混合营养型浮游生物生态学研究进展

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摘要:目前已知的混合营养型浮游生物集中在甲藻门、黄藻门、裸藻门、隐藻门、金藻门、绿藻门和原生动物界的纤毛虫门,根据营养特性可分为 3 个生理类群。混合营养型浮游生物分布广泛,从淡水湖泊到开阔海洋,从赤道到两极,无论是寡营养还是富营养环境都发现有它们的存在。混合营养型浮游生物可进行光合营养和吞噬营养,营养策略的采用受控于环境因子。在低光照、寡营养等特殊环境中,混养生物具有重要生态地位。它可以成为主要摄食细菌者,占总生物量和生产力的大部分,比光合营养的浮游植物或吞噬营养的浮游动物更具有竞争优势。20 世纪 90 年代以来对有害赤潮的研究,加深了对混合营养型浮游生物的认识。相信通过实验和模型的结合以及新技术的应用,将进一步推动混合营养型浮游生物生态学研究的深入。

关键词:混合营养;浮游生物;生态学;营养策略

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A review of ecological research on mixotrophic plankton

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Abstract: Mixotrophic plankton, which include the forms in Pyrrophyta, Xanthophyta, Euglenophyta, Cryptophyta, Chrysophyta, Chlorophyta and the Ciliophora of Protozoa, can be divided into three physiological types according to their nutrient strategy. The forms of Type I can grow well no matter which trophy they will take. The forms of Type II, i. e. heterotrophic microalgae, are generally phototrophic and sometime phagotrophic. The forms of Type III, i. e. autotrophic protozoa, are commonly phagotrophic and sometime phototrophic. Mixotrophic plankton are found to be ubiquitous, occurring in eutrophic, mesotrophic and oligotrophic waters, from freshwater lakes to the open ocean, from equator to the poles.

Phototrophy and phagotrophy are the nutritional strategy of mixotrophs which depends highly on a variety of environmental factors. When environmental factors are not suitable and the population density of pure heterotrophs is low, mixotrophs can be the important consumers of bacteria and become an important component of the microbial food web. It constitutes a significant fraction of the total biomass or production. Due to the competitive advantage of the nutritional strategy, mixotrophic plankton would outcompete the phototrophs or phagotrophs and play a important role in the nutritional dynamics of microbial food web.

However, in 1930's, the phenomenon of mixotrophy was regarded as "isolated and aberrant" cases and was ignored in the food web research. In the late 1980's feeding rates of mixotrophic plankton were also difficult to determine in the laboratory.

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Being lack of adequate quantitative techenique, the role of mixotrophic plankton in the dynamics of food web was poorly understood. Since 1990's some new techniques were applied to some mixotrophic species to answer the questions concerning the dynamics of food web including physiological processes and interaction. At the same time, harmful Algae Bloom (HAB) was the focus of global concern. Since a lot of HAB was caused by mixotrophic plankton, much attention has been devoted to their research works. The research works would be pushed forward through the technique improvement of experiment and modeling.

Key words: mixotrophy; plankton; ecology; nutritional strategy

混合营养型浮游生物是指既能进行光合作用合成有机物，又能通过摄食细菌或其它微小生物来满足其生长和繁殖所需的浮游生物类群[1~3]，它们属于各种单细胞藻类和原生动物的纤毛虫[4~5]。混合营养型浮游生物一方面可通过渗透吸收与微型浮游植物和细菌竞争水中溶解的营养物质，同时又可直接摄食微型浮游植物和细菌，这使得微食物网(microbial food web)各类群间的营养关系更为复杂。由于它既是生产者又是消费者，与异养原生动物相比，它能更有效地在微食物环与后生动物之间进行营养衔接，在食物网营养动力学中发挥着重要作用[1,6]。同时，不少混合营养型浮游生物可形成有害赤潮[7~9]。本文就混合营养型浮游生物的研究概况，分布及生物量，生态类群，对环境的适应等进行综述，并对混合营养型浮游生物研究存在的问题进行分析，对加强混合营养型浮游生物的研究提出几点思考与建议。

1 混合营养型浮游生物的研究概况

早在20世纪30年代，Hofeneder等人发现有的单细胞藻类能进行摄食或具食物泡[10]，后来人们又发现有的纤毛虫能保留摄入的叶绿素进行光合作用[11]。由于当时判断单细胞藻存在摄食现象主要是通过对其食物泡的观察，受实验手段的限制，观察到具色素浮游生物的摄食现象非常有限，因此，这种混养现象被认为是“孤立的、异常的”特例，没能引起足够的重视。

直到20世纪80年代后期，随着越来越多的混合营养型浮游生物被发现，科学家们意识到混合营养型浮游生物普遍存在并可能对食物网动力学产生重大影响[2~3,12]，应用放射性碳标记细菌、荧光标记细菌(FLB)、荧光标记藻类(FLA)和荧光标记微球(FLMs)等各种标记技术，对混合营养微型鞭毛藻的摄食进行研究[13~14]。

20世纪90年代对有害赤潮(Harmful Algae Bloom, HAB)研究的深入，推动了混合营养型浮游生物研究的发展。研究表明，很多有害赤潮是由混合营养型浮游生物引起，认为混合营养由于能充分利用额外的能源而使浮游生物大量繁殖，从而促进赤潮的形成和维持[15]。甚至在无机营养盐限制的环境中，混合营养型浮游生物也能形成赤潮，如在挪威西南沿海分别由多鳞金色藻 *Chrysochromulina polylepi* 和小土栖藻 *Prymnesium parvu* 引起的两次HAB中，可溶性磷甚至均低于检测下限，这两种混养鞭毛藻能通过摄食细菌获得磷而大量繁殖的[16]。

20世纪90年代后期以来，对混合营养型浮游生物与环境因子的相互关系的研究逐步深入，包括光强度、光照时间、营养盐浓度、食物(细菌和微型藻类等)浓度，甚至盐度和酸碱度对混合营养型浮游生物摄食、光合作用、生长生殖、毒性等的影响，以及混合营养型浮游生物对微食物网营养动力学的影响[17~22]，使得对混合营养型浮游生物生态特征有了较为深入的了解。

2 分布及生物量

混合营养型浮游生物分布广泛，从淡水湖泊到开阔海洋，从赤道到两极，无论是寡营养还是富营养环境都发现有它们的踪迹[2,23]。在寡营养等环境中，混养生物可以构成总生物量和生产力的大部分。例如，在太平洋赤道海域，混养生物对浮游生物的贡献率高达27%～56%[24]；在美国宾夕法尼亚洲东北部的一个寡营养湖泊，夏、秋季混合营养型纤毛虫丰度达751～33,600 cells/L，占纤毛虫总生物量的88%，在8月和10月，混合营养型纤毛虫对细菌的摄食率分别为30.6和17.4个/ciliate·h，分别是异养纤毛虫摄食率的近2倍和6倍[25]；在大西洋西北部的Georges Bank和Sargasso Sea，混合营养型鞭毛藻分别占微型鞭毛藻总量的38%和30%[26]。在智利Pirehueico湖，秋季混合营养型纤毛虫占纤毛虫总生物量的67%～69%，占自养生物总生物量的25%[27]；在阿尔卑斯山上的一个寡营养湖，混合营养型鞭毛藻分别占浮游植物总数量和总生物量的94%和79%[28]。可见，混合营养型浮游生物在食物网营养动力学中起着重要作用。

3 功能类群

目前已发现和记录的混合营养种类有62种(见表1)，主要属于甲藻门(Pyrrophyta)、黄藻门(Xanthophyta)、裸藻门(Euglenophyta)、隐藻门(Cryptophyta)、金藻门(Chrysophyta)、绿藻门(Chlorophyta)和原生动物界(Protozoa)的纤毛虫门(Ciliophora)。

依据主要营养途径，混合营养型浮游生物可分为“自由营养”、“主光合营养”和“主吞噬营养”三大类群[23]。其中，“自由营养”类群为“理想”的混合营养型浮游生物，无论是利用光合营养、吞噬营养还是混合营养，均能很好生长，如亚球形脆甲藻Fragilidium subglobosum。但这类混合营养型浮游生物的种类很少，主要可能与同时需要维持自养和异养细胞器，相对与纯自

养或异养需要消耗更多的能量,在竞争中不占优势[57]。

表 1　混合营养型浮游生物主要种类

Table 1　Mainly species of mixotrophic plankton

种类 Species	文献 Reference	种类 Species	文献 Reference
Akashiwo sanguinea =*Gymnodinium sanguineum* 红裸甲藻	[29] [30]	*Gymnodinium ordinatum*,横列裸甲藻	[28]
Alexandrium tamarense 塔玛亚历山大藻	[16]	*Gyrodinium galatheanum* =*karlodinium micrum* 米氏裸甲藻	[38]
Amphidinium poecilochroum 杂色前沟藻	[31]	*Gyrodinium instriatum* 环节环沟藻	[39]
Amphidinium cryophilum =*Gymnodinium cryophilum* 嗜寒裸甲藻	[32]	*Gyrodinium uncatenum* 非连环沟藻	[40]
Chlamydomonas sp. 衣藻	[28]	*Heterocapsa triquetra* 三角异囊藻	[41]
Chromulina sp. 金光藻	[28]	*Heterosigma akashiwo* 赤潮异弯藻	[16]
Chrysochromulina brevifilum 短丝金色藻	[33]	*Noctiluca scintillans* 夜光藻	[42]
Chrysochromulina leadbeateri 列氏金色藻	[17]	*Ochromonas* sp. 棕鞭藻	[43]
Chrysochromulina polylepis 多鳞金色藻	[33]	*Ochromonas minima* 细小棕鞭藻	[16]
Chrysochromulina sp. 金色藻	[18]	*Peridinium* sp. 多甲藻	[28]
Chrysochromulina ericina 刺猬金色藻	[19]	*Pfiesteria piscicida* 鱼毒费氏甲藻	[7]
Ceratium cornutum 具角角藻	[9]	*Poterioochromonas malhamensis* 默汉波得鞭金藻	[44]
Ceratium declinatum f. normale 偏斜角藻	[9]	*Prorocentrum minimum* 微型原甲藻	[45]
Ceratium furca 叉状角藻	[9]	*Prymnesium parvum* 小土栖藻	[16]
Ceratium fusus 纺锤角藻	[9]	*Prymnesium patelliferum* 土栖藻	[17]
Ceratium hirundinella 飞燕角藻	[9]	*Pyramimonas gelidicola* 塔胞藻	[46]
Ceratium longipes 弯顶角藻	[9]	*Rhodomonas* sp. 红胞藻	[28]
Ceratium lunula 新月角藻	[9]	*Uroglena Americana* 美洲辐尾藻	[47]
Ceratium teres 圆柱角藻	[9]	*Laboea strobila* 纤毛虫	[48]
Ceratium tripos 三角角藻	[9]	*Mesodinium rubrum* 红色中缢虫	[49]
Cryptomonas sp. 隐藻	[28]	*Ophrydium naumanni* 睫纤虫	[50]
Dinobryon cylindricum 圆筒锥囊藻	[20]	*Paramecium bursaria* 绿草履虫	[51]
Dinobryon balticum 波罗的海锥囊藻	[21]	*Pelagostrombidium mirabile* 奇异海游虫	[52]
Dinobryon sertularia 密集锥囊藻	[28]	*Perispira ovum* 卵形周纤虫	[53]
Dinophysis acuinata 渐尖鳍藻	[34]	*Stentor araucanus* 南美喇叭虫	[27]
Dinophysis norvegica 挪威鳍藻	[34]	*Stentor amethystinus* 紫晶喇叭虫	[27]
Fragilidium subglobosum 亚球形脆甲藻	[22]	*Strombidium capitatum* 头急游虫	[54]
Fragilidium mexicanum 墨西哥脆甲藻	[35]	*Strombidium* sp. 急游虫	[55]
Gymnodinium brevve 短裸甲藻	[36]	*Strombidium viride* 绿急游虫	[44]
Gymnodinium gracilentum 小裸甲藻	[31]	*Strombidium oculatum* 虹急游虫	[56]
Gymnodinium acidotum 尖形裸甲藻	[37]	*Strombidium stylifer* 楔尾急游虫	[56]

"主光合营养"类群,即异养微藻。以光合营养作为主要营养途径,在某些条件下辅以吞噬营养。根据吞噬营养的调节机制,该类群又可分为 3 个亚群。亚群 A,吞噬营养受无机营养盐浓度的调节,在无机营养盐受限制时进行摄食;亚群 B,吞噬营养受光的调节,当光成为限制因子时,混合营养型浮游生物通过摄食来获取碳源;亚群 C,吞噬营养的目的只是为了获得生长所需的微量有机物,因而不受溶解无机营养盐浓度和光照条件变化的影响。这类混合营养型浮游生物数量最多。

"主吞噬营养"类群,即自养原生动物。以吞噬营养作为主要营养途径,能辅以光合营养。根据生物体内光合质体的来源,该类群可分 2 个亚群。亚群 A,生物具有内源性质体;亚群 B:利用内共生藻类或保留被摄食藻类的质体进行光合作用。

4　调控因子

4.1　光

光是"主光合营养"型混合营养型浮游生物营养策略最重要的调节因子之一。Holen 发现默汉波得鞭金藻(*Poterioochromonas malhamensis*)从光环境转换到暗环境时,细胞内叶绿素 a 含量由 140 fg/cell 下降到 10 fg/cell,但对细菌的摄食率则由 3.2 个/flagellate·h 上升到 9.4 个/flagellate·h[44]。当光强度降至 50 μE/(m·s)时,亚球形脆甲藻叶绿素 a 含量下降了 53%,但由于异养作用,其生长率反而上升[22]。米氏裸甲藻 *Gyrodinium galatheanum*(=*Karlodinium miceum*)主要进行光合作用,但同时能摄食微藻并保留微藻的色素,在完全黑暗的条件下,仅靠摄食它无法存活,在有光的条件下,米氏裸甲藻靠混合营养比靠光合营养其生长率要高出 2～3 倍[58]。

某些混养生物如上面提到的米氏裸甲藻和红色中缢虫(*Mesodinium rubrum*)在光成为限制因子的环境中,能够靠吞噬来补充营养[3,13,49,58];而某些原生动物在光线充足而食物短缺时,能通过光合作用来获取其生长和繁殖所需的营养物质[11]。显然光影响着混合营养型浮游生物营养方式的选择。

4.2 营养盐

在营养盐受限的环境中,多数混合营养型浮游生物能够吸收溶解有机物或通过摄食来补充碳源和能源;而在有机物耗尽时,通过光合作用获取能量物质[59]。营养盐限制对摄食的影响,目前尚未能统一认识。有研究认为营养限制刺激混合营养型浮游生物的摄食活动[38,41],但有的则认为对摄食活动的影响有限[60]。Li 等人在研究米氏裸甲藻摄食与营养盐关系时发现,限制溶解无机磷或无机氮,或远离理想生长的值 P∶N=1∶10 时,均可刺激其摄食,但限制无机磷比限制无机氮更有效。人为添加氮或同时添加磷和氮,则会抑制其摄食[38]。赤潮生物混养叉状角藻(*Ceratium furca*)在营养盐缺乏时,通过摄食每天平均可得其体碳的 4.6%、其体氮的 6.5%和其体磷的 4.0%,最大可分别达到 36%、51%和 32%,这种在无机营养缺乏的条件下具摄取有机营养的能力,使叉状角藻比完全靠光合作用的浮游生物更具竞争优势[61]。

4.3 其它因素

除光和营养盐之外,被捕食者丰度和种类组成、水体酸碱度等也能影响混合营养型浮游生物的营养策略[19,31,44]。如 Hansen 在研究被捕食者丰度对亚球形脆甲藻营养策略的影响时发现,在被捕食者丰度小时,采用光合营养或吞噬营养对的生长并不影响,当被捕食者丰度大时,亚球形脆甲藻就选择吞噬营养策略,这是因为维持和运行光合作用器官所消耗的能量要比捕食和消化吸收过程所消耗的能量大得多,此时采用光合营养要消耗固定碳源的 46%用于呼吸作用,而吞噬营养策略只需要消耗固定碳源的 28%用于呼吸作用[22];Jakobsen 等人的研究表明,被捕食者的种类组成对混合营养型浮游生物的摄食也有影响,加入各种微藻对小裸甲藻(*Gymnodinium gracilentum*)的摄食影响不大,当加入一种隐藻时,小裸甲藻的摄食率立即上升[31]。Smalley 等人对叉状角藻的研究表明,细胞内 C∶N∶P 比率处于最佳值时,细胞生长良好,当 C∶N∶P 比率背离最佳值时,会诱导摄食[9]。因而,凡是影响细胞内 C∶N∶P 比率形成的生理过程或环境因素,都有可能对混合营养型浮游生物的摄食产生影响。

5 营养策略

现有研究表明,在没有生长限制的条件下,混合营养型浮游生物相对于完全利用光合营养自养生物和完全利用吞噬营养的异养生物并没有竞争优势,这是由于混合营养型浮游生物要消耗部分能量以维持光合作用的细胞器、同化无机营养的酶系统以及吞噬器官,因此,其最大生长率比完全利用光合营养自养生物和完全利用吞噬营养的异养生物的都要低[57]。

但在光、营养盐及食物成为限制因子时,混合营养型浮游生物相对于完全利用光合营养自养生物及完全利用吞噬营养的异养生物具有很大的竞争优势。当溶解性无机营养盐成为限制因子时,混合营养型浮游生物能通过摄食来补充营养而得以生存,如微型原甲藻(*Prorodentrum minimum*)[45]和米氏裸甲藻[38];有些混合营养型浮游生物还可通过摄食获得某些限制生长的微量有机物,如大洋中溶解铁浓度极低,往往成为光合浮游生物的限制因子,赤道太平洋的棕鞭藻(*Ochromonas*)通过摄食细菌,一方面获取铁(同化率达 30%)以维持光合作用,另一方面获取碳源(可占自身碳的 40%)以减少光合作用的压力,减少铁的消耗[62]。当光成为限制因子时,某些混合营养型浮游生物却能通过摄食来补充碳源,如短丝金色藻(*Chrysochromulina brevifilum*)[33]和嗜寒裸甲藻 *Amphidinium cryophilum*(=*Gymnodinium cryophilum*)[32]等,甚至能够吞噬其竞争对手[63]。当食物成为限制因子时,很多混合营养型浮游生物能够进行光合营养,包括很多保留有被捕食者质体的藻类,如:鱼毒费氏甲藻(*Pfiesteria piscicida*)[7],及纤毛虫类,如:纤毛虫 *Laboea strobila*[48]、红色中缢虫[49]和头急游虫(*Strombidium capitatum*)[54]。

正是由于混合营养型浮游生物具有双重营养策略,使得混合营养型浮游生物更能适应复杂多变的浮游生活环境,在环境不利的条件下,如寡营养的水体或光限制的环境中,能够更有效的生存与繁殖乃至于形成赤潮[16]。

6 混合营养型浮游生物生态研究的建议

(1)加强对混合营养型浮游生物实验生态研究 由于很多混合营养型浮游生物可摄食其它浮游动物和浮游植物,与桡足类等后生动物竞争同一食物来源,打破了经典食物链[浮游植物(硅藻)→浮游动物(桡足类)→鱼类]能量传递模式,能量不再是简单地从初级生产者传向消费者,加上很多混合营养型浮游生物不易被桡足类等后生动物捕食,这样由于混合营养型浮游生物的摄食活动而使营养传递的效率明显下降;同时混合营养型浮游生物还可通过渗透吸收与微型浮游植物和细菌竞争溶解性营养物质,使得食物网的营养动力学变得更加复杂。尽管目前有很多实验可以推测混合营养型浮游生物通过改变物质循环和能量流动来影响食物网动力学,但至今仍然没有充分的数据来定量说明这种营养动力学的变化。建立模型是阐明混合营养型浮游生物在食物网动力学中作用的较好方法,而目前仅有少数食物网模型中包括了混合营养型浮游生物[23,64],并且由于引用参数的限制使建立的模型留有遗憾。

由于不同混合营养型浮游生物的摄食行为和摄食目的存在很大的差异,并且混合营养型浮游生物进行光合作用和摄食的能力差别很大,通过实验生态学研究了解影响混合营养型浮游生物与其他浮游生物类群间的营养关系以及混合营养浮游摄食

的调节机制,有助于建立较为理想的营养动力学模型。对调节机制的研究,研究对象除目前研究相对较多的无机营养浓度,光辐射强度及其时间变化等之外,应特别重视如微量元素和溶解有机碳浓度的变化对混合营养型浮游生物的调节作用。

(2)探索高纬地区混合营养型浮游生物生态作用 相对于中、低纬度地区,对高纬地区混合营养型浮游生物的研究非常有限,并且对海洋混合营养型浮游生物尚未有相关的研究报道。考虑到高纬地区自然环境极昼与极夜的转化,极昼期间非常有利于光合作用,而在极夜期间则无法进行光合作用,浮游生物需依靠异养而生存,因而混合营养可能是一种较为有利的营养策略,在维持物种延续上具有重要意义。对南极湖泊的有限研究已表明,在南、北极持续低温、低光和营养限制的环境,混合营养是浮游生物能够生存的重要营养策略[65]。如南极泰勒谷的 Fryxell 湖和 Hoare 湖,隐藻类只依靠光合作用无法生存,必须依靠摄食细菌来补充营养[66],南极 Vestfold 山脉的一些盐湖,浮游生物优势种绿藻类(Pyramimonas)和在盐湖中广泛分布的红色中缢虫也是采用混合营养[65];塔胞藻 *Pyramimonas gelidicola* 每天所需的碳源 30%来自摄食细菌[46]。

开展对高纬海域混合营养型浮游生物生态特性的研究,有助于对海洋微食物网较为全面的了解。

(3)新技术将推动混合营养型浮游生物研究的发展 荧光标记法的应用,极大地推动了对混合营养型浮游生物的摄食研究。由于目前常用的荧光标记物都是人工合成或经灭活处理,与自然活体性状有较大的差别。而部分混合营养型浮游生物不摄食缺乏活性的食物,荧光标记法往往会造成摄食率和混合营养型浮游生物多样性的低估。Jacqueline 等人[66]采用基因工程技术克隆水母 *Aequorea victoria* 体内的一种自发荧光蛋白质(green fluorescent protein, GFP)基因 *gfp gene*,并在大肠杆菌 *Escherichia coli* 中表达,用这种大肠杆菌做为标记物,克服了标记物不活动的缺陷,得出的实验结果较符合自然状况。由于 *gfp gene* 在原核生物和真核生物中均能表达,并且没有毒性[67],因此,在研究微型浮游生物的摄食方面具有广阔的应用前景。

同时,由于混养鞭毛藻存在许多不同的摄食机制,传统研究原生动物摄食行为的方法已不适用于对混养鞭毛藻的摄食研究,故对混合营养鞭毛藻的研究大部分还停留在定性分析[31,33,60,62]。新技术的发展,预期将推动这方面的研究。

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