Dear Referee # 2,

Thank you very much for the comments. We have studied the comments and agree that the original manuscript (MS No.: bg-2013-653) lacked focus and was riddled with grammatical errors. We have made significant strides in streamlining the manuscript and have cut our original contribution (51 pages of our submitted file in word format) down to 36 pages. In doing so, we have focused content around a single guiding theme. In addition, we have passed this version of the manuscript along to an expert in English who has provided additional edits to improve its readibility.

While we agree with many of the comments/concerns of the reviewer, we do not agree that the manuscript presents trivial new insight into MCP. It is our feeling that this comment stems from the lack of focus on the guiding theme (i.e., the efficacy of the MCP in the light of ecosystem bioenergetics) and hope that this improves the reviewer's perception of this contribution.

Given our need to focus this contribution, we changed the title to "Perspectives on the Microbial Carbon Pump with Special Reference to Microbial Respiration and Ecosystem Efficiency in Large Estuarine Systems". We removed much of the content in the old version to make the revised manuscript more concise and clear. We deleted the whole section 3.2 "Compounding anthropogenic perturbations with impacts of climate change" in order to focus on our main theme and to remove material that may be too speculative or inconclusive. We also removed Figure 3 of the original manuscript as we found out that there was just too much information presented which may be an additional source of confusion.

In the following, we present our response to the comments item by item:

COMMENT: I have now read the manuscript by Dang and Jiao twice and, unfortunately, I am still not convinced that my time was spent well in doing so. In my humble opinion, a review is ideally concentrating the relevant literature into a coherent piece and detail conclusions from a higher vantage point than would be possible when only focusing on a specific original paper.
RESPONSE: Sorry that our original writing of the manuscript lacked focus and was not quite clear. We covered too many aspects of the MCP and we did not organize the original manuscript very well. We took the comments of this reviewer very seriously and we made substantial modifications to the manuscript. The MCP is a new concept in marine microbiology and carbon biogeochemistry. The microbial physiology of energy metabolism and its influence on the efficiency of MCP have not been studied and reviewed before. However, this aspect is very important for understanding the mechanisms and processes of the MCP for organic carbon transformation and sequestration in the ocean. It is our hope that our revised manuscript represents a better synthesis of these ideas.

COMMENT: Aside from the numerous grammatical errors and awkward formulations, the key words characterizing this review manuscript are: Complete lack

of focus.
RESPONSE: We agree with the reviewer that our previous submission lacked focus. We have taken substantial strides to streamline the text to better convey our message in a more focused manner. In addition, we have had an expert in English grammar read through our current manuscript. In doing these steps, we have reduced our original submission from 51 pages (in word format) to 36 pages.
However, we don't understand the comments on the key words, which were selected from a predefined set of index terms that define the journal subject areas. They were used **for assignment of submitted manuscripts to individual editors**. Please see the following table (copied from the journal's web site) for details.

Journal Subject Areas

The journal subject areas are defined by the following index terms below. These terms represent the keywords to be chosen for assignment of submitted manuscripts to individual editors.

Biodiversity and Ecosystem Function	- Freshwater - Terrestrial - Marine - Palaeo - Microbial Ecology & Geomicrobiology
Biogeochemistry	- Land - Land - Sea Coupling - Air - Sea Exchange - Air - Land Exchange - Greenhouse Gases - Wetlands - Coastal Ocean - Open Ocean - Stable Isotopes & Other Tracers - Organic Biogeochemistry - Limnology - Rivers & Streams - Sediment - Soils - Groundwater - Environmental Microbiology - Biomineralization - Bioremediation - Bio-Optics - Modelling, Aquatic - Modelling, Terrestrial
Paleobiogeoscience	- Marine Record - Terrestrial Record - Proxy use, Development & Validation - Organic Biomarkers - Past Ecosystem Functioning - Climate Connection
Biogeophysics	- Ecohydrology - Biota & Sediment Stability - Turbulence & Biota - Physical - Biological Coupling - Bioturbation - Benthic Boundary Layer Processes - Environmental Optics
Astrobiology and Exobiology	- Extreme Environments, Brines & Hydrothermal - Deep Biosphere - Extraterrestrial Biogeosciences
Earth System Science / Response to Global Change	- Models, Holocene/Anthropocene - Models, Geological History - Climate Change - Evolution of System Earth

COMMENT: I simply fail to see the scientific goal that the authors attempted to address. In other words, what is the message that a potential reader could take away from reading the manuscript?
RESPONSE: The primary goal of this review is to present new ideas to synthesize what is known of the MCP in the light of ecosystem bioenergetics. The microbial physiology of energy metabolism and its influence on the efficiency of MCP are important aspects of the newly proposed MCP concept. In order to avoid any further confusion, we have made substantial modifications in the revised manuscript, including significant streamlining of the content.

COMMENT: The manuscript is incredibly information intense, everything from biochemistry, viruses, to jellyfish is touched at one point or another. But the grand majority of this information is either trivial (in the sense that it is not new), needs to be substantiated with actual data, or is completely pointless in the light of the manuscript's title.
RESPONSE: Following these comments, we have reorganized our writing and focused our review on studies that aim to understand MCP efficacy in consideration of respiratory energy metabolism in estuarine ecosystems. In order to focus better, we also removed the writing that may be too speculative or inconclusive, including the sections about the influence of marine viruses and jellyfish on the MCP carbon sequestration. Hopefully the reviewer can see the merit and importance of our work following this substantial revision.

COMMENT: I am unable to detail every critique I would have as there would simply be too much and instead give some examples: p.5/l18-22: Stating that the concept of the microbial carbon pump has attracted great attention and than citing exclusively papers from the last author is too much for my plate.
RESPONSE: We agree and have deleted a large part of the writing, and leave the judgment on supporting or refuting the validity of this carbon sequestration mechanism in future researches. However, the MCP concept was originally proposed by the last author and the meeting members of SCOR-WG134 in the year 2010 (Jiao et al., 2010).

COMMENT: Chapter 2 and its subchapters deal exclusively with energy-dependent cellular biochemical processes that can be found in any reasonable biochemistry book of today. What's the significance of all of this information here?
RESPONSE: Chapter 2 is important as this section conveys the idea that some key microbial processes contribute to the MCP mechanisms and functioning. We agree that some of the materials are just too basic, which have been removed in the revised manuscript. The key point we want to make in this section is that the MCP has its physiological foundation and microbial respiration is intrinsically linked to the efficiency of the MCP.

COMMENT: Reviews generally do not contain many figures; that means that the

few figures should actually count. The figures in this review are a list of ATP-dependent cellular processes (Fig. 1), the copy of a scheme detailing oxidation-reduction pairs (Fig. 2), and a very confuse scheme supposedly detailing some processes in estuaries with ever mentioning the microbial carbon pump proposal.
RESPONSE: Thanks for the comments. What Figure 1 shows is not only a list of ATP-dependent cellular processes, but also the linkages of most of the cellular processes with the MCP mechanisms and functioning. Figure 2 shows the influence of the various respiration processes on the MCP efficiency. Please see the revised manuscript for the revised figure legends and Figure 2. We removed Figure 3 of the original manuscript as we found out that there was just too much information presented which may be an additional source of confusion.

COMMENT: Unfortunately, I have to conclude that this manuscript is pointless.
RESPONSE: It is clear that the lack of focus in our original submission and the poor grammar have made it difficult for the reviewer to see the merits of this work. We have made substantial improvement in the revised manuscript.

Perspectives on the Microbial Carbon Pump with Special Reference to Microbial Respiration and Ecosystem Efficiency in Large Estuarine Systems

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Abstract

Although respiration-based oxidation of reduced carbon releases CO_2 into the environment, it provides an ecosystem with the metabolic energy for essential biogeochemical processes, including the newly proposed microbial carbon pump (MCP). The efficiency of MCP in heterotrophic microorganisms is related to the mechanisms of energy transduction employed and hence is related to the form of respiration utilized. Anaerobic organisms typically have lower efficiencies of energy transduction and hence lower efficiencies of energy-dependent carbon transformation. This leads to a lower MCP efficiency on a per-cell basis. Substantial input of terrigenous nutrients and organic matter into estuarine ecosystems typically results in elevated heterotrophic respiration that rapidly consumes 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 discharge lead to enhanced anaerobic respiration processes such as denitrification and dissimilatory nitrate reduction to ammonium. Thus, some nutrients may be consumed through anaerobic heterotrophs, instead of being utilized by phytoplankton for autotrophic carbon fixation. In this manner, eutrophied estuarine ecosystems become largely fueled by anaerobic respiratory pathways and their efficiency is less due to lowered ecosystem productivity when compared to healthy and balanced estuarine ecosystems. This situation may have a negative impact on the ecological function and efficiency of the MCP which depends on the supply of both

organic carbon and metabolic energy. This review presents our current understanding of the MCP mechanisms from the view point of ecosystem energy transduction efficiency, which has not been discussed in previous literature.

1 Introduction

The microbial carbon pump (MCP) is a recently proposed biological mechanism for explaining the dynamics of dissolved organic carbon (DOC) transformation and sequestration in the ocean, which involves the production of recalcitrant DOC (RDOC) from labile DOC (LDOC) via microbial processing (Jiao et al., 2010). Millennial mean ages of marine DOC have been observed throughout the water column except in surface water (Loh et al., 2004; Hansell, 2013) and it has been estimated that approximately 155 Pg (10^{15} g) of RDOC are currently sequestered via MCP (Benner and Herndl, 2011). In addition to aquatic ecosystems, soil and sediment microbial communities may play similar roles in RDOC production and sequestration (Benner, 2011; Liang and Balser, 2011). The MCP potential of organic carbon sequestration on a global scale is likely to have profoundly impacted the Earth's carbon cycle and potentially also climate (Wang et al., 2014).

Carbon sequestration by the formation of RDOC is a basic ecosystem property in marine systems in a manner that is similar to what has been described for soil environments (Schmidt et al., 2011). Abiotic and biotic factors that influence the structure, composition, and functions of an ecosystem may also influence the functioning and efficiency of the MCP. Marine microbes differ substantially from one another in their genetic potential, gene expression, and thus their ability to utilize specific DOC compounds, with some microbes being generalists and others being specialists (Gómez-Consarnau et al., 2012). Changes in the abundance or composition of the DOC pool may act as selective pressures that structure the natural microbial communities in these systems (Gómez-Consarnau et al., 2012; Nelson and Carlson, 2012; Nelson et al., 2013). On the other hand, changes in the composition and structure of microbial communities may also impact the abundance and composition of the marine DOC pool, leading to the accumulation of different RDOC compounds with varying ages of persistence in distinct environments.

Heterotrophic bacteria and archaea play a dominant role in the MCP process (Jiao et al., 2010; Benner and Herndl, 2011), which putatively involves three distinct mechanisms including (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 grazing and viral lysis, and (3) the threshold mode pertaining to the retention of environmental DOC at low concentration due to its low metabolic efficiency (Jiao and Azam, 2011; Kattner et al., 2011). The synthesis and secretion of extracellular products including enzymes may consume respiratory metabolic energy in heterotrophic microbes. Grazing and viral lysis release LDOC into the environment, stimulating microbial respiration and thus the active mode of the MCP process. In the threshold mode, a DOC substrate must first be sensed or recognized at or above a threshold concentration before it can be utilized, likely at the expense of additional metabolic energy (the cost of synthesis of additional sensory gene products). Thus, energy metabolism seems to be essentially linked to the MCP processes.

Under natural environmental conditions, most of the environmental LDOC that is taken up by microbes is used for respiration (del Giorgio et al., 1997; Brune et al., 2000; Cotner and Biddanda, 2002; del Giorgio and Duarte, 2002; Carlson et al., 2007; Karl, 2007; Robinson and Ramaiah, 2011; Ducklow and Doney, 2013), which likely results in the simultaneous production and secretion of by-product and/or waste-product chemical compounds (often in the form of RDOC). The respiration process not only participates in the MCP via direct production of respiratory RDOC products but also provides metabolic energy to fuel the ecosystem for running MCP processes.

Microorganisms utilize a variety of respiration systems, including both aerobic and anaerobic pathways with distinctly different energy transduction efficiencies, for energy conservation (Burgin et al., 2011; Wright et al., 2012). In general, anaerobic respiration generates less metabolic energy than aerobic respiration (Burgin et al., 2011; Wright et al., 2012). Furthermore, some microbes may harbor several different respiration pathways. For example, *Paracoccus denitrificans,* a common environmental bacterium, employs the cytochrome aa_3 oxidase as the terminal enzyme in its respiratory chain in the presence of high oxygen concentrations to operate an energetically efficient electron-transfer pathway. However, in the presence of low oxygen concentrations, this bacterium mainly employs the high-affinity cytochrome cbb_3 oxidase (Richardson, 2000). Further, under anoxic conditions, *Paracoccus denitrificans* switches to an anaerobic respiration pathway that employs respiratory enzymes capable of reducing nitrate, nitrite, nitric oxide and nitrous oxide (Richardson, 2000). Thus, even for the same bacterium, different energy transduction efficiencies may pervade under distinct redox conditions. Given that the MCP is mainly fueled by respiratory metabolic energy, the efficiency of the MCP for DOC transformation and sequestration may be better understood by considering contrasting environments such as oxic, suboxic/hypoxic, and anoxic marine waters and sediments that harbor different microbial communities with distinctly different energy conservation efficiencies.

2 Linkages of cellular respiration to MCP

All microorganisms carry out respiration to generate adenosine-5'-triphosphate (ATP) and reducing equivalents, except for obligate fermenters which rely on substrate level phosphorylation (Carlson et al., 2007). ATP molecules produced by energy transduction processes such as respiration play critical roles in cellular carbon metabolism. ATP, along with proton-motive force (*pmf*) or sodium-motive force (*smf*) in certain microbes (Mulkidjanian et al., 2008), provides the metabolic energy for various essential cellular processes. These include (1) motility and chemotaxis in sensing, signaling and response to environmental cues such as utilizable LDOC substrates; (2) uptake, utilization and transformation of metabolic substrates such as LDOC; (3) biosynthesis and storage of cellular products, some of which may be converted into RDOC once released into environment; (4) DNA replication and cell reproduction; (5) secretion of extracellular compounds such as toxins, metabolic products, by-products and waste products, some of which may be RDOC; and (6) biosynthesis, modification and activity regulation of enzymes (including extracellular enzymes) and other proteins for carrying out the above mentioned processes (Fig. 1). Thus, the MCP-related microbial processes may be fueled in several ways by respiration-generated metabolic energy (in the form of ATP, *pmf* or *smf*).

2.1 Environmental DOC substrate sensing － A critical step of the MCP

In nature, microorganisms often encounter frequently changing or dynamic physicochemical conditions (e.g., temperature, pH, oxygen tension, redox, salinity, osmolarity, light, quorum sensing chemical signals, heavy metals, and other contaminants and biocides) and nutritional conditions (e.g., inorganic and organic substrates, N and P nutrients, oxidants (as electron acceptors), reductants (as electron donors), and trace element availabilities). The dynamics of these environmental parameters can occur at submillimetre spatial scales, and microorganisms have evolved the mechanisms and machinery to sense and adapt to the changing extracellular physicochemical and nutritional conditions (Stocker, 2012). For an environmental LDOC substrate to be taken up and utilized, it needs to first be sensed and recognized by a microbe resulting in the expression of cross-membrane transporters. Sensing may be the necessary first step for the MCP, i.e., for microbial uptake and transformation of environmental LDOC.

2.1.1 Two-component signal transduction

The two-component signal transduction systems (TCS) are elegant and predominant mechanisms by which many microorganisms cope with environmental changes and stresses (Capra and Laub, 2012). Upon activation by a stimulus, ATP-dependent autophosphorylation on a specific histidine residue of the TCS sensor histidine kinase and subsequent transfer of the phosphoryl group to an aspartate residue on the TCS cognate response regulator leads to changes in cellular transcriptional, enzymatic or mechanistic properties, thereby altering the physiology and/or behavior of the microorganism in response to environmental change (Gao and Stock, 2009; Capra and Laub, 2012).

TCS are present in greater than 95% and 50% of currently sequenced bacterial and archaeal genomes, respectively (Wuichet et al., 2010). Genomic analyses have shown that bacteria tend to encode for an average of more than 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). For example, the phosphate responsive PhoR/PhoB system, the nitrate responsive NarX/NarL system, and the oxygen responsive FixL/FixJ system are among the most common TCS in bacteria (Gilles-Gonzalez, 2001; Galperin, 2010; Hsieh and Wanner, 2010). Some other identified microbial TCS can sense simple organic compounds such as sugars and organic acids in the environment, triggering the activation of specific transporter systems for uptake (Galperin, 2010). These TCS may participate directly in MCP for environmental LDOC uptake, utilization, and transformation. To the extent that the rate of RDOC formation depends on the ability of microorganisms to sense organic compounds and respond to their presence at a metabolic level (Ogawa et al., 2001), the TCS may enhance the functionality and efficiency of the marine MCP for RDOC production and sequestration.

2.1.2 Chemotaxis

Chemotaxis systems coordinate the sensing, signaling and responsive motility of a bacterium or archaeon in response to chemical attractants or repellents (Szurmant and Ordal, 2004) and are among the most thoroughly studied TCS (Nixon et al., 1986). In natural aquatic environments, many physicochemical and nutrient conditions are highly dynamic at the micro-scale. Microbes with chemotactic capability may exploit this environmental heterogeneity much more readily than those lacking this capability (Blackburn et al., 1998; Stocker, 2012). The large energy cost of chemotaxis (typically in the form of ATP, *pmf* or *smf*) is ultimately compensated for with optimal resource accession and utilization (Stocker and Seymour, 2012; Taylor and Stocker, 2012). Chemotaxis provides chemotactic bacteria with a competitive advantage relative to non-chemotactic populations, enabling the uptake of nutrients and metabolic substrates that would otherwise be unattainable. Thus, chemotaxis may not only facilitate the microbial loop that channels more carbon into the organic particulate phase (Azam et al., 1983), but also enhance the MCP functioning and efficiency for RDOC production and sequestration in the ocean (Ogawa et al., 2001).

In contrast to the stimulating effect of chemotactic attractants on some microbial populations, repellent chemicals can drive chemotactic microorganisms away from a given environment. Thus, repellent chemicals may have reduced potential to be accessed, degraded, and/or utilized by environmental microbes. Organic chemotactic repellents may constitute an important source of RDOC or at least environmental context-specific RDOC ($\mathrm{RDOC}_{\mathrm{context}}$) (Jiao et al., 2014, this issue) and therefore may contribute to the sequestration of organic carbon in the ocean.

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, in order to achieve coordinated gene expression and behavior. These behaviors may include synchronized production and secretion of toxins (e.g. virulence factors and antimicrobials), extracellular polysaccharides (EPS), pigments, siderophores, biosurfactants and exoenzymes (West et al., 2012). The production or secretion of these compounds may contribute to the production and sequestration of RDOC or $\mathrm{RDOC}_{\mathrm{context}}$ in the ocean. The QS process is usually fueled by ATP (Keller and Surette, 2006) and thus has an effect on cellular energy budgets and represents a demand on energy transduction processes.

QS is typically activated when high microbial density is reached. In marine environments, high microbial population densities are often achieved via the formation of spatially structured multi-species biofilm communities which may live on surfaces or on suspended particles, detritus, aggregates and marine snows (Azam and Long, 2001; Simon et al., 2002).

Particle-associated bacteria tend to be larger volumetrically than their free-living counterparts, presumably due to the more favorable nutritive conditions associated with the complex microbial communities and the particles themselves (Simon et al., 2002). The majority of aquatic microbes are hypothesized to live as biofilms in association with particles (Grossart, 2010). Particle-associated microbes play important roles in the biogeochemical cycling of C, N and S, particularly in estuarine and coastal areas where organic or organically enriched particles are abundant (Dang and Lovell, 2002; Smith et al., 2013). Particle-associated microbes also dominate deep-sea microbial communities (Arístegui et al., 2002; Bochdansky et al., 2010; Eloe et al., 2011). Particle-associated communities contribute to the degradation of particulate organic matter (POM) and may account for as much as 90% of the total water column heterotrophic bacterial activity (Crump et al., 1999; Turley and Stutt, 2000; Simon et al., 2002). Particle-associated microbes provide LDOC substrates through the enzymatic decomposition of biopolymers (Cho and Azam, 1988). Biopolymer degradation may also produce RDOC directly (Jiao and Azam, 2011). For example, partial hydrolysis of bacterial cell wall peptidoglycan fragments yields D-amino acids, which constitute an important RDOC component in the ocean (Benner and Herndl, 2011). Higher bacterial activity may produce more RDOC or semi-recalcitrant DOC (semi-RDOC) in the form of slow-to-degrade dissolved organic matter (DOM) (Azam, 1998). Thus, particle-associated bacteria may have significant impacts on carbon sequestration in the ocean (Paerl and Pinckney, 1996).

Particle-associated bacteria have been found to produce acylated homoserine lactones (AHLs), the major type of QS autoinducers (Gram et al., 2002). AHLs have also been identified in marine surface-associated microbial communities (Decho et al., 2009; Huang et al., 2009). The bacterium *Kordia algicida* relies on QS-dependent excretion of an algicidal protein to suppress activity of marine diatoms such as *Skeletonema costatum*, *Thalassiosira weissflogii* and *Phaeodactylum tricornutum* (Paul and Pohnert, 2011). Algicidal bacteria, such as *K. algicida*, may contribute not only to the termination of algal blooms, but also to the release of algal particulate organic carbon (POC) and DOC, thus influencing the MCP process. QS may influence the activity of extracellular hydrolytic enzymes on marine 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 cycling of carbon (Arnosti, 2011). By participating in the regulation of POC degradation and DOC production, microbial QS may impact the marine biological pump (BP) (Hmelo et al., 2011) and the MCP as well.

2.1.4 Interwoven networks of cellular sensing, signaling and response

Bacteria and archaea employ complicated regulatory networks for extracellular resource utilization to achieve optimal growth and maintenance. For example, the utilization of chitin, the most abundant biopolymer in aquatic environments, by vibrio involves multiple levels of gene regulation and regulation of specific physiological responses. These include chemotaxis, type IV pili production (for attachment on chitin surfaces), biofilm formation, extracellular chitinase enzyme secretion and/or chitoporin expression (for transmembrane uptake of chitin oligosaccharides) (Li and Roseman, 2004; Meibom et al., 2004; Pruzzo et al., 2008; Blokesch, 2012). While chitin is highly insoluble, its degradation products represent an abundant source of carbon, nitrogen and metabolic energy for microbial communities. Microbial chitin utilization may also influence the relative contributions of BP and MCP to carbon sequestration in the ocean.

Environmental substrate sensing is not limited to vibrios. It has been found that the addition of high-molecular-weight (HMW) DOM to marine samples significantly stimulates microbial community gene expression of TCS, chemotaxis and motility (McCarren et al., 2010). It has also been found that some simple sugars such as glucose are not utilized by oligotrophic bacteria inhabiting the Sargasso Sea (Nelson and Carlson, 2012). The lack of a suitable glucose-sensing membrane apparatus and thus the incapability to recognize or sense glucose may be the cause of this phenomenon.

The sensing of LDOC represents a little explored area of research that is ripe for study and will enhance our understanding of the MCP. Thus, it is necessary to introduce and define a new concept, the microbial "recognitome" (i.e., the complete suite of sensory apparatus of a microbial assemblage that sense and recognize the whole spectrum of metabolizable extracellular substrates in a given environment), in order to fully understand the mechanism of the MCP. If a LDOC substrate cannot be sensed and recognized by a microbe, it is unlikely to be taken up and utilized. The microbial recognitome may ultimately determine the persistence of DOC in a given environment. Furthermore, if the concentration of a LDOC substrate is lower than a threshold concentration of the microbial recognitome, it may persist as $\mathrm{RDOC}_{\mathrm{context}}$ in the environment. Thus, the microbial sensing and response network, fueled primarily by respiratory processes as described above, may have profound impacts on the sequestration of organic carbon in the ocean.

2.2 Metabolic energy-fueled transmembrane transportation and secretion

Heterotrophic bacteria and archaea are the most important consumers of marine OM, driving the microbial loop and MCP (Azam et al., 1983; Azam and Malfatti, 2007; Jiao et al., 2010), primarily through the utilization of metabolic energy-driven transport systems for the uptake of organic substrates. Bacteria and archaea also utilize energy-driven transport systems for the secretion of extracellular enzymes and compounds (including certain RDOC) to meet their metabolic needs.

2.2.1 ATP binding cassette transporters

The ATP binding cassette (ABC) transporters, which translocate substrates across cell membranes at the expense of ATP consumption, constitute the most common and versatile transport systems in microorganisms (Lee et al., 2007; George and Jones, 2012; Rinta-Kanto et al., 2012). Interestingly, ABC importers have only been found in Bacteria and Archaea but not Eukarya (Rees et al., 2009). Some ABC transporters may have broad substrate specificity, although most ABC transporters exhibit high substrate specificity (Couñago et al., 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 (Couñago et al., 2012). This mechanism couples substrate trafficking with ATP hydrolysis and results in specific substrate uptake of environmental DOC compounds. Due to the specificity of ABC importers, certain DOC compounds may not be taken up and utilized by a microbial assemblage and may result in accumulation of this substrate in the environment.

Enrichment experiments with simple DOC substrates (e.g. amino acids, glucose, acetate, pyruvate and dimethylsulphoniopropionate) have shown that environmental bacteria differ substantially in their ability to utilize specific DOC compounds, with some bacteria acting as specialists (Gómez-Consarnau et al., 2012; Nelson and Carlson, 2012). Some DOC compounds, such as carbohydrates, carboxylic acids and polyamines may be taken up only by certain specialist bacteria (Poretsky et al., 2010).

Various ‘omic’-based approaches have provided further insights into organic carbon cycling in natural systems. The “eutrophic” *Roseobacter* clade, a numerically dominant and functionally important group of marine alphaproteobacteria, harbors diverse carbohydrate-related ABC importer genes, implying their involvement in the carbohydrate-related DOC utilization or transformation (Poretsky et al., 2010; Jiao and Zheng, 2011). On the contrary, the "oligotrophic" SAR11 clade, another important group of marine alphaproteobacteria, 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 cannot be utilized by SAR11 isolates (Schwalbach et al., 2010). The contrasting ABC importer machineries associated with the *Roseobacter* clade and the SAR11 clade may be closely related to their distinct niches and ecophysiological adaptations. Their different environmental DOC utilization profiles may also exemplify the potential for $\mathrm{RDOC}_{\mathrm{context}}$ accumulation in different marine habitats.

The cellular functions of ABC transporters go far beyond the uptake of nutrients and metabolic substrates. Bacteria and Archaea harbor diverse ABC exporters important in the 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 association of genes encoding biopolymer degradation enzymes with ABC exporters, usually within the same operon, facilitates efficient and tightly controlled 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. This is due to the fact that these compounds are toxic and often difficult to metabolize 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 (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* use QS and surface sensing mechanisms to regulate the activities of its T6SS to enhance environmental fitness via anti-bacterial activity when competing for a niche (Salomon et al., 2013). *Vibrio cholerae* can also out-compete other bacteria when using the T6SS (MacIntyre et al., 2010; Unterweger et al., 2012); lipase and muramidase were identified as the relevant effectors delivered by the T6SS (Dong et al., 2013). Recently, diverse novel phospholipases from a number of 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 result in 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 studied have been 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, are powered by *pmf* to coordinate with specific ABC importers or secondary transporters and function in microbial uptake 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 genome of *Bacteroides thetaiotaomicron* VPI-5482 (Hehemann et al., 2010), 147 glycoside hydrolase and 10 polysaccharide lyase genes in the genome of *Flavobacterium johnsoniae* UW101 (McBride et al., 2009), 137 glycoside hydrolase and 15 polysaccharide lyase genes in the genome of *Zobellia galactanivorans* DsiJT (Thomas et al., 2012), 125 glycoside hydrolase genes in the genome of *Zunongwangia profunda* SM-A87 (Qin et al., 2010), and 96 glycoside hydrolase and 15 polysaccharide lyase genes in the genome of *Formosa agariphila* KMM 3901^T (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). This indicates coordinated degradation, transportation and utilization of extracellular polysaccharides and their breakdown products. *Bacteroidetes* are frequently found in nutrient-rich (micro)environments and are 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; Pedrotti et al., 2009; Dang et al., 2011; 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 hypothesis, 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*. Likewise, 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 primarily encoded by marine *Flavobacteria* (Teeling et al., 2012). Furthermore, *Flavobacteria* TBDT dominated the expressed transport proteins during an 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 various ocean habitats, 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 biomacromolecules in both the particulate and dissolved fraction of the marine OM pool

(Bauer et al., 2006). They thus are likely to contribute substantially 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 *Gammaproteobacteria*, particularly in the *Alteromonadales* order, harboring diverse TBDT (Tang et al., 2012). The addition of HMW DOM to marine microbial communities 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 (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 (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 a mutualistic relationship with *Prochlorococcus*, the latter of which is one of the key populations driving biogeochemical cycles in the open ocean (Morris et al., 2011; Hunt et al., 2013). *Alteromonadales* 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 dominant 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, producing D-amino acids as byproducts (Dupont et al., 2012). However, unlike the copiotrophic and particle-associated *Bacteroidetes* and *Alteromonadales*, SAR86 bacteria are predominantly free living (planktonic) (Dupont et al., 2012). Niche differentiation between SAR86 and *Alteromonadales* or *Bacteroidetes* may therefore facilitate resource partitioning, exemplifying the basic principle of resource-driven competition and coexistence in the ocean.

Environmental LDOC substrate uptake constitutes a critical step in the MCP process. Thus, the transportome of a microbial assemblage may define the spectrum of utilizable substrates in a given environment. If an environmental LDOC substrate cannot be taken up by any microbe in an ecosystem, it is likely to persist as RDOC in the environment. The microbial transportome, along with the microbial recognitome, are useful to consider when characterizing the potential recalcitrance of DOC compounds in natural environments.

3 Biogeochemical linkage of microbial respiration and MCP in estuaries — Aerobic vs. anaerobic respirations and related shift of estuarine ecosystem functioning

Due to anthropogenic impacts and intense interactions between the terrestrial and marine compartments of the Earth system, estuaries represent some of the most complex and dynamic ecosystems on Earth. Rivers discharge large 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 in 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. In the past, large river estuaries sustained high marine productivity and fisheries; however, at present, many estuaries and their associated coastal seas have been experiencing frequent and intense environmental and ecological perturbations, including eutrophication, blooms of harmful phytoplankton and gelatinous zooplankton, hypoxia, anoxia, and seawater acidification (Anderson et al., 2002; Xian et al., 2005; Paerl et al., 2006; Breitburg et al., 2009; Rabalais et al., 2009; Rabalais et al., 2010; Condon et al., 2011; Anderson et al., 2012; Duarte et al., 2013). Many large river estuaries have become net heterotrophic hotspots of the ocean and net sources of CO_2 to the atmosphere. Over input of terrigenous nutrients and OM, mainly from crop fertilizer applications and wastewater discharge, generally constitute the major contributors to the deterioration of the estuarine ecosystems worldwide.

Estuaries are intensified areas of the global carbon cycle 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 even anoxic zones near estuaries. Estuarine waters are also characterized by high turbidity caused by 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 archaea, which divert the flow of available energy away from higher trophic levels (Diaz and Rosenberg, 2008). The difference in energetic efficiency of metabolism between anaerobic respiration and aerobic respiration appears to be consistent with research suggesting that hypoxic and anoxic zones are usually a net source of CO_2 (Doney et al., 2009; Cai et al., 2011; Melzner et al., 2013). Thus, eutrophied estuaries are usually net heterotrophic in nature and can become acidified due to production of CO_2 (Frankignoulle et al., 1998; Cai, 2011).

3.1 Varying MCP efficiency in distinct estuarine environments

Due to the intrinsic connection of respiratory energy transduction and MCP functioning, anaerobic and aerobic microbes are likely to have distinctly different DOC processing efficiencies and thus different contributions to RDOC production and sequestration in the ocean. In hypoxic and anoxic seawater and sediments, the flow of energy typically follows 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 potentials spanning oxic, suboxic and anoxic environmental conditions (Wright et al., 2012), but also determines the net energetics of community metabolism. 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 sequentially decreasing respiratory energy transduction efficiencies (Burgin et al., 2011; Lam and Kuypers, 2011; Wright et al., 2012), which may greatly impact MCP carbon sequestration efficiency in the ocean (Fig. 2). Although estuarine hypoxia and anoxia have already been recognized as a major global environmental problem with significant deleterious effects (Diaz and Rosenberg, 2008), the continually expanding estuarine and coastal hypoxic zones may interact with the expanding open ocean oxygen minimum zones (OMZs) which may potentially give rise to even more severe environmental and ecological consequences (Gilly et al., 2013). However, there is currently no research that links in situ microbial community respiration and energy transduction efficiency with the functionality and efficiency of MCP in different environmental statuses of an estuarine ecosystem.

3.2 A putative mechanism of the MCP for RDOC production in estuaries

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 and thus no longer utilizable by microbes (O'Brien and Herschlag, 1999; Ogawa et al., 2001). This mechanism could be responsible for much of the detrital carbon that is sequestered in the ocean (Ogawa et al., 2001). Steep physicochemical gradients and fluctuations of environmental conditions 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 may represent 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 compounds. Whether this scenario represents a realistic MCP mechanism of enhanced RDOC production in the estuarine microbiota remains unsolved and warrants further investigation.

3.3 Negative impacts of eutrophication on the estuarine MCP efficiency

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., 2009; Zehr, 2009). In certain coastal 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 mainly by heterotrophic microorganisms (especially by anaerobes) rather than being utilized 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 metabolic energy and fixed carbon can be produced through anaerobic pathways when compared to aerobic or phototrophic pathways. This may also negatively influence the ecological efficiency of MCP for carbon sequestration. 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 sequestration (Liang and Balser, 2012). Due to the increased overloading of nitrogenous nutrients from anthropogenic sources, nutrient eutrophication may also negatively influence the efficiency of the marine MCP for RDOC production and sequestration in estuarine environments.

4 Conclusions and perspectives

The MCP provides a fundamental framework for designing new studies aimed at improving understanding of carbon sequestration mechanisms different from that of the BP (Jiao et al., 2010), 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.

The incorporation of respiration into the MCP theoretical framework provides the basis through which marine carbon cycling and sequestration can be understood and evaluated in terms of energy flow and budget. This is important as both MCP and BP may have the potential to be engineered to enhance carbon sequestration in the ocean. However, any 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 transduction, the efficiency of the MCP in different environments 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.

It has been hypothesized that reduction of the discharge of excessive terrigenous nutrients and OM into the estuarine and coastal seas may enhance the MCP efficacy (Jiao et al., 2011). 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 engineering strategies to enhance carbon sequestration in the ocean and to mitigate anthropogenic impacts on the estuarine and coastal environments.

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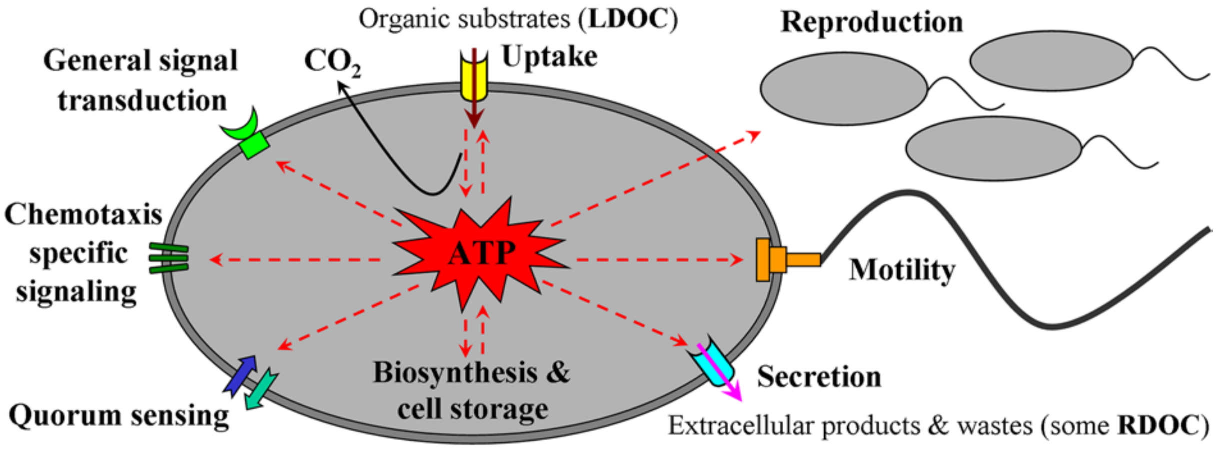

Figure 1. Schematic of metabolic energy transduction by microbial respiration and certain MCP-related cellular processes. These processes are fueled by respiration-generated ATP, which is consumed through the sensing, uptake, transformation and storage of environmental LDOC substrates and the secretion of extracellular products and waste materials that may be related to RDOC production.

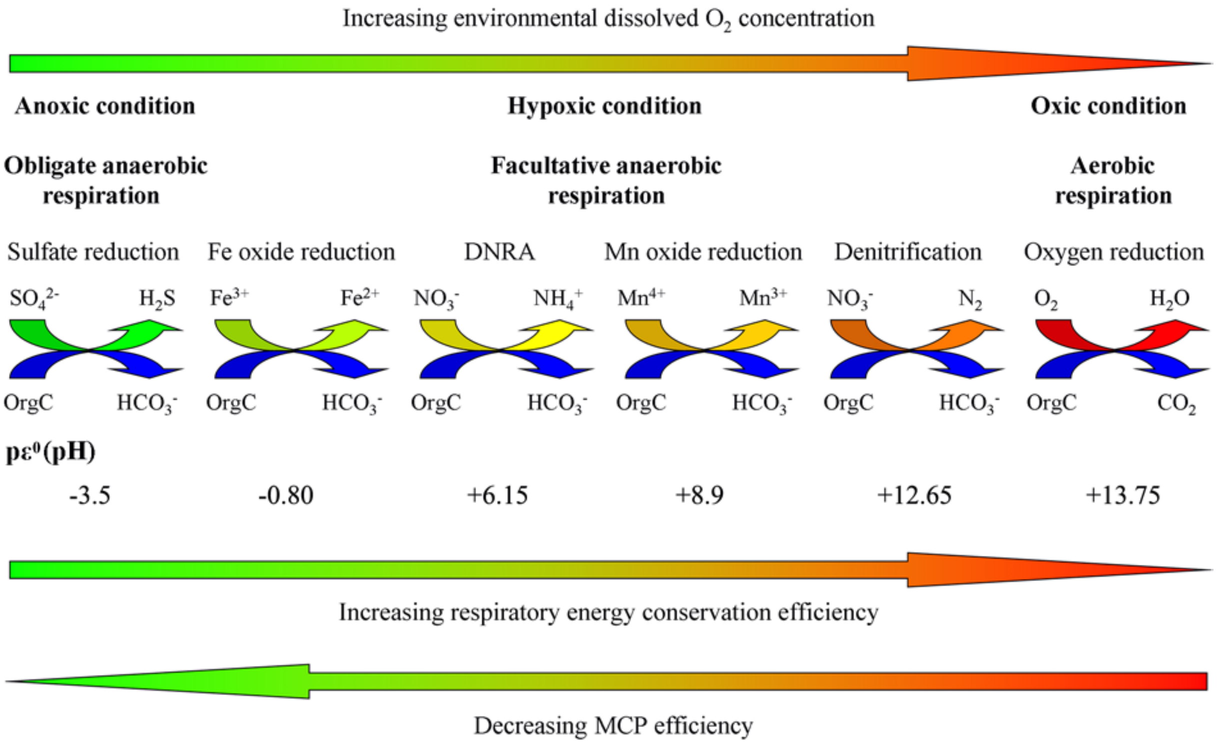

Figure 2. Schematic of microbial aerobic and anaerobic respiration pathways and their potentially different contribution to cellular metabolic energy transduction and MCP efficiencies. $p\varepsilon^0$(pH) values refer to the electron activity for unit activities of oxidants and reductants at neutral pH (Nealson and Saffarini, 1994).

Perspectives on~~of~~ the Microbial Carbon Pump with Special Reference~~s~~ to Microbial Respiration and Ecosystem~~Ecological~~ Efficiency in Large Estuarine Systems

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Abstract

Although respiration-based oxidation of reduced~~-consumes fixed~~ carbon releases~~and produce~~ CO$_2$ into the environment,~~,~~ it provides ~~energy for essential biological processes of~~ an ecosystem with the metabolic energy for essential biogeochemical processes,~~,~~ including the newly proposed 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 MCP in~~a~~ heterotrophic microorganisms is related to the mechanisms of energy transduction employed and hence is ~~thus~~ related to the form of respiration utilized. Anaerobic organisms typically~~its energy production efficiency and hence to its respiration efficiency. Anaerobically respiring microbes usually~~ have lower efficiencies of energy transduction~~production efficiency~~ and hence lower efficiencies of energy-dependent carbon transformation. This leads to a~~-efficiency, and consequently~~ lower MCP efficiency on a per-cell basis. Substantial input of ~~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 into~~,~~ estuarine ecosystems typically results in elevated~~usually experience intense~~ heterotrophic respiration ~~processes~~ that rapidly consumes 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 discharge lead to~~input prompt~~ enhanced anaerobic respiration processes such as denitrification and dissimilatory nitrate reduction to ammonium.~~.~~ Thus, some nutrients may be consumed through anaerobic heterotrophs,~~by anaerobically respiring heterotrophic microorganisms,~~ instead of being utilized by phytoplankton for autotrophic carbon fixation.~~, and primary production.~~ In this manner, eutrophied estuarine ecosystems become largely fueled by anaerobic respiratory pathways and their efficiency is less due to lowered ecosystem productivity when compared to healthy and balanced ~~situation, the ecological functioning of the~~ estuarine ecosystems. This situation may have a negative impact on~~ is altered and~~ the ecological function~~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 the supply of both organic carbon and metabolic energy. This review presents our current understanding of the MCP mechanisms from the view point of ecosystem energy transduction efficiency, which has not been discussed in previous literature.~~energy supply.~~

1 Introduction

The microbial carbon pump (MCP) is a recently proposed biological mechanism for explaining the dynamics of dissolved organic carbon (DOC) transformation and sequestration~~storage~~ in ~~water columns of~~ the ocean,~~global oceans,~~ which involves the production of recalcitrant DOC (RDOC) from labile DOC (LDOC) via microbial processing (Jiao et al., 2010). Millennial~~2010; Jiao et al., 2013, this issue). 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 water~~s~~ (Loh et al., 2004; Hansell, 2013) and it has been estimated that approximately 155 Pg (10^{15} g) of RDOC are currently sequestered via MCP (Benner and Herndl, 2011). In addition to aquatic ecosystems, soil~~. 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 sequestration on a global scale is likely to have profoundly impacted~~has profound impacts on~~ the Earth's carbon cycle and potentially also climate (Wang et al., 2014).~~change.~~

Carbon sequestration by the formation of RDOC ~~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 marine systems in a manner that is similar to what has been described for ~~the~~ soil environments (Schmidt et al., 2011). Abiotic and biotic factors that influence the structure, composition,~~processes~~ and functions of an ecosystem may also influence the functioning and efficiency of the MCP. Marine ~~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; Stoderegger and Herndl, 1999; Ogawa et al., 2001; Gruber et al., 2006; Kawasaki and Benner, 2006). Furthermore, marine~~ microbes differ substantially from one another in their genetic potential, gene expression, and thus their ability~~individual abilities~~ to utilize specific DOC compounds, with some microbes being generalists and others being specialists (Gómez-Consarnau et al., 2012). Changes~~Thus, changes~~ in the abundance or composition of the DOC pool may act as selective pressures that structure ~~forces structuring~~ the natural microbial communities in these systems (Gómez-Consarnau et al., 2012; Nelson and Carlson, 2012; Nelson et al., 2013). On the other hand,~~This also implies that~~ changes in the composition and structure of ~~the~~ microbial communities may also impact~~change~~ the abundance and composition of the marine DOC pool, leading to the ~~production and~~ accumulation of different RDOC compounds~~components~~ with varying ages of persistence in distinct environments.

Heterotrophic bacteria and archaea play a dominant role in the MCP process (Jiao et al., 2010; Benner and Herndl, 2011), which putatively involves three distinct mechanisms including (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 grazing and viral lysis, and (3) the threshold mode pertaining to the retention of environmental DOC at low concentration due to its low metabolic efficiency (Jiao and Azam, 2011; Kattner et al., 2011). The synthesis and secretion of extracellular products including enzymes may consume respiratory metabolic energy in heterotrophic microbes. Grazing and viral lysis release LDOC into the environment, stimulating microbial respiration and thus the active mode of the MCP process. In the threshold mode, a DOC substrate must first be sensed or recognized at or above a threshold concentration before it can be utilized, likely at the expense of additional metabolic energy (the cost of synthesis of additional sensory gene products). Thus, energy metabolism seems to be essentially linked to the MCP processes. ~~environment.~~

Under natural environmental conditions, ~~the consumed LDOC is partly used for microbial cell growth. However,~~ most of the environmental LDOC that is taken up~~used~~ by ~~the~~ microbes is used for respiration (del Giorgio et al., 1997; Brune et al., 2000; 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;~~ Robinson and Ramaiah, 2011; Ducklow and Doney, 2013), which likely results in the simultaneous ~~2011), which consumes organic carbon (usually in various forms of LDOC) for cellular energy production accompanied simultaneously by the~~ production and secretion~~accumulation~~ of by-product and/or waste-product chemical compounds (often~~(maybe~~ in the form~~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 metabolic 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 processes.~~(Robinson and Ramaiah, 2011).~~

Microorganisms utilize a variety of respiration systems, including both aerobic and anaerobic pathways with distinctly different energy transduction efficiencies,~~production efficiency~~ for ~~respiratory~~ energy conservation~~metabolism~~ (Burgin et al., 2011; Wright et al., 2012). In general, anaerobic respiration generates less metabolic energy than aerobic respiration (Burgin et al., 2011; Wright et al., 2012). Furthermore, some~~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 enzyme~~electron acceptor~~ in its respiratory chain in the presence~~conditions~~ of high oxygen concentrations~~tensions~~ to operate an energetically efficient ~~highly coupled~~ electron-transfer pathway. However, in the presence of ~~pathway, while in~~ low oxygen concentrations,~~tension situations,~~ this bacterium mainly employs the high-affinity cytochrome *cbb*$_3$ oxidase (Richardson, 2000). ~~.~~Further, under anoxic conditions, *Paracoccus denitrificans* switches to an anaerobic respiration pathway that employs respiratory enzymes capable of reducing nitrate, nitrite, nitric oxide~~nitrogen oxy-anions~~ and nitrous oxide~~ nitrogen oxides~~ (Richardson, 2000). Thus, even for the same bacterium, different~~In general, anaerobic respiration produces less metabolic~~ energy transduction efficiencies may pervade under distinct redox conditions. Given that~~than aerobic respiration does (Burgin et al., 2011; Wright et al., 2012). As~~ the MCP is mainly fueled by respiratory~~respiration produced~~ metabolic energy, ~~with the integration of microbial respiration into the MCP theoretical framework,~~ the efficiency of the MCP for DOC transformation and sequestration~~storage~~ may be better understood~~, especially~~ by considering~~comparative analyses of the MCP processes and mechanisms in~~ contrasting environments such as oxic, suboxic/hypoxic, and anoxic ~~zones and their interfaces in~~ marine waters and sediments that harbor different microbial communities with distinctly different energy conservation efficiencies.~~.~~

2 Linkages of cellular respiration to MCP

All~~The MCP has been reviewed about its major microbial processes and mechanisms (Jiao and Azam, 2011; Jiao et al., 2013, this issue), 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, this issue). 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 interconnections 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 carry out~~, rely on~~ respiration to generate~~-produced energy, mainly in the form of~~ adenosine-5'-triphosphate (ATP) and reducing equivalents,~~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 which rely on substrate level phosphorylation ~~, all microorganisms carry out respiration~~ (Carlson et al., 2007). ATP molecules produced by energy transduction~~metabolic~~ processes such as respiration play critical roles in cellular carbon metabolism. ATP,

~~ATP is the central molecule in energy metabolism, which~~ along with proton-motive force (*pmf*) or sodium-motive force (*smf*) in certain microbes (Mulkidjanian et al., 2008),~~*pmf*~~ provides the metabolic energy for various essential cellular processes. These include~~processes, such as~~ (1) motility and chemotaxis in sensing, signaling and response to environmental cues such as utilizable LDOC substrates; (2) uptake, utilization and~~,~~ transformation ~~or modification~~ of metabolic substrates such as LDOC; (3) biosynthesis and storage of cellular products, some of which may be converted into RDOC once released into environment;~~products;~~ (4) DNA~~cellular genetic material~~ replication and cell reproduction; (5) secretion of extracellular compounds such as toxins, metabolic products, by-products and waste products, ~~(~~some of which may be RDOC;~~RDOC);~~ and (6) biosynthesis, modification and activity regulation of enzymes (including extracellular 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 processes may be fueled in several ways by respiration-generated metabolic energy (in the form of ATP, *pmf* or *smf*).~~:~~

2.1 Environmental DOC substrate sensing — A critical step of the MCP

~~2.1 Energy-fueled cellular sensing, signaling and response~~

In nature, microorganisms often encounter~~usually live in a world with~~ frequently changing or dynamic physicochemical conditions (e.g.,~~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 (e.g.,~~(such as~~ inorganic and organic substrates, N and P nutrients, oxidants (as electron acceptors), reductants (as electron donors), and trace element availabilities). The dynamics~~change~~ of these environmental parameters can occur~~conditions is most frequent and rigorous~~ at ~~the~~ submillimetre spatial scales,~~scale,~~ and microorganisms have evolved the mechanisms and machinery to sense and adapt to the changing ~~steep gradients of small- and micro-scale~~ extracellular physicochemical and nutritional conditions (Stocker, 2012). For an environmental LDOC substrate~~In order~~ to be taken up and utilized, it needs to first be sensed ~~survive in~~ and recognized by a microbe resulting in the expression of cross-membrane transporters. Sensing may be the necessary first step for~~optimally exploit or escape from the changing environment, prokaryotes (bacteria and archaea) have evolved~~ the MCP, i.e., for microbial uptake and transformation~~capability~~ of ~~sensing and response to various~~ environmental LDOC.~~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 mechanisms~~means~~ by which many microorganisms cope with environmental changes and stresses (Capra and Laub, 2012). Upon activation by ~~way of~~ a stimulus, ATP-dependent autophosphorylation on a specific histidine residue of the TCS sensor histidine kinase and subsequent transfer of the phosphoryl group to an aspartate residue on the TCS cognate response regulator leads to changes in cellular transcriptional, enzymatic or mechanistic properties, thereby altering~~thus alter~~ the physiology and/or behavior of the microorganism in response to environmental change ~~the environment~~ (Gao and Stock, 2009; Capra and Laub, 2012).

TCS are present in greater than 95% and 50% of currently sequenced bacterial and archaeal genomes, respectively (Wuichet et al., 2010). Genomic analyses have shown that bacteria tend to encode for an average of more than~~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 2013.6.14) currently identifies 214,336 TCS proteins from a total of 3,075 bacterial and archaeal genomes (Ulrich and Zhulin, 2010). The P2CS (Prokaryotic 2-Component Systems) database (last accessed 2013.6.14) 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). For example, the

~~The PhoR/PhoB involved in response to~~ phosphate responsive PhoR/PhoB system, the nitrate responsive~~starvation,~~ NarX/NarL system,~~involved in nitrate assimilation~~ and the oxygen responsive FixL/FixJ system~~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 TCS can sense~~sensing and response systems to environmental~~ simple organic compounds such as sugars and organic acids in the environment,~~,~~ triggering the activation of specific~~ membrane~~ transporter systems for uptake (Galperin, 2010). These TCS may participate directly in MCP for environmental LDOC uptake, utilization, and transformation. To~~ or modification. With~~ the extent that the rate of

RDOC formation depends on the ability of microorganisms to sense organic compounds~~aids of these sensing, signaling and response systems for the changing environment~~ and respond to their presence at a metabolic level (Ogawa et al., 2001), the TCS may enhance the functionality~~nutritional condition, the function~~ and efficiency of the marine MCP for RDOC production and sequestration.~~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, this issue), the biological and environmental factors influencing their production, release and accumulation in the ocean are worth further investigation.~~

2.1.2 Chemotaxis

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) and ~~,~~ 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 2013.6.14) currently identifies 38,772 chemotaxis proteins from a total of 3,075 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 and nutrient conditions are~~and nutritional statuses exhibit~~ highly dynamic at the~~small-scale and~~ micro-scale.~~ gradients.~~ Microbes with chemotactic capability may exploit this environmental heterogeneity much more readily than those lacking this ~~without chemotactic ~~capability (Blackburn et al., 1998; Stocker, 2012). The large energy cost of chemotaxis (typically in the form of ATP, *pmf* or *smf*) is ultimately compensated for with optimal ~~maximum ~~resource accession and ~~, ~~utilization (Stocker and Seymour, 2012; ~~and optimal metabolic conditions (~~Taylor and Stocker, 2012). Chemotaxis ~~not only ~~provides chemotactic bacteria with a competitive advantage relative to non-chemotactic populations, enabling the~~s associated with higher~~ uptake of nutrients and metabolic substrates that would otherwise be unattainable. Thus, chemotaxis ~~, but also may have substantial influences on the ecological processes and biogeochemical consequences 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 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 the organic particulate phase (Azam et al., 1983), but also enhance the MCP functioning and efficiency for RDOC production and sequestration in the ocean ~~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).

In contrast~~Contrary~~ to the stimulating effect of chemotactic attractants on some microbial populations,~~,~~ repellent chemicals can drive chemotactic microorganisms away from a given~~their source~~ environment. Thus, repellent chemicals may have reduced potential to be accessed, degraded, and/or utilized by ~~most ~~environmental microbes. Organic chemotactic repellents may constitute an important source of RDOC or at least environmental context-specific~~situation-specific~~ RDOC (RDOC$_{context}$)~~(RDOC$_{specific}$)~~ (Jiao et al., 2014,~~2013,~~ this issue) and therefore may contribute~~, contributing~~ to the ~~accumulation and ~~sequestration of organic carbon in the ocean.~~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, in order to achieve coordinated gene expression and behavior. These behaviors may include~~behavior, such as~~ synchronized production and secretion of toxins (e.g. virulence factors and antimicrobials), extracellular polysaccharides (EPS), pigments, siderophores, biosurfactants and exoenzymes (West et al., 2012). The production or secretion of these compounds may contribute to the production and sequestration of RDOC or RDOC$_{context}$ in the ocean. The QS process is usually fueled by ATP (Keller and Surette, 2006) and thus has an effect on cellular energy budgets and represents a demand on energy transduction processes.~~, 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, this issue). 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).~~

QS is typically activated when high microbial density is reached. In marine environments, high microbial population densities are often~~density is usually~~ achieved via the formation of spatially structured multi-species biofilm communities which may live~~, such as biofilms~~ on ~~submerged~~ surfaces or on~~,~~ suspended particles, detritus, aggregates~~,~~ and marine snows (Azam and Long, 2001; Simon et al., 2002). Particle-associated~~In addition to the fact that~~ bacteria tend to be larger~~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 associated with the complex microbial communities and the~~of~~ particles themselves~~than those in the surrounding water~~ (Simon et al., 2002). The ~~It was hypothesized that the~~ majority of aquatic microbes are hypothesized to live as biofilms in association with particles ~~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 are abundant ~~is relatively high~~ (Dang and Lovell, 2002; Smith et al., 2013). Particle-associated microbes also dominate ~~the~~ deep-sea microbial communities~~overall metabolism~~ (Arístegui et al., 2002; Bochdansky et al., 2010; Eloe et al., 2011). Particle-associated communities ~~They~~ contribute ~~much~~ to the degradation of particulate organic matter (POM) and may account for as much as 90% of the total water column heterotrophic bacterial activity (Crump et al., 1999; Turley and Stutt, 2000; Simon et al., 2002). ~~2002), though sometimes they may constitute < 5% of total bacterial biomass (Cho and Azam, 1988).~~ Particle-associated microbes provide LDOC substrates through the~~, by organic polymer~~ enzymatic decomposition of biopolymers (Cho and Azam, 1988). Biopolymer degradation may ~~, to not only the attached microbial community but~~ also produce RDOC directly~~the free-living community of the surrounding water column (Cho and Azam, 1988), to fuel the MCP~~ (Jiao ~~et al., 2013, this issue). 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 peptidoglycan fragments yields D-amino acids, which constitute an important RDOC component ~~s by microbial degradation may produce slow-to-degrade DOM, resulting in carbon storage as RDOC or semi-RDOC~~ in the ocean (Benner and Herndl, 2011). Higher~~(Azam, 1998; Jiao et al., 2013, this issue). Interestingly, high~~ bacterial activity may~~could actually~~ produce more RDOC or semi-recalcitrant DOC (semi-RDOC) in the form of slow-to-degrade dissolved organic matter (DOM) ~~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).

Particle-associated~~Many marine Gram-negative~~ bacteria have been found to~~and certain Gram-positive bacteria~~ produce acylated homoserine lactones (AHLs), the major type of QS autoinducers (Gram et al., 2002).~~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). The bacterium~~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 suppress~~achieve the algicidal~~ activity of~~towards~~ marine diatoms such as *Skeletonema costatum*, *Thalassiosira weissflogii* and *Phaeodactylum tricornutum* (Paul and Pohnert, 2011). Algicidal bacteria, such as *K. algicida*, may contribute not only to the termination of algal blooms, but also to the release of algal particulate organic carbon (POC) and 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 marine~~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 and DOC production,~~,~~ microbial QS may impact the marine biological pump (BP) (Hmelo et al., 2011) and the MCP as well.~~MCP via the release of DOC that may have varying degree of resistance to further degradation (Jiao et al., 2013, this issue).~~

2.1.4 Interwoven networks of cellular sensing, signaling and response

Bacteria and archaea employ complicated ~~and interconnected~~ regulatory networks for extracellular resource utilization ~~and interspecies competition~~ to achieve optimal growth and maintenance. For example, the~~survival. A metatranscriptomic 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 biopolymer~~s on earth and possibly the most abundant~~ in aquatic environments, by vibrio involves~~presents an example of a successful bacteria-substrate interaction with~~ multiple ~~hierarchical~~ levels of gene regulation and regulation of specific ~~regulations in various cell metabolic and~~ physiological responses. These include ~~responses, such as~~ chemotaxis, type IV pili production (for attachment on chitin surfaces),~~surface),~~ biofilm formation, extracellular chitinase enzyme secretion and/or~~,~~ 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).~~2012; Sun et al., 2013).~~ While chitin is highly insoluble, its degradation products represent~~provide~~ an abundant source of carbon, nitrogen and metabolic energy for microbial communities. Microbial~~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 to carbon sequestration in the ocean.

Environmental substrate sensing is not limited to vibrios. It has been found that the addition of high-molecular-weight (HMW) DOM to marine samples significantly stimulates microbial community gene expression of TCS, chemotaxis and motility (McCarren et al., 2010). It has also been found that some simple sugars such as glucose are not utilized by oligotrophic bacteria inhabiting the Sargasso Sea (Nelson and Carlson, 2012). The lack of a suitable glucose-sensing membrane apparatus and thus the incapability to recognize or sense glucose may be the cause of this phenomenon.

The sensing of LDOC represents a little explored area of research that is ripe for study and will enhance our understanding of the MCP. Thus, it is necessary to introduce and define a new concept, the microbial "recognitome" (i.e., the complete suite of sensory apparatus of a microbial assemblage that sense and recognize the whole spectrum of metabolizable extracellular substrates in a given environment), in order to fully understand the mechanism of the MCP. If a LDOC substrate cannot be sensed and recognized by a microbe, it is unlikely to be taken up and utilized. The microbial recognitome may ultimately determine the persistence of DOC in a given environment. Furthermore, if the concentration of a LDOC substrate is lower than a threshold concentration of the microbial recognitome, it may persist as $\text{RDOC}_{\text{context}}$ in the environment. Thus, the microbial~~. In general, the cellular~~ sensing and response network,~~ of heterotrophic bacteria and archaea,~~ fueled primarily by respiratory processes as described above,~~energy production,~~ may have profound impacts on the ~~composition and~~ sequestration of organic carbon ~~compounds~~ in the ocean.

2.2 Metabolic energy-fueled~~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 marine ~~environmental~~ OM, driving the microbial loop and MCP~~, MCP and certain key biogeochemical pathways in the ocean~~ (Azam et al., 1983; Azam and Malfatti, 2007; Jiao et al., 2010), primarily ~~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 of extracellular enzymes and compounds (including certain RDOC) to meet their metabolic needs.~~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 at the expense of ATP consumption,~~,~~ constitute the most common and versatile transport systems in microorganisms~~the microbial world~~ (Lee et al., 2007; George and Jones, 2012; Rinta-Kanto et al., 2012). Interestingly, ABC importers have only been found in Bacteria and Archaea but not Eukarya~~prokaryotes~~ (Rees et al., 2009). Some ABC transporters may have broad~~er~~ substrate specificity, although~~specificity; however,~~ most ABC transporters exhibit high~~are highly~~ substrate specificity~~-specific~~ (Couñago et al., 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 couples~~provides not only the coupling of~~ substrate trafficking with ATP hydrolysis and results in specific ~~but also the~~ substrate ~~specificity for the prokaryotic~~ uptake of environmental DOC compounds. Due to the~~substrate~~ specificity of ~~in~~ ABC importers~~, for OM cross-membrane transport,~~ certain ~~environmental~~ DOC compounds may not be taken up and utilized by a~~the in situ~~ microbial assemblage and ~~thus~~ may result in accumulation~~accumulate in the environment, contributing to the pool~~ of ~~RDOC and especially RDOC$_{\text{specific}}$ (Jiao et al., 2013,~~ this substrate in the environment.~~issue).~~

Enrichment experiments with simple DOC substrates (e.g. amino acids, glucose, acetate, pyruvate and dimethylsulphoniopropionate) ~~in the Mediterranean Sea, Baltic Sea and North Sea~~ have shown that environmental bacteria differ substantially in their ability~~abilities~~ to utilize specific DOC compounds, with some bacteria acting as specialists ~~and leaving certain DOC compounds unutilized~~ (Gómez-Consarnau et al., 2012; ~~2012). It has also been found that simple sugar glucose is not utilizable by any oligotrophic oceanic clades of the Sargasso Sea bacterioplankton community (~~Nelson and Carlson, 2012). Some DOC compounds,~~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).

Various ‘omic’-based approaches have provided~~Genomic, metagenomic, metatranscriptomic, and metaproteomic analyses provide~~ further insights into organic carbon cycling in natural systems.~~.~~ The “eutrophic” *Roseobacter* clade, a numerically dominant and functionally important group of marine alphaproteo~~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 Zheng, 2011). On the contrary, the “oligotrophic” SAR11 clade, another important group of marine alphaproteobacteria,~~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 can~~, such as galactose, fucose, rhamnose, arabinose, ribose, mannose, maltose and trehalose, can~~ not be utilized by SAR11 isolates (Schwalbach et al., 2010). The~~se~~ contrasting ABC importer machineries associated with~~between~~ the *Roseobacter* clade and the SAR11 clade may be closely related to their distinct ~~respective~~ niches and ecophysiological adaptations. Their~~ to distinct living environments. The distinctly~~ different environmental DOC utilization profiles may also exemplify the potential for RDOC$_{context}$~~of RDOC$_{specific}$~~ accumulation in different~~distinct~~ marine habitats.~~environments (Jiao et al., 2013, this issue).~~

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~~archaea~~ harbor diverse ABC exporters important in the 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 genes encoding biopolymer degradation enzymes with ABC exporters, usually within the same operon, facilitates efficient and tightly controlled 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. This is due to the fact that~~environment, as~~ these compounds are toxic and often~~or~~ difficult to metabolize~~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* use~~s~~ 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 out-compete~~outcompete~~ other bacteria when using~~via~~ the T6SS (MacIntyre et al., 2010; Unterweger et al., 2012);~~2012), and~~ lipase and muramidase were identified as the relevant effectors delivered by the T6SS (Dong et al., 2013). Recently, diverse novel phospholipases from a number of~~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 result in~~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 studied have been~~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, are~~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 genome of *Bacteroides thetaiotaomicron* VPI-5482 ~~genome~~ (Hehemann et al., 2010), 147 glycoside hydrolase and 10 polysaccharide lyase genes in the genome of *Flavobacterium johnsoniae* UW101 ~~genome~~ (McBride et al., 2009), 137 glycoside hydrolase and 15 polysaccharide lyase genes in the genome of *Zobellia galactanivorans* DsiJT ~~genome~~ (Thomas et al., 2012), 125 glycoside hydrolase genes in the genome of *Zunongwangia profunda* SM-A87 ~~genome~~ (Qin et al., 2010), and 96 glycoside hydrolase and 15 polysaccharide lyase genes in the genome of *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). This indicates~~2013), indicating~~ coordinated degradation, transportation and utilization of extracellular polysaccharides and their breakdown products. *Bacteroidetes* are frequently found in nutrient-rich (micro)environments and are 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; Pedrotti et al., 2009; Dang et al., 2011; 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 hypothesis, 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*. Likewise,~~*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 primarily encoded~~dominated~~ by marine *Flavobacteria* (Teeling et al., 2012). Furthermore, *Flavobacteria* TBDT dominated the expressed transport proteins during an~~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 various ocean habitats,~~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 biomacromolecules in both the particulate and dissolved fraction of the marine OM pool (Bauer et al., 2006). They thus are likely to contribute substantially~~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 communities 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 a~~its~~ mutualistic relationship with *Prochlorococcus*, the latter of which is one of~~likely~~ the key populations driving biogeochemical cycles~~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 dominant~~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, producing ~~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* may therefore facilitate~~facilitates~~ resource partitioning, ~~for distinctly different components of the in situ microbial communities,~~ exemplifying the basic principle of resource-driven~~resource-driving~~ competition and coexistence in the ocean.

Environmental LDOC substrate uptake constitutes a critical step in the MCP process. Thus, the transportome of a microbial assemblage may define the spectrum of utilizable substrates in a given environment. If an environmental LDOC substrate cannot be taken up by any microbe in an ecosystem, it is likely to persist as RDOC in the environment. The microbial transportome, along with the microbial recognitome, are useful to consider when characterizing the potential recalcitrance of DOC compounds in natural environments.

3 Biogeochemical linkage of microbial respiration and MCP in estuaries — Aerobic vs. anaerobic respirations and related shift of estuarine ecosystem functioning

Due to~~ severe~~ anthropogenic impacts and intense interactions between the terrestrial and marine compartments of the Earth system, estuaries represent some of~~as land-ocean interface are usually~~ the most complex and dynamic ecosystems on Earth. Rivers discharge large~~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 in~~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 this issue (Jiao et al., 2013)).~~ In the past, large river estuaries sustained high marine productivity and fisheries; however, at~~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; Xian et al., 2005; Paerl et al., 2006; Breitburg et al., 2009; Rabalais et al., 2009; Rabalais et al., 2010; Condon et al., 2011; Anderson et al., 2012; Duarte et al., 2013). Many large river estuaries have become ~~the ~~net heterotrophic hotspots of the ocean and ~~the ~~net sources of CO_2 to the atmosphere. Over input of~~ Overloaded~~ terrigenous nutrients and OM, mainly from crop fertilizer applications and wastewater discharge,~~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 the global carbon cycle~~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 even anoxic zones near estuaries. Estuarine 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 archaea, which divert the flow of available energy away from higher trophic levels (Diaz and Rosenberg, 2008).~~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 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 to be consistent with research suggesting that hypoxic and anoxic zones are usually a net~~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 can become acidified due to production of CO_2 (~~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;~~ Frankignoulle et al., 1998; Cai, 2011).

3.1 Varying MCP efficiency in distinct estuarine environments

Due to the intrinsic connection of respiratory energy transduction~~production~~ and MCP functioning, anaerobic and aerobic microbes are likely to~~may~~ have distinctly different DOC processing efficiencies ~~efficiency~~ and thus different contributions~~contribute differently~~ to RDOC production and sequestration in the ocean. In hypoxic and anoxic seawater and sediments, the flow of energy ~~flows~~ typically follows 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 potentials spanning oxic, suboxic and anoxic environmental conditions (Wright et al., 2012), but also determines the net energetics of community metabolism.~~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 sequentially decreasing respiratory energy transduction efficiencies ~~production efficiency~~ (Burgin et al., 2011; Lam and Kuypers, 2011; Wright et al., 2012), which may greatly~~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), the continually expanding estuarine and coastal hypoxic zones may interact with the expanding open ocean oxygen minimum zones (OMZs) which may potentially give rise to even more severe environmental and ecological consequences (Gilly et al., 2013). However, there is currently no ~~relevant~~ research that links~~has been proposed to link~~ in situ microbial community respiration ~~physiology~~ and energy transduction efficiency with the functionality~~MCP functioning~~ and efficiency of MCP in different environmental statuses~~states~~ of an estuarine ecosystem.~~ecosystems.~~

3.2 A putative mechanism of the MCP for RDOC production in estuaries

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 the detrital~~fixed~~ carbon that is sequestered~~sequestration~~ in the ocean (Ogawa et al., 2001). Steep~~ Various steep~~ physicochemical gradients and ~~swift~~ fluctuations of environmental conditions 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 may represent~~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 compounds. Whether this scenario represents a realistic MCP mechanism of enhanced RDOC production in the estuarine microbiota remains unsolved and warrants further investigation.

3.3 Negative impacts of eutrophication on the estuarine MCP efficiency

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., 2009;~~2009b;~~ Zehr, 2009). In certain coastal OMZs,~~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 mainly~~, to varying degrees,~~ by heterotrophic microorganisms (~~, ~~especially by anaerobes) rather than~~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 metabolic energy and fixed carbon can be produced through anaerobic pathways when compared to aerobic or phototrophic pathways.~~.~~ 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 sequestration~~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 the 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, 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. 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 years (Hönisch et al., 2012).~~

~~Furthermore, the combination of the "deadly trio" impacts, along with other severe 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 functioning (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 (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, this issue), 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). 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 this issue) 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; Tinta et al., 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 framework for designing new studies aimed at improving understanding of~~schematic for~~ carbon sequestration mechanisms different from that of the BP (Jiao et al., 2010),~~2010; Jiao et al., 2013, this issue),~~ 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.

The incorporation of respiration into~~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 may have the potential~~are being considered~~ to be ~~eco-~~engineered to enhance carbon sequestration~~storage~~ in the ocean.~~(Jiao et al., 2013, this issue).~~ 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 transduction,~~production,~~ the efficiency~~efficacy~~ of the MCP in~~from~~ different environments 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).~~

It has been hypothesized~~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., 2011).~~ 2013, this issue).~~ 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 on~~in~~ the estuarine and coastal environments.

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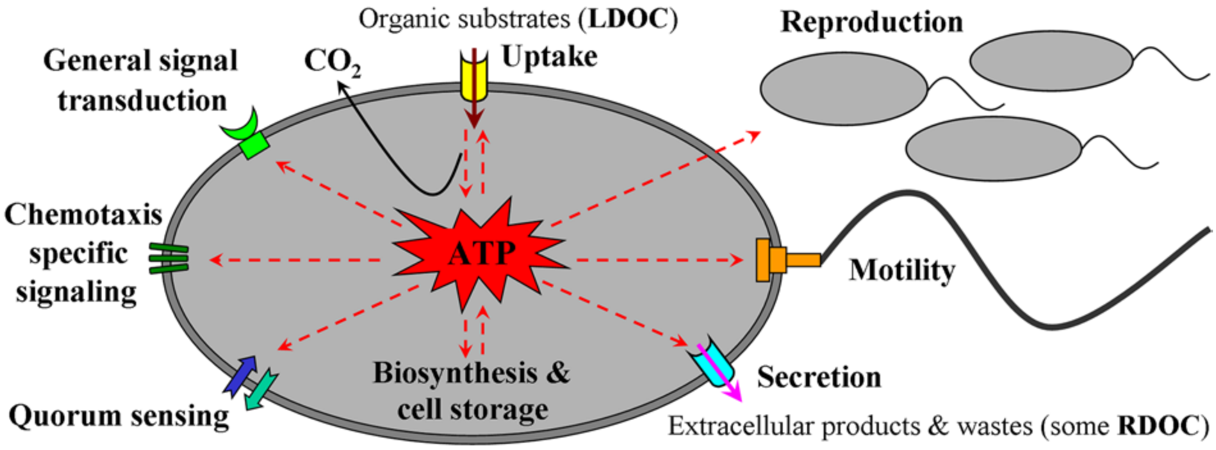
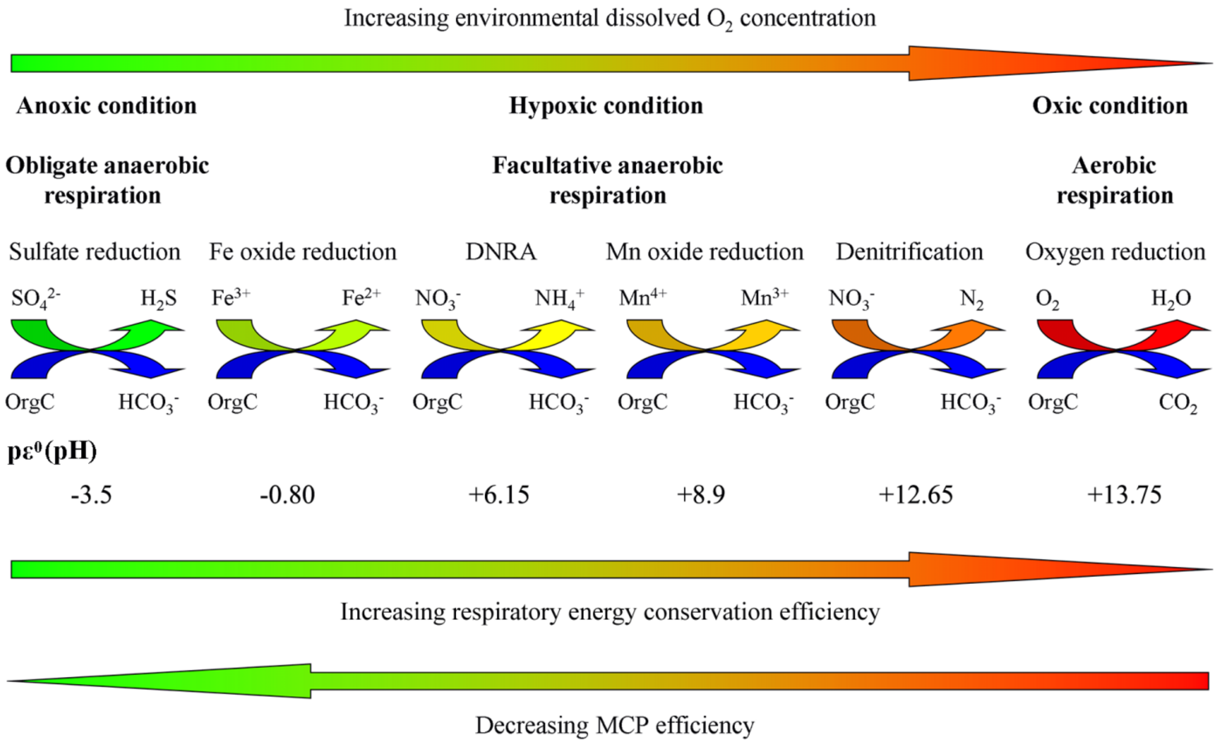


Figure 1. Schematic~~Simplified illustration~~ of metabolic energy transduction~~production~~ by microbial respiration and certain MCP-related~~key~~ cellular processes. These processes are fueled by respiration-generated ATP, which is consumed through~~ATP. The respiratory energy also fuels certain MCP processes, such as~~ the sensing, uptake, transformation and storage of environmental LDOC~~organic~~ substrates and the secretion of extracellular products and waste materials that may be related to RDOC production.~~.~~



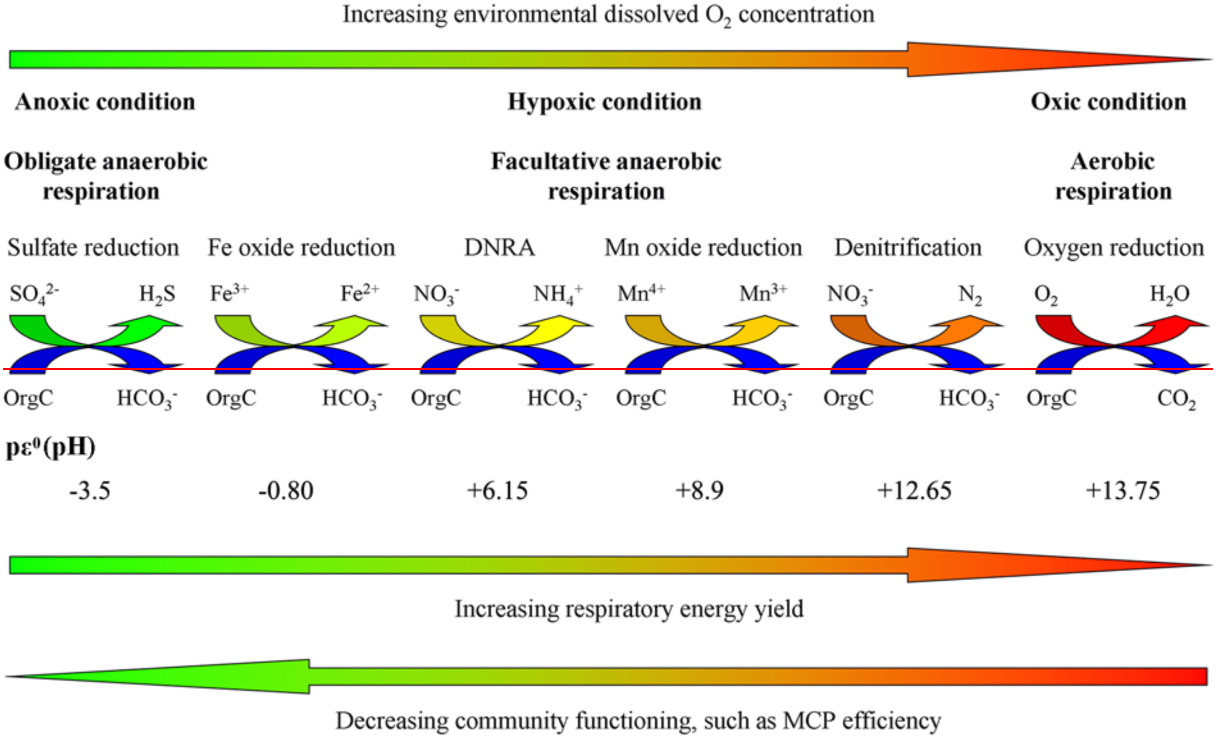
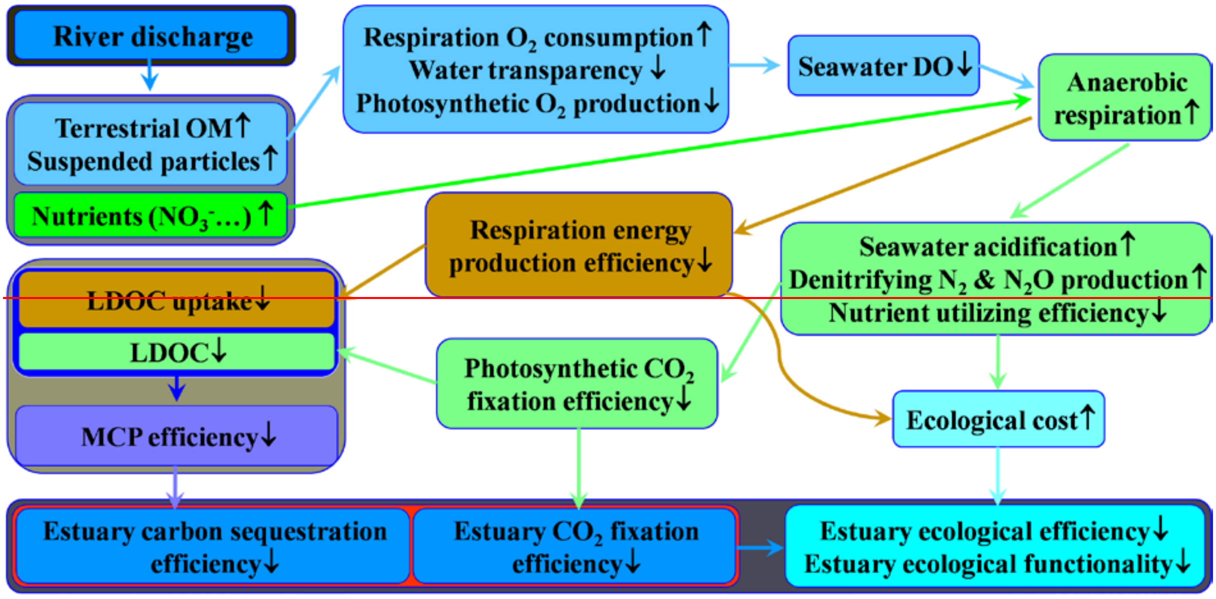


Figure 2. Schematic~~Simplified illustration~~ of microbial aerobic and anaerobic respiration pathways and their potentially different contribution to cellular metabolic energy transduction and MCP~~production and microbial community functioning~~ efficiencies. $p\varepsilon^0$(pH) values refer

to the electron activity for unit activities of oxidants and reductants at neutral pH (Nealson and Saffarini, 1994).



~~Figure 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.~~