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• HIGHLIGHT •

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Untangling the role that microbes play in ocean carbon cycle─A new paradigm in marine biogeochemistry

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An estimated amount of 3.7×10^5 petagrams (1 Pg=10^{15} g) of organic carbon is stored in marine sediments (Lipp et al., 2008), which supports an immense subsurface biosphere that contains approximately 2.9×10^{29} to 3.6×10^{30} cells of indigenous microorganisms (Kallmeyer et al., 2012; Whitman et al., 1997). The majority of that carbon is transported from surface oceans by a process called the "biological pump (BP)", which has been a prevailing doctrine in the ocean carbon cycle.

The term "biological pump" has been used by marine scientists to visually describe the ocean's capability in sequestering atmospheric CO_2 into the deep sea due to biological processes. Volk and Hoffert (1985) emphasize the importance of the sinking flux of biogenic carbon in the ocean in their definition of this term, which has been held as the core principle of BP until today.

While focusing on the transport of the small fraction of primary production into the ocean floor, marine scientists also have wondered about the remaining fraction of primary production after its majority has been respired back to CO_2. That remaining fraction is the dissolved organic carbon (DOC), which commonly has a concentration in the range of 30–80 μmol/kg in the open ocean (Hansell et al., 2009). This diluted food bank is like chaff unpalatable to the majority of living organisms in the ocean, and for a long time, the exact role of DOC in ocean biology has been uncertain. However, the total quantity of it is huge: at 662 Pg C, DOC exceeds the total carbon inventory of marine biomass by 200 fold and is almost equivalent to the total carbon dioxide in the atmosphere. Thus the role of DOC in the global carbon cycle is immensely important.

In 2010, a seminal paper was published by a group of eminent scientists led by Nianzhi Jiao from Xiamen University (Jiao et al., 2010). It presented a new conceptual framework called the microbial carbon pump (MCP), which changed our perception of DOC and the microorganisms producing it in the ocean. The essence of MCP stands on the refractory nature of the majority (~95%) of DOC, which resists biological degradation and thus can be persistent in the ocean for thousands of years.

Despite the long recognition of DOC as being "old", a wide chasm has existed between our understanding and the reality of the complexity of this biologically recalcitrant DOC (RDOC). MCP for the first time recognized the role that microorganisms play in transferring the labile or semi-labile DOC into RDOC by three fundamental pathways: (1) direct production of RDOC by microbial cells' own machinery (path 1); (2) release of microbial cells' macromolecules by viral lysis (path 2); and (3) degradation of organic substrates into recalcitrant compounds (path 3) (Figure 1). Jiao et al. (2014) further defined RDOC as "being environment-constrained" or "due to low concentration of a particular compound".

The significance of MCP lies in two pivotal aspects relevant to global climate change and marine biogeochemistry. One is its "pumping" of transient labile carbon into more stable and recalcitrant carbon, thus functioning to suppress it from escaping as CO_2 into the atmosphere. The other aspect is its selective remineralization of non-carbon elements (e.g., N, P) from dissolved organic matter (DOM), driving the RDOM

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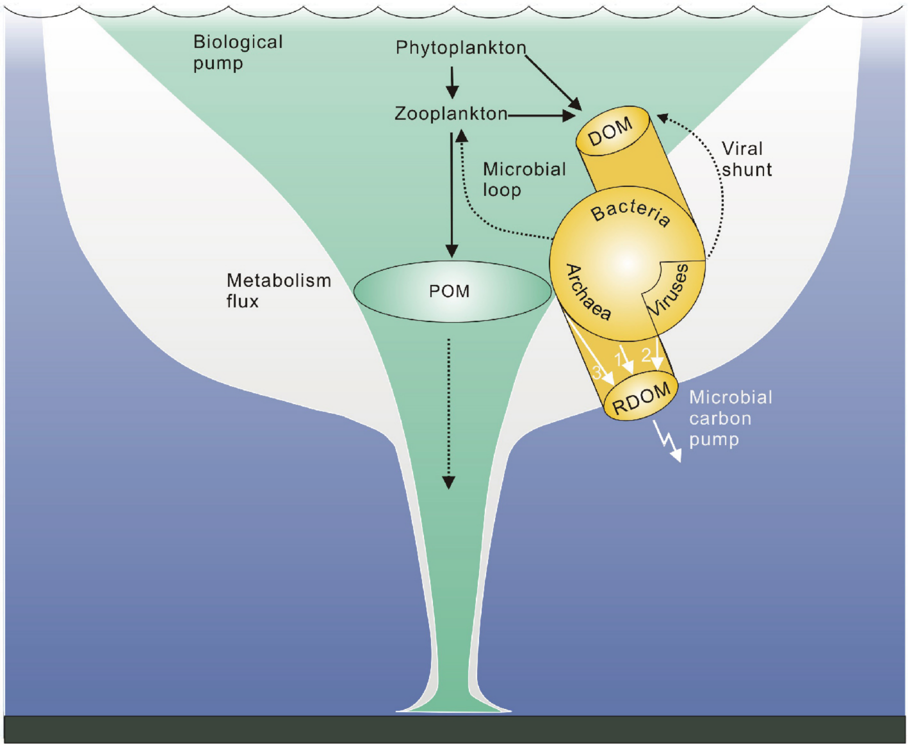

Figure 1 Redrawn based on Figure 1 of Jiao et al. (2010).

to be extremely dominant in carbon in the Redfield elemental molar ratio (C : N : P of ~3511 : 202 : 1) while preferentially releasing nitrogen and phosphorus into the water column, rendering primary production to be enhanced with more available nutrients.

The concept of MCP has been echoed by enthusiastic responses from the research community. The Jiao et al. (2010) paper has received over 380 citations within the past six years. More importantly, it has provided new incentives for ocean biogeochemistry research. This outcome is demonstrated by its recognition from the International Society for Advancing Science in Limnology and Oceanography, the establishment of a working group (WG134) on the MCP by the international Scientific Committee for Oceanic Research, a joint MCP-focused working group under the leadership of the North Pacific Marine Science Organization and the International Council for the Exploration of the Sea, and establishment of a Gordon Research Conference on Ocean Biogeochemistry in 2016 in Hong Kong.

Jiao et al. (2010) also recognized the importance of the linkage between MCP and BP, which are intrinsically intertwined in the marine carbon cycle. This helps to bring the two research communities into unity as these research fields expand into the future. Furthermore, MCP has an intimate reflection of the geological past, at times when ancient oceans might have contained a DOC pool that was 500–1000 times bigger than it is today. Thus MCP may also play an eminent role in linking modern microbial oceanography and paleoceanography for a better understanding of microbial functions in climate change over geological timescales.

It can be agreed that future research should focus on the following important aspects of MCP, which clearly need to be resolved: (1) the sources of DOC and RDOC, (2) the composition of RDOC, (3) the specific groups of microorganisms transforming DOC, and (4) the rate of carbon degradation and RDOC production in specific environments.

Fundamental knowledge gaps remain for each of the aspects mentioned above. For example, the relative contribution of external DOC input from degradation of particulate organic carbon (POC) and *in situ* DOC input from chemolithoautotrophic production need to be resolved in the vast deep ocean (Dang and Lovell, 2016); the different sources of DOC may have different molecular structures and bioreactivity, which influence the DOC biodegradability, carbon transformation rate, microbial metabolic pathways and the resulting RDOC composition and production rate. Recent scientific breakthroughs may help to identify some of the key microbial processes. For example, the increasing recognition of archaeal heterotrophy in degradation of POC (Zhang et al., 2015) and degradation pathways catalyzed by *Bacteroidetes* and the *Roseobacter* clade bacteria (Dang and Lovell, 2016) may be windows of opportunities for filling the knowledge gap between POC degradation and RDOC production.

Addressing those fundamental questions requires a collective and concerted effort from multiple disciplines. To our delight, this has become a new trend in microbial oceanography and biogeochemistry, which is driven by the growing effort to integrate microbiological and geochemical tools. In particular, we will likely see an increase in combining "omics" (e.g., genomics, transcriptomics, proteomics, metabolomics, lipidomics) and mass spectrometry (e.g, Fourier-transform ion cyclotron resonance mass spectrometry, gas- or liquid chromatography-mass spectrometry, isotope ratio mass spectrometry, accelerator mass spectrometry) tools in future research of microbe-DOC interactions. At a global scale, the study of microbial oceanography can be integrated under the framework of physical oceanography and chemical oceanography, and at geological timescales, geomicrobiology and paleoceanography can be integrated in the study of DOC in ancient oceans and past climate change. MCP can be the key thread linking all disciplines (Figure 2) and serve a central role in promoting future research in ocean biogeochemistry across time and space.

At the moment, field research in MCP is still in its infancy and our efforts and accomplishments have only allowed us to disclose the tip of the DOC iceberg in terms of its function in mitigating global climate change. While this research field is in relatively uncharted water, we are at the brink of a golden age for doing microbial oceanography and biogeochemistry. For example, a National Microbiome Initiative (NMI) was launched this year in the United States, which might be a direct outcome of strong campaigning from the microbiology community. In China, the microbiology community has successfully launched a "Microbial Hydrosphere Plan" within the National Natural Science Foundation of China (NSFC) while cautiously evaluating the US NMI. The Chinese Academy of Sciences and NSFC are also promoting the development of microbial oceanography programs in China, in which the MCP will be the corollary of future research. The Chinese research community has been preparing to take on these opportunities (Fang et al., 2015; Zhang F et al., 2016; Zhang Z et al., 2016). Thus, there is every reason to be optimistic about a bright future in microbial biogeochemistry for the Chinese research community, which hopefully helps regain global confidence in the currently challenging funding situations.

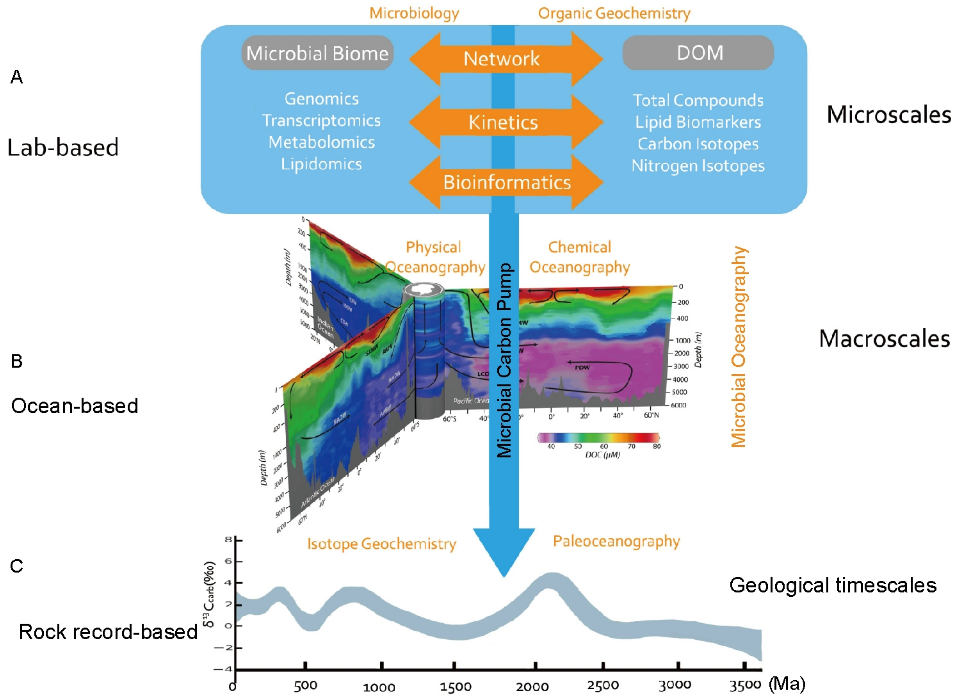

Figure 2 The role the microbial carbon pump (MCP) plays in linking different disciplines in studies of ocean biogeochemistry across time and space. A, At the microscales or lab-based studies, MCP links the disciplines of microbiology and organic geochemistry in unraveling the two grand black boxes "Microbial Biome" and "Dissolved Organic Matter (DOM)"; the former is studied using "omics" tools whereas the latter is addressed by using mass spectrometry tools such as Fourier transform ion cyclotron resonance mass spectrometry for examining a broad spectrum of organic compounds, gas chromatography-mass spectrometry and liquid chromatography-mass spectrometry for identifying specific lipid biomarkers, gas chromatography isotope ratio mass spectrometry for stable carbon and nitrogen isotope analyses, and accelerator mass spectrometry for radiocarbon isotope analysis. B, At the macroscales or ocean-based studies, MCP links the study of microbial oceanography to that of chemical and physical oceanography in untangling the interactions between microbes and dissolved organic carbon (DOC). C, At the geological timescales or rock record-based studies, MCP links geomicrobiology and paleoceanography in deciphering the geological record of DOC in ancient oceans that might have tuned past climate change. Figure 2B represents distribution of DOC in modern oceans (modified from Hansell et al., 2009). Figure 2C represents carbon isotopic compositions of carbonates in marine sediments from different ages (modified from Krissansen-Totton et al., 2015), which reflect possible impact of DOC on dissolved inorganic carbon (DIC) reservoir through geological time. Copyrights were obtained for using Figure 2B from Hansell et al. (2009) and Figure 2C from Krissansen-Totton et al. (2015).

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References

Dang H, Lovell C R. 2016. Microbial surface colonization and biofilm development in marine environments. Microbiol Mol Biol Rev, 80: 91–138

Fang J S, Zhang L, Li J T, Kato C, Tamburini C, Zhang Y Z, Dang H Y, Wang G Y, Wang F P. 2015. The POM-DOM piezophilic microorganism continuum (PDPMC)—The role of piezophilic microorganisms in the global ocean carbon cycle. Sci China Earth Sci, 58: 106–115

Lipp J S, Morono Y, Inagaki F, Hinrichs K U. 2008. Significant contribution of Archaea to extant biomass in marine subsurface sediments. Nature, 454: 991–994

Jiao N, Herndl G J, Hansell D A, Benner R, Kattner G, Wilhelm S W, Kirchman D L, Weinbauer M G, Luo T, Chen F, Azam F. 2010. Microbial production of recalcitrant dissolved organic matter: Long-term carbon storage in the global ocean. Nat Rev Micro, 8: 593–599

Jiao N, Robinson C, Azam F, Thomas H, Baltar F, Dang H, Hardman-Mountford N J, Johnson M, Kirchman D L, Koch B P, Legendre L, Li C, Liu J, Luo T, Luo Y W, Mitra A, Romanou A, Tang K, Wang X, Zhang C, Zhang R. 2014. Mechanisms of microbial carbon sequestration in the ocean—Future research directions. Biogeosciences, 11: 5285–5306

Kallmeyer J, Pockalny R, Ram Adhikari R, Smith D C, D'Hondt S. 2012. Global distribution of microbial abundance and biomass in subseafloor sediment. Proc Natl Acad Sci USA, 109: 16213–16216

Krissansen-Totton J, Buick R, Catling D C. 2015. A statistical analysis of the carbon isotope record from the Archean to Phanerozoic and implications for the rise of oxygen. Am J Sci, 315: 275–316

Volk T, Hoffert M I. 1985. Ocean carbon pumps: Analysis of relative strengths and efficiencies in ocean-driven atmospheric CO_2 changes. In: Sundquist E T, Broecker W S, eds. The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present. Geophys Monogr Ser, 32: 99–110

Whitman W B, Coleman D C, Wiebe W J. 1997. Prokaryotes: The unseen majority. Proc Natl Acad Sci USA, 95: 6578–6583

Zhang C L, Xie W, Martin-Cuadrado A B, Rodriguez-Valera F. 2015. Marine Group II Archaea, potentially important players in the global ocean carbon cycle. Front Microbiol, 6: 1108

Zhang F, Liu J H, Li Q, Zou L J, Zhang Y. 2016. The research of typical microbial functional group reveals a new oceanic carbon sequestration mechanism—A case of innovative method promoting scientific discovery. Sci China Earth Sci, 59: 456–463

Hansell D, Carlson C, Repeta D, Schlitzer R. 2009. Dissolved organic matter in the ocean: A controversy stimulates new insights. Oceanography, 22: 202–211

Zhang Z L, Zheng Q, Jiao N Z. 2016. Microbial D-amino acids and marine carbon storage. Sci China Earth Sci, 59: 17–24