Sinking Marine Particles: The Eukaryotic Groups Shaping Compositional Variability and POC Flux Dynamics

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ABSTRACT

Sinking marine particles, including detritus, fecal matter, and aggregates, represent a critical pathway for ocean carbon export and sequestration. However, the development of quantitative export models has been hindered due to an incomplete understanding of the biological mechanisms expediting or deterring sinking particles and their relative contributions to carbon export. One approach to advancing this understanding is to examine the relationship between particle composition and carbon export. Here, we use data collected during the EXport Processes in the Ocean from RemoTe Sensing (EXPORTS) field campaigns in the North Pacific and North Atlantic Oceans to analyze genetic material from bulk and individual sinking particles and assess heterotrophic eukaryotic community composition. Hierarchical clustering analysis reveals distinct compositional groups among individual particles, driven primarily by taxa such as Rhizaria and Stramenopiles in both oceanic basins despite differing environmental conditions. The functional and morphological roles of these taxa appear to influence carbon export processes significantly. Additionally, we observed that the composition of bulk samples differed from that of individual particles, suggesting that rapidly-sinking larger particles (>300 μm) are compositionally distinct from the bulk sinking organic carbon.

INTRODUCTION

The oceanic carbon pump removes a net 2-2.5 PgC of carbon from the atmosphere every year (Iversen 2023). In particular, the transport of particulate organic carbon (POC) via biological, physical, and chemical processes is collectively referred to as the biological carbon pump (BCP; Volk & Hoffert, 1985). A key pathway for carbon export within the BCP is the gravitational settling of marine particles. These particles are typically small aggregates consisting of organic material such as dead or decaying animals, phytoplankton, suspended sediments, fecal pellets, or other excrement and detritus. Just 5-25% of net primary production sinks below the euphotic zone and only 1% reaches the seafloor where they may be sequestered for thousands of years (Iversen 2023). As particles sink, several oceanic processes may intervene, including aggregation, consumption, and bacterial degradation. These processes may reshape aggregates and speed up, slow down, or prevent the transfer of these particles and their carbon to sequestration depths.

However, it has been difficult to quantify the individual contributions of different organic carbon sources to the BCP. Seasonality, organismal population dynamics, and depth-dependent interactions are just some of the factors that contribute simultaneously to informing BCP processes. Recent work has linked taxonomic community composition to POC flux by combining sequencing of bulk sediment, sequencing of individual sinking particles, flux measurements, and observations of particle type by microscopy (Durkin et al., 2022). Genetic material may belong to consumed, decaying, or living organisms and is a key piece of information for understanding the biological processes driving particle formation and export. These methods have been integrated to assess bacterial populations, finding successional changes in microbial communities on sinking particles (Stephens et al., 2024). Likewise, heterotrophic eukaryotic communities present broad taxa of interest due to their multifarious interactions with sinking particles. Unlike photosynthetic eukaryotic taxa, heterotrophs may originate at depths below the euphotic zone. In addition to remnants of consumed or fragmented heterotrophs, heterotrophic genetic material may remain in sinking particles from temporary or prolonged interactions with live heterotrophs at various depths as particles sink through the water column.

Here, observational and sequencing data were combined to evaluate the community compositional variability of individual and bulk particles collected as part of the EXport Processes in the Ocean from RemoTe Sensing (EXPORTS) field campaigns in the North Pacific

(Siegel et al., 2021) and North Atlantic Oceans (Johnson et al, 2023). In this study, we focused on observations of heterotrophic eukaryotic community composition. Hierarchical clustering was performed to determine if particles could be categorized into distinct compositional groups. The taxa driving cluster separation were investigated across collection types, depth, and time scales and related to mechanisms and quantity of carbon export. Comparisons of bulk particle composition vs. individual particle composition revealed that collection methods also captured different aspects of diversity in the carbon export process.

2. METHODS AND MATERIALS

2.1. EXPORTS FIELD CAMPAIGN OVERVIEW

Sequencing samples for this study were collected during the EXport Processes in the Ocean from RemoTe Sensing (EXPORTS) field campaigns at Ocean Station Papa in the North Pacific (Siegel et al., 2021) and at the Porcupine Abyssal Plain Sustained Observatory (PAP-SO) in the North Atlantic (Johnson et al, 2023). Samples at the North Pacific and North Atlantic sites were collected in three 2-6 day "epochs" (deployments) over consecutive weeks in August-September 2018 and May 2021, respectively. Collections included whole seawater samples and sediment traps. Neutrally-buoyant (NBST) and surface-tethered trap (STT) platforms were deployed in conjunction to collect bulk sinking particles and individual particles from polyacrylamide gel layers (Estapa et al., 2021; Durkin et al., 2021). STT platforms consistently collected sinking particles at five depths over all three deployments in both basins. Depths ranged from approximately 75-500 meters, where the shallowest trap depth was below the euphotic zone at 1% of the surface light level.

2.2. POC FLUX MEASUREMENTS

Out of four total tubes on both the STT and NBST platforms, two were dedicated to measuring particulate organic carbon (POC) flux. Tube contents and the bulk POC estimation procedure, conducted via combustion analysis after removing active swimmers and filtration, are described in detail in Estapa et al. (2021).

2.3. BULK PARTICLE COLLECTION

To collect bulk sediment for sequencing analysis, one of the four tubes on the sediment trap platform was filled with either RNAlater or 0.1% formalin (Estapa et al., 2021). In total, 52

bulk samples were collected across both basins, 17 in the North Atlantic and 35 in the North Pacific across both STT and NBST platforms.

To ensure consistent in-basin comparison, the bulk trap analysis in this paper uses data only from the STT platform and the primary preservation method used for that basin's bulk sampling: formalin in the North Atlantic (n = 13) and RNAlater in the North Pacific (n = 14).

2.4. INDIVIDUAL PARTICLE COLLECTION

Individual particles were captured on a polyacrylamide gel layer (Durkin et al., 2021). Particles were observed under a dissecting microscope at multiple magnifications. Based on visual analysis, particles were categorized as one of the following types: large loose pellets, dense detritus, aggregates, short pellets, long fecal pellets, and salp fecal pellets (Amaral & Durkin, *in prep*).

2.5. DNA EXTRACTION AND 18S rRNA GENE AMPLIFICATION

Total DNA was extracted from bulk particles as described in Stephens et al. (2024). Nucleic acids were extracted from individual particles in the gel polyacrylamide layer as described by Durkin et al. (2022). Primers for the eukaryotic 18S ribosomal RNA (rRNA) region were used to amplify eukaryotic sequences. All bulk and individual particle DNA can be found at: https://seabass.gsfc.nasa.gov/archive/MBARI/durkin/EXPORTS.

2.6. TAXONOMIC IDENTIFICATION AND FILTERING

As described in Durkin et al. (2022), amplified 18S rRNA reads were processed through the DADA2 denoising pipeline (Callahan et al., 2016) to produce amplicon sequence variants (ASVs) in the QIIME2 (Bolyen et al., 2019) workflow. ASVs were compared against the Protist Ribosomal Reference database (PR^2 v. 5.0.0) for taxonomic classification (Guillou et al. 2012). Occasionally, primers used in 18S rRNA amplification amplify non-eukaryotic sequences, such as prokaryotic bacterial sequences. PR^2 provides ASV labeling for a limited set of such sequences (Guillou et al. 2012). To filter out the majority of possible non-eukaryotic reads, we filtered out any ASVs within the domain "Bacteria," any ASV with an unknown domain, and those with an ASV confidence level of less than 70%.

Heterotrophic sequences were filtered by taxonomic class according to the list under photosythentic_taxa_v5_0_0.csv at https://github.com/sashajane19/EXPORTS_particle_DNA. Dinoflagellates represent the category of most trophic uncertainty, as approximately half of

dinoflagellate taxa are considered heterotrophic and half are considered phototrophic (Gabrielsen et al., 2011). Among these, an unknown percent of dinoflagellates can leverage both trophic modes, considered mixotrophs (Stoecker 1999). Due to the uncertainty in dinoflagellate trophic mode, in our analyses focused entirely on heterotrophic eukaryotic sequences, all dinoflagellates were categorized as heterotrophs. In this dataset, dinoflagellates were a significant contributor to ASV diversity and total raw reads. Thus, in our comparisons of autotrophic vs. heterotrophic composition, dinoflagellates were categorized as their own group. Despite these measures, a portion of the ASVs categorized as heterotrophic here may likely belong to some autotrophic or mixotrophic taxa.

2.7. DATA PROCESSING

Raw ASV reads were normalized in one of two ways. In-sample normalization was used to assess relative abundance. Raw reads belonging to an individual particle sample or a bulk trap sample were divided by the total read count in that sample.

Otherwise, following Gloor et al. (2017), we applied a closure to center and normalize the data, followed by a centered log-ratio transformation to particular subsets of the data (Atlantic individual reads, Pacific individual reads, Atlantic bulk reads, Pacific bulk reads) using scikit-bio composition library in Python. Centered log-ratio transformation (clr-transformation) is recommended for compositional data due to the constraint that compositional data components must sum to a constant value, where the increase in the proportion of one component in the data must lead to a decrease in another component. Therefore, clr-transformations, which represent log ratios relative to the geometric mean, reflect the relative differences between components.

2.8. COMPOSITIONAL ANALYSES

To visualize taxonomic composition via principal components analysis (PCA), we calculated the Aitchison distance, the Euclidean distance between clr–transformed samples (Gloor et al., 2017). PCA was performed using the sklearn.decomposition library and the first two components were plotted on a scatterplot. Similarly, PERMANOVAs were used to evaluate the dissimilarity between samples using Aitchison distances calculated between all groups collected under similar conditions (e.g., same depth, same deployment, same particle type), followed by pairwise PERMANOVAs with a Bonferroni p-value adjustment.

To compare average taxonomic composition across samples collected in either the North Atlantic or North Pacific, the abundances of major taxonomic groups (phototrophs, dinoflagellates, and heterotrophs) were averaged across all samples. Further, depth profiles tracked the difference in trophic mode with depth by averaging the proportions of the three groups across that collection depth. Similarly, depth profiles of specific taxonomic groups used each subgroups' relative abundance in relation to only that group's reads and considered the average proportions of each subgroup by depth.

2.9. CLUSTERING

Ward clustering (Ward 1963) was performed on individual particles and bulk particles by basin using the composition of each sample at the ASV-level. Ward clustering creates clusters on the basis of minimizing within-cluster variation. The number of clusters was determined by plotting a dendrogram from the clr-transformed data using SciPy's cluster library and identifying the cut point at the branch with the largest vertical distance. To compare compositions within clusters, relative abundances of taxa within clusters were plotted on stacked bar graphs.

Groups driving the variability between clusters were assessed by evaluating the taxonomic classes that had the highest variance between clusters. Raw ASV-associated reads were grouped by class and central-log transformed. Samples were then labeled by their associated cluster, and the mean variance by class for each taxonomic group was calculated using the numpy.var function, where variance is defined as:

$$\frac{\Sigma_i \left| x_i - \bar{x} \right|^2}{N} \quad ,$$

where N is the number of samples, $\bar{x}$ is the sample mean, and x_i is each cluster's relative abundance of the taxonomic group of interest.

RESULTS

3.1. ABUNDANCE BY TROPHIC MODE

Across both the North Atlantic and North Pacific, heterotrophic and dinoflagellates were relatively more abundant than phototrophs. The proportion of reads associated with phototrophic sequences, averaged across all samples by collection method, was between 5-80% lower than the

average proportion of heterotrophic sequences (Figure 1). Dinoflagellates, which have a highly variable trophic mode, made up a larger proportion of relative reads in the Pacific regardless of sampling method.

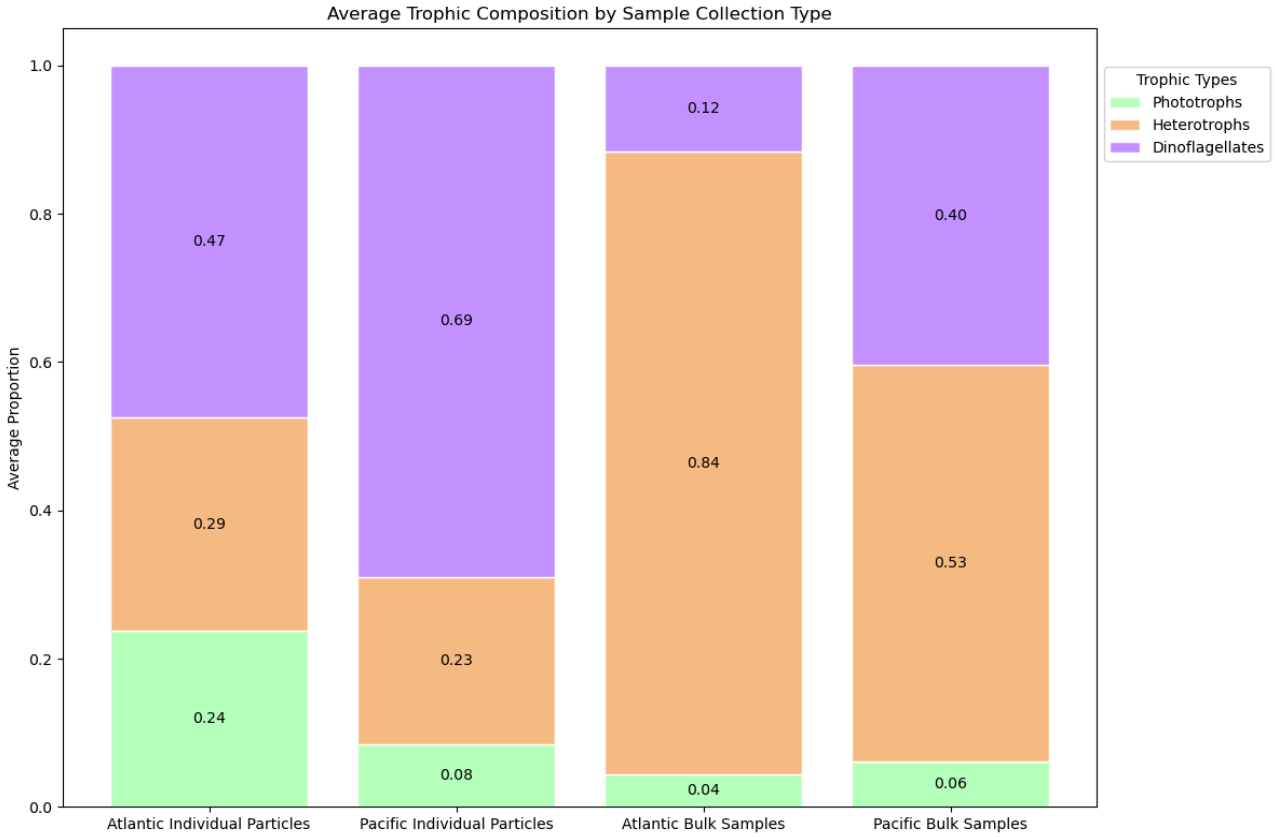

Figure 1. Comparison of trophic make-up in all samples by collection type. Each bar represents a specific basin (Atlantic vs.Pacific) and collection type (individual particles vs. bulk particles). In each category, the average proportion of phototrophs, heterotrophs, and dinoflagellates is shown. Dinoflagellates were a distinct trophic category in this analysis only.

3.2. ENVIRONMENTAL VARIATION

Analysis of taxonomic composition revealed significant variations across both the North Atlantic and North Pacific Oceans in relation to depth, sample collection time, and particle type ($p = 0.001$ in all cases). Pairwise PERMANOVAs indicated that data subsetting by sample size most consistently accounted for significant variance in composition ($p = 0.003$). In the North Atlantic, depth and particle type were good indicators of variability in particle sample composition, however, in the North Pacific, significant differences were predominantly observed only with specific particle types, such as salp fecal pellets and long fecal pellets.

3.3. CLUSTERING BY TAXONOMIC COMPOSITION

3.3.1 INDIVIDUAL PARTICLE CLUSTERING

Individual particle samples clustered into distinct groups across a small number of clusters. Three clusters were identified in the North Atlantic and four clusters in the North Pacific (Figure 2).

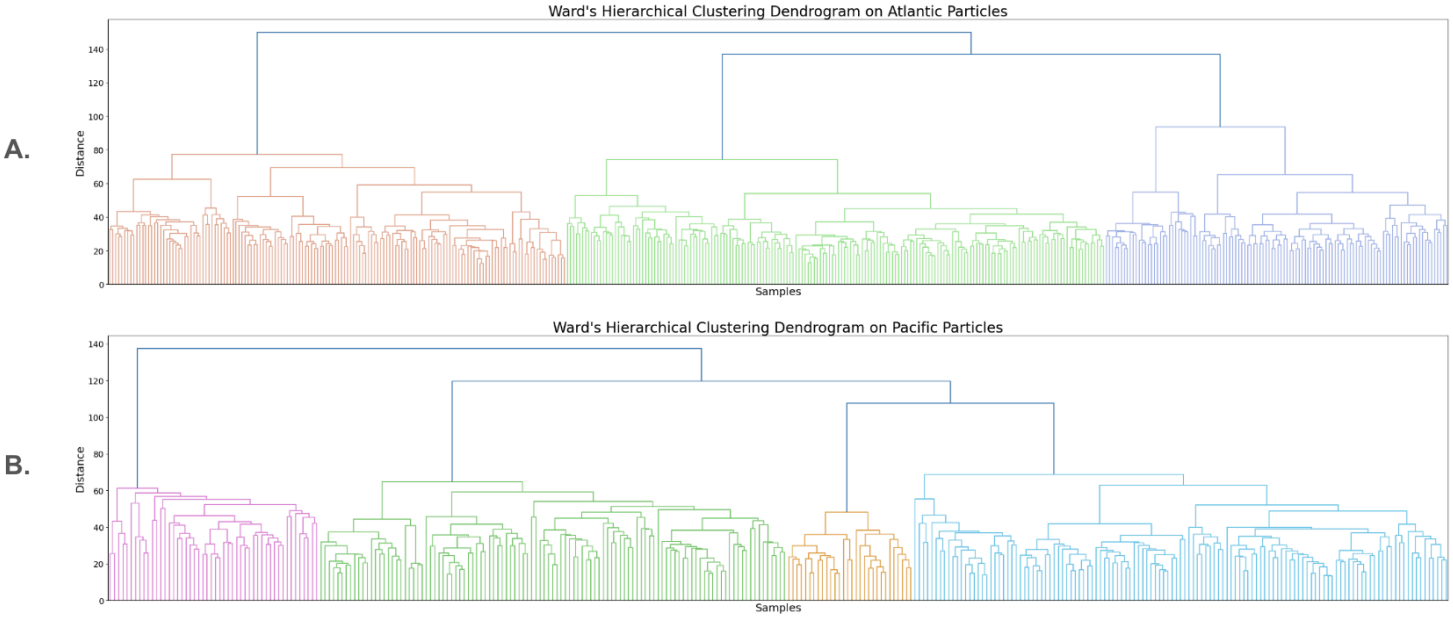

Figure 2. Hierarchical cluster analysis of individual particle samples in the North Atlantic (Fig. 2A) and in the North Pacific (Fig. 2B). Leaf nodes represent individual samples (n = 445, n = 318). Each cluster is differentiated by color. Three clusters separate from the North Atlantic samples (Fig. 2A) and four from the North Pacific (Fig. 2B).

Coloring the principal component analysis (PCA) plot for the North Atlantic and North Pacific by the corresponding cluster for each sample revealed distinct groups of samples (Figure 3). Clusters generally did not separate completely based on any single environmental variable (Figure 4). However, the North Atlantic compositional clusters appeared to most closely separate with time in the PCA, while North Pacific compositional clusters separated more clearly with depth (Figure 4). In addition, salps were observed in large numbers in Epoch 1 of the North Pacific expedition (Steinberg et al., 2023). Salp fecal pellets differed considerably from other individual particle samples. These samples made up the majority (76%) of cluster 3 in the North Pacific and were found minimally in other clusters (Figure 4).

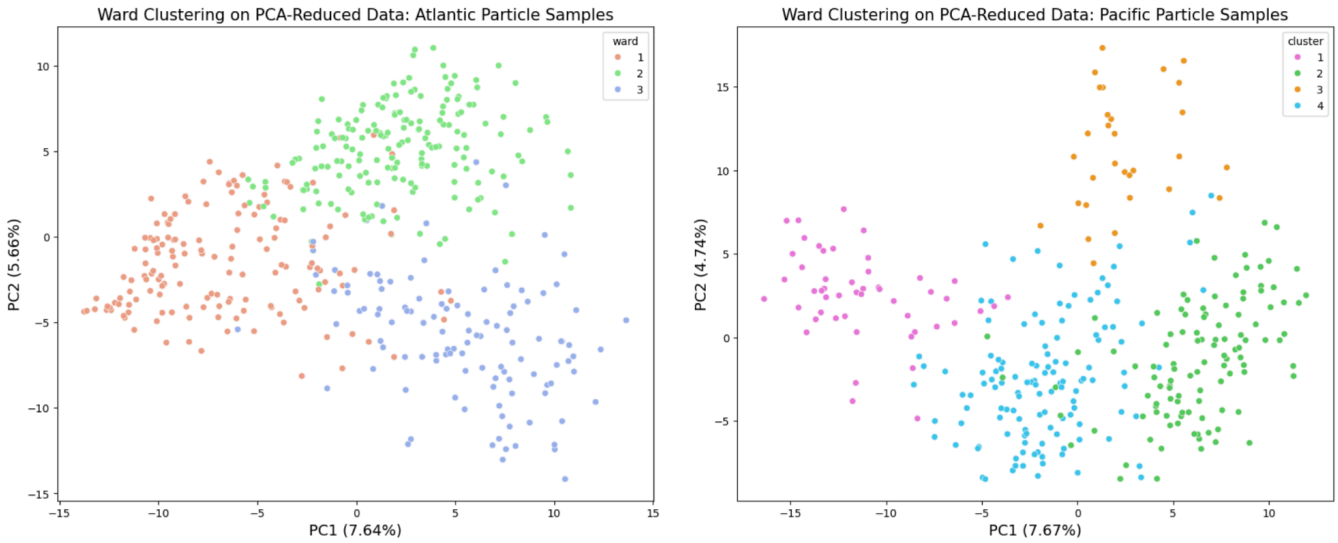

Figure 3. Principal component analysis (PCA) plots for each basin, with each dot representing one sample. Samples are colored by their associated ward cluster label (Figure 2).

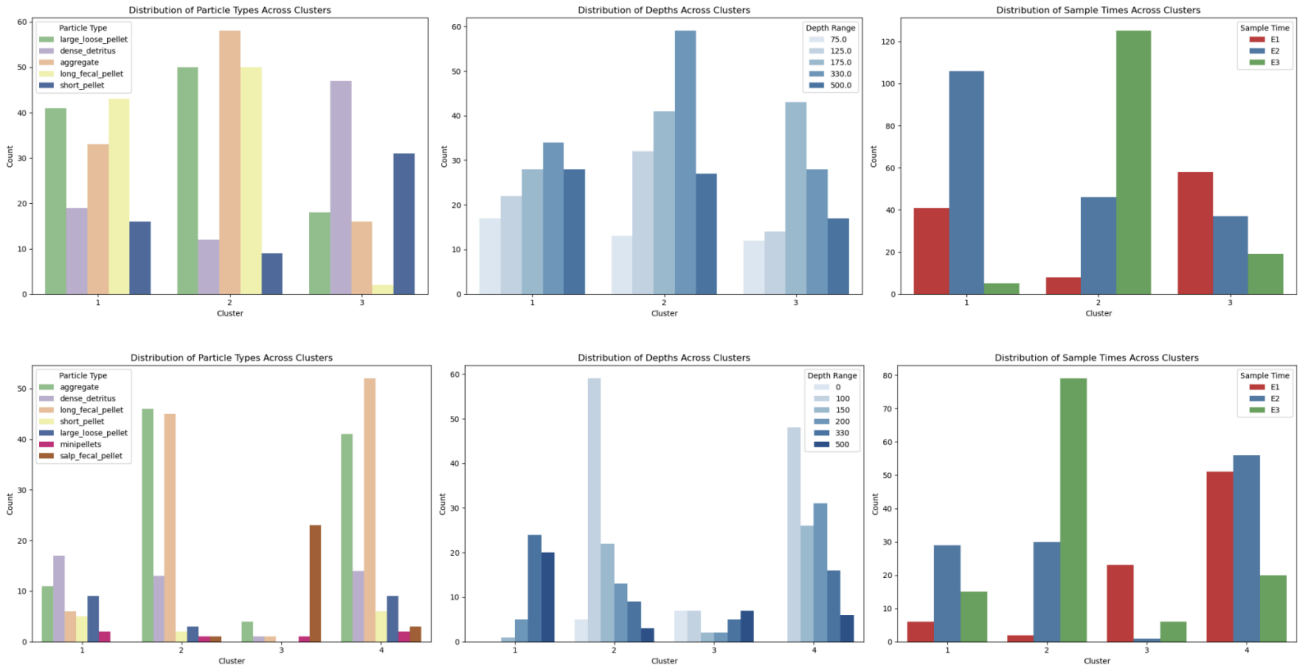

Figure 4. Number of samples per cluster by sample time (epoch), approximate depth, and particle type from visual analysis in (A) the North Atlantic and (B) the North Pacific.

3.3.2 BULK PARTICLE CLUSTERING

No clear clusters emerged from the bulk particle samples for either the North Atlantic or North Pacific (Figure 5). The structure of the dendrograms for these samples suggests that samples were highly distinct from one another and no clear groupings were observed. Each sample constituted its own cluster, indicating high levels of dissimilarity in bulk sample

composition. The greatest variation, as identified by the longest vertical node length, exists between samples at the individual level. Therefore, samples cannot be grouped into clusters of size greater than one.

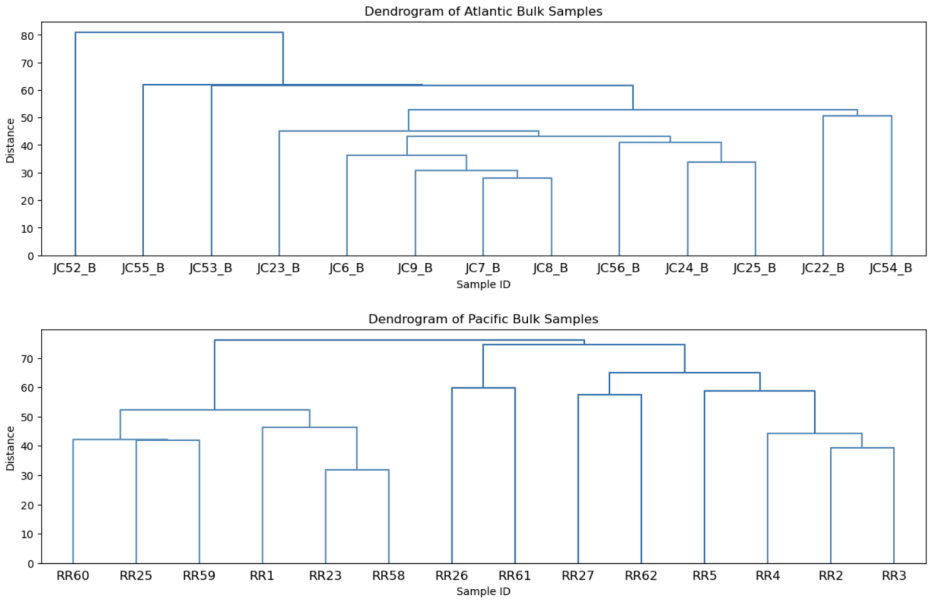

Figure 5. Dendrogram of Atlantic (n=13) and Pacific (n=14) bulk trap samples. Each leaf represents one sample.

3.4 DRIVERS OF INTER-CLUSTER VARIATION IN INDIVIDUAL PARTICLES

Similar taxonomic groups drove variance between clusters in the North Atlantic and North Pacific despite differences in environmental conditions and surface ocean primary productivity. Figure 6 highlights the top ten taxonomic classes that varied most strongly between clusters. Although broad groups like Alveolata generally constituted the largest percentage of relative reads per particle (Supplementary Figure 1), high variance groups were evaluated because they were represented highly in some clusters and less frequently in others.

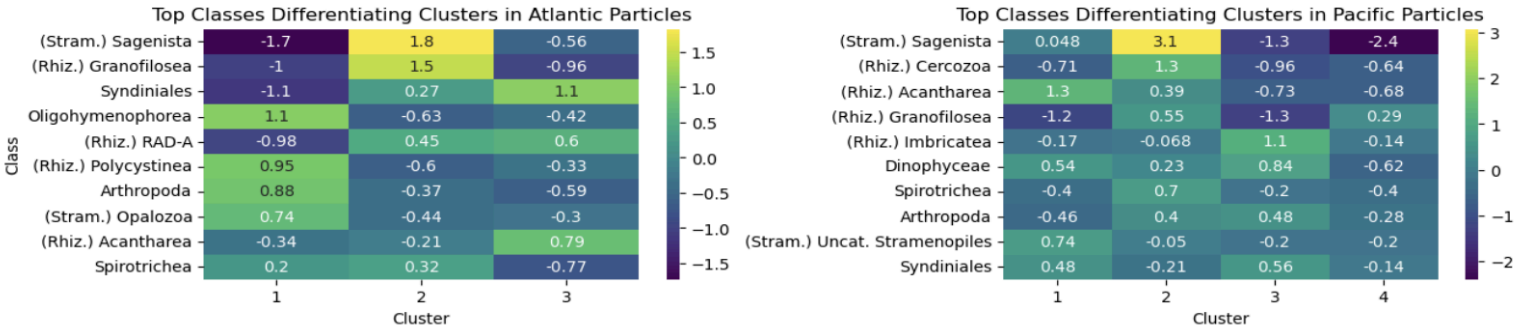

Figure 6. Heatmap of top ten classes with the greatest variance between clusters, ranked from most variable (top) to least variable (bottom). Each box contains the center log-ratio transformed value of a given taxonomic class within a given cluster. Classes belonging to Rhizarians and Stramenopiles are noted as (Rhiz.) and (Stram.).

In both basins, the class Sagenista, a Stramenopile subgroup, had the highest variance. For instance, in the North Pacific, cluster 2—comprising primarily particles from epoch 3 (Figure 4)—showed elevated levels of Sagenista. In contrast, cluster 4, which mainly consisted of particles from epochs 1 and 2 (Figure 4), displayed Sagenista levels significantly below the geometric mean (Figure 6). Notably, within the Sagenista class, 93.4% of raw reads were attributed to the genus Aplanochytrium, a spore-forming heterotroph within the order Labyrinthulomycetes.

Multiple Rhizaria classes also exhibited considerable variation across clusters. Despite functional and morphological differences, cercozoans (Granofilosea, Imbricatea, general cercozoans) and radiolarians (Acantharea, RAD-A, Polycystinea) appeared among the top ten variable groups (Fig. 6). Other, less repeated groups included dinoflagellates, arthropods, and ciliophora.

3.5. DEPTH VARIABILITY IN RHIZARIA AND STRAMENOPILES

3.5.1 RHIZARIA

When comparing the relative sequence abundance of Rhizaria subgroups averaged across depth strata, acantharea consistently accounted for at least 35% of the sample's relative read abundance, regardless of whether bulk or individual trap samples were analyzed (Figure 7). Although most acanthareans were concentrated in surface waters, their relative distribution among other Rhizaria groups exhibited stability across different depths or even showed an increase in the case of individual particles sampled in the North Pacific.

Phaeodaria, large cercozoans ranging in size from hundreds of micrometers to a few millimeters (Nakamura & Suzuki, 2015), were more prominent in North Pacific samples than in North Atlantic samples. In contrast, Spumellaria, a class of polycystines, were more prominent in the Atlantic. Other taxonomic groups that are less well-defined in the PR^2 database, such as RAD-A, constituted a significant portion of the relative reads in the Atlantic but could not be distinctly categorized (Figure 7).

3.5.2 STRAMENOPILES

Similar to the dominance of acanthareans among Rhizaria, Labyrinthulomycetes were the predominant group within the Stramenopiles (Figure 7). Both Labyrinthulomycetes and uncultured marine Stramenopiles (MAST) belong to the Sagenista class, which was the group

with the highest variance in the clusters (Figure 6). Labyrinthulomycetes are distinguished by their spore network-filament-forming ability. The vast majority (97.7%) of Labyrinthulomycetes reads were attributed to the genus Aplanochytrium. As illustrated in Supplementary Figure 2, when analyzed by sample time, composition may also vary in relation to POC flux and changing environmental conditions, with the highest POC flux in the North Atlantic correlating with the greatest abundance of Labyrinthulomycetes.

Though MAST are a largely understudied and loosely related group of species, they constitute a substantial portion of the Stramenopile abundance in the North Pacific (Figure 7).

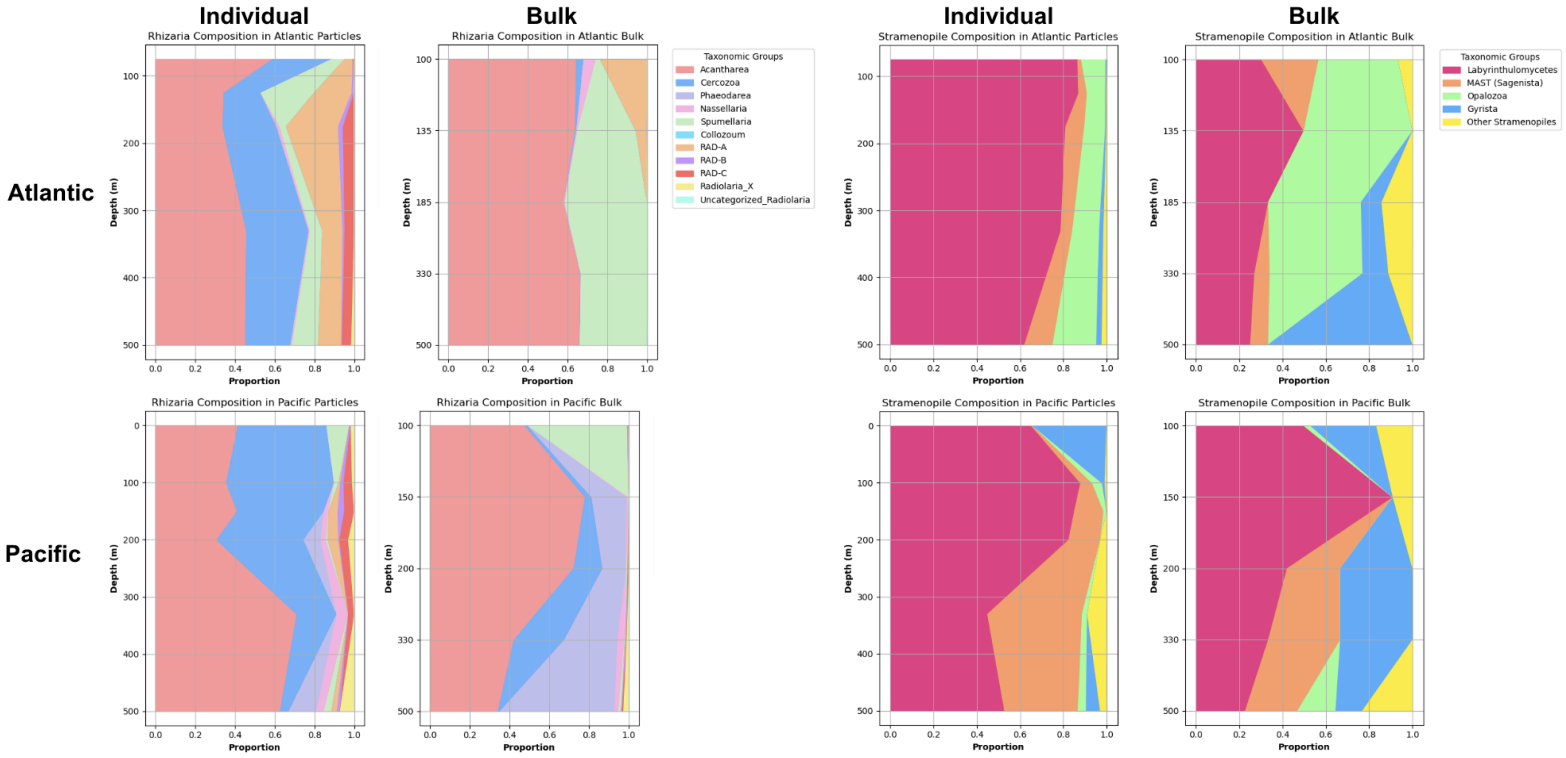

Figure 7. Depth profiles of Rhizaria composition (left) and Stramenopile composition (right) in both the Atlantic and Pacific basins. Relative abundances of subgroups in samples were averaged across sample depth (m).

3.6. BULK AND INDIVIDUAL COLLECTION IRREGULARITIES

At both collection sites, taxonomic composition differed notably between bulk particles vs. individual particles. When looking at all heterotrophic taxa, Atlantic bulk samples were dominated by Rhizaria reads, which were considerably less abundant in individual particle samples (Supplementary Figure 1). Conversely, Stramenopiles were significantly represented on

specific clusters of individual particles, yet were scarcely detected in the bulk samples (Supplementary Figure 1).

Comparing depth profiles reveals that individual and bulk samples highlight taxa in different proportions. For example, non-Phaeodaria cercozoans were significantly more prevalent in individual particle samples compared to bulk samples. In the Atlantic, Spumellaria constituted a much larger proportion of bulk particle composition than individual particle composition. Interestingly, while Labyrinthulomycetes were the dominant taxa in North Atlantic individual particles, Opalozoa, typically found in the gut of vertebrates, were observed in comparable or greater abundance with depth in bulk samples (Figure 7).

DISCUSSION

Sinking particles carried substantial amounts of heterotrophic genetic material to depth in this dataset. Individual particles could be successfully distinguished and clustered, into clusters that were driven by shared taxonomic groups in the North Atlantic and North Pacific, including Rhizaria and Stramenopiles. The functional roles of these taxa and their proposed relationship to carbon export are examined further in the discussion.

4.1. COMPOSITIONAL COMMUNITIES REVEALED BY CLUSTERING

Resolving carbon flux to the individual particle level helps elucidate export mechanisms and the communities of organisms creating their own niche ecosystems on particles. Clustering analysis provides an opportunity to evaluate compositional variability and check for associated environmental correlations, as opposed to an equally informative approach of segregating samples by environmental conditions prior to assessing compositional variability. Despite the presence of over 14,000 unique heterotrophic ASVs across all samples, the variance in individual particle composition was best captured by three or four clusters, suggesting that just a small subset of ASVs drives differentiable groups. It is likely that environmental changes were at least partially responsible for driving compositional variability, as seen by associations between clusters by epoch or with certain particle types, such as salp fecal pellets in the North Pacific.

In contrast, bulk particle samples, which encompassed higher ASV diversity and contained fewer samples overall, did not form distinct clusters beyond the individual sample level. This heterogeneity in composition may be a reflection of strong variability in environmental conditions. Given small sample sizes for bulk traps, individual differences may

also be overemphasized. On the other hand, bulk samples may lack distinguishable composition to form clusters beyond the individual sample level, highlighting the uniformity of bulk samples compared to highly variable individual particles.

4.2 POTENTIAL CARBON EXPORT MECHANISMS: RHIZARIA AND STRAMENOPILES

Sagenista, a Stramenopile group, along with various classes of Rhizaria, were identified as the primary drivers of cluster differentiation within individual particles. Recent studies have estimated that Rhizaria make up approximately 1.7% of mesozooplankton carbon biomass in the upper 500 meters of the water column (Laget et al., 2024). At PAP-SO, the North Atlantic study site, a thirty-year time series analysis linked Rhizaria blooms with enhanced sequestration flux (Lampitt et al., 2023). Other productive ecosystems, such as the California Current Ecosystem, have associated radiolarians (a type of Rhizaria) as significant contributors in POC flux, possibly due to some of their skeletons acting as ballasting minerals that facilitate rapid particle sinking (Gutiérrez-Rodríguez et al., 2019).

In line with these findings, Rhizaria constituted a substantial portion of the overall abundance within our samples, with acanthareans generally representing nearly half of the sample reads. Acantharea are typically found in high relative abundance in surface waters, though their abundance generally declines with depth (Decelle & Not, 2015; Mars Brisbin et al., 2020). Interestingly, the generally photosymbiotic, surface-dwelling acanthareans seemed to maintain or even increase their relative abundance compared to other Rhizaria with depth. Several possible export mechanisms may explain these observations. Acantharea found in large numbers at the surface may be transported through ingestion and subsequent excretion in fecal matter or via rapid sinking of particles following the organism's death to below epipelagic depth. Another key consideration is the use of swarmers in the reproductive phases of Rhizaria classes like Acantharea, Nassellaria, and Spumellaria (Mars Brisbin et al., 2020). If Acantharea reproduce at depth, their swarmer cells might be captured in sinking particles, remaining viable even at greater depths.

On the other hand, many heterotrophic Stramenopiles, particularly within the Sagenista class and Labyrinthulomycetes order, were found in our dataset. These taxa are predominantly recognized as decomposers (Pereboev & Bubnova, 2023). Aplanochytrium, the majority genus among Labyrinthulomycetes reads, is characterized by its spore-based reproduction and the formation of ectoplasmic nets that facilitate movement and nutrient intake (Leander et al., 2004).

Given that Labyrinthulomycetes ASVs in this data exhibit somewhat consistent abundance across depths and are not reliant on epipelagic light for energy, it is likely that many of these organisms were alive on the particles and actively impacting particle composition or export efficiency.

Labyrinthulomycetes possess multiple trophic strategies (Xie et al., 2022) that may contribute to varying impacts on particle export. For instance, these organisms could accelerate particle export by adding weight to the particles they attach to or by reproducing on those particles. On the other hand, they might deter export by decomposing or breaking up the particles and absorbing nutrients. Previous sediment sequencing studies have revealed that Labyrinthulomycetes are commonly present in bathypelagic sediments (Rodríguez-Martínez et al., 2020). At PAP-SO specifically, Labyrinthulomycetes and fungi were identified as the dominant eukaryotic taxa on sinking particles. Labyrinthulomycetes accounted for nearly one-fifth of the composition in some sediment trap samples and appeared to thrive in low-oxygen, high-carbon environments (Bochdansky et al., 2017). These findings agree with our observation of elevated levels of Labyrinthulomycetes correlated with higher POC flux measurements in the North Atlantic.

4.3. COLLECTION TYPE CAPTURES DIFFERENT ASPECTS OF COMMUNITY DYNAMICS

Although bulk and individual particle samples were collected simultaneously, compositional profiles revealed significant discrepancies in taxonomic proportions between the two sample types. Individual particles collected from the gel layer were over 300 micrometers in size (Durkin et al., 2021), larger than the average aggregate in the bulk. These larger, carbon-dense particles are likely to attract decomposers such as Labyrinthulomycetes, which may explain the higher prevalence of these taxa on individual particles. In contrast, Opalozoa—osmotrophic organisms typically associated with vertebrate guts (Cavalier-Smith & Chao, 2006)—were more likely to be found in aggregate sinking material within bulk traps.

Furthermore, bulk traps occasionally capture entire organisms. Genetic material associated with Phaeodaria, which appears more frequently in bulk traps, may be associated with whole Phaeodaria cells sinking into the trap. Therefore, sequencing bulk samples may offer a broader and more quantifiable perspective on carbon flux, while individual particle analysis could provide insights into specific export mechanisms.

CONCLUSION/RECOMMENDATIONS

In this study, we demonstrated that individual particles, representing distinct ecological niches, formed clusters driven by specific, shared taxa across multiple locations. In contrast, bulk samples, which encompassed a broader range of organisms and materials, obscured these niche-specific patterns and failed to cluster distinctly. However, the bulk particle samples presented a broad understanding of flux dynamics. Focusing on the specific taxa associated with these sinking particles provides insight into the mechanisms of carbon sequestration that cannot be observed only by visual analysis. Our work highlights how identifying enriched and highly variable taxa can reveal the organism-specific and particle-specific pathways for carbon export.

Many potential analyses may follow. Besides specific taxa, a more thorough analysis of the factors distinguishing these clusters—such as the role of environmental conditions versus taxonomic composition—could clarify whether taxa are primarily influenced by their environment or are themselves the key drivers of ecological patterns. Specific outlier groups, such as salp fecal pellets and the high abundance of Rhizaria in the Atlantic could be investigated for relation to carbon flux pattern. Generally, associating other flux measurements from the collection regions with taxonomic trends may provide insight into key POC-associated groups. Investigating clusters with the highest and lowest abundance of specific taxa to identify associated environmental variables would further elucidate these dynamics. Finally, examining the specific species within groups like Rhizaria or Stramenopiles could determine whether the same species drive observed variances or if these patterns vary regionally.

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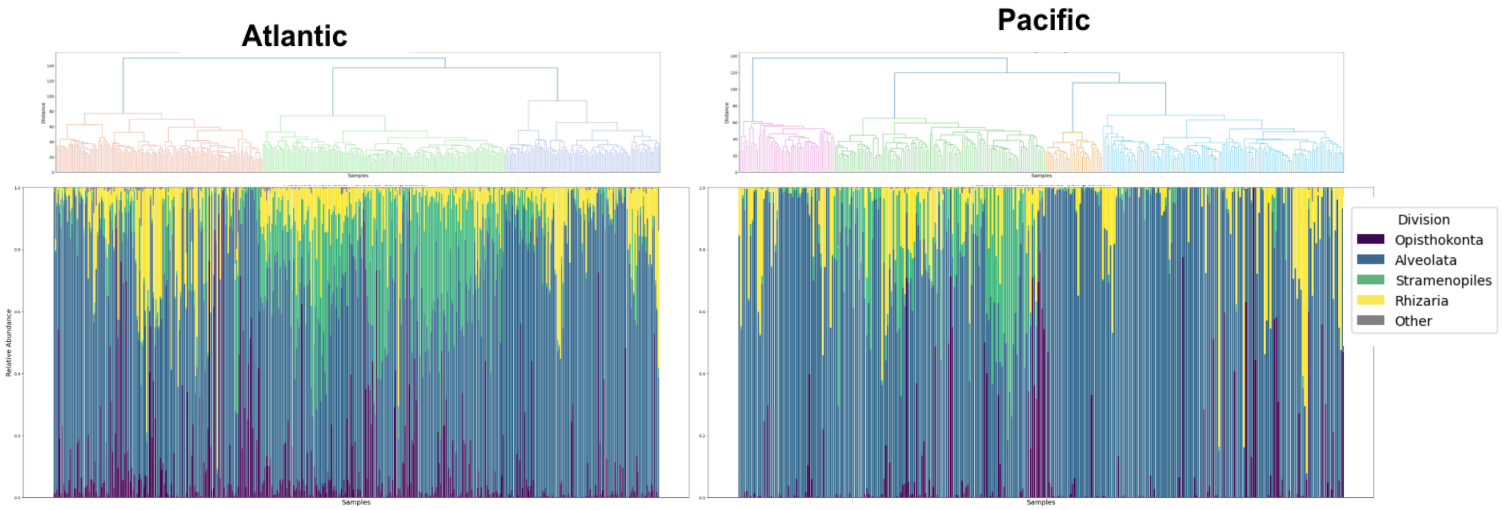
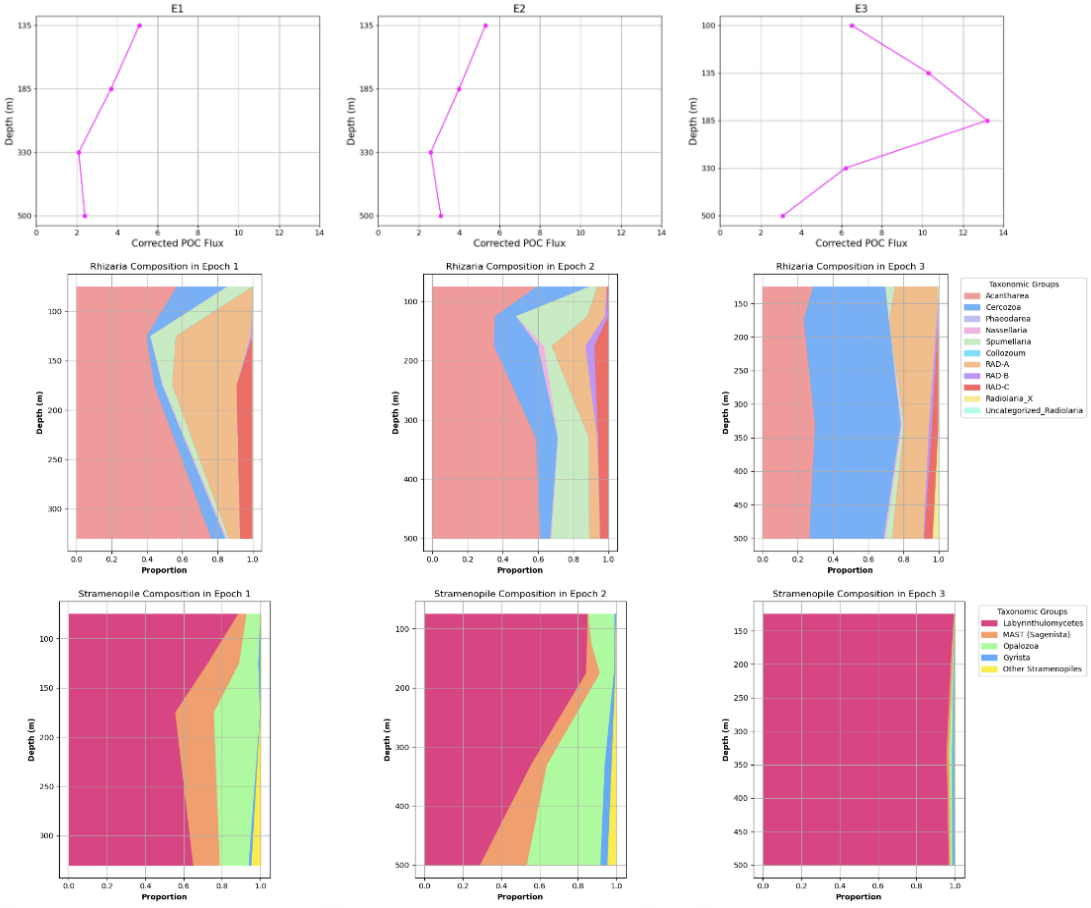
Supplementary Figures:



Supplementary Figure 1. Dendrograms are aligned with the relative abundance of each taxonomic division. Samples are shown in the same order for direct comparison between clusters and abundance.



Supplementary Figure 2. The top row shows changes in particulate organic carbon (POC) flux with depth in the North Atlantic across different sampling epochs. The second and third rows display the corresponding relative abundance of Rhizaria and Stramenopile taxa, respectively, with subgroup composition averaged across depth. Epoch 3 shows the highest recorded POC flux and the greatest variability in taxonomic composition.