the area of north Cleft (from about 44° 55.5'N to the end of the segment), resulting in very young lava flows and vigourous hydrothermal activity. These lava flows were likely produced by an along-axis source such as a dike intrusion along different parts of the same fissure system (Chadwick and Embley 1994; Embley and Chadwick 1994; Smith et al. 1994). In this chapter, I use 1986 as "time zero". I assume it is the year that the low temperature vents are initiated on north Cleft. This assumption follows the precedent of Butterfield and Massoth (1994) who describe marked changes in vent fluid chemistry on north Cleft and suggest that 1986 is the year venting was (re-) initiated.

Goals

My goals for this chapter are:

- to examine species richness, abundance, and distribution;
- to investigate reasons for observed community structure; and
- to document temporal changes in the faunal assemblage.

Summarising temporal change and community organisation on Cleft is a step towards comparing all active venting segments on the Juan de Fuca and other mid-ocean ridges. Comparing segments on the Juan de Fuca and comparing ridge systems is one method of investigating observed successional patterns. Comparing vent communities on different types of spreading segments (slow-, medium-, or fast-rate spreading) may answer the question of whether similar geophysical sources produce similar community structure. Comparative data allow investigation of the kinds of controls that may determine diversity in the vent environment.

A caution

My approach uses both image and collection data. There are a number of problems with these data. First, the program of study and sampling on Cleft was not developed with biology as a major focus. Therefore, any biological work that comes out of this program is destined to be haphazard. Second, work on north Cleft began before the importance of repeated, time-series measurements was recognised. There was no repeat-sampling programme for biology. Third, there is no pre-eruption survey of the segment that can be used as a baseline to compare information from the post-eruption period. Finally, broad exploration and sampling of Cleft did not begin until two years after the 1986 eruption.

Even with the above limitations, it is worthwhile to use the north Cleft data set. Sampling vents is difficult and often unsuccessful and thus sample sizes are small. The north Cleft data represent a large set of samples compared to what is available for other parts of the ridge. Also, there has been a lot of work to understand geophysically and geochemically the dynamics of Cleft and the eruption. This work is complementary to any biological investigation of temporal change. Finally, chronicling the composition and character of the Cleft community is an essential step towards an integrated understanding of the Juan de Fuca Ridge and all of its vent communities.

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2.2: The application of Geographical Information Systems to biological studies at hydrothermal vents

Tsurumi, M. 1998. *Cahiers de Biologie Marine* **39**: 263-266.

Introduction

Geographical Information Systems (GIS) are software tools to process spatial information. The output of GIS analyses takes the form of maps, statistical summaries, and derived data sets. Such results can be used in other tasks such as modelling, hypothesis testing or to provide easy access to attributes of the data for further analysis.

Most current GIS work on biological systems is in the fields of resource management and landscape ecology. There, it aids identification and explanation of disturbance patterns, effects of intervention on landscape structure, and neighbourhood interactions in natural populations. Outside of aquaculture, there is little application of GIS capabilities to biological systems in an aquatic environment. Wright (1996) and Wright et al. (1997) demonstrate GIS utility to geological studies of vents.

An important factor that enhances uses of GIS to hydrothermal studies is the inter-disciplinary nature of hydrothermal research. With the ever-increasing amount of oceanographic data collected in multi-agency, multi-disciplinary national and international research programmes, it may be more efficient to implement comprehensive data management techniques (Wright 1996). Moreover, the difficulty and expense of sampling vents makes it crucial to maximise the amount of data available per dive. Maximal data extraction includes observations derived from dive tapes and photographs on geological, chemical, and biological features associated with venting. In GIS software, notes about these features can be entered and coordinated with point locations. These data and notes can be further organised alongside other notations such as what was sampled where, and by whom.

Another incentive to explore applications for biological work is the current use of GIS a tool for data collection and processing by some organisations, notably, the VENTS Program of NOAA. Post-dive, VENTS researchers use GIS software to provide maps of dive and camera tow tracks and produce tables of features associated with point locations from the tracklines. NOAA provides an interactive link to some of its GIS database (World Wide Web, http://www.pmel.noaa.gov/vents/coax/gis_www.html). Off-site users have the capability to view, summarise, and make calculations on vent data held by various research institutions. A direct benefit derived from GIS organisation of vent data is more expeditious delivery of such data to researchers involved in related investigations.

Presented here are partial results of a GIS application to a temporal study of venting on north Cleft Segment, Juan de Fuca Ridge (Figure 1.1). The goal is to illustrate the use of this GIS software as a supplementary tool for analyses of temporal change and succession at vents.

Background on north Cleft segment

In 1986 and 1987 two distinct megaplumes were discovered over north Cleft segment. Modelling of the dynamics of both plumes was consistent with the sudden expulsion of fluids from a hydrothermal system (Embley et al. 1994). Towed camera and submersible observations located extensive diffuse venting and several black smokers between 44°53'N and 45°03'N (Figure 2.2.1). North Cleft was visited from 1988 until

1995 by camera tow and submersible. In 1990, submersible observers found areas of dead tube worms and moribund vent communities; the high temperature vents remained vigourous. By 1991, diffuse venting had ceased along this part of the segment. In 1994, a new vent on a recent lava mound was located but venting remained absent elsewhere except at high temperature chimneys.

Using GIS to document temporal change

The GIS software package used in this analysis is ArcView® 2.0 by ESRI™ which operates in the Microsoft® Windows™, Apple® Macintosh®, or UNIX® environments. Some of the tasks possible with ArcView include: 1) mapping, 2) displaying data from other GIS software databases, 3) displaying tabular data, 4) querying/searching/manipulating attributes of any features associated with a map in the database, 5) summarising and generating statistics on the attributes of features associated with a map, and 6) creating charts to show the attributes of features. In addition, there are ways of customising ArcView to suit specific work needs.

The series of maps presented in Figure 2.2.2 (a-d) show how information on the temporal state of venting on north Cleft can be displayed using this GIS mapping program. These figures were produced by ArcView using data from the NOAA GIS database and from review and annotation of all the dive tapes, dive logs, and still photographs available from north Cleft from 1988 until 1991. Within ArcView, each feature is mapped as a separate coverage called a "theme". Therefore, on Figure 2.2.2a-

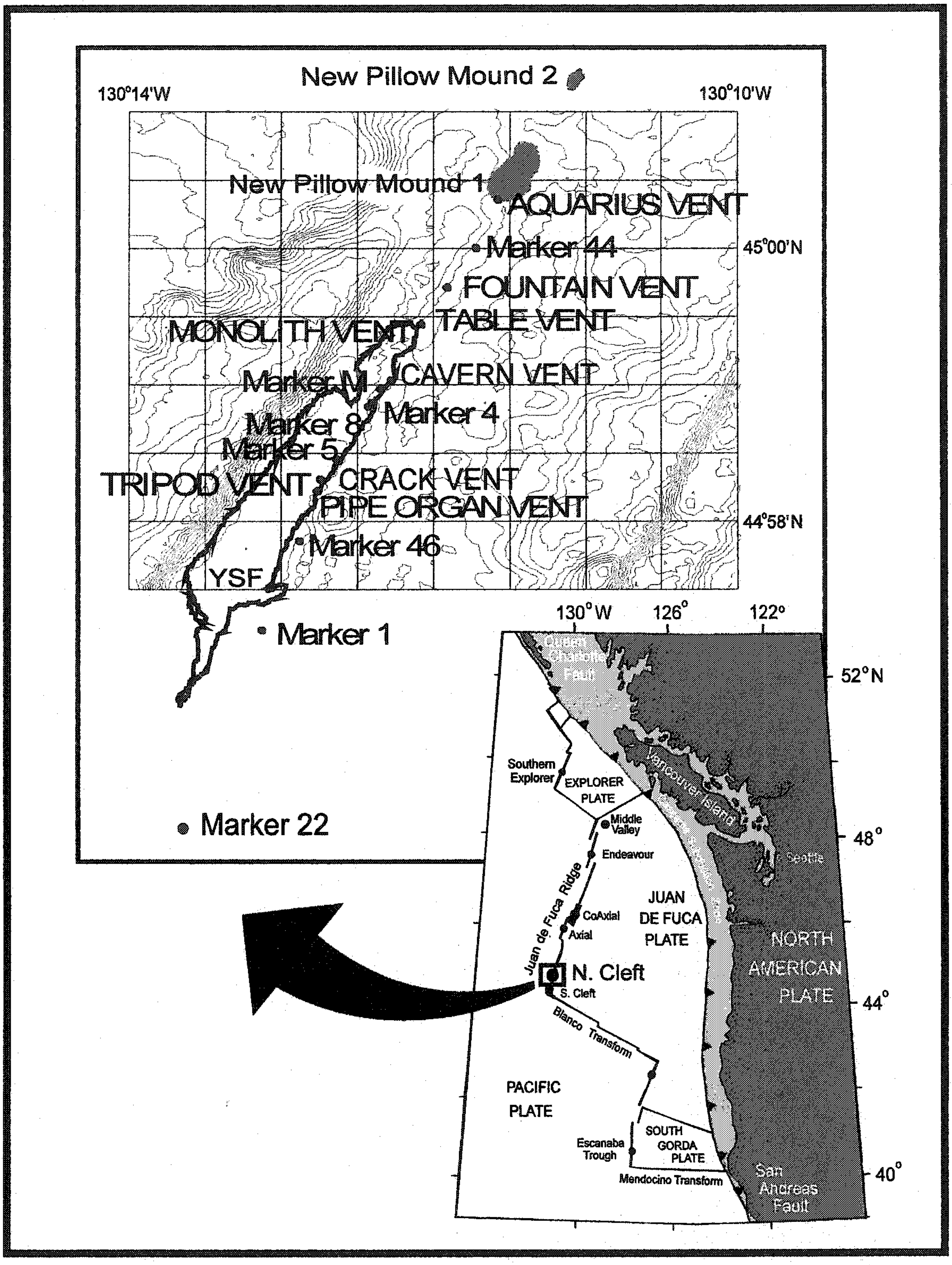
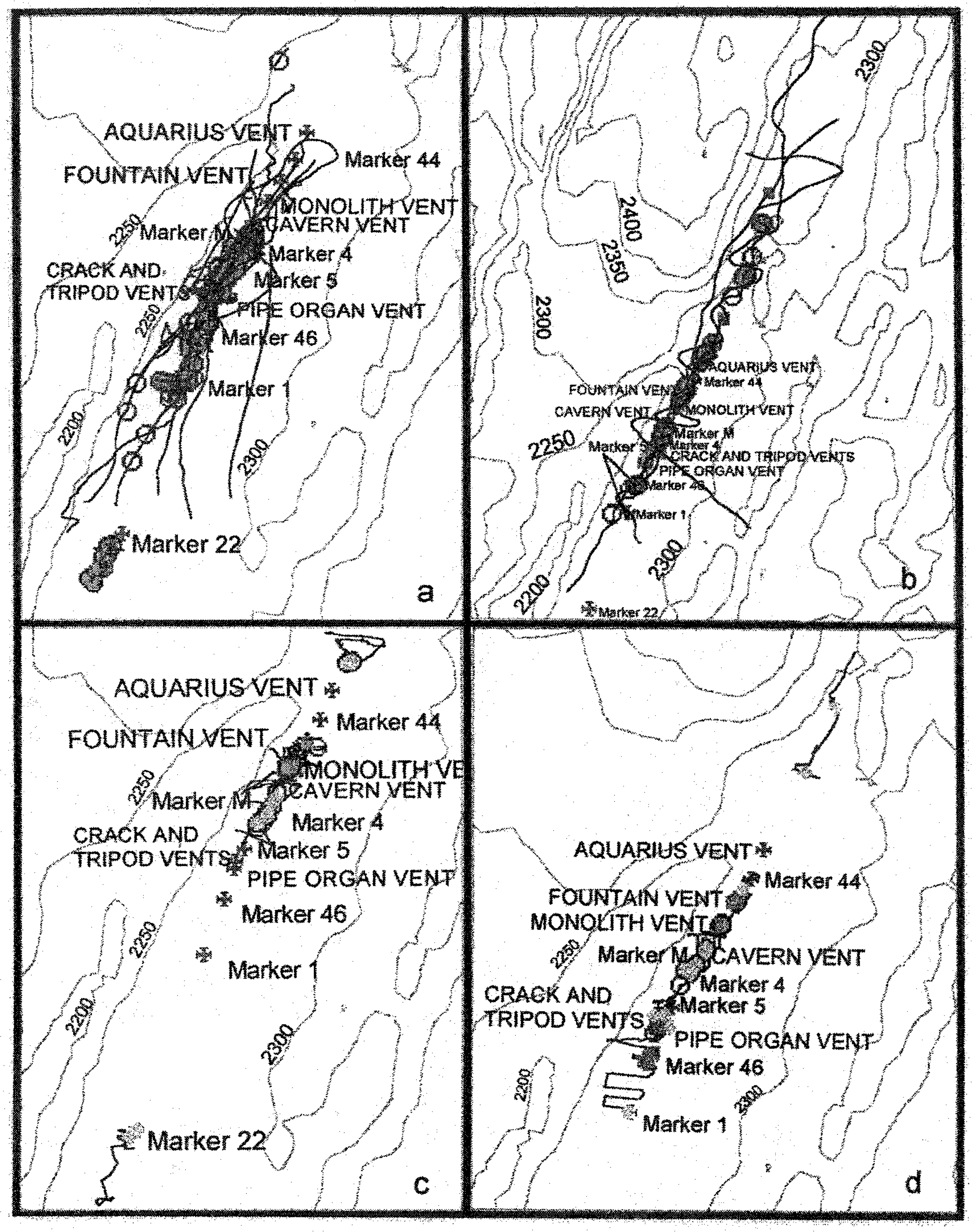


Figure 2.2.1. Location of the Juan de Fuca Ridge showing surrounding tectonic features. Inset shows a close-up of the vents, geological features, and bathymetry of north Cleft segment. The contour intervals are 10 m.

Figure 2.2.2. a-d show the temporal changes in venting extent from 1988 to 1991 at north Cleft segment. a: 1988 Alvin and camera tows. b: 1989 camera tows. c: 1990 Alvin. d: 1991 Alvin. The contour intervals are 50 m. Vents are shown by the Maltese crosses; high temperature vents in upper case and low temperature vents in lower case. Open circles indicate areas with bacteria. Dark grey squares indicate areas of tube worms. Light grey stippled diamonds indicate areas of dead tube worms. Black lines are Alvin and camera tow tracklines.


AQUARIUS VENT
Marker 44
FOUNTAIN VENT
MONOLITH VENT
Marker M
CAVERN VENT
Marker 4
CRACK AND TRIPOD VENTS
Marker 5
PIPE ORGAN VENT
Marker 46
Marker 1
Marker 22
2200
2250
2300
2350
2400
a
b
c
d

d, the bathymetry is one theme, the markers/vents locations another, the presence of bacteria yet another, and so on. These themes are then layered to produce a map. This is a qualitative means to convey the concept that at north Cleft, diffuse venting seemed to peak in 1988 and to be in rapid decline by 1991.

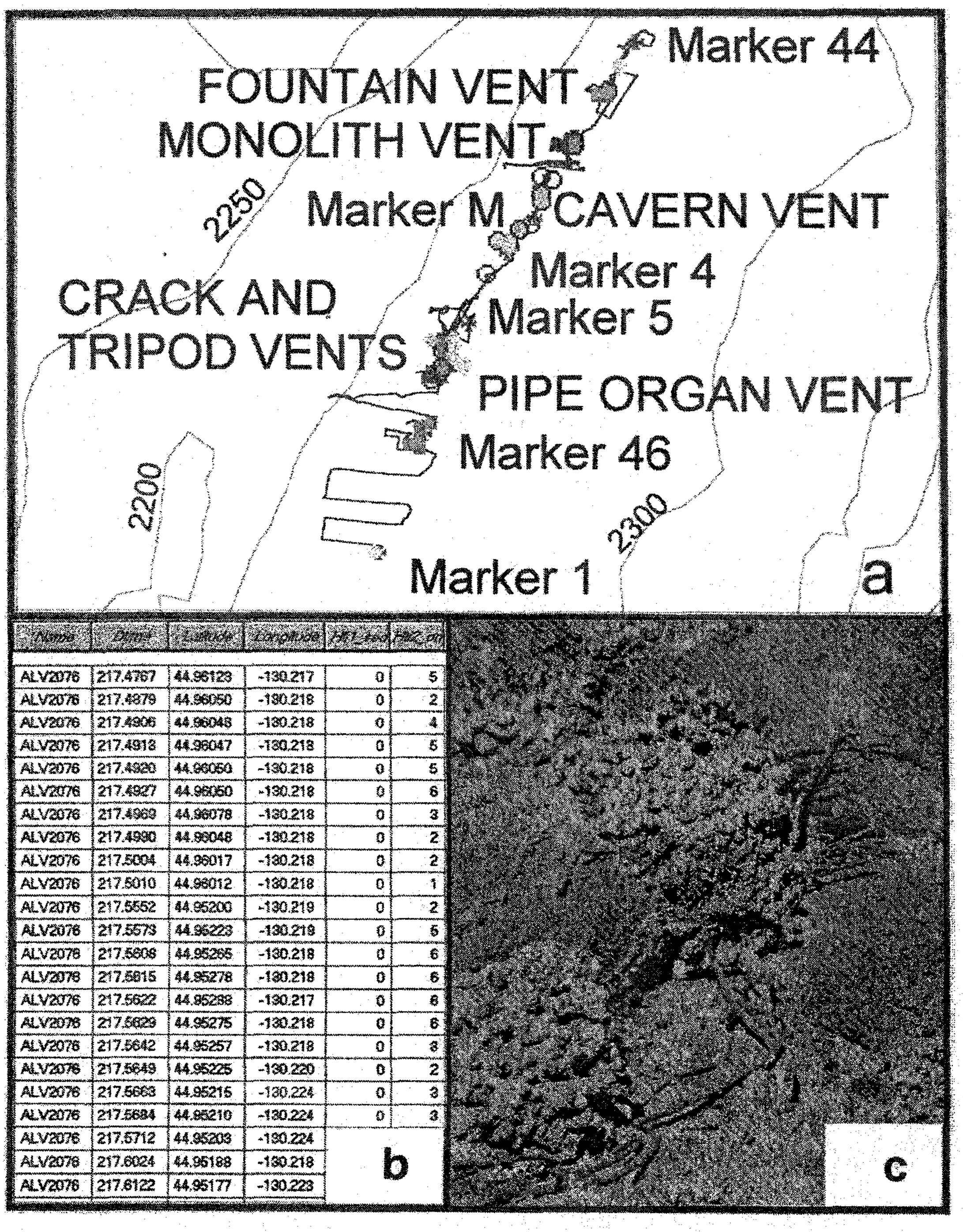
ArcView tables are a convenient way to store data associated with a map. These data can be manipulated statistically in other programs by exporting the ArcView attribute tables (Figure. 2.2.3b). Quantitative biological estimates can be made on the areal coverage of tube worms and or bacteria by using the same data that produced these maps. Basic statistics are possible within ArcView but I found that summary statistics were more easily generated by using Microsoft® Excel™.

Hot linking to other files is the facility in ArcView that allows access to other data sources or applications by clicking on a feature. For example, one could zoom in on one point location of an ArcView map and select one of the data points (e.g. the tube worms themes) to display a picture of that site, access a document or table describing it, or even play a video showing it (Figure 2.2.3a-c).

Summary

With respect to its potential as a tool for analysis, ArcView is an elegant way to display and inventory data about temporal changes in venting. At present however, it is unlikely that GIS will penetrate far into the spatial analyses domain of vent work. GIS was not intended in its inception to answer a "How is..?" type of question but rather to answer static problems such as "Where is..?" or "What is..?" (Ball 1994). The ability to handle time-dependent data (i.e. data in four-dimensions) is important for modelling such

Figure 2.2.3. a-c show an example of "hot linking" within ArcView. By clicking a point location on a, various data associated with that point location can be accessed. a: State of venting on a portion of north Cleft segment in 1991. b: An example of an ArcView attribute table with data associated with the map in a. c: A photo of the vent area at Marker 1 in 1991.



Name	Dtime	Latitude	Longitude	HF1_[illegible]	HF2_[illegible]
ALV2076	217.4767	44.96123	-130.217	0	5
ALV2076	217.4879	44.96050	-180.218	0	2
ALV2076	217.4906	44.96048	-130.218	0	4
ALV2076	217.4913	44.96047	-130.218	0	5
ALV2076	217.4920	44.96050	-130.218	0	5
ALV2076	217.4927	44.96050	-130.218	0	6
ALV2076	217.4969	44.96078	-130.218	0	3
ALV2076	217.4990	44.96048	-130.218	0	2
ALV2076	217.5004	44.96017	-130.218	0	2
ALV2076	217.5010	44.96012	-130.218	0	1
ALV2076	217.5552	44.95200	-130.219	0	2
ALV2076	217.5573	44.95223	-130.219	0	5
ALV2076	217.5608	44.95265	-130.218	0	6
ALV2076	217.5615	44.95278	-130.218	0	6
ALV2076	217.5622	44.95288	-130.217	0	6
ALV2076	217.5629	44.95275	-130.218	0	6
ALV2076	217.5642	44.95257	-130.218	0	3
ALV2076	217.5649	44.95225	-130.220	0	2
ALV2076	217.5663	44.95215	-130.224	0	3
ALV2076	217.5684	44.95210	-130.224	0	3
ALV2076	217.5712	44.95203	-130.224		
ALV2076	217.6024	44.95188	-130.218		
ALV2076	217.6122	44.95177	-130.223		

an highly dynamic marine environment as hydrothermal vent sites (Kucera 1995 and Wright 1996) and as yet GIS generally lack three- or four-dimensional display and analysis capabilities.

For the purposes of the work on temporal changes at north Cleft segment, ArcView is a useful application, supplementing descriptive and statistical analyses of change in the vent communities on this part of the Juan de Fuca Ridge. The ability to use this GIS software to augment work on the temporal ecology of north Cleft is a direct result of the effort NOAA has put into developing a database of seafloor maps of north Cleft which function as a convenient baseline from which to work.

Acknowledgments

I thank Bob Embley and the NOAA Vents Program for access to data and their GIS database. In addition, thanks are due to Larissa Lubomudrov for advice about ArcView, Laurel Franklin for technical support, and Verena Tunnicliffe for research support. This work was funded by NSERC Canada.

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2.3: Characteristics of a hydrothermal vent assemblage on a volcanically active segment of Juan de Fuca Ridge, northeast Pacific

Tsurumi, M. and Tunnicliffe, V. 2001. *Canadian Journal of Aquatic and Fisheries Research* **58**: 530-542.

Abstract

An eruption on Cleft segment, Juan de Fuca Ridge in 1986, provided an opportunity to observe potential successional patterns in vent animal colonisation. Other objectives were to describe the Cleft fauna, examine distribution and abundance of select taxa, and determine if the fauna reflected changes in water chemistry. Biological samples were tubeworm grabs collected by submersible and visual data were still photographs and video. Two years post-eruption, there were extensive diffuse vents and 23 of 44 species in the Cleft species pool were present. Five years post-eruption most low temperature vents were extinct. High temperature venting was maintained, and biological communities were reduced in visual extent. Four of the 44 species in samples from 1988-1994, accounted for over 90% of the individuals. Cluster analyses of species collected on tubes did not distinguish year or substratum differences, suggesting that a study of less than a year is necessary to document successional patterns at new vents. The Cleft subset of the Juan de Fuca species pool is likely adapted to episodic eruptive events on the decadal scale. Major changes in fluid chemistry did not result in detectable community changes other than habitat loss due to a decrease in dissolved sulphide availability.

Introduction

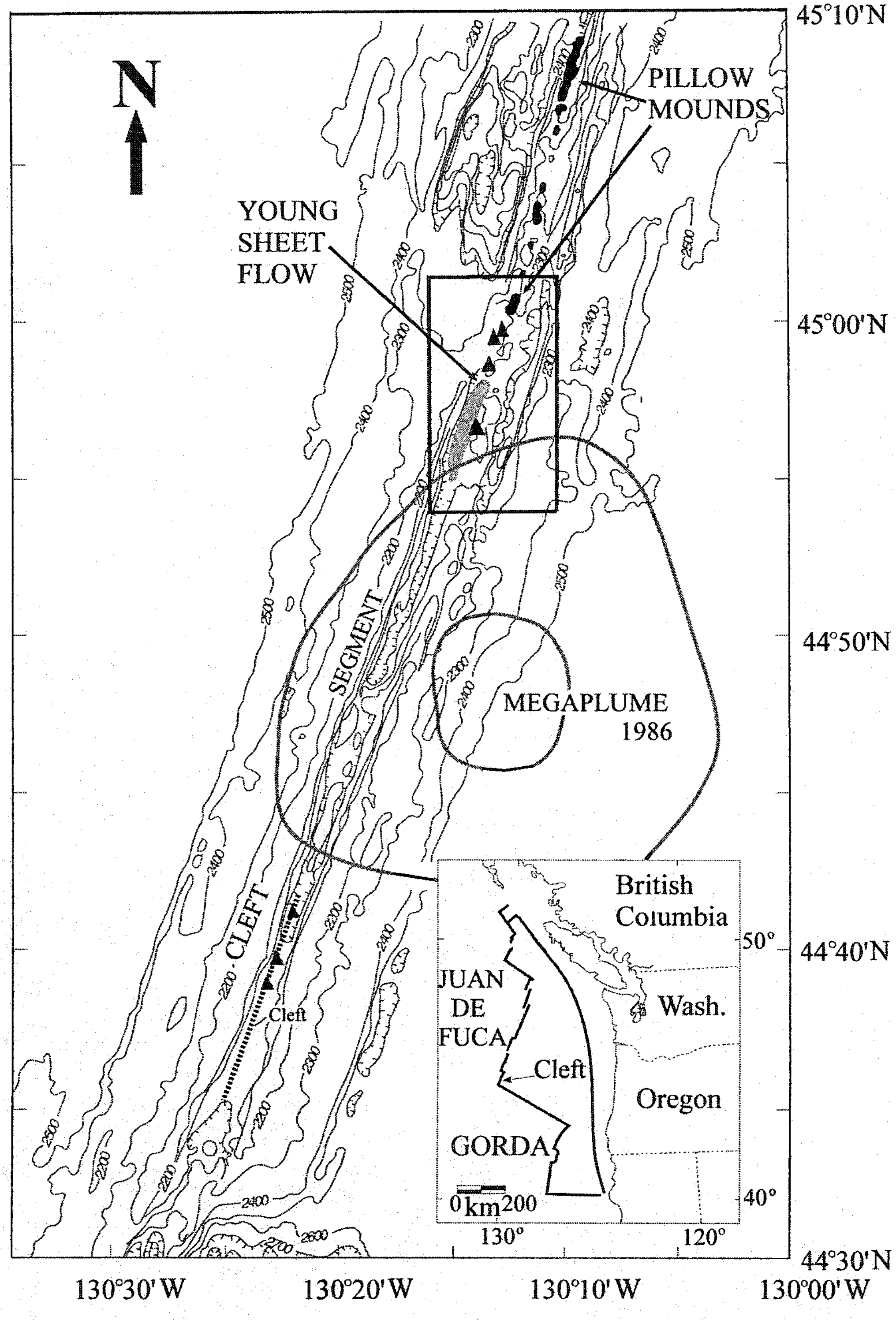
The appearance of empty habitat after a large disruption or disaster provides an opportunity to study the behaviour of the community in the subsequent colonization process. Some organisms are well-adapted to predictable disasters such as forest fires (Halpern 1989) and wave action in rocky intertidal communities (Dayton 1971), and colonization may proceed relatively rapidly. Massive landscape disruption may require decades before conditions are acceptable to a variety of organisms.

The hot vent habitat sits atop a highly dynamic ridgecrest where both tectonic and volcanic activity may frequently disrupt the community (Juniper and Tunnicliffe 1997). While these communities are difficult to access and study systematically, repeat visits note substantial changes in vent assemblages (Fustec et al. 1987; Hessler et al. 1988). The process of seafloor spreading includes the extrusion of new lavas to the seafloor above a magma chamber. Heat from the magma chamber induces hydrothermal circulation. An area prone to frequent eruptive activity usually has ongoing hydrothermalism and a local pool of vent species such as seen at the high spreading rate centres of the southeast Pacific (Embley et al. 1998). On the northern East Pacific Rise thick microbial mats, large uncolonized surfaces and even partly cooked animals indicated a recent eruption (Haymon et al. 1993). Within one year vestimentiferan tubeworms were among the first to recruit and many species appeared within five years (Lutz et al. 1994). On Juan de Fuca Ridge, even at a site where no adjacent communities were found, several species colonised eruption-induced venting in 1993 within one year (Tunnicliffe et al. 1997).

Vent animals rely on microbial production which, in turn, responds to chemical conditions in the venting fluids. A general model of post-eruption fluid evolution is presented by Butterfield et al. (1997): a change from a vapour-dominated phase of high heat flux to brine-dominated in a later time of low heat flux. Sulphide peaks sometime after the initial eruption event depending on the size of the system and longevity of the heat source. While temporal change in assemblages is observed at vents, the relationship of that change to chemical conditions is unknown. The current profile of post-colonization communities in the eastern Pacific includes: rapid appearance of macrofauna by larval recruitment, limited diversity with a changing dominance pattern in the succeeding years, very rapid growth of vestimentiferans and diminishing microbial mat coverage (Tunnicliffe et al. 1997; Shank et al. 1998).

The first seafloor eruption recognized on mid-ocean ridges occurred on northern Cleft segment of the Juan de Fuca Ridge. A huge bolus of hot water rose 800 m off the bottom in 1986 and disappeared within one month; a second megaplume was identified the following year (Baker et al. 1989). The plume character suggested sudden expulsion of fluid during seafloor extension. Subsequent side scan sonar and towed camera surveys identified very young lavas and vigorous hydrothermalism (Figure 2.3.1). These lava flows were in the form of pillow mounds and a southerly sheet (Embley and Chadwick 1994). Comparative bathymetric surveys constrained the pillow mounds' appearance between 1983 and 1987 but the sheet flow likely erupted before October 1982. The eruptive fissure lies mostly within the young sheet flow with vents concentrated along this feature (Embley and Chadwick 1994: Figure 2.3.2). Limited colonization by deep-

Figure 2.3.1. Simplified Sea Beam map of Cleft segment, the southernmost segment of the Juan de Fuca Ridge. Contour interval is 100 m except for the axial valley where it is 20 m. High temperature vents are indicated by the triangles and the young sheet flow and northern pillow mounds by grey and black shading respectively. The closest known venting is indicated on southern Cleft segment at 44° 42'N. The megaplume contour shows the extent of the temperature anomaly associated with the megaplume. This temperature anomaly is used to detect and define hydrothermal plumes. Adapted from Embley and Chadwick (1994). The box indicates the area shown in Figure 2.3.2.


N
PILLOW
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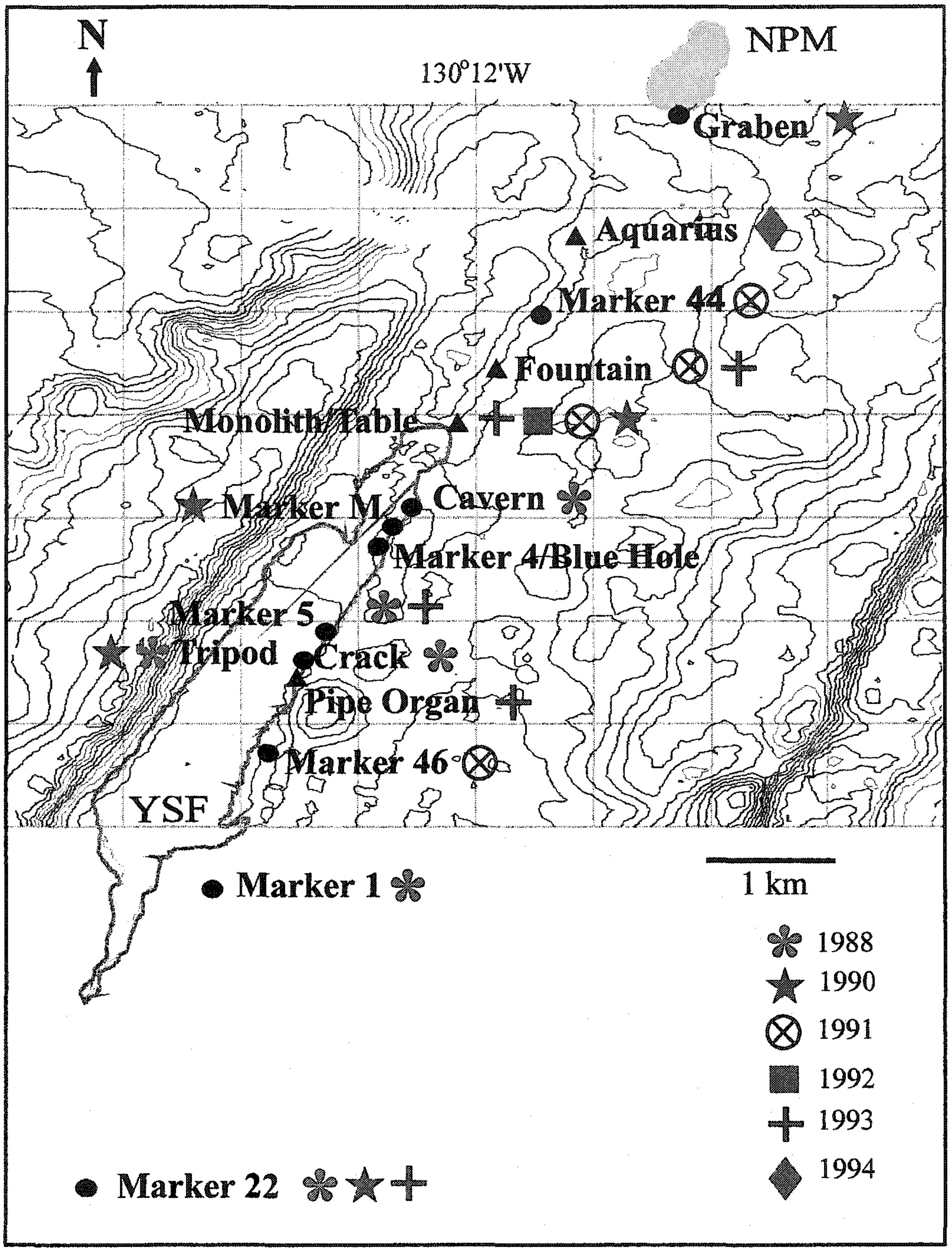


Figure 2.3.2. Map of north Cleft with sampling history for the region. The map was generated using the National Oceanic and Atmospheric Administration GIS database; detailed bathymetry is not available for the entire study area. Contour interval is 50 m. Triangles = high temperature venting; YSF = young sheet flows; NPM = northern pillow mound.

sea fauna and poor sediment cover suggest an age not much older than that date (Milligan et al. 1994).

A bottom exploration programme began in 1987 with camera tows and in 1988 with submersibles. A description of the eruption scenario arose as each year expanded the observations. Current interpretation is that the young sheet flow appeared in the 1970s. The 1986 and 1987 eruptions probably generated the northern pillow mounds but also initiated venting on the young sheet flow and, in limited areas, on the pillow mounds. Embley and Chadwick (1994) implicate a magma chamber below the young sheet flow that fed the northern pillow mound by dike injection. Subsequent cooling contracted the hydrothermal circulation to the sheet flow area during the 1990s. The steady-state chronic plume subsided to a relatively low level from 1991 through 1997 (E. Baker pers. comm., NOAA/PMEL, 7600 Sand Point Way NE, Seattle, WA). Mineralisation of the high temperature Monolith and Fountain sulphide structures (Figure 2.3.2) likely occurred prior to the eruption of the northern pillow mounds while Pipe Organ may be a product of this more recent event (Koski et al. 1994). Aquarius and Marker 22 ages are unknown.

We consider 1986 to be the year sheet flow venting was (re)initiated on north Cleft following the precedent of Butterfield and Massoth (1994). These authors describe marked changes in vent fluid chemistry in this system: they relate changes in water characters to a switch from vapour-dominated fluids in 1988 to brine-dominated fluids in 1990. Following the eruption, they speculate that widespread subseafloor boiling discharged vapour- and sulphide-rich fluids first, while brines enriched in metals accumulated deeper in the hydrothermal system. With the hindsight of the eruptions studied elsewhere and the pronounced water changes, we undertook to examine the biological collections for a successional pattern. Further objectives were to examine the distribution and abundance characteristics of select taxa at these hydrothermal vents, and determine if the fauna reflect the marked changes in water chemistry.

The data presented here extend post-eruption community observations from three (Tunnicliffe et al. 1997) to seven years. Our study is the first quantitative attempt to describe vent succession. Furthermore, this is the first study to illustrate the importance of including meiofauna in analyses of vent communities and to try to correlate evolution in water chemistry to changes in the faunal assemblage.

Methods

Study site

Cleft is the 80 km-long southernmost discrete segment of the Juan de Fuca Ridge (Figure 1.1). The smooth, shallow relief of the ridge flanks between 44° 50'N to 45° 02'N suggests a higher average rate of extensive volcanism than tectonism in the northern part (Embley and Chadwick 1994). Average depth in this area is 2200 m. North Cleft venting aligned on a trend of 020° (Figure 2.3.2) spans about 11 km. The nearest vent communities occur on the southern end of the segment at 44°42'N (Figure 2.3.1). Venting is not known on the next segment that overlaps to the north.

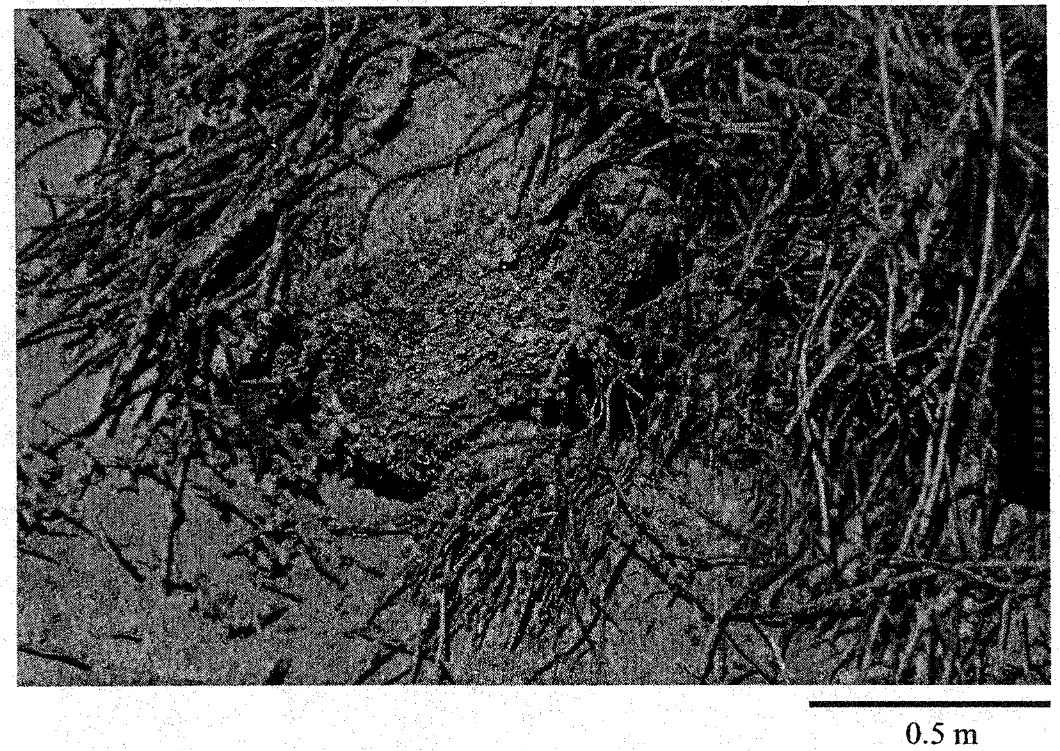
Sample collection

Samples were taken by submersible in the summers from 1988-1994. The manipulators grabbed one or two samples of tubeworms, plus associated biota, which were placed in closable boxes. Organisms on the tubeworms were potentially lost during the transfer from manipulator to sample box. There was relatively little overlap in biological sampling sites due to bottom time limitations and other commitments. While some vents were revisited, the exact sampling spot could not be identified. A 'vent' in this case, was either a concentrated area of flow through basalt over an area from 1-10 m^2 or venting through a mineralized chimney (sulphide) that usually had high temperature fluid orifices. It was not possible to sample a discrete bottom area on the rough hard terrain. Because the samples are vestimentiferan clumps, we present faunal statistics in relation to total surface area of the tubes.

Estimates of venting extent

Still photos and videos were scored for areal coverage by indicator groups. Three categories of vent "indicator groups" were chosen for their distinctive appearance: bacterial mats, live tubeworms (*Ridgeia piscesae*) and dead tubeworms. “Dead tubeworms” were tubeworm patches with no visible branchial plumes and extensive sediment cover (Figure 2.3.3). A class system of scores from one to six represented total percent coverage by these indicators in images as estimated by eye: 1, less than 5%; 2, 5-20%; 3, 20-40%; 4, 40-60%; 5, 60-80%; and 6 was greater than 80%. Figure 2.3.3, from a 1993 camera tow, had scores of 0 for bacterial mat and live tubeworm coverage and 5 for dead tubeworms. Geographic Information System (GIS) manipulations of spatial data allow visualization of venting changes and storage of information about venting conditions (Tsurumi 1998). The visual data cover more spatial and temporal ranges than the collections and thus allow a broader view of changes in venting. GIS manipulations

Figure 2.3.3. An example of a seafloor photo from a *ROPOS* dive on north Cleft. This image was taken at Marker 46 in July, 1993. The stick-like objects are tubeworms. Note the heavy cover of iron-rich sediment and the moribund appearance of the animals. The area of this photograph is about 2 m^2. The score for indicator species is 0 for both bacterial mats and live tubeworms and 5 for dead tubeworms.


0.5 m

were run in ArcView 2.1 from the database provided on-line (http://newport.pmel.noaa.gov/gis/data.html).

Sample processing

Samples were fixed in 7% seawater formalin at sea for transport to the lab for processing. All samples were sieved over a 1 mm mesh. The residue of one sample, Aquarius Vent, was sieved over a 63 µm mesh. Samples were sorted and counted to species. Meiofauna were not included in analyses but meiofauna from all samples are included in the species total.

Eighteen biological samples were selected for examination. Samples were culled to fit these criteria: manipulator grabs of tubeworm bushes, specimens available to confirm any prior identifications and tubeworm area measurable. Because numbers of species and individuals are not independent, and our data set has a large number of rare species (species in low abundance), only collections over 200 individuals were used. We set this minimum number of individuals to ensure inclusion of at least some of these rare species in all analyses in the hope that unrealistic clustering based on a few abundant species would not result. Subsamples of the 1988 specimens were used for other studies, thus, strict quantitative comparisons were not possible. Only presence/absence information was used from this year for cluster analyses and descriptive changes in venting. The 1988 data were adequate to present a relative assessment of the most abundant species and to include in overall diversity and rarefaction estimates. Missing species would lead to an underestimate of species diversity.

Analyses

Tubeworm area was measured to standardise sample size for comparison of the variable grabs. A digital image of all tubes in a sample was examined in the Bioscan Optimus 5.0 program. Plan area of each tube was converted to surface area by assuming a cylindrical shape. Density is the number of species per tubeworm surface area in a sample.

Rosenzweig (1995) suggests species number is the most appropriate measure of community diversity. We include the Shannon-Wiener (log base 2), Simpson's index of diversity (1-D), and Margalef indices for comparison with other studies. Rarefaction computes the expected number of species [E(Sn)] in a random sample of n individuals (drawn without replacement from N individuals distributed among S species) as the sum of the probability that each species will be included in the sample (Hurlbert 1971). The slope of the rarefaction curve (i.e. the rate of addition of new species with additional individuals) reflects the richness and evenness of distribution of individuals among species. The rarefaction method was used to describe deep-sea diversity (Sanders 1968; Grassle and Maciolek 1992; Cosson-Sarradin et al. 1998). Rarefaction calculations were made in the BioDiversity Professional Programme 2.0 (McAleece 1997).

The standardized density data (number of animals•cm^{-2} of tubeworm area) were log transformed. However, this transformation successfully normalized only two of the species chosen for analysis. No other transformations were able to normalize the data. Number of individuals, species, and *Ridgeia* were lognormally distributed as was *Ridgeia* area. Statistical tests were performed in SPSS and clustering in NTSYS 2.0: Jaccard and Bray-Curtis (flexible method; ß = -0.25) were used.

Results

Changes in venting

Towed camera images of the Marker 22 area revealed vigourous vent communities with large tubeworms in 1987. Marker 22 was south of the young sheet flow and venting in this area may have predated the 1986 eruption. Dives in 1988 on the southern part of the young sheet flow found diffuse vents with extensive bacterial mats, healthy tubeworms, shimmering flows to 25 °C and flocculated white particulates. On the cleft walls at Cavern Vent, gelatinous deposits up to 10 cm thick were embedded within microbial mats. Some Cavern tubeworms were over 180 cm in length in flows of 21 °C. Tripod Vent had temperatures up to 59 °C. In 1990, both camera tows and submersible dives recorded reduced venting and animal coverage. Iron-rich sediments smothered several marked sites such as Tripod and Marker 22. A few sites maintained reduced activity (Table 2.3.1) but extensive mats and floc were gone. Northern sulphide structures were discovered this year (1990). By 1991, five years post-eruption, most low temperature vents were extinct; the highest temperature was 30 °C. In the next three years most of the 1988 sites were revisited - only two of ten had any residual venting. Extensive fields of tubeworms were sedimented and decaying. The four high temperature chimneys maintained activity, albeit reduced, in this period. Monolith was sampled for five successive years and dropped from 324 °C to 295 °C.

Table 2.3.2 presents average percent coverage of indicator species on photographs for 1988, 1990 and 1991. Coverage by bacterial mats and tubeworms was greatest in

Table 2.3.1: Observations on vents visited by submersible and, for 1987 and 1989, by towed camera. *denotes biological sample; V = vigorous **community**; NV = not vigorous **community**; D = dead tubeworms, iron staining and maybe a few lingering animals; E = extinct, no signs of any venting or dead animals. Parantheses mean the marker was not located but worm fields in the vicinity were examined.

Vent	Substratum	1987	1988	1989	1990	1991	1992	1993	1994	1995
Marker 22 area	basalt	V	*V		*V			*D		E
North of Marker 1	basalt		*V					(D)		
Marker 46	basalt					*V		D		
Tripod area	basalt		*V		D	D			E	E
Crack	basalt		*V						E?	E
From Crack to Marker 4	basalt		*V		E			*V	D	
Cavern/Marker M	basalt		*V		*V			(D)	D/NV	
Marker 44 area	basalt					*D			D	
Graben	basalt			NV	*NV	NV				
Northern Pillow Mounds	basalt			NV		NV				
Pipe Organ Vent	sulphide					V			V	V
Monolith/Table Vents	sulphide				*V	*V	*V	*V	V	V
Fountain Vent	sulphide				V	*V		*V		
Aquarius Vent	sulphide								*V	

Table 2.3.2: Still images from the submersible Alvin were scored for cover estimates by three vent "indicator groups" over three years. Estimates for each indicator are presented as the average percentage cover of indicator species from all the images with indicator species.

Indicator	1988	1990	1991
Microbial mats (%)	22.5	3.90	5.84
Live tubeworms (%)	6.12	3.05	1.05
Dead tubes/sediments (%)	0.00	15.5	16.2

1988 and decreased markedly in 1990 and 1991. Average percent coverage of dead tubeworms increased from 1988 to 1991. Even these remnants disappeared in later years.

Taxonomic character

Eighteen collections of *R. piscesae* grabs yielded 140 418 individuals on the tubes. There were 28 species averaging over 1 mm adult size (Table 2.3.3) and another 16 meiofaunal species (Table 2.3.4). Seventeen species were new records for this part of the Juan de Fuca Ridge, another nine were possibly new to science and/or vents, three were newly described species, and two were new species records at vents. Across all samples, 16 out of a total of 44 species were meiofaunal (34.8%). The remaining 28 species are macrofaunal. In the one sample sorted carefully for meiofauna on a 63 μm sieve, ten of 27 species were meiofaunal.

Taxonomic diversity

Results for selected diversity indices were as follows: Margalef's (S-1/logN) was 8.68; Shannon-Wiener (H') was 1.73; and Simpson's (1-D) was 0.69. The shape of the Cleft rarefaction curve differed markedly from three other studies of deep-sea fauna (Figure 2.3.4). The shallow slope reflects the great unevenness in species distribution among individuals and the low richness at Cleft.

Dominance and dispersion

The four most abundant macrofaunal animals were two gastropods and two polychaetes that made up over 90% of the enumerated collections (Table 2.3.3). The

Table 2.3.3: a. Percent relative abundance of macrofaunal species in ten collections from 1990 to 1994 (samples with consistent collection/retention techniques); the value is the average over these samples. A "site" is a discrete geographical location of a vent.
b. Additional macrofaunal species recorded from samples not used for quantitative comparison. These species were found in samples that were subsampled and so %-average relative abundance could not be calculated.

Taxon	Species	Number of sites present (out of 14)	Percent-average relative abundance
a. Species from comparable samples.			
Gastropoda	*Lepetodrilus fucensis*	10	35.56
Gastropoda	*Depressigyra globulus*	11	18.66
Polychaeta	*Paralvinella pandorae*	10	18.25
Polychaeta	*Amphisamytha galapagensis*	11	18.07
Polychaeta	*Paralvinella sulfincola*	6	4.352
Polychaeta	*Paralvinella palmiformis*	8	1.857
Polychaeta	*Parougia wolfi*	8	1.224
Polychaeta	*Lepidonotopodium piscesae*	9	0.582
Polychaeta	*Branchinotogluma* sp.	10	0.321
Gastropoda	*Provanna variabilis*	6	0.226
Polychaeta	*Nicomache venticola*	4	0.201
Polychaeta	*Hesiospina vestimentifera*	3	0.198
Arachnida	*Ammothea verenae*	5	0.154
Aplacophora	*Helicoradomenia juani*	1	0.096
Polychaeta	*Levensteiniella kincaidi*	7	0.062
Ostracoda	*Euphilomedes climax*	4	0.047
Polychaeta	*Opisthotrochopodus tunnicliffeae*	3	0.046
Polychaeta	*Prionospio* n. sp.	2	0.033
Gastropoda	*Clypeosectus curvus*	2	0.030
Amphipoda	Amphipod spp.	4	0.028
Polychaeta	*Ophryotrocha globopalpata*	2	0.008
Polychaeta	*Protomystides verenae*	2	0.004
Polychaeta	*Hesiodeira glabra*	1	0.000
b. Additional species from other samples			
Polychaeta	*Paralvinella dela*	1	--
Amphipoda	Sp. nr. *Valettiopsis*	1	--
Scyphozoa	*Lucenaria* n. sp.	1	--

Taxon	Species	Number of sites present (out of 14)	Percent-average relative abundance
Gastropoda	*Temnocinclis euripes*	1	--
Nemertea	*Thermanemertes valens*	1	--

Table 2.3.4: Listing of all meiofauna recovered from Cleft samples. The unknown copepods are all harpacticoids. The relative abundance of these taxa in one carefully sorted sample is shown. The meiofaunal component in the Aquarius sample constituted 27% of all individuals and 44% of the taxa recovered.

Taxon	Species	Individuals in the Aquarius sample
Acarina Family Halacaridae	*Copidognathus papillatus*	80
Copepoda Family Pseudocalanidae	*Clausocalanus lividus*	0
Copepoda Family Ameridae	unknown	483
Copepoda Family Diosaccidae	unknown	1636
Copepoda Family Tisbidae	unknown	40
Copepoda Family Ectinosomidae	unknown	20
Copepoda Family Thalestridae	unknown	20
Copepoda Family Tisbidae	unknown	0
Copepoda Siphonostomatoida	*Aphotopontius forcipatus*	0
Copepoda Siphonostomatoida	*Benthoxynus spiculifer*	568
Copepoda Siphonostomatoida	*Stygiopontius quadrispinosus*	617
Copepoda Siphonostomatoida	*Collocherides brychius*	0
Copepoda Misophrioida	*Misophriopsis longicauda*	0
Ostracoda Myodocopida	Spp. unknown	780
Ostracoda Podocopida	*Microloxoconcha* sp. (?)	60
Nematoda	Spp. unknown	0

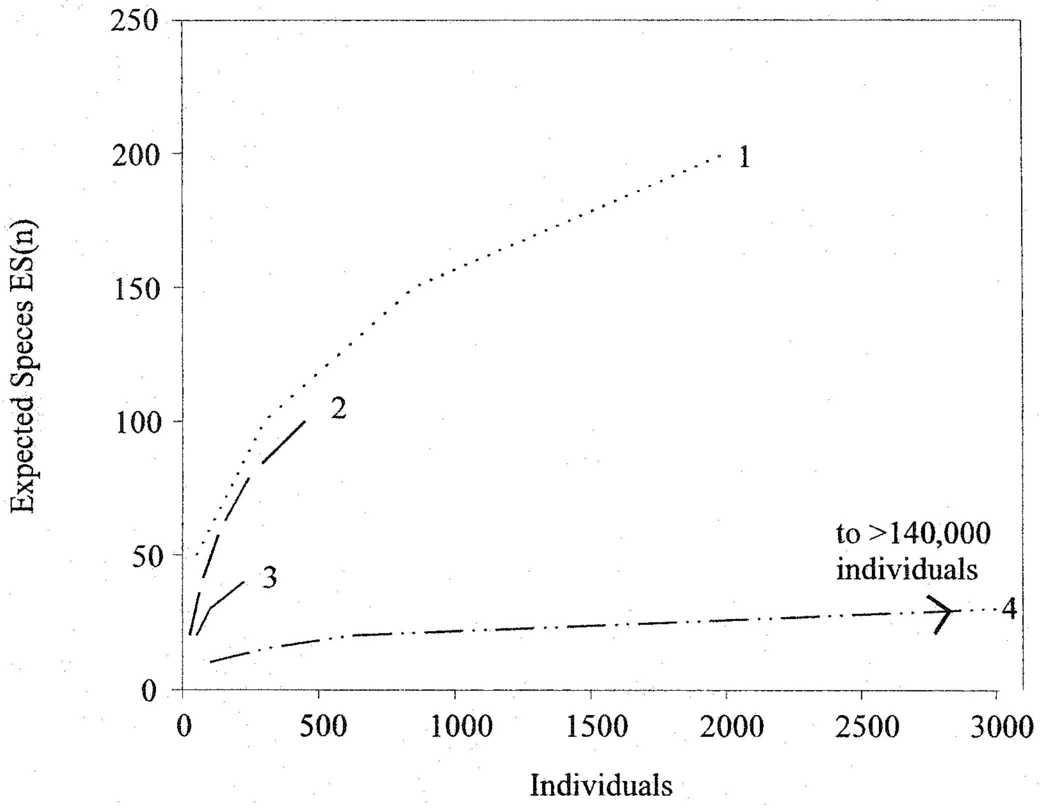


Figure 2.3.4. Rarefaction curve of the north Cleft data as well as curves reproduced from three other deep-sea studies. The curves of the non-vent fauna are of similar shape, indicating a similar pattern of species diversity and evenness. 1 = off New Jersey and Delaware, 1500-2500 m (Grassle and Maciolek 1992); 2 = Tropical northeast Atlantic, 1700-4600 m (Cosson-Sarradin et al. 1998); 3 = Newport Submarine Canyon, CA, 31-500 m (Maurer et al. 1995); 4 = north Cleft, 2200 m.

three next most abundant taxa were an order of magnitude lower than the top four (totalling 7.5%). These were followed by 16 species each representing much less than one percent average relative abundance. The limpet *Lepetodrilus fucensis* was the first, second or third most abundant animal in nine out of ten samples used and in the tenth it was not found (Figure 2.3.5). Similarly, *Depressigyra globulus* and *Amphisamytha galapagensis* were dominant in most collections.

The occurrence pattern of the polychaete *Paralvinella pandorae* differed. Although information for our 1988 collections was not complete for all species, the abundance of this animal could be assessed. *P. pandorae* represented 70% of the > 18 000 animals in this year; it occurred at all sites constituting 20 to 98% of the community. In 1990, this species was 88% of the > 70 000 animals identified. However, all but 10 specimens came from a single site: Monolith. In the combined 1991 to 1994 collections, *P. pandorae* occurred as less than 1% of the > 22 000 animals collected. The four most abundant species were also the most well-dispersed (Table 2.3.3) being found at 10 or 11 of the 14 sampled sites. Forty-six percent of the macrofaunal species in Table 2.3.3 were found at only one, two, or three sites. Three species were seen at only one site in 1988 and never again: *Temnocinclis euripes, P. dela* and *Thermanemertes valens.*

Substratum

Ridgeia area was not correlated to the number of species. Organism abundances were not affected by the type of substrate the *Ridgeia* occupied (basalt or sulphide).

A wide range of animal densities were encountered in the 1990 to 1994 samples: from 0.01 animals•cm^{-2} to 3.34 animals•cm^{-2} in one 1993 sample. Limpets alone in the

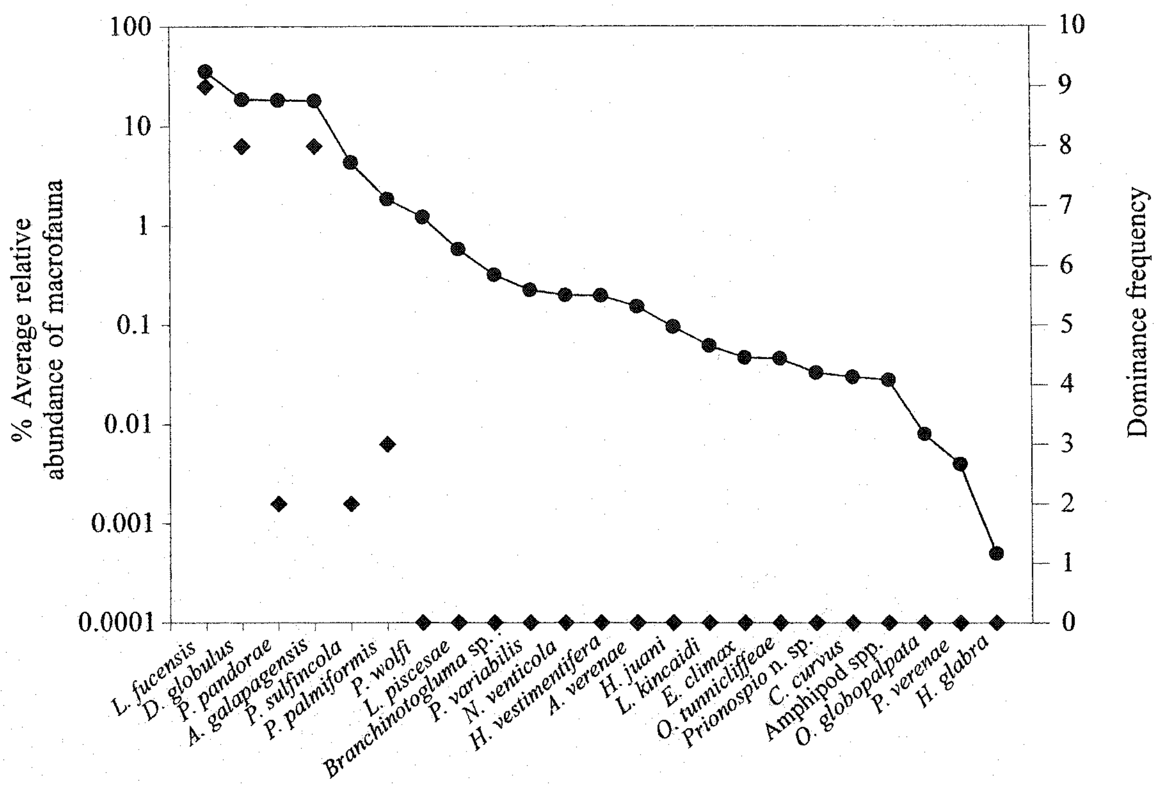


Figure 2.3.5. Rank abundance of the macrofauna in ten samples (circles). Frequency of their dominance in the samples is also recorded (diamonds). Rank abundance was calculated as the percent average relative abundance of each species across all eighteen samples. Dominance frequency is the number of times a species was among the three most abundant species in each sample.

latter sample reached nearly 3 animals•cm^{-2}; at about 0.5 cm long, these animals crowd a desirable substratum by stacking and, apparently, suspension-feeding. The base of Monolith sponsored high densities of *P.* (2.70 animals•cm^{-2}) where the deposit-feeding polychaetes built sheaths overlapping each other. The Fountain sample with fat, white tubeworms had the lowest density at 0.01 animals•cm^{-2} and was also depauperate in species (8 species from 728 individuals).

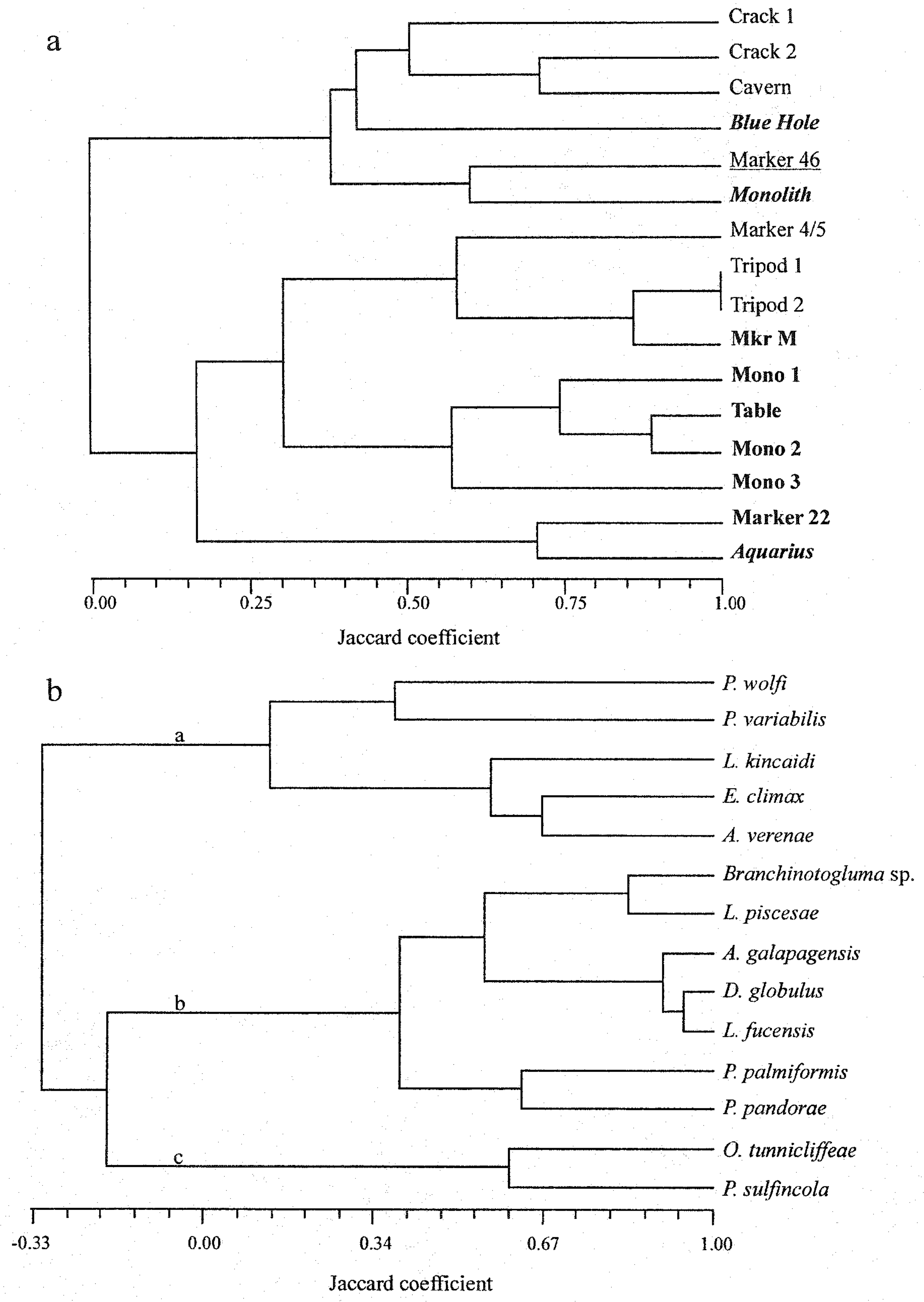
Community similarity

Data from sixteen collections from 1988 to 1994 were reduced to species presence/absence; singleton occurrences were converted to zeros. The Jaccard similarity coefficient indicated two major clusters (Figure 2.3.6a), but sites did not cluster by year. The major division separated lower from higher diversity groups. The only consistent cluster comprised the four Monolith and Table samples in 1990 (Table is only a few metres from Monolith); in 1992, Monolith differed enough to move to another part of the tree. Marker 22 and Aquarius were the most widely separated sites yet the most speciose.

Species associations

Possible associations among macrofaunal species were examined with cluster techniques. Only species that occurred at more than two sites were used. Figure 2.3.6b suggests three major clusters based on presence/absence data. Two-way analyses of associations were run (Kendall's Tau and Pearson's correlation) on the densities of the nine most abundant species in the 1990 to 1994 samples selected for analysis.

Figure 2.3.6. a. Cluster diagram of similarity matrix generated by the Jaccard Coefficient based on presence/absence of species in *Ridgeia* tube collections. Sample year is designated by font: normal = 1988; bold = 1990; underline = 1991; bold/italic = 1992 to 1994 inclusive. b. Cluster diagram of species associations generated by the Jaccard Coefficient based on the presence/absence of species in *Ridgeia* tube collections. Cluster "a" species are associated with low temperature habitats, cluster "b" species with warmer habitats, and cluster "c" species with the hottest environment. Mono 1, 2, and 3 are three different samples from Monolith in 1990. Samples from Pipe Organ and Graben vents were too comprised to use in the cluster analysis.


a
Crack 1
Crack 2
Cavern
Blue Hole
Marker 46
Monolith
Marker 4/5
Tripod 1
Tripod 2
Mkr M
Mono 1
Table
Mono 2
Mono 3
Marker 22
Aquarius
0.00
0.25
0.50
0.75
1.00
Jaccard coefficient
b
a
b
c
P. wolfi
P. variabilis
L. kincaidi
E. climax
A. verenae
Branchinotogluma sp.
L. piscesae
A. galapagensis
D. globulus
L. fucensis
P. palmiformis
P. pandorae
O. tunnicliffeae
P. sulfincola
-0.33
0.00
0.34
0.67
1.00
Jaccard coefficient

Associations among *A. galapagensis*, *L. fucensis*, and *D. globulus* were significant ($p < 0.05$), as was the association between *Branchinotogluma* sp. and *P. variabilis*. Densities of *P. palmiformis* and *D. globulus* were significantly associated as were *P. pandorae* and *P. sulfincola*. All associations were positive.

Discussion

Cleft segment may be subject to cyclical and periodic eruptions on the decade to century scale due to magma surges and declinations (Lichtman et al. 1983; Kappel et al. 1986; Baker et al. 1989). The 1986 eruption, the colonisation of new vents, and the eventual loss of tubeworm habitat likely represented a typical cycle for the vent communities in this geophysical setting. By five years post-eruption, most low temperature vents were extinguished and, by 1994, all were gone. Areas of focused flow at high temperature chimneys remained active although diminished in extent and temperature (Butterfield and Massoth 1994). These sites may sustain focused flow for much longer (Koski et al. 1994) and thus may provide a ready supply of propagules to populate periodic venting during episodes of crustal accretion.

The following changes in diffuse fluids were described from Cleft from 1988-1991: chloride nearly three-fold, sulphate up five-fold, sulphide from 6 $\text{mmol}\bullet\text{kg}^{-1}$ to nearly zero, iron up 30-fold and manganese up three-fold (Butterfield and Massoth 1994). Where diffuse vents survived, temperatures were generally lower. The shifts were related to a change from vapour-dominated fluids still undergoing phase separation to brine-dominated fluids. On a gross scale, these fluid changes had a great influence on the fauna as a direct result of the loss of available dissolved sulphide and smothering by iron-rich precipitates. Sulphide depletion likely occurs due to subsurface chemical and microbial oxidation; a similar abrupt drop in the heat to sulphide ratio was recorded at the CoAxial vents (Butterfield et al. 1997). Among the diffuse vents that remained, however, animals showed no detectable responses to fluid changes during the vapour to brine transition. Diffuse fluids are much diluted by subsurface seawater leakage. Pronounced hydrothermal changes in this milieu may have little effect.

The north Cleft fauna differed in one notable character from the other studied sites on Juan de Fuca: the species list of 44 species was shorter. For comparison, 61 species were found in one Endeavour segment field among 75 000 individuals and 62 species on Axial Volcano among 530 000 plus individuals (Tunnicliffe unpubl. data). There were no species endemic to the Cleft community (species that were newly recorded from Cleft, are now known from other sites). The fact that the north Cleft fauna was a subset of the entire Ridge species pool probably reflects the frequency of habitat turnover on this segment. In the larger context, Juniper and Tunnicliffe (1997) linked spreading rate, frequency of magmatic events and habitat unpredictability to partly explain differences in regional vent diversity around the world. North Cleft is a segment-scale expression of the same phenomenon. This assemblage may represent a “rapid response fauna” for the Juan de Fuca. The paucity of species on Cleft compared to the Ridge species pool may reflect the demands of a habitat that is continually turning over on the scale of a decade or less.

In 1988, north Cleft communities looked much like those at the post-eruptive vents on CoAxial segment (Tunnicliffe et al. 1997) and Axial Volcano (Tsurumi et al. 1998) at two years after eruption: i) extensive microbial mats and local areas with thick sacs of gelatinous polysaccharides; ii) large, fat *R. piscesae*; iii) large, abundant, and well-dispersed *P. pandorae*; and iv) flocculated particulates in cracks in the basalt. The presence of microbial mats, well-established tubeworms by the second year and an increase in species richness by three years post-eruption, were reported by Shank et al. (1998) from 9°N EPR. From 1988 to 1990, the coverage by microbial mats decreased, tubeworms became long and skinny, *P. pandorae* became smaller and localized, and flocculated particles disappeared. Dead tubeworms smothered in sediment were abundant and, by 1991, most diffuse habitat was lost.

However, despite dramatic shifts in vent visual and areal character, collections did not group by year in the cluster analysis. By 1988, we had already missed sampling the initial stages of colonisation. Within two years, most of the Cleft fauna had colonized, probably seeded from the chimneys. Subsequent vent deaths were so quick that the limited sampling of 1990 was insufficient to detect senescence. Small plumbing changes initiated one site near Marker 4 (Blue Hole) in 1993, that clustered with the 1988 vents; we cannot assume that heat flux diminished consistently. We show some geographic consistency as collections from the same site in the same years clustered. The vestimentiferan, *R. piscesae*, is a rapid colonizer (Tunnicliffe et al. 1997) and, by two years post-eruption, it formed extensive bushes with some individuals near 2 m long. *Ridgeia* tubes create a three-dimensional structure for other vent animals to inhabit. For some vent animals, the presence of tubeworms and the microhabitats created by their physical structure may be the main pre-requisite for colonisation. Even when there is no measurable sulphide or temperature anomaly at a vent, some vent fauna persist among the dead or dying tubeworms, perhaps until the tubes themselves are gone (Tsurumi, unpubl. data).

Two species may be very early colonizers. The nemertean *Thermanemertes valens* was an initial coloniser after the CoAxial eruption. It is otherwise known only at vents one to two years post-eruption on Axial (Tunnicliffe, unpubl. data) and at Cleft in 1988. It may be out-competed for resources by late-arriving species. The scyphozoan, *Lucenaria* n. sp. was found in small numbers at one site in the second year after eruption on CoAxial and was found in similar numbers at one site four years post-eruption at Cleft.

Most measures of species diversity from hard substratum vent sites are restricted to species lists and are statistically incomparable. Van Dover and Trask (2000) used a standardised sampling volume to compare mussel bed diversity between a Mid-Atlantic Ridge vent site and the intertidal. We chose tubeworm area to make north Cleft samples comparable as tubeworms provided most of the three-dimensional habitat for animals living at low temperature basalt venting and also covered substantial amounts of sulphide chimneys (Sarrazin et al. 1997; Sarrazin and Juniper 1999).

The Shannon-Wiener index (H') for Cleft (1.73) was comparable to that of the vent mussel bed (2.31 when converted to log base 2) (Van Dover and Trask 2000). The rank-abundance curves for their mussel beds and for Cleft were similar in shape, with five or less species accounting for 90% of the total individuals. Cleft H' was much lower than that reported for deep-sea soft sediments (converts to 19.3 in base 2) (Grassle and Maciolek 1992). The rarefaction curve for Cleft was markedly different from selected curves of deep-sea sediment studies. Grassle and Maciolek (1992) found very high evenness of fauna in deep-sea sediments and Maurer et al. (1995) found less evenness, but dominance was still spread over 24 taxa rather than five. Areas subject to frequent physical disturbance in the deep-sea have reduced species diversity and are more like shallow-water communities because they have species that are numerically dominant (Grassle and Maciolek 1992). The unevenness of the vent environment may be due to habitat that is both unpredictable and frequently disturbed.

The limpet, *L. fucensis,* had the highest dominance frequency and attained densities to 3 animals•cm^{-2} at Blue Hole. *Lepetodrilus* occurred (10.8 animals•cm^{-2}) as the most dense species on an Endeavour sulphide chimney (Sarrazin et al. 1999). This limpet will stack vertically on any substratum and may be suspension feeding. De Burgh and Singla (1984) reported bacterial colonisation and endocytosis on the gill of this species and stacking may be a way of bringing nutrients to its bacteria from the water column. They suggested the animal is both filter- and deposit-feeding. If *L. fucensis* has multiple food-gathering strategies but is not dependent on a symbiont, it may be able to live in a variety of vent habitats. Although nothing is known about *L. fucensis*' reproduction and dispersal, *L. elevatus,* a congener, is recorded to have had region-wide synchronous settlement on the EPR (Mullineaux et al. 1998).

Although it was the third most abundant species, *Paralvinella pandorae* dominated only two samples. Although *P. pandorae* appears dependent upon *Ridgeia* for substratum, there was no apparent correlation between its abundance and *Ridgeia* surface area. *P. pandorae*'s dispersion pattern changed markedly over five years. The phenomenon described by Tunnicliffe et al. (1997) was seen here: a body-size shift from large to small adults in later post-eruptive years. This feature, combined with the decreasing site occupation suggested that habitat suitability, not dispersal capability, may limit this species. The cause is not clear but may involve competition with *P.*

palmiformis and *Amphisamytha galapagensis*, species that share a similar habitat attached to tubeworms.

Two polynoid polychaetes, *Branchinotogluma* sp. (the species designations are under revision; S. Hourdez, pers. comm., 208 Mueller Lab., Pennsylvania State University, University Park, PA) and *Levensteiniella kincaidi*, were very well-dispersed despite low abundances. Both belong to a small subset of species (that includes *Amphisamytha galapagensis* and *Hesiospina vestimentifera*) shared with the East Pacific Rise. *Lepidonotopodium piscesae*, another polynoid polychaete, was also well-dispersed. A generalist/opportunist life history strategy may allow early entry into the vent sites and/or persistence in a specialised niche with a low carrying-capacity. Species with low local abundances may avoid extinction if they are widespread.

We did not see the distinct separation of chimney and basalt communities found by Jollivet (1996) on northern East Pacific Rise. While there was some separation of basalt and sulphide based assemblages, the location on a chimney appeared to be important. On Juan de Fuca, different flow/temperature regimes foster different assemblages (Sarrazin and Juniper 1999) and there is considerable overlap in species presence both among these groupings and with basalt-hosted assemblages. More work is required to define the habitat characters of the three clusters, but the groupings agreed with our observations of relative temperature.

Limitations on larval dispersal were not evident at the scale of the north Cleft community (about 11 km) as the same species occurred at the geographic extremes; the samples with the highest diversity were farthest apart. Because neither geographic location nor year of collection appeared to influence clusters, local habitat-scale features (sulphide supply, food availability and competition) may determine species composition. The wide ranges in both density and diversity may reflect the range of microhabitats available to the animals. Thus cooling of Monolith may have changed the 1992 habitat to resemble diffuse conditions rather than the Monolith of 1990. Marker 22's dissimilarity to all vents but Aquarius, may be due to its pre-eruption existence.

An oft-noted pattern in ecology is that the most abundant species tend also to be the most widely distributed (Hanski 1982). There was a positive relationship between average local densities and species' geographical distributions on Cleft. Although the underlying causes for a positive abundance-range relationship are not understood, abundant and widespread species may be those able to use a broader range of resources (Brown 1984). A few species on north Cleft such as *Branchinotogluma* sp., had low local densities, yet wide distributions. Hanski et al. (1993) suggest that species with low local abundances and wide distributions will have low local growth rates in relation to their emigration rate and will also have high mortality during dispersal. Species with both a small range and low local abundances should be at high risk of extinction. However, the 12 species with the narrowest distribution were also the ones with the lowest abundances on north Cleft. Establishment of a species at a particular vent site is a balance between local probabilities of extinction and colonisation. Species with a narrow distribution may maintain their metapopulations by having a very high colonisation rate. Further work on other sections of the Juan de Fuca Ridge are needed to see whether this pattern is repeated.

The inconsistent biological sampling at Cleft had at least two consequences. It reduced the number of samples available for statistical analyses and only allowed inclusion of macrofauna in those analyses. Because of the overwhelming dominance of four species, excluding meiofauna probably did not distort the overall community character. However, without the meiofauna, we do not have a complete picture of diversity and/or taxonomic character. In the one sample sorted to the 63 μm size class, over a third of the species were in the meiofauna which included mites, nematodes, crustaceans, and juveniles of most species. Sorting to meiofauna may alter our idea of vent community organisation and may be important in defining senescent from non-senescent assemblages (Tsurumi, unpubl. data). Small crustaceans that are a major component of non-vent deep-sea fauna, may be more prevalent and diverse at vents than previously recognised (Tsurumi, unpubl. data). Many crustaceans found at vents may not be vent endemic. For example, *Clausocalanus lividus*, a common mid- to deep-water calanoid copepod is reported here for the first time at vents (F. Ferrari, pers. comm., IZ/MSC, National Museum of Natural History, Smithsonian Institution, Washington, D.C.).

In summary, by two years post-eruption, more than half of the Cleft species pool was present on north Cleft. Only an investigative response in less than a year can map the pattern of arrival and replacement at new vents. An increase in diversity was seen neither in subsequent years nor at high temperature chimneys likely venting before the 1986 eruption. The north Cleft subset of the Juan de Fuca species pool is likely adapted to episodic and frequent eruptive events on the segment. Major changes in fluid composition at vents because of a shift from vapour- to brine-dominated fluids resulted in no detectable community changes other than habitat loss due to a large decrease in dissolved sulphide availability. Habitat loss from 1988 to 1991 was greater than 70%.

On the scale of the 20 km of the north Cleft vents, larval interchange homogenised the character of the community. This homogenisation made it difficult to distinguish temporal, spatial, or substratum differences. Cleft vents had low diversity and evenness, with 90% of the individuals contained in four species. These four dominants are responsible for the community character although small-scale habitat variability was likely important in determining exact assemblage compositions. Extreme unevenness of the Cleft community reflects the dominance pattern in frequently disturbed habitats such as the rocky intertidal and areas of the deep-sea subject to sediment eroding benthic storms. Assemblage diversity changes markedly when animals under 1 mm are considered: one-third of the species found on Cleft were meiofaunal.

Acknowledgements

Many thanks are due to R. W. Embley and the NOAA Vents Program, as well as to the pilots of Alvin and ROPOS and the crews of the Atlantis II and John P. Tully. Technical assistance was provided by B. Milligan and L. Frankin. Information from E. Baker and D. Butterfield on chemistry is greatly appreciated. Three anonymous reviewers provided thoughtful and useful comments. This research was funded by NSERC Canada.

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CHAPTER 3

Senescent vent assemblages

Introduction

Succession is a concept that has its roots in plant ecology (Menge 2000). This botanical origin influences ecologists' definitions of succession. Succession is most easily applied to an assemblage if there is an immobile quality to the community so that a study area can be delimited, and where space is often a limiting factor. Many studies of animal succession are of the rocky intertidal (e.g. Dayton 1971; Paine and Levin 1981) and document the arrival and replacement of invertebrates attached to rocks. The vent environment is an alluring system in which to observe succession as it is composed of a mostly endemic fauna confined to an area immediately adjacent to vents and largely distinct from the surrounding deep-sea.

One reason to study succession is to understand human impacts on the world in order to resolve environmental crises (Odum 1969). Understanding the patterns and causes of succession is critical to managing variability in landscapes increasingly dominated by anthropogenic disturbances, and key to understanding the regulation of nearly all aspects of biodiversity (Miles 1987; Huston 1994; Berlow 1997). Mortimer (1987) is interested in succession for the insight it may offer regarding causal explanations of species persistence. Theories of species persistence are often associated more with metapopulation theory than succession, but the two are related in that patch occupancy based on colonisations and extinctions is fundamental to both theories. One is at the population level and one at the community level of inquiry. Many researchers aim for consensus on the mechanisms that are most important in controlling processes of successional change (Tilman 1985; Tilman 1988; Pickett and McDonnell 1989; McCook 1994).

Studying succession in the vent system offers another opportunity to look for commonalties in patterns and processes of succession across ecosystems. Vent successional studies may be useful when considering management issues for the vent environment. Since the declaration of the Endeavour segment pilot Marine Protected Area by Canada's Department of Fisheries and Oceans in 1998, management and preservation of vent habitat is no longer a far-fetched idea. Studies of vent succession and, in particular, senescence, the final stage of the community, may increase understanding about vent export to, and import from, the surrounding deep-sea community.

In this chapter I define dying vent communities as senescent assemblages. This definition of senescence is biased by my perspective as a vent ecologist. In an absolute sense, the patch of habitat in question does not die and become azoic, but goes through a transition stage from vent to normal deep-sea community. From the perspective of non-vent deep-sea community succession, a senescent vent assemblage is the initial stage of colonisation after a catastrophic event that has wiped out the previous deep-sea community (i.e. the birth of the vent). I consider senescent assemblages to be vent communities. The species composition of senescent vents may differ from active vents but many of the component species are vent endemics and the primary substratum is *Ridgeia piscesae* tubes.

My objective is to distinguish senescent from non-senescent vent assemblages. I hypothesize that senescent assemblages are different in species composition, abundance of major taxa, and species relative abundances from non-senescent vents. Senescent vents are transition assemblages from active vent to non-vent deep-sea and this should be reflected by differences in diversity, distribution, and abundance of the constituent species compared to active vents. With a cessation in venting, temperature and fluids that prevent non-vent deep-sea species from invading the vent habitat disappear; I expect to see more non-vent deep-sea taxa at senescent vents than at active vents. Given the low diversity and evenness of vent communities and ubiquitous dominance of the vent limpet *Lepetodrilus fucensis* (Chapters 2 and 4), differences between senescent and non-senescent vents should be more clear when meio- and macrofauna are considered.

If rare species are more threatened with extinction than common species (Chapman 1999; Garcia and Laville 2000), rare species (low in local abundance and narrowly distributed) should be the first species to disappear with extinction of the vent habitat. Additionally, identification of rare vent species may provide candidates for future investigations into whether rare species share common biological attributes that can lead to species rarity. To further discussions of rarity, two questions will be addressed in this chapter: 1) do rare active vent species disappear from the community when venting ceases; and 2) which species are rare in the senescent environment?

Methods

Sample collection

For sampling purposes, a senescent habitat is determined visually and chemically: visually, by recumbent tubeworm tubes with no visible branchial plumes, by abundant scavenging spider crabs, and by the lack of bacterial production and shimmering water, and chemically, by no detectable temperature anomalies or sulphide.

Senescent samples were taken by submersible in the summers of 1996, 1998, and 1999 on Axial (South Rift Zone field), CoAxial, and Endeavour segments on the Juan de Fuca Ridge (Figure 1.1). Non-senescent samples were taken on Axial Seamount in 1986-88 and 1997-1999. Samples are submersible manipulator grabs of tubeworms, plus associated biota as per Tsurumi and Tunnicliffe (2000). Senescent tubeworm grabs EE and GG were accompanied by suction samples of the same location using a 63 µm mesh. The information from the suction samples is combined with the tubeworm grab data for EE and GG.

Non-vent samples consist of two sediment suction samples taken on basalt on Endeavour and Axial. Suction samples are taken by submersible into sample jars with a 63 µm mesh on the outlet. Non-vent samples are taken 30-50 m away from venting areas.

Sample processing

Samples were fixed in 7% seawater formalin at sea for transport to the lab for processing. All samples were sieved over a 63 µm mesh. Non-senescent South Rift Zone (Axial) samples and all senescent samples were sorted and counted to species down to the 63 µm mesh size. All other Axial samples were sorted down to 1 mm sieve size and meiofauna were not quantitatively processed. Therefore, comparisons of senescent samples with Axial samples are limited to macrofauna except for species richness and dispersion descriptors.

Thirty-six samples were selected for examination; two non-vent, five senescent, and 29 active vent (Table 3.1). All samples except for the two non-vent samples are used for presence/absence information for cluster analyses, total diversity, number of endemics, and rarefaction. After culling as described in Tsurumi and Tunnicliffe (2000), 23 non-senescent Axial samples and four senescent samples remain in the data set for statistical analyses (Table 3.1). Non-vent samples are used solely for a descriptive comparison because they are not quantitative and do not meet the sample culling criteria.

Axial as the non-senescent comparison community

Non-senescent Axial Seamount vents are chosen as the comparison community because these vents provide the largest data set from the Juan de Fuca available for comparison. Axial Seamount has been venting continuously since at least 1983 when it was first explored (Tunnicliffe et al. 1985). Samples from Axial span nearly two decades and several habitats. Secondly, three senescent vent samples come from Axial and so allow comparison between senescent and non-senescent samples from the same geographic location. Comparing vents on the same segment is important to make the argument that senescent vents host different assemblages because of their successional stage.

Analyses

Table 3.1: Senescent and non-senescent samples used in this chapter. Totals do not include the tubeworm *Ridgeia piscesae*; SRZ = South Rift Zone; *=samples culled from quantitative analysis; ^=senescent samples. Macrofauna are all species caught on a 1 mm sieve.

Sample designation	Vent field	Vent	Year	Substratum	Number of individuals	Number of species	Number of individuals	Number of species	Macrofaunal density (individuals•cm^{-2})
					All fauna		**Macrofauna**		
Axial									
A	ASHES	Goblin	1986	Basalt	11252	13	9766	10	2.179
B	ASHES	Bouquet	1986	Basalt	7821	26	7813	23	0.923
C	ASHES	Demon	1986	Basalt	28049	22	28046	21	2.599
D	ASHES	Sweet	1986	Basalt	1831	11	1830	10	1.554
E	ASHES	Limbo	1986	Basalt	2578	17	2578	17	0.390
F	ASHES	Miserable	1986	Basalt	408	19	401	14	0.614
G	ASHES	Not-so-miserable	1986	Basalt	18963	27	18937	21	1.208
H	ASHES	Bouquet	1988	Basalt	5283	21	5279	19	1.059
I	ASHES	ISCA	1997	Basalt	4759	19	1689	17	0.530
J*	ASHES	Hatfield	1997	Basalt	47128	41	37121	28	not available
K	ASHES	Bouquet2	1998	Basalt	33706	24	33643	19	1.938
L	ASHES	Hairdo	1998	Basalt	15385	33	143741	24	0.473
M	ASHES	Gollum	1998	Basalt	6262	19	6208	12	2.316
N	ASHES	Marker i	1998	Basalt	8945	24	8681	15	2.136
O	ASHES	Medusa	1998	Basalt	570	8	508	6	2.082
P	CASM	Post-	1986	Basalt	7018	17	7018	17	0.795

Sample designation	Vent field	Vent	Year	Substratum	Number of individuals	Number of species	Number of individuals	Number of species	Macrofaunal density (individuals•cm^{-2})
					All fauna		**Macrofauna**		
Q*	CASM	Taylor's Lamphere	1986	Sulphide	472+?	12	301+?	7	not available
R*	CASM	Lamphere	1986	Sulphide	508	7	508	7	not available
S	CASM	Lamphere	1988	Sulphide	3431	21	3280	18	1.053
T	CASM	Bob	1998	Basalt	1771	16	1655	11	1.382
U	CASM	T & S	1998	Sulphide	3378	16	767	9	0.113
V	CASM	Base of T & S	1999	Basalt	2995	16	2736	12	1.527
W*	SRZ	Vent #1	1986	Basalt	825+?	15	813+?	11	not available
X*	SRZ	Sonne	1997	Basalt	433	16	411	11	not available
Y*^	SRZ	10 m SE of Marker 113	1998	Basalt	159	10	147	8	0.039
Z^	SRZ	Near Marker 113	1998	Basalt	7139	29	7026	20	0.641
AA	SRZ	Flat Top	1998	Basalt	2098	13	2095	10	2.571
BB	SRZ	Oldworms	1998	Basalt	4420	25	3841	16	1.071
CC	SRZ	LargeTW	1998	Basalt	2551	21	2441	13	0.375
DD	SRZ	Old Flow	1998	Basalt	1766	10	1766	10	1.454
EE^	SRZ	Crevice	1999	Basalt	509	23	349	14	0.036
CoAxial									
XX	CoAxial	HDV	1995	Basalt	1856	10	1850	8	0.394
YY^	CoAxial	HDV	1996	Basalt	3586	25	2448	15	0.025

Sample designation	Vent field	Vent	Year	Substratum	Number of individuals	Number of species	Number of individuals	Number of species	Macrofaunal density (individuals•cm^{-2})
					All fauna		**Macrofauna**		
Endeavour									
GG^	Endeavour	Crab Gulley (Marker 5)	1999	Basalt	428	25	219	18	0.086
Non-vent									
HH*	SRZ, Axial	Near Marker 108	1999	Basalt	54	8	34	4	not available
II*	Endeavour	Marker 6,	1999	Basalt	97	14	30	7	not available

Tubeworm area is measured as per Tsurumi and Tunnicliffe (2000). *Ridgeia* abundances and presence/absence are not included in the analyses. Dominance frequency is the percent of samples in which a species is one of the three most abundant species.

The density data (number of animals•cm^{-2} of tubeworm area) were log transformed. However, this transformation successfully normalized only two of the Axial species chosen for analysis and none of the species from the senescent samples. No other transformations were able to normalize the data. For the senescent samples, no species distributions are normal with any transformation. Parametric statistical tests assume normally distributed data as well as random sampling. Nonparametric measures of species association are used to look for species associations (Spearman and Kendall correlation coefficients as well as multivariate analyses). Tests for normality, Friedman tests (to test whether species abundance distributions differ among sites), and pairwise correlations are performed in SPSS. Clustering, cophenetic correlation, and correspondence analysis in NTSYS 2.0. The Jaccard and Bray-Curtis coefficients are used to compute similarity matrices and the hierarchical, agglomerative algorithm of the flexible method (ß = -0.25) to cluster. Correspondence analysis and cophenetic correlation are used to check the validity of clusters. A discussion about the multivariate techniques used to analyse the data in this chapter is in Chapter 4, Methods. Complementarity calculations are after Colwell and Coddington (1994) with a modification that takes different sample sizes into account (Chapter 4, Methods).

Species diversity indices are as per Tsurumi and Tunnicliffe (2000). For both H' and (1-D), the higher the absolute number, the greater the diversity, although Simpson's index only ranges between zero and almost one. I also include Simpson's measure of evenness, $E_{1/D}=[(1/D)/s]$ where s is the number of species. Values of $E_{1/D}$ range from zero to one, with one representing maximum evenness. Simpson's measure of diversity is suggested to be better for small samples, than H' (Smith and Grassle 1977). Hill (1973) suggests use of Simpson's and total species. This measure is relatively unaffected by the rare species in a sample (Krebs 1999). Rarefaction is computed as per Tsurumi and Tunnicliffe (2000). Unequal sample size is also accounted for by species density: number of species divided by specified collection area (Magurran 1988).

Rare and endemic species

Rare species are those species that are present at only a few sites and low in overall abundance. I consider rare vent species to have less than 0.1% percent-average relative abundance and that are present at 25% or fewer sites. For Axial that means present at 1-5 sites out of 25 and for the senescent data set that means present at only one of four sampled sites. My definition of rare does not include species that are in low local abundance in some samples, but are in high abundance over the entire data set. Species that are not yet described or identified are not included as endemics even if they are commonly found in Juan de Fuca vent samples because they may turn out to be unrecognised non-vent deep-sea or mid-water species.

Results

Non-senescent (Axial) versus all senescent samples

Senescent samples are grabs of recumbent tubeworm tubes with little macrofauna visible on or around the tubes. Upon examination on the surface, most tubes are empty of live *Ridgeia piscesae*, there is very little bacterial mat or associated fauna on the tubes, and there are few macrofauna. There is high variation among the senescent samples with respect to the species present, dominant species, and species rank-abundance. Table 3.2 gives the species present in all five senescent samples and Appendix 3.5 lists species percent-average relative abundance for each senescent sample. There may be a shift in senescent samples from more vent-like to less vent-like (Z to YY to EE to GG: Appendix 3.5). A general senescent assemblage description is different from the Axial profile. Rank-abundance curves for senescent and Axial samples are different despite having the same animal (the limpet, *Lepetodrilus fucensis*) as the most abundant organism for both communities (Figures 3.1a and b). Rank-abundance for the senescent samples is more even than for non-senescent Axial samples: 11 species make up more than 90% of the community for senescent vents while only five species constitute more than 90% of the community for Axial. The dominance pattern of Axial samples follows the abundance curve closely while the senescent curve has dominance shared amongst more species so that species of lesser overall abundance are dominant in some samples (Figures 3.1a and b). The composition of major taxa indicates that gastropods and annelids are both at about the same abundance for senescent and non-senescent samples, but the senescent habitat hosts a greater abundance of both Crustacea and Other fauna (Figure 3.2). “Acoelomates” are present in senescent samples and not in Axial samples.

Multivariate cluster and correspondence analysis (CA) of senescent and non-senescent samples show senescent sample GG (Endeavour 1999) separates from all other

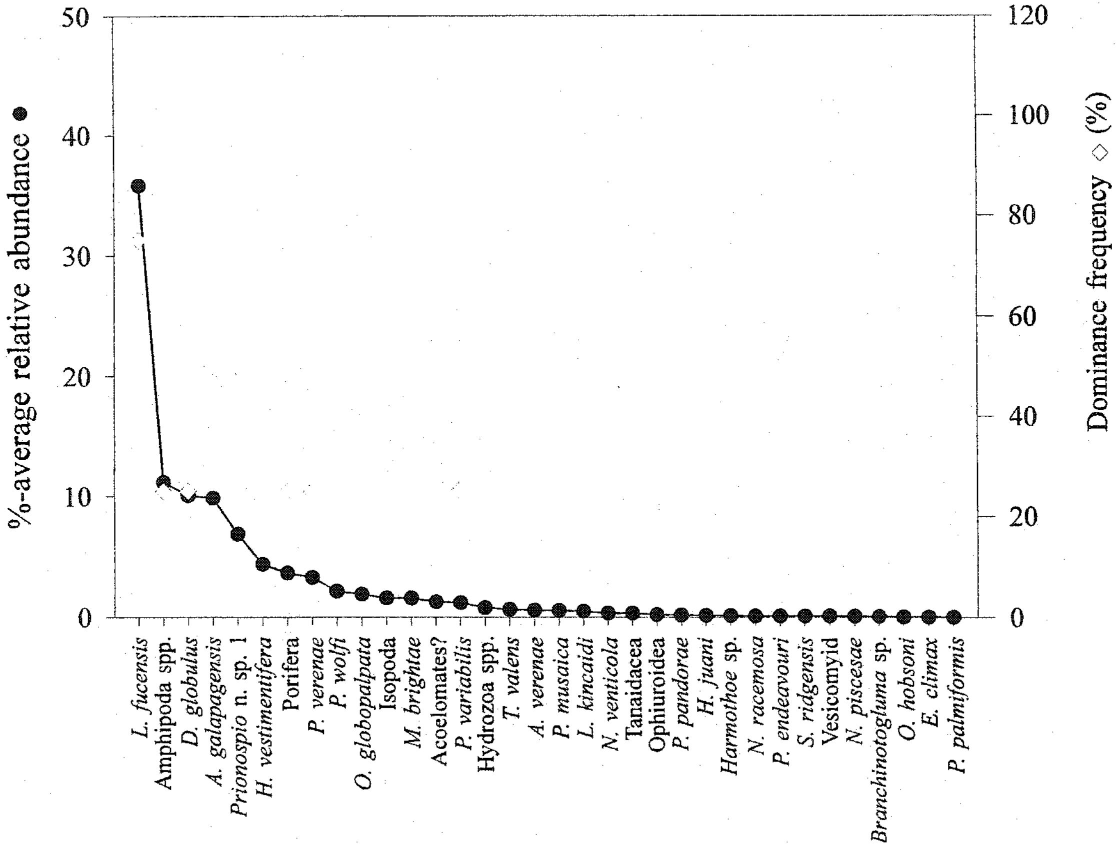
Table 3.2: Taxonomic listing of species from all senescent samples. The non-vent column shows species which are present in the qualitative non-vent samples HH and II, species that are known to be present in the non-vent environment, or if the species are unknown, are higher order taxa that are common in the deep-sea. For example, *Pyropelta musaica* has been reported on whale bones off California (Bennett et al. 1994).

Taxon	Species	**Samples**					
		YY	Y	Z	EE	GG	Non - vent
Polychaeta	*Nicomache venticola*					X	
Polychaeta	*Ophryotrocha globopalpata*	X		X	X		
Polychaeta	*Parougia wolfi*		X	X	X		
Polychaeta	*Orbiniella hobsonae*		X	X			
Polychaeta	*Branchinotogluma* sp.				X		
Polychaeta	*Harmothoe* sp.	X				X	X
Polychaeta	*Hesiospina vestimentifera*	X		X	X		
Polychaeta	*Levensteiniella kincaidi*	X		X	X		
Polychaeta	*Nereis piscesae*			X	X		
Polychaeta	*Protomystides verenae*		X	X		X	
Polychaeta	*Prionospio* n. sp.1	X	X	X	X		X
Polychaeta	*Amphisamytha galapagensis*	X	X	X	X		
Polychaeta	*Paralvinella palmiformis*			X			
Polychaeta	*Paralvinella pandorae*	X		X	X		
Arachninda	*Copidognathus papillatus*			X			
Calanoida	some are *Clausocalanus lividus*	X	X	X	X	X	X
Harpacticoida	Spp. unknown	X		X	X	X	X
Harpacticoida	Family Tisbidae, Copepoda Type 1	X	X	X	X	X	
Copepoda	Copepoda Type 2 (copepodites?)	X			X	X	
Copepoda	Copepoda Type 9	X					
Copepoda	*Aphotopontius forcipatus*	X		X	X		
Copepoda	*Bethoxynus spiculifer*			X		X	
Copepoda	*Barathricola rimensis*	X			X		
Copepoda	*Misophriopsis longicauda*	X		X	X		
Copepoda	*Stygiopontius quadrispinosus*	X					
Copepoda	Copepoda Type 11	X					
Copepoda	Copepoda Type 13				X		
Ostracoda	*Euphilomedes climax*	X					
Ostracoda	Spp. unknown			X	X	X	X
Pycnogonida	*Ammothea verenae*	X		X		X	
Hydrozoa	Spp. unknown					X	X

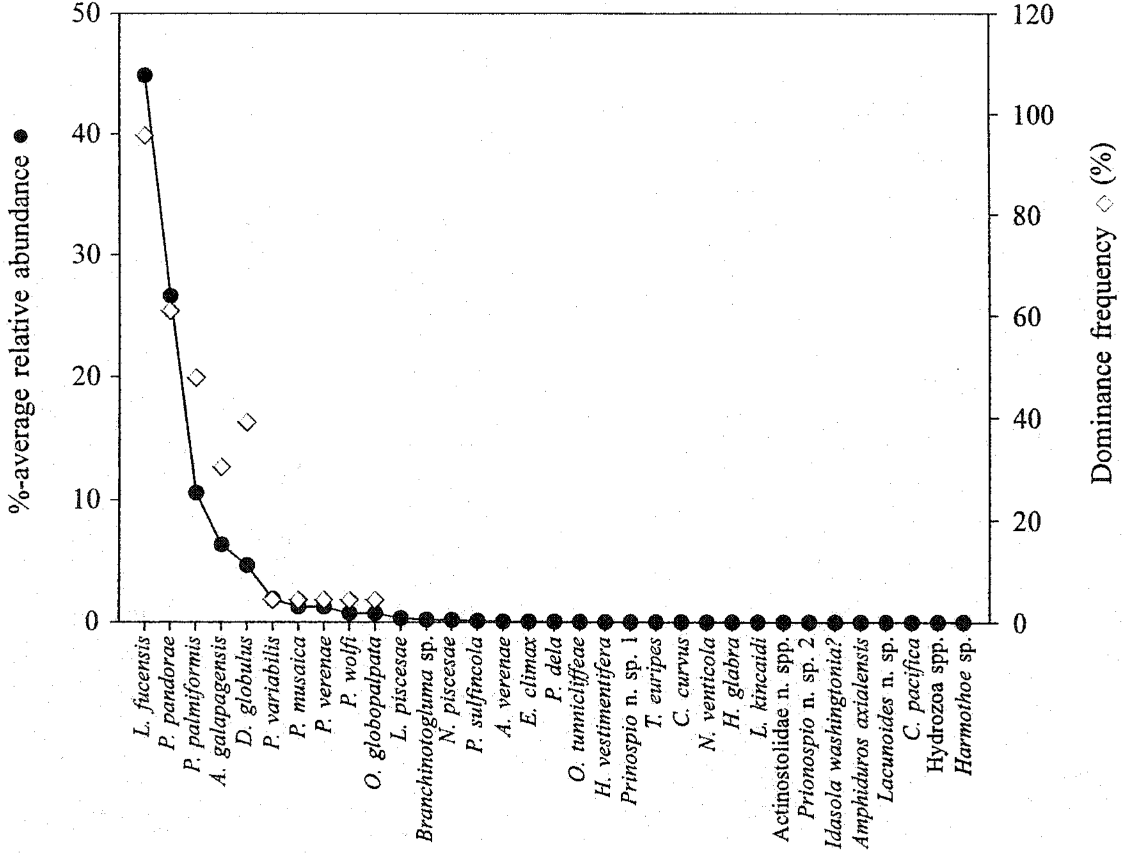
Taxon	Species	**Samples**					
		YY	Y	Z	EE	GG	Non - vent
Gastropoda	*Provanna variabilis*	X	X	X	X	X	
Gastropoda	*Depressigyra globulus*	X		X	X		
Gastropoda	*Melanodrymia brightae*					X	
Gastropoda	*Pyropelta musaica*			X			X
Gastropoda	*Lepetodrilus fucensis*	X	X	X	X	X	
Solenogaster	*Helicoradomenia juani*	X		X	X		
Nematoda	Spp. unknown			X		X	X
Nemertea	*Thermanemertes valens*	X			X		
Acoelomates?	?	X	X	X		X	X
Porifera	*Asbestopluma* n. sp.					X	X
Polychaeta	*Sphaerosyllis ridgensis*					X	X
Polychaeta	*Neolira racemosa*					X	X
Amphipoda	Spp. unknown 1			X		X	X
Amphipoda	Spp. unknown 2					X	X
Amphipoda	*Pardalisca endeavouri*					X	
Bivalvia	Vesicomyid					X	X
Isopoda	Sp. unknown					X	X
Ophiuroidea	Sp. unknown					X	X

Figure 3.1. a: Rank-abundance of senescent macrofauna. Total number of specimens is 10 034. Total number of samples is 4 and does not include culled sample Y. b: Rank-abundance of Axial macrofauna. Total number of specimens is 168 352 and does not include culled samples J, Q, R, W, and X. Abundance is expressed as percent-average relative abundance across samples. Dominance frequency is the percent of samples in which a species is one of the three most abundant species. For example, *Lepetodrilus fucensis* is in the top three abundance in three out of four samples (75.0%) for the senescent dataset. Taxonomic groups where the species are unknown but which probably contain more than one species are noted as “spp”.

a


%-average relative abundance ●
Dominance frequency ◇ (%)
0
10
20
30
40
50
0
20
40
60
80
100
120
L. fucensis
Amphipoda spp.
D. globulus
A. galapagensis
Prionospio n. sp. 1
H. vestimentifera
Porifera
P. verenae
P. wolfi
O. globopalpata
Isopoda
M. brightae
Acoelomates?
P. variabilis
Hydrozoa spp.
T. valens
A. verenae
P. musaica
L. kincaidi
N. venticola
Tanaidacea
Ophiuroidea
P. pandorae
H. juani
Harmothoe sp.
N. racemosa
P. endeavouri
S. ridgensis
Vesicomyid
N. piscesae
Branchinotogluma sp.
O. hobsoni
E. climax
P. palmiformis

b


%-average relative abundance ●
Dominance frequency ◇ (%)
0
10
20
30
40
50
0
20
40
60
80
100
120
L. fucensis
P. pandorae
P. palmiformis
A. galapagensis
D. globulus
P. variabilis
P. musaica
P. verenae
P. wolfi
O. globopalpata
L. piscesae
Branchinotogluma sp.
N. piscesae
P. sulfincola
A. verenae
E. climax
P. dela
O. tunnicliffeae
H. vestimentifera
Prinospio n. sp. 1
T. euripes
C. curvus
N. venticola
H. glabra
L. kincaidi
Actinostolidae n. spp.
Prionospio n. sp. 2
Idasola washingtonia?
Amphiduros axialensis
Lacunoides n. sp.
C. pacifica
Hydrozoa spp.
Harmothoe sp.

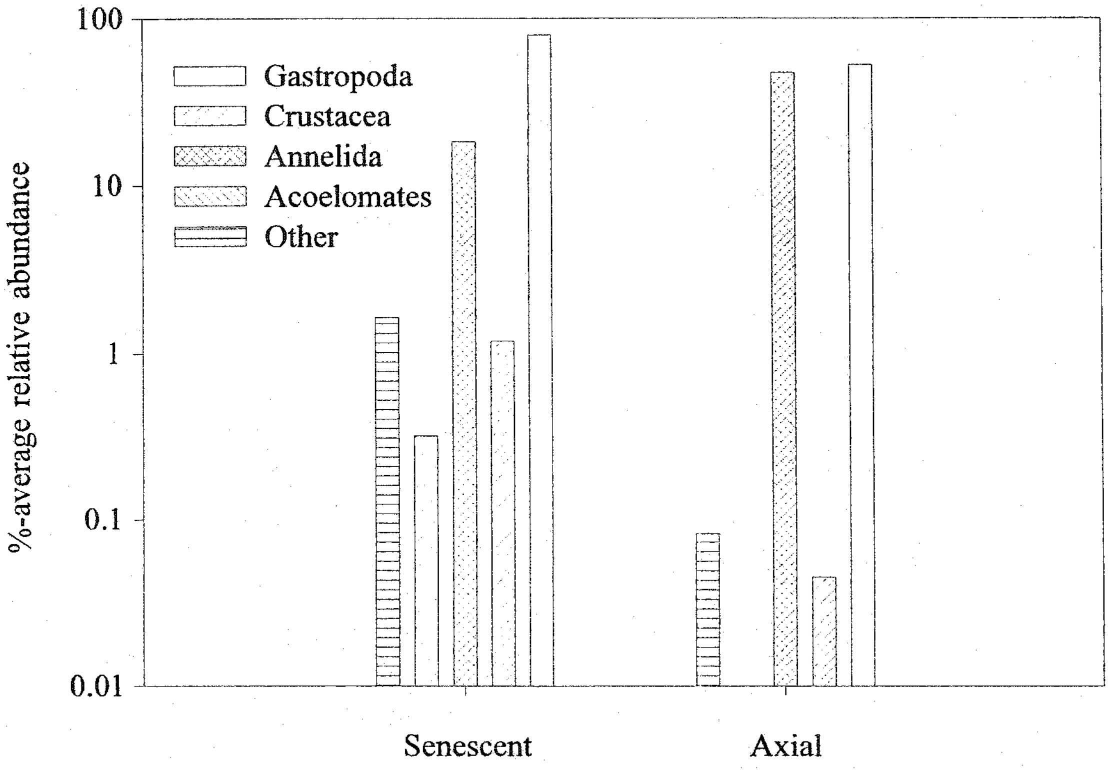


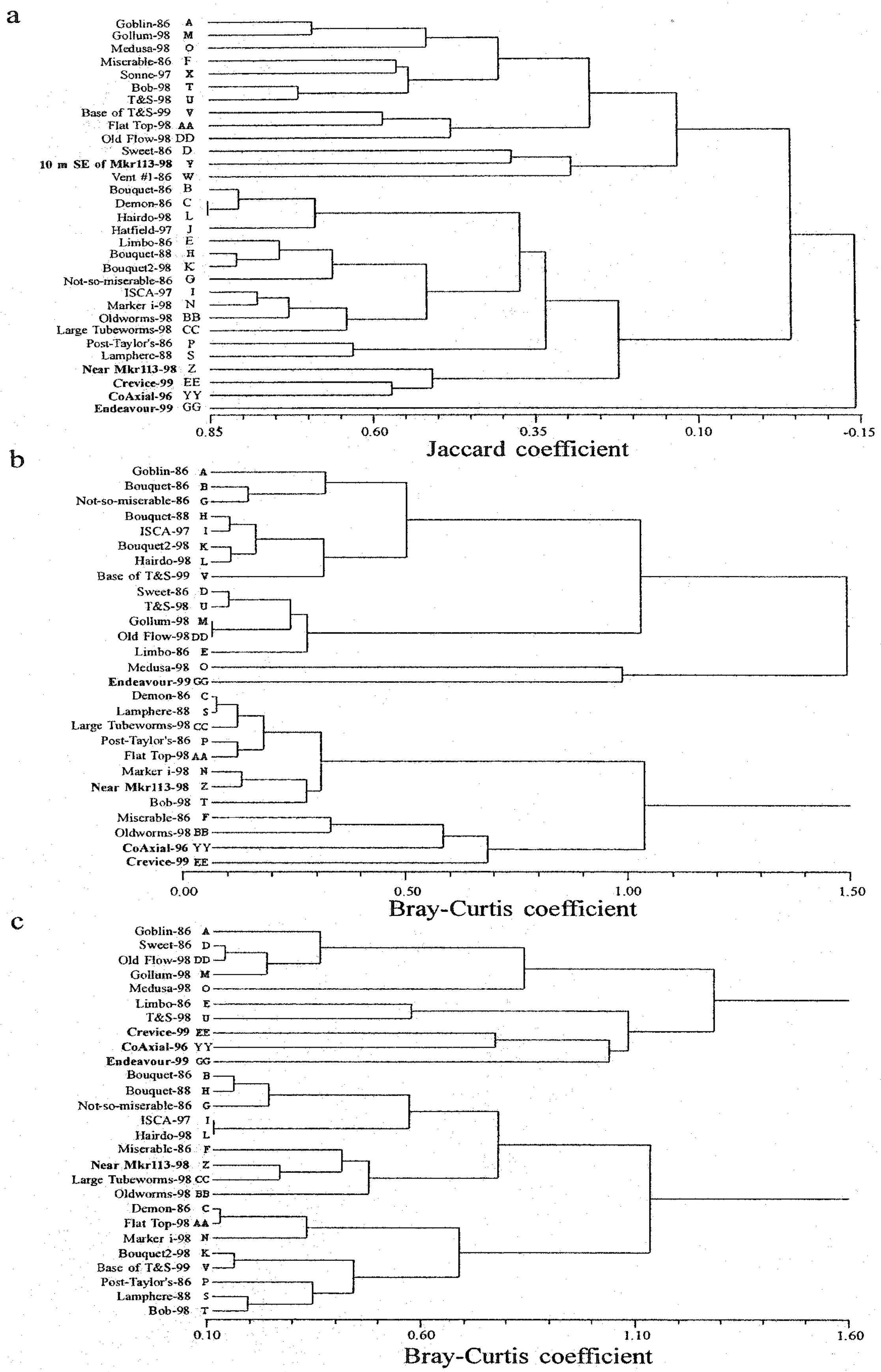
Figure 3.2. Comparing major taxonomic groups between senescent non-senescent (Axial) habitat. Different patterns indicate one of five taxonomic groups. Abundance is expressed as percent-average relative abundance across samples. The "Other" category encompasses Porifera, Echinodermata, Mollusca other than gastropods, Cnidaria, and Arthropoda other than Crustacea.

samples (Figures 3.3 and 3.4). Senescent samples YY (CoAxial 1996) and EE (SRZ, Axial 1999) cluster together (Figure 3.3). Clusters and CA based on percent relative abundance, density, and presence/absence all agree on these groupings. Senescent sample Z (SRZ, Axial 1998) falls out with YY and EE with the presence/absence data only (Figure 3.3). Sample GG is from Endeavour which is a ridge segment that is geographically removed from the other samples (it lies more than 100 km to the north of the nearest senescent site), hosts sedimented as well as hard substratum vents, and is hypothesised to have a very different geophysical source of venting from CoAxial and Axial (RIDGE 1999). These factors may explain why the senescent Endeavour sample is so removed from all other sample in the multivariate analysis.

The rarefaction curve is much steeper for the senescent samples and starts to plateau at a higher level, indicating that the species richness and evenness of the senescent samples is greater than for non-senescent Axial (Figure 3.5). The species richness and evenness of the senescent and Axial samples illustrated by species number, species density, and diversity indices (Table 3.3) are of similar values. However, rarefaction curves are a more useful comparison as the Axial calculations are based on 25 samples and the senescent calculations on only four.

A nonparametric Friedman test on the differences in distribution between species densities of Axial and senescent samples finds significant differences between Axial and senescent communities ($p<0.01$). The complementarity between Axial and senescent vents is 92.8% with 19 shared species. This figure is a percent-measure of distinctness between two sample sets. Average density (individuals•cm^{-2}) is 1.319 for Axial and 0.222 for senescent vents (Figure 3.6).

Figure 3.3. Cluster diagrams for senescent and non-senescent samples (sites). Only macrofauna are used in the analysis. The dash and number after each vent site indicates the year of sample collection. a: presence/absence data (all samples used). b: percent relative abundance data (culled samples J, Q, R, W, X, and Y not used). c: density data (culled samples J, Q, R, W, X, and Y not used). Plain and bold typefaces indicate non-senescent and senescent vents respectively. Flexible clustering method ($\beta = -0.25$) and the Jaccard similarity coefficient are used. Letters are sample designations (Table 3.1).


a
Goblin-86 A
Gollum-98 M
Medusa-98 O
Miserable-86 F
Sonne-97 X
Bob-98 T
T&S-98 U
Base of T&S-99 V
Flat Top-98 AA
Old Flow-98 DD
Sweet-86 D
10 m SE of Mkr113-98 Y
Vent #1-86 W
Bouquet-86 B
Demon-86 C
Hairdo-98 L
Hatfield-97 J
Limbo-86 E
Bouquet-88 H
Bouquet2-98 K
Not-so-miserable-86 G
ISCA-97 I
Marker i-98 N
Oldworms-98 BB
Large Tubeworms-98 CC
Post-Taylor's-86 P
Lamphere-88 S
Near Mkr113-98 Z
Crevice-99 EE
CoAxial-96 YY
Endeavour-99 GG
0.85
0.60
0.35
0.10
-0.15
Jaccard coefficient
b
Goblin-86 A
Bouquet-86 B
Not-so-miserable-86 G
Bouquet-88 H
ISCA-97 I
Bouquet2-98 K
Hairdo-98 L
Base of T&S-99 V
Sweet-86 D
T&S-98 U
Gollum-98 M
Old Flow-98 DD
Limbo-86 E
Medusa-98 O
Endeavour-99 GG
Demon-86 C
Lamphere-88 S
Large Tubeworms-98 CC
Post-Taylor's-86 P
Flat Top-98 AA
Marker i-98 N
Near Mkr113-98 Z
Bob-98 T
Miserable-86 F
Oldworms-98 BB
CoAxial-96 YY
Crevice-99 EE
0.00
0.50
1.00
1.50
Bray-Curtis coefficient
c
Goblin-86 A
Sweet-86 D
Old Flow-98 DD
Gollum-98 M
Medusa-98 O
Limbo-86 E
T&S-98 U
Crevice-99 EE
CoAxial-96 YY
Endeavour-99 GG
Bouquet-86 B
Bouquet-88 H
Not-so-miserable-86 G
ISCA-97 I
Hairdo-98 L
Miserable-86 F
Near Mkr113-98 Z
Large Tubeworms-98 CC
Oldworms-98 BB
Demon-86 C
Flat Top-98 AA
Marker i-98 N
Bouquet2-98 K
Base of T&S-99 V
Post-Taylor's-86 P
Lamphere-88 S
Bob-98 T
0.10
0.60
1.10
1.60
Bray-Curtis coefficient

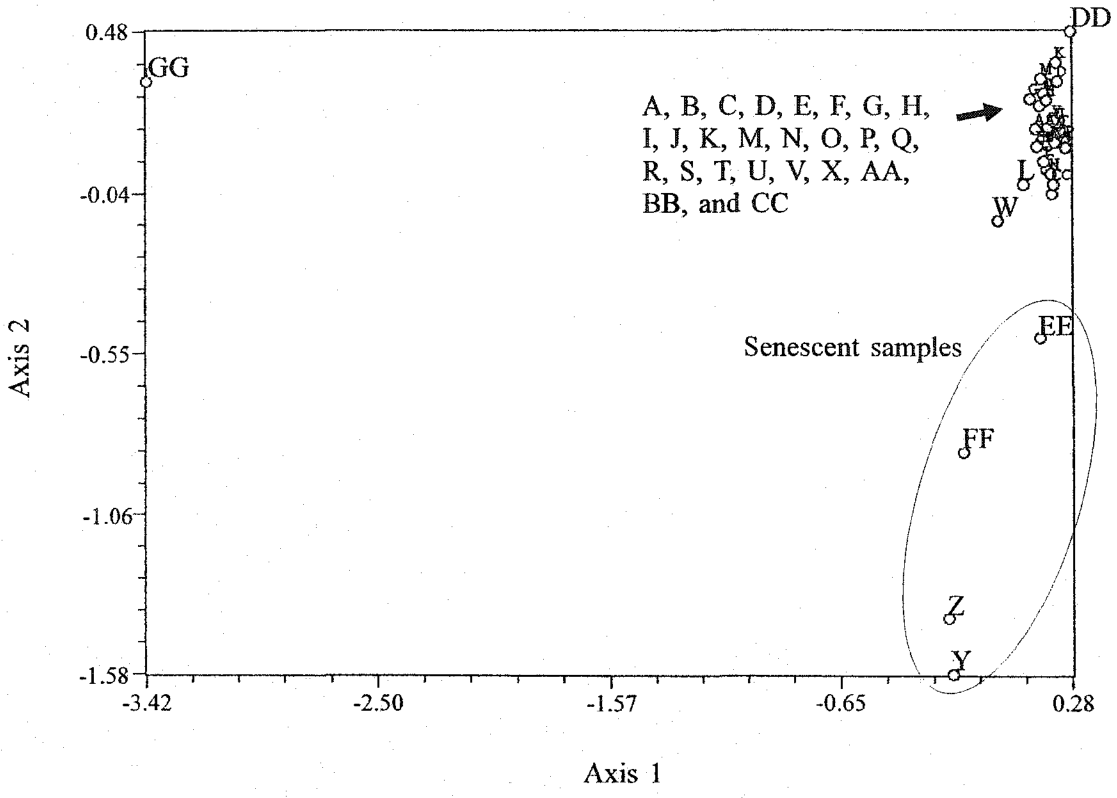


Figure 3.4. Correspondence analysis of senescent and non-senescent sample associations using presence/absence data. Thirty-one samples are included in the analysis. The senescent cluster from Figure 4a, is indicated on the graph. Note: Endeavour (GG) is in the upper left sector. Letters are site designations (Table 3.1).

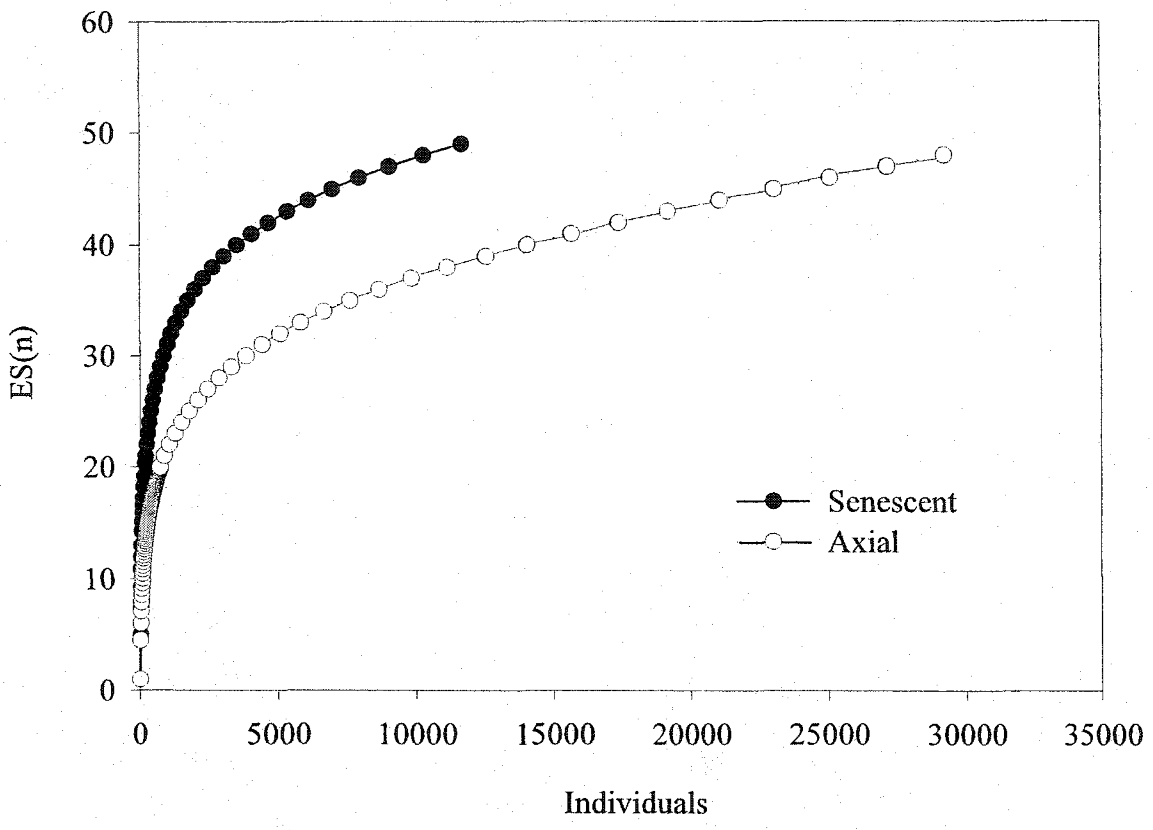


Figure 3.5. Rarefaction curves for senescent and non-senescent (Axial) samples ES(n) is the expected number of species in a random sample of n individuals. Each ES(n) estimate is based on 10 random samples for a given n.

Table 3.3: Species diversity characteristics for senescent and non-senescent communities. For Simpson's measure of diversity and evenness and Shannon-Wiener, H', all data are pooled. Numbers in parentheses are plus/minus standard deviations.

Habitat	No. of samples	Simpson's measure of diversity, 1-D	Shannon -Wiener, H'	Species density (no. of species• cm^{-2})	Species no. (macrofauna)	Species no. (all fauna)	Simpson's measure of evenness, $E_{1/D}$
Axial	23	0.702	2.424	0.006 (0.006)	36	48	0.093
Senescent	4	0.660	2.724	0.004 (0.003)	34	49	0.087
CoAxial 1995	1	--	--	0.002	8	9	--
CoAxial 1996	1	--	--	2.000 x 10^{-4}	15	25	--
Non-senescent South Rift Zone	4	0.690	2.521	0.007 (0.005)	20	32	0.101
Senescent South Rift Zone	3	0.442	1.533	0.004 (0.003)	21	33	0.054
Senescent sample GG from Endeavour	1	--	--	0.007	18	25	--

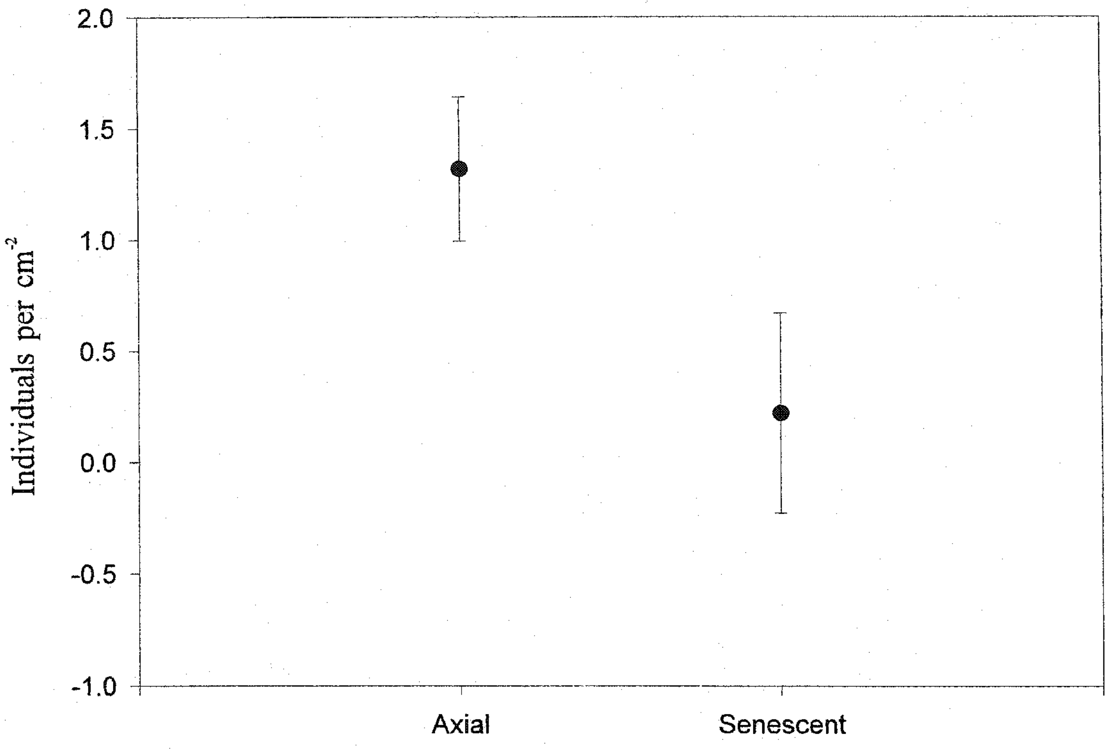


Figure 3.6. Average macrofaunal density in senescent and non-senescent (Axial) habitats. Calculated for Axial without culled samples J, Q, R, W, and X and for senescent samples without culled sample Y.

Overall, species at senescent vents appear to be less widely dispersed than most Axial species (Figure 3.7). A majority of the fauna from senescent vents are rare in dispersion (at 50% or fewer sites). The apparent greater rarity compared to the Axial community may, however, be due to the small sample size for the senescent data set. For Axial, the most widely dispersed species are the most common (Appendix 3.2). For the combined senescent samples, the same pattern is evident (Appendix 3.1). *Lepetodrilus fucensis* is present at all sites and dominant in abundance for Axial and senescent vents. The annelid, *Amphisamytha galapagensis*, is at 6 and 10% average relative abundance in Axial and senescent samples respectively, and is present at all but one site for both communities. The snail, *Depressigyra globulus* has about 5 and 10% average relative abundance at Axial and senescent vents respectively and is present at all Axial sites and all but one of the senescent sites. The snail, *Provanna variabilis*, comprises about 1-2% average relative abundance of both communities and is present at all but one site on Axial and all senescent sites. The polychaete, *Paralvinella pandorae* is present in vastly different average relative abundances at senescent (0.18%) and Axial (26.6%) communities, but is found at all but one of the senescent vents and at all Axial vents.

However, there is so much variation among the senescent vents (Appendix 3.5) that homogenising the samples may be misleading. For example, *D. globulus*, *A. galapagensis*, and *P. variabilis* are abundant and widely dispersed when all senescent samples are pooled (Appendix 3.1), but their relative abundance in each senescent sample ranges over three to four orders of magnitude (Appendix 3.5).

Twenty-nine of 39 macrofaunal species are endemics in the Axial community, whereas 23 of 34 macrofaunal species are vent endemics in the senescent habitat. Two

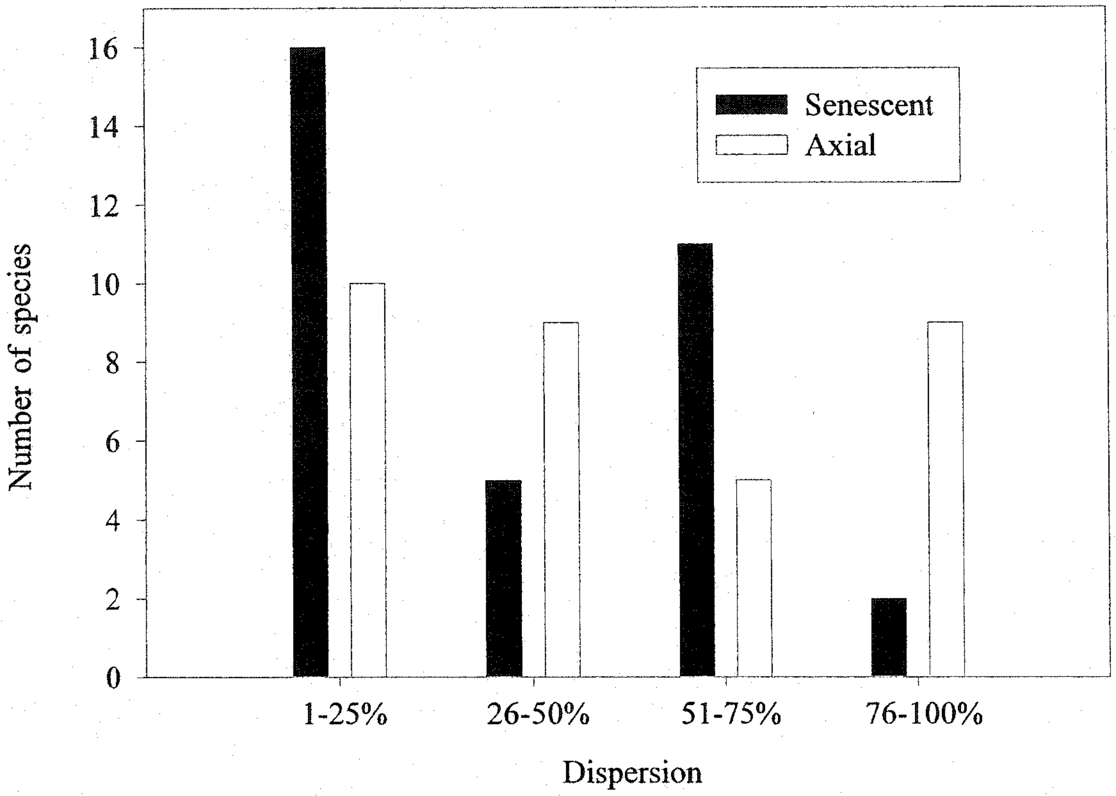


Figure 3.7. Comparison of dispersion between Axial and senescent macrofaunal species. Dispersion is divided into four classes: 1-25%, 26-50%, 51-75%, and 76-100%. These classes represent the percentage of sites where a species is found. The percentage is out of 23 total sites for Axial, and out of four total sites for the South Rift Zone. Black bars are senescent totals and white bars are Axial totals.

numerically dominant species in the senescent data set are not present in Axial samples, but all of the numerically dominant species from Axial are found at senescent vents.

Non-senescent versus senescent samples on the same segments

CoAxial 1995 versus CoAxial 1996

Cluster and correspondence analyses on macrofaunal percent relative abundance, density, and presence/absence do not group the CoAxial 1995 (non-senescent; sample XX) and 1996 (senescent; sample YY) samples. Collections at CoAxial in 1995 and 1996 were made within metres of each other so there is no question that these samples come from the same location. The CoAxial 1995 rank-abundance curve is less even than for 1996 (one species at CoAxial 1995 makes up more than 90% of the community compared to three species doing so in 1996). And the dominant species are different: *P. pandorae* is more than 90% of the community while *L. fucensis* is at about 0.1% abundance for CoAxial 1995 (Figure 3.8; Appendix 3.3). *Lepetodrilus fucensis* is the most abundant species for CoAxial 1996 while *P. pandorae* is only about 0.1% abundant (Appendix 3.3). The composition of major taxa is also different with CoAxial 1995 dominated by the Annelida, and CoAxial 1996, by the Gastropoda and Crustacea. CoAxial 1996 also has fauna in the "Other" category and a more even distribution among taxa.

The rarefaction curve for CoAxial 1996 is much steeper and reaches a higher plateau than for CoAxial 1995 indicating greater species richness and evenness (Figure 3.9). CoAxial 1995 has ten species, and 1996 has 25 species (Table 3.3). Friedman tests of percent-average relative abundance of species distributions indicate a significant

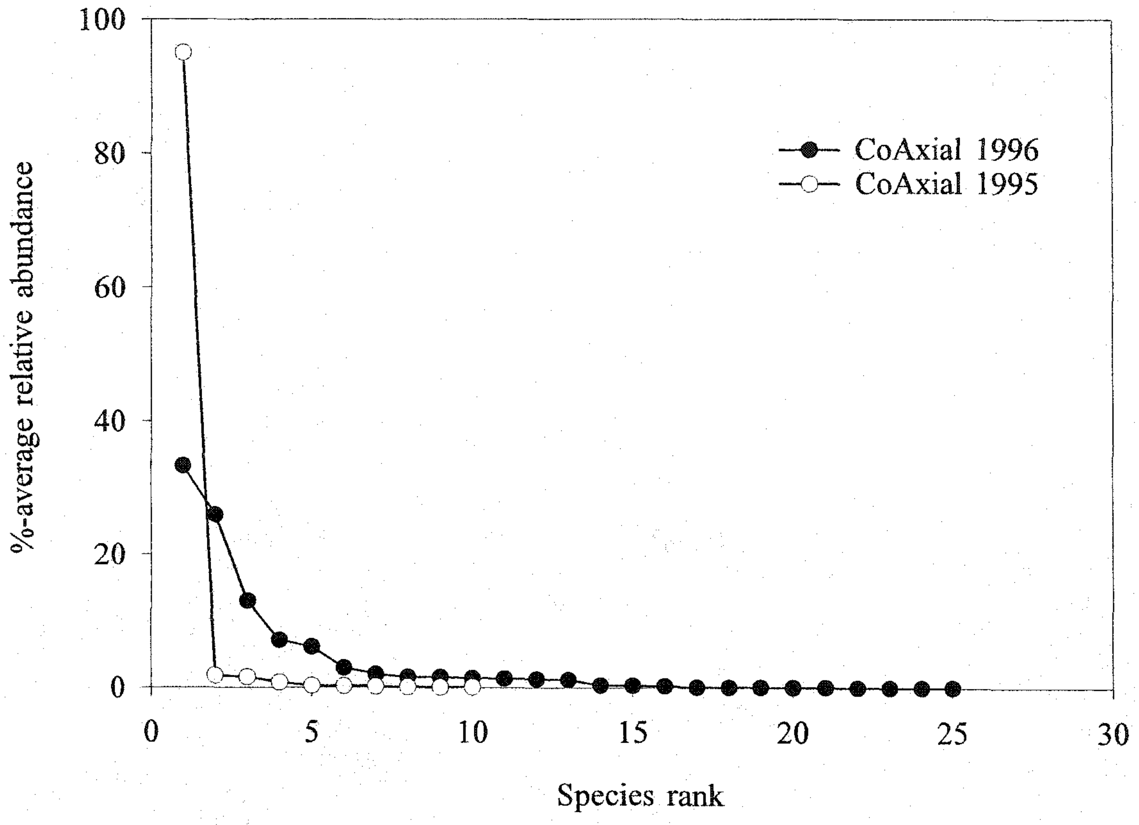


Figure 3.8. Rank-abundance curves for CoAxial 1995 and 1996. Macro- and meiofauna are used. Total number of specimens for CoAxial 1995 is 1850 and for CoAxial 1996 is 3586. Abundance is expressed as percent-average relative abundance across samples.

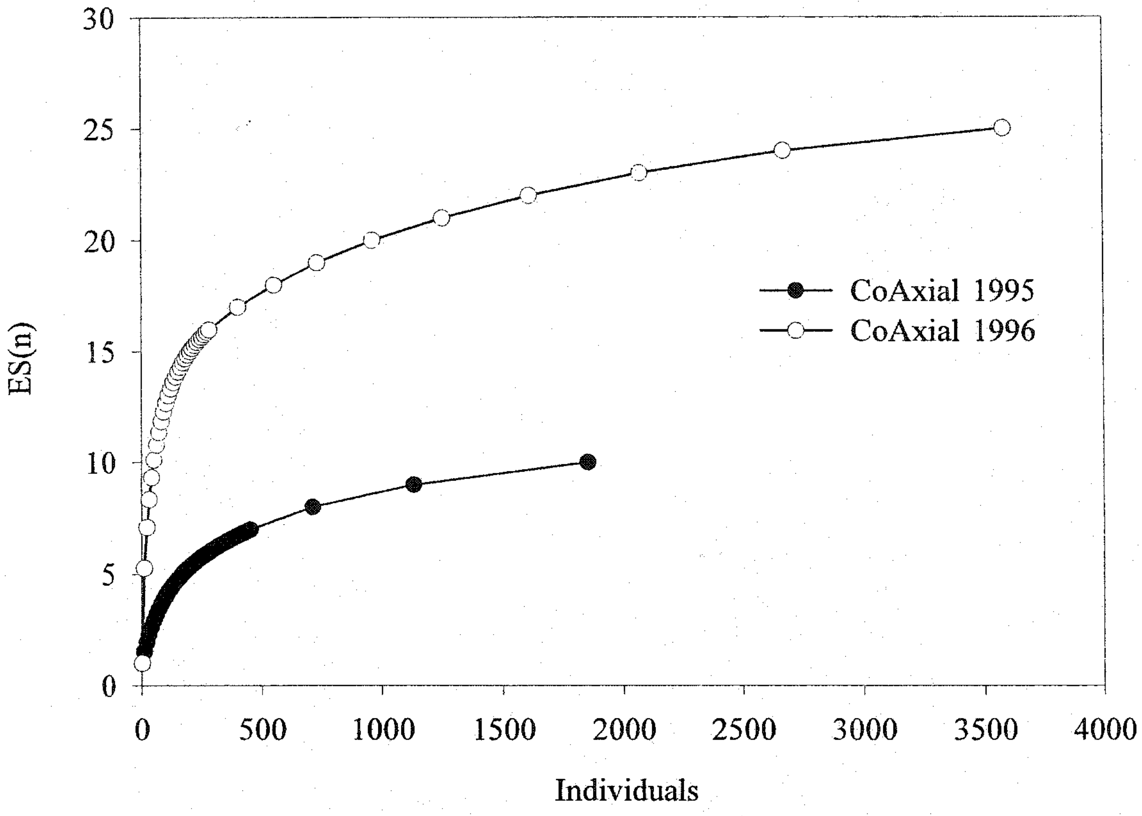


Figure 3.9. Rarefaction curves for CoAxial 1995 and 1996. ES(n) is the expected number of species in a random sample of n individuals. Each ES(n) estimate is based on 10 random samples for a given n.

difference between CoAxial 1995 and 1996 samples ($p<0.01$). Density of CoAxial 1995 fauna is 0.394 individuals•cm^{-2}; density for CoAxial 1996 is 0.025 individuals•cm^{-2}.

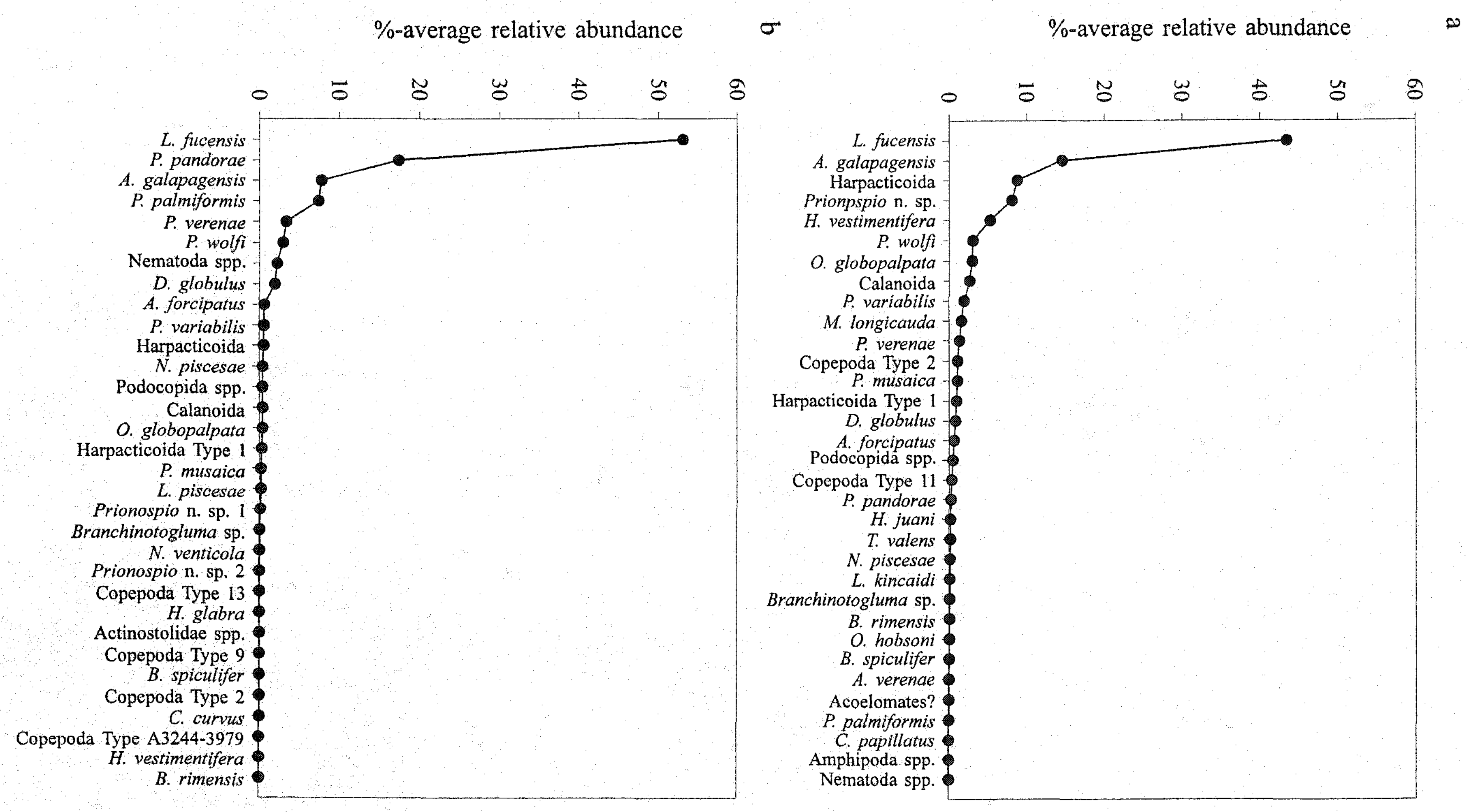
Non-senescent South Rift Zone versus senescent South Rift Zone

Cluster and correspondence analyses on percent relative abundance and density do not cluster non-senescent and senescent South Rift Zone samples together. Rank-abundance curves are the same shape for both data sets and *Lepetodrilus fucensis* is the most abundant organism (Figures 3.10a and b). In the non-senescent South Rift Zone community, six species make up more than 90% of the individuals and *Paralvinella pandorae* is the second most abundant animal at 17.4% (Appendix 3.4). In the senescent South Rift Zone samples, 11 species make up more than 90% of the individuals and *P. pandorae* is only at 0.2% abundance (Appendix 3.4). Gastropod and annelid abundances are about the same for both data sets. However, Crustacea are of an order of magnitude greater for senescent samples and Acoelomates are present (Appendix 3.4).

Non-senescent and senescent rarefaction curves have about the same slope (i.e. similar evenness) but the senescent curve is higher indicating greater species richness (Figure 3.11). Diversity indices, species density and number are listed in Table 3.3. Friedman tests show no significant differences between sample sets. Density for non-senescent South Rift Zone vents is 1.413 individuals•cm^{-2} and for senescent vents is 0.425 individuals•cm^{-2}.

Senescent samples YY, Z, EE, and GG

Figure 3.10. a: Rank-abundance of senescent South Rift Zone fauna. Total number of specimens is 7648. Total number of samples is two and does not include culled sample Y. b: Rank-abundance of non-senescent South Rift Zone fauna. Total number of specimens is 10 835. Total number of samples is four and does not include culled samples W and X. Abundance is expressed as percent-average relative abundance across samples. Taxonomic groups where the species are unknown but which probably contain more than one species are noted as "spp".


a
%-average relative abundance
0
10
20
30
40
50
60
L. fucensis
A. galapagensis
Harpacticoida
Prionpspio n. sp.
H. vestimentifera
P. wolfi
O. globopalpata
Calanoida
P. variabilis
M. longicauda
P. verenae
Copepoda Type 2
P. musaica
Harpacticoida Type 1
D. globulus
A. forcipatus
Podocopida spp.
Copepoda Type 11
P. pandorae
H. juani
T. valens
N. piscesae
L. kincaidi
Branchinotogluma sp.
B. rimensis
O. hobsoni
B. spiculifer
A. verenae
Acoelomates?
P. palmiformis
C. papillatus
Amphipoda spp.
Nematoda spp.
b
%-average relative abundance
0
10
20
30
40
50
60
L. fucensis
P. pandorae
A. galapagensis
P. palmiformis
P. verenae
P. wolfi
Nematoda spp.
D. globulus
A. forcipatus
P. variabilis
Harpacticoida
N. piscesae
Podocopida spp.
Calanoida
O. globopalpata
Harpacticoida Type 1
P. musaica
L. piscesae
Prionospio n. sp. 1
Branchinotogluma sp.
N. venticola
Prionospio n. sp. 2
Copepoda Type 13
H. glabra
Actinostolidae spp.
Copepoda Type 9
B. spiculifer
Copepoda Type 2
C. curvus
Copepoda Type A3244-3979
H. vestimentifera
B. rimensis

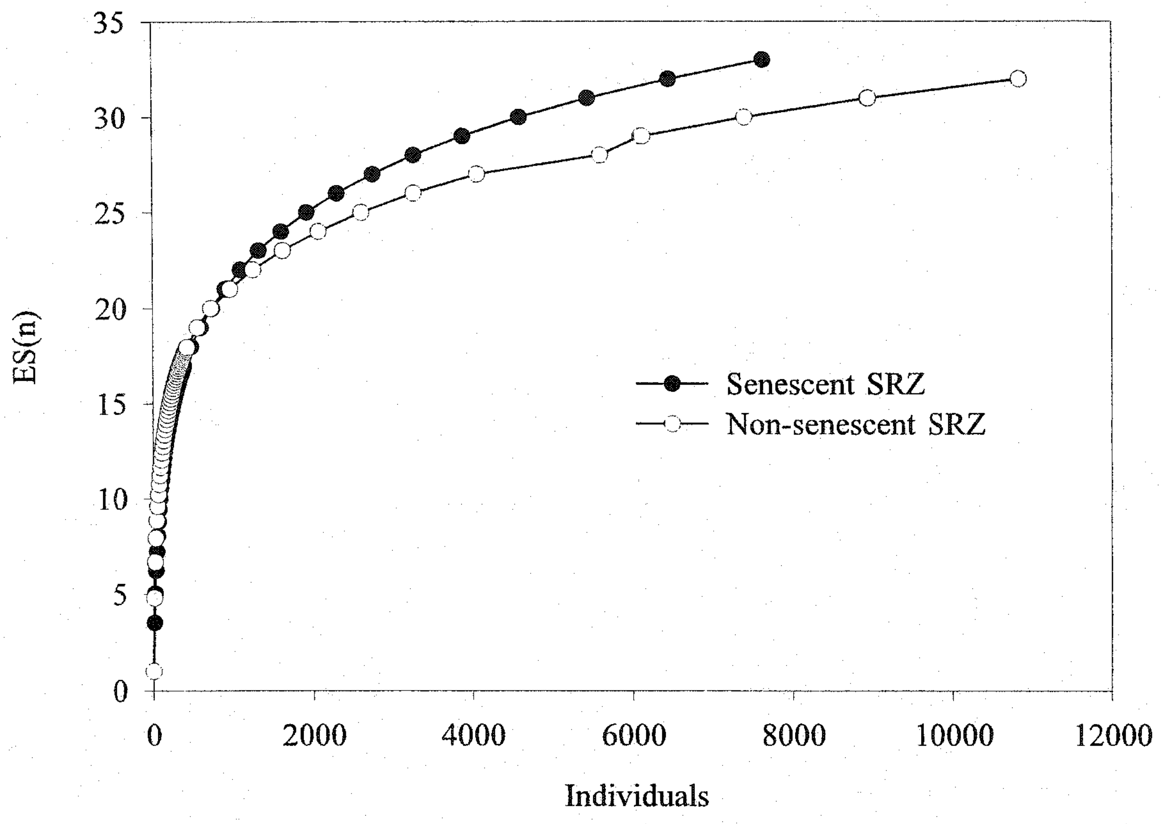


Figure 3.11. Rarefaction curves for senescent and non-senescent South Rift Zone samples. ES(n) is the expected number of species in a random sample of n individuals. Each ES(n) estimate is based on 10 random samples for a given n.

Rank-abundance curves for the four samples are different in the ranks of individual species (Appendix 3.5), but similar in shape to each other (Figure 3.12). Samples YY and EE have the most even distribution of percent-average relative abundance. *L. fucensis* is the most abundant species for samples YY and Z, and all samples have a completely different rank-order of species. These rank-orders are also different from Axial and non-senescent South Rift Zone curves (Figures 3.1b and 3.11b). Seven species make up more than 90% of the individuals for YY; four, eight, and ten species comprise more than 90% of the sample for samples Z, EE, and GG (Appendix 3.5). Composition of major taxa is evenly distributed in Sample E, including the Other category and Crustacea is the dominant taxon. Samples YY and Z are dominated by gastropods and sample EE by annelids (Appendix 3.5).

Rarefaction curves are given in Figure 3.13. Samples EE and GG are more even and species-rich than YY and Z. Curves YY and Z look similar and converge on each other. The species numbers are equivalent in the four samples (Table 3.3). Friedman tests of percent-average relative abundance and density do not detect any significant differences between samples. The samples in decreasing order of density are Z (0.641 individuals•cm^{-2}), EE (0.136 individuals•cm^{-2}), GG (0.0860 individuals•cm^{-2}), and YY (0.025 individuals•cm^{-2}) (Table 3.3). This follows the pattern of the rank-abundance curves which may indicate a shift from more vent-like to less vent-like (Z to EE to GG).

Senescent versus non-vent

Fauna typical of the non-vent deep-sea community such as isopods, tanaids, and ophiuroids were found in the senescent sample GG and in non-vent samples HH and II

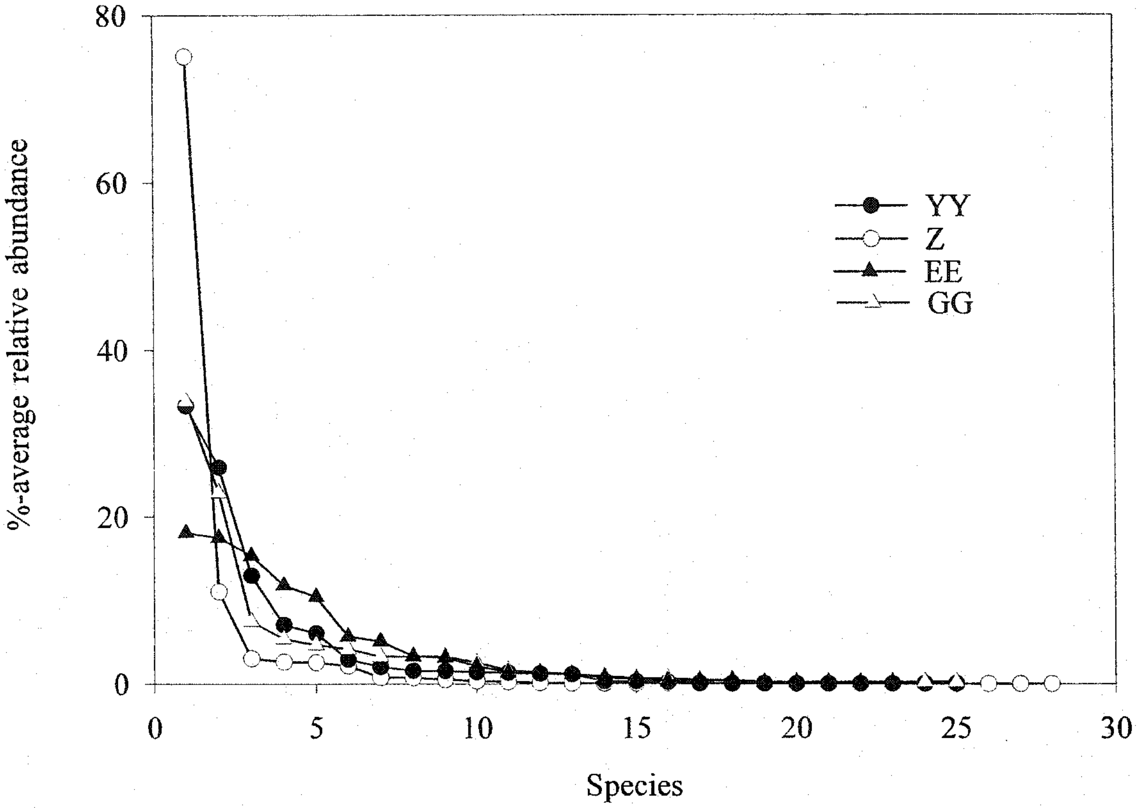


Figure 3.12. Rank-abundance curves for senescent samples. Macro- and meiofauna are used. Total number of specimens for sample YY is 3586, for sample Z is 7139, for sample EE is 509, and for sample GG is 428. Abundance is expressed as percent-average relative abundance across samples.

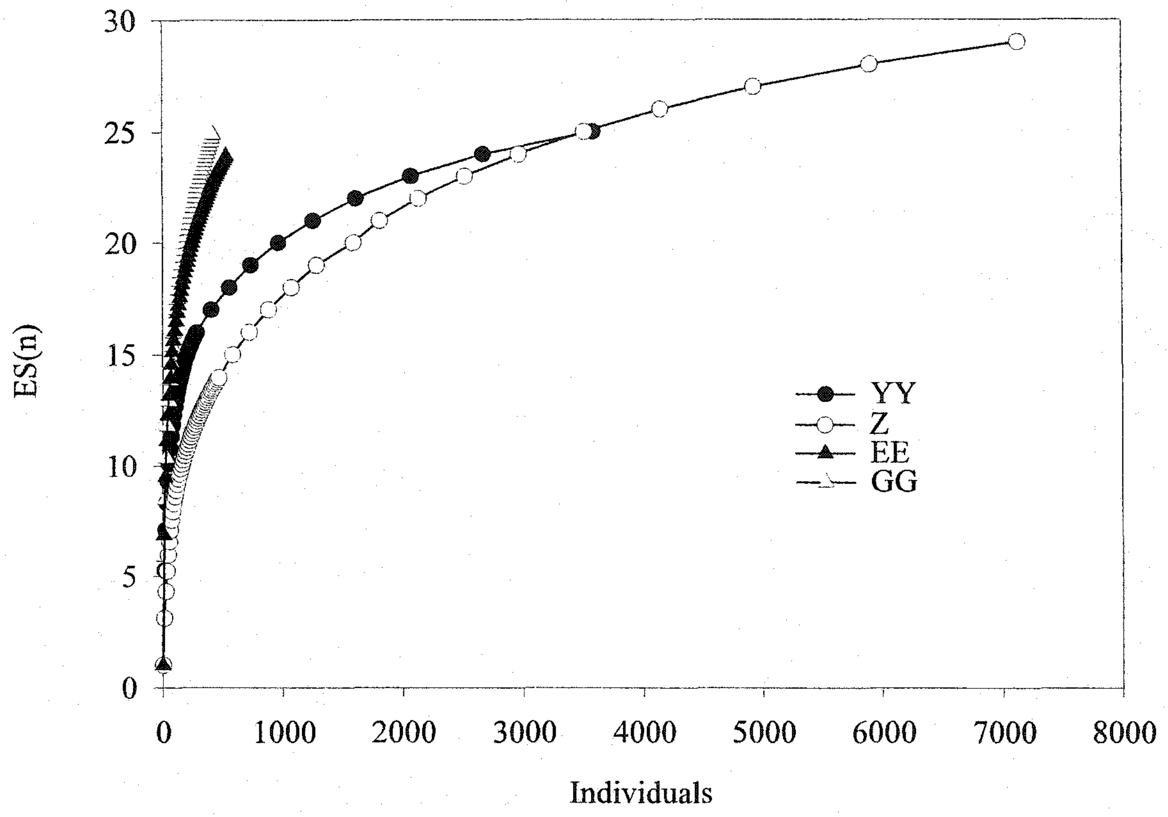


Figure 3.13. Rarefaction curves for senescent samples. ES(n) is the expected number of species in a random sample of n individuals. Each ES(n) estimate is based on 10 random samples for a given n.

(Table 3.1; Appendices 3.5 and 3.6). Calanoids, harpacticoid copepods, and ostracods (Podocopida) were found in non-vent samples as well as senescent and non-senescent vent samples.

Species associations

Cluster and correspondence analyses on the senescent samples cluster the pycnogonid, *Ammothea verenae*, with Acoelomates using percent relative abundance and density (Figure 3.14). The polychaetes *Ophryotrocha globopalpata* and *Amphisamytha galapagensis* are grouped together with correspondence analysis. Species associations are not similar to Axial (Chapter 4), but this may in part be because only some of the same species were used in both analyses. Pairwise correlations on density with Spearman's rank correlation, r_s, and Kendall's τ, are significant for a positive association between *A. verenae* and Acoelomates and between *O. globopalpata* and *A. galapagensis*.

Discussion

The senescent vent assemblage

Visually, senescent assemblages look different from active vents. Tubeworm tubes are relatively clean of bacteria, debris, and animals. Tubeworms are recumbent, sometimes covered in a heavy coat of sediment (Figure 2.3.3), *Ridgeia* branchial plumes are not visible, and spider crabs are found feeding in large numbers (Figure 3.15). There is no shimmering water, and no detectable temperature anomaly or sulphide. Statistically, senescent vents are distinguished by cluster analyses, have different distribution of species densities, and have low complementarity with non-senescent vents

Figure 3.14. a: Cluster diagram for senescent species using percent relative abundance data. b: Correspondence analysis of species associations using percent relative abundance data. Only species found in more than two samples (> 50%) are used. Flexible clustering method ($\beta = -0.25$) with Bray-Curtis coefficient is used to cluster. Total number of samples is four. Numbers are species designations (Appendix 1).

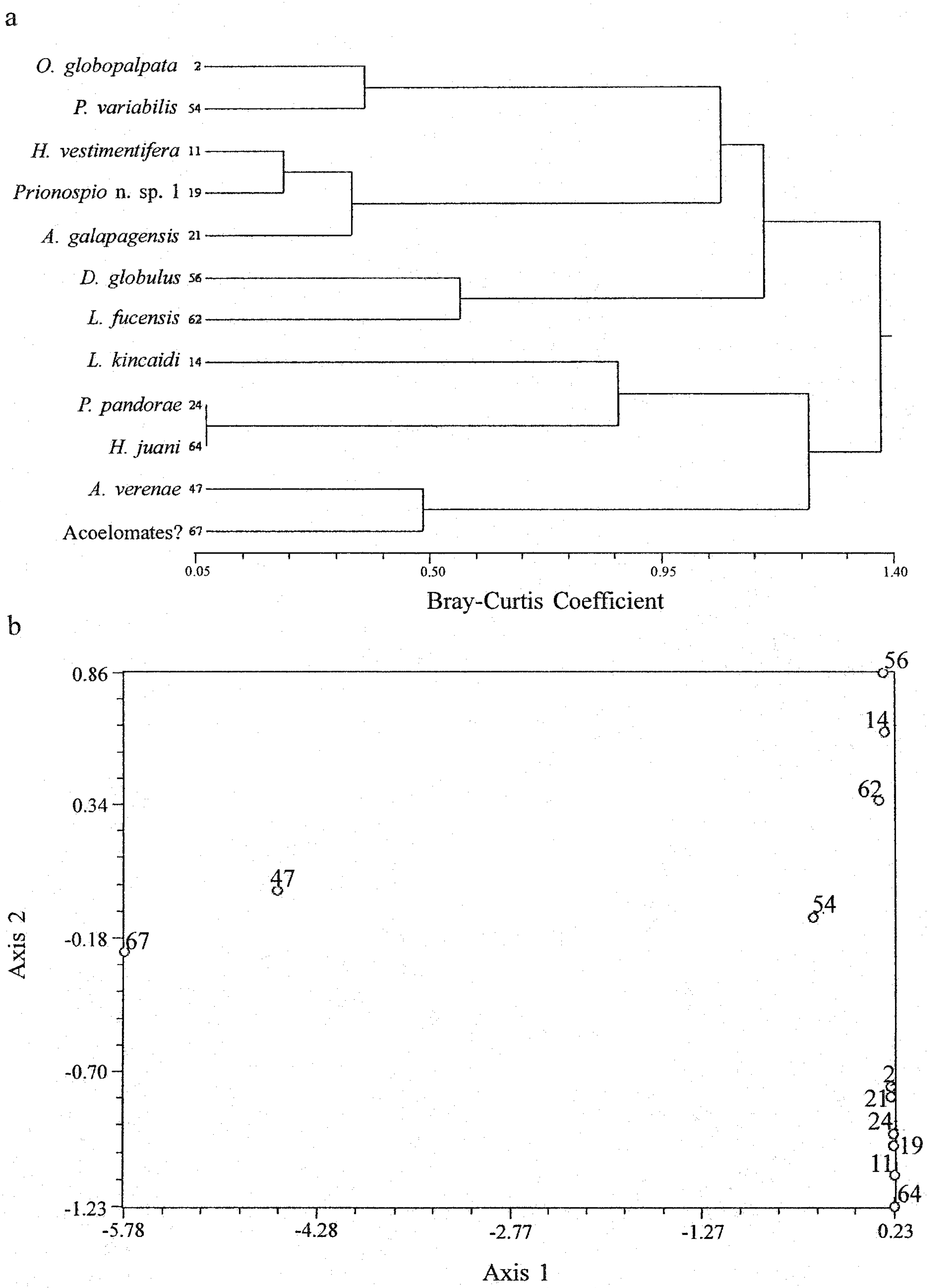

a
O. globopalpata 2
P. variabilis 54
H. vestimentifera 11
Prionospio n. sp. 1 19
A. galapagensis 21
D. globulus 56
L. fucensis 62
L. kincaidi 14
P. pandorae 24
H. juani 64
A. verenae 47
Acoelomates? 67
0.05
0.50
0.95
1.40
Bray-Curtis Coefficient
b
0.86
0.34
-0.18
-0.70
-1.23
-5.78
-4.28
-2.77
-1.27
0.23
Axis 2
Axis 1
56
14
62
47
54
67
2
21
24
19
11
64

Figure 3.15. Photograph of a senescent vent (CoAxial 1996; sample YY). Stick-like objects are *Ridgeia piscesae* tubes. Spider crabs crawling on the tubeworm tubes are a deep-sea species, *Macroregonia macrochira.* Note the absence of bacterial mats typical of active hydrothermal vents.

(93% distinct). A senescent vent has a more even distribution of species abundance than a non-senescent vent. Taxa present in large numbers in senescent samples are not found in non-senescent samples: Amphipoda spp. unknown and Porifera (Appendices 3.1 and 3.2). Species richness at senescent vents is higher than the non-senescent environment if unequal sample size is taken into account (Figure 3.5). Density, as measured by individuals per area of *Ridgeia* tube, is much lower than for non-senescent vents. There are fewer known vent endemics and more overlap taxa with the surrounding deep-sea. Composition of major taxa is similar for both active and senescent vent habitats except that the abundance of Crustacea is an order of magnitude higher at senescent vents.

The increased species richness and evenness of the senescent samples may be due to a change in environmental conditions that allows non-vent deep-sea fauna to invade the vent habitat and/or to changes in the ability of the dominant endemics to competitively exclude rarer species. Evidence for the former lies in the unrestrained movement of deep-sea spider crabs (*Macroregonia macrochira*) over senescent assemblages (Figure 3.15), in the fewer number of vent endemics, and the presence of isopods, tanaids, ophiuroids, hydrozoans, and Porifera, typical deep-sea fauna (Gage and Tyler 1991), in the senescent samples.

Studies in the literature on senescent assemblages relate increases in species richness and concomitant decreases in species abundance to changes in the physical and chemical environment (e.g. Odum 1960; Monk 1967; Bazzaz 1975; Woolhouse et al. 1985). Klimaszewski and Peck (1987) describe changes in insect fauna on a species of fungus. Abundance of individuals is highest at the initial stage (I), whereas the senescent stage (IV) supports the greatest species diversity (number of species). There is physical and chemical change over time in the fungal tissue due to aging, decomposition, and insect attack and there is a concomitant change in the insect community.

The intermediate disturbance hypothesis predicts a change in the ability of dominant species to competitively exclude other species due to a change in environmental conditions (Connell 1978). The increased abundance of vent endemics such as *Depressigyra globulus*, *Amphisamytha galapagensis*, and *Hesiospina vestimentifera* in some senescent samples, at the expense of *Lepetodrilus fucensis* and *Paralvinella pandorae*, may be a result of this process. Juniper and Tunnicliffe (1997) propose that species diversity increases with spreading rate, because the faster the spreading rate, the more frequent the disturbances and turnover of habitat. If habitat turnover creates vents in different successional states on a segment or ridge, then habitat turnover can increase regional species diversity at vents.

The decrease in animal density at senescent vents may be a result of the decrease in productivity that occurs with a cessation in venting. The trophic chain at vents is based on the primary productivity of chemosynthetic microbes that are dependent on the sulphide in the vent fluid. Without vent fluids, and sulphide in particular, resources are scarce for vent fauna and animal density should be lower. Remaining animals may be subsisting on bacterial mats produced when the sites were active and/or on each other. Macrofaunal density on the abyssal plains is about 0.1 $\text{individuals} \cdot \text{cm}^{-2}$ (Gage and Tyler 1991), the same order of magnitude seen in these samples.

Physical measurements such as temperature and H_2S are used to partially define a senescent vent before sampling. However, these physico-chemical factors are also the purported explanation for observed changes. It is axiomatic that changes in the composition of vent species will result with drastic changes in the venting. It is perhaps surprising that more changes are not evident and that some vent species persist in the habitat without active venting. Those that persist into the senescence vent stage, like *Lepetodrilus*, may have multiple food-gathering strategies, such as suspension- and deposit-feeding. Persistent species may be those that are competitively able to command the remaining food resources after venting ceases.

Rare species

Rare species are often assumed to be more threatened with extinction than common species (Chapman 1999; Garcia and Laville 2000). One might expect that rare species would disappear first with vent habitat extirpation. Eight of the 13 "rare" species (less than 0.1% abundance) disappear from the community when non-senescent and senescent South Rift Zone samples are compared (Appendix 3.4). Abundant vent species are also affected; *Lepetodrilus fucensis*, and the polychaetes, *Paralvinella pandorae*, *P. palmiformis*, and *Lepidonotopodium piscesae* are all species that dramatically decrease their percent-average relative abundance from intermediate to senescent stages.

The study of differences between common and rare species in their ecology and life history is one way to understand the causes of the species' rarity (Kunin and Gaston 1997). Kunin and Gaston (1997) suggest that rare species tend to differ from taxonomically related common species in a variety of biological traits. These traits include breeding systems, reproductive investment, dispersal ability, genetic polymorphism, competitive ability, resource usage (breadth or availability), trophic group and body size. Chapman (1999) reviews rarity and its application to marine invertebrates.

He concludes that little is known about the ecological attributes of rare marine species due to a scarcity of quantitative data sets on the occurrence of rarity in marine taxa. Samples from active and senescent vents provide quantitative data on the occurrence of rarity at Juan de Fuca vents. Are rare species from these vents poorer dispersers and colonizers of new habitat? Do rare species have more stringent habitat-requirements than common species?

Rare species from active and senescent habitat appear to be mostly diffusively rare (sensu Schoener 1987) in that they are present in low abundances and have narrow distributions. The twelve species on Cleft with the narrowest distributions are the ones present in the lowest abundances (Tsurumi and Tunnicliffe 2001). All ten macrofaunal species with the narrowest distribution (present at less than 25% of sites) at non-senescent Axial vents have very low abundances (<0.1%). An additional three species are present at only one or two sites but were from qualitative samples so relative abundance was not calculated, but were present in less than 10 individuals each. Twelve of 21 species with the narrowest distributions have the lowest abundances at senescent vents (<0.1%) and eight more have less than 1% abundance. Two of the 12 senescent species rare in distribution and abundance are only found at senescent vents (Table 3.4). These two species may be poor dispersers and/or colonisers, inadequately sampled, or excluded from vents until the senescent stage because of the chemical environment. Both species are known non-vent species and so restrictions due to habitat conditions likely explain their abundance-distribution.

Three species are common at Axial or Axial and Cleft and one species is common on Endeavour (Table 3.4). These four species may be adversely affected by the change

Table 3.4: Rarity of senescent vent species. Rare species are those present at 25% or fewer vent sites and less than 0.1% abundance in senescent samples (Appendix 3.1). "Rare at Axial or Axial and Cleft" mean species that are present at 25% or fewer vent sites and less than 0.1% abundance in Axial or Cleft samples not including senescent samples. "Common" means species that are not rare by the above definition.

Species rare in senescent samples	Common at Axial or Axial and Cleft non-senescent vents	Rare at Axial or Axial and Cleft non-senescent vents	Present on Endeavour, but not Axial or Cleft	Not at Axial, Cleft, or Endeavour non-senescent vents
Orbiniella hobsonae		X		
Branchinotogluma sp.	X			
Paralvinella palmiformis	X			
Copidognathus papillatus		X		
Copepoda Type 9		X		
Stygiopontius quadrispinosus	X			
Copepoda Type 11		X		
Euphilomedes climax		X		
Sphaerosyllis ridgensis				X
Neolira racemosa				X
Pardalisca endeavouri			X	
Vesicomyid		X		
Total	3	6	1	2

in habitat conditions going from an active to a senescent vent. Six of the 12 rare senescent species are rare at Axial or both Axial and Cleft (Table 3.4). For ecologists interested in what differentiates rare from non-rare species then I suggest *Orbiniella hobsonae*, *Copidognathus papillatus*, *Euphilomedes climax*, and Copepoda Types 9 and 11, as six candidate species from senescent vents to examine for common biological traits of rarity.

Dispersion of vent species

There are similarities between non-senescent and senescent vents other than in the species present. The limpet *Lepetodrilus fucensis*, is numerically dominant at both senescent and some non-senescent vents. The organism appears to compete well for resources: both as an intermediate stage coloniser and a hardy, late persistent species (Tsurumi and Tunnicliffe 2001), that once established in a community flourishes until a vent has senesced completely. The dispersion of the gastropods *L. fucensis*, and *Depressigyra globulus*, and the polychaete, *Amphisamytha galapagensis*, is similar for pooled senescent and pooled non-senescent samples. These species are ubiquitous, appearing at all or all but one site for both combined data sets. The most common species are often the most abundant in other systems (e.g. Gaston 1998) and both senescent and non-senescent fauna support this pattern (Appendices 3.1 and 3.2). Active and senescent vents are dominated by a few very abundant species and rare species make up the rest of the fauna with 65% rare species at senescent vents, and 63% rare at non-senescent Axial vents. The Cleft species pool also has mostly rare species. This is a fairly typical species abundance-distribution (Brown et al. 1995) for systems other than the benthic deep-sea.

Sample variability

One interesting difference between senescent and non-senescent samples is the amount of variation among senescent samples. There is much more variation among senescent samples than among non-senescent samples (Chapter 4). Differences in the taxonomic composition of individual senescent samples are not surprising, given that the specifics of succession are dependent on stochastic factors as well as deterministic mechanisms such as species-species interactions. Tsurumi et al. (1998) report different scenarios of initial colonisation after an eruptive event on the Juan de Fuca Ridge. There may be different scripts of succession that play out depending on invasion events or stage of senescence and that result in differences in senescent vent assemblages in terms of the specific fauna hosted.

Senescent versus non-vent deep-sea assemblages

Taxonomic similarity of samples at senescent vents to non-vent deep-sea communities is presented in Table 3.2. Crustacea, in particular copepods may be the first deep-sea species to move into a vent as it senesces. Abundances of some crustacean taxa at senescent vents are more like those found in the deep-sea. Harpacticoids comprise 2-3% of meiofaunal abundance in the abyssal zone and there may be global similarity in deep-sea harpacticoid fauna at family and/or generic levels (Gage and Tyler 1991). In the quantitative senescent samples, harpacticoids are at about 5% average relative abundance (Appendix 3.5). It is not surprising that this taxon may have cross-over species between vents and the deep-sea.

Early discussion of vent versus non-vent deep-sea suggested that large accumulations of biomass at hydrothermal vents affect the surrounding resource-starved deep-sea habitat in the same way that water at oases affects the surrounding desert (Cohen and Haedrich 1983). This idea is no longer relevant given the observations on productivity transfer from vents to deep-sea (Arquit 1990; Burd et al. 1992; Burd and Thomson 1994; Pond et al. 1997; Vereschaka and Vinogradov 1999; Pond et al. 2000). Senescent vents straddle the vent-deep-sea boundary and sometimes have more deep-sea species than non-senescent communities. This is one way senescence provides for productivity transfer between vent and pelagic and benthic deep-sea. Also, as tubeworms and other vent endemics die off, the organic material from their tubes and carcasses are left behind for the non-vent deep-sea community, increasing local productivity. Productivity may also be transferred further afield by deep-sea scavengers such as spider crabs, macrourid and zoarcid fish, and octopuses that move into vent fields as conditions allow (Voight 2000). Usually these far-ranging species must wait at the periphery for changes in fluid flow that allow them access to some vent animals. However, during senescence, fluid flow is drastically decreased and eventually ceases, allowing these animals unlimited access to organic remains.

Figure 3.16 graphs rarefaction curves for non-senescent Axial, senescent and deep-sea (Grassle and Maciolek 1992). Although senescent vents are more similar to deep-sea communities than are active vents, in terms of species richness and evenness they are still vent communities.

Although discussion of vent fauna is usually focused on distinctions between vent and non-vent, these differences may be less rigid than commonly believed. Some vent

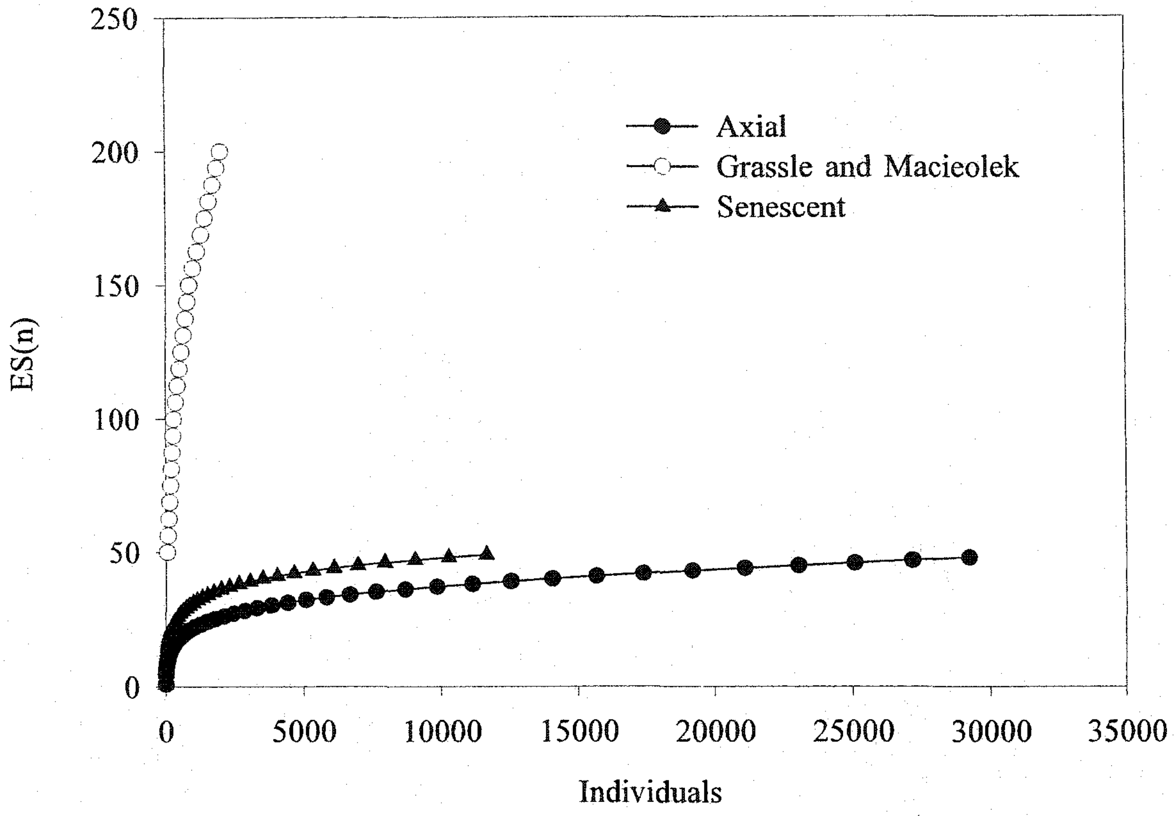


Figure 3.16. Rarefaction curves from different habitats. Both non-senescent (Axial) and senescent vent samples differ markedly from the non-vent deep-sea. Non-vent deep-sea curve is redrawn from Grassle and Maciolek (1992). ES(n) is the expected number of species in a random sample of n individuals. Each ES(n) estimate is based on 10 random samples for a given n.

endemics appear to be "hardy" species with individuals that persist beyond active venting, for example, *Lepetodrilus fucensis*. I do not think, however, that these species have persistent breeding populations at inactive vents. Some species may be considered vent species for historical reasons: considered vent endemics not because they are restricted to the vent environment, but because they happened to be sampled and described from vents and still await discovery in the non-vent deep-sea. These species may have higher densities at active vents, but would likely be present during a senescent stage as they are not restricted to just the vent habitat. Much effort has gone into sampling and classifying vent species. On the other hand, the majority of the deep-sea with very low densities of species, has been comparatively under-sampled (5-10% of the area explored and far less sampled; Lalli and Parsons 1993). It is likely that some purported vent endemic species are more cosmopolitan than first thought and are deep-sea inhabitants as well. For example, we now know that the snail *Pyropelta musaica* and the mussel *Idasola*, described from vents on Axial, are found on whale bones. Although whale bones are still considered a chemosynthetic habitat, the distribution of these two species is more cosmopolitan than their presence at Juan de Fuca vents might suggest. I suspect that as more of the deep-sea is sampled, a number of the vent crustacean taxa, in particular copepods and ostracods, will be found in the non-vent habitat.

With the inclusion of meiofauna in vent sample processing, more cross-over species between vent and non-vent are emerging. The vent calanoids are mostly a species of *Clausocalanus* (*C. lividus*) which is an epipelagic species otherwise found shallower than 1500 m (F. Ferarri, pers. comm.). Podocopid ostracods appear to be mostly common deep-sea ostracods (T. Jellinek, pers. comm.). Unidentified copepods, in particular harpacticoid copepods, are common in vent and in non-vent samples. It is likely that many of these species are deep-sea species taking advantage of the enhanced productivity at vents compared to the surrounding deep-sea.

Importance of meiofauna

Meiofaunal organisms are important in characterising the species diversity of vent communities (Tsurumi and Tunnicliffe 2001). Meiofauna are also important in characterising the abundance-distribution of vent communities (for example highlighting the number of rare species) and in elucidating differences between different successional stages and community types. Including meiofauna in species richness estimates increases this descriptor by 49% on average (Table 3.3). Meiofauna increase species diversity at senescent vents more than non-senescent vents. This is almost exclusively due to the increase in crustacean species. Smaller mesh sizes are needed to discover the diversity of small animals that comprise the bulk of deep-sea benthic fauna and that has resulted in an unexpected deep-sea species richness (Gage and Tyler 1991).

Meiofauna are a key element in broadening our understanding of vent to non-vent exchanges as discussed above. The identification of the most common calanoid species at vents, *Clausocalanus lividus,* as a common mid-water calanoid is an example of vent-non-vent exchange not previously recognised. Meiofauna help distinguish between temporally separated vent communities as shown here with observed differences between senescent and non-senescent communities.

Conclusions

Senescent vents are characterised by higher species richness and evenness, fewer endemics, and lower density of individuals than non-senescent vents. Cluster analysis differentiates between senescent and non-senescent vents. It may be useful to search for common biological traits in rare vent species to understand what traits, if any, can lead to species rarity. Senescent vents contain non-vent deep-sea taxa not present in samples of active vent assemblages, but species richness and evenness is much less than for deep-sea communities. The inclusion of meiofauna is important for discerning differences between vent successional states as well as differences among active vents on a segment or ridge. Meiofauna are also a source of productivity transfer between the vent and non-vent habitat.

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Appendix 3.1: Percent-average relative abundance of senescent species. Not including culled senescent sample Y. Dispersion is the percentage of sites at which the species is found.

	Species	Percent-average relative abundance	Dispersion (4 sites; n=4)
All fauna			
	Lepetodrilus fucensis	30.16	100
	Podocopida spp. unknown	8.705	75.0
	Amphisamytha galapagensis	7.591	75.0
	Depressigyra globulus	6.890	75.0
	Amphipoda spp. unknown	5.728	50.0
	Harpacticoida	5.593	100
	Prionospio n. sp. 1	4.762	75.0
	Calanoida	3.357	75.0
	Barathricola rimensis	3.291	50.0
	Copepoda Type 1	3.158	100
	Hesiospina vestimentifera	3.008	75.0
	Protomystides verenae	2.006	75.0
	Porifera	1.869	25.0
	Parougia wolfi	1.512	50.0
	Ophryotrocha globopalpata	1.504	75.0
	Misophriopsis longicauda	1.231	75.0
	Nematoda spp. unknown	1.055	50.0
	Provanna variabilis	1.040	100
	Copepoda Type 2	0.947	75.0
	Aphotopontius forcipatus	0.825	75.0
	Melanodrymia brightae	0.818	25.0
	Isopoda spp. unknown	0.818	25.0
	Acoelomates?	0.657	75.0
	Pyropelta musaica	0.540	25.0
	Thermanemertes valens	0.447	50.0
	Hydrozoa spp. unknown	0.409	25.0
	Levensteiniella kincaidi	0.342	75.0
	Ammothea verenae	0.321	75.0
	Nicomache venticola	0.175	25.0
	Tanaidacea sp. unknown	0.175	25.0
	Copepoda Type 13	0.147	25.0
	Paralvinella pandorae	0.126	75.0
	Ophiuroidea sp. unknown	0.117	25.0
	Helicoradomenia juani	0.109	75.0

	Species	Percent-average relative abundance	Dispersion (4 sites; n=4)
	Stygiopontius quadrispinosus	0.084	25.0
	Benthoxynus spiculifer	0.079	50.0
	Nereis piscesae	0.074	50.0
	Harmothoe sp.	0.072	50.0
	Sphaerosyllis ridgensis	0.058	25.0
	Neolira racemosa	0.058	25.0
	Pardalisca endeavouri	0.058	25.0
	Vescomyid	0.058	25.0
	Branchinotogluma sp.	0.049	25.0
	Orbiniella hobsonae	0.035	25.0
	Euphilomedes climax	0.014	25.0
	Copepoda Type 9	0.014	25.0
	Copepoda Type 11	0.007	25.0
	Paralvinella palmiformis	0.004	25.0
	Copidognathus papillatus	0.004	25.0
Macrofauna only			
	Lepetodrilus fucensis	35.79	100
	Amphipoda spp. unknown	11.19	50.0
	Depressigyra globulus	10.06	75.0
	Amphisamytha galapagensis	9.853	75.0
	Prionospio n. sp.1	6.863	75.0
	Hesiospina vestimentifera	4.383	75.0
	Porifera	3.653	25.0
	Protomystides verenae	3.299	75.0
	Parougia wolfi	2.166	50.0
	Ophryotrocha globopalpata	1.911	75.0
	Isopoda	1.598	25.0
	Melanodrymia brightae	1.598	25.0
	Acoelomates?	1.273	75.0
	Provanna variabilis	1.208	100
	Hydrozoa sp. unknown	0.799	25.0
	Thermanemertes valens	0.654	50.0
	Ammothea verenae	0.580	75.0
	Pyropelta musaica	0.549	25.0
	Levensteiniella kincaidi	0.497	75.0
	Nicomache venticola	0.342	25.0
	Tanaidacea	0.342	25.0
	Ophiuroidea	0.228	25.0
	Paralvinella pandorae	0.181	75.0
	Helicoradomenia juani	0.157	75.0

Species	Percent-average relative abundance	Dispersion (4 sites; n=4)
Harmothoe sp.	0.135	50.0
Neolira racemosa	0.114	25.0
Pardalisca endeavouri	0.114	25.0
Sphaerosyllis ridgensis	0.114	25.0
Vesicomyid	0.114	25.0
Nereis piscesae	0.097	50.0
Branchinotogluma sp.	0.072	25.0
Orbiniella hobsonae	0.036	25.0
Euphilomedes climax	0.020	25.0
Paralvinella palmiformis	0.004	25.0

Appendix 3.2: Percent-average relative abundance of Axial species, not including culled samples J, Q, R, W, and X and senescent samples Y, Z, and EE. Macrofauna only. Dispersion is the percentage of sites at which the species is found.

Species	Percent-average relative abundance	Dispersion (23 sites; n=23)
Lepetodrilus fucensis	44.88	100
Paralvinella pandorae	26.61	100
Paralvinella palmiformis	10.58	91.3
Amphisamytha galapagensis	6.352	95.7
Depressigyra globulus	4.642	100
Provanna variabilis	1.873	95.7
Pyropelta musaica	1.245	73.9
Protomystides verenae	1.236	82.6
Parougia wolfi	0.728	69.7
Ophryotrocha globopalpata	0.707	69.7
Lepidonotopodium piscesae	0.328	82.6
Branchinotogluma sp.	0.191	82.6
Nereis piscesae	0.185	65.2
Paralvinella sulfincola	0.102	43.5
Ammothea verenae	0.071	47.8
Euphilomedes climax	0.045	21.7
Paralvinella dela	0.043	26.1
Opisthotrochopodus tunnicliffeae	0.029	43.5
Hesiospina vestimentifera	0.027	52.2
Prionospio n. sp.1	0.026	26.1
Temnocinclis euripes	0.022	8.70
Clypeosectus curvus	0.020	47.8
Nicomache venticola	0.014	26.1
Hesiodeira glabra	0.013	26.1
Levensteiniella kincaidi	0.010	43.5
Actinostolidae n. spp (2)	0.007	17.4
Prionospio n. sp. 2	0.006	8.70
Idasola washingtonia?	0.003	13.0
Amphiduros axialensis	0.002	13.0
Lacunoides n. sp.	0.001	8.70
Calyptogena pacifica	0.001	8.70
Hydrozoa spp. unknown	0.0004	8.70
Harmothoe sp.	0.0003	4.35

Appendix 3.3: Percent-average relative abundance for CoAxial 1995 (XX) and CoAxial 1996 (YY). All fauna are included.

Samples	Species	Percent-average relative abundance
CoAxial 1995		
	Paralvinella pandorae	94.99
	Branchinotogluma sp.	1.778
	Thermanemertes valens	1.563
	Paralvinella palmiformis	0.754
	Hesiodeira glabra	0.269
	Lepidonotopodium piscesae	0.216
	Aphotopontius forcipatus	0.216
	Calanoida	0.108
	Amphisamytha galapagensis	0.054
	Lepetodrilus fucensis	0.054
CoAxial 1996	*Lepetodrilus fucensis*	33.30
	Depressigyra globulus	25.93
	Barathricola rimensis	12.97
	Calanoida	7.083
	Copepoda Type 1	6.079
	Prionospio n. sp.1	2.928
	Aphotopontius forcipatus	2.036
	Harpacticoida	1.590
	Hesiospina vestimentifera	1.561
	Thermanemertes valens	1.394
	Misophriopsis longicauda	1.339
	Amphisamytha galapagensis	1.255
	Levensteiniella kincaidi	1.143
	Stygiopontius quadrispinosus	0.335
	Ammothea verenae	0.307
	Copepoda Type 2 (copepodites?)	0.223
	Ophryotrocha globopalpata	0.112
	Paralvinella pandorae	0.084
	Provanna variabilis	0.084
	Harmothoe sp.	0.056
	Copepoda Type 9	0.056
	Euphilomedes climax	0.056
	Copepoda Type 11	0.028
	Helicoradomenia juani	0.028
	Acoelomates?	0.028

Appendix 3.4: Percent-average relative abundance for senescent and non-senescent South Rift Zone (SRZ) fauna. Not including culled samples W and X (non-senescent) and Z (senescent). All fauna are included.

Samples	Species	Percent-average relative abundance
Senescent SRZ (2 samples)		
	Lepetodrilus fucensis	43.43
	Amphisamytha galapagensis	14.56
	Harpacticoida	8.757
	Prionospio n. sp.1	8.062
	Hesiospina vestimentifera	5.234
	Parougia wolfi	3.024
	Ophryotrocha globopalpata	2.953
	Calanoida	2.589
	Provanna variabilis	1.921
	Misophriopsis longicauda	1.593
	Protomystides verenae	1.325
	Copepoda Type 2	1.081
	Pyropelta musaica	1.080
	Copepoda Type 1	0.940
	Depressigyra globulus	0.814
	Aphotopontius forcipatus	0.631
	Podocopida spp. unknown	0.470
	Copepoda Type 13	0.295
	Paralvinella pandorae	0.210
	Helicoradomenia juani	0.203
	Thermanemertes valens	0.196
	Nereis piscesae	0.147
	Levensteiniella kincaidi	0.112
	Branchinotogluma sp.	0.098
	Barathricola rimensis	0.098
	Orbiniella hobsonae	0.070
	Benthoxynus spiculifer	0.042
	Ammothea verenae	0.021
	Acoelomates	0.014
	Paralvinella palmiformis	0.007
	Copidognathus papillatus	0.007
	Amphipoda spp. unknown	0.007
	Nematoda spp. unknown	0.007

Samples	Species	Percent-average relative abundance
Non-senescent SRZ (4 samples)		
	Lepetodrilus fucensis	53.07
	Paralvinella pandorae	17.35
	Amphisamytha galapagensis	7.747
	Paralvinella palmiformis	7.380
	Protomystides verenae	3.311
	Parougia wolfi	2.917
	Nematoda spp. unknown	2.163
	Depressigyra globulus	1.902
	Aphotopontius forcipatus	0.610
	Provanna variabilis	0.547
	Harpacticoida	0.517
	Nereis piscesae	0.383
	Podocopida spp. unknown	0.374
	Calanoida	0.368
	Ophryotrocha globopalpata	0.361
	Copepoda Type 1	0.276
	Pyropelta musaica	0.158
	Lepidonotopodium piscesae	0.155
	Prionospio n. sp.1	0.118
	Branchinotogluma sp.	0.061
	Nicomache venticola	0.045
	Prionospio n. sp. 2	0.032
	Copepoda Type 11	0.031
	Hesiodeira glabra	0.028
	Actinostolidae n. spp (2)	0.028
	Copepoda Type 9	0.012
	Benthoxynus spiculifer	0.012
	Copepoda Type 2	0.011
	Clypeosectus curvus	0.011
	A3244-3979 type copepoda	0.010
	Hesiospina vestimentifera	0.010
	Barathricola rimensis	0.010

Appendix 3.5: Percent-average relative abundance for each senescent sample. Does not include culled sample, Y. All fauna are included.

Samples	Species	Percent-average relative abundance
YY		
	Lepetodrilus fucensis	33.30
	Depressigyra globulus	25.93
	Barathricola rimensis	12.97
	Calanoida	7.083
	Copepoda Type 1	6.079
	Prionospio n. sp.1	2.928
	Aphotopontius forcipatus	2.036
	Harpacticoida	1.590
	Hesiospina vestimentifera	1.562
	Thermanemertes valens	1.394
	Misophriopsis longicauda	1.339
	Amphisamytha galapagensis	1.255
	Levensteiniella kincaidi	1.143
	Stygiopontius quadrispinosus	0.335
	Ammothea verenae	0.307
	Copepoda Type 2	0.223
	Ophryotrocha globopalpata	0.112
	Paralvinella pandorae	0.084
	Provanna variabilis	0.084
	Harmothoe sp.	0.056
	Copepoda Type 9	0.056
	Euphilomedes climax	0.056
	Copepoda Type 11	0.028
	Helicoradomenia juani	0.028
	Acoelomates?	0.028
Z		
	Lepetodrilus fucensis	75.08
	Amphisamytha galapagensis	11.04
	Provanna variabilis	3.057
	Protomystides verenae	2.650
	Ophryotrocha globopalpata	2.566
	Pyropelta musaica	2.160
	Prionospio n. sp.1	0.799
	Podocopida spp. unknown	0.743
	Copepoda Type 1	0.505
	Parougia wolfi	0.351
	Depressigyra globulus	0.252

Samples	Species	Percent-average relative abundance
	Orbiniella hobsonae	0.140
	Nereis piscesae	0.098
	Aphotopontius forcipatus	0.084
	Benthoxynus spiculifer	0.084
	Calanoida	0.070
	Hesiospina vestimentifera	0.056
	Misophriopsis longicauda	0.042
	Ammothea verenae	0.042
	Levensteiniella kincaidi	0.028
	Paralvinella pandorae	0.028
	Harpacticoida	0.028
	Acoelomates?	0.028
	Paralvinella palmiformis	0.014
	Copidognathus papillatus	0.014
	Amphipoda spp. unknown	0.014
	Helicoradomenia juani	0.014
	Nematoda spp. unknown	0.014
EE		
	Amphisamytha galapagensis	18.07
	Harpacticoida	17.49
	Prionospio n. sp.1	15.32
	Lepetodrilus fucensis	11.79
	Hesiospina vestimentifera	10.41
	Parougia wolfi	5.697
	Calanoida	5.108
	Ophryotrocha globopalpata	3.340
	Misophriopsis longicauda	3.143
	Copepoda Type 2	2.161
	Copepoda Type 1	1.375
	Depressigyra globulus	1.375
	Aphotopontius forcipatus	1.179
	Provanna variabilis	0.786
	Copepoda Type 13	0.589
	Paralvinella pandorae	0.393
	Helicoradomenia juani	0.393
	Thermanemertes valens	0.393
	Branchinotogluma sp.	0.196
	Levensteiniella kincaidi	0.196
	Nereis piscesae	0.196
	Barathricola rimensis	0.196
	Podocopida spp. unknown	0.196
GG		
	Podocopida spp. unknown	33.88

Samples	Species	Percent-average relative abundance
	Amphipoda spp. unknown	22.90
	Porifera	7.477
	Protomystides verenae	5.374
	Copepoda Type 1	4.673
	Nematoda spp. unknown	4.206
	Harpacticoida	3.271
	Melanodrymia brightae	3.271
	Isopoda spp. unknown	3.271
	Acoelomates?	2.570
	Hydrozoa spp. unknown	1.636
	Copepoda Type 2	1.402
	Calanoida	1.168
	Ammothea verenae	0.935
	Nicomache venticola	0.701
	Tanaidacea sp. unknown	0.701
	Lepetodrilus fucensis	0.467
	Ophiuroidea sp. unknown	0.467
	Harmothoe sp.	0.234
	Benthoxynus spiculifer	0.234
	Provanna variabilis	0.234
	Sphaerosyllis ridgensis	0.234
	Neolira racemosa	0.234
	Pardalisca endeavouri	0.234
	Vesicomyid	0.234

Appendix 3.6: Deep-sea sample listing. Both samples HH and II are suction samples and are used qualitatively. All fauna are included.

	Species	Number of individuals
Sample HH		
	Prionospio sp.	1
	Harpacticoida	13
	Calanoida	2
	Unknown copepoda	4
	Ostracoda	1
	Isopoda	4
	Unknown polychaeta sp. 1	26
	Unknown polychaeta sp. 2	3
	?	1
Sample II		
	Lepetodrilus fucensis	6
	Buccinum thermophilum	1
	Pardalisca endeavouri	4
	Copepoda Type 2?	10
	Copepoda Type 14 (Harpacticoida?)	6
	Copepoda Type 15	5
	Harpacticoida	42
	Calanoida	2
	Podocopida	2
	Isopoda #2	9
	Tanaidacea	2
	Ophiuroida	1
	Misc. unk. polychaetes	6

CHAPTER 4

The Axial Seamount vent community

Introduction

Biological study of vent communities on the Juan de Fuca Ridge began in 1983, with the discovery of hydrothermal activity on Axial Seamount (Canadian American Seamount Expedition 1985) (Figure 1.1). Soon after this exciting find, more vents were found on Axial (Malahoff et al. 1984) and two other segments of the ridge: Cleft (Normark et al. 1983) and Endeavour (Merge Group 1984). Subsequently, venting was found on Explorer Ridge to the north of the Juan de Fuca Tunnicliffe et al. 1986).

Ecological work on vent communities began as natural history, with inventories of the species present and descriptions of their habitat. Juniper and Tunnicliffe (1997) describe three conceptual levels of ecosystem properties arranged in a hierarchy of complexity:

Composition (species present and habitat conditions)

↓

Structure (spatial distribution, biomass/abundance, population data, and trophic relationships)

↓

Dynamics (succession, growth and productivity, energy and material fluxes, and mortality and recruitment).

Early studies of vents were devoted to the first level of ecosystem properties, and studies at this level are still a major focus of ecological work at vents, as there remain many undescribed species and unmeasured habitat conditions. The logistic realities of working in the deep-sea mean that work on structure and dynamics of vent communities is technically challenging if not impossible (Juniper and Tunnicliffe 1997). As knowledge of vent species composition increases, ecological studies are becoming narrower, such as studies on species-species interactions (Mullineaux et al. 2000) and broader, for example biogeographical analyses (Tunnicliffe et al. 1996) and studies of temporal change (Tunnicliffe et al. 1997).

One goal for ecologists studying the Juan de Fuca vents is an integrated understanding of the composition, structure, and dynamics of the community at the ridge-scale. In order to gain such an understanding it is necessary to investigate communities on all segments of the ridge. The objective of this chapter is to describe the organisation of low temperature *Ridgeia piscesae* vent communities on Axial Seamount. I use species composition, diversity, and distributions and abundances to answer the question: are the three Axial vent fields distinguishable from each other?

The lack of differentiation within the Cleft fauna leads to the following prediction for Axial: there is no statistical difference among vent fields; all fields are dominated by the same most abundant species. The enhanced abundance of a few species results in similar values for diversity indices based on species evenness as well as on richness. This enhanced abundance may also cause tests of the difference among species distributions and abundances at different sites to be non-significant. Homogenisation of ridge-segment communities due to dominance by a few species is reported for Cleft (Tsurumi and

Tunncliffe 2001) and CoAxial (Tunncliffe et al. 1997; Tunnicliffe, unpubl. data) segments. Jollivet (1996) reports that specific diversity and faunal compositions are similar within 13°N vent fields on the East Pacific Rise. Jollivet believes that fauna within a ridge are grouped by microhabitat rather than by spatial location on the ridge.

A community is defined as a group of interacting organisms that exist within defined spatial boundaries (Magurran 1988). Species diversity, i.e. the number and relative abundance of the constituent species, is one of the most commonly examined aspects of biological communities (Caswell 1976). I use the term "community structure" as a description of the number of species and their abundances in a representative sample of a community. Community structure is used to refer to species present and their estimated diversity, abundances, and spatial distributions, but it is also used to refer to characteristics such as size and age structure of populations, population growth rates, species biomass, productivity, and information about trophic and guild relationships (e.g. Hessler and Kaharl 1995; Kelt et al. 1996; Menge 2000; Wilson et al. 2000). My data consist of species presence/absence, abundances, and locations. These data types limit evaluation of the data to composition, diversity, species associations, and distribution-abundance patterns.

Methods

Axial Seamount

Axial Seamount is a large, active, ridge axis volcano on the central segment of the Juan de Fuca Ridge approximately 430 km west of the B.C./Washington/Oregon coast (Johnson and Embley 1990). Axial lies at the intersection of the Cobb-Eickelberg

Seamount Chain and the Juan de Fuca Ridge (Figure 1.1). There are three known vent fields in the Axial caldera: ASHES, CASM, and the South Rift Zone (Figure 4.1). The ASHES system lies near the southwest corner of the caldera, about 60 m out into the caldera from the wall. Hammond (1990) suggests that this vent field is controlled both by the faulting associated with the wall formation and by the permeability of the lobate pillow flows that make up the caldera floor in this area. ASHES is a 100 m diameter area with active low (basalt) and high (sulphide) temperature vents.

The CASM vent field, the first area of hydrothermal activity discovered on Axial Seamount (Canadian American Seamount Expedition 1985), was the focus of the first manned submersible expedition to the Juan de Fuca (Figure 4.1). CASM lies below the northern rim of the caldera wall in a fissure that extends southwest from the wall into the caldera (Tunncliffe et al. 1985). There is a zone of diffuse venting associated with the eruptive fissure and concentrated in areas along the fissure where the walls widen out to form circular-shaped bowls (Embley et al. 1990). A few massive sulphide chimneys lie about 20 m west of the northern part of the primary fissure in an area of several smaller, parallel fissures. At least one of these chimneys has been active during intermittent visits over the past 17 years. Bob vent (Table 4.1) lies about 4 km to the north of CASM on the North Rift Zone. Bob vent is included in the CASM vent field data set.

The South Rift Zone vent field (SRZ) is the least well-known hydrothermal area on Axial (Figure 4.1). The SRZ covers a large area (almost 6 km north to south and on average about 0.5 km wide) running south from the caldera's eastern wall down to the south flank of the volcano. This area was visited briefly by submersible in 1987 and

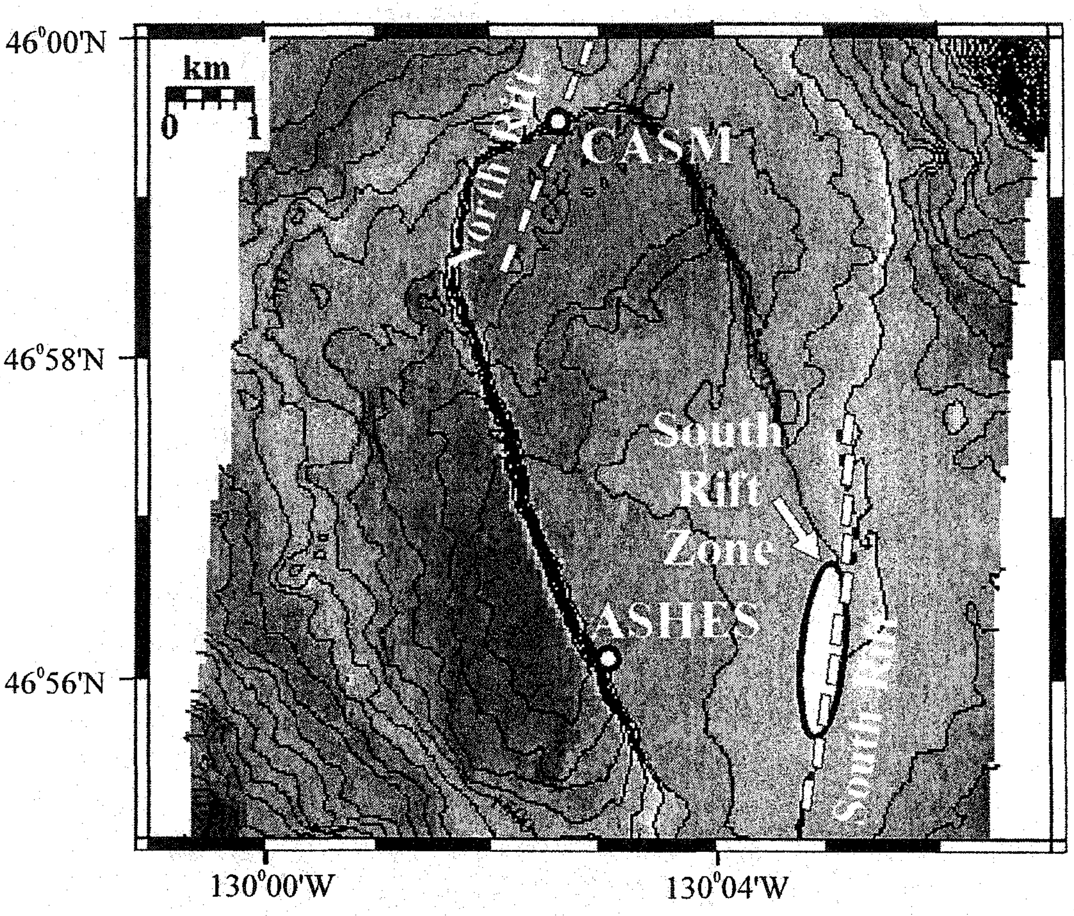


Figure 4.1. The Axial Seamount caldera. ASHES, CASM, and the South Rift Zone (SRZ) vent fields are indicated by the white and black circles. Courtesy of R.W. Embley, National Atmospheric and Oceanographic Administration.

Table 4.1: Axial samples. Totals do not include the tubeworm *Ridgeia piscesae*; SRZ = South Rift Zone; * = samples that are culled from quantitative analysis. Macrofauna are all species caught on a 1 mm sieve.

Sample designation	Vent field	Vent	Year	Substratum	All fauna		Macrofauna		Macrofaunal density (individuals•cm^{-2})
					Number of individuals	Number of species	Number of individuals	Number of species	
A	ASHES	Goblin	1986	Basalt	11252	13	9766	10	2.179
B	ASHES	Bouquet	1986	Basalt	7821	26	7813	23	0.923
C	ASHES	Demon	1986	Basalt	28049	22	28046	21	2.599
D	ASHES	Sweet	1986	Basalt	1831	11	1830	10	1.554
E	ASHES	Limbo	1986	Basalt	2578	17	2578	17	0.390
F	ASHES	Miserable	1986	Basalt	408	19	401	14	0.614
G	ASHES	Not-so-miserable	1986	Basalt	18963	27	18937	21	1.208
H	ASHES	Bouquet	1988	Basalt	5283	21	5279	19	1.059
I	ASHES	ISCA	1997	Basalt	4759	19	1689	17	0.530
J*	ASHES	Hatfield	1997	Basalt	47128	41	37121	28	not available
K	ASHES	Bouquet2	1998	Basalt	33706	24	33643	19	1.938
L	ASHES	Hairdo	1998	Basalt	15385	33	143741	24	0.473
M	ASHES	Gollum	1998	Basalt	6262	19	6208	12	2.316
N	ASHES	Marker i	1998	Basalt	8945	24	8681	15	2.136
O	ASHES	Medusa	1998	Basalt	570	8	508	6	2.082
P	CASM	Post-Taylor's	1986	Basalt	7018	17	7018	17	0.795
Q*	CASM	Lamphere	1986	Sulphide	472+?	12	301+?	7	not available
R*	CASM	Lamphere	1986	Sulphide	508	7	508	7	not available

Sample designation	Vent field	Vent	Year	Substratum	All fauna		Macrofauna		Macrofaunal density (individuals•cm^{-2})
					Number of individuals	Number of species	Number of individuals	Number of species	
S	CASM	Lamphere	1988	Sulphide	3431	21	3280	18	1.053
T	CASM	Bob	1998	Basalt	1771	16	1655	11	1.382
U	CASM	T & S	1998	Sulphide	3378	16	767	9	0.113
V	CASM	Base of T & S	1999	Basalt	2995	16	2736	12	1.527
W*	SRZ	Vent #1	1986	Basalt	825+?	15	813+?	11	not available
X*	SRZ	Sonne	1997	Basalt	433	16	411	11	not available
Y*	SRZ	10 m SE of Marker 113	1998	Basalt	159	10	147	8	0.039
Z	SRZ	Near Marker 113	1998	Basalt	7139	29	7026	20	0.641
AA	SRZ	Flat Top	1998	Basalt	2098	13	2095	10	2.571
BB	SRZ	Oldworms	1998	Basalt	4420	25	3841	16	1.071
CC	SRZ	LargeTW	1998	Basalt	2551	21	2441	13	0.375
DD	SRZ	Old Flow	1998	Basalt	1766	10	1766	10	1.454
EE	SRZ	Crevice	1999	Basalt	509	23	349	14	0.036

1997, but was not fully explored until after a 1998 eruption on Axial Seamount. Visits in 1998 and 1999 demarcated a new lava flow with vents initiated by the 1998 eruption (pers. obs.). One vent sampled in 1986 (Vent #1) and one vent sampled in 1997 (Sonne Vent) (Table 4.1) are now gone, smothered by the new lava. Vents just beyond the limits of the new lava flow are considered to pre-date the 1998 eruption (Embley and Baker 1999). None of the new vents initiated by the 1998 eruption are used in the SRZ data set.

Sample collection

Samples were taken on Axial in 1986-88 and 1997-1999 (Table 4.1). All samples are from low temperature (< 60 °C) vents. All samples are from basalt except for the 1988 sample from CASM (sample S, Table 4.1) and the 1998 samples from CASM (sample T, Table 4.1) and Flat Top (sample AA, Table 4.1).

Sample processing

Samples were fixed in 7% seawater formalin at sea for transport to the lab for processing. All samples were sieved over a 63 μm mesh. All ASHES samples except for sample J, Hatfield, (Table 4.1) were sorted down to 1 mm sieve size and meiofauna were not quantitatively processed (Table 4.1). CASM samples from 1986 (samples Q, R, and P) were sorted down to 1 mm sieve size. One SRZ sample, sample W, was sorted down to the 1 mm sieve size. All other CASM and SRZ samples were sorted down to 63 μm. Statistical comparisons of CASM and SRZ samples with ASHES samples are limited to macrofauna except for species richness descriptors. Discussion of dispersion for CASM and the SRZ includes meiofauna when looking at how many species are found at less than

50% of vents (a measure of rarity), but is limited to macrofauna when comparing the dispersion of particular species.

Thirty-one samples are selected for examination, 15 from ASHES, seven from CASM, and nine from the SRZ (Table 4.1). All samples are used for presence/absence information for cluster analyses, species richness, and rarefaction. After culling as described in Tsurumi and Tunnicliffe (2000), 25 samples remain in the data set for statistical analyses: 14, five, and six samples from ASHES, CASM, and the SRZ respectively (Table 4.1).

Analyses

The density data (number of individuals•cm^{-2} of tubeworm area) for some species from the three vent fields are normally distributed: three of the species at ASHES (*Lepidonotopodium piscesae*, *Opisthotrochopodus tunnicliffeae*, and *Paralvinella pandorae*); six of the CASM species (*Branchinotogluma* sp., *L. piscesae*, *Protomystides verenae*, *Paralvinella pandorae*, *Depressigyra globulus*, *Lepetodrilus fucensis*; and *Provanna variabilis*), and four of the SRZ species (*Ophryotrocha globopalpata*, *Branchinotogluma* sp., *D. globulus* and *P. variabilis*). Density data for all Axial species combined are not normal and are log transformed. However, this transformation successfully normalises only two of the Axial species (*L. piscesae* and *L. fucensis*). Log transformations of density data from ASHES, CASM, and the SRZ were only able to normalize one more species for ASHES (*Amphisamytha galapagensis*) and one more for the SRZ (*L. fucensis*). No other transformations were able to normalize the data successfully. Number of species and density per sample are normally distributed for

Axial (all three vent fields combined), ASHES, CASM, and the SRZ. Species abundance distributions are evaluated using a chi-square test for the log series in the BioDiversity Professional Programme 2.0 (McAleece 1997), a linear regression of observed versus expected abundance values for the geometric series (Magurran 1988), and tests for the lognormal in SPSS.

Multivariate techniques including clustering and ordination determine how an object or descriptor varies with some pre-defined distance, for example, Euclidean distance. Cluster analysis is used to find species or site groupings by bringing out partitions in ecological data (e.g. Poore et al. 1994; Lancellotti and Vasquez 1999). These techniques will cluster data even when there are no major discontinuities. Flexible clustering is a common clustering method (Bakus 1990) that is preferred for non-random or non-systematic sampling and is compatible with all association measures (Legendre and Legendre 1998). The flexible method fuses clusters by a measure of similarity that incorporates all species in each cluster. Grassle and Smith (1976) recommend the flexible method of clustering ($\beta = -0.25$). Similarity or association matrices are computed using similarity or dissimilarity coefficients. The Jaccard similarity coefficient is preferable for presence/absence data because it is intuitive and gives good results (Bakus 1990; Copley et al. 1996). Simultaneous non-occurrences of species are not included in the Jaccard equation and Legendre and Legendre (1998) recommend this coefficient for presence/absence data. Bray-Curtis is a dissimilarity coefficient that is commonly used in the literature for rank or abundance data (e.g. Burd and Thomson 1995; Walsh 1997; Somerfield and Gage 2000). This coefficient reveals species relationships driven by abundance: co-occurring abundant species yield higher similarity values than co-occurring rare species (Legendre and Legendre 1998). Bray-Curtis is considerably influenced by dominance (Bakus 1990). The Axial data set is numerically dominated by three species out of a total of more than 50 species. By using the Bray-Curtis similarity measure I hope to achieve realistic clusters based on the characteristics of the Axial fauna.

Legendre and Legendre (1998) recommend a plurality of methods when it comes to validating clusters. Cophenetic correlation measures the extent to which the clustering result corresponds to the original resemblance matrix. The higher the absolute value of the cophenetic correlation, the better the correspondence between the original matrix and the cophenetic matrix derived from the dendrogram. NTSYS 2.0 uses a Mantel test for evaluating matrix correspondence that computes a cophenetic value matrix with a user-defined number of random permutations to test the Mantel statistic. A cophenetic correlation cannot be tested for significance, however, because the cophenetic matrix is not independent of the original similarity matrix. Another way to validate clusters is to plot clusters onto an ordination diagram and look for separation of the clusters (Legendre and Legendre 1998). Correspondence analysis is one ordination method recommended in the literature to validate clustering (Jackson 1997; Balmer and Erhardt 2000). Clustering, cophenetic correlation, and correspondence analysis are done in NTSYS 2.0. The Jaccard and Bray-Curtis coefficients are used to compute similarity matrices and the hierarchical, agglomerative algorithm of the flexible method ($\beta = -0.25$) to cluster.

Complementarity is defined by Colwell and Coddington (1994) as the distinctness or dissimilarity of two local inventories. This is an easily calculated similarity measure for comparing species lists from two sites. Colwell and Coddington (1994) believe it is the simplest measure of similarity or difference that captures the meaning of complementarity of two species lists. Complementarity is the proportion of all species in two sites that occurs in only one or the other of them. The higher the percentage, the less similar two species lists are considered. Complementarity calculations are after Colwell and Coddington (1994). Diversity indices and species number are calculated as described in Tsurumi and Tunnicliffe (2001) and Chapter 3, Methods.

Results

Field characteristics

Samples from the three Axial vent fields, ASHES, CASM, and the SRZ, are tubeworm grabs. These tubeworm grabs are from low temperature vents, mostly on basalt, but the shape and appearance of the tubeworm communities vary between and within fields. A number of the ASHES samples (e.g. samples B, J, K, and L) are comprised of tightly-interwoven tubeworm tubes, analogous to a hedge. Some ASHES and SRZ samples are loose clumps of tubeworms, with the tubes growing up from a common base. These “looser” tubeworm communities are shrub-like in appearance and do not have anastomosing tubeworm tubes. Sample M from ASHES and sample U from CASM are made of even more loosely-growing tubeworms than the shrub-like ASHES and SRZ samples. There are fewer tubeworms and these *Ridgeia* are visually different from the other types of samples: short and fat, with very white tubes and prominent red plumes (Chapter 5). Visible sessile fauna on these types of communities are usually alvinellid polychaetes on the tubeworm tubes or among limpets at the base of the tubes on the basalt. For the hedge- and shrub-like tubeworm bushes, the limpet *Lepetodrilus* *fucensis* usually dominates the visual landscape, colonising most available tubeworm surfaces.

ASHES

Figure 4.2 shows the rank-abundance curve and dominance frequency for ASHES vent field. Five species are just over 90% of the total percent-average relative abundance. The limpet *Lepetodrilus fucensis* is the most abundant animal, followed by two alvinellid polychaetes, *Paralvinella pandorae* and *P. palmiformis*. Dominance frequency is spread amongst the top seven most abundant organisms. ASHES has 48 species in total and 31 macrofaunal species. Species density, the Shannon-Wiener index and Simpson's measure of diversity are given in Table 4.2. Average density of macrofaunal species is 1.428 individuals•cm^{-2} (Table 4.1). There is a six-fold range in density among samples but this is not related to the physical structure of the tubeworm bushes nor to area sampled in the field. Thirty-five percent of the species at ASHES are present at less than 25% of the samples (Appendix 4.1). The snails *Temnocinclis euripes* and *Provanna laevis*, the polynoid polychaetes *Lepidonotopodium intermedia* and *Harmothoe* sp., unknown hydrozoan(s), and the solenogaster *Helicoradomenia juani* are only found at one out of 15 sampled vents within ASHES vent field (Appendix 4.1). The snail, *Lacunoides* n. sp. is found at only two vents.

Cluster and correspondence analyses of presence/absence data, percent relative abundances, and density values agree on a grouping of *Paralvinella pandorae* and *P. palmiformis* with *Lepetodrilus fucensis* (Figures 4.3 and 4.4a). Cluster and correspondence analyses with percent relative abundance and density data place the

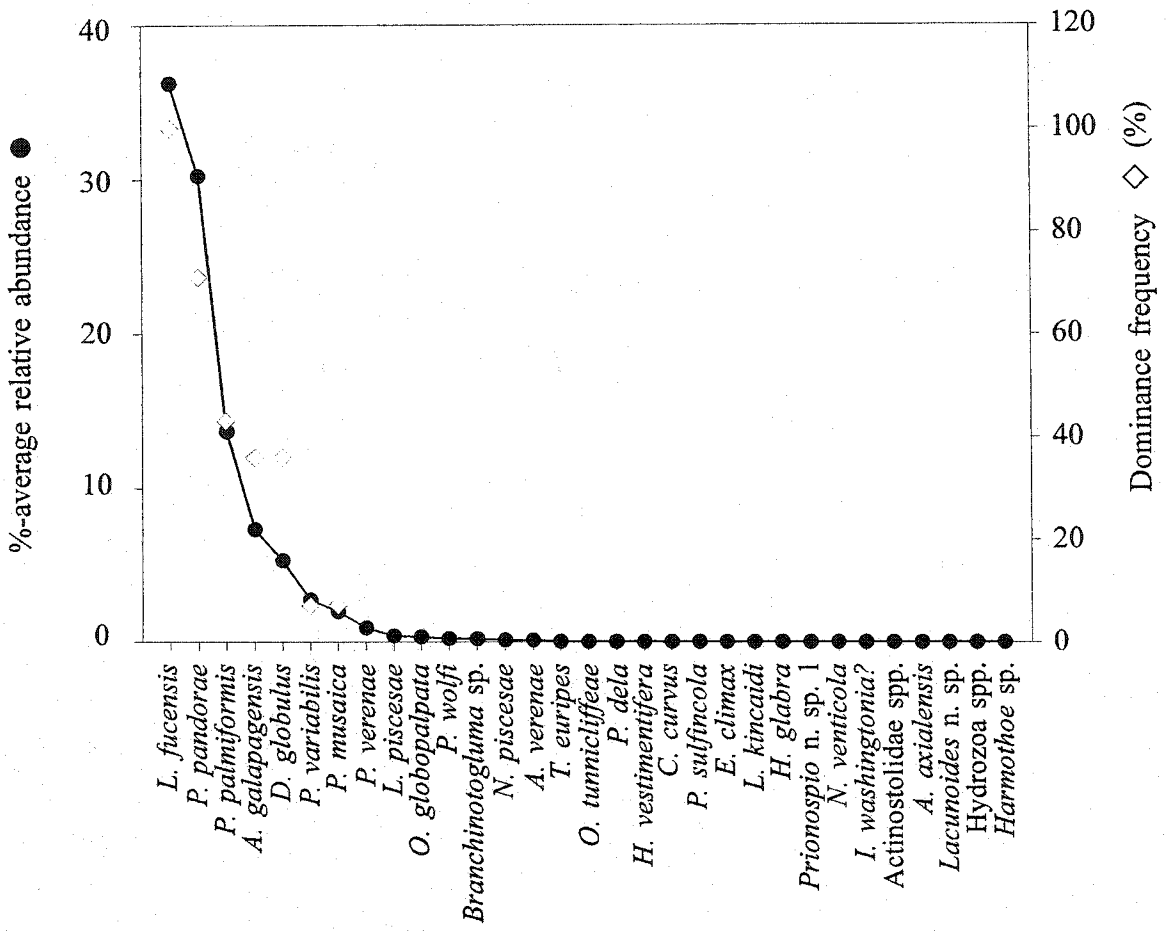


Figure 4.2. Rank-abundance of ASHES macrofauna. Total number of specimens is 142,753. Total number of samples is 14 and does not include culled sample, J. Abundance is expressed as percent-average relative abundance across samples. Dominance frequency is the percent of samples in which a species is one of the three most abundant species. For example, *Lepetodrilus fucensis* is in the top three abundance in all of the samples (100%). Taxonomic groups where the species are unknown but which probably contain more than one species are noted as "spp".

Table 4.2: Species diversity characteristics at Axial Seamount. For Simpson's measure of diversity and evenness and Shannon-Wiener, H', all data are pooled. Numbers in parentheses are plus/minus standard deviations.

Site	No. of samples	Simpson's measure of diversity, 1-D	Shannon -Wiener, H'	Species density (number of species•cm^{-2})	Species number (macro fauna)	Species number (all fauna)	Simpson's measure of evenness, $E_{1/D}$
ASHES	14	0.709	2.342	0.006 (0.008)	31	48	0.073
CASM	5	0.589	2.028	0.005 (0.003)	22	30	0.081
SRZ	6	0.618	2.376	0.006 (0.004)	28	47	0.056
Axial	25	0.698	2.433	0.007 (0.006)	39	55	0.060

polynoid polychaetes *Lepidonotopodium piscesae* and *Branchinotogluma* sp. together. The ampharetid polychaete *Amphisamytha galapagensis* and the snail *Depressigyra globulus* are clustered with all three data sets as well. Pairwise correlations (14 samples) agree well with the multivariate analyses: Pearson's r, Kendall's τ, and Spearman's r_s show significant positive relationships between *P. pandorae* and *P. palmiformis* ($p<0.01$) and between *L. piscesae* and *Branchinotogluma* sp. ($p<0.01$).

CASM

Three species have 90% cumulative percent-average relative abundance at CASM (Figure 4.5): *Lepetodrilus fucensis*, *Paralvinella pandorae*, and *Depressigyra globulus*. Three more species are in the top three abundances one to three times even though they are not the three most abundant species: *P. palmiformis*, *Ophryotrocha globopalpata*, and *Amphisamytha galapagensis*. Thirty species are found in the CASM samples, 22 of them macrofaunal species. Table 4.2 gives selected diversity indices and species density for CASM vent field. Density of individuals at CASM is 0.974 individuals•cm^{-2}. *Opisthotrochopodus tunnicliffeae*, a polynoid polychaete, and *Euphilomedes climax*, a myodocopid ostracod, are found at only one out of four vents sampled at CASM (Appendix 4.1).

Presence/absence-based Jaccard clustering is in good agreement with the correspondence analysis based on the same data and *Branchinotogluma* sp. and *Provanna variabilis* form a group to which *Lepidonotopodium piscesae* is subsequently added (Figures 4.6a and 4.4b). Clustering based on percent relative abundance data shows the same grouping although the correspondence analysis does not agree (Figure 4.6b).

Figure 4.3. Cluster diagrams for ASHES species. Only species found in seven or more (> 50%) samples are used. Flexible clustering method (β = -0.25) is used. a: dendrogram of presence/absence data using the Jaccard coefficient. b: dendrogram of percent relative abundance data using the Bray-Curtis coefficient. c: dendrogram of density data using the Bray-Curtis coefficient. Numbers are species designations (Appendix 1).

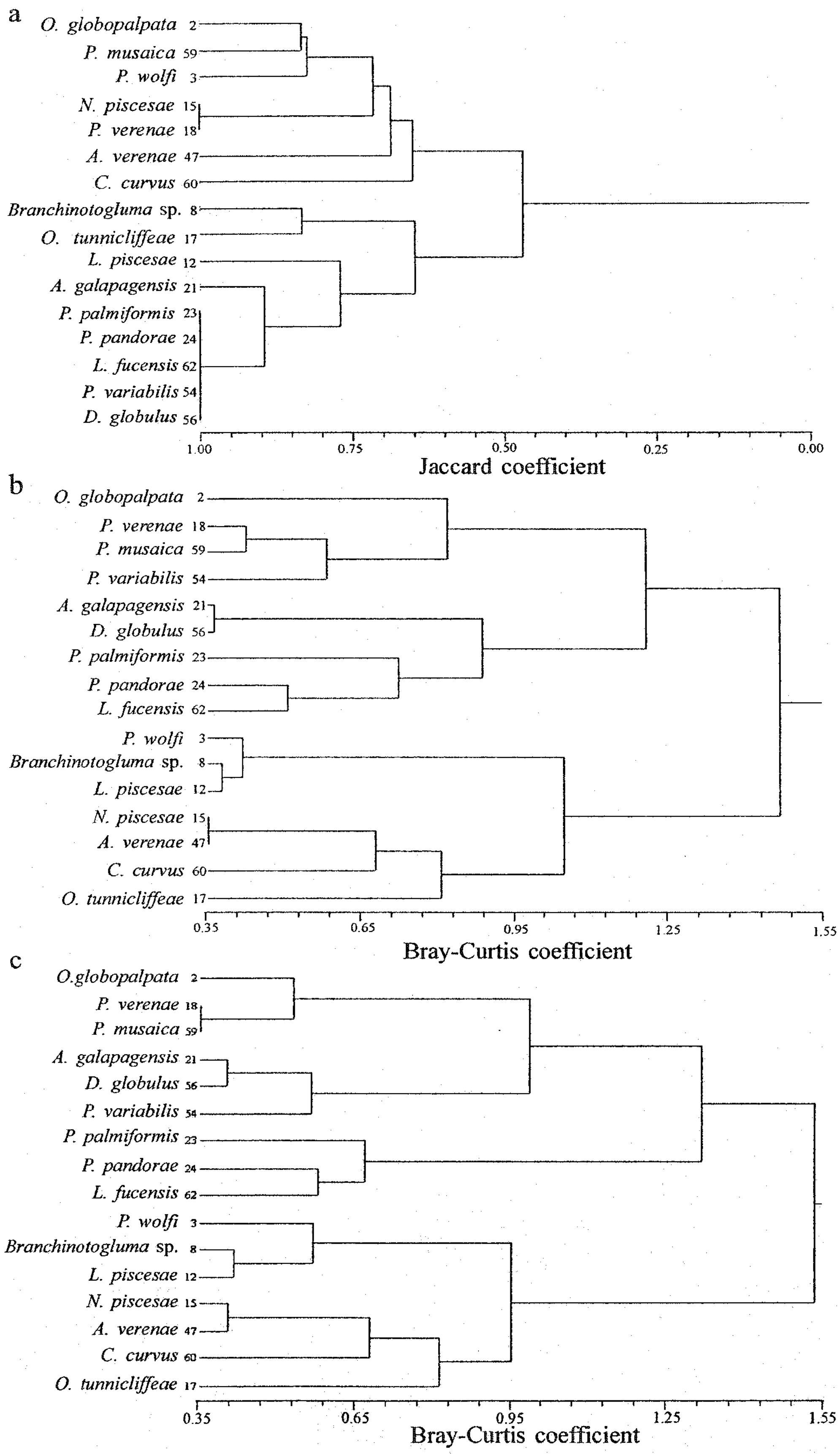
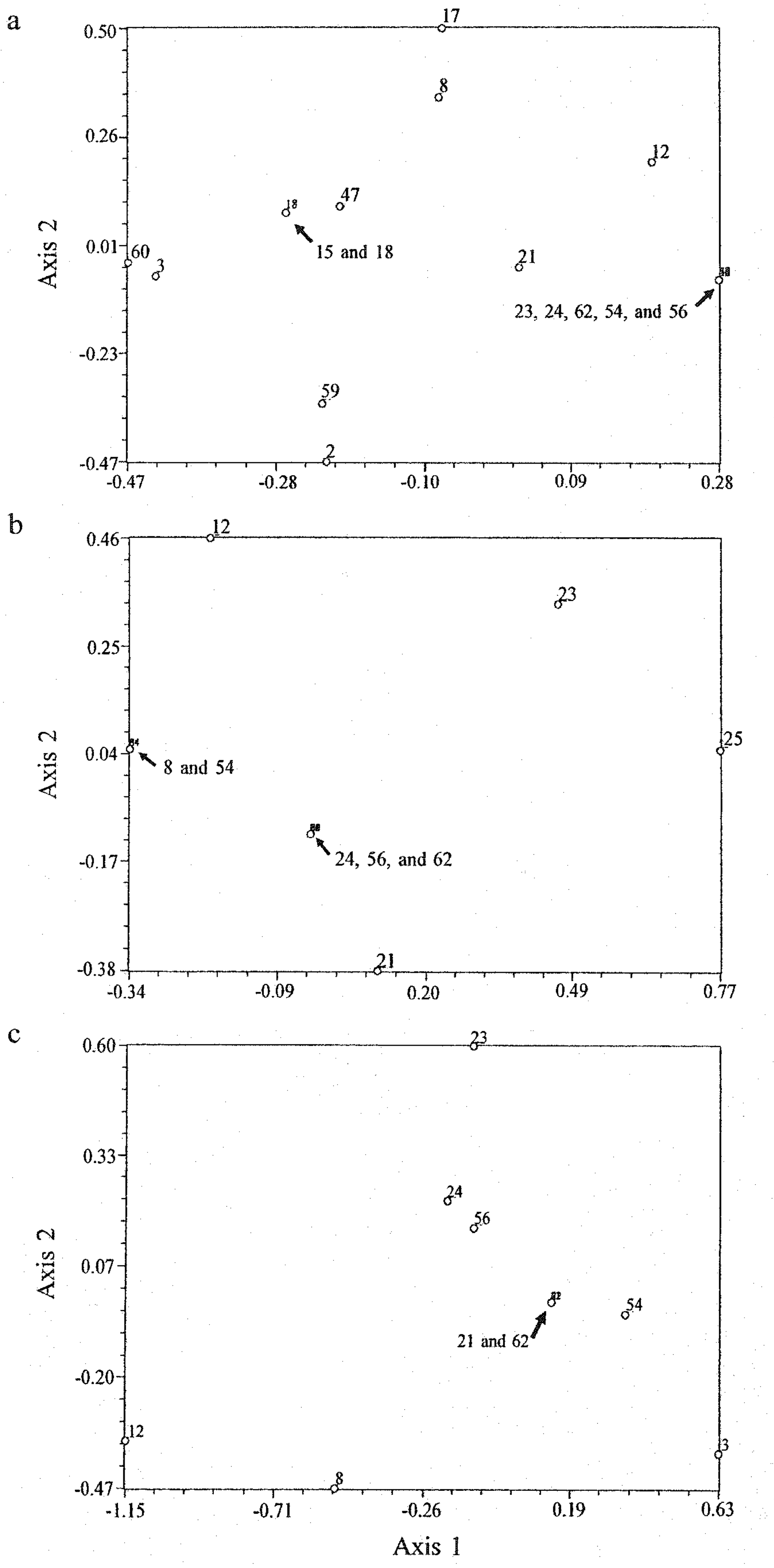

a
O. globopalpata 2
P. musaica 59
P. wolfi 3
N. piscesae 15
P. verenae 18
A. verenae 47
C. curvus 60
Branchinotogluma sp. 8
O. tunnicliffeae 17
L. piscesae 12
A. galapagensis 21
P. palmiformis 23
P. pandorae 24
L. fucensis 62
P. variabilis 54
D. globulus 56
1.00
0.75
0.50
0.25
0.00
Jaccard coefficient
b
O. globopalpata 2
P. verenae 18
P. musaica 59
P. variabilis 54
A. galapagensis 21
D. globulus 56
P. palmiformis 23
P. pandorae 24
L. fucensis 62
P. wolfi 3
Branchinotogluma sp. 8
L. piscesae 12
N. piscesae 15
A. verenae 47
C. curvus 60
O. tunnicliffeae 17
0.35
0.65
0.95
1.25
1.55
Bray-Curtis coefficient
c
O.globopalpata 2
P. verenae 18
P. musaica 59
A. galapagensis 21
D. globulus 56
P. variabilis 54
P. palmiformis 23
P. pandorae 24
L. fucensis 62
P. wolfi 3
Branchinotogluma sp. 8
L. piscesae 12
N. piscesae 15
A. verenae 47
C. curvus 60
O. tunnicliffeae 17
0.35
0.65
0.95
1.25
1.55
Bray-Curtis coefficient

Figure 4.4. Correspondence analysis of species associations using presence/absence data. Only species found in more than 50% of samples from each area are used. Numbers are species designations (Appendix 1). a: ASHES (total number of samples is 15). b: CASM (total number of samples is 5). c: South Rift Zone (total number of samples is 6).


a
Axis 2
0.50
0.26
0.01
-0.23
-0.47
-0.47
-0.28
-0.10
0.09
0.28
17
8
12
47
15 and 18
60
3
21
23, 24, 62, 54, and 56
59
2
b
Axis 2
0.46
0.25
0.04
-0.17
-0.38
-0.34
-0.09
0.20
0.49
0.77
12
23
8 and 54
25
24, 56, and 62
21
c
Axis 2
0.60
0.33
0.07
-0.20
-0.47
-1.15
-0.71
-0.26
0.19
0.63
Axis 1
23
24
56
21 and 62
54
12
3
8

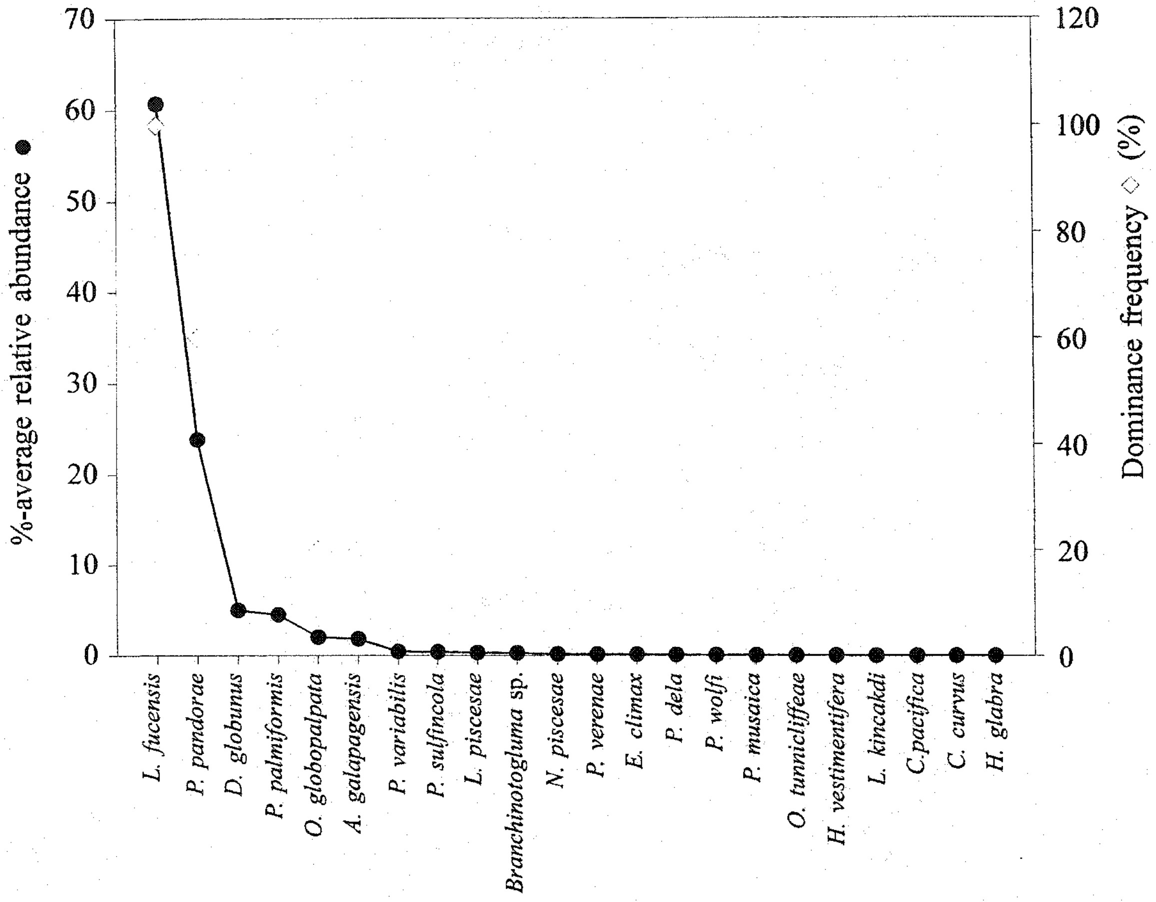


Figure 4.5. Rank-abundance of CASM macrofauna. Total number of specimens is 15,456. Total number of samples is five and does not include culled samples Q and R. Abundance is expressed as percent-average relative abundance across samples. Dominance frequency is the percent of samples in which a species is one of the three most abundant species.

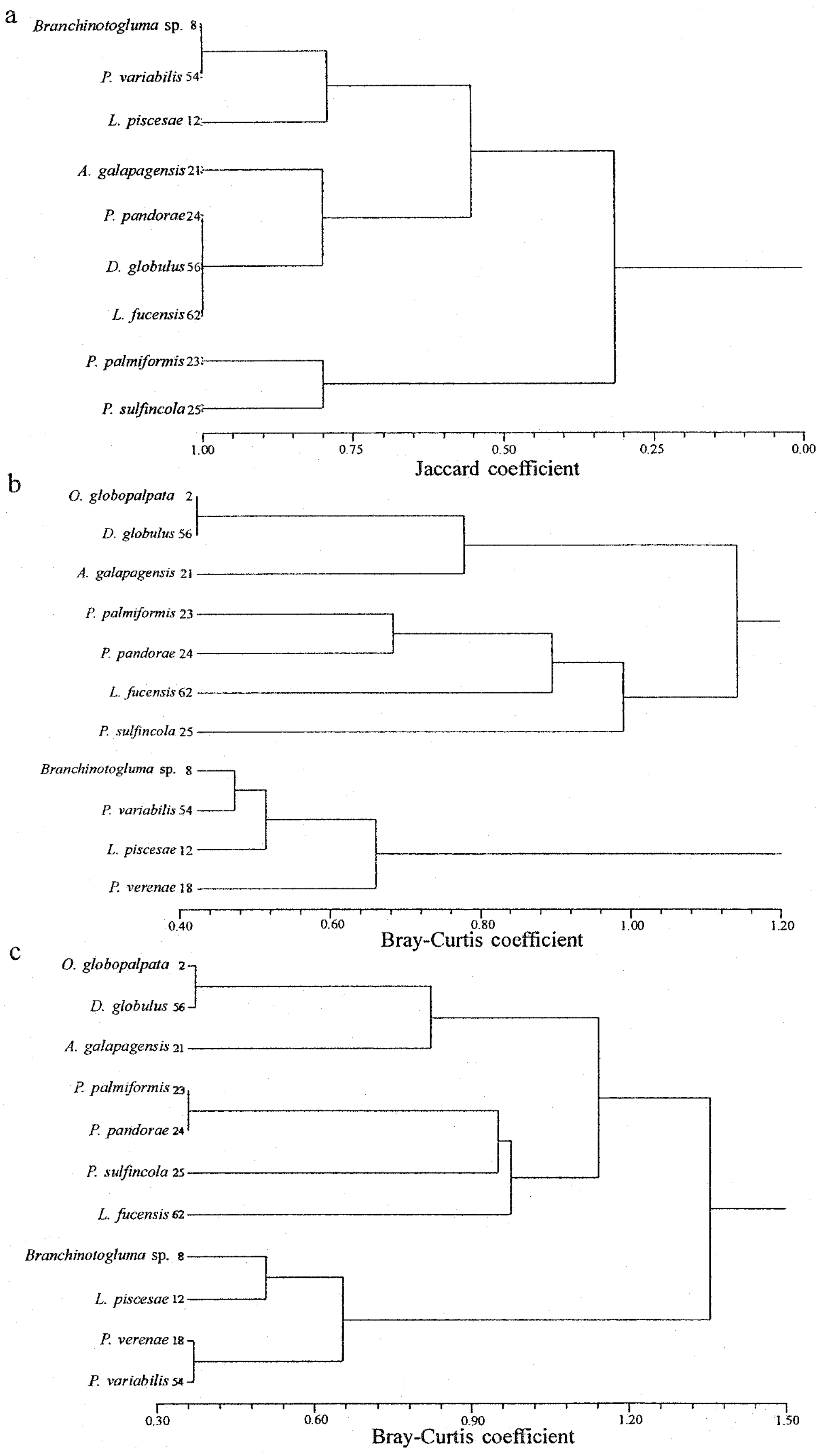
Clustering with density data gives *Branchinotogluma* sp. with *L. piscesae* and then with *P. variabilis* (Figure 4.6c). *Paralvinella pandorae* and *P. palmiformis* are clustered using percent relative abundance and density data. *P. palmiformis* and *P. sulfincola* cluster with all three data sets although at different levels.

The SRZ

The SRZ rank-abundance curve is slightly more even in distribution than rank-abundances for ASHES or CASM (Figure 4.7). Seven species make up just over 90% of the total abundance: *Lepetodrilus fucensis*, *Amphisamytha galapagensis*, *Paralvinella pandorae*, *P. palmiformis*, *Prionospio* n. sp. 1, *Parougia wolfi*, and *Protomystides verenae*. The dominance frequency generally follows the most abundant species, except for two species that are not among the seven most abundant, but are in the top three abundances in one sample each. The total number of species in SRZ samples is 47. Twenty-eight of these are macrofaunal. Species density, Shannon-Wiener and Simpson's measures are given in Table 4.2. Average density for the SRZ is 1.041 individuals•cm^{-2}. Thirteen species are only found at one of the eight vents sampled and another seven species at only two of the vents. Twenty-four species are found at 25% or fewer vents (Appendix 4.1), making species rare in distribution a more important component of this data set than for ASHES or CASM.

Branchinotogluma sp. and *Lepidonotopodium piscesae* are clustered together with presence/absence, percent relative abundance, and density data (Figure 4.8). Other than this grouping there is little concordance between clusters based on presence/absence and based on percent relative abundance and density. *Paralvinella pandorae* and *P.*

Figure 4.6. Cluster diagrams for CASM species. Only species found in three or four (> 50%) samples are used. a: dendrogram of presence/absence data using the Jaccard coefficient. b: dendrogram of percent relative abundance data using the Bray-Curtis coefficient. c: dendrogram of density data using the Bray-Curtis coefficient. Numbers are species designations (Appendix 1).


a
Branchinotogluma sp. 8
P. variabilis 54
L. piscesae 12
A. galapagensis 21
P. pandorae 24
D. globulus 56
L. fucensis 62
P. palmiformis 23
P. sulfincola 25
1.00
0.75
0.50
0.25
0.00
Jaccard coefficient
b
O. globopalpata 2
D. globulus 56
A. galapagensis 21
P. palmiformis 23
P. pandorae 24
L. fucensis 62
P. sulfincola 25
Branchinotogluma sp. 8
P. variabilis 54
L. piscesae 12
P. verenae 18
0.40
0.60
0.80
1.00
1.20
Bray-Curtis coefficient
c
O. globopalpata 2
D. globulus 56
A. galapagensis 21
P. palmiformis 23
P. pandorae 24
P. sulfincola 25
L. fucensis 62
Branchinotogluma sp. 8
L. piscesae 12
P. verenae 18
P. variabilis 54
0.30
0.60
0.90
1.20
1.50
Bray-Curtis coefficient

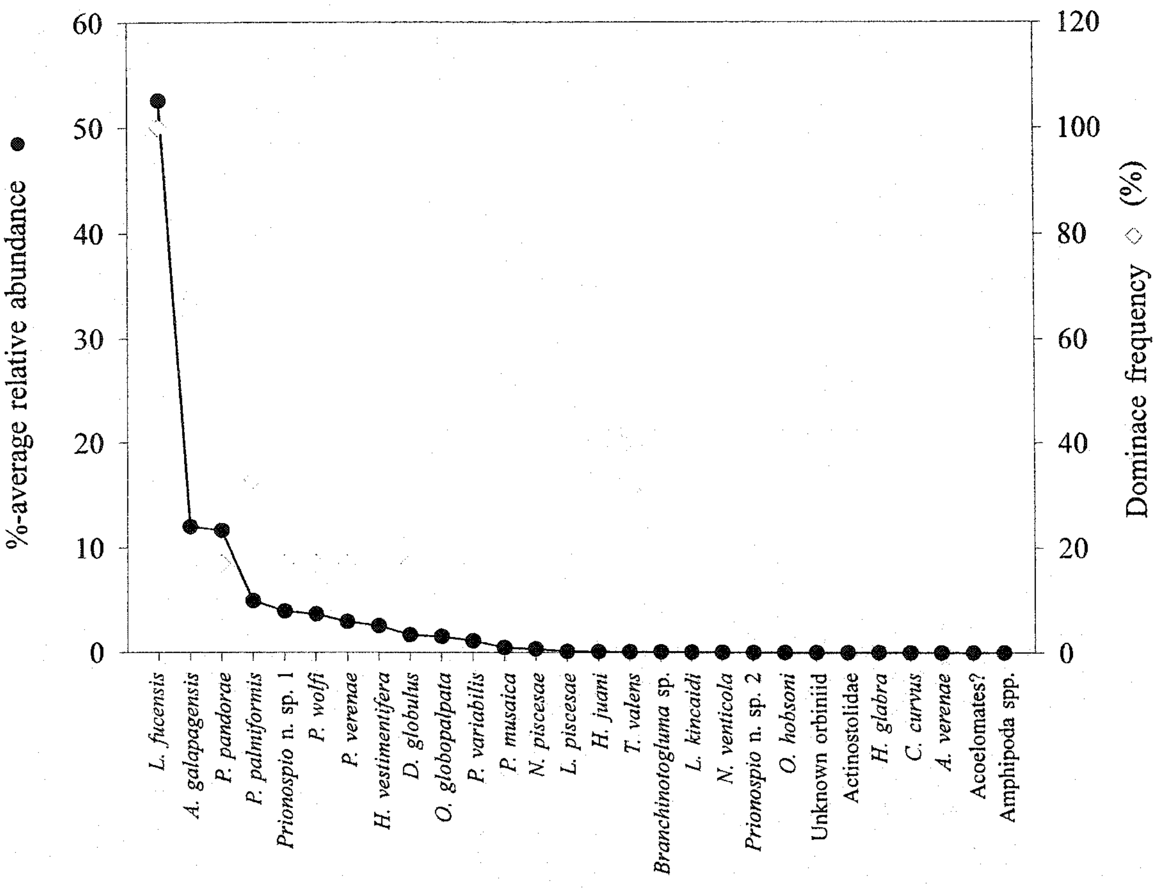


Figure 4.7. Rank-abundance of South Rift Zone macrofauna. Total number of specimens is 17,518. Total number of samples is six and does not include culled samples W, X, and Y. Abundance is expressed as percent-average relative abundance across all samples. Dominance frequency is the percent of samples in which a species is one of the three most abundant species. Taxonomic groups where the species are unknown but which probably contain more than one species are noted as "spp".

palmiformis are in the same higher cluster for the presence/absence and density data and are grouped together at the lowest clustering level for the abundance data (Figure 4.8). Correspondence analysis shows fair agreement with the Jaccard-based clusters (Figure 4.4c), but not for the percent relative abundance or density data.

Comparing the three vent fields

There is no agreement on vent clustering among trees created with the presence/absence, percent relative abundance, or density data (Figure 4.9). However, the one thing that all clusters and correspondence analyses do show is that no delineation can be made among ASHES, CASM, and the SRZ. Year of sample does not fall out in the clusters either. Samples from the three vent fields and from different years are grouped together at every level, including the initial pairing level. The Friedman test of the distribution of percent-average relative abundance is not significant for CASM and the SRZ and for the SRZ and ASHES, but is significant ($p<0.01$) between CASM and ASHES. Complementarity of macrofauna between all three sites is less than 50% (Table 4.3). ASHES and CASM are the most similar, with twenty-one shared species. Rarefaction curves for ASHES, CASM, and the SRZ are presented in Figure 4.10. The SRZ is the most species rich. Regressions of species number with type of substratum (basalt or sulphide) and with vent field are not significant.

Including meiofauna

If meiofauna are included in the rank-abundance curves, the curves do not change shape. Animals that are most abundant and dominant with just the macrofaunal data,

Figure 4.8. Cluster diagrams for South Rift Zone species. Only species found in four or more (> 50%) samples are used. a: dendrogram of presence/absence data using the Jaccard coefficient. b: dendrogram of percent relative abundance data using the Bray-Curtis coefficient. c: dendrogram of density data using the Bray-Curtis coefficient. Numbers are species designations (Appendix 1).

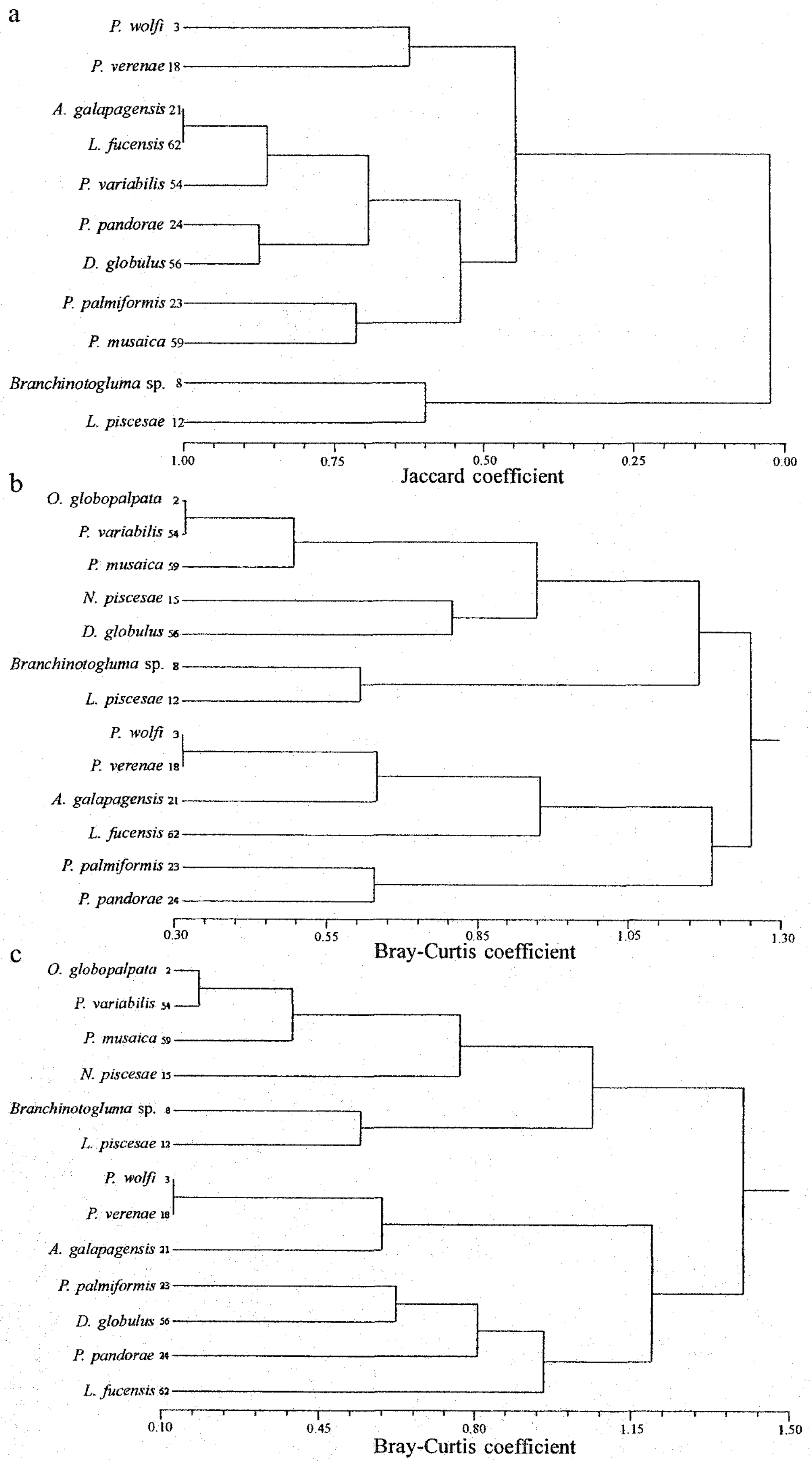

a
P. wolfi 3
P. verenae 18
A. galapagensis 21
L. fucensis 62
P. variabilis 54
P. pandorae 24
D. globulus 56
P. palmiformis 23
P. musaica 59
Branchinotogluma sp. 8
L. piscesae 12
1.00
0.75
0.50
0.25
0.00
Jaccard coefficient
b
O. globopalpata 2
P. variabilis 54
P. musaica 59
N. piscesae 15
D. globulus 56
Branchinotogluma sp. 8
L. piscesae 12
P. wolfi 3
P. verenae 18
A. galapagensis 21
L. fucensis 62
P. palmiformis 23
P. pandorae 24
0.30
0.55
0.85
1.05
1.30
Bray-Curtis coefficient
c
O. globopalpata 2
P. variabilis 54
P. musaica 59
N. piscesae 15
Branchinotogluma sp. 8
L. piscesae 12
P. wolfi 3
P. verenae 18
A. galapagensis 21
P. palmiformis 23
D. globulus 56
P. pandorae 24
L. fucensis 62
0.10
0.45
0.80
1.15
1.50
Bray-Curtis coefficient

Figure 4.9. Cluster diagrams for Axial vent sites from ASHES, CASM, and the South Rift Zone. Only macrofauna are used in the analysis. The dash and number after each vent site indicates the year of sample collection. Plain, bold, and italic typefaces indicate ASHES, CASM, and South Rift Zone vents respectively. Letters are site designations (Table 4.1). a: dendrogram of presence/absence data using the Jaccard coefficient (all 31 samples are used). b: dendrogram of percent relative abundance data using the Bray-Curtis coefficient (number of samples used is 25; culled samples J, Q, R, W, X, and Y are not included). c: dendrogram of density data using the Bray-Curtis coefficient (number of samples used is 25; culled samples J, Q, R, W, X, and Y are not included).

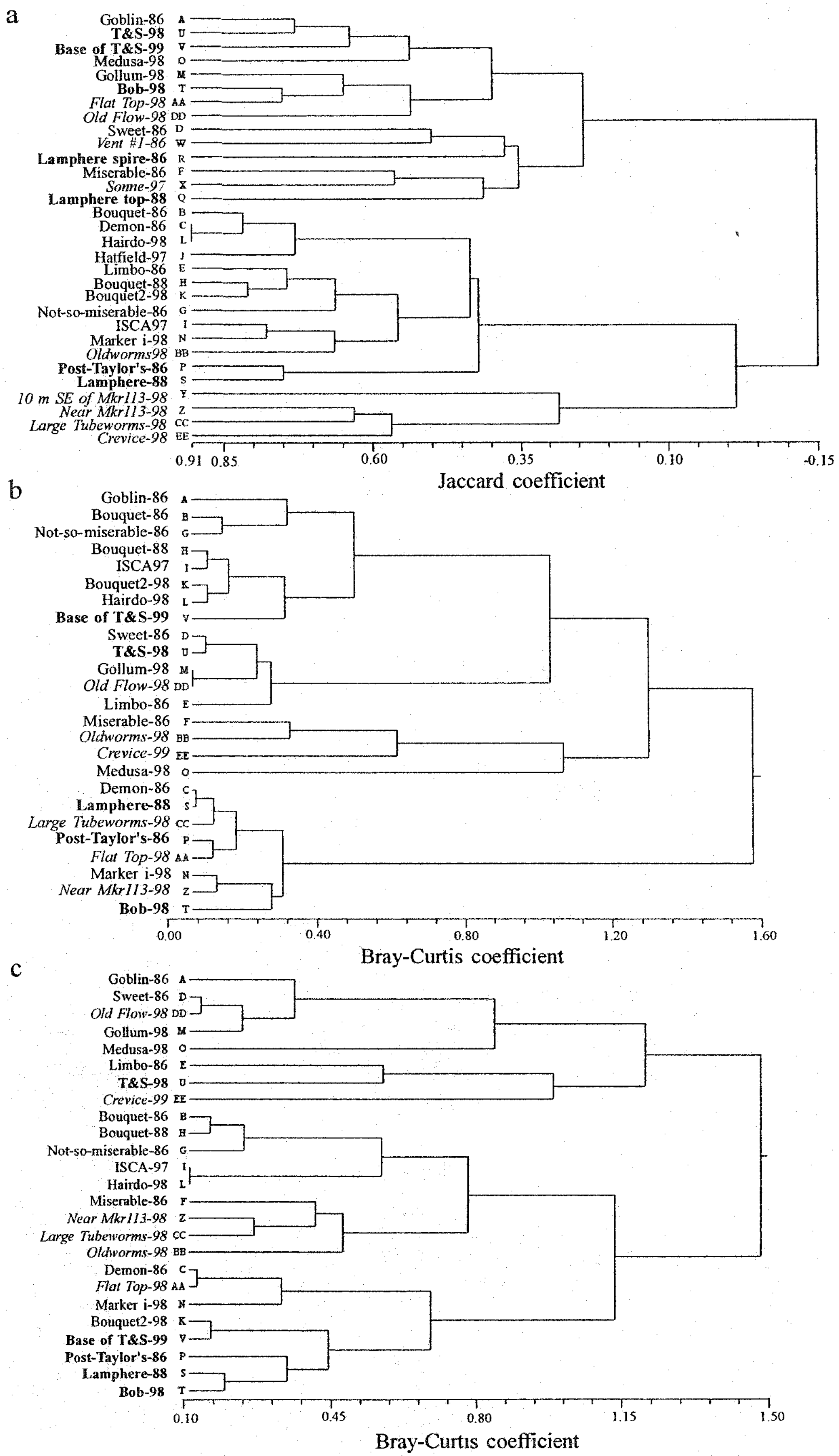

a
Goblin-86 A
T&S-98 U
Base of T&S-99 V
Medusa-98 O
Gollum-98 M
Bob-98 T
Flat Top-98 AA
Old Flow-98 DD
Sweet-86 D
Vent #1-86 W
Lamphere spire-86 R
Miserable-86 F
Sonne-97 X
Lamphere top-88 Q
Bouquet-86 B
Demon-86 C
Hairdo-98 L
Hatfield-97 J
Limbo-86 E
Bouquet-88 H
Bouquet2-98 K
Not-so-miserable-86 G
ISCA97 I
Marker i-98 N
Oldworms98 BB
Post-Taylor's-86 P
Lamphere-88 S
10 m SE of Mkr113-98 Y
Near Mkr113-98 Z
Large Tubeworms-98 CC
Crevice-98 EE
0.91 0.85
0.60
0.35
0.10
-0.15
Jaccard coefficient
b
Goblin-86 A
Bouquet-86 B
Not-so-miserable-86 G
Bouquet-88 H
ISCA97 I
Bouquet2-98 K
Hairdo-98 L
Base of T&S-99 V
Sweet-86 D
T&S-98 U
Gollum-98 M
Old Flow-98 DD
Limbo-86 E
Miserable-86 F
Oldworms-98 BB
Crevice-99 EE
Medusa-98 O
Demon-86 C
Lamphere-88 S
Large Tubeworms-98 CC
Post-Taylor's-86 P
Flat Top-98 AA
Marker i-98 N
Near Mkr113-98 Z
Bob-98 T
0.00
0.40
0.80
1.20
1.60
Bray-Curtis coefficient
c
Goblin-86 A
Sweet-86 D
Old Flow-98 DD
Gollum-98 M
Medusa-98 O
Limbo-86 E
T&S-98 U
Crevice-99 EE
Bouquet-86 B
Bouquet-88 H
Not-so-miserable-86 G
ISCA-97 I
Hairdo-98 L
Miserable-86 F
Near Mkr113-98 Z
Large Tubeworms-98 CC
Oldworms-98 BB
Demon-86 C
Flat Top-98 AA
Marker i-98 N
Bouquet2-98 K
Base of T&S-99 V
Post-Taylor's-86 P
Lamphere-88 S
Bob-98 T
0.10
0.45
0.80
1.15
1.50
Bray-Curtis coefficient

Table 4.3: Complementarity of macrofauna. Complementarity is a measure of differences in species composition between two sites. Number in parentheses is the number of shared species between vent fields. Right-hand side of diagonal is complementarity calculated with macrofauna only. Left-hand side of diagonal is complementarity calculated with all fauna.

	ASHES	CASM	SRZ
ASHES	--	34.3% (21)	44.7% (21)
CASM	44.0% (28)	--	48.5% (17)
SRZ	43.1 (33)	54.0% (23)	--

remain so when all fauna are used. The curves become longer as more species are added to the species totals and the individual rank-orders of the species in very low abundances change. Including meiofauna in complementarity calculations changes this index little (Table 4.3). Meiofauna can only be used to cluster qualitatively using the Jaccard coefficient with presence/absence data. The cluster for Axial sites is given in Figure 4.11 and the correspondence analysis in Figure 4.12. There are some differences in clustering between the analyses with and without meiofauna, but the results are the similar: ASHES, CASM, and the SRZ do not emerge as distinct groupings. There is one cluster that is mostly ASHES samples, but it also includes two CASM samples, and all other clusters include ASHES samples at all hierarchical levels. Senescent and SRZ samples do fall out better in the correspondence analysis with meiofauna than without.

The Axial community

Five species make up over 90% of the total individuals of the Axial community (Figure 4.13). As is the case for each vent field, *Lepetodrilus fucensis* is the most abundant species and *Paralvinella pandorae* and *P. palmiformis* are two of the top four most abundant species. Axial diversity indices are noted in Table 4.2. There are 55 total species and 39 macrofaunal species. Number of species versus log individuals by substratum shows no relation of species number for either basalt or sulphide. Density for Axial is 1.245 individuals•cm^{-2}. Eight species are found at only one of the 26 vents in the Axial data set (Appendix 4.1). Five of these species, *Orbiniella hobsonae*, unknown orbiniid species, unknown Amphipoda species, *Thermanemertes valens*, and unknown acoelomates are from the SRZ. The other three (*Harmothoe* sp., *Levensteiniella*

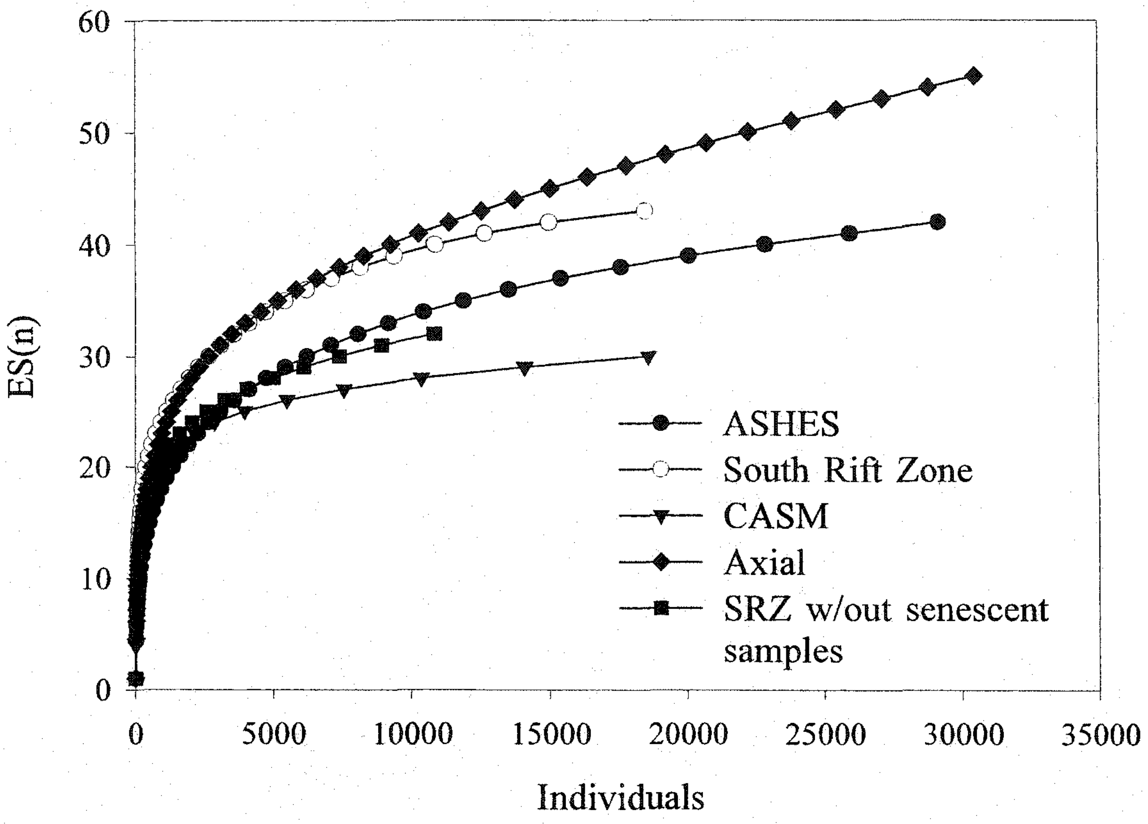


Figure 4.10. Rarefaction of ASHES, CASM, South Rift Zone, Axial, and the South Rift Zone minus the senescent samples. ES(n) is the expected number of species in a random sample of n individuals. Each ES(n) estimate is based on 10 random samples for a given n.

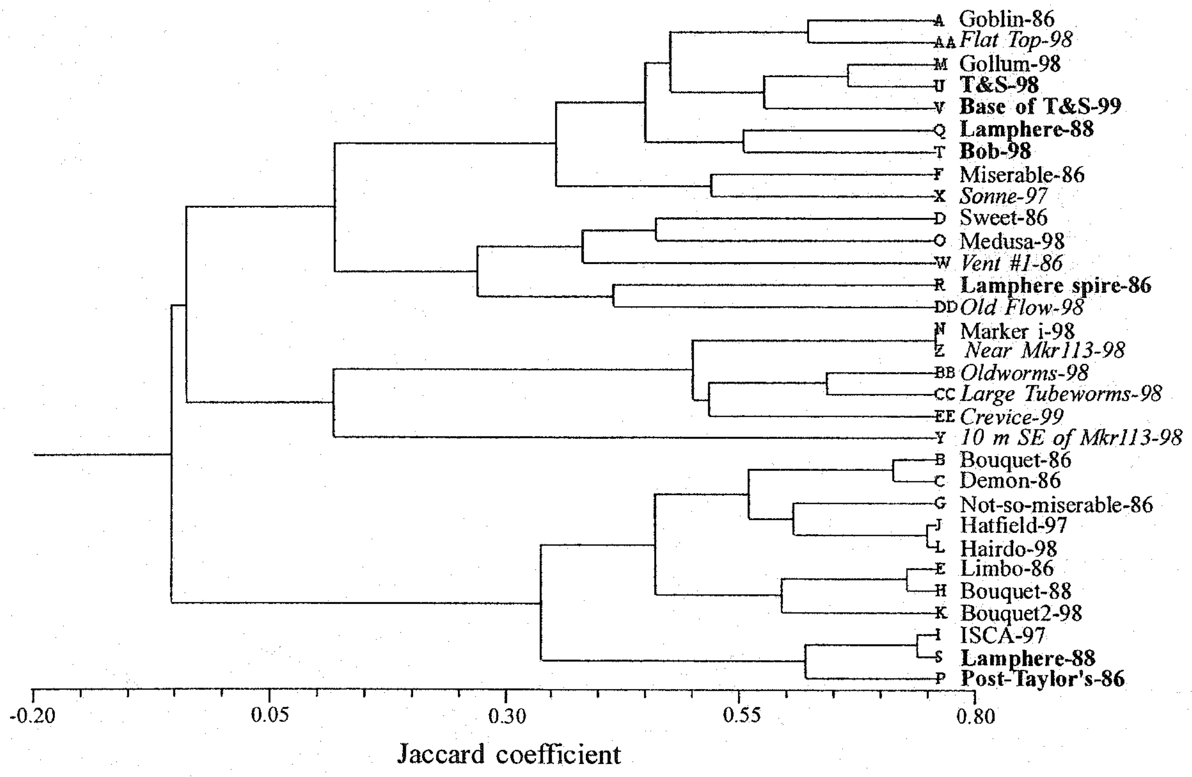


Figure 4.11. Cluster diagram for Axial vent sites using both meio- and macrofauna. Only presence/absence data are used. All 31 samples are included in the analysis. The dash and number after each vent site indicates the year of sample collection. Plain, bold,and italic typefaces indicate ASHES, CASM and South Rift Zone vents respectively. "Mkr" is short for "Marker". Letters are site designations (Table 4.1).

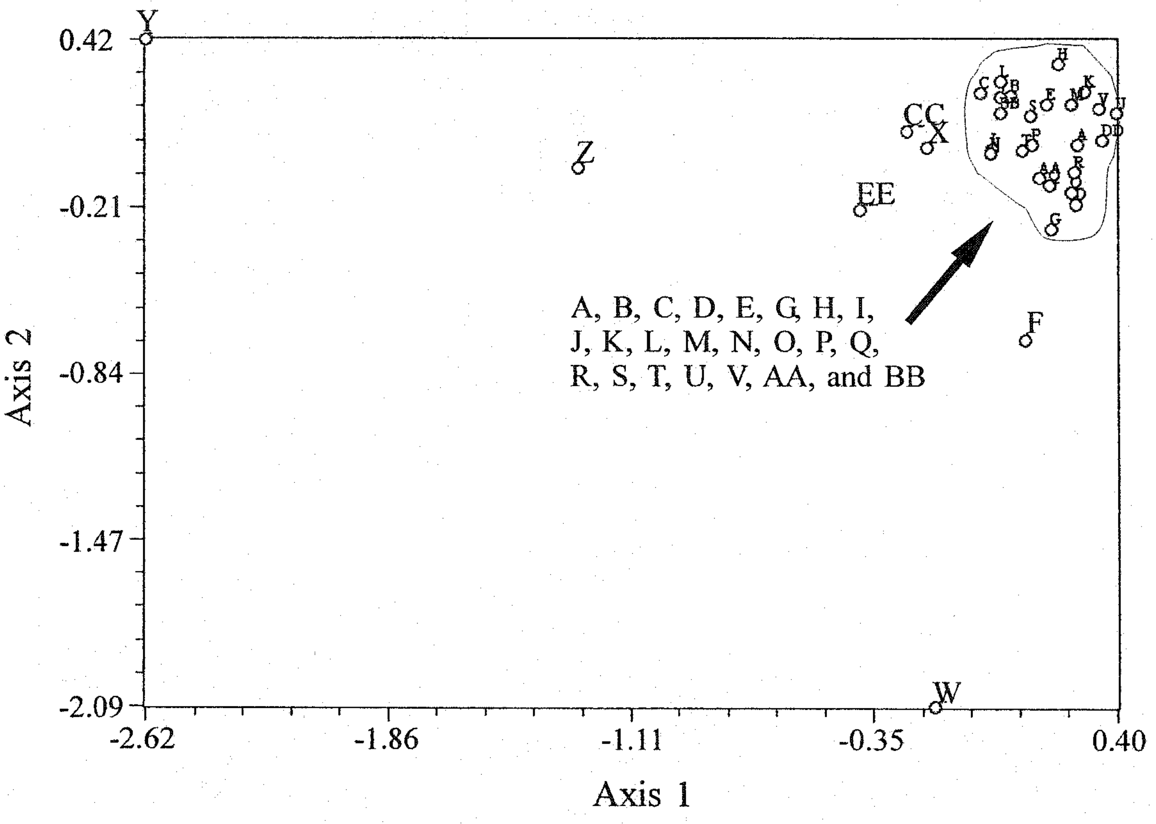


Figure 4.12. Correspondence analysis of Axial site associations using presence/absence data. All 31 samples are included in the analysis. Letters are site designations (Table 4.1).

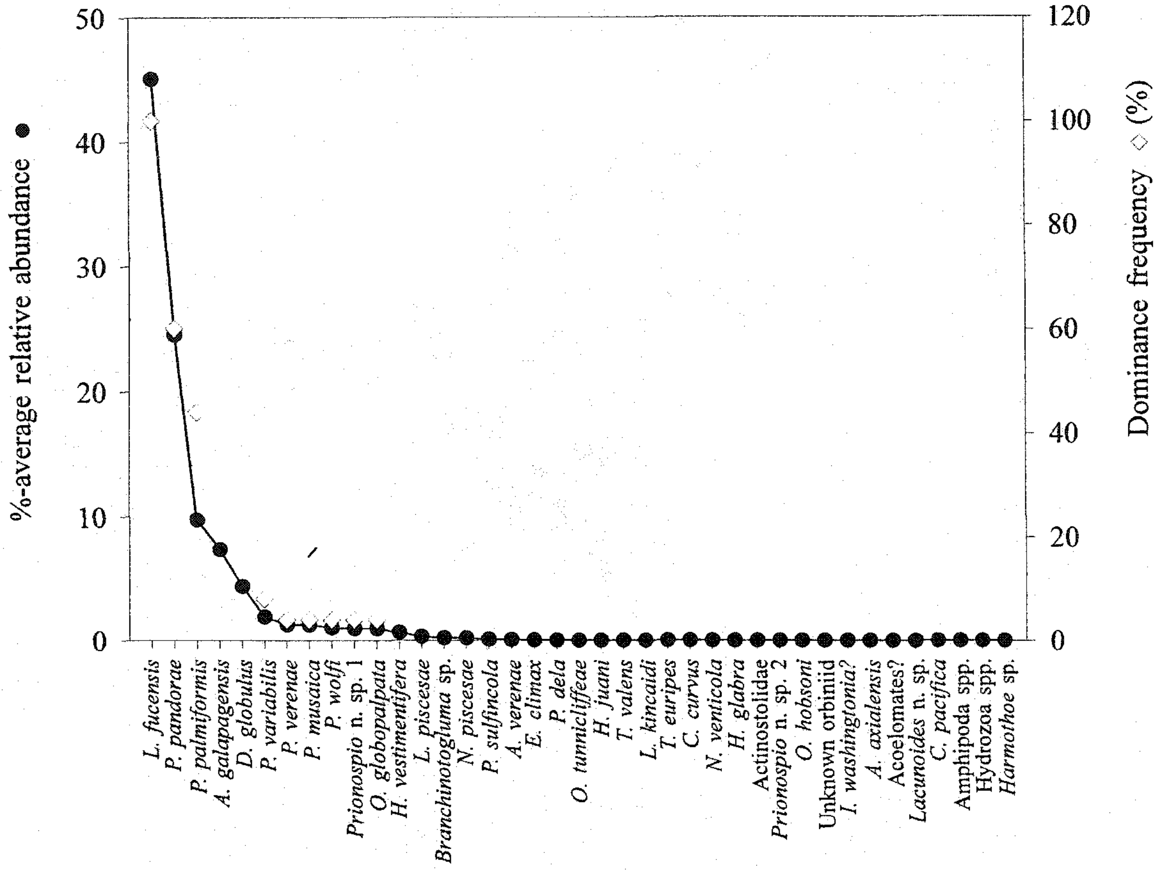


Figure 4.13. Rank-abundance of Axial macrofauna. Total number of samples is 25 and does not include culled samples J, Q, R, W, X, and Y. Abundance is expressed as percent-average relative abundance across all samples. Dominance frequency is the percent of samples in which a species is one of the three most abundant species. Taxonomic groups where the species are unknown but which probably contain more than one species are noted as "spp".

intermedia, and *Provanna laevis*) are from ASHES. The polychaete, *O. hobsonae* is reported from ASHES but is not present in this Axial data set. *Calyptogena pacifica*, a clam, is found only at two vents at CASM but it has been observed at the other two vent fields (pers. obs.). *Lacunoides* n. sp., a snail, is found at only two vents at ASHES. *Amphiduros axialensis*, a polychaete, and a mussel, possibly *Idasola washingtonia*, are found at three vents at ASHES only. The limpet *Temnocinclis euripes* is found at only one vent at ASHES and at the SRZ, as are unknown Hydrozoa. The polychaete, *Prionospio* n. sp. 2 is only found at the SRZ. Twenty-eight species out of 55 are found at less than 25% of the sites (Appendix 4.1). Similar to the SRZ vent field, species rare in dispersion constitute about half of the community. The species abundance model that best describes the Axial community is the geometric series (Figure 4.14; $p<0.000$; $r^2 = 0.803$).

Paralvinella pandorae and *P. palmiformis* are clustered using percent relative abundance and density (Figure 4.15) and the correspondence analysis agrees. These two species are positively significantly associated with Pearson's, Kendall's, and Spearman's pairwise correlations, as are *Amphisamytha galapagensis* and *Depressigyra globulus*. *Branchinotogluma* sp. and *Lepidonotopodium piscesae* cluster together with good agreement from the correspondence analysis with abundance, density, and presence/absence data (Figure 4.16). The *A. galapagensis-D. globulus* and *P. pandorae-P. palmiformis* groupings are supported at a higher clustering level with the presence/absence data (Figure 4.15).

Discussion

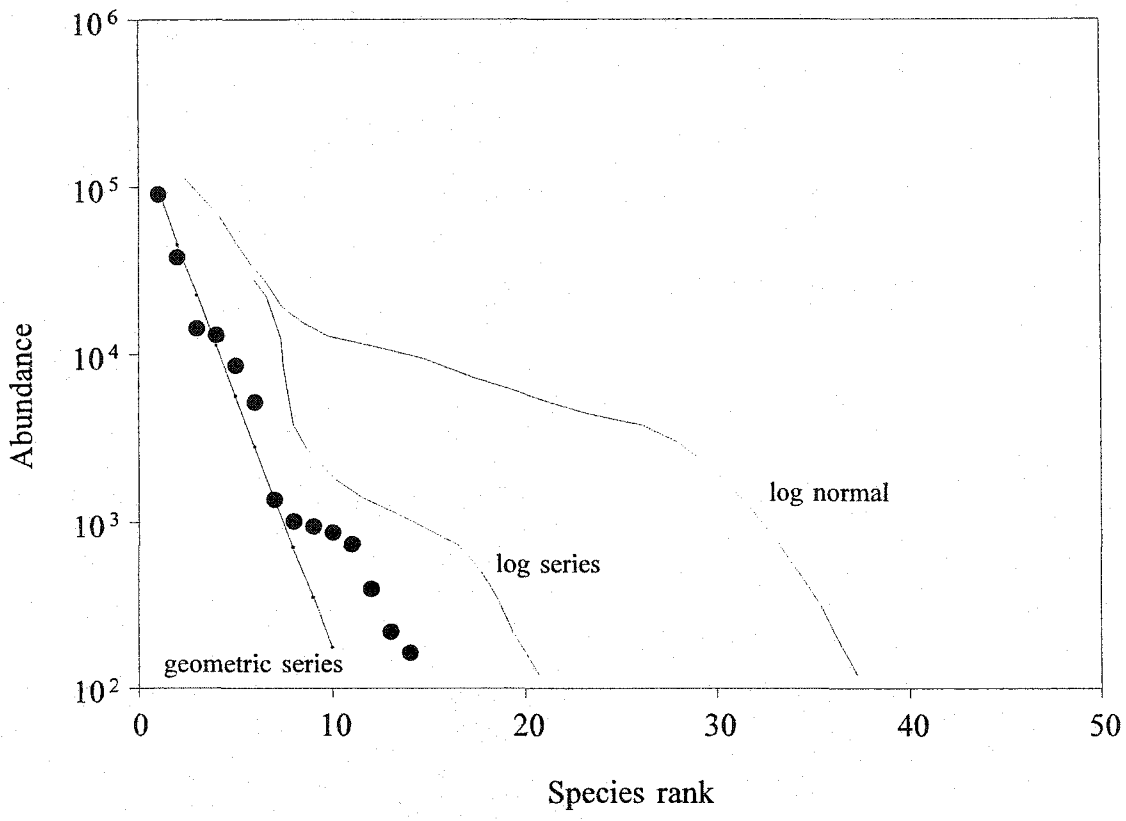
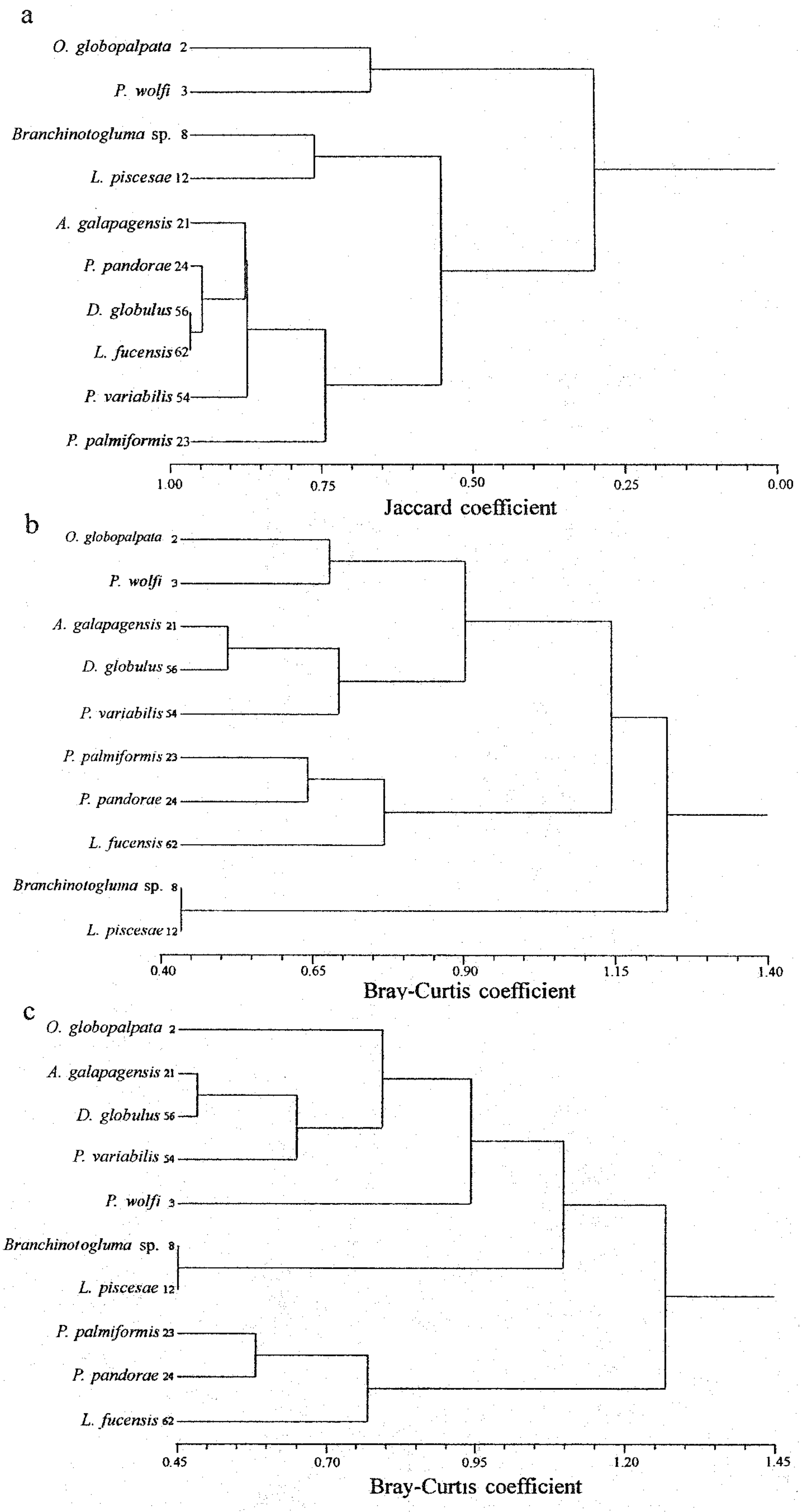


Figure 4.14. Axial species abundance-distribution. Abundance is the number of individuals. The straight line gives the fit to a geometric series distribution. The theoretical log series and log normal distributions are indicated on the figure.

Figure 4.15. Cluster diagrams for species at Axial. Only species found in more than 50% of the samples are used. a: dendrogram of presence/absence data using the Jaccard coefficient. b: dendrogram of percent relative abundance data using the Bray-Curtis coefficient. c: dendrogram of density data using the Bray-Curtis coefficient. Numbers are species designations (Appendix 1).


a
O. globopalpata 2
P. wolfi 3
Branchinotogluma sp. 8
L. piscesae 12
A. galapagensis 21
P. pandorae 24
D. globulus 56
L. fucensis 62
P. variabilis 54
P. palmiformis 23
1.00
0.75
0.50
0.25
0.00
Jaccard coefficient
b
O. globopalpata 2
P. wolfi 3
A. galapagensis 21
D. globulus 56
P. variabilis 54
P. palmiformis 23
P. pandorae 24
L. fucensis 62
Branchinotogluma sp. 8
L. piscesae 12
0.40
0.65
0.90
1.15
1.40
Bray-Curtis coefficient
c
O. globopalpata 2
A. galapagensis 21
D. globulus 56
P. variabilis 54
P. wolfi 3
Branchinotogluma sp. 8
L. piscesae 12
P. palmiformis 23
P. pandorae 24
L. fucensis 62
0.45
0.70
0.95
1.20
1.45
Bray-Curtis coefficient

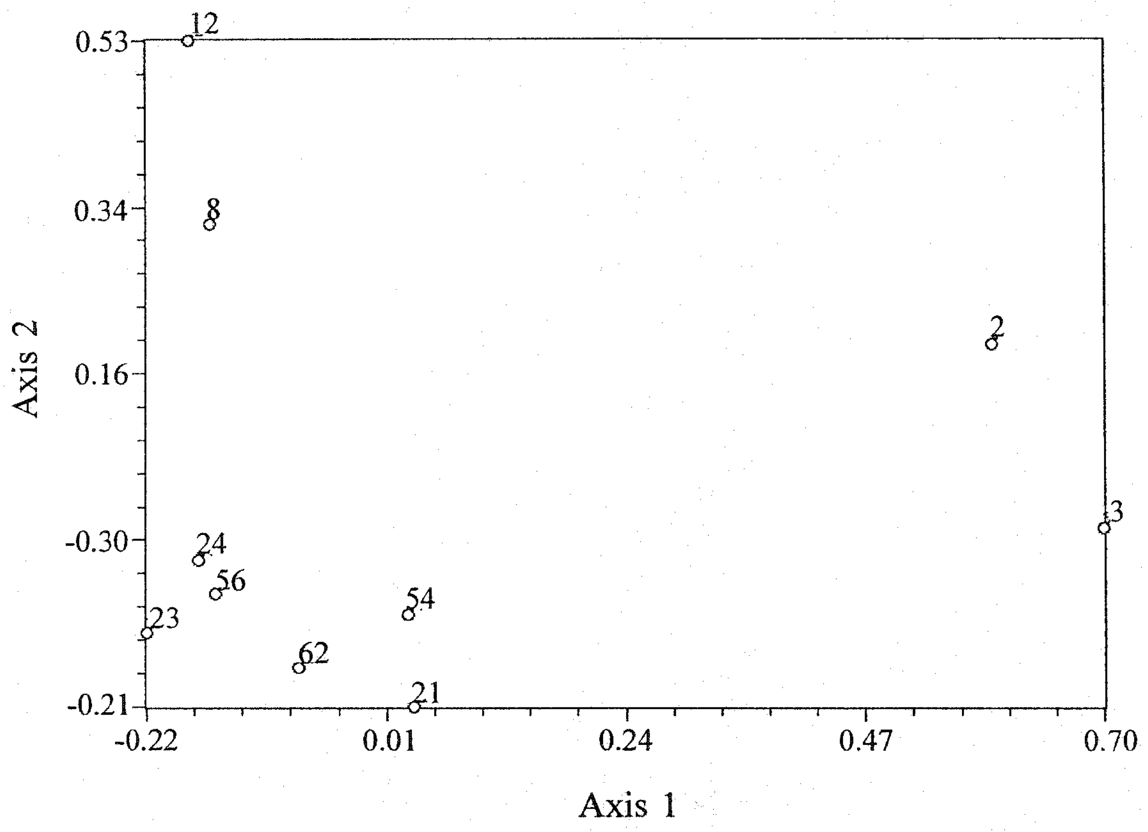


Figure 4.16. Correspondence analysis of Axial species associations using presence/ absence data. Total number of samples is 31. Only species found in more than 50% of samples from each area are used. Numbers are species designations (Appendix 1).

The Axial vent fields

The Axial samples do not group by vent field in the cluster and correspondence analyses and complementarity is low. The rank-abundances of all three vent fields are similar in shape with three or four species contributing more than 90%-average relative abundance. Most species are shared among ASHES, CASM, and the SRZ. There are more differences in individual species rank-order for CASM and the SRZ when these areas are compared to Axial, than for the ASHES data. This could be an effect of the larger sample size for ASHES. Almost all species at CASM and the SRZ are a subset of the ASHES species pool. There are five species at SRZ vents that are not recorded from ASHES, but of these, four are in senescent samples.

The diversity indices for all three fields are very similar, but these indices do not account for unequal sample sizes (Table 4.2). Rarefaction, which does account for unequal sample sizes, shows that ASHES, CASM, and the SRZ curves are alike and differ little in species richness or evenness (Figure 4.10). When the senescent vent samples are excluded from the rarefaction calculation, then ASHES and the SRZ have almost identical curves (Figure 4.10). Sampling of senescent vents in the SRZ, increased the estimated species diversity for this vent field and explains differences in species rank-abundance and composition between the SRZ and ASHES and CASM. Variability within the ASHES vent field is hypothesised to be a result of the relative successional stage of individual tubeworm bushes (J. Marcus, pers. comm.).

Density is slightly higher at ASHES than at CASM and the SRZ. The type of *Ridgeia* bush sampled may explain why: almost all ASHES samples come from large tube worm grabs of tightly interwoven *Ridgeia* tubes which tend to retain more specimens than loose clumps of tube worms when sampled (pers. obs.). At 1.245 individuals•cm^{-2}, density on Axial is high compared to other systems with high-productivity. For example, seagrass beds are considered very productive, but density of grazers on tropical seagrass plants in the Philippines is approximately 0.001 individuals•cm^{-2} (Klump et al. 1992) and 0.200 to 0.600 individuals•cm^{-2} on subtropical seagrasses in Florida (Knowles and Bell 1998). High density of Axial communities is primarily due to the number of *Lepetodrilus fucensis*.

Hanski's (1982) prediction that the most abundant species are the also the most-widespread is supported by the data: species most abundant at each vent field are also the ones found at most or all of the vents. However, some species are well-dispersed yet rare in abundance. *Branchinotogluma* sp. has less than 0.1 to 1%-average relative abundance at all three fields, yet it is widely dispersed (Appendix 4.1). *Lepidonotopodium piscesae*, another polynoid, and *Nereis piscesae*, another polychaete, are less than 1% abundant at all fields and also widely dispersed. All three species are found on both sulphide and basalt. These polychaetes may be a subset of vent fauna, distributions of which are not limited by dispersal ability, settling conditions, or substratum. Distributions of this group of animals may be more limited by microhabitat, life history characteristics, and/or species interactions. *Branchinotogluma* sp. is unusual by its presence at most senescent as well as active vents (Chapter 3). Ubiquitous dispersion in space and time suggests that the low abundance of this species is due to life history constraints and/or species interactions and not due to limitations on dispersal. One explanation of its wide dispersal yet low abundance, may lie in its trophic dynamics. Levesque and Juniper (2000) find *Branchinotogluma* sp. to be a trophic generalist. As a vent ages, *Branchinotogluma* sp.

diversifies its trophic sources. Trophic generalism combined with wide dispersal capabilities could account for its ability to persist at most vents. The ability to use a broad range of trophic resources may mean that this species is not able to dominate food resources, but that it can persist under a broad range of trophic conditions. Except for *L. piscesae*, which Levesque and Juniper (2000) also find to have a broad trophic niche, all other vent polynoids (*Harmothoe* sp., *O. tunnicliffeae*, *Levensteiniella intermedia*, and *L. kincaidi*) are present in low individual abundances and are not well-dispersed around Axial.

Is the similarity of the three vent fields in the Axial community due to the lack of statistical ability to discern a difference because of small sample sizes and non-normally distributed data? Some statistical methods are useful only when applied to small or large samples (Krebs 1999). For example, the Shannon-Wiener diversity index, H', can be indistinguishable for different species distribution patterns unless the assemblage contains of the order of 100 species (May 1975 in Lambshead et al. 1983). A seemingly homogeneous "community" at Axial may be due to sample collection methods that preferentially collect the same kinds of animals (and in the same relative abundances). Given that collection methods are limited by the inconvenient location of vents and by the development of technologies for working in the deep-sea, this point cannot be refuted. However, from my experience working with visual and biological vent data, I think this is unlikely.

A few species are so dominant in abundance and distribution on Axial that greater sample sizes are not likely to change the overall description of the community based on species diversity indices, abundance, and distribution. The ASHES data set has 14 samples, CASM five, and the SRZ six. Going from five to 11 to 25 samples increases the species richness (Figure 4.17), but the same species are almost all present at CASM, the SRZ, and all three vent fields. Variability in diversity and species presence within the ASHES vent field is low and does not seem to be influenced by physico-chemical and or spatial factors (J. Marcus pers. comm.; pers. obs.). Diversity does change somewhat among fields, however, and habitat heterogeneity may account for these differences. Rosenzweig (1995) explains that species probably differ in their abilities to use various habitats. A regional pool of species occupies a much greater variety of places and times than each species will by itself and species diversity increases with habitat variation (Rosenzweig 1995). I use collections of similar habitat (low temperature assemblages on basalt) to compare the three fields in order to minimise the effect of habitat heterogeneity on diversity. But, there must be microhabitat differences even among similar samples.

The Axial vent community

The Axial community has an uneven distribution of species relative abundances. The conspicuous numerical dominance of the community by a few species is comparable to descriptions from north Cleft (Tsurumi and Tunncliffe 2001) and CoAxial (Tunnicliffe et al. 1997), and to that described for Mid-Atlantic Ridge vent mussel beds (van Dover and Trask 2000). On the Mid-Atlantic Ridge, Van Dover and Trask (2000) found that four species contributed over 90% of the total abundance of fauna inhabiting vent mussel beds. Similarly, at Axial, three species are consistently the most abundant: *Lepetodrilus fucensis*, *Paralvinella pandorae*, and *P. palmiformis*.

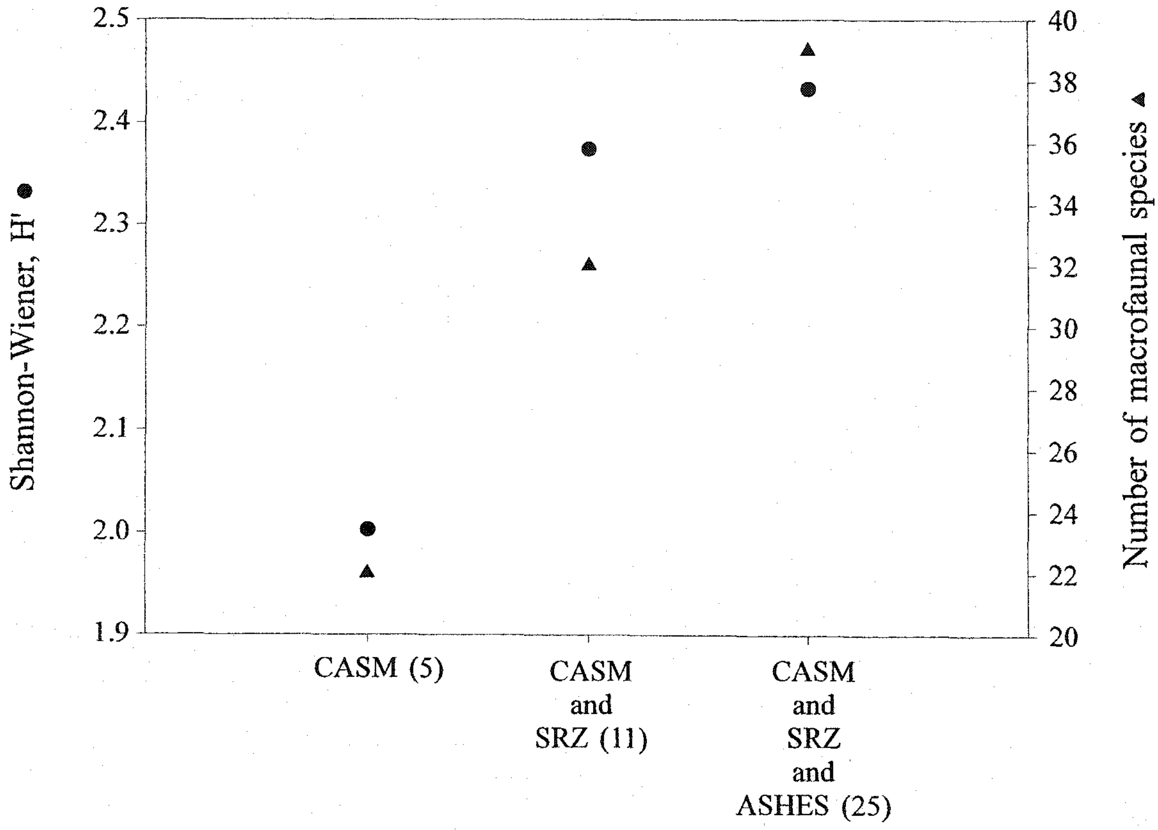


Figure 4.17. Cumulative Shannon-Wiener (H') and number of macrofaunal species for Axial vent fields. Number in parentheses after the vent field name(s) on the x-axis is the cumulative number of samples.

The species abundance model that best describes the Axial data is the geometric series. Assumptions that underlie all species abundance models are: 1) the total number of individuals in the community is equivalent to occupancy of the whole environment; and 2) all species represent niches (Safranyik et al. 1999). There are a couple of assumptions that are specific to the geometric series: 1) the most dominant species will pre-empt a proportion, *k*, of some limiting resource and the second most dominant species will pre-empt the same *k*, of the remainder and so on; and 2) the abundance of a species is proportional to the amount of resource it utilises. These are both reasonable assumptions to make in the vent system. The numerical dominance of a species like *Lepetodrilus fucensis* indicates that it is able to pre-empt some resource or resources. Living space may be a potential limiting resource as vent communities and microbial chemosynthetic production exist within the area reached by the vent fluid. *L. fucensis* are observed stacked on top of each other in tube worm bushes and around vent openings (pers. obs.) and this limpet may be able to out-compete other species for substratum. However, even if the niche-preemption hypothesis is not tenable as a model of community structure (Lambshead and Platt 1985), it may still be valid as a model of species abundance (Hughes 1986).

Communities with abundances in a geometric series are found primarily in environments that are species-poor and often harsh and structured by relatively few environmental factors (Whittaker 1970; Devan and Mucina 1986; Magurran 1988; Safranyik et al. 1999). The hydrothermal vent system is a species-poor habitat with a stressful physico-chemical environment, the fauna of which is dependent on the vent fluid for their existence. Vent faunal composition may be more influenced by the physical and chemical environment than by biological interactions (Sarrazin et al. 1997; Luther et al. 2001).

Unlike Axial (or ASHES or CASM), the SRZ community is best described by the log series model. The SRZ data include senescent vents that are responsible for most of the described differences in species composition and diversity. The fit of the log series model to the SRZ data could be explained by a more random arrival of colonising species (Simpson and Todzia 1990. The log series model fit for the SRZ is perhaps explained by the presence of senescent vents. As succession proceeds in a community from initial to late stages, a community is expected to grade into the log series from the geometric (Choi and Yim 1984; Magurran 1988). Examination of the senescent vent data from Chapter 3, shows that the log series abundance model describes the data (chi-square = 4.896; $p<0.75$).

Paralvinella pandorae and *P. palmiformis* are associated with each other at all three vent fields. *P. pandorae* is a pioneer species at new vents on the Juan de Fuca (Tunnicliffe et al. 1997; Tsurumi et al. 1998). *P. palmiformis* appears to arrive after *P. pandorae* establishes. Colonisation of *Ridgeia* tubes by *P. palmiformis*, does not appear to displace *P. pandorae*, but a decrease in body-size of *P. pandorae* occurred after the arrival of *P. palmiformis* at vents on CoAxial (Tunnicliffe et al. 1997). *L. fucensis* is not necessarily an early coloniser (Tsurumi et al. 1998), but once established it seems to compete well for resources (Chapter 3).

Similar to north Cleft (Tsurumi and Tunnicliffe 2001), dispersal of vent animals on Axial is not limited to the geographic distances between fields. The same species are present at ASHES, CASM, and the SRZ. Coarse calculations indicate that water moves around the caldera at a mean speed of 3 $cm{\bullet}s^{-1}$ and takes about 120 hours to complete one circuit (Cannon and Pashinski 1990; B. Lavelle, pers. comm.). Five days is enough time for planktonic larvae to move between vent sites. Even if larvae were to leave the caldera, one circuit around the perimeter of Axial is only about 10 days (Lavelle and Baker 2000) and re-entry at the south is probable. If dispersal is not an issue and habitat is indistinguishable, then one large Axial community is realistic. ASHES has more species because it has greater area (in terms of tubeworm area, geographic area, and number of samples) than CASM or the SRZ: the species-area phenomenon (Figure 4.17). Slight differences in the species pool between the SRZ and ASHES and CASM are probably due to the presence of different successional states on the SRZ. Differences in density and diversity may also arise from microhabitat differences based on dissolved sulphide or water temperature. Given the water circulation on Axial, regular and frequent dispersal of planktonic larvae around the caldera is likely.

Community descriptors

Descriptors other than species composition, distribution and abundance may be more appropriate when comparing vent communities if one is interested in differences in community structure. For example, a descriptor such as species biomass may be more informative than species abundance. Sarrazin and Juniper (1999) use biomass to define assemblages on a single sulphide structure. Using biomass, they differentiate among assemblages on the same structure as well as among vents on other ridge systems. Magurran (1988) believes biomass to be a more direct measure of resource use than the number of individuals and species. Biomass provides a more meaningful comparison between diversities of different taxonomic levels of organisms (Magurran 1988). If biomass is used as a descriptive variable instead of abundance data, this may mitigate the disadvantage of applying species abundance-based diversity measures across many taxonomic groups. The importance of rare species in vent communities may be better described and measured by factors such as biomass, role in maintaining diversity (e.g. keystone species concept of Dayton 1971), and functional group. Tokeshi (1990) suggests that biomass is intuitively plausible as an expression of species abundances in many communities because biomass is more closely related to the concept of resource utilisation and species abundance models are often related to niche approportionment (for example, the geometric series and broken stick models).

I did a rough calculation of percent-average relative biomass for the Axial macrofauna to compare the results with percent-average relative abundance in Figure 4.18. Using 10 specimens of each species, wet weights were estimated for species with more than 0.01% abundance and relative biomass calculated based on numbers of individuals. The results are given in Figure 4.18: *Paralvinella palmiformis* becomes the most important species in terms of biomass, surpassing even *Lepetodrilus fucensis*. Also, large polychaete species found in low abundances, move up dramatically in rank. *Lepidonotopodium piscesae* at about 0.3% abundance, moves above *P. pandorae* the second most abundant species. Similarly, *Branchinotogluma* sp. moves up from fourteenth rank to seventh. Some species are unaffected by ranking with biomass or abundance, for example, *Provanna variabilis*.

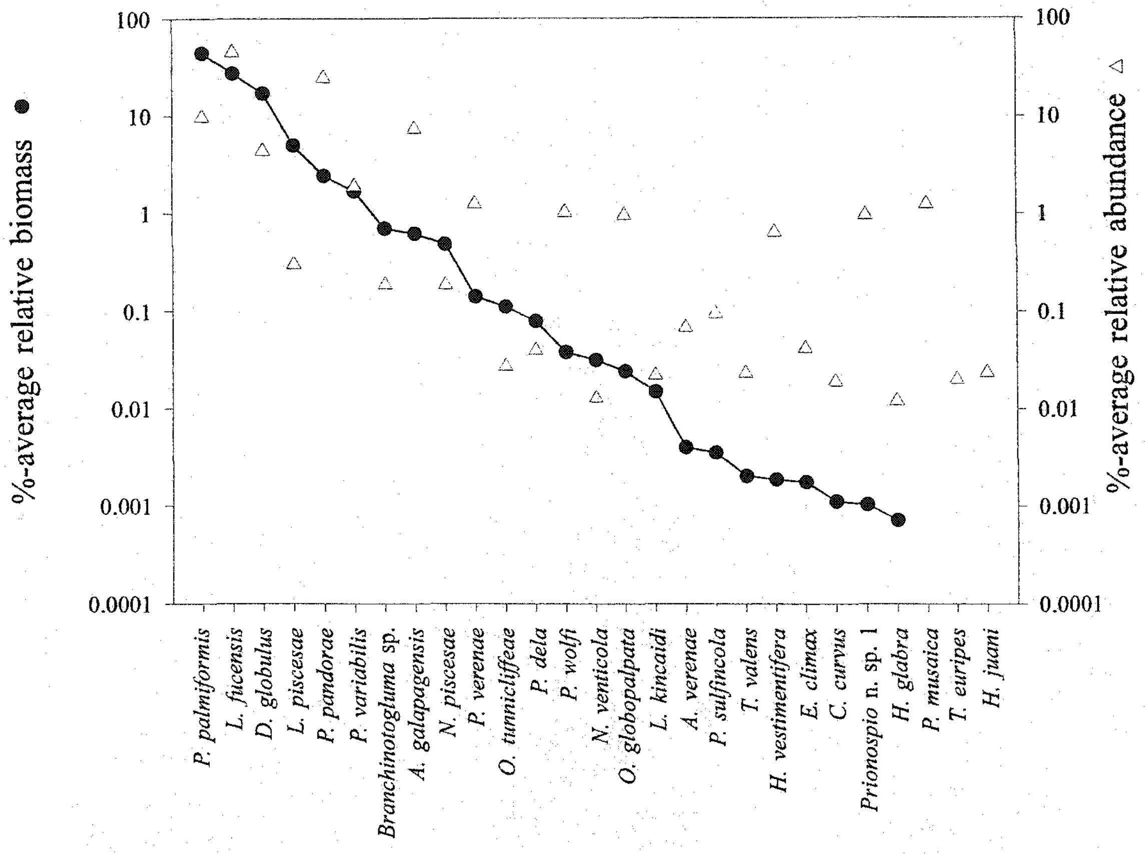


Figure 4.18. Percent-average relative biomass and abundance for Axial macrofauna. Biomass is estimated using wet weights. The line is percent-average relative biomass and the triangles represent percent-average relative abundance. Species hold different ranks depending on whether biomass or abundance is the measured parameter.

Making comparisons relevant

In terms of productivity, disturbance-regime, species diversity, and species abundances, the non-vent deep-sea and the vent habitat are dissimilar. The deep-sea has low productivity, small-scale and infrequent disturbance, high species diversity, and low species abundances. In terms of body-size, vent species are more like coastal water species than the deep-sea benthos (Rex and Etter 1998; pers. obs.). Initial ecological discussion of vent and non-vent deep-sea habitats centred on differences between these two systems (e.g. Cohen and Haedrich 1983; Tunnicliffe 1991). However, ecologists interested in understanding processes that structure communities are perhaps better served by comparing similar systems. Comparison of similar systems should allow detection of repeated ecological patterns and processes. It may be more informative for pattern detection and explanation to compare vent systems to environments that are comparable in terms of community structure.

Johnson et al. (1994) and van Dover and Trask (2000) identify the intertidal as a habitat with which to compare the vent habitat. Large changes in vent O_2 availability and temperature may impact vent communities in a manner analogous to the rise and fall of water in the intertidal zone (Johnson et al. 1994). Knowing that Axial vents fit a geometric series, we have another way to find ecological systems to compare with vents. Most assemblages described as geometric series are taxocenes [e.g. assemblages of dung-beetles (Davis 1993)] within a larger community. Although comparisons between ecotypes are usually between the entire array of species in each community, vent communities could also be compared to select taxocenes as well as other habitats.

Geometric and log series models are good fits to early successional stages of communities (Hughes 1986). Perhaps vent communities can be compared with primary successional states of other ecosystems rather than with a particular community per se. Comparing communities with similar productivity, disturbance, and diversity may make observed similarities and differences meaningful. Differences and similarities in patterns and mechanisms structuring communities may shed light on the ecology of both communities. Comparisons between communities with similar diversity and or functional parameters allow us to move forward with understanding ecological processes such as biotic and abiotic controls on community structure (van Dover and Trask 2000).

Conclusions

One cannot expect to find discontinuities when clustering sampling sites unless the abiotic environment is itself discontinuous, or unless sampling occurs at opposite ends of a gradient, instead of within a gradient (Legendre and Legendre 1998). The three vent fields on Axial Seamount are indistinguishable from each other using clustering, ordination, or other techniques suggesting that the conditions at each vent field are perceived similarly by the animals. The fauna comprises a single, caldera-wide community and most Axial species are widely distributed. Axial fauna has a very uneven species abundance distribution with three species making up more than 90% of the total relative abundance: *Lepetodrilus fucensis*, *Paralvinella pandorae*, and *P. palmiformis*. Positive species associations are described for *P. pandorae* and *P. palmiformis*, *Amphisamytha galapagensis* and *Depressigyra globulus*, and *Branchinotogluma* sp. and *Lepidonotopodium piscesae*. A few species are notable for their wide dispersion yet low overall abundances. One such species, *Branchinotogluma* sp., is widely dispersed in space and time and has a broad trophic niche. This species may be in low abundance due to life history constraints and/or species interactions not because of dispersal or settlement limitations. The Axial community fits a geometric series. This abundance distribution is consistent with literature predictions for low diversity communities in harsh environments. Rather than comparing vents with the non-vent deep-sea, an environment very different in productivity, disturbance regime, and diversity from vents, insights into processes at vents may be better served by comparisons to other communities, successional states, and/or taxocenes that follow a geometric or log series distribution.

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Appendix 4.1: Axial species. Percent-average relative abundance is for macrofauna and does not include culled samples J, Q, R, W, X, and Y. Number of sites present includes culled samples. Dispersion is the percentage of sites at which the species is found. NP = species not present in the dataset. NQ = species present in culled samples or meiofauna and not quantifiable. ^species found at only one site. *species found at only one vent field.

Species	**Axial**		**ASHES**		**CASM**		**SRZ**	
	Percent-average relative abundance (n=25)	Dispersion (26 sites; n=31)	Percent-average relative abundance (n=14)	Dispersion (14 sites; n=15)	Percent-average relative abundance (n=5)	Dispersion (4 sites; n=7)	Percent-average relative abundance (n=6)	Dispersion (8 sites; n=9)
Lepetodrilus fucensis	45.03	100	36.22	100	60.67	100	52.55	100
Paralvinella pandorae	24.50	96.2	30.24	100	23.83	100	11.67	87.5
Paralvinella palmiformis	9.736	65.4	13.68	100	4.473	75.0	4.926	75.0
Amphisamytha galapagensis	7.347	96.2	7.326	92.9	1.801	100	12.02	100
Depressigyra globulus	4.361	100	5.294	100	4.977	100	1.670	100
Provanna variabilis	1.893	96.2	2.749	100	0.436	100	1.100	87.5
Protomystides verenae	1.249	76.9	0.907	78.6	0.156	75.0	2.941	75.0
Pyropelta musaica	1.233	73.1	1.968	78.6	0.078	50.0	0.480	75.0
Parougia wolfi	1.016	61.5	0.208	64.3	0.096	50.0	3.668	62.5
Prionospio n. sp.1	0.951	30.8	0.008	28.6	NP	NP	3.942	50.0
Ophryotrocha globopalpata	0.949	61.5	0.326	64.3	2.015	75.0	1.514	50.0
Hesiospina vestimentifera	0.634	46.2	0.033	42.9	0.027	50.0	2.545	50.0
Lepidonotopodium	0.301	73.1	0.385	85.7	0.303	100	0.105	37.5

Species	**Axial**		**ASHES**		**CASM**		**SRZ**	
	Percent-average relative abundance (n=25)	Dispersion (26 sites; n=31)	Percent-average relative abundance (n=14)	Dispersion (14 sites; n=15)	Percent-average relative abundance (n=5)	Dispersion (4 sites; n=7)	Percent-average relative abundance (n=6)	Dispersion (8 sites; n=9)
piscesae								
Branchinotogluma sp.	0.187	65.4	0.198	78.6	0.272	100	0.091	62.5
Nereis piscesae	0.186	65.4	0.120	78.6	0.164	50.0	0.358	50.0
Paralvinella sulfincola	0.094	38.5	0.026	42.9	0.395	75.0	NQ	12.5
Ammothea verenae	0.071	42.3	0.117	71.4	NP	NP	0.007	12.5
Euphilomedes climax	0.041	19.2	0.022	28.6	0.146	25.0	NP	NP
Paralvinella dela	0.040	23.1	0.033	28.6	0.104	50.0	NP	NP
Opisthotrochopodus tunnicliffeae	0.027	57.7	0.034	64.3	0.041	25.0	NP	NP
Helicoradmenia juani	0.023	15.4	NQ	7.14	NP	NP	0.098	37.5
Thermanemertes valens^	0.023	3.85	NP	NP	NP	NP	0.096	12.5
Levensteiniella kincaidi	0.022	38.5	0.013	42.9	0.012	50.0	0.053	25.0
Temnocinclis euripes	0.020	7.69	0.036	7.14	NP	NP	NQ	12.5
Clypeosectus curvus	0.019	46.2	0.029	57.1	0.003	50.0	0.009	12.5
Nicomache venticola	0.013	23.1	0.008	35.7	NP	NP	0.035	12.5
Hesiodeira glabra	0.012	23.1	0.012	21.4	0.003	50.0	0.019	12.5
Actinostolidae n. spp (2)	0.006	15.4	0.003	21.4	NP	NP	0.019	12.5
Prionospio n. sp. 2*	0.006	7.69	NP	NP	NP	NP	0.024	25.0
Orbiniella hobsonae^	0.006	3.85	NP	NP	NP	NP	0.024	12.5
Unknown orbiniid^	0.005	3.85	NP	NP	NP	NP	0.020	12.5
Idasola washingtonia?*	0.003	11.5	0.005	21.4	NP	NP	NP	NP
*Amphiduros axialensis**	0.002	11.5	0.003	21.4	NP	NP	NP	NP
Acoelomates?^	0.001	3.85	NP	NP	NP	NP	0.005	12.5

Species	**Axial**		**ASHES**		**CASM**		**SRZ**	
	Percent-average relative abundance (n=25)	Dispersion (26 sites; n=31)	Percent-average relative abundance (n=14)	Dispersion (14 sites; n=15)	Percent-average relative abundance (n=5)	Dispersion (4 sites; n=7)	Percent-average relative abundance (n=6)	Dispersion (8 sites; n=9)
Lacunoides n. sp.*	0.001	7.69	0.001	14.3	NP	NP	NP	NP
*Calyptogena pacifica**	0.001	7.69	NP	NP	0.003	50.0	NP	NP
Amphipoda spp. unknown^	0.001	3.85	NP	NP	NP	NP	0.002	12.5
Hydrozoa spp. unknown	0.0004	7.69	0.001	7.14	NP	NP	NQ	12.5
Harmothoe sp.^	0.0003	3.85	0.0005	7.14	NP	NP	NP	NP
Copidognathus papillatus	NQ	26.9	NQ	35.7	NP	NP	NQ	25.0
*Levensteiniella intermedia^*	NQ	3.85	NQ	7.14	NQ	NP	NP	NP
*Provanna laevis^*	NQ	3.85	NQ	7.14	NP	NP	NP	NP
Aphotopontius forcipatus	NQ	73.1	NQ	57.1	NQ	75.0	NQ	87.5
*Barathricola rimensis**	NQ	7.69	NP	NP	NP	NP	NQ	25.0
Benthoxynus spiculifer	NQ	57.7	NQ	64.3	NQ	75.0	NQ	37.5
Misophriopsis longicauda	NQ	15.4	NQ	14.3	NP	NP	NQ	25.0
Stygiopontius quadrispinosus	NQ	42.3	NQ	57.1	NQ	50.0	NQ	12.5
Copepoda type 1	NQ	38.5	NQ	35.7	NP	NP	NQ	62.5
Copepoda type 2	NQ	15.4	NQ	14.3	NP	NP	NQ	25.0
Copepoda type 9	NQ	7.69	NQ	7.14	NP	NP	NQ	12.5
Copepoda type 10*	NQ	3.85	NQ	7.14	NP	NP	NP	NP
Copepoda type 11	NQ	15.4	NQ	7.14	NQ	25.0	NQ	25.0
Copepoda type 13*	NQ	3.85	NP	NP	NP	NP	NQ	12.5

Species	**Axial**		**ASHES**		**CASM**		**SRZ**	
	Percent-average relative abundance (n=25)	Dispersion (26 sites; n=31)	Percent-average relative abundance (n=14)	Dispersion (14 sites; n=15)	Percent-average relative abundance (n=5)	Dispersion (4 sites; n=7)	Percent-average relative abundance (n=6)	Dispersion (8 sites; n=9)
Copepoda type A3244	NQ	7.69	NP	NP	NQ	25.0	NQ	12.5
Calanoida	NQ	69.2	NQ	71.4	NQ	75.0	NQ	62.5
Harpacticoida	NQ	53.8	NQ	50.0	NQ	50.0	NQ	62.5
Nematoda	NQ	19.2	NQ	14.3	NP	NP	NQ	62.5
Podocopida	NQ	57.7	NQ	42.9	NQ	75.0	NQ	62.5

Appendix 4.2: ASHES species. Percent-average relative abundance for macrofauna only and does not include culled sample J. Number of sites present includes culled samples. Quantitative: macrofaunal species in the reduced data set. Qualitative: additional species (mostly meiofauna) from the culled samples.

Species	Percent-average relative abundance (n=14)	Number of sites present (14 sites total; n=15)
A. Quantitative		
Lepetodrilus fucensis	36.22	14
Paralvinella pandorae	30.24	14
Paralvinella palmiformis	13.68	14
Amphisamytha galapagensis	7.326	13
Depressigyra globulus	5.294	14
Provanna variabilis	2.749	14
Pyropelta musaica	1.968	11
Protomystides verenae	0.907	11
Lepidonotopodium piscesae	0.385	12
Ophryotrocha globopalpata	0.326	9
Parougia wolfi	0.208	9
Branchinotogluma sp.	0.198	11
Nereis piscesae	0.120	11
Ammothea verenae	0.117	10
Temnocinclis euripes	0.036	1
Opisthotrochopodus tunnicliffeae	0.034	9
Paralvinella dela	0.033	4
Hesiospina vestimentifera	0.033	6
Clypeosectus curvus	0.029	8
Paralvinella sulfincola	0.026	6
Euphilomedes climax	0.022	4
Levensteiniella kincaidi	0.013	6
Hesiodeira glabra	0.012	3
Prionospio n. sp.1	0.008	4
Nicomache venticola	0.008	5
Idosola washingtonia?	0.005	3
Actinostolidae n. spp (2)	0.003	3
Amphiduros axialensis	0.003	3
Lacunoides n. sp.	0.001	2
Hydrozoa spp. unknown	0.001	1
Harmothoe sp.	0.0005	1

B. Qualitative

Species	Percent-average relative abundance (n=14)	Number of sites present (14 sites total; n=15)
Copidognathus papillatus	--	5
Helicoradmenia juani	--	1
Levensteiniella intermedia	--	1
Provanna laevis	--	1
Aphotopontius forcipatus	--	8
Benthoxynus spiculifer	--	9
Misophriopsis longicauda	--	2
Stygiopontius quadrispinosus	--	8
Copepoda type 1	--	5
Copepoda type 2	--	2
Copepoda type 9	--	1
Copepoda type 10	--	1
Copepoda type 11	--	1
Calanoida	--	10
Harpacticoida	--	7
Nematoda	--	2
Podocopida	--	6

Appendix 4.3: CASM species. Percent-average relative abundance for macrofauna only and does not include culled samples Q and R. Number of sites present includes culled samples. Quantitative: macrofaunal species in the reduced data set. Qualitative: additional species (mostly meiofauna) from the culled samples.

Species	Percent-average relative abundance (n=5)	Number of sites present (4 sites total; n=7)
A. Quantitative		
Lepetodrilus fucensis	60.67	4
Paralvinella pandorae	23.83	4
Depressigyra globulus	4.977	4
Paralvinella palmiformis	4.473	3
Ophryotrocha globopalpata	2.015	3
Amphisamytha galapagensis	1.801	4
Provanna variabilis	0.436	4
Paralvinella sulfincola	0.395	3
Lepidonotopodium piscesae	0.303	4
Branchinotogluma sp.	0.272	4
Nereis piscesae	0.164	2
Protomystides verenae	0.156	3
Euphilomedes climax	0.146	1
Paralvinella dela	0.104	2
Parougia wolfi	0.096	2
Pyropelta musaica	0.078	2
Opisthotrochopodus tunnicliffeae	0.041	1
Hesiospina vestimentifera	0.027	2
Levensteiniella kincaidi	0.012	2
Calyptogena pacifica	0.003	2
Clypeosectus curvus	0.003	2
Hesiodeira glabra	0.003	2
B. Qualitative		
Aphotopontius forcipatus	--	3
Benthoxynus spiculifer	--	3
Stygiopontius quadrispinosus	--	2
Copepoda type 11	--	1
Copepoda type A3244	--	1
Calanoida	--	3
Harpacticoida	--	2

Species	Percent-average relative abundance (n=5)	Number of sites present (4 sites total; n=7)
Podocopida	--	3

Appendix 4.4: South Rift Zone species. Percent-average relative abundance for macrofauna only and does not include culled samples W, X, and Y. Number of sites present includes culled samples. Quantitative: macrofaunal species in the reduced data set. Qualitative: additional species (mostly meiofauna) from the culled samples.

Species	Percent-average relative abundance (n=6)	Number of sites present (8 sites total; n=9)
A. Quantitative		
Lepetodrilus fucensis	52.55	8
Amphisamytha galapagensis	12.02	8
Paralvinella pandorae	11.67	7
Paralvinella palmiformis	4.926	6
Prionospio n. sp.1	3.942	4
Parougia wolfi	3.668	5
Protomystides verenae	2.941	6
Hesiospina vestimentifera	2.545	4
Depressigyra globulus	1.670	8
Ophryotrocha globopalpata	1.514	4
Provanna variabilis	1.100	7
Pyropelta musaica	0.480	6
Nereis piscesae	0.358	4
Lepidonotopodium piscesae	0.105	3
Helicoradomenia juani	0.098	3
Thermanemertes valens	0.096	1
Branchinotogluma sp.	0.091	5
Levensteiniella kincaidi	0.053	2
Nicomache venticola	0.035	1
Prionospio n. sp.2	0.024	2
Orbiniella hobsonae	0.024	1
Unknown orbiniid	0.020	1
Actinostolidae n. spp (2)	0.019	1
Hesiodeira glabra	0.019	1
Clypeosectus curvus	0.009	1
Ammothea verenae	0.007	1
Acoelomates?	0.005	1
Amphipoda spp. unknown	0.002	1
B. Qualitative		
Copidognatus papillatus	--	2
Paralvinella sulfincola	--	1
Temnocinclis euripes	--	1
Aphotopontius forcipatus	--	7

Species	Percent-average relative abundance (n=6)	Number of sites present (8 sites total; n=9)
Benthoxynus spiculifer	--	3
Barathricola rimensis	--	2
Misophriopsis longicauda	--	2
Stygiopontius quadrispinosus	--	1
Copepoda type 1	--	5
Copepoda type 2	--	2
Copepoda type 9	--	1
Copepoda type 11	--	2
Copepoda type 13	--	1
Copepoda type A3244	--	1
Calanoida	--	5
Harpacticoida	--	5
Nematoda	--	3
Podocopida	--	5
Hydrozoa spp. unknown	--	1

CHAPTER 5

Axial, Cleft, and CoAxial vent communities

Introduction

Natural history and ecology of three segments of the Juan de Fuca Ridge, (Axial, north Cleft, CoAxial: Figure 1.1) are presented in chapters two to four. This chapter examines the idea that communities on the three segments are statistically indistinguishable and have similar patterns of species association, dispersion, and diversity. The three-segment region of the Juan de Fuca is also evaluated for the relative influence of mesoscale ecological versus local controls on local diversity and for the utility of nonparametric species richness estimators.

Ridge and interridge scale biological work at vents began as analyses of population genetics of various organisms. Studies examined amphipods (France et al. 1992), vestimentiferans (Black et al. 1994; Black 1995; Southward et al. 1996), bivalves (Craddock et al. 1995; Karl et al. 1996), polychaetes (Jollivet et al. 1995; Chevaldonne et al. 1998), and limpets (Craddock et al. 1997). Next came syntheses of these studies including Vrijenhoek's (1997) test of modes and patterns of dispersal on the East Pacific Rise and Galapagos Spreading Centre (Figure 2.1). The conclusion of this synthesis was that within a ridge, species are genetically homogenous but at the interridge scale, species are separated due to major fracture zones (Vrijenhoek 1997). These fracture zones effectively stop the transport of larvae and species between ridges. Similar conclusions have been made of ridge versus interridge community structure (Jollivet 1996).

Studies of the ecology and biogeography of vent fauna at the ridge and interridge scale are rarer than works on population genetics. Gebruk et al. (1997) give a broad overview of the ecology and biogeography of the Mid-Atlantic Ridge (Figure 2.1.1) vent fauna in which they describe the species composition, patterns of animal distributions, and community organisation. Food sources, behaviour, and distribution of vent shrimps on the Mid-Atlantic Ridge are investigated by Gebruk et al. (2000). Tunnicliffe et al. (1998) provide a biogeographical perspective of the deep-sea hydrothermal vent fauna; theirs is one of the first studies in which ridge communities are compared at a scale beyond that of their nearest neighbours. The primary reason for the scarcity of large scale ecological and biogeographical studies is the paucity of integrated comparative information available for entire ridge segments.

Axial, Cleft, and CoAxial data are used for a description of the ecology of communities on this approximately 150 km portion of the southern Juan de Fuca Ridge. Comparing Juan de Fuca segments is a step towards completing a description of the entire Ridge. Eventually, I would like to see an integrated account of all active vent areas on the Ridge. A description of the Juan de Fuca vent community will enable biogeographical comparisons between mid-ocean ridges and answer questions about diversity maintenance and species distribution and abundance at vents across oceanic basins and among oceans.

Although the region discussed in this chapter includes CoAxial segment, there are only two samples from CoAxial and community comparisons between segments are thus primarily between Axial and Cleft. Why should we expect differences among communities on the segments? Table 5.1 presents general physical, chemical and

Table 5.1: Physical, chemical, and biological features of Axial and Cleft segments. Estimated travel time is calculated as the time a larvae travels between the two furthest vents on the segment using measurements of prevailing current direction and speed (Cannon and Pashinski 1990; B. Lavelle, pers. comm.). The maximum age of low temperature venting is set by discovery of venting on Axial and Cleft. In the case of Axial, a hotspot on the ridge, venting was probably ongoing years before discovery. For Cleft, 1986 is the year of the eruption and this eruption probably initiated all subsequent low temperature venting.

Segment	Distance to Axial or Cleft	Estimated travel time (days)	Geophysical source mechanism	Low temperature *Ridgeia* bushes on basalt?	High temperature sulphide vents?	Age of low temperature venting
Axial	~130 km	5.0	shallow magma source	Yes	Yes	1983-2000
Cleft	~130 km	6.4	shallow magma source	Yes	Yes	1986-1993

biological features of Axial and Cleft. Both segments have a similar geophysical heat source due to shallow magma emplacement and have low (basalt and sulphide) and high (sulphide) temperature venting. In addition, tubeworm assemblages of *Ridgeia piscesae* with associated macrofauna dominate both communities. However, sustained low temperature venting on Axial is of greater duration than at Cleft, communities on Axial are somewhat closer to each other (as measured by travel time between the two furthest points) than north Cleft vents, Axial has a greater area of venting, the geometric relationship of the vents on Axial is circular but linear for Cleft, and the distance between the segments is about 130 km.

Local and regional diversity

Understanding the roles of regional (historical and geographical) and local processes in determining local patterns of species richness has been an important focus for ecologists since the 1980s (e.g. Terborgh and Faaborg 1980; Cornell 1985; Ricklefs 1987; Caswell and Cohen 1991; Cornell and Lawton 1992; Cornell and Karlson 1996; Caley and Schluter 1997). A main reason for this focus has been conservation: i.e. understanding what processes are involved in producing and maintaining diversity may lead to a better management strategy for maximising preservation of biodiversity (e.g. Ricklefs 1987; Harrison 1997).

Processes governing local diversity are varied. Biotic interactions have traditionally been used to explain the number of observed species in a particular habitat. Competition, predation, mutualism, parasitism, limited dispersal capabilities (e.g. pool exhaustion, Cornell 1993), and environmental stochasticity are thought to influence local diversity (Connell 1978; Ricklefs 1987). However, local diversity does not necessarily correspond perfectly to conditions of the local physical environment, and similar habitats on different continents often support strikingly dissimilar numbers of species. As well, non-equilibrium explanations for patterns of species richness suggest that species may only compete weakly, if at all (Schluter and Ricklefs 1993; Cornell and Karlson 1996). Patterns of diversity at the local level may be influenced by historical and geographical circumstances including speciation, dispersal, climate, and wide-spread extinction as well as local ecological factors (Ricklefs 1987; Cornell and Lawton 1992; Schluter and Ricklefs 1993).

One of the challenges of diversity studies is defining the "true" species pool from which a given local assemblage is drawn (Cornell 1985). In the ephemeral vent environment, we have the advantage of periodic naturally-occurring defaunation and (re-) colonisation; this gives researchers the opportunity to get a good approximation of the "true" species pool. Comparisons between local and regional species diversity are facilitated in the vent environment by a relatively small number of species confined to well-delineated habitat patches. These circumstances are coupled with a good understanding of the species present and their taxonomic relatedness (Tunnicliffe et al. 1996).

Vent communities have clearly defined boundaries on a local scale. In this analysis, "local" refers to the scale of an individual vent. On a larger scale, the vent habitat is linear and can be divided up into small or large regions. For example, a segment of a ridge could be one region or, for comparisons at the global scale, an entire ridge could be considered a region or province. It is important to carefully define regional boundaries (Westoby 1993; Angermeier and Winston 1998; Caley and Schulter 1998; Huston 1999). An ideal "region" is environmentally homogeneous, equally accessible to all species in the region, and has ecologically relevant boundaries (Morton 1993; Westoby 1993; Angermeier and Winston 1998). To investigate controls on local diversity maintenance I define gamma diversity, often equated with regional diversity, as the species richness of a vent field. The theoretical framework of "local versus regional diversity" is most often applied at the scale of a biogeographic province (i.e. a region equals one biogeographic area; e.g. Ricklefs 1987; Caley and Schluter 1997). However, gamma diversity (sensu Whittaker 1972) is the overall diversity of a group of local (= alpha) diversities of interest (Terborgh and Faaborg 1980; Cornell 1985; Magurran 1988) and does not have to be a region in the classical biogeographic sense. Cleft and CoAxial have nine and two quantitative samples respectively, and a depauperate fauna compared to Axial; I treat these sites as one vent field. Axial, while arguably one large vent field (Chapter 4), is divided into vent field regions (ASHES, CASM, and the South Rift Zone) based on spatial disjunction and past convention.

Species richness estimators

Colwell and Coddington (1994) argue that the magnitude and urgency of assessing global biodiversity requires that we make the most of what we know about species distributions through estimation and extrapolation techniques. Local species richness can be estimated by extrapolation of species accumulation curves, by fitting of parametric distributions of relative abundance, and by using non-parametric techniques based on the distribution of individuals among species or species among samples

(Colwell and Coddington 1994). A full evaluation of non-parametric methods needs to be done with real data sets for a diverse range of organisms and habitats (Colwell and Coddington 1994). Testing their suggested estimators with vent data from the Juan de Fuca Ridge is one method of evaluation.

Goals

I ask four questions in this chapter:

1) Are Axial, Cleft, and CoAxial (for a combined total distance of 150 km) distinguishable in terms of species composition, abundance, and community structure?
2) What are the patterns of species abundance, distribution, and diversity for the Axial, Cleft, and CoAxial region?
3) Are processes other than local biotic and environmental interactions also important in regulating local vent species richness?
4) Are the nonparametric species estimation methods of Colwell and Coddington (1994) good estimators of species richness for Juan de Fuca vents?

Methods

Geological setting

Axial Seamount

Axial Seamount (Figure 1.1) is described in Chapter 4, Methods. The summit of Axial, at 1500 m, has a well-defined, three-sided caldera with active hydrothermal systems. Axial Seamount's three hydrothermal vent fields (ASHES, CASM, and the South Rift Zone) are described in Chapter 4 (Figure 4.1).

Cleft segment

Cleft is the 80 km-long southernmost discrete segment of the Juan de Fuca Ridge (Figure 1.1; Figure 2.1.2). Average depth in this area is 2200 m and venting spans about 11 km (Figure 2.2.1). The recent volcanic and venting history of north Cleft is discussed in detail in Chapter 2.

CoAxial segment

CoAxial segment overlaps the northern rift of Axial Seamount to the south at 46° 05'N, 129° 53'W and terminates at Cobb segment to the north at 46° 42'N, 129° 30'W (Figure 1.1) (Embley et al. 1995). An eruption occurred on CoAxial in June of 1993 beginning near 46° 15'N, 129° 51'W and ending near 46° 32'N, 129° 35'W (Embley et al. 1995). Event plumes in July 1993 probably originated during the seismically active period (Baker et al. 1995). Seafloor observations in 1993 and 1994 revealed fresh lava on CoAxial in a band about 2.5 km long, oriented in a northeast 020° direction and up to 300 m wide. The CoAxial eruption was probably caused by initial magma injection and subsequent lateral dike injection analogous to the Cleft episode (Embley et al. 1995; RIDGE 1999).

Diffuse hydrothermal venting on eruptive lava on CoAxial was nearly continuous along the axis of the flow and ended at the flow's northern termination (Embley et al. 1995); it ceased in 1994. In 1994 and 1995, venting continued at least 4 km south of the new lava along fractures within a 20-40 m-wide graben that cut through older lavas (Embley et al. 1995). By 1996, this venting had ceased (Chapter 3).

Sample collection

Samples from Axial and north Cleft were taken as described in Chapters 2 and 4. CoAxial samples were taken by submersible in 1995 and 1996. All samples are from low temperature (< 60 °C) vents. Samples are from basalt and sulphide substrata (Table 5.2).

Sample processing

Samples were fixed in 7% seawater formalin at sea for transport to the lab for processing. All samples were sieved over a 63 µm mesh and sorted as described in Chapters 2, 3, and 4. Both CoAxial samples were sorted to 63 µm. Statistical comparisons of Axial, Cleft, and CoAxial samples are limited to macrofauna except for species richness descriptors. Discussion of dispersion and percent-average relative abundance for Axial, Cleft, and CoAxial is limited to macrofauna.

Fifty-one samples were selected for examination, 31 from Axial, 18 from Cleft and two from CoAxial (Table 5.2). All samples are used for presence/absence information for cluster analyses, species richness, rarefaction, and species richness estimators. After culling as described in Tsurumi and Tunnicliffe (2000), 34 samples remain in the data set for statistical analyses: 25, seven, and two samples from Axial, Cleft, and CoAxial respectively (Table 5.2).

Analyses

The density data (number of individuals•cm^{-2} of tubeworm area) are not normally or lognormally distributed for any species for all three segments. No transformations were able to normalize the data successfully. Analyses were performed as described in Chapter 2, 3, and 4.

Table 5.2: Axial, Cleft, and CoAxial samples. Totals do not include the tubeworm *Ridgeia piscesae*; SRZ = South Rift Zone; * = samples that are culled from quantitative analysis. Macrofauna are all species caught on a 1 mm sieve.

Sample designation	Vent field	Vent	Year	Substratum	**All fauna**		**Macrofauna**		Macrofaunal density (individuals•cm^{-2})
					Number of individuals	Number of species	Number of individuals	Number of species	
Axial									
A	ASHES	Goblin	1986	Basalt	11252	13	9766	10	2.179
B	ASHES	Bouquet	1986	Basalt	7821	26	7813	23	0.923
C	ASHES	Demon	1986	Basalt	28049	22	28046	21	2.599
D	ASHES	Sweet	1986	Basalt	1831	11	1830	10	1.554
E	ASHES	Limbo	1986	Basalt	2578	17	2578	17	0.390
F	ASHES	Miserable	1986	Basalt	408	19	401	14	0.614
G	ASHES	Not-so-miserable	1986	Basalt	18963	27	18937	21	1.208
H	ASHES	Bouquet	1988	Basalt	5283	21	5279	19	1.059
I	ASHES	ISCA	1997	Basalt	4759	19	1689	17	0.530
J*	ASHES	Hatfield	1997	Basalt	47128	41	37121	28	not available
K	ASHES	Bouquet2	1998	Basalt	33706	24	33643	19	1.938
L	ASHES	Hairdo	1998	Basalt	15385	33	143741	24	0.473
M	ASHES	Gollum	1998	Basalt	6262	19	6208	12	2.316
N	ASHES	Marker i	1998	Basalt	8945	24	8681	15	2.136
O	ASHES	Medusa	1998	Basalt	570	8	508	6	2.082
P	CASM	Post-Taylor's	1986	Basalt	7018	17	7018	17	0.795
Q*	CASM	Lamphere	1986	Sulphide	472+?	12	301+?	7	not available
R*	CASM	Lamphere	1986	Sulphide	508	7	508	7	not available
S	CASM	Lamphere	1988	Sulphide	3431	21	3280	18	1.053

Sample designation	Vent field	Vent	Year	Substratum	All fauna		Macrofauna		Macrofaunal density (individuals•cm^{-2})
					Number of individuals	Number of species	Number of individuals	Number of species	
T	CASM	Bob	1998	Basalt	1771	16	1655	11	1.382
U	CASM	T & S	1998	Sulphide	3378	16	767	9	0.113
V	CASM	Base of T & S	1999	Basalt	2995	16	2736	12	1.527
W*	SRZ	Vent #1	1986	Basalt	825+?	15	813+?	11	not available
X*	SRZ	Sonne	1997	Basalt	433	16	411	11	not available
Y*	SRZ	10 m SE of Marker 113	1998	Basalt	159	10	147	8	0.039
Z	SRZ	Near Marker 113	1998	Basalt	7139	29	7026	20	0.641
AA	SRZ	Flat Top	1998	Basalt	2098	13	2095	10	2.571
BB	SRZ	Oldworms	1998	Basalt	4420	25	3841	16	1.071
CC	SRZ	LargeTW	1998	Basalt	2551	21	2441	13	0.375
DD	SRZ	Old Flow	1998	Basalt	1766	10	1766	10	1.454
EE	SRZ	Crevice	1999	Basalt	509	23	349	14	0.036
Cleft									
FF*	A2075	Crack	1988	Basalt	270	6	255	4	5.000
GG*	A2077	Between Marker 5 and 4	1988	Basalt	671	14	663	10	1.542
HH*	A2079	Crack	1988	Basalt	805	10	798	6	0.062
II*	A2080	Tripod/Hidden	1988	Basalt	6044	8	6044	8	1.492
JJ*	A2082	Cavern	1988	Basalt	2046	10	1996	6	0.117
KK*	A2092	Tripod/Hidden	1988	Basalt	3008	13	2890	8	0.719
LL*	A2094	Cavern	1988	Basalt	3702	5	3696	4	0.913
MM	A2259a	Base of	1990	Sulphide	64722	21	64687	17	2.821

Sample designation	Vent field	Vent	Year	Substratum	**All fauna**		**Macrofauna**		Macrofaunal density (individuals•cm^{-2})
					Number of individuals	Number of species	Number of individuals	Number of species	
NN*	A2259b	Monolith Table	1990	Sulphide	5732	13	4921	9	0.398
OO	A2259c	Spout on Monolith	1990	Sulphide	424	11	264	7	0.066
PP	A2264	Marker 22	1990	Basalt	5240	32	4999	21	0.221
QQ*	A2265	Monolith	1990	Sulphide	1455	12	1398	8	0.471
RR	A2267	Marker M	1990	Basalt	353	15	315	10	0.039
SS*	A2429	Fountain	1991	Sulphide	148	7	114	6	0.012
TT	A2444	Marker 46	1991	Basalt	309	7	286	4	0.132
UU*	R202	Monolith	1992	Sulphide	142	6	141	5	0.097
VV	R232	Blue Hole	1993	Basalt	1312	18	1304	14	3.344
WW	A2781	Aquarius	1994	Sulphide	15818	27	10940	15	0.497
CoAxial									
XX	CoAxial	HDV	1995	Basalt	1856	10	1850	8	0.394
YY	CoAxial	HDV	1996	Basalt	3586	25	2448	15	0.025

Local versus regional diversity analyses in this chapter calculate alpha, beta, and gamma diversity as per Harrison (1997; 1999). Alpha diversity is calculated as the average species density per site (vent) (Harrison 1997) and as the average number of species per site (Kelt et al. 1996) in a given vent field. Gamma diversity is the total number of species for each vent field. Beta diversity calculations are for two types of habitat (patchy and continuous) and two spatial scales (total and local). North Cleft and the South Rift Zone (SRZ) vent fields are considered "patchy" and ASHES is considered "continuous". North Cleft and the SRZ have vents that are spatially separated (up to about 11 km) within the vent field. ASHES is a vent field that has vents contained within an approximately 60 m diametre area. Beta diversity averaged over all sites and is calculated in two ways: a) Whittaker's beta, which is gamma divided by average alpha diversity (Harrison 1997); and b) complementarity (Colwell and Coddington 1994). Whittaker's beta is calculated as: a) total beta diversity (β_T) where the total number of species in both patchy sites is divided by the number of species at each vent; and b) local beta diversity (β_L), the number of species in each habitat divided by the number of species at each vent. Complementarity is calculated at total (complementarity of a site with all other sites in its habitat type) and local (complementarity with all other sites in its segment) levels (Harrison 1997). Only macrofauna are used for alpha, beta, and gamma diversity calculations. Patchy versus continuous habitats are evaluated for diversity differences in order to distinguish the role of spatial isolation from that of environmental gradients.

If variation in regional processes is more important than local processes, the expected pattern is that the number of species in each local area will be correlated with the number of species in the entire region (Huston 1999). One way to test if local species richness is some predictable fraction of regional richness is to test for saturation. Terborgh and Faaborg (1980) demonstrate how to test for saturation. If number of species in a region is correlated with local conditions (e.g. habitat, biotic interactions) and is uncorrelated with regional species richness, local processes are thought to be regulating local species diversity (Huston 1999). In such a case, the curve of local diversity versus regional diversity will reach a plateau independent of regional species richness (Figure 5.1). The method suggested by Terborgh and Faaborg (1980) has been used by many other investigators interested in local and regional controls on maintenance of diversity (e.g. Ricklefs 1987; Cornell and Lawton 1992; Caley and Schluter 1997; Griffiths 1997). Tests of saturation can be done at various scales (Cornell 1985; Karlson and Cornell 1998). I follow Terborgh and Faaborg (1980)'s example and present local richness as alpha, or average number of species per vent. Gamma diversity is equal to the species pool available to individual vents and is the total number of species per vent field.

Colwell and Coddington (1994) discuss several methods for estimating local species richness and examine the effectiveness of these methods using an example data set. I apply the methods described in Colwell and Coddington (1994) using EstimateS 5.0 (Colwell 1997). Random subsamples of the data sets from Axial (25) and Cleft (nine) were examined at arbitrary levels (five and 15 for Axial; three and six for Cleft) and species richness estimates at these levels were compared to the total number of species observed in the complete data sets. Estimators that were close to the total number of species at both subsample sizes were considered to be good predictors.

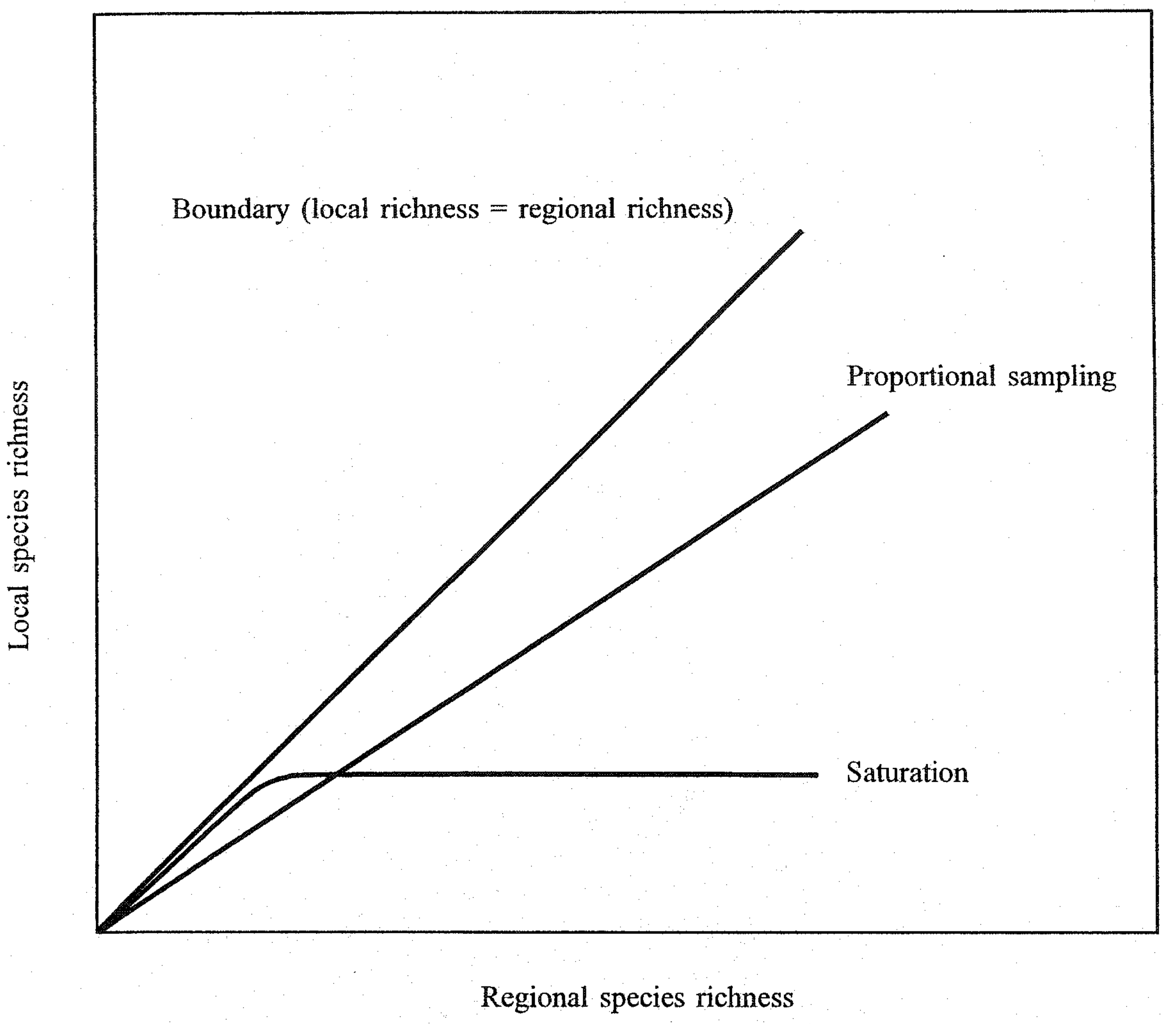


Figure 5.1. Diagram of local versus regional species richness. Theoretical relationships between communities exhibiting proportional sampling and saturation are shown. The line labelled "boundary" represents complete regional pool exhaustion where local richness equals regional richness. This line is the upper boundary on local richness.

Results

First impressions

Visual inspection of tubeworm (*Ridgeia piscesae*) grabs from Axial, Cleft, and CoAxial show samples to be indistinguishable by segment (Figure 5.2). The macrofaunal species lists from Cleft (Chapter 2), CoAxial (Chapter 3), and Axial (Chapter 4) are very similar (Table 5.3). A look at the available meiofauna reinforces this observation. Visual sample similarity may be more determined by vent environment than by spatial location. Senescent samples such as CoAxial 1996 (sample YY; Table 5.2) and Crevice 1999 from Axial (sample EE; Table 5.2), are more similar in appearance than CoAxial 1996 and 1995 (sample XX, Table 5.2). Both CoAxial 1996 and Crevice samples have long, thin tubeworm tubes with little visible tubeworm tissue, little sediment or bacteria, and few macrofauna or juvenile *Ridgeia* attached to the tubeworms (Chapter 3).

Ridgeia piscesae is a species with a high degree of phenotypic plasticity in its tube and body aspect (Southward et al. 1995). *R. piscesae* was first described as two species (Jones 1985) and believed to be three additional species (de Burgh 1986). However, Southward et al. (1995) determined that there is only one species on the ridge. Tubeworm tube morphotype is probably governed by local differences in vent chemistry (Southward et al. 1995; Urcuyo 2000). A sample of tubeworms will comprise one type of tube morphology, while a grab a few metres away will contain another type (Southward et al. 1995). Although there are many tubeworm morphotypes, two general types of tubeworm can be distinguished: a) loosely clumped forward-growing tubeworms with fat (high width-to-length ratio) white tubes, and prominent “fluffy”

Figure 5.2. Representative low temperature tubeworm bushes on basalt. a: Axial (from ASHES vent field). b: Cleft. c: CoAxial (from Huge Diffuse Vent). Low temperature High Diversity Knot-type tubeworm assemblages are similar in appearance on all three segments.

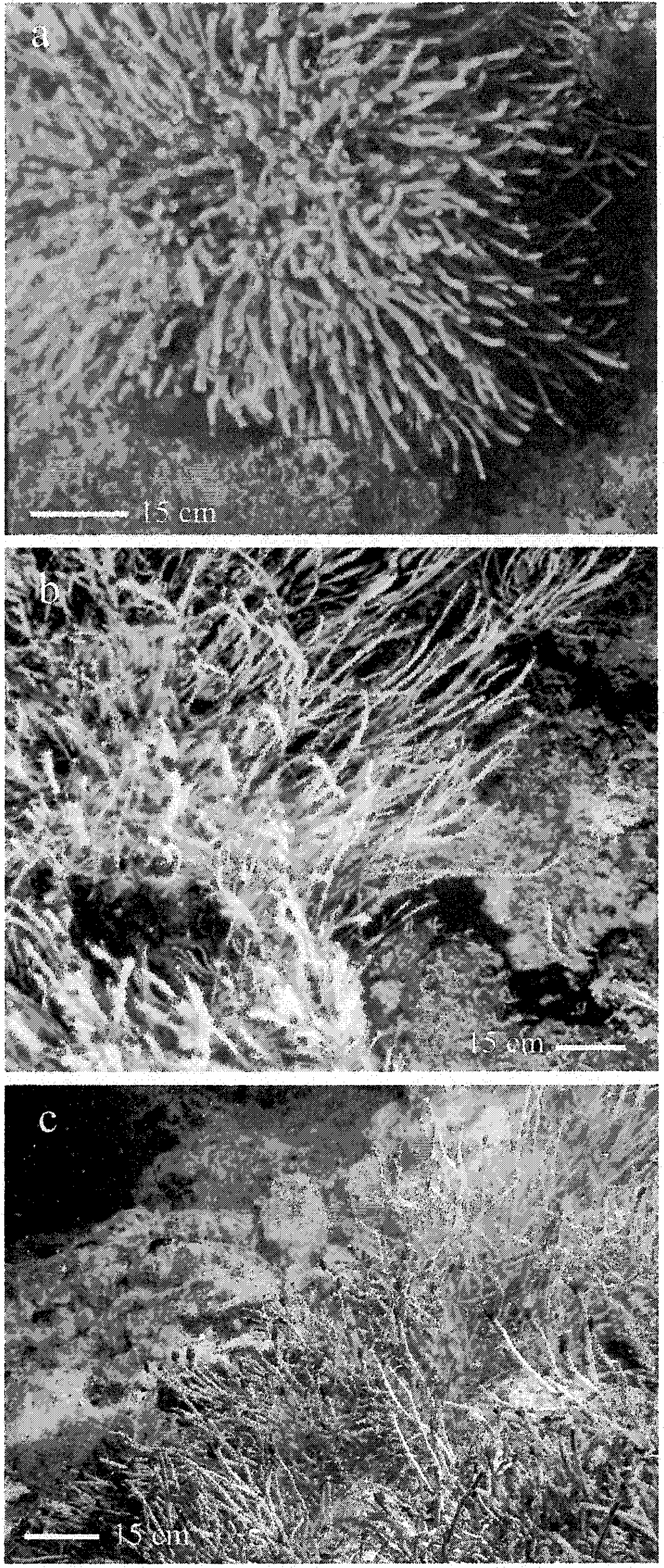

a
15 cm
b
15 cm
c
15 cm

Table 5.3: Species percent-average relative abundance for three southern segments of the Juan de Fuca Ridge, Axial, Cleft, and CoAxial. Percent-average relative abundance is for macrofauna and does not include culled samples (see Table 1). NP = species not present in the data set. NQ = species present in culled samples or meiofauna and not quantifiable.

Species	Three-segment region	Axial	Cleft	CoAxial
L. fucensis	41.09	45.03	35.56	24.41
P. pandorae	23.36	24.50	18.25	47.71
A. galapagensis	10.22	7.347	18.07	0.946
D. globulus	8.546	4.361	18.66	19.00
P. palmiformis	7.581	9.736	1.857	0.378
P. variabilis	1.423	1.893	0.226	0.061
P. sulfincola	1.339	0.094	4.352	NP
P. wolfi	1.104	1.016	1.224	NP
P. verenae	0.917	1.245	0.004	NP
P. musaica	0.907	1.233	NP	NP
Prionospio n. sp. 1	0.835	0.951	0.033	2.145
Ophryotrocha globopalpata	0.705	0.949	0.008	0.082
H. vestimentifera	0.583	0.635	0.198	1.144
L. piscesae	0.376	0.301	0.582	0.108
Branchinotogluma sp.	0.329	0.187	0.321	0.892
N. piscesae	0.137	0.186	NP	NP
A. verenae	0.096	0.067	0.154	0.225
L. kincaidi	0.082	0.022	0.062	0.837
T. valens	0.077	0.023	NQ	1.805
N. venticola	0.063	0.013	0.201	NP
H. juani	0.046	0.023	0.096	0.020
E. climax	0.041	0.041	0.047	0.041
O. tunnicliffeae	0.032	0.027	0.046	NP
P. dela	0.029	0.040	NQ	NP
C. curvus	0.023	0.019	0.030	NP
T. euripes	0.015	0.020	NQ	NP
H. glabra	0.009	0.012	0.0004	0.135
Cnidaria	0.008	0.006	NQ	NP
Prionospio n. sp. 2	0.004	0.006	NP	NP
O. hobsonae	0.004	0.006	NP	NP
Amphipoda spp. unknown	0.003	0.001	0.028	NP
Unknown orbiniid	0.003	0.005	NP	NP
Harmothe sp.	0.003	0.0002	NP	0.042
Acoelomates?	0.002	0.001	NP	0.020
Idasola washingtonia?	0.002	0.003	NP	NP

Species	Three-segment region	Axial	Cleft	CoAxial
A. axialensis	0.001	0.002	NP	NP
Lacunoides n. sp.	0.001	0.001	NP	NP
C. pacifica	0.0004	0.001	NP	NP
Hydrozoa spp. unknown	0.0003	0.0004	NP	NP
Amphipoda sp. nr. *Valettiopsis*	NQ	NP	NQ	NP
Copidognathus papillatus	NQ	NQ	NQ	NP
Levensteiniella intermedia	NQ	NQ	NP	NP
Provanna laevis	NQ	NQ	NP	NP
Aphotopontius forcipatus	NQ	NQ	NQ	NQ
Barathricola rimensis	NQ	NQ	NP	NQ
Benthoxynus spiculifer	NQ	NQ	NQ	NP
Misophriopsis longicauda	NQ	NQ	NQ	NQ
Stygiopontius quadrispinosus	NQ	NQ	NQ	NQ
Copepoda type 1	NQ	NQ	NQ	NQ
Copepoda type 2	NQ	NQ	NP	NQ
Copepoda type 9	NQ	NQ	NP	NP
Copepoda type 10	NQ	NQ	NP	NP
Copepoda type 11	NQ	NQ	NP	NQ
Copepoda type 13	NQ	NQ	NP	NP
Copepoda type A3244	NQ	NQ	NP	NP
Calanoida	NQ	NQ	NQ	NQ
Harpacticoida	NQ	NQ	NP	NP
Nematoda	NQ	NQ	NQ	NP
Podocopida	NQ	NQ	NQ	NP

branchial plumes (Figure 5.3a); and b) interwoven forward-and-backward-growing tubeworms (either at the base or throughout the bush) with thin (low width-to-length ratio) translucent and/or golden tubes, and branchial plumes that are not "fluffy" (Figure 5.3b). The latter *R. piscesae* morphotype is also called the "long-skinny" morphotype (Urcuyo 2000). The loosely-clumped, forward-growing tubeworm type is sometimes called "fat-type" because of the thick, wide appearance of its tubes compared to other morphotypes. I believe these two tubeworm morphotypes represent two different types of communities at Juan de Fuca vents. The fat-type community is low diversity with few juvenile tubeworms (Table 5.4) in areas of high fluid-flow (and perhaps sulphide), either on chimneys or at new vents. The interwoven (knot-type) community is a high diversity aggregation with many juvenile tubeworms (Table 5.4), typical of most low temperature diffuse tubeworm bushes. The knot-type community is in presumably lower sulphide environments away from high-temperature orifices on chimneys, and at well-established low temperature venting on basalt (Urcuyo 2000; pers. obs.). As tubeworm tube morphotype can be determined by flow regime, so too may tubeworm community type.

Questions 1 and 2: are Axial, Cleft, and CoAxial vents distinguishable from each other and what are the patterns of community organisation?

Sample analysis

Cluster analysis using macrofaunal presence/absence, percent relative abundance, and density (not shown) does not divide samples by segments (Figure 5.4). Samples do not cluster by year or substrata within segments or among segments. Cleft and Axial samples tend to fall out in higher (greater distance) level clusters with samples from the

Figure 5.3. Tubeworm community types. a: Low Diversity Fat-type community. Prominent “fluffy” red branchial plumes of *R. piscesae* are at the bottom of the photograph on a sulphide high temperature chimney. Small polychaetes between the tubeworms and the high temperature orifice are the sulphide worm, *Paralvinella sulfincola*. b: High Diversity Knot-type community. Sample from ASHES vent field, Marker i. Tubeworms are intertwined and inseparable. Some associated fauna can be seen in the bush (red objects) and in the sorting dish to the left of the sample. The ruler in the picture is 15 cm.

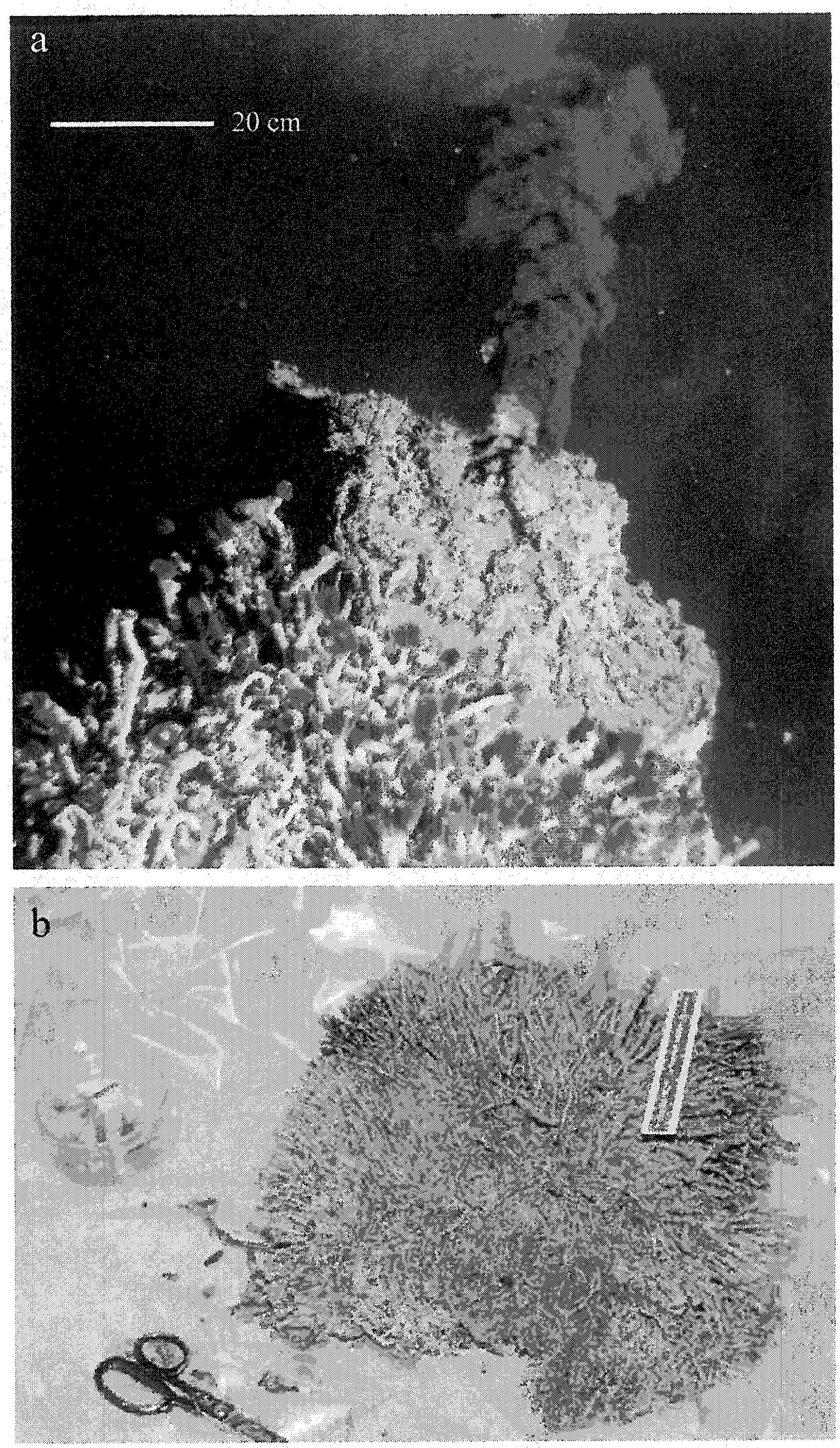
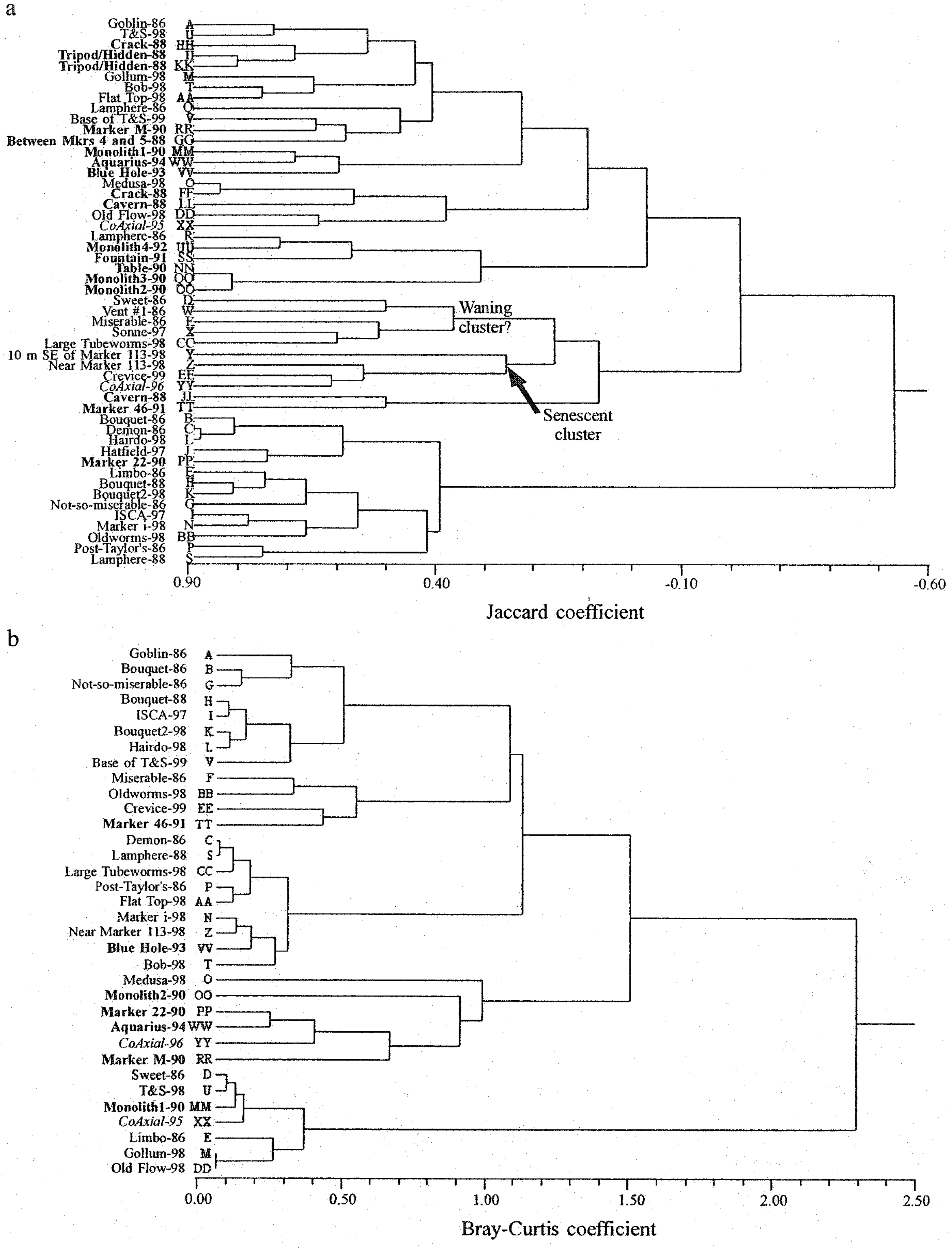

a
20 cm
b

Table 5.4: A comparison of *Ridgeia piscesae* communities. LDF is Low Diversity Fat-type community; HDK is High Diversity Knot-type community.

	No. of species	No. of species	Density (indivs. per cm^2)	Juveniles *Ridgeia* on tubes?	Chemical environment	Substratum
	All fauna	**Macrofauna**				
LDF						
Medusa (R472; O)	8	6	2.082	few	high-flow (new vent?)	basalt
T & S (R480; U)	16	9	0.113	few	high-flow	sulphide (chimney top)
Fountain (A2429; Cleft SS)	7	6	0.011	few	high-flow	sulphide (chimney top)
Average	10.33	7	0.735			
HDK						
Bouquet86 (P1728; B)	26	23	0.923	many	low-flow	basalt
Hatfield (R406; J)	41	28	?	many	low-flow	basalt
Bouquet2 (R466; K)	24	19	1.938	many	low-flow	basalt
Hairdo (R466; L)	33	24	0.473	many	low-flow	basalt
Average	31	23.5	1.111	many		

Figure 5.4. Cluster diagrams for vents on Axial, Cleft, and CoAxial. Only macrofauna are used in the analysis. The dash and number after each vent site indicates the year of sample collection. Plain, bold, and italic typefaces indicate Axial, Cleft, and CoAxial vents respectively. Letters are site designations (Table 5.1). a: dendrogram of presence/absence data using the Jaccard coefficient (all 51 samples are used). Purported waning and senescent clusters are indicated. b: dendrogram of percent relative abundance data using the Bray-Curtis coefficient (number of samples used is 34; culled samples are not included).


a
Goblin-86 A
T&S-98 U
Crack-88 HH
Tripod/Hidden-88 II
Tripod/Hidden-88 KK
Gollum-98 M
Bob-98 T
Flat Top-98 AA
Lamphere-86 Q
Base of T&S-99 V
Marker M-90 RR
Between Mkrs 4 and 5-88 GG
Monolith1-90 MM
Aquarius-94 WW
Blue Hole-93 VV
Medusa-98 O
Crack-88 FF
Cavern-88 LL
Old Flow-98 DD
CoAxial-95 XX
Lamphere-86 R
Monolith4-92 UU
Fountain-91 SS
Table-90 NN
Monolith3-90 QQ
Monolith2-90 OO
Sweet-86 D
Vent #1-86 W
Miserable-86 F
Sonne-97 X
Large Tubeworms-98 CC
10 m SE of Marker 113-98 Y
Near Marker 113-98 Z
Crevice-99 EE
CoAxial-96 YY
Cavern-88 JJ
Marker 46-91 TT
Bouquet-86 B
Demon-86 C
Hairdo-98 L
Hatfield-97 J
Marker 22-90 PP
Limbo-86 E
Bouquet-88 H
Bouquet2-98 K
Not-so-miserable-86 G
ISCA-97 I
Marker i-98 N
Oldworms-98 BB
Post-Taylor's-86 P
Lamphere-88 S
Waning cluster?
Senescent cluster
0.90
0.40
-0.10
-0.60
Jaccard coefficient
b
Goblin-86 A
Bouquet-86 B
Not-so-miserable-86 G
Bouquet-88 H
ISCA-97 I
Bouquet2-98 K
Hairdo-98 L
Base of T&S-99 V
Miserable-86 F
Oldworms-98 BB
Crevice-99 EE
Marker 46-91 TT
Demon-86 C
Lamphere-88 S
Large Tubeworms-98 CC
Post-Taylor's-86 P
Flat Top-98 AA
Marker i-98 N
Near Marker 113-98 Z
Blue Hole-93 VV
Bob-98 T
Medusa-98 O
Monolith2-90 OO
Marker 22-90 PP
Aquarius-94 WW
CoAxial-96 YY
Marker M-90 RR
Sweet-86 D
T&S-98 U
Monolith1-90 MM
CoAxial-95 XX
Limbo-86 E
Gollum-98 M
Old Flow-98 DD
0.00
0.50
1.00
1.50
2.00
2.50
Bray-Curtis coefficient

same segment, but there is no clear pattern as Cleft samples are found with Axial samples and vice versa. However, correspondence analyses for presence/absence indicate intersecting groupings of the Axial and Cleft samples (Figures 5.5a and 5.6b). The two Axial samples that are in the Cleft grouping are sulphide samples that may be falling out with Cleft because the Cleft data set has a higher ratio of sulphide to basalt samples than the Axial data set.

The two CoAxial samples are never found clustered. The presence/absence data clusters CoAxial 1996 with Crevice 1999 (both senescent samples) and two other senescent samples. This cluster is supported by correspondence analysis (Figure 5.5) and by cluster and correspondence analysis based on a data set without the dominant species (Figure 5.6). Cluster analysis with meiofauna does not cluster samples by segment, year, or substratum although the dendrogram differs from trees produced using only macrofauna (Figure 5.7). Cluster analyses without dominant species uses the data set with the six most abundant species deleted (*Lepetodrilus fucensis*, *Depressigyra globulus*, *Amphisamytha galapagensis*, *Paralvinella pandorae*, *P. sulfincola*, and *P. palmiformis*). Cluster analysis without dominants improves the cophenetic value of the percent relative abundance and the density data trees, but improves this value for the presence/absence data. Agreement from correspondence analysis is minimal. Although some first order clusters remain the same as for the entire data set (Figure 5.5), most of the samples move position in the dendrogram. However, there is no pattern by segment, year, or substratum using data without numerically dominant species.

Although there is no clear division by year, substratum, or segment, there is an argument to be made for some presence/absence clustering based on successional state.

Figure 5.5. Correspondence analyses of Axial, Cleft, and CoAxial site associations. a: presence/absence data with 51 samples. Senescent cluster is indicated. b: percent relative abundance data with 34 samples. Letters are site designations (Table 5.1). Samples Y, Z, EE, and YY (circled) are the senescent samples.

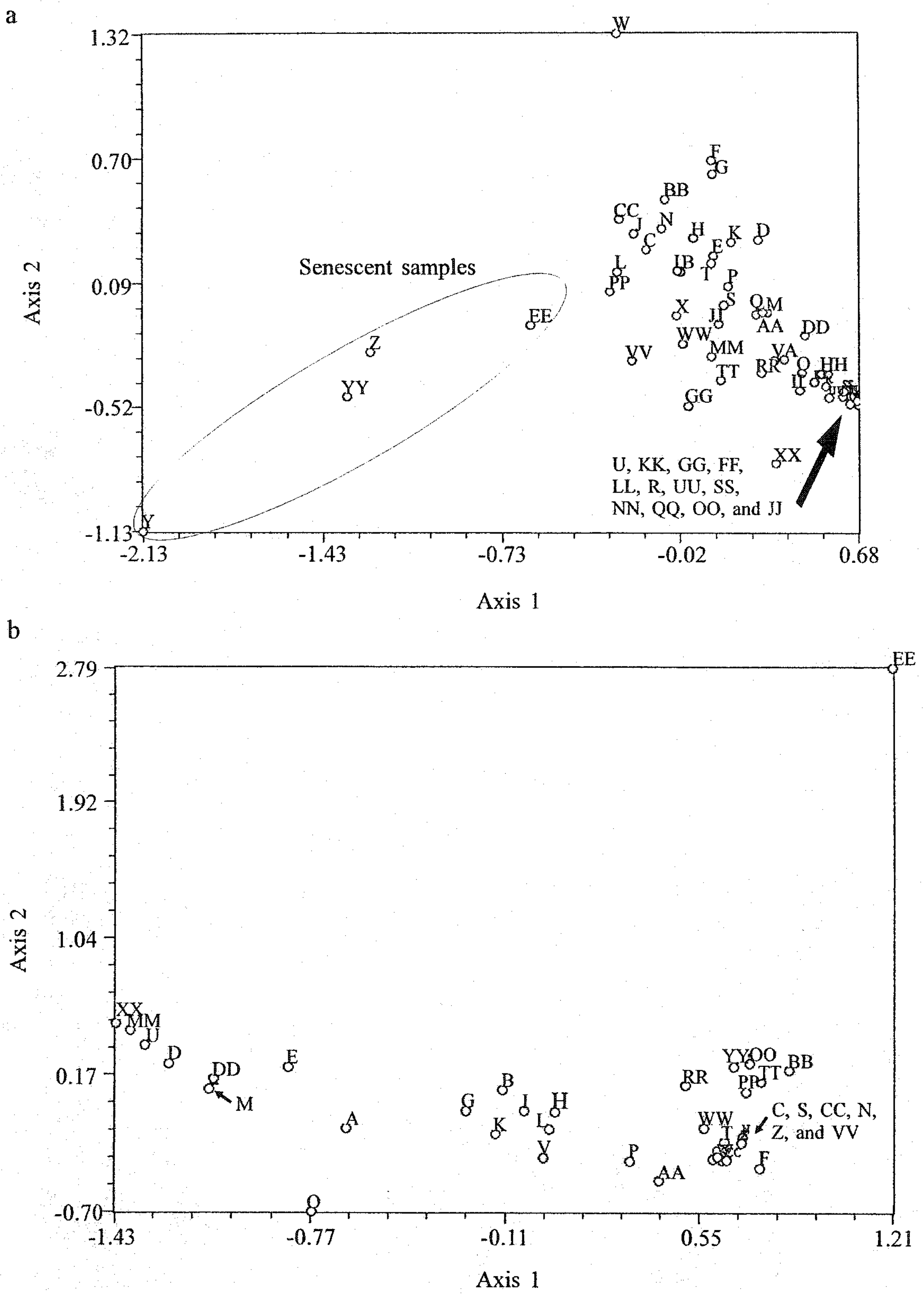
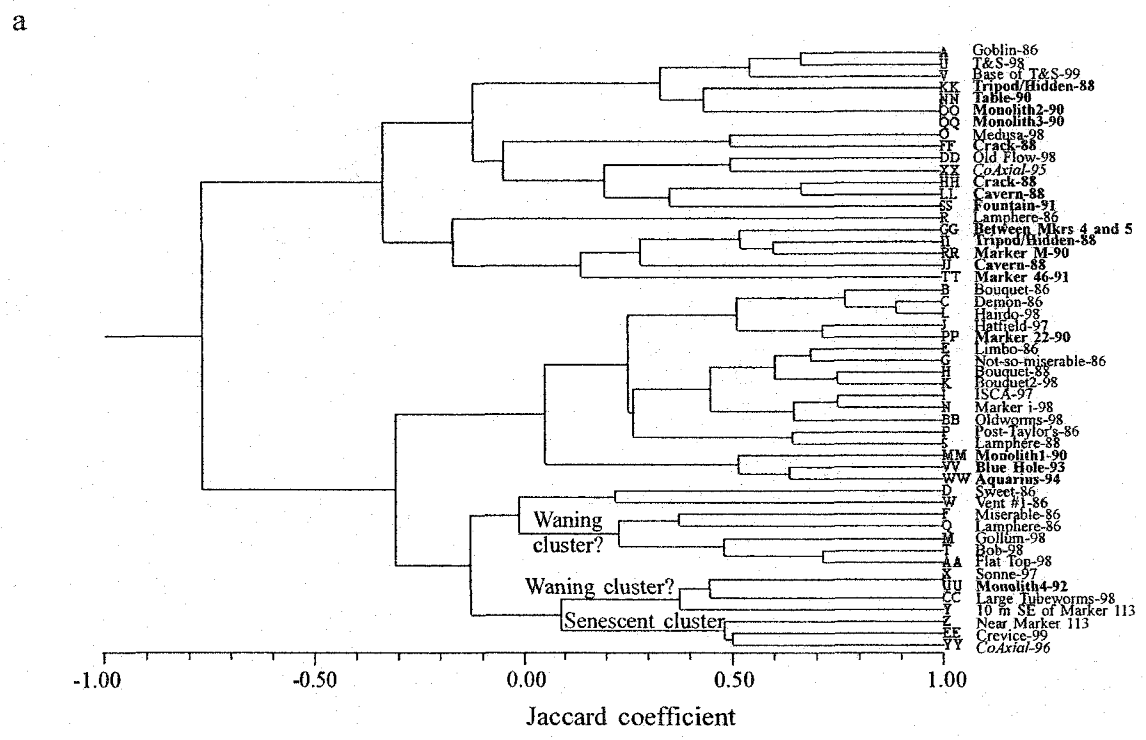

a
Axis 2
Axis 1
1.32
0.70
0.09
-0.52
-1.13
-2.13
-1.43
-0.73
-0.02
0.68
Senescent samples
W
F
G
BB
CC
J
N
C
H
K
D
E
L
IB
T
PP
P
S
QM
X
JJ
AA
DD
FE
Z
WW
MM
VV
VA
O
HH
RR
TT
II
YY
GG
XX
Y
U, KK, GG, FF,
LL, R, UU, SS,
NN, QQ, OO, and JJ
b
Axis 2
Axis 1
2.79
1.92
1.04
0.17
-0.70
-1.43
-0.77
-0.11
0.55
1.21
EE
XX
MM
U
D
DD
M
E
A
Q
B
G
J
H
K
L
Y
P
AA
RR
YYOO
BB
TT
PP
WW
T
F
C, S, CC, N,
Z, and VV

Figure 5.6. Cluster and correspondence analysis diagrams for Axial, Cleft, and CoAxial site associations without dominant species. Excluded species are *Lepetodrilus fucensis*, *Paralvinella pandorae*, *P. palmiformis*, *P. sulfincola*, *A. galapagensis*, and *D. globulus*. a: dendrogram of presence/absence data using the Jaccard coefficient. Plain, bold, and italic typefaces indicate Axial, Cleft, and CoAxial vents respectively. Purported waning and senescent clusters are indicated. b: correspondence analysis for a. Senescent cluster is indicated. Letters are site designations (Table 5.1).


a
A Goblin-86
U T&S-98
V Base of T&S-99
KK **Tripod/Hidden-88**
NN **Table-90**
OO **Monolith2-90**
QQ **Monolith3-90**
O Medusa-98
FF **Crack-88**
DD Old Flow-98
XX *CoAxial-95*
HH **Crack-88**
LL **Cavern-88**
SS **Fountain-91**
R Lamphere-86
GG **Between Mkrs 4 and 5**
II **Tripod/Hidden-88**
RR **Marker M-90**
JJ **Cavern-88**
TT **Marker 46-91**
B Bouquet-86
C Demon-86
L Hairdo-98
J Hatfield-97
PP **Marker 22-90**
E Limbo-86
G Not-so-miserable-86
H Bouquet-88
K Bouquet2-98
I ISCA-97
N Marker i-98
BB Oldworms-98
P Post-Taylor's-86
S Lamphere-88
MM **Monolith1-90**
VV **Blue Hole-93**
WW **Aquarius-94**
D Sweet-86
W Vent #1-86
F Miserable-86
Q Lamphere-86
M Gollum-98
T Bob-98
AA Flat Top-98
X Sonne-97
UU **Monolith4-92**
CC Large Tubeworms-98
Y 10 m SE of Marker 113
Z Near Marker 113
EE Crevice-99
YY *CoAxial-96*
Waning cluster?
Waning cluster?
Senescent cluster
-1.00
-0.50
0.00
0.50
1.00
Jaccard coefficient

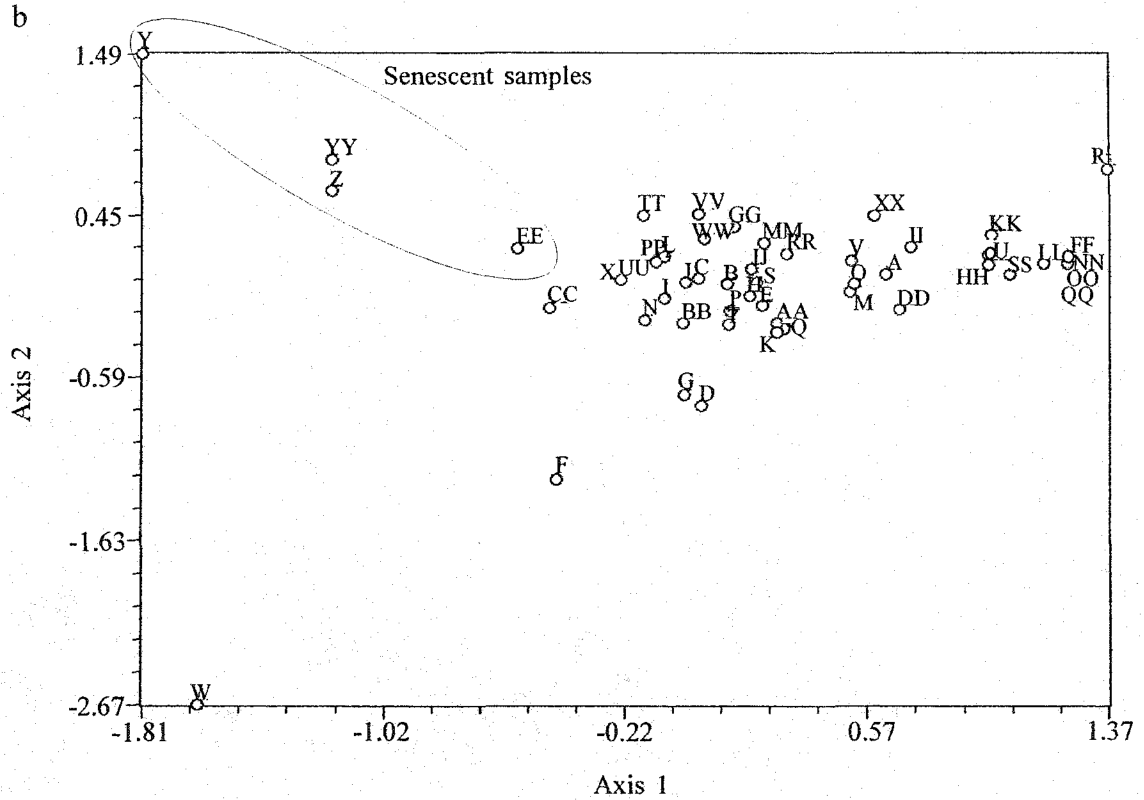

b
Senescent samples
1.49
0.45
-0.59
-1.63
-2.67
Axis 2
-1.81
-1.02
-0.22
0.57
1.37
Axis 1
Y
YY
Z
EE
CC
F
W
TT
VV
GG
WW
MM
RR
PP
XUU
IC
B
JJ
S
HE
N
J
BB
P
T
AA
OQ
K
G
D
XX
II
V
O
A
M
DD
KK
U
HH
SS
LL
FF
NN
OO
QQ
R

Figure 5.7. Cluster diagram for Axial, Cleft, and CoAxial site associations with all fauna (meio- and macrofauna). Presence/absence data with Jaccard coefficient are used. Plain, bold, and italic typefaces indicate Axial, Cleft, and CoAxial vents respectively. Letters are site designations (Table 5.1). Senescent cluster is indicated.

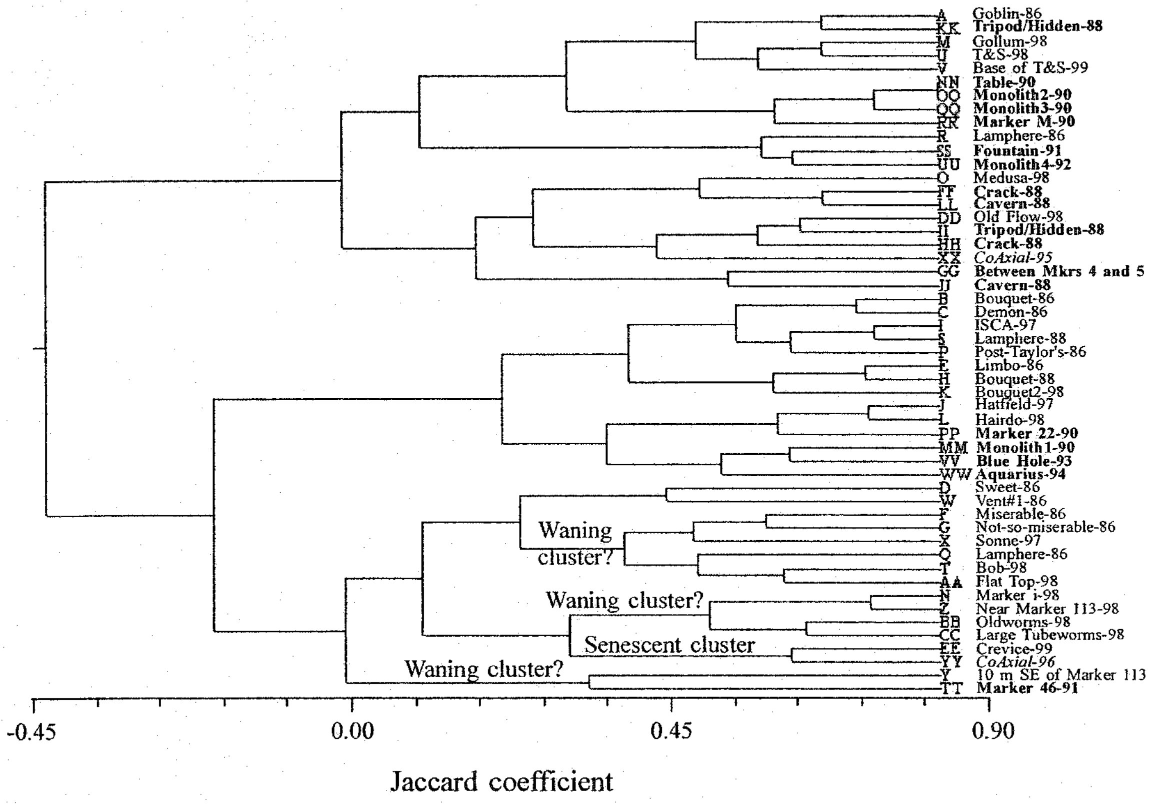

A Goblin-86
KK **Tripod/Hidden-88**
M Gollum-98
U T&S-98
V Base of T&S-99
NN **Table-90**
OO **Monolith2-90**
QQ **Monolith3-90**
RR **Marker M-90**
R Lamphere-86
SS **Fountain-91**
UU **Monolith4-92**
O Medusa-98
FF **Crack-88**
LL **Cavern-88**
DD Old Flow-98
II **Tripod/Hidden-88**
HH **Crack-88**
XX *CoAxial-95*
GG **Between Mkrs 4 and 5**
JJ **Cavern-88**
B Bouquet-86
C Demon-86
I ISCA-97
S Lamphere-88
P Post-Taylor's-86
E Limbo-86
H Bouquet-88
K Bouquet2-98
J Hatfield-97
L Hairdo-98
PP **Marker 22-90**
MM **Monolith1-90**
VV **Blue Hole-93**
WW **Aquarius-94**
D Sweet-86
W Vent#1-86
F Miserable-86
G Not-so-miserable-86
X Sonne-97
Q Lamphere-86
T Bob-98
AA Flat Top-98
N Marker i-98
Z Near Marker 113-98
BB Oldworms-98
CC Large Tubeworms-98
EE Crevice-99
YY *CoAxial-96*
Y 10 m SE of Marker 113
TT **Marker 46-91**
Waning cluster?
Waning cluster?
Senescent cluster
Waning cluster?
-0.45
0.00
0.45
0.90
Jaccard coefficient

Figure 5.4a shows a senescent cluster with the next closest cluster composed of vents that were active but showed signs of waning or transition to a senescent stage when sampled (Large Tubeworms, Sonne, and Miserable). The senescent cluster is supported by the correspondence analysis, but a pre-senescent, "waning" cluster is not well supported (Figure 5.5a). Presence/absence clustering without the dominant species has a senescent grouping supported by correspondence analysis (Figure 5.6). The two closest clusters to the senescent group also include a number of visibly waning vents (Miserable, Bob, Flat Top, Sonne, Large Tubeworms) as well as one senescent vent (10 m SE of Marker 113). Again, this is not well supported by the correspondence analysis. Clustering of all fauna shows a senescent grouping (Crevice and CoAxial 1996) and a possible larger clustering of waning with senescent vents (Figure 5.7).

Friedman tests of differences in sample distributions are significant between Axial and Cleft for density but not for percent-average relative abundance data. Friedman tests are also significant between Cleft and CoAxial for density but not for percent-average relative abundance data. Friedman tests with density and percent-average relative abundance are significant between Axial and CoAxial. However, as CoAxial is represented by only two samples, the usefulness of Friedman tests to distinguish between CoAxial and the other two segments is dubious. North Cleft and Axial share 23 species out of a total of 23 and 39 for Cleft and Axial respectively (Figure 5.8). Complementarity is 0.410, or 41%, which indicates that the samples are fairly similar. Between Axial and CoAxial complementarity is 51.3% with all 19 CoAxial species found at Axial. Cleft and CoAxial are most similar with 38.5% complementarity and 16 shared species (Figure 5.8).

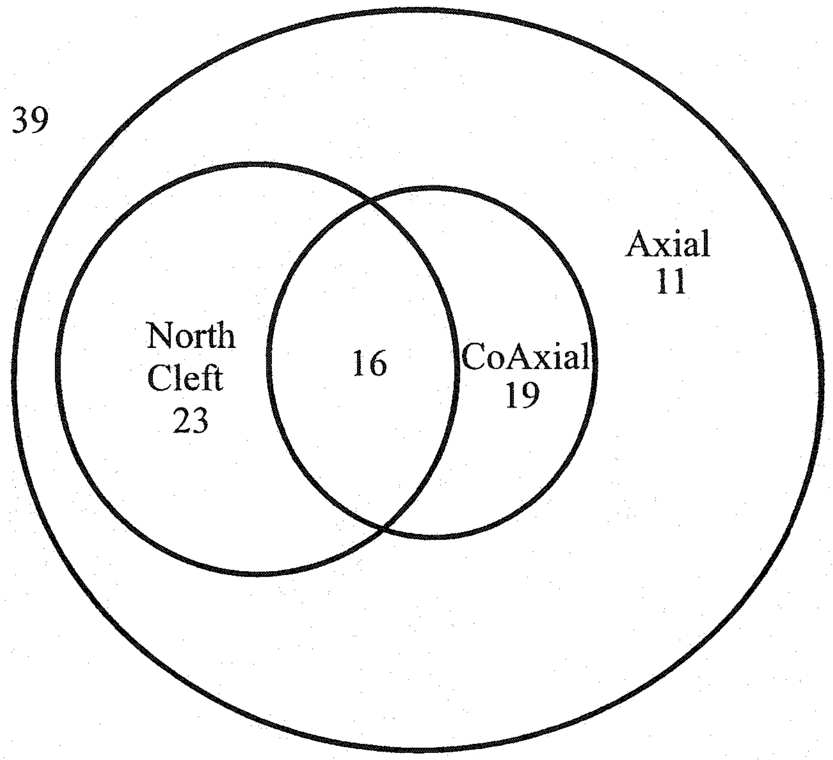


Figure 5.8. Diagram of macrofaunal species overlap between Axial, Cleft, and CoAxial segments. All 23 macrofaunal species from Cleft segment and 19 macrofaunal species from CoAxial segment are contained within Axial's 39 species. North Cleft and CoAxial segments have 16 species in common. Only quantitative samples were used to calculate the number of species for each segment.

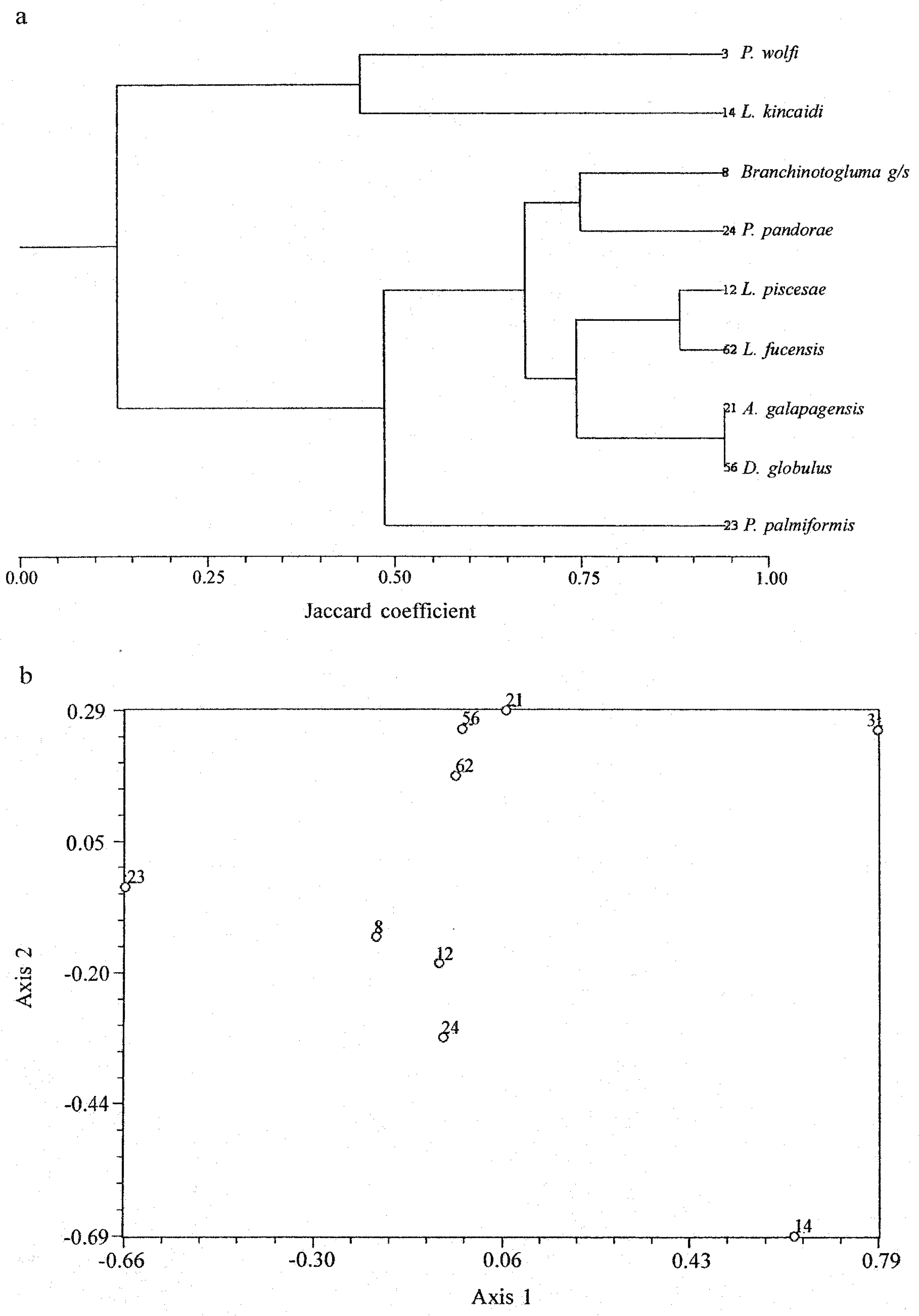
Community structure

Discussion of species associations and species dispersion apply to Axial, Cleft, and all three segments together and descriptions of community structure (rank-abundance, density, and diversity) also include CoAxial.

Pairwise correlations for Cleft macrofauna and Axial macrofauna with density data both show a significant positive association between the alvinellid polychaetes *Paralvinella pandorae* and *P. palmiformis* on both segments. Both segments also have a significant positive association between the gastropods *Lepetodrilus fucensis* and *Depressigyra globulus*. For Cleft, there is a significant negative correlation between *P. sulfincola* and *L. fucensis* and for Axial, a significant positive association between the polynoid polychaetes *Branchinotogluma* sp. and *Lepidonotopodium piscesae*. Pairwise correlations with density data for all three segments together indicate many significant positive associations, three of which reflect segment scale species associations: *P. pandorae* and *P. palmiformis*, *D. globulus* and *L. fucensis*, and *Branchinotogluma* sp. and *L. piscesae*. There is a significant negative correlation between *P. palmiformis* and another polychaete, *Parougia wolfi*.

Cluster and correspondence analyses of presence/absence, percent relative abundance, and density group *Branchinotogluma* sp. and *Lepidonotopodium piscesae* as well as *Paralvinella pandorae* and *P. palmiformis* for Axial (Figure 4.15). The same groupings are not seen in Cleft clusters with presence/absence data (Figure 5.9). However, *Branchinotogluma* sp. and *L. piscesae* are in the same higher order grouping. The Cleft dendrogram also groups *Depressigyra globulus*, *Lepetodrilus fucensis*, and

Figure 5.9. Cluster and correspondence analysis diagrams for Cleft segment species associations. a: dendrogram for presence/absence data. b: correspondence analysis for a. Numbers are species designations (Appendix 1).


a
3 P. wolfi
14 L. kincaidi
8 Branchinotogluma g/s
24 P. pandorae
12 L. piscesae
62 L. fucensis
21 A. galapagensis
56 D. globulus
23 P. palmiformis
0.00
0.25
0.50
0.75
1.00
Jaccard coefficient
b
0.29
0.05
-0.20
-0.44
-0.69
Axis 2
-0.66
-0.30
0.06
0.43
0.79
Axis 1
21
56
3
62
23
8
12
24
14

Amphisamytha galapagensis, an ampharetid polychaete. The Axial presence/absence and density data sets show these three species to be grouped as well. Clustering using all three data sets for all three segments groups the *P. pandorae* and *P. palmiformis* and *Branchinotogluma* sp. and *L. piscesae* associations (Figure 5.10). Species clusters for all three segments using the presence/absence, percent relative abundance, and density data also support the *D. globulus* and *L. fucensis* with *A. galapagensis* association.

Table 5.5 lists macrofaunal species and their dispersion for Axial, Cleft, and all three segments together. There is wide dispersion of the most abundant species on both segments. There is also wide dispersion (frequency of occurrence) for two species at less than 1% abundance: *Lepidonotopodium piscesae* and *Branchinotogluma* sp. Three species with wide distributions for the Axial, Cleft, and CoAxial (ACC) region that are relatively more locally abundant and widely distributed on Axial than on Cleft are: the snail *Provanna variabilis*, and the polychaetes, *Protomystides verenae* and *Hesiospina vestimentifera*. Two more species are more widely dispersed in Axial samples versus Cleft samples: the polynoid polychaete *Opisthotrochopodus tunnicliffeae* and the split limpet *Clypeosectus curvus*. Interestingly, despite their more restricted distributions on Cleft, *O. tunnicliffeae* and *C. curvus* are both approximately twice as abundant on Cleft as on Axial (Table 5.3).

The overall shape of the rank-abundance curves for Axial, CoAxial, and Cleft is similar (Figure 5.11). Five, four, and three species make up more than 90%-average relative abundance for Axial, Cleft, and CoAxial respectively. The same dominant species are present on all three segments although on CoAxial, *Paralvinella pandorae* is most abundant instead of *Lepetodrilus fucensis* which is most abundant on Axial and

Figure 5.10. Cluster diagrams for species on the three segments. Only species found in more than 50% of the samples are used. a: dendrogram of presence/absence data using the Jaccard coefficient. b: dendrogram of percent relative abundance data using the Bray-Curtis coefficient. c: dendrogram of density data using the Bray-Curtis coefficient. Numbers are species designations (Appendix 1).

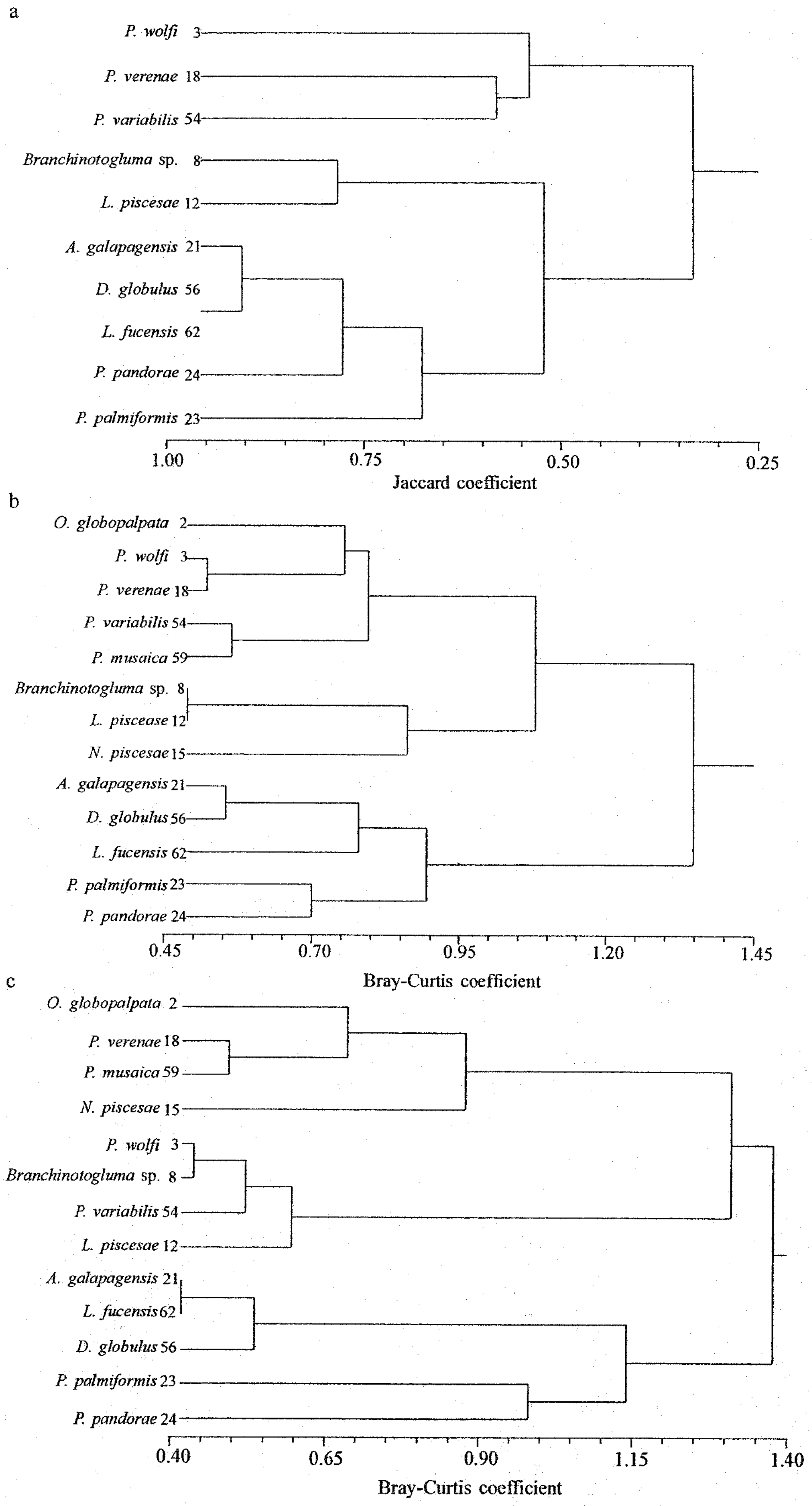

a
P. wolfi 3
P. verenae 18
P. variabilis 54
Branchinotogluma sp. 8
L. piscesae 12
A. galapagensis 21
D. globulus 56
L. fucensis 62
P. pandorae 24
P. palmiformis 23
1.00
0.75
0.50
0.25
Jaccard coefficient
b
O. globopalpata 2
P. wolfi 3
P. verenae 18
P. variabilis 54
P. musaica 59
Branchinotogluma sp. 8
L. piscease 12
N. piscesae 15
A. galapagensis 21
D. globulus 56
L. fucensis 62
P. palmiformis 23
P. pandorae 24
0.45
0.70
0.95
1.20
1.45
Bray-Curtis coefficient
c
O. globopalpata 2
P. verenae 18
P. musaica 59
N. piscesae 15
P. wolfi 3
Branchinotogluma sp. 8
P. variabilis 54
L. piscesae 12
A. galapagensis 21
L. fucensis 62
D. globulus 56
P. palmiformis 23
P. pandorae 24
0.40
0.65
0.90
1.15
1.40
Bray-Curtis coefficient

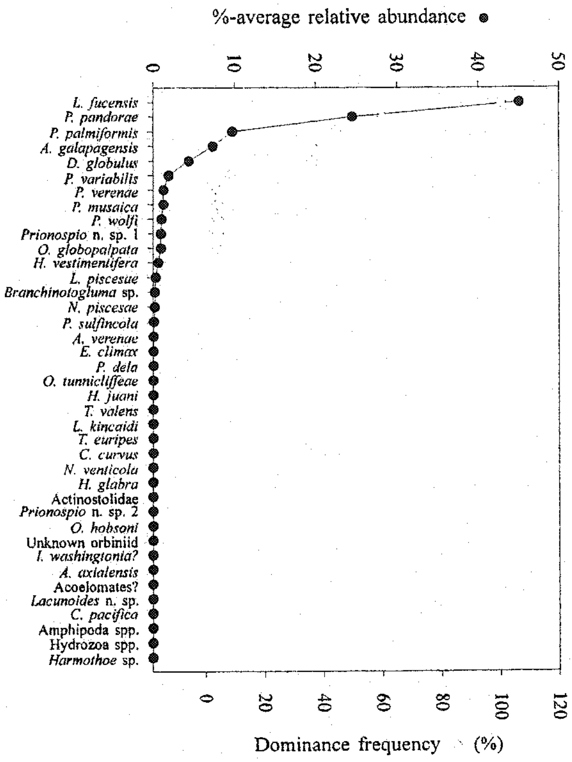
Table 5.5: Dispersion of Axial, Cleft, CoAxial, and the three-segment region. Dispersion is the percentage of sites at which the species is found. Species are in order from most abundant to least on Axial. Calculations include culled samples. *species found on only one segment.

Species	Axial (26 sites; n=31)	Cleft (14 sites; n=18)	CoAxial (1 site; n=2)	Total (41 sites; n=51)
Lepetodrilus fucensis	100	71.4	100	90.2
Paralvinella pandorae	96.2	71.4	100	87.8
Paralvinella palmiformis	65.4	57.1	100	63.4
Amphisamytha galapagensis	96.2	78.6	100	90.2
Depressigyra globulus	100	78.6	100	92.7
Provanna variabilis	96.2	42.9	100	78.0
*Pyropelta musaica**	73.1	NP	NP	46.3
Protomystides verenae	76.9	14.3	NP	53.7
Parougia wolfi	61.5	57.1	NP	58.5
Prionospio n. sp.1	30.8	14.3	100	26.8
Ophryotrocha globopalpata	61.5	14.3	100	46.3
Hesiospina vestimentifera	46.2	21.4	100	39.0
Lepidonotopodium piscesae	73.1	64.3	100	70.7
Branchinotogluma sp.	65.4	71.4	100	68.3
*Nereis piscesae**	65.4	NP	NP	41.5
Paralvinella sulfincola	38.5	42.9	NP	39.0
Ammothea verenae	42.3	35.7	100	41.5
Euphilomedes climax	19.2	28.6	100	24.4
Paralvinella dela	23.1	7.14	NP	17.1
Opisthotrochopodus tunnicliffeae	57.7	21.4	NP	43.9
Helicoradomenia juani	15.4	7.14	100	14.6
Thermanemertes valens	3.85	7.14	100	7.32
Levensteiniella kincaidi	38.5	50.0	100	43.9
Temnocinclis euripes	7.69	7.14	NP	7.32
Clypeosectus curvus	46.2	14.3	NP	34.1
Nicomache venticola	23.1	28.6	NP	24.4
Hesiodeira glabra	23.1	7.14	100	19.5
Actinostolidae n. spp (2)*	15.4	NP	NP	9.76
Prionospio n. sp. 2*	7.69	NP	NP	4.88
*Orbiniella hobsonae**	3.85	NP	NP	2.44
Unknown orbiniid*	3.85	NP	NP	2.44
Idasola washingtonia?*	11.5	NP	NP	7.32
*Amphiduros axialensis**	11.5	NP	NP	4.88
Acoelomates?	3.85	NP	100	4.88

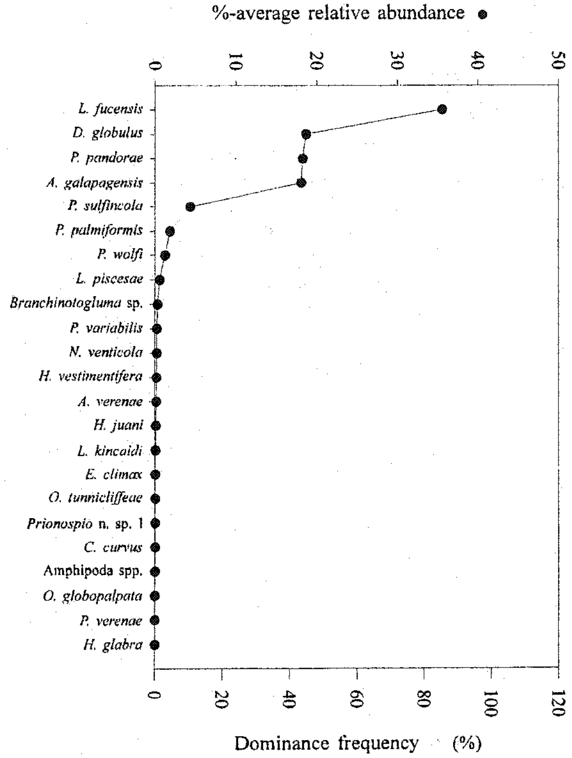
Species	Axial (26 sites; n=31)	Cleft (14 sites; n=18)	CoAxial (1 site; n=2)	Total (41 sites; n=51)
Lacunoides n. sp.*	7.69	NP	NP	4.88
*Calyptogena pacifica**	7.69	NP	NP	4.88
Amphipoda spp. unknown	3.85	28.6	NP	12.2
Hydrozoa spp. unknown*	7.69	NP	NP	4.88
Harmothoe sp.	3.85	NP	100	4.88
Amphipoda sp. nr. *Valettiopsis**	NP	7.14	NP	2.44
Lucenaria n. sp.*	NP	7.14	NP	2.44

Figure 5.11. Rank-abundance diagrams of macrofauna from the three segments. Abundance is expressed as percent-average relative abundance across all samples remaining after culling. Dominance frequency is the percent of samples in which a species is one of the three most abundant species. Dominance frequency for CoAxial is not given, as there are only two samples for this segment. Taxonomic groups where the species are unknown but which probably contain more than one species are noted as "spp". a. Axial. Total number of samples is 25. b: Cleft. Total number of samples is seven. c: CoAxial. Total number of samples is two.

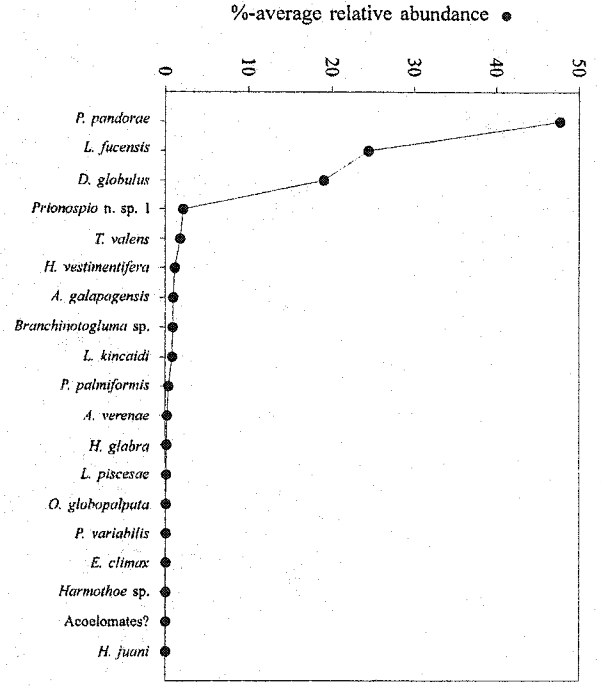
a


%-average relative abundance ●
0
10
20
30
40
50
L. fucensis
P. pandorae
P. palmiformis
A. galapagensis
D. globulus
P. variabilis
P. verenae
P. musaica
P. wolfi
Prionospio n. sp. 1
O. globopalpata
H. vestimentifera
L. piscesae
Branchinotogluma sp.
N. piscesae
P. sulfincola
A. verenae
E. climax
P. dela
O. tunnicliffeae
H. juani
T. valens
L. kincaidi
T. euripes
C. curvus
N. venticola
H. glabra
Actinostolidae
Prionospio n. sp. 2
O. hobsoni
Unknown orbiniid
I. washingtonia?
A. axialensis
Acoelomates?
Lacunoides n. sp.
C. pacifica
Amphipoda spp.
Hydrozoa spp.
Harmothoe sp.
0
20
40
60
80
100
120
Dominance frequency (%)

b


%-average relative abundance ●
0
10
20
30
40
50
L. fucensis
D. globulus
P. pandorae
A. galapagensis
P. sulfincola
P. palmiformis
P. wolfi
L. piscesae
Branchinotogluma sp.
P. variabilis
N. venticola
H. vestimentifera
A. verenae
H. juani
L. kincaidi
E. climax
O. tunnicliffeae
Prionospio n. sp. 1
C. curvus
Amphipoda spp.
O. globopalpata
P. verenae
H. glabra
0
20
40
60
80
100
120
Dominance frequency (%)

c


%-average relative abundance ●
0
10
20
30
40
50
P. pandorae
L. fucensis
D. globulus
Prionospio n. sp. 1
T. valens
H. vestimentifera
A. galapagensis
Branchinotogluma sp.
L. kincaidi
P. palmiformis
A. verenae
H. glabra
L. piscesae
O. globopalpata
P. variabilis
E. climax
Harmothoe sp.
Acoelomates?
H. juani

Cleft. The same species are present on all three segments, but there are more similarities between Cleft and Axial rank-abundance curves than between either of these segments and CoAxial.

Density and diversity values are given in Table 5.6. Axial has the highest density (not significant) and species richness of all three segments; CoAxial has the highest H' and Cleft and Axial have the same species density. Diversity indices for the ACC region are similar to that of Axial. This is not surprising given that Cleft and CoAxial species are both subsets of the Axial fauna and that Axial has a much larger number of samples. Cleft and Axial have relatively similar densities, five to six times greater than density for CoAxial. Rarefaction curves are shown in Figure 5.12. Rarefaction accounts for uneven sample size, but the maximum species detected for each segment sets the end point of the curve. Thus the increasing diversity from CoAxial, to Cleft, to Axial, to all three together may be an artefact of increasing sample size (i.e. area). An asymptote is not reached for the rarefaction curves but given the shallowness of the slope, and the fact that all individuals are not included in the analysis because of programming constraints, I believe we have found most of the species present.

Question 3: what scale of processes influence local diversity of Juan de Fuca vents?

Local diversity and saturation

Vents do not cluster by substratum, geographic area, or sampling date. Local diversity (alpha diversity) as a function of gamma diversity (regional diversity) is in Figure 5.13. If alpha diversity is the average species density per vent, R-squared is 0.578 and if alpha is the average number of species per vent, R-squared is 0.720 and a linear

Table 5.6: Species diversity characteristics at Axial, Cleft, CoAxial, and three-segment region. Two of the samples culled for quantitative analysis are used to calculate diversity indices for Cleft and all three segments combined. These samples were culled because they have fewer than 200 individuals but this does not affect their value in calculating diversity indices. For Simpson's measure of diversity and evenness and Shannon-Wiener, H', all data are pooled. Numbers in parentheses are standard deviations.

Site	No. of samples	Simpson's measure of diversity, 1-D	Shannon -Wiener, H'	Species density (number of species• cm^{-2})	Density (macro fauna)	Species number (macro fauna)	Species number (all fauna)	Simpson's measure of evenness, $E_{1/D}$
Axial	25	0.698	2.433	0.006 (0.006)	1.245 (0.766)	39	55	0.060
Cleft	9 for indices; 7 for species density and density	0.475	1.616	0.006 (0.013)	1.017 (1.426)	23	32	0.060
CoAxial	2	0.807	2.797	0.001 (0.001)	0.209 (0.260)	19	33	0.157
All three	36 for indices; 34 for species density and density	0.716	2.434	0.005 (0.008)	1.137 (0.929)	39	55	0.063

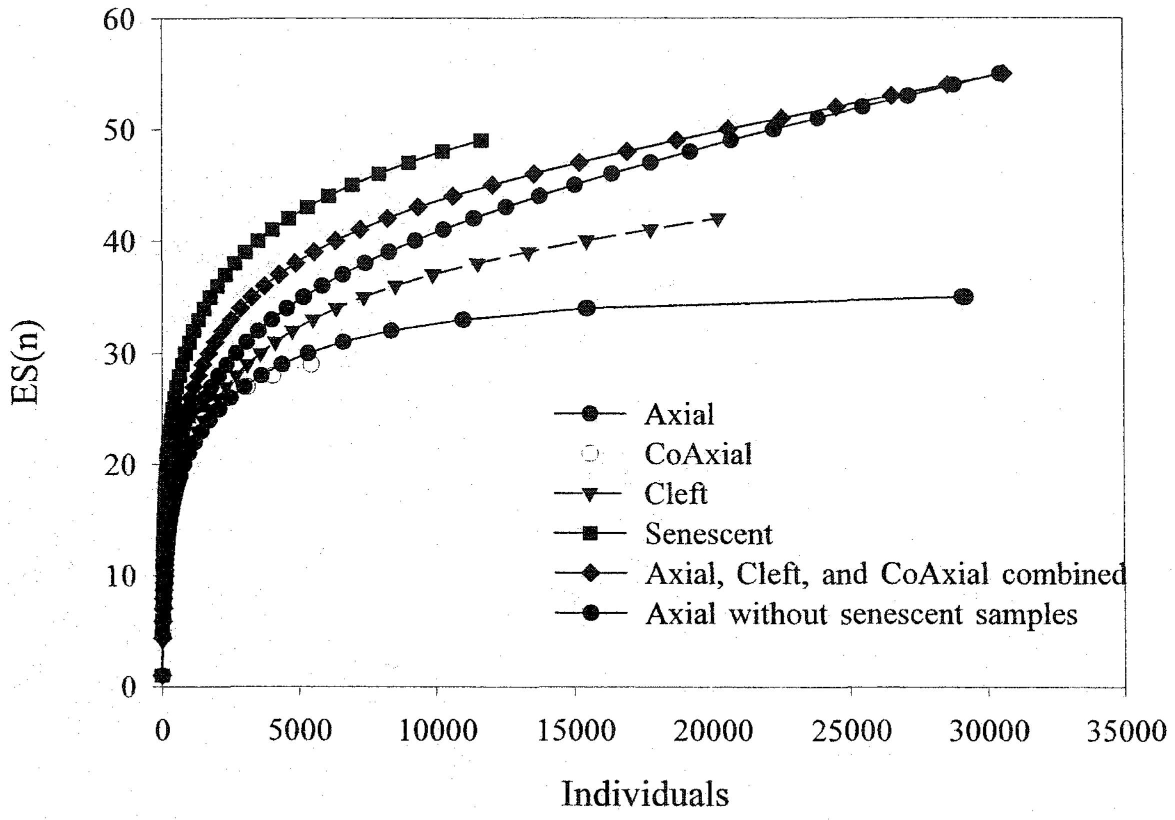


Figure 5.12. Rarefaction of Axial (including senescent samples), Cleft, CoAxial, senescent community, and the three segments combined. The senescent community is from Chapter 3. ES(n) is the expected number of species in a random sample of n individuals. Each ES(n) estimate is based on 10 random samples for a given n.

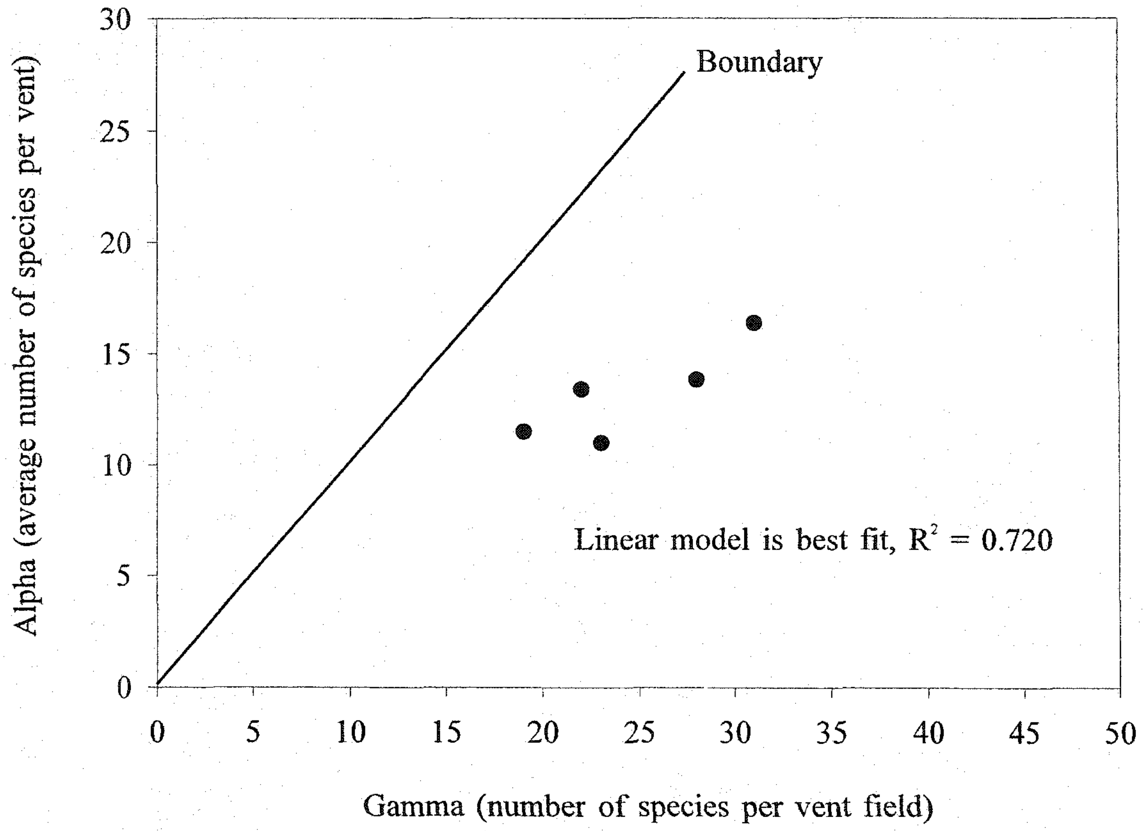


Figure 5.13. Alpha versus gamma vent diversity. The five data points on the graph, in order of increasing gamma diversity, represent CoAxial, CASM, Cleft, South Rift Zone, and ASHES. The line labelled "boundary" represents complete regional pool exhaustion where local richness is equal to regional richness. This line is the upper boundary on local richness.

model is the best fit by curve estimation. All values fall below the line that indicates local diversity equal to regional diversity. A linear relationship indicates that local diversity is not reaching a ceiling independent of the number of species in the regional pool. Values below the boundary line indicate that local diversity is not an exact reflection of regional diversity and that local factors also play a role in governing local diversity.

Alpha (α), beta (β), and gamma (γ) diversity

Alpha (local), beta (between-site), and gamma (regional) diversity of vents for two types of habitat and at two spatial scales are presented in Table 5.7. Beta diversity is the differentiation in species composition among sites. It has two explanations: a) the spatial turnover of species along environmental gradients (as per Whittaker 1960); or b) spatial turnover of species due to existence of different species in similar, but separated habitats (as per Colwell and Coddington 1994). Continuous venting habitat has higher alpha and gamma diversity and lower beta diversity than patchy habitat, although differences are not significant.

Question 4: which species richness estimators are most useful for vents?

Using percent relative abundance data, the Michaelis-Menten (MMMean) estimator is a good predictor of species richness for Axial and Cleft segments. The usefulness of a species richness estimator lies in its ability to estimate total community diversity from a small number of samples (n). Results for the non-parametric estimators are given in Table 5.8 for n equal to 5, 15, and 25 for Axial, where n_{max} equals 25.

Table 5.7: Patchy versus continuous vent habitat and components of diversity. P-values for tests for differences in beta (local) and alpha between habitat types are Friedman tests because the ASHES data are not normally distributed. P-values for complementarity (local) are from t-tests because all data are normally distributed. SRZ is South Rift Zone. Alpha diversity is given as average species density per site and average number of species per site (in parentheses).

Diversity component	**Patchy (north Cleft)**	**Patchy (SRZ)**	**Patchy (both north Cleft and SRZ)**	**Continuous (ASHES)**	**P-values**		
					N. Cleft vs. ASHES	SRZ vs. ASHES	N. Cleft and SRZ vs. ASHES
Alpha	0.005 (11)	0.006 (13.83)	0.005 (12.13)	0.006 (16.39)	$p<0.096$	$p\sim1.000$	$p<0.166$
Gamma	23	28	30	31	--	--	--
Beta (total)	--	--	3.130	--	--	--	--
Beta (local)	2.821	2.151	2.553	2.195	$p<0.739$	$p\sim1.000$	$p\sim1.000$
Complementarity (total)	--	--	0.609	--	--	--	--
Complementarity (local)	0.565	0.560	0.563	0.477	$p<0.960$	$p<0.463$	$p<0.797$

Results for n equal to three, six, and nine (= n_{max}) for Cleft are also given. The usefulness of the estimators is judged by how close to the total number of species at n_{max} the estimator is at sample sizes much less than n_{max}.

Discussion

High-flow versus low-flow *Ridgeia piscesae* communities

It is not surprising that different types of venting conditions produce different types of communities. Luther et al. (2001) describe significant differences in oxygen, iron, and sulphur speciation to be strongly correlated with distribution of specific taxa in different microhabitats on the East Pacific Rise. Low-flow, high diversity and high-flow, low diversity vent communities on sulphide chimneys are described in Sarrazin and Juniper (1999). Sarrazin and Juniper's (1999) Assemblage V-high-flow is has relatively high biomass but low species richness in a regime of vigourous fluid flow. The low diversity fat-type (LDF) community described in this chapter includes Assemblage V-high-flow type assemblages, but also includes assemblages in areas of high-flow on basalt (i.e. at newly eruptive vents). Urcuyo (2000) reports a biomass of 1 kg for one Juan de Fuca tubeworm bush with a surface area of 5.8 m^2 and suggests that this much surface area could provide a long lasting renewable substratum for new settlement and colonisation and a source of nutrition for vent endemic fauna in low-flow tubeworm bushes. The larger surface area and presumably greater resources and/or substratum available to HDK tubeworm bushes compared to LDF tubeworm assemblages may be one reason why the HDK type communities have higher species richness.

Table 5.8: Test results of non-parametric species richness estimators presented in Colwell and Coddington (1994). Estimators predict total species richness from samples including species not discovered in any sample. All fauna are used. Two samples culled from other quantitative analyses because of small numbers of individuals, are included in the Cleft data set here because of the low numbers of samples compared to Axial.

Estimator		Axial			Cleft	
	n=5	n=15	n_{max}=25	n=3	n=6	n_{max}=9
Species observed	37.0	49.5	55.0	26.0	31.1	33.0
ACE	37.0	49.5	55.0	26.1	31.2	33.0
ICE	48.6	60.1	66.3	46.0	36.6	34.5
Chao 1	37.0	49.5	55.0	26.1	31.2	33.0
Chao 2	49.5	64.2	68.1	37.9	34.9	33.4
Jackknife 1	47.2	60.8	66.5	34.2	37.0	35.7
Jackknife 2	51.4	66.7	73.2	37.0	37.4	33.2
Bootstrap	41.8	54.6	60.2	29.9	34.3	35.0
MMRuns	172	55.9	58.3	50.9	74.3	47.9
MMMean	48.1	54.0	57.3	39.9	39.2	39.0

Diversity is the major difference between the LDF and the HDK type communities. The LDF assemblages are presumably on new substratum (produced via changes in fluid flow through a chimney or eruption and new venting) and the lower species richness of this community type may be due to the early successional stage; many species may not have had time to recruit to the new substratum. However, although the presence and absence of juvenile *Ridgeia piscesae* is qualitative, this observation suggests differences between the community types may also be related to factors other than duration of venting, for example, fluid flow regime.

Axial, Cleft, and CoAxial vents

Multivariate analyses and descriptions of community structure including rank-abundance, dispersion, and diversity demonstrate that Axial, Cleft, and CoAxial are similar statistically, although there may be a general Cleft and Axial grouping according to the presence/absence correspondence analysis (Figures 5.5a and 5.6b) and a Friedman test on density. The same numerically dominant species are present on Axial and Cleft and when dominant species are excluded, samples still do not cluster by segment, substratum, or year (Figure 5.6). Without dominant species, senescent samples (CoAxial 1996, YY; Crevice 1999, EE) fall out together in the cluster and correspondence analyses. This result supports the assertion in Chapter 3, that differences between senescent and non-senescent vents are enhanced when meiofauna and species in the tails of the rank-abundance curves are considered.

The shape of the rank-abundance curves are similar for all three segments as are the identities of the numerically dominant species. CoAxial, nevertheless, differs in its rank-abundance curve from Axial or Cleft. The most abundant species on CoAxial is *Paralvinella pandorae*, not the limpet *Lepetodrilus fucensis*. This may be explained by the successional state of venting on CoAxial during the sampling period. CoAxial vents were newly colonised in 1994; the community in 1995 probably was more like early eruptive vents than well-established vents as on Axial and Cleft. High abundance of *P. pandorae* is often characteristic of early successional vents (Tunnicliffe et al. 1997; Tsurumi et al. 1998). The CoAxial vent sampled in 1996 was senescing and therefore animal densities in this sample were lower than for the 1995 sample. Thus, although *L. fucensis* was the most abundant organism in 1996, *P. pandorae* is more abundant overall. The one senescent CoAxial sample explains differences in species-ranks at CoAxial: *Thermanemertes valens* and *Prionospio* n. sp. 1 are present in greater relative abundance than at active vent sites on Axial and Cleft. Both these species are present in greater abundance at senescent vents than non-senescent vents (Chapter 3). Finally, the influence of sample size cannot be discounted here as the CoAxial profile is based on only two samples.

The distance between the two furthest segments (CoAxial and Cleft) is approximately 150 km and most Juan de Fuca species, even those rare in abundance and distribution, have dispersed along this length. The large degree of species similarity along the southern segment of the Juan de Fuca is not unexpected given similar results for Axial and Cleft segments (Chapters 4 and 2).

Species with restricted distributions are interesting. Eleven species are found only on Axial (Table 5.3). Of these 11, five are known elsewhere on the Ridge (Tunnicliffe, pers. comm.). Of the remaining six, five are either species currently under description or remain unidentified and await attention by a specialist. These five species could be endemic to Axial, but they also could be in samples from other areas but not recognised during sample processing. Species like the unknown Orbiniid polychaete, found only in senescent samples, may be a deep-sea species not usually found at vents. *Pyropelta musaica* appears to be truly endemic to Axial among Juan de Fuca vents. This limpet however, is present on decaying whale bones in the Pacific (Bennett et al. 1994). If this species is able to disperse long distances (e.g. between whale bones and/or Axial Seamount), why is it not found elsewhere on the Juan de Fuca? It seems unlikely that its presence or absence is influenced by the availability of an appropriate microhabitat as it is found at all three vent fields on Axial under varying conditions and whale skeletons are a sulphide-rich environment with a different rate and mechanism of sulphide delivery than at vents. The restricted distribution of *P. musaica* on the Juan de Fuca may be due to its competitive exclusion by vent endemics, or perhaps this species is not a good disperser. Two species from north Cleft are not found in Axial or CoAxial samples (Table 5.3), but one of these species is reported from CoAxial (Tunnicliffe et al. 1997) and the other may be a non-vent species (Hendricks, pers. comm.).

Over the ACC region, *Lepetodrilus fucensis* is the numerically dominant species (Figure 5.14). This dominance is not apparent at early eruptive vents (Tunnicliffe et al. 1997; Tsurumi et al. 1998), but emerges at active and senescent vents. *Lepetodrilus* is probably a good competitor for space due to its ability to stack vertically on any substratum. The vent environment is very productive compared to the deep-sea and can support many individuals; however, as many of the species live in and on tubeworm bushes where low temperature fluid flow is focused, available settling substratum is

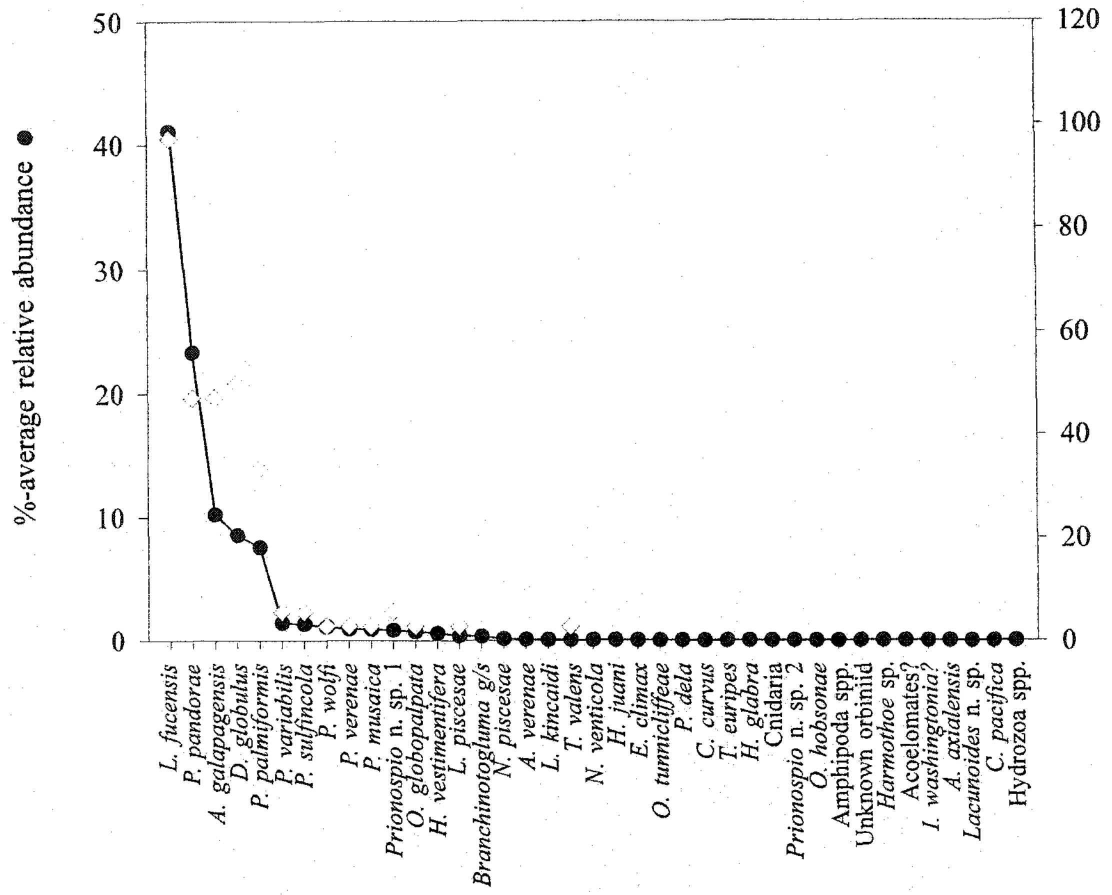


Figure 5.14. Rank-abundance diagram of macrofauna from the three-segment region (Axial, Cleft, and CoAxial combined). Total number of samples is 34 and does not include culled samples. Abundance is expressed as percent-average relative abundance across all samples. Dominance frequency is the percent of samples in which a species is one of the three most abundant species. Taxonomic groups where the species are unknown but which probably contain more than one species are noted as "spp".

limited. Furthermore, *L. fucensis* may have multiple food-gathering strategies that make it an efficient competitor for food resources (Chapter 2).

The East Pacific Rise (EPR) lies in the same geographic region as the Juan de Fuca, but is a different biogeographical province (Figure 2.1.1) and was probably separated from the EPR by a vicariant event about 30 million years ago (Tunnicliffe 1988). The faunas still have many similarities at the generic and familial levels (Tunnicliffe et al. 1998). Congeners of *Lepetodrilus fucensis* on the EPR are: *L. cristatus*, *L. elevatus*, *L. guaymasensis*, *L. ovalis*, *L. pustulosus*, and *L. tevnianus*. *Lepetodrilus elevatus* may be ecologically equivalent to *L. fucensis* in some low temperature tubeworm-dominated EPR assemblages, but faunal dominance of all vents by a single species does not appears to occur on the EPR (T. Shank, pers. comm.). The only other species of *Lepetodrilus* on the Juan de Fuca is *L. corrugatus*, found on Middle Valley, a segment with sediment rather than basalt as the main substratum.

Community structure

Species associations

Most patterns of species associations reoccur on Axial, Cleft, and the three-segment region. *Paralvinella pandorae* and *P. palmiformis* are positively associated. These species may occupy the same habitat on tubeworm tubes. If both species occupy the same habitat and occupy for the same spatial (pers. obs.) and trophic (Levesque and Juniper 2000) resources, why are they positively associated? The size shift of *P. pandorae* from a large-bodied form at early successional vents without *P. palmiformis*, to a small-bodied form at later successional stages hosting both alvinellid species

(Tunnicliffe et al. 1997), may explain why the species abundances are positively correlated. There may be competition for substratum between the two species and niche displacement of *P. pandorae* by *P. palmiformis* because of overlap in trophic niche (Levesque and Juniper 2000), but the abundance relationship remains positive because numbers of *P. pandorae* are unaffected. Total abundance of *P. pandorae* does not change because it can modify its phenotype.

The association between the polynoids *Branchinotogluma* sp. and *Lepidonotopodium piscesae* is due to their similar abundance and wide distribution at vents. Although *Branchinotogluma* sp. seems to be even more of a habitat and trophic generalist than *L. piscesae* (Levesque and Juniper 2000), they probably have similar ecological requirements and/or competitive abilities in active venting conditions.

Diversity

The ACC region has low species richness and low evenness. The low species richness and evenness are comparable to other systems with intermediate to high disturbance regimes where organisms must be able to tolerate harsh abiotic conditions. For example, species richness of plants on soils affected by the Mt. St. Helen's eruption ranged from a mean of just over two to around 17 species per 250 m^2 ten years post-eruption (del Moral and Bliss 1993). Turner et al. (1997) report average numbers of up to 15.9 species per 8 m^2 plot three to five years after disturbance by forest fires in Yellowstone National Park. Numbers ranging from 14 to 33 species are commonly reported for communities inhabiting sea-ice and sub-ice water in the Arctic Ocean and environs (e.g. Lonne and Gulliksen 1991; Werner and Arbizu 1999). Rocky intertidal communities have a high frequency of disturbance and have relatively low diversity compared to most marine environments (Huston 1994). Sousa (1979) reports average species richness of plants and sessile animals on intertidal boulders exposed to disturbance to be 6.7 to 87.7.

Axial has almost double the number of species as Cleft. I believe that greater species richness for Axial is not an artefact of sampling. Both Cleft and Axial samples are from low temperature habitats (basalt and sulphide) and both segments have low and high temperature venting. Although only nine samples are used to determine species richness and diversity on Cleft (as opposed to 25 for Axial), 18 samples from Cleft were processed and extensive videographic and photographic data were available (Chapter 2). The rarefaction curves, which take uneven sample size into account, are different for Axial and Cleft. Observed differences in diversity between Axial and Cleft may be a result of the species-area effect: Axial has a larger total area of venting as well as longer duration of venting than Cleft. Axial may have more habitat heterogeneity and/or opportunities for supporting a greater number of species. If differential area is accounted for using species density (Table 5.6), Cleft may be more species-rich per unit area than Axial. Greater total species richness at Axial may also be due to the sampling of the senescent successional stage (Chapter 4). Figure 5.12 shows the rarefaction curve for Cleft versus Axial without senescent samples in the Axial data set. Cleft and Axial are more similar in species richness without inclusion of the late successional samples.

Dispersion

The most abundant species of the ACC region are the most well-dispersed (Figure 5.15). Species with low local abundances have narrow distributions. This relationship is described for Cleft (Chapter 2) and Axial (Chapter 4). In general, species that are abundant or widespread at small scales tend to be so at larger scales, and vice versa (e.g. Gaston 1996; Loreau and Mouquet 1999), although there is some evidence that species rare in local abundance can also be regionally widespread (Brown and Maurer 1987; Pitman et al. 1999). The distribution-abundance relationship is found at two spatial scales (Table 5.5). Maurer (1999) describes the distribution-abundance relationship as a consequence of the geographic range structure of species and suggests that abundance is correlated with distribution because species with ecological adaptations that allow them to have large geographic ranges also tend to dominate local communities. *Lepetodrilus fucensis* fits this pattern. The exceptions are widespread species found in low numbers that specialise on resources across a large geographic range, and so are less common locally than their more narrowly distributed relatives. At Juan de Fuca vents, however, widespread but locally less abundant species such as *Branchinotogluma* sp. and *Lepidonotopodium piscesae* appear to be trophic generalists, not specialists (Levesque and Juniper 2000). A majority of tree species in the Amazon basin of Peru are geographically widespread yet low in local abundance (Pitman et al. 1999). Pitman et al. (1999) believe this is because most of their tree species are habitat generalists occurring over large areas of the Amazonian lowlands at low densities (Pitman et al. 1999).

Maurer (1999) argues that the productivity of an environment constrains the positive relationship between distribution and abundance and that the steepness of this relationship should increase in more productive habitats where it is harder for one or a

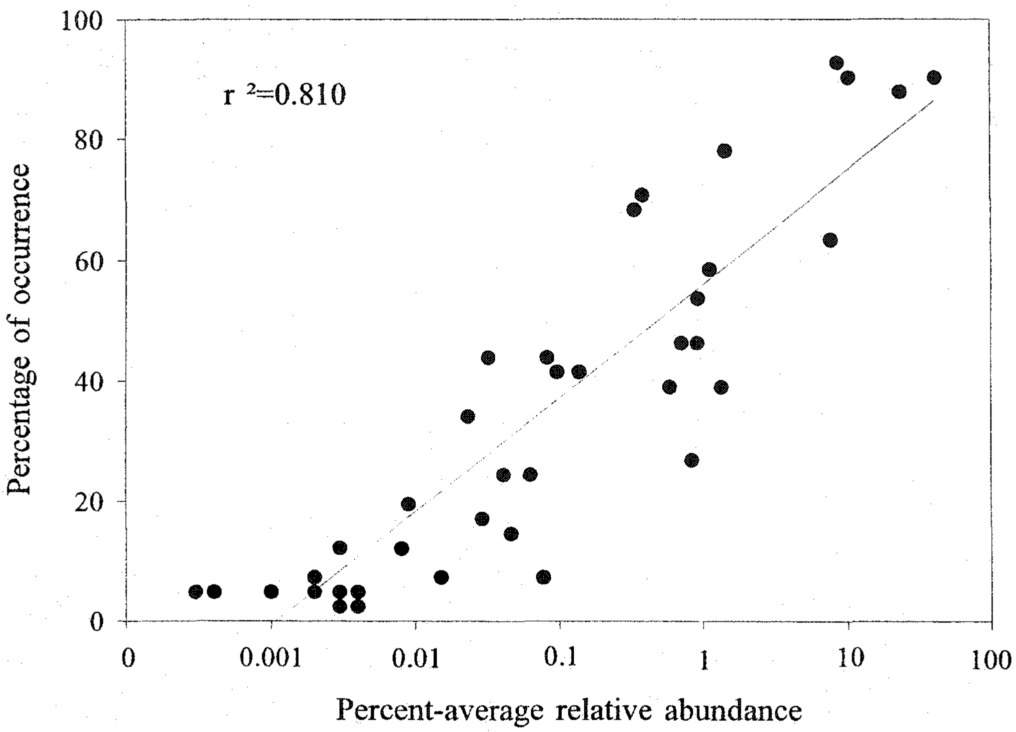


Figure 5.15. Interspecific abundance-distribution relationship for the three-segment region of Axial, Cleft, and CoAxial. Only macrofaunal species are included. Percentage of occurrence is the number of times out of the total number of sites a species is found. The relationship is linear and r^2 is 0.810.

few species to monopolise resources. However, in the productive Juan de Fuca vent environment there is a strong positive relationship between abundance and distribution (Table 5.5; Figure 5.15). The extreme nature of the vent habitat restricts the number of species able to take advantage of the resources and so the productivity-abundance relationship is perhaps modified.

The cause of the distribution-abundance relationship remains undetermined (Gaston 1996; Maurer 1999). The first step in resolving this issue is to analyse combinations of taxa, scales, and regions where the abundance-distribution relationship is unknown (Gaston 1996). The Juan de Fuca vent data contribute a new combination of taxa at two scales (intersegmental and intrasegmental) and are from the marine environment, a system for which few reports on species abundance-distribution relationships exist. Wright (1991) believes that it is more useful to focus on deviations from the abundance-distribution relationship. For example, how do some relatively rare (in local abundance) species manage to be widespread? I would also ask why species such as *Prionospio* n. sp. 1, *Paralvinella palmiformis*, and *P. sulfincola* are relatively abundant but not widely dispersed.

The widely dispersed animals in low relative local abundance for Axial, Cleft, and CoAxial are mostly large, mobile polychaetes: the polynoids *Opisthotrochopodus tunnicliffeae*, *Lepidonotopodium piscesae*, *Branchinotogluma* sp., and *Levensteiniella kincaidi* (Table 5.5). The one non-polychaete is the split limpet, *Clypeosectus curvus*. If we exclude *O. tunnicliffeae* and *C. curvus* from consideration because they only fit the pattern for Axial and not Cleft, then we are left with three polynoids. An analysis of trophic dynamics for *Branchinotogluma* sp. and *L. piscesae* shows both species to be trophic generalists (Levesque and Juniper 2000). *L. kincaidi* may be a trophic specialist, but interpretation of the results is difficult because of limited specimens available for analysis (Levesque and Juniper 2000). Qualitatively, *L. kincaidi* appears to be more common at senescent vents than non-senescent vents (Chapter 3) and it could be that this polychaete is either a trophic specialist that only does well in conditions at senescent vents and/or is limited to very low numbers at non-senescent vents due to competitive exclusion by other species. Observed vent distribution-abundance relationships may be due to a species density-independent response to environmental variation: species with higher density-independent growth rates may on average range over a larger fraction of habitats than those with lower density-independent growth rates (Holt et al. 1997). Species data on growth rates and density-independent responses are not yet available from the vent environment to evaluate this idea although it may be possible to evaluate using comparative data on the paralvinellids.

Opisthotrochopodus tunnicliffeae and *Clypeosectus curvus* are present on Cleft as well as Axial, yet the sample data from Cleft do not show the same pattern of wide-dispersion and low abundance. There is no trophic information on these two species, but one reason for the observed patterns may relate to limited dispersal abilities. These species may not be able to disperse as well as species that exhibit a wide-dispersion/low abundance pattern on both segments. Restricted dispersal may not matter on Axial where the travel time between vents may be shorter and more regular than for north Cleft. Cleft vents are aligned along a 020° trending axis and current movement appears complex, changing between south-southwest and north-northwest directions on west and east sides of the ridge respectively, with a variable lateral component (Cannon et al. 1991).

Another difference in species distribution-abundance patterns between Axial and Cleft is the low abundance and wide-spread occurrence of the predatory polychaete, *Nereis piscesae* and the snail, *Pyropelta musaica* on Axial and their apparent absence on Cleft (Table 5.5). *Nereis piscesae* is found only on Axial and Middle Valley (Juniper and Tunnicliffe 1992). *Pyropelta musaica* is an interesting puzzle because this species is found on whale bones far off the ridge axis and on Axial. The restricted distribution of *P. musaica* may be due to limited dispersal capabilities and/or low survivorship due to local interactions such as competition or predation at all other Juan de Fuca vent sites. The suggestion that *P. musaica* (and other vent species) have wide dispersal abilities can be tested by doing population level studies of gene flow for vent species. On the Juan de Fuca, *Ridgeia piscesae* is the only species for which such studies are available (Black 1991). This species is a wide disperser and there is no significant population differentiation along the ridge (Black 1991).

Finally, three species are narrowly dispersed but in relatively high abundance on Axial or Cleft: *Prionospio* n. sp. 1 and *Paralvinella palmiformis* (Axial) and *P. sulfincola* (Cleft). These species may have limited dispersal capabilities or survivorship, but once they arrive at a vent or settle beyond a certain threshold of numbers, they may be able to compete well for available resources. Information on the life histories of these species would be useful to evaluate this idea, but is only available for *P. palmiformis*, not *Prionospio* or *P. sulfincola*. *P. sulfincola*'s distribution-abundance pattern may be an artefact of sampling. Of the seven Cleft samples used to calculate percent-average relative abundance, three were from sulphide structures. Although the collections were of low temperature vents on the sulphide, *P. sulfincola* is known to preferentially colonise high temperature sulphide environments (Sarrazin et al. 1997). Therefore, *P. sulfincola* numbers may be artificially high in the Cleft samples due to some *P. sulfincola* living in marginal sulphide habitats.

Local versus regional diversity

Regional processes

The relationship between local and regional diversity on the Juan de Fuca in the sense intended by Ricklefs (1987) was not investigated in this thesis as data are only available from within one biogeographic province or region. However, a test for saturation can be applied to any defined area encompassing a group of areas (Cornell 1985; Magurran 1988). The goal is to determine whether factors operating at a larger scale than the local are important influences on local diversity. The scale of investigation here is not the macro-, but rather the mesoscale (Holt 1993). The mesoscale is in the gray zone between local mechanisms that are of traditional concern for community ecologists, such as detailed analyses of population dynamics in a single patch, and large scale processes of interest to biogeographers and systematists (Holt 1993). At the mesoscale, the influence of regional ecological processes on local communities can be determined for spatial processes important at the metapopulation or landscape level.

Communities in which local diversity (alpha) is linearly dependent on gamma diversity are referred to as "unsaturated" or exhibiting "proportional sampling" (Cornell 1985; Cornell and Lawton 1992; Cornell 1993; Caley and Schluter 1997). The communities on Axial, Cleft, and CoAxial are unsaturated (Figure 5.13). The absence of saturation in natural communities is reported in the literature for a diverse range of taxa

(Cornell and Karlson 1997; Karlson and Cornell 1998) and interpreted as evidence of the importance of factors at a larger than local scale in regulating local diversity (e.g. Ricklefs and Schluter 1993; Caley and Schluter 1997). Proportional sampling does not necessarily mean that a community's local richness is not regulated by local interactions, but it does mean that local factors are not sufficient to limit local diversity (Cornell 1993).

The slope of alpha to gamma diversity for the Juan de Fuca is below the point of complete regional pool exhaustion. Local versus regional relationships are expected to be less than one, either because species associated with the habitat are specialised to other habitats, which results in high beta diversity, or because periodic extinctions occur and are balanced by stochastic colonisation from a regional pool (Cornell 1993). High beta diversity is expected if species are specialised to microhabitats (Cornell 1993), but the Juan de Fuca vent data exhibit low beta diversity (Table 5.7). Brown et al. (2001) argue that if changes in species composition between habitats (i.e. beta diversity) are only stochastic, colonisations and extinctions should mostly be confined to rare species. Beta diversity at the Juan de Fuca vents is primarily due to the differential presence of rare species (Figure 5.11). Thus, periodic extinctions of fauna and/or the entire vent followed by stochastic recolonisation of a vent or newly created habitat from a regional pool, probably best explains the slope of the line in Figure 5.13 falling below the boundary value of one.

The mesoscale mechanism that I believe to be important in influencing local vent diversity is differential dispersal capabilities. Processes such as source pool effects, source-sink dynamics, and metapopulation dynamics are all possible explanations for persistence of certain species in a patch (Holt 1993). All of these processes are considered "regional" in that they operate at the metapopulation and/or landscape scale and dispersal is the spatial mechanism invoked (Holt 1993; Loreau and Mouquet 1999).

If local interactions are primarily responsible for local diversity, Schluter and Ricklefs (1993) predict that: 1) local diversity should be correlated with features of the environment; 2) if competition is a strong force, local diversity should reach a ceiling independent of the number of species in the regional pool (saturation); and 3) independently assembled communities in similar habitats on different continents should have similar numbers of species. The first two predictions can be addressed with the data presented in this chapter. Prediction 1) is not supported by the Juan de Fuca data as local diversity is not correlated with substratum, geographic area, or sampling date for Axial, Cleft, and the ACC. The samples, however, do not represent a full sulphide range of habitats or sedimented vents. Prediction 2) is also unsupported as Juan de Fuca communities are unsaturated. Prediction 3) is not addressed as species richness among mid-ocean ridges awaits comparison. Angermeier and Winston (1998) test Schluter and Ricklefs' (1993) predictions 1) and 2) for fish communities. Prediction 1) is not confirmed as regional diversity was the most consistent predictor of local diversity. Prediction 2) is partially confirmed as asymptotic relationships between local and regional diversity were evident for some fish communities depending on regional scale.

Local and mesoscale regional processes

Despite the debate over local *versus* regional controls on local diversity, local *and* regional processes are not independent of each other. A continuum of controls, from primarily local to primarily regional likely operate, varying with the community in question (Caley and Schluter 1997). The outcome of interspecific interactions such as competition and predation depends upon the number and types of local species (Smith 2001). Ecologists report combined effects of local and regional diversity on local diversity (e.g. Angermeier and Winston 1998; Karlson and Cornell 1998). Competitive equilibrium can reduce species richness (Huston 1994; Huston 1999) and immigration from an external source is able to maintain high local diversity (Loreau and Mouquet 1999) in a system that would otherwise tend towards competitive exclusion. The influence of local and regional controls on local diversity can vary on a geographic scale (Karlson and Cornell 1998). Both local and regional processes at the mesoscale are probably responsible for observed vent diversity. Local interactions such as competition are likely at Juan de Fuca vents. For example, the trophic overlap between *Paralvinella pandorae* and *P. palmiformis* that may cause the observed size shift and probable niche displacement of *P. pandorae* by *P. palmiformis*. Also, Axial vents follow a geometric species abundance distribution which suggests that a few physical factors may be important in structuring the community (Chapter 4).

Karlson and Cornell (1998) look at regional factors that affect coral species richness such as distance to nearest high diversity region, number of regional species and genera, distance to equator, and age of genera. Their results indicate that coral local species richness is sensitive to several large-scale regional factors as well as local environmental factors. If Juan de Fuca vent communities are unsaturated, then mesoscale regional factors are an important component in the regulation of local vent diversity. Future analyses of regional contributions to local vent species richness should explore more thoroughly historical and geographical explanations for regional-scale enrichment.

Local (e.g. sulphide level, substrata, or competition intensity) and regional (e.g. distance from each sampling site and the nearest highest diversity vent field, distance from each sampling site to the next ridge, average age and number of vent genera in the region) variables should be evaluated for their correlation to local vent species richness.

Components of diversity

Beta diversity, is an important aspect of diversity maintained at the local level independent of regional diversity. High beta diversity can explain local diversity reaching a ceiling independent of regional diversity. One definition of beta diversity is between habitat differences in species due to spatial turnover of species along environmental gradients (beta diversity of Whittaker 1960). This definition supports the idea that local interactions are most important in regulating local diversity. Beta diversity is also defined as between habitat differences in species because of spatial turnover due to the existence of different species in similar but separated habitats (ecological equivalency of Shmida and Wilson 1985). This definition supports the theory of regional diversity regulation via stochastic colonisation and extinction processes. For patchy and continuous vent habitat on the Juan de Fuca there is low overall beta diversity (beta and complementarity, Table 5.7; Figure 5.8). In addition, spatial isolation may be influential in producing the beta diversity detected as patchy habitat beta diversity is higher than continuous habitat beta diversity although this difference is not significant (Table 5.7). Greater beta diversity is not a factor of greater alpha or gamma diversity as alpha is highest for the continuous habitat and gamma values are almost equal.

Species richness estimators

The best non-parametric estimator of species richness from vent samples is the Michaelis-Menten (MMMean) richness estimator (Table 5.8). This estimator is good for Axial and north Cleft data using macro- and meiofauna. Colwell and Coddington (1994) found the Chao 2 and second order Jackknife estimators followed by the Michaelis-Menten to provide the least biased estimates for small numbers of samples. The Cleft data set is a small data set (total nine samples) and after the Michaelis-Menten, the next best estimators are the Chao 2 and Jackknife 2 methods. However, the latter two estimators do not predict Axial sample diversity well (Table 5.8). When only macrofauna are used, no estimator is a good predictor of sample richness. There may not be a set of universal species richness estimators that work in most environments. Different species richness estimators may prove useful for different habitats and communities, but will have to be established individually for each type of habitat or taxonomic assemblage. Colwell and Coddington (1994) are right in that a full evaluation of non-parametric methods with real data sets for a diverse range of organisms and habitats is necessary. However, estimators found by Colwell and Coddington (1994) to perform well, also do so somewhat in the vent environment.

Conclusions

Intersegmental analyses of Axial, north Cleft, and CoAxial segments give an overview of the community on this part of the Juan de Fuca Ridge. Multivariate analyses cannot distinguish between the communities on the three segments. Numerically abundant and widely dispersed species are similar for all segments and these species overwhelm any differences in rare species among segments. Community structure is similar in patterns of species association, diversity, and dispersion. The limpet *Lepetodrilus fucensis* is the most abundant organism and species diversity is similar to other disturbed and high energy environments. The most abundant species are widely dispersed, although there are a couple of exceptions such as the polynoids *Branchinotogluma* sp., *Lepidonotopodium piscesae*, and *Levensteiniella kincaidi* which are low in local abundance but widely dispersed. Seventy-five percent of the vent species are found over the 150 km scale of the study. The Juan de Fuca vent communities exhibit proportional sampling and are not saturated. A combination of local and mesoscale regional factors probably best explain the observed local diversity. Dispersal is suggested to be the important mechanism for the mesoscale processes. Beta diversity is low for patchy and continuous habitat; spatial isolation, not the turnover of species along an environmental gradient, appears to produce observed beta diversity. The best nonparametric method for estimating species richness from vent samples is the Michaelis-Menten.

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CHAPTER 6

Discussion and conclusions

Patterns and processes

Correlative patterns of community structure do not identify processes, but observations of patterns, or their lack, are the fundamentals of ecological study (Underwood et al. 2000). The primary purpose of this thesis is to describe and explain temporal and spatial patterns of distribution, abundance, and diversity of vent communities on the Juan de Fuca Ridge. My observations detailing community structure provide a basis for explanatory models about processes operating at the vent, segment, and intersegment scale. I describe vent communities on the Juan de Fuca and use observational data to test whether vent communities are structured similarly, whether local species richness is a function of local or regional diversity, and whether habitat diversity is responsible for observed between-habitat diversity.

Specifically, I learned that:

1) Vent communities are statistically indistinguishable at the segment scale (Axial and north Cleft) and at the intersegment scale for the Axial, Cleft, and CoAxial (ACC) region. *Lepetodrilus fucensis* is the dominant species in terms of distribution and abundance.
2) While communities are similar in composition within and among segments, different temporal communities can be described.
3) Distribution of most vent endemics is not limited at Axial, north Cleft, or the ACC region.

4) Abundances and distrbiutions of Axial, Cleft, and ACC species are correlated. The exceptions are the polynoids *Branchinotogluma* sp., *Lepidonotopodium piscesae*, and *Levensteiniella kincaidi.*
5) Both local and regional mechanisms explain observed local diversity. Spatial isolation, not habitat differences, influences between-habitat diversity (beta diversity) on Axial, Cleft, and ACC.
6) Vent communities should be compared to communities with similar diversity and evenness parameters as well as disturbance and productivity regimes. Candidate comparison communities include those in early successional states, selected taxocenes such as carabid beetles on fungi, or high disturbance/low diversity systems like the rocky intertidal.
7) Meiofauna are important to include in community analyses for an accurate estimate of species richness, to identify differences among structurally similar communities, and to understand input/output between vents and the deep-sea.
8) Measurements such as species richness and diversity indices may be poor at distinguishing vent communities because the communities are species poor and evenness is low. Biomass and species abundance distributions may be useful ways to reveal community differences.
9) The Michaelis Menten method of nonparametric species richness estimation is the most accurate estimator of total vent species richness. The Chao 2 and Jackknife 2 methods may also be useful.

What can be learned from the above?

Community structure

Communities on Axial, north Cleft, and ACC are similar in species richness, evenness, percent-average relative abundance, numerically dominant species, and species composition. *Lepetodrilus fucensis* is the dominant species in terms of distribution and abundance (Chapters 2, 4, and 5). This observation provides a basis to synthesize information on community ecology for the Juan de Fuca Ridge. To complete this synthesis, data from communities on Endeavour and Middle Valley are needed. Once these data are available we can begin to answer questions on the ridge scale. Are spatially disjunct Juan de Fuca vent assemblages distinguishable? If all Juan de Fuca communities are not the same in terms of community structure, what factors are responsible for observed differences? Can habitat diversity explain observed differences? Axial, Cleft, and ACC, have basalt and sulphide vents. While substratum does not affect differences in diversity among vents in these regions, perhaps if taken over the entire ridge, a basalt versus sulphide pattern would emerge.

Endeavour segment has both sedimented and hard substratum vents and Middle Valley is a sedimented basin with exposed massive sulphides. Does habitat turnover (e.g. different habitat types) along the ridge explain between-habitat diversity? At the scale of Axial, Cleft, and ACC it may not (Chapter 5), but maybe at the ridge scale it does. Juniper et al. (1992) suggest that high species diversity at one sedimented site at Middle Valley may be partly due to the mixture of hard and soft substrata. Tunnicliffe et al. (1996) believe that strong affinities among the faunas of three sedimented hydrothermal sites in the eastern Pacific provide further evidence for a strong substratum effect on faunal composition at vents. Variability of habitat conditions is often used to explain observed differences in patterns within a ridge (Juniper et al. 1992; Jollivet 1996; Tunnicliffe et al. 1996; Shank et al. 1998) and among ridges (Juniper and Tunnicliffe 1997; Desbruyeres 1998; Tunnicliffe et al. 1998), but this hypothesis remains untested.

Geophysical work on the Juan de Fuca suggests that two general "types" of vent subsurface controls exist. There are tectonised environments such as Endeavour where fluids are channeled and heat sources are deep and crack-accessed (Robigou et al. 1993). There are shallow magmatic volcanic environments such as Cleft and Axial, where fluids circulate freely within the extrusives, and much or most of the deposits may be hidden in the shallow crust (RIDGE 1999). There may be differences in the biological communities based on this geophysical division. Differences in geophysical heat source can cause differences in geochemistry and the extent and periodicity of venting. Chemical differences in fluid chemistry as well as relative stability and predictability in available vent habitat may influence the structure of communities. Trask and van Dover (1999) found differences in vent mussel isotopic composition between two chemically distinct sites within a Mid-Atlantic Ridge vent field. In Chapter 3, the one senescent sample from Endeavour falls out quite separately from the rest of the samples. Also, preliminary data from one basalt tubeworm community on Endeavour indicate that *Depressigyra globulus* is the dominant organism at 10% relative abundance while *Lepetodrilus fucensis* is at 4% (RIDGE 1999; Urcuyo, pers. comm.). Not only is the Endeavour sample rank-abundance different from Cleft and Axial rank-abundances (Chapters 2, 4, and 5), but the community appears to be much more even as well. However, equivalence in processing methods remains to be assessed.

Several researchers have linked spreading rate to community structure and in particular to diversity (Juniper and Tunnicliffe 1997; Desbruyeres 1998; van Dover and Trask 2000). Biogeographical comparisons among ridges are one way to test this idea. The Juan de Fuca Ridge appears to have a mixture of tectonic and volcanic environments as well as mechanisms of heat transfer typically predominant on either fast- or slow-spreading ridges (RIDGE 1999). Similar to testing habitat effects of sediment versus hard substratum, the effect of spreading rate on diversity can be tested. To begin, a regression of spreading rate versus standardised species richness (e.g. rarefaction estimates to a minimum sample size, species density, species richness) could be done for vent sites. Multivariate analyses to see if vents from ridges with similar spreading rates fall out together and pairwise correlations could also be done. Residuals of the regression between spreading rate and age can be done to can be done to account for historical factors.

Temporal differences in communities

A number of studies describe temporal change in vent communities (Chapter 2: Table 2.1). Most of these studies characterise the initial colonisation stage and some extend to later stages of venting. In Chapter 2, we attempted to document succession from the initial to final stages of venting on north Cleft. We did not see a pattern because the transition from initial to intermediate stage was more rapid than the interval of sampling and senescent vents were not sampled. In Chapter 3, I document differences in communities between active and senescent vents as a proxy for temporal succession (except at CoAxial where temporal succession of one vent can be described). There are differences between intermediate and senescent stages. In fact, in Chapter 4, I argue that vents of different successional states (intermediate and senescent) are responsible for the greater species richness of the South Rift Zone (SRZ) and for the differences among the SRZ and ASHES and CASM. The differences between SRZ communities and the rest of Axial are not due to spatial location. South Rift Zone senescent communities are different from non-senescent SRZ communities and community characteristics of senescent assemblages are similar for communities on Endeavour, CoAxial, and the SRZ (Chapter 4 and 5).

Distribution

The distribution-abundance relationship

The most abundant species on Axial and Cleft are the species with the widest distributions within a region and vice versa. Brown's (1984) explanation for the positive correlation between geographic range size and abundance is that species able to exploit a wide range of resources (i.e. species with broad niches) can become both widespread and abundant. If Brown's (1984) niche breadth hypothesis is correct, widespread species with wide trophic niches should have high local population densities. *Lepetodrilus fucensis* and *Depressigyra globulus* are two of the most abundant and widespread species on ACC and both may have broad trophic niches (Levesque and Juniper 2000; Chapter 2). At Axial, Cleft, and senescent communities however, the polynoids *Branchinotogluma* sp., *Lepidonotopodium piscesae*, and *Levensteiniella kincaidi* do not fit this pattern. These large, mobile species may have wide dispersal capabilities but be limited in local abundance by competitive interactions or life history characteristics. *Branchinotogluma* sp. and *L. piscesae* appear to have wide niche breadths: they are trophic generalists (Levesque and Juniper 2000) and *Branchinotogluma* sp. is present at active and senescent vents. *L. kincaidi* is often found at greater abundances at senescent vents and this species may be in low numbers at active vents because of competitive interactions that are reduced or alleviated when the habitat changes to a senescent state.

Wide distributions of species in low abundances are not necessarily unusual. Higher dispersal rates evolve in ephemeral habitats in response to fluctuating habitat availability (Keymer et al. 2000). Pitman et al. (1999) found a majority of tree species in the Peruvian Amazonian basin to be geographically widespread even with low average densities over the entire network of plots. However, the Amazonian basin is a species-rich forest, where a large number of rare species coexist and evenness is much greater than at vents. If species are in low abundance and widely dispersed over the uneven community of the ACC region, then this suggests two explanations. 1) that some species do not produce as many successful recruits as other species; and/or 2) recruitment and survivorship are limiting for populations low in abundance. Tunnicliffe et al. (2001) wonder whether "pioneer" species of new vents may be particularly suited to local dispersal and establishment and whether later species are less efficient in dispersal or whether habitat conditioning is more important for within region distributions. Studies of experimental recruitment to artificial settlement panels indicate that post-settlement interactions are important in structuring vent communities on the East Pacific Rise (EPR) (Mullineaux et al. 1998; Mullineaux et al. 2000). These post-settlement interactions include facilitation by early colonizers via a presumed mechanism of habitat modification that induces settlement of later species (Mullineaux et al. 2000). Desbruyeres (1998) states that colonisation rates after disturbances, the early settlement of a vent mussel species coincident with the revitalisation of a vent site, and the infrequency of abiotic active vent sites, suggest propagule supply is not a limiting factor for the settlement and development of EPR vent communities. Communities are more influenced by local factors such as habitat suitability and intraspecific competition for space and resources. Time-series sampling of artificial recruitment substrata at vents on Axial or Cleft as well as sampling of the water column above and around the vents is necessary to understand differential contributions of dispersal, recruitment, and survivorship to community structure.

The effect of insufficient sampling of the entire vent habitat cannot be discounted. The species I find to be widely distributed and in low abundances, may be in high abundance somewhere over their range. My work does not include the entire range of any Juan de Fuca species. Murray et al. (1999) find only 5% of Australian flowering plant species from dry sclerophyll woodland and temperate rainforest to be sparse when the species entire ranges are considered.

Interestingly, in productive habitats, an even distribution of species versus proportion of occupied sites is expected, while in less productive habitats where some species can monopolise resources, a core-satellite distribution is expected (Maurer 1999). An idea for future study is an investigation of other productive systems for bimodality in species distributions across abundances. If the vent environment is unique, then vent specific reasons for a core-satellite distribution can be evaluated. If the vent environment is not unique, then Maurer's (1999) prediction is not supported and the focus should shift to other explanations for the distribution-abundance patterns of species.

Seventy-five percent of the vent species on Axial (Chapter 4), north Cleft (Chapter 2), or the ACC region (Chapter 5) are widely distributed. This is not surprising given the dispersal potential of some vent species inferred from length of larval life, speed and direction of ambient currents, direct collections of planktonic larvae, and studies of genetic similarity between disjunct populations (Mullineaux and France 1995; Mullineaux et al. 1995; Tunnicliffe et al. 1997; studies reviewed in Vrijenhoek 1997). Population genetics work needs to be done on these species to understand exact movement patterns among the regional pool. Molecular techniques can tell us how widely populations are dispersed within the region. Only when we know the relatedness of intra- and intersegmental populations can we make inferences about the dispersal abilities of each vent species. Nonetheless, species, even some in low abundances, are distributed across this region.

Metapopulation theory

Models of population dynamics are constructed to predict how population sizes change under different conditions, including the effect of population size. Metapopulation models are a type of population biology model that emphasize the importance of the spatial structure of discrete patches of populations. Metapopulations are ensembles of interacting populations in discrete habitat patches that persist via processes of population turnover, extinction and establishment (Hanski 1991). Metapopulation theory assesses the effects of local extinctions and (re-) colonisations on the persistence of the regional population (Hanski 1996). Metapopulation models assume that: 1) space-occupancy is discrete; 2) ecological processes take place at two scales; and

3) discrete spatial units of habitat are large and permanent enough to enable persistence of local breeding populations for at least a few generations (Hanski 1999). In addition, no single population should be large enough to have a long expected lifetime in comparison with the expected lifetime of the metapopulation (Hanski and Kuussaari 1995).

Discrete space-occupancy and ecological processes at two spatial scales are two characteristics of vent community persistence. A metapopulation is a "population" of many local populations that are connected by dispersing individuals. Local populations exist in a regional network of habitat patches and each local population has a substantial probability of extinction. Hanski (1999) asserts that the metapopulation concept is of the greatest value when applied to species living in physically patchy environments with sufficiently large patches to support local breeding populations. Hydrothermal communities are made up of discrete habitat patches supporting locally breeding populations. Community persistence is dependent on dispersal between habitats and diversity maintenance occurs at two scales (Chapter 5). Although vents go extinct (Chapter 3), vent populations persist in a region. Vrijenhoek (1997) was the first to recognise the potential applicability of metapopulation models to vent populations. He discusses population genetics of vent animals in the context of metapopulation theory although he does not explicitly explain how metapopulation models could be applied to vent species.

Vent communities on the Juan de Fuca last from a few years (e.g. CoAxial) to tens of years (e.g. Axial, Endeavour). Even ephemeral vents on CoAxial were present long enough to enable persistence of local breeding populations for at least a few generations. The transitory nature of the vent system is not a problem for a metapopulation approach because extinction of populations in some patches is essential for the general model. Hanski (1987) discusses metapopulations inhabiting ephemeral dung and carrion habitats. However, the ephemeral nature of the vent habitat and his examples differ. Dung and carrion inhabiting species have larvae that tend to be fixed and it is the adults that move from patch to patch whereas vent species can immigrate/emigrate only via larval dispersal. Species on dung or carrion can use up or extinguish their resource. Although the amount of H_2S is a limiting resource, the vent animals themselves cannot cause the extinction of their habitat.

Vent extinction is due to abiotic factors such as cessation of heat source and changes in fluid chemistry. Many metapopulation models (e.g. the patch-occupancy model of Hanski 1994) ignore local population dynamics. Ignoring local population dynamics greatly reduces the realism of a model. At vents however, while species interactions are probably important, patch persistence is ultimately dependent on the chemical conditions of the vent fluid and so the abiotic environment is probably limiting.

Currently, most metapopulation models assume a set of habitats with an equal chance of extinction for each patch. The extinction and creation of habitat patches is considered to be uncorrelated. Vent extinction and creation, however, are frequently correlated in time and space along a ridge segment. Local vent populations fluctuate synchronously among habitat patches. Thus, the temporal distribution of vents is an important element that must be considered when looking at the maintenance of metapopulations. Simple metapopulation models that depict a finite or infinite set of populations, all of which are subject to extinction with equal and temporally independent probabilities (Harrison 1991) will be inappropriate.

The assumption that no single population is large enough to have a long expected lifetime in comparison with the expected lifetime of the metapopulation is not valid for populations in the Axial, Cleft, and CoAxial region (Chapter 5). Harrison et al. (1995) test conditions for metapopulation coexistence of competitors for a food resource. They find a metapopulation model unlikely to apply in their system. The application of the model is inappropriate because of the dispersal capability of the dominant competitor. Dispersal is so high that patches are unlikely to act as separate dynamic entities with respect to competition. The regional colonisation time scale appears much faster than the local competition time scale. Given the apparent widespread dispersal of most vent endemics on ACC, metapopulation theory is unlikely to successfully predict species persistence at the ACC scale. However, if vent metapopulations are considered on the scale of a entire ridge, then spatial and temporal correlation of vent patch existence may not be problematic as magma supply (i.e. vent persistence) to each ridge segment may be independent (MacDonald et al. 1988) and dispersal may be low enough that patches have different population dynamics.

Future work on understanding abundances and distributions of vent species could include application of a metapopulation model to selected species. The potential is two-fold: a useful model may emerge for describing patterns for some vent species and modifications can be incorporated into general metapopulation models to make them more realistic. Jollivet et al. (1999) use a metapopulation model to describe the role of dispersal in structuring gene flow of vent species. Their model is a compromise between existing conceptual models and what is currently known of the biology and ecology of one of the best-studied vent species, the polychaete *Alvinella pompejana* on the East

Pacific Rise. They find that exchanges among populations mainly depend on the habitat's movements along the ridge axis rather than the organism's dispersal. This leads them to propose a new model based on patch-network displacements in which transient contact zones allow low levels of genetic flow throughout the metapopulation (Jollivet et al. 1999).

Stelter et al. (1997) note a mismatch between theory and empirical studies of metapopulations: models assume a static landscape but patchy landscapes inhabited by metapopulations are often dynamic, presenting a "shifting habitat mosaic". In their study, grasshoppers on Northern Alps gravel bars had their substratum periodically wiped out by catastrophic floods or made uninhabitable by succession. Deterministic extinctions are also common in the vent system. By incorporating a dynamic system into the model, Stelter et al. (1997) are better able to predict realistic persistence times for their population. Keymer et al. (2000) show that metapopulation persistence in dynamic landscapes depends on the interactions of three factors: the amount of habitat in the landscape, the rate of change of the amount of habitat, and the life history of species living in the landscape. These three factors correspond to the area of venting on a segment or ridge, habitat turnover (a function of segment spreading rate), and dispersal capabilities of the vent organisms.

Hanski (1994) describes a minimalistic model that characterises the effect of patch area and isolation on occupancy that only requires data on species presence/absence, patch area, and inter-patch distances. This model is a generalised incidence function that describes how the fraction of occupied habitat patches depends on patch area and isolation. Parameter values are estimated and the equilibrium fraction of occupied patches in a system of habitat patches is predicted. The significance of particular habitat patches for the long term persistence of the metapopulation can be evaluated. It would be interesting to use such a model to predict the minimum patch size for occupancy by, and turnover rate of, selected vent species and see how well such predictions match observed distributions. Application of this kind of metapopulation model may help explain the role of patch area and inter-patch distance in determining the distribution of some vent species.

The selection of an appropriate species or population to study with a metapopulation approach is crucial to the successful application of the model. "Many populations appear to be patchy to the human eye, but critical examination is required to deduce the dynamic consequences of this patchiness." (Harrison et al. 1995). Candidate vent species should be species that are neither rare nor common in distribution. On the segment scale, a candidate population should be present at fewer than half of the vents in a region.

If we want to use the concept of metapopulation biology to describe population and species distributions and persistence, it is also critical to choose an applicable metapopulation model. I propose that vent populations will be best described by a mainland-island model. Vrijenhoek (1997) found the island model to explain gene flow in some vent endemics on the East Pacific Rise. The key process of classical metapopulation models is the regional process of extinction and colonisation. For a mainland-island model, local factors such as population size, habitat heterogeneity, and within-population dispersal are the important processes (Harrison 1991). Persistence of larger populations in "island" patches must be much longer than the time scale of interisland dispersal for the mainland-island model to be suitable. For the southern Juan de Fuca, the time for colonisation of new vent habitat is shorter than the persistence of populations. Post-eruption sampling at Cleft (Tsurumi and Tunnicliffe 2001) and CoAxial (Tunnicliffe et al. 1997) as well as temporal sampling of Axial has demonstrated this. Large differences in patch size suggests that populations will be similar in their dynamics to mainlands and islands (Harrison 1991). Different vent fields have large variations in habitat area and population size. If the pattern of patch occupancy for vent populations is explained by distance from a large area of sustained venting, then persistence of vent metapopulations may be relatively unaffected by population turnover on the small patches. For example, vent populations at low temperature north Cleft and CoAxial vents have probably gone extinct with extinction of the habitat, but populations of these species persist on Axial. Thus local extinction can be frequent and correlated, but may be relatively unimportant in terms of regional dynamics (Harrison 1991).

Future work could posit a relatively large vent field as a "mainland" and then look at population sizes of species on smaller habitat patches as a function of patch size and distance from this island. If population and species distributions are correlated with distance from the island then we will know that patch size for "island" patches may not be as important as isolation from the mainland in determining the species' distribution. The effects of population or patch size and isolation on species persistence can also be investigated with a metapopulation approach for species as described by Ouborg (1993). Abundances of species at sites from two different years can be compared to determine which of the populations went extinct in between sampling dates. Population sizes of species in the first sampling group and the degree of isolation of the patch (distance to nearest vent with the same species and the number of occupied sites with that species within a range of X kilometres) can be quantified. Habitat quality can also be quantified with fluid characteristics and/or an indicator such as amount of tubeworm biomass. An analysis using stepwise multiple logistic regression with presence or absence as dependent variables can assess the relative importance of the independent variables.

Local and regional dynamics

A combination of local and regional influences probably best explain observed local vent diversity. Holt (1993) classifies regional effects on local species richness: 1) source pool effects; 2) spatial dimension of species-specific autecological needs; 3) source-sink population structures in a heterogeneous environment; 4) habitat selection in heterogeneous environments; and 5) metapopulation dynamics. Holt (1993) argues that species in a community differ in the spatial scale they require for the successful completion of their life cycles and they differ in their ecological and evolutionary responses to spatial heterogeneity. I would also add that species vary in their responses to temporal heterogeneity; Holt (1993) implicitly recognises this factor by including metapopulation dynamics as a mechanism structuring local communities within a larger landscape.

Caley and Schluter (1997) posit that local diversity is a function of the continuum of relationships from primarily local to primarily regional control, depending on the community in question. The literature presents models predicting dominance of either local or regional processes; simple and consistent predictions are not available about the expected relationship between local and regional diversity patterns. Studies have examined the relationship between local and regional richness for a limited range of taxa and regional diversities. If there is a similarity between taxa and continents in the form of a local-regional diversity relationship, then there may be "rules" governing the assembly of local communities that are widely consistent. For Huston (1994), the critical issue is not whether regional or local processes are most important, but identifying the conditions under which local or regional components of diversity are most important.

For the Axial, Cleft, and CoAxial region, local diversity is linearly related to regional diversity and patchy habitat beta diversity is higher than continuous habitat beta diversity while gamma diversity is approximately the same for both habitat types (Chapter 5). On the ACC, regional processes such as dispersal, the regional species pool, and rates of immigration are probably more important than local interactions such as competition in determining local diversity. I predict that vent faunas on different ridge systems will have similar local interactions among species, but will have different species richness. Furthermore, local species richness will be a linear function of regional species richness for each ridge. Vent faunas on different ridges are different at the species level, but genera are almost identical along systems of connected ridges and nearly all species belong to a restricted number of specialised families occurring throughout the whole ridge network (Jollivet 1996). The narrow subset of conditions within a broader range of venting possibilities (Tunnicliffe 1991) combined with the similar phylogenetic composition of vents will lead to similar local interactions at vents on different ridges. Thus, given similar local processes influencing local diversity on all ridges, the pattern of proportional sampling for the ACC region will be repeated at the ridge and interridge scale.

Comparing vent systems to other habitats

Vent communities should be compared to communities with similar diversity and evenness parameters as well as disturbance and productivity regimes. Systems such as early successional states of communities, selected taxocenes on ephemeral substrata like beetles on fungi, dung, or carrion, organically polluted habitats such as soft sediments in areas of sewage outfall, oxygen minimum zones beneath upwelling regions in the deep-sea, or high disturbance and/or low diversity systems like the rocky intertidal or tundra are probably more relevant to compare with the vent habitat than the deep-sea (Chapter 5). The non-vent deep-sea is very different in diversity and representation of major taxonomic groups from vents (Tunnicliffe 1991; Chapter 3). Also, most sampling of the non-vent deep-sea is from soft-sediment communities while most vents are on hard substratum. Even studies of non-vent hard substratum communities, however, indicate a divergence between vent and non-vent deep-sea fauna. Tunnicliffe (1992) compares species distributions among taxonomic classes of vent and deep-sea ridge fauna from the northeast Pacific. Vent species are distributed among eight classes with most fauna in the Polychaeta, Vestimentifera, Gastropoda, and Crustacea. Non-vent ridge species are distributed among 13 classes, few to none contained in the four common vent classes. A study on a deep-sea hard substratum assemblage on glass sponges describes a fauna that is phyletically different in composition and much more even in abundance than the vent fauna (Beaulieu 2001).

Comparing similar communities makes observed similarities and differences meaningful. Differences and similarities in patterns and mechanisms structuring communities may shed light on the ecology of all communities being compared. For example, the keystone species concept of Paine (1966) was developed in the rocky intertidal. Is there a comparable set of interactions in the vent environment? With the numerical dominance of *Lepetodrilus fucensis* in the ACC region it is unlikely that there are any predators that maintain diversity at higher levels by paring down populations of dominants like the limpet, but the question awaits testing. Also, what happens if *L. fucensis* is excluded from a site? Species-specific removals and exclusions are impossible in the vent environment but it may be possible to exclude all adults and juveniles, in large part *L. fucensis*, and observe what larvae recruit and develop over a time-series. The observation that diversity peaks over intermediate disturbance levels (Connell 1978) is supported by a wide range of data. How does the concept hold up in the vent habitat? Juniper and Tunnicliffe (1997) use the intermediate disturbance hypothesis as one of their criteria in evaluating diversity of ridges with different types of spreading rates, but diversity peaking with intermediate disturbance frequency has not yet been demonstrated for vents. Investigations into this could be done at two levels: the intersegmental and local scale. The former would be a diversity comparison among segments with different spreading rates on the Juan de Fuca because spreading rate is linked to disturbance frequency (Juniper and Tunnicliffe 1997). The latter would be an experimental manipulation at a long-lived site such as ASHES vent field with sampling at different rates as the disturbance.

Meiofauna

Meiofauna are important to include in community analyses to obtain an accurate count of species richness, to identify differences between structurally similar communities, and to catalogue input/output between vents and the deep-sea. Species richness increases when meiofauna are considered (Chapter 2). Successional differences are also clearer when meiofauna are considered (Chapter 3). Species abundance distributions (Chapter 4) may be more correct if meiofauna are used. For example, sampling effects tend to produce a truncated lognormal pattern as rare species are often missed in sampling (Sageman and Bina 1997). A truncated lognormal can approximate a log series depending on where the sampling limit falls relative to the mode of a normal distribution (Hughes 1986). Including meiofauna increases the number of species represented by a sample and may reduce the chance of seeing a log series distribution when the community really follows the truncated lognormal. Including meiofauna may also reduce the chance of seeing the truncated lognormal when the community is lognormally distributed. Including meiofauna in diversity indices and rank-abundance curves may increase the accuracy of these measures.

Measurements of vent diversity

The Juan de Fuca vent communities discussed in this thesis have very uneven species representation and low diversity. In Chapter 4, I suggest that community descriptors such as biomass and species abundance distributions may be more useful parameters to elucidate differences among communities. Diversity indices and rank-abundances based on macrofauna do not distinguish vent communities well. An alternative to common indices such as the Shannon-Wiener and Simpson's is a measure of taxonomic distinctness proposed by Warwick and Clarke (1995). Taxonomic distinctness (Δ^*) is a measure of taxonomic distance between individuals of different species and is independent of sample size. Additionally, this measure is scale-independent and so can generalise data matrices that are species counts, biomass, or percent substratum cover. Although vent species are similar among vents on a ridge and genera are similar among ridges, taxonomic distinctness may be useful to distinguish between temporal stages of venting. The senescent community in Chapter 3 has greater species richness than the non-senescent community, but this difference is not striking. Senescent and active vents differ more in the suite of species present, than in their overall species numbers. If taxonomic distinctness is used to compare these communities, I predict more marked differences in the communities will be apparent.

Nonparametric methods of estimating vent species richness were evaluated in Chapter 5. Some of these methods may be useful for estimating vent species richness from a small number of samples. Another approach to estimating species richness is to estimate the minimum number of samples needed to find a preset number of species with a known degree of confidence (Tsurumi and Potter, unpubl.). A theoretical vent species distribution can be created as a sampling universe. This species distribution would follow the geometric series based on known vent species abundance distributions (Chapter 4). The user could then define the estimated number of species and number of samples. The computer then randomly samples the theoretical distribution for the specified number of samples and generates a species richness mean and variance. This whole process is then repeated 1000 times and a mean and variance for the number of species in the chosen number of samples and 95% confidence intervals around this estimate can be calculated. This program could be used *a priori* to estimate minimum sample size and *a posteriori* to give confidence limits around the species richness for a given number of samples and species count.

Conclusions

Rosenzweig (1995) implores researchers to make models as simple as possible: find the variables that really make the system behave and join them into the simplest of formal structures. In many ways, the vent environment is suited to this approach. Vent communities have clearly defined boundaries that are dependent on physico-chemical conditions for their vigour and sustenance and have relatively few species with a known degree of taxonomic relatedness. The underlying theme of my work is that patterns first need to be described. Once patterns are identified, we can take advantage of the unique features of hydrothermal communities to empirically test ecological theory about mechanisms producing observed patterns and to build formal models. I see my contribution to ecology with this thesis as two-fold: 1) I add and synthesise knowledge of species and their distributions in a three-segment region of the Juan de Fuca; and 2) I use this natural history to describe and compare vents at the intra- and intersegment scale and evaluate community patterns and processes within a framework of general ecology.

Major conclusions from this work are:

1) Active vent communities at the segment and three-segment scale have the same rank-abundances, dominant species, density, diversity, and species associations. Spatial differences between communities are not apparent with these parameters.
2) Active vents follow a geometric series species abundance distribution.

3) Three pairs of species are positively associated at both the inter- and intrasegment scale: *Paralvinella pandorae* and *Paralvinella palmiformis*; *Lepetodrilus fucensis* and *Depressigyra globulus*; and *Branchinotogluma* sp. and *Lepidonotopodium piscesae*.
4) The limpet, *Lepetodrilus fucensis* is the dominant species in distribution and abundance.
5) An initial stage of venting cannot be detected if sampling does not occur within two years of habitat generation.
6) Senescent communities can be identified. These communities are lower in density, more variable in species composition, have higher species richness, and are more even in rank-abundance. There are shifts in dominant species between senescent and non-senescent vents although *Lepetodrilus fucensis* is often dominant. Senescent communities are transition zones from vent to non-vent deep-sea community; dying vents have more non-endemic species and these species are in greater abundances than active vents.
7) Total vent diversity, as measured by the regional species pool, is increased by having vents in different successional states.
8) Almost 75% of Juan de Fuca vent species in the Axial, Cleft, and CoAxial (ACC) region are distributed throughout this region.
9) The most abundant vent species are the most well-dispersed and vice versa. Large mobile polynoid polychaetes are low in local abundance, but are widespread.
10) The ACC region is unsaturated. Spatial isolation, not habitat differences, influences between-habitat (beta) diversity.

11)A few large samples sorted to the meiofaunal (63 μm) level can give an accurate profile of community characteristics as measured by diversity, evenness, and species abundance models.

12)Species richness and diversity indices are not good for distinguishing vent communities because the communities are species poor and have low evenness.

13)The Michaelis Menten nonparametric species richness estimation method is an accurate species richness estimator for vent species.

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Appendix 1: Species list.

Species #	Phylum	Group	Order	Species
1	Annelida	Polychaeta	Capitellida	*Nicomache venticola*
2	Annelida	Polychaeta	Eunicida	*Ophryotrocha globopalpata*
3	Annelida	Polychaeta	Eunicida	*Parougia wolfi*
4	Annelida	Polychaeta	Orbiniida	*Orbiniella hobsonae*
5	Annelida	Polychaeta	Orbiniida?	Spp. unknown
6	Annelida	Polychaeta	Phyllodocida	*Amphiduros axialensis*
8	Annelida	Polychaeta	Phyllodocida	*Branchinotogluma* sp.
9	Annelida	Polychaeta	Phyllodocida	*Harmothoe* sp.
10	Annelida	Polychaeta	Phyllodocida	*Hesiodeira glabra*
11	Annelida	Polychaeta	Phyllodocida	*Hesiospina vestimentifera*
12	Annelida	Polychaeta	Phyllodocida	*Lepidonotopodium piscesae*
13	Annelida	Polychaeta	Phyllodocida	*Levensteiniella intermedia*
14	Annelida	Polychaeta	Phyllodocida	*Levensteiniella kincaidi*
15	Annelida	Polychaeta	Phyllodocida	*Nereis piscesae*
17	Annelida	Polychaeta	Phyllodocida	*Opisthotrochopodus tunnicliffeae*
18	Annelida	Polychaeta	Phyllodocida	*Protomystides verenae*
19	Annelida	Polychaeta	Spionida	*Prionospio* n. sp.1
20	Annelida	Polychaeta	Spionida	*Prionospio* n. sp. 2
21	Annelida	Polychaeta	Terebellida	*Amphisamytha galapagensis*
22	Annelida	Polychaeta	Terebellida	*Paralvinella dela*
23	Annelida	Polychaeta	Terebellida	*Paralvinella palmiformis*
24	Annelida	Polychaeta	Terebellida	*Paralvinella pandorae*
25	Annelida	Polychaeta	Terebellida	*Paralvinella sulfincola*
26	Arthropoda	Arachninda	Acarina	*Copidognathus papillatus*
27	Arthropoda	Copepoda	Calanoida	mostly *Clausocalanus lividus*
28	Arthropoda	Copepoda	Harpacticoida	4 families: Diosaccidae, Ectinosomidae, Thalestridae, and Tisbidae
29	Arthropoda	Copepoda	Harpacticoida	Family Tisbidae, Copepoda Type 1
30	Arthropoda	Copepoda	Harpacticoida?	Copepoda Type 2 (copepodites?)
31	Arthropoda	Copepoda	Harpacticoida?	Copepoda Type 9
32	Arthropoda	Copepoda	Siphonostomatoida	*Aphotopontius forcipatus*
33	Arthropoda	Copepoda	Siphonostomatoida	*Benthoxynus spiculifer*
34	Arthropoda	Copepoda	Siphonostomatoida	*Barathricola rimensis*
35	Arthropoda	Copepoda	Siphonostomatoida	*Misophriopsis longicauda*
36	Arthropoda	Copepoda	Siphonostomatoida	*Stygiopontius quadrispinosus*
37	Arthropoda	Copepoda	Unknown	Copepoda Type 10
38	Arthropoda	Copepoda	Unknown	Copepoda Type 11
39	Arthropoda	Copepoda	Unknown	Copepoda Type 12

Species #	Phylum	Group	Order	Species
40	Arthropoda	Copepoda	Unknown	Copepoda Type 13
41	Arthropoda	Copepoda	Unknown	A3244-3979 type copepoda
42	Arthropoda	Malacostraca	Amphipoda	Spp. unknown
43	Arthropoda	Malacostraca	Amphipoda	Lysianassid, near *Valettiopsis*
44	Arthropoda	Ostracoda	Myodocopida	*Euphilomedes climax*
45	Arthropoda	Ostracoda	Myodocopida	Spp. unknown
46	Arthropoda	Ostracoda	Podocopida	Spp. unknown
47	Arthropoda	Pycnogonida		*Ammothea verenae*
48	Cnidaria	Anthozoa	Actiniaria	Actinostolidae n. spp (2)
49	Cnidaria	Hydrozoa	Unknown	Spp. unknown
50	Mollusca	Bivalvia	Eulamellibranchia	*Calyptogena pacifica*
51	Mollusca	Bivalvia	Filibranchia	*Idasola washingtonia?*
52	Mollusca	Bivalvia	Thyassirid	Sp. unknown
53	Mollusca	Gastropoda	Caenogastropoda	*Provanna laevis*
54	Mollusca	Gastropoda	Caenogastropoda	*Provanna variabilis*
56	Mollusca	Gastropoda	Neomphalina	*Depressigyra globulus*
57	Mollusca	Gastropoda	Neomphalina	*Lacunoides* n. sp.
58	Mollusca	Gastropoda	Neomphalina	*Melanodrymia brightae*
59	Mollusca	Gastropoda	Patellogastropoda	*Pyropelta musaica*
60	Mollusca	Gastropoda	Vetigastropoda	*Clypeosectus curvus*
62	Mollusca	Gastropoda	Vetigastropoda	*Lepetodrilus fucensis*
63	Mollusca	Gastropoda	Vetigastropoda	*Temnocinclis euripes*
64	Mollusca	Solenogaster	Neomeniomorpha	*Helicoradomenia juani*
65	Nematoda	Unknown	Unknown	Spp. unknown
66	Nemertea	Enopla	Hoplonemertea	*Thermanemertes valens*
67	Acoelomates?			?
68	Porifera			*Asbestopluma* sp. unknown
69	Vestimentifera	Basibranchia	Tevniida	*Ridgeia piscesae*
72	Annelida	Polychaeta	Phyllodocida	*Sphaerosyllis ridgensis*
73	Annelida	Polychaeta		*Neolira racemosa*
74	Arthropoda	Malacostraca	Isopoda	Spp. unknown
75	Arthropoda	Malacostraca	Amphipoda	*Pardalisca endeavouri*
76	Mollusca	Bivalvia	Eulamellibranchia	Vesicomyid
77	Arthropoda	Malacostraca	Tanadaicea	Sp. unknown
78	Annelida	Polychaeta		Sp. unknown
79	Mollusca	Gastropoda		*Buccinum thermophilum*
80	Echinodermata	Ophiuroidea		Sp. unknown