Megafaunal Benthic Ecology of the Submarine Canyons of Southern California

Grant Duffy, University of Southampton/NOCS, UK

Mentors: Charlie Paull, Lonny Lundsten

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ABSTRACT

Submarine canyons have been studied to a very limited extent in spite of their important biological roles as hotspots of secondary production and organic matter conduits between the shelf and the deep sea. The heterogeneity and rugged terrain of submarine canyons makes them difficult to sample using traditional means such as trawling, however there has be a great deal of success in using ROVs to study these important yet poorly understood environments. A number of ROV dives were executed within the submarine canyons of Southern California during research expeditions in 2005 and 2010. Although these dives were planned and executed with geological research in mind, the video data obtained during these dives can be utilised for ecological research. Video transects from a range of depths in five submarine canyons have been analysed to produce presence/absence data for each site and a comparison of benthic communities in differing depths, locales, and canyons has been performed. No difference was found between canyons based on canyon activity however there was a significant trend for community composition to vary between water depths. This depth-related trend is in agreement with the findings of previous studies and is most probably tied to the depth ranges of the various organisms studied, which is dictated by their tolerances of depth depth-correlated variables such as temperature, salinity and oxygen concentration.

INTRODUCTION

Forming deep incisions into the continental shelf, submarine canyons are large topographic features with unique hydrographic, sedimentological, and geochemical characteristics. Most submarine canyons resemble terrestrial valleys with a V-shaped profile and high, steep walls with rocky outcrops (Shepard & Dill, 1969), for descriptive purposes they can be divided into upper, middle, and lower regions based upon water-depth and bottom-topography (de Stigter et al., 2007; Lastras et al., 2009; Vanney & Mougenot, 1990). Examples of typical submarine canyons include the Nazaré Canyon, off the coast of Portugal, the Monterey Canyon, off the Californian coast, and the Tokyo Canyon at the entrance to Tokyo Bay.

Submarine canyons exhibit a high degree of variability on both an intra-canyon and inter-canyon level (Gage & Tyler, 1992; Tyler et al., 2009). This heterogeneity is the result of a number of biotic and abiotic factors including shelf morphology, proximity to river systems, bottom topography, oceanographic conditions, large and small-scale canyon events, sedimentation rates, nutrient input, and depth.

While these larger canyons are prime examples of typical submarine canyons, they occur relatively infrequently along the World's continental margins. Smaller canyons, sometimes referred to as submarine valleys, pepper continental margins around the globe (DeLeo et al., 2010), and while these canyons are relatively small they still demonstrate the same heterogeneity, albeit on a much smaller scale. Canyons can be classified using various criteria and while attempts to classify quantitatively have occurred (eg. Goff, 2001), most classification is on a qualitative basis. One classification system of particular interest to biologists and geologist alike is that of canyon activity, where canyons are categorised based upon their rate of sediment throughput.

All submarine canyons intercept sediment being laterally transported along the continental shelf (Cúrdia et al., 2004). Large, active canyons, such as Nazaré, which

penetrates almost the entire width of the continental shelf, intercept a greater amount of sediment than those with reduced shelf penetration (Van Weering et al., 2002). This sediment interception results in almost all canyons experiencing high levels of organic matter input. Like continental margins, the amount of organic matter found within canyons depends upon the production of associated surface waters. Macrophyte communities, such as the kelp forests found near canyons along the Pacific Coast, contribute substantially to the total organic matter entering the canyon system (Vetter & Dayton, 1998).

The high levels of organic matter that accumulate in submarine canyons result in increased food for resident filter-feeders and detritivores (Sorbe, 1999), making them hotspots of secondary production (DeLeo et al., 2010). Secondary production is the rate at which biogenic energy stores are incorporated into heterotrophic organisms (Soliman & Rowe, 2008), where the energy source is effectively recycled carbon from detrital sources and faecal matter (Jannasch & Taylor, 1984). The heightened levels of secondary production within canyons may have resulted in the development of distinct faunal assemblages with high faunal and biomass densities relative to other deep-sea ecosystems at comparable depths (Ormond et al., 1999). Organisms that are able to alter their feeding strategies and take advantage of any feeding opportunities that may arise generally thrive in the unpredictable canyon environment (Cúrdia et al., 2004).

Many submarine canyons not only catch sediment but also channel it down from the continental shelf to the abyssal plain. While inactive canyons have little role in sediment transportation to the abyss, with sediment accumulating within the canyon channel over time, active canyons act as vital conduits for sediment. By channelling sediment and expediting its movement from the continental shelf to the associated basin (Vetter & Dayton, 1998) active canyons provide an important means to supply organic carbon to the deep sea.

The effect of canyon activity upon the faunal composition of communities inhabiting submarine canyons has yet to be discussed in published literature. This may be in part due to the difficulties of studying fauna in such complex environments or due to the opportunity to execute such a study not arising. It is hoped that this study will provide a means to test the faunal differences between active and inactive canyons and facilitate an improved understanding of the canyon faunal assemblages as a whole.

In spite of their importance as hotspots of secondary production and role in connecting the continental shelf to the deep sea (Vetter & Dayton, 1998), our understanding of submarine canyons, their formation, processes, and ecosystems, is relatively limited (Ramirez-Llodra et al., 2010). In recent years there have been a number of programmes targeting submarine canyons (e.g. EUROSTRATFORM, HERMES, HERMIONE), however complete multidisciplinary comprehension of these complex systems is still far away, with numerous submarine canyon systems remaining wholly unstudied. A number of studies have aimed to survey canyons from a geological perspective with minimal regard to the study of canyon ecology, however this does not mean that ecological details cannot be gleaned from the data collected on these expeditions.

As a matter of course video recordings are made during all MBARI ROV dives in order to provide a record of the dive for future reference. This results in a great deal of video data being collected during all dives that can potentially be used as part of a video survey of local fauna. There are a number of limitations associated with using this data that will be discussed later in this report.

MATERIALS AND METHODS

Over 67 hours of ROV footage was recorded during research expeditions to the submarine canyons off the coast of Southern California in 2005 and 2010. In total five submarine canyons were sampled (Figure 1) over the course of these two expeditions.
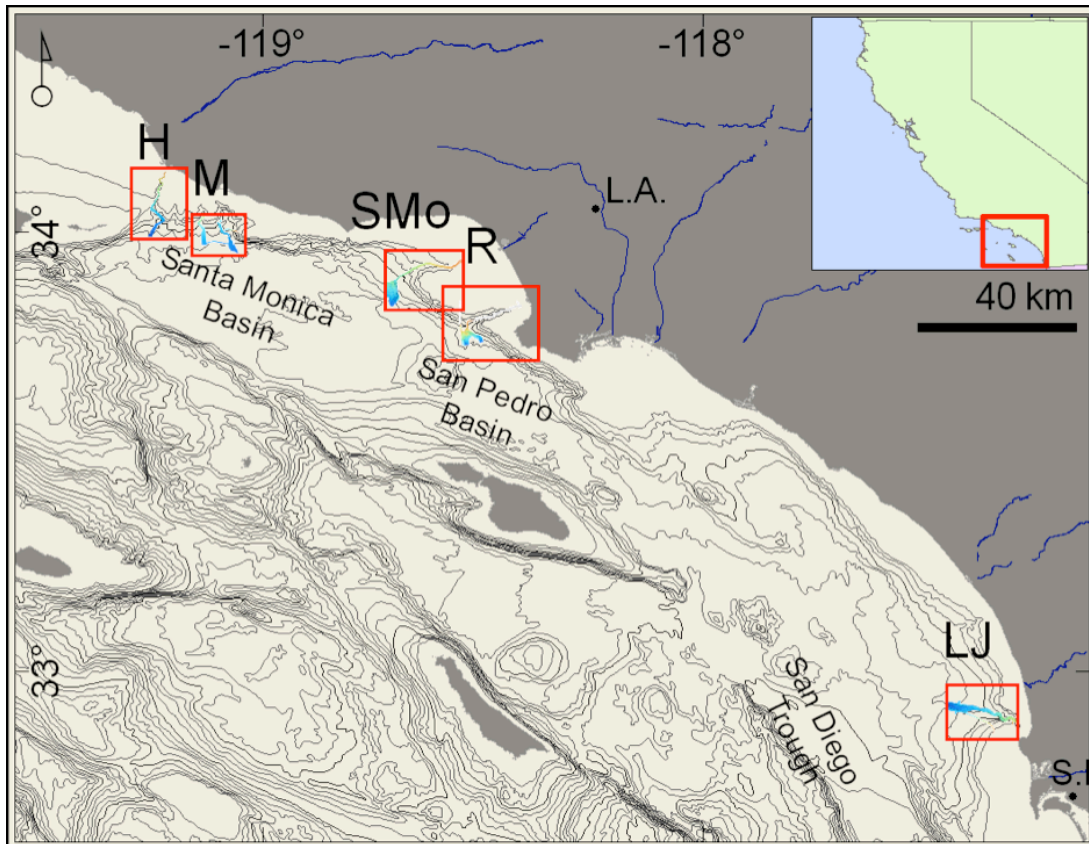

Figure 1: Map of study sites. H; Hueneme Canyon (28km long), M; Mugu (16km), SMo; Santa Monica (22km), R: Redondo (18km), LJ; La Jolla (27km).

Hueneme (Figure 2a), Redondo (Figure 2b), and Santa Monica (Figure 2c) Submarine Canyons were surveyed during the 2005 expedition using *ROV Tiburon*. *ROV Tiburon* was used for all dives during the 2005 expedition. This ROV was deployed from the *RV Western Flyer* and equipped with a standard definition (SD) camera, which was used to survey these submarine canyons. Footage was recorded to tape for subsequent analysis in the MBARI video lab.
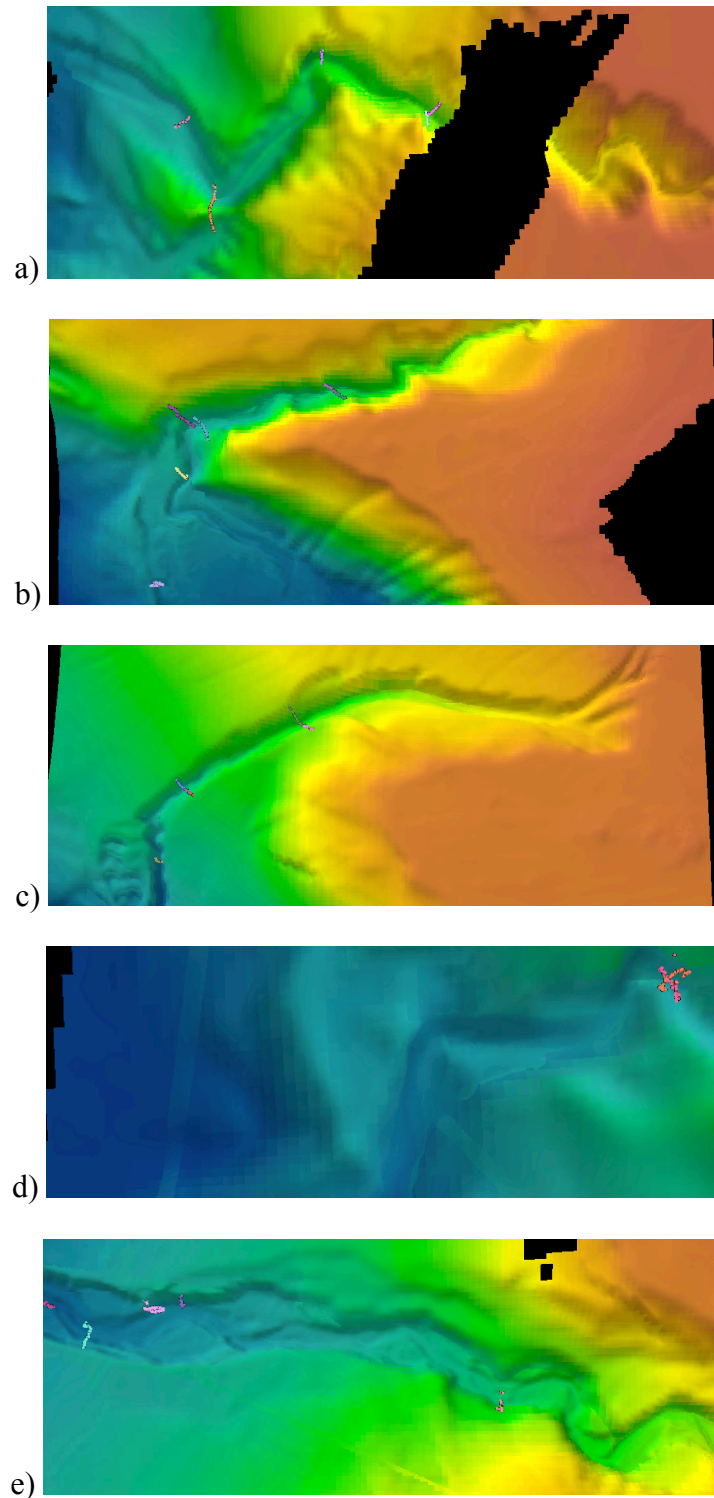
Figure 2: Bathymetric maps of the study canyons with dive tracks indicated by coloured dots. Coloured shading represents bottom depth ranging from 0m deep (Red) to 750m deep (Blue). Canyons in order are: a) Huenene; b) Redondo; c) Santa Monica; d) Mugu; e) La Jolla.

During the 2010 expedition Mugu (Figure 2d) and La Jolla (Figure 2e) Submarine Canyons were surveyed using *ROV Doc Ricketts*. Once again this vehicle was tethered to and piloted from *RV Western Flyer*. *ROV Doc Ricketts* was equipped with a high definition (HD) video camera, all footage was recorded onto high definition tape and analysed upon return to MBARI.

The duration and distance travelled during each dive varied greatly and was dictated by the geological sampling requirements of each dive and operational considerations, such as crew availability and sea conditions. For this reason each dive was divided into a number of randomly selected 50m long transects, this also aided in zone and substratum classification as many dives traversed a number of zones and substrata.

Three discrete zones were identified (<45° slope, >45° slope, and wall) with transects being classified using bathymetric data collected using an AUV equipped with a multibeam array, BPI index calculated using the Benthic Terrain Modeller plugin for ArcGIS, and observations made using video footage. Substratum (sand, soft, rocky, and hard) was identified using observations from ROV footage and knowledge of the substratum obtained during the primary geological survey.

Each transect was annotated using MBARI's proprietary Video Annotation and Reference Software (VARS). Initial outline annotations were performed by Lonny Lundsten, Linda Kuhnz, and Susan Von Thun. The author reviewed all footage in greater detail to identify any potential sources of error and to ensure consistency between dives. Due to the nature of this study no voucher specimens were collected during dives, the distance that the camera was from the benthos also varied substantially and while a limited number of organisms were viewed close-up many were observed at some distance. These reasons, coupled with the use of SD video during the 2005 dives and HD video during the 2010 dives meant that the level of certainty of identification of organisms was highly variable.

Due to this variability in identification certainty some organisms could be identified to lower taxonomic levels than others. Even without clear footage some organisms could be confidently identified to species level (eg. *Strongylocentrtotus fragilis*) or grouped as a morphologically-similar species (eg. *Asteroid sp. A*) while others had to be grouped to family level to ensure consistency between footage of varying quality (eg. *Sebastes spp.* and *Sebastolobus spp.* grouped into Sebastidae). For this reason analysis was performed using fauna classified as Operational Taxonomic Units (OTUs), with organisms identified to the taxonomic level that provide the most confidence that consistent identification occurred across all dives. Throughout the process of video analysis the substratum and zone indicative features were noted, if an OTU was numerically dominant this was also noted.

Annotations for all dives were sorted into the appropriate OTU as necessary and counted, this data was subsequently converted into presence/absence data. It was determined that analysis of presence/absence data was the most appropriate approach due to the variability of field-of-view. While it is known that all transects were 50m in length the distance from the benthos varied considerably making the total area observed difficult to determine and the collection of representative abundance data infeasible.

A resemblance matrix of the data was created based upon Bray-Curtis similarity and used to create a Multi-dimensional scaling plot using PRIMER statistical software (Plymouth Routines In Multivariate Ecological Research; Clarke & Gorley, 2006). Data were then analysed using a factorial analysis. Due to the unbalanced design of this study of opportunity it was decided that a PERMANOVA analysis (Anderson, 2005) using the PERMANOVA+ add-on for PRIMER provided the best approach as it is able to take into account a number of factors and accommodates for more complex experimental designs than an ANOSIM (Clarke, 1993) test.

The PERMANOVA design file was created with Canyon as the top tier factor. Nested within this was zone and depth. Average transect depths were grouped into 100m depth bins to be used as a factor for analysis. Temperature, oxygen concentration, and salinity were closely correlated to depth and as such only depth was used as a representative factor to reduce the total number of factors and therefore the computations power required to run the PERMANOVA. Substratum was additionally nested within zone. In order to assess the effect of canyon activity, a contrast was built into this design grouping Hueneme, Mugu, and La Jolla Canyons against Santa Monica Canyon. Redondo canyon was grouped either with the active canyons, the inactive canyons, or excluded altogether to test where this intermediate canyon lies. The PERMANOVA was run using 9999 permutations to produce a P(Perm) value indicating the significance of any effect that each factor may be having upon variability.

RESULTS

In total 127 50m transects were annotated totalling a 6.35km long stretch of benthos. Approximately 11 000 biological observations were made throughout the dives, these were classified into 35 OTUs (Table 1) or excluded. Organisms that were not observed to be in contact with the benthos for a prolonged period of time were excluded from analysis as they may have been drawn to the lights, noise, or movement of the ROV and may not be long-term residents. For this reason all gelatinous zooplankton, except *Dromalia alexandri*, which is anchored to the benthos, were excluded. Transient, fast moving fishes, such as the family Osmeriidae, and all squid species were also excluded on these grounds.

Table 1: Operational taxonomic units identified and used for faunal analysis for all video footage.

Actiniaria spp. (ex L. brevicornis)	Eptatretus spp.
Anoplopoma fimbria	F/H Complex
Anthozoa	Florometra sp.
Asteroidea sp. A	Galatheidae sp.
Asteronyx longifissus	Gastropoda
Brisaster spp.	Liparidae
Brisingida spp.	Lithodidae
Dromalia alexandri	Lycodes diapterus
Liponema brevicornis	Macrouridae
Majidae spp.	Octopoda
Pleurobranchaea	Other Pennatulacea (ex. f/h complex)
Pleuronectiformes spp.	Pannychia moseleyi
Porifera	Psolus squamatus
Pterasteridae	Scyliorhinidae spp.
Raja rhina	Strongylocentrotus fragilis
Rathbunaster californicus	Umbellula lindahli
Scorpaenidae spp.	Other Zoarcidae
Solaster sp.	

These transects covered a wide range of zones, substrata, and depth however not all factors were represented in all canyons. The MDS plot generated (Figure 3) suggests that Mugu Canyon may house different faunal assemblages to the other canyons however

these plots are often open to interpretation and the apparent dissimilarity requires testing especially given how the unbalanced sampling effort. A PERMANOVA test indicated that there was no significant difference between canyons (DF= 4, pseudoF= 1.2689, P(Perm)= 0.2353) or based on canyon activity, irrespective of whether Redondo was classified as active, inactive, or excluded altogether (DF= 1, pseudoF= 0.81419, P(Perm)= 0.6716; DF= 1, pseudoF= 0.75723, P(Perm)= 0.7009; DF= 1, pseudoF= 0.92151, P(Perm)= 0.5640 respectively).
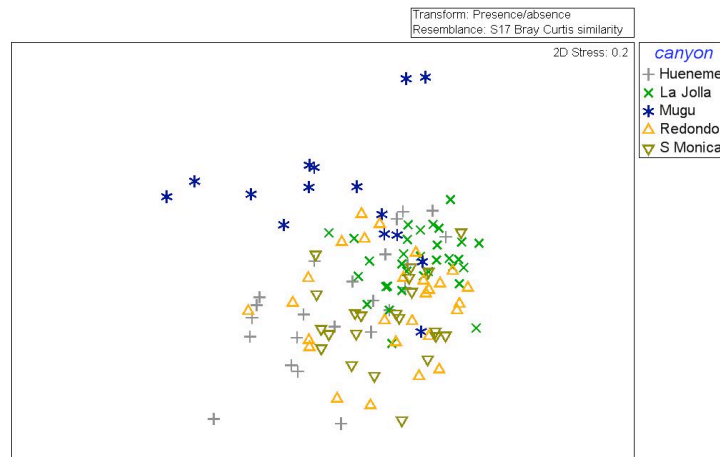
Figure 3: Two-dimensional MDS based on Bray-Curtis Similarity matrix created from comparison between all transects (n=127). Points categorised by canyon.

The effect of zone was not significant (DF= 9, pseudoF= 1.9404, P(Perm)= 0.0523) but a relatively high pseudoF value coupled with the near-significant P(Perm) value suggest that zone may still be having some influence upon community composition. Substratum was found to have no significant effect upon community dissimilarity (DF= 9, pseudoF= 1.9404, P(Perm)= 0.0523).
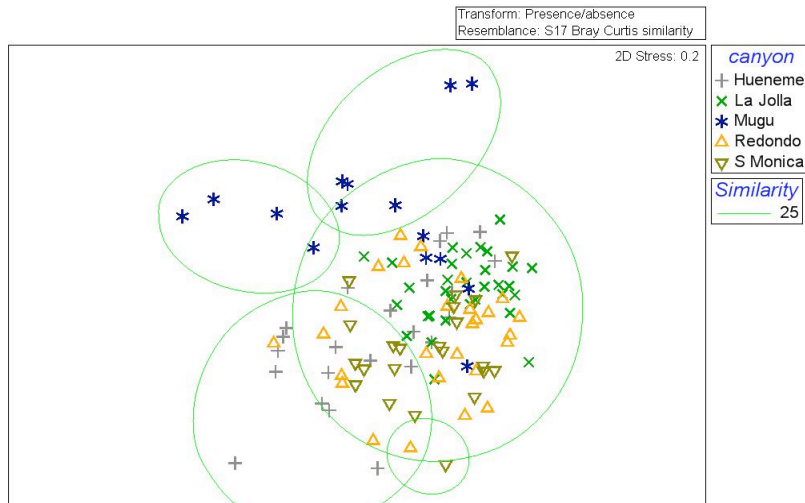
Figure 4: Two-dimensional MDS based on Bray-Curtis Similarity matrix created from comparison between all transects (n=127). Points categorised by canyon, points grouped together by the green line are 25% similar to one another based on transect depth.

Depth was found to have a significant effect upon the community composition of these canyons (DF= 9, pseudoF= 2.9992, P(Perm)= 0.002). This concurs with observation made by the author while reviewing video footage. This explains why Mugu Canyon appeared to vary from the other canyons when reviewing the MDS plot (Figure 3) although no significant variation was detected by the PERMANOVA. If one plots similarity of data based on depth (Figure 4) it becomes apparent that these Mugu transects were much deeper than most others. Plotting the depth of every observation of the ten most common OTUs (Figure 5) demonstrates that some species are only found within specific depth boundaries.
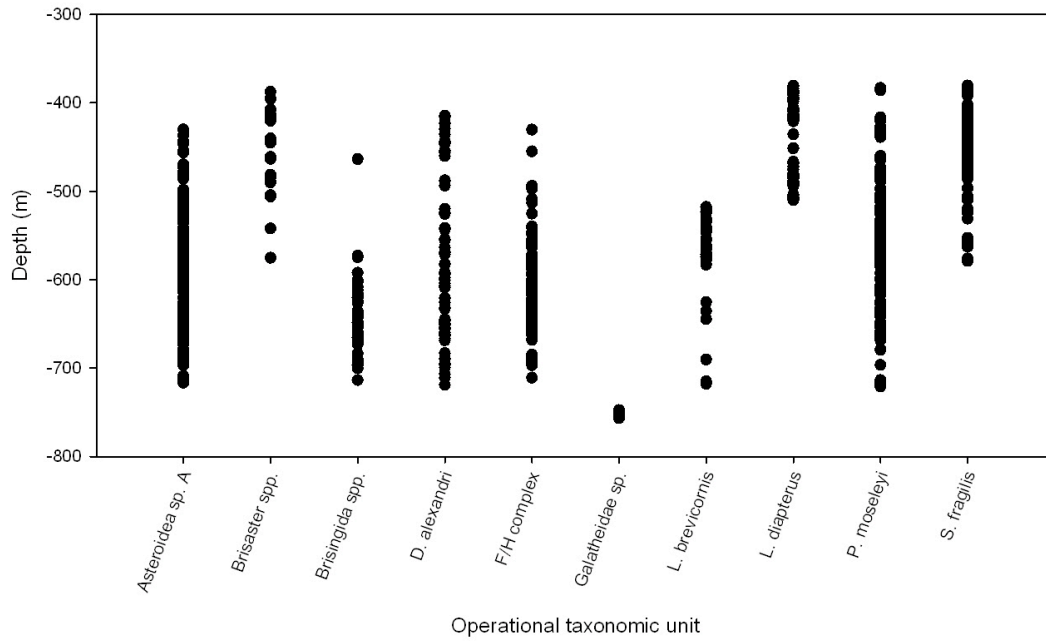
Figure 5: Depth of all recorded observations of the most frequently observed OTUs by number.

DISCUSSION

Based on the results of the PERMANOVA test if canyon activity does have any effect on community composition it has not been detected as part of this study. In the opinion of the author, this could be a result of the unbalanced study of these canyons as the depths and zones surveyed were not consistent between canyons. Based upon what is known about the effect that reduced canyon activity has upon the morphology of the canyon, reduction of main channel width and size, reduced steep slopes, build-up of soft muddy sediments, one would only expect to see differences when looking at the megahabitat (Greene et al., 1999; between-canyon) level of comparison as fewer smaller macrohabitats (eg. sandy flats) would occur in the less active canyons. Without equal and representative surveying of all canyons it is not possible to perform this analysis with confidence.

Although the trend was not significant, there is evidence of a correlation between zone and community composition. Fauna frequently found on gentle slopes and flats may be lack the necessary ability to remain affixed to the steeper topography of slopes greater than 45° and that of near-vertical walls. Fauna such as the sponges, Porifera, require the harder substratum commonly found forming walls in order to anchor themselves securely and as such are most commonly found within this zone. It is likely that the differences seen were not significant due to the continuous nature of the zones and frequent zone overlap during some transects (eg. small sections of flat terrace on walls) confounding the analysis.

The effect of depth upon community composition has been observed on numerous occasions in a wide variety of habitats over a range of fauna (eg. Haedrick et al., 1980; Cartes, 1993; Cartes and Sardá, 1993). Following plotting of observations by depth it is clear that the depth range of a number of the organisms observed is restricted. Based on observations made during video footage analysis this is not particularly surprising as trends can be observed while watching dives that traverse a range of depths. Based on the data from all five canyons it is possible to describe the trends that one observes in benthic

communities while travelling down the canyon from the head on continental shelf to the mouth emptying out to the basin below.

Some OTUs were found over the whole range of depths surveyed. The holothurian *Pannychia moseleyi* Theél 1882 was one such organism being found frequently in varying numbers between 375m and 725m deep. *Dromalia alexandri* Bigelow 1911, a benthic siphonophore that anchors itself to the seafloor, was also found at almost all depths ranging from approximately 400m-725m deep. This species was not found in the shallowest transects, however the majority of these shallow dives were focussed on the main canyon channel where currents may have been too strong for *D. alexandri* to remain tethered.

The shallowest transects (~375m-500m deep) were characterised by *Lycodes diapterus* Gilbert 1892, a teleost fish, being found in high numbers in the main canyon channel. This species was not observed at all below 525m water depth. *Brisaster spp.* were frequently observed on gentle slopes in shallow depths but there occurrence was sporadic below 500m and unobserved below 600m deep. The deep-sea urchin *Strongylocentrotus fragilis* Jackson 1912 was found in very high numbers on slopes and flats with soft muddy sediment shallower than 600m deep. Below this depth it was rarely observed, being usurped by *Asteroidea sp. A* as the numerically dominant organism.

Asteroidea sp. A was seen frequently in high numbers between 425m and 725m deep. Below 500m it numerically dominated a number of transects, occurring alongside *S. fragilis* at the shallower end of this range. Below 500m a large number of sea-pens belonging to the *Fuculina/Halipteris* Complex are observed on both gentle and steep muddy slopes. On almost all occasions, *Asteronyx longifissus* Döderlein 1927, an organism that was rarely seen on the benthos, is observed attached to these sea-pens.

The pom-pom anemone, *Liponema brevicornis* McMurrich 1893, was observed sporadically in footage recorded below 500m deep but was not seen at all above this depth. Basket stars belonging to the family Brisingida began to increase in number below 600m, often being seen alongside *Asteroidea sp. A* and *P. moselyi* on flat muddy terraces and gentle slopes.

The transects below 725m deep were dominated by the squat lobster *Galatheoidea sp.*, which was found in very high numbers and high densities in the deeper dives at the mouth of the canyon. These organisms were also seen in high numbers in footage taken from the Santa Monica Mounds that are located in the Santa Monica Basin, which a number of the studied canyons empty into. This suggests that conditions in the mouth of the canyon are similar to those of the basin, this is of little surprise due to their proximity to one another.

The restrictions in depth distributions of some OTUs may be an indication of their physiological tolerance limits with regard to depth-related environmental variables. A principal components analysis showed that within the studies canyons depth, and therefore pressure, temperature, and oxygen concentration all correlated so as to form one principal component accounting for 94% of environmental variability. Therefore while pressure itself may not be the limiting factor for each organism it is not possible to discern between depth and these other variables.

Another possible cause for the faunal zonation observed that requires further investigation is the nutrient availability of each depth zone, as this has been found to affect faunal distributions in the deep sea as some organisms thrive in higher energy environments (Cartes and Carrassón, 2004), this is another factor that could potentially co-vary with the survey depth. At the time of writing very little information regarding the nutrient availability at various depths within the canyon is available in order to test this theory.

Beyond the physiological limitations than may be controlling the depth distribution of the various fauna observed, there may also be some degree of interspecific competition dictating what fauna is found within each depth band, zone, or substratum. As an example, *L. diapterus* was found frequently within the main channel of the canyon while other organisms were not. As a teleost fish, *L. diapterus* is comparatively motile and so can quickly escape the channel should a large, potentially life threatening, sediment flow occur. Other, less motile, organisms while not excluded from the channel due to pressure, temperature, oxygen concentration, or salinity would be unlikely to survive long in the main channel and as such will be less frequently observed in this area.

CONCLUSIONS/RECOMMENDATIONS

While it has not been possible to determine the effect, if any, that canyon activity may have upon the communities found within them, this study has nevertheless shown an interesting result with regards to the varying communities encounters as one descends into the submarine canyons of Southern California. Submarine canyons are still relatively understudied environments that are poorly understood, as such, studies of opportunity like this can greatly benefit researchers and are a worthwhile scientific endeavour. Lessons learned from this work can be applied to future analysis of opportunistic video datasets such as this one and for planning of future ROV work in order to capitalise on any dive time that is available and ensure that surveys are perhaps performed in such a way as to appease both geologists and biologists resulting in a more comprehensive and multifaceted research programme.

In order to confidently determine if canyon activity affects community composition it is recommended that a more rigorous and uniform surveying technique is practised in order to encompass a more even spread of transects in a range of depth bands and zones within all canyons. This would require careful prior planning, ideally using detailed bathymetric maps, which have proven invaluable during this study. This will ensure that dive time is well-used and hopefully provide a dataset that is both robust and thorough for any subsequent data analysis. This should be entirely possible while still meeting the needs of geologists although some compromises may have to be made on both sides due to time and financial constraints.

ACKNOWLEDGEMENTS

References:

Anderson, M. J. (2005). *PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance*. Department of Statistics, University of Auckland, New Zealand.

Cartes, J. E. (1993). 'Deep-Sea Decapod Fauna of the Western Mediterranean: Bathymetric Distribution and Biogeographic Aspects', *Crustaceana* **65**(1), 29-40.

Cartes, J. E. & Carrassón, M., 'Influence of trophic variables on the depth-range distributions and zonation rates of deep-sea megafauna: the case of the Western Mediterranean assemblages'*, Deep Sea Research Part I* **51**(2), 263-279.

Cartes, J.E. & Sardá, F. (1993). 'Zonation of deep-sea decapod fauna in the Catalan Sea (Western Mediterranean)', *Marine Ecology Progress Series* **94**, 27-34.

Clarke, K. (1993), 'Non-parametric multivariate analyses of changes in community structure', *Australian Journal of Ecology* **18**, 117–143.

Clarke, K. & Gorley, R. (2006), *PRIMER v6: User Manual/Tutorial*, PRIMER-E, Plymouth, UK.

Cúrdia, J., Carvalho, S., Ravara, A., Gage, J., Rodrigues, A. & Quintino, V. (2004), 'Deep macrobenthic communities from Nazaré submarine canyon (NW Portugal)', *Scientia Marina* **68**, 171–180.

De Leo, F. C., Smith, C. R., Rowden, A. A., Bowden, D. A. & Clark, M.R. (2010), 'Submarine canyons: hotspots of benthic biomass and productivity in the deep sea'*, Proceedings of the Royal Society of London: B* **doi:10.1098/rspb.2010.0462**.

De Stigter, H. C., Boer, W., Mendes, P. A. d. J., Jesus, C. C., Thomsen, L., van den Bergh, G. D. & van Weering, T. C. E. (2007), 'Recent sediment transport and deposition in the Nazaré Canyon, Portuguese continental margin', *Marine Geology* **246**(2- 4), 144–164.

Gage, J. & Tyler, P. (1992), *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*, Cambridge University Press, Cambridge, UK.

Goff, J. A. (2001), 'Quantitative classification of canyon systems on continental slopes and a possible relationship to slope curvature', *Geophysical Research Letters* **28**(23), 4359.

Greene, H. G., Yoklavich, M. M., Starr, R. M., O'Connell, V. M., Wakefield, W. W., \ Sullivan, D.E., McRea, J. E. & Cailliet, G. M. (1999), 'A classification scheme for deep seafloor habitats', *Oceanologica Acta* **22**(6) 663-678.

Haedrich, R. L., Rowe, G. T. & Polloni, P. T. (1980), 'The megabenthic fauna in the deep sea south of New England, USA', *Marine Biology* **57**(3) 165-179.

Jannasch, H. & Taylor, C. (1984), 'Deep-sea microbiology', *Annual Reviews in Microbiology* **38**(1), 487–487.

Lastras, G., Arzola, R. G., Masson, D. G., Wynn, R. B., Huvenne, V. A. I., Huhnerbach, V. & Canals, M. (2009), 'Geomorphology and sedimentary features in the Central Portuguese submarine canyons, Western Iberian margin', *Geomorphology* **103**(3), 310–329.

Ormond, R., Gage, J. & Angel, M. (1999), *Marine Biodiversity: Patterns and Processes*, Cambridge University Press, Cambridge, UK.

Ramirez-Llodra, E. Z., Brandt, A.,Danovaro, R., De Mol, B., Escobar, E., German, C. R., Levin, L. A., Martinez Arbizu, P., Menot, L.; Buhl-Mortensen, P., Narayanaswamy, B. E., Smith, C. R., Tittensor, D. P., Tyler, P. A., Vanreusel, A., Vecchione, M. (2010). 'Deep, diverse and definitely different: unique attributes of the world's largest ecosystem', *Biogeosciences* **7**(9): 2851-2899.

Shepard, F. P. & Dill, R. F. (1969), *Submarine Canyons and Other Sea Valleys*, Rand McNally & Co., Chicago, USA.

Soliman, Y. & Rowe, G. (2008), 'Secondary production of *Ampelisca mississippiana* Soliman and Wicksten 2007 (Amphipoda, Crustacea) in the head of the Mississippi Canyon, northern Gulf of Mexico', *Deep-Sea Research Part II* **55**(24-26), 2692–2698.

Sorbe, J. (1999), 'Deep-sea macrofaunal assemblages within the Benthic Boundary Layer of the Cap-Ferret Canyon (Bay of Biscay, NE Atlantic)', *Deep-Sea Research Part II* **46**(10), 2309–2329.

Tyler, P., Amaro, T., Arzola, R., Cunha, M., de Stigter, H., Gooday, A., Huvenne, V., Ingels, J., Kiriakoulakis, K., Lastras, G., Masson, D., Oliveira, A., Pattenden, A., Vanreusel, A., Van Weering, T., Vitorino, J., Witte, U. & Wolff, G. (2009), 'Europe's Grand Canyon: Nazaŕe Submarine Canyon', *Oceanography* **22**(1), 46–57.

Van Weering, T., De Stigter, H., Boer, W. & De Haas, H. (2002), 'Recent sediment transport and accumulation on the NW Iberian margin', *Progress in Oceanography* **52**(2-4), 349–371.

Vanney, J. & Mougenot, D. (1990), 'A gouf-type canyon, the Canhao Da-Nazare (Portugal)', *Oceanologica Acta* **13**(1), 1–14.

Vetter, E. & Dayton, P. (1998), 'Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system', *Deep-Sea Research Part II* **45**(1-3), 25–54.