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SPATIAL VARIATION IN THE COMPOSITION AND DISTRIBUTION OF FAUNAL ASSEMBLAGES AT HYDROTHERMAL VENTS IN AN ANTARCTIC SEAFLOOR CALDERA

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As the nominated University supervisor of this M.Sc. project by Abbie Sarah Amy Chapman, I confirm that I have had the opportunity to comment on earlier drafts of the report, prior to submission of the dissertation for consideration of the award of M.Sc. Oceanography.

Signed:

Dr Jonathan T Copley

ABSTRACT

Recent exploration of hydrothermal vent fields on the East Scotia Ridge has revealed a new Southern Ocean province of vent biogeography. Whilst the newly discovered E2 and E9 vent fields are dominated by a new species of *Kiwa* crab, gastropods, barnacles and anemones, another hydrothermal vent field was discovered in 2010, in a seafloor caldera in the South Sandwich Island chain. Few caldera-hosted hydrothermal systems have been studied globally, and such systems appear to contrast with ridge-hosted systems nearby. This study provides a first characterisation of the dominant fauna at the active hydrothermal vent field of Kemp Caldera, South Sandwich Islands. The project aims to address how faunal assemblages within this caldera-hosted vent field compare with those of ridge-hosted vent fields in the Southern Ocean, and other calderas around the world. Remotely Operated Vehicle (ROV) *Isis* was used to obtain high-resolution video imagery along grids of 5-25 m lines, enabling creation of photomosaics of four distinct faunal assemblages, to examine faunal density variation across space, in detail, for the first time. Videos from larger scale transect lines are used in this project to define a wider faunal zonation across the vent field. *Lepetodrilus* sp., bacterial mat and vesicomyid clams (in excess of 125.2 m^{-2}) dominate assemblages closest to visible vent sources. Meanwhile, photomosaics predominantly represent fauna from areas of diffuse venting, with 'M1' mosaic dominated by pycnogonids and gastropods (*Lepetodrilus* sp. up to 549 m^{-2} and *Pyropelta* sp. in excess of 14292 m^{-2}), 'M2' by anemones ($\leq$21 m^{-2}) and gastropods, 'M3' by siboglinid tubeworms ($\leq$103 m^{-2}) and 'M4' by vesicomyid clams ($\leq$125 m^{-2}). The peripheral fauna mostly comprise echinoderms, in addition to midwater crustaceans and *Nematocarcinus lanceopes* shrimp. It is proposed that Kemp Caldera is a regularly disturbed site, with evidence for slope failure and a recent eruption. The site acts as an interaction point for Antarctic midwater, deep-sea and chemosynthetic fauna, analogous with calderas studied in the Caribbean and Samoa. The fauna of the caldera vent field contrasts with that of the nearby E9 vent field on the East Scotia Ridge, indicating that further exploration and investigation of caldera-hosted hydrothermal systems may be important, to obtain a full understanding of global vent biogeography.

KEYWORDS: Caldera; Hydrothermal Vents; Photomosaic; Remotely Operated Vehicle; Vent Biogeography.

This project is dedicated to the memories of my Grandad, Grandma and Grandfather.

'Shackleton's Nimrod', by Gordon Chapman

I hope that this work will make Gordon Chapman, Mau Chapman and Jim Samuels proud, as I am proud to be their granddaughter.
I will treasure our seaside memories, Grandma and Grandad.
Grandfather, I hope to visit Antarctica to tell you all about it one day…

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I. INTRODUCTION

In 2010, the Register of Antarctic Marine Species comprised more than 8,800 species (DeBroyer and Danis, 2010; Griffiths, 2010). However, understanding of Antarctic marine biodiversity is limited by physical accessibility (Brandt *et al.*, 2007; Griffiths, 2010). Since the advancement of Remotely Operated Vehicle (ROV) technologies, the deep Southern Ocean has become increasingly accessible, with research already conducted on several hydrothermal vent sites to date (e.g. E2 and E9, East Scotia Ridge – see Rogers *et al.*, 2012 and Marsh *et al.*, 2012, respectively). This report aims to provide a first characterisation of a site within an Antarctic submarine volcanic caldera, with the goal of improving understanding of Antarctic deep-sea ecology, broadening the research scope from chimneys and ridges to submarine volcanoes. It will begin by introducing key controls on vent fauna and the current status of vent biogeography (given the recent discovery of East Scotia Ridge vent fields). Suggestions will be made as to why calderas may lie outside existing biogeographic provinces, before explaining how video images have been utilised effectively in ecological analyses of vent sites. Finally, before presenting the methodology and findings of this study of Kemp Caldera vent field, the aims of this project are put forward and research hypotheses proposed.

Life at Hydrothermal Vents

Hydrothermal vent systems operate as a result of convection of seawater through newly forming upper lithosphere (Lutz and Kennish, 1993). Active hydrothermal vent systems are linked with volcanism and plate tectonics, situated at mid-ocean ridges, back-arc basins, and volcanoes (Van Dover, 2000). Vent sites are ephemeral features, particularly when disturbed by volcanic eruptions (Haymon *et al.*, 1993; Van Dover, 2000). Vent biomass is high, but faunal species richness tends to be low, when compared with other non-chemosynthetic habitats of the deep sea (Grassle and Macioleck, 1992; Snelgrove and Grassle, 2001; Ramirez-Llodra *et al.*, 2007). This relationship is commonplace in high-energy habitats, where physiological limits are pushed to extremes (Ramirez-Llodra *et al.*, 2007). Vent habitats are unique, characterised by: endemic species, habitat segregation, global spread, and close links between ecology and geodynamics (Van Dover, 2000). More specifically, hydrothermal vent habitats are distinct from others in the deep sea, as hydrothermal fluid circulation affects community composition, species richness and faunal spread (Van Dover, 2000).

Chemosynthetic vent fauna rely on microbes to oxidise reduced chemicals (e.g. hydrogen sulfide), harnessing hydrothermal fluid energy to make organic compounds to survive (Fisher *et al.*, 2007). They utilise microbial production, by direct feeding on microorganisms, by using microbes as symbionts, or by a mix of both processes (Van Dover, 2000). This chemosynthetic means of primary production supports a plethora of fauna at deep-sea hydrothermal vents, creating hubs for primary consumers, which cover any exposed surface and are often divided into 'zones', according to an overlying physico-chemical gradient (Jannasch and Wirsen, 1979; Hessler and Smithey, 1983; Sarrazin *et al.*, 1999; Van Dover, 2000). Environmental conditions at vents are highly variable, with temperatures fluctuating over unpredictable timescales (Lutz and Kennish, 1993). As a result, organisms must have rapid physiological responses: reproducing regularly or continuously; growing more quickly; being highly fertile; and remaining tolerant of an ever-changing environment (Johnson *et al.*, 1988; Lutz and Kennish, 1993). Van Dover (2011) summarizes the influences on deep-sea hydrothermal vent life, as shown in Table 1.

Table 1 – Key physical, chemical, and biological influences on deep-sea hydrothermal vent ecosystems.
(After Van Dover, 2011.)

Space	Distance between active sites
Time	Intervals between disturbance Duration of vent activity
Environment	Substratum Fluid chemistry Seasonality Geography Hydrography Topography
Biology	Species composition Time to sexual maturation Mode of fertilization Brood size Larval dispersal type Larval behaviour Duration of larval life Recruitment processes Predation and competition

Venting varies in appearance and temperature, ranging from 400°C black smokers to 30°C diffuse flows (Lutz and Kennish, 1993). On a larger scale, vent fields vary as a result of differences in geology and underlying plate tectonics. For example, back-arc spreading centres are found along active plate margins behind island arcs, where oceanic crust subducts beneath a continental plate and drags part of the continental plate with it, creating a split, or an extension zone (Van Dover, 2000). It is within this zone that magmas are upwelled, forming new crust by very different means to the more familiar process of seafloor spreading (Van Dover, 2000). Back-arc spreading is more erratic than spreading at mid-ocean ridges, with extension stopping and starting over millions of years (Van Dover, 2000; Tokeshi, 2011). It is the unique situation where water brought with the oceanic crust enters hot mantle that generates a different form of melt chemistry, creating a heterogeneous volcanic environment, less uniform than basalt-dominated mid-ocean ridge sites (Van Dover, 2000). This compound environment permits establishment of a wealth of invertebrates and microbes, with new taxa and assemblages often found at such sites (Martinez *et al.*, 2007). Also, back-arc geochemistry differs from ridge-hosted vent environments and it is likely that substratum, pH, and other factors impact back-arc basin community development (Luther *et al.*, 2001; Martinez *et al.*, 2007). The complexity of the back-arc environment ensures that its vent systems are unrelated to vents from other geodynamic settings (Tokeshi, 2011).

Back-arc basins, like the East Scotia Ridge, near which the Kemp Caldera vent field is situated, are perfect real-life laboratories, demonstrating the influence of varied geochemistry and geomorphology on biological diversity (Martinez *et al.*, 2007). Because they are isolated and undergo more frequent change within geological timescales, back-arc basins are important when investigating vent biogeography (Ramirez-Llodra *et al.*, 2007).

Biogeographical Provinces and the Discovery of the East Scotia Ridge Vent Fields

Vent biogeography involves the identification of patterns in present-day species distributions across the globe (Tunnicliffe *et al.*, 1991; 1996; 1997; 1998; Bachraty *et al.*, 2009; Desbruyères, 2009; Vrijenhoek, 2010; Moalic *et al.*, 2012 – see Appendix A). A view on the importance of vent 'provinces' as a component of our understanding of global hydrothermal systems is presented in the work of Tyler *et al.* (2003; see also: Gage and Tyler, 1991; Ramirez-Llodra *et al.*, 2007). Gene flow, dispersal and colonization can all be influenced by larval transport, affected by biotic and abiotic factors (e.g. swimming capability versus distance between sites; Cowen *et al.*, 2000; Tyler and Young, 2003; Ramirez-Llodra *et al.*, 2007; Vrijenhoek, 2010). Thus, biogeography is driven by a complex suite of factors, including: life history traits, geology, deep-ocean currents, and bathymetry (Van Dover *et al.*, 2002; Ramirez-Llodra *et al.*, 2007).

The Southern Ocean region is likely influenced by the Circumpolar Current, which would link species from the East Pacific Rise, East Scotia Ridge, Mid-Atlantic Ridge and Southwest Indian Ridge (Ramirez-Llodra *et al.*, 2007). However, this region has yet to be fully explored. It has been suggested that the Drake Passage may enable or prevent larval dispersal between the Atlantic and Pacific Oceans (Van Dover *et al.*, 2003; Ramirez-Llodra *et al.*, 2007; Tunnicliffe *et al.*, 2009).

Debates surrounding vent biogeography have been reignited following the discovery of vent fauna on the Antarctic East Scotia Ridge (ESR), which have been linked to and separated from other Pacific and Atlantic vent communities (Rogers *et al.*, 2012). Global deep-sea macrofaunal biodiversity trends allegedly indicate that species richness decreases poleward (Brandt, 2012). However, the Atlantic sector of the Southern Ocean (the location of the ESR) does not conform to this trend, and has been proposed to form the largest single benthic habitat on Earth (Brandt *et al.* 2012).

The ESR is an isolated, intermediate-rate back-arc spreading centre in the Southern Ocean, potentially representing a new province in vent biogeography (Marsh *et al.*, 2012; Rogers *et al.*, 2012). The ESR started spreading more than 15 million years ago and is 500 km long, forming the boundary between the Scotia plate and the Sandwich plate (Rogers *et al.*, 2012; Nicholson and Georgen, 2013). Its present day full spreading rate is 70 mm y^{-1}. Its nine second-order ridge components (named E1 to E9) are separated by non-transform discontinuities (Rogers *et al.*, 2012). To the south of E9, near Kemp Caldera, there are changes to the stress field on approach to strike-slip faults where the South Sandwich and Scotia plates meet the Antarctic plate boundary (Rogers *et al.*, 2012). Vent fields on the ESR differ from those of other known mid-ocean ridge systems in terms of community composition, with a notable lack of siboglinid tubeworms, alvinellids, clams, mussels and alvinocaridid shrimp (Rogers *et al.*, 2012).

Lutz *et al.* (2008) anticipated ESR sites to suffer the effects of both predation pressure (with more Antarctic fauna present in shallower environments such as those along the ESR) and inter-basin circulation (limiting larval dispersal). Antarctica and the Southern Ocean are isolated from the global ocean by the Polar Front, the Antarctic Circumpolar Current and ambient water temperatures below freezing (Orsi *et al.*, 1995; Rogers *et al.*, 2012; Thatje, 2012). Physiological limits are reached in this polar region, with most crustaceans unable to survive at polar temperatures and many invertebrates opting for direct or lecithotrophic modes of larval development (Rogers *et al.*, 2012; Thatje, 2012). This explains the findings of Rogers *et al.* (2012), where commonly identified vent fauna (e.g. mussels) were absent from the ESR, likely due to their planktotrophic larval development mode.

Calderas – outside existing provinces?

Volcanic arcs are common, equivalent to around one third of the length of mid-ocean ridges (Wishner *et al.*, 2005). However, they remain relatively unstudied (Wishner *et al.*, 2005). Due to their topography, submarine volcanic features can form unique environments, with localised currents retaining larvae and trapping animals and food (Embley *et al.*, 2004; Wishner *et al.*, 2005; Staudigel *et al.*, 2006; Tokeshi, 2011; Clark *et al.*, 2012). Thus, it can be assumed that faunal distribution within a venting caldera may differ from that on a large chimney, despite a common chemosynthetic energy supply.

Wishner *et al.* (2005) investigated hydrothermal venting in a shallow volcanic crater (Kick'em Jenny) in the Caribbean Sea, finding mesopelagic crustaceans below their depth. They discovered that fewer animals (shrimp and worms) were found in the main crater than in inactive, secondary craters (Wishner *et al.*, 2005). They concluded that volcanic arcs act as important interaction sites for midwater and deep fauna, but that this particular site's species richness was lowered by frequent volcanic disturbances or limited habitat availability (Wishner *et al.*, 2005). Caldera environments were identified as a habitat and burial ground for accidental entrants (Wishner *et al.*, 2005). Staudigel *et al.* (2006) worked on Vailulu'u seamount in Samoa and noted similar ecological features to those of Wishner *et al.* (2005); for example, they, too, observed dead midwater fauna, presumably killed on contact with toxic hydrothermal vent emissions.

Following on from these studies, it is reasonable to assume that, despite the shared back-arc basin setting of Kemp Caldera, it may differ from other ESR vent sites. Its unique shape and complex geology will likely drive dissimilarity and encourage mesopelagic Antarctic species into a deep, chemosynthetic environment.

Vent Ecology & Spatial Analyses Using Imagery

It is important to understand the species composition of an ecosystem before investigating spatial patterns and their potential drivers (Underwood *et al.*, 2000; Ramirez-Llodra *et al.*, 2007). This involves preliminary work, mapping spatial distribution across a variety of scales (e.g. Marsh *et al.*, 2012). It is vital to understand the factors shaping vent communities to appreciate our potential impact on the deep sea. This is especially important at present, as proposals for seabed massive sulfide mining and manganese nodule mining are being presented at a faster rate than deep-sea ecologists can keep up with (Ramirez-Llodra *et al.*, 2011; Van Dover, 2011; Marsh *et al.*, 2012).

Over small spatial scales, species distribution patterns correspond to physical and chemical conditions at a vent site (Gage and Tyler, 1991; Marsh *et al.*, 2012). This means that spatial analyses can be undertaken on scales ranging from centimetres to kilometres, to yield ecologically valuable results (Marsh *et al.*, 2012). Description of spatial patterns and characterisation of habitats are pre-requisites for experimental manipulation and understanding of process in deep-sea ecology (Underwood *et al.*, 2000; Podowski *et al.*, 2009). For example, the spatial distribution of vent fauna can be used as an indicator of intraspecific interactions on the seafloor (Gage and Tyler, 1991).

Unlike the study of shallow, coastal environments (e.g. Paine, 1974), deep-sea vents can only be explored by machine (Marsh *et al.*, 2012). As a result, Remotely Operated Vehicles (ROVs), Human-Occupied Vehicles (HOVs) and Autonomous Underwater Vehicles (AUVs) are often used to map and photographically survey the deep sea (Yoerger *et al.*, 2000; Yoerger *et al.*, 2007). However, the study of deep-sea habitats is limited by the difficulties presented in reconstructing seafloor viewed through a camera lens (Durand *et al.*, 2002). Thus, the creation of maps and photomosaics (composite images) enables relatively quick, detailed analysis of faunal distribution at vent sites across reasonably large spatial scales (Durand *et al.*, 2002; Pizarro and Singh, 2003; Podowski *et al.*, 2009; Marcon *et al.*, 2013a; 2013b; 2013c; Marsh *et al.*, 2013).

Image analysis is a less invasive means of exploring vent habitats than direct sampling (Van Dover and Lutz, 2004; Cuvelier *et al.*, 2012). It can be used to ensure any samples collected involve minimal environmental and ecological impact, as per InterRidge guidelines (InterRidge, 2006; Marsh *et al.*, 2013). Cuvelier *et al.* (2012) outline the ecological scope of image analysis, when compared with *in situ* sampling. They conclude that images can be used to examine: macrofaunal (>1 cm) abundances; assemblage distributions; diversity; biomass; behaviours and interactions; microbial mat coverage; environmental variables, such as currents and fluid flow; and temporal change (Cuvelier *et al.*, 2012). However, many studies to date have relied on towed camera sleds, limiting the resolution of images acquired and preventing reliable identification of fauna (Marsh *et al.*, 2013).

Few studies have used overlapping survey lines to gather imagery of sufficient quality for photomosaic generation across large-scale vent sites (Marsh *et al.*, 2013). Marsh *et al.* (2012; 2013), Rogers *et al.* (2012) and Amon *et al.* (2013) have used such techniques in the Southern Ocean deep sea to interpret zonation patterns, proportional coverage by dominant species on a vent chimney, and to provide typical faunal densities for particular localities. However, no research has yet seen the use of still images and videography to quantify and contour faunal densities across a site, as this is impossible to do when fauna are as densely populated and concentrated as at E2 and E9 vent chimneys, or on whale bones. Nonetheless, this should be achievable using horizontal mosaics at Kemp Caldera vent field.

Aims & Research Questions

This project forms part of a NERC-funded research programme, investigating the biogeography and ecology of chemosynthetic ecosystems south of the Polar Front, which has been highlighted as a priority area for improving understanding of global vent biogeography (Tyler *et al.*, 2003; German *et al.*, 2011). It is hoped that, by studying the ESR vent sites, the link between North Atlantic and East Pacific vent provinces will be determinable (German *et al.*, 2000).

The aim of this project is to determine the composition and spatial distribution of faunal assemblages at a hydrothermal vent field in Kemp Caldera, South Sandwich Islands, using similar videographic survey and photomosaicing methods to those applied at vent fields on the East Scotia Ridge (Marsh *et al.*, 2012; 2013). The study addresses the following research question:

> *"How do the faunal assemblages of a hydrothermal vent field in an Antarctic seafloor caldera compare with those of ridge-hosted vent fields in the Southern Ocean, and calderas across the globe?*

The specific objectives of this project are: to describe communities identified at Kemp Caldera at a range of scales; to use ROV imagery to delineate spatial distribution patterns and describe faunal assemblages; and to employ statistical methods to quantify patterns in community composition and faunal abundance across the caldera. As the data have been gathered from horizontal mosaic and transect lines, peripheral fauna are also considered (Marsh *et al.*, 2013).

The following research hypotheses are proposed:

- Based on the findings at the Caribbean and Samoan calderas, it is proposed that the dead remains of mesopelagic organisms will accumulate in Kemp Caldera vent field, providing a food source for bacteria and larger benthic organisms.
- Kemp Caldera vent field will likely be more affected by physical oceanography, pH and toxicity than other Antarctic vent sites, differentiating it from E2 and E9 fields, in terms of species presence/absence, faunal distribution, and environmental drivers.
- Some species identified at Kemp Caldera vent field will be endemic to caldera vent systems in the Antarctic, not found on nearby Antarctic ridge sites.

The overall goal of this work is to improve understanding of Antarctic deep-sea ecology, by expanding knowledge of habitat types in the region.

II. MATERIALS & METHODS

A Description of the Kemp Caldera Vent Field

Figure 1 – Location of the Kemp Caldera vent field, East Scotia Ridge, Antarctica. (A) Bathymetric map of the Scotia Sea and key oceanographic and geological features.
(B) Bathymetry of Kemp Caldera, with transect and mosaic locations marked on in the vent field, near the sub-cone.
(C) Bathymetry of the Kemp caldera vent field, displaying the location of transect lines and mosaic surveys. (A) is adapted from Marsh *et al.* (2012).
(B) and (C) were constructed in ArcMap (ESRI, CA) using unpublished ship-based bathymetry data from the British Antarctic Survey JCR224 research cruise.

Figure 1: Caption on page 7

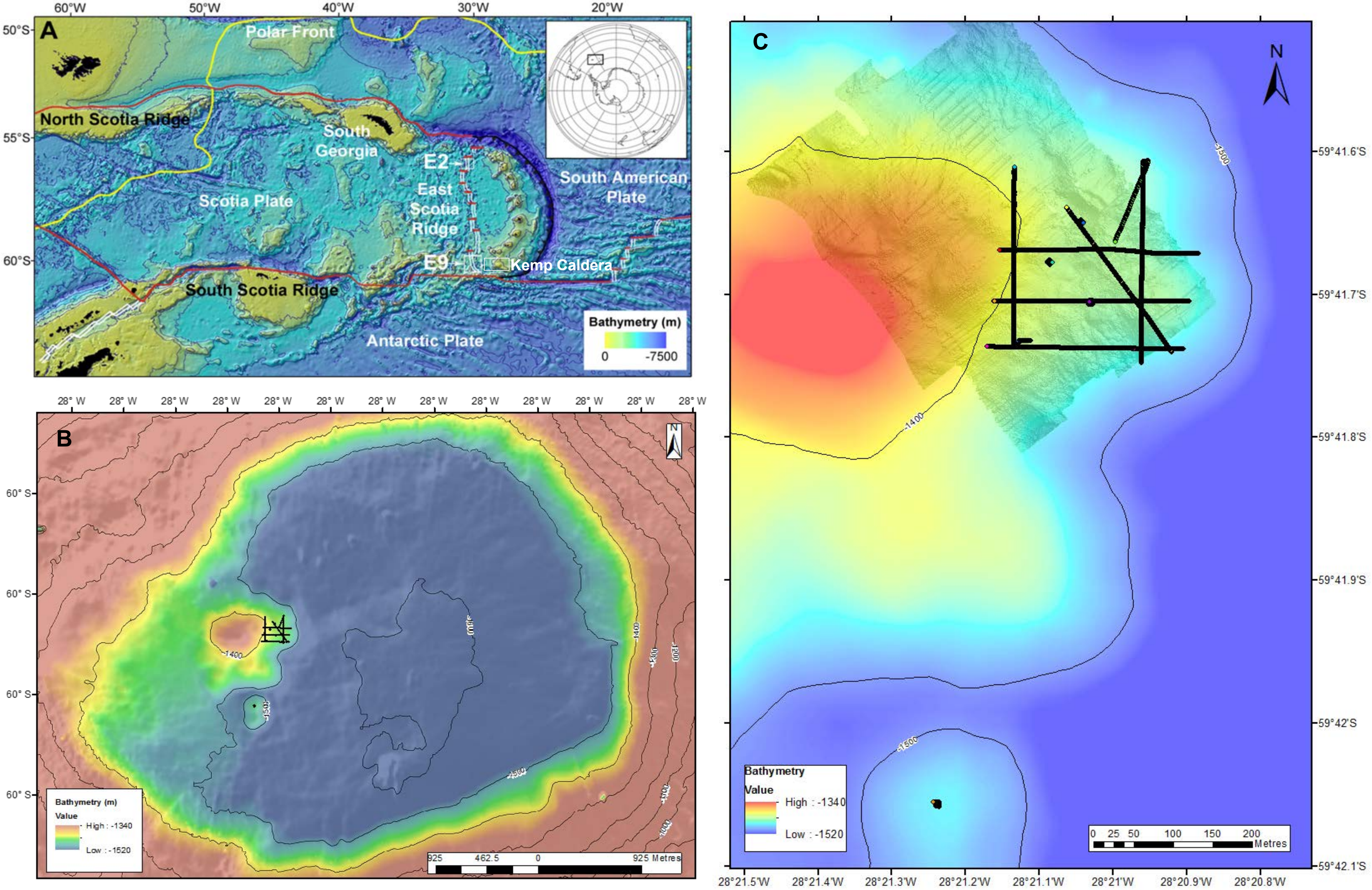


Table 2 – Summary of horizontal mosaic and transect surveys completed during ROV *Isis* Dive 148 of the JC042 research cruise and conditions.
Locations are given in decimal degrees (WGS1984). Depth and temperature data were collated from Dive 148 ROV-mounted CTD records (Cast 25). Transect 1 (T1) was not covered by CTD Cast 25 of Dive 148 and thus depth and temperature data are unavailable for this survey line.

MOSAIC / TRANSECT	START LOCATION (°longitude, °latitude)	END LOCATION (°longitude, °latitude)	MAXIMUM CTD DEPTH (m)	MINIMUM CTD DEPTH (m)	MAXIMUM TEMPERATURE (°C)	MINIMUM TEMPERATURE (°C)
M1	-28.35406, -59.700924	-28.353929, -59.700972	1456.35	1454.63	0.576	0.2627
M2	-28.351419, -59.694653	-28.351373, -59.69463	1428.64	1418.62	0.5144	0.2753
M3	-28.35072, -59.594132	-28.350662, -59.69416	1428.79	1425.61	0.388	0.2667
M4	-28.350542, -59.695087	-28.350462, -59.69507	1426.52	1427.55	0.3748	0.2632
T1	-28.34913, -59.694518	-28.352571, -59.694481	-	-	0.656	0.2674
T2	-28.348273, -59.69508	-28.352688, -59.69508	1445.41	1387.09	0.6091	0.2697
T3	-28.348669, -59.695675	-28.351047, -59.693989	1451.26	1421.27	0.594	0.2668
T4*	-28.349359, -59.695794	-28.349954, -59.694391	1456.04	1419.38	0.8322	0.2699
T5*	-28.351861, -59.695542	-28.352227, -59.693514	1425.58	1389.7	0.4266	0.2685
T6	-28.348411, -59.695637	-28.35285, -59.69561	1459.65	1400.87	0.3598	0.2665

Kemp Caldera (also known as McIntosh Caldera) is located to the west of Kemp seamount, 70 km north of the southern part of the East Scotia subduction zone, in the Atlantic sector of the Southern Ocean (with a maximum depth of 1600 m; Amon *et al.*, 2013; Hawkes *et al.*, submitted; InterRidge, 2013; Leat *et al.*, 2004). It is a protected site due to its known chemosynthetic habitats and potential for diverse benthos (GSGSSI, 2013). The ESR hosts 9 second-order ridge segments, referred to as E1-E9, within which E2 and E9 are most similar to conventional fast spreading mid-ocean ridges and the remaining, middle segments comprise a deep rift valley (German *et al.*, 2000).

Kemp Caldera is a collapse feature, formed in the crater of the volcano beneath as a result of magma removal from deep within the volcano (during a particularly large eruption or intrusion; NOAA, 2013). As a result, the site lies above a magma chamber and can likely be linked to a past pyroclastic eruption (Wright and Gamble, 1999). Kemp Caldera is located to the south of the South Sandwich Island Arc, at a similar distance from the main trench to other islands comprising the volcanic arc (Leat *et al.*, 2004).

With an approximately 7 km diameter, the rim of Kemp Caldera sits around 800 m above the seafloor, containing vent fluid emissions in a bowl-shaped environment (Hawkes *et al.*, submitted). According to Hawkes *et al.* (submitted), the caldera lies beneath a typical winter mixed layer depth, below the depth of an average island arc plume. It hosts sulfur-rich vents, stimulating the development of complex communities of clams, anemones, sponges, and ophiuroids, among other organisms (Rogers *et al.*, 2010). The area explored during RRS *James Cook* research cruise JC42 focused on a small sub-cone (reaching around 250 m above the base of the caldera), hosting diffuse hydrothermal fluids (<40°C; Rogers *et al.*, 2010; Hawkes *et al.*, submitted).

JC042, ROV *Isis* and Navigation: Image Acquisition

ROV 'Isis' was used to conduct systematic videographic surveys of selected areas (representing separate key assemblages) and transect lines at Kemp Caldera vent field, during the RRS *James Cook* cruise 42 (7th January – 24th February 2010; Marsh *et al.*, 2012; 2013). This ROV had a Doppler Velocity Log (DVL), used to enable precise control over vehicle positioning and movement (0.1 m precision in all directions), to ensure videographic survey lines had a minimum overlap of 50% (Marsh *et al.*, 2012). The ultra-short baseline (USBL) navigation system on *Isis* enabled absolute geographical positioning (accuracy: 0.32% of slant range); meanwhile, closed-loop vehicle control was employed using DVLNAV (see Marsh *et al.*, 2013).

Horizontal surveys were conducted using a downward-looking 3-chip charge-coupled device (CCD) video camera (Insite Pacific Atlas), with a laser scale set up by two lasers, mounted 0.1 m apart and parallel to the focal axis of the camera (Marsh *et al.*, 2012). The camera maintained an altitude of around 3 metres above the seabed, using acoustic altimetry (Marsh *et al.*, 2013). The ROV was moved forward and back along transect lines using Doppler-lock navigation to ensure maintenance of heading and distance above the seafloor (Marsh *et al.*, 2013). To ensure complete coverage and enable photomosaicing of still images taken from ROV video footage, *Isis* had to travel along parallel grid lines (set to overlap by 60%), at constant speed (0.01 ms^{-1}) and zoom (Marsh *et al.*, 2013). For information regarding imaging and lighting equipment and the setup of ROV *Isis*, see Marsh *et al.* (2013).

Seabed Mapping & CTD Data Acquisition

CTD temperature data were acquired 2 to 3 metres above the seafloor, using a ROV-mounted system (Idronaut Ocean Seven 320 CTD; Marsh *et al.*, 2012). Swath bathymetry data were acquired by the British Antarctic Survey, using a ROV-mounted SIMRAD SM2000 high-resolution, 200 kHz multibeam echosounder (see Larter *et al.*, 2009 – JCR224 research cruise). Bathymetric data were processed in CARAIBES (IFREMER; Marsh *et al.*, 2013).

Image Processing

Videos were imported into QuickTime Pro (version 7.6.6.) and exported as still images for use in mosaic image construction using Adobe Photoshop CS5 extended (version 12.0664) auto-align, auto-blend and manual transformation tools (Marsh *et al.*, 2012; Appendix B). If distortion had occurred (e.g. due to rough topography in 'M2'), still images were free-transformed to fit to the mosaic (Marsh *et al.*, 2013). Variations in image lighting and clarity were corrected for using automated image adjustment modes in Adobe Photoshop CS5 extended. The resolution of still images (72 x 72 in) was sufficient for identification of small fauna (e.g. 0.385 cm gastropods (Frame 447, M1) in mosaics and 0.721 cm gastropods (Frame 0318; T2) in transects) in most cases. Where fauna were not resolvable in some frames, their cells remained blank in the compiled datasets, so as not to interfere with statistical analyses or averages (thus, zeros represented a lack of observation, not a loss of resolution suitable for enumeration).

Mosaic Creation, ID, and Quantification of Faunal Abundances

A feature-based mosaic creation technique was employed, followed by blending, to render each mosaic quasi-seamless (Marcon *et al.*, 2013b).

Photomosaics constructed from ROV video footage were used to delineate faunal assemblage extents and as a reference when processing frames for quantification of faunal density. Frames were selected for counting by overlaying photomosaic strips onto each mosaic, to ensure that the selected frames covered the entire mosaic, without gaps. Any overlap between strips or individual frames was marked onto each frame before counting, to ensure that fauna were not double-counted. Then, individual frames were analysed, with species abundances counted using the Photoshop 'Count' tool. Areas were calculated using the 0.1 m laser scale, present in each frame, to convert counts per frame section to density per square metre (to ensure data were comparable with reports describing average faunal abundance at other vent sites, given in square metres).

If mosaics had been used directly, rather than raw data from selected frames, abundances would suffer error, as a result of inclusion of artifacts introduced by mosaicing algorithms. Automated mosaic creation software was not employed, as a human eye is required to notice introduction of compound errors, or be aware of any artifacts prior to counting (Singh *et al.*, 1998; Marsh *et al.*, 2013). In addition, one student (the author) completed all enumeration and image analysis tasks, reducing compound errors introduced by incorrect IDs, missing fauna, or other subjectivity issues.

Whilst compound errors are an inherent part of deep-sea image analysis (e.g. examining a 2D representation of a 3D surface), the patterns described in this work are based on large difference or repeated similarity and ecological interpretations are valid (as in Marsh *et al.*, 2013). Nonetheless, as emphasised by Gage and Tyler (1991), it is best to assume that all observations are minima.

Quantification of abundance was carried out at all four mosaic sites, but the resolution of gastropods in some M1 frames was too low to make representative counts. Thus, results from such frames were not included in statistical analyses. Zeros were input for fauna actually absent from frames, whilst frames with non-resolvable, but present, fauna were removed. This was a problem in gastropods of 'M1' because densities became so high, in concordance with bacterial mat cover, that it was impossible to confidently distinguish gastropods from each other and from mat beneath (Appendix B); here, a minimum abundance was included in the dataset, set at the highest count made in 'M1'.

Informal categories like 'anemones' and 'sponges' have been used in some analyses, as many of the species are new and in the process of being formally described. Most fauna could be named to genus level, using images alone. Live clams were identified by their siphons, extending up from soft sediment; dead clams were visible as shells on the surface (as identified in Olu *et al.*, 1996). Nonetheless, there may be species-dependent error in these assumptions, given that *Calyptogena magnifica* are found on bare basalt and can survive in rubble during their early life stages and *Calyptogena solidissima* bury around half to two-thirds of their shells in soft sediment (Desbruyères *et al.*, 2006).

ArcGIS, Digitisation and Surfer Contouring

CTD temperature data were interpolated and contoured in both ArcGIS (ESRI, CA; for transects) and Surfer 8.0 (Golden Software Inc., Colorado; for mosaics) to enable comparison between faunal distributions and temperature gradients. Using Surfer 8.0 (Golden Software Inc., Colorado), temperature data were gridded and interpolated using kriging, to specify a spherical variogram model (Appendix B – Table B1).

As all images were extracted from video footage, they had an associated timestamp, which could be matched to co-ordinates recorded by ROV *Isis* during each dive. In matching the centre point of each frame (used to compose a mosaic) to a time, temperature data could then be compared directly with contour plots, once geo-referenced to a UTM coordinate system in ArcMap (WGS 1984 UTM Zone 26 S; as per Podowski *et al.*, 2009). Temperature contour plots do not match those of species density exactly, due to the offset introduced by the positioning of the CTD at the side of *Isis*, compared with the cameras, located at the front (see Marsh *et al.*, 2013).

As per Marsh *et al.* (2012), whilst formal descriptions are awaited to confirm species identities, the dominant taxa presented in this project are distinguishable using image analysis.

Transect Data

As transects were too long to be mosaiced using non-automated techniques, a different method was employed for analysis of larger-scale zonation patterns across the Kemp Caldera vent field. Instead, videos and stills were analysed repeatedly to note changes to the visibly dominant fauna and match these to dive times. In doing this, it was possible to create a presence/absence dataset for cluster analyses, in addition to assemblage maps. Assemblage types were defined for transects using image stills, according to dominant visible fauna (as per Marsh *et al.*, 2012). 10 faunal assemblages and 6 substrata or chimney features formed the categories presented across all transects. In matching video time codes to ROV recorded times and co-ordinates, assemblages and 'dead zones' could be mapped using ArcGIS (ESRI, CA). This enabled interpretation of a zonation pattern for the Kemp Caldera study site. Following this, slope analysis was conducted using Spatial and Focal Analyst ArcMap 10.1 (ESRI, CA) tools, to identify any relationships between faunal assemblage and slope or rugosity (standard deviation of slope, used to determine topographic roughness).

Statistical Analyses

As data did not follow a normal distribution, non-parametric, Spearman's Rank correlation tests were deemed appropriate and run using SPSS Statistics (v.20, IBM Corp., 2011).

PRIMER-E (v.6, Clarke and Gorley, 2006) was used to generate a similarity matrix for mosaic abundance data and, separately, presence/absence data from E2, E9, Kemp Caldera whale fall and Kemp Caldera transects (using species lists from Rogers *et al.* (2012), Marsh *et al.* (2012) and Amon *et al.* (2013) alongside a Kemp Caldera dataset generated following transect image analysis). No transformation was applied, as the data were in the form of presence/absence. 18 fauna were included in the matrix and mobile fauna were excluded to ensure fairness despite differences in sampling effort (ROV dive time). Using these matrices, cluster analyses (group average clustering) were performed to generate dendrograms (representing Sorensen's Index similarity between sites), which were evaluated in terms of coherence using a SIMPROF test. For mosaic data, PRIMER-E (v.6, Clarke and Gorley, 2006) was also used to perform cluster analysis, following the aforementioned procedure but with a log(x+1) data transformation applied, to remove the impact of dominant fauna on output. Bray-Curtis similarity was represented by the output, as the input was in the form of abundances. MDS ordination plots were also created in PRIMER-E (v.6, Clarke and Gorley, 2006; 25 restarts), with mosaic environmental data used to create 'bubble plots' for the investigation of potential environmental influences on inter-mosaic similarity.

Table 3

PHYLUM	CLASS	ORDER	FAMILY	GENUS	SPECIES / DESCRIPTION	MOSAIC / NO. OF OBS.	MEAN ABUNDANCE (per m² ± STD. DEV.)	■ / ●
PORIFERA	indet.	indet.	indet.	indet.	2 spp. (?) or morphotypes	M1 / 119 M2 / 77 M3 / 64 M4 / 74	3.017 (±5.339) 10.479 (±16.630) 17.453 (±20.303) 0 (±0)	■
	Hexactinellida	Amphidiscosida	Hyalonematidae	*Hyalonema* (?)				■
					indet.			
FORAMINIFERA	Xenophyophorea	indet.	indet.	indet.	2 spp. (?) – 1 sp. counted	M1 / 119 M2 / 79 M3 / 67 M4 / 74	0 (±0) 0.611 (±5.433) 0 (±0) 65.919 (±58.874)	■
CNIDARIA	Anthozoa	Actinaria	indet.	indet.	> 2 spp. or morphotypes	M1 / 119 M2 / 79 M3 / 67 M4 / 74	0.008 (±0.092) 6.932 (±4.897) 0 (±0) 0.387 (±1.296)	■
		Ceriantharia	indet.	indet.				■
		Octocorallia	indet.	indet.	One observation			■
			Umbellulidae	*Umbellula*	One observation			■
		Pennatulacea	Kophobelemnidae (?)	*Kophobelemnon* (?)	One observation			■
					One observation			
NEMERTEA	indet.	indet.	indet.	indet.	One observation	M1 / 119 M2 / 79 M3 / 67 M4 / 74	0 (±0) 0 (±0) 0.018 (±0.144) 0 (±0)	■

Table 3

ANNELIDA	Polychaeta	Sabellida	Siboglinidae	indet.	1 sp.	M1 / 116	14.353 (±19.847)	●
						M2 / 76	0.545 (±2.771)	
						M3 / 67	9.613 (±16.010)	
						M4 / 74	0.020 (±0.175)	
MOLLUSCA	Cephalopoda	Oegopsida	Neoteuthidae	*Alluroteuthis*	*antarcticus*	M1 / 119	0 (±0)	■
			Onychoteuthid (?)	indet.	1 sp.	M2 / 79	0.125 (±1.111)	■
			Brachioteuthidae	*Slosarczykovia*	*circumantarctica*	M3 / 67	0.017 (±0.141)	■
						M4 / 74	0 (±0)	
	Bivalvia	Veneroida	Vesicomyidae	indet.	1 sp. (?)	Live:	Live:	●
						M1 / 119	0 (±0)	
						M2 / 79	0 (±0)	
						M3 / 67	0 (±0)	
						M4 / 74	6.989 (±12.411)	
						Dead:	Dead:	
						M1 / 119	0 (±0)	
						M2 / 79	0.390 (±1.489)	
						M3 / 67	0.225 (±1.022)	
						M4 / 74	20.303 (±23.405)	
	Gastropoda		Lepetodrillidae	*Lepetodrilus*	1 sp.	M1/ 113	101.744 (±123.157)	●
						M2 / 0	-	
						M3 / 67	0 (±0)	
						M4 / 61	1.018 (±5.549)	
			Pyropeltidae	*Pyropelta*	1 sp.	M1 / 119	7489.434 (±5370.976)	●
						M2 / 79	1221.774 (±861.015)	
						M3 / 67	0 (±0)	
						M4 / 62	5.879 (±18.494)	

Table 3

CHELICERATA	Pycnogonida	Pantopoda	Ammotheidae	*Sericosura*	3 spp. (?)	M1 / 114 M2 / 79 M3 / 67 M4 / 74	62.265 (±86.314) 4.592 (±7.067) 0.439 (±1.344) 1.200 (±3.292)	■
			Colossendeidae	*Colossendeis*	1 sp. (1 observation)			■
ARTHROPODA	Maxillopoda	Scalpelliformes	Eolepadidae	*Vulcanolepas*	*sp.* as per Rogers *et al.* (2012)	M1 / 119 M2 / 78 M3 / 67 M4 / 74	0.101 (±0.602) 1.525 (±3.455) 0.016 (±0.134) 0 (±0)	●
	Malacostraca	Decapoda	Nematocarcinidae	*Nematocarcinus*	*lanceopes*	Live: M1 / 119 M2 / 79 M3 / 67 M4 / 74 Dead: M1 / 119 M2 / 79 M3 / 67 M4 / 74	Live: 0 (±0) 0 (±0) 0.018 (±0.145) 0 (±0) Dead: 0 (±0) 0.290 (±2.072) 0.015 (±0.121) 0 (±0)	■
			Hippolytidae	*Lebbeus*	*antarcticus*	Live: M1 / 119 M2 / 79 M3 / 67 M4 / 74 Dead: M1 / 119 M2 / 79 M3 / 67 M4 / 74	Live: 0.050 (±0.255) 0.086 (±0.448) 0 (±0) 0 (±0) Dead: 0.008 (±0.092) 0.236 (±0.950) 1.615 (±3.147) 0 (±0)	■
		Euphausiacea	Euphausiidae	*Euphausia*	*superba* (?)			■
		Mysida	indet.		indet.			■

Table 3

ECHINODERMATA	Asteroidea	Forcipulatida	Stichasteridae	indet.	1 sp.			■
	Ophiuroidea	Ophiurida	Ophiacenthidae	*Ophiolimna*	*antarctica*			■
	Echinoidea	Camarodonta	Echinidae	*Sterechinus*	1 sp., pink			■
	Holothuroidea	Aspidochirotida	Holothuriidae	*Holothuria* (*Psolus*)	1 sp., with ‘feathering’	M1 / 119	0.152 (±1.662)	■
		indet.	indet.	indet.	1 sp. (?)	M2 / 79	0 (±0)	■
						M3 / 67	0 (±0)	
						M4 / 74	0 (±0)	
CHORDATA	Actinopterygii	Gadiformes	Macrouridae	indet.	1 sp.	M1 / 119	0.048 (±0.520)	■
		Aulopiformes	Paralepididae	*Notolepis*	*annulata* (?)	M2 / 79	0.037 (±0.329)	■
						M3 / 67	0.078 (±0.492)	
						M4 / 74	0 (±0)	

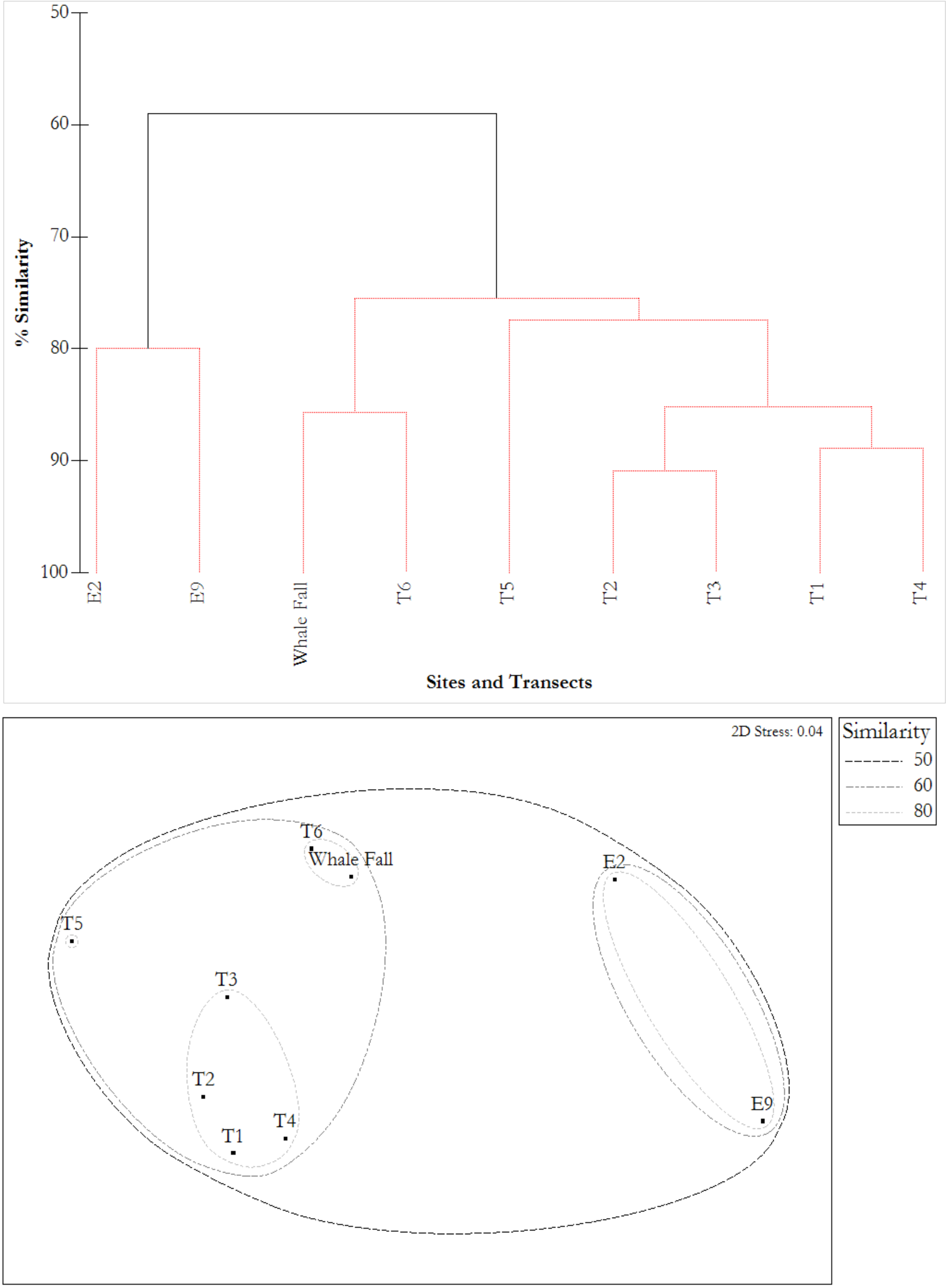


Figure 2 – Multivariate analyses of species presence/absence at the E2, E9 and Kemp Caldera vent fields, based on records from this project (see Table 3) and those of Amon *et al.* (2013 – whale fall site), Rogers *et al.* (2012 – E2 & E9) and Marsh *et al.* (E9).

(A) Dendrogram of hierarchical agglomerative clustering of Sorensen's similarity of presence/absence data using group-average linkage.

(B) Ordination following non-metric multidimensional scaling (MDS) of Sorensen's similarity values (ordination stress: 0.04). Dashed lines encompassing sites represent clusters formed on increasing Sorensen's similarity values (e.g. all sites share at least 50% Sorensen's similarity).

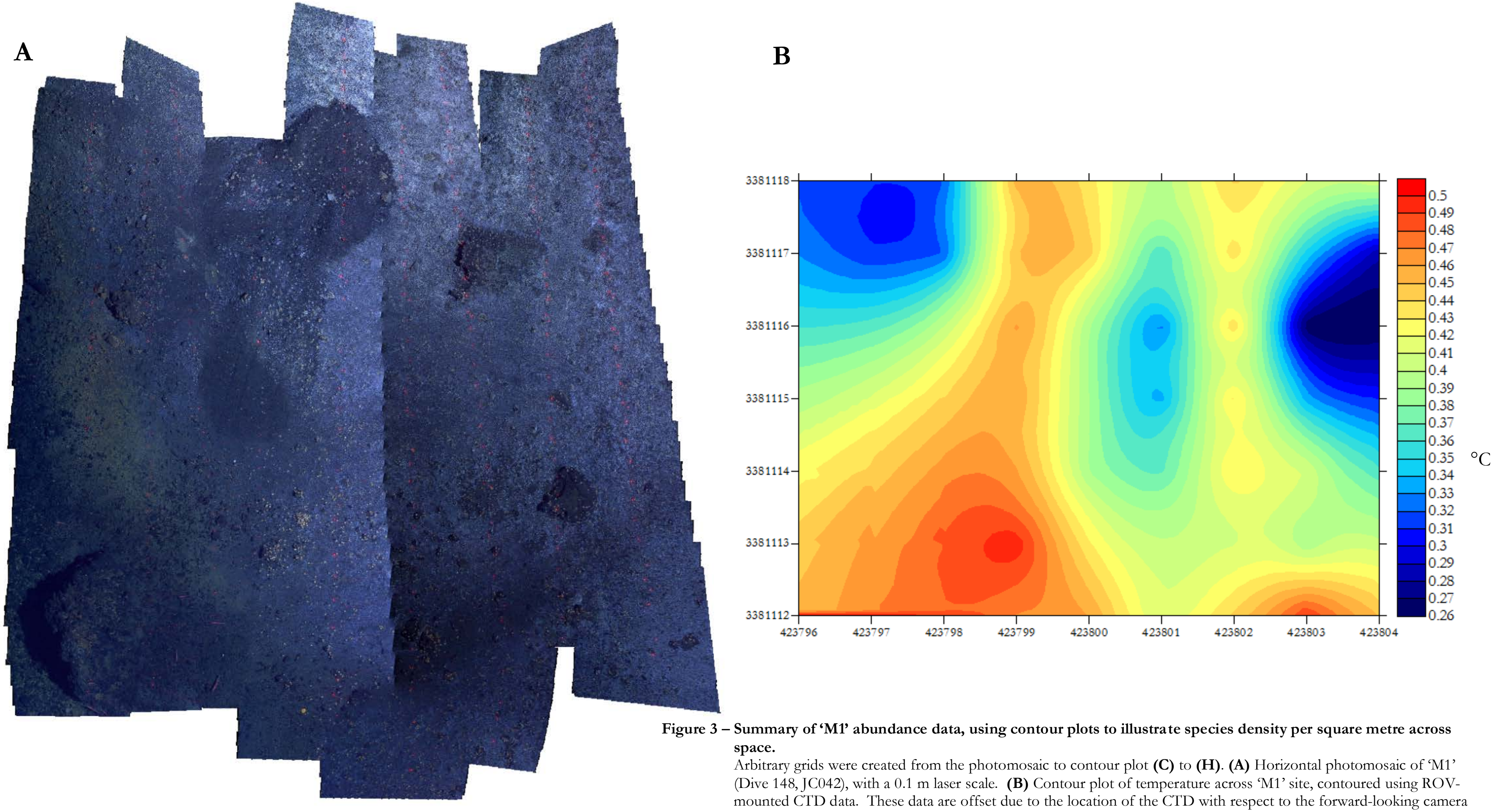


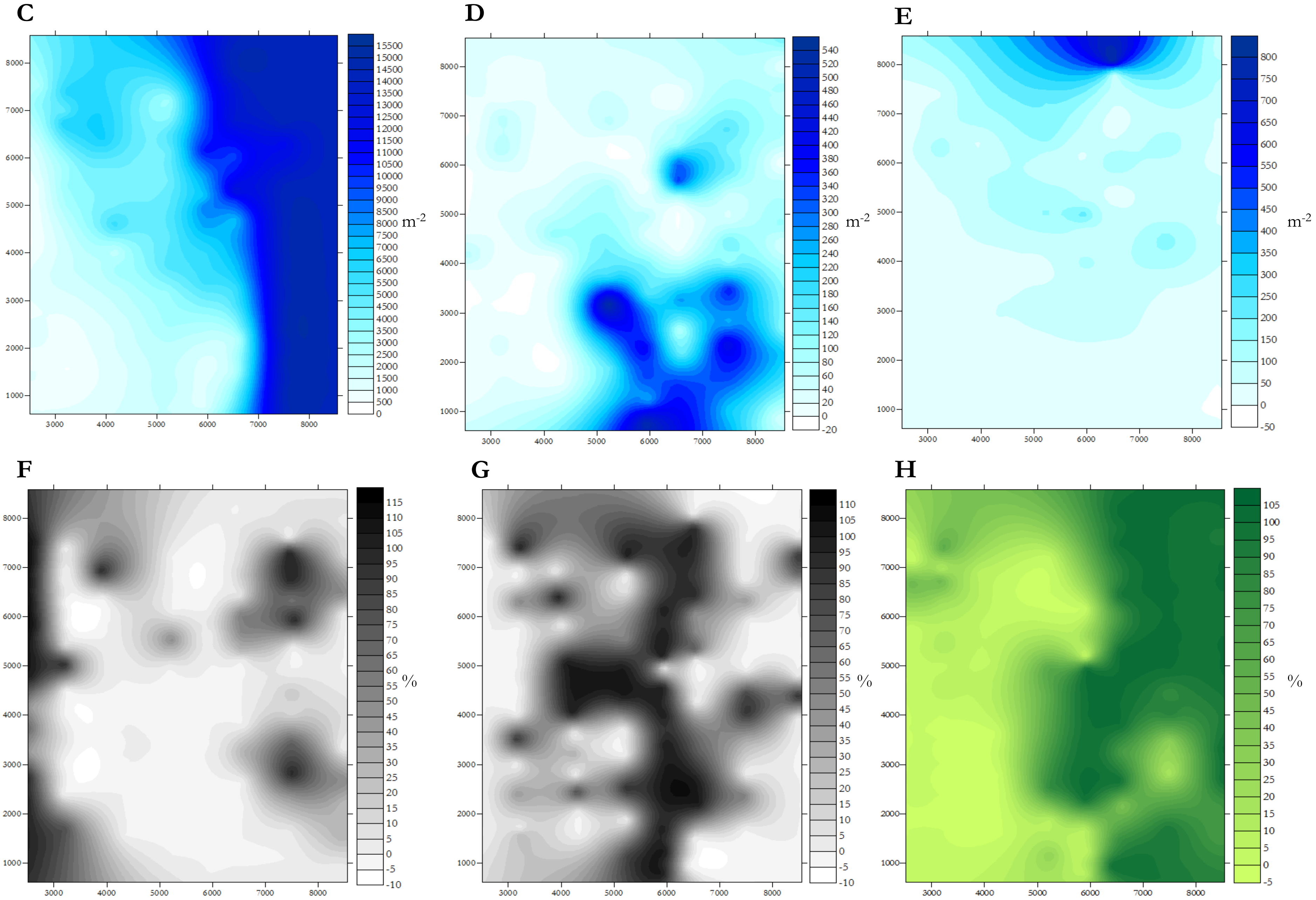
Figure 3 – Summary of 'M1' abundance data, using contour plots to illustrate species density per square metre across space.

Arbitrary grids were created from the photomosaic to contour plot **(C)** to **(H)**. **(A)** Horizontal photomosaic of 'M1' (Dive 148, JC042), with a 0.1 m laser scale. **(B)** Contour plot of temperature across 'M1' site, contoured using ROV-mounted CTD data. These data are offset due to the location of the CTD with respect to the forward-looking camera and are presented in UTM co-ordinates (UTM 26°S). Thus, they do not directly compare with mosaic and density contour orientations. Images could not be co-registered with ROV movement to map onto a shared UTM grid.

(C) to **(E)** are contour plots of density per square metre of the following fauna: **(C)** - *Pyropelta* sp.; **(D)** - *Lepetodrilus* sp.; **(E)** - *Sericosura* spp..

(F) and **(G)** are contour plots illustrating percentage space covered by hard and soft substrata, respectively.

(H) Contour plot of the percentage cover of microbial mat.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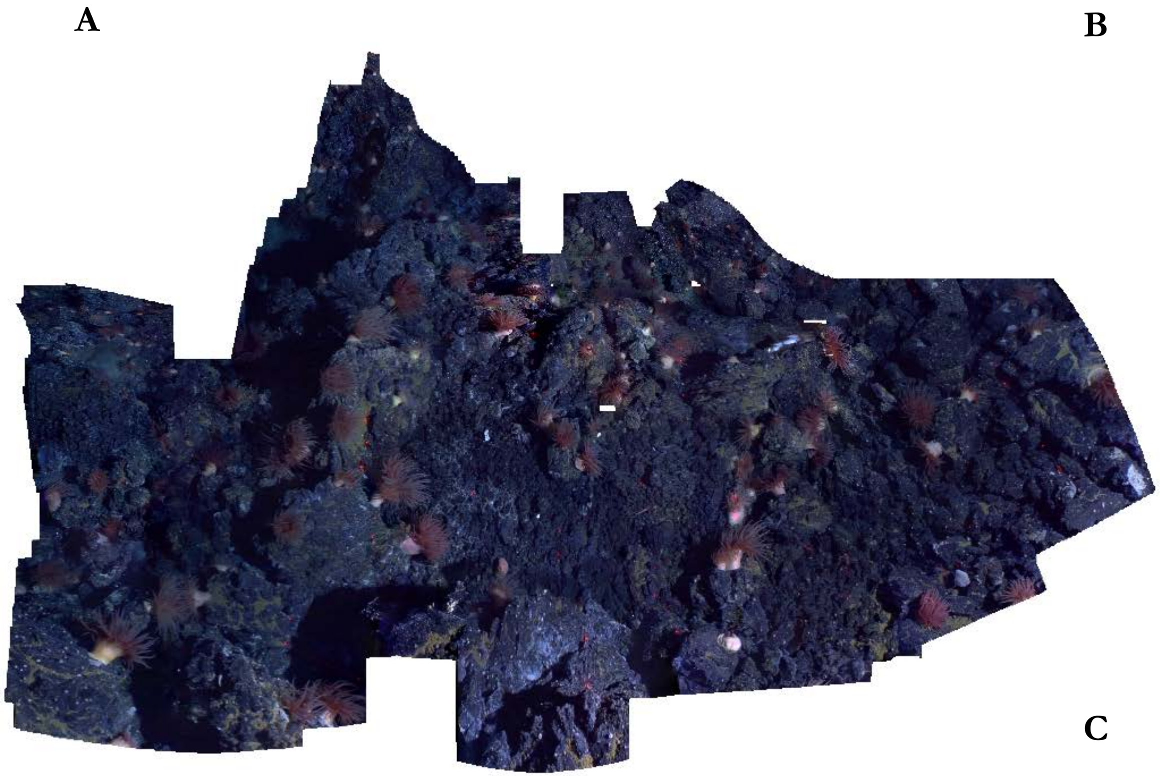


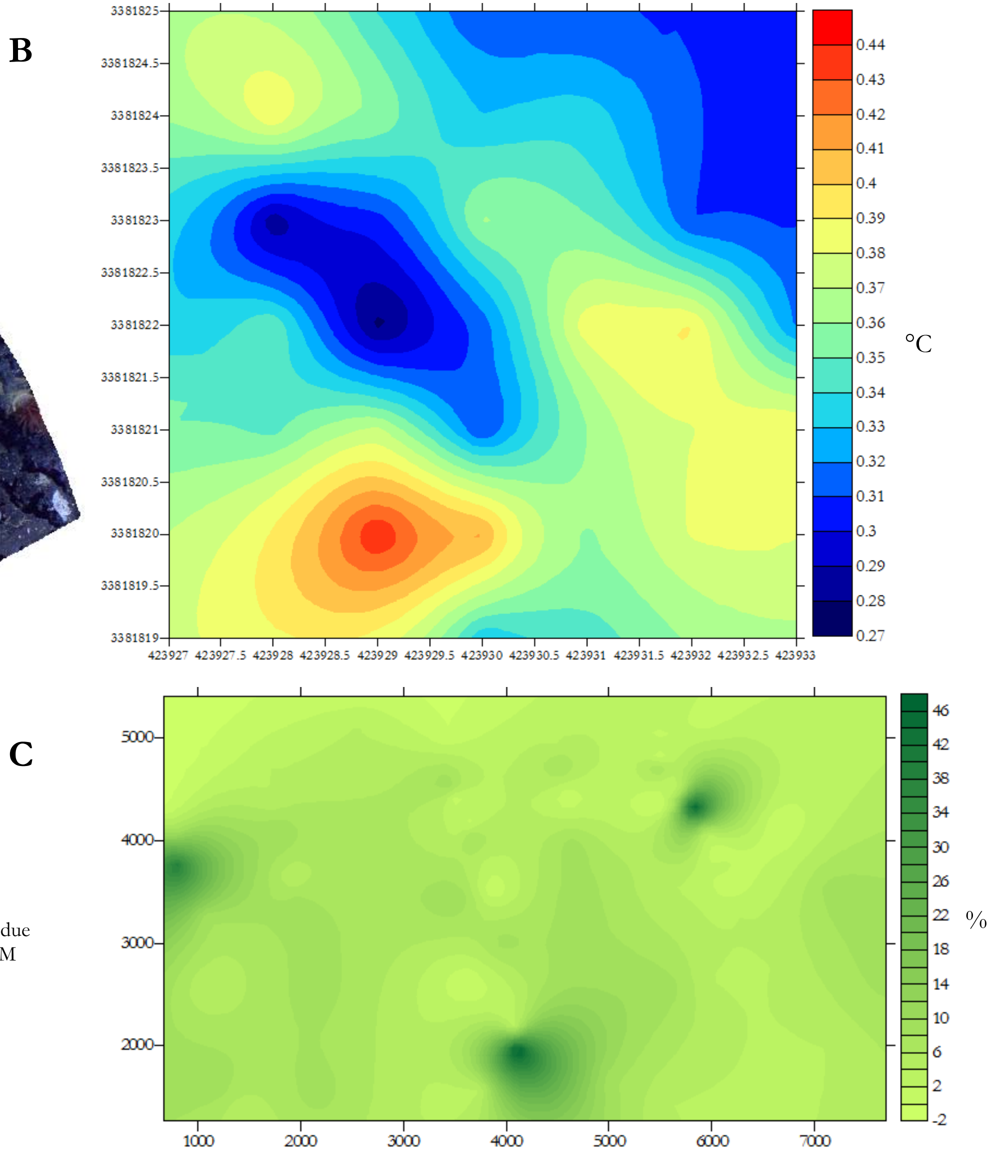


Figure 4 – Summary of 'M2' abundance data, using contour plots to illustrate species density per square metre across space.

Arbitrary grids were created from the photomosaic to contour plot **(A)** to **(F)** and **(H)**.

(A) Horizontal photomosaic of 'M2' (Dive 148, JC042), with a 0.1 m laser scale.

(B) Contour plot of temperature across 'M2' site, contoured using ROV-mounted CTD data. These data are offset due to the location of the CTD with respect to the forward-looking camera and are presented in UTM co-ordinates (UTM 26°S). Thus, they do not directly compare with mosaic and density contour orientations. Images could not be co-registered with ROV movement to map onto a shared UTM grid.

(C) Contour plot of the percentage cover of microbial mat across 'M2'.

(D) Contour plot of anemone density across 'M2'.

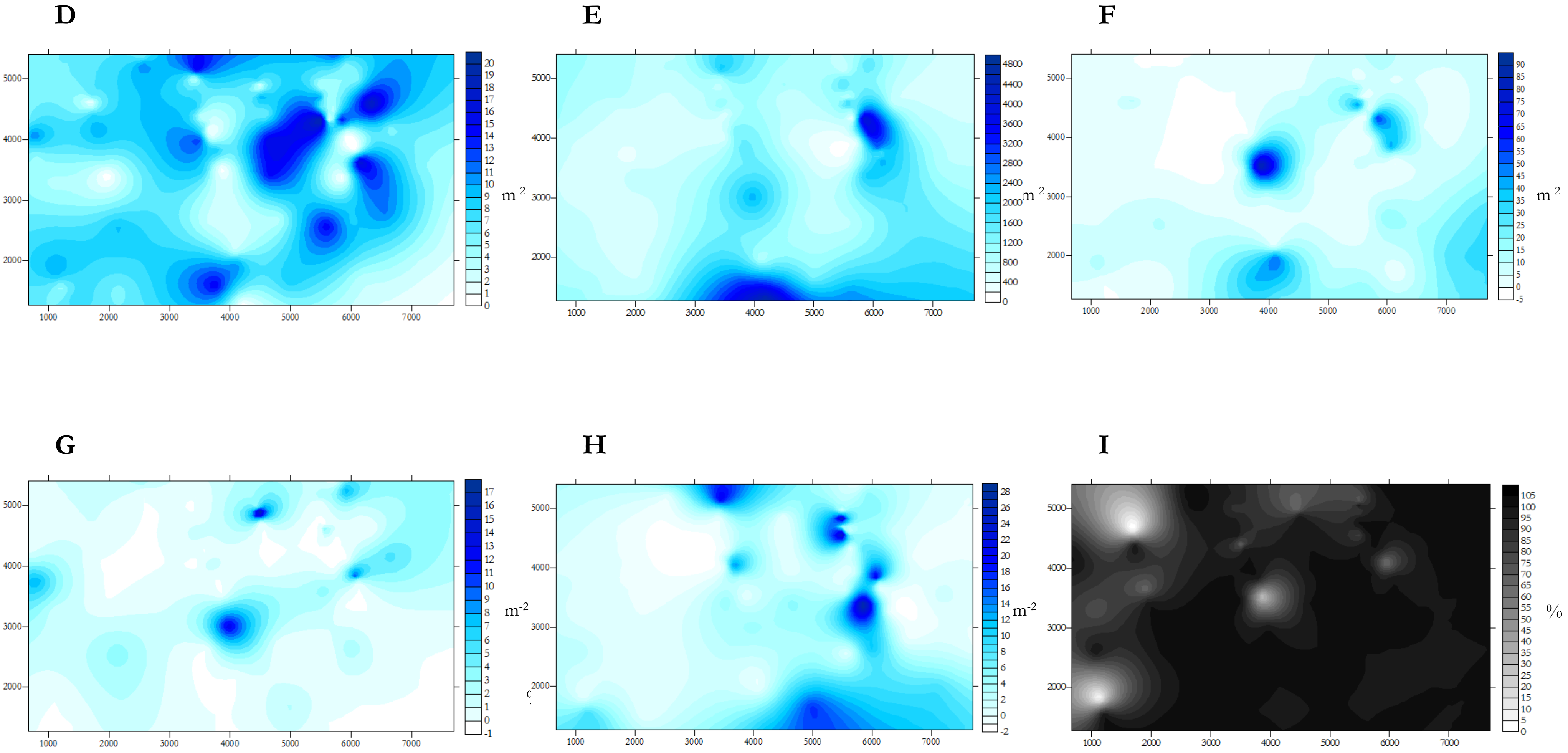
(E) Contour plot of *Pyropelta* sp. density at 'M2'.

(F) Contour plot of sponge density across 'M2'.

(G) Contour plot of stalked barnacle density across 'M2'.

(H) Contour plot of *Sericosura* spp. density across 'M2'.

(I) Contour plot representing proportional hard substratum cover (%).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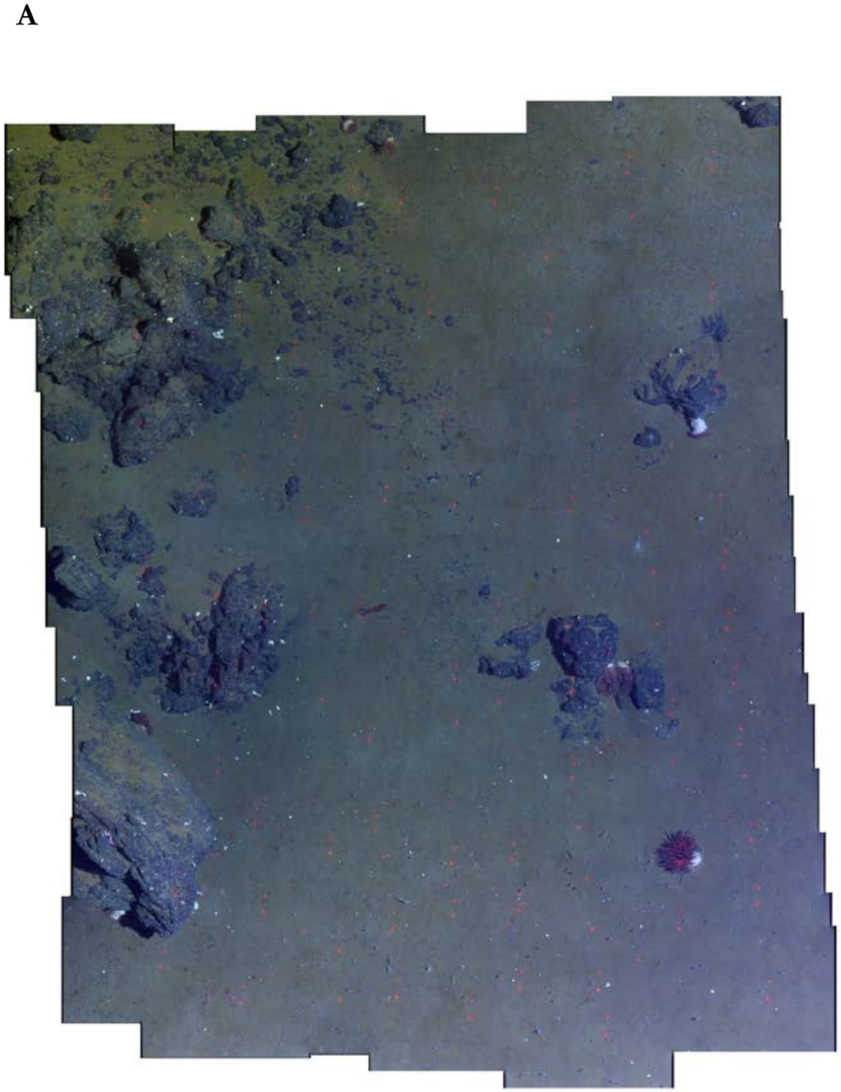


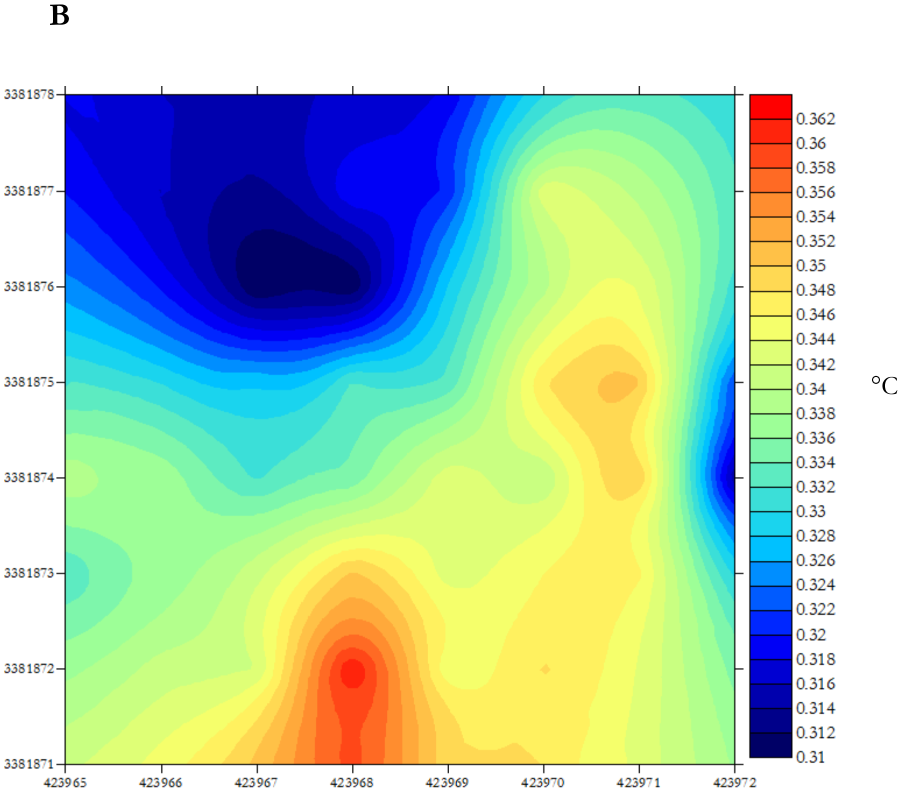
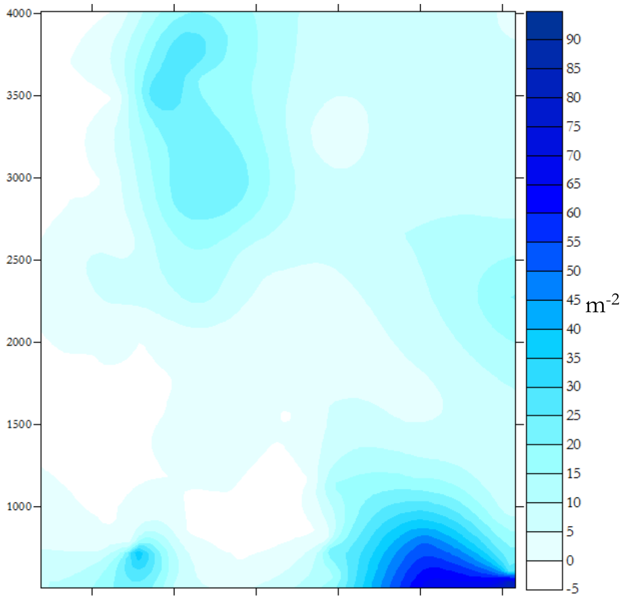


Figure 5 – Summary of 'M3' abundance data, using contour plots to illustrate species density per square metre across space. Arbitrary grids were created from the photomosaic to contour plot **(A)** to **(C)** and **(E)** and **(F)**.
(A) Horizontal photomosaic of 'M3' (Dive 148, JC042), with a 0.1 m laser scale. This photomosaic was generated by Leigh Marsh.
(B) Contour plot of temperature across 'M3' site, contoured using ROV-mounted CTD data. These data are offset due to the location of the CTD with respect to the forward-looking camera and are presented in UTM co-ordinates (UTM 26°S). Thus, they do not directly compare with mosaic and density contour orientations. Images could not be co-registered with ROV movement to map onto a shared UTM grid.
(C) Contour plot of siboglinid tubeworm density at 'M3'.
(D) Contour plot of *Sericosura* spp. density across 'M3'.
(E) Contour plot of sponge density across 'M3'.
(F) Contour plot of percentage bacterial mat coverage at 'M3'.
(G) Contour plot of percentage hard substratum cover at 'M3'.

C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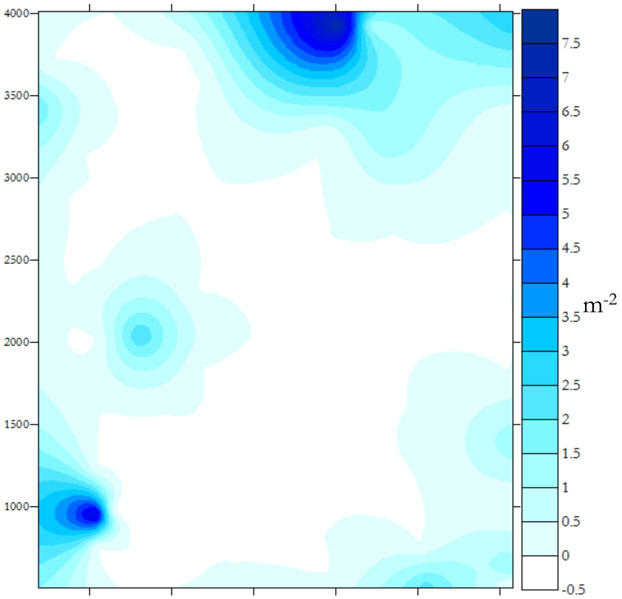
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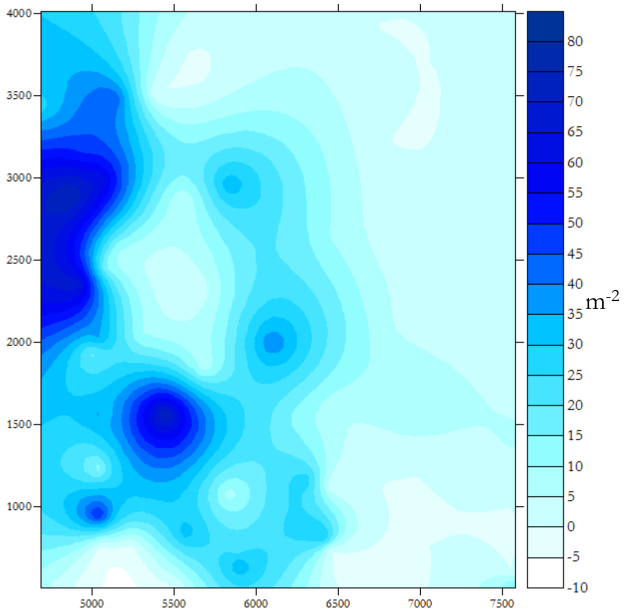
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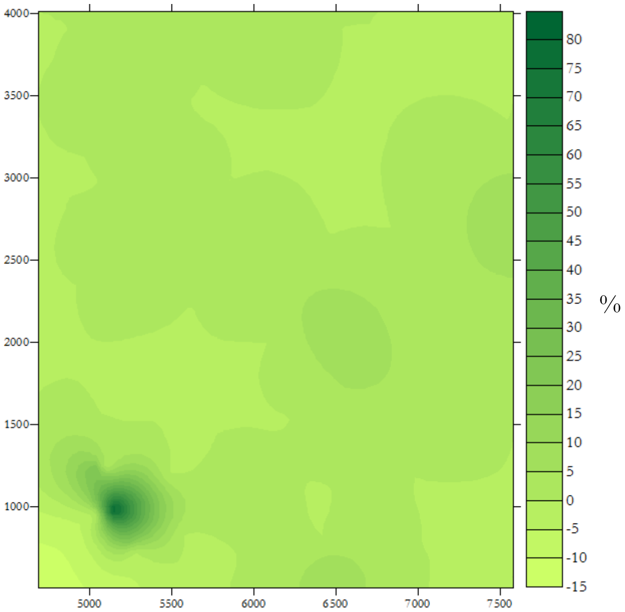
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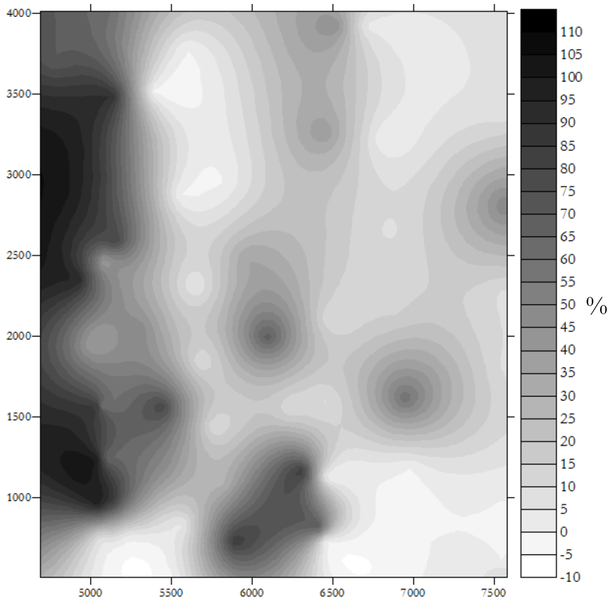
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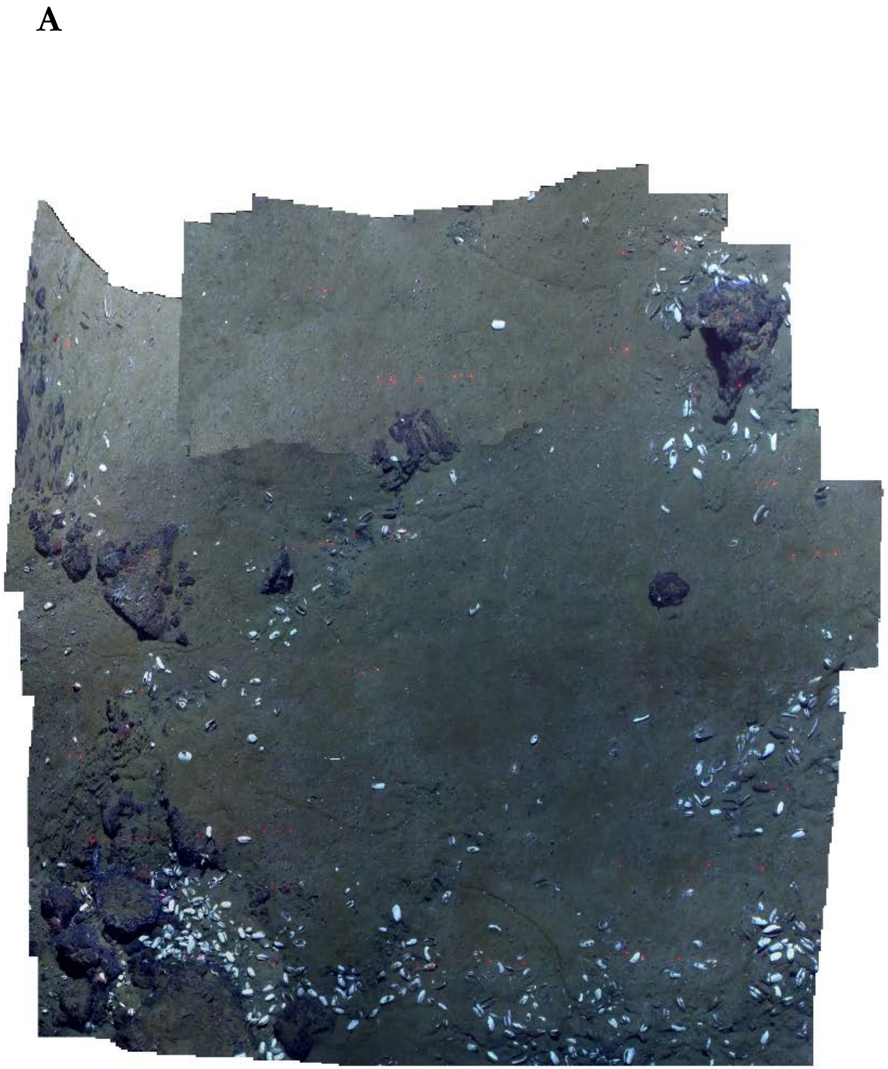


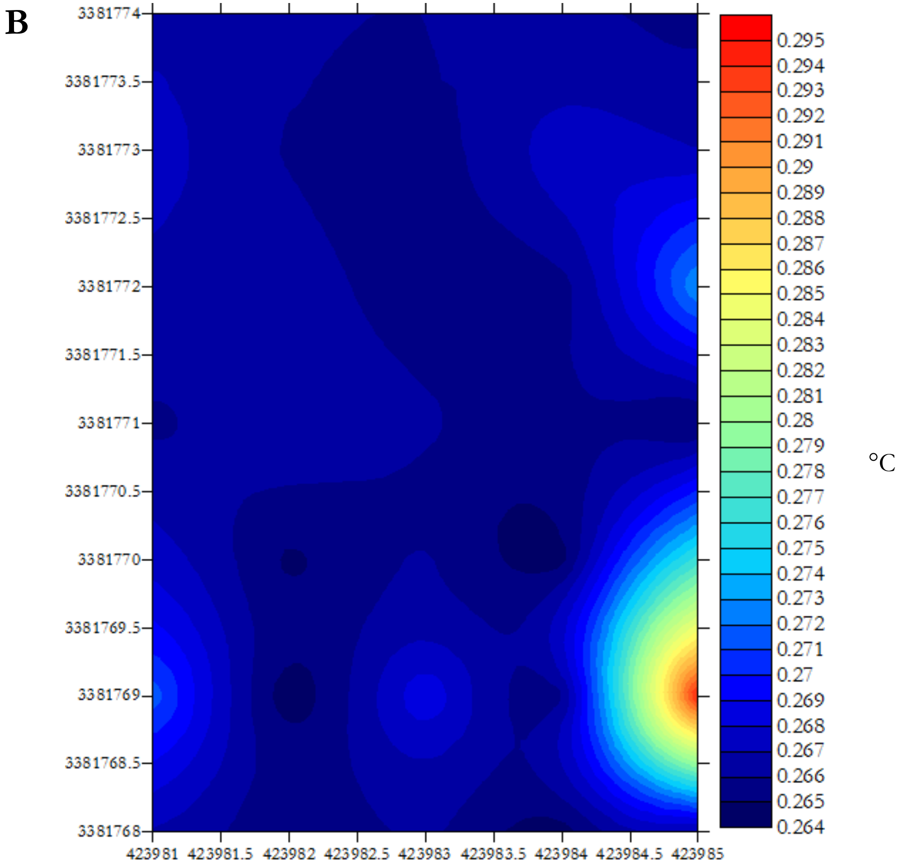


Figure 6 – Summary of 'M4' abundance data, using contour plots to illustrate species density per square metre across space.

Arbitrary grids were created from the photomosaic to contour plot **(B)** to **(E)**, **(G)** to **(H)** and **(I)** to **(K)**.

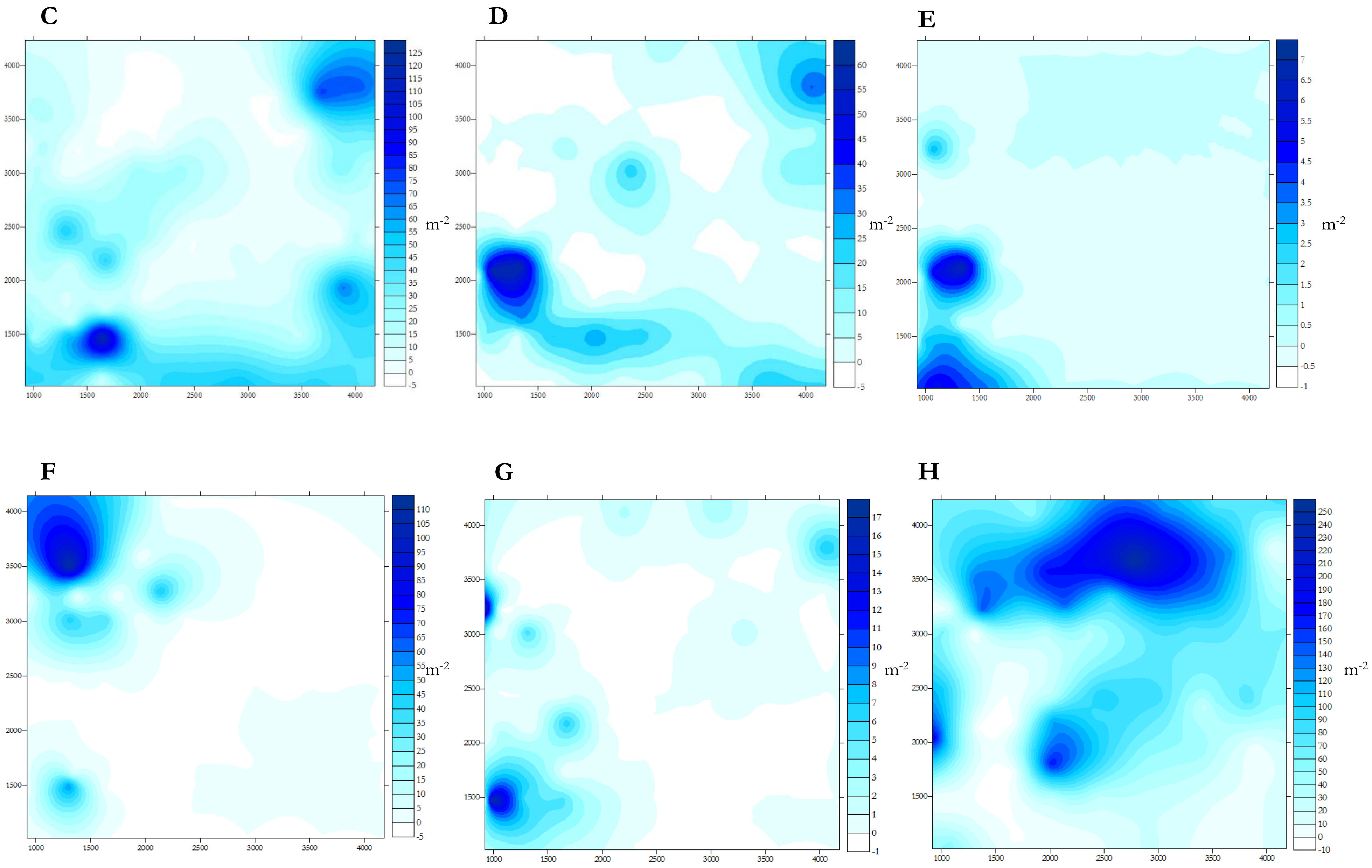
(A) Horizontal photomosaic of 'M4' (Dive 148, JC042), with a 0.1 m laser scale.

(B) Contour plot of temperature across 'M4' site, contoured using ROV-mounted CTD data. These data are offset due to the location of the CTD with respect to the forward-looking camera and are presented in UTM co-ordinates (UTM 26°S). Thus, they do not directly compare with mosaic and density contour orientations. Images could not be co-registered with ROV movement to map onto a shared UTM grid.

(C) to **(I)** are contour plots of density per square metre of the following fauna at 'M4': **(C)** – Dead clams; **(D)** – Live clams; **(E)** - Anemones; **(F)** - *Pyropelta* sp.; **(G)** - *Sericosura* spp.; **(H)** – Xenophyophores; **(I)** – *Lepetodrilus* sp.

(J) Contour plot of percentage cover of bacterial mat.

(K) Contour plot of percentage hard substratum cover.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1
0.5
-0.5
-1
17
16
15
14
13
12
11
9
8
7
6
4
3
2
250
240
230
220
210
200
190
180
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160
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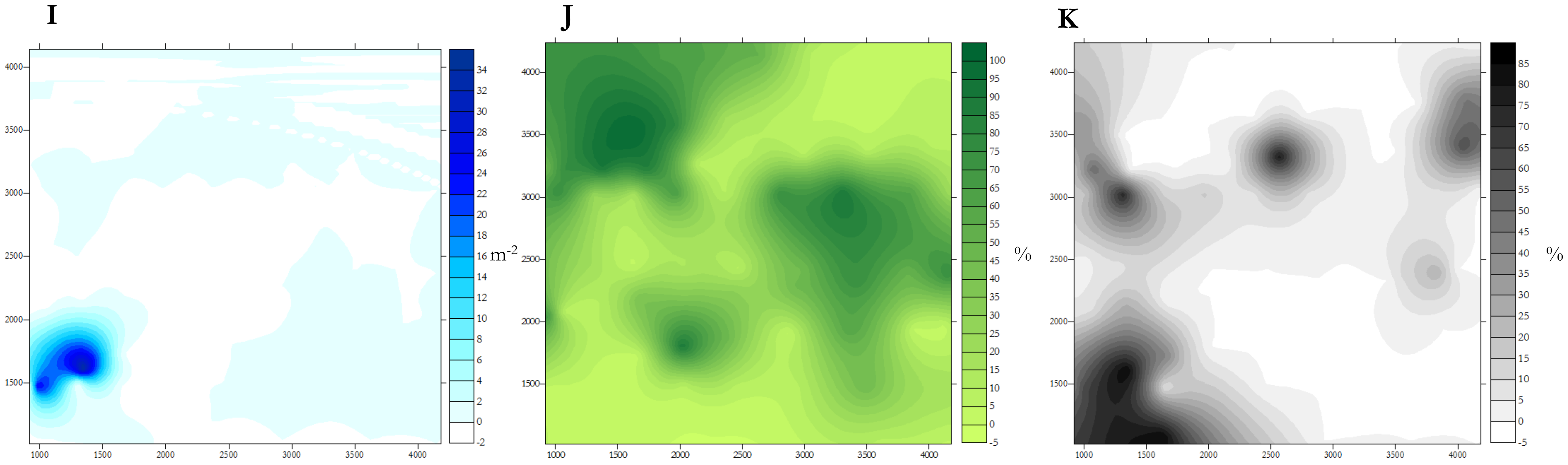
130
120
110
90
80
70
60
50
40
30
20
10
-10


I
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K
4000
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26
24
22
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18
16
14
12
10
8
6
4
2
0
-2
m-2
100
95
90
85
80
75
70
65
60
55
50
45
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30
25
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15
10
5
0
-5
%
85
80
75
70
65
60
55
50
45
40
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30
25
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15
10
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0
-5
%

Figure 7

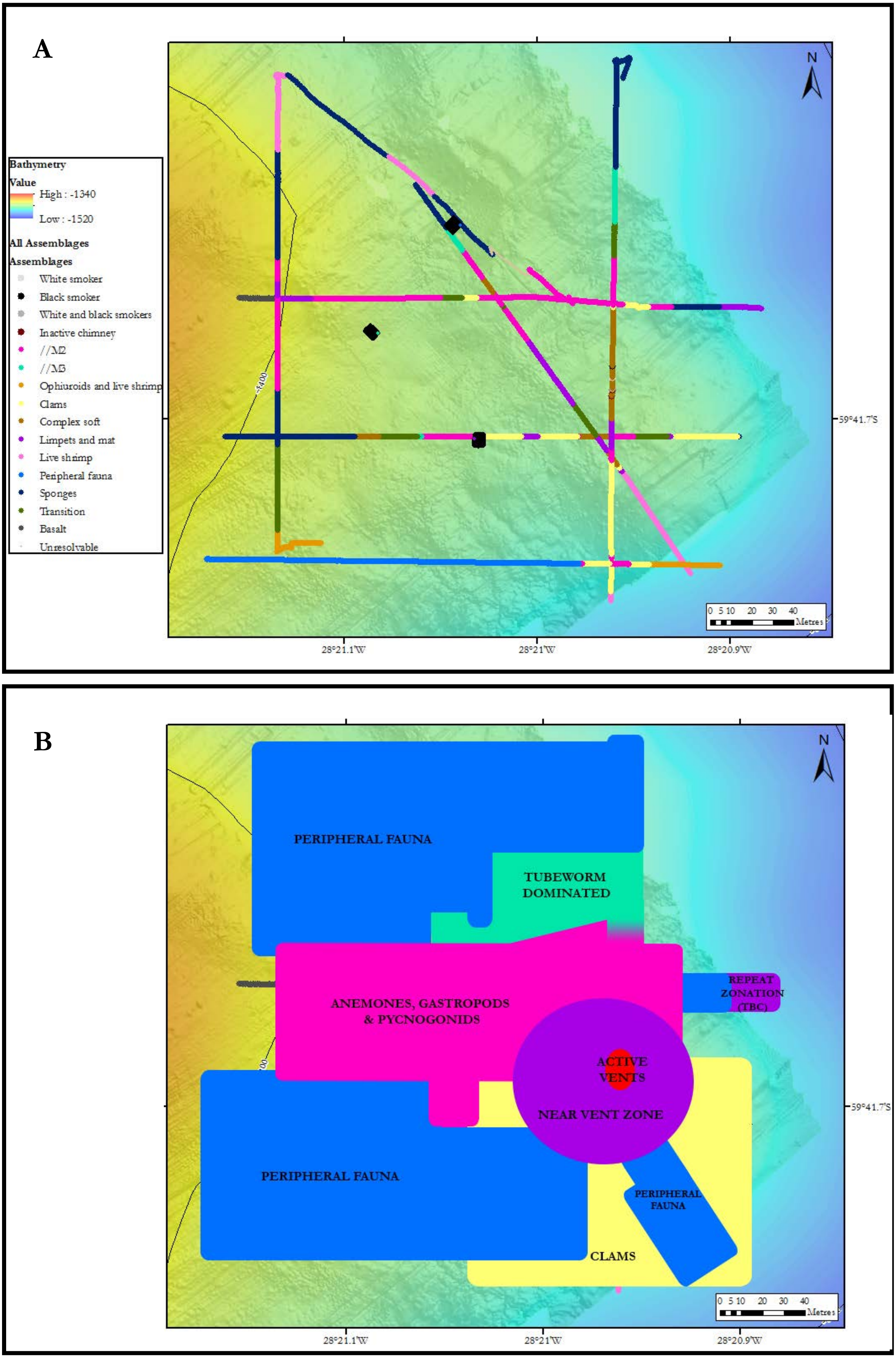
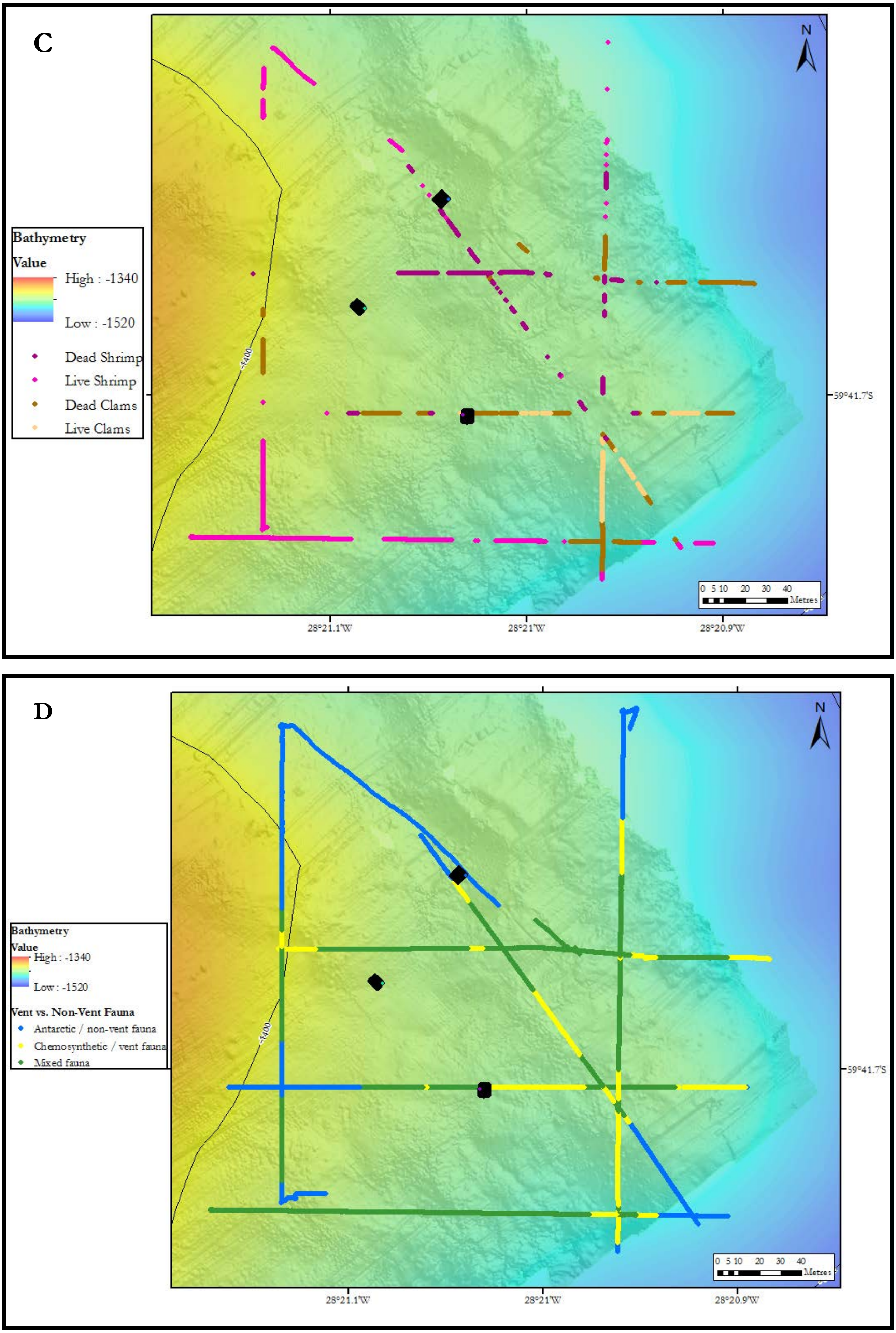

A
Bathymetry
Value
High : -1340
Low : -1520
All Assemblages
Assemblages
White smoker
Black smoker
White and black smokers
Inactive chimney
//M2
//M3
Ophiuroids and live shrimp
Clams
Complex soft
Limpets and mat
Live shrimp
Peripheral fauna
Sponges
Transition
Basalt
Unresolvable
-1400
N
0 5 10 20 30 40
Metres
59°41.7'S
28°21.1'W
28°21'W
28°20.9'W
B
PERIPHERAL FAUNA
TUBEWORM DOMINATED
ANEMONES, GASTROPODS & PYCNOGONIDS
REPEAT ZONATION (TBC)
ACTIVE VENTS
NEAR VENT ZONE
PERIPHERAL FAUNA
PERIPHERAL FAUNA
CLAMS
N
0 5 10 20 30 40
Metres
59°41.7'S
28°21.1'W
28°21'W
28°20.9'W

Figure 7 (cont.)



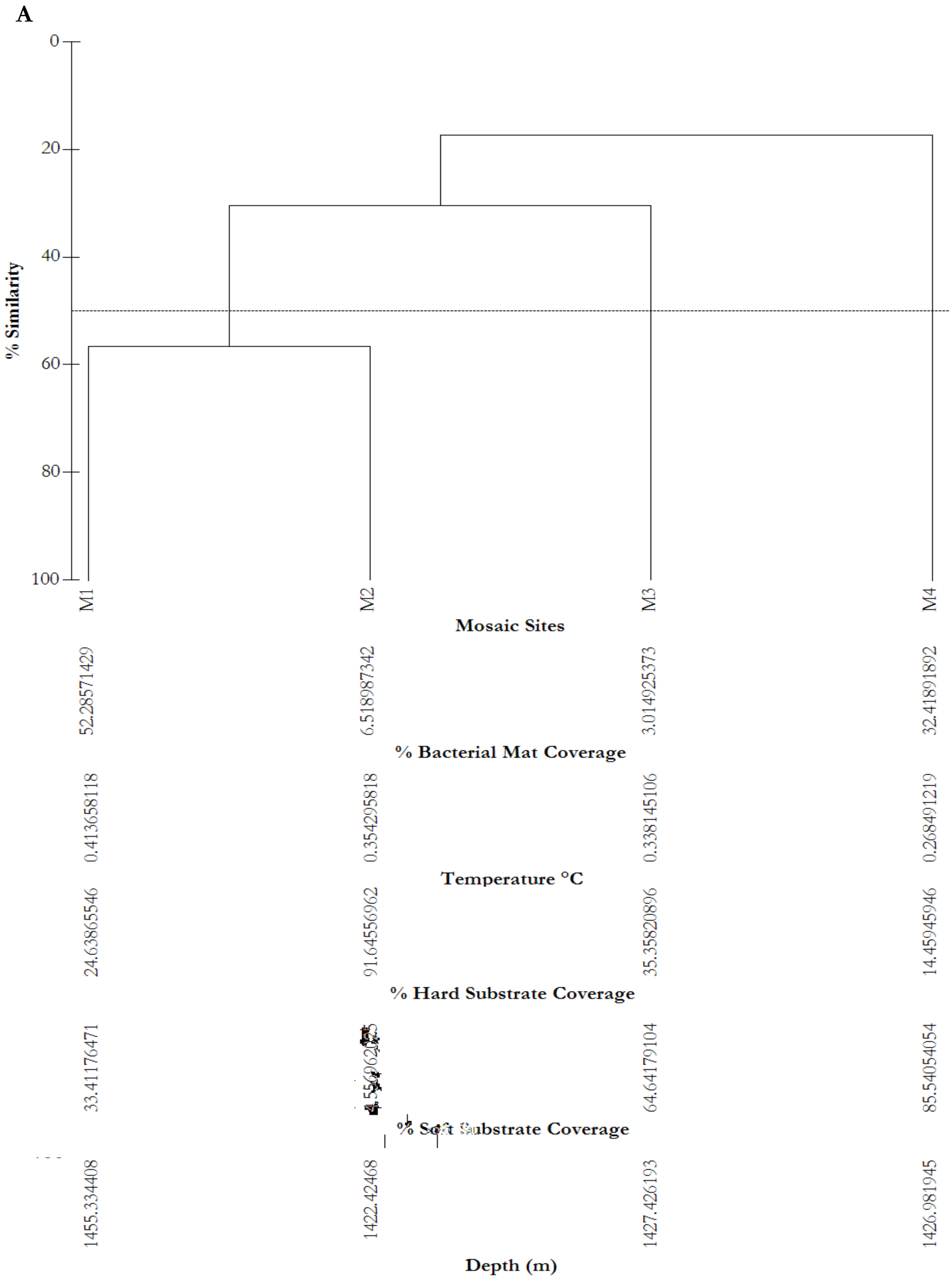
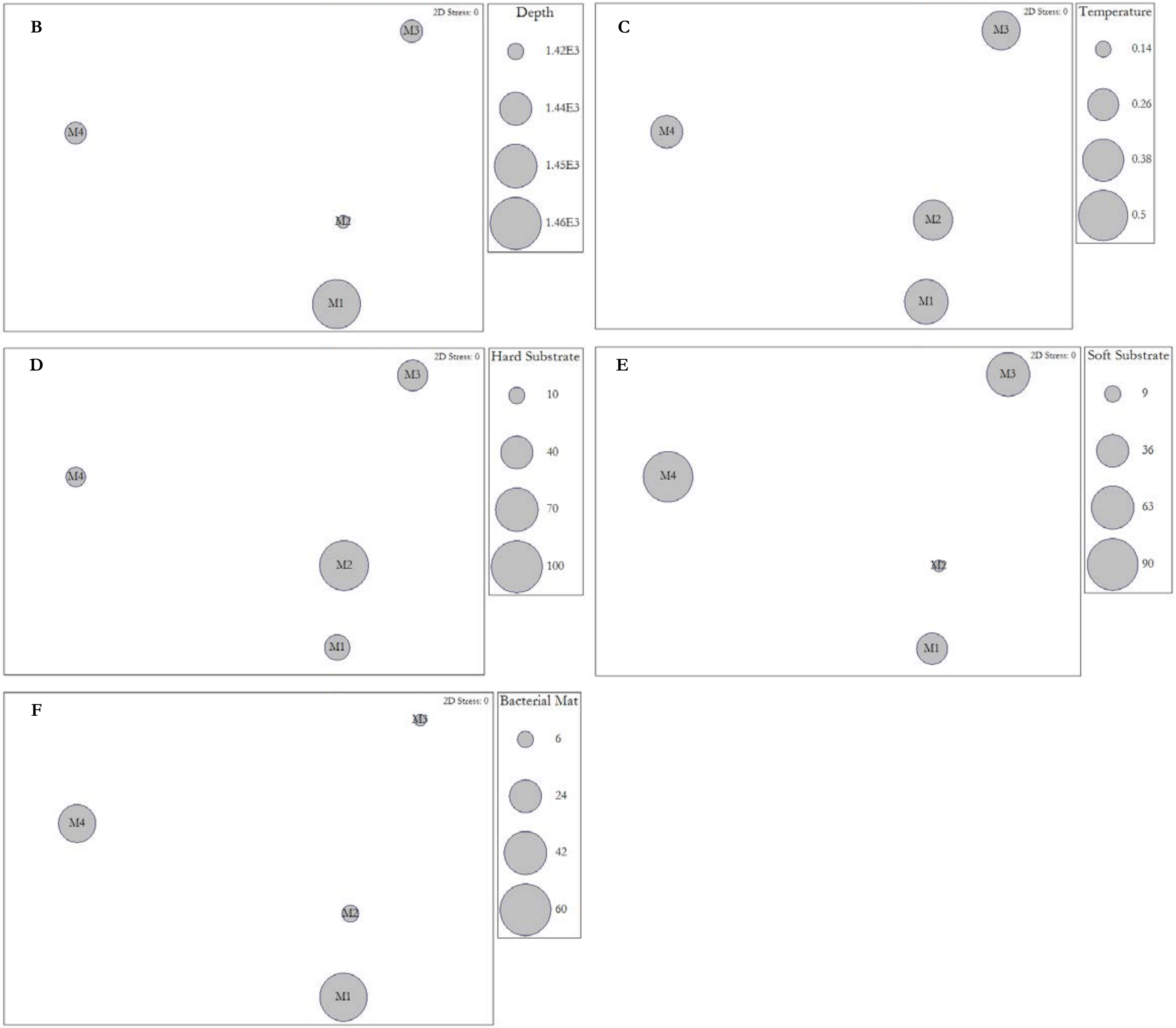


Figure 8 – Multivariate analyses of species abundance at mosaic sites on Kemp Caldera vent field, South Sandwich Islands.

(A) Dendrogram from hierarchical agglomerative clustering of Sorensen's similarity of log (x+1) transformed abundance data using group-average linkage. **(B-F)** Ordination from non-metric multidimensional scaling (MDS) of Sorensen's similarity values (ordination stress: 0). Bubble size is representative of environmental variables, as follows: **(B)** – depth; **(C)** – temperature; **(D)** – % hard substratum coverage; **(E)** - % soft substratum coverage; **(F)** - % bacterial mat coverage.


B
2D Stress: 0
M3
M4
M2
M1
Depth
1.42E3
1.44E3
1.45E3
1.46E3
C
2D Stress: 0
M3
M4
M2
M1
Temperature
0.14
0.26
0.38
0.5
D
2D Stress: 0
M3
M4
M2
M1
Hard Substrate
10
40
70
100
E
2D Stress: 0
M3
M4
M2
M1
Soft Substrate
9
36
63
90
F
2D Stress: 0
M3
M4
M2
M1
Bacterial Mat
6
24
42
60

III. RESULTS

Kemp Caldera within the Southern Ocean

There is an approximate 58% similarity (in Sorensen's Similarity Index, based on species presence/absence data) between the E2, E9 and Kemp Caldera sites (Figure 2). It is important to note that this is impacted by sampling effort, which might not be comparable between sites. In addition, the presence/absence dataset used to create Figure 2 was based on the species lists presented in Amon *et al.* (2013), Marsh *et al.* (2012) and Rogers *et al.* (2012), which might be incomplete (e.g. excluding peripheral fauna).

E2 and E9 vent fields share approximately 80% Sorensen's similarity. The transect and whale fall sites are identified as a separate coherent cluster from the E2 and E9 sites, according to a SIMPROF test. The whale fall site is approximately 86% similar (Sorensen's) to 'T6' and around 75% similar (Sorensen's) to all other transects.

A species list for all sites is presented in Table 3. Whilst many species are yet to be formally described, this list constitutes a first characterisation of the fauna of Kemp Caldera vent field, based on image analyses, cruise logs, and findings at E2 and E9 vent fields (and the already investigated whale fall site). The species list may increase following taxonomic identification and genetic analyses. For example, pycnogonids of various colours were observed and may represent colour morphotypes of the same *Sericosura* species, or different species altogether. 'M1' tubeworm abundance data (in Table 3) are to be treated with caution, due to the reduced visibility incurred as a result of high-density bacterial mat; these small tubes may be a morphotype of xenophyophore, microbial mat, or blurred gastropods, not siboglinid tubeworms observed in 'M3'. It is also worth noting that the description of *Calyptogena* and other vesicomyid clams is in the process of adjustment (see Decker *et al.*, 2012), though clams will be referred to as vesicomyids throughout this project.

Table 3 – List of Kemp Caldera vent field (South Sandwich Islands, Southern Ocean) megafaunal and macrofaunal taxa observed using ROV *Isis* video surveys.

Mean abundances counted at each location are provided where available (± standard deviation). ■ - Background fauna from the Southern Ocean. ● - Vent, or chemosynthetic, fauna. The majority of identifications are putative and awaiting taxonomic and molecular verification.

The following people are thanked for their contributions: Professor Paul Tyler (Sterechinus, nemertean worm, Kophobelemnon, Hyalonema); Dr Sven Thatje (midwater crustaceans and Nematocarcinus lanceopes); Dr Michael Vecchione (Alluroteuthis antarctica, Slosarczykovia circumantarctica); Professor Paul Rodhouse (Onychotheuthid sp.?). The following works were also used to identify taxa: Nye et al. (2013; Lebbeus antarcticus); Boschen et al. (2013; Ophiolimna antarctica); Amon et al. (2013), Marsh et al. (2012) and Rogers et al. (2012) for ESR fauna; and Rogers et al. (2010 – cruise report) for fish and holothurians.

Transect Comparisons and Assemblages

Table 4 – Summary of assemblages identified for each transect line (T1-T6) completed by ROV *Isis* during Dive 148 of research cruise JC042 (Kemp Caldera vent field, Southern Ocean).
Assemblages were defined according to dominant fauna, visible in ROV videographic surveys. These assemblages are mapped in Figure 7.
For original assemblages from which these assemblages were drawn, with example images, see Appendix C.

Transect	I	II	III	IV	V	VI	VII	VIII
T1	Limpets & bacterial mat	Sponge	Similar to (//) M2	Clams	Transitional (mixed fauna)	-	-	-
T2	Sponge	Clams	Limpets & bacterial mat	Transitional	//M2	Complex soft sediment (mixed fauna)	-	-
T3	Live shrimp	Limpets & bacterial mat	Clams	Complex soft sediment	Transitional	//M2	Sponge	-
T4	Live Shrimp	Clams	//M2	Limpets & bacterial mat	Complex soft sediment	Transitional	Similar to (//) M3	Sponge
T5	Ophiuroids & live shrimp	Transitional	Sponge	//M2	Limpets & bacterial mat	Live shrimp	-	-
T6	Ophiuroids & live shrimp	Clams	//M2	Peripheral vent fauna	-	-	-	-

Following cluster analysis (Figure 2), the following groups can be identified: 'T1' and 'T4'; 'T2' and 'T3'; 'T6' and the whale fall site; and 'T5' separately. The whale fall data are limited in value due to exclusion of bone-specialists and meiofauna from cluster analyses, as these were not comparatively resolvable at the Kemp Caldera vent field sites examined in this project. All transects share around 76% Sorensen's similarity, with 'T6' the least similar of the transects (~75%, along with the whale fall site). 'T5' is the next least similar, sharing approximately 78% Sorensen's similarity with transects 'T1-T4'. 'T2' and 'T3' (~91% similar) form a separate cluster to 'T1' and 'T4' (~88% similar), with an ~85% Sorensen's similarity between all four of these transects.

The dominant fauna of Kemp Caldera are: *Lepetodrilus* limpets, sponges, pycnogonids, *Pyropelta* gastropods, anemones, vesicomyid clams, midwater crustaceans, *Nematocarcinus lanceopes*, ophiuroids, and siboglinid tubeworms, most of which are represented in the selected small-scale mosaic sites. Also present at Kemp Caldera are macrourid and *Notolepis* sp. fish, three species of cephalopod, octocorals, holothurians, echinoderms and others, as listed in Table 3.

The visually dominant species present across each transect were used to define each of the 10 repeated assemblages shown in Table 4, which were grouped in spatial analyses. These ten assemblages represent the clearest, broad-scale changes in dominant visible fauna across the Kemp Caldera vent field and less dominant fauna may vary within assemblages between transects (see Appendix C).

Often concurrent with sulfidic material and vent chimneys, the 'limpets and mat' assemblage is dominated by thick, white bacterial mat and *Lepetodrilus* sp., with xenophyophores and vesicomyid clam shells often visible in the surrounding area. On occasion, this assemblage overlaps with the 'M2' assemblage, which is dominated by gastropods (*Pyropelta* sp. and *Lepetodrilus* sp.) and actinostolid anemones (as per the 'M2' mosaic). Also prevalent are *Sericosura* pycnogonids and sponges (with collections of clam shells occupying soft sediment between basalt outcrops). *Vulcanolepas* stalked barnacles are associated with this 'M2' assemblage at 'T1' and patchy bacterial mat with associated *Lepetodrilus* sp. are identified in concordance with this assemblage at 'T2' and 'T3'.

The 'sponge' assemblage occurs mainly on hard basalt topography, often comprising only sponges. However, where other species are also present, these include: bacterial mat, gastropods (*Pyropelta* sp. and *Lepetodrilus* sp.), xenophyophores, solitary actinostolid anemones, crustaceans (mixed dead *Nematocarcinus lanceopes* and *Lebbeus antarcticus* and alive *Nematocarcinus lanceopes*), siboglinid tubeworms and vesicomyid clams, in varying proportions. Basalt tends to be the defining feature; where soft sediment decreases, sponges become increasingly solitary and other fauna disappear.

'Clam' assemblage is dominated by vesicomyid (likely *Calyptogena* sp.) clamshells and, in some cases, live clams (with distinguishing features being protruding siphons, partially buried shells and bioturbated sediment). Other fauna found in association with high densities of clamshells are: anemones, *Nematocarcinus* and *Lebbeus* shrimp, gastropods (*Pyropelta* sp. and *Lepetodrilus* sp.), xenophyophores, *Sericosura* pycnogonids, fish (2 spp.), and light bacterial mat. A dead *Alluroteuthis antarctica* was observed amidst a clamshell bed at 'T1'.

The 'transition' assemblage was used to define any grouping comprising fauna from a mix of assemblages, often at the 'start' and 'end' of each assemblage along a transect line. It is an assemblage representing overlap and varies with each transect, commonly found near vent sources.

The 'complex soft sediment' assemblage comprises soft sediment with complexity added by basalt 'gravels', bioturbation and seemingly organic material or mat (which may be Fe floc, as mentioned in Staudigel *et al*., 2006). At 'T2' and 'T4', this assemblage hosts fewer fauna than neighbouring assemblages, with sulfides, sponges, anemones, dead shrimp and gastropods (*Pyropelta* sp. and

Lepetodrilus sp.) comprising its visible fauna. At 'T3', vesicomyid clamshells, pycnogonids and xenophyophores build upon these fauna.

'M3' assemblage was named after the 'M3' mosaic site and is thus dominated by siboglinid tubeworms on soft sediment. At 'T3', these are associated with aggregations of dead shrimp and dead clams (in addition to sponges and gastropods inhabiting any exposed basalt). At 'T4', dead shrimp and sponge fragments are associated with 'M3' assemblage.

Whilst live shrimp are motile organisms and thus not necessarily located in one place over a long timescale, a 'live shrimp' assemblage is defined at 'T3', 'T4' and 'T5', where *Nematocarcinus lanceopes* and *Lebbeus antarcticus* dominated the denoted larger-scale areas. At 'T3', these shrimp are associated with vesicomyid clamshells, sporadic anemones, *Ophiolimna antarctica*, live clams and xenophyophores; basalt is sediment covered and topography complex. At 'T4,' the picture is far simpler, with only live shrimp observed above soft sediments. At 'T5', the shrimp are associated with xenophyophores, sponge fragments and sporadic anemones.

The 'ophiuroid and live shrimp' assemblage comprises orange-coloured sediment, basalt outcrops and a mix of *Ophiolimna antarctica* and live *Lebbeus antarcticus* and *Nematocarcinus lanceopes*. At 'T6', patches of vesicomyid clamshells and occasional *Sterechinus* echinoids are also present.

Finally, the 'peripheral vent fauna' assemblage, observed only at 'T6', is composed of orange-coloured sediment and a mix of fauna. Anemones, live *Lebbeus* sp. and *Nematocarcinus* sp. shrimp, *Vulcanolepas* stalked barnacles, holothurians (2 spp.), regular echinoids, cephalopods (3 spp.) and *Ophiolimna antarctica* are all found in a shared proximity in this assemblage.

Mosaic Description

Four distinct areas were selected for videographic survey for smaller-scale analyses, based on their dominant visible fauna. 'M1' is visibly dominated by pycnogonids and gastropods, 'M2' by anemones and gastropods, 'M3' by siboglinid tubeworms and 'M4' by clamshells. A species list has been compiled for all of the mosaic sites ('M1-M4'), as shown in Table 3. Horizontal mosaics were created for each site, in addition to contour plots (representing density of dominant taxa per square metre) for each mosaic (M1 – Figure 3; M2 – Figure 4; M3 – Figure 5; M4 – Figure 6). As the mosaics and associated contour plots in Figures 3 to 6 are mostly shown on an arbitrary grid, references to areas within a contour plot or mosaic are made using compass directions for guidance only, and do not refer to ROV or data positioning within a UTM co-ordinate system.

‘M1’ is the furthest away from all transect and mosaic sites (~676.534 m from the nearest mosaic site – ‘M4’), located on a platform further southwest of visible vent sources (see Figure 7). ‘M1’ is visibly dominated by (in descending density): *Pyropelta* sp., *Sericosura* sp. and *Lepetodrilus* sp., with a predominantly ashy substratum. The temperature at this site ranges from 0.263°C to 0.576°C and depth ranges by approximately 2 metres, according to CTD-based records.

Pyropelta sp. densities are highest in the northeastern part of M1 (~17,000 m^{-2}) and lowest to the southwest (0-1000 m^{-2}). There is a visible NE-SW gradient in *Pyropelta* sp. density across ‘M1’. *Lepetodrilus* sp. abundances are greatest in the southern half of ‘M1’, with densities reaching 540 m^{-2} at their highest. Low numbers of *Lepetodrilus* sp. are recorded across ‘M1’ (20-60 m^{-2}) with a slight SE-NW gradient. Pycnogonids appear more concentrated, with highest densities recorded in the northeastern corner (800 m^{-2}); they demonstrate an overall NE-SW density gradient. Other fauna present at this site include shrimp, which are found in sparsely inhabited areas to the north and south, where substrata are mixed. The substratum is predominantly soft to the eastern half of ‘M1’, with hard basalt rocks scattered across an ashy base. Gravelly basalt overlies soft sediment to the western side of ‘M1’, excluding most fauna.

‘M2’ is the most central of all the mosaics. It is visibly dominated by anemones and gastropods (*Pyropelta* sp. and *Lepetodrilus* sp.), with a steep pillow basalt ledge and complex hard topography. Temperatures at this site range by around 0.2°C and depth is more variable, ranging by around 10 m.

Pyropelta sp. attain the highest recorded densities (4800 m^{-2}) in the southernmost portion of ‘M2’. The majority of ‘M2’ maintains *Pyropelta* sp. densities of around 1000 m^{-2}. Actinostolid anemones are, visibly, the dominant fauna at ‘M2’. As they are solitary fauna, their densities remain relatively low, reaching a maximum of 20 m^{-2}. However, they are spread across the whole of ‘M2’. Pycnogonids reach densities of 28 m^{-2} in small areas of ‘M2’, generally staying low in density across the site (~0-10 m^{-2}). Sponges are, again, focused on specific areas, reaching around 90 m^{-2} densities in one space. However, the majority of ‘M2’ sees low densities, of around 0-25 m^{-2}. Stalked barnacles (*Vulcanolepas* sp.) are present at ‘M2’, scattered and reaching densities of 17 m^{-2} in places. Microbial mat coverage is patchy at ‘M2’, focused at 3 main points across the mosaic. A dead squid (likely *Alluroteuthis antarctica* but view obscured by ledge) was observed at the ‘M2’ site. ‘M2’ is predominantly comprised of hard basalt rock, but some soft and mixed sediments can be identified to the western edge, where a light dusting of sediment covers this hard under layer.

‘M3’ is the furthest north of all the mosaic sites. With a temperature range of 0.121°C and a depth range of around 3 m, the site is predominantly soft sediment, with basalt outcrops to the western edges. ‘M3’ is visibly dominated by siboglinid tubeworms on soft sediment, and sponges on hard basalt.

Siboglinid tubeworms reach densities of up to 90 m^{-2}, with the highest densities to the southeastern corned of ‘M3’. Where hard substratum is present, tubeworms are not. Aside from this, the tubeworms tend to maintain densities of approximately 5-50 m^{-2} across the site. Sponges reach the second highest densities (up to 80 m^{-2}), where substratum is hard. They are found as fragments on soft substratum too, giving them a spread across the whole of ‘M3’. Pycnogonids are lower in density, reaching a maximum of 7.5 m^{-2} in peripheral areas of ‘M3’. The centre of ‘M3’ hosts no visible pycnogonids and bacterial mat is also low in central areas, only identifiable at a specific point to the southwestern edge. Anemones are also present at the ‘M3’ site, though their distribution is random and they occur singularly in most instances.

‘M4’ is visually dominated by vesicomyid clam beds, with a temperature range of approximately 0.1°C and the smallest depth range of all the mosaics (1.03 m). Dead clams visibly dominate the ‘M4’ site, reaching densities of 125 m^{-2}. Densities of the clamshells remain high around the periphery, particularly to the south and eastern edges, whilst the centre remains free of (or reduced in numbers of) these dead remains. Live vesicomyid clams, identified by their siphons and some slightly exposed shells, are more patchily distributed, reaching densities up to 60 m^{-2} to the western edge. Xenophyophores are less visually dominating but highest in density, with densities reaching 250 m^{-2}, particularly in the northern half of the site. Anemones are mostly found in the southwestern corner of the ‘M4’ site ($\leq 7\ m^{-2}$), whilst *Pyropelta* sp. are highest in density to the north and southwestern corners of the site ($\leq 110\ m^{-2}$). Pycnogonids are spread around the periphery, reaching densities of around 17 m^{-2} and *Lepetodrilus* sp. are concentrated in the southwestern corner ($\leq 34\ m^{-2}$). Hard basalt substratum, whilst scattered as small exposed rocks, is mainly found in the southwestern corner of ‘M4’. Microbial mat is more spread, covering the northwestern corner and more central portions of the site.

An Interpreted Zonation for the Kemp Caldera Vent Field

Figure 7 – Maps delineating the spatial distribution of faunal assemblages in Kemp Caldera vent field, South Sandwich Islands.
(A) Map of faunal and substratum assemblages, as identified using ROV *Isis* transect line video footage (Dive 148, JC042).
(B) A schematic representing an interpreted zonation of the Kemp Caldera vent field, based on the spatial distribution of faunal assemblages with increasing distance from visible vent fluid outflow (from chimneys). Here, active chimneys are 25.8 m from the nearest ‘limpets and mat’ assemblage, 31.6 m from the nearest ‘clam’ group, 43.8 m from the nearest ‘sponge’ assemblage (127.5 m from the furthest) and 74 m from the nearest ‘M3’ tubeworm group. Peripheral fauna are approximately 91.4 m from venting toward the east and 214.9 m away from venting westward. Live shrimp are found near inactive chimneys (47.1 m from

'dead' chimneys) but are at least 91.4 m from active venting more generally. The 'M2' assemblage to the west is around 160.6 m from active vent sources.
(C) Map showing the spatial distribution of dead and live taxa (shrimp and vesicomyid clams), as identified using ROV *Isis* transect line video footage (Dive 148, JC042).
(D) Map representing the spatial distribution of 'background' and chemosynthetic (or vent) fauna (and mixed groups of both), categorized as illustrated by symbols in Table 3.
Bathymetric data shown in (A) to (D) were collected on British Antarctic Survey JCR224 research cruise.
NB: white and black smokers, marked on maps refer to an appearance only and are not reflective of vent style. These smokers are, in fact, sulfide chimneys.

Whilst the aforementioned mosaics enable illustration of the microdistribution of fauna at a specific site, in using the interpreted zonation (shown in Figure 7), it is possible to see that these mosaics fit into a larger scale, repeatable zonation across the Kemp Caldera vent field.

As can be seen in Figure 7, a zonation can be interpreted for the Kemp Caldera study area, centred on visibly active venting to the east. Nearest the main venting, 'limpets and mat' and 'clam' assemblages dominate, along with 'transitional' groups. Moving outward, 'clam' and 'M2' assemblages thrive, before fauna become more mixed and separate clusters of 'M3', 'limpets and mat' and 'M2' assemblages are identifiable. There is a distinct boundary beyond this, separating vent and tolerant fauna from those from the wider Southern Ocean. The peripheral fauna are marginally shallower than those found within the main boundary line.

Dead crustaceans (predominantly shrimp) are found within the peripheral boundary, near vent sources. Meanwhile, live *Nematocarcinus lanceopes* and *Lebbeus antarcticus* shrimp are observed in the periphery, particularly to the south west of the study site.

Live vesicomyid clams are found near main vent sources (sulfide chimneys). Whilst dead clams, too, are found near these chimneys, they are also seen further afield. However, they do not extend to the peripheral zone, except where a potential 'other vent zone' (or repeated zonation out from venting towards the east) is highlighted in Figure 7, where limpets and bacterial mat are observed in abundance.

Material in Appendix C supports the interpretation of a zonation at the Kemp Caldera sub-cone site, with chemosynthetic fauna found within the vent area, predominantly south of the main smoker vent sources. Chemosynthetic or vent fauna are compared with non-vent, background fauna and are marked in Table 3. The categorization of fauna is in line with that of Reid *et al.* (2013). 'Background fauna' (observed at non-vent sites in the Southern Ocean) are restricted to the periphery. Mixed assemblages, comprising both vent and non-vent fauna, are found both within and outside of the periphery.

Following completion of slope analysis, it can be said that most of the aforementioned assemblages were found on an average slope of approximately 55º. The 'sponge' and 'limpets and mat' assemblages were found to occupy relatively steep slopes (>50º), whilst *Ophiolimna antarctica* and live *Nematocarcinus sp.* and *Lebbeus* sp. shrimp were found at slightly shallower depths and slopes (47º mean slope). Whilst error bars presented on the graphs in Appendix C suggest that shallower slopes are also occupied by all fauna, the median slope values hosting all assemblages lie steeper than 40º. This may result from the high resolution of the bathymetric data, which may pick up each small-scale change in surface roughness and topography, occurring repeatedly across the Kemp Caldera vent field. Perhaps, in future, a better representation of the overall topography could be obtained as suggested in Appendix C, though the reasons for not doing so in this project are also explained in this Appendix.

Environmental Factors and Inter-Mosaic Comparisons

All mosaics share around 18% Bray-Curtis similarity, with 'M1' and 'M2' the most similar to one another (~57%) and 'M3' the next most similar (30%).

According to factor-based analyses, mosaic clusters are not greatly affected by temperature. Instead, substratum, bacterial mat coverage and depth appear to influence similarity. Soft substratum may be most influential on community composition, as 'M1' and 'M2' have the least soft sediment and 'M4' has the most. Meanwhile, 'M1' is the shallowest site. 'M1' and 'M2' have the greatest bacterial mat coverage.

Using the contour plots illustrated in Figures 3 to 6, it is possible to describe relationships between different fauna and fellow fauna, temperature and substrata. At 'M1', *Pyropelta* sp. predominantly occupy soft substrata, where bacterial mat coverage is densest. *Lepetodrilus* limpets are high where *Pyropelta* sp. are low in density and are, too, found where bacterial mat is most dense; these fauna are associated with a hard substratum. Pycnogonid numbers are high in concurrence with *Pyropelta* sp.; these sea spiders seem less affected by substratum type. There are no clear relationships between fauna and temperature at 'M1' and shrimp appear randomly spread. All fauna appear to avoid gravelly, oxidized basalt.

At 'M2', anemones are associated with hard substrata. *Pyropelta* sp. are not found near anemones, in hotter zones, in most instances; instead they reflect the spatial distributions of pycnogonids and sponges, on hard substrata. Stalked barnacles are observed in cooler areas, like the sponges. Most fauna appear to avoid rougher topography, with gastropod numbers increasing on the lower basalt shelf and others demonstrating no preference.

In ‘M3’, tubeworm density follows a temperature gradient, on a soft substratum. *Sericosura* pycnogonids can occupy mixed substrata, with no clear associations (other than avoiding maximal temperatures). Sponges are tied to hard substrata, increasing in density at cooler temperatures.

‘M4’ hosts both dead and live vesicomyid clams, which occupy shared spaces in hotter areas where bacterial mat density is low. Where bacterial mat coverage is high, *Pyropelta* gastropods and xenophyophores are found. Anemones are associated with hard substrata. *Pyropelta* sp. mostly occupy medium temperature, high mat zones. Meanwhile, pycnogonids prefer medium temperatures, mixed substrata and occupy similar spaces to live clams. Xenophyophores are near ubiquitous across ‘M4’, on soft sediment and increasing where bacterial mat extends its coverage. *Lepetodrilus* sp. are focused on hard substrata, where temperatures are moderate.

Statistical Analyses

Following non-parametric correlation tests (Kolmogorov-Smirnov normality test failed), several strong (r_s=0.7 – 0.89 – see Fowler *et al.*, 1998 and Appendix D) significant relationships can be identified within mosaic sites. At ‘M1’, *Pyropelta* sp. are strongly positively correlated with bacterial mat (r_s=0.751, p<0.001, n=119). Meanwhile, at ‘M3’, sponges are significantly negatively correlated with siboglinid tubes (r_s=-0.745, p<0.001, n=64). Substratum-fauna relationships are also identifiable at ‘M3’, with sponges strongly positively correlated with hard substrata (r_s=0.824, p<0.001, n=64) and tubes strongly negatively correlated (r_s=-0.817, p<0.001, n=67).

The same non-parametric tests were applied to all fauna among all mosaics, identifying many moderate (r_s=0.4 – 0.69), significant relationships and some strong, significant correlations. (See Appendix D for results of all moderate to strong correlations and box plots illustrating the changing density of each species between mosaic sites.) The strongest, significant correlations were found between *Sericosura* pycnogonids and *Pyropelta* sp. (r_s=0.779, p<0.001, n=322) and *Lepetodrilus* sp. and *Pyropelta* sp. (r_s=0.805, p<0.001, n=239).

IV. DISCUSSION

This study presents the first characterisation of Kemp Caldera vent field and its associated fauna. Horizontal transect lines have been analysed to determine a broad-scale faunal zonation for the vent fauna and horizontal mosaics have been examined to quantify the faunal abundance and spatial microdistribution at sites representative of repeatable assemblages across the vent field. The results presented indicate that a faunal zonation centres on visibly active vent sources and mosaic sites fit into this zonation, repeating on occasion along transect lines. Thus, it can be suggested that environmental variables driving relationships identified in mosaics are influencing the zonation and composition of assemblages across the Kemp Caldera vent field.

Kemp Caldera within the Southern Ocean

The findings presented in Figure 2 demonstrate similarities between the Kemp Caldera vent field and neighbouring E2 and E9 vent fields. There are shared fauna between these sites. Nonetheless, Kemp Caldera vent field fauna are considered sufficiently dissimilar from E2 and E9 fauna that they were assigned a separate, coherent cluster following a SIMPROF test.

One of the main drivers of difference between Kemp Caldera vent field and the E2 and E9 vent fields is potentially introduced by the shape of Kemp Caldera, forming a filter on larval dispersal.
It was previously stated in work by Desbruyères *et al.* (1994) that *Bathymodiolus* are found in all back-arc basins, but Kemp Caldera and E2 and E9 observations suggest that this is not the case. Mussels are likely lacking in Kemp Caldera because the bowl-shaped, 'container' environment is unfavourable for pelagic larval stages, limiting planktotrophic larval movement and compounding the problems associated with Thorson's Rule in the Antarctic (Thorson, 1936; Clarke, 1992; Desbruyères *et al.*, 1994; Thatje *et al.* 2005). Another possibility is that the lack of *Bathymodiolus* mussels may echo the findings of Fabri *et al.* (2011), who suggested that an absence of these might result from a high abundance of suspended mineral particles restricting the filter feeding capability of mussels. Perhaps, whilst Thorson's Rule likely influences a lack of mussels at E2 and E9 vent fields, at Kemp, this is compounded by near-bottom current movement around Kemp Caldera's complex topography, combined with ashy soft sediment in suspension restricting filter feeding.

Meanwhile Kemp Caldera vent field also shares faunal affinities with E2 and E9. For example, stalked barnacles appear to have spread from E2 and E9 ridge vents to the caldera vent field. Their low numbers may be explained by their inability to sustain a larval mass. The stalked barnacles identified at the E2 and E9 ridge vents are likely a source for those barnacles randomly observed at Kemp Caldera vent field. However, at the E2 and E9 sites, stalked barnacles are in much higher abundance than at Kemp Caldera, visibly dominating the parts of the chimneys (Marsh *et al.*, 2012). Stalked barnacles are sessile filter feeders, living away from vent sources, as also found at Central Indian Ridge, SW Indian Ridge, and other western Pacific back-arc basins (again, in higher abundance than at Kemp Caldera; Marsh *et al.*, 2012). They are defined as chemosynthetic fauna in this study, due to their presence on E9 vent chimneys, in direct flow (Marsh *et al.*, 2012). Nevertheless, they do not increase in abundance proximal to visible vent sources. Stalked barnacles are another taxon shared between the South Sandwich Island sites, so it can be assumed that, as at E2 and E9 and their closest relations in Brothers Caldera in the Kermadec Ridge, stalked barnacles at Kemp Caldera vent field are sessile filter feeders that also use epibiotic bacterial food sources (Marsh *et al.*, 2012). Observations of these stalked barnacles are in line with the evaluation presented in Buckeridge (2012), where Scalpelliformes are deemed a resilient, adaptable cirripede, often acting as opportunists, establishing themselves in newly available niches, where available. Nonetheless, due to their sessile nature, they may be unable to tolerate environmental disturbances like volcanic eruptions, which may explain their low numbers and random spatial distribution in Kemp Caldera vent field observations (Buckeridge, 2012).

Peltospiroid gastropods are present at the ESR sites and Kemp Caldera, which may reflect the presence of a larval pool at one of the sites contributing to the dominance of gastropods across large distances. Peltospiroid gastropods are globally spread across hydrothermal vents, occurring on the Central Indian Ridge, East Pacific Rise, SW Indian Ridge, Mid-Atlantic Ridge and the Juan de Fuca Ridge in various guises (Marsh *et al.*, 2012). They were identified at E2 and E9 in high densities (up to 1000 m^{-2}), along with *Lepetodrilus* limpets, in the second nearest zone to venting (Marsh *et al.*, 2012; Rogers *et al.*, 2012). The limpets were commonly found in lower temperature diffuse flow, on bare rock, sulfides and other fauna (e.g. peltospiroid gastropods and stalked barnacles), grazing on associated microbes (Rogers *et al.*, 2012). These findings are echoed at Kemp Caldera, with *Pyropelta* gastropods reaching the highest densities of all fauna (exceeding 1000 m^{-2} in most instances) and limpets associated with bacterial mat and hard substrata. Both taxa are generally found in assemblages close to visibly venting chimneys at Kemp, and presumably in areas of more diffuse flow (though this is not determinable using ROV *Isis* footage).

Limpet densities exceeded those of *Pyropelta* gastropods at E9 (Marsh *et al.*, 2012). This does not seem to be the case for Kemp Caldera, on first look. However, this is likely the result of error in identification when counting, due to reflection of light off limpet shells giving them a white appearance, or by bacterial mat obscuring the appearance of limpets in images (Appendix B). Limpets are observed in high densities near active vent sources in transect images, where their shells are clearly brown against the reflective white mat 'background', so it is unreasonable to argue that they are lower in number than *Pyropelta* sp. without further, repeat counts completed by multiple researchers.

Rogers *et al.* (2012) describe an association between anemones (of which 5 morphospecies are recorded) and diffuse flow at chimneys and on pillow lavas. The association between anemones and hard substrata, like pillow lavas, was also identified using abundance data from Kemp Caldera mosaic sites. The 'M2 assemblage', dominated by anemones and gastropods, repeatedly occurred near vent sources at Kemp Caldera, though not at chimneys themselves; this perhaps implies that at Kemp, too, anemones are associated with more diffuse flow, which could not be observed in the available video, given the resolution. A future visit to Kemp Caldera would require use of a high-definition camera, as used for vertical chimney surveys at E9 (not available for horizontal imaging; Marsh *et al.*, 2013), to define sites of more diffuse flow, not associated with sulfide chimneys. These could then be mapped to determine the mean distances between fauna and hydrothermal fluid sources, as per Marsh *et al.* (2012). Nonetheless, it is well known that anemones can occupy peripheral, low temperature areas in vent sites such as E9, TAG, Mid-Atlantic Ridge sites and others (Marsh *et al.*, 2012). Their presence in warmer temperatures, in lower abundances than identified at the aforementioned sites (with the highest recorded density of ≤21 m^{-2} at Kemp and 20-30 m^{-2} at the other sites) perhaps suggests that anemones in the 'M2' assemblages are at their limit of thermal tolerance, staying close to vents to ensure prey availability (e.g. gastropods).

Peripheral fauna observed at E2 and E9 included: stichasterid sea stars, pycnogonids, zoarcid fish and an octopus (Marsh *et al.*, 2012). Three species of *Sericosura* pycnogonid were identified at E2 and E9, with the largest of these (*Colossendeis* cf. *concendis* and *C.* cf. *elephantis*) in more peripheral regions (Rogers *et al.*, 2012). At Kemp Caldera vent field, taxonomic verification of pycnogonid species is yet to be provided, but visual examination suggested that one (or more) species of *Sericosura* pycnogonid dominated wherever present. *Colossendeis* sp. indet. was observed on two occasions, at 'T2' and 'T5, respectively.

Echinoderms observed at E2 and E9 were mostly non-vent species, apart from a seven-armed sea star from the Stichasteridae family, which appeared vent-endemic, feeding on other vent life (e.g. barnacles; Rogers *et al.*, 2012). These observations are in line with those made of Kemp Caldera echinoderm species, though behavioural patterns would need to be observed over longer timescales using ROV dives specifically designed for behavioural study (e.g. close zoom, maintained depth).

Dominant fauna identified at E2 and E9 vent fields were *Kiwa* crabs, peltospiroid gastropods, eolepadid barnacles and carnivorous actinostolid anemones (Marsh *et al.*, 2012). Whilst the anemones, gastropods and stalked barnacles are shared with Kemp Caldera, *Kiwa* crabs are missing from Kemp Caldera observations. The reason for a lack of *Kiwa* in Kemp Caldera vent field is largely unclear, as they are vent-endemic. Depth is disregarded as a limiting factor on species unable to thrive at Kemp Caldera vent field (where they otherwise succeed at E2 and E9 vent fields) because temperature does not change dramatically with depth in Antarctic waters. However, work by Roterman *et al.* (2013) suggests that these crabs may have been prevented from entering Kemp Caldera due to the ridge surrounding the vent field, forming the caldera 'bowl' itself. Roterman *et al.* (2013) explain that vent communities are often similar among sites where larvae can disperse along ridges, using bottom currents to assist in their transport long-distance. It could thus be possible that the *Kiwa* crabs are prevented from colonising Kemp Caldera vent field by the rim of the caldera creating a barrier against larval dispersal.

Cephalopods, such as those observed at Kemp Caldera vent field, absent from E2 and E9 observations, are known to replace fish in the Polar Frontal Zone of the Scotia Sea (Tynan, 1998). However, at Kemp, both fish and cephalopods are present. Fish (macrourids and a zoarcid) were uncommon at E2 and E9, though Kemp Caldera vent field observations may suggest that this was a result of the limitations of videographic survey, where more dive time at the E2 and E9 sites would increase the likelihood of fish observations (Rogers *et al.*, 2012). The fish at Kemp Caldera were randomly distributed, though seemed to concur with live shrimp, implying a preference for peripheral, cooler conditions. This might explain a lack of fish observations at E2 and E9, if videographic survey limitations were not to blame. With regard to cephalopods, these are likely opportunists, seeking prey (or following the ROV lights). At Kemp Caldera vent field, their live presence supports the idea that calderas can be interaction sites for deep and midwater fauna. However, dead cephalopods observed in areas of diffuse flow suggest that cephalopods are not able to tolerate vent conditions.

A notable difference between the E2 and E9 sites and that studied at Kemp Caldera is the presence of vesicomyid clams in Kemp Caldera vent field. This is likely due to the presence of suitable soft sediment at Kemp, unavailable at E2 and E9, emphasising the influence of local geomorphology on community composition at vent sites. The difference is unlikely caused by dispersal limitations, as vesicomyids have shown evidence for long-distance dispersal, based on vent and whale fall observations (Baco *et al.*, 1999). Clams rely on reduced sulfur availability and, it now seems, on suitable substrata through which they can access this sulfur (Baco *et al.*, 1999). This argued, Kemp Caldera does host some clamshells (that may not be dead) on rocky terrains and live clams were observed off the study site, within the caldera, on rocky substrata (Copley, per. comm.). This would be worthy of future investigation, to constrain the reasons for these fauna establishing themselves successfully at Kemp Caldera and not being observed at neighbouring E9. It is proposed that those clams surviving on rocky substrata are on rubble-like substrata, with sufficient gaps between each rock for their foot to penetrate soft sediment and access sulfide beneath. This proposition is made under the proviso that live clams were not visible on solid sheet and pillow basalts at Kemp Caldera vent field and that clams would thus not be able to establish themselves on the solid substrata available at E2 and E9. It may even be the case that small-scale landslides create the rubble surfaces observed (through which clams can penetrate and reach soft sediment beneath), thereby linking Kemp Caldera's disturbed nature to the prevalence of vesicomyid clams.

Siboglinid tubeworms are another taxon observed at Kemp Caldera vent field, but not at the E2 and E9 vent fields of the East Scotia Ridge. This may be the result of a requirement for soft sediment, more so than vesicomyid clams (Hilário *et al.*, 2011). These worms have planktonic larvae, able to transmit across large distances and their larval pool might therefore encompass E2 and E9, but recruitment may be prohibited at those sites by lack of suitable habitat (Hilário *et al.*, 2011).

Rogers *et al.* (2012) suggest that the E2 and E9 vents share faunal affinities with western Pacific back-arc basins, the south East Pacific Ridge and the Mid-Atlantic Ridge. In addition, the dominant anomuran *Kiwa* crab is linked to species found off Costa Rica and at the Pacific-Antarctic Ridge (Rogers *et al.*, 2012; Roterman *et al.*, 2013). It could be argued that the presence of vesicomyid clams and siboglinid tubeworms further supports these faunal affinities, with fauna at Kemp Caldera vent field echoing observations from Pacific vent sites, though vesicomyid clams have a trans-oceanic spread (Krylova and Sahling, 2010; Audzijonyte *et al.*, 2012). Nonetheless, it has been proposed that the ESR is a new biogeographic province in vent ecology (German *et al.*, 2000), whereas the findings from Kemp Caldera vent field suggest that, within this province, smaller provinces may exist, with caldera environments possibly forming "subprovinces".

In addition, the Kemp Caldera vent field hosted the first natural whale fall ever found in the Southern Ocean, as presented in Amon *et al.* (2013). The findings illustrated in Figure 2 can be used to suggest that vent fauna have spread into the wider, non-venting caldera at Kemp, due to the presence of a chemosynthetic source – the whale fall. Whilst Amon *et al.* (2013) suggested that fauna surrounding the whale fall could not be said to be 'background fauna' until further analyses and identification had been completed, it can now be said, using Kemp Caldera data, that the fauna surrounding the whale fall reflect wider Kemp Caldera background taxa. The fact that the whale fall is not buried after 50 years on the seafloor may suggest that eruptive disturbance at Kemp Caldera is limited to a small area, surrounding the sub-cone, though this would require repeat visits to confirm.

As highlighted in the work of Amon *et al.* (2013), whale falls offer an intermediate habitat type for vent fauna to use as stepping-stones between vent fields. Whilst this is not the case at Kemp Caldera, as vent fauna have merely extended their range to this within-caldera whale fall, an important similarity between whale falls and caldera sites can be drawn. Thanks to disturbance creating ashy substrata and the varied topography of Kemp Caldera vent field, fauna are offered both hard and soft substrata, enabling more species to colonise this area of the 'Southern Ocean province'. The influence of substratum on faunal distribution is often neglected in ecological studies (Sarrazin *et al.*, 1999); here, it seems that substratum has a key role to play in the distribution of fauna in submarine calderas.

Transects & Zonation

On examining Figure 2 more closely, it is apparent that Kemp Caldera vent field varies within its own 'bowl', as well as when compared with E2 and E9 vent fields. For example, the selected transects were found to group into separate clusters (Figure 2).

It is likely that 'T5' was least similar to the other transects as a result of it lying mostly in the peripheral zone, comprising predominantly sponge and *Nematocarcinus* shrimp assemblages. Grouping 'T6' with the whale fall site is largely insignificant, as the in-fauna and whale bone specialists were excluded from the whale fall presence/absence data; however, 'T6' is predominantly comprised of peripheral fauna, perhaps suggesting that the whale fall, like Kemp Caldera, is an interaction site for Antarctic and chemosynthetic fauna. Grouping 'T1', 'T4', 'T2' and 'T3' highlights the dominance of chemosynthetic vent fauna towards the east of the study site.

Is there a zonation pattern across the transects?

A zonation pattern was interpreted across the transects by joining together repeated assemblages (Figure 7). This pattern suggests that venting is focused to the eastern side of the site, where both inactive and active sulfide chimneys were observed. This fits in with faunal observations, given that bacterial mat and limpets, along with vesicomyid clams (reliant on sulfides) dominated the areas surrounding this focal point and non-vent fauna were found further westward.

Succession at vents can be caused by episodic disturbance, like volcanic eruption, on annual to decadal timescales (Mullineaux *et al.*, 2003; 2010). Faunal groups can be indicative of successional stage; for example, dominance of a single symbiont-containing species (e.g. limpets) and low species richness, particularly lacking filter feeders (e.g. limpet and mat assemblages), suggests an early successional stage (Podowski *et al.*, 2010). Perhaps, the zonation interpreted for Kemp Caldera vent field represents a snapshot of various stages in succession, or community composition through time. In this case, limpets and mat near vents are an early stage, implying recent activation of the observed chimneys, whilst the filter feeders in the periphery have established over a longer time period. If this were the case, perhaps an eruption occurred further back in time than the time taken for sponges to colonise pillow basalts.

The zonation proposed for the Kemp Caldera vent field can be compared with that presented in Marsh *et al.* (2012). At E9 vent field (ESR), Marsh *et al.* (2012) suggest that *Kiwa* crabs dominate the areas closest to venting, with gastropods forming the next zone, stalked barnacles the next and anemones further afield, before the peripheral zone. A pictorial representation of this zonation is represented in Figure 7. The Kemp Caldera vent field zonation is similar to that proposed for the

E9 vent field. Nearest venting, whilst Marsh *et al.* (2012) suggest that *Kiwa* crabs dominate, limpets cover their carapaces. It could thus be argued that, at E9, limpets are the numerically dominant fauna of this near-vent zone. With this in mind, Kemp Caldera vent field's limpet and mat assemblage dominating the near-vent zone draws direct parallel with the E9 vent field, suggesting that the microbial mat formed proximal to warmest outflow provides a food source for limpets, which, at E9 is shared with the microbe-harvesting *Kiwa* crabs (Marsh *et al.*, 2012; Roterman *et al.*, 2013). Moving further away from venting, the gastropods dominating Zone II of the E9 vent field compare with the 'M2 assemblage' dominating the second zone at Kemp Caldera vent field, comprising gastropods, anemones and pycnogonids. Clamshells and live clams are an addition to this zone at Kemp Caldera vent field because of the availability of a suitable soft substratum, unavailable at E9. Further afield, stalked barnacles form a distinct zone at E9, whereas these are sporadically part of the 'M2 assemblage' zone at Kemp Caldera. The anemones assigned a separate zone at E9, too, fit in with the second zone 'M2 assemblage' at Kemp Caldera vent field. The periphery is identifiable at Kemp Caldera and highlighted in Figure 7. However, at Kemp Caldera vent field, tubeworms form an additional penultimate zone fauna, due to the availability of soft substrata, not present at E9.

In comparing the aforementioned zonation patterns and identifying differences between those of E9 and Kemp Caldera vent fields, it is possible to say that substratum is a key influence on faunal difference between these sites. Geological difference is driving biological variation across space (Kim and Hammerstrom, 2012). Thus, it is important that more interdisciplinary studies of vent fields in calderas are undertaken, combining geomorphology, geochemistry and ecology to identify substratum-induced differences between and within vent fields.

Cuvelier *et al.* (2011) suggest that temperature impacts species distribution more than sulfide. The diffuse flow from sulfide chimneys, similar in appearance to white and black 'smokers' (observed within 'T4'), indicate an area of higher temperature expulsion (Van Dover, 2000). The majority of Kemp Caldera site is supplied with diffuse vent flows (up to 115°C), where thermophilic microorganisms can thrive, supporting a variety of invertebrates (Van Dover, 2000). At Kemp Caldera vent field, most diffuse flow is ejected from fissures in basaltic lava, with some mineral precipitates (e.g. iron oxyhydroxides) visible as a coloured layer on the surface of bare rock (Van Dover, 2000). Bacterial mat is an appropriate indicator of hydrothermal venting, as supported by thick accumulations next to chimney sources (Wishner *et al.*, 2005).

Nonetheless, on inspection of the Kemp Caldera site as a whole, it cannot be said that either temperature or sulfide has a greater influence on species distribution, with both factors influencing the zonation, centring on hot, sulfur-rich vents. As a result, it could be argued that chemistry is key, as this is one factor likely to vary considerably with geology, despite geographical proximity of neighbouring vent sites and might explain the variation amongst Kemp and other ESR vent fauna.

'Background' Antarctic fauna are generally found at shallower depths than vent fauna, perhaps suggesting that depth is a limiting factor within the caldera for non-vent fauna. They are also not adapted to the chemical toxicity of the vent field. Meanwhile, chemosynthetic fauna tend to comprise the taxa that are shared with ESR vent fields, though clams are a notable addition at Kemp Caldera. This suggests that it was reasonable to suggest that chemosynthetic vent fauna are not depth-limited, as they are found at the Kemp site, despite it being relatively shallow compared with E2 and E9. Temperature may be less influential in the Antarctic than at other vent sites across the globe, as the waters of Kemp Caldera are relatively cool when compared with E2 and E9 'smokers', but fauna are still shared between sites. This idea is perhaps further supported by the presence of Kemp Caldera vent taxa at the whale fall, as the whale provides a chemosynthetic source but not a heat supply (Amon *et al.*, 2013). Small-scale physical oceanographic differences also seem to have little impact on vent fauna, according to the sharing of species between these structurally different sites. Thus, it is likely that habitat type or substratum plays a more important role in the spatial distribution of the chemosynthetic fauna.

Whilst limpets are found proximal to visible vent sources and yet seem temperature limited on the mosaic scale, bacterial mats are usually associated with temperatures below 50 °C, at the boundary between hot fluids and ambient temperature seawater (Van Dover, 2000). This suggests that the areas of thick microbial mat lie at an appropriate moderate temperature, within which limpets can survive (Barreyre *et al.*, 2012).

Limpets are regular inhabitants of vent environments, grazing on epizoic microbes (Gage and Tyler, 1991; Rogers *et al.*, 2012; Amon *et al.*, 2013). Experimental work conducted by Lee (2003) showed that *Lepetodrilus* limpets from the Pacific tend to dominate in areas of weaker venting. In fact, Lee (2003) found the limpets to be less thermotolerant than other vent species, unable to survive above around 35ºC. These findings were echoed in the work of Mills *et al.* (2007) at the East Pacific Rise, who identified *Lepetodrilus* species as abundant in concordance with suspension feeders and vestimentiferans, in cool and warm zones (temperatures around 3-6°C permitted a range of limpet species to thrive). At Kemp Caldera vent field, it is likely that the lack of 'smoker' vent sources provides a moderate, tolerable temperature for gastropod survival on actively venting areas.

Lepetodrilus sp. at Kemp, like *Lepetodrilus fucensis* in Northeast Pacific vent sites, are likely to have selected habitats nearest visibly venting chimneys to maximise reproductive output (Kelly and Metaxas, 2007). Their grazing on mat is usually a response to vent shutdown, which may be supported by the inactive chimneys located proximal to those currently active and the thick bacterial mat coincident with high limpet abundances (Kelly and Metaxas, 2007).

Matabos *et al.* (2008) discovered that peltospiroid gastropods dominated lepetodrilids when environments were acidic, sulfide-rich and hot. It was suggested following further analysis that lepetodrilid gastropods outcompete peltospiroid gastropods given the opportunity (Matabos *et al.*, 2008). The dominant drivers of gastropod distribution were considered to be: mean sulfide concentration, acidity, and maximum temperature, with peltospiroid gastropods able to withstand higher levels of each (Matabos *et al.*, 2008). These findings appear to be both supported and negated by observations at Kemp Caldera, perhaps implying an overlying biotic driver for the relative gastropod densities observed at each mosaic site and across the site as a whole. For instance, the *Pyropelta* sp. are not found in the most acidic, sulfidic, hot environments; instead, *Lepetodrilus* sp. graze on mat most proximal to venting sulfide chimneys. This may be a result of the finding of Matabos *et al.* (2008), that *Lepetodrilus* sp. outcompete *Pyropelta* sp. where possible. Here, it is perhaps likely that limpets were the first colonizers of an area of newly activated venting, outcompeting their *Pyropelta* sp. rivals. This idea is potentially supported in the work of Mullineaux *et al.* (2010, 2012), who highlight the opportunity for recolonisation presented by an eruption event. Potentially, *Lepetodrilus* larvae from E2 or E9 vent fields could have colonised the area surrounding the chimneys following an eruption that removed or reduced the numbers of their *Pyropelta* competitors.

Calyptogena spp. are chemosynthetic, reliant on microbial symbionts to reduce carbon dioxide for their nutrition (Gage and Tyler, 1991). Thus, their spatial distribution denotes that of hydrothermal fluid outflow (Gage and Tyler, 1991). They are forced into boundary zones, between ambient, oxygen-rich seawater and hydrothermal fluid (a source of reduced sulfide; Gage and Tyler, 1991). Chemical fluxes at submarine volcanoes are strongly influenced by microbial activity (Staudigel *et al.*, 2006). This may explain the presence of both dead and live clams (assumed *Calytogena* spp., though awaiting confirmation) near the 'limpets and bacterial mat' assemblages, as the mat impacting chemical flux would affect clams, who rely on vent fluids and sulfur, positioning themselves in the sediment according to the most suitable chemical environment (Olu *et al.*, 1996). Meanwhile, as dead clams can signify a change in substratum porosity or vent fluid exit deactivation, their absence from the periphery may suggest that the periphery has not been active in venting for the last 25 years at least (the approximate time taken for clam shells to decompose; Cuvelier *et al.*, 2009). Live clams were observed near the main source of visible venting, as expected (Gage and Tyler, 1991).

Following slope analysis, it appears that slope and rugosity (roughness) play a minimal role in the spatial distribution of organisms in Kemp Caldera vent field, though motile fauna (e.g. shrimp) are not inhibited by steep topography and may thus be able to avoid predators by seeking steeper slopes. Munilla and Soler-Membrives (2007) denote the influence of slope on the enhanced carriage of particulate organic matter in bottom currents, benefiting sponges and other filter feeders. Thus, were the small-scale physical oceanography of Kemp Caldera better understood, it might be possible to denote a relationship between small-scale bottom currents (perhaps circulating the crater 'bowl') and the positioning of sessile filter feeders (supported in Kim and Hammerstrom, 2012). Further still, the frequency of small-scale current changes may influence the success of such species in caldera environments.

Ophiuroids, anemones and holothurians are typical peripheral fauna (Micheli *et al.*, 2002; Desbruyères *et al.*, 2006; Fabri *et al.*, 2011). The presence of sponges in peripheral areas is unsurprising, as filter feeders, like sponges, comprise well-known deep-sea assemblages, acting as peripheral fauna, at the boundaries of separation between vents and the wider deep sea (Desbruyères *et al.*, 1994). Epifaunal species, like sponges, were found to attain greater densities near the Vailulu'u volcano peak, due to the increase in current speeds optimising conditions for filter feeding (Staudigel *et al.*, 2006). It might thus be interesting to map sponge density across the study site, to determine whether the sub-cone or caldera 'bowl' impact any small-scale water movements, improving or worsening conditions for filter feeding.

It is expected that the majority of the peripheral fauna are more influenced by biotic than abiotic factors, impacted by predator-prey and competitive processes (Micheli *et al.*, 2002). Actinostolid anemones are more central at Kemp Caldera, able to thrive in the venting zone. It would be interesting to compare anemone sizes across space, to determine whether juvenile anemones are concentrated in a particular area, or are rare (employing a similar analysis to Marcon *et al.*, 2013a). Non-vent anemones were more rare in Kemp Caldera than actinostolids, though this is likely a result of selecting transect lines focused on the vent field. Nonetheless, echinoderms do comprise a large proportion of the observed peripheral fauna. It is difficult to say whether biotic drivers affect these fauna without experimental manipulation or footage of a single, small-scale site over an extended time frame. However, relationships between fauna were investigable using small-scale mosaic sites following enumeration and statistical analysis.

Based on the transect analyses, it is clear that small-scale mosaics account for the majority of faunal groupings observed at Kemp Caldera. However, mosaicing of small areas of the 'ophiuroid and live shrimp' assemblages and the 'limpets and mat' assemblage (to quantify limpet abundance and examine body size) would prove fruitful for studies of predator-prey distribution and size distributions, respectively. The peripheral fauna would perhaps not be fairly represented by this small-scale, image-based mode of study, given their spread, and may require the use of automated mosaicing techniques.

Assemblages reflecting 'M2' and 'M3' mosaic sites suggest that these mosaics are representative of repeatable zones within Kemp Caldera vent field. 'M4' is perhaps most similar to the clam assemblages, which recur across the site. 'M1' is least similar to the assemblages observed along the transects, perhaps suggesting that, further south, a difference in venting style or geology impacts fluid outflow and affects community composition. The high abundances of gastropods and pycnogonids, in association with elevated levels of microbial mat, imply that venting does occur further south of the transect zonation. However, it might be the case that 'M1' forms part of another zonation, surrounding a more diffuse vent fluid source.

Mosaics: Microdistribution of Visible Fauna

Whilst is has been proposed, using the interpreted zonation for the Kemp Caldera vent field, that temperature does not appear to be a key driver on assemblage types on the vent field scale, small-scale studies are needed to identify relationships between environmental drivers and the spatial distribution of individual taxa. In generating photomosaics and quantifying fauna in smaller areas, a small-scale, high-resolution characterization of the faunal microdistribution at each mosaic site is now possible.

The PRIMER-E results illustrated in Figure 8 demonstrate that each photomosaic represents a distinct vent community. Depth, substratum type and bacterial mat coverage appear to have a greater influence on mosaic dissimilarity than temperature. 'M1' is the shallowest site and is furthest from the other sites, perhaps fitting into another zonation altogether, further south in the caldera.

Using the contour plots illustrated in Figures 3 to 6, it is possible to describe relationships between different fauna and fellow fauna, temperature and substrata. At 'M1', *Pyropelta* sp. predominantly occupy soft substrata, where bacterial mat coverage is densest. *Lepetodrilus* limpets are high where *Pyropelta* sp. are low in density and are, too, found where bacterial mat is most dense; these fauna are associated with a hard substratum. Pycnogonid numbers are high in concurrence with *Pyropelta* sp.; these sea spiders seem less affected by substratum type. There are no clear relationships between fauna and temperature at 'M1' and shrimp appear randomly spread. All fauna appear to avoid gravelly, oxidized basalt.

At 'M2', anemones are associated with hard substrata. *Pyropelta* sp. are not found near anemones, in hotter zones, in most instances; instead they reflect the spatial distributions of pycnogonids and sponges, on hard substrata. Stalked barnacles are observed in cooler areas, like the sponges. Most fauna appear to avoid rougher topography, with gastropod numbers increasing on the lower basalt shelf and others demonstrating no preference.

'M1' and 'M2' are likely to be most similar (see Figure 8) because of the dominance of gastropods at both sites. 'M1' and 'M2' are distant sites and a shared physico-chemical driver is perhaps unlikely. This argued, bacterial mat is also particularly high at both 'M1' and 'M2' sites, suggesting that sulfide levels (or high chemical toxicity) links these sites. 'M3' also saw presence of gastropods, whereas M4 was perhaps most different from other sites through the introduction of clams and xenophyophores, often at the expense of other shared fauna.

In 'M3', tubeworm density follows a temperature gradient, on a soft substratum. *Sericosura* pycnogonids can occupy mixed substrata, with no clear associations (other than avoiding maximal temperatures). Sponges are tied to hard substrata, increasing in density at cooler temperatures.

'M4' hosts both dead and live vesicomyid clams, which occupy shared spaces in hotter areas where bacterial mat density is low. Where bacterial mat coverage is high, *Pyropelta* gastropods and xenophyophores are found. Anemones are associated with hard substrata. *Pyropelta* sp. mostly occupy medium temperature, high mat zones. Meanwhile, pycnogonids prefer medium temperatures, mixed substrata and occupy similar spaces to live clams. Xenophyophores are near ubiquitous across 'M4', on soft sediment and increasing where bacterial mat extends its coverage. *Lepetodrilus* sp. are focused on hard substrata, where temperatures are moderate.

Cuvelier *et al.* (2009) relate faunal distributions to characteristics such as fluid outflow and depth. Temperature changes can drive habitat selection, spatial segregation and overall spatial distribution of vent fauna (Cuvelier *et al.*, 2009). However, as emphasised by Mills *et al.* (2007), it is often difficult to describe a preferred physicochemical habitat for a particular macrofaunal species, due to the nature of vents, with their steep thermal, chemical and biogenic gradients. Biotic factors (e.g. uptake of sulfides and predation), too, influence spatial patterns but are more difficult to elucidate to using image analysis (Cuvelier *et al.*, 2009). Given the small-scale and high resolution of the mosaic site data and the quantification of fauna across each mosaic, statistical tests and visual observations of possible relationships between a species and its habitat can be run and made. Using the findings of Cuvelier *et al.* (2009), relationships with geomorphology and substratum (which impacts porosity and thus fluid flow), as well as microbial mat (a proxy for hydrothermal fluid exit – see Barreyre *et al.*, 2012) were considered. The associations identified following the quantification of fauna at small-scale mosaic sites are shown in Figures 3 to 6. Relationships between species densities at sites are illustrated in Appendix D.

Gastropods may respond to temperature, chemicals, or bacterial mat presence; they may also choose a habitat for protection from predators or competition (Mills *et al.*, 2007). Increased space between individuals or aggregation can imply socially induced patterns (Gage and Tyler, 1991). Statistical tests showed that *Lepetodrilus* sp. and *Pyropelta* sp. are significantly positively correlated and both are positively related to bacterial mat coverage, on which they both rely for grazing.

Nonetheless, on inspection of the contour plots shown in Figures 3 to 6, it seems that *Lepetodrilus* sp. are more closely associated with hard substratum than *Pyropelta* sp., which can thrive on soft and mixed substrata. *Pyropelta* sp. in 'M4' seem to occupy a similar medium temperature niche as the limpets, but the limpets are focused on hard substratum and *Pyropelta* gastropods are found with high levels of microbial mat. Gastropods can move to settle in their preferred temperature niche, suggesting that observed locations relate to environmental conditions at that particular window in time (Mills *et al.*, 2007; Cuvelier *et al.*, 2009). As substrata do not tend to alter rapidly over time (except in the case of slope failure), it is likely that large aggregations of both gastropod types would, based on visual observations, be more associated with a preferred geology than rapid temperature change. Thus, whilst temperature and sulfide levels are linked variables, affecting faunal distribution, Kemp Caldera does not seem to support the hypothesis that temperature is a leading determinant of faunal spread, particularly in vent gastropods (Bates *et al.*, 2005; Podowski *et al.*, 2010). Perhaps, at Kemp Caldera vent field, the *Lepetodrilus* sp. are free to be more selective about substrata (preferring hard surfaces), as Reid *et al.* suggest that E2 and E9 limpets fulfil a 'scavenger' role, using more than one trophic food web pathway and being less limited by biotic factors (Johnson *et al.*, 2008). In fact, the success of *Lepetodrilus* limpets at vent sites is attributed by Kelly and Metaxas (2007) to their multiple feeding modes (grazing, filter feeding and use of chemosynthetic microbial symbionts).

At 'M2' and across the vent field, it would be interesting to examine the difference between large and small gastropods, to discover whether these are adults and juveniles or if size follows a gradient in concordance with distance from active venting. It would then be possible to map large and small gastropods across space, to determine whether age or size impact spatial distribution patterns (e.g. Marcon *et al.*, 2013a). Body size has been found to decrease with distance from active venting in *Lepetodrilus* sp. limpets, so it would be interesting to test at Kemp Caldera whether this seems food, substratum, or temperature driven (Marcus and Tunnicliffe, 2002 in Kelly and Metaxas, 2007). These analyses would require taxonomic identification of *Pyropelta* sp. and *Lepetodrilus* sp. samples and genetic coding, which are in progress for Kemp Caldera faunal groups (e.g. Chen *et al.*, submitted). 'M2' gastropod identification was limited in accuracy, as *Lepetodrilus* sp. and *Pyropelta* sp. were difficult to distinguish, given the interference of shadow introduced by the rougher topography at this site. However, the high similarity of 'M1' and 'M2' sites (Figure 8) is likely attributable to high gastropod densities, dominating the other fauna.

Some anemones will tolerate hydrothermal fluids to ensure that there is high prey availability near enhanced primary productivity (Podowski *et al.*, 2010). Podowski *et al.* (2010) have even suggested that some anemones may have chemoautotrophic symbionts, though this requires further investigation (Podowski *et al.*, 2010). Peripheral anemones are considered non-vent fauna in this project, though this is debated, given the categorisation of actinostolids as 'vent fauna' in Reid *et al.* (2013), following isotopic analyses. Thus, it can be said that Kemp Caldera vent field hosts actinostolids in venting areas like those of 'M2' assemblage and mosaic sites; meanwhile, non-vent, peripheral anemones remain less common, based on observations, and are limited to the periphery.

Actinostolids are associated with hard substrata across all mosaics in which they are present, making any relationships with other fauna likely related to substratum preference. This argued, in 'M2', *Pyropelta* prey are not found in high densities where anemones dominate, suggesting that prey abundance may also influence anemone distribution (Micheli *et al.*, 2002). However, behavioural observations are required to support or negate a predator-prey oriented proposition such as this.

Sponges, despite a similar preference for hard substrata (Figures 3 to 6), do not seem to share a habitat with non-vent anemones in the periphery. This may imply that these anemones need to be near a source of prey (whereas sponges can rely on particulates in the water column, readily available in Kemp Caldera; Micheli *et al.*, 2002). Reid *et al.* (2013) examined sponges and anemones from the E2 periphery, to find that these fauna were partially reliant on epipelagic photosynthesis for primary production. This was not identified at E9, nearer Kemp Caldera, suggesting that sites can vary in the proportional dependence of fauna on photosynthetic and chemosynthetic means of carbon fixation (Reid *et al.*, 2013). This required investigation at Kemp Caldera vent field.

Sericosura pycnogonids analysed by Reid *et al.* (2013) displayed evidence of isotopic mixing between chemosynthetic and photosynthetic primary production modes. This may explain their dominance at 'M1', further from the main study site and located at a slightly shallower depth, perhaps utilising the maximal gastropod abundances and epipelagic food sources for optimal growth and development. The abundance of pycnogonids increasing at a shallower site is supported by the work of Munilla and Soler-Membrives (2007), who identified a decreasing abundance with depth, relating to the proportional abundance of planktonic food at shallower and deeper sites.

Sericosura pycnogonids are positively correlated with both types of gastropod and this is likely a predator-prey interaction, given that the sea spiders are seemingly unaffected by substratum or temperature (though perhaps avoiding the hottest temperatures in 'M3'). The dominance of *Sericosura* spp. over *Colossendeis* sp. appears to be a factor of adaptation. *Colossendeis* sp. are not vent fauna, whereas *Sericosura* spp. are known scavengers, tending to feed on anemones at other vent sites (Desbruyères *et al.*, 2006). *Sericosura* pycnogonids dominate some areas of the Kemp Caldera vent field, which could be related to the high abundances of anemones, though no behavioural observations of feeding were made and the anemones seem rather large for these small pycnogonids to feed upon. In addition, *Sericosura* spp. numbers are particularly high at 'M1', despite absence of anemones. It could be suggested that recorded densities for this taxon are, instead, related to availability of bacterial mat. Alternatively, *Sericosura* spp. may have a predation-oriented relationship with gastropods, which may explain the statistically significant positive correlation found between these taxa. Further behavioural observations would be required to support or negate these hypotheses, perhaps suggesting a need for even more small-scale studies than those completed on the mosaic sites. Instead, ROVs could focus on one area, representative of an assemblage, and film for longer periods, to try and document behavioural interaction. The only viable alternative to this is manipulative experimentation.

The lack of visible pycnogonids near visible vent flow may enable limpets to dominate near vents, where temperatures are too high for the 'scavenger' sea spiders. Gastropod prey species are reduced by larger motile predators, causing a reduction in grazing pressure (Micheli *et al.*, 2002). Thus, an absence of predators able to survive in the extreme conditions near the chimney vent sources enables gastropods to thrive. While bacterial mat remains in areas of high grazing pressure, this is due to increased hydrothermal fluid supplies near vent exits. Meanwhile, larger sessile invertebrates may be negatively impacted by grazers (e.g. limpets), which consume sessile larvae and juveniles (or simply the biofilm on which these young organisms rely for a settlement cue; Micheli *et al.*, 2002). Based on observations at Kemp Caldera, it is likely that bacterial mat is limiting large sessile fauna.

Sponges demonstrate a negative correlation with bacterial mat at 'M1', perhaps also suggesting that this taxon cannot tolerate venting or high toxicity. In areas of high sedimentation, it is expected that filter and suspension feeders (e.g. sponges, reliant on smaller particles) will be selected against (Thatje *et al.*, 2005). Whilst sponges at 'M3' are negatively correlated with tubeworms, it is likely that this is a substratum-induced relationship, as sponges are associated with hard pillow basalts and tubeworms need a soft sediment substratum. Nonetheless, strengthening this negative relationship may be the higher fluid and chemical levels associated with tubeworms, to which sponges appear intolerant. It may be that sponges are actually more intolerant of high temperatures than sulfides, explaining their distribution in 'M3', where their densities are highest when temperatures are lower. Stalked barnacles, whilst randomly distributed, appear to occupy cooler zones, in concordance with seemingly heat intolerant sponges.

Following on from isotopic analyses, Reid *et al.* (2013) highlight the differences in end-member vent fluid chemistry both between and within E2 and E9 vent fields. In comparing the geochemistry of Kemp Caldera, E2 and E9, it is likely to be found that there is an underlying geological or chemical driver, forcing the spatial distribution of fauna.

A substratum link also brings xenophyophores into correlation with vesicomyid clams, as both inhabit soft substrata; at 'M4', this relationship is reversed, but this is likely because clams make any xenophyophores impossible to enumerate and data are being skewed by this factor. Vesicomyid clams are negatively correlated with bacterial mat at 'M4', though this is likely a substratum factor, with mat more detectable on solid, hard substrata, where clams do not tend to survive. Clams and their dead remains are mostly found in high temperature, low microbial mat areas, contrary to their presence near limpets and mat assemblages on the transect scale. Bacterial mat is a distinguishing feature of 'M4', according to factor-based ordination analyses, where bacterial mat coverage is relatively high compared to other mosaics. This is likely indicative of the high levels of sulfides that must be present to support the clam communities at this site (Olu *et al.*, 1996).

Clam siphons must be in contact with a highly permeable sediment layer to absorb sulfides through their foot (Olu *et al.*, 1996). As a result, Olu *et al.* (1996) discovered that clams respond to sediment thickness by positioning themselves shallower or deeper in the sediment. It was concluded that clams respond to both fluid flow variation and sulfide production in their habitat (Olu *et al.*, 1996). These findings appear wholly supported at Kemp Caldera, with live clams positioned relatively shallow in the sediment, perhaps due to a lack of permeability in the ashy basalt sediment type. The location of most live clams near sulfide sources in the near-chimney zone supports the idea that they respond to fluid flow and sulfide supplies.

Siboglinid tubeworms follow a similar density gradient to that exhibited by temperature at 'M3'. It appears that, as found by Cuvelier *et al.* (2009), temperature impacts symbiont-containing fauna to a greater degree than other vent and background fauna. The 'M3' site is perhaps most similar in community composition to that of a seep (Little *et al.*, 2013). The blurred line between vent and seep at Kemp Caldera is evermore smudged by the presence of vesicomyid clams (e.g. at 'M4), which were found to cluster in the Weddell Sea at a seep site established following the collapse of the Larsen B ice shelf (Little *et al.*, 2013). Regardless, the presence of tubeworms at 'M3' site and its associated repeat assemblage is indicative of venting, as, without this, the tubeworms would rapidly die (Van Dover, 2000). This argued, bacterial mat coverage is low, differentiating 'M3' from other mosaic sites, according to factor-based analyses. This may suggests that sulfides are supplied to the siboglinids deeper within the sediment.

In future, if transect analyses were to be carried out to a similar level of detail to the mosaic sites, with enumeration of visible fauna, it may then be possible to conduct nearest neighbour analyses as per Podowski *et al.* (2009; see also Cuvelier *et al.* 2009), to determine whether certain species are always located next to one another. This can provide a first step towards understanding biotic interactions at vent sites.

Findings from the Eastern Lau Spreading Centre (ELSC) suggest that lava characteristics (e.g. porosity) impact vent fluid diffusion, affecting the distribution of anemones, bivalves and zoanthids (Podowski *et al.*, 2010). For example, andesitic lavas contain more silica than basalts, making them more permeable (Podowski *et al.*, 2010). Pillow basalts are more solid, enabling the stabilisation of fauna requiring attachment; meanwhile, andesite permits hydrothermal fluid circulation across larger areas, instead of focusing fluid flow through small cracks and fissures (as per the less permeable basalts; Podowski *et al.*, 2010). Thus, it is possible that anemones prefer more permeable, andesitic substrata towards the vent chimneys and are within a zone where hydrothermal fluid circulates more freely and cools on mixing with ambient water. Meanwhile, sponges are found on pillow basalts, for stability.

High species richness is expected for Antarctic sponges, according to Griffiths (2010). On the other hand, gastropods and bivalves are expected to be lower in terms of richness (Griffiths, 2010). This is difficult to support or negate, given the limitations of image analysis; however, as taxonomic identification is provided for Kemp Caldera biological samples, species richness should be examinable in more detail with confidence.

Kemp Caldera as a Submarine Volcanic Vent Field

Following examination of Kemp Caldera vent field data on broad and small scales, it is possible to compare Kemp Caldera vent field with other volcanic vent sites, to determine whether Kemp Caldera is a unique site, or if caldera environments are, on the whole, different from ridge-hosted vent systems.

Signs of Eruption?

As Kemp Caldera is situated in a volcanic setting, it is natural to ask whether the vent communities appear disturbed by volcanic activity (e.g. see Haymon *et al.*, 1993; Tunnicliffe *et al.*, 1997; Fornari *et al.*, 2012). For a review of volcanic eruptions in the deep sea and their geological and geochemical impacts, see Rubin *et al.* (2012).

Following an eruption, microbial mats are the first colonisers, enabling larvae to settle and vent metazoans to begin to thrive (Lutz *et al.*, 2008; Adams *et al.*, 2012). Nees *et al.* (2008) found that, following an eruption, thick, white microbial mats (such as those observed at T1 and T2) colonise vents, in concordance with lower temperature, diffuse flow. These so-called 'biofilms' are suggested to control larval settlement and metazoan colonization (Lutz *et al.*, 2008; Adams *et al.*, 2012). In accordance with these findings, it could be argued that the 'limpets and mat' assemblages identified in the innermost zone, surrounding active smoker chimneys provide evidence for a recent eruption at Kemp Caldera. This may also explain the nearby 'clamslides', where clams appear to have been moved by mass wasting processes, falling down steep slopes with basalt rubble. Conversely, the presence of active vent sources may be driving the bacterial mat and limpet assemblages nearby, rather than these fauna being established as a result of a volcanic eruption. Perhaps microbial mat and its associated fauna are first to colonise a new vent, as chimneys reactivate at Kemp, providing fuel for vesicomyid clams to survive.

Nonetheless, the succession following eruption is said to progress to tubeworms, as immediate post-eruption fluids tend to be more toxic and hotter than those after several years (Nees *et al.*, 2008). This appears to be reflected in the 'M3' areas (dominated by siboglinid tubeworms) outside of the 'limpet and mat' assemblage and vent source inner zone. It could be argued that eruption and particularly hot fluid is the only way to explain the presence of siboglinid tubeworms in Kemp Caldera, where they are absent at E2 and E9. On closer inspection, though, it is likely that E2 and E9 do not provide a suitable substratum for these tubeworms, whereas Kemp Caldera's soft sediment availability enables a more varied fauna to thrive.

In addition, the post-eruption, scattered mussel communities described by Nees *et al.* (2008) reflect observations of clamshells at Kemp Caldera. These clams may also have been transported down slopes via lava flows or sediment slumps. As a result, clams may also increase in abundance at 'M3' assemblage sites, outcompeting tubeworms when sulfide and heat levels decline over time (as proposed by Nees *et al.*, 2008). This could be investigated following a repeat visit to Kemp Caldera sites, to produce time-series data for the area. Then, it would be interesting to determine whether the siboglinid tubeworms are sourced from a population outside of the Southern Ocean, endemic to soft sediments within the Southern Ocean, or a short-lived post-eruption community from either source.

Alternatively, seep communities are usually comprised of vestimentiferan tubeworms (e.g. *Lamellibrachia*), clams, mytilid mussels, sponges and empty shells (Gage and Tyler, 1991; Olu *et al.*, 1996; Tyler *et al.*, 2003; Little *et al.*, 2013; Marcon *et al.*, 2013c). In fact, at the higher taxonomic level, similarities between seeps and Pacific vents can be drawn, despite differences in diversity and abundance of species (Tyler *et al.*, 2003). Thus, it may not be unreasonable to compare 'M3' and its associated repeated assemblage with a seep-like environment. Marcon *et al.* (2013c) worked on a seep off West Africa and explain that tubeworms reduce the amount of methane and sulfide available at the boundary between sediment and ambient water, enabling non-endemic fauna to compete with chemosynthetic species. At their site, this was evidenced in a loss of mussel populations, following changes to seep flow (Marcon *et al.*, 2013c). They found that tubeworms persist in environments when fluid flow has declined, perhaps explaining the presence of tubeworms where clams are found dead at Kemp Caldera (Marcon *et al.*, 2013c).

The presence of dead *Calyptogena* shells in high densities at Kemp Caldera, too, implies that the site in its observed state is short-lived and changes regularly (Gage and Tyler, 1991). The low diversity of other species in clam assemblages, in addition to dead clam presence, suggests that hydrothermal fluids are irregularly vented in some areas (Olu *et al.*, 1996). As *Calyptogena* shells only take around 15 to 25 years to dissolve, dead shells imply a recent change in hydrothermal fluid exit location and clusters of dead shells may be useful for mapping past active vent sites (Lutz and Kennish, 1993).

Feeding and dying in a deep-sea caldera…

German *et al.* (2000) propose that shallower environments, like Kemp Caldera, may have increased predation pressure, due to the greater numbers of ambient fauna able to tolerate life a in shallower, less hostile environment. Kemp Caldera is not sufficiently shallow for all Antarctic fauna to access, but *Nematocarcinus* shrimp and ophiuroids can comprise vent 'halo fauna' because they can survive in deeper waters and the area is likely high in productivity.

Due to the variable nature of abiotic factors in deep-sea hydrothermal vents, it is often assumed that these are more important controls on community structure than biotic factors (Micheli *et al.*, 2002). Nevertheless, it would be naïve to assume that food supply plays no role in vent community structure (Micheli *et al.*, 2002). For example, Sokolova *et al.* (1994) observed high levels of consumption of dead euphausiids in the Scotia Sea and Weddell Sea, where the eyes of dead bodies formed a steady food supply for ophiuroids. The ophiuroids observed at Kemp Caldera have been described in work by Boschen *et al.* (2013), who identify *Ophiolimna antarctica* spread across basalts at 1546 m depth. They were deemed high density as a result of a lack of other Antarctic predators in such low temperatures; however, they are fewer in number than observed at other vent sites across the globe (Boschen *et al.*, 2013). Dead euphausiids and other midwater crustaceans may support these ophiuroids by means of 'dead body rain'; though, given their shared habitat with deposit-feeding *Nematocarcinus* shrimp, it is likely that these ophiuroids predominantly deposit feed (Boschen *et al.*, 2013). The iron-rich Kemp Caldera vent field is likely highly productive, providing for these peripheral taxa.

Nematocarcinus lanceopes is a Southern Ocean deep-sea shrimp found from continental slope depths to 4,000 m (Dambach *et al.*, 2013). Despite the highly adaptable nature of the ophiuroids (tolerant of mixed substrata, with three development modes and a range of feeding patterns – Boschen *et al.*, 2013), they appear to occupy a specific area to the west of the study site. The idea of a midwater crustacean food fall cannot be discounted, as the presence of a mix of crustacean species in video observations suggests that they do enter Kemp Caldera. However, perhaps the combination of more orange-coloured sediment and presence of various deposit feeders in the periphery implies that the area near the sub-cone, as with fertile land near terrestrial volcanoes, is particularly rich in organic material and thus a productive area. This idea is supported by the presence of holothurians in the peripheral zone, as this deposit-feeding taxon is indicative of an increased food supply (Jamieson *et al.*, 2010).

Nonetheless, crustaceans observed in Kemp Caldera also accidentally enter the venting zone, ranging in behaviour from an active state (swimming), to a stationary, comatosed one (with a shadow beneath in video footage), to dead (lying on their side or broken in video footage). Wishner (2005) attribute hydrogen sulfide to toxicity, perhaps explaining the presence of dead shrimp nearest sulfide chimneys. Meanwhile, where shrimp are stationary but live, this may be linked to high levels of carbon dioxide (Wishner *et al.*, 2005). It could be argued that, as clams require CO_2 to survive, their live presence concurrent with that of dead or comatosed shrimp supports this proposition; realistically, further chemical tests are required.

High nutrient levels in Antarctic waters may drive high abundances of crustaceans, increasing the likelihood of accidental entry to a deepwater hydrothermal system (Griffiths, 2010). The high oxygen levels of Antarctic bottom water may provide a false sense of security for these crustaceans, which are already adapted to the cold ambient water temperatures (Griffiths, 2010). Another explanation is a physical oceanographic driver impacting on surface biology. The Antarctic system is iron limited, so phytoplankton blooms (a food source for crustaceans) are known to concentrate near iron sources like islands and other landmasses (Griffiths, 2010). Perhaps Kemp Caldera's shallow rim and iron richness drives a biologically rich surface water, which, in turn increases crustacean numbers and augments the likelihood of accidental encounter with hydrothermal vents below. This hypothesis is potentially supported by work on the geochemistry of Kemp Caldera by Hawkes *et al.* (submitted).

The patchiness of dead shrimp accumulations may be driven by other physical oceanographic features, such as small-scale bottom currents impacted by the complex topography of the caldera (e.g. Kim and Hammerstrom, 2012). This would require further investigation and is beyond the scope of this study. Another factor worthy of future investigation is the time taken for crustaceans to decompose at around 1400 m depths, which could be recreated in a laboratory using the remains of fauna used in other studies. In doing this, it would be possible to see if Kemp Caldera and similar sites are a sink for midwater crustaceans, as Wishner *et al.* (2005) and Staudigel *et al.* (2006) have suggested, and to investigate whether the dead creatures observed in video footage are low in number, as they comprise accumulations that have been building over years; or, alternatively, if the dead fauna seen last for a week, implying high levels of predation or fast decomposition at the site.

Cephalopods have been excluded from discussion regarding death in the Kemp Caldera 'trap', not due to lack of observation, but due to the likelihood that they only ventured beyond their depth as attracted to ROV *Isis*' lights (Copley and Marsh, per.comm.).

Wishner *et al.* (2005) could not say whether midwater crustaceans observed in Kick'em Jenny were accidental entrants to the system or opportunistic vent fauna. However, based on observations at Kemp Caldera, both suggestions are plausible. For instance, *Nematocarcinus* shrimp were observed to opportunistically occupy and thrive in the shallower periphery, whilst they may also accidentally stray too far into the vent zone, where at Kemp Caldera they were observed either comatosed or dead.

How does Kemp Caldera compare with other calderas?

In addition to the aforementioned similarities to the findings of Wishner *et al.* (2005), who studied the Kick'em Jenny seamount in the Caribbean, Kemp Caldera can also be compared with Vailulu'u seamount, studied by Staudigel *et al.* (2006). Staudigel *et al.* (2006) identified similar peripheral habitat types to those seen at Kemp Caldera, with octocorals, sponges and echinoderms (including ophiuroids) found near the peak of the seamount, where filter feeders were put at an advantage, due to strong currents, and predator and scavenger species were deemed more common. Despite the similarities in faunal composition, this habitat type was found outside the crater of Vailulu'u seamount. At the summit, iron oxide mats at Vailulu'u and Kick'em Jenny reflect the thick bacterial mats and flocculated sediments established in the Kemp Caldera vent field (Staudigel *et al.*, 2006).

Contrastingly, dead zones in Vailulu'u were located in an acidic 'moat' environment; in Kemp Caldera, dead zones were patchy, relating to proximal venting. Staudigel *et al.* (2006) suggest that fish and crustaceans enter Vailulu'u at the crater walls, where stalked sponges are found. At Kemp

Caldera, the pattern might not be so uniform. As the whole site is relatively shallow for the deep sea, fish and crustaceans may enter across the site, not limited by a steep seamount obstruction. Their survival thereafter will likely be determined by their tolerances toward temperature, chemicals and other biotic factors. The differences between Vailulu'u and Kemp Caldera are likely influenced by a suite of factors, including: physical oceanography, as Kemp Caldera is a large bowl, whereas Vailulu'u currents are shaped around a seamount; temperature, as Kemp Caldera's ambient water temperature excludes physiologically-limited fauna; and geomorphology, as Kemp Caldera hosts a varied topography and geology, ranging from soft, ashy sediments to pillow basalts and andesitic rocks.

Kemp Caldera shares near-identical peripheral faunal groups with Kick'em Jenny, according to descriptions of echinoderms, holothurians and fish in Wishner *et al.* (2005). However, unlike at Kick'em Jenny, where these fauna occupy inactive craters outside the venting one, Kemp Caldera hosts these creatures proximal to active vent sources. This may be due to the presence of the sub-cone to the western edge of the peripheral zone, as the influence of localized currents on peripheral, filter-feeding fauna has been previously emphasised (see Wishner *et al.*, 2005).

Kemp Caldera is distinctly different from both the Kick'em Jenny and Vailulu'u seamounts as the latter both suffer low species richness, naming only three dominant fauna at each location (Wishner *et al.*, 2005; Staudigel *et al.*, 2006). This may be related to the acidic nature of these sites (mentioned in Staudigel *et al.*, 2006), as was identified at the venting Kolumbo submarine volcano in Greece (Carey *et al.*, 2013). This recent work identified a buildup of CO_2 in the Kolumbo crater, creating acidic conditions, intolerable for even vent-endemic macrofauna (Carey *et al.*, 2013). Wishner *et al.* (2005) suggest that low species richness may result from a lack of suitable habitat or regularity of disturbance, the former of which may be more likely given the plethora of fauna supported in the volcanically disturbed Kemp Caldera. This may be an indication that, on investigating more caldera environments, each may have unique attributes and endemic fauna, linked to geochemical and geological difference, in addition to variations in nearby larval pools (affecting communities comprising taxa similar to nearby ridge-hosted vents). This is not necessarily surprising, given the distinctive nature of volcanic geomorphology, altered by each eruption; introducing marine variables such as currents, depth, and nutrient levels enables more variation to be expected from any volcano-associated fauna.

The two aforementioned studies (Wishner *et al.*, 2005; Staudigel *et al.*, 2006) form the only other major ecological studies of submarine calderas, as most submarine volcano studies tend to focus on geochemistry and geodynamics (e.g. Kilias *et al.*, 2013). This emphasises the need for further exploration of caldera environments, should more exist. The differences identified between Kemp

Caldera and these other sites imply that each caldera may be unique. A potentially useful test of this would be examination of ridge-hosted vent sites near Kick'em Jenny (e.g. Cayman vents – Connelly *et al.*, 2012) and Vailulu'u, in addition to any nearby venting calderas (e.g. likely venting calderas in the Caribbean island arc, near Kick'em Jenny).

In conclusion, it seems that Kemp Caldera differs from shallower, equatorial calderas, as these seem to host fewer species (Jeng *et al.*, 2004; Wishner *et al.*, 2005). However, similarities can mostly be drawn in the dead crustacean falls, supplied from shallower waters. Even in a shallow, tidally impacted crater off Kueishan, *Xenograpsus* crabs were observed to swarm out from their sulfidic crevices to feed on zooplankton 'rain', so it is likely this is a common feature of caldera sites (Jeng *et al.*, 2004). Many caldera studies focus on the geochemistry or microbiology of the submarine volcanic environment (Kilias *et al.*, 2013; Stott *et al.*, 2008). Though, as caldera chemistry has been identified as unusual at many sites, impacting microbial community composition, it is likely that calderas across the world have unique faunal assemblages, shaped by these abiotic and biotic factors (Stott *et al.*, 2008).

V. CONCLUSION

This project aimed to investigate how faunal assemblages of Kemp Caldera vent field compare with those of Southern Ocean ridge-hosted vents, like E2 and E9, and other calderas.

In constructing high-resolution, small-scale photomosaics for enumeration of fauna and conducting standard image analysis techniques on larger-scale transect lines to create an interpreted zonation for an area of Kemp Caldera, this project has met its aims. Communities have been described at a range of scales, ROV footage has been used to define spatial distribution patterns and define faunal assemblages, and statistical techniques have been employed to quantify patterns in species composition and abundance. None of these goals could have been achieved without the use of ROV imagery, ArcGIS and photomosaicing tools, as outlined in Marsh *et al.* (2013).

On completion of this project, it is possible to support the hypothesis that dead remains of crustaceans are found trapped in caldera environments, forming a food source for background, peripheral fauna. Kemp Caldera has been shown to differ from other Antarctic vent sites, according to presence/absence data, faunal microdistribution patterns, environmental factors of influence and zonation. In addition, the site hosts vesicomyid clams, endemic to the caldera and yet to be formally described, to determine any genetic relationships with (likely *Calyptogena* sp.) clams from other vent sites around the world.

In conclusion, in characterising the spatial distribution of fauna at Kemp Caldera for the first time, it is important to highlight a need for future research into other caldera environments near hydrothermal vent sites. In investigating: the number of such sites; the similarities and differences between them and their neighbouring chimney and ridge vent sites; and the importance of these sites as points of interaction between midwater and deep-water, vent-adapted species, it is hoped that these "subprovinces" will improve our understanding of the complexity of vent biogeography and the variety of chemosynthetic environments around the globe.

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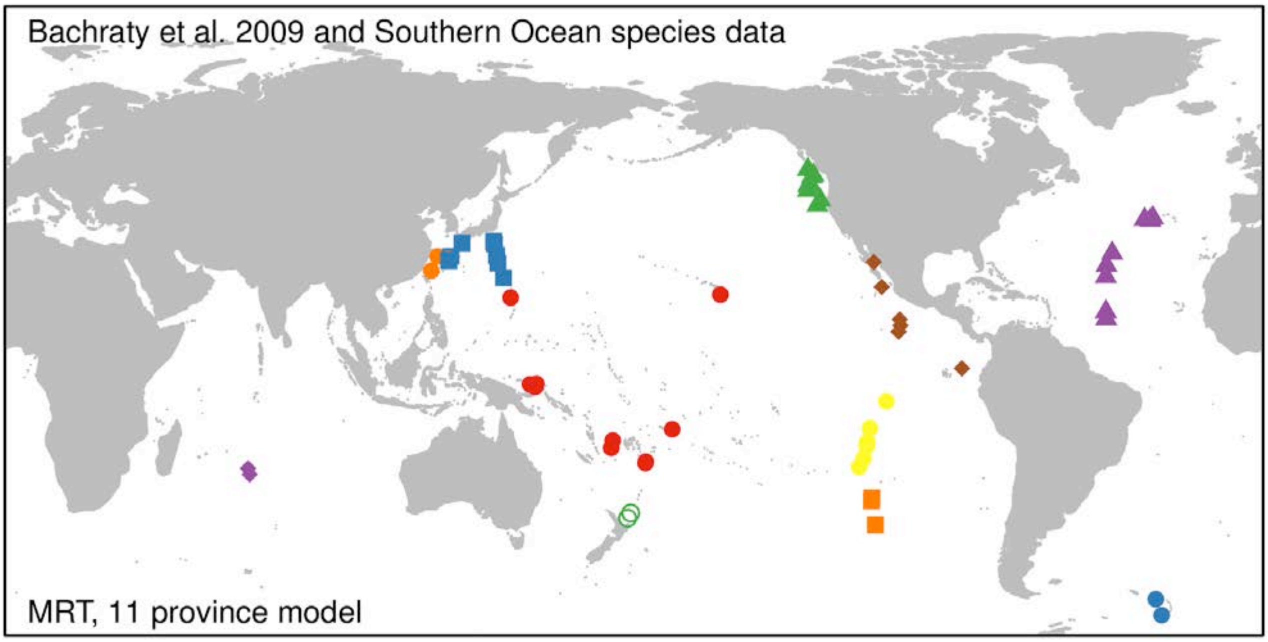
APPENDIX A: Vent Biogeography

Vent biogeography is the identification of patterns and drivers in present-day species distributions across the globe (Tunnicliffe *et al.*, 1991, 1998; Bachraty *et al.*, 2009). Since the first vent discovery in 1977 on the Galapagos Spreading Centre, numerous hydrothermal vent sites have been discovered and studied across ranging tectonic settings (e.g. mid-ocean ridges, back-arc basins and volcanic arcs; Bachraty *et al.*, 2009). Geological and hydrological barriers impact larval dispersal, isolating some vent faunas and seeing the development of separate provinces, occupied by different species filling the same niche as others in different geographic locations (Bachraty *et al.*, 2009). One of the most recent proposals for vent biogeographic provinces involved 6 major provinces in the world ocean, put forward by Bachraty and colleagues (2009; see also Moalic *et al.*, 2012). Nonetheless, as these researchers explain, the exclusion of Antarctic sites is likely to see revision of these provinces in the near future (Bachraty *et al.*, 2009).

Figure A1 – Map from Rogers *et al*. (2012, p.11) delineating the 'results of geographically constrained clustering using multivariate regression trees'.
This map depicts the 11-province model considered by Rogers *et al.* (2012) to be the optimal one following multiple cross-validations. Provinces are said to include: (1) Mid-Atlantic Ridge, (2) East Scotia Ridge, (3) northern East Pacific Rise (EPR), (4) central EPR, (5) southern EPR, (6) south of the Easter Microplate, (7-10) western Pacific provinces, and (11) Indian Ocean.



APPENDIX B: Data Acquisition & Processing

Figures B1 to B3 have been included in Appendix B to support the Materials and Methods presented in this project, by illustrating the photomosaicing, faunal abundance quantification and temperature data acquisition processes. Table B1 is provided to support Figures 3 to 6, as anisotropy adjustments were applied to ensure that all 'real' data were incorporated into the kriging interpolation process when gridding the contours presented.

Figure B1 – Figure from Marsh *et al.* (2013, p.6) depicting a 'simplified representation of […] image acquisition' and processing, as carried out in this project for the Kemp Caldera vent field mosaic sites.

(A) Image sequence used to generate photomosaic (resolution: 960 x 540 px), produced by exporting image stills from HD video footage using Quicktime Pro (Version 7.6.6.).

(B) A section of the full 'Carwash' edifice photomosaic, created by mosaicing and merging the image sequence in **(A)** using Adobe Photoshop CS5 extended (version 12.0 x 64).

(C) Complete vertical photomosaic of 'Carwash' edifice (E9 vent field), with a scale bar representing 1 m.

(D) Image used to depict the level of detail presented in raw images (pre-mosaicing), permitting identification of *Lepetodrilus* limpets. The scale bar equates to 0.1 m.

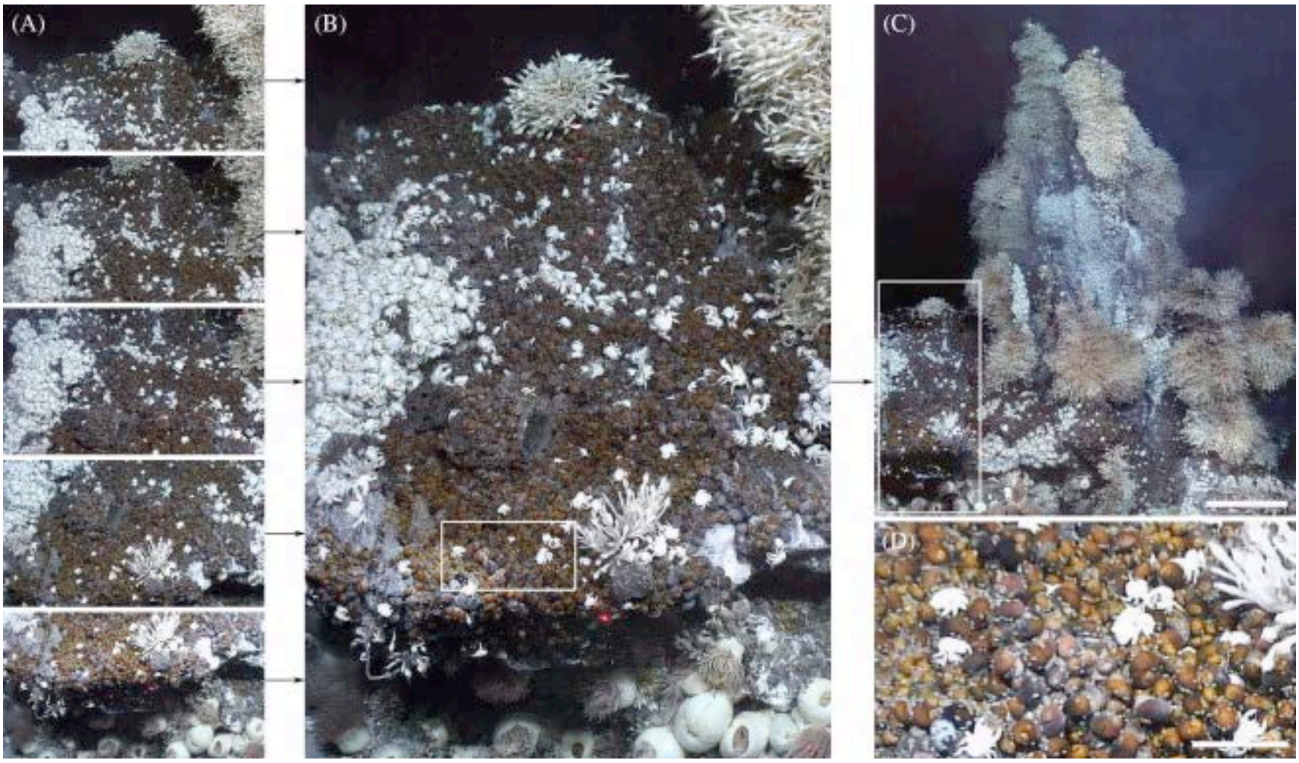


Figure B2 – Temperature data from mosaics 'M1' to 'M4', collected using ROV *Isis* CTD (Dive 148, Cast 25, JC042) and mapped using ArcGIS software (ESRI, CA).

(A) to **(D)** represent survey lines and temperature data for 'M1' to 'M4', respectively.

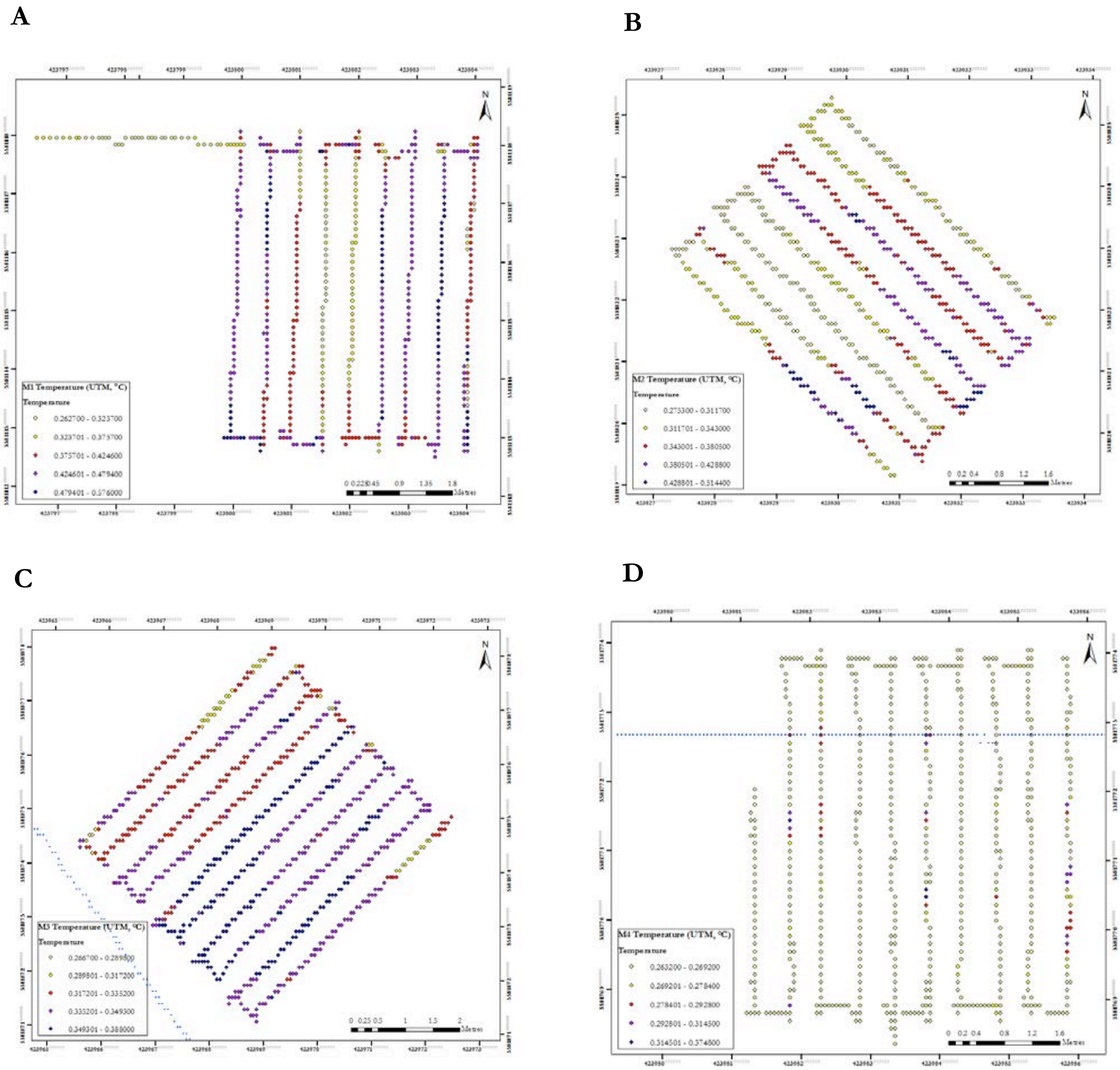


Table B1 – Table of search radii / anisotropy adjustments applied to grid contour plots using kriging, illustrated in Figures 4-7.

Mosaic	Radius 1	Radius 2	Angle (°)
M1	10000 / 10	5000 / 5	0
M2	8160	4080	45
M3	4540	2270	-45
M4	4580	2290	0

Figure B3 – Images taken from high-resolution video footage captured by ROV *Isis* during Dive 148 of research cruise JC042 at Kemp Caldera vent field.
Scale bars equate to 0.1 m but may be subject to marginal error introduced by uneven topography.
(A) Image taken from 'M2', depicting the counting process, whereby blue numbers are *Pyropelta* gastropod counts and pink numbers are counts of anemones.
(B) Image taken from 'M2' demonstrating how overlap between frames was accounted for and double counting avoided. Turquoise lines are guide lines used to mark out count areas for measurement (to enable calculation of density per square metre). Blue numbers, again, represent *Pyropelta* gastropod counts and beige a stalked barnacle.

Anemones have not been counted in this frame as another double count precaution. This taxon was only counted when its column-like body was visible.
(C) Image taken from 'M1' to illustrate how the high resolution of video recorded using the downward-looking camera enabled counts of *Lepetodrilus* limpets, *Pyropelta* gastropods and *Sericosura* pycnogonids to be made.
(D) Image taken from 'M1' to illustrate how bacterial mat and high gastropod abundance rendered some frames uncountable. Gastropods from these frames were assigned a minimal density value, based on the highest countable density from all other 'M1' frames.

See Overleaf

Figure B4 – Simplified, schematic representations of the mosaic sites within Kemp Caldera vent field, areas occupied by dominant visible fauna, and motile fauna observations.
(A) Simplified representation of the 'M1' site. The following colours correspond to the following groups: pink – pycnogonids and limpets; black – basalt; cream – sparse fauna; light blue – limpets; light green – basalt and bacterial mat; maroon – limpets and bacterial mat; dark blue – high densities of gastropods; light grey – oxidized sediment; medium grey – gravels and oxidized sediment; dark grey – gravelly basalt; red – pycnogonids dominant; medium blue – medium density gastropods.
(B) Simplified representation of the 'M2' site. Light grey represents bacterial mat, beige is soft sediment, dark grey is lower level basalt (beneath the ledge) and black is the upper ledge. Meanwhile, maroon represents areas of rubbly, rough topography.
© Simplified representation of the 'M3' site. The following colours represent the assigned groups: blue – basalt and sponges; black – basalt; purple – basalt with anemones; grey – spread basalt with sediment between; orange – mixed fauna on soft substrate; gradient colour – tubeworms in soft sediment, with the gradient corresponding to a species density gradient.
(D) Simplified representation of the 'M4' site. The following colours represent the assigned groups: red – small mixed basalt community (anemones and gastropods); yellow – soft sediment with dead clams; orange – basalt with sponges; black – basalt; grey – small mixed basalt rocks; dark grey – bacterial mat; green – live clams; cream – soft sediment and xenophyophores; light green – mixed assemblage (siphons, clam shells and pycnogonids); and brown – soft sediment with sparse fauna.
For **(A)** to **(D)**, 'A' = anemone; 'S' = shrimp; 'Sd' = dead shrimp; 'Sq' = squid; B = stalked barnacle and P = pycnogonid.
NB: The orientation of these representations is opposite of that presented in Figures 3 to 6. It is directly comparable with Figures 3 to 6 upon flipping upside down.

See Overleaf

Figure B3

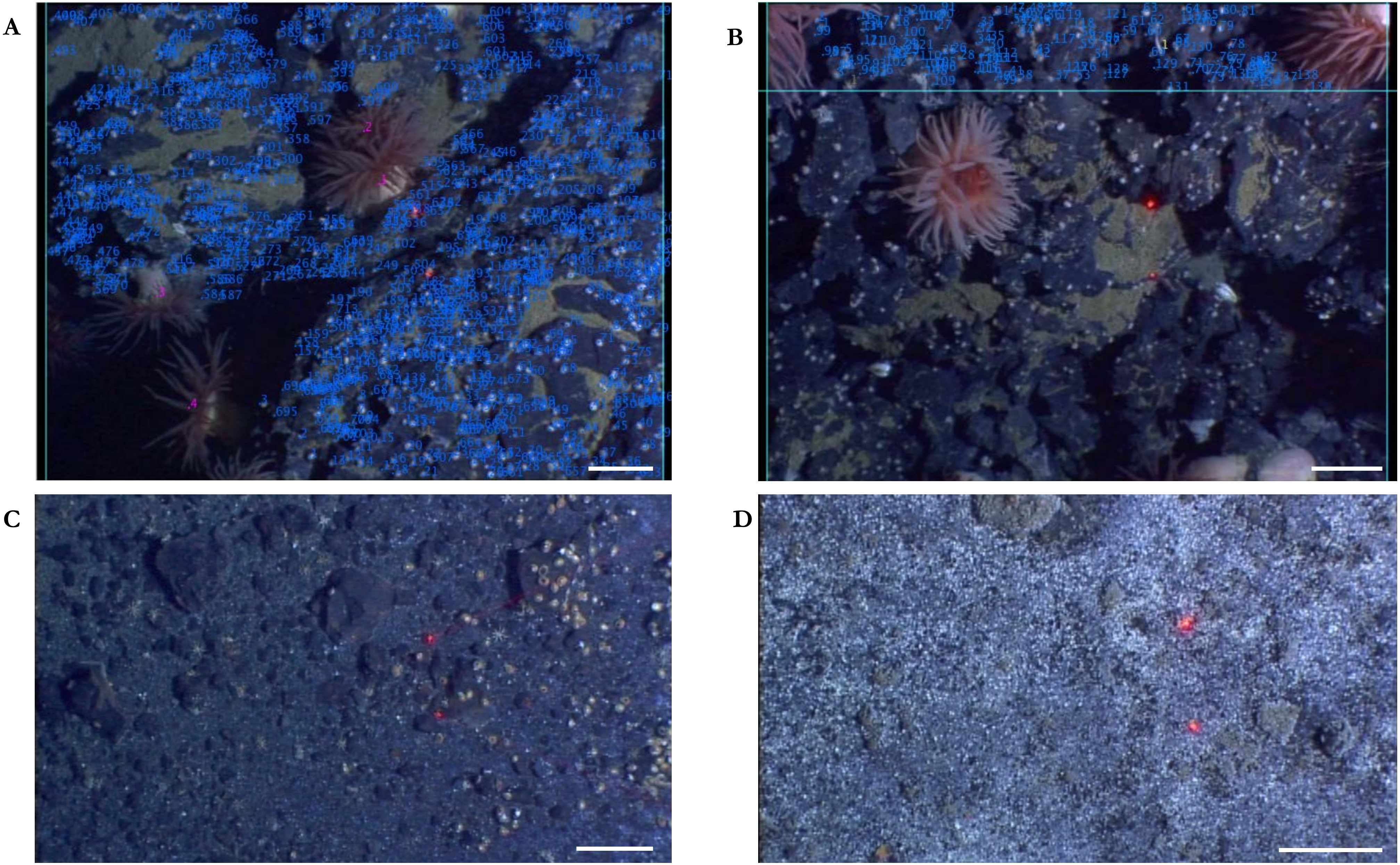


Figure B4 - A

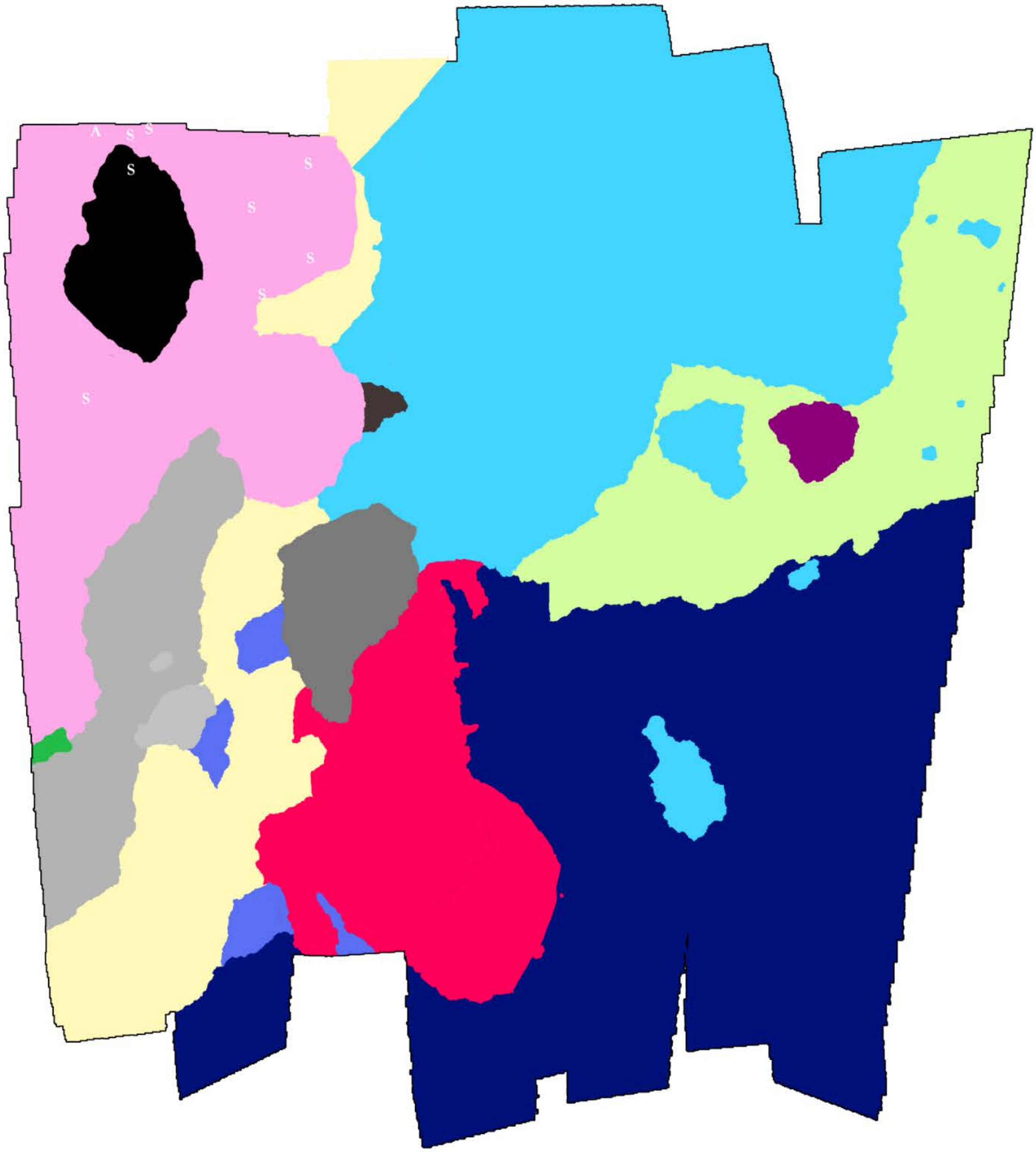


Figure B4 - B

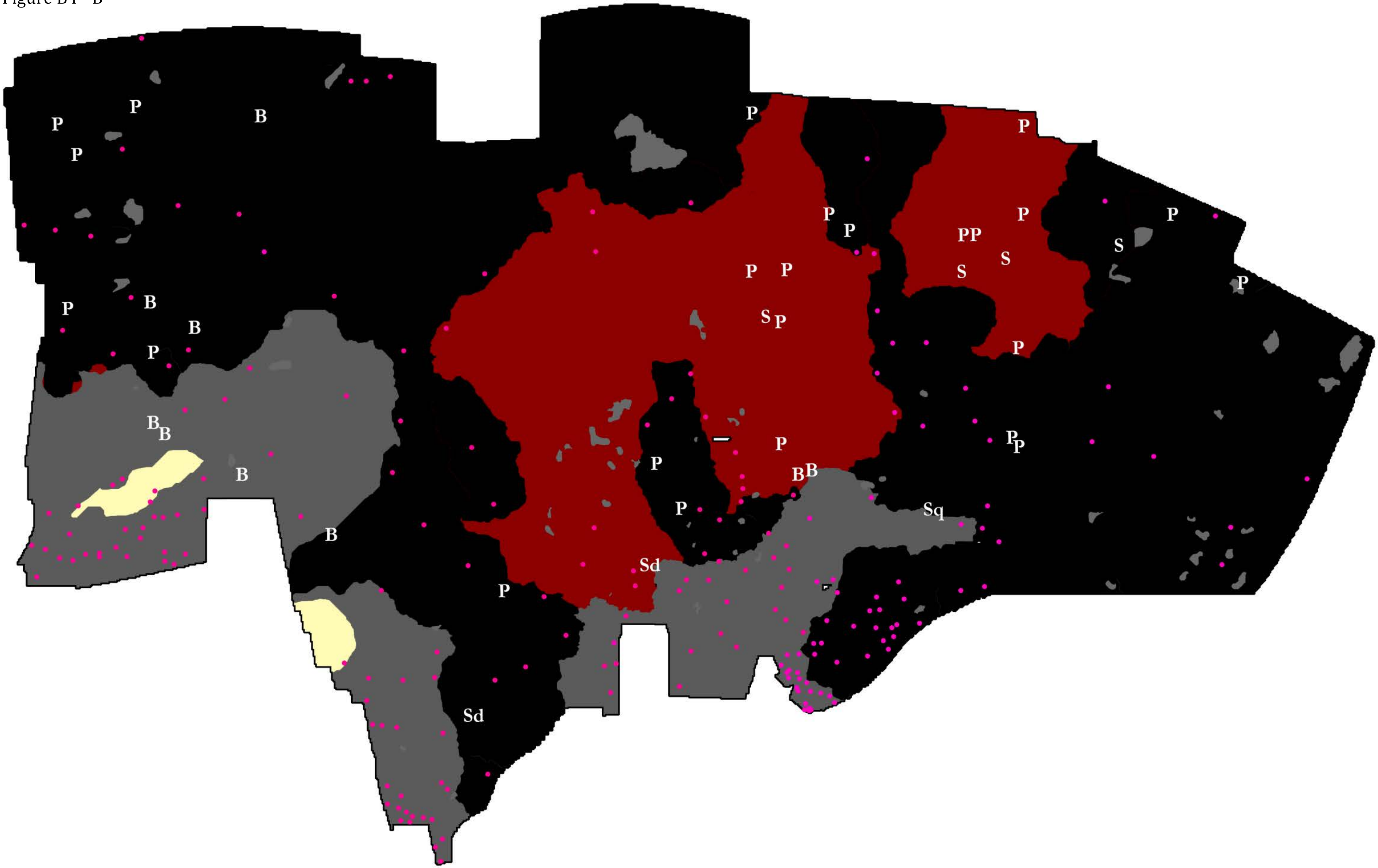


Figure B4 - C

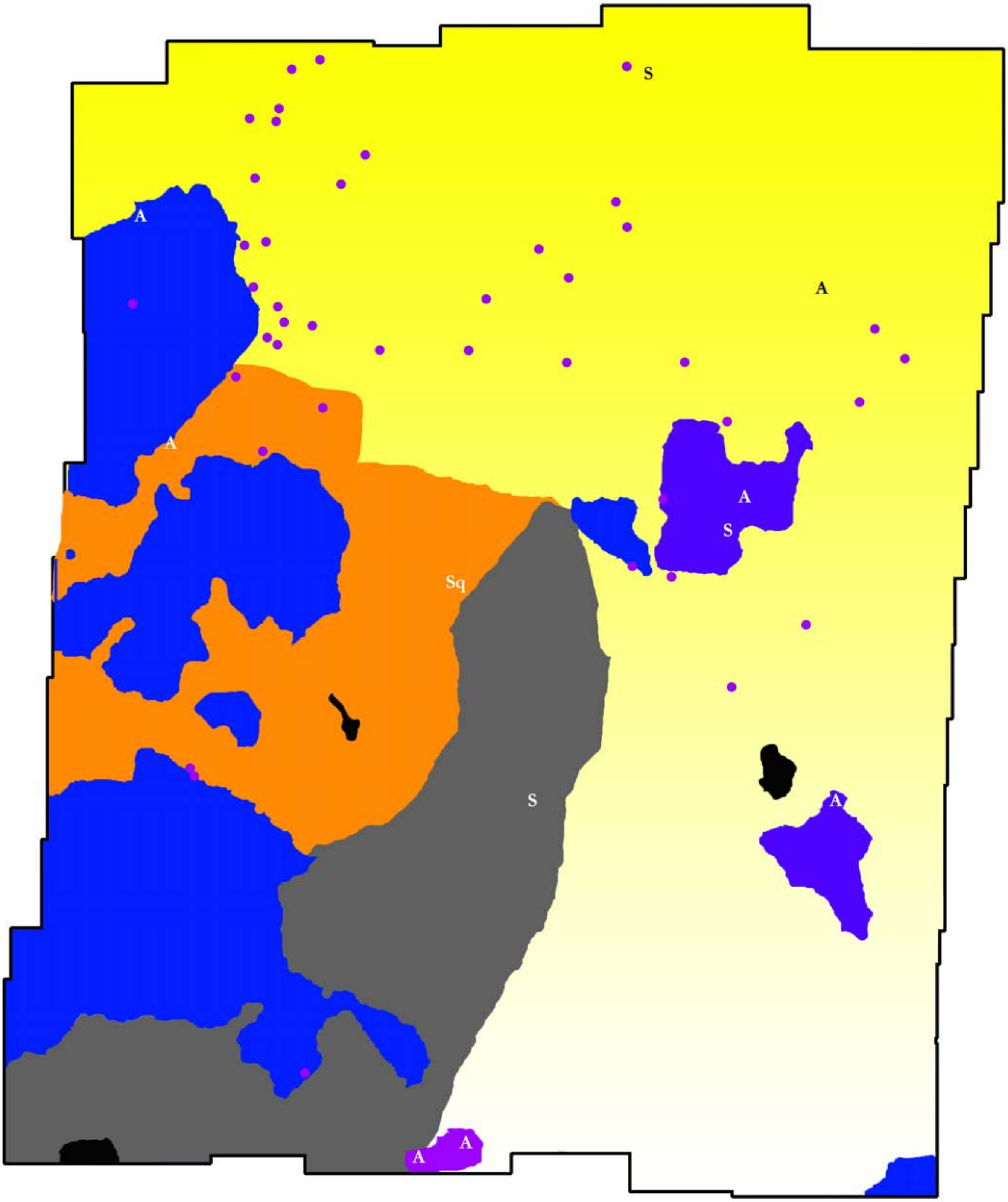
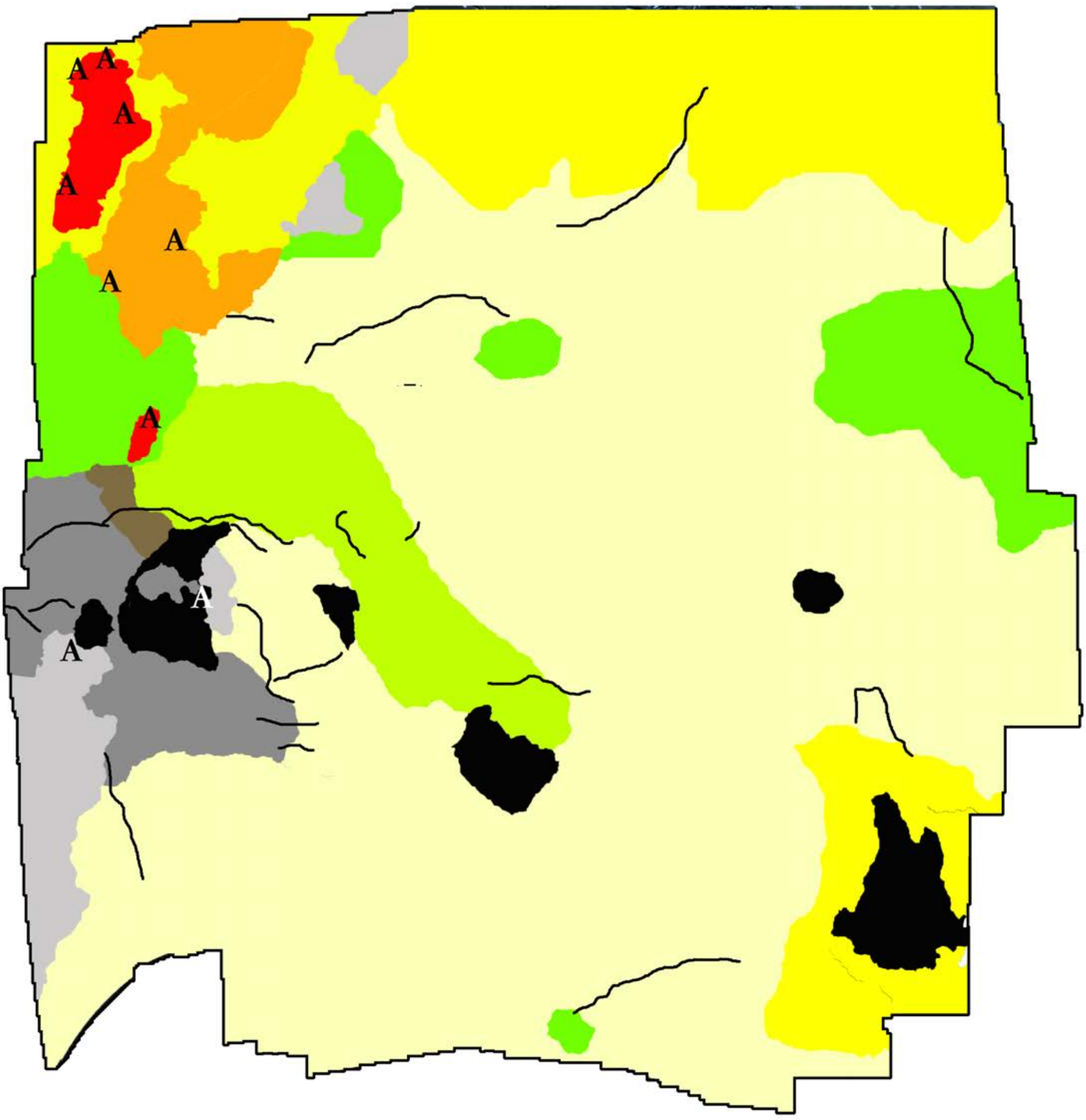


Figure B4 - D



APPENDIX C: Transect Assemblages, Zonation and Slope Analysis

Figure C1 is used to illustrate the smaller-scale changes identified in community composition using ROV *Isis* video footage. This information is useful when examining spatial distribution or zonation along a transect, but large-scale patterns like those represented by Figure 7 are more important when trying to understand the ecology of a vent field across a larger scale. Whilst community composition is, as illustrated in C1 and mosaic data, more complex than Figure 7 might suggest, Figure 7 can be used to compare broader scale zonation patterns at Kemp Caldera vent field with those identified at the ESR E2 and E9 vent fields.

Figure C1 – Transect lines T1 to T6, completed in Kemp Caldera vent field (South Sandwich Islands) using ROV *Isis* (Dive 148, JC042), with assemblages mapped across each line and representative frames for each assemblage.
These assemblages are more specific than those presented across the vent site in Figure 7 because they represent change across smaller spatial scales, inappropriate for broader-scale mapping and interpretation of zonation (as presented in Figure 7). The assemblages depicted in **(A)** to **(F)** were defined according to dominant visible fauna, as observed in ROV *Isis* videographic surveys.
Transects are depicted as follows: **(A) -** 'T1', **(B) -** 'T2', **(C) -** 'T3', **(D) -** 'T4', **(E) -** 'T5', and **(F) -** 'T6'.
Plots of presence/absence data to support each of the assemblage designations are shown in **(G)** to **(L).**

See Overleaf

Figures C2 and C3 were not included in the main body of this project because the slope and rugosity analyses, whilst highlighting the complexity of the Kemp Caldera vent field terrain, did not identify a potential relationship between slope or surface roughness and faunal assemblages. This is likely due to the high resolution of the bathymetric data containing too much noise and fine-scale detail. Mapping the faunal assemblages in a 3D caldera space using a combination of programmes like Petrel and ArcGIS may make interpretation of any relationships between topographic change and faunal assemblages possible. However, this is likely not a particularly useful exercise, given that slope and roughness are not key drivers of the spatial distribution of vent fauna. Until the small-scale currents of caldera environments are better understood, our comprehension of the impacts of complex geomorphology on vent and deep-sea fauna is limited.

Figure C2 – Map (and associated plots) of the slope of Kemp Caldera vent field (South Sandwich Islands), for comparison with the assemblage and zonation maps presented in Figure 3.

(A) Scatterplot of mean slope compared with faunal and substratum assemblages. Error bars represent ± 2 standard deviations.

(B) Box plot of slope compared with faunal and substratum assemblages, to illustrate variation about the median value and actual slope values, rather than the means presented in **(A)**. Error bars represent ± 2 standard deviations.

(C) Slope map, illustrating changing steepness across the Kemp Caldera vent field. Values of -9999 are given to areas lying outside the area for which 'hillshade' could be mapped in ArcMap (ESRI, CA) with the given bathymetry data. Bathymetric data are unpublished, from the British Antarctic Survey cruise JCR224.

The assemblage numbers given on **(A)** and **(B)** are linked to the following groups: 1 – limpets and mat; 2 – sponges; 3 – 'M2'; 4 – clams; 5 – transition; 6 – peripheral; 7 – complex soft; 8 – 'M3'; 9 – live shrimp; 10 – ophiuroids and live shrimp; 11 – basalt; 12 – dead chimney; 13 – active sulfide chimneys.

See Overleaf

Figure C3 – Map (and associated plots) of the rugosity (topographic roughness) of Kemp Caldera vent field (South Sandwich Islands), for comparison with the assemblage and zonation maps presented in Figure 3.

Rugosity is the standard deviation of slope, calculable following Focal Analysis of a slope map in ArcMap (ESRI, CA).

(A) Scatterplot of mean rugosity compared with faunal and substratum assemblages. Error bars represent ± 2 standard deviations.

(B) Box plot of rugosity compared with faunal and substratum assemblages, to illustrate variation about the median value and actual slope values, rather than the means presented in **(A)**. Error bars represent ± 2 standard deviations.

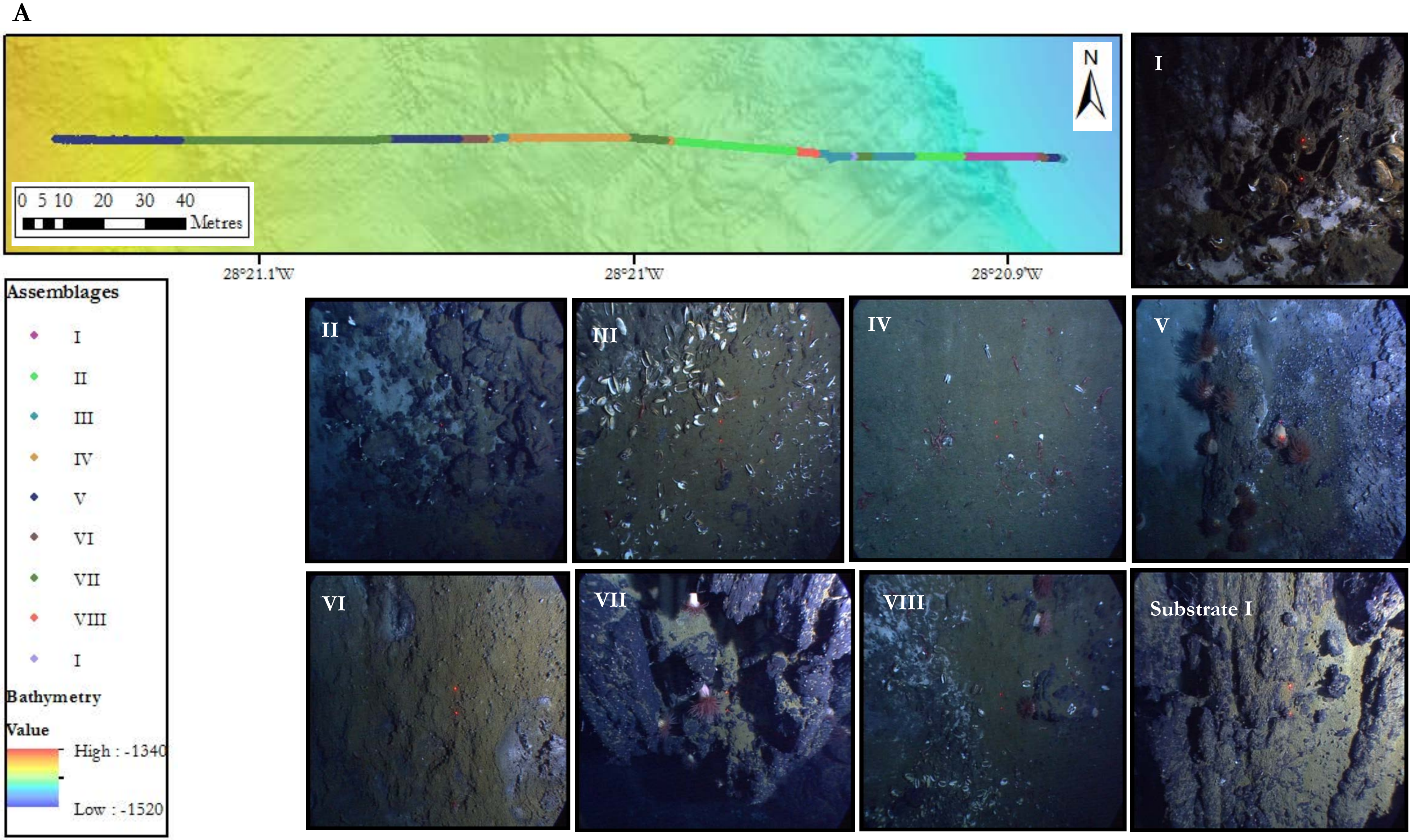
(C) Rugosity map, illustrating changing roughness across the Kemp Caldera vent field. Values of -9999 are given to areas lying outside the area for which 'hillshade' could be mapped in ArcMap (ESRI, CA) with the given bathymetry data. Bathymetric data are unpublished, from the British Antarctic Survey cruise JCR224.

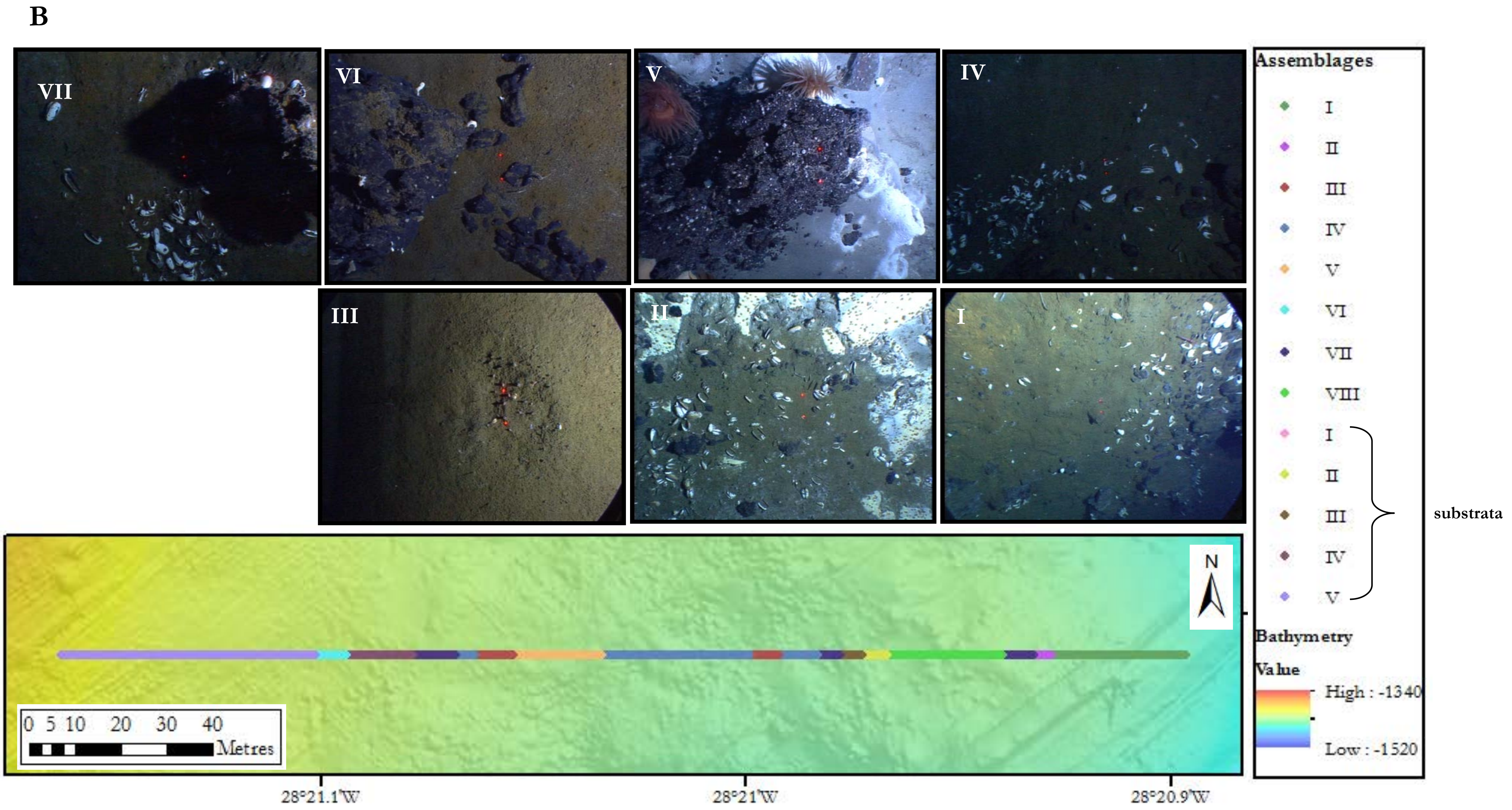
The assemblage numbers given on **(A)** and **(B)** are linked to the following groups: 1 – limpets and mat; 2 – sponges; 3 – 'M2'; 4 – clams; 5 – transition; 6 – peripheral; 7 – complex soft; 8 – 'M3'; 9 – live shrimp; 10 – ophiuroids and live shrimp; 11 – basalt; 12 – dead chimney; 13 – active sulfide chimneys.

See Overleaf

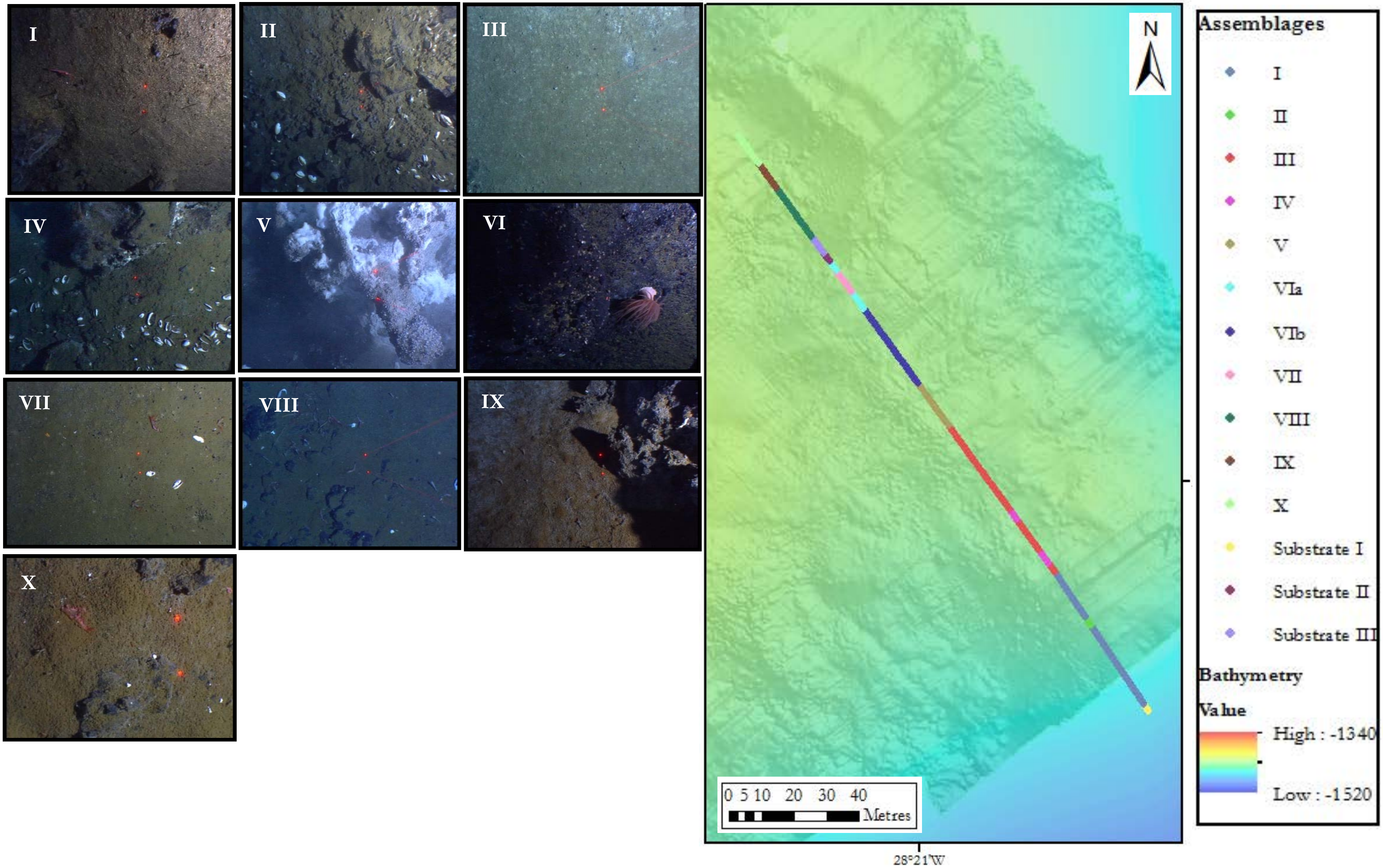
Figure C4 – Figure from Marsh *et al*. (2012, p.16) delineating an idealised zonation for the E9 vent field, applicable in both horizontal and vertical directions.

Figure C1

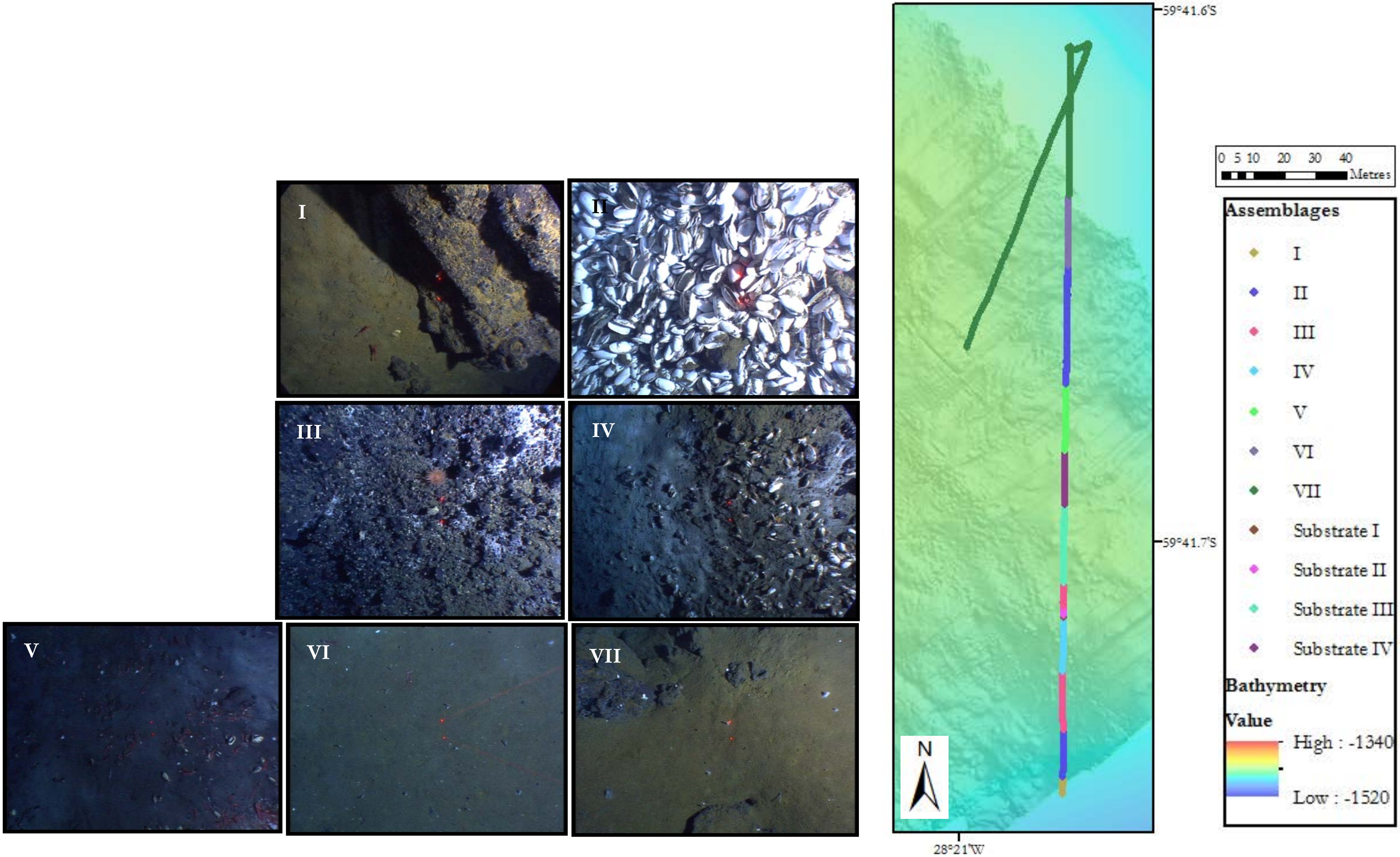

A
N
0 5 10 20 30 40
Metres
28°21.1'W
28°21'W
28°20.9'W
Assemblages
◆ I
◆ II
◆ III
◆ IV
◆ V
◆ VI
◆ VII
◆ VIII
◆ I
Bathymetry
Value
High : -1340
Low : -1520
I
II
III
IV
V
VI
VII
VIII
Substrate I

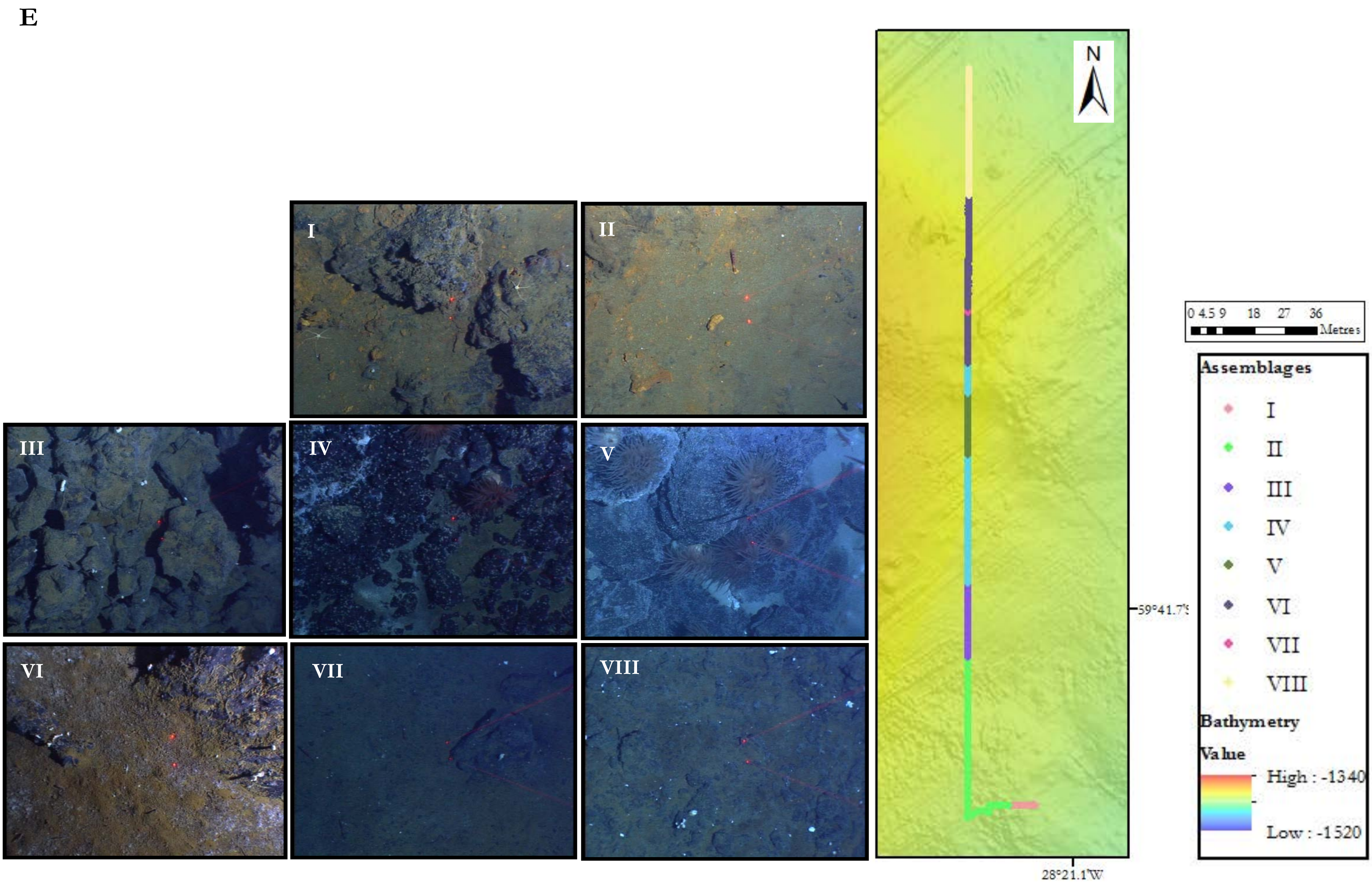

B
VII
VI
V
IV
III
II
I
Assemblages
I
II
III
IV
V
VI
VII
VIII
I
II
III
IV
V
substrata
Bathymetry
Value
High : -1340
Low : -1520
N
0 5 10 20 30 40
Metres
28°21.1'W
28°21'W
28°20.9'W

C


I
II
III
IV
V
VI
VII
VIII
IX
X
N
Assemblages
I
II
III
IV
V
VIa
VIb
VII
VIII
IX
X
Substrate I
Substrate II
Substrate III
Bathymetry
Value
High : -1340
Low : -1520
0 5 10 20 30 40
Metres
28°21'W

D


I
II
III
IV
V
VI
VII
59°41.6'S
59°41.7'S
28°21'W
N
0 5 10 20 30 40
Metres
Assemblages
I
II
III
IV
V
VI
VII
Substrate I
Substrate II
Substrate III
Substrate IV
Bathymetry
Value
High : -1340
Low : -1520


E
I
II
III
IV
V
VI
VII
VIII
N
0 4.5 9 18 27 36
Metres
Assemblages
I
II
III
IV
V
VI
VII
VIII
Bathymetry
Value
High : -1340
Low : -1520
59°41.7'
28°21.1'W

F

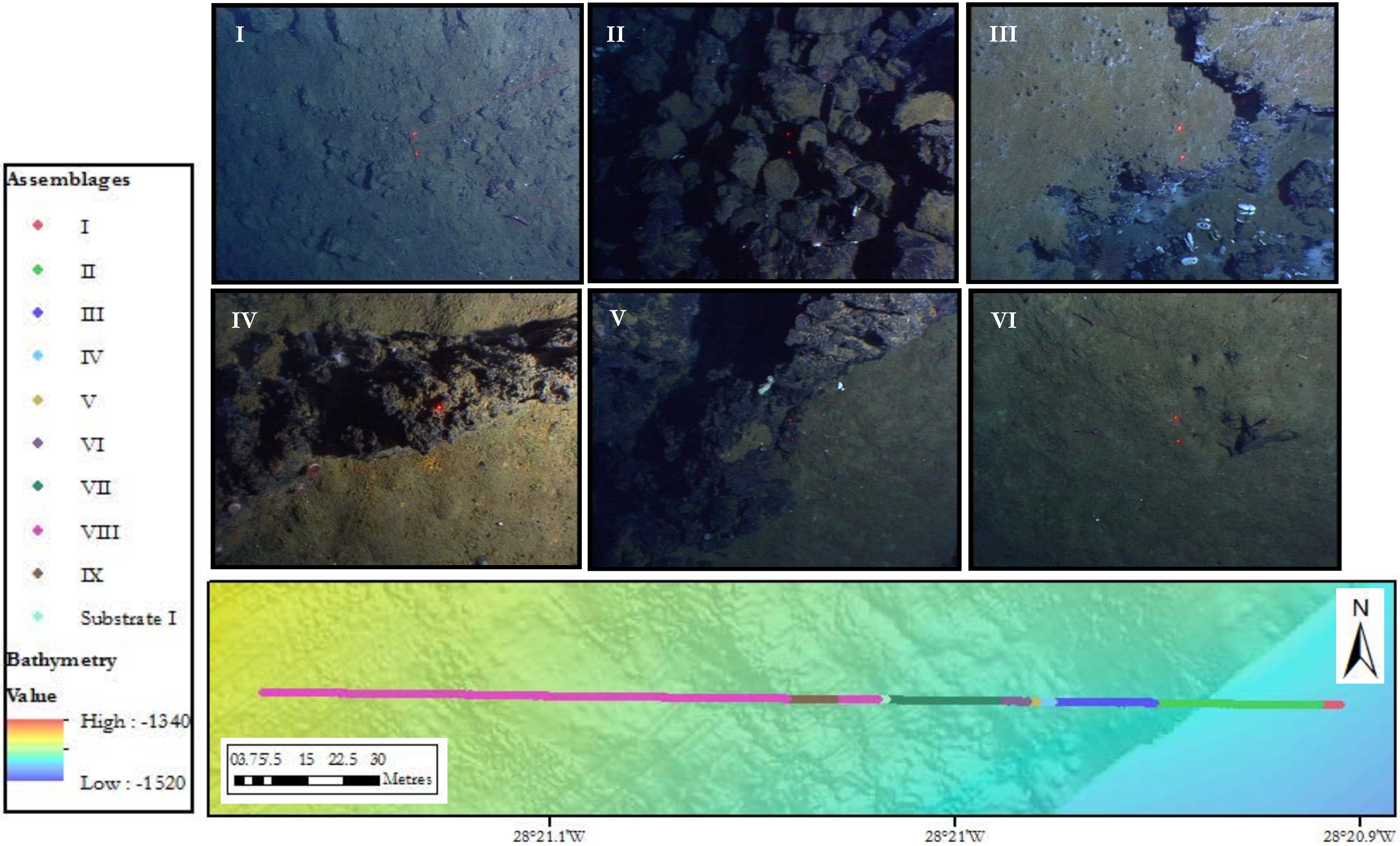

I
II
III
IV
V
VI
Assemblages
I
II
III
IV
V
VI
VII
VIII
IX
Substrate I
Bathymetry
Value
High : -1340
Low : -1520
N
0 3.75 7.5 15 22.5 30
Metres
28°21.1'W
28°21'W
28°20.9'W

Figure C2

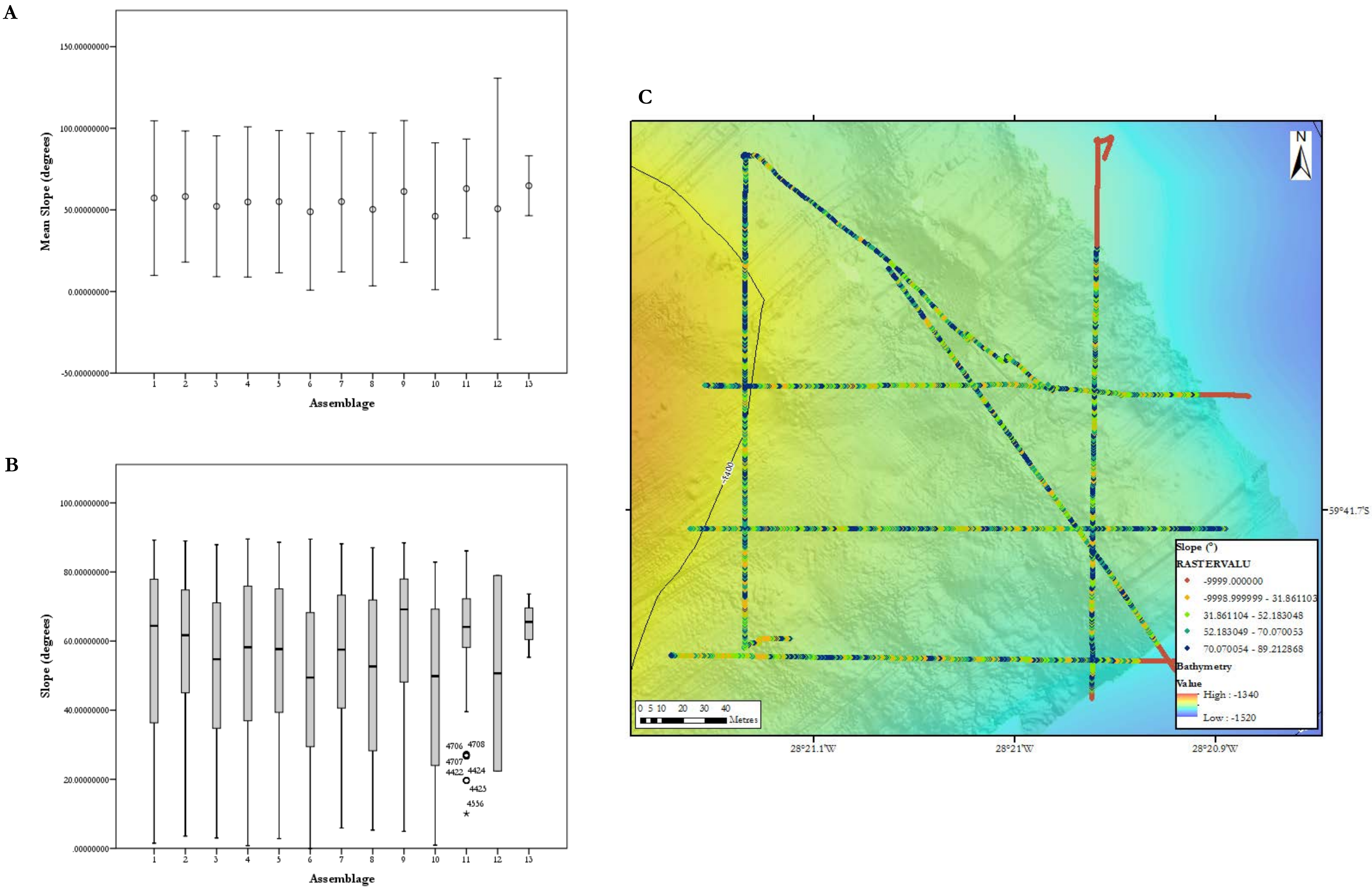

A
150.00000000
100.00000000
50.00000000
0.00000000
-50.00000000
Mean Slope (degrees)
1
2
3
4
5
6
7
8
9
10
11
12
13
Assemblage
B
100.00000000
80.00000000
60.00000000
40.00000000
20.00000000
.00000000
Slope (degrees)
4706
4708
4707
4422
4424
4425
4556
Assemblage
C
N
-1400
59°41.7'S
28°21.1'W
28°21'W
28°20.9'W
0 5 10 20 30 40
Metres
Slope (°)
RASTERVALU
-9999.000000
-9998.999999 - 31.861103
31.861104 - 52.183048
52.183049 - 70.070053
70.070054 - 89.212868
Bathymetry
Value
High : -1340
Low : -1520

Figure C3

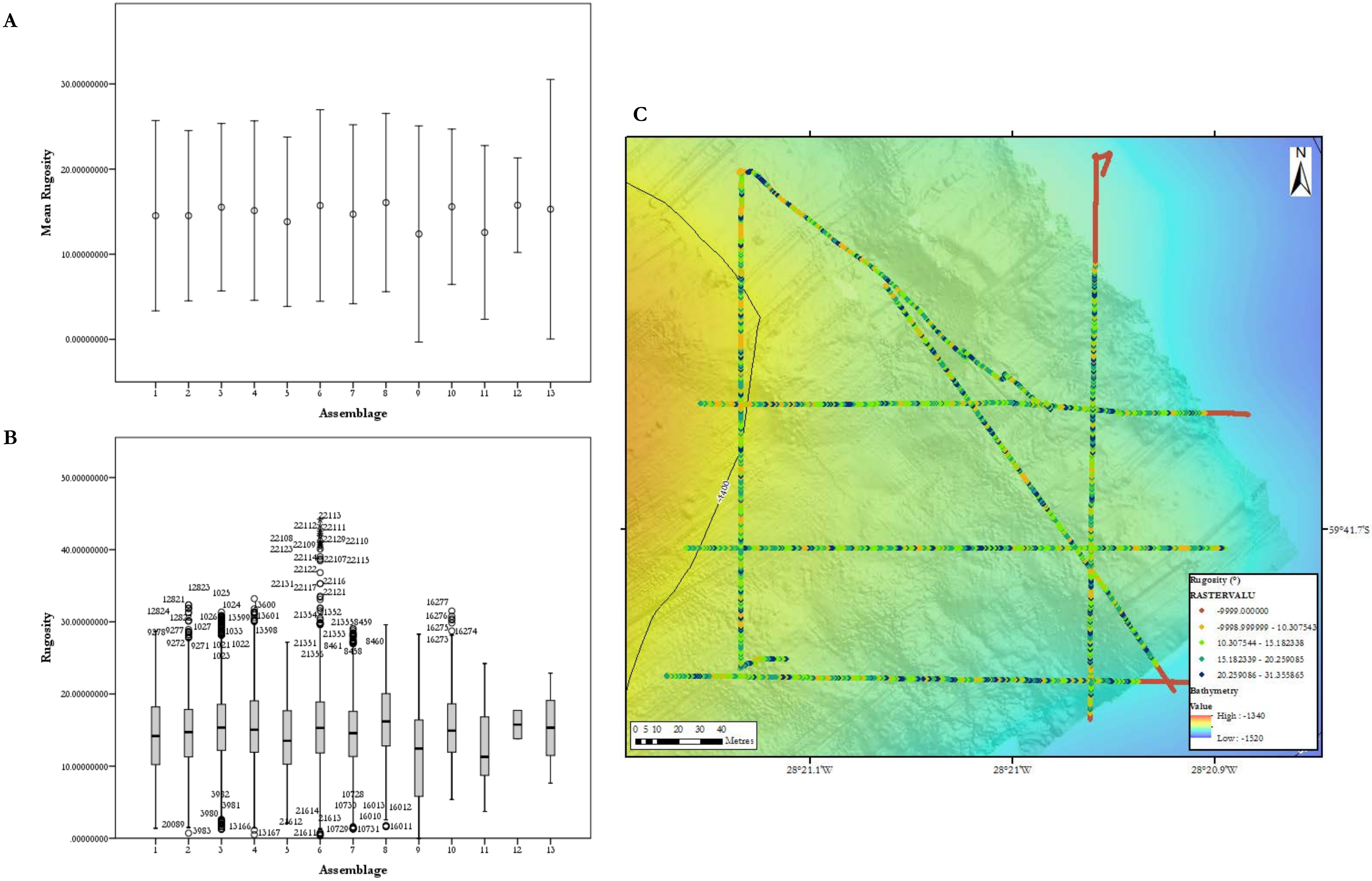
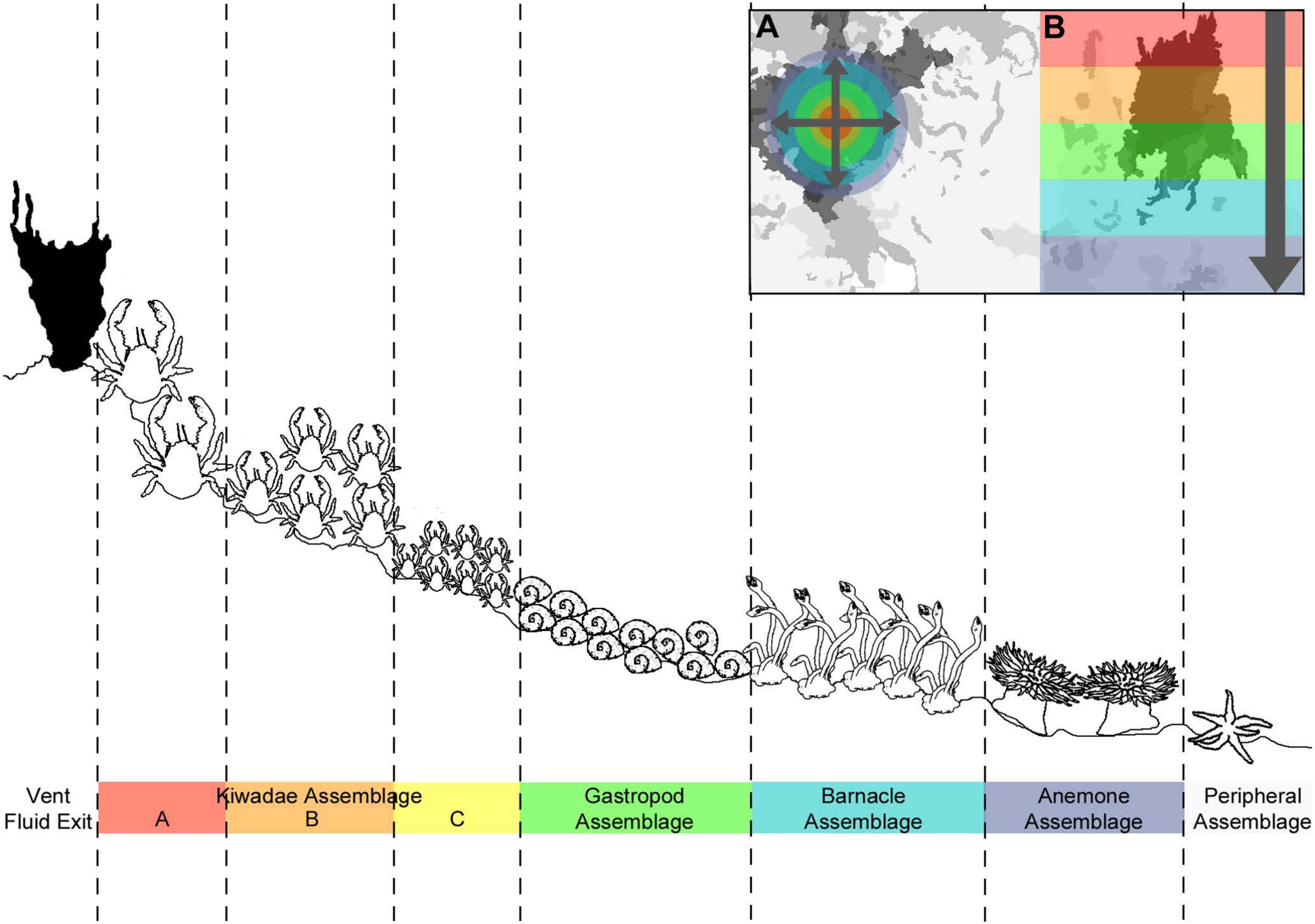

A
Mean Rugosity
30.00000000
20.00000000
10.00000000
0.00000000
1
2
3
4
5
6
7
8
9
10
11
12
13
Assemblage
B
Rugosity
50.00000000
40.00000000
30.00000000
20.00000000
10.00000000
.00000000
22113
22112
22111
22108
22109
22129
22110
22123
22114
22107
22115
22122
22131
22117
22116
22121
12823
1025
12821
1024
13600
12824
12822
1026
13599
13601
21354
21352
9278
9277
1027
1033
13598
21355
8459
9272
9271
1021
1022
21353
8460
1023
21351
8461
21356
8458
16277
16276
16275
16274
16273
3982
3981
3980
20089
3983
13166
13167
21614
21612
21613
21611
10728
10730
10729
10731
16013
16012
16010
16011
1
2
3
4
5
6
7
8
9
10
11
12
13
Assemblage
C
N
-1400
59°41.7'S
28°21.1'W
28°21'W
28°20.9'W
0 5 10 20 30 40
Metres
Rugosity (°)
RASTERVALU
-9999.000000
-9998.999999 - 10.307543
10.307544 - 15.182338
15.182339 - 20.259085
20.259086 - 31.355865
Bathymetry
Value
High : -1340
Low : -1520

Figure C4

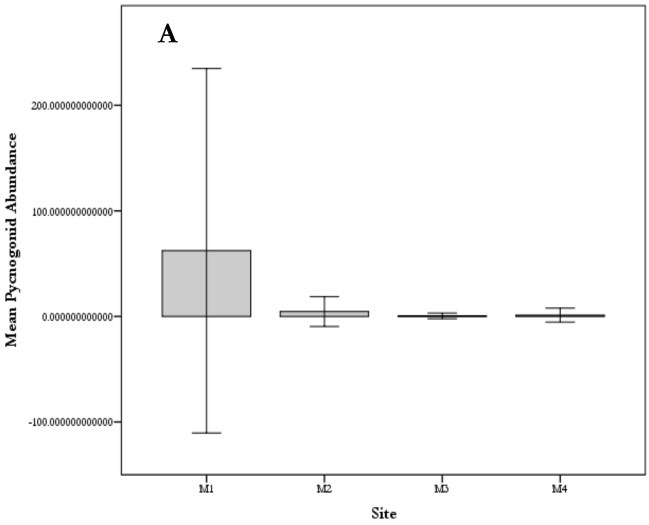

A
B
Vent
Fluid Exit
Kiwadae Assemblage
A
B
C
Gastropod
Assemblage
Barnacle
Assemblage
Anemone
Assemblage
Peripheral
Assemblage

APPENDIX D: Mosaic Fauna (Bar Charts and Statistics)

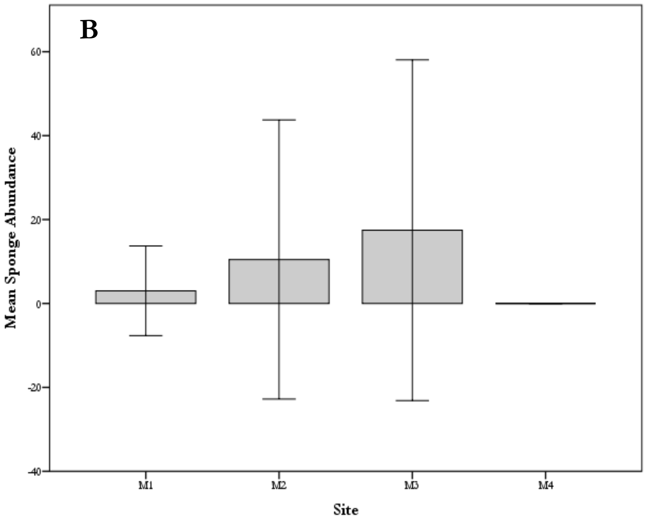
The bar charts presented in Figure D1 illustrate why each of the mosaic sites was selected for small-scale analyses of faunal microdistribution and the relationships between fauna and environmental variables. From the charts in Figure D1, it can be seen that species densities vary widely across mosaic sites, indicating that the community composition was different at each of the sites and that each site could bring a new variable for comparative analysis. Figure D1 supports the findings presented on the small, mosaic scale throughout this project.

Figure D1 – Bar charts illustrating changes in species densities across mosaic sites ('M1' to 'M4') in the Kemp Caldera vent field, South Sandwich Islands.
The bar charts presented depict the changing species densities of the following fauna: **(A)** – *Sericosura* spp.; **(B)** – sponges; **(C)** – *Lepetodrilus* sp.; **(D)** – siboglinid tubeworms ('M1' observations to be ignored, as likely misidentification); **(E)** – *Pyropelta* sp.; **(F)** – stalked barnacles; **(G)** – anemones; **(H)** – dead *Nematocarcinus* shrimp; **(I)** – live *Nematocarcinus* shrimp; **(J)** - bacterial mat (%); **(K)** – dead *Lebbeus* shrimp; **(L)** – xenophyophores; **(M)** – dead vesicomyid clams; **(N)** – fish; **(O)** – live vesicomyid clams.
Error bars represent ± 2 standard deviations.

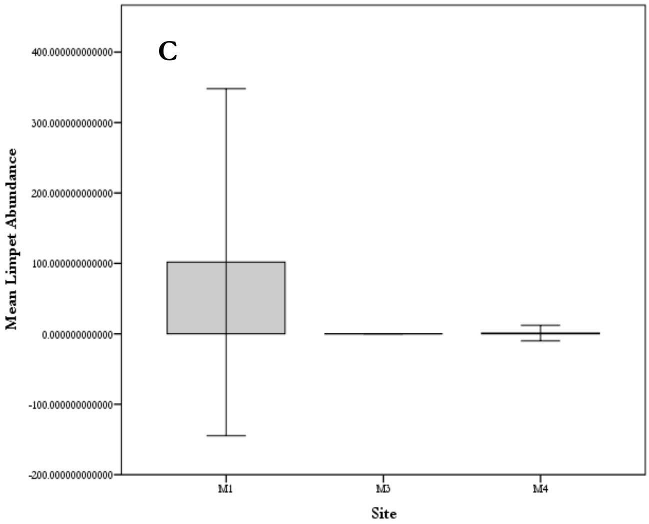
See Overleaf



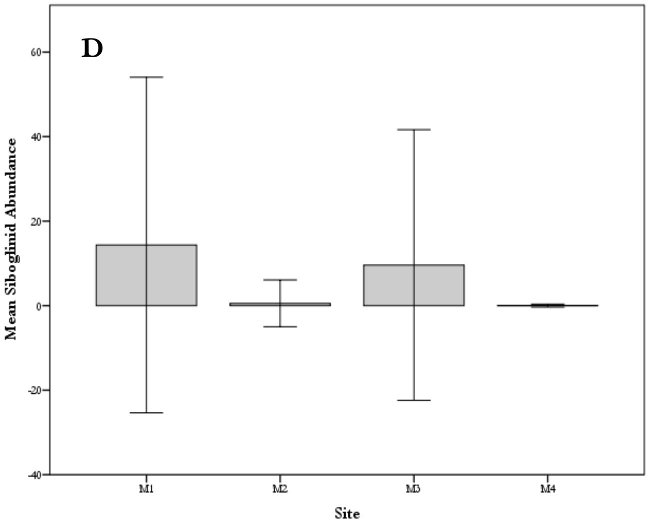
Error Bars: +/- 2 SD



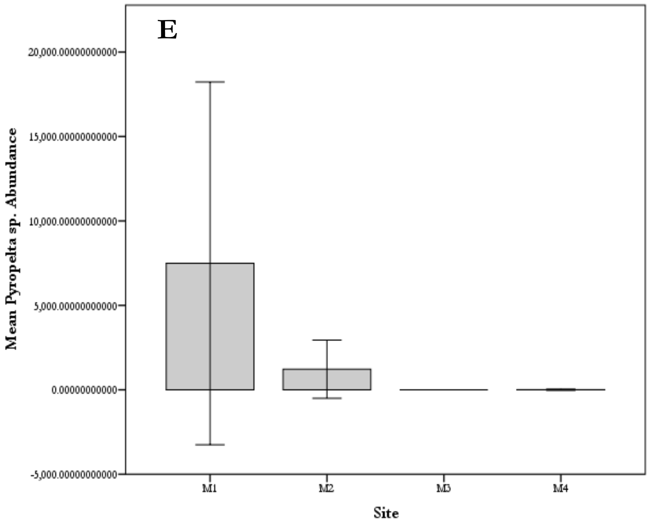
Error Bars: +/- 2 SD



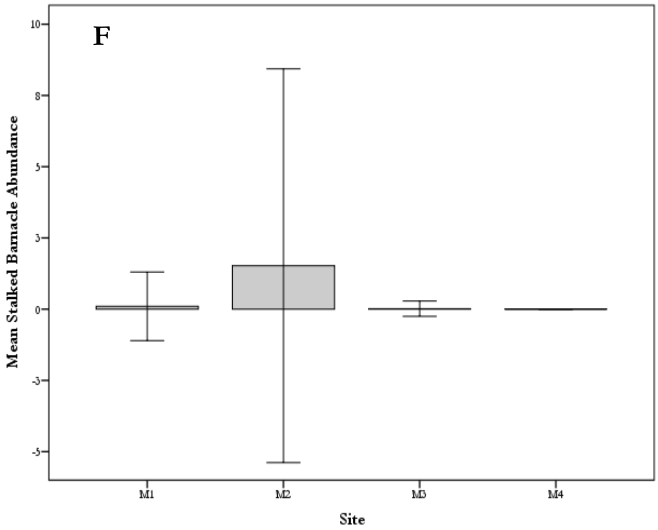
Error Bars: +/- 2 SD



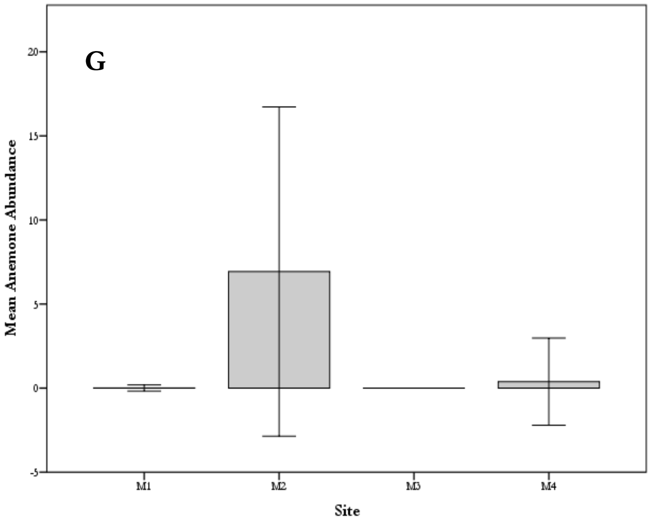
Error Bars: +/- 2 SD



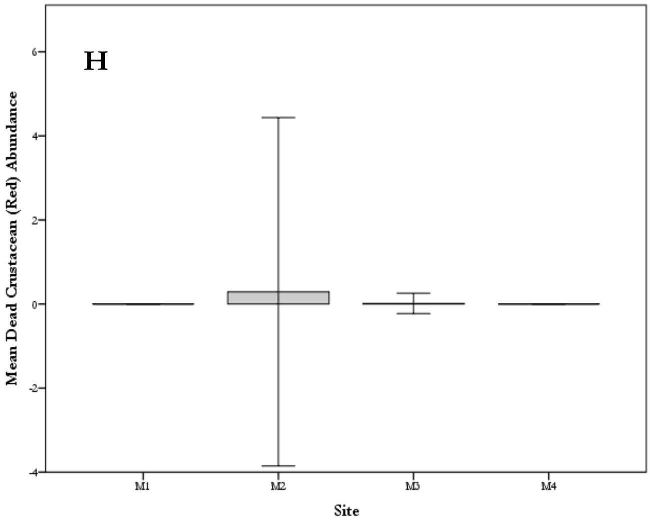
Error Bars: +/- 2 SD



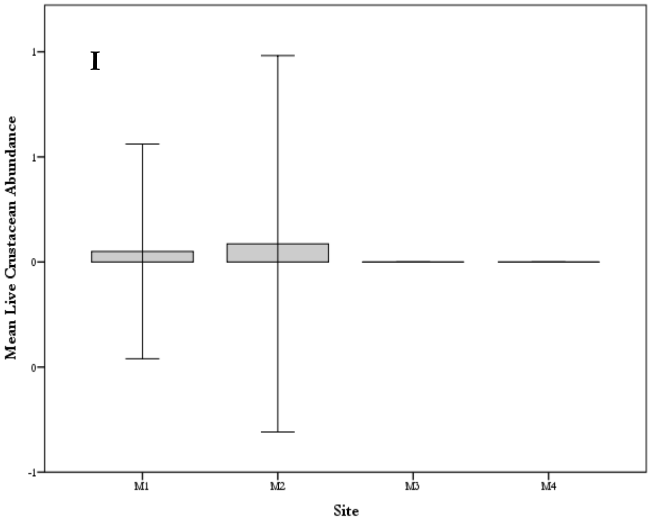
Error Bars: +/- 2 SD



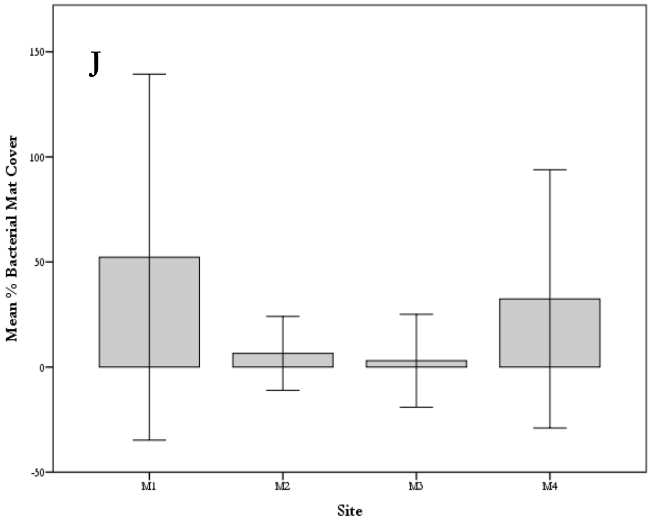
Error Bars: +/- 2 SD



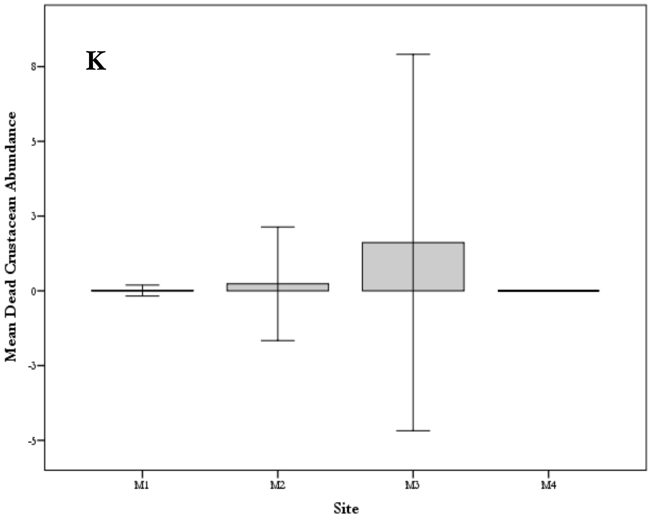
Error Bars: +/- 2 SD



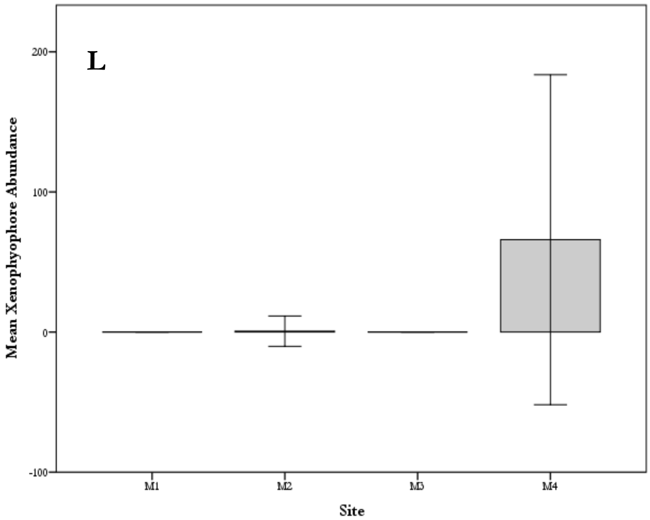
Error Bars: +/- 2 SD



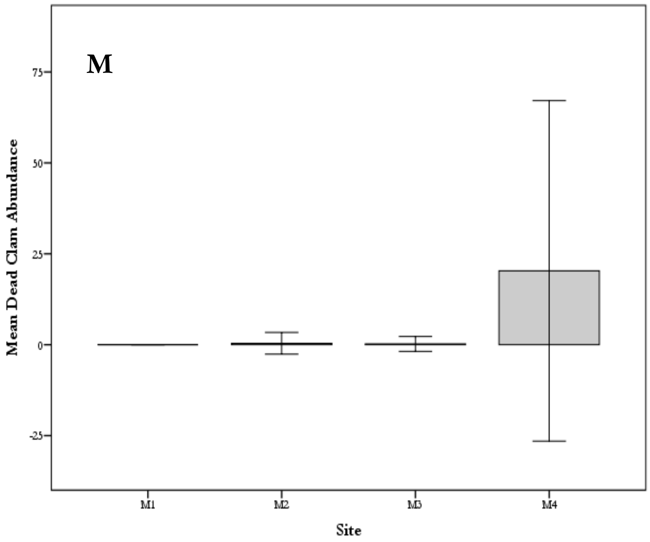
Error Bars: +/- 2 SD



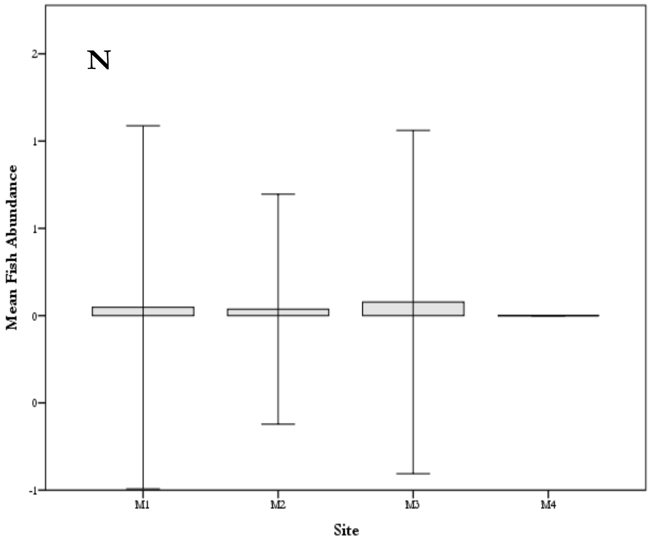
Error Bars: +/- 2 SD



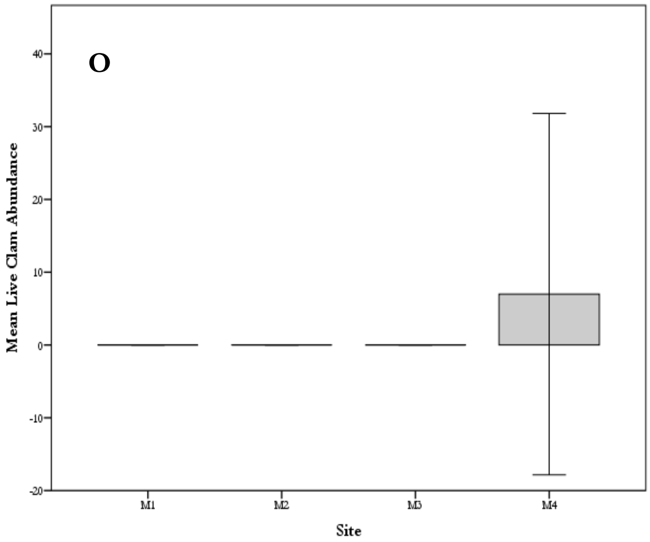
Error Bars: +/- 2 SD



Error Bars: +/- 2 SD



Error Bars: +/- 2 SD



Error Bars: +/- 2 SD

Table D1 depicts the results of the non-parametric statistical tests described in the Materials and Methods, Results and Discussion sections of this project.

Table D1 – Spearman's Rank Correlation test results, comparing faunal relationships between and within mosaic sites from Kemp Caldera vent field (South Sandwich Islands).

'Strength'	Site	Variable 1	Variable 2	r_s	p	n
Strong	M1	Bacterial mat	*Pyropelta* sp.	0.751	<0.001	119
Strong	M3	Sponges	Tubeworms	-0.745	<0.001	64
Strong	M3	Sponges	Hard substratum	0.824	<0.001	64
Strong	M3	Tubeworms	Hard substratum	-0.817	<0.001	67
Strong	M3	Sponges	Soft substratum	-0.824	<0.001	64
Strong	M3	Tubeworms	Soft substratum	0.817	<0.001	67
Strong	All	Pycnogonids	*Pyropelta* sp.	0.779	<0.001	322
Strong	All	Limpets	*Pyropelta* sp.	0.805	<0.001	239
Moderate	M1	Sponge	*Pyropelta* sp.	-0.513	<0.001	119
Moderate	M1	Tubeworms	Limpets	0.468	<0.001	110
Moderate	M1	Tubeworms	*Pyropelta* sp.	0.471	<0.001	116
Moderate	M1	Bacterial mat	Limpets	0.456	<0.001	113
Moderate	M1	Bacterial mat	Sponges	-0.531	<0.001	119
Moderate	M1	Bacterial mat	Tubeworms	0.430	<0.001	116
Moderate	M1	Anemones	*Lebbeus* sp. (live)	0.455	<0.001	119
Moderate	M2	Pycnogonids	*Pyropelta* sp.	0.518	<0.001	79
Moderate	M2	*Lebbeus* sp. (live)	Fish	0.585	<0.001	79
Moderate	M4	Pycnogonids	Limpets	0.446	<0.001	61
Moderate	M4	Limpets	*Pyropelta* sp.	0.541	<0.001	59
Moderate	M4	Limpets	Anemones	0.400	0.001	61
Moderate	M4	Pycnogonids	Hard substratum	0.416	<0.001	74
Moderate	M4	Anemones	Hard substratum	0.468	<0.001	74
Moderate	M4	Xenophyophores	Hard substratum	-0.469	<0.001	74
Moderate	M4	Bacterial mat	Dead clams	-0.523	<0.001	74
Moderate	M4	Bacterial mat	Live clams	-0.461	<0.001	74
Moderate	M4	Xenophyophores	Dead clams	-0.555	<0.001	74
Moderate	M4	Dead clams	Live clams	0.452	<0.001	74
Moderate	All	Pycnogonids	Limpets	0.689	<0.001	241
Moderate	All	*Pyropelta* sp.	Bacterial mat	0.467	<0.001	327
Moderate	All	Sponge	Bacterial mat	-0.430	<0.001	334
Moderate	All	Anemones	Hard substratum	0.602	<0.001	339
Moderate	All	*Pyropelta* sp.	Soft substratum	-0.472	<0.001	327
Moderate	All	*Pyropelta* sp.	Xenophyophores	-0.436	<0.001	327
Moderate	All	*Pyropelta* sp.	Dead clams	-0.429	<0.001	327
Moderate	All	Bacterial mat	Limpets	0.511	<0.001	241
Moderate	All	Dead clams	Live clams	0.630	<0.001	339
Moderate	All	Xenophyophores	Live clams	0.449	<0.001	339
Moderate	All	Dead clams	Xenophyophores	0.628	<0.001	339
Moderate	All	Xenophyophores	Soft substratum	0.505	<0.001	339