Determining variation in biological community structure due to environmental stressors around hydrothermal vent systems of Brothers volcano, Kermadec Arc, New Zealand

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Non-Technical Project Summary

Studies of hydrothermal systems have shown that their biological community structure is highly affected by physical and chemical ocean processes that are characteristic of hydrothermal vent environments. In the Southern Kermadec Arc, Brothers volcano contains two side-by-side vent sites with differing chemical concentrations and physical properties, making them ideal sites for assessing the effects these processes have on groups of fauna. In this study, a photographic survey of the biological communities within the two plume fields of Brothers was conducted, and manual and automated image analysis was performed, to determine whether groups of fauna differ in species density and composition between the two sites. Eight dominant types of organisms were tabulated, each of which were assessed for relationships with four potential environmental stressors: temperature, Eh levels (a substitute for chemical concentrations in the water column), salinity (salt content in the water column), and turbidity (suspended particles in the water column). Observed relationships suggest that three of the four factors significantly effect which species are able to live in particular areas. Temperature and Eh produced the same relative effects on vent specialized and non-vent specific organisms. Crustaceans (shrimp, crabs, and long-necked barnacles) were disproportionately found in strongly vent-influenced areas with high temperatures and low Eh levels. They were also associated with areas of high turbidity caused mainly by particles in vent fluid. Poriferans (sponges) and Hydrozoans (hydroids) were found at lower temperatures and higher Eh levels, properties generally found further from a vent source. Salinity did not appear to have major effects on groups of fauna. These environmental conditions are constantly changing, making hydrothermal vent systems extremely variable environments and requiring fauna inhabiting vent areas to be adaptable to these environmental stressors in order to survive in these extreme systems.

Abstract

Hydrothermal vent fauna community structure is highly affected by physical and chemical ocean processes influenced by hydrothermal fluids. Brothers volcano in the Southern Kermadec Arc contains two adjacent vent sites ideal for assessing the effects varying chemical concentrations and physical properties have on faunal assemblages, because they likely have similar accessibility to colonizing invertebrates and fish but their water properties differ from one another. In this study, the WHOI TowCam was used to execute a photographic survey of the biological communities within the two plume fields of Brothers and determine variations in macrofauna community density and species composition between the two sites. Manual and automated image analysis was performed to determine spatial distribution and taxonomy of faunal assemblages. Eight dominant types of organisms were tabulated and assessed for correlations with four potential environmental stressors: temperature, Eh levels, salinity and turbidity. Temperature and Eh had statistically significant effects on which species were found in areas with strong or weak vent influences. Crustaceans colonized areas of high temperatures and low Eh levels making them appear to be vent-specialized. These organisms were also found disproportionately in areas of high turbidity caused mainly by vent fluid particulate matter. Poriferans and Hydrozoans were found at lower temperatures and higher Eh levels, properties generally seen further from a vent source. Salinity did not appear to have major effects on distributions of any taxa. These environmental conditions are constantly changing, making hydrothermal vent systems extremely variable environments. These conditions require fauna inhabiting vent areas to be adaptable to these environmental stressors, otherwise their survival is at risk.

Introduction

The Kermadec Arc is a chain of submarine volcanoes which lies to the north of New Zealand in the South Pacific. Many of the 94 volcanoes in this chain are currently active, forming hydrothermal vents that add unique chemical, geological and biological components to the deep sea environment (de Ronde et al. 2005). This study focuses on Brothers volcano, located 400 km northeast of New Zealand (Fig. 1, Stott et al. 2008). Brothers volcano has the most extreme hydrothermal activity within the volcanic chain, and is the deepest volcano in the Southern Kermadec Arc, with a summit depth of 1,350 m (de Ronde et al. 2001). The volcano has a unique bathymetric structure, dominated by a caldera (3 km in diameter) that contains two emerging cones, the main cone and satellite cone. This structure has resulted in the formation of two major active hydrothermal venting sites, one on the northwest caldera wall, and the other on the Brothers cone (Fig. 2a).

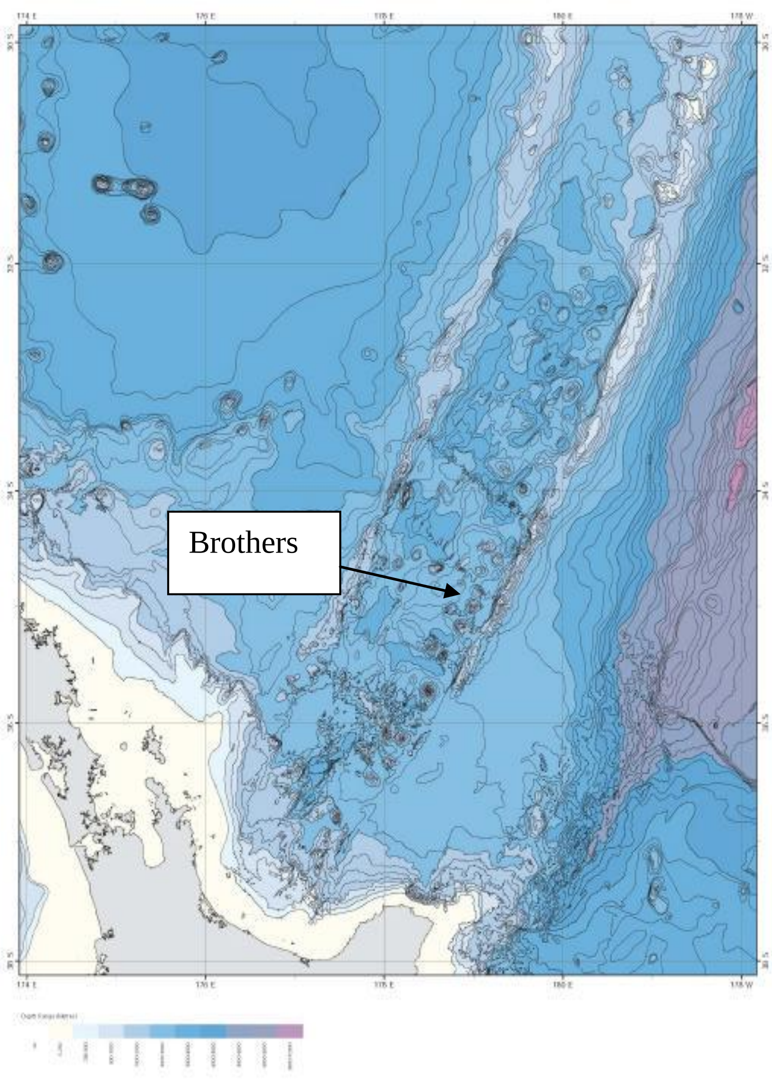

Figure 1. Location of study site, Brothers volcano in the Southern Kermadec Arc (map: Rowden et al. 2003)

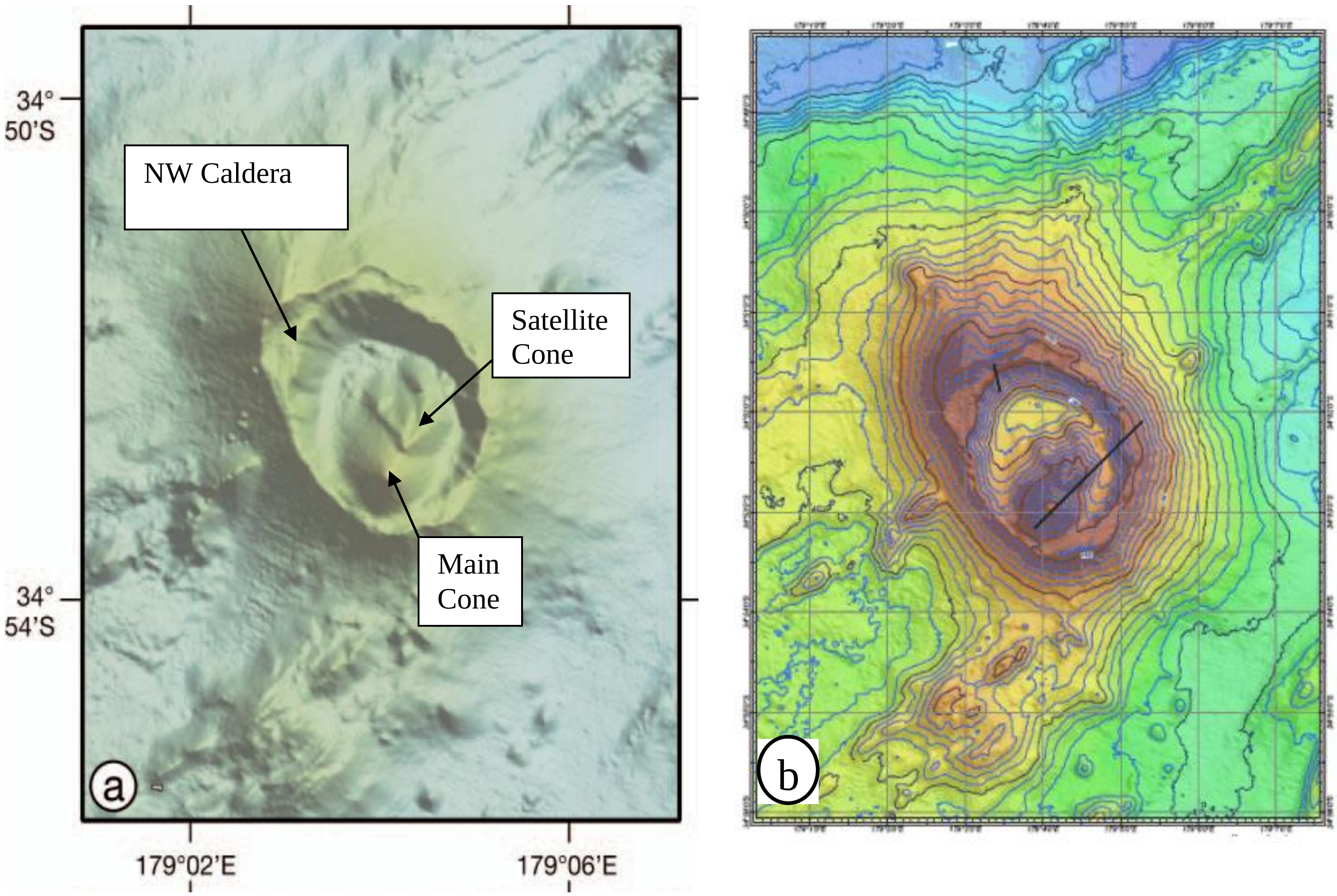

Figure 2. a) Two sites of hydrothermal venting within the Brothers volcano, the NW Caldera wall and the cone. Cone site is divided into the main and satellite cones (image from de Ronde 2005). b) TowCam tracklines for the two venting sites (image from NAZPlume III Kermadec Arc 2004).

Chemical and Physical Characteristics of the Brothers Vent Sites

Different types of venting occur at the cone and caldera plume sites. The NW caldera is characterized by high temperature black smoker venting, and the cone site is dominated by low temperature diffuse venting (de Ronde et al. 2005). Although the plumes are in close proximity, the hydrothermal fluids emerging from the plumes have very different chemical compositions (de Ronde et al. 2005). The NW Caldera plume is old and well established, and has two large areas of sulfide chimneys 1-2 m in height. Fluids expelled from the caldera vents are high in particulate Fe, Cu and Zn which increases water turbidity and indicates high temperatures (de Ronde et al. 2001). Though profuse venting was observed at this site, no signs of H_2S were previously present in the water column. The Brothers cone site had high concentrations of H_2S and lower turbidity because vent fluids had few metal particulates (Table 1, de Ronde et al. 2005).

I hypothesize that the distinct vent-associated water properties of the Brothers plumes, including temperature, salinity, turbidity and chemical composition, contribute vital survival resources to vent fauna, and therefore are likely to have an effect on species composition and spatial distributions of the vent fauna that live in these regions.

Hydrothermal Vent Ecosystems

Studies of hydrothermal communities at other vents around the world have shown that community structure is strongly affected by physical and geochemical processes under the influence of vents. Growth rate, reproduction/mortality, and colonization of vent fauna all depend upon physical water properties and fluid chemical composition (Lutz 1993). Vent communities are typically very high density, high biomass, low species diversity ecosystems, which is typical of habitats with high energy availability and a wide range in water property values including temperature and chemical concentrations (Ramirez-Llodra et al. 2007). Many are composed of vent organisms such as tube worms, bivalves, crabs and bacteria which have high metabolic rates and fast growth rates (Lutz 1993). Organisms inhabiting these areas must be well adapted to sudden environmental changes because large shifts in water properties can occur rapidly over very small distances (Scearce 2006). A large majority of hydrothermal vent species are endemic to these vent regions, and have evolved to show important physiological, morphological and ecological adaptations to vent-specific environmental factors.

Temperature Effects on Biology of Black Smoker and Diffuse Vent Fields

Black smoker and diffuse venting systems contribute different properties to the water column of their surrounding vent fields, which have large effects on the biology that can survive in these areas. Black smoker chimneys are formed as sulfide from vent fluids precipitates out of seawater to form solid chimney structures. These vents expel abiotic fluids of extreme temperatures (260°-400°C) and produce plumes rich in particulate metals (Fisher et al. 2007, Van Dover 2000). No organisms are able to survive at such extreme temperatures. However, the chimneys as well as cracks and channels around the chimneys and throughout the vent field allow hydrothermal fluids to circulate and support dense, productive faunal assemblages (Van Dover 2000). Major taxa found around black smokers include the giant tubeworm *Riftia pachyptila*, various species of shrimp, mussels and other bivalves (Scearce 2006).

Diffuse venting provides a more sustainable environment for supporting life than black smokers, so highest biomass assemblages are generally found near these vent fields (Fisher et al. 2007). Diffuse flows are supplied through porous seafloor substrates or through cracks and fissures (Van Dover 2000). As these flows occur, high temperature hydrothermal fluids mix with ambient seawater to form warm fluids (ambient- 40˚C) and the mineral particulates precipitate out, leaving dissolved H_2S and CH_4 behind as a resource to support organism communities (Ramirez-Llodra 2007).

Both types of vent environments are variable systems which are continuously changing. Due to constant mixing and turbulence, fluid temperatures can fluctuate within seconds over centimeter distances, requiring animals inhabiting these ecosystems to be adapted to large thermal gradients both temporally and spatially (Fisher et al. 2007). Many vent invertebrates are adapted to the high temperature environments allowing them to live closer in proximity to the vent source, whereas others are restricted to cooler temperature environments away from vent sources. These varying adaptations cause vent invertebrates to often be distributed into different zones spatially throughout vent fields (Van Dover 2000) and are restricted with respect to temperature and other environmental tolerances (Fisher et al. 2007).

Hydrothermal Vent Chemistry and Chemosynthesis

Hydrothermal vent communities depend on chemosynthetic free-living and symbiotic bacteria for primary production as an alternative to photosynthesis-based food chains. Chemosynthetic bacteria harvest inorganic compounds from the hydrothermal fluids and use them to fix CO_2 found in seawater to create energy and form organic compounds which are then used by macrofauna for survival (Ramirez-Llodra 2007). Vent bacteria depend on three important reduced inorganic compounds: H_2S, H_2 and CH_4 (Van Dover 2000). Through bacterial chemosynthesis, vent fauna communities depend on, and hence may be shaped by, chemical composition of the plume (Lutz 1993, Scearce 2006, Fisher et al. 2007). Variations in chemical composition may result in an alteration of the biological community structure in particular regions.

Although hydrogen sulfide is important to chemosynthesis and the survival of hydrothermal vent ecosystems, it is also potentially toxic. H_2S can be present in concentrations 10-100 times higher than concentrations which are generally toxic to most other macrofauna species (Fisher et al. 2007). This factor requires vent fauna to have yet another adaptation to the extreme environment. For those macrofauna lacking adaptations to the high concentrations, it may have a poisonous effect similar to cyanide (Scearce 2006).

One way of determining concentrations of chemicals (acting as resources for some organisms and toxins to others) in the water column is by looking at Eh levels. An Eh sensor on a CTD operating system detects reduction potential within the water. By responding to all ions in situ, Eh indicates how chemically reactive a fluid is in a particular area. Increases in H_2S and other chemicals cause reduction in Eh values. The lower the Eh, the stronger the chemical concentration in the water column is (www.divediscover.whoi.edu). Thus, Eh can be used as a proxy for H_2S and CH_4 when direct measurements are not available.

Salinity and turbidity are other factors that could potentially effect distribution and composition of vent faunal assemblages in the vent fields. Effects of these factors on biology have not been studied as extensively as temperature and chemical effects. Both salinity and turbidity could be proxies for water chemistry, and therefore could indicate resources to macrofauna and show potential effects these chemical resources have on biological communities. Light scattering is used to determine turbidity, which is greatly affected by the product of hydrothermal emissions. Turbidity could be variable depending on type of venting occurring within the vent field. Any differences found in light scatter show potential differences in vent fluid composition (de Ronde et al. 2001).

Biology of Vent Sites

The majority of vent biology research has been executed in mid-ocean ridge (MOR) systems. In contrast, little research has been done on the biology of volcanic arcs formed in back arc spreading centers. One extensive biological survey was performed on three Kermadec Arc seamounts, Brothers, Rumble III and Rumble V (Rowden et al. 2003). The combined survey revealed 308 different species, distributed among 10 phyla. The five dominating phyla included Cnidaria, Polychaeta, Crustacea, Mollusca, and Echinodermata. Together these phyla contained over 90% of total taxa. Of the three volcanoes, Brothers was found to have the lowest species diversity, with a mean diversity of 8.3 species (Rowden et al. 2003).

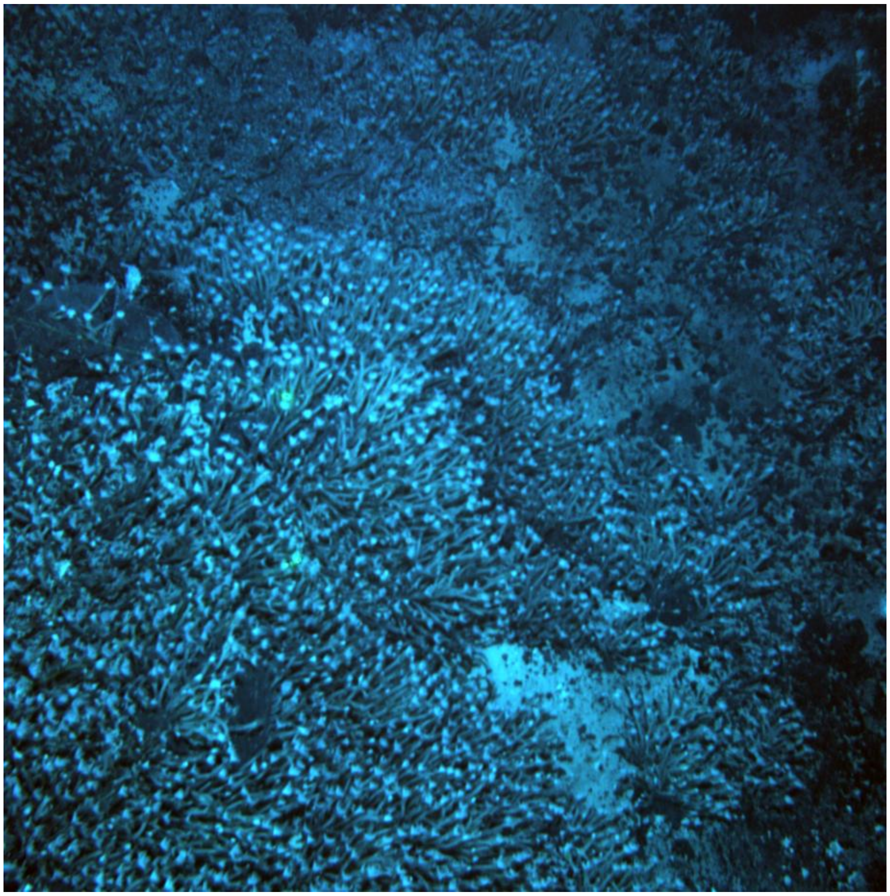

Figure 3. Long-necked barnacles discovered at the Brothers cone site, using WHOI TowCam system

Aside from this survey, little is known about the vent fauna of the Brothers volcano in general, and almost nothing is known about how biological assemblages vary between the two active vent fields. Observations on vent fauna made during chemistry studies by de Ronde et al. (2005) on Brothers volcano suggest community structure differs between the two sites. Macrofauna at the NW Caldera were not abundant. A limited number of long-necked barnacles were found (Fig. 3), along with filamentous bacteria and a single crab, but no high density vent communities were observed. In contrast, the Brothers cone had large assemblages of vent fauna including sulfide worms, limpets, shrimp, barnacles and bacteria. These de Ronde studies (2005) were incomplete observations, so it remains unknown exactly how community structure and densities of faunal assemblages differ between the two sites. However, the few existing observations along with the physical and chemical differences between plumes suggest that the distinct properties of the plumes and the resources they provide may have major effects on resident biological communities.

The objective of this study was to perform a survey of the biological community structure around the two Brothers volcano vent fields. Phyla present within the vent fields were identified and distributions were mapped out. By correlating biological densities and the presence/absence of particular phyla with the different extreme environmental stressors that occur in these deep sea ecosystems, a potential determination of environmental limitations individual phyla encounter within these systems is given.

Methods

Community structures near hydrothermal vents of the NW Caldera and cone of Brothers volcano were photographically surveyed during a cruise on the *R/V Thomas G. Thompson* from March 2-March 12, 2009. Spatial variations occurring in macrofauna density and diversity were quantified and biological data were examined for correlations with physical and chemical properties water properties: temperature, Eh, salinity and turbidity.

Sampling and Image Analysis

Methods followed those of Rowden et al.'s 2003 biological survey of Brothers, Rumble III and Rumble V volcanoes. The survey uses a WHOI TowCam system to photograph tracklines in the vicinity of the two vent sites (Gardner et al. 2006, Soule et al. 2007). The TowCam system was flown 3-5 meters above the seafloor and traveled upslope, taking 3.3 megapixel resolution images every 10 seconds.

Due to the large extent of the vent fields and limited sampling time, camera tracklines were set to execute the most accurate coverage possible of the hydrothermal sites. The tracklines were laid out relative to active venting regions found by de Ronde et al. (2005) because this was where previous biology was found and was a likely location for the formation of current biological assemblages. Two tracklines were surveyed, approximately 1 km in length, covering the NW caldera site and Brothers cone (Fig. 2b).

I performed a combination of manual and automated image analysis on the survey photographs to determine the presence and absence of taxonomic groups and density of faunal assemblages in particular environmental conditions (Gardner et al. 2006, Danny Grunbaum, pers. comm.). The imaging toolbox in MATLAB was used to manually identify biology based on taxonomic phyla and class in each individual photograph. MATLAB was then used to tabulate this information and determine presence/absence of fauna frame by frame along each track line. Densities of biological communities were determined visually by identifying and making note of regions containing higher than average numbers of organisms.

Once organism presence and biological community densities along the tracklines were determined, correlations were made with the data on physical and chemical plume characteristics. Box plots correlating five phyla individually with each environmental factor were made. The five different phyla and five classes plotted include Arthropoda (Class Malacostraca and Maxillopoda), Porifera, Cnidaria (Class Hydrozoa), Echinodermata (Class Asteroidea and Echinoidea) and Chordata. Each was correlated individually with one of four environmental factors. MATLAB was used to perform a Kruskal-Wallis one way ANOVA test on these data to reveal statistically significant relationships between physical and biological characteristics (Appendix 1). Spatial distributions and trends of environmental factors were visualized using multi-axis time series plots with locations of dense aggregations of organisms shown to help show organism distributions at each vent site.

Determination of Physical and Chemical Water Properties

Physical and chemical water properties were determined using a CTD located on the TowCam system. The CTD measured temperature, salinity, and turbidity every second. The TowCam was also equipped with an Eh sensor which was used to detect in situ redox potential. CTD and Eh data were paired with each image along with ship navigation data. This platform allows water properties to be spatially indexed with images along tracklines. I then performed statistical analysis to look for relationships between presence/absence of phyla with varying environmental factors.

Species Identification

Species identification depended on the classification through images and the collection of specimen samples using a dredge. The sampling location was determined using images from the TowCam. In the Brothers cone tow, we targeted a high density long-neck barnacle field (34.8704˚S 179.0802˚E to 34.8707˚S 179.0793˚E). Dredging tracklines were short to better resolve where specimens were collected. Material brought up from the seafloor was manually sorted. Specimens collected were identified on board by colleague Tim Shank (WHOI), or preserved in formaldehyde for future classification.

Results

Photographic Images

Due to time constraints, replications were limited at Brothers volcano. At the Brothers cone 2143 images were taken, of which 76% were of good quality and were able to provide accurate seafloor analysis. Of the seafloor images, 44% contained biology. At the NW Caldera site, the sample size was smaller, with a total of 770 images. Of these, 74% had visible seafloor and were of acceptable quality, and 68% had biology present. At both the cone and caldera site, biology that could not be accurately identified was noted as questionable and was not included in analysis. 24% and 26% of images were eliminated, respectively, due to being water column images or having poor quality.

Taxonomic Biodiversity

Due to lack of replication, it is likely that samples did not cover a large enough area to fully describe and classify the assemblages of invertebrate taxa at both the Brothers cone and NW Caldera sites. However, of the organisms observed, five dominate phyla were identified and

Table 1. Taxonomic groups identified during the survey of Brothers megafauna

Phylum	**Class**	**Common Name**
Chordata		Fish
Cnidaria	Anthozoa	Sea Anemone
	Hydrozoa	Hydroid
Crustacea	Malacostraca	Crab
		Shrimp
	Maxillopoda	Long Necked Barnacle
Echinodermata	Asteroidea	Sea star
	Echinoidea	Sea Urchin
	Ophiuroidea	Brittle Star
Mollusca	Bivalvia	Clam
	Gastropoda	Snail
Porifera		Sponge

composed over 95% of organisms present. These phyla include Crustacea, Porifera, Echinodermata, Cnidaria and Chordata (Table 1). This differs from what was found by Rowden et al. in their 2003 survey, in which species were distributed among 10 phyla. Similarly to this survey, Rowden et al. found five dominating phyla which contained over 90% of the total taxa. Two of these phyla, Polychaeta and Mollusca, were completely absent or composed a very small part of the overall biology found at Brothers.

The dominant taxon at both vent sites was Crustacea, which made up 55% of identifiable organisms. Similar to the Rowden et al. survey, Crustaceans were the most diverse phylum with two dominating classes found, Malacostraca (Decapods including shrimp and crabs) and Maxillopoda (long-necked barnacles). Of all visible organisms present, these appeared in greatest numbers at both sites, and formed the densest assemblages. The second dominant phylum was Cnidaria, with classes Hydrozoa and Anthozoa. Hydrozoans were found over a large range at both sites. At least two apparently distinct species were found, one inhabiting rocky habitats and the other inhabiting soft sediments. However, due to the lack of high image resolution and specimen samples, organisms could not be identified to the species level. Although this was one of the dominant classes at Brothers, no Hydrozoans were found in the 2003 study. Several Anthozoans were sighted mainly at the cone site, but were one of the least-frequent classes observed.

Individuals of the phylum Echinodermata were observed infrequently (0.03% of organisms identified). Of these, Echinoids were the most prevalent at both vent sites. Asteroidea were absent at the NW Caldera site, and only five individuals were observed at the Brothers cone. A third class, Ophiuroidea (brittle stars), may have been present at the NW Caldera site, but no individuals were identified with confidence.

Unlike the 2003 study in which mollusks were dominant in some places (59 species identified) only one possible individual of the class Bivalvia was observed in the current study, along with several Gastropod shells.

Differences in biological diversity between the NW Caldera and Brothers cone sites are not apparent. With the exception of Asteroidea, all phyla and classes appeared at both the cone and NW Caldera; however abundances between sites were variable. In 2009, vent fauna appeared to be more abundant and diverse at the NW Caldera site than during the de Ronde et al. study in 2005 (two phyla in 2005, five phyla in 2009). Diversity has apparently increased at the cone site as well, though two organisms, limpets and tube worms, observed by de Ronde et al. in 2005 were absent in 2009. In regards to density of faunal assemblages at each site, the cone had the two largest assemblages found during this survey. One assemblage was composed of thousands of long-necked barnacles. The second was composed of hundreds of vent shrimp. At the NW Caldera, two smaller assemblages of long-necked barnacles were observed.

Locations of Vent Sources

By using the temperature and Eh data from the TowCam CTD, a time series of these two variables was plotted. Strong correlations between these two environmental factors were found and used to identify the likely locations of vent sources at both the cone and NW Caldera. Vent sources were identified as the location with highest temperature and lowest Eh level observed along the track line. Three potential vent sources were found along the cone site and at NW Caldera, six potential sites total (Table 2). Images showing potential active venting support the idea of these high temperature, low Eh areas as the vent source. Specifically, along the Brothers cone tow, diffuse venting is apparent in images around 11:45 AM, due to the presence of highly turbid, cloudy water (Fig. 8, top right image).

Table 2. Potential locations of vent sources at Brothers cone and NW Caldera vent sites based off temperature and Eh data.

Brothers Cone				
Site #	Latitude (S)	Longitude (E)	Temperature (˚C)	Eh (mV)
1	-34.8796	179.0705	4.40	-133.0
2	-34.8814	179.0691	3.98	-74.8
3	-34.8837	179.0672	4.30	-49.2
NW Caldera				
Site #	Latitude (S)	Longitude (E)	Temperature (˚C)	Eh (mV)
1	-34.8617	179.0578	3.30	12.82
2	-34.8614	179.0577	3.40	34.80
3	-34.8604	179.0578	3.26	13.06

Table 3. Ranges of the four environmental variables at the Brothers cone and NW Caldera venting sites

	Environmental Stressor			
Site	**Temperature (˚C)**	**Eh (mV)**	**Salinity**	**Turbidity (nephels)**
Brothers Cone	3.15˚C-4.55˚C	-125-225	34.43-34.56	0.30-0.34
NW Caldera	3.12˚C-3.35˚C	10-190	34.55-34.56	0.31-0.39

Taxonomic Variability from Environmental Factors

Temperature

Temperatures were variable between the two sites, with warmest temperatures observed at the cone site. NW Caldera temperatures ranged from 3.12˚C-3.35˚C compared to a range of 3.15˚C-4.55˚C at the cone (Table 3). Of taxa present at the cone, the Crustaceans were found in the warmest temperature habitats, in areas thought to be close to diffuse vents. Time series plots of temperature variability along tracklines at both vent sites show temperature anomalies (Fig. 4, Fig. 5). At the cone site, two spikes in temperature were seen, corresponding to the satellite cone and the main cone. Dense Crustacean assemblages were found at these anomaly areas, specifically a high density barnacle field at the satellite cone and a large shrimp colony on the

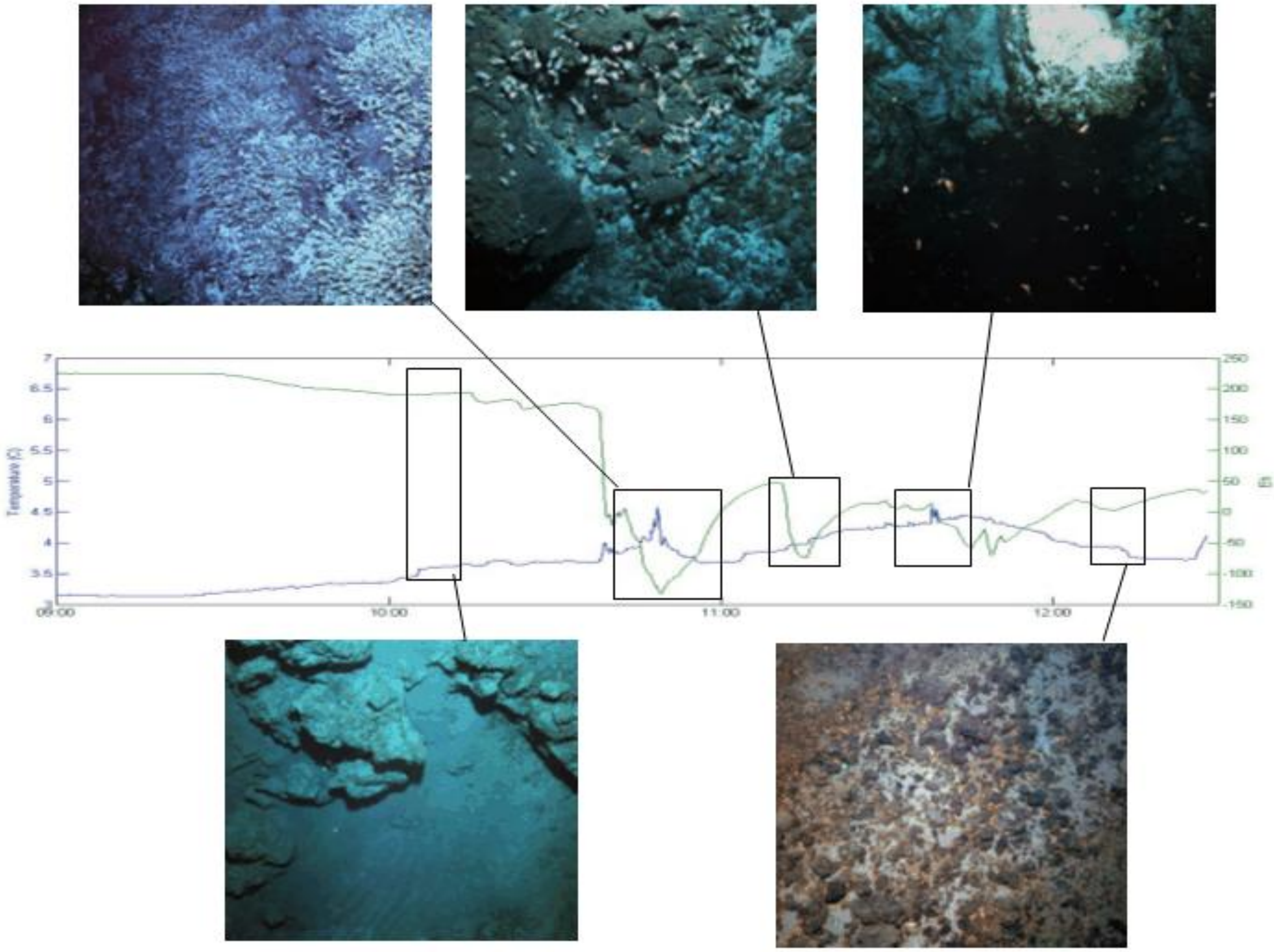

Figure 4. Temperature and Eh trends with image progression along track line of the Brothers cone site. Images are representations of biological assemblage density and types of organisms present in varying temperature and Eh conditions. Low density assemblage shown around 10:15 AM (bottom left image). High density long-necked barnacle assemblage at 10:45 AM (top left image). Shrimp colony around 11:30 AM (top right image). A second representative image lacking visible organisms occurs around 12:15 PM (bottom right image).

main cone (Fig. 4). Of all organisms, shrimp were observed in the most extreme temperature habitats, with a median temperature of 4.3˚C (Fig. 6a, p=0). Long-necked barnacles and crabs occupied the next highest temperatures, both occurring at a temperature of 3.9˚C (p=0, p=0.0003). Porifera and Hydrozoa followed similar trends to each other, living in cooler

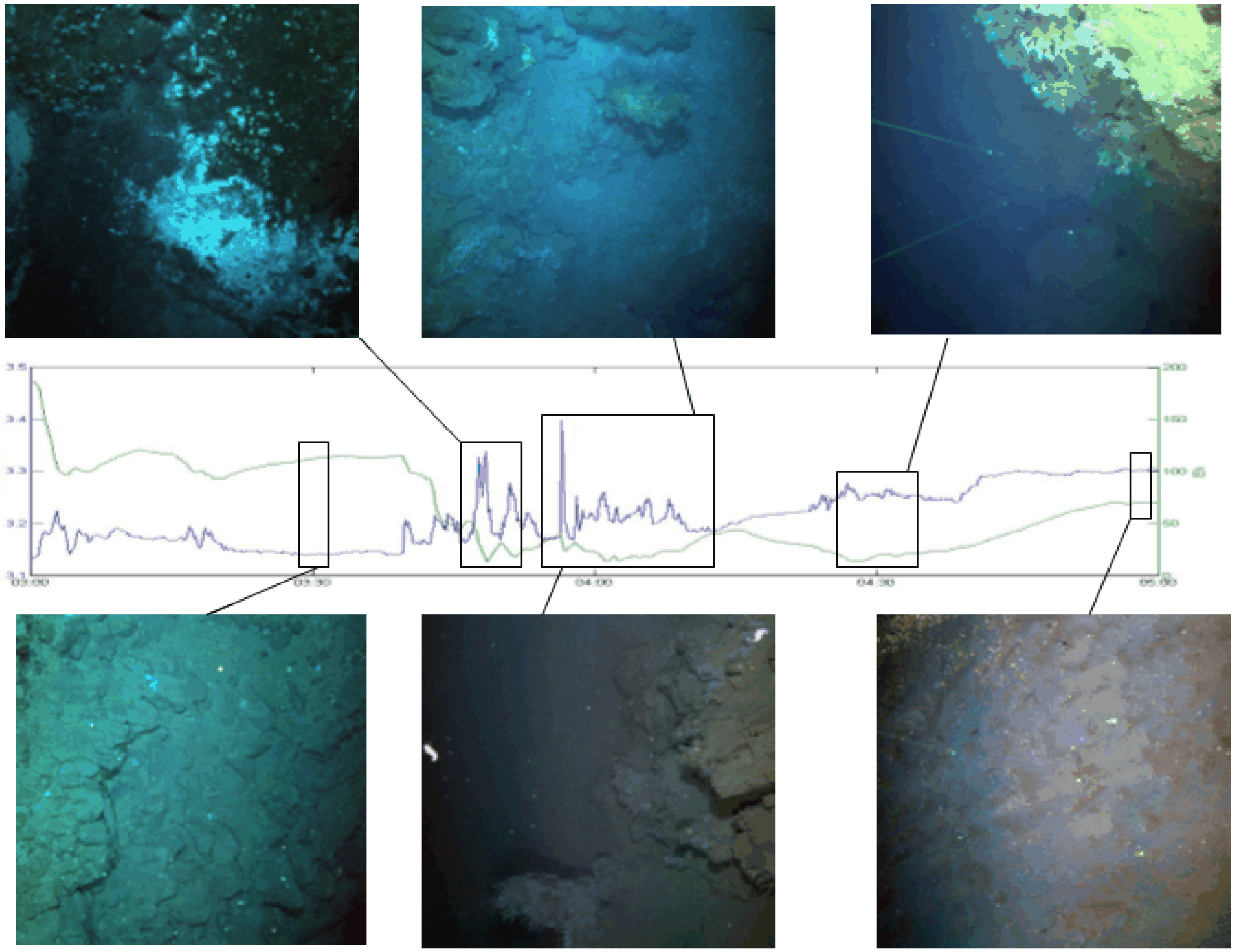

Figure 5. Temperature and Eh trends with image progression along track line of the NW Caldera site. Images are representations of biological assemblage density and types of organisms present in varying temperature and Eh conditions. Low density assemblage shown around 3:30 AM (bottom left image). High density long-necked barnacle assemblage at approximately 3:50 AM (top left image). Small shrimp colony and crab assemblage at 4:00 AM (top and bottom middle images). A second long-necked barnacle aggregation occurs around 4:30 AM (top right image). Sediment hydroid colony at 5:00 AM (bottom right image).

temperatures, 3.1˚C and 3.3˚C, respectively ($p=1.34e-6$, $p=1.28e-6$). The Echinoderms and Chordates did not show statistically significant relationships with temperature (Fig. 6b, $p=0.004$) with the exception of Asteroidea which were found at cooler temperatures of 3.15˚C.

Temperature effects on organisms at NW Caldera were very similar to the effects seen at the cone site, with slight variations seen in assemblage densities. The maximum temperature was lower at this site than at the cone. The smaller temperature range and lower maximum temperature had an effect on the areas colonized by some phyla. Shrimp and long-necked barnacles still populated the warmest temperature environments available, seen at temperatures 3.22˚C and 3.26˚C respectively (p=0.005, p=0). However, faunal assemblages were much less dense than seen at the cone. The temperature time series at this site showed the presence of one temperature anomaly, which was associated with the largest assemblage of long-necked barnacles found along the tow, as well as several crabs, hydroids and a small shrimp colony (Fig. 5). Crab distributions at this site did not show any relationship with temperature. Similar to the cone site, Porifera colonized cooler environments, 3.15˚C (p=7.52e-7). Hydrozoans were in cooler temperature zones than at the cone, 3.22˚C (p=4.81e-5).

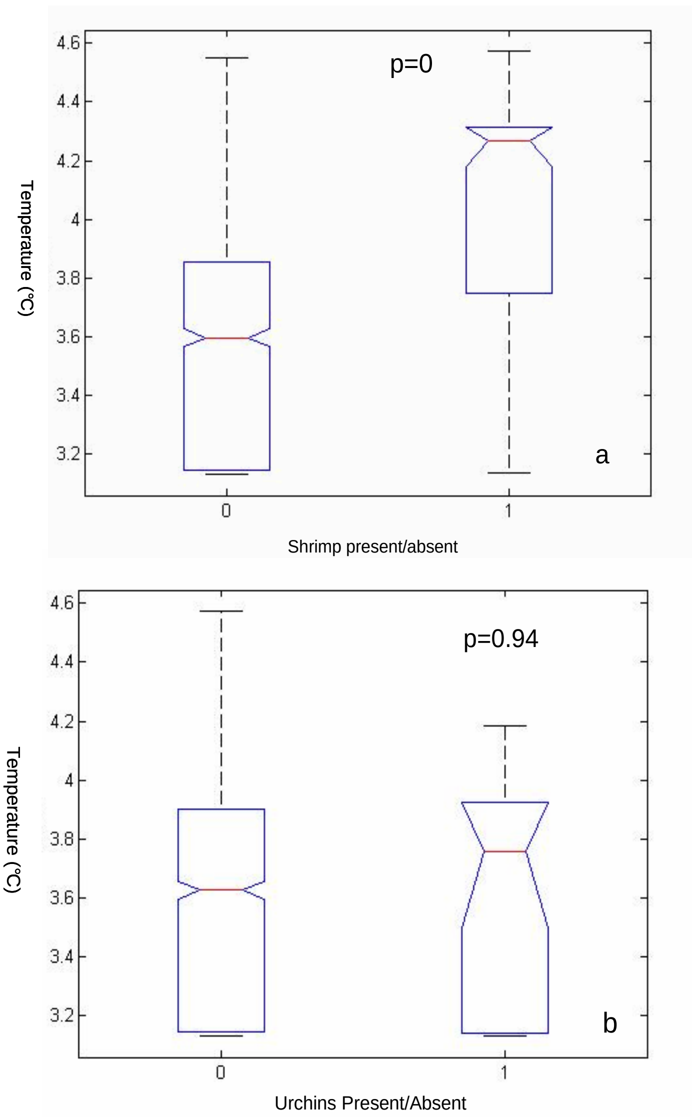

Figure 6. a) Box plot showing statistically significant relationship between temperature and presence/absence of shrimp (n= 80) at the Brothers cone site. b) Box plot showing non-statistically significant relationship between urchins (n=12) and temperature at the Brothers Cone.

Overall, Crustaceans appear to follow the same trends and colonize in the warmest available environments at each site. Poriferans and Hydrozoans also grew in the same temperature environments as one another. These taxa appeared to thrive in cooler temperatures compared to Crustaceans. No significant trends were found in habitat choices for Echinoderms or Chordates.

Eh levels

The Eh range at the NW Caldera was 10-190 mV compared to a range of -125-225 mV at the cone vent site (Table 3). Higher plume intensity and chemical concentrations were indicated by the extremely low Eh levels at the cone site. Both classes of Crustaceans were observed in low Eh environments. At the cone site, shrimp and long-necked barnacles formed dense aggregations in -10 mV environments (Fig. 7a, p=9.263-12, p=0). Crabs were fewer in number, but were found to have a significant relationship with lower Eh levels, around -80 mV (p=3.98e-9). Poriferans and Hydrozoans were present in high Eh

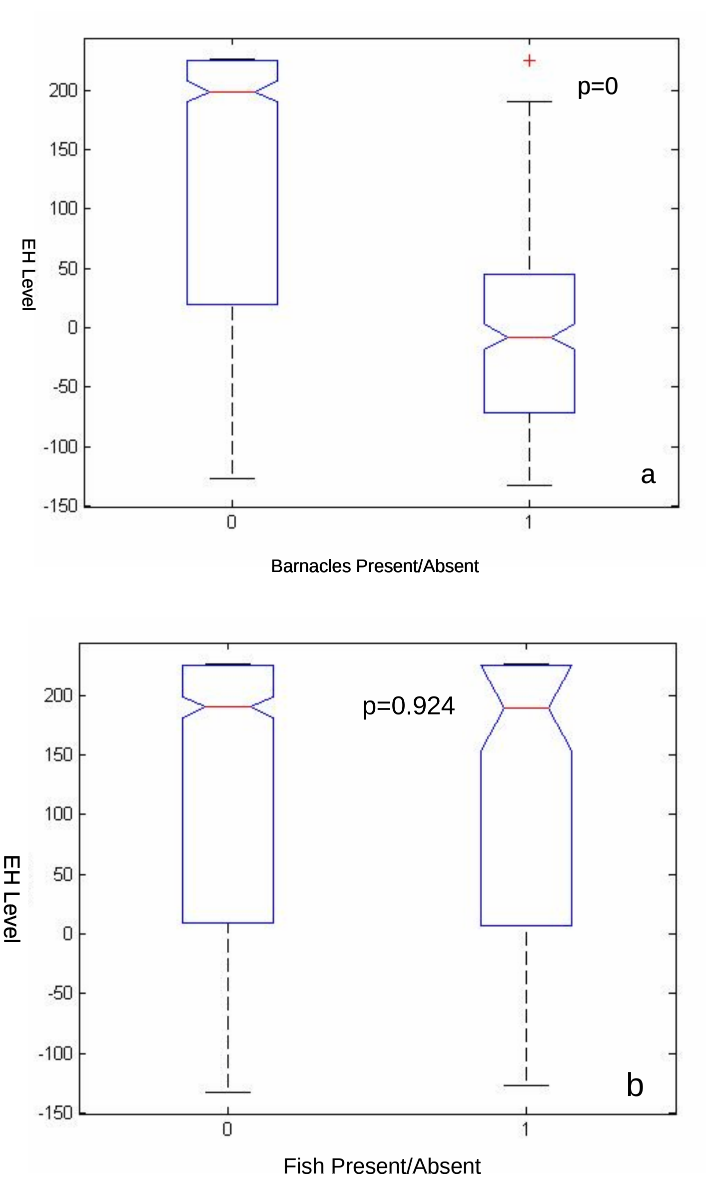

Figure 7. a) Box plot showing statistically significant relationship between Eh and presence/absence of barnacles (n=293) at the Brothers cone site. b) Box plot showing non-statistically significant relationship between Eh and fish (n=53) at the Brothers cone.

environments at this site, and were seen at levels of 200-225 mV ($p=2.79e-6$, $p=0.0001$).

The time series progression of Eh levels along the cone track line shows three areas of strong decreases in Eh to negative values, which is representative of high chemical concentrations (Fig. 4). Each of these three regions correlates with a dense colony of organisms. The first is associated with the large long-necked barnacle field found on the satellite cone, the second associates with a smaller assemblage of barnacles, and the third associates with a large shrimp colony. Mobile Echinoderms and Chordates showed no significant relationship with Eh level (Fig. 7b).

The weaker Eh signals at the NW Caldera site signify lower venting activity and lower chemical concentrations than those at the Brothers cone. All Crustaceans colonized low Eh environments around 20-30 mV (shrimp $p=1.96e-11$, barnacles $p=3.37e-12$, crabs $p=6.5e-6$). However, Eh levels did not drop to negative values as they did at the cone. At this site, Poriferans were in much lower Eh levels, Eh= 110 mV ($p=0.0004$), than at the cone site. However, these low levels were in the higher range of Eh values for the site. Hydrozoans were found in very low Eh levels around 40 mV ($p=0.016$). Chordates showed a statistical relationship with higher Eh levels, living in levels around 95 mV ($p=0.013$). Asteroidea were absent at this site, and Echinoidea showed no preference.

The time series plot for Eh at the NW Caldera site revealed two areas of decreased Eh level, however, these Eh drops were less drastic than the three drops found at the cone (Fig. 5). Both low Eh areas were correlated with the dense assemblages of long-necked barnacles found along the tow. A few crabs were also observed at these sites, along with several vent shrimp. Compared to the assemblages formed in the low Eh areas of the cone site, the densities of the NW Caldera assemblages were low.

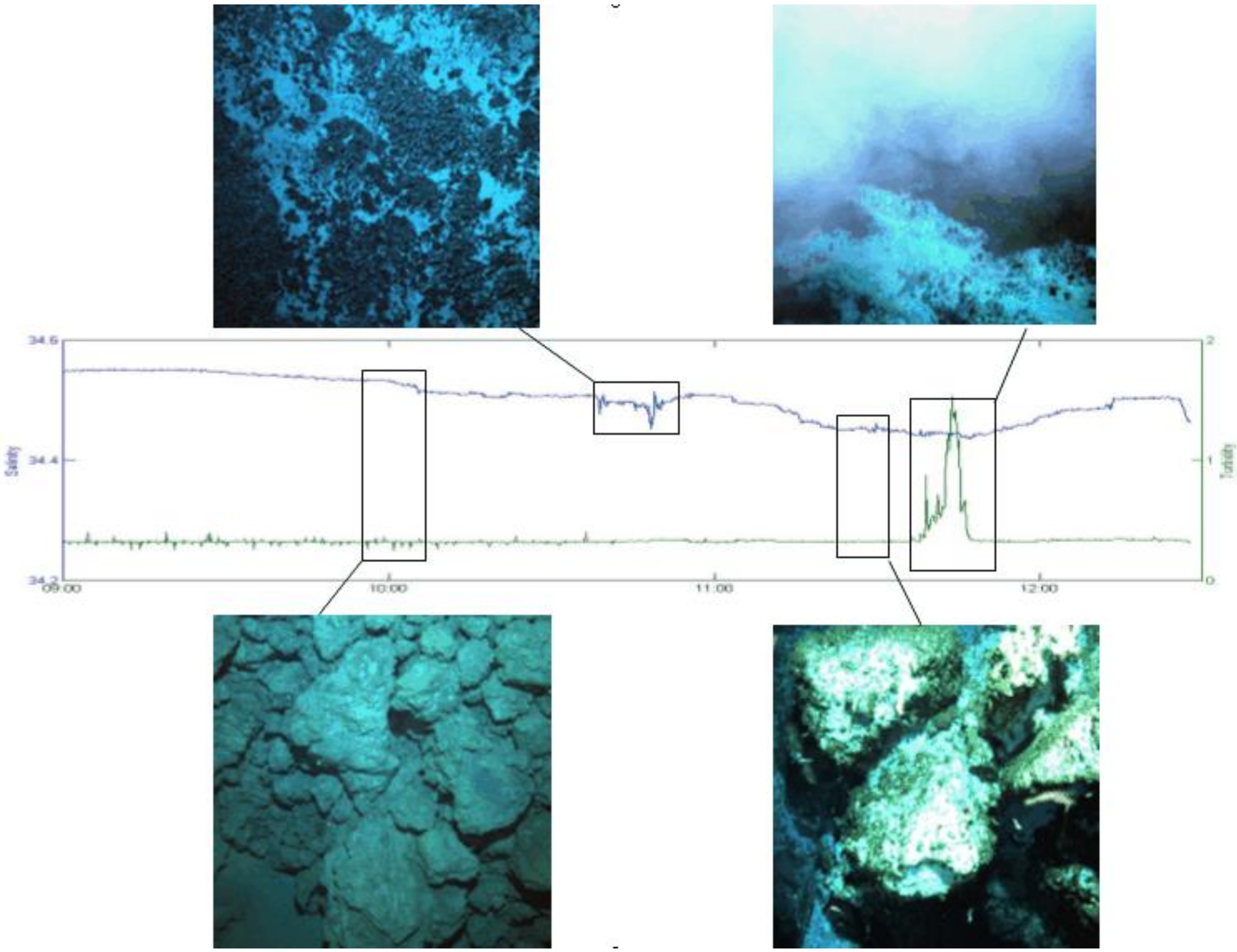

Figure 8. Turbidity and salinity trends shown with image progression along Brothers cone track line. Active venting occurring at large turbidity anomaly (top right image). Shrimp colony found outside this turbidity region (bottom right image). Salinity anomaly found at approximately 10:45 AM corresponds with dense barnacle assemblage (top left image). The absence of salinity or turbidity anomalies corresponds with a lack in biology (bottom left image).

Turbidity

The cone site had a slightly smaller range, 0.30-0.34 nephels compared to 0.31-0.39 nephels at the NW Caldera (Table 3). In general, relationships between turbidity and taxa were found only at the cone site, where the majority of phyla showed statistically significant relationships with higher turbidity regions.

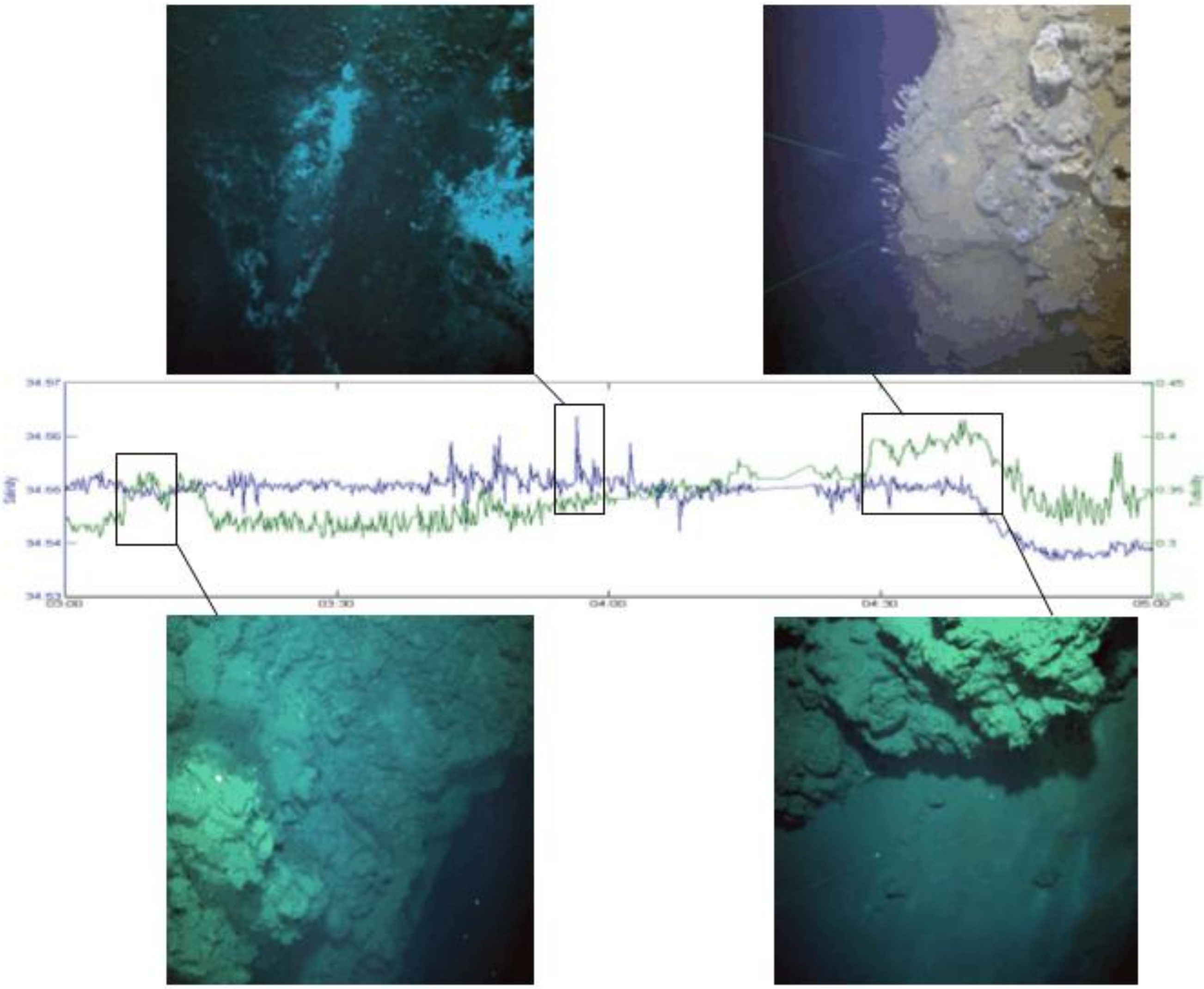

Figure 9. Turbidity and salinity trends shown with image progression along the NW Caldera track line. All turbidity and salinity anomalies shown correlate with small assemblages of long-necked barnacles. Assemblages also contain a few individuals of the class Malacostraca (top left image).

At the cone site, taxa did not follow the same trends seen with the other environmental variables. Both classes of Crustaceans were observed in the same environmental conditions as each other, colonizing high turbidity regions. Barnacles live in slightly less turbid waters, 0.324 nephels, than shrimp and crabs, 0.33 nephels (shrimp p=1.63e-6, barnacles p=2.58e-12, crabs p=0.001). With the other environmental stressors, Poriferans and Hydrozoans have followed the same trends. In this case, however, Poriferans follow the trends of Crustaceans and are found in the same turbidity level as Malacostraca (p=0.006). Hydrozoans appeared to colonize lower turbidity areas, 0.317 nephels (p=0.012). At the cone site, the turbidity progression plot showed turbidity as a rather constant factor throughout the tow until the peak of the main cone is reached, where a large turbidity increase is seen (Fig.8). This increase in turbidity correlated with the gradual temperature increase as well as a drop in Eh levels, and images showed potential active venting. The large shrimp colony was found outside this high turbidity region (Fig. 8).

There is no between-site correlation among the various taxa and turbidity levels. At the NW Caldera site, Crustaceans do not colonize the same turbidity habitats seen at the cone. Shrimp are found in levels of 0.373 nephels, which are higher than levels at the cone site (p=5.88e-8). Barnacles colonize higher turbidity levels as well, 0.336 nephels, although this value is on the lower end of the turbidity range at the caldera site (p=7.00e-13). Turbidity levels for Poriferans are lower, 0.324 nephels, and higher for Hydrozoans, 0.336 nephels. In the time series of turbidity along the NW Caldera track line three high turbidity anomalies are seen (Fig. 9). The first two anomalies occurring around 3:15 AM and 4:30 AM both correlate with small but dense assemblages of long-necked barnacles. These assemblages also contained several individuals of the class Malacostraca (Fig. 9 top left image). The third turbidity anomaly occurs at the end of the tow, around 5:00 AM, and correlates with an assemblage of Hydrozoans (not shown in figure).

Salinity

Salinity had slight effects on the areas colonized by taxa at the cone site, however, only one statistically significant relationship was found at the NW Caldera site, suggesting salinity is not an extreme environmental stressor on most vent fauna. The range of salinities observed at the cone site was 34.43-34.56 compared to the NW Caldera range of 34.55-34.56 (Table 3). The Crustaceans colonizing the cone vent field were found at lower salinities, with shrimp at 34.45 (p=0) and barnacles at 34.49 (p=0). Crabs at this site were not affected by varying salinity. Poriferans and Hydrozoans were found in regions of higher salinity, 34.46 and 34.51 respectively (p=1.27e-5, 1.76e-5). The remaining phyla, Echinoderms and Chordates, showed no relationship to salinity. The salinity time series at the cone site shows a small drop in salinity around 10:45 AM. This anomaly correlates with the large field of long-necked barnacles found on the satellite cone, an increase in temperature, and a decrease in Eh (Fig. 8).

Vent fauna in the NW Caldera vent field showed no significant impact by salinity, with the exception of long-necked barnacles. Like at the cone site, these organisms colonized lower salinity regions, 34.54 (p=2.89e-10). This salinity was the lowest at this site; however, it is high compared to that of the cone site. In the time series progression of the NW Caldera, the largest peak in salinity occurs around 4:00 AM and is found within one of the long-necked barnacle assemblages (Fig. 9). All other Crustaceans, Poriferans, Hydrozoans, Chordates and Echinoderms showed no statistical relationship with this environmental factor.

Discussion

Between-Site Biological Community Structures

Fluids expelled by hydrothermal vents influence the water properties in the surrounding vent fields and cause strong variability within the vent environments. These trends have been observed at hydrothermal vents around the world and also held up at Brothers volcano. Differences in faunas found in three different surveys at Brothers suggest that biodiversity of vent fauna as well as spatial distributions have in fact been affected by varying environmental stressors. Vent fauna biodiversity has shifted and major changes in composition and densities have occurred over a rather short time period for Brothers volcano as a whole, as well as between the two active venting sites. Nearly half of the phyla observed in the Rowden et al. 2003 study were not found in 2009. However, within the area of the volcano, biodiversity at each site has increased, with the greatest increase seen at the NW Caldera site. These shifts have occurred over a period of four years. However, the number of changes in biological community structure within that time period is unknown. These observations support the idea that vent fields are extremely variable environments, and shifts in habitat properties are substantial and frequent (Scearce 2006). The constant fluxing of environmental conditions requires strong adaptability of vent specialized organisms, otherwise small environmental changes may cause harm and put their survival in these extreme vent environments at risk. The shift in species diversity seen at both sites may be indicative that the species now absent from the vent environments were not adaptable to potentially shifted environmental conditions that have occurred within the past four years.

As environmental variables such as temperature and Eh change, organisms ill suited for the new conditions may die off, and others better suited for the new habitat will colonize. This mechanism allows particular phyla to become present or absent from a site within a short time. In 2005, observations of tube worms and limpets present at the cone site were made by de Ronde et al. These organisms were not observed during the recent survey. There are two potential explanations for this occurrence. Environmental shifts may have occurred since these past observations and these particular fauna were unable to survive in the new conditions, so populations were wiped out and have not been able to re-colonize the site (de Ronde et al. 2005). A second possibility is that these taxa require very specific environmental conditions which are highly localized. If that were the case, then organisms would likely occupy only small parts of the vent sites. Due to limited sampling, any single survey could miss these regions.

The changes in biological community structure suggest that significant fluctuations in the vent characteristics have occurred. Intensity of hydrothermal activity or chemical composition of fluids may have been altered, and affected the biological communities. Varying results of water properties from past studies by de Ronde et al. (2005) suggest the cone vent site is a constantly changing, unstable environment. However, few fluctuations in water properties have occurred at the NW Caldera site suggesting it is in a steady state condition (de Ronde et al. 2005). Based off these conditions, the changes in biological community structure at the cone site were expected because the environment is variable. The drastic changes in biological communities at the NW Caldera however, were unexpected. Given the past observations of steady state conditions at the NW Caldera site, it was predicted that vent fauna structure would have gone through very few changes in composition and density over this short time period. It is a possibility that the sites studied currently are different than those observed by de Ronde et al. (2005) and therefore the biology present varies. Another possibility is that the steady state conditions of the caldera site have shifted, causing changes in environmental stressors great enough to have strong positive impacts on the biology in this area, creating a more suitable environment, providing more resources, and allowing a wider variety and larger populations of organisms to colonize.

Given the fact that the NW Caldera and the cone site are dominated by different forms of venting, thus contributing different physical and chemical vent-specific properties to the water column, it was expected that the biological structure between the two sites would differ a great deal. This was not observed. The survey tabulated five major phyla composing the biological communities of Brothers. All five phyla occurred at both vent sites, and only one of the five classes, Asteroidea, was present at the cone but absent at the NW Caldera site. One possible explanation is the area sampled at the NW Caldera. Previously, NW Caldera has been classified as a black smoker dominant vent site (de Ronde et al. 2005). In this survey, no active black smokers were sighted, and very few remnant chimneys were observed. The absence of active black smokers suggests that the NW Caldera track line missed the black smoker vent field, and the survey was performed on the outer regions of the vent sites where potential diffuse venting was occurring. The type of venting is a likely explanation for species diversity. Diffuse vent sites are found to support a wider variety and larger populations of organisms (Fisher et al. 2007). If diffuse venting was surveyed at NW Caldera opposed to black smoker venting, which was observed in the de Ronde et al. (2005) study, this provides possible reasoning behind the increase in diversity and density of assemblages observed.

Between the two sites, highest density biological assemblages were found at the cone site, which is consistent with previous observations by de Ronde et al. (2005). This trend was expected considering the cone is dominated by highly active diffuse venting. Diffuse vent sites around the world have been found to support the highest density biological communities (Fisher et al. 2007). The presence of high density assemblages in these vent areas suggests that water properties created under the influence of diffuse vents provide the most resources and are most suitable for sustaining life of vent organisms.

Environmental Stressors

Although little variation was seen in between site species composition and diversity, the intensity of environmental stressors did vary between sites. This variation in vent properties was found to significantly affect some organisms present at each site. Vent environment variables are shown to have strong effects on the colonization of vent fauna in specific regions; some effects are stronger than others.

Salinity

Salinity appears to have the weakest overall effect on biology, suggesting that differences in salt ion concentration do not significantly impact the survival of organisms. This can be seen specifically along the NW Caldera tow, where one large increase in salinity was seen, and correlated with a dense assemblage of long-necked barnacles (Fig. 9). The long-necked barnacles colonizing the NW Caldera site showed significant relationships with lower salinity levels, however, considering the assemblage was still present under the highest salinity anomaly found in the NW Caldera survey, salinity was not a large enough contributing environmental factor to prohibit barnacle colonization in this area. Most likely the other environmental stressors such as temperature and Eh level had a larger effect on colonization, making salinity levels of minimal importance to the organisms.

Turbidity

It is known that turbidity normally increases in areas of active venting due to the expulsion of particulate matter in the hydrothermal fluids (de Ronde et al. 2007). The correlation of turbidity with higher temperatures and decreased Eh levels at the cone site follows the trends generally seen in areas of venting. However, being on the seafloor boundary, there is high probability of currents mixing up sediment and depositing them into the water column. This process has significant potential to increase turbidity levels, making it likely that turbidity measurements taken are not strictly a measurement of particulate matter caused by the hydrothermal plume, but rather a mixture of the two (de Ronde et al. 2007). Based off this, effects on macrofauna due to overall turbidity are possible to determine, however, plume specific turbidity effects caused by particulate metals cannot be determined.

The majority of taxa colonized regions of higher turbidity, which was predicted. High biological assemblages of vent specialized organisms seen in these areas suggests turbidity is a significant factor, and increased turbidity is a proxy for increased chemical availability in the water column, which is used in chemosynthesis and allows for the survival of macrofauna. I expected that Crustaceans would colonize high turbidity regions. However, it is surprising to find Poriferans in these areas because they are susceptible to clogging by particulates. Sponges filtering methods for survival would make turbid waters seen problematic, with threats of obstructing their pores. It appears that sponges have adaptations to survive in these turbid environments and prevent particulate matter from becoming an issue in their survival.

Temperature and Eh

Temperature and Eh levels had stronger effects and revealed a more definite pattern in taxa distributions than salinity and turbidity. The high temperature and negative Eh values recorded at the cone site indicate significant venting, and high chemical content (most likely H_2S) in the hydrothermal fluids. Lower temperatures and higher Eh levels at the NW Caldera site suggest that venting was less intense, or alternatively that we missed the vent field in our survey and were on the outer limits of the vent site. The temperatures recorded at the NW Caldera (range 3.12˚C to 3.35˚C) were unexpected. Black smoker vents release fluids up to 400˚C (Fisher et al. 2007), and although these fluids cool as they mix with ambient seawater, temperatures were expected to be higher than 3.5˚C. This is another observation which suggests we were outside the black smoker vent field.

At both sites, Crustaceans colonized the higher temperature and lower Eh environments available, suggesting they are vent specialized organisms and have highest survival rates in warm, high chemical venting environments. At the cone site, three areas of negative Eh values were discovered, all of which correlated with high density faunal assemblages. Two of these regions were also correlated with increased temperatures. These observations support the idea that many fauna are dependent upon venting regions for survival. Warmer than ambient temperatures and high chemical levels are byproducts of venting and contribute to organism survival.

This trend towards high temperature and low Eh levels is not the case for all vent fauna. The majority of Poriferans and Hydrozoans were found colonizing low temperature, high Eh environments at both the NW Caldera and the cone. The correlation between these taxa with low temperature and high Eh suggests that these macrofauna do not require highly concentrated resources from large inputs by hydrothermal vents. Survival is possible further from the vent source. It is likely that the effects of hydrothermal fluids on the surrounding water column are not strictly localized around the vents themselves, but rather diffuse through the water column to the outer regions of vent fields. Waters occurring at greater distances away from the vent source are more dilute in their physical and chemical properties. Temperatures are lower and high chemical levels are not likely to be present, however the diluted vent fluid was still sufficient enough to support certain types of life adapted to these conditions. There was also the possibility that high chemical concentrations, specifically H_2S, may be damaging to the specific organisms, which may lack the adaptations to survive in high concentrations (Fisher et al. 2007), and therefore colonize the more dilute chemical environments.

The variations in extent of environmental conditions particular organisms are able to colonize have implications for the ecological adaptations they have to these vent environments.

The Crustaceans are found colonizing the higher temperature and lower Eh (higher chemical concentration) areas of both the NW Caldera and the cone vent fields, whereas the majority of Poriferans and Hydrozoans are found colonizing lower temperature and higher Eh (lower chemical concentration) areas of each site. The mobile, non-vent specific phyla including the Echinoderms and Chordates, generally have no significant relationship to temperature and Eh. These observations imply that Crustaceans are better adapted to living in the extreme vent environments. They have greater tolerances to live in warmer temperatures and higher chemical concentrations, allowing them to colonize areas in close proximity to the vent source (Scearce 2006). The sessile Poriferans and Hydrozoans appear to have lower tolerances for and lack adaptations to the extreme conditions, and are more likely to colonize areas closer to ambient sea temperature with lower chemical concentrations. This seems to be their adaptation to vent environments, causing them to colonize further away from vent sources. The mobile Echinoderms and Chordates likely show no significant relationship because they can easily relocate throughout the vent field. There is potential that these mobile animals are not specialized for vent environments, and only move into the vent fields periodically to pursue food (Scearce 2006). These variations in colonization observed between different types of phyla suggest that temperature and chemical concentrations do in fact restrict colonization to many vent macrofauna (Fisher et al. 2007), however others are not greatly affected.

Isolating Environmental Factors

Strong correlations occurred between three of the environmental factors, making isolation of the factors and their individual effects on biological communities difficult to determine. In some instances turbidity correlated with temperature and Eh, however, this was not a reoccurring trend. Turbidity anomalies were not found at every temperature or Eh anomaly, allowing this factor to be isolated. Dense faunal assemblages formed in areas where turbidity anomalies were absent, suggesting turbidity contributes to assemblages, but is not the underlying factor in fauna growth and survival. Temperature and Eh appear to have a larger influence on community structure.

Temperature and Eh were the two factors with the strongest correlation. In nearly every instance of a temperature increase, a decrease in Eh level was seen, and the densest biological communities were found. The strong correlation between these two variables made it difficult to determine which one has a stronger effect on biological communities. One area along the Brothers cone tow showed the presence of a large Eh anomaly without an associated temperature increase. Although an increase in temperature was not seen, a dense assemblage of long-necked barnacles was observed in this area. This anomaly and the presence of biology suggest that Eh is potentially a stronger factor than temperature in its effects on macrofauna. This does not rule out temperature as a strong contributor to shaping faunal assemblages, however. Although there was an assemblage present at the isolated Eh anomaly, it was small compared to the assemblages observed where temperature and Eh are correlated (Fig. 4).

Based off these observations, Eh appears to be the strongest environmental factor contributing to large macrofauna communities. Being a proxy for chemical concentration in the water column, this means that the chemical resources available to vent specialized organisms are the most vital factor for their survival in these extreme ecosystems. Higher chemical concentrations throughout the water column may result in a chain of events through the food web. More chemical resources available to vent bacteria result in an increase in chemosynthesis and more food production for vent fauna. Food may become more readily available, and in turn support more life and denser biological communities.

Although evidence of chemistry being the most important factor in survival is reasonable, the fact that only one isolated Eh anomaly occurred during this survey, and no isolated temperature anomalies were observed, is not sufficient enough to draw any accurate conclusions on the issue of isolating environmental variables. Determination of the underlying cause of dense biological communities will require an approach that eliminates the effects of the other three environmental factors on biology. Similarly, quantifying exactly how much chemistry contributes to the colonization of biology of Brothers volcano can not be determined through this survey, and further research on organism utilization of resources is an appropriate next step to learn more about the biology of Brothers.

Future Research

Suggested future research for this study is to determine more specific properties of the hydrothermal vent influenced waters, in particular, larval settlement rates and food content. With proper species identification of the organisms found during this survey, larval settlement traits may be determined. Do larvae of the observed species settle in particular environmental conditions? If so, determining what conditions are suitable for different types of larvae may help explain more thoroughly why organism assemblages are found where they are. There is potential that assemblages are found based entirely off of the locations which are suitable for larval settlement. Another possibility is that the environmental stressors considered in this survey effect settlement rates and the number of larvae able to colonize an area.

Food content of fluids should also be considered. By determining the approximate distance of faunal assemblages from the vent source and gathering data on current flow rates through the NW Caldera and cone vent fields, the age of the vent water when it reaches the faunal communities can be determined. After fluids are expelled from the vents, chemosynthetic bacteria will begin to increase in population based off the chemical content of the water. As hydrothermal water ages, an increase in bacteria concentration will likely follow. By determining an approximate bacterial growth rate and the age of the water, bacteria content in the vent fluid as it reaches the faunal assemblages can be approximated. This may be one way to assess the food availability present in the water column, and to determine if this is another environmental factor that has an effect on biological communities. Both of these issues will contribute a great deal of knowledge about the biology colonizing the Brothers volcano vent site, however, extensive future research is necessary.

Conclusions

In comparison with past surveys, the phyla composing each site have changed. Species diversity as well as density of faunal assemblages has increased at both the cone and NW Caldera. This change in biological community structure suggests significant shifts in environmental conditions have potentially occurred, allowing the colonization of new taxa as well as the disappearance of others. This observation supports the idea that hydrothermal vent ecosystems are variable environments with constantly changing environmental stressors, requiring organisms to be adaptable to fluxing conditions.

Temperature, Eh, salinity and turbidity all acted as environmental stressors on vent macrofauna, however each factor affected different fauna in different ways. A comparison of environmental factors between the cone and NW Caldera sites suggests there is little variation in the effects environmental conditions have on faunal assemblages. At both sites, temperature and Eh had the strongest correlations with taxa. Crustaceans colonized areas with high temperature and low Eh, making them appear to be vent specialized organisms that prefer extreme vent environments in close proximity to vent sources. Poriferans and Hydrozoans colonized the less extreme vent environments with cooler temperatures and higher Eh levels, suggesting they are adapted to live in more dilute chemical environments further away from vent sources. Turbidity had significant effects on biology, but patterns were slightly variable and difficult to distinguish due to other environmental processes potentially contributing to turbidity levels. In most cases, Crustaceans and Poriferans colonized high turbidity environments and Hydrozoans colonized less turbid environments. Salinity had minimal effects on most phyla present at each site. Mobile organisms belonging to the phyla Echinodermata and Chordata generally showed no significant correlation with specific habitats.

Strong correlations between temperature, Eh and turbidity were observed. Significant trends were found between environmental stressors at each site, in which high temperatures were correlated with low Eh values and high turbidity. This strongly suggests these are areas of active hydrothermal vent activity. These areas are also the regions where highest density biological assemblages were found, suggesting increased venting and chemical input into the water column significantly impacts biological density. However, these strong correlations make it difficult to isolate effects each individual environmental factor has on macrofauna. Given high temperatures and low Eh levels are seen in some areas without the presence of turbidity, this rules out turbidity as the major underlying factor supporting dense communities. Temperature and Eh correlations are more difficult to isolate because they are so strongly correlated. Nearly every temperature increase is paired with a drop in Eh levels, with the exception of one in which a drop in Eh is observed without a temperature anomaly. The presence of a dense long-necked barnacle community suggests that Eh, and therefore chemical concentrations, are potentially the most important environmental factor effecting organism colonization and survival.

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References

De Ronde, C.E.J., E.T. Baker, G.J. Massoth, J.E. Lupton, I.C. Wright, R.A. Freely and R.R. Greene. 2001. Intra-oceanic subduction-related hydrothermal venting, Kermadec volcanic arc, New Zealand. Earth and Planetary Science Letters. **193**: 359-369.

De Ronde, C.E.J., E.T. Baker, G.J. Massoth, J.E. Lupton, I.C. Wright, R.J. Sparks, S.C. Bannister, M.E. Reyners, S.L. Walker, R.R. Greene, J. Ishibashi, K. Faure, J.A. Resing and G.T. Lebon. 2007. Submarine hydrothermal activity along the mid-Kermadec Arc, New Zealand: large-scale effects on venting. Geochem. Geophys. Geosyst. **8**, Q07007, doi: 10.1029/2006GC001495.

De Ronde, C.E.J., M.D. Hannington, P. Stoffers, I.C. Wright, R.G. Ditchburn, A.G. Reyes, E.T. Baker, G.J. Massoth, J.E. Lupton, S.L. Walker, R.R. Greene, C.W.R. Soong, J. Ishibashi, G.T. Lebon, C.J. Bray, and J.A. Resing. 2005. Evolution of a submarine magmatic-hydrothermal system: Brothers Volcano, Southern Kermadec Arc, New Zealand. Economic Geology. **100**: 1097-1133.

Fisher, C.S., K. Takai and N. Le Bris. 2007. Hydrothermal Vent Ecosystems. Oceanography. **20**: 14-23.

Gardner, J.P.A., M.J. Curwen, J. Long, R.J. Williamson, and A.R. Wood. 2006. Benthic community structure and water column characteristics at two sites in the Kermadec Islands Marine Reserve, New Zealand. New Zealand Journal of Marine and Freshwater Research. **40**: 179-194.

Lutz, R.A. and M.J. Kennish. 1993. Ecology of deep-sea hydrothermal vent communities: a review. Reviews of Geophysics. **31**: 211-242.

Ramirez-Llodra, E., T.M. Shank, and C.R. German. 2007. Biodiversity and biogeography of hydrothermal vent species: Thirty years of discovery and investigations. Oceanography. **20**: 30-41.

Rowden, A.A., M.R. Clark, S. O'Shea, and D.G. McKnight. 2003. Benthic biodiversity of seamounts on the souther Kermadec volcanic arc. Marine Biodiversity Biosecurity Report No. 3. 23 p.

Scearce, C. 2006. Hydrothermal Vent Communities. CSA Discovery Guides. http://www.csa.com/discoveryguides/discoveryguides-main.php

Soule, S.A., D. J. Fornari, M. R. Perfit, and K.H. Rubin. 2007. New insights into mid-ocean ridge volcanic processes from the 2005-2006 eruption of the East Pacific Rise, 9°46′N–9°56′N. Geology. **35**: 1079-1082, doi: 10.1130/G23924A.1.

Stott, M.B., J.A. Saito, M.A. Crowe, P.F. Dunfield, S. Hou, E. Nakasone, C.J. Daughney, A.V. Smirnova, B.W. Mountain, K. Takai, and M. Alam. 2008. Culture-independent characterization of a novel microbial community at a hydrothermal vent at Brothers volcano, Kermadec Arc, New Zealand. J. Geophys. Res., **113**, doi: 10.1029/2007JB005477.

Van Dover, C.L. 2000. The ecology of deep-sea hydrothermal vents. Princeton University Press.

APPENDIX 1

Summary of MATLAB Kruskal-Wallis one way ANOVA results for determination of statistically significant relationships between individual phyla and environmental stressor. Results for the cone and NW Caldera tows on Brothers volcano

Tow 4: Brothers Cone			Environmental Stressor											
			Temperature (˚C)			Eh			Salinity			Turbidity		
Phylum	Class		Median (˚C)	High/Low	p value	Median	High/Low	p value	Median	High/Low	p value	Median	High/Low	p value
Chordata			N/A	N/A	0.509	N/A	N/A	0.942	N/A	N/A	0.672	0.324	N/A	0.658
Cnidaria	Anthozoa		No statistical tests performed due to low population numbers											
	Hydrozoa		3.3	Low	1.28E-06	189	High	0.0001	34.51	High	1.76E-05	0.317	Low	0.012
Crustacea	Malacostraca													
		Crab	3.9	High	0.0003	-80	Low	3.98E-09	34.5	Low	0.002	0.33	High	0.001
		Shrimp	4.3	High	0	4	Low	9.26E-12	34.45	Low	0	0.33	High	1.63E-06
	Maxillopoda		3.9	High	0	-8	Low	0	34.49	Low	0	0.324	High	2.58E-12
Echinodermata	Asteroidea		3.15	Low	0.004	4.03	High	0.023	35.55	High	0.015	N/A	N/A	0.695
	Echinoidea		N/A	N/A	0.942	N/A	N/A	0.895	N/A	N/A	0.874	0.336	N/A	0.113
	Ophiuroidea		No statistical tests performed due to low population numbers											
Mollusca	Bivalvia		No statistical tests performed due to low population numbers											
	Gastropoda		No statistical tests performed due to low population numbers											
Porifera			3.1	Low	1.34E-06	200	High	2.79E-06	34.55	High	1.27E-05	0.33	High	0.006

APPENDIX 1 (*Cont.*)

Tow 6: NW Caldera						Environmental Stressor								
			Temperature (°C)			Eh			Salinity			Turbidity		
Phylum	Class		Median (°C)	High/Low	p value	Median	High/Low	p value	Median	High/Low	p value	Median	High/Low	p value
Chordata			N/A	N/A	0.199	95	High	0.014	N/A	N/A	0.696	0.342	Low	0.025
Cnidaria	Anthozoa		No statistical tests performed due to low population numbers											
	Hydrozoa		3.22	High	4.81E-05	40	Low	0.016	N/A	N/A	0.22	0.336	High	0.0008
Crustacea	Malacostraca													
		Crab	N/A	N/A	0.178	20-30	Low	6.50E-06	N/A	N/A	0.401	0.350	High	0.002
		Shrimp	3.22	High	0.005	20-30	Low	1.96E-11	N/A	N/A	0.127	0.373	High	5.88E-08
	Maxillopoda		3.26	High	0	20-30	Low	3.37E-12	34.54	Low	2.89E-10	0.336	High	7.00E-13
Echinodermata	Asteroidea		Absent from site											
	Echinoidea		N/A	N/A	0.389	N/A	N/A	0.301	N/A	N/A	0.495	N/A	N/A	0.724
	Ophiuroidea		No statistical tests performed due to low population numbers											
Mollusca	Bivalvia		No statistical tests performed due to low population numbers											
	Gastropoda		No statistical tests performed due to low population numbers											
Porifera			3.15	Low	7.52E-07	110	High	0.0004	N/A	N/A	0.447	0.324	Low	0.0002