

Review Article

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Bioavailability of Phosphorus in Marine Ecosystems: Sources, Transport, and Ecological Impacts

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Abstract Phosphorus is a fundamental and critical biogenetic factor in marine ecosystems, and its bioavailability directly affects the efficiency of marine primary productivity and biogeochemical cycles. In the marine environment, phosphorus mainly exists in two major forms: inorganic phosphates and organophosphorus compounds. Different sources and processes determine the input pathway and circulation mechanism of phosphorus. This study summarizes the main sources of ocean phosphorus and explores the characteristics of morphological transformation of phosphorus in the ocean. On this basis, the transportation and circulation mechanism of phosphorus are analyzed, covering the effects of physical processes such as ocean currents and upstream on phosphorus redistribution, as well as the impact of sedimentation-resuspension processes on phosphorus revenue and expenditure. Further, the status of phosphorus bioavailability in different sea areas and its ecological significance as a restricted nutrient salt is discussed, emphasizing the impact of changes in nitrogen-phosphorus ratio on the structure of phytoplankton community, the physiological adaptation strategies and gene regulation mechanisms of phytoplankton under phosphorus restriction. Finally, from the perspective of ecological and environmental, the impact of phosphorus circulation disorder on the coupling effect of marine food networks, the formation of marine hypoxic zones, and the feedback effect of phosphorus circulation in the context of climate change is discussed. Based on research progress in all aspects, this study emphasizes the core position of phosphorus in marine ecosystems and proposes prospects for future research on marine phosphorus cycles and sustainable marine management.

Keywords Phosphorus restriction; Bioavailability; Nutrient cycle; Primary productivity; Red tide

1 Introduction

Phosphorus (P) is an essential nutrient element that constitutes genetic material and energy molecules of biological cells, and plays an irreplaceable role in the structure and function of marine ecosystems. Compared with elements such as nitrogen (N), iron (Fe), phosphorus is considered to be the "ultimate" restrictive nutrient that limits ocean primary productivity on the geological time scale. Global phosphorus circulation profoundly affects marine biological pumps and global climate regulation through processes such as river output to the sea, internal ocean circulation, and marine sediment burial (Zhao et al., 2024).

Enhanced recirculation of phosphorus in paleomarine environments has led to double the burial rate of organic carbon and significant global climate cooling, accompanied by the expansion of marine hypoxic zones, and has profound impacts on biological evolution (Guilbaud et al., 2020). In modern oceans, the concentration of surface phosphate is extremely low in oligotrophic areas far away from terrestrial sources in the ocean. The strong absorption of phosphorus by phytoplankton makes phosphorus often one of the main factors limiting primary productivity in these areas. Although the phosphorus concentration in nearshore waters often has a high concentration due to terrestrial input, there is also a phenomenon of relative phosphorus deficiency in the context of eutrophication, resulting in an imbalance of nutrient structure of "excess nitrogen and phosphorus shortage" (Maslukah et al., 2021). Phosphorus restriction not only directly restricts the growth, reproduction and community composition changes of phytoplankton, but also indirectly couples the carbon and nitrogen cycles of the ocean by affecting nitrogen fixation and organic carbon fixation.

Therefore, in-depth study of the bioavailability of phosphorus in marine ecosystems is of great significance to understand the control mechanisms of global marine primary productivity and to address climate change and

marine eutrophication challenges. This study discusses the source, morphological transformation, circulation mechanism, bioavailability and ecological impact of phosphorus, and reviews relevant domestic and foreign research progress in recent years, aiming to provide a scientific basis for a comprehensive understanding of the marine phosphorus circulation and its ecological role.

2 The Main Sources of Marine Phosphorus

2.1 River input and land-source material contribution

Rivers are one of the important sources of ocean phosphorus. The phosphorus released by land weathering enters the estuary and nearshore waters through river runoff, and is transported to the ocean in the form of particulate phosphorus and dissolved inorganic phosphorus. Studies have shown that the total phosphorus delivered to the oceans by global rivers each year is about millions of tons, of which about half are settled or buried in the estuaries and continental shelf in the form of particulate phosphorus (Wallmann, 2010), and only partly enters the open ocean. The high sedimentation rate of the estuary and the complex physical and chemical environment cause the conversion of phosphorus during the sea entry: about 30% of the particulate phosphorus and a certain proportion of dissolved phosphorus will be intercepted in the estuary-near-shore area and become part of the phosphorus reservoir of the surface sediment. However, the impact of river input on offshore phosphorus supply varies by region: In high-nutrient estuaries such as the Yangtze River Estuary and the Pearl River Estuary, although the concentration of inorganic phosphorus (PO_4^{3-}) carried by river water is not as good as that of nitrogen salt, it still significantly increases the basal phosphorus level in the estuary and adjacent sea areas (Liu et al., 2022; Lan et al., 2024). Studies have found that the N/P ratio of water bodies in the estuary of the Yangtze River and the Pearl River Estuary is significantly higher, indicating that these areas are mainly restricted by phosphorus. In the estuary, sufficient freshwater phosphorus supply can promote the luxuriance of phytoplankton, but excessive N/P ratio may also trigger changes in the composition of plankton communities and potential ecological risks.

2.2 Atmospheric settlement (dust and phosphorus in aerosols)

Atmospheric transport is an important exogenous supply pathway for phosphorus away from land-sourced sea areas. Dust particles and aerosols contain a certain amount of soluble phosphorus, which can provide "airborne phosphorus reduction" to the surface seawater when they settle to the sea surface. It is reported that the phosphorus flux input to the ocean through atmospheric sedimentation worldwide accounts for about 10% of river input every year, but this proportion can reach even higher in ocean oligotrophic areas such as the mid-Atlantic Ocean. Increased soluble atmospheric phosphorus settlement may alleviate the demand for phosphorus by broad oceanic phytoplankton to a certain extent. However, atmospheric sedimentation is often accompanied by the infusion of large amounts of nitrogen nutrients, which will aggravate the excess of nitrogen and phosphorus in the surface seawater, thereby indirectly promoting the utilization of organophosphorus. Peripheral experimental research found that even in the case of relatively lack of phosphorus, the simulated aerosol settlement and nitrogen carried by river water input will further increase the N/P ratio of the water body and strengthen phosphorus restriction, thereby inducing phytoplankton to accelerate secretion and use alkaline phosphatase to decompose dissolved organophosphorus (DOP), making DOP the main source of phosphorus in phytoplankton (Figure 1) (Wang et al., 2022; Jin et al., 2024).

2.3 Seabed geological processes and phosphorus recharge from volcanic eruptions

In addition to land source input, geological processes inside the ocean are also one of the important sources of phosphorus. Subsea volcanic eruptions, hydrothermal activity and geological tectonic movements at continental edges can release phosphorus-containing fluids or promote phosphorus redissolution in sediments, replenishing nutrients to the upper water (Sai and Kakegawa, 2019; Rasmussen et al., 2021). At the hydrothermal vent of the Zhongyang ridge, although the concentration of phosphorus is not high, the hydrothermal fluid can carry certain reducing chemicals, which converts the phosphorus form in the local environment and releases usable phosphorus. Other coastal submarine groundwater leakage (SGD) will also bring phosphorus from land seepage into nearshore waters. Research shows that the dissolved phosphorus flux carried by SGD globally can be comparable to river flux in some areas, especially in densely populated and nutrient-rich coastal areas (Figure 2) (Kreuzburg et al.,

2023). In addition, the anaerobic decomposition of sediments in the continental shelf and slope areas can release phosphates, which suddenly pour into the water when geological disturbances (such as earthquakes, landslides) or overflow on the underlying anaerobic water body.

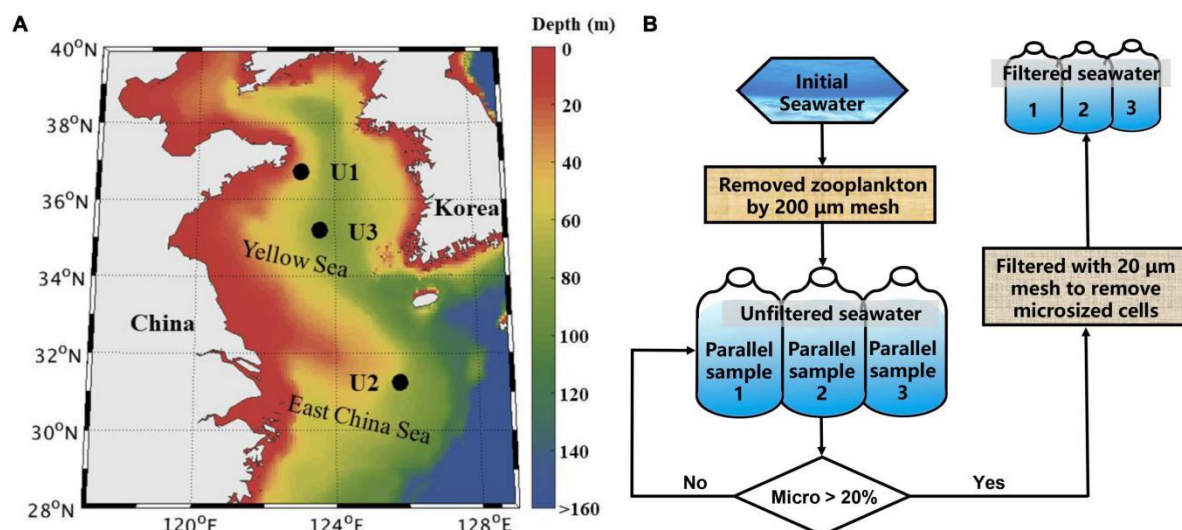


Figure 1 Water sampling stations used for the microcosm incubation experiments in the Yellow Sea and East China Sea (A) and the treatment procedure of the incubations (B). Where micro refers to the contribution of micro-sized Chl a to total Chl a (Adopted from Wang et al., 2022)

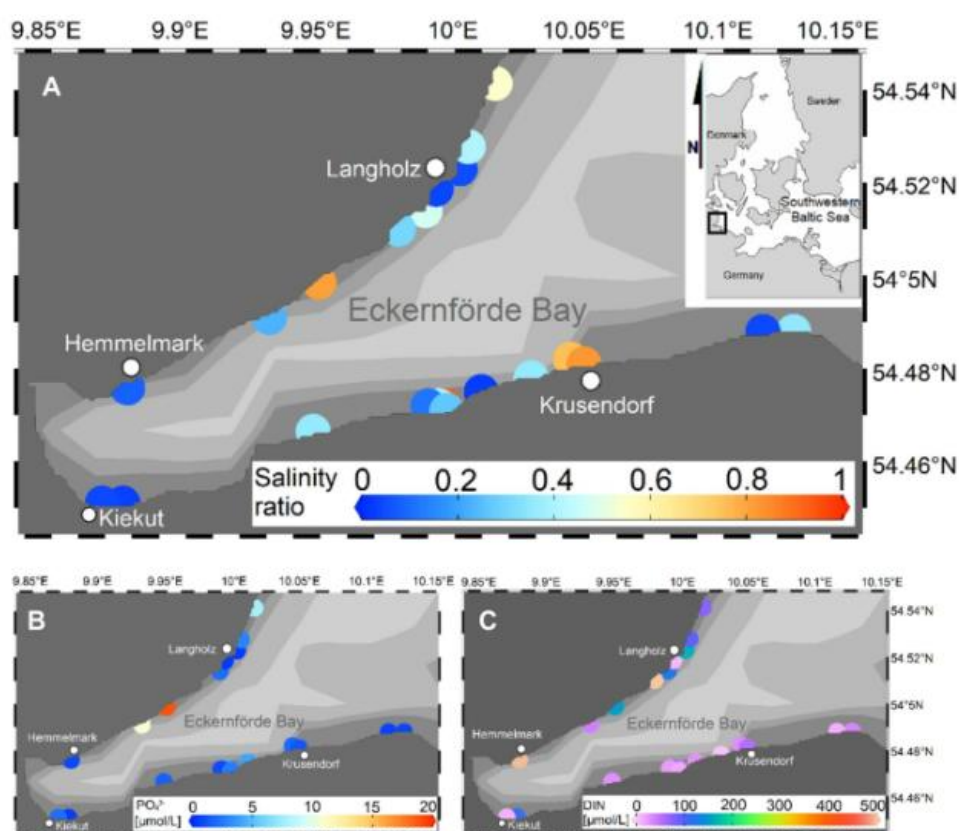


Figure 2 Eckernförde Bay with locations of a coastal SGD surveys. The insert in A shows the location of Eckernförde Bay in the southwestern Baltic Sea. A Salinity ratios of surface sediment pore water and ambient seawater; B phosphate (PO_4^{3-}) concentrations in pore water; C pore water dissolved total inorganic nitrogen ($\text{DIN} = \text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$) concentrations. Langholz, Hemmelmark, Kiekut, and Krusendorf are the location where depth profile studies were conducted (Adopted from Kreuzburg et al., 2023)

3 The Form and Transformation of Phosphorus in the Ocean

3.1 Distribution and utilization of inorganic phosphorus (phosphate)

Dissolved inorganic phosphorus (DIP) usually exists in the form of phosphate ions and is the most direct and easy-to-use phosphorus source for most marine organisms. The typical distribution of DIP in the ocean is the exhaustion of the surface and the concentration increases with the increase of depth. This is due to rapid uptake of phosphate for growth in the surface eutrophication layer, resulting in concentrations often as low as nanomolar levels (McLaughlin et al., 2013). In the oligotrophic sea areas in the middle of the ocean, surface DIP is often at the lower limit of detection for a long time, and phosphorus has become one of the restrictive nutrients (Liang et al., 2022). The surface phosphate concentrations in the nearshore and upflow areas are relatively high due to exogenous recharge and deep water upsurge. Phytoplankton has a high affinity and rapid uptake of phosphates to cope with the scarcity of phosphorus in the environment. In the classic "poor nutrition-rich" ecological condition conversion, phytoplankton usually feels phosphorus-limiting pressure when the environmental DIP concentration drops below about 0.1 $\mu\text{mol/L}$, and activates a series of physiological response mechanisms. Phosphate, as the preferred source of phosphorus for plankton, will be immediately absorbed by cells once it is sufficient and used to synthesize nucleic acids, phospholipids and energy molecule ATP. This is also why in some nearshore waters affected by rivers or pollution emissions, increased phosphate concentrations often directly drive the jump in primary productivity and even induce algae blooms.

3.2 Organophosphorus compounds and their degradation pathways

Dissolved organophosphorus (DOP) in seawater consists of various organophosphorus compounds, including nucleic acids, phospholipids, phosphoproteins, and specific metabolites. DOP accounts for a considerable proportion of the surface ocean phosphorus reservoirs, and even exceeds the content of inorganic phosphorus in the surface ocean water. However, most DOPs cannot be directly utilized by phytoplankton and need to be converted into inorganic phosphates first. Microbial communities play a key role in DOP degradation: they secrete various hydrolytic enzymes to break down organophosphorus compounds into available small molecules and phosphates (Adams et al., 2022). Common degradation pathways include: phosphorus in nucleic acids is released through nuclease reduction, phospholipids are hydrolyzed under the action of phospholipase, and compounds containing phosphoester bonds are cut off by phosphomonoesterase and phosphodiesterase, respectively. Recent studies have found that marine microorganisms have evolved into efficient strategies for decomposing phytic acid: by secreting phytase, gradually hydrolyzing hexaphosphate bonds, and phytic acid releases inorganic phosphorus. Studies have shown that marine macroalgae and seaweed are rich in inositol phosphoric acid such as phytic acid. Microorganisms can drive the metabolism of phytic acid and convert the phosphorus in it into phosphate for cell use (Sosa et al., 2019). This suggests that "hidden" organic phosphorus sources such as phytic acid may have the importance of being ignored in phosphorus-constrained sea areas. In addition, some marine bacteria also have a special pathway to utilize organic phosphonates, namely converting them into useful inorganic phosphorus through C-P lyase.

3.3 Enzymatic effects of microorganisms on phosphorus transformation

Microorganisms act as "enzyme library" in the marine phosphorus cycle, accelerating the morphological transformation and regeneration of phosphorus through the secretion of various enzymatic reactions. The most typical of these is alkaline phosphatase (AP), an enzyme that can hydrolyze organic phosphorus into inorganic phosphates under alkaline conditions. Both phytoplankton and heterotrophic bacteria express alkaline phosphatases, and AP inducible expression is activated when the external DIP concentration drops below a certain threshold (usually on the order of nanomolar). Therefore, alkaline phosphatase activity (APA) is often negatively correlated with the degree of environmental phosphorus deficiency and is considered as a valid indicator of phosphorus restriction status (Ma et al., 2019). Some studies compared the relative importance of AP and PDE to DOP hydrolysis in the upper water bodies of the North Pacific. The results showed that the two had their own emphasis when decomposing different types of organophosphorus compounds, and contributed to the DOP cycle in both the upper and middle water bodies. When the supply of phosphorus in different morphologies changes in the environment, these microorganisms are able to dynamically regulate the expression of related genes, thereby

optimizing phosphorus acquisition strategies. Research data at a global scale show that functional genes related to phosphorus circulation in the ocean have a hierarchical distribution in different regions and depths: for example, the surface is rich in *AP* genes and the deep layer is rich in genes related to organic phosphine degradation (Lidbury et al., 2022).

4 Phosphorus Transport and Circulation Mechanism

4.1 Physical process: redistribution of phosphorus by ocean currents, upstreams and mixing

Large-scale ocean currents and vertical mixing play a fundamental role in the spatial redistribution of ocean phosphorus. The hot salt circulation and surface circulation of seawater transport water mass containing phosphorus nutrient salts globally. The deep water in the Atlantic Ocean is rich in phosphorus produced by remineralization, and gradually spreads to the Indian Ocean and the Pacific Ocean through the ocean, making the Pacific deep water a "high stock area" of phosphorus (Teng et al., 2014). These deep high phosphorus water masses are brought back to the surface in the upflow area, becoming an important source of phosphorus for primary production of the surface. In typical upwelling systems such as Peru-Humboldt upwelling, continuous interannual coastal upwellings inject large amounts of deep phosphorus-rich water into the true light layer, supporting one of the world's highest fish yields. Observations show that the surface phosphate concentration in the upwelling area is significantly higher than that in the surrounding sea area. Compared with the oligotrophic area in the central Pacific, the phosphorus concentration in the oligotrophic area is often less than 0.1 $\mu\text{mol/L}$. The surface phosphorus caused by the upwelling along the coast of Peru can reach more than 1 $\mu\text{mol/L}$ (Glock et al., 2020). This sufficient supply of phosphorus greatly promotes local phytoplankton growth and forms highly productive waters.

4.2 Biological processes: recycling of phytoplankton, bacteria and zooplankton

Biological processes circulate phosphorus in the biosphere through growth-death and predation-metabolism, which is the link between inorganic and organic phosphorus banks. As primary producers, phytoplankton absorbs inorganic phosphorus from the environment to build biological tissues, a process that converts inorganic phosphorus into organic phosphorus and passes it in the food web. About hundreds of millions of tons of phosphorus are fixed to organic matter by global primary marine production every year. Some of these organic phosphorus enter a higher trophic level through the food chain (such as zooplankton and fish), achieving the flow and amplification of phosphorus in the food network, while the other part sinks into the true light layer with phytoplankton or feces particles. During the feeding and metabolism of zooplankton, some of the intake of organic phosphorus will be rapidly remineralized. The excretion and release of zooplankton converts the organophosphorus partly into dissolved inorganic phosphorus (such as phosphate) and dissolved organic phosphorus (Popendorf and Duhamel, 2015), and returns to the water body. Research points out that in eutrophied nearshore areas such as estuaries, the regenerated phosphorus contribution of microzooplankton can account for a certain proportion of the phosphorus demand of phytoplankton, thus playing an important regulatory role in the phosphorus cycle.

4.3 Deposition and resuspension process

When the phosphorus in the ocean settles to the seabed in particles, it enters the sediment reservoir and may undergo burial or re-release. Under normal oxidative environments, most iron-bound phosphorus (Fe-P) exists stably in the sediment, and only a small amount is released through pore water; while organic phosphorus is buried with organic matter or is decomposed and reused by benthic organisms. In an oxidative environment, sediments tend to be a sink of phosphorus; however, in an oxygen-deficient environment, the reduction and dissolution of iron oxides releases its bound phosphorus, thus making the sediment a source of phosphorus (Yang et al., 2020). The study found that in the hypoxic sediments in the northern outer Yangtze River estuary and southern near-shore Zhejiang, the iron-bound phosphorus content was significantly lower than the surrounding aerobic zone, while the proportion of weakly adsorbed inorganic phosphorus was higher, indicating that hypoxia enabled Fe-P to be activated and converted into easily released inorganic phosphate (Liu et al., 2020). On the other hand, the resuspension process also affects the fate of sediment phosphorus. When disturbances such as

strong storms, bottom trawls, etc. cause surface sediments to resuspend, the phosphorus adsorbed on the particles will reenter the water column. For example, the Bohai Sea and the East China Sea shallow Sea often observe an increase in the concentration of phosphorus in water after winter storms, that is, it is derived from the contribution of resuspended and remineralized sediments.

4.4 Case analysis: phosphorus cycle dynamics in peruvian upflow system

The Eastern Pacific Peruvian upflow system is a classical area for studying the ocean's phosphorus cycle. The sea area is known for its strong coastal uplift and extensive oxygen minimum belt, with extremely high primary productivity, and at the same time, the underlying water body is hypoxia or even anaerobic. Phosphorus has some unique characteristics in this cycle. During the upwelling season, a large amount of deep phosphorus-rich water surges to the surface, causing the phosphate concentration on the coastal surface to be much higher than that on the open ocean. Once reached the surface, these phosphorus is rapidly absorbed and utilized by explosive phytoplankton communities, supporting the growth of lush diatoms and dinoflagellates, and promoting the prosperity of fishery food webs. At the same time, due to the extremely low oxygen content of rising deep water itself, coupled with the loss and decomposition of phytoplankton consumes oxygen (Figure 3) (Maßmig and Engel, 2021), it is easy for a large-scale hypoxic or even anaerobic environment (commonly known as "dark zones") to form a large-scale hypoxic or even anaerobic environment (commonly known as "dark zones") on the bottom of the coast. Under such conditions, reducing dissolution of iron in the sediment results in the release of large amounts of phosphorus back into the water. The study found that the concentration of water phosphate in the bottom layer of the offshore oxygen-deficient sea areas in Peru is several times higher than that in normal aerobic sea areas. Some of these phosphates continue to return to the surface with the upflow, forming a positive feedback of "hypoxia-regenerated phosphorus supply"; the other part of the phosphorus combines with the upsurge of sulfides in the sediment to form minerals such as apatite, achieving permanent burial (Glock et al., 2020).

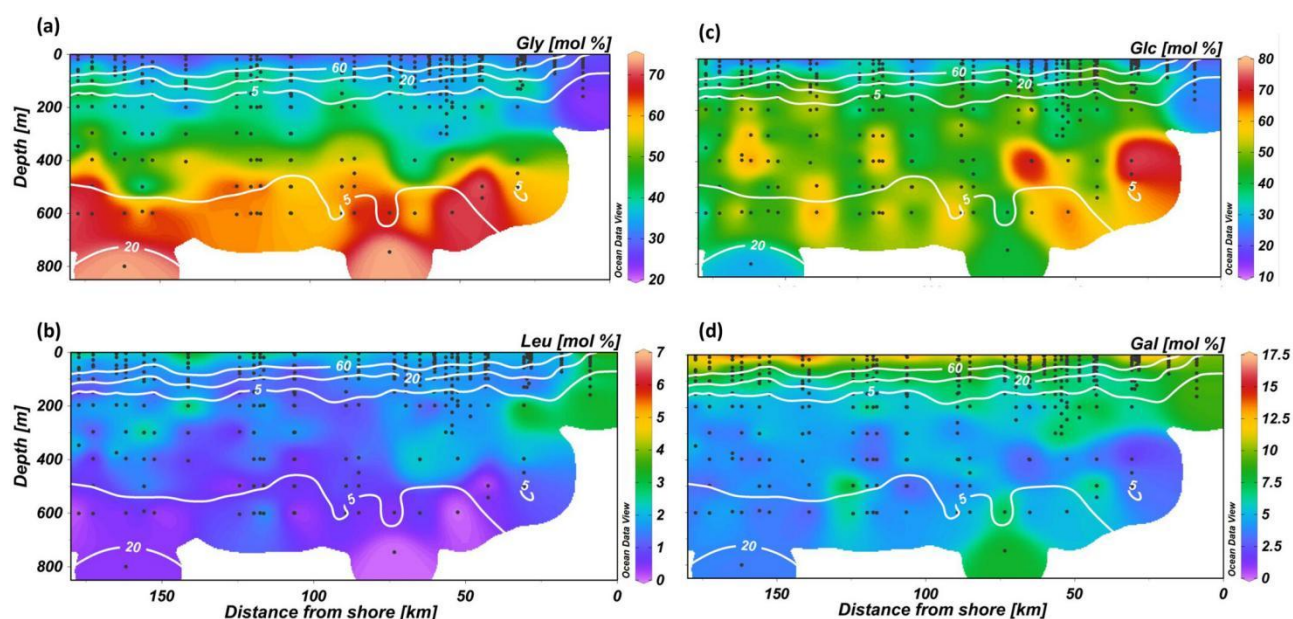


Figure 3 Percentage of the dissolved amino acids glycine (Gly) (a) and leucine (Leu) (b) and the dissolved combined carbohydrates glucose (Glc) (c) and galactose (Gal) (d) over depth for all stations sampled during the cruises M136 and M138 sorted by distance from shore. *In situ* oxygen concentrations are indicated with white contour lines (Adopted from Maßmig and Engel, 2021)

5 P Bioavailability and Limiting Effects

5.1 The ecological significance of phosphorus as a restricted nutrient

In the ocean, macronutrient elements mainly include nitrogen, phosphorus, silicon, etc., where nitrogen or phosphorus is usually the bottleneck nutrient that limits primary productivity. The classic Redfield ratio (C:N:P = 106:16:1) points out that the average demand for nitrogen and phosphorus in phytoplankton is 16:1, so when N/P is significantly higher than 16 in the environment, phosphorus is often shortened, and vice versa. In many tropical

and subtropical oceans, such as the North Atlantic and North Pacific subtropical circulation, surface phosphates are always low to approach detection limits, while nitrates are also low on the surface, but can be partially supplemented by nitrogen fixation, so these areas are closer to phosphorus restriction or nitrogen-phosphorus co-limitation. Global analysis by Browning and Moore (2023) shows that nitrogen limits are widely present in the distinctly stratified low-latitude subtropical circulation areas, iron limits are common in high productivity upstreams and the Southern Ocean, while single phosphorus limits are relatively rare, but in some closed waters (such as the Eastern Mediterranean), phosphorus limits are indeed dominated by phosphorus limits. As a restrictive nutrient, phosphorus has an ecological significance that once the supply of phosphorus is insufficient, the growth of phytoplankton will not be sustainable, and even if other nutrients are sufficient, it will be useless. Therefore, phosphorus restriction often leads to a decrease in phytoplankton biomass, a decrease in productivity, and a transformation in community composition.

5.2 Effects of changes in nitrogen and phosphorus ratio on the structure of phytoplankton community

Marine phytoplankton communities are very sensitive to changes in environmental nitrogen-phosphorus ratio (N:P). There are differences in the adaptability of phytoplankton in different groups to nutrient ratio imbalance, so changes in nutrient ratio often lead to succession of community structure. When the environment N/P is significantly higher (relatively lacking phosphorus), it is often favorable for some organophosphorus to be more efficiently utilized or stored phosphorus. For example, studies have shown that the relative advantage of dinoflagellates will increase under high nitrogen-phosphorus ratio conditions, because many dinoflagellates have strong organic phosphorus utilization and migration and predation ability, and can obtain the required phosphorus in a phosphorus-deficient environment. The nitrogen and phosphorus ratio also affects the internal stoichiometry and equilibrium of phytoplankton cells. When the N/P ratio increases, phytoplankton may accumulate more carbohydrates and reduce protein content in the body, which in turn affects its nutritional value and feeding rate, and thus affects the energy flow of the food web. Laboratory and field addition experiments have confirmed that the composition of phytoplankton community under different N/P supply will undergo significant changes (Redoglio and Radtke, 2022).

5.3 Adaptation strategies and gene regulation mechanisms under phosphorus restriction

Faced with phosphorus limitations, marine plankton and microorganisms have evolved a variety of adaptation strategies to maximize the acquisition and utilization of limited phosphorus sources. These strategies include physiological, biochemical and molecular genetic aspects. First, in cellular physiology, many phytoplankton reduce the proportion of phosphorus-related components in the cell when phosphorus is deficient, such as replacing part of phospholipids with sulfur or nitrogen lipids to reduce the need for phosphorus (Sebastián et al., 2015). Secondly, at the community level, there are synergistic and complementary mechanisms between plankton, such as organic matter decomposition bacteria release phosphate for algae, while algae release organic substrate for bacteria to utilize, forming a reciprocal relationship and improving the overall phosphorus utilization efficiency. At the molecular and gene regulation level, plankton's adaptation to the environment of phosphorus lacks is reflected in the changes in the transcriptional regulatory network. Many algae and bacteria have phosphorus starvation response regulation systems (PHO regulation systems). When the external phosphorus concentration decreases, a series of phosphorus acquisition gene expression will be activated, including phosphate high affinity transporter, alkaline phosphatase, phosphorus metabolism-related enzymes, etc. (Jha et al., 2018). In cyanobacteria, the transcription factor PhoB is the core of this regulatory network. Its activation energy triggers changes in the expression of dozens of genes, improving the cells' absorption of phosphorus and the resistance to phosphorus deficiency.

5.4 Case analysis: adaptation of phytoplankton to low phosphorus in mediterranean Oligotrophic Areas

The eastern Mediterranean is considered one of the most obvious sea areas in the world with phosphorus restriction. In terms of community composition, small cyanobacteria and pico-eukino algae dominate, such as *Prochlorococcus* and *Synechococcus*. These micro-photosynthetic autotrophs have a high surface area-to-volume ratio, which is conducive to improving phosphorus absorption efficiency at ultra-low phosphorus concentrations.

Mediterranean phytoplankton demonstrates significant biochemical adjustment capabilities. Sampling analysis showed that their intracellular phospholipid content was much lower than that of similar Atlantic populations, and instead increased the proportion of non-phosphorus membrane lipids (such as sulfhydryl lipids, glucoglycerides, etc.), which was seen as a strategy for phytoplankton to construct membranes with other elements in a low-phosphorus environment to reduce dependence on phosphorus. At the genetic level, plankton in the Eastern Mediterranean is enriched with many genes related to organophosphorus utilization. The study also found that the alkaline phosphatase activity in the eastern Mediterranean waters is much higher than that in the Atlantic Ocean sea area, indicating that the microbial community is actively decomposing and utilizing limited DOP (Van Wambeke et al., 2024).

6 Phosphorus and Marine Primary Productivity

6.1 Effects of phosphorus supply on algae growth and photosynthesis

Sufficient phosphorus supply is one of the necessary conditions to ensure the vigorous growth of phytoplankton and efficient photosynthesis. Algae undergo photosynthesis to fix CO₂, and a large number of phosphorus-containing molecules are required to synthesize, so the environmental phosphorus concentration often determines the maximum photosynthetic yield and upper biomass limit of phytoplankton (Hong and Huang, 2025). In phosphorus-rich water bodies, phytoplankton can reproduce at a near maximum specific growth rate, forming a "green water" area with high chlorophyll and high primary productivity; both field observations and culture experiments have proved that when phosphorus changes from lack to abundant, the photosynthetic rate and cell oxygen production rate of phytoplankton will increase significantly. Seasonal changes are similar. When the concentration of phosphorus in the estuary drops, sufficient light is sufficient but the algae are not prosperous, it indicates that phosphorus becomes a limiting factor, while the increase in phosphorus in winter and spring runoff promotes the prosperity of phytoplankton in spring. These all indicate that the phosphorus supply status is closely related to the photosynthesis intensity of algae.

6.2 The role of phosphorus in the formation of red tides and harmful algae blooms (HABs)

Red tides and harmful algae blooms are ecological abnormalities caused by the over-reproduction of certain phytoplankton algae, and their occurrence is often closely related to the nutrient condition. As one of the main fertilizer source elements, phosphorus plays an important role in the formation of red tides. Generally speaking, the increase in nitrogen and phosphorus load in eutrophied waters is the basic prerequisite for inducing red tides. Excessive nitrogen and phosphorus input will promote the rapid growth of nutrient-resistant algae, break the original ecological balance, and thus trigger algae blooms (Mackey et al., 2017). Especially in closed or semi-enclosed sea areas, when the concentrations of N and P in the water far exceed the needs of plants, high concentrations of algae are easily accumulated in the lower wind flow and develop into red tides. Many studies have shown that dinoflagellate red tide organisms are more competitive under high N/P and phosphorus restriction conditions, while diatom red tides tend to have slightly lower N/P ratio environments (Shen et al., 2022). This means that artificial changes in nutrient ratios may lead to a shift in red tide types. For example, along the East China Sea coast, the proportion of diatom-type red tides has been observed since the end of the 20th century, from about 70% to less than 30%, while the proportion of dinoflagellate red tides has increased from less than 20% to more than 50%. This trend is partly attributed to the increase in the N/P ratio and intensified phosphorus restrictions in nearshore waters, which has allowed dinoflagellates, which are good at snatching organic phosphorus, to gain the upper hand.

6.3 Indirect effect of phosphorus on carbon fixation and carbon cycle

As one of the limiting factors for primary marine productivity, the impact of phosphorus on carbon cycle is mainly reflected in regulating carbon fixation rates and changing the carbon flow path of the food web. The supply of phosphorus limits the photosynthesis of phytoplankton and will reduce the fixed flux of carbon dioxide. The global oceans fix approximately 50 Pg of carbon every year through photosynthesis, of which a considerable proportion settles to the deep sea to achieve carbon sink function. Second, phosphorus affects community structure, thereby changing the flow of carbon in the food web. When phosphorus restriction is severe, small

plankton and microbial rings dominate, and more carbon remains on the surface in the form of dissolved organic carbon or circulates through micro food rings, and less sinking into the deep sea through large particles. This reduces the efficiency of the biopump. Phosphorus restriction also has an indirect effect on carbon circulation by promoting the prosperity of nitrogen-fixing cyanobacteria and changing the system's carbon-nitrogen coupling. Nitrogen-fixing cyanobacteria (such as *wool*) generally has a C:P ratio above the average. When it is present in large quantities, it may change the local organic matter C:P, thereby affecting the organic carbon degradation rate and burial efficiency.

6.4 Case analysis: the relationship between red tide explosion in the East China Sea and phosphorus input

China's East China Sea coast, especially the Yangtze River Estuary - Hangzhou Bay, is one of the frequent red tides in the world, and its red tide evolution is closely related to changes in nutrient input. The Yangtze River has transported a large amount of freshwater and nutrients to the East China Sea. In recent decades, nitrogen and phosphorus emissions in the Yangtze River Basin have increased significantly and have changed the nutrient structure near the Yangtze River estuary. Under the phosphorus-restricted environment, dinoflagellates that are more suitable for low phosphorus are likely to increase significantly, which triggers a red tide of dinoflagellate. In addition to the nutrient ratio, the increase in total phosphorus concentration itself will also promote the occurrence of red tides. When the discharge of phosphorus fertilizer and domestic sewage in the basin increases, the phosphorus load entering the estuary increases, which can directly stimulate the extremely rapid growth of phytoplankton (Fang et al., 2025). The study at the Pearl River Estuary pointed out that the increase in phosphorus concentration is positively correlated with the outbreak of local dinoflagellate and algae blooms.

7 Ecological and Environmental Impacts of Phosphorus

7.1 Coupling effect between phosphorus and marine food network

The supply and circulation of phosphorus have an important impact on all trophic levels of the marine food network. The phosphorus condition of primary producers determines the quality and quantity of baits at secondary consumers and even higher nutritional grades. Phosphorus is an element necessary for nucleic acid and energy metabolism in zooplankton. If the food is relatively lacking in phosphorus, zooplankton will rebalance by increasing the excretion of carbon or nitrogen and retaining phosphorus, but it may still lead to growth restriction or decreased fecundity. Therefore, in low-phosphorus ecosystems, the population density of zooplankton is often low, or mainly small species that are good at low nutritional conditions, which in turn affects the supply of bait for higher trophic grades such as fish. This can partly explain why some oligotrophic ocean-sea fish yields are low because the phosphorus nutrients at the bottom of the food web restrict the transmission layer by layer, resulting in low productivity in the entire system (White and Dyhrman, 2013). The distribution of phosphorus affects the structure of the food web and the energy flow direction. In an environment where phosphorus is extremely lacking, small microorganisms are dominant, the trophic level may be extended and the energy transfer efficiency is reduced. In the case of sufficient phosphorus, the nutritional structure is simpler and direct. Large herbivorous zooplankton directly feeds on large algae, and the energy is transmitted to higher orders more quickly.

7.2 Phosphorus circulation disorder and the formation of marine hypoxic zones

When the ocean phosphorus circulation is disordered, such as excessive input of exogenous phosphorus causes eutrophication or large-scale release of endogenous phosphorus changes the nutrient structure, it often leads to the formation or expansion of marine hypoxic zones. Mechanistically, this involves the amplification of phosphorus on primary production and organic carbon sedimentation and decomposition of oxygen consumption processes. Coastal eutrophication is a typical example. Human activities allow rivers to transport excessive nitrogen and phosphorus to semi-enclosed sea areas such as bays and estuaries, prompting explosive growth of phytoplankton, and then a large amount of organic matter sinks into the bottom layer. In the process of bacteria decomposing these organic matter, dissolved oxygen in the water is consumed, and in severe cases, large areas of the underlying layer are hypoxic or even anaerobic environment (Tsandev, 2010). Phosphorus plays a "promoter" role in this process: if only nitrogen increases but phosphorus does not increase, the growth of algae will be limited by phosphorus; but when nitrogen and phosphorus increase together, the algae proliferation will reach a higher level,

more organic carbon is settled, and the hypoxia is more serious. Therefore, it is often emphasized in eutrophication management that "phosphorus control" is because reducing phosphorus can effectively reduce the intensity of algae blooms and prevent large-scale hypoxia.

7.3 Feedback effect of phosphorus cycle in the background of climate change

Global climate change may affect the ocean phosphorus cycle through multiple channels, which in turn will provide feedback on the climate system. Ocean warming and stratified enhancement may reduce upflow and vertical mixing, weaken deep phosphorus recharge, thereby reducing surface primary productivity and reducing marine biocarbon pump efficiency. This negative feedback mechanism means that warming causes less CO₂ to be absorbed by the ocean, which may accelerate the accumulation of atmospheric CO₂ (Niemeyer et al., 2016). Furthermore, ocean acidification may alter the chemical morphological availability of phosphorus. Some experiments have found that acidification reduces calcium carbonate deposition, causing the adsorption capacity of phosphorus on the particles to change, and at the same time affects the extracellular enzyme activity of phytoplankton. Terrestrial carbon-nitrogen coupled feedback is also involved in phosphorus, and warming may enhance the rate of phosphorus release on land weathering, which is part of the cooling feedback on the geological scale (Watson et al., 2017).

8 Conclusion

As an essential element in life, phosphorus has a core position in marine ecosystems and runs through all aspects of primary production, food web transmission and biogeochemical cycle. The supply of phosphorus and bioavailability often determine the upper growth limit of phytoplankton and the level of primary marine productivity. In many areas, phosphorus is a restrictive nutrient or together with nitrogen and iron limits the production function of the ecosystem. When phosphorus is sufficient, the marine ecosystem can efficiently fix CO₂ and support a prosperous food web; when phosphorus is scarce, primary production and energy transfer are significantly suppressed, the ecosystem is in a low productivity state and community structure changes may occur. The phosphorus cycle regenerates phosphorus between the various ocean circles through complex physical transport and biological processes: ocean currents and upstreams redistribute phosphorus globally, bioabsorption and decomposition promote the conversion of phosphorus between organic and inorganic forms, and sedimentation burial and re-release regulates the revenue and expenditure of phosphorus banks on a long-term scale. Together, these processes maintain the dynamic balance of the ocean's phosphorus cycle, making the global ocean's nutritional pattern generally stable despite regional and period differences. Phosphorus is not only important for its own circulation, but it is closely coupled with the circulation of elements such as nitrogen, carbon, and iron, which jointly determines the balance of the source elements and climate regulation functions of the ocean.

By reviewing the main sources of phosphorus, various forms and transformations in the ocean, circular transport mechanisms, bioavailability and restriction effects, and the ecological environment impact of phosphorus circulation disorders, we can see that ocean phosphorus circulation is a comprehensive system involving multiple scales and multiple processes. Land sources and seabed jointly provide marine phosphorus reservoirs. Different sources make different relative contributions in different regions. From coast to oceans, they gradually turn from rivers to atmospheric atmosphere. Geological sources cannot be ignored under local special environments. After entering the ocean, the phosphorus is constantly transformed between inorganic and various organic forms, and organisms play the main driver in it. Through enzymatic action, it converts difficult-to-use organic phosphorus into available phosphates to achieve nutrient regeneration. The ocean current and biological pump process migrate the phosphorus in a vertical and horizontal direction, making the surface-deep, near-shore-ocean related to each other.

Research on marine phosphorus cycle has many implications for future sustainable development of oceans. In terms of eutrophication and red tide management, controlling phosphorus emissions and imports is one of the key measures. Unlike nitrogen, there is currently no phosphorus storage in the atmosphere and it is difficult to survive

through biological sequestration from scratch. Every part of phosphorus emitted by man-made can eventually enter the water body to produce a cumulative effect. Therefore, strengthening the management of watershed phosphorus is crucial to protecting the offshore ecological environment and can effectively reduce the occurrence of harmful algae blooms and hypoxic areas. This not only maintains ecosystem service functions (such as fishery, tourism), but also requires the sustainable development of coastal socio-economics. In the context of climate change, nutrient factors need to be included in the forecast and planning of marine carbon sinks and fishery management. Scientific research should continue to promote the monitoring and mechanism research of the ocean's phosphorus cycle, such as developing new sensors and satellite remote sensing inversion of seawater phosphorus content, strengthening the monitoring of indicators such as marine alkaline phosphatase, and timely grasping changes in global nutritional status; at the same time, making full use of genomics and culture experiments to clarify the phosphorus metabolism mechanism of key species, and provide parameters for model construction.

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Conflict of Interest Disclosure

The authors confirm that the study was conducted without any commercial or financial relationships and could be interpreted as a potential conflict of interest.

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