Effects of Atolls on the Distribution and Composition of Suspended Particles in the Western Tropical Pacific

Ashleigh L.L. Steedman

University of Washington,

School of Oceanography,

Seattle, WA 98195

19 February 2024

asteed@uw.edu

Abstract

Atolls are unique geomorphic structures that influence suspended sediment dynamics and microbial communities through their interaction with wave energy, currents, and limited landmass. These factors create localized patterns of suspended particles, yet their impacts on microbial activity and nutrient cycling remain poorly understood. This study investigates how atolls influence suspended sediments' vertical distribution and composition by examining differences in organic and inorganic particle concentrations at varying depths. I hypothesize that atolls promote the accumulation of fine organic matter and microbial activity near the reef, while larger inorganic sediments dominate farther away due to hydrodynamic forces. Fieldwork was conducted near Nam2 Atoll in the western Pacific, where transmissometer data, Conductivity, Temperature, and Depth (CTD) profiles, and water samples were collected across different locations. The composition of suspended particles was determined through microscopy while the proportion between organic and inorganic materials was quantified by the Loss on Ignition (LOI) method. Results indicate a significant decrease in the organic-to-inorganic ratio with depth, with the highest organic concentrations occurring in surface waters (20–100 m) and inorganic sediments increasing at deeper layers (>500 m). Statistical analysis revealed a T-statistic was 0.4129 while the p-value was 0.6889 however, showed no significant difference in organic-inorganic ratios between shallow and deep samples. The observed organic-to-inorganic ratio trends help clarify how organic carbon is stored and transported in marine environments which can inform climate models and global carbon budget estimates.

Plain Language Summary

Atolls are unique ocean environments shaped by coral breakdown, wave action, and their small landmass. These factors influence how tiny particles, including sediments and microbes, move through the water. However, scientists still don't fully understand how atolls affect these suspended particles. This study investigated how atolls impact the amount and type of particles found in different depths of the ocean, particularly the balance between organic matter, microbes, and inorganic sediments, such as tiny rock fragments. The research was based near Nam2 Atoll in the western Pacific, where water samples were collected at different locations and depths. Instruments were used to measure water clarity, temperature, salinity, and sediment concentration. Microscopes helped identify microbes, and a method called Loss on Ignition (LOI) determined how much of the sediment was organic versus inorganic.

Results showed that organic matter was most concentrated in the upper ocean (20–100 meters), while inorganic material increased at greater depths (below 500 meters). However, statistical tests showed no significant difference between shallow and deep samples. These findings help explain how atolls influence the movement of sediments and microbes, which play an important role in ocean health. Understanding these processes can improve knowledge about nutrient cycling, carbon storage, and marine food webs, all of which are important for sustaining life in the ocean and responding to environmental changes.

Introduction

Atolls, including those around Guam, are a unique coral reef ecosystem that plays a crucial role in sedimentology and biogeochemistry (East et al., 2020). Their ring-shaped morphology influences suspended sediment distribution by altering wave energy and currents, which drive alongshore transport gradients and spatial variability (Shope et al., 2019). In the Western Pacific near Guam, suspended particles are influenced by fringing reefs, terrestrial runoff, and currents like the North Equatorial Current. These factors likely result in a mix of organic matter from primary production and reef ecosystems, resuspended inorganic sediments, and terrestrial inputs. The vertical distribution of these particles is critical for understanding nutrient cycling, carbon sequestration, and ecosystem function (Yan et al., 2024).

As wave energy and hydrodynamic forces disperse suspended material outward, the finer organic particles settle more quickly near the atoll, while coarser, heavier sediments remain in motion and are transported farther from the source (Bruni et al., 2022). Additionally, sediment resuspension near the seafloor may be intensified by interactions with deeper ocean currents farther from the sheltered environment of the atoll lagoon. These factors create a distinct gradient in sediment size distribution as distance from the atoll increases.

Atolls not only influence suspended particle distribution but also the microbial ecology and phytoplankton. Microbes, both Archaea and Bacteria, contribute significantly to the atoll ecosystem as they are ingested by coral reef organisms (Dinsdale et al., 2008). These microbial communities play a significant factor in biogeochemical cycles in near atoll ecosystems. Studies found that more than 60% of bacteria are inclined to attach to settled and suspended particles

(Yung et al., 2016). A high rate of bacterial attachment to the particles is important to the atoll ecosystems where the relationship between coral reefs, lagoons, and surrounding water creates a dynamic environment. This research also aligns with previous studies on the Island Mass Effect (IME), a phenomenon where islands and atolls act as biological hotspots in otherwise nutrient-poor ocean regions. The combination of physical factors, such as water turbulence, sediment resuspension, and nutrient upwelling, creates conditions that support higher phytoplankton concentrations near atolls (Gove et al., 2016).

In atoll environments, the upper layers of the water column experience elevated microbial activity and higher concentrations of fine organic particles (Stephens et al., 2024). This is largely due to the productive reef ecosystem, which supports photosynthetic microbes such as phytoplankton and cyanobacteria, contributing to organic matter production. These fine organic particles influence light penetration, nutrient availability, and overall water quality (Premarathne et al., 2021). Additionally, heterotrophic microbial activity plays a key role in breaking down organic matter and facilitating nutrient recycling within the ecosystem.

In contrast, the deeper layers of the atoll water column contain fewer fine organic particles but higher concentrations of resuspended inorganic sediments (Bruni et al., 2022). This shift can be attributed to wave energy, ocean currents, and bioturbation, which stir up bottom sediments, redistributing them into deeper waters (Sivkov, 2021). While microbial communities persist at these depths, heterotrophic bacteria dominate, breaking down sinking organic material and contributing to deep-sea nutrient cycling.

The resuspension of larger particles significantly influences sediment transport and the morphology of atoll systems. Research has shown that microbial community richness—defined as the diversity of microbial species within a given environment—decreases as particles age and sink (Stephens et al., 2024). This decline is attributed to the depletion of labile organic matter and increased colonization by specialized deep-sea microbes. Conversely, richness tends to increase with particle size and as carbon export diminishes, likely due to the retention of diverse microbial communities on larger aggregates. These findings suggest that the principles of island biogeography, which describe how diversity is influenced by area size and isolation, can also be applied to sinking marine particles (Stephens et al., 2024).

Atolls play a key role in shaping sediment dynamics and microbial community composition in the water column. Studying their influence helps us understand how atolls support biodiversity, regulate biogeochemical processes, and respond to environmental changes, aiding in the assessment of ecosystem health and resilience. This knowledge will guide conservation efforts and enhance our understanding of atolls' roles in carbon storage and marine sediment dynamics. Understanding these processes also helps predict how atoll ecosystems will react to climate change and other environmental pressures.

To test the hypothesis that atolls influence the vertical distribution of suspended particles, with higher concentrations of fine organic matter and microbial activity near the surface and larger resuspended inorganic sediments at depth, we conducted fieldwork near Nam2 Atoll in the western Pacific. We collected water samples and particle data at multiple depths using a

Conductivity, Temperature, and Depth (CTD) sensor, a transmissometer, and microscopy. The Loss on Ignition (LOI) method was used to quantify the proportion of organic versus inorganic material.

Our results revealed a significant decrease in the organic-to-inorganic ratio with depth, with organic material concentrated in surface waters (20–100 m) and inorganic sediments increasing at deeper layers (>500 m).

Methods

Study region-

Sampling processes were conducted from December 27th, 2024, to January 11th, 2025, aboard the RV *Thomas G. Thompson* (AGOR-23) in the western Pacific near Guam. Data was collected from four distinct sampling sites to evaluate variations in suspended sediment dynamics, comparing near-atoll environments with those of the open ocean (Figure 1). Nam2 Atoll (09º08'40''N, 148º07'50'' E) was our sampling area, including sampling sites 4, 5A, 5B, 5C, 5X, and 5D surrounding the atoll (Figure 2).

Sampling at Nam2 Atoll will involve transmissometer and CTD recordings at six sampling sites around the atoll, with water samples collected at each site to assess the influence of reef morphology on suspended particle distribution. Location 4 and 5A will be positioned as close to Nam2 Atoll as possible, although it is subject to change. Location 5B and 5C, located off the atoll, will encompass previous samples and be situated between atoll and off-atoll environments. Locations 5X and 5D will represent open-ocean conditions.

Sample collection-

Data collection will include transmissometer measurements, CTD profiles, and water samples collected with Niskin bottles. These methods are used to comprehensively analyze suspended particles in atoll and open-water locations. The transmissometer was deployed to measure water turbidity, which serves as an indirect indicator of suspended particle concentration. This instrument operates by passing a beam of light through a water sample and quantifying the fraction of light transmitted, which decreases in the presence of suspended particles. (Bartz and Milburn, 1983) The transmissometer measured turbidity from measurements of light attenuation, providing high-resolution data on suspended particle concentrations across the water column, while microscopy will identify particle size, type, and morphology, categorizing them into organic and inorganic groups to assess biological contributions.

Initially, the CTD sensor was used to record water dynamics, including light transmission and fluorescence, which helped identify chlorophyll peaks and suspended particles in the water column. At points where transmission values were at a minimum, Niskin bottles were deployed at pre-determined depths based on insitu CTD readings to collect water samples. These samples were then filtered to analyze suspended particles and microbial content. This approach provided a more targeted sampling strategy, reducing redundancy compared to randomly deploying Niskin bottles at various sites.

Data analysis-

After the transmission was measured in situ we were able to determine where Niskin bottles were fired. 10L of water was filtered from determined depths into 0.7 Whatman GF/A glass microfiber filters. After the filtering process was complete, filters were wrapped in aluminum foil and placed into liquid nitrogen for preservation. The oss on Ignition method (LOI) was used to quantify the organic and inorganic ratio of suspended particles (Stavn et al. 2019), offering precise compositional data. After returning to the lab, filters were dried in an oven at 60 °C for 24 hours. Crucibles were cleaned out and put into the desiccator for 4 hours.

Filters were folded and placed into crucibles, using tongs, after being preweighed and then placed into the desiccator for 5 hours at 500 °C. After 5 hours, the furnace was cooling down by turning off the muffle furnace and cracking the door. 30 minutes later crucibles were removed with tongs and post-weight was recorded on an analytical balance.

Microscopic analysis was conducted to visually assess the diversity and size of suspended sediments. Initially, water samples were filtered to concentrate suspended particles from various depths, ensuring a sufficient sample for examination. Following filtration, different types of suspended sediments were analyzed to characterize their composition and distribution throughout the water column.

Results

The highest phytoplankton concentrations were observed at the deep chlorophyll maximum (DCM), coinciding with the lowest transmission levels (Figure 4). The presence of high fluorescence at the DCM (around 100m at station 5B) supports active phytoplankton growth. Decreased transmission in this region confirms high particle density. Below the DCM, fluorescence declines, transmission slightly increases, and temperature continues to drop, indicating a shift towards fewer phytoplankton and increased inorganic suspended material.

The organic-to-inorganic ratio varied significantly across depths, generally decreasing with increasing depth. At shallow depths (20–100m), the ratio was highest, indicating elevated organic material near the atoll (Figure 9). At Station 4, the ratio at 20m was 0.0455, similar to 0.0477 at 100m, likely due to its proximity to the atoll and shallow depth. However, at 300m, the ratio dropped sharply to 0.8976, indicating a shift toward inorganic dominance. At Station 5A, which included samples from 50m to 80m, the ratio remained relatively stable (0.0343 at 50m, 1.0052 at 70m, and 0.0402 at 80m), suggesting moderate organic retention in mid-water depths. At Station 5B, deeper samples at 100m (0.0380) and 300m (0.0158) followed the trend of decreasing organic content, with further drops at 400m (0.0301) and 459m (0.0165), confirming the increasing dominance of inorganic particles with depth.

At greater depths (≥ 300m), a continued decline in organic matter was observed (Figure 8). At Station 5C (320–785m), the ratio decreased from 0.0298 at 320m to 0.0154 at 550m, 0.0126 at 600m, 0.0073 at 700m, and 0.0053 at 785m, reflecting significant organic degradation. At Station 5X (750–1200m), the trend continued, with values of 0.0043 at 750m, 0.0027 at 800m, 0.0022 at 900m, and 0.0015 at 960m, reaching the lowest recorded ratio of 0.0014 at 1200m, indicating minimal organic content. At Station 5D (60–2200m), moderate organic content was observed at 60m (0.0332) and 100m (0.0370), but the ratio declined at 170m (0.0206) and 920m (0.0190). Deeper samples at 1300m (0.0033) and 2200m (0.0065) confirmed significantly reduced organic material in offshore waters.

Statistical analysis revealed an R^2 value of 0.0243, with a T-statistic of 0.4129 and a p-value of 0.6889 when comparing shallow (≤100m) and deep (>100m) samples. The high p-value suggests that the difference between organic-to-inorganic ratios at shallow and deep depths is not statistically significant. However, trends across stations indicate depth-dependent organic matter loss, with near-atoll waters retaining more organic material at shallow depths while deeper, offshore regions become increasingly dominated by inorganic sediments. These findings highlight the role of depth and location in shaping sediment composition and organic material retention in atoll-associated marine environments.

Figures

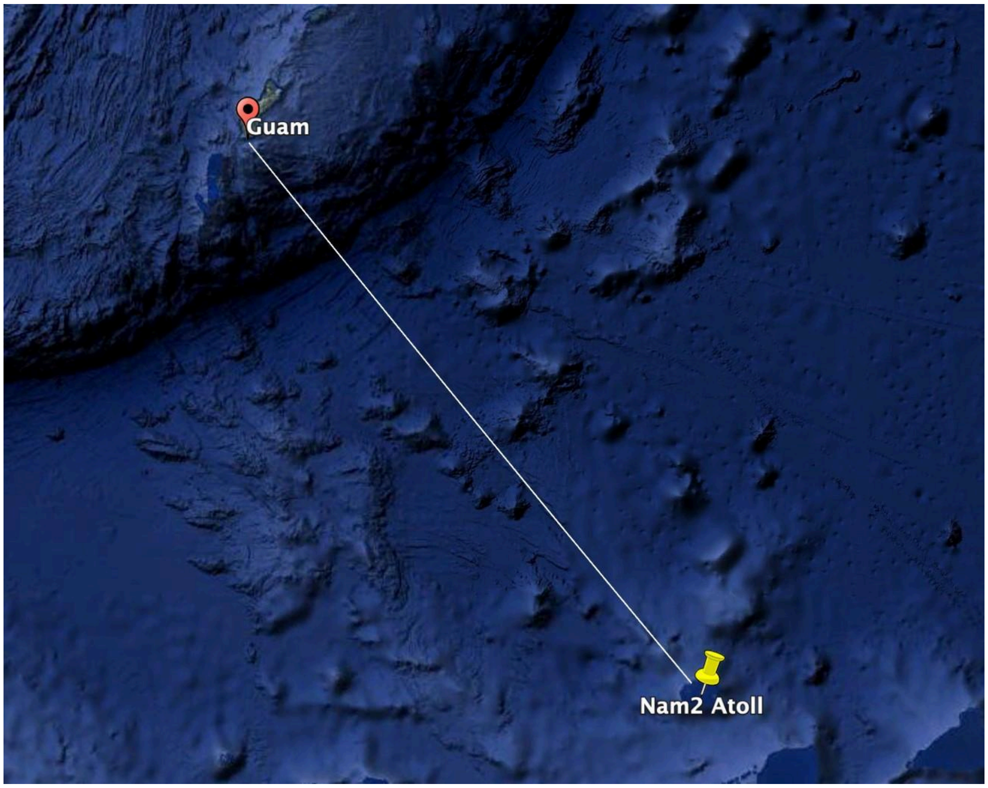

Figure 1: Nam2 Atoll (09º08’40”N, 148º07’50”E) is located in the Western Pacific Ocean, positioned relative to Guam to establish its geographic context within the region

Figure 2: 09º08’40’’N, 148º07’50’’ E is where data collection occurred with stations 4, 5A, 5B, 5C, 5X, 5D.

Sample ID	Station #	LOI (%)

A1	4	4.35
A2	4	4.55
A3	4	47.33
B1	5A	3.31
B2	5A	50.15
B3	5A	4.02
C1	5B	3.8
C2	5B	2.37
C3	5B	2.92
C4	5B	9.57
D1	5C	2.97
D2	5C	6.71
D3	5C	1.88
D4	5C	3.38
D5	5C	2.56
E1	5X	3.25
E2	5X	2.15
E3	5X	20.13
E4	5X	16.41
E5	5X	3.67
Ex 3	5D	3.32
Ex 4	5D	3.7
Ex 5	5D	2.06
Ex 6	5D	1.9
Ex 7	5D	3.34
Ex 8	5D	6.53

Figure 3- Each station number and sample identification used while conducting LOI method.

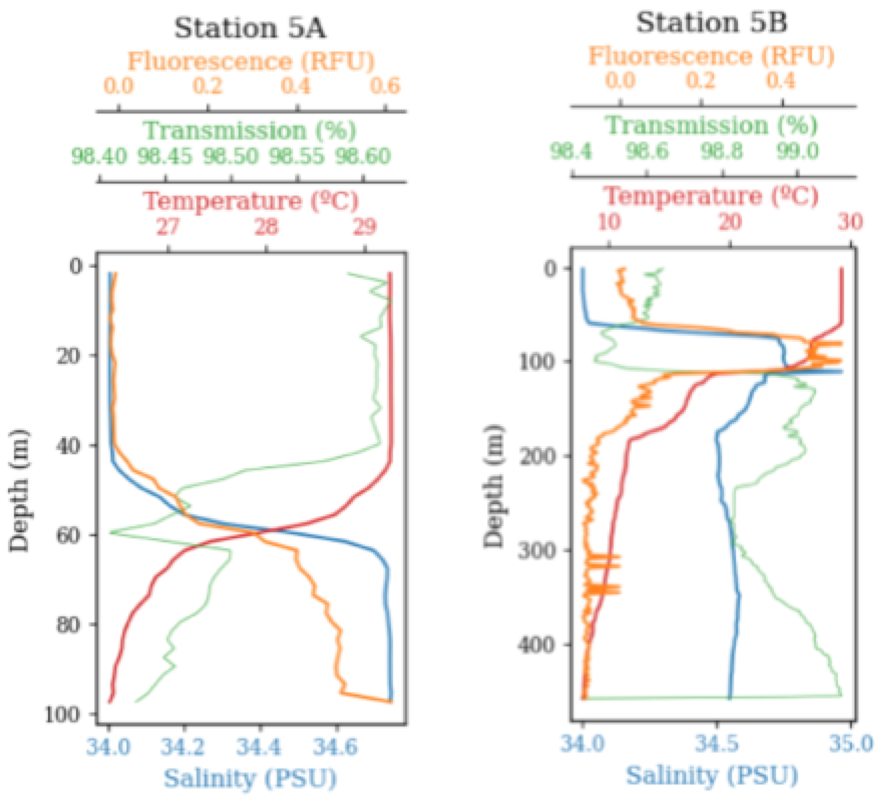

Fig 4: Station 5A showing Fluorescence, Transmission Temperature, and Salinity along Depth with data collection at 50m, 70m, 80m, and 98m. Station 5B showing Fluorescence, Transmission Temperature, and Salinity along Depth with data collection at 100m, 300m, 400m, 459m.

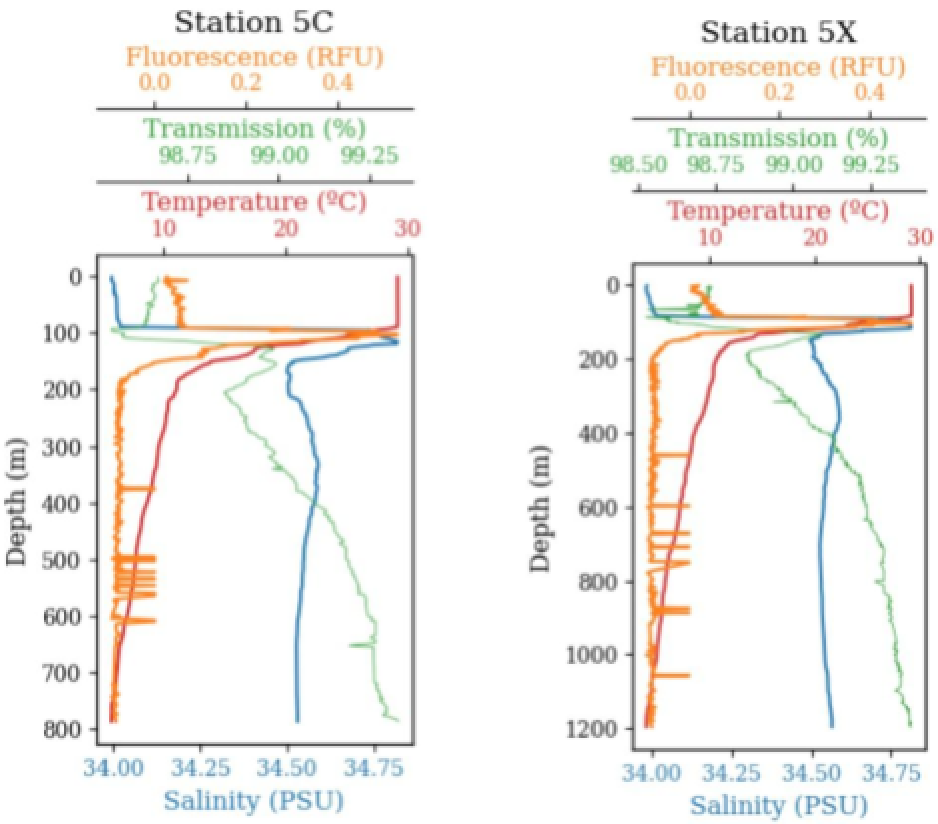

Fig 5: Station 5C showing Fluorescence, Transmission, Temperature, and Salinity along Depth with data collection at 320m, 550m, 600m, 700m, 785m. Station 5X showing Fluorescence, Transmission Temperature, and Salinity along Depth with data collection at 750m, 800m, 900m, 960m, 1200m

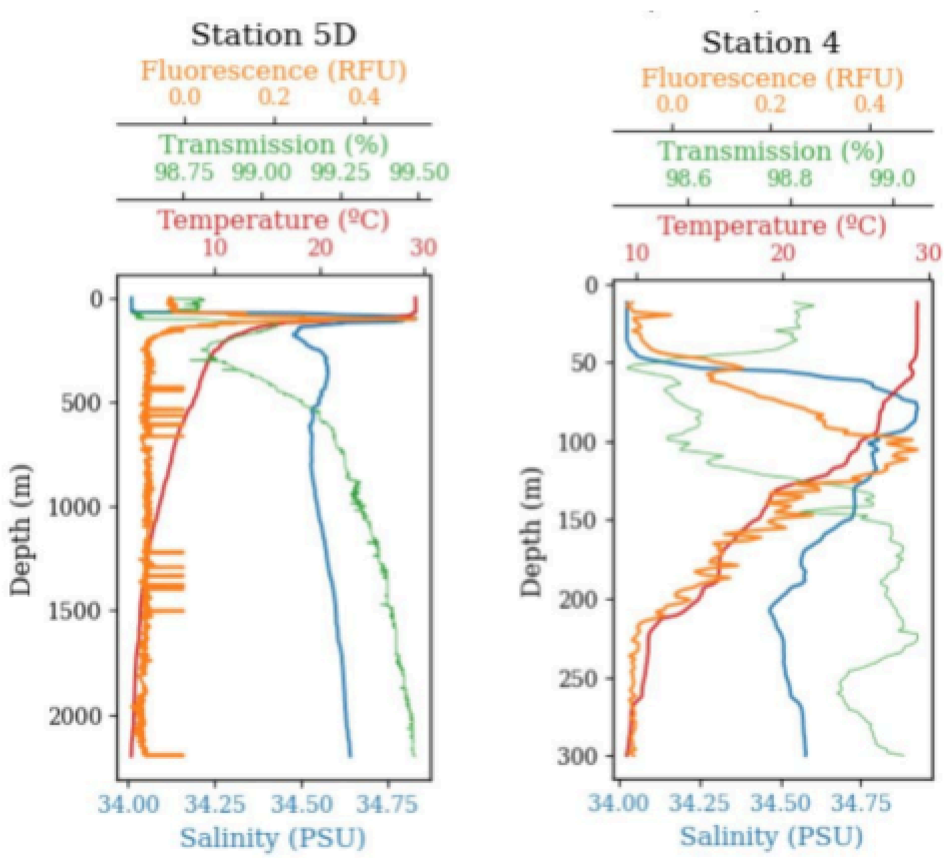

Fig 6: Station 5D showing Fluorescence, Transmission Temperature, and Salinity along Depth with data collection at 60m, 100m, 170m, 920m, 1300m, 2200m. Station 4 showing Fluorescence, Transmission, Temperature, and Salinity along Depth with data collection at 20m,100m, 300m

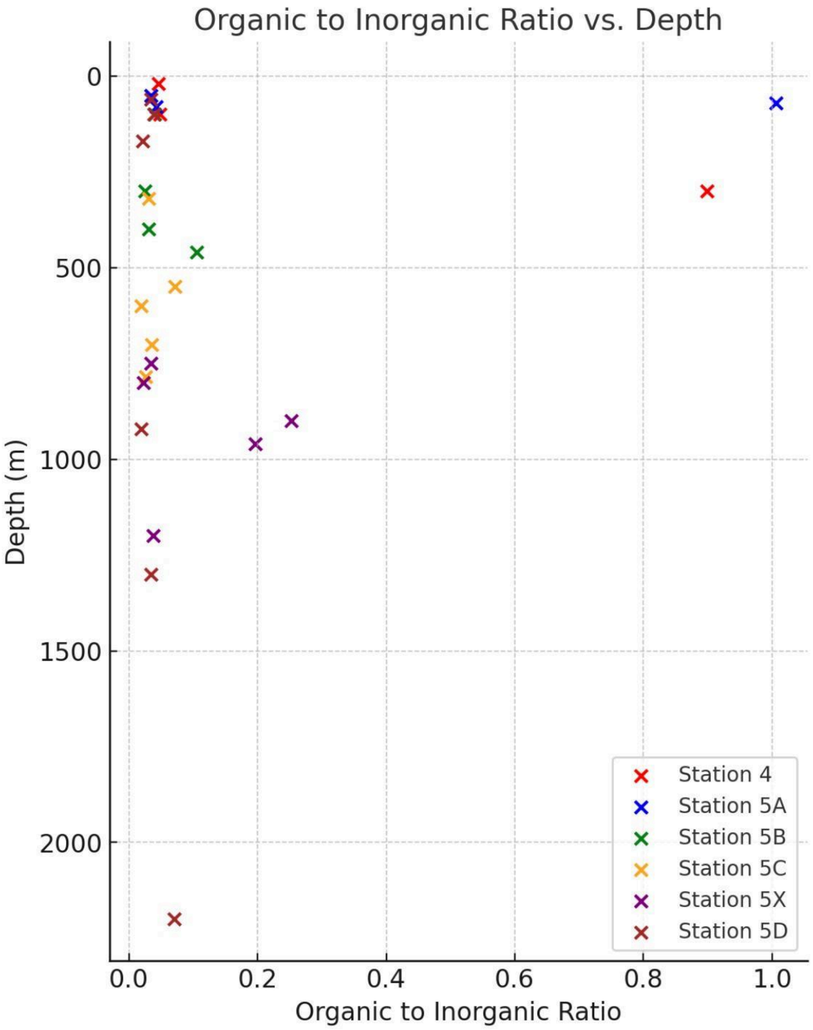

Figure 7: Organic to inorganic ratio vs Depth (m) with station numbers colored in the bottom right corner.

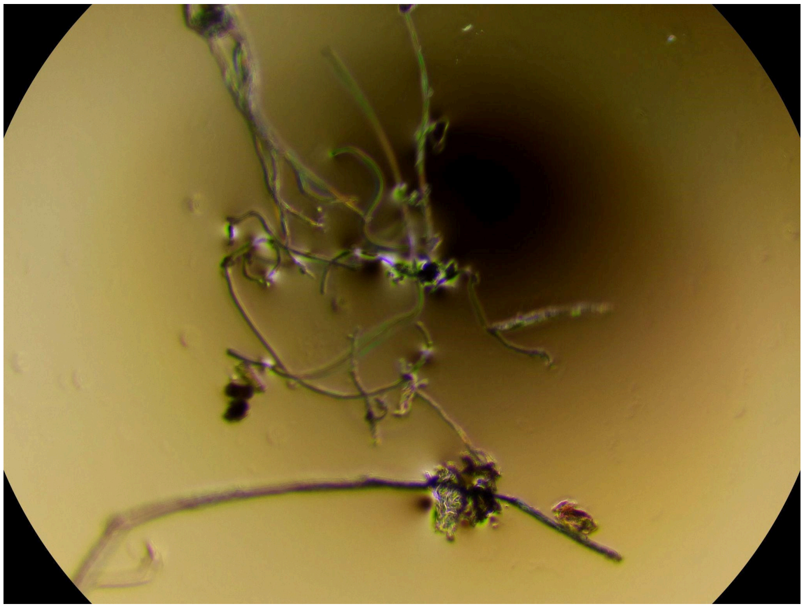

Figure 8: Larger suspended sediment attached to fibers at Station 5C at 785m.

Figure 9: Smaller dispersed suspended sediment attached to fibers at Station 5A at 100m.

Discussion

Influence of Atoll Morphology on Suspended Sediment Dynamics

The morphology of Nam2 Atoll significantly influences suspended sediment distribution. The unique ring-shaped structure alters wave energy and currents, leading to distinct spatial patterns in sediment composition. The proximity to the atoll promotes the accumulation of fine organic matter in shallow waters due to reduced hydrodynamic energy, while larger inorganic sediments dominate deeper waters. This aligns with previous studies (Shope et al., 2019) that suggest atolls create gradients in sediment size and composition driven by wave interactions and reef morphology.

Vertical Distribution of Organic and Inorganic Sediments

Our findings show a clear vertical stratification in suspended particle composition. The highest organic-to-inorganic ratios were observed in the upper 100 meters, where organic material from primary productivity and microbial activity is concentrated. The elevated organic content at these depths suggests active photosynthesis and particle aggregation near the surface, consistent with the Island Mass Effect (Gove et al., 2016).

In contrast, deeper samples (>500 m) exhibited a marked increase in inorganic sediments. This trend likely results from sediment resuspension and transport by deeper ocean currents, a phenomenon noted in similar environments (Bruni et al., 2022). The decrease in organic material with depth highlights the role of sedimentation and degradation processes in shaping the vertical distribution of suspended particles.

Microbial Community Influence on Organic Matter

The presence of microbes plays a critical role in the composition and dynamics of suspended sediments. High concentrations of microbial communities, particularly in surface waters, contribute to the production and transformation of organic matter. The elevated microbial activity near the atoll promotes organic particle aggregation, enhancing nutrient cycling and carbon storage within the ecosystem (Stephens et al., 2024).

Microscopic analysis revealed diverse microbial populations attached to suspended particles, supporting previous findings on the importance of particle-associated microbes (Yung et al., 2016). The observed decrease in microbial diversity with depth suggests a shift in community composition as labile organic matter is consumed and specialized deep-sea microbes colonize sinking particles.

Implications for Carbon Sequestration and Nutrient Cycling

The study’s findings have important implications for understanding carbon sequestration and nutrient cycling in atoll environments. The high organic content in shallow waters indicates active carbon storage, driven by primary production and microbial processes. However, the rapid decline in organic material at depth suggests significant carbon loss through degradation and export to the deep ocean.

These processes play a crucial role in global carbon budgets and climate models, as atolls contribute to the vertical transport of carbon in marine ecosystems. The retention of organic matter near the atoll supports local food webs and enhances nutrient availability, while the export of inorganic sediments influences the geomorphology and stability of atoll systems.

Statistical Analysis and Limitations

Although the organic-to-inorganic ratio decreased with depth, statistical analysis indicated no significant difference between shallow and deep samples (T-statistic = 0.4129; p-value = 0.6889). This suggests that while trends in sediment composition are apparent, variations within the dataset may reduce statistical power. Factors such as sampling variability, small sample sizes, and environmental heterogeneity could contribute to the lack of statistical significance.

Further research with larger sample sizes and longer-term observations is necessary to refine these findings. The integration of high-resolution spatial data and advanced analytical techniques could improve our understanding of sediment dynamics and microbial interactions in atoll environments.

Conclusion

This study highlights the critical role of atolls in shaping suspended sediment dynamics and microbial community composition. The results demonstrate a clear vertical gradient in organic and inorganic sediments, driven by atoll morphology, hydrodynamic forces, and microbial processes.

Understanding these patterns provides valuable insights into nutrient cycling, carbon storage, and ecosystem function in atoll environments. Although statistical significance was not achieved, the observed trends emphasize the importance of depth and location in influencing sediment composition. Future research should focus on expanding sampling efforts and exploring the long-term impacts of environmental changes on atoll-associated marine systems. Additionally, microbial DNA sequencing could provide deeper insights into community shifts with depth, refining our understanding of biogeochemical interactions in atoll environments. These findings contribute to our broader knowledge of how atolls influence ocean health, carbon sequestration, and resilience in the face of climate change.

Acknowledgments

I am deeply grateful to François Ribalet for his exceptional mentorship, helping shape my research project and guiding me through its realization. My sincere thanks to Kathy Newell for providing access to her lab and for her invaluable support during data processing. I also extend my appreciation to the marine technicians, crew, captain, officers, and chief scientists who assisted me throughout the research cruise. A special thanks to my fellow senior oceanography peers for their help with data collection and sample filtering, as well as for their unwavering support. I am forever thankful to my passionate instructors, Ginger Armbrust, François Ribalet, Kathy Newell, Alison Gray, Andrea Ogston, and Mark Warner, for their continuous guidance and support throughout this senior thesis. I am especially thankful to the University of Washington School of Oceanography for offering this incredible and life-changing opportunity.

References

Ai is used to improve the clarity and flow of writing, summarize key findings from articles, proofread documents:

Anon (n.d.). *RV Thomas G Thompson.* Available from: https://www.ocean.washington.edu/story/RV_Thomas_G_Thompson (Accessed 6 November 2024b)

Baker, E. T., & Milburn, H. B. (1983). An instrument system for the investigation of particle fluxes. *Continental Shelf Research,* 1(4), 425–435. Available from: https://doi.org/10.1016/0278-4343(83)90006-7 (Accessed 18 November 2024)

Boyd, P. W., & Ellwood, M. J. (2010). The biogeochemical cycle of iron in the ocean. *Annual Review of Marine Science,* 2(1), 179–207. https://doi.org/10.1146/annurev-marine-120709-142814

Bruni, E. T., T. M. Blattmann, N. Haghipour, D. Louw, M. Lever, and T. I. Eglinton (2022), Sedimentary hydrodynamic processes under low-oxygen conditions: Implications for past, present, and future oceans, *Frontiers*. Available from: https://www.frontiersin.org/journals/earth-science/articles/10.3389/feart.2022.886395/full

Dinsdale, E. A. et al. (2008). Microbial ecology of four coral atolls in the Northern Line Islands. *PLoS One.* Available from: https://pmc.ncbi.nlm.nih.gov/articles/PMC2253183/#s1

Goldberg, W. M., & Rankey, E. C. (2024). A global atlas of atolls. *CRC Press, Taylor & Francis Group,* Boca Raton.

Gray (2008). Microbial ecology. *Microbial Ecology - an overview | ScienceDirect Topics.* Available from: https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/microbial-ecology (Accessed 21 November 2024a)

Holly K. East et al. (2020), Modelling reef hydrodynamics and sediment mobility under sea level rise in Atoll Reef Island Systems, *Global and Planetary Change*. Available from: https://www.sciencedirect.com/science/article/pii/S0921818120300874#bb0255

Li, W., Sun, J., Wang, H., et al. (2024). Composition and concentration of suspended matter in the Zhongsha Great Atoll, South China Sea, before and during the summer monsoon. *Frontiers in Marine Science,* 11, 1268294. https://doi.org/10.3389/fmars.2024.1268294

OpenAI (2023). ChatGPT (November 2024 version). Accessed [November 1, 2024], from https://chat.openai.com/

Premarathne, C. et al. (2021), Low light availability reduces the subsurface sediment carbon content in Halophila beccarii from the South China Sea, *Frontiers*. Available from: https://www.frontiersin.org/journals/plant-science/articles/10.3389/fpls.2021.664060/full

Shah, D. R., Nikolic, D., & van Breemen, R. B. (2007). Post-collection sample processing: Effect of temperature and humidity on metabolite stability during the transport of biospecimens. *Analytical Chemistry,* 79(4), 1306–1313. https://doi.org/10.1021/ac0620633

Shope, J. B., & Storlazzi, C. D. (2019). Assessing morphologic controls on atoll island alongshore sediment transport gradients due to future sea-level rise. *Frontiers.* Available from: https://www.frontiersin.org/journals/marine-science/articles/10.3389/fmars.2019.00245/full?utm_source=chatgpt.com (Accessed 21 November 2024)

Sivkov, V., & Bubnova, E. (2021). Distribution of suspended particulate matter at the equatorial transect in the Atlantic Ocean. *Ocean Science,* 17, 1421–1435. https://os.copernicus.org/articles/17/1421/2021/

Stavn, R. H., Rick, H. J., & Falster, A. V. (2009). Correcting the errors from variable sea salt retention and water of hydration in loss on ignition analysis: Implications for studies of estuarine and coastal waters. *Estuarine, Coastal and Shelf Science,* 81(4), 575–582. Available from: https://libres.uncg.edu/ir/uncg/f/R_Stavn_Correcting_2009.pdf (Accessed 20 November 2024)
Stephens, B. M., Durkin, C. A., Sharpe, G., Nguyen, T. T. H., Albers, J., Estapa, M. L.,

Steinberg, D. K., Levine, N. M., Gifford, S. M., Carlson, C. A., Boyd, P. W., & Santoro, A. E. (2024). Direct observations of microbial community succession on sinking marine particles. *The ISME Journal,* 18(1). https://doi.org/10.1093/ismejo/wrad010

Thomas, P. D., Hughes, Z. J., Marani, M., & Schuerch, M. (2024). Coastal wetland resilience to sea-level rise and management interventions. *Current Research in Environmental Sustainability,* 6, 100264. https://doi.org/10.1016/j.crsust.2024.100264

Woodroffe, C. D., et al. (2007). Reef-island topography and the vulnerability of atolls to sea-level rise. *Global and Planetary Change.* Available from: https://www.sciencedirect.com/science/article/abs/pii/S0921818107001890

Gove, J. M., McManus, M. A., Neuheimer, A. B., Polovina, J. J., Drazen, J. C., Smith, C. R., Merrifield, M. A., Friedlander, A. M., Ehses, J. S., Young, C. W., Dillon, A. K., & Williams, G. J.
(2016). Near-island biological hotspots in barren ocean basins. *Nature Communications, 7*, 10581. https://doi.org/10.1038/ncomms10581