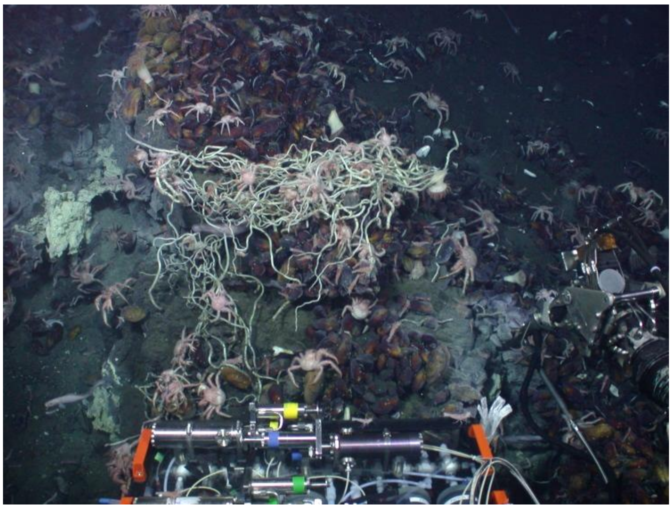

Benthic community structure and environmental drivers on Monowai Seamount, Kermadec volcanic arc

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ABSTRACT

Seamounts are spatially isolated, underwater topographical features that extend more than 1 km above the seafloor. They are products of geological processes, and exhibit diverse forms of venting as a result of volcanism due to plate tectonics. Environmental factors vary greatly on seamounts, due to which they support communities of specialist chemosynthetic invertebrates, suspension-feeding fauna, and large mobile megafauna including many commercially-important fish species. In addition to threats from benthic trawling, seamounts are now viewed as repositories for Seafloor Massive Sulphide (SMS) deposits, owing to their venting activity. The seamounts of the 2500 km-long Tonga-Kermadec volcanic arc are diverse in their hydrothermal activity and, therefore, are potentially of mining interest. Species diversity and abundances differ within and between seamounts of the Kermadec volcanic arc, according to prevailing environmental factors. Three abiotic variables (i.e. water depth, substrate type, proximity to vent sites) were chosen in order to examine their effect on taxa richness, abundances, and benthic community structure for the current study on Monowai Seamount, northern Kermadec volcanic arc.

Monowai Caldera was explored as part of the 2005 New Zealand-American Pacific Ring of Fire, using the submersible *Pisces V*. 4500 still images and 16 hours of video footage for three dives were acquired for recording data on substrate type, water depth, proximity to vent sites, taxa abundance, and composition. 166 workable samples were chosen for further analysis after excluding images that lacked clarity. Still images were matched with frame grabs from video footages for acquiring information on water depth, geographical coordinates, and small-scale distances to a vent opening within samples. OFOP (Ocean Floor Observation Protocol) was used for recording seafloor observations and mapping of habitat and associated taxa on to a calibrated map of the caldera.

Habitat maps and faunal distribution maps visually represented the spatial distribution of habitats, vent, and non-vent assemblages, along with identification of an area of the caldera that was hydrothermally active in 2005. Multivariate analyses, using PRIMER v.6 with PERMANOVA, distinguished key variables responsible for the variation in the faunal community structure. Substrate heterogeneity, composition, and associated vent- and non-vent taxa were also identified. Faunal zonation with distance to the nearest vent sample was evident, with the first 300 m from a vent site defined as the vent zone.

Univariate statistics, using R and JMP, tested for significant effect of environmental variables on taxa richness and abundance. The predictor variables showed a weak relationship with taxa richness. However, substrate differences and distance to the nearest vent site had a significant effect on taxa abundance. Small-scale examination of distances from a vent opening within samples did not show strong relationships to taxa richness and abundances. Despite a low sample size, an inverse relationship of vent fluid temperatures on taxa abundance was obvious.

Further biological explorations are needed to record the spatial and temporal changes on Monowai Caldera. Other baseline studies, similar to the current study, need to be widely undertaken when considering management and conservation strategies for the protection of such vulnerable ecosystems against seafloor mining.

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Christopher Paolini (*Eragon*):

"The sea is emotion incarnate. It loves, hates, and weeps. It defies all attempts to capture it with words and rejects all shackles. No matter what you say about it, there is always that which you can't."

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CHAPTER 1: INTRODUCTION

1.1 SEAMOUNTS AS A BENTHIC HABITAT

Seamounts are isolated topographical features (Staudigel & Clague, 2010), with vertical extents varying between 100–1000 m above the seafloor (Wessel, 2007). The exact number of seamounts in the world ocean is not known due to limited seafloor mapping. The Pacific Ocean, being the most tectonically active, is estimated to have around 30,000 seamounts (Smith & Jordan, 1988), with about 4000 in the South-West Pacific region (Allain et al., 2008). Current global estimates exceed 100,000 for seamounts > 1000 m (Wessel et al., 2010) and a similar number for those between 500–1000 m high (Yesson et al., 2011), while there may be over a million > 100 m (Costello et al., 2010; Wessel, 2007).

The origin of a seamount is associated with the Earth's geological processes. Seamounts occur near mid-ocean ridges, convergent margins (island arcs), and at upwelling mantle plume hotspots (Wessel et al., 2010). Upward convective flow of decompressed, molten mantle or thinning and expansion of the mantle forms seamounts at mid-ocean ridges, whereas lowering of the melting temperature of the descending slab at a subduction zone forms seamounts at convergent margins (Staudigel & Clague, 2010). Younger seamounts are areas of active volcanism while older seamounts that are dormant and have ceased venting still act as "conduits for fluid exchange between the rock mantle subsurface and the ocean" (Emerson & Moyer, 2010). Seamounts are normally self-sufficient with their own hydrothermal system and magma supply.

Seamounts are features of the seafloor that can be millions of years old, often mirroring the tectonics on which they are situated. The relative geographic isolation of seamounts has led many scientists to propose the 'Centres of Endemism' model (O'Hara, 2007). This model states that because of their isolation, "seamounts accumulate a distinctive fauna through ancient vicariant and rare dispersal events, which is then followed by accelerated evolution through genetic processes operating on isolated small populations" (O'Hara, 2007). Endemism rates of 30–40% and up to 52% for benthic invertebrates have been reported in various studies. Endemism rates as high as 44% and

51% for fish and invertebrate species respectively, have been reported from the seamounts of the Nazca and Salas y Gómez submarine ridges in Chile (Brewin et al., 2007; Parin et al., 1997). Seamounts from the Norfolk Ridge, Lord Howe Rise, and Tasmania have been reported to have potentially 16–33% of endemic species (de Forges et al., 2000), with no similarity in community composition found over areas containing similar habitat types, latitude, and depth (de Forges et al., 2000). However, various other studies have shown lower rates of endemism for invertebrates. Examples include endemism rates of 0–4.7% for the ophiuroid fauna of the south-western Pacific (O'Hara, 2007), <3% for corals of North-east Atlantic seamounts (Hall-Spencer et al., 2007), and ~6% for epibenthic megafauna when comparing three seamounts off southern and central California, USA (Lundsten et al., 2009).

It is possible that sampling bias or sampling in species-rich communities may be responsible for high rates of reported endemism. Because most benthic communities have few species that are very common whilst the rest are rare, collection of more rare species from seamounts may make them seem endemic. Other reasons attributed to this misconception are due to lack or uneven effort in collecting data, intensive sampling around seamounts instead of continental slopes, and lack of taxonomic knowledge for many benthic species (Samadi et al., 2006). On balance, it appears as if there is insufficient evidence to support the notion that seamounts are centres of endemism (Rowden et al., 2010). However, benthic communities on and among seamounts can vary greatly as a result of environmental factors.

1.2 ENVIRONMENTAL FACTORS INFLUENCING BENTHIC COMMUNITIES ON SEAMOUNTS

A number of environmental factors affect species richness and composition of seamount communities. These include geographic location, seamount topography, substrate type, local hydrographic conditions, current velocities, light levels, productivity, biogeochemistry, water temperature, and hydrostatic pressure (Clark et al., 2010).

A number of these factors are related to water depth. The depth threshold distinguishing shallow-water vents from deep-water vents is 800 m (Tarasov et al., 2005). The amount of light, organic matter, temperature and oxygen content declines with increasing water depth, while hydrostatic pressure increases with depth. With increasing depth, the temperature and chemistry of venting fluids also change (Tarasov et al., 2005). Consequently, the variation of such environmental factors along a bathymetric gradient affects benthic community composition and richness (Lundsten et al., 2009). The composition of benthic communities is also dependent on the availability of appropriate substrata. For example, areas of seamounts that are unsedimented and surrounded by fast currents show a dominance of suspension-feeding assemblages, such as corals which require hard substrata for attachment (Genin et al., 1986). There can be many types of substrata on seamounts, both hard (e.g. pavement, ridges, walls, ledges, and tubes), and soft substrates (sand waves, ripples, soft, fine-grained sediments) (Auster et al., 2005). Such habitat complexity and heterogeneity affects the number of species, and overall structure of benthic assemblages (Raymore, 1982). For volcanic seamounts, the occurrences of hydrothermal activity as well as associated geological and geomorphological variables are important (O’Hara & Tittensor, 2010). Hydrothermal venting from volcanic seamounts supports assemblages that rely on chemosynthesis (Van Dover, 2010), and the spatial and temporal patterns in composition and diversity of benthic assemblages are dependent on individual physiological tolerances of the fauna to hydrothermal fluids (Podowski et al., 2009).

Due to the extremely variable environmental conditions present around seamounts, abiotic factors are assumed to play key roles in structuring benthic populations that rely on POC flux (Genin et al., 1986; Samadi et al., 2007; Wilson & Kaufman, 1987), and those that rely on chemoautotrophy (Fisher et al., 2007; Galkin, 1997; Podowski et al., 2009; Van Dover, 2010). Even though the subject of the current study is the structuring of benthic communities on a chemosynthetic seamount, the role of abiotic factors such as water depth, substrate type, and hydrothermal venting are considered in more detail below for seamounts that are both photosynthetically and chemosynthetically driven.

1.2.1 WATER DEPTH

Factors such as temperature, hydrostatic pressure, availability of nutrients, and light, which all vary with water depth, are vital in establishing distinct faunal zonations in the deep sea (Yeh & Drazen, 2008). Zonation is defined as “the depth interval of the benthic domain where the ecological conditions related to the main environmental factors are homogeneous, and where the boundary between two adjacent vertical zones corresponds to a sharp change in the living assemblage composition” (Terlizzi & Schiel, 2009).

The effect of bathymetric gradients is most prominent at upper bathyal depths along continental slopes (Hessler, 1987), where there may be an overlap in the distributions by multiple species. As a result, it would be expected that the relationship between species richness and diversity (defined by the number of species and the evenness of the number of individuals distributed within those species; Sanders, 1968) would be unimodal, such that diversity and richness are highest at intermediate depths of ~2000–3000 m (McClain et al., 2010) and decline at bathyal depths (Levin et al., 2001). Comparison of change in the species composition of assemblages on Davidson Seamount showed a 50% change in assemblage composition for every 1500 m of depth, but no evidence was found of a significant decrease in species diversity or density with increasing depth (McClain et al., 2010).

Light and nutrient levels enhance productivity for seamounts that have summit depths stretching into the euphotic zone (Comeau et al., 1995; Dower et al., 1992; Genin & Boehlert, 1985). Even though low plankton residence times of 2.5–3 weeks over the summit of seamounts in the euphotic zone (Dower et al., 1992) may not be sufficient to sustain higher trophic levels, it is possible that the presence of certain hydrodynamic conditions (seamount-induced currents, internal waves) at shallow seamounts promotes the transfer of energy to intermediate and deeper waters. A good example of this and its effect on benthic communities can be seen at Jasper Seamount. This seamount is an oceanic intraplate volcano (Pringle et al., 1991) that forms part of the Fieberling-Guadalupe seamount chain off the coast of Baja California, Mexico (Konter et al., 2010). Here, the high abundance of suspension-feeders such as corals, anemones, and tunicates has largely been attributed to the seamount's ability to trap concentrations of food and larvae through water-flow impinging on the seamount (Genin et al., 1986). These conditions also support aggregations of local populations of demersal fish species (pelagic armorhead and alfonsino) at several seamounts, such as those in the Hawaiian-Emperor Ridge (Genin, 2004).

Benthic communities are largely sustained by organic matter sinking from the euphotic zone (Lampitt & Antia, 1997). The availability of particulate organic carbon (POC) with increasing depth is largely a reflection of surface productivity (Graf, 1989). Therefore, it would be expected that seasonal fluctuation in the amount of POC that is available to the benthos is directly proportional to the seasonal cycles in primary productivity. The flux of POC also varies with latitude, with the quantity of POC available to benthos in equatorial oligotrophic waters being much lower compared to benthos located under eutrophic waters at higher latitudes. Benthic response to POC arriving at the seafloor is rapid (Graf, 1989), with only 1–10% of the proportion of primary productivity left un-grazed by benthos in subtropical and tropical waters, compared to 30–96% in higher latitudes (Ambrose & Renaud, 1995). Benthic invertebrate communities exhibit changes in biomass and abundance through syncing of reproductive cycles (seasonal reproduction and recruitment) with seasonal influxes of POC to the seafloor (Gage & Tyler, 1985). The availability of POC also dictates growth rates, with most deep-sea mega fauna showing increased growth rates according to pulsed POC events (e.g *Echinus affinis*; Gage & Tyler, 1985).

In contrast, areas of the seafloor located under oligotrophic waters are limited in POC. The amount of POC arriving at the seafloor at eutrophic and oligotrophic sites to provide food for benthic organisms shows a decrease with increasing depth (Levin et al., 2001), largely because of mineralisation while descending through the water column (Desbruyères et al., 2000; Vanreusel et al., 2010). This results in a general decline in population densities extending from the continental shelf to the abyss (Rex & Etter, 2010). Although limitations in food can affect local species diversity by the presence of more opportunistic species being capable at adapting and taking advantage of the food-limited environment (Levin et al., 2001), the overall benthic diversity in the deep sea is generally high (Rex & Etter, 2010).

Amounts of POC flux to areas around deep-water seamounts of the central Pacific and eastern Pacific range from 0.4–1.7 mg C m^{-2} day^{-1} and 2–3 mg C m^{-2} day^{-1} respectively (Levin & Thomas, 1989). A low quantity of POC around Atlantic seamounts (Azores) translates to low species richness and abundances of infaunal organisms such as polychaetes, in comparison to other soft-bottom areas of the deep sea (Gillet & Dauvin, 2000). Furthermore, dominance by surface-feeding macrofauna instead of sub-surface feeders is seen due to the low quantities of POC at some seamounts (Levin & Thomas, 1989). Benthic fauna living around chemosynthetic seamounts/hydrothermal vents rely on products of microbial chemoautotrophy, and as such the decline in the amount of POC flux through the water column with increasing depth has no impacts on the overall patterns of abundances (Neubert et al., 2006). However, other environmental conditions (e.g. oxygen content) arising as a result of increasing water depth can impact faunal distributions.

Bottom-water oxygen concentration ranges from 0–7 ml $litre^{-1}$ in the deep sea, but can drop to as low as 0.5 ml $litre^{-1}$ between water depths of 100–1200 m (Levin et al., 1991; Levin et al., 2001). Where oxygen levels are this low, they are called Oxygen Minimum Zones (OMZs), and they usually occur beneath highly productive waters (Levin et al., 2001). Assemblages on seamounts within an OMZ show low species richness but high dominance (Levin et al., 1991). A good example is Volcano 7 in the eastern Pacific Ocean that has an OMZ on its summit (750–800 m). Biological assemblages on the summit are different to those at flanks depths, presumably due to differences in faunal tolerance to low oxygen levels (Levin et al., 1991).

Variable levels of dissolved oxygen and subsequent adaptations of fauna are not unique to seamounts relying on POC flux. Volcanic cones such as Nafanua, located within the summit crater of the Vailulu’u Seamount (Samoan archipelago), exhibit dissolved oxygen content of 2.5–3.0 mg $litre^{-1}$ between water depths of 600–750 m (Staudigel et al., 2006). At depths of over 740 m, highly turbid and acidic water carried due to anticyclonic currents from the ‘Moat of Death’ (East pit crater), creates low pH and low oxygen conditions. Such toxic conditions are tolerable to specialised polychaete species (Staudigel et al., 2006) that feed on crustaceans and fish that are entrained in anticyclonic currents and deposited in the moat.

Water depth is not a direct driver of species richness, diversity, and community composition because it acts by way of variation in physico-chemical parameters (hydrostatic pressure, current velocity, oxygen concentration) that influence species range distributions (Clark et al., 2010; McClain et al., 2010). But examinations of faunal change with depth are a useful way to understand what environmental factors influence species distributions in the deep sea (Olabarria, 2006; Rowe & Menzies, 1969). It is somewhat surprising then that relatively few studies have examined changes in benthic community structure with changes in water depth on seamounts. Depth-related studies of benthic fauna on an individual seamount are limited to those by Lundsten et al. (2009) and McClain et al. (2010).

1.2.2 SUBSTRATE HETEROGENEITY

Seamounts of a volcanic nature have predominantly rocky or hard substrata, while flat-topped eroded seamounts and those formed by tectonic uplift can have extensive areas of soft-sediment habitats (e.g. Horizon Guyot; Lonsdale et al., 1972). Soft sediments on seamounts are often the products of volcanic detritus, biogenic, and terrigenous sediments (Smith et al., 1989).

Axial Seamount on the Juan de Fuca Ridge (JdFR) in the North-East Pacific has been observed to support dense communities of suspension-feeders on the vertical walls of the caldera (Marcus et al., 2009). The presence of hard and rocky substrates, along with strong currents to sweep away sediments, facilitates the formation of benthic assemblages of suspension-feeders. Hard substrates provide a solid and erosion-free substratum for taxa such as corals and sponges to colonise and grow (Genin et al, 1986; Kaufmann et al., 1989; Levin & Thomas, 1989; Stocks, 2004). The presence of strong bottom currents aids the transport of large quantities of food particles, which in turn support large communities of suspension-feeding taxa (Young, 2009). Corals under particular conditions can form extensive reefs on hard substrata such as rocky outcrops, which can provide habitat for other invertebrate organisms, thereby leading to differences in community composition within and among seamounts (O'Hara et al., 2008; Tittensor et al., 2009).

Volcanic seamounts that support hydrothermalism produce substrates that are colonised by specialist taxa. Sulphide chimneys formed from active hydrothermalism support the settlement and attachment of many invertebrate fauna. Examples include black smoker chimneys of the Kairei vent field (Central Indian Ocean) that provide substrate for actiniarians, mytilids such as *Bathymodiolus marisindicus*, and scaly-foot gastropods (Cubelio et al., 2008); and sulphide chimneys in the Nolan's Nook and Fred's Fortress field (East Pacific Rise) which consist of few specialist species such as *Riftia pachyptila*, *Alvinella pompejana*, and bythograeid crabs (Hey et al., 2006). The change in frequency of volcanism is associated with substrate differences around volcanic seamounts/hydrothermal vents. Consequently, this reflects on the differences in species composition occupying those substrate classes. Diffuse-flow anhydrite chimneys ('Ghost chimneys') in the East Pacific Rise (EPR) vent fields support vent megafauna such as bathymodiolid mussels, bythograeid crabs, gastropods, anemones, and two species of siboglinid tubeworms (Hey et al., 2006). The vent field consists of "low-relief lobate glassy pillows with extensive hydrothermal alteration", that support microbial mats and actinostolids (Hey et al., 2006). Elsewhere, pillow basalts from vent sites of the Eastern Lau Spreading Centre support dense assemblages of zoanthids, which inhabit areas of low-temperature diffuse venting through fissures in the basalt (Zelnio et al., 2009).

Seamounts can also have extensive areas that are heavily sedimented. The presence of strong and periodic currents can affect the texture and stability of sediments, as well as affecting its organic content (Levin et al., 1994). Variation in these sediment characteristics leads to variation in abundance and species composition of infaunal organisms (Levin et al., 1994). Polychaetes are common infaunal organisms on most seamounts, and can account for up to 70% of individuals in macrofaunal communities (e.g. NE Atlantic seamounts; Surugiu et al., 2008). Polychaete standing stock is strongly correlated with high organic material content, which corresponds to the amount of sediment (Chivers et al., 2013). Sedimentation also greatly affects the diversity and composition of polychaetes. Extensive sedimentation supports deposit and sub-surface deposit-feeding polychaetes in the deep sea, that rely on carbon flux from surface waters. However, on seamounts where carbon flux is captured by organisms such as corals, anemones, and sponges, a change in the community composition of polychaetes has been observed. For example, a shift from deposit-feeding to predatory behaviour, with living and feeding on sponges is not uncommon for carnivorous polychaetes (Surugiu et al., 2008) in areas of low carbon flux.

When bottom-current speeds are low and sediment is deposited, large bioturbating organisms can dominate soft sediment habitats, as indicated by the biogenic structures they create (pits, burrows, mounds, trails, and fecal casts) on seamounts (Kaufmann et al., 1989). Taxa that make such ‘life traces’ or lebensspurren include holothurians, asteroids, ophiuroids, and gastropods. These organisms aid in nutrient mixing by their feeding and burrowing activities (Levin & Thomas, 1989).

Seamounts have patchy habitats which are composed of different substrate types. Because certain taxa are characteristic of those substrata, the heterogeneity of the substrate will influence the overall diversity found on a seamount. Studies of seamounts to date have usually described assemblage structure for predominantly hard or soft substrate types. There is a lack of study of changes in benthic structure with substrate type and how this might affect species richness on a spatial scale of an individual seamount (but see Raymore, 1982).

1.2.3 HYDROTHERMAL VENTING

Hydrothermal venting takes the form of black smoker hydrothermal vents, white smoker vents, and low-temperature diffuse venting on seamounts. Seamounts occurring along mid-ocean ridges (e.g. the northern EPR or Mid-Atlantic Ridge) are a result of hydrothermal circulation, largely induced by heat produced from the magma chamber (Tsurumi & Tunnicliffe, 2001). In comparison, seamounts at seafloor-spreading centres are characterised by production of pillow and sheet lava at depths of over 1000 m. Similar seamounts can be found along island arcs where subduction of oceanic crust under the continental crust leads to a release of carbon dioxide and other metal-rich fluids due to melting of rocks (Carey & Sigurdsson, 2007).

Seamounts with active hydrothermal venting support communities that rely on chemosynthesis. Primary production through chemosynthesis can support large populations of bivalves, vestimentiferan worms, and other taxa (Lutz & Kennish, 1993). Together, bivalves and tubeworms attain high biomasses around vent openings (Lutz & Kennish, 1993), followed by crustaceans and polychaetes (Wolff, 2005). Variability in a suite of environmental conditions (temperature, hydrothermal fluid flux, pH) over the lifespan of a vent leads to changes in the abundance and composition of the surrounding vent community, over particular spatial and temporal scales (Fisher et al., 2007; Lutz & Kennish, 1993). Habitats are created at centimetre and metre scales away from a vent opening due to steep gradients between conditions such as temperature, pH, oxygen content, and sulphide content, compared to ambient seawater (Fisher et al., 2007).

Spatial zonation

Benthic communities show a high degree of faunal zonation in response to differences in temperature and water chemistry, as well as the style of venting. For example, vent communities of the EPR are dominated by alvinellids and other polychaetes in areas of active venting (30–400 °C, H_2S concentrations of 12 mmol kg^{-1}), whereas diffuse venting areas (<30 °C, H_2S concentrations of 0.20–0.30 mmol kg^{-1}) are dominated by vestimentiferan tubeworms (Demina, 2010; Hunt et al., 2004; Mills et al., 2007). Bivalves such as bathymodiolid mussels, dominate areas where vent fluids are more diluted and have temperatures of less than 2 °C. The latter are also inhabited by other suspension feeders, such as barnacles and serpulids. Similarly, the White Lady hydrothermal field in the North Fiji Basin has a combination of both high temperature (91 °C and 296 °C) and warm, diffuse fluid-venting (~31 °C), which has led to different assemblages occupying the two habitats. For example, the anhydrite chimney walls in the presence of hot hydrothermal fluids are dominated by alvinellid polychaetes of the genus *Paralvinella*, whereas areas of low temperature (6.92–13.33 °C) diffuse venting show the presence of gastropods such as *Ifremeria nautilei* and *Alviniconcha hessleri*. Naganuma & Heki (1994) also found a dominance of bathymodiolid mussels at the base and walls of chimneys, where recorded fluid temperatures were 8.51–21.36 °C. Areas away from the venting field were dominated by large populations of the sessile cirripede *Eochionelasmus ohtai* along with the stalked cirripede *Neoleopas* sp. attached to basaltic rocks.

In addition to differences in vent temperature and chemistry, the distribution of benthic assemblages is also dependent on related biological factors (Hessler et al., 1988). Biological studies by Naganuma & Heki (1994) found higher bacterio-plankton abundance at active chimneys in the White Lady field in response to manganese concentration in plume waters. The high abundance of such plume-associated bacteria enhances the abundance of filter feeders such as bathymodiolid mussels and barnacles (Naganuma & Heki, 1994).

Temporal succession

Temporal changes in venting intensity on a seamount lead to varying degrees of succession and settlement of taxa, that mirror their individual physiological tolerances to the emanating hydrothermal fluids. JdFR vent sites undergo rapid changes in vent formation, such that species compositions on new vents start to resemble older vent communities within three years of their formation (Tsurumi & Tunnicliffe, 2003).

As on the JdFR, vents on EPR undergo changes in the flow of hydrothermal vent fluids, which is reflected in a succession of organisms colonising such areas. Successional sequence at vents on the EPR follows the initial colonisation by the tubeworm *Tevia jerichonana* that is replaced by *R. pachyptila.* The latter is subsequently replaced by bathymodiolid mussels (Hunt et al., 2004). In other studies, the giant tubeworm *A. pompejana* is thought to play a pivotal role by assisting in the establishment and settlement of other less tolerant species, by "modifying flow patterns, fluid composition, mineral precipitation, and the degree of hydrothermal mixing with seawater" (Pradillon et al., 2005).

Diffuse-flow vents

Areas that show evidence of fluctuations (and eventual cessation) of active venting have different community composition and abundances. This is largely due to constraints on nutrition from reduced venting activity, thereby prompting taxa to adapt to fluxes in hydrothermal flow (Podowski et al., 2009). The community structure shifts from largely sessile organisms such as vestimentiferan worms, as seen in areas of active venting in EPR, to mobile species such as bathymodiolid mussels in areas with diffuse venting (Podowski et al., 2009). Mobility aids in adapting and changing spatial distributions in response to changes in hydrothermal fluid flow. An example of such a community is seen in the diffuse-flow vents in the Lau back-arc Basin that are dominated by the bathymodiolin mussel *Bathymodiolus brevior* and two provannid snails, *Alviniconcha* sp. and *I. nautilei* (Podowski et al., 2009). While the benthic community composition remains relatively structured and characterised by symbiont-carrying taxa that dominate areas near venting, the community composition changes with distance from vents, with more mobile and non-symbiont taxa dominating such areas. Diffuse-flow areas are largely dominated by molluscan taxa (Kim & Hammerstrom, 2012), with certain gastropods (e.g. *Alviniconcha* spp., *I. nautilei*) showing greater tolerance to higher temperatures and sulphide concentrations than other species (e.g. *B. brevior*).

Peripheral taxa

Away from sites of low-temperature venting, extensive films of bacterial mats are common that co-occur with crustaceans, demosponges, large fish, and cephalopods (e.g. Vailulu’u Seamount in Samoa; Staudigel et al., 2006). Similarly, at distances of over 10 m from the site of venting in the Lau back-arc Basin, the species composition changes to give way to non-vent fauna such as filter-feeders (e.g. anemones, sponges, echinoderms at Lau back-arc Basin; Kim & Hammerstrom, 2012), mat-grazers (e.g. bresiliid shrimps, galatheids, lithodids; Desbruyères et al., 1994), scavengers (decapod crabs), and larger megafauna such as squids and fish. The harsh physico-chemical conditions of volcanic seamounts and vents typically restrict the distributions and abundances of larger megafauna such as fish. However, fish such as zoarcids and synaphobranchids have been reported from vent periphery sites (Micheli et al., 2002).

These taxa form an essential part of vent megafauna by grazing on vent gastropods (limpets) and feeding on crustaceans. The diversity of fish found around vent sites on seamounts is typically low, but there appears to be high endemism (Biscoito et al., 2002), with endemism rates of up to 12% reported from well-studied regions such as the Hawaiian Ridge, Mid-Pacific Mountains, Kyushu-Palau Ridge, and Verma Seamount (de Forges et al., 2000).

Cessation of venting allows the colonisation of a range of taxa that find the absence of hydrothermal fluids conducive for settlement and survival. For instance, old sulphide mounds and chimneys that have ceased venting offer attachment and hard substrata for non-vent suspension-feeding organisms. These invertebrate communities rely on products of chemosynthesis from nearby venting systems (Van Dover, 2010). Investigations of carbon and nitrogen isotopic composition by Erickson et al. (2009) on the invertebrates of the Manus Basin (bamboo corals, stalked barnacles) showed that such invertebrates attained high abundance and biomass, due to their primary reliance on nutrition from microbial chemoautotrophic production. In addition, the presence of hydroids and cladorhizid sponges at these sites was indicative of feeding on microzooplankton and other particulate organic material in the water column.

Hydrothermal venting on seamounts gives rise to a mosaic of habitats due to temporal variation in environmental conditions of the vent sites, as well as changes in the physical structure of mineral substrate from variability in hydrothermal fluid flow. This spatio-temporal variability has a direct impact on the species assemblage of seamounts (Matabos et al., 2008). Of the ~100,000 seamounts worldwide (Wessel et al., 2010), around 55 deep-water (> 200 m deep) seamounts with hydrothermal venting have had their biological communities described (Figure 1.1; Tarasov et al., 2005). However, there are many other known volcanic seamounts that are known to have hydrothermal venting, but lack adequate biological studies (Tarasov et al., 2005). Descriptions of the benthic communities of more seamounts with hydrothermal venting are required to better understand how venting influences the patterns of faunal composition on seamounts.

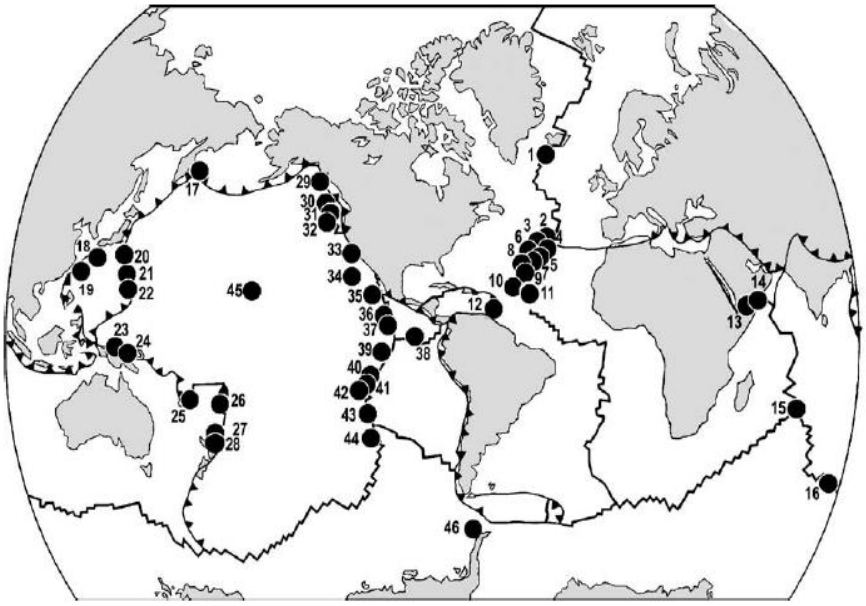


Figure 1.1: Location of deep-sea (> 200 m) hydrothermal vents with known data on biota (Tarasov et al., 2005).

1– Steinaholl, **2**– Menez Gwen, **3**– Lucky Strike, **4**– Mount Saldanha, **5**– Rainbow, **6**– Lost City, **7**– Broken Spur, **8**– TAG, **9**– Snake Pit, **10**– Logatchev, **11**–Ashadze, **12**– Kick’em Jenny Volcano, Grenada, **13**– Gulf of Aden, **14**– Tadjoura Rift, **15**– Rodryges Triple Junction (Kairei Edmond Fields), **16**– Amsterdam–St. Paul Plateau, **17**– Piip’s Volcano, **18**– Okinawa Trough (Fields Minami-Ensei Knoll, Iheya Ridge, Izena Caldron, Hatoma Knoll), **19**– Daiyon Knoll, **20**– Ogasawara North (Fields Myojin Knoll, Sumisi Caldera, Seamounts Suiyo, Moknyo and Kaikata), **21**– Ogasawara South (Nikko Seamount), **22**– Mariana Trough, North and South (Fields Daini Kasuga Seamount, Central Mariana Trough, South Mariana Ridge), **23**– Manus Basin, **24**– Edison Seamount, **25**– North Fiji Basin, **26**– Lau Basin, **27-28**– Kermadec Ridge (Fields Rumbe III and Rumble V, Brothers Caldera and Macauley Cone), **29**– Explorer Ridge, **30**– Juan de Fuca, **31-32**– Gorda Ridge, **33**– Guaymas Basin, **34**– EPR 21°N, **35**– EPR 13°N, **36**– EPR 11°N, **37**– EPR 9°N, **38**– Galapagos Rift, **39**– EPR 7°S, **40**– EPR 17°S, **41**– EPR 21°S, **42**– EPR 23°S (and Pito Seamount, Easter Microplate), **43**– EPR 27-32°S, **44**– Pacific–Antarctic Ridge 37°S, **45**– Loihi Seamount, **46**– Hook Ridge, Bransfield Strait

1.3 THREATS TO SEAMOUNTS

In recent decades, decreasing availability of land-based resources along with ever-advancing technology has led to increased interest in the exploration and exploitation of deep-sea systems. Unfortunately, such interest tends to outpace acquiring adequate scientific knowledge of such ecosystems (Ramirez-Llodora et al., 2011). Seamounts are no exception to this trend. The main anthropogenic activity on seamounts is fishing and, potentially, mining for mineral resources (Ramirez-Llodra et al., 2011).

In addition to the direct impact of fishing and the potential impacts from mining, other threats to seamount communities come from lost fishing gear, marine litter, and climate change related impacts. Trawl nets caught and lost on seamounts may continue ghost fishing for a long time (Gregory, 2009). Such gear can also lead to smothering of epifauna and infauna (Clark & Koslow, 2007; Clark & O'Driscoll, 2003). Marine litter in the form of plastic and glass (beer bottles) can be abundant on seamounts, with up to an average of 160 bottles km^{-2} reported on the summit of Condor Seamount in the Azores (Pham et al., 2013). Currently, no information exists on the impact of marine litter on seamount ecosystems (Pham et al., 2013).

Seamounts and their respective deep-sea biological communities are also vulnerable to changes in climate and ocean chemistry (Ramirez-Llodra, 2011). Atmospheric carbon dioxide (CO_2) levels are currently at levels significantly higher than in pre-industrial times. By being a natural carbon sink and absorbing most of the anthropogenic carbon, the oceans are now facing rising effects from acidification as a result of decreasing pH of seawater, with a decrease of 0.1 unit since the Industrial Revolution (IPCC, 2007; IPCC, 2013). Continuous release of anthropogenic CO_2 into the atmosphere is expected to lead to a decrease in ocean pH by up to 0.7 units by the end of this century (Caldeira & Wickett, 2003; Orr et al., 2005), which has serious implications for calcifying organisms due to a decline in carbonate ion concentration (Orr et al., 2005).

There are limited studies and experiments on calcification rates of deep-sea calcifying taxa. However, some studies have revealed variable survival rates in different taxa under low pH stress. For example, experiments by Barry et al. (2013) on abyssal megafauna off the central California coast. Calcifying organisms such as deep-water echinoderms that use high magnesium calcite for skeleton formation are highly sensitive to changes in pH concentration, and as such do not occur in areas that are under-saturated or in areas with low pH (Barry et al., 2013).These deep-sea taxa are at risk from acidification (Andersson et al., 2008; Ries et al., 2009), and have been found to be less resilient than other megafauna such as crustaceans, larger fish and molluscs due to physiological differences (Barry et al., 2013). Calcifying organisms are also at risk from changes in the lysocline depth due to ocean acidification (Hofmann et al., 2010). An increase in anthropogenic CO_2 in the surface waters would effectively lead to changes in carbonate saturation depths (Orr et al., 2005) within the next 50–100 years. The impact on seamount communities from ocean acidification is not certain, and has not been studied in detail. However, given the depths that seamounts occur and the bathymetric range preference of many deep-sea calcifying taxa in response to calcite saturation (Hofmann et al., 2010), it is very likely that these taxa would be the most vulnerable to shallowing of saturation boundaries through the water column. For instance, serious consequences exist for corals on deep-water seamounts which would be at an increased risk from increased dissolution, following the shoaling of saturation boundaries (Hofmann et al., 2010).

Corals produce calcium carbonate skeletons, and the impacts from increased acidification and other factors are already evident from shallow-water coral reefs in the Great Barrier Reef (De'ath et al., 2009). Similar impacts can be expected to be seen in deep-water scleractinian corals of the North Atlantic, which is predicted to undergo the largest change in saturation boundaries by the year 2100, due to shoaling by 1–2 km (Hofmann et al., 2010). Cold-water corals on seamounts such as *Lophelia pertusa* and *Solenosmilia variablis* can form dense thickets, isolated colonies or even extensive reefs that can be kilometres in length. These reefs provide complex habitat in the form of live coral framework and coral rubble which contributes to high faunal diversity of benthic invertebrates (O'Hara et al., 2008; Tittensor et al., 2009). Rising acidification would prevent such corals to form essential skeletal structures, which could have a cascading effect in the deep-sea ecosystem, including seamounts (Hofmann et al., 2010; Tittensor et al., 2010). In addition, rising temperatures from global climate change could alter oceanic currents, primary productivity levels, and carbon flux, which could in turn affect cold-water corals that do not rely on symbiotic algae for nutrition (IPCC, 2007). Furthermore, life-history characteristics such as slow growth and long lifespans

(Koslow et al., 2001) can potentially make cold-water corals on seamounts more vulnerable to climate change impacts.

While climate change and impacts from ocean acidification for seamount communities are likely to be widespread, the threat from benthic trawling is still very much in existence alongside the imminent potential impact on seamount communities from mining for mineral resources.

1.3.1 BENTHIC TRAWLING

Commercial fisheries often target mid-and deepwater fish species such as pelagic armorhead, redfish, alfonsino, pink maomao, orange roughy, and oreosomatids that form dense aggregations over seamounts for feeding and spawning (Boehlert & Sasaki, 1988; Hubbs, 1959; Koslow, 1997). Trawling over seamounts can be intensive with individual seamounts being subjected to 100s to 1000s of individual trawl tows (Althaus et al., 2009). Owing to their topography and predominant hard substrate, benthic assemblages on seamount are primarily composed of suspension-feeding taxa (such as corals) that are vulnerable to such physical disturbances (Koslow et al., 2001).

In New Zealand, commercial fishing for seamount-aggregating fish species, such as orange roughy, oreos, cardinalfish, and alfonsino contributes to a total catch amount of 40,000–45,000 tonnes each year (Clark & O’Driscoll, 2003), with trawling occurring primarily at depths of 600–1200 m (Clark, 1999). Bottom-trawling on seamounts for fish species such as orange roughy on the Chatham Rise for over two decades has given rise to large bycatch of sessile epifauna such as deep-water corals (Probert et al., 1997). The effects from bottom-trawling include creation of groves and gouges into the substrate due to the heavy trawl doors (Clark & Koslow, 2007), smothering of infauna from sediment resuspension, crushing of buried fauna (Clark & O’Driscoll, 2003), scraping, and ploughing of the seabed by trawl doors on hard substrates. Such impacts are all detrimental to habitat-forming corals and associated benthic communities (Clark & Rowden, 2009; Koslow et al., 2001). Scleractinian corals form an important component of seamount communities, by providing habitat complexity for benthic sessile and mobile assemblages, such as sponges, polychaetes, bryozoans, echinoderms, gastropods, bivalves, anemones, and foraminiferans (Probert et al., 1997). Repeated and intensive trawl tows over seamounts, therefore, lead to extensive areas of live coral-cover and associated benthic assemblages being stripped away (Koslow et al., 2001).

In New Zealand and Australia, compare-and-contrast studies of seamounts have revealed significant differences in benthic community structure between seamounts that have been fished and those that have either been lightly fished or unfished. Unfished seamounts were found to be more speciose than heavily fished seamounts (Koslow et al., 2001). Heavily fished seamounts in the Chatham Rise, such as Graveyard and Morgue seamounts have extensive areas of barren seafloor devoid of any coral cover and conspicuous megafauna compared to those that have been lightly fished/unfished. The latter show more live coral cover, and, therefore, more signs of invertebrate life (Clark & O'Driscoll, 2003; Clark & Rowden, 2009). Community shifts have been reported with fished seamounts transforming into being either urchin-dominated (Koslow et al., 2001) or dominated by sponges and anemones (Althaus et al., 2009).

Life-histories of seamount benthic organisms are largely unknown. However, certain species appear to be long-lived and slow-growing (Althaus et al., 2009; Koslow et al., 2001). Most deep-sea corals are slow growers (Van Dover, 2010), with growth rates of 4–35 mm yr^{-1} (Van Dover, 2010) as well as low growth rates of 0.18 mm yr^{-1} reported for bamboo coral colonies on New Zealand seamounts (Tracey et al., 2007). Other examples include those of calcareous sponges such as *Vaceletia* spp. found on seamounts of the Norfolk Ridge, that grow at the rate of 11 mm per 100 years (Vacelet et al., 1992). Similarly, reef-building deep-water corals such as *L. pertusa* that also occur on several seamounts(e.g. Galicia Bank, North-west Spain; Duineveld et al., 2004) grow at a rate of 4.1–7.5 mm yr^{-1}, and as such are estimated to be 200–360 years old (Wilson, 1979). The life-history characteristics make recovery of such deep-water corals and their associated benthic communities likely to be on decadal time scales, even after cessation of any trawling activity (Althaus et al., 2009; Williams et al., 2010).

Quantifying effects from bottom-trawling activities is difficult because of a lack of adequate baseline data on deep-water coral communities on seamounts, as well as knowledge on life-history traits of such benthic taxa (Althaus et al., 2009). This is largely due to the fact that offshore bottom-trawling commences before any habitat assessments could be conducted in most parts of the world (Hall-Spencer et al., 2007). Aside from gear modifications and closure of fishing areas to trawling, it is important to regularly monitor changes in benthic communities on seamounts over spatial and temporal scales that will aid in management of such fragile ecosystems. Prior to establishing monitoring surveys, it is necessary to conduct studies that establish baseline patterns of community structure and distribution.

1.3.2 SEAFLOOR MINING

Methods for extracting cobalt-rich crusts as well as poly-metallic sulphides on seamounts are being explored extensively, due to a shortage of land-based mineral resources. Crust deposits occur on the summits and flanks of seamounts at depths of 1500–2500 m (Glasby, 2002; Hein et al., 2000), and have economic potential due to their elevated concentrations of manganese, cobalt, nickel, lead, and rare earth elements (Hein et al., 2000; Hein et al., 2009). These cobalt-rich crusts are formed when minerals precipitate from hydrothermal fluids and interact with ambient seawater to form thick pavements on rocky surfaces, primarily on seamounts of the western and Central Pacific Ocean (Hein et al., 1988; Hein et al., 2009). The accumulation of cobalt-rich crusts on seamounts and active mountain chains is estimated to be able to meet over 20% of the world's cobalt demand (Rona, 2003). However, it is seamounts that have polymetallic sulphide deposits rich in gold, silver, zinc, and lead (Carey & Sigurdsson, 2007; Hoagland et al., 2010) that are of greater commercial interest at present.

Seafloor Massive Sulphide (SMS) deposits are sulphur-rich mineral deposits that form by precipitating out of hydrothermal fluids when the latter mixes with ambient seawater at hydrothermal vent sites (Hoagland et al., 2010). Such deposits are found in different tectonic settings such as convergent, divergent, and subduction-related regions (Herzig & Hannington, 2000).The mining of SMS deposits is currently the centre of an advanced exploration stage by two mining companies – Neptune, and Nautilus Minerals. Both companies have exploration licences for exploring vent areas of the

Kermadec volcanic arc, New Zealand (Neptune Minerals) and Solwara-1, Papua New Guinea (Nautilus Minerals) (de Ronde & Leybourne, 2007).

Most mining operations are likely to be limited to areas of older volcanic regions or areas that have ceased active venting, which have the advantage of having remained stable over time to support thicker and high-grade crusts (Hein et al., 2009), as well as to minimise impacts to hydrothermal vent communities (Van Dover, 2011). Up to 680 km^2 of a seamount area would be mined in 20 years (Hein et al., 2009), which could possibly include areas of diffuse-flow. However, diffuse emissions from cracks in the basalt/andesite substrate that spread over larger distances have been observed to be often surrounded by distinct high-biomass benthic assemblages (Fisher et al., 2007). Many studies have also pointed out the existence of such communities at inactive vent sites that could be supported by chemoautotrophically-based food webs from nearby venting (Van Dover, 2010). The diversity in these areas has been reported to be relatively high, dominated by a range of suspension-feeders such as corals, barnacles, and sponges (Van Dover, 2010).

The effects of mining are estimated to be similar to those from bottom trawling (Clark et al., 2012). Effects on the benthic community from mining disturbances range from substrate removal, dislodgment of sessile fauna, disruption of sediment and sediment suspension leading to smothering, and other effects from waste disposal through the discharge of return water (Levin et al., 2009). It is apparent that seamounts are now being viewed as repositories of precious minerals, and potentially may trigger activity analogous to the gold rushes of the 19th century (Van Dover, 2011). Over the 20-year life of a mine, it is unknown what impacts mining would have on the local benthic ecosystem. In order to better understand the potential impact from anthropogenic activities on seamount communities, it is important to record the natural state of these benthic communities before any mining activities commence.

1.4 STUDY REGION

The Tonga-Kermadec volcanic arc is ~2500 km long and forms part of the Lau-Havre-Taupo arc-backarc complex, arising from the convergence of the Pacific and Australian plates (de Ronde et al., 2001). The Kermadec volcanic arc is the southern 1220 km part of the Tonga-Kermadec volcanic arc (de Ronde et al., 2005). The volcanoes of the Kermadec volcanic arc consist of active and late Quaternary andesite and basalt (Hockstein et al., 1974), and were formed around 5 million years ago, as a result of “underthrusting of the oceanic crust”, raising of the “upper trench-facing slope”, and the depression of the Kermadec Trench to its current depth (Karig, 1970).

1.4.1 THE KERMADEC VOLCANIC ARC

The southern part of the Kermadec volcanic arc is dominated by twelve submarine volcanoes between 30°S and 37°S (de Ronde et al., 2005). The southern Kermadec volcanic arc is ~260 km long, with an average height of 900–2180 m and summit depths of 220–1350 m for volcanoes in this part of the arc (Massoth et al., 2003). Hydrothermal activity has been observed for seven southern Kermadec volcanoes: Brothers, Rumble III, Rumble V, Tangaroa, Clark, Rumble II West, and Healy (Massoth et al., 2003).

The 580 km mid-Kermadec volcanic arc consists of 12 volcanic centres, most of which are stratovolcanoes (Graham et al., 2008). The mid-Kermadec volcanic arc is composed of a mix of submarine and sub-aerial volcanoes, along with submarine calderas composed largely of silica (Shane & Wright, 2011). The term ‘caldera’ used for this study is defined similar to Lipman (1997), as a geological feature created “by some form of roof collapse over an underlying shallow magma reservoir”. Sub-aerial volcanoes include those that constitute the Kermadec Islands, formed by the emergent summits of Raoul, Macauley, and Curtis (Graham et al., 2008). Submarine volcanoes that lie in the northern section of the Kermadec volcanic arc and south of the Tonga arc (between 28.59°S 177.82°W and 25.19°S 177.06°W) include Hinetapeka, “OP”, Putoto, Gamble, Rakahore, Hinepuia, Monowai, “U”, and “V” (Graham et al., 2008).

Previous biological studies

Published results of ecological research on the seamounts of the Kermadec volcanic arc are relatively limited. Preliminary reports on biological investigations for three southern Kermadec seamounts, namely Brothers, Rumble III, and Rumble V, revealed highly variable species diversity, richness, and substratum type within and between the three seamounts (Clark & O’Shea, 2001). Large dissimilarities in taxa between areas of active and inactive venting were also observed. Further reporting by Rowden et al. (2003) on these three volcanoes of the southern Kermadec volcanic arc revealed that species richness varied between the three seamounts, with Rumble V showing a higher mean number of species than Rumble III and Brothers. Sampling for macro-invertebrates revealed 308 species from all three seamounts, with an estimated 5.5% of the species undescribed for the New Zealand region (Rowden et al., 2003). Such a result would indicate an apparently high endemicity within the southern Kermadec volcanic arc fauna. However, claims of high endemism do not seem appropriate due to the absence of other comparative studies on seamounts within the rest of the Kermadec volcanic arc, as well as for the rest of the New Zealand region with similar habitats/ substrata/ topography (Rowden et al., 2003).

Nevertheless, some endemism among the vent fauna has been reported. Examples include the chemosynthetic mussel *Gigantidas gladius* that occurs on Rumble III and Rumble V volcanoes (von Cosel & Marshall, 2003), along with the vent-associated bryozoan *Parachnoidea rowdeni* and the kamptozoan *Barentsia bulbosa* that encrusts live *G. gladius* shells (Gordon, 2013). Other vent-related taxa that are thought to be endemic to the Kermadec arc seamounts include the lucinid clam *Bathyaustriella thionipta* found at Macauley Caldera which is located on the north-western submarine flank of the sub-aerial Macauley Island (Glover et al., 2004), the vent mussel *Vulcanidas insolatus* from shallow (140–200 m) gas-venting summit sites on Macauley and Giggenbach volcanoes (Van Cosel & Marshall, 2010), the predatory asteroid *Sclerasterias eructans* from Rumble III and Rumble V volcanoes (Mah & Foltz, 2011;

McKnight, 2006), and the bythograeid crab *Gandalfus puia* from Macauley Caldera, Rumble III, and Brothers volcanoes (McLay, 2007).

Certain vent taxa are generally widespread at the genus level elsewhere in the North Pacific or southwest Pacific Ocean, but endemic to the Kermadec seamounts at the species level (Clark & O'Shea, 2001). Examples include the ophiuroid *Ophioscolex* sp. (Clark & O'Shea, 2001), eight species of barnacles, including *Vulcanolepas* [Neolepas] *osheai*, (Clark & O'Shea, 2001), the neolepadine (deep-sea stalked) barnacle *Ashinkailepas kermadecensis* from the sites of diffuse low-temperature venting on the south-eastern caldera walls of Wright Volcano (Buckeridge, 2009), the hippolytid shrimp *Lebbeus wera* from the Brothers Caldera (Ahyong, 2009), the vent crab *Xenograpsus ngatama* from Brothers and Maculey volcanoes (McLay, 2007), and the galatheid crab *Munidopsis maunga* from Macauley Caldera (Schnabel & Bruce, 2006).

Research focussed on the benthic ecology of Kermadec seamounts has been ongoing over the last decade (Rowden et al., 2008). However, there are still large gaps in our understanding of how the seamounts of the Kermadec volcanic arc function in their natural state. Such information is needed before effective conservation strategies can be put in place to protect seamount communities from human-induced disturbances.

1.5 RELEVANCE OF STUDY

The threat posed by fishing to seamount communities resulted in a call in 1999 to protect them as part of a wider deep-sea conservation strategy (Probert, 1999). Since then, conservation of some seamounts has been achieved. Seamounts in New Zealand waters were among the first to be protected. Nineteen seamounts were designated as "protected" and closed to all forms of trawling in 2001 (Brodie & Clark, 2004), including those that support hydrothermal communities on the Kermadec volcanic arc (Brothers, Rumble III). Up to 52% of seamounts in the New Zealand Exclusive Economic Zone (EEZ) are also protected from bottom trawling by being included in 1.13 million km^2 large Benthic Protection Areas that were established in 2007 (Helson et al., 2010).

Elsewhere two seamounts, namely the Formigas and D. João de Castro Bank in the Azores have been protected since 2006 (Probert et al., 2007) whilst Mediterranean seamounts, such as Eratosthenes Seamount which has been recorded to be highly diverse (Tudela et al., 2004), were included within a network of marine protected areas in 2005 (Probert et al., 2007). Other prominent examples of seamount conservation include: the protection of 15 seamounts in Australia in 1999 as part of the Tasmanian Seamounts Marine reserve; the closure from bottom trawling in 2005 of 1 million km^2 of seafloor, containing seamounts off the Aleutian Islands (USA); and designation of four seamounts off the southern edge of Georges Bank (US EEZ) for their cold-water coral as 'Habitat of Particular Concern' in 2005 (Probert e al., 2007).

The New Zealand region has over 800 seamounts, half of which lie within New Zealand's EEZ (Rowden et al., 2005), covering around 3% of the EEZ surface area (Clark & O'Driscoll, 2003). These include seamounts on the Kermadec volcanic arc which have hydrothermal vents that support chemosynthetic-based communities (Clark & O'Shea, 2001), and which are included within mineral prospecting licence areas of companies interested in mining for SMS deposits (Wright, 2005). While some of these seamounts have been sampled, and their benthic communities described (e.g. Beaumont et al., 2009; Rowden et al., 2003), seafloor imagery from others is yet to be analysed. Monowai Volcano is one of these seamounts. Monowai lies outside the New Zealand EEZ, but on the Extended Continental Shelf (which New Zealand has some governance over), and is potentially of future interest to mining companies.

Monowai Caldera (MoC1) is the largest caldera by volume in the northern Kermadec-southern-Tofua arc system (Graham et al., 2008; Leybourne et al., 2012). MoC1 is older than the current stratovolcano, as assumed due to the absence of dissecting faults on the stratovolcano (Wormald et al., 2012). The Monowai Volcanic Complex (MVC) consists of a combination of areas that have ceased venting and those that exhibit diffuse-flow/low-temperature venting (<60 °C) (Leybourne et al., 2012). Volcanism occurs through the secondary, basaltic cone situated ~2 km north of the stratovolcano, smaller parasitic cones situated within the rim of the caldera, and through cones (of diameters > 1 km) situated within 4 km south of the caldera centre (Wormald et al., 2012). Due to the fact that it exhibits different forms of venting ("explosive"/active type and diffuse) at different intervals, it can be assumed that the MVC consists of a range of habitats (hard substrates, soft sediments, diffuse-flow chimneys, inactive chimneys), and consequently, communities of different species composition adapted to those environmental conditions (Hessler et al., 1988).

Several other Kermadec seamounts exhibit variable patterns of species diversity, richness, and habitat heterogeneity. The Kermadec region forms one of the 11 major biogeographic regions (Bacharty et al., 2009), with its unique geological and tectonic history. The geographical location of Monowai places it separately and in isolation to the rest of the Kermadec seamounts. With its variable frequency of venting along with periods of quiescence (Wormald et al., 2012), of up to over a decade between 1979 and 1990 (Wright et al., 2008), it could possibly favour the deposition of thicker deposits. Older volcanic regions, where hydrothermal vent activity has ceased, contain thicker mineral deposits, which are the targets for mining companies (Collins et al., 2013; Hein et al., 2009). Monowai, with its active volcanic system and relative spatial isolation, makes it ideal to compare with many other seamounts that are spatially isolated in similar bathymetric ranges.

The biggest problem confronting conservation of seamount ecosystems is the lack of baseline data and a basic understanding of the main abiotic factors driving seamount community structure, diversity, and endemism (Morato et al., 2010). Studies of seamounts, and their chemosynthetic ecosystems, if they have them, initially focus on descriptive accounts: identifying species that dominate communities, examining similarities with other seamounts, biogeography, and endemism (Young, 2009). In addition and compared to active vent sites, tracking inactive vents (such as on Monowai Caldera) is difficult due to a lack of water column signal through venting (Van Dover et al., 2011), leading to relatively limited studies of benthic communities around such sites (Pruis & Johnson, 2004). Therefore, fewer such studies have examined relationships between abiotic factors and benthic community structure on seamounts (Young, 2009), primarily because of the difficulties in obtaining abiotic data at the appropriate spatial scale. In order to gain and understanding of how biological communities exhibit temporal change, it is important both to describe benthic communities and to evaluate abiotic factors, should environmental conditions alter due either to natural events or human activities (Khripounoff et al., 2006). Knowledge of species composition of communities also enables us to understand ecological processes, such as dispersal and migration events within and among seamounts, which can also inform us about how communities may recover from significant environmental change, and how to design effective networks of protected areas.

While the threat to seamounts from fishing remains, the current concern is that disturbance from deep-sea mining represents a significant potential threat to communities on seamounts that have, or had, active hydrothermal venting (Van Dover, 2011). The recovery of many inactive vent sites after mining is predicted to be on decadal scales (Van Dover, 2010). Gaining knowledge about the communities in the form of surveys on the spatial distribution of benthic fauna and patterns arising from abiotic factors on these types of seamounts before mining takes place is important, if the environmental effect of such mining is to be effectively managed (Collins et al., 2013). As seamounts in the Kermadec volcanic arc come in the spotlight for mining (Wright, 2005), having an unexploited seamount such as Monowai could allow for comparisons between an un-impacted/control site to ones that have been impacted through mining. As there are no current proposals for conducting mining due to its recent level of volcanic activity (Watts et al., 2012), Monowai Volcano could usefully serve to provide baseline information by which to assess recovery of other seamounts with hydrothermal venting that are currently the subject of proposed SMS mining elsewhere on the Kermadec volcanic arc.

1.6 STUDY SITE: MONOWAI VOLCANO

Monowai Volcano is located ~1400 km NNE of New Zealand (25°53’S, 177°11’W) and midway along the Tonga-Kermadec arcs, and is one of the 26 main volcanic centres of the Kermadec volcanic arc between 25°S and 36°30’S (Wright et al., 2008). It lies ~ 150 km to the west of where the Louisville Seamount Chain is being subducted into the Tonga-Kermadec Trench (Figure 1.2) (Watts et al., 2012; Wormald et al., 2012).

Studies by Graham et al. (2008), Timm et al. (2011), and Watts et al. (2012), have shown that the MVC consists of:

1) A 10–12 km wide, 1000 m high central volcanic cone reaching a summit depth of ~132 m.

2) A 7–10 km wide caldera.

3) Several parasitic cones composed of basalt and andesite.

4) A smaller, secondary basaltic cone that lies ~ 2 km north of the main volcanic cone.

Although lacking an obvious summit crater (Graham et al., 2008), Monowai’s volcanic cone is hydrothermally active and Monowai is known to be one of the three most active volcanoes of the Kermadec volcanic arc (Wright et al., 2008). Monowai Caldera was only discovered through swath mapping during the 2004 NZAPLUME III expedition (Leybourne et al., 2012), which is in contrast to the cone which has been surveyed on numerous cruises owing to its high hydrothermal activity. It was also noted that Monowai essentially consists of two calderas (MoC1 and MoC2), with the smaller, younger, and hydrothermally active caldera MoC2 nested within the larger and older MoC1 (Graham et al., 2008; Wright et al., 2008). The subject of this study is the main Monowai Caldera (MoC1) which is located ~ 12 km north-northeast of the summit (Timm et al., 2011). The caldera is a northwest-southeast elongated structural feature (Watts et al., 2012), and primarily composed of silicic material. The caldera outer rim and caldera floor occur at water depths of 800 m and 1250 m respectively (Timm et al., 2011). It is assumed that the two calderas were formed as a result of collapse due to the deflation of the magma chamber beneath the old Monowai stratovolcano, concurrent to its eruptions (Timm et al., 2011). The rim of the caldera is dissected by caldera-ring faults and caldera-wall collapse (Graham et al., 2008).

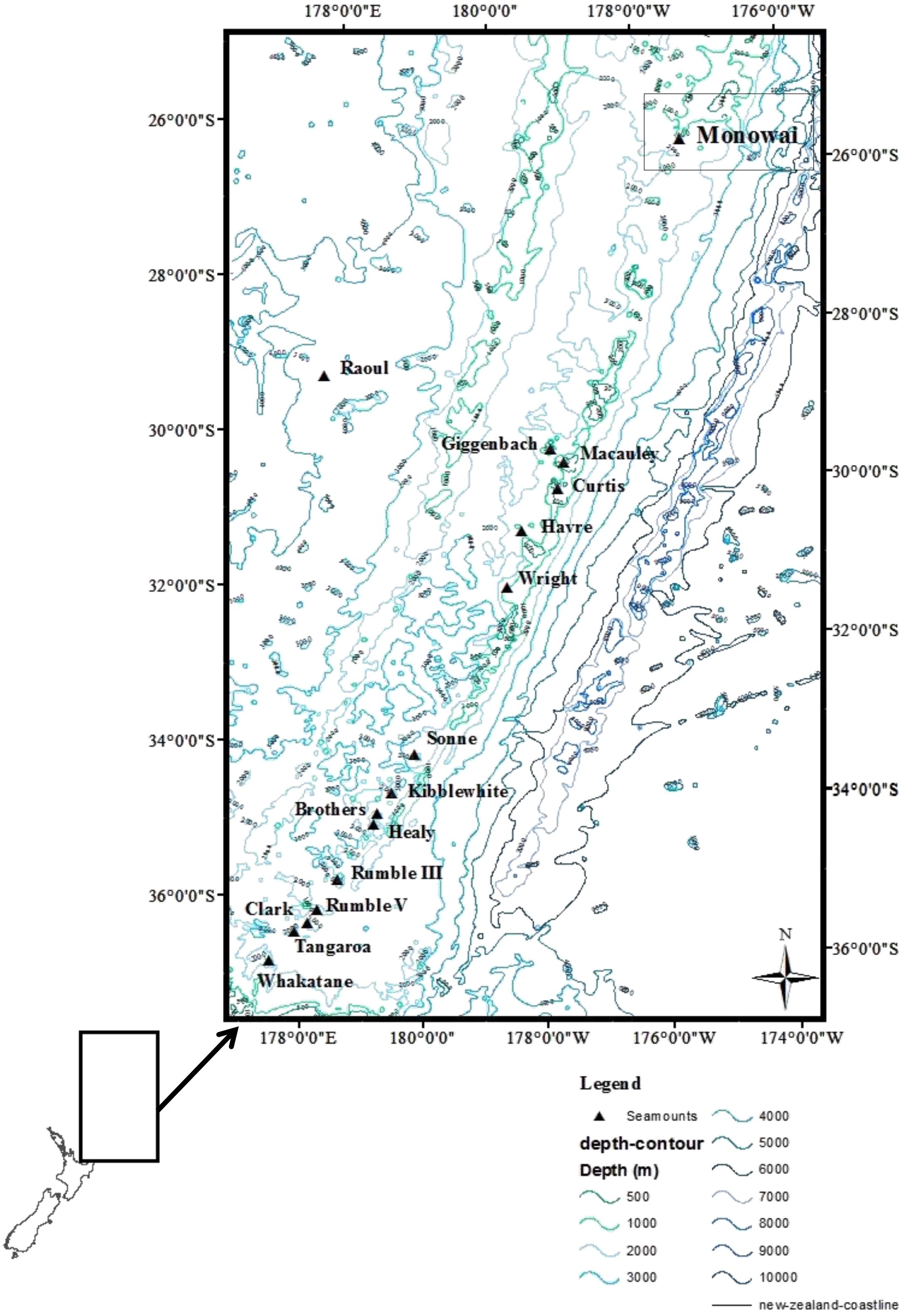


Figure 1.2: Bathymetric map showing the location of Monowai Seamount on the Kermadec volcanic arc.

1.6.1 MONOWAI GEOLOGY AND PREVIOUS STUDIES

Hydrothermal activity on Monowai was first recorded in 1877, with six major eruptions occurring between the periods of 1877–1928 (Mastin & Witter, 2000). Submarine eruptions have been recorded since 1944 both visually (discoloured surface water, gas emissions) and through T-wave activity by the Polynesian Seismic Network (Watts et al., 2012). Several aerial observations by RNZAF Orion were conducted in 1977, in response to discolouring of surface waters and vigorous gas emissions (Davey, 1980). This was followed by acoustic experiments and towed-array sonars between February 1978 and June 1979 by HMNZS *Tui* that recorded underwater volcanism signals (Davey, 1980). A bathymetric survey done in September 1978 calculated Monowai's summit to be at 117 m (sound velocity uncorrected), along with smaller parasitic cones charted on its flanks (Davey, 1980). Dredge samples from the summit were taken by Brothers et al. (1980) who described the mineralogy of the rocks to be primarily plagioclase and clinopyroxene basalt. The MANGO cruise in 2007 using the ROV *ROPOS* described the substrate from the caldera to be largely composed of well size-sorted lapilli, along with thickly sedimented caldera walls, and pillow lava blocks on the immediate caldera floor (Schwarz-Schampera et al., 2007). The Mussel Ridge hydrothermal field (western side of the Monowai Caldera) has been described as muddy with "slabs of sulphur-cemented ash, rich in hydrocarbons and massive anhydrite" (Short & Metaxas, 2011).

The central basaltic cone undergoes frequent cone collapse and rebuild because of its high eruptive activity, with significant events recorded in 1977, 1998, 2002, 2004, and 2005 (Wright et al., 2008). Wright et al. (2008) interpreted the explosions (as picked up from T-wave data), followed by estimation of the loss of edifice volume and regrowth between 2002 and 2004. The authors estimated that the eruptive phase from May 2002 led to cone collapse and displacement of ~0.085 km^3 of the upper edifice, followed by reconstruction of the cone from successive eruptive phases, resulting in a cone growth of 90 m in less than 2 years. Bathymetric surveys have shown changes in the summit depth (~45 m in 1998 to 130 m in 2004), with repeated shoaling and deepening occurring due to sector collapses and mass-wasting events in the form of sediment flows (Wright et al., 2008), and formation of newer structures such as cones, pyroclastic and lava flows (Watts et al., 2012). Consequently, a multi-beam survey in 1986 (RV *Thomas Washington*), and multi-beam surveys in 1998 (RV *Sonne*) and 2004 (NZA PLUME III expedition, RV *Tangaroa*) were all conducted in order to record summit collapse and rebuild (Wright et al., 2008). Such high geological activity and repeated eruptive cycles places Monowai in the "upper limits of Kermadec volcanic edifice growth in historical times" (Wright et al., 2008).

Additionally, morphometric studies on the two calderas were performed to examine the interaction between tectonic and magmatic processes (in relation to caldera formation and structural elongation) occurring within the MVC (Wormald et al., 2012). However, biological studies of Monowai are limited and very few biological data have been reported from previous expeditions. The most extensive biological sampling was conducted during the 2005 New Zealand American Pacific Ring of Fire, using the *Pisces V* submersible, but the biological communities of Monowai are yet to be described from this sampling effort. Subsequently, Monowai was further studied using the Remotely Operated Vehicle (ROV) *ROPOS* in 2007, and biological samples (*Bathymodiolus* sp. and *Lamellibrachia* sp.) were collected (Schwarz-Schampera et al., 2007). The data collected from this expedition enabled Short & Metaxas (2011) to examine the patterns of settlement behaviour of the vent tubeworm *Lamellibrachia* sp. on Monowai Caldera's Mussel Ridge. The authors also observed sites of low-temperature venting through cracks in the substrate which were largely surrounded by dense mussel beds, along with other megafauna such as sponges, anemones, crustaceans, and larger fish. Other studies on Monowai include comparison of survival rates and shell thickness of the vent mussel (*Bathymodiolus* sp.), when collected from low pH venting sites of Monowai, Lau basin, and NW Eifuku (Tunnicliffe et al., 2009).

1.7 AIMS AND HYPOTHESES

The primary aim of this project is to understand how the benthic community structure changes with abiotic factors (substrate type, water depth, and proximity to hydrothermal vent sites) on Monowai Caldera. As the MVC (including the caldera) is a site of hydrothermal activity, the focus will be on benthic fauna and associated communities which are likely to be chemosynthetically-driven. Therefore, the following hypotheses are tested to examine changes in vent taxa (hereafter referred to as simply ‘taxa’) richness, total number of individuals (hereafter referred to as simply ‘taxa abundance’), and community structure with each abiotic factor:

Water depth

Water depth has an impact on seamount communities that rely on photosynthetic products, with the rate of POC flux declining with increased depth. This has significant implications on the benthos. However, the effect of water depth would be minimal for benthic communities such as on Monowai that rely on chemoautotrophy.

Hypothesis 1: There is no relationship between water depth and the richness, abundance, and community structure of benthic vent taxa on Monowai.

Substrate type

Differences in the frequencies and periodicity of venting lead to the formation of a range of both hard and soft substrata. Consequently, these are colonised by different benthic faunas, with certain habitats more species depauperate than others.

Hypothesis 2: Substrate differences lead to differences in richness, abundance, and community structure of benthic vent taxa on Monowai.

Distance to a vent site

Differences in the temperature and chemistry of vent fluids contribute to a range of environmental conditions for vent taxa, which depending on individual tolerances, settle at different distances from a vent site, thus giving rise to spatial zonation.

Hypothesis 3: Distance to a vent site is inversely proportional to the richness and abundance of benthic vent taxa on Monowai, with vent taxa replacing non-vent taxa with decreasing distance to a vent site.

Small-scale patterns

Effects of venting can impact local vent taxa distribution and abundance, on smaller spatial scales of 1–10s of metres. The effect of small-scale distance and the temperature of venting fluids (within samples) on the richness, abundance and community structure of Monowai benthic vent taxa within samples will also be examined.

In addition, a secondary aim of this study is to map faunal communities on Monowai Caldera. Such spatial information on the distribution of the benthic communities would contribute to a baseline for future management of seamounts on the Kermadec volcanic arc and elsewhere in the Pacific.

CHAPTER 2: METHODS

2.1 DATA COLLECTION

The primary method of gathering data for studying the relationship between abiotic factors and benthic community structure on Monowai was through the analysis of seafloor images. Images were from the 2005 New Zealand-American Submarine Ring of Fire expedition. This expedition was a joint venture between National Oceanic and Atmospheric Administration (NOAA), National Institute of Water and Atmospheric Research (NIWA), and Geological and Nuclear Sciences (GNS) to study the submarine volcanoes of the Kermadec arc. The vessel used for this expedition was *RV Ka'imikai-o-Kanaloa* (KOK), from which the submersible *Pisces V* was deployed. Four submersible dives (PV-612, PV-613, PV-614 and PV-615) were undertaken by *Pisces V* on the flanks of Monowai Caldera. The submersible was equipped with a video camera that took continuous footage, and a still camera set to take pictures of the seafloor every 15 seconds (typically at an altitude of 2 m above the seafloor when in transit). The submersible also had a manipulator arm and a bio-box in order to collect substrate samples and benthic fauna. A depth sensor attached to the submersible provided information about maximum depth and location, relative to the support vessel. Table 2.1 shows the details of each dive conducted on Monowai Caldera, as acquired from the voyage report of this expedition. Summaries for each dive have been listed in Appendix A.

Table 2.1: Details from *Pisces V* dives on Monowai Caldera, KOK 2005 expedition

Dive number	Location	Date	Bottom time	Max. depth
PV 612	SW caldera area -25.795°S -177.170°W	07-04-2005	5 hrs 40 mins	1372 m
PV 613	SW caldera area -25.805°S -177.164°W	08-04-2005	6 hrs and 23 mins	1297m
PV 614	SW caldera area -25.804°S -177.166°W	09-04-2005	4 hrs and 59 mins	~1166 m
PV 615	SW caldera area -25.803°S -177.166°W	10-04-2005	5 hrs and 34 mind	1228 m

2.2 ANALYSIS OF STILL IMAGES

A total of 4500 still images and 15 hours & 52 minutes of video footages were available from all submersible dives on Monowai Caldera for analysis. Image quality varied, with some pictures being unclear and unsuitable for analysis. Lack of clarity in images was due to inadequate contrast, large distances from the seafloor making observation of the seafloor difficult due to inadequate lighting and camera resolution, formation of sediment clouds in the water column if the submersible accidentally collided against the muddy/sandy bottom, and fish swimming in front of the camera. Where the submersible encountered a site of interest and paused on the seafloor to collect a sample of the substrate and attached fauna, repeat images were generated. In these cases, only one representative image (the most clear) from that site was chosen to avoid repetitive sampling.

After screening for clarity, a total of 167 images were available to be used for quantitative analysis, with 30 images from PV-612, 75 images from PV-613, and 62 from PV-614. No images from PV-615 were of sufficient quality to be useful. There was no bias in choosing usable images according to bathymetric ranges. Although the submersible travelled over various substrate classes of the caldera, a lot of focus appeared to be on hard substrates that had visible megafauna. For the purpose of this study and statistical analysis (mentioned in Section 2.4), only images that had no visible fauna and singletons were excluded. Coincidentally, these were also images that contained extensive sedimentation or homogeneity of hard substrate (boulders). Images were loaded into ImageJ, a software that adjusts images for colour, contrast, exposure, and hue. If an image appeared slightly obscured or unclear, adjustments were made using Black & Contrast function tools. Such adjustments were no more than 3 units for Black & Contrast function and 2 units for Redness and Hue, in order to standardise all images and minimise bias. For examining small areas of the image, XnView was used. XnView has the ability to enhance a picture on a smaller scale along with magnification. ImageJ also has tools to scale the area of the seafloor imaged before analysis by using the distance between the laser lights (20 cm apart).

2.2.1 SUBSTRATE CLASSIFICATION

Despite using the laser lights from the submersible to standardise and calibrate the still images, it is important to note that the lasers were often not perpendicular to the visible substrate. This relates to areas where the substrate was of high-relief (outcrops) or sloped. In the absence of a third laser, measurements were carried out as normal using the two laser lights. However, due to this key point, the areas may have been over-estimated. The average image area from all 166 samples was 11.5 m^2 (± 0.43 m^2, standard error of the mean). Following clarity adjustments and scaling, the seabed was classified into several substrate categories, similar to those used in the study by Clark et al. (2010). For substrate covered by fauna (such as bathymodiolid mussels), the dominant substrate was chosen. Most often, this was bedrock (a continuous rock formation) covered by soft sediment, which provided a stable and erosion-free foundation for fauna. Therefore, mussels covering such substrate were recorded as ‘bedrock’ or ‘bedrock with sand/mud overlay’ unless the mussels occurred on high-relief outcrops, in which case they were recorded as ‘bedrock outcrops’. For images that had mixed substrates, percentage cover of each substrate type was estimated by using the ‘Freehand’ tool in ImageJ. A polygon was drawn around the margins of each particular substrate class, obtaining the area that it covered, and then turning it into a percentage value of the overall image area. Abiotic substrate was classed into hard and soft types, as well as biogenic (of biological origin) as shown in Table 2.2.

Table 2.2: Classification of observed abiotic and biogenic substrate types on Monowai Caldera, along with grade size (mm) according to the Wentworth scale (Fisher, 1961)

Hard substrate	Soft substrate	Biogenic substrate
Bedrock	Sand (2–0.063 mm)	Bacterial mat (green)
Sand overlaying bedrock	Mud (<0.063 mm)	Bacterial mat (white)
Mud overlaying bedrock	Sulphidic sediment (yellow/white/black)	Shell hash
Bedrock outcrop		Bathymodiolin shells
Boulder (>256 mm)		Crustacean remains
Cobbles (64–256 mm)		
Pebbles (2–64 mm)		
Pillow lava		
Volcanically altered bedrock/small chimneys		

The following definitions apply to all the substrate categories recorded during image analysis:

Hard substrate

a) Bedrock: A continuous and consolidated rock formation.

b) Bedrock with sand or mud overlay: Continuous stretches of bedrock covered by a veneer of sand or mud. Bedrock was often disrupted by numerous depressions, cracks, or fissures that were filled with soft sediment such as sand or mud.

c) Bedrock outcrop: A bedrock outcrop is typically a high-relief feature (such as a cliff-face) with minimal sediment cover, due to erosion from the prevailing water currents.

d) Boulder: Boulders are rounded fragments of rock that are larger than cobbles and are relatively of the same size (> 256 mm) (Wentworth, 1922).

e) Cobbles: Smaller fragments of rock, usually between the sizes of 64–256 mm (Fisher, 1961).

f) Pebbles: Small, rounded pieces of rock between the sizes of 2–64 mm (Fisher, 1961)

g) Pillow lava: Pillow lavas are the product of effusive eruptions (Wright et al., 2002). They occur as interconnected or closely-packed structures (Moore, 1975), where hot molten material spreads out on the terrain and subsequently cools to form the bulbous structures that eventually become pillow lavas/ pillow tallus, in response to hydrostatic pressure with increasing water depth.

h) Volcanically altered bedrock/small chimneys: Bedrock that is volcanically altered in nature (usually a light colour) from the surrounding bedrock areas. Small chimneys are those that form as a result of diffuse-style venting, emanate hot water, are covered with yellow sulphidic sediment, and green microbial cover (Figure 2.1).

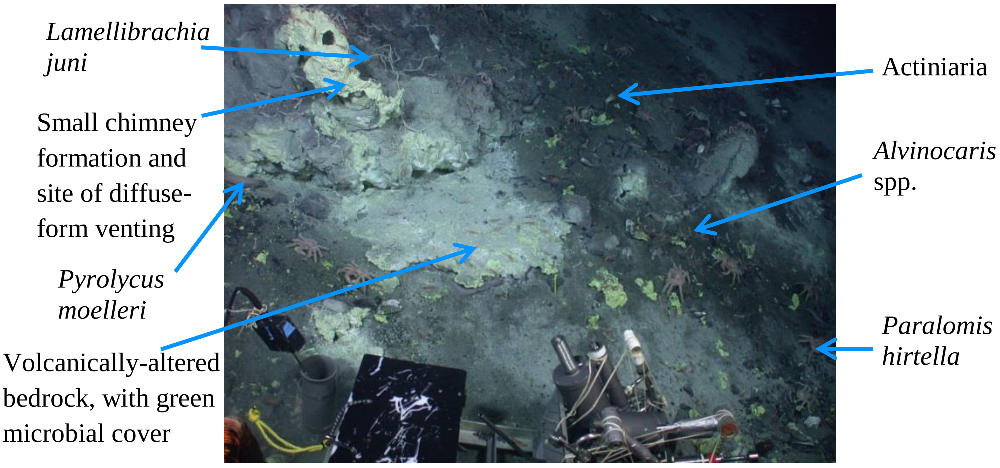


Figure 2.1: Sample picture showing chimney formation along with volcanically-altered bedrock on Monowai Caldera, dive 613, 9 April 2005, water depth= 1150 m, vent-fluid temperature= 56.5 °C, image area= 15 m^2.Vent fauna in the sample picture include the vent tubeworm (*Lamellibrachia juni*), lithodid crab (*Paralomis hirtella*), vent shrimp (*Alvinocaris* spp.), vent eelpout (*Pyrolycus moelleri*), vent mussel (*Bathymodiolus manusensis*), actiniaria, and green microbial cover.

Soft substrate

a) Sand: Sand encompasses epiclastic materials of sediment grade sizes between 2 mm and 63 µm (Folk, 1954). Visual observations indicate it to be less flocculent and ranging from coarse sand to find sand. Wave and ripple formations are more prominent.

b) Mud: Composed of materials finer than 63 µm, i.e. clay (4 µm) and silt (4–63µm) (Folk, 1954). Visually, mud is flocculent and easily resuspended. Invertebrate tracks are more prominent and noticeable.

c) Yellow/white sulphidic sediment: Soft sediment of the consistency of coarse-fine sand, usually located around areas of venting.

Biogenic substrate

a) Green/white bacterial mat: Films of microbial mat around vent openings. Green microbial mats were present on rocks surrounding vent openings, whereas white microbial mats were present on bedrock with mud overlay, and in areas away from sites of venting.

b) Shell hash: Areas of substrate that were littered in broken shells from gastropods and smaller fragments of mussel shells.

c) Bathymodiolin shell: An intact, but open, dead mussel shell- often completely intact and silvery in colour, able to reflect the light of the submersible.

d) Crustacean remains: Composed of fragments of carapace and appendages of lithodid crabs.

2.2.2 MONOWAI FAUNAL DATA

Visible surface fauna or signs of infauna (lebensspuren) per image were identified, counted, and entered into a spreadsheet. Lebensspuren are defined as “structures that are generated through the action of epi- and infaunal benthic organisms” (Kaufman et al., 1989). The multipoint tool in ImageJ was used to click on and count visible fauna such as crabs, anemones, and shrimps. For mussels that occurred in high density ‘beds’, however, an estimation of abundance was determined by first counting 15 mussels, then determining the area occupied by these mussels (using the rectangle box function), before obtaining an abundance estimate for the total area occupied by the mussel bed by extrapolation. The size frequency distribution of mussels was not consistent through all the samples, with mussels varying in shell lengths. The overall extrapolated figure for large mussel beds per sample is thus an approximation of the number of individuals (of all size classes) within the beds. Organisms were initially identified and classified into higher taxonomic groups, as shown in Table 2.3.

Table 2.3: Initial classification of observed sessile and motile fauna on Monowai Caldera.

Motile	Sessile	Lebenspurren/infauna
Decapod crabs	Unidentified bivalves (attached to pillow lava and large boulders)	Gastropod tracks
Lithodid crabs		Pits
Alvinocarid shrimps		Mounds
Gastropods	Bathymodiolid mussels	Burrow (< 25 mm)
Squid	Green limpets on mussels	
Eelpouts	Red, yellow, orange, white anemones	Burrow (> 25 mm)
Blue eels	Tubeworms	
Other fish		

2.2.3 FAUNAL IDENTIFICATION

Following the initial analysis of still images, taxonomic experts (see Acknowledgments) were consulted to obtain faunal identifications to the lowest possible taxonomic level. As a result of this consultation, a number of the initial faunal groups were combined. For example, anemones of different colours (red, white, orange), yet showing morphological similarities were combined into one group. Anemones of the Actinostolidae and Hormathiidae (deep-sea families) were especially hard to distinguish, as close observation and dissection of the columns are required to separate these families (D. Fautin, personal communication, 14 March 2012). According to the KOK expedition voyage report, more than one species of *Alvinocaris* shrimp were collected from Monowai. However, in the absence of biological samples, it is hard to identify which species was being observed in the still images. Therefore, alvinocarid shrimps were deemed *Alvinocaris* spp. for this study. The bathymodiolid mussel was considered to be *Bathymodiolus manusensis*, as only this mussel species has been sampled from Monowai to date. The zoarcid fish was considered to be *Pyrolycus moelleri*, because this species has been collected previously from vents elsewhere on the Kermadec volcanic arc. Similarly, the tubeworms *Lamellibrachia juni* and *Oasisia fujikurai*, the lithodid crab *Paralomis hirtella*, the squid *Pholiodoteuthis massyae*, and octopuses *Graneledone challengeri* and *Benthoctopus tegginmathae* were all identified by taxonomists to species level because of previous records from seamounts on the Kermadec arc. All other taxa were identified only to genus, family or class level (Table 2.4).

Table 2.4: A listing of all taxa observed and recorded from Monowai Caldera, after consultation with taxonomists

Sessile	Motile
Bathymodiolus manusensis (vent mussel)	*Paralomis hirtella* (vent crab)
Lepetodrilus sp. (green limpets on mussel shells)	*Alvinocaris* spp. (vent shrimp)
	Natant decapod
Lamellibrachia juni (tubeworm)	*Enigmaticolus* sp. (Buccinidae)
Oasisia fujikurai (tubeworm)	*Pyrolycus moelleri* (Zoarcidae)
Bivalves (attached to boulders)	Liparidae (snail fish)
Anemones (Actinistolidae/Hormathiidae)	Macrouridae (rat-tails)
	Synaphobranchidae
	Pholidoteuthis massyae (squid)
	Graneledone challengeri (octopus)
	Benthoctopus tegginmathae (octopus)

Taxonomic experts identified the fauna using images supplied from an ‘image library’. This image library was created using a combination of the still images and screen-grabs of video footage. Screen-grabs from the videos allowed for close-up pictures to be generated that made it easier for taxonomists to identify taxa, and for recording key morphological features. A range of the best quality images of each taxon was chosen for the library and sent to the taxonomists. Images of the common taxa found in this study can be found in the disc supplied with this thesis (CD-Appendix F).

2.3 OBTAINING POSITION AND DEPTH INFORMATION FOR EACH STILL IMAGE

The position and depth for each still image was obtained by relating the navigation files for each dive with the video along each transect.

Navigation files for each dive were acquired from NIWA. In order to use navigation files as position files (or *posi files) in OFOP (Ocean Floor Observation Protocol, see section 2.5), the time on the navigation files had to be first concatenated into the time format of hh:mm:ss. An Excel spread-sheet was created with headings: Date, Time, SHIP_Lat, SHIP_Lon, SUB1_Lat, and SUB1_Lon for each dive.

In order to arrive at the video footage that matched the still image of a particular station, the filename for each still image was used. The filenames provided an approximate time for where the matching image could be found on the video. Once the taking of the image had been identified from the video (by observing the flash near the approximate time), the precise time could be recorded for each image, and the navigation file was referred to in order to record coordinates matching the time when the image was taken.

The navigation file for Dive 613 had depth information from the submersible. Hence, it was easy to correlate latitude and longitude information to corresponding depth. However, for Dives 612 and 614, depth was not available in this format and, therefore, depth information had to be obtained from the dive log of the expedition. The average depth from all 166 samples was 1117.9 m (±3.86 m, standard error of the mean). Matching the time the image was taken to the nearest time in the log when depth was recorded meant that depth records for these dives were only approximate. Position or *posi files in Notepad were created with the time, depth, and location for each dive.

2.3.1 MEASURING THE DISTANCE TO THE NEAREST VENT SITE

One of the variables that was required for this study was the distance an image was from a vent site.

For this study, a vent is defined as an area of diffuse hydrothermal flow with associated biological communities, wherein each vent “occurs in discrete patches and are separated by areas of the seafloor not exposed to hydrothermal fluids” (Neubert et al., 2006). A vent opening was defined and classified as in Tsurumi (2003), as a concentrated area of flow observed through cracks in the basaltic seafloor, spreading over an area of 1–10 m^2. Vent openings on the video were identified by one of the following:

1) A clearly visible hole on the seafloor (often >5 cm in diameter), venting hot water;
2) Small cracks amongst boulders and bedrock outcrops, venting hot, shimmering water, but not vigorously as mentioned in (1).

All above-mentioned venting on Monowai Caldera was in the form of diffuse venting with black/grey smoke or hot shimmering water. Vent fluid temperatures ranged between 44–56 °C (as recorded by temperature probe deployed by the submersible, see dive logs), and often noticeable by the presence of microbial mats.

Aside from measuring the distance of images to the nearest vent site, at a smaller spatial scale, the distance a particular vent taxon was from a vent within an image was also required. Furthermore, the temperature of hydrothermal fluids (as recorded by temperature probe deployed by the submersible, see dive logs) was tested from a limited number of sites. Nevertheless, the temperature data were used for examining the effect on the benthic community composition surrounding those vent openings.

Video from each dive was observed using a VLC player and, using the ‘Take a Snapshot’ option, screen-grabs of vents and their surrounding taxa were taken. In order to measure the small-scale distance between a vent opening and a vent taxon within images, the screen-grab was first scaled (as for the still images), and then the “Straight line” and “Measure” tools in ImageJ were used to draw and measure a line from the vent opening to an indicator species (bathymodiolid mussels, alvinocarid shrimps). The indicator species differed from one vent to another, as vents previously described as holes on the seafloor had a higher abundance of vent shrimps and crabs in comparison to venting from cracks in boulders/bedrock which were surrounded by mytilid bed. A spreadsheet of maximum distances to the vents in addition to the species composition surrounding the vents was compiled.

For calculating the distance between an image and the nearest vent site, the start of a vent community was chosen as the point where there was a noticeable change in the substrate, with homogeneous substrate (extensive soft sediment/pebbles/boulders) being replaced by heterogeneneous substrate classes in the form of bedrock with sediment overlay/chimneys/outcrops. Consequently, a change in associated benthic fauna was observed, with vent mytilids prominently dominant, along with other vent taxa such as alvinocarid shrimps and lithodid crabs on heterogeneous substrate classes. Vent communities were frequently separated by expanses of soft sediment, with minimal hard substrates to foster any habitat heterogeneity, along with occurrences of several mobile non-vent taxa (larger fish, cephalopods). In several samples, large numbers of dead bathymodiolin shells connected two communities. Dead bathymodiolin shells also acted as the ‘outer boundary’ for many of the vent communities seen during image analysis, leading to either a second community or a non-vent habitat with homogeneous substrates.

Subsequent screen-grabs were taken in order to arrive at the next screen-grab that corresponded to the next still-image in which a vent community could be identified. This was done by noting the end of a community on an image to the beginning of a community on the next image. Distance between images containing vents was measured by scaling the image (as for the still images), and then using the ‘Straight Line’ and ‘Measure’ tools to calculate the distance from the bottom of an image to the top. It is important to note that the presence of a vent community in a screen-grab or a still-image does not necessarily indicate the nearest distance to a vent. A vent could be to either side of the submersible transect. This was not an issue for images that had signs of venting within the submersible’s field of view. However, for images where the site of actual venting was not obvious, an assumption had to be made that the vent could be to either side of the submersible transect. The location of every vent was not explored. Therefore, distance measurement for such images may not be accurate, as the distance calculations were based solely on the existence of a thriving vent community. Nevertheless, the method used is considered useful for estimating the approximate distance of an image to a vent.

2.4 STATISTICAL ANALYSES

As area estimates for each image (hereafter referred to as ‘samples’) varied considerably due to the variable altitude of the submersible, taxa richness and abundances had to be standardised to 1 m^2. Standardisation of faunal richness and abundance data was done by dividing the image area by the faunal richness or abundance count for every sample. Unlike other biodiversity studies, it was not possibly to carry out rarefaction curves on taxa richness due to the structure of the data. Rarefaction analysis works best when comparing assemblages collected independently and randomly through different sampling methods in the same area, but over large distances (individuals randomly spatially distributed) (Gotelli & Colwell, 2011). Samples that contained no fauna or had only one (singletons) individual were excluded from analysis. One sample from the data set was excluded from analysis as it contained bivalves attached to boulders. The bivalves were not encountered elsewhere, and the sample formed an obvious outlier during statistical analysis, producing a clustering of data points in multivariate analysis. This made it difficult to visualise overall patterns in the multivariate results outputs. Removing this sample changed the sample size from 167 to 166. Abundance data were log-transformed (natural log) for univariate stastistics. Linear and non-linear regressions were performed using R and JMP to test for statistically significant relationships between the predictor variables and taxa richness and abundance.

Abundance data were then square-root transformed for multivariate statistical routines, so that the patterns resulting from subsequent analyses were not just because of the presence of taxa that had high-value counts in the dataset (Clarke & Warwick, 1998). In order to examine benthic community structure and its relationship with abiotic factors, PRIMER v.6 (Clark & Gorley, 2006) with the PERMANOVA add-on (Anderson, 2001) was used. The following multivariate routines were conducted to allow for the grouping of samples, establishing the effects of predictor variables on the response variable, and testing for overall statistical significance:

1) Resemblance matrix (Clarke & Warwick, 1998): To measure the similarities between every pair of samples in the data set using the Bray-Curtis metric for faunal data, and Euclidean metric for substrate/habitat data.

2) CLUSTER with SIMPROF (McClain et al., 2010): To identify samples of similar faunal/habitat structure using Group-average hierarchical clustering through dendrograms, which group and sub-divide samples into small numbers of clusters of increasing/decreasing similarity. The SIMPROF (Similarity Profile) routine was used to determine statistically significant clusters of samples (i.e. communities), by assuming a null hypothesis that particular sets of samples are not different (P=5%) in a multivariate structure.

3) MDS (Multi-dimensional Scaling) (Clarke & Warwick, 1998; Clark et al., 2010): To visualise the relative dissimilarities between the samples depending on distance between sample points on a 2D/3D plane.

4) A one-way ANOSIM (Analysis of Similarity) (Clark et al., 2010): To examine the strength of the difference between the community and habitat groups identified by CLUSTER/SIMPROF, using a Global R statistic (across all groups of samples) and pairwise measures of R between the different groups. R ranges from 0 to 1, where values close to 1 indicate that sample groups are very different from one another.

5) SIMPER (Similarity Percentages) (Clark et al., 2010): To identify those taxa that contribute to the similarities or dissimilarities within and between community groups. Dissimilarity/SD or similarity/SD values of over 1.0 were used to identify taxa that can be deemed characterising or discriminating taxa for the similarity or dissimilarity respectively within or between community groups. The cut-off percentage for the analysis was set at 90%.

6) DistLM (Distance-based linear models) (Legendre & Anderson, 1999; McArdle & Anderson, 2001): To determine the relationship between the abundance data (response variable) as a resemblance matrix and predictor variables, and to calculate how much variation in the faunal data can be explained when a variable is considered

alone. A db-RDA (Distance-based redundancy analysis) plot of the key environmental variables was done to graphically represent the results from the DistLM routine.

2.5 MAPPING BENTHIC COMMUNITIES AND HABITAT

Position or posi* files from each dive were loaded into ‘Processing & Observations’ of the software program Ocean Floor Observation Protocol (OFOP, version 3.3.0 L) in order to map the dive tracks. Smoothing of the raw location data for each dive was done by changing the value of ‘Smooth’ to 0. Then each dive track was splined using the smooth posi data. Smoothing and splining ensures continuity of the submersible’s location and time, by filling in the blanks of its location. Once a dive had been smoothed and splined, the new posi file was loaded on OFOP to create a map of the submersible’s track on Monowai Caldera, using GPS coordinates and time stamps from the navigation files (CD: Appendix F).

Button files were created and customised in OFOP according to fauna and substrate classes observed during still-image analysis. Merging the submersible’s dive track to the biotic and abiotic observation file from OFOP enabled mapping of habitat and biological communities. A detailed methodology of OFOP for this study can be found in Appendix B.

CHAPTER 3: RESULTS

3.1 HABITAT AND FAUNAL MAPPING

The spatial distribution of substrate types and benthic communities on Monowai Caldera was plotted using OFOP by combining navigation information from each dive with observation files for each still image, and matched up with the corresponding video footage. Figure 3.1 shows the location of all samples (n=166) from all three dives on the caldera.

Gaps between observations along the dive track in Figures 3.2–3.4 correspond to *Pisces V* submersible being in transit over the seafloor, and exclusion of images that either had singletons or no fauna. The latter corresponds to the first hour of the footage from dive PV-613, that had no surface biota. Areas of focussed diffuse-flow venting have been indicated by a circle on all distribution maps. It is important to note that these areas were sites where there was visual evidence of hot shimmering water or black/grey smoke from small chimneys. It is possible that other areas of the caldera may have had diffuse-style venting. However, these were not encountered during image analysis.

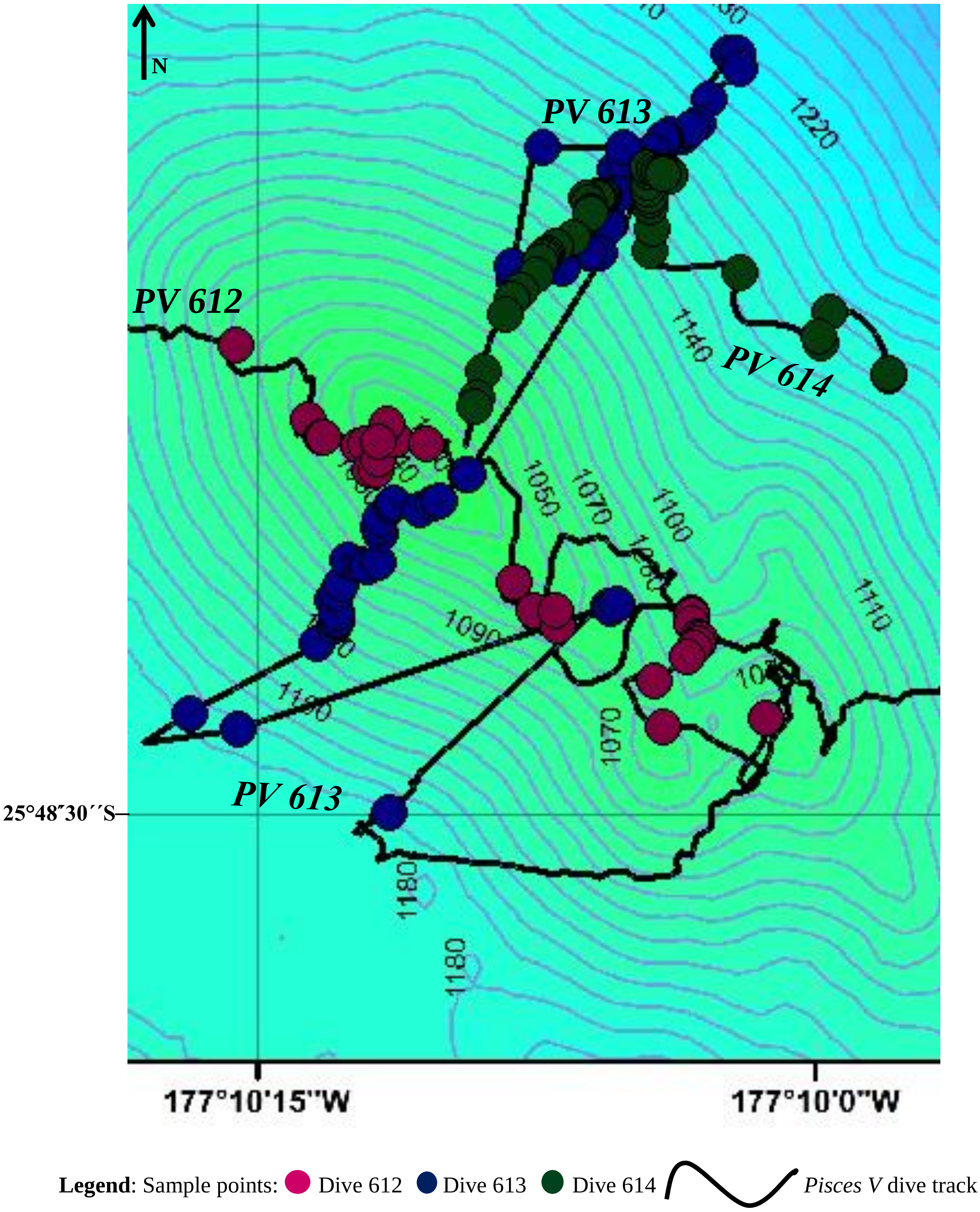


Figure 3.1: Spatial map of Monowai Caldera showing sample points from all the *Pisces V* dives used in the current study.

3.1.1 SUBSTRATE SETTING ON MONOWAI CALDERA

The distribution of hard substrates on the caldera is shown in Figure 3.2. Bedrock with mud or sand overlay occurred in much of the caldera, followed by larger substrates such as boulders and cobbles. High-relief outcrops had a patchy distribution. Pillow lava covered with a veneer of sediment occurred in only two samples. Similarly, chimneys (< 1 m high) and bedrock altered through hydrothermal activity occurred in only a few samples. During image analysis, these were areas that showed visual evidence of diffuse-flow venting in the form of hot shimmering water or black/grey smoke through cracks in among large boulders, outcrops or bedrock during the time period that the samples (still/video footages) were collected in 2005.

Figure 3.3 shows the distribution of soft sediments on Monowai Caldera, with most of the caldera showing extensive sedimentation (mud and sand). The few observation points of sand and mud for this map can be explained by the number of samples that consisted of such substrates, as there appeared to be a large focus on areas with hard substrate cover during the submersible dives. Furthermore, poor visibility during transit of *Pisces V* over such areas of heavy sedimentation is a contributory factor to the number of samples. The confinement of white and yellow sulphidic sediments (a product of hydrothermal activity) within the circled area is once again indicative of hydrothermal activity that was occurring when the caldera was explored in 2005.

The distribution of biogenic substrata (Figure 3.4) such as shell hash or bathymodiolin shell co-occurred consistently over areas of hard substrates such as boulders, cobbles and bedrock. The presence of bathymodiolin shells in most areas of the caldera coincides with the presence of well-established communities or where venting has shown cessation, possibly indicating a transition from an older community. In comparison, crustacean remains showed a very patchy distribution by being localised to areas near cobbles and cracks/crevices in boulders, and near areas of medium sedimentation. Similar to the confinement of white and yellow sulphidic sediments (Figure 3.3), microbial mats showed patchy distributions by being restricted to the circled area where there was visual evidence of venting. This confirmed visual observations during image analysis where green bacterial mats were found in areas of focussed diffuse-style flow and chimneys. However, white microbial mats also extended to areas outside of immediate venting, indicating possible differences between the microbial types forming such mats on the caldera.

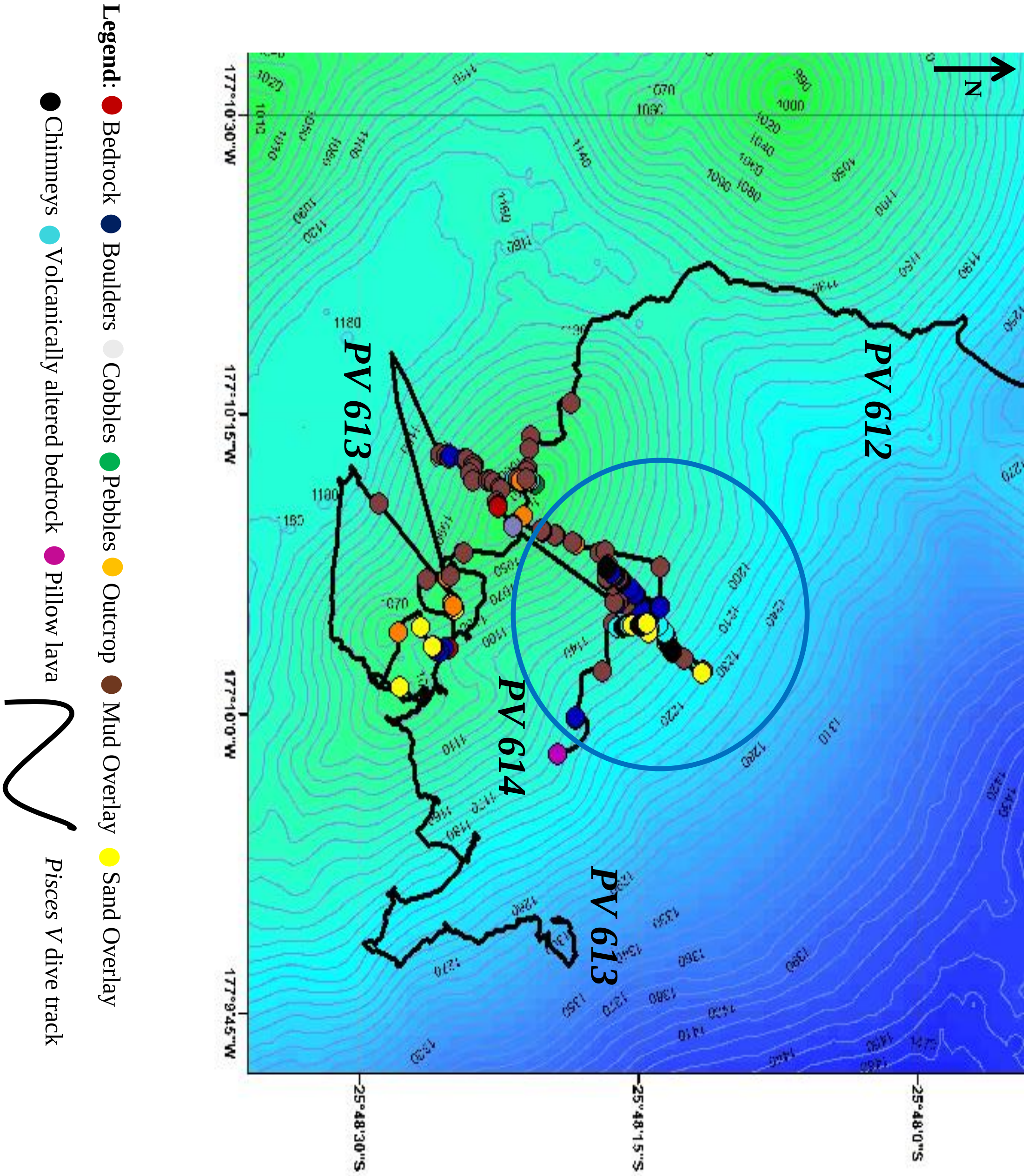


Figure 3.2: Habitat map showing the distribution of hard substrata around Monowai Caldera. The circle marks sites of the caldera where visual evidence of venting, in the form of hot shimmering water/black or grey smoke from small chimneys was noted.

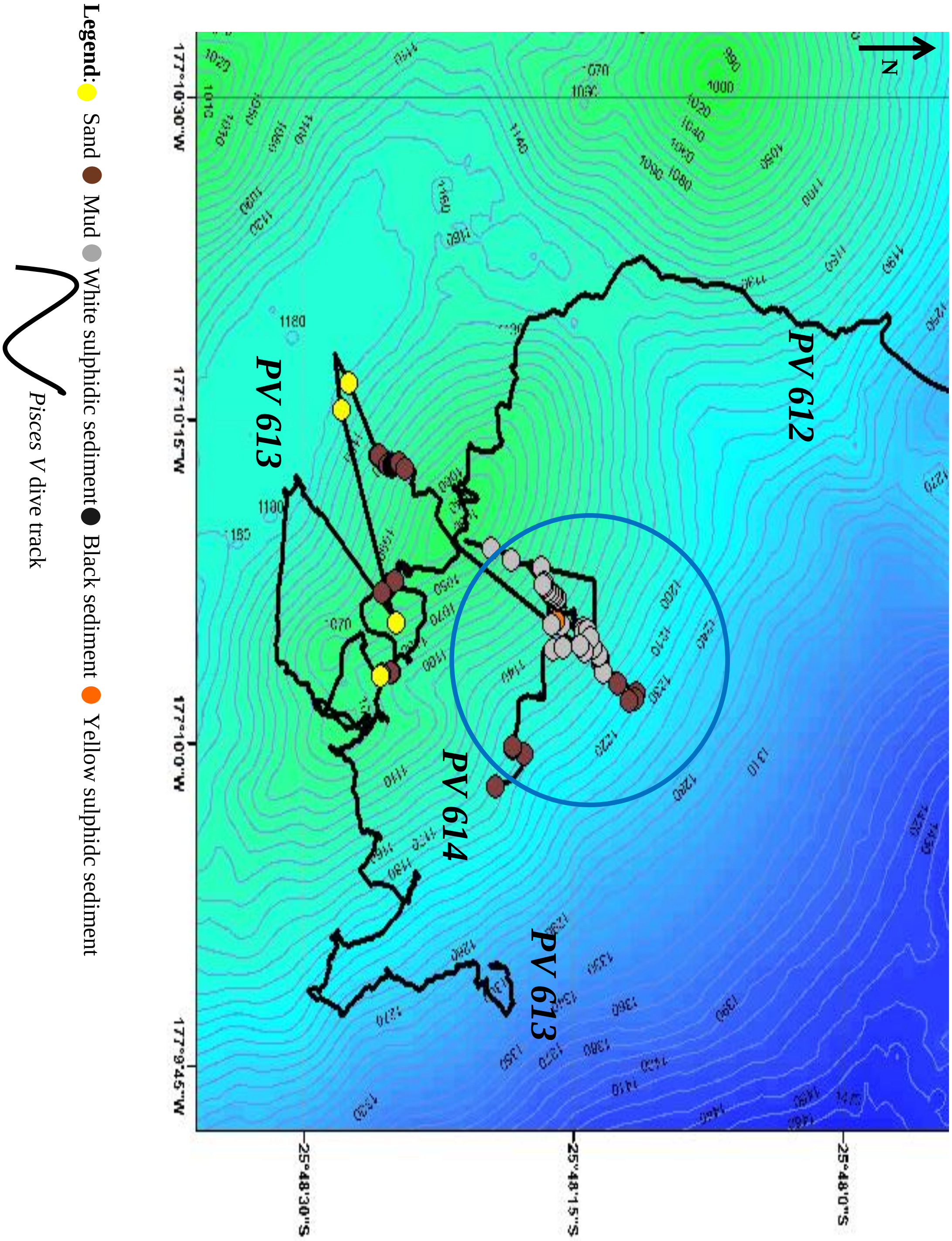


Figure 3.3: Habitat map showing the distribution of soft substrata around Monowai Caldera. The circle marks sites of the caldera where visual evidence of venting, in the form of hot shimmering water/black or grey smoke from small chimneys was noted.

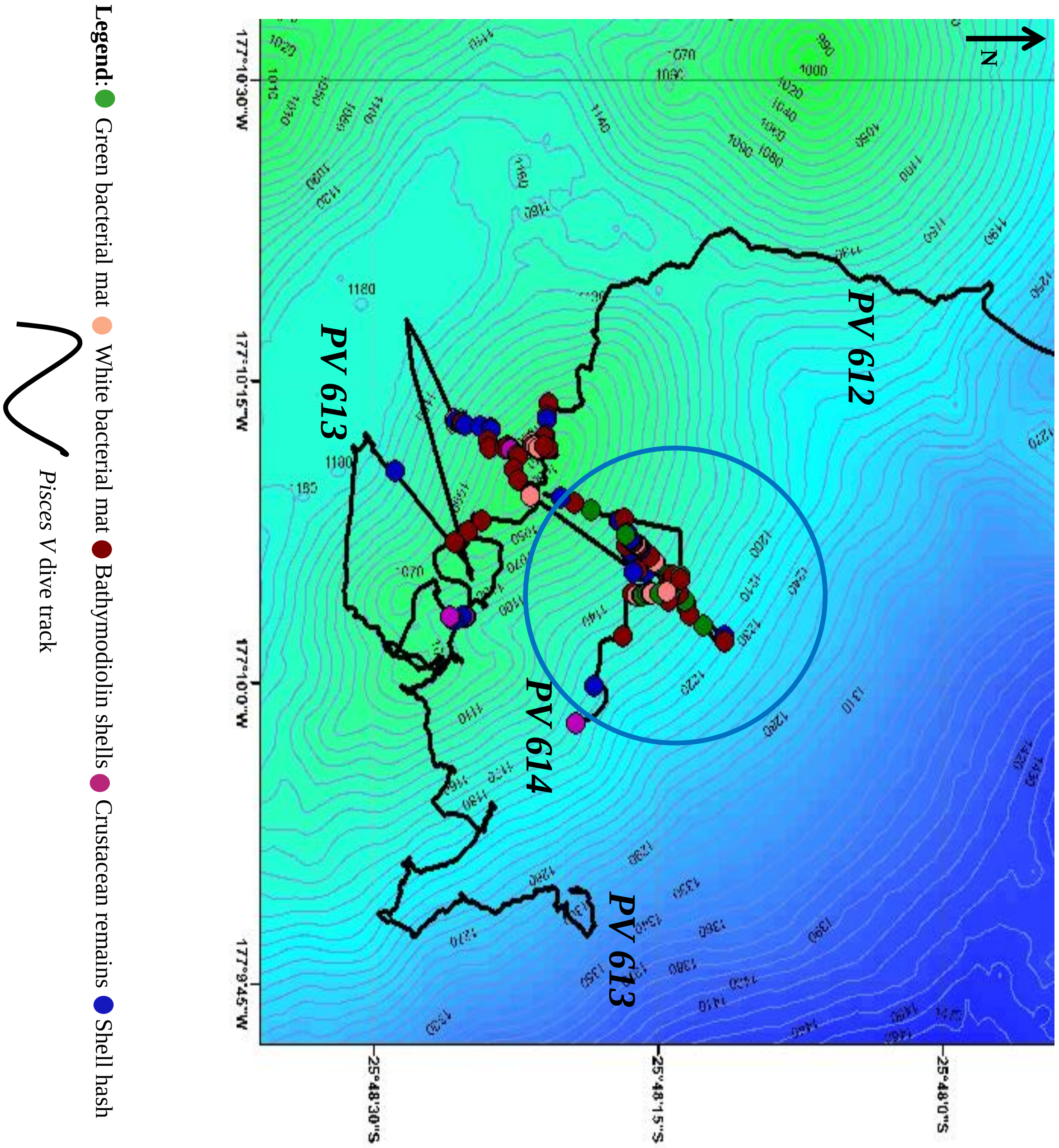


Figure 3.4: Habitat map showing the distribution of biogenic substrata around Monowai Caldera. The circle marks sites of the caldera where visual evidence of venting, in the form of hot shimmering water/black or grey smoke from small chimneys was noted.

3.1.2 FAUNAL ASSEMBLAGES ON MONOWAI CALDERA

The primary faunal groups of the caldera and their distribution are shown in Figures 3.5–3.7. Figure 3.5 shows the distribution of the four key vent taxa: the vent mussel *Bathymodiolus manusensis,* the vent shrimp *Alvinocaris* spp., the vent limpet *Lepetodrilus* sp., and the vent crab *Paralomis hirtella.* Vent mussels occurred as beds, and their distribution coincided with areas where there was adequate hard substratum cover in the form of bedrock, with a high number of observations seen in the circled area of venting. However, the mussel beds also occurred as isolated patches and did not quite equate to the spread of hard substrates in the caldera. In contrast, the vent shrimp and the crabs showed wide distributions into areas of the caldera that had a slightly higher percentage cover of soft substrate cover than hard substrate. In addition, these sites were not venting areas.

Wide distributions were also observed for larger motile megafauna (fish) (Figure 3.6); their occurrence was associated with the presence of expanses of soft substratum and isolated pockets of hard substrata. The vent zoarcid *Pyrolycus moelleri* was associated with mussel beds. Synaphobranchid fish occurred in a few samples. Macrourids generally did not occur along with any vent taxa, and as such showed very scattered distributions away from vent communities. Actinostolid and hormathiid anemones were observed alongside vent communities during image analysis. However, others (e.g. ‘fly-trap’ anemones, Family: Hormathiidae) occurred in isolation, on patches of poorly-sorted cobbles or attached to large boulders.

The two species of tubeworms recorded on Monowai were *Lamellibrachia juni* and *Oasisia fujikurai.* While *L. juni* occurred in small patches around the caldera and was restricted to areas of strong, focussed-diffuse flows often on high-relief outcrop areas, *O. fujikurai* was only recorded from two samples of hot shimmering water from cobbles and small pieces of volcanic rocks (Figure 3.7).

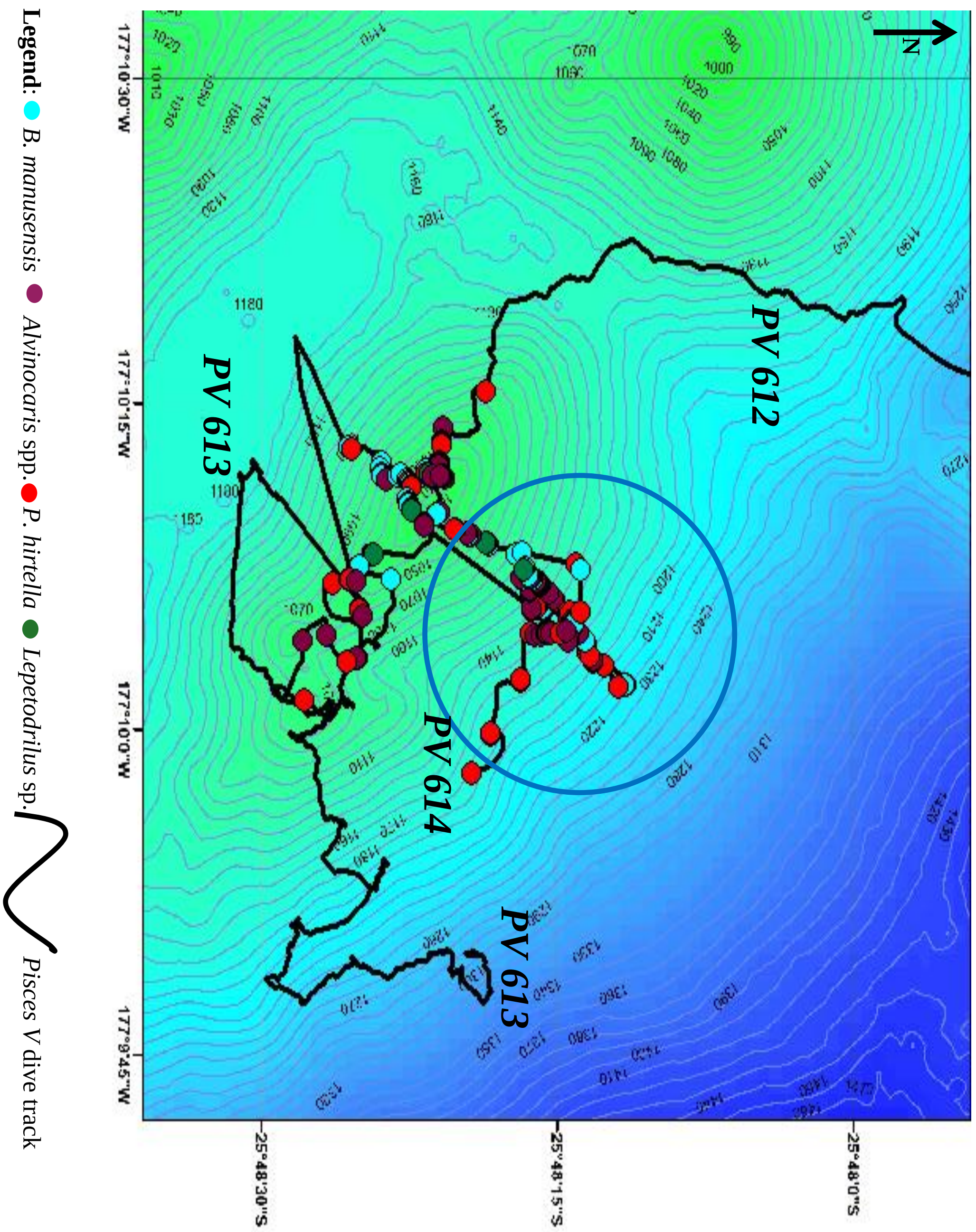


Figure 3.5: Distribution map of vent taxa as recorded on Monowai Caldera. The circle marks sites of the caldera where visual evidence of venting, in the form of hot shimmering water/black or grey smoke from small chimneys was noted.

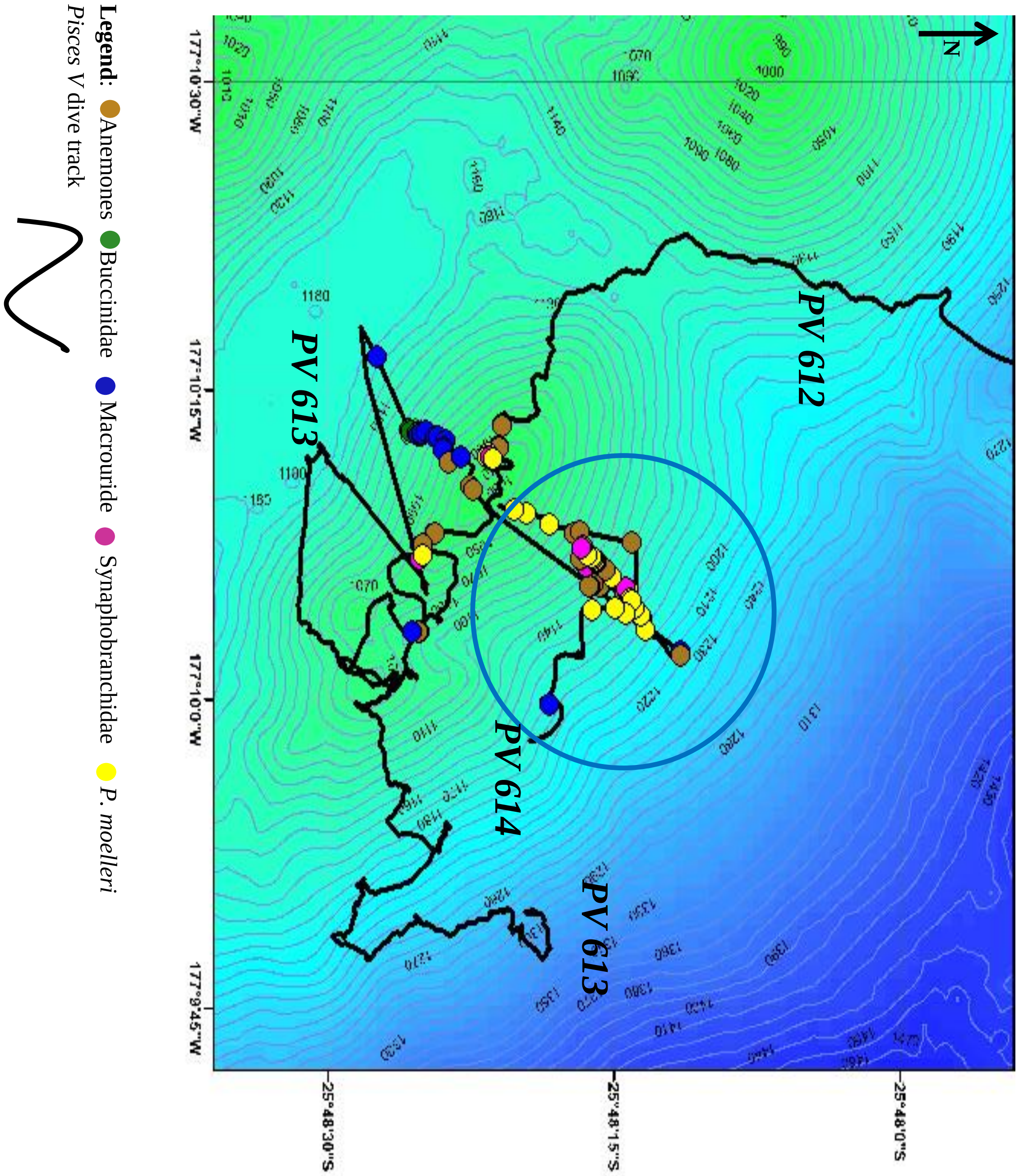


Figure 3.6: Distribution map of non-vent and larger megafaunal taxa on Monowai Caldera. The circle marks sites of the caldera where visual evidence of venting, in the form of hot shimmering water/black or grey smoke from small chimneys was noted.

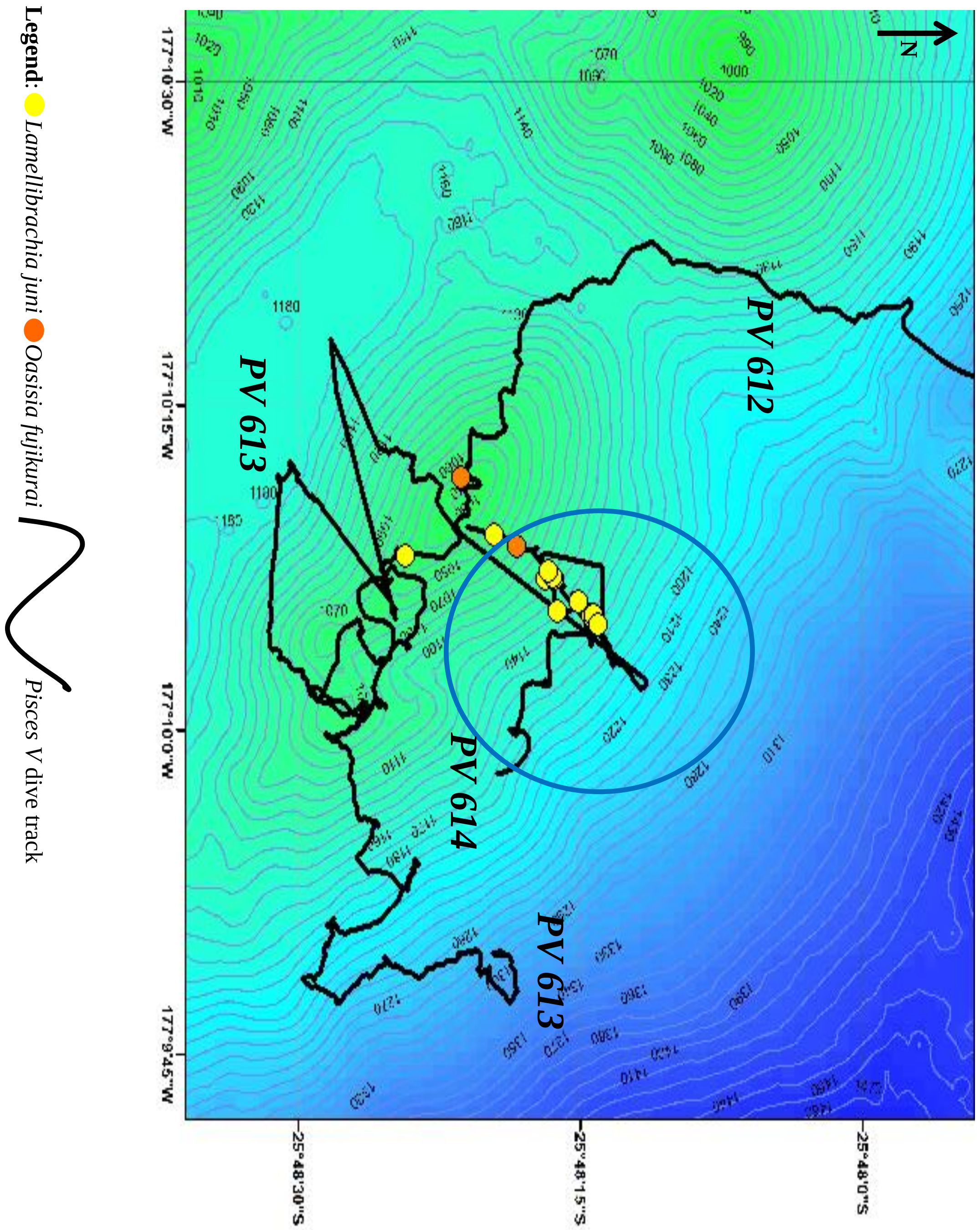


Figure 3.7: Distribution map of the two siboglinid (vent-tubeworm) species on Monowai Caldera. The circle marks sites of the caldera where visual evidence of venting, in the form of hot shimmering water/black or grey smoke from small chimneys was noted.

3.2 MULTIVARIATE ANALYSES OF COMMUNITY STRUCTURE AND ABIOTIC FACTORS

DistLM (Distance-based linear models) routine using Forward selection linked faunal data on Monowai to the three types of environmental factors recorded in this study, namely: substrate type, water depth, and proximity to vent sites. Table 3.1 lists all the abiotic variables (acquired from Forward selection sequential test) that had significant influence on the faunal community structure on Monowai Caldera. Marginal tests from this routine as well as results for other variables are listed in Appendix C. The key environmental variables responsible for the variation seen in the benthic community structure have been shown in a db-RDA plot (Figure 3.8). The two axes of the plot explained 72.9% of the variability in the faunal abundance data, and 25.2% of the relationship between faunal data and abiotic factors. The key variables contributing to the first axis of the plot (accounting for 45.1% of the variation) were mud, white bacterial mat, distance to vent sites, black sulphidic sediments, white sulphidic sediments, and sand. Water depth, green bacterial mat, chimneys, bedrock outcrop, bedrock with mud overlay, and crustacean remains correlated to the second axis of the plot (accounting for 27.8% of the variation). The results suggest that variables related to substrate and proximity to vent sites have a large effect on the benthic community structure on Monowai, in comparison to water depth. This supports Hypothesis 1: There is no relationship between water depth and community structure of vent taxa on Monowai.

Table 3.1: Results from DistLM routine showing permutation values (P) as well as increase in the proportion of variation linked to each environmental variable (Prop), and cumulative percentage contribution of each variable to the overall variation in the data set (Cumul).

Variables	R^2	SS Trace	Psuedo-F	P	Prop	Cumul
Mud	0.11	49200	21.29	0.001	0.11	0.11
Green bacterial mat	0.15	16667	7.49	0.001	3.89E-2	0.15
White bacterial mat	0.18	13513	6.27	0.001	3.15E-2	0.18
Bathymodiolin shell	0.20	10357	4.92	0.001	2.41E-2	0.20
Black sulphidic sediment	0.22	8258.3	4.002	0.005	1.92E-2	0.22
Sand	0.24	7540.8	3.71	0.007	1.76E-2	0.24
Bedrock outcrop	0.26	7432.7	3.72	0.002	1.73E-2	0.26
White sulphidic sediment	0.27	5213.6	2.64	0.017	1.21E-2	0.27
Crustacean remains	0.28	4700.7	2.40	0.052	1.09E-2	0.28
Bedrock with mud overlay	0.30	4128.5	2.14	0.04	9.64E-3	0.30
Chimneys	0.31	4893.4	2.56	0.02	1.14E-2	0.31
Distance to nearest vent	5.29E-2	22657	9.16	0.001	5.29E-2	5.29E-2
Water depth	6.48E-2	5129	2.08	0.04	1.19E-2	6.48E-2

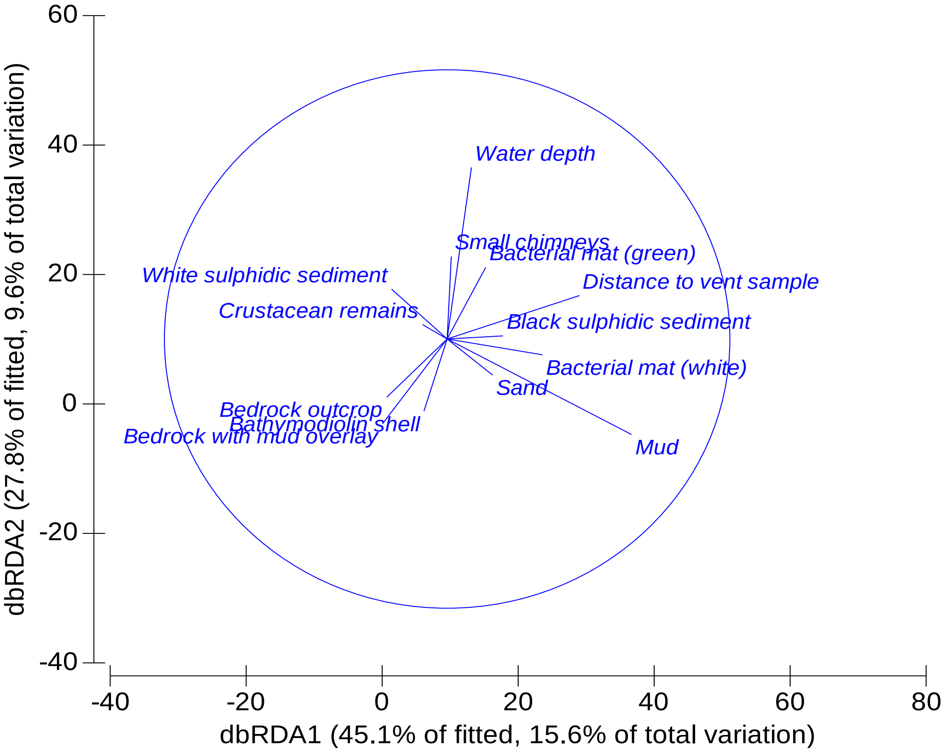


Figure 3.8: db-RDA plot of the primary environmental variables as recognised by the DistLM analysis, explaining the variation in the faunal abundance on Monowai Caldera. The length of each vector indicates the influence of that predictor variable on the faunal structure.

3.3 SUBSTRATE COMPOSITION AND HETEROGENEITY

Multivariate analysis (CLUSTER with SIMPROF) of the different substrate types on Monowai revealed seven groups of substrate types, i.e. groups **a**–**g** (Figure 3.9). At first glance, it appears that the composition of the groups as identified by SIMPER (Table 3.2) are similar, with only varying contribution percentages as points of difference. Nevertheless, these groups point to microhabitats within Monowai Caldera. The composition of Groups **e**–**g** essentially class them as areas of active venting (as already discussed in habitat mapping), due to the presence of volcanically altered bedrock, chimneys, bacterial mats, and sulphidic sediments (products of volcanism), alongside bedrock with sand/mud overlay. Furthermore, the CLUSTER analysis shows Euclidean distances of under 20 for all samples in groups **e** and **f**, pointing to obvious similarities between these samples. On the other hand, groups **a**–**d** represent areas of the caldera, located away from sites of venting. These groups were composed of a mix of soft sediment and larger hard substrate classes (e.g. boulders). Habitat heterogeneity and the strength of the difference between the substrate groups was further confirmed by a one-way analysis of similarity test (ANOSIM Global R = 0.969).

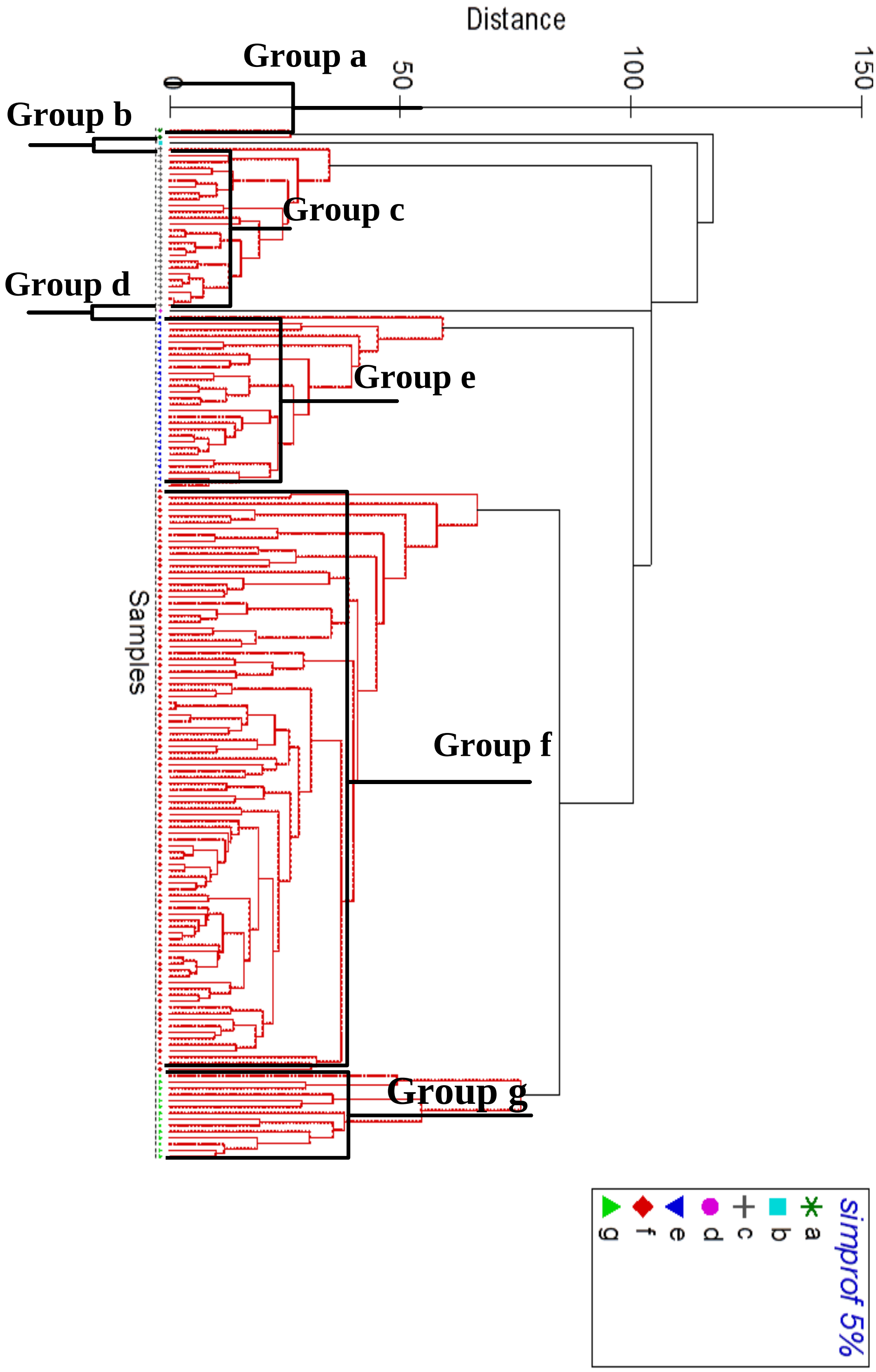


Figure 3.9: Dendrogram from a CLUSTER analysis of substrate types from all samples. Samples (labelled as Groups **a**–**g**) are listed on the horizontal axis, with Euclidean distance similarity percentage on the vertical axis (n= 166).

Table 3.2: SIMPER profile of the seven substrate groups, with substrate composition, average percentage cover values, and percentage contribution.

Group	Substrate type	Av. Value	Av. Sq distance	% Contribution
a	Sand	91.5	145	41.88
	Green bacterial mat	10	200	57.97
	Bedrock	0.5	0.5	0.14
b	Bedrock	86	7.4E3	-
	Bathymodiolin shell	36	1.17E3	-
c	Mud	76.9	101	35.82
	Shell hash	3.73	31.8	11.31
	Bathymodiolin shell	1.5	14.4	5.13
	Pebbles	1.31	23.3	8.30
	Boulders	1.12	12.4	4.04
	Yellow sulphidic sediment	1	26	9.25
	Black sulphidic sediment	0.92	11.4	4.04
	Crustacean remains	0.46	1.7	0.60
	Cobbles	0.30	1.26	0.45
d	Boulders	76	5.75E3	100
e	Bedrock with sand overlay	71.3	145	23.43
	Green bacterial mat	8.82	137	22.03
	White sulphidic sediment	5	64.1	10.34
	Bedrock	3.29	77.8	12.54
	Bedrock with mud overlay	2.18	67.1	10.82
	Volcanically altered bedrock	1.82	46.7	7.54
	Pebbles	1.43	43.7	7.05
	Bathymodiolin shell	1.43	17.7	2.86

Group	Substrate type	Av. Value	Av. Sq distance	% Contribution
	Small chimneys	1.36	6.31	1.02
	White bacterial mat	0.67	8.45	1.36
	Black sulphidic sediment	0.42	5.14	0.83
	Shell hash	0.25	0.417	0.07
f	Bedrock with mud overlay	67.6	235	30.62
	Bathymodiolin shell	5.88	53.74	7
	White sulphidic sediment	4.02	54.1	7.05
	Bedrock	3.53	61.3	8.00
	Shell hash	2.31	47.8	6.23
	Small chimneys	2.2	40	5.22
	Bedrock outcrop	2.14	55.9	7.29
	Green bacterial mat	1.96	29.1	3.80
	Mud	1.64	45	5.86
	Boulders	1.3	22.7	2.96
	White bacterial mat	1.27	77.4	10.09
	Bedrock with sand overlay	1.24	24.1	3.14
	Cobbles	0.61	8.35	1.09
	Volcanically altered bedrock	0.39	5.98	0.78
	Black sulphidic sediment	0.22	4.69	0.61

3.4 BENTHIC COMMUNITY STRUCTURE AND SUBSTRATE COMPOSITION

CLUSTER with SIMROF analysis of Monowai fauna revealed eight groupings in relation to the substrate heterogeneity/habitat diversity on Monowai Caldera (Figure 3.10). The resulting faunal groups mirrored the substrate groupings in Section 3.3. As in Table 3.2, the composition of the faunal groupings (Table 3.3) was very similar, albeit in different average abundances within groups. The separation of the groups, despite having similar compositions, is related to habitat differences, with certain taxa in areas of focussed-diffuse flows and weak-diffuse flows, and others in non-venting/background habitats. Given that the composition of groups **d**–**f** are exclusively vent taxa, these groups could be classed as vent communities. Group **f** encompassed a majority of the samples, with average similarity of faunal composition between samples in this group over approximately 90%.

From the mapping of faunal communities in Section 3.1.2, it was clear that the distribution of the vent crab *P. hirtella* and the vent shrimp *Alvinocaris* spp. extended beyond vent sites. Additionally, in several other samples, these two were the sole taxa near a focussed-diffuse flow vent. A similar result was seen in Table 3.3, with the composition of groups **a**–**c**, and group **g** being exclusively composed of these two taxa. These two taxa were often sighted on areas of isolated patches of hard substrates (e.g. boulders, cobbles) or expanses of soft sediment (sand/mud). On the other hand, group **h** was exclusively composed of non-vent taxa/background taxa (larger megafauna such as fish) that were recorded from the periphery of vent communities. The average dissimilarities between the faunal groups varied between 54% and over 90%, with the biggest dissimilarity percentage of 98.2% seen between group **e** and **h**. Dissimilarity percentage values for the eight faunal groups are listed in Appendix D. The strength of the difference in the composition of the assemblages with substrate change was confirmed (ANOSIM Global R = 0.851), thus supporting Hypothesis 2: substrate differences lead to differences in benthic community structure on Monowai.

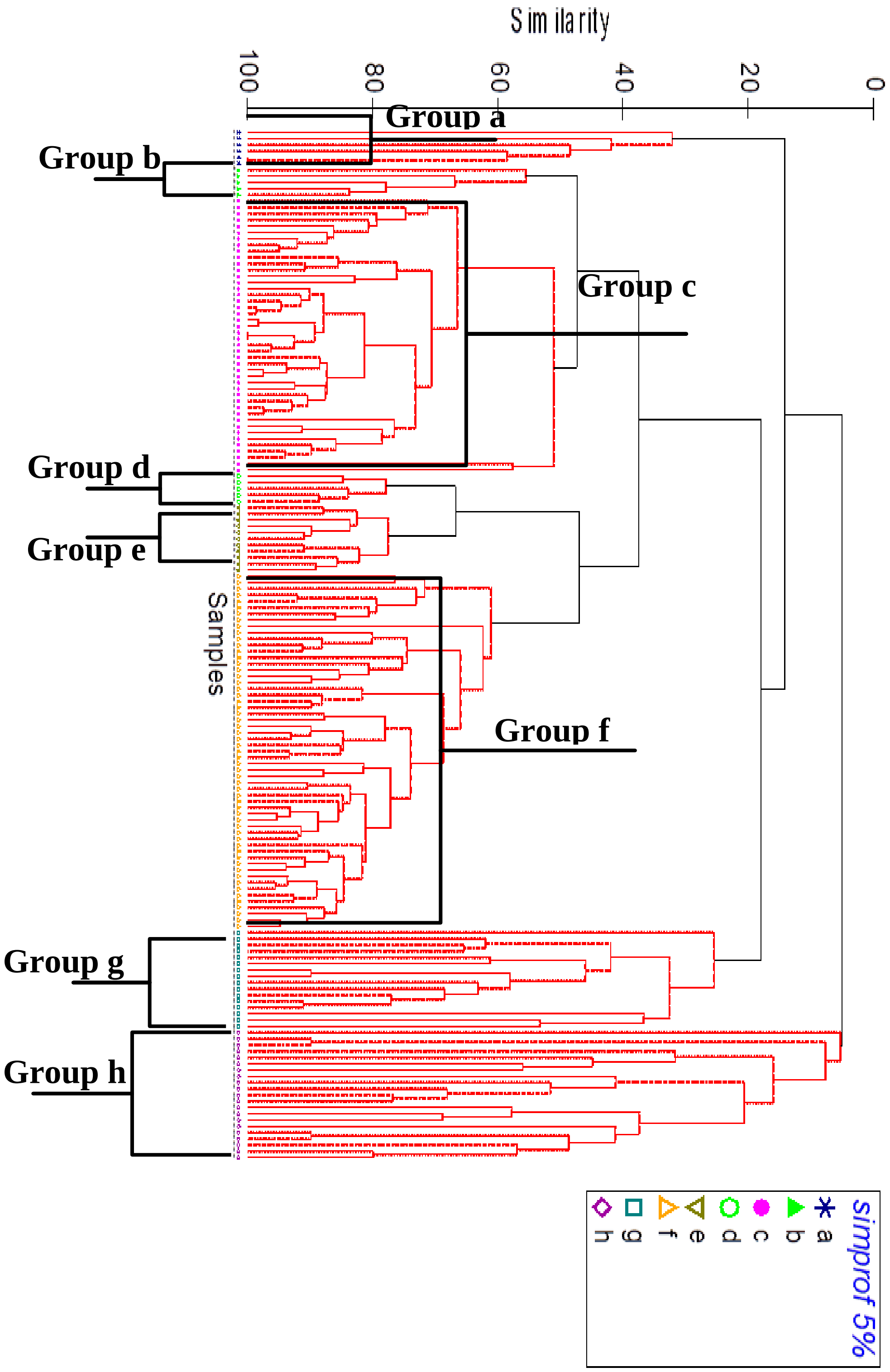


Figure 3.10: Dendrogram from a CLUSTER analysis showing eight groupings/ assemblages of samples. Samples (labelled as Groups **a**–**h**) are listed on the horizontal axis, with Bray-Curtis similarity percentage on the vertical axis (n= 166).

Table 3.3: SIMPER profile showing species composition, mean abundances[a], and percentage similarity contribution of the eight assemblages, according to substrate types. Only taxa with average abundances of 0.1 and over have been listed.

Group	Species	Av.abundance	Av similarity	Sim/SD	% Contribution
a	*Alvinocaris* spp.	0.59	46.07	2.41	100
b	*Alvinocaris* spp.	1.03	34.22	6.13	51.68
	Paralomis hirtella	0.88	30.79	5.29	46.49
c	*Alvinocaris* spp.	3.35	50.58	4.31	70.36
	Paralomis hirtella	1.35	19.13	1.66	26.62
d	*Lepetodrilus* sp.	6.76	34.86	6.16	43.12
	Bathymodiolus manusensis	4.11	19.81	6.54	24.50
	Alvinocaris spp.	3.89	14.89	2.31	18.41
	Paralomis hirtella	1.96	9.11	7.52	11.27
e	*Lepetodrilus* sp.	14.62	37.42	6.36	46.34
	Bathymodiolus manusensis	8.50	22.36	7.58	27.68
	Alvinocaris spp.	5.04	12.70	6.56	15.73
	Paralomis hirtella	2.15	5.47	3.01	6.77
f	*Bathymodiolus manusensis*	5.56	40.34	3.24	57.31
	Alvinocaris spp.	2.24	13.80	1.46	19.61
	Paralomis hirtella	1.51	11.07	2.46	15.73
g	*Paralomis hirtella*	0.84	39.17	2.19	92.40
h	Macrourids	0.35	14.30	0.88	63.68
	Synaphobranchids	0.13	2.26	0.23	10.08
	Invertebrate tracks	0.18	2.05	0.26	9.12
	Enigmaticolus sp.	0.42	1.93	0.21	8.58

[a] Data square-root transformed

3.5 BENTHIC COMMUNITY STRUCTURE AND DISTANCE TO THE NEAREST VENT SITE

The DistLM analysis indicated that distance to vents was one of the variables responsible for structuring the benthic communities on Monowai. In order to visualise the influence of distance to vents on benthic community structure, an MDS plot was produced that showed the samples coded for different distance bins. For ease of visualisation of the results within the MDS plot, samples were allocated to 50 m bins for distances up to 300 m from the nearest vent, followed by 500 m bins for distances over 300 m.

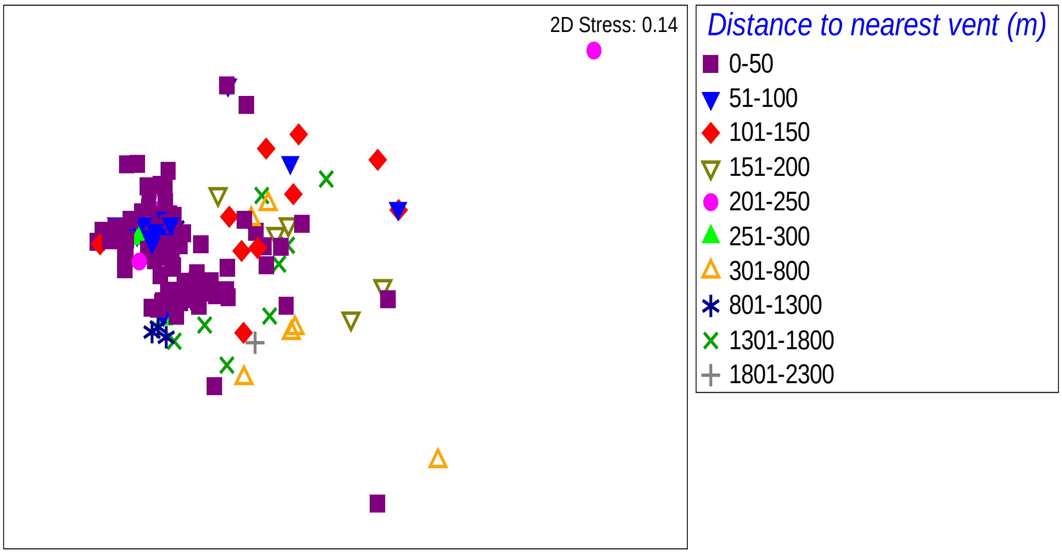


Figure 3.11: MDS plot of samples according to distance to the nearest vent (n= 166). Analysis performed on Bray-Curtis similarities of square-root transformed data.

A strong dominance was exhibited by taxa in samples that were less than 50 m from a vent (Figure 3.11), as evident from the tight clustering. Samples within 51–100 m, 101–150 m, 201–250 m, and 251–300 m were also components of this large cluster, indicating relatively similar assemblage composition. The similarity in the species composition of the groups but in different average abundances links to habitat differences and characteristics of individual vents. However, the presence of samples in the 801–1300 m bin next to the large cluster also indicates similar taxa composition, despite the distance from a vent (*Alvinocaris* spp.) The result from the MDS plot was reflected by the SIMPER analysis (Table 3.4) that identified samples in the 0–50 m bin to be composed exclusively of the three main vent taxa, i.e. *B. manusensis*, *Alvinocaris* spp., and *P. hirtella*. All subsequent groups up to 300 m also consisted of these vent taxa. As discussed previously, the presence of the vent shrimp *Alvinocaris* spp. (occurring in all samples, regardless of distance to a vent site) and the vent crab *P. hirtella* extended beyond areas that were sites of venting. These two taxa co-occurred with other mobile larger megafauna (macrourids), and sessile invertebrates (anemones) at distances of over 300 m. At distances of 1800–2300 m from a vent sample, the group consisted of alvinocarid shrimps and anemones, both taxa at low abundances of 0.2. Even though a one-way analysis of similarity (ANOSIM) revealed a weak assemblage group classification (Global R= 0.419), the above results support Hypothesis 3: The community structure changes in relation to distance to a vent site, with vent taxa replacing non-vent taxa with decreasing distance to a vent site.

Table 3.4: SIMPER profile of species composition, mean abundances[a], and percentage similarity contribution of groups located within 1800 m from the nearest vent. Only taxa with average abundances of 0.1 and over have been listed.

Group	Species	Av.abundance	Av. similarity	Sim/SD	% Contribution
0–50 m	*Bathymodiolus manusensis*	19.35	8.42	0.48	28.42
	Alvinocaris spp.	9.42	14.25	0.77	48.07
	Paralomis hirtella	2.60	5.99	0.88	20.22
51–100 m	*Bathymodiolus manusensis*	41.46	20.94	0.80	75.46
	Alvinocaris spp.	9.85	4.33	0.71	15.60
101–150 m	*Enigmaticolus* sp.	1.64	5.50	0.33	45.69
	Paralomis hirtella	1.47	3.92	0.29	32.53
	Macrourids	0.15	1.57	0.39	13
151–200 m	*Paralomis hirtella*	0.36	6.20	0.54	47.60
	Enigmaticolus sp.	0.24	1.63	0.32	12.53
	Invertebrate tracks	0.10	2.35	0.32	18.06
201–250 m	*Bathymodiolus manusensis*	28	20.59	0.81	87.63
	Alvinocaris spp.	6	2.21	0.90	9.40
251–300 m	*Alvinocaris* sp.	27.50	35.71	-	98.86
301–800	*Paralomis hirtella*	0.15	1.33	0.26	8.99
	Invertebrate tracks	0.12	2.67	0.26	17.98
	Macrourids	0.26	4.34	0.44	23.82
	Alvinocaris spp.	0.10	4.51	0.41	30.40
801–1300 m	*Alvinocaris* spp.	13.75	37.33	1.01	99.77

1301–1800 m	*Alvinocaris* spp.	1.37	7.22	0.41	45.01

[a] Data square-root transformed

3.6 SMALL-SCALE EXAMINATION OF BENTHIC COMMUNITY STRUCTURE AND VENT OPENINGS

Small-scale examination of the impact of distance from a vent opening on the benthic community structure identified four faunal groups. Group **a** formed the largest group with samples showing similarities of over 90%, composed exclusively of *Alvinocaris* spp. and *P. hirtella*. During image analysis, these two taxa were observed to be always present very near to the rim of vent openings that had strong, focussed diffuse-venting. Groups **b**–**d** consisted of similar taxa composition representing communities around low-temperature weak diffuse hydrothermal flow. These groups were composed of *Alvinocaris* spp., *P. hirtella, B. manusensis* and the vent limpet *Lepetodrilus* sp. The latter two taxa were located at distances of beyond 50 cm from a vent opening. Even though all the groups shared similar taxa (Table 3.5) in their respective samples, a one-way analysis of similarity (ANOSIM) revealed that the faunal group classification was relatively strong (Global R=0.876).

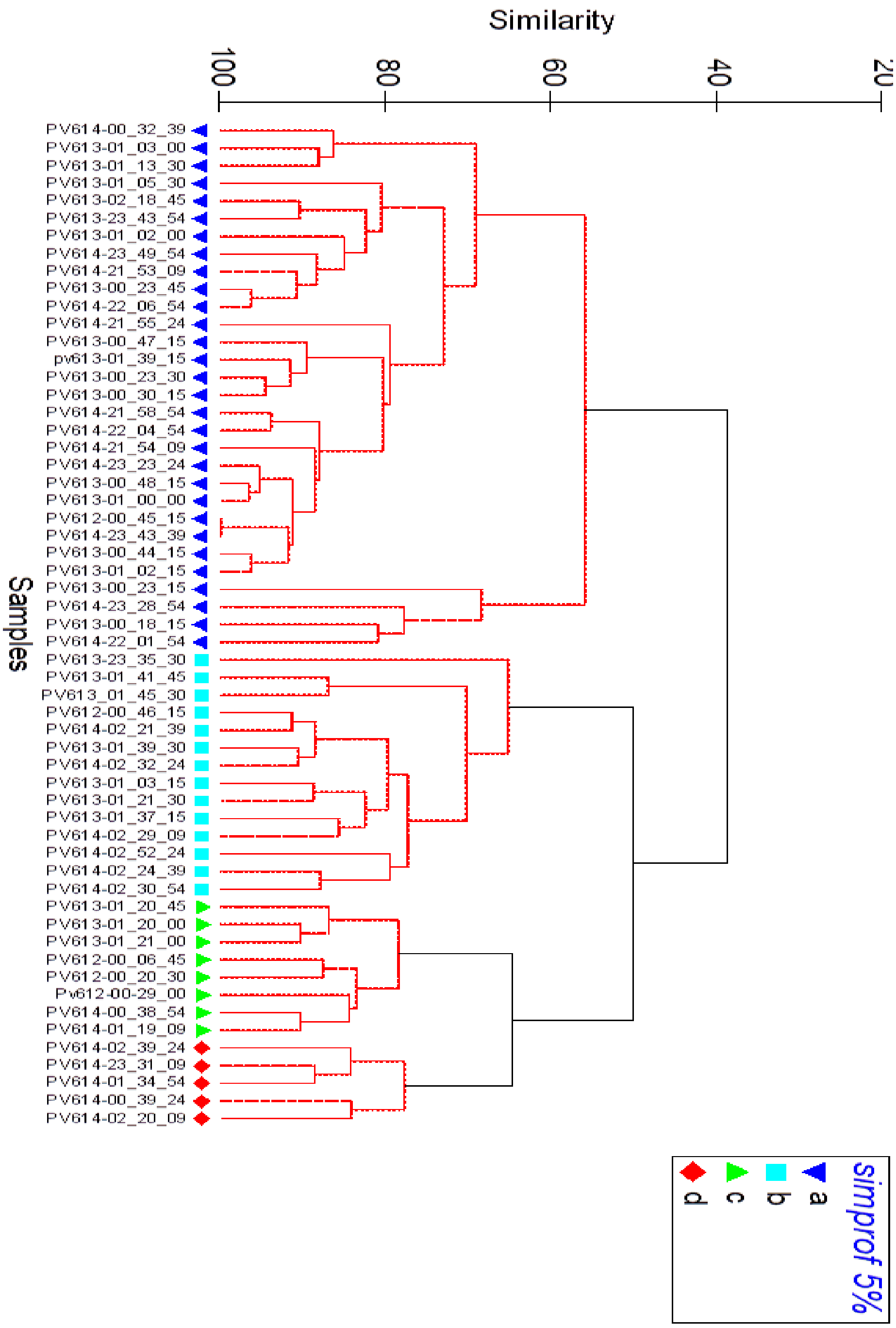


Figure 3.12: Dendrogram from a CLUSTER analysis of samples with vent openings, showing four groupings. Samples are listed on the horizontal axis, with Bray-Curtis similarity percentage on the vertical axis (n= 56).

Table 3.5: SIMPER profile of species composition, mean abundances[a], and percentage similarity contribution of the four assemblages, according to distance from a vent opening (within samples).

Group	Species	Av. abundance	Av. similarity	Sim/SD	% Contribution
a	*Alvinocaris* spp.	3.06	46.23	3.58	60.01
	Paralomis hirtella	1.54	26.32	4.56	36.54
b	*Paralomis hirtella*	1.68	12.71	4.78	16.76
	Bathymodiolus manusensis	5.67	41.25	4.60	54.43
	Alvinocaris spp.	2.86	17.69	2.09	23.33
c	*Lepetodrilus* sp.	15.76	39.00	7.39	47.72
	Bathymodiolus manusensis	8.50	21.79	9.40	26.67
	Alvinocaris spp.	5.40	12.67	5.30	15.50
	Paralomis hirtella	2.32	5.72	2.90	7.00
d	*Lepetodrilus* sp.	6.79	34.97	6.19	43.30
	Bathymodiolus manusensis	4.11	19.94	6.99	24.69
	Alvinocaris spp.	3.85	14.44	2.13	17.89
	Paralomis hirtella	1.89	8.75	7.97	10.83

[a] Data square-root transformed

3.7 BENTHIC COMMUNITY STRUCTURE AND TEMPERATURE OF VENT-FLUIDS

Three distinct faunal groups were identified by CLUSTER with SIMPROF analysis for samples (n=14) that had their vent fluids measured with a temperature-probe (Figure 3.13). Group **a** formed the largest group, representing taxa that showed tolerances to high vent-fluids temperatures (>30 °C), i.e. *Alvinocaris* spp. and *P. hirtella* (Table 3.6). These results follow on from Section 3.6 where these two taxa formed a distinct group by occurring closes to vent openings. The SIMPER routine (Table 3.6) identified similar taxa in groups **b** & **c**, with the exception of *P. hirtella* that did not occur in group **b**. Groups **b** and **c** consisted of taxa that were observed as part of a well-established vent community and around vents that showed low temperatures (<30 °C), and as such occurred at distances further away from the zone where the vent shrimps and crabs occurred (Table 3.5). Despite a small sample size for the analysis, an ANOSIM routine revealed the strength of faunal classification groups (Global R= 0.998). The above results support the hypothesis on small-scale changes to the community structure with distance to a vent opening, and vent fluid temperatures.

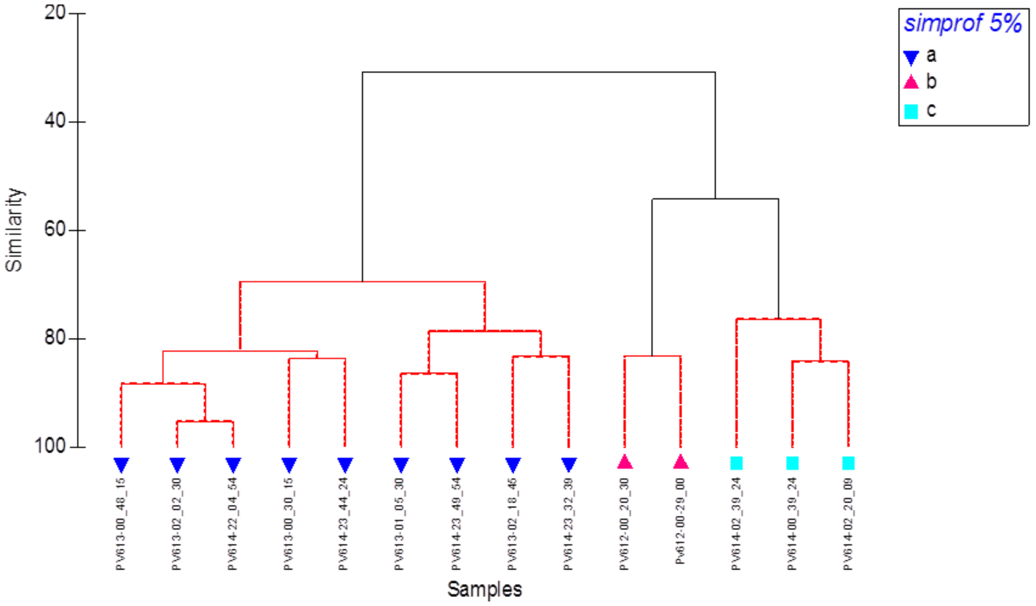


Figure 3.13: Dendrogram from a CLUSTER analysis of samples with temperature-sampled vents, showing three groupings. Samples are listed on the horizontal axis by stations numbers, with Bray-Curtis similarity percentage on the vertical axis (n= 14).

Table 3.6: SIMPER profile showing species composition, mean abundances[a], and percentage similarity contribution of the four assemblages, according to temperature of vent fluids.

Group	Species	Av. abundance	Av similarity	Sim/SD	% Contribution
a	*Alvinocaris* sp.	3.59	46.54	4.92	61.52
	Paralomis hirtella	1.62	25.08	4.52	33.15
b	*Lepetodrilus* sp.	20.18	47.34	-	56.90
	Bathymodiolus manusensis	8.34	20.65	-	24.82
	Alvinocaris sp.	5.62	11.55	-	13.88
c	*Lepetodrilus* sp.	6.87	38.64	5.09	48.92
	Bathymodiolus manusensis	3.72	19.63	6.08	24.86
	Alvinocaris sp.	2.80	10.52	2.25	13.32
	Paralomis hirtella	1.56	8.72	14.76	11.04

[a] Data square-root transformed

3.8 UNIVARIATE ANALYSES OF ABIOTIC FACTORS ON TAXA RICHNESS AND ABUNDANCE

3.8.1 Water depth

The relationship between taxa richness with changes in water depth (Figure 3.14A) was very weak, with insufficient evidence of a pattern to suggest that the overall number of taxa declined with increasing water depth (p-value=0.94). A similar weak relationship was seen in change of taxa abundance with water depth (Figure 3.14B). Although a slight decline in abundance was seen in samples greater than 1170 m, there was no evidence to establish this (p=0.05). Furthermore, the low r^2 values for both analyses suggest that water depth accounted and explained for a very small variance in the response variables. The results support Hypothesis 1: There is no relationship between water depth and taxa richness and abundance on Monowai.

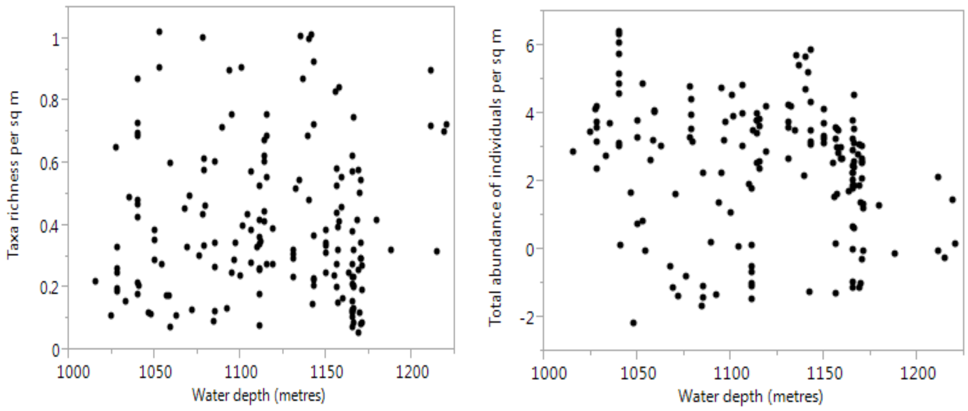


Figure 3.14A: Regression analysis of change in taxa richness (standardised to 1 m^2) with water depth (n= 166, r^2=2.988e–05, df=164, F=0.004, p=0.94).

Figure 3.14B: Regression analysis (2nd order) of change in taxa abundance (log transformed) per m^2 with water depth (n= 166, r^2= 0.04, df=163, F=3.04, p=0.05).

3.8.2 SUBSTRATE COMPOSITION ON MONOWAI CALDERA

Figure 3.15 shows the mean percentage cover of 13 main substrate types across all dives on Monowai Caldera. Only substrate classes with mean percentage covers of over 1% are displayed, with other substrate classes that occupied percentage covers of less than 1% listed in Appendix D. An overall dominance by mud overlaying bedrock (38%) was noticeable, followed by mud (13.5%) and bedrock with sand overlay (12.7%) that showed similar mean percentages, as observed from overlaps in their standard error bars. Similarly, bedrock and bedrock outcrops were not different due to overlap of their respective standard error bars. Bathymodiolin shells (4.2%) and shell hash (1.9%) contributed to the bulk of the biogenic substrates across all samples on Monowai Caldera.

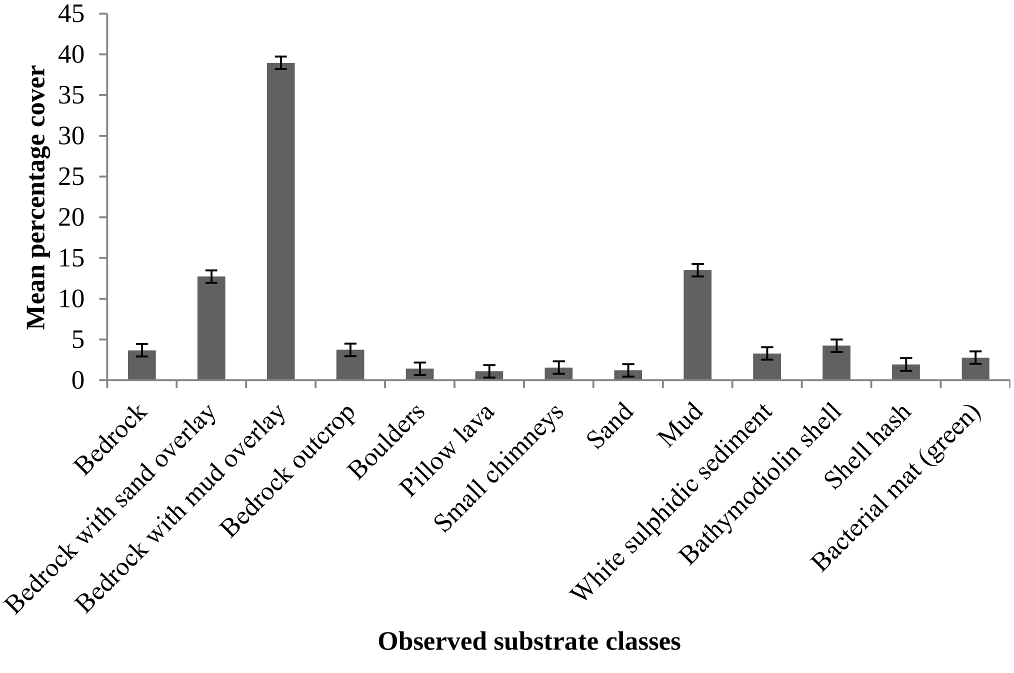


Figure 3.15: Mean percentage cover of observed substrate types (hard, soft, and biogenic) (n=166) on Monowai Caldera. Error bars are standard error of the mean.

3.8.3 EFFECT OF SUBSTRATE COMPOSITION ON TAXA RICHNESS AND ABUNDANCE

The relationship between taxa richness and percentage cover of hard substrate (Figure 3.16A) was not significant (p=0.97). Even though a slight increase in the number of taxa was seen in samples with more than 30% hard substrate cover, there was still an overall lack of clear evidence to suggest that the presence of hard substrates is responsible for variations in taxa richness (r^2=0.001). In comparison, a relatively strong relationship (p=<0.001, r^2=0.23) was seen between taxa abundance and hard substrate cover. Taxa abundance increased linearly, achieving peak numbers of individuals at intermediate percentage covers of 60%. However, taxa abundances plateaued at 75–80% percentage cover, such that samples exclusively composed of hard substrata did not necessarily translate to highest taxa abundances.

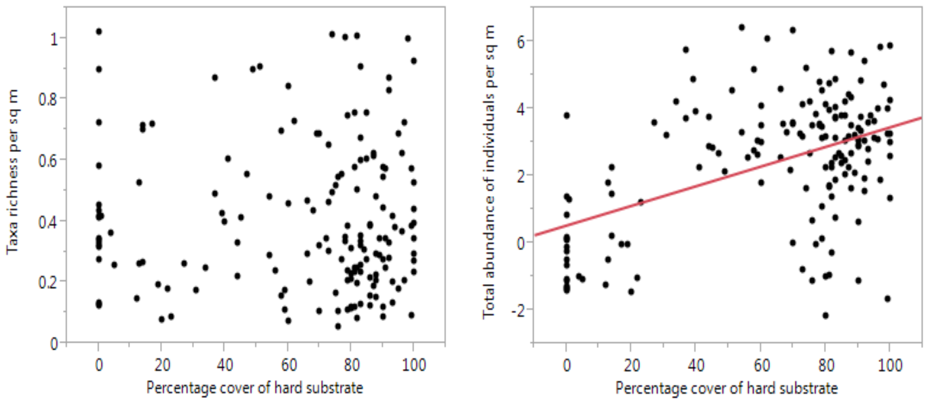
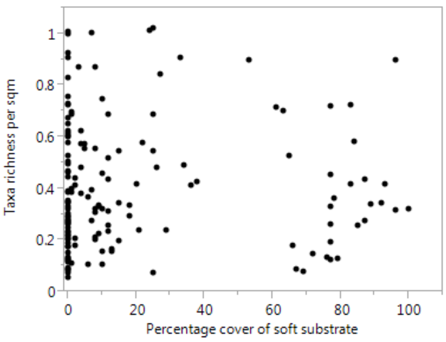


Figure 3.16A: Regression analysis (3rd order) of change in taxa richness (standardised to 1 m^2) with percentage cover of hard substrate (n= 166, r^2=0.001, df= 162, F=0.07, p=0.97).

Figure 3.16B: Regression analysis of change in taxa abundance (log-transformed) per m^2 with percentage cover of hard substrate (n=166, r^2= 0.23, df=164, F= 49.17, p= 5.83x10^{-11}, y = 0.029x+0.537).



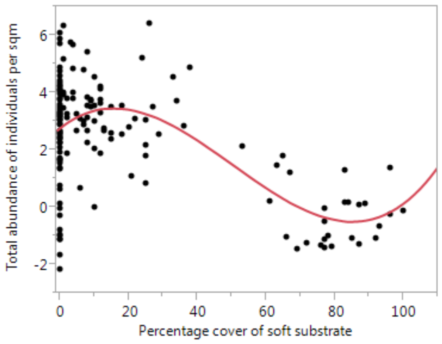


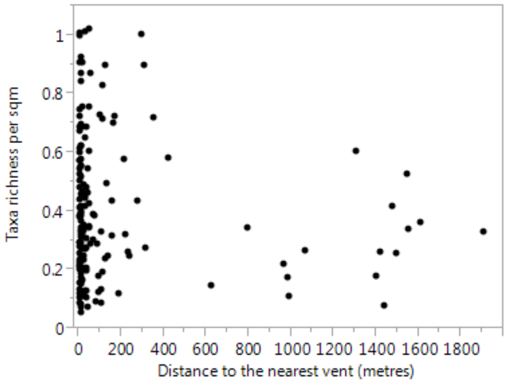
Figure 3.17A: Regression analysis (3rd order) of change in taxa richness (standardised to 1 m²) with percentage cover of soft substrate (n= 166, r²=0.03, df= 162, F=1.59, p=0.19).

Figure 3.17B: Regression analysis (3rd order) of change in taxa abundance (log-transformed) per m² with percentage cover of soft substrate (n=166, r^2= 0.39, df=162, F= 35.14, p= 2.2×10^{-16}, $y = 2E\text{-}05x^3 - 0.0036x^2 + 0.0941x + 2.7721$).

Taxa richness (Figure 3.17A) showed an overall inverse and weak relationship with soft substrates (p=0.19, r^2=0.03). There is slight evidence of a gradual decline in the number of species with increasing soft substrate cover. However, there appears to be no difference between taxa numbers in areas of 20% soft substrate cover and those of 60%–80% soft substrate cover. Figure 3.17B showed a decline in the total number of individuals after 40% soft substrata cover, such that at 100% soft sediment cover, the number of surface biota was reduced to fewer than 10 individuals. The above results suggest that differences in substrate do not have a strong effect on taxa richness, and as such accounted for a very small proportion in explaining variation of the response variable in the caldera. This does not support the first part of Hypothesis 2: Substrate differences lead to differences in richness of vent taxa on Monowai. However, the impact on taxa abundances due to changes in hard and soft substrate cover was evident, with the total number of individuals mirroring the change in percentage cover of the respective substrata over all samples. Therefore, the findings support the second part of Hypothesis 2: Substrate differences lead to differences in abundance of vent taxa on Monowai.

3.8.4 EFFECT OF DISTANCE TO NEAREST VENT ON TAXA RICHNESS AND ABUNDANCE

The relationship between taxa richness and the distance to the nearest vent site was not significant (p=0.34, r^2=0.02). High taxa richness was recorded in samples that were less than 300 m from a vent site, as seen from the clustering of sample points on the left-hand axis of the graph. Taxa richness gradually declined at distances of over 400 m, only to peak again at 800 m and 1400 m.



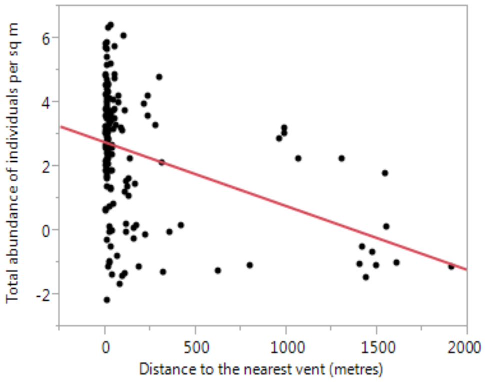


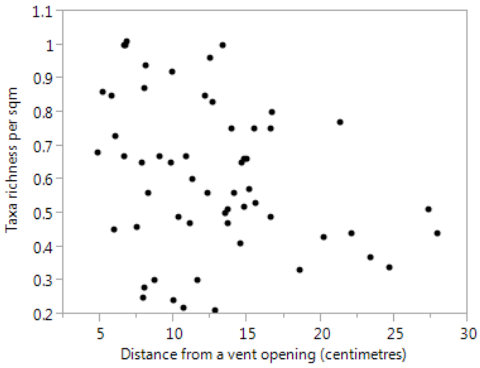
Figure 3.18A: Regression analysis (3rd order) of change in taxa richness (standardised to 1 m²) with distance to the nearest vent (n= 166, r²=0.02, df= 162, F=1.13, p=0.34).

Figure 3.18B: Regression analysis of change in taxa abundance (log-transformed) per m² with distance to the nearest vent (n=166, r^2= 0.19, df=162, F= 13.13, p= $1.02x10^{-7}$, y = -0.001x + 2.764).

Figure 3.18B showed a strong relationship between taxa abundance and distance to the nearest vent site (p<0.001, r^2=0.19). Similar to Figure 3.18A, the total number of individuals showed a negative relationship with distance to the nearest vent, with highest abundances seen in samples less than 300 m. A steady decline in abundance was recorded in samples more than 400 m from a vent site, followed by a slight increase in abundances at distances of over 1 km from a vent site. The results suggest that distance to vent does not have a strong effect on the number of species, thus rejecting the first part of Hypothesis 3: Distance to a vent site is inversely proportional to the richness of vent taxa on Monowai. However, distance to the nearest vent site strongly correlates to the abundance of taxa, with high abundances at distances of less than 200 m from a vent site (as also inferred from multivariate analyses). These findings support Hypothesis 3: Distance to a vent site is inversely proportional to the abundance of vent taxa on Monowai.

3.8.5 EFFECT OF SMALL-SCALE DISTANCE ON TAXA RICHNESS AND ABUNDANCE

On a small-scale, there was an overall decline in taxa richness with increasing distance from a vent opening (Figure 3.19A). However, this relationship was not significant (r^2=0.10, p= 0.12). Taxa richness was highest and remained unchanged at distances of up to 15 cm away from a vent opening, with few vent taxa located at distances of over 20 cm. The pattern for taxa abundance was similar to that for taxa richness (Figure 3.19B). The highest taxa abundance was recorded at distances of under 20 cm from a vent, and then decreased with increasing distance from a vent opening. However, this negative relationship was also not significant (r^2= 0.08, p-value=0.23).



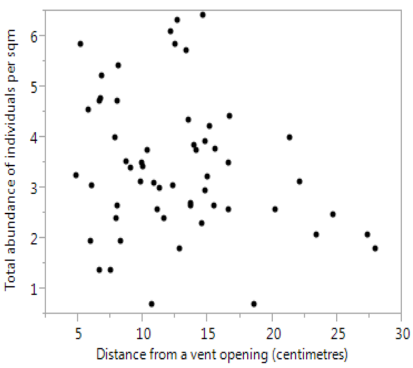
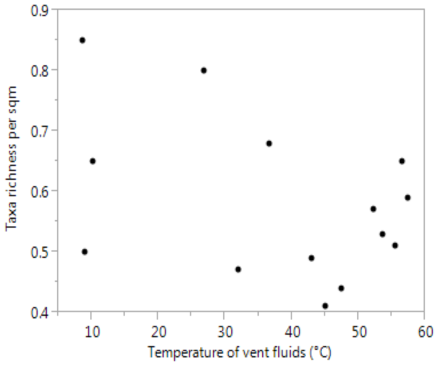


Figure 3.19A: Regression analysis (3rd order) of change in taxa richness (standardised to 1 m²) with distance from a vent opening (n= 57, r^2=0.10, df=53, F=1.98, p=0.12).

Figure 3.19B: Regression analysis (3rd order) analysis of change in taxa abundance (log-transformed) per m² with distance from a vent opening (n=57, r^2= 0.08, df=53, F= 1.48, p=0.23).

3.8.6 EFFECT OF VENT-FLUID TEMPERATURE ON TAXA RICHNESS AND ABUNDANCE

The number of vent sites that *Pisces V* sampled with a temperature-probe were relatively low (n=14), due to which the data presented here might not be a fair representation of the overall patterns. Nevertheless, the results provide an overview of faunal zonation with changes in vent-fluid temperature. Figure 3.20A shows a slight decline in taxa richness with increasing vent fluid temperature. The number of taxa that could tolerate surrounding (<30 cm) a vent emanating fluids of < 20 °C was higher than those at temperatures of over 30 °C. However the overall relationship was still weak (p-value= 0.14), as taxa richness increased at temperatures over 55 °C. A similar relationship was obvious when comparing taxa abundances and vent-fluid temperatures, with low numbers of individuals encountered at high temperatures (> 30 °C).



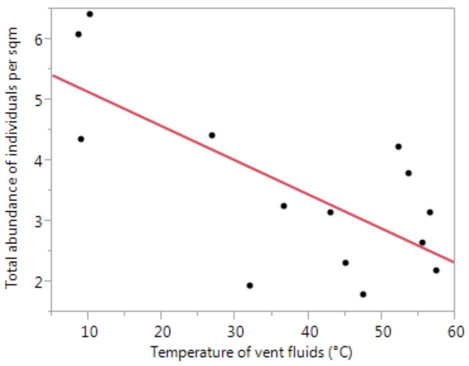


Figure 3.20A: Regression analysis (3rd order) of change in taxa richness (standardised to 1 m²) with temperature of vent fluids (n= 14, r^2=0.41, df=10, F=2.29, p=0.14).

Figure 3.20B: Linear regression of change in taxa abundance (log-transformed) per m² with temperature of vent fluids (n=14, r^2= 0.51, df=12, F= 12.29, p=0.004, y=-0.056x+5.697).

The above results suggest that on a smaller spatial scale, the effect of small-scale distances to a vent opening and the temperature of vent fluids do not have a significant effect on the taxa richness. However, the temperature of vent fluids has an impact on the total number of individuals surrounding a vent opening (r^2=0.51), and accounts for patterns of zonation seen within assemblages.

CHAPTER 4: DISCUSSION

The benthic community structure on Monowai is similar to that of many other chemosynthetic ecosystems that are characterised by high biomass and low diversity (Grassle, 1985). Taxa on Monowai such as *Bathymodiolus manusensis* (vent mussel), *Alvinocaris* spp. (vent shrimps), and *Lepetodrilus* sp. (limpets) can be characterised as vent-obligate, similar to Barry et al. (1996) who defined such taxa by their distribution being restricted to areas “in direct proximity to fluids rich in sulphide, methane, or other reducing inorganic compounds”. The lithodid crab *Paralomis hirtella*, although found in high abundances near venting areas, also had a wider distribution into non-venting background environments (stretches of soft substratum and isolated pockets of hard substrate such as boulders and cobbles.), as also reported by Ohta & Kim (2001). Although species in this genus have been classed as non-vent endemics (Watanabe et al., 2010), their presence around vents in high numbers suggests their tolerance to the chemical-laden environment near vents (discussed further in Section 4.4). *B. manusensis* also showed patchy distribution on Monowai and at linear distances of over 100 m from a source of diffuse-venting. This mytilid species has also been reported from the active hydrothermal vents of the South-Su and Solwara 1 sites in Papua New Guinea (Beaudoin et al., 2012), where it forms extensive beds in the outer zone (areas furthest away from actively venting chimneys). Larger megafauna such as synaphobranchid fish and the vent eelpout *Pyrolycus moelleri* (Zoarcidae) were observed co-occuring with vent taxa. *P. moelleri* was almost always associated with mussel beds. This species has been reported from upper slope depths of the Brothers Seamount, and on talus lava or near diffuse vents (Anderson, 2006). Elsewhere, *Pyrolycus manusanus* has been observed living in similar habitats amongst mussel beds on the hydrothermal vent fields of the Manus Basin (Machida & Hashimoto, 2002). Away from vent sites on Monowai Caldera, larger megafauna, such as macrourids and cephalopods occurred in low densities.

Previous faunal studies of Monowai are limited, with few studies such as by Short & Metaxas (2011) describing megafauna as largely dominated by mussel beds, anemones, crustaceans, and large fish. The current study confirms those observations.

However, differences arise when comparing Monowai's diffuse vents to other seamounts in the Kermadec volcanic arc. For example, the summit of the Brothers cone (de Ronde et al., 2005), unlike Monowai, has been reported as largely dominated by sulphide worms instead of mytilid mussels, along with limpets, alvinocarid shimps, bacterial mats, and stalked barnacles (de Ronde et al., 2005). The presence of microbial mats around diffuse-style vents, as well as inactive vents on Monowai has been reported elsewhere (e.g. southern Mariana Trough; Kato et al., 2010). Two types of bacterial mat cover were observed on Monowai Caldera: lime/olive green microbial mat cover was recorded from basaltic rocks near venting areas, whereas white microbial mat cover was present on bedrock with mud overlay, at a considerable distance from venting areas. This observation is consistent with general observations of bacterial groups that can thrive in a range of niches within hydrothermal vent environments, from hot vent fluid and plumes (black smokers) to rock surfaces in low-temperature diffuse-vent flow areas (Podar et al., 2002).

Suspension-feeding organisms such as anemones, sponges, and corals form an essential part of seamount benthic fauna (Stocks, 2004). No corals were recorded on Monowai. However, individual boulders were typically dominated by bivalve molluscs or predatory cnidarians (such as hormathiid anemones). Cnidarian abundance and diversity appeared to be low on Monowai compared to other studies such as that by Rowden & Clark (2010), who found at least 70 species of cnidarians occupying different substrata on seven seamounts in the southern Kermadec volcanic arc. However, the differences in the results could be because of differences in sampling effort, as most seamounts in the southern Kermadec volcanic arc have been relatively well sampled compared to seamounts in the northern Kermadec volcanic arc. Furthermore, the only way to identify anemones to species is by physical examination and dissection (D. Fautin, personal communication, 14 March 2012).

Other vent taxa found on Monowai included live bushes of the vent tubeworms *Lamellibrachia juni* and *Oasisia fujikurai*, which were present in a relatively small number of samples. Such scattered distributions of these two tubeworms species match previous records (Wysoczanski & Clark, 2012) for the Kermadec volcanic arc. *L. juni* were recorded primarily around strong, focussed diffuse-flow vents on bedrock outcrops. Patchy distributions of this species of tubeworms were also recorded by Short & Metaxas (2011) on Monowai's Mussel Ridge. Similar to this study, the authors noted the presence of tubeworms solely around areas of fluid venting indicated by “altered rocks and sulphur precipitation”. In other areas of the caldera, dead tubeworms were seen away from the sites of venting. *L. juni* has been reported from the Brothers Caldera in the southern Kermadec arc (Baco et al., 2010), DESMOS site in Manus Basin, and TOTO Caldera in the southern Mariana volcanic arc (Kojima et al., 2006). Their occurrence has also been reported in reducing environments of the western Pacific: vent fields of the Iheya Ridge and the North Iheya knoll in the Okinawa Trough, PACMANUS in the Manus Basin, seep areas of the Kuroshima knoll, and Nankai Trough off Muroto Point (Kojima et al., 2001). The second species of tubeworm identified on Monowai Caldera was *Oasisia fujikurai*, which also inhabits the Brothers Caldera, Kermadec volcanic arc (Kojima et al., 2006). A closely related species, *O. alvinae*, has been reported from the Eastern Pacific (Baker et al., 2010). Unlike *L.juni*, *O. fujikurai* was observed in only two samples in the present study. In comparison to other siboglinid species, there appears to be insufficient information on the habitat preference of this tubeworm species.

Lastly, no echinoderms were recorded on Monowai Caldera. This is unlike studies by Rowden et al. (2003) who found 35 species of echinoderms on three seamounts of the southern Kermadec arc. Other studies recorded large concentrations of the predatory sea star *Sclerasterias eructans* on Rumble III and Rumble V volcanoes (Mah & Foltz, 2011; McKnight, 2006), and dense patches of the echinoid *Dermechinus horridus* on the flanks of seamounts (Wysoczanski & Clark, 2012). Similarly, echinoderms have been observed in other studies as a component of the peripheral vent community; such as chiridotid holothurians associated with diffuse-vent openings of the North Fiji Basin and Manus Basin (Ohta & Kim, 2001), and predatory asteroids on the shell beds of Volcano 19, Tonga arc (Stoffers et al., 2006). The diffuse vents of Monowai are comparable to those found in the North Fiji Basin, Manus Basin and Okinawa Trough; all of which have records of echinoderms associated with either diffuse vent openings or the peripheral communities, due to the low heavy-metal content in the water column.

An explanation for the absence of certain classes of echinoderms on Monowai, such as holothurians, could be due to the absence of high temperature (>250 °C) vents in the vicinity, that elevate production and microbial biomass (Arquit, 1990). It is unclear whether the lack of echinoderms could be as a result of inadequate sampling or a true absence of this phylum on Monowai. If the latter is true, then this would warrant further investigation.

The subsequent sections of this chapter consist of detailed discussion of the influence of the three key environmental variables on faunal richness, abundances, and the overall benthic community structure on Monowai Caldera.

4.1 WATER DEPTH AND MONOWAI FAUNA

There was a lack of a significant bathymetric association with taxa richness on Monowai Caldera. Similarly, the relationship between water depth and taxa abundance was also weak. Such a result was expected as:

(1) The dives frequently encountered large vent fields with extensive mytilid beds and associated taxa, and

(2) The submersible did not explore a large bathymetric gradient of Monowai Caldera.

Benthic species show prominent zonation along with an inverse relationship of density and biomass with water depth (McClain et al., 2010). Such a zonation and, consequently, the structuring of the benthic community are as a result of a suite of abiotic conditions as well as biotic interactions that operate along particular bathymetric gradients (McClain & Etter, 2005; McClain et al., 2010). There are limited studies on the effect of the bathymetric gradients on the number of species, abundances of individuals, and the overall community structure on volcanic seamounts, as pointed out in Chapter 1 (Section 1.2.1). Decline in taxa richness and taxa abundance with increasing depth in the deep sea could be due to several factors, such as changes in oxygen concentration, hydrostatic pressure, ocean chemistry (McClain et al., 2010), and a decline in food availability (Levin et al., 2001). The role of hypoxic conditions (OMZ) occurring on the summits of seamounts under eutrophic surface waters has been discussed (Chapter 1, Section 1.2.1). For example, Wishner et al. (1990) found low faunal abundances at depths of < 750 m over the summit of Volcano 7 due to the presence of an OMZ, as well as below 1000 m, with highest abundances recorded at water depths of 750–810 m. However, unlike the current study on Monowai, the results from Volcano 7 were not in relation to other abiotic factors such as substrate type or hydrothermal venting (Wishner et al., 1990).

McClain et al. (2010) found compositional change between the summit (1299–1477 m) and base (2464–3276 m) of Davidson Seamount, NE Pacific. This was primarily attributed to the dominance and preference of habitat and reef-building octocorals on the summit, and their declining abundances with increasing depth. In contrast, the base of the seamount was dominated by soft-sediment dwelling deposit-feeders such as holothurians. When comparing the present study to that by McClain et al. (2010), and putting aside sampling differences where a much larger bathymetric gradient was explored on Davidson Seamount, similarities in habitat preferences of different taxa are obvious. *Pisces V* dives commenced from the deeper areas of the caldera floor that were sedimented extensively (see dive logs). Larger megafauna such as macrourid fish were reported swimming past isolated boulders/rocks, and from analysis of video images, commonly occurred either singly or in groups of 2–4 above soft substratum away from the sites of venting. This trend is indicative of generalist species (larger fish, motile invertebrates) that are less sessile and exhibit a range of lifestyles adapted to deeper waters amongst the homogeneous soft-sediment environments (Hoff & Stevens, 2005). The results seem to suggest that non-vent type habitats are localised to deeper waters on Monowai. However, the submersible did not cover more transects at water depths deeper than 1250 m and, therefore, such a conclusion does not seem apt.

Unlike other areas of the deep-sea, where a decline in carbon flux with increasing water depth coupled with seasonal productivity is obvious resulting in changes to benthic community composition, volcanic seamounts may not show any such relationship as the correlation of flux with water depth is rather weak (McClain et al., 2010). Instead, patterns of faunal zonation arise from differences in vent-fluid chemistry (temperature, oxygen/sulphide concentrations) and substrate/rock types (Kim & Hammerstrom, 2012). Hydrothermal alteration changes with depth, thereby leading to the formation of different mineralogical products (Webber et al., 2011). A good example is the change in lava type from basalt sites to andesite sites between 2100–2700 m in the Eastern Lau Spreading Centre (Podowski et al., 2010). Consequently, this would appear to influence habitat characteristics and subsequent preferences and spatial distribution of benthic vent taxa, with certain taxa leading to the exclusion of others. A second influence on faunal distribution and abundance with respect to water depth arises due to differences in larval dispersal. Whilst certain vent larva may restrict their distributions to adult conspecifics (e.g. *Lamellibrachia* sp. on Monowai; Short & Metaxas, 2011), others are carried by near-bottom vent plumes (e.g. *Lepetodrilus* larvae in Juan de Fuca Ridge, Mullineaux et al., 1995) to be deposited at high-relief features above the seafloor (Kim & Hammerstrom, 2012). Other studies have focussed on differences in faunal abundances and richness from hypoxic conditions due to the presence of high sulphide concentrations in the sediment through nearby venting (Bagarinao, 1992; Grassle, 1985). Hypoxia and organic matter show an inverse relationship (Levin et al., 2000). However, inferences on bottom-oxygen concentration, organic matter, sulphide concentration in sediments with increasing depth, and information on vent larval dispersal cannot be made for Monowai Caldera, as data for those variables were not available and/or unknown.

Due to the lack of differences in taxa richness and abundance within the narrow depth bands investigated, it is obvious that any benthic community composition differences on Monowai Caldera may be as a result of other prevailing abiotic factors (i.e. substrate differences and influence of venting), the results of which have been discussed in detail within this chapter.

4.2 SUBSTRATE COMPOSITION AND VENT TAXA

Analyses on the substrate classes revealed different microhabitats, with compositions of habitat groups mirroring sites of venting. The relationship between hard and soft substratum and taxa richness was not very strong. However, the percentage cover of hard and soft substrates showed an association with taxa abundance.

Amongst the homogeneous environment of soft substrata in the deep sea such as sand, mud, and benthic ooze, hard substrata can be found interspersed in the form of bedrock outcrops, areas of chemosynthetic activity such as hydrothermal vents and seamounts (Baco & Smith, 2003). Hard substrata such as rocks, boulders, and bedrock outcrops are stable and erosion-free. Therefore, they form ideal habitats for attachment and proliferation of a number of invertebrates, including the settlement of colonisers and subsequent succession of organisms, thereby contributing to benthic biodiversity and ecological functions (Taylor & Wilson, 2002). For seamount communities that depend on POC flux, many studies have examined the link between cold-water coral reefs occurring on the summit and flanks of seamounts amongst outcrops and to species richness and abundances (see Chapter 1, Section 1.2.2). Corals on seamounts thrive in areas, where owing to the topography, water currents help in bringing food-bearing organic matter, as well as clearing sediment from hard substrata that they attach to (Rogers et al., 2007). In turn, taxa richness amongst such cold-water coral reefs has been measured to be higher than that of background communities (Koslow et al., 2001).

For volcanic seamounts, species such as mussels and tubeworms often settle and colonise smaller areas of basalt/bedrock substrates. Over time, their spatial extension provides a larger substrate area which is conducive for the settlement of other invertebrate populations (Urcuyo et al., 2003). This leads to the creation of micro-habitats that provide food and protection for other species. The presence of diffuse-flow venting through cracks and fissures on hard substratum on Monowai Caldera and the subsequent distribution of vent taxa confirms other studies such as by Bates et al. (2005). According to these authors, substrata that are bathed in hydrothermal vent fluids offer the greatest source of food in the form of bacterial mat, flocculent, and particulate matter. Subsequently, this would reflect elevated productivity and high abundances of taxa.

Other examples of vent taxa on hard substratum and similar to Monowai include those of *B. manusensis* occuring as extensive beds on the hard substrates (chimneys, blocks, volcanic outcrops) of Su Su knolls, Eastern Manus Basin (Papua New Guinea) (Beaudoin & Smith, 2012), beds or isolated clumps of *B. thermophilius* at active and diffuse-vent of the Rose Garden site (Galapagos Rift) (Fisher et al., 1988), and aggregations of mussels around diffuse-flow vents of 9°50’N EPR (Le Bris et al., 2006). Hard substrates also provide ideal substratum for grazing alvinocarid shrimps that are important primary consumers in vent environments (Hashimoto et al., 1995). On Monowai Caldera, these were observed hovering over mussel beds or grazing on the substratum devoid of mytilid beds (pillow-lava/boulders). Similar occurrences of alvinocarid shrimps on mytilid beds and rocky surfaces have been recorded in the Hina Hina site of the Lau Basin (Desbruyères et al., 1994), over mytilid beds in Minami-Ensie knoll (Hashimoto et al., 1995), and in the Gulf of Mexico, where *Alvinocaris muricola* is regularly seen associated with seep mussels *Bathymodiolus* spp. on hard substrate (Lessard-Pilon et al., 2010).

The third distinct component of vent taxa were *Paralomis* crabs, which were observed in association with more than one substrate class. They formed an integral part of vent assemblages (alongside *B. manusensis* and *Alvinocaris* spp.), as well as non-vent assemblages (e.g. anemones, macrourid, zoarcid, and synaphobranchid fish). Although the crabs were primarily found in association with other vent taxa on bedrock with sediment overlay, they were also observed on soft substrates (muddy or sandy sediment), among biogenic substrates (shell hash, mytilid shells), and isolated basaltic rocks or boulders. Their extensive distribution could be due to their ability to feed, scavenge, or graze (depending on substrate types). Clark & O’Shea (2001) recorded *Paralomis* sp. on the Brothers Seamount which was similar but not conspecific to *Paralomis jamsteci*, a small lithodid that lives amongst mytilid beds near vent openings on the Minami-Ensei knoll (Chevaldonne & Olu, 1996; Hashimoto et al., 1995). Elsewhere, *P. hirtella* has been recorded from hydrothermal vent fields of the Indo-west Pacific Ocean, Lau Basin, Valu-Fa Ridge, Hine Hina site (Martin & Haney, 2005), and White Lady hydrothermal field of the North Fiji Basin (Desbruyères et al., 1994).

Hard substratum, combined with local hydrodynamics around a seamount can also provide both food and habitat to larger megafauna. For example, synaphobranchids (*Dysommina rugosa*) found on the Nafanua summit (Samoa), seek habitat in the crevices around mounds and pillars and rely on crustaceans for food. The crustaceans are delivered through anticyclonic currents around Vailulu'u Seamount (Staudigel et al., 2006). Aside from hard substratum, the presence of soft and biogenic substrates contributed to the overall habitat heterogeneity on Monowai Caldera

4.2.1 SOFT SUBSTRATA AND NON-VENT TAXA

With increasing distance from sites of venting on Monowai Caldera, a change in substrate type occurred from hard bedrock with some sediment overlay to large expanses of soft sediment such as mud or sand. The only islands of hard substrata occurring in such areas on Monowai Caldera were occasional expanses of boulders, cobbles, pebbles, or pillow lava, consisting of taxa such as buccinid gastropods, large fish such as macrourids and synaphobranchids, and cephalopods. Such taxa were recorded in areas that were a mix of hard and soft substrates. In areas away from venting activity and on substratum covered by white microbial mat cover, buccinid gastropods were present. Elsewhere, buccinids have been also recorded from the peripheral areas of the vent fields of Manus Basin (Galkin, 1997).

Even though soft sedimented areas supported limited fauna (anthozoans, gastropods, cephalopods, larger fish), the presence of lebensspurren (pits and burrows) on Monowai Caldera indicated the presence of infauna. Active digging by infauna was occasionally observed in video footages. Such infauna could be benefiting from the interaction of hydrothermal fluids with surrounding sediments, enabling “microbial activity and enhanced food supply relative to ambient sediments” (Levin et al., 2009). However, data on abundances of infaunal organisms are not available, as no samples or cores of infauna were taken for this study.

4.2.2 BIOGENIC SUBSTRATA

Dead mussel shells were encountered in isolated patches on soft sediments away from vent communities, as well as among live mussel beds. Mussel shells are generally associated with inactive vent sites. However, a larger proportion of dead mussel shells were observed amongst the large community of live mussel beds and other megafauna in many samples. An abundance of dead mussel shells may indicate increased predation by crustaceans or other large predators (cephalopods, predatory fish) (Tunnicliffe et al., 2009). Two vent communities were often connected by a chain of dead mussel shells pointing towards the transition from a past venting site to a current venting site. Shell hash consisting of dead mussel and gastropod shells was also frequently encountered in areas of extensive sedimentation. In addition, crustacean remains, indicative of recent predation, were recorded away from the vent sites and on soft substratum. Occurrences of larger megafauna such as eels and squids during image analysis were fairly common. However, no sign of active predation by these megafauna on crabs was observed during image analysis.

Benthic faunal distributions are a response to substratum type and flow intensities of hydrothermal fluids (Sarrazin et al., 1999). This holds true where the complexity and diversity of available substrata also dictate the amount of hydrothermal fluid flow in vent communities. The results of this study support the idea that this leads to the creation of a mosaic of microhabitats, each consisting of species that have variable tolerance to the temperature and composition of hydrothermal fluids (Kelly & Metaxas, 2008). Substrate heterogeneity, as observed on Monowai Caldera, was as a result of periodic venting. Therefore, the patterns seen on different substra work in concert with changes in venting activity, which possibly govern observed changes in benthic community composition and structure.

4.3 PROXIMITY TO A VENT SITE AND MONOWAI FAUNA

The effect of proximity to a vent sample was not very significant on vent taxa richness. Vent taxa such as *B. manusensis*, *Alvinocaris* spp., and *P. hirtella* were the dominant fauna observed in samples closest (up to 250 m) to vents. Therefore, these taxa contributed to a high percentage of biomass in samples located less than 300 m from a vent. Such a result matches previous studies as mentioned earlier (see Chapter 1, Section 1.2.3), as well as in the Snake Pit vent field (Mid-Atlantic Ridge) where the zone of high density benthos was observed to be between 50–100 m and 200–300 m from the nearest vent (Sudarikov & Galkin, 1995).

Whilst the relationship between vent taxa richness and distance to the nearest vent site was not significant, the effect of this predictor variable on the total abundances of individuals was strong. The abundance of fauna was highest at distances of less than 300 m, and then declined markedly with increasing distance from a vent sample. The definition of a vent sample for this study has been discussed previously (Chapter 2, Section 2.3.1), and as such the presence of a vent is related to the presence of a well-established vent community, as already identified in Section 4.2.2 (characterised by the presence of mytilid bed, shrimps, and crabs) surrounding the vent opening.

The supply of vent fluids is essential in maintaining vent-associated taxa (Tsurumi, 2003). Monowai Caldera consisted of sites with diffuse-style venting, similar to other diffuse vent sites elsewhere (Galapagos Rift, Guaymas Basin, Juan de Fuca Ridge, Explorer Ridge, vent locations between 9° and 21°N of the East Pacific Rise, Lau-Fiji Basin, Okinawa Trough, and the Mid-Atlantic Ridge) (Lutz & Kennish, 1993), exhibiting high biomasses of taxa around diffuse-flow zones (Lutz & Kennish, 1993), but low species diversity (Rhoades, 2009; Tunnicliffe, 1988). The presence of high biomass, low diversity communities with high productivity is typical of vent environments that have a simple trophic structure due to the abiotic conditions being so markedly different to non-vent areas of the seafloor (Tsurumi, 2003). The mytilid-dominated benthic community on Monowai Caldera is similar to vent communities elsewhere, where larger sessile organisms (tubeworm thickets and mussel beds) act as ‘habitat engineers’ by assisting in modifying and stabilising substrata, modifying hydrothermal fluid flow, “particulate food and larval deposition, buffering residents from potential physical stress, and providing refuge from predators" (Bertness et al., 1999). Van Dover & Trask (2000) compared the diversity of intertidal mussel beds with vent mussel beds on the East Pacific Rise. As with the current study, the authors found low diversity at the vent mussel beds, which was attributed to the chemical environment around vents that may deter potential invaders.

Diffuse venting leads to the dispersal of hydrothermal fluids over a large area, and therefore, approximates vent distribution (Juniper & Tunnicliffe, 1997). According to Tsurumi & Tunnicliffe (2003), there is a shift from high biomass and high production in active vent assemblages to low biomass and production in assemblages around vents that have ceased venting. Differences in community composition become apparent, such that there is an intrusion of more non-vent taxa (echinoderms, sponges) and large predators (crabs, isopods) into the community around such vents, and the fauna start resembling background communities. However, this was not the case for Monowai Caldera as there was evidence of areas of high biomass in areas where venting had ceased, albeit patchily distributed.

Based on the results of this study, the spatial distances from a vent sample have been divided into two zones for further explanation, namely the vent zone (0–300 m) and the non-vent zone (300–1800 m).

4.3.1 THE VENT ZONE (0–300 M)

On Monowai Caldera, bedrock outcrops and other sites of discrete venting were encrusted with beds of bathymodiolid mussels (Figure 4.1). Previous studies on benthic fauna around vents have stressed the dependence of chemosynthetic invertebrates on the supply of hydrothermal fluids, justified by their proximity to vent openings. While this was expected and observed on still and video images, it was noted that mussel beds were extensive and spread out away from venting sites, confirming the ability of diffuse-vent flows spreading over large areas. Tarasov et al. (2005) discussed the concept of a 'Diffuse flow biosphere' which is the zone of highest biomass found in vent communities. During image analysis for the present study, it was noted that no visual evidence of venting was apparent, and yet patchy clumps of mussels or a thriving mussel-bed community were present. Average abundances of mussels were highest (~1750 individuals per m^2) at 100 m from a vent sample, and then halved in abundance at distances of up to 250 m from a vent sample. Johnson et al. (1994) attributed this observation to the fact that bathymodiolid mussels have the capability to “laterally disperse vent fluids throughout the clump which increases their uptake of sulphide as well as allowing for the extension of mussel populations spatially”. Elsewhere, *B. manusensis* occurs as beds furthest away from active high-temperature vents on the Su-Su hydrothermal site of the Eastern Manus Basin (Beaudoin & Smith, 2012).

Fisher et al. (1988) noted that the vent mussel *Bathymodiolus thermophilus* in the Rose Garden and New Vent hydrothermal fields of the Galapagos Rift valley are capable of relying on heterotrophy when away from hydrothermal fluids, by filter-feeding on suspended particles (bacteria). This could also explain the presence of smaller clumps of mussels scattered on isolated basaltic rocks, away from sites of focussed diffuse venting on Monowai (Figure 4.2). Such wide distribution of bathymodiolids, irrespective of venting areas, reflects their ability to tolerate a wide range of environmental conditions (Desbruyères et al., 1994; Fisher et al., 1988; Lutz & Kennish, 1993).

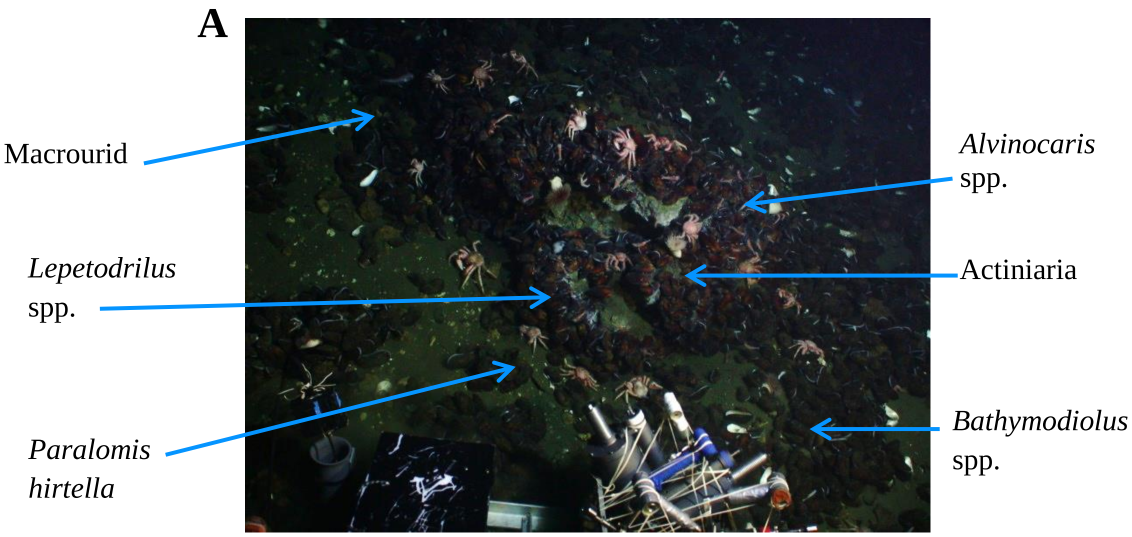


Figure 4.1: Mussel community (*Bathymodiolus manuensis*) along with vent crabs (*Paralomis hirtella*), vent shrimp (*Alvinocaris* spp.), vent limpet (*Lepetodrilus* sp.), actiniarian , and macrourids near 10 cm away from a diffuse vent, Monowai Caldera, dive 613, 8 April 2005, water depth=1027 m, image area= 9 m^2

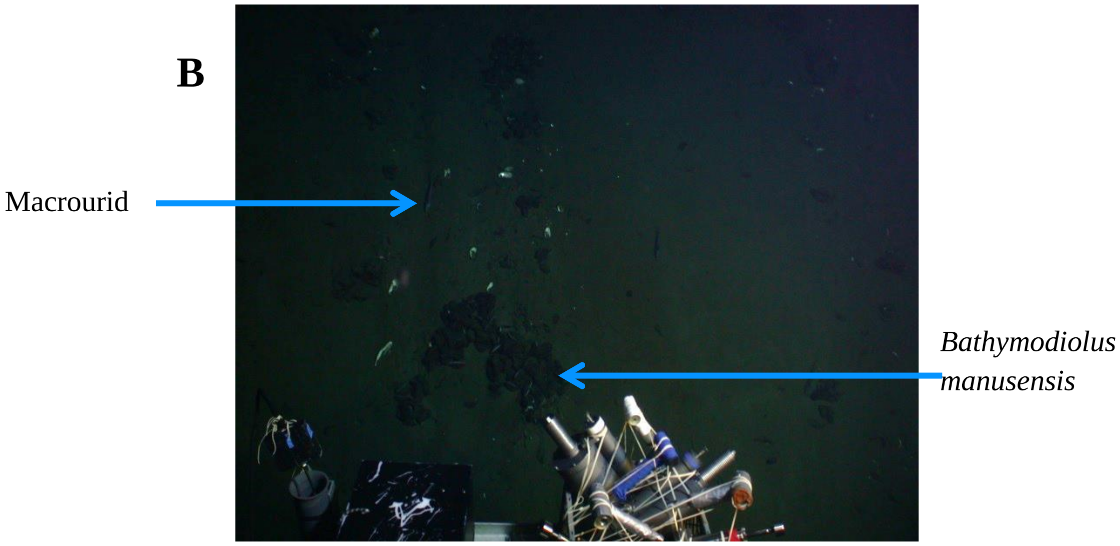


Figure 4.2: Isolated clump of mussels (*Bathymodiolus manusensis*) in an area of sedimentation, along with larger megafauna (macrourid fish), Monowai Caldera, dive 613, 8 April 2005, water depth= 1067 m, image area= 6.6 m^2

Compared to the extensive spatial distribution of bathymodiolid mussels, siboglinid tubeworms showed patchy distributions, being exclusively restricted to areas where the flow-intensity was highest (Figure 4.3). Such sites were uncommon which explains the occurrence of tubeworms in relatively few samples on Monowai Caldera. Patchy distributions of siboglinds have also been reported by Wysoozanksi & Clark (2012) for other seamounts of the Kermadec volcanic arc. The habitat preference of siboglinids for medium-high low intensity vents also matches studies by Arquit (1990).

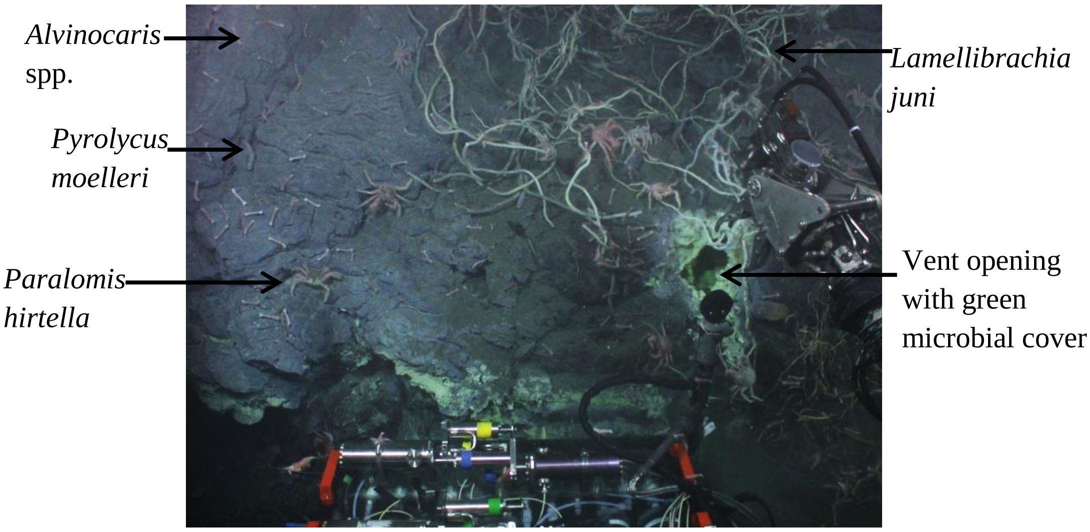


Figure 4.3: A thicket of vent tubeworms (*Lamellibrachia juni*) on an outcrop around a vent opening. Other fauna present include vent crab (*Paralomis hirtella*), vent shrimp (*Alvinocaris* spp.), and vent eelpout (*Pyrolycus moelleri*). Green microbial cover is seen present around the rim of the vent opening, Monowai Caldera, dive 614, 9 April 2005, water depth= 1079 m, temp= 26.8 °C, image area= 5.1 m^2

Decapod crustaceans account for nearly 10% of all vent-associated megafaunal taxa worldwide (Yang et al., 2013). Aside from bathymodiolid mussels, alvinocarid shrimps contributed to most of the biomass on Monowai Caldera. Alvinocarid shrimps assume the role of primary consumers by forming large swarms and hovering up to 1 m above the vents/mussel beds (Tarasov et al., 2005). Unlike results by Clark & O’Shea (2001), highest average abundances of alvinocarid shrimps (~ 750 individuals) on Monowai Caldera were observed to be correlated to sites over 300 m away, rather than within the first 100 m as would be expected. Samples over 300 m away from a vent showed no evidence of venting. However, this does not discount the spread of diffuse-flows, as indicated by the presence of large expanses of bacterial mat over basalt rock that were noted at such sites, and most probably being grazed by the shrimps. Similar mat-grazing behaviour by alvinocarid shrimps has also been found in areas of low-temperature diffuse venting in the Lau Basin (Desbruyères et al., 1994).

Paralomis crabs on Monowai Caldera were present in relatively high abundances around venting areas, and showed a slow decline in average abundances with increasing distance from vent samples. Other studies such as those by Tunnicliffe & Jensen (1987), recorded aggregations of *Paralomis* crabs and brachuyrans near low-temperature diffuse vents. They attain high densities on mytilid and vestimentiferan beds elsewhere (Chevaldonne & Olu, 1996; Tunnicliffe & Jensen, 1987). Unlike brachyuran and galatheid crabs near vent areas that feed on live mussels and clams or scavenge on dead mytilids (Michelli et al., 2002), *Paralomis* crabs from Monowai Caldera were never observed directly feeding on the vent mussels during image analysis. However, this does not mean these crustaceans do not participate in active predation, as *Paralomis* sp. from low-temperature vents elsewhere on Axial Seamount (Tunnicliffe & Jensen, 1987), Sagami Bay cold-seeps, and Okinawa vents have all been observed feeding on mytilid and vesicomyid bivalves (Chevaldonne & Olu, 1996). *Paralomis* crabs on Monowai Caldera were also observed around areas of sedimentation and patchy distributions of boulders, away from venting sites in low densities. Their distribution and contribution to vent- and non-vent assemblages on Monowai Caldera is perhaps evidence of their capability to thrive in areas not exclusive to vents.

Other larger megafauna in the vent zone included zoarcids in low numbers within mytilid beds on Monowai. This observation is in contrast to that reported by Desbruyères et al. (1994), who reported that predators of vent-associated taxa are usually concentrated at the peripheral zone of the vent field, thereby participating “in the outflow of organic matter from the vent environment”.

4.3.2 THE NON-VENT ZONE (300–1800 m)

Sites away from vent samples contained a high percentage of mud with isolated pockets of hard substrata, which in turn translated to low taxa richness and abundance.

Results from multivariate analyses suggest that alvinocarid shrimps and anemones were the prominent taxa within assemblages situated in the non-vent impact zone. Anemones were observed and recorded either occurring on solitary boulders or in most vent samples, on top of mussel beds. Even though data on current flows were unavailable for this study, it is clear that prevalent water currents have the capability to transport food-bearing particles, as well as hydrothermal fluids from diffuse-flow vents over a large area. During image analysis, this was evident by the presence of anemones on mussel beds that presumably orient themselves to the prevailing current in order to maximise food capture. As with the current study, anemones near chemosynthetic environments have been observed inhabiting ‘the vent zone’, as well as being considered peripheral fauna associated with vents and seeps (Rodríguez & Daly, 2010). Similar to this study, where anemones were observed on mussel beds and cobbles, Podowski et al. (2009) reported a preference for bare substratum within 5 cm of symbiont-containing fauna. However, from the results of multivariate analyses, anemones were not part of the vent communities in the first 300 m, even though they were sighted on mussel beds. Such a result could be due to their relatively low abundances in comparison to high numbers of other high density vent taxa (mussels and shrimps). The anemones at distances of up to 2300 m from a vent sample are likely to be predatory cnidarians, such as hormathiids (Figure 4.4), rather than actiniarians seen on mussel beds (Figure 4.5).

Figure 4.4: Hormathiid anemones on an isolated patch of bedrock in a heavily sedimented area, Monowai Caldera, dive 613, 8 April 2005, water depth= 1089 m, image area= 7.9 m^2

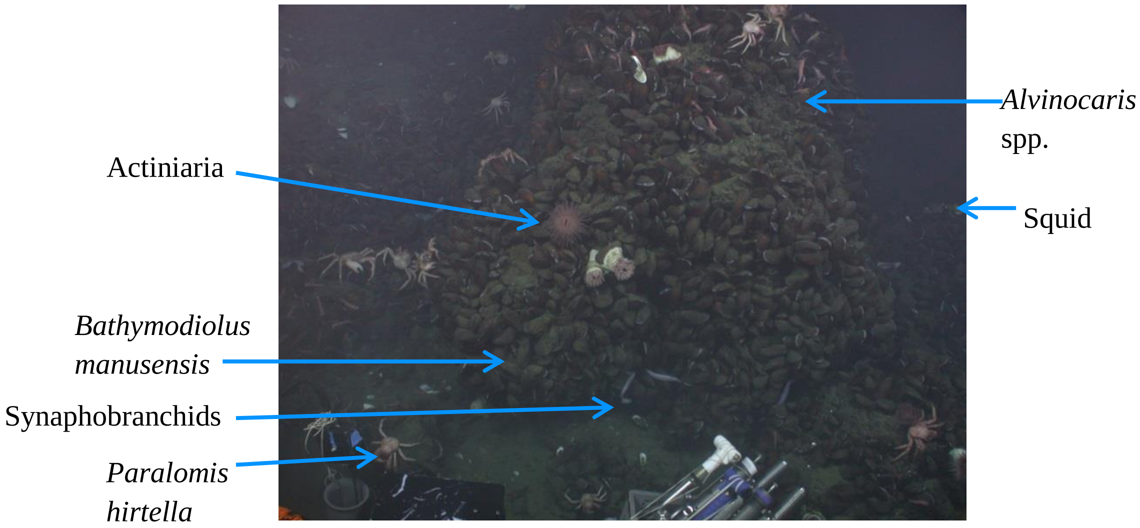


Figure 4.5: An actiniarian attached to an outcrop encrusted with vent mussels (*Bathymodiolus manusensis*). Other megafauna include vent crab (*Paralomis hirtella*), vent shrimp (*Alvinocaris* spp.), synaphobranchids, and squid, Monowai Caldera, dive 612, 7 April 2005, water depth= 1053 m, image area= 7.5 m^2

The presence of larger fish included in the peripheral faunal groups matches observations during image analysis of macrourids drifting around the periphery of vent communities in low densities. Cohen & Haedrich (1983) captured footages and live specimens of vent fish in the Galapagos vent region. Similar to the macrourids on Monowai Caldera, the authors stated that the macrourid *Coryphaenoides anguliceps* was always “seen in an oblique, head down attitude, swimming slowly, drifting, or resting”. Furthermore, Hoff & Stevens (2005) reported the occurrence of *C. acrolepis* and *C. cinereus* in association with larger substrates and fine sediment on the Patton Seamount, Gulf of Alaska.

Even though not detailed in statistical analyses but encountered in the video footages, other larger megafauna in the non-vent zone included two species of octopus (*Graneledone challengeri* and *Benthoctopus tegginmathae*), one species of squid (*Pholidoteuthis massyae*), an unidentified shrimp, and natant decapods which were larger than alvinocarid shrimps. Both *G. challengeri* and *B. tegginmathae* were observed resting on the seafloor on sedimented areas. *B. tegginmathae* has previously been recorded off the east coast of the North and South islands of New Zealand, and along the Chatham Rise at water depths of 777–1723 m (O’Shea, 1999). *Graneledone* sp. has been recorded from the caldera walls of Axial Volcano (Voight, 2000). In New Zealand, its distribution extends from the East Coast of the North Island, East Cape to Chatham Rise as well as the Kermadec Islands, and at water depths of 766–1500 m (O’Shea, 1999). Occasional sightings of synaphobranchid fish were also recorded during this study, although they were also observed to be associated with the vent community in low numbers. Similar observations have been reported by Desbruyères et al. (1994) who mentioned the preference of the synaphobranchid *Thermobiotes mytilogeiton* for mussel beds and gastropods in the Lau Basin.

The non-vent zone on Monowai was relatively depauperate in sessile and mobile megafauna. However, more transects will need to be undertaken in future to quantify the taxa richness of these background communities. While the effects of venting are largely restricted to the close proximity of a discharge or plume (Tarasov et al., 2005), there is evidence of localised structuring of vent communities on smaller spatial scales in response to vent emissions (Johnson et al., 1988), the details of which have been explained below.

4.4 EFFECT OF VENT-FLUID TEMPERATURE AND SMALL-SCALE SPATIAL VARIABILITY

Two kinds of vents were encountered in this study: small cracks in the bedrock with a weak diffuse-flow, and visible holes on the seafloor showing strong, focussed diffuse-style flows with black/grey smoke. Small-scale distances did not have a significant effect on the taxa richness. The occurrence of most taxa closer to vent openings suggests a well-established vent community, while the decline in abundance of individuals with increasing distance from a vent opening indicates a definite spatial pattern of zonation.

In comparison, taxa richness and abundance showed a very strong correlation with temperature of vent-fluids. Benthic community composition and structure around vent sites are dependent on the temperature and chemistry of hydrothermal fluids (Podowski et al., 2009). As a result, different microhabitats could be created on centimetre-scales. The species composition of the community around a vent opening on Monowai Caldera varied little. Analyses on the faunal data with small-scale distances identified four assemblages, three of which were composed of vent taxa (*B. manusensis*, *Alvinocaris* spp., *Lepetodrilus* sp., and *P. hirtella*). These assemblages shared similar taxa indicated by samples that had larger distances from a vent opening, and which marked the start of a vent community. Bathymodiolid mussels occurred in samples with distances of 0.5– 1 m from a vent opening, emanating weak diffuse-flow shimmering water. This observation is in contrast to other studies as well as those by Tokeshi (2011) where *Bathymodiolus platifrons* from the Okinawa Trough vent sites were positioned at distances of up to 2.5 m from the vent orifices. Elsewhere, Grassle (1985) reported the presence of mussels “at some distance from the central vent zone”. In certain sites on Monowai Caldera, the increase in mussel density was directly proportional to distance to venting sites as well as where venting was not obvious. Subsequently, the spread of the mussel bed was towards the outer periphery of the vent community, indicative of transport of hydrothermal fluids over a large area and/or reliance on filter-feeding. In general, bathymodiolid mussels tend to occur at some distance away from a vent opening, presumably due to their low tolerance to high sulphide content/temperature conditions (Dahlhoff et al., 1991;

Tokeshi, 2011). This observation matches those by Collins et al. (2008) who noticed the presence of beds of *B. manusensis* in the outer vent zone along with the barnacle *Eochionelasmus ohtai* at the Su Su knolls of the Manus Basin. As vent-fluid temperatures varied between samples, it is easy to infer that the mussel beds occurred around vents that had low temperatures. It is likely that the presence of well-established, long-lived mussel beds have ameliorated the toxicity of hydrothermal fluids, therefore justifying their close presence to vent openings in comparison to other studies.

Limpets belonging to the genus *Lepetodrilus* occurred in high densities on top of live bathymodiolid shells near areas of reduced fluid flow. However, the presence of mussels did not always indicate the presence of limpets. *Lepetodrilus* sp. were also present on rocks near venting areas (B. Marshall, personal communication, 27 February 2013). Such abundance patterns could be in response to different flow characteristics, such as sulphide-to-heat ratios (Bates et al., 2005). The presence of limpets in association with bathymodiolid mussels matches other studies where *Lepetodrilus* limpets were abundant both in “the presence of no hydrothermal fluid flow and low temperatures (0–10 °C) as well as visibly shimmering hydrothermal fluid flow (high flow vigour) and intermediate temperatures (10–20 °C)” (Kelly & Metaxas, 2007). This would indicate the ability of this species to utilise various feeding strategies, allowing it to exploit a range of nutritional sources in various hydrothermal fluid flow conditions to reproduce successfully (e.g. *L. fucensis* in the North East Pacific; Kelly & Metaxas, 2007). For gastropods of the size of *Lepetodrilus* sp., changes in the physical and chemical variables on decimetre scales have impacts on their densities (Bates et al., 2005). The occurrence of vent limpets even in samples away from vent effluents on Monowai Caldera suggests their capability to harness vent fluids efficiently regardless of the distance. For instance, the vent limpet *L. fucensis* in the JdFR maximises its utilisation of vent fluids by displaying stacking behaviour when occurring at high population densities (Bates et al., 2005).

However, the largest sample group that had a significant relationship with vent-fluid temperatures was composed primarily of *Paralomis* crabs and alvinocarid shrimps. The results possibly indicate a preference for vent fluids and physiological tolerance of high temperatures for these two taxa.

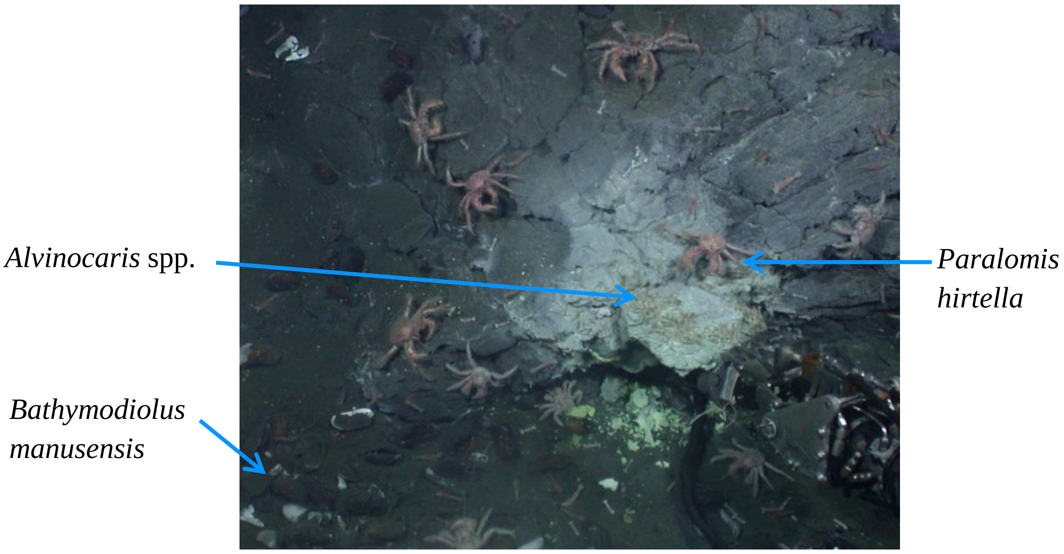


Figure 4.6: Swarms of *Alvinocaris* spp. occurring with the vent crab, *Paralomis hirtella* near a vent opening, several vent mussels (*Bathymodiolus manusensis*), and surrounded by white flocculent matter, green microbial cover, and hydrothermally-altered substrate, Monowai Caldera, dive 614, 9 April 2005, water depth= 1157 m, image area= 2.2 m^2, distance range from vent opening to indicator species (alvinocarid shrimps) = 5–11 cm

Vent openings of sizeable diameter (of up to 5 cm) were surrounded by green and/or white bacterial mats and flocculent materials where alvinocarid shrimps were almost always observed co-occurring with *Paralomis* crabs (Figure 4.6). Moreover, shrimps appeared the most tolerant to hydrothermal fluids, often positioning themselves against the opening of a vent. Video footage of focussed strong-flow of hot, shimmering water showed alvinocarid shrimps on the seafloor, orienting themselves towards the rim of the vent opening. Such behaviour has also been reported by Renniger et al. (1995) for the Mid-Atlantic Ridge shrimp *Rimicaris exoculata* which shows a chemosensory reception to pieces of sulphide from vent chimneys. Similarly, Copley et al. (1997) reported crawling behaviour by *R. exoculata* on substratum closest to vent orifices as a way to sustain chemosynthetic primary production by epibiotic bacteria harboured within the maxillae of the shrimps.

Co-occuring with alvinocarid shrimps around such vent openings were *Paralomis* crabs. Vent fields are ideal to observe competition for food and space (Michelli et al., 2002). This was evident in the behaviour of *Paralomis* crabs that appeared to compete with alvinocarid shrimps for a space near venting fluids. Compared to other scavenging crabs, it is possible that *Paralomis* crabs are more tolerant of temperatures associated with venting on Monowai. Another reason in addition to the availability of food for high abundances of crabs on vent sites could be due to the pH of the ambient seawater. The ambient pH on Monowai is 7.85 (KOK expedition dive log) compared to low pH values (5.88–7.29) found in other vent areas of the western Pacific (Tunnicliffe et al., 2009). Low pH conditions around a vent environment inhibit carapace formation, thereby correlating water chemistry to presence/absence of mobile predators such as crustaceans (Tunnicliffe et al., 2009). The presence of aggregations of *Paralomis* crabs on Monowai Calera near diffuse-style vents could be correlated to local pH conditions.

4.5 MONOWAI AND IMPLICATIONS OF FUTURE SEAFLOOR MINING

Seamounts are currently vulnerable to benthic trawling and seafloor mining for SMS deposits. Seafloor mining is detrimental to seamount habitats and their associated communities (Van Dover et al., 2011). Vent communities are unique to other ecosystems by being spatially discrete, geographically isolated, and ephemeral (Van Dover et al., 1988). The presence of fragmented and patchy populations of adult benthic organisms translates to spatially-restricted source populations for larvae, high local recruitment, and low potential for new colonisation after a natural or anthropogenic disturbance (Metaxas, 2011). Due to the close proximity of adult populations to mining activities and its effects (e.g. sediment plumes moving downstream on to nearby communities), the implication of future seafloor mining would be low numbers of recruitment and the inability to retain a seed population for recolonisation (Gwyther, 2008). Hydrothermal vents on Monowai are similar to vents on other seamounts in the Tonga-Kermadec volcanic arc (e.g Volcano 1 and Volcano

19) and the Western Pacific (e.g. NW Rota 1, NW Eifuku, and East Diamante) that have high-density, patchy, and spatially restricted adult benthic populations spread over large distances (Metaxas, 2011). Similar to other studies (e.g. JdFR, Sarrazin et al., 1999), the results from the current study also confirmed the dependence of benthic assemblages on appropriate substrata and the presence of hydrothermal fluids in relation to their spatial distribution.

Low-temperature vents and altered rocks on Monowai Caldera have previously been observed by Leybourne et al. (2012). The taxa attaining highest biomass on Monowai around such low-temperature diffuse vents were bathymodiolid mussels. The populations of such relatively sessile invertebrates are maintained through dispersive larvae which are dependent on spacing between habitats, ocean circulation or currents, duration of larval life, and larval behaviour in choosing recruitment sites (Van Dover et al., 2011). It has been suggested that larvae of vent species use temperature (Sarrazin et al., 1999) and hydrogen sulphide cues in the water column as physiological triggers to induce settlement (Kelly et al., 2007; Lutz et al., 1980). Furthermore, successional sequences are dependent on the strength of venting (Collins et al., 2008). Therefore, the transient nature of vents on Monowai Caldera may be crucial for the settlement of the benthic communities.

One of the greatest risks of seafloor mining is the possible loss of endemic fauna around volcanic seamounts, in particular those (such as bathymodiolid mussels and vestimentiferans) that act as ‘habitat engineers’ (Bertness et al., 1999). On Monowai, a high degree of endemism has been associated with the vent mussel *Bathymodiolus manusensis*, due to its distribution being limited to only two locations, namely the Su Su hydrothermal site of the Eastern Manus Basin and Monowai Volcano (Beaudoin & Smith, 2012; Collins et al., 2008). Aside from occurring at these two locations, *B. manusensis* has never been recorded on seamounts of the southern Kermadec volcanic arc. Instead, there appears to be a change with the occurrence of other species of *Bathymodiolus* as well as an entirely different genus and species of mussel (*Gigantidas gladius*) (von Cosel & Marshall, 2010) on the southern Kermadec seamounts (Wysoozanksi & Clark, 2012). In contrast, Monowai shares many benthic fauna (*Paralomis hirtella*, *Pyrolycus moelleri*, *Lamellibrachia juni*, and *Oasisia fujikurai*) with other southern Kermadec arc volcanoes, and elsewhere in the South-Pacific. Such local distribution of vent mussels could be a combination of local hydrodynamics and the geographical position of Monowai, being much further away from the other seamounts of the middle and southern Kermadec volcanic arc.

Geologically, Monowai rocks are mafic (basalt to basaltic-andesite) in composition, which possibly makes it globally one of the largest mafic calderas (Leybourne et al., 2012). The Kermadec volcanic arc forms an essential part of one of the 11 vent biogeographic regions (Bacharty et al., 2009). Several other volcanoes in the Kermadec volcanic arc (e.g. Clark, Rumble II West, Brothers, Volcano 1, and Volcano 19) host mafic calderas, and are also rich in massive sulphides (Leybourne et al., 2012). Leybourne et al. (2012) explained the presence of altered sulphur and hydrothermally-altered rocks on Monowai, as a product of previous high-temperature (~300 °C) acidic venting in the past. Such areas of altered sulphur in the caldera contain high concentrations of fluid-associated metals such as copper, lead, molybdenum, and gold (Leybourne et al., 2012), which are known to be primary components of SMS deposits (Hoagland et al., 2010). Most future seafloor mining is likely to be carried out in areas that consist of diffuse vents, presumably due to the concentration of thicker mineral deposits (Hein et al., 2009), and with minimal risk to biological communities (Van Dover, 2010). The concentrations of massive sulphides in certain parts of the Monowai Caldera could potentially make it a source of interest for mineral exploration. However, as this study shows, the presence of diffuse-flow vents can support extensive communities with high biomass, albeit low species richness when compared to other seamount communities around active black-smokers. Due to its reliance on fluids from other areas of active venting along with dependence on offspring or larvae produced at other habitat patches (Van Dover et al., 2011), the implications are that the recolonisation rates on Monowai and other similar seamounts, following any anthropogenic activity such as mining, could lead to longer recovery periods on decadal scales or even longer, and/or local extinction of certain species (Van Dover et al., 2011; Williams et al., 2010).

Seamounts, like Monowai, can be good candidates for studying the recovery potential and duration after mining. Isolated seamounts or ones that are separated by large distances warrant great protection, as they may be sites of high endemism (Clark et al., 2011; Stocks & Hart, 2007). A large factor for this endemism is oceanographic retention, where larvae are retained over a seamount due to Taylor columns (anti-cyclonic currents around a seamount), thereby inhibiting long-distance dispersal

(Brewin et al., 2009). Furthermore, the differences in life-history characteristics and larval dispersal mechanisms make it difficult to generalise and assess recovery periods for individual vent ecosystems (Clark et al., 2011; Boschen et al., 2013; Thaler et al., 2011). To truly conserve seamounts, it is essential to have control sites that are representative of different bathymetric ranges, habitats, and taxa diversity. Whilst Monowai does not resemble other high-diversity seamounts, it nevertheless represents an area which is still capable of supporting biological communities, and as such can act as a control site for other geologically- and biologically similar seamounts which may be at a risk from mining due to accumulated mineral resources.

In order to assign Monowai as a control site and use it as a baseline for impacts of mining, it is crucial to have complete information on the environmental parameters and the spatial and temporal changes of biological communities at every scale (meio- to megafauna) (Boschen et al., 2013). The reasons for the low taxa diversity on Monowai could be due to the nature of its venting (diffuse vs active). While the current study only highlights megafaunal abundance and diversity, the lack of data on soft-sediment fauna presents limitations on species diversity. This is a crucial point as meiofauna (organisms that can pass through 0.5 mm sieve) account for nearly 20% of the total diversity around hydrothermal vents (Gollner et al., 2010). Similarly, the absence of echinoderms on Monowai (regardless whether due to sampling inadequacy or true absence from the caldera) may not assign Monowai as a comparable control site. However, it is important to note that the samples for the current study were acquired as part of an initial exploration of the caldera, and as such the limitations stated previously can be overcome through future intensive sampling efforts on this seamount.

However, mitigation of mining operations and/or restoring of vent habitats cannot be executed as there is an overall lack of impact-assessment and baseline studies on chemosynthetic ecosystems lying outside of national jurisdiction, many of which cannot be tested until mining activities have been performed (Van Dover, 2011). Even though New Zealand has 1.13 million km^2 of Benthic Protection Areas in place (Helson et al., 2010), mid-water trawling and mining are in fact permitted at closed seamounts and those that are under BPAs. This fact indicates an inadequacy in the protection of these vulnerable habitats (Beaumont et al., 2009; Bors et al., 2012).

In order to truly conserve such ecosystems from anthropogenic influences, it is important:

1) To have an understanding of the underlying geology.

2) To obtain baseline data of distribution of biological communities and the various habitat types.

3) To gain an understanding how such communities are maintained through larval dispersal events and define source populations.

4) To have taxonomic expertise available to identify taxa.

Anthropogenic disturbance from deep-sea mining is likely to occur in the future for seamounts. Information on biological interactions between taxa, such as food webs, recruitment, growth, predation, and competition on Monowai Caldera was not available and is outside the scope of the present study. In the absence of adequate knowledge of the aforementioned factors, it seems plausible to defer mining activities on seamounts that are of mining interest. The number of ecological works similar to the current study is limited when compared to the number of seamounts that have been mapped globally (Tarasov et al., 2005). Even though mining on Monowai may not be imminent, future explorations on Monowai and similar studies on other isolated seamounts of similar geological history could pave the way for more information to be collected, in order to put in place appropriate conservations measures for such ecosystems.

4.6 GENERAL CONCLUSIONS

Monowai Caldera, situated in the Kermadec volcanic arc belongs to a larger volcanic complex consisting of a primary active volcanic cone, a secondary volcanic cone, several parasitic cones, and two calderas. The caldera investigated for this study during the 2005 KOK New Zealand-American Submarine Ring of Fire is the larger and older caldera (MoC1). The current study involved studying the effects of substrate type, water depth, and distance to vent sites on the taxa richness, abundance, and the overall community structure of the caldera.

Habitat mapping of Monowai Caldera showed spatial extent of different substrate classes. Distribution maps of faunal assemblages revealed patchy occurences of vent taxa such as bathymodiolid mussels, in comparison to wide distributions for *Paralomis* crabs and other larger motile megafauna (fish). The two species of tubeworms (*Lamellibrachia juni* and *Oasisia fujikurai*) also showed patchy distributions and were restricted to certain areas of the caldera that were actively venting. In addition, an area of the caldera where venting was occurring in 2005 was also noted. This was confirmed by the restricted distribution of small chimneys, yellow sulphidic sediments, and green bacterial mat, all of which are indications of venting sites.

Pisces V submersible explored a relatively small bathymetric gradient on the caldera (water depth range of 1050–1250 m). As a result, there was an overall lack of a significant effect on the taxa richness and abundance. Similarly, a noticeable pattern in the change of the benthic community structure may have been noticeable if a larger water-depth range was explored. For the purpose of this study, it was obvious that the patterns arising from changes in the benthic community structure were dependent on the change in substratum/habitat types and distance to the nearest vent.

Substrate heterogeneity was obvious, with a large portion of the samples being covered by bedrock (plain, sediment overlay, and outcrop), followed by other classes such as poorly-sorted cobbles and pebbles, soft sediments and different biogenic substrates. Similar substrate types have been recorded on other seamounts of the Kermadec volcanic arc. Substrate differences showed a strong relationship with taxa abundance, but not with taxa richness. Multivariate analyses identified seven groups of substrate types, representing possible micro-habitats. These were primarily a mix of hard, soft, and biogenic substrates. Consequently, eight assemblages of benthic fauna were also identified in association with those substrate groupings. The faunal groups consisted of bathymodiolid mussels, alvinocarid shrimps, and *Paralomis* crabs, and as such were characterised as vent-obligate. Other taxa such as macrourid fish and anemones were classed as non-vent or background megafauna. Forward selection of DistLM analysis showed a significant effect of a number of substrate categories that explained variations seen in the benthic community structure.

The distance between samples to the nearest vent ranged from less than 50 m to over 1500 m. The number of taxa did not show a strong relationship with changes in distance to the nearest site. However, the effect on taxa abundance with distance to the nearest vent was clear, with highest abundances noted in the first 250–300 m from a vent site. Furthermore, a significant effect of proximity to vents was identified in the DistLM analysis, with other multivariate analyses identifying the vent zone to 300 m from a vent site. There was a lack of dissimilarity in the species composition, being largely dominated by vent-taxa at distances of up to 250 m from a vent sample. However, certain taxa such as alvinocarid shrimps, *Paralomis* crabs, and macrourid fish showed wider distributions well into the non-vent, background community at distances of 800 m and beyond from a vent.

Upon examining small-scale spatial distances from a vent opening to the start of the vent community, no noticeable effect was observed. Taxa richness and abundance of individuals showed a weak relationship with distance from a vent opening within samples. In contrast, when the effect of vent fluid temperature was included, both taxa richness and abundance of individuals showed a strong correlation, with low vent-fluid temperatures (< 30° C) correlated to elevated species richness and abundances. Multivariate analyses on the spatial small-scale distances data revealed four faunal assemblages, with three of them consisting of vent-taxa (bathymodiolid mussels, alvinocarid shrimps, *Paralomis* crabs, *Lepetodrilus* limpets). The fourth group consisted exclusively of alvinocarid shrimps and *Paralomis* crabs. This result was to be expected as *Paralomis* crabs and alvinocarid shrimps were closest to, and often near the rim of vent openings. Similar grouping of faunal assemblages was seen when combined with the results from the small-scale spatial distances from a vent opening, thus pointing to the spatial distribution of benthic fauna on Monowai according to physiological tolerances to hydrothermal fluids.

The fragmented spatial distribution of populations of vent communities has serious implications for recovery and recolonisation through larval dispersal from isolated habitat patches. Mining in areas that have ceased active venting may prove conducive due to thicker mineral deposits, thereby enhancing profitability. However, as this study shows, seamounts such as Monowai can sustain extensive communities through low-temperature diffuse-venting, long after the cessation of active venting. Pinpointing the existence of such communities through tracking of diffuse-venting in the water column is difficult. Therefore, further studies emphasising the spatial and temporal changes in such communities, in addition to biotic interactions, are needed to put in place conservation measures for seamount ecosystems that could be vulnerable to future seafloor mining.

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APPENDICES

APPENDIX A-DIVE SUMMARIES

Dive summary PV 612

Location: SW caldera area

-25.795 °S, -177.170 °W

Date: 07-04-2005

Bottom time: 5 hrs 40 mins

Max depth: 1372 m

Objective: To explore the volcanic ridge at SW area of Monowai Caldera.

The dive began on the floor of the caldera near a SW-NE trending tectonic ridge that extended from the central cone of the caldera floor into the SW wall of the caldera. Subsequently, the dive track veered south to southwest and encountered alternating areas of pillow lavas, heavily sedimented areas, and talus slopes. At about 1200 m depth, those portions of lavas not covered with sediments were colonised by dense communities of small bivalves and limpets. At 11.37 am, the course was changed to the SE to transverse directly upslope to the crest of the target ridge. The remainder of the dive occurred at the top of the ridge. Mussel beds were mapped for more than 300 m along the crest of the ridge to the south east. Biological samples were collected during the dive.

Dive summary PV-613

Location: SW caldera area

-25.805 °S, -177.164 °W

Date: 08-04-2005

Bottom time: 6 hrs and 23 minutes

Max depth: 1297 m

Objectives: 1) To explore the eastern and western flanks of Mussel Ridge.

2) To sample any discovered hydrothermal vent fields on the ridge flanks.

3) To sample the diffuse venting associated with the dense mussel beds at the crest of the ridge.

The dive started on the lower south-eastern flanks of the ridge imaging pillow lavas and associated talus. The western flanks of the ridge comprised a similar geology to the lower slopes. Upper slopes consisted of volcanic talus and mussel shell detritus. The north-eastern flank comprised a NE-SW structurally controlled hydrothermal vent field, extending from a depth of 1170 m to the ridge crest. The field consisted of discrete events with associated mussel beds, crabs, shrimps, and tubeworms. Most vents occurred at outcrop bases with evidence of elemental sulphur extrusion on the seafloor. Vent temperatures ranged from 47 to 55 °C (as recorded by temperature probe deployed by the submersible, see dive logs).

Dive Summary PV-614

Location: Monowai volcano, southwest caldera area

-25.804 °S, -177.166 °W

Date: 09-04-2005

Bottom time: 4 hrs and 59mins

Max depth: ~1166 m

Objectives: 1) To sample fluids at HURL marker 8

2) To sample fluids along ridge crest.

3) To continue investigations along contour of HURL marker 8.

The dive began SE of HURL marker 8. Marker 8, on the south caldera wall was located at 10:59 am at a depth of 1165 m. A 44 °C vent fluid sample was taken at marker 8. The search for additional vents moved upslope, and further hydrothermal fluid sampling was conducted at 12:53 (1157 m), 14:01 (1143 m), and 14:33 (1140 m). The dive ended further upslope of marker 8 after another venting area was discovered at 15:41 (1079 m). The submersible left the bottom at 15:56 (1028 m).

Dive Summary PV-615

Location: Monowai Volcano, south-west caldera area

-25.803 °S, -177.166 °W

Date: 10-04-2005

Bottom time: 5 hours 34 minutes

Maximum depth: 1228 m

Objectives: 1) To sample vent fluids at the top of Mussel Ridge.

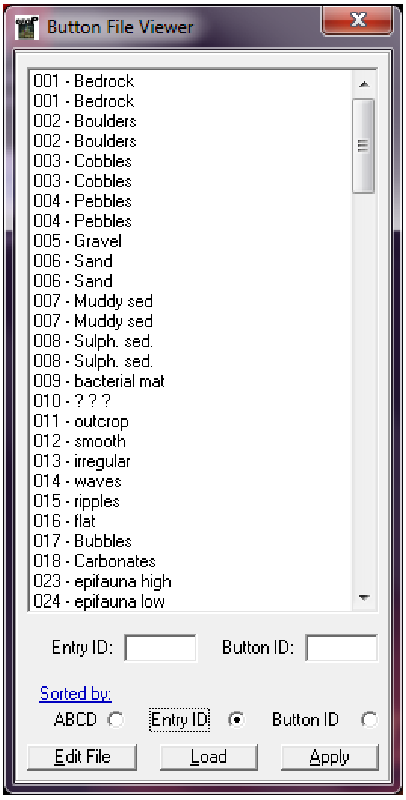
2) To sample hydrothermal animals and possible sulphides on the top of Mussel Ridge.

3) To conduct an Imagenex sonar survey over Mussel Ridge.

The dive began on the north-east slope of the volcanic ridge. *Pisces V* explored the top of the ridge, the cone located north-west of Mussel Ridge, and came across a distinct biological community on the southern flank. Unfortunately, images were highly unclear as they were from a handheld camera (the digital still camera was not turned on), no digital record of the sub depth was available due to the CTD data not being written on to a file, and the Imagenex scanning sonar was inoperational. Due to a loose connection, the video recording was in black and white.

APPENDIX B-OCEAN FLOOR OBSERVATION PROTOCOL (OFOP) METHODOLOGY

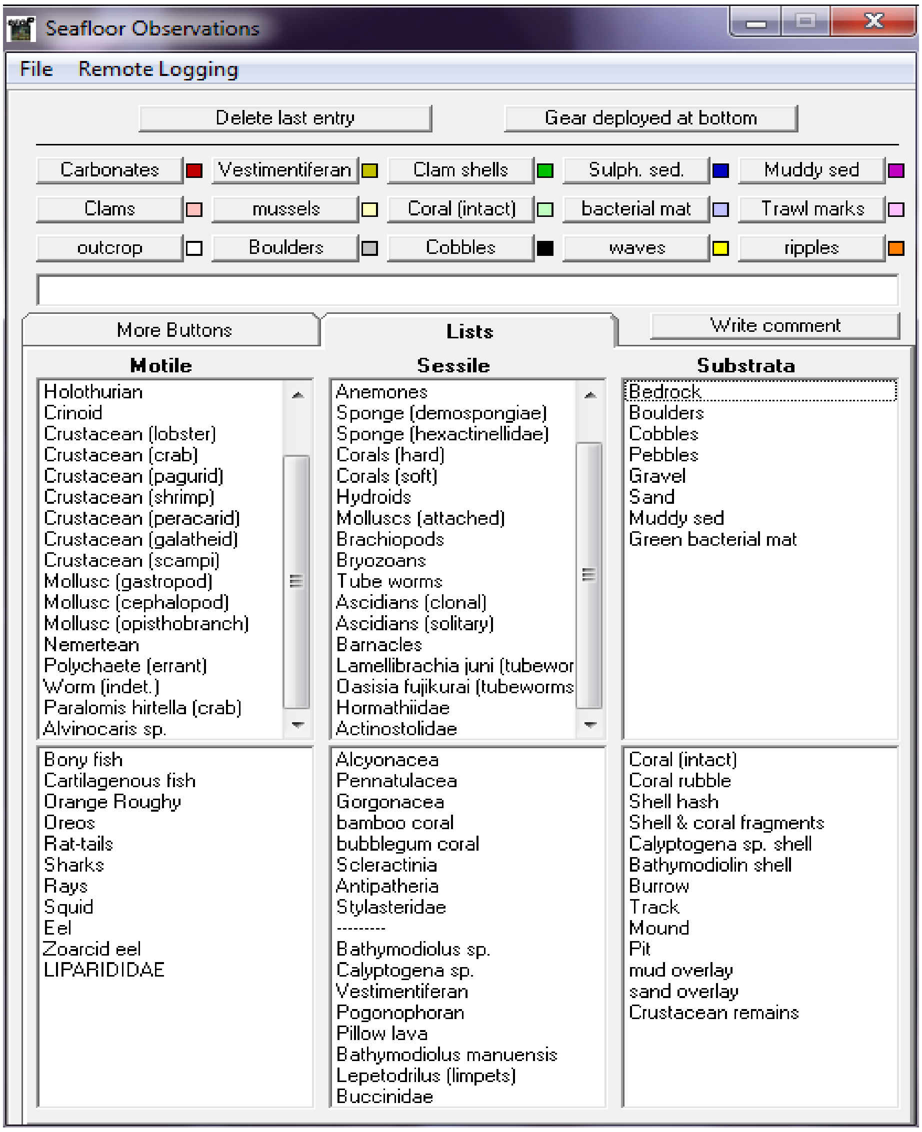
After creation and customisation of button files (Figure 1) according to faunal and substrate classes in OFOP, each taxon/substrate class on the button file list had its unique code (ID number) that aided in biological observations during image analysis. For example, an ID number of 7 corresponded to Muddy sediment on the Master Button file.



001 - Bedrock
001 - Bedrock
002 - Boulders
002 - Boulders
003 - Cobbles
003 - Cobbles
004 - Pebbles
004 - Pebbles
005 - Gravel
006 - Sand
006 - Sand
007 - Muddy sed
007 - Muddy sed
008 - Sulph. sed.
008 - Sulph. sed.
009 - bacterial mat
010 - ? ? ?
011 - outcrop
012 - smooth
013 - irregular
014 - waves
015 - ripples
016 - flat
017 - Bubbles
018 - Carbonates
023 - epifauna high
024 - epifauna low

Figure 1: Button File viewer for ID entry referencing in OFOP during mapping of habitat and faunal classes.

A new Protocol window was opened in OFOP, describing the name of the expedition, dive number, and the date. The Movie and Track Replay tool in OFOP was used to link the rendered video images to the corresponding navigation files. An observation file was created to record all fauna and substrate classes observed for every station as seen on the still-images on each dive transect, and the community and habitat type of each station. For example, a still-image showing a bedrock outcrop, with an extensive mussel bed, lithodid crabs, alvinocarid shrimps, and mobile megafauna was recorded by clicking on the corresponding items on the button file, so as to create a file that matched faunal/substrate data to the time/date stamp and coordinates on the navigation files for that station number. This file was stored as an observation file (*obser.txt), to be used for mapping particular faunal taxa, substrate classes, communities or habitat types on a calibrated map of Monowai Caldera.



Motile

Holothurian
Crinoid
Crustacean (lobster)
Crustacean (crab)
Crustacean (pagurid)
Crustacean (shrimp)
Crustacean (peracarid)
Crustacean (galatheid)
Crustacean (scampi)
Mollusc (gastropod)
Mollusc (cephalopod)
Mollusc (opisthobranch)
Nemertean
Polychaete (errant)
Worm (indet.)
Paralomis hirtella (crab)
Alvinocaris sp.

Bony fish
Cartilagenous fish
Orange Roughy
Oreos
Rat-tails
Sharks
Rays
Squid
Eel
Zoarcid eel
LIPARIDIDAE

Sessile

Anemones
Sponge (demospongiae)
Sponge (hexactinellidae)
Corals (hard)
Corals (soft)
Hydroids
Molluscs (attached)
Brachiopods
Bryozoans
Tube worms
Ascidians (clonal)
Ascidians (solitary)
Barnacles
Lamellibrachia juni (tubewor
Oasisia fujikurai (tubeworms
Hormathiidae
Actinostolidae

Alcyonacea
Pennatulacea
Gorgonacea
bamboo coral
bubblegum coral
Scleractinia
Antipatheria
Stylasteridae

Bathymodiolus sp.
Calyptogena sp.
Vestimentiferan
Pogonophoran
Pillow lava
Bathymodiolus manuensis
Lepetodrilus (limpets)
Buccinidae

Substrata

Bedrock
Boulders
Cobbles
Pebbles
Gravel
Sand
Muddy sed
Green bacterial mat

Coral (intact)
Coral rubble
Shell hash
Shell & coral fragments
Calyptogena sp. shell
Bathymodiolin shell
Burrow
Track
Mound
Pit
mud overlay
sand overlay
Crustacean remains

Figure 2: Buttons file with faunal and substrate data to correspond with seafloor observations from video images in OFOP

In order to plot any of the above, a depth contour and colour-shaded map was made for Monowai (see Acknowledgements), and supplied as .jpg image (Figure 3).

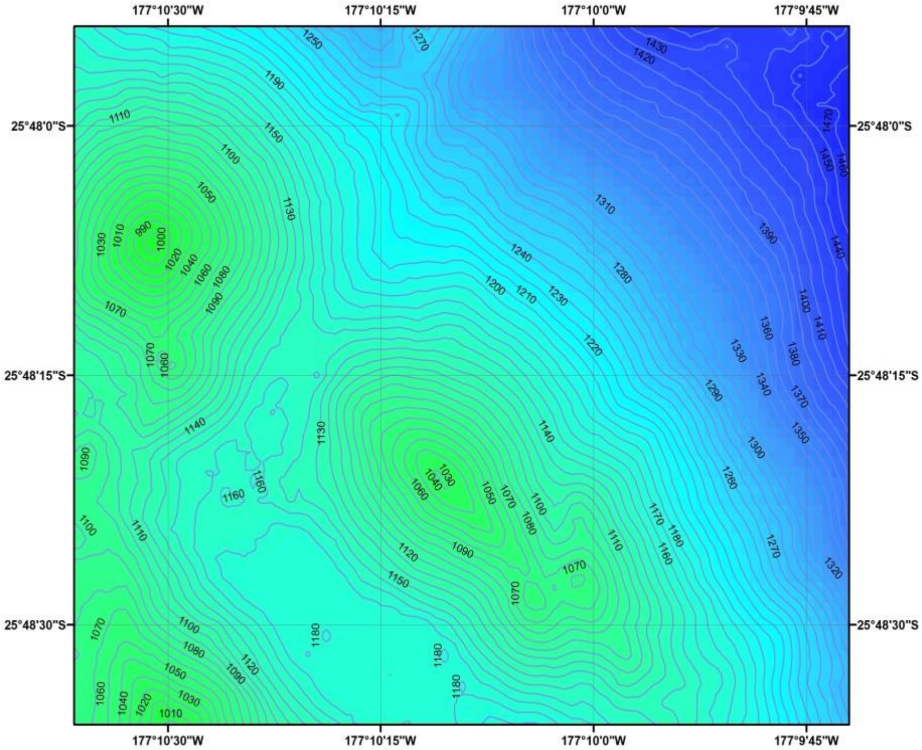
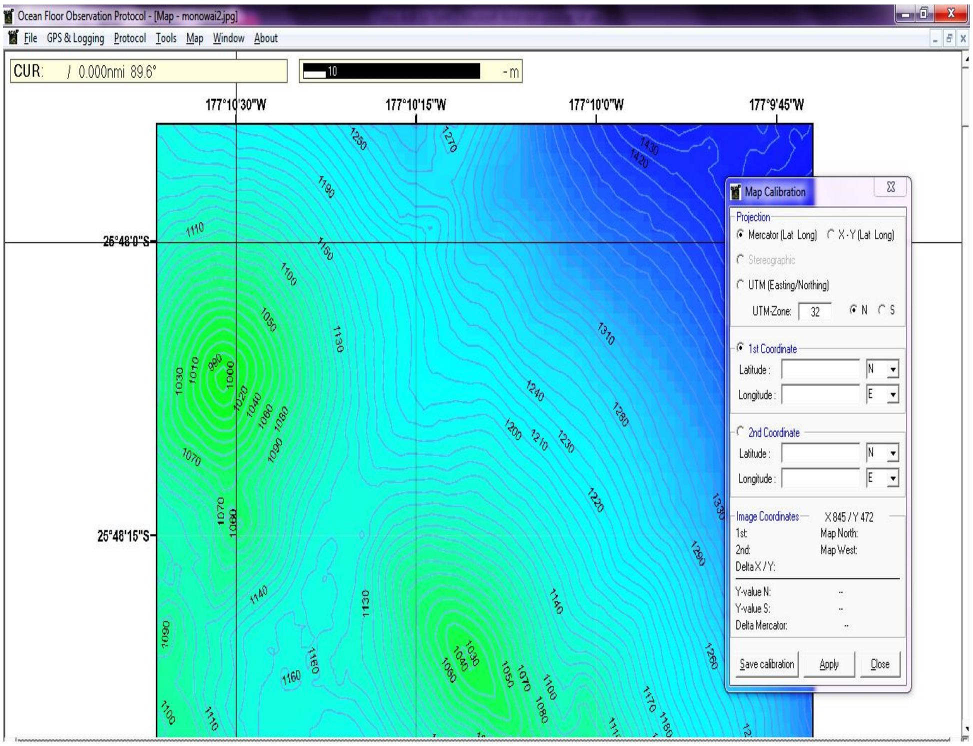


Figure 3: Colour shaded map of Monowai Caldera, with contour labels

The maps came complete with latitudes and longitudes but had to be calibrated (i.e. geo-referenced) in OFOP. To do so, two opposite corners of the map were chosen and the map cursor was aligned with the correct latitude and longitude values of the map for that corner (Figure 4). The coordinates were entered in the Map calibration window. The same steps were repeated in order to enter the values of the second coordinate on the opposite corner of the map. This calibration was saved for subsequent mapping.



Projection
● Mercator (Lat Long) ○ X - Y (Lat Long)
○ Stereographic
○ UTM (Easting/Northing)
UTM-Zone: 32 ● N ○ S

● 1st Coordinate
Latitude: N
Longitude: E

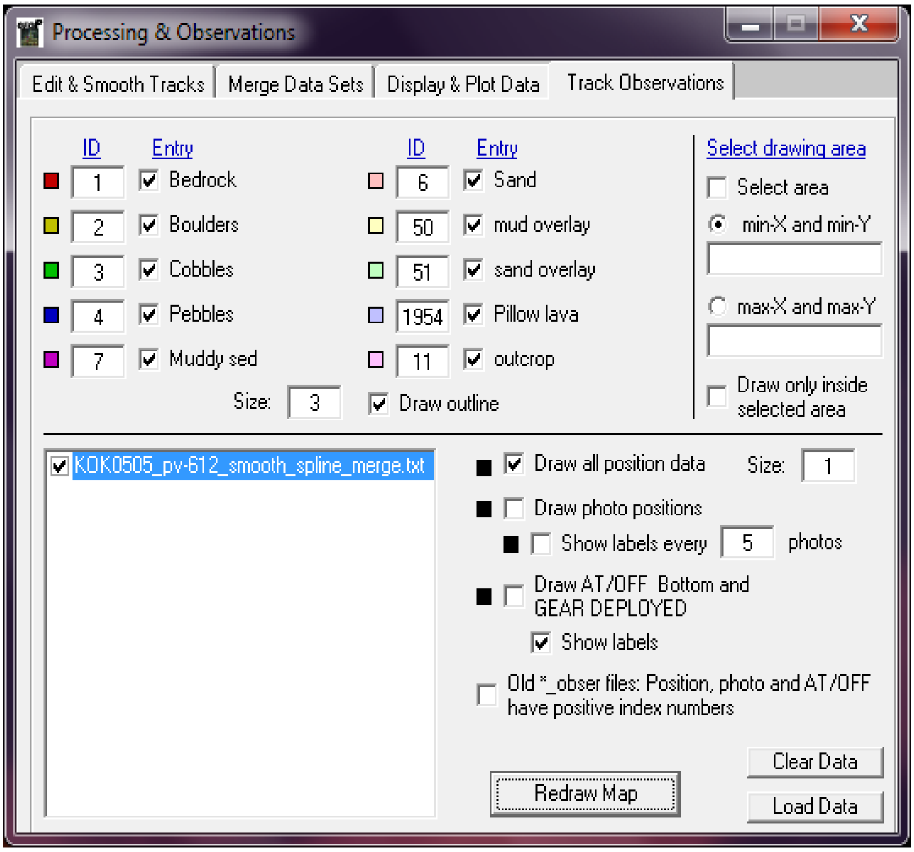
○ 2nd Coordinate
Latitude: N
Longitude: E

Image Coordinates X 845 / Y 472
1st: Map North:
2nd: Map West:
Delta X / Y:

Y-value N: --
Y-value S: --
Delta Mercator: --

Figure 4: Calibration (geo-referencing) of Monowai map in OFOP

Next, the submersible’s position file (smooth_spline_posi* file) was merged with the observation file that listed fauna and substrate classes per still-image in Processing & Observations in OFOP. Mapping of the faunal assemblages and substrates classes along the transect was done by entering the unique button ID for each observation (Figure 5).



	ID		Entry		ID		Entry
🟥	1	☑	Bedrock	🟥	6	☑	Sand
🟨	2	☑	Boulders	🟨	50	☑	mud overlay
🟩	3	☑	Cobbles	🟩	51	☑	sand overlay
🟦	4	☑	Pebbles	🟦	1954	☑	Pillow lava
🟪	7	☑	Muddy sed	🟪	11	☑	outcrop

Size: 3 ☑ Draw outline

Select drawing area

☐ Select area

● min-X and min-Y

○ max-X and max-Y

☐ Draw only inside selected area

☑ KOK0505_pv-612_smooth_spline_merge.txt

■ ☑ Draw all position data Size: 1

■ ☐ Draw photo positions

■ ☐ Show labels every 5 photos

■ ☐ Draw AT/OFF Bottom and GEAR DEPLOYED

☑ Show labels

☐ Old *_obser files: Position, photo and AT/OFF have positive index numbers

Figure 5: Track observations for mapping substrate classes in OFOP

APPENDIX C

Table 1: Results from sequential test of DistLM analysis for environmental variables with showing permutation values (P) of over 0.05, as well as increase in the proportion of variation linked to each environmental variable (Prop), and cumulative percentage contribution of each variable to the overall variation in the data set (Cumul)

Variable	SS (trace)	Pseudo-F	P	Prop.
Bedrock	2675.2	1.03	0.38	6.24E-2
Bedrock outcrop	10615	4.16	0.004	2.47E-2
Bedrock with sand overlay	15172	6.02	0.001	3.54E-2
Bedrock with mud overlay	21168	8.52	0.001	4.94E-2
Volcanically altered bedrock	3909	1.51	0.15	9.12E-3
Pillow lava	1401.1	0.53	0.78	3.27E-3
Boulders	1922.9	0.73	0.57	4.49E-3
Cobbles	1118.6	0.42	0.88	2.61E-3
Pebbles	4504.3	1.74	0.11	1.05E-2
Chimneys	8261.6	3.22	0.004	1.92E-2
Sand	6561.1	2.55	0.03	1.53E-2
Mud	49200	21.29	0.001	0.11
Black sediment	10336	4.05	0.005	2.41E-2
Yellow sulphidic sediment	6683.5	2.600	0.07	1.56E-2
White sulphidic sediment	15410	6.12	0.001	3.59E-2
Bathymodiolid shells	16803	6.69	0.001	3.92E-2
Broken Lamellibrachia tube	2676	1.03	0.39	6.25E-3

Shell hash	2618.6	1.009	0.41	6.11E-3
Crustacean remains	5839.2	2.26	0.05	1.36E-2
Green bacterial mat	14762	5.85	0.001	3.44E-2
White bacterial mat	11422	4.49	0.004	2.66E-2
Water depth	5205.8	2.018	0.057	1.21E-2
Distance to nearest vent	22657	9.163	0.001	5.29E-2

Table 2: Results from sequential test of DistLM analysis for environmental variables with an showing permutation values (P) of over 0.05, as well as increase in the proportion of variation linked to each environmental variable (Prop), cumulative percentage contribution of each variable to the overall variation in the data set (Cumul)

Variables	R^2	SS Trace	Pseudo-F	P	Prop	Cumul
Yellow sulphidic sediment	0.29	4374.8	2.25	0.08	1.02E-2	0.29
Bedrock with sand overlay	0.32	3186.3	1.68	0.11	7.44E-3	0.32
Bedrock	0.332	2854	1.50	0.16	6.66E-3	0.332
Cobbles	0.336	1806.4	0.95	0.40	4.21E-3	0.336
Shell hash	0.339	1352.7	0.71	062	3.15E-3	0.339
Pillow lava	0.342	1379.1	0.72	0.59	3.22E-3	0.342
Boulders	0.345	1181.8	0.62	0.64	2.76E-3	0.345
Pebbles	0.348	1176.6	0.61	0.70	2.74E-3	0.348
Broken Lamellibrachia tube	0.35	789.6	0.41	0.82	1.84E-3	0.35

APPENDIX D

Table 3: A list of other substrate classes with mean percentage covers of less than 1%, and standard errors of the mean (n=166)

Substrate classes	Mean percentage cover	Standard error
Volcanically-altered bedrock	0.45	0.19
Cobbles	0.43	0.17
Pebbles	0.44	0.26
Black sediment	0.35	0.18
Yellow sulphidic sediment	0.16	0.15
Broken lamellibrachia tube	0.04	0.02
Crustacean remains	0.07	0.04
Bacterial mat (white)	0.83	0.52

APPENDIX E

Table 4: Dissimilarity percentage values for faunal groups associated with different substrate classes, in decreasing order of overall dissimilarity. Taxa with dissimilarity/SD value of over 1.0 were deemed to be responsible for the dissimilarities between faunal community groups.

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Groups e & h						
Average dissimilarity = 98.26						
	Group e	Group h				
Species						
Lepetodrilus sp.	14.62	0.00	42.71	6.59	43.47	43.47
B. manusensis	8.50	0.00	25.21	4.66	25.66	69.13
Alvinocaris spp.	5.04	0.12	14.34	4.80	14.59	83.72
P. hirtella	2.15	0.04	6.52	2.39	6.63	90.35
Groups h & d						
Average dissimilarity = 97.73						
	Group h	Group d				
Species						
Lepetodrilus sp.	0.00	6.76	34.96	4.59	35.77	35.77
B. manusensis	0.00	4.11	20.69	7.85	21.17	56.94
Alvinocaris spp.	0.12	3.89	18.44	2.75	18.87	75.81
P. hirtella	0.04	1.96	9.60	5.79	9.82	85.63
L. juni	0.00	0.72	3.24	0.67	3.31	88.94
P. moelleri	0.00	0.46	2.21	1.70	2.26	91.20

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Groups f & h						
Average dissimilarity = 95.80						
	Group f	Group h				
B. manusensis	5.56	0.00	45.42	3.23	47.41	47.41
Alvinocaris spp.	2.24	0.12	17.62	1.80	18.39	65.80
P. hirtella	1.51	0.04	12.28	2.50	12.82	78.62
Anemones	0.62	0.10	4.55	1.38	4.75	83.37
Enigmaticolus sp.	0.00	0.42	3.17	0.49	3.31	86.68
Macrourids (Rat-tails)	0.02	0.35	2.91	1.32	3.03	89.71
P. moelleri	0.27	0.00	2.18	0.97	2.27	91.98
Groups e & a						
Average dissimilarity = 95.64						
	Group e	Group a				
Lepetodrilus sp.	14.62	0.00	43.28	6.71	45.25	45.25
B. manusensis	8.50	0.00	25.55	4.68	26.72	71.97
Alvinocaris spp.	5.04	0.59	13.06	4.41	13.65	85.62
P. hirtella	2.15	0.05	6.57	2.38	6.87	92.49

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Groups c & h						
Average dissimilarity = 94.39						
	Group c	Group h				
Alvinocaris spp.	3.35	0.12	47.74	3.28	50.58	50.58
P. hirtella	1.35	0.04	19.57	2.05	20.74	71.32
Macrourids (Rat-tails)	0.00	0.35	5.21	1.37	5.52	76.83
Enigmaticolus sp.	0.00	0.42	5.10	0.50	5.41	82.24
P. moelleri	0.23	0.00	3.12	0.89	3.30	85.54
Anemones	0.13	0.10	2.95	0.65	3.13	88.67
Synaphobranchids	0.10	0.13	2.80	0.73	2.97	91.64
Groups a & g						
Average dissimilarity = 93.83						
	Group a	Group g				
P. hirtella	0.05	0.84	29.17	1.93	31.09	31.09
Alvinocaris spp.	0.59	0.00	24.20	2.05	25.79	56.88
Anemones	0.07	0.18	6.42	0.74	6.84	63.72
Invertebrate Tracks	0.11	0.03	4.19	0.49	4.46	68.19
Natant decapod	0.00	0.10	4.15	0.50	4.42	72.61
Synaphobranchids	0.00	0.12	3.44	0.54	3.66	76.27
Enigmaticolus sp.	0.07	0.06	3.25	0.51	3.46	79.73
Mound <20cm	0.11	0.00	3.13	0.43	3.33	83.07
Burrow (<25mm)	0.00	0.13	3.06	0.32	3.26	86.33
Bivalvia	0.00	0.17	3.04	0.26	3.24	89.57

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
B. manusensis	0.00	0.10	2.55	0.37	2.71	92.28

Groups g & h

Average dissimilarity = 93.36

	Group g	Group h				
P. hirtella	0.84	0.04	27.89	1.66	29.87	29.87
Macrourids (Rat-tails)	0.00	0.35	11.97	1.14	12.82	42.69
Enigmaticolus sp.	0.06	0.42	9.70	0.54	10.39	53.09
Synaphobranchids	0.12	0.13	6.60	0.67	7.07	60.16
Anemones	0.18	0.10	6.57	0.73	7.04	67.19
Invertebrate Tracks	0.03	0.18	6.26	0.59	6.71	73.90
Natant decapod	0.10	0.02	4.09	0.52	4.38	78.28
Bivalvia	0.17	0.03	3.57	0.31	3.83	82.11
Burrow (<25mm)	0.13	0.03	3.55	0.38	3.80	85.91
Alvinocaris spp.	0.00	0.12	3.38	0.44	3.62	89.54
B. manusensis	0.10	0.00	2.36	0.36	2.53	92.07

Groups e & g

Average dissimilarity = 93.35

	Group e	Group g				
Lepetodrilus sp.	14.62	0.00	42.41	6.49	45.43	45.43
B. manusensis	8.50	0.10	24.75	4.50	26.52	71.94
Alvinocaris spp.	5.04	0.00	14.59	5.26	15.63	87.57
P. hirtella	2.15	0.84	4.15	1.56	4.45	92.01

Groups a & d

Average dissimilarity = 92.93

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
	Group a	Group d				
Lepetodrilus sp.	0.00	6.76	35.74	4.60	38.46	38.46
B. manusensis	0.00	4.11	21.14	8.32	22.75	61.21
Alvinocaris spp.	0.59	3.89	16.32	2.35	17.56	78.78
P. hirtella	0.05	1.96	9.74	6.26	10.48	89.26
L. juni	0.00	0.72	3.30	0.67	3.55	92.81

Groups b & h

Average dissimilarity = 92.47

	Group b	Group h				
Alvinocaris spp.	1.03	0.12	24.11	2.69	26.08	26.08
P. hirtella	0.88	0.04	21.67	2.54	23.44	49.51
Macrourids (Rat-tails)	0.00	0.35	8.34	1.35	9.02	58.53
Enigmaticolus sp.	0.00	0.42	7.32	0.51	7.92	66.45
B. manusensis	0.35	0.00	6.57	0.49	7.11	73.56
Anemones	0.18	0.10	6.23	0.66	6.73	80.29
Burrow (<25mm)	0.20	0.03	5.29	0.78	5.72	86.01
Invertebrate Tracks	0.00	0.18	4.03	0.59	4.36	90.38

Groups f & a

Average dissimilarity = 88.64

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
	Group f	Group a				
B. manusensis	5.56	0.00	47.00	3.34	53.02	53.02
Alvinocaris spp.	2.24	0.59	14.93	1.79	16.84	69.86
P. hirtella	1.51	0.05	12.59	2.59	14.21	84.07
Anemones	0.62	0.07	4.73	1.40	5.33	89.41
P. moelleri	0.27	0.00	2.25	0.98	2.54	91.94

Groups g & d

Average dissimilarity = 89.77

	Group g	Group d				
Lepetodrilus sp.	0.00	6.76	34.54	4.54	38.48	38.48
B. manusensis	0.10	4.11	19.99	6.26	22.27	60.75
Alvinocaris spp.	0.00	3.89	18.81	2.94	20.95	81.70
P. hirtella	0.84	1.96	5.59	2.19	6.23	87.92
L. juni	0.02	0.72	3.24	0.69	3.61	91.53

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%

Groups a & h

Average dissimilarity = 89.46

	Group a	Group h				
Alvinocaris spp.	0.59	0.12	24.18	1.70	27.03	27.03
Macrourids (Rat-tails)	0.00	0.35	14.05	1.21	15.70	42.73
Enigmaticolus sp.	0.07	0.42	11.95	0.62	13.35	56.08
Invertebrate Tracks	0.11	0.18	8.32	0.69	9.30	65.38

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Anemones	0.07	0.10	6.84	0.62	7.65	73.02
Synaphobranchids	0.00	0.13	5.97	0.53	6.67	79.70
P. hirtella	0.05	0.04	3.45	0.51	3.86	83.56
Mound <20cm	0.11	0.00	3.31	0.43	3.70	87.26
Squid	0.05	0.03	3.19	0.50	3.56	90.82

Groups b & e

Average dissimilarity = 85.77

	Group b	Group e				
Lepetodrilus sp.	0.00	14.62	41.28	6.50	48.13	48.13
B. manusensis	0.35	8.50	23.38	4.08	27.25	75.38
Alvinocaris spp.	1.03	5.04	11.18	3.72	13.03	88.42
P. hirtella	0.88	2.15	3.83	1.62	4.46	92.88

Groups f & g

Average dissimilarity = 83.48

	Group f	Group g				
B. manusensis	5.56	0.10	43.85	3.05	52.53	52.53
Alvinocaris spp.	2.24	0.00	17.96	1.85	21.52	74.04
P. hirtella	1.51	0.84	6.67	1.52	7.99	82.03
Anemones	0.62	0.18	4.39	1.33	5.26	87.29
P. moelleri	0.27	0.02	2.13	0.98	2.55	89.84
L. juni	0.27	0.02	2.11	0.59	2.52	92.36

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Groups c & a						
Average dissimilarity = 78.50						
	Group c	Group a				
Alvinocaris spp.	3.35	0.59	42.37	3.18	53.98	53.98
P. hirtella	1.35	0.05	20.43	2.18	26.03	80.01
P. moelleri	0.23	0.00	3.28	0.90	4.18	84.19
Anemones	0.13	0.07	2.76	0.62	3.52	87.71
Invertebrate Tracks	0.01	0.11	1.64	0.46	2.08	89.79
Synaphobranchids	0.10	0.00	1.57	0.46	2.00	91.79
Groups b & d						
Average dissimilarity = 77.32						
	Group b	Group d				
Lepetodrilus sp.	0.00	6.76	32.94	4.79	42.60	42.60
B. manusensis	0.35	4.11	17.94	4.01	23.20	65.81
Alvinocaris spp.	1.03	3.89	13.01	1.93	16.83	82.63
P. hirtella	0.88	1.96	5.00	3.01	6.47	89.10
L. juni	0.00	0.72	3.08	0.67	3.98	93.09
Groups c & e						
Average dissimilarity = 74.34						
	Group c	Group e				
Lepetodrilus sp.	0.00	14.62	38.44	6.20	51.71	51.71
B. manusensis	0.00	8.50	22.66	4.67	30.48	82.19
Alvinocaris spp.	3.35	5.04	5.19	1.45	6.98	89.17
P. hirtella	1.35	2.15	2.70	1.18	3.63	92.80

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Groups f & b						
Average dissimilarity = 65.84						
	Group f	Group b				
B. manusensis	5.56	0.35	38.69	2.73	58.77	58.77
Alvinocaris spp.	2.24	1.03	10.80	1.63	16.40	75.17
P. hirtella	1.51	0.88	5.28	1.59	8.02	83.20
Anemones	0.62	0.18	4.26	1.40	6.47	89.67
P. moelleri	0.27	0.06	1.95	1.02	2.97	92.63
Groups b & g						
Average dissimilarity = 64.67						
	Group b	Group g				
Alvinocaris spp.	1.03	0.00	24.79	3.24	38.34	38.34
P. hirtella	0.88	0.84	7.89	1.21	12.20	50.54
B. manusensis	0.35	0.10	7.53	0.59	11.64	62.18
Anemones	0.18	0.18	6.27	0.71	9.69	71.88
Burrow (<25mm)	0.20	0.13	6.22	0.79	9.62	81.49
Natant decapod	0.00	0.10	2.48	0.52	3.84	85.33
Bivalvia	0.00	0.17	2.36	0.26	3.65	88.98
Synaphobranchids	0.00	0.12	2.29	0.56	3.54	92.52

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Groups c & d						
Average dissimilarity = 64.09						
	Group c	Group d				
Lepetodrilus sp.	0.00	6.76	29.27	5.06	45.67	45.67
B. manusensis	0.00	4.11	17.40	7.72	27.15	72.82
Alvinocaris spp.	3.35	3.89	7.23	1.55	11.28	84.09
P. hirtella	1.35	1.96	3.03	1.13	4.72	88.82
L. juni	0.05	0.72	2.84	0.71	4.43	93.24
Groups b & a						
Average dissimilarity = 63.95						
	Group b	Group a				
P. hirtella	0.88	0.05	22.80	3.18	35.65	35.65
Alvinocaris spp.	1.03	0.59	11.97	1.69	18.71	54.36
B. manusensis	0.35	0.00	7.00	0.49	10.94	65.30
Anemones	0.18	0.07	6.31	0.64	9.87	75.17
Burrow (<25mm)	0.20	0.00	5.40	0.75	8.45	83.63
Invertebrate Tracks	0.00	0.11	2.35	0.43	3.67	87.30
Mound <20cm	0.00	0.11	2.35	0.43	3.67	90.97

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Groups c & f						
Average dissimilarity = 58.98						
	Group c	Group f				
B. manusensis	0.00	5.56	34.48	3.19	58.46	58.46
Alvinocaris spp.	3.35	2.24	10.81	1.32	18.32	76.78
P. hirtella	1.35	1.51	4.32	1.18	7.33	84.11
Anemones	0.13	0.62	3.53	1.38	5.98	90.10
Groups f & e						
Average dissimilarity = 55.41						
	Group f	Group e				
Lepetodrilus sp.	0.00	14.62	33.72	5.48	60.85	60.85
B. manusensis	5.56	8.50	8.27	1.47	14.92	75.77
Alvinocaris spp.	2.24	5.04	6.67	1.71	12.04	87.82
P. hirtella	1.51	2.15	2.19	1.21	3.94	91.76
Groups c & b						
Average dissimilarity = 52.55						
	Group c	Group b				
Alvinocaris spp.	3.35	1.03	28.25	2.41	53.76	53.76
P. hirtella	1.35	0.88	8.81	2.18	16.77	70.53
B. manusensis	0.00	0.35	3.86	0.49	7.35	77.88
Anemones	0.13	0.18	3.36	0.67	6.40	84.29
P. moelleri	0.23	0.06	2.74	0.97	5.20	89.49

	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Burrow (<25mm)	0.02	0.20	2.69	0.76	5.12	94.61

Groups f & d

Average dissimilarity = 47.54

	Group f	Group d				
Lepetodrilus sp.	0.00	6.76	23.88	5.01	50.23	50.23
Alvinocaris spp.	2.24	3.89	7.58	1.53	15.96	66.19
B. manusensis	5.56	4.11	6.98	1.20	14.68	80.87
L. juni	0.27	0.72	2.61	0.83	5.49	86.36
P. hirtella	1.51	1.96	2.38	1.30	5.01	91.37

Groups e & d

Average dissimilarity = 33.25

	Group e	Group d				
Lepetodrilus sp.	14.62	6.76	14.94	2.27	44.94	44.94
B. manusensis	8.50	4.11	8.58	1.98	25.80	70.74
Alvinocaris spp.	5.04	3.89	3.85	1.32	11.57	82.31
L. juni	0.26	0.72	1.53	0.83	4.60	86.90
P. hirtella	2.15	1.96	1.35	1.23	4.06	90.97