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### 南海水域不同深度非光合微生物的固碳潜能及其对不 同电子供体的响应

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摘要:通过对南海水域多个区域不同深度的海水分别以  $H_2$ 、 $Na_2S_2O_3$ 、 $NaNO_2$  为电子供体经过一定时间的驯化培养后,测定其中非光合微生物的固碳潜力,并统计南海水域不同深度非光合微生物在不同电子供体条件下固碳潜力的差异性,最后结合不同深度海水的主要固碳基因丰度差异,分析南海水域不同深度海洋非光合微生物在不同电子供体条件下固碳潜能差异的原因. 结果发现以  $NaNO_2$  为电子供体时,海洋非光合微生物固碳能力普遍较低,各深度之间没有显著差异;以  $H_2$  为电子供体时,表层海水中的非光合微生物的固碳潜力显著高于深层海水中的;而以  $Na_2S_2O_3$  为电子供体时,深层海水中的非光合微生物的固碳潜力显著高于表层海水中的. 基因分析结果表明,固碳基因 cbbL 在表层海水中的丰度高于深层海水,而 cbbM 基因在深层海水中的丰度高于表层海水。硫细菌大多以拥有 cbbM 基因为主,而氢细菌大多以拥有 cbbL 基因为主。因此不同海洋深度非光合微生物对不同电子供体响应的差异性可能和优势菌群结构的差异有关。海洋表层和深层溶解氧、无机碳含量的差异是导致菌群结构差异,乃至固碳潜力差异的重要原因。

关键词:南海水域:固碳潜力:基因丰度:海水深度:影响因素

中图分类号: X55; X172 文献标识码: A 文章编号: 0250-3301(2015)05-1550-07 DOI: 10.13227/j. hjkx. 2015. 05. 006

# Potential Carbon Fixation Capability of Non-photosynthetic Microbial Community at Different Depth of the South China Sea and Its Response to Different Electron Donors

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Abstract: The seawater samples collected from many different areas with different depth in the South China Sea were cultivated using different electron donors respectively. And the variation in the potential carbon fixation capability (PCFC) of non-photosynthetic microbial community (NPMC) in seawater with different depth was determined after a cycle of cultivation through the statistic analysis. In addition, the cause for the variation was clarified through analyzing key gene abundance regarding  $CO_2$  fixation and characteristics of seawater with different depth. The result showed that the PCFCs of NPMC in seawater with different depth were generally low and had no significant difference when using  $NaNO_2$  as the electron donor. The PCFC of NPMC in surface seawater was higher than that in deep seawater when using  $Na_2S_2O_3$  as the electron donor. The abundance of the main  $CO_2$  fixation gene cbbL in surface seawater was higher than that in deep seawater while the cbbM gene abundance in deep seawater was higher than that in surface seawater. Most hydrogenoxidizing bacteria had the cbbL gene, and most sulfur bacteria had the cbbM gene. The tendency of seawater cbbL/cbbM gene abundance with the change of depth revealed that there were different kinds of bacteria accounting for the majority in NPMC fixing  $CO_2$  at different depth of ocean, which led to different response of PCFC of NPMC at different depth of the sea to different electron donors. The distributions of dissolved oxygen and inorganic carbon concentration with the change of the depth of the sea might be an important reason leading to the difference of NPMC structure and even the difference of PCFC at different depth of the sea.

Key words: South China Sea; potential carbon fixation capability; gene abundance; depth of the sea; affecting factors

二氧化碳(CO,)过量排放而引起的全球变暖是 目前全球面临的重大环境问题. 生物固碳是 CO, 吸

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收与资源化的重要手段. 生物固定  $CO_2$  主要依靠植物和自养微生物  $^{[1]}$  ,但植物生长对环境要求较为严格,地球上有很多环境并不适合植物生长,此时,自养微生物固定  $CO_2$  的优势便显现出来了. 固碳微生物主要包括光合自养微生物  $^{[2]}$  和化能自养微生物. 目前很多研究利用藻类固定  $CO_2$  ,但是藻类培养中需要光照,且不耐高浓度  $CO_2$  ,因此,探索无需光照的高效固碳微生物对于更广泛环境条件下的微生物固碳具有重要意义. 化能自养微生物主要通过氧化无机化合物获得能量,能量的有效获得对于自养微生物的固碳效率具有举足轻重的作用. 自养微生物能够利用的无机化合物主要有一些还原性化合物,包括  $H_2$ 、 $H_2S$ 、S 以及含  $S_2O_3^{2-}$ 、 $NH_4^+$ 、 $NO^{2-}$ 、 $Fe^{2+}$ 的化合物等  $^{[3]}$ . 其中  $H_2$  是最好的能源物质(自由能最大).

至今已发现的微生物固定  $CO_2$  途径有 6 条,即卡尔文循环、还原柠檬酸循环、还原乙酰-CoA 途径、羟基丙酸循环、三羟基丙酸/四羟基丁酸酯循环以及二羧酸/四羟基丁酸酯循环[4]. 其中,卡尔文循环是光能自养生物和化能自养生物固定  $CO_2$  的主要途径[5,6]. 核酮糖-1,5-二磷酸羧化酶/加氧酶(RubisCO)是卡尔文循环中碳同化的限速酶. 目前自然界存在的不同类型 RubisCO 已被鉴定出来,按照其结构、催化性能和  $O_2$  的敏感性可分为  $I \sim \mathbb{N}^{[7]}$ . 其中有关 $\mathbb{II}$  和 $\mathbb{IV}$  的研究较少,大部分自养微生物主要以  $\mathbb{I}$  和  $\mathbb{II}$  型为主[8]. 固碳功能基因 cbbL 和 cbbM 分别表达关键酶 RubisCO 的  $\mathbb{I}$  、 $\mathbb{II}$  构型.

海洋是全球最大的碳库,溶解的无机碳储量约 为37 400 Gt<sup>[9]</sup>. 同时,海洋也是最大的微生物库,据 估计,海洋微生物种类可能多达1000万种. 迄今为 止,人类发现的微生物大约有150万种,除了7.2万 种存在于陆地外,其余都存在于海洋之中[10]. 由于 许多自养微生物都为古菌,而生物起源于海洋,因此 从生物进化角度来看,海洋中可能含有丰富的自养 微生物资源[11]. 胡佳俊[12]已从全球各大海域表层 海水筛选富集出非光合固碳微生物菌群,并通过电 子供体的优化,发现以 H<sub>2</sub>、Na<sub>2</sub>S<sub>2</sub>O<sub>3</sub>、NaNO<sub>2</sub> 这 3 种 还原性无机物作为电子供体能够较显著提高其固碳 效率[13]. 但是由于海水不同深度的自然环境差异 很大,如温度、压力、溶解氧、CO,浓度等,因此不 同深度的海水的微生物群落结构以及优势固碳菌 (基因)可能不同,其固碳潜能以及对不同电子供体 的响应也可能有异. 然而目前尚未有不同深度海洋 非光合微生物固碳潜能以及对不同电子供体响应的相关研究.

本文以 2013 国家自然科学基金南海西部开放 航次(航次编号: NORC2013-07) 从南海各海域不同 深度所采集来的海水为研究对象,以 H<sub>2</sub>、Na<sub>2</sub>S<sub>2</sub>O<sub>3</sub>、NaNO<sub>2</sub> 这 3 种还原性无机物作为电子供体,研究南海不同深度海水中非光合微生物在特定培养条件下的固碳能力及其对不同电子供体的响应,并将其定义为相应电子供体条件下的海水非光合微生物的固碳潜能.通过分析不同深度海水样品中固碳途径关键酶基因的丰度以及海水理化因素,讨论了不同深度海洋微生物固碳潜能差异的可能原因,以期为今后在普通培养条件下从海洋中筛选和驯化得到更有效的非光合固碳微生物菌群提供理论指导.

### 1 材料与方法

### 1.1 采样区域概况及采样点分布

图 1 为南海水域采样点分布,后期实验过程中 将海水样品按地理位置区域混合,分为 A、B、C、 D、E、F 共 6 个区. 各区域采样深度见表 1. 用温深 盐测量仪(SBE911PlusCTD)采集水样,并现场获取 深度、温度、压强、盐度相关理化数据,样品采集后 以 4℃保存带回实验室做后期实验.

由于 200 m 左右深度以内阳光可以透射,500 m 以下的深度区域不可见光<sup>[14]</sup>,故将每个区域的水

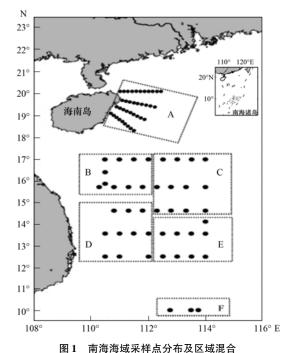


Fig. 1 Distribution of sampling sites and mixing areas in the South China Sea

样,按照表层(5 m 深度),次表层(25~200 m 深度),次深层(500~1000 m深度)和深层(1100~1500 m深度)共4个深度梯度进行分类归纳. 各区域的表层样品为5 m 深度采得的样品,次表层为25~200 m 深度范围采得的样品,次深层为500~1000 m深度范围采得的样品,深层为1100~1500 m深度范围采得的样品.

表1 各区域采样海水深度1)

Table 1 Sampling seawater depth of each area

		1 0		1			
深度/m	区域						
休及/m	A	В	С	D	E	F	
5		V	V	V	V	$\sqrt{}$	
25	$\sqrt{}$	$\checkmark$	_	_	_	_	
50	$\sqrt{}$	$\checkmark$	$\checkmark$	$\checkmark$	$\checkmark$	$\checkmark$	
75	$\sqrt{}$	$\sqrt{}$	_	_	_	_	
100	$\sqrt{}$	$\sqrt{}$	$\checkmark$	$\checkmark$	$\checkmark$	$\sqrt{}$	
150	$\sqrt{}$	$\sqrt{}$	$\checkmark$	_	_	_	
200	$\sqrt{}$	$\sqrt{}$	$\sqrt{}$	$\sqrt{}$	$\checkmark$	$\checkmark$	
500	$\sqrt{}$	$\sqrt{}$	$\checkmark$	$\sqrt{}$	$\sqrt{}$	$\checkmark$	
700	$\sqrt{}$	_	_	_	_	_	
800	_	_	$\sqrt{}$	_	$\checkmark$	_	
1 000	_	$\sqrt{}$	$\sqrt{}$	$\sqrt{}$	$\checkmark$	$\checkmark$	
1 200	_	_	_	_	$\sqrt{}$	_	
1 500	_	_	$\checkmark$	_	$\checkmark$	$\checkmark$	

1) "√"表示相应的深度有样品,"一"表示没有样品

### 1.2 海水非光合固碳微生物培养

将 1.1 节中采集自所有样点的样品按划分的地理位置区域及深度梯度等比例混合得到各区域 4 个不同深度的混合海水样品,每个样品设置为 3 个平行样,各按 10% 的比例转入装有 90 mL 海水基本培养基<sup>[15]</sup>的血清瓶中,用硅胶塞密封. 以  $H_2$  为电子供体条件培养,按混合气比例  $H_2$ :  $O_2$ :  $CO_2$  为 8.5: 0.5: 1 的比例注入气体,用封口膜封口. 其余电子供体条件按 2‰电子供体浓度<sup>[12]</sup>加入培养基,按混合气比例空气:  $CO_2$  为 9: 1. 置于摇床避光振荡培养(28%, 120  $\mathbf{r} \cdot \mathbf{min}^{-1}$ ),4 d 后重新充入混合气. 8 d 为一个周期<sup>[16]</sup>,8 d 后测定培养液中有机碳含量.

### 1.3 固碳潜能的测定

由于海水微生物的不完全可培养性,常规培养不能完全反映原位条件下的非光合微生物的固碳能力,因此将等量海水在等体积量的培养体系中经过一定时间特定培养条件培养后固定 CO<sub>2</sub> 的量,定义为固碳潜能,以此反映其相对固碳能力. 由于培养基中除了接种的海水并不存在有机碳源,所以在培养后总有机碳的增加量即为 CO<sub>2</sub> 的固定量. 在分析中采用 Shimadzu TOC-VCPH 有机碳分析仪(Shimadzu Seisakusho Co. Ltd., Kyoto, Japan)测定

总有机碳含量(total organic carbon, TOC),并以此 为测量指标,衡量微生物的 CO<sub>2</sub> 固定潜能.测量时 统计 3 个平行样的平均值及标准差,以此计算每个 实验样品的固碳潜能.

### 1.4 海水微生物采集及 DNA 提取

将所有地理位置点采集的海水样品按 1.1 节中的 4 个深度梯度等比例混合得到各深度范围的总混合海水样品,取 3 L 该混合海水样品过 0.22 μm 微孔滤膜采集海水微生物.

用 DNA 提取试剂盒(UltraClean ® DNA Isolation Kit, MoBio USA)根据其使用说明书<sup>[17]</sup>对过滤过海水的微孔滤膜提取总细菌 DNA. 通过NanoDrop ND-2000(Thermo, USA)测定 DNA 样品的浓度和纯度,之后将样品在 – 20℃保藏以用于分析.

#### 1.5 固碳途径关键酶基因分析

由于卡尔文循环是主要的固碳途径,本研究主要分析卡尔文循环的关键酶基因 cbbL、cbbM 的丰度. 表达基因 cbbL 和 cbbM 用 1.4 节中提取的总DNA 样品通过 ABI 7500 定量 PCR 仪(Life Technologies, USA)通过绝对定量的方法测定关键酶基因的数量. 基因 cbbL 的定量引物为 K2F(5'-ACCAYCAAGCCSAAGCTSGG-3') 和 V2F(5'-GCCTTCSAGCTTGCCSACCRC-3') [18], cbbM 定量引物为 cbbM-F(5'-TTCTGGCTGGGBGGHGAYTTYATY AARAAYGACGA-3') 和 cbbM-R(5'-CCGTGRCCR GCVCGRTGGTARTG-3') [19].

定量分析步骤:取 2 μL 1.4 节中提取得到的 DNA 样品混入 18μL SYBR Premix Ex Taq<sup>TM</sup> system (Takara, Japan).循环条件如下:95℃ 预变性 3 min;95℃延伸 30 s,62℃(cbbL 基因)/55℃(cbbM 基因)退火 60 s,进行 40 个循环;72℃延伸 10 min.

#### 1.6 数据统计

统计各区域不同深度海水样品3个平行样的固碳能力的平均值及标准差,将其作为各区域不同深度海水样品的固碳潜力.将所有区域各深度梯度的固碳潜力值按深度梯度统计,除在深层梯度(1100~1500 m)只有3个区域的平均值外,其余梯度排除1个最大区域值和1个最小区域值后取剩余区域的平均值,统计标准差,进行南海水域非光合微生物不同电子供体条件的固碳潜力深度差异分析.

采用 SPSS 13.0 统计软件对所测数据进行单因素方差分析(ANOVA),LSD 多重比较(P为 0.05 或 0.01)分析不同深度间指标的差异显著性.

#### 2 结果与讨论

# **2.1** 不同深度海洋非光合微生物的固碳潜力及其对不同电子供体的响应

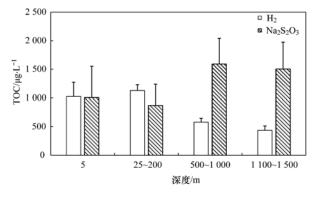
对南海水域 6 个采样区域的水样分别按 4 个深度梯度混合,并以 H<sub>2</sub>、Na<sub>2</sub>S<sub>2</sub>O<sub>3</sub>、NaNO<sub>2</sub>分别作为电子供体,按照 1. 2 节的方法进行培养,经过一个培养周期测定净固碳量. 所得的结果见表 2. 在一个

培养周期内,各区域及深度以 NaNO<sub>2</sub> 为电子供体的响应值普遍较低,且没有显著差异,这可能是由于 NaNO<sub>2</sub> 氧化时所产生的能量较低而且以其为电子供体的硝化菌世代时间长,生长缓慢,这与文献 [12,13]结果相符,故不对该电子供体的响应情况进行进一步的分析. 将所有区域的结果按照深度梯度整合统计得到不同深度海洋微生物固碳潜力对 H<sub>2</sub> 和 Na<sub>2</sub>S<sub>2</sub>O<sub>3</sub> 的响应的关系,见图 2.

表 2 各区域海水非光合微生物固碳潜力对不同电子供体响应情况

Table 2 Response of potential carbon fixation capability of non-photosynthetic microbial community in each area seawater to different electron donors

培养条件	深度/m	固碳量/μg·L <sup>-1</sup>					
477.7.	休及/III	A 🗵	B⊠	C区	D区	E区	F区
	5	975.5 ± 107.0	2 638.2 ± 104.1	$395.7 \pm 37.5$	$1\ 309.9 \pm 53.2$	1 221.7 ± 18.1	639.9 ± 156.8
H, 为电子供体	25 ~ 200	$1\ 202.\ 8\ \pm 114.\ 7$	2 782.4 ± 284.8	$1088.9\pm55.0$	$1\ 090.\ 2\pm67.\ 0$	$869.9 \pm 155.7$	$1056.9\pm102.4$
	500 ~1 000	$194.7 \pm 102.7$	$623.8 \pm 97.7$	$534.6 \pm 77.3$	$664.5 \pm 132.9$	$490.7 \pm 65.5$	$1\ 052.\ 7\ \pm 127.\ 5$
	1 100 ~ 1 500	_	_	$412.4 \pm 25.6$	_	$458.9 \pm 37.5$	$440.6 \pm 40.5$
	5	1 163.3 ±41.5	1 148.9 ± 252.4	959.6 ± 235.0	2 143.35 ± 169.8	594.6 ± 158.5	114.1 ± 36.5
Na <sub>2</sub> S <sub>2</sub> O <sub>3</sub> 为电子供体	25 ~ 200	1 658.2 ± 231.1	$723.2 \pm 165.8$	$406.5 \pm 6.5$	$771.2 \pm 103.9$	$394.2 \pm 122.9$	$923.5 \pm 149.2$
	500 ~1 000	$1555.3 \pm 243.5$	$398.2 \pm 94.2$	$883.5 \pm 108.5$	$2533.5 \pm 106.3$	1 821.8 ± 190.4	$2\ 103.\ 1\pm145.\ 1$
	1 100 ~ 1 500	_	_	$1\ 035.7\pm213.7$	_	$1976.2\pm256.9$	$1576.6\pm106.8$
	5	$519.5 \pm 78.6$	$458.4 \pm 65.3$	$367.8 \pm 45.6$	$434.8 \pm 54.7$	$345.6 \pm 69.3$	$420.8 \pm 42.3$
NaNO, 为电子供体	25 ~ 200	$429.5 \pm 53.2$	$450 \pm 62.4$	$364.4 \pm 50.2$	$301.2 \pm 49.6$	$420.8 \pm 58.6$	$426.3 \pm 47.2$
110107 22 1 1 1 1	500 ~1 000	$514.8 \pm 53.1$	$547 \pm 65.4$	$475.7 \pm 72.3$	$494.8 \pm 74.7$	$357.3 \pm 56.0$	$358.4 \pm 43.6$
	1 100 ~ 1 500	_	_	$472.1 \pm 50.7$	_	$359.5 \pm 61.1$	$330.7 \pm 42.6$



将表 2 中所有区域的净固碳量按各深度梯度平均,除1100~ 1500 m深度梯度外,其余排除 1 个最低区域值和 1 个最高区域 值,将余下的区域值统计平均值和标准差

### 图 2 不同电子供体条件下海水非光合 微生物固碳能力随深度变化

Fig. 2 Variation of carbon fixation capability of non-photosynthetic microbial community in seawater with the depth under different cultivation conditions using  $H_2/Na_2S_2O_3$  as electron donors

从图 2 可知,以 H<sub>2</sub> 为电子供体的培养条件下, 200 m 以内的表层海水的非光合微生物的固碳能力 要显著高于 500 m 以下深层海水.数据偏差分析表 明,5 m 深度的表层水的各区域的非光合微生物的 固碳量差异要明显大于其他深度梯度各区域间的差 异(标准差是其他深度区域 2 倍以上),这可能是由于外部环境条件(光照,温度,生物)变化对表层水的理化性质和微生物结构的影响较显著,因此表层海水相较于其他深度海水微生物固碳量的区域差异性较大.

以  $Na_2S_2O_3$  为电子供体的培养条件下,500 m 以下深层海水的非光合微生物的固碳能力要显著高于 200 m 以内表层海水,深层海水的非光合微生物 固碳量是表层海水的 1.5 倍左右.

数据偏差分析表明,以  $Na_2S_2O_3$  为电子供体的培养条件下的各深度梯度的非光合微生物固碳潜力的区域差异性要明显大于以  $H_2$  为电子供体培养条件下的区域差异性(以  $Na_2S_2O_3$  为电子供体的标准差基本上是以  $H_2$  为电子供体的 3 倍以上). 说明南海水域能够利用以  $S_2O_3^{2-}$  为电子供体的化能自养菌丰度的区域间差异性要高于能以  $H_2$  为电子供体的化能自养菌的区间差异性.

从南海水域不同深度海洋微生物固碳潜力对  $H_2$  和  $Na_2S_2O_3$  两种电子供体的响应效果看,表层水以  $H_2$  为电子供体的响应效果要略好于以  $Na_2S_2O_3$  为电子供体的响应效果,而深层水以  $Na_2S_2O_3$  为电

子供体的响应效果要明显好于以  $H_2$  为电子供体的响应效果,固碳潜力是后者的近 3 倍. 由于深层海水特殊的环境条件,大量的深海微生物多为嗜压、嗜冷微生物,在常温、常压下难以生存<sup>[20]</sup>. 使得大量深海环境生存的细菌在采集以及后期实验室培养的过程中,由于环境条件较大的变化,已经失活或死亡. 所以如果在原位生长环境,深海区域能利用  $S_2O_3^{2-}$  为电子供体固碳的微生物数量可能远高于表层海水,其固碳能力可能更大.

固碳潜力的差异肯定与不同深度海洋中的优势 固碳微生物数量有关,但是由于采集过程中环境条件的变化,一些深海微生物已失活或死亡,因此传统 的培养方法难以确定不同海洋深度各种固碳微生物 的数量.固碳途径的关键酶基因的丰度可以间接反 映固碳微生物的数量.为了阐明不同深度海洋微生 物固碳潜力差异的深层原因,进一步研究了2个关 键的固碳酶基因随海水深度变化的丰度差异.

### **2.2** 南海海域不同深度主要固碳基因的差异性及 其与微生物固碳潜能的相关性

对南海水域采集的样品按照深度梯度混合,按照1.4和1.5节的方法测定不同深度梯度海水中 cbbL、cbbM 基因的丰度,结果见图3. 固碳基因 cbbL 的丰度,随着海水深度的增加逐渐递减,在5m深度的表层水中,其数量显著高于其他的深度梯度(高于其他深度梯度数量1个数量级). 固碳基因 cbbM 的丰度随着海水深度增加逐渐递增,在500~1000 m的深度范围内,基因含量达到最高值,而且深层水 cbbM 基因丰度都高于表层水的10倍以上,5m深度表层水最低.

由基因 cbbL 表达的 RubisCO I 广泛存在于植物和一些原核生物中,其有 4 种类型: IA ~  $ID^{[21]}$ ,

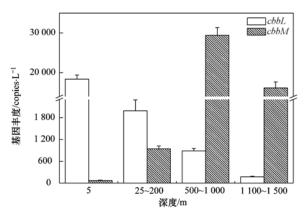


图 3 海水主要固碳基因随深度变化差异

Fig. 3 Differences of main  ${\rm CO_2}$  fixation gene abundance in sea water with the change of the depth

其中 IA 和 IC 多发现于变形菌门中, 而变形菌门中 有一部分菌属和 N, H, 代谢有密切联系[22], IB 和 ID 在蓝藻和真核生物中占优势[21,23,24]. 由基因 cbbM 表达的 RubisCO Ⅱ广泛分布于厌氧的 α-变形菌门 以及硫杆菌的一些种中,它们大多和硫代谢有 关[25]. 南海不同深度非光合微生物的固碳潜力与 两种主要固碳功能基因随海水深度上的分布趋势是 大致相符的,即表层水的 cbbL 基因丰度以及以  $H_2$ 为电子供体的固碳能力均高于深层水,同时,深层水 的 cbbM 基因丰度以及以  $Na_2S_2O_3$  为电子供体的固 碳能力均大于表层水. 因此表层水可能多以 cbbL 为 固碳功能基因的光合微生物、氢-氧化细菌为主,深 层水可能多以 cbbM 为固碳功能基因的 α-变形菌、 硫细菌为主,从而使得不同深度海洋非光合固碳微 生物的固碳潜力对不同电子供体的响应有显著差 异. 然而,从图2和图3结果可见,次表层的cbbL显 著低于表层,但以 H, 为电子供体的固碳潜力却无 显著差异(甚至略高于表层),这可能是由于表层中 大量的 cbbL 来源于光合细菌,因此在避光培养中未 发挥出其固碳能力,导致无光条件下的固碳能力 较低.

图 3 中深层海水的 cbbM 固碳基因丰度明显高于表层水,比表层水高了 1 个数量级,而图 2 中,以  $Na_2S_2O_3$  为电子供体的固碳量深层水仅是表层水的 1.5 倍左右. 而且次深层的 cbbM 丰度明显高于深层,但以  $Na_2S_2O_3$  为电子供体的固碳量却大致相当. 这进一步验证了 2.1 节中的推测,即深层海水的固碳微生物以能利用还原性硫为电子供体并以 cbbM 为固碳功能基因的硫细菌为主,但是由于特殊的环境条件,在常温、常压环境中不能生存. 如果能进行原位培养,其固碳能力可能远高于表层海水.

# 2.3 海洋不同深度优势固碳菌差异的环境影响因素分析

海洋生态系统中,不同的深度海水在各种理化性质及环境条件等方面都存在着显著差异,对于微生物的生长以及菌群结构组成等造成显著影响,表3为通过 CTD 对采样现场测定的环境理化数据按照深度区域整合做了统计,可以看出,深层水相比较于表层水,含盐量高,温度低,压强大. RubisCO I 多在好氧微生物中被发现,被认为是一种主要存在于光合生物和好氧化能自养微生物中的 RubisCO 酶<sup>[26]</sup>,而 Badger 等<sup>[27]</sup>通过生态学及对酶结构研究指出,RubisCO II 在低氧和高二氧化碳浓度下有较高活性,这与早期地球的大气环境极为相似,RubisCO II

表 3 海水各深度区域的物理化学性质特征1)

Table 3 Physico-chemical properties of seawater within each range of depth

深度/m	TDS/g·L <sup>-1</sup>	温度/℃	压强/kPa
5	24. 0 ± 0. 2	29. 49 ± 0. 09	50.1 ± 1.4
25 ~ 200	$25.9 \pm 0.5$	21. 17 $\pm$ 0. 11	$1\ 100\ \pm 800$
500 ~ 1 000	29. $8 \pm 0.4$	8. 88 $\pm$ 0. 07	$8\ 000 \pm 2\ 000$
1 100 ~ 1 500	29. $1 \pm 0.2$	$4.64 \pm 0.06$	$12\ 000\ \pm 1\ 800$

1)TDS(总溶解性固体),表示海水的含盐量

### 可能是 RubisCO 的共同进化祖先.

Alfrider 等 $^{[28]}$ 和 Videmšek 等 $^{[29]}$ 的研究表明,高 CO<sub>2</sub> 浓度的环境不利于 cbbL 为固碳基因的固碳细菌的生长,有利于以 cbbM 为固碳基因的细菌的生长.

因此可以推测,造成固碳基因 cbbL、cbbM 随深度变化的丰度差异原因可能和溶解  $O_2$  含量、溶解  $CO_2$  含量有关.

由于生物泵的作用,碳实现了从海洋表层向深层的转移<sup>[30]</sup>,并且深层海水低温、高压强等特殊的环境条件也有利于无机碳的储存. 因此底部的 CO<sub>2</sub>浓度远高于表层<sup>[31]</sup>,但氧气浓度极低,因此有利于以 cbbM 为固碳基因的微生物的生长. 反之,表层海水含氧量高,CO<sub>2</sub> 浓度相对较低<sup>[32]</sup>,从而有利于以 cbbL 为固碳基因的微生物的生长

另一方面,许多研究指出<sup>[33-36]</sup>,海洋深处可挥发性硫化物(AVS)的浓度较高,也有利于以 *cbbM* 为固碳基因的微生物的生长.

结合文献报道的有关 cbbL、cbbM 固碳基因存在的微生物类群的生存条件及代谢类型,可以推测海洋中不同深度的  $O_2$ 、 $CO_2$ 、还原性硫化物的含量差异可能是造成海洋中不同深度优势固碳菌菌群结构差异,乃至主要固碳基因丰度和固碳潜力差异的重要原因.

### 3 结论

- (1)南海水域不同深度海洋非光合固碳微生物 对不同电子供体的响应有显著差异. 以 H<sub>2</sub> 为电子 供体时,表层海水中的非光合微生物的固碳潜力高 于深层海水,反之以 Na<sub>2</sub>S<sub>2</sub>O<sub>3</sub> 为电子供体时,深层海 水微生物的固碳潜力高于表层海水.
- (2)两种主要的固碳功能基因 cbbL 和 cbbM 丰 度随海水深度变化而变化. 表层海水中 cbbL 基因丰 度显著高于深层水,相反,深层海水中 cbbM 的基因 丰度显著高于表层水,表明表层和深层海水中的非

光合固碳微生物的优势种有较显著差异. 这可能是 表层和深层海水中的非光合固碳微生物对不同电子 供体响应有显著差异的重要原因.

(3)导致不同的影响因素很多且复杂.海洋不同深度溶解  $O_2/CO_2$  和还原性硫化物浓度的差异可能是导致其优势非光合固碳微生物差异的重要原因.深层海水的低  $O_2$ 、高  $CO_2$  和高还原性硫化物环境适合于以 cbbM 为固碳基因的微生物生长,反之表层海水的高  $O_2$ 、低  $CO_2$  和低还原性硫化物环境适合于以 cbbL 为固碳基因的微生物生长.

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