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评 述

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海洋蓝细菌与异养细菌相互作用: 以原绿球藻为例

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摘要 蓝细菌(cyanobacteria)是海洋最主要的初级生产者, 贡献了海洋净初级生产力的25%. 海洋异养细菌具有多种代谢路径, 能够吸收和利用蓝细菌的光合作用产物. 海洋蓝细菌和异养细菌之间的相互作用关系影响海洋食物网、固碳和储碳, 具有重要的生态效应和生物地球化学意义. 原绿球藻(*Prochlorococcus*)作为蓝细菌的典型代表类群, 是海洋中体积最小、数量最大的光合自养原核微生物. 原绿球藻的基因组高度精简, 从而减少了细胞复制中所需的物质和能量, 同时减小了细胞体积, 因此在寡营养大洋表层环境中具有竞争优势. 然而, 基因组减小同时使得原绿球藻单个细胞基因多样性下降, 从而使其适应环境的潜能降低. 因此, 相比于其他蓝细菌, 原绿球藻更加依赖于海洋环境中其他微生物的协助, 以维持自身生存的需求. 本文根据国内外近期的相关研究成果, 从原绿球藻与异养细菌之间基因的互补关系和生理特性等角度, 归纳了两者之间存在的互利共生、偏利共生等多种相互作用关系及其生态效应, 并提出了未来的研究重点.

关键词 蓝细菌, 原绿球藻, 异养细菌, 相互作用, 互利共生, 偏利共生

蓝细菌又称蓝藻, 是地球上最早的产氧光合自养原核生物, 出现在距今大约35~33亿年前[1], 其光合作用使地球上的大气由无氧状态转变为有氧状态. 海洋蓝细菌仅占全球碳生物量的0.05%[2], 但贡献了25%的海洋净初级生产力[3]. 在开阔大洋, 蓝细菌甚至可以贡献超过80%的初级生产力[4], 是最主要的初级生产者. 通过光合作用, 海洋蓝细菌将无机碳转化为有机碳(高达200亿吨/年)[5,6], 而异养细菌通过呼吸矿化蓝细菌生产的有机碳, 释放无机碳, 参与以惰性溶解有机碳(recalcitrant dissolved organic carbon, RDOC)形式储碳的“海洋微型生物碳泵” (microbial carbon pump, MCP)和以颗粒有机碳(particulate organic carbon, POC)沉降储碳的“生物泵”(biological pump, BP)[7~9]. 因此, 自养蓝细菌和异养细菌构成了海洋食物网的基础, 驱动海洋生态系统的物质循环和能量流动.

在长期的演化过程中, 海洋蓝细菌和异养细菌群落之间形成了密切的相互作用关系. 地质记录表明, 至少在4.4亿年前蓝细菌和异养细菌就已存在相互作用关系[10]. 研究发现, 蓝细菌与异养细菌直接接触或间接物质交换的现象在海洋中普遍存在[11~13]. 蓝细菌和异养细菌的相互作用使得两者形成长久的共存关系, 从而维持了海洋微生物群落的稳定性与多样性. 随着全球气候变化的加剧, 蓝细菌和异养细菌的相互作用关系可能发生变化, 直接影响海洋生态系统的群落结构, 进而对海洋长期储碳和生物地球化学循环产生重要的影响.

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海洋蓝细菌有3个主要类群：原绿球藻(*Prochlorococcus*)、聚球藻(*Synechococcus*)和束毛藻(*Trichodesmium*)[14~16]. 其中，原绿球藻是海洋中细胞体积最小、数量最大的产氧光合微生物，其全球大洋的年平均总丰度为$(2.9\pm0.1)\times10^{27}$ cell[3]. 原绿球藻每年可固定约40亿吨的碳，是热带和亚热带寡营养开阔大洋中最主要的初级生产者[17~21]. 本文根据国内外近期的相关研究成果，以“原绿球藻-异养细菌”相互作用为例，在基因组、代谢和群落等层面归纳了两者之间存在的互利共生、偏利共生等多种相互作用关系及其生态效应，并提出了未来的研究重点.

1 原绿球藻基因组的特点

根据不同的生理生态和分子进化特征，原绿球藻可分为高光适应(high-light adapted, HL)和低光适应(low-light adapted, LL)两大类生态型(ecotype)[22,23]. HL型包括HLI、HLII、HLIII、HLIV、HLV、HLVI共6种，LL型包括LLI、LLII/III、LLIV、LLV、LLVI、LLVII共6种[22,23]. 不同生态型的原绿球藻表现出对光照、温度等适应的差异，与其生态位(ecological niche)特征相符[24~27]. 原绿球藻具有较小的基因组(1.6~2.6 Mb)和较低的GC含量(30%~51%)[27]. 在长期进化过程中, 原绿球藻发生了基因组流线型化(genome streamlining), 丢失了一些非必须基因. 例如, 与DNA修复、光合系统(*psbU/V*)和氧化应激等功能相关的基因簇[28,29]. 因为原绿球藻的基因组高度精简，所以减少了基因组和细胞复制过程中所需的物质和能量，在寡营养环境中具有竞争优势[24,30~34]. 此外，原绿球藻通过减少基因组的大小，减少了细胞体积，增加了表面积与体积比(S/V), 从而提高了光吸收和物质交换的效率[35,36]. 原绿球藻的基因组，包括保守的核心基因(core genes)和“灵活”(flexible)的非核心基因(non-core genes)，原绿球藻通过这些多样的非核心基因，一定程度提高了其对环境的适应能力. 综上, 原绿球藻基因组的流线型化使得原绿球藻在寡营养海区的真光层具有较大的竞争优势. 然而，基因组减小使得原绿球藻单个细胞基因多样性下降，从而使其适应环境的潜能降低. 因此，相比于其他蓝细菌，原绿球藻更加依赖于海洋环境中其他微生物的共生协助, 以维持自身生存的需求.

2 异养细菌促进原绿球藻生长

在原绿球藻12种生态型中，仅有5种生态型能够在实验室中人工培养[22,37~40]. 目前，实验室培养的原绿球藻株系大部分含有共生的异养细菌，并且这些共生菌很难被人工清除，成为原绿球藻培养体系中长期存在的“污染物”[41]. 有意思的是，一些初步的研究发现，这些“污染物”的存在能够使原绿球藻生长得更好(相对于无菌的纯原绿球藻培养体系)[41]. 例如，在HLII型的MIT9215和LLIV型的MIT1327等原绿球藻株系的无菌培养体系中，分别添加交替单胞菌EZ55(*Alteromonas* sp. EZ55)、海旋菌MIT1351(*Thalassospira* sp. MIT1351)、玫瑰杆菌MIT1352(*Roseobacter* sp. MIT1352)和海洋杆菌MIT1353(*Marinobacter* sp. MIT1353)等异养细菌后(如表1所示)，原绿球藻的生长均明显改善: 生长停滞期时间明显缩短; 生长所需要的起始细胞浓度下降, 生长速率提高, 稳定期的细胞浓度上升，以及使处于衰亡期的原绿球藻重新恢复生长[41~50]. 最近的研究发现, 异养细菌的存在对原绿球藻在黑暗和极限温度条件下的生长具有积极影响[45,46]. 麦氏交替单胞菌MIT1002(*Alteromonas macleodii* MIT1002)可以使原绿球藻在黑暗中维持生存长达11 d之久，而纯培养的原绿球藻存活则不超过1.5 d；同时，MIT1002还增加了原绿球藻MED4和NATL2A在黑暗条件下的生长速率[45]. 在共培养体系中，交替单胞菌EZ55能够提高原绿球藻在不同温度下的生长速率，特别是在生长极限温度(12°C)附近，促进效果更为明显[46].

3 原绿球藻与异养细菌相互作用机制

3.1 异养细菌去除原绿球藻的氧化压力

原绿球藻通过基因组流线型化，使其在寡营养环境中具有竞争优势，但同时失去了一些重要的非必须基因，使其应对环境的潜能降低[32,51~54]. 例如：原绿球藻丢失了编码过氧化氢酶(catalase peroxidase)的基因*katG*，这种缺失可以使每个细胞节约0.2%的铁需求量，从而提高生长速率，有利于其在铁限制的环境中生存[53,55~57]. 但是，这也导致了原绿球藻对活性氧类物质(reactive oxygen species, ROS)较为敏感, 其过氧化氢耐受浓度小于200 nmol/L[42,58,59]. 因此，原绿球藻的生存依赖于具有降低氧化压力能力的异养细菌. 进一步研究表明，在24°C，800 nmol/L的过氧化氢对混合层中发现的所有生态型原绿球菌株都是致死的，而交替单胞菌EZ55能消耗环境中过氧化氢，防止原绿球藻细胞和

表 1 异养细菌在共培环境下对原绿球藻的影响

Table 1 Effects of heterotrophic bacteria on *Prochlorococcus* strains in co-culture environment

原绿球藻	生态型	表型[a)]	异养细菌[b)]	对原绿球藻生长影响[c)]	培养基	文献
MED4	HLI	Sm^{r} (VOL7)	*Alteromonas* sp. EZ55	++	Pro99	[42]
		WT	Rhodobacterales*, Oceanospirillales*, OM60*, Alcanivoracacea*, Marinobacter*, Alteromonadales*	+/N, N, N, N, N, N	ProMM	[43]
		WT	*Alteromonas macleodii* HOT1A3	+	Pro99	[44]
		WT	*Alteromonas macleodii* MIT1002	++	Pro99	[45]
		Sm^{r} (VOL7)	*Alteromonas* sp. EZ55	++(不同温度)	Pro99	[46]
		WT	*Pelagibacterales* sp. HTCC7211	N	ProMS, ProMC	[47]
MIT9515	HLI	Sm^{r} (VOL8)	*Alteromonas* sp. EZ55	++	Pro99	[42]
MIT9215	HLII	WT	*Alteromonas* sp. EZ55	++	Pro99	[41]
AS9601	HLII	Sm^{r} (VOL5)	*Alteromonas* sp. EZ55	+	Pro99	[42]
MIT9312	HLII	Sm^{r} (VOL4)	*Alteromonas* sp. EZ55	++	Pro99	[42]
		Sm^{r} (VOL4)	*Alteromonas* sp. EZ55	-(CO$_2$增加)	Pro99	[48]
		Sm^{r} (VOL4)	*Alteromonas* sp. EZ55	++	Pro99	[42]
		WT	*Pelagibacterales* sp. HTCC7211	N	ProMS	[47]
UH18301	HLII	Sm^{r}	*Alteromonas* sp. EZ55	++	Pro99	[42]
MIT1314	HLII	WT	*Thalassospira* sp. MIT1351	+	Pro99	[47]
			Roseobacter sp. MIT1352	+		
			Marinobacter sp. MIT1353	+		
NATL2A	LLI	Sm^{r} (VOL3)	*Alteromonas* sp. EZ55	++	Pro99	[42]
		WT	*Alteromonas macleodii* MIT1002	++	Pro99	[45]
		WT	*Alteromonas macleodii* MIT1002	+	Pro99	[49]
		WT	*Alteromonas macleodii* MIT1002	+	ProMM	[50]
MIT0801	LLI	WT	*Pelagibacterales* sp. HTCC7211	N	ProMS	[47]
MIT9313	LLIV	Sm^{r}	*Alteromonas* sp. EZ55	+	Pro99	[42]
		WT	Rhodobacterales*, Oceanospirillales*, OM60*, Alcanivoracacea*, Marinobacter*, Alteromonadales*	+, N ++, ++, +/N/-, +/-	ProMM	[43]
		WT	*Alteromonas macleodii* HOT1A3	N(低浓度菌) -(高浓度菌)	Pro99	[44]
		WT	*Alteromonas macleodii* MIT1002	+	Pro99	[45]
		WT	*Pelagibacterales* sp. HTCC7211	N	ProMS, ProMC	[47]
MIT1327	LLIV	WT	*Thalassospira* sp. MIT1351	++	Pro99	[47]
			Roseobacter sp. MIT1352	++		
			Marinobacter sp. MIT1353	++		

a) Sm^{r}, 链霉素的抗性突变(streptomycin-resistant mutant); WT, 野生型(wild type); b) *表示开阔大洋同一科的菌; c) +表示具有对原绿球藻生长的速率提高等促进作用, ++表示效果显著, -表示抑制作用, N表示无作用

其光系统受到氧化损伤，从而保护原绿球藻，并且对其生长具显著的促进作用[42]．对比实验显示，使用发生*katA*基因突变的费式弧菌(*Virbio fischer*)无法帮助原绿球藻MIT9215的生长[41]．此外，转录组学研究表明，原绿球藻-交替单胞菌共培养体系中，原绿球藻的DNA修复酶(DNA repair enzymes)等应激反应的蛋白家族基因的表达水平，相较于纯培养条件明显减低，这进一步证实交替单胞菌可以帮助原绿球藻减少氧化损伤[44,49]．

在寡营养自然海洋环境中，具有过氧化氢酶的异养细菌群落，能够将过氧化氢浓度限制在低于200 nmol/L的水平，可能给原绿球藻和聚球藻等蓝细菌提供了交叉保护作用[39,60~63]．有研究表明，如果无异养细菌存在，海洋中过氧化氢的浓度可能高达800 nmol/L; 如果异养细菌群落对过氧化氢的清除效率为目前水平的一半，即过氧化氢的浓度为400 nmol/L，则原绿球藻的分布范围将缩减为目前的11%[46]．除了蓝细菌外，其他类群的微生物也可能从这种交叉保护中获益，例如远洋杆菌(*Candidatus Pelagibacter ubique*, SAR11)、氨氧化古菌(ammonia-oxidizing archaea, AOA)和氨氧化细菌(ammonia-oxidizing archaea, AOB)[62]．综上，某些异养细菌扮演着“帮助者”角色，产生过氧化氢酶作为环境中的“公共物质”，以帮助“受益者”原绿球藻应对氧化压力[55]，使两者形成偏利共生相互作用关系．

3.2 异养细菌和原绿球藻之间资源供求关系

异养细菌除了可以降低环境中原绿球藻面对的氧化压力，还存在复杂的资源供求关系．研究发现，在原绿球藻纯株培养中添加交替单胞菌后，原绿球藻生长速率和恢复能力高于只添加具有还原性的丙酮酸钠[45,46]; 具有过氧化氢酶基因的SAR11 HTCC7211对原绿球藻的生长没有显著影响[47]．结合共培养体系的转录组信息推测，交替单胞菌保护原绿球藻的机制不只局限在去除氧化压力．通过比较基因组学和代谢模型研究发现，原绿球藻和异养细菌之间的资源供求关系，主要包括有机物的再循环和生长因子的释放两大方面(图1)．

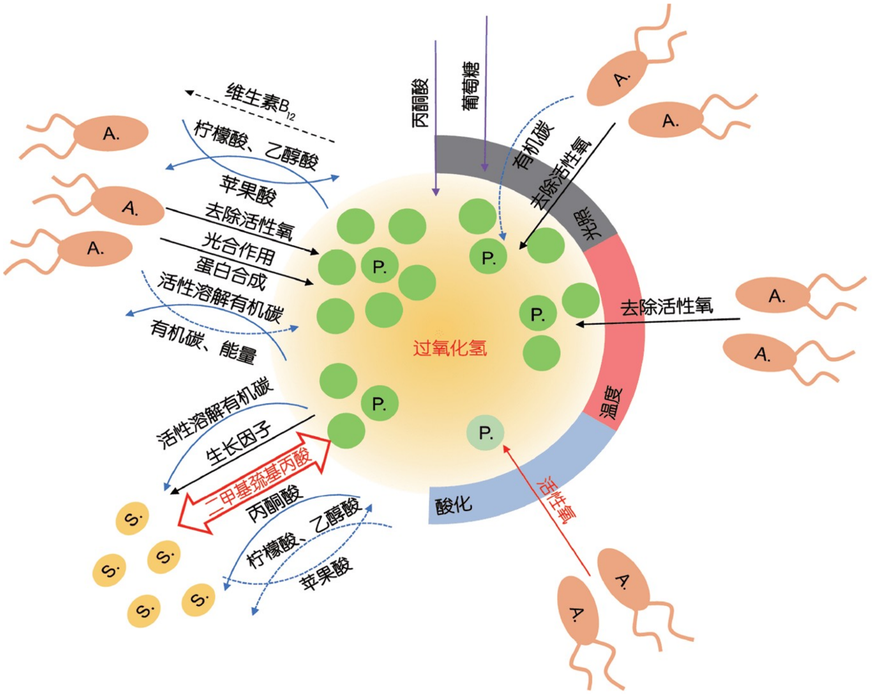

图 1 原绿球藻与交替单胞菌和SAR11的相互作用机制模式图．P.、A.、S.分别表示原绿球藻、交替单胞菌和SAR11．箭头表示两者的相互作用关系，黑色表示偏利关系，蓝色表示互利关系，红色表示不利影响; 紫色箭头表示添加丙酮酸和葡萄糖对原绿球藻的促进作用; 双箭头表示竞争关系; 虚线表示由基因组学分析获得的潜在关系

Figure 1 Schematic diagram of the interaction pattern between *Prochlorococcus* (P.) and *Alteromonas* (A.) or SAR11 (S.). Types of interactions are shown with different coloured arrows; the black arrows show commensalism, the blue shows mutualism and the red shows the negative influences. The purple arrow indicates the promoting effect of pyruvate and glucose on *Prochlorococcus*. The double arrow represents competition, and dashed lines imply that potential relationships are inferred from the genomic information

(ⅰ) 再循环有机物. 通过对原绿球藻的转运蛋白、生物合成途径和异养细菌中酶表达差异的研究, 揭示出柠檬酸(citrate)、乙醇酸(glycolate)和苹果酸(malate)等有机物可以在原绿球藻和异养细菌之间再循环[50,64]. 研究发现, 原绿球藻产生低分子量的羧酸(carboxylic acids)能被某些细菌群落利用[63,65], 而细菌*Oricola* sp.中也存在3种参与吸收聚球藻产生的溶解有机物(dissolved organic carbon matter, DOM)的转运体[66]. Becker等人[47]发现, 原绿球藻MIT9313可以产生甜菜碱(glycine betaine), 而该有机碳分子可能满足了SAR11对甘氨酸等特定营养物质的需求. 原绿球藻的代谢路径暗示, 细胞固碳后会向环境中释放丙酮酸(pyruvate)和乙醇酸等物质, 这些物质均为SAR11类群维持生存所必需的[64]. 相对地, SAR11会排出苹果酸盐, 可作为原绿球藻在夜间维持生存的潜在能量来源[47,67]. 此外, 在黑暗环境下, 交替单胞菌可能提供有机化合物, 作为原绿球藻的能量来源或必要的生物合成底物, 以提高其抵御黑暗和维持生存的能力, 甚至改变其新陈代谢和细胞节律[45,50,68~70].

(ⅱ) 释放生长因子. 通过原绿球藻和异养细菌的基因功能互补分析和共培养实验研究, 发现原绿球藻可能为异养细菌提供生长因子. 例如, 在自然环境中细菌通过与藻类的共生以获取维生素B_{12}[71], 表明维生素交换也是海洋微生物之间相互作用的过程之一. 海洋中某些微生物缺少维生素B_{12}, 而B_{12}作为辅助因子(co-factor)实现重要的生物学功能. 例如, 原绿球藻NATL2A基因组包含合成维生素B_{12}完整途径的相关基因, 而共生细菌麦氏交替单胞菌MIT1002具有依赖于维生素B_{12}的蛋氨酸酶合成(methionine synthetase)的基因(*metH*). 因此, 原绿球藻可能为交替单胞菌提供维生素B_{12}, 协助其蛋氨酸酶的合成, 从而促进其“助手”MIT1002的生长[44]. 现有的研究表明, 大部分蓝细菌中含有多种维生素合成的相关基因, 例如, 具有完整的B1、B7、B12维生素合成途径[72], 因此, 蓝细菌可能是寡营养海区中维生素B群的主要供应者. 此外, Becker等人[47]研究指出, 在共培养条件下, 原绿球藻使SAR11的生长速度比纯培养条件快15%~70%, 而原绿球藻的生长基本不受影响, 这表明共培养体系中的原绿球藻可能通过产生和释放生长因子促进了SAR11的生长, 形成了两者之间的偏利共生关系.

原绿球藻和异养细菌之间代谢产物的交换, 形成了两者互利共生和偏利共生的关系, 而长期保持这种相互作用关系可能促进微生物群落的协同进化, 最终将影响寡营养海区生态系统的群落组成和多样性. 微生物群落是一个复杂的系统, 而目前对“原绿球藻-异养细菌”关系的研究, 多数基于单藻和单菌简化的共培养体系, 因此, 仍存在较多不明确的地方, 如蓝细菌-异养细菌的群落动态变化及其协同进化的研究等. 随着基因组、转录组、蛋白质组和代谢组等多组学技术的发展和应用, 对原绿球藻和异养细菌之间共生关系也将有更加深入的认识.

4 原绿球藻-异养细菌关系的生态效应

蓝细菌是其所处海区的主要初级生产者, 所释放的溶解有机物是异养细菌群落生存所需的物质来源. 异养细菌利用这些有机物后, 转化成自身的生物量, 并将能量传递到更高的营养级. 因此, 蓝细菌和异养细菌以资源供求为主的协同作用, 驱动了海洋中的物质循环和能量流动. 另一方面, 蓝细菌利用异养细菌所提供的“公共物质”, 有效地补充了自身的能量需求, 提高竞争优势, 进而增加了环境适应能力. 例如, 原绿球藻受到海水的混合作用, 沉降到非透光区, 这时原绿球藻就需要异养细菌的协助来维持短暂的黑暗存活, 从而扩大其生存的时间和空间范围. 再例如, 在热带和亚热带寡营养开阔大洋的真光层中, SAR11与原绿球藻均为海洋表层的优势类群, 两者的生物总量在某些海区可占总细菌量的一半以上; 这两类微生物群落存在相同的生态位, 且均通过基因组流线型化来适应寡营养环境[39,47,73~75]. 如果原绿球藻和SAR11群落之间存在代谢潜能互补协同作用, 那么这两者之间的相互作用可能影响海洋生物地球化学循环. 总之, 蓝细菌和异养细菌在生态系统中各司其职, 构成互利共生和偏利共生的相互作用关系, 对维持海洋生态系统的稳定、多样性和生物地球化学循环起到了重要的作用.

随着CO_2排放量增加, 全球暖化和海洋酸化等问题日益严峻, 海洋蓝细菌在极端条件下将更依赖微生物群落. 以原绿球藻和异养细菌之间的相互作用为例, 两者之间互作关系因环境压力而改变, 最终可能影响原绿球藻的种群数量及其环境适应性. 例如, 极端温度和过氧化氢通过干扰原绿球藻光系统II(photosystem II, PSII)反应中心D1蛋白的合成及替换来影响光合作用. 因此, 在过氧化氢和极端温度双重压力下, 温度升高导致光系统II对过氧化氢的敏感性增强, 光合作用效率下降, 而交替单胞菌的存在扩大了原绿球藻的生长温度

范围[46,55]. 此外, 共培养实验的转录组数据显示, 在CO_2浓度升高时, 原绿球藻面对更大的氧化压力; 而在酸化条件下, 交替单胞菌表现出过氧化氢酶和过氧化物酶(peroxiredoxin)的基因表达量降低, 使得其在共培养环境中过氧化氢清除效率降低, 最终增加了原绿球藻的氧化压力[48]. 目前研究预测, 如果2100年大气CO_2浓度达到800 ppm(parts per million), 原绿球藻和交替单胞菌可能会从共生转向拮抗, 导致热带和亚热带海洋的初级生产力降低, 从而降低其对全球固碳及元素循环的贡献[48]. 因为蓝细菌有极大全球丰度和重要的生态学意义, 在全球气候变化的大背景下, "蓝细菌-异养细菌"的关系发生变化, 将直接影响寡营养海区的微生物群落结构, 进而影响海洋初级生产力和元素循环.

5 结论和展望

蓝细菌和异养细菌之间联系十分密切. 蓝细菌贡献了海洋近一半的海洋初级生产力, 是异养细菌群落的生存基础. 而异养细菌影响原绿球藻种群的规模及进化, 进而影响海洋生态系统、全球固碳和生物地球化学循环. 因此, 研究原绿球藻与异养细菌群落之间相互作用机制及其生态效应具有重要的科学意义. 未来对以原绿球藻为代表的蓝细菌和异养细菌相互作用研究的重点, 包括以下几个方面.

(1) 微生物群落之间的相互作用关系极为复杂, 利用已知菌藻关系, 促进对海洋异养细菌、蓝细菌及各自病毒的分离和培养. 目前, 病毒对菌藻关系的影响研究较为缺乏. 因此, 研究蓝细菌、异养细菌和自病毒之间相互作用关系, 有助于提高对整个海洋微生物群落结构和协同进化的认识, 建立起更完善的"蓝细菌-异养细菌-病毒"海洋生态学模型.

(2) 目前的研究大多基于简化的人工共培养体系, 而在自然海区中蓝细菌与许多重要异养细菌类群相互作用的研究则较少. 因此, 未来需要加强蓝细菌与海洋异养细菌群落的现场调查和研究, 通过(宏)基因组、(宏)转录组、(宏)蛋白质组和(宏)代谢组等多组学联用的技术和方法, 进一步揭示海洋中"蓝细菌-异养细菌"的相互作用机制.

(3) 在全球气候变化的背景下, 蓝细菌和异养细菌群落将面对多重环境压力胁迫. 但是, 目前对这种压力胁迫条件下两者相互作用变化的认识仍然较少. 通过设置不同环境因子, 结合现场调查, 探究气候变化条件下蓝细菌和异养细菌的相互作用关系的变化, 最终建立生态学模型, 进而预测未来海洋微生物群落的动态和对海洋生物地球化学循环的影响.

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Summary for “海洋蓝细菌与异养细菌相互作用: 以原绿球藻为例”

Interactions between marine cyanobacteria and heterotrophic bacteria: A case study of *Prochlorococcus*

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Cyanobacteria are the key primary producers in the global ocean and account for 25% of its net productivity. They play a vital role in the ocean by driving the circulation of matter and the flow of energy via the absorption of considerable amounts of carbon dioxide and the release of dissolved organic matter. This dissolved organic matter is converted into biomass by marine heterotrophs, which keeps the cycling of elements in oligotrophic waters at equilibrium. *Prochlorococcus,* an ecologically important genus of cyanobacteria, is the smallest and most abundant oxygenic phototroph in the global ocean. *Prochlorococcus* has highly streamlined genomes, which can provide a competitive advantage in the oligotrophic surface waters; however, the streamlined genomes also force *Prochlorococcus* to adapt to a narrow range of environmental parameters. Owing to these genomic characteristics, *Prochlorococcus* often establishes interactions with heterotrophic bacteria to survive in the challenging marine environment. Because cyanobacteria are abundant in the ocean, the cyanobacteria-heterotrophic bacteria relationship can significantly affect marine carbon sequestration and storage, which in turn has important ecological implications. Previous studies have reported on the relationships between *Prochlorococcus* and various heterotrophic bacteria. For example, *Prochlorococcus* establishes positive interactions with *Alteromonas* sp. that enhance its growth rate and environmental adaptability. In this review, we discuss the underlying mechanisms of the interaction patterns between *Prochlorococcus* and heterotrophic bacteria, as well as their genetic, physiological, and ecological significance. *Prochlorococcus* and heterotrophic bacteria tend to form mutualistic relationships in which they directly or indirectly exchange metabolites or recycle organic carbon through complementary excretion and crosstalk between pathways, such as citrate, glycolate, and malate pathways. *Prochlorococcus* and heterotrophic bacteria also commonly establish commensal relationships. For instance, heterotrophic bacteria protect *Prochlorococcus* by scavenging hydrogen peroxide, which *Prochlorococcus* is sensitive to. Although many heterotrophic bacteria cannot synthesize vitamin B_{12}, they require it as a cofactor for essential functions. Their genetic characteristics suggest that most cyanobacteria have the pathways for synthesizing vitamin B_{12}, but that they may provide vitamin B_{12} to heterotrophic bacteria to promote the growth of “helper” in the oligotrophic ocean. Therefore, the interactions between cyanobacteria and heterotrophic bacteria help maintain the stability and diversity of marine ecosystems. Global climate change may influence cyanobacteria-heterotrophic bacteria interactions, which could directly affect the structure and dynamics of the microbial community in the oligotrophic ocean, and therefore, primary productivity and element cycling in the ocean. Here, we suggest future research priorities and potential applications based on newfound knowledge of the subject. First, using the known “heterotrophic bacteria-cyanobacteria” relationships, the cultivation of marine heterotrophic bacteria, cyanobacteria and their viruses should be promoted to build a more comprehensive “cyanobacteria-heterotrophic bacteria-virus” ecological model for marine environments. Second, the interaction mechanisms between cyanobacteria and heterotrophic bacteria should be revealed by new biotechnologies, such as (meta) genomics, (meta) transcriptomics, (meta) proteomics, and (meta) metabolomics.Third, cyanobacteria-heterotrophic bacteria interactions should be studied against the backdrop of climate change using both *ex situ* (i.e., laboratory) and *in situ* investigations to predict changes in marine microbial community and its potential impact on biogeochemical cycling in oceans.

cyanobacteria, *Prochlorococcus*, heterotrophic bacteria, interaction, mutualism, commensalism

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