Community ecology of hydrothermal vents at Axial Volcano, Juan de Fuca Ridge, northeast Pacific

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

DOCTOR OF PHILOSOPHY

in the Department of Biology

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Abstract

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Hydrothermal vents are deep-sea hot springs. Vents are home to luxuriant assemblages of animals that colonize the warm venting fluids. High biomass is fed by microbes that use hydrogen sulphide and other reduced chemicals in the vent fluid as an energy source to fix inorganic carbon. Individual vents may persist for a few years to several decades. The specialized animals must find new vents, cope with changing fluid conditions and foster their offspring.

The composition and structure of vent communities vary in space and time. My research at Axial Volcano, a seamount on the Juan de Fuca Ridge (JdFR) in the northeast Pacific, aims to find pattern in this variation and to propose viable hypotheses of the mechanisms driving the patterns. Axial is an ideal location as it supports mature vent fields (venting for over 15 years) and young, developing vents initiated by a volcanic eruption in 1998. Thus, I was able to study both temporal and spatial variation in vent communities at the same site and relate patterns of developing assemblages to patterns observed at longer-lived vents.

Pattern detection is the first critical step in any community ecology study as it justifies and focuses the search for process. I have refined existing statistical methods and developed novel techniques to test for pattern in vent species distributions and abundances. I modified an existing null model approach and showed that species distributions among sixteen vents differ from random in a long-lived (>15 years) vent field. I also developed a novel null model to confirm that initial patterns of community assembly seven months following the Axial eruption differ from random recruitment of species and individuals to new vents.

My description of the community response to the Axial eruption is the first quantitative report of patterns of vent colonization and succession. My work documents that new vents are colonized quickly (within months) and that initial assemblages are variable. However, rapid community transitions and species replacements within the first few years cause new assemblages to resemble mature vents by 2.5 years post-eruption. Three habitat factors correlate with the development of nascent vent assemblages: the recruitment timing of the tubeworm *Ridgeia piscesae* post-eruption, vent age and vent fluid hydrogen sulphide content. I also describe a new polynoid polychaete discovered colonizing the new vents in high densities.

My major contribution to vent community ecology is revealing species patterns through extensive sampling and rigorous statistical methods. These patterns are a necessary step towards understanding the processes that structure vent communities: they direct future research effort towards the key species and generate hypotheses to be experimentally tested. My work also elucidates how vent species respond to habitat destruction and creation, which is critical information for effectively managing Canada's only hydrothermal vent Marine Protected Area on the JdFR.

Examiners:

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Acknowledgments

I wish to express my thanks to the many people who have helped me over the past five and a half years. Your support has been indispensable and you have made my life as a graduate student enjoyable and enriching. I am especially grateful to Verena Tunnicliffe for giving me the opportunity to work in such a fascinating field of biology, and for her patience, insight and guidance. Verena, you are an inspiration to women in science. Many thanks also to my committee members, Brad Anholt, Louise Page and Michael Whiticar for your open door policies and mentorship. A particular thank you to Brad who has offered many hours of his time answering statistical questions and commenting on manuscripts.

I also extend my thanks to those who have made UVic a great place to be a graduate student. To my lab mates past and present - Maia Tsurumi, Jacqueline O'Connell, Anja Schultze, Amanda Bates, Kristi Skebo and Laura Genn - your friendship, humour and support are so appreciated. A special thanks to Maia who has patiently answered many questions and continues to be a source of lively discussions about vent ecology. Laurel Franklin and Jonathan Rose provided lab assistance in countless ways. I thank Eleanore Floyd for administrative support. Heather Down and Tom Gore offered audio-visual assistance for various conference presentations. Thanks also to Darren Volger for brightening my afternoons in the basement of Petch.

Many people have assisted me with fieldwork, and have shared their knowledge of vents with me at sea. Bob Embley, Bill Chadwick and Susan Merle (NOAA) patiently answered many questions about vent geophysics and provided maps of my study site. Special thanks to Bob who was Chief Scientist on many of my cruises – you always made graduate students feel like an integral part of the team. David Butterfield (NOAA) and Gary Massoth (GNS, New Zealand) shared invaluable chemistry data; I thank you both for using precious sampling time and space to take fluid measurements for me. To Kim Juniper (Université du Québec à Montréal) and Anna Metaxas (Dalhousie University), thank you both for your enthusiasm about vent ecology and your support at sea. I also owe much of my positive experiences on research cruises to the many graduate students working on vents from various parts of the world. In particular, Julie Huber (University

of Washington), Christian Levesque (Université du Québec à Montréal) and Stéphane Hourdez (Penn State University) continue to be good friends and collaborators. Last but not least, a big thank you to the ROPOS Guys – Keith Shepherd, Keith Tamburri, Ian Murdock, Bob Holland, Kim Wallace, Mike Dempsey and Craig Elder - your technical expertise, sampling patience and friendships were very much appreciated.

Chuck Fisher (Penn State University) made my dream come true - a trip to the bottom of the ocean in a submarine! Thank you also Chuck for being a great host while I was working at your lab. Dale Calder (Royal Ontario Museum) graciously opened his lab to me for a four-month work visit midway through my degree. Ross Chapman (UVic, SEOS) introduced me to cold seeps - yet another fascinating deep-sea ecosystem - and let me play with ROPOS one more time.

I was supported by various funding agencies over the course of my degree. Reference letters were graciously provided by Don Bowen (BIO), Sara Iverson (Dalhousie University), Verena Tunnicliffe, Brad Anholt, Louise Page, Kim Juniper and Anna Metaxas. Many thanks to NSERC, the Maritime Awards Society of Canada, the Canadian Association of University Teachers, the University of Victoria and the families of Maureen de Burgh, Gordon Fields and Randy Baker for monetary support.

To end, I would like to acknowledge the personalities who inspired me to study marine biology and who have sustained me most throughout this degree. To my parents, Karl and Carol Marcus - thank you for introducing me to the wonders of the ocean and scuba diving at such a young age. Your adventurous spirits continue to be an inspiration, and your unconditional love, encouragement and support are so much appreciated. To my brother David, I thank you for your passion and your wonderful perspective. To my closest friends who have lived these past five years with me, Andrew Sloan and Deanna Mathewson - I thank you both so much for your love and support. Without you two, I doubt I would have made it!

CHAPTER 1

Introduction

Community ecology aims to understand the causes of variation in species distributions and abundances. A community is generally defined as an assemblage of species that occur together in space and time (Begon et al. 1990), although specific definitions may invoke more stringent criteria (Morin 1999). The temporal and spatial scales of a community ecological study are typically defined by the investigator and are dictated by the characteristics of the biological system or habitat under study. Community ecologists are generally not concerned with evolutionary processes that form the regional ensemble of species - the species pool - but rather strive to understand how subsets of that pool assemble in space and time into collections of coexisting species (Figure 1.1).

Three broad categories of processes structure communities: chance, species-environment interactions and biological interactions among species and individuals. Specific causes of community patterns may include competition, predation, facilitation, physiological constraints, indirect interactions and life history characteristics (Morin 1999). The role of recent history is also implicit since communities are dynamic entities that exist through time (Drake 1991).

Pattern detection is the first critical step in any ecological study as it justifies and focuses the search for process (Underwood et al. 2000). Observational and sampling studies coupled with statistical approaches can determine if community structure is nonrandom (Connor & Simberloff 1979) and can uncover the relative importance of abiotic and biotic controls (Schoener & Adler 1991). Although patterns allow for speculation of process, they are not definitive evidence of a particular ecological mechanism: different processes may generate the same pattern while variation in any community likely results from an intricate hierarchy of interacting causes (Quinn & Dunham 1983, Schluter 1984). Thus, experimental work is ultimately needed to ascribe process to community patterns legitimately (James & McCulloch 1990). As the relative importance of stochastic, abiotic and biotic controls on community structure emerges for individual systems, commonalities and differences in process across various systems can

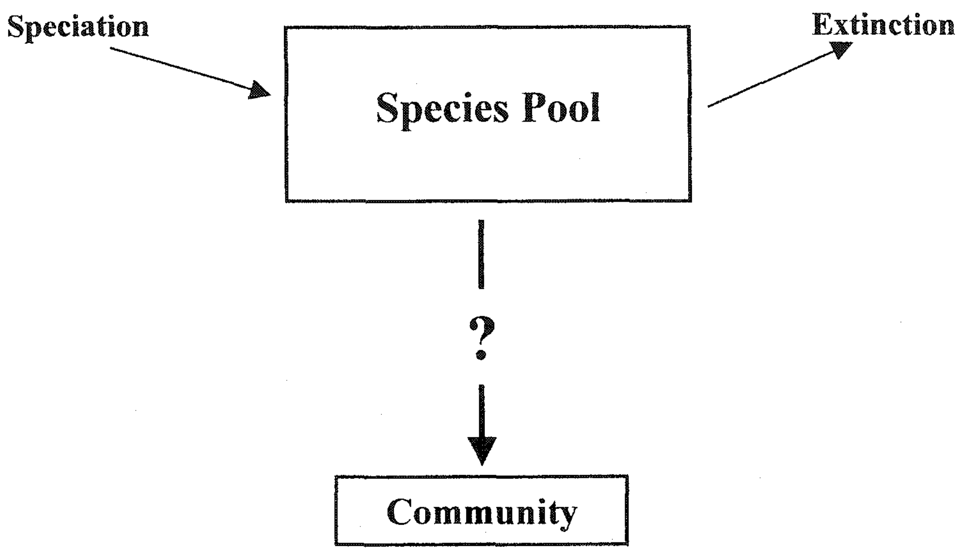

Figure 1.1. A central question of community ecology is how communities are assembled from species pools, whereas evolutionary biology questions the formation of the pool (adapted from Keddy & Weiher 1999). The processes driving community structure (?) fall under three main categories: chance, species-environment interactions and intra- and interspecific interactions.

be determined. Such a comparative approach facilitates a broader understanding of general ecosystem attributes that may underlie shared patterns.

In this dissertation, I explore the community characteristics of a relatively unknown habitat: deep-sea hydrothermal vents. These remote hot springs are home to luxuriant assemblages of animals that colonize the warm venting fluids. Although less than three decades have passed since their discovery (Lonsdale 1977), we now know seafloor venting is a global phenomenon. I proceed with a brief introduction to vents and define terms (*in italics*) that are used throughout this work. I follow with a brief overview of the current status of vent community ecology and introduce the biogeographical setting of this study. I end with my dissertation goals and contributions.

Hydrothermal vents: background and definitions

Vents are the seafloor manifestation of seawater circulation through the oceanic crust. This unique habitat occurs mainly along the Mid-Ocean Ridge (MOR) system where tectonic plates spread apart and new seafloor is formed (Figure 1.2). At spreading ridges, cold dense seawater percolates down through the seafloor deep into the crust where it is heated and chemically altered by water-rock reactions. This buoyant, altered seawater rises back the surface and exits the seafloor. Venting fluid is typically acidic, laden with metals and rich in reducing gases such as hydrogen sulphide. Chemosynthetic microbes use these reduced chemicals as an energy source to fix inorganic carbon and thereby fuel the high biomass of species associated with vents.

Venting occurs in two main forms (Figure 1.3). *High temperature vents* form when focused flow of metal- and sulphide-rich fluid 200°C to 400°C leaves the seafloor and mixes with the surrounding cold seawater. Upon contact, the metal sulphides precipitate from solution and generate a particle-rich 'black smoker' plume that, within a year, can form 5 m high sulphide structures called chimneys (Haymon et al. 1993). *Low temperature vents* do not generate sulphide structures and are typically defined by fluid temperatures up to ~60°C (van Dover 2000), although temperatures may be higher. They form when rising hot fluid is cooled subsurface by mixing with crustal seawater, though secondary processes also contribute to the final chemical character of the fluid (Butterfield et al. submitted). It is around these diffuse fluids that lush communities of

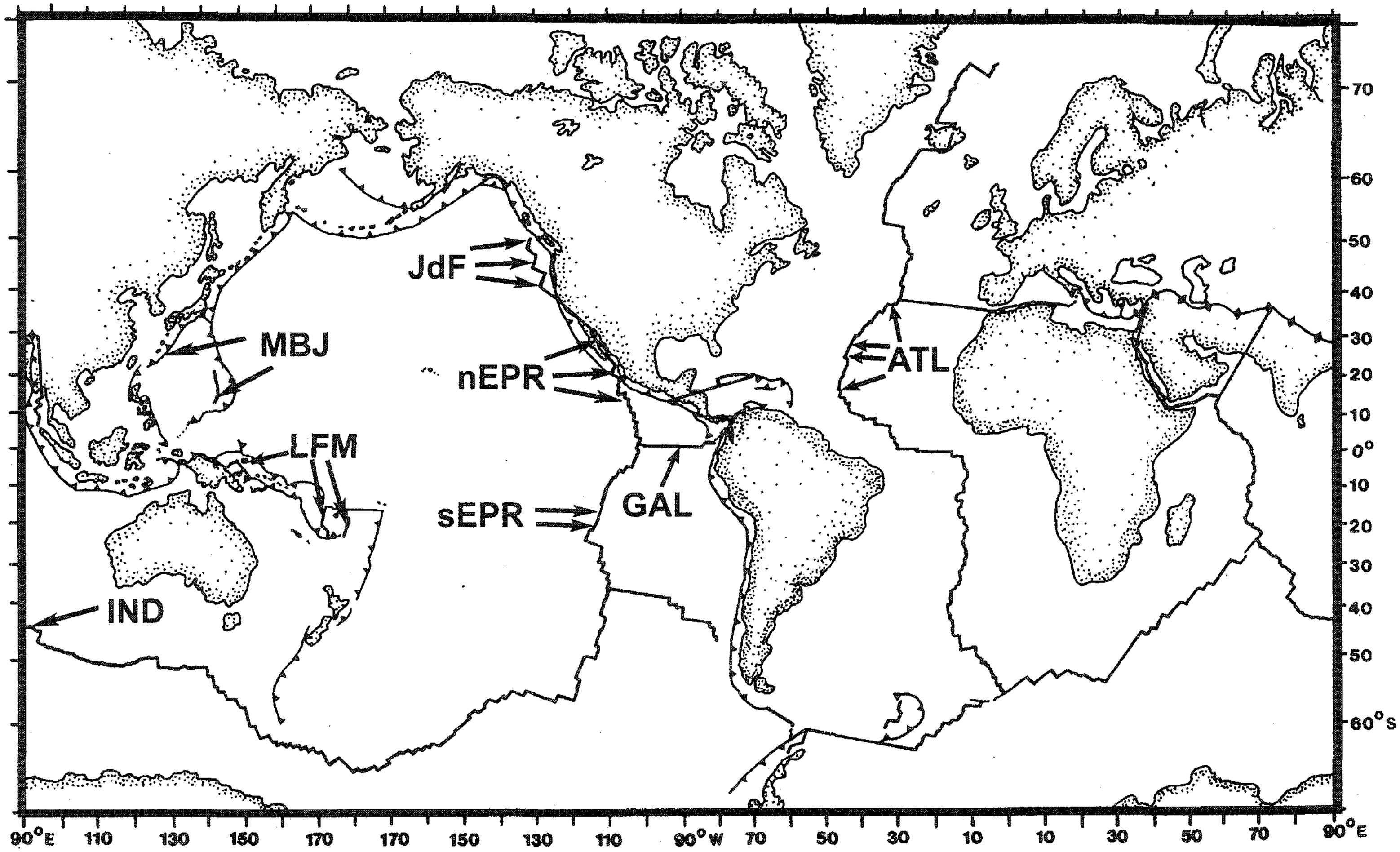

Figure 1.2. Distribution of major vent sites around the globe. Each arrow may represent several vent fields. JdF = Juan de Fuca Ridge; nEPR = north East Pacific Rise; sEPR = south East Pacific Rise; GAL = Galapagos Spreading Centre; ATL = Mid-Atlantic Ridge; IND = Indian Ridge; MBJ = Marianas, Bonin and Okinawa sites; LFM = Lau, Fiji and Manus back-arc basins. Adapted from Tunnicliffe et al. (1998).

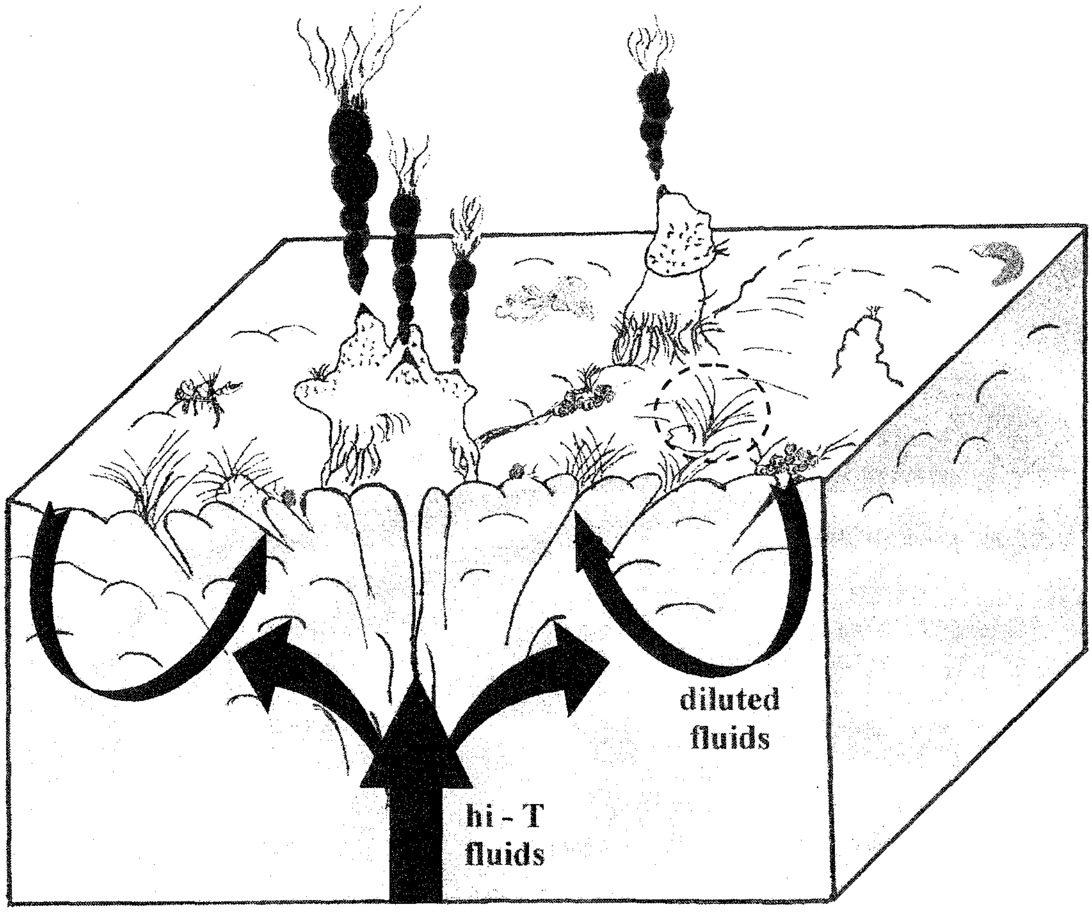

Figure 1.3. Schematic of a vent field. High temperature fluids build sulphide edifices and emit black, smoke-like plumes. Low temperature vents issue from crack or fissures in the basalt lava. Tubeworms (*Ridgeia piscesae*) form aggregations around diffuse flow at vents in the northeast Pacific (dashed circle).

vent invertebrates occur. Although low temperature fluids also issue from chimney (sulphide) substratum, I reserve the descriptors *diffuse* and *low temperature* for flow emanating from cracks and fissures in basalt lavas.

The spatial distribution of venting is patchy on several scales (Tunnicliffe 1991). A *vent* is a discrete stream of fluid emanating from the seafloor. Diffuse vents appear as visibly shimmering fluid and/or as clumps of animals such as tubeworms bushes or mussel beds with no apparent flow (Figure 1.3). A *vent field* is a collection of vents. Vents within one field are separated from one another by meters to hundreds of meters. Vent fields may range in size from a few hundred metres squared to several kilometres. Vents of smaller fields likely share a common subsurface plumbing system. A v*ent site* is a general area of venting along a ridge, and is separated from other sites by inactive areas tens to hundreds of kilometres long. Several vent fields may occur at one vent site.

The distribution of venting also varies in time. Individual vents may persist for a few years to several decades to possibly hundreds of years (Tunnicliffe 1991, Lalou 1995, Tunnicliffe et al. 1997). Globally, the turnover of larger-scale vent activity (e.g. vent fields) is likely related to seafloor spreading-rate; plume incidence increases with spreading rate (Baker et al. 1995) and the frequency of volcanism is higher at faster versus slower spreading centres (Fornari & Embley 1995, Juniper & Tunnicliffe 1997). Smaller-scale processes such as clogging, mineralization and/or shifting of flow conduits also affect vent longevity within vent fields (Tunnicliffe 1991).

The specialized animals that live at vents must thus contend with a habitat shifting in space and time. The vent *lifecycle* starts with the inception of flow and ends when flow ceases or chemically changes so that primary production via microbial chemosynthesis is no longer sustained. Vent species must find new vents, cope with changing fluid conditions and foster their offspring. Adults are typically restricted to the area around the vent opening, although a few highly mobile species, such as polynoid and nereid polychaetes, may swim to nearby vents. Dispersal between sites is primarily achieved via pelagic larvae.

The vent lifecycle is tracked by the species that live at vents. When a new vent is created, usually by a seafloor eruption or earthquake, vent larvae recruit to the new site within weeks to months (Tunnicliffe et al. 1997, Shank et al. 1998). Over time, a *community* (or an *assemblage*, I use the two words interchangeably) of species develops at the site. Vents up to 1 year in age, and their associated fauna, I define as *new*. Vents of unknown age, but which support healthy communities, I call *long-lived* or *mature*. A *senescent* vent refers to waning flow with no detectable temperature (or sulphide) anomaly that hosts an obviously dying vent assemblage.

Vents are also typified by high productivity and high habitat variability. Biomass estimates are orders of magnitude higher than the surrounding deep-sea and rival highly productive, photosynthetically based systems (Sarrazin & Juniper 1999). Vents also display large variations in physical and chemical fluid properties over space and time. Habitat variation operates on many scales; for example, temperature may vary at a single location within a diffuse vent by 10°C over 40-80 seconds (M. Pruis pers. comm.), while maximum temperatures between two diffuse vents separated by a few meters can be >60°C (pers. obs.). Many vent invertebrates have novel adaptations to capitalize on and cope with this unique environment. This is exemplified by the species that visually dominate the landscape (vestimentiferans, bivalves and shrimp): they harbour chemoautotrophic symbionts and have unique methods of managing high habitat variability (Fisher 1995). It is not surprising that this extreme and variable milieu has fostered a fauna that is highly endemic (>80%) and taxonomically distinct from the surrounding deep-sea (Tunnicliffe et al. 1998).

Despite high local productivity and community biomass, vent faunal diversity is low (Tsurumi in press). The latest count reports 443 invertebrates known from vents worldwide, with most species belonging to the Annelida (23%), Mollusca (34%) and Arthropoda (35%) (Tunnicliffe et al. 1998). Specific biogeographic regions, such as the northeast Pacific ridges, support less than 100 species. Species richness and evenness are also low at the local scale; species rank-abundance curves of individual vent communities show that a few species are very abundant while most are numerically rare (Tsurumi & Tunnicliffe 2001, Govenar et al. 2002).

Current status of vent community ecology

Vent ecology is in a relative early stage of development. Juniper & Tunnicliffe (1997) present three conceptual levels of information that are required for an integrated understanding of the vent ecosystem: (1) composition (species present, habitat conditions), (2) structure (spatial distribution, biomass/abundance, population data, trophic relationships), and (3) dynamics (succession, growth and productivity, energy and material fluxes, mortality and recruitment). The flow of information gathering through this hierarchy is typically progressive when a new ecosystem is under study. This has not been the case for vents; their extreme isolation continues to dictate the type of ecological questions that can be asked. Depths of 1.5 to ~3 km impose expense limitations and technological constraints on sampling and field experimentation, while the high habitat pressures pose major challenges for working with vent fauna in the laboratory.

Early ecological studies at vents focused on exploration, description and basic understanding of the principal fauna. Work included finding new vent sites, describing the habitat and the novel fauna and understanding the physiology of the dominant symbiont-bearing species. This descriptive or 'composition' phase continues today; exploring new sites (Hashimoto et al. 2001), measuring habitat properties and developing appropriate chemical sensors (Luther et al. 2001) and identifying new species (Marcus & Hourdez 2002) remain important tasks.

Early vent community work also described general patterns in species distributions and documented community organization with photographs and video (see Tsurumi 2001 for a chronological review of ecological studies at vents). For example, initial observations at Galapagos Rift vents reported a zonation pattern of species replacements with increasing distances from diffuse fluid flow (Hessler and Smithey 1983), while submersible dives to the same location separated by six years saw major shifts in species assemblages (Hessler et al. 1988). As with almost any system, this work revealed that the composition and structure of vent communities varies in space and time at many spatial scales. Some early studies speculated that shifts in fluid flow and changes in hydrogen sulphide content caused the observed faunal patterns (e.g. Hessler et al. 1985, Fustec et al. 1987, Johnson et al. 1988).

More recent efforts have assessed the spatial variability and temporal dynamics of community structure through sampling and/or repeated observations of a vent field over multiple years (e.g. Desbruyères 1995, Tunnicliffe et al. 1997, Shank et al. 1998, Tsurumi & Tunnicliffe 2001, Marcus & Tunnicliffe 2002). Many of these authors again suggest causal links between the physical and chemical properties of vent fluids and observed faunal variation, but only two studies to date statistically show such a correlation (Sarrazin et al. 1999, Micheli et al. 2002). The potential importance of biological interactions has also been addressed with community food web studies that use stable isotopes of carbon and nitrogen to deduce trophic relationships (Southward et al. 1994, van Dover & Fry 1994, Fisher et al. 1994) and infer potential competitive interactions among species (Levesque et al. 2003).

Experimental work aimed at understanding community patterns and processes is commencing at vents. So far, field experiments have used recruitment panels to assess the effects of microhabitat, predation and facilitation on the development of diffuse flow assemblages (Mullineaux et al. 1998, Mullineaux et al. 2000, Micheli et al. 2002). Laboratory experiments aimed at directly measuring physiological tolerances of the dominant mollusc and polychaete species are also beginning (B. Shillito, A. Bates, R. Lee: pers. comm.), but comprehensive data have yet to be published.

Although we are entering an era of experimentation, vent ecologists still face major challenges. First, life-history knowledge is virtually nonexistent for the majority of species, which complicates interpretation of observed patterns. Second, experimental work remains limited by technology, time and cost. Third, despite advances in abiotic and biotic habitat characterization, there is no efficient way to couple certain measurements, such as flow dynamics and productivity, with biological collections. Fourth, the problem of quantitative biological sampling has yet to be solved. C. Fisher (Penn State University) has developed a technique for sampling vestimentiferan aggregations on various substrata, but the sampling device does not take quantitative samples from all surfaces (Govenar et al. 2003). Further, since many attempts are needed to achieve one 'good' sample, it is not possible to efficiently sample multiple vents (pers. obs.). A compromise adopted here and elsewhere (Tsurumi & Tunnicliffe 2001) is to rely on semi-quantitative tubeworm grabs; some of the associated fauna are lost during collection, but the surface area of the tubeworm tubes can be used to estimate faunal density and numerous samples can be taken during one cruise.

Venting on the Juan de Fuca Ridge

My thesis examines vent communities from Axial Volcano, a seamount lying atop the Juan de Fuca Ridge (JdFR) in the northeast Pacific (Figure 1.4). Ridges in the northeast Pacific separated from their southern neighbour about 30 million years ago as the North American Plate drifted southwest and overran the continuous ancestral ridge (Tunnicliffe et al. 1998). This vicariant event created a dispersal barrier between the vent fauna of the northeast Pacific and the East Pacific Rise (EPR): less than 15% of the species known from northeast Pacific vents are shared with the EPR or Galapagos sites. Visually, vent communities of the northeast Pacific are unique: there is one main habitat forming species, the vestimentiferan tubeworm *Ridgeia piscesae*, at northeast Pacific vents while three species of tubeworms and two bivalve species may dominate the EPR landscape. On the JdFR, *R. piscesae* forms bush-like aggregations over diffuse flow in a range of microhabitats (see Figure 1.3).

Vent fauna was discovered on the JdFR at Axial Volcano in 1983 (Tunnicliffe et al. 1985). The proximity of the JdFR to the west coast of North America (~400 km) has facilitated numerous studies in this area over the past 20 years. To date, species representing seven phyla and eleven classes are known, but there are likely less than 100 species in the whole region (Tsurumi 2001). Fifty-five species are known from both high and low temperature vents at Axial Volcano (Tsurumi 2001).

The JdFR is unique among ridges as it lies within the U.S. Navy's SOund SUrveillance System. SOSUS is an underwater hydrophone array that can detect seismic activity. These data inform scientists of volcanic/tectonic events that may cause major changes to a vent system. For example, SOSUS detected the eruption of Axial Volcano in January 1998. Knowing the timing of a major disturbance is a novelty for vent community ecologists; besides Axial, only one other seafloor eruption that created new vent habitat has been remotely detected (CoAxial Segment in 1993, Figure 1.4). An understanding of the temporal dynamics of vent communities relies inherently on the ability to observe these communities assemble and develop over time.

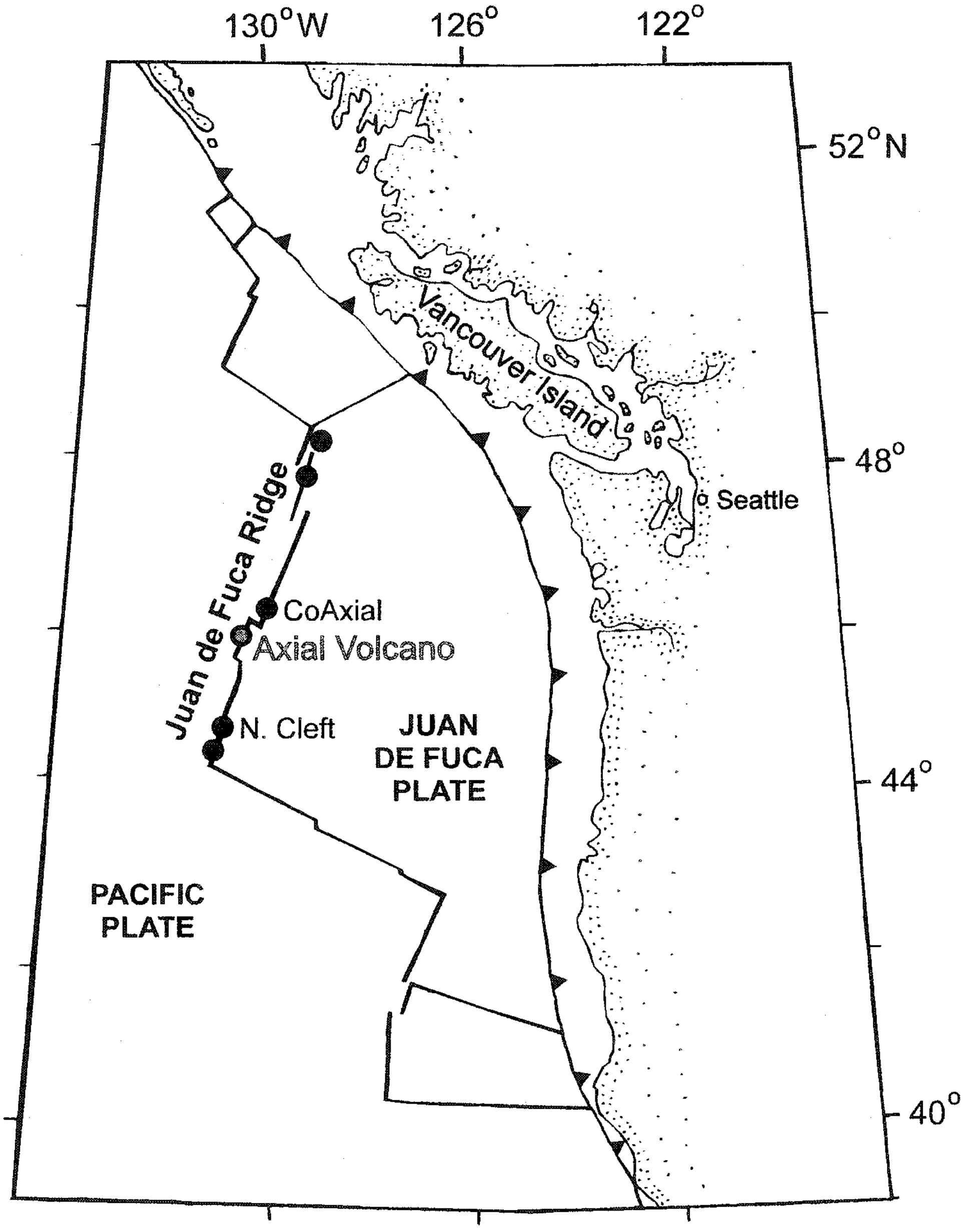

Figure 1.4. Location of Axial Volcano on the Juan de Fuca Ridge (JdFR) in the northeast Pacific. Black dots represent other vent sites along the JdFR; CoAxial Segment and North Cleft are indicated, as they are both known eruption sites. The solid line with pointers is the Cascadia Subduction Zone (pointers show direction of subduction).

Goals and Contributions

The ultimate goal of vent community ecology is to uncover the processing driving the observed species patterns. My goal is to advance our understanding of diffuse flow vent community composition and structure within the realm of current constraints. In particular, I aim to detect patterns of community organization and use these patterns to formulate hypotheses of the causes of variation among diffuse flow vent communities at Axial Volcano. To this end, I start by using statistical models to test if vent assemblages are random ensembles of coexisting species since confirmation of nonrandom structure justifies the proposal of causal hypotheses. In addition, I describe species patterns of developing nascent assemblages and relate these patterns to mature assemblages and measurable habitat characteristics. I also describe a new polynoid polychaete, as species identification underlies any community ecological endeavour. I therefore contribute to all three levels of knowledge of vent ecosystem properties with this dissertation: composition, structure and dynamics.

In Chapters 2 and 4, I use novel statistical methods to confirm that vent communities are nonrandomly organized. Nonrandom community structure has always been assumed for vents, but never tested. The detection of nonrandomness is much more than an academic exercise: it justifies the search for process and prevents ecologists from expending effort testing hypotheses based on community patterns that are indistinguishable from random. Chapter 2 assesses patterns among mature vent communities and is in revision with the *Marine Ecology Progress Series*. Chapter 4 asks if nascent vents are colonized by a random assortment of species and individuals, and is intended for publication in modified format.

In Chapter 3, I describe a new polynoid polychaete associated with nascent hydrothermal vents. The discovery and description of species remains a fundamental task; species are the basic unit of investigation for most ecological studies, from community ecology to biogeography. This paper is published in *Proceedings of the Biological Society of Washington.*

In Chapters 5 and 6, I describe the temporal development of nascent vent communities over three years. I document the formation of post-eruption vent communities with an adequate number of samples to tease out general trends, address variability in the succession process and compare developing assemblages to mature communities (Ch. 5). I also propose which mechanisms likely drive the observed species patterns based on correlations with habitat characteristics (Ch. 6). Analyses from both chapters are used to formulate a model of community development at diffuse flow vents. Both chapters are intended for publication in a modified format.

In the Appendix, I explore how the vent community changes with increasing distance from fluid flow. This is the first assessment of the proximate peripheral vent fauna at JdFR vents. This paper is published as an extended abstract in the *Cahiers de Biologie Marine*.

This thesis contributes to vent community ecology in three main ways. First, I highlight the importance of rigorous pattern detection and show that vent communities are not random assemblages of coexisting species. Second, I document spatial and temporal variation among diffuse flow communities at the scale of a vent field with sampling. I use these patterns to develop hypotheses of putative regulating processes. Third, the model of community development I propose incorporates biotic and abiotic controls and emphasizes unresolved questions. Overall, this work uncovers significant community patterns and generates hypotheses of causal mechanisms. The patterns I describe will focus and direct future research effort at vents.

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CHAPTER 2

Nonrandom species patterns in hydrothermal vent survey data: a null model approach

Marcus, J. and Anholt, B. R. In revision with the *Marine Ecology Progress Series.*

Abstract

Distribution patterns of species across sites are often attributed to nonrandom causes. Proponents of null models argue that causal mechanisms cannot be invoked to explain such patterns unless observed distributions deviate from a model of randomness. We use a null model approach to analyze species occurrence data from sixteen hydrothermal vent tubeworm aggregations sampled at a deep-sea volcano. Observed patterns of two faunal groups, the polychaetes and the macrofauna, are compared to results from simulated random distributions. We ask two questions: (1) does the distribution of species over sites differ from random expectations, and (2) are there significantly associated species pairs? To compare published randomization techniques we used five algorithms to create random matrices. All simulation algorithms except one (Knight's Tour) deem both faunal groups significantly nonrandom using the well-known community C- and S^2-score metrics. The same 10% of all species pairs free to vary in the simulations deviate from random with every analysis. We attribute positive associations to common habitat requirements and negative associations to potential predator-prey, competitive relationships, or differential abiotic requirements and/or tolerances. One algorithm (Sequential Swap) is not useful for association analyses since the method biases species pair results. Null models and association patterns are particularly useful for analyzing data and directing future research in systems like vents that are difficult to sample and not easily amenable to experimentation.

Introduction

When habitats are easy to sample, and their species are amenable to manipulation, we can gather data and perform experiments to test for community patterns and uncover the structuring processes. From such studies, we know that mechanisms such as competition, predation, priority effects and physiological tolerances organize communities into nonrandom patterns (Morin 1999). In the marine environment, measurable community patterns and processes are known from habitats such as coral reefs, soft sediments, salt marshes, seagrass beds, and the rocky inter- and subtidal (Bertness et al. 2001).

However, when habitats are difficult to access and associated species are difficult to maintain in the lab, our ability to explain perceived species patterns is typically limited. Here ecologists are frequently restricted to taxonomic information to interpret samples and reported community patterns are usually descriptive. Deep-sea hydrothermal vents are a good example of such a habitat: location, technology and financing are major challenges. Animal assemblages associated with hydrothermal vents were discovered in 1977 (Lonsdale 1977). Since then, ecologists have described vent communities from mid-ocean ridges and back-arc basins around the globe. Initial biological study of new venting areas documents the fauna present: over 443 species are known from vents worldwide (Tunnicliffe et al. 1998). Later ecological studies document spatial and temporal patterns in species assemblages, and a few relate these patterns to environmental factors (Sarrazin et al. 1999, Luther et al. 2001) or to biological mechanisms (Micheli et al. 2002, Levesque et al. 2003). However, most vent community studies are descriptive and little is known about most organisms except for a few well-studied species (van Dover 2000).

Since the hydrothermal vent habitat is remote and costly to visit, we should make maximal use of existing data to detect where species patterns likely lie prior to conducting experiments to test hypothesized processes. Although nonrandom community patterns should be rigorously tested rather than assumed in any system, this is particularly so in habitats like vents that are prone to such presumptions due to minimal instructive experimental work in the field and laboratory (but see Micheli et al. 2002 for an exception). In this paper we use a null model approach to test for nonrandom patterns in hydrothermal vent collections towards a dual end: to test if the assumption of pattern in vent ecological research is justified, and to reveal which species are most likely responsible for putative nonrandom patterns.

Null Models

Null models test for community structure by evaluating species occurrences in a species by site data matrix of a defined community. Null co-occurrence models stem from a paper by Connor & Simberloff (1979) where they critiqued Diamond's (1975) 'assembly rules' to explain patterns of bird distributions over islands of the Bismark archipelago. Connor & Simberloff argued that if the distribution data do not differ from random, then any attempt to attribute nonrandom causal mechanisms to patterns of species distributions is unwarranted. Jackson et al. (1992) further highlight that use of contemporary multivariate statistical analyses with survey data may be inappropriate because the techniques (cluster and ordination analyses) either assume or impose structure on the data.

We adopt a null model approach because it is currently the best available method to test if species distributions are nonrandom and it is well established in community ecology (Manly & Sanderson 2002). While the approach appears useful and justified, disagreement lingers over the mechanics of the null model test itself (Wilson 1987, Jackson et al. 1992, Sanderson et al. 1998, Gotelli & Entsminger 2001). There are three necessary components of a classic null model randomization approach: (1) an index to measure association in the presence/absence matrix, (2) an algorithm to create random communities, and (3) a method to compare the degree of association in the observed data to that measured in the simulated communities. With a randomization approach, step 3 is uncontested (Edgington 1987); significance is determined by comparing the test statistic calculated from the observed data to its null distribution generated by the randomization process. If the observed value lies in the extreme tail(s) of the null distribution of the test statistic, the null hypothesis is rejected.

However, the specifics of the first two steps remain controversial. First, there are almost as many measures of association as there are studies. Most try to summarize the mean level of association of the occurrence matrix into one global metric to test if the entire community differs from random expectations (e.g. Stone & Roberts 1990, Stone & Roberts 1992, Gotelli 2000). Any justifiable metric can be used with null models. Five metrics are offered by the EcoSim 6.0 program (website: homepages.together.net/~gentsmin/ecosim.htm): the C- and S^2-scores of Stone & Roberts

(1990, 1992), the V-ratio of Schluter (1984), the number of checkerboards, and the number of species combinations. Alternatively, species pair associations can be evaluated individually to determine which pairs contribute most to nonrandom community structure (Sanderson 2000). Manly (1995) argues that the latter is a more sensible approach; simply testing if an observed occurrence matrix is nonrandom contributes nothing to our understanding of which species associations are driving community structure. If the goal is to focus research effort, we need to know which species to study.

Second, and currently the most contentious issue, is how to create an appropriate null matrix. Most researchers agree that the observed species distributions (row totals) and site richnesses (column totals) must be retained in random matrices to maintain realism (e.g. Connor & Simberloff 1979, Wilson 1987, Sanderson et al. 1998): if constraints are relaxed the 'null space' becomes unreasonably large causing unwarranted rejection of the null hypothesis (but see Gotelli 2000 for an alternate view). Sanderson et al. (1998) believed they had solved the dilemma of random matrix generation (e.g. the problems of 'flat' and non-independent null matrices generated by swap algorithms) with their "Knight's Tour" (KT) method. But Gotelli & Entsminger (2001) recently argued that the KT method is flawed because it generates a biased subset of all possible random matrices. The importance of this step cannot be overemphasized: determining nonrandom structure depends on the ability to adequately generate random communities. We address the issue of random matrix generation by using five different algorithms and comparing the results.

Null models and their applicability to vents

Past studies have applied null co-occurrence models to, for example, the presence of bird species on islands in an archipelago (Connor & Simberloff 1979, Gilpin & Diamond 1984), flora on islands in a lake (Wilson 1988), fish species in lakes of a region (Jackson et al. 1992) and algae in rock pools in the intertidal (Wilson et al. 1992). We believe a null model approach is also useful for analysis of vent community structure for three reasons.

First, vents are patchy habitats. Lush assemblages of invertebrates colonize the discrete streams of venting fluid. High biomass is fed by bacteria that use reduced chemicals in the vent fluid as an energy source to fix inorganic carbon. Most animals congregate around low temperature vents (up to ~50°C) of dilute vent fluid. In the northeast Pacific, low temperature vents are dominated by tubeworms (vestimentiferans) forming intertwined bushes over diffusing fluid. These bushes provide habitat for most other vent fauna (Figure 2.1). The discrete tubeworm clumps thus act like islands for the associated biota and delineate discrete species assemblages. Null co-occurrence models were developed to analyze species distributions on islands; they are less applicable to a continuous landscape where the species assemblages are arbitrarily defined by the investigator. For such cases, lattice-type null models deal with issues such as spatial autocorrelation (Roxburgh & Chesson 1998, Roxburgh & Matsuki 1999).

Second, sampling at vents is difficult. Current technology limits recovery of fluid temperature and chemistry data coupled to biological collections. Even when such data are available, it is difficult to use short-term, point measurements to describe this highly variable habitat in space and time. Environmental data thus fail to explain a significant portion of variance in species patterns (e.g. Sarrazin et al. 1999). Density data are also difficult to retrieve in a replicated fashion for tubeworm bushes, although quantitative samples are now achievable at vent mussel beds (van Dover 2002). Thus, the best data currently available to vent community ecologists studying numerous tubeworm aggregations are species occurrences.

Third, vent community ecology, on the scale of vent to region, remains largely descriptive (e.g. Shank et al. 1998, Sarrazin et al. 1999, Tsurumi & Tunnicliffe 2001). Null models offer the opportunity to reliably test whether vent assemblages are indeed structured.

Objectives

This paper analyzes occurrence data from a hydrothermal vent field on Axial Volcano, Juan de Fuca Ridge (JdFR, Figure 1.4). Two data sets are analyzed: all the macrofaunal invertebrates and only the polychaetes. Our first goal is to test for pattern in the data; we ask two questions of both data sets: (1) does the distribution of all species

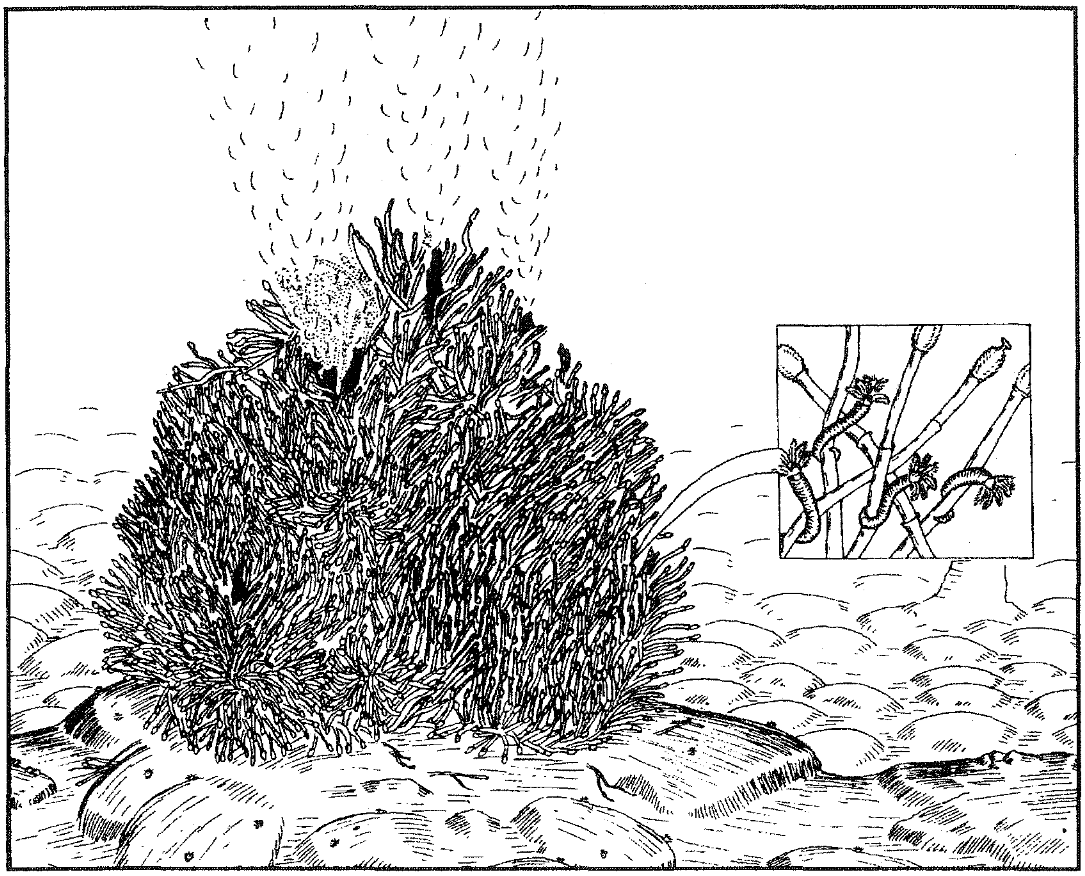


Figure 2.1. A low temperature "tubeworm bush" vent. Associated fauna live on and within the tubeworm aggregation. This is illustrated by the inset showing individuals of the polychaete *Paralvinella palmiformis* with their caudal ends wrapped around tubeworm tubes. Figure adapted from Tunnicliffe (1991).

over sites differ from random expectations (i.e. is the community nonrandomly structured?), and (2) are there species pairs in the community that are positively or negatively associated? The first question is interesting because variations in vent community structure are thought to be partly due to variations in larval dispersal and chance recruitment (e.g. Tunnicliffe & Fontaine 1987, Lutz & Kennish 1993). The second question teases out species pairs that may shape community structure, and thus may warrant further investigation. Our second goal is to assess the performance of five different random matrix algorithms. We compare four previously published methods, and a new version of one method programmed by JM. We believe our results contribute to the debate of null matrix generation by recommending a subset of the algorithms for analysis of species associations.

Methods

Site Description

Axial is a large, shallow ridge axis volcano located on a central segment of JdFR in the northeast Pacific (45°N, 130°W; Figure 1.4). It rises approximately 700 m above the seafloor and summits at a depth of 1500 m. The volcano's caldera supports three localized fields of hydrothermal activity. This paper analyses species occurrence data from one relatively small field called ASHES. ASHES is approximately 100 m in diameter, and supports tens of low temperature vents.

Field Methods / Data Collection

Sixteen low temperature vents ("tubeworm bushes", Figure 2.1) were sampled from ASHES between 1986-88 and 1997-98. Samples were grabs of tubeworm clumps taken with a clawed submersible arm; they were placed in closable boxes for transport to the ship. On board samples were bulk fixed in 7% seawater formalin. In the lab, samples were rinsed, sieved through a 63 μm mesh and sorted for all fauna. Only species whose adults would be retained on a 1 mm sieve are reported here (the macrofauna). The tubeworm was not included as it is the substratum. Species occurrence data were recorded in a matrix with rows representing species and columns representing individual vents: a '1' was assigned for presence and a '0' for absence.

Data Selection Rationale

We examined two data sets: the polychaetes alone and all the macrofauna. Community structuring forces, including competition, are assumed to be greater among ecologically similar species (e.g. guilds, Gilpin & Diamond 1982 or taxocenes, Legendre & Legendre 1998). Some authors argue that application of null models to whole communities, rather than specified subsets of that community, is not useful since interesting trends (i.e. a highly exclusive distribution of a species pair) will be lost in a mass of irrelevant data (the 'dilution effect', Diamond & Gilpin 1982). However, guild determination can be very difficult (Connor & Simberloff 1984). Detailed knowledge of the biology and ecology of a species is needed to adequately assign it to a specific guild, and controversy abounds over how to define a guild. Taxonomically related species are often assigned to the same guild since precise information is usually lacking (Connor & Simberloff 1983). As so little is known about most vent species on the JdFR, we follow this convention and analyse the vent polychaetes separately. However, we also analyse all the macrofauna because vent-associated species occur in small, dense, spatially restricted areas (the tubeworm bush) where they are exposed to similar physico-chemical conditions and the potential for interspecies interactions is likely high.

Statistical Methods

Random matrix generation

The two general approaches to generating random matrices with null row and column sums fixed to observed values are (1) algorithms that begin with an empty matrix and randomly fill in ones, and (2) algorithms that begin with the observed matrix and randomly swap the ones. Fill algorithms proceed until a marginal constraint is violated and then have some mechanism for backtracking before proceeding again; swap algorithms maintain observed totals by finding submatrices of the form

$$\begin{matrix} 1 & 0 \\ 0 & 1 \end{matrix} \quad \text{or} \quad \begin{matrix} 0 & 1 \\ 1 & 0 \end{matrix} \qquad [1]$$

anywhere throughout the matrix and changing the 0s to 1s and vice versa. Both approaches were used in this study. Since four of the five algorithms have been published elsewhere (see Gotelli & Entsminger 2001 for a review), only brief descriptions are given here.

Fill algorithms

1. The Knight's Tour (KT) method (Sanderson et al. 1998) randomly fills in 1s until a marginal total constraint is violated. At this point, all other possibilities for placing a one are tried. If no solution is found, the algorithm retreats sequentially by one step and proceeds forward again. The procedure is repeated until the matrix is filled.
2. The Random Knight's Tour (RKT) method (Gotelli & Entsminger 2001) also randomly fills in 1s until a marginal total constraint is violated. However, at this point only a random subset of all possible cells are tried to see if a placement does not violate marginal totals. If no solution is found, the algorithm retreats by randomly removing a previously filled cell from anywhere in the matrix. The procedure is repeated until the matrix is filled.

Swap algorithms

3. The Sequential Swap (SS) method (Gotelli & Entsminger 2001) begins by randomly swapping 30,000 submatrices. After this initial shuffle, a different null matrix is generated by each subsequent submatrix swap. This algorithm searches for submatrices by simply choosing two rows and two columns at random, and swapping the cells if possible.
4. The Independent Swap (IS) method (Gotelli & Entsminger 2001) swaps 30,000 submatrices to generate each null matrix. Selection of submatrices is identical to the SS method.
5. The SubMatrix Swap (SMS) method (this paper) is theoretically the same as the IS method, but uses a different algorithm to select submatrices. The SMS method begins by randomly choosing one cell in the matrix. The remainder of this row is then searched for all possible complementary matches (e.g. if a 1 was selected, the row is searched for all columns that have a 0). One of these complementary matches is then randomly chosen, and the first column and the randomly chosen column are searched for rows with complementary pairs (e.g. if the initial row pair is 1 0, a 0 1 in

> any row is a match). If more than one complementary pair is found, one is randomly selected and the cells are swapped. This maintains the row and column totals. If no matching pair is found, the algorithm randomly selects another complementary match. If the columns with complementary matches are exhausted, the algorithm chooses a new random cell in the matrix. For our study, one null matrix was completed when 1000 submatrices were successfully swapped.

Three programs were used to create null matrices: the KT method (program written by R. Selfridge) was implemented in J, the RKT, SS, and IS methods were implemented in EcoSim 6.0, and the SMS method was implemented in S-Plus 2000. One thousand random communities (null matrices) were simulated for each trial, and occasionally 10,000 times when computing time was not limiting (Table 2.1).

Community summary indices

We used the *C*-score (Stone & Roberts 1990) and the S^2-score (Roberts & Stone 1990) as measures of community structure. The *C*-score is recommended by Gotelli & Entsminger (2001), and both scores have been used in many null model analyses (e.g. Roberts & Stone 1990, Sanderson et al. 1998, Gotelli & Entsminger 2001) allowing for comparison of this study to others.

The *C*-score measures the degree to which species avoid sharing the same site (Stone & Roberts 1992). It is based on a measurement called a "checkerboard unit" (CU). A CU is the mutually exclusive occurrence of two species at two sites; in matrix form a CU is a swappable submatrix (see [1]). We used the formula proposed by Stone & Roberts (1990) to compute the checkerboard units for each possible species pair in the matrix:

$$\mathrm{CU}=(r_{\mathrm{i}}-\mathrm{S})(r_{\mathrm{j}}-\mathrm{S}) \qquad [2]$$

where r_{i} and r_{j} are the row totals for species i and j, and S is the number of sites shared by both species.

Table 2.1. Details of the number of trials executed per algorithm for the polychaete and macrofauna data sets. Abb. = algorithm abbreviation.

Algorithm	Abb.	# submatrix swaps / null matrix	# null matrices/trial	# trials
Knight's Tour	KT	na	1000	10
			10,000	1
Random Knight's Tour	RKT	na	1000	10
Sequential Swap	SS	1*	1000	10
			10,000	1
Independent Swap	IS	30,000	1000	10
SubMatrix Swap	SMS	1000	1000	10

* after 30,000 initial swaps.

The *C*-score is the mean number of CUs of an occurrence matrix: the total number of CUs divided by the total number of possible species pairs, [n•(n-1)/2]. The *C*-scores for the SS, RKT and IS methods were calculated in EcoSim 6.0. The *C*-scores for the SMS and KT methods were calculated in S-Plus2000.

The S^2-score is based on how species pairs share sites (Stone & Roberts 1992). For each species pair, the number of shared sites (S) is calculated. The S^2-score is the sum of S squared (S^2) for all species pairs divided by the total number of possible pairs (matrix mean S^2 score). EcoSim 6.0 was used to calculate the S^2-score for the SS, IS and RKT methods. S-Plus2000 was used for SMS and KT calculations.

If the observed data have a *C*- or S^2-score significantly greater than random values, the observed data are nonrandomly structured. The observed *C*- and S^2-scores were compared with scores calculated from either 1000 and/or 10,000 random matrices to determine if the observed species groups differed significantly from models of random distribution (Table 2.1). Significance was calculated by counting how many simulated scores were greater than or less than the observed value of the index; the upper-tail p-value determined if the observed index was significantly greater than the distribution of random values.

Species pair associations

The number of sites shared (S) was used as a test statistic to determine if species pairs are positively or negatively associated. S was calculated for each unique species pair. The observed number was compared to the distribution of S calculated for each comparable pair in each of 1000 (or 10,000) null matrices. The p-value was 2 times the proportion of the null distribution as extreme or more extreme than that observed.

All species pair analyses were preformed in S-Plus2000. Since EcoSim 6.0 only calculates summary statistics (*C*- and S^2-scores), the simulated matrices generated by the SS, IS and RKT algorithms were saved and subsequently analysed in S-Plus2000.

Comparison of Algorithms

To assess the variability associated with each method, and to enable comparisons between methods, we repeated all analyses for each algorithm ten times (Table 2.1).

Community results (*C*- and *S*-scores) of the five algorithms for each data set were compared with a one-way ANOVA and a post-hoc multiple comparison Tukey-test to determine homogeneous groups (implemented in SPSS 9.0). To compare how well the methods detected species pair associations we: (1) ranked the significance values of the pairs for each trial of each algorithm, (2) log transformed the ranks, and (3) clustered the transformed ranks (flexible method, $\beta = -0.25$, Euclidean distance measure; implemented in PC-Ord). Ranks were log transformed to emphasize the most significant pairs and underplay the lower ranking pairs. The KT method was excluded from this last analysis because it produced anomalous community results (see Results).

Testing the Dilution Effect

The potential of a dilution effect was evaluated by comparing the species pair results from analysis of the two data sets. If there is a dilution effect, the polychaete pair significance values determined by analysis of the macrofauna data set should be greater than the species pair p-values calculated by analysing only the polychaetes. We used an exact binomial test to test for a dilution effect. The proportion of the mean species pair p-values calculated from the macrofauna data set greater than the mean species pair p-values calculated from the polychaete data set should not differ from the expectation of 0.5 if there is no effect.

Results

From the sixteen samples, 29 macrofaunal species were identified from over 180,000 individuals. All species were invertebrates; 20 were polychaetes, and the remainder belonged to the classes Gastropoda, Bivalvia and Pycnogonida. The largest individuals were alvinellid and polynoid polychaetes (about 100 mm and 50 mm in length respectively). Most species were relatively small, with average lengths of less than 20 mm.

Community Analysis

The observed *C*-score for each data set was significantly greater than the null distributions of *C*-scores for each of the ten trials of the RKT, SS, IS and SMS algorithms. Both the macrofauna and polychaete data sets are nonrandomly structured. The mean *C*-score upper-tail p-values ranged from 0.007 to 0.020 for polychaetes and from 0.001 to 0.011 for macrofauna (Table 2.2). However, the KT method did not reject the null hypothesis of random colonization: the observed *C*-score of each data set was very near the expectation in all trials (Table 2.2; mean $p = 0.933$ for polychaetes, mean $p = 0.989$ for macrofauna).

The observed S^2-scores, for polychaetes and macrofauna, were also significantly greater than their null distributions for each of the ten trials of the RKT, SS, IS and SMS algorithms. Mean p-values ranged from 0.011 to 0.026 for polychaetes and from 0.003 to 0.015 for macrofauna (Table 2.2). Again, the KT method did not reject the null hypothesis of random colonization: the observed S^2-scores were not significantly greater than expected by chance (Table 2.2; mean $p = 0.325$ for polychaetes, mean $p = 0.410$ for macrofauna).

Community results (*C*- and S^2-scores) from both data sets were significantly different among all 5 algorithms (ANOVA, $p < 0.001$ in all four cases, Table 2.3). In 3 of the 4 cases, the RKT, SS and IS algorithm results formed one homogeneous group, while the SMS and KT algorithms produced results distinct from each other and the other three algorithms (Tukey test, Table 2.3). The RKT, IS, SMS and SS S^2-scores from analysis of the polychaete data set formed an indefinite group, distinct from the KT results (Table 2.3). Increasing the number of matrices simulated by the KT and SS algorithms to 10,000 produced similar results for both *C*- and S^2-scores.

C- and S^2-scores calculated from KT simulations always exceeded the values calculated from all other methods, and KT score variances were on average 3 to 5 times larger than those of the other algorithms for both data sets (Table 2.2). The KT method was excluded from further analyses since the large variances were consistent with the findings of Gotelli & Entsminger (2001) that this method is biased. We retained the SMS method since it is theoretically identical to the unbiased IS method; the fact that the SMS method produced significantly different community results from the SS, IS and RKT methods may indicate that the way in which an algorithm is programmed affects results.

Table 2.2. Community results for the polychaete and macrofauna data sets: mean simulated *C*- and S^2-scores, standard deviations and upper-tail p-values from ten trials of each algorithm (1000 simulations per trial in all cases). Observed scores are 2.884 (*C*) and 47.790 (S^2) for polychaetes; 2.254 (*C*) and 54.017 (S^2) for macrofauna. Algorithm abbreviations are the same as Table 2.1.

	KT	RKT	SS	IS	SMS
POLYCHAETES					
C-score	3.140	2.623	2.630	2.628	2.654
σ	0.184	0.087	0.089	0.089	0.096
obs $\geq$ exp p-value	0.933	0.007	0.009	0.009	0.020
S^2-score	47.574	47.073	47.101	47.082	47.097
σ	0.521	0.252	0.288	0.281	0.322
obs $\geq$ exp p-value	0.325	0.011	0.019	0.014	0.026
MACROFAUNA					
C-score	2.569	2.020	2.022	2.024	2.058
σ	0.155	0.060	0.059	0.062	0.070
obs $\geq$ exp p-value	0.989	0.001	0.001	0.002	0.011
S^2-score	53.946	53.391	53.400	53.409	53.445
σ	0.441	0.190	0.200	0.196	0.228
obs $\geq$ exp p-value	0.410	0.003	0.005	0.004	0.015

Table 2.3. One-way ANOVA results comparing community indices (*C*- and S^2-scores) from the five algorithms. Tukey test homogeneous algorithm groups are also listed.

	C-score				S^2-score			
	SS	df	F	P	SS	df	F	P
POLYCHAETES								
Algorithm	2.055	4	10421	0	1.895	4	1351	0
Residual	0.002	45			0.015	45		
Total	2.057	49			1.910	49		
Tukey post hoc test	RKT IS SS SMS KT				RKT IS SS SMS KT			
MACROFAUNA								
Algorithm	2.322	4	24590	0	2.311	4	1807	0
Residual	0.001	45			0.014	45		
Total	2.323	49			2.325	49		
Tukey post hoc test	RKT IS SS SMS KT				RKT IS SS SMS KT			

Species Associations

The community results show that species are distributed over sites nonrandomly. We defined a significant association as a species pair whose random S values deviated from the observed S in $\geq$ 90% of the simulations ($p \leq 0.2$, two-tailed test). We chose a more liberal level of significance because characteristics of our data sets (small size, nestedness, number of ubiquitous species) may hinder detection of nonrandom patterns (Diamond & Gilpin 1982, Manly 1991). Further, the goal of our analysis is to detect species pairs that are worth investigating; detected patterns will have to be substantiated by further investigation and experiments.

There are 190 possible polychaete species pairs. Since two species are ubiquitous, *Paralvinella palmiformis* and *P. pandorae*, and observed row totals were maintained in the random matrices, the number of sites shared (S) by every possible pair combination with the two ubiquitous species could not deviate from observed values (37 species pairs). Of the remaining 153 species pairs that were free to vary in the random simulations, 16 were significantly associated (five positive, 11 negative) by one or more algorithms (Table 2.4). Of the 16 pairs, nine were significantly associated across all algorithms, and 11 were significant across at least three algorithms. Three pairs were calculated as significant by only one algorithm; only the SS algorithm produced unique significant pairs.

There are 406 possible macrofaunal species pairs. However, the number of sites shared (S) by 135 species pairs could not deviate from observed values because five species were ubiquitous. Of the 271 species pairs that were free to vary in the random simulations, 21 were significantly associated (six positive, 15 negative) by one or more algorithms (Table 2.5). Of the 21 pairs, 13 were significantly associated across all algorithms, and 18 pairs were significant across at least three algorithms. Two pairs were significant by only the SS algorithm.

A cluster analysis of the polychaete species pair results groups all SS trials separately from the SMS, IS and RKT methods (Figure 2.2).

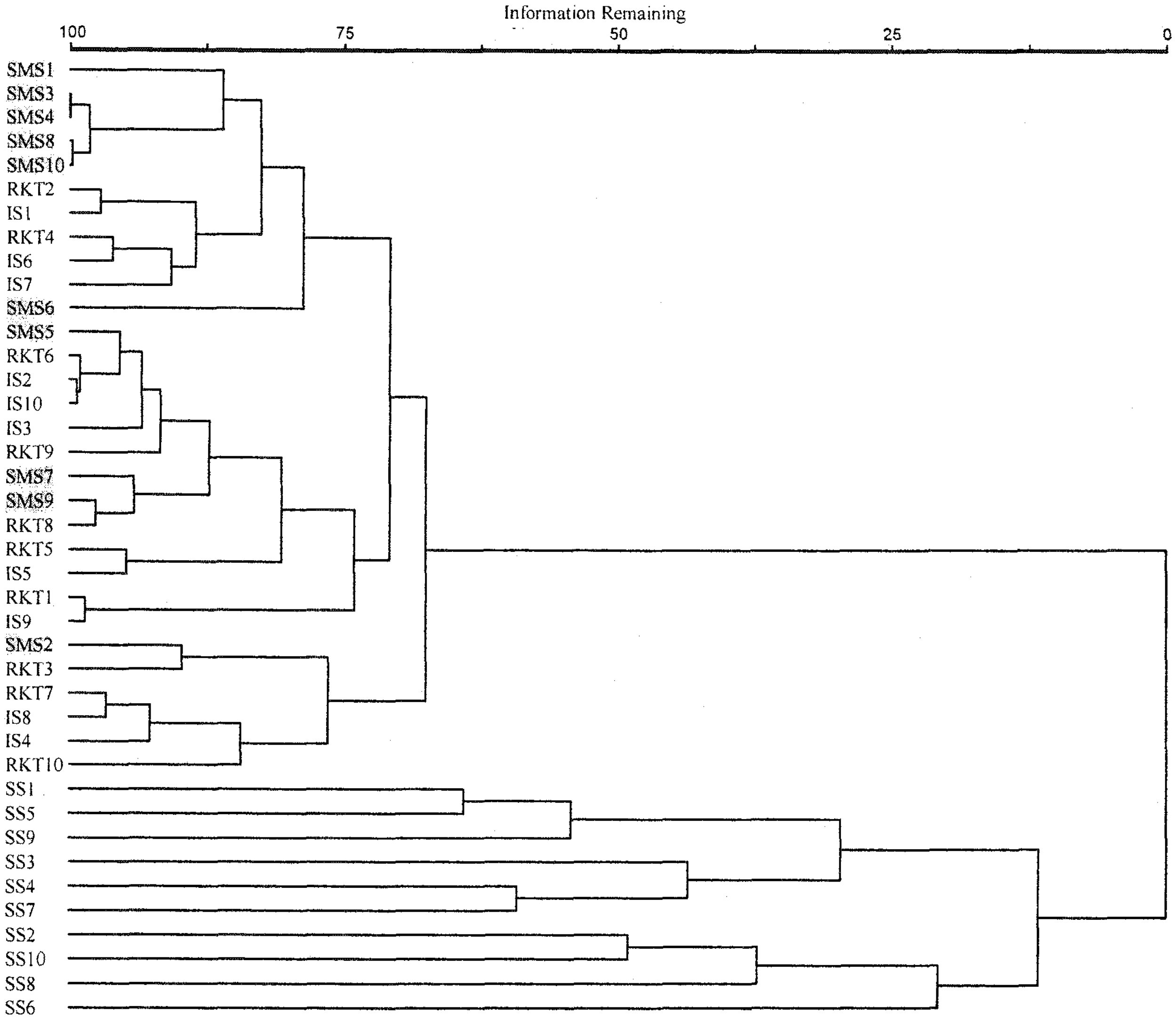
Table 2.4. Polychaete species pair associations. Ranks of mean p-values from 10 trials of each algorithm. All pairs significant at $0.1 \leq p < 0.2$.

		Null algorithm			
Species pair	Direction	RKT	SS	IS	SMS
Nicomache venticola – *Nereis piscesae*	-	1	2	1	1
Hesiospina vestimentifera – *Opisthotrochopodus tunnicliffeae*	-	2	4	2	2
Amphiduropsis axialensis – *Hesiodeira glabra*	-	4	1	3	3
Parougia wolfi – *N. piscesae*	+	3	5	4	6
O. tunnicliffeae – *Branchinotogluma grasslei*	+	5	9	5	7
H. glabra – *Levensteiniella kincaidi*	-	6	7	6	4
H. glabra – *Paralvinella sulfincola*	-	7	3	7	5
A. axialensis – *Prionospio* sp.	+	9	10	9	12
N. venticola – *Paralvinella dela*	-	12	6	10	8
H. glabra – *Lepidonotopodium piscesae*	-	8	8	8	
N. venticola – *L. kincaidi*	-	11		11	10
N. venticola – *P. sulfincola*	-	10			9
N. piscesae – *Protomystides verenae*	+			12	11
N. venticola – *P. wolfi*	-		11		
Prionospio sp. – *L. kincaidi*	+		12		
N. venticola – *O. globopalpata*	-		13		

Table 2.5. Macrofauna species pair associations. Ranks of mean p-values from 10 trials of each algorithm. Significance is indicated by font: bold text = $p < 0.1$ and normal text = $0.1 \leq p < 0.2$.

Species pair	Direction	Null Algorithm			
		RKT	SS	IS	SMS
Idasola washingtonia – Paralvinella dela	-	**2**	**1**	**1**	**1**
Nicomache venticola – Ammothea verenae	-	**1**	**2**	**2**	**2**
Idosola washingtonia – Hesiospina vestimentifera	-	**3**	**3**	**3**	**3**
N. venticola – Nereis piscesae	-	4	4	4	4
I. washingtonia – Lepidonotopodium piscesae	-	5	5	5	7
Amphiduropsis axialensis – Prionospio sp.	+	7	10	6	10
H. vestimentifera – Opisthotrochopodus tunnicliffeae	-	9	8	7	6
N. venticola – Clypeosectus curvus	-	8	12	8	5
Parougia wolfi – N. piscesae	+	6	6	9	14
O. tunnicliffeae – Branchinotoglum grasslei	+	11	9	10	12
Helicoradomenia juani – Ophryotrocha globopalpata	-	10	11	11	15
Lacunoides vitreus – O. globopalpata	-	12	7	12	16
A. axialensis – Hesiodeira glabra	-	13	16	13	11
I. washingtonia – Prionospio sp.	-	16		14	8
H. glabra – Paralvinella sulfincola	-	15		16	9
H. glabra – Levensteiniella kincaidi	-	17		17	13
Prionospio sp. *– L. kincaidi*	+	18	14	18	
Prionospio sp. *– Paralvinella dela*	+	19	17	19	
H. glabra – Lepidonotopodium piscesae	-	14		15	
I. washingtonia – Protomystides verenae	-		13		
N. piscesae – P. verenae	+		15		

Figure 2.2. Polychaete species pair log transformed ranked p-values from ten trials of four methods (RKT, SS, IS, SMS). SMS trials are highlighted. Clustered with flexible method ($\beta = -0.25$) using Euclidean distance in PC-Ord.


Information Remaining
100
75
50
25
0
SMS1
SMS3
SMS4
SMS8
SMS10
RKT2
IS1
RKT4
IS6
IS7
SMS6
SMS5
RKT6
IS2
IS10
IS3
RKT9
SMS7
SMS9
RKT8
RKT5
IS5
RKT1
IS9
SMS2
RKT3
RKT7
IS8
IS4
RKT10
SS1
SS5
SS9
SS3
SS4
SS7
SS2
SS10
SS8
SS6

Dilution Effect

The occurrence of a dilution effect is algorithm-dependent. The RKT and IS algorithms had almost the same frequency of increased significance (79 and 78 respectively; Table 2.6) for the smaller polychaete data set. This is very near the expectation of 76.5. The SS and SMS algorithms were also similar to each other: the smaller polychaete data set had more significant results for 88 and 87 species pairs ($p_{SS} = 0.026$ and $p_{SMS} = 0.038$) respectively (Table 2.6).

Discussion

Vent fauna community structure

There is strong support that at least some of the ASHES fauna are nonrandomly distributed across sites from both the C- and S^2-score indices. The models of random structure generated by all algorithms except the KT method support this conclusion. This discrepancy is not surprising: Gotelli & Entsminger (2001) argue that the KT method is biased due to its nonrandom selection of matrices from the realm of all possible matrices. One consequence seems to be that the KT method produces larger variances than the other algorithms (Gotelli & Entsminger 2001). Our results are consistent with this observation. Current understanding judges the other four algorithms to be reliable. The IS and SMS methods theoretically produce the entire set of possible matrices given marginal total constraints (Brualdi 1980). The RKT method generates a non-biased sample of random matrices (Gotelli & Entsminger 2001) and the SS method produces results consistent with these other methods (Gotelli & Entsminger 2001, this paper: Table 2.2). The consistent results among these four algorithms strongly suggest that both the polychaete and macrofauna data sets are structured.

It is encouraging that these algorithms are able to detect structure in the ASHES data sets. Both data sets are characterized by a large proportion of ubiquitous species, have a strong tendency towards nestedness, and are quite small. These characteristics are known to limit random matrix generation and hence pattern detection (Diamond & Gilpin 1982, Manly 1991). Further, all 16 vents were sampled within a small area (~100 m in diameter), with 1 to 5 meters separating most vents. We know only two other studies that used null models to detect community patterns at a comparable scale: Wilson et al.

Table 2.6. Exact binomial test results evaluating the presence of a dilution effect. Of the 190 polychaete pairs, 153 can vary in random simulations. # MF > Poly = the number of times the mean polychaete pair p-values calculated from analysis of the macrofauna (MF) data set are greater than the mean p-values calculated from the polychaete data set. Significance = the probability that # MF > Poly would be observed given no dilution effect (MF polychaete p-value has a 50% chance of being larger than the polycheate p-value).

Algorithm	# MF > Poly	Significance
RKT	79	0.373
SS	88	0.026
IS	78	0.314
SMS	87	0.038

(1992) analysed the algal flora of 15 rock pools along a 53 m transect, and Gotelli & Entsminger (2001) analysed ants from a grid of pitfall traps within a 5 x 5 m area. Both studies found no structure using *C*-scores and other metrics, and both argued that the small spatial scale was responsible. Wilson et al. (1992) chose the rock pools to control for environmental differences between sites, in an attempt to implicate species interactions for significant patterns. Since no pattern was found, and the pools seemed to be "genuinely equivalent habitats", Wilson et al. suggested that differences in species occurrences between pools were likely due to chance.

The detection of significant community structure at the local scale may be due to unique features of the vent ecosystem. First, although tubeworm bushes are regarded as a distinct vent habitat type (e.g. versus high temperature sulphide chimneys), environmental differences can be quite variable at small scales. For example, temperature was measured for nine of the 16 vents used in this study; maximum vent fluid temperature ranged from 6°C to 55°C, represented by two vents only 10-15 m apart. Second, most vent species are restricted to their particular bush once they have successfully settled. Compared to other systems where habitat is continuous and species have greater ability to move between arbitrarily defined patches (e.g. ants of the pitfall traps), there is perhaps a greater opportunity at vents for species interactions to shape assemblage structure.

We stress that a separation of 10 years between sampling dates is inconsequential for this analysis. The null model approach simply asks if occurrence patterns deviate from random; the causes of nonrandom distributions are open to interpretation. One driving factor of nonrandom patterns may be predictable temporal shifts in species composition due to succession. The exact ages of the vents used here are unknown. Although we cannot discount vent age as a contributing factor, Tsurumi (2001) reports no relation of year of sampling to variation in compositions of the vents analyzed here.

Vent species associations

The straightforward, Monte Carlo approach of Sanderson (2000) was adopted for this paper: significance was determined by comparing the observed distribution of each pair to its simulated distributions. A persistent problem, however, is that the random placement of species across sites may yield some significant associations due to chance alone (Gilpin & Diamond 1982, Sanderson 2000). The task is thus to determine which pairs are associated by chance, and which pairs are associated for ecological reasons. Consistency across different methods does not answer this question; rather it supports results from individual analyses that certain pairs are indeed nonrandomly distributed across sites for any reason. This knowledge can be used to direct future research efforts, and decisions on which associations make ecological sense should then be based on available knowledge of the species and system.

From both data sets, 26 distinct species pairs were significantly associated by at least one algorithm (Tables 2.4 and 2.5). The majority of associations are negative (77%). Interpreting the associations is difficult due to lack of information on species feeding modes, habitat preferences and interspecific interactions. Since ecological knowledge of vent species is sparse, we use information from related taxonomic groups. We invoke common habitat requirements to explain positive associations. Negative associations are attributed to interspecific interactions (e.g. competition, predation) and species' differential habitat requirements and/or tolerances.

Vent species have a strong positive relationship between distribution and abundance (Tsurumi 2001). In this study the most abundant species occurred at all sites. The association analysis thus excluded assemblage dominants since the number of sites shared by a species pair could not deviate from observed values if one member was ubiquitous. This analysis thus reveals relationships among the relatively rarer species. However, rare species can add substantially to community biomass (e.g. vent scale worms) and may have a large impact on community structure. Knowledge of a species' contribution to community abundance or biomass may be another way to select which associations are potentially meaningful. Below we discuss all polychaete associations that were significant across all algorithms.

Positive Associations

Three polychaete pairs co-occurred more often than expected by chance across all algorithms (Table 2.4). One pair, *Branchinotogluma grasslei* and *Ophisthotrochopodus tunnicliffeae*, are both scale-worms that were described as different species in different genera based on morphology (Pettibone 1985, Pettibone 1988). However, recent molecular work indicates that they are, in fact, the same species (S. Hourdez, pers. comm.), which readily explains their positive association. The other two pairs are (1) the nereid *Nereis piscesae* and the dorvilleid *Parougia wolfi*, and (2) the hesionid *Amphiduropsis axialensis* and the undescribed spionid, *Prionospio* sp. Both the nereid and dorvilleid are armed with jaws (Blake & Hilbig 1990) and presumed carnivorous (Fauchald & Jumars 1979). The hesionid and spionid are small, fragile species (Pleijel 2001, Blake & Hilbig 1990); nothing is known about their foraging habits, although hesionids usually feed on diatoms, bacterial debris and copepods, while spionids presumably feed on surface deposits (Fauchald & Jumars 1979). Common habitat requirements are a likely explanation for both their co-occurrences, and all other positive associations. Habitat needs may include specific foods or specific temperature and/or chemical gradients.

Negative Associations

Three of the six negatively associated polychaete pairs include large, active, presumably predaceous species coupled with much smaller, less motile species. Two scale-worm species, *Opisthotrochopodus tunnicliffeae* and *Levensteiniella kincaidi*, are negatively associated with two hesionid species, *Hesiospina vestimentifera* and *Hesiodeira glabra*, respectively (Table 2.4). Adult vent scale-worms on the JdFR are typically 30-50 mm long and are believed carnivorous because of the feeding habits of their shallow water relatives and their jawed muscular eversible pharynges (Fauchald & Jumars 1979). In contrast, *H. vestimentifera* is usually about 17 mm long (Blake 1985) while *H. glabra* is a small, fragile species, 2.5-5.5 mm long (Blake & Hilbig 1990). It is unknown whether scale-worms prey upon hesionids, but an author (JM) has observed a vent scale-worm eating a similar-sized vent ampharetid polychaete. The third pair is the maldanid *Nicomache venticola* and *Nereis piscesae* (Table 2.4). *N. venticola* reaches lengths of 130 mm (Blake and Hilbig 1990) and as a maldanid presumably lives a sedentary, tube-dwelling life feeding on sediment by eversion of a sac-like pharynx (Fauchald & Jumars 1979). Nereids are similar to scale-worms: some are well-known active, carnivorous predators (Fauchald & Jumars 1979). *N. piscesae* has a jawed eversible pharynx, is a capable swimmer, and reaches lengths of 70-80 mm (Blake & Hilbig 1990). The attributes of these three species pairs may suggest predator-prey relationships.

The negative association between *Hesiodeira glabra* and *Amphiduropsis axialensis* is more difficult to assess. Both are small, fragile hesionid polychaetes with unarmed proboscides (Blake & Hilbig 1990, Pleijel 2001). Nothing is known about their foraging habits. It is possible these species are competitors, but they may have different habitat requirements and/or tolerances. However, the negative associations of the alvinellid *Paralvinella sulfincola* with *Hesiodeira glabra* and *Nicomache venticola* are likely due to species-specific habitat preferences (Table 2.4). *P. sulfincola* inhabits the highest temperature niche (20-80°C) of any vent fauna on the JdFR (Tunnicliffe et al. 1993, Juniper & Martineu 1995). Although surprising to find *P. sulfincola* at low temperature vents, it is possible that these vents had comparably higher temperatures than the other sampled sites.

Comparison of Algorithms

Of the four algorithms that rejected the null hypothesis of random structure, the SMS algorithm usually generated C- and S^2-scores close to, but significantly different from the RKT, SS and IS algorithms (Table 2.3). If the SMS and IS algorithms are theoretically identical, why were there slight differences in their scores? The most obvious possibility is that the number of submatrix swaps used to generate one null matrix affects results: the IS method swapped 30,000 submatrices per null matrix, while the SMS method only swapped 1000 (Table 2.1). To test this idea, we first calculated the total number of possible submatrix swaps in the polychaete data set to ensure each one had the chance of being swapped; this number is 548 (simply the total number of CUs (see [2]) in the observed matrix), well below our value of 1000. We then reran the analysis with 550, 1000, 5000 and 10,000 submatrix swaps per null matrix to evaluate the effect, if any, on summary indices. C- and S^2-scores generated from these trials were no different than those reported from the 1000 submatrix swap runs. Excluding the number of submatrix swaps as the responsible factor, and confident that the SMS program is theoretically equivalent to the IS program, we are left to conclude that the difference lies in the nuances of the programming. This in itself is an interesting result, and raises the notion that 'random' may not be a truly objective function, but depends on factors such as the programming language (behaviour of random number generators) and the mechanical details of the algorithm. However, in our study these differences were small enough that the conclusion of the null hypothesis test was unaffected.

However, when species association results are used to compare the four algorithms, the SS results fall out separately from the results of the other three. The RKT, IS and SMS algorithms generate species associations that are qualitatively indistinguishable; variation among trials is expected, but all 30 trials of these three algorithms form one cluster and the trials interdigitate (Figure 2.2). This distinctness of the SS trials is not surprising since this method produces null matrices with 30,000 initial submatrix swaps followed by one swap for each subsequent null matrix. The species pair results thus depend heavily on the matrix configuration after the initial swap of 30,000; this starting point seems to dictate which species pairs will be deemed significant. The dendrogram reflects this phenomenon: variation among the SS trials is much higher than the other three, and the SS trials form a loose cluster clearly separate from the other three. Thus, we recommend that although the SS method may be an adequate and quick way to perform a null model analysis with summary indices (see Gotelli & Entsminger 2001), it is inadequate for determining species associations. Manly & Sanderson (2002) further argue that the SS method is not useful for community analysis: the method is not mathematically defensible since the test for significance is based on non-independent sequential steps.

Polychaete versus Macrofuana pairs: A dilution effect?

Did the significant associations from analysis of just the polychaetes get lost in a "mass of irrelevant data" (Gilpin & Diamond 1982) with analysis of the whole macrofauna data set? The answer depends on the algorithm: the SS and SMS methods produced results indicative of a dilution effect, while the RKT and IS algorithms did not (Table 2.6). However, the effect was not extreme enough with the SS and SMS algorithms to affect the ranking of significant pairs, so the main associations were not obscured (Tables 2.4 and 2.5). Thus, we suggest that in systems like vents, where information is too limited to warrant informed allocation of species to groups (like guilds), analysis of all the macrofauna is appropriate. It remains an open question whether the dilution effect is present in other types of data sets, as even with the addition of all other macrofauna our data set was small.

Conclusions and Current Challenges

Overall, the results of the null model analyses support the notion that species are nonrandomly distributed across diffuse vents at the scale of a vent field. However, the varied behaviour of the algorithms across different analyses suggests that the results of the null models still need to be applied with caution. No two algorithms produced identical results for community, association and dilution effect analyses. Summary indices calculated from the SS, IS and RKT algorithms were usually similar, and differed from summary results of the KT and SMS algorithms. However, the summary results were also index and data set dependent. For example, the SMS method was not a distinct group when the S^2-score was applied to the polychaete data (Table 2.3). In contrast, the SMS, IS and RKT algorithms produced similar species associations, while the SS algorithm differed. Finally, the SS and SMS algorithms produced a dilution effect and the RKT and IS algorithms did not. In any one study, researchers might be well advised to test their data with multiple approaches before proceeding to more expensive sampling or experimentation.

There are three further considerations when using this type of null model analysis. One, the species pair approach only teases out pairwise associations when multi-species relationships are known to be important in structuring communities (Dale et al. 1991). Second, decisions about which pairs are associated due to nonrandom causal forces and not chance remain subjective. This is particularly challenging when so little is known about the species in question, making selection of pairs and explanatory arguments speculative. Three, null models currently use presence/absence data. This limits their usefulness for smaller-scale studies where patterns likely occur with species abundances rather than species occurrences.

Regardless of these limitations, co-occurrence null models are an improvement over other approaches of pattern detection in survey data. The main advantage is that null models overcome problems associated with having to refer to a theoretical distribution to determine significance. Contemporary computing power allows probability distributions of a chosen community test statistic to be generated under the assumption that the null hypothesis is true by randomizing the observed data set thousands of times. The test statistic need not conform to a known distribution and the researcher is free to choose any reasonable measure(s) for the question under study.

Further, and we believe almost as crucially, null models are a useful tool for analysing data from environments that are not amenable to experimentation. The null model approach allows the ecologist to ask if species distributions are nonrandom thus justifying the search for process, and teases out patterns that can direct future research effort when time and money are limiting. Our analysis shows that hydrothermal vent species are nonrandomly distributed across sites, and we believe null models are a useful way to detect species patterns in challenging habitats like the deep-sea.

Acknowledgements

We thank J. Sanderson and R. Selfridge for kindly giving us their program for the Knight's Tour algorithm, and N. Gotelli and G. Entsminger for their comments on the SMS algorithm. All four gladly answered many questions. We thank V. Tunnicliffe for posing the original question, and for field support and samples. Thanks also to the crews of the R/V Pandora II, R/V Brown and the R/V Atlantis II, and to the *Pisces, Alvin* and *ROPOS* teams for field support. We also gratefully acknowledge the support of the NOAA Vents program. J. M. was funded by scholarships from Natural Sciences and Engineering Research Council of Canada, the Canadian Association of University Teachers and the University of Victoria.

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CHAPTER 3

A new species of scale-worm (Polychaeta: Polynoidae) from Axial Volcano, Juan de Fuca Ridge, northeast Pacific

Marcus, J. and Hourdez, S. 2002. *Proceedings of the Biological Society of Washington* 115(2): 341-349.

Abstract

Vampiropolynoe embleyi, a new genus and species of scale-worm (Polychaeta: Polynoidae), is described from hydrothermal vents created by the 1998 eruption of Axial Volcano (Juan de Fuca Ridge, NE Pacific). Based on this species we propose a new subfamily, the Vampiropolynoinae. This subfamily is closely related to the deep-sea subfamilies Macellicephalinae and Lepidonotopodinae. However, the Vampiropolynoinae differs by having a significantly greater number of segments, by lacking jaws, and by possessing a pair of strong curved acicular lobes on the tentacular segment. The mouth structure, along with sea-floor observations, suggests that *V. embleyi* grazes on bacterial mats. We propose that *V. embleyi* is a pioneer species adapted to living at new vents.

Introduction

Axial Volcano (Juan de Fuca Ridge) erupted in January 1998, initiating new venting along a lava flow over 3 km long (Embley & Baker 1999). Observations seven months after the eruption with the remotely operated vehicle ROPOS revealed new vents already colonized by numerous vent species (Tsurumi et al. 1998). Common Axial Volcano polynoids (*Branchinotogluma* spp., *Opisthotrochopodus tunnicliffeae*, *Lepidonotopodium piscesae*) were present in high numbers at most new vents (J.M. pers. obs.). Along with these typical vent polynoids, an unknown large bright red scale-worm was observed in high densities, feeding on the bacteria-covered basalt of vent peripheries. Here we describe this new species from collections made in the summers of 1998, 1999 and 2000.

There are nine subfamilies of polynoid polychaetes known from hydrothermal vents (Tunnicliffe et al. 1998). Of these, four are known from the Juan de Fuca Ridge.

We argue that the new species described herein is distinct enough from vent and other deep-sea subfamilies to warrant the formation of a new subfamily allied to the Macellicephalinae Hartmann-Schröder, 1971, emended Pettibone, 1976 and the Lepidonotopodinae Pettibone, 1983.

Materials and Methods

Type locality

Axial Volcano, Juan de Fuca Ridge, 45°56'N, 128°59'W, 1530 m depth ("South Rift Zone" venting area). Specimens were suctioned from bare basalt on vent peripheries.

Type material

Holotype (dive R488, 27 Jun 1999; USNM 1002015) and 3 paratypes (dive R473; USNM 1002016) are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Another paratype is deposited in the collections of the Canadian Museum of Nature, Ottawa, ON (dive R474; CMNA 2002-0001).

Additional Material

A total of 23 specimens were collected during ROPOS dives R462 (1 specimen, Marker 33 site), R473 (17 specimens, Marker 108 and Marker 33 sites), R474 (1 specimen, Milky site), R488 (2 specimens, Cloud site), R543 (1 specimen, Marker N41 site), R549 (1 specimen, Cloud site). Four specimens from R473 were deep-frozen for isotope analysis, and 1 specimen from R543 was preserved in ethanol for DNA analysis.

Specimen preparation

Two specimens, fixed with 7% seawater formalin and preserved in 70% ethanol, were prepared for scanning electron microscopy (SEM). They were critical point dried with carbon dioxide, sputtered with gold and examined with a Jeol scanning electron microscope (JSM-5200).

Systematics

Family Polynoidae
Vampiropolynoinae, new subfamily

Diagnosis

Polynoid with elongated body, up to 45 segments. Elytra 10 pairs, on segments 2, 4, 5, 7, 9 alternating to 19. Dorsal cirri on non-elytrigerous segments. Prostomium bilobed. Lateral antennae absent. Median antenna inserted in central notch of prostomium. Frontal filaments hooked. First segment fused to prostomium; a pair of strong, prominent acicular lobes curve toward midline of the body. Eyes lacking. Jaws absent. Keratinized teeth cover junction between mouth opening and pharynx. Curved conical papillae on the upper, lateral, and ventral lips surround mouth opening. Parapodia biramous. Digitiform dorsal tubercles present on all cirrigerous segments, starting on segment 6; absent from elytrigerous segments. Ventral nephridial papillae indistinct. Pygidium with a pair of anal cirri.

This subfamily comprises a single species described in this paper.

Vampiropolynoe, new genus

Diagnosis

Characters of the subfamily.

Type species

Vampiropolynoe embleyi, new species, by present designation.

Etymology

Vampiro is from the English vampire, in reference to the fang-like appearance of the acicular lobes on the first segment and papillae at the mouth, and *polynoe* is taken from the family name Polynoidae.

Vampiropolynoe embleyi, new species
Figures 3.1 - 3.5

Diagnosis

Characters of the subfamily.

Etymology

The species is named after Robert Embley, chief scientist of the 1998-2000 Axial cruises when specimens of this new species were collected.

Description

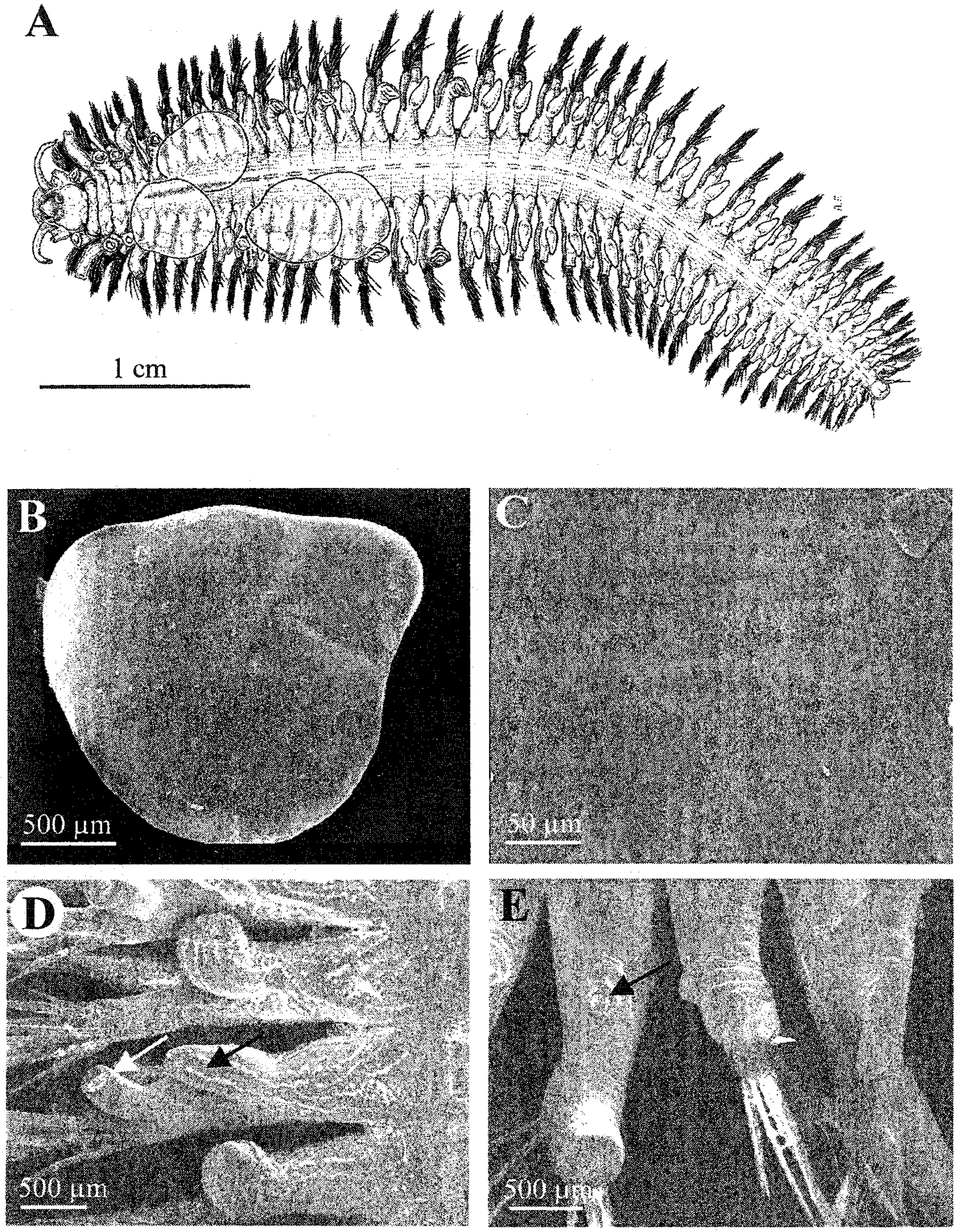
Preserved holotype 46 mm long for 45 segments, 12 mm wide including parapodia (excluding setae), and 3 mm wide without parapodia. Largest paratype 52 mm long for 43 segments; smallest paratype 36 mm long for 44 segments. Body long, tapers gently posteriorly (Figure 3.1A). Living specimens bright red, with white setae, and reach live lengths up to 55 mm. After preservation, specimens light brown.

Elytra 10 pairs on segments 2, 4, 5, 7, 9 alternating to 19. First pair of elytra overlap medially but leave a central notch through which the median antenna protrudes. Elytra overlap anteriorly and posteriorly, but leave a gap along the mid-dorsal line. Elytra attach eccentrically on prominent elytrophores. Elytra translucent, smooth, oval, and without ornamentation (Figure 3.1B). Elytral surface covered by numerous small circular pits about 5-10 μm in diameter (Figure 3.1C).

Dorsal cirri with cylindrical cirrophores attached dorso-posteriorly on the notopodia (Figure 3.1D). Cirri extremely long (up to half the length of the worm), and taper gradually to tips. Lines of cilia cover parapodia except on ventral side (Figures 3.1D, 3.4A-D, 3.5E). No transverse lines of cilia on the middorsum (Figure 3.1D). Digitiform dorsal tubercles on all cirrigerous segments (Figures 3.1A, D, E, 3.4C-F), starting on segment 6 (Figure 3.1E). Dorsal tubercles become dorso-ventrally flattened on the posterior segments of the worm.

Prostomium bilobed, with hooked frontal filaments (Figure 3.2A-C). Lateral antennae absent. Median antenna approximately 2-3 times the length of the prostomium; tapers gently to the tip. Median antenna with a short, cylindrical ceratophore inserted in

Figure 3.1. A. Drawing of paratype (R473-6096), dorsal view of whole specimen. Dorsal cirri have broken off. B-E, SEM views. B. Elytron from the mid-section, dorsal view. C. Detail of elytral surface. D. Dorsal view of segments 11 (bottom) –14 (top). White arrow points to cirrophore on segment 12, black arrow points to digitiform dorsal tubercle on the same segment. E. Detail of first dorsal tubercle on segment 6 (black arrow).


A
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E
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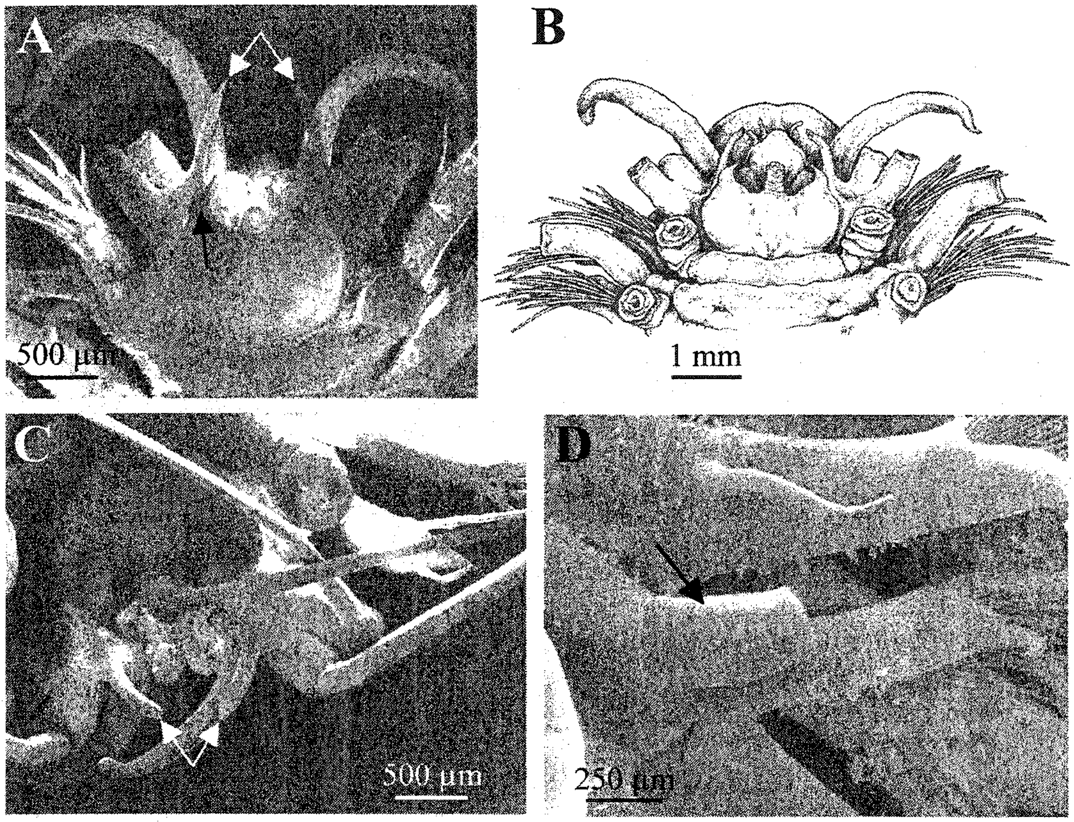
Figure 3.2. A, C, and D, SEM views. A. Dorsal view of anterior part of worm. White arrows point to the strong aciculae protruding from the 1st segment. Black arrow points to the left hooked frontal filament. B. Drawing of the anterior part of paratype (R473-6096), pharynx partially everted. C. Frontal view of prostomium showing median antenna, tentacular cirri, aciculae (white arrows). D. Detail of the buccal cirrophore (black arrow), and second ventral cirrus (3rd segment).


A
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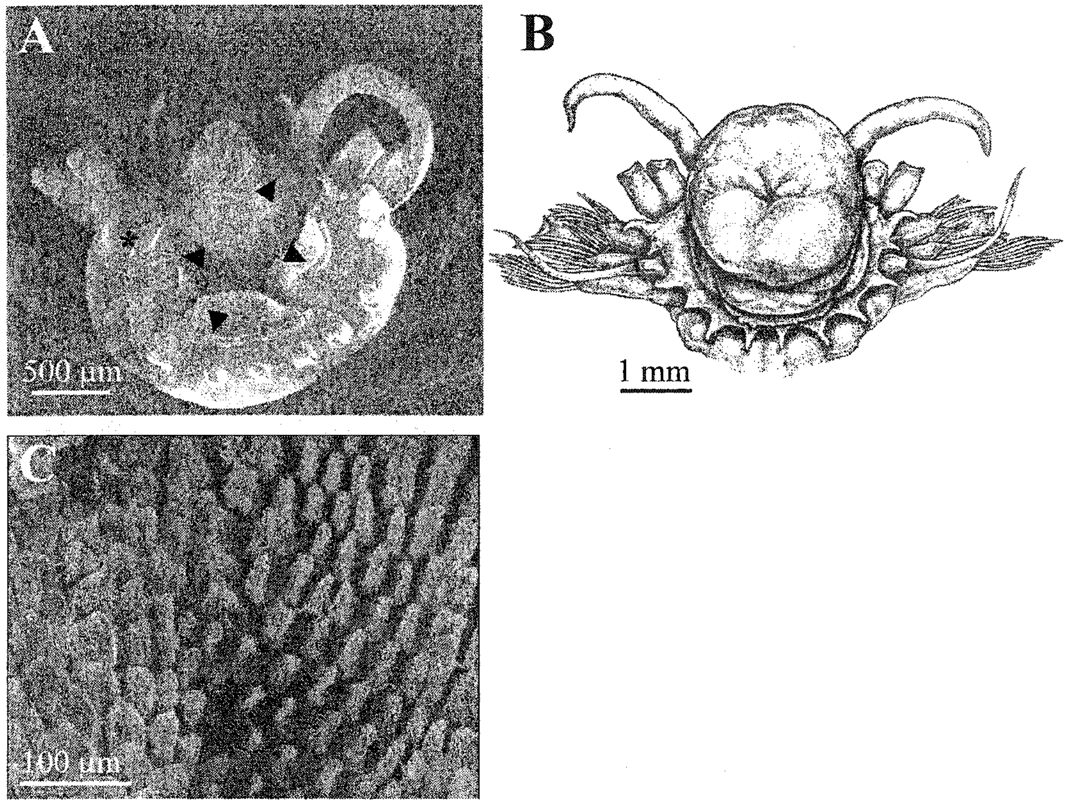
D
250 µm

Figure 3.3. A and C, SEM views. A. Ventral view of a partially everted pharynx showing upper, lateral and ventral lips with their papillae and ridges. Black arrowheads point to lip ridges, asterisk points to shared bulbous base of the two median papillae on the lateral lip. B. Drawing of paratype (R473-6096), ventral view of a more everted pharynx, with the buccal papillae forming a crown at the base of the pharynx. C. Keratinized teeth at the junction between the mouth opening and the pharynx.


A
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500 µm
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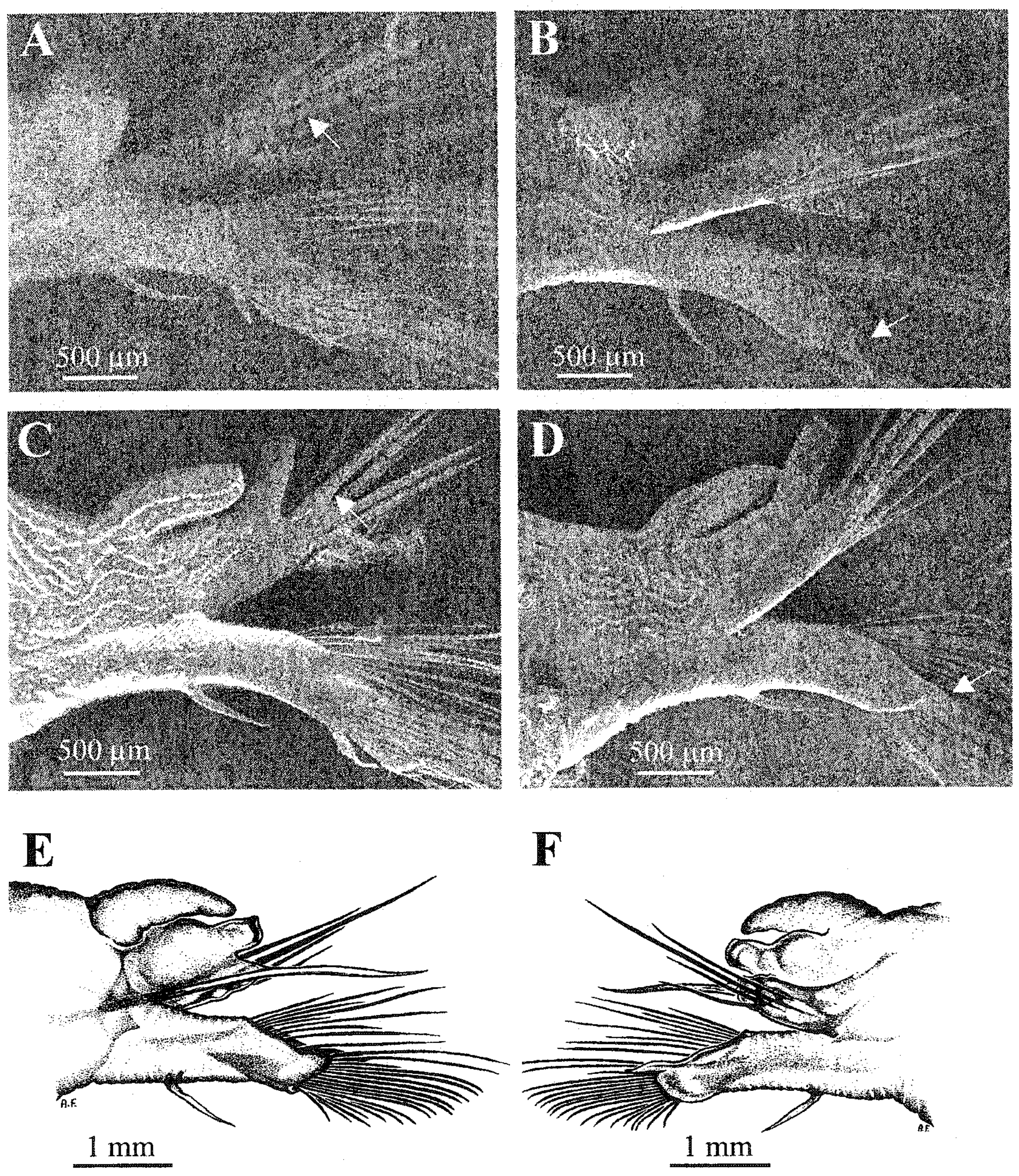
100 µm

Figure 3.4. A-D, SEM views; E and F, drawings. A. Posterior view of elytrigerous parapodium (segment 15). Arrow points to the ligule of the notopodium. B. Anterior view of the parapodium from the same segment. Arrow points to the ligule of the neuropodium. C. Posterior view of cirrigerous parapodium (segment 14). Arrow points to the ligule of the notopodium. D. Anterior view of the parapodium from the same segment. Arrow points to the ligule of the neuropodium. E. Posterior view of cirrigerous parapodium of segment 24, note the protruding acicula. F. Anterior view of the same parapodium depicted in E.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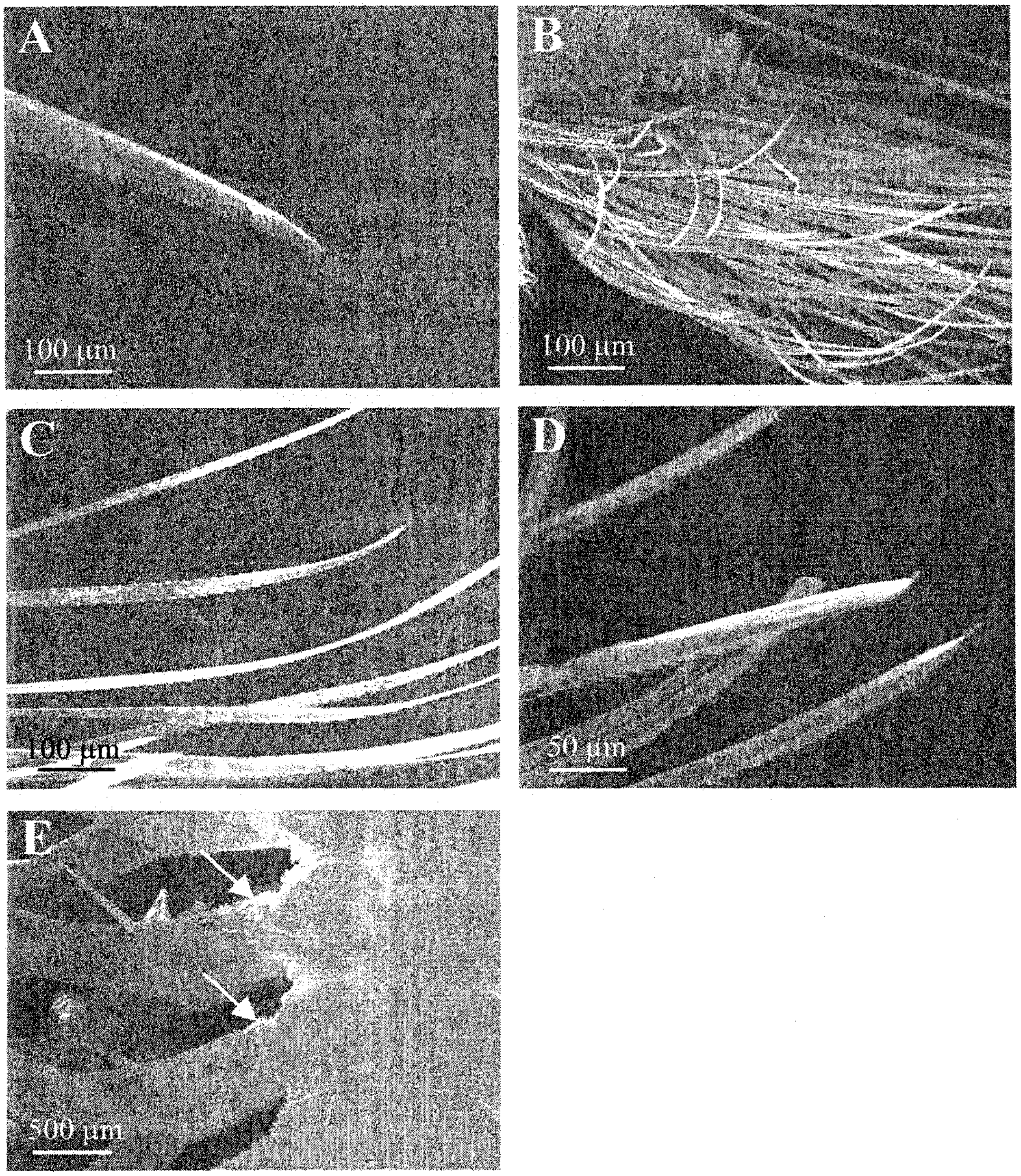
E
A.F.
1 mm
F
A.F.
1 mm

Figure 3.5. A-E, SEM views. A. Tip of a notoseta. B. Feather-like neurosetae on the lower side of the neuropodium. C. Upper neurosetae. D. Detail of neurosetae tips. E. Ventral view of segments 11-14 showing inconspicuous nephridial papillae (white arrows).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100 µm
B
100 µm
C
100 µm
D
50 µm
E
500 µm

the anterior notch of the prostomium (Figure 3.2A-C). Palps approximately twice the length of the prostomium; taper gradually to the tips (Figures 3.1A, 3.2A, B, 3.3A, B). Eyes lacking. First (or tentacular) segment not visible dorsally. Tentaculophores lateral to the prostomium; each bears one strong brown acicular lobe that curves towards the midline of the body (Figures 3.1A, 3.2A-C, 3.3A). Tentacular styles long (reaching 0.25 of the body length), slender, tapered. Facial tubercle lacking.

Second (or buccal) segment with first pair of large elytrophores and biramous parapodia (Figures 3.1A, 3.2A-C). Ventral or buccal cirri attached basally on prominent cirrophores lateral to the ventral mouth (Figures 3.2D, 3.3B). Buccal cirri similar in shape to the tentacular cirri; longer than the following ventral cirri. Mouth enclosed in upper, lateral and posterior lips between segments 1 and 3 (Figure 3.3A, B). Pharynx never fully everted in the studied specimens. A partially everted pharynx shows papillae at the mouth opening (Figure 3.3A). Upper lip with a group of 3 conical curved papillae similar in shape and size. Ventral lip with 3 pairs of conical curved papillae increasing in size from the median papilla to the most lateral one. Lateral lips with 4 pairs of conical curved papillae; the central pair shares a bulbous base (Figure 3.3A, B). A concentric ridge broken by the limits between the upper, lateral and ventral lips lies interior to the ring of papillae (Figure 3.3A). Ridge on the ventral lip divided into two symmetrical parts, each with 3 small, equidistantly placed papillae. Area between the mouth opening and the pharynx bears numerous small (approximately 40 by 50 by 10 μm), keratinized teeth (Figure 3.3C). No jaws at the opening of the pharynx.

Parapodia biramous. Notopodia short, on the anterio-dorsal side of the longer neuropodia (Figures 3.1D, 3.4A-F). Elytrigerous notopodia cylindrical (Figure 3.4A, B), the posterior lobe forms a ligule (Figure 3.4A). On posterior cirrigerous segments, the acicula protrudes from the acicular lobe (Figure 3.4E, F). On cirrigerous notopodia, the cirrophore projects at the emergence point of the notosetae (Figure 3.4C, D). Upper and lower margins of the neuropodia deeply cleft. Conical presetal lobes of neuropdia equal in length to the rounded postsetal lobes (Figure 3.4A-F). Presetal lobe extended by a ligule (Figure 3.4B, D, F). Ventral cirri short and tapered; located at the base of the neuropodia (Figure 3.4A-F).

Notosetae (approximately 10 per notopodium) stouter than neurosetae (Figure 3.4A-F), smooth, and taper to blunt tips (Figure 3.5A). Neuropodia with 2 types of setae. Lower neurosetae curved (Figures 3.4A-D, 3.5B); at a higher magnification setae appear feather-like. Upper neurosetae flattened with lateral teeth (Figure 3.5C). Teeth begin just above the emergence point of the setae, and continue to the tapered, curved, scoop-like tip (Figure 3.5C, D). Setae similar on all segments.

Nephridial papillae inconspicuous; begin on segment 5 and continue along length of the body (Figure 3.5E). Pygidium small, rounded, and with a pair of short anal cirri.

Ecology

Vampiropolynoe embleyi appears to specialize at colonizing new vents. This suggestion is supported by the species' absence from the numerous observations and collections of animals made at sustained venting sites at Axial since the mid-80s, and its presence in high densities at most new vents created by the Axial eruption (10 of 14 vents observed in 1998). The large size of *V. embleyi* and its conspicuous red coloring makes it highly unlikely that it would have been overlooked. Furthermore, *V. embleyi* is easily observed in photographs of CoAxial Segment (Juan de Fuca Ridge) vents one year after their initiation by an eruption, although specimens were not collected (V. Tunnicliffe, pers. comm.).

Vampiropolynoe embleyi lives on vent peripheries, beyond the immediate area of fluid flow. The species is strikingly more active than other vent polynoids: it crawls quickly across the basalt, and swims short distances when disturbed. At most vents in July 1998, *V. embleyi* was observed spaced at least a body length apart from other individuals (of both *V. embleyi* and other vent polynoid species), but at two sites it occurred in relatively dense monospecific patches, reaching densities up to 60 individuals/m^2 (Cloud and Mkr 108 vents). Densities decreased by June 1999 (highest was 30 individuals/m^2 at Cloud vent) and by July 2000, two and a half years after vent creation, *V. embleyi* was not evident in bottom observations, although still present in very low numbers (2 specimens found in 32 collections).

These observations strongly suggest that *V. embleyi* is a pioneer species, adapted to living at hydrothermal vents within the first two years after their creation. The feeding structures of *V. embleyi* are consistent with observations of it grazing on bacteria and gelatinous material. Many studies report the correlation between seafloor eruptions and subsequent proliferation of bacterial mats (see Delaney et al. 1999 for review). *V. embleyi* is likely capitalizing on this abundant food source which may last for months to years following an eruptive event.

Discussion

Vampiropolynoe embleyi is a deep-sea species collected from vents created by the eruption on Axial Volcano, Juan de Fuca Ridge. The new subfamily erected here, the Vampiropolynoinae, is closely related to the Macellicephalinae and Lepidonotopodinae. The bilobed prostomium and the lack of lateral antennae typify these two subfamilies. However, the Vampiropolynoinae is clearly distinguished from the Macellicephalinae and Lepidonotopodinae by the absence of jaws, the presence of keratinized teeth, and the presence of a pair of strong hooked acicular lobes on the first segment. The high number of segments of *V. embleyi* (up to 45) also clearly differentiates it from the Lepidonotopodinae (23 to 30 segments; Desbruyères & Hourdez 2000a, b), and the Macellicephalinae (15 to 28 segments; Pettibone 1989, Hourdez & Desbruyères 2000).

The suggestion that *Vampiropolynoe embleyi* is a vent pioneer species adapted to conditions following eruptive events awaits further confirmation from future eruptions on the Juan de Fuca Ridge.

Acknowledgments

We thank Aud Fischer for the exceptional drawings of this new species, and Rosemary Walsh for her assistance with the electron microscopy studies. Many thanks to Verena Tunnicliffe for field support and manuscript suggestions and Charles Fisher for use of his research facilities. Thanks are also extended to the crew of ROPOS and the NOAA Vents Program. This work benefited from the comments of Brigitte Hilbig and an anonymous reviewer. This research was supported by the Natural Sciences and Engineering Research Council of Canada (JM and VT), the NOAA West Coast National Undersea Research Program (SH) and the National Science Foundation (OCE-9633195 to CF).

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CHAPTER 4

Modelling colonization of nascent hydrothermal vents

Introduction

Ecological communities do not suddenly appear, but develop in time by a process called assembly (Lockwood et al. 1997). This process is initiated by an event that reopens or creates new habitat. Over time species recruit to and occupy this new habitat. The sequence of species arrivals and community structure early in the assembly process can influence community organization later in time (Drake 1990, 1991). Knowledge of historical events is thus desirable to interpret observed patterns of extant communities and correctly attribute process.

The pattern of initial assembly differs among systems. In some habitats, early assembly is predictable. In the intertidal environment, certain species are adapted to post-disturbance conditions and are the first to colonize new space (e.g. early successional species; Berlow 1997). Initial species may further influence assemblage structure by having a positive or negative effect on the success of other potential colonists. Priority effects such as facilitation and inhibition are present at many locales (McCook 1994, Blaustein & Margalit 1996).

In other habitats, initial assemblage structure is unpredictable. New assemblages are not correlated to environmental factors, or composed of predictable species, but seem to be random subsets of species drawn from a pool of potential colonists. For example, vegetation structure of Mount St. Helens pumice potholes (del Moral 1999) and vegetation of Mediterranean old fields (Lavorel & Lebreton 1992) are best described by stochastic models of species assembly. Chance events early in assembly are intriguing since initial stochasticity can produce persistent assemblages of different compositions in the lab (Drake 1991). Thus, knowing if initial assemblages are random may be important for understanding community variation later in time.

This hypothesis of random assembly has been called ‘lottery recruitment’ (Lavorel & Lebreton 1992). Lottery recruitment should not be confused with Sale’s (1977) lottery hypothesis of community structure. Sale proposed that certain species assemblages, such as fish on patch reefs, are stochastic entities at all times. His is a hypothesis of persistent community organization and thus can only be tested with temporal data of established assemblages (Sale & Steele 1986, Galzin & Legendre 1987). Here I use 'lottery' to refer to lottery recruitment, defined as the assembly of species at newly formed habitat patches by random draws of species from a regional species pool.

My objective is to test whether lottery recruitment applies to new hydrothermal vent communities. There is evidence that longer-lived or mature, low temperature vent assemblages are nonrandomly structured (Marcus & Anholt in revision), but the structure of nascent low temperature assemblages is not well known. The two studies that examine early post-disturbance assemblages suggest that vents are colonized by a predictable subset of the species pool (Tunnicliffe et al. 1997, Shank et al. 1998), and priority effects may be important for some species (Mullineaux et al. 2000). However, observations of a recent eruption of Axial Volanco on the Juan de Fuca Ridge (JdFR) show substantial variation among early vent assemblages (Tsurumi et al. 1998), implying that initial assembly is not as predictable as previously thought.

Testing whether initial vent communities are stochastic is important for three reasons. First, authors typically turn to the possibility of random assembly after other pattern detection methods such as ordination techniques (e.g. CCA, relating species patterns to environmental variables) fail to explain observed patterns (Kazmierczak 1995, del Moral 1999). Since multivariate community statistics are qualitative in nature, and either impose structure on (cluster analysis) or assume structure of (ordination) the data, nonrandom patterns should first be statistically validated before attempts to relate species patterns to abiotic factors (Jackson et al. 1992).

Second, although random assembly is known to set assemblages on different trajectories of development in the lab (Drake 1991), very few studies have addressed this question by following assembly of whole communities in the field (Drake 1990, Honnay et al. 2001). The first step towards answering this question in the field is to determine if initial assembly is random.

Third, random dispersal and random settlement may be the best strategy for species that contend with variable and unpredictable habitats in space and time (Sale 1977, Ferriere et al. 2000). Since vents are inherently variable and unpredictable habitats, random dispersal may be a good strategy for vent species. Variations in larval dispersal and chance recruitment have been suggested as potential drivers of vent community structure (Tunnicliffe & Fontaine 1987, Lutz & Kennish 1993).

The Axial Volcano eruption was a catastrophic disturbance. The lava flow paved over all organic matter in its path, and created new substratum supporting new vent habitat. In classic ecological terminology, this disturbance initiated the process of primary succession: the lava flow destroyed pre-existing faunal assemblages, necessitating species recruitment to new vents from afar. This chapter examines data from the Axial eruption to determine if the observed variability in initial assemblages could result from lottery recruitment. Determining whether initial vent assemblages are random subsets of the species pool is one further step towards understanding the processes driving vent community structure. I ask if vents sampled seven months after inception are colonized by species assemblages that are different from assemblages created by randomly drawing individuals from the pool of potential colonists.

Methods

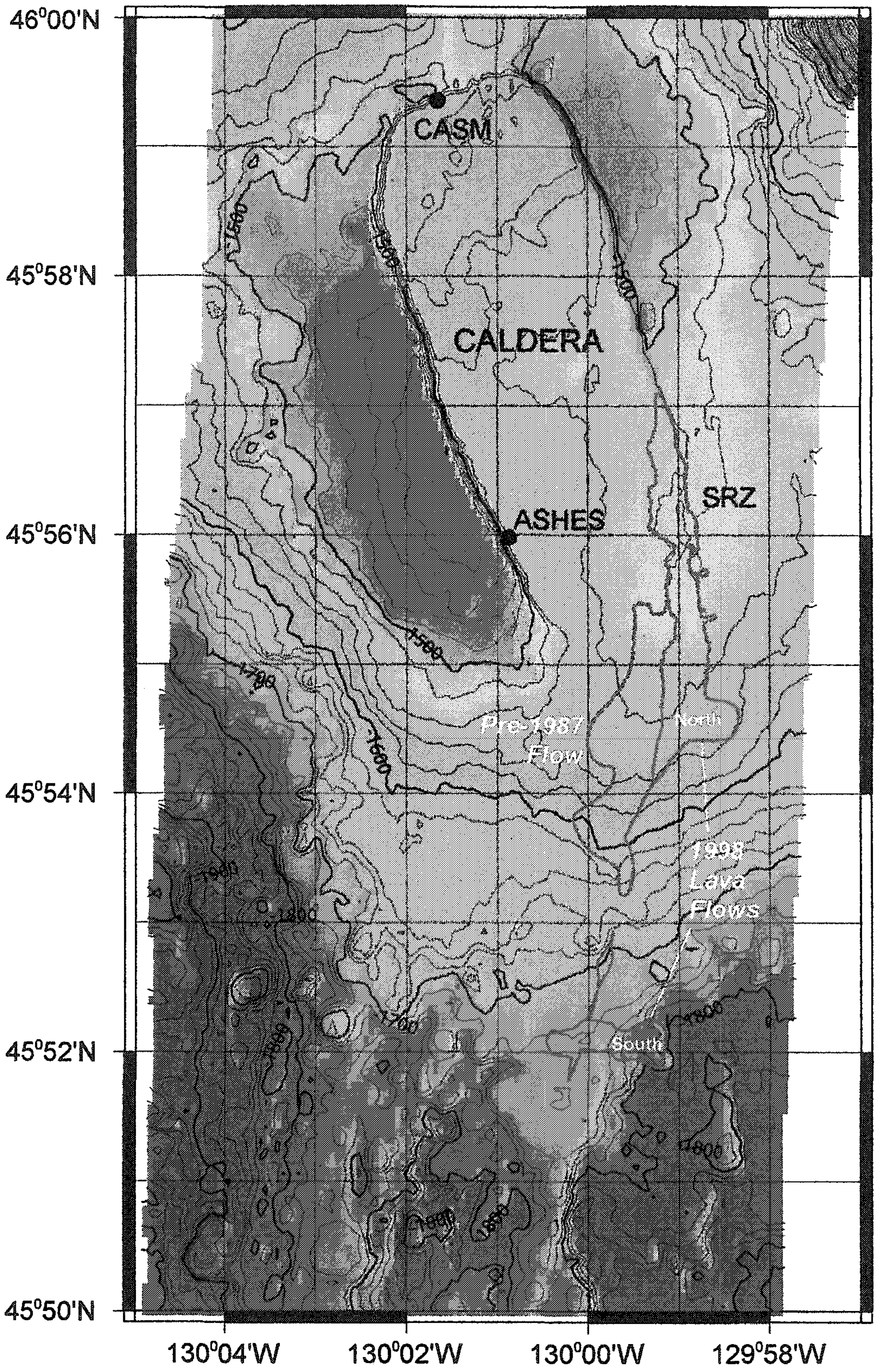
Site description

Axial Volcano is an active, ridge axis seamount situated on the central segment of the Juan de Fuca Ridge in the northeast Pacific (N45°57’, W130°00’; Figure 1.4). The summit, approximately 1500 metres depth, hosts a three-sided caldera. There are three areas of active venting within the caldera: ASHES, CASM and the South Rift Zone (SRZ) vent fields (Figure 4.1).

Venting was discovered at Axial in 1983 with submersible dives to the CASM field (Tunnicliffe et al. 1985). The ASHES field, an area about 100 m in diameter, was first visited in 1984. Both CASM and ASHES support high temperature chimneys and low temperature basalt-hosted habitats. The SRZ covers an area about 6 km north to south and on average about 0.5 km wide (Tsurumi 2001). The SRZ was briefly surveyed in the summers of 1985-87, and again in 1996-97; only low temperature venting was observed (R. Embley pers. comm.). The SRZ erupted in January 1998, and since then vents of this area have been intensively sampled.

The SRZ eruption created two lava flows (Figure 4.1). Animal assemblages in the path of the northern lava flow were destroyed and new vents were created (Embley

Figure 4.1. Map of the summit caldera of Axial Volcano. The location of the three vent fields (ASHES, CASM and the South Rift Zone) are shown with respect to the north and south lava flows created by the January 1998 eruption (outlined in red). A lava flow of unknown age, but formed prior to 1987 is also shown (outlined in purple). Map provided by B. Chadwick (Pacific Marine Environmental Laboratory, NOAA). Note: 1 minute latitude = 1.8 km.


46°00'N
45°58'N
45°56'N
45°54'N
45°52'N
45°50'N
130°04'W
130°02'W
130°00'W
129°58'W
CASM
CALDERA
SRZ
ASHES
Pre-1987
Flow
North
1998
Lava
Flows
South
1500
1600
1700
1800

& Baker 1999); no vents were found on the southern flow. In July and August 1998, seven months post-eruption, the northern end of the northern flow was explored and sampled with the remotely operated vehicle ROPOS. Over ten new vents were discovered on this portion of the flow.

Sampling

Faunal samples were collected from the three Axial fields in 1986-88 and 1997-1999. Selected samples for this study are all low-temperature (<50°C), basalt-hosted assemblages, except one (Flat Top, Table 4.1). Flat Top is a low temperature (~20°C) sulphide sample, and was included as it was initially mislabelled as a diffuse vent on basalt (Tsurumi 2001). Flat Top should not affect results: it only contributes ~1% to the total number of individuals used to estimate the species pool and its community structure is indistinguishable from basalt-hosted assemblages (Tsurumi 2001).

Samples were categorized as new or mature. I defined new assemblages as the fauna living at vents within the first year after their creation. The 1998 eruption is the only known major disturbance at Axial since 1983, thus the only data for new assemblages are from vents sampled seven months after the 1998 event. I defined mature assemblages as the fauna living at vents with sustained fluid flow for a number of years. Since the three fields have supported continuous venting since the mid-1980s, I referred all non-eruption samples to the mature category. While the exact ages of the mature assemblages are unknown, the Axial caldera has not experienced a major perturbation since the mid-80s through to 1998. A deflation of the caldera may have occurred in 1988, possibly caused by an intrusion or eruptive event (Fox 1990), but the evidence is ambiguous and no obvious biological changes were observed at CASM and ASHES (V. Tunnicliffe pers. comm.). Minor disturbances such as clogging and opening of subsurface flow conduits could have initiated venting, resulting in mature assemblages of different ages. However, all mature assemblages are characterized by a very similar structure (species composition, relative abundances), species contain several size classes and observed variability is not related to vent field location or year of sampling (Tsurumi 2001). Thus, although differences in mature assemblages may be associated with age,

Table 4.1. Axial samples used for random colonization analyses. The tubeworm *Ridgeia piscesae* is excluded. Only the macrofauna, defined as all species caught on a 1 mm sieve, are reported. SRZ = South Rift Zone. * indicates a sulphide sample, all other samples are from diffuse flow basalt-hosted vents.

Sample ID	Vent Field	Vent Name	Year	Number of Individuals	Number of Species
Mature Assemblages					
A	ASHES	Goblin	1986	9907	10
B	ASHES	Bouquet	1986	7815	23
C	ASHES	Demon	1986	28066	21
D	ASHES	Sweet	1986	1819	10
E	ASHES	Limbo	1986	2581	17
F	ASHES	Miserable	1986	401	14
G	ASHES	N-S-M	1986	18917	21
H	ASHES	Devil	1986	6256	17
I	ASHES	Bouquet	1988	5337	20
J	ASHES	ISCA	1997	4689	17
K	ASHES	Hatfield	1997	37121	28
L	ASHES	Bouquet2	1998	14395	24
M	ASHES	Hairdo	1998	33687	21
N	ASHES	Gollum	1998	6208	12
O	ASHES	Marker I	1998	8681	15
P	ASHES	Medusa	1998	508	6
Q	CASM	Post-Taylor's	1986	7018	17
R	CASM	Base of T & S	1999	2736	12
S	SRZ	Flat Top*	1998	2095	10
T	SRZ	Oldworms	1998	3841	16
U	SRZ	Old Flow	1998	2441	13
V	SRZ	Large TW	1998	1766	10
New Assemblages					
AA	SRZ lava	Easy	1998	32	5
BB	SRZ lava	Mkr N41	1998	81	8
CC	SRZ lava	Nascent	1998	161	5
DD	SRZ lava	Mkr 33	1998	288	11
EE	SRZ lava	Snail	1998	533	7
FF	SRZ lava	Cloud (N4)	1998	15	4
GG	SRZ lava	Mkr 108	1998	42	8
HH	SRZ lava	Mkr 113	1998	82	4

this possibility is inconsequential here. All mature assemblages include adults that contribute propagules to the Axial species pool. For this paper, I used data from eight new, and 22 mature assemblages (Table 4.1).

All mature vent samples were grabs of tubeworms taken with a clawed submersible arm. Samples were put in closed boxes for transport to the ship. On board, samples were fixed in 7% seawater formalin. In the lab, samples were sieved over a 1mm and then a 64μm mesh. All samples were sorted for the macrofauna defined as species whose adults would be caught on a 1mm sieve (all fauna except copepods, podocopid ostracods, nematodes and mites). For five samples (Table 4.1, samples A, C, E, G, I) all individuals caught on the 1mm sieve were sorted, but only one-quarter of the debris (64μm to 1mm size fraction) was processed. Total abundances of these five samples include extrapolated numbers from the quarter debris sorts.

New vent samples were either suctions or tubeworm grabs. Fauna were suctioned through a hose into a collection jar with the flow outtake fitted with either a 64 or 250μm mesh. Density data for suctions were unobtainable due to the friable substratum and the limited manipulation ability of the submersible. Samples were processed as above, except all new samples were sorted down to meiofauna (64μm mesh size), but only macrofauna are reported here. I justify the mixed sampling methods by a requirement for maximal assemblage representation: tubeworms were not present at some vents in 1998 and grabs on bare basalt are impossible.

Statistical Modelling

Testing random assembly of species from a species pool requires knowledge of the species pool and data on the structure of real new assemblages. Random assemblages can then be created using different models of assembly. Comparison of observed assemblages to these random assemblages determines if new assemblages are random.

Creating the species pool – I combined the species abundance data from the 22 mature vent samples to estimate the structure of the Axial species pool. All species were included except the tubeworm *Ridgeia piscesae*, which was excluded because it is the substratum for other species.

Creating random assemblages – To create meaningful random assemblages to compare to real assemblages, I set the number of individuals randomly drawn from the pool equal to the number sampled at each new vent. The additional constraint of maintaining observed species number was not adopted since differences in species number among the new assemblages probably do not reflect site differences, but are likely a consequence of unequal sampling effort.

I used two models to create one hundred random assemblages for each of the eight 1998 lava flow vents. The "lottery" model randomly assigned individuals to an assemblage assuming an equal probability of successful recruitment for each species. The "weighted lottery" model randomly assigned individuals to an assemblage assuming an unequal probability of successful recruitment equal to the species' relative abundance in the species pool. Both models were programmed with replacement and implemented in Splus 2000.

Although both models are clearly simplistic, data on dispersal, settlement and post-settlement processes for these species do not exist. Until they do, these two models are the only viable options for simulating random colonization. Conceptually, these models are random or 'null' because probabilities of successful recruitment are unaffected by intra- and interspecific interactions (such as possible effects of the sequence of species arrivals) and species interactions with the environment.

Comparing real to random assemblages – Three aspects of community diversity were measured to determine if real assemblages differed from randomly generated ones: species richness, assemblage composition and assemblage structure. For all three, significant differences were detected with a classic randomization test by comparing the number of times the metric calculated from the random assemblages was greater than, less than or equal to the comparable observed metric (two-tailed test). For example, to determine if the species richness of a real assemblage was significantly different from random, the real value was compared to the distribution of species richness values from its comparable random assemblages.

Assemblage compositions were compared using the Jaccard distance coefficient (J). This coefficient uses presence/absence data to calculate the distance between pairs of assemblages using the formula:

$$J = 1 - [a / (a + b + c)]$$

where a is the number of shared species, b is the number of species unique to one site and c is the number of species unique to the other site. J ranges from 0 (two sites have identical species lists) to 1 (two sites have no shared species). The Jaccard index is recommended since it is easy to understand and interpret and excludes double absences, which are ambiguous indicators of site similarity (Legendre & Legendre 1998).

Assemblage structures were compared using the Bray & Curtis distance coefficient (BC). This coefficient uses abundance data to calculate the difference between pairs of assemblages using the formula:

$$BC = 1 - [2W / (A + B)]$$

where W is the sum of shared species abundances, and A and B are sums of species abundances in the individual sites. BC ranges from 0 (two sites have identical species lists and species abundances) to 1 (two sites have no shared species). This is a popular coefficient (e.g. Mackie et al. 1997, Jorgensen et al. 1999). BC places more emphasis on numerically dominant species (Bakus 1990), which is a useful quality for vent data since assemblages are usually dominated by a few species.

For both J and BC coefficients, the mean distance of each random assemblage to all other random assemblages was computed using Outlier Analysis in PC-Ord4. The mean distance of the real assemblage to all random assemblages was compared to this distribution of random values to determine significance.

To visualize results, two multivariate techniques were also used: correspondence analysis (CA) and cluster analysis. CA is an ordination technique based on the chi-squared distance measure which simultaneously ordinates species and sites. It is useful for both species presence/absence and abundance data (Legendre & Legendre 1998). For all cluster analyses, the flexible method was used ($\beta = -0.25$) with the distance measures described above (J used for incidence data and BC used for abundances). Clustering is further described in Chapter 5 and CA is explained in detail in Chapter 6. Both CA and clustering were implemented in PC-Ord4.

Results

Characteristics of the species pool

Thirty-five macrofaunal species (excluding *Ridgeia piscesae*) were found from the 22 mature assemblages, totalling 206,285 individuals (non-extrapolated number, Tables 4.1). The relative abundance of each species was calculated from this combined data set (Table 4.2). Only six species have total relative abundances exceeding one percent. The limpet *Lepetodrilus fucensis* is by far the most abundant species, representing nearly 50% of all individuals. See Tsurumi (2001) for a more detailed description of the Axial fauna.

Characteristics of the new SRZ assemblages

Twenty macrofaunal species (excluding *Ridgeia piscesae*) were found from the eight new assemblages, totalling 1,234 individuals (Tables 4.1 and 5.4). All new SRZ species were members of the Axial species pool except two: an unknown orbiniid polychaete (*Orbiniella* unk. sp.) and a polynoid polychaete, *Vampiropolynoe embleyi*. The unknown orbiniid has not been reported from other tubeworm assemblages at Axial (Tsurumi 2001). *V. embleyi* is considered a pioneer species, adapted to post-eruption vent conditions (Marcus & Hourdez 2002). New assemblages were variable across the eight sampled vents. In terms of species relative abundances, new vents were dominated by one of three species groups: gastropods, polynoids and other polychaetes, or alvinellid polychaetes and the tubeworm *Ridgeia piscesae* (Table 4.3).

Comparing real and random assemblages

Species richness

The lottery model generated random assemblages with significantly higher numbers of species than real assemblages for each vent (Table 4.4). The weighted lottery model generated assemblages with species richnesses both significantly and not significantly different from real assemblages. For five of the eight vents, the mean

Table 4.2. Species list of mature samples from Axial. Relative abundance (RA) is based on the total extrapolated number of individuals collected. The Axial species pool was modelled using the mature species list (lottery model) and the mature species' relative abundances (weighted lottery). P=present.

Class	Species	Mature RA
Vestimentifera	*Ridgeia piscesae*	P
Gastropoda	*Lepetodrilus fucensis*	45.796
Polychaeta	*Paralvinella pandorae*	26.996
	Paralvinella palmiformis	7.494
	Amphisamytha galapagensis	7.432
Gastropoda	*Depressigyra globulus*	6.214
	Provanna variabilis	2.422
Polychaeta	*Protomystides verenae*	0.540
	Lepidonotopodium piscesae	0.527
	Ophryotrocha globopalpata	0.492
	Parougia wolfi	0.453
Gastropoda	*Pyropelta musaica*	0.408
Polychaeta	*Branchinotogluma* sp.	0.303
	Paralvinella dela	0.287
Ostracoda	*Euphilomedes climax*	0.222
Polychaeta	*Nereis piscesae*	0.122
Pycnogonida	*Ammothea verenae*	0.061
Polychaeta	*Opisthotrochopodus tunnicliffeae*	0.048
	Hesiospina vestimentifera	0.044
	Paralvinella sulfincola	0.031
	Levensteiniella kincaidi	0.027
Gastropoda	*Clypeosectus curvus*	0.018
Polychaeta	*Nicomache venticola*	0.015
	Prionospio n. sp. 1	0.013
Gastropoda	*Lacunoides vitreus*	0.009
Polychaeta	*Hesiodeira glabra*	0.008
	Amphiduropsis axialensis	0.005
	Prionospio n. sp. 2	0.002
Anthozoa	Actinostolidae n. spp (2)	0.002
Bivalvia	*Idasola* cf. *washingtonia*	0.002
Polychaeta	*Levensteiniella intermedia*	0.001
Hydrozoa	Unknown hydrozoan	0.001
Gastropoda	*Temnocinclis euripes*	0.001
Polychaeta	*Harmothoe* unk. sp.	0.001
Bivalvia	*Calyptogena pacifica*	< 0.001
Gastropoda	*Helicoradomenia juani*	< 0.001

Table 4.3. Percent relative abundance of taxonomic groups for the eight new vents sampled in 1998. The presence of the tubeworm *Ridgeia piscesae* is indicated with a P, absence with an A. Vents are grouped by the dominant (>50% of individuals) taxa.

Vent	Gastropods	Alvinellid polychaetes	All other polychaetes	Other	*Ridgeia piscesae*
Snail	91.18	0	8.82	0	A
Easy	0	0	100	0	A
Mkr 33	1.04	13.54	85.42	0	A
Cloud (N4)	6.67	0	93.33	0	A
Mkr 108	26.19	0	69.05	4.76	A
Mkr N41	0	53.09	45.68	1.23	P
Nascent	1.86	96.89	1.24	0	P
Mkr 113	7.32	91.46	1.22	0	P

Table 4.4. Observed species richness (SR) compared to the mean species richness of the 100 random assemblages using the lottery and weighted lottery models for each vent. Three vents have one species not in the pool: *Orbiniella* unk. sp. is present at Easy vent and *Vampiropolynoe embleyi* occurs at Mkr 33 and Mkr 108. Removing these species from observed SR estimates does not affect results (weighted lottery SR remains not significantly different from observed). Significance indicates if observed species richness differs from random. NS = not significant (p>0.05); *** p<0.001. SD = standard deviation.

		Lottery		Weighted lottery	
Vent	Observed	Mean (SD)	Significance	Mean (SD)	Significance
Easy	5	21.18 (1.80)	***	6.25 (1.23)	NS
Mkr N41	8	31.52 (1.50)	***	8.41 (1.44)	NS
Nascent	5	34.59 (0.62)	***	10.30 (1.54)	***
Mkr 33	11	35 (0)	***	12.59 (1.81)	NS
Snail	7	35 (0)	***	14.57 (1.46)	***
Cloud (N4)	4	12.49 (1.29)	***	4.97 (1.06)	NS
Mkr 108	8	24.72 (1.86)	***	6.96 (1.20)	NS
Mkr 113	4	31.70 (1.54)	***	8.32 (1.29)	***

number of species from a hundred random assemblages was not significantly different from the observed number of species. The observed species richness of the other three vents (Nascent, Snail and Mkr 113) was significantly lower than expected (Table 4.4).

Assemblage Composition

Only the weighted lottery model was assessed for assemblage composition. The lottery model generated random assemblages with species richnesses significantly different from observed in all cases, so nonrandom species composition was a certain outcome for observed assemblages.

The outlier analysis of mean Jaccard distances showed that all real assemblages have species compositions significantly different from weighted lottery assemblage compositions (Table 4.5). Mean Jaccard distances of random assemblages to one another ranged from 0.178 to 0.639, while the mean distance of real to random assemblages ranged from 0.506 to 0.892. For all vents, the mean distance of the real to the random assemblages exceeded all comparable random distances (Table 4.5).

However, multivariate techniques yielded qualitatively different results than the outlier analysis for some vents. Two of the eight observed vent assemblages (Nascent and Mkr 33) grouped with their random assemblages when analysed with correspondence and cluster analysis (Table 4.5). Two others (Cloud and Mkr 113) showed conflicting results between CA and clustering (Table 4.5). The real vent assemblages most similar and least similar to their random assemblages are illustrated with dendrograms in Figure 4.2.

Assemblage Structure

Real assemblage structure was significantly different from random assemblage structure for all vents and both models. For the lottery model, mean Bray & Curtis distances among random assemblages ranged from 0.128 to 0.801, and the mean distances of real to random assemblages ranged from 0.796 to 0.942 (Table 4.6). For each vent, the mean distance of the real to the random assemblages consistently exceeded all comparable random distances (Table 4.6).

Table 4.5. Mean Jaccard distances among random and observed assemblages for the weighted lottery model. Observed assemblage composition differs from random in all cases. Significance: *** = $p<0.001$. SD = standard deviation. Correspondence analysis or cluster analysis did (yes) or did not (no) ordinate or cluster the real assemblage separately in space from the group of random assemblages.

Vent	Range of random distances (min – max)	Grand mean of random distances (SD)	Distance of real to random assemblages	Sig.	Ordin-ation (CA)	Cluster Analysis
Easy	0.241 – 0.585	0.363 (0.076)	0.892	***	yes	yes
Mkr N41	0.307 – 0.509	0.379 (0.048)	0.885	***	yes	yes
Nascent	0.352 – 0.508	0.405 (0.036)	0.587	***	no	no
Mkr 33	0.252 – 0.460	0.346 (0.049)	0.506	***	no	no
Snail	0.178 – 0.401	0.266 (0.050)	0.765	***	yes	yes
Cloud	0.316 – 0.639	0.448 (0.091)	0.843	***	yes	no
Mkr 108	0.243 – 0.484	0.340 (0.067)	0.816	***	yes	yes
Mkr 113	0.276 – 0.485	0.359 (0.052)	0.611	***	no	yes

Figure 4.2. Cluster Analysis dendrograms of random and observed assemblages for the weighted lottery model based on presence/absence data. The two vents represented here (A = Snail, B = Mkr 33) are the extremes in similarity of real assemblages to random assemblages. Arrows depict the observed vent assemblage.

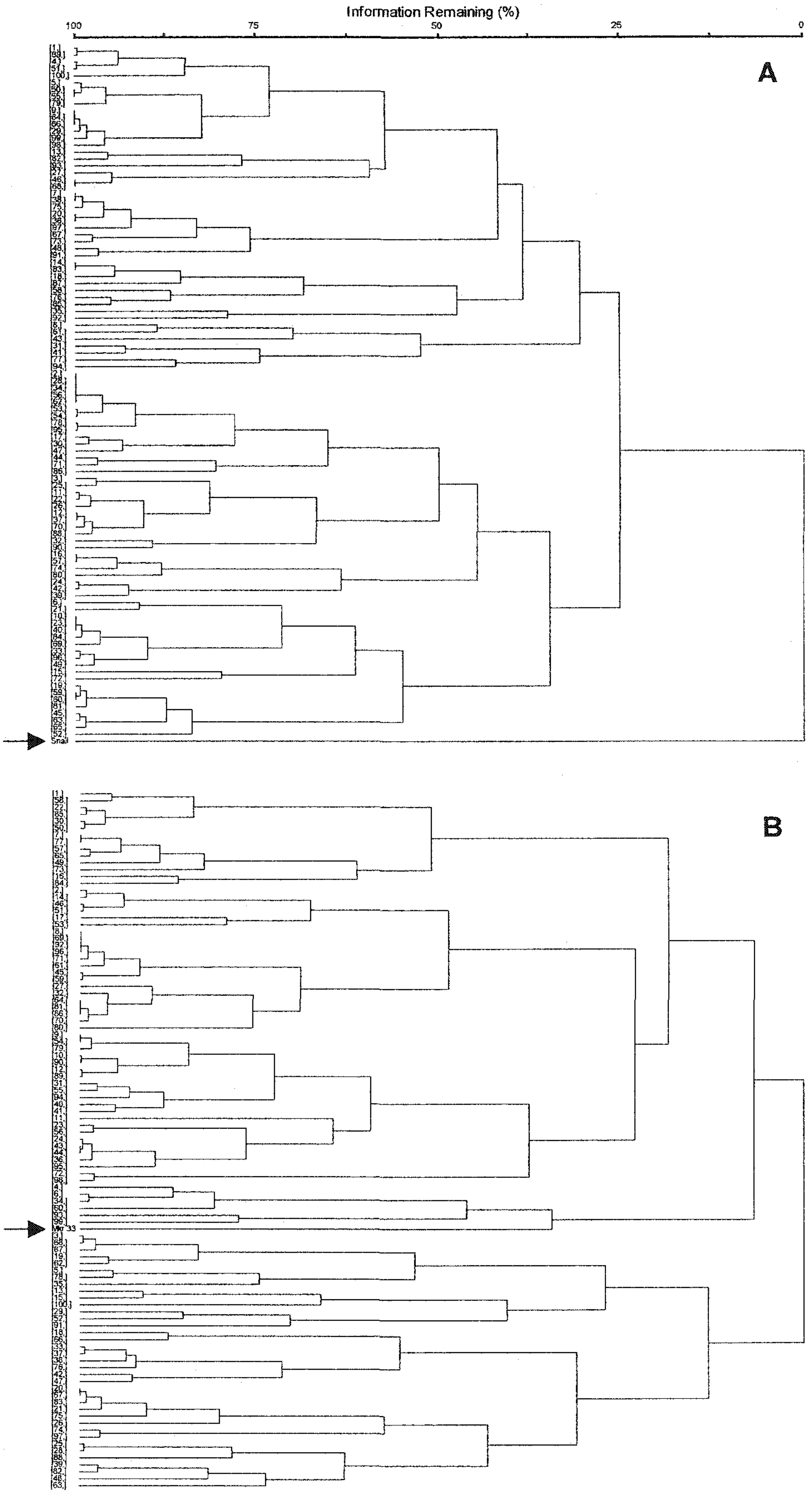

Information Remaining (%)
100
75
50
25
0
A
Snail
B
Mir 33

Table 4.6. Mean Bray & Curtis distances among random and observed assemblages. Observed assemblage structure differs from random in all cases ($p<0.001$). All cluster and ordination analyses are consistent with these results.

Vent	Range of random distances (min – max)	Grand mean of random distances (SD)	Distance of real to random assemblages
Lottery Model			
Easy	0.453 – 0.617	0.539 (0.029)	0.909
Mkr N41	0.301 – 0.418	0.353 (0.020)	0.833
Nascent	0.225 – 0.292	0.256 (0.014)	0.942
Mkr 33	0.170 – 0.241	0.196 (0.013)	0.796
Snail	0.128 – 0.165	0.147 (0.009)	0.901
Cloud (N4)	0.649 – 0.801	0.708 (0.027)	0.912
Mkr 108	0.423 – 0.551	0.483 (0.028)	0.824
Mkr 113	0.316 – 0.411	0.361 (0.019)	0.922
Weighted Lottery Model			
Easy	0.166 – 0.318	0.210 (0.031)	0.943
Mkr N41	0.112 – 0.211	0.149 (0.020)	0.719
Nascent	0.084 – 0.149	0.106 (0.014)	0.707
Mkr 33	0.061 – 0.120	0.078 (0.011)	0.813
Snail	0.049 – 0.090	0.061 (0.008)	0.553
Cloud (N4)	0.222 – 0.502	0.304 (0.054)	0.921
Mkr 108	0.125 – 0.302	0.176 (0.033)	0.658
Mkr 113	0.105 – 0.203	0.142 (0.022)	0.638

For the weighted lottery model, mean Bray & Curtis distances among random assemblages ranged from 0.049 to 0.502, and the mean distances of real to random assemblages ranged from 0.553 to 0.943 (Table 4.6). Again, for each vent, the mean distance of the real to the random assemblages exceeded all comparable random distances (Table 4.6).

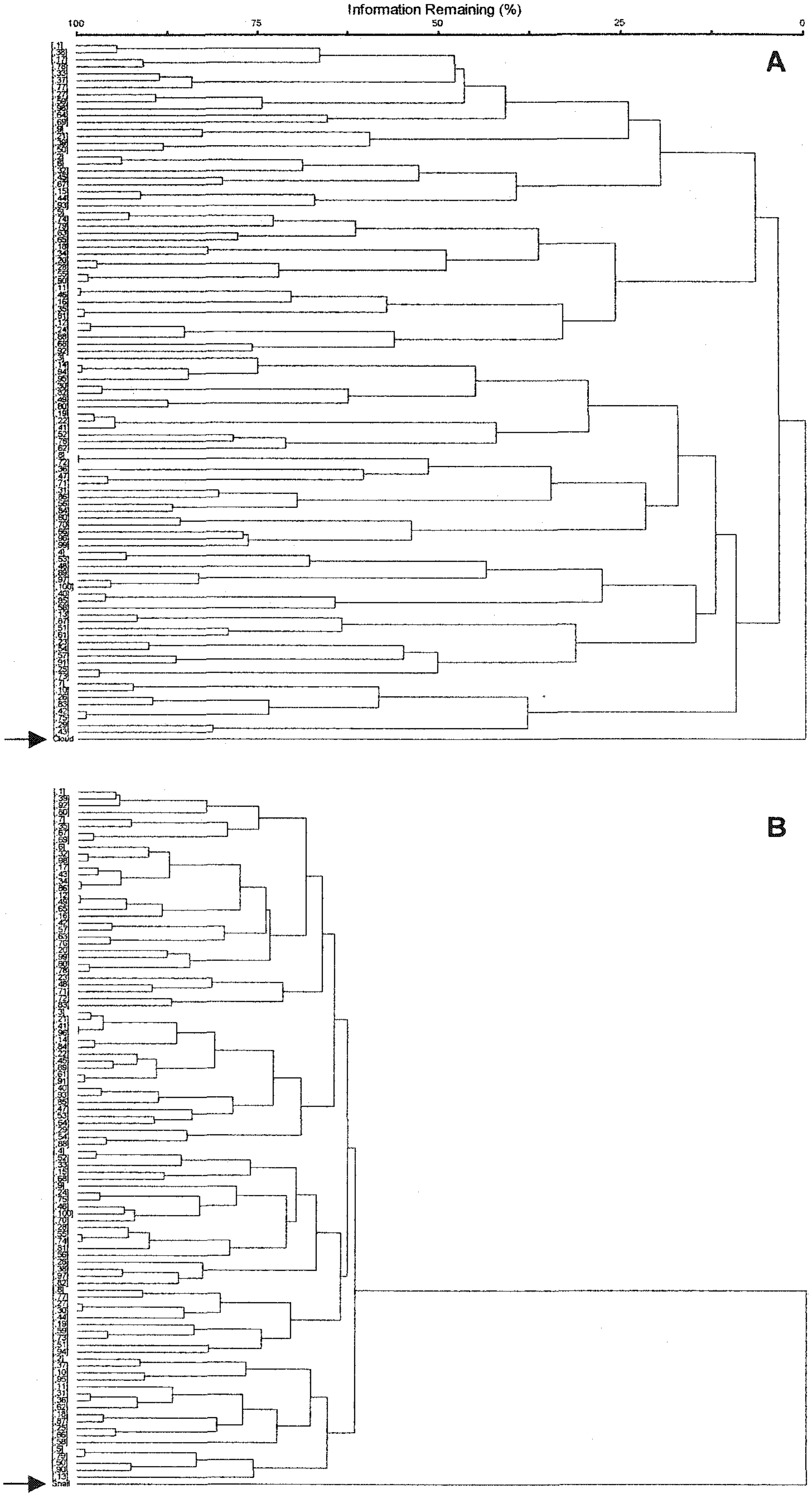
Cluster and correspondence analyses produced qualitatively identical results. All real assemblages were clustered or ordinated separately from their group of random assemblages. The only difference between vents and models was the degree separating real from random assemblages; to illustrate this, dendrograms of the most similar and the least similar vent to its randomly generated assemblages by the lottery model are presented in Figure 4.3.

Discussion

Random colonization models

Species richness. The weighted lottery model evaluated with the species richness metric was the only analysis that yielded observed vent diversity not significantly different from random: observed species richness of five vents did not differ from random expectations. One interpretation of this result is that dispersal drives species assembly for these five vents rather than local processes (Schoolmaster 2001). Local processes mean any biotic or abiotic interactions occurring within the spatial scale of the vent that cause species richness to differ from random expectations. Since dispersal (and hence recruitment) was modelled here by the distribution of relative abundances of the species pool, this suggests that the number of species present at nascent vents may be predictable if the structure of the regional species pool is known. The three vents (Nascent, Snail, M113) that differed significantly from expected had low species numbers for the number of individuals sampled. It is unlikely that sampling was biased only for these three vents (e.g. more rare species missed given the number of individuals sampled), thus these lower richnesses may reflect an influence of local processes such as predation on community assembly (see 'potential causes of non-random patterns' section).

Figure 4.3. Cluster Analysis dendrograms of random and observed assemblages for the lottery model based on relative abundance data. The two vents represented here (A = Cloud, B = Snail) are the extremes in similarity of real assemblages to random assemblages. Arrows depict the observed vent assemblages.


Information Remaining (%)
100
75
50
25
0
A
Cloud
B
Snail

Undoubtedly, both processes operating outside and inside the habitat patch (e.g. dispersal and local interactions) influence assemblage diversity. This modelling approach may be useful to test which of these scales is relatively more important in shaping vent species richness over time. Walker & Chapin (1987) argue that stochastic events and propagule arrival are likely more important during the early stages of community assembly of primary successions, while local processes become increasingly important over time. If so, one possible prediction is that local species richness would fall below the expected value due to negative interactions (e.g. competition) and/or abiotic constraints on species distributions. I tested this possibility by using the weighted lottery model to simulate one hundred randomly assembled communities for six vents that were consecutively sampled seven, 18 and 30 months post-eruption. By two and a half years after initiation, all six vents supported species richness below random expectations (Table 4.7), perhaps indicating that local processes become more important in shaping species richness as vents age.

Although Schoolmaster (2001) argues this is a viable method to test if local processes limit local communities, the interpretation is limited because the species pool was formed from samples of mature Axial assemblages. Any species interactions that shaped mature assemblages are thus inherently integrated into the model as species-specific colonization probabilities. I attempted to limit this bias by calculating the species pool by combining data from all mature assemblages, rather than taking the average relative abundance of a species across mature vents. Further, the 'regional pool of potential colonists' should ideally be measured directly but this is often too difficult, and perhaps impossible, to achieve (see 'model assumptions' section). Thus, the processes determining the distribution of relative abundances of the Axial pool are not addressed here. Rather, given this distribution, this analysis shows that as vent assemblages age, the species richness of a vent is not predictable by a simple model attributing colonization probabilities to species based on their relative abundance in the species pool, and assigning these species independently to assemblages.

In contrast to the weighted lottery results, random lottery assemblages had many more species than observed assemblages (Table 4.4). This result was not surprising since the lottery model by definition produced random assemblages with an even distribution

Table 4.7. Species richness of observed (OSR) and random (RSR) assemblages for six vents sampled consecutively for three years post-eruption. The species richnesses of real assemblages sampled at 18 and 30 months post-eruption (1999 and 2000 respectively) are compared to mean species richnesses of 100 random assemblages using the weighted lottery model. All vents have species richnesses significantly lower than random expectations except for two vents in 1999 (NS = not significantly different from random SR, p>0.05). See Table 4.4 for year 1 results.

	1999				2000			
	Obs # inds	OSR	Mean RSR	RSR range	Obs # inds	OSR	Mean RSR	RSR range
Mkr N41	16,991	14	27.42	24-31	58,213	18	31.38	28-34
Nascent	9,307	15	25.27	22-29	11,501	18	25.85	22-30
Mkr 33	1,645	19	18.71^{NS}	15-24	7,141	16	24.3	20-28
Snail	940	13	17.01	13-22	5,990	12	23.52	20-27
Cloud	424	11	14.23^{NS}	9-20	4,776	15	22.43	18-27
Mkr 113	16,715	22	27.92	24-34	27,493	15	29.1	26-33

of individuals across species. New vents were numerically dominated by a few species (Table 4.3), so the lottery model was not expected to accurately predict observed species richnesses. This result highlights that vent species do not have equivalent probabilities of successful recruitment.

Assemblage composition. Although species richness for five vents was not distinguishable from random with the weighted lottery model, their species compositions (species lists) were significantly different from the compositions of the random assemblages using direct comparisons of mean Jaccard distances. However, the multivariate analyses were only partially consistent with these results: half the observed vents were deemed no different from random with respect to species composition by one or both of ordination and clustering (Table 4.5, Figure 4.2a).

The discrepancy between the outlier analysis approach and the multivariate techniques arises because they evaluate the data differently. The outlier analysis summarizes the mean distance of each vent assemblage to all others, and thus is useful for asking if the real assemblage has a greater average distance from all other (random) assemblages than the average distances of random assemblages to each other. The reduction of the direct approach allows for a test of significance, but more detailed relationships between specific assemblages are lost. In contrast, the aim of multivariate approaches is to reveal the associations among the objects: cluster analysis examines pairwise distances among sites or groups of sites looking for fine-scale relationships, while ordination considers the variability of the whole distance matrix to reveal general trends (Legendre & Legendre 1998). The resulting dendrograms and/or ordination plots are useful because they depict the relative position of each vent to all others, allowing for a visual assessment of which random assemblages, and how many, are 'close' to the real assemblage. Both approaches reveal useful aspects of patterns among assemblages. I consider a pattern robust if it is supported by all the statistical methods, and I interpret contradictory results with caution.

Since the multivariate approaches contradict the results of the outlier analysis for half of the vents, it is not possible to resolve if the colonization probabilities attributed to the species in the Axial pool (weighted lottery model) do or do not accurately predict which species colonize early in the assembly process. The results of the qualitative multivariate statistics suggest that four vents (Nascent, Mkr 33, Cloud, Mkr 113; Table 4.5) were initially colonized by the numerically dominant species in the species pool. In contrast, the other four vents that deviated from random expectations (Easy, Mkr N41, Snail and Mkr 108; Table 4.5) occurred either because they had species uncommon in random assemblages (due to low colonization probabilities in the species pool) and/or did not support species common to the random assemblages (due to high colonization probabilities in the species pool). Since correspondence analysis ordinates species concurrently with sites, it is easy to visualize which species uncommon in the species pool are driving the real assemblages away from randomness (see Figure 4.4 for an example). Two to four of the top five colonizers from the species pool (see Table 4.2) were missing from the four vents that differed from random. Further, these vents supported species with very low colonization probabilities, such as *Opisthotrochopodus tunnicliffeae*, *Hesiospina vestimentifera*, *Prionospio* n. sp. 1 and *Amphiduropsis axialensis*. The vents that grouped with their respective random assemblages did support some rare species, but all supported most of the top five colonizers.

Overall these data indicate that the species purported to be most abundant in the species pool are not necessarily the most common colonizers of all individual nascent vents. However, their numerical dominance seems to make them more successful as initial colonizers in a general sense: abundant species in the pool were more likely to be present at any nascent vent than less abundant species. For example, five of the six species in the Axial pool that have relative abundances over one percent occurred at two or more of the new vents, and 73% (11 of 15) of the species with relative abundances over 0.1% in the Axial pool reached at least one of the new vents by seven months. In contrast, only 38% (8 of 21) of those with lower species pool relative abundances were present at any new vents. Thus, while some species with very low species pool abundances did colonize new vents quickly, their occurrences were more rare than species abundant in the Axial pool. In Chapter 5, I test whether abundant species pool species colonize new vents faster than rarer species with a different null model approach.

Assemblage structure. In terms of species abundances, all vent assemblages were significantly different from random with both models (Table 4.6). Since the lottery model generated assemblages with an even distribution of individuals across species,

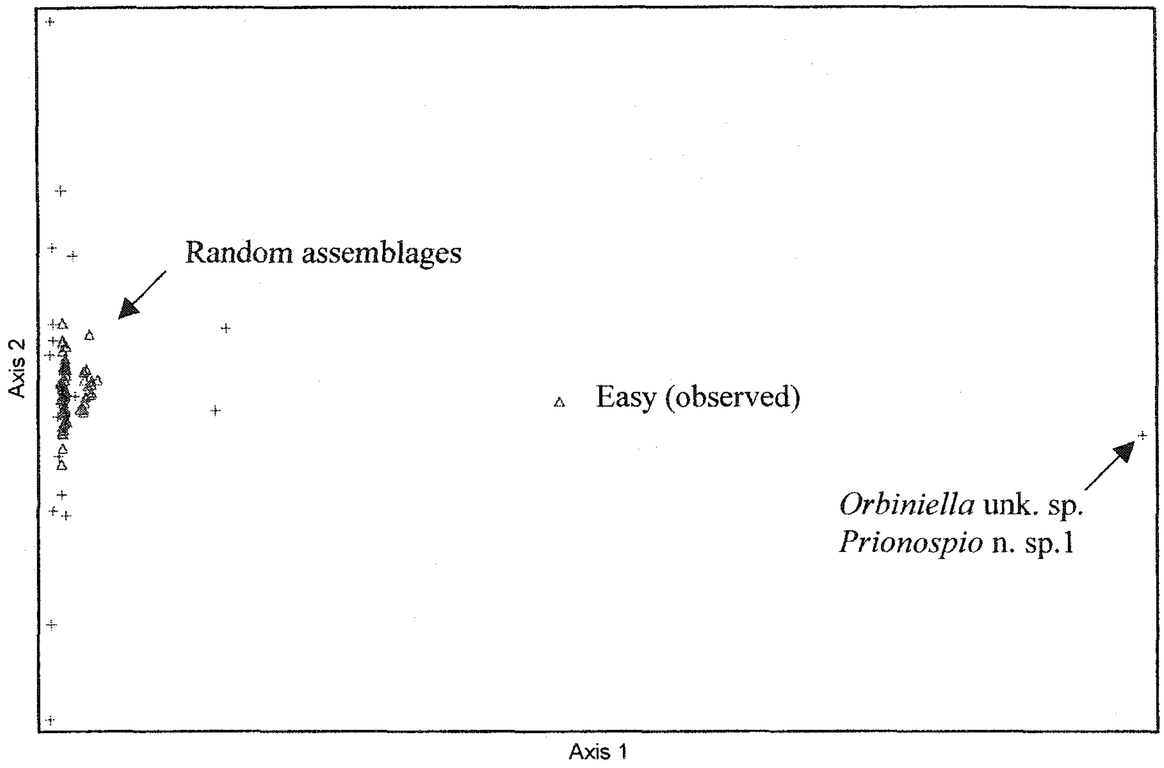


Figure 4.4. Correspondence Analysis biplot based on species compositions of Easy vent and its hundred random assemblages generated by the weighted lottery model. Assemblages are indicated by triangles and species by crosses. All random assemblages cluster together and away from the observed assemblage (Easy). The presence of the polychaetes *Orbiniella* unk. sp. (not in the Axial species pool) and *Prionospio* n. sp.1 (very low colonization probability in the Axial species pool) in the observed assemblage are partly responsible for the nonrandom composition of Easy vent.

observed assemblages were expected to differ from random since new vents were dominated by one or a few species. This outcome strongly suggests that not all vent species are equally successful at colonizing nascent vents. Rather, early vent habitats are dominated by a subset of species from the pool of potential colonists and harbour an uneven distribution of individuals among species.

The primary reason the weighted lottery model generated random assemblages with species abundances significantly different from observed was that the limpet, *Lepetodrilus fucensis*, had a colonizing probability of 0.45 (Table 4.2) due to its dominance of mature assemblages. Only two new vent assemblages, Snail and Mkr 108, had an observed relative abundance of *L. fucensis* near this number (31% and 26% respectively). The limpet represented 0% to 7% of all individuals sampled at all other new vents. Despite the variability among nascent assemblages, not one new vent was dominated by the species typically numerically abundant in mature assemblages. Thus, although the weighted lottery model correctly predicted the number, and in some cases the composition, of species occupying new vents, it did not accurately predict the structure of these assemblages.

Model Assumptions

The random colonization models presented in this study are obviously too simplistic to accurately reflect reality, but they represent the most parsimonious option for modelling vent community assembly at this time. The models assume that (1) complex settlement and post-settlement processes can be incorporated into simple probabilities of successful recruitment ('colonization') based either on a species presence in mature assemblages (lottery model) or a species relative abundance in mature assemblages (weighted lottery), (2) the composition and structure of the propagules in the Axial species pool are accurately represented by the adult populations of 22 mature vent samples, and (3) the propagules of the species pool are equally available spatially at the scale of the sampled lava flow (a few kilometres).

The first assumption is the most contentious, but cannot be reasonably addressed with our current understanding of Axial vent species biotic and abiotic interactions in space and time. Of the two models, the weighted lottery variant is likely more realistic since abundant species will have higher probabilities of successful recruitment due to their numerical dominance if individual propagules of all species have an equal chance of successfully recruiting. Although there are many examples of benthic marine invertebrates having different rates of successful recruitment due to various pre- and post-settlement processes (e.g. microhabitat preferences, post-settlement predation etc.; Booth & Brosnan 1995), and there are examples of rare and/or competitively inferior species adopting *r*-type life history strategies to overcome their competitive disadvantage as adults (e.g. early successional species; McCook 1994), such specific details of Axial species are unknown. When more information on vent species life histories and recruitment patterns and processes are known, more sophisticated and accurate colonization models can be developed.

I believe the last two assumptions are reasonable given the current state of information on Axial and vent species. Adults of invertebrate vent species are spatially restricted to the area immediately surrounding fluid flow. Dispersal between vents is thought to be primarily achieved by pelagic larvae, although some fauna such as scale worms may be able to swim to nearby vents. Invertebrates have either direct, lecithotrophic or planktotrophic development (Tyler & Young 1999). Roughly 10% of vent species have been studied for reproduction, or have had their larval modes inferred from, for example, gastropod protoconch morphology (Lutz et al. 1986). Although direct development has been reported for a few species (e.g. Zal 1995, Martel et al. 2002), most vent invertebrates are thought to produce pelagic larvae (primarily lecithotrophy; Tyler & Young 1999). Data on larval development exist for only six Axial species (Table 4.8); lecithotrophy is proposed for five of the six, and although one species (*Paralvinella pandorae*) is a purported brooder, this does not preclude the possibility that it releases pelagic larvae. These data support the assumption that Axial vent species produce larvae that disperse in the water column.

Another assumption of the models is that the species pool does not change over an annual time scale. For this to be true all species must have continuous gametogenesis and/or the combined populations have reproduction pulses that span all time. If vent species have discontinuous reproduction, where larvae are released into the water column at synchronized intervals rather than continuously, the result would be a temporally

Table 4.8. List of six invertebrate vent species from Axial Volcano that have been studied for reproductive traits. Information is given with respect to gametogenesis (continuous versus pulsed) and reproductive modes (pelagic versus direct developer). If available, the type of pelagic mode is indicated (L = lecithotrophic, P = planktotrophic).

Class	Species	Reference	Gametogensis	Reproductive mode
Solenogaster	*Helicoradomenia juani*	Savage (1997)	continuous	pelagic (L)
Polychaeta	*Paralvinella pandorae*	McHugh (1989)	continuous	brooder – unknown if pelagic (P or L) or directly benthic
	Paralvinella palmiformis	McHugh (1989)	pulsed	pelagic (L)
	Paralvinella sulfincola	Copley (1998)	continuous	pelagic (L?)
	Amphisamytha galapagensis	McHugh & Tunnicliffe (1994)	continuous	pelagic (L)
Vestimentifera	*Ridgeia piscesae*	Southward (1988)	continuous	pelagic (L)

shifting species pool. Both continuous and discontinuous recruitment are proposed for vent species (Van Dover 2000, Sadosky et al. 2001, Copley et al. 2001). Although the Axial data are scant, five of the six studied species have continuous reproduction (Table 4.8). Since the mature assemblages used here to construct the species pool were sampled between 1986-1999, I also assume that large temporal shifts in the composition and structure of mature assemblages do not occur, and that these data adequately represent the available species pool in the early months of 1998. The work by Tsurumi (2001) supports this assumption. She investigated possible causes of variability among Axial assemblages and found that mature vents are very similar in structure and composition, and year of sampling did not explain observed variation.

Axial vent species also seem to disperse easily within the geographic distances of the volcano's caldera. Tsurumi (2001) found no difference between the fauna of the three Axial vent fields, which are separated by distances of approximately 3 to 8 kilometres (Johnson & Embley 1990). Hydrographic data also support the suggestion that pelagic larvae are easily dispersed at this scale: water moves around the caldera at a mean speed of 3 cm/sec and takes about five days to complete one circuit (Cannon & Pashinski 1990, B. Lavelle pers. comm.). Although larval duration in the water column is a function of many factors, such as egg size, developmental mode and temperature, most lecithotrophic and planktotrophic larvae can survive for weeks to months (polychaetes, Beesley et al. 2000; archaeogastropods, Craddock et al. 1997), suggesting easy dispersal of vent larvae around the caldera.

If currents readily disperse vent larvae around Axial's caldera forming a well-mixed regional species pool, we would expect little spatial variation in the larvae that settle out of the water column. Preliminary data support this expectation: Metaxas (2001) deployed larval traps concurrently at ASHES and the SRZ and found no difference in larval supply within and between the two sites. Collected larvae were dominated by limpets (1000s m^2/day), followed by various stages of polychaete larvae and snails (100s m^2/day), further suggesting that larval abundances mirror adult populations at this coarse taxonomic scale.

These three lines of evidence - vent species developmental modes and gametogenesis, undifferentiated Axial fauna by time or location, and Axial larval trap data - point to a well-mixed Axial species pool whose structure parallels that of adult populations. Although it would be preferable to use plankton samples or larval traps to directly measure the species pool, such data are sparse and molecular information is needed to identify most larvae to species (A. Metaxas pers. comm., Mullineaux et al. 2000). Given these constraints, data on adult populations is the best available and most reasonable estimate of the Axial species pool, and existing data support the assumption that larval supply is not spatially variable at the scale of the caldera.

Once more information is available on various aspects of vent species, such as species-specific life history strategies, microhabitat preferences, and interspecific interactions, these data can be used to constrain and/or modify aspects of the species pool and/or species-specific recruitment probabilities. For example, the species pool could be modified to reflect temporal shifts in relative larval abundances, and microhabitat preferences could be incorporated into the models by restricting random dispersal of specific species to only those vents known to support the appropriate physico-chemical conditions (e.g. Palmer et al. 2000).

The models presented here are a first attempt to test statistically if vent assembly is nonrandom given our current state of knowledge. Axial Volcano is one of a few global vent sites for which enough samples exist to allow this type of analysis. The models provide a conceptual and working framework to test colonization patterns of new vents created by future eruptions in similar areas where a good estimate of the regional species pool already exists (e.g. 9°N, East Pacific Rise; Endeavour Segment, JdFR).

Potential causes of nonrandom patterns

The results for initial patterns of species richness and species composition are unclear, with evidence for both random and nonrandom patterns depending on the specific vent and the statistical approach used. The weighted lottery model may have some ability to predict the number of species occurring at nascent vents: the regional distribution of relative abundances (Axial species pool) accurately predicted local richnesses for over half of the new vents. When the identities of those species were evaluated with different statistical methods, half the real assemblages did not differ qualitatively from randomly generated ones by at least one method. This suggests that the numerically dominant members of the pool colonize some vents, but this result is vent specific.

However, the models unequivocally suggest that nascent vent assemblages are nonrandomly structured with respect to species relative abundances. The two general mechanisms that can drive nonrandom species patterns early in the vent assembly process are larval supply and recruit survival. Larval supply seems not to be spatially variable at the Axial caldera scale, however the data are preliminary (Metaxas 2001) and variable larval supply in space, along with the potential of a variable species pool in time, cannot be discounted. If larval supply were constant in space and time across vents at the scale of the SRZ, then initial patterns would be due to recruitment processes and post-recruitment survivorship at specific vents.

The most obvious possible factor affecting recruit survival is vent-to-vent differences in fluid properties. Temperature and chemistry vary with species distributions among diffuse vents at the vent field scale (e.g. Luther et al. 2001, Micheli et al. 2002), and are invoked as possible drivers of species associations at ASHES vents (Marcus & Anholt in revision). Although no direct evidence exists for fluid characteristics influencing larval recruitment to vents, changes in fluid chemistry and temperature are implicated for transformations of post-eruption vent assemblages on 9°N EPR (Shank et al. 1998). The nascent vents at Axial had variable fluid characteristics: maximum temperatures ranged from 10 to 55°C and maximum sulphide levels ranged from 0.1 to 2.1 mmol (no fluid data for Snail vent). This variability superimposed on the general post-eruption signature of vent fluid evolution (Butterfield et al. 1997) may cause among vent differences in initial colonizers. Physical variation at the local scale may also be important. The new vents ranged in size and lava type and Mullineaux et al. (1998) report that basalt morphology is important for tubeworm recruits.

Interspecific interactions may also shape nascent vent assemblage structure. Competition is an unlikely mechanism here, but predation and facilitation may have played roles. Neither competition for food nor competition for space seems likely by seven months post-eruption. The dominant fauna at nascent Axial vents have similar carbon and nitrogen isotope signatures, indicating consumption of a common, unlimited resource in 1998 (C. Levesque pers. comm.). Further, although population densities were not measured, visually they were distinctly lower than those of mature assemblages.

In contrast to competition, predation likely affected the structure of nascent assemblages. Settlement studies invoke predation as a likely mechanism affecting recruit success (van Dover 1988, Mullineaux et al. 1998), and recent work shows that limpet recruitment at East Pacific Rise vents is controlled by cropping by predatory fish (Micheli et al. 2002). Most new vents in this study supported numerous predatory polychaetes (polynoids and hesionids). The low abundance but wide distribution of common gastropods at new vents (present at six of eight vents) may suggest high post-settlement mortality by predation. There is a negative correlation between the relative abundance of gastropods and predatory polychaetes at the five vents without tubeworms ($p<0.05$).

Chance events of species arrivals through time may also affect vent assembly via predation. Early arrivals may have an advantage over subsequent species due to an absence of grazing pressure and/or unhindered access to resources. At Snail vent the limpets and snails may have reached a critical threshold (abundance or size) to withstand grazing pressure before predators arrived. There is also some evidence at vents for burst deliveries of batches of larvae (van Dover 2000). Even if predators are present under such conditions, a substantial proportion of recruits may successfully reach adulthood if they settle in large enough number to satiate the predators. Episodic batch recruitment is another unknown factor for most vent species, but if known, could be easily integrated into models of colonization.

The proposition that the tubeworm *Ridgeia piscesae* facilitates the successful recruitment of alvinellid and ampharetid polychaetes (Tunnicliffe et al. 1997) is supported here. Species that usually live on vestimentiferan tubes, such as *Paralvinella pandorae*, *P. palmiformis* and *Amphisamytha galapagensis*, occurred at all sites with visible tubeworms (Table 4.3). Only Mkr 33 hosted alvinellids without vestimentiferans, and the relative abundance of alvinellids was lowest here (Table 4.3).

Species-specific dispersal strategies may also contribute to nonrandom patterns. For example, the snail *Provanna variabilis* is the sixth most abundant species from mature assemblages, yet is absent from all seven month-old vents. Again, possibilities for its absence include constraints of larval supply (e.g. pulsed gametogenesis), and/or controls of settlement (e.g. cues) or post-settlement mortality (e.g. predation).

Conclusion

The main drawbacks of the random colonization models presented here are the lack of (1) a direct estimate of the species pool, (2) knowledge of larval supply variability in space and time, and (3) information on species-specific settlement and post-settlement processes. I argue that samples of adult populations likely provide a good estimate of the actual species pool, and that Axial currents can disperse planktonic larvae at the scale of the caldera, thus providing new vents with a well-mixed larval supply in space. Given these assumptions, the results of the models suggest that nascent vents are nonrandomly colonized in terms of species abundances. Available information points to post-settlement processes as the likely drivers of observed species patterns rather than larval supply. Processes likely include species-environment interactions and species-species interactions such as predation and facilitation, although species-specific life history strategies may also be important.

This analysis shows that observed patterns of nascent vent assemblages cannot be explained by a model that assigns an equal chance of successful recruitment to each species in the species pool. A model that assigns unequal chances of colonization to each species in the pool based on their relative abundances in mature assemblages also does not describe all aspects of observed patterns. While the weighted lottery model does correctly predict species richness for more than half of the new vents, it does not consistently explain observed patterns of species compositions and abundances. These results suggest that the structure of nascent assemblages is not determined by random colonization from the species pool. Further work on vent species development and dispersal, settlement, post-settlement processes and microhabitat distributions should increase our ability to predict the composition and structure of post-eruption vents. Such information can also be used to refine colonization models to more accurately test if initial communities are nonrandom.

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CHAPTER 5

Spatial and temporal patterns of post-eruption vent assemblages

Introduction

Hydrothermal vents are insular and ephemeral habitats. The dynamic nature of the underlying geological features causes individual vents to persist from years to decades (Hessler et al. 1988, Haymon et al. 1991, Tunnicliffe et al. 1997). To contend with spatially and temporally fluctuating habitat patches, vent species must successfully disperse to and colonize new sites. Dispersal and colonization are crucial processes that maintain and structure vent communities (Kim et al. 1994, Mullineaux et al. 1998).

Patterns of species establishment and community development can point to the abiotic and biotic controls on community structure and dynamics (McCook 1994, Sousa 2001). However, the histories of most vent communities are unknown. Despite this lack of historical knowledge, the recognition that vents turn on and off led to the idea early in the vent ecological literature that vent age may affect community structure. In 1985, Hessler et al. hypothesized that distributions of the dominant fauna at East Pacific Rise (EPR) vents relate to variations in fluid flow. Assuming that fluid flow is initially high, followed by a gradual or abrupt decline to lower flow conditions, Hessler et al. (1985, 1988) proposed that vestimentiferans dominate the early stages of the EPR vent community lifecycle, and bivalves replace them over time. These species replacements were attributed to species-specific tolerances to fluid properties and competitive abilities under varying flow regimes.

Continued observations at vents revealed that varying compositions and relative abundances of species typify most vent fields creating a mosaic of faunal assemblages in space and time (Tunnicliffe 1991). The speculation that flow alterations associated with vent age is one factor driving these community mosaic patterns is now well entrenched in the vent literature, both for diffuse vents (e.g. Van Dover & Hessler 1990, Desbruyères 1995, Tsurumi & Tunnicliffe 2001) and high temperature chimneys (Tunnicliffe & Juniper 1990, Sarrazin & Juniper 1999). However, the small-scale perturbations that create, alter or destroy individual vents are difficult to monitor. Subsurface flow conduits are altered by mineral accretion, clogging due to microbial or other growth, and tectonic events (Hessler et al. 1985), and surface disturbances such as falling pieces of sulphide and sampling can change flow patterns (Tunnicliffe 1990). Further, vents separated by mere meters may be affected differently. This complexity, along with the typically sporadic and infrequent visits to any given vent site, have precluded direct tests of the effect of vent age and historical processes in established vent fields.

To overcome these limitations, vent ecologists have turned to seafloor recruitment experiments or direct observations of seafloor eruptions to study vent community establishment and temporal development. Recruitment experiments reveal that early communities are influenced by biological processes such as priority effects and predation (Mullineaux et al. 2000, Mills et al. 2001, Micheli et al. 2002) and abiotic controls (Micheli et al. 2002), but are limited by practical concerns (e.g. many panels are never colonized, V. Tunnicliffe pers. comm.). They also fail to reveal long-term temporal patterns in naturally emerging assemblages, since panels are small and typically deployed within already well-established biological communities and are situated adjacent to flow rather than in optimal habitat conditions. *De novo* hydrothermalism, on the other hand, offers a natural laboratory for observing how vent species respond to habitat creation, and reveals how entire vent assemblages develop over time.

Ridge crest eruptions are large-scale disturbances that simultaneously create multiple vents. Despite the scale of the perturbation, detection is difficult. Volcanic events are unpredictable and occur hundreds of kilometres from shore and thousands of meters below the sea surface. Eight seafloor eruptions or tectonic events on mid-ocean ridges have been inferred or directly observed (Delaney et al. 1998, Johnson et al. 2000). Faunal development after two eruptions has been studied from the onset of habitat creation: the eruption at 9°N on the EPR in 1991, which was a chance discovery (Lutz et al. 2001), and the eruption at CoAxial Segment on the Juan de Fuca Ridge (JdFR, Tunnicliffe et al. 1997), which was detected by a military underwater hydrophone array. On the southern EPR, Embley et al. (1998) note distinct biota on different aged lavas. The community response to the 1986 eruption of Cleft Segment (JdFR) was also studied, but the absence of sampling during the first two years post-eruption precluded documentation of species arrival and replacement patterns (Tsurumi & Tunnicliffe 2001).

Synchronous colonization and/or community development typify both studied eruptions. At 9°N, all nascent vents were successively dominated by three megafaunal species: the tubeworm *Tevnia jerichonana* in year one, the tubeworm *Riftia pachyptila* in year two, and the mussel *Bathymodiolus thermophilis* in years three to five (Shank et al. 1998). At CoAxial, all nascent vents were colonized by the tubeworm *Ridgeia piscesae* and the alvinellid polychaete *Paralvinella pandorae* by one year post-eruption (Tunnicliffe et al. 1997). These coordinated patterns imply that vent community development is predictable (Shank et al. 1998, Van Dover 2000, Mullineaux et al. 2000). Synchronized changes in fluid chemistry following eruptive events may be the main driver of vent faunal succession. Initial fluids are vapour-dominated with elevated temperatures and hydrogen sulphide content, but over time become brine-dominated with lower temperatures and sulphide and higher concentrations of iron (Von Damm et al. 1995, Butterfield et al. 1997). This evolution of fluid properties is linked to initial community establishment on the JdFR (Tunnicliffe et al. 1997) and successive shifts of faunal dominance on the EPR (Shank et al. 1998). Experimental work also suggests that facilitation of *R. pachyptila* by *T. jerichonana* may contribute to megafanal shifts at EPR vents (Mullineaux et al. 2000).

This chapter adds to current knowledge of vent community assembly and succession by describing the post-eruption patterns in fauna following the 1998 eruption at Axial Volcano, JdFR (Figure 1.4). Axial is unique among eruption studies as the resident fauna was well studied prior to the disturbance (e.g. Tunnicliffe et al. 1985, Tsurumi 2001, Marcus & Anholt in revision). Species patterns of nascent vents can thus be related to patterns of longer-lived or mature vent assemblages from the same site. This study is also the first account of an *entire* vent community response to habitat destruction and creation. Since I evaluate species patterns by sampling multiple vents each year, I consider spatial and temporal responses of all components of the community (meio- and macrofauna), rather than restricting patterns to the megafauna (9°N, Shank et al. 1998) or making inferences from few samples (CoAxial, Tunnicliffe et al. 1997).

My overall objective is to describe vent community development at Axial for three years post-eruption. In particular, I report general trends in species patterns across the three years, I highlight within year community variation and I describe observed trajectories of community change. I also relate patterns at nascent vents to mature Axial communities and to faunal patterns from the other studied eruptions. This study extends our observation of vent colonization and community development to three sites. Since there are approximately 25 active hydrothermal sites recognized around the globe (Van Dover 2000, Hashimoto et al. 2001), additional vent initiation studies are needed to confirm the generality of emergent trends. Further, since vent species and community patterns differ markedly between biogeographic regions (e.g. EPR, northeast Pacific, Mid-Atlantic Ridge), study of future eruptions should reveal if post-eruption patterns and putative causal processes are system-specific, region-specific or simply contingent on specific site conditions.

Methods

Site Description

Axial Volcano (N45°57', W130°00') is an active, ridge-axis seamount located on the central segment of the JdFR in the northeast Pacific, approximately 250 miles off the coast of Oregon. The volcano rises 700 m above the mean ridge depth and its summit hosts a three-sided caldera (3 by 8 km) bordered by boundary faults (Figure 4.1). Two rift zones bisect the caldera to the north and south. Sustained hydrothermal activity is associated with the rift zones and the boundary faults (Johnson & Embley 1990); they provide access to the magma chamber that lies approximately 2 km below the caldera floor (Embley et al. 1990).

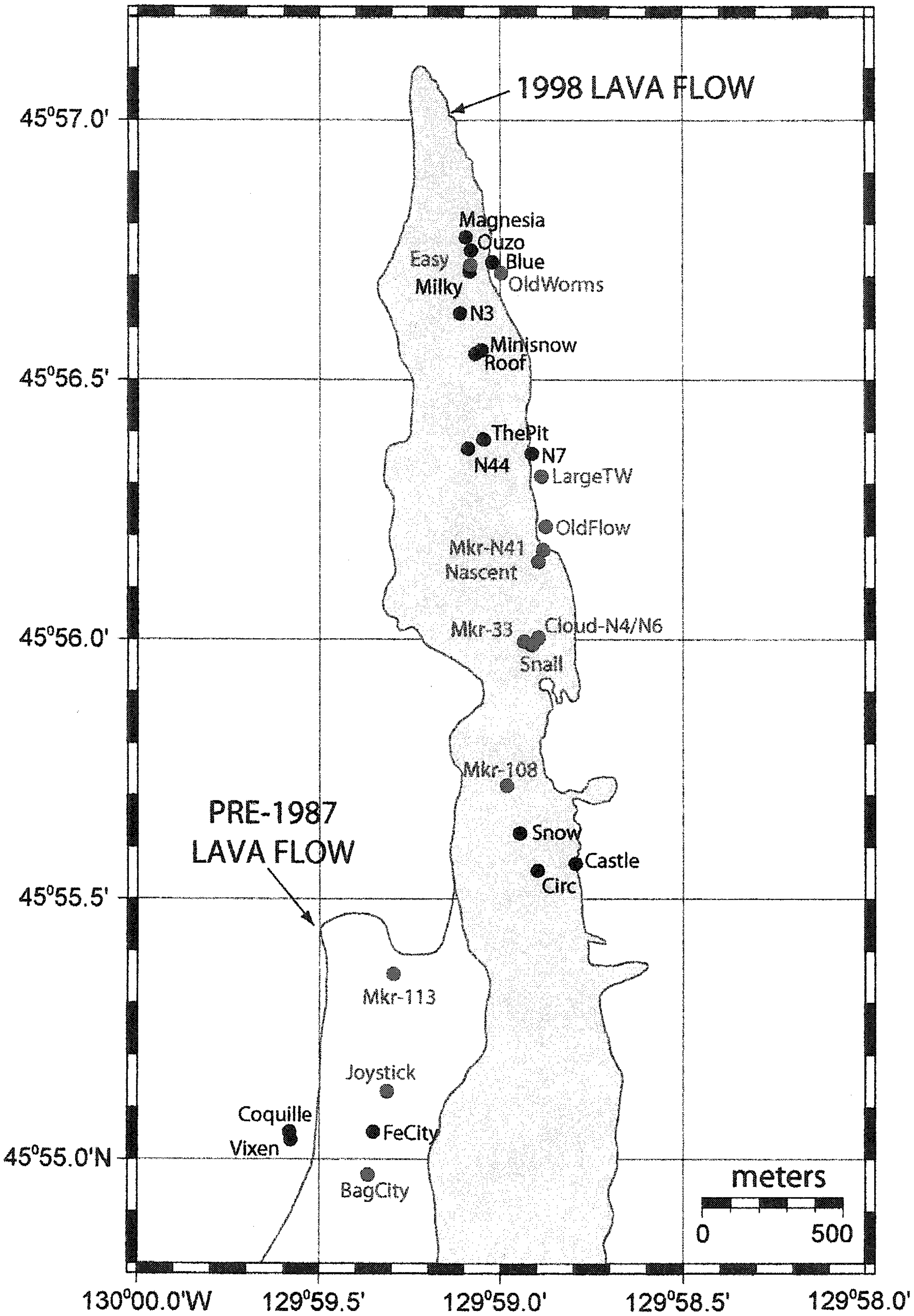
Most of the active venting at Axial is spatially restricted to three fields: ASHES, CASM and the South Rift Zone (SRZ). ASHES is adjacent to the western caldera wall and covers an area ~100 m in diameter, CASM is located in a fissure on the northern wall and the SRZ field covers an area about 6 km long and 0.5 km wide on the southeast portion of the caldera (Figure 4.1). Venting was discovered at Axial in 1983 with submersible dives to the CASM field (Tunnicliffe et al. 1985) and one year later in 1984 at ASHES. Ever since, both CASM and ASHES have supported sustained venting and associated biota in the form of high-temperature sulphide chimneys and low-temperature basalt-hosted vents. The SRZ was first observed in 1985 with camera tows and again in the summers of 1986-87 and 1996-97 with submersible visits. Discrete fields of active diffuse venting colonized by tubeworms and other vent fauna were found along the trend of the SRZ and the buried SE caldera wall (Embley et al. 1990, Butterfield et al. submitted). No eruptions have occurred at Axial since the discovery of venting in the early eighties until 1998, although seismic events have been reported (Fox 1990).

On January 28, 1998 intense earthquakes were detected on the summit of Axial. The seismic swarms lasted 11 days while they migrated 50 km south down the SRZ (Embley & Baker 1999). Two weeks later a rapid response cruise detected a large increase in the hydrothermal output at the summit (Baker et al. 1998). The occurrence of extrusive lava was confirmed in August, seven months after initial earthquake detection, when the remotely operated vehicle ROPOS visited the site. The 1998 eruption created two lava flows (Figure 4.1). The Northern Flow lava was extruded quickly, within an estimated time of one to two hours, and consequently formed a thin sheet flow (~5-6 m) about 5.5 km long and 300-600 m wide (B. Chadwick pers. comm.). This northern flow paved over animal assemblages observed the previous year in the vicinity of the Mkr 33 site (N45°56', W129°59', Figure 5.1). The Southern Flow formed more slowly (6-12 hours) creating a thick (~20-25 m) flow of pillow lavas 400 m long and 1.7 km wide.

New vents were created on the Northern Flow, while no hydrothermal activity was found on the Southern Flow. The Northern Flow was extensively surveyed and sampled in the summers of 1998-2001 by an interdisciplinary group of geologists, chemists and micro- and macrobiologists to investigate the effects of a seafloor eruption on the chemistry, microbiology and macrobiology of nascent vents (New Millennium Observatory project, www.pmel.noaa.gov/vents/nemo/). All new hydrothermal activity was in the form of diffuse, low-temperature (maximum recorded temperature of 55°C in 1998), basalt-hosted vents.

Since the 1998 event was remotely detected, the age of the nascent vents are precisely known. Vents sampled for fauna on the Northern Flow are shown in red in Figure 5.1. Seafloor topography adjacent to the Northern Flow is confusing with the occurrence of multiple lava flows of different ages. Although the ages of these other flows are unknown, they likely formed prior to 1987 (B. Chadwick pers. comm., Figure 5.1). Communities were sampled from three vents on the "pre-1987" lava (Mkr 113, Bag City and Joystick, Figure 5.1). As the fauna of these vents was typical of new assemblages and visually distinct from older, reinvigorated flow (Tsurumi 2001), they are

Figure 5.1. Map of the South Rift Zone venting area of the Axial caldera. The 1998 lava flow is show in grey and outlined in red. The pre-1987 flow is outlined in black. All vents observed between 1998-2000 are shown. Vents in red were sampled for fauna at least once between 1998 and 2000. See Table 5.1 for details of the biological collections.


1998 LAVA FLOW
PRE-1987 LAVA FLOW
Magnesia
Ouzo
Easy
Blue
OldWorms
Milky
N3
Minisnow
Roof
ThePit
N44
N7
LargeTW
OldFlow
Mkr-N41
Nascent
Mkr-33
Cloud-N4/N6
Snail
Mkr-108
Snow
Castle
Circ
Mkr-113
Joystick
Coquille
Vixen
FeCity
BagCity
meters
0
500
45°57.0'
45°56.5'
45°56.0'
45°55.5'
45°55.0'N
130°00.0'W
129°59.5'
129°59.0'
129°58.5'
129°58.0'

considered equivalent to vents sampled on the 1998 flow, in that we assume venting was initiated by the 1998 eruption.

Sampling and Processing

Faunal assemblages were sampled from nascent vents in the summers of 1998-2000. Throughout the text, 1998 to 2000 or years 1 through 3 refer to sampling dates of 7, 18 and 30 months post-eruption. Animals were collected by one of two methods: (1) fauna were suctioned through a hose into a jar with a flow outtake fitted with a 64-250 μm mesh (suction samples), or (2) tubeworms and associated fauna were grabbed with a clawed submersible arm (tubeworm grabs) and placed in closable boxes for transport to the ship. Table 5.1 lists vent collections by year and sample type. Tubeworms settle and grow directly over venting fluid, while suction samples ranged from directly in flow (for example, suctions coupled with a tubeworm grab) to within ~1m of venting fluid. Some vents were sampled multiple times in the same year (Table 5.1).

Suction sampling targeted the visible fauna, but sampling was ultimately dictated by the submersible's ability to reach specific locations. It was impossible to determine the surface area suctioned: new lava was very friable rendering suctioned areas indistinguishable from areas disturbed by other means. Suction sample data are thus qualitative. Faunal density was obtainable for tubeworm grabs as tubeworm tube surface area is considered the substratum for associated species. Three tubeworm samples (Nascent '99 and Mkr N41 in '99 & 2000) combined bushes separated by <2m; multiple grabs were necessary to retrieve a sample of reasonable size.

Markers were deployed at all new vents to facilitate their re-location in subsequent visits. When the same vent was sampled in successive years with suctioning (e.g. no tubeworm bushes present to grab), sampling was haphazard within the spatial boundaries of the vent. However, if tubeworms were present and sampled one year, the following year a grab was taken just adjacent to the sample location of the previous year.

On board, samples were fixed in 7% seawater formalin. In the lab, samples were sieved over a 64μm mesh. Fauna were sorted to the lowest possible taxonomic rank and individuals were counted. Macrofauna and meiofauna are reported separately. Macrofauna are species whose adults are caught on a 1mm sieve, and meiofauna are

Table 5.1. List of nascent vents sampled for fauna on the 1998 Axial Volcano northern lava flow and older vents sampled on the South Rift Zone beyond the reaches of the 1998 flow. X is a suction sample and $\underline{X}$ is a tubeworm grab. A blank cell indicates lack of a sample although the vent was still active that year. "Dead" indicates cessation of fluid flow. Years 1 through 3 represent the summers of 1998 to 2000 (seven, 18 and 30 months after the January 1998 eruption). Vents are ordered by location north to south along the lava flow, see Figure 5.1 for vent locations. Three vents (*) occur off the 1998 flow but are grouped with the new vents since they were very likely initiated by the 1998 eruption. ^ Tubeworm suction sample. ** Tubeworm grabs for which only ¼ of the debris (64μm to 1mm) was sorted. # Sample was kept in the claw of the submersible for transport to the ship, thus not a 'quantitative' tubeworm grab. $^{\$}$ Suction samples coupled with tubeworm grabs; superscript number indicates if more than one suction sample was collected. Abb.= vent name abbreviations used in dendrograms.

Vent	Abb.	Year 1	Year 2	Year 3
New vents on the 1998 lava flow				
Easy	Easy	X	dead	dead
Mkr N41	MN41	$X^{\wedge}$	$\underline{X}$	$\underline{X}^{**}$
Nascent	Nas	$\underline{X}$	$\underline{X}^{\$}$	$\underline{X}^{**}$
Mkr 33	M33	X^{6}	$\underline{X}^{2\$}$	$\underline{X}^{\$}$
Cloud Mkr N4	MN4	X	X^{3}	
Cloud Mkr N6	MN6			$\underline{X}^{\$}$
Snail	Snail	X	X	$\underline{X}^{\$}$
Mkr 108	M108	X		X
Mkr 113 *	M113	$\underline{X}$	$\underline{X}^{\$}$	$\underline{X}^{\$**}$
Joystick *	Joy		X	$\underline{X}^{\$}$
Bag City *	Bag		$\underline{X}$	$\underline{X}^{\$}$
Older vents on the SRZ beyond the lava flow				
Oldworms		$\underline{X}$		
LargeTW		$X^{\#}$		
Old Flow		$\underline{X}$		

species whose adults are caught on a 64μm sieve. Meiofauna include all copepods, nematodes, mites and small ostracods (Podocopida); all other species belong to the macrofauna category. All samples were completely sorted except for Nascent, Mkr N41 and Mkr 113 tubeworm grabs in year 3; here, all individuals greater than 1mm were counted, and one-quarter of the debris sized 64μm to 1mm was processed. Extrapolated numbers from the quarter debris sorts were used to estimate total sample abundance.

Density, total macrofaunal species biomass (g wet weight) and standardized biomass (g/cm^2 surface area) are reported for the tubeworm grabs. Digital images of all tubeworm tubes were examined in the Bioscan Optimus 5.0 program, and surface area was calculated by converting plan area of each tube to surface area by assuming a cylindrical shape (see Tsurumi & Tunnicliffe 2001).

All mature assemblages used in this chapter are low-temperature, basalt-hosted tubeworm grabs from Axial (n=21, the sulphide sample 'Flat Top' is excluded). See Chapter 4 for details of sampling and processing of mature vent collections.

Descriptive analyses of assemblage patterns

Annual trends in community development – To examine broad annual patterns of developing assemblages, all faunal samples were combined within each sample year. I report annual trends in (1) species composition and richness, (2) community dominance and evenness, and (3) species distributions. I use relative species abundances (rank abundance curves) to illustrate community dominance patterns. Hurlbert's PIE method is used to measure community evenness (implemented in EcoSim 6.0). Hurlbert's PIE calculates the probability that two randomly chosen individuals are two different species; a high probability thus reflects high assemblage evenness. Data for macro- and meiofauna are reported separately. Since the Snail vent assemblage differed substantially from other nascent vents in year 1, combined data for 1998 are presented with and without Snail.

Annual colonization rate is defined as the percentage of the species pool that is present at the nascent vents each year. Species-specific colonization rates refer to the year post-eruption each species is first sampled at the new vents. Extinctions refer to species that are present at the nascent vents in one year, but are absent the following year.

To test the hypothesis that species abundant in mature assemblages are faster colonizers of new vents than rarer species, I developed the following null model. For each year, I counted the number of species present in new assemblages that are also present in mature assemblages (excluding *Ridgeia piscesae*). I randomly drew this number of species with an equal probability and without replacement from the total number of species known from mature assemblages, and repeated this procedure to create 1000 null species lists (each species has an equal probability of colonization). I then compared the number of species in the null assemblages that occurred in two species abundance categories (>1% and >0.1% relative abundance in mature assemblages) to the observed number of species in these categories in each year. Support for the proposition that abundant species colonize faster than less abundant species is given if the observed number of species is greater than expected in each relative abundance category.

Annual species densities and biomass estimates of macrofauna are reported for tubeworm grabs.

Assemblage variation within years – Assemblage variability within each year was explored with clustering and correspondence analysis (CA). Analyses were based on relative species abundances and all collections (suctions and tubeworm grabs). Separate macro- and total fauna (macro- and meiofauna combined) analyses yielded indistinguishable patterns, so only the macrofauna results are reported for ease of comparison to mature samples (which lack complete meiofauna data).

Clustering (Bray & Curtis coefficient, flexible method β=-0.25) and CA were implemented in PC-Ord4. Dendrograms derived from clustering are scaled by percentage of information remaining. This reflects the amount of information lost when successive groups are fused into larger clusters; when all items are fused into a single group, no information remains. This scale is recommended by PC-Ord as it prevents reversals. I define 'main clusters' as groups of samples separated at the 50% information remaining scale. If I use a value other than 50%, I indicate so in the text. In the results, I refer to the main clusters in order from top to bottom. CA was used to confirm dendrogram clusters (Legendre & Legendre 1998); this method is described further in Chapter 6.

To assess the idea that macrofaunal differences among vents decrease with assemblage age, similarity indices (Jaccard and Bray & Curtis) were calculated for all pairs of vent assemblages in four data sets: (1) mature Axial assemblages (n=21), (2) seven month old assemblages (n=8), (3) 1.5 year old assemblages (n=8), and (4) 2.5 year old assemblages (n=9). See Chapter 4 for similarity index equations.

Assemblage variation among years: temporal patterns of individual vents – Cluster analyses of all samples from all years were performed to examine the similarity of vent assemblages with respect to location and age. All vents were clustered using presence-absence (PA) data, relative abundance (RA) data and macro- and total fauna. Mature assemblages were included in these analyses. For PA data, two older vents on the SRZ sampled beyond the reaches of the lava flow were included, each as a separate vent. For RA data, three composite mature assemblages were included as the average RA of: (1) three SRZ tubeworm bushes that were unaffected by the lava flow ("OLD"), (2) four tubeworm bushes from ASHES dominated by *Paralvinella pandorae* ("AshesPp"), and (3) 11 tubeworm bushes from ASHES dominated by *Lepetodrilus fucensis* ("AshesLp"). Subdivision of the ASHES data was based on a cluster analysis that divided the vents into two main groups driven by the relative dominance of the pandora worm or the limpet (Appendix 5.1).

To explore the possibility that the prior state of a vent assemblage influences its future state, I compared the similarity index between each vent 'X' in time one and time two, to the average similarity index between vent 'X' in time one and all other vent assemblages in time two. I predict that if a prior state influences a later state, then the similarity index between the same vent at two different times will be higher than the average index of pairwise comparisons between that vent in time one and all other vents in time two. Pairwise assemblage similarity was measured with the Jacaard coefficient for species composition and the Bray & Curtis coefficient for species relative abundances.

The above analyses use all available samples (suctions and tubeworm grabs) to explore species patterns, with the goal of accurately describing general spatial and temporal trends. To examine the potential bias of combining results from two sampling methods, I performed cluster analyses separately on tubeworm grab collections (RA, density and biomass data) and suction samples (RA data).

Results

Characteristics of the 1998 lava flow and new vents

Nascent vents varied in their physicochemical fluid properties and geological setting (Table 5.2). I follow the classification of Butterfield et al. (submitted), and categorize the new vents into two types based on lava morphology.

One type of venting occurs at the top of lava pillars in collapse areas, or in the crevices of intact lobate flows. Lava pillars support the roof of lobate flows and act like pipes by providing conduits for fluids to migrate up from reservoirs beneath the floor of drained out areas (Gregg & Chadwick 1996). Vent assemblages atop pillars are isolated islands meters off the seafloor, while discrete vents on intact lobate roofs may occur within meters of one another. Six of the 11 vents studied here are the lobate/pillar type (Table 5.2: Mkr N41, Nascent, Mkr 108, Mkr 113, Bag City, Joystick; see Figure 5.1); all persisted over the length of the study. Easy vent is a variant on the lobate/pillar type. It is located on the northern portion of the flow in complex terrain with pillars and collapsed areas and pressure ridges. Flow at Easy was undetectable in 1999 (Table 5.1). The second type of venting occurs in sheet flow areas where fluid escapes through linear cracks, or through cracks in jumbled flow. Two vents fall into this category: Marker 33 and Snail (Figure 5.1). Both vents persisted for the length of the study (Table 5.2).

Cloud vent is located in complex terrain with pillars and collapsed areas, and does not fit neatly into one of the two categories. Two discrete venting areas occur at Cloud, separated by a few meters: Mkr N4 and Mkr N6. Fluid vents through jumbled flow at Mkr N4. At Mkr N6, the vent orifice was obscured in 1998 due to smoky fluid. In 1999, the fluid was less cloudy, revealing a hole in the seafloor about 30 cm across and over 1.5 meters deep. Mkr N6 is unique among diffuse vents since yearly temperature measurements are extremely consistent; this suggests that Mkr N6 is analogous to a low temperature black smoker, with strong focused flow (Butterfield et al. submitted).

The possible influences of vent morphology and fluid properties on faunal assemblages are explored further in Chapter 6.

Table 5.2. Habitat characteristics (substratum and maximum temperature) of the new vents on the 1998 lava flow. *Temperature from a vent similarly colonized by gastropods (Circ) was 6.5°C in 1998.

		Maximum temperature (°C)		
Vent	Substratum	Year 1	Year 2	Year 3
Easy	complex lobate	10.2	dead	dead
Mkr N41	lobate roof	22.7	15.3	13.2
Nascent	lobate roof	23.5	15.3	14.7
Mkr 33	crack in sheet	55	74.6	33.4
Cloud Mkr N4	jumbled lobate	23.1	18.7	na
Cloud Mkr N6	jumbled lobate	27.3	20.3	16
Snail	crack in sheet	na*	13	17.2
Mkr 108	top of pillar	13	13.8	na
Mkr 113	top of pillar	25.2	27	19.8
Joystick	collapsed lobate	na	9.6	4
Bag City	lobate roof	na	23.4	19.3
Average per year		25.0	23.1	17.2

Annual trends in community development

Species composition and richness

The number of species present at new vents increases with time. Combining both macro- and meiofaunal species, 29 species were recorded in 1998, 39 in 1999 and 45 in 2000 (Table 5.3).

Macrofauna - Macrofaunal species richness increases from 21 to 27 to 33 for each successive year (Table 5.3). Seven species present at new vents are absent from mature vents (Table 5.4). Two of these species, an unknown amphipod and an unknown brittle star, are from waning Joystick vent in 2000, and are likely non-vent deep-sea species (Marcus & Tunnicliffe 2002). Two other species, the nemertean *Thermonemertes valens* and an unidentified ciliate protozoan (*Folliculina* sp.), are reported from other Axial vents not included in the mature samples (see Table 5.4). The remaining three species may be adapted to nascent vents: the scale worm *Vampiropolynoe embleyi*, an unknown orbiniid polychaete, and the snail *Hyalogyrina globularis* (Table 5.4). Omitting these seven species from annual richness estimates, and using mature assemblages to estimate the Axial species pool, 53% of the pool (n=19 species) arrived at nascent vents by 1998, 64% (n=23) by 1999 and 72% (n=26) by 2000.

Species differ in their colonization rates of new vents. Species abundant in mature assemblages tend to colonize new vents earlier than relatively rarer species. In 1998, there are more species in the mature RA categories of >1% and >0.1% than expected; respectively, 5 species are observed versus 3.084 expected (p=0.097) and 10 species are observed versus 7.694 expected (p=0.102). Furthermore, the only absent species in 1998 with an overall RA >1% in mature assemblages (the snail *Provanna variabilis*) is the least abundant of the top six species at mature vents (Table 5.4). In 1999, this trend is more significant: 6 species are observed with a RA >1% in mature assemblages, while only 3.74 are expected (p=0.043), and 13 species are observed with a RA >0.1% in mature assemblages, while only 9.45 are expected (p=0.014). Again, more species are observed than expected in 2000 (p=0.11 for >1% RA, p=0.014 for >0.1% RA). Species of note that colonized in abundance in 1998, but are relatively rare in mature assemblages are the scale worm *Branchinotogluma* sp. and the dorvilleid polychaete *Ophryotrocha globopalpata* (Table 5.4).

Table 5.3. Summary of data from collections of nascent vents on the South Rift Zone (SRZ). Bracketed numbers refer to macrofauna. Colonizations refer to the first time a species is sampled from the new SRZ vents. Extinctions refer to species present the previous year but absent the year in question. Recolonization means a species is present in 1998, absent in 1999 and present again in 2000.

Number	1998	1999	2000
Vents sampled	8	8	9
Individuals collected			
Macrofauna	1,234	85,960	139,665
Meiofauna	183	1,343	3,781
Total	1,417	87,303	143,446
Species	29 (21)	39 (27)	45 (33)
Colonizations	29 (21)	14 (8)	7 (5)
Extinctions	-	4 (2)	2 (0)
Recolonizations	-	-	1 (1)

Table 5.4. Species list of macrofauna from mature and new vent samples from Axial Volcano. Mature samples exclude Flat Top, the sulphide sample included in Chapter 4. Percent relative abundances are based on the total number of individuals collected from both sample groups. Total individuals exclude *Ridgeia piscesae* and unidentifiable individuals such as baby polynoids. P = present; NP = not present. Species are ordered by decreasing relative abundances in the mature assemblage. Years 1, 2 and 3 refer to vents sampled seven, 18, and 30 months post-eruption. Two species present at the new South Rift Zone (SRZ) vents occurred in other samples from Axial not included in the mature category: ^ present in one senescent SRZ sample, *present in two high temperature sulphide samples from ASHES. Continued on next page.

		Relative Abundance (%)			
Class	Species	Mature	Year 1	Year 2	Year 3
Number of vents sampled		21	8	8	9
Total number of macrofauna species		36	21	27	33
Total number of individuals sampled		204,190	1,234	85,960	139,665
Vestimentifera	*Ridgeia piscesae*	P	P	P	P
Gastropoda	*Lepetodrilus fucensis*	45.460	15.154	7.648	61.187
Polychaeta	*Paralvinella pandorae*	27.244	23.177	76.990	23.925
	Amphisamytha galapagensis	7.483	2.188	0.629	0.830
	Paralvinella palmiformis	7.455	5.186	1.130	1.161
Gastropoda	*Depressigyra globulus*	6.240	25.689	0.933	10.787
	Provanna variabilis	2.444	NP	0.006	0.067
Polychaeta	*Protomystides verenae*	0.544	0.081	0.007	0.080
	Lepidonotopodium piscesae	0.528	1.378	0.049	0.228
	Ophryotrocha globopalpata	0.497	11.588	10.798	0.914
	Parougia wolfi	0.458	NP	0.870	0.295
Gastropoda	*Pyropelta musaica*	0.411	NP	NP	0.004
Polychaeta	*Branchinotogluma* sp.	0.305	9.481	0.255	0.195
	Paralvinella dela	0.290	NP	NP	NP
Ostracoda	*Euphilomedes climax*	0.224	0.162	0.003	0.062
Polychaeta	*Nereis piscesae*	0.123	NP	0.001	0.004
Pycnogonida	*Ammothea verenae*	0.062	NP	NP	0.024
Polychaeta	*Opisthotrochopodus tunnicliffeae*	0.049	0.567	0.008	0.018

Table 5.4 continued

		Relative Abundance (%)			
Class	Species	Mature	Year 1	Year 2	Year 3
Polychaeta	*Hesiospina vestimentifera*	0.044	0.648	0.252	0.083
	Paralvinella sulfincola	0.031	NP	0.001	0.017
	Levensteiniella kincaidi	0.027	NP	0.036	0.019
Gastropoda	*Clypeosectus curvus*	0.018	NP	NP	NP
Polychaeta	*Nicomache venticola*	0.015	NP	NP	NP
	Prionospio n. sp.1	0.013	0.243	0.206	0.024
Gastropoda	*Lacunoides vitreus*	0.009	0.486	0.008	0.002
Polychaeta	*Hesiodeira glabra*	0.008	0.081	NP	0.039
	Amphiduropsis axialensis	0.005	0.162	0.059	0.014
	Prionospio n. sp. 2	0.002	2.026	NP	NP
Anthozoa	Actinostolidae n. spp (2)	0.002	NP	NP	NP
Bivalvia	*Idasola* cf. *washingtonia*	0.002	NP	NP	NP
Polychaeta	*Levensteiniella intermedia*	0.001	NP	NP	NP
Hydrozoa	Unknown hydrozoan	0.001	NP	NP	NP
Gastropoda	*Temnocinclis euripes*	0.001	NP	NP	NP
Bivalvia	*Calyptogena pacifica*	0.001	0.081	0.001	0.002
Polychaeta	*Harmothoe* sp.	< 0.001	NP	NP	NP
Gastropoda	*Helicoradomenia juani*	< 0.001	NP	0.002	0.005
Polychaeta	*Vampiropolynoe embleyi*	NP	1.540	0.002	0.001
	Orbiniella unk. sp.	NP	0.081	0.055	0.004
Nemertea	*Thermonemertes valens*	NP^	NP	0.045	0.004
Gastropoda	*Hyalogyrina globularis*	NP	NP	0.003	0.002
Amphipoda	Amphipoda unk. sp.	NP	NP	NP	0.001
Ophuroidea	Ophuroidea unk. sp	NP	NP	NP	0.001
Ciliata	*Folliculina* sp.	NP*	NP	NP	P

In 1999, there were eight colonizations and two extinctions (Table 5.3). Three of the eight new arrivals are typical members of mature assemblages (overall RA > 0.1%): the snail *Provanna variabilis* and the polychaetes *Parougia wolfi* and *Nereis piscesae* (Table 5.4). Two species with RAs >0.1% at mature vents had still not arrived by 1999: the limpet *Pyropelta musaica* and the alvinellid *Paralvinella dela* (Table 5.4). Only one of the two extinctions (*Hesiodeira glabra* and *Prionospio* n. sp. 2, Table 5.4) is undoubtedly real: due to identification problems, I cannot discount the possibility that a few individuals of *Prionospio* n. sp. 2 may be cited as *Prionospio* n. sp. 1 in 1999 and 2000.

By 2000, an additional five species had colonized the new vents (Table 5.3). Two are likely non-vent deep-sea species (Marcus & Tunnicliffe 2002), but the other three are typical vent members: the pycnogonid *Ammothea verenae*, the limpet *Pyropelta musaica* and the ciliate protozoan *Folliculina* sp. (Table 5.4). Since sampling was quite extensive in 1999 (> 85,000 individuals, Table 5.3), the slower rate of colonization of these three species is likely real. In year 3, no species had disappeared from the previous year, and one species, the polychaete *Hesiodeira glabra*, present in 1998 but not in 1999 had recolonized (Table 5.4).

Nine species known from mature communities never occur at nascent vents (1998-2000); all are relatively rare. Only three have an overall RA exceeding 0.01% at mature vents: the alvinellid *Paralvinella dela*, the split-limpet *Clypeosectus curvus*, and the polychaete *Nicomache venticola.* The other five species have an overall RA equal to or less than 0.002% (Table 5.4).

Meiofauna - Meiofaunal species richness increases from eight in 1998, to 12 in 1999 and 2000 (Tables 5.3 and 5.5). Seven (44%) of the 16 meiofaunal species known from Axial samples reached the new vents by 1998. By 1999, 62% (n=10) of the known Axial pool are present, and a subsequent colonization and extinction event maintains this number (n=10) in 2000 (Table 5.5).

Relative abundances of meiofauna are available for only seven mature assemblages (Table 5.5). The 1998 data support the hypothesis that abundant species in mature assemblages are faster colonizers than rarer species: on average, 2.138 and 3.868 species are expected within the mature RA categories of >1% and >0.1%, while 6 and 4

Table 5.5. Species list of meiofauna from mature and new vent samples from Axial Volcano. Only seven mature vents were completely sorted for meiofauna; mature relative abundances (RA) are calculated from these. The species list (P/A) is taken from a larger study of the Axial fauna (Tsurumi 2001); P = present; NP = not present. All relative abundances are based on the total number of individuals collected for each sample group. Species are ordered by decreasing relative abundance in the mature assemblage. Years 1, 2 and 3 refer to vents sampled seven, 18, and 30 months post-eruption. One hundred unsorted copepod individuals (Joystick vent, R548-10) were excluded from year 3 calculations as they are pending identification.

Class	Species	P/A	RA	RA		
		Mature		Year 1	Year 2	Year 3
Total number of meiofauna species		16	14	8	12	12
Total number of individuals sampled		na	11,015	183	1,343	3,781
Copepoda	*Benthoxynus spiculifer*	P	88.597	1.093	NP	NP
Nematoda	Nematoda unk. sp.	P	3.431	NP	NP	0.026
Copepoda	*Stygiopontius quadrispinosus*	P	2.351	1.093	0.521	5.766
	Harpacticoida (>1 sp.)	P	1.852	2.186	11.690	17.164
	Aphotopontius forcipatus	P	1.625	83.607	74.460	65.194
	Calanoida (> 1 sp.)	P	0.835	9.836	7.744	3.756
Ostracoda	Podocopida	P	0.681	NP	2.532	2.169
Copepoda	*Misophriopsis longicauda*	P	0.263	NP	0.447	0.635
	Copepoda Type 2	P	0.236	0.546	NP	NP
	Humesipontius arthuri	P	0.064	0.546	0.521	4.258
	Copepoda Type 9	P	0.036	NP	0.074	NP
	Barathricola rimensis	P	0.009	NP	0.447	0.423
	Copepoda Type A3244	P	0.009	NP	NP	NP
Acari	*Copidognathus papillatus*	P	0.009	NP	0.149	0.106
Copepoda	Copepoda Type 10	P	-	NP	NP	NP
	Copepoda Type 13	P	-	NP	NP	NP
	Copepoda Type 19	NP	-	NP	0.372	NP
	Cyclopoida (*Oithona* sp.?)	NP	-	NP	NP	0.132
	Unk. copepods (>1 sp.)	-	-	1.093	1.1042	0.370

species are observed (p=0.025 and p=0.066). However, the 1999 and 2000 data do not support this hypothesis. Fewer species in 1999 are observed than expected: 3 and 6 species are observed, while 3.552 and 6.439 species are expected in the RA categories of >1% and >0.1%, respectively (p=0.892 and p=0.864). Although more species are observed than expected in 2000, the difference is not significant (p=0.526 for RA>1%, and p=0.455 for RA>0.1%).

Rates of colonization also vary for meiofaunal species and the number of colonizations and extinctions is slightly greater than for macrofauna (Table 5.3). In 1999, there were two extinctions and six colonizations (Table 5.5). Extinction of the copepod *Benthoxynus spiculifer* is notable as it is the most abundant species from mature vents; it is absent in 1999 and 2000. In 2000, two new species colonized (Table 5.5) and two species were not resampled.

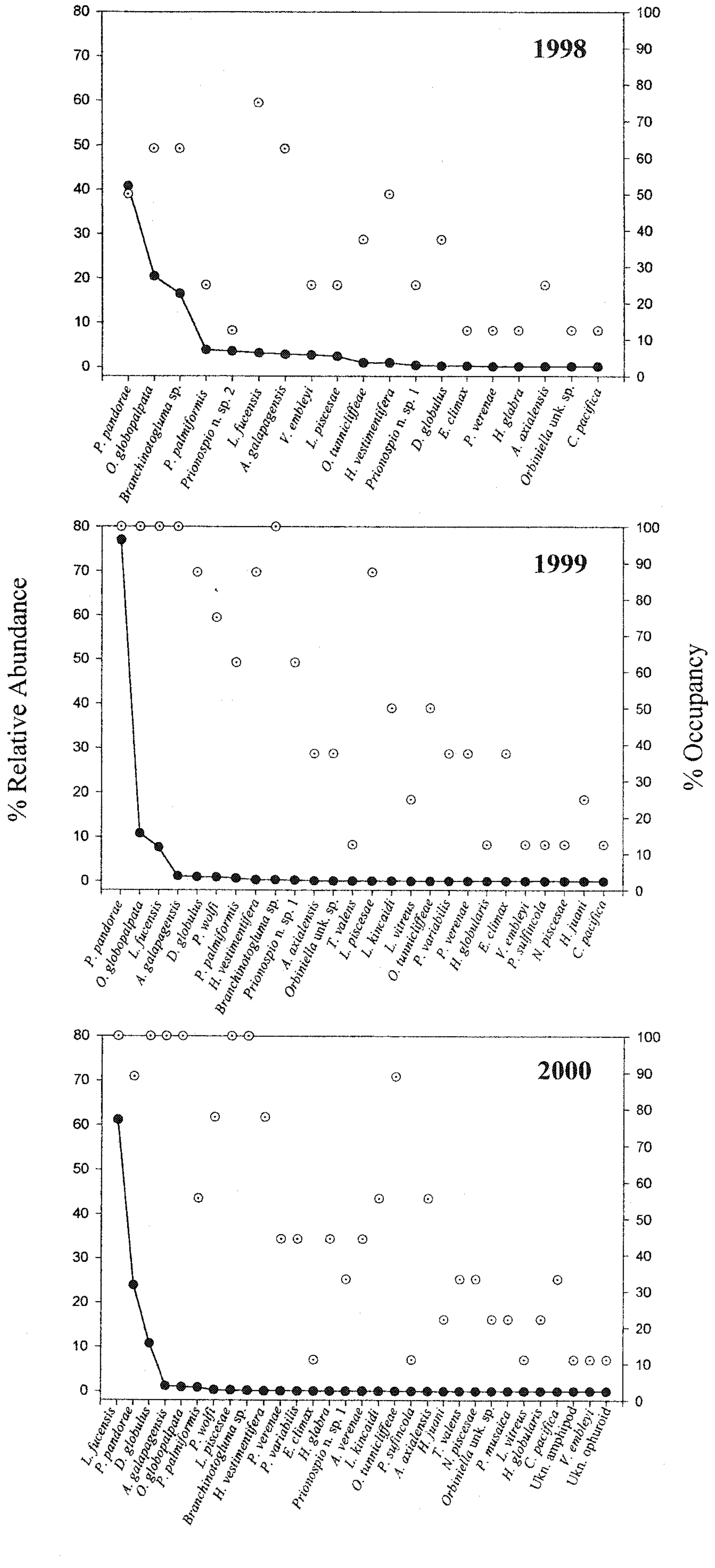
Two meiofaunal species only occur at nascent vents: Copepoda Type 19 and Cyclopoid copepods. Cylopoids are well-known pelagic copepods and may be contaminants (Tsurumi pers. comm.). Three other species known from mature assemblages are absent from nascent vents from 1998-2000: Copepoda Type 10, Type 13 and Type A3244 (Table 5.5).

Annual patterns of species dominance and evenness

Macrofauna – Annual patterns of species dominance are presented with species rank-abundance curves for each year using combined data from all vents (Figure 5.2 and Table 5.4). In year 1, the three most abundant species represent >64% of individuals; they are the alvinellid polychaete *Paralvinella pandorae* (23%), the snail *Depressigyra globulus* (26%) and the limpet *Lepetodrilus fucensis* (15%). In year 2, the top three species account for >95% of all individuals; they are *P. pandorae* (77%), the dorvilleid worm *Ophryotrocha globopalpata* (11%), and *L. fucensis* (8%). In year 3, the three most abundant species again account for >95% of individuals, but there is a shift in species dominance from the alvinellid polychate to the common limpet. The most abundant species in 2000 are *L. fucensis* (61%), followed by *P. pandorae* (24%) and the snail *D. globulus* (11%).

Snail vent greatly influences the structure of the overall rank-abundance curve in

Figure 5.2. Rank-abundance curves and species distribution data for macrofauna sampled from nascent vents in 1998, 1999 and 2000. Rank-abundance curves (solid black circles) are based on combined species abundance data from all vents sampled in each year. Percent occupancy (dotted open circles) is the proportion of sites occupied by each species. Snail vent is omitted from the 1998 rank-abundance curve, but is included for the 1998 species distribution data.


1998
P. pandorae
O. globopalpata
Branchinotogluma sp.
P. palmiformis
Prionospio n. sp. 2
L. fucensis
A. galapagensis
V. embleyi
L. piscesae
O. tunnicliffeae
H. vestimentifera
Prionospio n. sp. 1
D. globulus
E. climax
P. verenae
H. glabra
A. axialensis
Orbiniella unk. sp.
C. pacifica
1999
P. pandorae
O. globopalpata
L. fucensis
A. galapagensis
D. globulus
P. wolfi
P. palmiformis
H. vestimentifera
Branchinotogluma sp.
Prionospio n. sp. 1
A. axialensis
Orbiniella unk. sp.
T. valens
L. piscesae
L. kincaidi
L. vitreus
O. tunnicliffeae
P. variabilis
P. verenae
H. globularis
E. climax
V. embleyi
P. sulfincola
N. piscesae
H. juani
C. pacifica
2000
L. fucensis
P. pandorae
D. globulus
A. galapagensis
O. globopalpata
P. palmiformis
P. wolfi
L. piscesae
Branchinotogluma sp.
H. vestimentifera
P. verenae
P. variabilis
E. climax
H. glabra
Prionospio n. sp. 1
A. verenae
L. kincaidi
O. tunnicliffeae
P. sufincola
A. axialensis
H. juani
T. valens
N. piscesae
Orbiniella unk. sp.
P. musaica
L. vitreus
H. globularis
C. pacifica
Ukn. amphipod
V. embleyi
Ukn. ophuroid
% Relative Abundance
0
10
20
30
40
50
60
70
80
% Occupancy
0
10
20
30
40
50
60
70
80
90
100

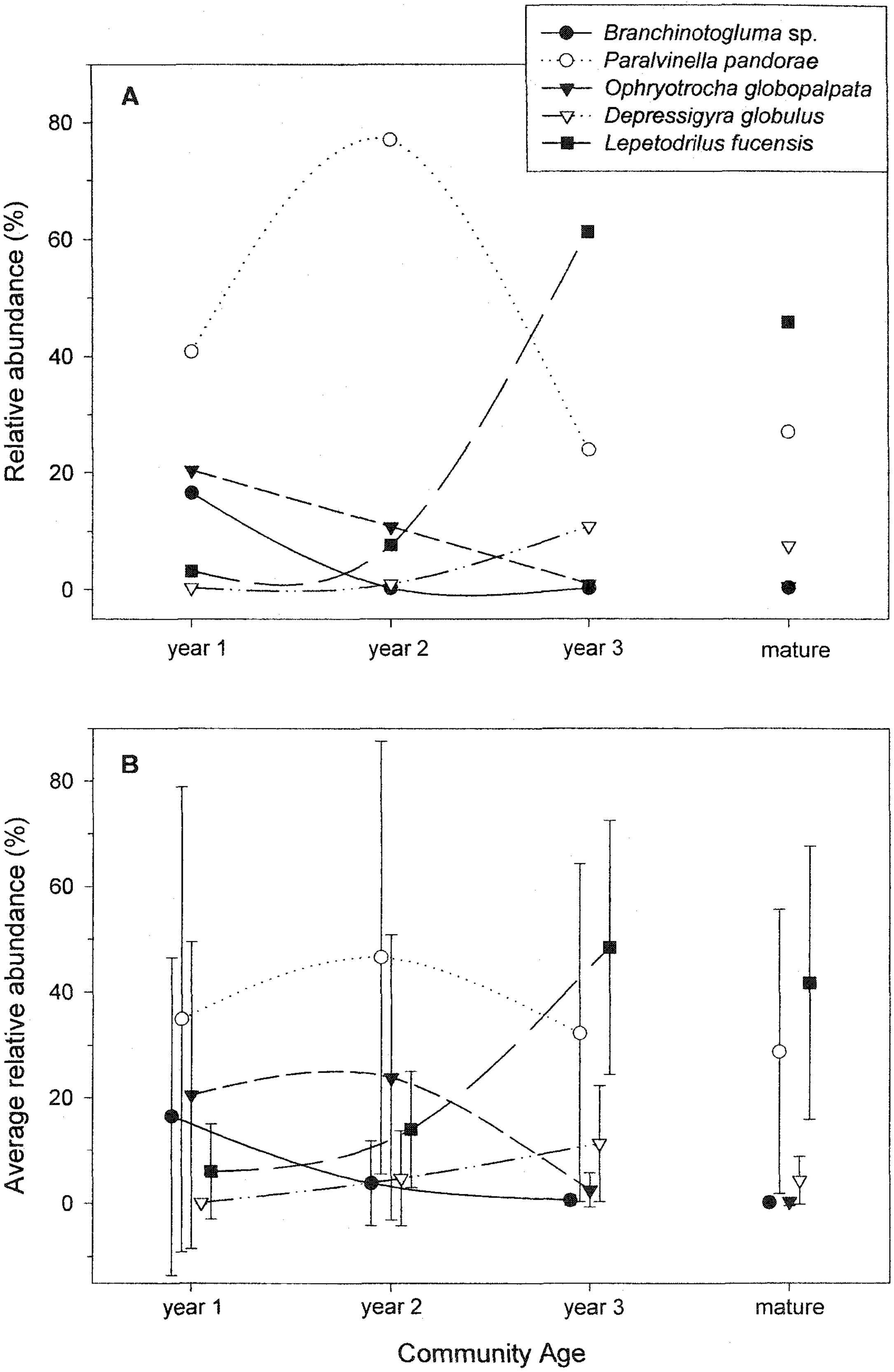
1998. Over 40% of all individuals sampled in year 1 are from Snail, and the dominant species are atypical compared to other nascent assemblages. Snail is dominated by gastropods while polychaetes dominate all other observed vents (Chapter 4, Table 4.3). When Snail vent is omitted from the 1998 rank-abundance curve, a different pattern of species dominance emerges: *Paralvinella pandorae*, *Ophryotrocha globopalpata*, and the scale worm *Branchinotogluma* sp. become the top three most abundant species, representing 41%, 20% and 17% of the total number of individuals, respectively (Figure 5.2A).

The shift in numerical dominance of the top ranked species over the three years is illustrated in Figure 5.3A,B. Omitting Snail vent from 1998, the pandora worm dominates seven and 18 month-old vents, but declines in overall relative abundance between 18 and 30 months. The two common gastropod species, *Lepetodrilus fucensis* and *Depressigyra globulus,* monotonically increase in relative abundance from year 1 to year 3, and the limpet replaces the pandora worm as the most abundant species by year 3. Both the dorvilleid worm *Ophryotrocha globopalpata* and the scale worm *Branchinotogluma* sp. decrease in relative abundance with increasing vent age. By 2000, the ranking of overall community dominants at nascent vents parallels their ranking in mature assemblages (Figure 5.3A). However, some notable differences persist: *O. globopalpata* and *Branchinotogluma* sp. are relatively more abundant in 2000 assemblages compared to mature vents, while species typically more abundant in mature assemblages (e.g. *Amphisamytha galapagensis, Provanna variabilis, Protomystides verenae* and *Pyropelta musaica*) remain numerically rare at new vents in 2000 (Table 5.4). Species replacement patterns are somewhat dampened when average relative species abundances are considered (Figure 5.3B).

Evenness declines with time at the nascent vents. In 1998, Hurlbert's PIE is 0.85 including Snail vent and 0.81 excluding Snail. In 1999 and 2000, evenness is 0.44 and 0.56, respectively. The shapes of the annual rank abundance curves reflect this decrease in evenness after 1998 (Figure 5.2); the 1998 distribution is significantly different from 1999 and 2000 ($p<0.001$ in both cases, Wald-Wolfowitz runs test) while the 1999 and 2000 curves do not differ ($p=0.1$).

Meiofauna – Annual rank-abundance curves for meiofauna are presented in

Figure 5.3. A. Overall relative abundances of the most abundant macrofaunal species (ranks 1 to 3) for the first three years post-eruption (omitting Snail vent in 1998). The relative abundances of the same species in mature assemblages are given for reference. B. Average relative abundance of species in A. Error bars represent one standard deviation. C. Overall relative abundances of the most abundant meiofaunal species (ranks 1 to 3) for the first three years post-eruption. The relative abundances of the same species in mature assemblages are given for reference. *Benthoxynus spiculifer* is included as it dominates mature assemblages.


Branchinotogluma sp.
Paralvinella pandorae
Ophryotrocha globopalpata
Depressigyra globulus
Lepetodrilus fucensis
A
Relative abundance (%)
0
20
40
60
80
year 1
year 2
year 3
mature
B
Average relative abundance (%)
0
20
40
60
80
year 1
year 2
year 3
mature
Community Age

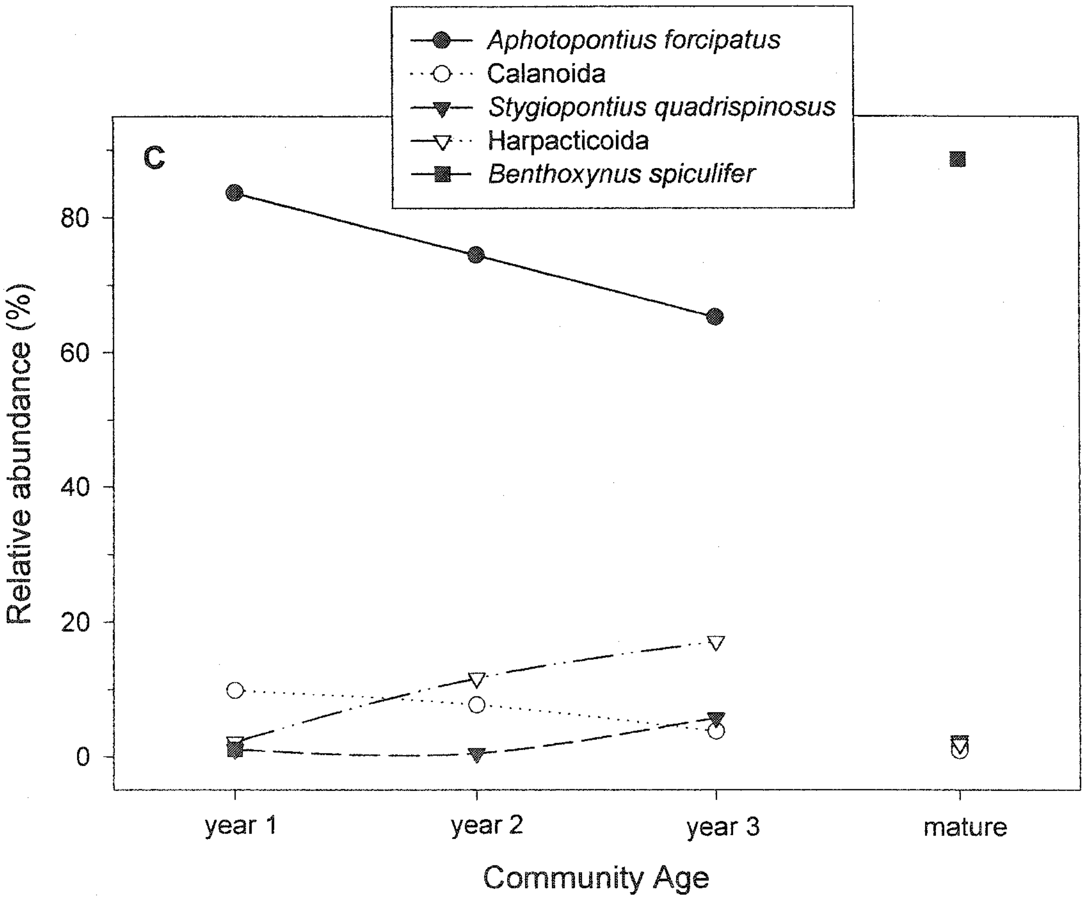

Aphotopontius forcipatus
Calanoida
Stygiopontius quadrispinosus
Harpacticoida
Benthoxynus spiculifer
C
80
60
40
20
0
Relative abundance (%)
year 1
year 2
year 3
mature
Community Age

Figure 5.4. In 1998, three copepod species account for >95% of all individuals: *Aphotopontius forcipatus* (84%), Calanoida (10%) and Harpacticoida (2%). In 1999, *A. forcipatus* remains numerically dominant (74%), followed by harpacticoid (12%) and calanoid (8%) copepods. By year 3, harpacticoids are relatively more abundant (17%), although *A. forcipatus* maintains its top ranking position (65%).

Unlike macrofauna, the overall relative abundances of meiofaunal species do not converge on the mature structure by year 3 (Figure 5.3C). *Benthoxynus spiculifer* accounts for >85% of individuals from mature vents, while *Aphotopontius forcipatus* is the dominant copepod at nascent vents seven months to 2.5 years old. *B. spiculifer* is absent from SRZ vents in years 2 and 3.

Meiofaunal evenness and annual dominance curves display an opposite trend to the macrofauna. Evenness increases with time (Hurlbert's PIE increases from 0.26 to 0.38 to 0.51 for 1998-2000) and species rank-abundance curves do not differ among the three years (Wald-Wolfowitz Runs Test, p>0.8 for all three comparisions).

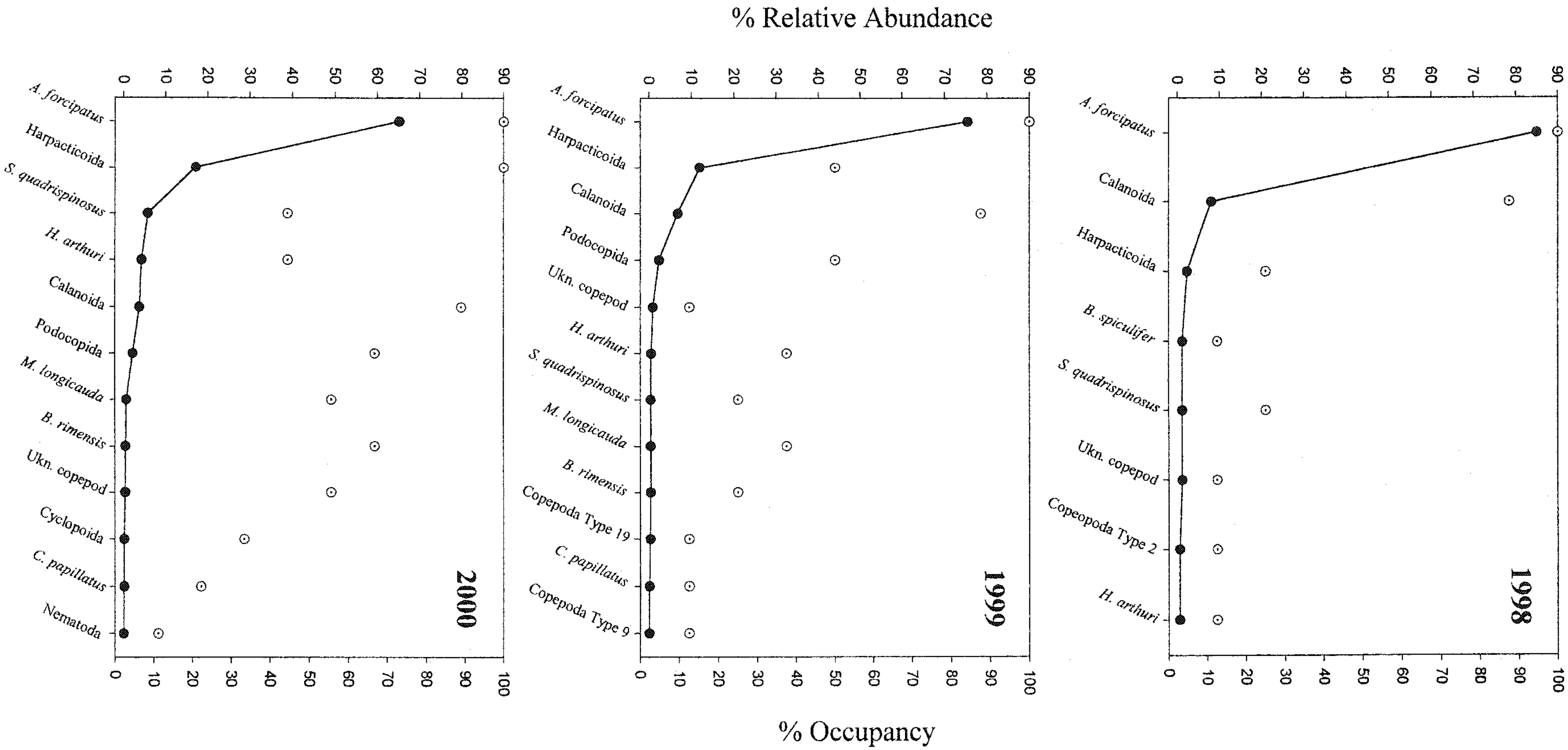
Annual patterns of species distributions

The tubeworm *Ridgeia piscesae* was present at three vents in 1998, and occurs at all sampled sites in 1999 except Snail vent. By 2000 the tubeworm was also present at Snail. However, tubeworms in 1999 occurred at some sites as sparsely distributed individuals. *R. piscesae* bushes, defined as an aggregation of tubeworms (see Figure 2.1), did not form at some vents until 2000 (e.g. Cloud vent).

More abundant species generally have wider distributions in all three years (Figures 5.2 and 5.4). In 1998, no macrofaunal species are found at all sampled vents. *Lepetrodrilus fucensis* has the widest distribution occurring at six of eight vents, and five additional species occur at 50% or more of the sites (*Paralvinella pandorae, Ophryotrocha globopalpata, Branchinotogluma* sp., *Amphisamytha galapagensis* and *Hesiospina vestimentifera*, Figure 5.2A). One meiofaunal species has a ubiquitous distribution in 1998 (*Aphotopontius forcipatus*) and calanoid copepods occur at all vents except one (Figure 5.4A).

In 1999, five macrofaunal species occur at all sites, while *A. forcipatus* remains the only meiofaunal species with a ubiquitous distribution, followed again by calanoid

Figure 5.4. Rank-abundance curves and species distribution data for meiofauna sampled from nascent vents in 1998, 1999 and 2000. Rank-abundance curves (solid black circles) are based on combined species abundance data from all vents sampled in each year. Percent occupancy (dotted open circles) is the proportion of total sites occupied by each species.


% Relative Abundance
% Occupancy
1998
A. forcipatus
Calanoida
Harpacticoida
B. spiculifer
S. quadrispinosus
Ukn. copepod
Copeopoda Type 2
H. arthuri
1999
A. forcipatus
Harpacticoida
Calanoida
Podocopida
Ukn. copepod
H. arthuri
S. quadrispinosus
M. longicauda
B. rimensis
Copepoda Type 19
C. papillatus
Copepoda Type 9
2000
A. forcipatus
Harpacticoida
S. quadrispinosus
H. arthuri
Calanoida
Podocopida
M. longicauda
B. rimensis
Ukn. copepod
Cyclopoida
C. papillatus
Nematoda
0
10
20
30
40
50
60
70
80
90
100

copepods (Figures 5.2B & 5.4B). Four of the five ubiquitous macrofaunal species are also the most abundant species, while the fifth species (*Branchinotogluma* sp.) has an unusually high distribution for its abundance. Of the new macrofaunal additions in 1999 (eight species), four occur at only one site; the polychaetes *Parougia wolfi* and *Levensteiniella kincaidi* are notable as they colonized four and six of the eight vents respectively, between 1998 and 1999 (Figure 5.2B). Of the six new meiofaunal additions in 1999, five are present at one to three sites, while one species (podocopid ostracods) successfully colonized half the sites (Figure 5.4B).

In 2000, six macrofaunal species occur at all sites. Three scale worm species have unusually high distributions for their abundances (*Lepidonotopodium piscesae, Branchinotogluma* sp., and *Opisthotrochopodus tunnicliffeae*), and although *Paralvinella pandorae* is the second most abundant species, it is absent from one site (Figure 5.2C). The pycnogonid *Ammothea verenae*, a new addition in 2000, had recruited to half the sites. In year 3, the top two ranked meiofaunal species occur at all sites (*Aphotopontius forcipatus* and harpacticoid copepods, Figure 5.4C). Of the three new meiofaunal colonizers, Copepoda Type 15 and an unknown nematode species are present at only one site, while cyclopoid copepods occur at 3 sites (Figure 5.4C).

Species density and biomass

Total macrofaunal densities increase at the new vents over time (Table 5.6). The average number of individuals per cm^2 of tubeworm tube surface area is 0.304 in 1998 (n=3). Total density increases to 4.168 individuals/cm^2 in 1999 (n=5) and declines to 3.332 individuals/cm^2 in 2000 (n=8). Average annual densities are significantly different between 1998 and the two subsequent years (p=0.025 for each comparison), but do not differ between 1999 and 2000 (p=0.662, Mann Whitney U Test).

Temporal patterns of macrofaunal biomass follow a similar trend (Table 5.7). Average biomass per cm^2 of tubeworm tube surface area increases from 0.005 g/cm^2 in 1998 to 0.052 g/cm^2 and 0.053 g/cm^2 in 1999 and 2000, respectively. Average macrofaunal biomass significantly differs between 1998 and the two subsequent years (p=0.025 and p=0.014 for 1999 and 2000, respectively), but does not differ between 1999 and 2000 (p=0.558, Mann Whitney U Test).

Table 5.6. Number of macrofuanal individuals per cm^2 of tubeworm tube surface area. Average annual densities differ significantly between 1998 and 1999 ($p=0.025$) and 1998 and 2000 ($p=0.025$), but not between 1999 and 2000 ($p=0.661$, Mann-Whitney U test). Total macrofaunal densities range from <0.5 to 2.6 individuals/cm^2 for mature Axial assemblages (Tsurumi 2001).

Vent	1998	1999	2000
Mkr N41	0.422	6.776	7.981
Nascent	0.228	3.058	0.808
Mkr 33		1.797	2.160
Cloud Mkr N6			1.085
Snail			3.323
Mkr 113	0.261	6.997	3.631
Joystick			7.366
Bag City		2.214	0.301
Average per year	0.304	4.168	3.332

Table 5.7. Biomass (wet weight) of macrofauna (g) per cm^2 of tubeworm tube surface area. Average annual biomass per cm^2 tubeworm area differs significantly between 1998 and 1999 ($p=0.025$) and 1998 and 2000 ($p=0.014$), but not between 1999 and 2000 ($p=0.558$, Mann-Whitney U test).

Vent	1998	1999	2000
Mkr N41	0.0048	0.0258	0.0977
Nascent	0.0002	0.0247	0.0287
Mkr 33		0.0688	0.0942
Cloud Mkr N6			0.0340
Snail			0.0463
Mkr 113	0.0115	0.1196	0.0804
Joystick			0.0306
Bag City		0.0208	0.0131
Average per year	0.0055	0.0520	0.0531

Assemblage variation within years

Cluster and correspondence analyses

In 1998, vent assemblages group into three clusters using macrofaunal relative abundances (Figure 5.5). These clusters reflect numerical dominance of each vent by one of three species or species groups: (1) the alvinellid polychaete *Paralvinella pandorae* (>50% RA at Mkr N41, Nascent, Mkr 113), (2) the dorvilleid polychaete *Ophryotrocha globopalpata* and the scale worm *Branchinotogluma* sp. (>70% RA at Cloud N4, Mkr 33, Easy), or (3) the limpet *Lepetodrilus fucensis* and the ampharetid polychaete *Amphisamytha galapagensis* (>35% RA at Mkr 108, Snail). Snail vent supports by far the largest proportion of gastropods of any vent sampled in 1998: 59% of individuals are the common snail *Depressigyra globulus* and 31% *L. fucensis*. Although Marker 108 groups with Snail vent, only one gastropod species is present (*L. fucensis,* 26% RA). The uniqueness of Snail vent in 1998 is better illustrated with a correspondence analysis biplot (Figure 5.6).

In 1999, vents group into two main clusters. Assemblages dominated by alvinellid polychaetes (first cluster) separate from vents with higher proportions of gastropods and *Ophryotrocha globopalpata* (second cluster, Figure 5.5). For example, >70% of total individuals from Bag City, Mkr N41, Nascent and Mkr 33 are the alvinellid polychaete, *Paralvinella pandorae*. The second cluster has two subclusters: Cloud N4 and Snail vents are co-dominated by *O. globopalpata* (38% and 34% RA, respectively) and the limpet *Lepetodrilus fucensis* (31% and 29% RA, respectively). Although *O. globopalpata* is dominant at Joystick and Mkr 113 (73% and 40% RA, respectively), the second most abundant species at Joystick is *Amphisamytha galapagensis* (6%) versus *P. pandorae* (35%) at Mkr 113.

In 2000, the separation of vents into two main clusters persists (Figure 5.5), but the species characteristic of each cluster changes slightly. The first cluster again groups vents dominated by alvinellids: >60% of individuals from Bag City, Mkr N6 and Nascent are *Paralvinella pandorae,* but the second most abundant species at each of these vents is now *Lepetodrilus fucensis* (16%, 13% and 29% RA, respectively). The limpet ranks first for each vent of the second cluster (range of 47% to 78% RA). Subdivision of this second cluster into two groups is due to the second most abundant species at each vent:

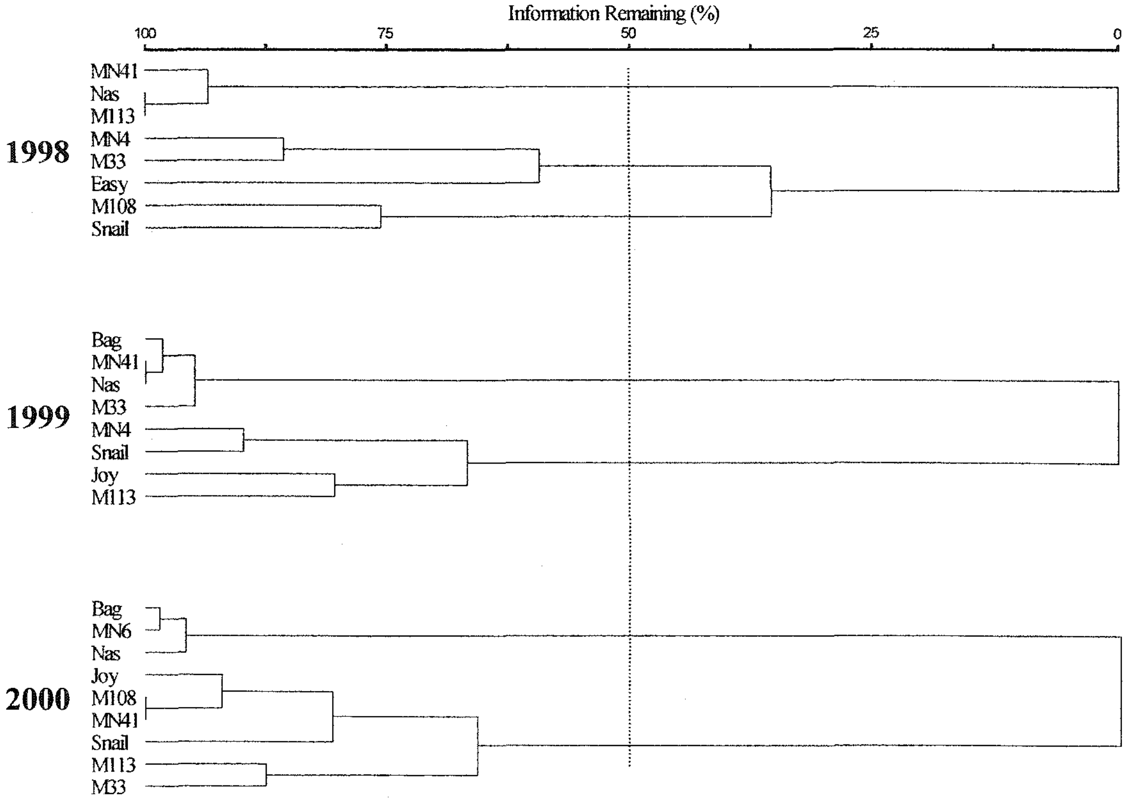
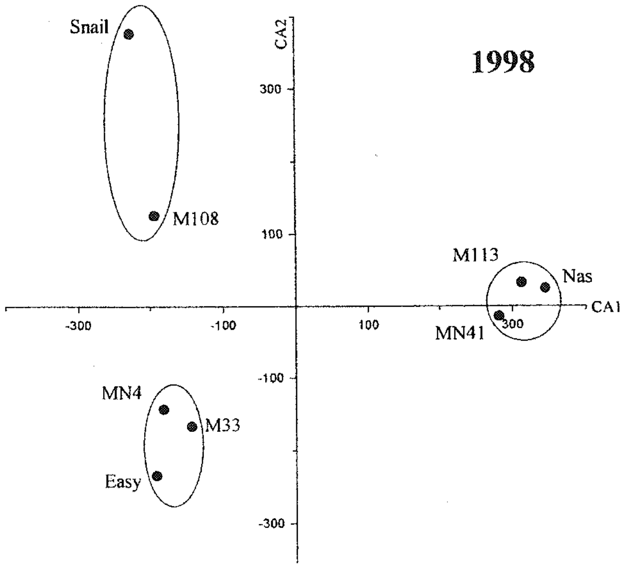
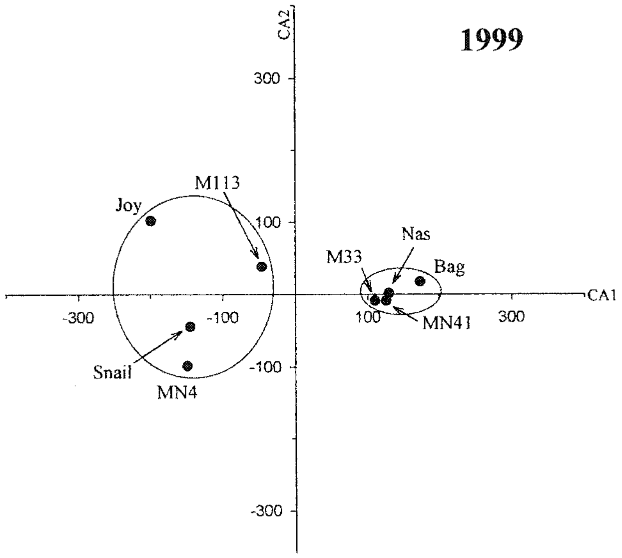
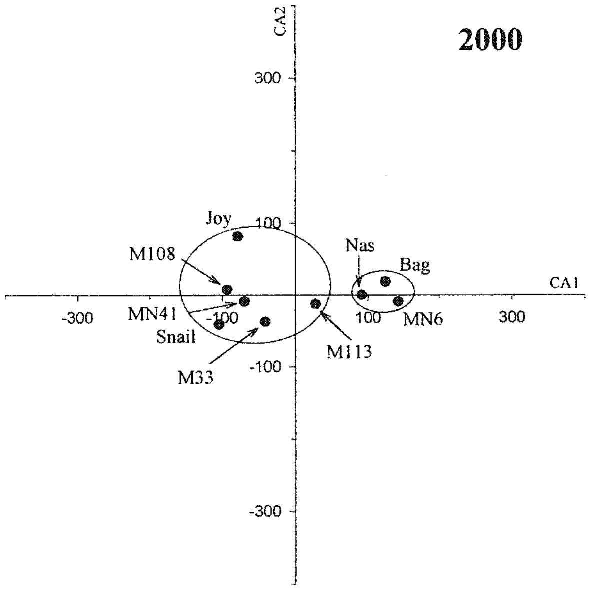


Figure 5.5. Cluster analysis of vents in 1998, 1999 and 2000 based on relative abundances of macrofauna (excluding *Ridgeia piscesae*). Three clusters fall out in 1998 and two clusters in both 1999 and 2000. See Table 5.1 for vent name abbreviations.

Figure 5.6. Correspondence analysis bipots (axes one and two) generated from macrofauna relative abundance data of all vents sampled in 1998, 1999 and 2000. Ovals depict the vent groups defined by the cluster analyses (Figure 5.5).


1998
CA2
CA1
300
100
-100
-300
-300
-100
100
300
Snail
M108
M113
Nas
MN41
MN4
M33
Easy


1999
CA2
CA1
300
100
-100
-300
-300
-100
100
300
Joy
M113
Snail
MN4
M33
Nas
Bag
MN41


2000
CA2
CA1
300
100
-100
-300
-300
-100
100
300
Joy
M108
MN41
Snail
M33
M113
Nas
Bag
MN6

Depressigyra globulus ranks second at Joystick, Mkr 108, Mkr N41 and Snail, while *P. pandorae* ranks second at Mkr 113 and Mkr 33. Correspondence analysis supports the main clusters depicted by the dendrograms (Figure 5.6).

Similarity analyses

Average pairwise similarity measures (Jaccard and Bray & Curtis) among vent assemblages increase with vent age and by 2.5 years are comparable to the same measures from mature vents (Table 5.8).

Nascent vents in 1998 support macrofaunal assemblages that are on average less similar to each other (Jaccard = 0.225, BC = 0.170) than vent assemblages 1.5 years old (Jaccard = 0.535, BC = 0.409) or 2.5 years old (Jaccard = 0.523, BC = 0.546). The average Jaccard index differs between 1998 and 1999 ($p<0.001$) and 1998 and 2000 ($p<0.001$), but not between 1999 and 2000 ($p=0.674$, Mann Whitney U Test). The average BC index is significantly different between all 3 years (1998-1999, $p=0.001$; 1998-2000, $p<0.001$; 1999 and 2000, $p=0.035$; Mann Whitney U Test).

The average pairwise similarity of vents based on species presence-absence data is comparable to mature vents at 1.5 years (0.534 versus 0.535, respectively; $p=0.989$), while the average pairwise similarity of vents based on species relative abundances reaches a similar value as mature vents (0.506) at 2.5 years (0.545) ($p=0.302$; Table 5.8). If only tubeworm grabs are used for year 3 vents, the average pairwise similarity (0.514) is even more similar to mature vents ($p=0.788$).

This pattern of decreasing among vent variability with increasing vent age is reflected in the correspondence analysis biplots of 1998-2000, as the vent groupings move closer together (Figure 5.6).

Assemblage variation among years: temporal patterns of individual vents

Cluster analyses of all new SRZ vents with mature vents

Presence-absence data - A cluster analysis of all new vents from 1998-2000 and two OLD SRZ vents, based on macrofauna presence/absence data, separates vents into two main clusters at the ~12.5% information remaining scale (Figure 5.7). The first cluster is very loose and contains seven of the eight vents from 1998. Shared low species

Table 5.8. The average pairwise similarity among vents increases with vent assemblage age. Both similarity indices use only macrofauna data (excluding *Ridgeia piscesae*); the Jaccard index is calculated from occurrence data and the Bray & Curtis index from species relative abundance data. There is at least one significant difference among years for both similarity indices (Kruskal-Wallis Test, $p<0.001$). Annual pairwise comparisons (Mann Whitney U Test) show the Jaccard index differs significantly between 1998 and 1999 ($p<0.001$), but not between 1999 and 2000 ($p=0.674$). Assemblages from 1999 and 2000 do not differ from mature vents ($p>0.05$ in both cases). The Bray & Curtis index differs significantly between 1998 and 1999 ($p=0.001$) and 1999 and 2000 ($p=0.035$), but there is no difference between 2000 vents and mature vents ($p=0.302$). If only tubeworm grabs from 2000 are analyzed (BC=0.514, SD=0.273), there is also no difference between year 3 vents and mature assemblages ($p=0.788$). SD = standard deviation.

	1998	1999	2000	Mature
Number of vents (n)	8	8	9	21
Number of pairs n*(n-1)/2	28	28	36	210
Jaccard				
Average	0.2254	0.5352	0.5232	0.5338
SD	0.1247	0.1028	0.0788	0.1292
Bray & Curtis				
Average	0.1703	0.4096	0.5458	0.5060
SD	0.2140	0.2906	0.2332	0.2240

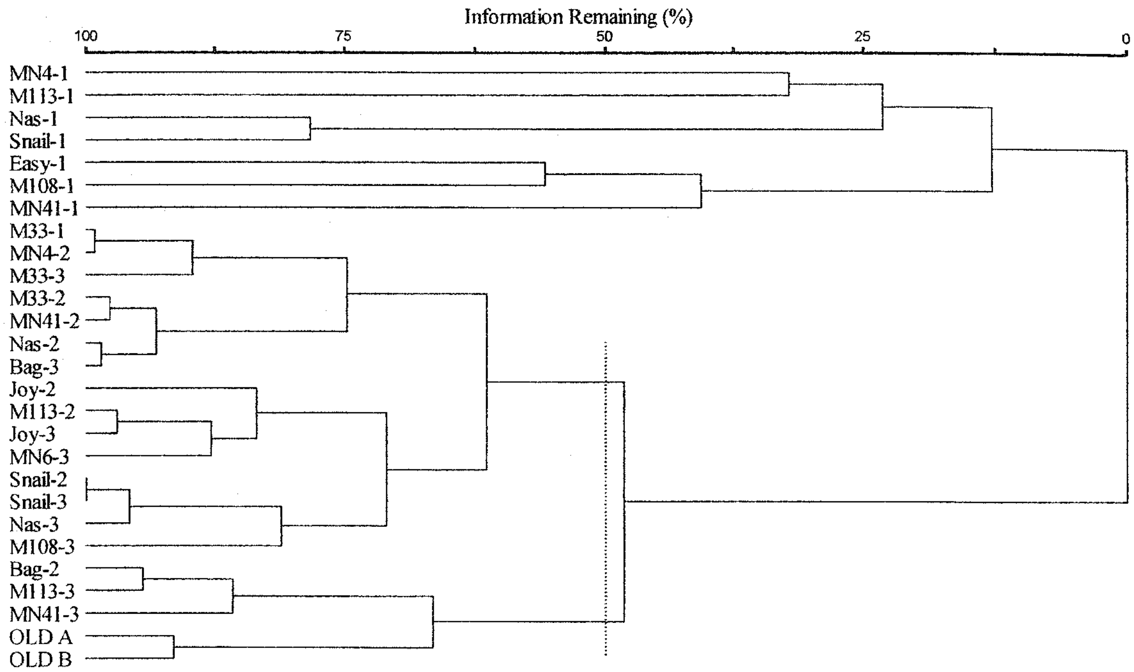


Figure 5.7. Cluster analysis based on macrofauna presence/absence data of all nascent South Rift Zone (SRZ) vents from 1998-2000. Two old vents on the SRZ beyond the lava flow are also included to represent mature vents. OLD A and OLD B refer to Oldworms and Old Flow, respectively. LargeTW vent (see Table 5.1) is not included since this tubeworm grab was not placed into the biobox for transport to the ship. Numbers 1, 2 and 3 refer to sampling years 1998, 1999 and 2000. See Table 5.1 for vent name abbreviations.

richness drives cluster membership rather than shared species identity: average species richness is 5.8 (range 4 to 8) versus an average species richness of 14.5 for the second cluster (range of 11 to 25). The second cluster includes all other samples and contains two subclusters at the 50% information remaining scale; the finer divisions suggest some effects of vent age and location. The first subcluster comprises vents from all three years and three vents appear to maintain a similar species composition with time (Joystick, Snail, Mkr 33). The second subcluster includes three vents from 1999 and 2000 and the two OLD vents. Two species typically rare at new vents, but present at all five of these vents, include the polychaete *Protomystides verenae* and the snail *Provanna variabilis* (both occur at only six of the other 22 vents). Also, the limpet *Pyropelta musaica* occurs at all old vents, but is only present at three of the new vents all years combined (n=25).

Relative abundance data – Using macrofaunal relative abundances all vents divide into four main clusters (Figure 5.8). The first cluster contains one vent (Easy in 1998) that is very different from all other assemblages: *Branchinotogluma* sp. accounts for 80% of total individuals. The second cluster fuses vents from 1998 and 1999 that are dominated by *Ophryotrocha globopalpata*. These assemblages are transitory and disappear by year 3, as vents subsequently die (Easy) or become dominated by either the pandora worm (e.g. Mkr 33) or the limpet (e.g. Mkr 113). The third cluster unites vents whose first or second most abundant species is *Lepetodrilus fucensis*. The limpet ranks first in all year 3 assemblages (51% to 78% RA), while it is the second most abundant species at Snail in 1998 and 1999 and Mkr 108 in 1998.

Paralvinella pandorae is the most abundant species in each assemblage of the fourth main cluster (RAs range from 53% to 99%), and membership includes vents sampled from all three years. The dominance of *P. pandorae* persists over time for some vents, but not for others. For example, Nascent vent is dominated by the pandorae worm all three years, despite strong recruitment of *Lepetodrilus fucensis* by 2000. In contrast, the pandora worm dominates Marker N41 in years 1 and 2, but the relative abundance of the limpet exceeds the pandora worm in year 3. Marker 113 also switches from a pandora-dominated vent in year 1 to a limpet-dominated vent by year 3. However, the opposite transition never occurs; for example, neither Snail nor Mkr 108 becomes dominated by alvinellid polychaetes over time (Figure 5.8).

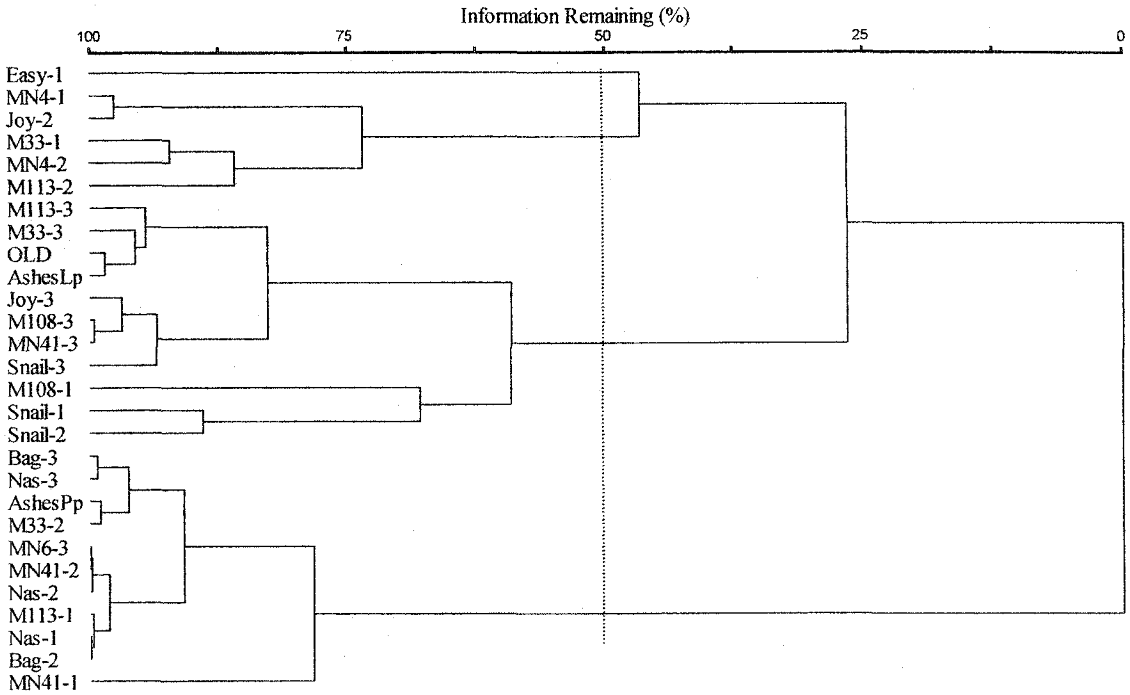


Figure 5.8. Cluster analysis of relative abundances of macrofauna (exluding *Ridgeia piscesae*) from all new South Rift Zone (SRZ) vents. Three compilations of 'mature' vents are included for reference: OLD refers to the average relative abundance of three SRZ vents unaffected by the lava flow (see Table 5.1), AshesLp refers to the average relative abundance of 11 ASHES vents dominated by *Lepetodrilus fucensis*, and AshesPp refers to four ASHES vents dominated by *Paralvinella pandorae*. See Appendix 5.1 for the cluster analysis of the ASHES fauna supporting division of the vents into these two groups. Numbers 1, 2 and 3 refer to sampling years 1998, 1999 and 2000. See Table 5.1 for vent name abbreviations.

The samples representing mature assemblages cluster with the expected SRZ vents: AshesPp groups with the 'pandora cluster' and OLD and AshesLP group within the 'limpet cluster'. No mature vents group with the transitory first or second clusters (Figure 5.8). Within the pandora cluster there is no obvious pattern associated with vent age: vents sampled in different years are most similar and year 1 vents do not group separately. However, the mature assemblage (AshesPp) does group most closely with vents from years 2 and 3 (Figure 5.8). In contrast, there is an obvious pattern of vent age within the limpet cluster: all year 3 vents form a tight cluster with the mature assemblages (OLD and AshesLp). The two vents initially colonized by gastropods (Snail-1 & -2 and M108-1) are most distantly associated with this mature cluster.

Does prior state influence future state?

Nineteen comparisons were made between the similarity of a given vent assemblage in 'time 1' (1998 or 1999) and 'time 2' (1999 or 2000), and the average similarity of that vent in time 1 to all other vents in time 2. Of these 19 comparisons, the Bray & Curtis (species relative abundances) similarity indices of 14 vent assemblages between time 1 and time 2 are higher than the average similarity between the given vent in time 1 and all other vents in time 2 (Table 5.9). However, species composition appears to be less influenced by historical states: only 11 of 19 comparisons yield Jaccard similarity indices higher between the same vent in two time periods than between that vent in time 1 and all others in time 2 (Table 5.9).

Of the five vents sampled in all three years (Mkr N41, Nascent, Mkr33, Snail and Mkr 113), only Snail shows evidence for historical influence in all paired year comparisons (1998-99, 1999-00, 1998-00) for both species identity and abundances (Table 5.9). With relative abundance data, no vent is more similar to Snail in 'time 1' than Snail in 'time 2'.

Separate analysis of tubeworm grabs and suction samples

Since tubeworms were either absent or low in numbers at some vents during the first two years post-eruption, it was necessary to combine data from two sampling methods for a more complete picture of the spatial and temporal variability of developing

Table 5.9. Vents sampled in more than one year are evaluated for effects of a 'prior state' on the structure and composition of the macrofaunal assemblage in successive years. 'Yes' indicates that the similarity index (Bray & Curtis for relative abundances, and Jaccard for occurrences) between the same vent sampled in two time periods (e.g. 1998 and 1999) is higher than the average index between that vent in the first time period (1998) and all others sampled in the later time period (1999). 'No' indicates the opposite. Bracketed numbers are the number of vents in the second time period that are more similar to the given vent in the first time period. For vents sampled in three consecutive years, 3 comparisons are made: 1998-1999, 1999-2000 and 1998-2000. One comparison is possible for vents sampled twice over the three years; blank cells indicate data are not available. Fourteen of the 19 comparisons for relative abundances are 'yes', and 11 of the 19 are 'yes' for presence/absence data.

Vent	Relative Abundance			Presence/Absence		
	1998-99	1999-00	1998-00	1998-99	1999-00	1998-00
Mkr N41	Yes (2)	No (5)	No (6)	No (5)	No (5)	No (6)
Nascent	Yes (1)	Yes (2)	Yes (2)	No (4)	Yes (2)	No (5)
Mkr 33	No (4)	No (4)	Yes (2)	Yes (5)	Yes (0)	Yes (0)
Cloud N4	Yes (2)			No (4)		
Snail	Yes (0)	Yes (0)	Yes (0)	Yes (1)	Yes (0)	Yes (4)
Mkr 108			Yes (1)			Yes (3)
Mkr 113	No (4)	Yes (2)	Yes (3)	No (6)	Yes (1)	Yes (0)
Joystick		Yes (0)			Yes (0)	
Bag City		Yes (1)			No (4)	

nascent assemblages. Although I believe this approach is justified given the realities of sampling, there are potential drawbacks. The methods may have different sampling biases and since tubeworm grabs recover the fauna living within a tubeworm bush, while suction samples recover animals from the lava substratum directly, the methods may sample different vent microhabitats.

Tubeworms may simply provide vent animals with additional substratum proximate to flow. However, the data presented here suggest that their three-dimensional bush structure influences community structure. For example, a tubeworm grab and a suction sample were taken from the same location at Marker N6 in 2000; the tubeworm grab recovered relatively more individuals of the pandora worm than limpets (88.8% versus 9.5% RA) while the suction sample recovered relatively more limpets than pandora worms (47.8% versus 11.5% RA). This pattern was observed for these two species at seven of nine vents where both tubeworm grabs and suction samples were taken (Table 5.10). The relative abundance of *Ophryotrocha globopalpata* is also influenced by sample type; it is more abundant in suction samples than grabs (Table 5.10).

Here I examine tubeworm grabs and suction samples separately to limit the possible confounding effects of sampling method. Analyses based on species relative abundance, density, relative biomass, and biomass (g) per cm^2 tubeworm tube surface area are presented for the tubeworm grabs. An analysis based on relative abundance is presented for suction samples.

Tubeworm grabs

Relative abundance - The pattern generated by a cluster analysis of tubeworm grabs using macrofauna relative abundances (Figure 5.9A) is similar to the pattern generated by a cluster analysis of all samples using combined data (Figure 5.8): vents are divided into clusters based on the relative dominance of *Lepetodrilus fucensis* (first cluster) or *Paralvinella pandorae* (second cluster). However, the 'transitory clusters' of Figure 5.8 are lost; likely because suction samples with high relative abundances of *Ophryotrocha globopalpata* are excluded (see Table 5.10). Also, two vents that group with the 'limpet cluster' in Figure 5.8 now cluster with vents dominated by *P. pandorae*

Table 5.10. Proportion of total macrofauna represented by the pandora worm *Paralvinella pandorae*, the common limpet *Lepetodrilus fucensis* and the dorvilleid polychaete *Ophryotrocha globopalpata* from vents where both a suction sample (SS) and a tubeworm grab (TWG) were used to collect animals. On average, 7.5x more *P. pandorae* are recovered from tubeworm grabs than suction samples and 1.7x times more *L. fucensis* and 17.3x more *O. globopalpata* are recovered from suction samples than tubeworm grabs.

Vent	*Paralvinella pandorae*		*Lepetodrilus fucensis*		*Ophyrotrocha globopalpata*	
	SS	TWG	SS	TWG	SS	TWG
Mkr 113 '99	0	71.3	2.2	23.8	78.6	0.5
Mkr 33 '99*	9.4	85.6	27.2	0.4	0	1.6
Nascent '99	12.9	91.9	51.3	6.9	27.0	0.2
Bag City '00	32.1	74.0	11.8	16.4	32.6	4.9
Joystick '00	4.2	2.3	57.1	85.1	10.7	1.5
Mkr 113 '00	0.3	58.2	83.7	34.3	0.02	0
Mkr 33 '00	1.6	69.3	64.4	14.6	0.2	0
Snail '00	0.8	3.2	62.1	52.6	0.1	0.1
Mkr N6 '00	11.5	88.8	47.8	9.5	6.5	0.3
Average	8.1	60.5	45.3	27.1	17.3	1.0

* suction sample values are the average of two samples.

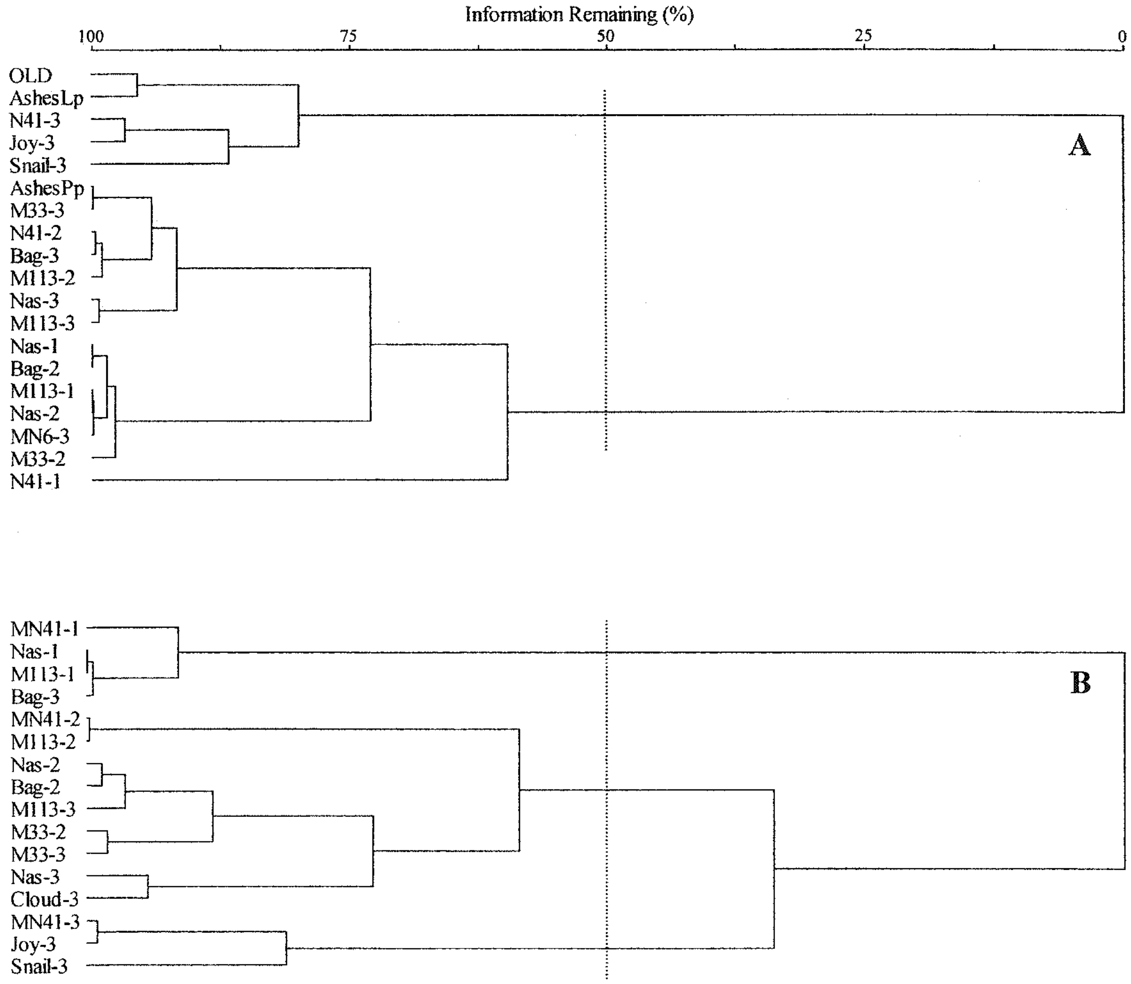


Figure 5.9. Cluster analysis of tubeworm grabs based on macrofauna relative abundance (A) and density (B). A. The first cluster unites vents with *Lepetodrilus fucensis* as the relatively most abundant species (range of 50% to 85%). The second cluster unites vents with *Paralvinella pandorae* as the relatively most abundant species (range of 53% to 99%). B. The first cluster unites vents with overall low densities (see Table 5.6). The second cluster unites vents with *P. pandorae* as the densest species, and the third cluster unites vents with *L. fucensis* as the densest species. Numbers 1, 2 and 3 refer to sampling years 1998, 1999 and 2000. See Table 5.1 for vent name abbreviations.

(Mkr 33-3 and Mkr 113-3, Figure 5.9A) since most limpets sampled from these vents in year 3 were from suction samples. Again, there is no obvious pattern of vent age within the pandora cluster, except that the vents that group most tightly with the mature sample (AshesPp) are not from 1998. All vents that group with the composite mature vents dominated by the limpet (OLD and AshesLP) are from year 3.

Density - Grouping vents with density data yields three main clusters (Figure 5.9B). The first cluster groups all the first year vents along with Bag City in 2000. Shared lower densities drive this cluster (see Table 5.6); Bag City individuals were very large in 2000. The second cluster unites vents with higher densities of *P. pandorae* relative to *L. fucensis*, while the third cluster unites vents with *L. fucensis* as the densest species (Figure 5.9B). Again, the obvious pattern with increasing vent age is the increase in limpet densities. Table 5.11 lists average densities of the most abundant species per year. Annual species densities generally parallel trends using total sample data and overall relative abundances (Figure 5.3) except *Ophyrotrocha globopalpata* shows no trend with year (Table 5.11).

Relative Biomass - Relative biomass data results in three main clusters (Figure 5.10A) rather than two main clusters when relative abundances are used (Figure 5.9A). Each cluster groups assemblages whose largest proportion of total biomass is *Paralvinella pandorae, P. palmiformis*, or *Lepetodrilus fucensis*. In general, these species dominate different-aged vents: *P. pandorae* dominates year 1 vents, *P. palmiformis* dominates year 2 vents, and *L. fucensis* dominates year 3 vents (Figure 5.11).

Two additional vents, Mkr 113 and Bag City, now group with the year 3 'limpet cluster' defined by abundance data (Figure 5.9). Although Mkr 113 and Bag City are numerically dominated by *P. pandorae* (58% and 74% RA) in year 3, this species contributes relatively little to total assemblage biomass (6% and 3%, respectively). In 2000, total biomass of Mkr 113 and Bag City is dominated by *Lepetodrilus fucensis* and *Paralvinella palmiformis* (species together = 87% and 84% total biomass, respectively).

Although the pandora worm remains numerically dominant in some aging assemblages, it rarely accounts for a large proportion of total macrofaunal biomass due to a shift to smaller body sizes over time (Table 5.12). Two vents, Bag City (1999) and Cloud N6 (2000) cluster with the year 1 vents (Figure 5.10A). Cloud N6 was observed in

Table 5.11. Average densities (number of individuals per cm^2 of tubeworm tube surface area) of the five most abundant species (ranks 1 to 3) from tubeworm grabs in any one year (see Figure 5.3). Standard deviation is shown in brackets. Due to high within year variability, there are no significant differences among the years for all species ($p>0.05$), except for *Paralvinella pandorae* ($p=0.008$, Kruskal-Wallis Test). *P. pandorae* densities are significantly higher in year 2.

Species	1998	1999	2000
Paralvinella pandorae	0.225 (0.012) n=3	3.381 (1.745) n=5	0.787 (0.707) n=8
Lepetodrilus fucensis	0.011 (0.011) n=2	0.598 (0.748) n=5	2.002 (2.641) n=8
Depressigyra globulus	0.001 n=1	0.044 (0.058) n=4	0.341 (0.511) n=8
Ophryotrocha globopalpata	0.026 n=1	0.015 (0.015) n=5	0.026 (0.042) n=6
Branchinotogluma sp.	0.008 (0.009) n=2	0.004 (0.005) n=3	0.004 (0.003) n=6

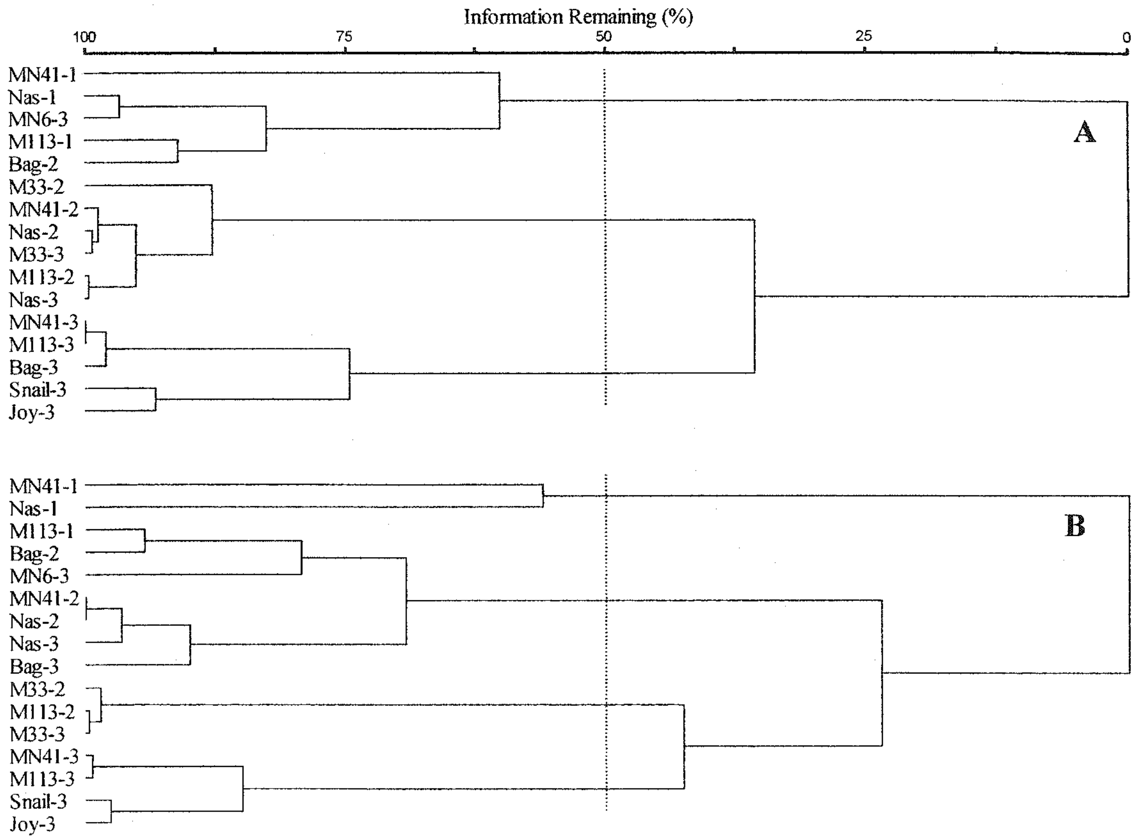


Figure 5.10. Cluster analysis of quantitative tubeworm grabs based on macrofauna relative biomass (A) and biomass (g) per cm^2 of tubeworm tube surface area (B). A. The first cluster unites vents with *Paralvinella pandorae* contributing most to total assemblage biomass (range of 46% to 76%). The exception is MN41-1, where the scale worm *Branchinotogluma* sp. accounts for 60% of total biomass, and *P. pandorae* only 26%. The second cluster unites vents with *Paralvinella palmiformis* contributing most to total assemblage biomass (range of 58% to 98%) and either *P. pandorae* or *Leptodrilus fucensis* as the second ranking species. The third cluster unites vents where *L. fucensis* dominates total biomass (range of 41%-89%), and either *P. palmiformis* or *Depressigyra globulus* ranks second. B. Four clusters fall out using standardized biomass to cluster vents. See text for a fuller description. Numbers 1, 2 and 3 refer to sampling years 1998, 1999 and 2000. See Table 5.1 for vent name abbreviations.

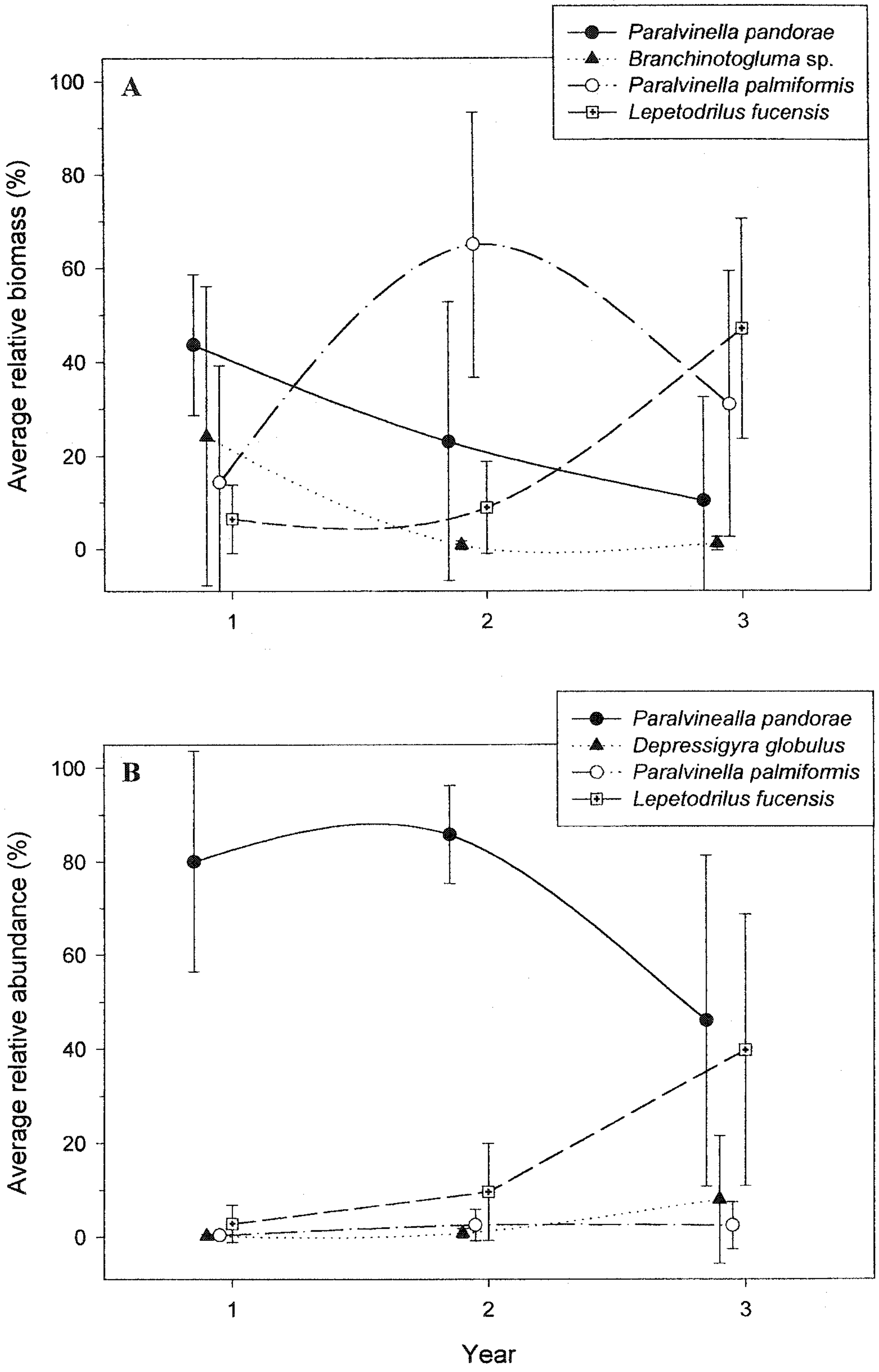


Figure 5.11. Average relative biomass (A) and average relative abundance (B) of the top ranking species (ranks 1 to 3) from South Rift Zone vents sampled by tubeworm grabs in 1998 (n=3), 1999 (n=5) and 2000 (n=8). Error bars represent one standard deviation. Note that one species differs between the graphs.

Table 5.12. Percent relative abundance (RA) and percent relative biomass (RB) of *Paralvinella pandorae* from three vents sampled by tubeworm grabs from 1998-2000. *P. pandorae* individuals decrease in size with vent age. On average, in year 1 assemblages *P. pandorae* accounts for 80% of total individuals and 44% of total biomass (n=3 vents below). One year later, the average relative abundance of *P. pandoare* is comparable (81%), but average relative biomass decreases to 12.5%.

Vent	Year	RA	RB	Ratio (RA:RB)
Mkr N41	1	53.1	27.5	1.9
	2	80.5	18.3	4.4
	3	9.3	0.5	18.6
Nascent	1	96.9	57.3	1.7
	2	91.9	12.5	7.3
	3	63.5	1.9	33.4
Mkr 113	1	90.2	46.3	1.9
	2	71.9	6.7	10.7
	3	58.0	6.4	9.1

1998 and 1999, and although tubeworms were present at N6 in 1999, they were sparsely distributed; a typical bush-like aggregation was first occured at Cloud N6 in 2000 (pers. obs.). Bag City was not visited in 1998, but its community in 1999 was typical of a new tubeworm bush assemblage.

There is a definite trend with age when relative biomass is used to analyse vent assemblage similarity: the same vent sampled in successive years is never found together in either the first ('pandora-dominated') or the third ('limpet-dominated') cluster. The pandora-dominated cluster disappears with age from time of tubeworm bush formation; all year 1 vents (Nascent, Mkr N41 and Mkr 113) and Bag City (year 2) are dominated by *Paralvinella palmiformis* and *Lepetodrilus fucensis* in the two subsequent years (Figure 5.10A).

Biomass per cm^2 of tubeworm tube surface area – Grouping vents using biomass standardized to area yields four main clusters (Figure 5.10B). The first cluster combines two year 1 vents with low standardized biomass relative to other assemblages (see Table 5.7). The second cluster unites vents from all three years with similar biomass values (0.01 g/cm^2 to 0.03 g/cm^2, Table 5.7) where either *Paralvinella pandorae* or *P. palmiformis* ranks first. The third cluster unites three vents from years 2 and 3 with relatively high overall biomass per unit area (0.07 g/cm^2 to 0.12 g/cm^2, Table 5.7) with *P. palmiformis* ranking first. The fourth cluster unites four vents all from year 3 with relatively moderate to high overall biomass values per unit area (0.03 to 0.10 g/cm^2, Table 5.7) and with *L. fucensis* as the top ranking species. Again, the temporal trend is clear: biomass increases with time and the palm worm and/or the limpet dominate overall biomass of all year 3 assemblages.

Suction Samples

Four main clusters fall out when only suction samples are used to group vent assemblages (Figure 5.12). The first and third clusters consist of single vents from year 1 that are dominated by a scale worm species: Easy vent by *Branchinotogluma* sp. and Mkr 108 by *Vampiropolynoe embleyi*. The second cluster unites five vents from all 3 years with *Ophryotrocha globopalpata* as the top ranking species (RAs range from 33% to 78%). The fourth cluster unites vents that are dominated by either *Lepetodrilus fucensis*

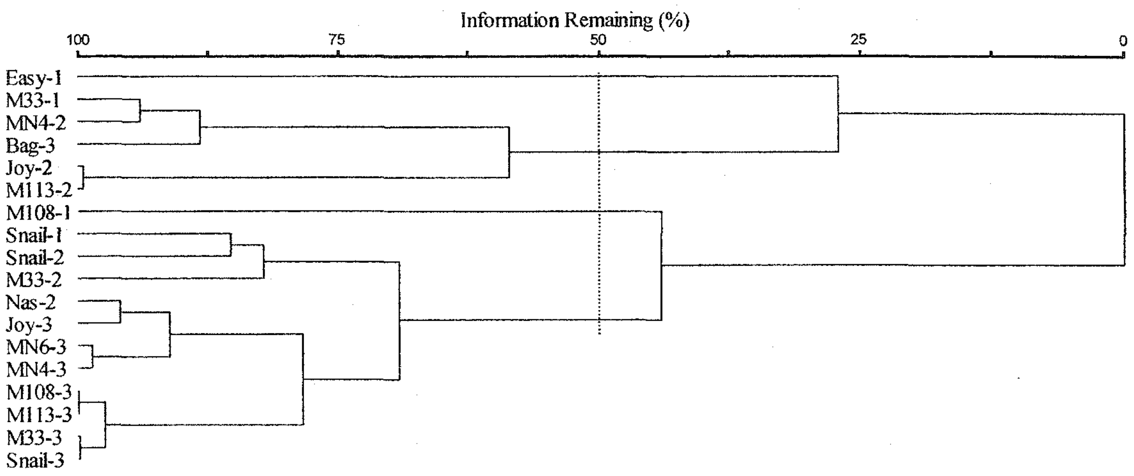


Figure 5.12. Cluster analysis of vents from all three years (1998-2000) using relative macrofaunal abundances from suction samples. Numbers 1, 2 and 3 refer to sampling years 1998, 1999 and 2000. See Table 5.1 for vent name abbreviations.

or the common snail, *Depressigyra globulus*. Subdivision of this cluster separates three vents that are equally dominated by limpets and snails (Snail-1, -2 and Mkr 33-2) from the remaining eight vents primarily dominated by the limpet (51% to 84% RA) (Figure 5.12). As with tubeworm bush assemblages, there is a strong indication that lava assemblages change with vent age: four of the five *O. globopalpata* dominated vents are from 1998 or 1999, and ten of the 11 gastropod dominated vents are from 1999 or 2000.

Discussion

Comparison to mature communities: assumptions

Axial's mature communities offer a unique backdrop for speculating on the mechanisms that control the colonization and accumulation of species at new vents and for interpreting the development of post-eruption vent assemblages. I use community data from prior Axial studies to (1) characterize the species pool (Chapter 4), and (2) characterize mature vent community structure. Mature vent collections are tubeworm grabs and community structure is defined by species relative abundances.

I compare the eruption data, which comprises mixed sampling methods, directly to the mature collections, and use the average relative abundances of species from multiple samples to create a few characteristic mature assemblages. I believe the first comparison is justified since the absence of tubeworm clumps from most vents in 1998, and almost half the vents in 1999, precluded the use of grabs for sampling. Culling the eruption data to include only tubeworm grabs would exclude informative data, such as high variability among early assemblages. My second use of mature samples was due to a practical concern of making cluster analyses interpretable (e.g. not including all 21 mature samples) and presumes that diffuse flow communities at Axial have two deterministic endpoints (or stages) of development. The ubiquitous dominance of diffuse flow vents by the limpet *Lepetodrilus fucensis* on the JdFR (Tsurumi 2001, Tsurumi & Tunnicliffe 2001), and the local shared dominance by the limpet and *Paralvinella pandorae* at Axial (this chapter), suggests that mature Axial communities may be predictably structured.

Processes that keep communities in other systems from reaching inevitable endpoints may be absent at JdFR diffuse vents. For example, frequent perturbations or predation of competitive dominants maintains some rocky intertidal assemblages in a state of non-equilibrium (Sousa 1979, Menge et al. 1994). Since the limpet and/or pandora worm numerically dominates diffuse Axial vents in less than a few years, disturbance regimes would have to be very frequent (months to two years) to disrupt this pattern. Although the frequencies of small-scale, within field disturbances are unknown and difficult to measure, the eruption frequency at any one location is estimated to be on the order of 50-150 years (B. Chadwick pers. comm.). A recent study at EPR diffuse vents also shows that densities of *Lepetodrilus elevatus*, a congener of *L. fucensis*, are significantly lowered by predation by a vent endemic fish (Micheli et al. 2002). Lack of a comparable predator at northeast Pacific vents could contribute to *L. fucensis* success.

Under ideal circumstances the ages and histories of these mature assemblages would be known. Since this information is unavailable, I believe my use of these samples to characterize typical mature, low temperature tubeworm aggregations is viable, and adds to our understanding of how vent communities develop in time.

Species colonization and extinction

During the first few years post-eruption, nascent Axial vents were colonized at a much faster rate than new vents at 9°N, EPR and CoAxial, JdFR (Figure 5.13). Annual colonization rates for CoAxial and 9°N may also be artificially high: the putative CoAxial source (Tunnicliffe et al. 1997) likely underestimates the true species pool (Tsurumi 2001), and the species pool at 9°N was determined by photographs and sparse sampling over the course of the eruption study (Shank et al. 1998).

Apparent differences in colonization rates between these three eruptions may be due to sampling, source proximity and site variability. First, only large fauna were documented in 9°N video and data at CoAxial derived from two tubeworm grabs each year (Table 5.13), while my study uses multiple grabs and suctions. Second, scattered tubeworm assemblages survived just meters beyond the flow at Axial, and established vent fields lay only a few kilometres away, while the nearest active hydrothermal site to CoAxial was >15 km distant. However, established vents survived just beyond the edges of the lava flow at 9°N, so sampling likely explains the lower colonization rate there rather than source proximity. Third, larger habitat differences among the 1998 Axial

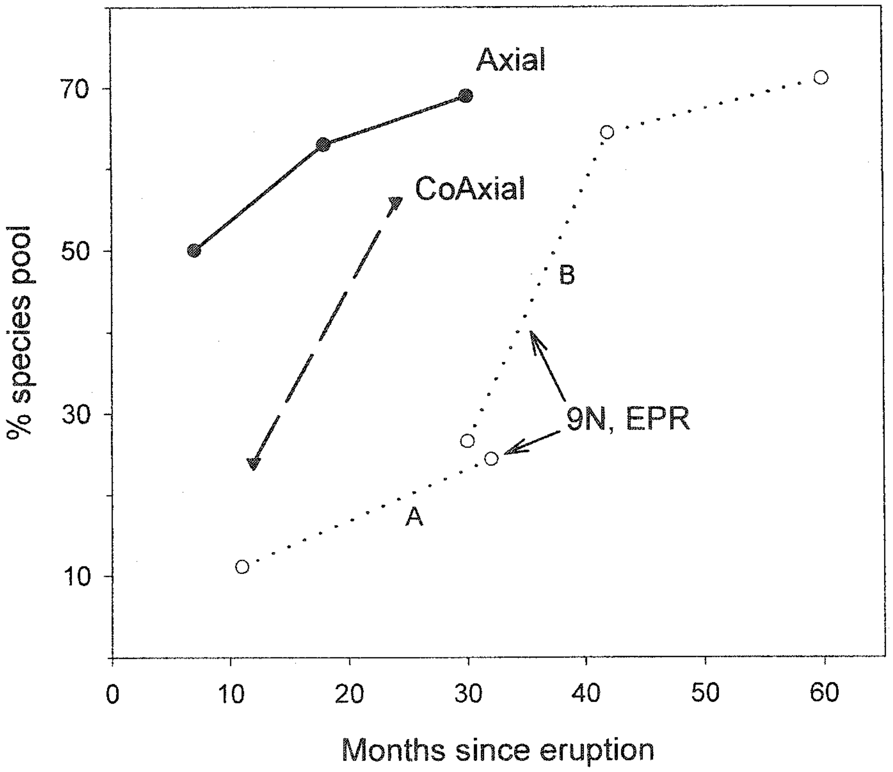


Figure 5.13. Percentage of the regional species pool present at nascent vents over time following three ridge crest eruptions. Shank et al. (1998) present two estimates of annual colonization rates at 9°N, EPR. One estimate is based on species identified from photographs of diffuse flow vents (A) and the other is from photographs and sampling of all vents within the vicinity of the eruption (B).

Table 5.13. Summary of the two eruptions studied to date for nascent vent community development. Continued on next page.

	9°N, EPR	CoAxial Segment, JdFR
Eruption	April 1991 Studied for 5 years (Shank et al. 1998)	June 1993 Studied for 2 years (Tunnicliffe et al. 1997)
Study Site	area of active venting prior to eruption: • lava flow overrode areas of established venting, some vents survived beyond flow	inactive area prior to eruption: • larvae recruited from a distal source >15 km away
Sampling Technique	photography, video • 1.7 km transect with markers for vent locations (11 vents sampled) • observations at ~2 weeks, 11 months, 2.5 years, 3.5 years and 5 years post-eruption	biological collections and video observations • year one: 2 vents sampled • year two: 2 vents near locations of year one sampled and more new vents discovered
Habitat data	fluid chemistry and temperature of a few vents: • no fluid data at 11 months, 3 and 5 vents sampled for fluid at 32 and 55 months, respectively	fluid chemistry and temperature of some vents: • 2 weeks, 3, 12, 24 months • not coupled with all collections
Main Conclusions	1. Thick microbial growth at new vents ~2 weeks, very high levels of hydrogen sulfide and iron 2. Motile vent and non-vent animals immediately present at new vents (presumably grazing on food source) 3. Sessile vent animals arrived by 11 months, tubeworm recruitment coincided with a decrease in hydrogen sulfide levels 4. Sequential pattern of dominant megafauna establishment (below)	1. Immediate prolific microbial growth at new vents (no vent animals) 2. No visible fauna after 3 months, temperatures decreasing 3. Recruitment from a distal source is rapid, tubeworms arrive after ~7 months; hydrogen sulfide levels increase 4. Similar initial colonization pattern for all vents observed (see below)

Table 5.13 continued

	9°N, EPR	CoAxial Segment, JdFR
Succession Model?	Yes • year one: establishment of one tube worm species (*Tevnia jerichonana*), 5 species total • year two: dominance by a second tube worm species (*Riftia pachyptila*), 12 species* • years 3-5: establishment and dominance by mussels (*Bathymodiolus thermophilis*), 29 species at 3.5 years, 32 species at 4.5 years* Process - hypothesis: • sequence ascribed to the differential ability of species to tolerate fluid characteristics * estimates based on all video, photographs and samples from entire eruption region (e.g. not limited to the eleven targeted vents)	No, description of initial colonization • year one: dominance by tube worms (*Ridgeia piscesae*), pandora worms (*Paralvinella pandorae*) and a new species of nemertean, total of 8 species sampled at all vents • year two: many new colonists, 21 species total Process - suggestions: • Colonization appears correlated with post-eruption peak in hydrogen sulfide levels and abundant microbial food source • Tube worms are considered a 'key' colonizer species: they provide substratum or food that other species seek • Initial colonizers likely represent a subset of the vent fauna adept at rapid recruitment
Limitations	• only ~25% of total species could be identified by video (11 of 45), thus succession story limited to megafauna • unclear if all vents had the same sequence of change, did not discuss differences between vents • fluid data coupled with <1/4 of the biological observations	• limited sampling • short-lived system: started to senesce after 2 years so limited to initial colonization • fluid samples not coupled with all biological collections

vents may have caused higher variability among the 1998 assemblages thereby increasing the overall initial colonization rate. Conversely, all vents at CoAxial were dominated by *Ridgeia piscesae* at one year post-eruption.

Trends in Species Colonization

Axial species differed in their colonization rates of nascent vents. Some species arrived by seven months, some by 18 months and some by 30 months post-eruption. By the last year of this study, 30% of Axial's species pool remained absent from the new lava flow vents.

The null model results suggest that colonization rates of macrofaunal species are explained in part by their relative abundances in mature assemblages. In general, abundant species were more likely to be present at nascent vents than less abundant species for each of the three years. Sheldon & Meffe (1995) observed a similar pattern for fishes recolonizing experimentally defaunated pools: abundant species colonized early and rarer species arrived later. However, there were also exceptions to this trend: some species rare in mature assemblages colonized early and some abundant species colonized late (Table 5.4).

To examine if distribution also relates to species-specific colonization rates, I plotted the distribution-abundance relationship for mature Axial assemblages. Macrofaunal species display a strong relationship between log abundance and occupancy (R^2=0.866, Figure 5.14). Nine species from mature vents never colonized by year 3. Most of these are numerically rare and eight fall on or below the distribution-abundance regression line, suggesting that abundance may be more important for colonization success than distribution (Figure 5.14). This interpretation is speculative though since six of these eight species had very low abundances, which directly affects distribution.

Besides rarity, other possible reasons for unsuccessful colonization of new vents include non-vent endemicity and preference for specific microhabitats. For example, *Idasola* cf. *washingtonia* and *Harmothoe* unk. sp. are not vent obligates, and anemones tend to occur on vent peripheries (see Table 5.4). Interestingly, two of the three relatively common species that never reached the lava flow have the largest deviations from the distribution-abundance regression line: *Paralvinella dela* occupies a smaller number of

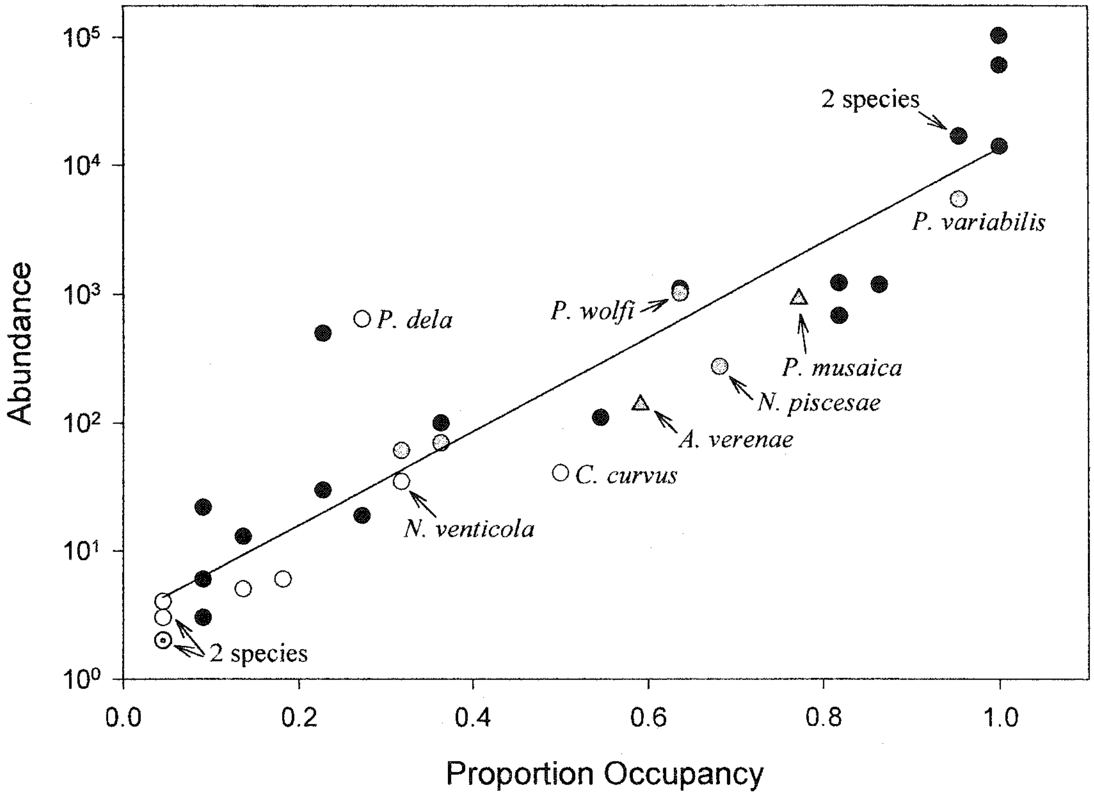


Figure 5.14. There is a positive relationship between log total abundance and proportion of sites occupied for the 21 mature vents from Axial ($R^2 = 0.866$). Each symbol is a species (35 species excluding *Ridgeia piscesae*); symbol type indicates year of arrival at the new vents. Only species referred to in the text are labeled. White circles are those nine species from mature vents that did not recruit to nascent vents over the course of this study (1998-2000). Solid black circles are species sampled in 1998, grey circles are species sampled in 1999, and triangles are species sampled in 2000. I indicate if a symbol represents two species; the dotted circle indicates one species was present (arrived in 1999) and one species was absent from the new vents.

vents than expected for its abundance and *Clypeosectus curvus* has very low abundance compared to its occupancy (Figure 5.14). *P. dela* may have very specialized habitat needs, while *C. curvus* may live preferentially in other vent microhabitats (*C. curvus* is commonly found on dead sulphide spires, V. Tunnicliffe pers. comm.). The other common species, *Nicomache venticola*, is an exception: all other species with similar abundance and distribution in mature assemblages had colonized by 2000 (Figure 5.14). Both *P. dela* and *N. venticola* have notable patchy distributions at the ridge scale (V. Tunnicliffe, pers. comm.).

Some species had delayed recruitment to nascent vents relative to other species with similar distributions and abundances. Despite their relative commonness, the provannid snail, *Provanna variabilis*, and the polychaetes *Parougia wolfi* and *Nereis piscesae* did not reach the lava flow until 1999, and the limpet *Pyropelta musaica* and the pycnogonid *Ammothea verenae* were first sampled in 2000 (Figure 5.14). These species may have life history characteristics that delay recruitment (e.g. pulsed gametogenesis, direct development) or perhaps the vents habitats were not appropriate for colonization until later in time.

Conversely, some macrofaunal species colonized quickly despite their rarity. Six of the seven rare species from mature communities (rare defined here as: <30% occupancy and <100 individuals) that occurred at the nascent vents over the course of the study recruited by seven months post-eruption (Figure 5.14). Since rare species are more prone to local extinction than more abundant species (Hanski 1999, Johnson 1998), adaptations for rapid recruitment to new habitat may help maintain their populations.

Meiofauna from mature communities have a much weaker relationship between distribution and abundance than macrofauna (R^2=0.181, Figure 5.15), and the null model results suggest that successful recruitment to nascent vents is not strongly influenced by relative species abundance in established assemblages.

Abundance and distribution at mature vents may not be correlated to meiofaunal recruitment due to sampling effects and life history constraints. Mature collections are tubeworm grabs, and less than one third of the samples were sorted for meiofauna. An inaccurate estimation of the meiofaunal species pool may have resulted from a combination of sample type - since the majority of meiofaunal individuals reported here

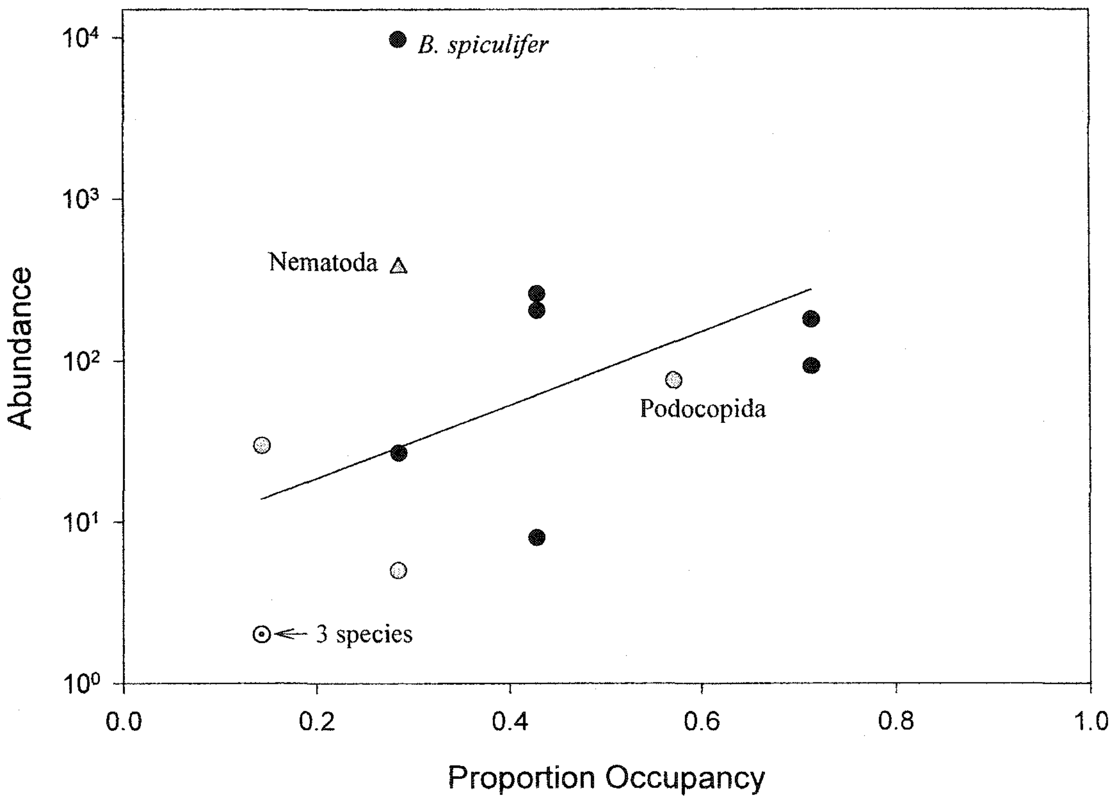


Figure 5.15. There is a weak, positive relationship between log total abundance and proportion of sites occupied for meiofaunal from the seven mature vents from Axial (R^2=0.181). Each symbol is a species (14 total); symbol type indicates year of arrival at the new vents. Only species referred to specifically in the text are labeled. Solid black circles are species sampled in 1998, grey circles are species sampled in 1999, and triangles are species sampled in 2000. One symbol represents three species; here, the dotted circle indicates 2 species present in 1999 and 1 species absent from nascent vents.

come from suction samples (~70%) - and limited data. The prevalence of copepods that are likely not vent endemics (e.g. calanoids and harpacticoids, Tsurumi et al. in review) also suggests that their relative dominance in mature samples is an inaccurate estimate of their propagule availability. Adaptations to nascent vent conditions may also be more important for meiofauna than larval supply for determining colonization success; Berg & van Dover (1987) propose that localized vent conditions may sponsor monospecific assemblages of copepods. Available data are too limited to reasonably speculate on the causes of meiofaunal recruitment to nascent vents.

Four macrofaunal species collected from nascent vents, that are unknown from mature communities, may be adapted to post-eruption conditions. The scale worm *Vampiropolynoe embleyi* is a conspicuous, bright red worm. It was present at new vents following both CoAxial and Axial eruptions on the JdFR, and is unknown from other locales (Marcus & Hourdez 2002). The polychaete *Orbiniella* unk. sp. and the snail *Hyalogyrina globularis* may also be vent pioneers, but both were absent from new vents at CoAxial, and their small size and low numbers increases their probability of being missed in mature collections. In contrast, the large nemertean *Thermonemertes valens* was observed after the CoAxial and Cleft Segment eruptions on the JdFR (Tunnicliffe et al. 1997, Tsurumi & Tunnicliffe 2001) and was collected at nascent SRZ vents in 1999 and 2000. The nemertean has not been recorded from mature Axial vents, but its presence in one senescent sample on the SRZ suggests it may respond to general eruption location rather than specific nascent vents.

Where would such pioneer species live between eruptions? The current estimate is that earthquakes causing intrusive dike injections or extrusive seafloor eruptions occur about every 2-3 years somewhere on the JdFR (B. Chadwick pers. comm.). These species may have larvae that can survive an unusually long time in the water column, or perhaps adults can survive at other reducing habitats such as seeps or whale falls. Over the timescale of this study (up to 2.5 years) none of these species went extinct, although *Vampiropolynoe embleyi* did become increasingly rare with time (Marcus & Hourdez 2002); *V. embleyi* abundance may be a viable indicator of approximate vent age.

Trends in Extinction

Annual extinctions were low for all the nascent vents combined. There were no macrofaunal extinctions between 1999 and 2000, and only two between 1998 and 1999. Thus, if a macrofaunal species successfully recruited to the new lava flow vents, it persisted. Meiofaunal extinctions were slightly higher: two species went extinct between both time intervals (1998-1999 and 1999-2000). Two of these species, *Benthoxynus spiculifer* and Copepoda Type 2, were recorded from year 1 vents but not in the subsequent two years. Lack of *B. spiculifer* persistence was unexpected as it numerically dominates mature vents (Tsurumi et al. in press). However, I note that *B. spiculifer* is only present in two of the seven fully sorted mature assemblages (Figure 5.15). Its low distribution (for its abundance) suggests that recruitment failure may be due to specific habitat needs or tolerances.

Although species extinctions were low overall, extinctions at specific vents were higher. For example, 26 macrofaunal extinctions occurred at the six sites sampled in all 3 years (average of 1.5 extinctions per vent from 1998-1999, and 2.8 per vent from 1999-2000, Table 5.14). Of the 28 species present at these six vents sometime over the 3 years, 12 never went extinct locally; all 12 were from the top 14 most abundant species in mature assemblages. Examples of species prone to local, but not regional extinction (i.e. did not go annually extinct at these six vents) include *Hesiospina vestimentifera* and *Amphiduropsis axialensis* (went extinct at three sites), and *Parougia wolfi* and *Vampiropolynoe embleyi* (went extinct at two sites). At the short time scale of this study, two mechanisms maintain overall populations of species with local extinction: (1) a portion of the occupied sites from the prior year go extinct (extinction without colonization), or (2) new sites are (re)colonized. *H. vestimentifera* and *P. wolfi* fall into the first category, while populations of *A. axialensis* and *V. embleyi* are maintained by colonization of new sites each year. Those species that fall into category two may be acting as metapopulations (Hanski 1999): they disappear at specific vents, but persist at the scale of the lava flow by colonizing new sites. Any species prone to local extinction will eventually go extinct at a larger spatial scale unless new sites are colonized.

Colonization/extinction data must be interpreted cautiously, since sampling intensity differed between sites and years, and sampling method may affect species

Table 5.14. Number of macrofaunal extinctions between 1998-1999 and 1999-2000 from the six vents sampled in all three years. Recolonizations (species present in 1998, absent in 1999, present again in 2000) are also listed. The average number of total extinction events for the two time periods is 4.3.

Vent	1998-1999	1999-2000	Recolonizations
Mkr N41	4	3	2
Nascent	0	2	0
Cloud (N4)	2	3	0
Mkr 33	2	2	1
Snail	1	1	0
Mkr 113	0	6	0
Total	9	17	3

composition. I cannot address the problem of sampling intensity, but the trend is still evident when I examine tubeworm grabs and suction samples separately. Combining all tubeworm grabs there were five extinctions overall, but three-fold more (17 extinction events) at individual vents sampled by grabs. Similarly, there were four extinctions combining all suction samples, but 21 extinctions at individual vents. Although cautious interpretation is warranted, the data suggest that extinction rates are locally high for some species, although they can persist at a larger spatial scale in a mosaic of sites. Only those species with patchy distributions and low to moderate abundance levels fall into this category, and are likely to persist as metapopulations.

Annual trends in species dominance

Annual patterns in species dominance and patterns of assemblage similarity were resolved by sampling multiple vents of the same age for three consecutive years. Low similarity among nascent Axial assemblages in 1998 was not predicted from prior studies. Eleven months following the 9°N eruption, the tubeworm *Tevnia jerichonana* and individuals of the *Lepetodrilus* genus dominated all observed vents (Shank et al. 1998). One year after the CoAxial eruption all vents were dominated by the tubeworm *Ridgeia piscesae* and the alvinellid *Paralvinella pandorae* (Tunnicliffe et al. 1997). In contrast, at seven months post-eruption at Axial, observed vents were dominated by one of three species or species groups and assemblages separated by as little as five meters were markedly different. Nonetheless, temporal replacements in macrofaunal species were apparent. Dominance of overall relative abundance shifted from *P. pandorae* in 1998 and 1999 to the common limpet *Lepetorilus fucensis* in 2000, and overall relative biomass shifted from dominance by *P. pandorae* in 1998, to *P. palmiformis* in 1999 and *L. fucensis* in 2000.

Factors driving patterns of species dominance during community successions can be conceptualized as a hierarchy of causes (Pickett & McDonnell 1989). Specific mechanisms fall under three general categories: site availability, species availability and species performance (Figure 5.16). In the following paragraphs, I consider which mechanisms most likely drive the general faunal shifts at Axial and evaluate current hypotheses of vent community succession. Ultimately, experiments are required to

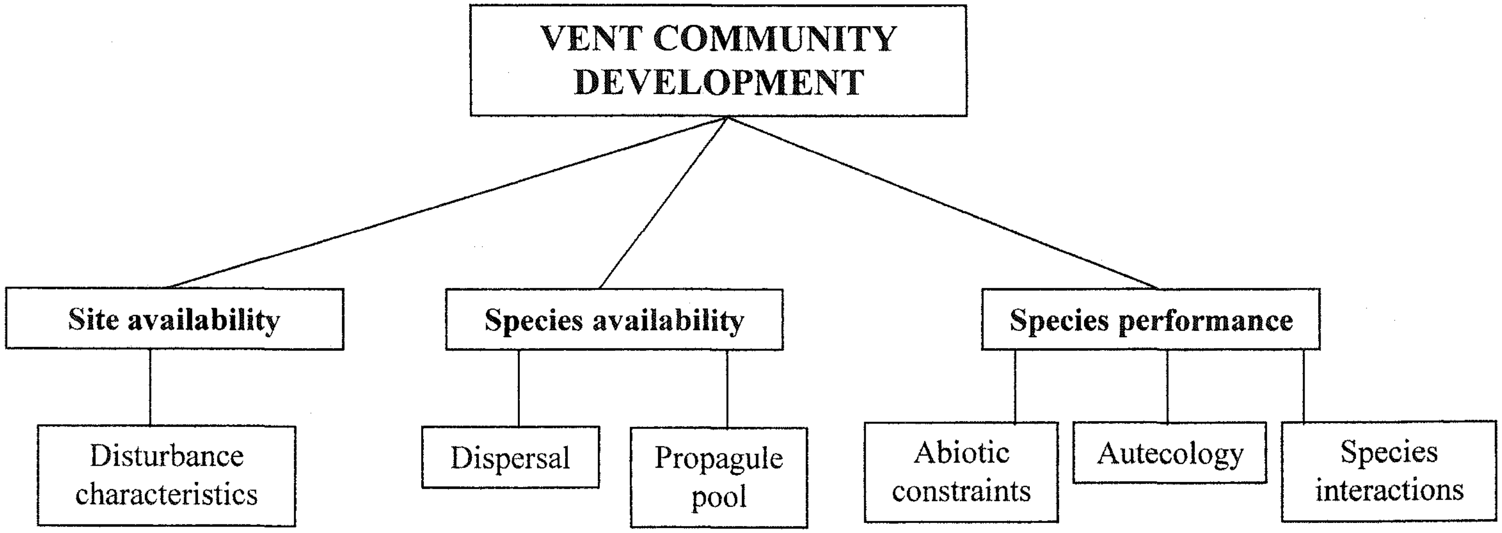


Figure 5.16. Hierarchy of causes of post-eruption vent community development. Disturbance characteristics include eruption size, number of vents created and vent dispersion. Factors affecting dispersal and propagule pool composition may cause differential species availability (larval supply). Differential species performance results from a combination of abiotic constraints, autecology and species interactions. Environmental constraints include resource availability and habitat characteristics such as fluid properties. Autecology refers to a species life history characteristics and physiological limitations. Species interactions include inter- and intraspecific interactions such as competition, predation and facilitation. Adapted from Pickett and McDonnell (1989).

substantiate proposed hypotheses.

Species-specific tolerances to changing fluid conditions may drive repeatable patterns of species replacements at 9°N, EPR. Shank et al. (1998) invoke an initial post-eruption peak in temperature and hydrogen sulphide concentrations, followed by a monotonic decline in both fluid properties, to explain faunal shifts. However, fluid measurements at 9°N were coupled with less than a quarter of the biological observations (Table 5.13). The hypothesis of Shank et al. thus relies on limited data and assumes that among vent variability in fluid properties of same-aged vents is insignificant. Available data suggest this assumption is unfounded since vent fluids separated by mere meters vary substantially (e.g. Johnson et al. 1988, Butterfield 1990, Butterfield et al. submitted). I propose that abiotic controls, interspecific interactions and chance dispersal events likely explain observed patterns of community development at Axial.

The initial stages of the fluid evolution model proposed by Butterfield in 1997 (Figure 5.17) and observed by Shank et al. (1998) also occurred at Axial (Butterfield et al. submitted). However, high variation among fluids of same-aged SRZ vents was also observed, suggesting that the hypothesis of Shank et al. (1998) is too simplistic to explain the faunal patterns described here. If annual variation is incorporated into the model of Butterfield, a general temporal trend in species patterns may still emerge if the majority of vents have fluid characteristics pertinent to the fauna that change in a similar way with time. For example, hydrogen sulphide content decreased in all sampled fluids over time, despite a four-fold range in values among 1998 vents (see Chapter 6). Eruption size may also be a factor, since the probability of vent-to-vent variation in fluid properties and other habitat characteristics likely increases with the number of vents created.

Thus, habitat variation superimposed on the general model of post-eruption fluid evolution may explain annual temporal shifts as well as within year assemblage variation. Limited recruitment of the limpet *Lepetodrilus fucensis* in 1998 may reflect non-optimal habitat conditions at most sites. Unfortunately, fluid data were not recovered from both year 1 vents with unusually high numbers of gastropods, but the available data suggest that temperatures were lower at these two sites compared to others (Table 5.2). Likewise, the relative success of *Paralvinella pandorae* and *P. palmiformis* at most vents in the first few years post-eruption may reflect suitable environmental conditions. On sulphide

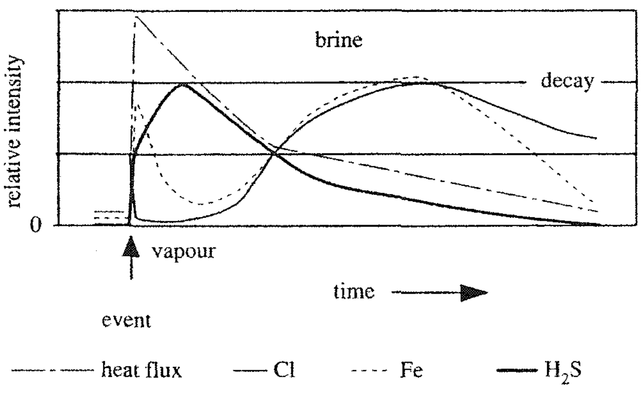


Figure 5.17. Proposed model of post-eruption fluid evolution. The time scale of change depends on the size of the eruptive event. From Butterfield et al. (1997).

chimneys, Sarrazin et al. (1999) report the presence of gastropods (*L. fucensis* and *Depressigyra globulus*) from temperatures below ~8°C, while healthy *Ridgeia piscesae* and the alvinellid worm *P. palmiformis* occur in areas with temperatures up to ~14°C. Moreover, 'low flow' tubeworm assemblages support *L. fucenesis* populations, while 'high flow' tubeworm aggregations do not (Sarrazin & Juniper 1999). High temperature tolerance of alvinellids is supported by i*n situ* observations and laboratory studies (Jollivet et al. 1995, Juniper & Martineu 1995).

However, life history characteristics and interspecific interactions are also likely important for the success of early colonizers and subsequent faunal shifts. Two polychaetes, *Ophryotrocha globopalpata* and *Branchinotogluma* sp. are markedly more abundant at new vents than in mature assemblages. Species of the genus *Ophryotrocha* are rapid colonizers of disturbed and organically enriched sites from many locales, but are typically out-competed over time (Gage & Tyler 1991). A pilot study at cold seeps showed that dorvilleid polychaetes (>80% *Ophryotrocha* sp.) colonized trays placed within bacterial mats high in hydrogen sulphide more often than trays placed beyond the mats (L. Levin pers. comm.). *O. globopalpata* may thus respond quickly to patchy, ephemeral resources and may be able to tolerate elevated levels of sulphide.

Paralvinella pandorae is also relatively more abundant at nascent vents than in mature assemblages, and *P. palmiformis* dominates assemblage biomass at year 2 vents. Tunnicliffe et al. (1997) argue that *Ridgeia piscesae* likely facilitates the colonization of alvinellids that use tubeworms for substratum. Although *Paralvinella pandorae* and *P. palmiformis* can exist without tubeworms present (Mkr 33 in 1998), the Axial data generally support this argument: all vents that hosted tubeworms in years 1 and 2 also supported alvinellid populations, and alvinellid relative abundances were lowest where tubeworms were absent. *P. pandorae* also appears to achieve highest relative abundance and biomass during the first year a tubeworm bush is present, followed by a decrease in dominance over time.

In a post-eruption scenario, what causes the eventual decline in the relative dominance of *Ophryotrocha globopalpata, Branchinotogluma* sp., *Paralvinella pandorae* and other such species? Early arrival may allow these species to reach unusually high densities since competition for food and/or space is unlikely in the early stages of community development (Walker & Chapin 1987). Carbon and nitrogen isotopes of the 1998 fauna support this hypothesis (C. Levesque pers. comm.). Resources may become limiting over time as density and biomass increase and more species accumulate. Competitively inferior species would suffer in such a scenario; this phenomenon is quite common in other community successions (e.g. Sousa 1984, Connell 1987). Density data from tubeworm grabs supports the decline in *O. globopalpata* with time and two years of time-lapse camera images from Mkr 33 show a gradual 3-fold decrease in *Branchinotogluma* sp. densities from deployment in 1998 to recovery in 2000 (V. Tunnicliffe, unpub. data). *P. pandorae* densities and relative biomass decline by 2000, and its downward size shift is attributed to competition with the later arriving palm worm (Levesque et al. 2003). No or low interspecific competition directly following an eruption may also explain the more even distribution of individuals among species early in the community assembly process. Somaschini et al. (1997) followed a polychaete community colonizing artificial habitats; they attribute a similar trend of declining species evenness with time to increasing interspecific competition. Differential predation of early successional species may also cause their eventual demise (Wooten 2002).

Small-scale variations in larval supply dictating the sequence of species arrival may also mediate interspecific interactions causing vent-to-vent variation in temporal macrofaunal shifts. The presence of *Lepetodrilus fucensis* at most sites in 1998 despite its numerical rarity implies that post-settlement mortality likely influenced this species in the early years; grazing by high densities of scale worms and other polychaetes may have affected recruit success. Chance arrival of snails and limpets to Snail vent before grazer recruitment may have contributed to early gastropod success at this vent. Micheli et al. (2002) report that predator exclusion from basalt recruitment blocks on the EPR caused gastropod abundances to increase by an order of magnitude, thereby indirectly increasing gastropod grazing and bulldozing sessile invertebrate recruits such as tubeworms. The delayed recruitment of tubeworms to Snail vent may also be related to elevated gastropod densities at this site.

Temporal shifts in meiofauna were less pronounced than macrofaunal shifts. The copepod *Aphotopontius forcipatus* dominates overall relative abundance of nascent vents for each of the three years. Since the copepod *Benthoxynus spiculifer* is thought to replace *A. forcipatus* as assemblages age (Tsurumi et al. in press), this transition may occur over longer time scales as *B. spiculifer* was absent from nascent vents in 2000.

Annual trends in species density and biomass

The density and biomass of tubeworm-associated species increases with time. In a trivial sense, this phenomenon is inherent to biological successions as species occupy new habitat patches and accumulate in space over time. However, a proposed criterion of community succession is the increase in total biomass to a stable level (Keeton & Gould 1993). At Axial, assemblage establishment is rapid and average density and biomass values appear to level by 1.5 years post-eruption (Tables 5.6 and 5.7). These data are also useful to establish the time scale of vent assemblage development to levels consistent with established communities. Half the macrofaunal densities at 2.5-year-old vents are higher than the maximum value reported by Tsurumi (2001) for mature Axial assemblages. A decrease in bulk food quality at vents on annual to decadal scales (e.g. C/N, protein, lipid content etc.; Levesque & Juniper 2002, C. Levesque pers. comm.) may be an explanation.

Although average density and biomass values seem to asymptote, there is substantial among vent variation within years 2 and 3. Biomass values may reflect local productivity regimes and/or the time since tubeworm bush formation: three vents with higher than average total biomass in 2000 had established tubeworm aggregations at least one year prior. Annual density ranges may reflect community structure; higher overall densities in 1999 and 2000 (>3 individuals/cm^2) occurred at vents with relatively high numbers of limpets. *Lepetodrilus fucensis* can stack atop one another and create chains 2-15 individuals long. Sarrazin et al. (1999) report *L. fucensis* up to 10.8 individuals/cm^2 on JdFR sulphide chimneys.

From nascent to mature vents: trajectories of assemblage development

Colonization and assemblage change at the new Axial vents occur quickly. Variation among nascent vent species lists is similar to mature vents by year 2 and relative species abundances are no longer more variable than mature vents by year 3. Decreasing among vent variability with increasing vent age likely results from initial assemblage heterogeneity, continued colonization of species to the new vents with time (by year 2) and the annual increase in the abundance of *Lepetodrilus fucensis* at all vents (by year 3). Berlow (1997) refers to processes that diminish initial variation in succession as canalizing or 'noise-dampening'. For example, in Oregon intertidal communities, recruitment of a competitively dominant mussel leads to its eventual dominance regardless of variations among patches in initial conditions and transient dynamics (Wooten 1993).

Composition and structure of nascent assemblages are also similar to mature vents by years 2 and 3 respectively (Figures 5.3, 5.7 and 5.8). This pace of community development is much faster than rates reported for corals and benthic macrofauna colonizing new lava flows in other marine environments (Grigg & Maragos 1974, Gulliksen et al. 1980, Tomascik et al. 1996), for the assembly of macroinvertebrates in new fresh water streams (Flory & Milner 2000) and for deep-sea assemblages developing on whale falls (Smith et al. 2002). A fundamental difficulty with interpreting the Axial results is our ignorance of what drives the variation among mature vent assemblages; variation in species distributions is non-random, but the structuring processes remain speculative (Marcus & Anholt in revision). Since 2.5 year-old nascent vents support assemblages similar to mature vents, causes of multiple community trajectories may explain part of the variation among mature assemblages.

Several trends are evident among the developing nascent vent faunas. First, assemblages characterized by scale worms or the dorveillid worm *Ophryotrocha globopalpata* become dominated by the limpet or pandora worm by year 3. Even though these 'transition' assemblages of 1998 and 1999 are only identified when suction samples are included in the analysis, limpets dominate all suction samples in year 3 except one. Second, some vents shift from being numerically dominated by the pandora worm to being dominated by the common limpet, but the reverse transition never occurs. Third, vent age is correlated to *Lepetodrilus fucensis* success (most assemblages dominated by limpets are from year 3), but vent age is less important for explaining the similarity among assemblages dominated by *Paralvinella pandorae*. Rather, similarity among pandora-dominated vents is linked to the establishment of *Ridgeia piscesae* aggregations. Fourth, the rate of assemblage change differs among vents. For example, both Nascent and Mkr N41 were initially colonized by *R. piscesae* and *P. pandorae*. Nascent vent maintains its overall character for three years (dominance by the pandora worm), while limpets dominate Marker N41 in 2000.

What may be the possible causes of these trends? Berlow (1997) proposes three models of how initial variation may be dampened, tracked or magnified during the course of community succession if the type and relative importance of abiotic and biotic interactions vary. Initial variation is minimized over time if species interactions are strong and consistent, leading to deterministic repeatable species patterns (see reference to Wooten 1993 above). This 'canalized' model of succession predicts that mosaic community patterns are best explained by time since the last disturbance (i.e. mosaic pattern would not arise if all sites were disturbed at the same time in the past). In contrast, if species are more influenced by extrinsic factors rather than deterministic species interactions, successional trajectories will vary depending on local site conditions (e.g. abiotic factors, propagule supply). This model of 'externally driven' succession proposes that current variation in community structure is best explained by a combination of current (e.g. environmental factors) and historic (e.g. initial community composition) site conditions, and models of external driving variables (e.g. seasonal supply of larvae). The third model asserts that the sign and magnitude of species interactions are highly context dependent, so patterns in community change are rarely repeatable. Under this 'contingency' model of succession, observed community mosaic patterns result from the interplay of species interactions and variation in extrinsic events.

Patterns observed at Axial fit aspects of both canalized and externally driven succession. Although the contingency model may also apply, the Axial data indicate that broad patterns of assemblage development are repeatable at vents (see next section). Recruitment of the limpet to all sites by year 3, and its dominance at these sites, agrees with the canalized model; *Lepetodrilus fucensis* ranks first or second in terms of abundance and biomass in all tubeworm grabs (Table 5.15), and ranks first from all suction samples except one (Table 5.16). Thus, despite differences in site characteristics and histories, the ubiquitous success of the limpet channels community development to some extent. Although abiotic factors and/or post-settlement processes may delay the success of the limpet within one to two years post-eruption, it is unknown why the limpet

Table 5.15. Ranks of relative abundance (A) and relative biomass (B) of selected species from tubeworm grabs. Species selection was based on the top 3 species each year calculated by average relative abundance/biomass across all tubeworm grabs. Relative abundance or biomass is shown in brackets. Outlined boxes indicate that *Ridgeia piscesae* formed a bush-like aggregation at the vent in the prior year (only shown for the first species; unknown for Joystick). *Bag City was not observed in 1998, but the 1999 assemblage in consistent with tubeworm bush formation the previous year. Blank cells = no sample, NP = not present, P = present.

Species	Year	Mkr N41	Nascent	Mkr 113	Mkr 33	Bag City*	Cloud N6	Snail	Joystick
A) RELATIVE ABUNDANCE									
P. pandorae	1998	1 (53%)	1 (97%)	1 (90%)					
	1999	1 (80%)	1 (92%)	1 (72%)	1 (86%)	1 (99%)			
	2000	3 (9%)	1 (63%)	1 (58%)	1 (69%)	1 (74%)	1 (88%)	4 (3%)	4 (2%)
L. fucensis	1998	NP	2 (1%)	2 (7%)					
	1999	2 (16%)	2 (7%)	2 (24%)	6 (0.4%)	2 (0.5%)			
	2000	1 (77%)	2 (29%)	2 (34%)	2 (15%)	2 (16%)	2 (10%)	1 (53%)	1 (85%)
D. globulus	1998	NP	3-5 (1%)	NP					
	1999	3 (2%)	6 (0.1%)	7 (0.2%)	3 (2%)	NP			
	2000	2 (12%)	4 (2%)	3 (5%)	4 (1%)	7 (0.5%)	4 (0.5%)	2 (40%)	3 (3%)
P. palmiformis	1998	NP	NP	3-4 (1%)					
	1999	4 (1%)	3 (1%)	3 (3%)	2 (8%)	3 (0.2%)			
	2000	5 (1%)	5 (1%)	4 (1.5%)	3 (15%)	4 (2%)	NP	NP	NP

Table 5.15 continued

Species	Year	Mkr N41	Nascent	Mkr 113	Mkr 33	Bag City	Cloud N6	Snail	Joystick
B) RELATIVE BIOMASS									
P. pandorae	1998	2 (27.5%)	1 (57%)	1 (46%)					
	1999	2 (18%)	2 (12.5%)	3 (7%)	2 (3%)	1 (75%)			
	2000	4 (0.5%)	4 (2%)	3 (6.5%)	4 (5%)	5 (3%)	1 (65%)	5 (0.5%)	5 (0.4%)
Branchinotogluma sp.	1998	1 (60%)	4 (12%)	NP					
	1999	6 (1%)	NP	5 (1%)	NP	3 (2.5%)			
	2000	6 (0.4%)	6 (0.2%)	6 (0.8%)	NP	4 (4%)	4 (2.5%)	4 (0.7%)	NP
L. fucensis	1998	NP	2/3 (15%)	4 (5%)					
	1999	3 (12%)	3 (7.5%)	2 (24%)	3 (0.2%)	5 (0.5%)			
	2000	1 (54%)	2 (31%)	1 (50%)	2 (14%)	2 (41%)	2 (30%)	1 (67%)	1 (89%)
D. globulus	1998	NP	2/3 (15%)	NP					
	1999	5 (1%)	P (<0.1%)	P (<0.1%)	P (<0.1%)	NP			
	2000	3 (6%)	5 (2%)	5 (2.5%)	6 (0.2%)	6 (0.5%)	5 (0.4%)	2 (29%)	3 (2%)
P. palmiformis	1998	NP	NP	2 (43%)					
	1999	1 (65%)	1 (79%)	1 (64%)	1 (97%)	2 (20%)			
	2000	2 (36%)	1 (58%)	2 (37%)	1 (74%)	1 (43%)	NP	NP	NP

Table 5.16. Relative abundance ranks of selected species from suction samples per vent per year (relative abundance shown in brackets). Species selection was based on the top 3 species calculated by average relative abundance across all suctions per year. Blank cells indicate no sample. NP = not present, P = present.

Species	Year	Mkr 33	Snail	Mkr 108	Mkr 113	Cloud N4	Joystick	Mkr N41	Nascent	Bag City
D. globulus	1998	P (<1%)	1 (59%)	NP				NP		
	1999	1 (29%)	3 (27%)		5 (1%)	P (<1%)	P (<1%)		4 (4%)	
	2000	2 (27%)	2 (33%)	2 (15%)	2 (15%)	2 (15%)	3 (10%)			P (<1%)
L. fucensis	1998	P (<1%)	2 (31%)	2 (26%)				2 (26%)		
	1999	2 (26.5%)	2 (29%)		4 (2%)	2 (31%)	3 (5.5%)		1 (51%)	
	2000	1 (64%)	1 (62%)	1 (78%)	1 (84%)	1 (63%)	1 (57%)			4 (12%)
O. globopalpata	1998	1 (42%)	NP	4 (9.5%)				4 (9.5%)		
	1999	NP	1 (35%)		1 (78.5%)	1 (39%)	1 (73%)		2 (27%)	
	2000	P (<1%)	P (<1%)	3 (3.5%)	P (<1%)	NP	2 (11%)			1 (33%)
Branchinotogluma sp.	1998	2 (30%)	P (<1%)	NP				NP		
	1999	3 (18%)	5 (2%)		P (<1%)	3 (25%)	P (<1%)		6 (2%)	
	2000	P (<1%)	P (<1%)	P (<1%)	P (<1%)	3 (15%)	P (<1%)			3 (18%)

achieves such dominance with time.

Lepetodrilus fucensis may be a competitively dominant species or it may simply fill a previously unoccupied niche. It is unknown whether resources and/or space are limiting at vents, but interspecific competition likely occurs between two JdFR alvinellid polychaetes (Levesque et al. 2003). The limpet has multiple feeding strategies; it can graze, suspension feed and perhaps gain nutrition from chemosynthetic bacteria living on its gills (de Burgh & Singla 1984, Fox et al. 2002, A. Bates pers. comm.). As a grazer and suspension feeder the limpet could exploit similar resources as other vent gastropods and polychaetes (e.g. JdFR alvinellids likely deposit and suspension feed; Desbruyères & Laubier 1986, 1991). However, if nutrition were derived from its episymbionts, then the limpet would likely compete for space rather than food. The densities of other tubeworm bush associated species may provide indirect evidence for interspecific competition; for example, if overall densities of all species (excluding the limpet) are lower where the limpet is in high abundance (year 3) versus where limpet abundances are more moderate (year 2). Although many factors are apt to affect community density at the same site over time, the data from Mkr N41 in 1999 and 2000 are intriguing. Overall macrofauna density is similar at N41 for both years (Table 5.6), but total density excluding the limpet shifts from 5.74 inds/cm^2 in 1999 to 1.85 inds/cm^2 in 2000, while the density of *L. fucensis* increases from 1.09 to 6.09 inds/cm^2. The success of *L. fucensis* may also be linked to fluid characteristics; temperature declines slightly between 1999 and 2000 at N41 (Table 5.2) and sulphide to heat decreases seven-fold.

Communities dominated by *Paralvinella pandorae* are not differentiated by year. Rather than vent age, the establishment of bush-like tubeworm aggregations seems to influence these assemblages. If tubeworm bush formation is considered as time zero, the pattern of assemblage development is very similar across vents: in year 1) *P. pandorae* dominates assemblage biomass and abundance, in year 2) *P. pandorae* decreases in size and relative abundance, and *P. palmiformis* usually recruits and dominates assemblage biomass and, in year 3) the relative abundance of *P. pandorae* continues to decline (although it may remain numerically the most dominant species) and either *P. palmiformis* or the limpet dominates assemblage biomass (Table 5.15). Thus, while the pattern of change is similar, the rate of succession among sites varies depending on the timing of tubeworm bush formation. Farrell (1991) reports a similar phenomenon in the succession of rocky intertidal communities; in his study, the order of species replacements was consistent, but the rate of change varied widely among sites due to the recruitment timing of a barnacle species.

Besides controls on successful tubeworm recruitment, the pattern of initial colonization may also cause varying rates of change among developing assemblages. Initial state seems to have limited the outcomes of certain assemblages: Snail and Joystick vents did not host large populations of alvinellid polychaetes even after the establishment of tubeworms (Table 5.15). Joystick was not observed in 1998, but Snail is unique among sites as it was initially dominated by gastropods. Of all the new SRZ assemblages, Snail vent changed the least with time; whether its slow rate of change is due to initial state or other unique site characteristics (e.g. fluid properties) is unknown.

Are patterns of community development predictable at JdFR diffuse vents?

To argue for predictable temporal patterns of community development at vents, patterns should be repeatable over multiple vents at one eruption site and over multiple eruptions. I restrict comparison of the post-eruption patterns at Axial to eruptions from other locations on the JdFR (CoAxial and Cleft) since faunal diversity and community structure differ between EPR and JdFR vents (Jollivet 1996). I make a comparison to CoAxial by limiting Axial data to the sampling method used at CoAxial (tubeworm grabs). I also compare community structure at 2.5 year-old Axial vents to vents at Cleft Segment from an equivalent time post-eruption.

Three months after the CoAxial eruption no macrofauna were visible at nascent vents, but nine months later all observed active sites (five vents) were colonized by *Ridgeia piscesae* (Tunnicliffe et al. 1997). Annual species richness estimates are comparable between Axial and CoAxial despite an order of magnitude difference in individuals in year 2, and temporal patterns in species composition and dominance are remarkably alike (Table 5.17). Five of the eight species at CoAxial in year 1 are also present in the seven month-old Axial tubeworm grabs, and 14 species are shared between the two sites in year 2. Notable differences are the absence of the nemertean (*Thermonemertes valens*) and the scale worm *Harmothoë* cf *globosa* from Axial samples

Table 5.17. Comparison of 1- and 2-year-old CoAxial (CoAx) tubeworm assemblages to seven and 18 month-old Axial tubeworm assemblages. For Axial, only those tubeworm grabs from 1999 that were sampled as tubeworm grabs in 1998 are used for comparison (Nascent, Mkr N41 and Mkr 113). Mkr N41 from 1998 is not included since it was a tubeworm suction sample. All abundances are presented as orders of magnitude (after Table 2 in Tunnicliffe et al. 1997) since quantitative data are not available from CoAxial. Abundance categories: X=1-10, XX=tens, XXX=hundreds, XXXX=thousands, XXXXX=tens of thousands.

Taxon	Species	CoAx	Axial	CoAx	Axial
		1 year	7 months	2 years	1.5 years
Stauromedusa	unknown			X	
Vestimentifera	*Ridgeia piscesae*	XXX	XXX	XXXX	XXXX
Polynoidae	*Branchinotogluma* sp.	X	X	XX	XX
	Levensteiniella kincaidi	X			X
	Harmothoë cf. *globosa*	X		X	
	Lepidonotopodium piscesae		X	X	XX
Ampharetidae	*Amphisamytha galapagensis*	X	X	X	XX
Alvinellidae	*Paralvinella pandorae*	XXX	XXX	XXXX	XXXXX
	Paralvinella palmiformis		X	XX	XXX
Lepetoddrilidae	*Lepetodrilus fucensis*	X	X	XXX	XXXX
Peltospiridae	*Depressigyra globulus*		X	XX	XXX
Provannidae	*Provanna variabilis*			X	
	Lacunoides vitreus				X
Nemertea	*Thermonemertes valens*	XX		XXX	X
Spionidae	*Prionospio* n. sp. 1			X	X
Hesionidae	*Hesiospina vestimentifera*			X	X
	Hesiodeira glabra			X	
Dorvilleidae	*Parougia wolfi*				X
Phyllodocidae	*Protomystides verenae*				X
Dorvilleidae	*Ophryotrocha globopalpata*			X	XX
Ostrocoda	*Euphilomedes climax*			X	
	Podocopida				X
Copepoda	Calanoida		X	X	XX
	Aphotopontius forcipatus		X	XX	XXX
	Benthoxynus spiculifer			X	
	Harpacticoida				X
Number of individuals		314	354	3,140 + ?	34,972
Species richness		8	10	20	20
Number of vents sampled		2	2	3	3

in 1998, and the absence of meiofauna from CoAxial year 1 samples.

If *Ridgeia piscesae* successfully establishes bush-like aggregations within 6-12 months after an eruption, the associated biota apparently has a predictable trajectory of development across JdFR sites. *Paralvinella pandorae* dominates biomass by the first year and is replaced by abundant smaller conspecifics the next year. *P. palmiformis* increases in numbers and dominates biomass in year 2, usurping the place of its congener *P. pandorae*. The concomitant downward size-shift of *P. pandorae* was observed at all JdFR post-eruption sites (Tunnicliffe et al. 1997, Tsurumi & Tunnicliffe 2001, this chapter). By three years post-eruption, the two common gastropod species (*Lepetodrilus fucensis* and *Depressigyra globulus*) recruit to new vents in increasing numbers. Other shared patterns include abundant scale worms (*Branchinotogluma* sp.) and copepods (*Aphotopontius forcipatius*) during the first two years post-eruption.

The observations of Tsurumi & Tunnicliffe (2001) suggest that *Paralvinella pandorae* may be out competed over time as more species encroach, and/or the habitat becomes unsuitable as vent fluids evolve. Following the Cleft eruption, the abundance pattern of *P. pandorae* changed markedly. At two years, *P. pandorae* was ubiquitous and represented 70% of total animals collected, and 20-98% of all individuals from each site. At five to eight years, less than 1% of all individuals were *P. pandorae*, although distribution remained high. However, since only two of the ten samples from the last time period were from vigorous diffuse flow vents (the remainder were sulphide or senescent samples), substratum effects and habitat demise may also explain the pattern.

In summary, at the two sites studied to date, nascent tubeworm assemblages have a similar pattern of development if *Ridgeia piscesae* colonizes and establishes aggregations within months to one year post-eruption. Also observed in this study is the effect of the timing of *Ridgeia piscesae* establishment: the same pattern of community change occurs but is delayed at sites if tubeworm bushes are formed 2-3 years post-eruption. It is unknown whether the limpet eventually dominates these diffuse vents if conditions remain stable. The observations at Cleft, the prevalence of limpet-dominated vents at ASHES (see Appendix 5.1), and the pandora worm to limpet shift at nascent Axial vents suggests that the pandora worm may only dominate young (<5 years) sites.

Proposed model of community development

Three general pathways of community development were observed, depending on the initial character of the fauna (Figure 5.18). Vent assemblages initially dominated by the pandora worm and polychaete grazers follow a similar trajectory of development after tubeworms arrive. In the year following establishment of *Ridgeia piscesae* aggregations, *Paralvinella pandorae* recruits in large numbers and achieves large body sizes. The next year, the pandora worm remains numerically dominant but decreases in size, the palm worm and limpet reach higher numbers, and the palm worm dominates assemblage biomass. In year 3 tubeworm bushes, *P. pandorae* or the limpet is numerically dominant, and either the limpet or the palm worm accounts for the largest proportion of assemblage biomass. The future fate of the assemblage is unknown, although data from mature vents suggests that numerical dominance by limpets and the pandora worm will persist. Initial colonization by gastropods seems to prevent progression through this pathway. After a tubeworm bush formed at Snail and Mkr 108 vents, alvinellids never became dominant (Figure 5.18).

The model presented in Figure 5.18 does not represent the developmental trajectories of two observed vents. Mkr 113 switched from a pandora assemblage in year 1, to a polychaete grazer assemblage in year 2, to a gastropod-dominated assemblage in year 3 if relative abundance data based on total collections are considered. However, data from just tubeworm grabs (abundance and biomass) suggest that Mkr 113 assemblage is dominated in year 1 by the pandora worm, by the palm worm in year 2 and limpets in year 3. Joystick vent is also excluded since the timing of tubeworm bush formation is unknown for that site.

This model emphasizes the decrease in variability among vent faunas with increasing vent age as three assemblage 'types' reduce to two 'types' by year 3. Faunal density and biomass also increase with time, primarily due to burgeoning limpet populations.

Conclusion

The 1998 eruption at Axial destroyed pre-existing assemblages, and created new vent habitat. Species colonized the new vents quickly, at rates two to three times higher

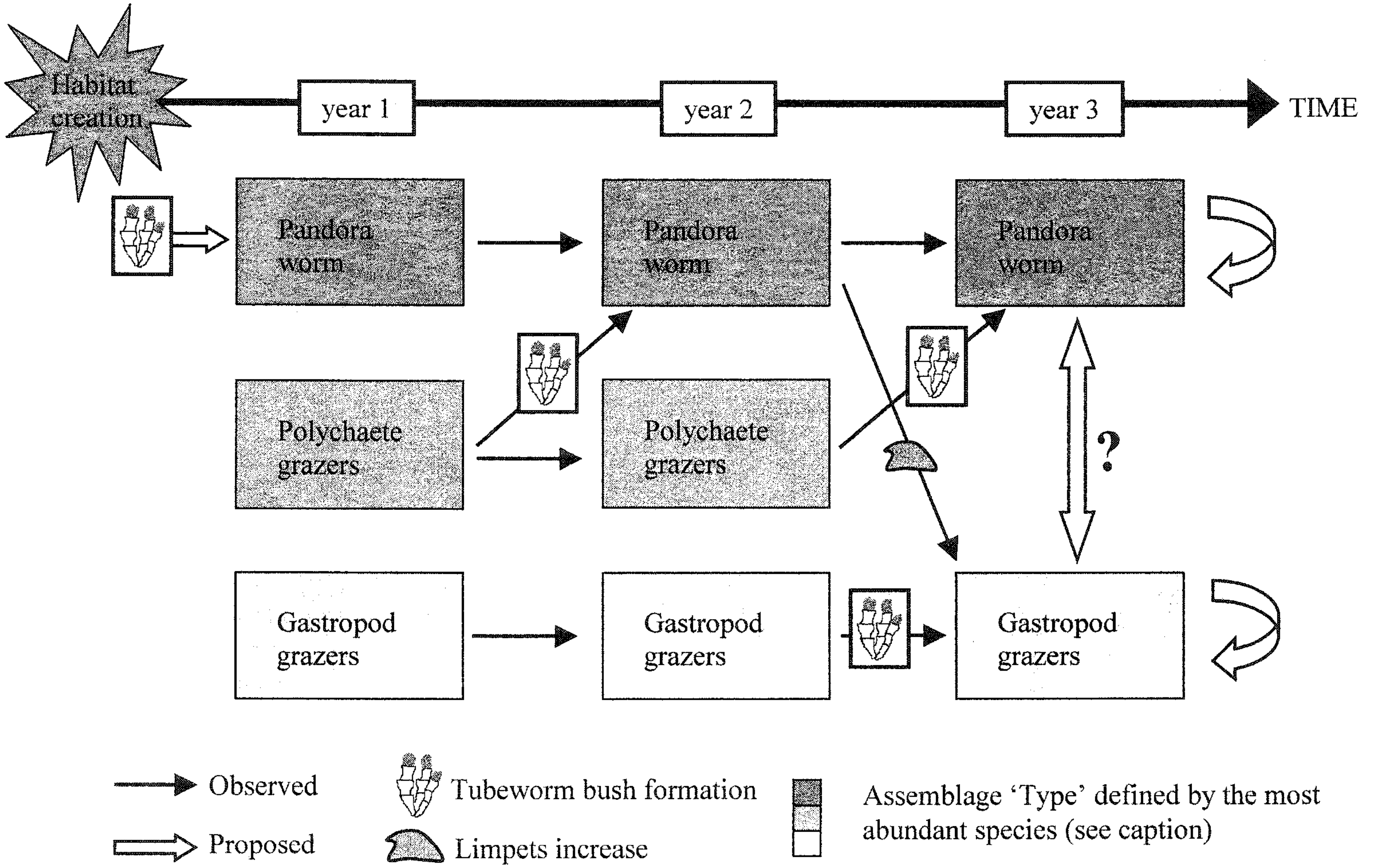


Figure 5.18. Proposed model of diffuse flow vent community development. Model is based on observed changes in relative species abundances at developing nascent Axial communities. Assemblage Type is defined by the collection groupings found with cluster and ordination analyses and refers to which species dominate total community abundance. Macrofaunal density and biomass increase with time. Curved arrows indicate that the two community types in year 3 may persist over time.

than reported for previous eruption studies. Colonization rates differed among species, and rates were generally related to species abundances in mature assemblages: abundant species colonized more quickly than rare species. Once species had arrived at the nascent vents, they persisted at the scale of the new lava flow although local extinction could be high. A general shift in the macrofauna was observed at the scale of the lava flow: *Paralvinella pandorae* and *P. palmiformis* dominated year 1 and 2 vents respectively, and *Lepetodrilus fucensis* dominated year 3 collections. Spatial variability among seven month-old assemblages was unexpected from synchronous patterns reported from prior eruption studies, but this initial variability decreased with time, and by year 3 nascent vent macrofauna resembled mature assemblages. However, meiofaunal patterns at year 3 vents remained distinct from mature collections. A general model for the temporal development of diffuse flow tubeworm assemblages is proposed. The rate and trajectory of development seems contingent on the timing of *Ridgeia piscesae* recruitment. Assemblages may not proceed through certain stages if tubeworms establish years after habitat inception or the vent was colonized by gastropods within the first year post-eruption. Observations of future eruptions are needed to test this model.

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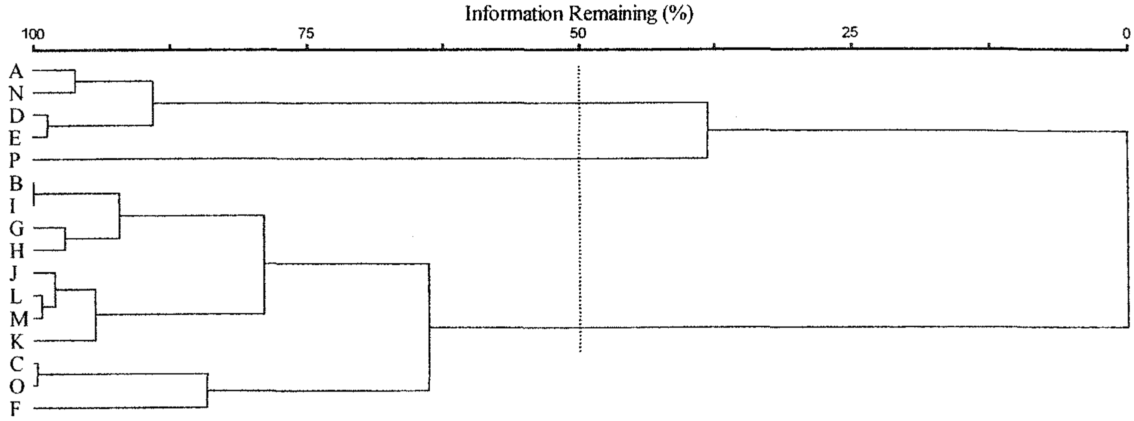


Appendix 5.1. Clustering of ASHES vents based on relative abundances of macrofauna (excluding *Ridgeia piscesae*). All samples are tubeworm grabs; see Table 4.1 for vent names. Three main clusters fall out. The first cluster unites four vents dominated by *Paralvinella pandorae* (50% to 80% relative abundance). The second cluster consists of only one vent, which differs from all other mature assemblages as it is dominated by *Paralvinella palmiformis* (81% relative abundance). The third cluster unites vents co-dominated by the limpet and pandora worm (both ~30% relative abundance), or dominated singly by *L. fucensis* (43% to 72% relative abundance). This cluster analysis was used to divide mature ASHES assemblage into two groups: AshesPp refers to the average relative abundance of the four samples in cluster 1, and AshesLp refers to the average relative abundance of the 11 samples in cluster 3.

CHAPTER 6

Species patterns and their relationship to habitat gradients at diffuse flow vents

Introduction

Biological communities are organized by the interplay of biotic interactions, abiotic factors and chance events. Community ecology aims to determine how much variation in community structure is caused by each of these general categories. Major processes such as recruitment, competition, predation, disturbance regimes and species-specific responses to environmental gradients influence the organization of both terrestrial (Morin 1999) and marine (Bertness et al. 2001) communities.

In the marine environment, the relative importance of abiotic and biotic controls can depend on community type and the intensity of environmental gradients. In the rocky intertidal, biological processes such as competition and predation should theoretically decrease in importance with increasing harsh environmental conditions, and increase along gradients of increasing recruitment intensity (Menge & Sutherland 1987, Menge & Farrell 1989). However, at hydrothermal vents the opposite trend may occur (Micheli et al. 2002); predation appears to have more influence on community structure in harsher rather than milder areas of the environmental gradient. Fundamental habitat characteristics likely underlie this difference; severe abiotic conditions at vents such as elevated temperature or sulphide levels are positively correlated with productivity due to the dependency of both these attributes on proximity to flow. The relative contributions of different types of structuring processes are thus habitat specific and theoretical expectations gleaned from one marine habitat may not apply to another.

Despite these habitat specific differences, marine benthic communities may share a common influence. Bruno & Bertness (2001) argue that many benthic assemblages are first and foremost structured by the presence of a foundation or habitat-forming species. Marine habitats generated by foundation species include coral reefs, kelp forests, intertidal and subtidal mussel beds (references in Bruno & Bertness 2001) and sponge reefs (Barthel 1992). Foundation species influence community structure of the associated fauna through facilitation. Specific mechanisms include provision of substrata for attachment, provision of refuges from predation, enhancement of propagule supply or retention, and reduction of physical and/or physiological stress (see Bruno & Bertness 2001 for a review).

Diffuse flow hydrothermal vents in the northeast Pacific may be another benthic marine habitat whose fauna are largely influenced by a foundation species. The vestimentiferan tubeworm *Ridgeia piscease* typically forms three-dimensional bush-like aggregations directly over low temperature fluid flow. These aggregations are so ubiquitous that they are used to locate vents; for example, fluid flow is inferred for some locations because tubeworms are present, although the flow itself is not visible (J. Marcus pers. obs.). Since *R. piscesae* is almost always present over or proximate to flow, diffuse flow assemblages with and without tubeworms have not been compared. Effects of tubeworm bush presence on the associated fauna are thus inferred. *R. piscesae* aggregations increase surface area proximate to flow for attachment by vent-obligate species (Sarrazin & Juniper 1999, Chapter 5), and variable tube morphology and bush complexity suggests that aggregations may create distinct microhabitats (Uruyco 2000) and possibly refuges from predation. Tsurumi & Tunnicliffe (in press) report a positive relationship between species richness and tubeworm bush complexity.

Other biotic and abiotic factors are also thought to influence vent community structure. Characterization of steep physical and chemical gradients at vents soon after their discovery led early researchers to propose that environmental factors are the main drivers of species patterns (e.g. Hessler & Smithey 1983, Grassle 1985, Hessler et al. 1985, Fustec et al. 1987, Tunnicliffe & Juniper 1990, Tunnicliffe 1991). In particular, variations in fauna between vents and vent sites have been attributed to temperature (Fustec et al. 1978, Sarrazin et al. 1997), hydrogen sulphide concentration (Tunnicliffe et al. 1986, Shank et al. 1998, Luther et al. 2001) and fluid flow patterns (Tunnicliffe 1991, Sarrazin et al. 1997). Although these early speculations were never directly tested, they are likely true in a general sense. Broad patterns of species abundances and distributions in flow and on the periphery correlate to species' relative exposure to fluid properties (Micheli et al. 2002, Marcus & Tunnicliffe 2002). More recent studies also suggest that biological processes such as predation (Micheli et al. 2002) and competition (Levesque et al. 2003) are important processes operating within the limits imposed by abiotic constraints.

Despite the suggestion by many authors that the spatio-temporal distribution of vent species is related vent fluid properties, only one study to date explores these putative links. Sarrazin et al. (1999) combined small-scale video observations of fauna living on sulphide edifices on the Juan de Fuca Ridge (JdFR) with *in situ* measurements of temperature, fluid flow intensity, substratum type, and concentrations of hydrogen sulphide, iron and manganese. They found that hydrogen sulphide, visible flow and substratum type influence species distributions, however less than 30% of the variance in their species data was explained by the measured factors. Sarrazin et al. (1999) recommended that future studies measure other factors such as dissolved oxygen, nitrogen compounds, food availability and biological interactions to account for the unexplained variance. They did not consider the presence of *Ridgeia piscesae* as a potential explanatory factor.

My objective is to determine if the organization of post-eruption diffuse flow communities is related to gradients in certain habitat variables. I test for possible influences of *Ridgeia piscesae* presence, tubeworm bush age, substratum type, vent age, vent location, and physical and chemical fluid properties, on faunal patterns. I am able to consider tubeworm presence and tubeworm bush age as habitat factors as aggregations of *R. piscesae* were established at different times at the nascent vents following the Axial eruption. The eruption thus offers a unique opportunity to test the potential significance of *R. piscesae*, since tubeworm bushes occur at all mature diffuse vents

Diversity among diffuse fluids within vent fields underlies the concept that physicochemical fluid properties may influence species patterns (e.g. Johnson 1988, Butterfield 1990, Luther et al. 2001). The primary source of variation among diffuse fluids is the character of the sulphide- and metal-rich high temperature fluid and the degree of mixing of this endmember fluid with crustal seawater (see Figure 1.3). Secondary processes include conductive heat exchange, mineral precipitation/dissolution, fluid-rock reactions at low temperature, and biologically mediated reactions (Butterfield et al. submitted).

In this chapter, I confirm which species are driving most of the variation among developing vent communities at Axial and report the habitat factors that relate to observed faunal variation. Luther et al. (2001) show that two species at East Pacific Rise

(EPR) vents, a tubeworm and an alvinellid polychaete, occur in microhabitats with different concentrations of free sulphide, oxygen and iron, but this study is the first to demonstrate a link between faunal patterns of entire communities and fluid properties at diffuse vents. This analysis is also the first to explicitly incorporate tubeworm bush age and vent age as habitat characteristics, although successional or time-mediated processes are frequently implicated as drivers of vent faunal patterns (Desbruyères 1998, Shank et al. 1998).

Methods

Site Description and Sampling

See Chapter 5 for a full description of Axial Volcano and faunal sampling. All nascent South Rift Zone (SRZ) vent samples, except those with less than 50 individuals, are analysed here. See Table 6.1 for the list of faunal samples and their letter abbreviations. Letters are used instead of the vent abbreviations in Chapter 5 to simplify presentation of results.

Habitat Characteristics

The habitat characteristics used in this analysis are listed in Table 6.2; they include qualitative binary variables (presence of *Ridgeia piscesae* and substratum type), semi-quantitative variables (year and timing of *R. piscesae* recruitment), and quantitative variables (six vent fluid properties). Table 6.2 also lists the potential significance of these characteristics to vent fauna.

Vent fluid properties were measured by the *in situ* chemical analyzer SAUVE (System Used to Assess Vented Emissions) or the vent fluid sampler HFPS (Hydrothermal Fluid and Particle Sampler). SAUVE measures temperature and dissolved concentrations of H_2S, Fe (II + III) and Mn (II) (Massoth et al. 1989). All SAUVE measurements presented here are from 1998. The HFPS measures temperature *in situ* and collects vent fluids into bags or bottles for immediate analysis on the ship (e.g. pH, H_2S) or later in the laboratory (major and minor elements). Some measurements from 1998, and all measurements from 1999 and 2000 are from the HFPS. See Butterfield et al. (submitted) for a detailed description of the HFPS system and chemical analyses.

Table 6.1. Abbreviations (Abb.) of the biological collections analysed in this chapter. *Samples excluded from analyses since collections include less than 50 macrofaunal individuals.

Vent	Year	Abb.
Easy	1	A*
Mkr N41	1	B
	2	C
	3	D
Nascent	1	E
	2	F
	3	G
Mkr 33	1	H
	2	I
	3	J
Cloud Mkr N4	1	K*
	2	L
Cloud Mkr N6	3	M
Snail	1	N
	2	O
	3	P
Mkr 108	1	Q*
	3	R
Mkr 113	1	S
	2	T
	3	U
Joystick	2	V
	3	W
Bag City	2	X
	3	Y

Table 6.2. Vent characteristics used in this chapter to correlate to faunal samples.

Vent Characteristic	Unit of Measurement	Potential Significance
Qualitative binary variables		
1. Ridgeia piscesae	Present or Absent (1/0)	Facilitation; habitat-forming species
2. Substratum type (lobate or crack sheet flow)	Lobate (0) or Crack (1)	Substratum effects
Semi-quantitative variables		
3. Year	Year of sampling post-eruption (1,2,3)	Successional processes
4. Timing of *Ridgeia piscesae* recruitment	Index of tubeworm bush age (1 to 3; 4 = absent)	Facilitation; successional processes
Quantitative variables		
5. Maximum hydrogen sulphide (H_2S) concentration	mmol/kg	Main energy source for primary producers; toxic at micromolar levels to metazoans
6. Maximum H_2S/heat (ratio)	nmol/J	As above, but better measurement of H_2S because independent of dilution
7. Maximum temperature	Degrees Celsius (°C)	Thresholds for metazoans; positively correlated with sulphide
8. Maximum H_2S/iron concentration (ratio)	$1000(H_2S/Fe)$ Fe in µM	Indicates if a vent is sulphide or metal rich; important for primary producers (if ratio is ~1, most sulphide complexes with iron as FeS, thereby depleting free H_2S)
9. pH	Standardized to 22°C	Significant for many biotic and abiotic interactions; i.e. affects calcification of mollusc shells and sulphide speciation
10. Chlorine (Cl) concentration at 0 Magnesium (Mg)	mmol/kg (endmember Cl)	Indicates if a vent is brine or vapour rich
11. Distance from north end of flow	meters	Measure of vent location and relative distance from putative source of larvae

Diffuse fluids are best compared by normalizing the chemical components to heat or to another chemical component that is minimally reactive on the time scale of sub-seafloor mixing (Butterfield et al submitted). H_2S/heat (see Table 6.2) is thus termed a pseudo-conservative property, as its dependence on the degree of dilution is negligible; comparing vent-to-vent differences in H_2S/heat is equivalent to comparing differences in sulphide concentration across vents at one temperature (D. Butterfield, pers. comm.). I use both measures of sulphide (H_2S concentration and H_2S/heat), since it is unknown which measurement may be more important to vent fauna.

If multiple *in situ* scans or fluid samples were taken at a vent in the same year, the maximum value measured for each fluid property was used for this analysis. At any vent, fluid sample location was determined by probing the flow for the highest temperature. Once this location was found, the submersible arm was locked into place. The aim was to retrieve a sample of vent fluid that was just exiting the seafloor and undiluted by above-surface seawater. Highest measured temperatures and extreme values of chemical properties are most representative of undiluted fluid characteristics (Tunnicliffe et al. 1997). Fluid measurements thus do not reflect the absolute values the fauna experience, but reflect physicochemical gradients among vents and hence a relative ranking of community exposure to the fluid property. HFPS samples were not coupled in time to faunal collections; the HFPS could not be fitted simultaneously with the biological sampling equipment on the submersible. Maximum time between a biological collection and fluid measurements at the same vent was approximately two weeks.

Due to fluid sampling constraints, the full suite of physical and chemical data is unavailable for some biological collections. For example, temperature was not recorded from Snail vent in 1998, and Mkr 108 in 2000, and sulphide concentration was not measured from Mkr N41 and Snail in 1999 and Joystick in 2000. If temperature was not measured, it was impossible to estimate other fluid properties. However, the strong positive association between temperature and sulphide concentration at diffuse SRZ vents ($n = 90$ fluid samples, $R^2 = 0.837$, Figure 6.1) was used to estimate sulphide data for the three biological samples with temperature but no sulphide data.

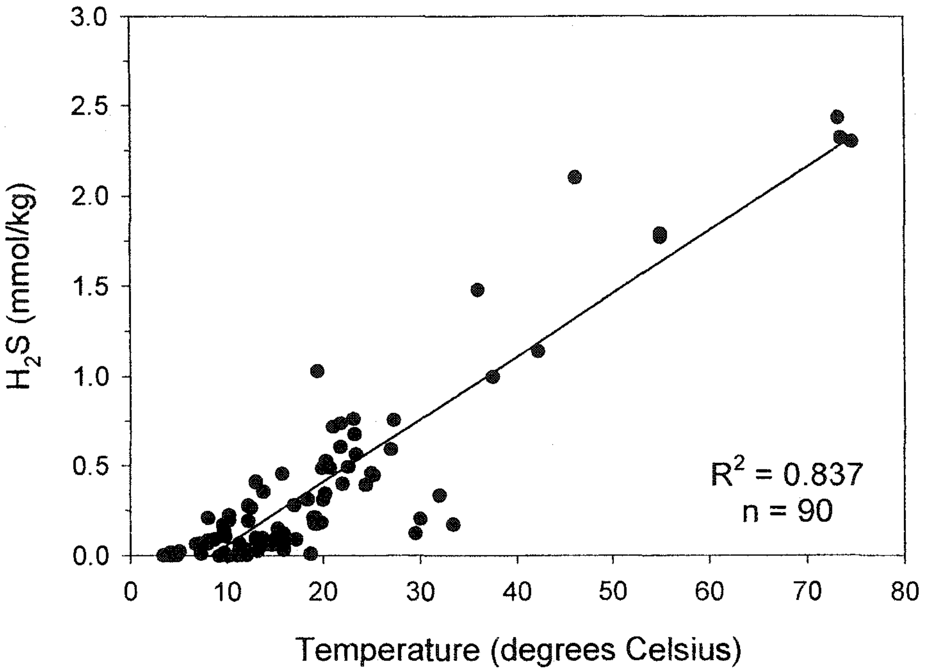


Figure 6.1. The concentration of hydrogen sulphide is positively related to vent fluid temperature at South Rift Zone vents on Axial Volcano. Data points are from 90 fluid samples taken from diffuse flow SRZ vents from 1998 to 2001 (from Butterfield et al. submitted). This relationship (H_2S = -0.288 + 0.035 temperature) was used to estimate H_2S concentration from temperature for three biological samples (Mkr N41 and Snail in 1999 and Joystick in 2000).

Analyses

A common way to determine patterns in species distributions and abundances at a defined spatial scale is to sample multiple sites and observe the associated species using some measure of species occurrence (e.g. presence/absence, density, relative abundance, relative biomass). As several species typically occur at each site, it would be ideal to represent the scatter of sites in a multidimensional diagram with the number of axes equal to the number of observed species. Although this is valid mathematically, it is impossible to represent more than three axes on paper. One option for teasing out trends in such multivariate data sets is thus to plot the sites against all possible pairs (or trios) of species, but this method is often too tedious and ineffective (Legendre & Legendre 1998). A better approach is to project the multidimensional scatter onto a bivariate graph whose axes represent the major trends of variation in the data (Legendre & Legendre 1998).

Ordination is the general term for techniques that calculate the main gradients of variation in multivariate data sets. Their overall aim is to effectively summarize the bulk of matrix variation in the first few ordination axes so that the sites (or species) can be meaningfully represented in two-dimensional space (Legendre & Legendre 1998). For example, sites most similar to one another (in terms of species data) are closely positioned in ordination space, while sites very different from one another are positioned distally. The ordination axes are mathematical constructs, but they usually represent ecologically meaningful gradients that can be revealed by relating potential explanatory variables (e.g. an environmental measurement) to the axes (Jongman et al. 1987).

Correspondence analysis (CA), a reduced-space ordination method, was used to examine relationships among the biological collections. CA simultaneously ordinates sites and species by maximizing the intercorrelation of their respective axis coordinates (Ludwig & Reynolds 1987). It is an unconstrained method since the ordination of the site by species matrix is not controlled by its relationship to another matrix (e.g. environmental variables). CA is widely used in ecology for ordinations of species presence-absence or abundance data, and is based on the χ^2 distance measure making it useful for data sets with a large number of null values (Legendre & Legendre 1998). Since only a few vent species have ubiquitous distributions, there are many zeros in the species by site matrices analysed here, making CA an appropriate method. Jackson

(1997) also recommends CA for proportional data (e.g. relative abundances) as the solution is unaffected by data standardization.

I present results from three data sets: (1) relative species abundances of total fauna (macro- and meiofauna combined) from all 22 samples (tubeworm grabs and suction samples combined), (2) species presence-absence data of total fauna from all 22 samples, and (3) relative biomass of macrofauna from 16 tubeworm grabs. Since ordinations based on macrofauna (relative abundances and presence-absences) of the 22 samples yielded very similar results as ordinations based on total fauna, they are not presented. CA analyses were implemented in PC-Ord4.

Prior to the analyses, three year 1 samples were omitted due to low sample size (less than 50 macrofaunal individuals were collected, Table 6.1). A shortcoming of CA is that it places more emphasis on abundance differences between rare species than the same difference between common species (Legendre & Gallagher 2001). To avoid this, species occurring in only one collection were excluded (Gauch 1982) and rare species were downweighted with the PC-Ord method (McCune & Mefford 1999).

All biological samples, defined as one vent in one year, were considered separately. Lack of complete independence among collections is possible since most vent sites were sampled in two or three subsequent years. However, faunal assemblages and vent habitat features varied substantially among sampling dates, supporting the assumption of independence. Furthermore, one goal of the present analysis is to determine if time explains variation in the species data; Fairchild et al. (2000) also treat samples separated in time but not space as independent in a similar type of ordination analysis.

To interpret ordination patterns, relationships of species and habitat characteristics to each of the first three CA axes were examined. Species-to-axis associations reveal which species are driving the ordination of sites in reduced space, while habitat-to-axis associations point to possible habitat gradients correlated with the CA axis. This is an 'indirect gradient analysis' (ter Braak 1986) since the unconstrained ordination pattern is secondarily related to the habitat variables. This allows for an expression of true community gradients, followed by an independent assessment of the importance of the habitat variables (McCune & Mefford 1999). For ordinal and quantitative data I examined Kendall's Tau rank correlations between (1) relative species abundance or relative biomass and the ordination axis scores for each faunal sample, and (2) the habitat variables and the ordination axis scores for each faunal sample. Significance levels were not adjusted for multiple comparisons, but the Bonferroni adjusted alpha level (for 0.05) is listed for all results.

Kendall's Tau (τ) is a nonparametric correlation coefficient analogous to Pearson's r as it only reveals linear associations. The square of τ (τ^2) is a measure of how much variability in one variable is accounted for by its correlation to a second variable (Zar 1999). Interpreting ordinations solely on the basis of correlation coefficients can be misleading since outliers can have a large effect and the coefficients do not capture non-linear relationships (McCune & Mefford 1999). These possibilities were managed by visually examining scatter plots of species and habitat data against the first three CA axes. I report the obvious nonlinear relationships or effects of outliers.

Kendall's Tau could not be used to interpret nominal data (species presence/absence data and binary habitat variables) as it is based on ranked values. For binary variables, I first explored the data by overlaying the species or habitat matrix on the site ordinations and visually determined which variables likely had significant associations with any one of the first three CA axes. Subsequent *t*-tests determined if the CA site values differed significantly between the presence (1) and absence (0) of the species or habitat variable. Only those variables with three or more observations in either the 0 or 1 category were examined. Rank correlations and *t*-tests were implemented in SPSS 11.0.

Direct relationships of species to habitat variables were also explored. The species and habitat variables significantly associated with the first 3 CA axes were examined with scatter plots and correlation coefficients. Species to habitat correlations (Kendall's Tau) were also calculated for the entire relative abundance and relative biomass data sets to determine if species other than those significantly associated with the ordination axes were related habitat variables.

I chose to use an indirect gradient analysis over a direct gradient analysis (e.g. CCA) for several reasons. First, the indirect approach allows for maximal use of the data since habitat variables with missing values can be correlated in a post-hoc fashion to the

CA axes simply by excluding the cases without data. CCA cannot accommodate data gaps in the habitat matrix, requiring either biological collections or habitat variables to be culled. Second, very strong relationships between the species and environmental matrices are inevitable with CCA if the number of samples is small and the number of habitat variables is large (McCune & Mefford 1999). I have too few samples (n=22 and n=16) relative to habitat variables (n=11) to be confident a CCA would be meaningful (G. Bradfield pers. comm.). Third, gradients in community structure can be distorted if noisy or unimportant environmental variables are included in the CCA analysis, and it is inappropriate to interpret CCA as a description of community structure per se (Økland 1996, McCune 1997). Habitat variables important to vent fauna are still unknown; the goal of this chapter is to describe community structure and determine which variables are related to, and hence *may* be important to, species patterns.

Results

Vent Characteristics

Annual means of the six quantitative vent fluid properties are presented in Figure 6.2, and the data for individual vents are presented in Figure 6.3 to illustrate spatial variation within years. Due to high among vent variability each year, there is no significant difference among the three years in temperature, H_2S/Fe and Cl at 0 Mg measurements ($p>0.05$, Kruskall-Wallis Test, Figure 6.2). H_2S/heat, H_2S concentration and pH show significant trends with time ($p<0.05$, Figure 6.2), despite vent-to-vent differences per year (Figure 6.3). Maximum H_2S/heat and H_2S concentrations decrease at the nascent vents over time: annual means between years 1 and 3 are significantly different ($p\leq0.01$), and annual means of H_2S/heat also differ between years 2 and 3 ($p=0.02$, Mann-Whitney U Test). The mean acidity of vent fluids also decreases significantly after the first year ($p<0.03$, Mann-Whitney U Test). Estimated H_2S concentrations (see Figure 6.1) are not included here (Figures 6.2 and 6.3), but they only slightly alter the significance of temporal trends: annual means of H_2S concentrations differ significantly between years 1 and 2 including the three vents with estimated H_2S ($p=0.03$) while the difference is not significant ($p=0.08$) if the three vents are excluded.

Some habitat variables are linearly correlated with each other. Correlation

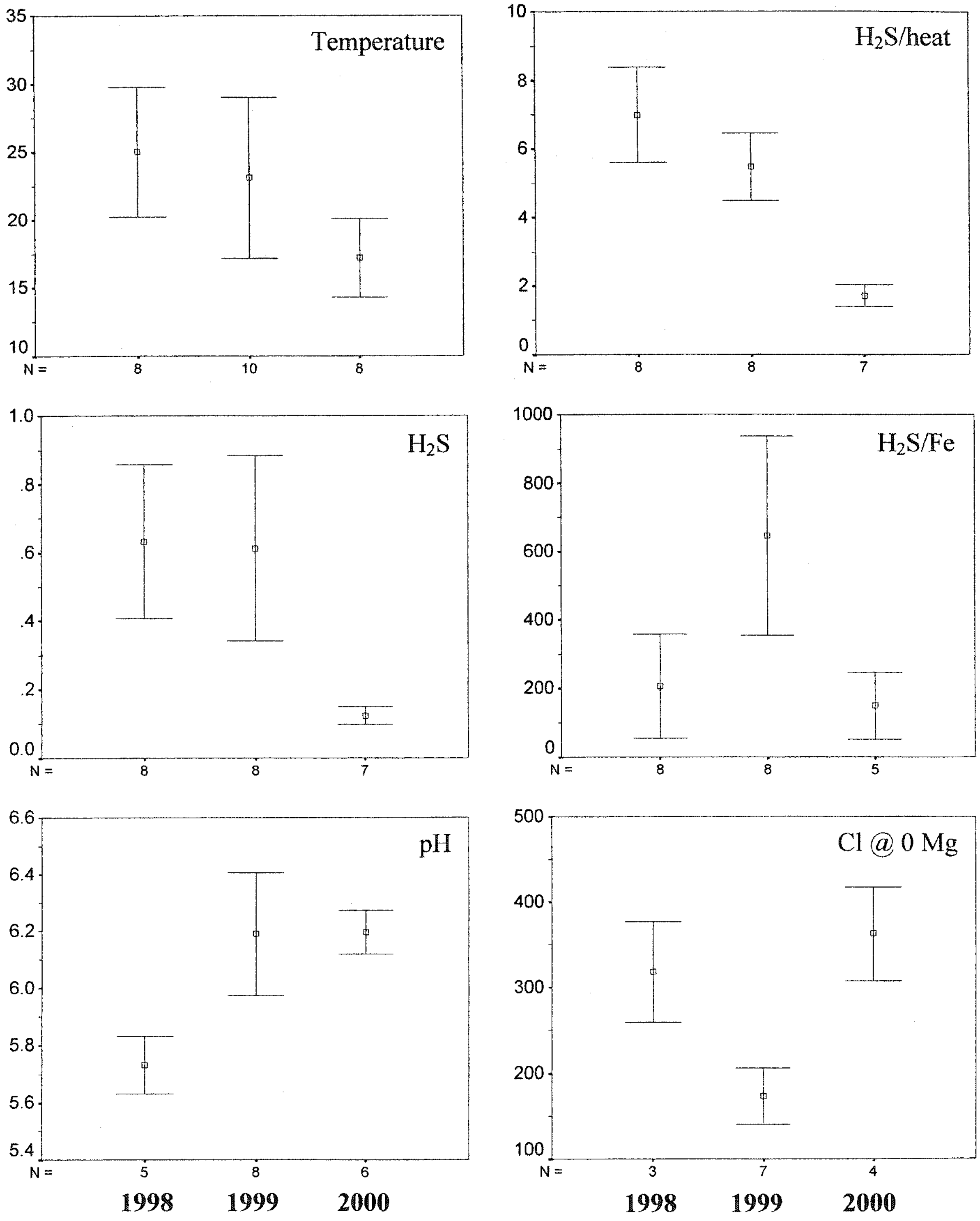


Figure 6.2. Annual means (+/- 1 standard error) of physical and chemical habitat characteristics at nascent vents sampled for fauna in any year. Maximum values per vent were used in calculations. See Table 6.2 for measurement units.

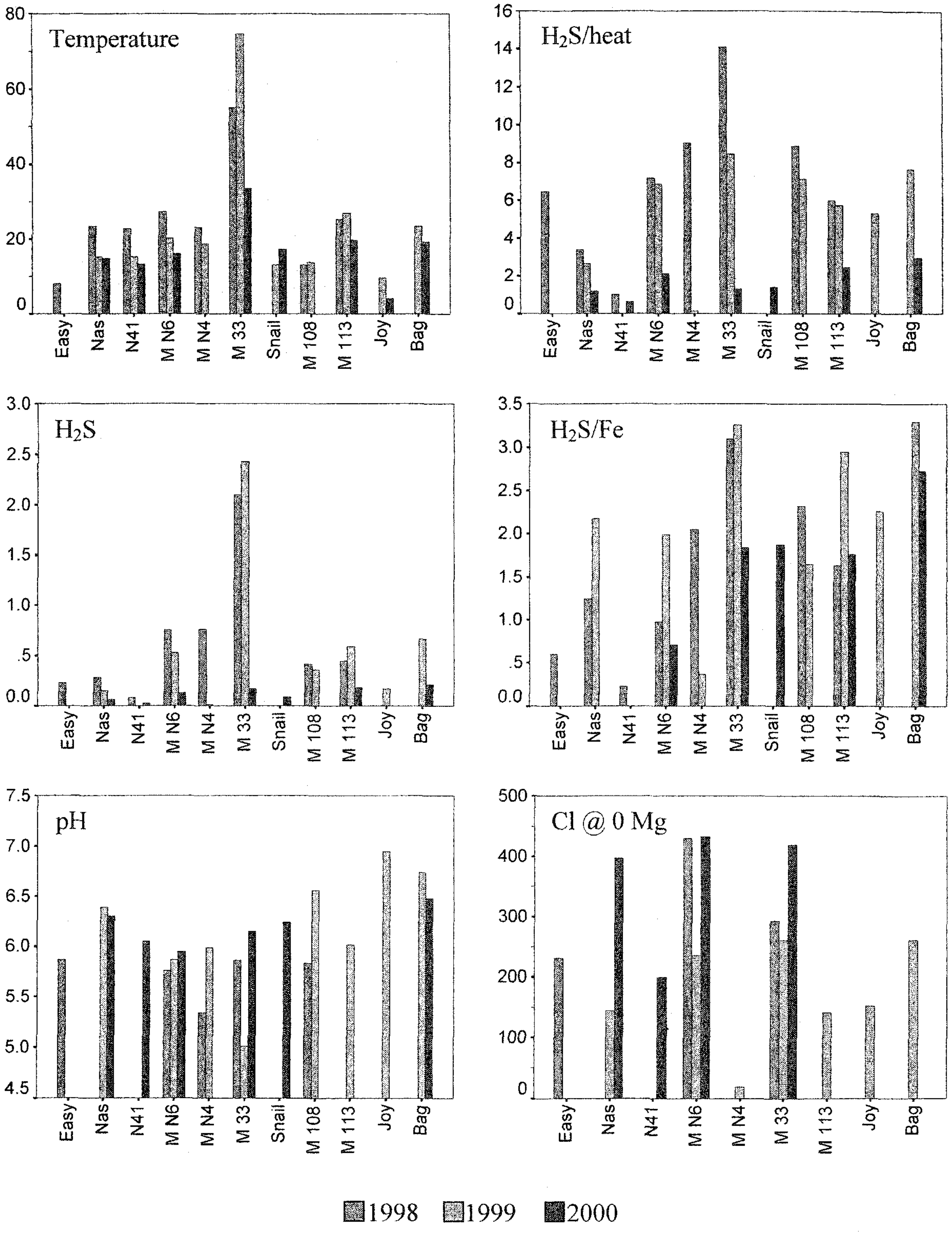


Figure 6.3. Maximum fluid measurements for South Rift Zone vents sampled for fauna in 1998, 1999 and 2000 (See Table 6.2 for measurement units). H_2S/Fe is a log scale; all others are a linear scale. Gaps indicate data are unavailable. See Figure 6.2 for annual means of each fluid property. Vents are ordered from north to south along the lava flow.

coefficients (Pearson's r and Kendall's τ), based on data from the 22 biological collections, show the following consistent trends: year is negatively associated with H_2S/heat, and temperature is positively associated with H_2S concentration and negatively associated with pH (Table 6.3). Some correlations between habitat factors are spurious since they share a common variable; for example, the correlation of H_2S/Fe and H_2S concentration (Table 6.3).

The timing of *Ridgeia piscesae* recruitment differed among nascent SRZ vents. Three vents had established tubeworm aggregations by year 1, two more vents supported tubeworm bushes by year 2, and aggregations formed at the remaining vents by year 3 (Table 6.4). Year of formation of tubeworm aggregations is unknown for two vents (Table 6.4). Vent morphology also differed: fluid vented through sheet flow cracks at Snail and Mkr 33, while all other vents occurred on lobate flows (pillars, roof or collapsed areas, Table 6.4).

Sample Numbers

After culling the three samples with less than 50 macrofaunal individuals (Table 6.1), five biological collections remained from 1998, eight collections from 1999 and nine collections from 2000. Forty-seven species were identified from these 22 samples, but seven species were omitted from the analysis due to single occurrences: *Prionospio* n. sp. 2, an unknown brittle star, an unknown amphipod, copepods Types 2, 9 and 19, and an unknown nematode. The remaining 40 species identified from 22 collections and 234,689 individuals were used for analyses.

Species patterns and habitat gradients

Total fauna, relative species abundances

The first and second CA axes explain 38% and 30% of the variance in the species data, respectively (Figure 6.4A). The relative position of the 22 faunal collections in ordination space parallels the grouping of samples found with cluster analysis (Figure 5.8): samples with high numbers of *Paralvinella pandorae* separate from vents dominated by gastropods and the dorvilleid worm *Ophryotrocha globopalpata* (Figure 6.4).

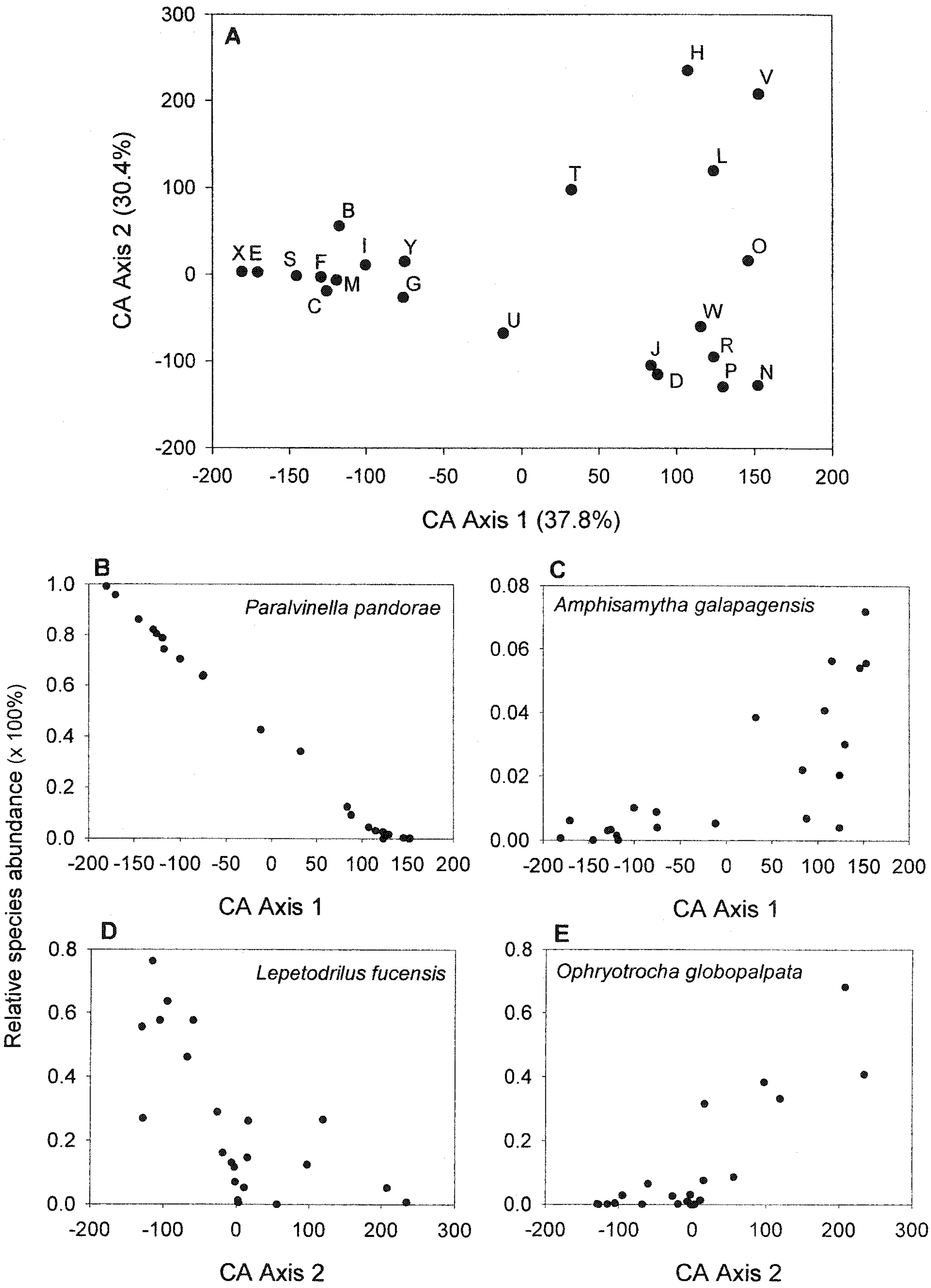
Table 6.3. Correlation of ordinal and continuous habitat variables to one another: Pearson (upper right) and Kendall's Tau (lower left) correlation coefficients. Data are taken only from the 22 biological collections (see Table 6.1). Spurious correlations between habitat factors that share a common variable are highlighted in grey. Refer to Figure 6.5 for the number of fluid samples with habitat information. Significance: * $0.01<p\leq0.05$, ** $0.001<p\leq0.01$, *** $p\leq0.001$. The presence-absence of *Ridgeia piscease* (Rp) is not significantly correlated to any of the measure habitat variables (*t*-test, $p>0.05$ in all pairwise comparisons).

	Year	Time of Rp	Temp.	H_2S	H_2S / heat	H_2S / Fe	pH	Cl @ 0 Mg	Dist.
Year		-0.02	-0.33	-0.38	-0.54 *	-0.13	0.13	0.49	0.15
Time of Rp	0.04		-0.08	-0.01	0.03	-0.04	-0.02	-0.36	-0.19
Temp.	-0.27	-0.23		0.93 ***	0.68 **	0.66 **	-0.79 ***	0.16	-0.17
H_2S	-0.37 *	-0.24	0.47 **		0.85 ***	0.77 ***	-0.65 *	0.09	-0.03
H_2S / heat	-0.45 *	-0.19	0.29	0.82 ***		0.74 ***	-0.22	0.03	0.20
H_2S / Fe	0.02	0.07	0.22	0.56 **	0.60 **		-0.29	0.07	0.30
pH	0.13	-0.17	-0.41 *	-0.05	0.05	0.09		-0.12	0.56 *
Cl @ 0 Mg	0.37	-0.27	0.09	0.13	0.13	0.06	-0.05		-0.23
Dist.	0.11	-0.03	0.01	0.26	0.27	0.45 *	0.22	-0.02	

Table 6.4. List of binary variables used to describe the habitat. The year of *Ridgeia piscesae* establishment refers to the year post-eruption when a tubeworm clump was first observed and sampled. For example, *R. piscesae* was present at Cloud N4 in year 2, but individuals were sparsely distributed rather than occurring in the typical intertwined bush aggregation. Bag City (*) was observed for the first time in year 2, but the morphology and colour of the *R. piscesae* tubes and the presence of very large *Paralvinella pandorae* strongly suggest that tubeworms had formed a bush aggregation within the prior year.

		Substratum	
Vent	Year of *R. piscesae* establishment	Crack in sheet flow	Lobate flow
Nascent	1		x
Mkr N41	1		x
Cloud N6	3		x
Cloud N4	3		x
Mkr 33	2	x	
Snail	3	x	
Mkr 108	na		x
Mkr 113	1		x
Joystick	na		x
Bag City	2*		x

Figure 6.4. A) Correspondence analysis biplot of 22 vent collections based on total species relative abundances. Total 'inertia' (variance) is 1.5691; together the first three axes explain 79.5% of the variance in the data (37.8, 30.4 and 11.3, respectively). See Table 6.1 for vent names. B-C) The relative abundances of *Paralvinella pandorae* (B) and *Amphisamytha galapagensis* (C) plotted against the first CA axis. D-E) The relative abundances of *Lepetodrilus fucensis* (D) and *Ophryotrocha globopalpata* (E) plotted against the second CA axis.


A
CA Axis 2 (30.4%)
CA Axis 1 (37.8%)
300
200
100
0
-100
-200
-200
-150
-100
-50
0
50
100
150
200
H
V
L
T
B
X
E
S
F
I
Y
M
G
C
O
U
W
J
R
P
N
D
B
Paralvinella pandorae
1.0
0.8
0.6
0.4
0.2
0.0
-200 -150 -100 -50 0 50 100 150 200
CA Axis 1
C
Amphisamytha galapagensis
0.08
0.06
0.04
0.02
0.00
-200 -150 -100 -50 0 50 100 150 200
CA Axis 1
Relative species abundance (x 100%)
D
Lepetodrilus fucensis
0.8
0.6
0.4
0.2
0.0
-200 -100 0 100 200 300
CA Axis 2
E
Ophryotrocha globopalpata
0.8
0.6
0.4
0.2
0.0
-200 -100 0 100 200 300
CA Axis 2

The first ordination axis is driven almost exclusively by *Paralvinella pandorae* (Figure 6.4B): the relative abundance of this species is negatively correlated with CA Axis 1 ($p<0.001$, Table 6.5A) and 91% of the variation in *P. pandorae* is explained by this correlation. The second ordination axis is driven by the relative abundances of the two common gastropods, *Lepetodrilus fucensis* and *Depressigyra globulus* and the dorvilleid polychaete *Ophryotrocha globopalpata*. The gastropods are negatively associated with CA 2 ($p<0.001$, Table 6.5A) and *O. globopalpata* is positively associated with CA 2 ($p<0.001$, Table 6.5A). The species to CA-axes correlations reveal that a few less abundant species are also important in ordering the samples (Table 6.5A). For example, *Amphisamytha galapagensis* is positively associated with CA Axis 1 ($p<0.001$, Table 6.5A), although it accounts for 0 to ~7% of all individuals collected at any given site. The relative abundances of *P. pandorae* and *A. galapagensis* are negatively correlated ($\tau = -0.613$, $p<0.001$).

A subset of the habitat variables is significantly related to the first three CA axes (Table 6.5B, Figure 6.5). The timing of *Ridgeia piscesae* recruitment is positively correlated with CA Axis 1 ($p=0.001$). Year and H_2S/heat are significantly correlated with CA Axis 2 ($p=0.014$ and $p=0.019$), and temperature and pH are associated with the third axis ($p=0.016$ and $p=0.010$). *R. piscesae* presence ($p<0.001$) and substratum type ($p=0.042$) also relate to the first CA axis (Table 6.5B).

Few species and no habitat characteristics display an obvious non-linear relationship with any of the first three CA axes. *Paralvinella pandorae* shows a humped relationship with CA axis 2 (Figure 6.6); relative abundances peak at intermediate CA2 values. However, none of the measured habitat variables follow this pattern.

Direct comparisons of the species and habitat variables significantly associated with the first three CA axes show that *Paralvinella pandorae* and *Amphisamytha galapagensis* are related in opposite directions to the timing of tubeworm bush formation (Figures 6.7A,B). Relative limpet abundances are positively correlated with year and negatively correlated with H_2S/heat (Figures 6.7C,E) and H_2S concentration (Table 6.6). The scaleworm *Levensteiniella kincaidi* is negatively associated with temperature (Figure 6.7H). Correlations of *Ophryotrocha globopalpata* to year and H_2S/heat and the snail *Depressigyra globulus* to H_2S/heat are not significant (Figures 6.7D,F,G). Correlations

Table 6.5. Species and habitat correlations to CA site scores generated using relative abundances of total fauna from 22 collections (see Figure 6.4A). A) Correlations of relative species abundances to CA axes 1-3. B) Habitat characteristic correlations to CA axes 1-3. Correlation direction and significance is listed for ordinal and continuous variables (Kendall's Tau) and for binary variables (*t*-test). See Figure 6.5 for number of measurements for each habitat variable. Significance: * $0.01<p\leq 0.05$, ** $0.001< p\leq 0.01$, *** $p\leq 0.001$ and NS = not significant. Only highly significant ($p\leq 0.01$) associations are shown for A. P-values are not adjusted for multiple comparisons; the Bonferroni correction is $p=0.001$ (A) and $p=0.005$ (B).

A)

Species	CA Axis 1	CA Axis 2	CA Axis 3
Paralvinella pandorae	-0.954***		
Amphisamytha galapagensis	0.625***		
Depressigyra globulus	0.471**	-0.540***	
Levensteiniella kincaidi	0.431**		0.410**
Lepetodrilus fucensis		-0.558***	
Ophryotrocha globopalpata		0.540***	
Branchinotogluma spp.		0.403**	
Orbiniella unk. sp.			0.520**
Vampiropolynoe embleyi			-0.442**
Aphotopontius forcipatus	0.463**		
Harpactocoida	0.513***		

B)

Habitat Characteristic	CA Axis 1	CA Axis 2	CA Axis 3
Binary variables			
Presence of *Ridgeia piscesae*	- ***	NS	NS
Substratum: crack in sheet flow	+ *	NS	NS
Substratum: lobate flow	- *	NS	NS
Ordinal and continuous variables			
Year	0.163	-0.425*	-0.005
Timing of *Ridgeia piscesae* recruitment	0.595***	0.007	-0.207
Maximum H_2S concentration	-0.305	0.284	0.053
Maximum H_2S/heat	-0.211	0.379*	0.168
Maximum temperature	-0.201	0.116	-0.392*
Maximum H_2S/Fe	0.048	0.105	0.105
pH	-0.051	-0.026	0.538**
Cl @ 0 Mg	-0.236	-0.309	-0.164
Distance from N end of flow	0.172	0.108	0.155

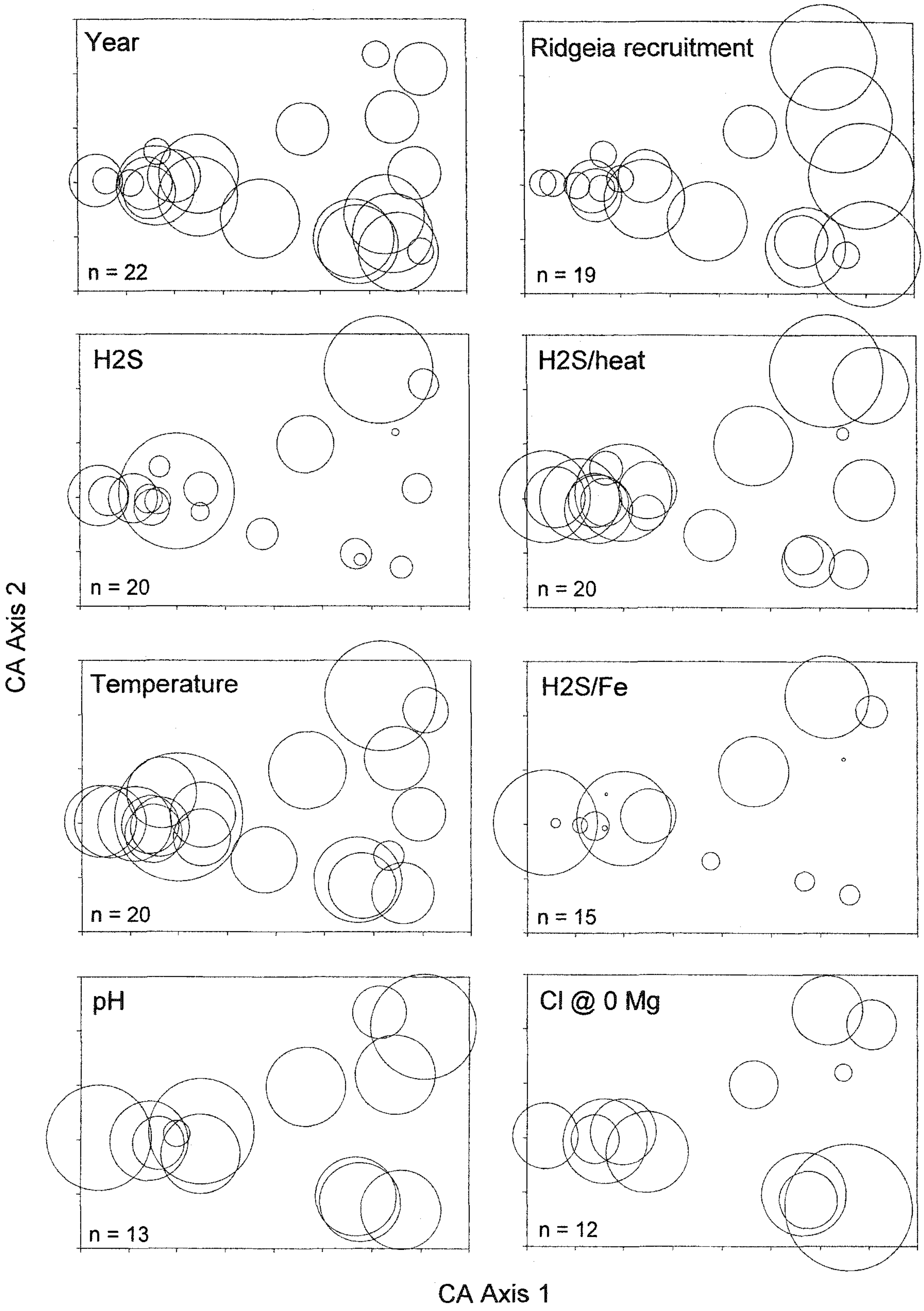


Figure 6.5. Habitat variables superimposed on the site ordinations (CA based on relative abundance of total fauna at 22 sites). Size of circle is proportional to magnitude of variable.

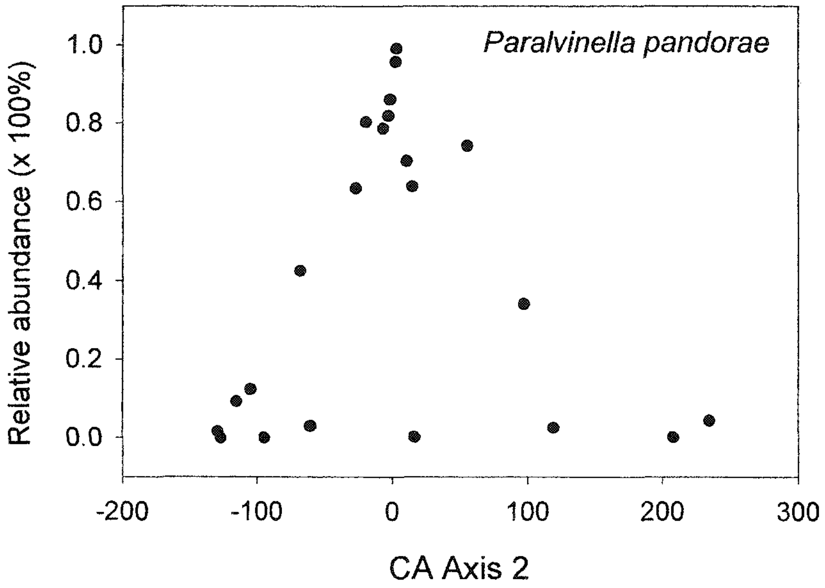
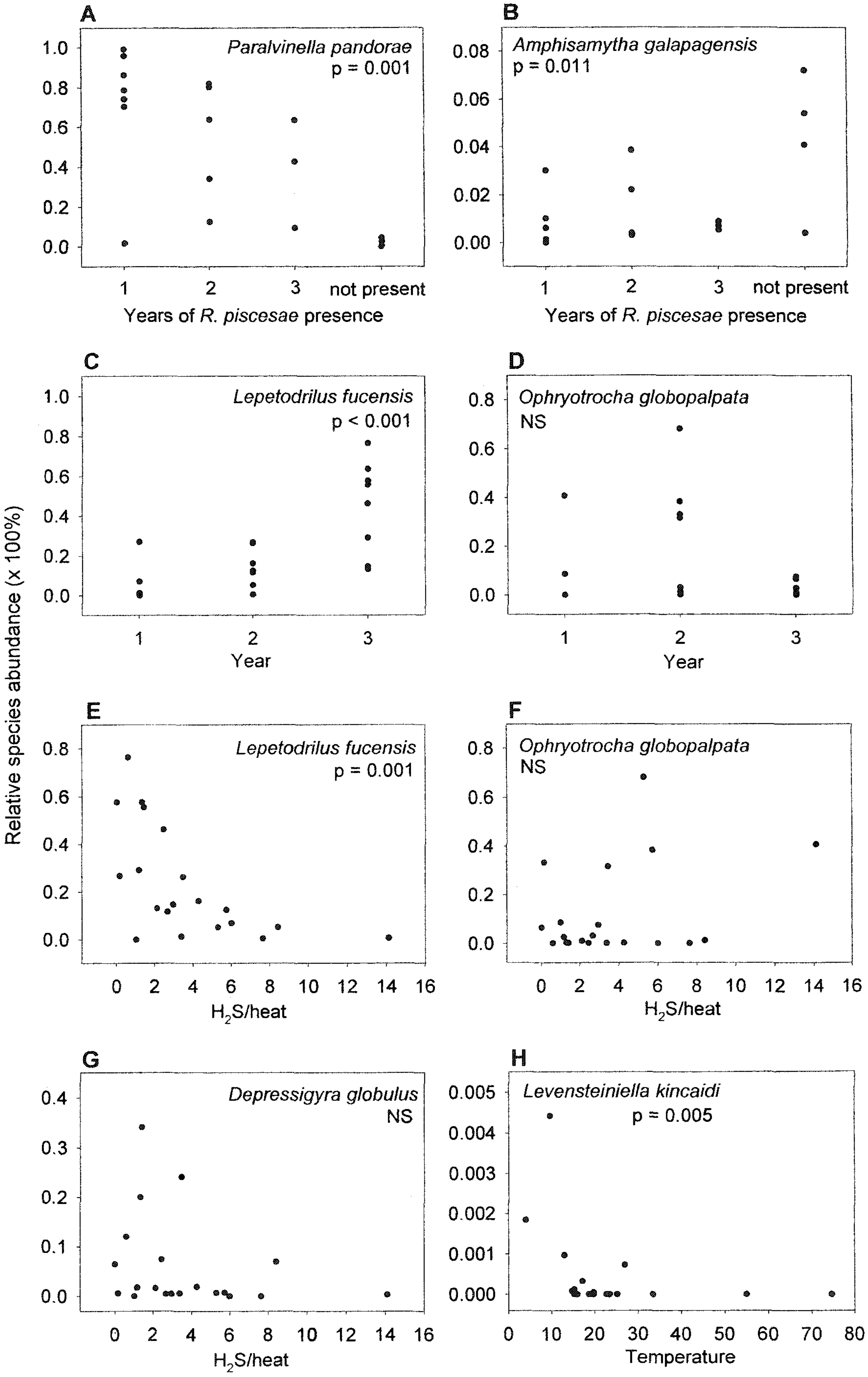


Figure 6.6. The relative abundance of *Paralvinella pandorae* displays a humped relationship with CA Axis 2 (see Figure 6.4A).

Figure 6.7. The relationship of selected habitat variables to selected relative species abundances. P-values indicate the significance of the correlation coefficient (Kendall's Tau). NS = not significant.


A
Paralvinella pandorae
p = 0.001
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
not present
Years of R. piscesae presence
B
Amphisamytha galapagensis
p = 0.011
0.08
0.06
0.04
0.02
0.00
1
2
3
not present
Years of R. piscesae presence
C
Lepetodrilus fucensis
p < 0.001
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
Year
D
Ophryotrocha globopalpata
NS
0.8
0.6
0.4
0.2
0.0
1
2
3
Year
Relative species abundance (x 100%)
E
Lepetodrilus fucensis
p = 0.001
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
14
16
H_2S/heat
F
Ophryotrocha globopalpata
NS
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
14
16
H_2S/heat
G
Depressigyra globulus
NS
0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10
12
14
16
H_2S/heat
H
Levensteiniella kincaidi
p = 0.005
0.005
0.004
0.003
0.002
0.001
0.000
0
10
20
30
40
50
60
70
80
Temperature

of the relative abundances of all species to non-binary habitat variables reveal other species-habitat associations not uncovered by the ordination analysis: *Paralvinella palmiformis* is positively associated with maximum temperature and H_2S concentration, and two meiofaunal species are significantly related to vent location (Table 6.6).

Total fauna, species presence-absence

The first and second ordination axes explain 16% and 13% of the variance in the species data, respectively (Figure 6.8A). There are no clear site groupings as in Figure 6.4A (relative abundance data); the sites are quite evenly positioned throughout the ordination space. The pattern of site associations in Figure 6.8 is not very consistent with the pattern found with cluster analysis (Figure 5.7). The contrasting patterns are likely due to the different distance measures used in the cluster (Jaccard index) versus CA (chi-square distance) analyses. Eleven species are positively correlated with CA Axis 1 (Table 6.7A), and none are negatively associated. Other species significantly correlated with CA Axis 2 and 3 are listed in Table 6.7A. The two species most significantly related to CA1 and CA3 are presented (Figures 6.8B-D).

Year and the presence of *Ridgeia piscesae* are positively correlated with CA Axis 1 (p=0.003 and p=0.024), substratum type is associated with CA Axis 2 (p=0.011) and temperature is negatively correlated with CA Axis 3 (p=0.019, Table 6.7B). Nine of the 11 species positively associated with CA 1 arrived at the nascent vents either in year 2 or year 3, while the other two species (*Opisthotrochopodus tunnicliffeae* and Harpacticoida) were present at only one or two sites in year 1 (see Figures 6.9A-D for examples). Only one of the nine species associated with CA Axis 2 is also significantly related to substratum type: *Protomystides verenae* only occurs at lobate vents (Chi-square test, p=0.05). Three of the five species associated with CA Axis 3 are significantly correlated with temperature: *Paralvinella palmiformis* presence is positively associated (p=0.045) while *Humesipontius arthuri* and *Lacunoides vitreus* are negatively associated (p=0.029 and p=0.044, Mann-Whitney U Test, Figures 6.9E-H).

None of the species nor any of the habitat characteristics display an obvious non-linear relationship with any of the first three CA axes.

Table 6.6. Kendall's Tau correlations of relative species abundances to non-binary habitat variables. Only associations significant at $p \leq 0.01$ are presented; no species are correlated with pH, H_2S/Fe and Cl @ 0 Mg at this level of significance. Rp clump = index of *Ridgeia piscesae* bush age. * Associations that were not uncovered by the ordination analysis. P-values are not adjusted for multiple comparisons; the Bonferroni correction is p=0.001.

Species	Rp clump (n = 19)	Year (n = 22)	Temp. (n = 20)	H_2S (n = 20)	H_2S/heat (n = 20)	Dist. (n = 22)
P. pandorae	-0.608 p = 0.001					
A. galapagensis	0.462 p = 0.011					
L. fucensis		0.604 p < 0.001		-0.442* p = 0.006	-0.516 p = 0.001	
P. palmiformis			0.470* p = 0.006	0.456* p = 0.007		
L. kincaidi			-0.498 p = 0.005			
B. rimemsis						0.459* p = 0.009
Podocopida						0.492* p = 0.004

Figure 6.8. A) Correspondence analysis biplot of 22 vent collections based on total species occurrences. Total 'inertia' (variance) is 1.0828; together the first three axes explain 40.4% of the variance in the data (15.9, 13.1 and 11.4%, respectively). See Table 6.1 for vent names. B-C) The presence and absence of Harpacticoida (B) and Podocopida (C) plotted against the first CA axis. D-E) The presence and absence of *Humesipontius arthuri* (B) and *Lacunoides vitreus* (C) plotted against the third CA axis.

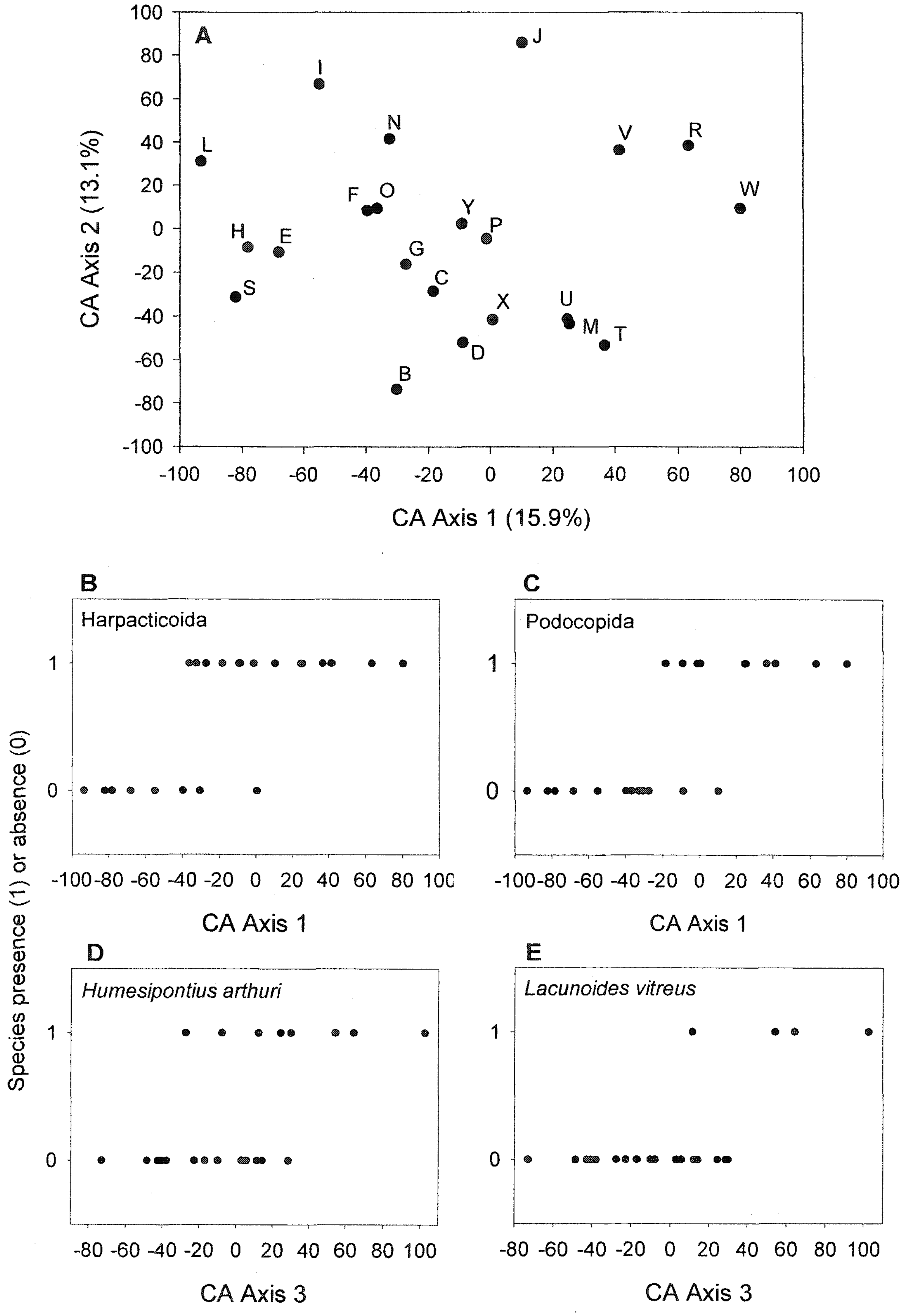

A
J
I
N
V
R
L
W
F
O
Y
P
H
E
G
S
C
X
U
M
T
D
B
CA Axis 2 (13.1%)
100
80
60
40
20
0
-20
-40
-60
-80
-100
-100
-80
-60
-40
-20
0
20
40
60
80
100
CA Axis 1 (15.9%)
B
Harpacticoida
C
Podocopida
1
0
-100-80 -60 -40 -20 0 20 40 60 80 100
CA Axis 1
-100-80 -60 -40 -20 0 20 40 60 80 100
CA Axis 1
Species presence (1) or absence (0)
D
Humesipontius arthuri
E
Lacunoides vitreus
1
0
-80 -60 -40 -20 0 20 40 60 80 100
CA Axis 3
-80 -60 -40 -20 0 20 40 60 80 100
CA Axis 3

Table 6.7. Species and habitat correlations to CA site scores generated using presence-absence data of total fauna from 22 collections (see Figure 6.8A). A) Direction and significance of the species significantly associated with CA Axes 1-3 (*t*-tests). B) Correlations of habitat characteristics to CA axes 1-3. Direction and significance of the association is shown for binary variables (*t*-test) and for ordinal and continuous variables (Kendall's Tau). See Figure 6.5 for number of sites measured for each habitat variable. Significance: * $0.01<p\leq 0.05$, ** $0.001<p\leq 0.01$, *** $p\leq 0.001$ and NS = not significant. See Table 6.5 for the Bonferroni correction. Continued on next page.

A)

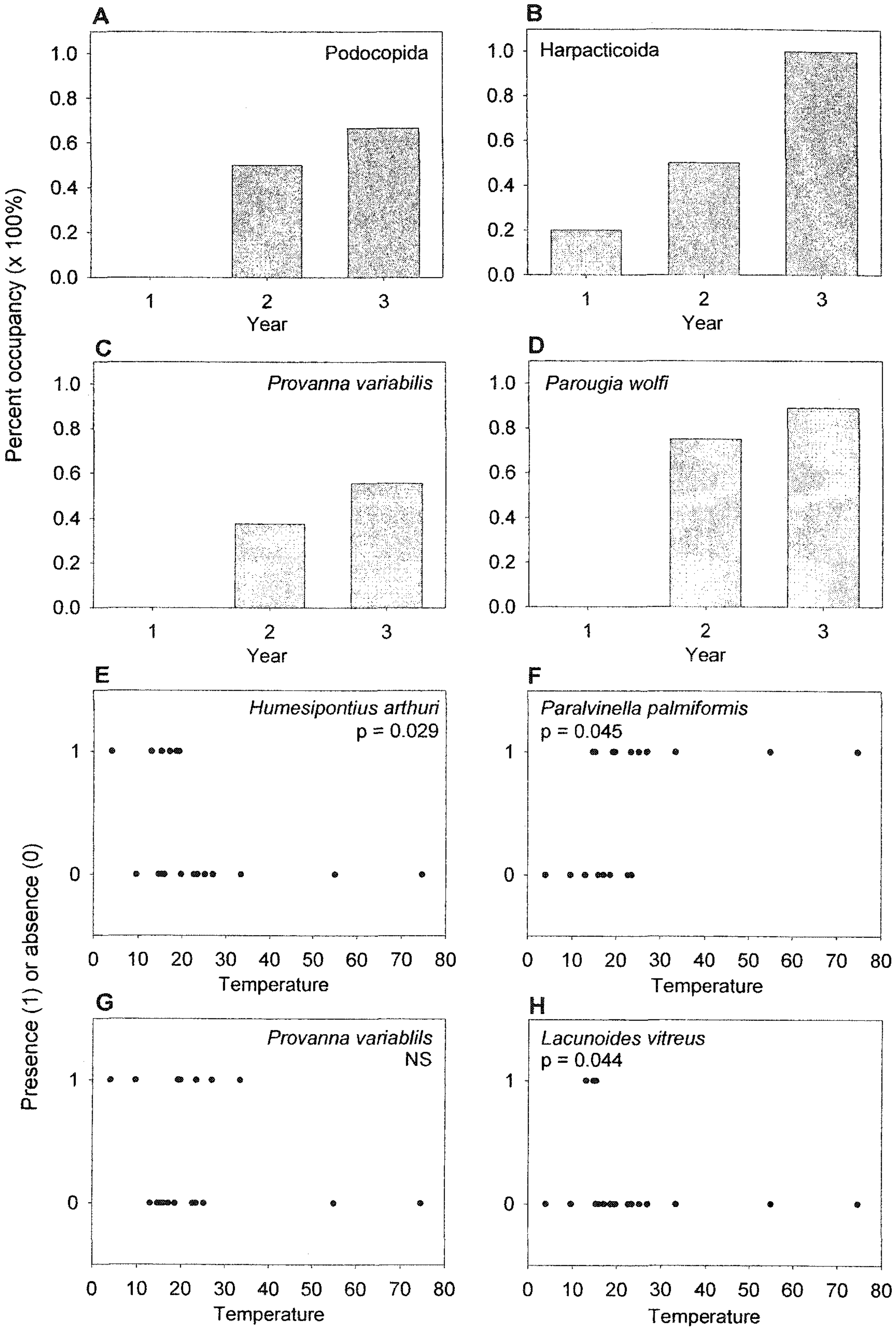
Habitat Characteristic	CA Axis 1	CA Axis 2	CA Axis 3
Levensteiniella kincaidi	+ *		
Nereis piscesae	+ *		
Ammothea verenae	+ *		
Opisthotrochopodus tunnicliffeae	+ **		
Parougia wolfi	+ **		
Provanna variabilis	+ **		- *
Pyropelta musaica	+ **		
Helicoradomenia juani	+ **		
Harpacticoida	+ ***		
Barathricola rimensis	+ ***		
Podocopida	+ ***		
Protomystides verenae		- *	
Hesiospina vestimentifera		+ *	
Depressigyra globulus		+ *	
Calyptogena pacifica		- *	
Stygiopontius quadrispinosus		+ *	
Misophriopsus longicauda		+ *	
Euphilomedes climax		- ***	
Paralvinella palmiformis			- *
Vampiropolynoe embleyi			- *
Lacunoides vitreus			+ ***
Humesipontius arthuri			+ ***

Table 6.7 continued.

B)

Habitat Characteristic	CA Axis 1	CA Axis 2	CA Axis 3
Binary variables			
Presence of *Ridgeia piscesae*	+ *	NS	NS
Substratum: crack in sheet flow	NS	+ *	NS
Substratum: lobate flow	NS	- *	NS
Ordinal and continuous variables			
Year	0.509**	0.058	-0.005
Timing of *Ridgeia piscesae* recruitment	-0.140	0.261	-0.007
Maximum H_2S concentration	-0.147	-0.021	-0.168
Maximum H_2S/heat	-0.137	0.011	-0.116
Maximum temperature	-0.201	-0.169	-0.381*
Maximum H_2S/Fe	0.105	0.162	-0.162
pH	0.231	0.051	0.205
Cl @ 0 Mg	0.164	0.055	-0.091
Distance from N end of flow	0.262	0.136	-0.018

Figure 6.9. The relationship of selected species and their percent site occupancy (A-D) to year, and the relationship of selected species occurrences to temperature (E-H). P-values indicate the significance of the *t*-test. NS = not significant.


A
Podocopida
B
Harpacticoida
C
Provanna variabilis
D
Parougia wolfi
Percent occupancy (x 100%)
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
Year
E
Humesipontius arthuri
p = 0.029
F
Paralvinella palmiformis
p = 0.045
G
Provanna variablils
NS
H
Lacunoides vitreus
p = 0.044
Presence (1) or absence (0)
1
0
0 10 20 30 40 50 60 70 80
Temperature

Macrofauna, relative species biomass

The first and second ordination axes explain 42% and 28% of the variance in the species biomass data, respectively (Figure 6.10A). The relative position of the 16 faunal collections in ordination space parallels the three grouping of samples found with cluster analysis (Figure 5.10A): samples with *Paralvinella pandorae* contributing most to total assemblage biomass separate from vents whose biomass is dominated by *P. palmiformis* or *Lepetodrilus fucensis*. Marker N41 in 1998 (sample B) is unique as scale worms dominate total assemblage biomass (Figure 6.10A).

The relative biomasses of the two species most highly correlated with the first two CA axes are illustrated in Figures 6.10B-E. The first axis is driven by *Paralvinella pandorae* and *Branchinotogluma* spp. (Figures 6.10B,C); the relative biomasses of these species are positively correlated with CA Axis 1 ($p<0.001$ for both species, Table 6.8A). The second axis is driven by the relative biomasses of *Paralvinella palmiformis* and the two common gastropods, *Lepetodrilus fucensis* and *Depressigyra globulus*. *P. palmiformis* is negatively associated and the gastropods are positively associated with CA 2 ($p<0.001$ in all cases, Table 6.8A). No species are highly correlated ($p\leq0.01$) with the third axis. To determine if the anomalous sample B (Marker N41 in 1998) influences the results, an analysis excluding this sample was performed. Overall, the effect of sample B is minor: the gastropod and alvinellid correlations to their respective CA axes become slightly stronger, *Branchinotogluma* spp. correlates less strongly to CA axis 1 ($\tau = 0.471$, $p=0.018$), and no other species show significant correlations with any of the axes.

The relationships of non-binary habitat variables to the first two ordination axes are illustrated in Figure 6.11. The timing of *Ridgeia piscesae* recruitment ($p=0.015$) and year ($p=0.033$) are negatively correlated with CA Axis 1 (Table 6.8B). Maximum H_2S concentration and H_2S/heat are negatively correlated with CA Axis 2 ($p=0.048$ and $p=0.024$, Table 6.8B). There are no significant correlations between CA Axis 3 and the non-binary habitat variables, and substratum type is not associated with any axis (Table 6.8B). None of the species nor any habitat characteristic displays an obvious non-linear relationship with any of the first three CA axes.

Species significantly associated with an ordination axis were directly compared to the habitat variables significantly associated with the same axis (see Figure 6.12 for

Figure 6.10. A) Correspondence analysis biplot of 16 vent collections (tubeworm grabs only) based on relative species biomass. Total 'inertia' (variance) is 1.4901; together the first three axes explain 91.6% of the variance in the data (42.1, 27.7 and 21.7%, respectively). See Table 6.1 for vent names. B-C) The relative biomasses of *Paralvinella pandorae* (B) and *Branchinotogluma* spp. (C) plotted against the first CA axis. D-E) The relative biomasses of *Paralvinella palmiformis* (D) and *Lepetodrilus fucensis* (E) plotted against the second CA axis.

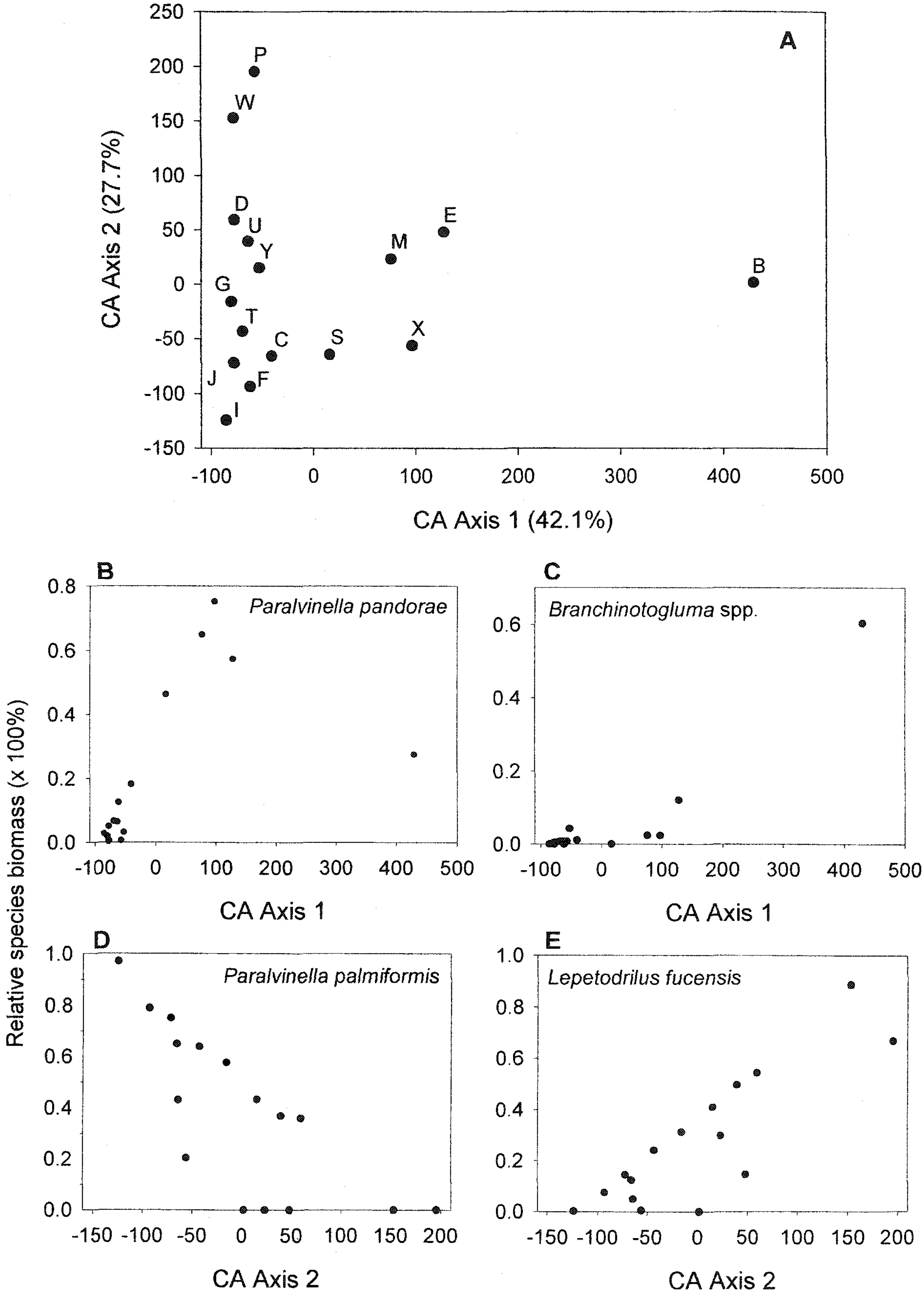

A
CA Axis 2 (27.7%)
CA Axis 1 (42.1%)
P
W
D
U
Y
G
T
C
S
X
M
E
B
J
F
I
250
200
150
100
50
0
-50
-100
-150
-100
0
100
200
300
400
500
B
Paralvinella pandorae
C
Branchinotogluma spp.
CA Axis 1
CA Axis 1
D
Paralvinella palmiformis
E
Lepetodrilus fucensis
CA Axis 2
CA Axis 2
Relative species biomass (x 100%)
0.0
0.2
0.4
0.6
0.8
1.0
-150
-100
-50
0
50
100
150
200

Table 6.8. Species and habitat correlations to CA site scores generated using relative biomass of macrofauna from 16 collections (see Figure 6.10A). A) Kendall's Tau correlations of relative species biomass to CA axes 1-3. B) Correlations of habitat characteristics to CA axes 1-3. Direction and significance of the association is shown for binary variables (*t*-test) and for ordinal and continuous variables (Kendall's Tau). See Figure 6.11 for number of sites measured for each habitat variable. Significance: * $0.01<p\leq 0.05$, ** $0.001<p\leq 0.01$, *** $p\leq 0.001$ and NS = not significant. Only highly significant (** and ***) associations are shown for A. P-values are not adjusted for multiple comparisons; the Bonferroni correction is p=0.003 (A) and p=0.005 (B).

A)

Species	CA Axis 1	CA Axis 2	CA Axis 3
Paralvinella pandorae	0.617***		
Branchinotogluma spp.	0.644***		
Paralvinella palmiformis		-0.714***	
Lepetodrilus fucensis		0.600***	
Depressigyra globulus		0.532***	

B)

Habitat Characteristic	CA Axis 1	CA Axis 2	CA Axis 3
Binary variables			
Substratum: crack in sheet flow	NS	NS	NS
Substratum: lobate flow	NS	NS	NS
Ordinal and continuous variables			
Year	-0.442*	0.318	0.134
Timing of *Ridgeia piscesae* recruitment	-0.521*	0.058	0.313
Maximum H_2S concentration	0.167	-0.367*	-0.150
Maximum H_2S/heat	0.217	-0.417*	-0.233
Maximum temperature	0.017	-0.303	0.101
Maximum H_2S/Fe	-0.424	-0.303	0.182
pH	0.333	0.022	-0.067
Cl @ 0 Mg	0.111	0.333	-0.111
Distance from N end of flow	-0.061	0.044	-0.131

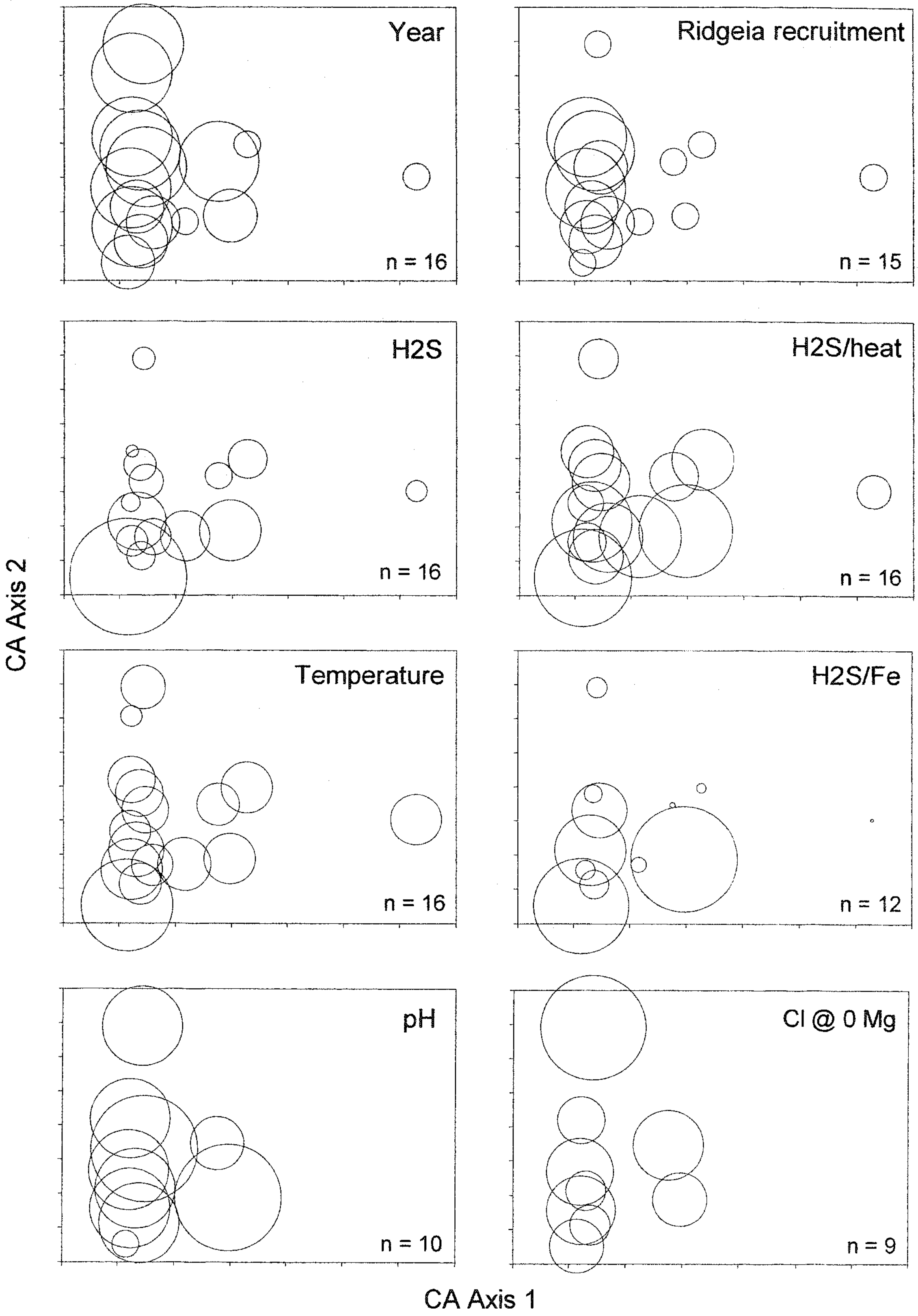
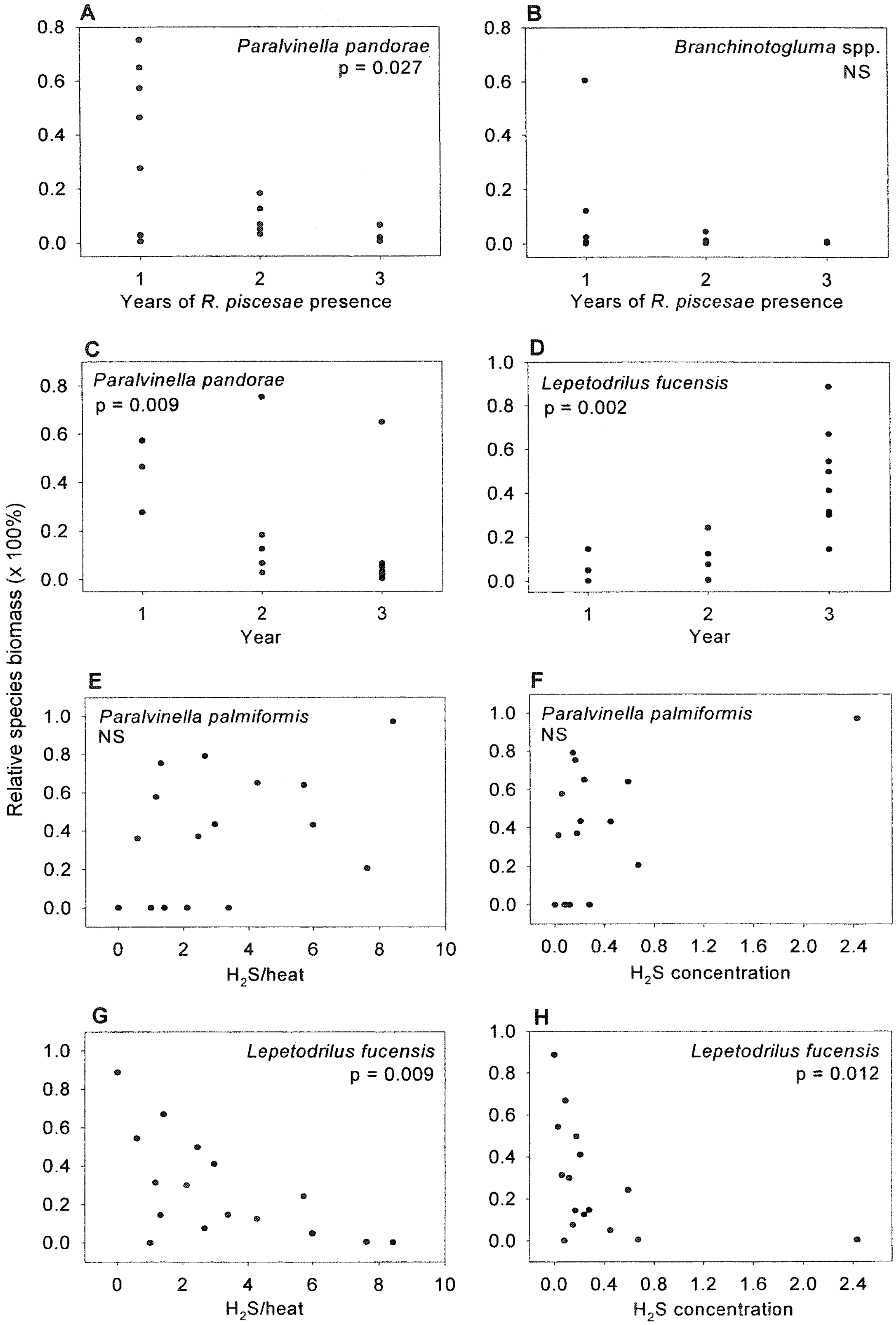


Figure 6.11. Habitat variables superimposed on the site ordinations (CA based on relative biomass of macrofauna in 16 samples). Circle size is proportional to variable magnitude.

Figure 6.12. The relationship of selected habitat variables to selected relative species biomasses. P-values indicate the significance of the correlation coefficient (Kendall's Tau). NS = not significant.


A
Paralvinella pandorae
p = 0.027
B
Branchinotogluma spp.
NS
Years of R. piscesae presence
C
Paralvinella pandorae
p = 0.009
D
Lepetodrilus fucensis
p = 0.002
Year
E
Paralvinella palmiformis
NS
F
Paralvinella palmiformis
NS
G
Lepetodrilus fucensis
p = 0.009
H
Lepetodrilus fucensis
p = 0.012
Relative species biomass (x 100%)
H2S/heat
H2S concentration
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
0
2
4
6
8
10
0.0
0.4
0.8
1.2
1.6
2.0
2.4

examples). *Paralvinella pandorae* relative biomass is negatively related to the number of years of tubeworm bush presence (p=0.027, Figure 6.12A) and year since eruption (p=0.009, Figure 6.12C). Relative limpet biomass is negatively correlated with H_2S/heat (p=0.009, Figure 6.12G) and H_2S concentration (p=0.012, Figure 6.12H). *Branchinotogluma* sp. relative biomass is not related to year (p=0.513, Figure 6.12B). Correlations of *Depressigyra globulus* and *Paralvinella palmiformis* to H_2S/heat and H_2S concentration are not significant, although *P. palmiformis* shows a trend of increasing relative biomass with both measures of sulphide (Figures 6.12E,F). Correlations of the relative biomasses of all species to non-binary habitat variables also reveal that *L. fucensis* is positively associated with year (p=0.002, Figure 6.12D). No other species were directly correlated with habitat variables at $p \leq 0.01$.

Community dominants and their relationship to tubeworm bush age, year and fluid sulphide content

Community dominants show trends with tubeworm bush age, time and fluid sulphide. I explored how *Paralvinella pandorae, P. palmiformis* and *Lepetodrilus fucensis* dominance varies in relation to these habitat factors. The relative biomass of these species varies with H_2S/heat and year post-eruption in first year tubeworm bushes (Figure 6.13): the palm worm only occurs at vents with high sulphide content, while limpet relative biomass is highest in year 3 and at low levels of sulphide.

Since limpet dominance is positively correlated with year and negatively correlated with H_2S/heat (Figures 6.7 and 6.12), and year and H_2S/heat are negatively correlated (Table 6.3), I examined the relationship of relative limpet abundance and biomass to sulphide within each year. The trend of decreasing limpet dominance with increasing H_2S persists for collections taken in the same year, although the relationship is only significant for relative limpet abundance (Figure 6.14). Further, as vent fluid H_2S/heat increases, relative limpet abundance and biomass declines and the relative contribution of the two common alvinellid polychaetes to total assemblage abundance and biomass increases (Figure 6.15). Although relative *Depressigyra globulus* abundance and biomass are not significantly related to sulphide or year, the snail follows the same trends as the limpet. Measures of snail and limpet dominance are positively

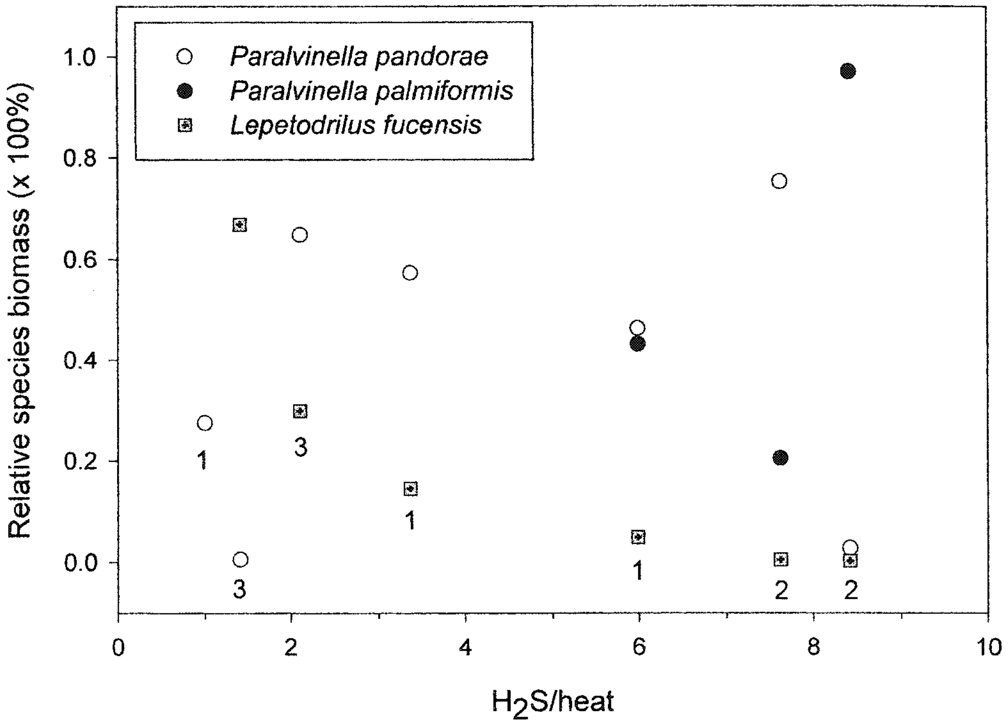


Figure 6.13. The relative biomass (and occurrence) of species in first year tubeworm bushes varies with H_2S/heat and year post-eruption (numbers indicate the year post-eruption of the sample).

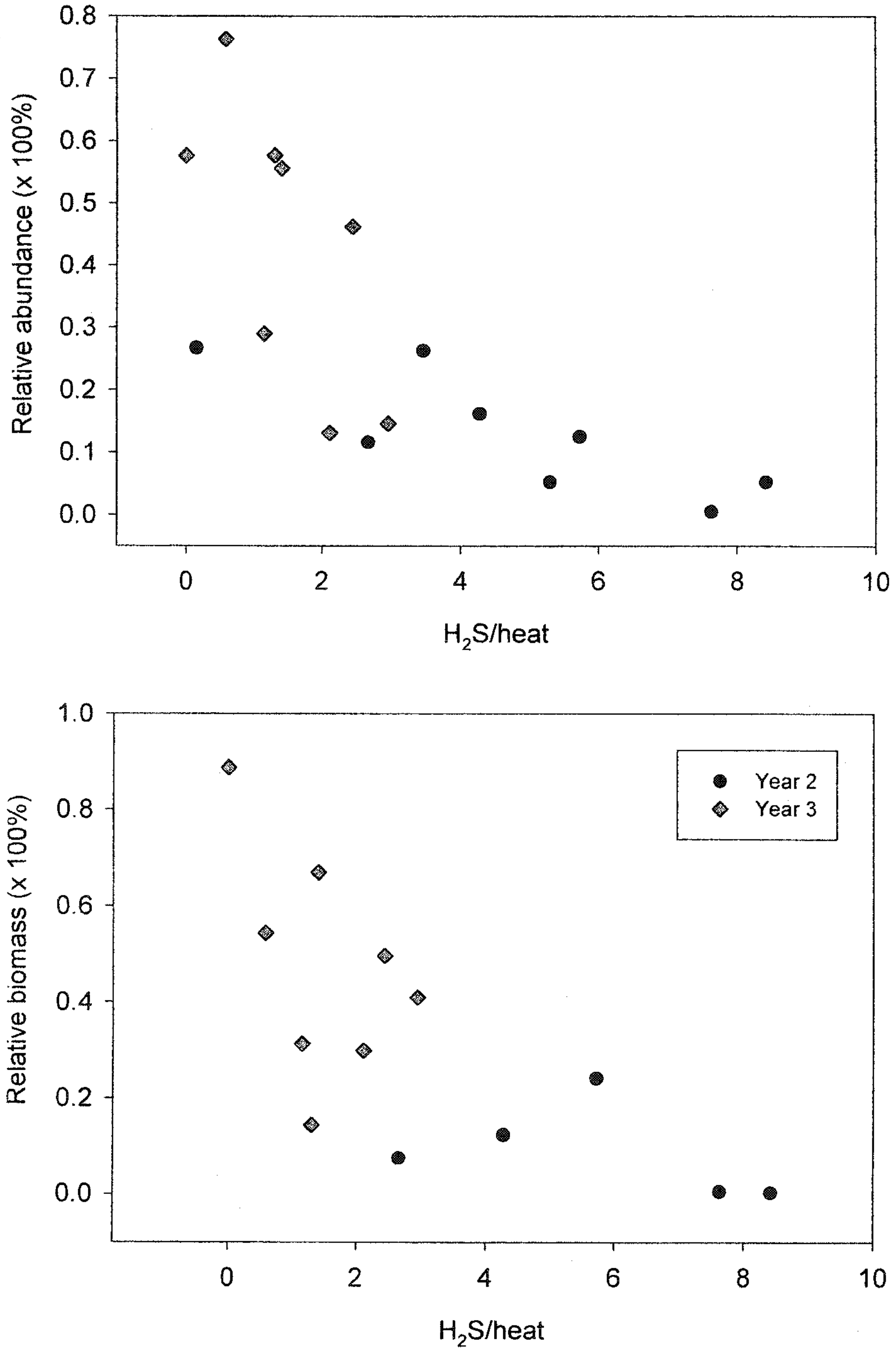


Figure 6.14. *Lepetodrilus fucensis* relative abundance (upper) and biomass (lower) decreases with increasing vent fluid H_2S/heat. This trend persists for collections taken in the same year, but is only significant for relative limpet abundance (year 2: Tau = -0.643, p=0.03; year 3: Tau = -0.500, p=0.08).

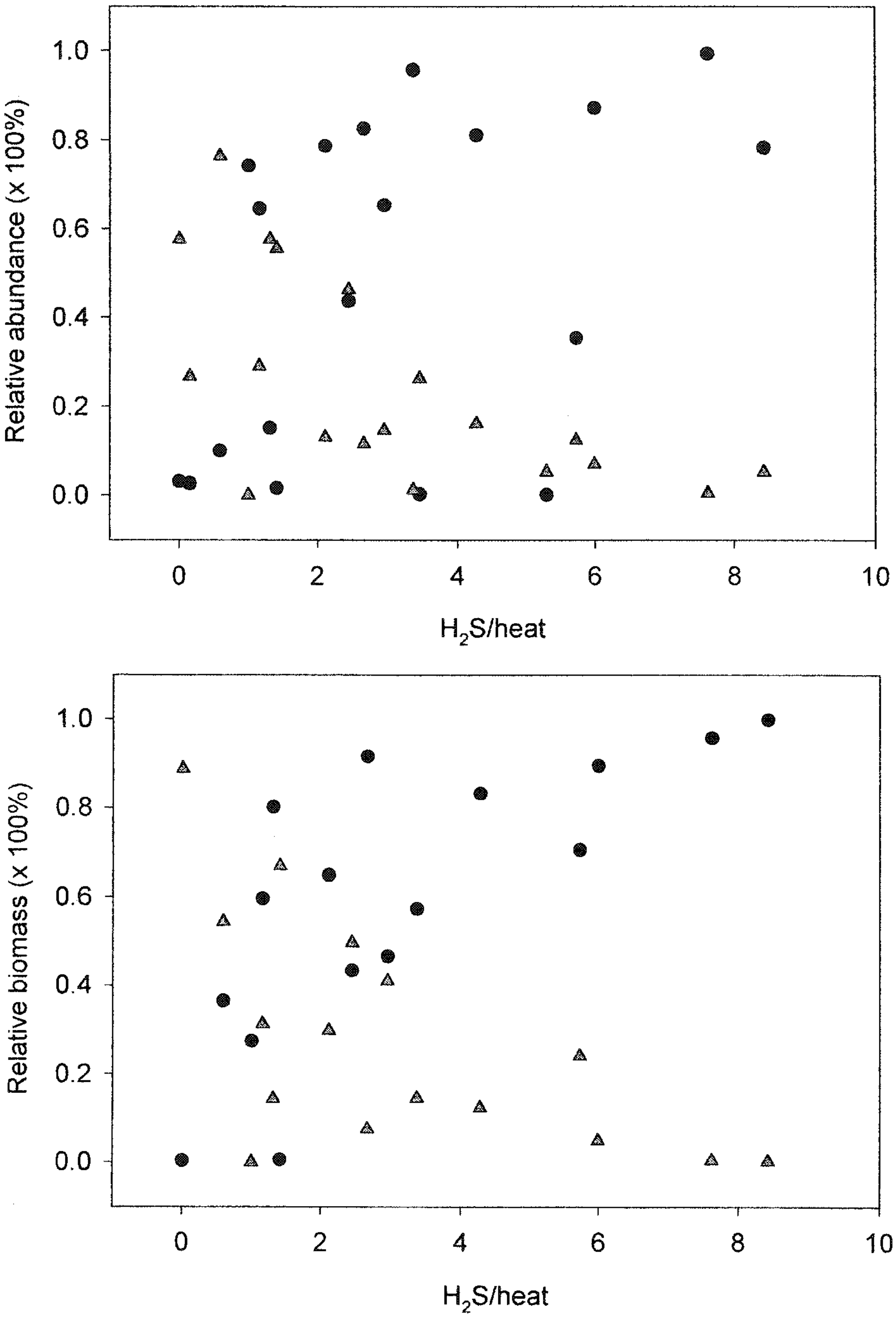


Figure 6.15. As vent fluid H_2S/heat increases, the relative contribution of the limpet *L. fucensis* to total assemblage abundance (n = 19) and biomass (n = 16) declines and the relative contribution of the two common alvinellid polychaetes to total assemblage abundance and biomass increases. H_2S/heat is positively correlated with relative alvinellid abundance (Tau=0.310, p=0.064) and biomass (Tau=0.633, p=0.001).

correlated across sites (relative abundance: Tau = 0.584, $p < 0.001$, n=22; relative biomass: Tau = 0.650, $p = 0.001$, n = 16).

Discussion

Fluid property trends and data considerations

Time-series measurements of Axial's post-eruption venting confirm that major disturbances, such as volcanic and tectonic events, have significant transient effects on the composition of diffuse fluids (Butterfield et al. submitted). Butterfield et al. (1997) propose that a predictable sequence of physicochemical changes follows an eruption (see Figure 5.17). Their model postulates that, immediately following a disturbance, heat flux and hydrogen sulphide rise, iron is variable, and chloride drops (vapour-enriched fluids). Over time, heat flux and H_2S decline, while iron and chloride increase (brine-enriched fluids). The relative time scale of change likely depends on the size of the volcanic event; the transition from the vapour- to the brine-enriched stage can occur over weeks to three or more years depending on the persistence of the heat source (Butterfield et al. submitted). This evolution of post-eruption fluid composition is linked to microbial production, faunal colonization and community development. Microbial blooms occur within days to weeks (Delaney et al. 1998), the post-eruption sulphide peak may be a settlement cue for some species, and quickly evolving fluids may reach the end of their 'lifecycle' before they sponsor thriving assemblages (Tunnicliffe et al. 1997). The pattern of post-eruption fluid evolution may also drive faunal succession (e.g. Shank et al. 1998).

However, Axial's post-eruption signature does not fully agree with the 1997 model proposed by Butterfield et al. (Butterfield et al. submitted). Six months after the Axial event, fluid composition coincided with the model: chlorinity was low and volatile content (H_2S, CO_2) was high. From 1998 to 2001, the vapour component of the fluids decreased (e.g. Figure 6.2), again consistent with the model. But by 2001, chloride concentrations of SRZ fluids remained lower than seawater; they had not evolved into the brine-rich phase. Butterfield et al. (submitted) argue that Axial may not support later-stage brine-dominated fluids, since all available data show that Axial's steady-state (fluids that have not been disturbed for many years) is vapour-rich. Butterfield's 1997 model is thus site dependent for the timing of evolution and for the return to steady state (D. Butterfield pers. comm.). An intriguing observation is that the nascent SRZ vent fluids returned to pre-eruption composition by 2.5 years after the event (Butterfield et al. submitted), coincident with the time observed for nascent assemblages to resemble mature communities (Chapter 5).

Hydrogen sulphide is particularly critical to vent communities as it sponsors microbial primary production and hence the success of the tubeworm. Moreover, H_2S may limit species distributions, as it is toxic to metazoans in micromolar concentrations (Fisher 1998). However, all forms of hydrogen sulphide are not equal with respect to their possible community effects. The relative concentration of fully reduced sulphur species (H_2S, HS^- and S^{2-}), commonly known as hydrogen sulphide, depends on fluid pH; in acidic fluids ($pH \leq 6$), dissolved H_2S gas dominates, while above this pH level, HS^- becomes the dominant form (D. Butterfield pers. comm.). This pH-mediated dissociation of sulphide likely impacts vent species. First, HS^- may be less toxic than H_2S, since it is the latter form that blocks cytochrome-*c* oxidase function in cellular aerobic respiration (Goffredi et al. 1997). Second, the hemoglobins of *Riftia pachyptila*, the dominant vestimentiferan on the EPR, bind HS^- not H_2S (Arp & Childress 1983, Goffredi et al. 1997). Circumstantial evidence implies that HS^- is also the form of sulphide bound by *Ridgeia piscesae* (J. Flores pers. comm.). Since pH generally increases with decreasing fluid temperature due to dilution with seawater, animals living at lower temperatures are likely exposed to the less toxic form of sulphide, and *R. piscesae* would have sulphide in its preferred form.

Another important chemical interaction is that the amount of biologically available sulphide depends on the relative concentration of sulphide to iron in the fluid. Luther et al. (2001) found no free sulphide (H_2S, HS^-) in high temperature fluids (~80°C), as all sulphur was complexed with iron (FeS). Organisms dependent on sulphide, such as tubeworms, cannot live in such microhabitats, while other species that can cope with high temperatures may benefit since FeS is not toxic. Since the sulphide measured for this study is a combination of all soluble species (e.g. H_2S, HS^- *and* FeS), it is important to know if the concentration of free sulphide is likely lower than measured H_2S because of complexing with iron. If the ratio of total H_2S to Fe is near one, then iron complexing will significantly reduce the amount of free sulphide in solution, but if the ratio is 10 or more, the effect is insignificant (D. Butterfield pers. comm.). In general, diffuse fluids at Axial have very low concentrations of iron, thus the lack of free sulphide is not an issue (Butterfield et al. submitted). This also holds for the specific subset of vents examined in this study (15 of the 22 collections have H_2S/Fe data): H_2S/Fe is greater than one for all samples, and only three vents have ratios under 10 (Figure 6.3: Easy and Mkr N41 in 1998 and Cloud N6 in 2000).

A final consideration is that fluid properties are not independent of the living community. Some hydrogen sulphide is oxidized below the seafloor (Butterfield et al. submitted). Mounting evidence for the existence of a subterranean biosphere suggests that sulphide-oxidizing microbes are present below the seafloor and that they likely play a part in this consumption of sulphide (Huber et al. 2002). Furthermore, H_2S uptake by large symbiont-bearing species can deplete fluid sulphide concentrations. Johnson et al. (1988) show that mussels on the EPR decrease fluid $[H_2S]$ before it reaches tubeworm plumes. Likewise, the presence of *Ridgeia piscesae* may decrease H_2S concentration. Animals at the base of tubeworm bushes may even benefit from this effect since H_2S uptake can be through the 'roots' as well as the branchial filaments of *R. piscesae* (C. Fisher pers. comm.).

Timing of tubeworm recruitment

Ridgeia piscesae takes up to three years to colonize the new vents, despite the proximity of uncolonized vents to on- and off-lava sources of recruits. The correlation of tubeworm presence and bush age to the main axes of community variation for both the relative abundance and relative biomass data sets suggests that *R. piscesae* markedly influences vent community development. This relationship is consistent with Bruno & Burtness' (2001) argument that foundation species are the most important structuring force of many marine benthic assemblages. The causes of variable *R. piscesae* recruitment are unknown. There is no significant association between the index of tubeworm bush age and year post-eruption, distance from larval source or any measured fluid property.

Despite this lack of association, abiotic factors may be important for tubeworm recruitment. On sulphide chimneys Sarrazin et al. (1997) report that *R. piscesae* establishment corresponds with a decrease to moderate fluid flow and low to medium temperatures (ambient to 20°C). This trend was observed at some nascent vents (e.g. first year tubeworm bushes coincided with a decrease in temperature at Cloud N6 and N4), but the opposite also occurred (e.g. tubeworm bush formation coincided with higher temperatures at Mkr 33). Although fluid property values (e.g. temperature, H_2S/heat, H_2S/Fe) for first year tubeworm bushes span the range of values for all other collections combined, it is difficult to speculate on potential abiotic effects since fluid measurements were taken months after tubeworm settlement. A possible 'threshold' effect, where *R. piscesae* recruitment is inhibited above or below some critical value is not evident, but would theoretically occur if the relative concentration of iron to sulphide were high enough to limit availability of free sulphide.

Other possible influences on the establishment of *Ridgeia piscesae* aggregations include post-settlement mortality, symbiont requirements and flow intensity. Studies manipulating predator access on the EPR report no difference in tubeworm recruit abundances between caged and uncaged plates (Mullineaux et al. 2000, Micheli et al. 2002), however pilot work with settling plates suggests that tubeworm recruit survival on the JdFR may depend on habitat refuges from predation (Tunnicliffe 1990). The presence of the appropriate free-living bacterial symbiont may also be a limiting factor if the hypothesis that *R. piscesae* acquires its symbionts through ingestion after settlement is correct (Southward 1988). Flow intensity and turbulent mixing are also critical factors; tubeworms require not only H_2S for their chemosynthetic endosymbionts, but also need access to oxygen in seawater. Although *R. piscesae* can acquire H_2S both through its posterior roots and its anterior gill, oxygen and carbon dioxide uptake is restricted to the gill-like plume. If fluid flow is too intense, tubeworms - especially small individuals - may be unable to successfully bridge this transition zone. Experimental work is needed to unravel which mechanisms underlie the successful recruitment of *R. piscesae*.

Effects of *Ridgeia piscesae*, vent age and hydrogen sulphide on community dominance patterns

Ridgeia piscesae: an influential foundation species

Tubeworm bush age explains the most variation in the community data mainly due to the response of one species, *Paralvinella pandorae*, to the formation and growth of *Ridgeia piscesae* aggregations. In general, the relative abundance and relative biomass of the pandora worm is highest in association with first year tubeworm bushes, and subsequently decreases with time. *P. pandorae*'s success in young tubeworm bushes likely results from a combination of life history characteristics (e.g. continuous reproduction, McHugh 1989), which make it a successful early recruiter, and the absence of its congener *P. palmiformis* at most new vents. Tunnicliffe et al. (1997) and Levesque et al. (2003) cite competition for food with the later-arriving *P. palmiformis*, and/or intraspecific competition due to increasing densities as likely causes of *P. pandorae*'s decrease in body size and assemblage dominance over time. Other possibilities include interspecific competition with *Amphisamytha galapagensis*, a similar-sized polychaete with a similar habit, and/or increased competition for space from burgeoning limpet populations.

The facilitation of *Paralvinella pandorae* by tubeworm aggregations is facultative. The pandorae worm does not have an obligate dependence on *R. piscesae*, but its relative abundance is higher when a tubeworm clump is present (Marcus & Tunnicliffe 2002). Snail vent is the only exception where relative *P. pandorae* abundance is similar to assemblages without tubeworms (Figure 6.7A). One mechanism of facilitation by foundation species is simply to increase habitable space (Bruno & Bertness 2001). Tubeworms provide substratum for attachment and perhaps create distinct microhabitats and/or refuges from predation for the pandora worm and other associated species.

Despite the trend of decreasing *Paralvinella pandorae* dominance with increasing tubeworm bush age, there is substantial community variation among same-aged tubeworm bushes. Three factors may contribute to this variation: (1) year of tubeworm recruitment post-eruption, (2) abiotic fluid characteristics (H_2S, temperature), and (3) tubeworm tube and bush morphology.

If tubeworm clumps establish later in time post-eruption, *Paralvinella pandorae* is less likely to dominate first year tubeworm bush assemblages. While all vents with tubeworm bushes in 1998 were dominated by the pandora worm, the relative abundance of *P. pandorae* at Snail vent, and its relative biomass at Marker 33 and Snail vents, were low in the first year of tubeworm bush presence (1999 and 2000, respectively). One cause may be increased interspecific competition with previously recruited species that occur in higher densities in later years. This is a common competitive mechanism in the rocky intertidal: an organism or species occupies space first thus making it unavailable for others ("preemptive exploitation", Menge & Branch 2001). The palm worm was twice as abundant as the pandora worm at Marker 33 in 1998, while the two common gastropods (snail and limpet) were three orders of magnitude more abundant than the pandora worm at Snail in 1999. Thus, these species had a numerical advantage over the pandora worm for using *R. piscesae* substratum once it became suitable for colonization.

Abiotic differences may also cause assemblage variation among same-aged tubeworm bushes. There is some evidence that *Paralvinella palmiformis* copes better with extreme fluid properties than *P. pandorae*. Dixon et al. (1992) report that palm worm rDNA denatures at higher temperatures than the pandora worm, and in this study, relative palm worm abundance is positively correlated to temperature and H_2S concentration while relative *P. pandorae* abundance is not. Further, *P. palmiformis* only occurs in first year tubeworm bushes with high sulphide (Figure 6.13). Higher sulphide flux translates into higher microbial production, which is likely needed by larger bodied animals like the palm worm. Abiotic factors may mediate competition between these two alvinellid polychaetes.

Highly plastic vestimentiferan tube and clump morphology may be yet another factor influencing faunal variation among same-aged tubeworm bushes. Tubes range from 'short and fat' to 'tall and skinny' with varying degrees of flutedness and recruit colonization, while clumps vary from tight, intertwined bushes to loose aggregations of individual worms. The 'short-fat' and 'long-skinny' morphotypes, that likely reflect different flow regimes, differ in their blood physiology (Flores et al. 2001). An intriguing possibility is that tube and bush morphology change with time and fluid flow alterations, thereby causing shifts in the associated fauna. Tsurumi & Tunnicliffe (in press) recently reported that species richness increases with tubeworm bush complexity at JdFR diffuse flow vents.

Although the precise mechanisms remain unidentified, this analysis suggests that *Ridgeia piscesae* aggregations strongly affect the structure of diffuse flow assemblages. This habitat-forming species appears to facilitate the pandora worm, while secondary processes likely cause variation among assemblages of same-aged tubeworm bushes.

Vent age and hydrogen sulphide content

The two other habitat descriptors significantly correlated with post-eruption assemblage structure are vent age and vent fluid H_2S content. The association of year since eruption to community variation was expected; Chapter 5 and other studies (e.g. Tunnicliffe et al. 1997, Desbruyères 1998, Shank et al. 1998) report sundry species patterns associated with vent age or shifts in fluid flow. The influence of sulphide was less expected. Although many studies stipulate that H_2S is important, only Luther et al. (2001) link free $[H_2S]$ to gross species distributions at diffuse vents. Of all the measured fluid properties, sulphide concentration should theoretically be the most significant as it is required for primary production and is toxic to metazoan life.

Vent age is difficult to interpret, as it does not directly imply process. Succession studies show that the mechanisms responsible for temporal species patterns are usually variable and complex (McCook 1994). At EPR vents, repeatable patterns of species replacements are thought to result from either (1) the predictable evolution of physicochemical vent fluid factors coupled with differing nutritional requirements and physiological tolerances among the dominant species (Shank et al. 1998), or (2) specific biological interactions that mediate the sequence (Hessler et al. 1988, Mullineaux et al. 2000). The current study suggests that the reality is more complex; substantial among vent variation is superimposed on the post-eruption pattern of fluid evolution at Axial, and species interactions with each other and the environment likely influence temporal patterns. Vent age is important, but is not very useful for identifying the mechanism(s) that structure community development.

Species patterns associated with a fluid property such as $[H_2S]$ point more clearly to potential process. However, both measures of H_2S content used here correlate negatively with year, which complicates the interpretation of the correlation of sulphide with assemblage variation. The most obvious annual species pattern is the increase in the relative abundance and biomass of the limpet *Lepetodrilus fucensis*. This temporal trend may be caused by biological factors related to time (e.g. recruitment pulses, initial high post-settlement mortality) and/or changing fluid conditions. The significant negative relationship between limpet dominance and [H_2S] suggests that sulphide level may affect *L. fucensis* populations. However, clearer support for this hypothesis would come from limpet abundance and biomass responding to sulphide gradients across vents of the same age. Although the number of samples per year is small, the inverse relationship of relative limpet dominance and H_2S/heat persists for collections from the same year (Figure 6.14). The common snail, *Depressigyra globulus*, follows the same trend as the limpet with [H_2S] and year, but the associations are not significant.

Two studies provide evidence consistent with the hypothesis that *Lepetodrilus fucensis* may be responding to vent fluid sulphide content. First, Sarrazin et al. (1999) report that *L. fucensis* and *Depressigyra globulus* have lower temperature and sulphide niche breadths (<10°C and <60µm H_2S) than some other vent species living on JdFR chimneys, such as alvinellid polychaetes (<15°C and <70µm H_2S). Second, experimental work by A. Bates (University of Victoria) shows that *L. fucensis* moves to temperatures below 15°C in the lab at sea level pressure. Although limpet relative abundance and biomass did not significantly correlate with temperature in my study, temperature is a reasonable proxy for sulphide concentration (D. Butterfield pers. comm., Figure 6.1).

Other species dominate assemblages with higher H_2S content. These include aggregations dominated by scale worms and/or the dorvilleid polychaete *Ophryotrocha globopalpata* in the first year, and one or both of *Paralvinella pandorae* and *P. palmiformis* in later years. Combined, the two alvinellid polychaetes display a trend of increasing dominance with H_2S/heat (Figure 6.15). Alvinellids are frequently cited as occupying the highest temperature niches at vents (e.g. Taghon 1988, Jollivet et al. 1995, Sarrazin et al. 1997), and may have a novel internal H_2S detoxification method (Jouin-Toulmond 1996). The relative success of gastropods versus alvinellids may thus be driven by fluid sulphide content. In addition to the post-eruption pattern of decreasing sulphide content with time, the continued proliferation of tubeworm clumps may also be important as *Ridgeia piscesae* may effectively decrease the amount of H_2S that reaches proximate fauna.

Sulphide to heat is stronger and more consistently correlated to assemblage variation than H_2S concentration, and both measures of sulphide correlate more strongly to species patterns than temperature. This suggests that temperature is relatively unimportant, and that species respond to fluid sulphide content independent of temperature. However, animals likely respond to the interaction of sulphide and temperature, especially when temperature approaches limiting levels. For example, *Lepetodrilus fucensis* may thrive at low temperature vents with low H_2S/heat, while their success at higher temperature vents with low sulphide may be limited by thermal constraints. Sarrazin et al. (1999) also report that species distributions and relative densities on chimneys are significantly influenced by H_2S but not temperature. Future studies aimed to relate environmental factors to species patterns should thus measure total and standardized fluid sulphide and not rely solely on temperature as a proxy for fluid characteristics.

Temperature and pH are also significantly associated with the third ordination axis derived from the relative abundance data set. The significant correlation with pH is suspect due to too few data ($n = 13$), but may be important as it drives sulphide speciation. The temperature correlation is likely robust ($n = 20$). Since the third CA axis only explains ~10% of community variation, none of the dominant species and only three rarer species are significantly associated with this gradient. Of these three species, the relative abundance of the polynoid polychaete *Levensteiniella kincaidi* is inversely related to temperature. Marcus & Tunnicliffe (2002) report that *L. kincaidi* is more abundant on vent peripheries than proximate to flow, which is consistent with the hypothesis that this polychaete may be unable to cope with elevated temperatures.

Effects of vent age and temperature on community occurrence patterns

In general, presence-absence data are less effective for detecting patterns at this scale. No distinct groupings of samples fall out, and much less variance is captured compared to analysis of the relative abundance and biomass data sets. However, the first ordination axis does broadly reflect a gradient of vents sampled from year 1 to year 3. It is not surprising that vent age relates to community species composition, as we know that species have differential colonization rates of post-eruption vents (Chapter 5, Tunnicliffe et al. 1997, Shank et al. 1998).

Substratum and temperature likely have little influence on species composition. Substratum effects are doubtful since sample size is small (only two vents are cracked sheet flows) and only one species has a significant substratum association. A possible effect of temperature may be more likely as the presence of three species varies significantly with temperature. The palm worm only occurs at vents with maximum temperatures >15°C, while the snail *Lacunoides vitreus* and the copepod *Humesipontius arthuri* only occur at vents with maximum temperatures <20°C. Although all species have a physiological temperature limit, this value is unknown for all but one vent animal: the brachyuran crab *Bythograea thermydron* dies at temperatures greater than 35°C at habitat pressures (Mickel & Childress 1982). Many studies report a correlation between a species' thermal tolerance and its *in situ* temperature regime (e.g. Taghon 1988, Toulmond et al. 1990, Dahlhoff et al. 1992, Dixon et al. 1992, Jollivet et al. 1995).

Finding a correlation between species distributions and temperature at diffuse flow vents (as opposed to sulphide chimneys) is challenging since tubeworm bushes are large, three-dimensional structures that host a wide range of temperature zones. Temperature is higher in areas proximal to flow - at the base of the bush and/or next to the flow conduit. Thermistors placed over diffuse flow at Endeavour Segment on the JdFR recorded average temperature differences up to 15°C over a spatial scale of 10 cm (M. Pruis pers. comm.), and temperatures at one location also vary on tidal and lunar cycles (Chevaldonné et al. 1991, Martel et al. 2002). If temperature does drive species segregation at diffuse flow vents, the pattern may be more manifest at the within bush rather than between bush scale. Thus, if the goal is to detect the major community gradients among diffuse vents, species occurrence data are likely most valuable when vent-to-vent variation in abiotic factors spans a large enough range to limit the distributions of one or more of the dominant species (e.g. the palm worm). Otherwise, presence-absence data are most useful for revealing biogeographic patterns at the segment and ridge scale (Tunnicliffe et al. 1998).

Unmeasured factors and unresolved issues

A number of potentially important habitat factors were not measured for this study. Vent size, substratum complexity, tubeworm clump morphology, productivity, food resources and species interactions are all likely important in structuring diffuse flow communities. Fluid flow intensity may also be influential. This complex variable, which integrates fluid properties such as temperature, particle delivery rate and sulphide content (and maybe even vent age in a post-eruption scenario), explained more of the variance of species distributions on chimneys than did measurements of individual fluid properties (Sarrazin et al. 1999).

Some of the habitat characteristics used here likely have no or little influence on the structure of diffuse flow assemblages. Although data gaps preclude unambiguous interpretation, measures of sulphide to iron, cholorinity and vent location (distance from putative larval source) did not correlate with any observed faunal patterns. The ratio of sulphide to iron would likely by important at other vent sites if iron limits the amount of free sulphide.

The species patterns reported here and their relationship to certain habitat factors depend on the temporal component of the data. Tubeworm bush age was determined by the timing of *Ridgeia piscesae* recruitment post-eruption, while the gradient of sulphide across samples was also affected by time. Although I show that vent-to-vent differences in [H_2S] coincide with dominance patterns in the limpet and alvinellid polychaetes, it is unclear whether this relationship arises because of other temporal processes or sulphide per se. A critical unanswered question is whether recruitment dynamics (e.g. larval supply, post-settlement mortality) and/or initially high levels of sulphide cause *Lepetodrilus fucensis* populations to be low at young vents. If sulphide does play a role in developing assemblages independent of time, then variation among mature vents at the vent field scale may also relate to fluid sulphide content.

Assessing faunal variation while controlling for confounding successional factors such as tubeworm bush age is likely impossible except for eruption scenarios, and even then post-eruption venting is typically shorter lived than stable fields. One possible solution is to use distinct faunal patterns to make a reasoned guess of tubeworm bush age. For example, young tubeworm aggregations may be inferred from large body sizes of *Paralvinella pandorae* or the relative contribution of this species to total assemblage abundance (e.g. >60% in first year assemblages). Another possibility may be to use

Ridgeia piscesae tube and/or bush structure if they are shown to vary predictably with age. The EPR may be an easier system to assess the relative influence of time and fluid properties as the dominant three or four habitat-forming species are related to vent age (Shank et al. 1998). One could thus compare communities within each stage to test which flow properties are correlated to assemblage variation.

Summary: Community Development Model revisited

The model presented in Chapter 5 is refined here with the insight that the timing of *Ridgeia piscesae* recruitment, vent age and hydrogen sulphide explain most of the variance in developing post-eruption diffuse flow vent assemblages. Year is also important for species composition, while temperature is related to smaller trends of variation in species relative abundances and occurrences. Since faunal patterns depend on whether abundance or biomass is used to describe community structure, I start by reporting the common patterns, and then present the trends in terms of abundance and biomass, respectively.

After the eruption, species recruit to the nascent vents within months. The timing of tubeworm recruitment and bush formation differed between vents; some vents were colonized by *Ridgeia piscesae* within a few months while others were colonized sometime between 2 and 3 years post-eruption. This contrasts the earlier suggestion that *R. piscesae* is a pioneer species occupying all new vents within one year (Tunnicliffe et al. 1997). Whether chance, abiotic factors or biological interactions drive differential tubeworm recruitment is unknown.

There are three main pathways of nascent vent community development based on relative species abundances (Figure 6.16). Pre-tubeworm assemblages are dominated by either polychaete or gastropod grazers (Figure 6.16A). This difference may be due in part to fluid properties: polychaete grazers occurred at high sulphide vents (Figure 6.16B), and although H_2S was not measured for Snail vent in years 1 and 2, relative *Lepetodrilus fucensis* abundances are negatively related to sulphide. The snail, *Depressigyra globulus*, is not as abundant as the limpet, but it follows roughly the same dominance pattern as *L. fucensis* across vents and hence shows similar trends with sulphide and year post-eruption.

Figure 6.16. A) Proposed model of nascent vent community development based on observed shifts in relative species abundances over time. Assemblage Type is defined by the collection groupings found with cluster and ordination analyses and refers to which species dominate total community abundance. Curved arrows indicate that the two community types in year 4 may persist over time. B) The same model as A, but this includes average H_2S/heat measurements for each assemblage type.

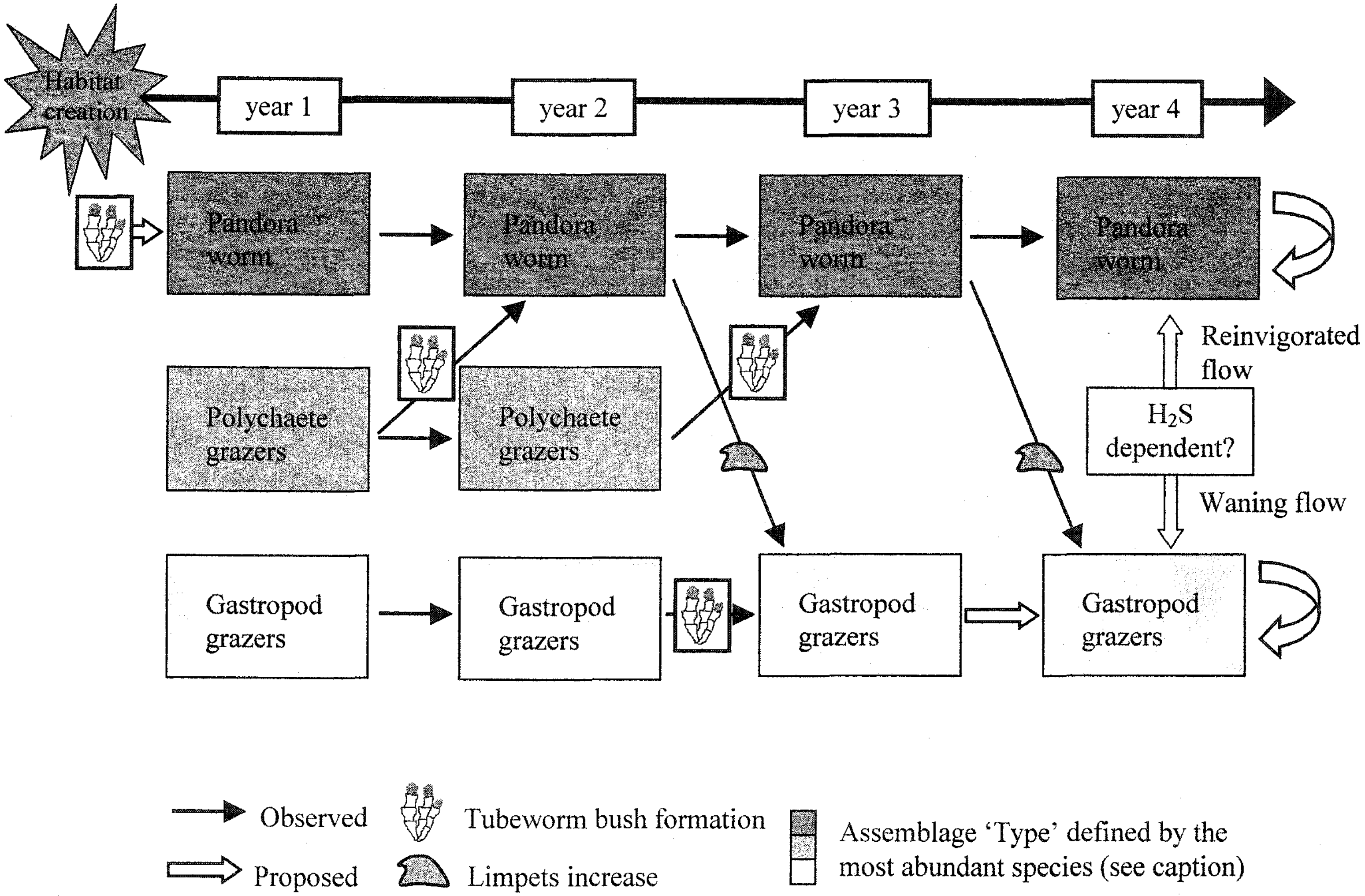

Habitat creation
year 1
year 2
year 3
year 4
Pandora worm
Pandora worm
Pandora worm
Pandora worm
Reinvigorated flow
Polychaete grazers
Polychaete grazers
H_2S dependent?
Waning flow
Gastropod grazers
Gastropod grazers
Gastropod grazers
Gastropod grazers
Observed
Proposed
Tubeworm bush formation
Limpets increase
Assemblage 'Type' defined by the most abundant species (see caption)

Figure 6.16 A

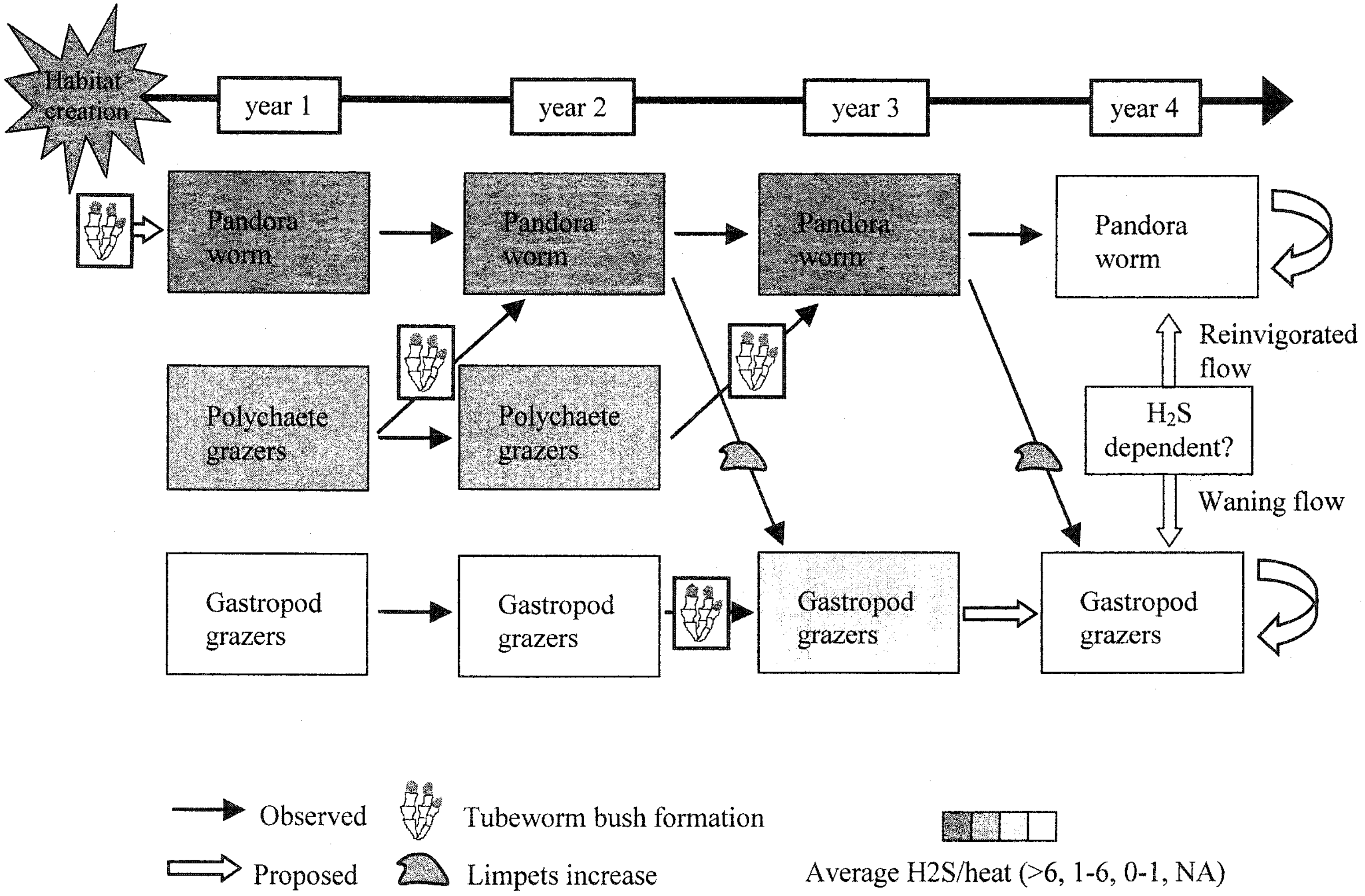

Habitat creation
year 1
year 2
year 3
year 4
Pandora worm
Pandora worm
Pandora worm
Pandora worm
Polychaete grazers
Polychaete grazers
Reinvigorated flow
H_2S dependent?
Waning flow
Gastropod grazers
Gastropod grazers
Gastropod grazers
Gastropod grazers
Observed
Proposed
Tubeworm bush formation
Limpets increase
Average H2S/heat (>6, 1-6, 0-1, NA)

Figure 6.16 B

After tubeworm aggregations form at a vent, there is a significant shift in the associated fauna. First year tubeworm bush communities are dominated by *P. pandorae*; Snail vent (and perhaps Mkr 108) is the only exception where bush formation was not associated with a major increases in the pandora worm (Figure 6.16A). As vents and tubeworm bushes age, *P. pandorae* either maintains its dominant position or the limpet *L. fucensis* increases in large numbers and becomes more abundant. This community shift - from dominance by alvinellid polychaetes to gastropods – is related to time (only occurs after year 2) and possibly vent fluid sulphide. The cause of delayed *L. fucensis* recruitment to most nascent vents is unknown, but may be due to initially high levels of sulphide.

Community transitions past 3 years will likely be alvinellid-dominated vents switching to limpet-dominated vents. Two vents with high relative abundances of alvinellids in 2000, Nascent and Cloud N6, were re-sampled the following year (data not presented); by 2001, Nascent had become numerically dominated by the limpet while Cloud N6 maintained high levels of alvinellids (see Figure 6.16A). If this alvinellid to gastropod shift is driven in part by a decrease in sulphide, a shift in the opposite direction from a gastropod to an alvinellid-dominated vent (which was never observed) may occur if flow is reinvigorated and sulphide levels increase (Figure 6.16A).

The pattern of community development is more complex when assemblage structure is measured with species biomass. With this measure, other species besides *Paralvinella pandorae* dominate first year tubeworm bushes (Figure 6.17). Vent age and sulphide likely contribute to this variability: *P. palmiformis* only occurs in first year bushes with high sulphide, and limpet relative biomass is only high in year 3 (Figure 6.13).

Biomass patterns in second and third year tubeworm bushes are less variable, but sample sizes are also very small, especially for third year bushes (Figure 6.17). In second year aggregations, *Paralvinella palmiformis* appropriates the largest portion of total biomass, followed by mid- to low contributions of the limpet and the pandora worm. This is due in part to *P. pandorae*'s decrease in body size, which may be concomitant with the arrival of the palm worm (Levesque et al. 2003). The palm worm and the limpet dominate third year aggregations, and *P. pandorae* contributes a small amount to total

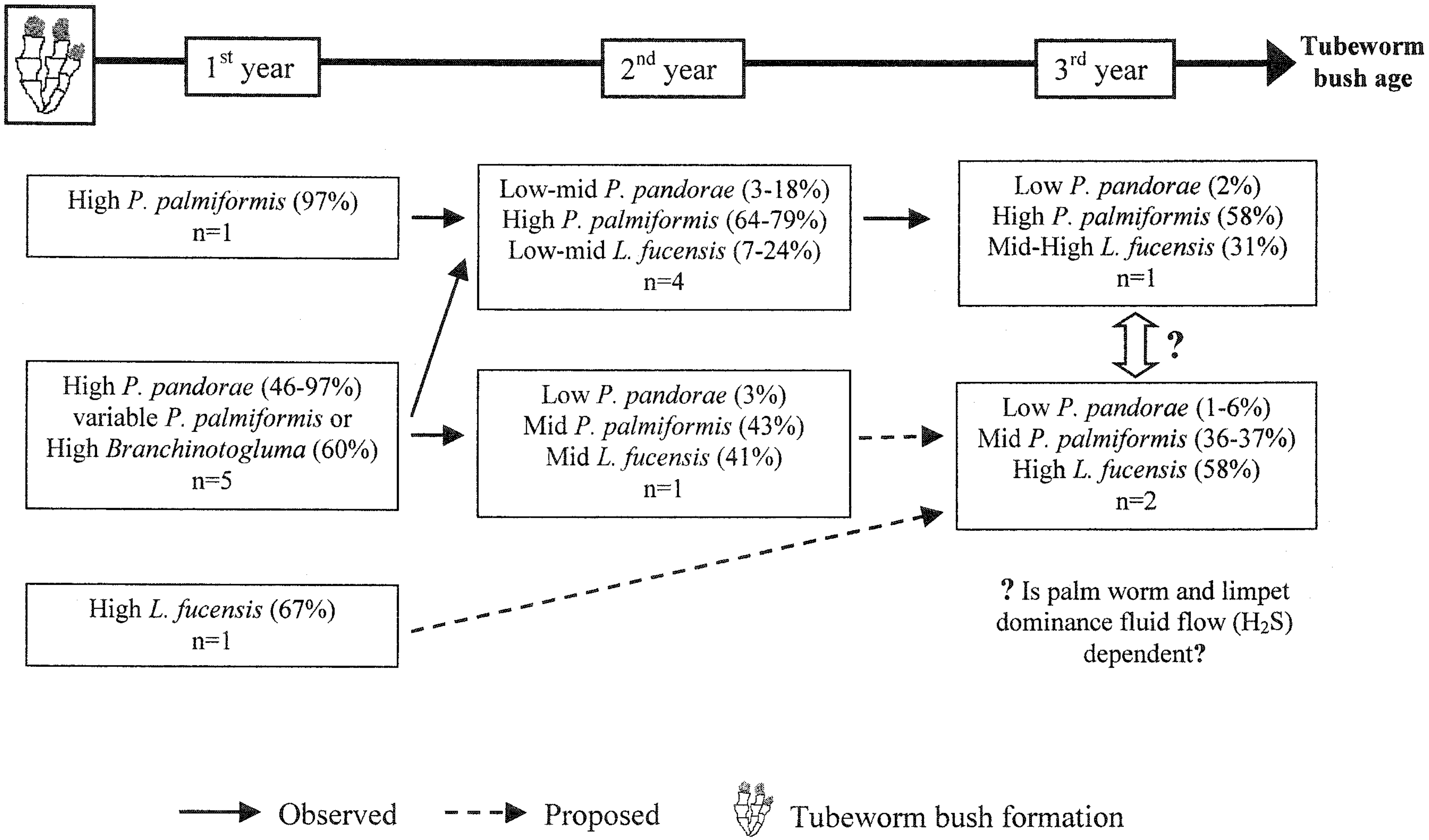


Figure 6.17. Proposed model of nascent vent community development based on observed shifts in relative species biomass with respect to tubeworm bush age. The boxes illustrate which species dominate (relative biomass in brackets) the sampled vents (n = number of vents).

biomass. Again, the relative dominance of the limpet versus the palm worm may be sulphide dependent (Figure 6.17).

In conclusion, this analysis suggests that the development of post-eruption diffuse flow vent assemblages is influenced by the interaction of tubeworm bush age, vent age, and fluid sulphide content. Although the main gradients of variation in the community data were anticipated to relate to temporal habitat factors, this is the first study that statistically shows the significant effect of time (tubeworm bush age and vent age) on vent communities. Further, although the habitat-forming species *Ridgeia piscesae* is hypothesized to influence community structure (e.g. Uruyco 2000, Tsurumi & Tunnicliffe in press), this is the first illustration of its effect on the relative abundance and biomass of associated species. Hopefully, future work will resolve whether the correlation of fluid sulphide to the relative dominance of alvinellids versus gastropods is independent of vent or bush age. Since faunal patterns are shown to be contingent on the species measure used, I recommend future studies use both species abundance and biomass as vent community descriptors.

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CHAPTER 7

Summary

Ecological observations and pattern detection are cornerstones of ecology; they form the basis of explanatory models and avert experimental analyses of improbable processes (Underwood et al. 2000). The species patterns that I describe throughout this dissertation take us one step closer to understanding the processes that organize diffuse flow hydrothermal vent communities in space and time. For systems like vents, which require much expense and effort to study, pattern detection based on observational studies is even more essential to develop reasoned hypotheses of processes to direct effectively future research efforts (Marcus & Anholt in revision).

My work focuses on the low-temperature vent communities of Axial Seamount, an active volcano lying atop the Juan de Fuca Ridge in the northeast Pacific. This site is an ideal location for exploring community patterns as it supports both long-lived vent fields (venting for over 15 years) and nascent vent habitat initiated by a volcanic eruption in 1998. I was thus able to examine temporal and spatial variation among vent communities at the same site and relate patterns of developing assemblages to patterns observed in mature communities. Axial is also a dedicated seafloor observatory (New Millennium Observatory, 'NeMO'[1]) for multidisciplinary research. Geologists, chemists and biologists work jointly to find the links among volcanic events, vent fluid properties and biological communities through multi-year observations. NeMO is the first collaborative effort of its type at deep-sea vents and is a boon from a community ecology perspective as critical habitat data are gathered concurrently with biological collections.

The overall objective of my dissertation is to reveal patterns that demand explanation: I describe species distribution and dominance patterns among diffuse flow vent communities and propose viable causal processes. In the next section, I highlight the major conclusions from my dissertation and follow with a discussion of the most obvious community patterns that should be explored with future observations and experiments.

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[1] NeMO web site: http://www.pmel.noaa.gov/vents/nemo.html

Conclusions

One – The null model results suggest that mature and nascent vent communities are nonrandom ensembles of individuals and species (Chapters 2 and 4). This is an important result for three reasons. First, in my experience, many vent researchers presume that vent communities are nonrandomly organized. Such claims must be tested for any new system, especially where experimental work is difficult, to substantiate the assumption. Second, rigorous statistical support for nonrandom community patterns justifies the use of descriptive multivariate techniques to describe vent communities (Jackson et al. 1992). Third, the nonrandom patterns validate speculation of - and search for - processes that structure both mature and nascent vent assemblages.

Two – The null model results of Chapter 2 suggest that one published matrix generation algorithm (Sequential Swap method, Gotelli & Entsminger 2001) is inadequate for evaluating species associations. I present a viable alternative algorithm for creating random matrices. This work contributes to the ongoing debate of null co-occurrence models in ecology.

Three – The new polynoid polychaete I describe in Chapter 3 appears to be a pioneer species adapted to post-eruption conditions. The absence of this species from mature vents is intriguing as we do not know where it lives between eruptions (Marcus & Hourdez 2002). Species identification remains a basic task for vent community ecologists as species are the fundamental unit of study. Further work is needed to understand why *Vampiropolynoe embleyi* can capitalize on ephemeral vent resources, but cannot persist at new vent sites for more than a few years.

Four – I describe the destruction and rebirth of a vent field (Chapter 5). I report the development of nascent vent communities over three years and compare the patterns I observe to those at mature vents. Main results include: (1) rapid colonization of new vents within months of vent inception, (2) variation in the composition and structure of early assemblages, (3) continued accumulation of species and an increase in community density and biomass over subsequent years, (4) high species persistence at the vent field scale, although some species may be prone to local extinction, (5) an overall shift in species dominance at most sites with time, (6) asynchronous rates of assemblage change among discrete vents, (7) a decrease in assemblage variability with time, due mainly to the ubiquitous success of the limpet *Lepetodrilus fucenesis* and (8) the demise and/or death of assemblages when flow wanes or fluid conditions become inappropriate. Knowledge of mature Axial assemblages also allowed for assessment of successional time scales and putative mechanisms driving some species patterns. Nascent vent community composition and structure converged on the mature state by 1.5 and 2.5 years respectively, and species-specific rates of colonization are positively linked to species abundances in mature assemblages. I also show that community patterns depend on whether abundance or biomass is used to evaluate species dominance and thus recommend future vent community studies use both measures.

Five – I relate the composition and structure of developing vent assemblages to abiotic and biotic habitat characteristics (Chapter 6). Habitat factors correlated most strongly with trends in community variation are tubeworm bush age, vent age and vent fluid hydrogen sulphide content. This is the first statistical attempt to link habitat data to diffuse flow vent community structure; I give support to prior speculations that temporal processes and fluid properties are influential and highlight the importance of a possible foundation species, the tubeworm *Ridgeia piscesae*. Based on these results, I propose a model of post-eruption community development at diffuse flow vents.

Overall, my work suggests that biotic and abiotic factors organize vent communities into nonrandom entities. I validate the supposition that time is important to community structure on the scale of a few years and propose various possibilities for the causes of community patterns.

Where to go next: current understanding and future work

Few studies address variation in community structure among diffuse flow vents at the scale of a vent field or vent site. Even fewer assess this variation with collections and adequate numbers of samples to examine complete assemblages, and use statistical analyses (Jollivet 1996, Tsurumi 2001, Tsurumi & Tunnicliffe 2001, van Dover 2002, Tsurumi & Tunnicliffe in press, Marcus & Anholt in revision, this thesis). The detection of species patterns from sampling multiple vents of the same habitat type over a scale of meters (field) to kilometres (site) is thus a relatively new direction of study for hydrothermal vent ecology. The ultimate aim of this approach is to understand what drives faunal variation among diffuse flow vents. Despite the limited number of studies, general trends are emerging: (1) diffuse flow communities are typically defined by the visually and structurally dominant species (e.g. tubeworm aggregations or mussel beds), (2) the same few species tend to represent the majority (60-90%) of individuals associated with the foundation species, (3) species abundance and distribution are positively related across vents and (4) faunal differences among vents are more pronounced during the initial, and maybe final, stages of a vent's lifecycle.

These trends give some insight into how and where to search for potentially meaningful species patterns. Trend 1 suggests that habitat-forming species at vents may have a major influence on community structure of the associated fauna, similar in effect to foundation species in other marine benthic systems (Bruno & Bertness 2001). Trend 2 suggests that since vent assemblages typically fit a geometric series species-abundance distribution (Tsurumi in press), the prevalent community gradients and hence, important mechanisms, may be best reflected in the relative proportions of the few dominant species. Similarly, Trend 3 suggests that species occurrences (presence-absence data) may be less useful for revealing major community patterns since abundant species tend to be ubiquitous. Finally, Trend 4 suggests that faunal differences among diffuse vents will likely be larger if sampling covers a range of vent ages and stages of community development.

Ultimately, the temporal and/or abiotic variation among the vent communities under analysis will dictate which aspects of the data are most useful for revealing important species patterns. For example, patterns among the dominant species may not be instructive if a few species occur at and dominate most or all vents, rendering small gradients in dominance across the sampled sites. This may arise if the range of conditions (e.g. vent age, fluid chemistry, fluid flow etc.) at the sampled vents does not limit the dominant species. In such a scenario, species occurrence data (Marcus & Anholt in review) or dominance patterns in the less abundant species may reveal more meaningful trends.

Since field observations and descriptions of patterns initiate explanations and underlie the study of biological systems (Andrew & Mapstone 1987), I list here the major patterns described throughout this work. I follow with possible general causes and end with a call for future investigations.

The major species patterns I report that demand explanation are:

1. Differential rates of colonization among species to nascent vents.
2. Differential timing of recruitment of the tubeworm *Ridgeia piscesae* to nascent vents.
3. Correlation of *Ridgeia piscesae* aggregation age and community structure.
4. Post-eruption faunal shift in species dominance over three years, from *Paralvinella pandorae* → *P. palmiformis* → *Lepetodrilus fucensis*.
5. Correlation of vent fluid hydrogen sulphide content to community dominance by *L. fucensis* or alvinellid polychaetes (*P. pandorae* and *P. palmiformis*).
6. Positive and negative associations between pairs of species in mature assemblages.

What may be causing these patterns?

1. *Larval supply.* At the large scale, species life history characteristics may cause a shifting species pool in space and time. Preliminary work suggests that Axial's species pool varies temporally, but not spatially (A. Metaxas pers. comm.). Species-specific colonization rates (patterns #1,4) may reflect life history traits based on tradeoffs in resource allocation. For example, species that have high gamete production, dispersal ability and growth rates may be inferior competitors in established communities (McCook 1994). At the smaller scale, local flow dynamics may mediate chance delivery of larvae to specific vents (pattern #2).
2. *Recruitment dynamics.* Processes that affect post-settlement survival include biological interactions and abiotic constraints (Booth & Brosnan 1995). Grazing or predation of recently settled juveniles (patterns #1,2) and facilitation (patterns #3,4) may affect recruit success, while abiotic factors, such as settlement cues and intolerable sulphide levels, may also play a role (patterns #1,2,4). The chance sequence of species arrival may also mediate the relative importance of these factors at specific vents.
3. *Abiotic and biotic interactions operating among established species.* There is evidence for competition between two alvinellid species (pattern #4, Levesque et al.

2003). This study also suggests that vent fluid hydrogen sulphide content may affect the relative success of common gastropods and alvinellid polychaetes (pattern #5), while species distribution patterns may result from both abiotic and biotic controls (pattern #6).

A dominant pattern, also described by Tsurumi (2001) and Marcus & Tunnicliffe (2002), is the remarkable numerical dominance of the limpet *Lepetodrilus fucensis* at Axial and at other sites on the JdFR. The biology of this species is currently being explored to understand which characteristics underlie its ecological success in different vent microhabitats (A. Bates pers. comm.).

We lack basic information for most vent species, such as life history characteristics, larval dispersal potential, settlement requirements, nutritional modes and abiotic tolerances. Community information on species interactions (e.g. predation, competition, facilitation) is also scarce (Mullineaux et al. 2000, Micheli et al. 2002, Levesque et al. 2003) and data on multispecies relationships (e.g. indirect effects) is nonexistent. Although progress is being made in measuring the biotic and abiotic habitat, it remains difficult to quantify certain variables, such as food resources and flow dynamics.

In light of this paucity of data, I recommend that future efforts aim to (1) understand basic biology of the dominant fauna by continuing to characterize their *in situ* habitats and use lab experiments to define specific species attributes, (2) understand species interactions using exploratory tools, such as isotopes, and possibly laboratory experiments investigating dynamics of paired species, and (3) understand community patterns using mensurative and manipulative field experiments to address possible processes. A laboratory approach using pressurized vessels successfully characterized the temperature limits of the embryos of one vent polychaete (Pradillon et al. 2001) and may also prove useful for characterizing physicochemical preferences/tolerances of various age classes of other vent fauna (R. Lee pers. comm.). The patterns described herein point to the obvious first candidates for such studies. New technologies, such as an *in situ* hydrogen sulphide probe (Butterfield et al. submitted), also allow future sampling to address hypotheses of community organization. Future collections on the

JdFR could target diffuse flow communities over a large sulphide gradient to determine if H_2S content influences species dominance patterns. *In situ* probes could also be used for selecting sites to deploy recruitment plates and larval traps.

In conclusion, the patterns detected by the observational approach adopted here are very useful for identifying the species and interactions most likely driving nonrandom community patterns among diffuse flow vents at Axial Volcano. Although interpretation of these patterns is limited by our current understanding of species attributes and community processes, this work highlights the dominant trends. Further work at other vent sites along the JdFR will reveal if these community patterns hold across regional spatial scales and future observations of eruptions will allow the proposed model of community development to tested and refined.

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APPENDIX

Living on the edges of diffuse vents on the Juan de Fuca Ridge

Marcus, J. and Tunnicliffe, V. 2002. *Cahiers de Biologie Marine* 43: 263-266.

Introduction

The first ecological studies at the Galapagos Rift vents invoked the concept of species zonation around diffuse vent openings (Hessler & Smithey 1983). Assemblages changed with increasing distance from hydrothermal influence: the direct flow dominated by vestimentiferans, clams, polynoids and limpets; mussels, serpulid worms and anemones in the next zone; and, a third peripheral zone dominated by siphonophores and ophiuroids. Other studies also relate patterns of species distributions to varying intensities of fluid flow properties (Fustec et al. 1987, Childress 1988, Desbruyères et al. 1994, Sarrazin et al. 1999, Gebruk et al. 2000).

Zonation is less visually evident at vents on the Juan de Fuca Ridge (JdFR). Species richness on the JdFR is lower compared to the East Pacific Rise and Galapagos Rift (Tunnicliffe et al. 1998); comparable megafaunal peripheral species such as suspension-feeding serpulids are absent. Nonetheless, hydrothermal influence decreases with increasing distance from the vent. Tubeworm clusters diminish and disappear, but many of the same species are present on adjacent rocks. We hypothesize that, with distance, faunal assemblages shift from a typical vent composition towards an assemblage less tolerant of vent conditions and less dependent on high rates of primary production. Our objectives are to determine whether vent assemblages are distinguishable from peripheral assemblages and, if so, to document the major differences.

Methods

The 1998 eruption on Axial Volcano, Juan de Fuca Ridge created numerous low temperature vents (Embley & Baker 1999). For this study, we sampled in July 2000 with the remotely-operated vehicle ROPOS. Two locations at each vent were targeted: within shimmering flow ('Flow' samples) and at distances of 0.5 to ~6m from the vent where no flow was evident ('Periphery' samples). 'Flow' samples were coupled with one 'Periphery' sample, except one vent where three Periphery samples were taken; three other collections were only Flow samples (Table A.1). The distance of Periphery samples from venting was estimated by video with scale indicators and cruise notes. Flow samples were tubeworm (*Ridgeia piscesae*, Jones 1985) grabs, sometimes coupled with suction samples; Periphery samples were suctions. We justify the mixed methods by a requirement for maximal assemblage representation.

Samples in 7% formalin were sorted to the lowest possible taxonomic rank and counted; although picked to 64 μm, only species whose adults would be retained on a 1 mm sieve are reported. Species evenness was calculated for Flow samples combined and Periphery samples combined using the Hurlbert's PIE measure (EcoSim 6.0, Acquired Intelligence Inc. & Kesey-Bear). Body weight data are reported for two species, *Lepetodrilus fucensis* McLean, 1988 and *Depressigyra globulus* Warén & Bouchet, 1989; bulk wet weight was measured for combined individuals from each microhabitat sampled at Cloud vent. Similarity among samples was investigated by cluster analysis using species presence/absence data (Jaccard similarity coefficient, flexible method, $\beta = -0.25$); only complete samples were included (see Table A.1). Clustering was preformed in NTSYS 2.0 (Exeter Software).

Results

I. Composition and distribution

The average relative abundances of taxa collected from the eight Flow samples and the seven Periphery samples are listed in Table A.2. More species were collected on the Periphery (n=36) than in Flow (n=31). All but 4 species sampled in Flow were also present in Periphery samples, while 9 species occurred exclusively in Periphery samples (Table A.2). Overall, species evenness is higher in Periphery samples: the probability that two randomly selected individuals are two different species is 0.75 for Periphery samples and 0.62 for Flow samples.

A striking similarity of the habitats is the abundance of two gastropods: the limpet, *Lepetodrilus fucensis,* and the snail, *Depressigyra globulus* (Table A.2). The

Table A.1. Collection listing; X denotes a sample. Distance from flow is given for Periphery samples. ID is the vent label, and * denotes a subsample from a complete collection.

Vent	ID	Flow	Periphery Near 0.5 m	 Mid. 1-3 m	 Far 5-6 m
Cloud	A	X	X	X	X
Mkr 33	B	X		X	
Mkr 113	C	X		X*	
Bag City	D	X		X	
Joystick	E	X	X		
Snail	F	X			
Nascent	G	X			
Bag City	H	X			

Table A.2. The average relative abundances of taxa from Flow and Periphery samples. *Ridgeia piscesae* is not included. * indicates species only found at Joystick Flow vent which is likely waning. ARA = average relative abundance, SP = sites present, NP = not present, P= present. Continued on next page.

Taxon	Species	Flow		Periphery	
		% ARA	# SP (of 8)	% ARA	# SP (of 7)
Gastropoda	*Lepetodrilus fucensis*	45.805	8	41.211	7
Polychaeta	*Paralvinella pandorae*	35.508	8	0.309	4
Gastropoda	*Depressigyra globulus*	10.938	8	11.487	7
Polychaeta	*Ophryotrocha globopalpata*	2.466	8	12.662	7
	Amphisamytha galapagensis	1.830	8	9.345	7
	Paralvinella palmiformis	0.924	5	NP	-
	Branchinotogluma sp.	0.675	8	0.537	2
	Parougia wolfi	0.671	7	5.697	6
	Lepidonotopodium piscesae	0.319	8	0.171	3
	Hesiospina vestimentifera	0.198	6	9.375	7
Ostracoda	*Euphilomedes climax*	0.152	1	0.105	3
Gastropoda	*Provanna variabilis*	0.147	5	1.234	6
Polychaeta	*Paralvinella sulfincola*	0.067	1	NP	-
	Prionospio sp.	0.064	3	1.554	6
	Opisthotochopodus tunnicliffeae	0.058	5	0.407	2
	Hesiodeira glabra	0.045	4	0.006	1
Pycnogonida	*Ammothea verenae*	0.038	3	0.004	1
Polychaeta	*Levensteiniella kincaidi*	0.032	4	0.417	6
	Protomystides verenae	0.029	4	NP	-
	Amphiduropsis axialensis	0.019	4	0.421	3
	Unknown spionid	0.009	2	0.109	3
Aplacophora	*Helicoradomenia juani*	0.008	1*	0.048	3
Gastropoda	*Pyropelta musaica*	0.007	1*	0.242	3
	Lacunoides vitreus	0.007	1	0.021	1
	Hyalogyrina globularis	0.006	2	NP	-
Polychaeta	*Nereis piscesae*	0.006	3	0.079	2
Nemertea	*Thermanemertes valens*	0.006	3	0.142	3
Bivalvia	Vesocomyid clam	0.005	3	0.040	2
Amphipoda	Amphipod sp.	0.005	1*	0.117	3
Ophiuroidea	Ophiuroid sp.	0.003	1*	0.019	1
Polychaeta	Unknown polynoid # 1	0.001	1	0.021	1
	Unknown polychaete #1	NP	-	2.978	4
	Unknown polychaetes	NP	-	0.476	3

Taxon	Species	Flow		Periphery	
		% ARA	# SP (of 8)	% ARA	# SP (of 7)
	mixed				
Gastropoda	*Provanna laevis*	NP	-	0.227	1
Bivalvia	Juvenile clams	NP	-	0.215	3
Polychaeta	Unknown orbiniid	NP	-	0.123	2
	Unknown nereid?	NP	-	0.082	3
	Nicomache venticola	NP	-	0.045	1
?	Unknown psuedocoelomate?	NP	-	0.032	1
Polychaeta	*Leitoscoloplos pachybranchiatus*	NP	-	0.014	1
	Harmothoe macnabi	NP	-	0.013	1
Ciliata	Folliculid sp.	NP	-	P	1
Hurlbert's PIE		0.62		0.75	

limpet ranks as the first or second most abundant species in every Periphery sample (range from 23.5% to 55.1% relative abundance) except in the farthest Cloud sample (2.5% relative abundance). Several differences occur between the Flow and Peripheral locales. First, the alvinellid polychaete, *Paralvinella pandorae* Desbruyères & Laubier, 1986 shifts from ubiquity and high abundance (35.5%) in Flow to lower occurrence and lower abundance (under 1%) on the Periphery. Its congener, *Paralvinella palmiformis* Desbruyères & Laubier, 1986 is absent in Periphery samples. Second, four polychaete species are relatively more abundant on the Periphery than in Flow: *Amphisamytha galapagensis* Zottoli, 1983, *Ophryotrocha globopalpata* Blake & Hilbig, 1990, *Parougia wolfi* Blake & Hilbig, 1990 and *Hesiospina vestimentifera* Blake, 1985 (Table A.2). *A. galapagensis*, an ampharetid, forms a conspicuous Periphery "belt" of tubes covering the basalt. Third, the polynoid polychaete *Levensteiniella kincaidi* Pettibone, 1985 typically rare in visible flow (JM unpub. data) occurs in all complete Periphery samples (Table A.2; missing from Mkr 113 Periphery sample, Table A.1).

II. Size structure

Individuals of the dominant gastropod species display marked size differences between the Flow and Periphery areas. The body sizes of *Lepetodrilus fucensis* and *Depressigyra globulus* at Cloud Vent decrease with increasing distance from vigorous flow. Average wet weight for the former species drops by three orders of magnitude and the latter by two orders (Table A.3). This trend was observed for both species in all Periphery samples.

III. Sample similarity

A cluster analysis of presence/absence data of all collections groups Periphery samples and visible Flow samples separately (Figure A.1). The one Periphery collection that clusters with Flow samples is the closest peripheral sample from Cloud vent taken only ~ 0.5 m away from the visible flow (Figure A.1). One Flow collection (Joystick) clusters with Periphery samples; visual observations suggest that this vent was waning at the time of sampling: the maximum temperature detected was 4°C, the thin tubes of

Table A.3. Average wet weight (g) of *Lepetodrilus fucensis* and *Depressigyra globulus* individuals from Cloud vent. For both species there is a trend of decreasing size with increasing distance from visible flow. n = number of individuals used for bulk measurements.

Species	Flow	Near	Mid.	Far
L. fucensis	0.1153 n=100	0.0721 n=100	0.0002 n=100	0.0002 n=7
D. globulus	0.0215 n=46	0.0244 n=69	0.0007 n=75	0.0002 n=25

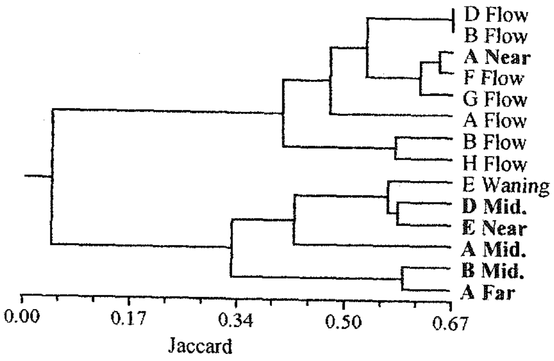

Figure A.1. Cluster diagram of species occurrences in collections. Font indicates sample type: normal are Flow and bold are Periphery samples. Table A.1 gives vent name labels and Periphery distances from vent.

Ridgeia piscesae held shriveled trophosomes, and alvinellid polychaetes were low in relative abundance (3.5%). Table A.2 indicates that, of the Flow samples, only Joystick hosts four species that are otherwise found on the Periphery.

Discussion

The assemblage sampled beyond the edges of visible vent flow differs from vent openings where temperatures ranged between 13°C and 39°C (excluding waning Joystick vent). The Flow samples retrieved over 85% of the macrofauna recorded from a larger study of Axial vent fauna (Tsurumi 2001). At the scale of this study, cluster analysis identifies a peripheral fauna. However, that fauna retains a 'vent' character: over 75% of the species are known from active vents and *Lepetodrilus fucensis* dominates both habitats.

The physicochemical attributes of the habitat are likely key factors. Although water characteristics were not measured until the following summer, we detected no temperature or sulphide anomalies at any peripheral sites. The close Cloud periphery may be an exception as fluid was advecting over the adjacent substratum during sampling. This moderate environment likely facilitates the occupation of peripheral areas by species precluded from the harsher vent habitat. Conversely, the disappearance of alvinellid polychaetes in the periphery may be in part due to loss of tubeworm substratum, changing resources, and increased competition from ampharetids.

Two and a half years post-eruption may not be enough time for encroachment by the normal deep-sea fauna to vents. There is no evident reason why they are not more abundant. We assume that the major food source is organic detritus from nearby vents. The most abundant animals are grazers/deposit feeders. However, the average relative proportion of potentially predatory and scavenging worms (polynoids, hesionids, dorvilleids, nereids and nemerteans) is greater from Periphery (29.9%) than Flow (4.5%) samples. A large nereid or polynoid predator may have a substantial influence on community structure. Apart from localized mats of folliculid protozoans, we find no suspension feeders.

The limpet, *Lepetodrilus fucensis*, is the most abundant animal in all collections except the most distal Cloud sample. This animal has multiple food gathering strategies and ranges from vent periphery to high temperature smoker habitats. It is ubiquitous on the Juan de Fuca Ridge (Tsurumi & Tunnicliffe 2001). The marked size differences in *L. fucensis* and *Depressigyra globulus* between Flow and Periphery may reflect the different habitat; body size may also be related to flow proximity for mytilid bivalves from the Mid-Atlantic Ridge (Comtet & Desbruyères 1998). Abundant small individuals of these species are uncommon in Flow samples (JM pers. obs.); juveniles may be excluded from Flow areas by predation or active venting conditions, or the small stage is very transitory. Low spatial variability in limpet larval arrival to the bottom (Metaxas, pers. comm.) implies that recruit supply is similar. However, size differences may also be due to stunted growth or predation of larger adults on the periphery.

At ~6 m from Cloud, the number of vent obligate animals decreased. While vent larvae may be arriving over wide spatial ranges, they are not surviving in large numbers. Tsurumi (2001) examined suction samples of surfaces beyond vent influence (~20-30 m away) to verify the absence of the Flow species listed here. She also found animal assemblages similar to the Periphery among tubeworm collections from failing vents where fluid flow is not visible and vestimentiferans are in poor condition. These waning vents also have higher species richness and evenness, fewer vent obligate species, the presence of deep-sea taxa, and a lower density of individuals. The vent temporal sequence may have some analogy in the spatial array.

The vent peripheral assemblage has many of the same species found in venting fluids. However, the small size and low abundance of these animals form a poorly visible band around the vents on Axial Volcano although patches of ampharetids and ciliates occur. There appears to be some incursion from the ambient deep-sea fauna. Spatial competition at the vents may relegate some individuals to this peripheral zone while other species may find it an optimal zone for foraging. Further comparative work on size and maturity characteristics of select species should better define the role of this habitat.

Acknowledgements

We thank R.W. Embley and the NOAA Vents Program and the logistical support of the *Ronald H. Brown* and *ROPOS*. This study was supported by NSERC Canada.

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