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# 生态学报

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# 生态学报

(SHENGTAI XUEBAO)

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封面图说:黄河的宁夏段属于中国的半荒漠地区,这里气候干燥、降水极少(250mm 以下)、植被缺乏、物理风化强烈、风力作用强劲、其蒸发量超过降水量数十倍。人们从黄河中提水引水灌溉土地,就近形成了荒漠中的绿洲。有水就有生命,有水就有绿色。这种独特的条件形成了人与沙较量的生态关系——不是人逼沙退就是沙逼人退。

彩图提供:陈建伟教授 国家林业局 E-mail: cites.chenjw@163.com

何剑锋, 崔世开, 张芳, 何培民, 林凌. 北冰洋海域微食物环研究进展. 生态学报, 2011, 31(23): 7279-7286.

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## 北冰洋海域微食物环研究进展

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**摘要:** 海洋微食物环在海洋生态系统中起着重要作用。北冰洋因常年为海冰所覆盖, 对微食物环的研究较为有限。现有研究表明, 微食物环在北冰洋生态系统中的作用与海域和季节相关。近年来环境的快速变化、特别是夏季海冰覆盖面积的迅速减少, 会对微食物环的结构和功能产生重大影响, 已有研究显示其生态作用有望进一步提高。综合近年来已有的研究成果, 对北冰洋微食物环的主要类群: 原核生物、真核浮游植物、原生动物和浮游病毒等的基本生态特征进行了概述, 讨论了各类群间的相互关系, 并对未来的研究重点进行了展望。

**关键词:** 北冰洋; 微食物环; 研究进展

### Progress in research on the marine microbial loop in the Arctic Ocean

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**Abstract:** The microbial loop plays an important role in the marine ecosystem. Studies of the microbial loop in the Arctic Ocean are limited because of sea ice coverage. Investigations have shown that the role of the microbial loop in the arctic marine ecosystem varies depending on season and region. Rapid changes in the environment, especially the decrease in sea ice coverage in summer, have been found to lead to changes in the microbial loop structure. Some studies, showing an increase of bacterial abundance and a shift in phytoplankton size structure towards small microbial eukaryotes, suggest a potential enhancement of the role of the microbial loop in the Arctic Ocean. The study of the microbial loop is an important research component, essential to the understanding of the structure and function of the Arctic Ocean ecosystem.

Results show that, for example, the structure of the arctic microbial loop is simple compared to those in low latitude areas. Bacterial production is controlled by protozoan grazing in winter, but regulated by DOM concentrations in spring and there is divergence in the ecological role of viruses in the microbial loop. However, to date most studies focus on the shelf waters of the Canadian Arctic, Chukchi Sea, Beaufort Sea and Barents Sea, few examine the central Arctic Ocean. Little research has investigated seasonal variation in the microbial loop in the basins due to logistical limitations. Apart from *prochlorococcus*, almost all assemblages found in the marine microbial loop occur in the Arctic Ocean. Prokaryotes are rarely reported except for bacteria.

Based on these prior studies and on the environmental changes occurring in the Arctic Ocean, the following questions should be addressed in the near future: 1) What are the consequences of the grazing of protozoa on phytoplankton and bacteria? Why does the importance of the microbial loop vary and what is the main course of these variations? Are

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community structure, biomass, environmental factors and / or the recent environmental changes the main factors underlying these variations; 2) What is the importance of the different assemblages in the microbial loop, such as the viruses and Archaea, which are abundant in Arctic waters but for which few data are available; 3) What are the seasonal and inter-annual variations in microbial loop processes? How do microbes of Arctic microbial loop respond and adapt to environmental change, especially to sea-ice change?

**Key Words:** microbial loop; Arctic Ocean; research progress

海洋微食物环概念由 Azam 等人于 1983 年首次提出,即物质和能量可通过溶解有机物(DOM)→异养细菌→原生动物→桡足类的摄食关系传递<sup>[1]</sup>,是海洋经典食物链浮游植物→浮游动物的重要补充。经过近 30 a 的深入研究,其结构已得到很大程度的完善:海洋聚球藻、原绿球藻、微微型真核浮游植物、光合异养细菌和浮游病毒等成为其“新成员”,使得其中的物质传递和能量流动变得更为复杂<sup>[2]</sup>,而且其在海洋浮游生态系统中的重要生态地位也得到了进一步验证。我国科研人员的研究同样证实了海洋微食物环在我国近海海洋生态系统中的重要作用<sup>[3-5]</sup>。

常年海冰覆盖以及低温、极昼和极夜交替等极端环境,限制了对北冰洋微食物环结构及其生态作用的了解。已有研究表明:相对低纬度海域,北冰洋微食物环结构较简单,聚球藻仅在北冰洋近岸海域有发现<sup>[6]</sup>,缺少原绿球藻,其在生态系统中的重要性具有一定的季节和区域性<sup>[7-10]</sup>。由于北冰洋环境正在发生着诸如气温升高、夏季海冰覆盖率下降、陆地淡水输入增加等快速变化,会导致微藻细胞小型化和细菌丰度增加<sup>[11]</sup>,研究微食物环可以作为了解北冰洋生态系统结构和功能及其变化趋势的一个有益补充。本文主要对北冰洋已有相关研究结果进行概述和分析,旨在为北极环境快速变化背景下海洋生态系统研究提供参考。

## 1 北冰洋微食物环各类群基本特征

### 1.1 原核生物

异养浮游细菌是海洋 DOM 库最重要消费者,同时也是海洋中重要的生产者。北冰洋表层海水浮游细菌平均丰度为  $10^8$ — $10^9$  个/L,其最高值约为最低值的 5—25 倍<sup>[12]</sup>。在加拿大北极海域,春季浮游细菌主要利用浮游植物新生产的 DOM,而冬季期间则能利用更为复杂的有机物<sup>[13]</sup>。细菌生长是否受温度的支配并没有取得一致的研究结果<sup>[14-16]</sup>。

目前对除异养细菌外的其它类群多有发现,但了解非常有限,需要进一步深入研究。研究表明,北冰洋至少存在一类泉古菌和两类广古菌,而表层海水中古菌的丰度要高于低纬度海域<sup>[17-18]</sup>;好氧不产氧光合细菌(AAPB)和含视紫质(PR)细菌的丰度在冬季明显下降,但相对于严格异养的细菌仍有竞争优势<sup>[19]</sup>。聚球藻(*Synchococcus*)和原绿球藻(*Prochlorococcus*)广泛分布于低纬海域,但在北冰洋尚未有原绿球藻的报道。对波弗特海和楚科奇海的调查发现,夏、冬季聚球藻平均丰度没有明显变化,分别为  $8 \times 10^4$  个/L 和  $4 \times 10^4$  个/L,显示聚球藻在冬季可能利用 DOM 而生存<sup>[19]</sup>。

### 1.2 真核浮游植物

真核浮游植物生产的颗粒有机物(POM)部分转化为活性 DOM<sup>[20]</sup>,后者可被异养浮游细菌所吸收,并且其中的小粒径浮游植物(0.2—20  $\mu\text{m}$ )可直接被原生动物摄食而进入微食环。北冰洋常见的真核浮游植物类群包括:硅藻、甲藻、青绿藻、金藻、定鞭藻和绿藻<sup>[21]</sup>。北冰洋近岸海域,春、夏季水华期间小型浮游植物(>20  $\mu\text{m}$ )占主导地位<sup>[22-23]</sup>,但在其它季节和海域,微型和微微型浮游植物(<20  $\mu\text{m}$ )明显占优。在春季巴伦支海北部冰缘区,微型浮游植物(<10  $\mu\text{m}$ )对初级生产力的贡献率平均为 46%,且藻华前、后分别高达 82% 和 87%<sup>[24]</sup>。北冰洋中心区浮游植物水华期间,小细胞浮游植物和未被鉴定的微型鞭毛藻处于优势地位<sup>[25]</sup>。并且研究表明,北冰洋中微胞藻(*micromonas*)和葡萄藻(*Bathycoccus*)属微微型青绿藻取代了中、低纬度聚球藻和原绿球藻的生态位而大量存在,并能在冬季黑暗环境中生存而成为来年旺发的“种子”源<sup>[26-27]</sup>。在波弗特

海和楚科奇海,冬季和夏季的微微型真核生物丰度分别为  $0.02 \times 10^6$  个/L 和  $5.4 \times 10^6$  个/L<sup>[19]</sup>。微型和微微型浮游植物是北冰洋、特别是海盆区值得重点关注的类群。

### 1.3 原生动物

原生动物是连接微食物环和经典食物链的关键中间环节。北冰洋原生动物主要类群有:微型异养和混合营养鞭毛虫、异养腰鞭毛虫、领鞭毛虫和纤毛虫,其中腰鞭毛虫和纤毛虫是北冰洋常见的食植者<sup>[8]</sup>,而异养鞭毛虫和领鞭毛虫则主要摄食细菌<sup>[28]</sup>。在楚科奇海,原生动物主要为纤毛虫和腰鞭毛虫,现存量可高达  $60 \mu\text{g C/L}$ <sup>[29]</sup>;在北冰洋中心海域,原生动物的平均生物量为  $120\text{—}1120 \text{ mg C/m}^2$ ,而在粒径  $<20 \mu\text{m}$  的原生动物中,微型异养鞭毛虫、腰鞭毛虫、领鞭毛虫的贡献率分别为 80%、16% 和 4%<sup>[28]</sup>。微微型鞭毛虫 ( $1.5\text{—}2 \mu\text{m}$ ) 丰度在  $100\text{—}1600$  个/mL 之间,占微型原生动物 ( $<20 \mu\text{m}$ ) 总丰度的 52%<sup>[8]</sup>。Lovejoy 等人报道了北冰洋微微型异养真核生物 ( $<3 \mu\text{m}$ ) 群落生物多样性很高<sup>[30]</sup>。

### 1.4 浮游病毒

浮游病毒是海洋中丰度最高的一类生物类群,它们通过感染导致藻类和异养微型生物死亡,释放细胞中的 DOM,从而改变海洋微型生物群落结构、推动生物地球化学循环。与除异养细菌外的其它原核生物类群类似,对北冰洋浮游病毒的研究很有限。已有研究表明,北冰洋病毒具有高丰度、强活性和高多样性等特点<sup>[31-33]</sup>。波弗特海春、夏季浮游病毒丰度的变化范围为  $0.13 \times 10^6\text{—}26 \times 10^6$  个/mL,病毒丰度与叶绿素 a 含量、细菌丰度和海水温度呈正相关,而与海水的深度和盐度呈负相关<sup>[34]</sup>。

## 2 北冰洋微食环各类群间的关系

### 2.1 浮游植物和异养原核生物

异养细菌的丰度、生物量与浮游植物的现存量呈明显相关性。在楚科奇海和加拿大海盆,春季表层海水的细菌丰度从  $0.3 \times 10^9\text{—}0.4 \times 10^9$  个/L 上升至藻华期间的  $0.9 \times 10^9$  个/L<sup>[32]</sup>,夏末时达到最大<sup>[33]</sup>。北冰洋中心海域藻华期间的细菌生物量明显增加,且无长的滞后期<sup>[8]</sup>。但在相同的叶绿素 a 浓度情况下,高纬海域的细菌丰度要低于低纬<sup>[35]</sup>。另外,低纬海域细菌能利用 50% 的初级生产力<sup>[36]</sup>,而北冰洋细菌生产力和初级生产力的比值相对较低<sup>[37]</sup>,这种弱相互作用最初被归结于北冰洋低温对细菌生长的限制<sup>[38]</sup>。但最近研究认为,北冰洋细菌的低生长率是受到了低温和活性 DOM 的交互影响<sup>[14]</sup>,并得到了实验室和北冰洋现场实验的验证<sup>[39-40]</sup>。细菌的丰度和生物量还受原生动物摄食和病毒致死的调控<sup>[41]</sup>,此外细菌的生长还取决于细菌和浮游植物竞争营养盐时,影响细菌“竞争力”的一切条件<sup>[42-43]</sup>。叶绿素 a 浓度小于  $2 \mu\text{g/L}$  时,细菌对硝酸盐和铵盐的吸收量可占其被吸收总量的 44%—78%,而当以硅藻为优势类群的藻华爆发时,因消耗大量营养盐会限制细菌生长,细菌丰度并没有随着 DOM 浓度的上升而明显增加<sup>[42,44]</sup>。随着北冰洋温度、光强和海水垂直稳定性的变化,会造成真光层营养盐变化,从而改变细菌和浮游植物的竞争关系<sup>[45]</sup>。

### 2.2 原核生物和原生动物

表 1 显示了北冰洋各海域原生动物对细菌的摄食情况。在一年的大部分时间,原生动物的摄食可消耗全部的细菌生产力,是细菌的主要控制因子;但在藻华期间,细菌的生长受到营养盐的限制,致使原生动物不喜好摄食细菌,摄食率几乎为零<sup>[12]</sup>。在北极富兰克林湾,相对春季而言,冬季细菌受到的摄食压力更大,细菌生产几乎完全被原生动物消耗(每天原生动物摄食量平均占细菌生产的比例为  $(152 \pm 159)\%$ )<sup>[46]</sup>。所以,目前认为北冰洋冬季的细菌生产力主要由原生动物控制,而春季细菌生产力主要受 DOM 调控。

关于北冰洋细菌和原生动物间的营养级结构研究较少。普遍认为粒径  $<5 \mu\text{m}$  的微型异养鞭毛虫 (heterotrophic nanoflagellates, HNF)、包括动基体目鞭毛虫和领鞭毛虫,与细菌的丰度相关性较大,是细菌的主要摄食者<sup>[50]</sup>。不同粒径的微型异养鞭毛虫对细菌的影响各异,细菌和 HNF ( $<5 \mu\text{m}$ ) 生物量具有重要的相关性,暗示粒径较小的 HNF 是细菌的主要摄食者,而较大的 HNF ( $>5 \mu\text{m}$ ) 主要摄食藻类<sup>[39]</sup>。不过对北极斯瓦尔巴群岛王湾海域的研究表明,藻华期间,异养腰鞭毛虫和纤毛虫可能也是细菌的主要摄食者<sup>[51]</sup>。

表 1 北冰洋原生动物对细菌摄食压力的时空变化

Table 1 The spatial and seasonal variations of protozoan grazing to the bacteria in the Arctic Ocean

地点 Locations	时间 Seasons	细菌生 长率/d <sup>-1</sup> Bacterial growth rates	原生动物 摄食率/d <sup>-1</sup> protozoan grazing rates	生长与被 摄食比/% Growth rate/ Grazing rate	实验方法 Methods	参考文献 References
利索鲁特湾 <sup>(1)</sup> Agile Root Bay	3—4 月	0.08—0.62	0.14—0.55	88—187	稀释法	[12]
	5 月末	0.1	—	—	FLB *	[47]
	5—6 月	0.22—0.85	不明显	—	稀释法	[12]
	8 月	0.62—1.02	0.76—0.88	86—93	稀释法	[12]
	9 月	0.38—1.0	不明显	—	稀释法	[12]
富兰克林湾 <sup>(2)</sup> Flanklin Bay	2—3 月	—	不明显	—	稀释法	[31]
	3—4 月	-0.5—0.5	0.05—0.53	0—300	FLB	[46]
	3—5 月	-0.5—0.5	0.65—1.21	5—57	FLB	[46]
波弗特海 Beaufort Sea	3—5 月	—	—	57	FLB	[48]
弗朗海峡 Fram Strait	6—7 月	—	—	2.9—65.9	FLB	[49]
北冰洋中心海域 central Arctic Ocean	7—9 月	0.03—0.09	0.002—0.009	4—22	FLB	[28]

\* : 荧光标记细菌法; (1): 加拿大北极海域, (2): 北冰洋西部; —: 缺乏数据

### 2.3 原生动物和浮游植物

迄今对北冰洋植食性原生动物在微食物网中的重要性的认识并不一致。1994 年夏季对北冰洋中心海域的研究显示, 粒径 < 5 μm 的异养鞭毛虫、腰鞭毛虫和纤毛虫均可摄食浮游植物<sup>[28]</sup>; 丰度较高的鞭毛虫 (2 μm) 和领鞭毛虫也能摄食微胞藻<sup>[8]</sup>, 而这些类群通常被认为主要摄食细菌<sup>[52]</sup>。因此, 北冰洋所有粒径级的原生动物都有可能是浮游植物的重要摄食者。早期的研究表明, 1992 年格陵兰岛近岸水华期间, 原生动物对浮游植物的摄食相当、甚至超过了桡足类的摄食压力<sup>[53]</sup>, 巴伦支海夏初原生动物的摄食可消耗浮游植物生产量的 64%—97%<sup>[54]</sup>。但近期的研究表明, 在北冰洋楚科奇海、波弗特海及加拿大海盆, 春、夏季微型原生动物 (< 20 μm) 平均只消耗了浮游植物生产力的 1/5<sup>[55]</sup>; 2007 年夏季格陵兰海棕囊藻水华期间, 微型浮游动物的摄食率仅占浮游植物总量的 8%<sup>[56]</sup>。低摄食率可能源于群落的衰亡、棕囊藻对摄食的影响或实验方法本身<sup>[56]</sup>, 或因食植性原生动物的生长受低温制约<sup>[57]</sup>。原生动物生态作用在早期和近期结论的差异是源于不同海域、还是近年来北冰洋环境变化导致的, 有待于进一步分析研究。

### 2.4 浮游病毒与其它类群

有关浮游病毒在微食物环中的作用研究非常有限, 结论不一, 应是今后研究的重点之一。在北冰洋部分海域, 病毒对细菌的致死量会超过摄食者对细菌的摄食量<sup>[31, 58]</sup>, Wells 等人的研究发现, 北极富兰克林湾冬季, >60% 的细菌生产力由病毒裂解而被消耗, 消耗量是细菌被摄食量的 2 倍<sup>[31]</sup>。白令海近岸海域病毒消耗细菌生产力的 9%—36%<sup>[59]</sup>。因大面积侵染宿主, 病毒可能成为北冰洋微生物多样性和生物进化的“推进器”<sup>[60]</sup>。但在楚科奇海, 病毒对细菌的致死量只占其总死亡量的 2%—10%<sup>[58]</sup>; 在北冰洋中心海域, 病毒平均只消耗细菌生产力的 4%<sup>[61]</sup>。

对波弗特海的调查发现, 病毒的一亚类群 V1 和真核浮游植物密切相关, 其主要侵染浮游植物<sup>[34]</sup>。而有关病毒和原生动物的相互关系尚还未见报道, 相关研究需要进一步加强。

### 2.5 微食物环物质与能量传递

通常认为微食环有两个起点, 一是以被细菌利用的 DOM 为起点, 另一个是以被原生动物摄食的光合营养生物 (微微型和微型浮游植物、聚球藻、原绿球藻) 为起点。北冰洋与细菌等粒径的光合营养生物丰度较低, 所以大多数海域微食物环是由细菌来主导的。异养细菌依赖于 DOC 的生产, 有研究表明, 北冰洋浮游植物净生产力的 30%—50% 是通过 DOC 的形式释放到海水中<sup>[62]</sup>, 北冰洋西部海域活性 DOC 的浓度和初级生产力大小密切相关<sup>[63]</sup>。与浮游植物相比, 异养生物对 DOC 生产的贡献大小尚未有定论, 在夏季巴伦支海的

研究表明,59%的 DOC 来自原生动物的<sup>[64]</sup>。虽然北冰洋部分海域春、夏季细菌与浮游植物表现出弱的相互作用,细菌只利用较少的初级生产力,但 DOC 得以储存或输出到寡营养海域,为冬季的细菌生产提供有机碳,从而维持北冰洋生态系统的正常运行<sup>[65]</sup>。

过去认为,微食物环含有数个营养级,大量有机物质在微食物环内传递过程中被生物呼吸所消耗,有机物传递效率较低,但北冰洋部分海域微食物环在物质和能量传递中显示了重要作用。对巴伦支海浮游生态系统的模式研究表明:春季原生动物摄食等量的浮游植物和细菌,而夏季原生动物消耗的细菌生物量是浮游植物的 4 倍,桡足类 80%—90% 的食物来自于原生动物,桡足类幼体能量来源的 60% 是通过微食环传递的<sup>[64]</sup>。再者,尽管大型浮游植物和冰藻是后生动物关键的食物来源,但在浮游植物现存量较低,小粒径浮游植物细胞占优势地位时,原生动物作为后生动物的食物也发挥同样的作用<sup>[66]</sup>。对北极斯瓦尔巴群岛近岸王湾海域的调查表明,各季节微食物环均起着重要作用,尽管大部分时期,微食物环均发挥着提供“再生生产力”作用,但在春季藻花期间,由于后生动物不能完全消耗浮游植物生物量,其发挥着提供“新生产力”作用<sup>[10]</sup>。

### 3 微食物环与环境变化

微食物环各类群对环境变化十分敏感,北冰洋微食物环对其环境变化具有重要的“指示”作用<sup>[67]</sup>;而气候环境变化将会改变微食物环结构、细胞粒径大小和代谢过程,从而影响微食物环的能流与效率。部分太平洋种会随着太平洋入流水分布至距白令海峡较远的北冰洋陆架海域<sup>[68]</sup>,而部分淡水种会随着淡水输入而进入北冰洋近岸海域<sup>[69]</sup>,从而改变该海域微食物环的结构与功能;同时,北冰洋温度的升高将加速微生物的碳通量和呼吸作用<sup>[70]</sup>。Li 等人对波弗特海连续监测数据的分析显示,北冰洋融冰加速和河流淡水输入的增加降低了表层海水的盐度、增强了水体稳定性,导致了细菌丰度的增加和浮游植物向微藻型青绿藻等小粒径真核细胞转化<sup>[11]</sup>;光照的增强会导致初级生产和微食物环活性的增加,但稳定跃层的存在和对流的减弱会造成对高营养级生物的支持并不会因此而增加<sup>[33]</sup>。鉴于近年来北冰洋环境的快速变化,微食物环对环境变化的响应及其对其生态地位的影响,是今后微食物环研究的重点。

### 4 小结与展望

北冰洋特殊的环境条件,限制了对北冰洋微食物环及其生态作用的了解。现有研究主要集中在加拿大北极海域、楚科奇和波弗特海、巴伦支海等近岸海域,对除异养细菌外的其它原生生物少有报道,并且在病毒生态作用、原生动物摄食压力等问题上结论不一<sup>[19,31,58,61]</sup>。除近岸海域外,微食物环的季节变化尚无法开展<sup>[10,19]</sup>。同时,近年来北冰洋海冰在春季的提前消退以及夏季海冰覆盖率的快速下降,对微食物环及其生态地位的影响尚无相关研究。根据已有研究结果,结合北冰洋生态系统的潜在变化,今后北冰洋微食物环研究可重点考虑以下几个方面内容:(1) 原生动物的摄食压力,包括对浮游植物和浮游细菌的摄食压力,重点阐明现有结论不一致的原因,是不同海域浮游生物群落结构的差异、海域环境的差异、还是近年来环境变化造成的?(2) 除最基础类群外其它类群生态特性的了解,从类群的重要性考虑,重点研究古菌和病毒的类群特征和生态作用;(3) 微食物环的季节和年际变化,重点解决微食物环重要类群对北冰洋环境变化、特别是海冰变化的响应和适应性问题,探讨其生态地位的潜在变化。

北冰洋现有环境变化导致了细菌丰度的增加和微藻粒径的小型化<sup>[11]</sup>,会导致微食物环作用的增强。而现有的一些国际计划,如北极临界点计划(ATP/Arctic Tipping Point)、北冰洋生物多样性计划(ArcOD/Arctic Ocean Diversity)等均包含了对微食物环研究。北冰洋生物学监测断面计划(DBO/Distributed Biological Observatory)等国际合作项目的实施<sup>[71]</sup>,为研究微食物环季节和年际变化提供了契机。可以预见,随着北冰洋海冰对考察阻碍的减少和研究投入的增加,对北冰洋微食物环结构和生态作用以及对环境变化响应的了解会更加深入。

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