

Marine Biogeochemical Processes and Ecosystem Evolution: Observational and Predictive Approaches

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Abstract This study provides an overview of the importance of marine biogeochemical cycles and their impact on ecosystem evolution, explores major biogeochemical processes such as carbon, nitrogen, phosphorus, sulfur, and iron, and analyzes how these processes drive the long-term evolution of marine ecosystems. It also summarizes observational methods for studying marine biogeochemistry, including remote sensing, in situ measurement, and long-term observational networks, and discusses the application of climate models and ecosystem predictive models in describing the evolution of marine ecosystems, as well as the challenges encountered in modeling. The study emphasizes the development of observation and prediction methods to support long-term monitoring and scientific management of ecosystems.

Keywords Marine biogeochemical processes; Carbon cycle; Ecosystem evolution; Remote sensing; Predictive models

1 Introduction

Marine biogeochemical cycles are fundamental processes that govern the transformation and movement of bioessential elements such as carbon (C), nitrogen (N), and phosphorus (P) within marine ecosystems. These cycles are driven primarily by microorganisms through their metabolic activities, which include energy harvesting from light and inorganic chemical bonds for autotrophic carbon fixation. The interconnectedness of these cycles with energy fluxes across the biosphere is crucial for maintaining the structure and function of marine ecosystems (Dang and Chen, 2017; Grabowski et al., 2019). For instance, the marine nitrogen cycle involves multiple biogeochemical transformations mediated by microorganisms, which play a critical role in primary productivity and the uptake of atmospheric carbon dioxide (Pajares and Ramos, 2019). Similarly, the phosphorus cycle, which is tightly controlled by microbial processes, is essential for marine productivity and ecosystem structure (Duhamel et al., 2021).

Understanding the evolution of marine ecosystems is vital for predicting how these systems will respond to environmental changes. Marine microorganisms, which drive biogeochemical cycles, are currently facing unprecedented anthropogenic changes, including shifts in seawater pH, temperature, and nutrient availability. These changes can have profound impacts on the biogeography, community structure, and adaptive evolution of marine microorganisms, ultimately affecting large-scale biogeochemical cycles (Hutchins and Fu, 2017). The role of redox-active compounds in aquatic systems highlights the importance of fluctuating redox conditions in maintaining high reactivity and influencing biogeochemical element cycles (Peiffer et al., 2021). The evolution of these processes over time is crucial for understanding the resilience and adaptability of marine ecosystems in the face of global change.

This study comprehensively analyzes marine biogeochemical processes and ecosystem evolution through observation and prediction methods, exploring the coupling of carbon and energy fluxes in the marine environment, especially in the subtropical circulation of the North Pacific. It evaluates the application and limitations of biogeochemical models in different marine environments, further discusses the thermodynamic principles behind marine biogeochemical cycles and their impact on ecosystem modeling, in order to enhance our understanding of the mechanisms and predictions of marine biogeochemical cycles and their role in ecosystem evolution.

2 Major Marine Biogeochemical Processes

2.1 Carbon cycle and oceanic carbon sequestration

The carbon cycle in marine environments is a complex interplay of biological, chemical, and physical processes that regulate the movement and storage of carbon. One of the key components of this cycle is the sequestration of carbon in the ocean, which involves the uptake of atmospheric CO₂ by marine organisms and its subsequent storage in various forms. The PISCES-v2 model, for instance, simulates the lower trophic levels of marine ecosystems and the biogeochemical cycles of carbon and other nutrients, providing insights into how carbon is cycled and stored in the ocean (Aumont et al., 2015; Zhang et al., 2024). The chemoattraction of marine fauna to dimethyl sulfide (DMS) plays a crucial role in natural iron fertilization, which in turn enhances carbon sequestration in high-nutrient, low-chlorophyll (HNLC) areas. This process highlights the interconnectedness of the carbon, iron, and sulfur cycles in marine ecosystems.

2.2 Nitrogen and phosphorus cycles

The nitrogen and phosphorus cycles are fundamental to marine biogeochemistry, influencing primary productivity and ecosystem dynamics. Nitrogen cycling, driven by microbial processes, includes nitrogen fixation, nitrification, and denitrification. These processes are sensitive to environmental changes such as ocean acidification, which can alter the rates of nitrogen transformations and impact microbial community composition (Wannicke et al., 2018). The eco-energetic strategies of chemolithoautotrophic microorganisms, which participate in the nitrogen cycle, are essential for understanding how these processes respond to global change. Phosphorus, on the other hand, is a limiting nutrient in many marine environments. Recent advances have revealed a more dynamic and interconnected phosphorus cycle than previously understood, with significant implications for marine productivity and ecosystem structure. The coupling of phosphorus with carbon, nitrogen, and metal cycles underscores its integral role in marine biogeochemistry.

2.3 Sulfur and iron cycles

Sulfur and iron cycles are closely linked with other biogeochemical processes in marine environments. Sulfur cycling, primarily driven by sulfate reduction, is a major component of the microbial ecology in marine sediments. This process is interconnected with the cycles of carbon, nitrogen, and iron, influencing both cellular and ecosystem-level processes (Wasmund et al., 2017). The role of sulfur-transforming microorganisms in these cycles is critical for understanding the overall biogeochemical dynamics of marine sediments. Iron, a limiting nutrient in many ocean regions, is recycled by marine biota, enhancing carbon assimilation and linking the iron and carbon cycles (Savoca, 2018). The interaction between sulfur, iron, and carbon cycles is further exemplified by the chemoattraction of marine fauna to DMS, which triggers iron recycling and augments carbon sequestration in HNLC waters. These interconnected cycles highlight the complexity and interdependence of marine biogeochemical processes.

3 Ecosystem Evolution in Response to Biogeochemical Changes

3.1 Long-term shifts in marine ecosystem structure

Marine ecosystems are undergoing significant structural changes due to various biogeochemical alterations. Ocean acidification (OA) and warming are primary drivers of these shifts, leading to a simplification of ecosystem structure and function. This simplification is characterized by reduced energy flow among trophic levels and limited acclimation potential for many species (Gamfeldt et al., 2015). Habitat-forming species such as coralligenous reefs and *Posidonia oceanica* meadows are experiencing biomass reductions, which in turn affect the entire marine community and ecosystem services (Zunino et al., 2021). These changes suggest a reorganization of energy flows and a decrease in ecosystem size, indicating a high degree of ecosystem development but potentially suboptimal conditions from an anthropocentric perspective.

3.2 Impact of ocean acidification on ecosystem dynamics

Ocean acidification is profoundly impacting marine ecosystems by altering the biogeochemical cycles and the structure of biogenic habitats. The decline in pH and carbonate saturation affects habitat-forming organisms, leading to decreased biodiversity in coral reefs and mussel beds, while potentially increasing it in seagrass and

some macroalgal habitats. These habitat changes exacerbate the direct negative effects of OA on coastal biodiversity, although the predicted biodiversity increases in certain habitats are not always observed (Sunday et al., 2017; Wang, 2024). OA impacts nitrogen cycling processes, enhancing diazotrophic nitrogen fixation and reducing nitrification rates, which may shift the relative nitrogen pools and affect the upper water column's nutrient dynamics.

3.3 Changes in biodiversity and food webs

3.3.1 Shifts in marine predator-prey relationships

The combined effects of ocean warming and acidification are altering predator-prey dynamics within marine ecosystems. Increased temperatures and CO₂ levels affect primary production and metabolic rates, leading to mismatches between herbivores and carnivores. For instance, while temperature increases consumption and metabolic rates of herbivores, secondary production decreases with acidification, creating a mismatch with carnivores whose metabolic and foraging costs increase with temperature (Nagelkerken and Connell, 2015). These changes in predator-prey relationships can lead to shifts in community compositions, favoring non-calcifying species and microorganisms.

3.3.2 Adaptations of marine species to nutrient changes

Marine species are adapting to nutrient changes driven by biogeochemical alterations such as ocean acidification. For example, the enhancement of diazotrophic nitrogen fixation under OA conditions suggests that certain nitrogen-fixing species may thrive, potentially altering microbial community compositions. However, the responses are species- and strain-specific, indicating that some species may be better adapted to these changes than others (Wannicke et al., 2018). The shifts from calcified to non-calcified habitats under OA conditions lead to decreased diversity of associated fish species, favoring those better adapted to simplified ecosystems dominated by algae (Cattano et al., 2020). These adaptations highlight the complex interplay between biogeochemical changes and marine species' responses, which ultimately shape ecosystem dynamics and biodiversity.

4 Observational Approaches to Studying Marine Biogeochemistry

4.1 Remote sensing and satellite observations

Remote sensing and satellite observations have revolutionized the study of marine biogeochemistry by providing rapid and synoptic data across multiple spatial and temporal scales. These technologies are particularly useful for monitoring biodiversity in critical coastal zones, where human activities and climate change are causing rapid alterations (Figure 1) (Kavanaugh et al., 2021). Satellite-derived data, such as ocean color properties, allow for the observation of surface ocean biogeochemical processes with unprecedented coverage and resolution (Jönsson et al., 2023). However, challenges remain due to complex bio-optical signals and suboptimal algorithms, which can hinder accurate data retrieval. Recent advancements in remote sensing, such as the use of the Wasserstein distance, have improved the comparison of satellite data with model simulations, enhancing our understanding of temporal dynamics in the ocean (Hyun et al., 2021).

This set of images presents a comprehensive study assessing the distribution, biomass, and environmental parameters of coastal ecosystems (such as kelp forests, coral reefs, and seagrass beds) using remote sensing and field observation techniques. It includes spectral reflectance data at different depths and the spatiotemporal variations of spatial distribution. Remote sensing and satellite observation technologies have greatly enhanced our ability to monitor and understand coastal ecosystems, especially in response to rapidly changing climate and human disturbances. Through these technologies, scientists can quickly and comprehensively obtain information on ecosystem health, providing a scientific basis and decision support for the conservation and management of coastal biodiversity.

4.2 In situ measurement technologies

In situ measurement technologies are essential for obtaining high-resolution data on marine biogeochemical processes. Autonomous platforms, such as the Biogeochemical-Argo (BGC-Argo) floats, are equipped with sensors that measure key biogeochemical variables like oxygen, nitrate, pH, and chlorophyll a (Chai et al., 2020; Claustre et al., 2020). These platforms provide temporally and vertically resolved observations, filling large gaps

in ocean-observing systems and supporting the management of ocean resources. Cost-effective in situ sensors have emerged, driven by advancements in miniaturization and mass production, enabling large-scale deployments and high-resolution data collection (Organelli et al., 2019). These technologies are crucial for understanding complex system processes and rapidly evolving changes in ocean biogeochemistry.

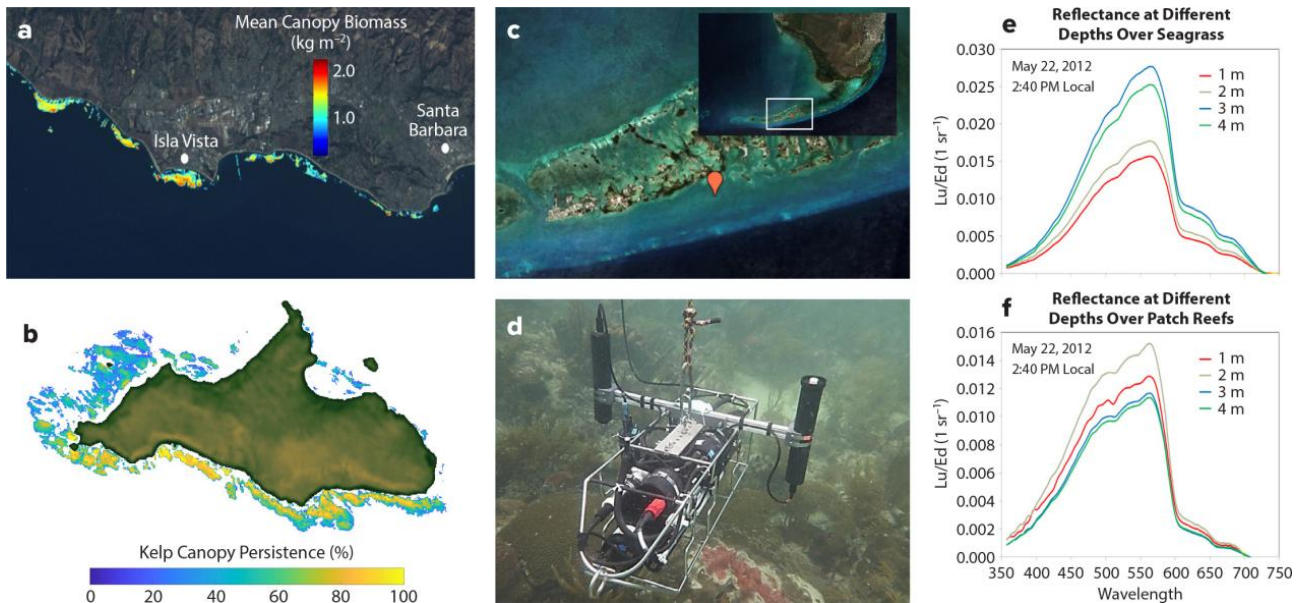


Figure 1 Development of foundation species algorithms for moderate spectral resolution, higher spatial resolution sensors (Adopted from Kavanaugh et al., 2021)

Image caption: (a) Mean macrocystis canopy biomass derived from Landsat satellite sensors. (b) Kelp persistence for San Miguel Island, California, using kelp canopy data derived from Landsat sensors. (c) Sentinel-2 composite image of the Florida Keys region where MBON surveys are regularly conducted. (d) Instrument used for in situ measurements of upwelling and downwelling irradiances above a patch reef during a field campaign in May 22, 2012, near Sugarloaf Key (red marker in c). (e) Reflectances over different depths above seagrasses. (f) Reflectances over different depths above patch reefs (Adopted from Kavanaugh et al., 2021)

4.3 Long-term observational networks

Long-term observational networks are vital for monitoring changes in marine ecosystems and biogeochemical cycles over extended periods. The BGC-Argo project is building a global network of autonomous floats that provide continuous, high-quality data on biogeochemical properties. These networks support the evaluation of ongoing changes due to anthropogenic pressures, such as acidification and deoxygenation, and contribute to sustainable ocean management. Additionally, the European Marine Omics Biodiversity Observation Network (EMO BON) aims to establish standardized, coordinated, and long-term omics observation networks to assess biodiversity and ecosystem functioning on a large scale. Such networks enhance observational power and provide structured, comparable data, which are essential for effective conservation measures and sustainable use of marine resources (Santi et al., 2023).

5 Predictive Modeling of Marine Ecosystem Evolution

5.1 Climate models and ocean biogeochemistry

Climate models play a crucial role in understanding and predicting the impacts of climate change on marine biogeochemical processes. These models integrate various environmental drivers such as ocean warming, acidification, and oxygen depletion to simulate the responses of marine ecosystems. For instance, process-based models have been developed to quantitatively integrate physiological and ecological processes, thereby advancing research and informing management strategies for marine fish populations (Koenigstein et al., 2016). Biogeochemical models are employed to simulate key ecosystem components like chlorophyll-a, nutrients, carbon, and oxygen cycles across different marine environments, although they still face limitations and assumptions that need addressing (Ismail and Al-Shehhi, 2023).

5.2 Predictive models of ecosystem changes

Predictive models of ecosystem changes are essential for forecasting the future trajectories of marine ecosystems under various climate change scenarios. Tools like EcoOcean (v2) have been developed to simulate spatial-temporal ecosystem dynamics, linking species productivity, distributions, and trophic interactions to the impacts of climate change and fisheries (Coll et al., 2020). These models use Earth-System Models (ESMs) and Representative Concentration Pathways (RCPs) to project future changes, showing how different configurations and environmental drivers can lead to varying ecological outcomes. The integration of adaptive evolution into these models can provide a more accurate representation of ecosystem responses over evolutionary timescales, which is particularly relevant for understanding past extinction events and future anthropogenic disruptions (Ward et al., 2019).

5.3 Challenges in modeling ecosystem evolution

Despite the advancements in predictive modeling, several challenges remain in accurately forecasting marine ecosystem evolution. One significant challenge is the sparse biogeochemical observation streams, which hinder the development and validation of biogeochemical and ecological models (Fennel et al., 2019). The complexity of marine ecosystems, influenced by multiple stressors and interacting processes, makes it difficult to achieve reliable predictions. For example, the lack of a clear understanding of physical and biological processes, coupled with insufficient observations for forecast initialization and verification, limits the predictability of ecosystem states on sub-seasonal to interannual timescales (Capotondi et al., 2019). Existing models often show discrepancies in local variability and interannual patterns, highlighting the need for improved model robustness and appropriateness for different applications (Ramirez-Romero et al., 2020).

6 Case Studies: Observational and Predictive Approaches in Action

6.1 The role of biogeochemical cycles in coral reef decline

Coral reefs are experiencing significant declines due to various stressors, including changes in biogeochemical cycles. Microorganisms play a crucial role in these cycles, influencing nutrient dynamics and ecosystem health. For instance, nutrient enrichment, particularly nitrogen (N) and phosphorus (P), has been shown to negatively impact invertebrate populations, which are essential for coral reef ecosystems. Microbial communities in coral reefs, such as those in the Great Barrier Reef, are highly sensitive to nutrient loads and temperature changes, which can serve as indicators of reef health. However, current predictions about coral reef decline are based on sparse datasets, highlighting the need for more comprehensive and uniform data collection to improve our understanding and predictive capabilities (Hochberg and Gierach, 2021).

6.2 Predictive models for polar ecosystem changes

Predictive models are essential for understanding and forecasting changes in polar ecosystems, which are particularly vulnerable to climate change. Biogeochemical models, such as PISCES-v2, simulate the interactions between various components of marine ecosystems, including phytoplankton and zooplankton, and the cycles of key nutrients like carbon, nitrogen, and phosphorus (Aumont et al., 2015). These models have been successful in simulating current global carbon and nutrient cycles and are increasingly used to project future changes under different climate scenarios (Ward et al., 2019). However, the incorporation of adaptive evolution into these models is crucial, as evolutionary processes can significantly alter ecosystem responses to environmental changes over long timescales. Expanding biogeochemical observation systems in polar regions will further enhance the accuracy and applicability of these predictive models (Fennel et al., 2019).

6.3 Observations of nutrient cycling in coastal zones

Nutrient cycling in coastal zones is a critical aspect of marine biogeochemical processes, influencing ecosystem health and productivity. Observational studies have shown that nutrient enrichment, particularly from human activities, can lead to declines in invertebrate populations, which are key players in nutrient cycling and ecosystem functioning (Nessel et al., 2021). Microbial communities in coastal zones exhibit distinct spatial patterns and are influenced by nutrient dynamics and temperature, which can serve as indicators of ecosystem health (Frade et al., 2020). The integration of omics approaches with traditional ecological studies can provide a more comprehensive

understanding of how environmental changes impact microbial communities and nutrient cycling. This integrated approach will improve our ability to predict and manage the impacts of nutrient enrichment and other stressors on coastal ecosystems.

7 Conclusion

Marine ecosystems are undergoing significant changes due to both natural and anthropogenic factors. A meta-analysis of 110 marine experiments revealed that species richness generally enhances ecosystem function, although the effect varies depending on the specific ecosystem process being measured. Ecological niche models (ENMs) and species distribution models (SDMs) have become crucial tools for understanding species distribution patterns and their underlying processes, with significant applications in conservation and climate change impact assessments. Biogeochemical models have been instrumental in simulating key ecosystem components such as chlorophyll-a, nutrients, and carbon cycles across various marine environments, although they still face limitations and require further refinement. The integration of biogeochemical and ecological models with ocean circulation models has shown promise in monitoring and managing ecosystem health, despite challenges related to sparse biogeochemical observation streams. Additionally, the role of adaptive evolution in marine ecosystems is increasingly recognized as a critical factor that can influence the accuracy of model projections

Future research should focus on expanding biogeochemical and ecological observation systems to improve the accuracy and applicability of predictive models. Incorporating adaptive evolution into marine ecosystem models is essential for better understanding long-term ecosystem responses to environmental changes. There is also a need to integrate omics data with earth system science to enhance our quantitative understanding of marine microbial roles in biogeochemical cycles. The use of advanced data assimilation techniques, such as those involving BGC-Argo measurements and satellite-derived phytoplankton functional type data, can significantly improve model predictability and reduce uncertainty. Moreover, exploring multiple post-extinction compensatory scenarios can provide more realistic projections of ecosystem futures, aiding in the development of effective management strategies.

Integrating biogeochemical and ecological models with conservation efforts is crucial for developing effective strategies to mitigate the impacts of climate change and other anthropogenic stressors on marine ecosystems. Predictive models can guide conservation policies by providing insights into the potential outcomes of different management scenarios. The use of ENMs and SDMs can help identify critical habitats and species at risk, informing targeted conservation actions. Additionally, understanding the functional responses of ecosystems to biodiversity loss and community reorganization can improve the reliability of ecological projections and support adaptive management practices. By combining observational data with advanced modeling techniques, we can enhance our ability to protect and sustain marine biodiversity and ecosystem functions in the face of ongoing environmental changes.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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