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The POM-DOM piezophilic microorganism continuum (PDPMC)—The role of piezophilic microorganisms in the global ocean carbon cycle

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The deep ocean piezosphere accounts for a significant part of the global ocean, hosts active and diverse microbial communities which probably play a more important role than hitherto recognized in the global ocean carbon cycle. The conventional biological pump concept and the recently proposed microbial carbon pump mechanism provide a foundation for our understanding of the role of microorganisms in cycling of carbon in the ocean. However, there are significant gaps in our knowledge and a lack of mechanistic understanding of the processes of microbially-mediated production, transformation, degradation, and export of marine dissolved and particulate organic matter (DOM and POM) in the deep ocean and the ecological consequence. Here we propose the POM-DOM piezophilic microorganism continuum (PDPMC) conceptual model, to address these important biogeochemical processes in the deep ocean. We propose that piezophilic microorganisms (bacteria and archaea) play a pivotal role in deep ocean carbon cycle where microbial production of exoenzymes, enzymatic breakdown of DOM and transformation of POM fuels the rapid cycling of marine organic matter, and serve as the primary driver for carbon cycle in the deep ocean.

carbon cycle, deep ocean, DOM, PDPMC, piezophilic microorganisms, POM

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1 Introduction

1.1 Ocean carbon cycle, biological pump, and microbial carbon pump

The oceans play a critical role in the global carbon cycle. The coupling between the upper ocean and the atmosphere results in increasing concentrations of dissolved CO_2 in surface seawater. A small fraction of this carbon is transported to the deep ocean via the "solubility pump" through the formation and sinking of dense water at selected high latitude sites. However, most of the carbon is moved through the processes of the "biological pump" (Volk and Hoffert, 1985) which begins with the growth of phytoplankton and the production of marine organic matter in the surface ocean. Organic matter thus produced is exported from the surface waters to the deep ocean and the seabed through, mostly, the sedimentation of particulate organic matter (POM) and to a less extent, export of dissolved organic matter (DOM) in overturning circulation of the ocean water column (e.g., advection, downwelling). The latter represents about 20% of total organic flux to the deep ocean (Carlson et al., 1994; Hansell, 2002).

Carbon cycle in the ocean is driven largely by unicellular microorganisms—bacteria and archaea (Aristegui et al., 2009). A large portion of surface ocean primary production is almost exclusively accessible to heterotrophic bacteria and archaea (Azam et al., 1983; Azam and Ammerman, 1984; Ducklow and Carlson, 1992). Bacteria represent an important component of the global oceanic ecosystems and dominate the abundance, diversity and metabolic activity of the ocean (Azam and Malfatti, 2007). Bacteria mediate a significant flux of organic matter, from DOM to POM (Ducklow, 2009), and account for a substantial fraction of heterotrophic respiration in the oceans (del Giorgio et al., 1997). For example, around 50% of the organic carbon produced by photosynthetic organisms in the euphotic zone is processed by bacteria and used to produce new bacterial biomass and meet the energy requirements for bacterial respiration (Azam et al., 1983).

Archaea, once known as extremophiles, have been discovered throughout the water column in the ocean (DeLong, 1992; Fuhrman et al., 1992). Based on cell counts and molecular studies, archaea accounts for 20% of the prokaryotes in the ocean water column (Offre et al., 2013). The abundance of pelagic archaea increases with depth in the ocean (Karner et al., 2001; Herndl et al., 2005; Kirchman et al., 2007; Sato et al., 2009), suggesting that marine archaea probably play an important role in deep ocean carbon cycle.

The recently proposed "microbial carbon pump" (MCP) (Jiao et al., 2010) provides a conceptual framework in understanding the role of microorganisms in cycling of marine organic matter. The MCP emphasizes the formation of recalcitrant DOM (RDOM) and the thus created stock of carbon storage in the process of microbial utilization of DOM. Microorganisms transfer organic matter from a biologically reactive state (labile DOM, LDOM) to a non-reactive state (RDOM), contributing to the storage of carbon in the ocean. Thus, the biological carbon pump emphasizes the passive vertical transport of organic matter, driven by primary production in the surface ocean (Hansell et al., 2009), and the MCP highlights the importance of heterotrophic microbial activity in biotransformation of organic matter. However, there are still significant gaps in our knowledge and understanding of microbial processes that control secretion, transformation, degradation, and export of marine organic matter in the water column. Our present understanding of these important processes is speculative at best. This is particularly true for processes occurring in the deep ocean, which are likely mediated mainly by piezophilic microorganisms. Recent studies suggest that deep ocean microorganisms play a more important role in mineralization of marine organic matter than hitherto recognized (Tamburini et al., 2003, 2009, 2013; Nagata, 2000; Glud et al., 2013). Here we propose a conceptual model, POM-DOM piezophilic microorganism continuum (PDPMC), to illustrate the mechanistic processes of piezophilic microorganism-mediated carbon cycle in the deep ocean (Fang et al., 2012).

1.2 Marine organic matter

Marine organic matter is produced mostly by photosynthetic plankton in the surface ocean. Operationally, marine organic matter is divided as particulate organic matter (POM) and dissolved organic matter (DOM) based on filtration of seawater using a 0.7 m filter. POM is comprised of various components that include organic and inorganic constituents such as phytoplankton and bacterial cells, organic detritus, fecal pellets, and inorganic particles. In general, the nonliving POM (i.e., detritus) exceeds that of plankton by a ratio of detritus/plankton 10∶1 (Kirchman et al., 1993). Yet, heterotrophic bacteria can be a major part of the living biomass of POM, particularly in oligotrophic areas (Caron et al., 1995). Thus, POM is a complex mixture of living and nonliving organic matter, having a broad range in size, form, and reactivity (Volkman and Tanoue, 2002). POM amounts for up to 30×10^{15} g C, and forming the second largest organic carbon pool in the ocean (Hansell and Carlson, 2001; Verdugo et al., 2004).

DOM represents one of the largest active pools of organic carbon in the global carbon cycle (Hedges, 1992; Hopkinson et al., 2002). DOM is produced from POM through mechanisms such as direct exudation from phytoplankton, from cell lyses due to viral infection, from "sloppy" zooplankton feeding, and from predator grazing or from particle solubilization. The amount of carbon in oceanic DOM, 700×10^{15} g C, is approximately equal to that of carbon in the atmosphere (750×10^{15} g C) (Ogawa et al., 2001). The dissolved organic carbon (DOC) is the carbon component of the DOM. Most of the marine DOC, about 90%–95%, is present in the deep ocean, with concentrations of 35–45 M DOC (e.g., Hopkinson et al., 1997; Hansell and Carlson, 1998; Ogawa et al., 1999). Therefore, it is imperative to study the deep ocean carbon cycle and the processes mediated by piezophilic microorganisms in order to gain a mechanistic understanding of the global ocean carbon cycle.

1.3 Hydrostatic pressure and piezophilic microorganisms in the deep-ocean piezosphere

The deep-ocean piezosphere is the volume of the ocean with hydrostatic pressure over 100 atm or 10 MPa (Bartlett, 2008; Fang et al., 2010). It is the largest aquatic habitat on earth, and is probably the most understudied oceanic environments (Aristegui et al., 2009; Tambuiri et al., 2006, 2009). The deep ocean contains the largest pool of microbes, harboring 75% of the prokaryotic biomass and 50% of the prokaryotic production of the global ocean (Aristegui et al., 2009). It is also the largest reservoir of inorganic carbon, containing greater than 98% of the global dissolved inorganic carbon (Gruber et al., 2004). The importance of the deep piezosphere in global ocean carbon cycle is manifested by the fact that it is the largest reactive component of the global carbon cycle (Hedges, 1992; Hansell and Carlson, 1998; Benner, 2002).

The deep ocean houses the most voluminous high hydrostatic pressure environment on earth and represents a major fraction of the biosphere (~62%) (Jannasch and Taylor, 1984). Piezophily is a general feature of bacteria in the deep ocean (Yayanos, 1998). Piezophiles are pressure-loving microorganisms which reproduce preferentially or exclusively at pressures greater than atmospheric pressure (Bartlett, 2008; Kato et al., 2008). The majority of the piezophilic microorganisms reported thus far are Gram-negative, facultative anaerobic Bacteria, and only a few piezophilic archaeal species have been isolated, which are either hyperthermo-piezophiles or hyperthermo-hyperpiezophiles (Fang et al., 2010). Most of the reported piezophilic bacterial isolates are within the orders Alteromonadales and Vibrionales, including *Colwellia, Moritella, Photobacterium, Pyschromonas,* and *Shewanella* (Kato et al., 1995, 1998; DeLong et al., 1997). Other piezophilic isolates include a moderately piezophilic sulfate-reducing bacterium, *Desulfovibrioprofundus,* from sediment in the Japan Sea (Bale et al., 1997), *Desulfovibriohydrothermalis* from a hydrothermal vent chimney in the East Pacific Rise (Alazard et al., 2003), *Desulfovibriopiezophilus* from wood falls in the Mediterranean Sea (Khelaifia et al., 2011; Pradel et al., 2013), *Marinitogapiezophila* of the Thermotogales isolated from a deep-sea hydrothermal vent (Alain et al., 2002), and two piezophilic Gram-positive bacteria, member of genus *Carnobacterium,* isolated from the Aleutian Trench and the Kermadec Trench (Lauro and Bartlett, 2007).

There are a few piezophilic archaeal species isolated from the deep ocean thus far. These species include *Pyrococcusabyssi*, a moderate piezophileisolated from the Fiji Basin at 2000 m (Erauso et al., 1993), *Thermococcusbarophilus*, a hyperthermo-piezophilic archaeon isolated from the Mid-Atlantic Ridge (MAR) (Marteinsson et al., 1999), *Methanopyruskandleri*strain 116, a methanogen isolated from the Central Indian Ridge, and achemoorganoheterotrophic, hyperthermo-hyperpiezophilicarchaeon, *Pyrococcusyayanosii* CH1, also isolated from the MAR (Zeng et al., 2009). It appears that the diversity and abundance of deep-sea piezophiles are likely much greater than what we know today (Fang and Bazylinski, 2008: Fang et al., 2010). The majority of the microorganisms in the deep ocean is poorly represented in our current microbial databases simply because of a lack of breadth and scale in sampling, but may be responsible for key metabolic processes in global biogeochemical cycles (Brown et al., 2009).

2 The POM-DOM piezophilic microorganism continuum (PDPMC) model

2.1 The model

The deep ocean is a huge bioreactor, holding a unique reservoir of high genetic and metabolic diversity of microorganisms that play a central role in ocean's carbon cycle. The endless "rain" of marine aggregates has long been considered as one of the major processes linking the surface and deep ocean and a critical component in the global ocean carbon cycle (Volk and Hoffert, 1985). However, marine organic matter is not a static pool of isolated substances in the ocean, but a dynamic assemblage of organic molecules that interact with microorganisms at various spatial and temporary scales (Hedges, 2002). Microbial activity in the ocean is coupled to, and largely fueled by, the sinking marine aggregates from the surface ocean and thus, is limited by the flux of POM delivered to the depth (Martin et al., 1987; Anderson and Williams, 1999; Nagata, 2000; Azam and Long, 2001; Tamburini et al., 2003).These processes in turn regulate the flux of sinking particles to depth. Here we propose the PDPMC conceptual model (Figure 1) which entails the interactions among descending marine particulates, particulate-attached and free-living microorganisms, the transport and degradation of marine organic matter, and implications for the global ocean carbon cycle, a dynamic continuum of microbiological and biogeochemical processes mediated by piezophilic bacteria in the ocean. The main points of the PDPMC model include:

(1) The POM microniche and microbial attachment. The descending marine particulates (POM) from the surface ocean to the deep ocean act as a carbon- and nutrient-rich microenvironment for preferred microbial colonization and attachment, which further promotes the coupling and interactions between POM and microorganisms.

(2) Microbial extracellular enzymatic activities. Attach-

ment of microorganisms to the descending particulates tends to alter microbial physiology and stimulate microbial metabolism including up-regulating microbial production of extracellular enzymatic activity (EEA).

(3) Microbial disintegration of POM and the formation of carbon- and nutrient-enriched plume. The increased EEA enhances the disintegration of the descending particulates, biotransformation of POM and production of DOM, regeneration of nutrients, mobilization of carbon, and biodegradation of DOM. This continuum of dynamic microbial processes serves as the primary driver for carbon cycle in the deep ocean. The carbon- and nutrient-enriched plume formed around the sinking particulates stimulates metabolism of free-living piezophilic microorganisms in the surrounding water column and leads to increased biotransformation and biodegradation of DOM.

(4) The PDPMC model. The PDPMC model embodies the mechanistic processes of the coupling and dynamic interactions among marine POM, DOM, and piezophilic microorganisms in the deep ocean. Thus, piezophilic microorganisms play a critical role in the global ocean carbon cycle.

2.2 The role of deep ocean piezophilic microorganisms in depolymerization of marine macromolecules—transformation of POM and production of DOM

The slowly sinking particulates from the surface ocean serve as hot-spots of microbial communities and activity as microorganisms preferentially attached to the descending particulates (Alldredge and Gottschalk, 1990; Azam, 1998; Simon et al., 2002; Grossart et al., 2007) (Figure 1). As a result, the density of microorganisms colonizing marine particulates can be orders of magnitude higher than the surrounding waters, reaching up to 10^9 cell/mL (Alldredge and Gottschalk, 1990; Anderson and Williams, 1999). On one hand, microbial attachment increases and stabilizes particle

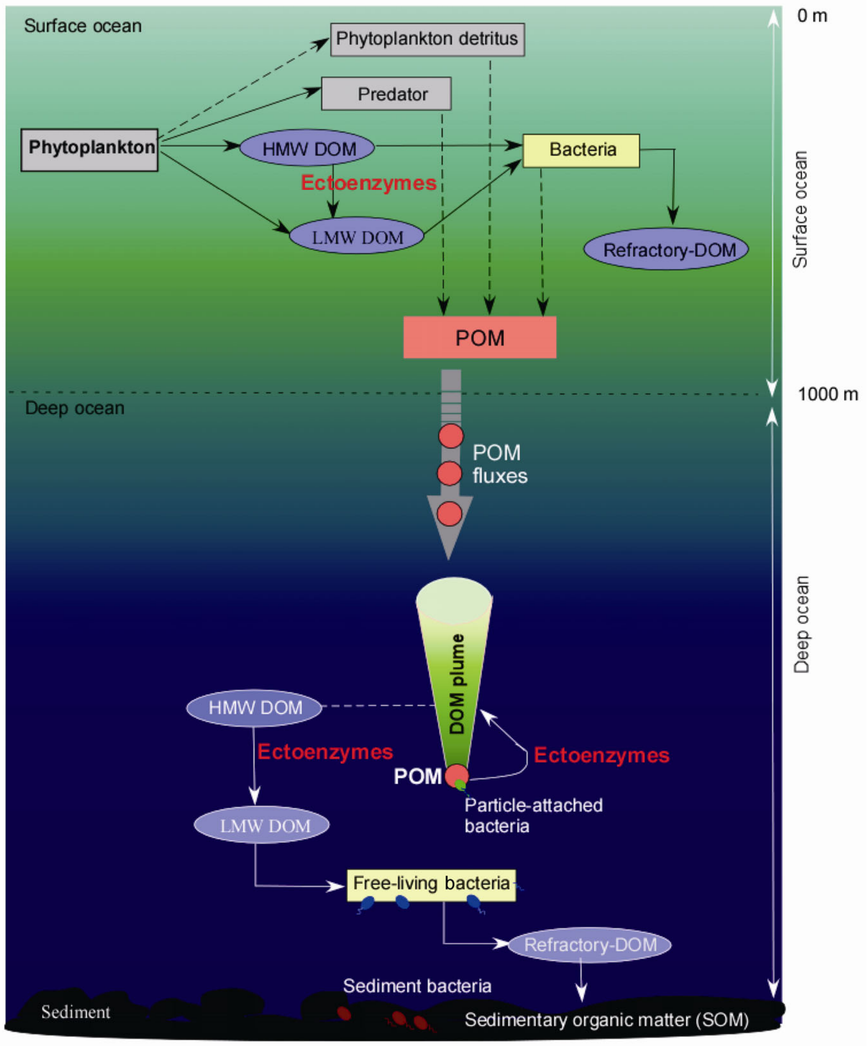

Figure 1 The POM-DOM piezophilic microorganism continuum (PDPMC). Shown are major microbiological and biogeochemical processes, mediated by piezophilic microorganisms, in transformation of POM to HMW DOM, from HMW DOM to LMW DOM intermediates, and in degradation and cycling of DOM. POM, particulate organic matter; DOM, dissolved organic matter; HMW, high molecular weight; LMW, low molecular weight.

aggregation (e.g., Gardes et al., 2011) and therefore, efficiently increases sedimentation and removal of marine organic matter from the surface ocean to the deep ocean. On the other hand, the attached microorganisms produce copious extracellular enzymes such that the particulates retain much higher microbial extracellular enzyme activity than the surrounding seawater (Smith et al., 1992; Ploug et al., 2008; Ziervogel and Arnosti, 2008). Thus, microbial attachment to particulates represents a biochemical mechanism that has multifaceted biogeochemical consequences, including the transform of organic carbon from particle phase (POC) to dissolved phase (DOC) and thus, increasing the quality and quantity of bioavailable organic carbon, and enhancing the potential of microbial degradation of DOC and carbon cycling in the ocean.

The sinking organic detritus is a composite of macromolecular compounds that include structural carbohydrates, proteins, nucleic acids, and lipid complexes (Jorgensen, 2009). Microorganisms are unable to take up particles or even large organic molecules in size greater than ca. 600 Daltons (Da) (Weiss et al., 1991). A simple depolymerization (e.g., hydrolysis) of these large molecules to monomeric products is necessary. This depolymerization process is initiated by exoenzymes produced by the particulate-attached microorganisms. The depolymerized products are either released freely into the surrounding environment or associated with the outer membrane or cell wall of the microorganisms (Arnosti, 2011). The extracellular enzymes break down high molecular weight (HMW) biopolymers into low molecular weight (LMW) (<600 Da) DOM intermediates. As a result, the marine particulates enroute to the deep ocean gradually release DOM through enzymatic processes of the attached microorganisms (Figure 1). The released LMW DOM intermediates forms a nutrient-rich plume streaming behind the marine particulates (Alldredge, 2000; Simon et al., 2002), constituting the POM-DOM piezophilic microorganism continuum (Figure 1).

2.3 The free-living microorganisms (FLM) and their role in degradation of DOM

From a biogeochemical perspective, the deep ocean can also be viewed as a large, dilute organic carbon bioreactor that operates at low-temperature and high-pressure conditions. It has been a widespread view that microbial activities in the deep ocean are extremely low and largely suppressed under the dark, cold, high pressure conditions, and the reduced quantity and quality of organic matter and nutrient content (Jannasch and Wirsen, 1973). Thus, marine microbes display minimum responses to the inputs of organic matter and likely play only a minor role in ocean biogeochemical cycles. The PDPMC model suggests the otherwise: the quality and quantity of organic matter and nutrients in the surrounding water of a descending particulate increases as a result of microbial disintegration of POM. In fact, recent studies suggest that the deep ocean is a heterogeneous habitat (Hewson et al., 2006) with distinctive and previously unknown communities of remarkably diverse microorganisms (Sogin et al., 2006; DeLong et al., 2006). Furthermore, the deep ocean microbial assemblages are adapted to high-pressure conditions and display unique molecular architectures and metabolic capabilities (Vezzi et al., 2005; DeLong et al., 2006; Lauro and Bartlett, 2007) that allow them to thrive under high-pressure conditions in the deep ocean (Lauro and Bartlett, 2008) and play an important role in mineralization of marine organic matter (Glud et al., 2013). Activity of deep ocean piezophilic microorganisms is higher than our laboratory decompressed measurements have showed. Cell-specific *in situ* measurements of microbial activities (ectoenzymatic activity, heterotrophic microbial production and dark fixation of CO_2) suggest that microbial metabolic rates in the deep ocean are as much as 11-fold higher than previous estimates obtained under surface decompression conditions (Tamburini, 2006; Tamburini et al., 2006, 2009). These ectoenzymatic activities are considered to be the limiting step for the heterotrophic mineralization of organic matter (Chrost, 1991). Specific metabolic genes related to the degradation of refractory pools of organic matter (e.g., chitin, cellulose and pullulan) metabolic pathways have been recovered from the deep ocean (DeLong et al., 2006; Martin-Cuadrado et al., 2007). Vezzi et al. (2005) showed that piezophilic bacterium *Photobacteriumprofundum* SS9 degraded many refractory compounds such as chitin, cellulose and pullulan. Additionally, when the measured rates are integrated over the entire water column of the deep ocean, the mineralization fluxes mediated by microbial populations in the deep sea are far from negligible (del Giorgio et al., 1997; Lefevre et al., 1996; Bianchi et al., 1998; Tamburini et al., 2002). These results suggest that the deep ocean piezophilic microorganisms are more resilient and expressing higher ectoenzymatic activities in degrading recalcitrant organic matter.

3 Summary and future research directions

The PDPMC represents a dynamic model of piezophilic microorganism-mediated deep ocean carbon cycle (Fang et al., 2012). The model is different from the BP and the MCP in a number of different ways. First, it elucidates the mechanistic processes of carbon cycle at the molecular level and emphasizes the dominated role of piezophilic microorganisms in the entire continuum of microbiological and biogeochemical processes of the deep ocean carbon cycle. Second, the model provides a conceptual framework for illustrating the interactions between marine organic matter and piezophilic microorganisms, entailed in the transformation of POM to DOM and the partitioning between POM and DOM, regulation of the channeling and export flux of organic matter from the surface ocean to the deep ocean, degradation of DOM, and the biogeochemical dynamics of carbon cycling in the deep ocean. Finally, the PDPMC emphasizes the interactions between marine particulates and piezophilic microorganisms in the broader biogeochemical and enzymatic context of carbon cycling at *in situ* environmental conditions, particularly, the *in situ* hydrostatic pressure. Within the POM-DOM piezophilic microorganism continuum, marine particulates are continuously transformed to HMW DOM which are further transformed into LMW DOM intermediates. The LMW DOM are either remineralized directly to CO_2 within the microbial food web, supporting heterotrophic microbial production, or converted to recalcitrant DOM and ultimately, incorporated into marine sediment as sedimentary organic matter (SOM). Chemolithoautotrophic microorganisms may utilize the released CO_2 for *in situ* dark fixation (Figure 1). Thus, the chemistry and reactivity of DOC, the quality, quantity, and degradability of marine organic matter changes dynamically with changes in the physic-chemical condition and the microbiology of the deep ocean environment.

Given our current limited understanding of these microbiological and biogeochemical processes under high pressure conditions in the deep ocean, future research should focus on:

(1) Determining the abundance, composition and diversity of piezophilic microorganisms in the deep ocean, including those attached to and free-living microbes around the sinking particulates. Additionally, the distribution and stratification of distinct microbial populations in different water masses and pressure regimes must be determined, in relation to changes in the chemistry and biological reactivity of organic matter with depth, and adaptations to pressure and temperature must be revealed. Further, quantitative linkages between microbial diversity, activity and ecosystem function must be determined. Combining modern molecular microbiological techniques, such as catalyzed reporter deposition-fluorescence *in situ* hybridization (CARD-FISH) which reveals spatial distribution of the microbial community (e.g., Scrippers et al., 2005), and single-cell genomics and metatranscriptomes which uncover metabolically active and dormant microorganisms of microbial populations (Siegl et al., 2011), with imaging secondary ion mass spectrometry on a nanometer scale (Boxer et al., 2009), can be a powerful approach to link microbial community structure, enzyme production, and microbial degradation activity at the submicromolecular scale (Hermann et al., 2007; Amstalden et al., 2010). The uptake and transformation of organic matter by heterotrophic piezophilic microorganisms is a major carbon-flow pathway and therefore, the variability of microbial abundance, diversity, metabolic activity, and ecosystem function can change the overall patterns of organic matter flux and carbon cycle in the oceans (Azam, 1998; Williams, 1998). Currently, the microbial diversity of piezophilic microorganisms is seriously underestimated because of various problems in (i) sampling and preservation of deep ocean samples at *in situ* conditions, (ii) preferential use of rich, heterotrophic growth media in the isolation of piezophilic microbes, (iii) the currently used piezophile-culturing devices incapable of reproducing the chemistry of the microorganisms' surrounding environment in the deep ocean; and (iv) inappropriate techniques used in microbial identification and quantification (Fang et al., 2010). It is predicted that the diversity of deep ocean piezophilic microorganisms will increase significantly as the use of new types of growth media, novel culturing strategies, and novel molecular sequencing techniques are employed (Fang et al., 2010).

(2) Addressing the mechanism of bacteria attachment to and interaction with marine particulates, and the associated changes in bacterial physiology, metabolism, enzymology, and ecological dynamics with increasing depth (pressure). It is essential that relevant experiments characterizing microbial physiology, metabolism, and enzymology be carried out under *in situ* pressure conditions, so that microbial metabolic activity and enzymatic processes in transformation of POM, uptake and degradation of DOM can be accurately determined. Furthermore, the interaction between phytoplankton and heterotrophic bacteria may affect the formation and disintegration of particulates, microbial enzyme production, and the production and interconversion of POM and DOM and therefore, the export of organic carbon from the surface ocean to the deep ocean. Thus, it is crucial to quantify the POM and DOM pools, fluxes, and microbiological controls in order to understand oceanic carbon cycling mediated by microorganisms. It is clear that the activity of deep-sea piezophilic microbes under *in situ* conditions is higher than our laboratory decompressed measurements have showed. The gross underestimation of microbial activities in the deep ocean can be attributed to two main factors: (i) our inability to take uncompressed deep ocean water/sediment samples to preserve the microbial physiology and metabolic lifestyles for land laboratory measurements; and (ii) our inability to measure the *in situ* microbial activity. Thus, collecting non-decompressed deep ocean samples and accurately measuring deep ocean microbial physiologies and activities are crucial to better assess the real impact of deep ocean microbial activity in global carbon cycle. Combining the traditional enzymatic approach and the new genetic and protein-based tools (e.g., enzymatic gene expression) enable the revelation of microbial community composition and functioning, particularly, linking microbial abundance to the rates and pathways of DOM processing and transformation (von Mering et al., 2007).

(3) Determining the chemistry and biological reactivity of DOM in different pressure/ecological regimes of the deep ocean. The chemistry (chemical composition and structure) of marine organic matter is one of the biggest black-box problems in chemical oceanography. Marine DOM is a complex mixture of thousands of compounds consisting of intact and transformed biomolecules from living and dead

organisms (Mopper et al., 2007), yet the common components of marine biomass, such as lipids, amino acids, and carbohydrates, represent less than 10% of DOM (Hedges et al., 2000). Furthermore, the chemistry of POM and DOM changes with depth and DOM ages in the ocean (Flerus et al., 2012). Additionally, microbial degradation of marine organic matter, one of the most important components of ocean carbon cycle, is dependent upon the chemistry of the organic matter, as well as the composition and diversity of the microbial community. Indeed, the recalcitrance of marine organic matter is not only a molecular chemical property, but also an ecosystem (microbiological) and environmental (geochemical) property. Thus, the chemistry of DOM affects the relative biological reactivity, the potential storage capacity and turnover times of the deep ocean carbon pool, whereas the *in situ* microbiology and microbial metabolism of the deep ocean affects the recalcitrance of marine organic matter. However, the mechanisms of the production, digenesis, and preservation of DOM in the ocean are unknown (Flerus et al., 2012). In addition, we know little about how deep ocean microorganisms respond to shifts in the composition, distribution and supply of organic carbon (Azam, 1998). Therefore, characterizing the chemical composition and molecular structure of DOM is imperative for determining the dynamics of microbial utilization of DOM. The recently developed Fourier transform ion cyclotron resonance mass spectrometry (FT-ICR-MS) is a powerful analytical technique for molecular-level characterization of the complex composition and structure of DOM (e.g., Kim et al., 2003; Koch et al., 2005; D'Andrilli et al., 2010; Flerus et al., 2012). It has the capacity to resolve the thousands of components in DOM, assign exact molecular formula, reveal the structural relationships among families of compounds, and determine the biological reactivity of DOM (Kim et al., 2003; Flerus et al., 2012). Results from our recent analysis of DOM samples from the South China Sea demonstrate the power of this technique, where different families of compounds and the reaction pathways leading to the groups of compounds can be identified (Figure 2).

Radiocarbon dating provides another constrain on the production and export of DOM, microbial degradation state, and the accumulated molecular structural changes of DOM (Druffel et al., 1992; Loh et al., 2004; Beaupre et al., 2009; Flerus et al., 2012). This presumably reflects a good correlation between recalcitrance of DOM and the Δ^{14}C of bulk DOM and its components (Siegl et al., 2011).

(4) Finally, assessing the capacity of the PDPMC in the processing of POM and DOM and the role of piezophilic microorganisms in the global ocean carbon cycle. The capacity of PDPMC can be determined accurately only when the microbiology of piezophilic microorganisms, the chemistry and reactivity of marine organic matter, and metabolism and enzymology of piezophilic microorganisms in transformation and degradation of DOM are determined in different pressure regimes and integrated in the global ocean. Until then, the PDPMC will provide a mechanistic basis for our understanding of the piezophilic microorganism-mediated deep ocean biogeochemical processes and the global carbon cycle (Fang and Kato, 2008; Fang et al., 2012). We propose that piezophilic microbialenzyme production, enzymatic breakdown and transformation of marine particulates fuels the rapidly cycling of dissolved organic matter pool, and serve as the primary driver for carbon cycle in the deep ocean. The PDPMC conceptual framework will help to unravel the variation of the dynamics of deep ocean carbon cycle at different depths and in different regions of the ocean, and provides a significant step in integrating the emerging paradigm regarding high-pressure microbiology and enzymology of piezophilic microorganisms with global ocean carbon cycle. We foresee that the integration of high-pressure microbiological, molecular chemical and biogeochemical information will provide global ocean carbon cycle science with a more mechanistic basis for predictions of carbon cycle dynamics in, e.g., climate change.

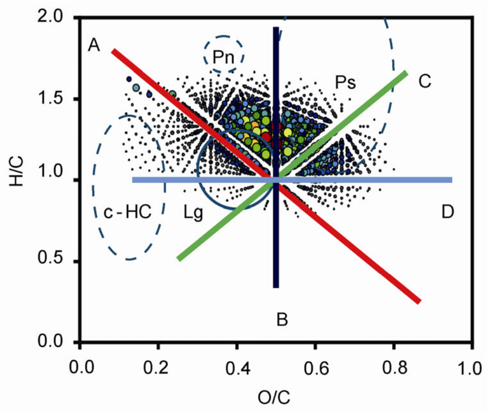

Figure 2 The van Krevelen diagram, showing results of Fourier transformion cyclotron resonance mass spectrometry (FT-ICR-MS) analysis of a seawater sample collected at depth of 1500 m in South China Sea in 2012. A broad range of organic compounds were detected in the sample. Shown are positions of major biomolecular components: Pn, protein; Ps, polysaccharides; c-HC, condensed hydrocarbons; Lg, lignin. Trend lines represent reaction pathways that results in the formation of the families of compounds. Line A: methylation/demethylation/alkyl chain elongation; Line B: hydrogenation/ dehydrogenation; Line C: hydration/condensation; Line D: oxidation/reduction (Kim et al., 2003; Koch et a., 2005).

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