THE UNIVERSITY OF EDINBURGH

SCHOOL OF GEOSCIENCES

Eunice worm from Mingulay Coral Reef (Henry, 2003).

ENVIRONMENTAL VERSUS SPATIAL DRIVERS OF COLD-WATER CORAL REEF-ASSOCIATED BIODIVERSITY IN THE SEA OF HEBRIDES (SCOTLAND)

BY

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ABSTRACT

The dynamic between spatial and environmental variability with biodiversity is well studied in shallow tropical reefs. Cold-water coral (CWC) reefs hold similarly high levels of biodiversity and are important sites of marine biogeochemical cycling, however, the processes that create biodiversity in these systems are less studied. These systems face threats of habitat destruction from deep-sea fishing, fossil fuel extraction and mining. Thus, for their effective conservation it is necessary to know which factors can capture and predict biodiversity in CWC reefs. This study aims to explain the extent to which spatial and environmental variables can reveal patterns in biodiversity in a *Lophelia pertusa* (Scleractinia) reef, as well as determine which level of taxonomic resolution is necessary to distinguish these ecological patterns. I tested remotely sensed environmental data with benthic community diversity data at three varying taxonomic levels obtained from the Mingulay Reef Complex, in the Sea of the Hebrides, Scotland. Canonical correspondence analysis (CCA) outputs revealed that gradients in bathymetry and hydrography explained a significant ($p=0.03$) proportion of mollusc species assemblage (83.92%), with a marked change in feeding type. Phylum-level ($p=0.66$, 54%) and class-level ($p=0.6$, 60%) analyses were insignificant, but indicate that increasing taxonomic resolution is necessary to extract meaningful outcomes from biodiversity data. These results confirm that remotely sensed environmental and spatial data is useful to explain significant proportions of species diversity in cold-water coral reefs.

CONTENTS

ACKNOWLEDGEMENTS

LIST OF ABBREVIATIONS

[CWC] – Cold Water Coral

[MPA] – Marine Protected Area

[OA] – Ocean Acidification

[RQ] – Research Questions

[MRC] – Mingulay Reef Complex

Data and Analysis

[C_{AVE}] - Average Current Speed

[C_{MAX}] – Maximum Current Speed

[C_{SD}] – Standard Deviation of Current Speed

[BPI] – Bathymetric Position Index

[BTM] - Benthic Terrain Modeler

[CCA] – Canonical Correspondence Analysis

[pCCA] – Partial Canonical Correspondence Analysis

[ANOVA] – Analysis of Variance

1. INTRODUCTION

Figure 1. Aggregation of live *Lophelia pertusa* in Mingulay Reef Complex (Roberts, 2013).

1.1 Background and Rationale

Scientific literature regards tropical coral reefs as sites of significant biodiversity and nutrient cycling which justifies their economic and ecological importance. Cold water coral (CWC) reefs receive significantly less attention in published literature, but research shows that they harbor similarly high levels of biodiversity (Jensen and Fredriksen, 1992; Henry and Roberts, 2007; Roberts *et al.*, 2008) while being more globally distributed than their tropical counterparts (Roberts 2006; Roberts *et al.*, 2009a, 2009b; Davies and Guittone, 2011). Unlike tropical reefs, CWC reefs do not rely on photosynthesis but rather on the delivery of phytoplankton, zooplankton and organic matter from the primary productivity of surface waters (Duinveld *et al.*, 2004, 2007; Kiriakoulakis *et al.*, 2005; Davies *et al.*, 2009). Independence from photosynthetic symbionts allows CWC reefs to occur below the photic zone, often at depths > 50 m. CWC reefs are formed globally by only six species of azooxanthellae scleractinian coral species capable of building reef frameworks (Appendix A., Table A.1*)* (Cairns, 2007; Roberts and Cairns, 2014; Henry and Roberts, 2015). One of these species is *Lophelia pertusa* (Linnaeus, 1758), which will be the focus of this study (Figure 1).

L. pertusa reefs grow under specific biological, physical and geochemical requirements which enhance food delivery from the surface and support the recruitment of young corals (Flögel *et al.*, 2014). They engineer carbonate mounds over glacial-interglacial time (Roberts, 2006; William *et*

al., 2006; Kano *et al.*, 2007; Raddatz *et al.*, 2011) which creates a structural habitat that modifies the local hydrography and seafloor (Davies *et al.*, 2009). Although these reefs are formed by one primary species of coral, the coral framework provides an environment in which many marine fauna can establish, creating high levels of biodiversity (Henry and Roberts, 2007; van Oevelen *et al.*, 2009; Lessard-Pilon *et* al., 2010; Cathalot *et al.*, 2015; Rovelli *et al.*, 2015). These habitats often include benthic fauna such as filter-feeding sponges, predatory worms as well as pelagic fish and shark species, many of which are commercially valuable (Costello, 2005; Henry *et al.*, 2013b).

1.2 Threats to Cold Water Coral Reefs

CWC reefs are valuable to conserve because they maintain high biodiversity and are sites of regional biogeochemical cycling (Jobsvogt *et al.*, 2004; van Oevelen *et al.*, 2009; Findlay *et al.*, 2014). However, they face long-term threats through human-induced industrial and environmental processes. A study examining CWC sites in the NE Atlantic discovered that 82% of fish species recorded were commercially valuable (Costello, 2005). It has also been observed that CWC sites are used by recreationally valuable shark species for lifecycle propagation (Henry *et al.*, 2013b). Studies have also discussed the medical potential of the genomic diversity from the deep sea (Jobsvogt *et al.*, 2004). Still, the lack of widespread knowledge surrounding CWC reefs leads them to be undervalued in the market. Industrial processes can damage CWC reef habitats through bottom trawling fishing methods, fossil fuel extraction and deep-sea mining (Koslow *et al.,* 2000; Roberts, 2006; Hennige *et al.,* 2015; Büscher *et al.,* 2017). Even reefs that do occur in MPAs show historical damage through evidence of trawl marks and human waste (Roberts et al., 2009a). As many species are dependent on coral reef frameworks, damage to CWC sites can result in a loss in biodiversity.

Human induced environmental changes also threaten CWC reef, most notably through ocean acidification (OA). Unlike tropical corals, cold-water corals are not vulnerable to the loss of photosynthetic symbionts; however OA stresses the biomineralisation of carbonate skeletons in *Lophelia pertusa* (Hall-Spencer *et al.*, 2008). On short timescales (21-89 days) *L. pertusa* is resilient to it's effects(Roberts et al., 2005; Roberts et al., 2009b; Hennige *et al.*, 2014) but *L. pertusa* is threatened by long-term exposure to acidic waters (Hennige et al., 2015). Although the effects on OA in CWC reefs as a whole are still not fully understood, it is likely the effects of

climate change are being felt at all levels in the ocean. The loss of biodiversity and ecological functioning through the mechanisms listed above highlight the importance of studying CWC reefs; through scientific study, we can close the discrepancy between their real value and their perceived industrial value.

1.3 What we Already Know about Biodiversity

The high biodiversity that *Lophelia* reefs maintain are a product of the unique environmental and spatial characteristics they create (Serrano *et al.*, 2006; Henry *et al.*, 2009; Henry *et al.*, 2010; Henry and Roberts, 2014b), most of which enhance the delivery of food-rich waters to the benthic boundary layer (Ritzrau *et al.*, 1997; Kiriakoulakis *et al.*, 2005; Duinveld *et al.*, 2007; Davies *et al.*, 2009). This is why the abundance and biodiversity of reef-associated species have niches dependent on both the delivery of nutrients through gradients in hydrology and topography (Wigham *et al.*, 2003; Witte *et al.*, 2003; Ruhl and Smith, 2004; Ruhl, 2008, van Oevelen *et al.*, 2009; Cathalot *et al.*, 2015; Rovelli *et al.*, 2015). Many of these environmental parameters interact however; with many combinations of biotic and abiotic factors it is difficult to separate which factors are important.

Our lack of knowledge surrounding the ecology of deep-sea fauna limits our ability to understand the structuring of biodiversity; still, studies done on *Lophelia* can be useful as many of its associated species like bivalve molluscs and filter feeding tunicates share a similar trophic level (Duinveld *et al.*, 2007). The reef relies on particle delivery for its food, and often CWC reefs will occur in areas with above average primary productivity (Guinotte *et al.*, 2006). Because reefs are driven by food particle delivery (Frederiksen *et al.*, 2004; Mortensen and Fosså, 2006; van Soest *et al.*, 2007; Cordes *et al.*, 2008), the surrounding hydrology of these reefs is one of the most important ecological processes to consider when concerning biodiversity; several studies point to this being the case. In the Mingulay Reef Complex (MRC), a reef off the west coast of Scotland, currents move from east to west (Davies *et al.*, 2009), and research on the biodiversity of this site reveals that community assemblage is also structured from east to west (Roberts *et al.*, 2009). In the same reef complex, aspect (direction of steepest slope) had some associations with biodiversity as well, likely due to how these slopes encounter water currents (Henry *et al.*, 2009). Variances in community assemblage have also been observed with seafloor structure such as slope and rugosity (Flach and Thomasen, 1998; Gage *et al.*, 2000; Hughes and Gage, 2004), which can create current amplification or turbulence that suspends particles and enhances food delivery (Thorpe, 1992; Davies *et al.*, 2009).

Still, there is more to learn about what creates beta diversity on CWC reefs, as there are so many interacting factors, and information on the ecology of the deep-sea species associated with *Lophelia* reefs is not widely available. This is partly because access to reefs require expensive technology. Yet, it is still useful to study CWC biodiversity and attempt to discover which factors are the most important in driving biodiversity on these reefs. Not only will this expand our knowledge of deep-sea ecosystems, but it will aid in predicting and modelling deep sea biodiversity in the future. By understanding what creates biodiversity, we can better conserve it. Fortunately, access to technology capable of studying coral reefs has improved and become more widely available, which increases our research capabilities and scientific understanding.

1.4 Using Remote Sensing to Study Reefs

The advancement of remote sensing technology has been monumental in the discovery and study of coral reefs. By combining field-based study and remotely sensed observations, some studies have been able to explain differences in species composition and model biodiversity in tropical coral reefs (Becking et al., 2006; Harborne et al., 2006; de Voogd *et al.*, 2006). Remote sensing is done commonly through optical methods (light and images) or through acoustic methods. In CWC reefs, only acoustic methods are applicable as optical methods do not work at the depths in which CWC commonly occur (Knudby et al., 2007). This is partly why deep-sea coral reefs are relatively less studied than their tropical counterparts as ecological information is significantly harder to obtain. The study of CWC reefs has been greatly advanced through multibeam echosounder technology. Acoustic data has been used to discover, map and model CWC reefs (Wilson, 2006; Wilson et al., 2007; Davies et al., 2008; Dolan et al., 2008), and explain patterns of coral reef composition (Roberts et al., 2003). Integrating remotely sensed data with ground-truthed data in the form of images or benthic samples improves the quality of information gained from acoustic remote sensing.

1.5 Study Objectives

This study aims to investigate the extent to which spatial and environmental variables can explain biodiversity at the Mingulay Reef Complex, as well as investigate which level of taxonomic resolution is appropriate to do this. The Mingulay Reef Complex (MRC) is a *Lophelia pertusa* reef located in the Sea of the Hebrides (Figure 2), occurring between ~120-180m. Using benthic samples from the MRC, I will identify its main taxonomic groups. Using a database of remotely

sensed environmental variables, I aim to identify which variables are ecologically related to species assemblage. I pose two main research questions regarding biodiversity.

1.6 Research Questions and Hypotheses

RQ1: Do spatial and environmental variables influence β Diversity on cold water coral reefs?

H$_1$ – Spatial and environmental variables will explain a significant (p>0.05) proportion of biodiversity.

H$_{10}$ – There will be no significant effect of spatial and environmental variables on biodiversity.

RQ2: Does taxonomic resolution have a significant effect on the outcomes of this analysis when using data from the same samples?

H$_2$ – Increasing taxonomic resolution (species/phylum) will increase significance of analysis with data from the same sites.

H$_{20}$ – There will be no significant change in model fit with increasing taxonomic resolution.

2. METHODS

2.1 Cruise, Obtaining Samples and Extracting Environmental Variables

2.1.1 *Obtaining Benthic Samples*

Benthic samples were obtained from the RRS *Discovery* cruise D366/D367 which departed on June 2011. Among other experiments, several benthic samples were taken and stored for later study (*see cruise report by* Achterberg and Richier, 2012). Locations were sampled from the MRC (Figure 2) on the 8-9th of June (9 samples) and the 7-8th of July, 2011 (7 samples). Benthic samples were collected using a van Veen grab sampler, (model and make not recorded in the cruise report) taking benthic samples of 100 cm^2. Due to the nature of this sampler, only benthic, slow-moving organisms were captured.
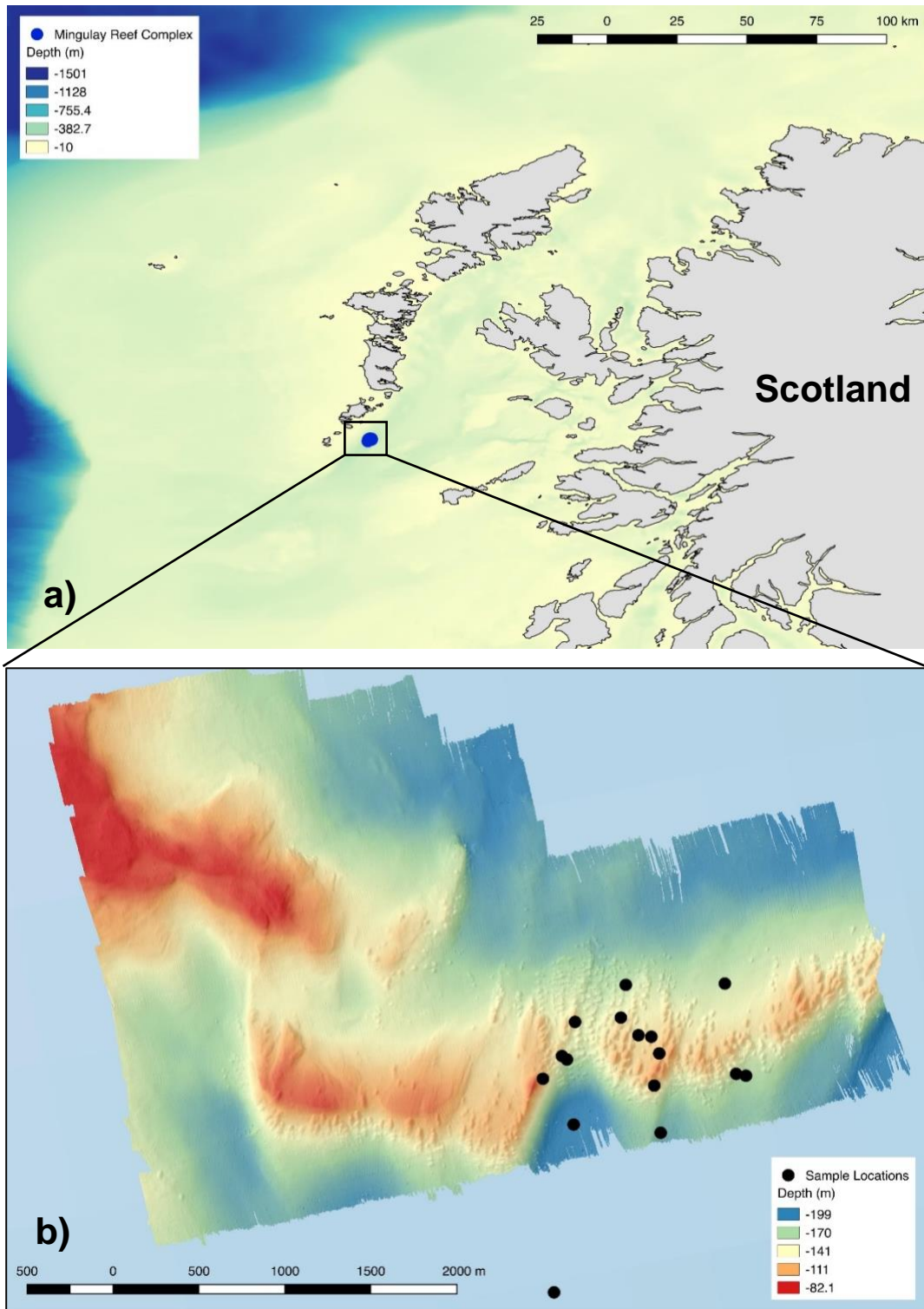
Figure 2. Map of study sites: a) Regional position of Mingulay Reef Complex in the sea of the Hebrides and b) Bathymetric map of sample sites in the MRC using multibeam acoustic data. Note one sample is outside the map boundary, this site was a dead coral site at 164 m depth.

The 16 samples were brought to the surface and stored in sealed buckets at -20ºC in ethanol and 4% borax-buffered formalin for preservation (Achterberg and Richier, 2012). It is important to note that samples were obtained in early June and July, during which temporal variation may have taken place. Sample locations were mapped in QGIS version 2.18.15 using data from a multibeam acoustic survey done in June and July, 2003 (Figure 2) (Roberts *et al.*, 2005).

2.1.2 *Collecting Hydrographical Variables*

I obtained data on current speed from a 3-D hydrodynamic model of the Mingulay reef complex created by Henry *et al.* (2013). This was a fine-scale model with a 100m horizontal resolution. As hydrography is tidally driven and varies over time (Davies *et al.*, 2009; Navas *et al.*, 2014), the model was run for two weeks over half a lunar cycle to capture the variability of currents (for detailed methods see Henry *et al.*, 2013a). The outputs of the model were average current speed (C_{AVE}), maximum current speed (C_{MAX}) and the standard deviation (C_{SD}) to represent variability in current. The outputs were coordinate-specific to the grab sites and were recorded in m s^{-1}. Current speed is a useful parameter to record as current speed has been observed to affect the uptake and delivery of food to *Lophelia pertusa* communities which has ecological implications for similar filter-feeding fauna (Mortensen, 2001; Davies *et al.*, 2009; Purser *et al.*, 2010).

2.1.3 *Extracting Bathymetric Variables*

All spatial variables used in the dataset (bathymetric position index (BPI)), rugosity, aspect, slope and depth) were obtained from a multibeam sonar survey conducted in June and July, 2003 (Roberts *et al.*, 2005). Multibeam sonar surveys were done using an EM2000 Multibeam Echo Sounder (MBES, Kongsberg-Simrad Ltd.), which works by sending out acoustic signals and measuring the strength of the reflected acoustic signal (Figure 3). The reflectivity can change with topography and substrate type, which produces a greyscale image. This can be inputted into a geographical information system to create a bathymetry model of the seafloor (Figure 3)(details in Roberts *et al.*, 2005). This data was analysed in ArcGIS 9.2, ESRI with a benthic terrain modeler (BTM) using routines from Jenness (2002) to calculate BPI, rugosity, aspect, slope and depth. Bathymetric variables were extracted for each of my 16 grab stations with a 10m buffer diameter. Detailed information on using GIS to calculate these variables is also available in Evans (1980) and Wilson *et al.* (2007).

Bathymetric Position Index

Bathymetric Position Index (BPI) is a marine version of Topographic Position Index (TPI) and represents how elevated or depressed a location is in the context of the surrounding seafloor. Positive values represent a peak in the seafloor and negative values represent a depression (Wilson *et al.*, 2007). BPI can affect the hydrology and delivery of nutrients to a reef (Frederiksen *et al.*, 1992; White *et al.*, 2005; Thiem *et al.*, 2006). As it's been demonstrated that certain animals show compatibility with certain types of terrain (Roberts *et al.*, 2003), it is a useful parameter to capture the spatial variability between sites.
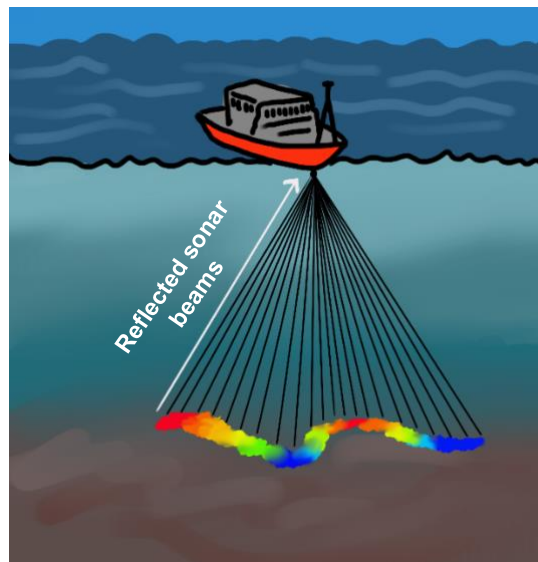
Figure 3. Remotely sensed multibeam sonar surveys are done by measuring reflectance and angle of acoustic signals using a multibeam echosounder. This creates a bathymetry map of the seafloor which can then be used later in GIS programs (adapted from British Antarctic Survey, 2015).

BPI is relative variable which is directly influenced by the spatial scale at which it is being calculated. It is calculated using a raster grid of a defined spatial scale, it is then calculated to indicate which specific pixel is at an elevation or depression. In this case, it was calculated both at broadscale and finescale, and was later standardised.

$$\textbf{BPI} = \textbf{Z}_{\textbf{grid}} - \textbf{focalmean} (\textbf{Z}_{\textbf{grid}}, \textbf{circle, r})$$

Where Z_{grid} is the raster bathymetry grid and focalmean is the mean of the raster values in a circle of a given radius.

<u>Rugosity</u>

Rugosity, or 'roughness' of the seafloor, is a ratio between the surface area and planar area of a 3x3 square. It was calculated as thus:

**rugosity = Surface area of 3x3 neighbourhood /
Planar area of 3x3 neighbourhood**

With this calculation, flat areas will have a value of 1 and rougher areas will have higher rugosity values. Rugosity has been used in several marine studies (Lundblad *et al.*, 2006; Henry *et al.*, 2010), and often, the supply of food particles and larvae is determined by topography and seafloor relief (Flach and Thomsen, 1998; Gage *et* al., 2000; Hughes and Gage, 2004). While BPI is useful for estimating relative position on the seafloor, rugosity is useful for estimating the overall variability in the surrounding terrain (Wilson *et al.*, 2007) and was thus included as a variable.

<u>Aspect</u>

Aspect describes the direction of the steepest slope in a given window, facing in degrees, and although it has been used in other marine studies (Hirzel *et al.*, 2002; Patthey 2003; Cleary and de Voogd, 2007), it has not been used as extensively as other indices such as slope have (Wilson *et al.*, 2007). This is because aspect is only relevant as an explanatory variable if the surrounding hydrography is understood, which isn't true for many deep sea systems. Fortunately, the hydrography of the Mingulay reef complex has been studied and modeled (Davies *et* al., 2009; Henry *et* al., 2013a; Navas *et al.* 2014), which enhances the interpretation of aspect. For analysis, this was later transformed into radians; the rationale and methods for this are described later in section 2.3.1.

<u>Slope</u>

The slope of the seabed can determine substrate composition as well as local hydrodynamics which both affect the present benthic community (Mortensen, 2001; Mohn and Beckmann, 2002; Dartnell and Gardner, 2004; Iampietro *et al.*, 2004; Lundblad *et al.*, 2006; Davies *et al.*, 2009; Purser *et al.*, 2010). Consequently, it is important to include in this analysis. Slope was calculated in ArcGIS 9.2 using methods described by Evans (1980) and Wilson *et al.* (2007).

<u>Depth</u>

Lastly, depth (m) was obtained at grab sample site. Depth may be correlated with BPI and rugosity, but it is nonetheless important to sample as studies have noted changes in community

composition with depth (Kazanidis *et al.*, 2015). Depth has implications for the delivery of nutrients from the sea surface and the abundance of live and dead *Lophelia pertusa* (Roberts *et al.*, 2003; Davies *et al.*, 2009).

2.2 Lab Work and Identification

All lab work was done in the Changing Oceans Lab in the University of Edinburgh Grant Institute under the supervision of Dr. Georgios Kazanidis and Dr. Lea-Anne Henry. The purpose of lab analysis was to identify the main taxonomic groups and assemblages in benthic samples to be used alongside environmental data from the 2011 cruise.

To avoid unsafe exposure to formalin, sample buckets were first strained and washed with water using a 0.5mm sieve. The contents of the samples were then placed in a large Pyrex dish and placed in separate jars by phylum. The samples were stored in 75% IMS (Industrial Methylated Spirit) after sorting for preservation. All taxonomic identifications were carried out using a taxonomic key by Hayward and Ryland (2017) (Figure 4). Fauna living attached to corals, such as polychaete worms or bivalve molluscs were removed and placed into jars, however, smaller organisms such as byrozoans or sponges encrusting on other fauna were left intact for future research on species associations in Mingulay. The body size cut-off was > 0.5 mm in length, and those organisms that were not clearly visible to the naked eye

Figure 4. Examples of deep-sea fauna the MRC. a) *Placostegus tridentatus* (Fabricius, 1779), a polychaete worm. b) Actinaria sp., an sea anemone. c) Cheilostomatida sp., an encrusting bryozoan. (Henry, 2003).

were sorted using a simple microscope. Phylum sorting took several months to complete as several buckets had large abundances of fauna. The phyla observed were recorded as
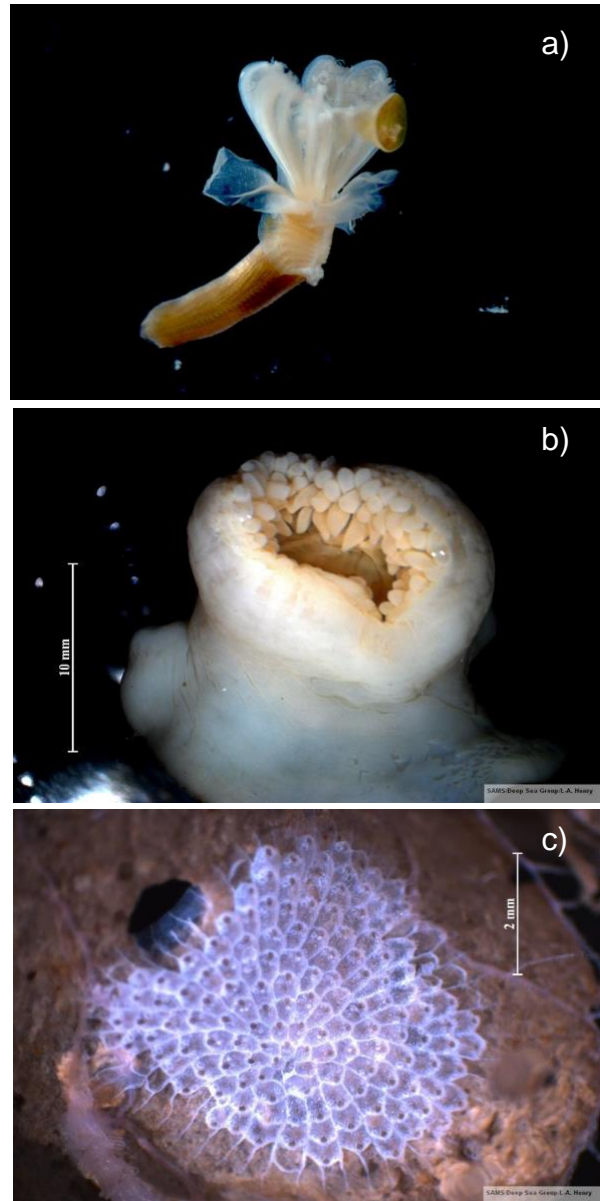
present/absent for each sample. I analysed the largest 6 samples myself and the remaining 10 samples were sorted to phylum with the help of post-doctorate Dr. Georgios Kazanidis.

After phylum sorting, I sorted all samples to class level using the same methods noted above. For most phyla, this was possible, however for Porifera, Nematoda, and Bryozoa, this was not achievable as taxonomic identifications were too advanced for the time constraints of the project. For samples with only one specimen of the above phyla, this would not affect the data as classes were recorded as present/absent, however in samples with multiple species of Porifera, Nematoda or Bryozoa, it was difficult to determine how many classes were present and absent. In these cases, the data remained at phylum level for their classifications.

Specimens in the phylum Mollusca were identified to species-level (see Appendix A, Table A.2). I chose Mollusca as species in this phyla had distinguishing characteristics, allowing for fluid identification. I also observed that species abundances showed significant variation in the samples, and thus it could be used to capture the variability between coral sites. Abundance and presence of the Mollusca species in each sample was recorded (Appendix C). Species were identified using the key by Hayward and Ryland (2017), and accepted taxonomic names were checked using the WoRMS website (World Register of Marine Species) (WoRMS Editorial Board, 2018).

Lastly, it has been noted in several studies that certain species are associated with the amount of live or dead *Lophelia* in CWC reefs (Mortensen and Fosså, 2006; van Soest *et al.*, 2007; Roberts *et al.*, 2008; Kazanidis *et al.*, 2015). Some of the variation in my data may be a result of this, therefore I included this as a category in my data. Each sample was sorted into three categories: live coral, dead coral, and mixed (Figure 5).

Figure 5. Categorical classifications of coral colonies. Coral samples were classified into three categories dependent on the amount of live and dead coral present. A=live, all or most of the sample is live coral. B= mixed, classified as the sample is a mix of both live and dead coral. C=dead, all or most of the sample is comprised of dead coral rubble (Kazanidis, 2018).

2.3 Data Analysis

2.3.1 *Data Transformations*

I transformed several parameters from their original values to allow for fluid analysis and meaningful outcomes. Aspect dictates the direction a slope is facing in degrees, which is problematic as the difference between values of 359º and 0º is 1 unit, but in statistical software it is recognized as 358º. To account for this, aspect was transformed into 'northing' and 'easting' radians which range from -1 to 1. This has been used in several studies when using aspect as a variable (Hirzel *et* al., 2002; Patthey 2003; Wilson *et al.*, 2007). They were calculated as such:

Northing = cos (Aspect)

Easting = sin (Aspect)

Furthermore, abundance data for Mollusca species were highly variable, with values ranging from 0 to 150+. To standardize the dataset and partially handle sampling error, abundance values were transformed by taking the square root ($\sqrt{Abundance}$). This would not affect the significance of the results.

2.3.2 *Diversity Analysis*

To determine the effects of environmental/spatial variables on biodiversity, I used a Canonical Correspondence Analysis (CCA). Many datasets that combine biodiversity data and environmental variables typically yield noisy data which is challenging to interpret (ter Braak and Verdonschot, 1995), and often natural data fail to meet parametric assumptions (Legendre, 2008). CCAs are useful as they can identify the major environmental contributors to patterns in the data while handling natural variation well (ter Braak, 1995). CCAs will linearly combine and extract synthetic environmental gradients and provide a visual representation which can be used to characterize species 'niches'. First described by ter Braak (1986), CCAs can provide a p-value (test of significance), describe which environmental variables are the most important (individual canonical eigenvalues), and explain what percentage of the variation is described by the given environmental variables (constrained proportion of variance) (Makarenkov and Legendre, 2002). CCAs are similar to RDAs (Redundancy Analyses) in the way they function, however a CCA was more appropriate as we captured the majority of the variation in depth range of coral sites in the MRC (121-185m).

CCAs were run using R Studio Version 1.0.153 (R Core Team, 2018) with the community ecology package "vegan" (Oksanen *et al.*, 2017) (R script in Appendix B). The constraining variables used were average current speed, maximum current speed, category of live/dead/mixed coral, standardized fine-scale BPI, aspect (northing/easting), slope and depth. CCAs were run three times, once with the phylum level presence/absence data, again with the class level presence/absence data, and lastly with the transformed abundance species level data for molluscs. CCAs were run at these varying taxonomic levels to investigate if taxonomic resolution influences outcome of results.

2.3.3 *Checking for Collinearity and Excluding Variables*

To test whether certain environmental variables were correlated with each other and could thus be excluded, I ran non-parametric Spearman rank correlations using RStudio. Environmental variables that were significantly correlated and did not add any ecological meaning to the data were excluded. These are the variables that were excluded:

- Rugosity was excluded due to correlation with slope ($p=2.1e^{-8}$, $R^2 = 0.89$).
- Broad-scale BPI was excluded due to correlation with fine-scale BPI ($p=1.3e^{-9}$, $R^2 = 0.97$).
- Current Standard deviation (C_{SD}) because it was redundant with C_{AVE} and C_{MAX}.

It is important to exclude redundant variables, as having multiple correlated environmental variables can over-fit the model and reduce the extent to which they explain the data. This is also necessary as the degrees of freedom present in this dataset are lower, thus including too many variables diminishes the significance of the analysis.
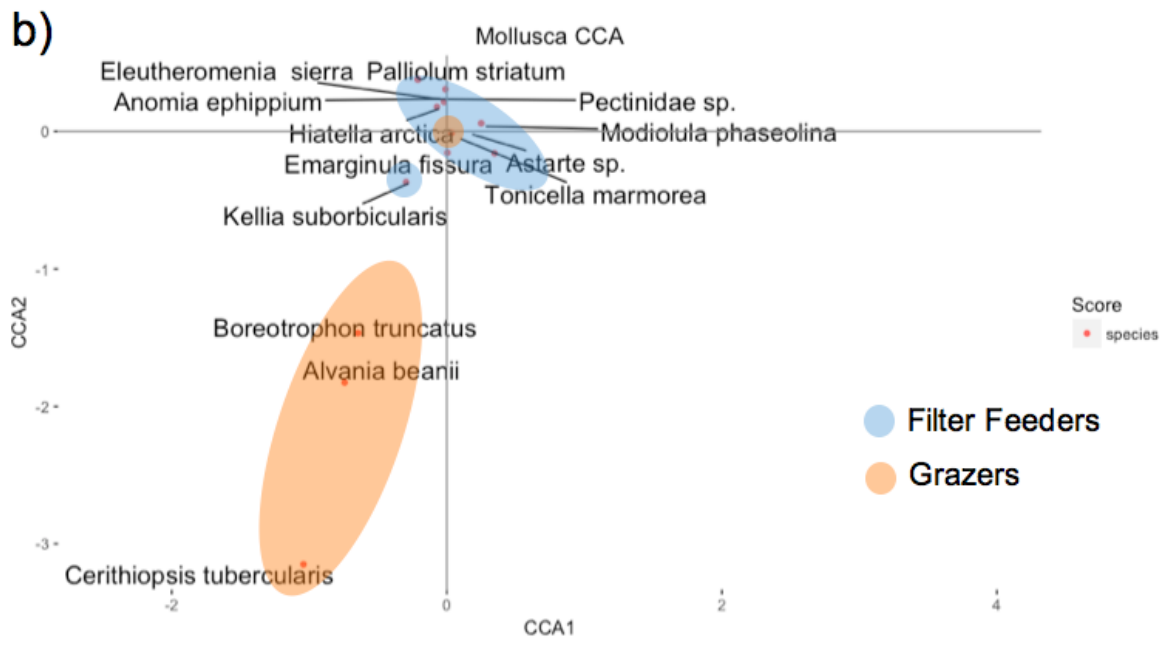
3. RESULTS

3.1 Do Spatial and Environmental Factors influence β diversity?

Table 1. Environmental variables at 16 Lophelia coral sites and mollusc species richness. Most sites consisted of mixed or dead coral, and depth range was between 121-185m. C_{MAX} is omitted from this table.

Sample No.	C_{AVE} m s^{-1}	BPI	Northing (rad)	Easting (rad)	Slope %	Depth (m)	Coral Type	Mollusc Richness
1	0.27	-11	0.39	0.92	3.59	162	dead	8
2	0.27	3	0.58	-0.82	8.92	150	live	4
3	0.30	-11	0.97	-0.25	4.08	167	mixed	5
4	0.31	-11	0.97	-0.25	4.08	124	mixed	7
5	0.30	-18	0.34	-0.94	2.01	185	dead	3
6	0.32	47	-0.18	0.98	11.57	121	dead	4
7	0.34	-3	0.85	-0.52	6.06	153	dead	5
8	0.34	-3	0.85	-0.52	6.06	131	dead	10
9	0.31	47	-0.18	0.98	11.57	147	dead	7
10	0.31	47	-0.18	0.98	11.57	135	dead	4
11	0.34	-3	0.85	-0.52	6.06	162	dead	3
12	0.30	-5	0.90	0.44	5.05	154	mixed	6
13	0.34	-3	0.85	-0.52	6.06	164	dead	6
14	0.34	46	0.39	-0.92	10.44	154	dead	2
15	0.33	47	-0.18	0.98	11.57	134	dead	7
16	0.31	-3	0.85	-0.52	6.06	159	mixed	8

3.1.1 *Species-Level CCA for Mollusca*

a)

Mollusca CCA

b)

Mollusca CCA

15
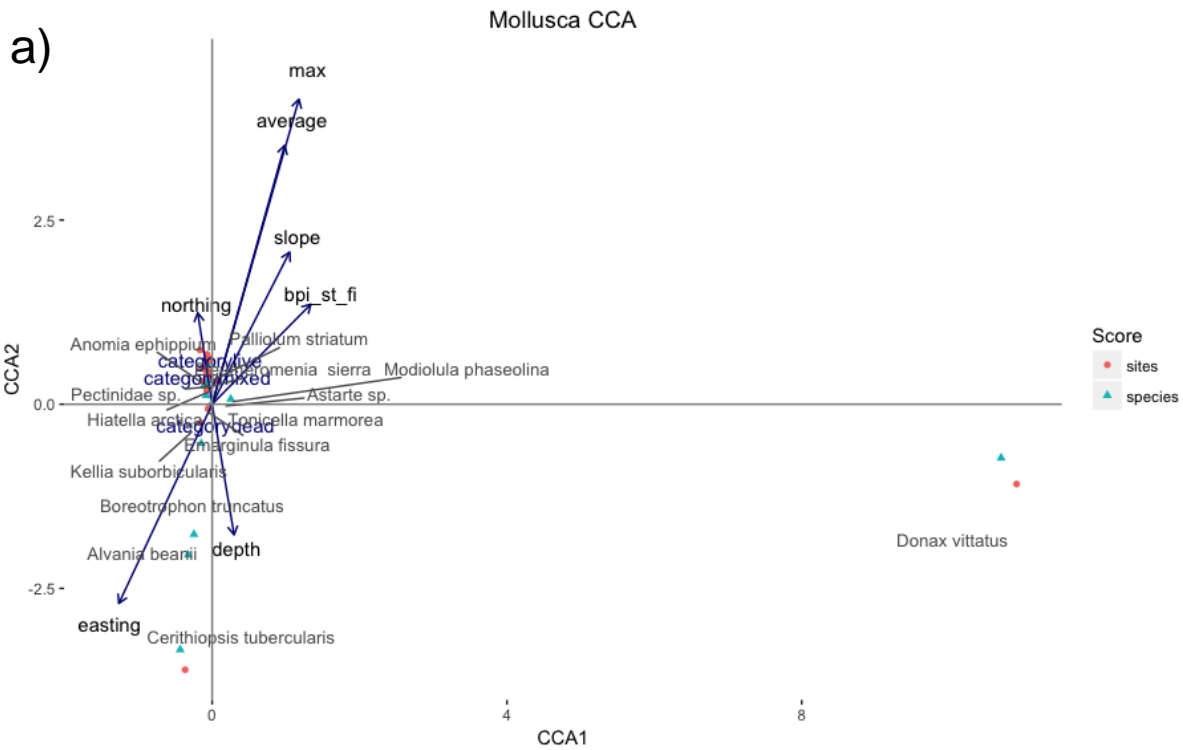
c)

Figure 6. Canonical Correspondence Analysis plots for Mollusca species data showing a) complete plot with species and biplot arrows, b) only species scores and c) only biplot arrows. (Results are on 5/10 degrees of freedom, n = 16, F=3.4782, p=0.03). The plots were separated into their components for ease of viewing. Axes CCA1 and CCA2 represent synthetic pairings of environmental variables that explain the most variance in the dataset. Length of biplot arrows (dark blue) demonstrate the respective weight of a constrained variable on variance, and their direction represents their linear relationship with the data. Similarly, weightings of categorical variables (live, mixed, dead) are represented as a single point by distance from 0. Axes of biplot arrows continue past (0,0). This is not typically shown on CCA plots but is important to note that each axis will extend in both directions on the plot. Species scores (blue triangles) are represented as points, and their nearness to biplot arrows symbolises an association with that specific environmental variable. For more information on interpreting CCA outputs, see ter Braak and Verdonschot (1995).

The species richness of Molluscs ranged between 2 and 10 in coral samples (Table 1), with 14 total species observed (Appendix B). The number and abundance of species showed considerable variation between samples. An analysis of variance (ANOVA) of the CCA showed spatial and environmental variables explained a significant (p=0.03, $F=3.4782_{5/10\ df}$) proportion of mollusc diversity at the Mingulay CWC reef, capturing 83.92% of the data (Figure 6a-6c).

Variables associated with hydrography (average current speed, max current speed, and easting) showed the largest effect on species distribution, distributed most widely on axis 2 (CCA2). Bathymetrical variables (slope, BPI and depth) also affected the distribution of species, however from the plot, it is evident that slope and BPI affect species distribution on a similar axis to easting and current sped, which is different from depth. Northing (northerly aspect) and category (live, mixed and dead coral) showed little effect on the distribution of species. Axis 2 (CCA2) showed most of the environmental variance characterized by gradients in hydrological and bathymetrical variables (for full CCA outputs, see Appendix D).

Those species associated with negative CCA2 values characterised by west-facing slopes with low current speeds, slope, and BPI, were mostly all deposit feeder/ grazer gastropod mollsucs that use a radula to scrape food from surfaces (Figure 6b). Differently, those species associated with higher CCA2 values, characterized by faster current speeds, steeper slopes and high BPI values, were mostly filter feeding bivalves. There was little variation on the x axis (CCA1 axis) of species assemblage, bar the presence of *Donax vitattus*. However, this presents that mollusc species assemblage and abundance is distributed by spatial and environmental variables.

3.2 Does taxonomic resolution affect model fit?

3.2.1 *Phylum-Level CCA*

There were 11 phyla present in the benthic samples, and there was little variance in the presence/absence of phyla. Presence-Absence data at phylum level showed no significant patterns when constrained by environmental variables ($p=0.665$, $F=0.805_{on\ 5/10df}$), explaining 54.70% of the data (Figure 7a,b). Filter feeding phyla (Porifera and Tunicates) were more associated with faster current speeds and east-facing slopes, similar to filter-feeding molluscs in Figure 6. However, the constraining environmental variables show similar length (weightings on the data) and extend in most directions, similar to the species scores. It is thus difficult to extract any meaningful information from this analysis.
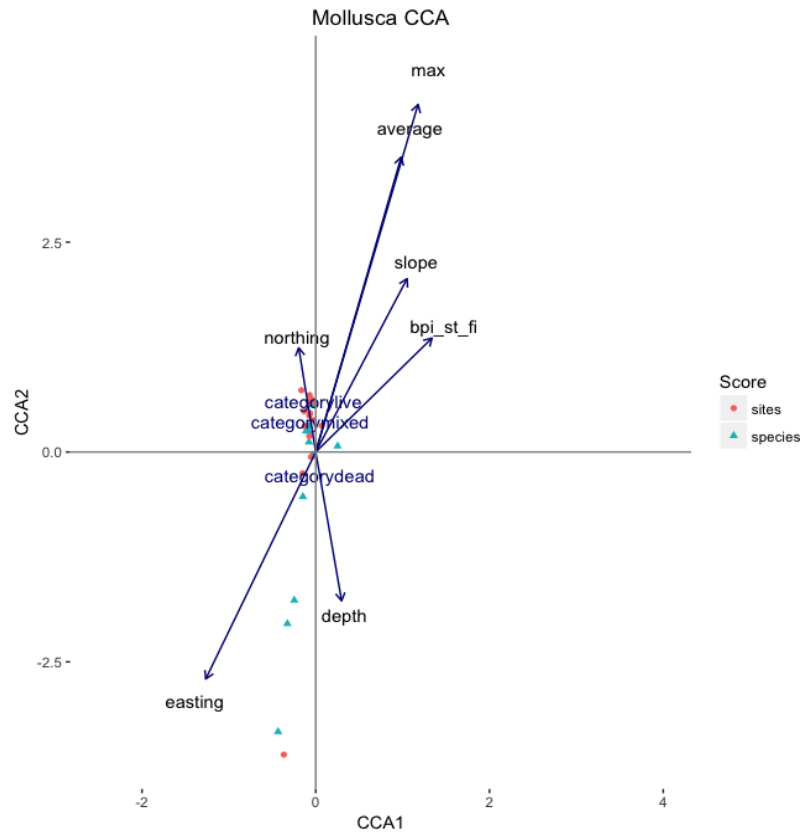
Figure 7. Canonical Correspondence Analysis plots for presence-absence phylum data showing a) complete plot with species and biplot arrows, b) only species scores. The plots were separated into their components for ease of viewing, note scales for axes are different between 2a and 2b.

3.2.2 *Class-Level CCA*

There were 14 taxonomic classes present in the benthic samples, with class diversity ranging between 7 and 13. Similarly to the phylum-level analysis, there was not a significant amount of variance between samples. The constraining environmental variables explained 58.41% of the variance in data, and this was not statistically significant (p=0.61, $F=0.9251_{5/10\ df}$). Yet unlike the phylum-level analysis, easting, BPI, slope, average and max current speed all showed to have more weight on the data than northing and coral category (Figure 8a,b), which is similar to the species-level mollusc analysis. This indicates that increasing taxonomic resolution reveals these trends.
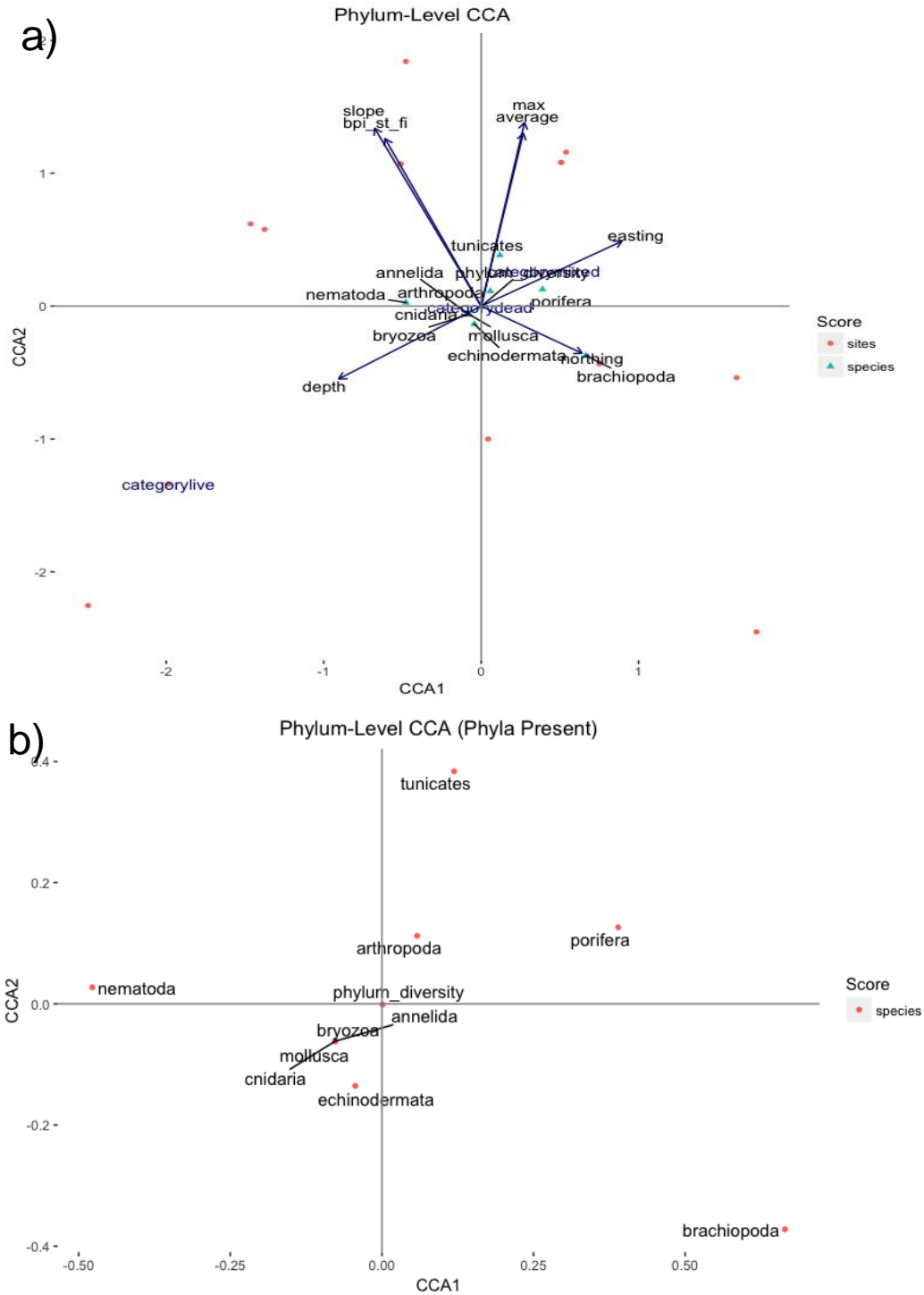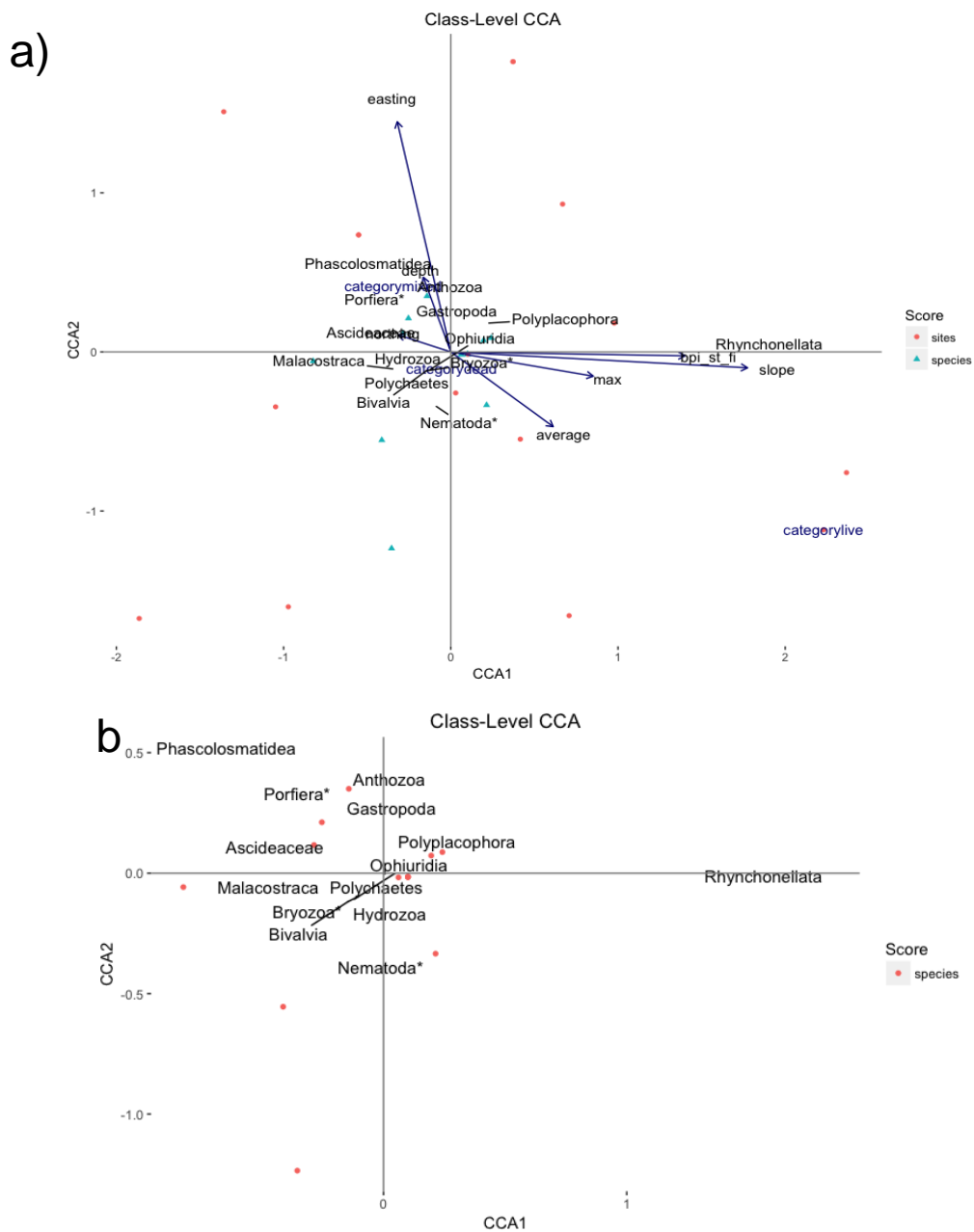
a)

b)

Figure 8. Canonical Correspondence Analysis plots for presence-absence class-level data showing a) complete plot with species and biplot arrows, and b) only species scores. The plots were separated into their components for ease of viewing, note scales for axes are different between 3a and 3b. It must be noted that Porifera, Bryozoa and Nematoda were left at phylum level while the rest are identified to class.

3.2.3 Comparing taxonomic resolution

Table 2. Results of CCA test at 3 different taxonomic levels

Taxonomic Level	% Variance explained	% Residual Variance	p-value
Phylum	54.70%	45.30%	0.665
Class*	58.41%	41.88%	0.61
Species **	83.92%	16.08%	**0.03**

* Some classes were unidentifiable and left at phylum level (Porifera, Nematoda and Bryozoa)
**Species level analysis was done only for phylum Mollusca

Comparing the three CCA outputs at phylum, class, and species level, it is evident there is a stepwise increase in model fit (% variance explained) and significance (p-value) with increasing taxonomic resolution (Table 2), when using the same environmental data. It must be noted that species-level analysis would have been more comparable to phylum and class if all phyla had been identified, but this was not possible with the time constraints. Nevertheless, even with Molluscs identified to species, the significance of CCA analysis increased significantly.

4. DISCUSSION

The study results conclude that the selected environmental variables (northing, easting, current speed (ms^{-1}), slope, BPI, depth and coral type) significantly affect mollusc community assemblage ($p < 0.05$) and capture 83.92% of biodiversity in the MRC (Figure 6). Current speed (average and maximum) and easting had the largest effect on species assemblage, with topographical variables such as slope, BPI and depth having medium effect. Northing and coral type had the least effect on the data. Overall, it is evident from this analysis that the selected environmental variables do drive beta diversity of molluscs, in which I reject the null hypothesis

(H_{10}) and accept H_1, that my selected environmental variables explain a significant proportion of biodiversity in the Mingulay Reef Complex.

When using the same environmental data with phylum and class level presence/absence data, the results were insignificant (Figures 7,8, Table 2). Although species level data was only available for Molluscs, the results suggest that increasing taxonomic resolution improves the significance of biodiversity analysis (Table 2), in which I reject null hypothesis 2 (H_{20}) and accept the alternative (H_2), that increasing taxonomic resolution increases the significance of biodiversity analysis.

4.1 Species-Level Analysis for Molluscs

Mollusca are among the most abundant phyla in my samples, which is consistent with findings from other studies (Kazanidis *et al.*, 2015). Although species-level analysis was only possible for this taxonomic group, I am confident it was ecologically significant to sample, as their identification is straightforward, they are present in every sample, and their abundances and diversity was variable throughout the dataset. It was found that Mollusca species assembly was linearly related to the environmental variables ($n = 16$, $F=3.478_{5/10\ df}$, $p=0.03$, pseudo $R^2 = 83.92\%$) (Figure 6).

4.1.1 *The effects of hydrography on species assemblage*

Aspect and current speed had the strongest effect on species assemblage overall. While aspect is not directly a hydrographical variable, it functioned on the same axis as current speed in the CCA (Figure 6), and there is evidence from studies to suggest that hydrography has a relation to aspect in the MRC (Davies *et al.*, 2009). Tidal currents cycling from the Sea of the Hebrides pass over the MRC from NE to
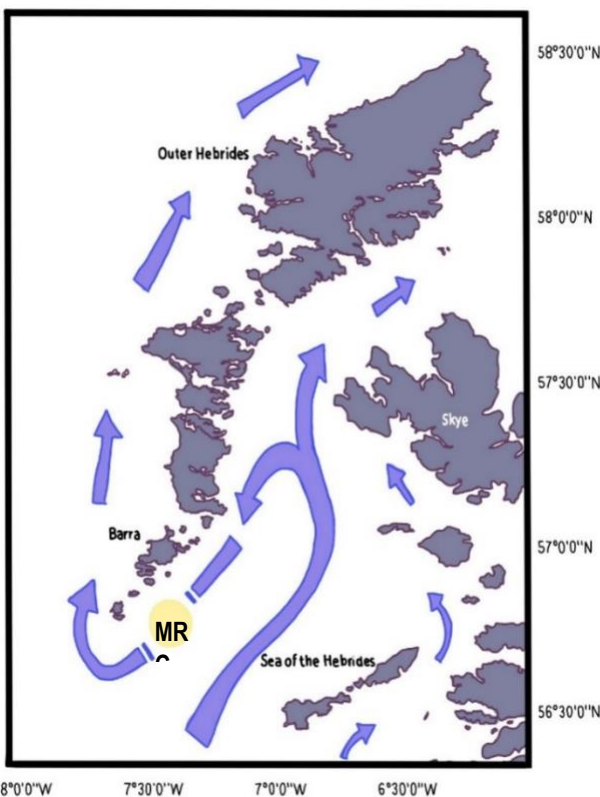

Figure 9. Map of surface water currents in the Sea of the Hebrides (adapted from Navas et al., 2014)

SW (Figure 9), which structures hydrographical variables from east to west (Davies *et al.*, 2009), with higher current speeds occurring in the west near the island chain than in the east (Navas *et al.*, 2014). The interaction between internal waves, seafloor topography and currents have been documented to affect downwelling in marine systems, which increases food delivery to the benthic fauna (Flach and Thomasen, 1998; Gage *et* al., 2000; Frederiksen *et* al., 2004; Hughes and Gage, 2004; Mortensen and Fosså , 2006; van Soest *et al.*, 2007; Cordes *et al.*, 2008; Duinveld *et al.,* 2012). As *Lophelia pertusa* reefs rely on advected particles from surface waters (Roberts, 2006; Guinotte *et al.*, 2006; Roberts et al.,2009), the spatial structuring of hydrography and downwelling will decidedly play an important role on the species assemblage of these systems (Henry *et al.*, 2009. This is may explain why easting aspect had a larger effect on biodiversity in comparison to northing aspect, as east-facing slopes will be encountering different current speeds and downwelling resulting from the east to west currents that pass. Other studies have also observed that aspect influences the structuring of diversity (Glasby, 2000; Cleary and de Voogd, 2007, Wilson *et* al., 2007; Henry *et al.*, 2009)

Interpreting why current speed has an effect on mollusc assemblage is challenging as there is little available information on the feeding patterns and ecology of the mollusc species present in the samples. The only obtainable information was feeding method: whether the molluscs are filter feeders or grazers that use a radula to eat. In the samples emerged a pattern of feeding mode changing from grazers to filter feeders on as current speed increased on topographic highs and slopes became steeper and more east-facing (Figure 6, 10). This may suggest that the spatial structuring of hydrology impacts the feeding mechanisms of molluscs.
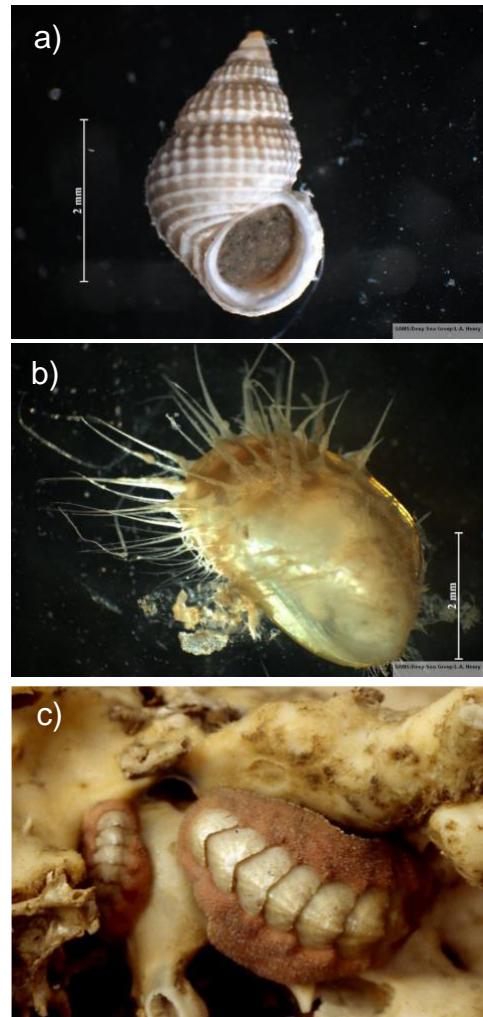

Figure 10. Mollusca species from the MRC.a) *Alvania beanii* (Hanley in Thorpe, 1844), a grazer mollusc. b) *Modiolula phaseolina* (Philippi, 1844), a filter-feeding bivalve. c) *Hanley hanleyi* (Bean, 1844), a chitin grazing on Porifera sponge (Henry, 2003)

Most studies on current speed and food uptake in CWC reefs focus on *Lophelia pertusa* polyps. Lab-based experiments find that low flow speeds (<7 cm s^{-1}) enhance the food uptake by corals, and faster flow speeds decrease the capture efficiency of food by *L. pertusa* (Mortensen, 2001; Purser *et* al., 2010; Orejas *et al.*, 2016). The sites studied here had an average flow speed of 31.3 cm s^{-1}, which is significantly higher than the ideal flow speed for *Lophelia pertusa* predation, however, this measurement is broad, and flow speeds may vary at the benthic boundary layer where molluscs are likely to be wedged in-between pieces of coral and the substrate. It is important to consider, however, that the model used in the study was run for half a lunar cycle (~2 weeks), and that hydrography can vary on the long-term (Navas *et al.*, 2014). Though there is little information on how flow speeds affect the feeding ability of marine molluscs, it is evident that there may be a relationship between hydrography and feeding type.

4.1.2 *Bathymetry and biodiversity (slope, BPI and depth)*

Bathymetric variables are important to the structure and ecological functioning of reefs, and have been used in studies to model and explain significant portions of biodiversity (Hewitt *et* al., 2005; Harborne *et al.*, 2006; de Voogd *et al.*, 2006). In this analysis, slope, depth and BPI were used to investigate how the spatial structuring of the seafloor can influence biodiversity of molluscs (Figure 6). All variables had an equal weight on the data, however slope and BPI functioned on a similar axis to hydrography and aspect, whereas depth affected the data on the opposite axis. Although I consider slope and BPI to be spatial variables, their similar effect to current speed and aspect hints that it is essential to analyse them with consideration to hydrology. Sloped areas alter the surrounding environment (Dartnell and Gardner, 2004) and can cause the amplification of currents (Mohn and Beckmann, 2002, White, 2006), this relationship was also apparent in my own results (Figure 6).

As *L. pertusa* reefs are dependent on tidal downwelling for food delivery, and bathymetric structures that enhance currents and create turbulence will increase the delivery of food to these systems. A study examining the hydrology of the MRC found that *L. pertusa* reefs occurred on sloped areas with high turbulence (Davies *et al.*, 2009). The localised strong currents and mixing created by the rough topography of coral reefs is ecologically important to re-suspend sediments and keep corals clean of sediment (Frederiksen *et* al., 1992; White, 2006). In this case, BPI can be used as a representative of rugosity (as the two are significantly correlated in my dataset). As rugosity increases, turbulence and wave action also increase (Thorpe, 1992).

Because of the relationship between turbulence, food delivery, rugosity and current speed, it is evident that this ecological function may be able to explain why slope and BPI affect mollusc biodiversity in this analysis. If the high current speeds and turbulence created by the topography of the seafloor enhance the food delivery to filter feeding organisms, it does then explain why I found a change in feeding method from grazers to filter feeders with increasing current speed and slope/BPI. This relationship is important enough that it has been used to model and predict locations of CWC systems (Dolan *et al.*, 2008).

Although depth influenced the data, its effect was weaker than the other measured environmental variables, and the method in which it affected the data was hard to distinguish (Figure 6a,6c). Although in tropical reef ecosystems, depth, or variance in depth can influence subsequent biodiversity (Harborne *et* al., 2006; de Voogd *et al.*, 2006), this relationship is less clear when examining deep sea ecosystems. In a study examining the biodiversity of deep sea sponges in the NE Atlantic, there were marked differences in sponge diversity with depth (Kazanidis *et al.*, 2015). However, the depth range between the two studied reefs was large (127m to 800m), and differences in biodiversity could be due to the differing environmental conditions rather than depth. In the MRC, there is little variation in the abundance or distribution of live and dead coral until depths below ~300m (Roberts *et al.*, 2003). Since my study site only ranged from depths 121-185m, it could explain why depth didn't show a significant contribution to mollusc community composition as opposed to other factors such as current speed or aspect; environmental parameters are not likely to change much with this narrow depth range. Yet, it is likely that depth does not affect species community as much as other environmental factors, which is consistent with another study done on the Hebrides seamount (Henry *et al.*, 2014).

4.1.3 *Coral cover and other environmental factors*

Examining the type of coral cover present at study sites is an important factor to as the amount of live coral cover has been shown to affect beta diversity in coral systems (Jonsson *et al.*, 2004; Raes and Vanreusel, 2005; Henry and Roberts, 2007; Henry *et al.*, 2009). Studies show that *L. pertusa* reefs will encounter higher diversity and abundances of fauna in areas with less live coral cover (Mortensen and Fosså, 2006; van Soest *et al.*, 2007; Roberts *et al.*, 2008; Kazanidis *et al.*, 2015). This is because dead coral structures provide niches for encrusting organisms to establish. In my samples, I often found small bivalves nestled inside dead coral polyps. Although coral type is important to biodiversity, in my analysis it had the least impact on the data (Figure 6). This may

be because of several reasons. Firstly, coral types were not evenly distributed throughout my samples. Only one sample contained mostly live coral, a few were mixed, but most samples consisted of coral rubble (Table 1). This may have been inadequate for the statistical program to analyse due to small variance in samples. Secondly, the amount of live or dead coral itself may not be an independent variable, but may be driven by the same environmental conditions that affect molluscs. Since It's been established that hydrology, bathymetry and other environmental factors affect the distribution and viability of *L. pertusa*, it is likely that the amount of live or dead coral cover is not an independent variable. It may still be true that live/dead coral cover is important, but perhaps other environmental conditions such as current speed, aspect and BPI drive more variance than coral cover would.

4.2 How Valuable is Taxonomic Resolution to Studying Biodiversity?

Overall, increasing taxonomic resolution improved the significance of CCA outputs, and increased the pseudo R^2 value (Table 1). The Phylum-level CCA explained 54.70% of the variance with was not significant (p=0.67) (Figure 7), and the class-level CCA explained 58.41% of the variance which was also not significant (p=0.61) Figure 8, table 2). Although the phylum and class level analyses were not significant, the selected environmental variables still explained a distinguishable amount of variance in the data, and the patterns were similar to the ones observed in the species-level analysis (Figure 6). For example, in the class level CCA (Figure 8), bathymetric factors (BPI, slope) and hydrological factors (current speed and easting aspect) showed the highest weight on the data. This hints that the same patterns that drive species assembly in molluscs could be affecting all taxonomic groups as a whole. This may be the case as although there is a high diversity of fauna in deep sea coral reefs such as the MRC, the functional diversity of animals is quite low (Henry *et al*., 2013a), with most species being sessile suspension feeders. Although particular niches are different, the effect that the environment has on the fauna of the MRC as a whole may not be so different, because most species are dependent of the same water currents and such for the delivery of nutrients. However, this cannot be concluded from the present study.

Furthermore, the levels of taxonomic resolution may not be adequate to answer this research question. I included two opposing levels of taxonomy, phylum and class vs species. Phylum and class level may not be the most useful as ecological differences within class groups can still be quite variable. It is possible that an intermediate level of taxonomic resolution, such as order or

family, will be enough to distinguish distinct ecological patterns. However, applying this taxonomic level to my data would not have been possible with the time constraints of the project. Nevertheless, from my results, I would argue that identification to low taxonomic resolution is necessary to extract significant ecological relationships from biodiversity data, in which I accept my second alternative hypothesis, H_2. This is important to know, as lab identification of fauna to species takes time and resources, thus knowing the appropriate level of taxonomic resolution makes the process more efficient.

4.3 Study Evaluation and Considerations

There are several methodological limitations in this study that may have affected the quality of the research. Firstly, there may have been some sampling error. Using grab samples is a good way to acquire benthic samples, but sometimes have issues sampling live organisms as they can disturb sediments (Woods Hole Oceanographic Institution, 2018). Some sampling error could also be a result of faulty or incomplete taxonomic identification on my part. With consideration to my analysis, I used a relatively small dataset consisting of 16 sites, which gives low degrees of freedom. In the CCA, I used 7 constraining variables with my species data, which may have over-fitted my model and led to a type I error (false positive) with the species-level mollusc data. It is difficult to know at which point to omit or include certain variables, especially since I had already omitted several variables from my analysis and there is no 'accepted' ratio of constraining variables to independent data points. In addition to this, I was not able to do a partial CCA (pCCA) through my statistical program. This is usually done when running CCA's to partial out what % of variance is explained by which environmental factors (Henry *et al.*, 2009) therefore, I cannot compare the extent to which spatial or environmental factors explain biodiversity.

Furthermore, some temporal variation could have affected my results. The samples from Mingulay were collected in early June and July (see section 2.1). During the one-month gap, seasonal changes in current, temperature and surface productivity at could have taken place Mingulay (Davies *et* al., 2009; Navas *et al.*, 2014). Resulting changes in coral growth (Mienis *et al.*, 2007), migration of predation which would affect both the species richness and abndace counts for those sites. It is therefore necessary to consider that some variation in the dataset may not be due to the selected environmental variables. Lastly, it would have been useful to collect other environmental variables such as turbidity or temperature, as studies have documented they affect ecological functions in CWC reef systems (Frederiksen *et al.*, 1992; White, 2006; Davies *et al.*,

2009; Roberts *et al.*, 2009b). Any increases in environmental parameters would require an increase in independent samples as well, as to not over-fit the data. Overall, there are several methodological limitations to this study that could have created a type I error in the results.

5. CONCLUSIONS

Linear combinations of current speed, aspect, slope, depth, BPI and coral type explained a significant proportion of mollusc species assemblage. There was a distinct environmental gradient in the sample locations, moving from deeper south/west facing slopes with slow current speeds and low BPIs to shallower north/east facing slopes with faster current speeds and high BPIs, through which mollusc feeding type changed from grazers to filter feeders. Based on information from other studies, it is likely that this gradient is created by increasing food delivery from surface waters, which indicates that the interaction between environmental variables and hydrology is a very important process in creating deep-sea biodiversity. When examining all fauna at phylum or class level, these patterns were not detectable, but it is evident that increased taxonomic resolution is necessary to extract ecological patterns from these types of datasets. These results, and studies like these are important for understanding what drives deep sea reef ecology.

In the future, more research should focus on examining the species-species relationships in deep sea sites. This study was limited as it was focused on the effects of abiotic factors on deep sea biodiversity, but the high trophic diversity present at deep sea sites should hint to the fact that there are many intra and inter-specific interactions that aren't explored to their full potential in marine science. Furthermore, it would be useful to conduct studies that integrate remote sensing, bathymetry, hydrology and species biodiversity in varied *Lophelia* reef locations, as the MRC cannot capture the true diversity of environmental conditions that *Lophelia* reefs actually constitute. By studying deep sea reefs, we can not only improve our own knowledge, but we can help bring to the public attention how valuable these ecosystems are, and perhaps a new understanding of their value will help us protect CWC reefs from human exploitation in the future.

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APPENDIX

Appendix A. Taxonomic Information

Table A.1. Table of major framework-building cold water coral species

Species	
Oculina varicosa	Le Sueur, 1820
Solenosmilia variabilis	Duncan, 1873
Goniocorella dumosa	(Alcock, 1902)
Lophelia pertusa	(Linnaeus, 1758)
Enallopsammia profunda	(Pourtalès, 1867)
Bathelia candida	Moseley, 1881

Table A.2 Taxonomic list of Mollusca species recorded

Species	
Alvania beanii	(Hanley in Thorpe, 1844)
Boreotrophon truncatus	(Strøm, 1768)
Cerithiopsis tubercularis	(Montagu, 1803)
Hiatella arctica	(Linnaeus, 1767)
Anomia ephippium	(Linnaeus, 1758)
Kellia suborbicularis	(Montagu, 18030
Modiolula phaseolina	(Philippi, 1844)
Palliolum striatum	(O.F. Müller, 1766)
Pectinidae sp.	Rafinesque, 1815
Astarte sp.	J. Sowerby, 1816
Donax vittatus	(da Costa, 1778)
Eleutheromenia sierra	(Pruvot, 1890)
Tonicella marmoreal	(O. Fabricius, 1780)

Appendix B*. R Code*

Package Library

```
library(readr)      # for reading my data
library(ggplot2)    # for making plots
library(dplyr)      # for formatting and cleaning data
library(devtools)   # for installing packages from altenative sources
library(permute)    # package needed for ggvegan
library(lattice)    # package needed for ggvegan
library(vegan)       # for running canonical correspondence analysis
library(ggvegan)    # integrating vegan with ggplot2
library(ggrepel)    # avoids overlapping labels
library(praise)
```

Reading in Data

```
phylum <- read_csv("mingulay_biodversity_data.csv")
View(phylum)
class <- read_csv("class_diversity.csv")
View(class)
mollusca <- read_csv("mollusca_transformed v2.csv")
View(mollusca)
praise()
```

Checking correlation

```
object_name <- cor(mollusca$x, y, method="spearman")
summary(object_name)
```

Creating Matrices

```
species_matrix <- as.matrix(mollusca[,21:34])   # matrix of species
phylum_matrix <- as.matrix(phylum[,21:31])      # matrix of all my phyla
class_matrix <- as.matrix(class[,20:33])        # matrix of all my classes
```

Phylum-Level CCA

```
phylum_cca <- cca(phylum_matrix~average+max+bpi_st_fi+category+northing+ easting+slope+depth,
data=phylum)
plot(phylum_cca)                    # Plots CCA using base R
summary(phylum_cca)                 # Summary of CCA outputs ->
                    gives coefficients and more
anova.cca(phylum_cca)               # permutation test results
```

Class-Level CCA

```
class_cca <- cca(class_matrix~average+max+bpi_st_fi+category+northing+ easting+slope+depth, data=class)
plot(class_cca)
summary(class_cca)
anova.cca(class_cca)
```

Species-Level CCA

```
cca <- cca(species_matrix~average+max+bpi_st_fi+category+northing+easting+ slope+depth, data=mollusca)
plot(cca)
summary(cca)
anova.cca(cca)
```

***Appendix C**. Raw Data*

Table C.1. *Raw abundance data for Mollusca species. Complementary environmental data for sites is available in results section (Table 1).*

	Boreotrophon truncatus	*Emarginula fissura*	*Cerithiopsis tubercularis*	*Hiatella arctica*	*Anomia ephippium*	*Modiolula phaeolina*
			Abundance			
1	*6*	*3*	*1*	*3*	*3*	*1*
2	*0*	*0*	*0*	*3*	*2*	*1*
3	*0*	*1*	*0*	*2*	*22*	*1*
4	*0*	*21*	*0*	*32*	*169*	*22*
5	*0*	*1*	*0*	*0*	*0*	*1*
6	*0*	*0*	*0*	*5*	*13*	*0*
7	*5*	*0*	*0*	*5*	*3*	*2*
8	*0*	*2*	*0*	*172*	*97*	*81*
9	*0*	*3*	*0*	*3*	*15*	*2*
10	*0*	*2*	*0*	*2*	*2*	*0*
11	*0*	*2*	*0*	*2*	*1*	*0*
12	*0*	*5*	*0*	*13*	*32*	*13*
13	*0*	*2*	*0*	*16*	*50*	*7*
14	*0*	*0*	*0*	*0*	*0*	*1*
15	*0*	*2*	*0*	*3*	*22*	*1*
16	*0*	*6*	*0*	*49*	*112*	*24*

	Palliolum striatum	*Pectindae sp.*	*Astarte sp.*	*Donax vitattus*	*Euleutheromenia sierra*	*Tonicella marmorea*
1	*0*	*0*	*0*	*0*	*0*	*0*
2	*1*	*0*	*0*	*0*	*0*	*0*

3	1	0	0	0	0	0
4	29	0	0	0	0	2
5	0	0	0	0	0	1
6	2	0	0	0	0	1
7	2	0	0	0	0	1
8	28	1	0	0	1	0
9	4	0	1	0	0	1
10	1	0	0	0	0	0
11	0	0	0	0	0	0
12	1	0	0	0	0	0
13	7	0	0	0	0	0
14	0	0	0	1	0	0
15	2	0	0	0	0	0
16	7	0	0	0	0	1

Appendix D. *Canonical Correspondence Analysis Outputs for Mollusca Species*

	Inertia	Proportion
Constrained	1.0023	0.3039
Unconstrained	0.1921	0.1608

		CCA2	CCA2
Importance of Components	Eigenvalue	0.5019	0.3039
	Prop. Explained	0.4202	0.2545
	Cumulative Prop.	0.4202	0.6747
Accumulated Constrained Eigenvalues	Eigenvalue	0.5019	0.3039
	Prop. Explained	0.5008	0.3032
	Cumulative Prop.	0.5008	0.8040

Species Scores	CCA1	CCA2
Alvania beanii	-0.32630	-2.04482
Boreotrophon truncatus	-0.24701	-1.76558
Emarginula fissura	-0.03698	-0.03723
Cerithiopsis tubercularis	-0.43332	-3.33170
Hiatella arctica	-0.07810	0.11892

Anomia ephippium	-0.08280	0.24703
Kellia Suborbicularis	-0.14748	-0.53258
Modiolula phaseolina	0.25222	0.07051
Palliolum striatum	-0.07107	0.30929
Pectinidae sp.	-0.04291	-0.04998
Astarte sp.	-0.03456	-0.56170
Donax vitattus	10.70618	-0.72910
Eleutheromenia sierra	-0.04291	-0.04998
Tonicella marmorea	-0.11177	0.25142

Site Constraints (linear combinations of constraining variables)

Site	CCA1	CCA2
1	-0.04332	-3.331696
2	-0.02757	0.597863
3	-0.19121	1.383129
4	-0.04794	0.452696
5	0.26778	-0.896443
6	-0.28260	0.299469
7	-0.49218	0.740974
8	-0.04291	-0.049979
9	-0.03456	0.561702
10	0.34130	-0.003614
11	0.13294	0.231372
12	0.03866	-0.185621
13	0.07029	0.325591
14	10.70618	-0.729102
15	-0.27233	0.335568
16	-0.10756	0.266769

Biplot scores for constraining variables

	CCA1	CCA2
C_{AVE}	0.13739	0.4902
C_{MAX}	0.16442	0.5776
BPI	0.18687	0.1894
Live Coral	-0.00410	0.0889
Mixed Coral	-0.05301	0.2943
Northing	-0.02733	0.2943
Easting	-0.17669	-0.3773
Slope	0.14677	0.2881
Depth	0.04158	-0.2474

Centroids for factor constraints

	CCA1	CCA2
Dead Coral	0.04607	-0.2725
Live Coral	-0.02757	0.5979
Mixed Coral	-0.06473	0.3594