BIOGEOGRAPHICAL ANALYSIS OF ABYSSAL BOTTOM HABITATS: USING AN ABIOTIC PROVINCE SCHEME AND METAZOAN OCCURRENCE DATABASES

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DEDICATION PAGE

Dedicated to all the workers who went out and explored our vast oceans. To paraphrase a well read book, “They that go down to the sea in ships, that do business in great waters; These see the works and wonders in the deep”. I can say that I am honored to have had the opportunity to work on data that represents the majority of scientific effort in the Deep-Sea. Thousands of women and men more capable than I, contributed to this work. Mahalo.

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I thank: My committee for their guidance and help along the way. Dr. Camilo Mora for giving me the opportunity to work on this project. Les for his enthusiasm in providing Province boundary files. My family for giving me the support over the years to pursue my interests and passions. The good Dr. Laws for her patience and understanding.

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LIST OF ABBREVIATIONS AND SYMBOLS

Important terms are **bolded** within the text, where they are defined or explained. The majority are found within the Background section of Chapter One. Below are the most important to questions and study of this thesis:

Abbysal habitats: All habitats within a depth zone below the bathyal zone, but above the hadal zone. For this study: 3500m - 6500m. Also used in reference to benthic habitats within the depth zone that are dominated by soft sediments with limited hard substrate and topographic features.

ABS 3.0: The abyssal province geospatial boundaries developed from the proposed province scheme (Watling et al. 2013). The shapefiles of boundaries.

BEPs: The benthic environmental parameters used in the proposed province scheme: salinity, dissolved oxygen, temperature, particulate organic carbon flux, and depth.

CeDAMar: The Census of Diversity of Abyssal Marine Life. Name of the biological datasets on metazoans in the deep-sea used to test provinces boundaries in this study (Stuart et al. 2008). Two forms are used: one unpublished, and one available online. CeDAMar is used within to explicitly refer to the unpublished version that contains secondary factors including gear and individuals per species. Records start at 1872 and go to the year 2005.

Deep-sea: Biological habitats of the ocean below the photic zone. Depth wise below ~200 meters, or the thermocline.

GBIF: The version of the CeDAMar dataset available online published by the Global Biodiversity Information Facility. Includes higher spatial coverage and numbers of samples, but no secondary information. Records go past the year 2005, start at 1872.

Ideal error: Or Ideal error equation ($E_\mathbf{x}$). Determined within Chapter One. It gives the height/width parameters for the resolution of a hypothetical feature that would be missed with satellite altimetry methods given an average regional depth.

MDE Mid-domain effect. The MDE is an emergent statistical distribution for diversity within a discrete spatial unit. With higher species diversity located in the geometric center of a spatial domain (Colwell et al. 2004).

Proposed province scheme: The biogeographic delineations of the deep-sea into province units, separated into three major depth zones, bathyal, abyssal, hadal (Watling et al. 2013). Used to indicate the theoretical underpinnings of the ABS 3.0 boundaries.

Satelite altimetry: Used to measure sea surface heights using space based radar. This information is used to measure gravity anomalies of the seafloor. Anomalies can be correlated to bottom topography. The main source of bathymetry for most of the open ocean.

PREFACE

Layout: This thesis is an integrative and theoretical study focused on a region of the planet that is still underexplored. It contains three chapters of analysis, and an initial introductory chapter containing two main sections. The introduction section contains all necessary information for the analysis and topic presented. The background section provides a broad overview of information which may be pertinent to deep-sea biology and biogeography, with some original synthesis. That pertinent information includes the context of the primary fields that are integrated, and possible sources of error inherent in analysis. The possible sources of error are too varied and complex to fully and satisfactorily discuss in the remaining chapters. This overview is included to balance, and give context to, the analytical chapters.

Chapter Two focuses on summary analysis for datasets used, but is supplementary to the core analysis. Basic analyses are found within, such as the spatial resolution of bathymetry used, and information on quality of biologic data used. A considerable amount of effort was directed at developing a method to use regional ocean depth to determine resolution errors in satellite derived topography. At a basic level, without a sound knowledge of the surface of the earth upon which the biota reside, biogeographical study is not possible. The bathymetric analysis as presented gives a numeric indication of error in satellite derived bathymetry. The second section of that chapter is supplementary to Chapters Three and Four, and describes the biological databases. The core thrust of the biogeographic analysis (subsection 3.4.2) of this work, diversity patterns of metazoans as a function of site distance from the center of the abyssal provinces, is contained within Chapter Three. Chapter Four contains a case study of spatial patterns of gastropod diversity at the landscape scale, and a discussion on subprovince designations.

The general layout follows guidelines published by University of Hawaiʻi at Mānoa, Office of Graduate Education (Appendix A). In following those guidelines, when appropriate, style and formatting is that of the Journal of *Global Ecology and Biogeography* (e.g, citation style).

Motivation: The scale and scope of this project is best suited for a much experienced deep-sea scientist, yet paradoxically no one person can claim true expertise of the vast under-explored deep-sea. The alluring nature of this field is that it has a rich history, marked by great intellectual feats and monumental physical effort, yet even today a sampling tow in any random section of the ocean may completely redefine understanding of these systems. There is much progress to be made in developing a robust theoretical framework for biogeography in the deep-sea. Where, appropriate elucidation of patterns proceeds the more alluring task of discerning processes. I embarked on this project because of circumstance, and a desire to contribute to the general knowledge of the fundamentals of evolution and geographic distribution of life in the Earth's largest expanse. It is my hope that this work may contribute to efforts to understand, and to conserve this planet's last great wilderness.

1 INTRODUCTION AND BACKGROUND

Introduction

The open ocean and associated deep-sea depths are the largest biological realms on the planet, and encompass many unique ecosystems and habitats that are not found in terrestrial and shallow marine realms (Ramirez-Llodra et al. 2010). Benthic habitats between ~ 3500m and 6500m depth (Figure 1.1), known as the abyssal habitats, may account for approximately 35% of the Earth's surface and are predominately characterized by soft sediments, and limited topographic variance at local or regional areal scales (Harris et al. 2014; Menzies et al. 1973). Though these habitats are under-sampled, available data suggest high endemic invertebrate diversity exists at small spatial scales. The geographic patterns of animal life in these relatively pristine sections of the earth are understudied.

Biogeographical understanding of deep-sea habitats lags behind equivalent terrestrial research, despite the large extent of these habitats (Kennish 2000). Logistical constraints prohibit extensive sampling in the remote deep ocean. The methods, theories, and substance of scientific study of biogeography therefore stem from the terrestrial realm. Recent progress in marine biogeography is closing the gap between the two realms, and has benefited from global collaborative databases and the emergence of satellite oceanographic methods (Priede 2014). The United Nations (UN) recognizes the importance of integrating biogeographical frameworks into conservation plans. The UN also recognizes the need to develop a biogeographical classification for the deep-sea (Briones et al. 2009).

This work is a biogeographical analysis with a focus on the validity of a deep-sea abiotic province scheme (Watling et al. 2013), and specifically the congruence of abyssal zone (3500m – 6500m) province delineations to species diversity patterns. Provinces are the second largest spatial unit in many marine biogeographical classifications. Provinces are defined as having a discrete or endemic biota within. The biota of provinces are considered to have a shared evolutionary history due to the role of environmental variables within provinces, and in defining province boundaries (Spalding et al. 2007). Testing the legitimacy of actual delineations of provinces lends itself to empirical methods, as it is more difficult to test the theoretical basis underlying the rationale for province delineations. The province scheme of Watling et al. (2013) provides the conceptual and theoretical framework for deep-sea province delineations (Watling et al. 2013; Table 2 & Figure 20). This province scheme includes two other deep ocean zones, lower bathyal (800–3500m), and hadal (>6500m). Only the abyssal zone was examined in this study because this large zone best encompasses factors unique, but representative, of all open ocean deep habitats.

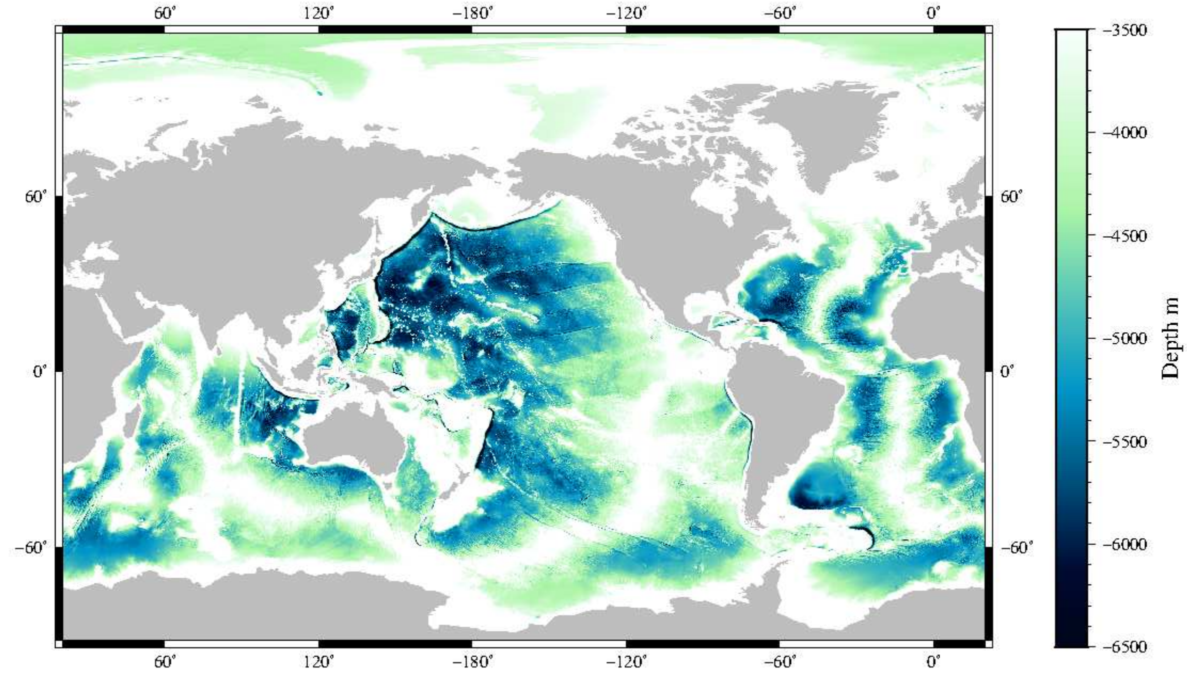


Figure 1.1: Global abyssal depths
Abyssal depths are vast, yet pattern and connectivity varies greatly from landmasses. Black > 6500 m. 0 m >= white < 3500 m. Grey is all non-ocean habitats: terrestrial and fresh water. See Appendix B for materials and methods.

The abiotic province scheme of Watling et al. 2013 is based on a combined physiographic (topographical and hydrological), and physiognomic approach (geophysical, environmental, and geomorphological relationships to biota). Topographic features are used to delineate provinces within basins, and abyssal habitats fall within the depth range of 3500 – 6500 meters. Provinces were also delineated based on environmental variables that are associated with oceanographic (hydrographic) water mass features, and known to impact the physiology and general distribution of deep-sea animals. The physiognomic approach is fundamentally an extrapolation method given that actual biological data across taxa, and explicit relationships to environmental variables need further study, especially spatially. Many taxa distribution patterns correlated to environmental variables are known from studies at varying depths, not at similar depths (Rex & Etter 2010). The environmental variables used are salinity, dissolved oxygen, temperature, particulate organic carbon (**POC**) flux, and depth which is linearly related to pressure. These variables are collectively referred to here as benthic environmental parameters **BEPs**.

The proposed province scheme of Watling et al. (2013), is effectively the third iteration of the original scheme developed from a UN workshop in 2009: Global Open Oceans and Deep Seabed (GOODS) biogeographic classification (Briones et al. 2009). The original **GOODS** classification scheme is based in part on expert incorporation of published, and unpublished, taxon distribution data and BEPs. Concepts regarding regions and provinces from older zoogeographies are utilized to help define provinces (Briones et al. 2009). The exact methods used to delineate provinces using taxonomic data in the GOODS work are not well explained or reproducibly presented. The authors of the more current proposed province scheme (Watling et al. 2013), updated the GOODS province boundaries with high-resolution BEP data. The geospatial dataset of abyssal province boundary polygons, from the scheme of Watling et al. (2013), are referred to as **ABS 3.0** in this work.

To test the validity of the ABS 3.0 provinces two versions of a species occurrence database were used. The biological database (Stuart et al. 2008), The Census of Diversity of Abyssal Marine Life, was compiled by the Census of Marine Life initiative. It is an attempt at a comprehensive database of metazoan records spanning from 1872–2005, with the lowest resolution being morphospecies. Due to both the nature of these environments, and that of sampling methods, the majority of records are invertebrata with fishes being poorly represented. Two versions of this database exist and are utilized. The first is the original unpublished version (referred to within as **CeDAMar**), which includes a variety of factors (including: sampling gear used, date of sampling, and recorded depth at site) in addition to species records. The second is the version available online through the Global Biodiversity Information Facility (Appendix A; ref. 1) (referred to within as **GBIF**), which includes records updated after 2005, but data are limited to species occurrence and geospatial coordinates (Appendix A; ref. 2 and 3). These datasets represent the cumulative effort of the entire field of deep-sea metazoan biologists since the field came into being more than 130 years ago.

These biological databases allow for global synthesis of the full range of known taxa, as biogeographical analysis in the abyss is often done for select and well known taxa only. Current knowledge of biogeographical patterns in the deep-sea are possible because of detailed study at specific taxon resolution; however biogeographical classifications based on a single taxa are more accurate biogeographies of that taxon rather than general biogeographies of the majority of animals in the abyss. This study is unique in that it tests biogeographic provinces using the majority of the metazoans that exist in these habitats.

1.1 Objectives

This project is an attempt to investigate the abiotic biogeographical province scheme by testing whether the defined abyssal provinces agree with taxonomic data. Watling et al. (2013) state their goal as delineating province centers and boundaries, this study seeks to test those provinces delineations, and not the exact boundaries. Depending on the fit of biological data to provinces, conclusions can be drawn on major, or 1st order, evolutionary trends over ~ 35% of the planet. The results may be used to build a more complete ecological geography (Longhurst 2010; Watling et al. 2013). This project is only implicitly a historical biogeographic study, as current species distributions are the apparent sum of ecological and historical factors, historical factors may be deterministic or random.

Main question: Do taxon distributions (CeDAMar & GBIF) align with the abyssal provinces (ABS 3.0), and therefore are provinces meaningful delineations biologically in terms of the abyssal biome?

Working hypothesis: Taxon spatial diversity patterns will be congruent with province delineations, as the province scheme is based on a sound theoretical framework, which synthesizes important environmental factors.

1.2 Approaches and structure

The main question is addressed in Chapter Three, with Chapters Two and Four including secondary analyses to provide a more comprehensive and integrative biogeographical approach. The province delineations and associated approximate centers of diversity are addressed in Chapter Three. Using an expected mid-domain effect (MDE) null hypothesis structure (Colwell et al. 2004), taxon rarefied diversity and distance relationships to province centroids were analyzed, and conclusions on province validity were determined by total taxa patterns. For diversity patterns, rarefaction of species by individuals and genera by species was performed for CeDAMar and GBIF, respectively.

Within Chapter Two, is a mathematical approach to presenting resolution issues in global bathymetry data, and details on the two biological databases. The mathematical approach, Ideal error equation, gives dimensional values of a hypothetical feature not detected for a regional depth. This investigation gives a numerical estimation of resolution error in the spatial domain of the bathymetric data used to create the abyssal provinces (ABS 3.0). This addresses errors in fit between the biological databases and provinces that could result solely from data resolution issues, and not factors related to the distribution of biota. In Chapter Four semivariance distance relationships were explored for diversity metrics of gastropods in the North Atlantic province, in relation to BEPs. These exploratory analyses provide a study at the subprovince spatial scale.

The CeDAMar database was used in analyses where secondary factor information was needed. Other standardization and cross-validation methods were calculated as needed using the two databases and species records. Chapter Four relies on the CeDAMar dataset only.

1.3 Implications for conservation

An understanding of biogeographic patterns is important to the implementation of effective conservation and management plans. Proper ecosystem management and conservation of ocean systems requires a comprehensive knowledge of whole ecosystems, sound baselines, and the ability predict future changes. Conservation efforts operate by using spatial units to integrate scientific knowledge and management capability. Deep-sea metazoans need to be conserved (Watling & Norse 1998). Watling et al. (2013) indicate creation of their province scheme was for "high seas management purposes." The United Nations intends to amend the United Nations Convention on the Law of the Sea, to specifically address proper legal and regulatory mechanisms for administering conservation areas in the open ocean (including the abyss) beyond national jurisdiction, which are currently deemed insufficient ("General Assembly resolution A/RES/69/292"). Climate Change is predicted to impact the deep-sea through changes in BEPs (Jones et al. 2013; Levin & Le Bris 2015). If BEPs are indeed important in determining geographic patterns of deep-sea life, than those patterns could change due to the indirect impact of a changing climate. In the abyss, mineral and gas extraction and disposal of waste (e.g., nuclear, CO_2 sequestration, and sewage), are forecast to be the issues of major concern that will have direct disturbance impacts (Glover & Smith 2003; Hollister et al. 1981; Smith et al. 2008a).

Of immediate concern for abyssal habitats is mining for polymetallic nodules in the Clarion-Clipperton Fracture Zone (CCZ), an area of similar size to the continental United States, in the Pacific Ocean (Wedding et al. 2015). The potential areas impacted by mining are the same size as abyssal provinces. Proper implementation of the precautionary principle discussed by Wedding et al. (2015) includes setting aside reserve areas within the CCZ, to mitigate the impacts of mining on regional biological diversity. This concern has prompted high quality sampling within the CCZ (Amon et al. 2016; Smith et al. 2008b). Even with recent work, a consensus on biogeographical patterns within the CCZ, and in the deep-sea in general, is lacking. Possible mining locations (McKelvey et al. 1983) are global in scope, and therefore conservation needs may be as well. Without a robust biogeographical framework, neither predicting the scale of impact, nor mitigating that impact is possible. If taxon spatial diversity patterns are congruent with province delineations, the provinces may be more useful for use in conservation.

Background

In this section is a basic overview of the concepts important to study of the deep-sea including a short overview of the history of the field, sampling methods, bathymetry, zonation, and biological diversity in the deep. The section on 'Measurement of bathymetry," and specifically the material on geophysical properties of ocean crust is a useful supplement to the relevant analysis in Chapter

Two. Additionally, a section on biogeography is included at the end of this chapter. An annotated review of key background sources is found in Appendix B.

1.4 Deep-sea science

1.4.1 History

The geopolitical histories of the major maritime empires and economic centers, over the last two centuries, have shaped the modern study of deep-sea biology. Those actors which have the resources, and technology to fund and equip large state of the art ocean going vessels, are the key players in the research field (Menzies et al. 1973). Given the cost and logistics involved in deep-sea biology, the most well studied oceans are those close to major ports and the shipping lanes of richest maritime powers.

Deep-sea research has historically experienced paradigm shifts due to the fact that the collection of new data can be so slow coming. It is still common to read introductions in deep-sea literature on how Edward Forbes, in the mid-1800s, mistakenly theorized that there was no life below 550 meters. A mistake due to large mesh sizes in sampling nets that did not capture the smaller sized deep fauna. This issue was compounded by the sampling in the low oxygen zones of the Mediterranean, which are faunistically disparate as compared to other oxygen replete areas of similar depths. Unfortunately, for Forbes his other valid discoveries receive less attention than his honest mistake (Menzies et al. 1973; pg. 1-7).

Deep-sea biology, typically used to describe oceanic biology below 200 meters, is a unique field in biology, and ecology, as its scale differs vastly from terrestrial and even shallow water work. The deep-sea is extremely difficult to study due to the logistical restraints of placing equipment in very extreme environments, and the associated costs. Because of these constraints, data collected ranges from opportunistic and incomplete to massive international, multi-institutional endeavors. There is a heavy connection between deep-sea biologists, oceanographers and engineers, meaning that the analysis of ecological patterns is often done with analytical tools from biology, as well as robust mathematical tools used in physical oceanography and applied engineering. The limited and uneven sampling, coupled with the mathematical rigor has selected for a high level of standardization, as well as a heavy use of extrapolation techniques to decipher patterns, and fill holes in knowledge, regarding vast stretches and regions of the planet. Current standardization of size classes used for invertebrates/organisms, collected by sled or dredges and separated by sieves, began which historic expeditions over 150 years ago (e.g., the Challenger Expedition).

Major contributors to the field include the United States and England with Germany, the low-countries, Scandinavia, France, and Russia being the other countries with deep-sea programs. The geographical realities of place and expertise inherent to the major players in deep-sea exploration means the most sampled ocean basins are the North Atlantic, Atlantic and North Polar Seas. The South Pacific and especially the Indian Ocean are under sampled in comparison.

The future of deep-sea exploration includes the emergence of Remotely Operated Vehicles (ROVs). Japan and China are the newcomers to the field. China, as it has done in so many other fronts, has become a global player in deep-sea exploitative capability with the launch of its manned submersible *Jiaolong*, China now leads the world in maximum depth (7000 meters) capability, of a fully autonomous, manned research submarine. With the recent launch of the NOAA Okeanos, in 2008, live ROV telepresence gives shore based educators and scientists immediate access to a depth of 6000 meters. Modern study of the deep-sea is considered by many to have been initiated by diversity studies and epibenthic sled work in the Northwest Atlantic in the late 1960s (Snelgrove & Smith 2002).

Historical expeditions of great importance have been that of the first scientifically oriented circum-global HMS Challenger expedition, 1872-1876, and the first dedicated deep-sea, Galathea expedition of the 1950's. The Galathea expedition was a Danish initiative that set out to sample the deepest ocean habitats and to bring up specimens intact. As indicative of other famous oceanographic missions, this expedition accomplished its initial yet broad goals. The team sampled fauna from the Philippine trench and established that there is indeed an assemblage of metazoan animals that live in Hadal depths. The question; if that assemblage is just an abyssal incursion or its own unique assemblage, began with that discovery. It is also a question still pertinent in the present literature.

The HMS Challenger was a Royal Navy military corvette, which was modified into a research vessel by the British Navy for the sole mission of a global oceanographic cruise to sample physical and biological process in the deep-sea. The motivation and political pressure that brought this endeavor to fruition, was fueled by sentiments of nationalism and a desire within the British scientific community to maintain its current lead at the forefront of oceanographic research (Deacon 1971). The breadth of new, and still relevant, discoveries made by Challenger Expedition is spread across the disciplines of the biological, geological, and earth sciences.

The scope and scale of the expedition cemented this cruise as the key starting point for the study of the our deep oceans. The most indisputable finding was that of the existence of life in the abyss, and throughout the oceans regardless of depth, thereby sending Forbes' Azoic theory into the waste bin. New species discovered by the expedition topped 4,000, and the cumulative reports took two decades to publish. There is a rich and unique biota in the depths of the planet's oceans, and the Challenger expedition launched that idea into the sphere of human knowledge.

The geological information that was collected by the expedition was useful at a variety of scales. At the simplest mapping level; the Challenger discovered one of the deepest spots located within the Marianas Trench, (only to be topped ever so slightly by Japanese researchers in the late

20th century) and also sounded the general structure of the Mid-Atlantic Ridge, well prior to theories and eventual knowledge regarding plate tectonics. Along with biological samples collected by specially constructed sampling devices, scientists collected a wealth of information on patterns of sediment type and distribution, as well as chemical composition within these sediments. Careful attention was paid to the presence of manganese and manganese nodules in stations sampled. This sparked debate on the geological and chemical forces at play in the creation and deposition of nodules (Murray 1891). Whereas currently questions on biological communities associated with nodules, and removing nodules for minerals contained within, are major issues for those whose study the deep-sea.

Importantly, species identifications and samples taken during the Challenger expedition, as well as other major expeditions, where analyzed for this thesis work. The logistical constraints, and historical factors of deep-sea expedition help explain patterns in the spatial and temporal dimensions of the data structure of the CeDAMar and GBIF datasets. Furthermore, an understanding of historical factors gives context to data collection methods. The paucity of data encourages reanalysis of older data.

1.4.2 Sampling methods

Biological sampling

The largely inaccessible abyss requires complex sampling and the type of sampling equipment comes with inherent biases that need to be recognized. A variety of sampling methods have been employed to capture the different size classes and animal types evenly in the deep-sea. Within the benthic boundary layer invertebrate fauna of the abyss are not distributed uniformly upon nor within the top few meters of sediment. Sampling gear types have as such been designed for more focused purposes, which workers describe as qualitative or quantitative. Quantitative gears give reliable estimates on species densities, or volumes, per sampling effort. Qualitative gears do not give the same estimates reliably, being more useful for detecting presence of animals, than for measures of animal density or volume. Gear types can be split into two general spatial categories, those that sample a specific spot or those that cover a transect by being towed (or in the case of remotely operated vehicles, driven), across the seafloor. With the three major point based methods being corers, grabs, and traps. The transect gears being, trawls, dredges/sleds, and ROVs or camera sleds. With the point based methods (excluding traps) relatively more quantitative (corers the most so) and interested in the smaller size class, while transect methods more qualitative and interested in large size classes (Clark et al. 2012; Table 2.1).

A monumental effort has gone into engineering and innovating to improve sampling efficiency and reduce errors of specific gears, improving the quantitative ability of qualitative gears. Transect methods, especially towed methods suffer from the issues involved by towing large amounts of wire attached to equipment a great depths over ocean bottom, namely gear may skip and bounce off bottom, or become fouled, without knowledge of the location where those errors occurred. The continuous attempt to correct for shortcomings in gear, means that gear types do not always fit into clean qualitative or quantitative bins, and should be more generally considered points on a continuum. Gear types within categories may differ greatly in design and deployment per expedition, given the time between expeditions and gear evolution, as well as logistics involved with deploying and maintaining more sophisticated gear. For comprehensive sampling of all possible species in an area, or site, the most straight forward solution is to use a suite of complimentary gear.

In describing the CeDAMar dataset Stuart et al. (2008) state, “In total, there are only about 1600 documented sites: 60% for quantitative samples (grabs, box corers, and multicorers), and 40% for qualitative samples (trawls and epibenthic sleds).” Unfortunately, for the analysis conducted here the issues surrounding variability in gear selectivity cannot be ignored nor fully accounted for. (See Clark et al. 2012, for a thorough description and comparison of gear types.)

Species size classes Gear type is strongly related to the size groupings in deep-sea biology, most basically related to mesh size, and size of spatial unit, i.e. kilometer tows versus sub cubic meter volumetric sampling. The biota of the deep-sea are generally small (with the trend of decreasing size with increasing depth). The megafauna of the abyss are orders of magnitude smaller than the megafauna that have roamed the planet in the past, and those associated with the surface of the planet in this epoch. From smallest to largest is bacteria, nanobiota, meiofauna, macrofauna, and megafauna. Nanobiota, generally poorly studied and made up of protozoans and fungi which are bigger than bacteria. The meiobenthos is dominated by nematodes, and protozoan foraminiferans. Macrofauna are dominated by polychaetes, crustaceans, bivalves and gastropods by density. Echinoderms and crustaceans dominate the megafauna (Clark et al. 2012). Structure forming sponges and corals, and demersal fishes belonging to the megafauna (Rex & Etter 2010).

Megafauna are generally in the size range of less than one mm to one meter, and macrofauna ranging in size from less than a millimeter to a centimeter, while meiofauna generally range in size from 32 to 1000 µm (Rex & Etter 2010). Snelgrove & Smith (2002) define the macrofauna as “organisms retained on a 300 pm or 500 pm sieve but too small to be identified in photographs.” with Europeans using 250 µm meshes and American programs using 300 µm meshes without seeming to make a significant difference in organisms retained (Rex & Etter 2010). Megafauna are identifiable in photographs and caught by trawls with 1-3 cm mesh size (Rex & Etter 2010).

The use of size classes dominates deep-sea research, in fact it may be more prevalent than in other field of habitat specific ecology. However, as biological proxies they are imperfect categories. Taxa may be represented in all three major sizes class (e.g., crustaceans) or only in one size class (e.g., nematodes and fishes). Adults species of one size class may have juveniles in an adjacent size class. (See Gage & Tyler 1991, which includes chapter designations on size classes, with background information on life history of many groups, and Rex & Etter (2010); pg. 10-13, and appendices.)

The heavy use of size classes dovetails with the use of biomass in the study of spatial patterns, as size class are useful bins, and generally provide a standardization across sampling studies. Biomass per size class is used repeatedly in study of beta diversity (Rex & Etter 2010), and environmental gradients. It is also used to for predictive modeling and macroecology (Ichino et al. 2015; Jones et al. 2013).

1.4.3 Measurement of bathymetry

The history of deep biology is intimately tied to the understanding about the sea-floor's shape, its depth, and features of its topography, collectively known as bathymetry. Only recently have deep-sea biogeographers had global maps with the accuracy and resolution needed to construct reliable biogeographic schemes. A variety of methods have been used to measure the sea-floor since antiquity. In the recent scientific period, sounding methods utilized lines or poles to directly measure the distance from ship to benthos. Mechanical improvements increased the accuracy, and quality, of line based sounding devices during the industrial revolution. In the early 19th century echosounder devices were developed, which measure the time a single sound pulse takes to travel from a transducer on a ship, contact the bottom (frequencies commonly used can penetrate the sea-floor), then reflect back to a receiver on the ship. This method may be improved, for example by adjusting for the value for speed in saltwater with local profiles of salinity and temperature, or post processing techniques e.g., waveform interferometry (Clark et al. 2012; Priede 2014),

In the 1970s multibeam sonar came into the public sphere. This method can provide high resolution swaths, as the sonar beam ensonifies an arc below a transducer, as opposed to a single ping path, therefore a two dimensional and a three dimensional area, respectively along a ship transect. Beam width is a proportional function of depth of the survey site below transducer (sonar systems may be towed, for example sidescan sonar, and therefore not located at the height of research ship). The swath of benthic area surveyed may be in the range of two times water depth. When multiple surveys of the same area utilize georeferencing and post-processing, which removes ship movements, one cm accuracy "pictures" of the sea-floor can be produced (Clark et al. 2012). Other methods are used e.g., LiDAR: light detecting and ranging, but multibeam systems are the primary means for creating high resolution bathymetry surveys. Importantly as depth increases a sonar system must be towed at lower speeds in order to maintain a constant resolution.

The cost of deploying ship-based methods, the logistics involved in deploying them in remote areas, and the shear enormity of the ocean, means large areas have not been mapped by ships. It has been estimated that to render a complete map of the ocean sea-floor it would take 120 years of continuous ship surveying (Becker et al. 2009). Given the relationship of depth to areal coverage, a majority of that ship time would be in shallow and complex bathymetric areas. The seafloor that has been mapped contains a “shoal” bias (Smith & Sandwell 2004); shallow waterways where bathymetry is important to safe travel of commercial, or military shipping, have been preferentially mapped. Whereas areas of sea bottom deeper than could directly impact a ships hull are often left blank on charts and navigation aids. This bias is further exacerbated by historical location of naval powers and unequal distribution of global equity, meaning large North American and European ports and shipping lanes have a greater coverage than the global south. The charting bias also includes another major artifact, that of “terracing” of depth contour distributions, as charting needs dictate extrapolation of specified depth contours, which leads to over estimation of specific depths e.g., the 25m isobath. Depth contours are drawn in areas of no measurements to connect actual sample sites.

Until recently global charts included these hand drawn contours. This allowed human experts to synthesize information prior to the use of computers (earth quake epicenters to infer tectonic features), and the ability to produce charts based on classified naval information known to specific cartographers and oceanographers with clearance to high resolution data, but unable to reproduce it fully because of censorship. Naval bathymetric data may be the only information available in many areas surveyed. Because of the hand drawn nature of products, often variation in sea-floor texture is a result of input by different individuals as opposed to actual geological features. Hand drawn contour maps have the benefit that they can be digitized, and then can be input into machine algorithms that can produce equal spaced gridded numerical values for the surface of the earth (Smith & Sandwell 2004). The digitalization of hand drawn maps may inadvertently propagate errors.

Linear extrapolation of plate tectonic 1st order trends have been used in contour maps, notably in Marie Tharp’s artistic maps. Working with Bruce C. Heezen, Marie produced the first global ocean bottom maps that integrated echo soundings and expert information. This resulted in the discovery of major geological features greater in size and scope than many continental features, most notably the mid-ocean ridge system, which circumscribes the planet. When the mid-ocean ridge system was first plotted it was essentially discovered, as while the data existed it had yet to be synthesized. This integration of cartographic license based on actual data, was a major earth science breakthrough, and depicted fine scale resolution despite actual lack of data over major bottom areas of the planet.

These factors give a false impression of the state of knowledge of bathymetry, and the resolution for which it is known. Taken together they may propagate errors at each step of the process. However current global maps utilize satellite derived altimetry to infer gravitational anomalies, and are pictures of sea-floor topography that are limited on methods, physics, and data. Therefore the error is largely quantitative in nature, not based on human error or subjectivity. It is only with recent satellite alimentary data that global deep-sea biogeographic delineations can proceed.

Satellite altimetry

Satellite altimetry is a space based bathymetry method that measures deflection of the equipotential surface, (deviations from the geoid), of the ocean surface using radar. The magnitude and shape of the radar returns are measured as waveforms (shortwave or long wave). This gives spatial information about the characteristics of the surface that caused the reflection and the resultant deviation of the ocean surface. These deviations are caused by heterogeneous mass distributions in the plane orthogonal to the deflections. The plane being the underlying sea-floor, crust and mantle section. Sea surface gravity anomalies then can be correlated with topography, but do not give an exact fit (Sandwell 1984). Local mass variations cause water to bulge around high gravity areas and spread away from low gravity areas in respect to the geoid. These water masses are what are measured by satellite radar.

Gravity induced inflections are caused by the underlying planetary section, specifically the mass/density differences between seafloor and the seawater interface. The planetary section of variance is the lithosphere, which includes surface topography and through to underlying solid mantle, or the total mass of the solid earth. Solid earth excludes those layers whose mechanical characteristics are dominated by viscosity and therefore behave like a fluid or plasma at geological time scales, or the ~ liquid mantle below the lithosphere.

When a load, a large mass such as a seamount, exists on top of the earth's crust the additional mass is compensated by a mechanism called isostasy, or it is in isostatic equilibrium. This phenomenon is most analogous to buoyancy, as it is a type of hydrostatic equilibrium, where the mass 'sinks' below the average compensation depth of the bottom of the solid mantle. However the flexural rigidity properties of the lithosphere, elasticity, act to redistribute the weight of a load, altering the relative compensation depth. Since the mass of the load can change over time by processes independent of earth's geology e.g., weathering or coral growth, the compensation depth can change over time. Lithosphere formation processes (primarily heat flow e.g., hot spot formation sites), and age of lithosphere contribute to crustal support of mass. Whereas older cooler material better distributes force, and bends less than younger hotter material, changing the flexural rigidity. Hydrostatic equilibrium is a restoring process. The restoring force is the summation of fluid and solid properties of the lithosphere and load, these vary in magnitude based on inherent physical properties of a specific section of lithosphere. (See Sandwell 1984 figure one, and section two, for further information on isostatic compensation. Additional explanation is found in Appendix C of Sandwell et al. 2001.)

The importance of these compensation mechanisms is that undulations of the geoid caused by local mass irregularities do not translate directly to actual topography. Increased mass is compensated by the mantle layer below via viscosity or mechanical properties in reaction to the supported load. For determining topography from gravity, this presents variability of overall density of a region measured, as theoretically a tall low density topographic feature could present similar gravitational signatures, a function of mass, as a flat but denser section of sea-floor.

Crustal flexing and buoyancy mechanisms generally operate at different spatial scales. Minimum resolution or wavelength signals are dominated by plate flexing characteristics, and large wavelengths and features are dominated by crustal buoyancy. Various isostatic compensation mechanisms may alter the strength of the gravity topography correlation relationship. Given the relative homogeneous formation of ocean crust, as opposed to continental formation and the stronger weathering above water, the topography gravity relationship is stronger in the ocean than on continental land masses.

There are several other factors that affect the relationship between measured sea surface height and undulations of the geoid (Yale et al. 1998). They can be classified as either oceanographic and atmospheric, or satellite based. Simply environmental or sampling error. Individual environmental factors include, tides, ocean waves, variable water masses, atmospheric water vapor and clouds, western boundary currents, other geostrophic flows, ENSO variability, and upper atmospheric effects (Fu & Cazenave 2001). The study of each of individual environmental factor, as subdisciplines of satellite oceanography, helps to correct for the errors in derived topography. Sensor error may be a result of, altimeter precision, coverage (repeat swaths), a satellite orbit and inclination, and near shore tracking (Sandwell et al. 2001).

The cost of satellite missions and the estimates of ship based sampling, has been suggested as an economical reason to invest in space based missions. There is a minimum resolution of satellites and correlations of topography to gravity must rely on sediment sampling, yet global coverage of sediment sampling is sparse. While satellite alimentary is the most viable means for global coverage, the accuracy of produced topographic information relies on adequate ground-truthed data, at local scales to constrain models.

Ground-truthing can be done with remote sensing robotic methods. Robotic technologies, whether remotely operated vehicles (ROVs) or autonomous underwater vehicles (AUVs), are currently a major component of deep-sea science and resource extraction (Ocean Studies Board et al. 2015). These range from, tethered mini-submarines and nektonic buoyancy driven torpedo like contraptions, to benthic crawlers (Purser et al. 2013; Sherman & Smith 2009). Especially relevant to echo sounding is the class of long range AUV's available (Aoki et al. 2001). The Boeing airplane company will begin sea trials in Fall of 2017 of its 51 foot 'Echo Voyager', an AUV with a range of 12,000 kilometers and an ability to operate at depths below 3300 meters, powered by hybrid diesel-electric rechargeable lithium ion batteries and a surface diesel generator (Davies 2016).

Robotic technologies like heavy AUVs and benthic crawlers could be used in tandem with satellite coverage to improve best available interpolated topographies, with increased ground-truthed soundings and sediment profiles. These new technologies reduce the logistical constraints associated with utilizing crewed research ships, and the tedious nature of operating in the vast regions of the oceans. Satellite data became declassified in 1995, sparking the interest in this method, a vast improvement in our knowledge regarding seafloor topography quickly followed. However like all methodologies, satellite alimentary has its own limitations, as without increased field measurements satellite based methods will reach a maximum precision in resolving topography of the seafloor.

1.5 Deep-sea systems

1.5.1 Topographic features

The importance of measuring bathymetry is to detect the topographic features of the seafloor. The biogeographer is interested in the major bathymetric features as unique habitats in themselves, or boundaries of regions. The following is a description of major oceanic features.

Starting from the coast and moving towards the ocean the first feature is the **continental shelf**, the relative shallow and low slope seabed adjoining the continents. The shelf may vary geographically in horizontal extent, being almost non-exist, to several hundred kilometers in length. The seaward border of the shelf is the **continental slope**, while the angle of the slope varies (Kennish 2000), it is steeper than the shelf, and in some locations can approach vertical. At the base of the slope is the **continental rise**, an area comprised of sediment deposition accumulated from continents and the currents associated with them. Together the three previous designations make up the **continental margin**, they are the submarine edge of the **continental crust**. Cut transversely into the face of the continental margin are found the incised **submarine canyons**. These canyons are formed primarily by turbidity flows. Other factors include land slides, mass wasting of continental shelves, and in some cases remnants of riverine erosion and changing sea levels. Turbidity flows, or slides, are water and suspended sediment which form a dense sinking solution, akin to montane avalanches. Canyons are known to be unique deep-sea habitats, which may be important sites of biological heterogeneity across the slope (De Leo et al. 2012; Escobar Briones et al. 2008; Matabos et al. 2014; McClain & Barry 2010; Purser et al. 2013; Vetter & Dayton 1998; Vetter et al. 2010). Those canyons associated with frequent landslides or fluvial deposits may accompanied by large depositional features known as **abyssal fans** or **submarine fans**, which spread out over the adjoining oceanic crust.

Submarine fans may fill sections of ocean basins creating the flat **abyssal plains**, features most relevant to deep-sea biogeography in the open ocean. These plains are generally found at the foot of the continental rise, and are formed as the oceanic crust created at the global undersea mountain system, the **mid-ocean ridge**, is covered by sediment. The mid-ocean ridge is generally found in the center of ocean basins, where it rises to bathyal depths. The rugose ocean plate is covered by depositional factors, submarine fans and sedimentation of biological sinking material from surfaces waters, these factors in summation give abyssal plains their characteristic undulating, and relatively flat surface.

The term **ocean basin** has different meanings, throughout this work it should be taken to mean the large areas of the planet covered by ocean and are geological separate from continental crusts (open ocean excluding shelf and slope areas). This is concurrent with a three part physiographic province designation of ocean areas into basin, margin and mid-ocean ridge put forth by Kennish 2000.

The abyssal plains are punctuated by minor and major bathymetric features. The most prominent major features are **seamounts**, defined by the International Hydrographic Organization as "An isolated or comparatively isolated elevation rising 1000 meters or more from the sea floor and of limited extent across the summit." Seamounts are often created through volcanic processes, and by definition are completely submerged. In a similar category as seamounts are **guyots**, which differ in that they are flat toped rather than peaked.

These two features may, but not always, differ from the surrounding sedimentary plains by domination of hard substrate, given rise to ecological communities that vary vastly in composition (Clark et al. 2014), prompting genuine interest for conservation (Clark et al. 2011). In the same category as seamounts, are island chains and islands, which punctuate the vast abyssal plains, and whose underwater flanks may have the biota of both seamounts and continental systems.

The minor features of the abyss are those features which do not rise up to one km above the surrounding seafloor, which include the most common geomorphological feature on earth, **abyssal hills**. These prevalent features may be important to the ecological landscapes of the abyssal plains (Durden et al. 2015). Recent work by Harris et al. (2014) redefines those features above 1000 meters, but formed within abyssal hill zones, not as seamounts, but as abyssal mountains. This classification is likely more apt, as generally abyssal hills and seamounts are formed through different processes. Abyssal hills are formed by foldings of crust due to volcanic, and tectonic activity of the mid-ocean ridge, with their individual characteristics defined by the ridge site of formation (Buck & Poliakov 1998; Goff et al. 2004). Most Seamounts are formed via localized volcanic activity (Harris et al. 2014).

Other major features such as extensive ridges, fracture zones, and trenches, permeate the abyssal plains adding interesting 2^{nd} order habitat heterogeneity to ocean basins. Harris et al. 2014 provide 25 geomorphological features relevant to deep-sea. Approximately 15 of 25 are of relevance to the abyss. (See Figure 4 of aforementioned work, as the color coded geomorphological features are a useful visualization of ocean bathymetry data.)

At scales between habitats and provinces there are major bathymetric features within the abyssal plains of each ocean basin. These features likely have some import on species geographic distributions, despite an incomplete knowledge of what that may be. The topographic layout of continents and ocean basins differ, thereby differentially impacting the biogeographic patterns in these two realms. Oceanic systems have the added complexity of a third dimension, in depth.

1.5.2 Vertical zonation

Pelagic

Vertical Zonation of both pelagic and benthic ocean biomes has been well studied. While the focus of this work is on benthic zones, the pelagic and benthic systems are interconnected, both through interacting biota and in terms of similar abiotic factors. The attenuation of available solar energy and related organic molecules, increase in pressure, and decrease in average temperature, as a function of depth are the same for pelagic and benthic depth zones.

Classic zones of open-water zonation are the Epipelagic (0 - 200 meters), Mesopelagic (200 - 1000 meters), Bathypelagic (1000 - 4000 meters), Abyssalpelagic (4000 - 6000 meters), and the Hadalpelagic (>6000 meters). These zones are primarily based on light availability, therefore the top two may vary in exact depth depending on local conditions. For example highly productive upwelling temperate zones may attenuate down-welling light at a much greater rate, through absorption and scattering by biological elements, and thereby reduce the maximum depth at which light is available.

In the Epipelagic primary production is generated, which sinks to create the rain of carbon which fuels the energy demands of the depths below. The lower depth of this zone marks the limit of adequate light for photosynthesis. It is the primary production zone for the open ocean. Depending on latitude and water mixing, this is also the area of highest temperature values and variability.

The Mesopelagic zone is a transitional band where light is still dimly available from the zone above. Other factors of importance include a permanent thermocline, and oxygen minimum zones which are brought on by the high oxygen demand of detrital decomposers (Herring 2002). Into the Bathypelagic (the upper limit being ~ 1000 meters, while the lower limit varies by author, with some not including the Abyssalpelagic at all), and light is lost, temperature is mostly uniform and available food is low. In this sparse habitat the physical parameters are more uniform, and the paucity of animals is apparent. Microbial processes dominant with the lower densities of metazoans in this zone. Below this zone are the Abyssalpelagic and Hadalpelagic, which are perpetually dark and are generally directly removed from surface weather, and currents. Fishes appear to be absent below 8400 meters, which may be due to biochemistry limitations and pressure (Yancey et al. 2014).

The above delineations are useful for a simple stratified 'bathtub' view of ocean zonation, yet do not fully encompass current understanding of the dynamic physical properties of water masses in the ocean. The 'bathtub' view of the ocean is analogous to the earth centric view of the solar system which dominated western thought prior to Copernicus. However it is vertical zonation of the deep-sea, which has dominated much of the macroecological research (Rex & Etter 2010), as patterns in the vertical are real and intriguing.

Benthic

The gradient of photosynthetic energy and impingement of surface physical factors as a function of depth found in the pelagic zone may be applied to the underlying benthos. However because of the ephemeral nature of water masses versus the stationary nature of the benthos, the transitory principle must be applied with great caution, and often abandoned completely. Benthic studies of deep-sea biology almost exclusively focus on changes across the extreme range of the continental margin to the abyss, and to a lesser degree between the abyss and hadal trenches. In studying biomass to depth, the decrease of biomass of metazoans from the surface to the lower of bounds of the abyss is unmistakable (Rex et al. 2006). Furthermore, a curve of this decrease shows varying slopes in the typical size classes of deep-sea fauna. Hadal depths and specifically the bottom of trenches, do not fit the pattern of decreased biomass and depth due to increased biomass associated with topographic forcing, the funneling of organic matter (Ichino et al. 2015). The trend in the rest of the deep-sea is likely due to the correlation of increasing depth with decreasing organic matter (Rex & Etter 2010). This decrease is a function of both use by the pelagic biome and increasing distance away from productive coastal waters following the slope of the continental margin, a spatial conflation of of all three dimensions.

The correlation between depth and biomass indicates a major theme in deep-sea studies (Menzies et al. 1973), that is analogous to the macroecological phenomena of latitude altitude gradients in the terrestrial sphere. Indeed patterns of latitude and diversity, so pivotal to the study of ecology in other realms (Willig et al. 2003) have been documented in the deep-sea (Rex et al. 1993). While much work has utilized depth gradients as a proxy for associated patterns in various environmental variables of ecological and evolutionary significance, the linear increase in pressure and its importance on the metabolic functioning of benthic animals cannot be ignored (Carney 2005; Yancey et al. 2014). Benthic zonation exists, a review of studies suggests vertical distance is more likely to explain variance than horizontal distance on the continental shelf (Rex & Etter 2010). This is likely because of several interrelated environmental factors, that are confounding, synergistic, and correlated. The factors involved in zonation are hypothesized to be important mechanisms responsible for speciation and the geographic distribution of diversity, providing the rationale to create deep-sea provinces partitioned by depth ranges (Watling et al. 2013).

1.5.3 Diversity and species distribution

Deep-sea benthic systems have high species diversity. In comparing deep-sea systems and shallow marine systems as opposing points on the zonation spectrum, seminal work motivated a greater interest in diversity and the responsible processes in the deep-sea, when the deep-sea was found to have higher than expected diversity (R. Hessler & L. Sanders 1967). The exact number of deep-sea taxa are still unknown, which is due to lack of sampling, and the variability in global estimates of species (Mora et al. 2011). The abyss does contain a high number of species (Snelgrove & Smith 2002). It is unclear if this applies equally over the global domain, and it can't be concluded that the deep-sea has higher diversity than shallower marine environments (Mcclain & Schlacher 2015).

The number and geographic distribution of species is convoluted by the issue of cryptic species (two separate closely related species described as a single species using morphological methods) and the resultant taxonomic error. The concept of cryptic species is not new, but according to Bickford et al. (2007), publications describing cryptic species have shown an exponential increase since the rise of genetic methods to compliment morphological ones. It is unclear if this work standardized by increases in total scientific publications (Bornmann & Mutz 2015). The number of cryptic publications is positively correlated (weakly) to the number of described species across taxa, however specific taxa such as arthropods show higher than average cryptic species, while molluscans show lower than average (Bickford et al. 2007; Pfenninger & Schwenk 2007).

Cryptic species do exist in the deep-sea (Vrijenhoek 2009). Especially interesting is cryptic species in taxa (Etter et al. 1999) which are often described as cosmopolitan (McClain & Hardy 2010). Given sampling issues, and a large number of taxa described before genetic methods were implemented in biology, it is fair to conclude that species estimates in the deep-sea are hampered by cryptic species issues. Given the dominance of small invertebrates, and the vastly diminished importance of light sensing and production in deep-sea benthic organisms (Johnsen et al. 2012), many deep-sea species present difficulties in distinction through visual means or are quite literally morphologically cryptic animals. Given the aforementioned issues, combined with the dominance of higher taxa such as arthropods, the problem of cryptic species in the deep-sea is a very large one indeed.

High expected diversity at local ecological spatial scales, yet undersampling, suggests that observed species richness has not come near measuring actual species richness in the deep ocean (Grassle & Maciolek 1992). However, Lambshead & Boucher (2003) suggest that extrapolating global estimates by local diversity fails to acknowledge the role of repeated patches at regional scales and question the hyper diversity theory of the deep-sea. Other mechanisms for localized diversity include the importance of the tempo of disturbance and the extremely wide range of life history dynamics of deep-sea animals, which creates unique patch scale dynamics over time (Smith 1994). The likelihood that vastly improved estimates for total number of species known in the deep-sea will be forthcoming in the near future is low. This is because of limited observational data, not issues (Gotelli & Colwell 2001) in estimation curves. One possible avenue of research that should be encouraged, in parallel to basic species identification, is using alternative methods of inferring local diversity. One candidate could be dark diversity.

Dark diversity is a measure of species available in a regional pool not observed in local sampling (Pärtel et al. 2011). The authors of this measure suggest using ratios of observed diversity to dark diversity, and calculating the dark diversity via suitability filters based on known habitat, or ecological criteria indicating the possibility that a species from a regional pool could be found at the local site. Predicting available colonizers requires better understanding of regional species estimates, as well as accurate estimations on dispersal potential, which varies immensely for disparate deep-sea taxa (Gage & Tyler 1991).

1.6 Biogeography

Previous sections have outlined the factors involved in the study and distribution of deep-sea biological diversity. The integration of these factors is the study of biogeography. Biogeography is a field which encompass many subdisciplines. The main term better encompasses the resultant patterns in an inclusive manner, the more focused subfields prove more useful in elucidating causal relationships.

If the various studies of biogeography exist as a gradient on the time space continuum, than ecological biogeography exists at the smaller scales and historical at the larger end. (Myers & Giller 1988). **Ecological Biogeography** is interested in the factors that explain current distributions of biology. These factors include biological ones, as in genetics or behavior. They may also be abiotic/environmental for example, temperature, or precipitation. **Historical Biogeography** conversely is interested in past factors that explain current distributions. Bridging these two is biological dispersal potential, while unique to historical is geological and evolutionary factors (Monge-Nájera 2008). Falling within historical is **Phylogentic biogeography** which utilizes genetic tools to determine distributions of closely related taxa or species, or populations within species (Eckelbarger & Watling 1995; Hickerson et al. 2010).

The emerging field of **Functional Biogeography** seeks to describe the geographic patterns of trait diversity, often synonymous with biogeochemical diversity in microbial studies (Violle et al. 2014). Of the benefits of this approach is independence for fully describing all species for biogeographic analysis, and the ability of integration of the study of the earth system, and biogeochemical parameters. A study on island faunas showed related scaling relationships with measures of functional diversity and species diversity (Whittaker et al. 2014). Diversity in functional traits may be a good proxy for ecosystem resilience (Longhurst 2010).

There are several different, and complimentary, ways to conduct geographic study of biota. Utilizing the appropriate lens is a challenge for conservation, and the study of patterns of life as a whole. This thesis is most interested in analysis in shorter time scales, and at the ecological and species level for tractability. As, for example functional trait diversity data do not exist at the global scale for deep-sea metazoans.

Current conservation efforts in biogeography rely heavily on nested spatial classifications. Managing geographic units is conveniently similar to established governmental spatial bureaucratic practices. The seminal work of Udvardy (1975) forms the theoretical basis for many major global schemes, and was drafted for the international union for the conservation of nature and nature resources. The GOODS classification, as well as other major classification schemes both terrestrial (Olson et al. 2001) and marine (Spalding et al. 2007), are built upon Uvardy's foundation. The nested **Hierarchical Spatial Classification**, utilized by these various schemes begins with largest to smallest, realm, biome, province, and ecoregion. This is the system which the proposed deep-sea biogeography utilizes (provinces). The definitions for these nested classifications given by (Spalding et al. 2007), being what will be generally adopted here and throughout. Despite the convenience of nested geographic schemes for conservation means, there effectiveness may be of concern based on untested assumptions inherent to underlying theories on diversity and spatial relationships (Boeklin 1997; Margules et al. 1982). Work at exploring the biogeographic structure of biota in deep-sea samples of the North Atlantic sub-basin, suggests that despite lack of continuous spatial coverage, approximate centers of biogeographic units can be found (Watling 2009).

Complimenting basic pattern description and correlation to explanatory factors, is analysis in terms of distributions of inherent spatial properties. Specific species distributions at the landscape scale (e.g., clumped vs. evenly distributed) may indicate underlying ecological mechanisms. Inherent spatial properties may indicate a fit to a specific hypothesis model (e.g., neutral or null spatial ecological models (Leigh Jr. et al. 2010), or may be linked to properties of scale with no underlying ecological mechanism. One spatial explanation, mid-domain effects suggests distribution patterns are resultant proprieties between the spatial domain geometry and range of biota (Colwell & Lees 2000; Colwell et al. 2004).

1.7 Conclusion

This thesis explores basic patterns of biogeography in the deep sea, and builds upon the background presented here. The proposed biogeographic scheme (Watling et al. 2013) is primarily an ecological spatial classification partitioned by BEPs and topographic features. However, it is informed by a thorough understanding of historical factors. Unfortunately the historical assumptions are more difficult to test via repeatable independent analytical means. The core question of ABS 3.0 provinces as centers of diversity and testing its inherent spatial properties, addresses the aforementioned issues. Analysis in the following chapters does not address multiple biogeographic lenses as that is more challenging, but was chosen to maximally integrate information available. The following chapters explore in more detail and focus, issues in data quality, the specific environmental factors used in the proposed province scheme, the role of topography in province delineations and in shaping diversity, and subprovince spatial patterns of biota. These focused thrusts are integrated in Chapter Five “Discussion and Conclusion”.

2 BATHYMETRIC DATA ERROR & BIOLOGICAL DATASETS SUMMARY

The core analysis of this work is dependent on the data quality of BEPs that were used in creating the province boundaries of ABS 3.0 and the quality of the taxonomic databases used to test them, this chapter examines those data. The two biological datasets are reviewed and explored within. Of the BEPs that were used to create the ABS 3.0 boundaries, depth and topographic features are the most pertinent to this study. The proposed province scheme divides ocean basins into provinces using major topographic features, and depth. The bathymetric data used to do so, is likely of the highest relative quality across the global domain of study because of the use of specific satellite methods employed in its determination.

Described in this chapter is the Ideal error equation. It was calculated to provide a tractability method to give insight into bathymetry resolutions issues, and to allow for the spatial error to be calculated using only regional average depth as input. A review of the literature found only less practical ways to account for satellite altimetry resolution error, which primarily require raw data and the expertise needed to analyze it. Using the Ideal error equation does not require those things. For transparency the Ideal error calculation is shown in detail (Subsection 2.2.3). See Figure 2.1 and Figure 2.3 for spatial error characteristics of a hypothetical three-dimensional topographic feature for a given regional depth, derived from this equation. These figures may be cross referenced with Figure 1.1 and Figure 3.1 to give a numerical estimation to depth errors, which because of propagation may cause errors in province delineations.

2.1 Bathymetry error

The continents and tectonic features of earth are recognized as major vicariance features in terrestrial biogeography. It is likely that major bathymetric features are also of 1^{st} order importance in marine biogeography. The global bathymetry data available is a compilation of actual measurements and satellite derived features. Satellite data is used to constrain interpolations of actual measurements for globally complete coverage (Smith & Sandwell 2004). Use of this data in analysis requires a basic understanding of data resolution and limitations (subsection 1.4.3). In particular using satellite data alone, in regions of limited ship-based measurements, may fail to pick up small bathymetric features, single features such as seamount or abyssal hill (< ~ one kilometer in height or < ten kilometers in length) in the abyssal depth range. For the proposed province scheme (Watling et al. 2013) the authors used the globally available 30 arc-second resolution SRTM30 PLUS (Becker et al. 2009) bathymetric data.

Ship-based measurements of bathymetry are limited in global coverage, and have inherent geolocational accuracy issues. Smith (1993) categorizes bathymetric data available in the Lamont-Doherty Observatory database, collected by academic ships, and show that of ~ 15 million ship soundings taken from 2,253 cruises during 1955-1992, only 5% were taken after the advent of multibeam sonar and GPS. Much of the older soundings, from that database, are in the Southern Ocean, an area that has not been well sampled since prior to the use of electronic positional equipment.

2.1.1 Satellite altimetry error

Satellite altimetry measures the magnitude (given as gravitational units) and wavelength properties (spatial characteristics of target surface) of radar returns. This information is used to correlate ocean surface height and shape with topography below. This is caused by the gravitational pull of the mass of an undersea feature on the local ocean water mass. (See subsection 1.4.3; Satellite altimetry).

Satellite derived bathymetry does not have the geopositional errors nor coverages problems, of older ship-based data, but does have resolution limitations (Smith & Sandwell 2004; Figure 9). Since the satellite altimetry data was released into the public domain via military declassification in 1995 (Sandwell et al. 2001), its analysis and use in determining bathymetry has progressed rapidly. A variety of factors create resolution limitations in this data (Yale et al. 1998). Some factors relating to resolution, satellite track coverage, data correction, and sensor technology, are improving such that an ideal error could shortly be approached (Sandwell et al. 2013).

An idealized error is based on optimal measurement conditions and assumes only the physics of attenuation of the gravitational signal based on depth. No improvement in measurement technology or methods can address the loss of signal due to attenuation. Gravitational strength diminishes as a function of the distance between objects. As depth increases the gravitational signal decreases. This diminishes the resolution of observable topography as the magnitude of the gravitational signal (mGal) is positively related to the size of the feature. If all possible factors involved in the environmental corrections in altimetry are optimally achieved, than the gravitational error range is $+-1\,mGal$. The Gal is a unit of acceleration used in the science of gravimetry. Where, $1\,mGal = 1 \times 10^{-5}\,ms^{-1}$, as 1 Gal = 1 cm/s^2, and is approximately 1/1000 of standard Earth gravity. Importantly mean sea surface height errors caused by a turbulent sea surface, can be corrected for by repeat satellite tracks with diverse orientation, and therefore are assumed to be optimized in the Ideal error.

Assuming error is parameterized, as above, or reduced in the environmental noise at the altimetry stage, the remaining error is located in the transfer function and the signal attenuation by depth. The transfer function utilized in SRTM30 PLUS varies spatially by inclusion of local filters for various isostatic mechanisms (Smith & Sandwell 1994), the gravitational models used improve every successive iteration of new SRTM PLUS versions, as they are corrected by inclusion of actual ship-based measurements and increased satellite swath coverage (Sandwell et al. 2014). Not addressed in this initial analysis is regional sedimentation, which affects the accuracy of gravity to topography conversion. This accuracy can be accounted for in location specific transfer functions (which have the range of zero to one in terms of correlation between gravity and topography) if they are calibrated with actual measurements of sediment cover at subregional scales, and corrections as such are currently utilized in the global topography predictions (Smith & Sandwell 1997).

For this work the transfer function is assumed to have a 100% correlation, varying from actual correlations. This leaves resolution error to be described as function of attenuation of signal by increasing depth only. The resolution loss is for the width and height of an undersea feature, as a function of depth.

For the purposes of equating gravitational error to topographic features several assumptions and simplifications were made which make converting the $+-1\,mGal$ gravity error to topographic resolution more tractably. Only small scale topographic features (large scale topographic features include ridge systems, a small scale feature might be a single seamount within a ridge system) are of interest so a transfer function was utilized that was spatially invariant to isostatic compensation mechanisms which vary by crustal age and formation, and operate at larger wavelengths varying by region. Following a spatially invariant framework, no accounting for variation in sedimentation was made. Only loss of features due to resolution was considered.

The loss of resolution may be considered more important than increased noise, or not finding a feature, rather than a false feature. As such, the following analysis is interested in the error rate of false negative rather than false positive. Given that abyssal depths are the focus here, the loss of signal at abyssal and average ocean depths skews errors to be false negatives, as features will be underestimated due to signal attenuation. In practice signal attenuation can be accounted for in the topography transfer function, but noise does limit possible resolution, and no transfer function can account for positive height features which fall below a detection limit due to the 1 mGal error.

The following analysis does not account for depressions in in mean topography, nor gravitational noise, only those positive features that would be missed. It is useful for a basic understanding of the limitations of satellite altimetry, such as the loss in ability to detect abyssal hills and other small scale rugosity/topography features. The determination of this Ideal error ($E_{\mathbf{x}}$) gives a method to produce a numerical approximation of spatial error by adjusting a few easily obtained input parameters. It was undertaken in part as a first step towards creating a method for applying a standard error filter to global bathymetric data for future use in more focused biogeographic/macroecological study. This method also allows for any worker utilizing publicly available gridded bathymetric data, to apply a systematic error estimate to the data without needing to analyze raw satellite altimetry data.

2.1.2 Determination of Ideal error

The **Ideal error** equation ($E_{\mathbf{x}}$), is based on an simplified topographic feature with average ocean crustal density, in an approximately conical shape, with a perfect circular base. An empirical relationship of abyssal hill heights to widths (but not lengths), and a sinusoidal profile was adopted for the idealized feature's shape. These steps are a basic mathematical simplification, which gives the base width (can be rearranged for height) of a hypothetical feature that would be missed with satellite altimetry given an average depth for a larger grid square, in an area of interest. No other information is needed.

For calculations of ideal gravitational error in bathymetry the following equations, unless otherwise stated, are from Smith & Sandwell (1994), Smith (1998), and Sandwell et al. (2001). (See appendices in **Sandewell2001**, for more on equations used.) Because there is not 100% similarity in the satellite altimetry literature for symbols used in equations, the reader should be vigilant in moving between the primary literature and this section.

In converting gravity anomalies to predicted topography workers employ two dimensional Fourier transforms of the spatial field data into the spectral domain. This transfer facilitates ease of analysis, as the calculations used for converting satellite radar altimetry measurements into gravity anomalies, become algebraic as opposed to a series of differential equations. It also allows, high, low, and passband filtering of gravity data (Sandwell & Smith 1997), and recombinations of longwave (including longwave data derived from other sources) and shortwave processed data to be gridded. Utilization of the spectral domain has been chosen to avoid assumptions on the characteristic wavelengths of signals (Fu & Cazenave 2001). Fourier transforms are from the spatial domain to the spectral domain, where in the spatial domain $\mathbf{x}$ is the x and y dimensions, (x,y) of a Cartesian gravity field, not to be confused with a specific location on the earth or geoid. In the spectral domain $\mathbf{k} = [k_x,k_y]$ in the wavenumber plane, the wavenumber (k) is related to the wavelength by $k_i = 2\pi/\lambda_i$. Importantly at small wavelengths, or spatial scales, the gravity anomaly can be considered a flat approximation of earth's surface, and spherical and harmonic complexities of calculating localized gravity anomalies can be ignored (Smith 1998). The flat earth approximation is implicit in the following equations.

Calculation of Ideal error (E_X)

The following is the derivation of the horizontal width scale Ideal error $E_{\mathbf{x}}$, at location $\mathbf{x}$ as described by $f(d,g)$. Where, d is regional depth, and g is the 1mGal gravity error. The predicted bathymetry from satellite altimetry derived gravity at a real location $\mathbf{x}$, coordinate point (x,y), is defined as:

$$b_p(\mathbf{x}) = p_l(\mathbf{x}) + S_t(\mathbf{x}) \times a_g(\mathbf{x}) \tag{2.1}$$

$b_p(\mathbf{x})$ = Predicted bathymetry.

$p_l(\mathbf{x})$ = Passband prediction and long-wavelength regional depth (spectral).

$S_t(\mathbf{x})$ = True scaling function (input parameter inclusive), gravity to topography transfer function, also known as admittance.

$a_g(\mathbf{x})$ = Downward continued gravity (attenuation based on depth).

In this framework the formula is not spatially invariant as $S(\mathbf{x})$ may go to zero based on sediment cover at $\mathbf{x}$ (Smith & Sandwell 1994), $p_l(\mathbf{x})$ becomes spatially invariant for the Ideal error, because only the short wave band is of interest, which excludes the longwave regional variation. (See Smith (1998); Figure 6, which demonstrates convergences of different isostatic transfer models ($S_t(\mathbf{x})$) at short wavelengths.) The above equation is simplified to a more ideal form below :

$$b_p(\mathbf{x}) = p(\mathbf{x}) + S(\mathbf{x}) \times a_g(\mathbf{x}) \tag{2.2}$$

Where, $p(\mathbf{x})$ = A passband prediction with no explicit wavelength cutoff, yet assumed to be smaller than affected by regional compensation mechanisms, and large enough such that noise is does not impact it.

$S(\mathbf{x})$= Invariant transfer function, ignoring variation in sedimentation, not spatially variable to lithosphere compensation mechanisms. As described above, workers assume that the geoid and topography are linearly related in the spectral domain (Fu & Cazenave 2001), so after Fourier transforms, into the spectral domain, the above equations become:

$$\hat{g}(\mathbf{k}) = f(k) \times \hat{h}(\mathbf{k}) \tag{2.3}$$

The explanation for this equation is given by Fu & Cazenave (2001); pg. 411 equation (13), in Smith & Sandwell (1994); pg. 21,807 equation (2), and in Appendix C of Sandwell et al. (2001); equations C1-C3. However, it is the explanation and form of equations 14-16 from Smith (1998) that is adopted here.

$\hat{g}(\mathbf{k})$ = The Fourier transform of the gravity anomaly at position $\mathbf{x}$.

$\hat{h}(\mathbf{k})$ = The Fourier transform of the height, above the local depth (d) of the topography at position $\mathbf{x}$. Given that $h << d$ in this setting, the first approximation of C1 fromSmith (1998)is utilized which gives:

$f(k)$ $=C \times exp(q)$. C is considered a constant (Bouguer constant) if no compensation mechanism is utilized, and $C = 2\pi G(\rho_c - \rho_w)$. G= the Newtonian gravitational constant, ρ_c is the underlying crustal density, and ρ_w is seawater density. Assumed to be spatially invariant here, but actual density values vary in a nonlinear fashion. This leaves $exp(q)$, to vary, and $exp(q) = exp[-2\pi d\backslash\lambda] = e^{(-2\pi d\backslash\lambda)}$. And $\lambda^{-1} = \sqrt{\lambda_x^{-2} + \lambda_y^{-2}}$ (Smith 1998), and if the assumption that $\lambda_x = \lambda_y$, so horizontal scales are equal, as in the base diameter of a conical feature. Then for the Ideal calculation : $\lambda_{width} = \lambda$:

$$f(k) = C \times e^{(-2\sqrt{2}\pi d/\lambda)} \tag{2.4}$$

It is not possible to solve for λ at a given depth and gravity anomaly, without knowing h, as mathematical they are independent. However at this step, it is possible to invoke a deterministic ratio between height and width scales from empirical data, as the Ideal error is interested in the small scale features of the ocean, and abyssal hills are considered the most pervasive small global feature (Goff et al. 2004). The literature contains ratios of abyssal hills width by height ratios, determined empirically. As such a simple inverse relationship is utilized from the published work, which was derived from a linear regression equation produced using ~ 400 empirical surveys. The authors give the number of sites, but indicate that not all values are published. (See Goff et al. (2004), as this includes geographic extent of several major field sites, see other publications by Goff for further information.) From Goff 2010; Equation 3, and Figure 10:

$$H_{rms}(\mathbf{x}) = \frac{5}{101}\lambda_{hw} - 60.9 \tag{2.5}$$

$\lambda_h w$ = Abyssal hill width.

H_{rms}= The abyssal hill root mean square height in meters as a function of wavelength in meters. The H_{rms} is useful as an integrated height measure of an ideal feature, if the feature is assumed to have a sinusoidal shape, then amplitude, or peak height is given by: $\sqrt{2} * H_{rms}$. To make solving the following equations more tractable using Mathematica the y intercept term was removed, given that actual abyssal hill width scales are in kilometers the likely error introduced by this approximation is considered acceptable.

If equations (2.5) and (2.4) are substituted into Equation (2.3) then the only unknown for a given depth becomes λ, as such the Ideal error $E_\mathbf{x}$ can be solved for λ as a $f(d)$ only. From Equation (2.3) $\hat{g}(\mathbf{k})$ and $\hat{h}(\mathbf{k})$ can be simplified to $g(\mathbf{x})$ and $h(\mathbf{x})$. By removing the Fourier transform term $exp[]$ from both sides giving:

$$g = C \times e^{(-2\sqrt{2}\pi d/\lambda)} \times \frac{5}{101}\lambda \qquad (2.6)$$

g = The gravity anomaly, which is $1{\times}10^{-5}\,m/s^2$.

$C = 7.84165 \times 10^{-7}\,s^{-2} = (2\pi * 6.674 \times 10^{-11}\,m^3/kg * s^2) \times (1870\,kg/m^3)$

Where, $(1870\,kg/m^3) = (\rho_c - \rho_w)$ and $\rho_c = 2900\,kg/m^3$ and $\rho_w = 1030\,kg/m^3$ (Carlson & Raskin 1984; Smith 1998).

$$g/C = \frac{5}{101}\lambda \times e^{(-2\sqrt{2}\pi d/\lambda)} \qquad (2.7)$$

Using the software *Mathematica 10.0* and the "Reduce function" the proceeding equation was rearranged for λ in terms of depth (constrained with logical parameters $\{d > 0 \;\&\; \lambda > 0\}$). Results did not differ from solving using wolfram's free online Mathematica portal, or the proprietary software:

$$\lambda_m = (8.88577\,d_m)/(F_w[(11564952\sqrt{2}\,d_m\Pi)/1489558387)]) \qquad (2.8)$$

$F_w[z]$ =The Lambert W Function = Product Log Function= gives the principal solution for w in $z = w \times e^w$ and in this case $z = -0.0344946\,d$, for $d > 0$ & $\lambda > 0$ (rounded). This is the $E_{\mathbf{x}}$ equation (**Ideal error**) (Figure 2.1).

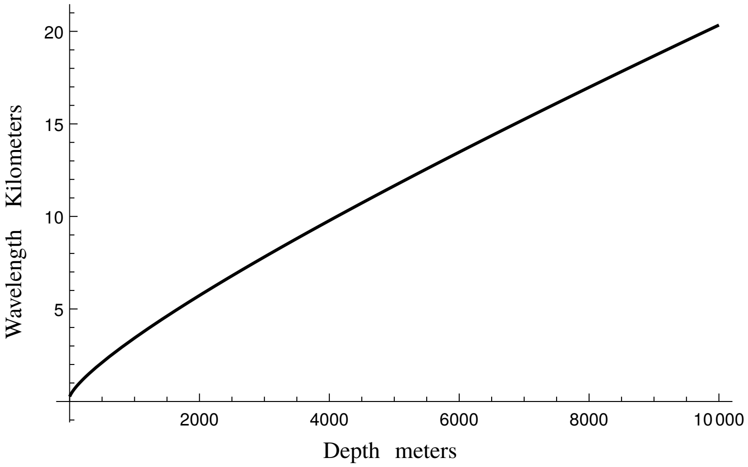


Figure 2.1: Ideal error - wavelength size by depth
Error width (λ) in kilometers. Depth is meters, 1-10,000 plotted. From Equation 2.8 Ideal error.

Equation 2.8 gives full wavelength (the horizontal scale of a feature), practically the Nyquist frequency most be taken into account. To avoid aliasing, any frequency must be measured at least twice per wavelength ($\lambda/2$). This becomes relevant for actual ship-based measurements to ground truth gravity width anomalies. The Ideal error assumes continuous satellite swath coverage, and so the Nyquist frequency does not directly affect the calculations above.

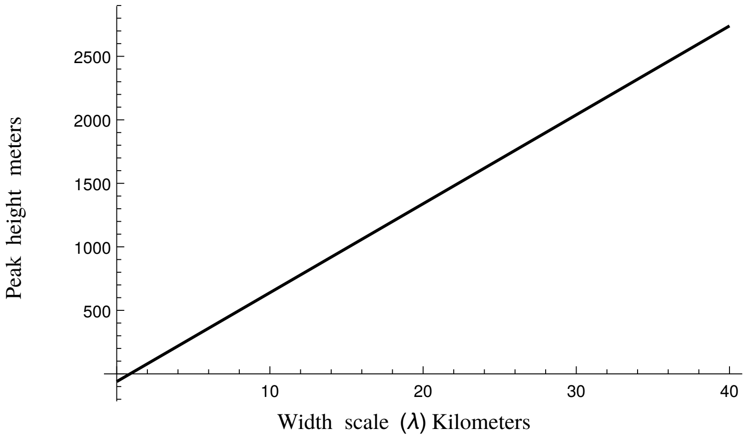


Figure 2.2: Ideal error - peak height by wavelength
Peak height as a function of horizontal width scale (λ) from the linear regression, Equation 2.5. Height in meters by width in kilometers is plotted from ~ 0 - 40. This range is two times greater than the Ideal error wavelength for a depth of 10 kilometers, see Figure 2.1.

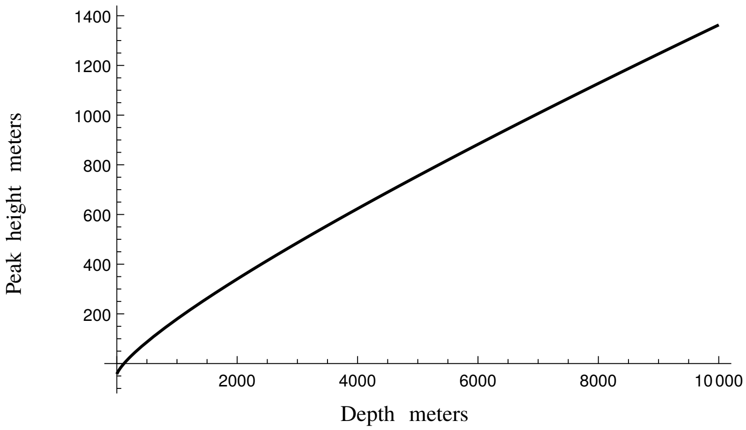


Figure 2.3: Ideal error - peak height by depth
Peak height as a function of depth, defined by the Error width scale at a given depth. Calculated by inputing Equation 2.8 into Equation 2.5. Negative values on the curve have no meaning.

The product of $E_{\mathbf{x}}$ equation, can be used to give an estimate of the peak height of a hypothetical missed feature. The sinusoidal Ideal peak height as function of wavelength at $\mathbf{x}$ is $\sqrt{2} \times H_{rms}(\mathbf{x})$, and $H_{rms}(\mathbf{x})$ is defined by combining Equations 2.8 and 2.5, which is plotted in Figure 2.2. Figure 2.3 is peak height plotted as a function of depth.

The $E_{\mathbf{x}}$ equation (2.8) was also calculated using the R statistical program (R Core Team 2014), version 3.1.2, using the package Lambert W version 0.6.4. The two programs (R & Mathematica) produced ~ 0.01 to 0.1 meter discrepancies in predicted wavelength when a non systematic comparison for abyssal depth values was undertaken. This error was considered acceptable. This may be relevant as R is more heavily utilized by ecologists and biologists than Mathematica.

2.1.3 Incorporation of Ideal error

The Ideal equation was calculated to give a numerical approximation for spatial error in the bathymetric data used in creating abyssal province delineations. The figures within (Figures 2.1-2.3) may be compared with results in subsequent chapters and sections. As this may be a new method for determining error in satellite bathymetry data it might be useful for many unintended purposes. The equations for Ideal error features outlined here are simple enough, and can be applied to gridded modeled data without having to conduct analysis of raw satellite data. For example the current gravity anomaly data accuracy in polar regions is closer to $3 \times 10^{-5}\, m/s^2$ (Sandwell et al. 2013), which can be substituted into Equation 2.7 to produce a regional Ideal error. Similarly, seamount density values input into the C term of Equation 2.7, could be used for an $E_{\mathbf{x}}$ equation that is applied to resolution issues in detecting of Seamounts. The use of a conical sinusoidal simplification for shape of features is more applicable to seamounts than abyssal hills. Abyssal hills are formed as a series of ridges, and through a variety of processes (mass wasting, sedimentation, secondary crustal tectonics) become isolated hills. For this reason the length dimension regression to rms height shows no strong relationship (Goff et al. 2004). As such, the hypothetical feature should not be used to accurately represent the real shape of abyssal hills.

The location of ABS 3.0 boundaries need to be considered in the context of bathymetric accuracy errors. The upper depth bounds for abyssal provinces is 3500m. The peak height calculated for the Ideal error at a regional depth of 3500 meters is ~ 555 meters (with an ideal hypothetical feature of ~ 8.8 kilometers in base diameter). If this number is used as an approximate error for depth, errors in assumed bathymetry may have significant import on the location of province boundaries. Habitat heterogeneity at mid-ocean ridge boundaries likely being less well sampled by ships than continental margins. Importantly, the complex topography of the two major boundaries of most provinces are obscured by issues inherent in satellite altimetry. While the attenuation errors are more pronounced on the lower bounds, of the 6500 meter abyssal depth delineations, the limited relative coverage of trench areas globally, the higher use of ship-based measurements at those locations, and the greater slope of depth increase in those locations, make the Ideal error more applicable at upper bounds than the lower bounds of the abyss. The boundaries of abyssal provinces were calculated using an older version than the currently available global satellite derived bathymetry, and data quality should increase with each new release. It would be useful if methods used in creating boundaries were better known and publicly available, in order to update them with new bathymetric data and it's associated error. Additionally this would allow future incorporation of other BEPs, and biological data.

This section includes a hypothetical error, which warrants further investigation, in order for non-specialists to better utilize modeled global topography. Correlation of topography to gravity however relies on increased sampling (subsection 1.4.3; Satellite altimetry) , and regional values would need to be obtained from appropriate agencies and individuals. Resources listed prior give various estimates for the correlation of gravity to bathymetry, indicating a low correlation between topography and gravity anomalies at wavelength values similar to Ideal error width calculated here.

2.2 Biological databases

The two biological datasets used to test the abyssal provinces are CeDAMar & GBIF, and represent most of the taxon occurrence information in the deep-sea. They are generally representative of the entire metazoan community within abyssal habitats; chordates are primarily represented by lesser evolved forms, but fishes are present. However, pelagic associates that are present in the benthic boundary layer (for example cnidarian medusae & fishes), are not as accurately sampled by all means used to collect benthic organisms. Due to chronic undersampling in relation to both area of the habitats, and possible high diversity of specific taxon (e.g., nematodes (Lambshead & Boucher 2003)) the true numerical extant of some unique abyssal taxa is unclear (Smith et al. 2006). As such the databases used are not fully inclusive of all abyssal metazoans.

As in all other fields of ecology, individual sampling methods in the deep-sea are selective in what taxa they capture. In comparing any metric of community composition or diversity across samples for a global database, this leads to several difficulties. Gear selectivity is well documented in the primary and review literature. Specific sampling methods are intentionally designed to collect select taxa, or more generally the size class designations of the deep-sea, which are in themselves lose groupings for adults of those taxa. Sampling bias is unavoidable, based on traditional methods. Specific attempts were made throughout analyses in Chapters Three and Four, to address this issue.

2.2.1 Gear to taxon correlations

Samples taken by similar gear type allows for comparison of biological data across studies. To conduct the main analyses of Chapter Three a proxy for gear type was used given uneven spatial-temporal sampling in the CeDAMar dataset, and lack of gear information in the GBIF dataset. Higher taxon level was used as replicates in the Chapter Three, as a proxy for gear type. Analysis of the CeDAMar dataset indicates that higher taxonomic levels may be an appropriate proxy for sampling methods.

Within the Animal (kingdom) records of the CeDAMar dataset, Chi-Squared tests of taxon levels to gear category violated independence, with p vales $< 2.2 \times 10^{-16}$. This was for Phylum, Class, Order, and Family. For the gear categories: Corer, Sled, Trawl, Grab, Dredge, Manual/Robotic collection, Trap, Hook and Line, Camera/video, or Other. When computing Chi-Squared tests per individual class to gear types listed above, (excluding Other), a few classes had higher p values (Table 2.1).

Table 2.1: Gear & select taxonomic class chi-squared values

Specific classes with Chi-Squared test values, less significant in rejecting in independence to gear category. Frequency data per category, counts represents unique species listing, not individual species. All had a degrees of freedom value of eight.

Class:	Camera / video	Corer	Dredge	Grab	Hook and Line	Manual / robotic collection	Sled	Trap	Trawl	P-Value	X-squared
Craniata	0	0	2	1	0	6	0	0	3	0.001278	25.5
Enopla	0	5	0	5	0	0	0	0	0	2.674e-05	35
Monoplacophora	0	0	1	0	0	0	0	0	0	0.4335	8
Sagittoidea	0	2	0	0	0	0	0	0	0	0.04238	16
Stenolaemata	0	5	0	0	0	0	0	0	6	5.11e-06	38.909

Outliers in gear-taxon dependence, Table 2.1: Craniata encompasses the hagfishes, not a major invertebrate taxa of interest, and the remainder of taxa showing limited dependence represented by few samples. Manual/Robotic collection is not a common method (296 records total in the full dataset), for collecting multiple animals, and taxon selected varies based on the desires of operators and principal investigators per dive. The class Stenolaemata, belongs to the bryozoan phylum, and encrusting forms could be imagined to be associated with rock debris in trawls, and small sized animals caught by corers, with the first method quantitative, and the latter qualitative.

Indeed other specific classes (e.g., gastropods) showed affinity for multiple collection methods (some being similar in nature e.g., trawls and dredges), yet violated independence to all gear categories. More thorough calculations of measures of association may be used to decipher gear selectivity at various taxonomic levels (Theil's U meets several important criteria). However, the scope of this analysis is for general relationships, as such no sufficient evidence was found to reject the assumptions for utilizing class as a replicate in analysis as outlined in Chapter Three.

2.2.2 Data quality

No metadata files were available during analysis, and there were errors within fields of both biological datasets. The CeDAMar dataset was compiled by a team of researchers, this may explain variation of syntax and the resultant lack of standardization and errors. For example for missing values, NaNs, NAs, blank spaces, and 9999's were listed. Data cleaning and munging was carried out at various steps in analysis because errors were not systematic.

Within the CeDAMar dataset three fields were attributed to species, "SPECIES", "ORIGINAL_NAMES_ID", and "WORMS_FullName" (WoRMS Editorial Board 2016). The "SPECIES" field was not limited to Latin binomials, common in the database were working species designated by numbers only for a specific genus, making this field useful within sites for diversity analysis (rarefaction methods, Chapter Three), but not between locations. Without a metadata file, lack of correlation with the two other fields, and given the large number of NAs for "ORIGINAL_NAMES_ID", this field was not used in analysis.

At the time of downloading (2015-10-12), GBIF contained fields for 200 + variables, almost all blank. Unfortunately no data on sampling effort or individuals collected per species was available. GBIF is in general a cleaner dataset, which includes numerical keys associated with each taxa level, yet for analysis in Chapter Three unique names for, class, genera, and species were more complete than associated numerical keys, and so those were used.

2.3 Discussion

Analyzing and assessing the GBIF and CeDAMar datasets independently, and then comparing results allows for a more thorough study as they complement each other in some respects, this is done in Chapter Three. Differences include scope, number of samples, and secondary variables of interest, in addition to taxonomic and location data. By utilizing the gear information and associated taxon information available in the CeDAMar, some proxy of gear category can be used for standardizing GBIF data. The inclusion of both gives some measure of robustness to the analysis in following chapters. Links to data are available in Appendix A.

Bathymetric resolution and accuracy is variable over the global domain. Using bathymetric data to define horizontal extant of provinces should include some measure of this inaccuracy. For reasons unrelated to bathymetry, strict adherence to specific boundary delineations in ocean biogeography is discouraged (e.g., fronts and gyre variability). The issues in biological data coverage and possible bathymetry inaccuracies at proposed province boundaries discouraged intended analysis of those boundaries for the global domain, in this study. The results of this section support the choose of MDE analysis of province centroids as a robust response to data inaccuracies with physical and biological data. The bathymetric resolution issues indicated by Figures 2.1-2.3, are significant enough that results from Chapter Three may be influenced by data inaccuracy due to its use in creating ABS 3.0 boundaries, but not necessarily rejected. Chapter Four addresses issues in bathymetric data by providing a case study of province boundaries where ship-based bathymetric data quality has high local accuracy.

Any attempt to correct for missing depth data within biological databases must account for depth variability. The variability in resolution in the currently available global bathymetric dataset is likely higher than the values given for the Ideal error. Calculating that error for a specific area needs to take into account local survey data, as well as the correlation of gravity anomalies to bathymetry. Use of the Ideal error formula could be applied to upscaled gridded satellite products, which then could be used for many purposes. For example a geospatial analysis of Ideal error with known ship tracks, would be useful in directing future cruises to areas that may harbor abyssal mountains and seamounts, not captured due to coarse satellite resolution. The Ideal error and the satellite derived bathymetry could be added to GBIF dataset, in order for future macroecological study interested in the relationship of patterns of biota to depth. It could be used with CeDAMar data to collaborate depth values, and subsequently be used in determining other spatial errors. Workers in the deep-sea could utilize the Ideal error to quantitatively parameterize error for any biotic analysis dependent on satellite derived bathymetric data. Some accounting for the bathymetric error should be used in future versions of ABS 3.0.

3 ABYSSAL PROVINCE SCHEME & DIVERSITY MID-DOMAIN EFFECT ANALYSIS

The core analysis of this thesis is presented in this chapter. The testing of the ABS 3.0 boundaries with the two biological datasets. Prior to the sections on analyses, are separate background sections. These sections are related specifically to marine and then deep-sea biogeographies. These two sections are followed by sections on the proposed abyssal province scheme (Watling et al. 2013) and the theoretical basis for each BEPs used in its creation.

3.1 Marine and deep-sea biogeographies

Oceanic biogeographies generally focus on specific realms within oceans and rarely encompass the complete marine system. The three major oceanic realms are coastal and shelf areas (pelagic and benthic), deep-sea benthic, and open ocean pelagic. The midwater pelagic zone is lacking in relative biogeographical analysis due to lack of sampling density, while coastal areas are the most heavily sampled (Webb et al. 2010). The commercial significance of coastal areas likely explains why work there (e.g., on fishes (Briggs & Bowen 2012)), has made the most progress of all the ocean realms .

A hierarchical and nested biogeographic system for coastal systems has recently been developed that includes realms, provinces, and ecoregions (Spalding et al. 2007). Traditionally ecoregions are accepted subdivisions of provinces, synonymous with the older term of regions. Ecoregions have been created for surface coastal regions, 0 to 300 meters depth, utilizing the marine ecosystems of the world classification **MEOW** (Spalding et al. 2007), which further divides provinces based on relatively homogeneous species composition and a distinct suite of hydrological factors. Those factors include: isolation, upwelling, nutrients, freshwater influx, ice coverage, sediment characteristics, coastal complexity, and bottom topography. The authors acknowledge that an optimal biogeographic system must allow for quantitative analysis at varying scales of a nested hierarchy. MEOW builds upon the coastal large marine ecosystems of the world (LME), which was constructed using a combination of biogeographical analysis as well as geopolitical borders (Briones et al. 2009). Most biogeographical work in the ocean is focused on shallow or coastal systems.

Biogeography of the pelagic realm is best represented by the seminal work of Longhurst (2010). This scheme was built by analyses of satellite data, relating to ocean surface chlorophyll, to derive biomes compromised of smaller provinces, which are defined by biogeochemical cycles, climatic patterns, ocean circulations patterns, and depth of mixing of surface water masses. The emphasis on fronts and eddies is well explained by Priede (2014). The importance of climate and geostrophic flow dominates the designation of biomes, where geostrophic processes allow casual delineations by latitude.

While the deep-sea lacks the fine scale biogeographical work of shallower systems, biogeographical work has been repeatably attempted. (See the description of past biogeographies by Watling (2009) and Watling et al. (2013), and the general reviews of McClain & Hardy (2010) and Smith et al. (2006).) Workers have produced various biogeographical classifications based on depth ranges for deep-sea ecosystems (Menzies et al. 1973; Watling et al. 2013). Authors interested in defining vertical zonation generally acknowledge a set boundary based on a numerical depth value derived solely on physical factors is not concurrent with nature, and instead suggest using rapid zones of species turnover as useful transition zones (e.g., Carney 2005). This is parallel to terrestrial work. A list of proposed depth proxies for the abyssal zone is found in Menzies et al. (1973). Newer work that contains additional depth categories is referenced in Table One of Watling et al. (2013). In the most complete recent taxonomically derived zoogeography of the abyss (Vinogradova 1997), the author suggests the upper limit of the abyss is centered at 3000 meters but with a kilometer of variance, based on analysis of Coelenterata and isopods.

Biogeographical work which has focused on taxonomic groups with high regional endemicity and low dispersal potential e.g isopods, or cumaceans, has been extremely useful in defining the importance of factors such as water masses as vicariance factors (Watling & Gerken 2005). Work in this vein includes analysis in both abyssal and bathyal habitats, and extrapolation of patterns to all deep taxa requires further analysis.

The proposed province scheme of Watling et al. 2013 is the most recent biogeographic scheme for the deep benthos. It follows general theoretical approaches of other oceanic schemes, yet is specifically designed with an understanding of deep-sea systems. This chapter tests the congruence of the abyssal zone province boundaries with taxon occurrence data.

3.2 Objectives and methodology

The objective of here is to test an ecological biogeography of the deep-sea and specifically the abyssal depth zone of Watling et al. (2013) using biological spatial data. Testing the proposed deep-sea biogeographical scheme is a focused endeavor in its own right, but by doing so results may be placed in the broader context of other biogeographical schemes in different ocean realms. The objective is to explore the general theoretical basis for the ABS 3.0 boundaries by testing all available metazoan occurrence data to all provinces. This is different to focusing on the specific boundaries of a single province. By testing the cumulative fit of all provinces the general scheme is tested. To test congruence, rarefied alpha diversity to distance relationships within provinces were calculated, using an expected mid-domain effect (MDE) null hypothesis with class replicates per province. This was down in parallel for GBIF and CeDAMar. This method may be more robust to issues in defining exact boundaries in the abyss. This approach tests the assumptions of a core premise of biogeographic provinces across realms, that provinces encompass centers of diversity. In this way the assumption is that the definition of provinces is equally applicable in the abyss as other realms and, but the BEPs that may be responsible for observed distribution patterns are unique to this depth habitat.

3.3 Proposed deep-sea biogeography

The proposed abiotic framework of Watling et al. (2013) was primarily created using abiotic factors of importance. It was also built upon the GOODS framework, which used previous zoogeographies for delineations as well as unpublished data (Briones et al. 2009). The methods of the GOODS report seem to be incorporation of expert opinion of previous work from the literature, rather than re-analysis of data. The proposed scheme divides the deep ocean (>800m) by vertical zonation into three distinct zones: bathyal, abyssal, and hadal. Watling et al. (2013) acknowledge the use of recent work in defining and updating previous depth classification schemes, but do not indicate a quantitative method for doing so and arrive at the abyss as delineated between 3500 – 6500. Deeper than 6500m, is classified as hadal, and 3500m - 800m is bathyal.

Only the abyssal zone provinces were tested in this study. The validity of bathyal, abyssal and hadal classifications for the deep-sea as proposed by Watling et al. (2013), is assumed here, but this study makes no assumptions on where those delineations should occur. In testing the strength of the horizontal delineations of the proposed biogeography, the depth zonations are implicitly tested. Hadal zones are dominated by trenches, ecosystems that are known to be unique, cover a small percentage of the ocean floor, exist as discreet units separated by vast distances, and are not considered threatened by direct anthropogenic disturbance. Bathyal zones exist primarily on the steep slopes of the continental margin and mid-ocean ridges, and have complex small habitat scale heterogeneity, less total area than abyssal systems, and are influenced on both depth boundaries by adjacent contrasting zonal ecosystems. The abyssal systems were chosen as representative of the open ocean, which lack confounding factors for analysis.

Watling et al. (2013) indicate regional and taxon differences are likely responsible for varying classifications schemes, undertaken here is an average of available data, as opposed to extrapolation and refinement based on single studies, or classes. For the abyss, they cite Menzies et al. (1973), and Vinogradova (1979), as their primary sources, yet do mention use of Vinogradova (1997), in defining provinces. Menzies et al. (1973) uses isopod genera for analysis, and Vinogradova (1979) uses easily identifiable species, mainly from the Pacific and from Russian expeditions.

The work by Menzies et al. (1973) is impressive, and judging by its scope took several years to complete. Their isopod species analysis coming from intensively studied transects down the continental margins into the abyss. The work is replete with additional information such as elaborate sketches of animals in-situ, detailed sediment descriptions, and in-depth descriptions of bottom current scouring along the area under study. However, transects at bathyal depths at the mid-ocean ridge system and into the abyss are not included. The authors designate boundaries of vertical zones using locations of high species turnover. Then from those locations they indicate habitat features that are spatially correlated. The authors use well studied sites at each region of interest, as opposed to pooling all data, and creating a global average. The benefit of this method is that it better captures regional differences and environmental factors which may explain those differences, yet extrapolation of single sample sites to large ocean regions should be undertaken with caution. While the authors include numerous reviews of other work, their own analysis is not geographically representative to sufficiently test the province scheme they propose.

Vinogradova (1997),updated her previous biogeographical scheme with an extensive review of current biogeographical work, discussing various theoretical assumptions on deep-sea biogeography and details of Russian expeditions not available in the west at that time. Her analysis is limited to Macrofaunal taxa, yet she reviews work for other size classes. She does not alter her previous work's delineations, but does suggest based on her analysis that a species' horizontal range increases as a positive function to that species' depth range regardless if the species is eurybathic (has a large depth ranges) or a stenobathic species (those with limited depth ranges). Table One of her work indicates the taxa she analyzed, listing 27 groupings of metazoans, ranging from phylum to order. Her work is the only multi-ocean basin zoogeography to included such a wide sampling of metazoans. Based on her review of work on specific megafaunal taxa, a circumcontinental scheme is discussed. While this particular scheme may be limited to echinoderms, it does not seem to be present in either the GOODS delineations or the proposed province scheme.

The GOODS provinces, and therefore ABS 3.0 provinces, were designed in part by biological occurrence data, but without complete taxon representation, the potential for sampling bias, and not in a reproducible manner. Watling et al. (2013) present an independent test of their province scheme, utilizing occurrence data. They reanalyzed protobranch data, a subclass of marine bivalves found throughout the ocean (search of OBIS 2016 records) but common in the deep-sea. The authors found within the Atlantic Ocean basins clustering did occur, with congruence to depth zones and province designations.

Full biological occurrence testing of abyssal provinces is needed. Incorporating underrepresented taxa and regions provides an inclusive test of provinces. Using the available biological data to test the scheme indicates whether it may be used in a predictive manner, given lack of full biological data coverage in the deep-sea. The lack of biological data is cited as the motivation of province scheme based on abiotic factors, or BEPs.

3.3.1 Benthic Environmental Parameters (BEPs) - abiotic factors

There are several core benthic environmental variables that are likely important in deep-sea biogeography. The following subsections outline factors that the authors of the proposed province scheme have used in creating provinces. In the abiotic work delineating abyssal provinces, the authors state, “We have adopted the concept that changes in key ecological (chemical, physical, environmental) parameters, as well as water-mass connectivity, drive the turnover and distribution of marine species and communities.” (Watling et al. 2013). They delineate abyssal provinces into fourteen distinct units which average $\sim 26 \times 10^{26}\, km^2$. These regions are separated based on: temperature, salinity, modeled particular carbon flux, ocean basin, and bathymetric features. Salinity and temperature not only indicate thermohaline water masses but also density variations, which define frontal areas. Fronts vary in terms of temporal permanence and spatial scale.

Fronts have been shown to act as barriers to dispersal across frontal zones, while distributing animals along isopycnals (Longhurst 2010; McManus & Woodson 2012; McManus et al. 2008; Thornhill et al. 2008; Woodson et al. 2012), yet animal behavior complicates this pattern (McManus et al. 2008; Woodson & McManus 2007; Woodson et al. 2005). Fronts, especially as they relate to major ocean gyres or western boundary currents, have annual or seasonal permanence within shifting spatial bounds. Furthermore, they may indeed impinge on the benthos in specific locations (Hollister & Nowell 1991).

In the deep-sea habitats, hydrodynamic processes may have several effects on the benthos including: dispersal conduits (or dispersal barriers), turbulence and sediment interactions, abiotic variability (oxygen, nutrients, etc.), and changes in delivery of carbon energy based compounds from surface and shelf areas (POC). Hydrodynamic processes range in scale from turbulent eddies to large-scale climatic fluctuations. The synergistic nature of these factors is important in studying patterns of biology in deep ocean bottom habitats; however, they may be more important in bathyal depths than abyssal in terms of biogeographic classification (Watling et al. 2013). It is likely that the major hydrodynamic forces in the deep oceans do affect geographic patterns of species in the abyss.

Meridional Overturning Circulation

Hydrodynamic processes in surface waters of the oceans are primary a result of unequal surface irradiation, wind patterns, differences in water mass properties, tidal cycles, and geostrophic effects. These factors interact with shelf and bottom topography, creating complex heterogeneity in coastal and shelf waters. Due to the various scales and interactions of these factors, ocean circulation and hydrodynamic processes are more spatially temporally dynamic than once thought. A paradigm shift away from the concept of a “bathtub” ocean has occurred in physical oceanography. While progress has been made in understanding the interplay of these causal factors in shallow systems, less is known about deep water processes.

In general it can be assumed that relative to the surface, deep benthic habitats do not experience the magnitude or severity of surface hydrodynamic processes, but they do experience both synaptic events and major ocean flows. The paradigm shift rejecting stability in the surface waters is echoed by work in the deep-sea. Work on the HEBBLE site on the Nova Scotia continental rise in the Northwest Atlantic in abyssal depths has documented severe benthic storms and resedimentation events associated with deep water western boundary currents (geostrophic flow) (see reviews in Rex & Etter (2010), and Hollister & Nowell (1991)). While these currents are known to be associated with continental land masses, the major source of currents in the the deep-sea are related to the Thermohaline circulation, which will be refereed throughout as the **Meridional Overturning Circulation** (MOC), which is a more exact term when referring to the movement of water masses in the abyss (Wunsch 2002). Thermal and salinity profiles of water masses define the mass transport of the MOC. Surface wind is the driving force, and vertical density gradients, primarily at the poles, are responsible for the global flow. The abyssal circulation component of the MOC is primarily horizontal in nature.

The abyssal flow has a defined direction as a function of integration across much of the deep ocean, but only at large time and volume scales. The immense scale and limited speed of the deep water flows makes the downscaling of a net global flow at local scales, and sub-monthly time frames, more difficult. At synaptic or daily scales mean Eulerian velocity generally exhibits a random pattern. The importance of the MOC in larva dispersion (Hilário et al. 2015) at ecological time scales, as well as its role in evolution via oscillation between thermohaline, halothermal conditions (McClain & Barry 2010), is thought to be important, but direct evidence is lacking.

In the absence of sufficient data coverage, numerical modeling has been utilized with available float coverage to model deep water circulation associated with topography of ridge systems. Results from one model (Speer et al. 2002) suggest that general circulation flows are strongly affected along mid-ocean ridges, such that yearly mean flow travels along ridges, largely impacted by the MOC in the Northern Atlantic. In the Atlantic, meridional flow wanes towards lower latitudes, with zonal flow caused by equatorial Rossby waves creating an oscillating pattern over several hundreds of kilometers (Speer et al. 2002). This pattern is repeated in all ocean basins. General results from this model, when compared to available drifter data, suggest that circulation patterns are well modeled in seasonal time frames and at regional scales; however, smaller scale statistical diffusive flow deviating from along ridge flow is not well resolved at local scales. The authors caution that dispersal of oceanic flows cannot be determined solely from the mean velocity field. In this regard, smaller scale flows are more complex than the models can resolve.

Numerical models, and observational data, have led to a general acceptance of the importance of large bathymetric features impacting deep water circulation. The Samoan Passage is a key bathymetric feature which funnels a major portion of the abyssal circulation from the Southern

Ocean into the South Pacific. Abyssal circulation through the passage is immense (~ steady mean $5 \times 10^6\, m^3 s^{-1}$ of water) and shows climatic variation at the scale of years and months (Voet et al. 2016).

Bathymetric features primarily separate abyssal regions in the form of spreading centers and mid-ocean ridges. However, the current province scheme demarcates some regions based on ridges, and in some regions ridges are of less importance. These features interact with the MOC, and may interact or redirect major benthic currents. The Atlantic basin provinces (ABS 3.0) likely incorporate the deep water flow and a poleward reversal through the equatorial region of the Atlantic passing through the Romanche and Chain fracture zones (Messias et al. 1999; Shank 2004). The ridge is not considered a separating feature in the North Atlantic Province, nor is the mid-ocean Indian ridge a separating feature in the province scheme. The Indian ridge system is known to be seismically active (Hashimoto et al. 2001). The Indian Ocean is unique in that it also includes a ridge system running latitudinally (Ninety East Ridge) that is considered aseismic, such that seismic activity is limited and it is a separate feature from the Mid-Indian ridge system. This dominant oceanographic feature may act as a topographic barrier to gene flow. Ridge features may vary in importance based on dispersal capabilities of deep-sea animals, in large part due to currents associated with those features.

In addition to MOC and basin scale ocean flows interacting with ridge topography, ridges may indeed impact biogeography through the factors relating to water mass differences, hydrothermal vent plumes, and the unique biological communities associated with vents. Vent plumes are typically caused by geothermal heating associated with active seismic areas of the seafloor, ridge systems, back-arc basin, and underwater volcanoes. They are found throughout the world's oceans. The metazoan communities associated with them depend on mutualistic and predatory relationships with the photosynthetic microbes that synthesize energy and carbon based structures from the effluent of the geothermal activity.

These ecosystems are regionally dominated by a few functionally important metazoan taxa, which show biomass abundance values several orders of magnitude higher than surrounding areas. With the exception of mobile demersal fishes, community composition, trophic coherence, and specific species are generally unique to active hydrothermal vents at regional scales. Additionally, there is a strong similarity of these communities to other deep-sea reducing environments, (e.g. whale falls, methane seeps).

The uniqueness of these communities and the high abundance of specialized animals suggest a competitive advantage over non-specialized animals such that existence of an endemic assemblage, through competitive exclusion, likely limits survivorship to any abyssal animals that may settle in reducing ecosystems. This factor may create a biological barrier to stepping stone gene flow that might occur across topographic features with active vent communities for abyssal plain habitats at the base of such features.

The interplay of recruitment and dispersal, a major theme in shallow water ecology, is likely of importance in the deep-sea. Watling et al. (2013), in creating provinces, assume that water masses which "bath" a region, are associated with abyssal flows and the MOC and indicate connectivity. The authors use that as a criteria for delineating provinces.

Oxygen and Salinity

While oxygen and salinity are BEPs used to determine the flow of the MOC, they have important impacts on the distribution of biota. Specifically oxygen availability in bathyal regions is associated with oxygen minimum zones (Levin 2003; Levin & Gage 1998; Levin et al. 2009). However, the lower limit of these regions is generally above the upper limit of the abyss (Helly & Levin 2004; Paulmier & Ruiz-Pino 2009). While oxygen is indeed fundamental to the distribution of deep-sea animals, its importance in the province scheme of the abyss is less likely, as the proposed province scheme was developed to include BEPs that are important for the hadal, abyssal, and bathyal zones.

POC Flux

Given that the decreasing trend of POC with depth is most pronounced with the depth decrease in the bathyal zone, and POC is of documented importance in the abyss (Smith & Leo 2008), this BEP is likely a strong candidate for horizontal geographic variation in the abyss, lacking confounding relationships to other major variables and their relation to defining water masses. The importance of POC is analogous to the role a theoretical combination of precipitation and solar energy would have in structuring terrestrial plant systems. It behaves in part like falling water, in that it sinks from above due to climactic and seasonal patterns which affect the surface water ecosystems, and it is the basis for the detrital food web (Moeseneder et al. 2012).

Regional differences in ocean current patterns may impact POC export. This is in part due to export's association with mesoscale eddies (O'Brien et al. 2013). POC flux variability is usually associated with upwelling along continental margins, but in fact variability does occur in the open ocean (Ebersbach et al. 2014). Watling et al. (2013) give a well summarized rationale for the use of POC in a regional abiotic biogeography of Cumacea. The bounds of Equatorial Pacific Province are strongly defined on the upwelling of that region, and the subsequent horizons of POC flux differences, in the proposed global biogeography (Watling et al. 2013).

Piezo-thermal

Pressure and temperature piezo-thermal thresholds may be more important on ecological scales than the individual values of temperature and pressure. The piezo-thermal equation may be dominated by pressure in most of the ocean, with temperature more important in the poles especially on continental margins (Carney 2005). It is known that pressure and temperature affect biological membranes and the structure of proteins, which are biogeochemical limitations related to the most basic metabolic needs and structure of core biological molecules. In fact the effect of pressure has been shown to affect the distribution of fishes in the hadal depths, via specifically adapted molecules (Yancey et al. 2014). Some authors suggest that the diversification of certain invertebrate taxa in the deep-sea is directly related to mechanisms related to the effect of pressure on biogeochemical pathways. There is little dispute that piezo-thermal thresholds are important when considering the depth domain from the surface to the bottom of trenches, but the role within the abyss for species patterns is not well explored.

Temperature

Temperature affects growth rates and metabolisms, as well as the aforementioned piezo-thermal thresholds. Polar seas exhibit a shallower upper limit of bathyal taxa as compared to tropical areas (Rex & Etter 2010). Watling et al. (2013) indicate that temperature changes at isobaths, rather than regions of variable temperature are used in province boundary creation.

Summary

The importance of BEPs as biogeographical factors is not tested directly in this chapter. Analysis instead is for the provinces and the fit of biota. This is in part for tractability, and because of the fact that BEP data for the abyss is hampered by sampling and accuracy issues. Errors with BEP data may exaggerate data quality issues with the biological databases. Other factors, such as species area relationships or historical factors unrelated to BEPs give credence to proposed provinces. The relative importance of individual BEPs is difficult to explore at the globally scale, as these may vary regionally and for specific taxa. Therefore analysis is for the boundaries themselves, which are the cumulative result of all BEPs. The basis for using BEPs in creating ABS 3.0 boundaries is theoretically sound.

3.4 Provinces

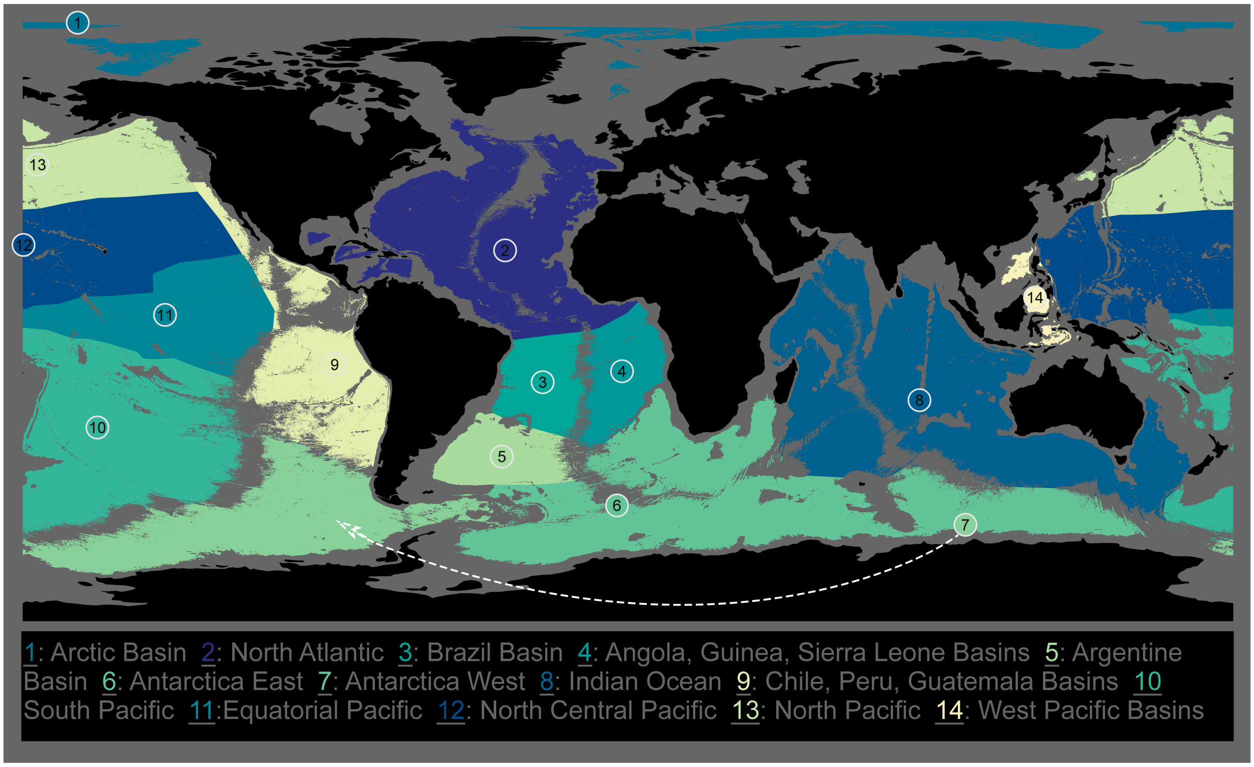


Figure 3.1: Abyssal provinces ABS 3.0

Abyssal provinces from Watling et al. 2013, and used in this study. Numbers and colors correspond to names listed. Numbered circles are located at each province centroid. Geographic centroid of Province Seven, as indicated by white arrow, does not fall within that province boundary. Black is land; Grey is ocean not within abyssal delineations.

Figure 3.1 maps ABS 3.0 provinces and their centroids. Watling et al. (2013) provide tables related to the characteristics of each province. Taken together, these provinces cover a vast area of the earth. Presented in Figure 3.2 and, Figure 3.3 are two alternative center points with two different projections, in order to visualize geographic extent, and connectivity of the abyssal depth zone, which differs from the more traditionally viewed continental framework of terrestrial realms and provinces.

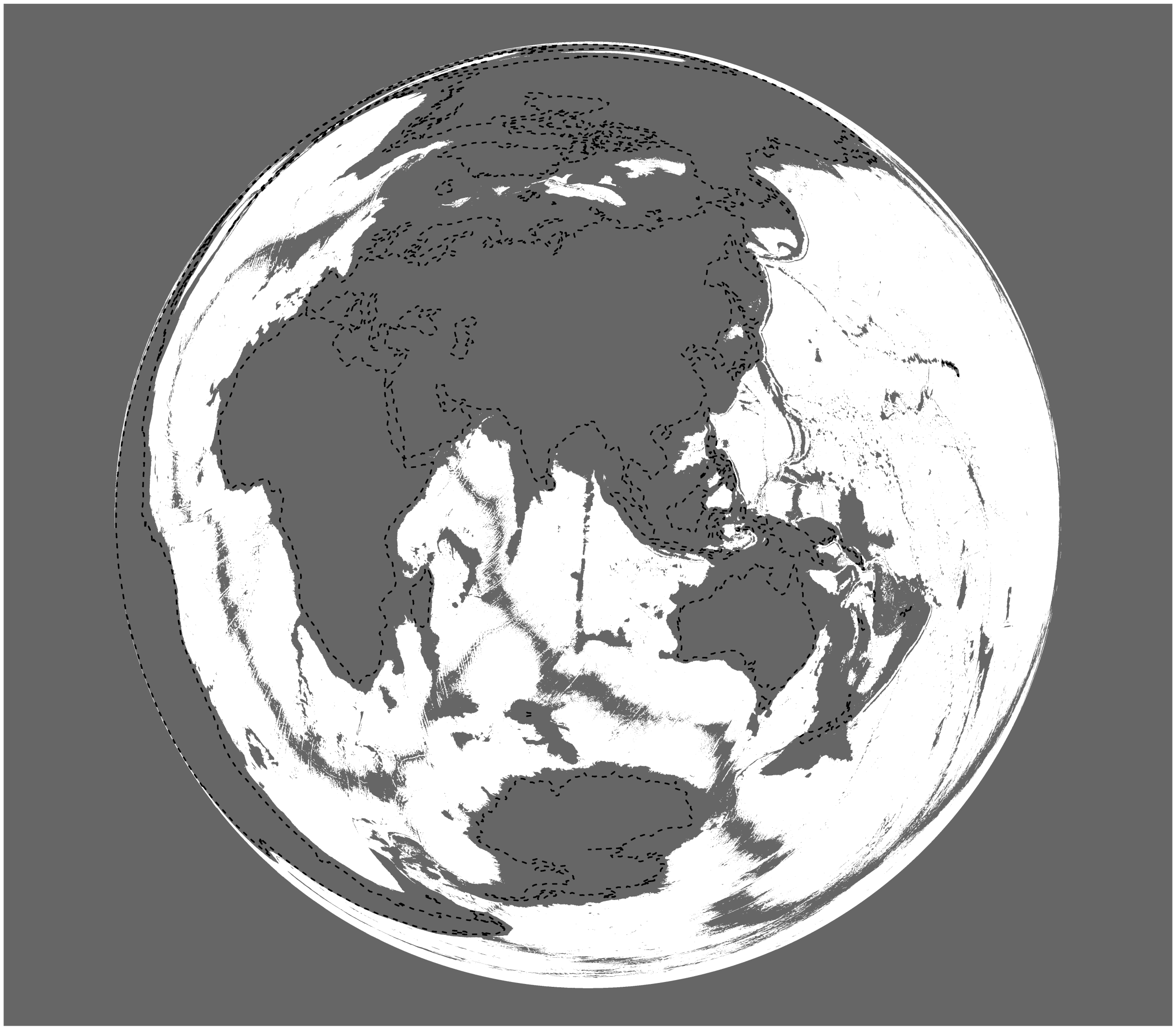
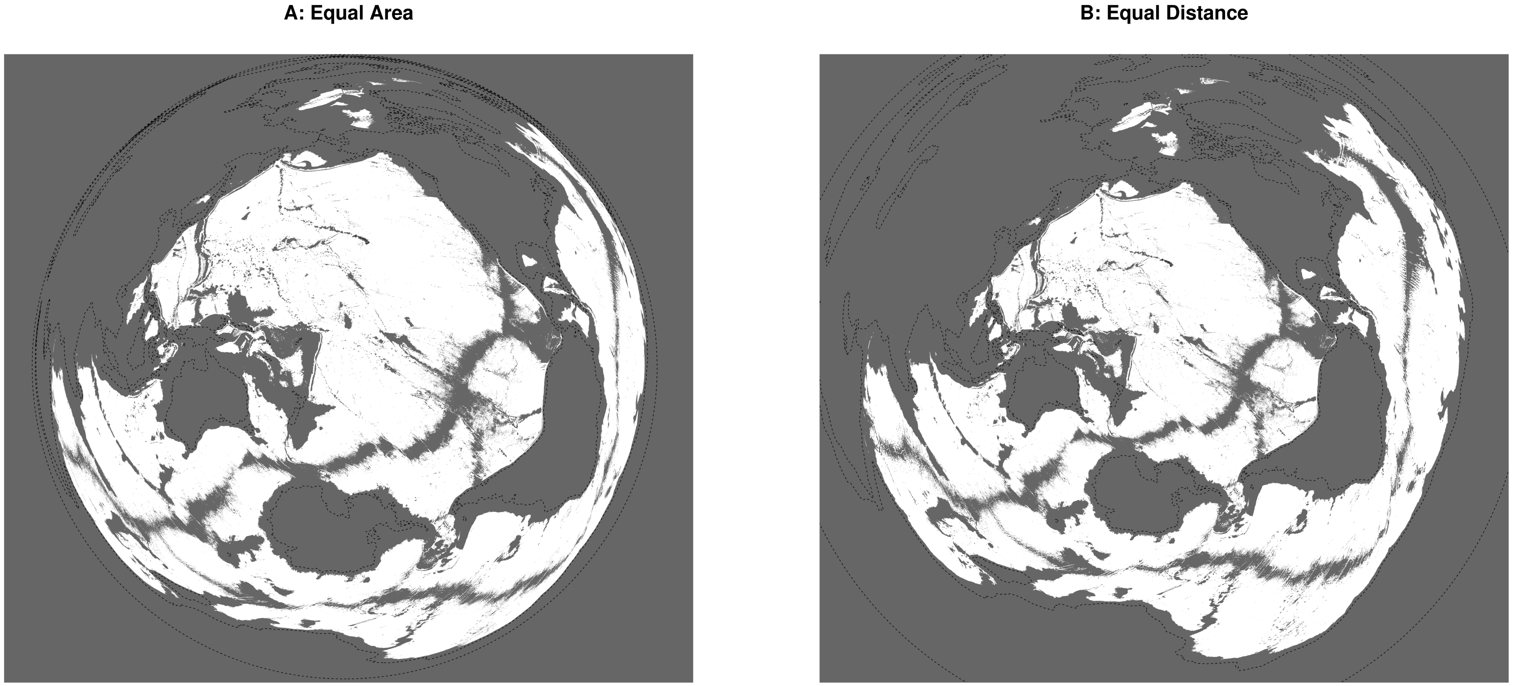


Figure 3.2: Province area

Lambert azimuthal equal-area projection, center at 90° East and the Equator. White is abyssal habitats. Coastlines shown with dotted lines. Grey is non-abyssal land, water and ocean. Land defined by dotted lines. Low resolution coastline data (1:110m). Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com.


A: Equal Area

B: Equal Distance

Figure 3.3: Equal area & Equidistant abyssal projections

Lambert equal area (A) and equidistant (B) projections of abyssal provinces (ABS 3.0) in white. Grey is non-abyssal land, water and ocean. Land defined by dotted lines. Center, is at 27.75° South, 163.5° West, and is the approximate centroid for 13 of 14 provinces combined (excluding the Arctic province). For equidistant, all points are proportionally correct distances and directions from center point. Low resolution coastline data (1:110m). Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com.

3.5 CeDAMar and GBIF

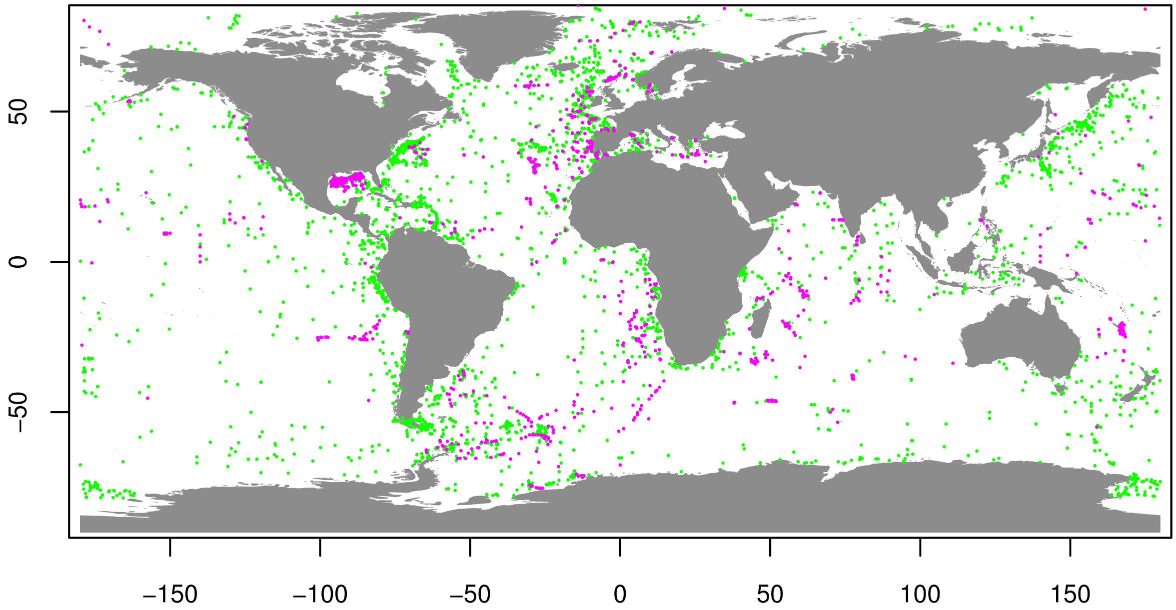


Figure 3.4: Biological databases ocean sites
All unique sites in the ocean. CeDAMar sites in magenta; GBIF sites in green. Medium resolution coastline data (1:50m). Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com.

The two databases differ in content and coverage (Figure 3.5), and as of 2016, I am unaware of other studies using the CeDAMar dataset, aside from an initial publication (Stuart et al. 2008). It is informative to present a basic comparison of the two datasets. Note the differences in global and province coverage in Table 3.1 and Figure 3.5. Abyssal regions are not well sampled over much of their area, and most sites are near the continental margin.

Table 3.1: Biological database site statistics
Unique site values for CeDAMar and GBIF. Determined using Natural earth land polygons version 3.0, 1:10m - high resolution (free vector and raster map data @ naturalearthdata.com.), and ABS 3.0. Differences in all sites and ocean, are due to incorrect positional data in datasets, and in some coastal locations may be due to proximity to land or islands, and polygon resolution. Total sites are those with geospatial coordinates.

Database	Total sites	Ocean sites	Abyssal province sites total
CeDAMar	2449	2420	657
GBIF	5051	5024	1776

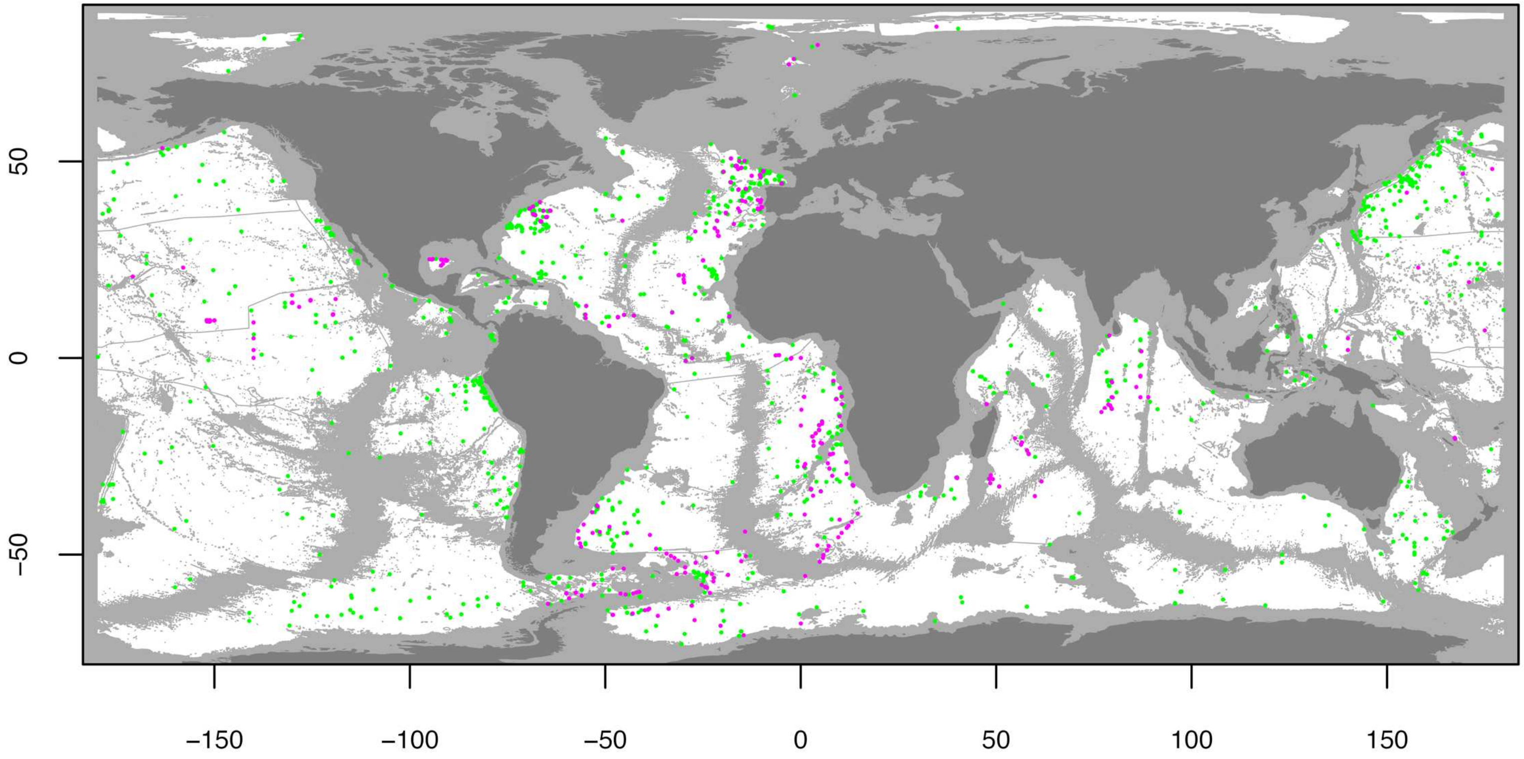


Figure 3.5: Biological databases abyssal sites
Sites within province boundaries only (ABS 3.0). Abyssal zone in white; continents in dark grey, all other ocean in light grey. CeDAMar sites in magenta; GBIF sites in green. Sites are properly mapped, bur some abyssal zones abutting the mid-ocean ridge are not discernible. Medium resolution coastline data (1:50m). Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com.

Table 3.2: Biological database sites by abyssal province

Provinces (row two) are listed with associated numerical identifier (row one). Unique sites are for the individual dataset and province (ABS 3.0). Values are total per dataset, not unique sites.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	Arctic Basin	North Atlantic	Brazil Basin	Angola, Guinea, Sierra Leone Basins	Argentine Basin	Antarctica East	Antarctica West	Indian Ocean	Chile, Peru, Guatemala Basins	South Pacific	Equatorial Pacific	North Central Pacific	North Pacific	West Pacific Basins
CeDAMar	4	273	0	73	15	85	18	40	0	4	79	62	4	0
GBIF	22	635	4	106	55	153	85	142	229	42	22	66	194	11

There is a large coverage and numerical difference between the two databases for total ocean sites (Figure 3.5), and for those sites that fall within the ABS 3.0 polygons (Figure 3.5). Table 3.2 indicates site differences between GBIF and CeDAMar per province. CeDAMar lacks the coverage that GBIF has.

3.6 Centroids and mid-domain effects

The core analysis of this thesis is testing province boundaries using an expected mid-domain effect (MDE) for diversity patterns. A MDE distribution is a statistical mathematical model in the spatial domain of a variable of interest, in the same a way Gaussian distribution is a statistical mathematical model in non-geographic space for the same variable. (See Montero et al. (2015); pg. 10, for formal descriptions on spatial mathematical models.) The MDE is an emergent statistical distribution which suggests higher species diversity is located in the geometric center of a spatial domain of interest. This is the result of stochastically located species ranges having the most overlap in the center of an inclusive geographic unit with some definable boundaries (e.g., islands or lakes). This assumes environmental gradients within the domain do not affect species distribution, or that they do not exist within the domain. Often MDEs are tested using simple and well defined geographic boundaries e.g., continental bounds for bird species (Aliabadian et al. 2008). Nothing prohibits redefining a domain based on climatic or environmental gradients. MDEs may be considered null mathematical conditions (Colwell et al. 2004). There is some ambiguity in the literature surrounding the use and understanding of MDE. This may be due to inclusion of the term 'mathematical model'.

Testing for MDEs and provinces as biogeographic centers of speciation is less dependent on the host of issues regarding the exact edge of any biogeographical areal unit. This is in line with the core of the proposed province scheme (Watling et al. 2013) in which the authors explicitly indicate the fallibility of boundaries, but emphasize the importance of provinces as indicating centers of diversity. To investigate if provinces are indeed correctly delineated, MDEs represent a promising and basic analysis. This is especially true given the issues discussed throughout regarding data quality.

Deep-sea diversity and depth patterns have been the subject of MDE analysis as reviewed by Carney (2005) and Haedrich et al. (2008). The effect has been invoked to explain a mid-depth maximum of diversity in work on continental margins. However, MDEs were rejected in favor of environmental gradients by several authors. This was in part given the variability in null models used in comparison to empirical data on diversity distribution patterns in gastropods and polychaetes (Pineda & Caswell 1997), and in gastropods, bivalves, and polychaetes (McClain & Etter 2005).

McClain & Etter (2005) conclude fit of null models to empirical data is dependent on assumptions inherent to model creation. They find poor fit when domains are improperly defined, and this does not preclude an MDE. While they reject that diversity depth patterns can be explained by null models, they do indicate that null models with similar characteristics to taxa of interest can be qualitatively correct. They also conclude that fit is a function of model parameters, thereby implicitly allowing that a MDE model built with correct assumptions may indeed correctly fit observed patterns. Conversely over fitting models, whether null or otherwise, is to be avoided. One factor that was found to be important to MDE fit by the proceeding work was whether or not actual animal ranges were continuous or patchy. Pineda & Caswell (1997) also find MDE null models fit data in a qualitative manner. They found the strength, and parabolic curve of diversity within bounded domains becomes increasingly flat when species with large range sizes are removed from their model.

Haedrich et al. (2008) conduct a thorough MDE null model comparison to their sophisticated multivariate regression analysis on megafauna and macrofauna collected systematically in the Gulf of Mexico, mainly in the bathyal depth range of the continental margin. They compared their environmental models to null models and depth diversity gradients. The authors rule out MDE models as proximal causes of diversity patterns with, environmental factors being better predictors for the majority of taxa. They found that increasing range size of taxon did correlate with greater null model fit, and given the general relationship with increased mobility to megafauna versus macrofauna, found megafauna fit null models better than macrofauna with high variability between groups within size classes.

In the limited use of MDE in deep-sea depth diversity gradients, MDE models cannot be completely rejected; however, they are likely not ultimate causes of the observed patterns, which are correlated strongly to environmental gradients. Perhaps the MDE should be considered not as a binary mutually exclusive option to environmental factors, but as a factor unto itself. In a review of MDE studies, Colwell et al. (2004) report percentage variance explained by correlation of observed richness versus MDE predicted richness. Values range from zero to 96%, and most studies are concerned with a one dimensional domain; elevation, latitude, and depth being the most common domains (Colwell et al. 2004; table 1). Fewer studies utilize a two dimensional domain. This review suggests there is not a strong precedent for stringent statistical criteria, nor standard, to use in the following analysis in two dimensions in the abyss.

The following use of MDE is analogous to an a priori expectation for a Gaussian normal distribution, where fit may not be one to one in analysis but deviation from that null indicates other processes are responsible for observed distributions. The working null hypothesis is that biogeographic provinces are likely to exist in the abyss given their acceptance as meaningful spatial partitions over the majority of other realms of the planet. Since the proposed province scheme delineates boundaries based on both physiographic and environmental gradients, the expectation is that the domain is correctly established to test MDE, as those gradients do not exist within the domain. To reject a MDE requires the lack of a meaningful observed effect, yet does not rely on MDEs dominating the observations. A priori, there is an expectation that a MDE will be stronger in the abyss than for the depth gradient to diversity analyses discussed above, given that relative to continental margins abyssal habitats have less intense environmental gradients.

3.6.1 Centroids

Centroids were calculated per individual province using shapefiles of provinces ABS 3.0. Shapefiles were provided by Dr. Les Watling (Watling, pers. comm.). Centroids are the midpoint of a province's spatial domain. To avoid centroid calculation errors, several steps were utilized based on the R (R Core Team 2014) package rgeos (Bivand & Rundel 2016). Initial centroids were calculated on a global Mercator projection; this value was used per province as the center for a Lambert equal distant projection. Next, the centroid was recalculated. This method gave the final center for a Lambert equal area projection to provide best extent for calculating the final centroid based on area. This method was chosen given the import of area in centroid calculations, and the assumptions of species ranges in the MDE. While this method is not needed for all provinces due to projection issues, it provided a standard method to apply to all provinces, facilitating more robust cross analysis. Other methods could have alternatively been used (3-dimensional Cartesian

Table 3.3: Province centroids

Location of centroids per province as calculated by multi-step re-projection method. Negative values indicate West longitudes, and South latitudes.

Province	Longitude	Latitude
1	-163.6441	87.69607
2	-36.53221	20.07618
3	-25.36893	-19.06573
4	-1.761114	-15.80678
5	-37.51722	-41.13108
6	-3.24587	-55.65838
7	100.3662	-61.4053
8	86.70003	-24.39749
9	-87.24032	-13.83895
10	-157.8009	-32.51781
11	-137.675	0.9266538
12	-179.7621	21.70342
13	-175.5923	45.5173
14	121.0676	6.105142

re-projection, alternate software, or using an appropriately parameterized cylindrical projection). See Table 3.3, and Figure 3.1.

Centroids were calculated based solely on province polygon geometry; resultant centroids are therefore not always in meaningful locations, but provide useful hypothetical proxies (Figure 3.1). For example, the Arctic province is a series of non contiguous polygons, and as such its centroid falls between abyssal basins in bathyal depths. Province Seven's (Antarctica West) centroid location is a result of its shape in relation to the Antarctica landmass.

3.6.2 Taxon analysis

Ideally, for this analysis province sampling would include replicate sampling by all major gear types throughout the spatial domain. Additionally, it would include taxonomic experts at all lower level taxonomic designations of the major groups of deep-sea metazoans. Logistical realities have limited efforts proceeding as such.

The following analyses take a compromised approach to various issues. To compare sites with different sampling effort, the well known species rarefaction by individuals technique was used (Heck et al. 1975). Rarefaction gives estimates of number of species (alpha diversity) observed as a function of individuals collected. A resampling curve of actual data is employed (statistically derived by taking the average of many resampling efforts) to develop this function. The curve is calculated per site, but to compare sites a standard number of individuals is chosen. This standardizes for sampling effort, but allows diversity numbers per site to reflect specific site alpha diversity. A major caveat to this method, which is used commonly in the deep-sea (Rex & Etter 2010; 55), is that it fails when comparing samples collected by different gear methods. Since the GBIF database does not contain information by collection method, or number of individuals per species, it was not possible to perform sub-analysis by gear type. Higher level taxonomic group was used as a proxy for gear type, in this case class. Alternatives could be chosen, namely order, or family. While CeDAMar does list gear type, exploratory analysis indicates that even in well sampled locations (Chapter Four), not all taxa which were likely captured by a gear type were recorded. Often studies are targeted for a specific taxonomic level, and information on other animals present is not taken. Not all CeDAMar samples had gear type designation listed. To compare the results from the independent analysis of the two datasets, the class proxy was used for both.

Several options were considered when selecting which taxonomic level to use. The taxon category must be strongly correlated to a limited number of major gear types. If this is the case a child category will likely be similarly constrained; this applies generally to the majority of taxonomic grouping at the same hierarchical level, but not necessarily within a specific subtaxon. The lower the taxonomic category chosen, the more comparable diversity metrics are between sites due to biological metrics, as well as reduced error in species designations by workers. The higher the taxon level, the greater number of overall samples sites to compare, and the better the overall spatial coverage.

Each of the three possible taxonomic levels represents trade offs within these scalable restraints. Family is a useful proxy for life history and functional trait similarities. Orders, especially those of the arthropods, represent traditionally defined expertise and previous biogeographical analysis. Class provides high site comparability. Family, and below, may suffer from taxonomic re-designations and unequal sampling distributions. Orders vary in relative importance by phylum. Class is the most coarse, and class diversity may not be comparable between sites. The goal was to test the general theoretical fit of provinces for the majority of metazoans, and not any ensemble or assemblage. Given the major limitations of sampling coverage and areal extent of provinces, class was chosen. The assumptions of gear selectivity and its correlation to class were not overturned by basic analysis given in Chapter Two.

3.6.3 Diversity spatial analysis

Two main analyses were undertaken and duplicated for the two datasets, those being diversity distance relationships per class per province. The results were then compared for specific significant classes between provinces. Diversity was calculated through the rarefaction technique (Heck et al. 1975), using the R package Vegan (Oksanen et al. 2016). Rarefaction of species by individuals was done for CeDAMar. For GBIF, no measure of sampling effort was available (individuals per species). This was addressed using genus richness, calculated using species numbers, for rarefaction. Rarefaction methods were originally developed for deep-sea analysis making them a clear choice in this work. At large spatial scales rarefaction, when compared to other methods, has been found the most robust method of removing sampling bias when correlating diversity to environmental factors (Engemann et al. 2015). For both datasets, analysis was carried out within class. CeDAMar contained both officially described species as well as working species. Working species were used for rarefaction. Considerable effort was written into R code to limit errors which could have occurred for duplicate working species names belonging to different taxa. Working species was chosen to account for high diversity in the deep-sea.

The main analysis was a regression of average rarefied richness for class replicates by site scalar great circle distance to local centroids. Within province diversity was calculated per class for each site. Three rarefied richness values were calculated for each class per site: (1) richness rarefied by maximum individuals collected per class in a province; (2) 100 individuals ($E(S_{100})$); and (3) the median number of individuals per site plus one. The geometric mean of the three values was taken as the value for the regression of expected richness to distance. The rationale for the three values, was that rarefaction to 100 individuals is a common number in deep-sea studies, while the median plus one was chosen to include class replicates with low representation and to avoid meaningless rarefaction values based on sampling only one individual. The maximum number was computed given high expected local diversity and possible under sampling issues. Replicates were excluded if a class was not represented at more than one site, and the minimum individual and species criteria which nullify rarefaction methods was not met. This geometric mean was used for general MDE analysis for both datasets.

To compare within class variability by province, the spatial diversity regression was recalculated for E(S_{100}) only, for both CeDAMar and GBIF. This was to done to better compare spatial regression slope values between classes. Rarefaction of genera diversity by species is less common, as such the 100 value rarefaction has no strong basis here, but was kept for standardization purposes. P-values (alpha = 0.10) for each replicate regression were criteria for MDE testing. Species rarefaction is preferred to using to genus rarefaction, but the differences in spatial coverage between GBIF and CeDAMar (Figure 3.5, Table 3.2) prompted its use in analysis.

CeDAMar MDE results

General MDE For class analysis for CeDAMar, an initial rejection of sites which failed to meet rarefaction criteria left 70 total pooled replicates across 10 of the 14 provinces. However, when linear regression (richness to increasing distance from centroid) was undertaken low sampling in terms of number of sites returned NaN values for p-values for slope coefficients. This was used as criteria to remove those samples which were poor candidates for analysis due to lack of data, or rejection by the default parameters of the statistical software (Table 2.4).

This left 52 replicates across eight provinces with 22 of 45 metazoan classes represented in the dataset (~ 48%). Province One, the Arctic Basin, was excluded being comprised of only two different sites, and the South Pacific consisting of one class represented by two sites. Of this remainder, 23 (44%) had significant p-values for 90% confidence level, and 29 (56%) had higher than acceptable p-values for a spatial trend. Of the 23 replicates which had meaningful spatial trends only eight had negative slope values, negative values indicate decreasing diversity as distance from centroid increases, in line with a MDE. Fifteen percent of pooled samples is slightly higher than 10%, which would be expected if MDE were only due to chance. However, 15 of 52 (~29%) replicates indicated a positive slope. Without standardizing by province, class, or any measure of sampling effort, this analysis is inconclusive, and the MDE effect is not statistically rejected under a liberal structure (10% MDE could be explained by chance alone). However, the number of positive regression slopes would indicate an opposite pattern of a MDE. The correlation between model fit (r squared) and slope was stronger for the positive slope versus the negative slopes, 0.413 and 0.171 respectively, with a correlation of r = 0.362 for the two combined. If MDE is real, then low slope values would indicate larger average species ranges.

Patterns were not equally distributed across provinces, with the heavily sampled North Atlantic representing 40% of all the 52 pooled replicates. The four statistical measures of sampling effort per replicate were number of sites, site range, median distance between sites, and standard

Table 3.4: MDE results per replicate - CeDAMar

Replicates sorted by province. P-values for regression slope significant for alpha of 0.10 are bolded, with associated replicates underlined. Slope is mean rarefied species diversity for increasing distance away from centroid. Number of sites is sites used in analysis per replicate. Columns 9-11 refer to statistical values for distances between sites.

Province	Class	Regression slope	Regression intercept	R squared	P value slope	P value intercept	Number of sites	Site range km	Median distance km	Standard deviation distance km
2	Asteroidea	0.00009	2.24619	0.00356	0.69694	0.00959	45	3781	3651	868
2	Hexactinellida	-0.00409	24.66238	0.21756	0.69108	0.67235	3	117	5659	66
2	Lingulata	-1.74E-20	1.00000	0.50298	0.67735	0.00000	17	3413	1888	1386
2	Gastropoda	-0.00050	7.58504	0.00636	0.50558	0.00507	72	5100	3652	823
2	Ophiuroidea	0.00008	1.33120	0.01055	0.39065	0.00001	72	4954	3293	1114
2	Adenophorea	0.00065	0.20211	0.20738	0.36413	0.93408	6	2677	3893	1092
2	Anthozoa	0.00066	2.25481	0.02523	0.24225	0.26776	56	4949	3657	929
2	Echiuroidea	-0.00031	2.48321	0.07102	0.20810	0.00756	24	2959	3656	707
2	Actinopterygii	0.00079	-0.46681	0.07253	0.17434	0.83161	27	2016	3654	520
2	Phascolosomatidea	0.00000	1.00000	0.50682	0.16939	0.00000	34	2446	3655	950
2	Pycnogonida	-0.00346	14.34236	0.11511	0.15530	0.11130	19	251	3652	60
2	Malacostraca	0.00023	2.88479	0.01917	0.10791	0.00000	136	5150	3295	1357
2	Maxillopoda	0.00069	-0.22549	0.09489	**0.05642**	0.85830	39	2755	3659	673
2	Sipunculidea	0.00020	1.22739	0.04029	**0.04007**	0.00015	105	3409	3655	911
2	Ascidiacea	0.00059	1.27335	0.06209	**0.00898**	0.06703	109	3409	3648	1085
2	Crinoidea	-9.08E-19	1.00000	0.50594	**0.00854**	0.00000	20	1430	3653	419
2	Bivalvia	0.00065	0.64503	0.16120	**0.00691**	0.46626	44	5151	3756	1573
2	Polychaeta	-0.00407	21.01559	0.33390	**0.00028**	0.00000	35	5148	3652	1429
2	Holothuroidea	0.00071	1.56339	0.18549	**0.00010**	0.00659	76	5100	3651	1236
2	Echinoidea	-0.00045	2.73445	0.98725	**0.00006**	0.00001	6	2258	3829	894
2	Cephalopoda	-2.97E-19	1.00000	0.00E+00	**2.43E-14**	2.87E-104	8	2123	3650	747
4	Scaphopoda	2.60E-19	1.00000	0.57980	0.83437	1.86E-185	15	199	1564	50
4	Gastropoda	-0.00063	3.81720	0.00666	0.67982	0.05761	28	1082	1312	423
4	Holothuroidea	0.00311	-3.00274	0.22403	0.16706	0.34360	10	484	1446	170
4	Anthozoa	0.00382	-4.97041	0.99946	**0.00027**	0.00042	4	196	1565	96
4	Malacostraca	-0.03660	63.44762	0.46356	**0.00005**	0.00000	29	1053	1558	350
4	Echinoidea	0.01444	-21.52985	0.99829	**4.09E-08**	5.63E-08	7	199	1560	74
4	Maxillopoda	0.72125	-452.48253	0.94691	**1.15E-09**	7.64E-09	15	91	773	46
4	Polychaeta	0.27558	-411.71260	0.97610	**1.41E-13**	3.02E-13	17	199	1564	47
4	Sipunculidea	0.00895	-12.99158	0.99620	**1.14E-14**	2.88E-14	13	199	1565	54
4	Bivalvia	0.09964	-154.59413	0.99339	**5.64E-20**	7.08E-20	19	199	1564	45
5	Gastropoda	-0.04313	72.21014	0.56490	0.45857	0.35903	3	354	1296	197
6	Bivalvia	0.00027	0.68457	0.09572	0.69061	0.64210	4	1325	2269	578
6	Ascidiacea	-0.00241	8.97719	0.11745	0.50606	0.35247	6	393	2516	156
6	Gastropoda	-0.00046	2.76387	0.11148	0.22389	0.00580	15	1886	2179	646
6	Pycnogonida	0.00379	-8.20101	0.59892	0.12459	0.18483	5	393	2515	207
6	Sipunculidea	0.00093	-1.34774	0.42150	0.11458	0.34183	7	381	2517	179
6	Holothuroidea	0.00951	-21.40112	0.73358	**0.02941**	0.04445	6	393	2516	156
6	Malacostraca	-0.01076	44.67835	0.51180	**0.00018**	0.00000	22	3351	2169	877
7	Malacostraca	0.07908	-473.59424	0.45168	0.21399	0.23463	5	251	6340	104
7	Gastropoda	-0.01945	128.64234	0.30342	0.12428	0.11366	9	143	6442	66
8	Ascidiacea	-0.00002	2.28360	0.00011	0.95386	0.00487	33	2892	2839	967
8	Anthozoa	-0.00007	1.67407	0.01035	0.63621	0.00083	24	2892	2855	896
8	Bivalvia	0.00759	-28.17154	0.84784	0.25510	0.28427	3	518	4353	296
8	Ophiuroidea	0.00098	-0.57963	0.39787	**0.00042**	0.41383	27	2892	2839	1027
8	Malacostraca	0.00111	-0.66422	0.42912	**0.00009**	0.35305	30	2892	2875	940
11	Maxillopoda	0.07475	-94.75352	0.06259	0.16728	0.29294	32	188	1669	33
11	Polychaeta	-0.01430	47.60809	0.31019	**0.00139**	0.00000	30	1756	1853	514
11	Malacostraca	0.01506	-22.74805	0.46078	**0.00019**	0.00178	25	366	2025	179
12	Malacostraca	0.00123	0.49853	0.01302	0.40677	0.91897	55	2524	3322	327
12	Polychaeta	-0.00266	19.68432	0.01834	0.33838	0.03596	52	1208	3322	157
12	Anthozoa	-0.00040	2.36803	1.00000	**0.00030**	0.00014	3	2524	3451	1457

deviation of site distance; all showed negative correlations to regression slopes. Those values respectively were: -0.0959, -0.2406, -0.2825, and -0.2546. This indicates increased sampling effort, scope and spatial patterns all alter the likely observance of MDE, with better overall sampling and increased effort more likely to report a negative trend.

Table 3.5: Per province MDE results - CeDAMar
Per province summary. Numbers are class replicates per column. Positive and negative regressions listed for significant class replicates only.

Province	Number classes total	Classes with a significant spatial linear regression	“” Not significant	Negative regression	Positive regression
2	21	9	12	4	5
4	10	7	3	1	6
5	1	0	1	1	1
6	7	2	5	1	1
7	2	0	2	0	0
8	5	2	3	0	2
11	3	2	1	1	1
12	3	1	2	1	0

When comparing classes within provinces, results were either inconclusive or likely rejected a MDE pattern (Table 3.5). Values were sufficiently low within provinces to exclude further statistical analysis of numbers presented. Of the three provinces with seven or more classes represented, only Province Four showed a majority of meaningful linear spatial relationships, which was dominated by an increase in diversity as a function of distance way from its centroid.

Class MDE Regression values differed when computing rarefaction by geometric mean versus by 100 individuals (with some classes showing significant slope values in one analysis but not another), but general patterns were similar. Plotted in Figure 3.6 are box-plots that indicate the variability in slope values for those class replicates with significant regressions. Slopes per class are from multiple provinces. Most classes show median positive slope, followed by almost no slope, and only the polychaetes have a median negative slope.

Figure 3.7 is slopes per province for all classes. Replicates with non significant regressions have been recoded as having a slope of zero. The trend of limited linear relationship for most replicates is shown. Comparison for same class between different provinces may be more relevant than comparing different classes. In general province designations could not be supported, as MDE was not easily observed within or across provinces, or at the class level.

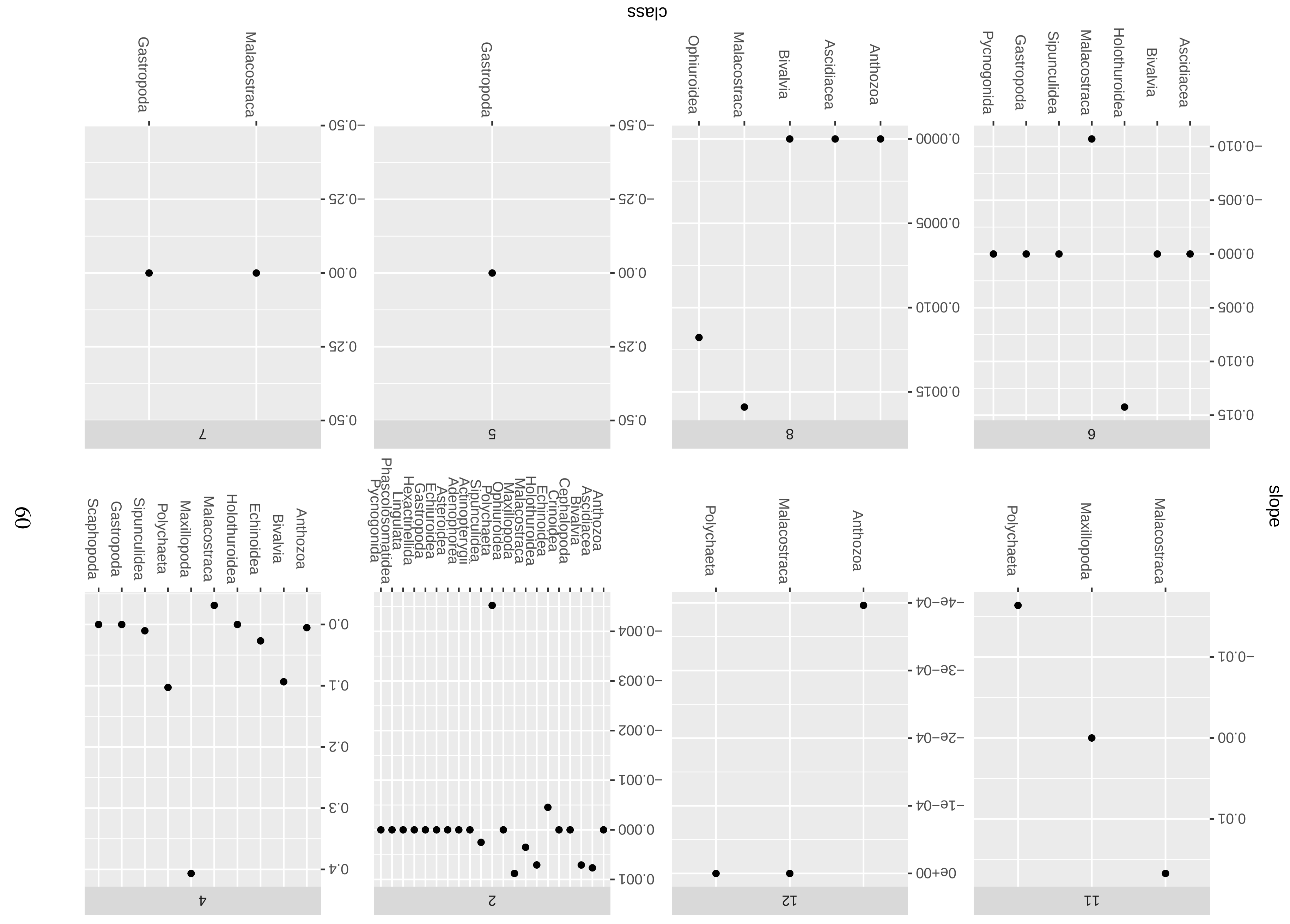


Figure 3.6: Class replicates adjusted species slopes per province - CeDAMar

Subfigures are labeled by numerical province. All non-significant slopes were converted to zeros. Slopes is mean rarefied diversity as a function of increasing distance in kilometers from province centroid.

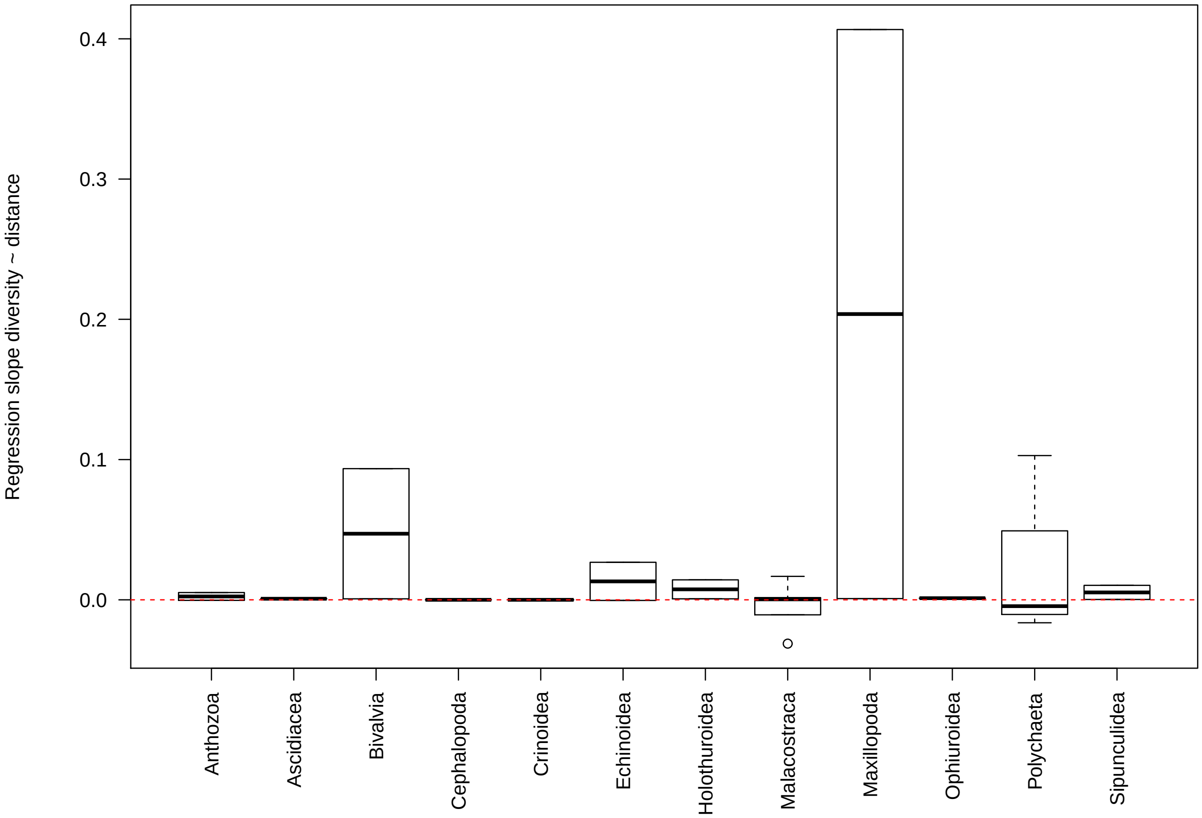


Figure 3.7: Box-plots per class replicates - CeDAMar

Box-plots for regression slopes per class, for class replicates per province with significant fit to regression. Dotted red line is zero slope. Slopes is mean rarefied diversity as a function of increasing distance in kilometers from province centroid.

3.6.4 GBIF MDE results

The GBIF results were similar to the CeDAMar results, yet a MDE was rejected. Initially, there were 83 class replicates across all provinces which met rarefaction standards. Limited data excluded 14 replicates, leaving 69 replicates for 13 provinces (Table 3.6). With Province Three, Brazil basin, not represented. Only 10 replicates showed significant p-values (alpha = 0.10) for a spatial relationship, and of those only two showed a negative slope.

Table 3.6: MDE results per replicate - GBIF

Replicates sorted by province. P-values for regression. slope significant for alpha of 0.10 are bolded, with associated replicates underlined. Slope is mean rarefied genera diversity for increasing distance away from centroid. Number of sites is sites used in analysis per replicate. Columns 9-11 refer to statistical values for distances between sites.

Province	Class	Regression slope	Regression intercept	R squared	P value slope	P value intercept	Number of sites	Site range km	Median distance km	STD distance km
1	Adenophorea	-0.00034	1.92479	0.37394	0.19708	0.02077	6	1376	2321	641
1	Bivalvia	0.01421	-10.47195	0.03678	0.71586	0.76122	6	37	880	14
1	Malacostraca	0.00356	-1.64896	0.16363	0.32021	0.57151	8	188	879	71
2	Bivalvia	0.00027	1.42597	0.02102	**0.06568**	0.00471	162	3166	3729	871
2	Malacostraca	0.00013	1.04888	0.01219	**0.09489**	0.00008	230	5256	3655	790
2	Adenophorea	-0.00004	1.41093	0.00484	0.64589	0.00000	46	2882	1887	1037
2	Arachnida	-0.00053	2.21446	0.93652	0.16215	0.07626	3	1521	2066	789
2	Ascidiacea	-0.00024	4.58382	0.00329	0.66340	0.01083	60	2966	3323	767
2	Demospongiae	-0.00030	2.01417	0.10416	0.43557	0.04708	8	2509	2175	853
2	Hexactinellida	0.00001	1.08220	0.00119	0.92978	0.01504	9	3454	2863	1099
2	Maxillopoda	0.00002	1.60506	0.00012	0.94216	0.04223	48	3129	3770	966
2	Phascolosomatidea	0.00012	0.70443	0.05873	0.15444	0.02656	36	2930	3669	682
2	Rhynchonellata	-6.95E-19	1.00000	0.42461	0.40472	0.00000	5	379	4039	156
2	Sipunculidea	0.00006	1.13960	0.00801	0.31506	0.00000	128	3347	3546	811
4	Adenophorea	-0.00736	16.01322	0.93886	**0.03105**	0.01918	4	818	1681	440
4	Ascidiacea	-0.00375	7.95723	0.25633	0.16430	0.04848	9	687	1312	235
4	Bivalvia	-0.00089	3.24158	0.00996	0.63501	0.21655	25	686	1317	163
4	Malacostraca	-0.00107	2.78637	0.04632	0.11809	0.00008	54	1326	773	307
4	Sipunculidea	0.00069	0.37188	0.04413	0.49091	0.77710	13	638	1259	166
5	Sipunculidea	-0.00086	1.96252	0.61636	**0.02099**	0.00044	8	961	1036	322
5	Ascidiacea	-0.00055	2.05963	0.01059	0.80837	0.42228	8	496	1050	181
5	Bivalvia	0.00103	1.02203	0.03318	0.59194	0.64447	11	905	1275	276
5	Malacostraca	-0.00063	2.17566	0.05695	0.19605	0.00010	31	1188	1035	344
6	Adenophorea	0.00095	-0.32390	0.59209	**0.00925**	0.68003	10	3486	2501	1185
6	Maxillopoda	0.00044	0.28959	1.00000	**0.00001**	0.00004	3	2264	1608	1307
6	Ascidiacea	0.00001	1.55049	0.00029	0.93699	0.00597	24	4900	2498	1405
6	Bivalvia	-0.00011	1.51191	0.01461	0.63285	0.02338	18	2581	2513	604
6	Demospongiae	-5.51E-20	1.00000	0.45566	0.42610	0.00000	6	4603	3350	1632
6	Hexactinellida	0.00004	1.03716	0.02272	0.56363	0.00059	17	4756	2621	1374
6	Malacostraca	-0.00002	1.44336	0.00246	0.73763	3.20E-09	48	6505	2187	1646
6	Sipunculidea	-0.00002	1.21776	0.00319	0.75865	1.02E-08	32	5156	2379	1463
7	Ascidiacea	0.00028	-0.19996	0.05363	0.37113	0.91367	17	1803	6061	509
7	Malacostraca	0.00017	-0.00093	0.06272	0.11909	0.99893	40	2038	6462	478
7	Rhynchonellata	0.00070	-3.55083	0.91346	0.19009	0.26698	3	2486	6930	1275
7	Sipunculidea	-0.00019	2.32920	0.03228	0.37980	0.08461	26	1463	6144	410
8	Bivalvia	0.00027	1.08704	0.14670	0.05878	0.09306	25	6046	4312	1905
8	Ascidiacea	-0.00005	1.87832	0.00716	0.50956	0.00000	63	5821	3615	1596
8	Demospongiae	0.00035	-0.11751	0.57151	0.24401	0.90393	4	2218	3788	1079
8	Hexactinellida	-0.00005	1.41275	0.03963	0.74823	0.11647	5	5081	4228	1845
8	Malacostraca	0.00005	1.23751	0.00540	0.68937	0.02415	32	5552	3820	1579
8	Sipunculidea	0.00004	1.04751	0.03301	0.31161	0.00002	33	5402	4808	1965
9	Rhynchonellata	0.00027	1.00880	0.47560	**0.00635**	0.01538	14	6363	3686	2432
9	Adenophorea	-0.00168	4.29887	0.01980	0.28359	0.00126	60	1486	759	193
9	Ascidiacea	-0.00002	1.32598	0.00796	0.65156	2.95E-09	28	5467	1015	1767
9	Bivalvia	-0.00001	1.46459	0.00032	0.93411	0.00010	24	6017	2182	2127
9	Demospongiae	-0.00033	2.18001	0.26562	0.29538	0.06642	6	1504	3022	558
9	Hexactinellida	-0.00007	1.19155	0.05207	0.43268	0.00001	14	2536	1368	860
9	Malacostraca	-0.00004	1.57067	0.00453	0.57420	2.16E-14	72	5952	938	1431
9	Maxillopoda	-0.00031	1.79736	0.02897	0.74716	0.19047	6	1463	904	590
9	Monoplacophora	-0.00004	1.14446	0.00438	0.78775	0.00001	19	1784	908	463
9	Sipunculidea	-0.00003	1.21269	0.00415	0.80589	0.00002	17	2428	946	922
10	Ascidiacea	-0.00016	1.68962	0.15277	0.23461	0.00195	11	4398	2842	1325
10	Bivalvia	0.00039	1.19590	0.02370	0.74175	0.59083	7	1655	1794	607
10	Demospongiae	-0.00154	3.90231	0.94074	0.15655	0.10731	3	598	1794	311
10	Malacostraca	-0.00006	1.48123	0.00661	0.78229	0.00996	14	3115	1946	836
10	Sipunculidea	0.00001	1.29908	0.00044	0.96840	0.19951	6	2176	3166	955
11	Bivalvia	-8.49E-21	1.00000	0.55675	0.91163	1.01E-47	5	4668	1274	1816
11	Hexactinellida	-0.00006	1.23292	0.01825	0.74975	0.01244	8	2710	1935	808
11	Maxillopoda	0.00659	-3.28422	0.30318	0.20025	0.75209	7	1858	1877	656
12	Bivalvia	0.00003	1.09519	0.00756	0.79933	0.06627	11	4746	3795	1371
12	Malacostraca	0.00001	1.14484	0.00230	0.77811	0.00000	37	5877	3258	1806
12	Maxillopoda	0.00007	2.87766	0.00265	0.88774	0.09931	10	4908	2180	1761
13	Bivalvia	0.00020	0.67467	0.21943	**0.00079**	0.00003	48	3834	2244	967
13	Hexactinellida	0.00058	0.27682	0.44467	**0.03520**	0.57913	10	2345	2065	778
13	Ascidiacea	0.00006	1.01417	0.01409	0.60835	0.00038	21	2366	1686	621
13	Demospongiae	3.02E-06	1.22567	0.00005	0.97687	0.00009	20	3247	2197	949
13	Malacostraca	-0.00004	1.91537	0.00037	0.85223	0.00027	96	3393	2254	730
13	Sipunculidea	0.00025	0.78223	0.08504	0.11791	0.03251	30	2838	2356	623
14	Maxillopoda	-0.00576	13.74871	0.23904	0.51108	0.31584	4	533	1434	225

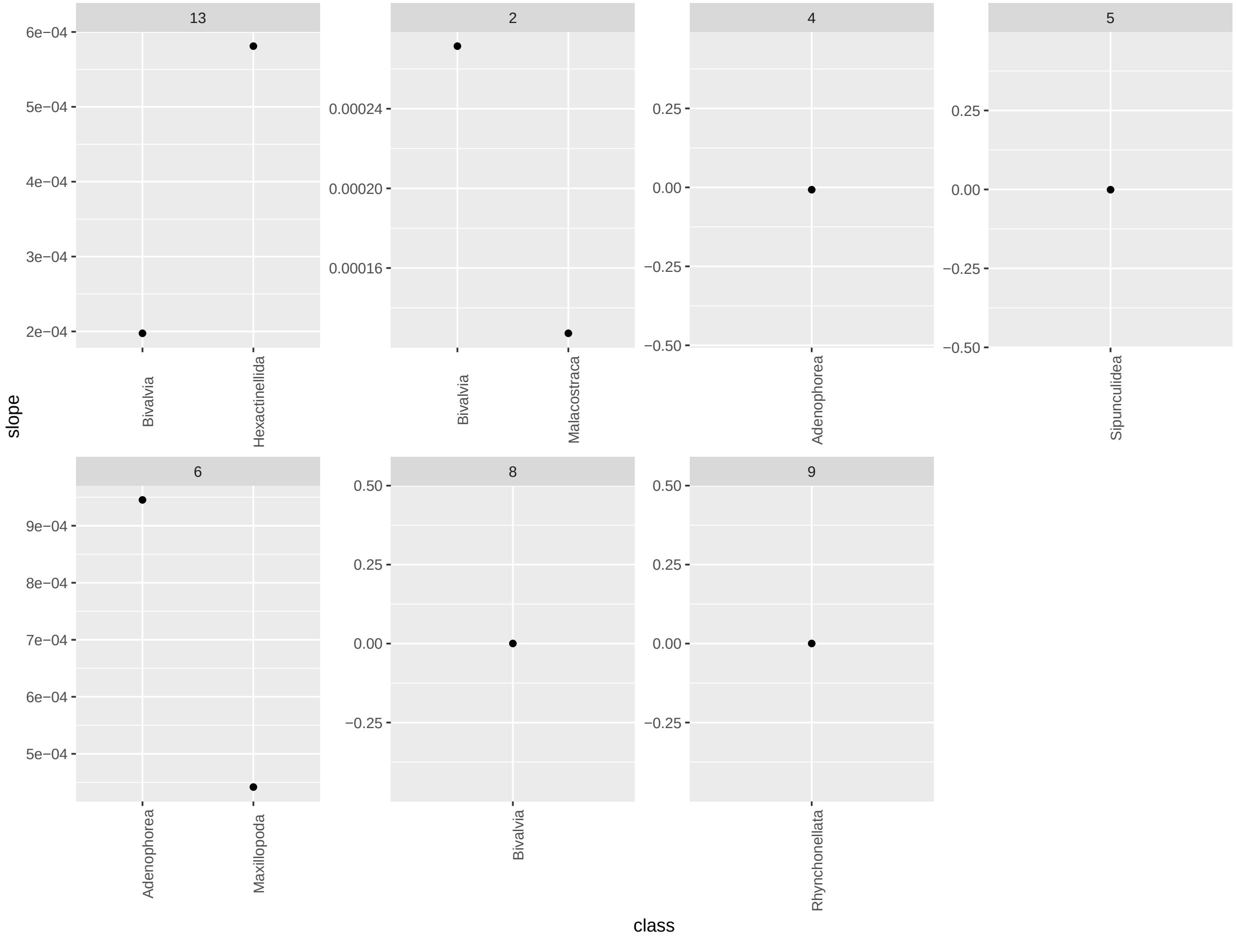


Figure 3.8: Class replicates genus slopes per province - GBIF
Subfigures are labeled by numerical province. Only significant regressions shown. Slopes is mean rarefied genera diversity as a function of increasing distance in kilometers from province centroid.

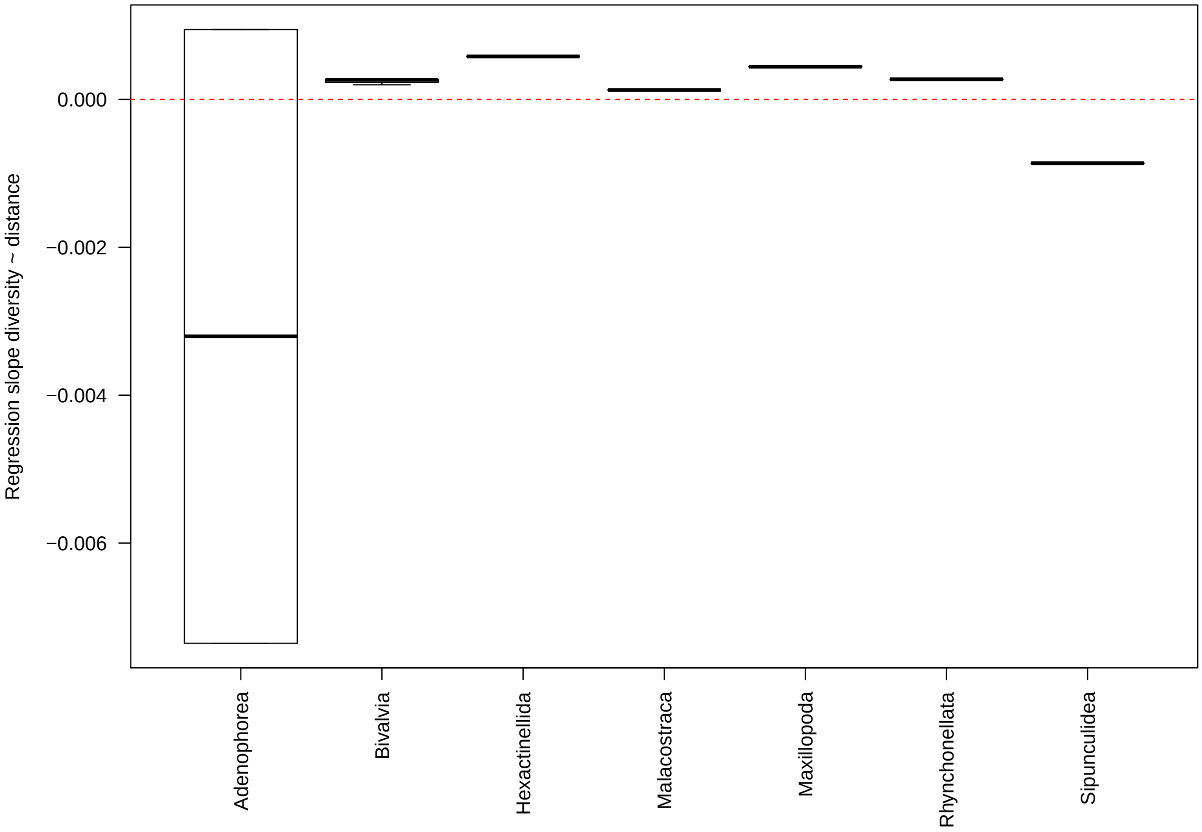


Figure 3.9: Box-plots per class replicates - GBIF

Box-plots for regression slopes per class, for class replicates per province with significant fit to regression. Dotted red line is zero slope. Only Bivalves and Adenophorea have more than one replicate. Slope is mean rarefied genera diversity as a function of increasing distance in kilometers from province centroid.

The four statistical measures of sampling effort per replicate (number of sites, site range, median distance between sites, and standard deviation of site distance) all showed weak positive correlations to regression slopes. Those values respectively were: 0.1933, 0.5128, 0.3525, and 0.4173. This is opposite, to the correlation patterns for CeDAMar. The most meaningful correlation was the scope of sampling (site range).

Figure 3.8 is box-plots that indicate the variability in slope values for those class replicates with significant regressions. Only two classes are represented by more than one replicate: Bivalves (3) and Adenoporha (2). Figure 3.9 is slopes per province, for significant classes only. Values of slope are low, regardless of sign. Comparison for same class between different provinces may be more relevant than comparing different classes.

3.7 Discussion

The total pattern in slope values for the class replicates' regression of diversity by distance to province centroids, was expected to confirm or reject a mid-domain effect. The results do neither satisfactorily, and strength of an opposite spatial diversity pattern, increasing diversity away from centroids, questions the validity of the assumptions inherent in an expected MDE. The assumption of provinces as centers of diversity may need to be differentiated by taxa, as for some deep-sea taxa evidence suggests high diversification on continental margins with radiation and subsequent extinction in the abyss, i.e., bivalves and gastropods (Rex et al. 2004). In the MDE analysis of Province Two for both GBIF and CeDAMar, bivalves showed a significant positive diversity slope, supporting this theory, yet data on gastropods was less clear or missing. This pattern was variable by class replicate and province. Class variability should be investigated further. Because of data limitations, comparisons to the relative fit between provinces was not performed. Some province delineations may be more real than others. As such, higher diversity observed on boundaries of provinces which abut continental margins requires vector analysis to province centroid, not a scalar analysis. Yet the majority of class replicates showed no significant spatial trend. The results of this analysis provide no indication for the observed lack of a spatial trend.

Differences in province patterns for class replicates' regressions could be due to complex biogeographical patterns or sampling bias, due to the classes selected after rejection for statistical reasons (Table 3.4 & 3.6), limited total spatial coverage (Figure 3.5), low total samples sites (Table 3.2), or diversity patterns, which are biased due to heavy sampling near continental margins (Figure 3.5). There are physiographic differences which could explain the difference in trends between provinces. For example, Province Two and Province Seven have very different edge characteristics in relation to adjacent ocean basins and provinces, the mid-ocean ridge system, and abutting continents. It seems likely that that differences in province delineations which are bounded by continents, versus those bounded by BEPs or mid-ocean ridges within basins, have different MDE results. However, comparing diversity regressions between provinces is difficult due differences in sampling effort, as statistics listed indicate the slopes are affected by scope of sampling. Spatial coverage was not well investigated beyond summary statistics, and this may impact the fit to MDE models.

The most tractable future analysis would be in the Atlantic basin, by either splitting or dividing provinces based on the mid-ocean ridge e.g., Province Two (Dr. Watling, pers. comm). The change in centroid locations could alter strength of various regressions. Future analysis could compare patterns between Provinces Four and Two, as sampling coverage is relatively high and they occur adjacent to each other, yet are delineated differently, primarily due to the mid-ocean ridge.

While MDE effects may be rejected here, this may not indicate that province schemes are nullified. In general the analysis of MDE was similar between GBIF and CeDAMar; however, they differed in spatial coverage, number of sites, and classes represented. Patterns were duplicated (had significant spatial relationships) in several classes in both investigations. The concept of provinces as units of speciation may be valid, but speciation may occur on boundaries not at the center of current provinces. The greater relative appearance of a MDE for species diversity over genera diversity indicates that inclusion of historical factors may be needed to explain current distributions of taxa in the Deep-Sea. Further analysis may provide evidence that provinces are useful spatial designations, but the assumption that these current provinces contain centers of diversity seems inappropriate. This would be a pattern in the ocean which dismisses the transitive application of biogeographic theory from the terrestrial realm to the ocean realm.

To objectives to test the congruence of province boundaries to biological data was completed, but the results are inconclusive. It is unclear form this particular analysis, if that is due to the theory driving the delineations, poorly defined provinces, the assumptions in the methods, or biological distributional factors unique to the abyss. Material presented in the following chapter may help explain these results.

4 SUBPROVINCE SCALE & GASTROPOD DIVERSITY CASE STUDY: NORTH ATLANTIC PROVINCE

The chapter investigates spatial patterns of biology at areal or distance scales below a province, or subprovince scales. Primarily through a case study in the North Atlantic province using gastropod species distribution information from the CeDAMar dataset. This is followed by a discussion on candidates for ecoregions in the abyss. Ecoregions are the next smallest hierarchal classification unit below provinces in a unified biogeographic scheme. The previous chapter investigated the provinces as discrete units and they were built based on factors that define edges. Biological provinces may be the emergent realization of sub-province factors, or provinces may be defined by BEPS within, not by those factors defining their boundaries. The case study on gastropods is an exploratory analysis that provides insight relevant to province boundaries, data used in the CeDAMar dataset, and general spatial structure of diversity at the ecological landscape scale.

4.1 Case Study: Gastrapods - Northwest Atlantic

This Case study provides an opportunity to investigate BEPs, and spatial patterns of biota within provinces. At subprovince or landscape spatial scales specific environmental effects (BEPs) might be stronger or easier to observe, via isolation or prevalence of one particular dominant factor. Specifically, the literature of the deep-sea is focused on patterns at scales from 10 meters to 100 kilometers. At sub-decameter distances distribution patterns are thought to be mostly a result of ecological factors and sediment characteristics. Bioturbation of sediments and burrows built by large animals are known to directly to affect distributions of smaller animals; non-equilibrium dynamics may dictate sediment community structure with the perturbation of sediment fostering diversity via niche creation through non-competitive and facilitative interactions.

At scales over 100 kilometers basin scale variation related to topography and oceanographic parameters are thought to explain large scale patterns, the basis of the proposed province scheme boundaries (ABS 3.0). The role of both ecological, and abiotic factors at the middle scales, is less known. To investigate this medium scale domain geostatistical methods were used, variograms and semivariograms. Since these methods may be more robust when sampling effort is completed in an appropriate fashion (gridded, with nodes of clustered sample sites Montero et al. 2015)), the CeDAMar database was searched for suitable regional locations which met those criteria.

A Keyhole Markup Language file of the CeDAMar dataset was created, and then inspected. This allowed for visual analysis of CeDAMar dataset, to select for sites that showed suitable layout for the desired criteria. Using this very basic exploratory method, a series of samples from the North Atlantic, Province Two, were selected for this case study (Table 4.1). The sites selected are

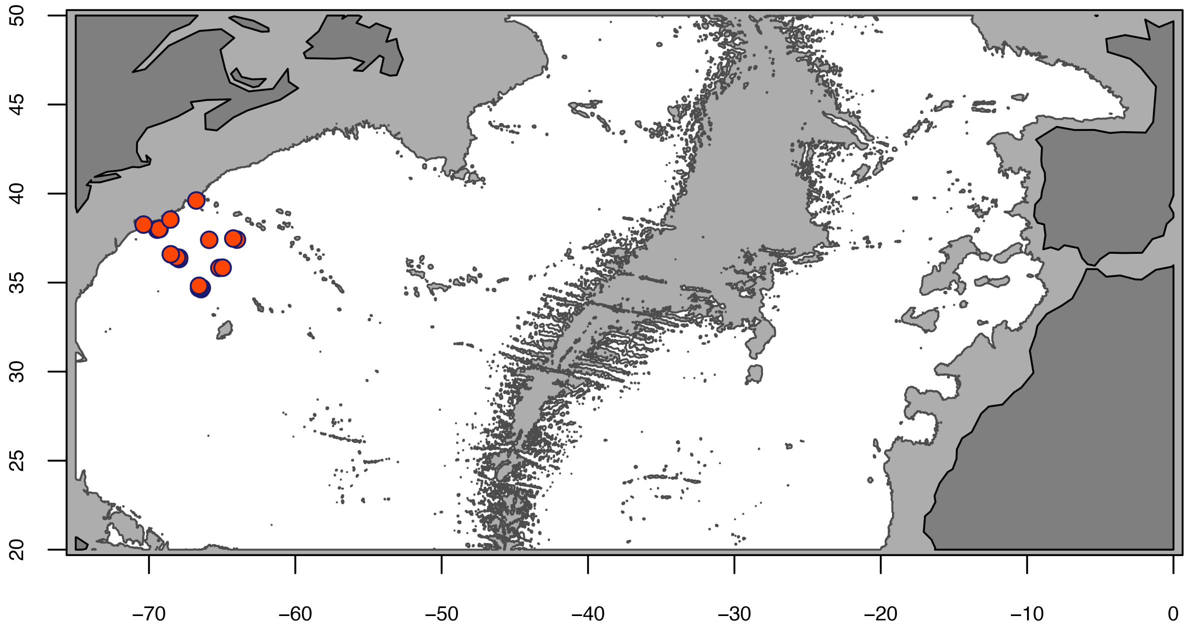


Figure 4.1: Case study sites and North Atlantic province
Case study sites in orange, Northern Atlantic. One site falls outside the boundaries (ABS 3.0) of the North Atlantic province (Province Two). Full province not shown. Province in white, land is dark Grey, all other ocean in lite Grey. Low resolution coastline data (1:110m). Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com.

in fact a well-studied sample area (Rex & Etter 2010; Sanders et al. 1965). It was reanalyzed in order to approach questions on spatial organization that are generally unknown. The case study area encompasses sites in the abyssal zone primarily, but on the continental margin and edge of a province boundary making it a useful location to look for boundary effects.

The transition down the continental slope to the deeper abyss, is the most drastic elevation change on Earth. A ribbon of undersea cliff walls, many of which are greater than 3.5 kilometers high, circle the continents of earth. The increase in depth in theses locations correlates to clines in BEPs, and therefore is a useful 1^{st} order proxy of underlying spatial patterns that may be caused by BEPs. (See subsection 1.5.3)

Objectives and initial hypothesis:

Question: Is there a spatial relationship in patterns of total diversity, or abundance at the species level, at the study site? The working hypothesis is that spatial relationships do exist and they will exhibit anisotropy most correlated to the change in depth across the sample sites. The depth and topography gradient is approximately in the Northwest to Southeast direction moving across the

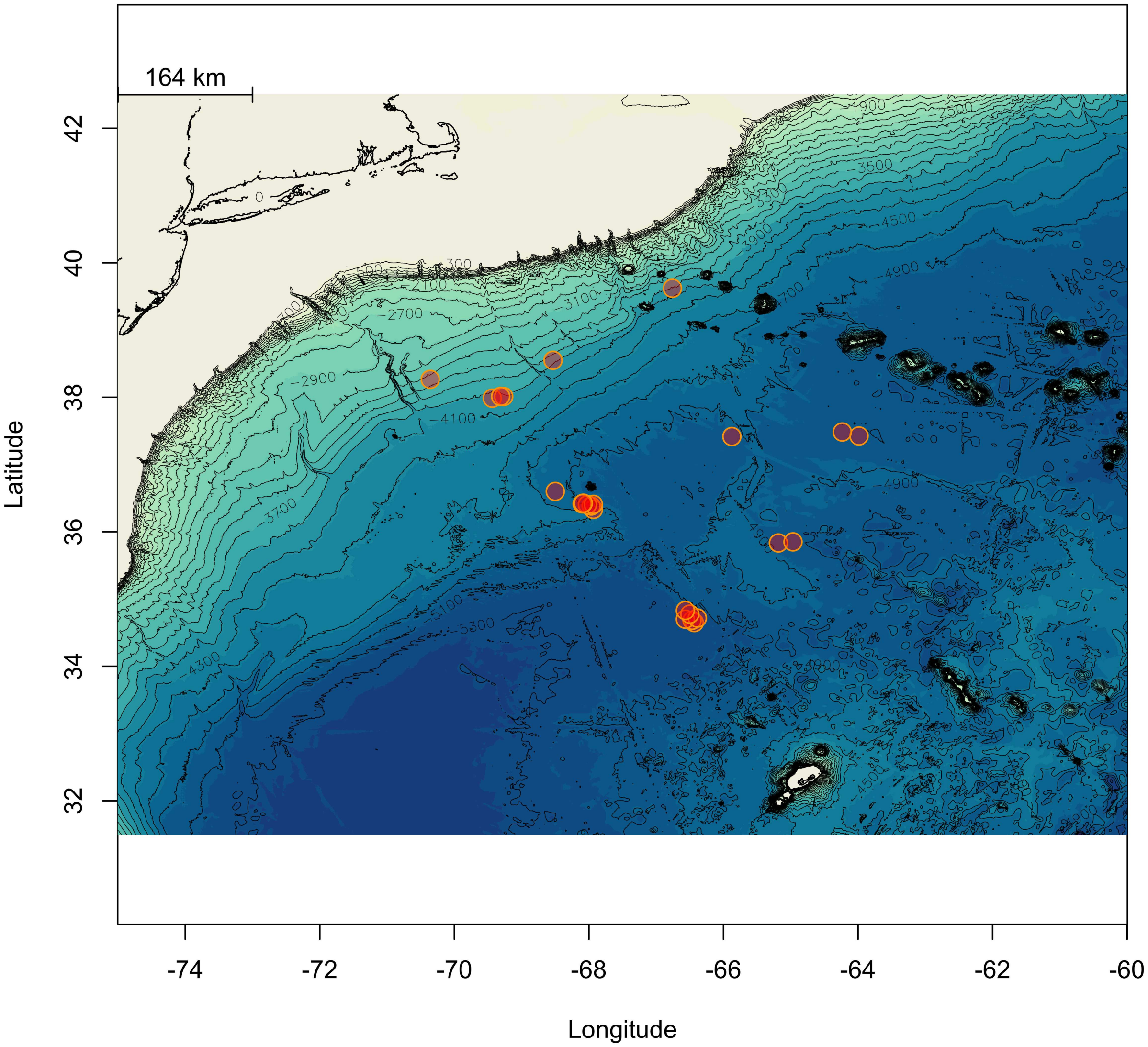


Figure 4.2: Study Site: NW Atlantic - 24 sites.
Map of sample sites, in abyssal zone, orange circles. Isobaths plotted every 200m from shelf break to 6500m. New England and Mid Atlantic coasts discernible. Notice clumping of transect sites.

continental margin and into the abyss. A second directional trend in line with North to South MOC flow is also expected.

Analysis

Semivariogram analysis of gastropods species diversity metrics was conducted for sites (Figure 4.2, Table 4.1) within the North Atlantic Province. (Figure 4.1) that exist near the province boundary, in order to determine spatial patterns that may be correlated to local environmental variables.

Table 4.1: Locations of sample sites

Location of sites used for case study. Species richness is number gastropod species. Depth values come from dataset. Negative values indicate West Longitude.

Site	Species Richness	Longitude	Latitude	Depth meters
1	4	-66.433	34.65	4967
2	4	-66.467	34.683	5042
3	3	-66.567	34.7	5021
4	3	-66.388	34.717	4977
5	4	-66.5	34.775	5000
6	9	-66.567	34.83	4970
7	10	-65.183	35.833	4800
8	6	-64.967	35.85	4833
9	9	-67.933	36.333	4694
10	9	-67.967	36.383	4680
11	5	-68.022	36.403	4700
12	14	-67.933	36.407	4749
13	8	-68.1	36.417	4750
14	6	-68.083	36.425	4740
15	12	-68.5	36.6	4680
16	14	-65.875	37.417	4825
17	8	-63.985	37.425	4862
18	11	-64.233	37.483	4853
19	32	-69.437	37.987	3834
20	15	-69.267	38.012	3806
21	11	-69.312	38.013	3828
22	44	-70.358	38.267	3310
23	6	-68.533	38.55	3753
24	23	-66.758	39.622	3806

Maximum distance between two sites was 568 km, minimum distance was 1.17 km. The sites were sampled utilizing one single gear type for collection of animals at all sites during the sampling period which occurred on 19 different dates from 1964 -1973 (first date: 1964-08-23, last date: 1973-11-24. mean: 1966-06-21, median:1966-05-03). The sampling gear was an epibenthic sled, a towed gear, providing semi-quantitative information on area sampled.

Gear type is semi-qualitative. Sampled area is the multiple of the standard width of the epibentic sled's opening, the average depth into surface sediment that the cutting edge penetrates, and length of a tow across the bottom. In reality however the sled may bounce across bottom due to factors such as, speed of tow, wire out, surface weather, and bottom topography that can cause sled to lift off the bottom, or cut too deeply into the sediment at different depths. The analysis proceeded under the assumption of quantitative sampling and this may negatively affect the interpret ability of results.

Data on tow length was not available. Based on common procedures, tow length can be assumed to be 1-10 kilometers per site. Analysis proceeded under the assumption a standard length was used across samples, due to the continuous role of the principal investigator (PI) involved and collaboration with workers who designed and perfected the WHOI epibenthic sled, (CeDAMar, includes a field of PI who was responsible for compiling data). Therefore count data was used as a surrogate for abundance assuming that bottom area sampled at each site was approximately equal for all sites.

Due to the nature of the data, and logistical realities of deep-sea sampling, spatial errors cannot be ignored. Possible errors in positional accuracy of tows and the associated ship are not addressed here. Geographic coordinates are reported for the start of tow field (all end of tow coordinate fields were blank), which for the sake of analysis is considered the central point of the site. Decimal degrees for sites was reported with precisions from one to five decimal digits, indicating spatial accuracy of 11km to approximately one meter. Decimal degrees values indicated that raw data had been in degree minutes seconds and converted. The majority of sample points had five decimal places reported (Table 4.1). If the assumption of 10 kilometer tows are assumed at a 10 kilometer spatial error, and the center of the tow is the best indicator for the center of the site, than sites correspond to circles of a 30 kilometer diameter of possibility. If no spatial error, and one kilometer tows, the circle of possible sampling site has a diameter of two kilometers. Even estimating tow direction is difficult as logistically towing up slope is likely, but weather and tides could alter this pattern, and as towing along loran lines for orientation (used prior to GPS) is common in offshore fishing practices. All simulations were run without correcting raw data, nor addressing propagations of errors. Because of the errors in determining site location, the over interpretation of nugget variance was avoided in the following geostatistical analysis.

Diversity is alpha (α) diversity, simply the number of species at each site. For diversity, directional and omnidirectional semivariograms were computed. Semivariance is spatial variance (Montero et al. 2015). Several empirical variograms were fitted. Key to the analysis was measuring anisotropy, or the vector component of scalar semivariance. Abundance values were calculated for three random species. Given there are a total of 81 species, three was chosen as more workable number. They were chosen at random in order to minimize bias. Bias could have resulted by picking species whose possible life history could be inferred, skewing results. Practical ranges were calculated to compare species in order to indicate variability between species and validate the methods used.

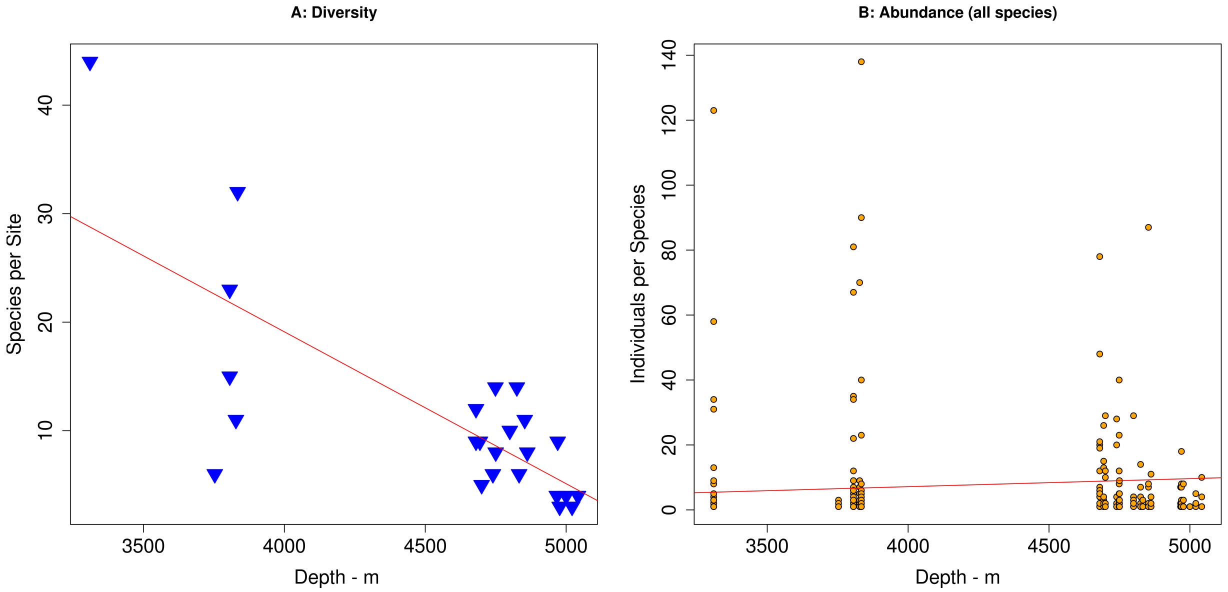


Figure 4.3: Diversity and abundance by depth
Diversity per site by depth (A). Individuals per species, per site by depth (B). In both plots red line is linear regression. Regression is significant for diversity and depth, but not for abundance and depth. With an adjusted R squared value for diversity and depth = 0.544.

Diversity was not standardized for abundance or sampling. Taxonomic diversity was limited by data available, which is the class Gastropoda. It is assumed all gastropods were identified regardless of order, family, or genius. Diversity showed a decrease with depth, with high spread at mid depths. Adjusted R-squared: 0.5437 for regression of diversity by depth, with a p value of 2.38e-05. There is a relationship with increasing depth and decreasing diversity (Figure 4.3-A). The shelf abyss transition shows the highest variability (continental rise), and where the linear relationship is less apparent. There are six sites along the rise, depth range of 524 meters, max depth = 3834, minimum depth = 3310, median depth = 3806, and the average = 3723. These summary statistics include the one site at bathyal depths. Figure 4.2 maps their position, minus the bathyal site.

For use in geoR (Ribeiro Jr. & Diggle 2015), Geographic coordinates were changed to UTM zone 19 north. Importantly the data fell within this zone, but because of the range between sites, at large distances there will be loss of true distances between pairs. No attempts were made to calculate along surface topography distances, distances are only in two dimensions. In exploratory graphs, the quartiles showed the greatest depth trend along the Gayhead to Bermuda transect with the two dimensional spatial pattern less simple (not presented here).

For the omnidirectional semivariograms the semivariance shows a general trend of being lower than the variance until the range reaches very high values, but a few outliers complicate this pattern

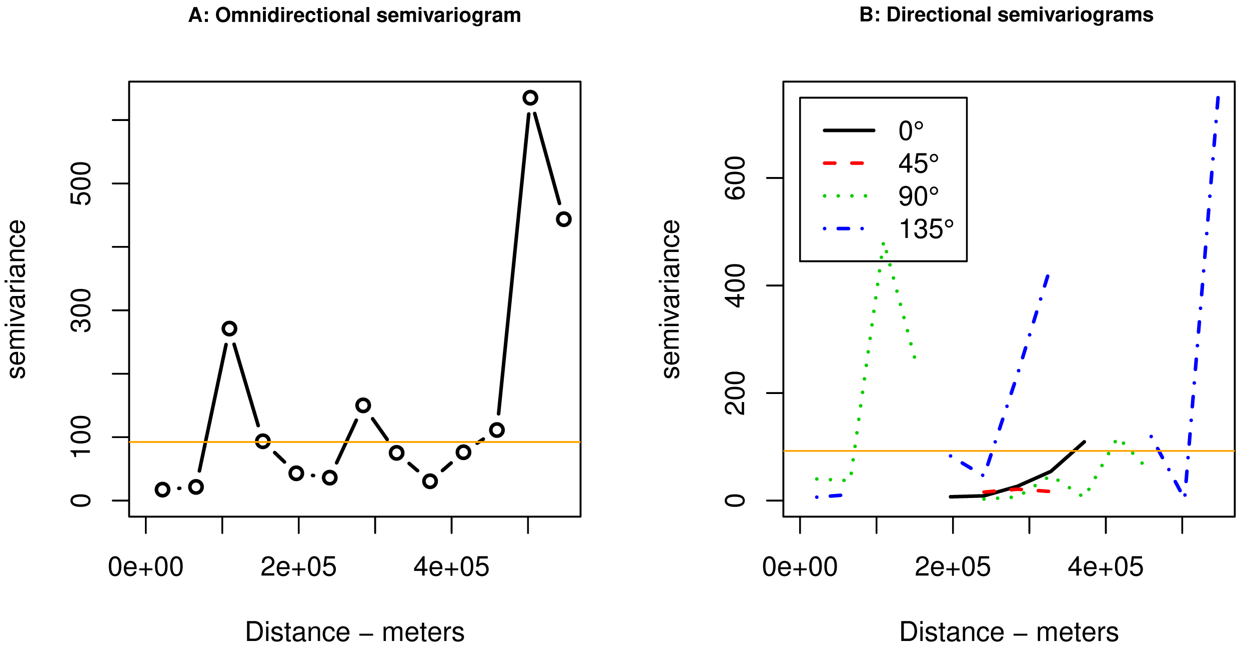


Figure 4.4: Diversity semivariograms
Omnidirectional semivariogram (A) and directional semivariograms (B) of species diversity of case study sites. Legend indicates cardinal direction in degrees. Semivariograms of diversity. Distance is in meters. Orange horizontal lines are non spatial variance per subfigure.

(Figure 4.4-A). The point at which the variograms intersect the variance indicates at what distance spatial or non spatial factors explain variance. The semivariance distance relationships below variance should not be considered significant. Semivariance generally increases with increasing distance between sites. For the directional variograms some directionality seems to exist, but not in a linear pattern (Figure 4.4-B). The directional components indicate the variability in the omnidirectional semivariogram. The 45 degree, North East - South West, semivariance corresponds to along isobaths, which show little change yet far below the non spatial variance. The 0 degree, North - South, semivariogram indicates a pattern which is most like an increase as a function of distance. The 90 degree, East-West, semivariogram has two significant independent inflection points where the semivariance function changes sign. Finally the 135 degree, North West - South East, semivariogram at largest distances explains the distance variability in the omnidirectional plot. This cardinal direction was expected to show the most pronounced anisotropy, in accordance with the working hypothesis, as it corresponds to the depth and bathymetric gradients. In plotting a Matern model visual estimation suggests nugget variance approaches the variance near zero distance, but for calculating semivariograms ranges it was a poor fit. While directional trends were expected to show some fit to the position of the continental margin, the observed pattern was too complex to infer simple spatial trends based on cardinal direction for other BEPs. Both directional and omnidirectional variograms intersect variance lines in a non linear fashion, making it difficult to separate variance by its spatial and non-spatial components. The noise in the results suggest that total variance between specific site pairs and corresponding samples explains much of the variance. It is only at the largest distances between sites that variance in diversity can be explained spatially.

Abundance The three Species chosen were, *Acteon melampoides*, *Benthonella tenella*, and *Theta lyronuclea*. In general all three species were rare (represented by few individuals), as were all species for all sites (data not shown). There was a high range of abundances per depth, (Figure 4.3-B) likely due to differences between species, with the highest variance at the junction of continental rise and the abyss, which was shown for diversity as well.

The matern models (Figure 4.5) may be useful for extrapolating possible nugget variances, importantly the semivariance axis vary by a factor of a thousand for the three species. This warrants more exploration. For the directional variograms anisotropy cannot determined. Like the diversity results, directional variograms show differences in anisotropy, but the noise is much higher. The noise prohibits making useful conclusions on directionality, but alternating patterns are apparent between the three species.

Table 4.2: Matern model parameters for three species

Values predicted by a matern model for each species. Range and practical range values are model predictions. Sum of squares shows model fit.

Species	Range km	Practical Range km	Variance	Sum of squares
Theta lyronuclea	369.36	1106.36	2.157609	121.22
Aceteon melampoides	16987.76	50890.79	43.12	479773.3
Benthonella tenella	99.99	1198.29	1669.362	199031645

The most significant result of the three species analysis (Table 4.2), is the difference between species' ranges and practical ranges, model fit, and variance. The range value being the maximum distance at which semivariance can be explained by distance between sites. The practical range indicates the extrapolated range within a $+-5\%$ confidence of the sill (location on the curve where model becomes asymptotic, used for determining the range). The poor fit of models and associated error, in conjunction with the model predicting ranges being much larger than actual observed distances is responsible for these values being larger than the range values. Only *Theta lyronuclea* comes close to fitting its model (low sum of squares values). This indicates the two other species modeled values should be used with caution. The order of magnitude differences between the three species ranges and practical ranges indicate that despite poor model fit, there is at least a qualitative difference in spatial patterns.

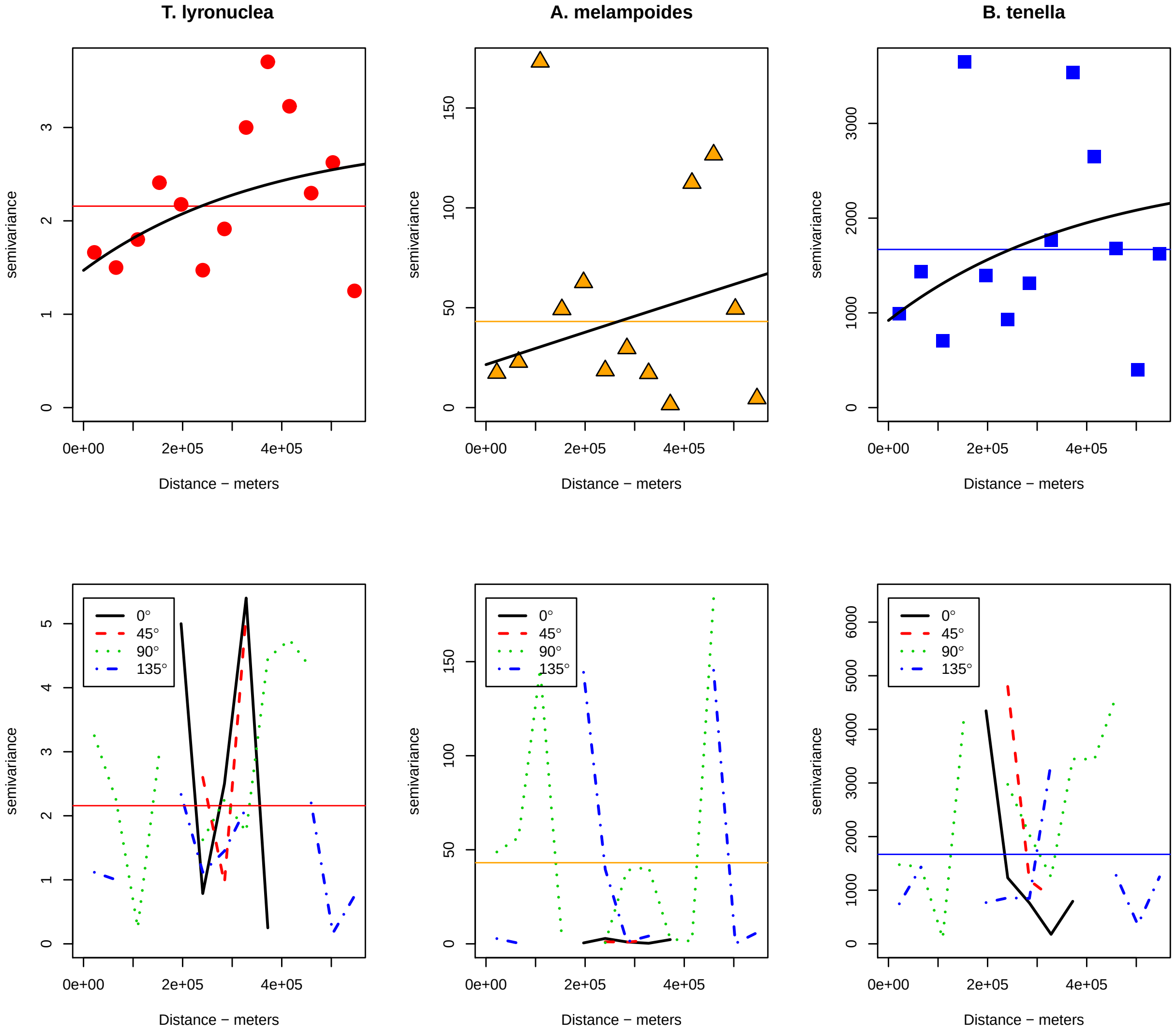


Figure 4.5: Three species semivariograms
Columns correspond to each species. Omnidirectional row one, directional row two. Distance is meters. The semivariograms axis for the three species differ by three orders of magnitude. Legend indicates cardinal direction in degrees. Horizontal lines are non spatial variance per subfigure.

The sites variability in diversity and abundance, suggests that an important boundary exists in at depths between 3500 and 4000 meters, with the mean depth of ~ 3800 meters. Inspection of that map indicates that these sites are located at the boundary, 3800m isobath, of the continental rise and the continental slope, which can be identified by isobaths (Figure 4.6). The diversity directional semivariance at the distances between the sites along the 3800 isobath corresponds to the diversity differences at those sites (Figure 4.4-B ; 45 degree semivariogram). The depth data used to create the isobath maps included localized ship measurements, to constrain satellite derived data (Becker

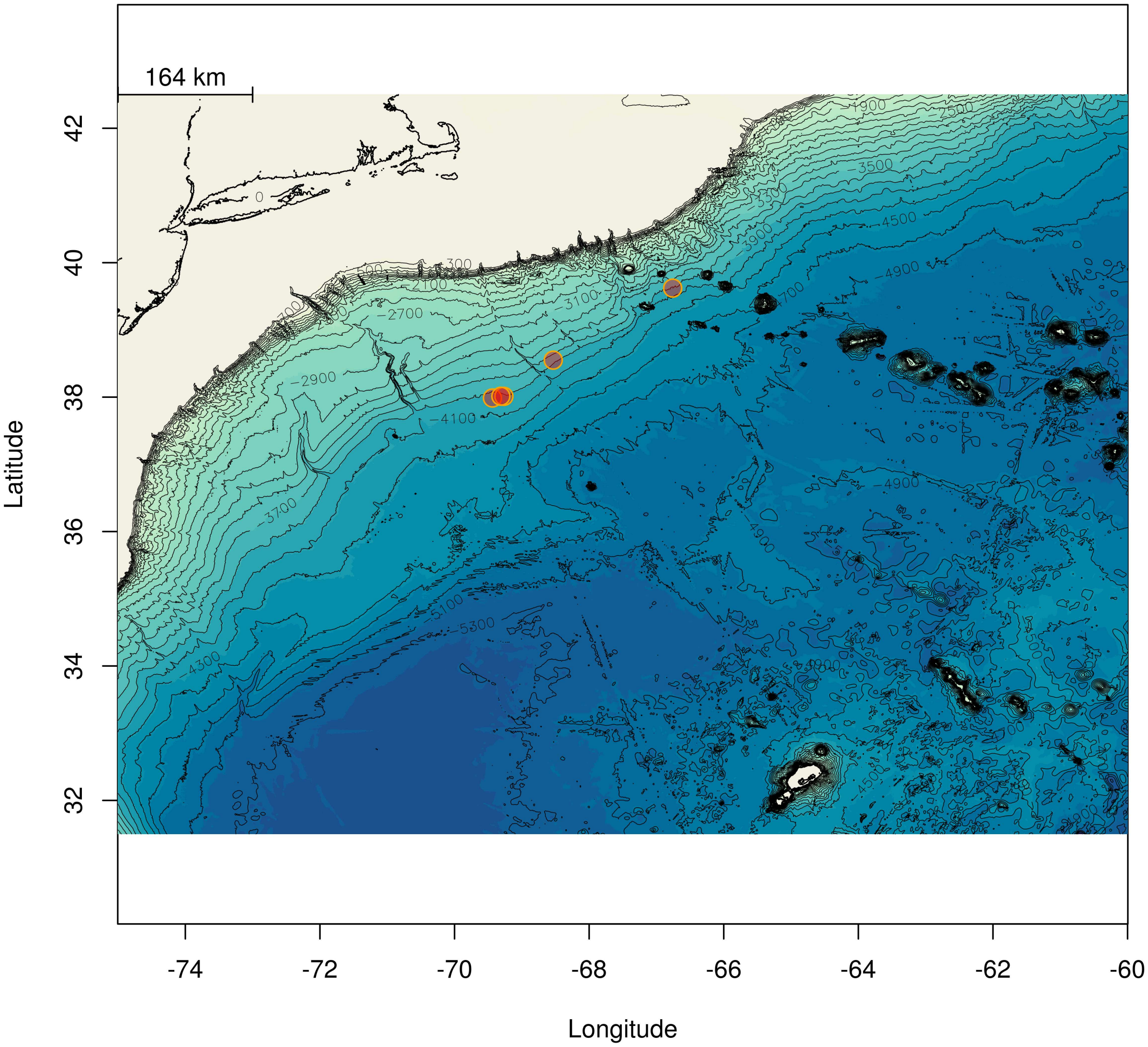


Figure 4.6: Continental rise sites
Case study sites with high richness and abundance variability. Notice locations in terms of isobath rate of change. Isobaths plotted every 200m from shelf break to 6500m.

et al. 2009), and the congruence of sample sites with the 3800m isobath is collaborated by the actual depth values in the biological dataset (Table 4.1).

4.1.1 Discussion

This case study supports what is known on the patterns of biology in the deep-sea in regards to depth diversity gradients. The strongest directional signal was the diversity semivariogram

(135 degree) across the depth change of the continental margin into the abyss. The 45 degree directionality was limited in significance but did show no change along isobaths, supporting the relationship of changing depth and diversity (Rex & Etter 2010). While anisotropy was present, it was not as apparent as expected and could not easily be compared to expected BEPs. The omnidirectional variogram for diversity indicates high dispersal of abyssal species in the abyss, as variance only becomes impacted at the largest distances between sample sites, in line with the current consensus.

The use of the the epibenthic sled along the Bermuda to Gay head transect (this general series of sites and the cluster of sites along the depth gradient) caused a paradigm shift in deep-sea biology, when it was shown through rarefaction methods that the deep sea may be as diverse as tropical shallow environments, when area is considered. The misconception of low diversity has been shown to be due in part to inadequate sampling (Mcclain & Schlacher 2015; R. Hessler & L. Sanders 1967; Sanders et al. 1965). However the diverse taxa that have been documented at this site were not present in the CeDAMar dataset. The CeDAMar dataset contained samples on gastropods only. This illustrates a general issue with the completeness of the dataset, as it is surprising that such a well studied location was lacking in species records. The goal of multiple taxon analysis was unable to be pursued here, but the accuracy of taxonomic description within this clade was assumed to be high. Therefore individual gastropods were likely consistently identified to species, across sites and time.

The order of magnitude differences in the results of species ranges may explain why patterns are hard to discern. The variability between the three species can be assumed to be related to differences in the scale of the spatial structure related to the biology and ecology of the individual species listed. Alternatively, the semiquantitative nature of sampling is responsible for the observed noise.

Further analysis into differences between species is warranted due to the variability between the range values found for abundance distance relationships. Previous work by Rex & Etter (1990) on *Benthonella tenella* suggests this species' distribution patterns may be due to planktonic larva dispersal potential, and the authors found limited population differentiation of phenotypic characteristics, of this species, in the abyss despite being widely distributed. Other pertinent life history traits of this species include, depositional feeding, continuous reproduction, and variable recruitment (Rex & Etter 2010). The traits of this species corresponds to the semivariance distance relationship results in this analysis. A literature search found no pertinent records on relevant life history characteristics for *Acteon melampoides*, but some information could possibly be gleaned from descriptions of congeners (e.g, Marcus 1974). *Theta lyronuclea* belongs to a widely distributed predatory family of deep-sea gastropods that specializes on polychaetes. A study including this species and other members of its family, suggests that increasing oxygen and depth correlates to increased shell size (McClain & Rex 2001). Body size trends could impact abundance values via biological mechanisms e.g., reproduction rates and recruitment, or through higher catch rates in sampling. The differences and observed patterns for the three species, in their distance abundance analysis may be due to any number of the life history strategies known for each species.

The life history information of these three species is not at odds with the geospatial results. However, spatial errors must be accounted for. Tows could have been unequal in sampling effort, and are generally considered qualitative methods, which would skew abundance values. This would explain noise in anisotropy. This noise indicates variance between sample sites is high, this could be due to sampling, or environmental variables at each site. The three species results are less accurate quantitatively within species, but the differences between each may be qualitatively real.

Directionality in semivariograms of diversity and abundance in line with directional water masses did not appear. However if the location of the sites was associated with the boundary of water masses, which are the most variable in terms of mean Eulerian flow, the apparent randomness in anisotropy in models could be related to complexity of currents. Comparing these results between two opposing displacement models, diffusive dispersal and the affect of episodic eddy formation, would be a way to explore that concept that is not reliant on increased biological sampling. Other ocean current models beside mean MOC flow could also be of use.

For this study site and the analysis above, more work should be directed at exploring empirical variograms (e.g., the standard model), No analysis was done looking at the nugget variance, but the geopositional accuracy of the data at the smaller scale was more questionable than at larger scales (eg., mixed precision in the geographic coordinates of sample sites). Further geostatistical analysis is needed, for example higher level taxa groupings, or Bayesian methods. Regression kriging using depth as an explanatory variable could be attempted with occurrence and diversity data. To explore the role of the MOC, a surface of potential density could be created which indicates the net movement of bottom water masses which may impact dispersal of animal larva and propagates, a candidate for regression kriging. To apply kriging software beyond the scale of a single UTM require three dimensional kriging, but that step would require accounting for error in bathymetric data. By investigating this location, the issues of the CeDAMar dataset as well as variability in dispersal potential is apparent. The work here sheds some light on boundary issues in provinces, which is discussed further in the Discussion and Conclusion Chapter. Spatial variability between 10 and 1000 meters is not explained by the results of this analysis, which is still not well understood in the deep-sea.

4.2 Ecoregions

Below province, ecoregions are the next nested hierarchical spatial division. Ecoregions are suggested as a useful biogeographical unit for both national and international conversation efforts

(Giakoumi et al. 2013). Ecoregion designations have been made in terrestrial and shallow marine biogeographies. Ecoregions are synonymous with ecological landscapes. Landscape scale geographic study in ecology is primarily interested in matrices of patches (Krzanowski & Raper 2001). Spalding et al. (2007)defines marine ecoregions as:

> "Areas of relatively homogeneous species composition, clearly distinct from adjacent systems. The species composition is likely to be determined by the predominance of a small number of ecosystems and/or a distinct suite of oceanographic or topographic features. The dominant biogeographic forcing agents defining the ecoregions vary from location to location but may include isolation, upwelling, nutrient inputs, freshwater influx, temperature regimes, ice regimes, exposure, sediments, currents, and bathymetric or coastal complexity."

Are Ecoregions applicable in the deep-sea? They are the logical extension in a hierarchal nested province scheme, yet are not present in the proposed deep-sea biogeography. Following the criteria of Spalding et al. (2007), it may be possible to develop candidate factors for ecoregions in the abyss. There is sufficient evidence to describe, unique and discrete ecosystem types (Ramirez-Llodra et al. 2010), and environmental features (Harris et al. 2014), which indicates that abyssal provinces can be divided into ecoregions. One method of moving towards integrating the frameworks of Watling et al. (2013) and Spalding et al. (2007)Spalding et al. 2007 is to use benthic parameters within the abyssal zones, namely major topographic or benthic features, and sediments characteristics. These could be tested using large biological databases, and the ecosystem types of Ramirez-Llodra et al. (2010).

4.2.1 Abyssal hills

The vast abyssal hills of the deep ocean may be important biogeographical factors. Abyssal hills are estimated to occur over ~ 60% of the global seafloor (Turnewitsch et al. 2015), and are primarily located in the abyssal depth zone. Dividing a province by subunits of abyssal hill rugosity may provide a simple ecoregion designation. According to Goff et al. (2004), "Geological information is contained in the small-scale fabric of altimetric gravity data. This fabric, which has the appearance of the skin of an orange peel, or the surface of a football, exists everywhere in the altimetry data." Predictions on abyssal hills zones and structural characteristics are distributed differently between, and within, provinces (Goff 2010; Figure 13). (See Ramirez-Llodra et al. 2010; Fig 1, for a relevant three dimensional presentation of bathymetry of the North Atlantic.)

Abyssal hills are known to vary from adjacent abyssal plains by altering sediment characteristics and water flow. Sediment characteristics and flow regimes do impact the distribution, and ecosystem dynamics, of abyssal metazoans. Abyssal hills have been found to have significant differences in type and amount of organic content, as well as grain size, of their sediments in relation to surrounding plains (Turnewitsch et al. 2015). These types of sediment characteristics are known to be important to deep sedimentary ecosystems (Etter & Grassle 1992; Watling 1991).

Work on the biological patterns in abyssal hills areas is limited, yet revealing. Durden et al. (2015) looked at these landscapes and found significant diversity and biomass differences of megafauna between abyssal hills and plains. Correlations to sediment structure explained the patterns (Durden et al. 2015). The majority of the hills at the site are 300m tall with one taller hill at 1000m. The authors state that their results indicate "abyssal hills may increase beta and gamma-diversity in abyss". They did not find differences in phytodetritus cover between hills and plains at their study site, but indicate this may be due to the limited temporal scope of sampling (Durden et al. 2015).

Abyssal hills may impact distribution patterns of POC via impingement of benthic currents and flows. Phytodetritus and POC, can be redistributed via resuspension and benthic currents (Lampitt 1985). If the benthic boundary layer and dominate currents are impacted significantly by hills then they may increase heterogeneity of available carbon input independent from surface processes. Medium scale topographic features (~2000 meters) near the mid-ocean ridge, have been found to alter tidal flows and surrounding hydrodynamic regimes in a localized manner (Dale & Inall 2015). When taken in total the small scale features of the ocean bottom account for a loss in tidal energy that has been missing from the global geophysical budget (Dale & Inall 2015), indicating the small abyssal features fundamentally impact the main flow of the MOC. Analysis of critical seafloor slope suggests abyssal hills flanking mid-ocean ridges account for much of the deep ocean mixing, and hence a majority of the deep water flow regime (Becker & Sandwell 2008). Any hydrological process which controls distribution of benthic carbon could also impact dispersal of biological propagules.

Abyssal hills could explain 1 - 10 kilometer scale geographic patterns of biota in the abyss, by creating habitat heterogeneity. They are known to exhibit fractal behavior at scales smaller than 2 to 10 km (Goff 2010). Hills are extremely prevalent in number and global coverage. They are consent in existence through geological time, yet change in type as they move from their sites of creation near mid-ocean ridges towards continental margins. They are shaped by tectonic and geomorphological processes in their formation and location. Sediment cover characteristics are mostly independent of tectonic processes, being caused by biological and oceanographic processes controlling export flux above, and major tidal and MOC flows along the benthos. Sediment cover and structure being independent of hill formation, allows for a high diversity of abyssal hill types, which increase habitat heterogeneity in the abyss.

4.2.2 Seamounts and Islands

Island and seamounts have similar physical properties as abyssal hills, including high global coverage, and can be theorized to impact species diversity patterns via the same mechanisms. They differ primarily in regards to their connection to surface waters, and a dominance of hard substrate. Seamounts may have the same effects as abyssal hills, but their large individual sizes increase theses effects. Groupings of seamounts or islands may divide, or be ecoregions.

The exact unique biological nature of seamounts is disputed, with theories on, endemism, biomass, and diversity in general lacking sufficient evidence for specific claims given the geographic variability of features (McClain 2007). Despite lacking a unified theoretical framework for these biological habitats they are considered ecologically and biological significant (Clark et al. 2014). In regards to impacting abyssal ecoregions, they may provide a source of evolutionary input as they are ecological distinct communities with increased biomass (Hardy et al. 2015; Rex et al. 2004).

Islands cause increased productivity in surrounding surface waters. This is due to the island mass effect; localized increases in phytoplankton biomass near island and atolls , caused by a suite biogeophysical factors (Andrade et al. 2014; Doty & Oguri 1956; Gove et al. 2015). This localized productivity impacts the benthic areas near these features. The occurrence of increased organic delivery to the benthos via export flux associated with the increased surface production caused by the mass island is documented (Pollard et al. 2007). If the mass island effect is responsible for productivity “oases” (Gove et al. 2013) in otherwise oligotrophic areas, export flux is documented, and the tight coupling of benthopelagic coupling of surface production is known for global abyssal sites (Smith Jr et al. 2009), islands may have a meaningful influence on abyssal biogeography due to increased areas of local organic carbon compound availability. This may be of import in the Pacific ocean, which contains groupings of island chains in regional oligotrophic surface waters.

4.2.3 Substrate

Deep benthic areas may be divided into hard or soft sediment substrate types, which may impact ecoregion scale patterns of life. Sediment types are known to be important to the abyssal faunal (Etter & Grassle 1992; Watling 1991), and transitions in sediment type have been previously suggested as zonal delineations (e.g., Menzies et al. 1973). Given the variable input of sediment can either be classified either by planktonic sedimentation or terrigenous inputs, these two types may be worth exploring as major soft sedimentary differences for ecoregions (Thistle 2003). Clay types should be considered as one possibility (Menzies et al. 1973).

Many hard substrate types in the abyss are associated with 1^{st} or 2^{nd} order topographic features e.g., seamounts. Hard substrate regions in the abyssal plain regions, devoid of major topographic features, should be considered as regions unto themselves. Abyssal plains regions scoured by the Antarctic Circumpolar Current, and lacking in sediment cover, in the Southern Ocean may be at the scale of ecoregions (Kennish 2000). Manganese nodule fields (hard substrate on top of soft sediments) in the Pacific have been shown to influence the community composition, distribution, and density of metazoans (Amon et al. 2016). Nodule fields are also known to exist in other ocean basins (McKelvey et al. 1983), making them applicable in multiple provinces.

4.2.4 Discussion

Distinct suites of oceanographic or topographic features exist in the abyssal zone which may be likely candidates for ecoregions. The examples given were restricted to major topographic features and sediment cover, as these stationary variable are more easily mapped in the deep-sea than other more transitory oceanographic features. Evidence exists that links these topographic features to BEPs from the proposed province scheme (Watling et al. 2013). Inclusion of ecoregions to the province scheme could strengthen it, and may be important for conservation efforts. However, data availability in some variables, such as sediment cover, may be a limiting factor in the near-term.

5 DISCUSSION AND CONCLUSION

5.1 Disscussion

This study provided an initial analyses on fundamental questions about spatial distribution of the majority of metazoans in the deep-sea. This is this first large scale biogeographic analysis of metazoan records in the abyss that was constructed around reproducibility and access to data used. This should encourage further study. The main MDE results did not strongly support or reject the ABS 3.0 boundaries nor provide a definitive answer on the theoretical basis province schemes, but instead in the context of the supplementary analysis and material presented within should be reviewed to stimulate further thinking on fundamental questions evolutionary/distribution porcessesses in the abyss. Refinement and development of the MDE analysis begun here could in the future better provide more conclusive answers to questions of congruences of biological occurrence data to province delineations. The findings should help in the construction of updates biogeographical classifications and units in the deep-sea.

The MDE results may be due to methodological or theoretical factors. Those factors include the location of specific boundaries, the methods used, general assumptions of mid domain effects, and the importance of individual BEPs used to delineate boundaries. However, historical and evolutionary factors may also be important in shaping current species distributions, and diversity patterns. The theoretical framework used to create boundaries may need to be amended to account for the unique role of ecoregions and diversity distribution processes in the deep-sea.

5.1.1 Biological congruence to provinces

The core goal when testing congruence of boundaries with the biological datasets used was to use all metazoan information available. This was done to test the general fit rather than any one taxon's patterns. When summing patterns for total taxa spatial distributions no single trend is apparent, but trends are well documented for specific taxa, and were echoed in diversity distance slope results for known taxa (e.g., polychaetes, and bivalves) an appearance of Simpson's paradox. It may be that information on specific taxa distribution patterns is lost by trying to create a scheme which generalizes for a majority of species. Future analysis could focus on taxa endemic only to the abyssal zone. In this work, class replicates for taxa were chosen to address spatial coverage issues. Class replicates may not be meaningful for specific classes, or in general.

Spatial coverages was not equal between or within provinces, making meaningful comparisons between provinces difficult. The majority of available biological occurrence data collected over much of the abyssal zone may be insufficient to test all the province boundaries. Lack of biological data was the rationale for creation of the proposed province scheme, indicated by the authors of the province scheme (Watling et al. 2013). Higher relative spatial coverage of biological sampling in the North Atlantic however could be used to test future versions of updated province boundaries in that basin.

The low diversity distance slope values for MDE analysis, was supported by the geospatial results in the case study on gastropods. Geostatistical results did not provide a conclusive answer to questions on specific BEPs for the case study analysis. They do however represent an interesting method to apply in a subsequent study. The semivariance and spatial variability between just three species suggests how little is known about dispersal and species ranges in the abyss. General theories on connectivity and dispersal could be investigated by completing a computational intensive kriging map for all species in the datasets, with sufficient data. As of now connectivity theories abound, yet a general trend has not been agreed upon. A kriging analysis would also indicate whether species ranges are patchy or continuous. The assumption inherent in the MDE tests undertaken is that species have continuous ranges within a domain (section 3.4).

5.1.2 Depth and province boundaries

There also may be confounding factors in species horizontal ranges and depth zonation. Vinogradova (1997) suggests greater horizontal range with increasing depth range, and it is plausible that species at the abyssal-bathyal interface have greater depth ranges, than truly abyssal species, and so transitively greater horizontal ranges. This would complicate mid-domain effects within ocean basins.

The import of depth is undeniable in relation to patterns of biology in the deep-sea, and as such it should play an fundamental role in defining biogeographical units. However, most authors agree that a single depth value for zonation lacks meaning due to biotic variability at regional and local scales. Even if there were a single depth value for a boundary, the error in placing the 3500 meter isobath accurately over much of the under-measured seafloor is indeed large. As is shown in Chapter Two (subsection 2.1.3). The inaccuracy of bathymetric data validates focusing on province delineations generally, as opposed to focusing of specific boundaries.

While not an extensive test of the boundaries the case study in the NW Atlantic illuminates an important concept, that the location not of depth but of change in the derivative of depth is indeed a real location of biotic variability. The junction of the continental rise and slope may be more important than an exact depth. A more meaningful boundary could be created for abyssal zones abutting bathyal zones. This could be achieved by taking a topographic inflection point, approximated by higher level derivatives of a function depth by orthogonal horizontal distance to the coast/shelf. This would be calculated within some agreed upon range (2500-4000 meters). Additionally, this approach would be less prone to satellite altimetry errors. These new boundaries could be tested for by measuring species turnover in available biological data, following Menzies et al. (1973).

5.1.3 Efficacy of spatail analysis

Increased geostatistical and computational methods could be used to further test and determine province boundaries. Truly vectorized spatial scale analysis of species patterns could illuminate uncertainties in the MDE analysis, and help solidify appropriate boundaries. An iterative Monte Carlo algorithm method could be used to find province domains which show the strongest MDE to all taxa. The domains from this analysis could be used to tests correlations between individual BEPS. If these results proved inconclusive, it would be likely the assumptions of finding discrete spatial domains would need to be investigated.

The BEPs that define the proposed province scheme's boundaries have all been documented as important factors in biological patterns of deep-sea. As such they cannot be rejected here. Yet province delineations were not supported by MDE analysis. Either lack of any trend or a slope in the opposite direction was found.

The scalar method used may inadvertently find no spatial pattern when in fact a single vectorized trend is present in a province. A hypothetical replicate could have an increase in diversity by distance only in a East to West direction across the full domain of a province, but as a function of distance to a centroid the diversity slopes would cancel (Traveling East to the centroid would be a positive slope, traveling West to the centroid would be a negative slope). Factors within a domain may disrupt species continuous ranges, also producing no significant spatial trend.

5.1.4 Evolutionary Porcesses

Mid-domain effects may not be a useful null model in the abyss. If real MDE should likely be less evident (flatter curves) for genera than species, which was observed in this analysis. The suggestion that the abyss is an evolutionary sink, while bathyal areas are thought of as evolutionary sources (Rex et al. 2004), would explain the diversity trends which were opposite (positive) to an expected MDE. This concept is taxon variable, with certain megafauna exhibiting possible radiations in the abyss. Modeling analysis suggests a key components of this theory, limited organic delivery and net food deficiencies, can be accounted for by seasonal pulses and temporal variability of POC flux in the abyss (Hardy et al. 2015).

The source-sink hypothesis may explain some of the trends found, but not the general lack of spatial trends for most taxa. The major topographic feature of the continental margin does impact geographic patterns. However, study of a similar major topographic feature, the mid-ocean ridge, is lacking. The bathyal zones of mid-ocean ridges share a similar heterogeneity of substrate, and environmental variability to those same depth zones on continental slopes. It is possible they impact the abyss in similar ways. Mid-ocean ridge hydrothermal sites are known to be areas of high productivity, and some authors provide evidence to support the theory that these sites are possible locations for the origin of life (Martin et al. 2008). Mid-ocean ridges play some role in speciation and extinction in the deep-sea. Increased diversity near the junction of mid-ocean ridges and the abyss, would be in lines with observed positive trends in the MDE analysis. These 1^{st} order features may impact MDE analysis, in some cases masking real trends if provinces are improperly delineated.

5.1.5 Subprovince scale

Internal masking of MDE within provinces would be caused by any factor that influences biological distribution patterns. Those factors could be ecological (recruitment and settlement), or diversity process (variable speciation/extinction rates). Ecoregions within provinces could be areas where specific local factors alter ecological or diversity processes.

The review in section 4.2 suggests that ecoregions may indeed exist in the deep-sea. The evidence for including abyssal hills as ecoregions is convincing. Their role in impacting distributions of species is documented. When taken in the context of, mid-ocean ridges, and continental margins they provide smaller scale habit heterogeneity spanning across much of the seafloor. Abyssal hills could be replicate cauldrons of speciation, which bridge the gap between the high environmental variability of the 1^{st} order topographic features that delineate and divide ocean basins. This would be in line with the concept of patch dynamics, temporally out of phase, fostering high diversity in the deep-sea (Smith 1994).

Perhaps connectivity, scale, and the unique evolutionary trends in the deep-sea make provinces ephemeral, with the spatial hierarchal system consisting of basin, subbasin and ecoregions. By standardizing, via stratification of replicates by ecoregions, future biogeographical testing of the province scheme may show a greater fit than was found here and within. It also may be that ecoregions are not viable concepts in the deep-sea, due to issues of connectivity and larva dispersal, or evolutionary source sink issues. However, at the landscape scale unique habitats do exist. Designation of unique ecoregions does not explicitly require clear resolution on the validity of provinces, as they can be tested for independently. Yet, the acceptance or rejection of one or the other spatial unit does have strong implications for the existence of the other.

5.1.6 Alternative biogeographical approaches

This work was a first attempt at an ecological biogeography of the abyss, but was incomplete as it made no effort to address ecological interactions and subsequently their role in shaping community structure. For example presence and abundance of one species may have causal relationship with another through trophic or direct interactions. Data resolution over the time scale of sampling per site is not sufficient to adequately address regimes shifts at the ecological level, over time, which could skew sampling between sites (Smith Jr et al. 2009).

This work was not explicitly a historical biogeography. Taxon approaches and specific taxon biogeographies take into account historical factors, for example phylogeny, and distributions in current and fossil space. A dedicated historical/evolutionary analysis was not in the scope of this study, as neither phylogenetic analysis, nor accurate geological time scale methods were employed. Historical biogeographic factors may explain current species occurrences that cannot be explained by ecological factors. The GBIF rarefied genera analysis was included due to the greater spatial coverage of GBIF however, it does account for a great time period of diversification as genera diversification is more derived than species. Menzies et al. (1973) also utilized genera as a means for investigating historical trends, yet Vinogradova (1997) suggest genera may not be useful. Fundamental to the concept of a provinces is that biota within share a similar evolutionary history. In order to investigate that property paleontological methods must be employed. For example tracking province centroids using paleo-coordinates and relevant fossilized fauna using the expected MDE method of this study. This will be difficult due to problems of adequate representation of the small soft-bodied marine fauna in the fossil record (Sperling 2013). However, that issue could be addressed by using pale-coordinates and higher taxonomic levels from the current biological databases.

5.2 Conclusion

The legitimacy of the province scheme, via testing of province delineations, was not supported by this work. However, it is not possible to reject the theoretical basis of the province scheme by the means presented here. The MDE was not observed for species diversity, and was rejected for genera diversity. It is unclear what is responsible for observed geospatial diversity patterns, but lack of mid-domain effects cannot solely be attributed to poor data coverage, or quality. The ABS 3.0 boundaries therefore need further study, and perhaps redesign. Evaluation of important habitat features within and abutting abyssal zones, and related speciation processes, may help explain the results. Including ecoregions and other import topographic features provide future directions for the study of patterns of life in the deep-sea. Resolution issues in the satellite derived bathymetry, lead to failures in capturing small scale habitat heterogeneity at the landscape scale. This gives a false impression of the shape of the seafloor, and the error must be incorporated into future biogeographic classifications. Multiple evolutionary theories may need to be integrated to fully account for diversity patterns. The theoretical rationale for BEPs seems correct, but results within are unable indicate the role of BEPs as vicariance factors, or in defining province boundaries.

While spatial classifications of diversity have practical applications (Briones et al. 2009), study of biogeography has additional intrinsic scientific value in that understanding the processes that shape the patterns of life are directly related to basic questions on evolution. Are basic assumptions of biogeographic theory and spatial classifications supported by actual data? The application of biogeographical theory across realms (terrestrial, oceanic) needs further study. What was tested here, and the results produced, possibly indicate that assumptions fundamental to theory of biogeographical units, which mostly were developed on land, seem a poor fit in the Abyss.

5.3 Prospects

Using quantitative means to address spatial scaling, and utilizing newer biogeographic perspectives in the context of updated conceptually framework, can progress the field of biogeography towards greater unification (Barton et al. 2013). The field of biogeography has developed enough that new subdisciplines provide sufficient diversity in explanatory viewpoints and mechanisms. Assuming this is true, improved unification might benefit from increasing the integration of subdisciplines through quantitative means, methods analogous to component analysis. For example a hypothetical specie's distribution could be described as 45% historical, 30% ecological, and 25% related to spatial stochastic factors.

The methods of this work can be improved and then standardized for automation, in order to incorporate the many streams of relevant data for real-time use in conservation. Biological databases are continually being updated as samples are added, and species appropriately identified. Every day earth science satellites circle the globe adding to large quantities of data on environmental variables in the ocean. The pace of academic publishing cannot compete with the speed at which private organizations race toward extracting resources and impacting the deep-ocean. Methods such as assigning Digital Object Identifiers to datasets allow for appropriate citation of academic work.

To move forward in the deep-sea, more basic sampling and species descriptions are needed, in addition to quantitative integration of mechanisms. Considering the limits to new sampling, species distributions must be complemented by other measures of biological distribution. Some agreement of whether or not basic biogeography concepts are applicable, will allow for use of models and methods deployed in other realms. Without a clear picture on the general spatial patterns of deep-sea biota, any attempt at conservation in the light of pending threats, will face a high failure probability. It is trite, but it is true; more sampling and analysis is needed to solidify the many unanswered biogeographical questions in the deep-sea.

Appendix A DATA SOURCES & REPOSITORY OF PRESENTED WORK

Biological datasets Numbers one - three are references for GBIF.

1: Martinez Arbizu, P. Smith, C. R., Keller, S. and Ebbe, B. (Editors). Biogeographic Database of the Census of Abyssal Marine Life. [Oct 12 2015]. World Wide Web electronic publication. Available online at http://www.cedamar.org/ doi:10.15468/oc9tsb

2: Senckenberg -CeDAMar Provider: Senckenberg - CeDAMar Resource. doi:10.15468/oc9tsb Accessed via http://www.gbif.org/dataset/96180cd0-f762-11e1-a439-00145eb45e9a on Oct 12 2015

3: GBIF.org (12th October 2015) GBIF Occurrence Download http://doi.org/10.15468/dl.ru90yk Query: Dataset Senckenberg - CeDAMar Resource

4: Unpublished CeDAMar is available via github data repository.

Data repository All data used, data produced, and the code used are available at the authors github repository: https://github.com/bmgenco/thesis/

Main softaware used

- R
- Python (analysis not shown)
- GMT tools
- ArcMap
- LaTeX and Lyx
- Google Earth Pro
- Mathematica

Style guidelines University of Hawai‘i at Mānoa 2014 (Electronic Thesis and Dissertation) Style and Policy guide :

https://manoa.hawaii.edu/graduate/sites/manoa.hawaii.edu.graduate/files/documents/misc/tdstylepolicy_e.pdf

Appendix B NOTES

Figure 1.1 Global abyssal depths Shorelines are crude resolution from global self-consistent, hierarchical, high-resolution shoreline database version 2.3.5. (GSHHG). Produced from 15 arc-second gridded (gridline node registration) global topography dataset, SRTM15 PLUS V1. Constructed using GMT tools version 5.3.0.

SRTM15 Topography: `http://topex.ucsd.edu/WWW_html/srtm30_plus.html`
GSHHG: `https://www.ngdc.noaa.gov/mgg/shorelines/gshhs.html`
GMT tools: `http://gmt.soest.hawaii.edu`

Annotated bibliography from Background section (Myers & Giller 1988), provides an in-depth overview of the two traditional pillars of biogeography, ecological and historical study. Furthermore this resource contains much discussion on the major themes and issues that are intertwined in biogeographical study. The contributors of this reference, repeatedly warn against the burden of excessive narrative, which is prevalent in biogeography, often at the expense of more rigorous quantitative analysis.

For a detailed review and synthesis of the primary studies and literature, relating to ecological processes, and diversity studies in the Deep-Sea see Rex & Etter 2010. For a review paper succinctly describing the field, its history and the relevant work related to species estimation see Snelgrove & Smith 2002. A textbook on Deep-Sea biology (Gage & Tyler 1991) contains much at the organismal denizens of the deep. The size class delineations used in Deep-Sea biology are well explained, as well as the importance of microhabitat niches and the nature of factors relevant to the sediment ecology of these systems. A useful complimentary companion to Gage & Tyler 1991 is the ecological themed book on abyssal environments by Menzies et al. 1973, whose body includes sections partitioned by major ocean basins (synonymous with biogeographic realms) as well analysis and background on patterns of genera zonation in isopods. Together these two references provide information on the primary gear and methods used to collect the animal samples, which are the basis of this thesis work. The more recently published work by Clark et al. 2012 specifically tackles sampling methods with inclusion of newer technologies (e.g. submersibles and remotely operated vehicles). This reference is far more comprehensive, as for example Menzies et al. 1973 does not adequately cover coring and meiofaunal sampling methods. Additionally the authors provide a current review and synthesis of ecological, and biological factors important in deep-sea study.

Herring 2002 provides a very concise Deep-Sea marine biological introductory work, the author achieves a near optimum level of reduction of complex issues without information loss of pertinent subject matter. There is much on the physiological challenges and adaptations of Deep-Sea animals. Watling et al. 2013 provides a short a review of Deep-Sea biogeographical studies most relevant to their proposed biogeography and the work undertaken here.

The aforementioned works represent extremely useful reference texts in the field, and are utilized in the Background section. Synthesizing all work, at smaller spatial scales, in is not feasible in this work. Dr. Holly Bik has compiled a list of "Seminal Literature in Deep-Sea Biology", which provides a good sampling of key studies and theoretical underpinnings in regards to the ecology and evolution of these systems.

Dr Holly Bik's Seminal Literature in Deep-Sea Biology:

Dayton & Hessler 1972; Etter et al. 2005; Fauchald & Jumars 1979; Grassle & Sanders 1973; Hessler & Thistle 1975; Levin 2003; Levin & Gage 1998; Levin et al. 2009; R. Hessler & L. Sanders 1967; Rex 1981; Rex 1976; Rex & Etter 1998; Rex et al. 1990; Rex et al. 1993, 2006; Thistle 1983, 1998; Thistle & Eckman 1988; Thistle & Levin 1998; Thistle et al. 1991, 1993; Wilson & Hessler 1987; Wishner et al. 1990

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