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Carbon fixation in sediments of Sino-Pacific seas-differential contributions of bacterial and archaeal domains

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ABSTRACT

Oceanic stretches experiencing perpetual darkness and extreme limitation of utilizable organic matter often rely on chemosynthetic carbon (C)-fixation. However, C-fixation is not limited to carbon-deplete environments alone but might also occur in varying degrees in carbon-replete locales depending on the nature and concentration of utilizable carbon, electron donors and acceptors. Quantification of microbial C-fixation and relative contribution of domains bacteria and archaea are therefore crucial. The present experiment estimates the differential rates of C-fixation by archaea and bacteria along with the effects of different electron donors. Four Sino-Pacific marine sediments from Bashi strait (Western Pacific Warm Pool), East China Sea, South China Sea and Okinawa Trough were examined. Total microbial C-uptake was estimated by doping of aqueous $NaH^{14}CO_3$. Total bacterial C-uptake was measured by blocking archaeal metabolism using inhibitor GC7. Archaeal contribution was estimated by subtracting total bacterial from total microbial C-uptake. Effect of electron donor addition was analyzed by spiking with ammonium, sulfide, and reduced metals. Results suggested that C-fixation in marine sediments was not the function of archaea alone, which was in contrast to results from several recent publications. C-fixing bacteria are also equally active. Often in spite of great effort of one domain to fix carbon, the system does not become net C-fixing due to equal and opposite C-releasing activity of the other domain. Thus a C-releasing bacterial or archaeal community can become C-fixing with the change of nature and concentration of electron donors.

1. Introduction

The global continental shelves alone absorb CO_2 continuously to fix about 0.25–0.36 Pg C yr^{-1}, equivalent to 16–23% of the net annual open-ocean CO_2 uptake (Chen and Borges, 2009; Takahashi et al., 2009). C-cycle is affected by other elemental cycles like the N-cycle (Falkowski, 1997; Nicolas and Galloway, 2008), S-cycle (Canfield and Thamdrup, 2009) and P-cycle (Biche et al., 2017). The inner shelf areas and the 'continental shelf pump' at the land-ocean-atmosphere interface exports dissolved inorganic carbon (DIC), through extensive oxidation of organic-C (Hopkinson and Smith, 2004). Biological pumps help in uptake of CO_2, resulting in C-enriched waters flowing subsequently to the open ocean (Thomas et al., 2004; Tsunogai et al., 1999).

In contrast to the photic zone, the perpetually dark ocean basins, with scanty organic detritus could be constrained to fix carbon from accessible reduced inorganic substrates (Das et al., 2011a; Das et al., 2011b). Here dissolution of carbonates and oxidation of dissolved organic fractions are important suppliers of inorganic-C. While the first process aids autotrophic C-uptake, the latter could support both mixotrophs and heterotrophic. Microbial C-fixation at the expense of reduced inorganic substrates (reduced Ni, Co, Mn, Fe) has previously been evaluated in deep-sea sediments of Central Indian Basin (Das et al., 2011b), Atlantic abyss and Mediterranean sediments (Molari et al., 2013). The recently highlighted widespread chemosynthetic C-fixation beyond classical vents and seeps implicates the necessity of estimating the differential amount of carbon fixed by bacterial and archaeal communities (Molari et al., 2013; Varela et al., 2011). Some of these studies project the importance of archaeal C-fixation complementing to bacterial fixation. The capacity of the "Third Domain of Life" in controlling the biogeochemistry of C-fixation is poorly understood. Archaeal C-fixation rates might actually surpass those of the more abundant bacterial domain.

The long shorelines, extensive marginal shallow seas and deeper oceanic realms bordering Chinese mainland and neighbouring regions are marked by diverse geological features (Chen, 1988). Tectono-climatic couples could have cradled these Sino-Pacific basin sediments with rich microbial biodiversity and activity through geological ages. C-fixation is a prime biogeochemical process that impacts the litho-hydro-bio-atmospheric shuttles in these environments. Intriguingly, though extensive efforts to estimate microbial diversity of these

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sediments are in records (Dang et al., 2009; Feng et al., 2009; Jiang et al., 2007; Nunoura et al., 2010; Zhang et al., 2010), relatively fewer initiatives on sediment microbial activity are observed.

Microbes, including archaea broadly effect processes like ammonium oxidation and subsequently nitrification (Dang et al., 2009; Martin et al., 2005), thus influencing the C:N:P or Redfield ratio. In addition to availability of CO_2, dissolved inorganic carbon (DIC) and utilizable organic matter, C-fixation in the sea-floor is controlled by the availability of electron donors, such as reduced metals like Fe^{2+} and Mn^{2+}. Similarly, NH_4^+ and S^{2-} provide energy for C-fixation by getting oxidized to nitrite and nitrate (for NH_4^+) and sulphite, thiosulphate or sulfate (for HS^-, S^{2-}). Concentrations of these reductants greatly influence C-fixation rates in sediments. Reductant availability varies widely due to a multitude of processes involving diagenesis/putrefaction of organic matter or emission of reduced gases from seeps, fractures and plate boundaries (Canfield and Thamdrup, 2009; Wang et al., 2000b).

Quantification of microbial C-fixation along the continental shelves and deep-seas of the Sino-Pacific region was thus considered crucial. These sediments were examined for differential contributions of the domains of bacteria and archaea to C-fixation along with the effects of added electron donors NH_4^+, S^{2-}, Fe^{2+} and Mn^{2+}.

1.1. Geological setting of the sino-pacific marine region

The Bashi Strait of the Western Pacific margin is the origin of the strong, warm and more saline Kuroshio Current, significantly impacting regional ecosystem, fishery and climate (Lee et al., 2004). Located on an active convergent plate boundary between the Eurasian and Philippine Sea plates, this part of the 'Pacific Seismic Rim' is characterized by frequent active volcanoes and earthquakes (Ozawa et al., 2004). The region is affected by recurrent heavy rains and tropical storms (Lansigan et al., 2000), tsunamis, floods and landslides (Liu et al., 2007) causing significant influx of terrigenous material along with intensified transport of terrestrial microbes into the ocean (Dang et al., 2009). Lithologically, these are silty-clay sediments, with porosity of around 80%. Si is <30% and P and S are around 0.27 and 0.14% respectively.

The evolution of the South China Sea (SCS) is linked to the continental-oceanic interaction of the Eurasian, Pacific and Indo-Australian plates. Despite its small size and short history, the SCS has undergone a complete Wilson cycle from continental breakup to seafloor spreading to subduction (Hayes et al., 1995; Taylor and Hayes, 1983; Zhou et al., 2008). Interesting geological past of the SCS exposes a mosaic of interrelated processes. The region records mesozoic interaction between the Tethys, Paleo-Pacific and East Asia, both geologically and climatically. Development of the western Pacific marginal seas, deep mantle processes associated with tectonic extrusion, magmatism, magnetization, seawater infiltration and serpentinization make the SCS an enigmatic site catering to global scientific interest.

The Bashi Strait and the South China Sea have some common characteristics like elevated concentrations of Fe, Mn, Ca, Al. Mo, Cu and Zn. The $\sum$ REE ranged wider as compared to the ECS and Okinawa regions. These regions also harboured more dissolved CO_2 as expected, being at layers below the Aragonite Compensation Depth (Chen et al., 1999; Wang et al., 1997). Dissolved ammonium in pore-waters was also higher in these two regions increasing the propensity of greater nitrifying rates as compared to the sulfur dominated ECS and Okinawa Trough regions (Table 1).

The semi-closed East China Sea (ECS) lying between the Chinese mainland and the Pacific Ocean is bounded by the Kuroshio Current on the eastern slope side and the coast of China on the west. Here, the Taiwan Warm Current (TWC), a branch of the Kuroshio Current, mixes with Yangtze River Diluted Water (Ichikawa and Beardsley, 2002) carrying away >70% of the fresh water discharge into the Japan Sea (Isobe et al., 2002) controlling the productivity and bottom water oxygenation levels. The ECS shelf is known as a high-productivity area, where estuarine circulation driven by Yangtze River discharge sustains nutrients upwelled from Kuroshio sub-surface waters (Chen and Wang, 1999). The continental shelf covers 460,000 km^2 of the total area (~60%) with average water depth of 72 m. The seabed terrain of the ECS mainly consists of the northwest continental shelf and the southwest Okinawa Trough (OT).

Table 1
Lithology and other geochemical properties of the surface sediments of Sino-Pacific seafloor obtained from literature.
Data from (Chen et al., 1992; Huh et al., 2006; Ishibashi et al., 1995; Kang et al., 2014; Kao et al., 2005; Lei et al., 2013; Li et al., 2015; Lin et al., 2007; Liu et al., 2013; Lu et al., 2013; Mackin and Aller, 1984; Pu et al., 2007; Qin et al., 1987; Ryota et al., 2014; Sohrin et al., 1999; Takai et al., 2012; Wang et al., 2000a; Wang et al., 2000b; Wang et al., 1983; Wu et al., 2014; Yan et al., 2008; Yusuke et al., 2012; Zeng et al., 2007).

	Representative regions near sampling stations			
	Okinawa Trough	*East China Sea*	*Bashi Strait*	*South China Sea*
Sand (%)	~20	8.9	3.61	6.85
Silt (%)	~35	59.1	66.1	59.5
Clay (%)	~45	32.1	30.3	33.3
Porosity (%)	~45.5	10–35	80	55–70
P (%)	0.08	0.06	0.27	0.19
Si (%)	20–30	>30	20.9	21.2
S (%)	>99 (in chimneys)*	0.5	0.14	~0.1
Fe (%)	2–4	2–4	5.95	6.01
Mn (%)	0.06	0.06	0.15	0.14
Ca (%)	5–15	3–10	9.76–22.02	9.76–22.02
Al (%)	6- > 8	4–5	8.6	8.0
Ba (%)	0.05–0.06	0.04–0.08	~0.065	~0.055
Mo(μg/g)	0.0099 ± 0.0006	0.0099 ± 0.0006	2–6	2–6
Cu (μg/g)	20–30	<10	74.9	39.8
Zn (μg/g)	60–80	40–80	107.0	122.6
Rb (μg/g)	100–130	80–100	56.6	118.7
Sr (μg/g)	400–1000	300	217	301
$\sum$ REE (μg/g)	174.9	175.2	160–190	100–130
CO_2 (μM/kg)	55	2040	20,455	11,364–20,455
HS^- (μg/l)	$(136–272)\times10^3$	0.02–3.32	–	10×10^3
NH_4^+ (μg/l)	$(3.4–11.4)\times10^3$	$(3.4–11.4)\times10^3$	17×10^3	17×10^3
Mn/Fe	0.015–0.03	0.015–0.03	0.025	0.023
Ba/Al	0.0062–0.01	0.008–0.02	0.0075	0.0069

* Present sample is surface sample near a chimney area. Exact surface sediment data is not available presently.

The Okinawa Trough (OT) is located behind the zone of convergence between the subducting Bashi Strait plate and the over-ridding Eurasian plate. It is a back-arc basin behind the Ryukyu arc and is one of the rare examples of an incipient continental back-arc basin (Fournier et al., 2001; Gungor et al., 2012). Complex geology of seabed terrain and influence of currents like Kuroshio are vital features making the OT an exciting spot for scientific investigations. The ECS and OT are richer in native sulfur than the Bashi Strait and SCS while the dissolved sulfide concentrations were variable (Table 1).

The prolific biogeochemical details (Table 1 and Table 2) along with good amount of data of microbial diversity, but relatively fewer records of microbial rate instigated the necessity to estimate microbial carbon fixation by bacteria and archaea, under the influence of four important electron donors, two reduced metals (Fe and Mn) and two non-metallic electron donors (NH_4^+ and HS^-) in the surface sediment layers. The importance of these electron donors is imperative from the regional biogeochemistry. Earlier studies had revealed varying concentrations of HS^-, from 0 to 9 mM in northern parts of South China Sea [e.g. ODP site 1144 and RV Sonne Site SO-177;(Suess, 2005; Wang et al., 2000a)]. Surface sediments contained 2% FeS, total nitrogen ~0.1% and pore-water NH_4^+ ~1 mM. In general the Sino-Pacific sediments are Fe-rich and Mn-poor with Mn:Fe ratios <1 indicating hydrogenetic metal precipitation, with presence of significant NH_4^+ and HS^- (Tables 1 and Table 2). Considering such biogeochemical backgrounds the sediment microbial community C-fixation was estimated for domains bacteria and Archaea using e^- donors Fe^{2+}, Mn^{2+}, NH_4^+ and HS^-.