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Marine diatom species richness and diversity at different latitudes during the Paleocene-Eocene thermal maximum: implications for future warming

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SUMMARY

Modeling diversity of marine diatom communities by latitude for the late Paleocene and early Eocene provides context for future warming climates. The Paleocene-Eocene Thermal Maximum (PETM) transition spans ~57 to 48 million years ago with global temperatures ranging from ~9 to 23°C higher than pre-industrial times. There are differing views whether modern carbon increases will lead to similar patterns in temperature and how it may impact global communities. This research used data provided by the International Ocean Discovery Program (IODP). The study examines how marine diatom communities responded to the rapid warming of the PETM as a potential analog for future marine diversity under a warming climate. Statistical analyses assess potential changes in diversity of diatom abundance data from existing marine sediment cores from Lomonosov Ridge in the Central Arctic Ocean, Blake Nose in the Western North Atlantic Ocean, and Broken Ridge in the Eastern Indian Ocean. Examining changes at different latitudes provides a more comprehensive picture of how rapid warming impacted diatom species richness and diversity across the globe. The Shannon-Wiener Diversity Index details change in diatom communities. Principal Component Analysis and Hierarchical Cluster analysis further refine variance between datasets. Results suggest diatom communities were negatively affected by the rapid warming of the PETM in middle latitude locations, while the Central Arctic Ocean diatom communities showed an increase in diatom species richness and diversity. The Central Arctic Ocean diatom community response may result from the more terrestrial paleogeography of the location during the PETM providing increased nutrient availability from runoff as well as poor diatom preservation. Changes in the Indian Ocean diatom If marine diatom communities suffer in middle latitude locations as the data suggests, then likely decreases in diatom species richness and diversity support a positive feedback loop for further warming. Challenges include inconsistent abundance

measures complicating comparisons between datasets, lack of Antarctic samples, and some evidence diagenesis has limited diatoms preservation during the PETM in some locations.

INTRODUCTION

Diatoms are the most diverse protists on Earth and the most common phytoplankton accounting for 40% of ocean productivity (Tréguer et al. 2018). They play a critical role in the marine carbon cycle fixing surface carbon in their shells and transporting it to the deep ocean for long-term burial. Warming oceans decrease productivity which in turn triggers a positive feedback loop resulting in decreased carbon absorption (Boot et al. 2023). As such, diatoms are a staple proxy of marine paleoclimate (Crosta et al. 1998). The Paleocene-Eocene Thermal Maximum (PETM) is a geologic period of rapidly increasing carbon dioxide and global temperatures of 4-5°C 56 million years ago (Burkea et al. 2018; Tian et al. 2021). The PETM is a particularly important time period as it is among the most intense intervals of global warming in the last 65 million years caused by a massive and abrupt change to the global carbon cycle (Rohl et al. 2007; Tierney et al. 2022) and provides a potential analog to current global warming trends (Haynes and Hönisch 2020).

Current diatom studies focus on changes in dominant diatom species with little attention directed to changes in species richness and diversity (Cherapanova et al., 2006; Davies and Kemp, 2016). Analysis of marine diatoms from before and after the PETM boundary is limited due in part to lack of sampling sites. This study employs analysis of Species Richness, Shannon-Wiener Diversity Index, Principal Components Analysis (PCA), and Hierarchical Cluster Analysis (HCA) to analyze diatom communities before and after the Paleocene-Eocene Thermal Maximum (PETM). Utilizing the Shannon-Wiener Diversity Index (SWDI) provides an analysis of marine diatom species diversity and evenness before and after the PETM.

The additional analytical methods of PCA and HCA support the Shannon-Weiner Diversity Index by refining species drivers of variance and identifying community groupings, respectively. PCA further identifies community structure and drivers of variance. HCA provides additional aspects of community structure (Chen et al. 2019). The multiple statistical approaches provide a range of perspectives on diatom communities before and after significant change in global climate. This approach identifies potential community changes in marine environments across the PETM warming. Comparing changes in diatom species richness, species diversity and statistical results at different latitudes improves understanding of the global nature of impacts on marine environments and serves as an analog for ocean dynamics in future global warming.

MATERIALS AND METHODS

Samples

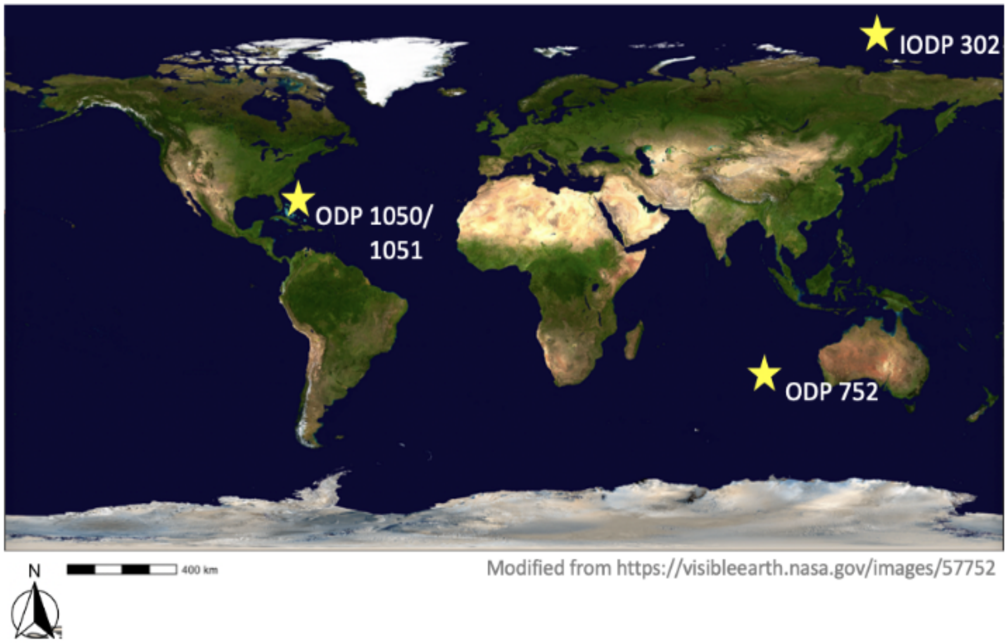
The location of sediment cores from one International Ocean Drilling Program (IODP) site and two Ocean Drilling Program (ODP) sites span latitudes and hemispheres for a global representation of ocean conditions reflected by trends in diatom communities across the Paleocene-Eocene Thermal Maximum (Fig. 1). Selection criteria emphasized availability of dated diatom abundance data across the PETM time period, and the latitude of the drilling locations. Diatom dissolution limited the available drilling sites for consideration. Latitude was important consideration when assessing a global climate shift and as evidence suggests rapid warming during the PETM varied in intensity depending on latitude (Zachos et al. 2001). As important indicators of global primary productivity, marine diatoms from these sites are assessed by multiple assays to explore potential changes in species diversity and community structure pre- and post- the PETM boundary.

Central Arctic Ocean IODP 302

Sediment cores from IODP Expedition 302 Hole M0004A provide the diatom abundance data for the Central Arctic Ocean (Backman et al. 2006) (Fig. 2A). This drilling site is on the Lomonosov Ridge (87°51.99'N, 136°10.64'E; WGS84) which is composed of continental crust. The ridge separated the Eurasian plate at approximately 56 Ma and subsided as it moved northward before marine sedimentation began (Backman et al. 2006). The coring location is currently approximately 1300 meters below sea level, whereas the surrounding abyssal plain lies at three kilometers below sea level (Backman et al. 2006). Diatom abundance counts provide the abundance data for the majority of the core, with sections of poor preservation being analyzed using abundance approximations (Backman et al. 2006).

Western North Atlantic Ocean ODP 1050 and 1051

Sediment cores from ODP drill holes 1050 (30°06’N, 76°14.1’W; WGS84) and 1051 (30°03.17’N, 76°21.46W; WGS84) were the source of the Western North Atlantic Ocean diatom abundance data (Witkowski et al. 2020) (Fig. 2B). These drilling locations located on Blake Nose are a projection of the Blake Plateau extending from the eastern margin of the plateau with a maximum depth of approximately 2700 meters below sea level (Norris et al. 1998). Site 1050 is located 2300 meters below the sea level (mbsl), while site 1051 is located at 1983 mbsl (Norris et al. 1998). Sediment cores from both drilling locations have diatom abundance data across the PETM. Diatom abundance counts for all core sections comprise the abundance data and considered representative of diatom communities in the Western North Atlantic Ocean across the PETM.



Modified from https://visibleearth.nasa.gov/images/57752

Figure 1. Drilling locations of IODP cores utilized in assessment of diatom communities across the PETM. Image modified from https://visibleearth.nasa.gov/images/57752/.

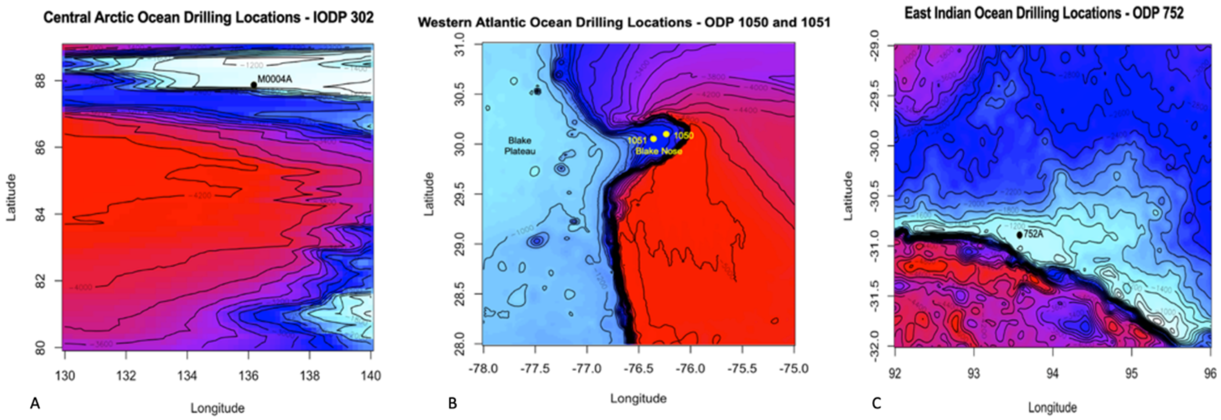


Figure 2. Bathymetric maps illustrating the locations and depths of IODP coring sites; A. 302 Hole M0004A; B. ODP sites 1050 and 1051; and C. ODP 752. Depths are in meters below sea level. Maps were generated by A. Hentzen in R using bathymetric data from NOAA.

Eastern Indian Ocean ODP 752

Diatom abundance data from the Eastern Indian Ocean comes from OPD Leg 121, Hole 752A sediment cores (Fourtanier 1991) (Fig. 2C). The drilling occurred at Broken Ridge (30°53.46'S, 93°34.68'E; WGS84). This drilling location located at Broken Ridge, is an oceanic platform remaining relatively shallow through time with rift-related uplift resulting in parts of Broken Ridge being exposed above sea level (Shipboard Scientific Party, 1989). Descriptions of Eastern Indian Ocean diatom abundance approximations comprise the abundance data. The approximations separated into diatoms categories are: abundant (A) when there were at least 20 specimens in one horizontal transverse at 500x magnification, common (C) when 19 to three specimens were present in one horizontal transverse, few (F) when one or two specimens were present in one horizontal transverse, and rare (R) when less than one specimen was present in one horizontal transverse (Fourtanier 1991).

Species Richness

Diatom species richness is the number of species present in a sample and is one of the simplest ways to characterize community diversity (Gotelli and Colwell 2001; Whittaker et al. 2001). Species richness is an indicator of species diversity. Diversity in marine species is a critical indicator of fundamental community structure and ecosystem functioning (Lotze 2021). Biodiversity supports productivity, community stability, and ecosystem resilience to pollution and climate changes. However despite its widespread use in ecological studies, species richness is highly dependent on sample size resulting in underestimates of richness at all sample sizes, but underestimation decreases as sample size increases (Hellmann and Fowler 1999).

Microsoft Excel calculated diatom species richness for each sediment core section extending across the PETM time period. Species richness graphs aid in the identification of changes in species richness across the PETM and between the study areas. Species richness provides information on how the rapid warming characteristic of the PETM affected diatom communities at each location.

Species Diversity

Species diversity plays a suggested critical role in the stability of ecological communities and increasing resilience to ecological stress. Species diversity characterizes community structure and is a function of species richness and evenness, with less even communities being less diverse than species richness alone would suggest (Maurer and McGill 2011). The diversity-stability hypothesis suggests as species diversity increases within a community so does the collective ability of community populations to maintain their abundances after disturbances (Johnson et al. 1996). Changes in species diversity can indicate changes in environmental conditions. Boyd et al. (2013) demonstrated polar diatoms experienced rapid decrease in growth rate when temperature increases exceeded 3°C followed by mortality indicating changes in the temperature of their environments affect diatoms.

Diatom Species Abundance Data

Sites at each region handled data collection and recording differently. Steps in data preparation allowed for comparison between datasets. This is especially true for the Central Arctic Ocean dataset where, differences in data logging occurred by core section. Preparation included processing diatom abundance data in RStudio before calculating species richness and diversity in Microsoft Excel. Splitting each dataset into two separate pre-PETM and post-PETM datasets allowed comparison by Principal Components Analysis (PCA) and Hierarchical Cluster Analysis (HCA). For each of these smaller datasets, only diatom species occurring in both datasets were included in the analysis. This may negatively bias the occurrence of warming extinctions.

The diatom species abundance data removed or replaced special characters and spaces to avoid interference with data processing. Data removed from depths due to dissolution reduced the effect of dissolution on the results. Diatom counts denoted by "+" for fragments converted to 1 the minimum number of individuals (MNI) present in the sample, then transferred to RStudio for PCA and HCA. Missing values were masked from analysis using the na.omit function. Data normalization utilized the scale function, which utilizes the equation:

$$\frac{X - \mu}{\sigma}$$

in which X is the original value, μ is the mean, and σ is the standard deviation.

Abundance data from Central Arctic Ocean ODP 302 excluded samples from core sections 2X, 3X, 20X, 21X, and 22X due to poor preservation provided no diatom data. Abundance data from core sections 15X, 18X, and 19X recorded abundance approximations, requiring the use of random number generation in Microsoft Excel to convert the diatom abundance approximates to approximate diatom counts. Western North Atlantic Ocean ODP 1050 and 1051 and Eastern Indian Ocean ODP 752 used similar preparation of abundance data. It is important to note any differences in data collection and interpretation may obscure some trends. Namely, in the use of random number generation in diatom abundance data for portions of the Central Arctic Ocean Eastern the dataset and the Indian Ocean dataset. While the use of random number generation reduced the presence of statistical bias in the analysis, it also introduced noise to the data. Another analysis using the minimum number of individuals method may provide useful data despite the bias it would introduce.

Shannon-Weiner Diversity Index

The Shannon-Weiner Diversity Index (SWDI) is a quantitative metric commonly used in environmental studies (Omayio and Mzungu 2019; Han et al. 2025) including assessments of the ecological condition of marine environments (Jing et al. 2015). The SWDI is not highly correlated to sample size when the samples contain at least 25 individuals (Cruz-Uribe 1988). While it incorporates both species richness and evenness to captures community structure, the SWDI puts more weight on rare species, primarily emphasizing evenness relative to richness (Chen et al. 2025). It is considered a top index, especially for marine biodiversity.

Diatom species diversity for each of the locations used Microsoft Excel to calculate the Shannon-Wiener Diversity Index,

$$H' = -\sum p\text{i} (\ln p\text{i})$$

where pi is equal to the portion of individuals of each species is divided by the total number of individuals in the population (Nair and Ngouajio 2012). These calculations used diatom abundance data from the appropriate sediment core sections at each location. Graphing calculated diatom species diversity H' across time allows ease of comparison through time and between study area locations.

The need for improved diversity knowledge is increasing the scrutiny of indices for bias. While the SWDI focuses heavily on rare species and small sample sizes it is important to combine it with additional assessments (Qiao et al. 2024). Here we employ both Principal Components Analysis to simplify data structure, highlighting similarities and differences and Hierarchical Cluster Analysis which groups data based on shared characteristics for a more robust assessment.

Principal Components Analysis

Principal Components Analysis (PCA) uses multivariate data analysis to reduce the number of dimensions while retaining the data's variation, allowing for the visualization of these new variables to help identify similarities and differences between samples (Groth et al. 2013). PCA identified factors of diatom preservation in saline lakes in Spain suggests pH was less significant to diatom preservation in saline lakes than factors such as permanence, water depth, conductivity, and turbidity (Reed 1998). A study of 28 Pyrenean springs characterized groupings of diatom taxa using PCA based on the speed of spring flow (fast or quiet waters) and water hardness (Sabater and Roca 1990). These studies indicate PCA can identify clusters of diatom taxa based on environmental characteristics, making it particularly useful in analyzing changes in diatom communities across the PETM, a time of rapid temperature increase.

PCA performed on each dataset used RStudio producing biplots for each dataset and location. PCA used the prcomp function in the stats package. The fviz_eig function from the factoextra package produced scree plots. The fviz_pca_ind, fviz_pca_var, and fviz_pca_biplot functions from the factoextra package produced the PCA plots and biplots for each location. The get_eigenvalue, get_pca_var, and get_pca_ind functions from the factoextra package extracted eigenvalues, the PCA results for variables and individuals.

Hierarchical Cluster Analysis

The Hierarchical Cluster Analysis (HCA) is a multivariate statistical method used to classify indexes according to commonalities within the data (Yang et al. 2021). One study involving the use of the Ward method for HCA to examine diatom distribution patterns showed the use of genus level diatom taxonomic composition has the potential to identify environmental change (Lu et al. 2020). This is of particular importance as many of the datasets used included diatoms identified at the genus level, but not always the species level. Another study examined benthic diatoms in the Kowie Estuary in South Africa indicated the tolerance of diatoms to different environmental factors may be indicated by clusters produced in hierarchical cluster analysis (Dalu et al. 2016).

Hierarchical Cluster Analysis of each dataset used RStudio. The dist function of the stats package using the Euclidean method of distance measurement and the hclust function of the stats package using Ward D2 agglomeration method, or Ward's Method of minimum variance with dissimilarities squared before clustering produced the cluster dendrograms. The plot function from the graphics package visualized the results in a dendrogram.

RESULTS

Central Arctic Ocean IODP 302

The Central Arctic Ocean IODP 302 (Supplementary File S1) species richness dataset records nine diatom species preserved pre-PETM and 20 species representing post-PETM, a 122% increase in species richness post-PETM. The species diversity record while not identical, very closely mirrors species richness in pattern and scale with a steady increase in richness and diversity from pre- to post-PETM, doubling and remaining high through the early Eocene (Figs. 3A and 3B). The Arctic record has many fewer species than the middle and lower latitude sites with species ranging from a single species pre-PETM to a peak of 26 species post-PETM. The Central Arctic Ocean highest species abundance had many fewer species than lower latitude locations.

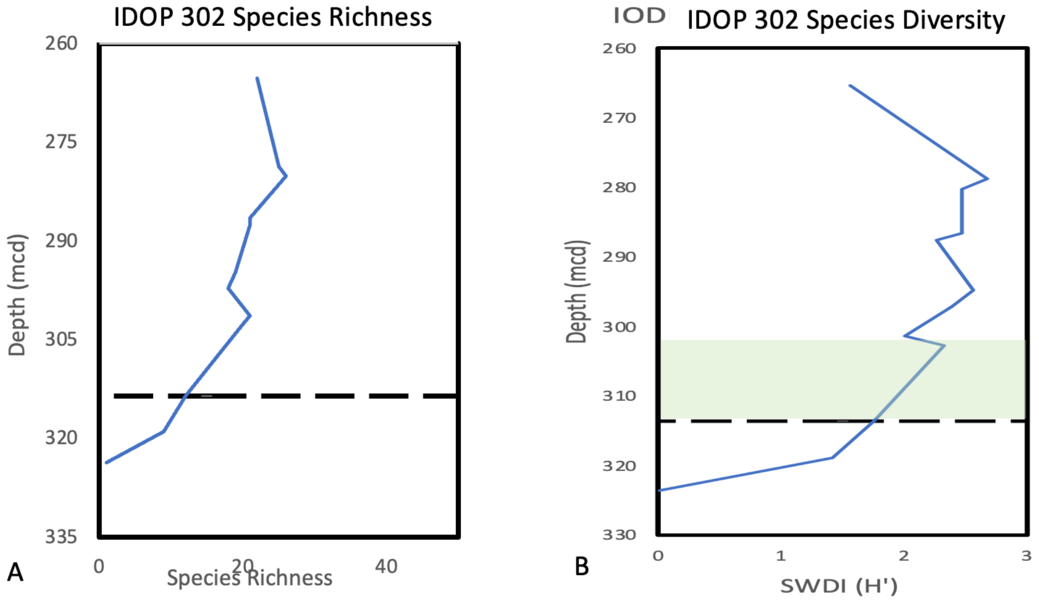


Figure 3. Central Arctic Ocean IODP 302 A. distribution of species richness across PETM marked by dashed line. B. distribution of species diversity across PETM marked by dashed line, post PETM increase in diversity highlighted in green.

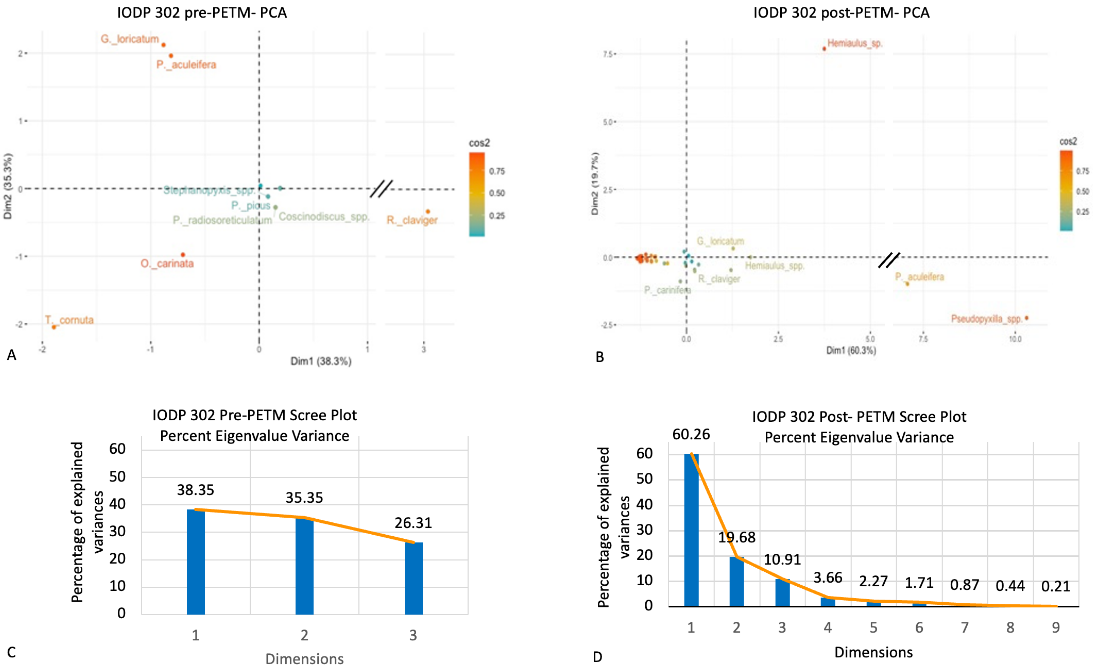


Figure 4. Central Arctic Ocean IODP 302 Principal Components Analysis plots visualize loading differences in principal components: A. pre-PETM and B. post-PETM. Scree plots quantify variance for each principal component: C. pre-PETM and D. post-PETM.

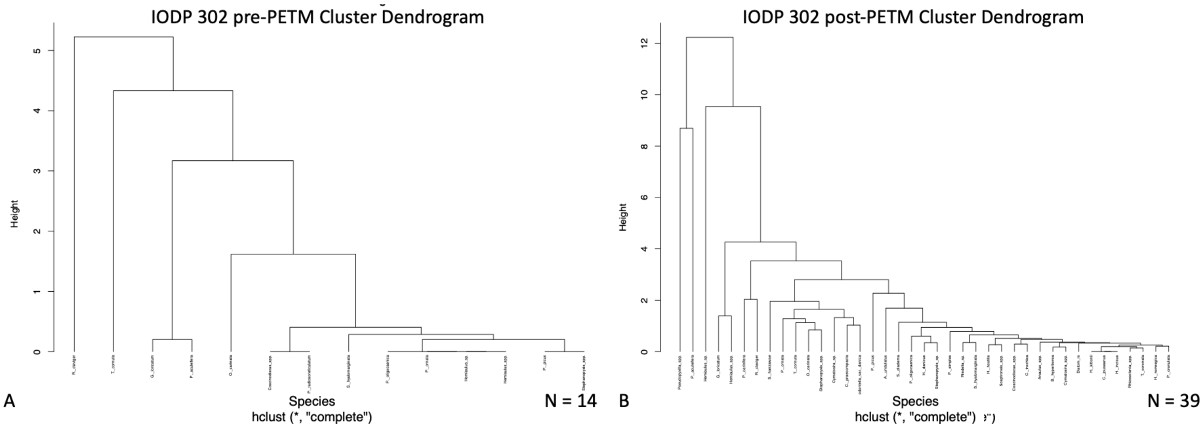


Figure 5. Hierarchical Cluster dendrograms; A. pre-PETM and B. post-PETM identify relationship structure.

The Principal Components Analysis of the Central Arctic Ocean IODP 302 data identify differences in variance between the pre-PETM (Fig. 4A) and post-PETM (Fig. 4B) datasets. The pre-PETM PCA confirm R. claviger shares little similarity with the rest of the species and is the most distant positive loading species. G. loricatum, P. aculeifera, T. cornuta, and O. carinata are distantly and negatively loaded in relation to the major grouping of species and strongly negative to R. claviger. The remainder of the species cluster closely about the center. The outliers from the pre-PETM PCA form a loose grouping close to the center with the remaining species forming two tightly clustered groups, one with slightly negative loading. Scree plots of the pre-PETM (Fig. 4C) and post-PETM PCA (Fig. 4D) demonstrate 38% and 60% variance, respectively, within the first principal components.

Hierarchical Cluster Analysis results for the Central Arctic Ocean IODP 302 differ greatly between pre-PETM (Fig. 5A) and post-PETM (Fig. 5B) datasets. Fourteen diatom species were observed before the PETM. Similar to the PCA *Rhabdolithus claviger* (*R. claviger*) was the least clustered of the diatoms. *Trinacria cornuta* (*T. cornuta*) also shared little similarity with the diatoms present before the PETM. *Goniothecium loricatum* (*G. loricatum*), *Pterotheca aculeifera* (*P. aculeifera*), and *Odontotropis carinata* (*O. carinata*) also cluster separately from the rest of the species. Only the remaining nine diatom species observed before the PETM form more closely clustered groups. Thirty-nine diatom species, a 178% increase from the number of pre-PETM species, comprise the post-PETM dataset. In the post-PETM species more dissimilarity is observed with *Pseudopyxilla* spp., *Pterotheca aculeifera* (*P. aculeifera*), and *Hemiaulus* spp., which have the greatest linkage distances. The remaining 36 species form one of four classes with two subclasses of closely clustered groups. Overall, more species in the post-PETM are more tightly grouped linkages.

Central Arctic Ocean 302 data contained the lowest number of diatom species with only 39 species being characterized, nearly 78% of which are unique to the Central Arctic Ocean. They are a mix of marine and freshwater/brackish species (Stickley et al., 2008). *Pseudopyxilla* spp., *Pterotheca aculeifera*, *Hemiaulus* sp., and *Goniothecium loricatum* are the four most prominent diatoms in the Central Arctic Ocean dataset (Figs. 6A and 6B). Not only is *Pseudopyxilla* spp. one of the most abundant species (78%) in both the Arctic and Western North Atlantic records, but it is also a strong positive outlier in these records as well. Distribution of the four most abundant species shows limited long-term pattern in their fluctuations which occur primarily in the post-PETM due to a lack of pre-PETM data, limiting their comparative value.

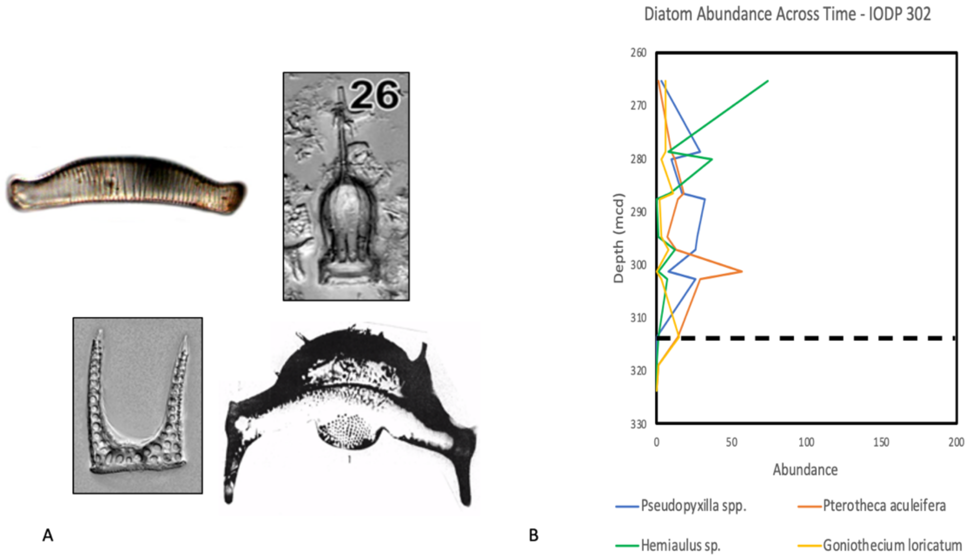


Figure 6. Central Arctic Ocean IODP 302. A. the four most abundant diatoms: *Pseudopyxilla* spp. (top left), *Pterotheca aculeifera* (top right), *Hemiaulus* sp. (bottom left), and *Goniothecium loricatum* (bottom right) (Schrader and Fenner, 1976); and B. distribution of the four most abundant diatom species post-PETM with limited pre-PETM data.

Western North Atlantic Ocean at ODP 1050 and ODP 1051

Diatom species richness in the Western North Atlantic Ocean ODP 1050 (Supplementary File S1) displayed patterns of frequent, sharp oscillations increasing and decreasing in species richness and species diversity (Figs. 7A and 7B). Both records decline at the PETM boundary with strong increases into the early Eocene. These records display high frequency fluctuations throughout their records with several significant declines and peaks post-PETM. The ODP 1051 site records of species richness and species diversity (Fig. 7C and 7D) present the most frequent sharp oscillations compared to the ODP 1050 records. In both datasets the decreases in species richness are greater than the decreases in species diversity at the PETM boundary. Overall diatom species diversity in the Western North Atlantic Ocean datasets record patterns similar to each other.

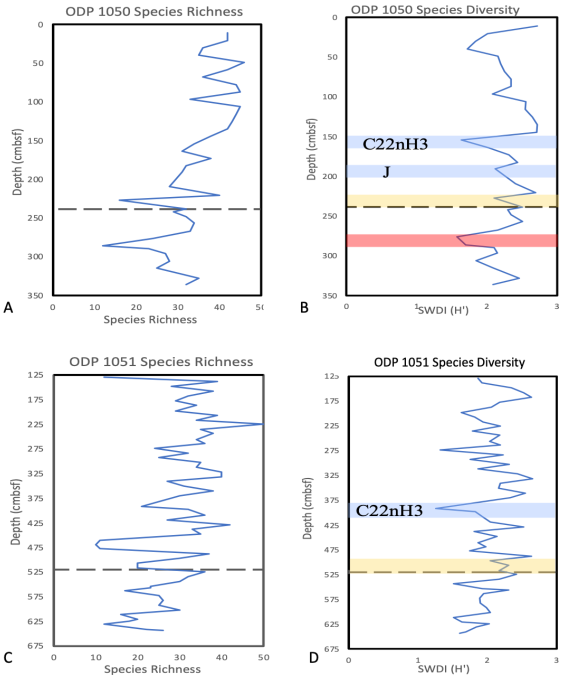


Figure 7. Western North Atlantic Ocean ODP 1050 distributions of species richness (A) and species diversity (B). Species diversity decreases across PETM (highlighted in yellow), additional decreases in the Early Eocene hyperthermal events J and C22nH3 (highlighted in blue), and pre-PETM species diversity decrease (highlighted in red). ODP 1051 species richness (C) decreases across the PETM. ODP 1051 species diversity (D) decreases across PETM (highlighted in yellow), additional decreases in the Early Eocene hyperthermal event C22nH3 (highlighted in blue).

There are larger decreases before the PETM which are greater in magnitude than at the PETM boundary and several after the PETM which are not as significant in amplitude. The ODP 1051 dataset has four instances of greater decreases in species richness than at the PETM boundary. Two occur before and two after the PETM. In ODP 1050 the two post-PETM decreases in species richness correlated to two early Eocene hyperthermal events (J and C22nH3) (Fig. 7B). Lower numbers of diatom species diversity are observed in both datasets prior to the PETM. The ODP 1050 pre-PETM dataset contains 90 species, and the post-PETM dataset peak has 176 species, a nearly 96% increase in species from the pre-PETM. The increase in species in ODP 1051 from pre- to post-PETM was 110%.

The Principal Components Analysis results for Western North Atlantic Ocean ODP 1050 pre-PETM and post-PETM (Figs. 8A and 8B) show similar patterns of component loadings and identify *Pseudopodosira* spp., *Paralia* spp., and *Pseudopodosira bella* to be strong outliers. The scree plots for ODP 1050 pre-PETM and post-PETM (Figs. 8C and 8D) are very similar to each other with 85% variance of both explained by the first principal component. *Paralia* spp. and *Pseudopodosira bella* are very distant and strongly negatively correlated to each other.

Principal Components Analysis results for ODP 1051 pre-PETM and post-PETM (Figs. 8E and 8F) show component loading patterns very similar to OPD 1050 pre-PETM also identifying *Pseudopodosira* spp., *Paralia* spp., and *Pseudopodosira bella* as strong outliers; and in post-PETM *Paralia* spp. and *Pseudopodosira bella* are distant and strongly negatively correlated to each other. ODP 1051 scree plots for pre-PETM (Fig. 8G) and post-PETM (Fig. 8H) explain slightly less variance of the first principal component than ODP 1050 at 81% and 79%, respectively. Species are tightly grouped at both the Western North Atlantic Ocean sites and outliers are similar with strong percentage of variance explained in the first component.

The Hierarchical Cluster Analysis of ODP 1050 differs between the pre-PETM (Fig. 9A) and post-PETM (Fig. 9B) in number of observed species, 90 species pre-PETM to 134 species post- PETM in a 49% increase. The pre-PETM species form 16 groupings of two, three, and four species with short branches indicating low levels of dissimilarity. While many small clusters with short branching occurred, there were taller branching groups indicating higher levels of dissimilarity among outliers identified as *Paralia* spp., *Pseudopodosira bella* (*P. bella*), *Pseudopodosira* spp., and *Acanthodiscus* spp.

The HCA for ODP 1051 pre-PETM dataset contains 81 species, and 170 species comprise the post-PETM clustering, more than doubling at 110% from the pre-PETM dataset. ODP 1051 pre-PETM and post-PETM (Figs. 9C and 9D) plots both demonstrate very short clustering distances indicating low levels of dissimilarity. Outliers *Paralia* spp. and *P. bella* are present in ODP 1050 pre-PETM with *Pseudopodosira* spp. occurring in a single cluster. ODP 1051 post-PETM has two clusters very distinct from the rest containing *Paralia* spp. and *P. bella*., and *A. concentrica*, and *Pseudopodosira* spp. In the post-PETM ODP 1051 clustering *Acanthodiscus* sp. and *Hemiaulus* *curvatulus* each forms their own clusters. HCA results of both Western North Atlantic Ocean sites differ similarly between pre-PETM and post-PETM clustering patterns. In general, the post-PETM clusters (Figs. 9B and 9D) have increased by 49% and 110%, respectively, from the number of pre-PETM species with species forming very short distances and tightly clustered groups. *Paralia* spp., *P. bella*, *A. concentrica*, and *Pseudopodosira* spp. clusters occur in both the post-PETM dendrograms.

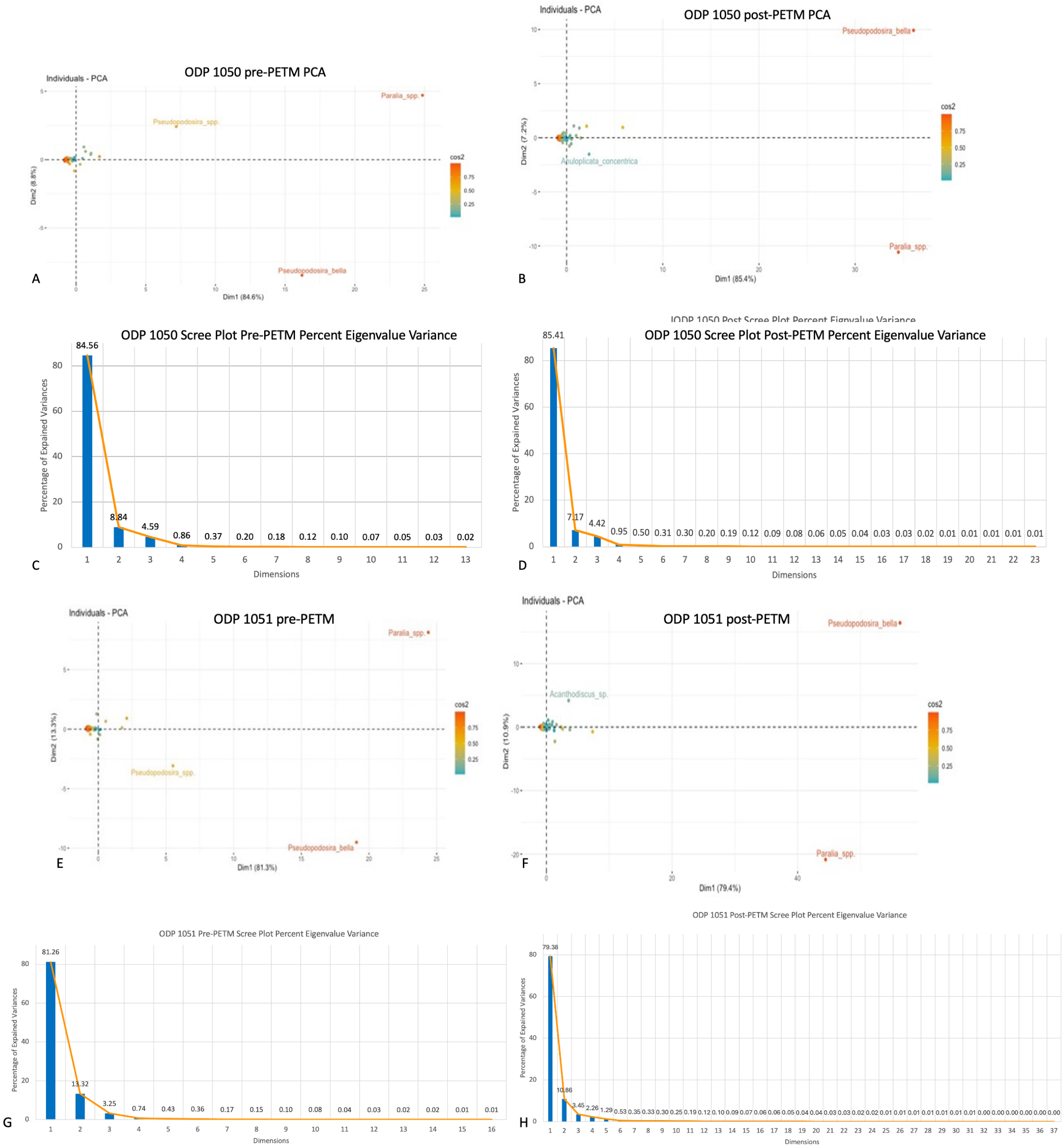


Figure 8. Principal Components plots for the Western North Atlantic Ocean exhibiting component loading for ODP 1050; A. pre-PETM and B. post-PETM; Scree Plots for illustrate percent of variance of the components (C and D). PCA component loadings for ODP 1051 pre-PETM (E) and post-PETM (F) also show similar patterns of similar loading. Screen Plots for ODP 1051 pre-PETM (G) and post-PETM (H) are similar to each other and to the results of the OPD 1050 PCA.

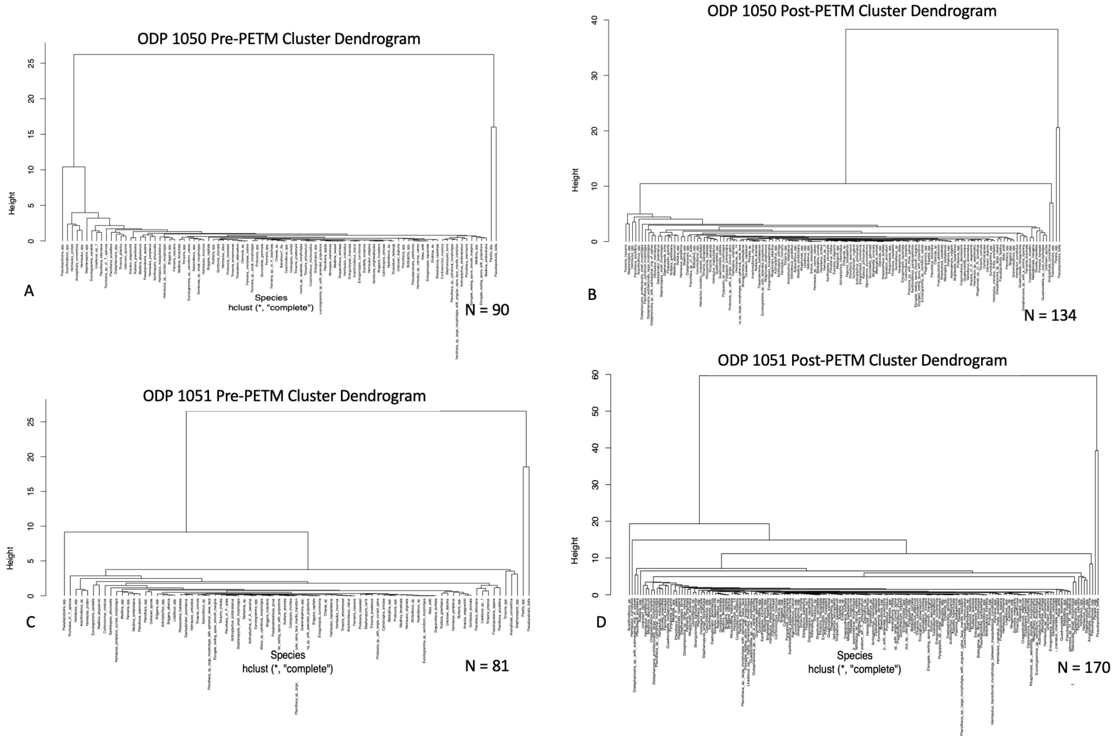


Figure 9. Hierarchical Cluster Analysis dendrograms for Western North Atlantic Ocean ODP 1050; A. pre-PETM and B. post-PETM. Western North Atlantic Ocean ODP 1051 HCA dendrograms; C. pre-PETM and D. post-PETM.

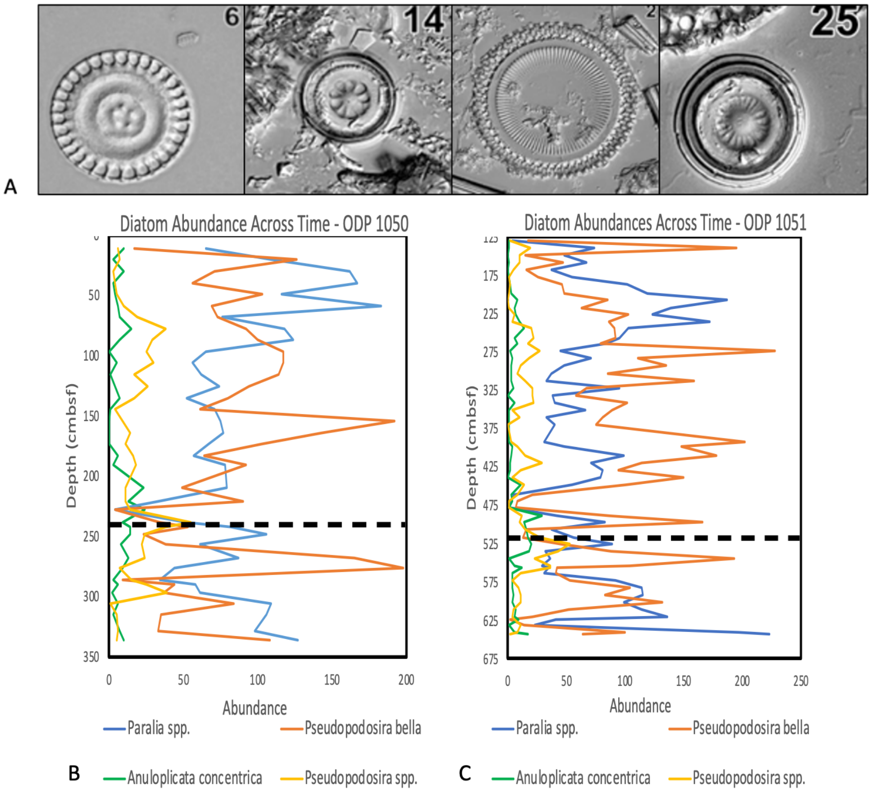


Figure 10 A. Four most abundant diatom species in both Western North Atlantic Ocean ODP 1050 and ODP 1051; *Anuloplicata concentrica* (far left), *Pseudopodosira bella* (middle left), *Paralia* sp. (middle right), and *Pseudopodosira* spp. (far right) (Witkowski et al. 2020); distributions of the four most dominant species across PETM; B. OPD 1050 and C. ODP 1051.

The Western North Atlantic Ocean 1050 and 1051 datasets have the most diatoms of all sites with 176 species and 187 species identified, respectively. Diatom species occurring only in the Western North Atlantic Ocean datasets number 206. *Paralia* spp., *Pseudopodosira bella*, *Pseudopodosira* spp., and *Anuloplicata concentrica* are the four most prominent diatoms and frequent outliers in both Western North Atlantic Ocean datasets (Fig. 10A). These most abundant diatoms vary in broadly similar fluctuations and amplitudes. They both share a pattern of steep decline at the PETM boundary, OPD 1050 (Fig. 10B) and ODP 1051 (Fig. 10C). At both sites *Paralia* spp. and *Pseudopodosira bella* abundance fluctuates strongly pre- and post-PETM, but the deepest declines are at the PETM boundary.

Eastern Indian Ocean ODP 752

The Eastern Indian Ocean ODP 752 dataset (Supplementary File S1) has the longest pre-PETM record of all site locations with sixty-one diatom species identified, but the shortest post-PETM record. Many small amplitude fluctuations characterize the pre-PETM species richness gradually increasing to the PETM boundary (Fig. 11A). At the PETM boundary species richness decreases with species deceasing 52% from 27 to 13 species. Other decreases in species richness are observed after the PETM during the early Eocene period. Species richness never returns to pre-PETM peak values. The ODP 752 species diversity reveals a trend similar to the species richness record, gradually increasing in the pre-PETM before a sharp decrease in at the PETM (Fig. 11B). The ODP 752 species diversity record also decreases significantly across the PETM. While there is some recovery post-PETM, species diversity does not return to pre-PETM levels in richness or diversity.

The Principal Components Analysis of ODP 752 species are not highly correlated pre-PETM (Fig. 11C), but post-PETM (Fig. 11D) species are tightly grouped with *Stephanopyxis* spp. sharing very little similarity with the rest of the diatoms in both pre-PETM and post-PETM. The pre-PETM PCA (Fig. 11C) returned a broadly distributed species plot while the post-PETM species are tightly clustered around the center (Fig. 11D). In both datasets *Stephanopyxis* spp. has little similarity with the remaining diatoms present. *Stephanopyxis* spp. is strongly positive and has the greatest distance in both pre-and post-PETM. In the post-PETM, *Triceratium* sp. is also distant from the main components. In the pre-PETM scree plot the first component explains 69% of the variance with 31 very small additional components (Fig. 11E). In the post-PETM scree plot the first two components explain the variance by 54% and 15%, respectively, totaling 69% with an additional ten increasingly smaller components (Fig. 11F).

The ODP 752 Hierarchical Cluster Analysis of the pre-PETM consists of 61 diatom species (Fig. 12A) with 42 species observed in post-PETM data, a decrease of 19% (Fig. 12B). The small clusters characterizing the pre-PETM linkages increase incrementally in branch height demonstrating steadily increasing dissimilarity. The post-PETM dendrogram has a range of cluster sizes and branch heights revealing a more complex dataset composed of a mix of distinct subgroups and gradual, overlapping relationships.

Forty-nine of the 61 diatom species (80%) are unique to the Eastern Indian Ocean dataset. *Stephanopyxis* spp., *Hemiaulus polycystinorum*, and *Triceratium* sp. are the three most abundant species (Fig. 13A). The pre-PETM and post-PETM fluctuation of these three species correlate closely (Fig. 13B). Their decrease at the PETM boundary is significant, but it is not the only deep decrease. There are at least five equally deep decreases before the PETM.

DISCUSSION

Species Richness and Diversity Over Time

The Central Arctic Ocean ODP 302 diatom record differs from the Western Atlantic Ocean and Eastern Indian Ocean records being much sparser in abundance, species richness, and species diversity. Poor diatom preservation in ODP 302 pre-PETM was recorded in core sections 15X, 18X, and 19X which may obscure some trends of species richness and diversity (Backman et al. 2006). The record has many fewer species than the middle and lower latitude sites with species ranging from a single species pre-PETM to a peak of 26 species post-PETM.

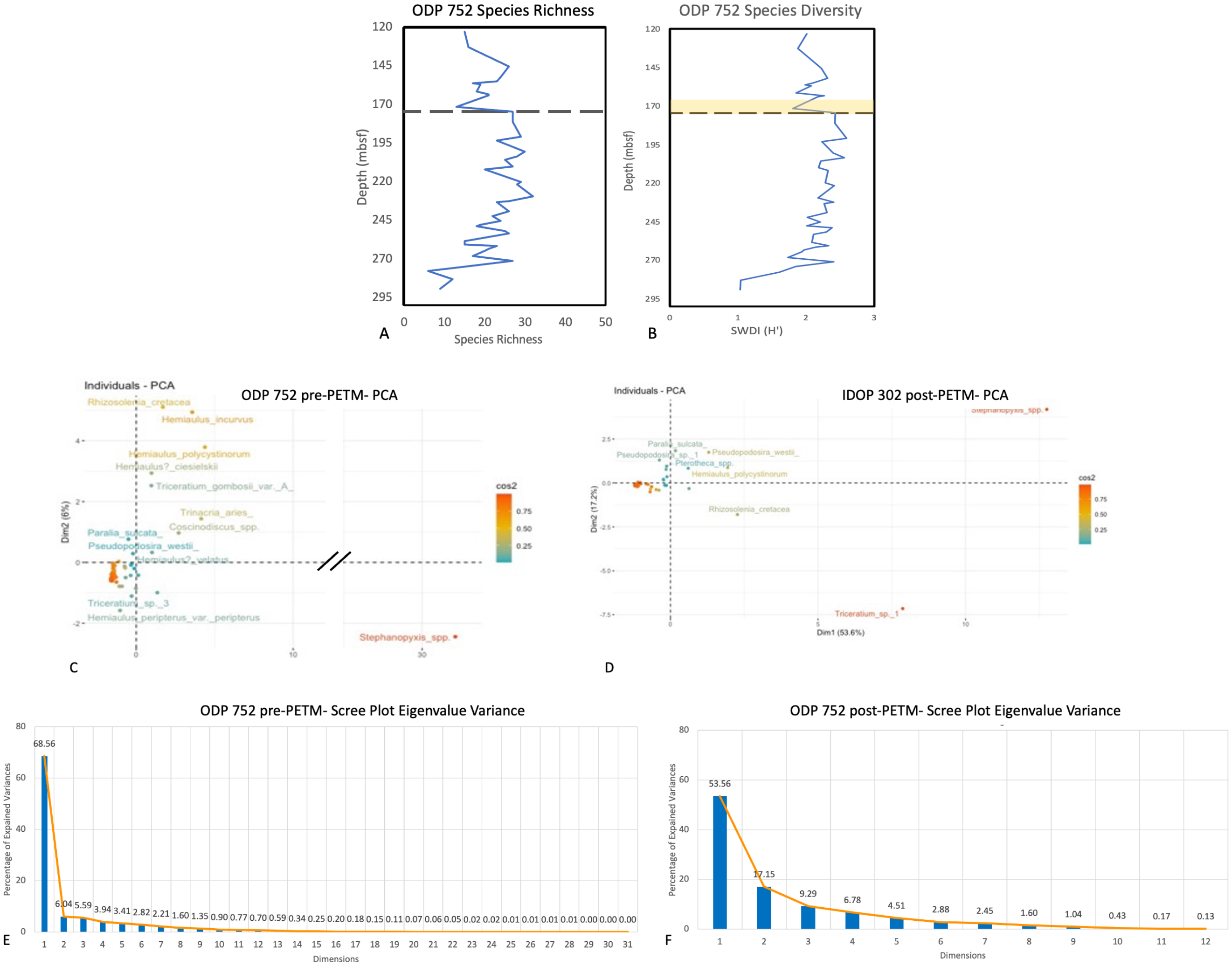


Figure 11. Eastern Indian Ocean ODP 752 distribution of A. species richness across PETM marked by dashed line; and B. distribution of species diversity across PETM, decrease in diversity at PETM highlighted in yellow. ODP 752 Principal Components Analysis C. Pre-PETM and D. Post-PETM graphs of component relationships. Scree Plots demonstrating percent variance of principal components E. pre-PETM and F. post-PETM.

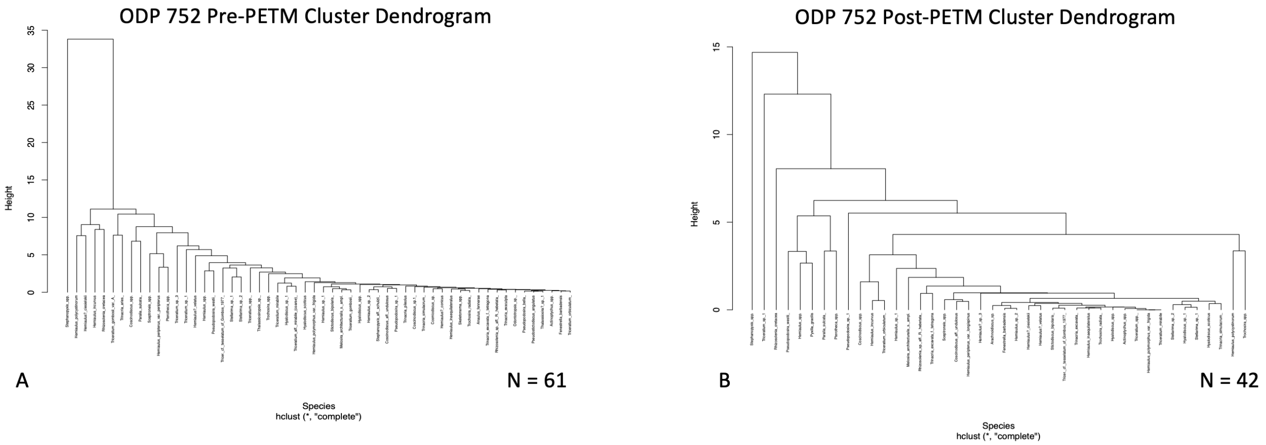


Figure 12. Hierarchical Cluster dendrograms of ODP 752; A. pre-PETM and B. post-PETM.

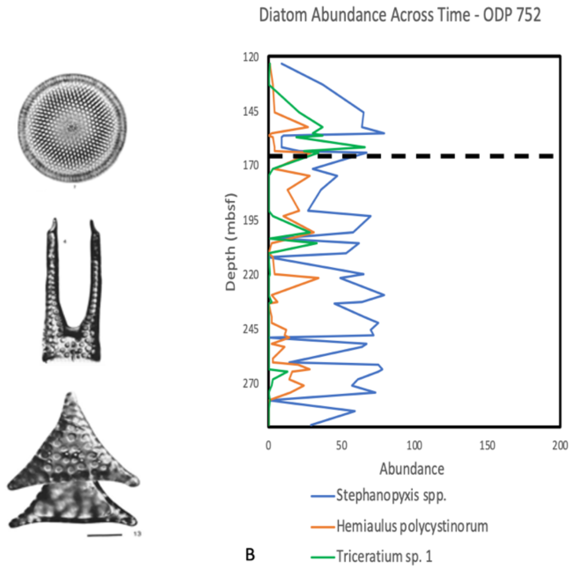


Figure 13. Eastern Indian Ocean ODP 752; A. the three most abundant diatoms: *Stephanopyxis* spp. (top), *Hemiaulus polycystinorum* (middle), and *Triceratium* sp. (Fourtanier, 1991), and B. distribution of the four most abundant diatom species across PETM with the longest pre-PETM record and limited post-PETM data.

Current research indicates polar ecosystems with cold nutrient rich waters are particularly abundant in marine diatom communities (Malviya et al. 2016). The orders of magnitude lower abundance in the Central Arctic Ocean 302 record surrounding the PETM may be explained by lack of preservation of the sediment record or dissolution of the diatom record by acidification through warming Arctic waters rather than an overall lack of primary productivity (Westacott et al. 2021). Marine diatoms are subject to dissolution which can negatively impact the preservation of diatom communities over time (Ryves et al. 2006). Dissolution can also be caused by low-salinity or low-oxygen conditions (Willard et al. 2019). Another potential cause of the lower diatom abundance and diversity for this site is its possible terrestrial geographic location at 56 million years (Backman et al. 2006) discussed further in the Paleogeography section.

The Central Arctic Ocean ODP 302 species richness and diversity datasets also differ from the other datasets by being the only records steadily increasing in across the PETM boundary. It is the only site increasing in richness and diversity at the PETM boundary in each of its four dominant species (Schrader and Fenner 1976; Witkowski et al. 2020). However, the isolated nature of the Central Arctic site on the Lomonosov Ridge may also have played a part in the observed trends. The Central Arctic Ocean location, while geographically closer to the Western North Atlantic sites than the Indian Ocean site, may have had limited or no exposure to the Atlantic Meridional Overturning Circulation (AMOC) (Fig. 10A). This is discussed further in the Paleogeography section.

The Principal Components Analysis of the Central Arctic Ocean ODP 302 data supports the community structure identified in the HCA with differences between the pre-PETM (Fig. 3E) and post-PETM (Fig. 3F) datasets. The post-PETM PCA confirms the HCA clustering with outliers, *Hemiaulus* sp., *Pseudopyxilla* spp., and *P. aculeifera*, strongly and positively distant from the rest of the dataset.

The middle latitude locations (ODP 1050 and ODP 1051) in the Western North Atlantic are in close physical proximity to each other along the same topographic promontory of Blake Nose. It is not surprising they reflect similarity in their records, but they are not identical. Both middle latitude locations record multiple sharp increases and decreases in diatom species richness and diversity throughout their records, greater decreases in species richness than observed at the other sites. At the PETM boundary both sites record sharp decreases indicating a steep decline in diatom communities. Recovery of species diversity to pre-PETM levels and other Early

Eocene hyperthermal event levels appear to be rapid in the Western North Atlantic Ocean datasets and community resilience is demonstrated by both sites recovering quickly in abundance and diversity. The PETM decrease is also not the greatest decline at both sites. The most notable decrease in species diversity in both datasets dates to the C22nH3 hyperthermal event at approximately 49.2 Ma (Kirtland-Turner and Ridgwell 2014). Another notable decrease in species diversity, appearing only in ODP 1050, dates to near the C24n.2rH1 or J event at approximately 53.260 Ma (Westerhold et al. 2018). These fluctuations suggest diatom communities in this region suffer large decreases in species richness somewhat frequently, but the magnitude of these declines vary greatly.

The records also demonstrate the communities can recover geologically quickly. When examining the individual records of the four most abundant species they follow similar patterns of decline and recovery, but do not align well with specific events after the PETM. The PCA and HCA analyses support the pre- and post-PETM pattern and scope of species richness and diversity. These analyses provide detailed species relationships and identify community groups and outliers. It is notable the most abundant species do not cluster with the majority of species and yet these isolated species are the most strongly positively or negatively aligned with structural factors. The Western North Atlantic PCAs are the most tightly clustered of all the sites.

The Eastern Indian Ocean 752 HCA differs from the other sites with greater species richness in the pre-PETM dataset (Fig. 9C). The record, while not as long post-PETM as the other sites, records its greatest decline at the PETM boundary. The PETM decrease in species richness and species diversity is greater than the decreases observed in the Western North Atlantic Ocean datasets. This location shows some recovery before the end of the record. However, there is insufficient data to examine their behavior during later Eocene warm phases seen in the Western Atlantic records. The Eastern Indian Ocean record has three moderately abundant species, but they are not the same species as the most abundant species from the Atlantic and share one (*Hemiaulus* sp.) in common with abundant Arctic species.

The Eastern Indian Ocean PCA is the most broadly distributed of all the PCA datasets (Fig. 9E) with the fewest outliers of all sites while the post-PETM species are tightly clustered around the center (Fig. 9F). The HCA is the least closely clustered. Global circulation effects are felt in the Eastern Indian Ocean as they are a part of the Atlantic Meridional Overturning Circulation (AMOC). The general similarity of pattern with records from the Western North Atlantic may reflect this association. During the PETM high latitude meltwater weakened the effect of the AMOC in the Indian Ocean and likely reduced the impact at the Eastern Indian Ocean ODP 752 location (Weldeab et al. 2022). Diatom communities in the Eastern Indian Ocean as a whole take longer to recover when compared to those from the Western North Atlantic Ocean and this may be related to the impacts of a weakened AMOC during rapid warming events such as the PETM.

Paleogeography

Species diversity and response to warming or cooling episodes may also be a factor of changing paleogeography. The difference in Arctic Ocean diatom species patterns may correlate to the location of the Lomonosov Ridge during the PETM (Fig. 14A). The Lomonosov Ridge formed around 56 Ma during the PETM (Backman et al. 2006). The site transitioned from terrestrial or shallow marine to deep marine during the PETM (Stickley et al., 2008). Perhaps the geological processes involved in the breaking away and isolation of the Lomonosov Ridge resulted in reduced preservation of diatoms within the core sections from this period, or for greater pre-PETM species diversity. The emerging Arctic Ocean was comparatively isolated from other oceans during the Early Eocene period. It is only with the tectonic opening of the Fram Strait during the early Miocene the isolated Arctic Ocean was connected to the Atlantic Ocean (Hossain et al. 2021). The Central Arctic Ocean ODP 302 is the only drilling location which may have been almost entirely landlocked. One explanation of this difference, the Central Arctic Ocean may have experienced increased nutrient availability due to terrestrial runoff during the PETM and other hyperthermal events (Willard et al. 2019).

Figures 14B and 14C shows the paleogeography of the Western North Atlantic Ocean and Eastern Indian Ocean drilling locations (Arreguín-Rodríguez et al. 2018). The Eastern Indian Ocean ODP 752 location was much further south than today. Comparing these paleomaps, the Western North Atlantic Ocean drilling location exhibits the

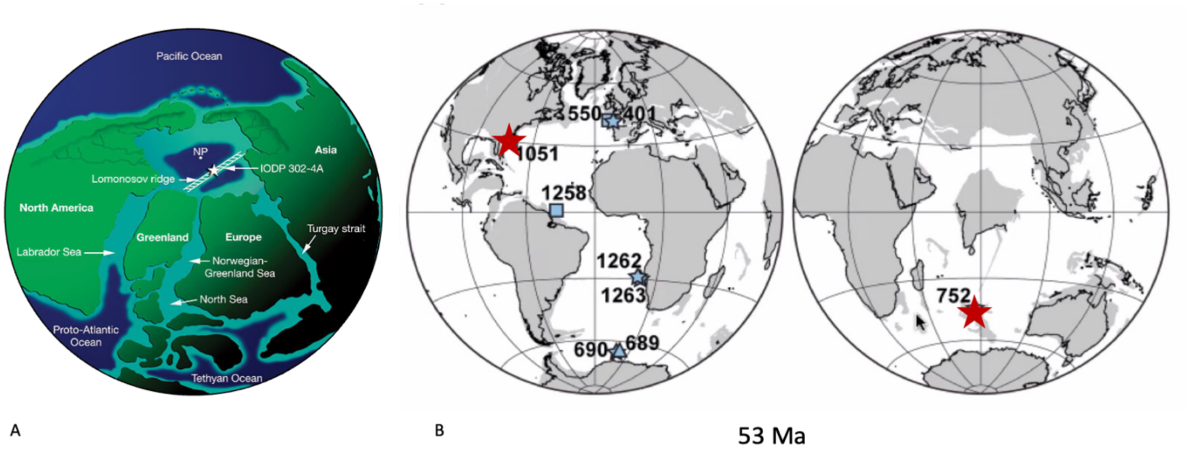


Figure 14. A: Location of the Lomonosov Ridge and the Central Arctic Ocean IODP location during the PETM (Backman et al., 2006), B: Paleogeography of the core locations for Western North Atlantic Ocean ODP 1050 and ODP 1051 and Eastern Indian Ocean ODP 752 (Arreguín-Rodríguez et al. 2018).

least change in geography to the present day, while the Eastern Indian Ocean drilling location has migrated north over the past 53 million years with the subcontinent of India (Verma and Singh 2024). This tectonic journey may also have contributed to the more limited diatom preservation.

Global Implications

Both the Western North Atlantic and Eastern Indian Ocean datasets show a decrease in diatom species richness and diversity across the PETM. The Western North Atlantic, with a longer post-PETM archive, records similar responses to other Early Eocene hyperthermal events. The PETM decrease is not observed in the Central Arctic Ocean. A study suggests the PETM was accompanied by intensification of the Atlantic Meridional Overturning Circulation (AMOC) (Batenburg et al. 2018). Perhaps this change in ocean and nutrient circulation led to swifter and more pronounced declines in the Western North Atlantic Ocean with its proximity to the AMOC. Multiple other hyperthermal events record further decreases in diatom species richness, and to a greater degree in species diversity than at the PETM. The rapid recovery of species richness after the PETM and following hyperthermal events suggests the diatom communities in the western North Atlantic Ocean were also resilient or able to evolve recovery adaptations to these rapid warming periods. It may also reflect the long-term geographic stability of this location.

The more pronounced decrease in diatom species richness and diversity in the Eastern Indian Ocean dataset may in part be related to differences in nutrient circulation in the Eastern Indian Ocean when compared to the Western North Atlantic Ocean and distance from the AMOC. While the Western North Atlantic Ocean diatom communities showed a quick recovery in diatom species richness and diversity after the PETM and subsequent Early Eocene hyperthermals, a full recovery was not observed in the Eastern Indian Ocean dataset possibly due to the limited record available.

Implications for Future Warming

The data suggests current global climate warming will negatively affect marine diatom species richness and diversity and ultimately the global carbon cycle. The PETM diatom communities most impacted were the Western North Atlantic sites. Of the locations studied, the Western North Atlantic was the most geologically stable during the PETM and with the longest preserved records. The Arctic Ocean location was the most isolated marine location, and the Indian Ocean location was trailing the tectonic migration of the Indian subcontinent. These two locations are today more geographically stable. Current research shows global oceans are warming four times faster than in 1990 with the Arctic Ocean warming the fastest (Rantanen et al. 2022). This dataset shows the middle latitude diatom communities changed the most during the PETM. The most abundant species were also negatively affected by rapid warming.

The significantly different paleogeography of the Central Arctic Ocean during the PETM compared to the open Arctic conditions of today resulted in a different diatom record. Better high latitude PETM records would improve understanding of how high latitude diatom communities will react to the rapid warming now occurring in the Arctic Ocean and into the future. Better representation of southern high latitude locations is also necessary. If future middle latitude marine diatom communities suffer as the data suggests, warming oceans are likely to decrease diatom species richness and diversity across the global oceans and have the potential to lead to a strong positive feedback loop of community collapse with further warming.

CONCLUSIONS

The results of the diatom species analysis at the community level provide insights into community responses that individual diatom records may not. Globally synchronous community declines are more robust evidence of global changes, and community level declines are indicators of significant environmental change. The data suggest the rapid warming characteristic of the PETM had a negative impact on marine diatom species richness and diversity at middle and southern latitude locations. Other early Eocene hyperthermal events also had negative impacts on diatom species richness and diversity in the Western North Atlantic Ocean. The dominant species abundance data are a more difficult to interpret as their records are more chaotic which supports the application of community scale analyses. Additional assessment of rare species dominance and sample size sensitivity could further elucidate these records. The Central Arctic Ocean displayed an increase in diatom species richness and diversity across the PETM, with most of the dominant species continuing to increase in abundance after the PETM. Poor diatom preservation in the Central Arctic Ocean around the PETM may obscured trends in the high latitude location. It is possible the isolated nature of the Central Arctic Ocean during this period may affect the results due to lack of connection with the AMOC or increased terrestrial nutrient availability during the PETM and other Early Eocene hyperthermals. The Western North Atlantic Ocean displayed the most geographic stability of all the core locations during and since the PETM, making it is a significant analogue of future warming for temperate locations. However, future studies should gather data from high latitude locations to provide a better model of how the rapidly warming in polar climate effects diatom communities and the transfer of carbon to the ocean bottom. This area is currently experiencing significant and exponentially faster warming.

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AUTHOR CONTRIBUTIONS

Davies contributed to conception and methodology, manuscript preparation, analytical review, and editing. Hentzen, contributed to conception, statistical analyses and graphics as part of a master's thesis.

Statement of Competing Interests

The authors have no competing interests.

List of Abbreviations

cmbsf- combined meters below sea floor

mcd- meters composite depth

HCA- Hierarchical Cluster analysis

PCA- Principal Components analysis

PETM- Pliocene-Eocene Thermal Maximum

SWDI- Shannon-Weiner Diversity Index

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