Geological Effects on Faunal Distributions on the Cleft Segment, Juan de Fuca Ridge

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Barry Milligan
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[redacted]

Dr. V.J. Tunnicliffe, Supervisor (Department of Biology)

[redacted]

Dr. P.T. Gregory, Departmental Member (Department of Biology)

[redacted]

Dr. M.J. Whiticar, Outside Member (School of Earth and Ocean Sciences)

[redacted]

Mr. P. Lambert (M.Sc.), External Examiner (Royal British Columbia Museum)

University of Victoria

Supervisor: Dr. Verena Tunnicliffe

ABSTRACT

Biological samples comprising high and low temperature vents ranging from a few to hundreds of years of age were taken within a few years of an eruption on the Cleft Segment of the Juan de Fuca Ridge. Cleft Segment is characterized by four active venting areas ranging from years to hundreds of years old. I hypothesized that older venting areas on Cleft Segment would be more speciose than younger areas. Cleft Segment is characterized by a very low number of species (24), although Cleft Segment represents the greatest areal extent, the most vents sampled, and the most specimens processed. Cleft Segment is taxonomically dominated by phyllodocid and terebellid polychaetes and archaeogastropods, and numerically dominated by 6 species (*Ridgeia piscesae*, *Paralvinella pandorae*, *Lepetodrilus fucensis*, *Depressigyra globulus*, *Amphisamytha galapagensis*, and *Paralvinella sulfincola*). Poor species richness may be explained by young age and very recent magmatic and tectonic activity, less habitat heterogeneity (possibly reducing niche availability), and regional current patterns that may not foster larval influx. The species composition of Cleft Segment is similar to that of other Northeast Pacific vents, suggesting good dispersive ability of Cleft inhabitants. The presence of vent organisms on the New Pillow Mounds (NPM) demonstrates that vent animals are colonizing new vents within at most 2 to 6 years.

There is a significant difference in species composition, but not species diversity or richness, among active venting areas of Cleft Segment. *P. pandorae* and *L. fucensis* is more abundant at South Cleft and *D. globulus* is more abundant at Young Sheet Flow (YSF) and Older Northern Lavas (ONL). *Ridgeia piscesae* dominated at South Cleft and ONL while *A. galapagensis* was absent from South Cleft and *P. sulfincola* was absent from YSF. Differences in species assemblages corresponded to differences in temperature and/or substratum, and distance the sample was taken from the active venting source or orifice. Within areas, and even within vents, there are differences in community structure corresponding to differences in temperature or substrata to which vent organisms are exposed. *Paralvinella pandorae*, *L. fucensis*, and *A. galapagensis* appear adapted to low temperature venting whereas *R. piscesae*, *D. globulus*, and *P. sulfincola* appear adapted to high temperature venting. Factors such as restricted settling space and competition do not appear to be important in structuring community assemblages at Cleft Segment. However, one cannot rule out the possibility that competition is occurring, or has occurred, at Cleft Segment. The documented decline of vent flow and vent fauna during this study indicate that underlying geological and chemical processes have a serious effect on community composition.

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ACKNOWLEDGEMENTS

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VENT ECOSYSTEM

Since the discovery of hydrothermal vents (Lonsdale, 1977), hundreds of vents, invertebrate species, and bacteria have been described from this type of environment (Tunnicliffe, 1991). The understanding of the special conditions there and how they have influenced the evolution of the fauna has also improved. The hydrothermal vent ecosystem experiences extremes in geological, physical, and chemical conditions which have an immediate effect on associated fauna. Vent fauna has evolved to exploit a narrow range of conditions varying in time and space. A basic characteristic of the hydrothermal vent habitat is the large and rapid temporal and spatial changes in the various factors supporting it (Tunnicliffe, 1991).

Hydrothermal venting with associated biota has been found in both the Pacific and Atlantic Oceans. At spreading centers, cold sea water moves through the crust becoming altered by contact with surrounding rock. Heating causes the water to become buoyant, which forms vents by upwelling through the seafloor. Underlying geological and physical processes are of major importance to vent fauna because they govern the survival of vent communities (Tunnicliffe, 1988). Variability in the activity of magma chambers influences the stability of venting, which supports biota. Degree of continuity of magma supply, flow through central conduits, and lateral diffusion of vent water may affect the community composition (Massoth et al., 1988).

Vents fall into two main groups : 1) warm vent fields with maximum exit temperatures of less than 100°C and flow rates of 0.5-2 cm sec^{-1} and 2) hot vents with maximum exit temperatures of 270°-380°C and flow rates of 1-2 m sec^{-1} (Jannasch and Mottl, 1985). Both types of vents have been found to occur along spreading ridge crests of the EPR (East Pacific Rise) and JDFR (Juan de Fuca Ridge; Rona et al., 1984). Hot vent fields commonly include warm- and intermediate-temperature vents (<300°C; "white smokers") as well as high-temperature vents (350° +/- 2°C; "black smokers"). The chemistry of vent waters indicates that both warm and hot vent fields are fed at depth by a high-temperature end-member solution at about 350°C and that the mixing of this solution with largely unreacted and unheated ocean bottom water in the shallow regions of the crust is responsible for the wide range of exit temperatures (Corliss et al., 1979).

Chemosynthesis and symbiosis are the basis for the concentration of biomass in the vent ecosystem (Tunnicliffe, 1991; Southward, 1989). Sulfur-oxidizing bacteria are ubiquitous in deep-sea hydrothermal vent communities (Tuttle, 1985). Microbial mediation of the oxidation of dissolved sulfide results in the transfer of chemical bond energy to biologically useful molecules such as ATP and NAD(P)H (Jannasch, 1985). These molecules are then fed into the Calvin-Benson cycle where carbon dioxide is fixed into usable sugars. Using nitrogen isotope ratios and carbon isotope ratios, Rau (1981) and Van Dover and Fry (1989), respectively, showed that distinct isotopic compositions from the East Pacific Rise reflect local sources of organic carbon and nitrogen. Microbial activity occurs mainly within subterranean vent systems at moderately elevated temperatures and decreases rapidly as emitted plume water mixes with cold ocean-bottom water (Tuttle, 1975). In terms of animal tissue mass, the most important sites of bacterial production seem to be bacterial mats and where bacterial symbionts inhabit tissues of megafauna such as the vestimentiferan *Riftia* and clam *Calyptogena*.

The hydrothermal vent ecosystem is characterized by a high degree of endemicity. Vent fauna are endemic at the level of 95% of its species and 22% of its families (Tunnicliffe, 1992). The vent fauna has developed from four sources: from the nearby deep-sea community, from a widespread fauna of generalists, from a sulphophillic fauna, but mostly from long-term in situ evolution. This ecosystem is also taxonomically dominated by vestimentiferans, phyllodocid and terebellid polychaetes, archaeogastropods, siphonostome copepods, and decapods (Tunnicliffe, 1991). Echinoderms, sponges, xenophyophores, all coelenterates (except anemones), brachiopods, bryozoans, phoronids, chaetognaths, ctenophores, and echiurans are lacking.

The vent habitat poses problems for colonization because of toxicity of vent emissions, high-temperature gradients, isolation, temporal and physical instability of the habitat, and a constant rain of particulates (Tunnicliffe, 1991). Numerous animals show adaptations such as the likely detoxification role of alvinellid epibionts (Gaill et al., 1988), the radiation sensitive organ in Mid-Atlantic Ridge shrimp (Van Dover et al., 1988), and the sulfide binding capability of blood in vent vestimentiferans (Arp and Childress, 1983). The physical and chemical environment may select for a protective cuticle, shell or tube that is more common in solitary organisms. A complex blood vascular system needed for detoxification and sulfur and oxygen binding may exclude most echinoderms, coelenterates, and sponges. The heterogeneity of the system may also select for sexually reproducing organisms that can colonize new habitats (Grassle, 1986).

Vent fields contain individual vents with large differences in vent water chemistry over short geographic distances (Von Damm, 1990). However, some common differences between pure hydrothermal fluids and ambient sea water that are of biological significance include : temperatures up to 400°C (Delaney et al., 1989), pH values to 3.2 and salinities from one-third to twice that of sea water and hydrogen sulfide to 19.5mmol/Kg (Butterfield et al., 1990), and the presence of a large number of cations normally depleted in sea water (Von Damm, 1990). Oxygen, nitrates, and phosphates are low or absent while carbon dioxide is variable (Edmond and Von Damm, 1985). Trace metals such as iron and manganese may be extremely enriched (Von Damm, 1990) while magnesium is used as an indicator of venting activity because it is absent from pure hydrothermal fluid.

SPATIO-TEMPORAL DISTRIBUTION OF VENT ANIMALS

Vent systems are thought to be relatively short-lived with a lifetime of less than 100 years (Lalou and Brichet, 1982) to a maximum of 40,000 years (Converse et al., 1984), with individual vents lasting one to ten years (Macdonald, 1982) due to mineral precipitate clogging the vents. This coincides with age estimates of bivalve molluscs indicating life spans of approximately 20 years at EPR (21°N) (Lutz et al., 1983). In a six-year time-series study of hydrothermal venting activity at EPR (21°N) Campbell et al. (1988) found little or no change in the major element composition of fluids at three out of four vents found there. Small variations between vent fields may be a function of the amount and type of sediment the fluid must pass through to exit onto the seafloor as well as entrainment of seawater in the mound plumbing system (Campbell et al., 1988). The time scale for significant changes in flow rates appears to be on the order of years to tens of years for individual vents.

Butterfield et al. (1990) believe that spatial variation in chemical composition and flow at Cleft Segment can best be explained by a single hydrothermal fluid undergoing phase separation while rising through the ocean crust, followed by partial segregation of vapor and brine phases. This phenomenon known as phase separation is inferred from chemical composition of vent fluids. Separation of hydrothermal effluent into liquid (brine) and vapor phase is attributed to differential functional stress between the flowing medium and the surrounding rock, which is, in turn, a function of the viscosity of the flow medium and the intrinsic permeability of the rock (Fox, 1990). Brine phase fluids are discharged from major conduits such as high-temperature sulfide chimneys. The vapor phase is discharged via diffuse flow from the sea-water or surrounding chimneys.

Type of venting influences the species composition of vent communities (Fustec et al., 1987). Certain species appear adapted to diffuse, low-temperature flows emanating from cracks in the seafloor, whereas others appear to require the habitat associated with high-temperature plumes venting from massive sulfide chimneys. Low-temperature, diffuse flow vent communities are characterized by zonation of the vent fields into three distinct habitats. The warm-water "vent" region of a diffuse flow field is typically dominated by dense clusters of megafaunal species that rely, to a large extent, on chemoautotrophic endosymbiotic bacteria for their nutrition. Beyond the central region are "near-field" populations of suspension-feeding and grazing megafaunal species that are presumably dependent on primary chemosynthetic production by free-living microorganisms. Boundaries of vent and near-field populations are sharp and appear to be defined by gradients of water chemistry as well as by the hydrodynamic regime within the vent field. Anemones, serpulid worms, gastropods, and galatheid crabs often characterize these regions. The "peripheral" region of a diffuse flow field has the least well defined boundaries. It is in this region that certain non-vent species may occur in greater abundance than elsewhere in the deep sea.

Chimneys comprise a fourth habitat within a vent field. Physical and chemical gradients are at their most extreme and most complex within this habitat. Characteristic fauna associated with the chimneys are alvinellids and vestimentiferans. Fustec et al. (1987) believe that heterogeneity produced by processes altering vents, causing precipitation of polymetallic sulfides, and creating edifices which block and divert flow, promote species diversity within chimney environments. As hot hydrothermal fluid mixes with seawater rich in sulfate, one of the first minerals to precipitate is anhydrite ($CaSO_4$) which remains insoluble between about 130° and 330°C at 2300 m depth (Haymon and Kastner, 1981). Tunnicliffe and Juniper (1990) found that the rapid growth of sulfide structures could cause drastic changes in the location and intensity of water flow as well as the deposition of rock on animals.

Tunnicliffe and Juniper (1990) believe that the growth of chimneys and associated fauna go through four successional stages: 1) high-temperature venting probably associated with tectonic activity that opens fluid conduits; 2) sulfide accumulation reducing porosity and encouraging colonization, (most notably of vestimentiferan tubes, Tivey and Delaney, 1986); 3) increasingly heterogeneous pattern of hydrothermal flow resulting from irregularities in chimney growth and mineralization associated with an increase in species number; and 4) formation of very large sulfide deposits with a few active smokers and their associated fauna. Finally, flow is restricted until it could no longer support fauna.

Variability in the geochemistry of venting water among vent fields is expressed in the availability of reduced chemical species, which in turn, influences the species composition of vent communities (Van Dover and Hessler, 1990). Chemoautotrophic organisms of vent communities need both oxidized and reduced chemicals to complete redox chemical cycles (Johnson et al., 1988a). Elements and gases determine quantity and quality of food supply for chemolithotrophic bacteria (Baross and Deming, 1985). Temperature can be used to estimate the chemical concentrations present in the mixture because it is positively correlated with sulfide and negatively correlated with oxygen (Johnson et al., 1988a). Temperature acts both by itself (a limiting condition on enzymatic and transport processes) and as a semi-conservative factor of the fluid dilution by affecting oxygen and sulfur contents (Chevaldonne et al., 1991). Dissolved oxygen is quickly scavenged by reduced chemical compounds in temperatures exceeding 8-12°C (Johnson et al., 1988a).

Tunnicliffe et al. (1985) found temperature on top of a sulfide chimney to be highly variable, suggesting stochastic turbulent mixing of vent and ambient waters. Likewise, Johnson et al. (1988a) found fluctuations in mean temperature at Rose Garden to be correlated significantly with values measured up to 1.25 h later, indicating that some external process is driving the fluctuations in temperature on a time scale of several hours. Chevaldonne et al. (1991) found periodicities in temperature ranging from tens of seconds to tens of hours at vents from EPR (13°N), Lau Back-Arc Basin, and the North-Fiji Basin. A combination of tidal cycles, turbulent mixing, and variance in hydrothermal discharge seem responsible. Changes on a scale of hours imply that vent animals are capable of withstanding changes in body temperatures and long stays in anoxic and hypoxic conditions (Chevaldonne et al., 1991).

Like few others, the hydrothermal vent habitat is totally dependent upon the sea-floor manifestation of geophysical processes of the substrata (Tunnicliffe and Juniper, 1990). Vent communities are isolated and greatly limited, both spatially and temporally, to habitats of tolerable temperature (< 40-50°C) that contain sufficient hydrogen sulfide and oxygen to support chemosynthesis. The specialized nature of the animals and their limited diversity (Grassle, 1986) represent an uncommon and extreme habitat. Huston (1979) and Pielou (1975) suggest that harsh environments (environments dominated by extreme abiotic factors) have broader niches which allow for fewer species, as well as causing a greater chance of extinction for marginal populations. At local scales, other processes, such as recruitment, competition, and predation, may control faunal composition and relative abundance of species at vent sites (Van Dover and Hessler, 1990).

At EPR, Johnson et al. (1988b) believe that the gradient of organisms around a vent may be partly self-regulating, especially among symbiont hosts competing for dissolved sulfides. Hessler et al. (1988) documented changes in an animal community at Rose Garden, Galapagos. Between 1979 and 1985 vestimentiferans had almost disappeared, mussel abundance and size had increased, clam distribution had expanded, and anemone, serpulid, siphonophore, and enteropneust densities had decreased. Hessler et al. (1988) believe that changes were due to mussel populations blocking flow and consuming sulfide. Johnson et al. (1988b) believe that the niches of the three major symbiont-hosts at East Pacific Rise, *Riftia*, *Calyptogena*, and the mussel *Bathymodiolus*, may be defined by their differential abilities to take up sulfide and separate that uptake in space and time. Mussels are able to thrive over a wider range of conditions than either *Calyptogena* or

Riftia and this is due to a lesser reliance on their symbiotic bacteria as a source of nutrition (Fisher et al., 1988). However, there is probably also a large component of history and chance associated with the colonization and domination of new sites which have a large effect on subsequent community development (Tunnicliffe, 1991).

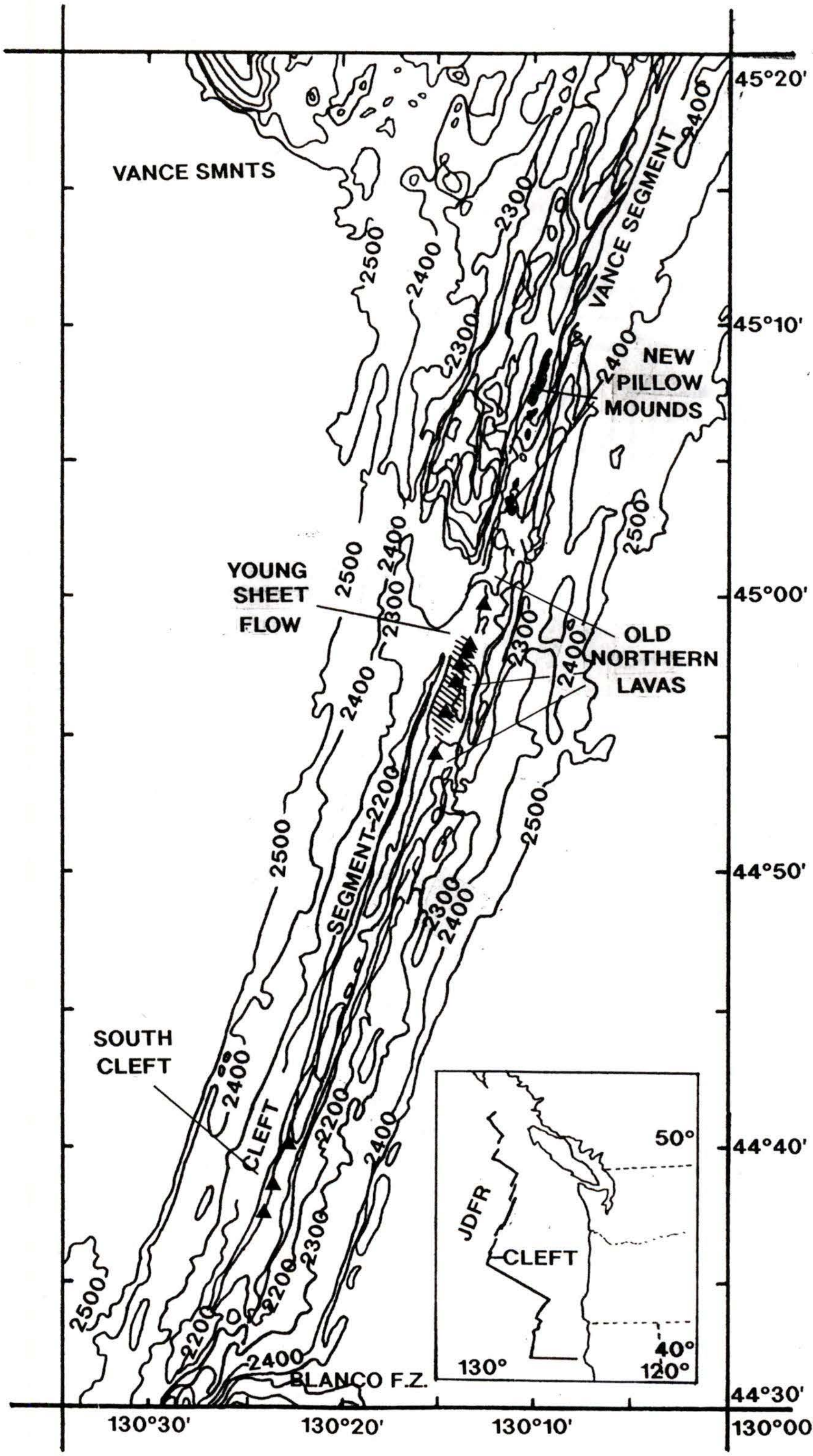
Some chemical or physical indicator of vents, such as sulfide or temperature gradient, may serve as a cue for recruitment (Tunnicliffe, 1992). Yamaguchi and Newman (1990) suggest that the disjunct nature of vents requires that vent animals must have excellent dispersability. This ability does not have to be exceptional because vents are probably more common than we think and because habitat specificity is a frequent requirement for benthic animals (Tunnicliffe, 1992). Although a few vent species undergo planktotrophic, high-dispersal modes of development, most have a relatively low dispersal capability and possess a free-swimming, nonplanktotrophic larval stage (Lutz, 1988). Despite the large distances separating the various deep-sea hydrothermal vent regions, several characteristic species are present at all of the sites studied. The free-swimming, nonplanktotrophic larvae of a number of these species may possibly have a dispersal capability sufficient to maintain chains of far-flung populations through stepwise larval dispersal (Lutz, 1988). However, at present, a knowledge of the frequency with which active hydrothermal vent areas occur along spreading centers and the understanding of deep-ocean circulation patterns are inadequate to determine whether or not such dispersal is feasible.

It has been hypothesized that, in an unpredictable environment, selection favors early maturity, high fecundity, semelparity, large reproductive effort, and reduced parental care (e.g., Grassle and Grassle, 1974). Desbruyeres and Laubier (1983) suggest that vent fauna should be expected to display all of these life-history characteristics in the form of r-type ecological strategies. Although the peculiar characteristics of the vent habitat may be expected to impose selective forces for certain life-history traits, many vent species may not be capable of adopting such traits due to limitations imposed by ancestry, particularly with regard to modes of larval development (Tunnicliffe, 1992).

STUDY SITE

The Cleft Segment is approximately 60 km long at a depth of 2200-2300 m, with a structurally well-defined, 2-3 km-wide axial valley bounded by steep, faulted walls with up to about 150 m relief. It is bounded by the Blanco Fracture Zone to the south and is overlapped by the Vance Segment by about 10 km to the north (Baker and Hammond, 1991). Its name is derived from the presence of a nearly continuous cleft that is 10 km long, 30 to 50 m wide, and 20 m deep, extending from about 44°35′ to 44°44′N within a broad, 3-km-wide axial valley (Figure 1). Recent lavas erupted between

Figure 1: Map of southern Juan de Fuca Ridge (Cleft Segment). Contour interval is 100m. Depths are in meters. Adapted from Embley et al. (1991). Older Northern Lavas occur between YSF and NPM, on the eastern edge of the YSF and to the south of the YSF above 44°50′N.


45°20'
VANCE SMNTS
VANCE SEGMENT
2400
2300
2500
45°10'
NEW
PILLOW
MOUNDS
2500
YOUNG
SHEET
FLOW
2400
2300
45°00'
OLD
NORTHERN
LAVAS
SEGMENT-2200
44°50'
SOUTH
CLEFT
CLEFT
2200
44°40'
JDFR
CLEFT
50°
40°
130°
120°
BLANCO F.Z.
44°30'
130°30'
130°20'
130°10'
130°00'

1983 and 1987 on the northern end of the segment. Associated with this eruption was the occurrence of "Megaplume", strengthening the hypothesis that megaplumes are caused by sea-floor extension events (Embley et al., 1991). Megaplume was a 20-km-diameter plume of hydrothermal origin discovered at a height of 700m over Cleft Segment in 1986 (Baker et al., 1987).

Vents on South Cleft (Figure 2) are located in a fissure which has been active for a relatively long time, judging by the sulfide accumulations present when visited in 1984, and are estimated to be less than a few hundred years old (Normark et al., 1983). The other area of active venting on the Cleft Segment occurs between about 44°54′N and 45°03′N (Figure 3). The northern vents are associated with three geological settings. The youngest lavas are a chain of pillow mounds (new pillow mounds or NPM; Figure 4) which were erupted between 1983 and 1987 (Chadwick et al., 1991; Embley et al., 1991; Fox et al., 1992). The NPM vents are characterized by diffuse flow from the pillow lavas and are not associated with any distinct geological structure (Chadwick and Embley, 1994). The most vigorous venting is associated with a fissure system on the eastern edge of a young sheet flow (YSF) estimated to be only years to decades old (Embley et al., 1991) and consists of both diffuse, low-temperature vents and focussed, high-temperature chimneys (Embley and Chadwick, 1994). The diffuse vents usually have

Figure 2: Map of southern Cleft Segment. Contour interval is 20m. Depths are in meters. Adapted from Von Damm and Bischoff (1987).

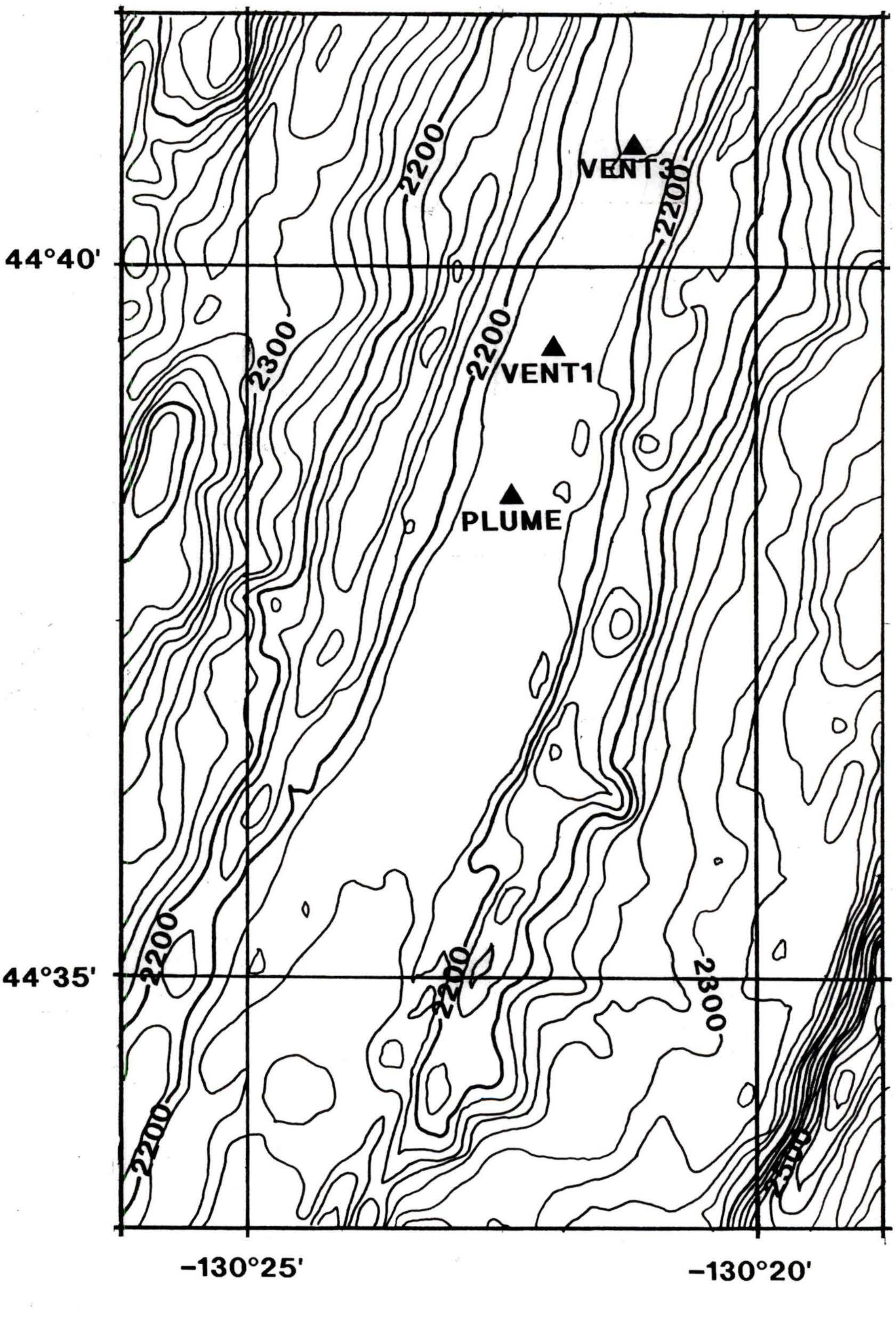

44°40'
44°35'
-130°25'
-130°20'
VENT3
VENT1
PLUME
2200
2300

Figure 3: Map of northern Cleft Segment. Contour interval is 10m. Depths are in meters. Adapted from Embley et al. (1991).

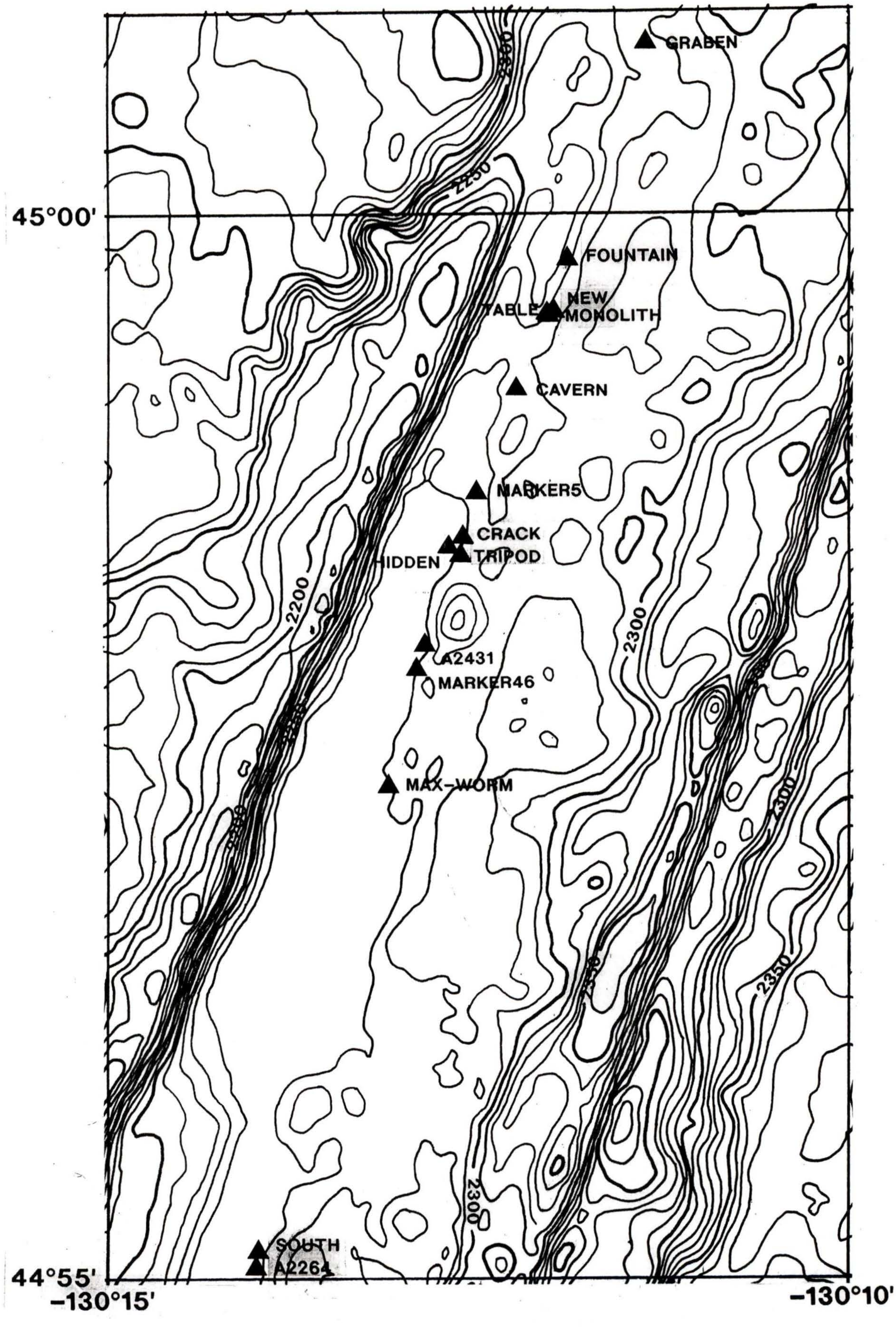
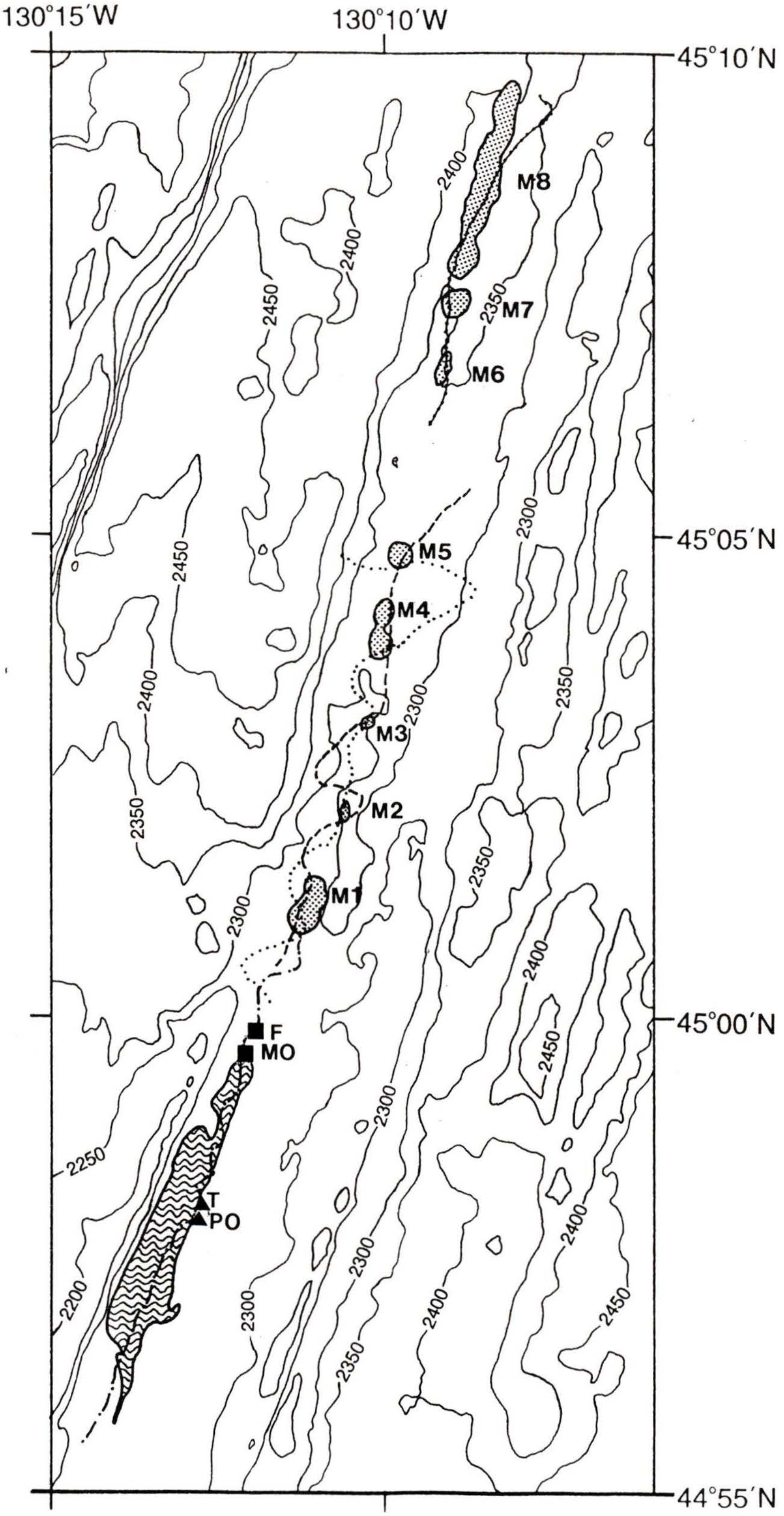

GRABEN
FOUNTAIN
TABLE
NEW MONOLITH
CAVERN
MARKER5
CRACK
HIDDEN
TRIPOD
A2431
MARKER46
MAX-WORM
SOUTH
A2264
2300
2250
2200
2250
2300
2300
2350
2300
2350
2300
45°00'
44°55'
-130°15'
-130°10'

Figure 4: Map of northern Cleft Segment depicting camera tow tracklines (denoted by dotted lines) used to document animal abundance (Milligan and Tunnicliffe, 1994). Striped feature to south is Young Sheet Flow (YSF) and the eight New Pillow Mounds are stippled. Depths are in meters. Adapted from NOAA Seabeam map in GPS coordinates.


130°15'W
130°10'W
45°10'N
45°05'N
45°00'N
44°55'N
M8
M7
M6
M5
M4
M3
M2
M1
F
MO
T
PO
2200
2250
2300
2350
2400
2450

exit temperatures of no more than 30°C (Embley et al., 1991). Venting also occurs along fissures within Older Northern Lavas (ONL) south of the sheet flow and between the sheet flow and the southernmost of the NPM. Although the basalts from the entire length of the neovolcanic zone of the Cleft segment appear to have been derived from the same mantle source, a systematic northward increase in magnesium concentration along the segment within the neovolcanic zone indicates less shallow-level differentiation to the north, possibly related to the development of new magma chambers during the recent phase of sea-floor spreading that has occurred there (Embley et al., 1991). Table 1 classifies the four major areas of venting along with lava type, location, distribution, and estimated and relative ages.

Table 1: Type of lava substrata, location, distribution, estimated age, and relative age from oldest (1) to newest (4) for the four major active venting areas on Cleft Segment. Vents are classified as South, Older Northern Lavas (ONL), Young Sheet Flow (YSF), and New Pillow Mounds (NPM).

Lava Name	Lava Type	Location	Distribution	Estimated Age (yrs)	Relative Age
South	basalt, chimneys	South	sheets, mounds	100's	1
ONL	basalt, chimneys	North	sheets, mounds	<100's, >10's	2
YSF	basalt	North	sheet flow	10's	3
NPM	basalt	North	8 mounds	6-12	4

While there are very important differences in vent fluid composition between ridge-crest sites (Von Damm, 1990), and sometimes large gradients in composition within single vent fields (Butterfield et al., 1990), until recently, the evidence from time-series measurements at specific vents (Campbell et al., 1988; Butterfield et al., 1990) indicated that vent fluid compositions changed very slowly and were apparently controlled by equilibrium with an alteration mineral assemblage. However, Butterfield and Massoth (1994) found that very large changes in vent fluid composition occurred on a time scale of years on the YSF and ONL, and that the primary differences in composition are related to phase separation and segregation of vapor and brine phases.

Vent fluids from South Cleft are uniquely high both in chloride, which ranges up to twice seawater value, and in metal content (Von Damm and Bischoff, 1987). The composition of vented fluids at North Cleft changed significantly between 1988 and 1990 (Butterfield and Massoth, 1994) and is believed to be related to the evolution of the hydrothermal system in this area following a tectonic or volcanic event which led to the 1986 and 1987 megaplume eruptions. Decreasing chlorinity and metal contents at one high-temperature vent suggest that the proportion of brine decreased from 1990 to 1992, either by mixing with low chlorinity vapor or with circulating seawater. Taken together, the Li, B, and Mn variations with chloride suggest that the spatial and temporal variations in chemical composition of the high-temperature vent fluids collected at North Cleft between 1990 and 1992 can be explained by mixing of a hydrothermal brine with convecting seawater, with the possible involvement of a vapor phase. The diffuse fluids located more than 50 meters away from known high-temperature vents had significantly lower levels of iron and were nearly totally depleted of hydrogen sulfide, consistent with a history of sub-seafloor precipitation of iron sulfides and iron oxides/hydroxides. In contrast, the diffuse vents located only a few meters from Monolith Vent had zero-magnesium endmembers for iron and hydrogen sulfide virtually identical to the high-temperature source, indicating mixing very near the seafloor and little precipitation prior to venting.

PROJECT OBJECTIVES

The hydrothermal vent ecosystem is an extreme environment where vent fauna have evolved to exploit a narrow range of conditions varying in time and space. Vent fauna are characterized by a high degree of endemicity and have largely developed from long-term in situ evolution. Like few others, the hydrothermal vent habitat is totally dependent upon the sea-floor manifestation of substratum geophysical processes (Tunnicliffe and Juniper, 1990). An understanding of community assemblages and ecology is important in understanding species interactions, evolution and physiological adaptations that are truly unique to the hydrothermal vent ecosystem.

Since the original discovery of hydrothermal vents on the Galapagos Ridge (Lonsdale, 1977), biological investigations have largely been concerned with taxonomic and physiological questions. More recently, several authors have raised questions concerning ecological dynamics of these communities (Hessler et al,. 1988; Tunnicliffe and Juniper, 1990; Fustec et al., 1987). Despite substantial reasons for suspecting community changes, little direct evidence has been available (Hessler et al., 1988). Temporal changes in faunal composition are rarely and poorly observed. To date, no one has tried to reconstruct and compare whole vent community assemblages. Community studies have been limited to photographic analysis (Fustec et al., 1987 and Hessler et al., 1988). Such studies limit analysis to large species easily identifiable in photographs and are often limited to only a few vents.

Many limitations are inherent in a study involving sampling of the hydrothermal environment. Due to the inaccessibility of the hydrothermal vent environment, and the expense incurred by submersible expeditions, samples do not represent equal bottom area, equivalent location in a vent, or even equal collection effort; they are 'samples of opportunity'. Faunal samples are taken using hydraulic submersible claws, thus excluding quantitative sampling of a vent. One must assume that a community sample taken in this manner represents a random sample, and is not biased towards any particular portion of the community, e.g., larger species. Time constraints and technical difficulties encountered during a submersible dive can sometimes prevent the sampling of water or temperature at a vent. Consequently, many faunal samples lack supporting physico-chemical data. Despite the cost of submersible bottom time, biological interpretations would be less suspect with better techniques. Better replicate samples from the same vents in the same years along with microhabitat measurements of chemistry, temperature, and flow regimes are required for further studies.

This study presents results derived from faunal samples obtained by submersible from Cleft Segment, Juan de Fuca Ridge during 1984, 1987, 1988, 1990, 1991, and 1992. The Cleft Segment provides an ideal opportunity for analyzing vent community assemblages because it is comprised of four distinct and differently aged environments (Table 1), of which three have been sampled on multiple occasions, - sometimes on different years. It is obvious that the underlying geological processes behind venting on Cleft are changing on a year-to-year scale. Juniper et al. (1990) believe that the relative isolation and short life of hot vents may mean that historical accidents due to geographical position and dispersal have great importance to community development. The main objective of this study is to examine the stages of community development and evolution at vents of varying type and age. Specifically, I compare community assemblages from South Cleft, YSF, and ONL. Because of the terminal location of Cleft Segment on the JDFR, the apparent isolation from possible sources of recruitment to the north and south, and the poor dispersive capabilities of many vent organisms, I predicted that South Cleft would be more specious than the NPM, YSF, and ONL, with decreasing species diversity and richness in that order.

Certain vent species appear adapted to diffuse, low-temperature flows emanating from cracks in the seafloor, while others appear to require the habitat associated with high-temperature plumes venting from massive sulfide chimneys. A comparison of vents from high (sulfide substrata) and low (basalt substrata) temperature vents is provided to determine if temperature or vent substratum has an effect on species composition. A comparison of vents from the same venting area, and in some cases a comparison of the same vents from different years, is also provided. A further comparison of samples from the same vent, but different distances to the actual emission site, is provided to determine the effect of microhabitat on species composition.

MATERIALS AND METHODS

- SAMPLE COLLECTION AND TREATMENT

Samples of hydrothermal vent communities were collected from South Cleft in 1984, 1987, 1990, and 1991, and from North Cleft in 1988, 1990, and 1991 using the ALVIN submersible (Table 2). One sample was taken from North Cleft in 1992 with the Canadian HYSUB 5000 ROV (remotely operated vehicle) operated from the NOAA (National Oceanic and Atmospheric Administration) ship DISCOVERER. This joint Canadian/American expedition marked the first time that high-temperature vent fluids were sampled from an ROV. All samples were attained by a mechanical arm. Samples were sorted through a 1 mm sieve. All species were identified and catalogued by the author (Appendix A). Catalogue data and voucher specimens are presently stored at the University of Victoria. All samples are presently preserved in either 5% sea-water formalin or 70% Ethanol or frozen at -70°C. Only sedentary (slow-moving adults) and sessile (animals that disperse only by larvae and are permanently attached as adults) invertebrates are examined.

No samples are available from vents on Mound lavas. Colonization is assessed from photographs taken from camera tows in 1989 and 1991 that covered all mounds and from ALVIN dives in 1990 and 1991 that traversed Mounds 1 and 2.

Table 2: Name, date, X, Y, and Z coordinates, and latitude and longitude of dive (A = ALVIN, H = HYSUB) faunal samples were taken from.

DIVE	NAME	Mo/Dy/Yr	X(m)/Y(m)/Z(m)	LATITUDE/LONGITUDE
A1455	VENT1A	09/16/84	?	44°39.2'/130°22.0'
A1461	PLUME	09/28/84	?	44°38.3'/130°22.2'
A1463	VENT1B	09/30/84	?	44°39.2'/130°22.0'
A1910	VENT1B	09/16/87	?	44°39.6'/130°21.8'
A1914	VENT3	09/20/87	?	44°40.8'/130°22.3'
A2075	CRACK	08/03/88	1447/14218/2270	44°57.6'/130°13.8'
A2076	MAX-WORM	08/04/88	1400/13200/2280	44°57.5'/130°13.8'
A2077	STATION2	08/05/88	1615/14669/2275	44°57.6'/130°13.8'
A2078	SOUTH	08/06/88	1086/7981/2280	44°57.3'/130°13.8'
"	STATION4	"	957/7222/2280	44°57.3'/130°13.8'
A2079	TRIPOD	08/07/88	1450/14185/2265	44°57.6'/130°13.8'
A2080	TRIPOD	08/08/88	1415/14171/2270	44°57.6'/130°13.8'
"	CAVERN	"	1793/15603/2270	44°57.7'/130°13.8'
A2082	CAVERN	08/10/88	1793/15603/2270	44°57.7'/130°13.8'
A2092	HIDDEN	08/20/88	1460/14185/2280	44°57.6'/130°13.8'
A2093	LAVA LK	08/21/88	1500/14750/2260	44°57.6'/130°13.8'
A2094	CAVERN	08/22/88	1835/15600/2270	44°57.7'/130°13.8'
A2259	MONOLITH	08/19/90	3655/11668/2259	44°58.9'/130°13.3'
A2259	TABLE	"	3659/1176/2257	44°58.9'/130°13.3'
A2259	MONOLITH	"	3655/11668/2259	44°58.9'/130°13.3'
A2262	GRABEN	08/22/90	4645/13890/2271	45°00.2'/130°12.6'
A2263	?	08/23/90	?	44°38.6'/130°21.2'
A2264	MARKER22	88/24/90	1144/3828/2283	44°54.0'/130°15.5'
A2265	MONOLITH	08/26/90	3642/11661/2259	44°58.9'/130°13.3'
A2267	?	08/28/90	3252/10636/2266	44°57.7'/130°13.8'
A2269	MONOLITH	08/30/90	3650/11662/2261	44°58.9'/130°13.3'
A2427	?	??/??/91	?	44°39.6'/130°21.8'
A2429	FOUNTAIN	07/19/91	4022/11447/2265	44°58.9'/130°13.3'
A2431	?	07/21/91	2530/8572/2277	44°57.5'/130°13.8'
A2433	MONOLITH	07/23/91	3810/11600/2255	44°58.9'/130°13.3'
A2434	TABLE	07/24/91	3808/11618/2255	44°58.9'/130°13.3'
A2435	?	07/25/91	4104/12381/2247	44°58.9'/130°13.3'
A2436	FOUNTAIN	07/26/91	4013/12090/2252	44°58.9'/130°13.3'
A2443	?	08/04/91	3410/10976/2270	44°57.6'/130°13.8'
A2444	MARKER46	08/05/91	2577/8656/2278	44°57.5'/130°13.8'
H202	MONOLITH	07/11/92	3810/11600/2255	44°58.9'/130°13.3'

- VENT COMMUNITY ANALYSIS

Data were analyzed by inspection of species lists to examine taxonomic composition and dominant species, calculation of species diversity and other community characteristics, multivariate analysis of covariance (MANCOVA) and univariate analysis of variance (ANOVA) to test for the significance of spatial and group differences, and numerical classification to identify patterns of faunal similarity. Measures of diversity and other community characteristics consisted of numbers of individuals, number of species (S), the Shannon information function (H′; Shannon and Weaver, 1963), and the associated evenness component (J′; Pielou, 1975). Evenness is a fraction of the maximum possible diversity which would be obtained at a given site if the individuals there were equally divided among the taxa present. Natural logarithms were used to calculate H′. Systat (Wilkinson, 1990) was used for MANCOVA, univariate ANOVA, analysis of covariance (ANCOVA), and stepdown analysis models.

Underlying multivariate and univariate procedures and most statistical tests of their outcomes is the assumption of normality and homogeneity of variances (Tabachni~~ck~~ and Fidell, 1989). In most community analyses in which species abundances are usually sparse, multivariate normality can be attained only by a transformation coupled with a substantial reduction in species considered to be the most abundant ones (Clarke and Green, 1988). Normality is the assumption that each variable and all linear combinations of the variables are normally distributed. When a distribution is normal, the values of skewness (pileup of cases to the left and right tails) and kurtosis (too few or too many cases in the tails) are zero (Tabachnick and Fidell, 1989).

A multivariate analysis of covariance (MANCOVA) was used to test for the significance of area (South, YSF, and ONL) on the fourth-root transformed proportions of the five most abundant species (*P. pandorae*, *R. piscesae*, *L. fucensis*, *Depressigyra globulus*, and *Amphisamytha galapagensis*) using sample size as the covariate. Originally, I had used all species comprising over one per cent of the total abundance, but *Paralvinella sulfincola* was later dropped from the analysis because it could not meet assumptions of normality or homogeneity of slopes. To reduce variability, only tubeworm grabs from active vents were used in the analysis. All YSF samples were from low-temperature vents. Almost all of the ONL samples, except the samples obtained on A2264, 2262, and 2078, were from high-temperature vents. All samples from the South (except the sample obtained on A1455) were also from high-temperature vents (Table 3). Therefore, samples obtained on dives A1455 and A2264 were eliminated from the first MANCOVA. This allowed me to compare the three areas and eliminate within area variability caused by differences in substrata. An alpha level of 0.05 was selected as the significance level for the main effect test. For the following statistical tests a Bonferroni-adjusted acceptance level was used (Tabachnich and Fidell, 1989).

Table 3: Area (see Table 2 or text for definitions), year, dive, vent temperature (High or low), number of individuals (#Ind) and species (#Sp), species diversity (H'), and evenness (J') for each faunal sample. Stn = to alphabetical ordering of stations used in statistical analysis. Grp = to group classification resulting from cluster analysis. Area refers to Older Northern Lavas (ONL), Young Sheet Flow (YSF), and South Cleft (Sth).

Dive	Vent	Stn	Area	Yr	#Ind	#Sp	H′	J′	Temp	Grp
H202	Monolith	A	ONL	92	637	5	0.81	0.45	Hi	1
A2444	Marker46	B	YSF	91	467	5	1.17	0.73	Lo	2
A2436	Fountain		ONL	91	68	5	0.42	0.26	Hi	
A2434	New		ONL	91	158	6	1.40	0.78	Hi	
A2431	?		YSF	91	252	4	0.22	0.16	Lo	
A2429	Fountain	C	ONL	91	694	7	0.56	0.29	Hi	1
A2427	?		Sth	91	64	6	1.25	0.70	Lo	
A2269	Monolith		ONL	90	38	1	0.00	0.00	Hi	
A2267	?	D	YSF	90	962	12	1.00	0.40	Lo	1
A2265	Monolith	E	ONL	90	1520	9	1.20	0.55	Hi	2
A2264	MARKER22	F	ONL	90	8182	19	1.50	0.51	Lo	2
A2263	?	G	Sth	90	2661	8	0.82	0.40	Hi	1
A2262	Graben		ONL	90	57	8	1.54	0.74	Lo	
A2259C	Monolith	H	ONL	90	2057	8	0.56	0.27	Hi	1
A2259B	Table	I	ONL	90	2871	10	1.62	0.70	Hi	2
A2259A	Monolith	J	ONL	90	32734	17	0.85	0.30	Hi	3
A2094	Cavern	K	YSF	88	4110	6	0.40	0.23	Lo	3
A2092	Hidden	L	YSF	88	2437	10	1.23	0.53	Lo	3
A2082	Cavern	M	YSF	88	2476	9	1.19	0.54	Lo	3
A2080	Tripod	N	YSF	88	6262	9	0.86	0.39	Lo	3
A2079	Tripod	O	YSF	88	1124	9	0.94	0.43	Lo	3
A2078	South		ONL	88	121	2	0.12	0.17	Lo	
A2077	Marker5	P	YSF	88	598	14	1.47	0.56	Lo	2
A2076	Max-Worm	Q	YSF	88	2332	4	0.54	0.39	Lo	3
A2075	Crack	R	YSF	88	308	6	1.29	0.72	Lo	2
A1914	Vent3		Sth	87	36	2	0.45	0.65	Hi	
A1911	Vent3		Sth	87	28	2	0.15	0.22	Hi	
A1910	Vent1B		Sth	87	84	5	1.45	0.90	Hi	
A1463	Vent1B	S	Sth	84	183	9	0.76	0.35	Hi	1
A1461	Plume	T	Sth	84	397	4	0.88	0.64	Hi	1
A1455	Vent1A	U	Sth	84	1571	10	1.35	0.59	Lo	2

Once the main effect and specific comparisons in MANCOVA were tested, I assessed the importance of dependent variables (DVs) by a combination of univariate ANOVA tests and stepdown analysis (Tabachnick and Fidell, 1989). If pooled within-group correlations among DVs are zero, univariate ANOVAs, one per DV, give the relevant information about their importance. However, when DVs are correlated, DVs measure overlapping aspects of the same variable and univariate F's are not independent and no straightforward adjustment of the error rate is possible. In stepdown analysis, the highest-priority DV is tested in univariate ANOVA, with appropriate adjustment of alpha. Priority of DVs was assigned according to proportion of the total fauna. The rest of the DVs are tested in a series of ANCOVAs; each successive DV is tested with higher-priority DVs as covariates to see what, if anything, it adds to the combination of DVs already tested. Species were entered into stepdown analysis in the following order: *P. pandorae*, *R. piscesae*, *L. fucensis*, *D. globulus*, *A. galapagensis*. An alpha level of 0.01 was selected as the significance level.

Widespread in community analysis is the use of a variety of descriptive clustering techniques which are not based on underlying distributional assumptions (and largely lack a framework for hypothesis testing, in consequence). Clustering can be defined as an analysis on a data matrix whereby a partitioning of the n samples into subsets is found, numbering less (usually much less) than n, such that the relationships among the subsets optimally predict the relationships among the original samples (Clarke and Green, 1988). For clustering, the package COMM (Piepenburg and

Piatkowski, 1992) was used. Fourth-root transformations of the relative proportions of the five dominant species were used in the cluster analysis. The 'Bray-Curtis' coefficient and 'Unweighted Pair Group Method using arithmetic Averages' (UPGMA) were used for station classification. The 'Bray-Curtis' dissimilarity (Bray and Curtis, 1957) is defined as the absolute differences between the species count for two samples, summed over all species, and then divided by the total count over both samples and all species. UPGMA is defined as the difference between the arithmetic median of the similarity of the objects within one cluster, but during the arithmetic calculation the number of objects (Cluster) is not put into account (Piepenburg and Piatkowski, 1992). Group membership, as an independent variable, was then used in a MANCOVA followed by stepdown analysis to test for the significance of groups on the fourth-root transformed values of the five most abundant species after numerical classification (see below). For the second MANCOVA all of the tubeworm grab samples were used to determine if group formation was the result of area or vent temperature or substrata sampled (Table 3).

An ANOVA model was used to test for the significance of area and cluster group membership (separately) on the log-transformed number of individuals, species diversity (H'), and evenness (J'). An ANCOVA model was used to test for the significance of area and group on the number of species. An alpha level of 0.05 was selected as the significance level.

If a significant effect was found among the levels of a factor following an ANOVA, a Tukey's test was used to make pairwise comparisons (Zar, 1984). Pearson correlations of species variables (transformed and untransformed) were also performed. An alpha level of 0.005 was selected as the significance level for correlations.

RESULTS

SPECIES BIOLOGY

What follows is the description of the 6 species comprising more than 1.0% of all the individuals sampled (Table 4). Reproductive and feeding biology and geographic range are included where known.

Paralvinella pandorae (Desbruyeres and Laubier, 1986; Terebellida, Polychaeta)

Paralvinella pandorae inhabits a self-constructed mucous sheath and is always found attached to the parchment-like tubes of vestimentiferans. Worm sheaths are not attached to very small vestimentifera, nor to the extreme bases of the tube-worms. *Paralvinella pandorae* is a tube-dweller with large yolky eggs, and presumably exhibits the capacity to brood its young (McHugh, 1989). The anterior end of the worm emerges to expose four pairs of branchiae and the buccal apparatus with numerous retractile feeding tentacles. These structures act as a respiratory surface for the animal and may also function in nutrition by gathering organic debris, which is then gleaned by the feeding tentacles (Desbruyeres et al., 1985). The feeding tentacles are grooved and may be retracted into the mouth. *Paralvinella pandorae* is presumably a modified indirect deposit feeder, collecting particulate organic matter.

Table 4: Cleft Segment vent species classification. Number and percentage of total fauna sampled for each species. [a] = samples used in statistical analysis only, [b] = all samples.

Classification	#ind.[a]	%	#ind.[b]	%
Phylum Annelida				
Class Polychaeta				
Order Capitellida				
Nicomache venticola (Blake and Hilbig, 1990)	103	0.14	100	0.13
Order Phyllodocida				
Branchinotogluma grasslei (Pettibone, 1985)	55	<0.10	55	<0.10
Branchinotogluma sandersi (Pettibone, 1985)	17	<0.10	17	<0.10
Hesiospina vestimentifera (Blake, 1985)	92	0.12	84	0.11
Lepidonotopodium piscesae (Pettibone, 1988)	399	0.53	395	0.53
Levensteiniella kincaidi (Pettibone, 1985)	17	<0.10	16	<0.10
Opisthotrochopodus tunnicliffeae (Pettibone, 1988)	25	<0.10	25	<0.10
Protomystides verenae (Blake and Hilbig, 1990)	4	<0.10	4	<0.10
Order Eunicida				
Parougia wolfi (Blake and Hilbig, 1990)	421	0.56	421	0.56
Order Terebellida				
Amphisamytha galapagensis (Zottoli, 1983)	1456	1.93	1185	1.59
Paralvinella dela (Detinova, 1988)	42	<0.10	42	<0.10
Paralvinella pandorae (Desbruyeres and Laubier, 1986)	37076	49.11	37074	49.68
Paralvinella palmiformis (Desbruyeres and Laubier, 1986)	549	0.73	511	0.68
Paralvinella sulfincola (Tunnicliffe et al., 1993)	1047	1.39	885	1.19
Phylum Arthropoda				
Class Pycnogonida				
Ammothea verenae (Child, 1987)	64	<0.10	59	<0.10
Class Crustacea				
Subclass Ostracoda				
Order Mydocopida				
Euphilomedes climax (Hornicker, personal communication)	4	<0.10	4	<0.10
Phylum Mollusca				
Class Gastropoda				
Order Archaeogastropoda				

Clypeosectus curvus (McLean, 1989)	27	<0.10	27	<0.10
Depressigyra globulus (Waren and Bouchet, 1989)	5065	6.71	4946	6.63
Lepetodrilus fucensis (McLean, 1988)	10504	13.91	10440	13.99
Temnocinclis euripes (McLean, 1989)	3	<0.10	3	<0.10
Order Mesogastropoda				
Provanna variabilis (Waren and Bouchet, 1986)	69	<0.10	68	<0.10
Class Solenogaster				
Order Neomeniomorpha				
Helicoradomenia juani (Scheltema and Kuzirian, 1991)	57	<0.10	47	<0.10
Phylum Nemertea				
Taxa not identified	24	<0.10	24	<0.10
Phylum Vestimentifera				
Class Basibranchia				
Order Tevniida				
Ridgeia piscesae (Jones, 1985)	18368	24.33	18188	24.37
Total	75489	97.38	74621	97.45

Bacterial matter probably makes up a large portion of the worm's diet.

The known geographic distribution of *P. pandorae* extends over a 350km long portion of the Northeast Pacific, and is limited to the JDFR, Axial Seamount and Endeavor Segment. The unimodal size-frequency distributions of *P. pandorae* (McHugh, 1989) may reflect continual low recruitment to the populations studied or infrequent or irregular recruitment, as has been suggested for populations of the deep-sea holothurian *Peniagone azorica* (Tyler et al., 1985). Each of the distributions may represent a single cohort, as has been hypothesized for *Kolga hyalina*, another deep-sea holothurian (Billett and Hansen, 1982).

Paralvinella sulfincola (Tunnicliffe et al., 1993; Terebellida, Polychaeta)

Although *P. sulfincola* does construct a tube, it is not sedentary and will abandon the tube. Little is known of the food requirements but the oral apparatus indicates an ingestion mode similar to that of other alvinellids (Tunnicliffe et al., 1993). Particles and bacteria are captured with oral tentacles in both deposit-feeding and modified suspension-feeding modes (Desbruyeres et al., 1985). It is possible that the worms may be culturing bacteria that live on their tubes. Such bacterial associations with *Alvinella* form an important food source (Saulnier-Michel et al., 1990). *Paralvinella sulfincola* tissues do, however, show sulfide-oxidase activity (Juniper et al., 1992) and it appears that sulfide oxidation augments the concentration of elemental sulphur thus allowing formation of substantial iron sulfide crusts in the form of the mineral marcasite. Tunnicliffe and Juniper (1990) implicate *P. sulfincola* in alteration of the chimney growth process because of its apparent ability to change the substratum porosity.

This species is restricted to the Northeast Pacific (Tunnicliffe, 1992). All localities listed under the species description are vents characterized by high-temperature fluids. All collections containing this animal came from sulfide edifices, where the animal occupies a distinct microhabitat. Its preferred substratum is recently deposited sulfide rock. These surfaces are found at active chimneys and lateral accretion flanges from under which hot water emerges. *Paralvinella sulfincola* is the dominant, and often only, inhabitant of this part of the sulfide structure. Previously, *P. sulfincola* has been recorded only from sulfide structures (Tunnicliffe et al., 1993). Of the four *Paralvinella* species at JDFR, *P. sulfincola* is the only one to produce a tube and the tube may provide the greatest protection near smokers and tube abandonment could be a mechanism for escaping accumulating toxins. It is possible that competition from both the palm worm (*P. palmiformis*) and other members of its own species enforces a peripheral existence near the hot water.

Amphisamytha galapagensis (Zottoli, 1983; Terebellida, Polychaeta)

Amphisamytha galapagensis live in mucus-lined tubes covered by detritus. The bulk of their food is from chemoautotrophic bacteria and fecal pellets of other animals (Zottoli, 1983). Mucus, secreted in the ventral part of each tentacle, traps detritus which is carried by ciliary action along the ventral tentacular groove to the mouth. Tentacles are extended from the tube onto the sediment surface and, once laden with detritus, are retracted towards the mouth. *Amphisamytha galapagensis* takes advantage of vestimentiferan tubes to increase substratum area but also colonizes active smokers, sediments and other animals. A significant positive correlation with vestimentiferan abundances is most likely due to the increased substratum area provided by the vestimentiferan tubes. The few samples in which it is found in great abundances (over 25%) are old chimneys with diminished flow and many dead tubeworms (McHugh and Tunnicliffe, 1994).

Amphisamytha galapagensis is hypothesized to produce larvae that swim or crawl along the bottom in the area where they are released. This would allow continuous repopulation without relying on larvae from geographically separated areas. Larvae would probably be swept by bottom currents to new vent areas (Zottoli, 1983). McHugh and Tunnicliffe (1994) propose that *A. galapagensis* undergoes continuous reproduction with external fertilization resulting in demersal, lecithotrophic larvae. Active dispersal between northern and equatorial Pacific vent fields is compromised by the apparently short life of the larvae. Intermediate sites such as seeps may provide the answer and there is also the possibility of adult dispersal by rafting or wafting (Tunnicliffe, 1992). Broad ecological tolerances, niche flexibility and reduced dispersal may be important in allowing establishment of the species at new sites once it arrives (McHugh and Tunnicliffe, 1994).

Ridgeia piscesae (Jones, 1985; Vestimentifera)

All vestimentiferans share a lack of a gut or mouth except during early development stages (e.g., Southward, 1988), presence of a trophosome and the reliance on bacterial oxidation of sulphur (or methane) compounds for their metabolic energy (Childress et al., 1991). Trophosomal bacteria have been observed as intracellular symbionts in *R. piscesae* (Tunnicliffe et al., 1985). Reproductive and developmental biology of vestimentiferans is still unknown. A larval stage and early juveniles have been identified (Southward, 1988). Both possess a complete digestive tract which subsequently atrophies as the worm matures. The larva may exist as a planktonic dispersal stage with the capacity for delayed (environmentally triggered) settlement (Jones and Gardiner, 1989). Gardiner et al. (1992) have found that gametogenesis in *Riftia pachyptila* (vestimentiferan) occurs continuously.

R. piscesae is found only in the NE (North East) Pacific (Jones, 1988). Vestimentiferans are clearly a prominent and likely dominant member of the JDFR communities. The worms likely provide a substrate for other attached fauna, grazing surfaces for numerous species and a a food source for other animals ranging from vent endemics such as species of polynoids, to deep-sea species such as large majid crabs.

Depressigyra globulus (Waren and Bouchet, 1989; Gastropoda)

The intestine of *D. globulus* contains no mineral particles, only amorphous organic matter (Waren and Bouchet, 1989). The gill is larger than in most deep sea archaeogastropods, but its position in the rear 2/3 of the pallial cavity suggests that filter feeding does not occur. Direct and planktotrophic development is rare in archaeogastropods so it is assumed that larval development in *D. globulus* is lecithotrophic (Waren and Bouchet, 1989). *Depressigyra globulus* is only known from the JDFR.

Lepetodrilus fucensis (McLean, 1988; Gastropoda)

Lepetodrilus fucensis cluster together adjacent to thermal vents, predominantly in stacks of up to 6 individuals with the stacks closely aggregated. *Lepetodrilus fucensis* is a suspension feeder and also gathers particles loosened from the substratum: the two methods of feeding may proceed concurrently (Fretter, 1988). Food is captured on cilia that transport it to a groove on the dorsal body wall which leads to the mouth. Masses of bacteria present on the gill surfaces have been found undergoing endocytosis and being uptaken directly into gill filaments (DeBurgh and Singla, 1984). *Lepetodrilus fucensis* is found only on Explorer and JDF Ridges.

FIELD DESCRIPTIONS

What follows is a detailed description of the four venting areas on Cleft Segment (Table 1, Figures 1-4) derived from published literature, personal communications, and video analysis. Sample location and description are included.

Mound Lavas

Three sites of tube worm colonization were seen on Mound lavas. About 100 m from the northern end of Mound 1, a 1989 camera tow and a 1991 ALVIN dive recorded faint seepages and tubes over a distance of about 40 m. Tubes were about 10 cm long and no obturacula were evident. Some scattered white and blue patches suggested sulfide emissions still supported some bacterial and protozoan activity. Two spider crabs were nearby. The number of apparently empty tubes suggest a vent in decline. Similarly, near the south end of Mound 2, ALVIN observers record "straggly dead-looking worms" although the several nearby crabs indicate a possible food source. Living worms are evident in 1989 photographs near the northern boundary of Mound 2 (Milligan and Tunnicliffe, 1994). Flow is seeping around basalt lobes. The following species were present: *R. piscesae*, *L. fucensis*, two polynoid species (one most likely *Lepidonotopodium piscesae*) and the blue mat characteristic of a folliculinid protozoan. The source for these animals could have been a vent on ONL about 200 m farther north that supported lush clumps of vestimentiferans, limpets, and polychaetes.

South Lavas

Three active hydrothermal discharge sites along the southern JDFR were investigated in 1984. All of the hydrothermal vents were located within a 10- to 30-m-deep, 30- to 50-m-wide cleft marking the center and eruptive focus of the axial valley (Normark et al., 1987). The hydrothermal activity is most extensive at 3 vent sites, denoted Plume, Vent 1 and Vent 3, from south to north (Figure 2). The Plume Site was located primarily on the floor of the cleft at the base of the eastern wall. The Vent 1 site was more than 500 m long and consisted of 3 main areas of sulfide mineralization and at least 4 smaller vents having extensive vent-related biota but no sulfide deposits (which may be indicative of lower temperature discharge). Vent 3 included at least 3 discharge sites spread over a distance of about 500m along the floor. Chimney structures were typically 20-40 cm in diameter and 1-2 m high and had a profile widening toward the top with each vent area surrounded by extensive faunal communities.

Eight biological samples were collected from South Cleft (Table 3), including one collected from a low-temperature vent (Vent 1A) on ALVIN dive 1455. On ALVIN dive 2263 the "asparagus" vents originally sampled in 1984, found quiet in 1987, and almost dead in 1988, were found heavily covered in sediment and apparently dead. Upslope from the dead vents 9 m^2 of tubeworms with temperatures ranging from 10 - 20°C and a smoker with temperatures ranging from 40 - 210°C and no biota, were found.

There is a great deal of variation in vent samples collected from South Cleft (Table 5; Figure 5). In 1984 the low-temperature basaltic vent (Vent1A) had a higher proportion of *L. fucensis*, *D. globulus*, and *A. galapagensis* and a lower proportion of *R. piscesae* than the two high-temperature vents sampled (Figure 5). In 1987 it was obvious that venting was in a state of decline which is indicated by the samples obtained with low numbers of species and individuals (Table 3). Except for the sample obtained on A2263, venting ceased at South Cleft in 1990. The one sample obtained was dominated by *D. globulus* and *R. piscesae*, similar to samples obtained in 1984 (Figure 5). Venting in 1991 was also nearly absent except for one small sample obtained from an apparently unhealthy vent on A2427 near Vent 1A. This sample was also dominated by *R. piscesae* and *D. globulus* (Table 5).

Young Sheet Flow (YSF)

The vents along the eastern edge of the YSF (Figure 6) are all diffuse vents with maximum temperatures <60°C and most are <30°C (Embley and Chadwick, 1994). Most of the vent samples from the young sheet flow come from an Alvin dive series in 1988 (Table 3). All of the vents sampled were low-temperature vents with no active sulfide

Table 5: Counts of species for each sample. Refer to Tables 2 and 3 for sample information.

Species Dive	H202	A2444	A2436	A2434	A2431	A2429	A2427	A2269	A2267	A2265	A2264
N. venticola											88
P. verenae											2
B. grasslei						1			2	4	11
B. sandersi											7
L. piscesae				3			1		4	18	51
L. kincaidi									1		11
O. tunnicliffeae										3	1
H. vestimentifera											84
P. wolfi		3							11		380
A. galapagensis	49	149			240	2	3		44	79	382
P. dela											
P. sulfincola	1		62	60		8	5	38	1	1	1
P. pandorae			2			95			5		
P. palmiformis	11		1	37		5			7	8	
A. verenae					1						53
E. climax											3
D. globulus	55	5	1	4		3	33		221	483	759
L. fucensis	25	129		45	1				16	780	2973
C. curvus											15
P. variabilis									3		42
H. juani					10						47
nematode											
R. piscesae	496	181	2	9		580	19		647	144	3272
Total no. of individuals	637	464	68	158	252	688	61	38	934	1487	7387

A2263	A2262	A2259C	A2259B	A2259A	A2094	A2092	A2082	A2080	A2079	A2078	A2077	A2076	A2075
				2									
		3	7	16		3		6	1		1		
				8	1						1		
2		7	92	176	1	9	2	5	13		9		1
	1			2			1				1		
		1	17	2		1							
	8												
				18			1	3			4		
2	2	108	25	171		12	29	8	12		42		
						42							
81	19	92	377	265									
			16	24320	3648	1180	1040	4075	718		10	1898	62
			162	91	55	48		63	29			15	2
1				1							1		
1				1									
1583	21	26	327	629		26	41	40	3		57		40
9	3	27	735	1230	6	825	880	1844	20	12	285		150
3													
	1								3				3
				1							7		
											8	16	
980	2	1793	1113	5801	399	291	479	218	327	47	169	403	53
2593	32416	4053	2194	2469	6185	1080	121	563	2301	305	36	28	84

A1914	A1911	A1910	A1463	A1461	A1455
					11
			1		4
					1
6		20	3		68
		16		20	
			1		6
			3	12	
	1		3		
30		30	15	103	530
		15			506
			3		
					3
					15
	27	3	151	262	429
36	28	84	177	400	1539

Figure 5: Relative proportion of the 6 most abundant species present in South Cleft samples. For sample details see Tables 2 and 3 and Field Description. Vent1A is a low temperature vent.

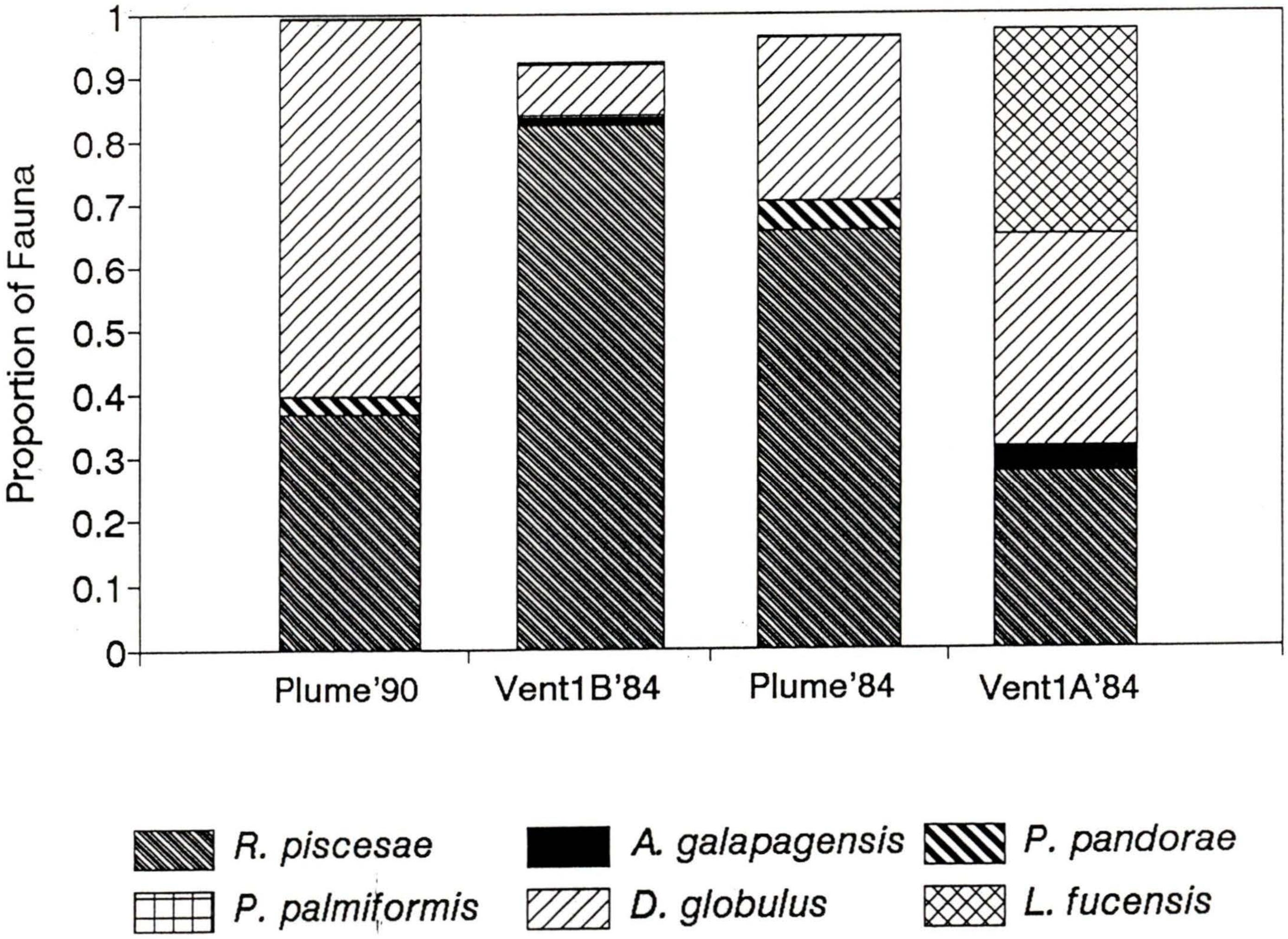
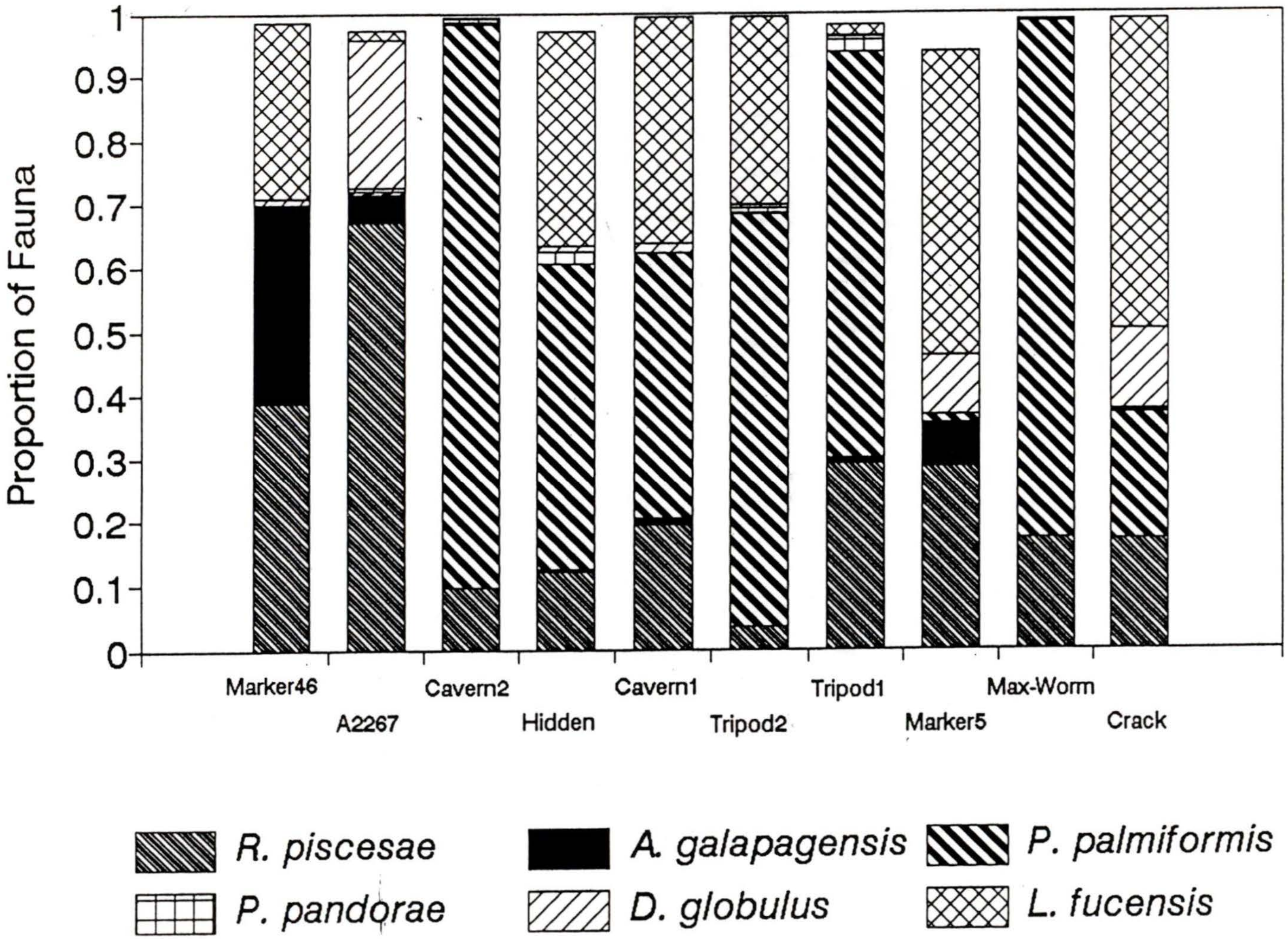

Proportion of Fauna
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Plume'90
Vent1B'84
Plume'84
Vent1A'84
R. piscesae
A. galapagensis
P. pandorae
P. palmiformis
D. globulus
L. fucensis

Figure 6: Relative proportion of fauna each of the 6 most abundant species represent from Young Sheet Flow samples. For sample details see Tables 2 and 3 and Field Description.


Proportion of Fauna
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Marker46
A2267
Cavern2
Hidden
Cavern1
Tripod2
Tripod1
Marker5
Max-Worm
Crack
R. piscesae
A. galapagensis
P. palmiformis
P. pandorae
D. globulus
L. fucensis

production. At Crack, Max-Worm, Station 5, Tripod, Cavern, and Hidden vents in 1988 lots of venting, worms, shimmering water, and staining in cracks with bacteria and worms were seen. Max-Worm is actually a combination of two samples taken from two heavily stained worm clumps 250 m apart. The Tripod and Hidden vents (observed on A2265) and Cavern vent area (A2267) were found covered in sediment and apparently dead in 1990. However, a new vent (Marker M) was found near Cavern (A2267) with shimmering water, no active sulfide production and relatively healthy worms. The vent fauna found on this dive appeared similar to fauna discovered in 1988 (Embley, personal communication). In 1991 (A2431) dead worms were sampled and another area of dead worms was observed in the area of Tripod. Vent fauna was found near newer flows only (newer pillow mounds) while only apparently dead vent fauna was found on the older ropy lava. It is likely that the absence of venting, the presence of hydrolyzed iron, and the dead worms (no H_2S) indicate a dead or dying hydrothermal system (pers. comm., I. Jonasson).

Venting water found at 60°C between Markers #3 and #6 in 1988 was found at 30°C in 1990. In 1991 (observed on A2437) the same area was covered with an orange-yellow fluffy sediment and the venting had virtually ceased (R. Embley, personal communication). Dead tubeworms littered the area and only a few very localized spots of diffuse venting were observed, and the only active vent was Hidden Vent. A hundred meters southwest of this site a large high-temperature vent was discovered, a line of smokers about 40′ to 60′ in length emanating from the collapsed lava cleft in new sheet flows with tops of several very delicate pipes on this edifice up to 10 to 12 m high. On dive A2443 between Marker 4 and Tripod vents the abundant worms observed in 1988 were gone; instead dead worms and a reduction in venting vigor and biomass was observed. At Marker 46 sampled in 1991 (A2444) recumbent scattered worms were sampled and lots of very diffuse venting with worms was also seen.

Paralvinella sulfincola and *D. globulus* are absent or small in all samples obtained from the YSF (Figure 6; Table 5). In 1988 there appeared to be a taxonomic domination by *P. pandorae* and *L. fucensis*. However, *L. fucensis* vary from dominant (Crack and Marker5) to near absent (Max-worm, Tripod, and Cavern). Likewise, *P. pandorae* proportions vary from dominant (Max-worm, Tripod, Cavern) to small (Crack) or near absent (Marker5). Although present in all samples, *R. piscesae* occurs in larger proportions only in the samples obtained from Marker5 in 1988 (A2077), the Cavern area in 1990 (A2267), and the sample from Marker46 in 1991 (A2444). In these samples *A. galapagensis* proportions are also high. The sample obtained on A2267 has the highest *R. piscesae* proportion of any YSF sample and its composition most closely resembles that of the Vent1B and Plume obtained from South Cleft in 1984. The sample of dead worms taken on A2431 in the Tripod area consisted primarily of *A.*

galapagensis, several *Helicoradomenia juani* and one *Ammothea verenae* (Table 5).

Older North Lavas (ONL)

The known high-temperature vents along the northern Cleft Segment occur along the fissure system on the east side of the YSF (Embley and Chadwick, 1994). The Monolith high-temperature site was discovered and sampled in 1990 and again in 1992 and consists of a 4-m high sulfide structure with approximately 12 high-temperature (275-325°C) gray and black smoker orifices, along with Table and Brigadoon vents, two nearby (~5 and 20 m away, respectively) low-relief sulfide mounds with weak high-temperature (~275°C) discharge. The morphology and mineralogy of the Monolith vent has led Koski et al. (1994) to propose that it is an older, lower temperature structure that has been rejuvenated by an increased flow rate and temperature.

Fountain vent, about 600 m North of Monolith, was seen during a traverse in 1990, and was sampled in 1991. Fountain consists of a single split sulfide structure ranging from 1 to 3 m in height, with ~6 high-temperature (275-310°C) orifices and several areas of diffuse flow covered with ridgeid and alvinellid worms. Several diffuse vents and groups of extinct sulfide chimneys are found within a few hundred meters north of Fountain Vent (Embley and Chadwick, 1994). Pipe Organ vent, located ~2-3 km South of Monolith and within 200 m of diffuse vents sampled in

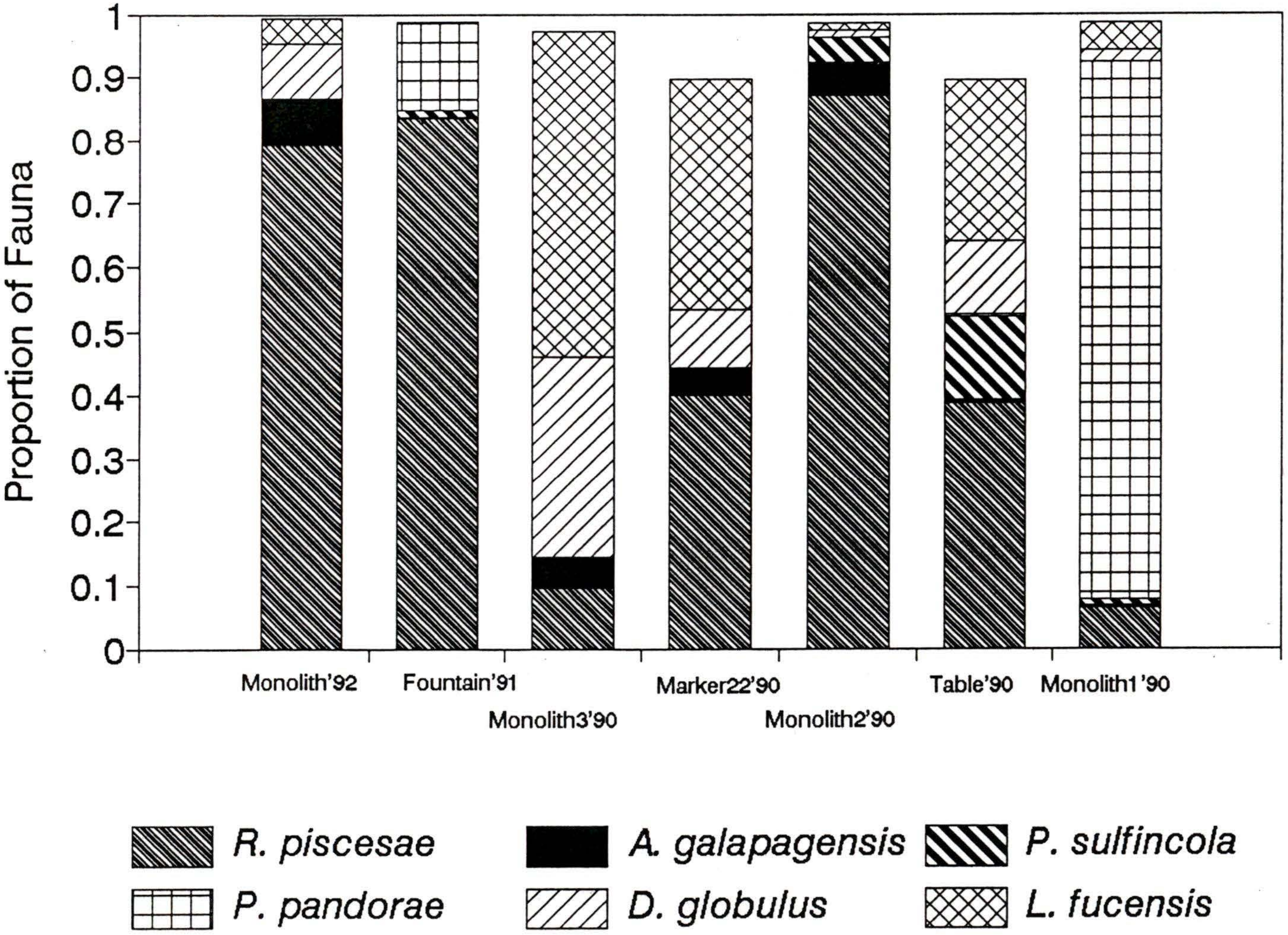
1988 and 1990, was discovered and sampled in 1991. Pipe Organ consists of several narrow, 4-5 m-tall sulfide chimneys with maximum measured temperatures of 260°C.

In 1990, Monolith vestimentiferan clusters were covered in brownish-red precipitate and were only found clustered around the chimneys. Worm clusters were moderate to rare, and appeared very scraggly and "almost dead" looking (W. W. Chadwick, personal communication). One sample was taken from a tubeworm clump on the southern face of Monolith (A2259"A") and another was taken from the same area but nearer the active venting orifice (A2259"C"). Table Vent was also sampled on the same dive (A2259"B"). On a later dive (A2269) the orifice near A2259"A" was sampled. At Table vent, the vestimentiferans were thicker and spread over a 3-4 m diameter around the vent source. The vestimentiferans were blackened and "sooty" looking and did not appear to have the high proportion of juvenile worms attached to their tubes as in the sample A2259"A". Monolith was also sampled from the northern face in 1990 (A2265) and in 1992 (H202). Sample A2265 was under a flange while H202 was similar in nature to A2259"C". A sulfide sample with worms was also sampled from Table Vent in 1991 (A2434). A tubeworm grab (A2429) and sulfide sample (A2436) were taken from the northern lobe of Fountain in 1991. North of Fountain vent about 250 m, a depression surrounded by worms (Depressed Vent) was sampled.

Differences in faunal composition at the high-temperature vents in the ONL appear to be caused by distance of sample from the venting orifice or degree of venting activity (Figure 7). Samples taken near (within 1 or 2 m) an active venting orifice (A2259"C", A2429, and H202) appear to be dominated by *R. piscesae*. One sample taken even further away from the orifice (A2259"A") was dominated by *P. pandorae*. One sample taken from a nearby diffuse vent (A2259"B") was comprised of high proportions of *R. piscesae* and *L. fucensis* and smaller proportions of *D. globulus* and *P. pandorae*. Another sample taken from Monolith (A2265) was dominated by *L. fucensis* and *D. globulus*. These last three samples closely resemble samples taken from the YSF (Figure 6). Sample A2259"A" was unusual because it had *P. pandorae* numbers in excess of 24,000 individuals and was comprised of 17 megafaunal species (Table 5). Two samples taken from high-temperature orifices (A2269 and A2436) were comprised entirely and almost entirely of *P. sulfincola*, respectively. Likewise, the sulfide sample from Table vent (A2434) was dominated by *P. sulfincola* (Table 5).

Three low-temperature diffuse vents were also sampled on the ONL (Table 3, Figure 7). Sparse worm colonies were found in a graben to the north of Monolith vent on A2262. Two vents to the south of the YSF (still on ONL) were sampled on dives A2264 and A2078. On A2264 a dense worm cluster about 2-3 m wide and 5-8 m long with more scattered worm clumps around the dense core was discovered.

Figure 7: Relative proportion of fauna from each of the 6 most abundant species represent from Older North Lava samples. For sample details see Tables 2 and 3 and Field Description.


Proportion of Fauna
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Monolith'92
Fountain'91
Monolith3'90
Marker22'90
Monolith2'90
Table'90
Monolith1'90
R. piscesae
A. galapagensis
P. sulfincola
P. pandorae
D. globulus
L. fucensis

There were many crabs in among the worms and the vestimentiferans appeared alive and healthy and up to a meter long (W. Chadwick, personal communication). On A2078 a vent with small clumps of worms and lots of heavy staining, floc, and sediment was discovered although a large clump of worms was discovered to the south.

The faunal composition of A2264 (Marker 22) is unique because it is comprised of 19 different megafaunal species, which is the highest of any processed Cleft sample. This sample also has the highest number of individual *Helicoradomenia juani* (47), *Hesiospina vestimentifera* (84), *Ammothea verenae* (53), and *Parougia wolfi* (380) from any Cleft sample. The dominance of A2264 by *L. fucensis* and *R. piscesae* with smaller numbers of *A. galapagensis* and *D. globulus* closely resembles that of Marker5 and is somewhat similar to Marker46 and A2267. The Graben sample was dominated by dead *R. piscesae*, *P. sulfincola*, and *D. globulus*. The South sample was comprised solely of *R. piscesae* and *L. fucensis*.

Taxonomic composition

Raw results are shown in Table 5. A total of 24 species representing 5 phyla (Table 4) have been identified among 75,489 specimens encountered in all 31 samples. All but the nemertean were identified to the species level. The nemertean is recognized as a distinct taxon but is not known to species at present. There is a taxonomic domination by polychaetes (phyllodocids and terebellids) and gastropods (archaeogastropods). Most species found at Cleft are endemic to the Northeast Pacific. Actual and relative abundances of species are presented in Table 4. Six species (*P. pandorae*, *R. piscesae*, *L. fucensis*, *D. globulus*, *A. galapagensis*, and *P. sulfincola* in decreasing order) account for more than 97 % of all individuals sampled (Table 4) and 90 % or more of the cumulative percent abundance of all species in a given sample (Table 6).

Statistical Analysis

With the use of Wilks' criterion, the combined DVs were significantly affected by area, (MANCOVA $\underline{F}(10, 22) = 3.789$, $\underline{P} = 0.004$). Sample size did not have a significant effect on the combined DVs (MANCOVA $\underline{F}(5, 11) = 2.199$, $\underline{P} = 0.128$). Although none of the species made a unique contribution to predicting differences between areas, if tested alone transformed values of *P. pandorae*, *R. piscesae*, and *D. globulus* were significantly different between venting areas (Table 7). Once the effect of higher priority species variables were removed in stepdown analysis, transformed values of *L. fucensis* would also be significantly different between areas if tested alone. There was no significant difference in transformed proportions of *P. pandorae*, *D. globulus*, *R. piscesae*, or *L. fucensis* when any two venting areas were compared (Table 7). However, *P. pandorae*

Table 6: Number of individuals and cumulative percentage of the six most abundant species for samples used in statistical analysis. Letters correspond to dive number (Table 3).

Species			#Ind.	%	#Ind.	%	#Ind.	%
			A		**B**		**C**	
R. piscesae (A)			496	77.68	181	38.76	580	83.57
P. pandorae (B)			0	0.00	0	0.00	95	13.69
L. fucensis (C)			25	3.92	129	27.62	0	0.00
D. globulus (D)			55	8.63	5	1.07	3	0.43
A. galapagensis (E)			49	7.69	149	31.91	2	0.29
P. sulfincola (F)			1	0.16	0	0.00	8	1.15
Total			626	98.27	464	99.36	688	99.13
	D		**E**		**F**		**G**	
(A)	647	67.26	144	9.47	3272	39.99	980	36.83
(B)	5	0.52	0	0.00	0	0.00	0	0.00
(C)	16	1.66	780	51.32	2973	36.34	9	0.34
(D)	221	22.97	483	31.78	759	9.28	1583	59.49
(E)	44	4.57	79	5.20	382	4.67	2	0.08
(F)	1	0.10	1	0.07	1	0.01	81	3.04
Total	934	97.08	1487	97.84	7387	90.29	2655	99.78
	H		**I**		**J**		**K**	
(A)	1793	87.17	1113	38.77	5801	17.72	399	9.71
(B)	0	0.00	16	0.56	24320	74.30	3648	89.49
(C)	27	1.31	735	25.60	1230	3.76	6	0.15
(D)	26	1.26	327	11.39	629	1.92	0	0.00
(E)	108	5.25	25	0.87	171	0.52	0	0.00
(F)	92	4.47	377	13.13	265	0.81	0	0.00
Total	2046	99.46	2593	90.32	32416	99.03	4053	99.35
	L		**M**		**N**		**O**	
(A)	291	11.90	479	19.35	218	3.48	327	29.09
(B)	1040	42.68	1040	42.00	4075	65.08	718	63.88
(C)	825	33.85	880	35.54	1844	29.45	20	1.78
(D)	26	1.07	41	1.66	40	0.64	3	0.27
(E)	12	0.49	29	1.17	8	0.13	12	1.07
(F)	0	0.00	0	0.00	0	0.00	0	0.00
Total	2194	89.99	2469	99.72	6185	98.78	1080	96.09
	P		**Q**		**R**		**S**	
(A)	169	28.26	403	17.28	53	17.21	151	82.51
(B)	10	1.67	1898	81.39	62	20.13	1	0.55
(C)	285	47.66	0	0.00	150	48.70	0	0.00
(D)	57	9.53	0	0.00	40	12.99	15	8.20
(E)	42	7.02	0	0.00	0	0.00	3	1.64
(F)	0	0.00	0	0.00	0	0.00	0	0.00
Total	563	94.14	2301	98.67	305	99.03	170	92.90
	T		**U**					
(A)	262	65.99	429	27.30				
(B)	0	0.00	6	0.38				
(C)	0	0.00	506	32.21				
(D)	103	25.94	530	33.74				
(E)	0	0.00	68	4.33				
(F)	20	5.04	0	0.00				
Total	385	96.97	1539	97.95				

Table 7: Analyses of Venting Region (Area) effects (univariate and stepdown analysis) on fourth-root transformed abundances of *P. pandorae* (FPPAND), *R. piscesae* (FRPIS), *L. fucensis* (FLFUC), *D. globulus* (FDGLOB), and *A. galapagensis* (FAGAL) with sample size as a covariate. Tukey tests to test for differences in *P. pandorae*, *L. fucensis*, and *D. globulus* between areas. Correlations between dependent variables (DV's). * = P < 0.05. ** = P < 0.005.

One-way ANCOVA

		Univariate		Stepdown		
IV	DV	F	df	F	df	alpha
Area	FPPAND	7.225*	2,15	7.225*	2,15	0.01
	FRPIS	4.585*	2,15	1.123	2,14	0.01
	FLFUC	3.051	2,15	4.729*	2,13	0.01
	FDGLOB	3.648*	2,15	4.320*	2,12	0.01
	FAGAL	1.309	2,15	0.520	2,11	0.01

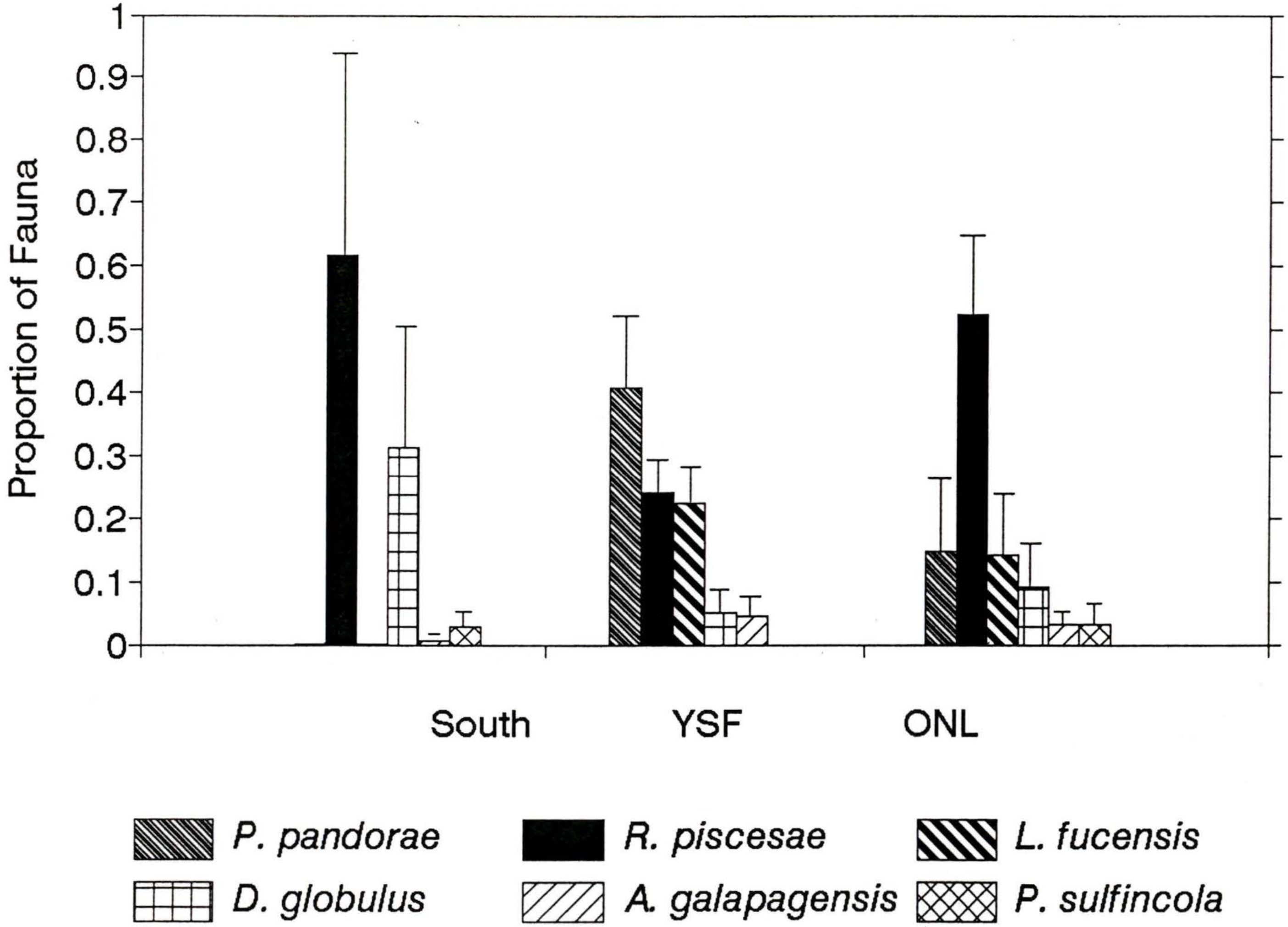
Contrasts

(DV)	Comparison	Mean Difference	SE	q	$q_{0.01,15,3}$
(FPPAND)	Sth vs. YSF	0.572	0.157	3.643	4.836
	Sth vs. ONL	0.211	0.169	1.249	4.836
	YSF vs. ONL	0.361	0.123	2.935	4.836
(FRPIC)	Sth vs. YSF	0.209	0.066	3.176	4.836
	Sth vs. ONL	0.069	0.071	0.976	4.836
	YSF vs. ONL	0.140	0.052	2.713	4.836
(FLFUC)	Sth vs. YSF	0.478	0.132	3.621	4.836
	Sth vs. ONL	0.384	0.142	2.704	4.836
	YSF vs. ONL	0.094	0.104	0.904	4.836
(FDGLOB)	Sth vs. YSF	0.373	0.106	3.519	4.836
	Sth vs. ONL	0.236	0.099	2.384	4.836
	YSF vs. ONL	0.137	0.077	1.780	4.836

DV Correlations

	FPPAND	FRPIS	FLFUC	FDGLOB
FRPIC	-0.611*			
FLFUC	0.014	-0.518*		
FDGLOB	-0.711**	0.301	0.193	
FAGAL	-0.519*	0.324	0.391	0.201

Figure 8: Mean relative proportions of fauna for each of the 6 most abundant species from South Cleft (South; n = 3), Young Sheet Flow (YSF; n = 10), and Older North Lavas (ONL; n = 6). Bars represent one standard error.


1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proportion of Fauna
South
YSF
ONL
P. pandorae
R. piscesae
L. fucensis
D. globulus
A. galapagensis
P. sulfincola

occurred at the greatest proportions at the YSF vents and was nearly absent from South vents (Figure 8). *Ridgeia piscesae* occurred at the greatest proportions at the ONL and South vents. *Depressigyra globulus* occurred in greater proportions at South vents and *L. fucensis* occurred in greater proportions at YSF vents and was nearly absent from South vents.

Pooled within-cell correlations among DVs for different areas are shown in Table 7. There is a significant and negative correlation between transformed values of *D. globulus* and *P. pandorae*. Although not signficant, there is a highly negative correlation between transformed values of *P. pandorae* and *R. piscesae*, *P. pandorae* and *A. galapagensis*, and *R. piscesae* and *L. fucensis*. There is a significant and negative correlation between untransformed proportions of *P. pandorae* and *R. piscesae* (Table 8). Although not significant, there was a highly negative correlation between *R. piscesae* and *L. fucensis* and between *D. globulus* and *R. piscesae*.

Table 8: Correlations between untransformed proportions of *P. pandorae* (PPAND), *R. piscesae* (RPIS), *L. fucensis* (LFUC), *D. globulus* (DGLOB), and *A. galapagensis* (AGAL). * = P < 0.05. ** = P < 0.005.

	PPAND	RPIS	LFUC	DGLOB	AGAL
PPAND	1.000				
RPIS	-0.625**	1.000			
LFUC	-0.157	-0.555*	1.000		
DGLOB	-0.503*	0.066	-0.004	1.000	
AGAL	-0.359	0.121	0.193	-0.117	1.000

A summary of diversity and other community characteristics for the various samples across area is given in Table 3. Area had no significant effect (Table 9) on species diversity (Figure 9), evenness (Figure 10), number of species (Figure 11), and transformed values of number of individuals (Figure 12). Species richness and proportions of *P. pandorae* are positively and significantly correlated with number of individuals (R = 0.618; N = 19; P = 0.005: R = 0.992; N = 19; P < 0.005), respectively. Species diversity (R = -0.307; N = 19; P = 0.201) and species richness (R = -0.154; N = 19, P = 0.506) were not significantly correlated with proportions of *R. piscesae*.

Table 9: Analysis of Area effects on species diversity (SD), evenness (EVEN), and log-transformed number of individuals (LN). Analysis of Area effects on species richness (SR) with sample size as a covariate.

	Source	SS	df	MS	F	P
SD	Area	0.105	2	0.052	0.433	0.656
	Error	1.939	6	0.121		
SR	Area	2.394	1	2.394	0.315	0.583
	N	71.278	1	71.278	9.369	0.007
	Error	121.722	16	7.608		
EVEN	Area	0.020	2	0.010	0.373	0.695
	Error	0.436	16	0.027		
LN	Area	3.551	1	1.776	1.280	0.305
	Error	22.194	16	1.387		

Figure 9: Mean species diversity (Shannon-Weiner index) for South Cleft (South), Older North Lavas (ONL), Young Sheet Flow (YSF) and the three groups (Grp1, Grp2, Grp3) resulting from cluster analysis (see Results). Bars represent one standard error. Groups with the same letter were not significantly different with respect to species diversity.

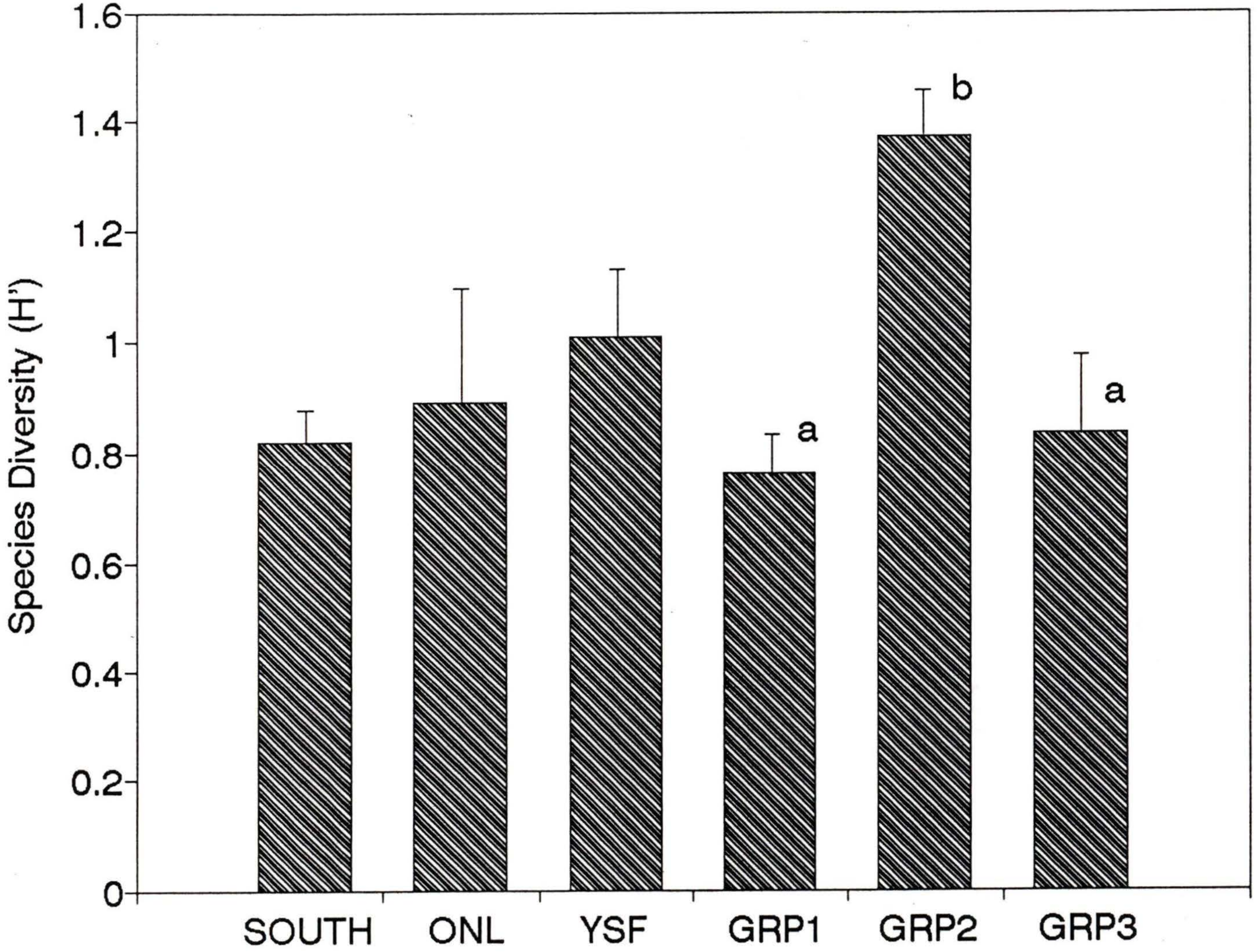

Species Diversity (H')
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
SOUTH
ONL
YSF
GRP1
GRP2
GRP3
a
b
a

Figure 10: Mean evenness index for South Cleft (South), Older North Lavas (ONL), Young Sheet Flow (YSF) and the three groups (Grp1, Grp2, Grp3) resulting from cluster analysis (see Results). Bars represent one standard error. Groups with the same letter were not significantly different with respect to evenness.

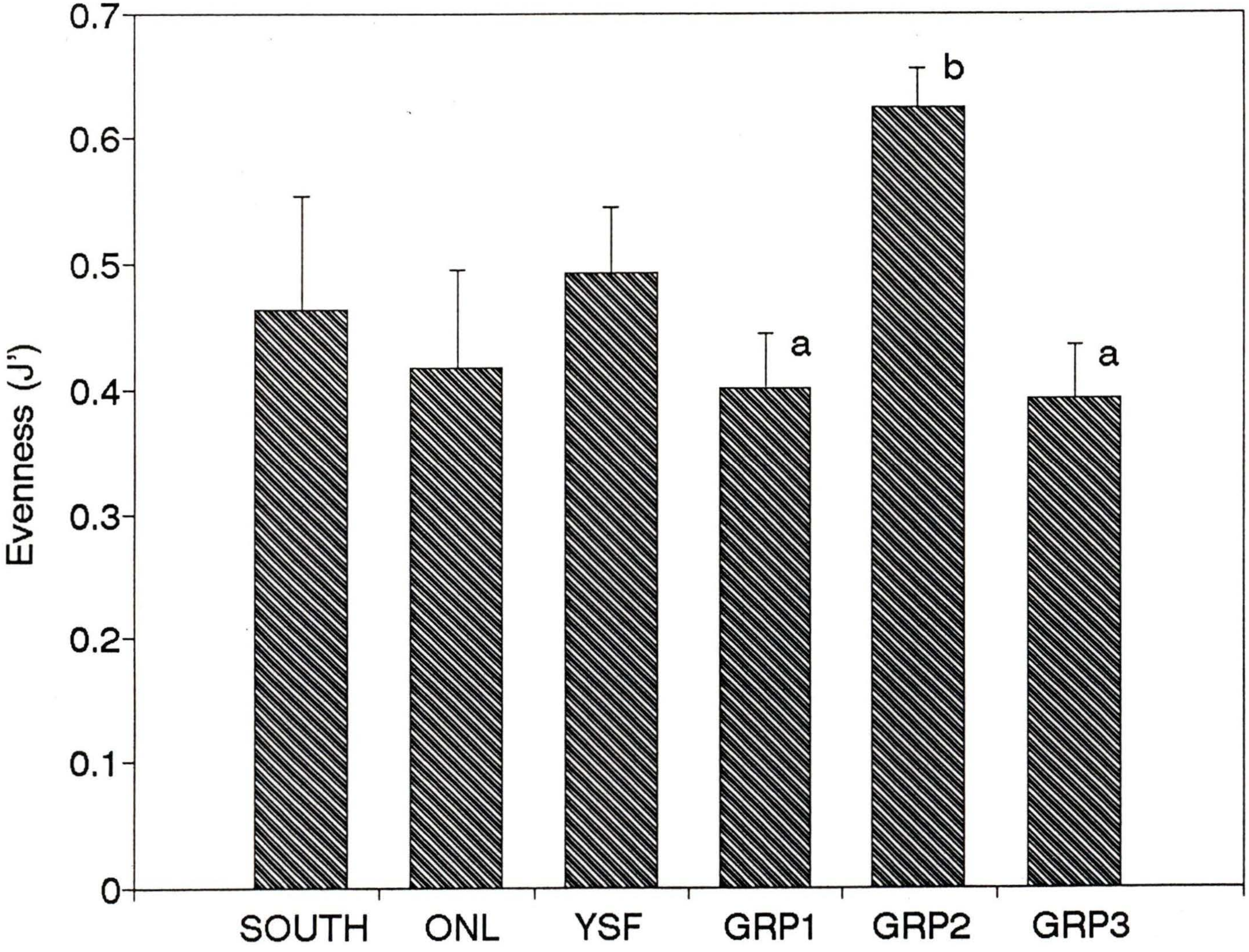

Evenness (J')
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
SOUTH
ONL
YSF
GRP1
GRP2
GRP3
a
b
a

Figure 11: Mean number of species for South Cleft (South), Older North Lavas (ONL), Young Sheet Flow (YSF) and the three groups (Grp1, Grp2, Grp3) resulting from cluster analysis (see Results). Bars represent one standard error. Niether venting region (area) or cluster group membership (Group) had a significant effect on species richness.

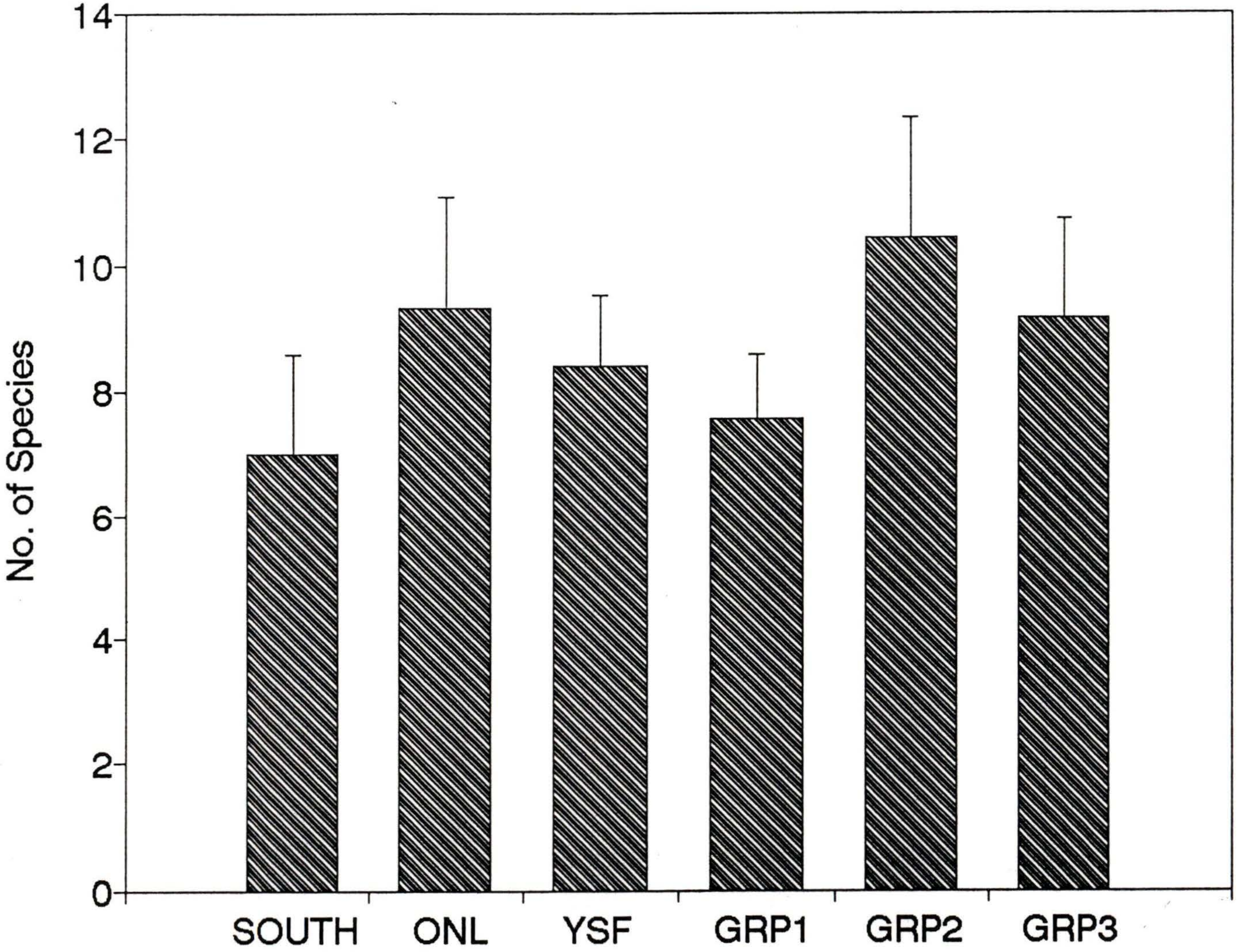
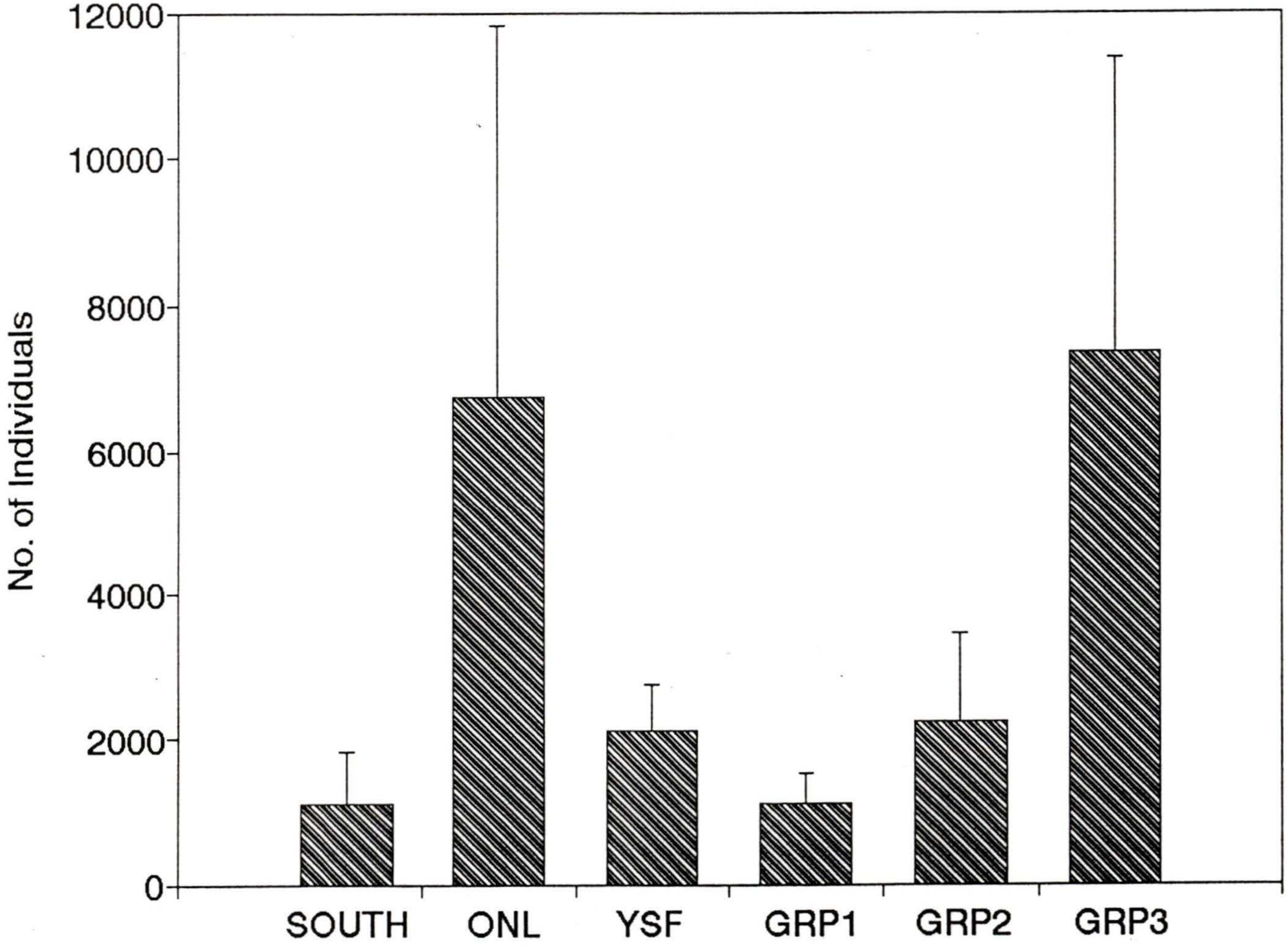

14
12
10
8
6
4
2
0
No. of Species
SOUTH
ONL
YSF
GRP1
GRP2
GRP3

Figure 12: Mean number of individuals for South Cleft (South), Older North Lavas (ONL), Young Sheet Flow (YSF) and the three groups (Grp1, Grp2, Grp3) resulting from cluster analysis (see Results). Bars represent one standard error. Niether venting region (Area) or cluster group membership (Group) had a significant effect on species richness.


12000
10000
8000
6000
4000
2000
0
No. of Individuals
SOUTH
ONL
YSF
GRP1
GRP2
GRP3

Numerical classification of samples from different years on North and South Cleft and high and low-temperature vents defines 3 major groups largely reflecting temperature differences (Figure 13). Cluster Group 1 consists of high-temperature vents (A, C, G, S, T) with the exception of the sample obtained on A2267 (D). Cluster Group 2 consists of a mix of high and low-temperature vents (B, E, F, I, P, R, U). Cluster Group 3 consists of only low-temperature vents (K, L, M, N, O, Q, R).

With the use of Wilks' criterion, the combined DVs were significantly affected by cluster group (MANCOVA $\underline{F}(10, 26) = 9.660$, $\underline{P} < 0.005$). Sample size did not have a significant effect on the combined DVs (MANCOVA $\underline{F}(5, 13) = 0.313$, $\underline{P} < 0.896$). Transformed values of *P. pandorae* and *R. piscesae* made unique contributions to predicting differences between cluster groups (Table 10). Transformed values of *P. pandorae*, *R. piscesae*, *L. fucensis* and *D. globulus* were significantly different between cluster groups (Table 10). Once the effect of higher priority species variables were removed in stepdown analysis, transformed values of *L. fucensis* were also significantly different between cluster groups when tested alone (Table 10).

Proportions of *P. pandorae* differed significantly between cluster groups 1 and 3 and groups 2 and 3, but not groups 1 and 2 (Table 10). *Paralvinella pandorae* was most abundant in group 3 and nearly absent in groups 1 and 2

Table 10: Analyses of Cluster Group effects (univariate and stepdown analysis) on fourth-root transformed abundances of *P. pandorae* (FPPAND), *R. piscesae* (FRPIS), *L. fucensis* (FLFUC), *D. globulus* (FDGLOB), and *A. galapagensis*(FAGAL) with sample size as a covariate. Tukey tests to test for differences in *P. pandorae*, *L. fucensis*, and *D. globulus* between groups. Correlations between dependent variables (DV's). * = P < 0.05. ** = P < 0.005.

One-way ANCOVA

		Univariate			Stepdown	
IV	DV	F	df	F	df	alpha
GROUP	FPPAND	23.347**	2,17	23.347**	2,17	0.01
	FRPIS	19.924**	2,17	10.296**	2,16	0.01
	FLFUC	12.712**	2,17	4.900*	2,15	0.01
	FDGLOB	9.263**	2,17	3.329	2,14	0.01
	FAGAL	2.360	2,17	0.414	2,13	0.01

Contrasts

(DV)	Comparison	Mean Difference	SE	q	$q_{0.01,18,3}$
(FPPAND)	1 vs. 2	0.058	0.076	0.763	4.703
	1 vs. 3	0.730	0.076	9.605**	4.703
	2 vs. 3	0.672	0.076	8.842**	4.703
(FRPIS)	1 vs. 2	0.196	0.032	6.125**	4.703
	1 vs. 3	0.304	0.032	9.500**	4.703
	2 vs. 3	0.108	0.032	3.375	4.703
(FLFUC)	1 vs. 2	0.585	0.079	7.405**	4.703
	1 vs. 3	0.270	0.079	3.418	4.703
	2 vs. 3	0.315	0.079	3.987*	4.703
(FDGLOB)	1 vs. 2	0.024	0.068	0.353	4.703
	1 vs. 3	0.342	0.068	5.029**	4.703
	2 vs. 3	0.366	0.068	5.383**	4.703

DV Correlations

	FPPAND	FRPIS	FLFUC	FDGLOB
FRPIC	-0.599**			
FLFUC	-0.065	-0.484*		
FDGLOB	-0.707**	0.283	0.255	
FAGAL	-0.546*	0.321	0.433*	0.251

Figure 13: Station dendrogram resulting from cluster analysis using Bray-Curtis index and UPGMA-linkage on transformed proportions of the six most abundant species.

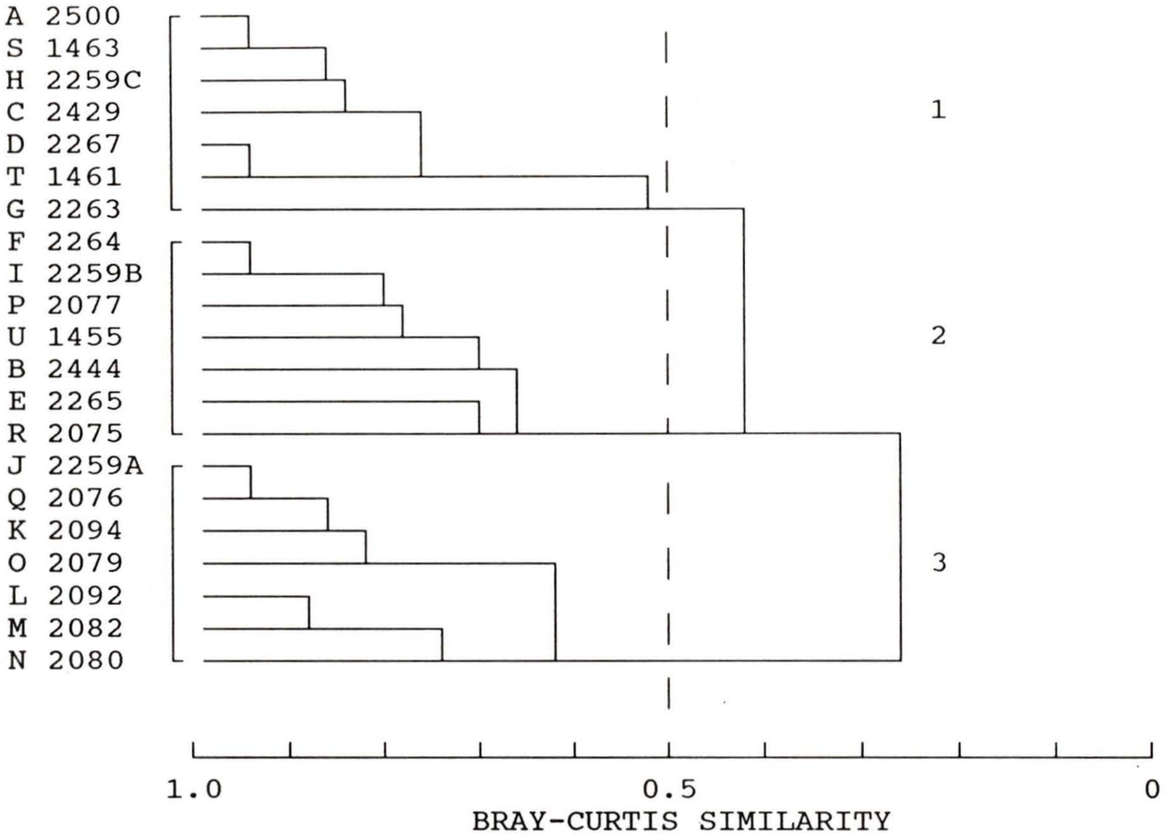
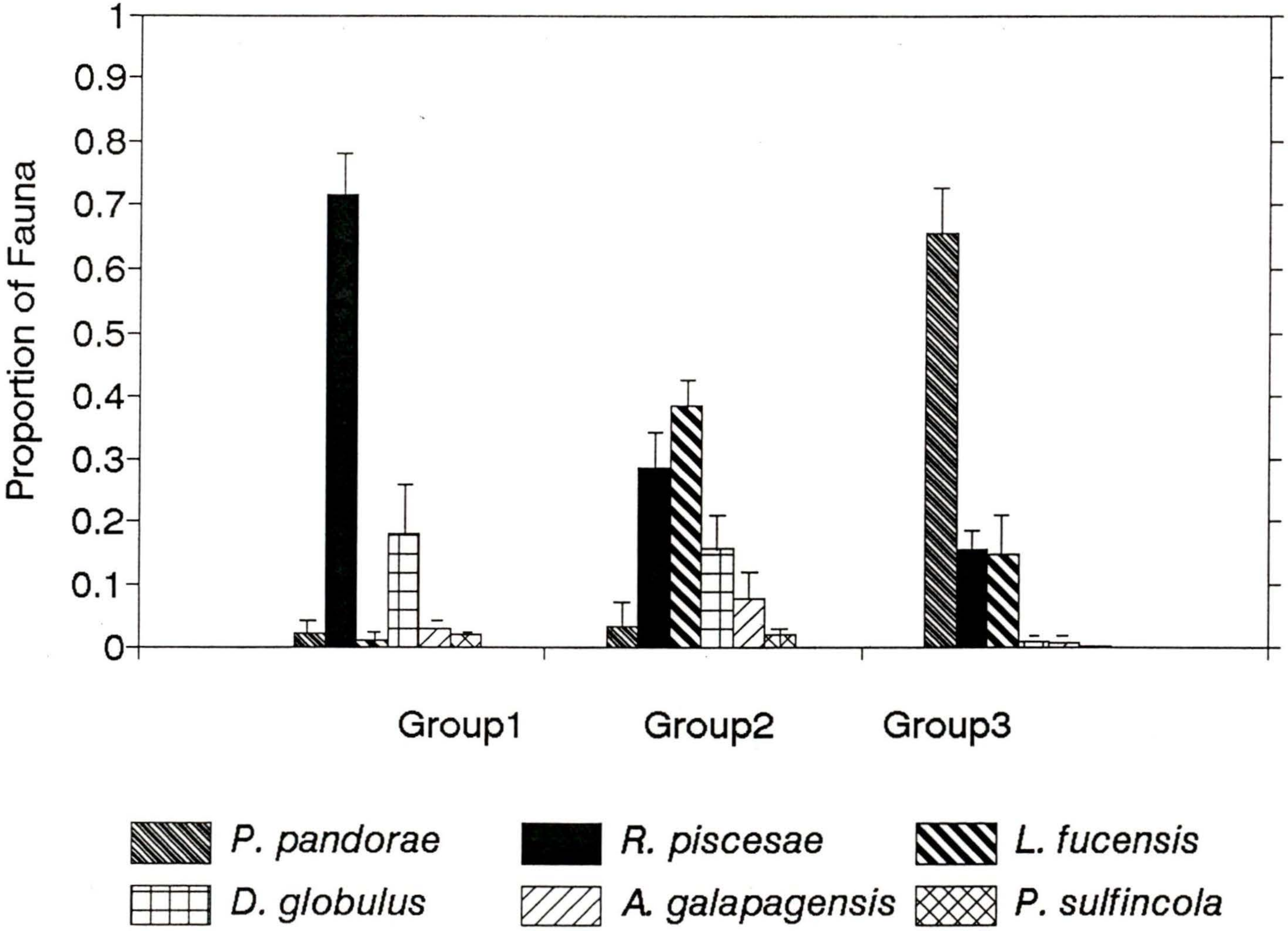

A 2500
S 1463
H 2259C
C 2429
D 2267
T 1461
G 2263
F 2264
I 2259B
P 2077
U 1455
B 2444
E 2265
R 2075
J 2259A
Q 2076
K 2094
O 2079
L 2092
M 2082
N 2080
1
2
3
1.0
0.5
0
BRAY-CURTIS SIMILARITY

Figure 14: Mean relative proportions of fauna for each of the 6 most abundant species from the three groups (Grp1, Grp2, Grp3) resulting from cluster analysis. Bars represent one standard error.


Proportion of Fauna
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Group1
Group2
Group3
P. pandorae
R. piscesae
L. fucensis
D. globulus
A. galapagensis
P. sulfincola

(Figure 14). *Ridgeia piscesae* proportions differed significantly between groups 1 and 3, but not between groups 1 and 2 or groups 2 and 3. *Ridgeia piscesae* proportions were highest in group 1 and lowest in group 3. *Lepetodrilus fucensis* proportions differed significantly between groups 1 and 2, but not between groups 1 and 3 or groups 2 and 3. *Lepetodrilus fucensis* values were highest in group 2 and lowest in group 1. *Depressigyra globulus* proportions were significantly different between groups 2 and 3, but not between groups 1 and 2 or groups 1 and 3. *Depressigyra globulus* proportions were similar for groups 1 and 2 and almost zero in group 3.

Pooled within-cell correlations among DVs for different groups are shown in Table 10. There is a significant and negative correlation between transformed values of *D. globulus* and *P. pandorae*, and between *R. piscesae* and *P. pandorae*. There is a highly negative correlation between transformed values of *P. pandorae* and *A. galapagensis*, and *R. piscesae* and *L. fucensis*. There is a negative and significant correlation between untransformed proportions of *P. pandorae* and *R. piscesae* (Table 11). Although not significant, there is a highly negative correlation between *R. piscesae* and *L. fucensis* and between *D. globulus* and *P. pandorae*.

Table 11: Correlations between untransformed proportions of *P. pandorae* (PPAND), *R. piscesae* (RPIC), *L. fucensis* (LFUC), *D. globulus* (DGLOB), and *A. galapagensis* (AGAL). * = $P < 0.05$. ** = $P < 0.005$.

	PPAND	RPIC	LFUC	DGLOB
RPIC	-0.590**			
LFUC	-0.213	-0.544*		
DGLOB	-0.512*	0.031	0.047	
AGAL	-0.358	0.119	0.197	-0.104

A summary of diversity and other community characteristics across groups for the various samples is given in Table 3. Cluster group had a significant effect on species diversity, evenness, and transformed number of individuals (Table 12). Species diversity (Figure 9), evenness (Figure 10), and number of species (Figure 11) were highest in Group 2. Number of individuals was highest in Group 3 (Figure 12). Proportions of *P. sulfincola* differed between venting area and cluster group. *P. sulfincola* occurred only at high-temperature vents. Therefore, it occurred only in South and ONL vents (Figure 8) and in Groups 1 and 2 (Figure 14). Of the rarer species comprising 0.1% or greater of the overall abundance, *N. venticola*, *P. wolfi*, and *H. vestimentifera* appear to occur predominantly at low-temperature vents in the ONL and YSF while *L. piscesae*, *A. verenae*, and *Paralvinella palmiformis* appear to occur ubiquitiously. Species comprising less than 0.1% of the overall abundance did not occur often enough for me to confidently make statements about their habitat preferences.

Table 12: Analysis of Cluster Group effects on species diversity (SD), evenness (EVEN), and log-transformed number of individuals (LN). Analysis of Area effects on species richness (SR) with sample size as a covariate. Tukey tests to test for differences in species diversity, evenness, and log-transformed number of individuals between groups.

One-way ANOVAS

	Source	SS	df	MS	F	P
SD	Group	1.560	2	0.780	15.309	0.000
	Error	0.917	18	0.051		
SR	Group	36.759	2	18.380	1.858	0.186
	N	110.121	1	110.121	11.132	0.004
	Error	168.165	17	9.892		
EVEN	Group	0.240	2	0.120	9.135	0.002
	Error	0.236	18	0.013		
LN	Group	9.350	2	4.675	4.356	0.029
	Error	19.318	18	1.073		

Comparisons

(DV)	Comparison	Mean Difference	SE	q	$q_{0.01,18,3}$
(SD)	1 vs. 2	0.611	0.085	7.188**	4.703
	1 vs. 3	0.073	0.085	0.859	4.703
	2 vs. 3	0.538	0.085	6.329**	4.703
(EVEN)	1 vs. 2	0.222	0.043	5.163**	4.703
	1 vs. 3	0.008	0.043	0.186	4.703
	2 vs. 3	0.230	0.043	5.349**	4.703
(LN)	1 vs. 2	0.481	0.392	1.227	4.703
	1 vs. 3	1.593	0.392	4.064*	4.703
	2 vs. 3	1.112	0.392	2.837	4.703

Summary of Results

1) A total of 24 species representing 5 phyla have been identified among 75,489 specimens from Cleft Segment samples. There is a taxonomic domination by polychaetes (phyllodocids and terebellids) and gastropods (archaeogastropods). Six species (*P. pandorae*, *R. piscesae*, *L. fucensis*, *D. globulus*, *A. galapagensis*, and *P. sulfincola* in decreasing order) account for more than 97 % of all individuals sampled and 90 % or more of the cumulative percent abundance of all species in a given sample.

2) Venting area, but not sample size, had a significant effect on relative abundances of the five most abundant species. *Paralvinella pandorae* occurred in the greatest proportions at the YSF vents and was near absent from South vents. *Ridgeia piscesae* occurred in the greatest proportions at the ONL and South vents. *Depressigyra globulus* occurred in greater proportions at South vents and *L. fucensis* occurred in greater proportions at YSF vents and was near absent from South vents.

3) There was a significant and negative correlation between untransformed proportions of *P. pandorae* and *R. piscesae*. Although not significant, there was a highly negative correlation between *R. piscesae* and *L. fucensis* and between *D. globulus* and *P. pandorae*.

4) Area had no significant effect on species diversity, evenness, number of species, and transformed values of number of individuals. Species richness and proportions of *P. pandorae* are positively and significantly correlated with number of individuals. Species diversity and species richness were not significantly correlated with proportions of *R. piscesae*.

5) Numerical classification of samples from different years on North and South Cleft and high and low-temperature vents defines 3 major groups, largely reflecting temperature differences.

6) Cluster group, but not sample size, had a significant effect on relative abundances of the five most abundant species. *Paralvinella pandorae* was most abundant in group 3 and nearly absent in groups 1 and 2. *Ridgeia piscesae* proportions were highest in group 1 and lowest in group 3. *Lepetodrilus fucensis* values were highest in group 2 and lowest in group 1. *Depressigyra globulus* proportions were similar for groups 1 and 2 and almost zero in group 3.

7) Cluster group had a significant effect on species diversity, evenness, and transformed number of individuals. Species diversity, evenness, and number of species were highest in Group 2. Number of individuals was highest in Group 3.

8) Paralvinella sulfincola proportions differed between areas and groups. *Paralvinella sulfincola* occurred only at high-temperature vents. Therefore, it occurred only in South and ONL vents and in Groups 1 and 2. Of the rarer species comprising 0.1% or greater of the overall abundance, *N. venticola*, *P. wolfi*, and *H. vestimentifera* occured predominantly at low-temperature vents in the ONL and YSF.

DISCUSSION

The Cleft collections are low in species numbers compared to collections from three other segments on the Juan de Fuca Ridge; moving northward, they are Axial Seamount, Endeavour Segment and Middle Valley. There, species numbers presently stand at 34, 30 and 47 (copepods, nematodes and nemerteans not included) compared to 25 at Cleft. The Cleft collections represent the greatest areal extent, the most vents sampled and the most specimens processed (Tables 2 - 4). Endeavour is poorly processed and Middle Valley has only three samples (Juniper et al., 1992). Cleft lacks the diversity of errant polychaetes and several small crustaceans such as ostracods and amphipods. The most abundant species at Cleft are also the most abundant elsewhere in the Northeast Pacific, suggesting good dispersive ability in these animals.

The reasons for such a small pool of species at Cleft may be three-fold. The young age of the vents combined with the very recent magmatic and tectonic activity may discourage accumulation of species. Second, compared to Endeavour and Middle Valley (large sulfide accumulations and variable sediment cover), there is less habitat heterogeneity, possibly reducing niche availability. Third, regional current patterns may not foster larval influx. At Cleft Segment, long-term mean currents of 2-3 cm/s parallel the ridge, flowing northward on the west side and southward on the east (Cannon et al., 1991). Significant along-axis flows (southerly vector in the order of 2 cm/s) also exist on Axial (Cannon and Pashinski, 1990) and Endeavour (Thomson et al., 1990). However, Cannon et al. (1991) also measured weak and variable currents in the Cleft axis that would slowly advect a larva off-axis. Given the terminal location on the ridge, new recruits from northern segments may be rare and larvae may be advected off-axis and, therefore, poorly dispersed within the segment.

There is further reason for low species diversity at the Cleft Segment and the rest of the JDFR. Geophysical evidence shows that North America interposed as a barrier between the northeast and equatorial Pacific spreading ridges about 35 Ma BP. The vicariating vent fauna of the JDFR has since formed an endemic assemblage of generally lower diversity than that found at EPR vents (Tunnicliffe, 1988). The vent fauna of the NE Pacific can be characterized as an assemblage of limited diversity dominated by a few vestimentiferan, polychaete and gastropod groups. Despite the large size of JDF vent collections (Cleft Segment has the most individuals and vents of any venting region processed to date), species numbers are low. At least ten orders represented at EPR and Galapagos vents are absent. Another feature of JDFR animals is their relatively small size with analagous species tending to be smaller than elsewhere. The fauna inhabiting hydrothermal vents of the NE Pacific has the same "vent character" seen elsewhere with old taxa and adaptations to chemosynthetic production.

Closer comparison of Northeast Pacific fauna to that of EPR vents show: a) similar functional and constructional niches in the assemblages, b) differentiation predominatly at the species level with some higher level separation, c) lower diversity at JDFR in number of higher taxa represented and in number of species within a taxon (Tunnicliffe, 1988). The EPR species list is at least twice as long as that of JDFR, a diversity difference that suggests that the Oligocene separation of the spreading ridges "sampled" only part of the ancestral assemblage. The JDFR vent habitat differs from the EPR areas studied in that it is associated with large accumulations of polymetallic sulfides. Cleft Segment is the newest and most active venting region in the Pacific characterized by a high degree of active venting, high-temperatures, unstable sulfide substrata, and particulate plumes which is probably responsible for the low species diversity at Cleft.

Unpredictable and severe environments such as hydrothermal vents have low diversity because unpredictability forces organisms to have broader niches which allow fewer species to be "packed in", as well as causing a greater chance of extinction for marginal populations (Pielou, 1975). An extreme condition is one that requires, of any organism tolerating it, a morphological structure or biochemical mechanism which is not found in most related species, and is costly, either in energetic terms, or in terms of the compensatory changes in the biology of the organism that are needed to accommodate it (Grime, 1973; Townsend et al., 1983). Although the H_2S of the hydrothermal environment is toxic to most marine animals (Powell and Somero, 1986), the species living in close proximity to the vents have mechanisms by which they avoid sulfide poisoning (Felbeck et al., 1985). However, the toxicity of the environment prevents the encroachment of species from the ambient deep-sea fauna (Hessler and Smithey, 1983). Sulfide toxicity with respect to immigrants should, therefore, promote stability and longevity within the community over long periods of geological time. Taxonomic domination by phyllodocids, terebellids, and archaeogastropods (Table 4) and numerical domination by six species suggests that only a few certain groups of species have adapted to living in a hydrothermal environment. This, along with long term in situ evolution and similarity between North East Pacific sites, suggests that the North East Pacific vent ecosystem has been stable over a long period of geological time.

Where disturbances are frequent and large, the community will tend to be dominated by opportunistic, fast-colonizing species (Connell, 1978). Where disturbances are rare and small, the diversity will depend on "compensatory mechanisms" such as predation, competition, and resource-partitioning (Connell, 1978). At intermediate levels of disturbance, there will be the highest diversity with a few adults of fast-colonizing species, many individuals of mid-succession, secondarily colonizing species, and possibly juveniles of late-succession species. Relatively stable or predictable environments may permit fragile, species-rich communities to exist, whereas relatively unstable or unpredictable environments will support only a dynamically robust and relatively simple ecosystem (May, 1979).

The presence of vent organisms on the NPM demonstrates that vent animals are capable of colonizing new vents on Cleft within two to six years (Milligan and Tunnicliffe, 1994). The NPM venting vigor appears to be in a state of decline already, providing further evidence that the hydrothermal vents are ephemeral and unpredictable environments (Milligan and Tunnicliffe, 1994). Lateral dike injection and subsequent rapid cooling of the mounds may have resulted in a rapid decline in hydrothermal venting over the NPM compared to the YSF (Embley and Chadwick, 1994). It is quite likely that vent animals have a locator cue, such as hydrogen sulfide, for vent water (Cuomo, 1985). Vent larvae are highly constrained by currents and we know little about local flow patterns or even where in the water column the larvae travel (Tunnicliffe, 1991).

Very little is known about locations of source populations or the extent to which supply of larvae to individual vents is independent of proximity to other vents (McLean, 1988). Active dispersal between northern and equatorial Pacific vent fields is compromised by the apparently short life of the larvae. Intermediate sites such as seeps may allow stepwise dispersal and there is also the possibility of adult dispersal by rafting or wafting (Martel and Chia, 1991). Few accounts of reproduction and development of vent fauna have been published (Tunnicliffe, 1991). Many of these studies show that vent species exhibit a wide range of reproductive and developmental modes, reflecting phylogeny of the species rather than the opportunistic life history strategies predicted in such an ephemeral and patchy environment (Grassle, 1985). Therefore, it is difficult to establish the importance of recruitment and source populations in community development.

There was a significant difference in species composition between the active venting areas of Cleft Segment (Table 7). There was a significant difference between South Cleft and YSF, but not between South Cleft and ONL or ONL and YSF, although the comparison between South Cleft and ONL was almost significant. The significant difference between areas appears to be due to the lack of *P. pandorae* and *L. fucensis* at South Cleft and the relative lack of *D. globulus* at YSF and ONL (Table 7, Figure 8). *R. piscesae* also appeared to dominate at South Cleft and ONL whereas *A. galapagensis* was absent from South Cleft and *P. sulfincola* was absent at YSF (Figure 8). I found no significant difference in species abundances, species richness, species diversity, evenness, or number of individuals among the three areas, on Cleft (Table 9, Figures 10 - 13). Although there was a significant difference in species assemblages between the three areas it was not due to an increase in species richness or diversity at South Cleft as I had predicted.

South Cleft is different from the ONL and YSF because it is dominated by *R. piscesae* and *D. globulus* whereas the YSF appears to have a greater predominance of *P. pandorae* and *L. fucensis* and the ONL has a combination of "South Cleft type" and "YSF type" assemblages. It is possible that the South Cleft vents are representative of an older vent ecosystem whereas the YSF vents are representative of a young vent ecosystem and the ONL vents are intermediate in species composition and age between the two. It is unfortunate that no samples are available from the youngest mounds; it may be that 'equilibrium composition' had been reached already in the YSF and ONL collections, which are thought to be slightly older than the NPM (Embley and Chadwick, 1994). The lack of knowledge about vent dispersal and frequency of venting and possible sources of recruitment makes difficult comparisons between different aged lavas, with respect to recruitment. The presence of vent organisms on the NPM suggests that recruitment occurs more quickly than once thought. This and the fact that there was no differences in species diversity, richness, or evenness suggests that community age with respect to recruitment is not an important factor in structuring community assemblages at different aged vents. There may be differences in chemistry or substrate between the different aged lavas to explain the difference in species compositions.

The categorization of vent communities by relative age (Table 1) may be only partly legitimate. When an episode of sea-floor spreading occurs, there is, by definition, extension with associated fissuring and faulting. However, eruptions do not necessarily occur throughout the area of extension. Venting occurs where there are open conduits to a deep heat source, and these fractures can be through older lava as well as associated with eruptions. This is undoubtedly the case at the northern Cleft site, where extensions of the eruptive fissure system cuts through older lavas to the north (Embley and Chadwick, 1994). There is no reason to think that vent communities on the fissures through older lava are any older than the fissure associated with the young sheet flow. The similarity between YSF and ONL faunal assemblages provides further support that vents on the YSF and ONL likely resulted from the same tectonic event and are fed from the same magmatic source (Embley and Chadwick, 1994).

Differences in species assemblages among the three areas is due to differences in temperature of the vent or substrate sampled, or in distance the sample was taken from the main venting source or orifice. Fustec et al. (1987) recorded distinctly different assemblages on the East Pacific Rise between basalts and chimneys. Tunnicliffe and

Juniper (1990) qualitatively document four stages of development in chimneys and associated fauna on Juan de Fuca Ridge. Both papers comment on the heterogeneity of the chimney habitat and the patchy organism distributions. In this study, several species such as *A. galapagensis*, *P. pandorae*, and *L. fucensis*, comprised a smaller proportion of the total fauna at high-temperature vents. Conversely, *R. piscesae*, *P. sulfincola*, and *D. globulus* comprised a greater proportion of the total fauna at high-temperature vents. Previously, *P. sulfincola* was recorded only from sulfide structures (Tunnicliffe et al., 1993), but its presence at three non-chimney vents (albeit in small numbers) suggests a broad adaptability.

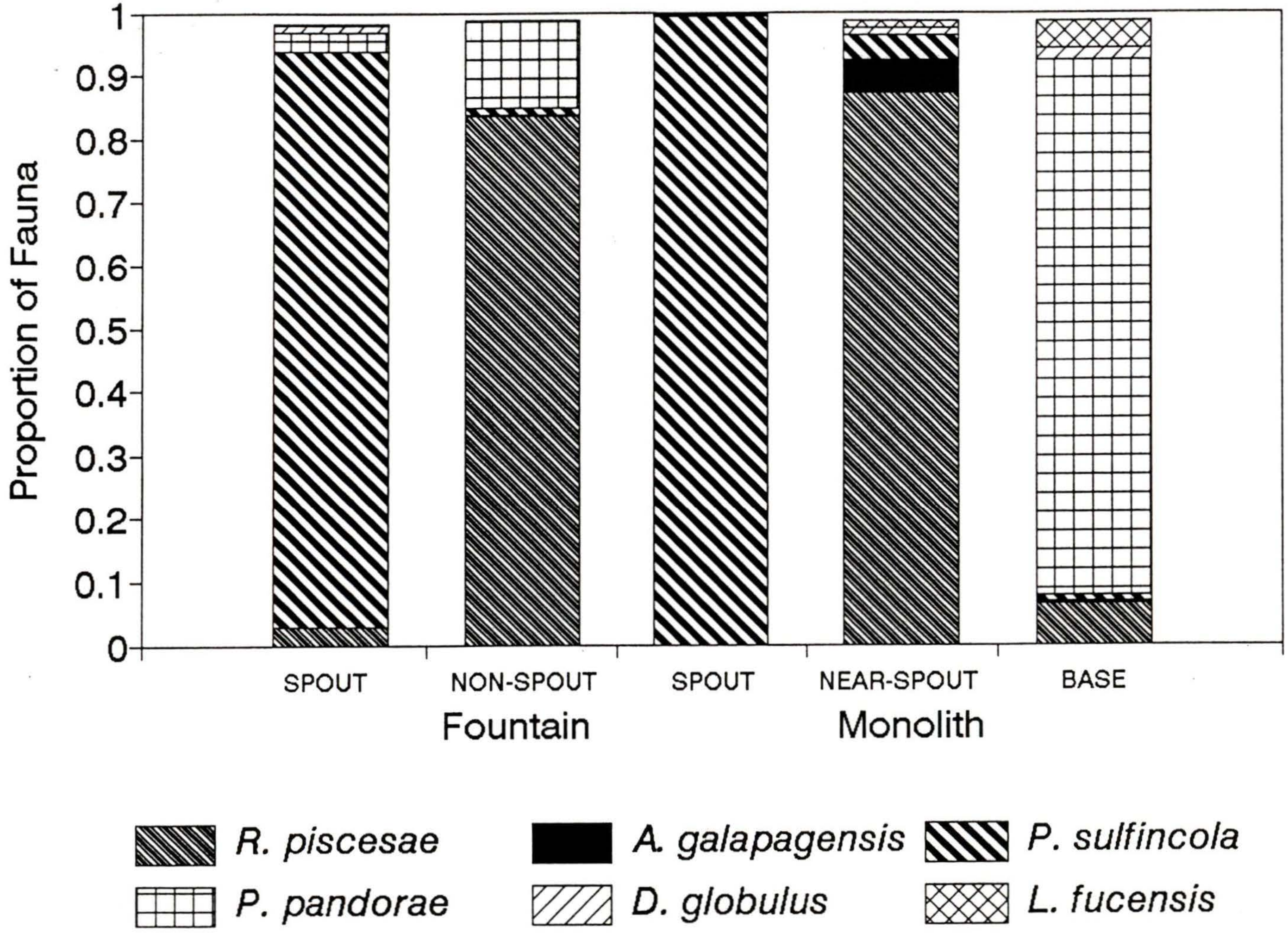
Both low and high-temperature microhabitats can occur in association with a sulfide chimney (Tunnicliffe and Juniper, 1990). Faunal zonation in response to temperature appears to be supported by organismal distribution within specific vents. At Axial, vestimentiferans, alvinellids, and snails are nearest vent exits whereas limpets, polynoids, and galatheid crabs are outside vestimentiferan clumps (Arquit, 1990). At older chimney bases on JDFR where temperatures are low (<10°C) *Ridgeia* sp. and *A. galapagensis* usually colonize. Higher on the chimney and in warmer water, a third vestimentiferan, *L. piscesae* and *P. palmiformis* live at temperatures over 25°C. Nearest the hot water spouts, *P. sulfincola* and another species of polynoid are common (Tunnicliffe and Juniper, 1990). At Cleft, *P.*

sulfincola appears to dominate near hot water spouts, *R. piscesae* dominates in warm water away from the spout, and *P. pandorae* dominates at the chimney base where temperatures are lower (Figure 15).

The faunas of the two low-temperature vents not included in the statistical analysis, one from South Cleft (Vent1A, Figure 2) and one from ONL (A2264, Figure 7), were both comprised largely of *L. fucensis*, *D. globulus*, and *R. piscesae*. Table vent is a diffuse vent while A2265 is a sample taken away from active venting. This suggests that within areas, and even within vents, there are differences in community structure corresponding to differences in temperature or substrate to which vent organisms are exposed.

The separation of Cleft vent samples into 3 groups is also likely due to heterogeneity within high-temperature vents. The 3 cluster groups (Figure 13) consist solely, with the exception of A2267, of high-temperature vents (cluster group 1), both high and low-temperature vents (cluster group 2), and solely, with the exception of Monolith (A2259A), of low-temperature vents (cluster group 3). The two high-temperature vents in cluster group 2 (Table and Monolith) are a diffuse vent and a vent sample away from active venting, respectively. The high-temperature vent sample in cluster group 3 (A2259A) is a sample taken at the base of Monolith, several meters away from active venting.

Figure 15: Relative proportion of fauna each of the 6 most abundant species represent from Monolith and Fountain vents. For sample details see Tables 2 and 3 and Field Description.


Proportion of Fauna
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
SPOUT
NON-SPOUT
SPOUT
NEAR-SPOUT
BASE
Fountain
Monolith
R. piscesae
A. galapagensis
P. sulfincola
P. pandorae
D. globulus
L. fucensis

The 5 dominant species are more abundant in cluster group 3 (Figure 14). In comparing cluster groups, I found that *L. fucensis*, *A. galapagensis*, and *P. pandorae* are less abundant in cluster group 1, whereas *D. globulus* and *R. piscesae* are more abundant in cluster group 1 and *P. sulfincola* is nearly absent from cluster group 3 (Figure 14). These organism distributions suggest that all species occur in greater abundances where there is a high degree of vent flow, characteristic of high-temperature vents, without the extreme temperatures found near hot-water spouts. Species such as *P. sulfincola*, *R. piscesae*, and *D. globulus* appear better adapted to living at high-temperature vents while species such as *P. pandorae*, *L. fucensis*, and *A. galapagensis* appear better adapted to living at low-temperature vents.

Tunnicliffe and Fontaine (1987) suggest that basalt-based vents on the Southern Cleft harbor more species than the chimney habitat. More species might be expected at low-temperature vents because physical circumstances are less extreme (Hessler et al., 1988). However, the spatially heterogenous environment of high-temperature vents should accommodate more species than the low-temperature vents because it provides a greater variety of microhabitats and range of microclimates (Huston, 1979). In this study Cluster group 2 (a mixture of high and low-temperature vents) had the highest species diversity (Figure 9), species richness (Figure 11), and evenness (Figure 10). This appears to be the result of a relatively more even distribution of species with a domination by *L. fucensis* (Figure 14) compared to a domination by *R. piscesae* and *D. globulus* at high-temperature vents alone (cluster group 1) or domination by *P. pandorae* and *L. fucensis* at low-temperature vents alone (cluster group 3). The high species diversity in cluster group 2 probably arises from a vigorous enough vent source to support a large proportion of *R. piscesae*, *D. globulus*, and *P. sulfincola* and temperatures low enough for species such as *L. fucensis* and *A. galapagensis* to tolerate them.

Competition and predation are thought to play significant roles in determining population dynamics and nature of the vent community in terms of species composition and relative abundance of species in relation to geochemistry and water flow (Van Dover et al., 1988). Species may not compete at present because selection in the past favoured an avoidance of competition and thus a differentiation of niches. Distribution of potential competitors in space should be negatively associated; each should tend to occur only where the other is absent (Connell, 1980). The negative correlation between untransformed proportions (Table 11) of *D. globulus* and *P. pandorae*, *R. piscesae* and *P. pandorae*, and *R. piscesae* and *L. fucensis* implies that there is competition occurring between these species. However, a negative association between two species could also mean that the two species have dissimilar habitat requirements (Tonn and Magnuson, 1982). Interspecific competition is a possible explanation for the organization of many communities, but it is not often a proven explanation (Connell, 1980). The negative correlations are likely due to the fact that *P. pandorae* and *L. fucensis* occur predominantly at low-temperature vents and *R. piscesae* and *D. globulus* occur predominantly at high-temperature vents. The presence of *P. pandorae* did not exclude the presence of *D. globulus* or *R. piscesae*, or vice versa (Figures 5 - 7). Likewise, the presence of *R. piscesae* did not exclude *L. fucensis*, or vice versa. This suggests that relative species abundance is a result of ability to adapt to a certain substrate or temperature.

McHugh and Tunnicliffe (1994) found a significant positive correlation between abundancess of *R. piscesae* and *A. galapagensis* and believe it is most likely due to the increased substratum area provided by the vestimentiferan tubes. However, I did not find a significant correlation (0.121) between *R. piscesae* and *A. galapagensis*. I also did not find a significant correlation between *R. piscesae* and species diversity (-0.307) or species richness (-0.154). Depletion of settling space at a suitable vent may be caused by the secretion of large amounts of mucus by *P. palmiformis*, which, along with high densities of *L. fucensis*, often smothers the tubes of vestimentiferans at low-temperature (McHugh, 1989). Although *P. palmiformis* did not occur in large abundance, *L. fucensis* was highly negatively (-0.555) correlated with *R. piscesae* abundance, suggesting that *L. fucensis* and *R. piscesae* occur in dissimilar habitats. *Paralvinella pandorae* is always found coiled around vestimentiferan tubes (McHugh, 1989). Proportion of *P. pandorae* is very strongly associated with sample size (0.992), but is negatively correlated with *R. piscesae* (-0.625) abundance. Although *P. pandorae* occurred in large numbers, it did not appear to be restricted by available vestimentiferan or substratum area. Therefore, it appears that depletion of vestimentiferan tubes as settling space is not a problem for recruitment of species such as *P. pandorae* and *A. galapagensis*.

Fisher et al. (1988) believe that symbiont-hosts are restricted to vent areas that provide sufficient hydrogen sulfide and oxygen. This may explain why *R. piscesae* dominates at high-temperature vents and is less abundant at low-temperature vents. This is supported by observations of recumbent vestimentiferans at several low-temperature vents and erect vestimentiferans at high-temperature vents, suggesting that vestimentiferans at low-temperature vents are relatively limited by hydrogen sulfide concentrations. The tube of *R. piscesae* may also provide some protection from high-temperatures, particulates, and toxicity found near high-temperature vents. *Ridgeia piscesae* cannot abandon its tube and would, therefore, suffer mortality from falling sulfides and/or extreme temperatures if it inhabited areas near active venting.

Paralvinella sulfincola is the only *Paralvinella* species (1 of 4) from the JDFR that constructs a tube. The tube, and the ability to abandon it, may allow *P. sulfincola* to inhabit environments close to active venting sources. *Paralvinella sulfincola* has been implicated in actually changing the nature of the substrate (Tunnicliffe and Juniper, 1990). Although *P. pandorae*, *A. galapagensis*, and *P. sulfincola* are deposit feeders, *P. pandorae* and *A. galapagensis* lack the tube of *P. sulfincola* and, therefore, may not be able to survive near the active venting source. Likewise, *L. fucensis* lacks the hard shell and operculum of *D. globulus* and may be limited to lower temperature vents. However, these adaptations do not explain why *R. piscesae*, *P. sulfincola*, and *D. globulus* do not occur in large abundances at low-temperature vents. Productivity at low-temperature vents may not be high enough to support these species. It is also possible that these species dominate at higher temperature vents because they cannot compete at lower temperature vents.

The patchy occurrence of *P. pandorae* has been linked to its reproductive strategy: continual production of brooded young serves to maintain a local population, but limits dispersal to other vents (McHugh, 1989). *Paralvinella pandorae* occurs in large numbers only at the YSF and the ONL vents with chimneys. That these vents are in close proximity suggests a local source of recruits. The ONL venting probably dates from the same event that initiated the Sheet lavas and we may be seeing simultaneous recruitment events. However, it is likely that *P. pandorae* is recruiting to low-temperature vents that are occurring in the YSF and ONL and are largely absent from South Cleft. The low abundances and frequent absences of *P. palmiformis* are surprising given its ubiquity at other vent sites. This species releases gametes and recruits in pulses (McHugh, 1989); its distribution again suggests weak dispersal agents and/or unstable venting conditions.

Over a 26-day period of observing vestimentiferans on two vents along JDFR, mortality of the worms was 44% by falling sulphate/sulfide spires or mortality for other reasons (Tunnicliffe et a., 1990). Organisms with the ability to avoid heavy mortality at high-temperature vents are likely dominating there. Predation is very common and rat-tail fish and polynoid polychaetes are implicated (Tunnicliffe et al., 1990). Following formation of a high-temperature edifice, alvinellid worms first colonize the walls at points that are sufficiently thick and clogged as to reduce the surface fluid temperature to near 40°C (Fustec et al., 1987). When mineralization further reduces fluid supply to critically low levels, the worms leave their tubes to build on a new part of the edifice. Broad ecological tolerances, niche flexibility and reduced dispersal are important in allowing establishment of *A. galapagensis* (McHugh and Tunnicliffe, 1994). It is likely that the extreme environment experienced by organisms on Cleft

Segment has selected for species with broad ecological tolerances, niche flexibility, and the ability to recruit to patchy environments. This is probably why there is such low species richness and high taxonomic and numerical domination by a few species (or groups of species) at Cleft. It is possible that competition between species has occurred in the past, pressuring species into adapting to slightly different microhabitats. However, at present it is impossible to determine if competition is occurring, or has occurred, at hydrothermal vents.

Change in degree of flow over the lifetime of an individual vent should also affect community composition. Tunnicliffe and Juniper (1990) found that anhydrite spires in the initial stages of "solidifying" are colonized by *P. sulfincola* that secretes a white mucus, beneath which forms a 2mm thick mineralized shell over the central fragile anhydrite. As anhydrite spires grow around hot water conduits, localized water flow changes from an open jet to a more diffuse emission. In response to spire accumulation/collapse, mobile animals can move around sulfide structures, but vestimentiferans are subject to unpredictable flow, and presumably H_2S changes. McHugh and Tunnicliffe (1994) found that the greatest abundances of *A. galapagensis* occurred at old chimneys with diminished flow and many dead tubeworms. One vent sampled (A2431) with dead tubeworms was found with a high number of *A. galapagensis* (Table 5). It was impossible to determine the flow regime to which organisms were exposed. There were no obvious trends observed in samples taken from the same vent or vent field in different years (Figures 6 - 8).

CONCLUSION

The biological samples collected within a few years after an eruption on the Cleft Segment provide some intriguing insights into the geological controls on hydrothermal vent communities. Cleft Segment is characterized by the lowest species richness of any vent system studied to date, although the Cleft Segment represents the greatest areal extent, the most vents sampled, and the most specimens processed. The species composition is similar to that of other Northeast Pacific vents, suggesting good dispersive ability of Cleft inhabitants. The poor species richness may be explained by the young age and very recent magmatic and tectonic activity, less habitat heterogeneity, possibly reducing niche availability, and regional current patterns that may not foster larval influx. The vicariating event 35 Ma BP, separating the North East and Equatorial Pacific spreading centers "sampled" only a portion of the original assemblage of the North East Pacific. The Cleft Segment is the newest and most active venting region in the Pacific, characterized by high-temperatures, unstable substrata, a high degree of venting, and particulate plumes.

The vent ecosystem is characterized by an upredictable environment that supports a dynamically robust and relatively simple ecosystem. Cleft Segment is taxonomically dominated by phyllodocids, terebellids, and archaegastropods, and numerically dominated by 6 species (*Ridgeia piscesae*, *Paralvinella pandorae*, *Lepetodrilus fucensis*, *Depressigyra globulus*, *Amphisamytha galapagensis*, and *Paralvinella sulfincola*). The presence of vent organisms on the NPM demonstrates that vent animals are colonizing new vents within at most 2 to 6 years. However, the lack of information about location of source populations and reproduction and development of vent fauna make it difficult to establish the importance of recruitment and source populations to community development.

There is a significant difference in species composition between active venting areas of Cleft Segment. The greatest difference occurs between South Cleft and YSF. Differences appeared to be caused by the lack of *P. pandorae* and *L. fucensis* at South Cleft and the lack of *D. globulus* at YSF and ONL. *Ridgeia piscesae* also appeared to dominate at South Cleft and ONL whereas *A. galapagensis* was absent from South Cleft and *P. sulfincola* was absent from YSF. There was no difference in species diversity or richness among the venting areas on Cleft Segment. The older South Cleft was not more speciose than the YSF and ONL as I had predicted. This suggests that age, with respect to recruitment, is not the driving factor behind community development, and some other characteristic of the areas is responsible for differences in community assemblages.

Vents on the YSF and ONL likely resulted from the same tectonic event and are fed from the same magmatic source.

This is one possible explanation for the difference between South Cleft and the ONL and YSF. However, this does not explain the similarity between South Cleft and ONL species assemblages and the results attained from a cluster analysis using all the samples, including a low-temperature sample from both South Cleft and ONL. Differences in species assemblages result from differences in temperature and/or substratum, and distance the sample was taken from the active venting source or orifice. Within areas, and even within vents, there are differences in community structure corresponding to differences in temperature or substrata to which vent organisms are exposed. *Paralvinella pandorae*, *L. fucensis*, and *A. galapagensis* appear adapted to low-temperature vents whereas *R. piscesae*, *D. globulus*, and *P. sulfincola* appear adapted to high-temperature vents. Within vents, *P. sulfincola* dominates near hot water spouts, *R. piscesae* dominates in warm water away from the spout, and *P. pandorae* dominates at the chimney base where temperatures are lower.

The highest species diversity at Cleft Segment occurs where there is enough vigorous vent flow to support populations of *R. piscesae*, *D. globulus*, and *P. sulfincola*, and temperatures low enough to allow species such as *P. pandorae*, *L. fucensis*, and *A. galapagensis* to tolerate them. The relative species abundances appear to be a result of the ability of species to tolerate a certain substrate or temperature. Factors such as restricted settling space and competition do not appear to be important in structuring community assemblages at Cleft Segment. However, one cannot rule out the possibility that competition is occurring, or has occurred, at Cleft Segment.

Further studies involving replicate samples and physico-chemical data between vents and within vents over a number of years are necessary to look at changed in vent communities on a year-to-year scale. Further knowledge of vent fauna feeding biology, reproduction, development, and dispersive ability are also required to assess the importance of geology, chemistry, and interspecific effects such as competition on community assemblages at Cleft Segment and other hydrothermal vent systems.

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Dive Number	Name	Catalogue Number	Animal	Number
A1455	Vent1A	133	*R. piscesae*	200
		134	*R. piscesae*	200
		135	*R. piscesae*	5
		288	*D. globulus*	500
		315	*P. variabilis*	14
		316	*P. variabilis*	1
		482	*A. galapagensis*	1
		483	*A. galapagensis*	1
		484	*A. galapagensis*	3
		485	*A. galapagensis*	1
		486	*A. galapagensis*	1
		554	*N. venticola*	6
		555	*N. venticola*	1
		556	*N. venticola*	1
		557	*N. venticola*	1
		558	*N. venticola*	1
		559	*N. venticola*	1
		1612	nematode	5
		1614	nematode	6
		2000	*L. fucensis*	415
A1461	Plume	132	*R. piscesae*	250
		136	*R. piscesae*	1
		159	*R. piscesae*	10
		287	*D. globulus*	103
		432	*P. sulfincola*	5
		1617	nematode	10
A1463	Vent1B	130	*R. piscesae*	150
		131	*R. piscesae*	1
		285	*D. globulus*	2
		431	*P. palmiformis*	1
		481	*A. galapagensis*	3
		615	*L. piscesae*	1
		1400	*C. curvus*	3
A1910	Vent1	1724	*A. galapagensis*	20
		2081	*L. fucensis*	15
		2465	*P. sulfincola*	10
		2824	*D. globulus*	30
A1914	Vent3	1926	*A. galapagensis*	6
		2813	*D. globulus*	30
A2075	Crack	1634	nematode	15
		2122	*L. fucensis*	90
		2486	*P. palmiformis*	2
		2497	*P. pandorae*	50

		2701	*R. piscesae*	20	125
		2858	*D. globulus*	40	
		3259	*L. picsesae*	1	
A2076	Max-Worm	2481	*P. pandorae*	1900	
		2696	*R. piscesae*	170	
		2697	*R. piscesae*	170	
A2077	Station2	739	*A. verenae*	1	
		2555	*P. pandorae*	10	
		2765	*R. piscesae*	20	
		3619	*B. sandersi*	1	
		3620	*B. grasslei*	1	
		3621	*L. kincaidi*	1	
		3622	*L. piscesae*	9	
		2859	*D. globulus*	57	
		2925	*P. variabilis*	7	
		3714	*A. galapagensis*	12	
A2078	Station4	740	*A. verenae*	3	
		2774	*R. piscesae*	118	
A2079	Tripod	576	*N. venticola*	1	
		672	*L. piscesae*	13	
		674	*L. kincaidi*	1	
		2084	*L. fucensis*	20	
		2479	*P. pandorae*	600	
		2480	*P. palmiformis*	4	
		2695	*R. piscesae*	242	
		2826	*D. globulus*	3	
		3623	*B. grasslei*	1	
A2080	Tripod	671	*B. grasslei*	6	
		1929	*A. galapagensis*	8	
		2083	*L. fucensis*	1700	
		2121	*L. fucensis*	380	
		2375	*P. wolfii*	3	
		2477	*P. palmiformis*	15	
		2478	*P. pandorae*	4075	
		2694	*R. piscesae*	188	
		2825	*D. globulus*	40	
A2082	Cavern	1466	*C. curvus*	1	
		1633	nematode	50	
		2125	*L. fucensis*	300	
		2495	*P. pandorae*	75	
		2766	*R. piscesae*	190	
		2767	*R. piscesae*	190	
		2860	*D. globulus*	15	
		3223	*P. wolfii*	1	
		3257	*L. piscesae*	2	
		3258	*L. kincaidi*	1	
		3715	*A. galapagensis*	4	

A2092	Hidden	1930	*A. galapagensis*	8	126
		2085	*L. fucensis*	775	
		2124	*L. fucensis*	775	
		2483	*P. palmiformis*	10	
		2484	*P. pandorae*	1180	
		2485	*P. dela*	2	
		2698	*R. piscesae*	241	
		2827	*D. globulus*	1	
		3624	*B. grasslei*	3	
		3625	*O. tunnicliffeae*	1	
		3626	*L. piscesae*	9	
A2093	Lave Lake	2772	*R. piscesae*	100	
		2773	*R. piscesae*	77	
A2094	Cavern	2123	*L. fucensis*	6	
		2556	*P. pandorae*	3700	
		2557	*P. palmiformis*	20	
		3627	*B. sandersi*	1	
		3628	*L. piscesae*	1	
A2259A	Monolith	737	*A. verenae*	1	
		1042	*E. climax*	1	
		2117	*L. fucensis*	1230	
		2289	*P. sulfincola*	3	
		2290	*P. palmiformis*	4	
		2291	*P. pandorae*	285	
		2292	*P. sulfincola*	38	
		2757	*R. piscesae*	100	
		2758	*R. piscesae*	100	
		2852	*D. globulus*	629	
		2924	*P. variabilis*	1	
		3362	*P. wolfi*	18	
		3363	*P. verenae*	2	
		3611	*L. piscesae*	176	
		3612	*L. kincaidi*	2	
		3613	*B. grasslei*	16	
		3614	*B. sandersi*	8	
		3615	*O. tunnicliffeae*	2	
		3708	*A. galapagensis*	2	
A2259B	Monolith	2116	*L. fucensis*	750	
		2286	*P. sulfincola*	377	
		2287	*P. palmiformis*	162	
		2288	*P. pandorae*	16	
		2754	*R. piscesae*	150	
		2755	*R. piscesae*	150	
		2756	*R. piscesae*	750	
		2851	*D. globulus*	4000	
		3608	*L. piscesae*	92	
		3609	*O. tunnicliffeae*	17	
		3610	*B. grasslei*	7	
		3707	*A. galapagensis*	25	

A2259C	Monolith	2115	*L. fucensis*	27	127
		2285	*P. sulfincola*	92	
		2752	*R. piscesae*	1100	
		2753	*R. piscesae*	700	
		2850	*D. globulus*	26	
		3606	*L. piscesae*	7	
		3607	*O. tunnicliffeae*	1	
		3706	*A. galapagensis*	108	
A2262	Graben	2114	*L. fucensis*	3	
		2751	*R. piscesae*	2	
		2849	*D. globulus*	21	
		2923	*P. variabilis*	1	
		3361	*H. vestimentifera*	8	
		3605	*L. kincaidi*	1	
		3705	*A. galapagensis*	1	
A2263	?	736	*A. verenae*	1	
		1465	*C. curvus*	3	
		2113	*L. fucensis*	9	
		2284	*P. sulfincola*	77	
		2750	*R. piscesae*	940	
		2848	*D. globulus*	1583	
		3603	*B. grasslei*	4	
		3704	*A. galapagensis*	2	
A2264	Marker22	578	*N. venticola*	88	
		735	*A. verenae*	53	
		1041	*E. climax*	2	
		1464	*C. curvus*	15	
		1784	*H. jauni*	47	
		2110	*L. fucensis*	3000	
		2279	*P. sulfincola*	1	
		2768	*R. piscesae*	1600	
		2769	*R. piscesae*	1600	
		2845	*D. globulus*	800	
		2921	*P. variabilis*	42	
		3294	*L. kincaidi*	11	
		3295	*L. piscesae*	51	
		3296	*B. grasslei*	11	
		3297	*B. sandersi*	7	
		3356	*H. vestimentifera*	84	
		3357	*P. verenae*	2	
		3359	*P. wolfi*	380	
		3701	*A. galapagensis*	400	
A2265	Monolith	2112	*L. fucensis*	800	
		2282	*P. sulfincola*	21	
		2283	*P. palmiformis*	8	
		2748	*R. piscesae*	70	
		2749	*R. piscesae*	70	
		2847	*D. globulus*	483	
		3601	*L. piscesae*	19	
		3602	*O. tunnicliffeae*	3	

		3703	*A. galapagensis*	79	128
A2267	?	2111	*L. fucensis*	16	
		2280	*P. sulfincola*	1	
		2281	*P. palmiformis*	7	
		2745	*R. piscesae*	100	
		2746	*R. piscesae*	100	
		2747	*R. piscesae*	450	
		2846	*D. globulus*	221	
		2922	*P. variabilis*	3	
		3298	*L. kincaidi*	1	
		3299	*B. grasslei*	1	
		3360	*P. wolfi*	11	
		3600	*L. piscesae*	4	
		3702	*A. galapagensis*	44	
A2269	Monolith	2292	*P. sulfincola*	28	
A2427	?	579	*N. venticola*	3	
		2293	*P. sulfincola*	5	
		2759	*R. piscesae*	19	
		2853	*D. globulus*	33	
		3364	*L. pachybranchiatus*	1	
		3616	*L. piscesae*	1	
		3709	*A. galapagensis*	3	
A2429	Fountain	2294	*P. sulfincola*	8	
		2295	*P. palmiformis*	5	
		2296	*P. pandorae*	95	
		2770	*R. piscesae*	290	
		2854	*D. globulus*	3	
		3617	*B. grasslei*	1	
		3710	*A. galapagensis*	2	
A2431	?	738	*A. verenae*	1	
		1785	*H. jauni*	10	
		3711	*A. galapagensis*	240	
A2434	Table	2119	*L. fucensis*	5	
		2297	*P. palmiformis*	37	
		2298	*P. sulfincola*	60	
		2761	*R. piscesae*	9	
		3618	*L. piscesae*	3	
		2855	*D. globulus*	4	
A2436	Fountain	2299	*P. sulfincola*	62	
		2553	*P. sulfincola*	1	
		2554	*P. palmiformis*	1	
		2762	*R. piscesae*	2	
		2856	*D. globulus*	1	
A2444	Marker46	2763	*R. piscesae*	181	
		12	*A. galapagensis*	149	

H202	Monolith	2120	*L. fucensis*	10	129
		2764	*R. piscesae*	496	
		2857	*D. globulus*	20	
		3713	*A. galapagensis*	49	

VITA

Surname: Milligan Given Names: Barry, Nelson

Place of Birth: Edmonton, Canada Date of Birth: July 7, 1969

Educational Institutions Attended:

University of Victoria	1991 to 1993
University of Regina	1987 to 1991

Degrees Awarded:

B.Sc. (Distinction)	University of Regina	1991

Honours and Awards:

NSERC Graduate Research Awards (PGSA)	1991 to 1993
NSERC Graduate Research Awards (PGSB)	1994 to 1995
President's Award, U. of Victoria	1991 to 1993
Graduate Teaching Fellowship	1993
W. C. Gordon Fields Scholarship	1993
NSERC Undergraduate Research Award	1991
Bamfield Marine Station Awards	1990
General Proficiency Awards, U. of Regina	1988, 1989
Sheldon Williams Collegiate Award, Regina	1987

Publications:

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Author:
Signature

Barry Nelson Milligan
Name

December 17, 1993
Date

Examiners: [redacted]

Dr. V.J. Tunnicliffe, Supervisor (Department of Biology)

[redacted]

Dr. P.T. Gregory, Departmental Member (Department of Biology)

[redacted]

Dr. M.J. Whiticar, Outside Member (School of Earth and Ocean Sciences)

[redacted]

Mr. P. Lambert (M.Sc.), External Examiner (Royal British Columbia Museum)