J. Lake Sci.(湖泊科学),2018,**30**(4):881-896
DOI 10.18307/2018.0402

刚毛藻(*Cladophora*)生态学研究进展*

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摘　要:刚毛藻(*Cladophora*)在全球海洋及淡水中普遍存在,它为沿岸带微生物和无脊椎动物提供了生产力和微生存空间. 随着水体富营养化程度的加剧,刚毛藻在沿岸带出现暴发现象,造成严重的环境污染,同时刚毛藻的存在也影响了湖泊生态修复过程中沉水植被的恢复. 本文从刚毛藻形态与种类鉴定、生长与分布影响因素、生长周期与种群动态、种间关系及生物去除等研究前沿方面进行综述,并对相关研究领域进行展望,为进一步研究刚毛藻生态生理特征、有效控制和去除提供科学依据.

关键词:刚毛藻;富营养化;生态;水动力;营养盐;竞争;摄食;种间关系

A review on the ecology of *Cladophora*

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Abstract: *Cladophora* is found in a variety of marine and freshwaters worldwide and provides productivity and micro habitat for numerous microorganisms and invertebrates in littoral zone. This filamentous green alga can reach nuisance levels as a result of eutrophication and also impedes the recovery of submerged vegetation in the lake ecological restoration. In this review, recent literatures concerning its morphological and taxonomic identification, abundance and distribution, species interactions, and biological control are summarized. Meanwhile, we discussed the future research directions in related field, which will provide some scientific information for further studies on the ecophysiology, effective controls and removal of *Cladophora*.

Keywords: *Cladophora*; eutrophication; ecology; hydrodynamics; nutrients; competition; grazing; species interactions

刚毛藻是一种典型的底栖附着藻类,广泛分布于全球淡水或沿海浅水水域,在周丛藻类群落中占据优势[1-5],其藻丝或漂浮于水柱中或松散的附着于软基质上,使沿岸带的功能性表面积增加,为所支持的附植生物和底栖动物提供重要的微生境[6]. 刚毛藻的生存环境跨幅较大,从超贫营养化到富营养化水体[7],从寒冷北极到温带海洋[3]. 潮间带刚毛藻某些种类能耐受 5‰~30‰的盐度环境[8],另有部分种类能在 100‰盐湖中存活[9].

刚毛藻的异常增殖是水体富营养化的直观表象,这种现象在淡水和海洋浅水区普遍存在[5,10-13]. 刚毛藻水华会堵塞渔网和工业取水管道,造成一定的经济损失;分解腐烂后的藻丝漂浮于水面,影响景观且产生难闻气味. 北美五大湖沿岸带刚毛藻生物量曾上升到令人厌恶的程度[14],造成严重的环境污染. 迄今为止,国内鲜有关于刚毛藻引起自然水体环境问题的报道. Shahrizim 等[15]研究显示,一旦刚毛藻附着在稳定基质上,能在该点位上持续生长多年. 虽然刚毛藻与沉水植物具有相同生态位,但刚毛藻能更快适应环境,与其竞争光照、营养盐及生长空间等资源[6,16-17],因此在国内水生态修复过程中,重建和恢复沉水植物阶段,刚毛藻的大量滋生在一定程度上阻碍了湖泊修复进程. 本文系统综述了刚毛藻生理生态学特征,重点阐述了刚毛藻生长的影响因素以及与其他生物之间的相互关系,旨在了解刚毛藻在湖泊生长中的利弊,为探寻控制刚毛藻异常增殖的方法提供理论依据.

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* 国家自然科学基金项目(41671096)和中国科学院南京地理与湖泊研究所自主部署项目(NIGLAS2016QY04)联合资助. 2017-08-03 收稿; 2017-10-11 收修改稿. 刘霞(1983~),女,博士,助理研究员;E-mail: xliu@niglas.ac.cn.

1 刚毛藻形态与种类

刚毛藻属绿藻门,细胞多呈核管状,植物体为分枝或不分枝丝状体. 细胞内含许多盘状色素体,或紧密排列在细胞侧壁,或扩散到细胞中央,或连成一个网状结构. 一些色素体内含一个双透镜形的蛋白核. 刚毛藻植物体的生长靠顶端或居间细胞分裂. 分枝侧面生长或生活于母细胞顶端. 植物体的固着是通过丝状体基细胞或基部区域的细胞所形成的假根;或通过由基细胞形成的简单的盘状固着器;有些种类缺乏固着器官,仅幼时营着生,长成后漂浮.

刚毛藻的种属鉴定一直存在着难题,因此分类并不完善. 正如荷兰藻类学家 van den Hoek[3]所描述的:几乎所有的刚毛藻分类系统都有一个定量标准(如依据顶端细胞的直径大小),每一个定量标准却又存在着种属间重复而分级的多变量表达. 除此之外,依据株龄和周围环境差异,刚毛藻会发生生态变异[1,3,18]. Van den Hoek[3]对 13 株海洋刚毛藻进行室内培养,仅有 5 株保存了原有形态,其他植株均发生了形态变异. 加勒比海刚毛藻(*Cladophora jongiorum* van den Hoek)与蒙氏刚毛藻(*C. montagneana* Kütz.)在野外环境中有极大的形态相似性,而经过一段时间的室内培养之后,形态差异显著. 通过室内培养也可区分散束刚毛藻(*C. vagabunda* van den Hoek)和浅滩刚毛藻(*C. vadorum* (Aresch.) Kütz.)[3]. 因刚毛藻属生态变异幅度较大,致使其分类学遗留问题较多,例如黑孢藻科(Pithophoraceae)黑孢藻属(*Pithophora*)、湖球藻属(*Aegagropila*)和阿诺藻属(*Arnoldiella*)的一些种类早期均被归于刚毛藻属,仅刚毛藻属下的种名就有近 400 个[19]. 拟湖球藻(*Aegagropilopsis*)和湖球藻亲缘关系较近,也隶属于湖球藻分枝黑孢藻科,拟湖球藻属常着生于淡水蚌类或螺丝壳上. 与阿诺藻属相比,拟湖球藻假根系统弱化,多形成长的次生假根. 由于早期对拟湖球藻属缺乏详细了解,仅依据形态特征而将其一些种类归于刚毛藻属或湖球藻属. 据记载,我国淡水刚毛藻目的名录为 6 属 31 种 11 变种 2 变型,其中新属 1 个、新种 7 个、新变种 3 个、新变型 2 个[19].

随着细胞分子生物学技术的完善,该技术也逐步应用于藻类鉴定研究中. 采用脱氧核糖核酸(DNA)-DNA 杂交技术显示细丝刚毛藻(*C. sericea* (Huds.) Kütz.)与岩生刚毛藻(*C. rupestris* (L.) Kütz.)[20],以及苍白刚毛藻(*C. albida* (Huds.) Kütz.)与岩生刚毛藻的种间差异显著[21]. Verma[22]以染色体的数量差异区分了 *C. crystalina* (Roth.) Kütz.与中型刚毛藻(*C. intermedia* Fosl.)和绉刚毛藻(*C. crispata*(Roth.) Kütz.)等藻种. 将藻类提取物中可溶性蛋白的抗体用于交感实验中,结果显示不同刚毛藻种间的免疫距离差异显著,由此验证了它们是不同种的集合体[23]. 相较于 rDNA ITS、叶绿素 *rbcL* 基因等序列,核糖体小亚基(SSU)和核糖体大亚基(LSU)在进化上更为稳定和保守,是刚毛藻目多数藻类及其相关类群系统发育研究采用的主要基因组片段序列,也是近期学者研究刚毛藻分类常用的技术手段[24-27].

2 影响刚毛藻生长与分布的环境因素

2.1 着生基质

刚毛藻可着生在泥沙、木桩、石头及沉水植物等各类型基质上. 淡水刚毛藻还可附着在蚌类[28]和鱼类[5]等生物体上,它在稻田里也时有出现[29],同时也可作为其他生物的附着植物[30]. 海洋刚毛藻能聚集成无定形团状,漂浮于盐沼池塘表面或附着于沉积物表面[3]. 另有刚毛藻以软基质为核心聚集形成球体[31-33],生长到一定程度后藻丝与固体基质分离漂浮于水面[34-35]. 着生在海洋叠层石上刚毛藻与蓝藻群落可拦截高镁方解石沉积物,使其成为附着基质的一部分[36].

着生基质的特性包括基质倾斜度、表面粗糙度、基质化学成分和稳定性及其相关水动力因素等. Konno[37]认为固体基质的倾斜度是影响刚毛藻生长的重要因素,倾斜度超过 120°时,乌氏刚毛藻(*C. wrightiana* Harvey)在海洋藻类群落中的优势地位下降,底部刚毛藻因光遮蔽效应(self-shading)生长受到抑制. 刚毛藻对附着基质的选择有一定的倾向性,Castenholz[38]没有发现夏季 Falls 湖泊中玻片基质上附着的脆弱刚毛藻(*C. fracta* (Muller ex Vahl) Kütz.),而 Tees 河流中玻璃载体上却能附着团集刚毛藻(*C. glomerata* Kütz.)[39]. Bellis 等[40]发现实验室内刚毛藻游动孢子可附着在玻璃载体上. 关于钙质岩石基质对刚毛藻生长的影响,其实验结果也不尽相同. 刚毛藻的生长需要矿物质,故此类型的岩石可能更易于被刚毛藻附着,但在 Kialing 河流中发现,团集刚毛藻游动孢子避开了富含钙质的岩石基质[41],选择了其他附着基质,然而

Thurman 等[42]发现美国达拉斯市溪流中含石灰岩的天然基质附着了大量团集刚毛藻．

2.2 水动力条件

水动力条件的变化会导致水体物质输移变化，从而影响藻类生长，Whitton[5]综述了流速大小和污水浓度对藻类生长的影响，结果显示在最大污水浓度条件下，团集刚毛藻生长偏好于流速为 20 和 80 cm/s 的水环境，对流速 5 cm/s 不响应，如果降低污水浓度，团集刚毛藻仅在流速 80 cm/s 下增殖，对流速 20 cm/s 不响应．水流流速对刚毛藻光合作用效率会产生直接影响，当流速增加至 2.1 cm/s，藻类光合效率增加[43]；当流速增加至 8 cm/s 时，光合效率成倍增加；但当流速超过 8 cm/s 时，光合效率下降[44]．研究显示随着流速增加，水体中藻类可利用物质的传输效率增加，藻类光合效率和生产力均明显增加[45-47]．例如水体流动增加促进了刚毛藻对 CO_2 碳源的利用，降低了其对 HCO_3^- 碳源的利用[48]．高流速状态下，刚毛藻藻丝间紧密接触，可利用物质进出刚毛藻藻丝的浓度降低，同时光遮蔽效应导致光合效率降低，以上称为“精简效应”（streamlining effect）．同理，当附着基质上的刚毛藻生物量显著增加后，藻丝间变得紧密，也会产生相似效应[43]．

水动力在一定程度上影响刚毛藻的附着率、附着丰度及生物量．Dodds[49]发现岩石大小与刚毛藻丰度之间呈不显著的正相关关系，大型岩石较稳固，其上表面抗紊流作用强，不易因强洪水冲击而翻转，易于刚毛藻着生，因此大型岩石上刚毛藻丰度高于小型岩石．刚毛藻附着成功的首要条件是耐受湖泊、河流底栖生境及其潮间带的水流剪应力，生长过程中藻丝的耗损也与其耐受水动力干扰的能力密切相关[50]．研究表明强洪水冲刷能显著减少河流刚毛藻的生物量[51-54]；海浪强冲刷使蓄潮池中刚毛藻藻丝脱落、藻丛疏松[34]；生长在河流飞溅区的刚毛藻生物量远小于浸没区生物量[55]．另一方面，洪水冲刷能移除基质上覆盖的沉水植被，有利于刚毛藻游动孢子附着[56]．不同海洋刚毛藻具备不同的抗浪能力[57]，这是固着器差异导致，还是叶状体柔韧性差异造成，抑或是其他因素，目前尚不清楚．

水动力对刚毛藻的形态发展有一定塑造作用，如后期分枝的多寡、分枝角度、“湖球”的形成等．频繁的海洋波塑造了刚毛藻较丰富的分枝形态[3]，剧烈的紊流作用使藻丝单细胞长度变短[18]．水流流速的增加也引起刚毛藻分枝数量的增加[58]，分枝与主枝之间的夹角减小[59]．水流运动可促进相似性质的非活性物质聚集[60]，“湖球”的形成正是水流的纵横旋转作用结合叶状体自身形态所产生的一种非活性物质聚集过程[61]．刚毛藻叶状体柔韧[62]，低流速下叶状体上下浮动，高流速下水流冲击加强，叶状体充分伸展，此类形态响应在其他大型藻类和陆生植物上均可见[63-64]．

2.3 光照

光照是影响刚毛藻规律性季节变化的重要环境因素．Wood[65]原位培养伊利湖和安大略湖中相同生物量的刚毛藻，并测定所需光照条件，结果显示 5 月份全日光照条件下刚毛藻最大光合效率超过 1200 mol CO_2/（g·h），藻类光合利用率最高；非全日光照条件下刚毛藻的最大光合效率为 400 mol CO_2/（g·h）；而 7 月份全日光强环境中，刚毛藻产生光抑制效应导致光合效率降低．刚毛藻的生长更依赖于高光照环境，但研究显示分枝长而稀疏的河流刚毛藻（*C. basiramosa*）是耐阴种[1]，常附着于悬石形成垂直藻带．长时间暴露于强光照环境中的刚毛藻会产生相应的生理响应机制，如细胞直径显著减小、叶绿体内质网膜厚度降低、叶绿素 a 浓度及叶绿素 b/a 比值的降低、最大光合效率的降低、活性碳酸氢盐吸收机制的出现等[66]．

光谱组成是影响刚毛藻生长繁殖的另一个重要因素．Cook 等[67]对绉刚毛藻和团集刚毛藻进行光照光谱试验，结果显示光照强度对两者游动孢子的释放时间没有影响，而光谱组成对其影响明显．以团集刚毛藻为例，将藻体分别暴露于 25℃时白光、黑暗、红、蓝及绿光等各种光谱中，以上各光谱中游动孢子的释放时间分别为 6~7、8~9、9~10 和 10~11 d，而绿光环境中团集刚毛藻没有释放游动孢子．光周期长短显著影响刚毛藻游动孢子释放数量，Hoffmann 等[68]设置光周期为 8 h∶16 h 时，孢子囊释放孢子释放数量最多．

前期已开展了大量关于淡水刚毛藻光合作用-辐射照度（P-I）曲线的试验研究．P-I 曲线中包含了最大光合速率（P_M）、上升曲线斜率（α）、下降曲线斜率（β）、维持净光合速率的临界光照度（I_{CR}）及最大光合作用的半饱和辐射度（$I_K=P_M/\alpha$）等参数．美国五大湖中刚毛藻的最大光合速率与其干重相关，其变化范围为 13.4~38.4 mg C·g/（DM·h）（DM 表示干物质）[69-70]，而最大光合作用的半饱和辐射度变化范围介于 15~600 μmol photon/（m^2·s）之间[70-72]．Davies 等[73]研究了伊利湖中刚毛藻原位最大光合速率的最大面积率为 197

或 66 mg O_2/(m^2·h). 休伦和密歇根湖中刚毛藻 P-I 曲线上升斜率值范围介于 0.11~0.26 mg O_2/(DM·h)/(μmol/(m^2·s))之间[70],净光合速率的临界光量子通量密度变化范围为 6~44 μmol/(m^2·s). 结合 Lorenz 等[74]和 Higgins 等[75]的研究方法,可用上述参数值估测刚毛藻在湖泊中的分布深度.

Dodds[44]采用中性密度滤光镜进行光衰减试验,同时结合$^{14}CO_2$培养测定,结果显示来自 2 条不同河流的刚毛藻,其光量子利用效率差异显著. Graham 等[71]测定休伦湖中刚毛藻各项生理指标,结果表明温度超过 5℃且光量子通量密度大于 35 μmol/(m^2·s)时,刚毛藻产生净光合速率,最优光合效率发生在光量子通量密度范围在 300~600 μmol/(m^2·s)之间. Lester 等[70]研究了密歇根湖团集刚毛藻光饱和点发生在 7 月和 8 月,对应的光补偿点分别 44 和 104 μmol/(m^2·s),此时光量子通量密度分别为 345 和 1125 μmol/(m^2·s). 河口苍白刚毛藻的净光合速率发生在光量子通量密度超过 25 μmol/(m^2·s),12℃和 30℃光合速率饱和时,光量子通量密度分别为 100 和 750 μmol/(m^2·s).

2.4 温度

淡水刚毛藻生物量或丰度的季节性变化往往是对温度的响应[5,76-78]. 春季低温抑制了苏必利尔湖中刚毛藻的生长[79],其生长所需的最低温度约为 5℃[71]. 水温 13~31℃是北美五大湖中团集刚毛藻最优生长温度,30~35℃是其最高临界生长温度[70-71]. Wong 等[76]研究显示夏季水温超过 23.5℃时,刚毛藻逐渐死亡. 而 Brock 等[80]研究显示水温为 27℃时,刚毛藻光合效率最高;水温达到 35℃时,部分种类刚毛藻可进行短暂光合作用. Lester 等[70]研究了密歇根湖中团集刚毛藻发生最大净光合产氧时的水温为 28~31℃. 另有研究表明,22~24℃水温下北美五大湖刚毛藻死亡[75,81],该值比室内试验的临界温度值低 10℃. Graham 等[71]证实当水温超过 25℃时,休伦湖中刚毛藻净光合产氧量下降,但因其光合放氧和暗呼吸作用已适应夏季高温,故能维持正常生长[15].

不同湖泊中刚毛藻对夏季高温响应不同,原因有(ⅰ)刚毛藻种间差异导致,不同种类刚毛藻对相同温度的响应不同;(ⅱ)光合作用对辐照度响应和对温度响应的协同效应[71],在相同温度条件下,光强改变,藻类生长趋势改变;(ⅲ)夏季水体的低营养盐浓度以及捕食者的牧食行为抑制了刚毛藻的生长[77,82].

2.5 营养盐

前期研究普遍认为磷是刚毛藻生长的关键因子,刚毛藻在水体中的异常增殖与磷的大量输入密切相关[52,83-88]. Auer 等[89]利用城市废水处理系统去除磷后,休伦湖中刚毛藻生物量降低 80%;实施磷减排措施或控制溶解性磷后,安大略湖和 Windermere 流域刚毛藻生物量分别降低 60%[86]和 90%[90]. 以往针对氮营养盐对刚毛藻生长影响的研究较少,结果显示氮营养盐限制刚毛藻的初级生产力,但是对其丰度没有影响[13,49,77]. Gerloff 等[91]研究了团集刚毛藻细胞组织氮、磷含量分别为 0.83%~4.89%和 0.04%~0.54%. Gordon 等[92]研究了苍白刚毛藻细胞内氮、磷含量临界值分别为 1.50%和 0.05%. 当细胞组织中氮、磷含量分别为 1.10%和 0.06%时[91],团集刚毛藻生长率最大,低于该临界值后其生长受限. 安大略南部溪流中刚毛藻细胞组织内、外磷浓度显著相关,而氮浓度不相关[83]. 哥伦比亚河流中刚毛藻细胞内氮含量与细胞外溶解性无机氮相关,细胞内磷含量与环境中磷浓度的相关性因藻类“奢侈”吸收作用被掩盖,表现出无相关[93].

刚毛藻的磷吸收速率与细胞内磷配额(Q_P)、环境中磷浓度及温度等密切相关. 某些特定种刚毛藻产生磷酸酶降解吸收环境中溶解性有机磷[94],故能耐受低磷浓度[7,95]. 刚毛藻细胞潜在增长率对 Q_P变化的响应遵循下垂模型[96],当 Q_P值>0.16% DM 时,潜在增长率对 Q_P值的微弱变化响应不敏感,磷的额外吸收为“奢侈”消耗[93];当 Q_P值<0.16% DM 时,潜在增长率对细微变化的 Q_P值响应敏感;Q_P值为 0.05%~0.06% DM 时是细胞内最小磷配额,低于该值细胞停止生长[96]. 处于生长旺季的刚毛藻细胞 Q_P值降低,说明刚毛藻对外界磷吸收作用不足以抵消其对细胞内磷的利用稀释作用,故最终表现为细胞内磷限制. 细胞内 Q_P值较低时,刚毛藻碱性磷酸酶活性(APA)表达,通过此响应关系可探索刚毛藻生长的磷限制条件[52]. 但细胞 Q_P值与 APA 的关系相对复杂,在某些研究中低 Q_P值与高 APA 直接相关,而某些研究中刚毛藻生长阶段的 Q_P值持续降低,而 APA 值先增后减[15]. 利用细胞最小氮配额(Q_N)与 APA 的关系也可探究刚毛藻生长的氮限制条件,结果显示美国安大略湖、伊利湖和休伦湖等五大湖中极少发生氮限制状况[75,85,97],维持刚毛藻正常生长的 Q_N约为 1.1% DM[91]. 伊利湖中刚毛藻 Q_N与其临界值 1.1% DM 相当[98].

自然条件下藻类生长受多环境因子的协同影响. 如育枝刚毛藻(*C. prolifera* (Roth) Kütz.)耐受高 H_2S

浓度的特性使其能在富营养化海洋环境中占优势[95]. 除氮、磷营养盐外,团集刚毛藻生长同时需要硅[99]、硼、锌、维生素 B_1 和 B_{12}[100]等多种营养元素. Wong 等[76]研究表明刚毛藻生长率的变化与周围光场密不可分. 另外,盐度也是限制刚毛藻分布的重要因素[101-102].

3 刚毛藻生长周期与种群季节动态

刚毛藻无性繁殖产生双鞭毛或四鞭毛的游动孢子,游动孢子的形成或孢子囊的发育需要短暂光照[103]. 研究表明,自然条件下孢子囊的萌发贯穿刚毛藻完整生长周期,每个孢子囊中含有上百个游动孢子,游动孢子释放后通过前端鞭毛附着在硬质基质上[40],在合适的环境下萌芽生长[5,40]. 高温、维生素不足及光周期缩短等因素均能诱发游动孢子的形成[103],从游动孢子萌发到藻株形成所需最低光量子通量密度为 25 μmol/(m^2·s)[74]. 刚毛藻主枝垂直发育,中间或顶端细胞不断生长延伸[5];依据流速或紊流状况,刚毛藻可产生分枝或亚分枝[14,104],分枝刚毛藻的生长方式是典型向顶式,顶尖细胞垂直延长,根尖细胞水平延长形成侧枝[1],发育年轻的分枝集中在刚毛藻顶端,厚壁孢子紧紧附着在基质上,这种生长方式有利于刚毛藻低温越冬,一旦环境水温超过 5℃时,刚毛藻复苏萌发[71],与主枝中间细胞相比,分枝中间细胞生长速度较缓慢[40].

北温带刚毛藻生长遵循双季节模式,其生物量出现短暂夏季高峰后,藻丝逐渐与基质分离、死亡,最终表现为生物量降低. 夏季高水温及营养盐不足等因素直接影响了刚毛藻的新陈代谢[105],游动孢子的形成、释放及附着过程. 游动孢子的形成会导致刚毛藻母细胞的裂解,因此夏季刚毛藻生物量呈先增后减趋势. 双季节模式中第 2 个峰值出现在秋季[5,40,75],秋季刚毛藻生物量峰值相对较低,且因水体透明度下降和光周期缩短等因素,刚毛藻通常附着在水深相对较浅的沿岸带[16].

刚毛藻在室内生长环境下最大净比生长率可达 0.7~0.8 d^{-1}[96,106],而在自然环境中,因遮蔽效应、溶解性气体减少等不利因素的负反馈作用,刚毛藻净比生长率极少达到该值[107-109]. 与其他季节相比,春季刚毛藻的比生长率最大,此时光遮蔽效应较弱,藻类的营养盐利用率最高[105,110]. 夏季刚毛藻的生长与死亡同时存在,因夏季湍流剪应力影响,衰落的藻丝或与基质分离或沿纤维轴断裂死亡[5,40,75,81,111]. 温度应力、营养不足和刚毛藻藻株及其细胞代谢失衡等等因素均可导致藻丝衰落[105]. 刚毛藻丝体与基质分离后,可能因其夹带的气泡或表面张力而漂浮于水面,或因水动力作用再悬浮输移. 大部分自由漂浮的刚毛藻丝体沉降至沉积物表面死亡分解;少部分丝体仍具有光合活性,缠绕在石头或树枝等基质上,继续新陈代谢.

4 刚毛藻群落与生态系统

4.1 生物地球化学循环

刚毛藻藻丛的快速生长能增进不同介质间物质和能量交换,促进水生态系统的生物地球化学循环. 藻丛增殖期是各形态营养盐的“汇”,可吸收去除水柱中大量碳、氮、磷等营养盐. 通过组织化学计量测算,春季伊利湖中处于生长期的刚毛藻去除碳、氮量分别约为 3000 和 230 t. 伊利湖 100 km 沿岸线的刚毛藻藻丛在 30 d 内可去除 15 t 磷,其细胞组织仍处于不饱和状态[75]. 刚毛藻藻丛衰亡期是各形态营养盐的“源”,波罗海中刚毛藻在有氧或无氧环境 14 d 后,其分解速率及营养盐释放速率相当,生物量和营养盐均减少了 50%[112]. 磷的释放速率依赖于水柱中溶解氧浓度,数据显示无氧条件下磷的损失速率较快,7 d 后细胞组织中磷含量为初始磷含量的 50%,30 d 后细胞组织中的磷含量为 20%,有氧条件下磷损失速率较慢,14 d 后细胞组织磷含量无显著变化,30~35 d 后磷含量仅减少 40%[112].

大型丝状藻类对碳源的吸收主要受水中无机碳浓度的调控[113]. 当藻丛暴露在空气中时,空气中 CO_2 将成为大型丝状藻类光合作用的主要碳源[114-117]. 刚毛藻露出水面时的最大光合作用高于浸没在水中时的最大光合作用[114,118],这种对环境中无机碳吸收的适应或许可以解释为什么刚毛藻漂浮在水面还能正常生长. 刚毛藻吸收无机碳主要有 3 种机制[109]:第一,通过胞浆内的碳酸酐酶 HCO_3^- 脱水作用转化成 CO_2,之后通过扩散进入细胞;第二,通过特定的转运机制直接吸收 HCO_3^-;第三,通过氢离子泵吸收无机碳. 因此,当刚毛藻大量繁殖时,水中无机碳含量减少,pH 值升高.

4.2 种间关系

4.2.1 刚毛藻与附着生物　刚毛藻与其附着生物之间可能存在共生、寄生或竞争关系. 大量研究表明,刚毛

藻为微生物[119-120]、附着藻类[49,121-123]及无脊椎动物[14,49,124-125]提供了必要的生存环境和栖息地. 严格来讲,无脊椎动物并不完全是刚毛藻的附着生物,为了章节结构特将无脊椎动物部分归类于此.

(1)微生物. 大肠杆菌及其他人类致病菌极易附着在刚毛藻丝体上[119-120,126-127]. 密歇根湖沿岸刚毛藻中,97%的样品附着了大肠杆菌和肠球菌[119],将晒干后的刚毛藻置于4℃下,大肠杆菌和肠球菌存活时间可超过6个月,且水化后可继续生长[119]. 附着病原性细菌的刚毛藻极易成为人类可接触的病源载体.

(2)藻类. 刚毛藻与其附着藻类之间可能是共生或资源(如营养盐和光照等)竞争关系[14],刚毛藻为附着藻类提供附着基并缓解强水流对其冲刷作用[128],而附着藻类分解释放的营养物质为刚毛藻利用,这种相互作用关系随着营养盐浓度、附着藻类密度及组成而改变. 北美五大湖中附着刚毛藻的优势藻类有席藻(*Phormidium diguetti*)、附生莱包藻(*Leibleinia epiphytica* (Hieronymus) Anagnostidis et Komarek)和硬壳管孢藻(*Chamaesiphon incrustans*)等,占附着藻类细胞丰度的53%~90%,其他藻类有虱形卵形藻(*Cocconeis pediculus* Ehr.)和弯楔藻(*Rhoicosphenia curvata*)[122]等. 休伦湖中刚毛藻的附生硅藻种类和生物量呈季节性变化[123],5月附生硅藻生物量约占总附生藻类生物量的30%;6-7月刚毛藻生物量显著增加,附着硅藻生物量减少,占总附生藻类生物量的20%;秋季刚毛藻生长率下降,附生藻类生物量比例增加至60%[123]. Stevenson等[123]推测附着在刚毛藻上藻类细胞过多,会对刚毛藻产生光遮蔽效应,刚毛藻的衰落加速,这种光抑制效应对附着于基质底部的刚毛藻更加明显. Dodds[44]研究认为淡水刚毛藻与其附生藻类的竞争压力促使了某种水溶性提取物的产生,该提取物能有效抑制其附生硅藻的光合作用效率. 刚毛藻与其附生藻类的光竞争性仅表现在低光照条件下,当光照充足时两者之间的竞争性减弱. 刚毛藻与其附生藻类之间的相互作用关系也会受到食藻动物的影响,Dudley[129]和Kupferberg[130]发现团集刚毛藻的附生藻类生物量因食藻动物的牧食作用而显著减少,而团集刚毛藻生长率和生物量增加.

群落的自然演替中不同物种的取代顺序是可预测的. 褐藻和绿藻耐受低光强,同时它们也是生存空间的"掠夺者",但是褐藻和绿藻淡水种罕见,故淡水刚毛藻的藻类竞争者较少;海洋无脊椎动物对底栖生存空间的竞争能力强于淡水无脊椎动物,但是海洋底栖动物摄食刚毛藻,而淡水底栖动物不以刚毛藻为食. 因此研究认为淡水刚毛藻是中晚期演替者[51,54,131-132],而海水刚毛藻是早期演替机会主义者[133-135].

(3)无脊椎动物. 刚毛藻藻丛为颤蚓、钩虾、龙虾、枝角类和软体动物类等无脊椎动物提供了良好的栖息环境[14,124-125]. 研究显示刚毛藻藻丛是钩虾的优先聚集地[136],伊利湖东部刚毛藻上附着最常见的无脊椎动物为端足类钩虾(*Gammarus fasciatus*)以及各种摇蚊[137]. 通过胃内容物和稳定同位素分析,钩虾和摇蚊主要以刚毛藻上的附着硅藻为食;控制实验结果显示,钩虾可直接以刚毛藻丝体为食[137]. Canale等[81]认为无脊椎动物对刚毛藻的摄食并不能显著减少其现存量. 刚毛藻与牧食者、附生生物之间的关系错综复杂. 在加利福尼亚北部某河流中,鱼类捕食以摇蚊幼虫为食物来源的昆虫,摇蚊幼虫牧食刚毛藻并将其作为避难场所[138],而刚毛藻又是鱼类的避难场所[139]. 洪水冲刷减少了食草动物的数量,刚毛藻的被牧食压力减小,发生水华的潜在可能性增加[140].

4.2.2 刚毛藻与其他藻类　北美五大湖中暗紫红毛菜(*Bangiadulcis atropurpurea*)以及环丝藻(*Ulothrix zonata*)也常出现在沿岸带[141],刚毛藻并不是唯一的大型附着藻类. 当两种或两种以上大型丝状藻类共存时,它们对环境压力的应对可能有不同策略. 丝藻对低温有更强的耐受力[89,141-142],因此早春丝藻在苏必利尔湖沿岸带占优[91,143]. Sheath等[144]发现休伦湖总藻类现存量中刚毛藻占92%,普生轮藻(*Chara vulgaris*)占7%,其他藻类如奈氏席藻(*Phormidum retzii*)、环丝藻、双星藻(*Zygnema* spp.)和水绵(*Spirogyra* spp.)等贡献量小于1%. 轮藻的附着基质主要为鹅卵石,与刚毛藻没有直接的空间竞争,但两者生长机制极为相似,近年来休伦湖沿岸带刚毛藻逐渐被轮藻取代. 刚毛藻对强风浪扰动环境具有强竞争性,Higgins等[17]发现伊利湖和安大略湖曾发生过短暂水绵水华,水华期间湖面平静,水绵丝状体假性附着在刚毛藻藻丛表层,随着风浪扰动加强,水绵丝状体与假性附着基质分离,而刚毛藻生物量无显著变化.

刚毛藻对其他大型海藻具有竞争优势,海洋团集刚毛藻可显著降低墨角藻(*Fucus vesiculosus* L.)幼殖体的数量[145]. Lavery等[146]调查发现刚毛藻在澳大利亚富营养化Peel-Harvey河口沿岸带占优势,松散藻丛覆盖在河口深水区富含有机质的沉积物表面,因光合作用产生的气泡将深水区部分藻丛携带至浅水区水面,对其他藻类产生了光遮蔽效应. 1978年Peel-Harvey河口冬季风暴去除了大量深水区的刚毛藻,沉积物表面

与氧气充分接触后,营养盐再生量不足以维持刚毛藻生长,逐渐被硬毛藻(*Chaetomorpha*)取代.

刚毛藻与浮游藻类存在竞争关系,漂浮于水面的浮游藻类优先利用进入水柱中的太阳光,减少了刚毛藻的可利用光照,而底栖丝状藻截留沉积物中的营养盐,使得进入水柱的可利用营养盐减少[147]. Spencer等[148]研究证实控制湖泊中浮游藻类的生长,能增强水下光照,有利于刚毛藻生长. 刚毛藻与某些固氮藻类存在共生关系. 研究显示刚毛藻耐受缺氮环境,而固氮蓝藻在此类水体中非常普遍. 海洋固氮蓝藻泡沫节球藻(*Nodularia spumigena*)死亡降解后氮释放,引起水柱中可利用氮源增加,刚毛藻生物量增加[149]. 刚毛藻上的附着藻类也存在固氮种[44],如含异形胞的胶团念珠藻(*Nostoc parmelioides* Kützing)以及与固氮蓝藻内共生的鼠形窗纹藻(*Epithemia sorex*)等[150].

4.2.3 刚毛藻与水生植物　刚毛藻喜附着在篦齿眼子菜(*Potamogeton pectinatus* L.)和芦苇(*Phragmites australis* (Lav.) Trin. ex Stevd)等水生植物上,被刚毛藻缠绕的芦苇脆性增加易折断[30],死亡后的刚毛藻分解释放出一种未知的水溶性化合物,抑制芦苇幼苗的形成[151]. Ozimek 等[152]发现团集刚毛藻通过对光的竞争,能有效抑制伊乐藻(*Elodea canadensi*s)和篦齿眼子菜的生长,且在高 pH、低 CO_2环境下,刚毛藻能完全取代伊乐藻[153].

4.2.4 刚毛藻与贝类　湖泊、河流和河口等水体中斑马纹贻贝(*Dreissena polymorpha*)和斑马贻贝(*D. bugensis*)的引入,使底栖藻类和水生植物的生物量显著增加[75,154-157]. 其主要原因有:第一,斑马纹贻贝和斑马贻贝增加了湖底三维表面积,刚毛藻游动孢子和厚壁孢子的可附着面积增加,随着贝类外壳上游动孢子萌发生长成藻丝,其他附着生物的可利用栖息地增加. 另外,刚毛藻初始现存量的增加直接影响其面积增长率,春季刚毛藻的营养盐吸收量和磷储量也随之增加,这将直接影响夏季刚毛藻的潜在最大现存量. 第二,斑马纹贻贝和斑马贻贝新陈代谢所释放的废弃物中,有大量刚毛藻可利用的生物磷[156,158-159];第三,贝类可吸收水体中悬浮物,提高水体透明度[160-162],故附着藻类着生深度、光饱和深度及其生物量均增加[75,105,163]. 第四,斑马纹贻贝和斑马贻贝对浮游藻类的摄食[164-165],减少了刚毛藻生物可利用性磷的竞争者,同时贝类也阻止了结合颗粒态磷进入湖底沉积物,减少水体可利用磷的损失[166].

4.3 刚毛藻生物防治研究

Patrick 等[167]研究了一系列淡水刚毛藻的生物控制措施,列出了一些可能会牧食刚毛藻的动物,如池塘蜗牛(*Physa heterostropha*)、淡水龙虾(*Orconectes propinquus*)、蝌蚪(*Rana pipiens*)、鲶鱼(*Ictalurus punctatus*)以及黑头呆鱼(*Pimephales promelas*)等等,研究结果显示上述动物并不以刚毛藻为食,但该结果存在着一定的争议. LaLonde 等[168]发现团集刚毛藻中低含量的氨基酸类和有毒脂肪酸物质(月桂酸、肉豆蔻酸和棕榈油酸等)增加了其对食草动物的不适口性,因此淡水牧食者不喜以刚毛藻为食. 然而依据 Dethier[34]对海洋潮间带的研究,虽然食草动物不会优先摄食刚毛藻,但腐烂的海洋刚毛藻却是模范大吉猛水蚤(*Tachidius discipes*)的充足食物来源. Bird 等[169]研究也发现蜉蝣稚虫喜以腐烂刚毛藻为食,片脚类动物(*Gammarus pseudolimnaeus*)和小蜉(*Ephemerella subvaria*)喜以腐烂硬毛藻和枫树叶子为食.

以真菌为主导的生物防治措施可能会成为未来的控藻手段. Patrick 等[167]发现基利支顶孢菌(*Acremonium kiliense*)可显著抑制刚毛藻的生长,而这种抑制作用在夏季更加明显. 据研究基利支顶孢菌能分泌使刚毛藻变色的具有水溶性、可透析、热稳定性的中间产物,从而抑制其生长[170]. Raghukumar[171]发现壶菌(*Coenomyces* sp.)可感染匍匐刚毛藻(*C. repens*(Agardh.) Harvey)和根枝藻(*Rhizoclonium* sp.),离壶菌(*Sirolpidium bryopsidis*)和油壶菌(*Olpidium rostiferum*)可感染刚毛藻 *C. franscatii* Collins et Harvey,但是对根枝藻或其他刚毛藻无效. 海洋种鞘丝藻(*Lyngbya*)、刚毛藻以及根枝藻极易受到网粘菌属(*Labyrinthula* sp.)感染[172],真菌 *Blodgettia bornetii* 与链状刚毛藻(*C. catenata* (L.) Kütz.)和硬管枝藻(*Siphonocladus rigida*)专性共生[173].

Caffrey 等[174]报道向沟渠岸边投放大麦杆,丝状藻类就不会出现,而水域内的高等水生植物繁盛. Irene[175]通过室内外实验,验证了不但大麦杆可抑制团集刚毛藻,而且其腐叶也有抑制大型丝状藻的作用.

5 国内刚毛藻研究进展

刚毛藻在国内的研究尽管较少,但在分类、生理生态及环境生物学方面均有涉及. 淡水刚毛藻的分类学

研究最早可追溯到1990s,刘国祥等[19]对其进行了系统研究,并发现了刚毛藻目的3个中国新记录种,厚壁刚毛藻(*Cladophora pachydermum* (Kjellmann) Brand)、邱园黑孢藻(*Pithophora kewensis* Wittrock)和贝生阿偌藻(*Arnoldiella conchophila* Miller). 随着分子生物学的发展,赵志娟等[176]基于SSU和LSU rDNA序列构建的系统发育树,重新鉴定了湖北境内4株刚毛藻HB1209、HB1304、TS1304以及HB1416的分类归属. 滕林宏[177]以海洋刚毛藻为材料,从形态和分子学两方面进行了分类及系统发育学研究,同时对国际DNA条形码技术在刚毛藻目的应用进行了初探.

关于生理生态及环境生物学方面的研究,主要集中在刚毛藻对光照、营养盐及CO_2等环境条件改变的生理响应性. 郭亮亮等[178]研究了光照强度和磷浓度对寡枝刚毛藻(*Cladophora oligoclona*)生长的影响,结果显示相对于磷浓度,光强对刚毛藻生长影响更大,且高光强不利于刚毛藻的生长. 与叉节藻(*Amphiroa* sp.)相比,刚毛藻对高CO_2浓度的响应表现为生长率的增加,日光紫外线辐射(UVR)对刚毛藻光化学效率造成的抑制率显著低于对叉节藻的抑制率[179]. 韩志国等[180]利用叶绿素荧光技术研究了束生刚毛藻(*Cladophora fascicularis*)在脱水和复水过程中光合作用变化,实验表明脱水可引起束生刚毛藻光合作用降低,但光合器官并未受到不可逆损伤,复水后光合活性迅速恢复. 刚毛藻对水体中N、P的控制及其重金属的吸附也有一定作用[181],在不同磷源纯培养条件下,刚毛藻能够有效直接去除无机磷和聚合磷酸盐;磷源为有机磷时,刚毛藻优先利用通过微生物分解作用和藻类磷酸酶转化有机磷产生的无机磷[182]. 刚毛藻腐烂过程对水质和沉水植物生长影响明显,在丝状绿藻腐烂过程中,水体溶解氧、pH值、水下光强水面光强比均降低,温度、TN、TP和高锰酸钾指数上升,且随着刚毛藻的腐烂,黑藻亦慢慢腐烂,最后消失[183]. 向贤芬等[184-185]研究了高原湖泊洱海和滇池沿岸带刚毛藻种群结构及其分布特征,寡枝刚毛藻、脆弱刚毛藻、疏枝刚毛藻(*Cladophora insignis*)和绉刚毛藻是滇池刚毛藻主要种类,滇池西岸以寡枝刚毛藻为优势种,东岸在秋、冬季以脆弱刚毛藻和绉刚毛藻为优势种,春、夏季优势种演替为寡枝刚毛藻.

6 结论与展望

刚毛藻在不同的生态系统中扮演不同角色,因此仅研究单一系统中刚毛藻的表现性,很难全面探究其生态表现特征. 刚毛藻形态差异是对环境适应性的响应,不同形态刚毛藻所具有的功能不同. 迄今为止,关于刚毛藻生态仍存在诸多值得研究探索的方向,其中包括:贻贝的引入改变了水体透明度、磷浓度以及栖息地等环境因素,由此导致刚毛藻再繁盛的机制机理;刚毛藻丝状体脱落和死亡的机制及死亡后对沉积区底栖生物的影响;夏季刚毛藻出现低现存量的影响因素;刚毛藻与其附生植物之间的竞争作用;刚毛藻附着的指示细菌(如大肠杆菌*E. coil*)与附着的人类病原体之间的相互作用关系;刚毛藻对沿岸带生物地球化学循环及食物网的重要作用.

结合我国湖泊环境现状,为了更好的控制刚毛藻异常增殖,除了探清各形态(颗粒态、溶解态等)磷来源及其在沿岸带的滞留时间,应从刚毛藻的生活史(繁殖方式、生长发育等)、生长周期以及不同生长阶段与光、温度、营养盐等的关系方面着手,如研究氮磷比和底泥沉积磷释放与刚毛藻的生长繁殖关系等,同时也需加强对贝类等底栖动物现存量的监测,更重要的是深入探究刚毛藻生态特性,全面模拟其季节生长模式以及藻体与基质分离后的丝状体生长特征. 另外,我国生态修复后的富营养化湖泊中过度增殖的刚毛藻对不同沉水植物的生长影响,包括刚毛藻和沉水植物的竞争优势各自阶段的主要生理活性等,以及衰亡腐烂后对沉水植物的生长和繁殖影响等方面值得深入研究. 最后,刚毛藻生态控制方面,如鱼类、贝类和浮游动物等对其摄食关系,以及其他水生植物对刚毛藻的生长繁殖等方面的影响仍需加强探索.

7 参考文献

[1] van den Hoek C ed. Revision of the European species of *Cladophora*. Leiden, the Netherlands: E. J. Brill, 1963: 1-31.

[2] van den Hoek C ed. Criteria and procedures in present-day algal taxonomy. In: Jackson DF ed. Algae and man. New York: Plenum, 1964: 31-58.

[3] van den Hoek C. The distribution of benthic marine algae in relation to the temperature regulation of their life histories. *Biological Journal of the Linnean Society*, 1982, **18**: 81-144.

[4] Collins FS. The green algae of North America. In: Cramer J ed. Bibliotecha phycologia(Vol. Ⅱ). New York: Charles Hyde Olmstead Fund, 1970: 331-357.

[5] Whitton BA. Biology of *Cladophora* in freshwaters. *Water Research*, 1970, **4**: 457-476.

[6] Stevenson RJ, Stoermer EF. Seasonal abundance patterns of diatoms on *Cladophora* in Lake Huron. *Journal of Great Lakes Research*, 1982, **8**: 169-183.

[7] Stanford JA, Prescott GW. Limnological features of a remote alpine lake in Montana, including a new species of *Cladophora* (Chlorophyta). *Journal of the North American Benthological Society*, 1988, **7**: 140-151.

[8] Jansson AM. Wintertime fluctuations in the epifauna of *Cladophora rupestris* in a rock pool on the Swedish west coast. *Annales Zoologici Fennici*, 1974, **11**: 185-192.

[9] Borowitzka LJ. The microflora. Adaptations to life in extremely saline lakes. *Hydrobiologia* (*Buchar.*), 1981, **81**: 33-46.

[10] Millner GC, Sweeney RA. Lake Erie *Cladophora* in perspective. *Journal of Great Lakes Research*, 1982, **8**: 27-29.

[11] Pogreboff S, Ronnberg O. Notes on benthic macroalgae off the northeast coast of the Bothnian Sea. *Memoranda Societatis pro Fauna et Flora Fennica*, 1987, **63**: 85-89.

[12] Kautsky H, Kautsky U, Nellbring S. Distribution of flora and fauna in an area receiving pulp mill effluents in the Baltic Sea. *Ophelia*, 1988, **28**: 139-155.

[13] Lapointe BE, O'Connell J. Nutrient-enhanced growth of *Cladophora prolifera* in Harrington Sound, Bermuda: eutrophication of a confined, phosphorus-limited marine ecosystem. *Estuarine Coastal and Shelf Science*, 1989, **28**: 347-360.

[14] Dodds WK, Gudder DA. The ecology of *Cladophora*. *Journal of Phycology*, 1992, **28**: 415-427.

[15] Shahrizim Z, Alissa H, Erica BY *et al*. The epiphytic microbiota of the globally widespread macroalga *Cladophora glomerata* (Chlorophyta, Cladophorales). *American Journal of Botany*, 2012, **99**: 1541-1552.

[16] Mantai KE. Energy relations in *Cladophora glomerata* from Lake Erie. *Journal of Great Lakes Research*, 1987, **13**: 279-284.

[17] Higgins SN, Malkin SY, Howell ET *et al*. An ecological review of *Cladophora glomerata* (Chlorophyta) in the Laurentian Great Lakes. *Journal of Phycology*, 2008, **44**: 839-854.

[18] Ronnberg O, Lax PE. Influence of wave action on morphology and epiphytic diatoms of *Cladophora glomerata* (L.) Kütz. *Ophelia*(*Suppl*), 1980, (1): 208-218.

[19] Liu GX, Hu ZY. Three new records of freshwater cladophorales from China. *Acta Hydrobiologica Sinica*, 1999, **23**: 93-96. [刘国祥, 胡征宇. 淡水刚毛藻目三个中国新记录种. 水生生物学报, 1999, **23**: 93-96.]

[20] Bot PVM, Stam WT, Boele-Bos SA *et al*. Biogeographic and phylogenetic studies in three North Atlantic species of *Cladophora* (Cladophorales, Chlorophyta) using DNA-DNA hybridization. *Phycologia*, 1989, **28**: 159-168.

[21] Bot PVM, Holton RW, Stam WT *et al*. Molecular divergence between North Atlantic and Indo-West Pacific *Cladophora albida* (Cladophorales: Chlorophyta) isolated as indicated by DNA-DNA hybridization. *Mar Biol* (*Berl*), 1989, **102**: 307-313.

[22] Verma BN. Karyomorphological studies on three species of *Cladophora* Kütz. *Cytologia* (*Tokyo*), 1985, **50**: 25-30.

[23] Olsen-Stojkovich J, West JA, Lowenstein JM. Phylogenetics and biogeography in the *Cladophorales complex* (Chlorophyta): Some insights from immunological distance data. *Bot Mar*, 1986, **29**: 239-249.

[24] Murray S, Jorgensen MF, Ho SY *et al*. Improving the analysis of dinoflagellate phylogeny based on rDNA. *Protist*, 2005, **156**(3): 269-286.

[25] Feau N, Hamelin RC, Bernier L. Attributes and congruence of three molecular data sets: inferring phylogenies among Septoria-ralted species from woody perennial plants. *Mol Phyl Evol*, 2006, **40**(3): 808-829.

[26] Leliaert F, De Clerck O, Verbruggen H *et al*. Molecular phylogeny of the *Siphonocladales* (Chlorophyta: Cladophorophyceae). *Mol Phylogenet Evol*, 2007, **44**(3): 1237-1256.

[27] Boedeker C, Leliaert F, Zuccarello GC. Molecular phylogeny of the Cladophoraceae (Cladophorales, Ulvophyceae), with the resurrection of Acrocladus Nageli and Willeella Borgesen, and the description of *Lurbica* gen. nov. and *Pseudorhizoclonium* gen. nov. *J Phycol*, 2016, **52**(6): 905-928.

[28] Curry MG, Everitt B, Vidrine MF. Haptobenthos on shells of living freshwater clams in Louisana. *Wasmann J Biol*, 1981, **39**: 56-63.

[29] Pantastico JB, Suayan ZA. Algal succession in the ricefields of College and Bay, Laguna. *Philipp J Agric*, 1973, **57**(7/

8): 313-326.

[30] Utermöhl VH. Phragmites stands damaged by periphyton of *Cladophora* in the lake GroBer Ploner See. *Archiv für Hydrobiologie*, 1982, **95**(1/4): 487-490.

[31] Nakazawa S. The time and cause of extermination of lake balls from Lake Zeller. *Bull Jpn Soc Phycol*, 1974, **22**: 101-103.

[32] Gordon DM, Birch PB, McComb AJ. The effect of light, temperature and salinity on photosynthetic rates of an estuarine *Cladophora*. *Bot Mar*, 1980, **23**: 749-755.

[33] Niiyama Y. Morphology and classification of *Cladophora aegagropila* (L.) Rabenhorst (Cladophorales, Chlorophyta) in Japanese lakes. *Phycologia*, 1989, **28**: 70-76.

[34] Dethier MN. Pattern and process in tidepool algae: factors influencing seasonality and distribution. *Bot Mar*, 1982, **25**: 55-66.

[35] Power ME. Benthic turfs vs floating mats of algae in river food webs. *Oikos*, 1990, **58**: 67-79.

[36] Braithwaite CJR, Casanova J, Frevert T *et al*. Recent stromatolites in landlocked pools on Aldabra, Western Indian Ocean. *Palaeogeogr Palaeoclimatol Palaeoecol*, 1989, **69**: 145-165.

[37] Konno T. Effects of inclination of a rock surface on the distribution of sublittoral sessile organisms. *J Tokyo Univ Fish*, 1985, **72**: 99-109.

[38] Castenholz RW. Seasonal changes in the attached algae of freshwater and saline lakes in the Lower Grand Coulee, Washington. *Limnology and Oceanography*, 1960, **5**: 1-28.

[39] Butcher RW. Survey of the river tees. Part Ⅲ. The non-tidal reaches. In: Butcher RW, Longwell J, Pentelow FTK eds. Chemical and biological. London: HMSO, 1937: 1-189.

[40] Bellis VJ, McLarty DA. Ecology of *Cladophora glomerata* (L.) Kütz in Southern Ontario. *Journal of Phycology*, 1967, **3**: 57-63.

[41] Jao C. Studies on the fresh-water algae of China Ⅶ. The attached algal communities of the Kialing River. *Sinensia Acad Sinica*, 1944, **15**: 61-91.

[42] Thurman MH, Kuehne RA. An ecological study of *Cladophora glomerata* (Chlorophyceae) near Dallas. *Field Lab*, 1952, **20**: 26-28.

[43] Pfeifer RF, McDiffett WF. Some factors affecting primary productivity of stream riffle communities. *Archiv für Hydrobiology*, 1975, **75**: 306-317.

[44] Dodds WK. Community interaction between the filamentous alga *Cladophora glomerata* (L.) Kützing, its epiphytes and epiphyte grazers. *Oecologia* (*Berl*), 1991, **85**: 572-580.

[45] Lehman JT. Enhanced transport of inorganic carbon into algal cells and its implications for the biological fixation of carbon. *Journal Phycology*, 1978, **14**: 33-42.

[46] Wheeler WN. Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. *Mar Biol* (*Berl*), 1980, **56**: 103-110.

[47] Dodds WK. Photosynthesis of two morphologies of *Nostoc parmelioides* (Cyanobacteria) as related to current velocities and diffusion patterns. *Journal of Phycology*, 1989, **25**: 258-262.

[48] Raven J, Beardall J, Griffiths H. Inorganic sources for *Lemanea*, *Cladophora* and *Ranunculus* in a fast-flowing stream: measurement of gas exchanges and of carbon isotope ratio and their ecological implications. *Oecologia* (*Berl*), 1982, **53**: 68-78.

[49] Dodds WK. Factors associated with dominance of the filamentous green alga *Cladophora glomerata*. *Water Research*, 1991, **25**: 1325-1332.

[50] Power ME, Stewart AJ. Distribution and recovery of an algal assemblage following flooding in an Oklahoma stream. *Am Midl Nat*, 1987, **117**: 333-345.

[51] Fisher SG, Gray LJ, Grimm NB *et al*. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs*, 1982, **52**: 93-110.

[52] Freeman MC. The role of nitrogen and phosphorus in the development of *Cladophora glomerata* (L.) Kützing in the Manawatu River, New Zealand. *Hydrobiologia*, 1986, **131**: 23-30.

[53] Entwisle TJ. Phenology of the *Cladophora stigeoclonium* community in two urban creeks of Melbourne. *Aust J Mar Frshwater Res*, 1989, **40**: 471-489.

[54] Sand-Jensen K, Jeppesen E, Nielsen K *et al*. Growth of macrophytes and ecosystem consequences in a lowland Danish stream. *Freshwater Biology*, 1989, **22**: 15-32.

[55] Oertel N. Heavy-metal accumulation in *Cladophora glomerata* (L.) Kütz. in the river Danube. *Ambio*, 1991, **20**: 264-268.

[56] Chudyba H. *Cladophora glomerata* and accompanying algae in the Skawa River. *Acta Hydrobiol*, 1965, **7**: 92-126.

[57] Kapraun DF. Summer aspect of algal zonation on a Texas jetty in relation to wave exposure. *Contrib Mar Sci*, 1980, **23**: 101-109.

[58] Parodi ER, Cάceres EJ. Variation in number of apical ramifications and vegetative cell length in freshwater population of *Cladophora* (Ulvaceae, Chlorophyta). *Journal of Phycology*, 1991, **27**: 628-633.

[59] Whitton BA. Algae. In: Whitton BA ed. River ecology. Oxford: Blackwell Scientific, 1975: 81-105.

[60] Smith GM. The fresh water algae of the United States. New York: McGraw-Hill, 1933: 716.

[61] Nakazawa S. Distribution of lake-balls considered from experiments. *Bull Yamagala Univ* (*Nav Sci*), 1976, **9**: 75-83.

[62] Dodds WK. Micro-environmental characteristics of filamentous algal communities in flowing freshwaters. *Freshwater Biology*, 1991, **25**: 199-209.

[63] Vogel S. Life in moving fluids. Princeton: Princeton University Press, 1981: 352.

[64] Vogel S. Life's devices. Princeton: Princeton University Press, 1988: 367.

[65] Wood KG. Photosynthesis of *Cladophora* under unnatural condition. In: Jackson DF ed. Algae, man and the environment. New York: Syracuse Univ Press, 1968:121-133.

[66] Choo KS, Nilsson J, Pederson M *et al*. Photosynthesis, carbon uptake and antioxidant defence in two coexisting filamentous green algae under different stress conditions. *Mar Ecol Prog Ser*, 2005, **292**: 127-138.

[67] Cook WRI, Price IR. The effect of aeration and light on the development of the zoosporangia in the genus *Cladophora*. *J Roy Microscop Soc*, 1928, **48**: 274-282.

[68] Hoffmann JP, Graham LE. Effects of selected physicochemical factors on growth and zoosporogensis of *Cladophora glomerata* (Chlorophyta). *J Phycol*, 1984, **20**(1): 1-7.

[69] Wood KG. Photosynthesis of *Cladophora* in relation to light and CO_2 limitation; $CaCO_3$ precipitation. *Ecology*, 1975, **56**: 479-484.

[70] Lester WW, Adams MS, Farmer AM. Effects of light and temperature on photosynthesis of the nuisance alga *Cladophora glomerata* (L.) Kütz. from Green Bay, Lake Michigan. *New Phytol*, 1988, **109**: 53-58.

[71] Graham JM, Auer MT, Canale RP *et al*. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 4. Photosynthesis and respiration as functions of light and temperature. *Journal of Great Lakes Research*, 1982, **8**: 100-111.

[72] Higgins SN. Modeling the growth dynamics of *Cladophora* in Eastern Lake Erie[Dissertation]. Waterloo: University of Waterloo, 2005: 153.

[73] Davies JM, Hecky RE. Initial measurements of benthic photosynthesis and respiration in Lake Erie. *Journal of Great Lakes Research*, 2005, **31**(Suppl. 2): 195-207.

[74] Lorenz RC, Monaco ME, Herdendorf CE. Minimum light requirement for substrate colonization by *Cladophora glomerata*. *Journal of Great Lakes Research*, 1991, **17**: 536-542.

[75] Higgins SN, Howell ET, Hecky RE *et al*. The wall of green: the status of *Cladophora glomerata* on the northern shores of Lake Erie's eastern basin, 1995–2002. *Journal of Great Lakes Research*, 2005, **31**: 547-563.

[76] Wong SL, Clark B, Kirby M *et al*. Water temperature fluctuations and seasonal periodicity of *Cladophora* and *Potamogeton* in shallow rivers. *J Fish Res Bd Can*, 1978, **35**: 866-870.

[77] Muller C. Uptake and accumulation of some nutrient elements in relation to the biomass of an epilithic community. In: Wetzel RG ed. Periphyton of freshwater ecosystems. Development in Hydrobiology. Dordrecht: Springer, 1983: 147-151.

[78] Robinson PK, Hawkes HA. Studies on the growth of *Cladophora glomerata* in laboratory continuous-flow culture. *Br Phycol*, 1986, **21**: 437-444.

[79] Sheath RG, Cole KM. Biogeography of stream macroalgae in North America. *Journal of Phycology*, 1992, **28**: 448-460.

[80] Brock TD, Hoffmann J. Temperature optimum of algae living in the outfall of a power plant on Lake Monona. *Trans Wis Acad Sci Arts Lett*, 1974, **62**: 195-203.

[81] Canale RP, Auer MT. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. *Journal of Great Lakes Research*, 1982, **8**: 112-125.

[82] Feminella JW, Resh VH. Herbivorous caddisflies, macroalgae, and microalgae: dynamic interactions in a stream grazing system. *Oecologia* (*Berl*), 1991, **87**: 247-256.

[83] Wong SL, Clark B, Painter DS. Application of underwater light measurements in nutrient and production studies in shallow rivers. *Freshwater Biology*, 1976, **6**: 543-550.

[84] Birch PB, Gordon DM, McComb AJ. Nitrogen and phosphorus nutrition of *Cladophora* in the Peel-Harvey estuarine system, Western Australia. *Bot Mar*, 1981, **24**: 381-387.

[85] Neil JH, Jackson MB. Monitoring *Cladophora* growth conditions and the effect of phosphorus additions at a shoreline site in northeastern Lake Erie. *Journal of Great Lakes Research*, 1982, **8**: 30-34.

[86] Painter DS, Kamaitis G. Reduction of *Cladophora* biomass and tissue phosphorus in Lake Ontario, 1972-83. *Can J Fish Aquat Sci*, 1987, **44**: 2212-2215.

[87] Jackson MB. The dominant attached filamentous algae of Georgian Bay, the North Channel and Eastern Lake Huron: field ecology and biomonitoring potential during 1980. *Hydrobiologia* (*Buchar*), 1988, **163**: 149-171.

[88] Painter DS, Jackson MB. *Cladophora* internal phosphorus modeling: verification. *Journal of Great Lakes Research*, 1989, **15**: 700-708.

[89] Auer MT, Canale RP, Grundler HC *et al*. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 1. Program description and field monitoring of growth dynamics. *Journal of Great Lakes Research*, 1982, **8**: 73-83.

[90] Parker JE, Maberly SC. Biological response to lake remediation by phosphate stripping: control of *Cladophora*. *Freshwater Biology*, 2000, **44**: 303-309.

[91] Gerloff GC, Fitzgerald GP. The nutrition of great lakes *Cladophora*. United States Environmental Protection Agency, EPA 60013-76-044, 1976:111.

[92] Gordon DM. Effects of inorganic phosphorus and nitrogen on the growth of an estuarine *Cladophora* in culture. *Bol Mar*, 1981, **24**: 93-106.

[93] Lohman K, Priscu JC. Physiological indicators of nutrient deficiency in *Cladophora* (Chlorophyta) in the Clark Fork of the Columbia River, Montana. *Journal of Phycology*, 1992, **28**: 443-448.

[94] Lin CK. Accumulation of water soluble phosphorus and hydrolysis of polyphosphates by *Cladophora glomerata* (Chlorophyceae). *Journal of Phycology*, 1977, **13**: 46-51.

[95] Schramm W, Booth W. Mass bloom of the alga *Cladophora prolifera* in Bermuda: productivity and phosphorus accumulation. *Bot Mar*, 1981, **24**: 419-426.

[96] Auer MT, Canale RP. Ecological and mathematical modelling of *Cladophora* in Lake Huron: 3. The dependence of growth rates on internal phosphorus pool size. *Journal of Great Lakes Research*, 1982, **8**: 93-99.

[97] Bootsma HA, Young EB, Berges JA. Temporal and spatial patterns of *Cladophora* biomass and nutrient stoichiometry in Lake Michigan. In Cladophora Research and Management in the Great Lakes (Workshop Proceedings). GLWI Special Report No. 2005-01. Great Lakes Water Institute, University of Wisconsin-Milwaukee, 2005:81-88.

[98] Lorenz RC, Herfendorf CE. Growth dynamics of *Cladophora glomerata* in western Lake Eire in relation to some environmental factors. *Journal of Great Lakes Research*, 1982, **8**: 42-53.

[99] Moore LF, Traquair JA. Silicon, a required nutrient for *Cladophora glomerata* (L.) Kütz. (Chlorophyta). *Planta* (*Berl.*), 1976, **128**: 179-182.

[100] Hoffman JP. Dependence of photosynthesis and vitamin B_{12} uptake on cellular vitamin B_{12} concentration in the multicellular alga *Cladophora glomerata* (Chlorophyta). *Limnology and Oceanography*, 1990, **35**: 100-108.

[101] Thomas DN, Collins JC, Russell G. Interpopulation differences in the salt tolerance to two *Cladophora* species. *Estuarine Coastal Shelf Sci*, 1990, **30**: 201-206.

[102] Thomas DN, Collins JC, Russell G. Physiological responses to salt stress of two ecologically different *Cladophora* species. *Bot Mar*, 1989, **32**: 259-265.

[103] Hoffmann JP, Graham LE. Effects of selected physicochemical factors on growth and zoosporogenesis of *Cladophora glomerata* (Chlorophyta). *Journal of Phycology*, 1984, **20**: 1-7.

[104] Bergey EA, Boettiger CA, Resh VH. Effects of water velocity on the architecture and epiphytes of *Cladophora glomerata* (Chlorophyta). *Journal of Phycology*, 1995, **31**: 264-271.

[105] Higgins SN, Hecky RE, Guildford SJ. Environmental controls of *Cladophora* growth dynamics in eastern Lake Erie: appli-

cation of the *Cladophora* growth model (CGM). *Journal of Great Lakes Research*, 2006, **32**: 629-644.

[106] Rosemarin AS. Phosphorus nutrition of two potentially competing filamentous algae, *Cladophora glomerata* (L.) Kütz. and *Stigeoclonium tenue* (Agardh) Kütz. from Lake Ontario. *Journal of Great Lakes Research*, 1982, **8**: 66-72.

[107] Hill WR, Boston HL. Community development alters photosynthesis-irradiance relations in stream periphyton. *Limnology and Oceanography*, 1991, **36**: 1375-1389.

[108] Dodds WK, Biggs BJF, Lowe RL. Photosynthesis-irradiance patterns in benthic algae: variations as a function of assemblage thickness and community structure. *Journal of Phycology*, 1999, **35**: 42-53.

[109] Choo KS, Snoeijs P, Pedersen M. Uptake of inorganic carbon by *Cladophora glomerata* (Chlorophyta) from the Baltic Sea. *Journal of Phycology*, 2002, **38**: 493-502.

[110] Canale RP, Auer MT. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 7. Model verification and system response. *Journal of Great Lakes Research*, 1982, **8**: 134-143.

[111] Higgins SN, Hecky RE, Guildford SJ. Modeling the growth, biomass, and tissue phosphorus concentration of *Cladophora glomerata* in eastern Lake Erie: model description and field testing. *Journal of Great Lakes Research*, 2005, **31**: 439-455.

[112] Paalme T, Kukk H, Kotta J *et al*. ‘In vitro’ and ‘in situ’ decomposition of nuisance macroalgae *Cladophora glomerata* and *Pilayella littoralis*. *Hydrobiologia*, 2002, **475/476**: 469-476.

[113] Andría JR, Brun FG, Pérez-Lloréns JL *et al*. Acclimation response of *Gracilaria* sp. (Rhodophyta) and *Enteromorpha intestinalis* (Chlorophyta) to changes in the external inorganic carbon concentration. *Botanica Marina*, 2001, **44**: 361-370.

[114] Madsen TV, Maberly SC. A comparison of air and water as environments for photosynthesis by the intertidal alga *Fucus spiralis* (Phaeophyta). *Journal of Phycology*, 1990, **26**: 24-30.

[115] Surif MB, Raven JA. Photosynthesis gas exchange under emersed conditions in eulittoral and normally submerged members of the *Fucales* and *Laminariales*: interpretation in relation to C isotope ratio and N and water use efficiency. *Oecologia*, 1990, **82**: 68-80.

[116] Raven JA, Johnston AM. Photosynthetic inorganic carbon acquisition by *Prasiola stipitata* (Prasiales, Chlorophyta) under emersed and submersed conditions: relationship to the taxonomy of Prasiola. *Br Phycol J*, 1991, **26**: 24-25.

[117] Gao K, Ji Y, Aruga Y. Relationship of CO_2 concentrations to photosynthesis of intertidal macroalgae during emersion. *Hydrobiologia*, 1999, **398/399**: 355-359.

[118] Oates BR, Murray SN. Photosynthesis, dark respiration and desiccation resistance of the intertidal seaweeds *Hesperophycus harveyanus* and *Pelvetia fastigiata* gracilis. *Journal of Phycology*, 1983, **19**: 371-380.

[119] Whitman RL, Shively DA, Pawlik H *et al*. Occurrence of Escherichia coli and enterococci in *Cladophora* (Chlorophyta) in nearshore water and beach sand of Lake Michigan. *Appl Environ Microbiol*, 2003, **69**: 4714-4719.

[120] Ishii S, Yan T, Shively DA *et al*. *Cladophora* (Chlorophyta) spp. harbor human bacterial pathogens in nearshore water of Lake Michigan. *Appl Environ Microbiol*, 2006, **72**: 4545-4553.

[121] Lowe RL, Rosen BH, Kingston JC. A comparison of epiphytes on *Bangia atropurpurea* (Rhodophyta) and *Cladophora glomerata* (Chlorophyta) from Northern Lake Michigan. *Journal of Great Lakes Research*, 1982, **8**: 164-168.

[122] Sheath RG, Morison MO. Epiphytes on *Cladophora glomerata* in the Great Lakes with particular reference to the red alga *Choodactylon ramosum* (= *Asterocystis smargdina*). *Journal of Phycology*, 1982, **18**: 385-391.

[123] Stevenson RJ, Stoermer EF. Luxury consumption of phosphorus by five *Cladophora* epiphytes in Lake Huron. *Trans Am Microsc Soc*, 1982, **101**: 151-161.

[124] Taft CE. History of *Cladophora* in the Great Lakes. In: Shear H, Konansewich DE eds. *Cladophora* in the Great Lakes. Windsor, Ontario, Canada: International Joint Commission, 1975: 5-16.

[125] Chilton EW, Lowe RL, Schurr KM. Invertebrate communities associated with *Bangia atropurpurea* and *Cladophora glomerata* in western Lake Erie. *Journal of Great Lakes Research*, 1986, **12**: 149-153.

[126] Byappanahalli MN, Shively DA, Nevers MB *et al*. Growth and survival of Escherichia coli and enterococci populations in the macroalga *Cladophora* (Chlorophyta). *FEMS Microbiol Ecol*, 2003, **46**: 203-211.

[127] Olapade OA, Depas MM, Jensen ET *et al*. Microbial communities and fecal indicator bacteria associated with *Cladophora* beds at beach sites along Lake Michigan shores. *Appl Environ Microbiol*, 2006, **72**: 1932-1938.

[128] Moore JW. Seasonal succession of algae in rivers. Ⅰ. Examples from the Avon, a large slow-flowing river. *Journal of Phycology*, 1976, **12**: 342-349.

[129] Dudley TL. Beneficial effects of herbivores on stream macroalgae via epiphyte removal. *Oikos*, 1992, **65**: 121-127.

[130] Kupferberg S. Facilitation of periphyton production by tadpole grazing: functional differences between species. *Freshwater Biology*, 1997, **37**: 427-439.

[131] Simons J, van Beem AP. Spirogyra species and accompanying algae from pools and ditches in the Netherlands. *Aquat Bot*, 1990, **37**: 247-269.

[132] Dudley TL, D'Antonio CM. The effects of substrate texture, grazing, and disturbance on macroalgal establishment in streams. *Ecology*, 1991, **72**: 297-309.

[133] Wanders JBW. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) Ⅲ: the significance of grazing. *Aquat Bot*, 1977, **3**: 357-390.

[134] Taylor PR, Litter MM. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced rocky intertidal community. *Ecology*, 1982, **63**: 135-146.

[135] Menge BA, Ashkenas LR, Matson A. Use of artificial holes in studying community development in cryptic marine habitats in a trophic rocky intertidal region. *Mar Biol* (*Berl*), 1983, **77**: 129-142.

[136] Van Overdijk CDA, Grigorovich IA, Mabee T *et al*. Microhabitat selection by the invasive amphipod *Echiniogammarus ischnus* and naïve *Gammarus fasciatus* in laboratory experiments and in Lake Erie. *Freshwater Biology*, 2003, **48**: 567-578.

[137] Szabo R. The benthic food web on nearshore hard substrates at Peacock Point, eastern Lake Erie[Dissertation]. Waterloo, Ontario, Canada: University of Waterloo, 2004:86.

[138] Power ME. Effects of fish in river food webs. *Science*, 1990, **250**: 811-814.

[139] Power ME, Marks JC, Parker MS. Variation in vulnerability of prey to different predators: community level consequences. *Ecology*, 1992, **73**: 2218-2223.

[140] Power ME. Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. *Arch Hydrobiol*, 1992, **125**: 385-410.

[141] Blum J. Colonization and growth of attached algae at the Lake Michigan water line. *Journal of Great Lakes Research*, 1982, **8**: 10-15.

[142] Kirby MK, Dunford WE. Attached algae of the Lake Erie shoreline near Nanticoke Generating Station. *Journal of Great Lakes Research*, 1981, **7**: 249-257.

[143] Jackson MB, Vandermeer EM, Heintsch LS. Attached filamentous algae of northern Lake Superior: field ecology and biomonitoring potential during 1983. *Journal of Great Lakes Research*, 1990, **16**: 158-163.

[144] Sheath RG, Hambrook JA, Nerone CA. The benthic macro-algae of Georgian Bay, the North Channel and their drainage basin. *Hydrobiologia*, 1988, **163**: 141-148.

[145] Berger R, Henriksson E, Kautsky L *et al*. Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquatic Ecology*, 2003, **37**: 1-11.

[146] Lavery PS, McComb AJ. Macroalgal-sediment nutrient interactions and their importance to macroalgal nutrition in a eutrophic estuary. *Estuar Coastal Shelf Sci*, 1991, **32**: 281-295.

[147] Hansson LA. Effects of competitive interactions on the biomass development of planktonic and periphyton algae in lakes. *Limnology and Oceanography*, 1988, **33**: 121-128.

[148] Spencer CN, King DL. Role of fish in regulation of plant and animal communities in eutrophic ponds. *Canadian Journal of Fisheries and Aquatic Sciences*, 1984, **41**: 1851-1855.

[149] Birch PB, Gabrielson JO. *Cladophora* growth in the Peel-Harvey estuarine system following blooms of the cyanobacterium *Nodularia spumigena*. *Bot Mar*, 1984, **27**: 17-21.

[150] Bahls LL, Weber EE. Ecology and distribution in Montana of *Epithemia sorex* Kütz.a common nitrogen-fixing diatom. *Proc Mont Acad Sci*, 1988, **48**: 15-20.

[151] Schröder VR. Reed decay at Lake Constance (Untersee) observations and investigation. *Arch Hydrobiol Suppl*, 1987, **76** (1/2): 53-99.

[152] Ozimek T, Pieczynska E, Hankiewicz A. Effects of filamentous algae on submerged macrophyte growth: A laboratory experiment. *Aquat Bot*, 1991, **41**: 309-315.

[153] Simpson PS, Eaton JW. Comparative studies of the photosynthesis of the submerged macrophyte *Elodea canadensis* and the filamentous algae *Cladophora glomerata* and *Spirogyra* sp.. *Aquat Bot*, 1986, **24**: 1-12.

[154]　Lowe RL, Pilsbury RW. Shifts in benthic algal communitystructure and function following the appearance of zebra mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research*, 1995, **21**: 558-566.

[155]　Skubinna JP, Coon TG, Batterson TR. Increased abundance and depth of submerged macrophytes in response to decreased turbidity in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research*, 1995, **21**: 476-488.

[156]　Orlova M, Golubkov S, Kalinina L *et al*. *Dreissena polymorpha* (Bivalvia: Dreissenidae) in the Neva Estuary (eastern Gulf of Finland, Baltic Sea): Is it a biofilter or source for pollution? *Mar Pollut Bull*, 2004, **49**: 196-205.

[157]　Zhu B, Fitzgerald DG, Mayer CM *et al*. Alteration of ecosystem function by zebra mussels in Oneida Lake: impacts on submerged macrophytes. *Ecosystems*, 2006, **9**: 1017-1028.

[158]　Arnott DL, Vanni MJ. Nitrogen and phosphorus recycling by the *zebra mussel* (Dreissena polymorpha) in the western basin of Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, 1996, **53**: 646-659.

[159]　Conroy JD, Edwards WJ, Pontius RA *et al*. Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralization in western Lake Erie. *Freshwater Biology*, 2005, **50**: 1146-1162.

[160]　Holland RE. Changes in planktonic diatoms and water transparency in Hatcher Bay, Bass Island area, Western Lake Erie since the establishment of the *zebra mussel*. *Journal of Great Lakes Research*, 1993, **19**: 617-624.

[161]　Fahnenstiel GL, Lang GA, Nalepa TF *et al*. Effects of *zebra mussel* (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research*, 1995, **21**: 435-448.

[162]　Howell ET, Marvin CH, Bilyea RW *et al*. Changes in environmental conditions during Dreissena colonization of a monitoring station in eastern Lake Erie. *Journal of Great Lakes Research*, 1996, **22**: 744-756.

[163]　Malkin SY, Guildford SJ, Hecky RE. Modeling the growth of *Cladophora* in a Laurentian Great Lake in response to changes due to the exotic invader Dreissena and to lake warming. *Limnology and Oceanography*, 2008, **53**: 1111-1124.

[164]　Nicholls KH, Standke SJ. Effects of *Zebra Mussels* on chlorophyll, nitrogen, phosphorus, and silica in north shore waters of Lake Erie. Ministry of the Environment and Energy, Toronto, Canada, 1997: 37.

[165]　Barbiero RP, Rockwell DC, Warren GJ *et al*. Changes in spring phytoplankton communities and nutrient dynamics in the eastern basin of Lake Erie since the invasion of *Dreissena* spp. *Canadian Journal of Fisheries and Aquatic Sciences*, 2006, **63**: 1549-1563.

[166]　Hecky RE, Smith REH, Barton DR *et al*. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 2004, **61**: 1285-1293.

[167]　Patrick R, Rhyne CF, Richardson RW *et al*. The potential for biological controls of *Cladophora glomerata*. United States Environmental Protection Agency, EPA 600/3-83-065, 1983: 153.

[168]　LaLonde RT, Morris CD, Wong CF *et al*. Response of *Aedes triseriatus larvae* to fatty acids of *Cladophora*. *J Chem Ecol*, 1979, **5**: 371-381.

[169]　Bird GA, Kaushik NK. Processing of decaying maple leaf, *Potamogeton* and *Cladophora* packs by invertebrates in an artificial stream. *Archiv fur Hydrobiology*, 1985, **105**: 93-104.

[170]　Bott TL, Rogenmuser K. Fungal pathogen of *Cladophora glomerata* (Chlorophyta). *Appl Environ Microbiol*, 1980, **40**: 977-980.

[171]　Raghukumar C. Fungal parasites of the marine green algae, *Cladophora* and *Rhizoclonium*. *Bot Mar*, 1986, **29**: 289-297.

[172]　Raghukumar C. Fungal parasites of the marine algae from Mandapam (South India). *Dis Aquat Org*, 1987, **13**: 137-145.

[173]　TeStrake D, Aldrich HC. Ultrastructure of two associations involving marine fungi and green algae. *Bot Mar*, 1984, **27**: 515-519.

[174]　Caffrey JM, Monahan C. Filamentous algal control using barley straw. *Hydrobiologia*, 1999, **415**: 315-318.

[175]　Irene M, José MO, Morgens R *et al*. The effect of salinity on the growth rate of the macroalgae *Enteromorpha intestinalis* (Chlorophyta) in the Mondego estuary (west Portugal). *Acta Oecologica*, 1999, **20**: 259-265.

[176]　Zhao ZJ, Liu GX, Hu ZY. A new combination species of freshwater Cladophorales and its phylogenetic analysis. *Plant Science Journal*, 2015, **33**(3): 281-290. [赵志娟, 刘国祥, 胡征宇. 淡水刚毛藻目—新组合种及其系统发育分析. 植物科学学报, 2015, **33**(3): 281-290.]

[177]　Teng LH. Study on morphology and molecular phylogeny of Cladophorales (Chlorophyta) along China sea coast[Dissertation]. Qingdao: Institute of Oceanology, Chinese Academy of Sciences, 2011. [滕林宏. 中国刚毛藻目海藻的形态及系

统发育学研究[学位论文]. 青岛：中国科学院海洋研究所，2011.]

[178] Guo LL, Zhou WC, Zhou QC *et al*. Effects of light intensity and phosphorus concentration on the growth of *Cladophora oligoclona*. *China Environmental Science*, 2015, **35**(7): 2153-2159. [郭亮亮，周维成，周起超等. 光照强度和磷浓度对寡枝刚毛藻生长的影响. 中国环境科学，2015，**35**(7)：2153-2159.]

[179] Li P, Su HH, Guan WC. The effect of high CO_2 concentrations and UVR on growth and photochemical efficiency in *Amphiroa* sp. (Rhdophyta) and *Cladophora* sp. (Chlorophyta). *Acta Hydrobiologica Sinica*, 2014, **38**(4): 636-641. [李平，苏海虹，关万春. 高 CO_2 和 UVR 对叉节藻和刚毛藻生长及光化学效率的影响. 水生生物学报，2014，**38**(4)：636-641.]

[180] Han ZG, He LJ, Gu JG. *Cladophora fascicularis* during its dehydration and rehydration. *Chinese Journal of Ecology*, 2005, **24**(11): 1291-1294. [韩志国，贺立静，顾继光等. 束生刚毛藻脱水和复水过程中光合作用的变化. 生态学杂志，2015，**24**(11)：1291-1294.]

[181] Li H. The study of toxic effect, enrichment and tolerance mechanism between heavy metal and *Cladophora*[Dissertation]. Hefei: Anhui Agricultural University, 2013. [李浩. 重金属的刚毛藻毒害效应及藻体富集机理[学位论文]. 合肥：安徽农业大学，2013.]

[182] Zhang XL, Sun LP, Zhong Y. Removal of different forms of phosphorus by *Cladophora*. *Chinese Journal of Environmental Engineering*, 2017, **11**(5): 2743-2747. [张新龙，孙力平，钟远. 刚毛藻对不同形态磷的去除. 环境工程学报，2017，**11**(5)：2743-2747.]

[183] Li DH, Shi LX, Li GB. Effect of decomposed filamentous green algae on water quality and the growth of submerged macrophyte *Hydrilla verticillata*. *Environmental Science and Management*, 2006, **31**(6): 27-30. [李敦海，史龙新，李根保等. 丝状绿藻腐烂过程对水质和沉水植物黑藻生长的影响实验研究. 环境科学与管理，2006，**31**(6)：27-30.]

[184] Xiang SF, Lan B, Yang JY *et al*. The characters of Cladophora community in the littoral zone of Lake Erhai. *Acta Hydrobiologica Sinica*, 2011, **35**(6): 1049-1055. [向贤芬，兰波，杨娇艳等. 洱海沿岸带刚毛藻群落的特性分析. 水生生物学报，2011，**35**(6)：1049-1055.]

[185] Yang K, Dong J, Guo LL *et al*. The population structure and the distributing characteristics of *Cladophora* in the littoral zone of Dianchi Lake. *Journal of Hydroecology*, 2013, **34**(3): 8-16. [杨凯，董静，郭亮亮等. 滇池沿岸带刚毛藻种群结构及分布特征. 水生态学杂志，2013，**34**(3)：8-16.]