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牡蛎礁碳源-汇功能研究进展与展望*

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摘要 针对当前全球气候变暖趋势, 中国提出“双碳”目标, 体现了我国主动承担应对全球气候变化责任的大国担当。海洋在实现碳中和目标中具有重要作用。牡蛎礁作为全球海岸带典型生态系统, 具有巨大碳储量和强大固碳能力。牡蛎礁在生物钙化、呼吸作用等过程中向大气释放二氧化碳, 但在生物合成、沉积作用等过程中却可以埋藏大量碳。目前, 全球牡蛎礁是大气碳的源还是汇尚不明确。为探究牡蛎礁碳源-汇功能, 本文综述了牡蛎礁碳源-汇功能研究现状, 分析了影响牡蛎礁碳源-汇功能的关键生态过程, 探讨了在不同环境条件下牡蛎礁碳源-汇特征。研究表明, 牡蛎礁不仅可以成为大气碳的汇, 还可以提高盐沼植被、海藻、海洋动物等生物的碳汇功能。未来应尽快开展牡蛎礁碳汇功能评估技术等研究, 形成以提高牡蛎礁碳汇为目的的牡蛎礁保护与修复技术, 提升我国海洋生态系统碳汇能力。

关键词 牡蛎礁; 碳源-汇功能; 储碳; 气候变化; 保护与修复

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气候变化是当今人类面临的重大全球性挑战(余碧莹等, 2021)。由于全球温室气体浓度持续增加, 引发全球变暖、海洋酸化、极端天气多发等一系列环境问题(Orr, 2005; Pachauri *et al.*, 2014)。控制大气中温室气体的浓度是减缓气候变化的关键(赵鹏等, 2019)。中国是全球第一大碳排放国, 在全球气候治理中起着关键作用。2020年9月, 习近平主席在第七十五届联合国大会一般性辩论上表示: “中国努力争取2030年前碳排放达峰, 2060年前实现碳中和”, 这是我国对全世界做出的庄严承诺。为实现“双碳”目标, 我国面临着巨大的压力与挑战(丁仲礼, 2021)。

蓝色碳汇是一种利用海洋生物及海洋活动吸收清除大气中的二氧化碳, 并将其固定在海洋中的过程、活动和机制。海洋每年可吸收约1/3左右由人类活动排放到大气中的二氧化碳(IPCC, 2019), 在实现我国碳中和目标中具有重要作用。海草床、红树林和滨海沼泽被列为世界三大海岸带蓝碳生态系统, 具有固碳量巨大、固碳效率高、碳存储周期长等特点(Donato *et al.*, 2011; Fourqurean *et al.*, 2012; Ouyang *et al.*, 2014)。牡蛎礁生态系统是全球海岸带典型生态系统之一, 被称为温带地区的珊瑚礁(Grabowski *et al.*, 2007), 具有很强的固碳功能和巨大的碳储量(沈新强等, 2011)。牡蛎礁牡蛎在生成贝壳、呼吸作用过程中向大气释放二氧化碳, 但牡蛎礁生物沉积、物理沉积作用等过程却可以固定大量的碳。尽管全球牡蛎礁是大气碳的源还是汇尚不明确, 但有研究表明, 某些特定区域的牡蛎礁为大气碳的汇(Fodrie *et al.*, 2017)。牡蛎礁还具有净化水体、生物生产、提供栖息生境、维持生物多样性与海洋碱度、保护岸线和防浪减灾等多种重要生态功能(Dame *et al.*, 1989; Meyer *et al.*, 1997; Tolley *et al.*, 2005; Waldbusser *et al.*, 2014; Ridge *et al.*, 2015)。据估算, 牡蛎礁生态服务价值可高达\$99 000 hm²/a (Grabowski *et al.*, 2012)。

在世界范围内, 牡蛎礁主要分布区域包括: 亚洲东部由辽东半岛至珠江三角洲的太平洋沿岸, 美洲由加拿大新斯科舍省以南至南美洲的大西洋、太平洋沿岸, 欧洲从挪威至摩洛哥的大西洋沿岸以及地中海和黑海沿岸, 以及澳洲温带和亚热带的滨海区域等地方(Beck *et al.*, 2009)。近一个世纪以来, 由于受过度捕捞、海岸带开发、环境污染和气候变化等因素影响, 全球范围内85%的牡蛎礁生境已退化或消失, 是被破坏最为严重的海岸带生境之一(Beck *et al.*, 2011; Lee *et al.*, 2020)。历史上, 我国沿海有丰富的牡蛎礁资源, 与全球牡蛎礁状况相似, 我国全海域天然牡蛎礁都出现明显衰退现象(Beck *et al.*, 2011)。为保护现有牡蛎

礁, 我国相继建立江苏蛎蚜山、天津大神堂牡蛎礁国家级海洋特别保护区, 并在天津大神堂、江苏小庙洪、长江口、浙江三门、香港深圳湾等多地开展了牡蛎礁修复工作。牡蛎礁作为海洋牧场重要生境, 我国海洋牧场建设也构建了大量人工牡蛎礁生境(杨红生, 2021)。据调查, 在我国北方黄渤海域, 通过投放人工鱼礁形成硬底质生境后, 常有大量牡蛎附着生长形成牡蛎礁。根据中华人民共和国农业农村部《国家级海洋牧场示范区建设规划(2017—2025年)》, 从2017—2025年, 我国将在黄渤海区建设超过600 km²的人工鱼礁区。投放的人工鱼礁吸引牡蛎附着生长与繁殖, 将形成大面积的人工牡蛎礁。牡蛎礁与牡蛎养殖系统具有相似的生物地球化学功能(Ray *et al.*, 2021)。综合海岸带、海洋牧场牡蛎礁和海水养殖贝类碳汇功能, 形成以海洋贝类为主导的海洋碳汇, 可以成为我国海草、盐沼、红树林和大型海藻碳汇的重要补充。开展牡蛎礁碳汇功能研究, 提高牡蛎礁碳汇, 对提升我国蓝色碳汇将具有重要意义。

1 牡蛎礁碳源-汇功能研究现状

目前, 世界范围内对牡蛎礁碳汇功能的研究较少, 仅Fodrie等(2017)对美国北卡罗莱纳州 Rachel Carson National Estuarine Research Reserve 潮间带和潮下带牡蛎礁碳源-汇功能开展了研究。通过测定潮间带、潮下带人工牡蛎礁、自然牡蛎礁有机碳、无机碳埋藏量, 量化了牡蛎礁沉积物中有机、无机碳埋藏速率。该研究中牡蛎贝壳的形成被认为是一个释放二氧化碳的过程, 有机碳的埋藏是碳汇过程, 基于每年有机碳埋藏量减去因形成牡蛎贝壳释放的碳, 获得牡蛎礁每年的净碳埋藏量。研究结果显示, 潮间带沙底质区牡蛎礁是大气二氧化碳的源, 二氧化碳释放量为(710±120) g C/(m²·a); 潮下带以及盐沼边缘牡蛎礁则是大气二氧化碳的汇, 二氧化碳吸收量分别为(100±40) g C/(m²·a)和(130±40) g C/(m²·a)。潮下带牡蛎礁由于呈贴面结构, 受生物捕食、侵蚀等因素影响较大, 牡蛎生长速度较慢, 沉积物有机碳积累速率较高; 沙地潮间带牡蛎礁则呈胶合簇团结构, 受生物捕食、侵蚀等因素影响较小, 牡蛎生长速度较快, 沉积物有机碳积累速率低。该研究表明, 牡蛎礁在不同分布区域具有不同的碳源-汇特征, 牡蛎礁既有可能是二氧化碳的汇, 也有可能是二氧化碳的源。当牡蛎礁有机碳沉积速率较低, 牡蛎生长速度较快时, 由于钙化作用较强, 碳释放量较高, 牡蛎礁更有可能是二氧化碳的源; 相反, 当牡蛎礁有机碳沉积速率较高, 牡蛎生长

速度较慢时, 沉积作用带来更多有机碳, 牡蛎礁则更有可能是二氧化碳的汇。其他牡蛎礁碳源-汇相关研究多数是关于牡蛎礁固碳量的研究, 沈新强等(2011)评估了长江口深水航道整治工程导堤及丁坝牡蛎礁贝壳的固碳量, 发现长江口牡蛎礁贝壳年固碳量达 450 g/m^2 。胡学东(2020)评估了我国海洋牧场人工牡蛎礁固碳量, 发现人工牡蛎礁区牡蛎贝壳年固碳量约为 540 g/m^2 。公丕海等(2014)和李娇等(2016)评估了不同类型人工鱼礁附着牡蛎贝壳的固碳量。Phillip 等(2019)评估了牡蛎礁钙化、生物合成、沉积作用固定的有机碳量。Dame 等(1989)评估了牡蛎礁生物、物理沉积作用对礁区碳沉积的影响。另外, Veenstra 等(2021)研究了潮间带牡蛎礁周边区域沉积物的碳积累速率。Ridge 等(2016)研究了盐沼边缘牡蛎礁对盐沼植被碎屑的埋藏速率, 表明牡蛎礁对稳固盐沼边缘生境、提高盐沼植被碳埋藏速率具有重要作用。

2 影响牡蛎礁碳源-汇功能的关键生态过程

2.1 牡蛎钙化作用

牡蛎钙化作用是指当牡蛎幼体固着以后, 牡蛎生长过程中利用水体中的碳酸氢根和钙离子形成碳酸钙的过程。经钙化过程封存于牡蛎壳内的无机碳可以在自然状态下存在上千年之久, 因而钙化作用被认为是牡蛎实现碳封存的主要生态过程(沈新强等, 2011; 李娇等, 2016; 张永雨等, 2017)。目前, 贝类形成贝壳的机制还不是完全清楚, 其主要包括 2 个过程: 一是通过合成分泌大分子有机物形成贝壳的有机质框; 二是将形成贝壳相关的无机盐离子(Ca^{2+} 、 HCO_3^- 等)运输至钙化地点合成碳酸钙(Johnstone *et al*, 2015)。

人们通常认为, 贝类钙化作用去除碳酸盐和重碳酸盐离子, 可以使海水中无机碳不饱和, 进而吸收大气中的二氧化碳。事实上, 该过程会向大气释放二氧化碳, 因贝类每形成 1 摩尔的 CaCO_3 , 就生成 1 摩尔的二氧化碳。该过程中的化学反应式为: $\text{Ca}^{2+} + 2 \text{HCO}_3^- = \text{CaCO}_3 + \text{CO}_2 + \text{H}_2\text{O}$, 不过, 由于海水的缓冲作用, 每形成 1 摩尔 CaCO_3 , 大约仅向大气释放 0.6 摩尔二氧化碳(Arrhenius, 1896; Taylor *et al*, 1991)。该过程与珊瑚礁中碳酸钙的形成过程类似(Ware *et al*, 1992)。海洋生物形成碳酸钙并释放二氧化碳的过程为人们所广泛关注, 据 Saderne 等(2019)研究发现, 全球海草床中每年因形成碳酸钙向大气释放的二氧化碳(8~37 Tg C)约占因埋藏有机碳而封存二氧化碳的 30%。另外, 据 van Dam 等(2021)对美国佛罗里达海草床的研究发现, 每年该海草床由于形成大量碳酸

钙而释放二氧化碳, 使得该海草床成为大气二氧化碳的源。但匡耀求等(2011)也指出, “碳酸盐泵在短的时间尺度上是大气二氧化碳的源”的认识值得商榷, 海洋碳酸钙的形成涉及一连串海洋化学反应, 在碳酸钙形成过程中, 每放出 1 摩尔二氧化碳需要从大气中吸收 2 摩尔二氧化碳, 所以碳酸盐泵应该是大气二氧化碳的汇。尽管如此, 贝类钙化过程中去除重碳酸盐和碳酸盐离子, 使水体酸度增加, 降低了海水二氧化碳的溶解度, 进而会降低海洋吸收大气二氧化碳的能力(Broecker *et al*, 1966; Stumm *et al*, 1981)。综合来看, 贝类钙化作用过程到底是大气碳的源还是汇, 尚存一定的争议。量化贝类钙化作用对海洋二氧化碳吸收能力的影响, 是查明该过程为大气碳源或汇的关键。贝类钙化过程中海水 pH 值、碱度、溶解无机碳含量、二氧化碳分压的变化则是查明该过程需要测定的关键参数(唐启升等, 2016)。

2.2 牡蛎生物沉积作用

牡蛎礁生物沉积作用指牡蛎依靠其生物泵功能, 不断把水体中悬浮颗粒物以粪便和假粪形式输入水体底层, 进而把水体有机碳和无机碳埋藏到沉积物中的过程(Newell *et al*, 1986; Dame *et al*, 1992; 沈新强等, 2011)。该过程增强了水体-沉积物之间的能量耦合关系, 把能量物质从水体中上层转移到水体底层(Dame *et al*, 1992; Smyth *et al*, 2009; Jud *et al*, 2020)。另外, 牡蛎的滤食和促进沉积物矿化作用可以增加浮游植物周转率, 提高水体浮游植物初级生产力, 该过程可以进一步加速牡蛎对水体中碳的移除(肖乐等, 2010)。据 Deslous-Paoli 等(1992)、Bayne 等(1998)和 Cranford 等(2011)的研究报道, 滤食性贝类的粪便和假粪生成量占总食物摄入量的比例随着水体颗粒物浓度变化而变化, 在水体颗粒物浓度较低时, 滤食性贝类摄入的颗粒有机物几乎都被机体吸收, 当水体颗粒物浓度超过一定阈值后, 贝类开始有假粪排出。滤食性贝类形成假粪的水体颗粒物浓度阈值在 1~6 mg 干重/L 之间(Bayne *et al*, 1983)。另外, 水体温度、浊度、贝类个体大小和颗粒物碳含量等因素也会影响贝类假粪的生成速率(Grant, 1996; Blomberg *et al*, 2017; Levinton *et al*, 2019)。随着水体颗粒物浓度的升高, 滤食性贝类粪便和假粪生成比例也有所不同, 据 Deslous-Paoli 等(1992)研究报道, 当水体中颗粒物浓度低于 10 mg/L 时, 长牡蛎粪便与假粪生成量的比例高于 1; 当浓度高于 10 mg/L 时, 长牡蛎粪便与假粪生成量的比例低于 1。在一定饵料浓度范围内, 滤食性贝类假粪生成量随水体颗粒物浓度的增加而增加

(Bayne, 1998)。大量研究表明,贝类具有选择性摄食的能力,其摄食选择受水体颗粒物粒径大小、形状、浓度、营养价值和化学成分等因素影响。贝类的选择性摄食对假粪中碳的含量也具有较大影响(Barillé *et al.*, 1997; Ward *et al.*, 1997; Arapov *et al.*, 2010; Cranford *et al.*, 2011)。总体来看,牡蛎礁通过牡蛎生物沉积作用埋藏有机碳的过程受水体颗粒物浓度与化学组成、水体温度、牡蛎个体大小等多重因素影响。Bernard(2011)研究发现,在加拿大启航湾牡蛎礁牡蛎过滤的颗粒有机物中,只有11%被机体吸收,绝大部分以粪便或假粪的形式排放到沉积物中。Newell 等(2005)、Kellogg 等(2013)、Pollack 等(2013)和 Chambers 等(2018)研究也发现,牡蛎生物沉积作用可将大量水体有机碳转移至牡蛎礁沉积物中。Fodrie 等(2017)通过研究牡蛎礁埋藏活动带(taphonomically active zone)下有机碳含量,发现其有机碳积累速率达30~270 g C/m²。这些有机碳位于牡蛎礁生物活动层以下,基本脱离了牡蛎礁生物地球化学循环过程,可以实现很长时间的埋藏。这说明由牡蛎礁所固定的沉积物碳有很大一部分是可以实现长期封存的。

2.3 牡蛎生物合成作用

牡蛎通过软体组织的生长实现对碳的固定,该过程在短期内可以被认为是二氧化碳的汇(肖乐等, 2010; 唐启升等, 2016)。贝类软体组织的生长同样也受温度、盐度、水体颗粒物浓度等因素的影响(Dame, 2016)。牡蛎死亡后,其软体组织可能会被快速分解,或成为海洋生物的食物来源,部分未被完全分解的有机物被埋藏在沉积物中,成为沉积物有机碳的一部分。

2.4 牡蛎呼吸作用

牡蛎作为牡蛎礁生物群落中的优势种,其呼吸作用是牡蛎礁区重要的碳源。Boucher 等(1988)研究发现,牡蛎礁区牡蛎年平均呼吸量占沉积物中生物呼吸量的35.82%。Bahr (1976)发现,牡蛎礁区牡蛎呼吸量占牡蛎礁群落呼吸量的48.1%。Dame(1992)发现,牡蛎呼吸量约占牡蛎礁生态系统总呼吸量的10%。Jackson 等(2018)发现,牡蛎礁中大部分二氧化碳排放来自牡蛎的呼吸作用。由于以上各研究中涉及的牡蛎密度、生物量、沉积物等特征有所差异,牡蛎呼吸排放的二氧化碳量占牡蛎礁群落总呼吸排放量比例也各有不同。柴雪良(2006)和任黎华(2014)分别开展了自然海水中牡蛎的能量收支研究,发现长牡蛎(*Crassostrea gigas*)年呼吸耗能占总能量摄入量的比

例分别在14%~25%、11%~22%之间,这说明牡蛎呼吸作用释放的碳可能抵消了很大一部分经生物沉积作用固定的碳。

2.5 牡蛎礁物理沉积作用

牡蛎礁区基于物理作用的物质沉积也是牡蛎礁碳沉积的一个重要过程(Newell *et al.*, 2005)。牡蛎礁具有复杂的物理结构,据 Bahr (1976)研究报道,水平面上每平方米牡蛎礁的总表面积可高达50 m²。牡蛎礁复杂的物理结构有利于减缓水流速度、消减波浪能量和水体悬浮物沉积,进而促进牡蛎礁区沉积物的积累和有机碳的埋藏(Kristmanson *et al.*, 1997; Lenihan, 1999; Chowdhury *et al.*, 2019)。Ridge 等(2016)研究发现,盐沼边缘的牡蛎礁在其物理沉积作用下埋藏了大量的盐沼植物碳。Dame 等(1989)研究发现,牡蛎礁区水体颗粒物在物理作用下引起的碳沉积量远高于牡蛎生物沉积作用引起的碳沉积量。

牡蛎礁对提高礁体周围沉积物的碳埋藏速率具有明显作用。据 Veenstra 等(2021)的研究报道,牡蛎礁对沉积物碳的影响远远超出了牡蛎礁本身的边界,牡蛎礁周边约2倍牡蛎礁面积范围内沉积物碳积累速率可以达到为131 g/(m²·a),这与全球盐沼、红树林和海草的碳年平均积累速率相当(Nellemann *et al.*, 2009; McLeod *et al.*, 2011)。另外, Kellogg 等(2013)、Fodrie 等(2017)和 Feinman 等(2018)研究也发现,牡蛎礁建设后礁体周边的沉积物粒径更小,有机碳含量更高。这表明牡蛎礁周边区域可能是重要的碳汇区。值得注意的是,在 Ridge 等(2016)和 Veenstra 等(2021)研究中的牡蛎礁分别位于盐沼和陆地森林的边缘,盐沼和森林输出了大量有机碳至牡蛎礁区,为牡蛎礁物理沉积作用埋藏碳提供了大量碳源。

2.6 牡蛎礁沉积物再悬浮作用

水体流速是影响牡蛎礁沉积物再悬浮的一个关键因素。在水体流速较大时,牡蛎礁沉积物会被冲刷离开牡蛎礁区或再悬浮返回水体(Dame, 1987; Ullman *et al.*, 2013; Chowdhury *et al.*, 2019)。据 Dame (1985)对河口潮间带牡蛎礁的研究发现,15 cm/s 是该牡蛎礁区沉积物再悬浮的临界流速。当水体流速小于15 cm/s 时,牡蛎礁沉积物-水界面以颗粒物沉降为主;当水体流速大于15 cm/s 时,牡蛎礁沉积物-水界面以颗粒物再悬浮为主。15 cm/s 同时也是该牡蛎礁区水体发生湍流混合现象的临界流速。在水体流速较低的牡蛎礁区,更有利于实现对沉积物中碳的长期埋藏。

2.7 牡蛎礁沉积物分解矿化作用

牡蛎的生物沉积作用可能会促进牡蛎礁区沉积物中有机碳的分解矿化和二氧化碳、甲烷等温室气体的释放(Ray *et al.*, 2021)。牡蛎礁区沉积物中有机碳的分解矿化主要源于沉积物中小型底栖动物和异养细菌的呼吸分解作用(Dame *et al.*, 1992)。目前, 仅有少数学者开展了对牡蛎礁沉积物中有机碳的分解矿化研究。Jackson 等(2018)通过开展牡蛎礁沉积物中无机碳的释放通量研究发现, 牡蛎组和牡蛎+沉积物组释放的二氧化碳通量比值约为 1:1, 说明牡蛎礁区沉积物释放的二氧化碳所占比例很低。相反, Green 等(2012)通过在潮间带沙质底质中开展牡蛎投放实验, 发现牡蛎投放区沉积物中二氧化碳和甲烷的释放速率分别增加了 13 倍和 6 倍, 牡蛎投放区温室气体的释放主要来源于沉积物, 牡蛎则显著促进了沉积物中二氧化碳等温室气体的释放。另外, Bahr (1976)研究发现, 牡蛎礁沉积物中小型底栖动物和细菌呼吸排放的二氧化碳约占牡蛎礁总呼吸量的 20%左右。这些研究表明, 在不同的沉积物环境下, 牡蛎对沉积物中有机碳分解矿化作用的影响明显不同。Ray 等(2021)还开展了一个为期 7 年的牡蛎养殖实验, 发现牡蛎促进底泥沉积物释放温室气体的现象只发生在养殖实验早期, 说明牡蛎可能只是在短期内促进沉积物释放温室气体。由于牡蛎养殖和牡蛎礁对沉积物的影响规律相似(Ray *et al.*, 2021), 在牡蛎礁生态系统中, 处于不同发育阶段牡蛎礁, 其沉积物中二氧化碳等温室气体的释放量可能也会有所不同。

综合以上研究, 发现在与牡蛎礁碳源-汇功能相关的生态过程中, 牡蛎生物沉积、生物合成作用、牡蛎礁物理沉积作用等主要表现为固定二氧化碳的过程, 牡蛎呼吸作用、牡蛎礁沉积物再悬浮和分解矿化作用等则主要表现为释放二氧化碳的过程, 牡蛎钙化作用则可能同时包括固定、释放二氧化碳的过程。

3 牡蛎礁碳源-汇功能分析

确定牡蛎礁是大气碳的源还是汇需要综合考虑影响牡蛎礁固定碳(生物沉积、物理沉积、生物合成、贝壳形成)和释放碳(沉积物再悬浮、沉积物呼吸分解作用)有关生态过程中的碳通量。牡蛎作为形成牡蛎礁的关键生物、牡蛎礁生物群落的绝对优势种(杨心愿, 2019), 量化自然条件下牡蛎的碳收支过程是查明牡蛎礁碳源-汇功能的重要内容。任黎华(2014)研究了自然养殖环境下桑沟湾长牡蛎(*Crassostrea gigas*)的碳收支过程, 发现 1 只软体部干重 0.25 g 的长牡蛎经

过 1 年成长, 可以利用水体中 7.53 g 碳, 其中, 被利用碳的 39.16%通过呼吸和钙化作用释放到环境中, 21.33%形成贝壳和软体部, 39.51%形成生物沉积物。因而, 被牡蛎利用的碳最终形成了 3 部分的碳埋藏出口: 1.42 g 的贝壳碳、0.19 g 的软体部碳和 2.98 g 的生物沉积碳。纵使不考虑长牡蛎由于钙化作用固定的碳, 长牡蛎通过生物沉积和生物合成作用固定的碳依然高于牡蛎钙化和呼吸作用释放的碳。另外, 在水体流速较缓的牡蛎礁区, 水体颗粒物物理沉积作用也会给牡蛎礁带来大量碳沉积(Dame *et al.*, 1989)。综合考虑这些因素, 牡蛎礁很可能是大气二氧化碳的汇。不过, 在沉积物有机碳分解速度较快, 水体流速较大, 沉积物再悬浮强度较高的牡蛎礁区域, 牡蛎礁则可能是大气二氧化碳的源。牡蛎礁区水体颗粒物浓度与化学组成、温度、深度、流速、牡蛎密度、个体大小与年龄、牡蛎礁物理结构和礁区底质特征等是影响牡蛎礁碳源-汇功能的重要因素。

牡蛎礁碳汇功能不仅体现在牡蛎礁生境对碳的埋藏, 还体现在牡蛎礁可提高其他初级、次级生产者的生产力, 进而提高海洋碳汇。牡蛎礁通过滤除水体颗粒物、提高水体透明度、稳定水流、减弱海浪侵蚀、加快生态系统生物地球化学循环速率、提供附着基等作用, 可以促进礁区底栖硅藻、大型海藻等生长, 提高海洋初级生产力(全为民等, 2006; Sousa-Dias *et al.*, 2007; Croce *et al.*, 2014), 进而增强海洋碳汇能力。河北唐山祥云湾海洋牧场通过构建人工牡蛎礁生境, 为大型海藻繁殖生长提供适宜的附着基和良好生态环境, 形成近 200 hm²牡蛎、大型海藻相依而生的贝藻礁生态系统, 显著增强了近岸海洋生态系统碳汇能力(杨红生, 2021)。Chowdhury 等(2019)研究发现, 在盐沼边缘建设牡蛎礁, 显著促进了盐沼植被向海一侧生长扩张, 盐沼植被面积和生物量得到明显提高。另外, 牡蛎礁还具有提高牡蛎礁区鱼类、甲壳类、头足类、贝类等生物生产力的作用(Peterson *et al.*, 2003; Xu *et al.*, 2019; Zhang *et al.*, 2020)。海洋动物通过繁殖实现自我延续, 并不断生长产生新的生物量, 因而, 被恢复的海洋动物种群中储存的碳被认为是隔离的, 可以达到碳封存目的的碳(Mariani *et al.*, 2020; Martin *et al.*, 2021)。综合而言, 牡蛎礁与大型海藻、盐沼植物、海洋动物等可以相互协同、共同提高海洋生态系统的碳汇能力。

4 牡蛎礁碳汇功能研究展望

与海草床、盐沼和红树林等蓝碳生态系统相似,

牡蛎礁作为海岸带生境可以存在数百年甚至上千年之久(王建等, 2009; Moulton *et al.*, 2015)。在牡蛎礁不被破坏的情况下, 牡蛎礁埋藏的有机碳可以实现长期埋藏。然而, 由于全球牡蛎礁被人类活动破坏严重, 牡蛎礁埋藏的有机碳被大量释放。这些有机碳很容易被分解并以二氧化碳形式再次回到大气(Fodrie *et al.*, 2017)。据 McLeod 等(2011)估计, 全球每年约有 20% 的二氧化碳排放是由于栖息地改变和被破坏导致的。从 1700 年至今, 全球由于贝壳礁被破坏引起的碳排放约为 4 亿 Mg (Fodrie *et al.*, 2017)。这严重破坏了牡蛎礁的固碳、储碳功能。如果全球现存牡蛎礁生境得不到有效保护, 牡蛎礁沉积物中将会有更多的碳被释放到大气中。因而, 对现有的牡蛎礁进行保护, 阻止牡蛎礁被进一步破坏, 不仅在维持海洋生物多样性、保护岸线、净化水体等方面具有重要作用, 同时也是一种减少全球大气碳排放的重要举措(Miteva *et al.*, 2015)。

美国国家科学院在 2021 年 12 月 8 日发布的《A research strategy for ocean-based carbon dioxide removal》报告中, 将保护与恢复近海生态系统、恢复鱼类、鲸类等海洋生物作为实现海洋碳汇的重要方法。报告认为, 牡蛎礁等底栖生态系统在实现二氧化碳移除与封存方面的作用被严重忽视, 牡蛎礁在应对全球变暖等气候变化方面的作用应该得到更多的关注(Solan *et al.*, 2020; National Academies of Sciences, Engineering, and Medicine, 2021)。考虑到牡蛎礁与盐沼植被、海藻、海洋动物在实现海洋碳汇方面具有协同促进作用, 采取基于生态系统方法、统筹考虑不同物种、生境间协同效应的牡蛎礁保护与恢复措施, 可以更好地实现牡蛎礁碳汇功能。

牡蛎礁中牡蛎的钙化、生物沉积、生物合成、呼吸作用和牡蛎礁物理沉积作用、牡蛎礁区沉积物的再悬浮和有机碳分解矿化作用是影响牡蛎礁碳汇功能的关键生态过程。目前, 与牡蛎礁碳汇有关的研究均未综合量化各关键生态过程对牡蛎礁碳汇功能的影响, 国际上尚未形成统一的牡蛎礁碳汇功能评估方法。在当前全球气候变暖、海洋酸化背景下, 为查明牡蛎礁碳汇量、提升牡蛎礁碳汇功能, 作者认为需重点开展以下研究:(1)不同时间尺度下牡蛎钙化作用对海洋-大气间碳交换的影响;(2)牡蛎礁中牡蛎的碳收支过程及其动态变化规律;(3)牡蛎礁沉积物中被埋藏有机碳的分解释放速率;(4)牡蛎礁与大型海藻、盐沼植被、浮游植物、海洋动物间协同固碳作用;(5)全球变暖、海洋酸化和海平面上升对牡蛎礁碳循环的影响;(6)牡蛎礁碳汇功能评价技术与方法构建。

通过开展以上研究, 查明牡蛎礁碳汇形成机制, 量化牡蛎钙化、生物沉积、生物合成、呼吸作用和牡蛎礁物理沉积、沉积物再悬浮和有机碳分解矿化作用等生态过程对牡蛎礁碳汇的影响规律, 综合牡蛎礁水体颗粒物浓度与化学组成、水温、水深、水体流速、礁体牡蛎密度、个体大小、年龄、礁体物理结构、礁区底质特征等因素构建牡蛎礁碳汇功能评估技术, 形成以提高牡蛎礁碳汇为目的的牡蛎礁保护与修复技术, 开展牡蛎礁保护与修复, 提升我国海洋生态系统的碳汇能力。

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Research Progress and the Prospect of Oyster Reef Carbon Source and Sink Functions

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Abstract In view of the current global warming trends, China has a "double carbon" goal, which reflects China's initiative in assuming the responsibility of dealing with global climate change. Oceans play an important role in achieving carbon neutrality. Oyster reefs are typical coastal ecosystems that contain huge carbon reserves and strong carbon sequestration ability. Due to overfishing, coastal engineering construction, environmental pollution, and climate change, the global oyster reef is in a seriously degraded state and urgently needs to be restored and protected. Oyster reefs released CO₂ to the atmosphere in the processes of calcification and respiration and also bury large volumes of carbon during biological and physical deposition, which makes it uncertain whether oyster reefs are a source or sink of CO₂. To explore the carbon source and sink function of oyster reefs, we summarized the research status of the carbon source-sink functions by oyster reefs, analyzed the key ecological processes affecting it, and discussed the characteristics of oyster reef carbon source-sink functions in different conditions. We aim to provide opinions and suggestions for research, restoration, and protection of oyster reefs. Until recently, few studies have reported the carbon source-sink functions of oyster reefs. A study of an oyster reef in Rachel Carson Reserve of North Carolina found oyster reefs have different carbon source-sink characteristics under different environmental conditions. The reefs on intertidal sandflats were net sources of CO₂ [(710±120) g C/(m²·a)], whereas shallow subtidal reefs [(-100±40) g C/(m²·a)] and saltmarsh-fringing reefs [(-130±40) g C/(m²·a)] were net carbon sinks. The concentration of seston, water temperature, depth, hydrodynamic regime, oyster density, individual size, age, reef size and structure, and sediment are important factors affecting the carbon source-sink function of an oyster reef. The oyster calcification, biological deposition, biosynthesis, and respiration processes, sediment resuspension and decomposition processes, and the physical sedimentation of oyster reefs are the key ecological processes affecting the carbon source-sink function of an oyster reef. In the process of calcification, oysters absorb

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bicarbonate to form calcium carbonate shells and release CO_2 to the atmosphere. Whether this process is the sink or source of atmospheric CO_2 is controversial. Biological deposition by oysters can transport large volumes of organic carbon to the oyster reef sediment, the organic carbon accumulation rate can reach $30\sim 270 \text{ g C}/(\text{m}^2\cdot\text{a})$, which is equivalent to the carbon sink rate of blue carbon ecosystems. Meanwhile, juvenile oysters have higher biological deposition rates than older oysters. The physical sedimentation in oyster reefs is also an important process of carbon deposition, the complex physical structure of an oyster reef can slow water flow, attenuate wave energy, and facilitate the deposition of particulate organic carbon. The influence of physical sedimentation by oyster reefs reaches far beyond the boundary of the oyster reef, the area with a carbon accumulation rate higher than $100 \text{ g C}/(\text{m}^2\cdot\text{a})$ surrounding the reef can be over twice the size of the oyster reef. Water velocity is a key factor affecting the resuspension of oyster reef sediments. A study of an oyster reef in an estuarine intertidal zone found that most uptake of particulate material by the oyster reef took place at velocities below 15 cm/s , and the release of particulates mainly occurred at velocities above 15 cm/s . It is more conducive to achieving long-term burial of sedimentary carbon in oyster reefs with low water velocities. The highest CO_2 emissions from oyster reefs may come from the oysters themselves. Therefore, oyster respiration should be one of the main sources of CO_2 from an oyster reef ecosystem. An evaluation of oyster reef carbon source-sink function needs to comprehensively consider multiple and complex biological processes. The oyster reef carbon sink functions do not only include the ability of the oyster reef habitat to bury carbon, but also their ability to improve the primary and secondary productivity of other organisms. Oyster reefs can promote the growth of macro-algae or salt marsh plants in the reef area by improving water transparency, stabilizing water flow, weakening wave erosion, and accelerating the biogeochemical cycle. Oyster reefs can also improve the productivity of fish, crustaceans, cephalopods, shellfish, and other organisms in the oyster reef ecosystem. In general, oyster reefs and macroalgae, salt marsh plants, and marine animals can jointly improve the carbon sink capacity of a coastal ecosystem. If the oyster reef is not damaged, the organic carbon buried by the reef can be preserved for a long time. The serious destruction of oyster reefs by human activities causes large volumes of organic carbon buried in oyster reefs to be released, which easily decomposes and returns to the atmosphere. The estimated global carbon emission caused by the destruction of shellfish reefs is approximately 400 million Mg, which destroys the carbon sink and storage functions of oyster reefs. Therefore, protecting the existing oyster reefs and preventing them from being damaged is important for reducing global atmospheric carbon emissions. At present, the formation of oyster reef carbon sinks have not been completely clarified, and a unified evaluation method of oyster reef carbon sink functions have not been established. There is no clear conclusion whether the global oyster reef is a sink or source of CO_2 . To clarify the carbon sink function of oyster reefs, we suggest research of oyster reef carbon sinks should be given priority in the future, including: 1. the effects of oyster calcification on carbon exchange between seawater and the atmosphere at different time scales; 2. the dynamic carbon budget of oysters in oyster reefs; 3. the carbon metabolism beneath the taphonomically active zone of oyster reefs; 4. the synergistic carbon sequestration effects between the oyster reef and macroalgae, salt marsh, phytoplankton, and marine animals; 5. the effects of global climate change on the carbon cycle of oyster reefs; and 6. the construction of carbon sink evaluation technology for assessing oyster reefs. These researches will determine the formation mechanisms of oyster reef carbon sinks, build oyster reef carbon sink evaluation technology, and establish oyster reef protection and restoration technology to improve the carbon sink capacity of oyster reefs.

Key words Oyster reef; Carbon source-sink function; Carbon storage; Climate change; Protection and restoration