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Editorial

Marine Nitrogen Fixation and Phytoplankton Ecology

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Many oceans are currently undergoing rapid changes in environmental conditions such as warming temperature, acidic water condition, coastal hypoxia, etc. Obvious warming and acidification in various oceans, from polar oceans to tropical oceans, was well reported in the fifth Assessment Report (AR5) by the Intergovernmental Panel on Climate Change [1]. These climate-driven environmental changes could lead to dramatic alterations in the biology and ecology of phytoplankton as major primary producers and biogeochemical drivers and subsequently impact the growth and survival of other marine organisms [2–5]. Consequently, the entire marine ecosystem and global biogeochemical cycles would be very different from what we have now.

Marine phytoplankton are an important indicator of marine ecosystem changes in response to climate-induced environmental change [2,4–6], since they are major primary producers that consolidate solar energy into organic matter and transfer it to marine ecosystems throughout the food web. Recently, increasing numbers of roles of small phytoplankton as a major contributor to primary production have been reported in various oceans, and it has been found that small phytoplankton could become more prominent under an ocean warming scenario [2,4,6–9]. The ecological and biogeochemical traits of small phytoplankton are very different from those of large phytoplankton [3,4,9]. Therefore, it is urgent to verify the different biological and chemical properties of small phytoplankton and understand their ecological roles under ongoing environmental changes.

It is widely known that nitrogenous nutrients are key components of primary production in the ocean, and the only biological source of such nutrients is diazotrophic N_2 fixation. Similar to primary producers, N_2 fixers (diazotrophs) are also vulnerable to changing environmental conditions. It was found that the polar regions can be introduced to diazotrophic activity under warming conditions, and the increased N availability can lead to elevated primary productivity [10–12]. However, if ocean acidification continues in the future, the diazotrophic activity is likely to decrease [13]. The documentation and processing of information on N_2 fixation is highly important as its role in the N cycle of the oceans is critical for preparing future projections on the effects of global environmental changes on the biogeochemical balance of the ecosystems. The employment of enriched isotopic tracers of dinitrogen ($^{15}N_2$) [14], natural abundance studies of the N_2 isotopes in particulate and dissolved forms of N, and the introduction of a simple enzyme-based assay, the acetylene reduction method, have opened possibilities expand our knowledge of biological N_2 fixation in the global oceans. The measured N_2 fixation rates in a *Trichodesmium* bloom in the Arabian Sea showed the highest depth-integrated values, ranging from ~0.1 to 34 mmol N m^{-2} d^{-1} [15]. The highest depth-integrated N_2 fixation rates in non-bloom conditions are obtained in the western tropical South Pacific (638 ± 1689 µmol N m^{-2} d^{-1}), which are higher than those of the subtropical North Atlantic (182 ± 479 µmol N m^{-2} d^{-1}) and North Pacific (118 ± 101 µmol N m^{-2} d^{-1}). N_2

fixation rates in the eastern South Pacific are measured to be 86 ± 99 µmol N m^{-2} d^{-1}, whereas the southern Indian Ocean (<20 µmol N m^{-2} d^{-1}, [12]) rates are low.

Recent genetic studies on microbial communities report niches of diazotrophic activities which were previously unknown. Most measurements on N_2 fixation rates are from bulk samples, which might have possibly comprised cyanobacteria and other diazotrophs. The infusion of the cell-specific N_2 fixation method using a nanoscale mass spectrometer gave a high-definition perspective of cellular-level N_2 fixation; more importantly, it provides knowledge about diazotrophy on an individual-species basis [16]. This novel method helps to identify the species that are capable of N_2 fixation, and to determine their role in transferring fixed N_2 to the autotrophs in association with them. However, information on global N_2 fixation rates and cell-specific N_2 fixation so far is scant, and inconsistent in different spatio-temporal scales due to a lack of sufficient measurements. To tackle the perplexing response of diazotrophs, a detailed assessment of the diazotrophic community response toward the changing environmental conditions needs to be recorded thoroughly. Considering the fundamental roles of phytoplankton in marine ecosystems and global biogeochemical cycles, it is important to understand phytoplankton ecology and N_2 fixation as a potential N source in various oceans.

This Special Issue covers a wide range of geographic study regions from pole to pole and from coastal systems to open oceans, including Terra Nova Bay, Ross Sea in the Antarctic Ocean, Northern Bering Sea, Chukchi Sea, Canada Basin, and Kongsfjorden, Svalbard in the Arctic Ocean, Western South China Sea, Northern East China Sea, Northwestern Pacific Ocean, and Jaran Bay in South Korea. In this Special Issue, we present a total of 11 articles offering ecological and biogeochemical baselines as indicators for the changes in marine environments and ecosystems driven by global climate changes. In particular, articles on the compositions of intracellular biochemical components such as proteins, lipids, and carbohydrates of phytoplankton could provide important information for their physiological conditions and the nutritional value of organic matter available to grazers [17,18]. Recently, phytoplankton-derived transparent exopolymer particles (TEPs) are known for making a considerable contribution to the organic matter pools and thus marine biogeochemical cycles in aquatic environments [19]. Ref. [20] investigated monthly TEPs concentration and particulate organic carbon (POC) concentration in Jaran Bay, a large shellfish aquaculture site in a southern coastal region of Korea. They found that the contribution of TEPs ranged from 2.4% to as high as 78.0% of the POC concentration, which indicated that TEPs-C could be a significant contributor to the POC pool in a coastal bay. Since little information on the monthly variation in TEPs is available, their investigation on the TEPs could be a very important baseline in a coastal bay system. Moreover, in Jaran Bay, ref. [21] also observed the seasonal and spatial variations in the biochemical compositions of phytoplankton. They found that the dominant biochemical component was carbohydrates (51.8 ± 8.7%), followed by lipids (27.3 ± 3.8%) and proteins (20.9 ± 7.4%). Large phytoplankton and the $P \times (PO_4^{3-} 1/16 \times NO_3^{-})$ and NH_4^+ concentrations were identified as major controlling factors for food material (FM) in Jaran Bay. Over a year at Jang Bogo Station (JBS) in Antarctica, ref. [18] measured bi-weekly biochemical compositions of particulate organic matter (POM) and concentrations of TEPs. The high composition of lipids and proteins indicated a good food source in summer, whereas stably low concentrations of carbohydrates and lipids were utilized for long-term energy storage in the survival of phytoplankton in winter. They found that TEPs have a longer residence time than POC, and the contribution of TEPs-C to the POC pool could be important in the Ross Sea. The biochemical composition of POM deriving mainly from phytoplankton in the Chukchi Sea, Arctic Ocean were presented by [22]. They investigated the biochemical components of phytoplankton and their spatial pattern. Carbohydrates were the predominant macromolecules, accounting for 42.6% in the Chukchi Shelf and 60.5% in the Canada Basin, followed by lipids and proteins. Based on their study, the biochemical compositions of phytoplankton could be considerably different in the regions of the Arctic Ocean. In a similar region, ref. [23] estimated the bioavailable fraction of POM through enzymatic hydrolysis that can be utilized by higher trophic levels. Based on their results, nutrient, temperature, meltwater and different size classes of phytoplankton (micro and picophytoplankton) were the main factors of the compositional variations and the spatial distributions. More studies on the changes in the biochemical compositions of phytoplankton should be conducted under future environmental changes.

In terms of elemental composition and primary productivity driven by phytoplankton, ref. [24] determined the combined physiological–elemental ratio changes in two phytoplankton species, *Scrippsiella trochoidea* (Dinophyceae) and *Heterosigma akashiwo* (Raphidophyceae). They found higher average ratios of particulate organic nitrogen (PON) to chlorophyll-a (Chl-*a*) and POC to Chl-*a* in *S. trochoidea* than those of *H. akashiwo.* However, the authors observed similar ratios of POC/PON of the two microalgae. These results can be used to develop physiological models for phytoplankton, with implications for the marine biogeochemical cycle. In Kongsfjorden's high-latitude open fjord systems, ref. [25] found that the turbidity associated with glacier meltwater impacted the penetration depth of light and that nutrients could cause the lower productivity rates of phytoplankton. They found that picophytoplankton was largely based on regenerated nutrients, even more productive than that suggested by their biomass contribution and their nitrogen uptake. For a better understanding of the biochemical traits of small phytoplankton, ref. [26] conducted field measurements in the biologically productive northern Bering and Chukchi seas. The contributions of small phytoplankton to the total primary production were 38.0% (SD = ±19.9%) and 25.0% (SD = ±12.8%) in 2016 and 2017, respectively. They found that small phytoplankton synthesize different biochemical compositions with nitrogen-rich POC from large phytoplankton.

The three articles below on phytoplankton communities and cyanobacterial contributions provide significant ecological predictions under expected warming ocean conditions. In the North Pacific Ocean, ref. [27] determined the picocyanobacterial contribution and the total primary production. The average picocyanobacterial contributions to the carbon uptake rates were 45.2% in the tropical Pacific region and 70.2% in the subtropical and temperate Pacific region, respectively. In addition, their contributions to the nitrogen uptake rates were significantly higher than those of carbon uptake rates. Based on high-performance liquid chromatography (HPLC) pigment analysis, ref. [28] investigated spatiotemporal variations in phytoplankton community compositions in the northern East China Sea (ECS), the largest marginal sea in the north-western Pacific Ocean. Overall, the two major phytoplankton groups were diatoms (32.0%) and cyanobacteria (20.6%) in the northern ECS, and the two groups were negatively correlated. In the western South China Sea, ref. [29] investigated the distinct seasonal variation in phytoplankton community structure related to different oceanographic conditions and observed a major shift from a diatom-dominated regime in winter to a cyanobacteria-dominated system in summer. The authors found that the increased overall abundance of phytoplankton and cyanobacteria during the summer was caused by upwelling and enriched eddy activity, whereas the abundant symbiotic cyanobacteria–diatom association during the winter was mainly due to the influence of the cool temperature. Long-term monitoring of the phytoplankton communities and the picocyanobacterial contributions should be conducted for a better understanding of the ecological impacts of the global warming scenario, with a focus on the ecological roles of picocyanobacteria.

This Special Issue covers various articles on N_2 fixation and aspects of marine phytoplankton ecology, such as biodiversity, distribution, biomass, photosynthetic traits, biochemical compositions, productivity, etc., in various oceans, including polar oceans. Finally, we hope that this Special Issue provides ecological and biogeochemical baselines that broaden our existing knowledge on the current and ongoing changes in marine ecosystems in response to global climate change.

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References

1. IPCC. Climate change 2014: Synthesis report. In *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*; IPCC: Geneva, Switzerland, 2014; ISBN 978-92-9169-142-5.
2. Li, W.K.W.; McLaughlin, F.A.; Lovejoy, C.; Carmack, E.C. Smallest Algae Thrive as the Arctic Ocean Freshens. *Science* **2009**, *326*, 539. [CrossRef] [PubMed]
3. Lee, S.H.; Yun, M.S.; Kim, B.K.; Saitoh, S.I.; Kang, C.K.; Kang, S.H.; Whitledge, T. Latitudinal Carbon Productivity in the Bering and Chukchi Seas during the Summer in 2007. *Cont. Shelf Res.* **2013**, *59*, 28–36. [CrossRef]
4. Kang, J.J.; Jang, H.K.; Lim, J.H.; Lee, D.; Lee, J.H.; Bae, H.; Lee, C.H.; Kang, C.K.; Lee, S.H. Characteristics of Different Size Phytoplankton for Primary Production and Biochemical Compositions in the Western East/Japan Sea. *Front. Microbiol.* **2020**, *11*, 560102. [CrossRef] [PubMed]
5. Sun, Y.; Youn, S.H.; Kim, Y.; Kang, J.J.; Lee, D.; Kim, K.; Jang, H.K.; Jo, N.; Yun, M.S.; Song, S.K.; et al. Interannual Variation in Phytoplankton Community Driven by Environmental Factors in the Northern East China Sea. *Front. Mar. Sci.* **2022**, *9*, 1–19. [CrossRef]
6. Lee, S.H.; Ryu, J.; Lee, D.; Park, J.W.; Kwon, J.-I.; Zhao, J.; Son, S. Spatial Variations of Small Phytoplankton Contributions in the Northern Bering Sea and the Southern Chukchi Sea. *GISci. Remote Sens.* **2019**, *56*, 794–810. [CrossRef]
7. Morán, X.A.G.; López-Urrutia, Á.; Calvo-Díaz, A.; LI, W.K.W. Increasing Importance of Small Phytoplankton in a Warmer Ocean. *Glob. Chang. Biol.* **2010**, *16*, 1137–1144. [CrossRef]
8. Bhavya, P.S.; Lee, J.H.; Lee, H.W.; Kang, J.J.; Lee, J.H.; Lee, D.; An, S.H.; Stockwell, D.A.; Whitledge, T.E.; Lee, S.H. First in Situ Estimations of Small Phytoplankton Carbon and Nitrogen Uptake Rates in the Kara, Laptev, and East Siberian Seas. *Biogeosciences* **2018**, *15*, 5503–5517. [CrossRef]
9. Bhavya, P.S.; Kang, J.J.; Jang, H.K.; Joo, H.; Lee, J.H.; Lee, J.H.; Park, J.W.; Kim, K.; Kim, H.C.; Lee, S.H. The Contribution of Small Phytoplankton Communities to the Total Dissolved Inorganic Nitrogen Assimilation Rates in the East/Japan Sea: An Experimental Evaluation. *J. Mar. Sci. Eng.* **2020**, *8*, 854. [CrossRef]
10. Blais, M.; Tremblay, J.É.; Jungblut, A.D.; Gagnon, J.; Martin, J.; Thaler, M.; Lovejoy, C. Nitrogen Fixation and Identification of Potential Diazotrophs in the Canadian Arctic. *Glob. Biogeochem. Cycles* **2012**, *26*, GB3022. [CrossRef]
11. Sipler, R.E.; Gong, D.; Baer, S.E.; Sanderson, M.P.; Roberts, Q.N.; Mulholland, M.R.; Bronk, D.A. Preliminary Estimates of the Contribution of Arctic Nitrogen Fixation to the Global Nitrogen Budget. *Limnol. Oceanogr. Lett.* **2017**, *2*, 159–166. [CrossRef]
12. Shiozaki, T.; Kodama, T.; Furuya, K. Large-scale impact of the island mass effect through nitrogen fixation in the western South Pacific Ocean. *Geophys. Res. Lett.* **2014**, *41*, 6413–6419. [CrossRef]
13. Hong, H.; Shen, R.; Zhang, F.; Wen, Z.; Chang, S.; Lin, W.; Kranz, S.A.; Luo, Y.-W.; Kao, S.-J.; Morel, F.M.M.; et al. The complex effects of ocean acidification on the prominent N_2-fixing cyanobacterium Trichodesmium. *Science* **2017**, *357*, 527–531. [CrossRef] [PubMed]
14. Montoya, J.P.; Voss, M.; Kahler, P.; Capone, D.G. A simple, high-precision, high-sensitivity tracer assay for N_2 fixation. *Appl. Environ. Microbiol.* **1996**, *62*, 986–993. [CrossRef] [PubMed]
15. Gandhi, N.; Singh, A.; Prakash, S.; Ramesh, R.; Raman, M.; Sheshshayee, M.S.; Shetye, S. First direct measurements of N_2 fixation during a Trichodesmium bloom in the eastern Arabian Sea. *Glob. Biogeochem. Cycles* **2011**, *25*, 1–10. [CrossRef]
16. Musat, N.; Musat, F.; Weber, P.K.; Pett-Ridge, J. Tracking Microbial Interactions with NanoSIMS. *Curr. Opin. Biotechnol.* **2016**, *41*, 114–121. [CrossRef] [PubMed]
17. Lee, J.H.; Kang, J.J.; Jang, H.K.; Jo, N.; Lee, D.; Yun, M.S.; Lee, S.H. Major Controlling Factors for Spatio-Temporal Variations in the Macromolecular Composition and Primary Production by Phytoplankton in Garolim and Asan Bays in the Yellow Sea. *Reg. Stud. Mar. Sci.* **2020**, *36*, 101269. [CrossRef]
18. Park, S.; Park, J.; Yoo, K.C.; Yoo, J.; Kim, K.; Jo, N.; Jang, H.K.; Kim, J.; Kim, J.; Kim, J.; et al. Seasonal Variations in the Biochemical Compositions of Phytoplankton and Transparent Exopolymer Particles (Teps) at Jang Bogo Station (Terra Nova Bay, Ross Sea), 2017–2018. *Water* **2021**, *13*, 2173. [CrossRef]
19. Passow, U. Transparent Exopolymer Particles (TEP) in Aquatic Environments. *Prog. Oceanogr.* **2002**, *55*, 287–333. [CrossRef]
20. Lee, J.H.; Lee, W.C.; Kim, H.C.; Jo, N.; Jang, H.K.; Kang, J.J.; Lee, D.; Kim, K.; Lee, S.H. Transparent Exopolymer Particle (TEPs) Dynamics and Contribution to Particulate Organic Carbon (POC) in Jaran Bay, Korea. *Water* **2020**, *12*, 1057. [CrossRef]

21. Lee, J.H.; Lee, W.C.; Kim, H.C.; Jo, N.; Kim, K.; Lee, D.; Kang, J.J.; Sim, B.R.; Kwon, J.-I.; Lee, S.H. Temporal and Spatial Variations of the Biochemical Composition of Phytoplankton and Potential Food Material (Fm) in Jaran Bay, South Korea. *Water* **2020**, *12*, 3093. [CrossRef]
22. Choe, K.; Yun, M.; Park, S.; Yang, E.; Jung, J.; Kang, J.; Jo, N.; Kim, J.; Kim, J.; Lee, S.H. Spatial Patterns of Macromolecular Composition of Phytoplankton in the Arctic Ocean. *Water* **2021**, *13*, 2495. [CrossRef]
23. Kim, B.K.; Joo, H.M.; Jung, J.; Lee, B.; Ha, S.Y. In Situ Rates of Carbon and Nitrogen Uptake by Phytoplankton and the Contribution of Picophytoplankton in Kongsfjorden, Svalbard. *Water* **2020**, *12*, 2903. [CrossRef]
24. Liu, X.; Liu, Y.; Noman, M.A.; Thangaraj, S.; Sun, J. Physiological Changes and Elemental Ratio of Scrippsiella Trochoidea and Heterosigma Akashiwo in Different Growth Phase. *Water* **2021**, *13*, 132. [CrossRef]
25. Kim, B.K.; Jung, J.; Lee, Y.; Cho, K.H.; Gal, J.K.; Kang, S.H.; Ha, S.Y. Characteristics of the Biochemical Composition and Bioavailability of Phytoplankton-Derived Particulate Organic Matter in the Chukchi Sea, Arctic. *Water* **2020**, *12*, 2355. [CrossRef]
26. Park, J.W.; Kim, Y.; Kim, K.W.; Fujiwara, A.; Waga, H.; Kang, J.J.; Lee, S.H.; Yang, E.J.; Hirawake, T. Contribution of Small Phytoplankton to Primary Production in the Northern Bering and Chukchi Seas. *Water* **2022**, *14*, 235. [CrossRef]
27. Lee, H.W.; Noh, J.H.; Choi, D.H.; Yun, M.; Bhavya, P.S.; Kang, J.J.; Lee, J.H.; Kim, K.W.; Jang, H.K.; Lee, S.H. Picocyanobacterial Contribution to the Total Primary Production in the Northwestern Pacific Ocean. *Water* **2021**, *13*, 1610. [CrossRef]
28. Kim, Y.; Youn, S.H.; Oh, H.J.; Kang, J.J.; Lee, J.H.; Lee, D.; Kim, K.; Jang, H.K.; Lee, J.; Lee, S.H. Spatiotemporal Variation in Phytoplankton Community Driven by Environmental Factors in the Northern East China Sea. *Water* **2020**, *12*, 2695. [CrossRef]
29. Ding, C.; Sun, J.; Narale, D.D.; Liu, H. Phytoplankton Community in the Western South China Sea in Winter and Summer. *Water* **2021**, *13*, 1209. [CrossRef]