Summer 2020

Hydrothermal Vent Periphery Invertebrate Community Habitat Preferences of the Lau Basin

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Recommended Citation

Soto, Kenji Jordi, "Hydrothermal Vent Periphery Invertebrate Community Habitat Preferences of the Lau Basin" (2020). *Capstone Projects and Master's Theses*. 892.
https://digitalcommons.csumb.edu/caps_thes_all/892

HYDROTEHRMAL VENT PERIPHERY INVERTEBRATE COMMUNITY HABITAT PREFERENCES OF THE LAU BASIN

A Thesis
Presented to the
Faculty of
Moss Landing Marine Laboratories
California State University Monterey Bay

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Marine Science

by
Kenji Jordi Soto
Spring 2020

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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HYDROTHERMAL VENT PERIPHERY INVERTEBRATE COMMUNITY HABITAT PREFERENCES OF THE LAU BASIN

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The *Trochophores* are larval tops the Polychaetes set spinning
With just a ciliated ring – at least in the beginning –
They feed, and feel an urgent need to grow more like their mothers,
So sprout some segments on behind, first one, and then the others.

–*Walter Garstang,* “The Trochophores” from *Larval Forms*

ABSTRACT

Hydrothermal Vent Periphery Invertebrate Community Habitat
Preferences of the Lau Basin
by
Kenji Jordi Soto
Master of Science in Marine Science
California State University Monterey Bay, 2020

The Eastern Lau Spreading Center (ELSC), located between 19°20’S and 22°45’S, is a back-arc basin containing active hydrothermal vents, and is characterized by gradients of several geological and chemical variables that follow along a north – south axis. The northern section of the ELSC spreads faster than the southern section resulting in farther distance from the Tofua Arc and vent geology and chemistry more akin to mid-oceanic ridges. In the Southern section, where distance from the arc is less, substrates are more heavily influenced by water resulting in andesitic substrates as opposed to basaltic substrates in the north. There are also north to south biological patterns, where in the northern vent peripheral zone communities are dominated by anemones, and by sponges in the south. This project used a replacement type experiment to test whether the anemone and sponge community distributions are due to substrate preferences (either basalt or andesite) or location effects. In September 2006, 17 basalt and 18 andesite rock blocks were set out in the peripheral vent zone at three locations in the Lau Basin; 42 months later, in May 2009, the rocks were recovered. After collection and identification (to lowest taxonomic level) of all invertebrates, rock block surface area and roughness was determined. This report found that while the basalt rock blocks used were smaller and had smoother surface roughness than andesite rocks, both rock types were evenly distributed throughout each location. Through this conclusion, rock type was determined not to affect the invertebrate community and that there was some other location specific effect responsible for the invertebrate community, possibly sulfide distribution. Southern locations had more brecciated substrates, allowing for more sulfide to distribute farther laterally, resulting in more primary productivity, and thus an increase in taxa belonging to groups Copepoda, Polychaeta, and Gastropoda. Specifically, southern sites showed higher densities of the copepod *Amphiascus* sp. and from the family Dirivultidae, the molluscs *Lepetodrilus* sp. and from the family Sutilizonidae, and polychaetes from the families Serpulidae, Ampharetidae, and Hesionidae.

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ACKNOWLEDGEMENTS

Wow! What a journey! A journey of so many ups and downs that I was only able to complete with the support of my friends, family, and the wonderful MLML community.

Thank you to my entire thesis committee, not just for guiding me through this academic endeavor, but also through a significant phase of my life. Thank you Stacy for being the most considerate advisors I could ever ask for; thank you for your unwavering support, patience, and openness and for sticking around even though you retired. Thank you Ivano for being a genuine human being, an enthusiastic instructor, and always finding time to answer my questions; I have always appreciated how you supported any student in need. Thank you Kenneth for being an overall positive force in my life, keeping things light, and teaching me how to make custom etched glasses; your passion for science is an inspiration.

I would also like to give a special thanks to a few others who were instrumental in me finishing my thesis. Thank you Kamille Hammerstrom for helping me analyze my community data, teaching me Primer, and being a welcoming lab manager. Thank you Gema Garcia for all the lab work you put in, being an enthusiastic learner, and putting up with the extra work I assigned to you during your internship. Thank you John Oliver for helping me figure out what types of polychaetes were in my samples and for all your stories.

Although I did not have the pleasure to meet the crews of the research vessels that conducted my experiment, I extend my thanks to Charles Langmuir and the crew aboard R/V Kilo Moana for collecting the rock substrates in 2004, Charles Fisher and the crew of the R/V Melville for deploying the rocks in 2006, and C. Fisher and the crew of the R/V Thomas G. Thompson for collecting the rocks in 2009. Thank you to the crew of the ROV Jason II for deploying, and collecting my samples and spending extra time searching for them when they were ultimately discovered to have been buried under a collapsed vent.

MLML is one of the most positive places I’ve been; there are so many people make this place special; I’m going to miss it. Thank you Val Loeb for being an awesome lab buddy during the summer and winter breaks; chatting with you before starting a day of staring through a microscope was always uplifting and kept me sane. Thank you Terra Eggink for helping me navigate the CSU system and for your unyielding positivity. Thank you Kris Machado for being readily available to help me and any the student body with any shop related problems with a smile. Thank you James Cochran for checking up on me during my late night lab sessions. Thank you Sam Hulme for bringing me aboard the R/V Atlantis and showing me first-hand how deep sea research gets done. Thank you Michelle Keefe, Di Steller, and Kathleen Donahue just for being cheery and saying ‘Hi’ to me.

Thank you to the entire MLML student body, it’s been a treat getting to know all of you; I cherish all the friends that I have made throughout this process. Because I did

not get to go out into the field for my project, I’m especially thankful to Jake Cline, Angela Zepp, June Shrestha, Alex Olson, Pamela Neeb Wade, Tyler Barnes, Dan Gossard, and Greg Bongey for letting me tag along during your field work. Thank you for the diversions from my thesis!!

Thank you to Kim Swan, Athena Barrios, and the WATCH program for helping me remember what it was like being a young scientist and for giving me the opportunity to give back.

Thank you to the entire Monterey Bay ultimate frisbee crew. Your presence was a refuge from the stresses of it all.

Thanks most of all to my parents for their love, support, encouragement, understanding, patience, and for constantly asking ‘how’s that thesis going?’

INTRODUCTION

HISTORY OF HYDROTHERMAL VENT DISCOVERY, STUDY, AND GOVERNANCE

Thousands of years after humans took to the sea, the nature of submarine features and the life supported there remained largely unknown and provided a source of scientific and popular speculation. As recently as the mid 1800s it was proposed that and the oceans below 550 meters were devoid of animals ("azoic hypothesis") and the ocean floor was simply a uniform plane of sand only sparsely covered with life (Hessler & Sanders 1967). Yet as oceanographers probed the depths with more sensitive equipment, clues such as slight anomalies in ocean bottom water temperatures (0.1 °C), and elevated concentrations of mercury, manganese, and methane provided evidence for nearby hydrothermal circulation over mid-ocean ridges (Williams *et al.* 1974) and a more complex picture of ocean life began to emerge. In 1977 the first hydrothermal vents were discovered, observed, and photographed using the manned submersible, ALVIN, at the Galapagos spreading center (Lonsdale 1977). The presence of fauna at vents fundamentally changed our understanding of life in the sea, and on the planet (Anderson & Rice 2006). Life at vents showed that organisms could thrive under conditions of extreme pressure, temperature, and pH. Because of these extreme conditions, some scientists have suggested that vents may be the location where life originated (Van Dover 2000, Gage & Tyler 1992). The discovery of vents has driven a considerable amount of new exploration and research, but still only 10% of the discovered ridge systems have been explored for hydrothermal vents (Baker & German 2004). For the first 30 years (1977-2007) after discovery, on average two new vent species were being described each month (Ramirez-Llodra & Shank 2007).

Since the construction of the first submersible, The Turtle, in 1775 by David Bushnell, there have been many advances in underwater transportation, navigation, and exploration. However, *in situ* study of vents is only possible because of the technological advances that have been made in the last sixty years. More recently, advances in robotics, computing, high definition cameras, navigation, and 3D imaging have allowed for detailed exploration of the deep sea. The use of Remotely Operated Vehicles (ROVs) allows for close up inspection via real-time high definition cameras; sample collection and habitat sampling with instruments such as chemical and temperature probes, slurp guns, and push cores; photo-mosaicking that stitches together multiple photographs into a single image enabling researchers to assess patterns in community structure; and *in situ* experiments in the deep sea (Yoerger *et al.* 2007). For this project, the ROV Jason II was used to place and retrieve the outplanted rock substrates. Jason II is equipped with a 10 kilometer fiber optic cable, sonar, HD video and still imaging systems, manipulator arms, sampling trays and is capable of diving to depths of 6,500 meters and for multiple days at a time.

While such technological advances have been a boon to the scientific community, they have also put deep-sea ecosystems at risk of degradation and exploitation. The past forty years of exploration, surveys, and experiments in the deep-sea have not been harmless. Deep-sea expeditions can negatively impact the natural environment through the littering of plastics and lead ballast, construction of permanent observatories/data loggers, auditory and visual impacts from sampling vehicles, and actual physical destruction of vents through crashing into vent spires and small scale drilling of the seafloor, to name a few (Van Dover 2014). However, these impacts are believed to be negligible compared to effects that will come with the deep-sea mining of sulfide deposits, ocean acidification and warming.

Interest in deep-sea mining began to grow once it was deemed to be economically feasible. The combination of technological advancements reducing the cost to reach the deep sea and an increase in demand for the rare earth metals necessary for computer fabrication have added up to potential profits on the order of billions of dollars (Rosenbaum 2011). Mining the deep sea is of particular interest because deep sea ores contain higher grades of rare earth metals than terrestrial sources (Collins *et al.* 2013). Both terrestrial and deep-sea mining methods necessitate massive destruction of the environment. At large spatial- (tens of kilometers) and long time- (years to millennia) scales, deep-sea mineral extraction will directly kill the native fauna, destroy the hard substrate that the fauna live upon, and create massive sediment plumes by disturbing the seafloor and discharging the fluid used in processing of mined ores (Van Dover 2014, Lallier & Maes 2016, Levin *et al.* 2016).

These severe environmental impacts, the growing interest in deep-sea mining, the fact that many of the mineable deep-sea environments lay in areas without national jurisdiction, and the lack of an international body capable of managing the deep-sea necessitated massive international cooperation. Thus, in 1982 the United Nations Convention on the Law of the Sea (UNCLOS) and in 1994 the International Seabed Authority (ISA) were created (Van Dover *et al.* 2012). Both helped create an official framework, at an international level, for the governance of deep-sea ecosystems inside and out of areas beyond national jurisdiction. The ISA is responsible for granting sea floor mining contracts; currently (August 2019), 29 contracts have been granted, five of which are in the southwest Pacific (www.isa.org). This regulatory body, proceedings, and framework, are of particular interest to this study because of this study's proximity to areas with active mining contracts and its own potential for mineral extraction.

Introduction to Hydrothermal Vents

Hydrothermal vents are geologic formations that occur globally at oceanic spreading centers and subduction zones (Ramirez-Llodra & Shank 2007). In general, vents form when the cold ocean waters percolate down through the oceanic crust and are heated and recirculated back out into the ocean as warm, buoyant, sulfide- or metal-rich fluid (sometimes referred to as "effluent") (Van Dover 2000). The recirculated fluid can be extremely hot (350°C) to only slightly warmer than the ambient water (5°C). The rate at which the fluid flows can vary as well (40-240 cm/s) (Figure 1) (Converse *et al.* 1984, Grassle 1987, Hey *et al.* 2006).

There is a 60,000 km long system of mid-ocean ridges (MORs) that encircles the earth (Ramirez-Llodra & Shank 2007); on average they occur at great depths (2500 m) where there is no sunlight and ambient seawater is very cold (1-2°C) (Rothschild 2001). These ridges are spreading centers where new oceanic crust is formed. The rate of spreading usually determines if there will be hydrothermal activity. Faster spreading increases the chance for venting and volcanic activity (Grassle 1987), but creates shallow-narrow rifts that do not constrain the exiting vent fluid, which due to its low density rises in the water column in the form of a buoyant plume until it reaches neutral buoyancy (Ramirez-Llodra & Shank 2007). Slow spreading ridges such as the Mid-Atlantic Ridge (20-50mm/yr.) create deep (1-3 km) and wide (5-15 km) rift valleys that can constrain the vent plumes.

The ability to constrain a plume is important in affecting the distribution of chemosynthetic organisms. A deep, wide valley will constrain the plume and the larvae of chemosynthetic organisms along the spreading axis, increasing the chance that the larvae will reach another hydrothermal vent. Adult life forms in these systems rely, either symbiotically or as the base of the food web, on bacterial chemosynthetic primary producers that use the chemically enriched effluent to produce energy.

Back-arc Basins

Hydrothermal vents also occur at convergent margins in back-arc basin (BAB) systems at depths between 1,500 and 3,000 meters where sea floor spreading occurs behind a subduction zone. This geologic setting is found at Western Pacific island arcs, such as Japan, Mariana, Fiji, and Lau; outside of the Pacific, they occur in the southern Atlantic along the Scotia Ridge and in the Northwest Indian Ocean along the Andaman Ridge (Van Dover 2000). Back-arc spreading centers are only active for tens of millions of years, which is relatively short geologically (Hessler & Lonsdale 1991). At a local scale, individual vents are active on the order of decades (Grassle 1987, Tivey *et al.* 2012). Subduction at BABs occurs when a colder, older, denser, oceanic lithospheric plate dives under an island arc (wet side), which is between the subducting plate and the spreading center (dry side) where new crust is being formed (Figure 2). The distance between the subducting plate and the magma chamber influences the amount of water available, which influences crustal thickness, extent of melting, rock type formation at the spreading center, and end member fluid composition (Tivey *et al.* 2012). The water brought down by the subducting plate is heated indirectly by a magma chamber; this heating induces chemical reactions between the down-flowing water and the surrounding rocks and results in a buoyant fluid that rises back up through the crust (Figure 1) (Kelly & Metaxas 2007, Tivey 2007, Tivey *et al.* 2012). Effluent temperatures at BABs can range from near ambient away from the vent in a diffuse flow manner up to 360°C when the fluid is coming from pinnacle structures directly above the vent (Ferrini *et al.* 2008, Tivey *et al.* 2012).

The contribution from the subducting plate to the extruded magmas and effluent is a main factor that discriminates BABs from MORs. The addition of water via subduction lowers the melting point of the surrounding rock, which will eventually melt and be extruded as new crust (flux melting). In contrast to BABs, subduction does not occur at MORs, the separating of two oceanic plates away from a spreading axis results in the upward movement of the underlying rock. This rock, now at a shallower depth and thus under less pressure, but the same temperature and so, can also melt and be extruded as new crust (decompression melting). In addition to the different processes of crust formation, these two tectonic settings also differ in extruded magmatic compositions, mainly due to elemental transportation and enrichment via water (Pearce 2006). In general, BAB rocks exhibit enrichment of Al_2O_3, SiO_2, Ti, Zr, Y, Hf, and Nb and are depleted in FeO, TiO_2, and MgO, whereas MOR rocks are the opposite (Langmuir *et al.* 2006). Convergent margin melts not only have more water than divergent margin melts, but water also affects each system oppositely. At BABs, more water is associated with a greater extent of melting and lower TiO_2, whereas at MORs, more water is associated with less melting and more TiO_2 (Langmuir *et al.* 2006). However, even with these generalizations, BABs show a high degree of variation in melt composition due to the large range in melt temperatures (100°C) and extent of melting (Langmuir *et al.* 2006). For example, the Lau Basin (Figure 3) tends to be more mid-ocean ridge-like than other BABs. In comparison to the Manus and Mariana Basins, the Lau Basin has a lower degree of melting and less water, thus less variation in melt composition, and is depleted in heavy rare earth elements, but compared to the Scotia and Mariana basins, Lau has faster spreading rates and hotter mantle temperatures (Taylor & Martinez 2003).

The Eastern Lau Spreading Center (ELSC) (Figure 3), located between 19°20’S and 22°45’S, is characterized by gradients of several geological and chemical variables, which are due to differing spreading rates along the ridge axis. From north to south, spreading rate decreases from 95 mm/yr to 40 mm/yr, distance from the active Tofua arc decreases from 110 km to 40 km, axial depth decreases from 2,700 m to 1,740 m, crustal thickness increases from 5 km to 9 km, the ridge faulting decreases, hydrothermal activity decreases, and rock type changes from basalt to andesite (Table 1) (Martinez *et al.* 2006, Ferrini *et al.* 2008, Tivey *et al.* 2012, Kim & Hammerstrom 2012). In the north, the spreading center is farther from the subducting plate (Tofua arc) and is influenced less by water, resulting in extrusion of higher temperature basaltic lavas that have less MgO (less than 5.5%) and slightly more SiO_2 than the subducting plate. The stronger influence of water on the subducting plate in the south results in andesitic lavas composed of more SiO_2 (5%) and less MgO (2-3%) than the subducting plate (Podowski *et al.* 2010, Tivey *et al.* 2012). Additionally, in the north the basaltic rock type elements such as Ba, Rb, La, Th, and U are depleted, resembling MOR rocks, and in contrast, the southern andesitic region is enriched in those elements (Tivey *et al.* 2012). Extruded basalt rocks can also be described as smoother, less friable, and have less surface complexity (rugosity) compared to andesitic rocks; such physical characters may have an influence on fauna settlement (Podowski *et al.* 2010). These gradients create a compelling natural laboratory.

In the Lau Basin along the different spreading centers, several study sites have been established (Figure 4). Along the northern-ELSC lie the sites Kilo Moana (20°3' S, 176°8' W) and Tow Cam (20°19' S, 176°8' W). ABE lies on the northern portion of the Central-ELSC (20°45' S, 176°11' W); just north of ABE is the transition from basalt substrates in the north to andesitic substrates in the south (see red arrow in Figure 4). In the southern Lau Basin along the Valu Fa Ridge lies the Mariner site (22°11' S, 176°36' W). North of Mariner, but still along the Valu Fa Ridge lies the site Tu'i Malila (21° 59'S, 176° 34'W).

Hydrothermal Vent Chemistry

A significant control on faunal presence is the enabling and inhibiting influence of the vent effluent. The chemosynthetic symbiont-containing fauna must be able to live in proximity to the vent so that their endosymbionts can extract sulfide from the effluent to make energy, but not so close that the symbionts as well as the hosts' physical and chemical tolerances are exceeded; the latter is also true for the non-symbiont containing fauna. Different physical and chemical tolerances help determine the distribution of fauna near the vent.

The chemistry of the vents in Lau Basin have some along-axis patterns, but do not follow the North-South gradient as neatly as the geologic patterns. There are many factors that influence the final composition of the vent effluent. A main control on vent chemistry is the characteristics of each chemical species. Chemical species can be solubility-controlled or equilibrium/steady state-controlled (Von Damm 1995). The solubility of a chemical species dictates which variables control it. Soluble/mobile species are controlled by water/rock ratio and substrate composition. Solubility-controlled species are added from the initial sources of the hydrothermal fluid, and can be the seawater that is brought below the seafloor, the rock that the water passes through, or the composition of the magma that heats the incoming water (Von Damm 1995). Soluble components of the rock will be leached away into the downflowing water and will be encompassed into the final vent fluid product. However, most chemical species are not soluble and are only incorporated into the end-member fluid after being subjected to high pressure (150-350 bars) and high temperatures (250-450°C); these species are referred to as reversible species or equilibrium/steady state-controlled species (Mottl & Holland 1978, Von Damm 1995).

A main chemosynthetically-important molecule is hydrogen sulfide (H_2S). Along the ELSC, H_2S levels decrease in a southerly direction from Kilo Moana to Tu'i Malila, but increase at Mariner. At Kilo Moana H_2S ranges between 5.4 and 6.0 mmol/kg, at ABE from 2.6 to 3.6 mmol/kg, and at Mariner from 4.2 to 9.3 mmol/kg (Mottl *et al.* 2011).

Maximum temperatures along the ELSC decrease slightly in a southerly direction from 333°C at Kilo Moana to 229°C at Tu'i Malila (Mottl *et al.* 2011). South of Tu'i Malila, the Mariner site has a large range of temperatures between 240°C to 363°C (Table 2 in Mottl *et al.* 2011). This is consistent with the reasoning that deeper circulation at northern sites results in higher temperatures than shallower circulation at southern sites (Martinez *et al.* 2006). Circulation depth, however, is not the only control on effluent temperature, as observed at the Mariner site, which may attribute its higher temperatures to input from an actively degassing magma chamber (Mottl *et al.* 2011).

Another factor important to faunal distribution is the pH of the effluent from the vent. The physical tolerances to lower pH levels can also determine the proximity to the vent where the fauna can live. Generally, pH increases as you move south from Kilo Moana to Tu'i Malila; there is a decrease in pH at the Mariner site. In 2011, Mottle measured pH values at Kilo Moana between 2.9 and 4.0, at ABE between 4.3 and 4.6, and at Mariner between 2.5 and 2.7.

General Hydrothermal Vent Ecology

Hydrothermal vent ecosystems, like other ecosystems, are influenced by the regional and local geology. Geologic processes determine vent plume chemistry, ridge morphology, effluent discharge time and rate, and substrate composition and characteristics, all of which are key to defining the vent ecosystem. The stability of venting is also important. Faster spreading ridges have higher rates of venting, but are more unstable and do not vent for as long as a slower venting ridge (Grassle 1987, Martinez *et al.* 2006).

The vents that occur at spreading centers are at great depths, such that there is no light penetration and the vent organisms do not rely directly on the photosynthetically-derived biomass that drives almost all other ecosystems. Even other light-limited deep-sea environments such as the abyssal plain are closely connected to the photosynthetic processes of the epipelagic zone, for example, through the food input of marine snow. Marine snow reaches the abyssal plain in the form of particulate-organic-carbon in spatially and temporally limited pulses, the amount of which is dependent on the primary productivity of the overlying surface waters and the depth of the plain (Smith *et al.* 2008, Van Dover 2000). Oligotrophic surface waters and a deep water column can result in abyssal communities having 1% of the abundance of nearby productive continental slope communities (Smith *et al.* 2008). Because of this low input of energy, biomass is also low and averages less than 1 gram of wet weight per square meter (Desbruyères *et al.* 2000). The abyssal plain community does not include abundant primary producers but has consumers that are deposit feeders, suspension feeders, and predators or scavengers (Iken 2001).

In contrast, hydrothermal vent communities do have *in situ* primary producers in addition to grazers, scavengers, and predators. Instead of relying on photosynthesis to form the base of the food web, chemoautotrophic microbes are the primary producers for hydrothermal vent ecosystems. Free living, mat forming, and endo/ecto-symbiont bacteria use energy from sulfur compounds emitted from vents to build organic materials that are utilized by metazoan heterotrophs. The bacteria may be grazed upon or eaten through filter feeding by gastropods (e.g. *Depressigyra globulus*), polychaetes (e.g. *Nicomache venticola*), pycnogonids (e.g. *Ammothea verenae*), and planktonic and benthic crustaceans (e.g. *Ventella sulfuris*) (Bergquist *et al.* 2007, Micheli *et al.* 2002). The fauna in vent ecosystems do diversify their diets; some grazers and predators supplement their diets with non-vent derived detritus, however other fauna such as some nematodes are solely detritivores/ scavengers (Bergquist *et al.* 2007). Predators such as eel pouts (*Thermarces cerberus*), brachyuran crabs (*Bythograea thermydron)*, and galatheid crabs (*Munidopsis subsquamosa*) mostly eat other metazoans (Micheli *et al.* 2002).

Vent fauna are faced with the challenge of living in a dynamic as well as extreme ecosystem. Temperature fluctuation occurs on varying temporal (seconds to days) and spatial (centimeters to meters) scales; fauna must even be able to survive intense temperature gradients along their bodies. In 2007 Fisher *et al.* observed the chimney dwelling worm, *Paralvinella sulfonica*, living in conditions where one part of its body was in water near 60°C and the rest of it was in 10°C water. In addition to coping with varying temperatures, vent fauna must be able to tolerate varying pH and oxygen concentrations whenever they are within a vent plume. Vent effluent has been recorded with pH as low as 2 and as high as 10 (Fisher *et al.* 2007). Being exposed to the vent plume results in low oxygen to anoxic conditions.

Such extreme conditions differentiate the vent environment from a neighboring ecosystem, the “typical deep-sea.” The typical deep-sea physical environment (at 3000 m) can be characterized by ambient temperatures of 1-2°C, currents of 1 cm/s, salinity of 34.8 PSU, a nearly saturated oxygen concentration of 225-270 µM, and no light except for bioluminescence (Van Dover 2000). But because non-vent and hydrothermal vent habitats are proximal and share some physical characteristics such as depth, currents, and light, does not mean they have similar ecosystems. Van Dover (2000) argues that vent ecosystems are more akin to the rocky intertidal than to non-vent deep-sea habitats because both can be described as high biomass, high density, space limited ecosystems (Beck 1998, Van Dover 2000). Johnson *et al.* (1994) adds that the gradients in physical factors that determine species distribution are sharp and dynamic, whether they be the tidal exposure and temperature gradients of the rocky-intertidal, or the chemical and temperature gradients at vents. However they are not completely analogous in that vent organisms experience short term environmental changes on the order of minutes to hours (pulses of venting) and long term changes on the order years to decades (stoppage of venting) and the intertidal experiences short term environmental changes on the order of minutes to hours (waves and tides) and long term changes on the order of millennia (sea level fluctuations).

As there are different rocky-intertidal species assemblages across the world, variation in vent communities corresponding with location and vent habitat also exist. There are six symbiotic community types of vents around the world, each at a spreading ridge or subduction zone. At the Juan de Fuca Ridge the community is dominated by skinny tube worms (*Ridgea piscesae*), the East Pacific Rise is dominated by fat tube worms (*Riftia pachyptila*), the deep Mid-Atlantic Ridge is dominated by shrimp (*Rimicaris exoculata*), the shallow Mid-Atlantic Ridge is dominated by mussels (*Bathymodiolus* spp.), the Western Pacific Ridge is dominated by hairy snails, and the Central Indian Ridge contains species from both the Western Pacific and North Atlantic communities (Ramirez-Llodra & Shank 2007). Examining the species within each community along the entire segment of the ridge, taking note of the physical gradients, can provide information on the dispersal potential of each species. Important factors in determining the dispersal success of vent organisms are the distance between active venting sites, ridge morphology (i.e. if the ridge is shallower, the plume will not be constrained), the currents within the ridge system, and larval survival.

Lau Faunal Assemblage Patterns

Macroscopic Near Vent Fauna

The distribution and zonation of the symbiotic fauna in the Lau Basin has been extensively studied (Desbruyères *et al.* 2006, Henry *et al.* 2008, Podowski *et al.* 2009, 2010, Kim & Hammerstrom 2012, Tivey *et al.* 2012). There are three main species of symbiotic fauna, the snails *Alviniconcha* spp. and *Ifremeria nautilei*, and the mussel *Bathymodiolus brevior*, all of which are motile, which is different from many other hydrothermal ecosystems (Podowski *et al.* 2009, 2010). Their mobility and the natural laboratory of the ELSC provide an opportunity to study the factors affecting the distribution of each species, whether they be chemical/thermal effluent tolerances, interspecies interactions, or substrate preferences. At vents along the ELSC, the symbiotic fauna are arranged in concentric rings around a vent with *Alviniconcha* closest to the vent, *I. nautilei* in the next closest ring, and *B. brevior* in the outer ring. *In situ* studies (Desbruyères 1994, Podowski *et al.* 2010, Kim & Hammerstrom 2012, Tivey *et al.* 2012) and laboratory experiments (Henry *et al.* 2008) have elucidated the factors determining this distribution. Because *Alviniconcha* has the highest thermal tolerances (up to 45°C in the laboratory) it can live closest to the vent. Sulfide concentration was not found as a contributing factor to distribution, although *Alviniconcha* does have the highest tolerance to sulfide (400 µM) among the three symbiotic fauna. In addition to being able to live closest to the vent, *Alviniconcha* must live closest to the vent because it relies mostly on its endosymbionts for nutrition and less on filter feeding (Henry *et al.* 2008). *Alviniconcha*'s metabolic rate and H_2S uptake rate increase in increasing sulfur conditions. It is hypothesized that *Alviniconcha*'s high sulfur uptake rate may be facilitated by having an elaborate gill structure that allows for a greater diffusion area as well as space to hold more symbionts, having gill hemoglobins that increase uptake and transport of oxygen and H_2S, and/or living in the optimal temperatures for their symbiont's enzymes to function at (13°C) (Henry *et al.* 2008). The high rate of H_2S uptake is amazing especially if you consider that it rivals that of *Riftia pachyptila*, the vent dwelling tube worm that relies *solely* on its symbiont for nutrition and has lost its gut entirely. Although both snail species have the ability for heterotrophism, *I. nautilei* does not rely on its symbiont as much as *Alviniconcha.* Both species can filter feed on the free-living bacteria, but in extreme instances of starvation *I. nautilei* has been seen to cannibalize the feet of its neighbors (Henry *et al.* 2008). The laboratory experiments by Henry *et al.* (2008) found that sulfide was the limiting factor (100 µM), not temperature, for the distribution of *I. nautilei*. This contrasts with Podowski's findings in 2010, who determined that temperature limits *I. nautilei's* distribution (33°C). *Ifremeria nautilei* has higher thermal and chemical tolerances than *B. brevior* and a lower metabolic rate, thus it makes up the middle ring. The mussel *B. brevior's* upper limit temperature is 18°C. All three species are limited by lower sulfide limits of 4 ± 2 μM, the necessary level of sulfide for chemosynthesis.

Occasionally, mixed aggregations of *I. nautilei* and *B. brevior* are seen, significantly more on andesite substrates rather than basalt substrates. Podowski *et al.* (2010) hypothesizes this is because *B. brevior* can successfully exclude *I. nautilei* on basalt because the mussel's byssal threads attach better on the smooth textured basalt. Also, the northern Lau Basin is characterized by hydrothermal fluid escaping via visibly expressed sources such as faults and fissures (Ferrini *et al.* 2008). The southern Lau Basin lacks these faults; hydrothermal fluid escapes from permeable pathways in collapsed volcanic structures such as calderas and domes (Ferrini *et al.* 2008). These permeable pathways allow for a greater horizontal distribution of effluent, which contrasts the basaltic northern sites, where hydrothermal fluid comes from point source emissions. Mussels can more easily exclude snails from hydrothermal fluid coming from point source emissions as opposed to fluid that is not limited to single emission points (Podowski *et al.* 2010). This finding concerning the permeability of the substrate in determining sessile faunal in peripheral regions (sponges and gorgonians) settlement was not supported by findings by Kim and Hammerstrom (2012).

Macroscopic Peripheral Zone Fauna/Pattern

Not as widely studied are the non-symbiotic fauna living in the near vent environment. This environment is commonly referred to as the peripheral zone and includes the areas surrounding the vents, but outside of their main influences. These areas are near enough to the vents to benefit from the increase in primary production, but far enough away that concentrations of sulfides and hydrogen are too low to support chemosynthesis. In these areas, normal deep sea (not associated with vents) fauna are found, but in higher densities compared to the normal deep sea due to the increase in production from the vents (Sen 2016, Fisher *et al.* 1994). Peripheral zone sizes and distances are site specific and vary starting from tens of meters to thousands of meters away from the vent source (Sen 2013).

One study specific to Lau Basin peripheral communities done during the same time period (2006-2009) (Sen 2013) examined the changes in temperature, sulfide, and macroscopic community via ROV photo transects of Kilo Moana (KM), ABE, Tow Cam, and a near-Mariner site called Tu’i Malila (Figure 4). Sen (2013) found that peripheral communities resembled late successional stage vent communities; northern and southern regions had distinct communities, with northern communities having higher taxonomic richness; and both regions had mostly stable communities that did not change much over three years. Regarding the physical environment, in both 2006 and 2009, temperature anomalies (higher temperatures) were present at all sites, but sulfide anomalies (higher sulfide) were only present at KM sites in 2009 (Sen 2013). Normally, when hydrothermalism is present, both temperature and sulfide anomalies occur in synchrony. This particular case is peculiar because in 2006 at KM sites, there were temperature anomalies but no sulfide anomalies (Table 2). One out of two stations (KM1P) within the KM site recorded temperature anomalies in 2006, but not in 2009. Over this three year time period, one cladorhizid sponge, *Asbestopluma* sp., exhibited relatively rapid growth and mortality, and communities at station KM1P exhibited a decline in anemones and the symbiont-containing *B. brevior*, Sen (2013) determined this decline to be a reflection of the declining temperature.

In general, in the Lau Basin, peripheral communities are dominated by anemones on the northern basaltic substrates and sponges on the southern andesitic substrates. North to South community zonation is not thought to be limited by dispersal due to the observed small scale eddies and tidal flows that allow for dispersal of larvae in all directions, despite the general northward current within the basin (Speer & Thurber 2012, Kim & Hammerstrom 2012). And the anemones found in the northern region are also found in the South, but in far lower densities (Sen 2013). Additionally, most of the species along the ELSC are also found at other vents in the western Pacific, so dispersal is not thought to limit distribution of fauna.

Rugosity (surface roughness) differences between the two rock types are thought to be a potential driver of the community differences (Podowski *et al.* 2010). A number of studies have shown that larvae select settlement substrates based on a variety of substrate characteristics from the centimeter to less than millimeter scale (Dean 1981, Hills & Thomason 1998, Qian 1999, Underwood *et al.* 1994). In this instance, it is unknown if the surface complexity differences between the two rock types are affecting the community composition and if there is a particular scale at which surface complexity has an effect. Aiello (2018, Personal communication) found that large scale surface complexity correlated with smaller scale complexity originating from rock source geology. Thus we would expect to see the smoother textured basalts to have less surface complexity compared to andesite at all scales.

In the north basalt sections of the ELSC, anemones were seen to be on bare substrate, adjacent to symbiotic fauna (40% of population within 5 cm), and to have increased density in locations with less hydrothermal activity (Podowski 2009). Anemones were found to be in groups of 0.3-74.9 individuals/m^2, at temperatures averaging between 0.2 and 4.4 °C (highest being 8 °C), average sulfide levels of 3 µM (highest 19 µM), and occasionally on shells of *B. brevior* (Podowski *et al.* 2010). The point sources of effluent found in basalt are thought to favor anemones because anemones benefit from being near hydrothermal activity, but not in it (Podowski *et al.* 2010). Their low tolerance to high temperatures and high sulfide levels would make living on substrates with high lateral diffusion of hydrothermal fluid, such as the andesitic southern Lau Basin, difficult. The anemones found along the ELSC are *Zoanthidea* sp*., Amphianthus* sp*., Actinostolidae* sp*., Cyanthea hourdezi, Alvinactis chessi, Chondrophellia orangina, and Sagartiogeton erythraios*.

Sponges prefer hard, vertical to near vertical substrates with little to no sedimentation (Arquit 1990, Leys 2004). Camera tows by Arquit in 1990 at the Ashes Vent Field, off of the Juan de Fuca Ridge, found that the highest densities (82.4 individuals/m^2, 3.2 times the average) of sponges were found in the Non-vent Impact Zone (800-1300 m from the vent). Despite the name, this zone was still affected by hydrothermalism and exhibited both biotic (bacterial mats, vestimentiferan tube worms) and abiotic (10-60 °C temperatures, vent-derived sediments) evidence for this. The increased distance from the vent and substrate pillow flow morphology limited the sediment accumulation in this area. Arquit (1990) determined that substrate was one of the most important factors in determining sponge colonization and found strong negative correlations between sponge density and sediment cover.

In general, deep-sea sponges are slow growing and long lived. Both, substrate and water characteristics can influence sponge growth rate and lifespan. Siliceous sponges (hexactinellids and some demosponges) need high amounts of dissolved silica in the water; concentrations below 30-40 µM can limit growth (Leys 2004). Oxygen levels must be above 45 µM in order to support sponge respiration; along the ELSC O_2 does not limit sponge distribution. Water temperature can affect sponge filter feeding; in sponges off the coast of British Columbia, Canada, Leys (2004) discovered that temperatures below 7 °C cause the sponge to stop pumping water and temperatures above 12 °C do not allow the sponge to stop pumping water. The ability to stop pumping water is necessary and avoids clogging of ostia (pores) if too much sediment is in the water. The sponges found along the ELSC are *Abestopluma* sp. (stick sponge) and *Abyssocladia dominalba* (lollipop sponge) (Kim & Hammerstrom 2012).

There are very few data available concerning the temperature and chemical tolerances of peripheral vent species, including the sponges and anemones of the Lau Basin. Sponges are expected to be one of the more low-oxygen tolerant organisms (Kim & Hammerstrom 2012), which may allow them to survive closer to vents. However, according to Kim & Hammerstrom 2012 (Table 3) sponges were observed farther from vents than anemones in both the northern and southern study sites. The mean of means distance of sponges from vents were 17.4 m in the northern sites and 10.4 m in the southern sites. The mean of means distance of anemones was 8.4 m at both northern and southern sites. Since anemones are living closer to vents, this may mean that they have higher temperature and sulfide tolerances than sponges.

Microscopic Peripheral Zone Fauna

Even less studied are the meio-/microscopic fauna that cannot be directly observed with an ROV. Some taxonomic work has been done on some of the meiofauna from the near-vent environment (Gollner *et al.* 2010, Gwyther & Wright 2008), however information regarding meiofauna of the Lau Basin is lacking. In the following sections I highlight some of the major groups of meiofauna and present some background on their vent/deep sea ecology. Images of some of the fauna can be found in the appendix**.**

Copepods

Copepoda is a subclass of crustaceans that is organized into nine orders, has 11,500 valid species, are the most abundant metazoan, found in all aquatic habitats, and are ecologically important due to their role as primary consumers, nutrient cyclers, and as a food source (Boxshall 2004, Turner 2004, Desbruyères *et al.* 2006, Gollner *et al.* 2010). As of 2010, there were 80 described species from vents alone, with 50 coming from the family Dirivultidae (Order Siphonostomatoida), most of which came from washings of tube worms, gastropods, bivalves, crabs and shrimp (Gollner *et al.* 2010, Boxshall 2004). Less specious are the benthic harpacticoid copepods which is mostly made up of the families Aegisthidae, Ameiridae, Argestidae, and Laophontidae (Boxshall 2004). Not much is known about the biology of each species, only recently has work begun on their taxonomy, morphometrics, and genetics.

At vents, they are found to be free-living on and above active chimneys and in association with tube worms where the effluent is emitted, showing a tolerance for high temperature and sulfide (Boxshall 2004, Gage & Tyler 1992). Additionally, they are found at inactive chimneys, in lower densities but more diverse assemblages than in the higher flow areas. Parasitic and symbiotic copepods have been found on and in crustaceans, fish, molluscs, and bryozoans. Studies have shown that they consume bacteria and detritus. Planktonic naupliae have been observed above the vent.

From the Lau Basin, the most studied family is Dirivultidae and is represented by *Stygiopontius lauensis*, *S. brevispina*, and *Chasmatopontius thescalus*; these taxa may have a high frequency of observance because they are usually found in high sulfide environments such as the washings of the snail *A. hessleri* (Gollner *et al.* 2010, Lorenzo personal comm.). These three species can be distinguished from each other by comparing the urosome shape and the rami characteristics. Contrasting the environmental preferences of the copepods from Dirivultidae, is *Amphiascus aff. varians,* (family Miraciidae) a copepod found in lower sulfide and higher oxygen environments such as washings of the mussel *B. brevior*.

Polychaetes

Polychaetes are mostly marine, mostly dioecious, segmented annelids with parapodia that usually contain setae, and there are at least 9000 species organized into 72 families (Fauchald 1977, Rouse & Pleijel 2001). Polychaetes are some of the most iconic and well-represented groups found at vents; when one thinks of vents, images of clusters of the giant tube worm, *Riftia pachyptila*, surrounding active chimneys come to mind. Because of their abundance, gregariousness, large size, and immobile adult lifestyle, species like *R. pachyptila* have become model organisms in studying the biogeography, gene flow, and habitat connectivity of vents.

As of 2006, 111 vent polychaete species had been described, 30% of which belonging to the scale worm family, Polynoidae. Like most polychaetes, the polychaetes at vents come in a large variety of shapes, sizes, and lifestyles. At vents, polychaetes fill niches as active predators (Hesionidae: *Hesiospina vestimentifera*), mobile scavengers/bacteria grazers (Polynoidae: *Branchinotogluma segonzaci*, from Lau), associated with other fauna (Amphinomidae: *Archinome rosacea*), sessile solitary tube builders (Serpulidae: *Hyalopomatus mironovi*), sessile burrowing deposit feeders (Ampharetidae: *Amphisamytha galapagensis*, from Lau), and tube building endosymbiotic habitat providers (Siboglinidae: *Tevnia jerichonana*), to name a few (Desbruyères *et al.* 2006, Kupriyanovaetal 2010).

Polychaete larvae are known to show selectivity in settlement location and cues to either induce or inhibit settlement can be a result of the presence of adult con-specifics, juvenile hormones, bacterial films, and physical factors such as current speed, substrate color, angle, or surface roughness (Qian 1999). In Toonen and Pawlik's 2001 study refuting the 'Desperate Larvae Hypothesis', at least for planktotrophic invertebrate larvae, the serpulid, *Hydroides dianthus*, was shown to have two main variants of larvae, a 'founder' that searched for uninhabited space of rock and an 'aggregator' that settled with conspecifics. Both variants responded to biological cues (biofilms and presence/absence of conspecifics); environmental factors were not shown to describe larval settlement. Correlation with surface complexity at vents most likely varies at a species level as it did in Dean's 1981 experiment examining how estuarine fouling tunicates, hydroids, bivalves, and polychaetes responded to bare or complex settlement plates. Dean's experiment showed that one sessile serpulid, *Hydroides dianthus*, preferred to settle on bare substrates, while another polychaete, the mobile polynoid

Leptodonotus squamutus, was found to associate itself with higher surface complexity habitats.

From the Lau Basin, a mix of mobile and sessile polychaetes have been characterized and all are associated with high sulfide environments. The polynoids *Branchinotogluma segonzaci* and *B. trifurcus*, are found on active chimney walls and I. nautilei washings, respectively. Paralvinella unidentata (family Alvinellidae, order Terebellida) is a tube dweller often found living in A. hessleri shells. Also from Alvinellidae, *P. fijiensis* is a solitary tube builder found on actively venting chimney walls. *Amphisamytha galapagensis* (Ampharetidae) makes gelatinous mucus tubes that are covered in mud or volcanic glass chips.

Molluscs: Gastropods and Bivalves

Phylum Mollusca, the second largest phylum (~200,000 extant species), contains Class Gastropoda — represented by the snails, slugs, and limpets — which is the most diverse molluscan class and contains at least 30,000 (up to 100,000) extant species, and is found in terrestrial, fresh, and brackish environments, but mostly marine habitats from intertidal to hadal depths (Ruppert *et al.* 2004, Carlton 2007). Gastropods are mostly benthic but some are pelagic (Bianchi & Fields 2011, Carlton 2007). Most gastropods have a muscular foot that is used for locomotion, a head with sensory tentacles and eyes, a rasping radula used for feeding, a mantle that secretes a shell, and a pelagic larvae known as a veliger; the one characteristic all gastropods share is torsion: the 180° rotation of the visceral mass in relation to the foot (Ruppert *et al.* 2004). Compared to other groups at vents, substantially more work has been done on the gastropods of hydrothermal vents. At all vents, 60 genera and at least 100 species of gastropods have been described (Desbruyères *et al.* 2006).

One of the most cosmopolitan genera is *Lepetodrilus*, 13 different species of limpets of this genus can be found at vents of the NE and SW Pacific, North Atlantic, and Indian Ocean. Most are vent-endemic detritivores and can be found living in association with symbiont-containing mussels and tube worms; some are bacterial grazers and filter feeders (Desbruyères *et al.* 2006, Kelley *et al.* 2007, Bates 2007). In the Lau Basin, *Lepetodrilus* is represented by *L. elevatus*.

In addition the well documented symbiont-containing *A. hessleri* and *I. nautilei,* several other snails from family Provannidae are also present in the Lau Basin. Such taxa belong to the genera *Provanna* and *Desbruyeresia*, are vent-endemic detritivores, have high spiraled shells, and can be distinguished externally through different levels of articulation and sculpture.

Barnacles

Infraclass Cirripedia (sometimes called a subclass), is composed of more than 1000 strictly marine species, found from the intertidal to the deep sea. Barnacles are hermaphroditic with internal fertilization, have a sessile adult stage (unless attached to something mobile i.e. whale, turtle, wood, boat etc.) and a planktonic larval stage, and mostly filter-feed particulate organic matter and bacteria with their cirri, although some vent species “grow” ectosymbiotic filamentous bacteria on their cirri (Southward 1998, Brusca 2003, EOL (encyclopedia of life)). Barnacle larvae have been shown to preferentially settle with conspecifics and exhibit substrate selectivity based on rock type and substrate texture (Caffey 1982, Prendergast *et al.* 2008). Despite the high dispersal capability of lecithotrophic larvae (up to four months), vent barnacles are limited to the Pacific Basin (Desbruyères *et al.* 2006). The Lau Basin is considered a diversity hot-spot for vent barnacles and contains four suborders of barnacles; in particular, it hosts Brachylepedamorpha, a suborder once thought to have gone extinct in the Miocene, and *Eochionelasmus ohtai*, the most primitive balanomorph (Newman & Yamaguchi 1995, Desbruyères *et al.* 2006).

Miscellaneous arthropods: Amphipoda, Tanaidacea, Ostracoda, and Isopoda

Order Amphipoda is composed of 5 suborders with the largest and most cosmopolitan being Gammaridea, which are found at in coastal terrestrial habitats and fresh, brackish, and marine waters at all depths (Chapman 2007). Amphipods are detritivores, scavengers, and predators of smaller amphipods, copepods, and polychaetes (Cadien 2004), function as environmental indicators, nutrient cyclers, and food for larger animals, and show complex sexual behaviors such as hermaphroditism, mate defending, and mate attraction via sound (Chapman 2007). At vents, amphipods are found in large numbers swarming in hydrothermal fluid and in mussel and tube-worm assemblages. As of 2006, 24 vent species had been described, with all but one coming from the Eastern Pacific and Mid-Atlantic and most being from the subfamily Lysianassoidea (Desbruyères *et al.* 2006). The one species, *Cyclocaris tahitensis*, not from the two mentioned regions, was found at a depth of 1447 m off of Tahiti, in the vent environment, but is not believed to be vent-obligate (Desbruyères *et al.* 2006).

Tanaids are found globally in fresh, brackish, and salt water from depths as shallow as the intertidal to waters as deep as 5000 meters. Most tanaids are very small (2-5 mm), marine, benthic detritivores that use their relatively large chelipeds for feeding (Desbruyères *et al.* 2006, Holdich & Jones 1983). A few families are planktonic and some can supplement their diet with filter-feeding. They can be free-living or tube-dwelling within the sediment or on hard surfaces as varied as turtle shells to volcanic rocks (Holdich & Jones 1983). They show sexual dimorphism, hermaphroditism, and have no pelagic life-stages (other than the holoplanktonic species) because the females brood their larvae within a marsupium until larval appendages begin to form (Blazewicz-Paszkowycs *et al.* 2012). Deep-sea tanaid sexual dimorphism is not as pronounced as it is in other habitats where males become non-feeding individuals with large chelipeds used for fighting other males and females primarily remain inside a burrow or tube (Larsen 2006). Tanaid adults and larvae have been shown to be able to survive limited anaerobic conditions and highly variable salinities (0-52 ppt), allowing them to live in burrows and tubes, which can become anaerobic, until the larvae have developed fully (Gamble 1970, Holdich & Jones 1983). As of 2012, the conservative estimate for number of species is 1200, with most new species likely to be found in the deep-sea (Blazewicz-Paszkowycz 2012 *et al.*). At vents, there are seven known species from the Mid-Atlantic Ridge and two at the Western Pacific BAB vents. *Typholotanais* sp. and *Leptognathia ventralis* were found in non-vent, diffuse vent, and sulfide rubble habitats in the Western Pacific BABs (Desbruyères *et al.* 2006). Not much is known about either species' ecology.

Ostracods, also called "seed shrimp," are small crustaceans enclosed in two valves that range in size from 0.3 – 3 mm, can be detritivores or filter-feeders, live benthically and pelagically in fresh, salt, and brackish waters globally, and can be found in extreme environments like hot springs, cave lakes, and can even survive for up to six days in dried up lakes waiting for the next rain (Benvenuto *et al.* 2013, Riisgard 2013, Karanovic 2014). There are 8,000 extant species, however including the extinct species results in a number closer to 50,000 species (Schram 2013, Tanaka & Yasuhara 2016); these extinct species play an important role in paleontological studies because their magnesium calcite shell preserves well and thus is used for stratigraphic dating (Wilson 2013). Additionally, their shell can keep them alive through a fish's digestive tract, is a place to brood eggs, helps resist desiccation, and can help determine which environment they live in (Schram 2013, Taylor 2013). Only 10 species are known at vents with six being vent-endemic from the North Eastern Pacific vents. Ostracods in particular are thought not to disperse very far and most likely ostracods at vents are most closely related to ostracods from the near-vent deep sea; extremely rare basin-to-basin connectivity is expected to occur once every tens to hundreds of thousands of years (Mitarai *et al.* 2016, Tanaka 2016). Recently in 2016 a new species was discovered at the Miojin-sho caldera off of Japan (Tanaka 2016). These ostracods are not vent-obligate, but live in association with and feed on the mucus and sloughed-off tissue of vent-obligate polychaetes and barnacles (Tanaka 2016).

There are over 9,500 species in order Isopoda, and species can be found at all depths in brackish and marine waters, on and within substrates like hard rocks, fine sands, corals, and sea grasses, and act as predators, detritivores, scavengers, and parasites (del Espinosa 2002, Brandt *et al.* 2015, Elsner *et al.* 2015). In the deep-sea, isopods can be the most common crustacean found; epi-/benthic trawls of the Kuril-Kamchatka Trench showed depth to be a controlling factor of faunal composition, with isopods being the dominant crustacean at depths from 5000 – 9000 m and amphipods being the most dominant crustacean deeper than 9000 m. The most dominant group of isopods in the deep-sea is Suborder Asellota, (contains 90% of deep-sea isopods), which contains 22 families, with some of the most cosmopolitan being Munnopsidae and Desmosomatidae (Brusca 1997, WORMS, Elsner *et al.* 2015, Riehl *et al.* 2014).

HYPOTHESIS

This thesis describes the sponge- and anemone-dominated communities along the ELSC, and possible factors determining their distribution. Through the use of a replacement-type experiment, this project is testing if northern and southern communities are affected by substrate (**H_{O1}** below) or location (**H_{O2}** below) or an interaction between these two factors. Elucidating recruitment on substrate type will help determine if larval preferences for substrate exist. Location is tested in this experiment to see if other site-specific factors such as sediment accumulation, vent fluid characteristics, or substrate permeability influence recruitment. The interaction factor tests whether recruitment is affected by substrate type and location together.

H_{O1}: Rock Type Does Not Affect Faunal Recruitment.

Rock type is expected to affect faunal recruitment. According to the community structure cluster analysis done by Kim (2012), rock type was found to be the factor responsible for the most similarity for communities in the peripheral zone. Kim (2012) found basalt communities to show 84% similarity with 67% similarity due to presence of anemones, and andesite communities to show 50% similarity with 70% similarity due to presence of sponges. If organisms do preferentially settle on certain rock types, this may be attributed to differences in rock type texture. Other factors such as bathymetric features, current direction, plume incidence and composition, and energy supply from the vent were considered, but were not found to explain the manner in which the communities were clustered (Kim & Hammerstrom 2012).

H_{O2}: Location Does Not Affect Faunal Recruitment.

Location is expected to affect faunal recruitment. Because the currents in the Lau Basin are not strong enough to limit dispersal unidirectionally, the multidirectional small scale eddies will be the prevailing dispersal factor. The dispersal potential is even at both locations, so larval supply of each region will influence faunal composition in each community. If anemones and sponges are found on andesite and basalt evenly, this will indicate that either larger scale geologic processes or larval supply is controlling the observed pattern of sponge-dominated communities in the north and anemone-dominated communities in the south.

While it is expect that substrate type will be the dominant factor in determining sponge community and anemone community recruitment, some effect from an interaction between the two factors is also expected. It is expected to see more sponge community fauna on andesitic rocks in the south compared to andesitic rocks in the north. It is expected to see more anemone community fauna on basaltic rocks in the north than basaltic rocks in the south.

MATERIALS AND METHODS

Outplant Experiment

Initial Rock Collection

The rocks to be used as outplanted settlement substrates (hereafter referred to as "substrate/s") were initially collected in 2004 by Charles H. Langmuir aboard the R/V Kilo Moana (expedition: KMO0417). Rock samples were collected with dredges at four different sites (TABLE 4). After collection, substrates were classified as andesite or basalt (full rock composition data table and analysis methodology can be found in Bezos *et al.* 2009), defaunated, dried out, and fitted with a rope handle plus visible marker label to allow detection and recovery by ROV. From each dredge, nine substrates were created, except from dredge 52 from which eight substrates were created.

Rock Deployments

Thirty-five substrates were available for the experimental layout, 17 basalt and 18 andesite. These were set out at in the peripheral vent zone at three locations in the Lau Basin: Kilo Moana, ABE, and Mariner, in September 2006 on cruise MGLN07MV (PI C. Fisher) aboard the RV Melville. Kilo Moana is a basaltic location that hosts hydrothermal vent fauna, ABE is an andesitic location with similar faunal abundance, and Mariner is an andesitic location that was undergoing rapid change, with motile fauna but minimal sessile species. Kilo Moana (most northern) is about 80 km from ABE (central) and ABE is about 241 km from Mariner (most southern) (Figure 4, Table 1). Within each location, the ROV Jason II was used to set out substrates in groupings of four containing two basalt and two andesite substrates, at three sites (Table 4). Within each site, substrates were separated by no less than 1 m and no more than 5 m. All sites (i.e. ABE1, ABE2, ABE3) were about 10 meters from each other, except for the Mariner 3 site which was about 280 meters from Mariner 1 & 2 (~5 m apart).

Rock Recoveries

Substrates were recovered 42 months later, in May 2009, again using the ROV Jason II (cruise TN235, PI C. Fisher, RV Thomas G. Thompson). Substrates were collected into separate sealed containers, and returned to the surface and processed as quickly as possible, to prevent warming and sample degradation. Substrates and fluid in the recovery containers were placed in a MgCl solution in a refrigerated van to relax organisms and display morphological characteristics. Fluid was filtered over a 300 µm mesh screen and the substrate and residue preserved in 5% buffered formaldehyde in seawater. After a suitable time for tissue penetration (at least 24 hours), the preservative solution was rinsed away over a 300 µm sieve, and replaced with a 70% ethanol storage solution. Of the 35 substrates set out, nine were stored individually in plastic screwtop jars, and 21 were stored by double wrapping each substrate in a cloth sheet and then placed into sealed 5 gallon buckets (~7 substrates per bucket), with fluid and residue stored in jars. The cloth storage method was necessary because those 21 rocks were too big to fit into the screw top jars. The four substrates (HB1M, LB1M, MA3M, AA2M) at Mariner 1 were not relocated despite excellent navigational data and visual markers; it is believed that rapid growth and collapse of hydrothermal chimneys in the area buried them. And one substrate at ABE (AA1A) was located, but was unrecoverable because it fell into a hole. Figure 5 shows images taken during the rock block recovery at the three locations.

Sample Processing

Invertebrate Sorting

In the laboratory, the collected rock samples were examined under a dissecting scope at magnifications between 20x and 80x. Invertebrates were manually removed from the rocks under the microscope with the use of forceps and probes. A dissecting scope on a boom was used to scan the entirety of each rock in a “mow-the-lawn” pattern. To insure that all of each rock was examined, a referenced gridded image of each face of the rock was used. When present, the cloth wrapping and the substrate was rinsed over a 50 µm sieve to remove any fauna that collected on the cloth. Fluid and residue from jars was also sieved through a 50 µm mesh. Invertebrates were sorted and counted to the lowest taxonomic level: mostly family for polychaetes and copepods and genus for gastropods, and other crustaceans to order/suborder. Smaller (<200 µm) fauna such as copepods and mites were examined under a compound scope from 100x to 400x. All groups from each substrate were then stored in their own 0.5 dram vials of 70% ethanol.

When possible, taxa were identified to the genus/species level. Due to the dearth of species-specific taxonomic guides, many fauna were identified to only the family level. Such was the case for many of the copepods, polychaetes, and amphipods; however, when formal taxonomic distinctions beyond family did not occur but specimens were morphologically distinct, the analysis did consider a more exact level of identification to “type” (i.e. hesionid 1, hesionid 2, etc. where Hesionidae is a family within Polychaeta). Other groups were only identified to Class/Order due to being rare or requiring micro-dissection for identification; Order Isopoda, Order Tanaidacea, and Class Ostracoda each contained several identifiable “types” within each taxa. Additionally, gastropods that were small (<2 mm) and had translucent, flat, spiral shells (protoconchs) and most likely included a few different gastropods (Appendix I p.13) were grouped into the “wastebasket/purgatory” group Skeneiform; this polyphyletic classification describes clear, minute, planispiral, undifferentiable shells (Hickman 2013).

Many photographs were taken (~1300, each specimen was photographed more than once) of most of the fauna found using a microscope camera attachment from the Leica Application Suite EZ (v. 3.1.1, Build: 490, Copyright 2015). Photos were taken of fauna while still attached/within the substrate using a microscope attached to a boom. Most pictures of unattached fauna were taken on the stage of a compound microscope with the Leica camera attachment.

Photogrammetry and Surface Area

Three dimensional models of each substrate were created using the program AutoDesk Remake (now called ReCap Photo 2017 v 18.2.0.8). Remake uses the process of photogrammetry to stitch together large numbers of 2D photographs into a complete 3D model. For each rock, 70-90 images were taken using a DSLR camera (Olympus C-5060); after each picture, the rock was rotated 5-10 degrees, and then another picture was taken until every side of the rock had been photographed. The substrates were placed on a matte white stage with a curved background and lit with two microscope lights. It is important to use a curved background and a matte surface to reduce the shadows and glare which can cause trouble in the photogrammetry process. The 10 mm holes that were drilled into the rock were used to set the size scale, these 10 mm holes were initially used to loop the rope handle so that the ROV could recover the substrate. AutoDesk Remake was then used to calculate the surface area of each substrate using its standard program features (Table 5). Two-way ANOVAs were done to test for differences in surface area by substrate placement location and substrate source in JMP (Table 6). Figure 6 shows some images of this process.

Rugosity Calculations

Surface roughness was determined using a Matlab script (I. Aiello, personal communication) at different scales and at different locations along the rock's surface (referred to as moving windows). To do this, XYZ points of each rock are exported from AutoDesk's PhotoRecap program into the script, which calculates the Root Mean Square Deviation (RMSD), Surface to Planar Ratio, and a scaling value, "D" of that rock. For this study, only RMSD was used; RMSD is a quantitative value of roughness that looks at the deviation, positively and negatively, of the XYZ points from an interpolated plane of a particular window. The moving window calculates RMSD at one window size at different portions of the rock, after canvassing the entire rock using different central window points, the window size increases and begins to move to different portions on the rock; this process keeps repeating. Fourteen different window sizes were used, measuing from about 1 cm^2 to size to 40 cm^2 with each window having a minimum resolution of about 12 points per 1 mm^2. Different window sizes were used to verify relative surface complexity at multiple scales and to help determine if the relative complexity at scales that were not measured remained the same (i.e. KM HiTi Basalt had the lowest rugosity at scales below 1 cm^2 and above 40 cm^2).

Statistical Analysis

Pre-Testing for Bias

All statistical tests were performed using JMP10 (ANOVAs) or PRIMER6 (non-parametric tests), and significance assessed at the $p < 0.05$ level except when Bonferroni corrections were needed for multiple tests. To test whether rock surface areas differed between rock source and type or placement site and location, a two-way analysis of variance was performed. Rock source (dredge number) was nested within rock type (andesite or basalt), and placement site (1-3) was nested within placement location (KM, ABE, and Mariner). Tukey HSD tests with Bonferroni corrections were done for pairwise comparisons between placement sites, placement locations, and rock sources.

It was not possible to run a three factor PERMANOVA (site[location] X source[rock type] X rugosity) in PRIMER because a continuous variable (rugosity values) creates a test with zero replication. Because rugosity co-varies with rock source, rugosity was removed from the three factor model. One-way nested ANOVAs were done comparing the source[rock type] rugosities at the smallest window size (1 cm^2) to see if rugosity could be removed from the three factor model. MANOVA tests in JMP were done comparing the rugosity of each source type and location at each window sizes.

Hypothesis Testing

Non-parametric PERMANOVA on Bray-Curtis similarity matrices from 4^{th}-root transformed densities of fauna sorted to the lowest taxonomical level were done to test for community differences due to rock type and source, and location and site. The factors were rock source nested within rock type (source[type]) and site nested within location (site[location]). Similarity Percentage Analysis (SIMPER) was used to determine contributions of individual taxa to community similarities. MultiDimensional Scaling (MDS) plots and SimProf Dendrograms were used for visualization.

Caveats

As discussed earlier in the methods, many rock substrates were too large to be placed in individual jars and were instead wrapped in a sheet and placed in 5 gallon buckets filled with ethanol. During transport, one bucket developed a small crack, the ethanol leaked out, and the samples dried out. All of these samples were found to have a very high number of mites (100-500); no other samples had > 9 mites (AA3M). To complicate things, all of these samples were also from Kilo Moana. Other samples from Kilo Moana that were not wrapped in cloth had few to no mites. Samples from other locations that were wrapped in cloth, but did not dry out, had few to no mites. It was undeterminable if the same sheet was used to wrap all of the rocks and if the sheet was washed/rinsed before it was used to store the samples. Because of the high correlation between mite presence and samples drying out, it is believed that the mites are a contaminant and thus they were not included in the analysis.

RESULTS

Rock Characteristics

The two-way ANOVA for bias in surface area was significant for rock type and rock source nested within rock type, but not significant for location or for site nested within location (Table 6). Substrates placed at all three locations measured around 35000 mm^2 (2-Way ANOVA, $F_{2,2} = 0.825$, $p = 0.4532$). Andesite (43000 mm^2) substrates were significantly ($p = 0.0038$) larger than basalt (29000 mm^2) substrates (Table 7), with all of the significant contribution ($p<0.0001$, Table 9) coming from the difference between Mariner andesite (49000 mm^2) and Kilo Moana basalts (19000 mm^2) (Table 8).

Rugosity was determined at multiple scales (1 – 40 cm^2) and as scale increased, rugosity also increased and variation decreased. Rugosity differences at the 1 cm^2 scale were analyzed further because it was the smallest resolution that the photogrammetry process was able to accurately measure and the most ecologically relevant to the very small fauna encountered. Unfortunately, the methods were not able to capture roughness at a “micro-texture” scale (1 – 100 µm), a resolution that barnacle ciprids can differentiate between (Berntsson 2000). At the 1 cm^2 window size, 1-way nested ANOVAs showed that rugosity is affected by both rock type (1-Way ANOVA, $F_{1,1} = 30.36$, $p < 0.0001$) (Table 10) and source[rock type] (1-Way ANOVA, $F_{2,1} = 4.97$, $p = 0.015$) (Table 10). Andesite (-1.58) had higher rugosity than basalt (-2.29). Rock source rugosity followed suit, with ABE andesites having the highest mean rugosity ($\mu = -1.27$)

and were statistically different compared to all other sources (Table 10). Mariner andesite had the second highest rugosity (μ = -1.84), then KM low Ti basalt (-2.21), and then KM high Ti basalt (-2.39). Statistical group and pairwise comparisons between sources can be found in Table 10.

Multivariate Community Analysis

Multivariate community analysis using a 4th root transformed Bray Curtis Similarity matrix of the fauna density using the PERMANOVA test in Primer found only location to have an effect on fauna density (PERMANOVA, Pseudo- F_2 = 2.35, p = 0.044); other factors such as rock type (F_1 = 0.800, p = 0.668), site[location] (F_5 = 1.31, p = 0.085), source[rock type] (F_2 =1.012, p = 445), and the interaction term rock type X location (F_2 = 4.414, p = 0.113) did not have a significant effect on fauna density (Table 11) . Results of the pair-wise analysis using the ANOSIM test, was used to compare differences between sites and showed that location had an effect on faunal distributions due to the differences between ABE versus Mariner (p = 0.001) and ABE versus Kilo Moana (0.011), Kilo Moana and Mariner did not differ significantly (p = 0.239) (Table 12).

Multivariate Figure Visualizations

Figures 17, 18, and 19 help visualize the statistical analysis and numerical values of the multivariate tests and use the same Bray Curtis similarity matrix. The MDS plot (Figure 17) shows a tight clustering of rocks placed at ABE locations, Mariner blocks show slight clustering, and Kilo Moana are variably distributed throughout the plot; rock type does not have an effect on fauna distribution, and the plot shows both andesite and basalt rocks to be mixed throughout all locations. The Principal Co-Ordinate figure (Figure 19) shows the same MDS plot overlaid with some of the more populous fauna and how they contribute to each groupings clustering. All taxa were included in the PCO analysis, any taxa not visible in this diagram clustered around the area where serpulids, *Amphiascus sp.*, and Sutilizonidae labels are; including them in the diagram would have made the diagram illegible. Some of the taxa not shown in this figure are: *Bathymodiolus* sp. (Bivalvia), *Provanna* sp. (Gastropoda), *Archinome sp.* (Polychaeta), unknown polychaete1, unknown copepod1, unknown copepod2, unknown juvenile polychaete, and unknown Cirripedia ciprid. Large numbers of serpulids, limpets, and *Provanna* gastropods cluster together and contribute to the ABE rock block clustering; Asellota isopods, gammarids, and hesionid2 polychaetes group together and contribute to Kilo Moana and Mariner clustering; syllid, glycerid, and hesionid1 polychaetes also show clustering together and contribute to ABE and some Kilo Moana clustering. The dendrogram (Figure 18) helps further illustrate the tight clustering of communities on rocks placed at ABE sites as well as some clustering of Kilo Moana sites and the high variance of Mariner sites.

SIMPER on Density Data

Similarity percentages (SIMPER) were calculated to examine the contribution of each taxa to the overall similarity of each location (Table 13) and rock type (Table 14). All substrate types from ABE were the most similar to each other (41.01%), with most of the contribution coming from the copepod *Amphiascus sp.* (21%), serpulid polychaetes (17%), and balanomorph barnacles (10%). Substrates from Mariner were the next most similar (35%), with the most contribution coming from Tegastidae copepods (23%), *Amphiascus* sp. (17%), and Asellota isopods (12%). Kilo Moana substrates were the least similar to each other (15%), where *Amphiascus* sp. contributed to 37% similarity, unknown polychaetes (12%), and an unidentified "copepod1" (9%). SIMPER analysis also showed pairwise dissimilarities between locations and showed that Kilo Moana and Mariner were 83% dissimilar, Kilo Moana and ABE were 80% dissimilar, and Mariner and ABE were 77% dissimilar. Andesite and basalt rock types were both 30.3% similar to themselves, with the top three contributions of andesite's similarity contribution coming from *Amphiascus* sp. (~22%), Asellota isopods (~9%), and serpulid polychaetes (~8%). Basalt rock type similarity comes from *Amphiascus* sp. (~27%), serpulids (~12%), and unknown polychaetes (~8%). All fauna contribute between 1 and 7% dissimilarity.

DISCUSSION

Rock Type and Source Effects

For all tests, rock type did not have a significant effect on the distribution of fauna. Physical characteristics such as surface area and surface roughness did differ by rock type and source. Surface area differed by rock type, with andesite (~ 43000 mm$^{2)}$ substrates being larger than basalt (~ 30000 mm^2) substrates. At the source level, Mariner andesites (~ 49000 mm^2) were larger than Kilo Moana low titanium basalts (~ 19000 mm^2). These potential biases must be kept in mind when assessing the community analysis.

Surface roughness was also affected by rock type and source. All roughness measurements had higher variations at smaller window sizes due to using fewer points to obtain a roughness measurement at those smaller window sizes; larger window sizes also had higher surface roughnesses due to using larger measurement areas allowing for greater chances of larger elevation differences. Mean surface roughness at all window sizes from 1 – 40 cm^2 was nearly identical at all placement locations (Figure 9). Surface roughness was affected by substrate source at all window sizes, where each source type consistently remained at a relatively higher/lower roughness than the other source types (i.e. ABE andesite substrates always had higher roughness than Mariner andesites etc., Figure 11, 12): ABE andesites had higher roughness than any other substrate; Mariner andesites were also rougher than KM high Ti basalt. These small scale relative roughness values also reflect the larger scale patterns for each location to a certain extent, where the basalt hosted Kilo Moana region has lower relief pillow basalts (smoother) and the andesitic regions have higher relief environments (rougher); the deviation occurs where, at large scales, the Mariner region has a higher relief (rougher) than the ABE region.

In the experimental design portion of this study, only location and rock type factors were planned to be tested. The direct test of rugosity sought a statistical confirmation of the assumed difference between basalt and andesite, and showed that while andesite from ABE was clearly different from all other substrates, andesite from Mariner was not statistically more rugose than basalt from KM (low Ti). This subtle difference must also be attended to while interpreting results of community analysis.

Because the communities were not statistically significantly different by rock type or source, it is concluded that substrate roughness did not influence the fauna. This pattern does not support Podowski *et al.*'s (2010) hypothesis that smoother basalt substrates would provide a better anchoring surface than the friable andesite surfaces for fauna such as cnidarians. However, supporting this hypothesis was the finding that barnacles, a taxa known to show larval settlement preferences, settled primarily on basalt (KM High Ti) substrates, the rock source with the lowest surface roughness, though this was not statistically significant (Figure 15, Table 17).

Three other taxa where surface roughness could play a role due to a sessile adult lifestyle with a motile larvae capable of testing for optimal substrate settlement are serpulid, terebellid, and ampharetid polychaetes. The serpulids that were found were encased in calcareous tubes that were attached to the surface of the rocks and did not differentiate significantly between andesite (SIMPER 2.02 indv./m^2) and basalt (1.93 indv./m^2) rock blocks. The presence of serpulids is interesting because as of 2010, only four species of serpulids have been found at vents, two of which are from the North Fiji Basin (Kupriyanova 2010). One genus, *Hyalopomatus,* found in the Fiji Basin has also been found in 4100 m waters off of California and attached to the glass sponge, *Hyalonema* (Kupriyanova 2010).

The availability of quality sediment also affects the settlement of sessile polychaetes such as the terebellid *Eupolymnia nebulosi,* whose larvae settled preferentially in areas with sediments fine enough to be used for tube building (Bhaud 1990). Of the substrates collected, some rocks had more sediment than others, however sediment levels and character were not accounted for, so it is not possible to determine if sediment had an effect faunal distribution. While sediment levels were not accounted for, tube-building fauna were (ampharetids, tanaids, terebellids), and were not shown to contribute significantly to site or rock type dissimilarity (SIMPER, ~2-3% for each group). In my samples, ampharetids, sabellids, terebellids, and tanaids were found to be living in gelatinous sediment-covered tubes that were on and within the rock substrates. In addition to the sediment, tanaid tubes were covered in foramnifera (Appendix p. 6). It is also not known what these tube-builders were using to cover their tubes, possible sources could be material from the vents, surface waters, or nearby erosion of rocks. Although not shown in the results, perhaps a more friable/erodible habitat with finer textures would be preferential and provide material for a tube-builder to use. Such was the case for *Typhlotanais* sp. and *Leptognathia ventralis,* two western Pacific BAB tanaids, found in a diffuse sulfide rubble environment, a habitat containing available sediment for tube building (Desbruyères *et al.* 2006).

Perhaps there is an effect of roughness for each polychaete group at a more precise level (genus/species), as Dean (1981) and Bhaud (1990) found, and generalizations cannot be made for all sessile, tube-dwelling worms. Such specialization is exhibited at a species level for the polynoids at Lau that either are found in or avoid patches of anhydrite precipitate on effluent edifices (Sen 2013). Although rock preference was not observed for these polychaete families in this study, rock hardness and texture may be a settlement factor because some worms will settle inside the cracks and crevices of rocks (Desbruyères *et al.* 2006, Appendix I 2.f p.9). Or maybe there are other factors influencing these polychaetes' settlement such as microbial cues, tube-building sediment availability, or hydrothermal fluid concentrations.

It was important to test for surface area and roughness effects because, although rock type and source did not affect fauna distribution, different types/sources may have shared similar roughnesses or surface areas and grouping rocks according to shared characteristics may have been a possibility. Making sure all sites/locations had similar sized substrates with similar roughnesses was also important. Validation for roughness differences between rock type/source was also necessary (i.e. andesites have higher roughness than basalts).

Location Effects

The distinct community differences of the macrofaunal periphery environment between the three locations that were observed by Kim (2012) can be seen in photographs of Figure 5. From the ROV footage, ABE appears to be the most densely populated, then Kilo Moana, and then Mariner that looks mostly barren, at least at a macroscopic level. This is reflected in Sen's photomosaic study (2013), where the Lau Basin's communities differed between northern and southern regions in the near vent environment as well as the peripheral region at the macroscopic level. Thus, it is not surprising that the meiofauna communities also show a strong location effect.

In this study, the ABE location was consistently statistically different from the other two sites in community composition (Table 11, 13). For gastropods and polychaetes, ABE had the highest mean density, then Kilo Moana, and then Mariner; for barnacles, and copepods, ABE had the highest mean density, and then Mariner; “Other fauna” were highest at ABE and nearly identical at Mariner and Kilo Moana; arthropods were the one group that was highest at Mariner, then ABE, and then Kilo Moana (Figure 14, Table 16).

It is likely that the primary reason for ABE having much higher meiofauna densities than the other sites is the increased availability of sulfide to the microbial primary producers, initiating a cascade of higher metazoan density in the peripheral vent environment (Grupe 2009). Sen (2013) hypothesized that the in situ measurements of the southern sites (ABE and Tu’i Malila) having a lower concentration of sulfide than the northern sites was a result of the manner in which the effluent was distributed and *not* a reflection of overall hydrothermalism. Effluent in the south is diffused laterally through the porous and brecciated substrates into a larger surface area, providing a better environment for microbes to oxidize sulfide, thus resulting in lower sulfide to temperature ratios. The point source chimneys in the north have a more limited spatial diffusion, facilitating either avoidance or exploitation of effluent, depending on the fauna. In fact, Kilo Moana was the only location to consistently have positive sulfide and temperature anomalies (Table 2), and it had some of the lowest fauna densities (arthropods, barnacles, copepods, Figure 14, Table 16).

The Mariner region, known to be over a degassing magma chamber and the most unstable of the three locations (4 samples were lost to a collapsing chimney and 1 fell into a hole), also did not show much evidence for the hydrothermal fluid presence reaching the peripheral environment. Maybe the high relief nature of the surrounding environment limited the exposure of the experimental substrates to fluid by elevating or blocking the substrates to where the effluent would flow? For all sites, the distance between the substrates and the nearest effluent source is not known (this would be difficult to measure), but it is presumed that all substrates were all placed in an appropriate “peripheral environment” due being where other peripheral fauna were encountered. Obtaining reliable temperature and sulfide concentrations at sites was not always possible due to instrument failure or disruptive environmental conditions (Table 2). Also, due to the difficulties and expensive nature of studying the deep sea in such a remote area, sulfide and temperature data exist only at two time points, 2006 and 2009. A continuous measurement of the physical and chemical characteristics for the entire 42 months when the substrates were outplanted does not exist. Evidence for the ephemeral nature of vents is exhibited by the rapid growth and mortality of cladorhizid sponges at the ABE sites, suggesting a period of increased hydrothermalism and primary productivity and then cessation of flow (Sen 2016). This paucity of information severely limits any determinative conclusions on what exact location effects may be causing these community differences. However, other evidence of location effects can be gleaned from the fauna assemblages collected combined with the natural history of each taxa and some ecological guesswork.

At a location level, according to SIMPER analysis, ABE was most similar to itself at ~ 41%, then Mariner at ~ 35%, and then Kilo Moana at ~ 15%; all pairwise comparisons were ~ 80% dissimilar to each other. ABE owes its high similarity to generally high abundances of all fauna, but in particular the copepod *Amphiascus aff. varians* (family Miraciidae) (5.25 indv./m^2 average abundance), serpulid polychaetes (4.15 indv./m^2), barnacles (3.73 indv./m^2), and Sutilizonidae limpets (3.35 indv./m^2). All of these taxa are known to occur in higher hydrothermal effluent areas (in the near vent environment) (Desbruyères *et al.* 2006). Two other taxa found in the near vent environment (Desbruyères *et al.* 2006), ampharetid polychaetes and *Lepetodrilus* limpets, were also found in slightly lower abundances.

The presence of the symbiont-containing mussel *Bathymodiolus* spp. at ABE is a strong indicator of sulfide. Only three of these mussels were found, all at ABE (one at each site i.e. ABE 1, 2, 3) and all on different types of rocks (ABE andesite, KM HiTi basalt, KM LoTi basalt). Such limited abundance is not enough to make a conclusion of habitat preference, but the fact that these mussels were found on different rock types could hint at having no preference for substrate. During initial sample processing, a few (about five) mysterious thread like “growths” coming from some of the rocks were found, initially they were presumed to be microbial strands, and thus were not recorded on which substrates they were found. However, after further inspection and help from Stacy

Kim, they were determined to actually be the byssal threads of mussels that had been removed from the rocks (Appendix I p.13). It is not known how the mussels were removed, whether it was by a predator, ROV, or other natural causes; it is possible that they decided to move themselves as they are known to do (Podowski *et al.* 2010). Finding mussels in this environment of this region may be a novel event, Sen (2016) did not encounter any mussels in the southern peripheral sites.

Another prominent near-vent taxa observed *only* at ABE and on both basalt and andesite substrates is the barnacle, *Eochionelasmus ohtai*. Adults of *E. ohtai* were one of the few macroscopic fauna found and ranged from ~1 mm to ~ 10 mm (Appendix I p.3). Some microscopic cyprid stage individuals (some unsettled and some recently settled) less than 1 mm in size were also found, a few of which might be pedunculate barnacles though it was not determined to which species they belong. They are most likely *E. ohtai*, but could also be one of the pedunculate barnacles found in the area, such as the vent obligate bacteria-farmer *Vulcanolepas parensis* (Desbruyères *et al.* 2006). *E. ohtai* is not vent obligate but is commonly found in the near-vent environment in close proximity to mussels and another barnacle, *Neoverruca brachylepadoformis* (Newman 1995, Desbruyères *et al.* 2006).

The Mariner location owes its similarity to moderate to low levels of fauna, primarily Tegastidae copepods ($\mu = 2.43$ indv./m^2), *Amphiascus* sp. ($\mu = 2.29$ indv./m^2), and Asellota isopods ($\mu = 1.97$ indv./m^2). Tegastidae, *Amphiascus* sp. (Miraciidae), Dirivultidae ($\mu = 1.13$ indv./m^2), and terebellids ($\mu = 1.13$ indv./m^2) have all been found in the near vent environment. Because the terebellids that were found were larger (5 - 10 mm) than most of the other fauna found, it is hypothesized that they need more energy than the smaller organisms, and thus be in areas of higher primary productivity due to the presence of hydrothermalism. Also large (~ 1 mm), were the Asellota isopods, a group found mostly at Mariner (some at Kilo Moana) and on all substrate types. Like other benthic peracarids (tanaids, amphipods), they lack a pelagic life stage — except in a few certain instances where some species are holoplanktonic — and brood their young, thus having limited dispersal, making them model organisms to study speciation (Brandt 2016). Finding these isopods at the two locations of potentially the lowest primary productivity is not a surprise since they are commonly found in abyssal plain, a habitat of low nutrient input (Riehl 2013).

Kilo Moana locations were more variable and fauna were not found in high abundance, the highest being *Amphiascus* sp. (Copepoda) (2.35 indv./m^2), unidentified copepod 1 (1.04 indv./m^2), hesionid1 (0.99 indv./m^2), and unknown polychaetes (0.90 indv./m^2). Low abundances may reflect lower primary productivity in the region.

Of particular note, for the ABE and Mariner locations, are the copepods from families Miraciidae and Dirivultidae. “Mussel pot” samples from the near vent environment at the ABE location were taken by the ROV Jason II and later studied by Lorenzo (2018), who found that the copepod distributions vary by environmental conditions on a species specific level. The harpacticoid, *Amphiascus* aff. *varians*, were found in association with the vent-obligate symbiont-containing mussel, *Bathymodiolus brevior*, in low sulfide (2.4-8.6 µM)/high oxygen (71 – 135 µM) environments and Siphonostomatoida copepods from family Dirivultidae were found in association with the vent obligate symbiont-containing snails *Alviniconcha hessleri* and *Ifremeria nautilei* in high sulfide (94-130µM)/low oxygen conditions (0-13.6 µM). At all locations, higher *Amphiascus* sp. and lower dirivultid abundances were encountered, hinting at a low sulfide high oxygen environment populated by *B. brevior* where enough sulfide is present to allow for chemoautotrophy, but not so high that faunal chemical and thermal tolerances are exceeded. Intriguingly, Mariner locations had higher dirivultid abundances than ABE, perhaps in some instances Mariner had a stronger sulfide presence? Kilo Moana had substantially fewer dirivultids than the other locations, could this provide some evidence that sulfide levels were indeed lower at KM than at the other two locations?

Further evidence for the effect of hydrothermal incidence on community composition comes from Sen’s (2016) photomosaic study of the macrofauna of the near vent and peripheral environments in the Lau Basin. Sen found that communities differed by location (north vs south) and chemical environment (near vent vs peripheral region) and concluded that increased sponge, anemone, and vent-obligate mussel abundance and overall taxonomic richness was most likely due to increased primary productivity from higher venting incidence. The importance of enriched fluid to these communities is illustrated in the observation that after venting stopped at a near-vent site, that site no longer resembled other near vent communities and instead was more like peripheral communities. In 2009, Grupe conducted a similar experiment to this study examining factors affecting fauna community aggregations through a replacement type experiment of out-planted substrates (authigenic carbonate, wood, and biogenic tubes and shells) at seeps near Costa Rica. He concluded that proximity to the enriched fluids was the main driver of colonization and fauna distribution and that substrate did not have an effect at inactive seep sites, but did at active seep sites. Although his study was examining the near-vent faunal assemblages, this project's results follow the same pattern.

CONCLUSION

This experiment looked to investigate factors influencing community distribution in the northern basaltic anemone-dominated region and the southern andesitic sponge-dominated region of hydrothermal vents of the Lau Basin. Initial hypotheses for these community differences were of potential substrate effects from the differing host rock types or other location specific effects. To investigate these hypotheses, a replacement experiment was done placing both andesitic and basalt rock blocks in three locations along the Eastern Lau Spreading Center. Physical rock block characteristics such as surface area and roughness were measured and found to vary by rock type and source but not location or site placement; this ensured that all locations received rocks with similar physical characteristics. The communities found were mostly meiofauna belonging to Copepoda, Polychaeta, and Gastropoda groups and did differ by location, but not by rock type. Despite being placed in locations dominated by macroscopic anemones and sponges, no sponges were collected and only three anemones were collected. The three anemones collected were very small (~1mm), could not be identified to a lower taxonomic rank, and were all found at the middle site, ABE, that is in the andesitic "southern andesitic sponge-dominated" region. Using taxa specific habitat preferences, it was hypothesized that the highest densities of barnacles, copepods, polychaetes, and gastropods found at ABE were due to higher concentrations of hydrothermal fluid in the peripheral environment. One of the most concrete pieces of evidence was finding, at ABE, the only vent-obligate chemosynthetic symbiont containing species, *Bathymodiolus* *brevior*. The “Other Arthropods” group was the only group to occur in the highest densities at a non-ABE location, Mariner.

Other factors like geology, depth, and topography of each location may also help explain the distribution of the fauna, but were not explicitly tested for. The crumbly texture and vesicular nature of the andesitic substratum in the southern Lau Basin allow for more diffuse flow of enriched fluids. This may allow for a more diluted and farther distributing fluid, which benefits the peripheral fauna that have lower tolerances for toxic sulfide and higher temperatures. Effluent from point sources in the northern basalt regions do not diffuse laterally as far as fluid from andesitic substrates (Podowski *et al.* 2010). The rift’s topography, as a result of the geology, can influence how the effluent is transported throughout the basin. The faster spreading northern portion of the ELSC results in an axial peak with a shallow narrow rift that does not constrain the enriched fluid, contrasting with the deeper wider valley formed at the slower spreading rates found in the southern region. Increased densities of fauna found in the southern sites may be a result of this deeper valley that has a higher potential to entrain the enriched fluid and planktonic larvae along the spreading axis. Effluent and taxa propagule transportation distance can be a function of height of the vent plume from the sea floor; plumes at heights of 200 m above the sea floor can travel up to one order of magnitude greater than near bottom fluids (Mullineaux 2005).

Depth can also affect vent fluid chemical properties where shallower depths will be less chemically enriched through increased phase separation at lower hydrostatic pressures (Desbruyères 2001). The deep sea fauna themselves are highly affected by depth, for instance, lecithotrophic larvae metabolism will decrease at deeper depths as a result of lower temperatures and some adult fauna will die if brought to shallower depths due to not being adapted to lower pressures (Marsh 2001, Sen 2013). For this study, the variable depth between the three locations is not believed to affect faunal distribution, at least not for explaining why ABE, the mid-depth site had the highest faunal abundance. If depth differences between the locations affected the fauna, it would be expected to see an abundance gradient following a depth gradient (either shallow to deeper or deeper to shallower), but this was not observed.

The weak, overall northward flow of the currents in the Lau Basin are not thought to provide a dispersal barrier preventing northern fauna traveling to the South. In the similar way that ABE is at a mid-depth between Kilo Moana and ABE, it is also mid-stream between the two sites. Because the middle site had the highest abundance and species richness, the general northward flow is not believed to influence the distribution of fauna. Further, many of the macrofauna found at the Lau vents are also found in other Western Pacific Back-Arc Basins.

Mining and Broader Impacts

Chemosynthetic-driven ecosystems face a number of anthropogenic disturbances with the potential to irrevocably harm not only the surrounding biota, but the geologic deposits responsible for the diverse communities as well. Initially, it may seem that due to vent's volatility, the communities would be resistant to a highly mutable habitat. This is true for the vents along the Mid-Atlantic Ridge, which experience catastrophic disturbances in the form of sulfide edifices collapsing multiple times a year (Van Dover *et al.* 2012, Du Preez 2018). However, the BAB vents of the Western Pacific have been proven to be "remarkably stable", on the order of decades, where current spires are believed to have taken 20 to 40 years to form (Du Preez 2018). It is important to take note of this difference in stability because the Western Pacific vents are the systems closest to facing threats of deep-sea mining. Other even slower forming deep-sea ecosystems under threat of mining and thus less resistant to disturbances, include deep water coral reefs (taking hundreds to thousands of years to form) (Barbier 2014) and manganese nodules (taking millennia to form) (Levin *et al.* 2016).

Deep-sea mining operations seek to extract minerals such as copper, zinc, gold, silver, manganese, and cobalt via dredge, drill, and/or ROV. These minerals are used in the production of computers, batteries, and mobile devices (Rosenbaum 2011). Mining of the deep-sea is particularly attractive because the deep-sea metal deposits contain higher grade ores and the mining process is less destructive compared to terrestrial mining (Collins *et al.* 2013). Collection of these ores in the deep-sea necessitates the destruction of the precipitated deposits, resulting in the loss of physical benthic habitat, production of kilometers of excess sediments into the overlying waters (to at least 10 km away), and toxic waste waters associated with the washing of ores (Steiner 2009). Further harm may come from the excessive noise produced from mining and is estimated that sound from such operations extends to 600 km underwater (Steiner 2009). Excess light is also needed to mine the deep sea; at depth, fauna may be attracted to the light used to operate the mining tool, putting them in danger of the surrounding heavy machinery and collapsing edifices (Boschen 2013). It is also unknown what effect having a "permanent" – mining operations are estimated to last around 5 years – light source at the surface will do to the behavior and navigation to fauna like sea birds and turtles.

Already twenty-nine 15-year contracts (as of August 2019) have been given out to explore deep-sea mining in the Clarion-Clipperton Fracture Zone (central Pacific), Southwest Indian Ridge (south of Madagascar), and South Pacific (Papua New Guinea) (ISA website: https://www.isa.org.jm/deep-seabed-minerals-contractors, Van Dover *et al.* 2012). Mining at one such site in Papua New Guinea, Solwara 1, is estimated to earn the Nautilus mining company $1 billion per year with the copper (80,000 tons) and gold (150,000 tons) reserves expected to last 2.5 years (Rosenbaum 2011). All mining operations must complete an environmental impact assessment (EIA) (done by the contractors) and be approved by the International Seabed Authority (ISA) in accordance with the mining code of 1994 (Lallier & Maes 2016). Under the United Nations Convention on the Law of the Sea of 1982 (LOSC), the ISA has general guidelines to consider *environmental good practice* when choosing whether to approve or not a mining project, but not all standards to follow such *good practices* are mandated. Surprisingly, such *good practices* that are only *recommended* to be followed, particularly because they are standard for most nation states and industries, are an independent review of the EIA by independent experts and a period for public comment (Lallier & Maes 2016).

Both an independent review and public comment are important aspects in insuring that an EIA has done a thorough job in considering all impacts of a project before natural resource exploitation begins. A complete review process informs a government/company/community that the correct decision has been made and all benefits of natural resource acquisition and associated incomes has been weighed against the costs of the destruction of the environment and potential mining related disasters. An independent review of the EIA of the Solwara 1 project concluded that while the direct site impacts were correctly assessed and description and classification of the benthic communities was extensive, not enough study was given to the to the genetic connectivity of fauna to nearby sites, the deep-water pelagic community above the site, and how waste water would be treated, for example (Steiner 2009). Such reports inform the public on what will happen to their environment and have real influence; in November 2012, Papua New Guineans and anti-mining NGOs organized enough support to successfully oppose a deal between the PNG government and the Nautilus mining company (Pemberton in Greenleft.org 2012). This deal to mine at the Solwara 1 site would earn the PNG government $40.8 million of the ~ $1 billion (~ 4.1%), was opposed via a petition with around 24,000 signatures (Pemberton 2012, Milman 2012 in The Guardian). The independent review and comments showed and highlighted the lack of scope of Nautilus' EIA; hopefully, future mining projects will be more encompassing and will continue to include those two aspects of the review process even if they are not explicitly necessitated by the LOSC.

Further opposition to mining has been shown in other parts of the globe within and without areas where mining could begin. Public surveys in Scotland (2012), Ireland (2007), and Portugal (2011)all have shown that a majority of people in those countries were willing to pay up to $115, $14, and $605, respectively, to protect marine habitats, including the deep-sea/chemosynthetic ecosystems (Barbier 2014). Public motivations for protecting the deep-sea from operations like mining and deep trawling included use in future biomedical applications, the deep-sea's role as a carbon sink and fish habitat, and its intrinsic value where it provides habitat for a unique species that should be preserved for future generations (Jaeckel *et al.* 2017). The ISA has set goals of protecting 10% of all (international and national waters) marine habitats by 2020, with experts suggesting the establishment of a network of Marine Protected Areas resulting in 30-50% conservation (Jaeckel *et al.* 2017). Already, some deep-water MPAs have been established, the Canadian Endeavor MPA, Mexican Guyamas Basin Sanctuary, and American Mariana Trench National Monument (Van Dover *et al.* 2012). In addition to preventative measures, deep-water restoration measures, like cold-water coral transplant experiments, are being explored (Barbier 2014). While deep-sea restoration is believed to be a worthwhile pursuit, drastically increased costs due to the logistical difficulties of operating in the deep sea must also be considered before such measures are necessary, thus most deep-sea ecology advocates press for a precautionary approach.

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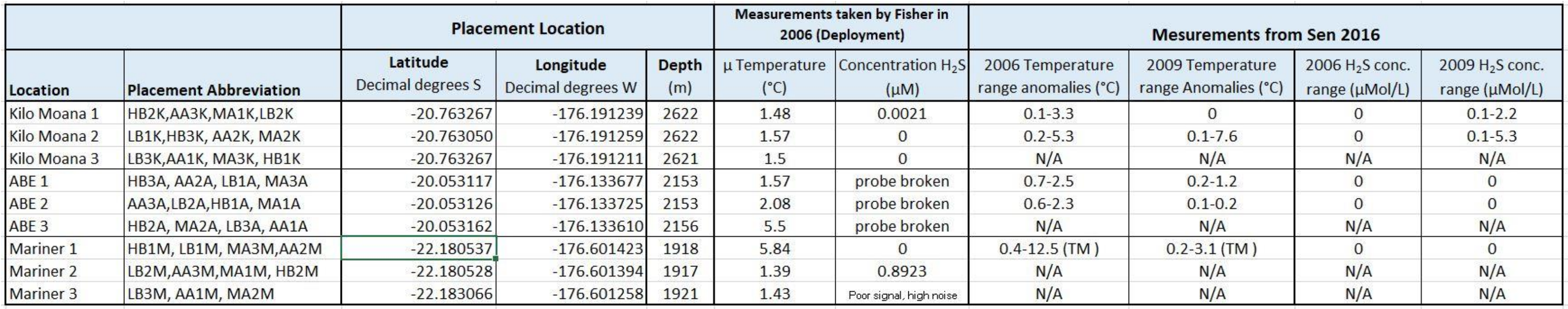
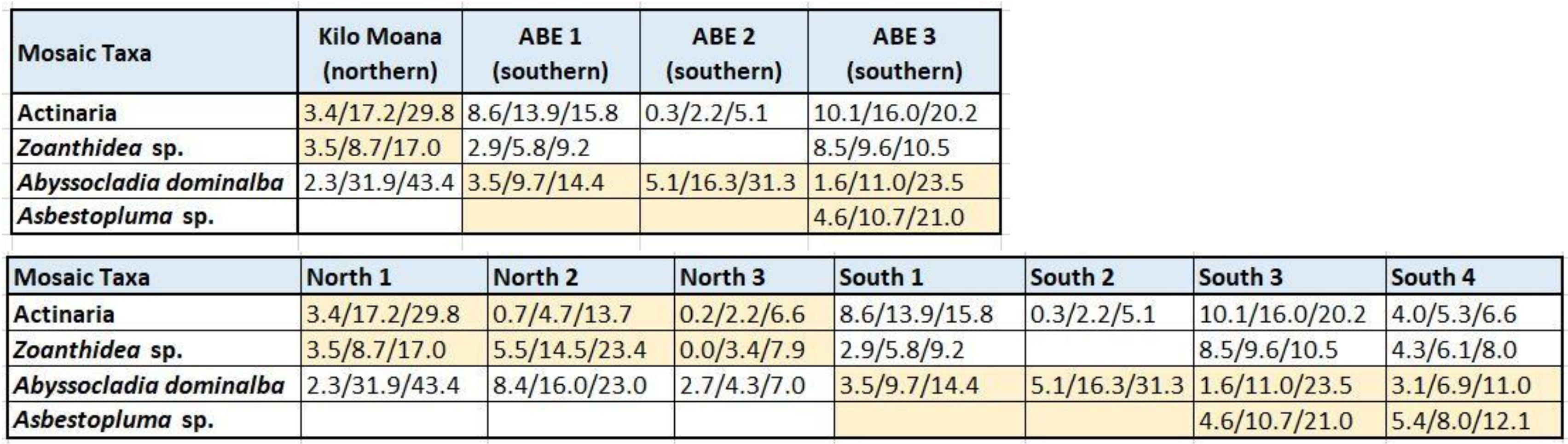
Vent Field	Distance along axis (km)	Distance to next field S (km)	Opening rate (cm/yr)	Character of axis	Axial area (km^2)	Crustal thickness (km)	Volcanic Morphology		Faulting		Plume incidence
							Flows	Domes	Near axis large	In vent field	
N. end of ELSC	0	90	97			~6					
Kilo Moana	90	79	87	No high	-3.8		Pillow and Lobate	Low Relief	Many	Yes	0.44
ABE	169	163	75	Rounded	-0.3		Pillows, aa	Medium	Some	Yes	0.38
Mariner	332	65	52	Peaked	1.8	9	aa	High relief	None	None	0.24
S. end of ELSC	397		39								

Table 1: Excerpt from Mottl (2011). Table showing the vent locations, relative distances to each other, spreading rate, and geological characteristics at a particular vent field. Plume incidence is a unitless value defined as “the percentage of ridge-axis length overlain by a significant hydrothermal plume” (Baker 1995).



		Placement Location			Measurements taken by Fisher in 2006 (Deployment)		Mesurements from Sen 2016			
Location	**Placement Abbreviation**	**Latitude** Decimal degrees S	**Longitude** Decimal degrees W	**Depth** (m)	µ Temperature (°C)	Concentration H_2S (µM)	2006 Temperature range anomalies (°C)	2009 Temperature range Anomalies (°C)	2006 H_2S conc. range (µMol/L)	2009 H_2S conc. range (µMol/L)
Kilo Moana 1	HB2K,AA3K,MA1K,LB2K	-20.763267	-176.191239	2622	1.48	0.0021	0.1-3.3	0	0	0.1-2.2
Kilo Moana 2	LB1K,HB3K, AA2K, MA2K	-20.763050	-176.191259	2622	1.57	0	0.2-5.3	0.1-7.6	0	0.1-5.3
Kilo Moana 3	LB3K,AA1K, MA3K, HB1K	-20.763267	-176.191211	2621	1.5	0	N/A	N/A	N/A	N/A
ABE 1	HB3A, AA2A, LB1A, MA3A	-20.053117	-176.133677	2153	1.57	probe broken	0.7-2.5	0.2-1.2	0	0
ABE 2	AA3A,LB2A,HB1A, MA1A	-20.053126	-176.133725	2153	2.08	probe broken	0.6-2.3	0.1-0.2	0	0
ABE 3	HB2A, MA2A, LB3A, AA1A	-20.053162	-176.133610	2156	5.5	probe broken	N/A	N/A	N/A	N/A
Mariner 1	HB1M, LB1M, MA3M,AA2M	-22.180537	-176.601423	1918	5.84	0	0.4-12.5 (TM)	0.2-3.1 (TM)	0	0
Mariner 2	LB2M,AA3M,MA1M, HB2M	-22.180528	-176.601394	1917	1.39	0.8923	N/A	N/A	N/A	N/A
Mariner 3	LB3M, AA1M, MA2M	-22.183066	-176.601258	1921	1.43	Poor signal, high noise	N/A	N/A	N/A	N/A

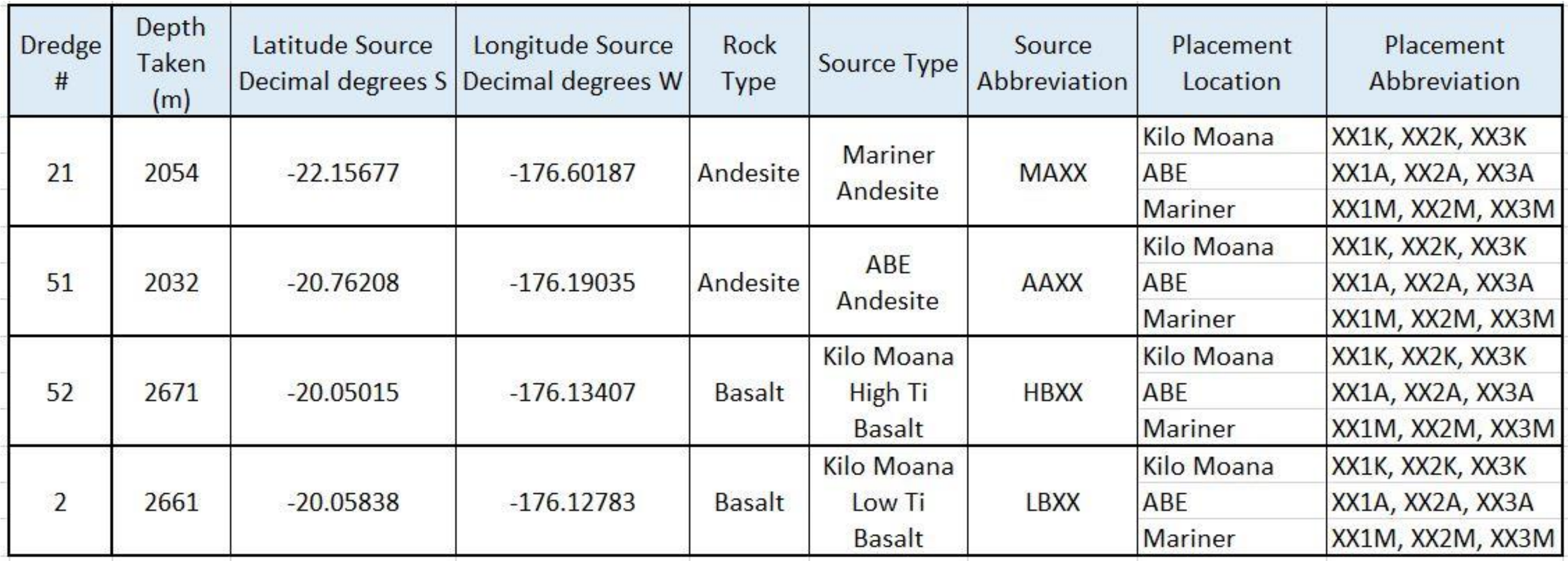
Table 2: Data from Fisher's 2006 ROV dives and Figure 1-4 from Sen 2016. Some data were not available due to environmental interference (Mariner 3 H_2S conc.), instrument malfunction (ABE H_2S conc.), or not all sites were sampled (Sen 2016 KM3 and ABE 3). The temperature measurements from Sen in 2006 and 2009 at Mariner are actually from a nearby site Tu'i Malila (4 km North of Mariner). The column "Placement Abbreviation" is the name assigned to each rock block; the first two letters signify the rock type (HB = high titanium basalt, LB = low titanium basalt, MA = Mariner andesite, AA = ABE andesite), the number is a replicate number, and the last letter is the location (K = Kilo Moana, A = ABE, M = Mariner).



Mosaic Taxa	**Kilo Moana (northern)**	**ABE 1 (southern)**	**ABE 2 (southern)**	**ABE 3 (southern)**
Actinaria	3.4/17.2/29.8	8.6/13.9/15.8	0.3/2.2/5.1	10.1/16.0/20.2
***Zoanthidea* sp.**	3.5/8.7/17.0	2.9/5.8/9.2		8.5/9.6/10.5
Abyssocladia dominalba	2.3/31.9/43.4	3.5/9.7/14.4	5.1/16.3/31.3	1.6/11.0/23.5
***Asbestopluma* sp.**				4.6/10.7/21.0

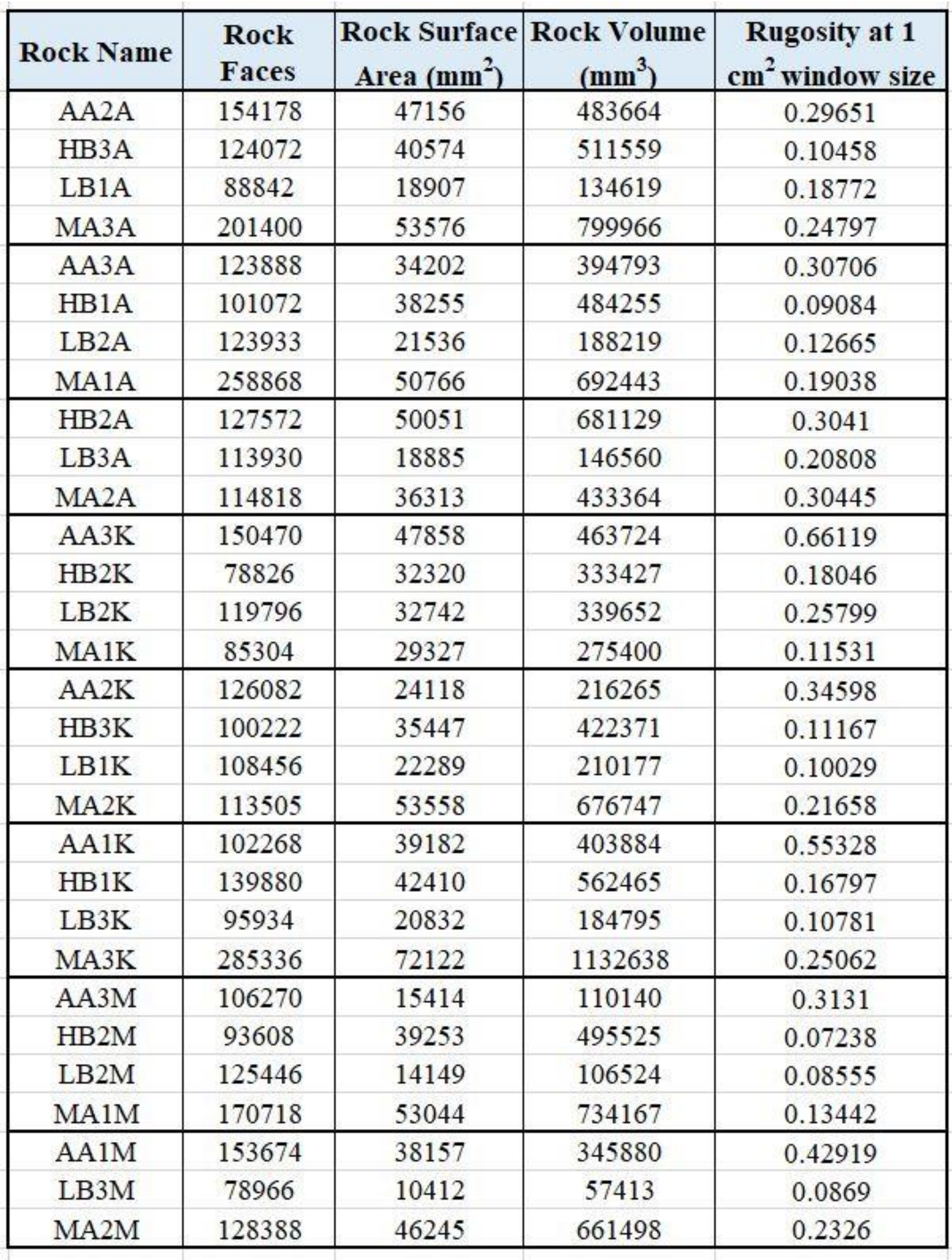
Mosaic Taxa	**North 1**	**North 2**	**North 3**	**South 1**	**South 2**	**South 3**	**South 4**
Actinaria	3.4/17.2/29.8	0.7/4.7/13.7	0.2/2.2/6.6	8.6/13.9/15.8	0.3/2.2/5.1	10.1/16.0/20.2	4.0/5.3/6.6
***Zoanthidea* sp.**	3.5/8.7/17.0	5.5/14.5/23.4	0.0/3.4/7.9	2.9/5.8/9.2		8.5/9.6/10.5	4.3/6.1/8.0
Abyssocladia dominalba	2.3/31.9/43.4	8.4/16.0/23.0	2.7/4.3/7.0	3.5/9.7/14.4	5.1/16.3/31.3	1.6/11.0/23.5	3.1/6.9/11.0
***Asbestopluma* sp.**						4.6/10.7/21.0	5.4/8.0/12.1

Table 3: Excerpt table from Kim & Hammerstrom (2012) benthic ROV surveys: Table of the minimum, mean, and maximum distances (m) each taxon was from a diffuse flow source at each site. The highlighted boxes show anemone (Actinaria and *Zoanthidea sp.*) distances in northern Lau Basin and sponge (*Abyssocladia dominalba* and *Asbestopluma* sp.) distances in the southern Lau Basin.



Dredge #	Depth Taken (m)	Latitude Source Decimal degrees S	Longitude Source Decimal degrees W	Rock Type	Source Type	Source Abbreviation	Placement Location	Placement Abbreviation
21	2054	-22.15677	-176.60187	Andesite	Mariner Andesite	MAXX	Kilo Moana	XX1K, XX2K, XX3K
							ABE	XX1A, XX2A, XX3A
							Mariner	XX1M, XX2M, XX3M
51	2032	-20.76208	-176.19035	Andesite	ABE Andesite	AAXX	Kilo Moana	XX1K, XX2K, XX3K
							ABE	XX1A, XX2A, XX3A
							Mariner	XX1M, XX2M, XX3M
52	2671	-20.05015	-176.13407	Basalt	Kilo Moana High Ti Basalt	HBXX	Kilo Moana	XX1K, XX2K, XX3K
							ABE	XX1A, XX2A, XX3A
							Mariner	XX1M, XX2M, XX3M
2	2661	-20.05838	-176.12783	Basalt	Kilo Moana Low Ti Basalt	LBXX	Kilo Moana	XX1K, XX2K, XX3K
							ABE	XX1A, XX2A, XX3A
							Mariner	XX1M, XX2M, XX3M

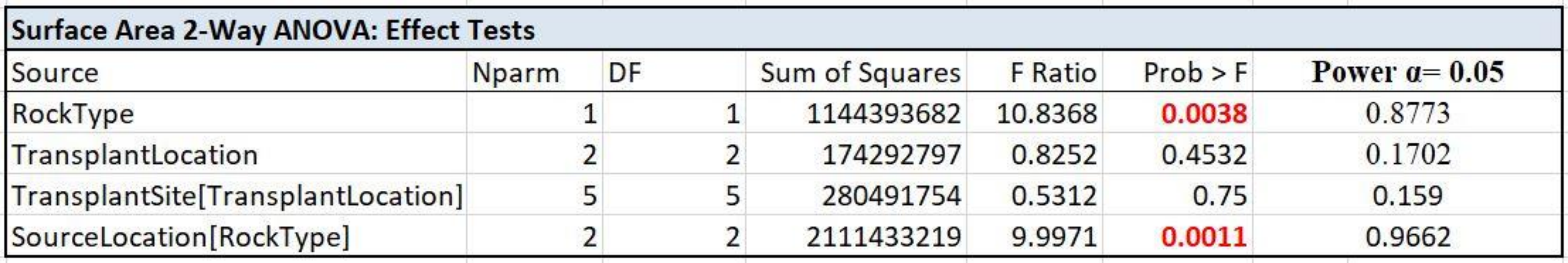
Table 4: Source information of rock blocks collected, including location (Decimal degrees), depth (m), and dredge number of collection. Naming convention for Source and Placement location are also listed; X is a placeholder. Dredge numbers are from Charles Langmuir cruise in 2004 aboard the R/V Kilo Moana (KMO0417).



Rock Name	Rock Faces	Rock Surface Area (mm^2)	Rock Volume (mm^3)	Rugosity at 1 cm^2 window size
AA2A	154178	47156	483664	0.29651
HB3A	124072	40574	511559	0.10458
LB1A	88842	18907	134619	0.18772
MA3A	201400	53576	799966	0.24797
AA3A	123888	34202	394793	0.30706
HB1A	101072	38255	484255	0.09084
LB2A	123933	21536	188219	0.12665
MA1A	258868	50766	692443	0.19038
HB2A	127572	50051	681129	0.3041
LB3A	113930	18885	146560	0.20808
MA2A	114818	36313	433364	0.30445
AA3K	150470	47858	463724	0.66119
HB2K	78826	32320	333427	0.18046
LB2K	119796	32742	339652	0.25799
MA1K	85304	29327	275400	0.11531
AA2K	126082	24118	216265	0.34598
HB3K	100222	35447	422371	0.11167
LB1K	108456	22289	210177	0.10029
MA2K	113505	53558	676747	0.21658
AA1K	102268	39182	403884	0.55328
HB1K	139880	42410	562465	0.16797
LB3K	95934	20832	184795	0.10781
MA3K	285336	72122	1132638	0.25062
AA3M	106270	15414	110140	0.3131
HB2M	93608	39253	495525	0.07238
LB2M	125446	14149	106524	0.08555
MA1M	170718	53044	734167	0.13442
AA1M	153674	38157	345880	0.42919
LB3M	78966	10412	57413	0.0869
MA2M	128388	46245	661498	0.2326

Table 5: Individual rock block surface area in mm^2, volume in mm^3, and individual surfaces counted by AutoDesk ReCap. The last column shows the average surface roughness at $1cm^2$ window size as calculated by Aiello's MATLAB script. Rocks are grouped by site deployed.

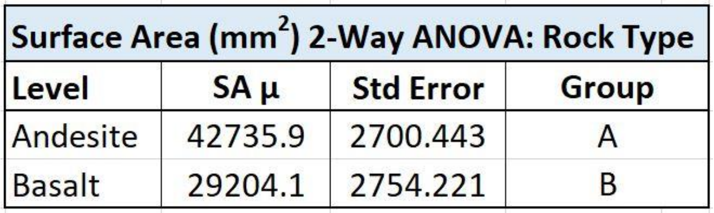
Table 6 - 15 Guide: The statistical model included the factors of each rock block: Rock Type, block Source Location nested within Rock Type, block Transplant Location, and Transplant Site nested within Transplant Location. Here are the variables and abbreviations for each factor. **Rock Type**: Andesite or Basalt. **Transplant Location**: ABE, Kilo Moana (KM), or Mariner (Mar). **Source Location**: ABE Andesite (ABE And.), Mariner Andesite (Mar. And.), Kilo Moana High Titanium Basalt (KM HiTiB), or Kilo Moana Low Titanium Basalt (KM LoTiB). **Transplant Site**: ABE 1, ABE 2, ABE 3, KM 1, KM 2, KM 3, Mar 2, or Mar 3. When fauna community data was being analyzed, the fauna density corrected values of number of individuals per 1 m^2 was used (Tables 11 – 14).



Surface Area 2-Way ANOVA: Effect Tests

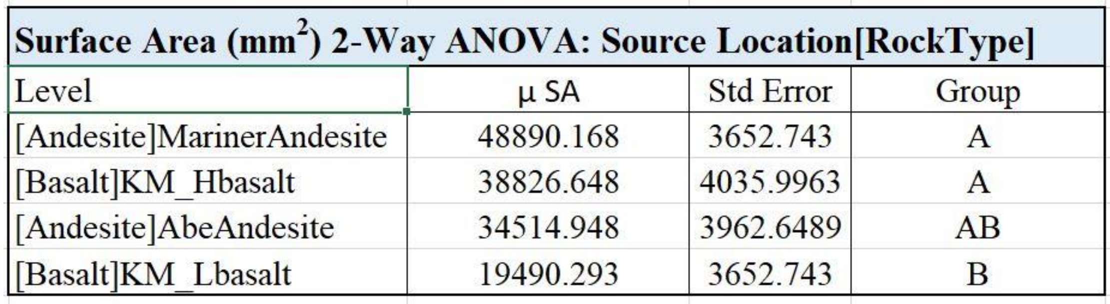
Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F	**Power α= 0.05**
RockType	1	1	1144393682	10.8368	**0.0038**	0.8773
TransplantLocation	2	2	174292797	0.8252	0.4532	0.1702
TransplantSite[TransplantLocation]	5	5	280491754	0.5312	0.75	0.159
SourceLocation[RockType]	2	2	2111433219	9.9971	**0.0011**	0.9662

Table 6: **Rock Block Surface Area**: Whole model results from two-way nested ANOVA testing for effects of factors: Rock Type, Transplant Location, Rock Source Type, and Transplant Site of each rock block’s surface area. See tables A.1-A.6 for means, SE, pair-wise comparisons, and statistical group for each factor’s variables.



Surface Area (mm^2) 2-Way ANOVA: Rock Type			
Level	**SA µ**	**Std Error**	**Group**
Andesite	42735.9	2700.443	A
Basalt	29204.1	2754.221	B

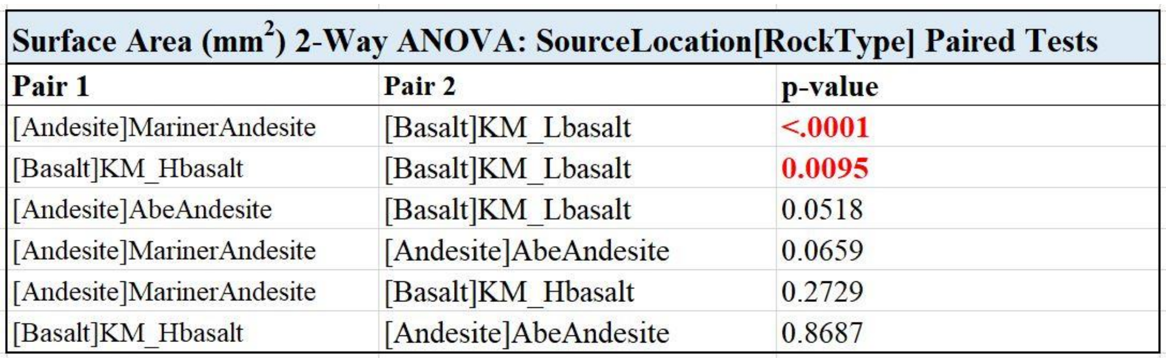
Table 7: Rock block surface area comparisons for each rock type with mean (µ) surface area and standard error of each rock type.



Surface Area (mm^2) 2-Way ANOVA: Source Location[RockType]

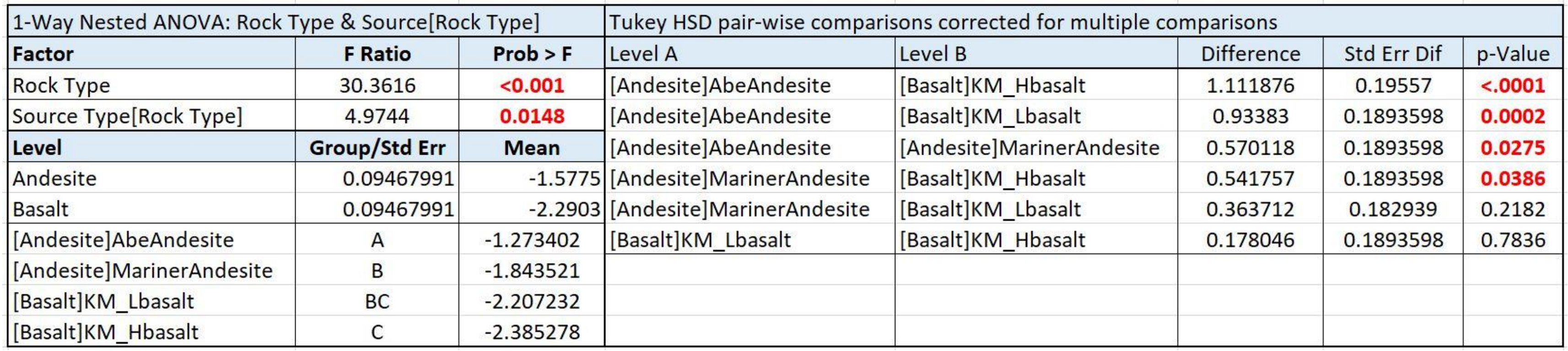
Level	µ SA	Std Error	Group
[Andesite]MarinerAndesite	48890.168	3652.743	A
[Basalt]KM_Hbasalt	38826.648	4035.9963	A
[Andesite]AbeAndesite	34514.948	3962.6489	AB
[Basalt]KM_Lbasalt	19490.293	3652.743	B

Table 8: Rock block surface area comparisons for each rock source type with mean (µ) surface area, standard error, and group of each source type. Source pair-wise comparisons in Table 9.



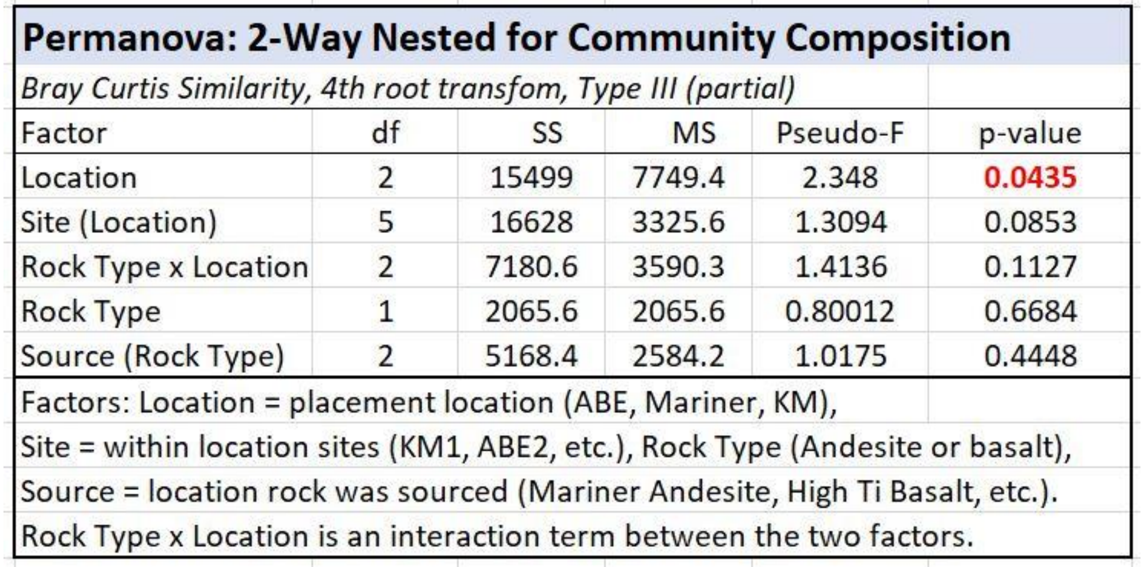
Surface Area (mm^2) 2-Way ANOVA: SourceLocation[RockType] Paired Tests		
Pair 1	**Pair 2**	**p-value**
[Andesite]MarinerAndesite	[Basalt]KM_Lbasalt	**<.0001**
[Basalt]KM_Hbasalt	[Basalt]KM_Lbasalt	**0.0095**
[Andesite]AbeAndesite	[Basalt]KM_Lbasalt	0.0518
[Andesite]MarinerAndesite	[Andesite]AbeAndesite	0.0659
[Andesite]MarinerAndesite	[Basalt]KM_Hbasalt	0.2729
[Basalt]KM_Hbasalt	[Andesite]AbeAndesite	0.8687

Table 9: Rock Block surface area pair-wise comparisons between each rock source type.



1-Way Nested ANOVA: Rock Type & Source[Rock Type]			Tukey HSD pair-wise comparisons corrected for multiple comparisons				
Factor	**F Ratio**	**Prob > F**	Level A	Level B	Difference	Std Err Dif	p-Value
Rock Type	30.3616	**<0.001**	[Andesite]AbeAndesite	[Basalt]KM_Hbasalt	1.111876	0.19557	**<.0001**
Source Type[Rock Type]	4.9744	**0.0148**	[Andesite]AbeAndesite	[Basalt]KM_Lbasalt	0.93383	0.1893598	**0.0002**
Level	**Group/Std Err**	**Mean**	[Andesite]AbeAndesite	[Andesite]MarinerAndesite	0.570118	0.1893598	**0.0275**
Andesite	0.09467991	-1.5775	[Andesite]MarinerAndesite	[Basalt]KM_Hbasalt	0.541757	0.1893598	**0.0386**
Basalt	0.09467991	-2.2903	[Andesite]MarinerAndesite	[Basalt]KM_Lbasalt	0.363712	0.182939	0.2182
[Andesite]AbeAndesite	A	-1.273402	[Basalt]KM_Lbasalt	[Basalt]KM_Hbasalt	0.178046	0.1893598	0.7836
[Andesite]MarinerAndesite	B	-1.843521					
[Basalt]KM_Lbasalt	BC	-2.207232					
[Basalt]KM_Hbasalt	C	-2.385278					

Table 10: 1 – Way ANOVA comparing Rock Type and Source[Rock Type] surface roughness differences at the 1 cm^2 scale resolution. The top left show the test results: F-Ratio and Prob > F. The lower left shows the statistical group each source falls into as well as the mean and standard error natural log transformed surface roughness. The right side shows the multiple comparison corrected pairwise results between each source.



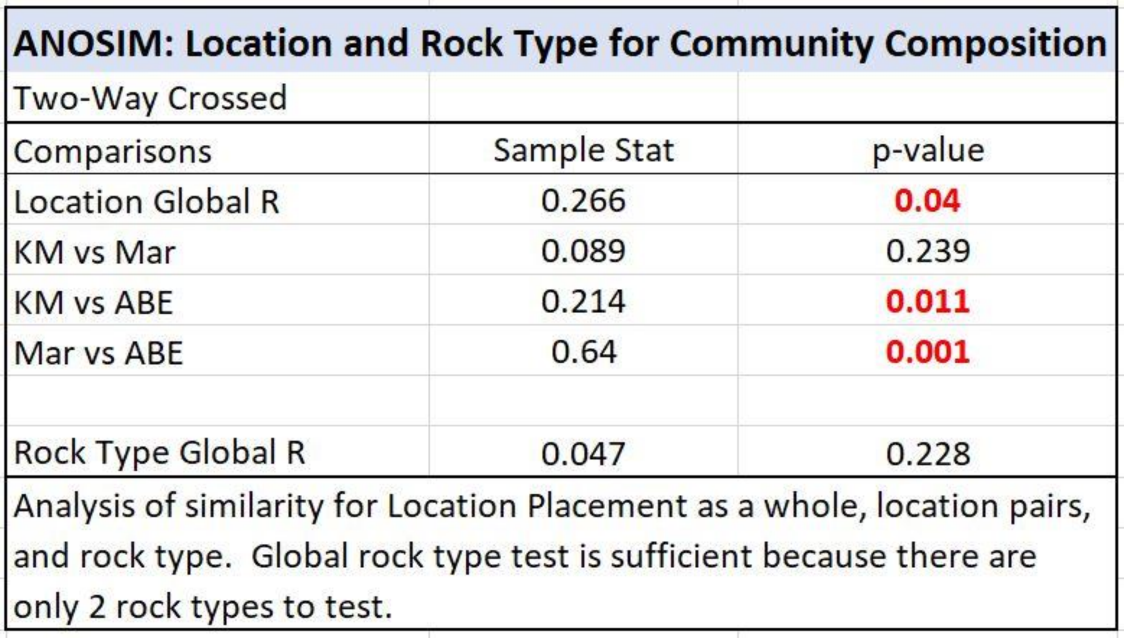
Permanova: 2-Way Nested for Community Composition

Bray Curtis Similarity, 4th root transfom, Type III (partial)

Factor	df	SS	MS	Pseudo-F	p-value
Location	2	15499	7749.4	2.348	**0.0435**
Site (Location)	5	16628	3325.6	1.3094	0.0853
Rock Type x Location	2	7180.6	3590.3	1.4136	0.1127
Rock Type	1	2065.6	2065.6	0.80012	0.6684
Source (Rock Type)	2	5168.4	2584.2	1.0175	0.4448

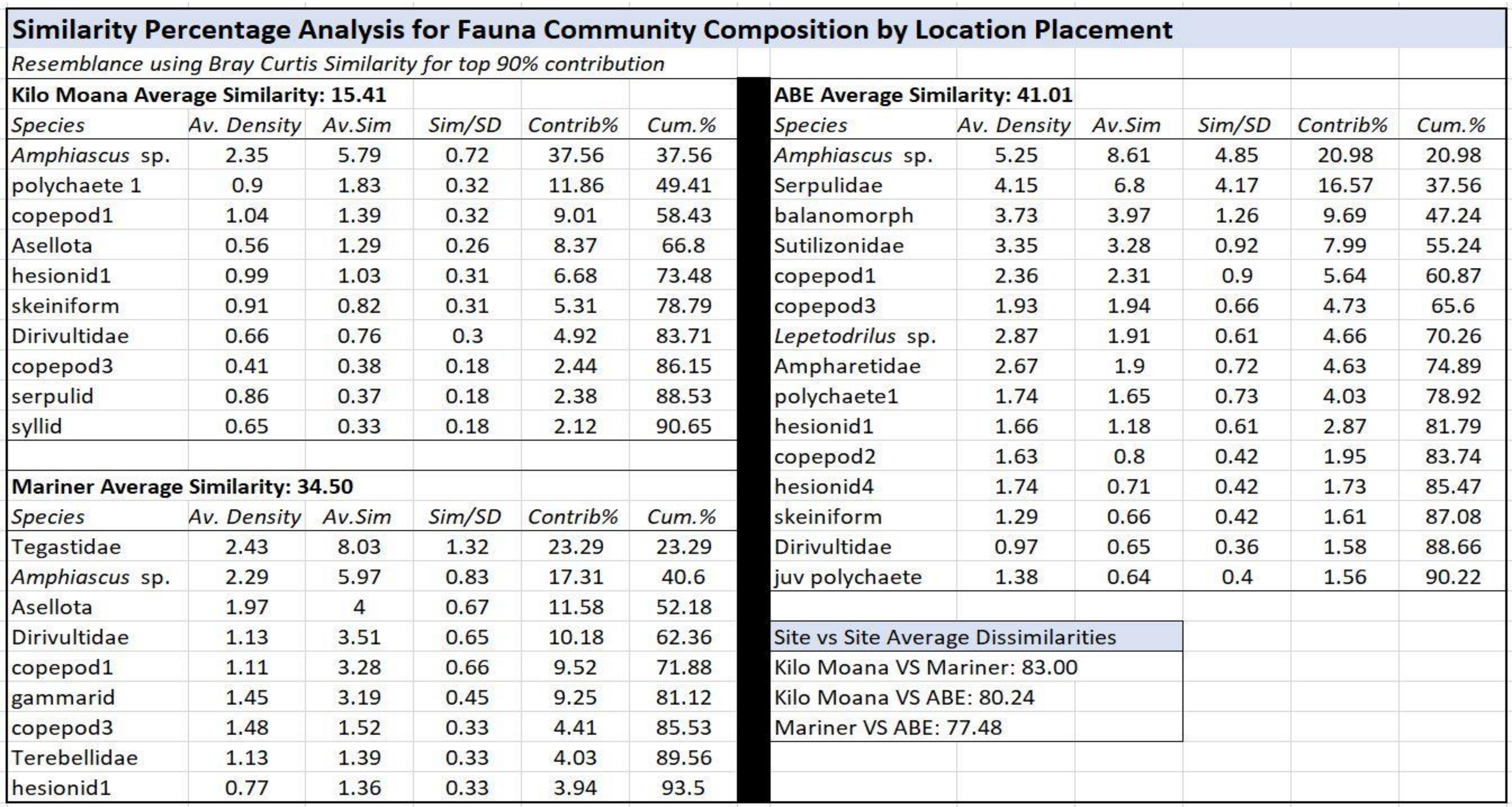
Factors: Location = placement location (ABE, Mariner, KM),
Site = within location sites (KM1, ABE2, etc.), Rock Type (Andesite or basalt),
Source = location rock was sourced (Mariner Andesite, High Ti Basalt, etc.).
Rock Type x Location is an interaction term between the two factors.

Table 11: 2-Way Nested PERMANOVA in PRIMER 6 testing all factors: Location, Site[Location], Rock Type, and Source[Rock Type] on fauna community. Test based on Bray-Curtis similarity table using 4^{th} root transformation, df = degrees of freedom, SS = Sum of Squares, MS = Means Squares, and Pseudo-F = F test statistic. Only Location is a significant factor on fauna community composition.



ANOSIM: Location and Rock Type for Community Composition		
Two-Way Crossed		
Comparisons	Sample Stat	p-value
Location Global R	0.266	**0.04**
KM vs Mar	0.089	0.239
KM vs ABE	0.214	**0.011**
Mar vs ABE	0.64	**0.001**
Rock Type Global R	0.047	0.228
Analysis of similarity for Location Placement as a whole, location pairs, and rock type. Global rock type test is sufficient because there are only 2 rock types to test.		

Table 12: Community Analysis of Similarity (ANOSIM) in PRIMER 6 using each taxon’s area corrected value for its particular rock. Results show test statistic for Rock Type and Location and pair-wise comparisons for Location



Similarity Percentage Analysis for Fauna Community Composition by Location Placement

Resemblance using Bray Curtis Similarity for top 90% contribution

Kilo Moana Average Similarity: 15.41

Species	*Av. Density*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*
Amphiascus sp.	2.35	5.79	0.72	37.56	37.56
polychaete 1	0.9	1.83	0.32	11.86	49.41
copepod1	1.04	1.39	0.32	9.01	58.43
Asellota	0.56	1.29	0.26	8.37	66.8
hesionid1	0.99	1.03	0.31	6.68	73.48
skeiniform	0.91	0.82	0.31	5.31	78.79
Dirivultidae	0.66	0.76	0.3	4.92	83.71
copepod3	0.41	0.38	0.18	2.44	86.15
serpulid	0.86	0.37	0.18	2.38	88.53
syllid	0.65	0.33	0.18	2.12	90.65

Mariner Average Similarity: 34.50

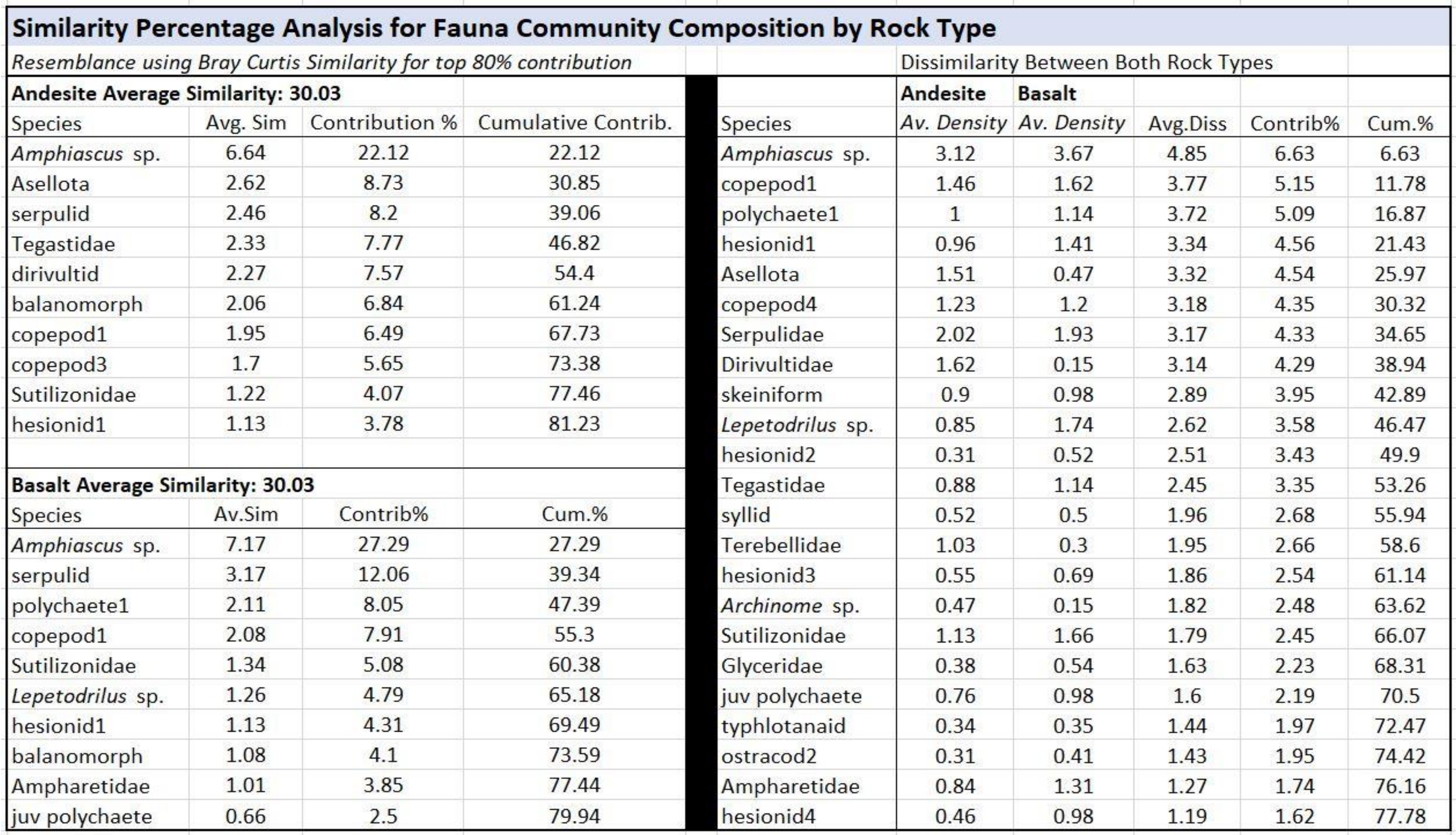
Species	*Av. Density*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*
Tegastidae	2.43	8.03	1.32	23.29	23.29
Amphiascus sp.	2.29	5.97	0.83	17.31	40.6
Asellota	1.97	4	0.67	11.58	52.18
Dirivultidae	1.13	3.51	0.65	10.18	62.36
copepod1	1.11	3.28	0.66	9.52	71.88
gammarid	1.45	3.19	0.45	9.25	81.12
copepod3	1.48	1.52	0.33	4.41	85.53
Terebellidae	1.13	1.39	0.33	4.03	89.56
hesionid1	0.77	1.36	0.33	3.94	93.5

ABE Average Similarity: 41.01

Species	*Av. Density*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*
Amphiascus sp.	5.25	8.61	4.85	20.98	20.98
Serpulidae	4.15	6.8	4.17	16.57	37.56
balanomorph	3.73	3.97	1.26	9.69	47.24
Sutilizonidae	3.35	3.28	0.92	7.99	55.24
copepod1	2.36	2.31	0.9	5.64	60.87
copepod3	1.93	1.94	0.66	4.73	65.6
Lepetodrilus sp.	2.87	1.91	0.61	4.66	70.26
Ampharetidae	2.67	1.9	0.72	4.63	74.89
polychaete1	1.74	1.65	0.73	4.03	78.92
hesionid1	1.66	1.18	0.61	2.87	81.79
copepod2	1.63	0.8	0.42	1.95	83.74
hesionid4	1.74	0.71	0.42	1.73	85.47
skeiniform	1.29	0.66	0.42	1.61	87.08
Dirivultidae	0.97	0.65	0.36	1.58	88.66
juv polychaete	1.38	0.64	0.4	1.56	90.22

Site vs Site Average Dissimilarities
Kilo Moana VS Mariner: 83.00
Kilo Moana VS ABE: 80.24
Mariner VS ABE: 77.48

Table 13: Similarity Percentage Analysis for taxa responsible for the top 90 % contribution to Bray-Curtis dissimilarity for each rock block placement location. Each Location has a similarity value showing how similar a location is to itself and the fauna that are responsible for the top 90% of that similarity. The data source is each taxon’s density corrected value from a particular rock and “Av. Density” is the number of individuals present per m^2. The bottom right sub-table shows pair-wise comparisons between Locations showing that all Locations are around 80% dissimilar to each other.



Similarity Percentage Analysis for Fauna Community Composition by Rock Type

Resemblance using Bray Curtis Similarity for top 80% contribution

Andesite Average Similarity: 30.03

Species	Avg. Sim	Contribution %	Cumulative Contrib.
Amphiascus sp.	6.64	22.12	22.12
Asellota	2.62	8.73	30.85
serpulid	2.46	8.2	39.06
Tegastidae	2.33	7.77	46.82
dirivultid	2.27	7.57	54.4
balanomorph	2.06	6.84	61.24
copepod1	1.95	6.49	67.73
copepod3	1.7	5.65	73.38
Sutilizonidae	1.22	4.07	77.46
hesionid1	1.13	3.78	81.23

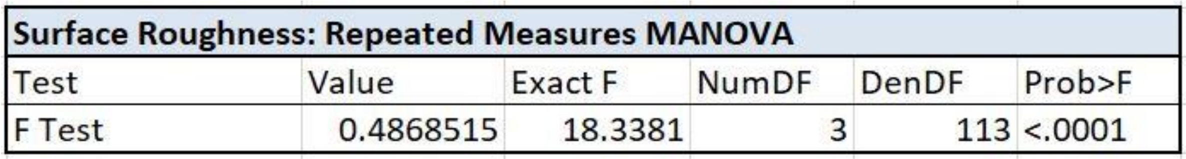
Basalt Average Similarity: 30.03

Species	Av.Sim	Contrib%	Cum.%
Amphiascus sp.	7.17	27.29	27.29
serpulid	3.17	12.06	39.34
polychaete1	2.11	8.05	47.39
copepod1	2.08	7.91	55.3
Sutilizonidae	1.34	5.08	60.38
Lepetodrilus sp.	1.26	4.79	65.18
hesionid1	1.13	4.31	69.49
balanomorph	1.08	4.1	73.59
Ampharetidae	1.01	3.85	77.44
juv polychaete	0.66	2.5	79.94

Dissimilarity Between Both Rock Types

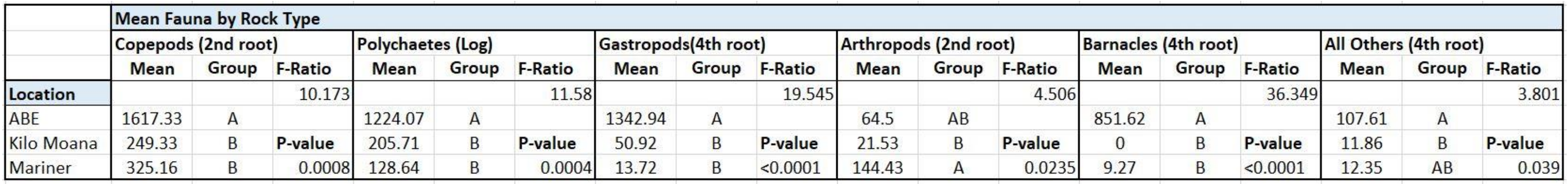
	Andesite	**Basalt**			
Species	*Av. Density*	*Av. Density*	Avg.Diss	Contrib%	Cum.%
Amphiascus sp.	3.12	3.67	4.85	6.63	6.63
copepod1	1.46	1.62	3.77	5.15	11.78
polychaete1	1	1.14	3.72	5.09	16.87
hesionid1	0.96	1.41	3.34	4.56	21.43
Asellota	1.51	0.47	3.32	4.54	25.97
copepod4	1.23	1.2	3.18	4.35	30.32
Serpulidae	2.02	1.93	3.17	4.33	34.65
Dirivultidae	1.62	0.15	3.14	4.29	38.94
skeiniform	0.9	0.98	2.89	3.95	42.89
Lepetodrilus sp.	0.85	1.74	2.62	3.58	46.47
hesionid2	0.31	0.52	2.51	3.43	49.9
Tegastidae	0.88	1.14	2.45	3.35	53.26
syllid	0.52	0.5	1.96	2.68	55.94
Terebellidae	1.03	0.3	1.95	2.66	58.6
hesionid3	0.55	0.69	1.86	2.54	61.14
Archinome sp.	0.47	0.15	1.82	2.48	63.62
Sutilizonidae	1.13	1.66	1.79	2.45	66.07
Glyceridae	0.38	0.54	1.63	2.23	68.31
juv polychaete	0.76	0.98	1.6	2.19	70.5
typhlotanaid	0.34	0.35	1.44	1.97	72.47
ostracod2	0.31	0.41	1.43	1.95	74.42
Ampharetidae	0.84	1.31	1.27	1.74	76.16
hesionid4	0.46	0.98	1.19	1.62	77.78

Table 14: Similarity Percentage Analysis for taxa responsible for the top 80 % contribution to Bray-Curtis dissimilarity for each rock block type. The left tables show each Rock Type's similarity value showing how similar a rock type is to itself and the fauna that are responsible for the top 80% of that similarity. The data source is each taxon's density corrected value from a particular rock and "Av. Density" is the number of individuals present per m^2. The right table shows the fauna responsible for the dissimilarity between the two Rock Types and the average abundance at each Rock Type.



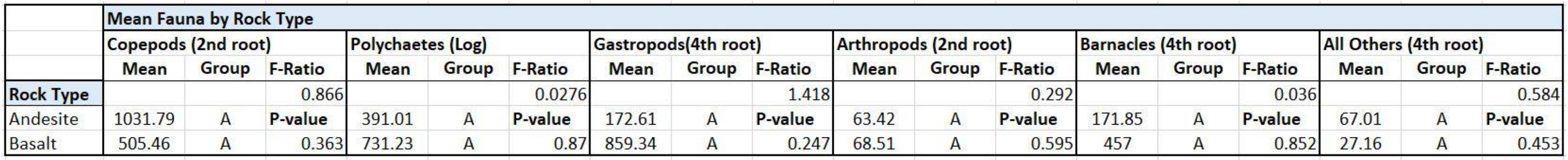
Surface Roughness: Repeated Measures MANOVA					
Test	Value	Exact F	NumDF	DenDF	Prob>F
F Test	0.4868515	18.3381	3	113	<.0001

Table 15: Repeated measures MANOVA result for surface roughness at multiple scales. Figure 11 shows graphical representation of test.



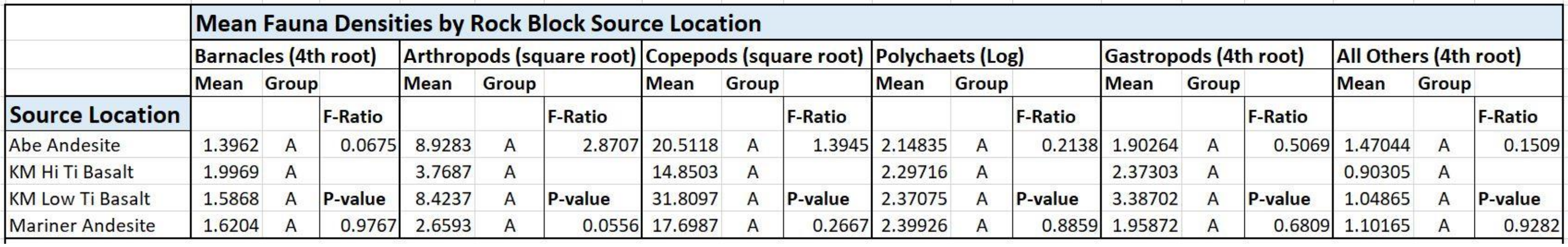
	Mean Fauna by Rock Type																	
	Copepods (2nd root)			**Polychaetes (Log)**			**Gastropods(4th root)**			**Arthropods (2nd root)**			**Barnacles (4th root)**			**All Others (4th root)**		
	Mean	**Group**	**F-Ratio**	**Mean**	**Group**	**F-Ratio**	**Mean**	**Group**	**F-Ratio**	**Mean**	**Group**	**F-Ratio**	**Mean**	**Group**	**F-Ratio**	**Mean**	**Group**	**F-Ratio**
Location			10.173			11.58			19.545			4.506			36.349			3.801
ABE	1617.33	A		1224.07	A		1342.94	A		64.5	AB		851.62	A		107.61	A	
Kilo Moana	249.33	B	**P-value**	205.71	B	**P-value**	50.92	B	**P-value**	21.53	B	**P-value**	0	B	**P-value**	11.86	B	**P-value**
Mariner	325.16	B	0.0008	128.64	B	0.0004	13.72	B	<0.0001	144.43	A	0.0235	9.27	B	<0.0001	12.35	AB	0.039

Table 16: Three-way ANOVA results by rock block transplant location for each major taxonomic group. Figure 14 shows graphical representation of results.



	Mean Fauna by Rock Type																	
	Copepods (2nd root)			Polychaetes (Log)			Gastropods(4th root)			Arthropods (2nd root)			Barnacles (4th root)			All Others (4th root)		
	Mean	Group	F-Ratio	Mean	Group	F-Ratio	Mean	Group	F-Ratio	Mean	Group	F-Ratio	Mean	Group	F-Ratio	Mean	Group	F-Ratio
Rock Type			0.866			0.0276			1.418			0.292			0.036			0.584
Andesite	1031.79	A	**P-value**	391.01	A	**P-value**	172.61	A	**P-value**	63.42	A	**P-value**	171.85	A	**P-value**	67.01	A	**P-value**
Basalt	505.46	A	0.363	731.23	A	0.87	859.34	A	0.247	68.51	A	0.595	457	A	0.852	27.16	A	0.453

Table 17: T-test results comparing rock block type for each major taxonomic group. Figure 15 shows graphical representation of results.



	Mean Fauna Densities by Rock Block Source Location																	
	Barnacles (4th root)			Arthropods (square root)			Copepods (square root)			Polychaets (Log)			Gastropods (4th root)			All Others (4th root)		
	Mean	Group		Mean	Group		Mean	Group		Mean	Group		Mean	Group		Mean	Group	
Source Location			**F-Ratio**			**F-Ratio**			**F-Ratio**			**F-Ratio**			**F-Ratio**			**F-Ratio**
Abe Andesite	1.3962	A	0.0675	8.9283	A	2.8707	20.5118	A	1.3945	2.14835	A	0.2138	1.90264	A	0.5069	1.47044	A	0.1509
KM Hi Ti Basalt	1.9969	A		3.7687	A		14.8503	A		2.29716	A		2.37303	A		0.90305	A	
KM Low Ti Basalt	1.5868	A	**P-value**	8.4237	A	**P-value**	31.8097	A	**P-value**	2.37075	A	**P-value**	3.38702	A	**P-value**	1.04865	A	**P-value**
Mariner Andesite	1.6204	A	0.9767	2.6593	A	0.0556	17.6987	A	0.2667	2.39926	A	0.8859	1.95872	A	0.6809	1.10165	A	0.9282

Table 18: Four-way ANOVA results by rock block source for each major taxonomic group. Figure 16 shows graphical representation of results.

Figure 1: From Tivey (2012). Back-arc system in Lau Basin along the Eastern Lau Spreading Center in the North (a) and the South (b). Due to the proximity differences, the north receives less subducting slab influence and the south, more.

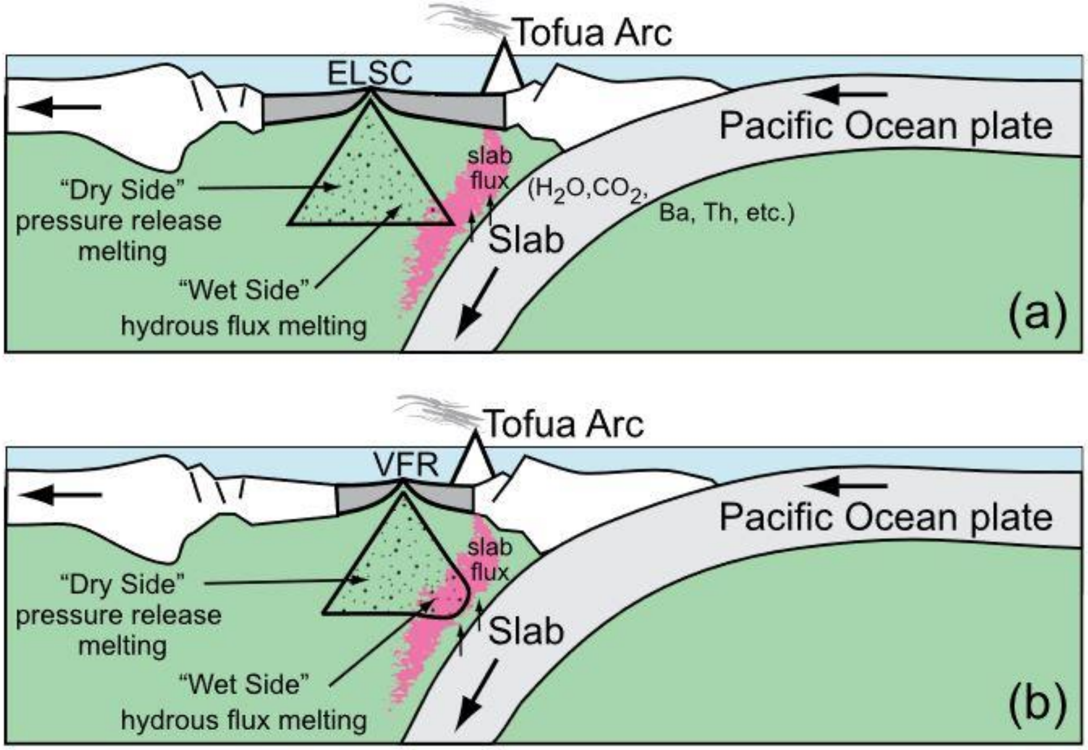


Figure 2: From Tivey (2007). Process of hydrothermal fluid creation and incorporation of chemical elements.

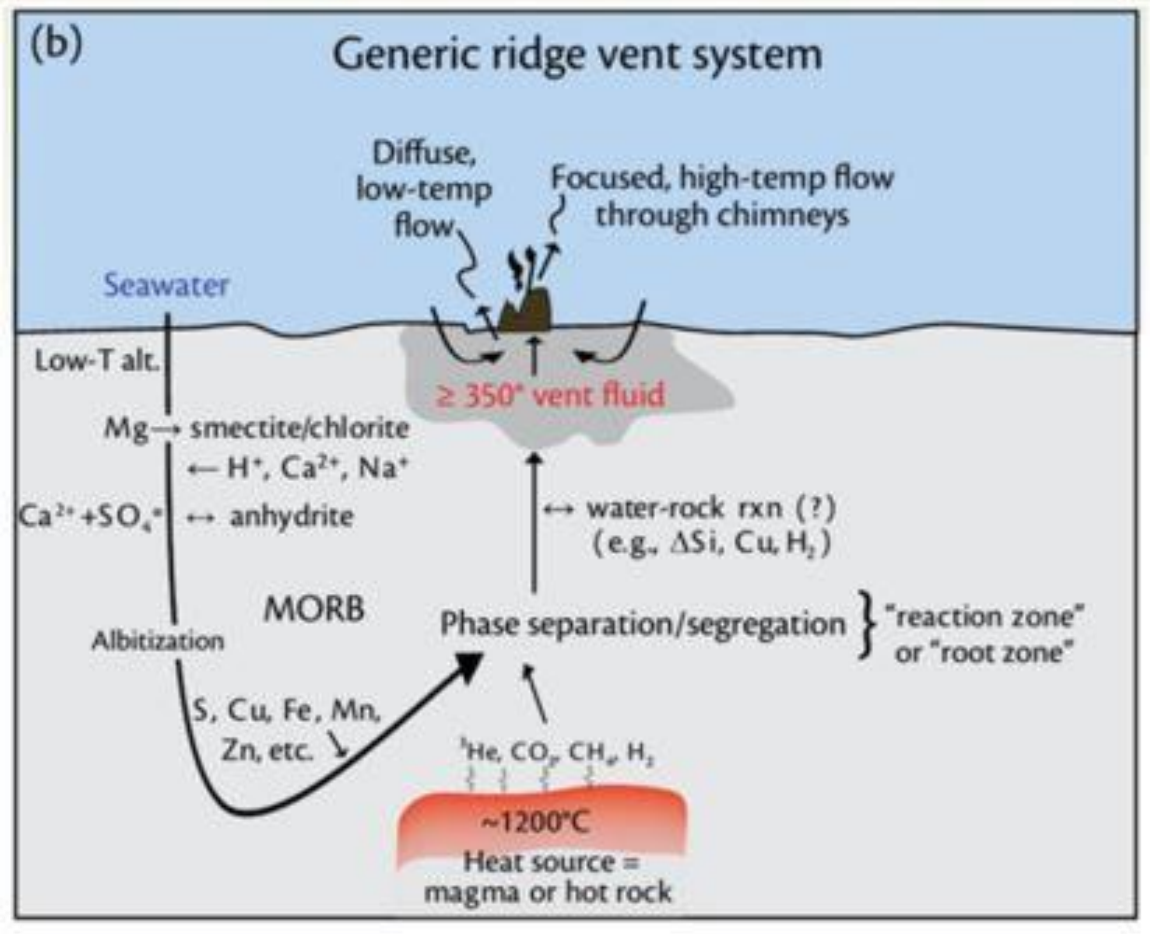


Figure 3: From Martinez (2006). Tectonic setting of the Lau Basin. The ELSC axis is shown by the bold line. Open white triangles represent volcanoes of the arc volcanic front. Grey areas are shallower than 2000 m.

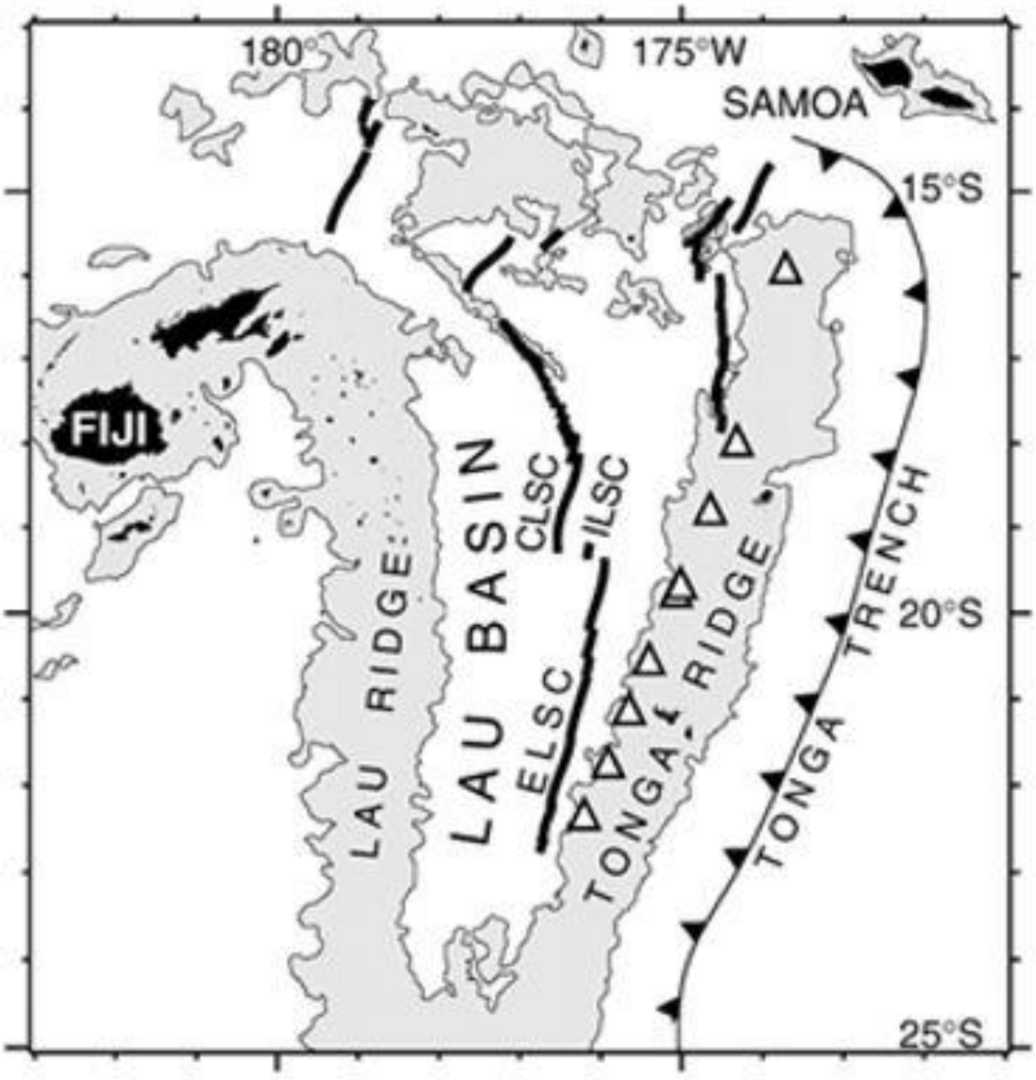


Figure 4: From Kim & Hammerstrom (2012). Location of vent fields. Red arrow indicates break between basalt (north) and andesite (south) type substrates. Highlighted sites (Kilo Moana, ABE, and Mariner) are the locations the rock blocks used in this study were placed.

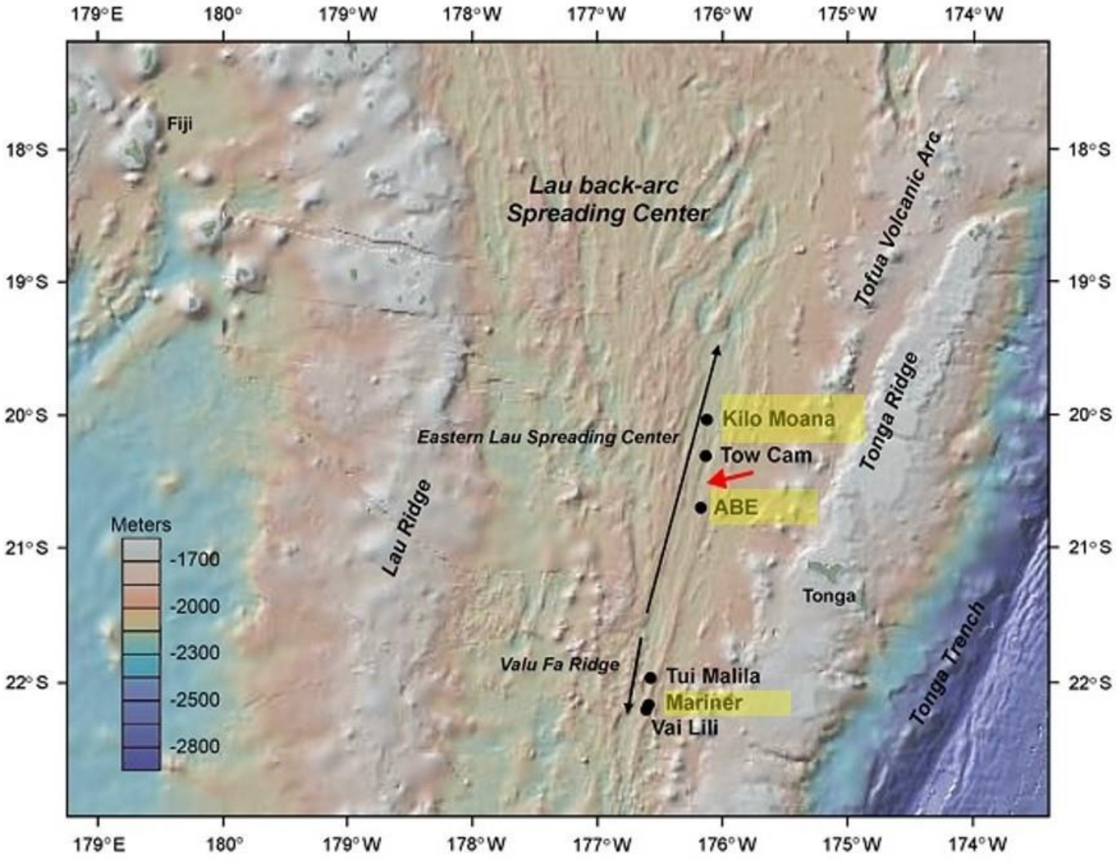


Figure 5: Images taken at a Site from each Location during the recovery portion of the project. Images from Jason II Virtual Van. A) Second Kilo Moana Site. B) Second ABE Site. C) Second Mariner Site. D) Notes and screen capture of Virtual Van, pilots unable to find Mariner 1 site.

DAQ.tn235.Jason
Lowering: J2-429
Time: 2009/05/30 21:31:51
Hdg: 331.68
* Lat: 22 10.843891 S
* Lon: 176 36.100072 W
Alt: 3.20
Depth: 1916.62
Bathy: 1919.82
DegC: 2.504
Cond: 3.170
Salin: -999.000
SVel: -999.000
MagX: -23626.7
MagY: -48126.7
MagZ: -1386.7
MagT: 53631.3
Type: EVT NavSrc: RNV.JAS2.DVL.v1 AttSrc:
ReNav OrigLat: 22 16.844970 S OrigLon: 176 36.100398 W
OrigX: 4978.65 OrigY: 5822.58 DeltaX: 4.11 DeltaY: 1.92
X: 4982.76 Y: 5824.50 Z:
Pitch: -11.9 Roll: 2.5
Event: DLG Can't find Mar1 (buried?)
Goto 8239
RefreshRate: 5

```
8239. 2009/05/30 21:31:51 EVT Can't find Mar1 (buried?)
8240. 2009/05/30 21:32:04 ASNAP
8241. 2009/05/30 21:34:04 ASNAP
8242. 2009/05/30 21:36:04 ASNAP
8243. 2009/05/30 21:36:10 EVT Aborting search for Mar1
```

Figure 6: Photogrammetry process. A) Initial set up highlighting stationary camera, even and strong lighting, and a matte white environment. B) One of 70-90 images of a rock block; each subsequent image was taken after the rock had been rotated ~5°. C) Whole 3D rock model created in AutoDesk ReCap using the many rock images; one function of ReCap is creating and exporting its mesh points for further analysis. D) Model of points exported into MatLab for rock face complexity analysis.

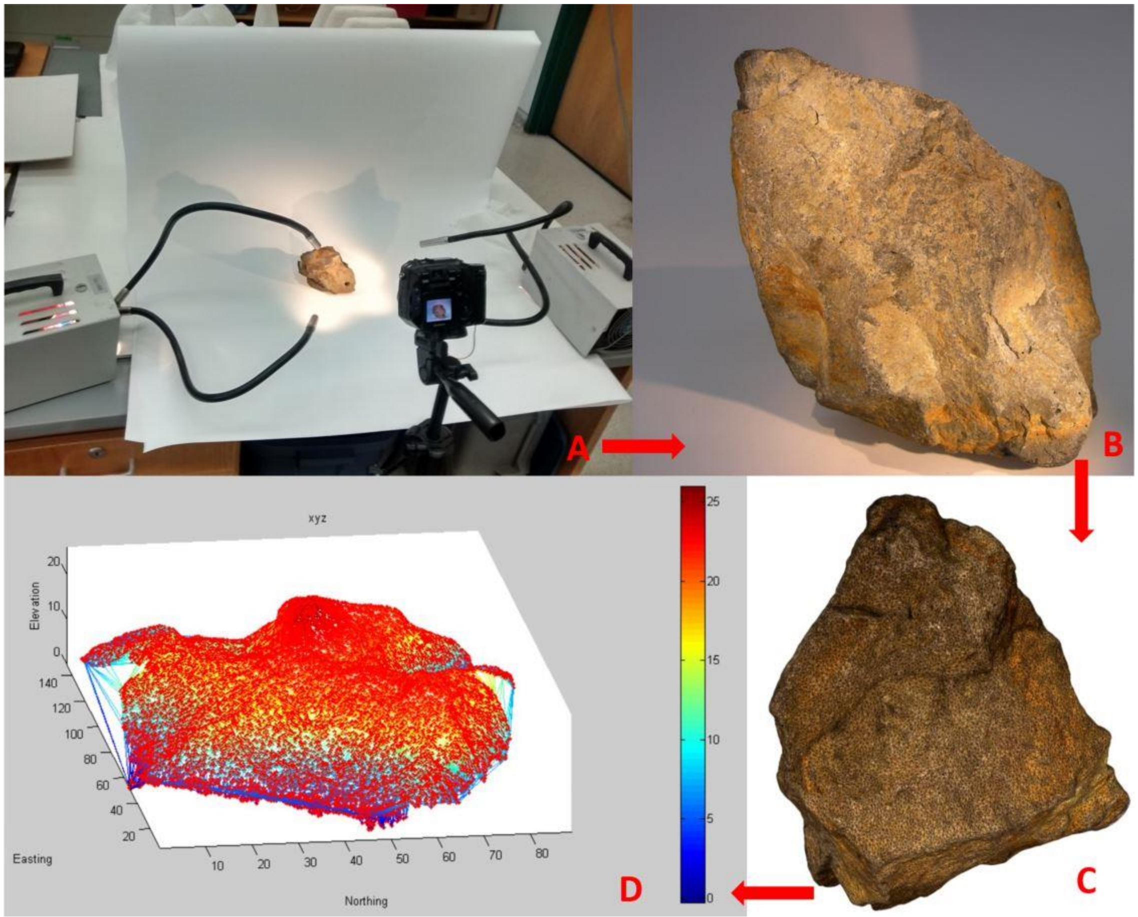


Figure 7: Box-plot of Rock block mean surface area in mm^2 (y-axis) separated by Transplant Location (x-axis) with standard error bars. All Locations are statistically similar to each other and blocks placed at KM show high upper surface area variation.

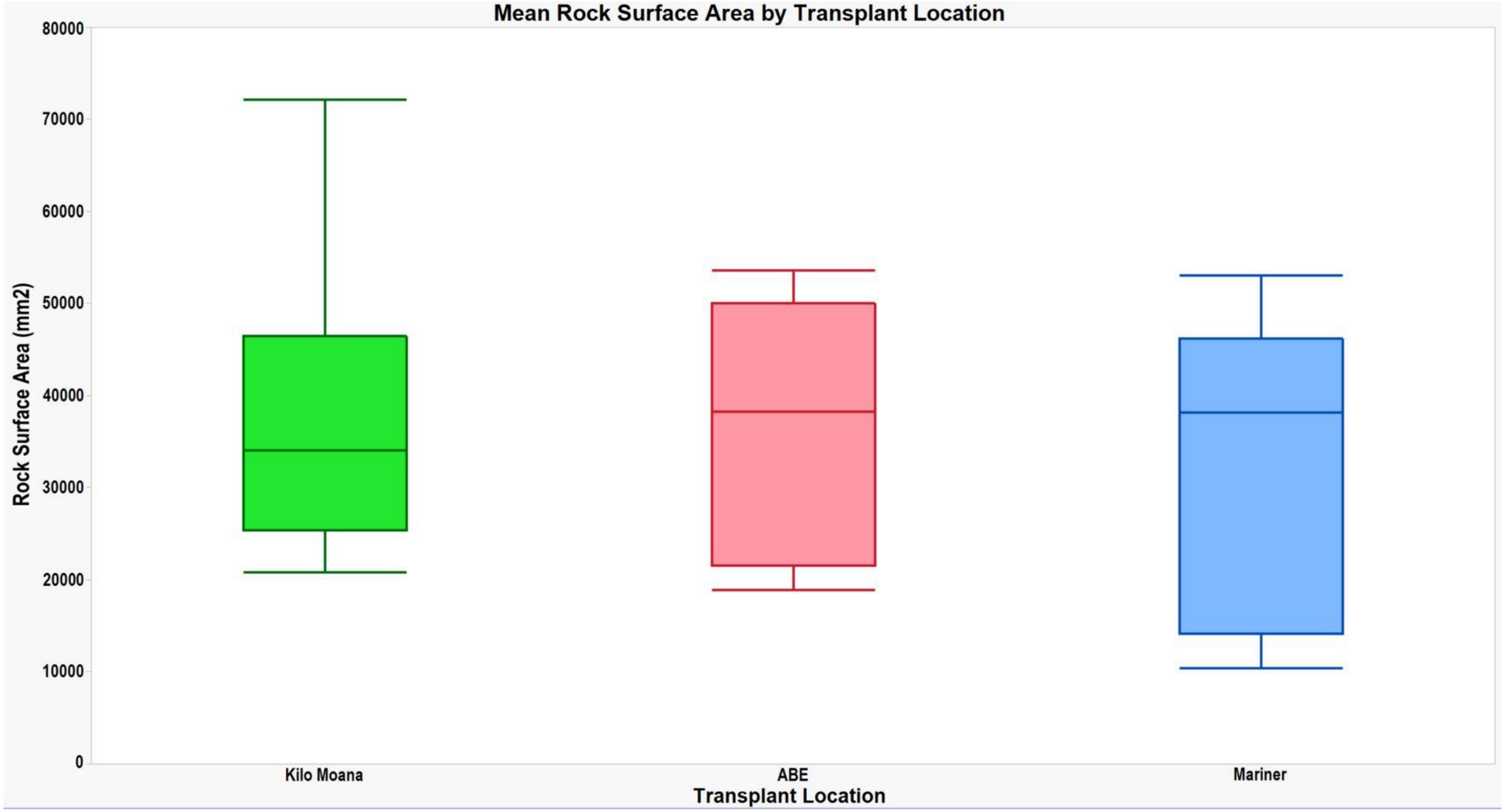


Figure 8: Box-plot of Rock block mean surface area (SA) in mm^2 (y-axis) separated by Rock Source Location nested within Rock Type (x-axis) with standard error bars. See Table 8 for exact means and SE.

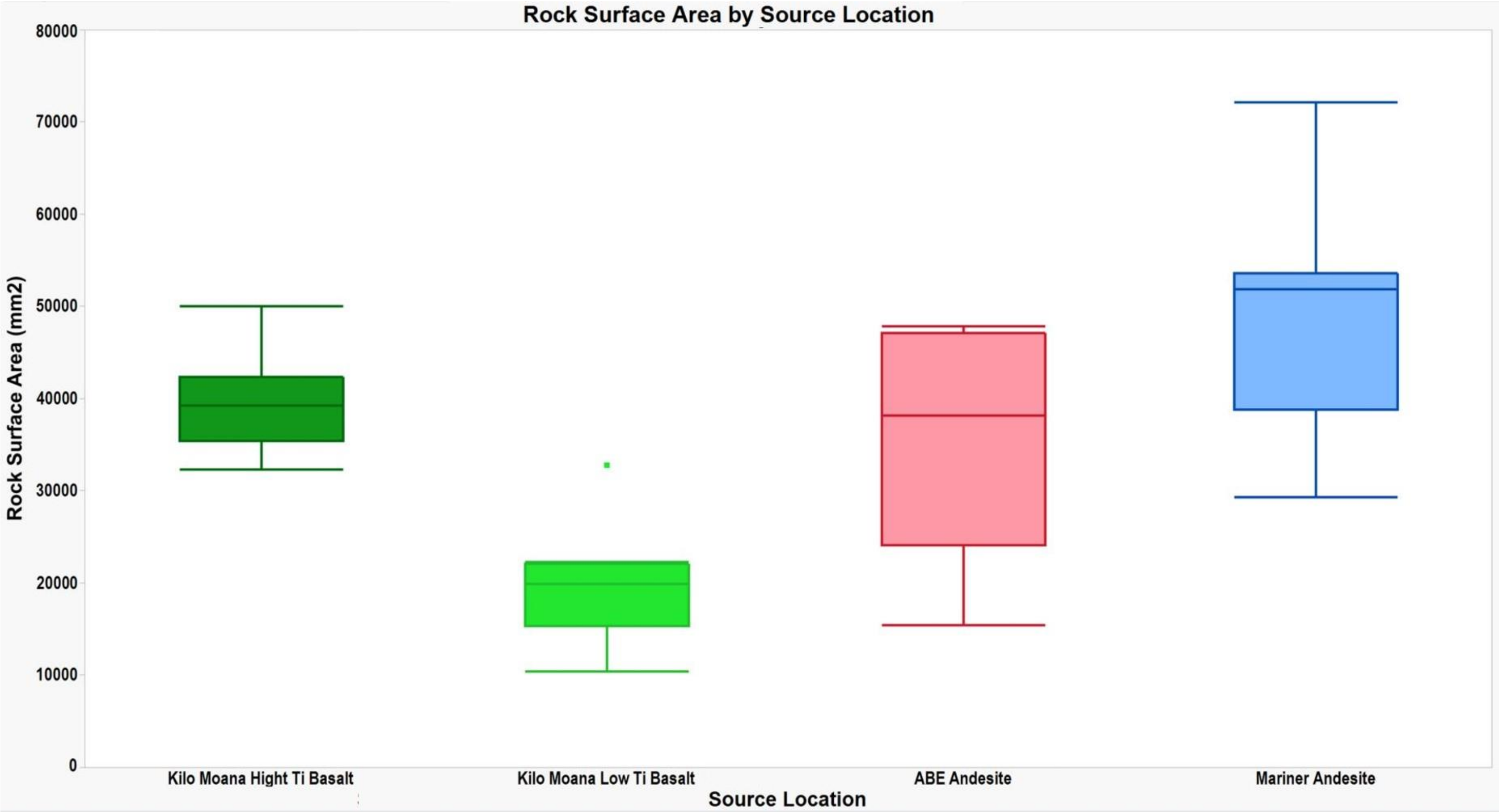


Figure 9: MANOVA of the rugosity of each rock block at different window sizes (x-axis) from 1 cm^2 (Win0) to 40 cm^2 (3.688…) and rugosity values on the y-axis.

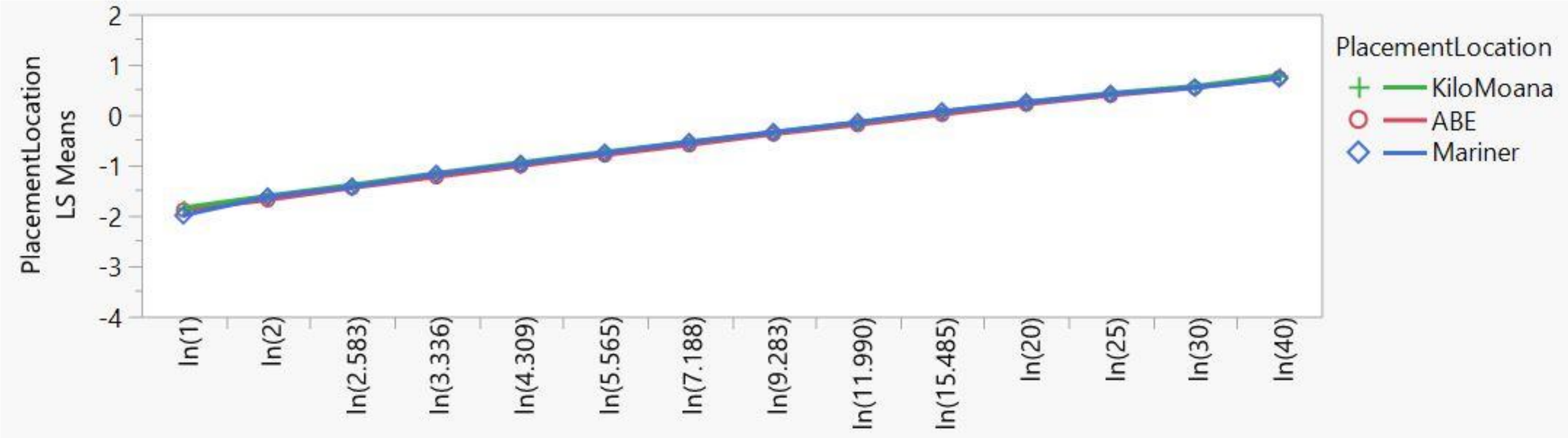


Figure 10. Mean rugosity (surface roughness, y-axis) of each Location's rock block at a particular scale (y-axis).

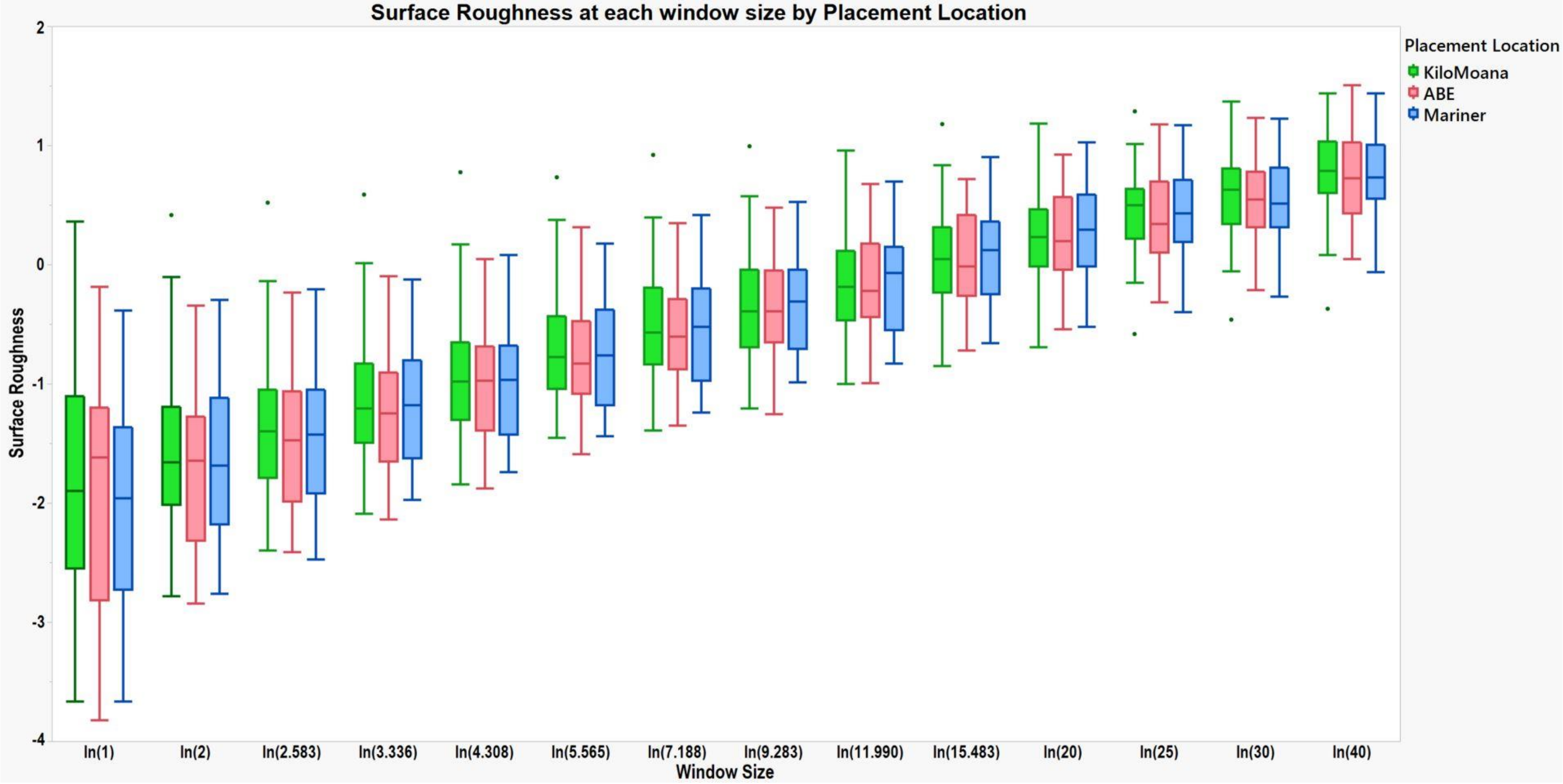


Figure 11: MANOVA of the rugosity of each rock block at different scale (x-axis) from 1 cm^2 (Win0) to 40 cm^2 (3.688…) and rugosity values on the y-axis. Table 15 has corresponding MANOVA test results.

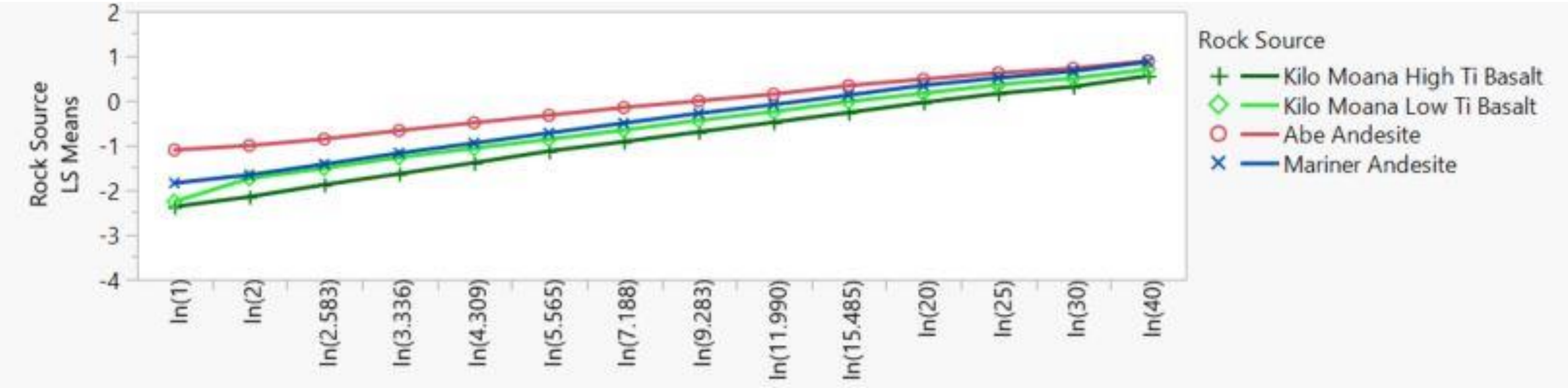
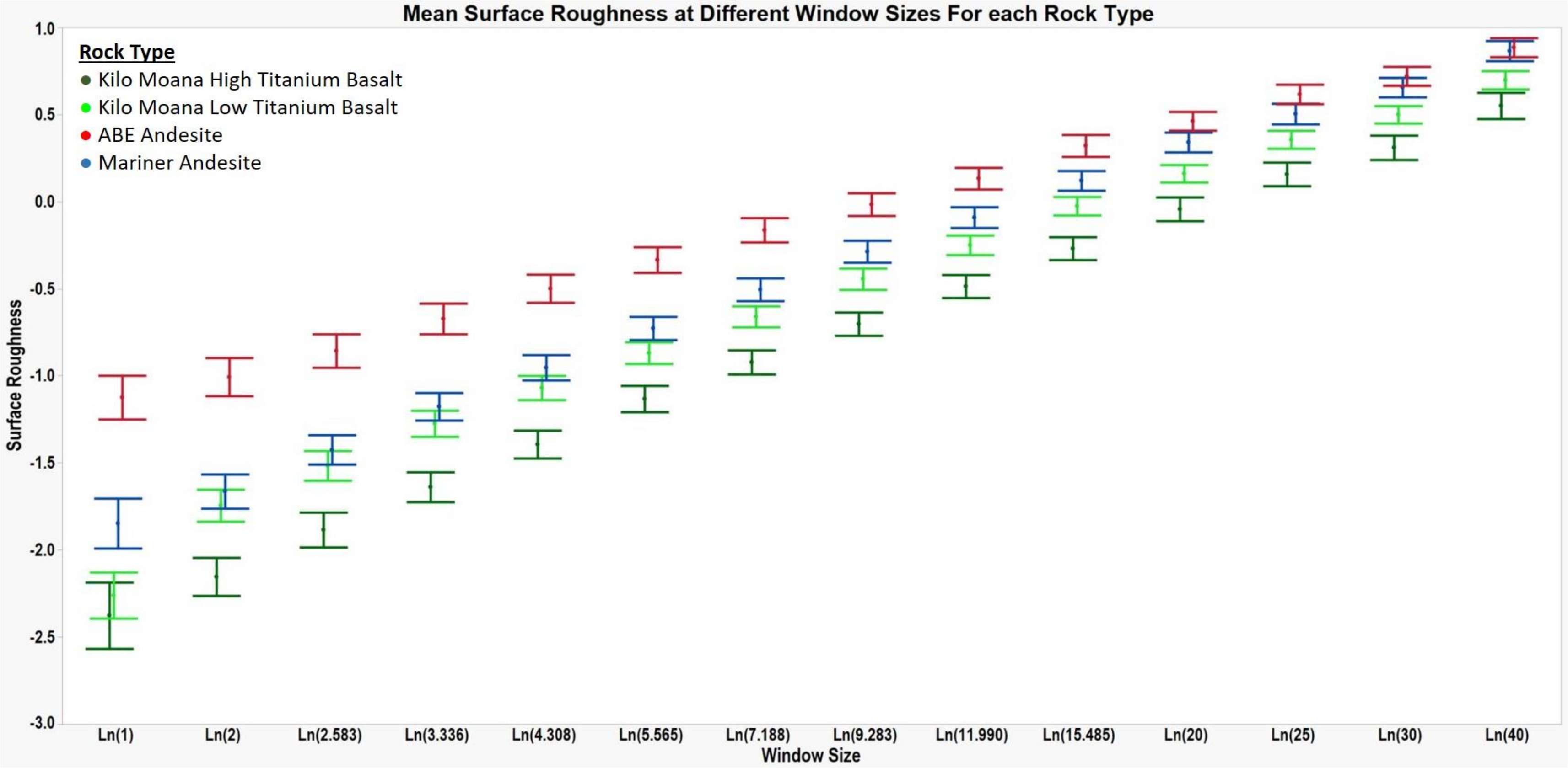


Figure 12. Mean rugosity (surface roughness, y-axis) of each Rock Source Type at a particular scale (y-axis).



Figures 13a – 13d: Show line graphs of the rugosity, where each rock is represented by a single line and scale is the points along the line. The figures are grouped by Source Rock Type. The bolder black line with yellow dots is the mean rugosity at a particular scale.

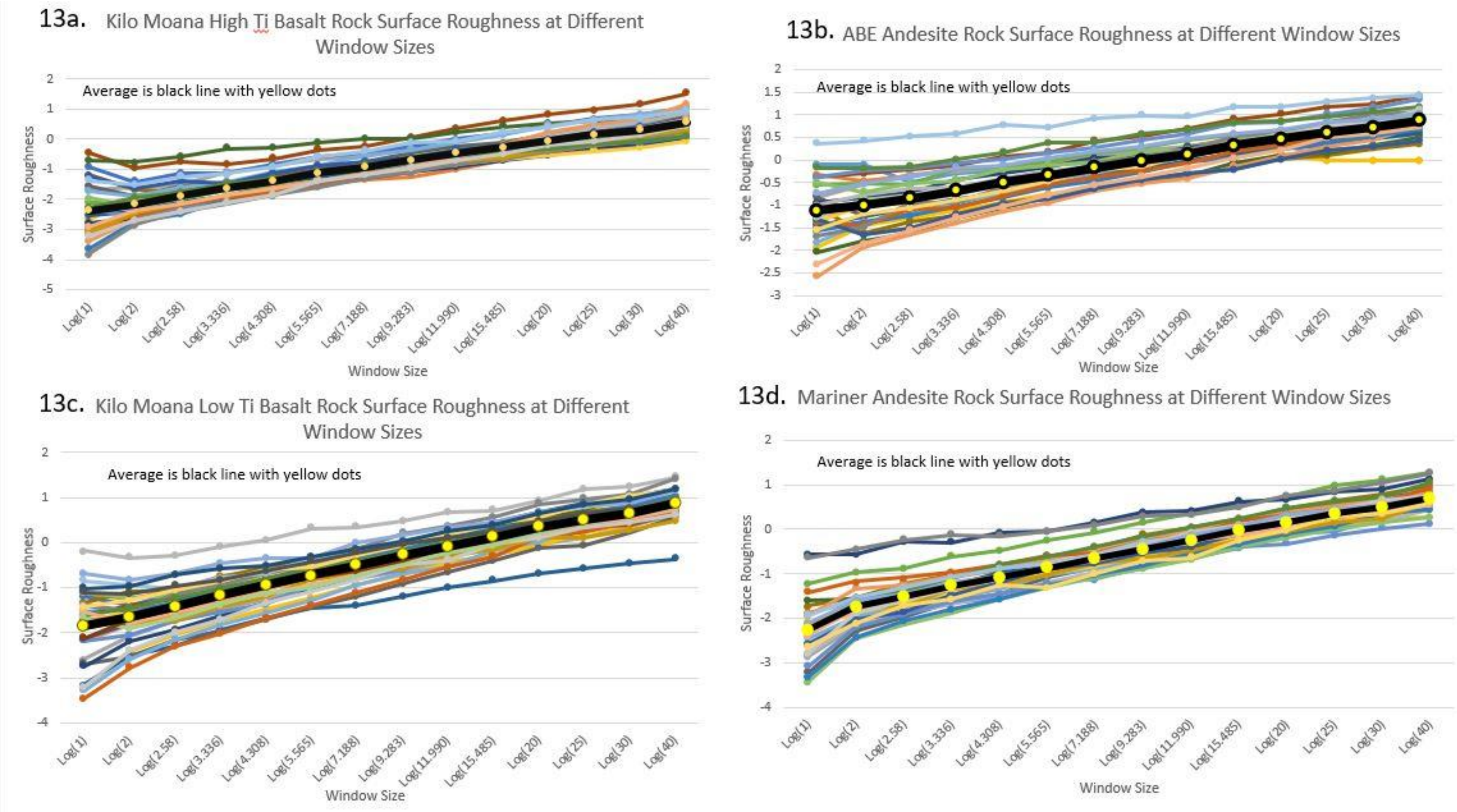


Figure 14: Mean Faunal Density (y-axis) with Standard Error bars by Transplant Location (x-axis) of each fauna group. Table 16 shows three-way ANOVA results.

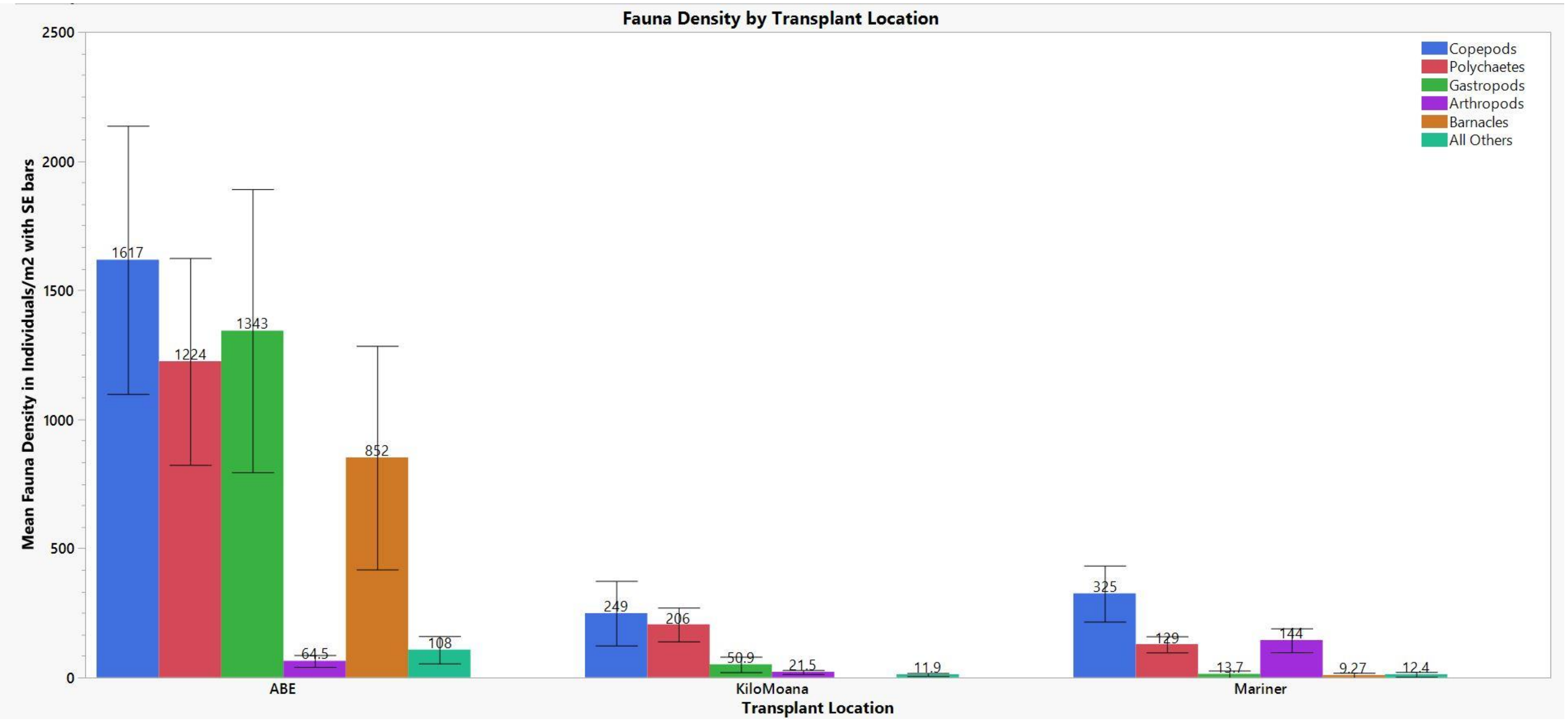


Figure 15: Mean Faunal Density (y-axis) with Standard Error bars by Rock Type (x-axis) of each fauna group. Table 17 shows t-test results.

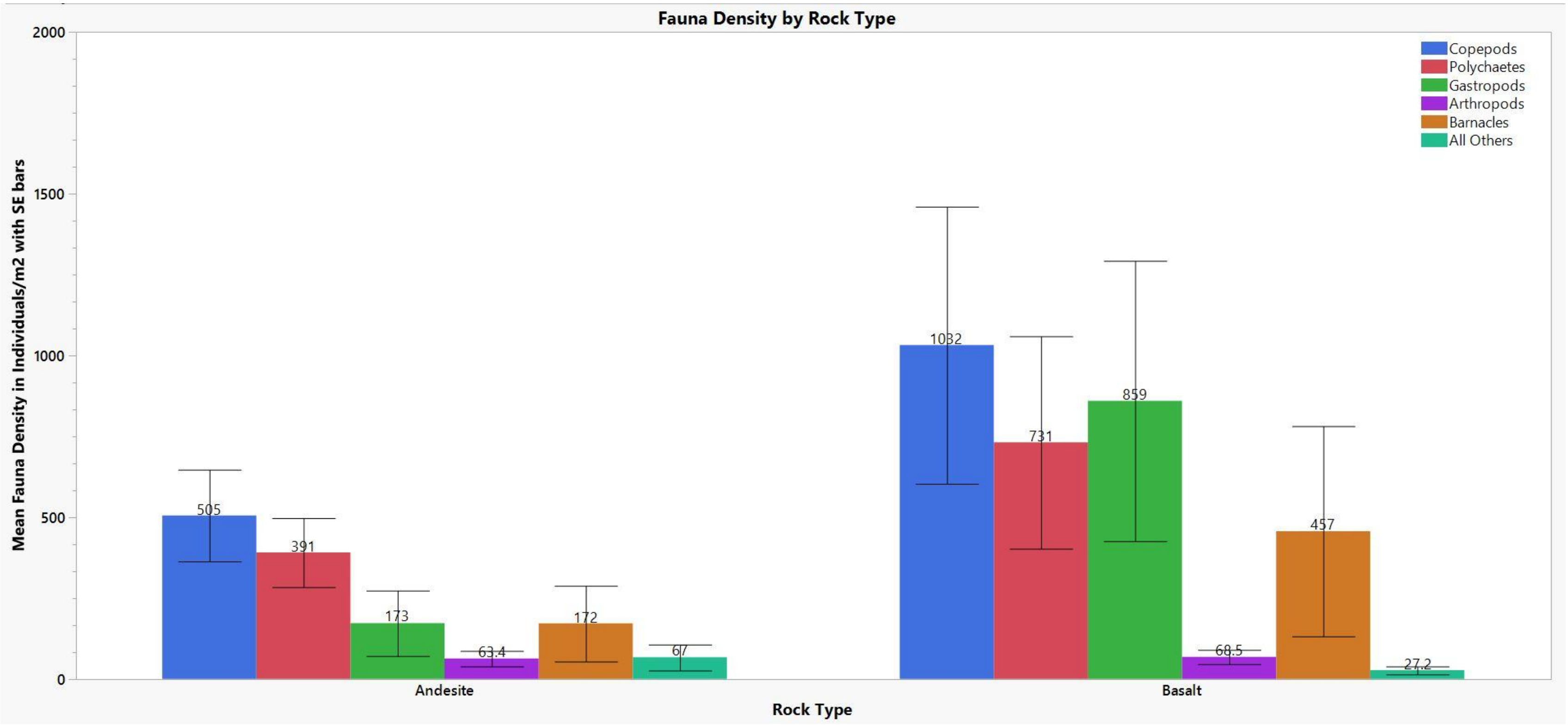


Figure 16: Mean Faunal Density (y-axis) with Standard Error bars by Rock Source Type (x-axis) of each fauna group. Table 18 shows four –way ANOVA results

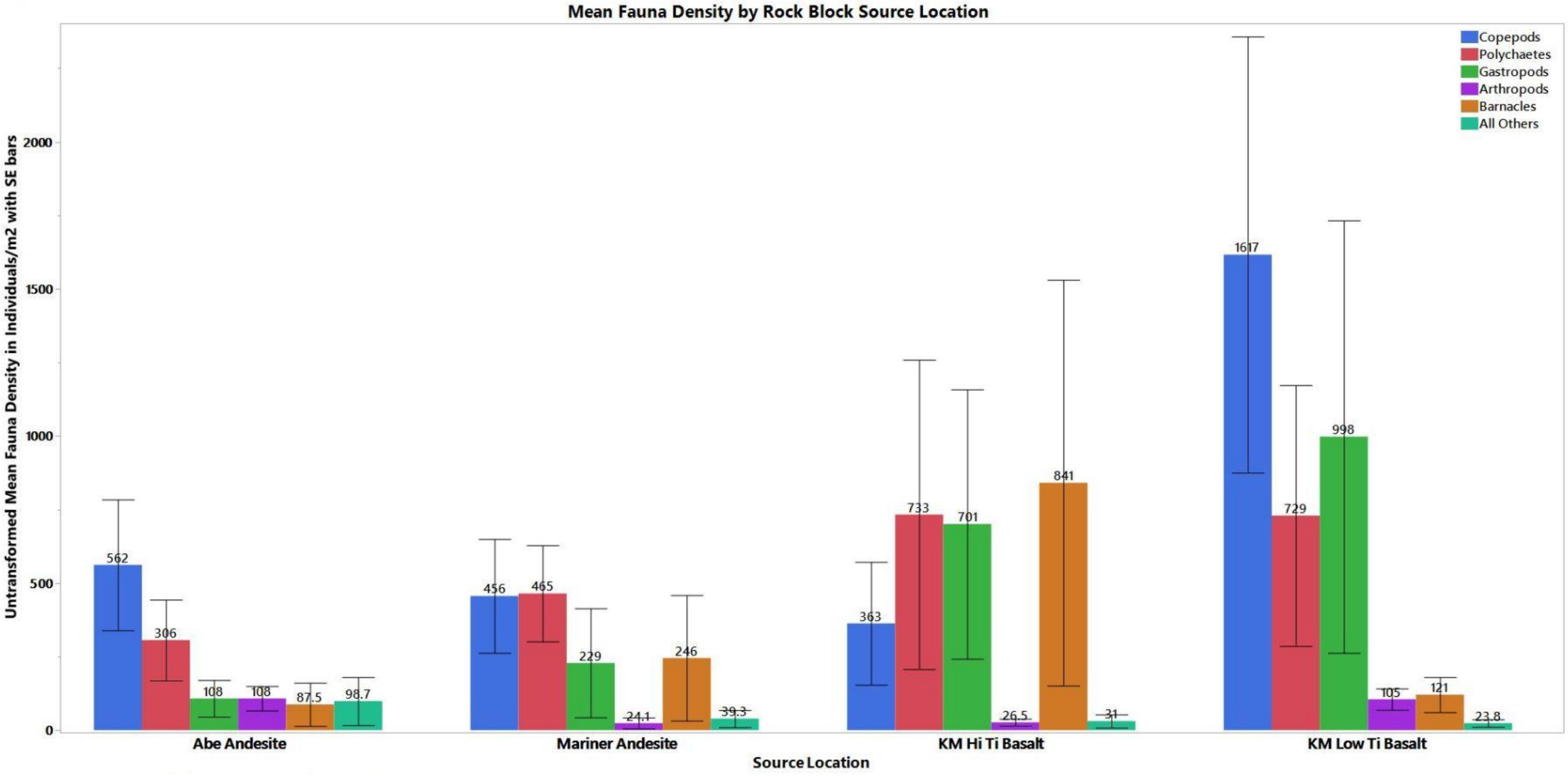


Figure 17: 4th root transformed – Bray Curtis Similarity- Non-Metric MultiDimensional Scaling (NMDS) plot of out planted rock blocks with Transplant Location signified by shape and colors (Green Triangles = Kilo Moana, Blue Triangle = Mariner, Teal Square = ABE) and Rock Type signified by letters (A = Andesite, B = Basalt).

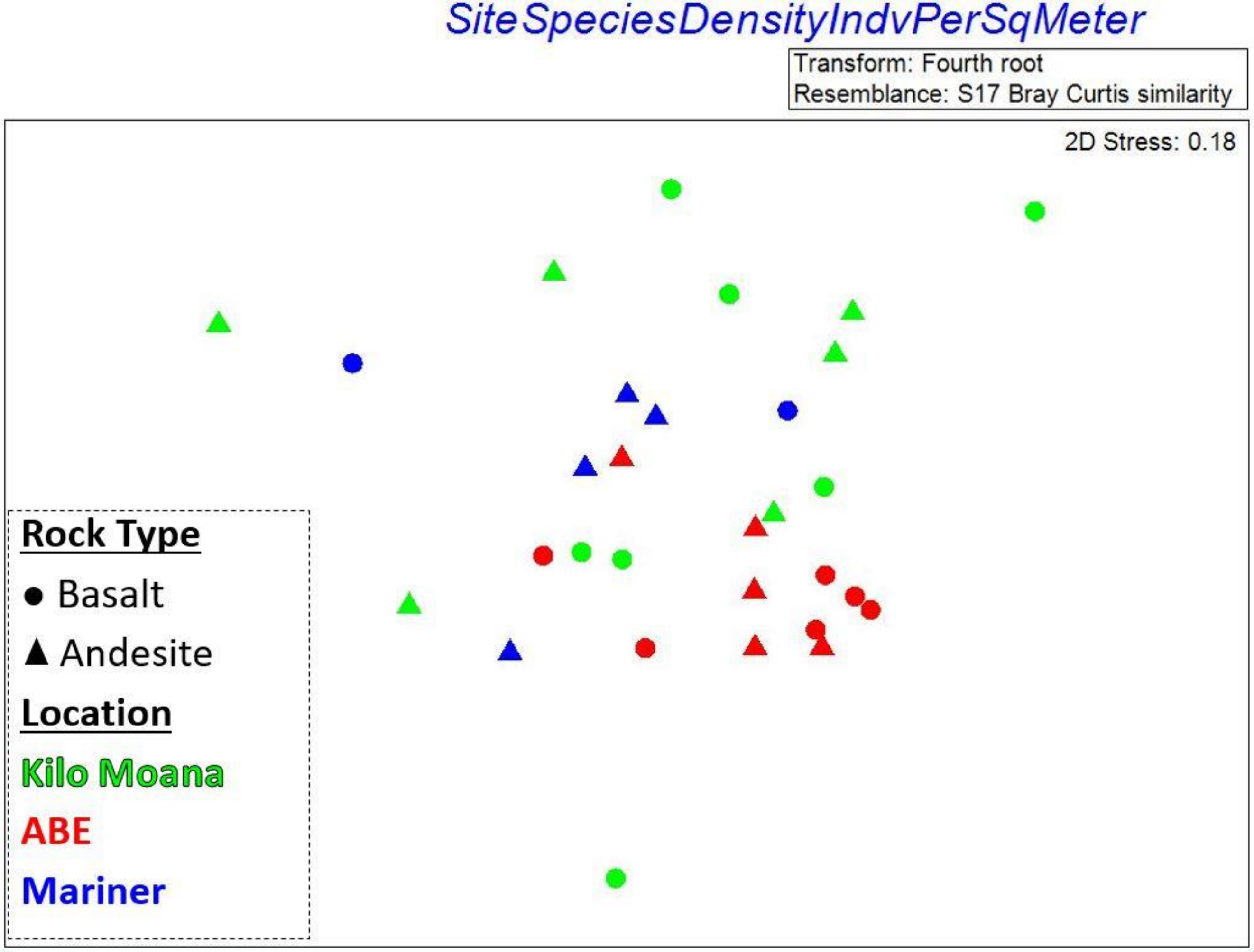


Figure 18: Simprof dendrogram using the same Bray-Curtis similarity results as Figure 9 showing the similarity grouping of each rock block's Placement Site (i.e._ Mariner 1, 2, or 3, ABE 1, 2, or 3 etc.). Green triangles signify Andesite rocks and blue triangles signify Basalt rocks. Red dotted lines show significant similarity at a particular similarity percentage at the 0.05% significance level.

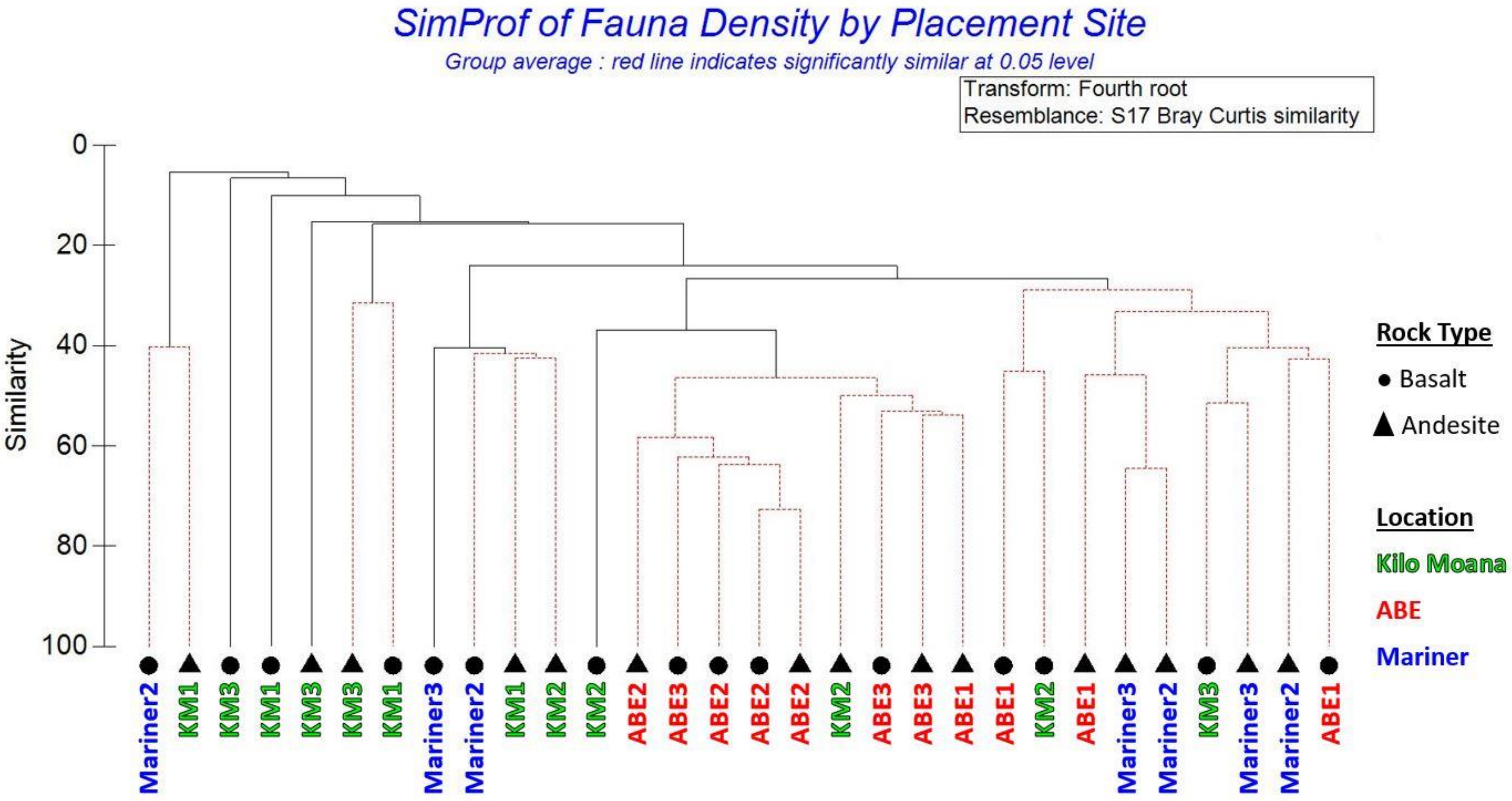
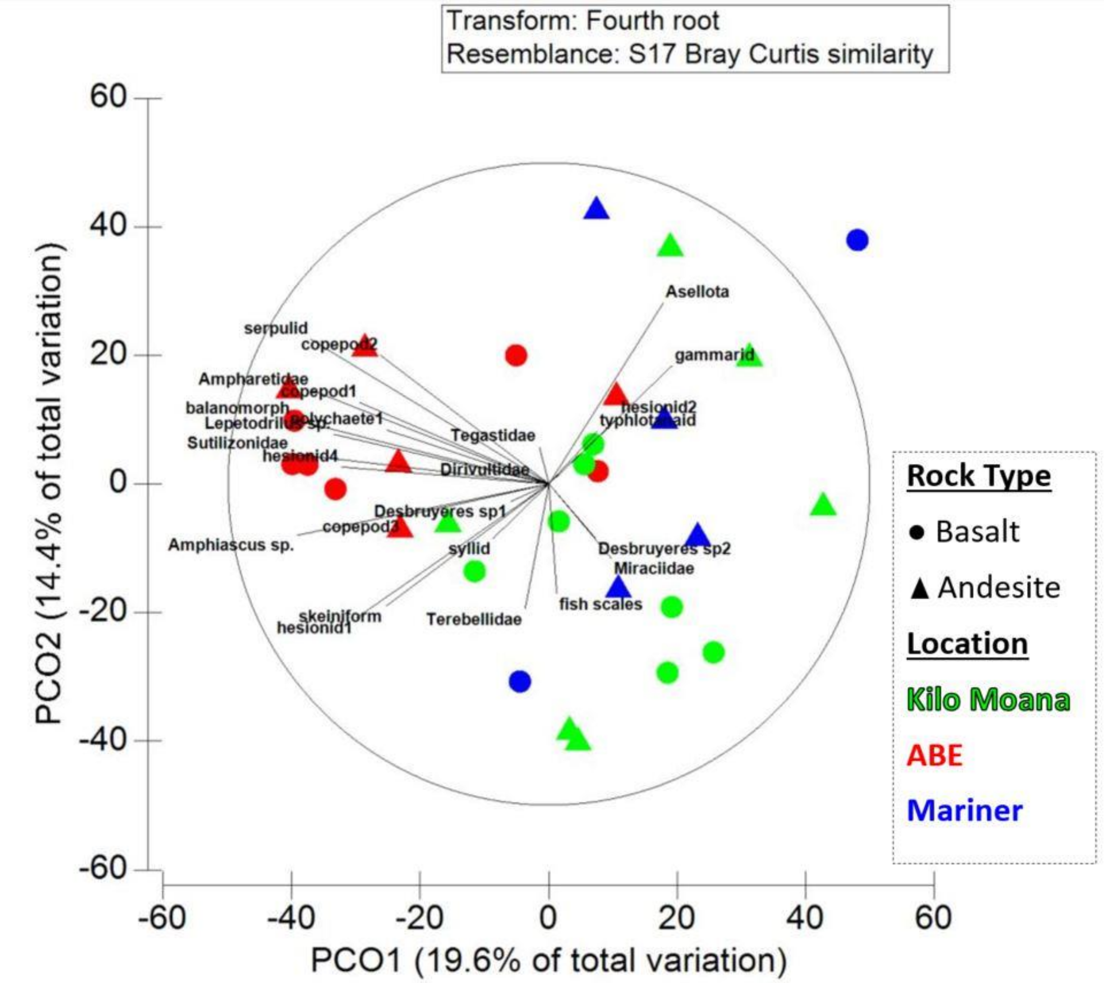


Figure 19: Same nMDS as Figure 17, but with Principal CoOrdinate axes showing the variation explanation of the two major coordinates as well as the top 90 % most abundant fauna for each of the three locations. Most of the omitted species grouped around the red circles and triangles. Results here, reflect the results from the SIMPER analysis (Table 18). Some notable (because of their known association with hydrothermal environments) omitted taxa are: *Archinome* sp., polynoid1, anemone1, *Bathymodiolus* sp., *Provanna* sp., and unknown barnacle ciprid.



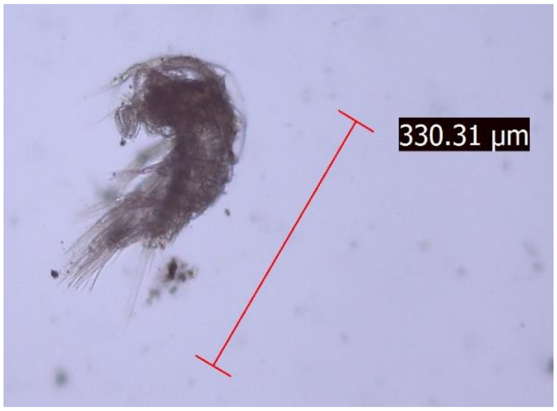
APPENDIX

IMAGES OF SELECTED FAUNA

1. Crustaceans
    a. Copepods
        i. Harpacticoid
            1. **Miraciidae 1**
            (*Amphiascus sp.*)

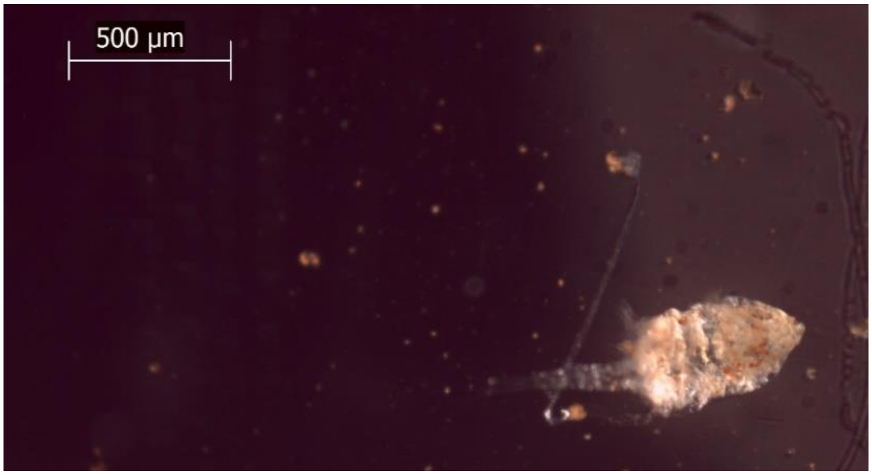
Miraciidae2

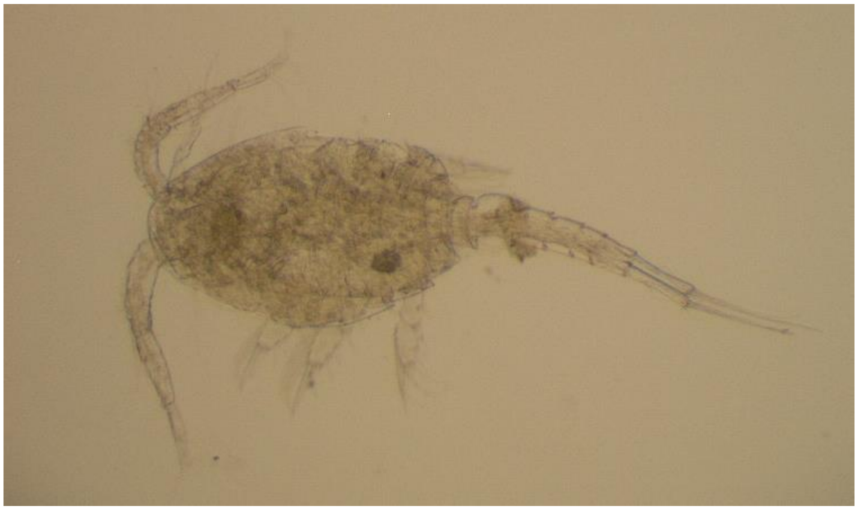
2. Tegastidae



ii. Siphonostomatid

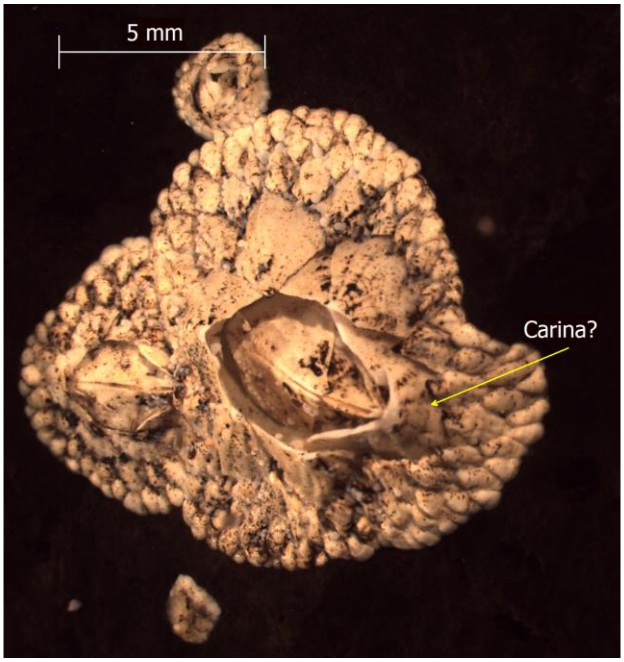
1. Dirivultidae





b. Barnacles

i. ***Eochionelasmus ohtai***



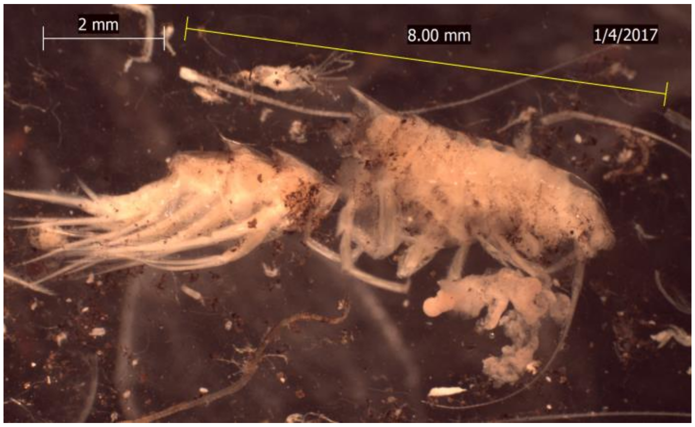
c. Isopods

i. **Suborder: Asellota**

d. Amphipods

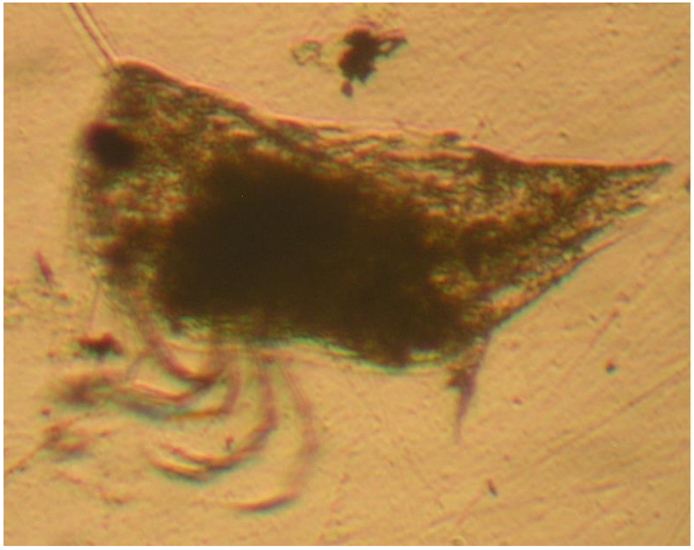
i. **Gammaridea**

1. **Eusiroidea**



e. Ostracods

i. **Order Podocopida**

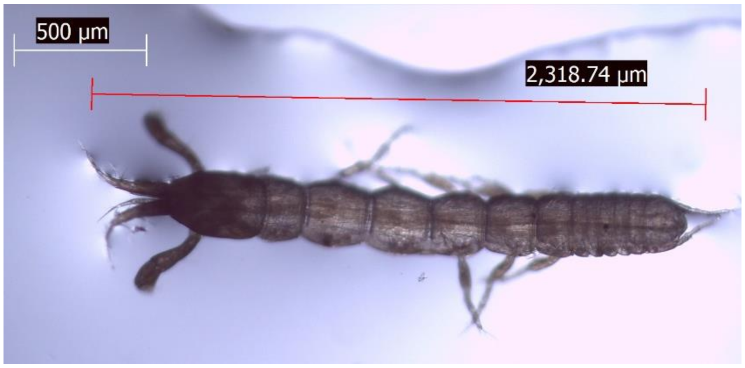


ii. **Order Platycopida**

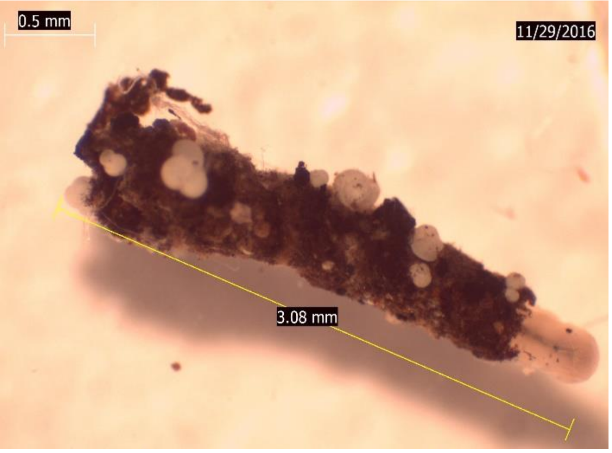
f. Tanaids

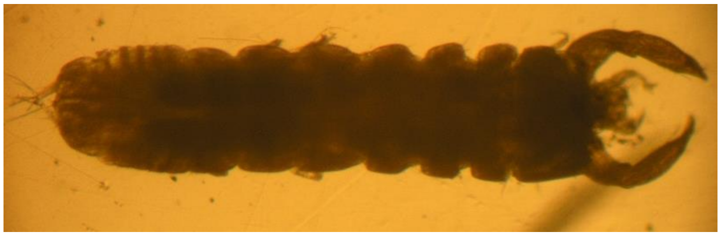
   i. Suborder: Tanaidomorpha

      1. ***Leptognathia ventralis***



2. ***Typhlotanais*** **sp.**



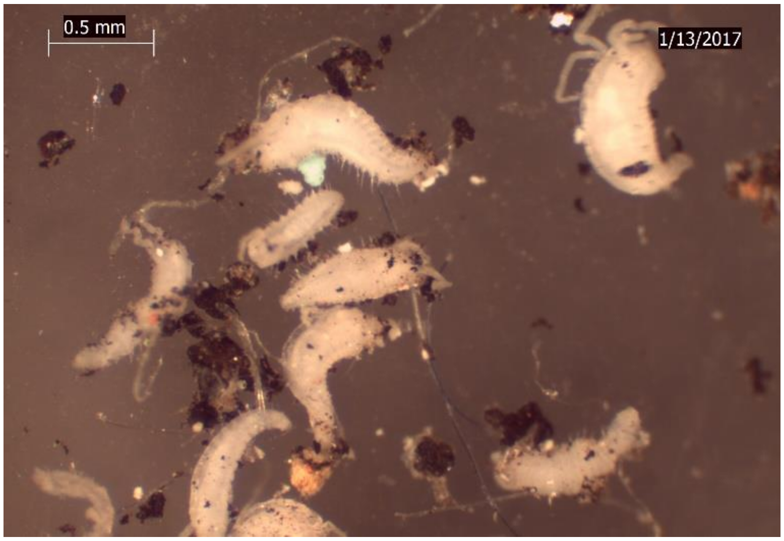


g. Acari (mites)

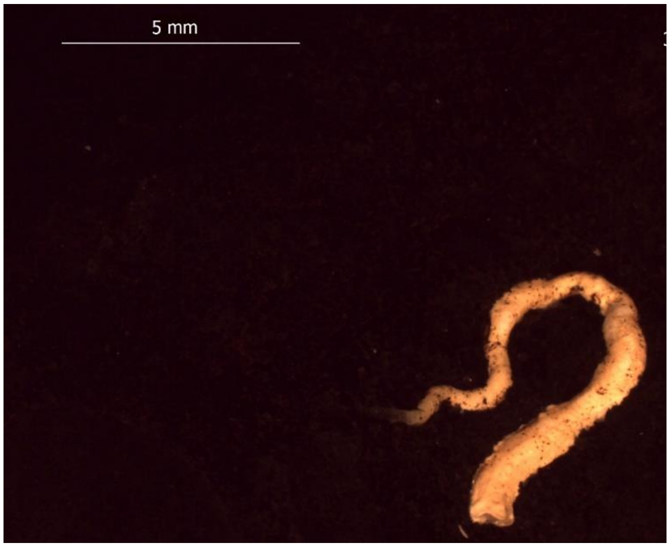
  i. ***Copidognathus papillatus???***

2. Polychaetes

a. **Ampharetidae**

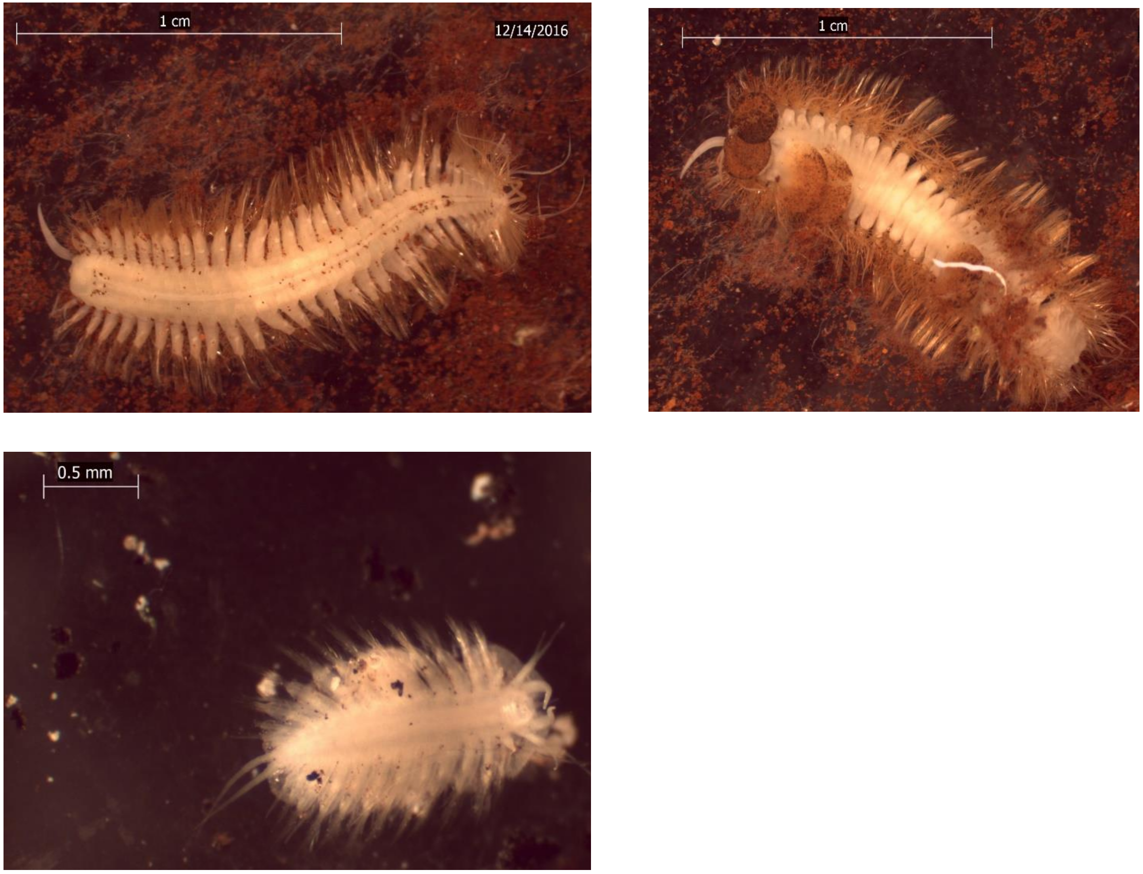


b. **Serpulidae**

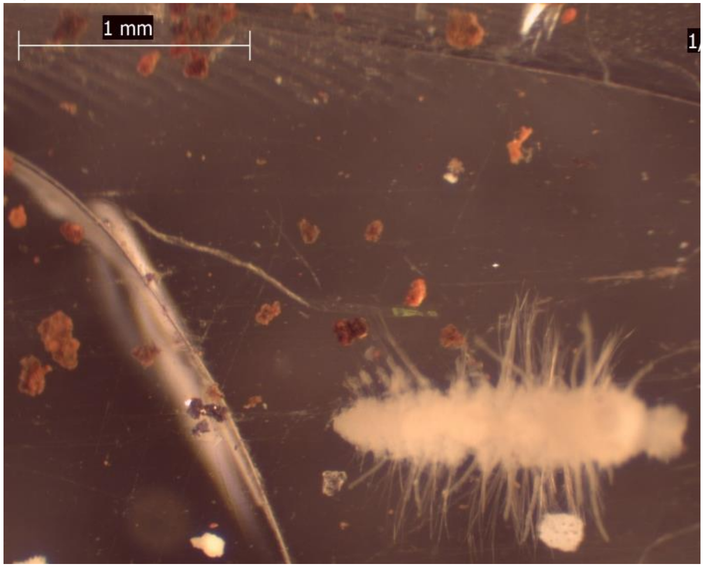


c. **Terebellidae**

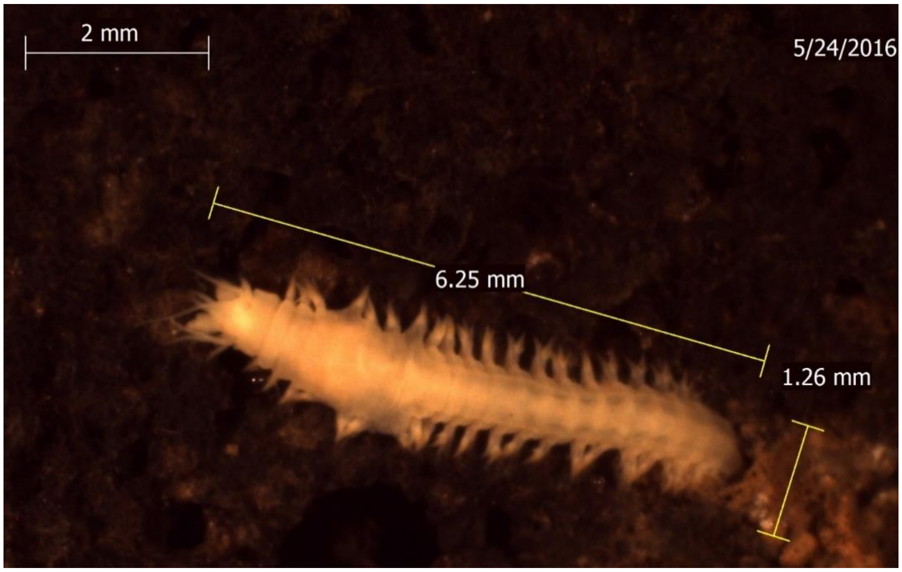
d. **Polynoidae**



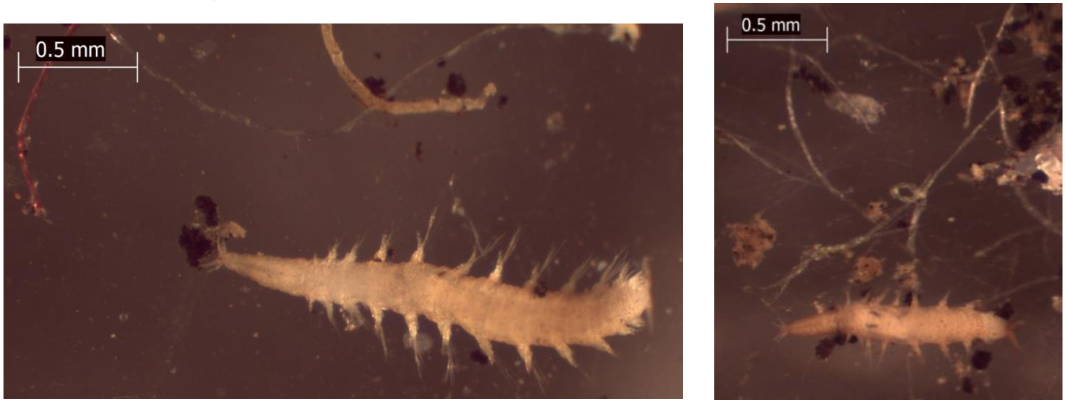
e. Syllidae



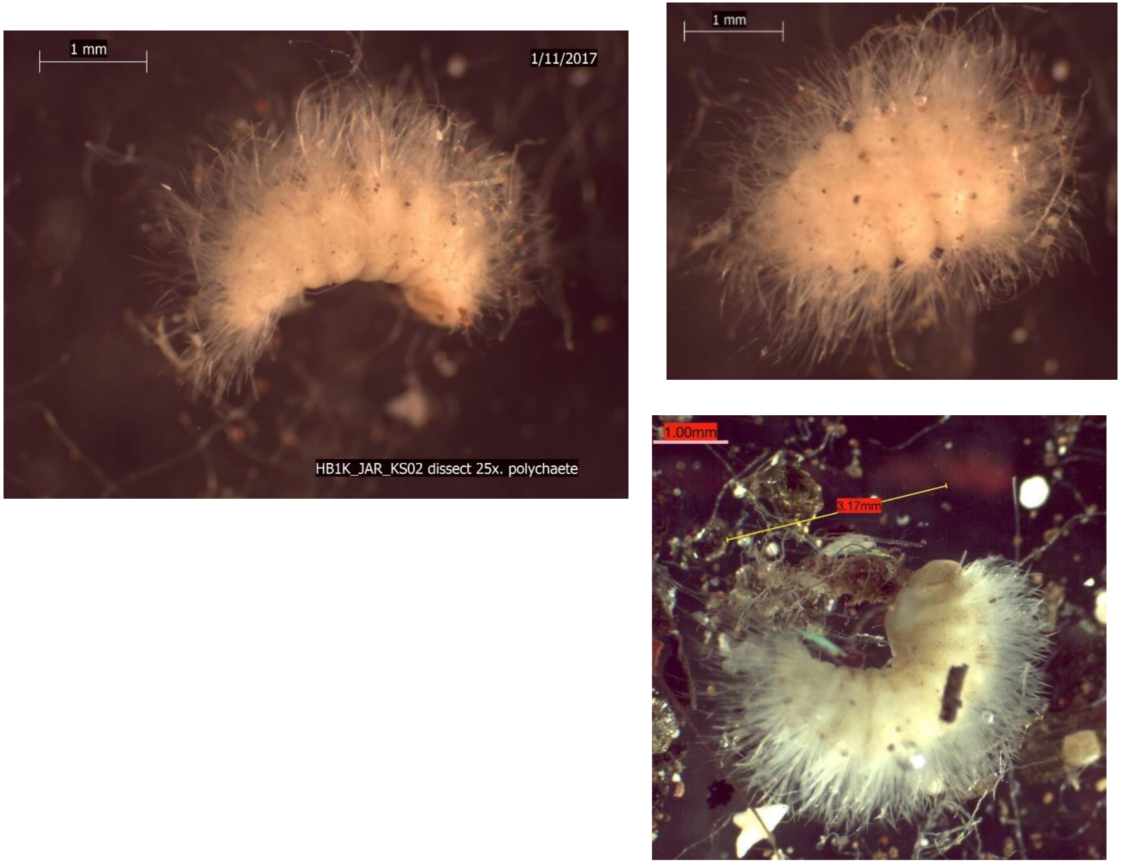
f. Hesionidae



g. **Glyceridae**

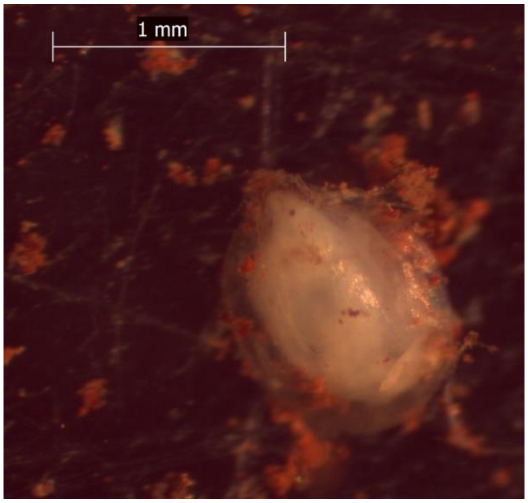


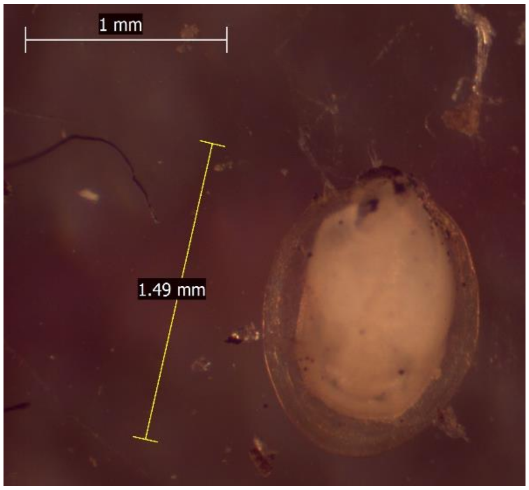
h. **Amphinomidae (*Archinome* sp.)**



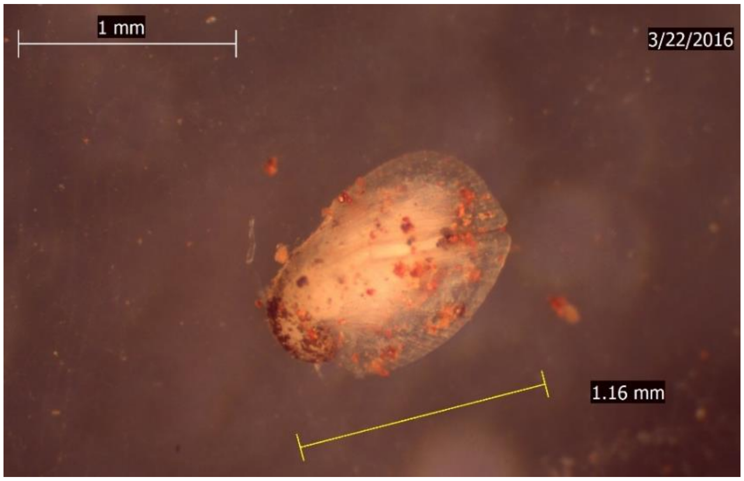
3. Molluscs
    a. Gastropods
        i. Limpets
            1. **Nodopelta**

2. **Lepetodrilidae**



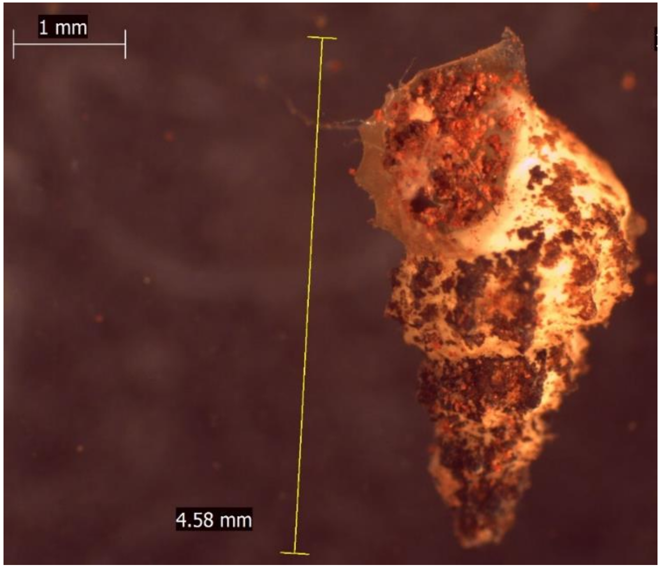


3. **Sutilizonidae**

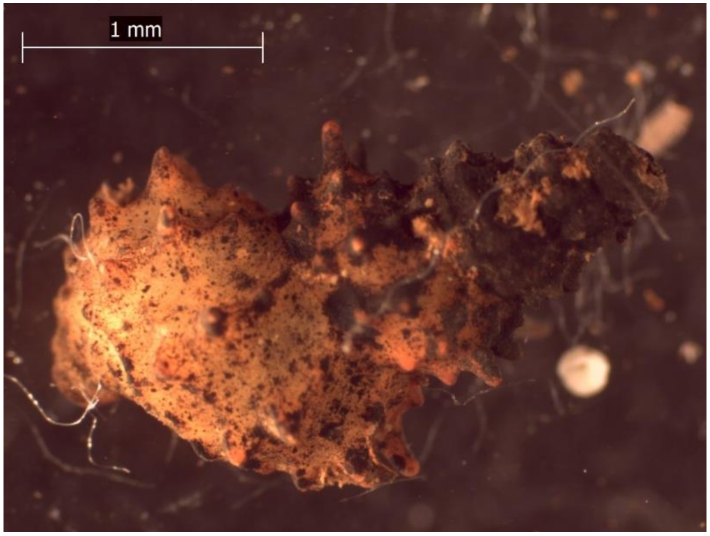


ii. Provannidae

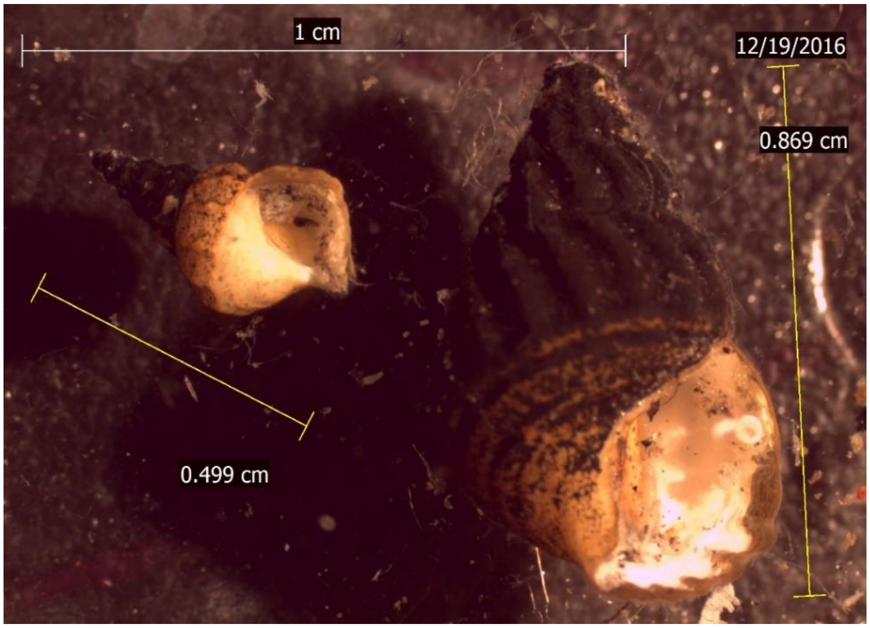
1. ***Desbruyeres* sp.** 1



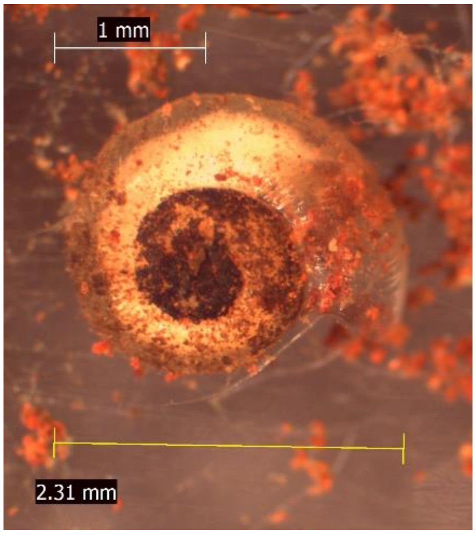
2. ***Desbruyeres* sp. 2**

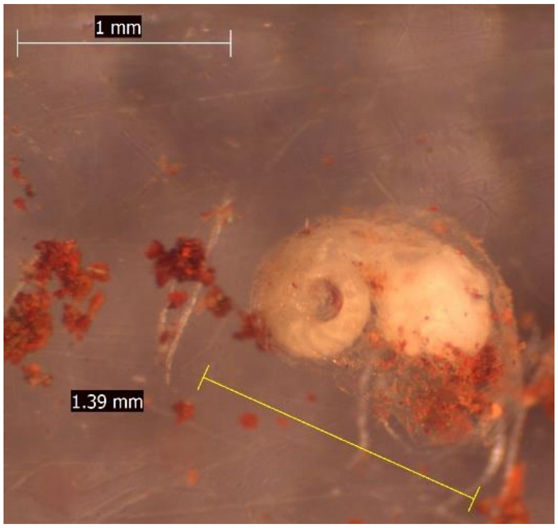


3. ***Provanna***



iii. **Skeneiform**





b. Bivalves

i. ***Bathymodiolus***

4. Cnidarian
    a. **Anemone**