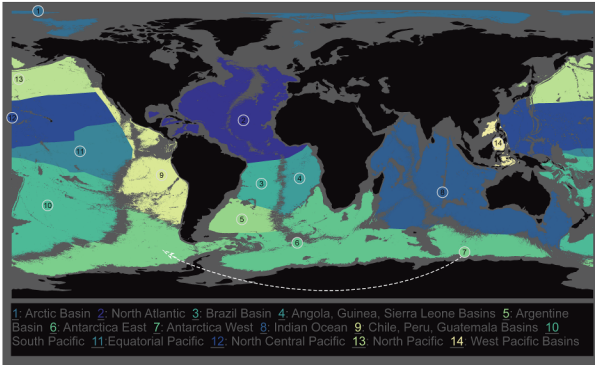


# Biogeographical analysis of abyssal bottom habitats: using an abiotic province scheme and metazoan occurrence databases

Brandon M. Genco, Berkeley CA. Masters Spring 2017, Geography Department, University of Hawai'i at Manoa.

## Introduction

The Deep-Sea is largest biological realm on the planet. Benthic habitats between 3500m and 6500m depth, known as abyssal habitats or abyssal plains, cover ~35% of the Earth's surface and are predominately characterized by soft sediments and limited topographic variance. The geographic patterns of animal life in these relatively pristine sections of the earth, are understudied but, available data suggests high endemic species diversity at small spatial scales [1,2].



Map 1: Abyssal provinces from [4] and used in this study. Numbers and colors correspond to names listed. Numbered circles are located at each province centroid. Geographic centroid of province 7, indicated by white arrow, does not fall within province boundary. Black land, grey ocean not within abyssal delineations.

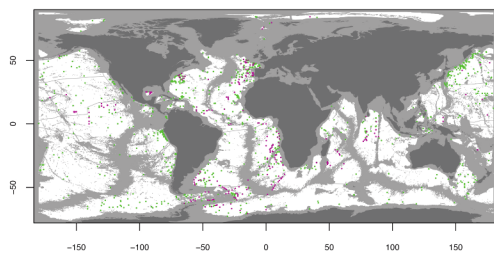
The United Nations recognizes the importance of biogeographical frameworks in conservation matters, prompting several iterations of proposed spatial schemes for the Deep-Sea [3], with the most recent abiotic scheme by Watling et al. [4] developed using the UN framework.

For this abiotic province scheme (ABS 3.0) [4], biogeographical provinces were delineated based on major bathymetric features within ocean basins as well as environmental variables that are associated with oceanographic water mass features and known to impact the physiology and general distribution of Deep-Sea animals: salinity, dissolved oxygen, temperature, particulate organic carbon (POC) flux, and depth. These variables are predicted to be impacted by climate change [5]. No attempt has been made to test the validity of provinces using the majority of animal taxa found within. **Are the abiotic provinces concurrent with taxon distributions?**

## Methods

Two biological databases of Deep-Sea metazoan records were used to test the abiotic province scheme. The original unpublished version of the Census of Diversity of Abyssal Marine Life (CeDAMar) [6]. This includes species records and additional factors. The second database is the published version [7] (GBIF), which includes records after 2005, but primary data is limited to species occurrence and geospatial coordinates. Both datasets are dominated by invertebrates due to sampling methods.

Using an expected mid-domain effect (MDE) null hypothesis structure, rarefied diversity (richness) and scalar distance (km) relationships to province centroids were analyzed, to test the validity of provinces as centers of diversity.



Map 2: Site locations of two databases that are within province boundaries. CeDAMar in magenta. With better spatial coverage and more total sites, GBIF in green.

The geometric mean of three rarefied species richness [8] values was calculated for each taxonomic class per site and used for the regression.  $Slope = G_{mean} / (rarefied\ richness) / km$ , where  $G_{mean}$  was calculated using  $E(S_{100})$ ,  $E(S_{max\ ind.})$ , and  $E(S_{median\ ind. + 1})$ .

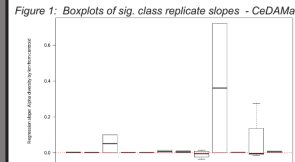
A priori biogeographic provinces are likely to exist in the abyss given their acceptance as meaningful spatial partitions in other realms. The MDE is an emergent statistical distribution [9], which suggests higher diversity is located in the geometric center of a spatial domain as a result of stochastically located species ranges having the most overlap in the center.

Because of differences in datasets, species diversity for CeDAMar and genus diversity for GBIF was calculated. Classes where chosen as replicates to account for intrinsic biological differences in diversity and to address known sampling bias [10]. Analysis not presented here, indicates classes are useful proxies for different sampling methods.

A case study is presented at the sub-province scale using geostatistical methods. This secondary approach is data driven in scope and limitation, and is constrained by the spatial extent of sites in the database, and to a lesser degree by the quality of taxonomic data in the databases. CeDAMar data used here.

## Results I: MDE

**CeDAMar MDE:** 52 replicates in 8 provinces representing 22 of 45 classes. 23 (44%), had significant regression slopes for a spatial trend ( $p$ -value = 0.1). Slopes are the number of rarefied species per kilometer from the province centroid. Of replicates with meaningful spatial trends,



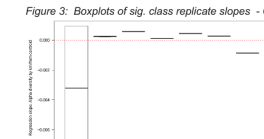
only eight had negative slope values. Negative values indicate decreasing diversity as distance from centroid increases, in line with a MDE. Yet, 15 of 52 (~29%) replicates had positive slopes. The correlation between model fit ( $r$  squared) and slope was stronger for the + slopes, 0.413 and 0.171 respectively, with a correlation of 0.362 for the two combined. If MDE is real, then low slope values would indicate larger average species ranges.

**Figure 1** indicates the variability in diversity slope. Significant regressions only. Replicates are individual taxonomic classes, slopes vary by province. Most show median positive slopes, followed by almost no slope. Only the polychaetes have a median negative slope.

**Figure 2** is slopes per province (numbered subplots) for all classes. Replicates with non significant regressions have been recoded as zero. MDE was not easily

observed, within or across provinces, nor at the class level. To compare within class variability by province the regression was recalculated for  $E(S_{100})$  only for CeDAMar.

**GBIF MDE:** Findings were similar to the CeDAMar results, yet MDEs were rejected. 69 replicates for 13 provinces. Only 10 replicates showed significant  $p$  values ( $p$ -value = 0.1) for a spatial relationship, and of those only two showed a negative slope.



correlation patterns for CeDAMar. The most meaningful correlation being the scope of sampling, the range of distance between sites.

**Figure 3** is box-plots that indicate the variability in slope values for those class replicates with significant regressions. Only Bivalves (3) and Adenopora (2) are represented by more than one replicate.

**Figure 4** is significant class slopes only. Values of slope are low, regardless of sign.

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. Opposite to the

correlation patterns for CeDAMar.

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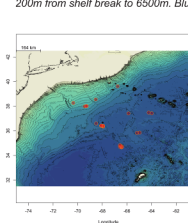
## Results II: Case Study

A series of samples from the Northwest Atlantic were selected for this case study, a well-known site [11]. Castrapods were the only taxa present. A single sampling gear was used for collection of all samples.



Map 3: Case study sites in orange. Province 2, Province white, land is dark grey, all other ocean life grey.

Map 4: Sample sites. Isobaths plotted every 200m from shelf break to 6500m. Blue/



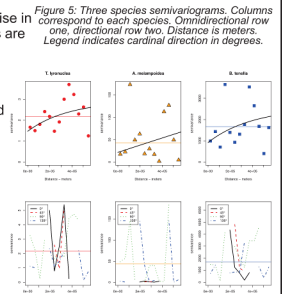
Spatial relationships in patterns of total diversity, or abundance, at the species level were explored using geostatistical methods [12]. The strongest directional variance correlated to the change in depth across the sample sites, which was expected. The depth and topography gradient is approximately in the Northwest to Southeast direction. A second directional trend, North to South, due MOC flow was expected but not found.

In general analysis found no discernible patterns for abundance or diversity. Semivariance of

abundance values for three randomly selected species: *Aceteon melampoides*, *Benthonella tenella*, and *Theta lyronuclea* is shown here.

**Figure 5**, the values for the semivariance axis vary by 1000 for the three species' omnidirectional semivariograms. For the directional semivariogram anisotropy cannot be determined. The semivariance variation indicates species ranges vary immensely. Noise in anisotropy indicates ranges are not continuous. Only *T. lyronuclea* had an acceptable sum of squares fit to the matern geostatistical model (plotted curve row 1).

The location of sites with the highest variability in diversity and abundance patterns by depth (analysis not shown), suggests that an important boundary exists at depths between 3500 and 4000 meters along the 3800m isobath



## Conclusions and Discussion

**The validity of the province scheme was not supported by this work.** The MDE was not observed for species diversity, and rejected for genera diversity. If real MDE should likely be less evident (flatter curves) for genera than species, which was observed. Some important Deep-Sea taxa (e.g., polychaetes) showed significant spatial relationships. The ABS 3.0 boundaries need further study, and possible redesign.

Species distributions by being non continuous may account for lack of MDE (case study). Habitat features within and abutting abyssal zones and related speciation processes, may explain results. The suggestion that the abyss is an evolutionary sink, while shelf areas are evolutionary sources [13], would explain the diversity trends that were opposite (+) to an expected MDE. The source-sink hypothesis may explain some of the trends found, but not the general lack of spatial trends for most taxa.

Multiple evolutionary theories may need to be integrated to fully account for diversity patterns. The theoretical rationale for environmental variables

seems apt. Results within are unable indicate the role of abiotic variables as vicariance factors, or in defining province boundaries.

The case study suggests that the location not of depth, but of change in the derivative of depth is a real location of biotic variability. The junction of the continental rise and slope may be more important than an exact depth for province boundaries. A more meaningful boundary could be created for abyssal zones, using local topographic inflection points as opposed to global depth boundaries.

Future work will look at the directional components of diversity distance relationships and the importance of ecoregions within provinces (e.g., abyssal hills). The environmental variables used to create the abiotic scheme, may be impacted by climate change, and thereby impact distribution of biota. This study indicates that assumptions fundamental to theory of biogeographical units, which mostly were developed on land, seem a poor fit in the Abyss.

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With guidance and support from my Thesis Committee:

David W. Beilman, Chairperson  
Matthew McGranahan  
Les Watling

bmgenco@gmail.com

1-857-231-1238

www2.hawaii.edu/~bmgenco/  
www.brandongenco.com  
https://github.com/bmgenco/thesis/