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## Deep-Sea Research II

journal homepage: [www.elsevier.com/locate/dsr2](http://www.elsevier.com/locate/dsr2)

# Macrobenthos community structure and trophic relationships within active and inactive Pacific hydrothermal sediments

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## ARTICLE INFO

## Keywords:

Benthos  
Hydrothermal fields  
Microbial mat  
Species diversity  
Isotopes  
Invertebrates  
Middle Valley  
Papua New Guinea  
Manus Basin

## ABSTRACT

Hydrothermal fluids passing through sediments create a habitat hypothesized to influence the community structure of infaunal macrobenthos. Here we characterize the density, biomass, species composition, diversity, distributions, lifestyle, and nutritional sources of macroinfauna in hydrothermal sediments in NE and SW Pacific settings, and draw comparisons in search of faunal attributes characteristic of this habitat. There is increasing likelihood that seafloor massive sulfide deposits, associated with active and inactive hydrothermal venting, will be mined commercially. This creates a growing imperative for a more thorough understanding of the structure, dynamics, and resilience of the associated sediment faunas, and has stimulated the research presented here. Macrobenthic assemblages were studied at Manus Basin (1430–1634 m, Papua New Guinea [PNG]) as a function of location (South Su vs. Solwara 1), and hydrothermal activity (active vs. inactive), and at Middle Valley (2406–2411 m, near Juan de Fuca Ridge) as a function of habitat (active clam bed, microbial mat, hot mud, inactive background sediment). The studies conducted in PNG formed part of the environmental impact assessment work for the Solwara 1 Project of Nautilus Minerals Niugini Limited. We hypothesized that hydrothermally active sites should support (a) higher densities and biomass, (b) greater dominance and lower diversity, (c) a higher fraction of deposit feeders, and (d) greater isotopic evidence for chemosynthetic food sources than inactive sites. Manus Basin macrofauna generally had low density ( $< 1000 \text{ ind. m}^{-2}$ ) and low biomass ( $0.1\text{--}1.07 \text{ g m}^{-2}$ ), except for the South Su active site, which had higher density ( $3494 \text{ ind. m}^{-2}$ ) and biomass ( $11.94 \text{ g m}^{-2}$ ), greater dominance ( $R1D = 76\%$ ), lower diversity and more spatial (between-core) homogeneity than the Solwara 1 and South Su inactive sites. Dominant taxa at Manus Basin were Spionidae (*Prionospio* sp.) in active sediments, and tanaids and deposit-feeding nuculanoid bivalves in active and inactive sediments. At Middle Valley, hot mud sediments supported few animals ( $1011 \text{ ind m}^{-2}$ ) and low biomass ( $1.34 \text{ g m}^{-2}$ ), while active clam bed sediments supported a high-density ( $19,984 \text{ ind m}^{-2}$ ), high-biomass ( $4.46 \text{ g m}^{-2}$ ), low-diversity assemblage comprised of largely orbinid and syllid polychaetes. Microbial mat sediments had the most diverse assemblage (mainly orbinid, syllid, dorvilleid, and ampharetid polychaetes) with intermediate densities ( $8191 \text{ ind m}^{-2}$ ) and high biomass ( $4.23 \text{ g m}^{-2}$ ). Fauna at both Manus Basin active sites had heavy  $\delta^{13}\text{C}$  signatures ( $-17\%$  to  $-13\%$ ) indicative of chemosynthetic, TCA-cycle microbes at the base of the food chain. In contrast, photosynthesis and sulfide oxidation appear to fuel most of the fauna at Manus Basin inactive sites ( $\delta^{13}\text{C} = -29\%$  to  $-20\%$ ) and Middle Valley active clam beds and microbial mats ( $\delta^{13}\text{C} = -36\%$  to  $-20\%$ ). The two hydrothermal regions, located at opposite ends of the Pacific Ocean, supported different habitats, sharing few taxa at the generic or family level, but both exhibited elevated infaunal density and high dominance at selected sites. Subsurface-deposit feeding and bacterivory were prevalent feeding modes. Both the Manus Basin and Middle Valley assemblages exhibit significant within-region heterogeneity, apparently conferred by variations in hydrothermal activity and associated biogenic habitats.

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## 1. Introduction

Most hydrothermal ecosystems have substrates consisting of exposed rock (volcanic or precipitated mineral deposits) with little or no sediment cover. Hydrothermal activity in ridge-crest environments is characterized by low sedimentation rates

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involving the chemical interaction of seawater with basalts, whereas in regions of high sedimentation, hydrothermal fluids also react with sediments that blanket the seafloor, yielding distinct hydrothermal fluid composition and environmental conditions. These conditions likely promote chemosynthetic microbial activity and generate an enhanced food supply for infauna relative to background (ambient) sediments. Thus, they potentially may support a specialized fauna. The first work on these distinctive habitats (active hydrothermal sediments) was conducted by Fred Grassle and Rose Petrecca, who studied infauna of Guaymas Basin (1800–2000 m, Gulf of California) and Escanaba Trough (3250 m, Gorda Ridge), finding previously unidentified infaunal assemblages (Petrecca and Grassle, 1990; Grassle and Petrecca, 1994). Subsequently, Juniper and Tunnicliffe (1997) reported on the larger biota of Middle Valley (2400 m, Juan de Fuca Ridge). Quantitative studies of hydrothermal sediments remain relatively rare. Most relevant analyses of infauna focus only on actively venting sediments, identifiable by surface manifestations of microbial mats, elevated temperatures, venting chimneys or the presence of certain symbiont-bearing megafauna (Petrecca and Grassle, 1990; Grassle and Petrecca, 1994; Sudarikov and Galkin, 1995; Juniper and Tunnicliffe, 1997; Gebruk et al., 2000; Biscoito et al., 2006). Kamenev et al. (1993) found similar macro- and meiofaunal composition in active and adjacent shallow hydrothermal sediments off New Zealand. However, abundances decreased towards vents and symbiont-bearing pogonophorans and Stilbonematinae nematodes were present only in hot, venting sediments. The best comparison to date of active and inactive vent infauna (based on ~10 samples) is a study by Vanreusel et al. (1997), which examined meiofauna (mainly nematodes) in hydrothermally active sediments, inactive hydrothermal sediment, and non-vent deep-sea sediments of the North Fiji Basin. Key findings were that composition at the genus level was similar in hydrothermal and non-hydrothermal areas, with all genera previously known to science, but none of the species in hydrothermal sediments occurred in control areas, and diversity was much lower in the hydrothermal sediments. Vanreusel et al. (1997) noted (a) extreme patchiness (with some cores having zero density) in all settings, (b) similar dominant genera in active and inactive sediments, but (c) notably lower meiofaunal density in inactive relative to active sediments. Understanding the ecology of active and inactive hydrothermal sediments has taken on added importance with greatly increased likelihood that hydrothermal sites will be mined for valuable metal-bearing sulfides. Knowledge of species' identity, distributions, lifestyles, trophic requirements and reproductive characteristics should be helpful in assessing resilience of these ecosystems in the face of anthropogenic disturbance such as dredging, trawling or mining.

The primary objectives of the present study were to (1) identify community attributes of macrofaunal assemblages inhabiting hydrothermally active sediments at Manus Basin and Middle Valley, specifically with respect to density, species composition, diversity, distributions, and lifestyle, (2) assess within-system habitat heterogeneity conferred by location and hydrothermal activity or by biogenic features such as clam beds and microbial mats (*sensu* Levin et al., 2003), and (3) evaluate and compare nutritional sources of vent infauna using stable isotope analyses. Specifically we identify fauna nutritionally reliant on chemosynthetically fixed C, i.e. those with isotopically light (methane-influenced) or heavy (TCA cycle-influenced sediments)  $\delta^{13}\text{C}$  signatures, and distinguish these from taxa using photosynthetically fixed organic matter. The Manus Basin study presented here is the result of work conducted for the Nautilus Minerals Niugini (Nautilus) environmental impact assessment. Nautilus is a company exploring seafloor massive sulfide deposits for future development. In this context we compared the Manus Basin and

Middle Valley faunas and attempted to evaluate compositions, lifestyles or taxon features that could influence resilience or potential to recover from mining disturbance. We hypothesized that hydrothermally active sites should support (a) higher densities and biomass, (b) greater dominance and lower diversity, (c) a higher fraction of deposit feeders, and (d) greater isotopic evidence for chemosynthetic food sources than inactive sites.

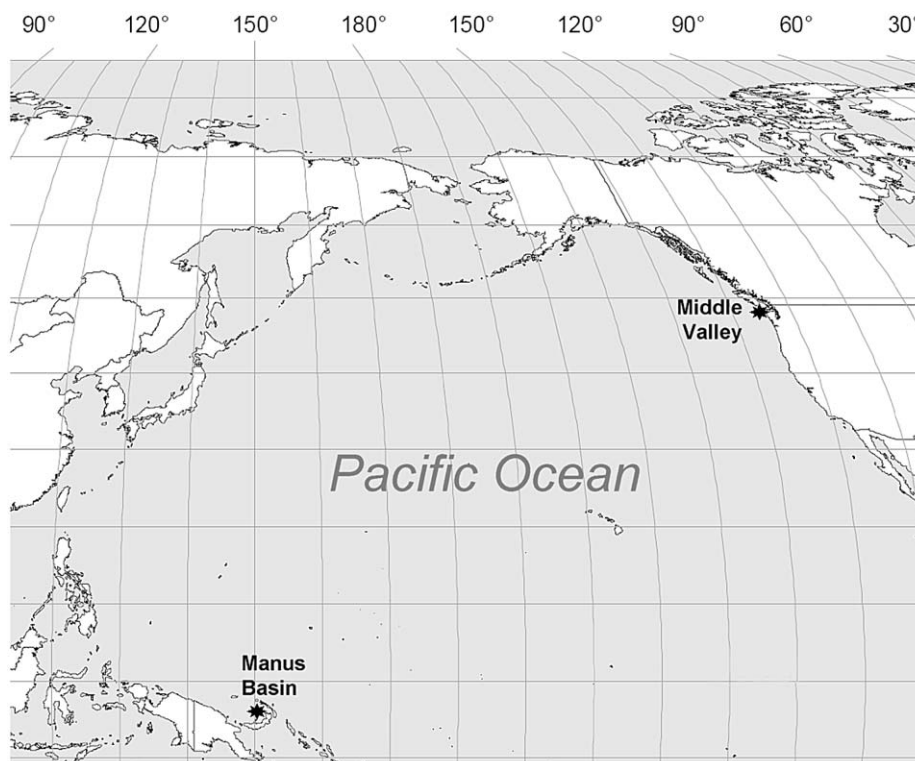
## 2. Methods

### 2.1. Manus Basin, Papua New Guinea

Sampling was conducted to quantify and compare macrofaunal invertebrate assemblages (>0.3 mm) in active and inactive hydrothermal sediments surrounding sulfide precipitates at two locations in Papua New Guinea (Fig. 1): Solwara 1 (a proposed site for mining, located at 3°47'18.7"S 152°5'38.2"E; 1504–1634 m) and South Su (a proposed reference site, located at 3°48'33.2"S 152°6'16.4"E; 1312–1430 m). A key objective in making the between-site comparisons was to assess the suitability of South Su as a control (or undisturbed) area for evaluating Solwara 1 mining impacts. Solwara 1 is located in the Bismarck Sea about 50 km north of Rabaul, Papua New Guinea. South Su is about 2 km SE of Solwara 1. Active mining at Solwara 1 has not yet occurred but is likely within the next few years. Active status of sediments was determined by close proximity (<20 m) to actively venting (shimmering), sulfide-rich environments; inactive status was defined as being >50 m (a somewhat arbitrary distance) from active venting. No clear color differences between active and inactive sediments were noted during sampling.

Samples were collected in conjunction with Nautilus personnel on board the CS Wave Mercury operated by Global Marine Systems during March and April 2007. Hydrothermal sediments were sampled using a Perry Slingsby ST200 series ROV (operated by Canyon Offshore and Global Marine Systems) using tube cores 7 cm in diameter (38.5 cm<sup>2</sup> surface area). Thirty-five tube cores were collected. Seventeen cores were taken at Solwara 1, 7 from inactive sediments and 10 from active sediments. At South Su, 10 cores were retrieved from active sediments and 8 from inactive material (Table 1). When possible, cores were sectioned vertically at intervals 0–1, 1–2, 2–3, 3–5, and 5–10 cm to examine vertical distribution of fauna within the sediment column. However, core depth in the sediment varied from 3 to 10 cm; hence, not all fractions were available for all cores. Macrofaunal abundance data are typically expressed as number or grams per square meter, and not in volume units. Thus, no correction was made for different core volumes that might have resulted from variable vertical penetration. Data for all cores >3 cm in depth were included in estimations of density, biomass, and composition. Since no animals were recovered in sediments collected below 5 cm depth, and 94% of all fauna were present in the top 3 cm, core depth was not considered a significant factor in this analysis for cores that contained sediments >3 cm deep. However, only tube cores that recovered sediments to at least 5 cm were included in the quantitative analysis of macrofaunal vertical distribution. In addition to tube cores, 16 non-quantitative scoop samples were collected to provide additional material for faunal characterization, including 2 from each of the active sites and 6 from each of the inactive sites (Table 1). These collected near-surface sediments (5–10 cm deep) from a larger area of sediment (~200–1000 cm<sup>2</sup>) than tube cores.

Onboard ship tube core samples were preserved unsieved (sections from 0 to 10 cm) and the fraction >10 cm was sieved on a 0.3-mm mesh with filtered seawater. All scoop samples were



**Fig. 1.** Location of Pacific hydrothermal sites studied: Solwara 1 and South Su in Manus Basin, Papua New Guinea, Southwestern Pacific Ocean, and Middle Valley near Juan de Fuca hydrothermal vents, Northeastern Pacific Ocean.

**Table 1**

Location and numbers of samples collected for community and isotope analyses.

<b>Manus Basin</b>	<b>Solwara 1 active</b> 3.79°S 152.095°E	<b>Solwara 1 inactive</b> 3.79°S 152.095°E	<b>South Su active</b> 3.81°S 152.105°E	<b>South Su inactive</b> 3.81°S 152.105°E	
Preserved samples					
Tube cores	10	7	11	7	
Scoops	2	6	2	6	
Isotope samples <sup>a</sup>					
No. individuals	1	6	16	10	
<b>Middle Valley</b>	<b>Microbial mat</b>	<b>Active clam bed</b>	<b>Inactive clam bed</b>	<b>Hot mud</b>	<b>Background</b>
	48°27.358N 128°42.574W	48°27.325N 128°42.557W	48°27.344N 128°42.573W	48°27.363N 128°42.586W	48°27.339N 128°42.538W
<b>Tube cores</b>					
Sorted live	3	2	0	2	0
Preserved	3	2	0	2	1
<b>Scoop samples</b>					
Sorted live	3	2	1	0	0
Preserved	0	0	0	0	0
<b>Isotope samples<sup>b</sup></b>					
Tube core	2	7	0	0	1
Scoop	4+1 slurp	1	1	0	1
No. individuals	83	59	4	0	11

<sup>a</sup> Manus Basin isotope samples were formalin-preserved specimens that were removed from preserved tube cores after counting, identification, and biomassing.

<sup>b</sup> Middle Valley isotope samples were sorted live and frozen unpreserved at  $-20^{\circ}\text{C}$  until analysis.

sieved on a 0.3-mm mesh prior to preservation. All samples were preserved in 8% buffered formalin and seawater.

In the laboratory at Scripps Institution of Oceanography, samples from all sites were re-sieved on a 0.3-mm mesh and invertebrates were sorted from retained material under a dissecting scope at  $12\times$  magnification. Animals were counted,

identified to species or putative species, and then weighed wet (having been in dilute formalin) on an analytical balance to obtain biomass. Each taxon was weighed separately. No attempt was made to remove shells or hard parts. Representative preserved specimens from each site were separated for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses as described below.

## 2.2. Middle Valley collections

Fifteen quantitative tube core samples (6.4-cm diameter; 32.1 cm<sup>2</sup> and 10 cm deep) and six scoop samples (to 10 cm depth) were collected in July 2006 by the DSRV *ALVIN* during dives 4338 and 4339 in Middle Valley near Juan de Fuca Ridge (48°27.3'N 128°42.5') (Fig. 1). Samples were collected from active sediments at three habitats: an 'active clam bed' (with an unidentified vesicomyid species), 'microbial mat' (comprised primarily of orange and white sulfide-oxidizing bacteria), and 'hot mud' (where venting bubbles were observed and sediments had elevated temperature readings of 37 °C at 1 cm and 94 °C at 5 cm). Inactive sediments were sampled at two habitats: 'inactive clam bed' (as evidenced by dead clam shells) and 'background sediments' (defined by the absence of surface vent organisms). Tube cores were sectioned at 0–1, 1–2, 2–5, and 5–10 cm intervals. A subset of tube core samples and all scoop sediments were sorted live to obtain animals for stable isotope analyses; the remainder were sectioned as indicated as above and preserved in 8% buffered formalin and seawater. The numbers of each type of sample are given in Table 1. In the laboratory, preserved specimens were sorted, identified to species or putative species, enumerated, and weighed wet for biomass determination as described for Manus Basin.

## 2.3. Stable isotope analyses

Living specimens from Middle Valley were allowed to clear guts overnight in filtered seawater. These and preserved individuals from Manus Basin were washed in Milli-Q (18 Ω) water and placed in pre-weighed tin boats or combusted vials (500 °C for 4 h). Middle Valley specimens were transported frozen at –20 °C to the laboratory. In the laboratory, specimens were oven dried (60 °C), weighed and acidified with 1% PtCl<sub>2</sub> to remove inorganic C. Stable isotope measurements ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) were made on 0.2–1 mg of dry tissue from single individuals. Samples were analyzed on a Costech elemental analyzer interfaced with a continuous-flow Micromass Isoprime isotope ratio mass spectrometer at Washington State University. Isotope ratios are expressed as  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  in units of per mil (‰). Standards were Pee Dee Belemnite for  $\delta^{13}\text{C}$  and nitrogen gas for  $\delta^{15}\text{N}$  (atmospheric). We recognize that formalin preservation will change  $\delta^{13}\text{C}$  of infauna slightly (~0.5‰) but there should be little effect on  $\delta^{15}\text{N}$  (Levin et al., 2006; Bergquist et al., 2007). Given the broad range of isotopic values present among hydrothermal infauna, and the fact that no quantitative comparisons were drawn between preserved and non-preserved specimens, we did not deem it necessary to correct for a preservation effect.

## 2.4. Statistical analyses

A non-parametric Kruskal–Wallis test followed by an *a posteriori* test (Student's *t*-test or Tukey's HSD test) was performed to evaluate differences in macrofaunal density and biomass among sampling sites and habitats, as data did not follow a normal distribution, even after transformation. Multivariate analyses of community similarity and dissimilarity were carried out using the Bray Curtis Index to draw assemblage comparisons between (1) the two Manus Basin sites, Solwara 1 and South Su, (2) active and inactive Manus Basin sites, (3) active clam bed, microbial mat and hydrothermal hot mud habitats at Middle Valley, and (4) Manus Basin vs. Middle Valley. Specifically, the statistical routines MDS, ANOSIM, and SIMPER were employed using PRIMER Software (v. 6.2) (Clarke and Gorley, 2006). For within-region comparisons we evaluated community similarity based on both

species presence and counts; thus, only quantitative tube core samples (with identical surface area) were used. To permit the comparison between Middle Valley and Manus Basin assemblages, we used tube core data resolved at the family level for annelids, mollusks, and tanaids and at the class level for other taxa.

Macrofauna diversity analysis, determined for quantitative tube core samples, involved evaluating average species richness per core (*S*), Shannon's diversity index (*H'*; log base *e* and 10) and Pielou's evenness (*J'*) using the DIVERSE routine in PRIMER. Rank 1 dominance was calculated as the proportion of the total of the most abundant species. Rarefaction curves, designed to compare diversity in samples having different numbers of individuals, were generated from scoop samples pooled from each Manus Basin site and from tube core samples taken in each Middle Valley habitat. Rarefaction curves estimate the number of species present for a given sample size. The very low number of individuals and species collected from tube core samples made the Manus Basin tube core data unsuitable for rarefaction analysis.

Stable isotope data were averaged by species and then mean  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values were calculated along with standard error. Differences between activity level, sites, or habitats within a region were evaluated using non-parametric Kruskal–Wallis tests.

## 3. Results

### 3.1. Manus Basin

#### 3.1.1. Density and biomass

Faunal densities in Manus Basin hydrothermal sediments were extremely low for the bathyal depths studied (1300–1600 m). Only 220 individuals belonging to 15 species were collected in 35 tube cores taken in this study. Densities (expressed as mean no. individuals m<sup>-2</sup> ± 1 Standard Error to allow comparisons with Middle Valley and other sites) were 935 ± 404, 445 ± 379, 3494 ± 1215, and 890 ± 487, at Solwara 1 active, Solwara 1 inactive, South Su active, and South Su inactive sites, respectively (Table 2). Within each study area, the active site densities were higher than the inactive site densities, by a factor of 2 at Solwara 1 and by a factor of 4 at South Su. However, due to high levels of variability, the difference between active and inactive site densities was significant only at South Su (*P* < 0.05). South Su active sediments had higher macrofaunal densities than the other three sites, which were not significantly different from one another ( $\chi^2 = 11.28$ , *df* = 3, *P* = 0.010). Tanaids and nuculanoid bivalves were the dominant taxa at both Solwara 1 sites and at the South Su inactive site (Table 2). The tanaids belong to two species: near *Paraleptognathia* sp. (Family Anarthruridae, Subfamily Akanthophoreinae) and *Pseudotanaia* sp. (Family Pseudotanaidae). The spionid polychaete *Prionospio* (*Minuspio*) sp. was the dominant taxon at the active South Su site, comprising 76% of the total number of individuals.

Average macrofaunal wet weight in the four study areas ranged from 0.26 to 11.95 g m<sup>-2</sup> (Table 2). In contrast to density, the Solwara 1 active biomass (0.26 g m<sup>-2</sup>) was lower than at the inactive site (1.07 g m<sup>-2</sup>), though, due to high between-core variability, this difference was not statistically significant. The South Su active site (11.95 g m<sup>-2</sup>) had biomass over 100 times higher than the inactive site (0.10 g m<sup>-2</sup>) (*P* < 0.05). South Su active macrofaunal biomass was significantly higher than that observed at the three other sites ( $\chi^2 = 15.89$ , *df* = 3, *P* = 0.001). Biomass dominants were the tanaid *Paraleptognathia* sp. (40% of total) in active Solwara 1 sediments, a sigalionid polychaete (81%) in Solwara 1 inactive sediments, *Prionospio* (*Minuspio*) sp. in active South Su sediments (69%), and a nuculanoid bivalve (66%) in

**Table 2**  
Density and biomass of macrofauna collected from active and inactive hydrothermal sediments of Manus Basin.

n	Solwara 1_active 10			Solwara 1_inactive 7			South Su_active 11			South Su_inactive 7		
	Average	S.E.	Percentage	Average	S.E.	Percentage	Average	S.E.	Percentage	Average	S.E.	Percentage
Counts = no. individuals/38 cm <sup>2</sup> core												
<i>Heteromastus</i> sp.	0.5	0.31	13.89%	0.14	0.14	8.33%	0.00	0.00	0.00%	0.00	0.00	0.00%
Glyceridae	0.1	0.10	2.78%	0.00	0.00	0.00%	0.00	0.00	0.00%	0.00	0.00	0.00%
<i>Cossura</i> sp.	0	0.00	0.00%	0.14	0.14	8.33%	0.00	0.00	0.00%	0.29	0.29	8.34%
Sigalionidae	0	0.00	0.00%	0.14	0.14	8.33%	0.00	0.00	0.00%	0.00	0.00	0.00%
<i>Prionospio</i> ( <i>Minuspio</i> ) sp.	0	0.00	0.00%	0.00	0.00	0.00%	10.18	4.32	75.68%	0.29	0.18	8.34%
<i>Nereis</i> sp.	0	0.00	0.00%	0.00	0.00	0.00%	0.09	0.09	0.68%	0.00	0.00	0.00%
<i>Spiochaetopterus</i> sp.	0.1	0.10	2.78%	0.00	0.00	0.00%	0.00	0.00	0.00%	0.00	0.00	0.00%
Lumbrineridae	0	0.00	0.00%	0.00	0.00	0.00%	0.00	0.00	0.00%	0.14	0.14	4.17%
Cumacea	0	0.00	0.00%	0.00	0.00	0.00%	0.00	0.00	0.00%	0.14	0.14	4.17%
<i>Paraleptognathia</i> sp.	1.3	0.26	36.11%	1.00	0.85	58.33%	0.18	0.18	1.35%	0.86	0.40	25.02%
<i>Pseudotanaïs</i> sp.	0.2	0.13	5.56%	0.00	0.00	0.00%	0.00	0.00	0.00%	0.00	0.00	0.00%
Isopoda	0.7	0.40	19.44%	0.00	0.00	0.00%	0.00	0.00	0.00%	0.14	0.14	4.17%
Gammaridea	0	0.00	0.00%	0.00	0.00	0.00%	0.09	0.09	0.68%	0.00	0.00	0.00%
Nuculanoid bivalve	0.7	0.26	19.44%	0.29	0.18	16.67%	2.82	0.57	20.95%	1.57	0.57	45.87%
<i>Leptodrilus</i> sp.	0.00	0.00	0.00%	0.00	0.00	0.00%	0.09	0.09	0.68%	0.00	0.00	0.00%
<b>Total</b>	<b>3.60</b>	<b>1.56</b>	<b>1.00</b>	<b>1.71</b>	<b>1.46</b>	<b>1.00</b>	<b>13.45</b>	<b>4.68</b>	<b>1.00</b>	<b>3.43</b>	<b>1.87</b>	<b>1.00</b>
<b>No./m<sup>2</sup></b>	<b>934.92</b>	<b>404.39</b>		<b>445.20</b>	<b>378.68</b>		<b>3494.15</b>	<b>1215.40</b>		<b>890.40</b>	<b>486.73</b>	
BIOMASS = mg/38 cm <sup>2</sup> core												
<i>Heteromastus</i> sp.	0.060	0.041	6.10%	0.014	0.041	0.35%	0.000	0.000	0.00%	0.000	0.000	0.00%
Glyceridae	0.110	0.110	11.19%	0.000	0.011	0.00%	0.000	0.000	0.00%	0.000	0.000	0.00%
<i>Cossura</i> sp.	0.000	0.000	0.00%	0.013	0.009	0.31%	0.000	0.000	0.00%	0.023	0.012	6.11%
Sigalionidae	0.000	0.000	0.00%	3.341	2.339	80.93%	0.000	0.000	0.00%	0.000	0.000	0.00%
<i>Prionospio</i> ( <i>Minuspio</i> ) sp.	0.000	0.000	0.00%	0.000	0.000	0.00%	31.535	10.724	68.54%	0.011	0.012	3.03%
<i>Nereis</i> sp.	0.000	0.000	0.00%	0.000	0.000	0.00%	2.822	2.691	6.13%	0.000	0.000	0.00%
<i>Spiochaetopterus</i> sp.	0.106	0.106	10.78%	0.000	0.011	0.00%	0.000	0.000	0.00%	0.000	0.000	0.00%
Lumbrineridae	0.000	0.000	0.00%	0.000	0.000	0.00%	0.000	0.000	0.00%	0.020	0.019	5.34%
Cumacea	0.000	0.000	0.00%	0.000	0.000	0.00%	0.000	0.000	0.00%	0.023	0.021	6.11%
<i>Paraleptognathia</i> sp.	0.403	0.282	41.00%	0.134	0.291	3.25%	0.016	0.016	0.04%	0.033	0.020	8.78%
<i>Pseudotanaïs</i> sp.	0.008	0.008	0.81%	0.000	0.001	0.00%	0.000	0.000	0.00%	0.000	0.000	0.00%
Isopoda	0.155	0.086	15.77%	0.000	0.069	0.00%	0.000	0.000	0.00%	0.016	0.015	4.20%
Gammaridea	0.000	0.000	0.00%	0.000	0.000	0.00%	0.007	0.007	0.02%	0.000	0.001	0.00%
Nuculanoid bivalve	0.141	0.078	14.34%	0.626	0.405	15.16%	11.541	6.414	25.18%	0.249	0.116	66.41%
<i>Leptodrilus</i> sp.	0.000	0.000	0.00%	0.000	0.000	0.00%	0.048	0.046	0.10%	0.000	0.000	0.00%
<b>Total</b>	<b>0.983</b>	<b>0.711</b>	<b>100.00%</b>	<b>4.129</b>	<b>3.176</b>	<b>100.00%</b>	<b>46.013</b>	<b>15.470</b>	<b>100.00%</b>	<b>0.374</b>	<b>0.116</b>	<b>100.00%</b>
<b>mg/m<sup>2</sup></b>	<b>255.285</b>	<b>184.638</b>		<b>1072.190</b>	<b>824.878</b>		<b>11948.196</b>	<b>4017.095</b>		<b>97.117</b>	<b>30.122</b>	
<b>g/m<sup>2</sup></b>	<b>0.255</b>	<b>0.185</b>		<b>1.072</b>	<b>0.825</b>		<b>11.948</b>	<b>4.017</b>		<b>0.097</b>	<b>0.030</b>	

S.E. = standard error.

South Su inactive sediments. At most of the sites only a few species comprised most of the biomass in tube cores. Single large individuals (like the sigalionid at Solwara 1 inactive site) have the potential to dramatically increase between-sample variability; however, this accounts for only part of the high-biomass variability between cores.

### 3.1.2. Composition and diversity

Besides the previously noted density dominant species of tanaid and polychaete, other taxa present at the two study sites included polychaetes from 7 families, peracarid crustaceans (gammarid amphipods, cumaceans, isopods), and limpets (*Leptodrilus*) (Table 2). Although they were not counted as macrofauna, a single species of allogromid (protozoan – soft-bodied foraminiferan) was also very abundant in active South Su hydrothermal sediments. Despite overlap in major taxa, the South Su and Solwara 1 communities were different. Of the 9 species collected at Solwara 1 and the 10 species at South Su, only 4 species were collected in common (the tanaid *Paraleptognathia* sp., the nuculanoid bivalve, *Cossura* sp., and an isopod). Even within a site there were only 2–3 species in common between the active and inactive sites. Limited species overlap may be due to the low number of animals sampled.

Assemblage composition, assessed by multivariate analysis, differed between active and inactive sites (Global  $R = 0.315$ ;  $P = 0.001$ ) (ANOSIM: Solwara 1  $R = 0.211$ ;  $P = 0.031$ , SIMPER 81% dissimilarity; South Su  $R = 0.249$ ;  $P = 0.004$ ; SIMPER 71% dissimilarity), and between the two active sites (ANOSIM: Solwara 1 vs. South Su  $R = 0.658$ ;  $P = 0.001$ ; SIMPER 83% dissimilarity) but not between the two inactive sites (ANOSIM: Solwara 1 vs South Su  $R = 0.016$   $P = 0.304$ ). Macrofaunal composition in South Su active sediments is clearly distinct from the other sites, as reflected in MDS plots based on density (Fig. 2A) and biomass (Fig. 2B). Difference in densities of tanaids, nuculanoid bivalves, and *Prionospio* sp. accounted for most of the among-site differences (SIMPER). Within a site, among-core homogeneity was greatest in the South Su active sediments (48% similarity) and least in Solwara 1 inactive sediments (6% similarity).

Scoop samples, which are non-quantitative, contained a total of 664 individuals belonging to more than 31 taxa (some groups have not yet been identified to species) (Table 3). Thirty-seven percent of the individuals collected were tanaids (*Paraleptognathia* sp. and *Pseudotanaïs* sp.) and 24% were nuculanoid bivalves (Table 3). In general, dominant taxa in scoops (Table 3) resembled those in tube cores (Table 2). Tanaids were the most abundant group at the Solwara 1 sites (2 species) and nuculanoids (1 sp.) were most abundant at South Su. Isopods, found mainly at

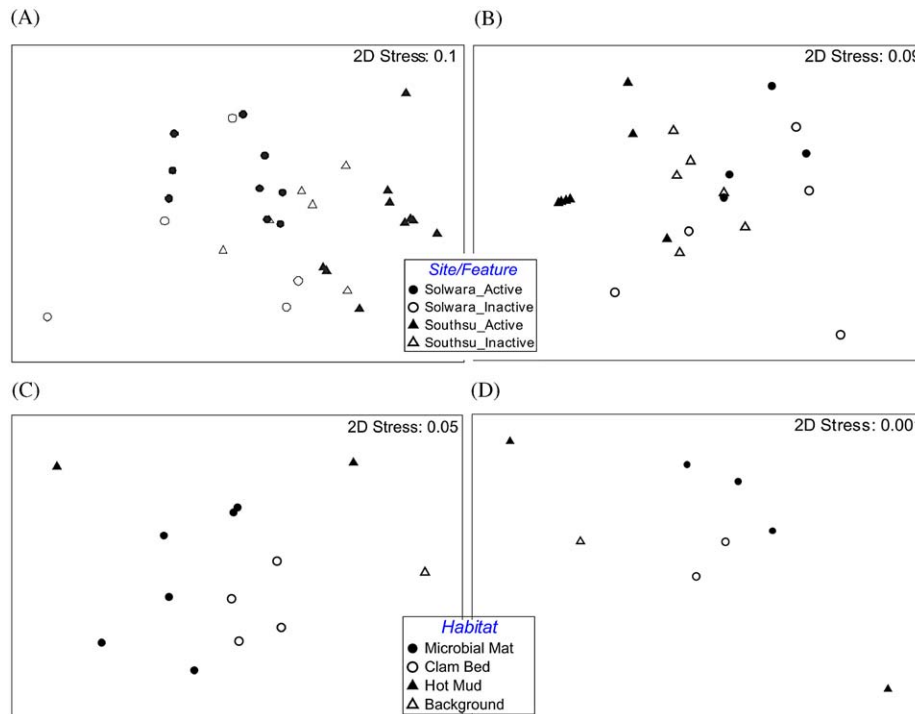
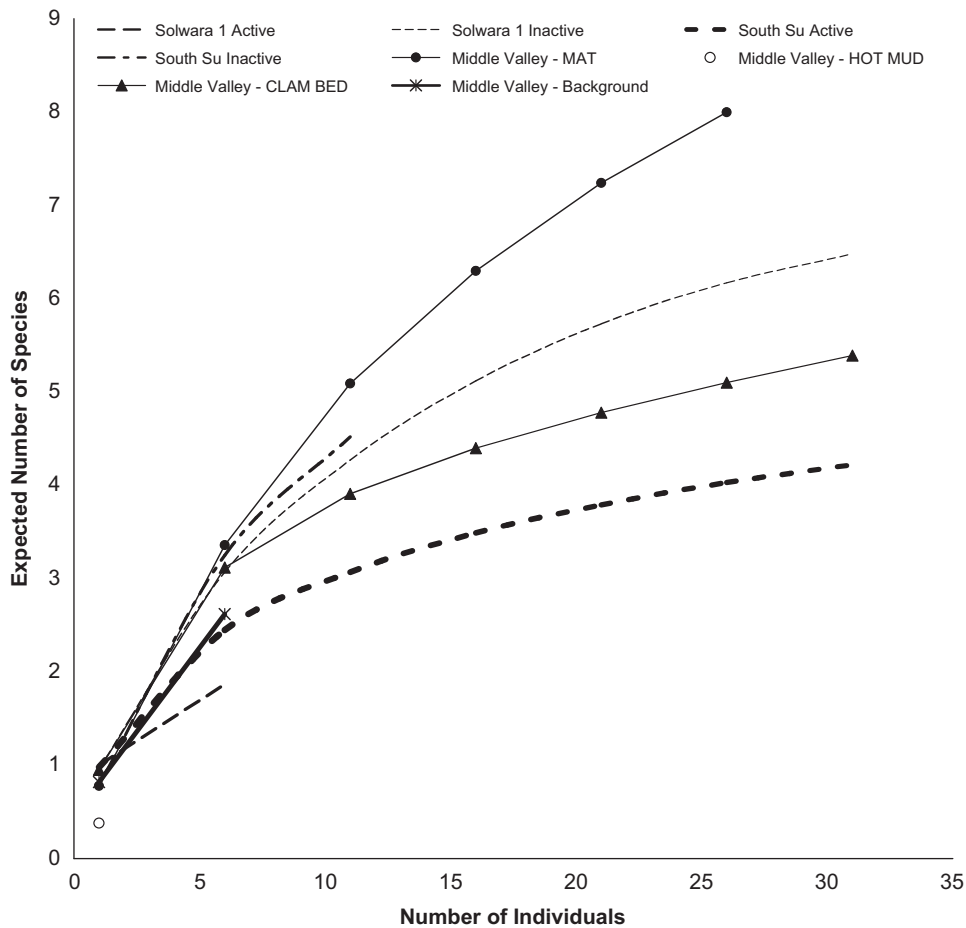


Fig. 2. MDS plots illustrating macrofaunal community differences for active and inactive sites at South Su and Solwara 1, Manus Basin (A) density (B) biomass and in three habitats at Middle Valley, Juan de Fuca vents (C) density (D) biomass.

Table 3  
Macrofauna in Manus Basin scoop samples (upper 10 cm of sediment).

Location	Solwara 1	Solwara 1	Solwara 1	Solwara 1	South Su	South Su	South Su	South Su	Total	
Activity	Active	Active	Inactive	Inactive	Active	Active	Inactive	Inactive		
Depth range (m)	1515		1510–1601		1312–1369		1334–1452			
n (no. of scoops)	2		6		2		6			
	SUM	Percentage (%)	SUM	Percentage (%)	SUM	Percentage (%)	SUM	Percentage (%)	Percentage (%)	
<i>Heteromastus</i> sp.	0	0.000	42	12.389	0	0.000	1	1.010	43	6.480
cf. <i>Scyphoproctus</i> sp.	0	0.000	0	0.000	1	0.541	0	0.000	1	0.150
<i>Nicomache</i> sp.	0	0.000	0	0.000	15	8.108	0	0.000	15	2.260
Glyceridae	0	0.000	1	0.295	0	0.000	3	3.030	4	0.600
<i>Cossura</i> sp.	0	0.000	17	5.015	0	0.000	14	14.141	31	4.670
Polynoidae	0	0.000	0	0.000	0	0.000	1	1.010	1	0.150
Sigalionidae	1	2.439	3	0.885	0	0.000	3	3.030	7	1.050
<i>Prionospio</i> (?) sp.	0	0.000	31	9.145	36	19.459	0	0.000	67	10.090
<i>Prionospio</i> ( <i>Minuspio</i> ) sp.	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Nereis</i> sp.	0	0.000	0	0.000	0	0.000	1	1.010	1	0.150
<i>Spiochaetopterus</i> sp.	3	7.317	0	0.000	0	0.000	0	0.000	3	0.450
Lumbrineridae	0	0.000	0	0.000	0	0.000	2	2.020	2	0.300
Hesionidae	0	0.000	1	0.295	0	0.000	0	0.000	1	0.150
Opheliidae	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
Phyllodocidae	0	0.000	0	0.000	0	0.000	2	2.020	2	0.300
Ampharetidae	2	4.878	3	0.885	6	3.243	2	2.020	13	1.960
Nemertinea	0	0.000	0	0.000	0	0.000	1	1.010	1	0.150
Cumacea	0	0.000	1	0.295	0	0.000	1	1.010	2	0.300
<i>Paraleptognathia</i> sp.	11	26.829	175	51.622	1	0.541	23	23.232	210	31.630
<i>Pseudotanais</i> sp.	3	7.317	24	7.080	1	0.541	8	8.081	36	5.420
Isopoda	3	7.317	23	6.785	0	0.000	1	1.010	27	4.070
Gammaridea	1	2.439	1	0.295	0	0.000	1	1.010	3	0.450
Lyssianasid gammarid	0	0.000	0	0.000	0	0.000	1	1.010	1	0.150
Phoxocephalid gammarid	0	0.000	0	0.000	0	0.000	1	1.010	1	0.150
Alvinocaridid decapod	1	2.439	0	0.000	0	0.000	0	0.000	1	0.150
Nuculanoid bivalve	2	4.878	14	4.130	120	64.865	26	26.263	162	24.400
<i>Cuspidaria</i> sp.	1	2.439	2	0.590	0	0.000	0	0.000	3	0.450
unid. bivalve	0	0.000	0	0.000	0	0.000	0	0.000	0	0.000
<i>Lepetodrilus</i> sp.	8	19.512	0	0.000	5	2.703	7	7.071	20	3.010
<i>Olgasolaris</i> sp.	5	12.195	0	0.000	0	0.000	0	0.000	5	0.750
Turritelid gastropod	0	0.000	1	0.295	0	0.000	0	0.000	1	0.150
<b>Total</b>	<b>41</b>		<b>339</b>		<b>185</b>		<b>99</b>		<b>664</b>	



**Fig. 3.** Comparative rarefaction curves illustrating macrofaunal diversity in four Middle Valley habitats (based on tube core collections) and inactive and active sediments from two Manus Basin settings (based on scoop collections).

Solwara 1, belonged to 3 species in 3 families: *Notoxenoides* sp. (Paramunnidae), *Janirella* sp. (Janirellidae), and *Ilyarachna* sp. (Munopsidae). All 3 are new to science.

Average species richness per tube core, evaluated via univariate analysis, was greatest at the Solwara 1 active site (2.50), intermediate at South Su active (1.90) and inactive (2.13) sites, and lowest at the Solwara 1 inactive site (1.0) (Table 7). Both diversity ( $H'$ ) and evenness ( $J'$ ) were highest in Solwara 1 active sediments ( $H' = 0.81, J' = 0.94$ ) while evenness was lowest in South Su active sediments ( $J' = 0.68$ ). Rank 1 dominance (R1D) is the proportion of the most abundant species, a parameter inversely correlated with  $H'$  and  $J'$ . R1D was highest in South Su active sediments (*Prionospio* (*Minuspio*) sp. 76%), and in Solwara 1 inactive sediments (*Paraleptognathia* sp. 58%), and slightly lower (but still high) in South Su inactive sediments (nuculanoid bivalves 46%) and active Solwara 1 sediments (*Paraleptognathia* sp. 36%). Rarefaction analyses conducted on pooled scoop samples revealed a slightly different trend from the per core analyses. Rarefaction diversity was greatest in Solwara 1 and South Su inactive sediments, and lowest at Solwara 1 and South Su active sites (Fig. 3).

### 3.1.3. Vertical distribution and feeding modes

Over 80% of the Manus Basin fauna were collected in the top 2 cm of the sediment column; this proportion was 100%, 82%, 85%, and 86% at the Solwara 1 active, Solwara 1 inactive, South Su active, and South Su inactive sites, respectively. In general,

macrofauna had deeper dwelling depths in the inactive than active Solwara 1 sediments, and in the active than inactive South Su sediments.

Feeding modes were assigned to species based on knowledge of congeners using Fauchald and Jumars (1979), information provided by systematists and on accumulated information acquired by the authors from 15 years of live-animal behavior and gut content observations and stable isotope (enrichment and natural abundance) studies conducted at bathyal depths. Despite the small number of species present, a diversity of feeding modes was represented in the hydrothermal sediments examined. The polychaetes include subsurface-deposit feeders (*Heteromastus* sp. and Lumbrineridae), surface-deposit feeders (*Prionospio* and *Cossura*), and carnivores (Sigalionidae, Nereididae, and Glyceridae). Most of the crustaceans are probably omnivorous (detritivores and scavengers), the limpet probably is a grazer, and the nuculanoid is a deposit feeder. In scoop samples the majority of the most common species were deposit feeders. These include *Heteromastus* sp., *Prionospio* sp., *Cossura* sp., the nuculanoid bivalve, and possibly the tanaids.

### 3.2. Middle Valley

#### 3.2.1. Density and biomass

A total of 428 individuals belonging to 37 taxa were collected in 14 tube cores sampling the Middle Valley active hydrothermal

sediments (Table 4). Only 12 individuals belonging to 6 taxa were collected in a single core from inactive background sediments (no cores were taken from the inactive clam bed). Macrofaunal densities at Middle Valley ranged from 10,010 to 19,984 ind. m<sup>-2</sup> depending on habitat (Table 4); these were 5–15 times higher than those in Manus Basin except in hot mud habitat, where densities were comparable. Total macrofaunal densities in active clam bed sediments (19,984 m<sup>-2</sup> ± 2689 ind m<sup>-2</sup>) were significantly higher than those in hot mud (1011 ± 664 ind m<sup>-2</sup>) but the microbial mat (8191 ± 2042 ind m<sup>-2</sup>) and hot mud faunal densities did not differ ( $\chi^2 = 13.24$ , df = 2,  $P = 0.0013$ ).

Clam bed sediments exhibited higher densities of *L. pachybranchiatus* ( $\chi^2 = 11.7$ ,  $P = 0.003$ , df = 2) and exogonid syllids ( $\chi^2 = 9.3$ , df = 2,  $P = 0.010$ ) than hot muds. Microbial mat sediments exhibited higher densities of Ampharetidae ( $\chi = 6.7$ , df = 2,  $P = 0.035$ ) and Hesionidae ( $\chi^2 = 9.3$ , df = 2,  $P = 0.003$ ) than in active clam bed sediments, and higher densities of Pycnogonida ( $\chi^2 = 6.8$ , df = 2,  $P = 0.034$ ) than in hot muds. Dorvilleidae ( $\chi^2 = 7.3$ , df = 2,  $P = 0.026$ ) and *Sphaerosyllis ridgiensis*

( $\chi^2 = 6.0$ , df = 2,  $P = 0.051$ ) also had highest densities in microbial mat sediments but *a posteriori* tests did not reveal significant differences with those in active clam bed or hot mud sediments.

Average macrofaunal biomass ranged from 1.34 g m<sup>-2</sup> in hot muds to 4.46 g m<sup>-2</sup> in active clam bed sediments with background (2.13 g m<sup>-2</sup>) and microbial mat-covered sediments (4.23 g m<sup>-2</sup>) having intermediate values (Table 5). There were no significant differences in biomass among habitats ( $\chi^2 = 5.11$ , df = 2,  $P = 0.077$ ). In each habitat a single species accounted for over 50% of the biomass: *Leitoscoloplos pachybranchiatus* in microbial mats (57%) and active clam beds (52%), *Depressigyra globulus* in hot muds (92% with shell), and tanaids (52%) in inactive background sediments. Only in the active clam beds did a second species, *Sphaerosyllis ridgiensis*, also exhibit high biomass (30% of total or 1 g m<sup>-2</sup>) (Table 5). Among individual taxa, only *Capitella* sp. exhibited significant biomass differences among habitats ( $\chi^2 = 5.833$ ,  $P = 0.054$ ); densities in active clam beds were higher than in microbial mats (Tukey's HSD,  $P = 0.048$ ).

**Table 4**  
Macrofaunal density and composition in microbial mat, active clam bed, hot mud, and inactive background sediments of Middle Valley determined from quantitative tube cores (32.2 cm<sup>2</sup>).

Habitat	Microbial mat			Hot mud			Active clam bed			Inactive sediments	
	6			4			4			1 <sup>a</sup>	
	Average	S. E.	Percent	Average	S. E.	Percent	Average	S. E.	Percent	Average	Percent
Taxon											
Unid. Spionidae sp.	0.00	0.00	0.00	0.75	0.75	23.08	0.00	0.00	0.00	0	0.00
<i>Prionospio</i> spp.	0.67	0.42	2.53	0.00	0.00	0.00	0.25	0.25	0.39	2	16.67
<i>Laonice</i> sp.	0.67	0.67	2.53	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
Unid. Dorvilleidae spp.	0.67	0.42	2.53	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
<i>Parourgia</i> nr <i>wolffi</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
<i>Ophryotrocha</i> n. sp. (dead dog)	1.67	1.05	6.33	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
<i>Ophryotrocha globopalpata</i>	1.17	0.75	4.43	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
<i>Ophryotrocha</i> sp. (shovelnose)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
Unid. <i>Ophryotrocha</i> sp.	0.17	0.17	0.63	0.50	0.50	15.38	0.00	0.00	0.00	0	0.00
Unid. Ampharetidae	3.67	2.32	13.93	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
Ampharetidae sp. 2	0.17	0.17	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
Ampharetidae sp. 1	0.17	0.17	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
<i>Amphysamytha galapagensis</i>	1.67	0.80	6.33	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
<i>Leitoscoloplos pachybranchiatus</i>	5.17	1.40	19.62	0.00	0.00	0.00	19.00	2.86	29.57	0	0.00
Maldanidae	0.33	0.21	1.27	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
<i>Sphaerosyllis ridgiensis</i>	4.00	3.61	15.19	0.00	0.00	0.00	23.50	8.37	36.58	0	0.00
Syllidae	2.00	1.26	7.60	1.25	1.25	38.46	1.25	1.25	1.95	0	0.00
Cirratulidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	8.33
Hesionidae	0.33	0.21	1.27	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
<i>Capitella</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.71	1.56	0	0.00
Capitellidae	0.67	0.42	2.53	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
Exogoninae	0.00	0.00	0.00	0.00	0.00	0.00	10.50	10.50	16.34	0	0.00
Oeonidae?	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.25	0.39	0	0.00
Paraonidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	8.33
Nerillidae	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.78	0	0.00
cf. Amphidurops	0.67	0.33	2.53	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
cf. Eulalia	0.00	0.00	0.00	0.00	0.00	0.00	4.75	4.42	7.39	0	0.00
<i>Hyalogyrina</i> sp.	1.00	0.63	3.80	0.00	0.00	0.00	1.25	1.25	1.95	0	0.00
<i>Depressigyra globulus</i>	0.00	0.00	0.00	0.50	0.50	15.38	0.00	0.00	0.00	0	0.00
<i>Provanna</i> sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.25	0.39	0	0.00
<i>Provanna</i> sp. 2	0.33	0.33	1.27	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
Unid. Buccinid gastropod	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.75	1.17	0	0.00
Unid. Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.78	0	0.00
Bivalves	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.25	0.39	0	0.00
Tanaidacea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5	41.67
Nemertean	0.00	0.00	0.00	0.25	0.25	7.69	0.25	0.25	0.39	2	16.67
Pycnogonid	1.17	0.40	4.43	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00
Unid. spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	8.33
<b>Total macrofauna per core</b>	<b>26.33</b>	<b>6.57</b>		<b>3.25</b>	<b>2.14</b>		<b>64.25</b>	<b>8.64</b>		<b>12</b>	
<b>No. macrofauna per m<sup>2</sup></b>	<b>8190.72</b>	<b>2042.26</b>		<b>1010.88</b>	<b>664.38</b>		<b>19,984.32</b>	<b>2688.82</b>		<b>2218.92</b>	
<b>No. species per core</b>	<b>7.50</b>	<b>1.67</b>		<b>1.50</b>	<b>1.00</b>		<b>5.50</b>	<b>0.87</b>		<b>6</b>	

<sup>a</sup> Core is 54.08 cm<sup>2</sup>.



**Table 5**

Biomass of Middle Valley macrofaunal assemblages in microbial mat, active clam bed, hydrothermal mud, and inactive habitats.

n (g/32.2 cm <sup>2</sup> core)	Microbial mat 3			Hot mud 2			Active clam bed 2			Inactive sediments <sup>a</sup> 1	
	Average	S.E.	Percentage (%)	Average	S.E.	Percentage (%)	Average	S.E.	Percentage (%)	Average	Percentage (%)
cf. <i>Capitella</i>	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0003	0.0001	1.95	0.0000	0.00
Unid. Cirratulidae	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0003	2.55
Unid. Paraonidae	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0002	1.56
<i>Laonice</i> sp.	0.0007	0.0007	5.15	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
<i>Prionospio</i> spp.	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0002	0.0002	1.22	0.0017	15.43
cf. <i>Amphidurops</i>	0.0011	0.0006	7.96	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
cf. <i>Eulalia</i>	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0013	0.0009	8.86	0.0000	0.00
<i>Leitoscoloplos pachybranchiatus</i>	0.0078	0.0040	57.41	0.0000	0.0000	0.00	0.0073	0.0001	51.15	0.0000	0.00
<i>Ophryotrocha globopalpata</i>	0.0014	0.0011	10.20	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
<i>Ophryotrocha</i> nov. sp.	0.0000	0.0000	0.00	0.0003	0.0003	6.40	0.0000	0.0000	0.00	0.0000	0.00
Unid. <i>Ophryotrocha</i> sp.	0.0000	0.0000	0.00	0.0001	0.0001	1.74	0.0000	0.0000	0.00	0.0000	0.00
<i>Amphysamytha galapagensis</i>	0.0010	0.0010	7.18	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Ampharetidae sp. 1	0.0002	0.0002	1.59	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Ampharetidae sp. 2	0.0004	0.0004	2.77	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Nerillidae	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0001	0.0001	0.45	0.0000	0.00
<i>Sphaerosyllis ridgiensis</i>	0.0005	0.0005	4.00	0.0000	0.0000	0.00	0.0043	0.0002	29.76	0.0000	0.00
Nemertean	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0001	0.0001	0.63	0.0017	15.01
Turbellarian	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Unknown Crustacea	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Cumacea	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Isopoda	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Amphipoda	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Decapoda	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Tanaidacea	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0058	51.68
<i>Sericossura</i> sp.	0.0003	0.0003	1.91	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
Bivalvia	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0004	0.0004	2.86	0.0000	0.00
<i>Provanna variabilis</i>	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0004	0.0004	3.07	0.0000	0.00
<i>Provanna</i> spp.	0.0002	0.0002	1.76	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.00
<i>Depressigyra globulus</i>	0.0000	0.0000	0.00	0.0039	0.0039	91.74	0.0000	0.0000	0.00	0.0000	0.00
Echiuroidea	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0000	0.0000	0.00	0.0015	13.45
<b>Total (g/32.2 cm<sup>2</sup> core)</b>	<b>0.0136</b>	<b>0.0089</b>		<b>0.0043</b>	<b>0.0043</b>		<b>0.0143</b>	<b>0.0025</b>		<b>0.0113</b>	
<b>g/m<sup>2</sup></b>	<b>4.23</b>	<b>2.77</b>		<b>1.34</b>	<b>1.34</b>		<b>4.46</b>	<b>0.76</b>		<b>2.13</b>	
<b>mg/m<sup>2</sup></b>	<b>4227</b>	<b>2771</b>		<b>1336</b>			<b>4456</b>	<b>764</b>		<b>2130</b>	

<sup>a</sup> Core is 54.08 cm<sup>2</sup>.

### 3.2.2. Composition and diversity

Middle Valley infauna was comprised largely of polychaetes (87%). Two species dominated the Middle Valley sediment fauna: the syllid polychaete *Sphaerosyllis ridgiensis* and the orbinid polychaete *Leitoscoloplos pachybranchiatus*, accounting, respectively, for 37% and 30% of the total infauna from active clam bed sediments, and 20% and 15% of the fauna from microbial mat sediments. Also common were multiple species of (other) syllid, ampharetid, and dorvilleid polychaetes (Table 4). In contrast, the fauna from inactive background sediments, based on admittedly limited sampling (1 core), contained only 33% polychaetes. Of the 12 individuals collected, 5 were tanaids, 2 were nemerteans, with 2 spionids (*Prionospio* sp.), 1 cirratulid and 1 paraonid polychaete, and 1 unidentified taxon (Table 4).

Assemblage differences, examined by multivariate analysis (Fig. 2C, D), were evident between macrofauna in active clam bed and hot mud sediments (ANOSIM,  $R = 0.466$ ;  $P = 0.029$ ) and between microbial mat and hot mud sediments ( $R = 0.656$ ;  $P = 0.005$ ), but not between active clam bed and microbial mat faunas ( $R = 0.274$ ;  $P = 0.081$ ). With only a single core from inactive, background sediments, no differences could be detected by the ANOSIM test between this habitat and the hydrothermally active habitats (all comparisons  $P > 0.14$ ), despite dissimilarities of >90% (SIMPER). MDS plots reveal considerable assemblage heterogeneity within as well as across habitats. Assemblage composition differences between habitats (determined by SIMPER) were largely a function of variations in orbinid (*Leitoscolo-*

*plos*), syllid (*Sphaerosyllis*), hesionid (*Amphidurops*), dorvilleid (*Ophryotrocha*), and phyllodocid (*Eulalia*) densities.

Scoop samples were sorted live in a non-quantitative mode, but provide useful qualitative insight (Table 6). Three scoops from microbial mat sediments netted 27 individuals from 10 species. Of these, 33% were dorvilleids, 22% were syllids, and 15% were hesionid polychaetes. A single active clam bed scoop yielded 29 individuals from 7 species. *Sphaerosyllis ridgiensis* and *L. pachybranchiatus* together comprised almost 70% of the individuals (Table 6). Samples from an inactive clam bed yielded only 6 individuals, but these were different from species in the live clam bed. They included the dorvilleid *Parourgia wolffi*, the alvinellid *Paralvinella palmiformis*, and a hesionid polychaete (Table 6).

Unexpectedly, the microbial mat habitat had the most diverse macrofauna, with the highest number of species collected per core ( $7.3 \pm 1.6$  on average) ( $\chi^2 = 7.8$ ,  $df = 2$ ,  $P = 0.020$ ), the highest  $H'(\log_e)$  (1.56), the greatest rarefaction diversity (Fig. 3) and the lowest Rank 1 dominance (19.6%) (Table 7). The top 3 taxa in microbial mat sediments, namely *L. pachybranchiatus*, *S. ridgiensis*, and an ampharetid species, comprised 49% of the total density. The active clam bed macrofauna was somewhat less diverse with  $5.5 \pm 0.86$  species per core. The Rank 1 dominant; *S. ridgiensis* (36.58% of the fauna) and the next 2 top taxa, including *L. pachybranchiatus* and another exogonid syllid, comprised 83% of all individuals collected. The hot mud habitat was the least diverse. Of the four hot mud cores collected, 2 contained no

**Table 6**  
Macrofauna collected in Middle Valley sediment scoops.

Habitat	Microbial mat			Total mat	Percent	Inactive clam bed	Active clam bed	Total clam bed	Percent
	2406	2410	2409						
Water depth (m)						2414	2400		
Site	Clam chowder	Dead dog	Dead dog			Dead dog	Clam chowder		
Spionidae sp.				0	0.00		1	1	2.86
Prionospio sp.				0	0.00		1	1	2.86
Parugia nr wolffi				0	0.00	2		2	5.71
Unid. Dorvilleidae spp.		3		3	11.11			0	0.00
Ophryotrocha globopalpata	2		2	4	14.81			0	0.00
Ophryotrocha sp. (shovelnose)			2	2	7.41			0	0.00
Unid. Ampharetidae		1		1	3.70			0	0.00
Amphysamytha galapagensis			Present	0	0.00			0	0.00
Leitoscoloplos pachibranchiatus		2	Present	2	7.41	Present	7	7	20.00
Syllidae	5	1	Present	6	22.22			0	0.00
Sphaerosyllis ridgiensis				0	0.00		17	17	48.57
Paralvinella palmaeformis				0	0.00	3		3	8.57
Hesionidae	3		1	4	14.81	1		1	2.86
Arabellidae?	1			1	3.70			0	0.00
Nemertinea				0	0.00		3	3	8.57
Unid. Gastropoda	3			3	11.11			0	0.00
Sericossura sp.			1	1	3.70			0	0.00
<b>Total Macrofauna</b>	<b>14</b>	<b>7</b>	<b>6</b>	<b>27</b>	<b>100.00</b>	<b>6</b>	<b>29</b>	<b>35</b>	<b>100.00</b>

**Table 7**  
Diversity measures for macrobenthos from (A) Manus Basin Papua New Guinea and (B).

n	Solwara 1 active 10		Solwara 1 inactive 7		South Su active 11		South Su inactive 7	
	Average	S.E.	Average	S.E.	Average	S.E.	Average	S.E.
<b>(A) Manus Basin</b>								
Species richness	2.50	0.27	1.00	0.31	1.90	0.23	2.13	0.52
N (no. individuals)	3.60	0.64	1.71	0.78	14.40	5.06	3.50	0.85
J'	0.94	0.01	1.00	0.00	0.68	0.04	0.92	0.04
ES(20)	2.50	0.27	1.00	0.31	1.90	0.23	2.13	0.52
H' (log <sub>e</sub> )	0.81	0.12	0.20	0.13	0.40	0.11	0.71	0.18
H' (log <sub>10</sub> )	0.35	0.05	0.09	0.06	0.17	0.05	0.31	0.08
Simpson's 1-Lambda	0.81	0.05	0.67	0.22	0.30	0.07	0.75	0.07
Rank 1 dominance (%)	36.11		58.33		77.08		42.86	
n	Microbial mat 6		Active clam bed 4		Hot mud 4		Inactive sediments <sup>a</sup> 1	
	Average	S.E.	Average	S.E.	Average	S.E.	Average	S.E.
<b>(B) Middle Valley</b>								
Species richness	7.33	1.56	5.50	0.87	1.25	0.75	5.00	
N	26.04	6.75	64.25	8.64	3.25	2.14	7.81	
J'	0.82	0.05	0.66	0.06	0.93	0.05	0.88	
ES(20)	6.27	1.11	3.81	0.24	1.25	0.75	5.00	
H' (log <sub>e</sub> )	1.56	0.25	1.10	0.11	0.41	0.24	1.41	
H' (log <sub>10</sub> )	0.68	0.11	0.48	0.05	0.18	0.10	0.61	
Simpson's 1-Lambda	0.75	0.08	0.60	0.05	0.65	0.01	0.82	
Rank 1 dominance (%)	19.62		36.58		38.46		45.45	

Middle Valley, Juan de Fuca. Values are average and standard error (S.E.) calculated per tube core.

<sup>a</sup> Core is 8.2cm diameter, all others are 6.4cm diameter.

individuals; the other two contained 13 individuals for an overall average of 1.25 species per core. These samples had the lowest  $H'(\log_e)$  (0.41) but highest  $J'$  (0.93). As in the active clam bed, Rank 1 dominant species in the hot mud habitat was *S. ridgiensis* (38%). The second most abundant taxon was an unidentified spionid (23%); *Ophryotrocha* sp. and *Depressigyra globulus* were tied for rank 3. Together these formed over 92% of the individuals; the only other taxon present was a nemertean (Table 4). Microbial mat species richness was higher than the hot mud richness, but active clam bed richness did not differ from either of the others.

( $\chi^2 = 7.83$ ,  $df = 2$ ;  $P = 0.0199$ ). One background (inactive) core contained 6 taxa with tanaids forming 41% of the total individuals; the tanaids have not been identified and hence it is unclear how many species they represent.

### 3.2.3. Vertical distribution and feeding modes

Vertical distribution of Middle Valley infauna was assessed for 3 microbial mat cores, 2 active clam bed cores, 1 hot mud, and 1 background core. Sixty-seven percent of all Middle Valley infauna

were collected in the top 2 cm of sediment. While replication is insufficient for statistical testing, habitat differences were evident. Over 86 percent of the 66 individuals from microbial mat habitat cores were found in the upper 2 cm; in contrast, only 56% of the 136 individuals in active clam bed cores were found in the upper 2 cm. Only 4 individuals were present in the hot mud sediments examined; 3 were in the upper 2 cm, 1 was present between 3 and 5 cm. Animals from one background core had vertical distributions similar to the active clam bed cores; 54% were present in the top 2 cm and 30% were present between 3 and 5 cm. Overall, animals from active clam bed cores had the deepest distribution, with almost 12% of individuals (16) present below 5 cm. In the other habitats only a single individual, a dorvilleid from a microbial mat core, was found below 5 cm.

The dominant taxa at Middle Valley appear to represent a range of feeding modes. Both syllids and dorvilleids have proventriculus or jaws capable of grabbing and cutting large bacteria or small metazoans, and it is assumed that they can

function as scavengers and bacterivores. The ampharetid and spionid polychaetes are surface-deposit feeders that may graze on mat bacteria or surface phytodetritus. The orbiniid polychaete is a subsurface-deposit feeder. The representation of infaunal feeding groups differed in each setting. Microbial mat sediments supported the greatest trophic diversity among infauna, with similar proportions (23–27%) of surface-deposit feeders, subsurface-deposit feeders, bacterivores and carnivores/omnivores. The hot muds had the greatest fraction of carnivores/omnivores (46%), intermediate numbers of bacterivores (31%), and surface-deposit feeders (23%) and had no subsurface-deposit feeders. The active clam bed and background sediments both had primarily carnivores/omnivores (64–65%) and few bacterivores. However, the clam bed had many subsurface-deposit feeders (32%) with no surface-deposit feeders, whereas the background community had surface-deposit feeders (27%) with no subsurface-deposit feeders. With respect to dwelling modes, the microbial mat, clam bed, and background sediments had mainly motile species (46%, 66%, and 64%, respectively) with fewer, similar numbers of tube builders

**Table 8**  
Stable isotope signatures of dominant taxa in hydrothermal sediments.

	<i>n</i>	$\delta^{13}\text{C}$	C St. error	$\delta^{15}\text{N}$	N St. error			
<b>Manus Basin</b>								
<b>Solwara 1 active</b>	<b>1</b>	<b>-16.46</b>		4.15				
<i>Paraleptognathia</i> sp.		-16.46		4.15				
<b>Solwara 1 inactive</b>	<b>6</b>	<b>-23.88</b>	<b>4.95</b>	<b>11.03</b>	<b>3.67</b>			
<i>Paraleptognathia</i> sp.	2	-20.14	1.32	14.63	2.01			
<i>Heteromastus</i> sp.	2	-25.22	3.15	9.40	0.71			
<i>Prionospio</i> sp.	2	-26.28	5.29	9.08	3.13			
<b>South Su active</b>	<b>16</b>	<b>-15.03</b>	<b>1.73</b>	<b>8.25</b>	<b>3.55</b>			
<i>Nereis</i> sp.	3	-15.92	1.60	9.29	2.18			
<i>Prionospio</i> sp.	3	-14.31	0.40	10.76	2.96			
cf. <i>Prionospio</i> sp.	2	-17.22	0.79	5.70	3.77			
Nuculanoidea	5	-14.57	0.51	7.08	1.00			
<i>Lepetodrilus</i> sp.	2	-13.76	0.81	8.44	1.55			
<b>South Su inactive</b>	<b>10</b>	<b>-19.76</b>	<b>3.90</b>	<b>12.89</b>	<b>5.69</b>			
<i>Cossura</i> sp.	1	-20.98		24.49				
<i>Heteromastus</i> sp.	2	-22.85	0.31	12.15	0.72			
Nuculanoidea	2	-22.09	0.78	17.83	1.28			
<i>Lepetodrilus</i> sp.	3	-14.5	1.50	7.17	0.31			
<i>Paraleptognathia</i> sp.	2	-21.63	0.50	11.45	0.19			
<b>Middle Valley averages<sup>a</sup></b>								
Inactive sediment	10	-22.12	1.09	6.59	1.65			
Active clam bed	54	-26.01	0.86	-1.13	1.71			
Inactive clam bed	4	-28.41	1.39	-0.7	0.77			
Microbial mat	77	-29.54	2.37	-0.57	0.59			
<b>Key Middle Valley taxa</b>								
	<b>Microbial mat</b>		<b>Active clam bed</b>		<b>Inactive clam bed</b>		<b>Background (inactive sediments)</b>	
Average values	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Leitoscoloplos pachybranchiatus</i>	-25.95	0.10	-27.69	-0.11			-24.69	4.68
<i>Sphaerosyllis ridgensis</i>	-26.88	1.40	-25.73	0.46			-21.56	2.52
<i>Prionospio</i> sp.	-29.87	-0.23	-26.06	4.11	-30.64	0.56	-18.78	11.02
Tanaidacea							-24.34	4.79
Ampharetidae								
<i>Ophryotrocha</i> sp. (dead dog)	-23.71	-4.50	-26.63	-10.57				
<i>Amphysamytha galapagensis</i>	-25.78	0.23	-22.53	0.52				
<i>Provanna variabilis</i>			-29.42	-0.61				
Buccinid gastropod	-36.33	-1.83						
Capitellidae	-49.43	0.63						
<i>S. grasslei</i> (Hesionidae)	-26.00	-1.65						
<i>Nicomache</i> sp. (Maldanidae)	-32.62	0.08						
Pycnogonida	-20.52	2.25						
Nematoda	-27.92	-2.74	-24.04	-1.69	-28.72	-0.57	-21.25	9.95
Hesionidae					-25.87	-2.10		
<b>Microbial mat (orange)</b>	<b>-27.01</b>	<b>-4.33</b>						

<sup>a</sup> Species averages were averaged.

and burrowers. The hot muds had only motile (77%) and tube-building species (23%) with no burrowers.

### 3.3. Stable isotope signatures and nutrition

Species from the active sites at Manus Basin typically had average  $\delta^{13}\text{C}$  signatures between  $-13\text{‰}$  and  $-17\text{‰}$ . These values were heavier than those of species from inactive sites, which, with one exception, had  $\delta^{13}\text{C}$  signatures between  $-26\text{‰}$  and  $-20\text{‰}$  (Table 8, Fig. 4). The exception was the limpet *Lepetodrilus fucescens*, which had a vent-type  $\delta^{13}\text{C}$  signature ( $-14.5\text{‰}$ ). There were no site-specific isotopic differences detected between Solwara 1 and South Su ( $\chi^2 = 7.66$ ,  $df = 3$ ;  $P = 0.054$ ). Among all Manus Basin between-site comparisons, only Solwara 1 inactive and South Su active signatures were different (Tukey's HSD) (Table 8). The relative diet homogeneity across species within a site spanned taxa known to be surface-deposit feeders (e.g., *Prionospio*), subsurface-deposit feeders (e.g., *Heteromastus*), carnivores or detritivores (*Paraleptognathia*), and omnivores (*Nereis*). Average  $\delta^{15}\text{N}$  signatures did not differ among the 4 regions, despite the fact that active site faunal values (7–8‰) appeared lower than inactive site faunal values (11–12‰) ( $\chi^2 = 6.56$ ,  $df = 3$ ,  $P = 0.087$ ).

Despite possible differences in feeding modes, most of the dominant taxa at the different Middle Valley settings (active clam bed, inactive clam bed, and microbial mat) had similar  $\delta^{13}\text{C}$  signatures, consistent with consumption of chemosynthetic, sulfur-oxidation-based nutrition (Fig. 4). Average  $\delta^{13}\text{C}$  across all species in each habitat ranged from  $-26\text{‰}$  to  $-29.5\text{‰}$  (Table 8, Fig. 4), values similar to values measured for the sulfide-oxidizing bacteria in the microbial mats ( $-27.87\text{‰}$  and  $-26.14\text{‰}$ ). Only the microbial mat faunal average  $\delta^{13}\text{C}$  differed significantly from background values ( $\chi^2 = 8.83$ ,  $df = 3$ ,  $P = 0.032$ ). In contrast, all of the vent habitats had macrofauna with average  $\delta^{15}\text{N}$  values significantly lighter (average =  $-1.13\text{‰}$  to  $-0.57\text{‰}$ ) than background values ( $6.59 \pm 1.65\text{‰}$ ) ( $\chi^2 = 11.29$ ,  $df = 3$ ,  $P = 0.010$ ). The mat-forming bacteria  $\delta^{15}\text{N}$  values ( $-4.43$ ,  $-4.23\text{‰}$ ) are about 3–4 per mil lighter than the vent infauna, consistent with animal consumption of these microbes. Many of the animals sampled are surface or subsurface-deposit-feeding polychaetes. For some, such as the spionid *Prionospio* sp. and nematodes, variation in the

isotope signatures reflects changing food availability in background vs. vent sediments (Table 8). However, others, such as *Sphaerosyllis ridgiensis*, have similar  $\delta^{13}\text{C}$  values in active and background habitats, suggesting that they have selective ingestion or selective assimilation of nutritional sources within sediments.

## 4. Discussion

### 4.1. Active vs. inactive sediments

We hypothesized initially that heterotrophic macrofaunal assemblages at hydrothermally active habitats should exhibit higher densities and biomass, greater dominance, lower species richness, extensive deposit feeding, and greater isotopic evidence for chemosynthetic food sources than those at inactive sites. However, our results suggest no consistent enhancement of density or biomass by hydrothermal activity. In Manus Basin, South Su active sediments exhibited enhanced densities and biomass relative to inactive sites, but Solwara 1 active sediments did not. In Middle Valley, active clam bed sediments exhibited enhanced densities and biomass, whereas hot mud sediments had reduced densities and biomass relative to the other active and background habitats. The more extreme temperature and sulfide conditions of the most active sites appear to reduce rather than enhance abundance and biomass. Similarly, diversity did not vary with sediment activity in a consistent manner. The sites with highest abundances (South Su active, Middle Valley active clam bed) exhibited low evenness ( $J'$ ), while the low-density habitats, Solwara 1 inactive and Middle Valley hot mud sediments, had the lowest species richness and diversity indices (Table 7). A range of feeding modes was represented in active and inactive sediments. Many of the abundant species in Manus Basin sediments were deposit feeders, particularly at South Su, but the importance of deposit feeding did not appear to vary with sediment activity. Deposit feeding was less prevalent in Middle Valley, where carnivory and bacterivory appeared to be more common. With respect to chemosynthetic food sources, we observed  $\delta^{13}\text{C}$  signatures indicative of chemosynthetic food sources at all of the Manus Basin and Middle Valley active sites, but also among a few individuals from Solwara 1 inactive sediments and Middle Valley inactive clam bed and background sites (Table 8). These results suggest that hydrothermal influence can extend to some components of inactive sediments and thus our original hypothesis was not fully supported.

### 4.2. Relationship to other sedimented vents

#### 4.2.1. Densities and biomass

Most past studies of hydrothermal sediment macrofauna at bathyal depths have been conducted by Fred Grassle and Rose Petrecca in the eastern Pacific Ocean. The macroinfauna of hydrothermal vent sediments have been described from the Galapagos Mounds (2700 m), in Guaymas Basin in the Gulf of California (1800–2000 m), and in Escanaba Trough on Gorda Ridge (3250 m), in addition to the sites described here (Table 9). All of the eastern Pacific hydrothermal sediment sites are deeper than those sampled at Solwara 1 and South Su in the Manus Basin, yet they exhibited higher macrofaunal densities than found in 3 of the 4 sampled Manus Basin sites (Table 9). Only in hot muds (up to  $94^\circ\text{C}$ ) from Middle Valley were macrofaunal densities as low as those at Solwara 1 and South Su inactive sites ( $< 1000 \text{ ind. m}^{-2}$ ). The South Su active site ( $3500 \text{ ind. m}^{-2}$ ) resembled the Middle Valley, Escanaba and Guaymas vent sediments in having somewhat higher densities (Table 9), and in exhibiting dominance by a few species, with rare species being absent. The lower Manus

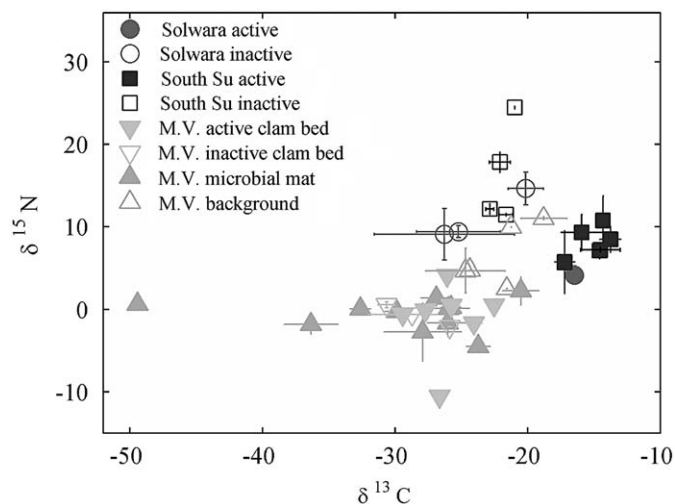


Fig. 4. Dual isotope plot showing stable isotope signatures of macrofaunal species collected from active and inactive hydrothermal sediments at two sites in Manus Basin, and from active and inactive (dead) clam beds, microbial mats and non-vent sediment in Middle Valley (M.V.), Juan de Fuca region. Each point reflects the average and standard error for a single species in a particular setting.

**Table 9**  
Summary of macrobenthos community structure in bathyal Eastern Pacific hydrothermal vent sediments.

Location	Habitat	Region	Depth (m)	No macrofauna/ m <sup>2</sup>	Rank 1 dominance (density) (%)	Dominant taxa	Other taxa	Diversity patterns	Reference	
<b>Escanaba Trough</b>	Hydrothermal sediment+Near background	NE Pacific	3254	18,709	<8	Ampharetidae, Orbinidae, Spionidae	Nuculanoid, <i>Provanna</i> , <i>Neolepetopsis</i>		Grassle and Petrecca (1994)	
	Near wood			16,932		Dorvilleidae, Hesionidae, <i>Provanna</i>			Grassle and Petrecca (1994)	
	Mounds		3274	Cirratulidae, Spionidae, Paraonidae		Similar to ambient	Grassle and Petrecca (1994)			
<b>Gorda Ridge</b>			3200			<i>Calypptogena phaseoliformis</i>	No species in common with non-vent sediments	Petrecca and Grassle (1987)		
<b>Guaymas Basin</b>	Combined hydrothermal Petroleum sed clam bed	Gulf of CA		3722–5443 1200–1900		Hesionidae, Dorvilleidae Nuculanid bivalves <i>Amphisamya</i> (Ampharetidae)			Petrecca and Grassle (1990) Petrecca and Grassle (1990) Petrecca and Grassle (1990)	
	Microbial mat									
	Background								3270	
<b>Galapagos Mounds</b>	Sulfidic sediments		2700			<i>Aurospio</i> (Spionidae)	Reduced species richness and density relative to non-vent	Grassle et al. (1985)		
<b>21°N, EPR</b>	Hydrothermal sediments		2717			<i>Anobothrus</i> sp. (Ampharetidae) Thyasiridae	Low diversity	Grassle et al. (1985)		
<b>Middle Valley, Juan de Fuca</b>	Bacterial mat	NE Pacific	2406–2414	8191 ± 2042	14	<i>Leitoscoloplos pachybrachiatus</i> , Dorvilleidae spp., Ampharetidae spp.	Dorvilleidae, Gastropoda		This study	
	Hot mud			1011 ± 664	50	<i>Sphaerosyllis ridgiensis</i> , Spionidae	Exogoninae		This study	
	Clam bed			19,984 ± 2689	34	Orbinidae, Syllidae	<i>Prionospio</i> sp.		This study	
	Background			2219		Tanaidacea			This study	
<b>Solwara 1, Manus Basin</b>	Active	Papua New Guinea	1511–1575	934	36	<i>Paraleptognathia</i> (Tanaidacea)	Isopoda, Nuculanoid bivalve, <i>Heteromastus</i>		This study	
	Inactive		1504–1634	445	58	<i>Paraleptognathia</i> (Tanaidacea)	Nuculanoid bivalve		This study	
<b>South Su, Manus Basin</b>	Active	Papua New Guinea	1312–1369	3740	77	<i>Prionospio</i> ( <i>Minuspio</i> )	Nuculanoid bivalve		This study	
	Inactive		1356–1452	908	43	Nuculanoid bivalve	<i>Paraleptognathia</i> sp., <i>Prionospio</i> sp.		This study	

Basin densities may be due to (a) more oligotrophic conditions in overlying waters off Papua New Guinea than in the eastern Pacific regions, which are upwelling areas (Herring, 2002) and/or (b) lesser hydrothermal activity and associated microbial food availability than in the sampled sediments of Guaymas, Escanaba Trough, and Middle Valley. Macrofaunal density in Middle Valley active clam beds was high (19,984 ind.m<sup>-2</sup>), comparable to those in hydrothermal sediments at Escanaba Trough (Grassle and Petrecca, 1994) and to densities in clam bed sediments of Hydrate Ridge methane seeps, located closer to the Oregon margin (Levin et al., in press). Middle Valley microbial mat densities were one quarter to one third lower (8190 ind.m<sup>-2</sup>), comparable to those in Guaymas hydrothermal sediments (Petrecca and Grassle, 1990) (Table 9).

The average macrofaunal biomass (wet weight) of Manus Basin sites varied greatly (0.1–12 g m<sup>-2</sup>), and encompassed the range found at Middle Valley (1.3–4.5 g m<sup>-2</sup>). Unfortunately, no comparable biomass data are available for hydrothermal sediment infauna from sites other than those studied here.

#### 4.2.2. Composition

Despite density differences between the Manus Basin, Middle Valley and the other eastern Pacific hydrothermal sediments, there were some similarities observed in taxonomic composition, most notably the abundance of the genus *Prionospio* (*Minuspio*) (South Su active, Middle Valley active clam bed and microbial mat, Escanaba Trough) and nuculanoid bivalves (most sites at Manus Basin, Escanaba Trough, Guaymas Basin) (Table 9). The genus *Prionospio* (*Minuspio*) is also reported from hydrothermal vents in the Indian Ocean and E. Pacific Ocean (21°N). This widespread and speciose genus is very abundant in hypoxic sediments on the Oman margin (Levin et al., 2000), and in polluted harbors, but even occurs in N. Atlantic abyssal plains (Levin and Gooday, 2003). Some specimens of *Laonice* sp., a genus in the “*Prionospio* complex” (Sigvaldadottir, 1998), were present in microbial mat and inactive background sediments at Middle Valley. *Prionospio* sp. was a dominant colonizer in organically enriched sediments at 2160 m in the Bay of Biscay (Desbruyeres et al., 1980). The limpet *Lepetodrilus* sp., typically attached to hard substrates or siboglinid tubes, was present at Manus Basin but not at Middle Valley. The genus *Lepetodrilus* is broadly distributed in eastern Pacific hydrothermal vents (Desbruyeres et al., 2006). This taxon and the gastropod *Olgasolaris* sp. are likely to be associated with sulfide precipitates. Nuculanoid bivalves, which comprised 17–43% of the fauna at the four Manus Basin sites, are abundant in Guaymas Basin hydrothermal clam bed sediments (*Nuculana* sp.) as well (Petrecca and Grassle, 1990). The maldivian polychaete *Nicomache* sp., common in South Su active scoop sediments, is characteristic of vent environments and some methane seeps (e.g., Florida Escarpment) globally (Desbruyeres et al., 2006).

Peracarid crustaceans (mainly tanaids and isopods) appeared more abundant in the Manus Basin than in other hydrothermal sediments, but related taxa (*Pseudotanaid* species and *Leptognathia* spp.) are reported from Escanaba Trough. In Middle Valley, a small, unidentified species of tanaid was the only crustacean collected, and comprised half of the fauna in the single inactive background core sampled. Orbiniid, ampharetid, dorvilleid, and hesionid polychaetes were abundant in Middle Valley and in other eastern Pacific hydrothermal sediments (Table 9). These taxa were less common, rare or absent in Manus Basin. However, we acknowledge that the spatial coverage, habitat coverage and number of individuals sampled in the Manus Basin are insufficient to assess taxon absence, or to enable a complete comparison.

A broad comparison of composition at the family level (Fig. 5) suggests that Manus Basin assemblages are distinct from those at

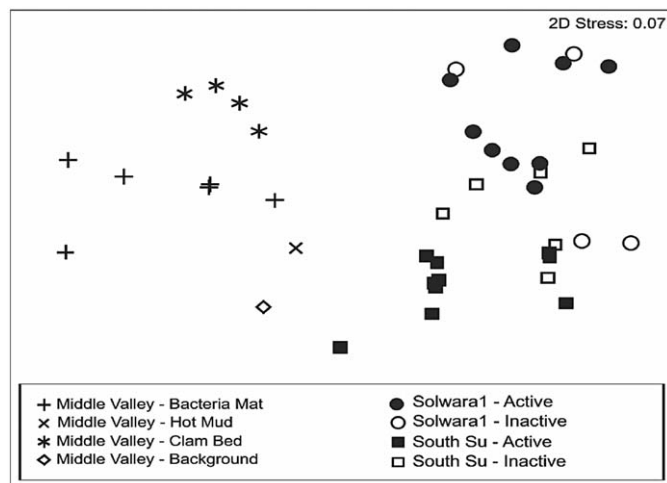


Fig. 5. MDS plots illustrating macrofaunal community composition based on density determined at the family level, for active and inactive sites at South Su and Solwara 1, Manus Basin and for Middle Valley habitats. Six outlier Manus Basin core samples (four from Solwara 1 samples and two from South Su) are omitted from the plots, due to zero or low density.

Middle Valley (ANOSIM, Global  $R = 0.709$ ,  $P = 0.001$ ). At the habitat level, macrofauna in the Middle Valley clam bed and microbial mat habitats differ from macrofauna at all of the Manus Basin sites (ANOSIM all  $P < 0.05$ ), but the Middle Valley background and hot mud assemblages do not ( $P = 0.09–0.18$ ). Higher-level differences between regions are largely due to greater abundances of Syllidae, Orbiniidae, Dorvilleidae, and Ampharetidae in hydrothermal sediments of Middle Valley and of tanaids, nuculanoid bivalves, and spionids in Manus Basin (SIMPER). The shared presence of spionids (hot mud) and tanaids (background) at Middle Valley and Manus Basin contributes to those assemblage similarities. However, even with some similarities at the genus and family level, there appears to be no overlap in species composition between the two hydrothermal sites studied here. To our knowledge, all of the Manus Basin macrofauna sampled appear to be new to science. This is not altogether surprising given this is the first time such a detailed study has been conducted in this previously unstudied part of the seafloor.

#### 4.2.3. Diversity

Reduced diversity (relative to inactive background sediments) and high dominance are characteristic of all active hydrothermal sediments sampled thus far (Table 9). Overall rarefaction diversity was lowest at the two hydrothermal active sites in Manus Basin, intermediate in the Solwara 1 inactive and Middle Valley clam bed sites, and highest at the South Su inactive and Middle Valley microbial mat sites (Fig. 4). It has been proposed that sulfide-oxidizing microbes detoxify sediments by removing H<sub>2</sub>S, possibly contributing to broader species diversity through facilitation (Gallardo, 1968). Macrofauna in the Manus Basin active and inactive sites hydrothermal sediments had relatively high dominance (R1D = 36–76%). Rank 1 dominance at Middle Valley was slightly lower, ranging from 14% to 38% in the different habitats. R1D data from both sites suggest effects of hydrothermal influence via food and stress; this effect appears greatest at the South Su active site. The number of species expected from a collection of 100 individuals ( $E_{S100}$ ) in Manus Basin ranged from 6 (South Su Active) to 20 (South Su Inactive). Similar  $E_{S100}$  values were observed in Middle Valley data pooled for microbial mats (18.4) and clam beds (10.7). These are comparable to or higher than diversity recorded at Guaymas Basin and Escanaba Trough

hydrothermal sediments (Grassle and Petrecca, 1994; Petrecca and Grassle, 1990). Wood falls in the vicinity of other vents appear to support slightly higher diversity (Petrecca and Grassle, 1990). It is not possible to draw comparisons with Solwara 1 active and Middle Valley hot mud results because the numbers of individuals collected were insufficient to calculate  $Es_{100}$ .

#### 4.3. Relation to non-vent fauna

Most of the literature on western South Pacific non-vent infauna is for deeper sites (>2000 m) (Alongi, 1992) or focuses on metazoan and protozoan meiofauna (Shirayama, 1984a, b; Alongi, 1987, 1990; Alongi and Pichon, 1988). Use of a 0.5 mm mesh yielded 736 macrofaunal ind. m<sup>-2</sup> and biomass of 2.44 g m<sup>-2</sup> at 695 m on the Papuan Barrier Reef Slope (roughly 11°S 151°E), and 120 individuals m<sup>-2</sup> and 0.33 g m<sup>-2</sup> at 1454 m on the Coral Sea Plateau (roughly 14°S 146°E), south of Papua New Guinea (Alongi, 1992). The Coral Sea density (from depths comparable to those sampled in the present study) was 4–30 times lower than the South Su and Solwara 1 densities, but the biomass was of the same order of magnitude at 3 out of 4 sites. Notably, Shirayama (1983) reported ~1000 ind m<sup>-2</sup> and biomass of 1–2 g m<sup>-2</sup> at 2100–2200 m on the Solomon Rise (roughly 0–3°S 159°E). In general, density is more sensitive to sieve size than is biomass (Gage et al., 2002). Our use of a 0.3-mm mesh may contribute to (but probably does not fully account for) the observation of higher densities in the Manus Basin hydrothermal sediments. Greater food supply associated with hydrothermal activity is also likely to elevate densities compared to inactive sites.

While no quantitative background (non-vent) macrofaunal data are available for 2400 m on the Oregon margin, densities of Middle Valley microbial mat assemblages are comparable to those reported for other bathyal Pacific locations >1000 m (5000–10,000 ind. m<sup>-2</sup>; Smith and Demopoulos, 2003) and to Oregon margin macrofaunal densities at 1200 m (5200 ind m<sup>-2</sup>; Levin et al., unpublished). The clam bed macrofaunal densities are about three times higher and probably reflect enhanced food supply, while the hot mud sediments, with temperatures of 37 °C at the surface and 94 °C at 5 cm, are much lower and almost certainly reflect the effects of heat and/or metal stress.

Many of the genera identified in this study are commonly found in non-vent, deep-sea sediments. For example, *Heteromastus (filiformis)* is a dominant taxon from 1100 to 1437 m, and the nuculanoid *Deminucula cancellata* is dominant from 1707 to 1815 m on the New England margin (Rowe et al., 1982). *Cossura* sp., present only in inactive Manus Basin hydrothermal sediments, is reported broadly from continental margins around the world, including many oxygen-minimum zones (Levin, 2003). *Leitoscoloplos*, *Sphaerosyllis*, and *Ophryotrocha* are also examples of widespread, speciose genera that can be found in enriched or sulfidic shallow-water settings (e.g., estuaries and harbors) as well as at vents. In contrast, the ampharetid *Amphisamytha galapagensis*, and the gastropods *Provanna*, *Depressigyra*, and *Hyalogyrina* are all specialists in vent or seep environments. Thus, evolutionarily there appears to be a mix of vent specialists and non-specialists inhabiting hydrothermal sediments. However, the abundant Middle Valley species, even those from widespread genera, appear to be associated with active hydrothermal vents as reported in Desbruyeres et al. (2006).

#### 4.4. Nutrition of macrobenthos at hydrothermal vents

On average Manus Basin macrofauna exhibited distinct isotopic patterns, with heavier  $\delta^{13}C$  signatures at the Solwara 1 and South Su active sites, than found in the inactive Manus Basin

sites, in the macrofauna of Middle Valley, or in typical background fauna fueled by photosynthesis (Fig. 4). The majority of macrofaunal taxa at the Manus active sites had  $\delta^{13}C$  signatures of –16‰ to –14‰, consistent with TCA-cycle C fixation mechanisms (Sievert et al., 2007a, b). Similar values are reported for siboglinid tube worms (*Ridgeia piscesae*) and its predators at Juan de Fuca Ridge (near Middle Valley; Bergquist et al., 2007), but were not observed for any of the species collected in the hydrothermal sediments of Middle Valley (Fig. 4, Table 8). The  $\delta^{13}C$  values reported for larger, epibenthic organisms (megafauna) by Erickson et al. (this issue) from Solwara 1 active (–29.7‰ to –19.9‰) and inactive (–25.8‰ to –17.2‰) sites resembled values we obtained for macrofauna at the Manus Basin inactive sites and at Middle Valley (Table 8). The South Su inactive site macrofauna had  $\delta^{13}C$  signatures (–23‰ to –19‰), suggestive of a phytoplankton-based diet, although without  $\delta^{34}S$  data it is difficult to rule out chemosynthetic food sources (Erickson et al., this issue). In contrast, most Middle Valley species in hydrothermal sediments had isotopically light  $\delta^{13}C$  (–26‰ to 29‰) consistent with the consumption of sulfide-oxidizing bacteria. Two deep-dwelling, deposit-feeding polychaetes, the maldanid *Nicomache* sp. and a capitellid had much lighter  $\delta^{13}C$  values than the other species (–32‰ and –49‰, respectively), possibly reflecting contributions to the C pool from methane and associated microbial consortia.

The  $\delta^{15}N$  signatures were substantially lighter (by 4–10‰) among macrofauna at Middle Valley hydrothermal sites than in Manus Basin (Fig. 4, Table 8). This may reflect consumption at a lower trophic level, with Middle Valley consumers feeding directly on primary producers, bacteria that fix carbon and local nitrogen, and Manus Basin consumers feeding on recycled organic matter. Exceptionally light  $\delta^{15}N$  values were observed among the dorvilleid *Ophryotrocha* sp. (Table 8), suggesting they have a specialized food source. Bergquist et al. (2007) recorded similar light  $\delta^{15}N$  values for *O. globopalpata* and *Paralvinella* spp. collected from tube worm (*Ridgeia*) aggregations at Juan de Fuca Ridge. Van Dover and Fry (1994) documented depleted  $\delta^{15}N$  values in megafauna and microbes from Gorda Ridge and Juan de Fuca vent sites. However, except for *Provanna variabilis*, they did not document species with the light  $\delta^{13}C$  values (<–25‰) characteristic of Middle Valley infauna. Thus, the nutritional sources of the animals in hydrothermal sediments at Middle Valley appear to be distinct from those associated with sulfide deposits at nearby Juan de Fuca Ridge.

Overall the hydrothermal sediments in this study supported taxa with 3 distinct nutritional patterns as reflected in heavy (TCA cycle), intermediate (phytoplankton-based) and light  $\delta^{13}C$  (sulfide oxidation- or anaerobic methane oxidation-based) signatures. The latter two types of signatures are common among infauna at methane seeps on the Aleutian, Oregon, and California margins (Levin and Michener, 2002; Levin and Mendoza, 2007), on whale falls (Goffredi et al., 2008) and in some hydrothermal sediments (Van Dover and Fry, 1994), but the heavy signatures appear unique to hydrothermal settings. These signatures do not appear related to the mechanical mode of feeding (e.g., surface deposit, subsurface deposit, grazer), but rather reflect the C fixation pathways of the organic matter assimilated by the organisms. Deposit feeders, filter feeders, grazers and carnivores all appear to have similar signatures within a specific habitat in Middle Valley and Manus Basin sediments; these signatures change with the microbial food sources in different habitats.

We acknowledge the likelihood that individual animal isotope values reflect diets including a combination of food sources. However, the available source signatures at the base of the food chain are not sufficiently constrained to permit the application of mixing models for either the Manus Basin or Middle Valley systems. This remains a target for future research.

#### 4.5. Hydrothermal sediment communities in the context of mining

Over the past decade, with a changing economic landscape, mining at hydrothermal vents has gone from a distant possibility to a likely reality (Smith et al., 2008). While mining is currently in the exploration stage, Nautilus has commissioned an environmental impact assessment for a potential seafloor mining project at Solwara 1 ([www.cares.nautilusminerals.com](http://www.cares.nautilusminerals.com)). This work has enabled scientific studies, such as this, to gain better understanding of hydrothermal environments that may otherwise remain unstudied. Exploratory activities by Neptune Minerals are also occurring to evaluate the potential of seafloor mining in the Kermadec region further south. Forms of mining disturbance could include removal of substrate and associated organisms, physical disruption of sediment, plume presence and deposition, return water, and waste disposal. Thus, there is a growing imperative to develop a knowledge base concerning the animal communities associated with hydrothermal sediments and their resilience to disturbance. Substrate removal should have the greatest negative effect on those species that (a) are endemic to the local area and have small population sizes or (b) are species without significant dispersal stages, or both.

No information is available on the endemism or broader distribution of the infaunal species recovered from Papua New Guinea; we identify this as a significant scientific need for effective management. While it is impossible to know the exact response of individual species to these disturbances without conducting pilot studies, some relevant information can be gleaned from lifestyle information, and behaviors of similar taxa elsewhere. Many of the Middle Valley species are apparently vent endemics, present at a variety of sites in the Juan de Fuca region (Desbruyeres et al., 2006). Peracarid crustaceans have direct development and lack larval stages; thus dispersal may be restricted on ecological time scales. Spionids, including species in the *Prionospio* complex, typically have mixotrophic development with initial brooded stages and later development by feeding larval stages that may remain planktonic for 1–3 weeks. This strategy typically allows rapid recolonization when source populations are nearby (Levin, 1984). Nuculanoidea typically have planktonic larvae, though brooding has been documented. Two *Nuculana* species colonized defaunated sediment trays placed at 1800 m in the NW Atlantic and one of these, *N. cancellata*, grew to maturity in 2 years (Grassle and Morse-Porteous, 1987). While plumes of turbid water produced by mining are likely to negatively affect suspension and surface feeders by clogging the feeding apparatus (Rhoads and Boyer, 1982), only a subset of species such as the spionids, ampharetids, and the grazing gastropods might be affected. The majority of the other abundant species present at Manus Basin or Middle Valley (e.g., bivalves, orbiinids, dorvilleids, syllids, caprellids, and maldanids) are likely to be subsurface-deposit feeders, bacterivores or carnivores and more tolerant to limited burial by resuspended sediments.

## 5. Conclusions

Hydrothermal sediments at both study areas exhibit a range of macrofaunal densities that are elevated above or comparable to background sediments. Macrofaunal assemblages in these sediments often have low diversity with high dominance by one or a few species. The hydrothermal sediments are clearly heterogeneous, exhibiting differences in macrofaunal community structure both between broadly separated vent sites and within a site. Within-site heterogeneity is associated with abiotic and biotic factors, including proximity to vent activity, presence of symbiont-bearing clams and microbial mat cover. In this study,

macrofaunal communities from the South Su active site stood apart from those of the Solwara 1 sites and the South Su inactive site in having (a) higher density, (b) higher biomass, (c) greater dominance and lower diversity, and (d) more spatial homogeneity. At Middle Valley, vesicomid clam bed sediments supported macrofauna that were distinctive in having higher density (but not biomass), a deeper vertical distribution and a greater proportion of subsurface-deposit feeders than microbial mat or hot sediments. The hydrothermal sediments sampled support a mix of vent and seep genera, but the majority of specimens belong to groups not normally associated exclusively with reducing environments. The community traits observed at South Su active and Middle Valley clam bed and microbial mat-covered sediments are characteristic of chemosynthetic ecosystems, and appear to reflect elevated food availability. However, the composition of the fauna at the family, generic and species level differs broadly between Manus Basin and Middle Valley. This is consistent with the very distinct megafaunal communities found on hard substrates at vents of Manus Basin (Bruns et al., 1997) and Juan de Fuca Ridge (Juniper and Tunnicliffe, 1997; Sarrazin and Juniper, 1999), and suggests the existence of distinct biogeographic provinces with limited dispersal potential across the Pacific (Van Dover et al., 2002). Nutritional sources for infauna also differed within and between regions. Heavy  $\delta^{13}\text{C}$  signatures of macrofauna ( $> -17\text{‰}$ ), characteristic of TCA-cycle C fixation, were observed at the active Manus Basin sites, whereas Middle Valley active sites exhibited light  $\delta^{13}\text{C}$  values ( $< -22\text{‰}$ ) characteristic of Calvin–Benson sulfide oxidation. Clearly, more research is required to develop a mechanistic understanding of the biotic and abiotic forces that shape infaunal hydrothermal communities and their food sources in the deep sea.

## Acknowledgements

This paper is dedicated to Fred Grassle, who provided the inspiration for this work. Among his many other accomplishments, he laid the groundwork for future study of hydrothermal vent communities, and drew attention to the hydrothermal sediment fauna. Assistance at sea for the Manus Basin work was provided by Nautilus Minerals (including vessel, ROV and personnel time, photos and tube core development). We thank Elitsa Hrischeva (University of Toronto), Samantha Smith (Nautilus), Alison Swadling (Nautilus), Patrick Collins (Duke University), and Carol Logan (Duke University) for help with sample collection and onboard processing of samples on board the Wave Mercury. We thank the crew of the R.V. *Atlantis*, ALVIN pilots and crew, P. Girgius, W. Ziebis, K. Halanych, and participating scientists on AT 15–22 for assistance with sample collection and shipboard processing of Middle Valley material. Assistance in the laboratory with sample sorting was provided by Shira Maezumi and Jennifer Gonzalez. Jennifer Gonzalez and Sarah Wheeler provided help with data compilation. Species/genus identifications were provided by Buz Wilson (isopods), Graham Oliver (bivalves), and Isabelle Williams (tanaids). We thank A. Rowden and two anonymous reviewers for comments on an earlier draft of the manuscript. Support for the research was provided by Nautilus Minerals Niugini (Manus Basin), NSF OCE 04 35217 and OCE 26254 to LAL, NSF DBI-0116203 to RL (Mass spectrometer instrumentation) and NSF OCE-0623554 to RL and P. Girgius (dives at Middle Valley).

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