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棘冠海星暴发及其对珊瑚礁的生态影响研究进展

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摘要:棘冠海星的反复暴发是导致印度—太平洋区域珊瑚礁生态系统退化的最主要原因之一。然而,我国对棘冠海星的研究非常有限。本文综述了国内外关于棘冠海星及其暴发的生态影响和应对策略的研究进展,得出以下主要结论:1)雌性棘冠海星个体每年产卵数量高达 50 万—2 亿个,环境因素变化只要导致幼虫和幼体存活率的轻微提高,成体就将得到大量补充;2)棘冠海星暴发的阈值为 1000—1500 个/km^2,暴发周期为 10—27 a,每次暴发持续 1—10 a,最终可能以“种群集体感染疾病而崩溃”结束;3)棘冠海星暴发对印度洋及太平洋东部和北部珊瑚礁的破坏性非常小,却直接导致太平洋的西部和南部珊瑚礁 90%以上的珊瑚死亡,并通过改变珊瑚群落组成、减少珊瑚和鱼类多样性而对珊瑚礁产生间接影响;4)关于棘冠海星暴发原因的假说中“陆地营养物质输入假说”和“捕食者过度捕捞假说”得到了最普遍的认可,但都不能解释所有的暴发事件;5)应对棘冠海星暴发的主要策略有改善水质、设立保护区、投放天敌和人工清理等,其中人工清理是最直接有效的策略,但迄今并没有发现可长期抑制棘冠海星暴发的方法。因此,急需加强对棘冠海星的深入研究,探查其暴发的根本原因和对策。

关键词:棘冠海星;珊瑚天敌;珊瑚礁退化;暴发特征;应对策略

A review of research on crown-of-thorns starfish and their ecological effects on coral reefs

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Abstract: Crown-of-thorns starfish (CoTs) outbreaks remain a major cause of coral mortality in the Indo-Pacific, contributing to widespread and accelerating degradation of coral reef environments. Coral reefs in the South China Sea also outbreak CoTs, but research on CoTs in our country is limited. In this study, we reviewed the advances in research on CoTs physiology and ecology, the ecological effects of CoTs outbreaks, and the measures used to manage such outbreaks. The main conclusions are as follows: 1) Each CoTs female produces approximately half a million to two-hundred million eggs per year, indicating a high reproductive potential. Consequently, if an environmental change leads to a marginal increase in the survival rate during the growing period of CoTs, a substantial number of adults will recruit, and thus lead to a CoTs outbreak. 2) The CoTs outbreak threshold is defined as 1000—1500 starfish/km^2 in areas with more than 20% coral cover. Outbreaks usually persisted for 1—10 years, and the time gap between the start of two outbreaks ranged from 10 to 27 years. Outbreaks were most likely to end with population precipitous decline caused by the rapid transmission of disease. 3) Incidences of large-scale destruction (>90% coral mortality) of scleractinian corals by CoTs outbreaks occurred primarily

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within the southern and western Pacific, but not in the Indian Ocean or in the northern and eastern parts of the Pacific Ocean, which may be explained by the relative dominance of *Acropora* in the southern and western Pacific. Outbreaks also indirectly destroy coral reefs by changing the benthic composition of the reefs, increasing the abundance of soft coral and macroalgae, and reducing the fish and coral diversity. 4) Whereas the *terrestrial run-off hypothesis* and *predator removal hypothesis* are the most biologically probable among numerous hypothesized outbreak causes, so far no single hypothesis could account for all the outbreaks. 5) Measures to manage outbreaks of CoTs include improving the water quality in marine environment, increasing the extent of no-take marine protected areas, releasing the predators of CoTs larvae to coral reefs, and directly removing CoTs from coral reefs. Among these, removing CoTs is the most direct and effective measure. However, irrespective of the improvements in the efficiency of direct control of CoTs populations, these measures will possibly only provide temporary or short-term solutions for minimizing the effects of CoTs outbreaks on coral reefs. Therefore, further research will be required to understand the ultimate cause(s) of CoTs outbreaks, which will provide long-term or permanent solutions.

Key Words: crown-of-thorns starfish; coral predators; coral reef degradation; outbreak characteristic; measures to manage and control outbreaks

棘冠海星(Crown-of-thorns starfish (CoTs); *Acanthaster planci*)是珊瑚的天敌,其反复暴发是导致印度—太平洋海区珊瑚礁退化的主要原因之一[1]。调查显示,1985—2012 年间澳大利亚大堡礁的活珊瑚覆盖度下降了 50.7%,其中 42%的珊瑚死于棘冠海星暴发[2]。虽然目前全球气候变暖所引起的珊瑚白化受到了广泛关注,但棘冠海星暴发对珊瑚的破坏程度并不比珊瑚白化小[2]。此外,棘冠海星暴发的时间间隔也越来越短,已由 1960s 前的 60—80 a/次缩短至 1960s 后的 15 a/次[3]。棘冠海星的频繁暴发叠加于环境恶化、珊瑚白化等因素,导致珊瑚礁恢复所需的时间越来越长,甚至可能难以恢复[3—4]。

2006—2010 年南海西沙群岛暴发了棘冠海星,导致其活珊瑚覆盖度从 60%下降至不足 5%[5]。2018 年西沙群岛再次暴发了棘冠海星[5—6],与上一轮暴发结束的时间间隔不足 10 a。由于我国对棘冠海星的研究非常少、认识程度也非常低,因此本文基于国内外研究成果综述棘冠海星及其生态影响的研究进展,一方面希望能够促进我国棘冠海星的科学研究,另一方面也希望能够为我国管理部门应对棘冠海星的暴发提供科学依据。

1 棘冠海星的生命周期及其生理特征

1.1 棘冠海星的生命周期

棘冠海星的生命周期过程大致如下:受精 8—9 h 后受精卵发育成囊胚,约 1d 后受精卵生长成可自由移动的原肠胚幼虫[7];2—4 d 后幼虫的消化道形成,开始摄食单细胞藻类和浮游生物[8],之后幼虫发育出腕足,用于附着前的底质探测[9];9 d 后进入晚期幼虫阶段[10];22—23 d 后幼虫达到附着高峰[11]。附着 2 d 后变态为直径 0.3—0.7 mm 的五腕幼体,其中每个腕有 2 对管足,管足末端有触须和红色视垫[8,10];3 周后幼体每 2 周增长一个腕[8,12]。变态后的前 6 个月内,棘冠海星幼体主要摄食钙化藻,身体呈粉红色,生长速度较慢,直径增长速率为 1.5—2.6 mm/月[13—14]。6 个月之后,棘冠海星转为摄食珊瑚,生长速度加快,直径增长速率为 16.7—25.0 mm/月[12]。24 个月后,棘冠海星进入性成熟阶段,生长速度明显放缓,通过摄食所获得的能量主要用于繁殖[12]。为了躲避天敌,在成功受精后的前 20 个月,棘冠海星通常在夜间活动[14]。野外评估的棘冠海星年龄通常在 4—14 岁之间,但它们的真实寿命尚无定论[11,15—17]。

1.2 棘冠海星繁殖力和存活率的影响因素

1.2.1 繁殖能力及其影响因素

棘冠海星 2 岁左右开始繁殖[14]。其繁殖能力非常强,大堡礁的雌性个体平均产卵约 1 亿个/a,最高产

2 亿个/a[18]。棘冠海星的繁殖能力随个体直径的增加而增加，直径<30 cm 的雌性个体产卵 50—2500 万个/a，平均直径为 39 cm 的个体产卵 29—3800 万个/a，>40 cm 的个体产卵 4600—6500 万个/a[12, 19]。棘冠海星的繁殖能力也与性腺大小密切相关，而性腺的发育状况既受年龄、体型大小和营养状况等生物体因素影响，也受温度、光照和食物等环境因素影响，但目前影响棘冠海星性腺发育的因素的深入研究较少[1]。

1.2.2　产卵及其影响因素

南半球的棘冠海星产卵集中在 12 月至次年 1 月[20]，北半球集中在 5—8 月[21]。在大堡礁，温度升高和光周期变长后棘冠海星的排卵更活跃[22]。由此，学者们认为温度是诱发棘冠海星繁殖的关键信号，当海水温度达到 27℃的阈值时它们开始产卵[1]。然而，在赤道附近，无论温度是否达到 27℃，棘冠海星都能够产卵[23]。在相对高纬度海区（如夏威夷、新喀里多尼亚），海水温度全年<27℃，它们则会集中在温度升高的几个月产卵[23]。棘冠海星只在海水温度相同并且距离较近的海区发生同步产卵，而温度相同但相距较远的海区之间不发生同步产卵[24—25]，这表明温度升高可能只加速了棘冠海星的性腺成熟，产卵信息素才是导致群体繁殖的关键信号[26]。

1.2.3　受精及其影响因素

棘冠海星属于雌雄异体，卵子和精子在水中受精，其受精率受种群密度、雌雄个体间距、性别比例等因素影响。如果种群密度较低、雌雄比例失衡或雌雄个体距离较远，则配子的受精率较低。例如，若棘冠海星的密度小于 300 个/km^2，受精率几乎为零[27]。暴发的棘冠海星种群中雌雄个体的丰度基本相等[28—29]，但也存在雄性偏多的现象[30]。在生物特征方面，棘冠海星的配子从母体释放后其活力退化的速度比其他无脊椎动物慢得多[20]，因此其受精能力比其他无脊椎动物强得多。

1.2.4　食物与幼虫生长发育的关系

棘冠海星暴发被认为与其幼虫的食物增加密切相关，因此食物丰度与棘冠海星幼虫的生长发育、存活率的关系受到广泛关注。室内实验表明，叶绿素浓度<0.25 μg/L 时棘冠海星幼虫的存活率较低，>2.0 μg/L 时幼虫发育较快，达到 3.0 μg/L 时存活率增加 8 倍[3,31]。然而，有研究发现，野外幼虫可以通过营养良好的母体提高配子营养、调整形态提高捕食率以及利用水体游离氨基酸等方式提高的存活率[32—34]。此外，室内模拟实验的结果也表明，棘冠海星幼虫发育的最佳叶绿素 a 浓度是 0.4—1.0 μg/L，浓度过高反而不利于幼虫发育[11]。因此，棘冠海星幼虫的发育、存活率与食物丰度之间的关系目前尚未定论，甚至存在相反的观点[1, 11,35—36]。这可能是因为，棘冠海星幼虫主要摄食直径>5.0 μm 甲藻和硅藻，而热带珊瑚礁水体以直径<2.0 μm的微型浮游植物为主[37]。因此，水体叶绿素 a 的指标不一定能反应野外棘冠海星的真实食物资源[35—38]，而目前反应野外幼虫食物资源的指标仍在探索之中。

除了上述室内实验之外，确定幼虫食物增加对棘冠海星暴发的作用还需要加强野外水体营养盐浓度、浮游植物的组成和浓度以及棘冠海星幼虫存活率和丰度等指标的调查，以探索水体营养物质输入引发的幼虫食物增加与棘冠海星暴发的关系[33,39]。然而，野外幼虫的采样和识别是开展此类监测工作的难点，但随着分子技术的持续进步，开发的特异性遗传标记和荧光标记的单体克隆染色法已实现了野外棘冠海星幼虫的定性和定量分析[1, 40—41]，使相应的监测工作得以深入。

1.2.5　盐度和温度对幼虫发育的影响

澳大利亚大堡礁的研究发现，盐度会影响棘冠海星幼虫的存活率。当洪水输入导致海水的盐度<30‰时，该区域的棘冠海星幼虫存活率比周围正常盐度区高 3 倍，这表明盐度的短暂降低可能会提高幼虫的存活率，盐度的降低可能诱导棘冠海星暴发[42]。棘冠海星从受精到各个阶段的幼虫发育对盐度变化都非常敏感，当盐度低于 25‰时受精率显著下降[43]，而在 30‰—34‰之间卵裂率较高[33]；原肠胚幼虫适应的盐度范围是 21‰—45‰；后期短腕幼虫只能在 26‰的盐度下完成变态，在 22‰以下则不能变态[22]；羽腕幼虫能适应 21‰—50‰的盐度范围[1]。

温度也是影响棘冠海星生长发育和存活率的重要因素。棘冠海星幼虫的不同发育阶段分别存在着最佳

的发育温度范围。胚胎在 20℃时完成发育需 31 h,但在 32℃时仅需 11 h[1]。胚囊幼虫的最佳发育温度是 13—34℃,羽腕幼虫则是 14.5—32℃[1]。中晚期幼虫的最佳发育温度为 26—30℃[44—45],当温度高于 32℃时幼虫会死亡,低于 25℃时则停止发育并退回早期发育阶段[9, 22]。新变态的幼体在 30℃时的存活率和摄食率都最高[46—47]。

1.2.6 棘冠海星幼虫的附着基底

基底是幼虫成功附着的关键,合适附着的基底越丰富则棘冠海星暴发的几率越大[48]。但由于在野外很少观察到新附着的幼体,因此目前关于幼虫附着基底的认识非常有限[1]。在斐济苏瓦礁、日本琉球群岛以及大堡礁的调查都表明,棘冠海星幼虫主要选择钙化藻表面附着,且孔石藻(*Porolithon onkodes*)是最受欢迎的附着基底之一[14,49—51]。室内附着实验也显示,棘冠海星幼虫均选择由钙化藻包裹的珊瑚碎石附着[8, 11,52]。钙化藻是通过附生细菌产生的代谢物质诱导棘冠海星幼虫附着[53],然而目前关于棘冠海星幼虫选择附着的钙化藻种类和起诱导作用的细菌种属及其代谢物的认识都非常有限。

2 棘冠海星暴发

2.1 暴发的标准

虽然棘冠海星暴发时密度明显增加,但很难从密度的角度定义暴发标准[1]。以“维持大堡礁正常生态(Exceeding the sustainable limits on GBR)”为标准计算棘冠海星暴发的密度阈值是 1500 个/km^2,超过这个阈值珊瑚就会大量死亡[54]。根据“棘冠海星摄食率和珊瑚增长率”的标准计算暴发的阈值是 1000 个/km^2[55]。根据“活珊瑚覆盖度>20%”的标准计算的棘冠海星暴发阈值是 1000—1500 个/km^2[56]。然而,除了棘冠海星的密度和珊瑚覆盖度外,棘冠海星暴发对珊瑚的破坏还取决于它们的平均大小及分布状况。活珊瑚覆盖度和棘冠海星密度很难量化也是暴发标准难以确定的原因之一,因为不同礁区或同一礁区在不同年份的活珊瑚覆盖度可能显著不同[1]。此外,棘冠海星种群具有高度聚集的特征,其密度可能仅在某些调查断面超过暴发阈值,而整个礁区的棘冠海星的平均密度却仍远低于暴发阈值[54,57—58]。

2.2 暴发的基本情况

棘冠海星群体暴发时,其个体数量能够在 1—2 a 内增加 6 个数量级[12]。在大堡礁、印度尼西亚和东萨摩亚的图图伊拉(Tutuila)等礁区的平均暴发密度在 20000—30000 个/km^{2}之间[57,59—60],有记录的最高暴发密度是波利尼西亚的莫雷阿岛(Moorea),达 150000 个/km^2[61]。

棘冠海星暴发的持续时间可能与珊瑚的消耗速率有关,一般 1—10 a 不等[1,61—63]。保护程度较高的大堡礁分别在 1966—1975 年、1981—1989 年、1995—2005 年和 2012—2020 年发生了 4 次有记录的大规模棘冠海星暴发,都持续 9—10 a 之久,这可能与大堡礁的活珊瑚覆盖度高及岛礁规模巨大有关[62—63]。据估算,发生棘冠海星暴发后的珊瑚群落通常需要 5—100 a 才能完全恢复[64],恢复时间的长短取决于被破坏珊瑚的种属和整体的破坏程度。被破坏较严重的礁区即使珊瑚覆盖度恢复到暴发前的水平,其珊瑚群落组成也很难恢复到暴发前的状态[1]。

大部分的棘冠海星暴发事件发生的间隔一般为 10—20 a[5—6,62—63],大洋洲的法属玻里尼西亚(French Polynesia)的暴发间隔却达 27 a 之久[61,65]。已有统计结果表明,印度—太平洋海区棘冠海星暴发的时间间隔从 1960s 以前的 80 a/次缩短至约 15 a/次[12]。有研究认为这可能是由于人为活动对珊瑚礁生态系统的破坏导致的,也有研究认为棘冠海星暴发频率的增加是由于调查和监测日益频繁所导致的假象,因为具有长期监测调查历史的大堡礁的棘冠海星暴发频率在 1960s 前后并未发生明显变化[1,60]。

2.3 暴发的方式

棘冠海星的暴发分初级暴发和次级暴发两种方式。初级暴发是幼虫连续几年增加补充而积累形成的暴发[14,16,57,65];次级暴发是初级暴发的群体产生大量的后代在附近和下游的珊瑚礁附着形成的暴发[14,66—67]。初级暴发种群的直径大小组成呈“多峰状”的形式,种群中最大的个体和最小的个体之间的直径相差大于 150

mm[12,57]；而次级暴发则由大小相似的个体组成，种群中最小个体和最大个体之间的直径相差小于 150 mm，其大小组成呈“单峰状”的形式[12]。因此，初级暴发是整个暴发的源头，找出导致初级暴发的原因是治理大规模暴发的关键[1]。然而，目前发现的初级暴发案例非常有限，唯一有记录的初级暴发发生在大堡礁北部的蜥蜴岛(Lizard)，暴发的棘冠海星种群是 6 年间连续补充积累形成的，个体直径在 110—620 mm 之间[57,68]。即便如此，这次初级暴发的原因也没有被最终探明[57]。

2.4　暴发的原因

目前，关于棘冠海星暴发原因的解释可大致归为两类：一类强调人类活动对海洋环境的破坏，如陆源营养物质输入假说、幼虫饥饿假说和天敌过度捕捞假说等[3, 28,31]；另一类则强调自然环境因素的周期性变化[66,69]。迄今还没有任何一种解释能得到直接证据的支持。

2.4.1　人为活动

(1)营养物质输入假说

陆地营养物质输入假说(幼虫饥饿假说)认为，一般情况下海水中浮游植物的丰度较低，使以浮游植物为食的棘冠海星幼虫长期处于饥饿状态，因此存活率较低；但陆地营养物质输入海水后棘冠海星幼虫的食物资源增加，幼虫的存活率因此大幅度提升，最终导致棘冠海星成体大暴发[3, 28,31]。有学者发现在西太平洋的密克罗尼西亚(Micronesia)和法属玻里尼西亚(French Polynesia)，棘冠海星暴发发生在当地特大暴雨事件之后的第 3 年，这正是棘冠海星幼虫生长至性成熟所需的时间[42]，由大暴雨携带入海的沿岸营养物质为棘冠海星的浮游幼虫提供更多食物资源，这促使幼虫的存活率大幅度提高，并最终导致成体暴发。然而，印尼-澳大利亚群岛或处于印度洋-太平洋交汇区的珊瑚三角区内，其水体营养物质从未增加，但该区域棘冠海星的暴发频率却也在增加[70]；另外，大堡礁中相对偏远的北部礁区和斯温斯岛(Swains)的水体叶绿素浓度常年高于棘冠海星幼虫发育的阈值(>0.25—0.5 μg/L)，但这些礁区的棘冠海星却只在大堡礁发生周期性暴发时才会暴发[31]。由此可见，陆地营养物质输入假说(幼虫饥饿假说)虽然可以解释比较多的棘冠海星暴发事件并得到广泛支持，但并不能解释所有的暴发事件[70—71]。

(2)天敌过度捕捞假说

统计结果表明，过去 75%的棘冠海星暴发事件发生在渔业区，20%在 5 a 以上的禁渔区[58]。“天敌过度捕捞假说”认为，棘冠海星的丰度通常受其天敌所控制，但当天敌被过度捕捞后棘冠海星的丰度就大量增加，导致暴发[72—73]。棘冠海星配子和幼虫的天敌主要包括豆娘鱼(*Abudefduf curacao*)、耳带蝴蝶鱼(*Chaetodon auripes*)和纹带蝴蝶鱼(*Chaetodon falcula*)；而附着和变态期间的主要天敌是底栖多毛类和滤食性动物[74—75]；成体海星的公认天敌是大法螺(*Charonia tritonis*)[75]，鱼类、虾和海葵也主动捕食棘冠海星[76—81]。其中鱼类包括纹腹叉鼻魨(*Arothron hispidus*)、星斑叉鼻魨(*Arothron stellatus*)、褐拟鳞魨(*Balistoides viridescens*)、黄边副鳞魨(*Pseudobalistes flavimarginatus*)、波纹唇鱼(*Cheilinus undulatus*)[76—78]；虾包括蓝拳击虾(*Hymenocera elegans/picta*)和小丑虾(*Hymenocera picta*)[74,79]；海葵包括大型宝石海葵(*Paracorynactis hoplites*)和(*Pseudocorynactis sp.*)[80—81]。1960s 棘冠海星的首次大规模暴发被认为是由于大法螺被过度捕捞所引起[28]，但室内实验表明每只大法螺平均每周仅捕食 0.7 只棘冠海星。因此，即使大法螺没有被大量捕捞，它们也不能有效控制棘冠海星成体的丰度[28]。目前，天敌过度捕捞假说的关注对象已逐渐从棘冠海星成体的天敌扩展到早期生命阶段的天敌，因为该阶段的天敌被过度捕捞也提升幼虫和幼体的存活率，并最终导致成体暴发[58,82—83]。

2.4.2　自然原因

人们最初关注棘冠海星暴发时，认为这是从未发生过的新现象，所以把暴发的原因归为人类活动破坏海洋环境的结果[84—86]。然而，早在 1940s 棘冠海星就曾经在某些区域大量存在[1]，这似乎表明在没有人类活动破坏海洋环境的情况下棘冠海星已有暴发，并推测其周期性暴发可能是自然环境周期性变化的结果[87—89]。地质学者在大堡礁的沉积物中发现了棘冠海星骨骼，表明棘冠海星在 8000 多年前就已经存在于大堡礁中，并

在过去 1000—2000 a 的沉积物中其骨骼的丰度较高[89]。也有研究者对大堡礁沉积物所记录的棘冠海星丰度信息提出质疑[3,90]。总之,关于棘冠海星暴发是人为影响或是自然现象的问题目前仍然没有定论。

2.5 暴发末期

暴发末期,高密度的棘冠海星种群集体消失。关于这种现象有三种解释:1)由于珊瑚被全部消耗,棘冠海星集体饿死;2)种群集体迁移至其他礁区寻找食物;3)棘冠海星种群因感染疾病而集体死亡[72]。1999 年在大堡礁北部蜥蜴岛的暴发结束时,平均珊瑚覆盖率仍然高达 22%[63]。由此可见,即使仍然有食物,爆发末期棘冠海星也出现集体消失的现象[63,72]。另外,野外棘冠海星的移动速度较慢(每天移动距离<35 m,并且仅在周围珊瑚被耗尽的情况下才移动)在礁区之间的迁移需要较长时间,加上迁移途中没有食物供应,它们能成功迁移的可能性极小[91]。当前,“暴发末期棘冠海星由于感染疾病而快速消失”的观点得到普遍关注。棘冠海星的免疫能力非常弱,它们对革兰氏阳性和阴性菌几乎没有抵抗力,暴发末期高密度的棘冠海星极易传染病原体而引发集体疾病,导致种群快速消失[15,92—93]。然而,暴发末期感染棘冠海星疾病的病原体仍然没有查明,查明这些病原体有利于开发控制棘冠海星暴发种群的新技术。

3 暴发的生态危害

3.1 直接破坏

棘冠海星只捕食珊瑚,它们把胃平铺在珊瑚表面,通过分泌消化酶消化珊瑚组织[94]。在大堡礁,直径 20—39 cm 的棘冠海星个体在夏季每天约消耗 155—234 cm^2 的珊瑚,这比其他同等大小的生物快 2—5 倍[91]。因此,棘冠海星暴发会导致珊瑚大量死亡[28,95]。在太平洋关岛(Guam),1967—1969 年间棘冠海星暴发导致沿岸长 38 km 的珊瑚礁中 90%造礁石珊瑚死亡[91]。2003—2010 年,棘冠海星在莫雷阿岛(Moorean)暴发,前后 8 a 时间内导致该珊瑚礁区(132 km^2)的活珊瑚覆盖度从大于 40%下降至小于 1%,造成了该区域约 96%的珊瑚死亡[61]。1985—2012 年间,澳大利亚大堡礁的活珊瑚覆盖度下降了 50.7%,其中 42%的珊瑚损失是由于棘冠海星暴发所致,比高温导致珊瑚白化的危害更严重[2]。2006—2010 年间我国西沙群岛也暴发了棘冠海星,导致该海域的活珊瑚覆盖度从超过 60%下降至不足 5%,造成超过 90%的活珊瑚死亡[5]。自 2018 年起,西沙群岛和东沙群岛又暴发了棘冠海星,导致大量珊瑚死亡[5,95]。然而,并非所有的棘冠海星暴发都导致珊瑚大量死亡,如在夏威夷莫洛凯岛(Molokai),1969—1970 年间棘冠海星连续暴发 18 个月,但并没有导致明显的珊瑚死亡[96]。东太平洋巴拿马(Panama)珊瑚礁区的棘冠海星暴发也仅导致了少量珊瑚死亡[97]。在整个印度—太平洋区域,包括东太平洋的巴拿马(Panama)、西太平洋的密克罗尼西亚群岛(Micronesia)、日本南部、我国南海、澳大利亚大堡礁和科科斯(基林)群岛(Cocos-Keeling)、南太平洋的萨摩亚群岛(Samoa)以及印度洋的红海等都反复爆发了棘冠海星[29,56, 96—98],但仅太平洋西部和南部的珊瑚礁遭严重破坏[12,99],这可能与太平洋西部和南部的珊瑚礁区均以鹿角珊瑚为优势种属有关[63,100]。

3.2 间接影响

棘冠海星的摄食有选择性,暴发初期它们优先摄食鹿角珊瑚和杯型珊瑚[60,63,100],而非滨珊瑚[61],它们的选择性摄食会改变珊瑚群落的组成和多样性。但是,当优先摄食的珊瑚被耗尽之后,棘冠海星会继续摄食其他珊瑚,并最终导致绝大部分珊瑚死亡[55,71]。珊瑚大量死亡后,因为生存空间加大,软珊瑚和大型藻类的覆盖度迅速增加,海胆和草食性鱼类的丰度也明显增加[101—102]。相反,以珊瑚为食或栖息在珊瑚中的鱼类和无脊椎动物的数量则显著下降[61,103]。统计数据表明,珊瑚礁中至少有 133 种鱼类摄食珊瑚[104],320 种鱼类以珊瑚为栖息地[105],棘冠海星的暴发会间接导致 8%—10%珊瑚礁鱼类数量减少,甚至消失[1,61]。因此,棘冠海星暴发间接改变了珊瑚礁底栖的群落结构,降低其恢复力。

4 棘冠海星暴发的应对策略

4.1 珊瑚礁生态环境保护

如果棘冠海星暴发由人为活动的破坏导致,那么减少甚至消除人为活动才能降低未来暴发的频率或消除

爆发[3]。近年来，不少国家已投入大量资源改善珊瑚礁区水质，且世界各地的珊瑚礁区所设置的以保护鱼类丰度和多样性为目的的禁渔保护区规模也大幅增加。虽然，营养盐输入和鱼类的过度捕捞与棘冠海星暴发之间的生态联系仍不清楚，但这些措施能提高珊瑚和鱼类的丰度与多样性，减少大型藻类覆盖度，增加珊瑚礁生态系统的恢复力[106—107]，是降低棘冠海星暴发频率和保护珊瑚礁生态系统的必要措施[108—110]。

4.2　投放天敌

研究发现，棘冠海星具有逃离天敌存在区域的生物特性[111]。近来，澳大利亚政府投资 56.8 万美元用于人工繁殖大法螺，并计划将所繁育的大法螺投放到珊瑚礁区用于驱散棘冠海星的聚集产卵，以预防暴发。截止至 2017 年，该项目已繁育了近 10 万只大法螺幼虫（https://www.aims.gov.au/docs/media/latest-releases/-/asset_publisher/8Kfw/content/giant-sea-snails-join-the-fight-to-save-the-reef），但迄今尚未见控制效率的相关报道。此外，李元超等人提出了“向珊瑚礁区投放棘冠海星幼虫天敌（如雀鲷和蝴蝶鱼）”的建议[5]，但是该的措施仍处于理论阶段。

4.3　人工清理及其效果

棘冠海星暴发是少数能直接干预的珊瑚礁灾害之一[112—113]。人们长期以来都在尝试各种方法直接清除这些敌害生物[114]。最普遍的做法是将海星抓捕后暴晒至死或注射毒性化学物质就地杀死[53,115—117]。早期的注射剂或者对潜水员和其他的礁栖生物都有毒（如甲醛、硫酸铜），或者需要多次注射才能杀死海星（如硫酸氢钠），控制效率较低[12]。胆汁酸盐虽然安全且高效[76]，但它价格昂贵并且它的使用受管制普通公益组织难以获取。近来发现，用普通家用食醋注射能使棘冠海星在 24 h 内 100%死亡，并对其他的礁栖生物和礁区环境没有负面影响[117—118]。注射食醋会使棘冠海星无法调控其体内的 pH 值，导致其组织和细胞膜腐烂，但是食醋注射只能杀死被注射的个体，不能达到少量注射引发集体死亡的效果[119]。目前，人们正尝试找出特异性的棘冠海星病原体，利用特异性疾病群体性地清除棘冠海星[1]。此外，澳洲训练了机器人识别棘冠海星并注射毒性化学物质，以提高清理效率[120]。

1970s 以来，虽然国际上付出了大量努力，但人工清理在阻止珊瑚损失方面收效甚微[1]。人工清理只在面积<1 km^{2}的珊瑚礁中才能防止珊瑚大量死亡[121]，并且即使小规模的珊瑚礁也需要长期、持续的清理才能达到保护珊瑚和抑制棘冠海星的效果[122]。人工清理时，直径<15 cm 的棘冠海星幼体的清理效率几乎为零，直径>40 cm 的个体也只能达到 75—85%，因此一次清理后仍有约 20%的棘冠海星没有被清除[123]。自 2018 年起，我国组织了首次大规模人工清理棘冠海星以应对新一轮暴发。虽然清理达到了 3 位潜水员 7 天共清理了 4.5 万个棘冠海星的高效率（https://page.om.qq.com/page/Oipkc1Og52cO37e0YeQVt8IQ0），但由于人工潜水安全深度的限制，水深 15 m 以下的棘冠海星不能清理，这次大规模清理对暴发的控制效果不显著。Hall 等[111]确定了棘冠海星用于种群聚集交流的化学信号因子，并成功利用这些化学信号因子诱导棘冠海星聚集，利用这些信号因子对棘冠海星进行集体诱捕，将大幅度提高棘冠海星的清除效率。

5　结语与展望

棘冠海星的周期性暴发是印度—太平洋珊瑚礁生态系统退化的主要原因之一[1]。虽然直接清理的效率越来越高，但这只能暂时缓解暴发造成的破坏，难以从根本上消除暴发[1]。关于暴发原因的假说都认为，棘冠海星生长阶段存活率的提高是暴发最重要的机制，这强调了对生长阶段的生理和生态过程认识的重要性[28,31,72—73]。随着技术的进步，关于棘冠海星的生理和生态过程有望开展以下几方面研究：

（1）暴发之初，人们认为棘冠海星是单一物种（*Acanthaster planci*）[100]，然而近来的分子研究发现珊瑚礁区至少存在四种棘冠海星[124]。暴发时，只有西太平洋的物种（*Acanthaster cf. solaris*）造成严重破坏，因此目前关于棘冠海星的研究都仅基于西太平洋的种[100]。然而，根据暴发的不同破坏程度可见，四种棘冠海星的生理和生态过程存在显著差异。往后的研究需要理清不同种棘冠海星的繁殖能力、浮浪幼虫发育和浮游期的时间以及生长函数等，为暴发的管理提供依据。

（2）近年来，分子技术的进步使研究人员确定了与棘冠海星繁殖相关的关键基因[125]，还识别了棘冠海星物种聚集的特定信息素，这为暴发提供了潜在的控制方案[123]。然而，目前关于棘冠海星的发育和生长对生态因素变化的响应机制仍然不清楚。未来的研究可以利用生物分子技术找出棘冠海星发育特征的关键基因和信号通路，研究这些基因和信号通路对各种环境因素变化（如温度升高、盐度降低、以及海洋酸化等）的响应机制和棘冠海星钙化的分子机制等。

（3）建立种群动态模型是棘冠海星暴发管理的重要工具[11]。然而，前期的模型研究要么只在单个珊瑚礁的尺度上建模，要么基于不切实际的假设和幼虫扩散过程建模，都不能为管理所用[11]。最近，大堡礁的连接网络模型虽然能应用于管理[126]，但这类模型仅基于幼虫的扩散，没有结合种群动态和捕食等生态系统因素，并且使用这类模型之前需要使用调查数据进行验证，这限制了它的应用[11]。今后的模型研究应尽可能扩大模型区域，使单个珊瑚礁的模型能为大空间的模型提供信息（如棘冠海星的聚集和分布等），同时大空间的模型也能为单个珊瑚礁的模型提供礁区的边界条件信息（如与邻近礁的迁移率等）。

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