

A CHARACTERIZATION OF A HYDROTHERMAL VENT COMMUNITY FROM A
DIFFUSE FLOW VERTICAL WALL OF “THE TOWER”
SULFIDE EDIFICE AT THE
JUAN DE FUCA RIDGE

A Thesis
Submitted To
the Temple University Graduate Board

In Partial Fulfillment of the Requirements of the Degree
MASTERS OF SCIENCE

By
Michele Grinar
August, 2011

Thesis Approvals:

Erik Cordes, Ph.D. Thesis Advisor, Biology

Department _____

Robert Sanders, Ph.D. Biology

Department _____

ABSTRACT

The Juan de Fuca Ridge, located 400 km off the coast of Washington State, is home to unstable and unpredictable hydrothermal vent sites where chemosynthetic communities flourish. In 2007 the manned submersible ALVIN retrieved a *Ridgeia piscesae* tubeworm community in its entirety from the side of the Tower sulfide edifice from the Endeavor segment of the Juan de Fuca Ridge (47 55.416720 N, 129 6.487020 W, at a depth of 2269 m) using the Bushmaster Jr. collection device. The collection was analyzed for community structure and the data collected were compared to that from several other hydrothermal vent communities. It was determined that substrate composition is a factor that heavily influences community structure. The data were then compared to the community succession model developed by Sarrazin et. al. in 1997 and 1999 (Sarrazin et. al. 1997, Sarrazin and Juniper 1999). The Tower community was found to expand the model as a new community succession classification; that of community iii low flow. The Tower community was then analyzed for diversity, structure and tubeworm morphology in conjunction with two other communities from differing substrata. The *Ridgeia piscesae* tubeworms were found to be of the “long skinny” morphotype, one that was previously thought to only reside on basaltic substrate. The Tower community has similar species richness and higher species evenness than those from basaltic substrate, but similar richness and lower evenness than those from sulfide. This community type combines the characteristics of those from both substrata, resulting in a community with diversity and structure that is an intermediary between sulfide and basaltic substrates.

ACKNOWLEDGEMENTS

Erik Cordes, Ph.D.

Amy Freestone, Ph.D.

Joel Sheffield, Ph.D

Robert Sanders, Ph.D.

Katherine Songile

Sarah Kazarnowicz

TABLE OF CONTENTS

ABSTRACT..... ii

ACKNOWLEDGEMENTS..... iii

LIST OF TABLES vi

LIST OF FIGURES vii

CHAPTER PAGE

1. INTRODUCTION AND BACKGROUND

 Introduction.....1

 Hydrothermal vents.....3

Ridgeia piscesae.....5

 The Juan de Fuca Ridge8

 Hydrothermal vent community succession.....11

 The Tower hydrothermal vent community13

2. METHODS AND MATERIALS.....15

 Collection, preservation and processing15

 Measurements and biomass of *Ridgeia piscesae* and associated fauna.....16

 Multi-dimensional scaling analysis of community structure between the Tower community and six community types described by Sarrazin et. al.....17

 Multi-dimensional scaling analyses of community structure between The Tower community and several others previously described18

 A comparison of communities from the Tower and the Easter Island hydrothermal site19

 Measurement of diversity19

 Sample and data collection20

3. RESULTS

Multi-dimensional scaling plot of the Tower community and six community types previously described by Sarrazin et. al.....	21
Multi-dimensional scaling plot of the Tower community and several others previously studied.....	22
<i>Ridgeia piscesae</i> analysis.....	24
A comparison of communities from the Tower and the Easter Island hydrothermal sites.....	26
Diversity indices of the Tower, Easter Island and Hell 1 communities.....	28

4. DISCUSSION

Community succession classification of the Tower community	30
The Tower community's role as an intermediary community between basalt and sulfide substrata	31
Conclusion	33
REFERENCES	38

LIST OF TABLES

Table	Page
1: Community succession model (Sarrazin et. al. 1997)	12
2: Diversity indices for the Tower, Easter Island and Hell 1	28
3: All communities listed in this study including site name, location, temperature, and substrate and fluid flow type.....	35
4: Species list for the Tower community	36

LIST OF FIGURES

Figure	Page
1: Undersea Ridges and subduction zones of the world's oceans (Qiu 2010).....	3
2: Underwater volcanic eruption at the East Pacific Rise (Qiu 2010).....	3
3: Hydrogen sulfide rich hydrothermal fluid spewing from a sulfide edifice chimney (photo credit: Erik Cordes)	3
4: Examples of various structures that can be found on hydrothermal vent chimneys (Modified from Sarrazin et. al. 1999).....	5
5: <i>Ridgeia piscesae</i> and associated fauna (ALVIN Framegrabber).....	8
6: The Juan de Fuca Ridge (Tsurumi 2003) (Yau et. al. 2009) (Yau et. al. 2009)	10
7: The Faulty Towers (Edifice Rex Sulfide Recovery Project, Delaney et. al.).....	11
8: The Bushmaster collecting the Tower community (ALVIN Framegrabber)	15
9: Multi-dimensional scaling analysis of community succession between The Tower and six others previously studied by Sarrazin et. al.....	21
10: Multi-dimensional scaling analysis of community structure between The Tower and several others based on substrata	22
11: Multi-dimensional scaling analysis of community structure between The Tower and several others based on fluid flow and collection method.....	23
12: Size frequency distribution of <i>Ridgeia piscesae</i> from The Tower	24
13: Bray- Curtis similarity profile between the entire Tower tubeworm aggregation and the different spatial orientations of the Easter Island tubeworm aggregation	26

CHAPTER 1

INTRODUCTION AND BACKGROUND

1.1 Introduction

One of the greatest advances of oceanography and marine biology has been the discovery of hydrothermal vents and the species that are endemic to them. Hydrothermal vents (Fig. 1), some of the most geologically active habitats in the deep sea, are considered model systems for population study (Kelly et. al. 2007). In stark contrast to the desert of most of the deep sea, hydrothermal vents are unstable areas that result in sudden community extinctions (Tunnicliffe et. al. 1997) and colonizations (Levesque et. al. 2006, Kelly et. al. 2007, Kelly and Mataxas 2008). Here, volcanic eruptions (Fig. 2) result in the emission of fluid rich in reduced chemicals such as sulfide which vents through cracks in the basaltic crust of the sea floor. High jagged sulfide edifices are created from these precipitated chemicals, and fluid emits diffusely through the sulfide walls, or vents through smoking chimneys that protrude from the top and sides (Sarrazin et. al. 1999) (Fig.3). This chemical-rich fluid ranges in temperatures from 1°C above ambient up to 300°C (Van Dover 2000).

It is at these sites that colonies of bacterial symbiont-dependent tubeworms, under certain environmental conditions, settle and flourish, utilizing hydrogen sulfide as their energy source (Bergquist et. al 2007, Sarrazin et. al. 1997, Tsurumi 2003). The surface area of their chitinous tubes provides ample habitat for scavengers, grazers and predators (Fig. 5), creating dense communities of endemic species (Urcuyo et. al. 1998, Urcuyo et. al. 2003, Tunnicliffe et. al. 1997, Govenar et. al. 2002, Kim and Mullineaux 1998).

Extensive studies have been conducted on hydrothermal vents at sites throughout the world including the Mid Atlantic Ridge (Cuvelier et. al. 2011), the East Pacific Rise (Spiess et. al. 1980) and the Juan de Fuca Ridge. The Juan de Fuca Ridge is among the most intensively studied hydrothermal vent centers worldwide (Kelley et. al. 2001, Yao et. al. 2009, Govenar et. al. 2002, Bergquist et. al. 2007, Sarrazin et. al. 1997, Sarrazin and Juniper 1999, Urcuro et. al. 2003, Tunnicliffe et. al. 1997, Tsurumi 2003, Limen et. al. 2007) and several communities from various sites featuring different combinations of substratum and fluid flow and have been described and categorized (Sarrazin et. al. 1997, Govenar et. al. 2002). A community retrieved in its entirety in 2007, however, was collected from a vertical edifice that had not previously been sampled, and its substrate (sulfide) and fluid flow (low) combination have not previously been as well categorized as others. This community may serve as an intermediary community, linking the faunal characteristics of community types from sulfide edifices to those from the basaltic sea floor.

Understanding how hydrothermal vent species interact with each other on a community scale is a key component of developing a framework from which their relationship with the rest of the deep sea can be conceptualized. Larval dispersal among chemosynthetic communities occurs between the patchy vent environments over stretches of kilometers of barren deep sea, and vents can occasionally be colonized by non endemic species (Sarrazin et. al. 1997). Anthropogenic activities such as fishing and mineral harvest are beginning to affect the deep sea environments, and understanding how the hydrothermal vent community interacts with the rest of the deep sea is necessary if we are to determine the effect of increased anthropogenic activity on chemosynthetic

communities. A structural and functional description of this previously unexamined community will add to the existing foundation of knowledge of hydrothermal vent community interactions at the Juan de Fuca Ridge.

1.2 Hydrothermal vents

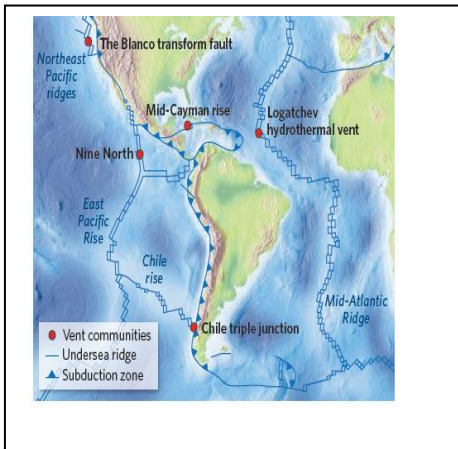


Fig. 1: Undersea Ridges and subduction zones of the world's oceans (Qiu 2010).



Fig. 2: Underwater volcanic eruption at the East Pacific Rise (Qiu 2010)

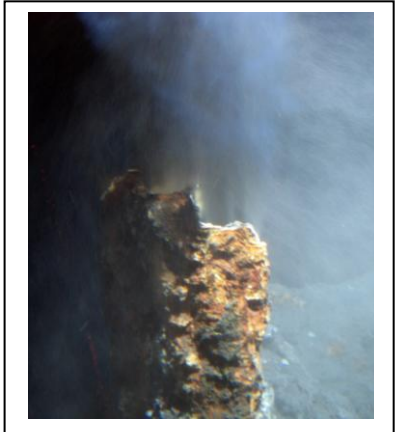


Fig 3: Hydrogen sulfide rich hydrothermal fluid spewing from a sulfide edifice chimney (photo credit: Erik Cordes)

The first hydrothermal vents were discovered in 1977 (Lonsdale 1977) at the East Pacific Rise (Spiess et. al. 1980) (Fig.1, 2). Since then vents have been found virtually worldwide (Fig.1) (Qiu 2010, Van Dover 2000), at mid ocean ridges and the back arc basins associated with subduction zones (Yao et. al. 2009, Van Dover 2000). The mid ocean ridges of the world are areas of sea floor spreading and part of an almost continuous volcanic mountain chain that extends more than 75,000 km worldwide (Van Dover 2000). Seismic activity such as earthquakes, and magmatic activity such as underwater volcanic eruptions (Tunnicliffe et. al. 1997) (Fig. 2) and magma extrusion

during sea floor spreading (Tsurumi 2003, Davis et. al. 2004) occur along these ridges (Davis et. al. 2004). These tectonic settings cause extreme temperatures and toxicity (Kim and Mullineaux 1998) from the hydrothermal vent fluid, which reaches temperatures of 300°C and has high concentrations of reduced chemicals, emitting from the fractured sea floor and mixing with the cold ambient seawater (4°C) (Sarrazin et. al. 1999, Van Dover 2000). These cracks are scattered along the sea floor, which is composed of basalt and has a glass like appearance. In the oceanic crust, sulfate (SO₄) is reduced to hydrogen sulfide (H₂S) through high temperature rock- seawater interactions (Sievert et. al. 2007), and then exits the sea floor via hydrothermal fluid and mixes with the ambient seawater. Anhydrite mounds are formed (Van Dover 2000) until the hydrothermal fluid bonds with iron, which precipitates out of the fluid to form pyrite (FeS₂) structures with a jagged spire-like appearance (Fig. 3,7) called sulfide edifice chimneys (Sarrazin et. al. 1997, Van Dover 2000). The hydrogen sulfide rich hydrothermal fluid is emitted in a diffuse manner from porous portions of the edifice at moderate temperatures (under 30°C) or vents at high temperatures (up to 300°C) (Sarrazin and Juniper 1999, Van Dover 2000) in a geyser-like fashion out of openings in the sides and top of the chimney (Fig.3, 4a). A variety of structures can form on these chimneys such as beehives and flanges (Fig.4). Beehives (Fig. 4b) are mostly comprised of mounds of anhydrite, sulfate molecules that have precipitated over a smoking chimney that holds hydrothermal fluid (under 150°C) (Sarrazin et. al. 1997, Sievert et. al. 2007, Van Dover 2000). Flanges (Fig. 4c) are structures that jut from the side of the vertical wall and hold a pool of hydrothermal fluid (Sarrazin et. al.1997, Van Dover 2000). Chemosynthetic communities have been observed to occupy an entire flange (Sarrazin et.

al. 1999) with venting fluid, flourish directly above or below a smoking chimney with venting fluid, protrude from porous sulfide (FeS_2) walls with diffuse fluid flow (Fig. 5), or settle next to or on a crack in the basaltic crust of the sea floor that is venting fluid.



Fig. 4: Examples of various structures that can be found on hydrothermal vent chimneys: a- smoker vent, spewing hot fluid from which minerals will precipitate, building the edifice. b- beehive, anhydrous substrate topping the edifice. c- flange, extruding from the side of the edifice, d- vertical wall of the edifice. e- base of the edifice (modified from Sarrazin et. al. 1999)

1.3 *Ridgeia piscesae*

Ridgeia piscesae (Jones 1985) (phylum annelida, class polychaeta, order sabellida, family siboglinidae) and other tubeworms are sometimes referred to as vestimentiferans, a specific group of siboglinids with a vestimentum, a collar like structure below the plume which houses the brain, heart and reproductive organs and anchors the tubeworm into its tube. *Ridgeia piscesae* (Fig. 5) is the most common tubeworm species as well as being the biomass dominant species at Northeast Pacific hydrothermal vents. In contrast to *Riftia pachyptila*, the giant tubeworms of the East Pacific Rise which can reach up to three meters in length (Govenar et. al. 2005), *Ridgeia*

piscesae range in length from a few centimeters to just over one meter (Urcuyo et. al. 2003, Urcuyo et. al. 1998). Their exoskeletons consist of a chitinous tube which covers the entire body. The tubes have pronounced horizontal flares of chitin which result in a segmented appearance. The posterior ends of the tubes typically tangle together in what has been described as a rootball (Urcuyo et. al. 2003), which anchors at the substrate. These ends are more flexible and translucent than the rest of the tubes. Each tube has a flared anterior end to allow for the emergence of the feathery plume. The plume has been described as the site for the uptake of sulfide, its energy source (Somero et. al. 1989), and is bright red in color due to the presence of hemoglobin, the transport protein molecule for sulfide. It has also been suggested that the posterior ends, with their thinner chitinous walls and close proximity to venting or diffusing hydrothermal vent fluid, may be the site of sulfide uptake in the some morphotypes of *Ridgeia piscesae* (Urcuyo et. al. 2003). *Ridgeia piscesae* does not have a gastro-intestinal system, and instead a symbiotic relationship between the tubeworm and sulfur oxidizing bacteria exists (Sievert et. al. 2007, Flores and Hourdez 2006). This γ proteo bacteria is housed in the tubeworm's body in a structure called the trophosome. The bacteria uses energy from sulfide in the same way that plants use energy from photons of light, as a means of transforming carbon in from its inorganic form (CO_2) to an organic form (glucose) as the tubeworms' nutrition source. It accepts hydrogen sulfide and oxygen molecules after they have been bound to and transported by hemoglobin molecules, the protein molecule in vestimentiferan polychaetes that binds sulfide (Somero et. al. 1989). Tubeworms have two types of hemoglobin, a small spherical and a large hexagonal, both being capable of binding hydrogen sulfide and oxygen at the same time. This crucial simultaneous binding of

sulfide and oxygen is reversible (Flores and Hourdez 2006), a necessary aspect of tubeworm metabolism as the compounds must be released inside the trophosome housing the symbiotic bacteria to allow the organism to acquire nutrition and exist unharmed by its toxic environment.

It was first thought that *Ridgeia piscesae* tubeworms were actually members of several species, due to their differences in morphology, but it was determined that one species did in fact exist (Southward 1995). Urcuyo et. al. described one specific morphotype of *R. piscesae* as “long skinny”, hypothesized their mode of sulfide uptake, and determined that the “long skinny” morphotype is found primarily on basalt and not on sulfide substrate (Urcuyo et. al. 1998). The same group later examined a *Ridgeia piscesae* “long skinny” community from 1994 to 1996 to determine the tubeworms’ growth rate, size frequency distribution, predation rate, mortality and anatomical site of sulfide uptake. Urcuyo et. al. hypothesized that “long skinny” *Ridgeia piscesae* acquired sulfide through the rootball primarily, with the secondary uptake site being the plume. This was due to the structure of the “long skinny” tubeworm as well as the typical substrate composition and fluid flow conditions found in association with the “long skinny” tubeworm community. “Long skinny” tubeworms are the longest of the *R. piscesae* morphotypes, with their plumes sometimes extending far beyond the scope of hydrothermal fluid flow. The flow around this morphotype has been seen as diffuse as opposed to venting (or in between basalt cracks with venting), and this morphotype has been associated with diffuse flow areas of the basaltic sea floor with the rootballs of these aggregations found nestled directly on the basalt at the site of the diffuse flow (or in between basalt cracks) (Urcuyo et. al. 2003).

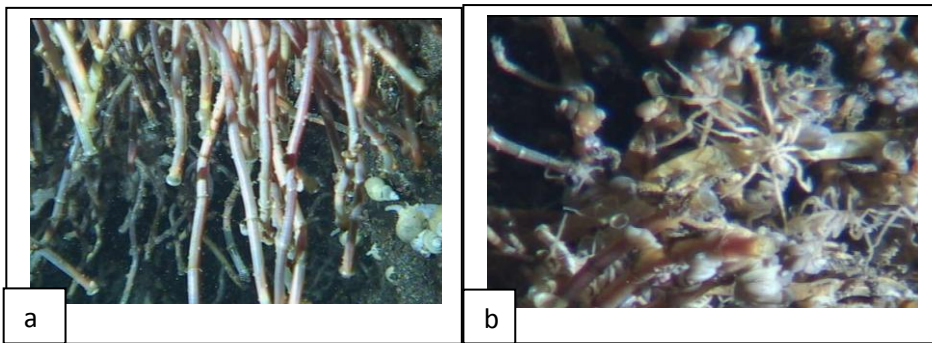


Fig.5 a- *Ridgeia piscesae* anterior ends b-pycnogonids (*Ammonothea verena*) and gastropods (*Provanna variabilis*) on the tubes of the *Ridgeia piscesae* (photo credit: ALVIN framegrabber)

1.4 The Juan de Fuca Ridge

The Juan de Fuca Ridge is located on a mid ocean spreading center in the northeast Pacific Ocean 350- 400 km from Washington state (Fig. 6a) (Sarrazin et. al. 1997, Yao et. al. 2009), with depths reaching up to over a mile below the surface. Six distinct geographic segments make up this ridge (Tsurumi 2003); Middle Valley, Endeavor (Fig. 6b), Cobb, Axial, CoAxial, Vance and Cleft. Segments are partitioned into hydrothermal fields (Fig. 6c) and each field contains clusters of vent sites within an area.

The Endeavor Segment of the Juan de Fuca Ridge (Fig.6a) is located in the northern part of the ridge, at a depth of 2200 m (Sarrazin et. al. 1997). In the Endeavor segment, the Mothra hydrothermal vent field is the southern-most field (Fig.6b,c), lying 2.7 km south of the Main Endeavor field (Yau et. al. 2009, Kelley et. al. 2001) and its communities have not been studied as thoroughly as those from the rest of the Endeavor segment, or other segments such as Axial or CoAxial. Mothra's geology differs somewhat from the rest of the Endeavor segment in that it's edifices are much taller (up to 20 m) (Yau et. al. 2009, Kelley et. al. 2001), they are surrounded by diffuse hydrothermal flow, and they feature fewer smoking chimneys than those from the rest of

the Endeavor segment (Kelley et. al. 2001). Mothra contains clusters of hydrothermal vent sites (Kelley et. al. 2001). One of these clusters, a sulfide chimney edifice group called the Faulty Towers (Fig.6c, 7), was first mapped in 1997 (Kelley et. al. 2001). In keeping with Mothra's geological composition, the Faulty Towers is a cluster of very steep and tall sulfide chimney edifices. Seismic events cause edifices to fall frequently, but currently, the tallest and most centralized is named The Tower (Fig.7a, 8) ($47^{\circ}55'N$, $129^{\circ}06'W$) (Edifice Rex Sulfide Recovery Project, Delaney et. al.).

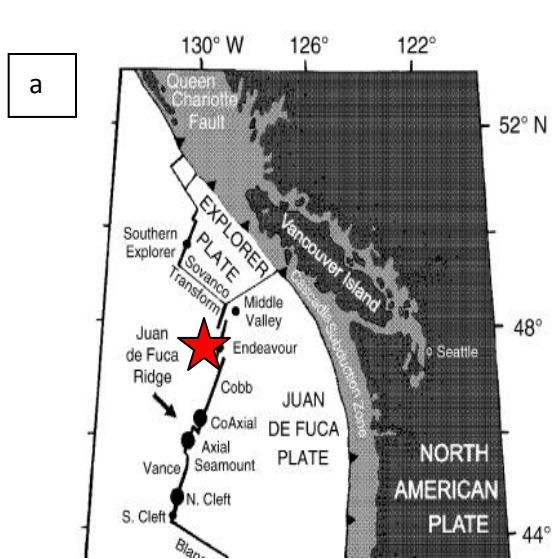


Fig. 6: a- The Juan de Fuca Ridge (Tsurumi 2003) b- The Endeavour Segment (Yau et. al. 2009) c- The Mothra Hydrothermal Field (Yau et. al. 2009)

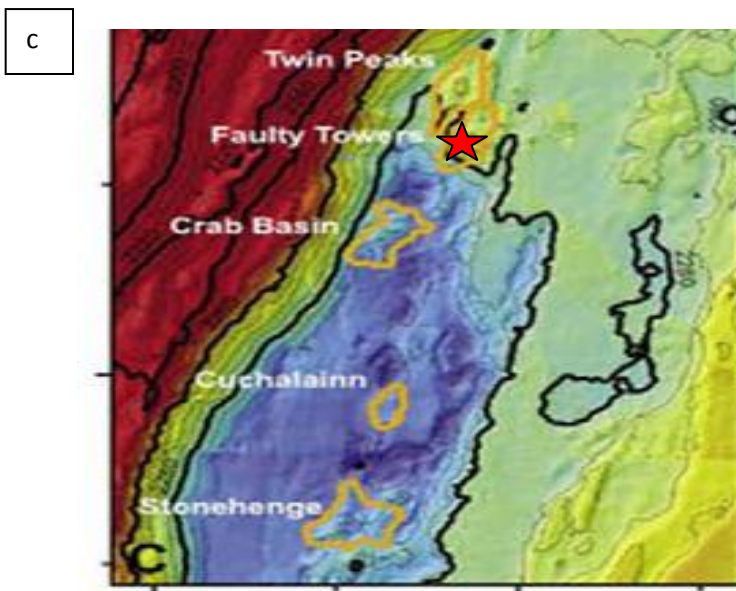
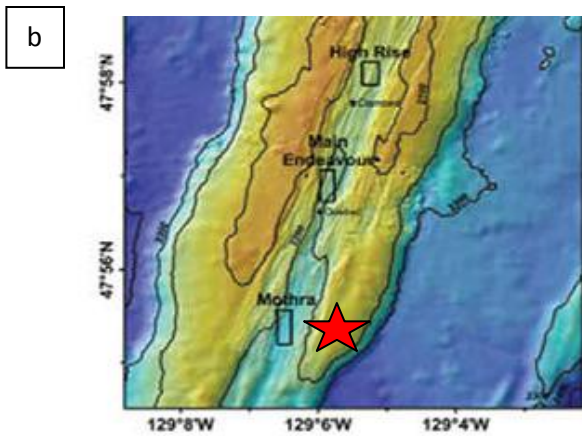
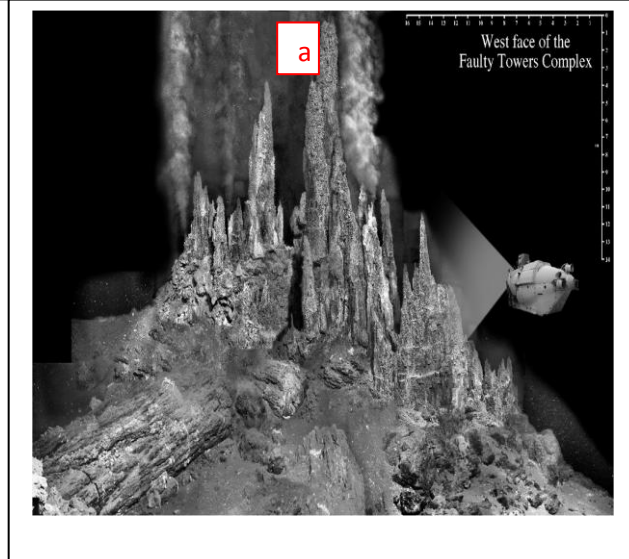


Fig. 7: The Faulty Towers. (Edifice Rex Sulfide Recovery Project, Delaney et. al.)
a-The Tower.



1.5 Hydrothermal vent community succession

It has been determined that the organisms in tubeworm assemblages can be referred to as a community due to the established interactions observed between the species (Bergquist et. al. 1997). There are six hydrothermal vent community types (Table 1) (Sarrazin et. al. 1997) that have been described as a succession model affected by fluid flow, temperature and substrate. Community i has only the alvenillid polychaete *Paralvinella sulfincola* in low flow, high temperature areas such as new sulfide chimneys. Community ii features the addition of *Paralvinella palmiformis* and is found at diffuse flow, medium to high temperature environments on sulfide. In community iii, *Paralvinella palmiformis* is the dominant annelid, with the introduction of gastropods, polynoid polychaetes and a small amount of small tubeworms. This community can be found on both sulfide and basalt substrata with high or diffuse flow, and medium to high temperature. Community iv is composed of mostly gastropods and small tubeworms and is found at low temperature medium flow areas on both sulfide and basalt. Community v is dominated by tubeworms and gastropods but has a number of alvenillid polychaetes,

and is found in diffuse flow areas on basalt or sulfide substrate. Community vi of the 1997 model was composed of dead tubeworms (Sarrazin et. al. 1997), but this model was modified in 1999 with the removal of community vi and the addition of a community called v high flow, a type of community v that includes *Paralvinella palmiformis* and high fluid flow (Sarrazin and Juniper 1999).

	I	II	Community			
			III	IV	V	VI
Organisms						
<i>Ridgeia piscesae</i>	-	-	(+)	+++	+++	++
<i>Paralvinella sulfincola</i>	+++	+++	-	-	+	-
<i>Paralvinella palmiformis</i>	-	+++	+++	-	++	-
Gastropods	-	-	+++	+++	+++	+
Bacterial mats	-	-	-	-	(++)	(++)
Polynoids	(+)	(+)	+++	(+)	+	+
Pycnogonids	-	-	+	(+)	+	+
Protozoans	-	-	-	-	(+)	(++)
Habitat characteristics						
Flow features						
Visible shimmering flow	+	+	+	(+)	(+)	-
Relative temperature	high	medium-high	medium	low	low	low
Substratum						
Sulfide	+	+	+	+	+	+
Basalt	-	-	+	+	+	+

Table 1: Community succession model (Sarrazin et. al. 1997)

This model has been basically supported, and the difference in structure between three of the model's community types, assemblages iii, iv, and v high flow has been effectively distinguished, demonstrating that the distinct communities can be part of a single mosaic community (Govenar et. al. 2002).

The first colonizers to newly formed vents are tubeworms and alvinellid polychaetes. This colonization occurs very rapidly due to the ephemeral nature of these environments (Tunnicliffe et. al. 1997).

Energy transfer flows from microbial primary producers to tubeworms, and upwards to bacterivores and ultimately to predatory polynoid polychaetes (Bergquist et. al. 2007),

and a single tubeworm aggregation can be home to different organisms with a variety of needs (Urcoyo et. al. 2003).

Community succession in hydrothermal vent ecosystems is influenced more by abiotic factors such as fluid flow (Limen et. al. 2007, Kelly et. al. 2007), substrate and temperature (Sarrazin et. al. 1997) than by chronological factors, and it has been suggested that it may be subject to reversion as environmental conditions change back to a previous state (Govenar et. al. 2002). Ambient water temperature is one of the abiotic factors that affect community structure and succession at hydrothermal vents (Sarrazin et. al. 1997), and designations of what low, medium and high vent temperatures are have varied throughout published work (Tsurumi 2003, Tunnicliffe et. al. 1997). The classifications of ambient seawater temperature (high: > 20°C, medium: 10-20°C, low: < 10°C) developed by Sarrazin et. al. are used by Govenar et. al., Limen et. al., and this present study. Collection and processing techniques for tubeworm aggregations have changed over the last several years with the advent of new equipment, and it should be noted that the aggregations included in this study were not retrieved in a consistent manner.

1.6 The Tower hydrothermal vent community

We hypothesize that the diffuse flow sulfide wall “Tower” community is a characterization that expands the model previously described by Sarrazin et. al., as well as being an intermediary community type between sulfide edifice and basalt communities. To test this hypothesis, the aggregation sampled was characterized by tubeworm physiology, biomass measurements of all community members and a complete

species list. Data from these measurements and observations was subjected to a comparison with existing community succession models (Sarrazin et. al. 1997), tubeworm physiological evaluations (Urcuyo et. al. 2003) and descriptions of communities that fit the existing succession model (Sarrazin and Juniper 1999, Bergquist et. al.2007, Tunnicliffe et. al. 1997, Kelly et. al. 2007, Govenar et. al. 2002, Limen et. al. 2007). The results of the comparisons yielded **(1) the similarities of the Tower community, residing on a vertical sulfide wall with diffuse hydrothermal flow to those from other more frequently visited sites with various fluid flows and substrata compositions (Sarrazin and Juniper 1999, Bergquist et. al. 2007, Tunnicliffe et. al. 1997, Kelly et. al. 2007, Govenar et. al. 2002, Limen et. al. 2007); (2) the description of a new community type which expands the succession model described by Sarrazin et. al. (Sarrazin et. al. 1997, Sarrazin and Juniper 1999) 3); a description of the habitat-forming species *Ridgeia piscesae* population from the Tower in relation to the *R. piscesae* population from a diffuse flow basaltic environment (Urcuyo et. al. 2003).**

CHAPTER 2

MATERIALS AND METHODS

2.1 Collection, preservation and processing

In 2007 the manned submersible ALVIN retrieved a *Ridgeia piscesae* community in its entirety using the Bushmaster Jr. collection device (Fig.8). The collection device, with its 63 μm mesh, made it possible to retrieve the community without noTable loss of organisms. The ALVIN *framegrabber* (<http://4dgeo.whoi.edu/alvin>) captured still photographs of the collection. This aggregation was found on the side of the Tower (47 55.416720 N, 129 6.487020 W), at a depth of 2269 m and an altitude of 4.5 m from the sea floor, in a diffuse flow environment with no flanges, beehives, chimneys or shimmering water observed. Previous sampling has indicated that the Bushmaster is ideal for retrieving tubeworm aggregations from flat hard sea bottom (Bergquist et. al. 2002), but photos show that the Tower aggregation was retrieved successfully as the Bushmaster's first vertical collection. Gastropods and arthropods could be seen on the chitinous tubes of *Ridgeia piscesae* (fig 5b).

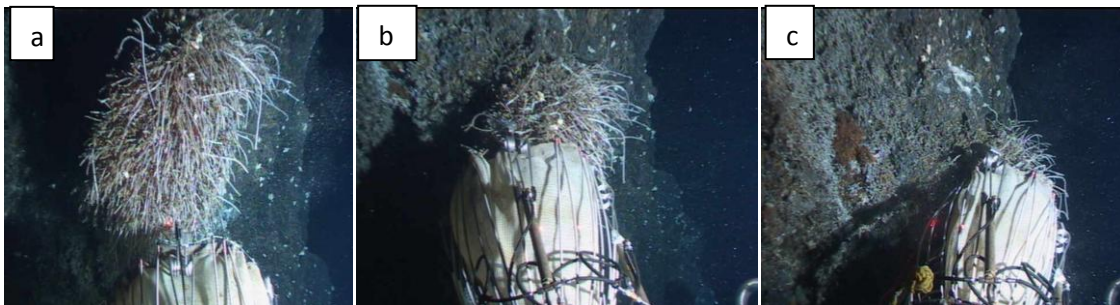


Fig. 8: a) The bushmaster approaches the aggregation. b) With its 63 μm mesh, the Bushmaster is able to encompass the community in its entirety. c) The tubeworm bush complete with its associated fauna is collected. (Photo credit: ALVIN Framegrabber)

The aggregation was brought to the surface and preserved in 7% seawater-buffered formalin, with the exception of a small percentage of fauna which was fixed and kept in 95% ethanol for molecular analysis. After transport to the lab, the collection was rinsed, sorted by size through a decreasing series of sieves (>2mm, 1-2mm, 500µm-1mm, 250µm-500µm), and transferred to 70% ethanol.

All tubeworms were identified as *Ridgeia piscesae* and separated, counted and visually inspected for attached macrofauna. All associated faunal species were separated from the aggregation, sorted, counted, and identified to the lowest possible taxonomic level.

2.2 Measurement and biomass of *Ridgeia piscesae* and associated fauna

For *Ridgeia piscesae*, length was standardized by measuring from the anterior end down the tube to a width of 2mm. Anterior diameter was measured with calipers at the interior opening of the anterior end. All tubeworms were measured and 100 were randomly selected and examined for sex determination and plume cropping damage.

Total biomass was determined for the aggregation by weighing a random sample of 53 individuals in their tubes after patting them dry and using an exponential relationship ($y = ax^b$) to convert length to mass for the rest of the population. This wet weight (WW) was converted to ash free dry weight (AFDW) by applying a conversion factor of 4.25 from current literature (Bergquist et. al. 2007). This likely underestimated the biomass since the rootball was not included. The 53 tubeworms were then weighed without their tubes to determine soft tissue biomass and condition index. Soft tissue wet weight and biomass for the aggregation was determined in the same manner as in-tube

weight and biomass. The condition index of the tubeworms was measured as a ratio of soft tissue ash free dry weight to tube volume (Urcuyo et. al. 2003). Tube volume was measured as $PI() * (B2/3) * (((A2/2)^2) + A2 + 1 + (1^2))$.

To estimate the amount of habitat provided by *Ridgeia piscesae* for the associated fauna, tubeworm surface area was calculated using the equation for a cone frustrum (surface area = $(2\pi) \cdot ((radius\ 1 + radius\ 2)/2) \cdot length$). The anterior diameter/2 was used as radius 1 and 1 mm was used as radius 2 (Urcuyo et. al. 2003, Govenar et. al. 2002).

Wet weight for all other species was measured by patting the individuals dry and weighing. To determine the biomass of the aggregation, ash free dry weight for each taxon was calculated using wet weight of all organisms including tubeworm soft tissue weight, based on published AFDW conversions (Bergquist et. al. 2007).

All individuals were sorted and counted from the sample. Each taxon was assigned a trophic guild classification based upon previous studies (Bergquist et. al. 2007).

2.3 Multi-dimensional scaling analysis of community structure between the Tower community and six community types described by Sarrazin et. al.

Relative abundances of individuals in certain populations of the Tower community and those from the sulfide edifices S&M and Salut which have been categorized as communities i-v high flow by Sarrazin and Juniper (Sarrazin and Juniper 1999) were calculated and transformed to the fourth root. Bray-Curtis similarity values were calculated for each pair of samples and the similarity matrix was used as the basis

for a multi-dimensional scaling analysis. The organisms selected for this analysis were those counted in the community succession analysis conducted by Sarrazin et. al. in 1997, are referred to as “community succession organisms” and include: the siboglinid polychaete *Ridgeia piscesae*, the alvinellid polychaetes *Paravinella palmiformis* and *sulfincola*, all gastropods, all polynoid polychaetes and all pycnogonids in each community.

2.4 Multi-dimensional scaling analyses of community structure between the Tower and several others previously described

To determine the abiotic factor that has the most influence on community structure, relative abundances of “community succession organisms” were calculated for the Tower and several other communities existing under different abiotic factors such as temperature, substrate composition, fluid flow type and collection device used. The selection of studies to be included in the abiotic factor analysis (Sarrazin and Juniper 1999, Bergquist et. al. 2007, Govenar et. al. 2002, Limen et. al. 2007, Tunnicliffe et. al. 1997, Kelly et. al. 2007) was based on the inclusion or accessibility of relative abundances of community succession species published. If all species were not accounted for (Tsurumi 2003) or if abundances were published as approximate numbers (Sarrazin et. al. 1997), the study data was excluded. For the purpose of basalt communities being sufficiently represented, data from Tunnicliffe et. al. 1997 was included, despite approximate numbers of abundances. These approximate numbers (written as “x” for 1-10 individuals, “xx” for tens, “xxx” for hundreds, “xxxx” for thousands (Tunnicliffe et. al. 1997)) were specific enough to calculate accurate relative abundances. Relative abundances for these communities were calculated and transformed to the fourth root.

Bray-Curtis similarity values were calculated for each pair of samples and the similarity matrix was used as the basis for a multi-dimensional scaling analysis.

2.5 A comparison of communities from the Tower sulfide edifice and the Easter Island hydrothermal site

The tubeworm population of the Tower was comparatively analyzed with that from the Easter Island hydrothermal site (Urcuyo et. al. 2003), who's community shared the most structural similarity with the Tower's, despite having different substrate composition. Size frequency distributions of anterior diameters as well as minimum, maximum and average lengths were compared. Condition index, mortality and measurements of the Tower tubeworms were compared to tubeworms from several different locations of the same Easter Island tubeworm population. The Bray Curtis values were calculated and the similarity matrix was used as a basis for a cluster analysis. Lastly mortality, predation, sex ratio and biomass as well as rank abundance of species, population and community biomass and diversity indices of the entire Easter Island community were compared to that of the Tower.

2.6 Measurement of diversity

Measures of diversity were conducted on three communities that span the substrate composition and fluid flow range; one that resides on basalt (Easter Island) (Urcuyo et. al. 2003), one from a sulfide edifice with diffuse flow (the Tower) and one from a sulfide edifice with high hydrothermal fluid flow (Hell 1) (Limen et. al. 2007). Species richness was calculated as $d = (S - 1) / \text{Log}(N)$ with (S) being total species and (N) being total individuals in the sample. Pielou's evenness was calculated as

$J' = H'/\text{Log}(S)$, with H' being the Shannon-Weiner diversity index and calculated as $H' = -\text{SUM}((ni/N)\text{Log}(ni/N))$. The ES 100 value (estimated number of species in a group of 100 individuals) for each community was calculated as $E(S_{100}) = \text{SUM} (1 - (N - Ni)/(N))$ (Rex and Etter 2010).

2.7 Sample and data collection

It has been suggested that inconsistency in sample collection and processing has prevented an accurate measure of species richness at hydrothermal vents (Gauthier et. al. 2010). For this analysis, due to the increased potential for discrepancies, identified meiofauna are excluded from all lists, and the fauna over 1mm will be included. Observations from the Tower aggregation suggest that most individuals of macrofauna such as polynoids and gastropods are retained on the 1mm sieve, and macrofauna visible to the naked eye are not present in the 500 μ m fraction. Due to differences in sample sizes, collection techniques and processing systems of the published analyses, relative abundances will be used for direct comparative analyses and these factors will be taken into consideration when formulating conclusions. Published temperatures of ambient seawater will be categorized consistently (high: > 20°C, medium: 10-20°C, low: < 10°C).

CHAPTER 3

RESULTS

3.1 Multi-dimensional scaling analysis of community succession between The Tower and six others previously studied by Sarrazin et. al.

On the multi-dimensional scale plot (Fig. 9), the Tower community maintains a position of distinctness among the other six described communities. It is in the closest proximity to communities iii and iv, both of which have an abundance of gastropods, although community iii does not contain tubeworms.

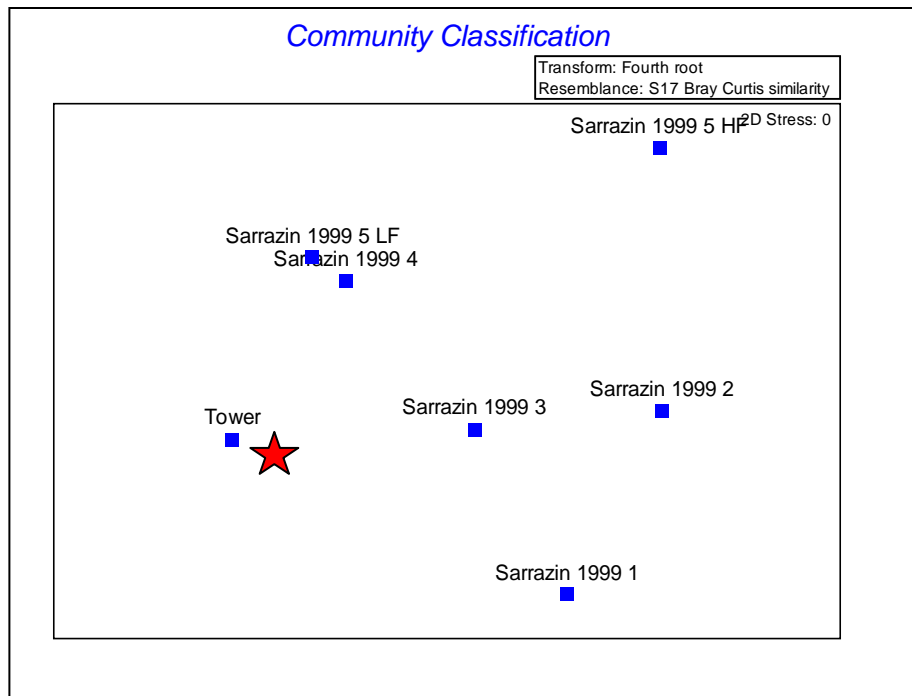
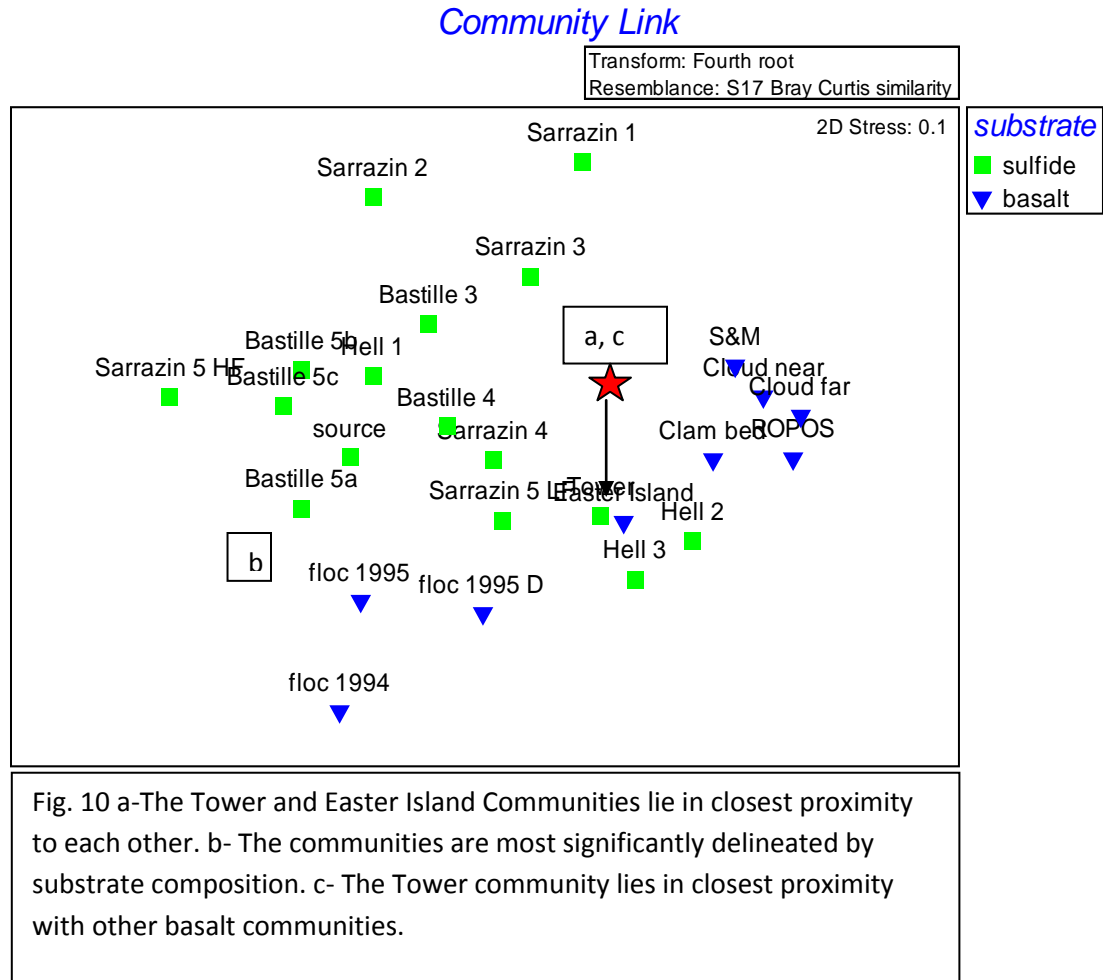


Fig. 9: The Tower community stands distinct from the classifications developed by Sarrazin et. al.

3.2 Multi-dimensional scaling analysis of community structure between The Tower and several others



Community Link

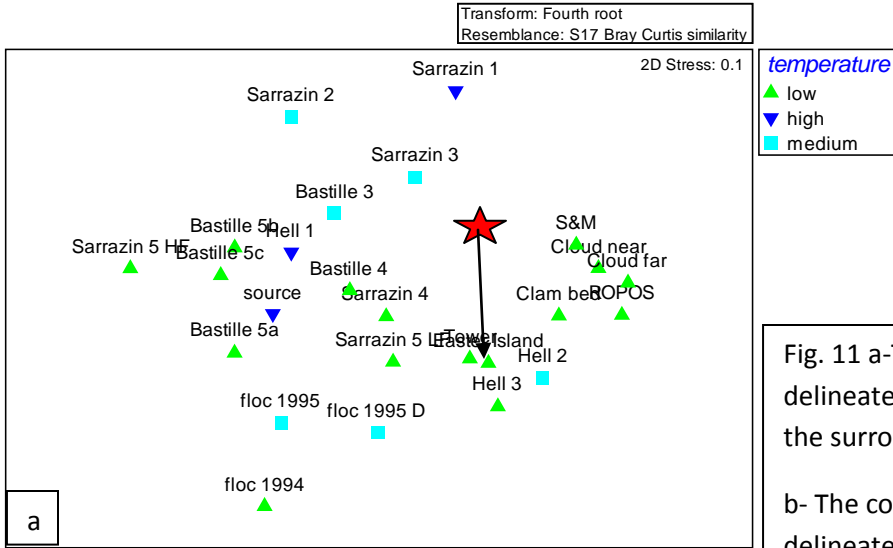
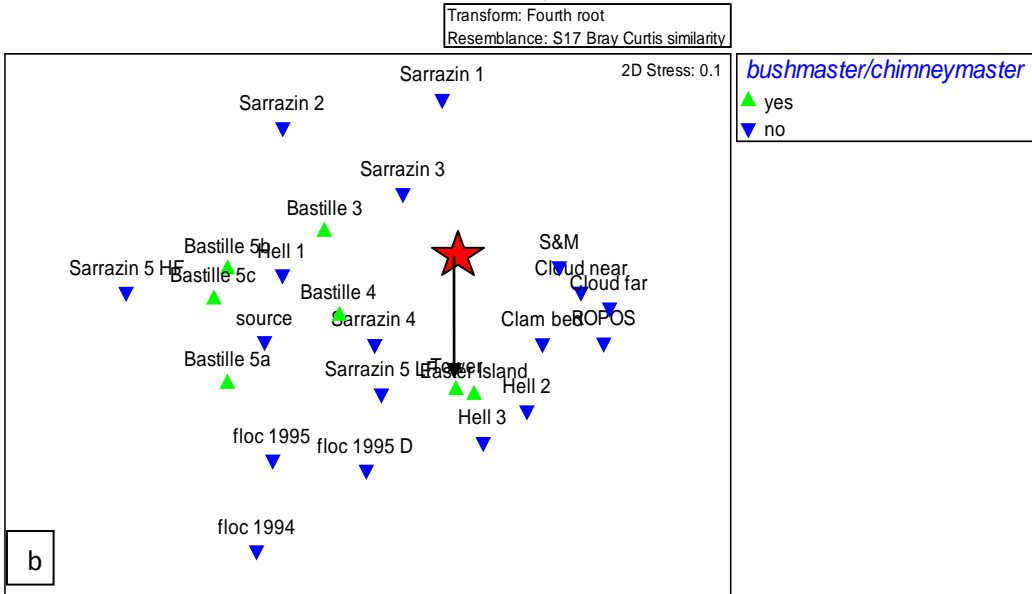


Fig. 11 a-The communities are not delineated by the temperature of the surrounding fluid.
b- The communities are not delineated by the mode of collection.

Community Link



On the multi-dimensional scaling plot, the communities are most clearly delineated by substrate composition (Fig. 10) in relation to other abiotic factors (Fig. 11). The Tower community lies within the grouping of those from sulfide substrate, but also in close proximity to those from basalt. It shares this distinction with two others, Hell 2 and Hell 3, both of which share fluid flow and substrate composition make-up with the Tower (Fig. 10). The Tower community lies in closest proximity with the Easter Island community, which is from basaltic substrate.

3.3 *Ridgeia piscesae* analysis

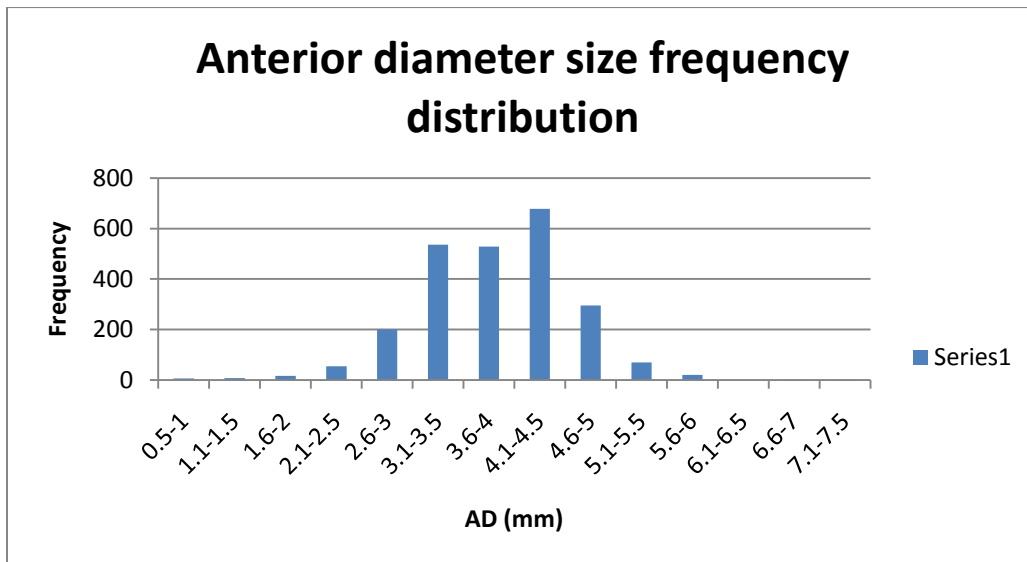


Fig. 12: The size frequency distribution of the *Ridgeia piscesae* from the Tower is unimodal.

There were 2397 tubeworms in the aggregation. The size frequency distribution for anterior diameter appeared to have a single mode (Fig. 12) from 3.5-4.5 mm with an average anterior diameter of 3.87 mm (± 0.73 mm). The mean standardized length was 175.78mm (± 82.0 mm) and lengths ranged from 10 to 785 mm. Out of the roughly 2400 tubeworms, 52 had an anterior diameter of less than 2.5mm and were considered “small”.

The outside tube diameter of the small tubeworms was < 2 mm throughout the length, so the standardized length of these worms was considered zero, but recorded as the length of the entire tube. Most of these were attached to larger tubes. The external surface area of the tubes above the rootball provided for associated fauna was 5.5 m^2 . The rootball was a tangled mass of posterior ends which were very thin walled and flexible. The wet weight of the aggregation was calculated as 1.9 kg, not including the rootball. The biomass (ash free dry weight) of the aggregation was calculated as .46 kg. The average calculated condition index of the tubeworms was measured as 0.0580 g/ml ($\pm 0.026 \text{ g/ml}$). Of the 100 tubeworms examined for gender and plume damage, 51 were males and 49 were females. There was no evidence of plume damage, but 91 tubes (3.7% of the population) in the aggregation were empty.

3.4 A comparison of communities from the Tower and the Easter Island hydrothermal site

The community at the Easter Island hydrothermal vent site studied by Urcuyo et. al. ($47^{\circ}57'N$, $129^{\circ}06'W$) was the most similar in community structure to that from the Tower, despite residing on different substrate. There were approximately 4300 individuals in the Easter Island tubeworm population, 1000 of which appeared to be very small and newly settled. Easter Island's tubeworm population had several clumps of newly settled colonizers, while the Tower's population of roughly 2400 was mainly comprised of larger sized tubeworms. The Easter Island tubeworm population's size frequency distribution is thus bimodal, so average measurements for length, anterior diameter, wet weight and biomass were performed for the two groupings. The Tower's tubeworm population of roughly 2400 showed one size frequency mode, so one set of

measurement averages was taken. Large Easter Island tubeworms with an average anterior diameter of 4 mm had an average standardized tube length of 147 mm, a length range of 6 to 544 mm, and an average biomass of 0.04 g. The average anterior diameter of the Tower tubeworms was 3.87 mm with an average standardized tube length of 175 mm, a length range of 10 to 785 mm, and an average biomass of 0.046 g. Both aggregations had similar tangled rootball bases comprised of small, thin walled cylindrical posterior ends. These transparent ends held some of the body and were in contrast to the sturdy and opaque portion of the tubes that emerged above them and held the majority of the organism. The Tower's rootball was anchored to a vertical sulfide wall while Easter Island's sat in a depression in the basalt.

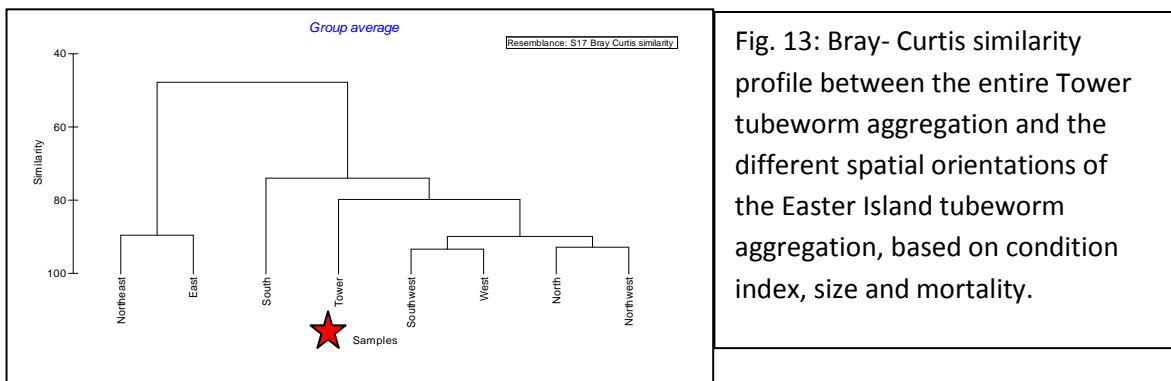


Fig. 13: Bray- Curtis similarity profile between the entire Tower tubeworm aggregation and the different spatial orientations of the Easter Island tubeworm aggregation, based on condition index, size and mortality.

The Easter Island tubeworm population was almost 45% more abundant than the Tower's, and was split into seven sub groups (North, Northeast, East, South, Southwest, West, Northwest) for analysis in terms of measurements, condition index and mortality. For these indicators, Tower tubeworms were closest on the Bray-Curtis similarity matrix to those from the North, Northwest, West and Southwest portions of the Easter Island aggregation (fig 13), which experienced almost no rise in plume level temperature above ambient, and therefore low levels of sulfide at plume level due to the positive correlation between sulfide levels and temperature (Urcuyo et. al. 2003). The surface area for

associated fauna provided by the Easter Island tubeworms was 6 m² compared to the 5.4 m² provided by the Tower tubeworms, an only 10% increase despite the Easter Island's aggregation having a 45% larger abundance. Associated fauna therefore had a total density of 252 individuals per square centimeter of surface area while The Tower's associated faunal density was 122 individuals per square centimeter of surface area.

The Tower community as a whole had 53,862 individuals compared to Easter Island's 151,533. There were 14 macrofaunal species in the Tower collection and 37 macrofaunal species found at the Easter Island site. For both communities, the numerically dominant species were gastropods, and *Ridgeia piscesae* made up the majority of biomass, although tubeworms made up 82.88% of the AFDW of the Easter Island sample while comprising only 70% of the Tower's.

In the Easter Island community, the ampharetid polychaete *Amphisamytha galapagensis* outnumbered *Ridgeia piscesae* by 59% while at the Tower, the reverse was true by 54%. In terms of rank abundance, both communities featured the gastropods *Depressigyra globulus*, *Provanna variabilis* and *Lepetodrilus fucensis*, the polychaete *Amphisamytha galapagensis* and the vestimentiferan *Ridgeia piscesae* in the top five ranks. The mollusk *Helicoradomenia juani* shared the same rank in both communities.

3.5 Diversity indices of the Tower, Easter Island and Hell 1 communities

Community	S	N	d	J'	H' (log e)	ES 100
Easter Island	36	1.52E+05	2.9341	0.34226	1.2265	8.2708
Tower	14	78875	1.1529	0.46276	1.2213	6.2112
Hell 1	6	55	1.2477	0.85338	1.5291	6

Table 2: diversity indices for the Tower, Easter Island and Hell 1. (S)- number of species in the sample. (N)- number of individuals in the sample. d- species richness index. J'- Pielou's evenness index. H'- Shannon-Weiner diversity index to the log of e. ES100: estimated number of species that would be found in each sample if 100 individuals were in the sample.

Out of the three samples chosen for measurements of diversity (Table 2), the community residing on basalt and bathed in diffuse hydrothermal flow from the Easter Island hydrothermal site (Urcoyo et. al. 2003) had the greatest number of species (36) and individuals (152,000+). Its richness index (d) (2.9341) was the highest of the three as well, and it had the highest expected number of species in a sample of 100 individuals (ES 100) (8.2708). Its Pielou's evenness index (J'), however, was the lowest of the three (0.34226) and its Shannon-Weiner diversity index (H') (1.2265) was in between the other samples. In the Tower community, on a sulfide edifice at the Faulty Towers site and subject to diffuse hydrothermal flow away any venting orifices, there were 14 species and 78, 875 individuals. Its richness index was 1.1529 and its ES 100 value was 6.2112. Its

evenness index was 0.46276 and its Shannon-Weiner index was 1.2213. At the Axial Volcano sulfide edifice directly above a venting orifice, the Hell 1 community (Limen et. al. 2007) had the lowest number of species (6) and individuals (55). Its richness index fell between the other sites (1.2477) and its ES 100 value was the lowest (6.0). The evenness index was the highest (0.85338), as was the Shannon –Weiner index (1.5291).

CHAPTER 4

DISCUSSION

The Tower hydrothermal vent community represents a new succession stage (community iii low flow), an intermediary sulfide habitat community with an abundance of “long skinny” tubeworms as its habitat forming species. Larvae of more sulfide tolerant species from basaltic substrate can settle in these communities, making the transition from basaltic to sulfide substrate.

4.1 Community succession classification of the Tower community

The Tower community adds a new succession stage to the existing succession model for hydrothermal vent communities. It is most similar to community types iii and iv. In the Tower community, tubeworms make up the largest amount of biomass, but do not share numerical dominance with gastropods as is the case in community iv. The Tower community's similarity to community iii extends only to gastropod abundance. Pycnogonids are present, or occasionally present, in very low abundances in succession model communities iii and iv, but are present in moderate numbers in the Tower community with 791 individuals making up 1% ($\pm 0.17\%$) of the community's individuals, wet weight and density. There is a low abundance of polynoids in the Tower sample in comparison to large amounts in community iv. Polynoid presence and low abundance, pycnogonid moderate abundance in addition to tubeworm presence and moderate numbers contribute to the Tower community's distinctness in the succession model and thereby the model's expansion. Community iii, found on sulfide edifices and basaltic substrate with visible fluid flow and medium temperatures, has large abundances

of the alvinellid polychaete *Paralvinella palmiformis*, in keeping with higher flow regimes. Community iv, however, features low temperature and low fluid flow on basaltic substrate as well as large numbers of tubeworms and no alvinellid polychaetes, in keeping with low flow regimes. The Tower community can therefore be classified as community iii low-flow, in keeping with its sulfide edifice substrate, tubeworm abundance and low abundance of alvinellid polychaetes.

4.2 The Tower community's role as an intermediary community between basalt and sulfide substrata

Communities that form at the mouth of ephemeral venting edifice chimneys are able to recruit from species pools from communities at more stable basaltic substrates. The diffuse flow environment of basaltic substrate is tolerable to more species, allowing basaltic communities to experience higher diversity. Higher diversity, especially species richness, and greater abundance both indicate that basaltic communities feature a large pool of organisms from which species that are more sulfide tolerant can spawn.

The diversity decrease from basaltic to edifice chimney communities is apparent when one considers the ES 100 index, which falls from 8.3 estimated species per 100 organisms at the Easter Island Community to 6.2 at the Tower community, and ultimately to 6.0 at the Hell 1 community. The richness index falls from 2.9 at the Easter Island community to 1.2 at both the Tower and Hell 1 communities, emphasizing the similarity of the Tower community to another sulfide community. The Tower and Easter Island communities experience less evenness at 0.4 and 0.3 respectively, while the Hell 1 community experiences the most evenness at 0.9. This emphasizes the similarities the

Tower shares between communities from both substrate types while indicating that when species spawn from basaltic substrate and settle on sulfide substrate, thereby creating a community of organisms that have the same sulfide tolerance, the abundances of populations become more similar to each other. The Tower type community (iii low flow) serves as an intermediary where a portion of a basaltic community species pool that is more sulfide tolerant can settle, before sending out new larvae that can ultimately settle at a newly forming community on a sulfide edifice chimney with venting fluid. It is at a community iii low flow site that species such as *Amphisamytha galapegensis* can colonize in fewer numbers than at their basaltic origin, without sending larvae further to actively venting sites. A preponderance of tubeworms in the Tower community in contrast to other edifice community types results in a large amount of surface area for larvae to colonize. Species settling at this community iii low flow, that are even more sulfide tolerant, ultimately emit larvae which can colonize at chimneys.

The MDS profiles of abiotic factors that have the most effect on community structure indicate that substrate composition has the greatest effect upon which organisms, and in what numbers, populate a hydrothermal flow environment. Therefore larvae that originate at a community on basaltic substrate can effectively transition to a sulfide structure by settling at a community which serves as an intermediary, spanning the characteristics of both substrates, such as the Tower community iii low flow.

The Tower community shares some characteristics with the other diffuse flow sulfide (Hell 3) community, but is most similar in structure to the Easter Island community. The portion of the Easter Island tubeworm population that was most similar to the Tower's tubeworm population in terms of tubeworm condition index, mortality and

size was that from where the lowest temperatures were recorded, indicating that a low level of sulfide is present in the ambient seawater at the Tower community. This similarity in sulfide use between the Tower sulfide community and the basaltic Easter Island community emphasizes the links between the Tower community and the basalt habitat.

The Tower tubeworms belong to the “long skinny” morphological subset of *Ridgeia piscesae*, expanding the habitat preferences of this morphotype to sulfide in addition to basalt. The “long skinny” Tower tubeworms provide more surface area per individual than the Easter Island tubeworms, leading to the establishment of this distinct community type and new succession stage on sulfide structures.

4.3 Conclusion

The Tower community, sustained by diffuse hydrothermal flow, with no vent orifice in close proximity, yet on a vertical sulfide edifice represents a new succession stage of Juan de Fuca Ridge hydrothermal vent communities. The broadening of the succession model expands our understanding of chemosynthetic communities.

The Tower community (community type iii low flow), a newly discovered community characterization, maintains a vital function in the hydrothermal vent ecosystem. This function extends to the rest of the deep sea as vent environments are occasionally visited by non endemic fauna and the patchy distribution of hydrothermal vent sites often results in larval dispersal extending through kilometers of deep sea. The Tower community iii low flow serves as a settlement point for less sulfide tolerant fauna, either from the basaltic substrate at its base or from the reaches of the deep sea, to ultimately colonize a

sulfide edifice. The Tower sulfide edifice is from a hydrothermal field which has been described as distinctive from other fields (Kelley et. al. 2001). One of the sites from the Axial Volcano (Limen et. al. 2007) and some of those from the Bastille edifice (Govenar et. al. 2002) and the Smoke and Mirrors edifice (Sarrazin and Juniper 1999) share some physical similarities with the Tower sample site (sulfide edifice substrate with diffuse flow). However, the Axial Volcano site which shares similarity to The Tower site, is only 70 cm from a high flow chimney (Limen et. al. 2007), while there were no chimneys visible from the photos taken during the retrieval of the Tower aggregation.

This addition to the hydrothermal vent community succession model allows for an additional community type intermediate between stable basaltic environments and harsher sulfide chimney environments. This intermediate community type may be colonized by larvae from either environment, and potentially allows for dispersal of mobile species among the habitats. The study of the Tower community has increased our knowledge and understanding of how hydrothermal vent communities interact. The truth is we still do not fully grasp the ecology of high biomass hydrothermal vents within the diversity of the deep sea, and how one habitat may affect the other. These ephemeral and unpredictable cradles of life must be better understood if they are to be effectively protected while man continues to conquer the abyssal deep.

Table 3: All communities listed in this study including site name, location, temperature, and substrate and fluid flow type.

author	site name	location	segment	substrate	temperature	fluid type
Grinar	Tower	47°55'N, 129°06'W	Endeavor	sulfide	low	diffuse
Tunncliffe et. al. 1997	Source	46°09'N,129°35'W	CoAxial		high	vent
Sarrazin et. al. 1999	S&M 1	47°57'N,129°08'W	Endeavor		high	vent
	Salut 2		Endeavor		medium	diffuse
	S&M 3		Endeavor		medium	diffuse
	S&M 4		Endeavor		low	diffuse
	S&M 5LF		Endeavor		low	diffuse
	S&M 5HF		Endeavor		low	diffuse
Govenar et.al. 2002	Bastille 3	47°57'N,129°08'W	Endeavor		medium	diffuse
	Bastille 4		Endeavor		low	diffuse
	Bastille 5a		Endeavor		low	diffuse
	Bastille 5b		Endeavor		low	diffuse
	Bastille 5c		Endeavor		low	diffuse
Limen et. al. 2007	Hell 1	46°55'N,130°00'W	Axial		high	vent
	Hell 2		Axial		medium	diffuse
	Hell 3		Axial		low	diffuse
Kelly et. al. 2007	ROPOS	47-47°N,129-130°	Axial	basalt	low	vent
	Cloud near		Axial		low	vent
	Cloud far		Axial		low	diffuse
	Clam Bed		Endeavor		low	vent
	S&M		Endeavor		low	vent
Bergquist et. al. 2007	Easter Island	47°57'N,129°06'W	Endeavor		low	diffuse
Tunncliffe et. al. 1997	floc 1994	46°09'N,129°35'W	CoAxial		low	vent
	floc 1995		CoAxial		medium	vent
	floc 1995 dying		CoAxial		medium	vent

Below: Table 4 : Species list of the Tower community. #- number of individuals. %#- percentage of total individuals. TG- trophic guild of species. (H= symbiont bearing host, B= bacterivore, S= scavenger/detrivore, P= predator, d= surface deposit feeder or grazer, s= suspension feeder) (Bergquist 2007) WW- wet weight of population. %WW- percentage of total wet weight. Con.- ash free dry weight conversion factor. AFDW- ash free dry weight. %AFDW- percentage of total ash free dry weight. Faunal density- number of individuals per square centimeter of surface area on the tubes of *Ridgeia piscesae*. % faunal density- percentage of total density.

organism	#	%#	TG	WW (g)	%WW	Con.	AFDW(g)	%AFDW	faunal density	% faunal density
polychaete										
alvinellid										
<i>Paralvinella sulfincola</i>	1	0.001	B (d,s)	0.17	0.005	6.25	0.03	0.004	0.002	0.001
<i>Paralvinella palmiformis</i>	20	0.029	B (d,s)	0.048	0.002	6.25	0.008	0.001	0.04	0.03
ampharetin										
<i>Amphisamytha galapegensis</i>	1452	2.08	S (d)	2.59	0.09	8.92	0.29	0.04	2.64	2.15
dorvilleid										
<i>Parougia wolffi</i>	52	0.074	P	0.59	0.02	6.25	0.094	0.01	0.1	0.08
phyllodocid										
<i>Protomystides verenae</i>	3	0.004	P	0.01	<.001	8	0.001	<.001	0.005	0.004
polynoid										
<i>Branchinotogluma tunicliffe</i>	172	0.246	P	10.1	0.35	7	1.44	0.22	0.31	0.25
<i>Lepidonotopodium piscesae</i>	54	0.077	P	9.03	0.32	6.32	1.43	0.22	0.1	0.07
siboglinid										
<i>Ridgiewia piscesae</i>	2397	3.43	H	1955.4	68.66	4.25	460.1	70.58	n/a	n/a
aplacophoran										
simrothiellid										
<i>Helicoradomenia juani</i>	437	0.625	P	0.257	<.001	21	0.01	<.001	0.79	0.65
pycnogonid										
ammotheadae										
<i>Ammothea verenae</i>	791	1.13	B	24.2	0.85	6.51	3.72	0.57	1.44	1.17
gastropod										
buccinid										
<i>Buccinum viridium</i>	12	0.017	P,S (d)	0.76	0.03	8.13	0.1	0.01	0.021818	0.02
lepetodrilid										
<i>Lepetodrilus fucensis</i>	32,341	46.25	B	325.14	11.42	6.71	48.46	7.43	58.80182	47.89
loxonematoid										
<i>Provanna variabilis</i>	6843	9.79	B	220.17	7.73	5.4	40.77	6.25	12.44182	10.13
peltospirid										
<i>Depressigyra globulus</i>	25,350	36.25	B	299.59	10.52	3.14	95.41	14.64	46.09091	37.54

Works Cited

- 1) Bergquist DC, Eckner JT, Urcuyo IA, Cordes EE, Hourdez S, Macko SA, Fisher CR (2007) Using stable isotopes and quantitative community characteristics to determine a local hydrothermal vent food web. *Mar. Ecol. Prog. Ser.* 33: 49-65
- 2) Bergquist DC, Urcuyo IA, Fisher CR (2002) Establishment and persistence of seep vestimentiferan aggregations on the upper Louisiana slope of the Gulf of Mexico. *Marine Ecology Progress Series* 241: 89- 98
- 3) Canfield DE, Thordrop FS, Kristensen E. Advances in Marine Biology. Elsevier: San Diego, CA. 2005
- 4) Cuvelier D, Sarradin PM, Sarrazin J, Colaco A, Copley J, Desbruyeres D, Glover A, Santos RS, Tyler P (2011) Hydrothermal faunal assemblages and habitat characterisation at the Eiffel Tower edifice (Lucky Strike, Mid-Atlantic Ridge). *Marine Ecology* 32: 243-255
- 5) Davis E, Becker K, Dziak R, Cassidy J, Wang K, Lilley M (2004) Hydrological response to a seafloor spreading episode on the Juan de Fuca ridge. *Nature* 4:30
- 6) Fisher, CR (1990) Chemoautotrophic and methanotrophic symbioses in marine invertebrates. *Reviews in Aquatic Sciences* 2: 399-436
- 7) Flores JF, Hourdez SM (2006) The zinc-mediated sulfide-binding mechanism of hydrothermal vent tubeworm 400-kDa hemoglobin. *Cah. Biol. Mar.* 47: 371-377
- 8) Gauthier O, Sarrazin J, Desbruyeres D (2010) Measure and mis-measure of species diversity in deep-sea chemosynthetic communities. *Mar. Ecol. Prog. Ser.* 402: 285-302

- 9) Govenar BW, Bergquist DC, Urcuyo IA, Eckner JT, Fisher CR (2002) Three *Ridgeia piscesae* assemblages from a single Juan de Fuca Ridge sulphide edifice: structurally different and functionally similar. *Cah. Biol. Mar.* 43: 247-252
- 10) Govenar B, Le Bris N, Gollner S, Glanville J, Aperghis AB, Hourdez S, Fisher CR (2005) Epifaunal community structure associated with *Riftia pachyptila* aggregations in chemically different hydrothermal vent habitats. *Mar. Ecol. Prog. Ser.* 305: 66-77
- 11) <http://4dgeo.who.edu/alvin>
- 12) Jones ML (1985) On the vestimentifera, new phylum: six species, and other taxa, from hydrothermal vents and elsewhere. *Bulletin of the Biological Society of Washington* 6: 117-158
- 13) Kelley DS, Delaney JR, Yoerger DR (2001) Geology and venting characteristics of the Mothra hydrothermal field, Endeavour segment, Juan de Fuca Ridge. *Geology* v. 29, p. 959-962
- 14) Kelly N, Mataxas A, Butterfield DS (2007) spatial and temporal patterns of colonization by deep-sea hydrothermal vent invertebrates on the Juan de Fuca Ridge, NE Pacific. *Aquatic Biology* 1: 1-16
- 15) Kelly N, Mataxas A (2008) Diversity of invertebrate colonists on simple and complex substrates at hydrothermal vents on the Juan de Fuca Ridge. *Aquatic Biology* 3: 271-281
- 16) Kim SL, Mullineaux LS (1998) Distribution and near-bottom transport of larvae and other plankton at hydrothermal vents. *Deep Sea Research* 45: 423-440

- 17) Levesque C, Juniper SK, Limen H (2006) Spatial organization of food webs along habitat gradients at deep-sea hydrothermal vents on Axial Volcano, Northeast Pacific. *Deep-Sea Research I* 53: 726-739
- 18) Limen H, Levesque C, Juniper SK (2007) POM in macro/meiofaunal food webs associated with three flow regimes at deep-sea hydrothermal vents on Axial Volcano, Juan de Fuca Ridge. *Mar. Biol.* 153:129-139
- 19) Lonsdale, P (1977) Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep Sea Research* 24: 9
- 20) Marcus J, Tunnicliffe V, Butterfield D (2009) Post-eruption succession of macrofaunal communities at diffuse flow hydrothermal vents on Axial Volcano, Juan de Fuca Ridge, Northeast Pacific. *Deep-Sea Research II* 56: 1586-1598
- 21) Qui J (2010) Death and rebirth in the deep. *Nature* 465
- 22) Rex M, Etter R. Deep Sea Biodiversity: Pattern and Scale. Harvard University Press: Cambridge Ma. 2010
- 23) Sarrazin J, Juniper SK, Massoth G, Legendre P (1999) Physical and chemical factors influencing species distributions on hydrothermal sulfide edifices of the Juan de Fuca Ridge, northeast Pacific. *Mar. Ecol. Prog. Ser.* 190: 89-112
- 24) Sarrazin J, Juniper SK (1999) Biological characteristics of a hydrothermal edifice mosaic community. *Mar. Ecol. Prog. Ser.* 185: 1-19

- 25) Sarrazin J, Robigou V, Juniper K, Delaney JR (1997) Biological and geological dynamics over four years on a high temperature sulfide structure at the Juan de Fuca Ridge hydrothermal observatory. *Mar. Ecol. Prog. Ser.* 153: 5-24
- 26) Sievert SM, Kiene RP, Schulz-Vogt HN (2007) The Sulfur Cycle. *Oceanography* 20: 2
- 27) Somero GN, Childress JJ, Anderson AE (1989) Transport, metabolism, and detoxification of hydrogen sulfide in animals from sulfide-rich marine environments. *Critical Reviews in Aquatic Sciences* 1: 591
- 28) Southward EC, Tunnicliffe V, Black M (1995) Revision of the species *Ridgeia* from northeast Pacific hydrothermal vents, with a redescription of *Ridgeia piscesae* Jones (Pogonophora: Obturata = vestimentifera). *Canadian Journal of Zoology* 73: 282-295
- 29) Speiss FN, MacDonald KC, Atwater T, Ballard R, Carranza A, Cordoba D, Cox C, Garcia VM, Francheteau J, Guerrero J, Hawkins J, Haymon R, Hessler R, Juteau T, Kastner M, Larson R, Luyendyk B, Macdougall JD, Miller S, Normark W, Orcurr J, Rangin C (1980) East Pacific Rise: Hot Springs and Geophysical Experiments. *Science* 207: 4438
- 30) Tsurumi M (2003) Diversity at hydrothermal vents. *Global Ecology and Biogeography* 12: 181-190
- 31) Tunnicliffe V, Embley RW, Holden JF, Butterfield DA, Massoth GJ, Juniper SK (1997) Biological colonization of new hydrothermal vents following an eruption on the Juan de Fuca Ridge. *Deep-Sea Research* 44: 1627-1644

- 32) Urcuyo IA, Massoth GJ, Julian D, Fisher CR (2003) Habitat, growth and physiological ecology of a basaltic community of *Ridgeia piscesae* from the Juan de Fuca Ridge. *Deep Sea Research* 50: 763-780
- 33) Urcuyo IA, Massoth GJ, MacDonald IR, Fisher CR (1998) In situ growth of the vestimentiferan *Ridgeia piscesae* living in highly diffuse flow environments in the Main Endeavor Segment of the Juan de Fuca Ridge. *Cah. Biol. Mar.* 39: 267-270
- 34) Van Dover, CL. The Ecology of Hydrothermal Vents. Princeton University Press: Princeton, NJ. 2000
- 35) Yao HQ, Zhou HY, Peng XT, Bao SX, Wu ZJ, Li JT, Sun ZL, Chen ZQ, Li JW, Chen GQ (2009) Metal sources of black smoker chimneys, Endeavour Segment, Juan de Fuca Ridge: Pb isotope constraints. *Applied Geochemistry* 24: 1971-1977