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悬浮物对造礁石珊瑚营养方式的影响及其适应性研究进展

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摘要:营养方式是造礁石珊瑚获取能量与营养物质的基础,影响其生长与分布。近年来珊瑚礁区悬浮物含量与组分结构发生显著变化,其对造礁石珊瑚营养方式的诸多影响正成为当前研究热点。研究系统综述了珊瑚礁区悬浮物变化特征、悬浮物对造礁石珊瑚营养方式的影响及其适应性研究现状。发现近年来人类活动加剧与强降雨事件频发是驱动珊瑚礁,尤其是近岸珊瑚礁区悬浮物含量递增、组分改变与变频加剧的主因;悬浮物变化对造礁石珊瑚光合自养与异养营养的影响存在显著的种间差异,这主要与悬浮物消光效应、生物可利用性及造礁石珊瑚种类密切相关。虽然少数种类造礁石珊瑚具光合可塑性或异养可塑性,能在高含量悬浮物存在的弱光环境中较好生长。然而对绝大多数造礁石珊瑚而言,其营养方式适应性较差,无法在悬浮物影响下较好地获取生命活动所需的能量与营养物质,进而难以生存。总体来说,悬浮物被认为是近年来影响造礁石珊瑚生长与分布的重要环境因子之一,而关于造礁石珊瑚营养方式对悬浮物变化的响应及其适应机制,当前研究仍较薄弱,需要进一步加强相关研究。

关键词:悬浮物;造礁石珊瑚;营养方式;影响;适应性

Effect of suspended sediment on the nutritional mode of scleractinian corals and their adaptability: state of knowledge and research

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Abstract: The nutritional mode is the basis for scleractinian corals to obtain energy and nutrients, which affects their growth and distribution. In recent years, the content and composition of suspended sediment in coral reefs have changed significantly, and many effects on the nutritional mode of scleractinian corals are becoming the focus of current research.

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This article reviewed the characteristics of the suspended sediment changes in coral reefs, the effects of suspended sediment on the nutritional mode of scleractinian corals and their adaptability. The results show that the intensification of human activities and the frequent occurrence of heavy rainfall events in recent years are the main reasons driving the increase in suspended sediment concentration, composition changes and frequency conversion in coral reefs, especially in fringing reefs. The influences of suspended sediment on autotrophy and heterotrophy of scleractinian corals are significantly different, which are mainly related to the extinction effect and bioavailability of suspended sediment, and the species of scleractinian corals. Although some species of scleractinian corals have photosynthetic plasticity or heterotrophic plasticity, they can grow well in low-light environments where high levels of suspended sediment exist. However, for the majority of scleractinian corals, the adaptability of nutritional mode is poor, so they can't obtain the energy and nutrients needed for living better under the influence of suspended sediment, which makes them difficult to survive. Overall, suspended sediment is considered to be one of the important environmental factors affecting the growth and distribution of scleractinian corals in recent years. However, the present studies on the response and adaptability mechanism of the nutritional mode of scleractinian corals to the change of suspended sediment are still rare, and further research is needed.

Key Words: suspended sediment; scleractinian corals; nutritional mode; effect; adaptability

造礁石珊瑚是典型的混合营养型生物,即在其通过共生虫黄藻进行光合自养的同时[1],也能以触手、粘液和刺细胞等结构捕获食物进行异养营养[2]。两种营养方式紧密相连、互为补充,共同为造礁石珊瑚提供生命活动所需的能量与营养物质[3-6]。近年来全球各地造礁石珊瑚覆盖率的急剧下降与群落结构的显著改变[7-11],即与部分造礁石珊瑚营养方式受环境影响密切相关[12-15]。

当前,研究报道影响造礁石珊瑚营养方式的主要因素有海水升温[16-17]与酸化[18]、水体富营养化[19]、有机物污染[20]、生物病害[21]和沉积物覆盖[22]等,而关于水体悬浮物变化对造礁石珊瑚营养方式影响的研究则相对较少。悬浮物作为珊瑚礁区水体重要组分,正常情况下其含量较低且组分稳定[23-24]。然而,随着热带地区人类活动干扰加剧[25-27]和强降雨事件频发[28-30],外源物质的大量输入显著地改变了珊瑚礁区悬浮物含量与组成[31-32],进而对造礁石珊瑚生长产生重要影响[13,33-34]。当前,虽然已有大量研究认为水体悬浮物增加降低了造礁石珊瑚幼体补充率[35-36]、钙化速率[37-38]、生长速率等[39-41],是导致大多造礁石珊瑚死亡、覆盖率减低,进而引发珊瑚礁急剧退化的主因[13-14,42-44]。但事实上,随着人们对全球珊瑚白化与水体浑浊事件的持续关注,陆续有报道指出部分珊瑚礁,尤其是邻近人口密集区的近岸珊瑚礁,其水体浑浊却有少数种类造礁石珊瑚能在其中生长良好,珊瑚群落整体呈低多样性、高覆盖率特征[34,39,45-48]。这表明悬浮物变化对造礁石珊瑚生长的影响效应存在明显的种间差异[49-51],近年来,越来越多的学者认识到这种差异主要与造礁石珊瑚营养方式对悬浮物变化的响应及其适应性有关[50,52-55],进而积极地开展相关研究。

悬浮物变化对造礁石珊瑚营养方式的诸多影响正成为当前研究热点。为此,本文结合国内外相关研究,系统地综述了珊瑚礁区悬浮物变化特征、悬浮物对珊瑚营养方式的影响及其适应性等研究现状,在此基础上指出当前存在的问题,并提出未来的研究展望。这将有助于明确珊瑚礁区悬浮物变化特征及其驱动主因,预判悬浮物影响下的造礁石珊瑚群落演变趋势,进而为造礁石珊瑚生存环境的改善及下一步研究提供参考。

1 珊瑚礁区悬浮物变化特征

与以往相比,当前珊瑚礁区悬浮物变化显著。关于引发珊瑚礁区悬浮物变化的原因,国内外虽然已有大量研究报道,但其实质却与悬浮物来源发生异常有关。这主要体现在两方面,其一是近岸森林砍伐[56]、土地开垦[57]、海岸工程建设[58]、城市污水排放[59]等人类活动加剧与强降雨事件频发导致的大量泥沙[60-62]、重金属[63]、人类排泄物[32]、植被碎屑[64]、持久性污染物[65]等陆源性物质注入珊瑚礁区,使其外源性悬浮物显著增加所致;而另一方面则与航道清淤[66]、填海造岛[67]、船舶尾流[68]、海啸[69]、风生海流或潮汐[70]等扰动引发的

底表细颗粒沉积物再悬浮[71-72]有关。

总体看,近年来珊瑚礁区悬浮物变化主要有 3 方面特征。首先,其主要特征是悬浮物含量递增。目前,国内外已有较多学者通过野外现场调查[73]、卫星遥感技术[67,74]、沉积物埋藏速率[75]、数值建模反演[20,56]等方式报道了珊瑚礁区悬浮物含量递增的事实。如与欧洲人定居澳大利亚以前相比,2012 年 Kroon 等[20]报道指出大堡礁泻湖内悬浮物年平均负荷量增加了 5.5 倍,达 17000 t/a。而新加坡自 20 世纪 70 年代以来,其近岸珊瑚礁区悬浮物沉降速率也从 3.2—5.9 mg cm^{-2} d^{-1}增至 14—30 mg cm^{-2} d^{-1}[76]。其次,悬浮物组分改变。大量报道显示,近年来珊瑚礁区悬浮物陆源组分显著增加,尤其是微塑料[77-78]、杀虫剂[20]和多氯联苯[79]等有机污染物,不仅在近岸珊瑚礁区丰度较高,同时也广布于离岸珊瑚礁区。如 Ding 等[65]在我国西沙群岛 3 个环礁的外礁斜坡、礁滩和潟湖海水中皆检测到了微塑料,其丰度分别为 0.2—11.2 个/L、1.0—12.2 个/L、1.0—45.2 个/L。而 Tan 等[80]最新研究也指出,尽管南沙群岛远离大陆污染来源,但微塑料依然广泛分布于其珊瑚礁区,浓度为(55.6±35.5)个/L。再者,悬浮物变频加剧。这主要与人类活动干扰[25,66]和暴风雨、台风等极端天气[29,61,81]愈见频密引发的悬浮物变异频率、强度与持续时间加剧等有关。当前,全球各地关于珊瑚礁区悬浮物变频加剧的报道较多,且主要见于邻近人口密集地区的近岸珊瑚礁区。如 Reichelt 等[82]研究指出,1991 年 5 月 20 日和 9 月 13 日克利夫兰海湾(Cleveland Bay)的挖掘事件分别导致水体浊度在 13—77NTU(NTU, nephelometric turbidity units)和 32—215NTU 之间波动,显著高于对照海域的波动范围(1—25NTU)。而 Thomas 等[83]观测显示,巴布亚新几内亚(Papua New Guinea)利希尔岛(Lihir Island)珊瑚礁区悬浮物含量较低(<5 mg/L),但由于受挖泥活动影响,珊瑚礁区悬浮物含量长期(数月)高于 25 mg/L,影响严重区域其悬浮物常高达 500—1000 mg/L。上述可知,珊瑚礁区悬浮物来源异常是驱动其变化的主因,而含量递增、组分改变与变频加剧是其变化的主要特征。

2　悬浮物对造礁石珊瑚光合自养的影响

光合自养是绝大多数造礁石珊瑚主要营养方式,可为其提供 50%—95%的能量与营养物质[84]。水体中高含量悬浮物的存在,显著地消减水下光合有效辐射(PAR),进而影响造礁石珊瑚光合自养能力。例如,澳大利亚昆士兰北部的伯德金(Burdekin)沿岸珊瑚礁区长期处于浑浊状态,50%PAR 的衰减会降低该区域造礁石珊瑚 70%的净光合作用[85]。Tamir 等[86]也进一步指出,浅水造礁石珊瑚(<40 m)光合作用所需的 PAR 不低于水面 PAR 的 1.25%,否则将会使其失去光合自养能力。目前,已有较多学者通过野外现场观测或室内模拟研究,明确了悬浮物消光效应与其浓度、粒度、颜色和有机组分占比等因素有关[31,87]。例如,Fourney 等[88]以来自埃弗格雷斯港(Port Everglades)和佛罗里达群岛(Florida Keys)珊瑚礁区表层沉积物开展不同含量(30、60、90、120mg/cm^2)的消光效应模拟实验,结果显示采集于埃弗格雷斯港的表层沉积物,由于其细颗粒(<63 μm)和有机物组分占比高,相同含量水平其消光效应显著高于佛罗里达群岛珊瑚礁区,且随着沉积物含量的递增,消光效应越加显著。由此可见,悬浮物消光效应对造礁石珊瑚光合自养产生明显的负面影响,与其浓度与组分结构有关。

此外,也有少数学者注意到,悬浮物在水动力或微生物作用下释放的无机组分或有机组分生物矿化生成的氮、磷等营养物质[89-91],也是影响造礁石珊瑚光合自养的重要因素[92]。目前,有研究认为水体营养物质的过量增加并不利于造礁石珊瑚生长,尤其是营养物质本底值较高的近岸珊瑚礁区[93-95]。其原因主要为氮、磷等营养物质的过量存在,不仅可直接促进共生虫黄藻的增殖,导致其光合作用产物被用于其自身生长和繁殖而减少对宿主的供给量[96]。更为重要的是这也促进了其他浮游植物或大型藻类的生长,进而产生遮阴效应间接地影响共生虫黄藻光合作用效率[36,97]。再者,在溶解无机氮含量显著增加的情况下,氮、磷比例失衡也将导致共生虫黄藻处于磷酸盐饥饿状态,降低其温度与光照胁迫的耐受力[98]。例如,Ferrier-Pagès 等[99]通过实验发现,培养体系中高含量铵盐和磷酸盐存在会导致柱状珊瑚(*Stylophora pistillata*)生长速率在 1 周内至少降低 10%,而时翔等[100]也指出佳丽鹿角珊瑚(*Acropora pulchra*)和多孔鹿角珊瑚(*A. millepora*)最大可以忍受

30 μmol/L 的磷酸盐浓度,且在 30 μmol/L 浓度的耐受范围内,随着磷酸盐浓度的不断增高,虫黄藻叶绿素荧光指数(F_v/F_m)和密度呈显著降低趋势。上述可知,水体悬浮物的增加,其消光效应与氮、磷等其他营养物质的释放影响造礁石珊瑚光合自养过程,不利于其生长。

3 悬浮物浓度和组分结构改变对造礁石珊瑚异养营养的影响

异养营养是造礁石珊瑚重要的营养补充。虽然已有大量研究证实大多数造礁石珊瑚具有异养可塑性,即在其光合自养受阻时通过异养营养供给能量与营养物质[15,101-102]。但珊瑚礁区悬浮物浓度与组分结构的改变,对造礁石珊瑚异养营养的影响则利弊兼有。一方面,地面径流[87]、生活污水[103]、养殖废水[104]等输入常携带大量有机物, 这些有机组分的补充不仅增加了悬浮物浓度,同时也显著地提高了其生物可利用性,进而可被造礁石珊瑚大量摄食。Anthony 等[54]通过富集^{14}C 标记的悬浮物添加实验证实,网状菊花珊瑚(*Goniastrea retiformis*)和细柱滨珊瑚(*Porites cylindrica*)在高浓度悬浮物水体中可摄食悬浮物进行异养营养,且还进一步指出相对于离岸或低浓度悬浮物海域,近岸高浊度水体中鹿角杯形珊瑚(*Pocillopora damicornis*)和多孔鹿角珊瑚(*A.millepora*)摄食悬浮物能力高 10—20 倍[55]。此外,Grover 等[105]在 2006 年和 2008 年通过实验分别证实柱状珊瑚(*S.pistillata*)可吸收利用尿素(Urea)和溶解游离氨基酸(DFAAs,dissolved free amino acids),而有机组分占比高的悬浮物在细菌等微生物作用下可将其降解生成 Urea 和 DFAAs 等小分子溶解有机物[106-107]。因此,颗粒有机物的增加在一定程度上也间接地有利于部分造礁石珊瑚异养营养。

而另一方面,随着人们对造礁石珊瑚异养营养的关注,越来越多的学者注意到近年来挖泥[66]、工程建设[108]等人类活动加剧导致的泥沙等无机组分及微塑料[109]等有机物污染物的大量注入,显著地降低了悬浮物生物可利用性,进而导致其无法被造礁石珊瑚摄食利用。例如,Cunning 等[14]报道,在 2013—2015 年迈阿密(Miami)港口建设期间,高含量泥沙、重金属[33]等物质生成,无法被其摄食利用,是造成其 0.5 km 范围内的 560000 株造礁石珊瑚死亡重要原因之一。而 Ding 等[65]在我国西沙群岛的造礁石珊瑚体内中检测到微塑料为 0.02—1.3 个/g,证明微塑料虽然能被造礁石珊瑚误食,但却不能利用它。综上,珊瑚礁区悬浮物的增加,可能会提高悬浮物的生物可利用性,从而促进造礁石珊瑚异养营养。但实际上,珊瑚礁区悬浮物的增加大多为人类活动或径流输入引起,主要以无机或有害组分为主,且并非所有的造礁石珊瑚都具有异养可塑性。因此,总体来说珊瑚礁区悬浮物增加对造礁石珊瑚异养营养的弊大于利,这也是导致近岸珊瑚礁退化的重要原因之一[14,87]。

4 造礁石珊瑚营养方式对悬浮物的适应性

珊瑚礁区悬浮物的增加,虽然以往的研究已明确指出不利于造礁石珊瑚生长,且不少学者也通过野外研究提出了珊瑚礁或造礁石珊瑚对悬浮物的耐受阈值[110]。如 Rogers[111]认为人类活动影响生成的悬浮物浓度不能超过 10 mg/L,否则将影响珊瑚礁的结构与功能,而 Li 等[112]也研究指出,悬浮物中细颗粒组分(0—63 μm)沉降速率 5—6 mg cm^{-2} d^{-1}是影响造礁石珊瑚群落结构的阈值浓度。尽管如此,实际上目前大多室内研究已证实少数种类造礁石珊瑚能暴露在悬浮物浓度为 10—1000 mg/L 的环境中数小时到一年而不会死亡[51],且近年来此类现象也同样在野外有发现,如在巴西阿波罗荷斯(Abrolhos)[48]、婆罗洲(Borneo)米里(Miri)[47]、大堡礁帕鲁玛浅滩(Paluma Shoals)[39,46]和新加坡南部[113]等珊瑚礁区,其水体浑浊,但以团块状和皮壳状生长型为优势类群的造礁石珊瑚群落却生长较好,群落整体呈低多样性、高覆盖率特征。这表明少数种类造礁石珊瑚对悬浮物具有一定耐受性,能在高含量悬浮物存在的弱光环境中较好生长[49-50]。

关于此现象,当前已有学者运用稳定同位素[12,114]或放射性元素[54]示踪、生物标志物[6,115]和分子生物学技术[116-118]等方法,通过室内研究或野外调查证实与造礁石珊瑚营养方式对悬浮物的适应性有关。这主要表现在以下 2 方面:

①光合可塑性。造礁石珊瑚种类繁多,不同种类造礁石珊瑚其共生虫黄藻形态、生理代谢、基因组成及垂

直分布[119]存在差异。因此,每种造礁石珊瑚皆有特定的光生态宽度,对 PAR 变化表现出不同的响应特征[120]。在高含量悬浮物存在的弱光环境中,光合可塑性较强的造礁石珊瑚可通过调节共生虫黄藻系群[121]、绿色荧光蛋白[122]、非光化学猝灭[123]、有效光量子产量[124]、虫黄藻密度及其体内光合色素含量[125]等方式以适应 PAR 的变化,进而保持恒定的光合作用效率。例如,柱状珊瑚(*S.pistillata*)是备受学者关注与研究的模式种之一,大量研究证实其具有较强光合可塑性,能快速地适应大幅度波动的 PAR(95%—0.8%水面 PAR)[125]。Cohen 等[126]也通过深水区(30 m)和浅水区(3 m)的交互移植证实,当共生虫黄藻暴露于其边界区外的深度时,其适应机制会发生显著变化,显示该种造礁石珊瑚具有较强光合可塑性。

②异养可塑性。造礁石珊瑚是珊瑚与虫黄藻共生体,尽管共生虫黄藻光合作用可为其提供主要的能量与营养物质,但其本质上仍属于异养动物[127]。在高含量悬浮物存在的弱光环境中,部分造礁石珊瑚可转光合自养为异养营养或加快异养摄食速率等方式以补充其生命活动所需的能量与营养物质[2,128]。Titlyanov 等[129]研究发现,柱状珊瑚(*S.pistillata*)在低 PAR 并投喂饵料时,可观察到其共生虫黄藻数量稳定增加,且在不同 PAR 条件下,饵料投喂有助于其保持一定的呼吸速率,这表明在弱光调节下,柱状珊瑚(*S.pistillata*)可通过异养营养维持其自身的能量代谢。而 Anthony 等[54]通过富集^{14}C标记的悬浮物添加实验,不仅证实了网状菊花珊瑚(*G.retiformis*)和细柱滨珊瑚(*P.cylindrica*)在高浓度悬浮物水体中能进行异养营养,且还指出网状菊花珊瑚(*G.retiformis*)在悬浮物含量为 16mg/L 的水体中,为了应对光合自养能力的降低,通过加快其摄食速率 2 倍多来补偿了光合自养 35%—47%的营养损失,进而使其能更好地适应弱光环境。近年来全球各地报道的浑浊水体能显著降低热应力影响下的造礁石珊瑚白化面积[46-47],即可能与造礁石珊瑚摄食悬浮物补偿其能量与营养物质有关。

综上,悬浮物变化影响造礁石珊瑚生长与分布。虽然绝大多数造礁石珊瑚对悬浮物敏感、耐受浓度较低。但同时,也注意到少数种类造礁石珊瑚,如团块状和皮壳状生长型类群,具有光合可塑性或异养可塑性,能在浑浊水体中较好生长。

5　小结与展望

悬浮物作为珊瑚礁区水体重要组分,由于近年来其来源异常,表现出含量增加、组分改变与变频加剧的变化特征。悬浮物变化显著地影响了造礁石珊瑚营养方式,进而对其生长与分布产生重要影响。虽然已有研究证实少数种类造礁石珊瑚具光合可塑性或异养可塑性,可在高含量悬浮物存在的弱光环境中生长良好。但对于大多数造礁石珊瑚而言,其营养方式适应性较差,无法在悬浮物影响下较好地获取生命活动所需的能量与营养物质,进而难以生存。悬浮物变化对造礁石珊瑚光合自养与异养营养的影响存在显著的种间差异,这也被认为是导致近年来近岸造礁石珊瑚覆盖率急剧下降与群落结构显著改变的重要原因之一。

当前,关于造礁石珊瑚营养方式对悬浮物的响应及其适应性,虽已开展了较多室内模拟或原位观测研究,但仍有一些问题尚不清晰,需进一步开展相关研究。主要有:①造礁石珊瑚营养方式对悬浮物适应性的分子机制。造礁石珊瑚适应多变环境与其基因表达的可塑性有关[130],而长期暴露于浑浊水体中的造礁石珊瑚,其适应的内在分子机制如何却鲜有报道,有待于进一步揭示;②光合自养与异养营养在悬浮物影响下的互作机制。部分造礁石珊瑚,尤其是悬浮物耐受类群,其营养方式对悬浮物的适应性存在互作效应,而这内在互作机制却仍不明朗,需进一步明确;③误食微塑料的影响效应。微塑料是当前备受关注的污染物,广布于全球珊瑚礁区。虽然已有研究指出造礁石珊瑚摄食悬浮物的同时,常误食水体中的微塑料[131],但微塑料对造礁石珊瑚生理代谢的影响效应如何? 是否会在其体内长期累积,进而阻碍其营养物质的获取等并不明晰,有待进一步开展相关研究。

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