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学术信息与动态
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封面图说: 藏酋猴(*Macaca thibetana*)属猴科(Cercopithecidae)猕猴属(*Macaca*)又名四川短尾猴、大青猴,为我国特有灵长类之一,被列为国家二级保护野生动物;近年来,由于人类活动加剧,栖息环境恶化,导致藏酋猴种群数量和分布日趋缩小;本照片摄于四川卧龙国家级自然保护区(拍摄时间:2010年3月)。

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北冰洋微型浮游生物分布及其多样性

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摘要:近年来随着全球气候变化对北冰洋生态环境的影响日益显现, 北极微型浮游生物生态学研究得到了广泛的重视和实质性的进展。对北冰洋微型浮游生物的主要类群: 异养细菌、古菌、光合异养原核生物和微型真核生物的分布及其多样性研究进展做了概述, 并在此基础上展望了未来北冰洋微型浮游生物学研究。

关键词:北冰洋; 微型浮游生物; 异养细菌; 古菌; 丰度; 多样性

The abundance and diversity of nanoplankton in Arctic Ocean

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Abstract: As the most abundant and the most taxonomically and genetically diverse organisms in the marine ecosystem, nanoplankton predominate in the marine system concerning their bioactivity, biomass, and production. They play an important role in the carbon fixation process in the Arctic Ocean, and are an important component to regulate the biosphere. Furtherly, nanoplankton can be an important indicator of the changing environment, since the changes in the community, structure and biomass of nanoplankton reflect the changes in the pathways of nutrient and energy transferring in the food web and the changes in the biogeochemical cycle. Recently, ecology study of the Arctic nanoplankton has been paid more attention due to the increasing impacts of climate change on the Arctic marine ecosystems. Substantial progress has been achieved.

The Arctic heterotrophic bacteria were reported to resemble those in the seas of lower altitudes in their high abundance and biomass with seasonal successions. Particle-associated bacteria often show a higher specific metabolic activity than the free-living communities. So far, there are few reports on the proteorhodopsin (PR)-containing bacteria. High diversity has been reported for this group in the Chukchi Sea, which can be attributed to variable bacteria communities. A large number of aerobic anoxygenic phototrophic (AAP) bacteria have been found in the Chukchi Sea with a distinctly seasonal succession. The photosynthetic group in the Arctic Ocean was found to be mostly composed with the nanoplankton ($\leq 20\mu\text{m}$), described as a polar ecotype of the small prasinophyte *Micromonas*. The high correlation between the abundance of coccoid cyanobacteria and temperature results their low abundance at the high latitudes. There are only a few studies of *Synechococcus* in the coastal Arctic Ocean. The *Micromonas* is proved to be ubiquitous throughout the Arctic Ocean, especially at the chlorophyll-maximum layer, and may be a major contributor to the primary production in the Arctic Ocean. Until now little is known about the distribution of heterotrophic nanoflagellates in the Arctic Ocean, compared with phytoplankton and prokaryotes.

Many scientific questions, which deserve special attention, remain unsolved due to lack of continuous sampling and the complexity of the nanoplankton characteristics. Some of them have been highlighted here in the Arctic nanoplankton ecology. (1) More attention should be paid to the effect of the climate change on the nanoplankton community in the Arctic

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Ocean, considering its major and often dominant contribution to the total ecosystem. (2) Most of the investigations of nanoplankton community are focused on the Atlantic Arctic Ocean of the Arctic Ocean. It is necessary to investigate the community structure of the nanoplankton in the entire Arctic Ocean. (3) As a photoheterotrophic microbe, AAP bacteria may play a special role in the ecology in the Arctic Ocean. However, little is known about the distribution, abundance, and diversity of the AAP bacteria in Arctic Ocean. (4) Archaea seems to be of special significance in the Arctic waters with large population existing in the surface water. More work need to be done on their diversity and their functions in the energy flow.

Key Words: Arctic Ocean; nanoplankton; heterotrophic bacteria; archaea; abundance; diversity

20世纪70年代后期海洋微型浮游生物生态学研究迅猛发展,颗粒计数器的应用导致了粒径谱概念的产生。海水中微型浮游生物类群($\leq 20\mu\text{m}$)主要包括异养细菌、古菌、光合异养原核生物、单细胞真核藻类和原生动物。习惯上根据浮游生物的粒径谱的划分^[1],又可以将其分为微型浮游生物(nanoplankton, $2\text{--}20\mu\text{m}$)和微微型浮游生物(picoplankton, $<2\mu\text{m}$),但本文将这两类统称为微型浮游生物。

微型浮游生物在北冰洋生态系统的碳固定过程中扮演着至关重要的角色^[2],以往认为,北冰洋中主要的初级生产力是小型硅藻($20\text{--}200\mu\text{m}$);但是近年来越来越多的研究表明,微型浮游植物是北冰洋水体中生物量和生产力的重要贡献者^[3]。同时,北冰洋气候的快速变化使其生态系统正在发生深刻的变化,而作为高纬度浮游生态系统中最为脆弱环节之一的微型浮游生物可能更容易受到冲击。因此国内外在北冰洋海域针对微型浮游生物的丰度、时空分布特点以及多样性已经陆续展开研究并取得一些进展,但总体来说还是初步的,与其它温、热带海域的研究水平相距甚远。

1 浮游异养细菌和古菌

已有研究表明,北冰洋异养细菌与低纬度海域类似,同样具有很高的丰度和生物量,并存在明显季节演替。春季楚科奇海和加拿大海盆表面混合层浮游异养细菌从 $0.3\times 10^6\text{--}0.4\times 10^6$ 个/ mL 增加到藻华后的 0.9×10^6 个/ mL ^[4],然后在夏季末达到最高值^[5-7]。北冰洋各个海域的浮游异养细菌丰度分布总结于表1。总体上看,北冰洋细菌丰度分布有明显的季节波动,秋冬季比春夏季要低,白令海和楚科奇海夏季浮游异养细菌的丰度最高,可能与该地区的太平洋入流带来的丰富的营养盐、细菌活性高和高浓度的可溶性DOM^[4]有关。

表1 北冰洋各海域细菌丰度分布
Table 1 Bacteria abundance in the Arctic Ocean

地点 Location	丰度($\times 10^6$ 个/ mL) Abundance	深度/m Depth	时间 Time	实验方法 Methods	参考文献 References
楚科奇海北部	0.20—0.94	10	6—7月	EFM	[4]
白令海和楚科奇海	2.1—21	≤ 10	8—9月	TEM	[5]
波弗特海富兰克林湾	0.87—11	≤ 10	11—3月	EFM	[14]
	1.0—6.8	10—200	11—3月	EFM	[14]
	5.7—13.6	≤ 3	6—7月	EFM	[12]
波弗特海	1.9—18.1	≤ 3	9—11月	EFM	[11]
加拿大群岛西北通道	1.23—6.56	≤ 42	9月	EFM	[13]
喀拉海	2.3—4.7	1—2	8—9月	EFM	[15]
北冰洋中心区	1.9—6.7	$Z_{eu} \leq 40$	6—9月	EFM	[16]
	1.3—2.9	≤ 40	12/1—3月	EFM	[6]
	3—15 ^c	≤ 30	7—8月	EFM	[17]
巴伦支海	3.6 ± 3.0	$Z_{eu} \leq 50$	7—8月	FCM	[18]
斯瓦尔巴群岛王湾	6.0—22.3	≤ 200	7—8月	EFM	[19]

Z_{eu} : 真光层; EFM: 表面荧光显微术; FCM: 流式细胞术

浮游附着异养细菌是一类专性附着在颗粒物上的特殊类群,相对于非附着细菌而言,它们能够有着较高的特异性代谢活动^[8-9],所以是北极沿岸生态系统重要的功能组成部分。每年约有300万t颗粒有机碳通过沿岸淡水河注入北冰洋沿岸峡湾^[10],对其细菌群落组成和丰度影响非常明显^[11-12], β -变形杆菌的丰度随着采样位点离岸距离的增加而减少, α -变形杆菌、 γ -变形杆菌和噬纤维菌-屈挠杆菌-拟杆菌(CFB)3个类群的变化则与之相反^[11]。近岸的颗粒附着细菌在总细菌的活力中处于支配地位,其生产力最高占总细菌生产力的98%^[12]。噬纤维菌-拟杆菌(CF)类群(1.23×10^6 — 6.56×10^6 个/mL)由于其特殊的复杂颗粒代谢物降解能力,被认为是北冰洋表层海水,特别是沿岸水体浮游细菌的代表类群,占到异养浮游细菌总量的30%—41%^[4, 13]。

北冰洋表层非附着浮游异养细菌系统发生组成与其他海域的类似,主要由以下7大类群: α -、 γ -、 δ -、 ε -变形杆菌、CFB、疣微菌、绿色非硫菌^[20]。 α -变形杆菌中的SAR11类群广泛分布于表层海水中,但在盐跃层中非常少见^[20],而Yager^[4]等报道在爆发藻华的海域中SAR11类群消失,直到藻华结束后才出现。与之相反,CF类群在藻华期间数量会突然增多^[4]。另外与已知序列的相似性小于94%的玫瑰杆菌(RCA)类群^[20-21],与CF类群相似,在藻华期间的丰度也增加^[4]。Selje^[22]等在比较了各个典型海域的RCA类群后认为这是一类具有明显特殊地理分布的新类群,并且可以作为不同水团的示踪。北冰洋深海浮游细菌类群与表层不同,相对丰度较高的类群有SAR11(α -变形杆菌)、SAR406、SAR202(绿屈挠菌)和SAR324(δ -变形杆菌),而这些深海细菌群落分布与不同水团相耦合,可作为水团鉴定的一个重要指标^[23]。

分子生物学研究表明,颗粒附着浮游异养细菌和非附着浮游异养细菌在分类学上存在显著差异^[24-25]。北冰洋海域的颗粒附着浮游异养细菌包括梭杆菌/拟杆菌、 γ -变形杆菌^[26]、浮霉状菌^[27],和与一些浮游植物相关的玫瑰杆菌^[24]。水体中颗粒物的浓度和成分不仅仅影响颗粒附着细菌占总细菌生产力份额^[28],而且也是颗粒附着细菌和非附着细菌群落之间相似性与否的主要因素之一^[29]。Rieman和Winding^[30]认为颗粒物作为选择性进化动力的主要因子,使得细菌群落由颗粒微环境的内部向周围水体转变,从而造成颗粒附着与非附着浮游异养细菌在系统发育方面的明显差异。

最早在1992年通过分子生物学手段发现海洋浮游古菌在海洋生态系统中广泛存在并占据着重要的生态地位,并在海洋微微型浮游生物中占相当比例^[31]。北冰洋的加拿大海域阿蒙森湾古菌的丰度(0.34×10^3 — 20.6×10^3 个/mL)占原核生物总量的0.1%—6.7%,且在颗粒丰富层中丰度最高^[13]。Wells和Deming^[32]推断北冰洋加拿大海域的古菌可能来自于北冰洋沿岸河流,例如马更些(Mackenzie)河,但北冰洋其他海域的古菌分布及其是否也受到沿岸河流的影响至今尚未见报道。北冰洋水体中存在海洋古菌包括类群I泉古菌、类群II广古菌、类群III广古菌和类群IV广古菌^[33]。表层海水古菌的多样性低于深海,且大部分属于类群I泉古菌^[32-34],特别是在冬季,其约占总古菌16S核糖体RNA总量的20%^[32],但到了夏季末,海水表层中类群II广古菌所占的份额逐渐上升^[33]。古菌类群的这种季节性演替可能与其不同类群的生理活性有关,例如类群I泉古菌中的某些类群能够在有氧的情况下氧化水体中的氨^[35]来获得氮源,而类群II广古菌含有视紫质蛋白,这种跨膜蛋白可以利用光能驱动质子泵来获得能量^[36]。

2 光合异养原核生物

光合异养类群普遍存在于微生物中,是指既能通过光驱动获得能量又可以利用环境中的溶解性无机物质(DOM)来满足自身的碳需求^[37]的一大类群。光合异养微生物包括含视紫质蛋白(PR)浮游细菌、好氧不产氧光合异养细菌(AAPB),以及蓝细菌。

PR作为类光驱动的质子泵,利用质子梯度势合成ATP。这种新的不依赖叶绿素的光能合成ATP途径使得PR细菌对高纬地区环境持续的夏季极昼、冬季极夜以及季节性冰盖的消退而引起的盐度急剧变化有其特殊的适应性,但是北冰洋海域的PR细菌相关报道却寥寥无几。Cottrell和Kirchman^[38]比较分析了楚科奇海与其他海域包括南极海域的PR基因片段,表明楚科奇海含PR的基因组片段来源于浮游 α -变形杆菌的一个独立分支,其它海域同源性非常低。这些数据表明北冰洋的含视紫质蛋白细菌具有很高的多样性,且广泛分

布于不同的细菌类群中。另外 PR 细菌的丰度和多样性并没有受到北冰洋极昼与极夜交替出现的特殊生境以及海冰季节性冻融的影响^[38],说明影响其分布的因素不仅仅是光照,更可能是溶解性有机物(DOM)。总之,北冰洋 PR 细菌对生境的特异适应机制可能与其它温、热带水域有很大的不同。

AAPB 作为一类光合异养细菌,其丰度在北大西洋(从中央环流到格陵兰岛附近)随纬度的增加而减少^[39]。但在 2009 年,AAPB 首次被报道在楚科奇海大量存在,并存在明显的季节变化,冬季和夏季占总原核生物的比重在 5%—8% 之间^[38]。研究表明,高辐照度能抑制细菌叶绿素(BChla)的合成^[40],但是在持续光照的北冰洋夏季 AAPB 仍能产生细菌叶绿素,说明高纬度海洋环境中光对 AAPB 色素合成的影响与纯培养有很大不同^[38]。北冰洋 AAPB 的光反应中心复合物中的 *puf-M* 亚基的基因序列也和其他低纬度海域的序列存在较大的差异^[38],来自南极永冻湖^[41]中的 AAPB 序列与其相似度最高,但也仅有 83%。Yutin^[42]等根据 *puf-M* 亚基序列将 AAPB 分为 12 个(A—L)类群,北冰洋中的夏季和冬季的 AAPB 主要属于 E,F,I 类群^[38]。

海洋中的聚球藻和原绿球藻作为海洋蓝细菌最主要的两个代表性类群,最早发现于 20 世纪 70 年代。原绿球藻丰度较大,在除极地海域(丰度较低,通常为 10³ 个/mL)以外的其他海域,丰度通常为 10³—10⁵ 个/mL^[43]。原绿球藻的分布与温度具有强相关性^[44],在极区海域少有分布,目前为止原绿球藻出现的亚北极海域的界限分别在北纬 60°^[45] 和 61°^[46],丰度比温热带海域低至少一个数量级(10³ 个/mL)。原绿球藻在整个北冰洋的几乎不存在^[38, 47],这种全球地理分布差异的一方面可能是由于北冰洋低温生境造成的生态分化所引起的,另一方面可能是由于一定的地理隔离及水域的自然选择造成的种群分化也会引起这种差异。聚球藻广泛分布于海洋水体中,从热带海洋到极地海洋都有分布^[48],其丰度范围为 5×10²—1.5×10⁶ 个/mL^[49]。北冰洋聚球藻丰度总体比温带、热带海域的分布要低,在北冰洋的中心区域甚至没有聚球藻的存在^[50]。波弗特海近岸海域中聚球藻丰度(3.503×10^3 — 6.713×10^3 个/mL^[51])比其他北冰洋海区要高,如楚科奇海(4—80 个/mL)^[38]、格陵兰海(0 — 1.079×10^3 个/mL)^[50] 和加拿大海盆(0 — 6.0×10^2 个/mL)^[52]。关于北冰洋聚球藻多样性的研究还非常有限。在对聚球藻的 16S 核糖体基因测序研究发现,加拿大海盆中富含藻蓝蛋白的聚球藻与淡水常见种—华美微囊藻(*Microcystic elabens*)最为相似(98%—99%)^[47],而在近岸海域中的聚球藻则与温带的湖泊和近岸水体的淡水种相似,目前尚没有发现任何典型海洋种聚球藻和原绿球藻的存在^[51]。

3 真核浮游微型生物

浮游硅藻是北冰洋浮游生物的重要组成部分,种类繁多,至今为止已报道近 400 种(56 属)^[53],是北冰洋真核微型浮游生物中具有较长研究历史的一类。目前对浮游硅藻的研究主要依赖于光镜和电子显微镜技术,而其粒径范围主要集中于 5—50 μm。随着分子生物学的发展,Lovejoy 等^[54] 和 Hamilton 等^[55] 相继证实了北冰洋微型浮游硅藻的存在。绝大部分的浮游硅藻分布及丰度随着季节变化而变化^[56];它们在夏季楚科奇海的丰度相对较高,且以中心纲硅藻为主(角毛藻和海链藻居多)^[57],但是在北冰洋中心区域则非常少见^[6]。

北冰洋的微型浮游真核生物分布、丰度是随着表面荧光显微技术(EFM)和流式细胞术(FCM)的发展而被陆续报道。Beattie 和 Booth^[57] 报道在北冰洋海域中类似微单胞藻(*Micromonas*)的微型浮游植物(<2 μm)占总光合类群丰度的 93%,其中在加拿大海盆区域的丰度最高(4.96×10^6 个/mL),楚科奇海的丰度最低(1.3×10^3 — 1.51×10^3 个/mL);2—5 μm 粒径的微型浮游植物主要以鞭毛状的普氏棕囊藻(*Phaeocystis pouchetii*)为主,而其群体胶质囊状仅在楚科奇海中被发现;5—20 μm 粒径的类群主要是自养甲藻(autotrophic dinoflagellates),以裸甲藻(*Gymnodinium*)居多。在北冰洋中心区域,微型浮游植物主要是自养鞭毛藻(1.0×10^2 — 2.8×10^4 个/mL),其中包括微单胞藻(*Micromonas*)、鞭毛状普氏棕囊藻、自养甲藻和隐藻^[6]。Schloss 等人^[3] 利用流式细胞术报道了波弗特海微微型浮游植物的丰度为 1.38×10^4 个/mL,平均占总微型浮游植物的 71%。Trondsen 等^[58] 通过培养技术(稀释法)报道了微单胞藻在巴伦支海的丰度超过 10^4 个/mL,而与微单胞藻同属于青绿藻纲的 *Bathycoccus prasinos* 夏季末也大量存在^[59]。最近,微单胞藻被证实广泛大量存在于整个北冰洋海域,特别是在叶绿素的最大层,其生物量平均占到总叶绿素的 92%,所以有可能成为北冰洋初级生产力的主要贡献者^[52]。总体来说,微型浮游植物各粒径分布存在明显的空间差异,即与北冰洋其他海域不

同,楚科奇海和白令海峡的海域中,<2 μm 的微型浮游植物丰度低于 2—20 μm 的微型浮游植物(表 2),这可能与该海域的溶解性无机物(DOM),特别是无机氮丰富有关^[3]。另外,夏季的白令海峡和楚科奇海南部水体温度较高,营养盐丰富,属于变性的白令海上层水^[60],聚球藻作为外来物种^[61]对氨氮的吸收具有更强的竞争性^[38],对营养盐响应更迅速,因此可能取代与之在微食物环中具有相同生态位的微型浮游植物(<2 μm)而快速增长。

微型浮游原生动物广泛分布于世界海洋中,是微食物环中重要的类群,它包括异养和混养的鞭毛虫、异养甲藻和纤毛虫^[62]。近年来对北冰洋近岸和大洋研究表明,微型浮游原生动物在北冰洋的微食物环中发挥着与温、热带海域同样甚至更重要的作用^[6]。Paranjape^[63]研究表明,纤毛虫大量存在于加拿大海盆中,且对浮游植物有很高的摄食率。同样,在楚科奇海和白令海中异养鞭毛虫和纤毛虫具有很高的摄食率,是微食物环中能量循环流动的主要贡献者^[64]。在格陵兰岛近岸海域,夏季微型鞭毛虫和纤毛虫具有相对较高的生物量和活性,它们对浮游植物的摄食率等于甚至高于桡足类对浮游植物的摄食率^[65]。北冰洋中心区域也有微型异养原生动物大量存在,甚至在冬季其丰度达到了 4.9×10^2 个/mL,其中<5 μm 的异养鞭毛虫占整个微型异养鞭毛虫的 87%;但领鞭毛虫的丰度相对较低($0\text{--}1.5 \times 10^2$ 个/mL)^[6, 66]。

北冰洋微型浮游真核生物的多样性研究明显少于原核生物,且研究主要集中在≤2 μm 的微型浮游真核生物中。Lovejoy 等^[54]通过构建 18S 核糖体基因克隆文库,分别研究了波弗特海、加拿大海盆和格陵兰海微型真核浮游生物的多样性。随后在北冰洋的其他海域和近岸也逐步开展相关的多样性研究工作^[52, 67-69]。北冰洋微型真核浮游生物多样性非常高,几乎所有的纲在微型粒级中都有相应的代表。在克隆文库中获得的 42% 序列与已知的其他海域的微型浮游真核生物序列相似性较低^[54],其中一部分序列代表着一类新的进化类群(Picobiliphyte)^[68]。异养的微型放射虫和有孔虫在北冰洋特别是加拿大海盆具有非常高的多样性和丰度^[54]。在微型真核浮游生物中,研究最为深入的是青绿藻纲,无论是基因文库还是高效液相色谱(HPLC)的数据均显示青绿藻纲的 *Mantoniella*、微单胞藻 (*Micromonas*) 和 *Bathycoccus* 是在北冰洋最好的代表,其中 *Bathycoccus* 的序列与其他海域的序列共同形成一个独立的系统进化分枝;与 *Bathycoccus* 相反,微单胞藻的系统发育相当复杂,至少有 5 个独立的发育分枝^[70],而北冰洋的微单胞藻则区别于其他海域的类群独立形成一个分枝 E^[52]。Lovejoy 等^[52]认为微单胞藻 (*Micromonas*) 这种适冷、地理分布独特且丰度高的基因型有可能取代蓝细菌在北冰洋食物链底层的生态位,并在微食物环生态系统的能量流动和物质循环中起重要的作用。

表 2 北冰洋各海域微型浮游植物丰度分布

Table 2 Nanophytoplankton abundance in the Arctic Ocean

地点 Location	类群 Groups	丰度/(10 ³ 个/mL) Abundance	实验方法 Methods	参考文献 References
王湾斯瓦尔巴群岛	APF	0.046—35.2	EFM	[19]
	ANF	0.036—4.6		
北冰洋中心区域	APF	0.003—28	EFM	[6]
	APF	1.5—13.8	FCM	[3]
波弗特海	ANF	0.003—2.90		
	APF			
楚科奇海-波弗特海	APF	$5.37 \pm 1.83^*$	FCM	[38]
楚科奇海	APF	0.001—7.5	EFM	未发表
	ANF	0.025—11.85		

* : 平均值; APF: 微型浮游植物(<2 μm); ANF: 微型浮游植物(2—20 μm)

4 问题与建议

尽管对海洋生态系统中微型浮游生物和微食物环的重要性已经被广泛接受,但是相对于温热带海洋来说,目前对北冰洋及其周边海域的微型浮游生物还知之甚少。另外,由于受到采样连贯性和研究方法以及微型生物本身动态复杂性的制约,还有许多问题尚未解决。根据现有文献,作者认为在今后的调查和研究中以

下4个方面是重点。

(1) 北冰洋微型生物系统对气候快速变化的响应

北冰洋气候快速变化已经对该地区的植物和动物生态系统产生了深刻的影响,特别是物种分布、种群动态及其在食物网中的相互作用^[71]。尽管微型生物在整个生态系统生物量、生物多样性、营养物质循环和能流中起着巨大的甚至决定性的作用,但是,气候变化对北冰洋微型生物群落的影响方面的研究相对较少。一些北冰洋微型生物生态系统似乎在迅速地衰退,而另一些则转化为新的状态,这些包含了食物网和包括温室气体释放在内的生物地球化学通量的信息。考虑到北冰洋气候变暖的速率^[72]和它对大尺度微型生物过程的潜在影响^[73-74],北冰洋的微型生物群可以看作为全球变化的指示器。

(2) 微型浮游生物群落结构的研究

就目前的资料而言,对北冰洋微型浮游生物群落结构的调查主要集中在北大西洋扇区,太平洋扇区的部分只见零星报道,所以对整个北冰洋海域的跨时间跨区域的全面微型浮游生物群落结构的研究很有必要。研究领域不但需要包括对原核生物、原生动物和浮游植物生物量的信息,更需要利用分子生物学技术来确认哪些重要类群在特殊的水体环境(营养盐、POM、DOC等)的动态变化以及对这种环境的应对策略。总而言之,微型浮游生物多样性研究得出大量的关于“有什么”的信息,同时也需要知道微型浮游生物是“做什么”的信息。两种新方法旨在不用微生物培养将生物多样性和功能联系起来。一是用连接¹³C的生长基质孵育环境样品^[75];二是用溴脱氧尿苷连接DNA分析法^[76]。这些方法目前为止还没有应用到极地微生物的代谢功能研究中,但是它们为人们更好地了解复杂微型浮游生物多样性与其功能提供了依据。

(3) 北冰洋中典型功能细菌群-AAPB 的研究

尽管在25a前就已经发现AAPB的存在,其广泛分布在温、热带海域的真光层中。AAPB作为好氧异养细菌,依靠溶解有机质(DOM)作为有机碳的来源维持生长代谢,同时它作为具有光合作用功能的细菌,以光合作用作为异养代谢的能量补充。AAPB光合作用产生的ATP减少了其在吸收溶解有机质的过程中对呼吸代谢产生能量的需求,这样既减少了被异养呼吸代谢释放的二氧化碳的量,又增加了进入细胞的DOM的量。北冰洋是一个极端多变的生境,特殊的地理位置决定了其持续低温和极昼-极夜更替现象,极昼期间气温相对较高,光线充足,非常有利于光合作用;而在漫长的极夜期间由于可能无法进行光合作用,生物需依靠异养而生存,因而AAPB这种独特的生理特征和生态功能可能在北冰洋环境中占有其特殊的生态位。目前对AAPB的分布、丰度及其多样性等方面的研究都还处于起始阶段,仅2009年有一篇关于楚科奇海AAPB的相关报道。

(4) 北冰洋古菌在碳、氮循环中的作用

以往研究认为古菌主要大量存在于深海极端区域。近年来古菌被发现大量存在于北冰洋的表层,并且可能是表层浮游原核生物的重要类群之一,但是其具体的参与能流循环的作用还尚未可知。深海水体的环境与北冰洋表层在某种程度上类似,两者均经历长期的极夜和终年可利用无机营养盐的缺乏,所以北冰洋表层古菌的大量出现使人们充分了解海洋古菌的生态学功能成为可能。

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