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Roles of Marine Microorganisms in the Carbon, Nitrogen, and Sulfur Cycles

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Abstract Marine microorganisms play a core role in the global biogeochemical cycle, especially in the cycles of the three key elements of carbon (C), nitrogen (N), and sulfur (S), which are of great significance for maintaining the functions of Marine ecosystems and regulating the global climate. This study systematically reviews the diversity, ecological distribution and metabolic mechanisms of Marine microbial communities involved in the C-N-S cycle. Through empirical cases in the anoxic zone of the Black Sea, the thermocline of the Pacific Ocean and polar sea areas, it demonstrates the regulatory role of microbial communities in specific Marine regions on regional element cycles. Meanwhile, this study also explored the application prospects of emerging approaches such as metagenomics, stable isotope probe technology, and synthetic biology in the functional research of Marine microorganisms. This study aims to provide a microbiological perspective for a deeper understanding of the Marine element cycle and offer theoretical support for Marine carbon sink management and climate regulation policies.

Keywords Marine microorganisms; Carbon cycle; Nitrogen cycle; Sulfur cycle; Biogeochemical processes

1 Introduction

The ocean, this blue area that covers most of the Earth's surface, is not merely a landscape. The cycles of key elements such as carbon, nitrogen and sulfur often take place here. They are related to the operation mode of the entire ecosystem and also influence the direction of the climate. Although these cycles are driven by the joint efforts of physical, chemical and biological processes, they are not clearly distinct but interrelated. Processes like carbon sequestration and nutrient regeneration, in the final analysis, are also closely related to the release and transformation of greenhouse gases (Dong et al., 2024).

As for who is behind the scenes working on the transformation of these elements? It's not really large organisms, but rather those Marine microorganisms that we usually can't see - bacteria, archaea, phytoplankton, all of which are the main force. Whether it is photosynthesis, nitrogen fixation, nitrification, denitrification, or even sulfate reduction, all these processes cannot do without their intervention. In the past, people might have focused on some "mainstream paths", but now more and more research is beginning to pay attention to those small prokaryotes and facultites that were not well studied in the past. They perform well in some obscure but important cyclic links and are widely distributed, almost covering all kinds of Marine environments (Pajares and Ramos, 2019). But then again, this system is actually not that stable. Once the activity of microorganisms is affected, the entire cycle may go hayline. The factors influencing them are not simple at all - ocean warming, acidification, and hypoxia. These environmental changes may disrupt the rhythm of the microbial community, thereby affecting the transformation efficiency and circulation path of the entire system (Hutchins and Capone, 2022).

This study aims to comprehensively analyze the current understanding of the role of Marine microorganisms in the carbon, nitrogen and sulfur cycles, with a focus on elaborating their functional diversity, ecological significance and response to global change. This study will review the mechanisms by which microorganisms mediate key transformation processes in the cycles of various elements, explore the progress made in identifying novel microbial groups and metabolic pathways in recent years, point out knowledge gaps and future research directions, especially in the context of human influence and climate change. By integrating the achievements of molecular, ecological and model studies, this research aims to comprehensively expound how Marine microbial processes shape Marine biogeochemistry and thereby influence the Earth system.

2 Diversity and Ecological Functions of Marine Microbial Communities

2.1 Classification of microorganisms: bacteria, archaea, and planktonic eukaryotes

Whether it is seawater, sediment or suspended biofilms, there are indeed many types of microorganisms in the ocean, which are generally classified into three major categories: bacteria, archaea and plankplankton eukaryotes. Most of the metabolic functions you can think of can find their "specialized players" among them. Bacteria and archaea are very common in most Marine environments, especially in seabed sediments, where their types and functions are rich. In contrast, planktonic eukaryotes (such as some protozoa and microalgae), although not necessarily in large numbers, are one of the main forces maintaining primary production and nutrient cycles. These three types of organisms do not act independently of each other. Instead, they interact and influence each other in the food web, and their metabolic activities are linked together, supporting the material cycle of the entire Marine ecosystem (Herve et al., 2025).

2.2 Distribution patterns of microorganisms in different marine niches

When it comes to where microorganisms are abundant, merely looking at seawater is not enough. Factors such as depth, salinity and temperature have a significant impact. Microorganisms living in open seas, nearshore areas, sediments or biofilms also vary. For example, in sediments, the types of microorganisms are usually more numerous than in water bodies. Some types are almost exclusively "sediment-specific", while others prefer open waters (Ul-Hasan et al., 2019; Zhang et al., 2019). In terms of planktonic eukaryotes, their distribution is more significantly affected by nutrient ratio, mixed layer depth and pH. For instance, the high-yield upwelling region is their "dense area" (Liu et al., 2025; Yanez et al., 2025). Another point that is easily overlooked is that the types of microorganisms in biofilms are completely different from those in water bodies, which is also a "hidden corner" of Marine microbial diversity.

2.3 Functional redundancy and ecosystem stability in microbial communities

In fact, the scientific community has long been debating whether microorganisms have a "backup mechanism". Functional redundancy refers to the situation where multiple species can perform the same task. In the early days, some people thought it was fine that the system could still function normally without one species. But recent studies have begun to challenge this "foolproof" idea - once the community structure changes, the functional performance may also change accordingly. Although functional traits are much more stable than taxonomic structures in different environments, which helps maintain ecological balance, the degree of "redundancy" actually varies by location and function (Song et al., 2022). The more complex the microbial community is, the stronger its theoretical ability to cope with external disturbances. However, it is not the case that the more complex, the better - too much interconnection and mutual disturbance may instead become an unstable factor of the system (Royalty and Steen, 2021; Lee et al., 2025).

It is precisely for this reason that issues such as the diversity of Marine microorganisms, where they are distributed, and what each can do are worth continuous tracking. After all, the way they exist directly determines whether the Marine ecosystem can operate stably and withstand environmental pressure.

3 Roles of Marine Microorganisms in the Carbon Cycle

3.1 Carbon fixation mechanisms of photosynthetic microorganisms

If we talk about who is the main force behind Marine carbon fixation, cyanobacteria and phytoplankton definitely have to be on the list - they contribute nearly half of the global photosynthesis output. But things are not as simple as they seem. Because there is not much dissolved carbon dioxide in seawater to start with, and enzymes like Rubisco have a relatively low "affinity" for CO_2, many microorganisms have long evolved their own carbon concentration mechanisms (CCMs) to address this "efficiency bottleneck". By actively absorbing bicarbonate (HCO_3^-) and utilizing carbonic anhydrase, these mechanisms can help them "work efficiently" under various water conditions and are less likely to fail (Kupriyanova et al., 2023; Beer and Beardall, 2025). Interestingly, these CCMs exhibit extremely high diversity and flexibility in cyanobacteria and phytoplankton. This "adaptability" precisely reflects their long-term adaptation to CO_2 fluctuations and light changes (Lu et al., 2023; Jaffe et al., 2024).

3.2 Microbial carbon pump and remineralization of dissolved organic carbon (DOC)

Primary production is only half the story. Microorganisms also play an indispensable role in the "post-treatment" aspect - especially in the conversion and long-term storage of carbon. The so-called microbial carbon pump (MCP) refers to the transformation of easily decomposable dissolved organic carbon (DOC) into a more stable and refractory form by microbial communities. These "stubborn molecules" can exist in the deep sea for thousands of years, providing unexpected support for carbon sequestration (Hach et al., 2020). During this process, heterotrophic bacteria and archaea are the main forces. They can not only efficiently degrade organic matter but also transform some DOC into long-term inventory through mutual feeding and metabolic collaboration in a "back-and-forth" manner. However, these mechanisms do not work unconditionally - community composition, environmental gradient and substrate source all affect the efficiency of remineralization (Kong et al., 2021).

3.3 Contributions of deep-sea microbes to carbon storage

Compared with the surface area, the carbon cycle in the deep sea has always seemed more covert, but in fact, it cannot be ignored. Especially those rare but "resilient" prokaryotic microbial communities, they have a knack for converting unstable DOC into stable and highly oxidizing molecules. This stable DOC is an important component of deep-sea carbon inventory, and the "main force behind maintaining this inventory" is these low-key microorganisms. Furthermore, it is precisely their community succession and diverse metabolic capabilities that support the efficient operation of the microbial carbon pump (MCP) in the deep sea, making the deep sea truly a reliable carbon sink and also an important link influencing global climate regulation (LaBrie et al., 2022).

4 Roles of Marine Microorganisms in the Nitrogen Cycle

4.1 Nitrogen fixation and conversion of atmospheric nitrogen by microorganisms

In the past, people always thought that only a few blue-green algae were responsible for nitrogen fixation in the sea. But the actual situation is not that simple. It has now been discovered that, apart from chain-like cyanobacteria, many single-celled cyanobacteria and heterotrophic bacteria can also "grab" nitrogen (N_2) from the air and convert it into ammonia. More importantly, they do not all live in the traditionally believed areas, but are more widely distributed and have more complex environments (Fernandez et al., 2011; Zehr and Capone, 2020). Although this process is quite energy-consuming, it is indeed an important "dark pipeline" for the ocean to replenish nitrogen sources. Especially in the context of denitrification and anaerobic ammonium oxidation consuming a large amount of nitrogen, this replenishment becomes even more crucial. Without these nitrogen-fixing microorganisms, Marine primary production might have run out of food long ago.

4.2 Microbial regulation of nitrification and denitrification processes

Nitrogen is running around in the ocean. In fact, it is the microorganisms at both ends that are "fiddling" - on one side is nitrification, which oxidizes ammonia into nitrate, and on the other side is denitrification, which reduces nitrate back to nitrogen gas. It sounds like "reverting to the original state". But things in between were not so smooth. The driving forces of these two processes are ammonia-oxidizing archaea, nitrite-oxidizing bacteria, and various denitrifying bacteria and archaea. These microorganisms are distributed in areas with thin oxygen, such as sediments or Marine "oxygen zones" (Pajares and Ramos, 2019). These processes are greatly influenced by the environment. The amount of oxygen and organic matter will both affect their "working efficiency". In addition, incidentally, these two mechanisms also release nitrous oxide, a potent greenhouse gas, during the "operation" process (Wang et al., 2025). To understand exactly how nitrogen circulates in the sea, the spatiotemporal "coordination degree" of these two processes is an unavoidable issue (Muck et al., 2019).

4.3 Role of anaerobic ammonium oxidation (Anammox) in deep-sea nitrogen loss

In those oxygen-deficient or even oxygen-free areas of the ocean, a portion of nitrogen will "disappear out of thin air", and the driving force behind this is anaerobic ammonia-oxidizing bacteria. Their operation method is rather "straightforward" - they directly combine ammonium and nitrite to form nitrogen gas and then volatilize it. This kind of path is particularly active in deep-sea sediments. Even in some areas, they contribute half of the nitrogen loss. Moreover, these types of bacteria not only have a large number but also strong adaptability. Many of them even hide in extreme environments and work quietly (Wang and Wang, 2025). For this reason, their position in the global nitrogen cycle cannot be ignored, and it also makes us rethink how much role the deep sea plays in the nitrogen balance of the entire earth.

5 Roles of Marine Microorganisms in the Sulfur Cycle

5.1 Sulfur-oxidizing bacteria and the oxidation of hydrogen sulfide

The microorganisms in Marine systems are "well aware" that H_2S itself is toxic. Sulfur-oxidizing bacteria (SOBs) have been striving to convert these reduced sulfides, such as hydrogen sulfide, into milder and more oxidized sulfates (SO_4^{2-}) - a form of sulfur that is both stable and practical for Marine ecosystems. However, it is not only the chemoautotrophic SOBs mentioned in textbooks that are involved in this work. Those often overlooked heterotrophic prokaryotes, especially certain proteobacteria, are also "very active" in the sediment. They use various enzymes, such as SQR (sulfide: quinone oxidoreductase) and PDO (persulfide dioxygenase), to gradually oxidize the sulfides. During this process, it will pass through "intermediate stations" such as zero-valent sulfur and sulfites, and ultimately generate sulfates that do not volatilize easily, avoiding H_2S directly escaping into the water body (Wang et al., 2019). Moreover, among these different types of microorganisms, sulfur intermediates can be transferred to each other. This "relay race" mechanism makes sulfur oxidation in sedimentary environments more efficient and stable (Figure 1) (Alamoudi et al., 2025; Chen et al., 2025; Ogola et al., 2025).

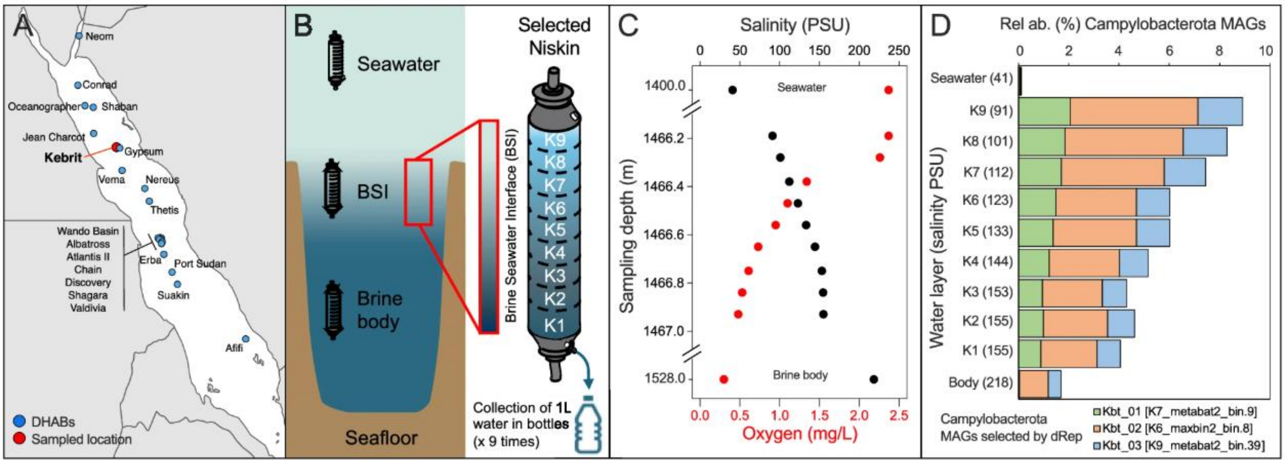

Figure 1 Chemocline of Kebrit Deep BSI and associated *Campylobacterota* diversity (Adopted from Alamoudi et al., 2025)

5.2 Sulfate-reducing bacteria and metabolic pathways in anaerobic environments

In anoxic environments, sulfate-reducing bacteria (SRB) always play a key role. This type of anaerobic bacteria can reduce sulfates to sulfides, completing the "final step" of organic matter decomposition. Especially in Marine sediments, this step is almost the end of the mineralization process. They are not confined to a certain group. In fact, they can also be found in various uncultured lineages, especially in surface sediments and deeper anoxic zones. SRB also has a rather diverse diet, with a wide variety of substrate species. Coupled with the fact that they often form biofilms in groups, this enables them to better withstand environmental changes and also participate in beneficial reactions such as heavy metal precipitation. Of course, sometimes it can also bring troubles like corrosion (Saxena et al., 2025). However, SRBS do not act alone. They often mix with methanogens and sulfur-oxidizing bacteria to jointly shape the appearance of the entire sulfur cycle and also affect the ecological stability of the system (Jørgensen et al., 2019).

5.3 Dimethyl sulfide (DMS) formation and its climatic implications

Regarding DMS (i.e., dimethyl sulfide), it is often linked in discussions about climate regulation. This gas comes from DMSP, a small molecule synthesized by phytoplankton. After being released into seawater, it is "taken over" by some Marine bacteria and transformed into DMS. Once DMS volatilizes, it may participate in the formation of sulfate aerosols in the atmosphere, thereby affecting cloud formation and even potentially fine-tuning the climate (Jackson and Gabric, 2022). But not all DMS can escape from the sea surface - most of them have actually been "eaten" by other microorganisms long ago or disintegrated in the sunlight. Therefore, the actual release of DMS in the ocean largely depends on this delicate balance between transformation and consumption. This balance is controlled by factors such as temperature, light and changes in microbial populations. Moreover, it is very likely to be reshuffled by climate change (Qian et al., 2024).

6 Case Studies: Microbial Contributions to Elemental Cycles in Specific Marine Regions

6.1 Community structure and functions of sulfur-oxidizing bacteria in the black sea anoxic zone

The Black Sea, a large oxygen-deficient sea area without seasonal improvement, has long attracted the attention of researchers for its unique features. Near its chemical stratosphere, there lives a type of sulfur-oxidizing bacteria (SOB) that rely on an anaerobic environment. Among them, the most common ones are the SUP05 branch of γ - Proteobacteria, as well as thiomonas and *Microspira vulcanis* (Vliet et al., 2020). They do not rely on oxygen but use nitrates or manganese oxides to oxidize sulfides. These microorganisms not only participate in carbon fixation, but also support a part of the main productivity at the bottom of the Black Sea - contributing up to nearly half of the primary production (Henkel et al., 2022). The microbial community in the Black Sea is not uniform but rather layered: SOAs are mainly concentrated in the transitional zone of the REDOX cascade, forming complex interactions with the surrounding sulfate-reducing bacteria, methane-oxidizing bacteria and denitrifying bacteria, jointly promoting the cycle among sulfur, carbon and nitrogen.

6.2 Microbial nitrogen cycling characteristics in the pacific thermocline layer

The thermocline of the Pacific Ocean serves as a dividing line, where oxygen and nutrients show significant differences between the upper and lower layers, and this precisely provides their respective positions for various nitrogen cycle microorganisms. Archaea like Thaumarchaeota dominate the upper layer of ammonia oxidation, while Nitrospinae are the "experts" in the downstream treatment of nitrite. Further down, in the area where oxygen is nearly depleted, anaerobic ammonia-oxidizing bacteria such as Scalindua and denitrifying bacteria come into play (Pajares and Ramos, 2019). Metagenomic data show that water depth almost determines who stays - the frequent occurrence of certain genes among different populations suggests possible functional redundancy, but ecological selection remains obvious (Figure 2) (Song et al., 2022). The balance between nitrogen supply and loss is quietly achieved among these microorganisms and also affects the primary productivity of the entire sea area.

6.3 Empirical study of carbon uptake by photosynthetic plankton in polar oceans

The polar regions are not deserts for life. On the contrary, small photosynthetic phytoplankton thrive there quite vividly. Their ability to absorb carbon largely depends on light, nutrient concentration and ice coverage. In some in-situ experiments in the Arctic and subarctic, researchers, using isotope labeling and fluorescence assays, found that these small phytoplankton sometimes contribute more than 80% of total carbon and nitrogen fixation. However, the efficiency of carbon fixation fluctuates greatly in different years and even under different ice conditions. For instance, microphytoplankton and micro-phytoplankton take turns to "take the center stage", which is closely related to light conditions, nitrate consumption rate and phytoplankton size (Zhu et al., 2019). In other words, whether polar phytoplankton communities can adapt to global warming may depend on whether they can flexibly respond to these constantly changing factors.

7 Application of Advanced Techniques in Marine Microbial Research

7.1 Use of metagenomics and metatranscriptomics in functional analysis

In the context where many Marine microorganisms cannot yet be cultivated, metagenomic and metatranscriptomic technologies have become shortcuts to directly understand them without culturating them. Researchers have used these techniques to reconstruct the transcriptome of Marine plankton eukaryotes. Some key metabolic processes, such as DMSP synthesis or nitrogen fixation, have thus identified the core "behind-the-scenes players" (Xu et al., 2024). In deep-sea hydrothermal environments, some species, although having similar functions, clearly divide their roles through metabolic differences. Such niche division and collaboration mechanisms have gradually emerged in this type of research. Tools like HUMAnN2 have been able to break down community functions to the species level, saving time and being precise. The emergence of long-read sequencing technology has "stitched together" many previously difficult-to-assemble full-length biosynthetic gene clusters, and the diversity of secondary metabolites has thus been presented more completely (Huang et al., 2023).

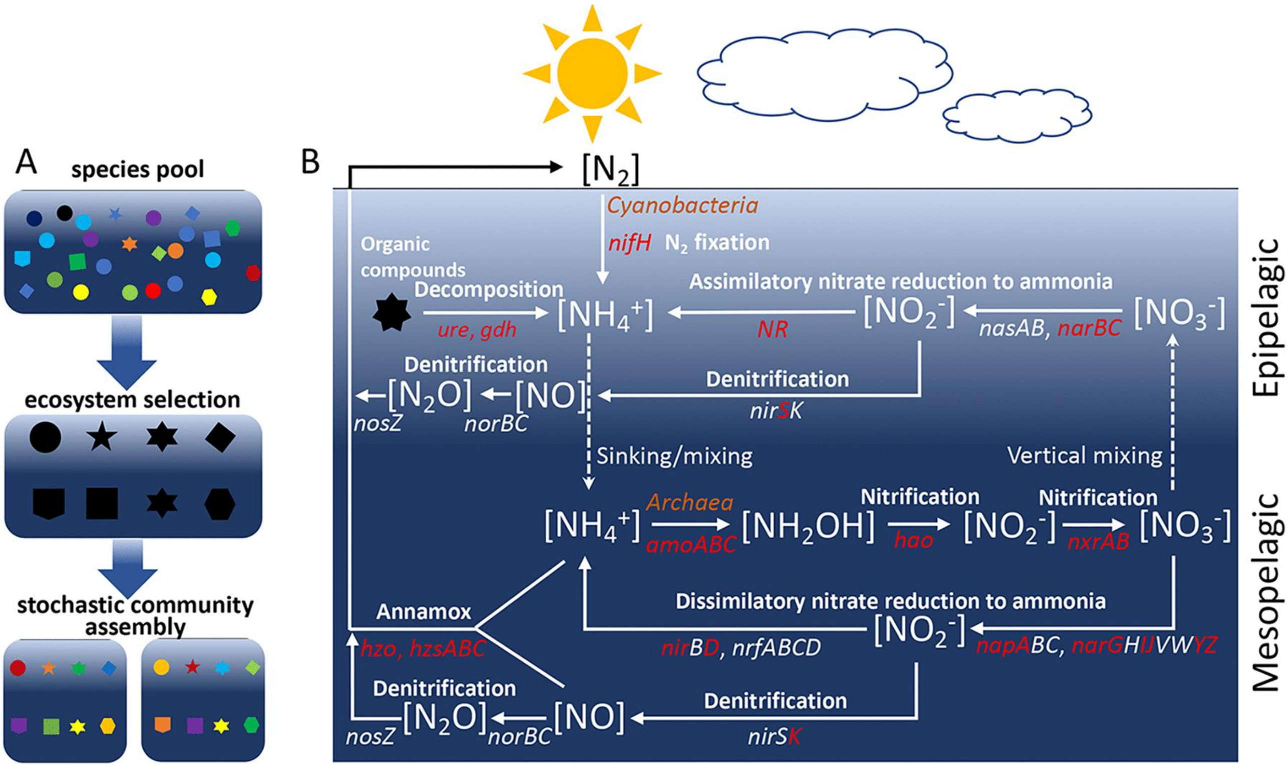

Figure 2 Conceptual models illustrating the community assembly and distribution of N-cycling pathways in the oceanic ecosystem (Adopted form Song et al., 2022)

7.2 Stable isotope probing (SIP) for tracing metabolic fluxes

If you want to know exactly what a certain Marine microorganism "eats" and which metabolic reactions it participates in, SIP technology is very useful. It relies on feeding microorganisms "labeled" substrates (such as ^{13}C, ^{15}N, D_2O), and then observing which biological macromolecules these labels have landed on. For instance, early on, the role of methylphagocytes in methanol and methylamine metabolism was determined by SIP. In addition to DNA and RNA, lipids and proteins can also be used for SIP labeling. These methods can complement each other and enable people to clearly see the specific destinations of carbon and nitrogen, which is particularly valuable when studying methane oxidation and sulfate reduction in sediments. Sometimes it is necessary to reach the nanoscale to see clearly - NanoSIMS, in combination with FISH and SIP, can track the nutritional interactions between microorganisms at the single-cell level (Yan, 2025).

7.3 Frontiers in synthetic biology and artificial ecosystem simulation

Not all research relies on "observation". Nowadays, more and more approaches are to "build a system and take a look". Synthetic biology is like equipping microorganisms with a "program". Some modified Marine bacteria or cyanobacteria can already be applied in biomanufacting, pollution remediation, and even ecological restoration (Bourgade and Stensjo, 2022). Some strains, such as Vibrio natriegens and Halomonas bluephagenesis, which grow fast and have flexible metabolism, are perfectly suitable to be used as "platforms" (Hoff et al., 2020; Von Borzyskowski, 2023). Simulating a complete algal-microbial community is no longer a difficult problem. With the advancement of artificial ecosystem design, researchers have been able to control the population ratio and interaction relationship relatively well (Deter and Lu, 2022; Jiang et al., 2022). Combined with techniques such as spectral analysis and dynamic modeling, it is not only possible to observe community changes in real time, but also to predict how they respond to environmental changes (Meirkhanova et al., 2024).

8 Conclusion and Future Perspectives

The microbial system in the ocean is very complex. After all, they are not just some invisible little creatures. From bacteria to archaea and then to planktonic-eukaryotes, they drive the cycle of carbon, nitrogen and sulfur - for instance, key steps such as carbon fixation, nitrogen fixation, nitrification and denitrification basically all rely on their participation. The role these microorganisms play in removing carbon dioxide from the atmosphere, releasing oxygen, and maintaining the Marine food chain is actually much greater than people imagine (fixing carbon, catalyzing the sulfur cycle, supporting nutrient regeneration, etc.).

However, to be fair, although technological progress has brought about many new tools, our understanding of most areas of the ocean remains limited, especially the deep sea and the polar regions. The functions of many microorganisms are still unclear at present, especially those groups that cannot be cultivated. Many questions remain unanswered to this day, such as what their genes are used for, how they react to environmental changes, or what role they play in global-scale ecological models. This requires more solid long-term observation, more sensitive single-cell technology, and it would be best to consider both "who it is" and "what it is doing" in combination.

As climate change intensifies, trends such as ocean warming, acidification and hypoxia are quietly reshaping the landscape of the microbial world. Some groups, such as nitrogen-fixing cyanobacteria, might live better as a result; But others, such as calcifying organisms or nitrifying bacteria, may not be so fortunate. The adaptability of microbial communities is of great significance as it is related to whether the entire ecosystem can maintain stability. However, if climate pressure continues to intensify, the biogeochemical cycle is likely to be disrupted, and the service functions of the ocean will be affected as a result. So the future direction, I'm afraid, cannot rely solely on traditional means. More genomic support is needed, mesoscale ecological experiments are relied upon, and closer international cooperation for monitoring is required. These not only help us clearly understand the changes in the microbial community, but also enable us to design more scientific response strategies. It is even possible that by mobilizing certain functions of microorganisms, they can be used for carbon sequestration or the restoration of Marine ecology.

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Conflict of Interest Disclosure

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