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

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## Introduction

The open ocean and associated Deep-Sea depths are the largest biological realms on the planet, and habitats within are under-sampled [1,2]. Despite low sampling, available data suggests high endemic diversity at small spatial scales.
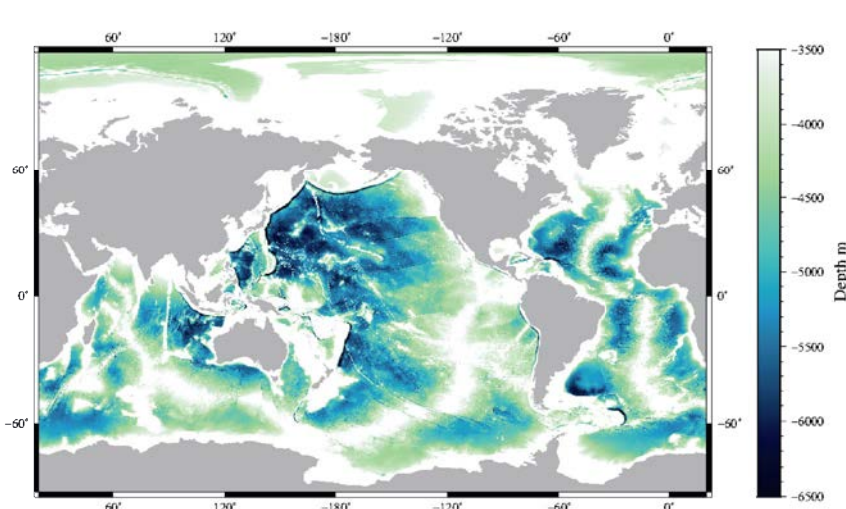
Benthic habitats between ~ 3500m and 6500m depth, known as abyssal habitats or abyssal plains, may account for approximately 35% of the Earth's surface and are predominately characterized by soft sediments and limited topographic variance, with no local photosynthetic production.

The geographic patterns of animal life in these relatively pristine abyssal sections of the earth, are not sufficiently studied. 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 [4] developed using the UN framework as a basis.

For this abiotic scheme [4], biogeographical provinces were delineated based on major bathymetric features within ocean basins as well as environmental variables which are associated with oceanographic water masses and flows (fronts and the meridional overturning circulation), and known to impact the physiology and general distribution of Deep-Sea animals.  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, and therefore meaningful delineations biologically in terms of the Abyssal Biome?*
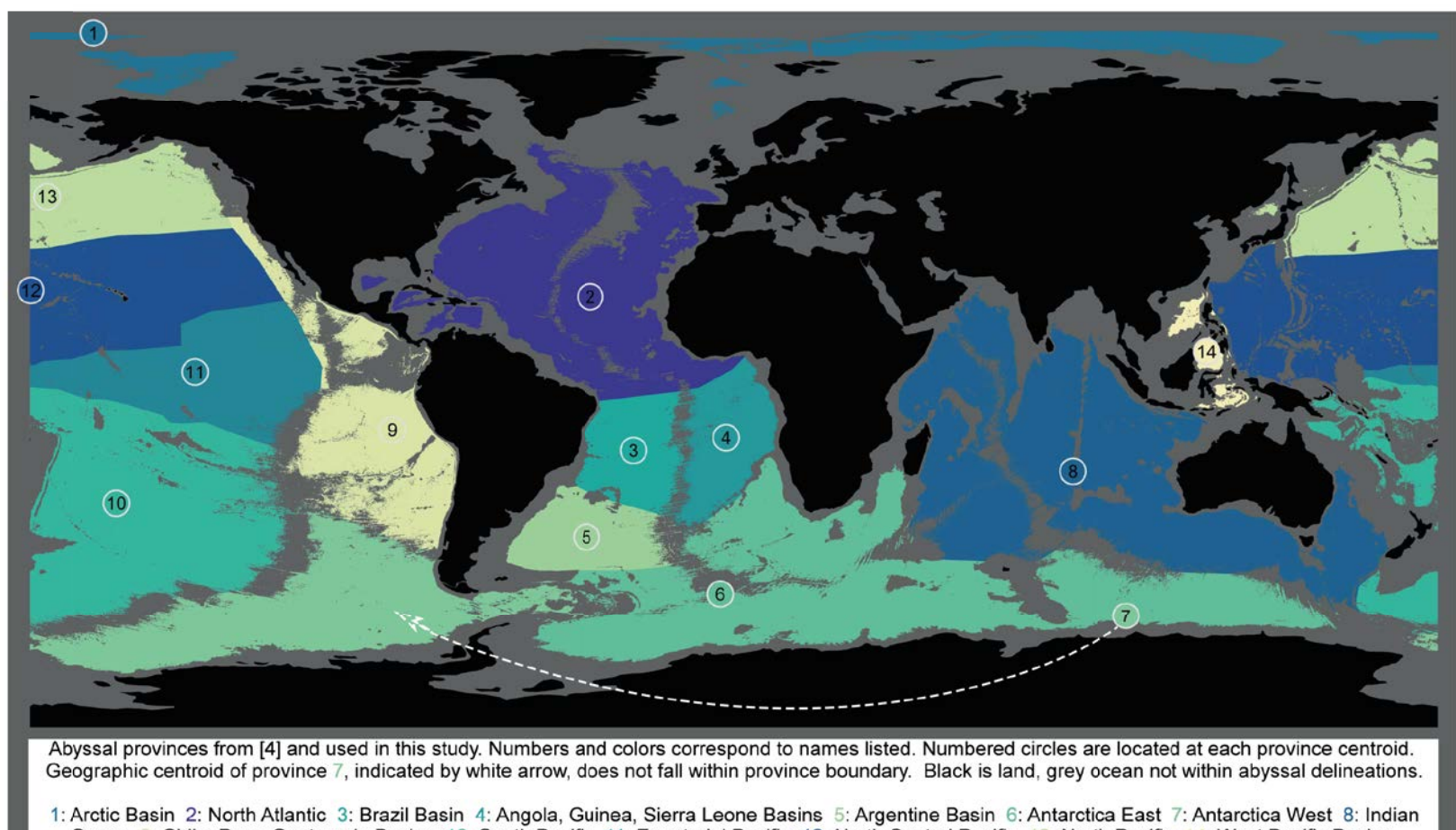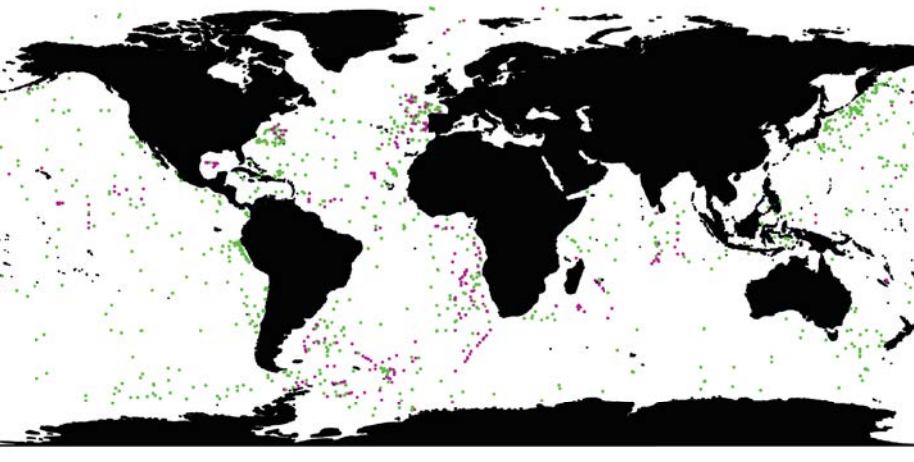


Abyssal provinces from [4] used in this study. Numbers and colors correspond to names listed. Numbered circles are located at each province centroid. Geographic centroid of province is indicated by white arrow, does not fall within province boundary. Black is land, grey ocean not within abyssal delineations.

1: Arctic Basin 2: North Atlantic 3: Brazil Basin 4: Angola, Guinea, Sierra Leone Basins 5: Argentine Basin 6: Antarctica East 7: Antarctica West 8: Indian Ocean 9: Chile, Peru, Guatemala Basins 10: South Pacific 11: Equatorial Pacific 12: North Central Pacific 13: North Pacific 14: West Pacific Basins

## Methods

Two biological databases of Deep-Sea metazoan records (lowest resolution morphospecies) where used to test the abiotic province scheme [4]. The original unpublished version of the Census of Diversity of Abyssal Marine Life (CeDAMar) [5]. This includes species records and addtional factors  (e.g. sampling gear used, and individuals collected per species record). The second database is the published version available online [6] (GBIF), which includes records after 2005, but primary data is limited to species occurrence and geospatial coordinates.



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

Site locations of databases records within province boundaries. CeDAMar is in magenta, and has better spatial coverage and more total sites. GBIF is in green.

A priori, biogeographic provinces are likely to exist in the abyss given their acceptance as meaningful spatial partitions in other realms of the planet**. The MDE is an emergent statistical distribution [7] which suggests higher diversity is located in the geometric center of a spatial domain, this is the result of stochastically located species ranges having the most overlap in the center. This assumes environmental gradients within the domain do not affect species distributions, or that they do not exist within the domain, and distributions of animals are continuous.

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 [8]. Analysis not presented here, indicates classes are useful proxies for different sampling methods.

Secondly 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.

* Three rarefied richness values were calculated for each class per site. Richness rarefied by max individuals collected per class in a province, 100 individuals - Es(100) and 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 richness to distance. To compare within class variability by province the regression was recalculated for Es(100) only for CeDAMar.

** No attempt was made to systematically test province boundaries due to variability in biota patterns to depth, and the ephemeral nature of water masses [4,9–12]. Additionally there is uncertainity in globally resolving bathymetry, where at one location depth may vary by 500 meters for a regional average depth of 3500m (**see attached supplement; Satellite altimetry error** ).

## Results I: MDE

**CeDAMar MDE:**  52 replicates in 8 provinces representing 22 of 45 classes. 44%, had significant p-vales for regression slopes for a spatial trend. Of replicates with meaningful spatial trends, only 8 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 indicated a positive slope.

The correlation between model fit (r squared) and slope was stronger for the + slope versus the - slopes, 0.413 and 0.171 respectively, with a correlation of 0.362 for the two combined. If MDE is real, than low slope values would indicate larger average species ranges.

Figure 1 indicates the variability in slope values for those class replicates with significant regressions. Most show median positive slope, followed by almost no slope. Only the polychaetes have a median negative slope.

Figure 2 is slopes per province, for all classes. Replicates



Figure 1: Box plots per class replicates - CeDAMar



Figure 2: Species MDE test CeDAMar

Per province regression slopes (rarefied, Es(100), species diversity as a function of increasing distance away from local province centroid), by class for CeDAMar dataset. All non significant slopes, p value > 0.1, were converted to zero for visualization. Sub figures are numbered by province. Slopes are + and -.

with non significant regressions have been recoded as zero. MDE was not easily observed, within or across provinces, nor at the class level.

**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 (alpha 90%) for a spatial relationship, and of those only 2 showed a negative slope.
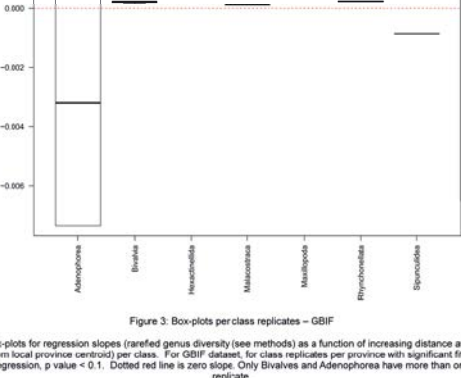
The four statistical measures of sampling effort per replicate, number of sites, site range, median distance between sites, and standard deviation of site distance, all showed weak positive correlations to regression slopes. Opposite to the correlation patterns for CeDAMar. The most meaningful correlation being the scope of sampling, the range of distance between sites.



Figure 3: box-plots per class replicates - GBIF

Figure 3 is box-plots which indicate the variability in slope values for those class replicates with significant regressions. Only Bivalves (3) and Adenoporha (2) are represented by more than one replicate. Figure 4 is significant classes only. Values of slope are low, regardless of sign. *(see attached supplement, for tables of all class replicate regression values)*



Figure 4: Genus MDE test GBIF

Per province regression slopes (rarefied genus diversity, see methods, as a function of increasing distance away from local province centroid), by class for GBIF dataset. Only significant slopes, p value < 0.1, shown. Sub figures are numbered by province. Slopes are + and -.

## Results II: Case Study



Bottom Map: Case study area, southern Atlantic. All but one of the sites falls within the boundaries of the North Atlantic province. The full province is not shown. Province in grey, land in black, all other ocean in white.

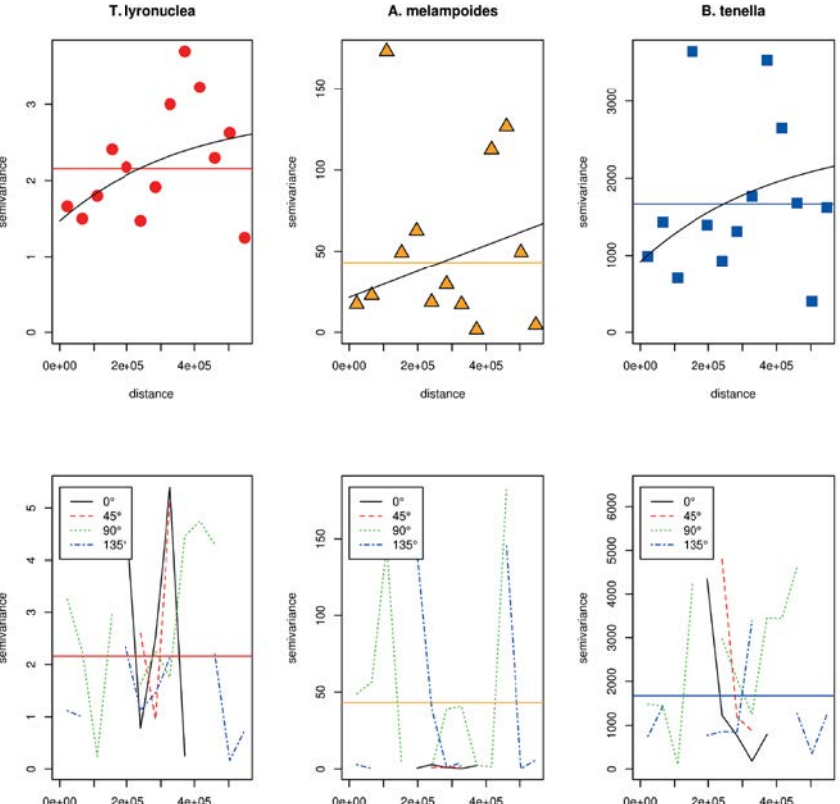Top Map: Case study sites in orange, northern Atlantic.

A series of samples from the Northwest Atlantic, off the Northeast coast of the United States, were selected for this case study, a well-known site [13]. Gastropods were the only taxa present. A single sampling gear was used for collection of all samples.

Geostatistical methods were employed [14], to explore  spatial relationships in patterns of total diversity, or abundance at the species level. Anisotropy correlated to the change in depth across the sample sites 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.

In general geospatial analysis found no discernible patterns for abundance or diversity. However presented is semivariance of abundance values for three randomly selected species: *Aceteon melampoides*, *Benthonella tenella*, and *Theta lyronuclea*.

In figure 5,  the values for the semivariance axis vary by a factor of a thousand for the three species' omindirectional semivariograms. For the directional semivariogram anisotropy cannot be determined. The semivariance variation indicates species ranges vary immensely, but noise in anisotropy indicates ranges are not continuous. Only *T. Lyronuclea* had an acceptable sum of squares fit to the mattern geostatstitical model (the curve shown in row 1).



Columns correspond to each species. Omnidirectional abundance semivariogram, with mattern model fitted row 1, directional abundance semivariogram row 2. Distance is meters. The semivariograms axis for the three species differ by 3 orders of magnitude. Semivariance is similar to variance, but for spatial data. Mattern model is a statical correlation model of semivariance by distance between pairs of sites, analogous to a regression model. Legends in bottom row plots refer to pattern in each of four cardinal directions. Colored horizontal lines are varinace values.

The  location of sites with the highest variability in diversity and abundance patterns by depth (analysis not shown), suggested that an important boundary exists at depths between 3500 and 4000 meters along the 3800m isobath located at the boundary of the Continental rise and the Continental slope. Those sites can been seen one the edge of province in the top map, and running along the isobath in the bottom map.

## Conclusions

**The validity of the province scheme was not supported by this work.** Yet, it would be improper to reject them entirely by this study. A MDE was not observed for species diversity, and was rejected for genera diversity, however significant spatial relationships coincided with important Deep-Sea taxa (e.g. polychaetes). Species distributions by being non continuous may account for lack of MDE, as indicated by the case study.

If real, MDEs should likely be less evident (flatter curves) for genera than species, which was observed in this analysis. Mid-domain effects may not be a useful null model in the abyss [15–17], given suggestions that the abyss is an evolutionary sink, while bathyal areas of continental margins are thought of as evolutionary sources. This concept is taxon variable, with certain megafauna exhibiting possible radiations in the abyss. There also may be confounding factors due to conflation of horizontal ranges related to depth ranges

[12]. Alternatively, area and connectivity properties of the Deep-Sea, may negate the usefulness of provinces. (see inset map projections)

The case study  suggests 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 for province boundaries. A more meaningful boundary could be created for abyssal zones, abutting bathyal zones, by using the 2nd derivative of depth change within a range of likely depths (2500-4000 meters).
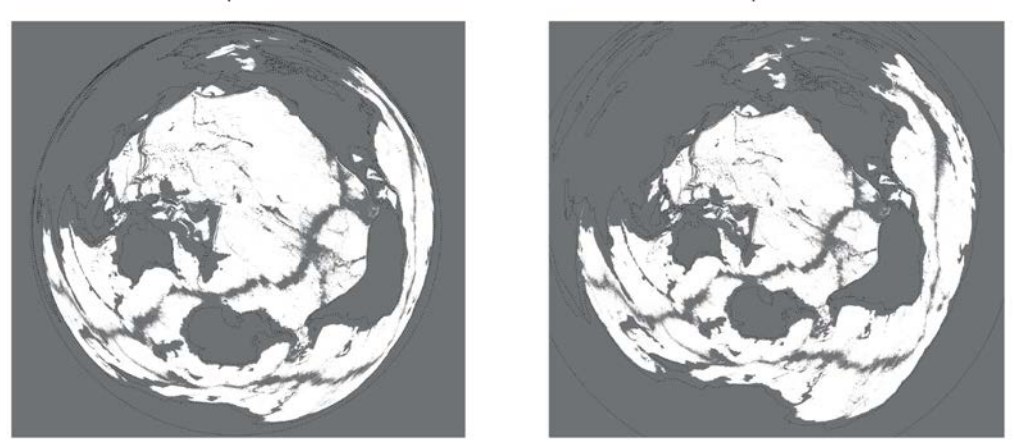


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