第 44 卷　第 4 期
2023 年　8 月

渔　业　科　学　进　展
PROGRESS IN FISHERY SCIENCES

Vol.44, No.4
Aug., 2023

DOI: 10.19663/j.issn2095-9869.20221229001　http://www.yykxjz.cn/

杜建国，陈炜霖，邱广龙，张涵，陈彬，胡文佳，郭玉清. 海草有性繁殖成花诱因研究进展与展望. 渔业科学进展，2023, 44(4): 01–11

DU J G, CHEN W L, QIU G L, ZHANG H, CHEN B, HU W J, GUO Y Q. Research progress and prospects of flowering induction for seagrass sexual reproduction. Progress in Fishery Sciences, 2023, 44(4): 01–11

海草有性繁殖成花诱因研究进展与展望*

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摘要　海草是一类生活在热带至温带浅海、完全适应海洋环境的沉水被子植物的总称。海草床作为连接珊瑚礁与红树林的纽带，具有重要的生态功能与经济价值。近年来，随着人们对海草认识的不断加深，海草的有性繁殖行为逐渐受到关注，而成花诱导是海草从营养生长向生殖生长过渡的重要环节。本文综述了海草有性繁殖中成花诱因的研究进展，探讨了温度、光照、盐度等相关因子对海草成花诱导的影响，分析了海草响应外界环境刺激与内源信号启动开花途径可能集中在光周期途径、春化途径和自发途径上。建议未来海草床保护修复工作应加强对海草有性生殖行为的研究，明确不同海域海草的集中开花和结果时间，对海草床生态系统的修复与保护具有重要意义。

关键词　海草；有性繁殖；成花诱导；开花途径

中图分类号　Q948.8　**文献标识码**　A　**文章编号**　2095-9869(2023)04-0001-11

海草(Seagrass)是一类生活在热带至温带浅海、完全适应海洋环境的沉水被子植物的总称(Unsworth *et al*, 2022; 张沛东等, 2020)。海草生态系统作为连接珊瑚礁与红树林生态系统的纽带，在改善水质、提供育幼场、保护海岸带、提供蓝碳、缓解气候变化等方面有着重要贡献(Macreadie *et al*, 2019; Du *et al*, 2020a、b)，海草也为鱼类、海龟、儒艮等海洋生物直接或间接提供食物来源(黄小平等, 2006; Du *et al*, 2016、2019)。但是，自 20 世纪 80 年代以来，由于全球气候变化以及区域性围填海、破坏性挖捕、水体富营养化等人为活动影响，全球海草面积减少约 29%，并正以每年 1%~7% 的速度继续减少(Waycott *et al*, 2009; Unsworth *et al*, 2022)。与此同时，我国海草床也面临着不断退化的风险(郑凤英等, 2013; Hu *et al*, 2021)。截至 2020 年，我国海草床总面积约为 2.6×10^4 hm^2，近岸海域超过 80%的海草床已经消失(于硕等, 2022)。以海南岛为例，2009—2019 年期间，黎安港海草床面积减少约 114 hm^2，占黎安港海草床总面积的 55% (吴钟解等, 2014; 陈石泉等, 2020)；2016—2020 年新村港海草床面积减少约 79 hm^2，约占新村港海草床总面积的 16% (Li *et al*, 2022)。此外，海南岛其他海草床的面积、盖度、密度、生物量也有所降低。分布在中国北方的温带海草床，其面积、种类、生物量等也存在着不同程度的下降(刘伟妍等, 2017)。

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* 国家自然科学基金(42176153、41676096)和自然资源部项目(HR04-210705)共同资助。杜建国，E-mail: dujianguo@tio.org.cn

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收稿日期: 2022-12-29, 收修改稿日期: 2023-04-07

为了缓解海草床面临的威胁，了解海草的繁殖特性并积极开展海草床保护修复工作尤为重要(Du *et al*, 2023)。海草的繁殖方式分为无性繁殖与有性繁殖，其中，无性繁殖主要以克隆生长的方式(张沛东等, 2020)，有性繁殖则包括了植株开花、传粉、受精、种子发育等过程，少部分海草还具有胎生和假胎生行为(Kuo *et al*, 1990; Ballesteros *et al*, 2005)。当前对海草床的修复大多基于其克隆生长的繁殖模式，虽然这种方式生育成本低、个体存活率高，但易造成海草遗传多样性降低，一旦环境超过某种优势海草的抵抗阈值，便易造成海草床大面积的退化。相比之下，基于海草有性繁殖开展的修复工作能够维持海草床种群遗传多样性、建立当地新的海草斑块，基于此构建的土壤种子库也有利于海草床干扰后快速恢复(邱广龙等, 2022)。成花过程是海草有性繁殖的关键阶段，包括成花诱导、花发育和开花3个过程(周琴等, 2018)。其中，成花诱导是海草从营养生长向生殖生长过渡的重要环节，也是成花过程中最关键的步骤(宋杨等, 2014)。当前对海草成花诱导的机制与影响因素大多停留在野外观测与记录阶段，但基于有性繁殖的海草床修复方式已被公认为是较好的海草床修复方式。本文综述了近年来国内外关于海草成花记录与研究的相关文献，概述了影响海草成花的环境因素，拟为海草床监测、评估与修复提供理论参考。

1 海草有性繁殖特点

海草的有性繁殖具有以下几个特点：(1)有性繁殖具有策略性：海草为雌雄同株或雌雄异株(表1) (Ackerman, 2007)。Cox等(1988)调查发现，龟裂泰来草(*Thalassia testudinum*)雄花与雌花比例为60∶1，这可能是因为在海洋环境中，花粉易因接收不足而产生花粉限制，以及产生雄花所需能量远低于产生雌花和果实的能量(van Tussenbroek *et al*, 2010、2016a)。海草的雌雄性器官成熟的先后不同，海草可以通过这种方式促进异交，保证基因的多样性(Ruckelshaus, 1995; Ackerman, 2007; Entrambasaguas *et al*, 2017)。(2)授粉方式独特：与陆生植物不同，海草的花小且构造上大多退化(柯智仁, 2004)。部分海草产丝状花粉，这种花粉形态更有利于在海水动态流动的状态情况下进行水上或水下授粉(表1) (Cox, 1983; Ackerman, 2007)。此外，花粉的释放、运输、捕获受到水流与海草冠层之间相互作用的影响(Ackerman, 2002)。之前观点普遍认为，海草授粉仅通过海水流动进行，海洋生物不参与海草的授粉过程，但van Tussenbroek等(2016b)通过室内实验发现，在夜间没有水流的情况下，无脊椎动物在花朵附近觅食时，黏性的花粉粒会附着在无脊椎动物身上，当其靠近雌花柱头时被捕获并成功授粉。(3)海草植株的成熟时间较长：海草具有一年生与多年生的生长形式，不同的生长形式对海草群落的生物多样性与遗传多样性具有重要的贡献(邱广龙等, 2022)。在对菲律宾的海草床调查中发现，圆叶丝粉草(*Cymodocea rotundata*)与泰来草(*Thalassia hemprichii*)开花率分别为5.6%和17.0%，且开花株年龄皆为0.5年以上(Duarte *et al*, 1997)，而鳗草(*Zostera marina*)的开花株

表1 不同属海草有性生殖特性

Tab.1 Selected reproductive characters in seagrass genera

属名 Genus	授粉方式 Pollination mode	雌雄同株/雌雄异株 Dicliny	花粉 Pollen
丝粉草属 *Cymodocea*	水下 Submarine	雌雄异株 Dioecious	丝状 Filiform
二药草属 *Halodule*	水下 Submarine	雌雄异株 Dioecious	丝状 Filiform
针叶草属 *Syringodium*	水下 Submarine	雌雄异株 Dioecious	丝状 Filiform
全楔草属 *Thalassodendron*	水下 Submarine	雌雄异株 Dioecious	丝状 Filiform
海菖蒲属 *Enhalus*	水面 Surface	雌雄异株 Dioecious	球状 Spherical
喜盐草属 *Halophila*	水下 Submarine	雌雄同株、雌雄异株 Monoecious and dioecious	椭圆状 Ellipsoidal
泰来草属 *Thalassia*	水下 Submarine	雌雄异株 Dioecious	球状 Spherical
川蔓草属 *Ruppia*	水面 Surface	雌雄同株 Monoecious	丝状 Filiform
虾形草属 *Phyllospadix*	水下、水面 Submarine and surface	雌雄异株 Dioecious	丝状 Filiform
鳗草属 *Zostera*	水下、水面 Submarine and surface	雌雄同株 Monoecious	丝状 Filiform

注：改自Ackerman (2007)。Note: Adapted from Ackerman (2007).

年龄均为 1 年以上(Duarte *et al*, 1997; Blok *et al*, 2018)。(4)受多因素影响：海草有性生殖行为不仅受单一因素影响，而是多种因素共同作用的结果。研究表明，温度(McMillan, 1980; Qin *et al*, 2020a)、光照(Collier *et al*, 2012; Olesen *et al*, 2017)、盐度(Fernández *et al*, 1999; Ankel *et al*, 2021)、水深(Cox, 1988; Tongkok *et al*, 2017)、营养盐(Smith *et al*, 2016; Jackson *et al*, 2017)等相关因素均会对海草有性生殖造成影响。

2　海草成花的研究趋势分析

2.1　研究数量趋势

本研究基于文献计量手段对海草成花研究发展趋势进行了分析与归纳总结。研究选择了美国科学信息研究所(Institute for Scientific Information, ISI)的 Web of Science 核心合集的 SCIE 数据库为检索源，选择已发表的国际期刊作为研究对象。以“seagrass flowering”作为检索关键词，共检索出相关文献 300 篇。从 2008—2021 逐年文献发表数量上看，海草成花相关文献整体呈增长趋势，并在近年来逐渐得到更多的关注(图 1)。

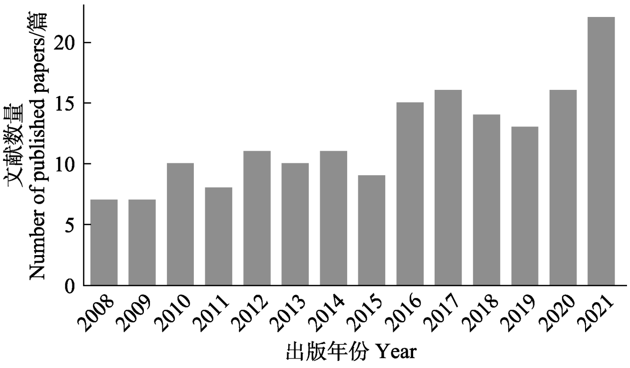

图 1　在 Web of science 检索 2008—2021 年关键词“seagrass flowering”文献数量

Fig.1　Number of literatures searched for the keyword “seagrass flowering” from 2008 to 2021 in Web of Science

2.2　海草有性繁殖与成花研究热点分析

高频关键词反映了该研究领域的热点主题与发展方向。利用 VOSviewer (Version 1.6.18)软件中的聚类算法对高频关键词进行统计和共现分析，并构建共现网络(图 2)。结果显示，1991—2022 年关于海草有性繁殖研究的高频关键词依次包括种群、发育、种子、遗传多样性、动力学、成花和发芽等。对出现频率>3 的关键词(共有 204 个)进行共现分析，通过关键词共现关系聚类，近 32 年来，海草有性繁殖领域的研究热点主题可归纳为相关因子研究、种群遗传研究、种群保护研究。3 个研究主题之间存在交叉联系。

本研究对海草成花研究热点进一步进行筛选，并对高频关键词进行统计和共现分析，并构建共现网络(图 3)。结果显示，从 1991—2022 年关于海草成花研究的高频关键词依次包括种子、生物量、授粉、花粉、气候变化、物候、营养物、光、食草活动、幼苗、季节性、温度、沉积物和盐度等。对出现频率>3 的关键词(共有 250 个)进行共现分析，通过关键词共现关系聚类，近 32 年来海草成花领域的研究热点主题可归纳为以下 3 个主题：(1)成花条件研究：主要关键词包括温度、光照、盐度、沉积物、营养盐、密度、生物量等；(2)种子发育研究：主要关键词包括种子、物候学、气候变化、水质、纬度等；(3)海草授粉研究：主要关键词包括授粉、花粉、DNA、雌雄比例、资源分配等。

3　影响海草成花的相关因子

尽管当前关于高等植物的成花诱因的研究多集中于模式生物与经济作物上，对海草的关注度相对较少，但已有相关研究表明，海草中同样存在诱导其成花的相关因子。这些因子主要分为两个方面，一方面主要与生物自身遗传、生理特性等因素相关，另一方面则主要与非生物因素(如温度、盐度、光照等)间接调控有关(Diaz-Almela *et al*, 2016)。

3.1　温度

海草对温度的适应性较强，除了北冰洋沿岸外，全球几乎所有海岸都有海草的分布(Short *et al*, 2007)。热带海草的最适温度为 23~32 ℃，温带海草的最适温度约为 12~26 ℃ (林显程等, 2019)。全球气候变化可能通过影响海草成花而影响海草的物候学(Diaz-almela *et al*, 2007)。当海水温度升高时，海草可能通过减少碳储备、降低有性繁殖的强度，以应对热胁迫造成的生理反应，过高的温度可能导致分生组织缺氧而造成植物死亡，从而影响越冬种群的规模，并对下一年海草种群的开花时间、强度、规模产生影响(Greve *et al*, 2003; Qin *et al*, 2020b)。如泰来草的成花与低温表现出显著相关性(McMillan, 1980; 许战洲等, 2008)，这种低温促使植物开花的现象成为春化作用，春化途径也是一些植物诱导开花的途径之一(孙昌辉等, 2007; 刘永平等, 2015)。但不同种类的海草对温度的响应不同。对大洋波喜荡草(*Posidonia oceanica*)研究发现，其开花率、开花强度与全年最高海表温存在显著正相关关系(Diaz-Almela *et al*, 2007)。Ruiz 等

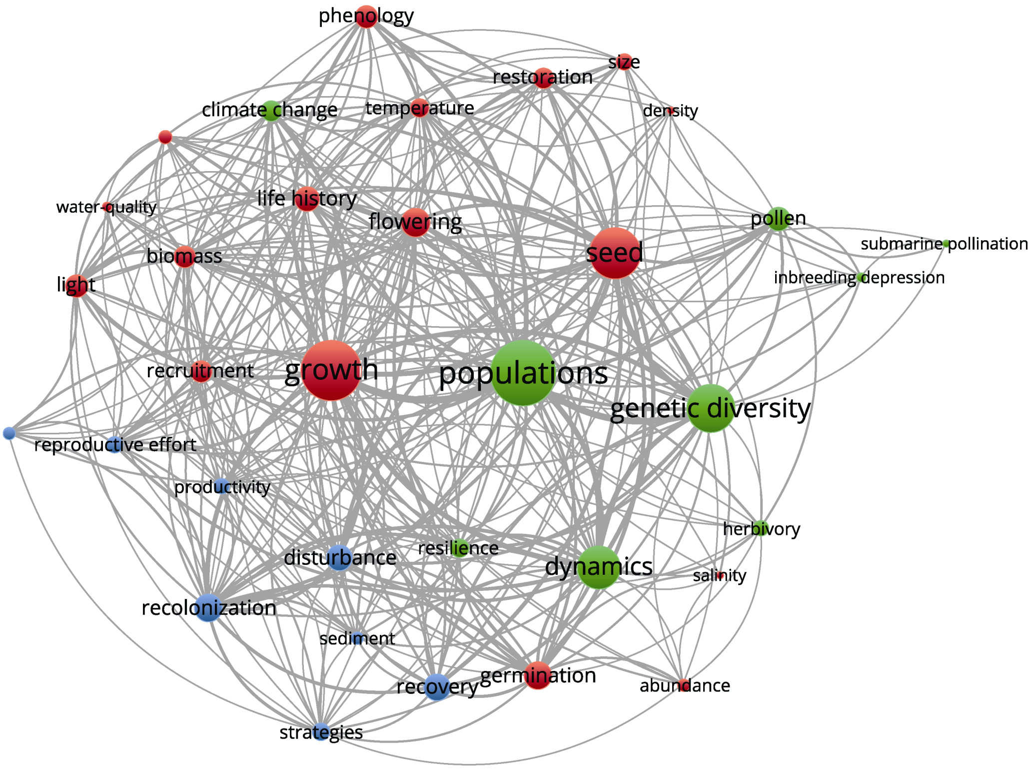

图 2　1991—2022 年海草有性繁殖研究的主要关键词及其共现关系

Fig.2　Main keywords and their co-occurrence in the seagrass sexual reproduction research in 1991–2022

红色为相关因子研究，绿色为种群遗传研究，蓝色为种群保护研究；字号与圆圈大小表示关键词的共现强度。
Red is the study of relevant factors, green is the study of population genetics, and blue is the study of population protection. Word size and circle size indicate the co-occurrence strength of keyword.

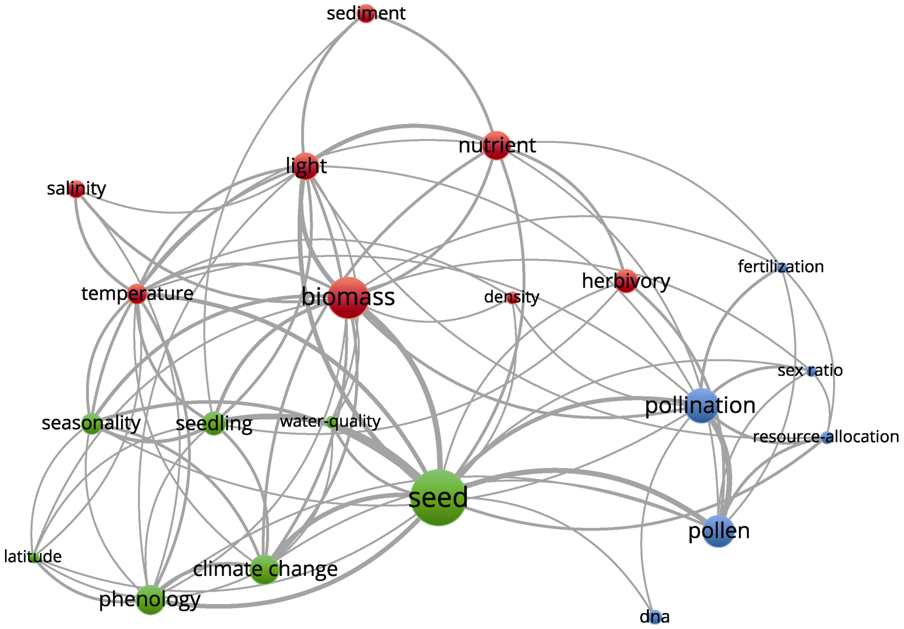

图 3　1991—2022 年海草成花研究的主要关键词及其共现关系

Fig.3　Main keywords and their co-occurrence in the seagrass flowering research in 1991-2022

红色为成花条件研究，绿色为种子发育研究，蓝色为海草授粉研究；字号与圆圈大小表示关键词的共现强度。
Red is the study of flowering conditions, green is the study of seed development, and blue is the study of seagrass pollination; word size and circle size indicate the co-occurrence strength of keyword.

表 2　我国不同种类海草成花温度

Tab.2　Flowering temperature of different seagrass in China

属名 Genus	种名 Species	成花温度 Flowering temperature/℃	参考文献 Reference
丝粉草属 *Cymodocea*	圆叶丝粉草 *Cymodocea rotundata*	27~31	McMillan (1982)
	齿叶丝粉草 *C. serrulate*	27~31	McMillan (1982)
二药草属 *Halodule*	羽叶二药草 *Halodule pinifolia*	–	–
	单脉二药草 *H. uninervis*	24~27	McMillan (1982)
针叶草属 *Syringodium*	针叶草 *Syringodium isoetifolium*	22~26	McMillan (1982)
全楔草属 *Thalassodendron*	全楔草 *Thalassodendron ciliatum*	–	–
海菖蒲属 *Enhalus*	海菖蒲 *Enhalus acoroides*	23~33	Kenyon 等(1997)
喜盐草属 *Halophila*	贝克喜盐草 *Halophila beccarii*	30~38	Zakaria 等(2002)
	毛叶喜盐草 *H. decipiens*	–	–
	小喜盐草 *H. minor*	–	–
	卵叶喜盐草 *H. ovalis*	–	–
泰来草属 *Thalassia*	泰来草 *Thalassia hemprichii*	22~26	McMillan (1982)
川蔓草属 *Ruppia*	川蔓草 *Ruppia* sp.*	18~25	Silberhorn 等(1996)
虾形草属 *Phyllospadix*	虾形草 *Phyllospadix* sp.*	15~21	Williams (1995)
鳗草属 *Zostera*	宽叶鳗草 *Zostera asiatica*	–	–
	丛生鳗草 *Z. caespitosa*	10~16	Lee 等(2005)
	具茎鳗草 *Z. caulescens*	–	–
	日本鳗草 *Z. japonica*	18~22	Lee 等(2005)
	鳗草 *Z. marina*	7~21	Lee 等(2005)

注：*表示未在中国分布的同属海草成花温度。–表示无成花温度数据。

Note: * It indicates the seagrass flowering temperature of the same genus not distributed in China. – indicates no flowering temperature data.

(2018)在室内人工环境下对大洋波喜荡草(*Posidonia oceanica*)进行了热暴露实验，同样表明热暴露是大洋波喜荡草成花的主要诱因。因此，温度的升高或降低都可能诱导海草成花，作者通过收集我国不同种类海草成花温度数据(表 2)，推测低温可能是海草受到春化作用而诱导成花，但高温可能是通过环境压力导致海草受迫，从而诱导成花。

3.2　光照

海草为沉水性植物，除部分浅海海草床在潮汐过程中出现短时间裸露外，大部分种类海草终生沉水生活。光照强度的变化一方面直接影响海草植株的形态特征、元素含量、生物量等(符妙等, 2022)；另一方面海草可以通过感知光照时间的周期变化调节自身新陈代谢及生理过程，如植株生长发育、固碳能力、相关基因表达等(Collier *et al*, 2012; Trevathan-Tackett *et al*, 2018; Wong *et al*, 2020; Ruocco *et al*, 2022)。Wong 等(2020)对鳗草海草床进行人为遮阴，遮阴后的鳗草通过改变植株形态、降低密度以维持低光照下的碳平衡。对有性繁殖而言，光照强度不足减少了海草对有性繁殖的投入，限制海草繁殖芽的诱导，导致海草的营养枝与开花枝的密度下降(Olesen *et al*, 2017; Qin *et al*, 2020b)。McMillan(1982)曾在实验室连续光照的环境下观察到多个属的海草开花，表明海草可能是长日照植物，即在长日照条件下可以促进开花，短日照则会抑制开花。海草的有性繁殖整体呈季节性，在一年四季中，夏季的日照时间长、温度高，较高温度和较高光照强度是海草进入有性繁殖的诱因，这也与温带海草多集中在夏季开花相符合(Ramage *et al*, 1998)，但同时将温度与光照作为变量对海草有性繁殖的研究较少。因此，未来对海草有性繁殖诱因研究过程中，应将温度与光强、光周期、光质等光照条件综合探讨。

3.3　盐度

海草长期生活在近岸海域，盐度的耐受范围为 5~35 (Nejrup *et al*, 2008)。盐度通过影响海草细胞渗透压而影响海草的生理生化结构(杨冉, 2015)。对混合种海草床而言，盐度的升高与降低对不同种类海草的生长动态产生影响，甚至可能会发生物种演替(Qiu *et al*, 2017)。关于盐度对海草成花的影响，相关文章记载较少且说法不一。McMillan (1980)研究表明，齿叶丝粉草(*Cymodocea serrulata*)的开花量随着盐度降低至25而增加。Ramage(1998)则认为，盐度下降会导致海草无法繁殖。此外也有研究表明，诺氏鳗草(*Zostera noltii*)在低盐度与高盐度情况下表现出较为相似的物候学(Ankel *et al*, 2021)。这表明盐度对海草成花的影响并不直接，可能通过对相关酶活性、光合速率等因子对海草产生影响(Fernández *et al*, 1999)。对多数海草种类而言，降低盐度可以提高海草种子的萌发率并缩短萌发历期(韦梅球, 2017)，故在受到低盐度胁迫时，海草植株可能更倾向于增加有性繁殖的投入。对不同种类、地域的海草在受到盐度胁迫响应是否一致仍然需要进一步研究。

3.4 水深与潮汐

海草一般栖息于潮下带6 m以上的近岸浅水区，最深也可分布至90 m，分布深度主要受到光照的影响(Duarte, 1991)。浅层海草与较深层海草的有性繁殖策略相似，但浅层海草开花芽发育早于较深层海草，可能通过这种方式影响种群内的基因交流与遗传结构(von Staats *et al*, 2020)。潮汐导致的深度变化会影响授粉的成功与否。对部分海草而言，雄花花粉释放后浮于水面，借助水流在水面上漂浮运输，花粉与同样浮于水面雌花柱头完成授粉过程，此时水深若大于雌花花梗长度，雌花将无法浮于水面从而影响授粉过程(Rollón *et al*, 2003)。Cox等(1988、1991)研究发现，全楔草(*Thalassodendron ciliatum*)与龟裂泰来草的开花与当地的极低潮有关，这可能是潮间带海草长期适应的结果，通过在低潮时期海草密集开花，更多的花粉与浮于水面的雌花授粉，通过低潮将立体授粉过程转为平面授粉过程，以提高授粉效率(Cox, 1983)。但潮汐在海草有性繁殖过程中可能并不起主导作用，可能通过改变水深影响光照与温度并对海草产生刺激。Tongkok (2017)研究发现，处于花期的泰来草对不同潮位、不同时间段的响应不同，在低潮位的夜间，泰来草的花开得最盛。

3.5 营养盐

海草生长于近岸，土地肥料使用与养殖尾水的排放易造成近岸海草床底质有机物富集。相关研究发现，在沉积物营养富集区域的鳗草的开花枝、开花枝高度、子房数量等都随着沉积物营养盐的富集而增加，较高的生殖枝能获得来自更远的花粉，一定程度上避免了近亲杂交，而子房数量则是直接影响海草种子产量(Jackson *et al*, 2017; Johnson *et al*, 2017)。营养盐过多富集还可能导致底质缺氧，产生有毒物质，并对海草床系统造成生存压力，通过胁迫诱导海草开花(Smith *et al*, 2016; Guerrero-Meseguer *et al*, 2021)。而水体的营养盐富集引发的大型海藻与附生藻类大量繁殖，使得海草可利用光能大幅度减少，从而对有性繁殖产生抑制(黄驰等, 2017; 刘伟妍等, 2017)。

3.6 其他

除以上主要环境因素外，地理位置(如纬度)也会对海草成花有一定影响。研究表明，广泛分布于不同纬度的温带海草鳗草，其开花物候与繁殖策略略有不同(Qin *et al*, 2020b)。未来海洋变暖一方面可能导致温带海草物种北移，另一方面可能导致海草有性繁殖提前，增强高纬度地区海草的有性繁殖能力(Blok *et al*, 2018; Wang *et al*, 2022)。此外，近年来一些研究也表明，海草具有逆境诱导开花的现象，即在受到胁迫时提前开花，通过调节自身生长与发育应对外界环境变化(张敏等, 2016)。如日本鳗草(*Zostera japonica*)在沉积物掩埋的干扰下，有性繁殖率随着掩埋程度的增加呈先上升后下降的趋势(Henderson *et al*, 2015)。Lekammudiyanse等(2022)研究也表明，修剪至1 cm的牟氏鳗草(*Zostera muelleri*)的开花率显著高于修剪至3 cm牟氏鳗草的开花率，这些结果均表明，在逆境条件下，海草会将个体更多资源分配给有性繁殖以抵御环境干扰。

4 海草有性繁殖在海草床修复与保护方面的应用

海草床修复最早记录于1947年，随着近年来海草床持续退化以及人们对海草床重要性认识的深入，海草床的修复与保护逐渐成为关注的热点(陈石泉等, 2021)。海草床修复方式可分为3种：生境恢复法、种子法和植株移植法(张剑, 2022)。其中，种子法被认为是成本低、破坏少，并能够维持遗传多样性的修复方式(于硕等, 2019)。但现阶段仍然面临种子收集难度大、数量不稳定等问题(韦梅球, 2017)。明确海草有性繁殖的成花诱因、准确判断成花时间，对使用种子法进行海草修复具有重要意义。

水生植物形成新种群更易依赖单一基因型的克隆生殖(Silvertown, 2008)。当一个特定基因型的海草非常适合当地的环境，那么可能会更多选择通过克隆生殖来扩大种群量，减少有性繁殖，降低可能改变关键性状的风险；不适应当地环境的基因型则可能会通

过有性繁殖产生新性状以提高适应能力(Henderson *et al*, 2015)。海草大多为雌雄异株，广泛的无性繁殖可能构成较多单性海草种群，这可能也是众多野外观察中果实与种子数量较少的原因(Rasheed, 2004)。海草在适宜的环境下进行大规模克隆生殖，意味着其面对胁迫时的承受能力较低，对大面积海草床而言，可以将基因型作为一项评估指标。

海草在生长过程中需要将有限的资源分配在生长、繁殖、抵御环境变化等方面，以保证其在当前环境下拥有适应能力(Rasheed, 2004)。海草床有性繁殖情况可能是对当地海草床压力状况的一种反映，长期处于高资源可利用地区的海草个体相较于低资源可利用地区的个体更可能将自身大部分能量用于海草有性繁殖(Johnson *et al*, 2017)。然而，现阶段关于逆境对海草有性繁殖的研究较少，在海草床长期监测过程中也未将其应用，建议未来在对海草床监测中可将有性繁殖率与一些受迫指标共同分析，更加全面对海草床健康状况进行评估。

5　总结与展望

近年来，国外研究者对海草有性繁殖关注度在逐步提升，我国关于海草研究起步较晚，对海草有性繁殖行为关注较低。本文整理了国内外海草成花相关文献，列出 6 项直接或间接影响海草成花的因素，认为海草响应外界环境刺激与内源信号启动开花途径可能集中在光周期途径、春化途径和自发途径上。但海草不同种类、不同种群间有性繁殖差异较大，现阶段对海草成花诱因与机理的认识仍不充分。

针对目前国内外海草有性繁殖成花诱因研究存在的主要问题，建议在以下几方面开展重点工作：(1)国内外对海草有性繁殖研究较少，野外海草的有性繁殖行为可能比目前认为的更常见，明确主要海草床集中开花时间对研究海草成花诱因、保护海草种子库等有促进作用；(2)开展海草成花诱因室内相关模拟实验，明确海草成花诱因，为室外海草有性生殖行为提供参考依据；(3)海草在逆境环境下进行有性繁殖的行为可用于指示气候与环境的变化，但现有的调查研究对海草有性繁殖的关注度较低，也未将有性繁殖率作为一项长期监测指标，建议在海草床长期监测、评估健康时将有性繁殖率与环境因子相结合，共同评估海草床状况。

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(编辑 冯小花)

Research Progress and Prospects of Flowering Induction for Seagrass Sexual Reproduction

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Abstract Seagrass is a group of flowering plants capable of completing their life cycle in a marine environment. It not only provides a refuge for biodiversity and essential fish spawning and

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nursery grounds, but also provides ecologically and socioeconomically important services for urban coasts. Seagrass is widely distributed along temperate and tropical coastlines globally. The biodiversity corresponds with differences in the relative importance of sexual (seed production) and asexual (clonal growth) life history strategies in the maintenance of seagrass populations. Sexual reproduction in predominantly clonal marine plants increases recombination favoring adaptation and enhancing species resilience to environmental change. Flowering induction is an important link in the transition from vegetative growth to reproductive growth of seagrasses. Recent studies on seagrasses suggest that flowering intensity and frequency are correlated with global climate change, and the response of seagrasses will be more complex, and potentially more resilient than previously imagined.

Seagrass environments are characterized by physical conditions, such as temperature, salinity, currents, waves, turbulence, and light. Each of these parameters has the potential to affect vegetation from the smallest (molecular and physiological) to the largest (ecosystem as well as global) scale. Based on bibliometric methods, this study summarized the development trend of seagrass flowering formation research. The SCIE database of the Web of Science core collection of the Institute for Scientific Information (ISI) was chosen as the retrieval source, and select published international journals were chosen as the research object. With "seagrass flowering" as the search keyword, a total of 300 related publications were retrieved. In terms of the number of relevant publications each year, there was an overall increasing trend, indicating that this topic has gradually received more attention in recent years, which has great research potential.

This review summarizes the research progress of flowering inducement in the sexual reproduction of seagrasses and discusses the influence of physical factors on the flowering induction of seagrasses. It was previously thought that the flowering pathway initiated by seagrasses in response to environmental factors and endogenous signals may focus on the photoperiod, vernalization, and spontaneous pathways. However, the sexual reproduction of different species is different, and studying the interaction between seagrasses and their physical environment may improve understanding of the processes that influence their biology. This review focuses on the following aspects: 1) Clarifying the period of concentrated flowering of the seagrass bed, which is conducive to studying the inducement of flowering of seagrass and protecting the seagrass seed bank. 2) Discussing whether more genotypes of seagrass should be introduced for planting in the process of seagrass bed repair to avoid large-scale clonal reproduction of a single genotype of seagrass. 3) How sexual reproduction of seagrasses under adverse environments can be used to indicate changes in the climate and environment. However, existing studies have paid little attention to the sexual reproduction of seagrass beds, and do not consider the sexual reproduction rate as a long-term monitoring indicator. It is suggested that the sexual reproduction rate should be combined with environmental factors in the future long-term monitoring and assessment of the health status of seagrass beds to jointly assess their pressure status.

Key words Seagrass; Sexual reproduction; Flowering induction; Flowering pathway