海草生态学研究进展

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摘要：海草床生态系统是生物圈中最具生产力的水生生态系统之一，具有重要的生态系统服务功能。作者根据海草生态学及相关领域的最新研究进展，对世界范围内海草床的空间分布、海草床的生态系统服务功能以及外界因素对海草床的影响等研究进展进行了综述。海草床生态系统服务功能主要包括净化水质、护堤减灾、提供栖息地和生态系统营养循环等。对海草床影响较大的外界环境因素包括盐度、温度、营养盐、光照、其他动物摄食、人类活动和气候变化等。海草普查、海草生态功能研究，影响海草床的主要环境因素，海草修复研究等将是我国海草研究的主要方向。

关键词：海草床；生态功能；环境因子
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Progress in the study of seagrass ecology

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Abstract: Seagrass beds are highly productive coastal ecosystems and provide habitat for a diverse and abundant range of associated flora and fauna. In this paper the spatial distribution of seagrasses throughout the world has been described and the effects of various environmental factors on seagrass health have been reviewed. The ecosystem services provided by seagrasses include nutrient cycling, provision of fish habitats, protection from coastal erosion and buffering of the impacts of poor water quality. Major environmental factors influencing seagrass distribution and abundance include temperature, salinity, nutrients, light intensity, grazing and climate change. Further research is required on Chinese seagrasses to examine the ecology, ecosystem functioning and, the environmental factors influencing distribution and abundance. In addition, at some locations, the possibility of restoring degraded seagrass beds could be investigated.

Key Words: seagrass; ecology; environmental factors

海草是单子叶草本植物[1]，通常生长在浅海和河口水域[2]。海草床作为最具生产力的生态系统[3]，对海岸带区域具有重要作用[4]，不仅可以为海洋生物提供重要的栖息地[5]和食物来源[6]，而且在全球 C、N、P 循环中具有重要作用[7]。全世界的海草包括 12 个属，约 50 多种，隶属于沼生目（Helobiae）的眼子菜科（Potamogetonaceae）和水鳖科（Hydrocharitaceae）[8]。南中国海分布了 20 多种[7]，我国分布有 8 属，包括大叶

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藻属(*Zostera*)、虾形藻属(*Phyllospadix*)、二药藻属(*Halodule*)、海神草属(*Cymodocea*)、针叶藻属(*Syringodium*)、海菖蒲属(*Enhalus*)、海黾草属(*Thalassia*)和喜盐草属(*Haliphila*)[9]。

近年来,国外学者在海草生态学领域开展了许多卓有成效的工作,研究领域主要涉及海草时空分布[10],食物链[11]、能量流动[12,13]和物质循环[14]等方面,为海草生态系统研究奠定了基础。我国海草生态学研究尚处于起步阶段,较有代表性的研究成果是中国科学院南海海洋研究所的 Huang 等[15]对我国华南沿海海草床进行了系统研究。本文对海草床的生态功能和生态学相关研究进展进行了系统的回顾,以期为我国海草生态学研究提供参考,同时也为我国海草资源的可持续利用提供科学依据。

1 海草的分布

关于海草空间分布区系学术界还存在争议。Hemminga 和 Duarte[10]将全球海草分为九大区系:温带北大西洋区系、温带南大西洋区系、温带东太平洋区系、温带西太平洋区系、地中海区系、加勒比海区系、印度-太平洋区系、南澳大利亚区系和新西兰区系。Short 等[16]根据物种丰度、物种分布范围、热带和温带影响等将全球海草分为六大区系:温带北大西洋区系、温带北太平洋区系、地中海区系和温带南大洋区系、热带大西洋区系和热带印度-太平洋区系。我国海草主要分布在温带北太平洋区系和印度-太平洋区系。我国华南地区海草床主要分布在广东的流沙湾、湛江东海岛和阳江海陵岛等,广西合浦和珍珠港海域,海南黎安港、新村湾、龙湾和三亚湾等,面积约为 2400hm^2[15],中国其他地区海草床分布和面积还未见文献报道。

海草的分布被限制在比较浅的海水中,最大海草分布深度为水下 90m 处[5],大多数的海草种类分布在 20m 以浅海域内[17]。

2 海草的生态功能

2.1 净化水质功能

海草可以调节水体中的悬浮物、DO、叶绿素、重金属和营养盐[18,19]。Lewis 等[20]对美国佛罗里达州 13 处海草床的水质、沉积物和海草个体组织的研究表明,有海草区域的沉积物比没有海草区域的沉积物富集的重金属浓度高,说明海草具有富集重金属的功能。大洋聚伞藻(*P. oceanica*)被证明是很好的重金属生物指示因子[21,22],大洋聚伞藻比贝类具有更好的生物储存能力[23]。海草还可以通过地上和地下组织吸收无机营养盐[24,25]。

2.2 护堤减灾功能

海草被证明能降低来自于波浪和水流的能量[13],从而可以防止海岸侵蚀[26]。海草还可以改变沉积物的沉积速率[27],主要通过在生长季提高沉积物中的淤泥量,一年生海草对沉积速率的影响取决于海草遮蔽(canopy)的密度。海草还可以通过根和茎增加沉积物的沉降速率[28],对沉积物起到稳定作用[29,30]。Bos 等[27]研究发现:鳗草(eelgrass)能通过在自身生长过程中增加沉积物中淤泥的量改变自身的生存环境。

2.3 栖息地功能

海草床结构的复杂性决定了其重要的栖息地功能,主要包括决定深海群落的组成,增加海草床区域物种丰度和生物多样性等[31,32]。海草床生态系统具有相对复杂的物理结构,能为重要的商业鱼类提供食物来源和育苗场所,海草床可以为幼苗提供庇护场所已经被科学家广泛的接受[11,33]。海草也为临近区域的盐沼、贝类、珊瑚礁和红树林的很多物种提供重要的育苗场所[34]。海草能提供关键栖息地,为儒艮(Dugong)、长须鲸、贝类和海鸟等提供营养基础[35]。

海草与其他海洋植物相比具有竞争力的优势是因为:海草可以固定在松软的海洋底质上面,从沉积物中补给所需要的营养物质,从而储存资源[36]。研究表明,上百种的浮游植物和深海洄游种靠海草床维持生存[11],一些草食动物直接以海草为食,使得海草床中的 C 通过微生物过程和颗粒有机碎屑进入浅海和河口食物网[14]。

2.4 生态系统营养循环

海草生长所必须的营养盐主要来源于水体和沉积物中有机物质的分解[37]。海草碎屑是海草床中可以再

利用的营养物质的主要有机来源,海草床中的有机物质循环可以通过有机物质的快速降解来完成[38]。海草床中存储的营养盐可能在0.3~6d内迅速转化,在龟草(*T. testudinum*)床内,溶解性无机N在水体和沉积物中的转化时间少于2d[39]。研究表明,海草贡献了全球海洋中有机碳的12%[40]。

3 外界因素对海草床生态系统的影响

3.1 盐度和温度对海草的影响

盐度可以对海草群落的健康产生潜在影响。Gacia 等[41]研究了盐水对大洋聚伞藻的影响,证明大洋聚伞藻对富营养化和高盐度具有较高的灵敏度,而且受影响的海草叶片中具有较高的附生菌类负荷和N含量、较高的坏疽爆发频率、较低的谷氨酸合成酶活动,却没有引起海草床的明显衰退。其他研究也表明,盐度可能并不是导致海草灭绝的唯一原因,高的盐度能改变植物体内C和O的平衡,从而对海草群落的健康产生潜在影响[42]。Biebel 等[43]研究表明,大叶藻在淡水和2倍正常海水盐度的水体中几乎不能进行光合作用,在4倍海水盐度的水体中,其叶子在24h内死亡。

海草对温度的适应范围很大,除了北冰洋沿岸,全世界几乎所有的海岸都有海草分布[44]。温度通过影响有机体的生物化学过程,从而成为控制海草生长的主要因素[45]。研究表明,温度和海草生物量在水温低于海草存活的最佳温度时,呈明显的正相关,而在夏季高温对海草生长产生抑制的情况下,温度与海草的生物量呈负相关[46]。温度对不同海草光合作用的影响程度不同,总的来说,海草在25~30℃时显示出最大饱和光强的光合作用[47]。

3.2 营养盐对海草的影响

无机营养盐N和P被认为是控制海草生长的主要因素[45]。海草及在海草床中的生物生长、繁殖与海草床中营养物质含量有着密切的关系[48]。营养盐的浓度会对海草的生长产生限制。通常的研究表明,生长在砂质和有机沉积物中的海草受到N限制,生长在碳酸盐沉积物中的海草受到P限制[49,50],在某些特定条件下,海草可能受到N和P的双重限制[51]。N的限制可以解释为海草和其他群落如微藻、大型藻类和其他微型异养生物在自然生态系统内的竞争,那些微型异养生物能吸收较高比重的再生氨[52]。

由于沉积物间隙水中营养盐浓度比水体中高很多[46,53],因此沉积物间隙水通常被认为是海草中营养盐的主要来源[54]。沉积物中增加的营养盐,通过改变海草的光合作用效率和提高叶绿素浓度,促进海草的生长,提高海草的生物量[55]。

尽管海草可以从水体和沉积物中利用无机营养盐,但是提高水体中营养盐浓度会刺激浮游植物和附生植物的生产力,从而对海草产生负面影响[56,57]。水体中营养物质的富集引起的竞争性初级生产者的繁盛,可以造成海草可利用光的降低[56]。过量的营养盐负荷对近岸水质产生有害影响,从而对海草床产生不利影响[57]。陆源污染带来的大量营养盐会影响海草的存活率和水体中DO的含量[58]。有研究表明水体中NO_3^-的富集能引起鳗草的衰退[59]。Caba[60]的研究结果表明,在有人类排放的营养盐干扰的地区,大叶藻的生物量和密度之间具有明显的相关关系,在无人类营养盐干扰区域,大叶藻的生物量和密度之间不相关。

N和P的过量输入海洋被认为是世界范围内海草消失的重要原因[61]。研究表明,海草栖息地水体中NH_4^+浓度在3~220μmol/L,沉积物间隙水中为500~1600μmol/L时就会引起海草的死亡[62]。

3.3 光照对海草的影响

光的利用是控制海草生产力、分布和存活最重要的因子[63,64]。海草对于光的适应性能通过支持生长和降低限制条件的易感性,改善海草的恢复能力[58]。Campbell 等[58]的工作表明,光子流量作为控制海草生长的初始因子具有重要意义,同时,海草对于光的生理调节也能被用来评估海草适应和容忍周围环境的能力。

与陆地植物相比,海草具有较低的光合速率,一般为3~13mgO_2(gDW·h)[65]。海草也具有较低的光补偿点和光饱和点,如二药藻属和喜盐草属普遍具有较低的光补偿点,较低的光饱和点保证了海草一天中有较长的时间达到净光合生产,来保证其正常生长[66]。

水下光环境的变化被认为是海草衰退的重要原因[2]。海草对光的反应包括生物化学[67]和生理[68]的适

应,这种适应主要影响生长率、海草的生理结构、形态特性(包括海草高度,枝径密度,地上和地下生物量比值(AG/BG))以及海草的分布等[69,70]。海草生长需要的最小光强非常重要,它的重要性表现在不同的海草种类在最低的光水平上能存活的时间,实验已经表明:一些海草种类可以在所需要的最小光强度以下存活几周到几个月[71,72]。

3.4 其他动物摄食对海草的影响

研究表明,海草密度的变化取决于其他物种的数量[73],科学家认为食草动物 *Scarid herbivory* 对印度太平洋海草床生态系统动力学具有重要作用[74],*Scarid herbivory* 不仅可以直接以海草为食,将海草床中的 C 纳入食物链,而且通过对海草碎屑材料的输出,对碎屑食物链具有重要贡献。研究表明其他动物对海草种子的掠夺对海草床生态系统中种子的稳定具有明显的负面影响[75]。Orth 等[76]的研究表明,甲壳类的不同种群在大多数海草床中都对海草种子具有较高的掠夺率。

海草床作为儒艮重要的栖息地[77],儒艮的捕食压力会对海草群落的结构和功能产生影响[78,79,80]。Masini 等[79]对西澳大利亚鲨鱼湾二药藻的研究表明,从 1 ~4 月份,受保护不受儒艮捕食的海草床的生物量是临近未保护区域的 1.8 倍。海草可以通过自身的结构和功能选择海草床内的捕食者,例如,海草的根和茎能防止一些类型的底栖生物在海草床内定居[81]。

3.5 硫化物的影响

Borum 等[82]认为沉积物中的硫化物可能是硫含量较高的水生环境中控制海草生长和存活的主要因素。硫化物通过影响区域内的微生物呼吸率,根周围沉积物氧化区的范围,以及当地沉积物生物地球化学循环等[83],对海草的生长产生重要影响。

Calleja[84]等人研究发现:间隙水中的 H_2S 浓度超过 10μmol/L 时,就会引起大洋聚伞藻的衰退,而且该研究也证实了大洋聚伞藻对硫化物具有较高的敏感性。尽管沉积物中较高的硫化物浓度会对海草产生负面影响[85],科学家研究表明可以通过铁络合物去除硫来改善海草的生长状况[86,87]。

3.6 人类活动的影响

人类活动如海水养殖、填海、溢油和船舶活动等提高了水体的浑浊度,导致藻类的过量繁殖,最终造成了海草的消亡,和人类相关的其他变化如全球变暖、外来物种入侵等也会导致海草床的衰退[88]。

海水养殖会使海草生长率降低,海草床扩散受到限制[89],养殖 3a 后,甚至会引起海草床灭绝[90]。养殖活动通过降低光的穿透作用来降低海草叶片的光合作用[91]。养殖活动产生的过量 N、P 等营养物质造成浮游生物和藻类的过量繁殖,会吸收大量的营养物质和光,造成海草生长缓慢[92]。养殖物种排泄物质的不断排放,导致有机物质的累积,改变了沉积物特性,也会对海草床产生不良影响[93]。

疏浚和挖沙对海草的影响主要包括对海草个体的物理去除和掩埋,以及增加海水的混浊度和悬浮物的沉降[94]。海草对于海水混浊度和悬浮物沉降的临界极限,在不同海草种类之间差别很大,大型且生长缓慢的储存有较多种类碳水化合物的海草种类,比其他小型海草种类具有较好的恢复能力。但是,小型的海草种类在海水水质恢复到被影响以前水平时,表现出较快的恢复能力。

掩埋和侵蚀也会对海草产生不利影响[95],实验室研究已经证实,海草在完全掩埋情况下,存活不超过 2 周[95],在掩埋实验中,叶和根茎中的 C,以及非结构碳水化合物的含量会明显下降,叶片的 N 含量也会明显下降,而根茎中的 N 含量却持续增加,叶片中损失氮的 50% 会被根茎重新吸收[95]。

娱乐船只以及船只的相关设备被证明可以增加海水的混浊度、海岸侵蚀和营养物质富集[96],从而对海草床造成机械损伤[97,98]。最明显的生态影响是码头等建筑物阻挡住栖息地的光,妨碍海草的光合作用,导致海草的衰退[99]。Fyfe 和 Davis[100]研究了沿岸建筑物对海草空间分布的影响,结果表明,海草床周围建筑物建成 46 个月后,海草枝径密度下降到 30% 以下。Giulia[101]等模拟了锚对大洋聚伞藻的短期影响,结果表明,锚的扰动对大洋聚伞藻具有强烈的影响。

3.7 气候变化对海草的影响

全球气候变化主要包括海平面,温度和大气中 CO_2 的变化[102],上述变化可以改变海草的分布、生产力和

群落组分[103]。海水温度的变化直接影响海草的新陈代谢和海草 C 平衡的维持[104],从而引起物种丰度和分布的地理和季节模式变化[105]。海平面上升对海草床的直接影响是海水深度的提高和海底可利用光的降低[106],已研究的海草栖息地表明,海平面上升引起海草分布区域减少,生产力下降,生态系统结构改变,生态系统服务功能降低[107]。CO_2浓度的提高可引起海草生物量的增加[108]。海草对于 CO_2增加的反应主要取决于和其他环境因素的关系,当营养盐、温度和光被限制时,这种反应被减弱[109]。

4　我国海草研究概况及展望

我国的海草研究始于 20 世纪 80 年代,中国科学院海洋研究所的杨宗岱等[9,110,111]对中国海草床的分布、生产力及其结构与功能等进行了分析,但是并未对中国海草的具体分布、种类和生物学特征等进行深入研究。自 2003 年以来,中国科学院南海海洋研究所的 Huang 等[15]在联合国环境规划署/全球环境基金(UNEP/GEF)项目的资助下,对我国华南地区主要海草的分布、种类、生物量、生产力和所面临的主要威胁等进行了较为系统的研究。韩秋影等[112,113]也对广西合浦海草床生态系统服务功能价值进行了系统评估。总体上看,我国海草研究目前仍处于起步阶段,未来我国海草的研究应集中在以下几方面。

4.1　海草普查

尽管 Huang 等[15]对我国华南地区海草床进行了较为系统的普查,目前学术界并未对我国东部和北方海域海草的基本状况进行研究,应利用现代监测技术对海草床及海草床生物进行调查,积累我国海草床的基础数据,建立海草数据库,为加强我国海草床的研究和管理提供支持。

4.2　海草生态功能研究

海草具有多种生态系统服务功能已经得到国际学术界的普遍认同,大多数关于海草生态系统服务功能的认识只是从某几种物种的研究中获得,但是,从已经进行很好研究的海草中得出的结论不能被应用到其他区域和其他海草物种中[114]。因此,学术界应对我国近岸海域的海草生态系统服务功能进行研究,为充分利用和保护其服务功能提供科学依据。

4.3　影响我国海草床的主要环境因素

学术界普遍认为海草的分布和丰度受一定的环境条件限制,包括地理位置[115]、营养物质情况[116]、温度[117]、盐度[48]、光的利用[117]、水流动模式[115]、水质透明度[118]、以及以海草为食的动物[119]等。还有学者认为导致海草床退化的自然原因主要包括沙子的移动[120]、地震,火山喷发和飓风[121]等。学术界应对影响我国海草床的主要环境因素进行系统的分析,为海草床的保护和修复提供理论依据和技术支持。

4.4　海草修复研究

尽管世界范围内海草床的衰退已经在学术界达成共识,但是很少关于受影响海草恢复效率的研究[122]。主要是由于长期监测项目的缺乏,和衰退海草床恢复实验的失败[121]。我国目前海草研究尚处于起步阶段,还没有开展海草床的修复研究。由于不同区域海草种类及控制海草生长的主要因素如光照、盐度、营养水平、竞争等表现出很强的地域性,因此需要对影响海草生长的因子做进一步的研究,针对我国海草床的特点,制定出科学合理的恢复方案。

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