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Perspectives of the microbial carbon pump with special references to microbial respiration and ecological efficiency

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Abstract

Although respiration consumes fixed carbon and produce CO_2, it provides energy for essential biological processes of an ecosystem, including the microbial carbon pump (MCP). In MCP-driving biotransformation of labile DOC to recalcitrant DOC (RDOC), microbial respiration provides the metabolic energy for environmental organic substrate sensing, cellular enzyme syntheses and catalytic processes such as uptake, secretion, modification, fixation and storage of carbon compounds. The MCP efficiency of a heterotrophic microorganism is thus related to its energy production efficiency and hence to its respiration efficiency. Anaerobically respiring microbes usually have lower energy production efficiency and lower energy-dependent carbon transformation efficiency, and consequently lower MCP efficiency at per cell level. This effect is masked by the phenomena that anoxic environments often store more organic matter. Here we point out that organic carbon preservation and RDOC production is different in mechanisms, and anaerobically respiring ecosystems could also have lower MCP ecological efficiency. Typical cases can be found in large river estuarine ecosystems. Due to strong terrigenous input of nutrients and organic matter, estuarine ecosystems usually experience intense heterotrophic respiration processes that rapidly consume dissolved oxygen, potentially producing hypoxic and anoxic zones in the water column. The lowered availability of dissolved oxygen and the excessive supply of nutrients such as nitrate from river input prompt enhanced anaerobic respiration processes. Thus, some nutrients may be consumed by anaerobically respiring heterotrophic microorganisms, instead of being utilized by phytoplankton for carbon fixation and primary production. In this situation, the ecological functioning of the estuarine ecosystem is altered and the ecological efficiency is lowered, as less carbon is fixed and less energy is produced. Ultimately this would have negatively impacts on the ecological functioning and efficiency of the MCP which depends on both organic carbon and energy supply.

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1 Introduction

The microbial carbon pump (MCP) is a recently proposed biological mechanism for dissolved organic carbon (DOC) transformation and storage in water columns of the global oceans, which involves the production of recalcitrant DOC (RDOC) from labile DOC (LDOC) via microbial processing (Jiao et al., 2010, 2013, 2014). Approximately 155 Pg (10^{15} g) of RDOC are currently sequestered via the marine MCP (Benner and Herndl, 2011), and millennial mean ages of marine DOC have been observed throughout the water column except in surface waters (Loh et al., 2004; Hansell, 2013). Soil and sediment microbial communities may play similar roles in RDOC production and carbon sequestration (Benner, 2011; Liang and Balser, 2011). Thus, the MCP conceptual framework can be considered universally valid for the Earth's major ecosystems. The MCP potential of decadal to millennial deactivation and sequestration of organic carbon on a global scale has profound impacts on the Earth's carbon cycle and climate change.

As a major process that may control the biogeochemical cycling of carbon and particularly its long-term storage, the MCP is a basic ecosystem property of the ocean as similarly illustrated in the soil environment (Schmidt et al., 2011). Abiotic and biotic factors that influence the structure, processes and functions of an ecosystem may also influence the functioning and efficiency of the MCP for RDOC production and storage. Accumulating evidence indicates that microbes, when growing on LDOC, produce RDOC that is resistant to further biochemical degradation and utilization (Taylor et al., 1985; Brophy and Carlson, 1989; Heissenberger and Herndl, 1994; Stoderegger and Herndl, 1998, 1999; Ogawa et al., 2001; Gruber et al., 2006; Kawasaki and Benner, 2006). Furthermore, marine microbes differ substantially in their individual abilities to utilize specific DOC compounds, with some microbes being generalists and others being specialists (Gómez-Consarnau et al., 2012). Thus, changes in the abundance or composition of the DOC pool act as selective forces structuring the natural microbial communities (Gómez-Consarnau et al., 2012; Nelson and Carlson, 2012; Nelson et al.,

2013). This also implies that changes in the composition and structure of the microbial communities may change the abundance and composition of the marine DOC pool, leading to the production and accumulation of different RDOC components with varying ages of persistence in the environment.

5   Under natural environmental conditions, the consumed LDOC is partly used for microbial cell growth. However, most of the environmental LDOC is used by the microbes for respiration (del Giorgio et al., 1997; Cotner and Biddanda, 2002; del Giorgio and Duarte, 2002; Carlson et al., 2007; Karl, 2007; Ducklow and Doney, 2013). Microbial respiration is a fundamental life process (Brune et al., 2000; Carlson et al., 2007; Robin-
10 son and Ramaiah, 2011), which consumes organic carbon (usually in various forms of LDOC) for cellular energy production accompanied simultaneously by the production and accumulation of by-product and/or waste-product chemical compounds (maybe in various forms of RDOC). The respiration process not only participates in the MCP via direct production and accumulation of respiratory RDOC products but also provides
15 energy to fuel the ecosystem for running the MCP process. Thus, there is an intrinsic linkage of microbial respiration and the MCP at subcellular, cellular, organism, population, community and ecosystem levels, and heterotrophic microbial metabolic rates constrain the MCP (Robinson and Ramaiah, 2011).

Microorganisms utilize a variety of respiration systems, including both aerobic and
20 anaerobic pathways with distinctly different energy production efficiency for respiratory energy metabolism (Burgin et al., 2011; Wright et al., 2012). Some microbes may harbor several different respiration pathways. For example, Richardson (2000) has reviewed that, *Paracoccus denitrificans*, a common environmental bacterium, employs the cytochrome aa_3 oxidase as the terminal electron acceptor in conditions of high
25 oxygen tensions to operate a highly coupled electron-transfer pathway, while in low oxygen tension situations, this bacterium mainly employs the high-affinity cytochrome cbb_3 oxidase. Further under anoxic conditions, *Paracoccus denitrificans* switches to anaerobic respiration pathway that employs respiratory enzymes capable of reducing nitrogen oxy-anions and nitrogen oxides (Richardson, 2000). In general, anaero-

bic respiration produces less metabolic energy than aerobic respiration does (Burgin et al., 2011; Wright et al., 2012). As the MCP is mainly fueled by respiration-produced metabolic energy, with the integration of microbial respiration into the MCP theoretical framework, the efficiency of the MCP for DOC transformation and storage may be better understood, especially by comparative analyses of the MCP processes and mechanisms in contrasting environments such as oxic, suboxic and anoxic zones and their interfaces in marine waters and sediments.

The MCP has been reviewed about its major microbial processes and mechanisms (Jiao and Azam, 2011; Jiao et al., 2013, 2014), which include (1) the active mode pertaining to the release of RDOC via direct microbial secretion or environmental production through extracellular enzymatic activities, (2) the passive mode pertaining to the release of RDOC via virus lysis and grazing, and (3) the threshold mode pertaining to the retention of environmental DOC due to its low metabolic economics under extremely low concentration conditions. Heterotrophic bacteria and archaea play a dominant role in the marine MCP process (Jiao et al., 2010; Benner and Herndl, 2011). In the active mode, the secretion of cellular products and the synthesis and secretion of extracellular enzymes may need to consume metabolic energy, which is mainly produced by cellular respiration in heterotrophic microbes. The MCP concept and framework have called great attention in the scientific realm since they were formulated in 2010 (Jiao et al., 2010), and many previous puzzling geochemical phenomena and questions, especially those related to the marine carbon cycle, may find answers or clues by employing the MCP theoretical framework (Jiao et al., 2013, 2014). However, the MCP-related microbial processes and mechanisms, especially those pertaining to cellular physiology and energy metabolism, have not yet been fully explored. In addition, as a fundamental and important biogeochemical process, the ecological efficiency of the MCP pertaining to marine carbon cycling and carbon sequestration may need to be further fathomed with the consideration of microbial energy metabolism efficiency. This review attempts to present an overview, though still waiting to be fully substantiated by future in depth researches due to the general lack of relevant investigations at present, of the inter-

connections of the MCP, microbial heterotrophic respiration and ecological efficiency at large river estuaries, where diverse and complicated geochemical settings and perturbations may enrich our understanding of the MCP mechanism and its eco-engineering potentials.

2 Fundamental linkage of cellular respiration to MCP

Microbial respiration is a fundamental metabolic process that consumes organic carbon to produce energy for life sustaining. Many cellular and physiological processes, especially in heterotrophic microorganisms, rely on respiration-produced energy, mainly in the form of adenosine-5′-triphosphate (ATP) or proton motive force (*pmf*), to carry out their functions. As the key energy transfer molecule in cells, ATP is the central intermediate between energy-yielding (exergonic) and energy-requiring (endergonic) reactions, serving as the "molecular unit of currency" of intracellular energy transfer. Oxidative phosphorylation in respiration, substrate-level phosphorylation in fermentation and photophosphorylation in photosynthesis are the major mechanisms of ATP biosynthesis in living organisms. However, except for obligate fermenters, all microorganisms carry out respiration (Carlson et al., 2007). ATP molecules produced by energy metabolic processes such as respiration play critical roles in cellular carbon metabolism.

ATP is the central molecule in energy metabolism, which along with *pmf* provides energy for various essential cellular processes, such as (1) motility and chemotaxis in sensing, signaling and response to environmental cues such as utilizable LDOC substrates; (2) uptake, utilization, transformation or modification of metabolic substrates such as LDOC; (3) biosynthesis and storage of cellular products; (4) cellular genetic material replication and cell reproduction; (5) secretion of extracellular compounds such as toxins, metabolic products, by-products and waste products (some maybe RDOC); and (6) biosynthesis, modification and activity regulation of enzymes and other proteins for carrying out the above mentioned processes, of which many are related to

carbon metabolism (Fig. 1). Thus, ATP and *pmf* generated by heterotrophic respiration participate in the MCP-related microbial process in several ways:

2.1 Energy-fueled cellular sensing, signaling and response

In nature, microorganisms usually live in a world with frequently changing physico-chemical environment (such as temperature, pH, oxygen tension, redox, salinity, osmolarity, light, quorum sensing chemical signals, heavy metals, and other contaminants and biocides) and nutritional conditions (such as inorganic and organic substrates, N and P nutrients, oxidants (as electron acceptors), reductants (as electron donors), and trace elements). The change of these environmental conditions is most frequent and rigorous at the submillimetre spatial scale, and microorganisms have evolved the mechanisms and machinery to adapt to the steep gradients of small- and micro-scale extracellular physicochemical and nutritional conditions (Stocker, 2012). In order to survive in and optimally exploit or escape from the changing environment, prokaryotes (bacteria and archaea) have evolved the capability of sensing and response to various environmental signals.

2.1.1 Two-component signal transduction

The two-component signal transduction systems (TCS), also known as histidyl-aspartyl phosphorelay systems, are typically composed of a sensor histidine kinase that receives the input stimuli and a cognate response regulator that effects an appropriate change in cellular physiology. TCS are an elegant and predominant means by which many microorganisms cope with environmental change and stress (Capra and Laub, 2012). Upon activation by way of a stimulus, ATP-dependent autophosphorylation on a specific histidine residue of the sensor histidine kinase and subsequent transfer of the phosphoryl group to an aspartate residue on the cognate response regulator leads to changes in transcriptional, enzymatic or mechanistic properties, thus alter the phys-

iology and/or behavior of the microorganism in the environment (Gao and Stock, 2009; Capra and Laub, 2012).

TCS are present in > 95 % of bacterial genomes and some 50 % of archaeal genomes, while the only bacteria lacking TCS are pathogens (e.g. *Mycoplasma* species) and endosymbionts (e.g. *Amoebophilus* species) with severely reduced genomes (Wuichet et al., 2010). The MiST2.1 Microbial Signal Transduction Database (last accessed 14 June 2013) currently identifies 214 336 TCS proteins from a total of 3075 bacterial and archaeal genomes (Ulrich and Zhulin, 2010). The P2CS (Prokaryotic 2-Component Systems) database (last accessed 14 June 2013) identifies 126 012 TCS proteins including 54 188 histidine kinases and 62 731 response regulators (Barakat et al., 2011). Bacteria that live primarily in steady environments typically harbor relatively few TCS genes, while bacteria that inhabit rapidly changing or diverse environments typically harbor large numbers of TCS genes. Thus, the number of TCS genes appears to correlate strongly with environmental complexity and ecological niche diversity (Capra and Laub, 2012). Genome analyses have shown that a bacterium usually has an average of > 50 TCS (Krell et al., 2010), and a single bacterial cell may contain up to hundreds of TCS that operate in parallel for adaptive responses to changing environmental and nutritional conditions, such as those caused by the alterations of abundance and composition of inorganic nutrients and organic substrates (Laub and Goulian, 2007).

The PhoR/PhoB involved in response to phosphate starvation, NarX/NarL involved in nitrate assimilation and FixL/FixJ involved in O_2 adaptation and nitrogen fixation are among the most common TCS in bacteria (Gilles-Gonzalez, 2001; Galperin, 2010; Hsieh and Wanner, 2010). Some other identified TCS function as microbial sensing and response systems to environmental simple organic compounds such as sugars and organic acids, triggering the activation of specific membrane transporter systems for uptake (Galperin, 2010). These TCS may participate directly in MCP for environmental LDOC uptake, utilization, transformation or modification. With the aids of these sensing, signaling and response systems for the changing environment and nutritional condition,

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the function and efficiency of MCP for RDOC production and storage may be enhanced in the ocean, as the rate of RDOC formation may be dependent on the rate of microbial activity (Ogawa et al., 2001).

Some TCS, such as WalK/WalR, are essential to peptidoglycan metabolism, such as cell wall biosynthesis and turnover, in some bacteria (Dubrac and Msadek, 2008). Cell wall remodeling may release D-amino acids into the environment (Lam et al., 2009a; Cava et al., 2011a). Diverse bacteria synthesize and release D-amino acids, which regulate cell wall remodeling in stationary phase and cause biofilm dispersal in aging bacterial communities (Cava et al., 2011b). D-amino acids may be accumulated in the ocean in several ways, including active release of D-amino acids by bacterial metabolic activities, passive release of D-amino acids by viral lysis and protozoan grazing of bacterial cells and by extracellular enzymatic degradation of bacterial cell wall fragments (Kawasaki and Benner, 2006; Azúa et al., 2013). As D-amino acids are regarded as important RDOC components in the ocean (Benner and Herndl, 2011; Jiao et al., 2013, 2014), the biological and environmental factors influencing their production, release and accumulation in the ocean are worth further investigation.

2.1.2 Chemotaxis

The chemotaxis systems, which coordinate the sensing, signaling and responsive motility of a bacterium or archaeon in response to chemical attractants or repellents in environment (Szurmant and Ordal, 2004), are among the first and most thoroughly studied TCS having been identified (Nixon et al., 1986). The MiST2.1 Microbial Signal Transduction Database (last accessed 14 June 2013) currently identifies 38 772 chemotaxis proteins from a total of 3075 bacterial and archaeal genomes (Ulrich and Zhulin, 2010). Microbial chemotaxis systems are highly sensitive and efficient processes. These processes, however, result in the expenditure of a relatively high amount of cellular energy in the form of ATP, *pmf* or sodium-motive force, especially for the synthesis and operation of the flagellum, one of the most complex organelles of a bacterium or archaeon (Berg, 2000; Ghosh and Albers, 2011; Stocker and Seymour, 2012).

In natural aquatic environments, many physicochemical conditions and nutritional statuses exhibit highly dynamic small-scale and micro-scale gradients. Microbes with chemotactic capability may exploit this environmental heterogeneity much more readily than those without chemotactic capability (Blackburn et al., 1998; Stocker, 2012).

5 The large energy cost of chemotaxis is ultimately compensated for with maximum resource accession, utilization and optimal metabolic conditions (Taylor and Stocker, 2012). Chemotaxis not only provides chemotactic bacteria competitive advantages associated with higher uptake of nutrients and metabolic substrates, but also may have substantial influences on the ecological processes and biogeochemical consequences

10 in the ocean (Stocker and Seymour, 2012). Due to rapid response to and exploitation of changes in environmental inorganic nutrients, DOC, dissolved organic nitrogen (DON) and organic sulfur compounds, such as ammonium, nitrite, nitrate, urea, phosphate, sulfate, thiosulfate, simple sugars, amino acids, peptides, carboxylic acids, dimethylsulfoniopropionate, hydrocarbons, simple aromatic compounds, extracellular products and

15 exudates from phytoplankton, chitin monosaccharide N-acetylglucosamine and chitin oligosaccharides from zooplankton, chemotactic microorganisms may play a potentially pivotal role in the marine C, N, P and S cycling (Stocker, 2012; Stocker and Seymour, 2012). Chemotaxis may not only facilitate the microbial loop that channels more carbon into particulate phase (Azam et al., 1983), but also enhance the MCP functioning and

20 efficiency for RDOC production and storage in the ocean, as this sensing, response and exploitation-enhancing mechanism for nutrients and metabolic substrates may improve the fueling of the MCP process (Ogawa et al., 2001).

Contrary to the stimulating effect of chemotactic attractants, repellent chemicals drive chemotactic microorganisms away from their source environment. Thus, repel-

25 lent chemicals may have reduced potential to be accessed, degraded, and utilized by most environmental microbes. Organic chemotactic repellents may constitute an important source of RDOC or at least situation-specific RDOC (RDOC$_{specific}$) (Jiao et al., 2013, 2014), contributing to the accumulation and sequestration of organic carbon in marine waters and sediments.

2.1.3 Quorum sensing

Microbes utilize quorum sensing (QS) as a specialized cell-to-cell communication mechanism for population density-dependent sensing, signaling and response, to achieve coordinated gene expression and behavior, such as synchronized production and secretion of toxins (e.g. virulence factors and antimicrobials), extracellular polysaccharides (EPS), pigments, siderophores, biosurfactants and exoenzymes, biofilm formation, bioluminescence, competence, conjugation, nodulation, symbiosis, sporulation, antibiotic resistance, programmed cell death, and changes in motility (Redfield, 2002; Erental et al., 2012; West et al., 2012), of which many processes may contribute to the production and accumulation of RDOC or RDOC$_{specific}$ in the ocean (Jiao et al., 2013, 2014). A typical QS process is characterized by the secretion and detection of small signal molecules collectively called autoinducers within a bacterial population, resulting in the establishment of coordinated behaviors once a sufficient quorum size is reached. The QS process is usually fueled by ATP. For example, it is estimated that the production of a QS signal peptide in *Staphylococcus aureus* requires 184 ATP molecules (Keller and Surette, 2006). Via QS, bacteria are able to determine their population densities and react appropriately by switching on or off specific population physiology and behavior, usually via activation or deactivation of specific gene expression (Miller and Bassler, 2001). Autoinducers and QS systems have also been reported, though only occasionally, in archaeal species (Paggi et al., 2003; Tommonaro et al., 2012; Zhang et al., 2012), indicating QS as a universal strategy to achieve group benefit and social behavior in the prokaryotic world (Schuster et al., 2013).

In marine environments, high microbial population density is usually achieved via the formation of spatially structured multi-species communities, such as biofilms on submerged surfaces, suspended particles, detritus, aggregates, and marine snows (Azam and Long, 2001; Simon et al., 2002). In addition to the fact that bacteria on particles are usually enriched as compared to the abundance of free-living bacteria in surrounding water, particle-associated bacteria are usually volumetrically larger than their free-

living counterparts, presumably due to the more favorable nutritive conditions of particles than those in the surrounding water (Simon et al., 2002). It was hypothesized that the majority of aquatic microbes lead a particle-associated lifestyle (Grossart, 2010). Particle-associated microbes play important roles in the biogeochemical cycling of C, N, and S, particularly in estuarine and coastal areas where the abundance of organic or organically enriched particles is relatively high (Dang and Lovell, 2002; Smith et al., 2013). Particle-associated microbes also dominate the deep-sea overall metabolism (Arístegui et al., 2002; Bochdansky et al., 2010; Eloe et al., 2011). They contribute much to the degradation of particulate organic matter (POM) and may account for as much as 90 % of water column heterotrophic bacterial activity (Crump et al., 1999; Turley and Stutt, 2000; Simon et al., 2002), though sometimes they may constitute < 5 % of total bacterial biomass (Cho and Azam, 1988). Particle-associated microbes provide LDOC substrates, by organic polymer enzymatic decomposition, to not only the attached microbial community but also the free-living community of the surrounding water column (Cho and Azam, 1988), to fuel the MCP (Jiao et al., 2013, 2014). Microbes act on seawater particles to cause quantitatively major POM to dissolved organic matter (DOM) flux, some of which may become RDOC (Jiao and Azam, 2011). For example, partial hydrolysis of complex biopolymers such as polysaccharides and bacterial cell wall peptidoglycans by microbial degradation may produce slow-to-degrade DOM, resulting in carbon storage as RDOC or semi-RDOC in the ocean (Azam, 1998; Jiao et al., 2013, 2014). Interestingly, high bacterial activity could actually produce more RDOC or semi-RDOC in the form of slow-to-degrade DOM (Azam, 1998). Thus, particle-associated bacteria may have significant impacts on microbial productivity, nutrient regeneration and carbon sequestration in the ocean (Paerl and Pinckney, 1996).

Many marine Gram-negative bacteria and certain Gram-positive bacteria produce acylated homoserine lactones (AHLs), the major type of QS autoinducers (Gram et al., 2002; Wagner-Dobler et al., 2005; Martens et al., 2007; Golberg et al., 2011; Zan et al., 2011; Biswa and Doble, 2013). AHLs have also been identified in marine surface-associated microbial communities (Decho et al., 2009; Huang et al., 2009). It was

recently found that QS controls phosphorus acquisition in *Trichodesmium* consortia by regulating the activity of alkaline phosphatases for dissolved organic phosphorus degradation (Van Mooy et al., 2012). Bacterium *Kordia algicida* relies on a QS-dependent excretion mechanism of an algicidal protein to achieve the algicidal activity towards marine diatoms such as *Skeletonema costatum*, *Thalassiosira weissflogii* and *Phaeodactylum tricornutum* (Paul and Pohnert, 2011). Algicidal bacteria may contribute not only to the termination of algal blooms, but also to the release of algal DOC, thus directly influencing the MCP process. The QS mechanism may contribute vastly to marine carbon cycling as a recent study provides evidence that QS may influence the activity of extracellular hydrolytic enzymes on sinking particles (Hmelo et al., 2011). Extracellular enzymatic hydrolysis is often referred to as the rate-limiting step in organic matter (OM) utilization or remineralization, and thus extracellular enzymes play a central role in marine heterotrophic microbial cycling of carbon (Arnosti, 2011). These enzymes catalyze the initial step in conversion of high-molecular-weight (HMW) OM to small substrates to be transported further into a microbial cell for incorporation into biomass, respiration to CO_2, or transformation and excretion into the environmental RDOC pool (Arnosti, 2011). By participating in the regulation of sinking POC degradation, microbial QS may impact the marine biological pump (BP) (Hmelo et al., 2011) and MCP via the release of DOC that may have varying degree of resistance to further degradation (Jiao et al., 2013, 2014).

2.1.4 Interwoven networks of cellular sensing, signaling and response

Bacteria and archaea employ complicated and interconnected regulatory networks for resource utilization and interspecies competition to achieve optimal survival. A meta-transcriptomic study has found that the addition of HMW DOM to marine microbial communities could significantly stimulate gene expressions of TCS, chemotaxis and motility (McCarren et al., 2010). *Vibrio* utilization of chitin, one of the most abundant biopolymers on earth and possibly the most abundant in aquatic environments, presents an example of a successful bacteria-substrate interaction with multiple hierarchical levels

of regulations in various cell metabolic and physiological responses, such as chemotaxis, type IV pili production (for attachment on chitin surface), biofilm formation, extracellular chitinase secretion, chitoporin expression (for transmembrane uptake of chitin oligosaccharides), nutrient cycling, competence induction, symbiosis, and pathogenicity (Li and Roseman, 2004; Meibom et al., 2004; Pruzzo et al., 2008; Blokesch, 2012; Sun et al., 2013). While chitin is highly insoluble, its degradation products provide an abundant source of carbon, nitrogen and energy for marine microorganisms. Sensing and response to environmental cues and population density that involve the TCS, chemotaxis and QS systems provide vibrios the advantage of optimal substrate utilization and survival. *Vibrio* chitin utilization may also influence the carbon sequestration processes and the relative contributions of the BP and MCP. In general, the cellular sensing and response network of heterotrophic bacteria and archaea, fueled primarily by respiratory energy production, may have profound impacts on the composition and sequestration of organic carbon compounds in the ocean.

2.2 Energy-fueled transmembrane transportation and secretion

Prokaryotes dominate the abundance, diversity and metabolic activity of the ocean (Azam and Malfatti, 2007). Heterotrophic bacteria and archaea are the most important consumers of environmental OM, driving the microbial loop, MCP and certain key biogeochemical pathways in the ocean (Azam et al., 1983; Azam and Malfatti, 2007; Jiao et al., 2010) mainly through the utilization of a variety of metabolic energy-driven transport systems for the uptake of organic substrates from the surrounding environment. Bacteria and archaea also utilize a variety of metabolic energy-driven transport systems for the secretion processes to achieve specific activities.

2.2.1 ATP binding cassette transporters

The ATP binding cassette (ABC) transporters, which cost energy in the form of ATP to translocate substrates across cell membranes, constitute the most common and versa-

tile transport systems in the microbial world (Lee et al., 2007; George and Jones, 2012; Rinta-Kanto et al., 2012). Interestingly, ABC importers have only been found in prokaryotes (Rees et al., 2009). Some ABC transporters may have broader substrate specificity; however, most ABC transporters are highly substrate-specific (Couñago et al.,
5 2012). High-affinity substrate-binding proteins that specifically associate with their ligands, together with their cognate ABC importers, facilitate the unidirectional translocation of specific substrates in prokaryotes (Couñago et al., 2012). This mechanism provides not only the coupling of substrate trafficking with ATP hydrolysis but also the substrate specificity for the prokaryotic uptake of environmental DOC compounds. Due
10 to substrate specificity in ABC importers for OM cross-membrane transport, certain environmental DOC compounds may not be taken up and utilized by the in situ microbial assemblage and thus may accumulate in the environment, contributing to the pool of RDOC and especially $RDOC_{specific}$ (Jiao et al., 2013, 2014).

Enrichment experiments with simple DOC substrates (e.g. amino acids, glucose,
15 acetate, pyruvate and dimethylsulphoniopropionate) in the Mediterranean Sea, Baltic Sea and North Sea have shown that environmental bacteria differ substantially in their abilities to utilize specific DOC compounds, with some bacteria acting as specialists and leaving certain DOC compounds unutilized (Gómez-Consarnau et al., 2012). It has also been found that simple sugar glucose is not utilizable by any oligotrophic oceanic
20 clades of the Sargasso Sea bacterioplankton community (Nelson and Carlson, 2012). The lack of suitable membrane importers for glucose uptake in these bacteria may be the major reason for this observed ecophysiological phenomenon. Similarly, some DOC, such as carbohydrates, carboxylic acids and polyamines, may be taken up only by certain specialist bacteria (Poretsky et al., 2010).

25 Genomic, metagenomic, metatranscriptomic, and metaproteomic analyses provide further insights. The "eutrophic" *Roseobacter* clade, a numerically dominant and functionally important group of marine alphaproteobacterial bacteria, harbors diverse carbohydrate-related ABC importer genes, implying their involvement in the carbohydrate-related DOC utilization or transformation (Poretsky et al., 2010; Jiao and

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Zheng, 2011). On the contrary, the "oligotrophic" SAR11 clade, another important marine alphaproteobacterial group, harbors a great deal more ABC importer genes for the uptake of amino acids and other nitrogenous compounds than for the uptake of carbohydrates (Sowell et al., 2009; Poretsky et al., 2010; Jiao and Zheng, 2011; Sowell et al., 2011; Zeigler Allen et al., 2012; Ottesen et al., 2013). Many common carbohydrate compounds, such as galactose, fucose, rhamnose, arabinose, ribose, mannose, maltose and trehalose, can not be utilized by SAR11 isolates (Schwalbach et al., 2010). These contrasting ABC importer machineries between the *Roseobacter* clade and the SAR11 clade may be closely related to their respective niches and ecophysiological adaptations to distinct living environments. The distinctly different environmental DOC utilization profiles may also exemplify the potential of RDOC$_{specific}$ accumulation in distinct marine environments (Jiao et al., 2013, 2014).

The cellular functions of ABC transporters go far beyond the uptake of nutrients and metabolic substrates. They also play important roles in pathogenicity and in maintenance of cell integrity, responses to environmental stresses, cell-to-cell communication, and cell differentiation (Eitinger et al., 2011). Bacteria and archaea harbor diverse ABC exporters important in secretion of extracellular enzymes, polysaccharides, toxins, antimicrobial agents and other compounds (Binet et al., 1997; Omori and Idei, 2003; Davidson and Chen, 2004; Dawson et al., 2007; Cuthbertson et al., 2009; Lalithambika et al., 2012). The gene association of biopolymer degradation enzymes with ABC exporters, usually within the same operon, facilitates secretion of extracellular enzymes (Omori and Idei, 2003). Thus, ABC exporters participate in POC decomposition and DOC production, contributing to the MCP process and forming a linkage between the POC-based BP and the RDOC-based MCP. ABC transporters are also involved in the secretion of recalcitrant EPS and capsular polysaccharides and the extrusion of various waste products, toxins and antimicrobial compounds, which may persist as RDOC in the environment, as these compounds are toxic or difficult to be utilized by environmental microbes (Martín et al., 2005; Dawson et al., 2007; Cuthbertson et al., 2009; Martinez et al., 2009; Jiao and Zheng, 2011).

Many Gram-negative bacteria use special ABC exporter-based Type I secretion systems (T1SS) for the secretion of various extracellular proteins, including toxins and hydrolases such as proteases, phosphatases, glucanases, nucleases and lipases (Delepelaire, 2004). The ABC transporter component forms a channel through the bacterial inner membrane and energizes the T1SS secretion process, which is likely involved in the regeneration of nutrients and degradation of environmental POC and HMW DOC.

A number of bacteria use the type VI secretion system (T6SS), which may be partially ATP-dependent, to kill other bacteria that co-exist in the same microhabitat to win resource competition (Basler et al., 2013; Casabona et al., 2013). For example, *Pseudomonas aeruginosa* utilizes the T6SS to inject cell wall lytic enzymes into the periplasm of other bacterial cells to hydrolyse peptidoglycans, thus compromising the integrity of cellular function in competing bacteria (Russell et al., 2011). Marine *Vibrio parahaemolyticus* uses QS and surface sensing mechanisms to regulate the activities of its T6SS to enhance its environmental fitness via anti-bacterial activity upregulation when competing for a niche in the presence of other bacterial populations (Salomon et al., 2013). *Vibrio cholerae* can also outcompete other bacteria via the T6SS (MacIntyre et al., 2010; Unterweger et al., 2012), and lipase and muramidase were identified as the relevant effectors delivered by the T6SS (Dong et al., 2013). Recently, diverse novel phospholipases from various bacteria have been identified to be T6SS effectors that specifically target and disrupt recipient bacterial cell membranes (Russell et al., 2013). The T6SS-mediated antibacterial activities undoubtedly cause the release of cellular LDOC and some RDOC (such as certain refractory bacterial cell wall components) into the environment from lysed bacteria, contributing to the functioning of the MCP. More than a quarter of bacteria are found to harbor the T6SS (Bingle et al., 2008), indicating its importance in bacterial survival and competition (Schwarz et al., 2010) and its potential role in mediating carbon cycling in natural environments.

2.2.2 TonB-dependent transporters

TonB-dependent transporters (TBDT), another type of energy-dependent transmembrane transportation mechanism, is powered by *pmf* to coordinate with specific ABC importers or secondary transporters and function in microbial uptake, from environment, of ion complexes (such as Fe, Ni, Co and Cu), vitamin B_{12}, vitamin B_1, heme, carbohydrates, lipids, aromatic hydrocarbons and/or their breakdown products (Schauer et al., 2008; Miller et al., 2010; Noinaj et al., 2010; Dupont et al., 2012). *Bacteroidetes* are particularly rich in carbohydrate-assimilation TBDT (Blanvillain et al., 2007; González et al., 2008; Hehemann et al., 2010; Tang et al., 2012) and biopolymer degradation enzymes. For example, the CAZy database (Cantarel et al., 2009) putatively identifies 269 glycoside hydrolase and 16 polysaccharide lyase genes in the *Bacteroides thetaiotaomicron* VPI-5482 genome (Hehemann et al., 2010), 147 glycoside hydrolase and 10 polysaccharide lyase genes in the *Flavobacterium johnsoniae* UW101 genome (McBride et al., 2009), 137 glycoside hydrolase and 15 polysaccharide lyase genes in the *Zobellia galactanivorans* DsiJT genome (Thomas et al., 2012), 125 glycoside hydrolase genes in the *Zunongwangia profunda* SM-A87 genome (Qin et al., 2010), and 96 glycoside hydrolase and 15 polysaccharide lyase genes in the *Formosa agariphila* KMM 3901^T genome (Mann et al., 2013). Many of the *Bacteroidetes* glycoside hydrolase genes are organized in polysaccharide utilization loci, usually clustered with genes for TonB-dependent receptors, SusD-like proteins, sensors/transcription factors, transporters and frequently with genes for sulfatases (McBride et al., 2009; Hehemann et al., 2010; Qin et al., 2010; Thomas et al., 2012; Mann et al., 2013), indicating coordinated degradation, transportation and utilization of extracellular polysaccharides and their breakdown products. *Bacteroidetes* are frequently found in nutrient-rich (micro)environments and abundant and even dominant in marine algae- and particle-attached microbial communities (Crump et al., 1999; Riemann et al., 2000; Kirchman, 2002; Grossart et al., 2005; Bauer et al., 2006; Woebken et al., 2007; Dang et al., 2008, 2011; Pedrotti et al., 2009; Gómez-Pereira et al., 2012). Some genes that

encode HMW biopolymer degradation enzymes are located in close association with the TBDT genes in *Bacteroidetes* genomes, suggesting an integrated regulation of surface colonization and extracellular degradation of biopolymers (Fernández-Gómez et al., 2013). In line with this, the abundance of marine *Flavobacteria*, a major bacterial subgroup of *Bacteroidetes*, was found to be significantly correlated with in situ chlorophyll *a* in seawater dilution cultures (Alonso-Sáez et al., 2010). In another study during a phytoplankton bloom, the most abundant and diverse carbohydrate-active enzymes (Cantarel et al., 2009) were found to be associated with marine *Flavobacteria*, and the genes that encode sulfatases, necessary for the degradation of recalcitrant sulfated algal polysaccharides such as carragenans, agarans, ulvans, fucans and other sulfate-modified algal cell wall polymer components (Gómez-Pereira et al., 2012), were also found to be dominated by marine *Flavobacteria* (Teeling et al., 2012). Furthermore, *Flavobacteria* TBDT dominated the expressed transport proteins during the studied algal bloom (Teeling et al., 2012). Environmental sequences of *Bacteroidetes* TBDT-related proteins, genes and their transcripts have been frequently found in abundance in metaproteomic, metagenomic and metatranscriptomic sequences from the world oceans, especially in coastal waters (Morris et al., 2010; Ottesen et al., 2011; Tang et al., 2012). *Bacteroidetes* also harbor diverse genes for the degradation of proteins, chitin, and bacterial cell wall peptidoglycans (Cottrell and Kirchman, 2000; McBride et al., 2009; Qin et al., 2010; Gómez-Pereira et al., 2012; Mann et al., 2013). Thus, *Bacteroidetes* have been regarded as specialists for degradation of HMW biomacro-molecules in both the particulate and dissolved fraction of the marine OM pool (Bauer et al., 2006), contributing to the transformation of POC to DOC, HMW DOC to low-molecular-weight (LMW) DOC, and the accumulation of certain RDOC (such as D-amino acids) in the ocean.

Certain *Proteobacteria* subgroups are also rich in TBDT (Blanvillain et al., 2007; Tang et al., 2012). Genomic and metagenomic studies have identified bacteria in *Gammaproteobacteria*, particularly in the *Alteromonadales* order, harboring diverse TBDT (Tang et al., 2012). The addition of HMW DOM to marine microbial communi-

ties could significantly stimulate the expression of TBDT-related genes in *Alteromonas* and *Idiomarina* (McCarren et al., 2010), suggesting a role of TBDT in environmental DOM uptake and assimilation in marine *Alteromonadales* (Tang et al., 2012). A study showed that DOM released from mimicked jellyfish blooms of *Mnemiopsis leidyi* and *Chrysaora quinquecirrha* tremendously increased the growth of *Gammaproteobacteria* (Condon et al., 2011). Another study showed that mimicked jellyfish blooms caused by *Pelagia noctiluca* and *Rhizostoma pulmo* stimulated rapid response and growth of marine *Pseudoalteromonadaceae* (Tinta et al., 2012). Most *Alteromonadales* bacteria are copiotrophic and ubiquitous in the temperate and tropical oceans and abundant or even dominant in nutrient-rich (micro)environments (García-Martínez et al., 2002; Tada et al., 2011; Smedile et al., 2013). Even in relatively oligotrophic open ocean surface waters, *Alteromonas* was found to possess high specific activities, possibly due to its mutualistic relationship with *Prochlorococcus,* likely the key biogeochemical driver in the open ocean (Morris et al., 2011; Hunt et al., 2013). *Alteromonadales* bacteria harbor diverse extracellular hydrolytic enzymes and prefer living in a marine particle-associated lifestyle (Ivars-Martinez et al., 2008; Thomas et al., 2008; Oh et al., 2011), thus contributing to POC degradation and fueling of the marine microbial loop and MCP (Azam and Long, 2001; Jiao et al., 2010).

SAR86, another major marine *Gammaproteobacteria* subgroup, also harbor abundant TBDT, which may be involved in the uptake and metabolism of large polysaccharides and lipids (Dupont et al., 2012; Ottesen et al., 2013). SAR86 may also degrade peptidoglycans with D-amino acids produced as byproducts (Dupont et al., 2012). However, unlike the copiotrophic and usually particle-associated *Bacteroidetes* and *Alteromonadales*, SAR86 bacteria are predominantly free living (planktonic) (Dupont et al., 2012). Niche differentiation between SAR86 and *Alteromonadales* or *Bacteroidetes* facilitates resource partitioning for distinctly different components of the in situ microbial communities, exemplifying the basic principle of resource-driving competition and coexistence in the ocean.

3 Biogeochemical linkage of microbial respiration and MCP in estuaries

Due to severe anthropogenic impacts and intense interactions between the terrestrial and marine compartments of the Earth system, estuaries as land–ocean interface are usually the most complex and dynamic ecosystems on Earth. Rivers discharge huge amount of terrigenous materials, such as nutrients, organic matter, suspended particles, wastes, and pollutants, into estuaries and coastal seas. The flow of material and energy through the estuarine system of the land-ocean continuum strongly impacts the metabolism and functioning of the in situ ecosystem, which, in turn, determines the net autotrophic or heterotrophic status of the coastal system and its role in the global carbon cycle (see Fig. 4. The impact of nutrient supply on carbon sequestration in the ocean in the synthesis paper of 2014, Jiao et al., 2013). In the past, large river estuaries sustained high marine productivity and fisheries; however, in present day, many estuaries and their associated coastal seas have been experiencing frequent and intense environmental and ecological perturbations, including eutrophication, blooms of harmful and nuisance phytoplankton and gelatinous zooplankton, hypoxia, anoxia, and seawater acidification (Anderson et al., 2002, 2012; Xian et al., 2005; Paerl et al., 2006; Breitburg et al., 2009; Rabalais et al., 2009, 2010; Condon et al., 2011; Duarte et al., 2013). Many large river estuaries have become the net heterotrophic hotspots of the ocean and the net source of CO_2 to the atmosphere. Overloaded terrigenous nutrients and OM, mainly from crop fertilizer applications and wastewater discharges, generally constitute the major contributors to the deterioration of the estuarine ecosystems worldwide.

3.1 Aerobic vs. anaerobic respirations and related shift of estuarine functioning

Estuaries are intensified areas of global carbon cycling activity due to anthropogenic eutrophication (Doney, 2010). Excessive riverine supply of nutrients and OM strongly stimulates microbial respiration that may rapidly consume dissolved O_2 in impacted seawater and sediments, producing hypoxic and anoxic zones near estuaries. Estuar-

ine waters are also characterized by high turbidity caused by intense input of riverine suspended particles, creating low-light habitats and suboxic and anoxic microhabitats with varying micro-scale redox and nutrient gradients (Stocker, 2012). O_2-limited or O_2-depleted conditions enhance the metabolic activities of anaerobic bacteria and ar-

5 chaea, which divert the flow of energy away from higher trophic levels into microbial pathways (Diaz and Rosenberg, 2008). Many anaerobic microbes are heterotrophs that utilize simple chemicals other than O_2, such as NO_3^-, NO_2^-, Mn^{4+}, Fe^{3+}, and SO_4^{2-}, as alternative terminal electron acceptors to carry out anaerobic respiration. These inorganic compounds have lower reduction potentials than O_2, thus anaerobic respiration

10 is less efficient and leads to lower cellular energy production than aerobic respiration (Burgin et al., 2011; Wright et al., 2012). Anaerobic microbes may need to consume more organic carbon and produce more CO_2 or HCO_3^- to achieve similar growth rate to that of aerobic microbes. The difference in energetic efficiency of metabolism between anaerobic respiration and aerobic respiration appears consistent with research sug-

15 gesting that hypoxic and anoxic zones are usually the source environment of CO_2 that further exacerbates the problem of ocean acidification (Doney et al., 2009; Cai et al., 2011; Melzner et al., 2013). Thus, eutrophied estuaries are usually net heterotrophic in nature and are acidified systems that constitute a significant source of CO_2 to the atmosphere, although they represent < 1 % of the total marine habitats (Heip et al., 1995;

20 Frankignoulle et al., 1998; Cai, 2011).

Due to the intrinsic connection of respiratory energy production and MCP functioning, anaerobic and aerobic microbes may have distinctly different DOC processing efficiency and thus contribute differently to RDOC production and sequestration in the ocean. In hypoxic and anoxic seawater and sediments, energy flows typically follow

25 a well-defined sequence of redox reactions determined by the amount of free energy extractable from each reaction (Wright et al., 2012). For microbial respiration, free oxygen is the most favorable electron acceptor while sulfate is utilized as an electron acceptor only after nitrate, nitrite, manganese oxides and iron oxides are exhausted. This sequential order not only defines specific metabolic niches and biogeochemical poten-

tials spanning oxic, suboxic and anoxic environmental conditions (Wright et al., 2012), but also determines the in situ microbial community respiratory energetics and thus the microbiota ecofunction. For example, different forms of anaerobic respiration, such as denitrification, manganese oxide reduction, dissimilatory nitrate reduction to ammonium (DNRA), iron oxide reduction and sulfate reduction, have distinctly different and decreasing respiratory energy production efficiency (Burgin et al., 2011; Lam and Kuypers, 2011; Wright et al., 2012), which may have an impact on the MCP's carbon sequestration efficiency in the ocean (Fig. 2). This may seemingly be contradictory to the palaeoceanographical observations that anoxic conditions might be favorable for organic carbon storage in the ocean, especially in the early Earth history (Rothman et al., 2003). However, organic carbon sequestration might be caused mainly by the lack of oxidants in the ancient ocean, which was vastly ferruginous (Shen et al., 2003; Canfield et al., 2008) and thus even favorable for LDOC preservation. However, LDOC is readily remineralized in modern oceans. For marine DOC sequestration, the key is actually to store carbon as RDOC (Jiao et al., 2010). Although estuarine hypoxia and anoxia have already been recognized as a major global environmental problem with significant deleterious effects (Diaz and Rosenberg, 2008), currently no relevant research has been proposed to link in situ microbial community respiration physiology and efficiency with MCP functioning and efficiency in different environmental states of estuarine ecosystems.

It has been suggested that microbial enzymatic activity plays an important role in the formation of small-molecule RDOC (Amon and Benner, 1996; Ogawa et al., 2001). Nonspecific or promiscuous enzymatic activities may produce abnormal organic molecules that may no longer be recognizable as substrates to microbial enzymes and thus no longer utilizable by microbes (O'Brien and Herschlag, 1999; Ogawa et al., 2001). This mechanism could be responsible for much of fixed carbon sequestration in the ocean (Ogawa et al., 2001). Various steep physicochemical gradients and swift fluctuations of environmental condition exist in estuarine systems. Rivers may also transport heavy metals, toxic organic compounds, and other antimicrobial substances to

estuaries. The harmful and varying environmental conditions and the combinations of these factors may present as physiological stressors to estuarine microbes. Under such conditions, microbes may be prone to produce more abnormal compounds caused by suboptimal or even disrupted enzymatic synthesis or transformation of metabolic com-
pounds. Whether this scenario represents a realistic MCP mechanism of enhanced RDOC production in the estuarine microbiota remains unsolved and warrants further investigation.

Although many questions remain concerning the MCP efficiency and capacity for carbon sequestration in estuaries, the multitude of harmful environmental effects caused
by escalated anthropogenic activities and global climate change have been established with high certainty. Estuarine hypoxia and repletion of nutrients such as nitrate originating anthropogenically from soil and river systems may stimulate enhanced anaerobic respiration such as denitrification, which may increase the production and release of N_2O and other greenhouse gases (Naqvi et al., 2000; Wright et al., 2012). Nitrogenous
nutrients, such as nitrate, nitrite, and ammonium, are also consumed to produce N_2 by marine anaerobic ammonium oxidizing bacteria in suboxic and anoxic aquatic and sediment environments, and are likely coupled to respiratory DNRA or denitrification (Jetten et al., 2009; Lam et al., 2009b; Zehr, 2009). In certain coastal oxygen minimum zones (OMZs), there exists a cryptic S cycle, coupled to intensified denitrification and
organic carbon mineralization processes (Thamdrup et al., 2010). Many heterotrophic microbes in general also assimilate nitrate and ammonium for biomass production (Cabello et al., 2004; Luque-Almagro et al., 2011; Zehr and Kudela, 2011). Thus, estuarine nutrients such as nitrate may be consumed, to varying degrees, by heterotrophic microorganisms, especially by those anaerobically respiring members instead of being
utilized principally by phytoplankton for carbon fixation and primary production. In this situation, the ecological function of the estuarine ecosystem is altered and the ecological efficiency is lowered, as less energy and fixed carbon can be produced. This may also negatively influence the ecological efficiency of MCP and BP for carbon sequestration (Fig. 3). In line with this logic, it has been found that short-term nutrient

disturbances such as those caused by wind-driven upwelling, forest fires and desert dust depositions can stimulate coastal microbial respiration significantly and thus shift coastal ecosystems strongly towards net heterotrophy (Bonilla-Findji et al., 2010). On the global scale, it has been found that the ecosystem organic carbon pool exhibits consistent and negative correlations with nitrate accrual along a hydrologic continuum from soils, through freshwater systems and coastal margins, to the open ocean (Taylor and Townsend, 2010). Another study has shown that the increase of nitrogen deposition in soils may negatively influence the terrestrial MCP for RDOC storage (Liang and Balser, 2012). Due to the increased overloading of nitrogenous nutrients from anthropogenic sources, nutrient eutrophication may also negatively influence the efficiency of marine MCP for RDOC production and sequestration in estuarine environments.

3.2 Compounding anthropogenic perturbations with impacts of climate change

The massive consumption of fossil fuels since global industrialization has brought about an enormous increase in the emission of CO_2 into the atmosphere, and it has caused a number of detrimental environmental effects as carbon perturbations. Global warming, ocean acidification, and hypoxia, colloquially referred to as the "deadly trio", are the major consequences of the ongoing anthropogenic carbon perturbation (Bijma et al., 2013). Due to global warming, the surface water of the ocean is becoming more and more stratified, causing ocean deoxygenation and rapid expansion and shoaling of the open ocean OMZs (Doney, 2010; Keeling et al., 2010; Wright et al., 2012). The continually expanding estuarine and coastal hypoxic zones may interact with the expanding open ocean OMZs, potentially giving rise to even more severe environmental and ecological consequences (Gilly et al., 2013). Ocean acidification is another consequence of the anthropogenic carbon perturbation (Doney et al., 2009), causing significant changes to marine biota and their ecofunctions. Ocean acidification has become a major contributing factor to the declines in the oceanic nitrification rate (Huesemann et al., 2002; Beman et al., 2011) and possibly also the rate of autotrophic CO_2 fixation via nitrification on a global scale. Reduced nitrification may also reduce the ocean's

new production (Hutchins et al., 2009). Ocean acidification causes the increase of respiration and thus increased carbon loss in several studied phytoplankton (Wu et al., 2010; Li et al., 2012; Yang and Gao, 2012). pH decrease caused by ocean acidification may make the affected bacterial or archaeal cell difficult to pump the protons out,

5 thus reducing the cellular energy production and the efficiencies of microbial sensing, signaling, chemotaxis, substrate uptake and many other physiological processes and ecological functions (Danovaro et al., 2011). However, limited research data observed no clear trend for ocean acidification effect on bacterial respiration (Teira et al., 2012; Motegi et al., 2013). Thus, how ocean acidification affects the MCP remains unclear.

10 According to Bijma et al. (2013), the current magnitude of carbon perturbation and the concurrent ocean acidification are unprecedented in the Earth's history and are occurring at a much higher rate than at any time in the past 55 million (Kump et al., 2009) or possibly even 300 million yr (Hönisch et al., 2012).

Furthermore, the combination of the "deadly trio" impacts, along with other severe

15 anthropogenic environmental perturbations, including pollution, eutrophication, and overfishing, exerts the strongest influence on the environment and ecosystem of the ocean and Earth (Bijma et al., 2013). How these perturbations and their combinations influence the ecophysiology (such as respiration and carbon heterotrophic assimilation or autotrophic fixation) of the estuarine microbiota and their biogeochemical function-

20 ing (such as nutrient regeneration and MCP) is currently not clearly understood. This lack of information and knowledge adds to the uncertainty in predicting the future carbon cycling of the planet and may cause serious delay in strategy formulation and the taking of appropriate action to prevent or lessen carbon-perturbation-induced catastrophes, which may be much more severe and urgent than what is usually perceived

25 (Bijma et al., 2013).

Global warming, which poses a serious threat to the Earth's environment and ecosystem, is now well accepted within the scientific realm as an undeniable fact. In terrestrial soils and freshwater wetlands, it has been found that the increase of temperature may negatively influence the MCP for RDOC storage (Liang and Balser, 2012;

Wang et al., 2012). This warming effect may have a similar impact on MCP function for organic carbon sequestration in shallow waters of the ocean, especially in estuarine and coastal areas. Elevated temperature and nutrient inputs may accelerate microbial respiration and organic carbon mineralization (Rivkin and Legendre, 2001; Wohlers et al., 2009; Danovaro et al., 2011; Yvon-Durocher et al., 2012), stimulating enhanced biodegradation of semi-recalcitrant DOC (SRDOC) in estuaries. This priming effect may be an important factor in estuarine carbon cycling (Bianchi, 2011), which may not only accelerate microbial decomposition of terrestrial organic carbon but also produce RDOC via MCP for long-term storage as new organic compounds that may be structurally different from their terrigenous source molecules. Although marine mesocosm experiments have shown that warming can shift the partitioning of organic carbon between the particulate and dissolved phase toward an enhanced accumulation of DOC under both current and increased CO_2 conditions (Wohlers et al., 2009; Kim et al., 2011), this hypothesis has not yet been fully investigated.

Global warming has a seemingly negligible direct impact on the MCP and its carbon sequestration capacity in deep oceans and sediments, which constitute the largest ecosystem on earth (Whitman et al., 1998). However, some indirect influences, such as those via the interactions of shallow water with deep water, coastal water with open ocean water, and seawater with sediments, are entirely possible. Global warming may also influence the interactions of the heterotrophic bacteria and archaea with the marine viral community, flora and fauna. The exchange of carbon between POC and DOC throughout the water column of the ocean (Jiao et al., 2013, 2014), presents one of the possibilities that the global warming effect may influence the deep ocean MCP, via its direct influence on the BP and the interaction of BP and MCP.

Most marine waters harbor high abundance of viruses, the majority of which are specific to bacteria, archaea or phytoplankton (Breitbart and Rohwer, 2005; Danovaro et al., 2011). Viral activities have substantial influences on the ecosystem's flow of energy, nutrients, OM, trace elements (such as Fe) and genetic information and viruses are a major force behind marine biogeochemical cycles (Fuhrman, 1999; Suttle, 2007).

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Viral lysis of microbial cells enhances the transfer of microbial biomass into the DOM pool and enhances the bacterial production and respiration (Fuhrman, 1999; Danovaro et al., 2011). A rough estimate indicates that as much as one-quarter of the ocean's primary production flows through the "viral shunt", mostly being ultimately respired to CO$_2$ by heterotrophic microbes (Breitbart and Rohwer, 2005; Suttle, 2007). However, viral lysis may enhance the marine MCP efficiency (Jiao et al., 2010; Jiao and Azam, 2011; Jiao et al., 2013 2014) by increasing RDOC production directly from refractory lysates and from facilitated transformation of viral-lysis-released LDOC to RDOC via the increased supply of LDOC compounds as metabolic substrates for both carbon biochemical transformation processes and respiratory energy production processes.

Estuarine waters usually harbor higher viral, prokaryotic and phytoplankton abundance than open ocean and deep ocean waters (Danovaro et al., 2011, and references therein). Thus, the viral production and viral lysis effect may both be stronger in estuaries, implying higher carbon flux through the viral shunt. It is generally observed that the virus-to-prokaryote ratio (VPR) increases with increasing environmental nutrients (Weinbauer et al., 1993). However, this trend seems not to hold in estuaries (Jiao et al., 2006; He et al., 2009). Estuaries usually harbor mixed viral communities that are composed of autochthonous viruses and allochthonous viruses from both river water and seawater. In addition, because of the shallow water depth at estuaries, enhanced sediment resuspension and viral particle release from sediments may also contribute to the variation of the estuarine VPR. However, how these factors affect the estuarine viral activity and carbon cycling is not yet resolved. Thus, the contribution of viruses to the estuarine MCP ecological efficiency needs to be further investigated, by taking into account the complexity and dynamics of estuarine processes under a variety of natural and anthropogenic influences.

Global warming, along with coastal eutrophication, also stimulates the occurrence of harmful blooms of algae and jellyfish (Heisler et al., 2008; Richardson et al., 2009; Kudela et al., 2010; Paerl and Scott, 2010; Prieto et al., 2010; Anderson et al., 2012; Purcell, 2012). Rapid production and massive biomass of algae and jellyfish enhance

DOM secretion into seawater, stimulating microbial respiration and organic carbon transformation by the MCP. Decayed bloom biomass further channels most of the organic matter and energy into microbial metabolic pathways, likely causing dissolved O_2 exhaustion and the prevalence of anaerobic microbial respirations in the impacted aquatic environment.

Jellyfish blooms have become an increasingly serious marine environmental and ecological problem (Purcell, 2012), exemplifying the influence of changes of marine zooplankton composition and abundance on microbial communities and carbon cycling in the ocean. Jellyfish blooms occur in many estuarine and coastal seas, and their magnitude and harmful effects are increasing worldwide (Condon et al., 2011). Overfishing, eutrophication, climate change, translocations, hypoxia, and habitat modification may all stimulate the outbreak of jellyfish blooms, which may also occur due to a self-enhancing feedback mechanism and a likely natural decadal rise and fall oscillation pattern of the global jellyfish populations (Richardson et al., 2009; Dupont and Aksnes, 2010; Purcell, 2012; Condon et al., 2013).

Jellyfish consume large quantities of phytoplankton-fixed carbon into gelatinous biomass, thus jellyfish blooms may change the marine trophic structure and efficiency as jellyfish are not readily consumed by other predators in the ocean (Condon et al., 2011). Jellyfish also produce and secrete large amounts of colloidal and dissolved organic matter (jelly-DOM), which may further influence the functioning of coastal ecosystems by altering DOM pathways (Condon et al., 2011). Decaying jellyfish biomass and jelly-DOM may stimulate the activity and growth of some bacteria while inhibiting some others, thus changing the composition and structure of in situ marine microbiota (Titelman et al., 2006; Tinta et al., 2010, 2012). Jellyfish blooms were found to specifically stimulate the growth and activity of *Flavobacteria*, *Alteromonadales,* and *Vibrionaceae* (Condon et al., 2011; Dinasquet et al., 2012; Tinta et al., 2012). Jellyfish were also found to release substantial quantities of extremely labile, carbon-rich DOM, quickly and readily metabolized by bacterioplankton at uptake rates two to six times that of the marine bulk DOM pools (Condon et al., 2011). More importantly, the consumed

jelly-DOM is shunted toward bacterial respiration rather than production, significantly reducing bacterial growth efficiencies by 10 % to 15 %, indicating that jellyfish blooms cause a large efflux of carbon toward bacterial CO_2 production and away from higher trophic levels (Condon et al., 2011). However, the contribution of the putative jelly-DOM-enhanced MCP to RDOC production currently remains unknown. Further, more thorough investigation of the intricacies of the MCP as a universal mechanism for DOC transformation and RDOC production is required to gain a better understanding of marine carbon cycling, in both normal and highly perturbed conditions.

4 Conclusions and perspectives

The MCP provides a fundamental schematic for carbon sequestration mechanisms different from that of the BP (Jiao et al., 2010; Jiao et al., 2013, 2014), which is more distinct in estuarine and coastal seas where light availability is limited but nutrients and DOC are replete. However, impacts induced by anthropogenic perturbations and climate change may alter the efficacy of the MCP in the estuarine and coastal environments.

Microbial respiration is a basic cellular physiological process that connects DOC mineralization to metabolic energy production. Respiration-produced CO_2 is an important component in the marine and global carbon cycle, counteracting carbon sequestration in marine and terrestrial environments. Furthermore, the incorporation of respiration within the MCP theoretical framework provides the basis through which marine carbon cycling and sequestration can be understood and evaluated in terms of the association of energy flow and budget. This is important as both MCP and BP are being considered to be eco-engineered to enhance carbon storage in the ocean (Jiao et al., 2013, 2014). However, any potential strategy targeting climate change mitigation must be harmless to the environment and ecosystem (Lawrence, 2002; Glibert et al., 2008; Lampitt et al., 2008; Smetacek and Naqvi, 2008). With the consideration of respiratory CO_2 emission and metabolic energy production, the efficacy of the MCP from different environments

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or ecosystems, such as the estuarine, coastal, continental shelf and open ocean areas, and the distinctly different oxic, suboxic and anoxic water zones, can be compared. For example, the estuarine ecosystems frequently exhibit a high level productivity. However, considering the intense release of CO_2 to the atmosphere and the potentially low metabolic energy production efficiency due to anaerobic respirations, most estuaries in the world are, in fact, sources of atmosphere CO_2 and currently not favorable for natural carbon sequestration by the BP and MCP mechanisms (Fig. 3).

In summation, we hypothesize that reduction of the discharge of excessive terrigenous nutrients and OM into the estuarine and coastal seas may enhance the MCP efficacy (Jiao and Zheng, 2011; Jiao et al., 2013, 2014). Thus, reducing anthropogenic inputs may not only mitigate various environmental and ecological problems but also enhance carbon sequestration in estuaries. The integrated consideration of marine microbial community respiration and MCP functioning may help to develop optimized eco-engineering strategies to enhance carbon sequestration in the ocean and to mitigate anthropogenic impacts in the estuarine and coastal environments.

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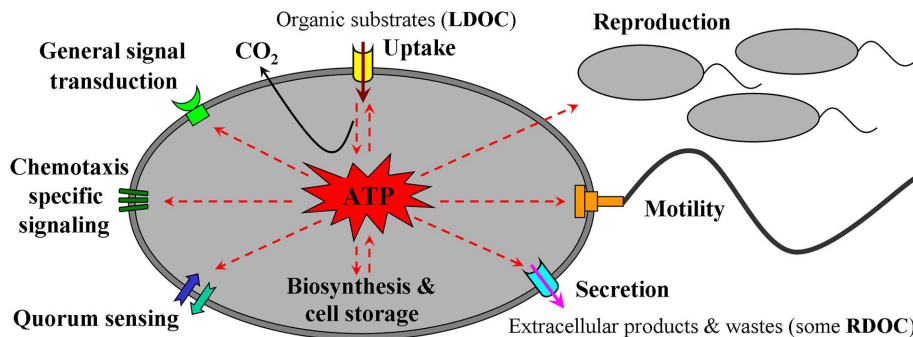
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Interactive Discussion

Zeigler Allen, L., Allen, E. E., Badger, J. H., McCrow, J. P., Paulsen, I. T., Elbourne, L. D., Thiagarajan, M., Rusch, D. B., Nealson, K. H., Williamson, S. J., Venter, J. C., and Allen, A. E.: Influence of nutrients and currents on the genomic composition of microbes across an upwelling mosaic, ISME J., 6, 1403–1414, 2012.

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Interactive Discussion

Fig. 1. Simplified illustration of metabolic energy production by microbial respiration and certain key cellular processes fueled by respiration-generated ATP. The respiratory energy also fuels certain MCP processes, such as the sensing, uptake, transformation and storage of environmental organic substrates and the secretion of extracellular products and waste materials.
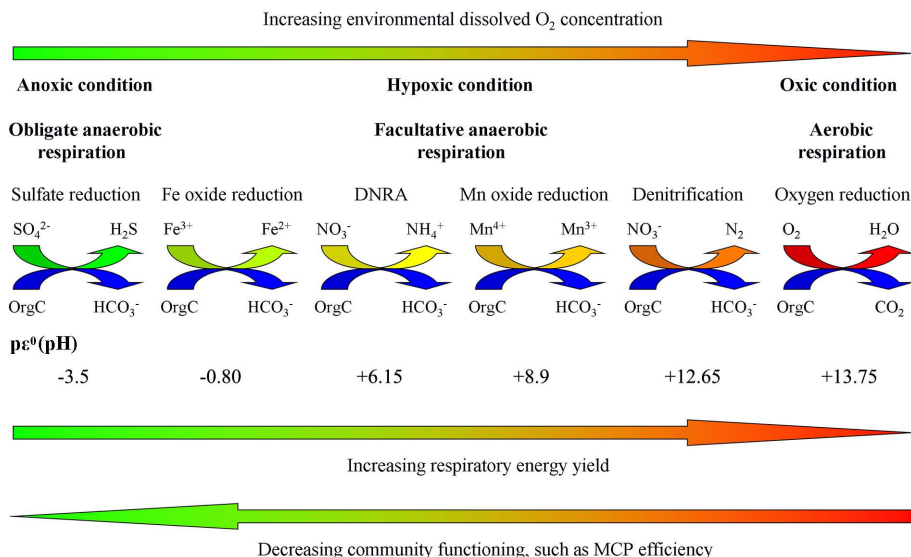
Fig. 2. Simplified illustration of microbial aerobic and anaerobic respiration pathways and their potentially different contribution to cellular metabolic energy production and microbial community functioning efficiencies. $p\varepsilon^0$ (pH) values refer to the electron activity for unit activities of oxidant and reductant at neutral pH (Nealson and Saffarini, 1994).
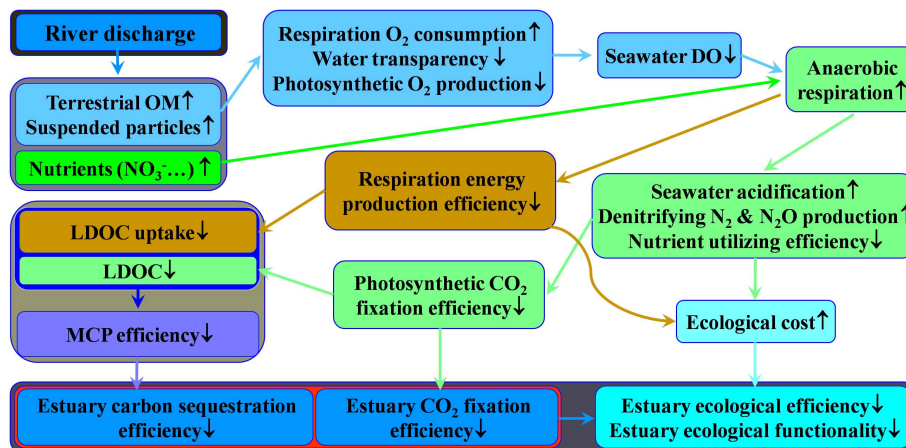
Fig. 3. Simplified schema showing the influence of excessive river discharges of terrestrial materials, such as nutrients, organic matter and suspended particles, on the ecological processes and efficiency of estuarine ecosystems, emphasizing on the incorporation of microbial cellular physiology and metabolic energy production efficiency into the prediction of ecosystem services.