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生 态 学 报

（SHENGTAI XUEBAO）

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封面图说:高寒草甸牦牛群——三江源区位于青藏高原腹地, 平均海拔 4200m,是长江、黄河、澜沧江三条大河的发源地,也是全球气候变化最敏感的地区。三江源区高寒草甸植被状况对该区的生态环境、草地资源合理利用和应对全球气候变化具有十分重要的意义。2005 年以来,国家投资 70 多亿元启动三江源生态保护工程。监测显示,近年来,三江源湖泊湿地面积逐步扩大,植被覆盖度得到提高,三江源区高寒草甸的生态恶化趋势得到遏制。图为冒着风雪在三江源高寒草甸上吃草的牦牛群。

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藤壶金星幼虫附着变态机制

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摘要:藤壶属节肢动物门(Arthropoda)甲壳亚门(Crustacea)蔓足下纲(Cirripedia)围胸总目(Thoracica), 具备特殊的形态结构、生活史和种群生态特征,是最主要的海洋污损生物。其幼虫阶段通常经历 6 期无节幼体和 1 期不摄食的金星幼虫,从浮游的金星幼虫附着变态成固着的稚体是藤壶生活史中的一个关键环节。外界化学和生物因子中成体提取物、水溶性信息素、足迹、神经递质、激素、生物膜等均影响藤壶金星幼虫的附着变态;内在因子即金星幼虫的生理状态(能量储量和年龄)决定了其对外界因子的反应程度。概括了近年来藤壶附着变态生理机制和分子机制研究的进展,可为深入了解藤壶金星幼虫附着变态机制提供参考,也为开发新型、高效、环保的防污剂提供理论指导。

关键词:藤壶;金星幼虫;附着;变态

A review on the mechanism of attachment and metamorphosis in barnacle cyprids

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Abstract: Barnacles are the most successful group of fouling organisms in the marine environment because of their morphology, life history and population ecology. Like many benthic marine organisms, barnacles have a complex life cycle. In general, the larval phase includes six planktotrophic naupliar stages followed by one non-feeding cypris larval stage. The lecithotrophic cyprids are specialized for locating suitable attachment sites and commencing metamorphosis (both processes are often referred to as "settlement") to juvenile barnacles.

It is believed that pelagic cyprids have active behavioral responses to the physical, chemical and biological properties of a substratum surface, which lead to their gregarious settlement. Furthermore, endogenous factors, such as the physiological condition of the cyprids, determine how their attachment and metamorphosis is affected by exogenous stimuli. Thus, this article reviews recent discoveries on the physiological and molecular mechanisms of attachment and metamorphosis in barnacle cyprids.

A wide variety of chemical and biological exogenous factors (adult conspecific extract, waterborne pheromones, footprints, neurotransmitters, hormones and biofilms) affect the attachment and metamorphosis of barnacle cyprids. For example, adult conspecific extract is a water-soluble glycoprotein that induces conspecific cypris settlement in its substratum-bound conformation. This adult conspecific extract, which was previously known as arthropodin, is now known as the settlement-inducing protein complex (SIPC). This complex has been isolated from the adult extract, biochemically characterized, genetically cloned, and its expression pattern has been examined during barnacle larval development, attachment and metamorphosis. Similarly, waterborne pheromone is released into the water column by adults and can be detected by cyprids in solution. The waterborne pheromone is a small peptide with a basic carboxy terminus and a neutral,

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or basic amino terminus, which induces cypris settlement. Cyprids also secrete an antennular footprint, which acts as a secondary cue in larval-larval interactions during settlement. The material basis of footprints for inducing settlement either contains, or is equivalent to SIPC. Neurotransmitters (e. g. acetylcholine, dopamine, serotonin, catecholamines, and noradrenaline) stimulate the secretion of adhesive granules from the cement glands, and the attachment and (or) metamorphosis of cyprids. Likewise, hormones (e. g. methyl farnesoate, juvenile hormone III, 20-hydroxyecdysone and ecdysone mimic RH5849) are reported to induce attachment and (or) metamorphosis of cyprids. Finally, biofilms, which are assemblages of microorganisms and organic molecules, play a key role in the cypris settlement process. Biofilms can facilitate, inhibit or have no effect on attachment and metamorphosis of cyprids, with their role determined by density, composition, physiological condition, and growth phase of the bacteria.

The physiological condition of cyprids is mainly controlled by their energy reserves and age, with their energy reserves a major determinant of their physiological quality. A cyprids energy status is measured as an index of their lipid, nucleic acid and protein content. Additionally, the age and ageing temperature of cyprids significantly affects their settlement ability. For example, newly molted cyprids would not yet have gained their settlement ability, but cyprids progressively lose their settlement ability with age.

This review provides new insights into the attachment and metamorphosis mechanisms of barnacle cyprids, providing a foundation for developing new, efficient, and less environmentally damaging antifoulants.

Key Words: barnacle; cyprid; attachment; metamorphosis

海洋污损生物又称海洋附着生物,是生长在船底和海中一切设施表面的动物、植物和微生物。当污损生物大量繁衍且未能及时清除,会对海洋设施如码头、港口、运输管道、船舶等造成极大的破坏并祸及水产养殖业,给沿海各国的经济造成巨大损失[1-2]。蔓足类中的许多种类如藤壶、茗荷、铠茗荷等均属于污损生物,其中无柄蔓足类——藤壶属节肢动物门(Arthropoda)、甲壳亚门(Crustacea)、蔓足下纲(Cirripedia)、围胸总目(Thoracica)[3], 具备特殊的形态结构、生活史和种群生态特征,是最主要的海洋污损生物[4-9]。美国、英国、日本以及其它沿海国家对藤壶等污损生物的防除问题非常重视,以纹藤壶(*Balanus amphitrite*)为模型生物对藤壶的附着变态机制进行了大量研究[2,5,9-15],以期为海洋污损生物的防治特别是开发高效环保无毒的防污剂提供理论依据。

蔓足类的生活史通常要经过营浮游生活的 6 期无节幼体(naupliar)、不摄食的金星幼虫(cyprid)、固着的稚体和成体几个发育阶段[3,11,15-16]。浮游的金星幼虫发育到固着的稚体阶段,其形态结构及生活习性发生了很大的变化。金星幼虫是蔓足类生活史中的一个重要阶段,其唯一的作用是选择适宜附着的基质并完成变态[6,16-17]。在附着变态过程中,金星幼虫的游泳足快速划动,以规律性的“步伐”在基质表面行走,通过第一触角探测附着基质,分泌临时胶体形成足迹;如果基质条件适宜,金星幼虫即分泌永久胶体附着,进而变态为稚体,个体进入固着阶段[17-19]。Lagersson 等把金星幼虫的固着行为分为 5 个分离的阶段:游泳、基质的探测、广泛的探索、紧密的探索、白垩腺的分泌及永久附着[17]。自然状态下金星幼虫的固着行为包括两个连续的过程,即附着和变态[11,16]。因此,浮游的金星幼虫附着变态成固着的稚体是蔓足类发育过程中的一个关键环节,如果金星幼虫不能完成附着变态,最终只有死亡。

一般认为自由游泳的金星幼虫通过基质表面的物理因子、化学因子和生物因子的诱导产生一种特别的行为反应,导致聚集固着的发生[6,9,16,20-21]。早期的研究主要侧重于各种物理因子对金星幼虫附着变态影响的探讨,底质类型[22]、颜色和光照、表面张力、温度和盐度[12,23]、表面湿度[24]、超声波[25]等因子均能影响金星幼虫的附着变态。进一步的研究表明,与物理因子相比化学和生物因子对金星幼虫附着变态的影响更为显著,近年来国外更多的研究集中在化学和生物因子方面[2,10,16, 26-27]。同时金星幼虫在附着变态过程中对外界因子的反应程度还依赖于其内在因子,即生理状态(如能量储量和年龄)[28-29]。本文概括了近年来藤壶附着变

态生理机制和分子机制研究的进展,从成体提取物、水溶性信息素、足迹、神经递质、激素、生物膜和金星幼虫的生理状态等对藤壶金星幼虫附着变态的影响进行综合阐述,希望能对我国相关工作的进一步开展提供借鉴与参考。

1 外界化学和生物因子的影响

1.1 成体提取物

藤壶的聚集固着行为已被人们认识很久,实验室和野外的实验都表明金星幼虫喜欢固着在同种个体的周围,这一行为称为聚集[30]。早在20世纪50—60年代就有实验表明藤壶(*Semibalanus balanoides*)能诱导其金星幼虫的附着变态,人们把其中未知的诱导因子称为节肢蛋白(与角质层相联系)[31];该因子的化学性质类似于肌动蛋白,是一种粘性蛋白,但在水溶液中不能独立诱导金星幼虫的附着变态,必须与基质结合[16]。Larman等进一步指出*S. balanoides*的诱导因子是由5000—6000 Da和18000 Da亚基组成的多态蛋白[32],随后更多的研究表明藤壶成体提取物能诱导金星幼虫的附着变态[12,24],目前开展的各种因子对金星幼虫附着变态影响的许多实验也都是在成体提取物的诱导下进行的[2,10-11,27]。

近年从纹藤壶中分离纯化出的“诱导固着蛋白复合物(SIPC)”是一种高分子量的糖蛋白,主要由分子量为76、88、98 kDa的3个亚基组成,每个亚基与整个SIPC一样具有诱导金星幼虫固着的活性[26]。藤壶成体粗提物[33]或纯化物SIPC的亚基[26]中能与小扁豆凝集素结合的特殊糖链在金星幼虫的附着变态中起重要作用,但环境中各种单糖和二糖对金星幼虫附着变态的影响取决于糖的种类和浓度[10]。SIPC可在藤壶无节幼体发育过程中合成并积累在金星幼虫体内,而后金星幼虫分泌SIPC至第一触角的附着盘[34]。SIPC是一种固着诱导信息素,SIPC(或类SIPC蛋白)在纹藤壶固着时参与了成体与幼虫间及幼虫与幼虫间的相互作用[34-35]。

序列分析结果表明,SIPC与α_2-巨球蛋白(α_2-macroglobulin)家族有30%的相似性,其cDNA (5.2 kb) 编码包含1547个氨基酸的蛋白质前体,可能是由一个α_2-巨球蛋白基因的祖先复制进化而来;SIPC的mRNA不仅在成体的各个器官表达,也在稚体和幼虫阶段广泛表达[35]。在幼虫和成体角质层中表达的糖蛋白与SIPC的mRNA同时出现;表明SIPC由上表皮细胞产生并分泌到角质层,SIPC在金星幼虫的附着变态中作为接触信息素起作用[36]。现在,一般认为早期命名的节肢蛋白就是现在的SIPC,它是一种角质层糖蛋白[26,34,36]。

藤壶不同部位(外壳、软体部、整体)提取物的诱导活性有所不同,一般整体提取物比外壳和软体部提取物的诱导活性高[10]。不仅同种藤壶的提取物具有诱导作用,异种藤壶的提取物也表现出诱导作用[11,37]。SIPC样的糖蛋白在藤壶中普遍存在,但是异种藤壶间SIPC的诱导活性有所不同[37]。采用成体粗提物和纯化物SIPC[38]进行的实验均表明金星幼虫在附着变态中对同种提取物的反应比异种提取物的强烈。因此,藤壶固着诱导信息素活性的强弱可以反映它们的系统亲缘关系[24,37]。

1.2 水溶性的信息素

除了以SIPC为代表的接触信息素(须与基质表面结合)能对金星幼虫产生诱导作用外,藤壶还可产生改变金星幼虫行为的水溶性信息素[31],Rittschof率先证实了水溶性信息素的存在[39],认为纹藤壶体内3000—5000 Da的多肽能诱导金星幼虫的固着[39-40]。一般水溶性的信息素是指从藤壶体内释放的能诱导金星幼虫附着行为和变态的分子量小于500 Da的多肽[16],它所含有的一个碱性羧基端和一个中性或碱性氨基端对其生物活性是重要的[40-41]。几个具有这种结构特征的二肽或三肽如甘氨酸-甘氨酸-精氨酸(GGR)具有类似的诱导能力[40]。虽然在野外GGR能诱导金星幼虫的固着[42],但在实验室内并不能证实GGR的活性[43]。最近许多的研究表明水溶性的信息素在金星幼虫的固着中起重要作用[44-46],它的生态作用可能是通过刺激金星幼虫的附着行为进而促进浮游阶段向固着阶段的转变,而不是与SIPC一样直接诱导金星幼虫的永久附着和变态[46]。从纹藤壶的成体提取物中还纯化出另一种诱导蛋白,其分子量为(31600±500)Da,但与SIPC无关;它能迅速诱导金星幼虫的探索行为,这种诱导蛋白被认为可能是一种水溶性的信息素[47]。有关水溶性信息素的生态作用、来源以及理化特性等仍有许多工作要做。

1.3 足迹

Walker 等发现 *S. balanoides* 的金星幼虫在探测基质时,在基质表面会留下触角分泌物——即蛋白质“足迹”[48]。Nott 等认为这种“足迹”是金星幼虫的临时胶体,由单细胞腺产生并分泌至第一触角附着盘[18]。在纹藤壶的金星幼虫中也证实了“足迹”的存在,其除了起临时胶体的作用外,还有第二种功能即行使固着诱导信息素的作用[49]。一般认为“足迹”的存在可以提高基质表面的吸引力,在基质表面不存在同种成体的情况下,金星幼虫也可以产生聚集固着[48-49]。免疫染色法显示金星幼虫的 “足迹” 含有 SIPC,金星幼虫整体免疫组织化学的实验结果也证明了金星幼虫的“足迹”与 SIPC 之间的化学关系,从而说明金星幼虫的“足迹”为什么可以诱导金星幼虫的固着[34]。使用 SIPC 的 N-端与 C-端多肽制备的多克隆抗体检测金星幼虫的“足迹”,同样证明 SIPC 是足迹蛋白的一个成份或两者是同样的蛋白[50]。

总之,研究结果表明金星幼虫“足迹”对其附着变态起诱导作用的物质基础仍是 SIPC。

1.4 神经递质和激素

有关神经递质和激素等信号传导物质在金星幼虫附着变态中的作用一直受到人们的重视。Clare 等认为第二信使(cAMP)参与金星幼虫附着变态的调节[51]。乙酰胆碱和多巴胺通过参与纹藤壶金星幼虫肌肉收缩及白垩腺胶体物质的分泌进而调节金星幼虫的附着变态[52-53];同样,儿茶酚胺包括多巴胺是参与红巨藤壶(*Megabalanus rosa*)金星幼虫白垩腺胶体物质的分泌而不是直接诱导附着变态的发生[54]。多巴胺能诱导纹藤壶金星幼虫产生没有附着的变态[55]或抑制金星幼虫的附着变态[56],5-羟色胺的作用仅调节金星幼虫的附着[56]或是诱导金星幼虫附着和变态[53,55]。这两种神经递质对致密藤壶(*B. improvisu*)的效应则截然不同,多巴胺能诱导其金星幼虫的固着,而 5-羟色胺却抑制其金星幼虫的固着[57]。去甲肾上腺素能诱导纹藤壶金星幼虫产生没有附着的变态且变态过程比自然过程延长许多,其机理是去甲肾上腺素能干扰金星幼虫白垩腺胶体物质的分泌,导致其放弃探索行为而不能粘附在基质表面,进而直接变态成为稚体[7]。一些研究进一步从分子水平证明胞内合成的 5-羟色胺和多巴胺至少部分参与了金星幼虫附着变态的调节[58]。

蛋白激酶 C(PKC)在纹藤壶金星幼虫的变态中可能起重要作用,但没有参与其附着行为[59]。甲基法尼酯(methyl farnesoate)和保幼激素(juvenile hormone III)能诱导金星幼虫产生没有附着的变态即早熟变态[60-61],前者可能通过蛋白激酶 C 信号传导系统诱导金星幼虫的变态[60]或是在金星幼虫体内起保幼激素的作用[61]。20-羟基脱皮酮(20-hydroxyecdysone)在低浓度时能促进金星幼虫的附着变态,但在其高浓度的作用下金星幼虫只附着却不变态[62]。蜕皮激素类似物 RH5849 也能诱导金星幼虫正常附着变态[63]。钙调蛋白(CaM)是一种主要的胞内钙结合蛋白,可以调节钙偶联信号传导途径,在金星幼虫附着变态中参与包括肌球蛋白轻链激酶和钙调蛋白激酶在内的酶促反应,也是金星幼虫变态时的一种调节剂[64]。

1.5 生物膜

生物膜往往是藤壶金星幼虫在野外附着变态的先决条件,在金星幼虫栖息地的选择和固着中起重要作用[20-21,28,65-67]。研究生物膜对藤壶附着变态的影响主要通过单种细菌膜和自然生物膜两种类型的实验。在室验室中许多工作研究了从自然生物膜中分离的在人工基质上培养的单种细菌膜对金星幼虫附着变态的影响[2,14,67-69]。单种细菌膜显示了不同的效应[20],由于细菌种类的不同可以是促进[66,68-70]、抑制[68-69,71-72]或不产生任何影响[73]。

在单种细菌膜的基础上,人们还进一步研究了多种人工生物膜[27,67]及自然生物膜在野外[28,65,70,73-74]或在室验室[2,66,68-69,74-75]对金星幼虫附着变态的影响。自然生物膜对金星幼虫附着变态的影响也是复杂的[20],可以是刺激作用[66,72]、抑制作用[28]或没有效果[73]。生物膜的细菌群落结构在决定生物膜对金星幼虫的吸引力方面起重要作用[66,73],而生物膜的年龄则影响其细菌密度[66,73]、种类组成[68]、生理状况及生长阶段[20,66,69,73,75]等群落参数。因此,一般老化的生物膜对金星幼虫的固着有促进作用而形成不久的生物膜却起抑制作用。这是由于细菌密度的增加、细菌多样性的增加以及生物膜代谢活力的变化引起的[69],但也有完全相反的效应[21,28],这取决于生物膜的来源[73-74]。另外,自然生物膜附着的基质[68]、环境条件(水温和盐

度[75]、底质特性[21])、潮位(群落结构在生物量、丰度、多样性等方面不同)[66]等均影响生物膜的效应。虽然表面湿度和生物膜的群落组成在金星幼虫的固着过程中起关键作用[21,76],但不论在哪种湿度的基质上老化的生物膜均能诱导金星幼虫的固着,说明表面湿度并不能改变自然生物膜在金星幼虫固着中的积极作用[68]。

除了生物膜本身的作用外,细菌分泌的胞外产物也能影响金星幼虫的固着行为[13,65,71,76]。细菌分泌的产物如培养上清液[2,13,67,69]和胞外多糖[2,67,72,76]在金星幼虫附着变态中的效应也被广泛研究,但胞外产物的效应还受到许多其他因素的影响。不同种类的细菌[13,72]或不同培养基培养的同种细菌[2,67]分泌的胞外产物效应不同;不同的盐度条件[67]、成体提取物存在与否[67]同一胞外产物的效应有所不同;同种细菌产生的表面结合的诱导物和水溶性的诱导物的效应也不同[67]。另外在凝集素的作用下细菌膜的效应会发生变化,凝集素能从两个方向改变诱导信号[72]。凝集素通过与胞外产物特定的糖分子反应能调节细菌膜的效应,在引导金星幼虫趋向固着终点上起重要作用[72]。特别是小扁豆凝集素能阻断细菌膜的促进作用,说明细菌膜产生的胞外产物可能含有一种类似于藤壶成体提取物 SIPC 特性的特殊糖链[72]。

以往对生物膜的研究多集中于细菌,近年也有一些研究关注生物膜中的其它生物类群(如硅藻)[77-78]。不同种类的硅藻对金星幼虫的效应不同,有的抑制、有的促进、有的没有明显作用[77]。研究表明对金星幼虫固着起促进作用的硅藻含有与小扁豆凝集素结合的糖链,说明硅藻中能与小扁豆凝集素结合的糖链化合物可能与从藤壶成体中分离纯化的 SIPC 的作用相似[77]。

2 金星幼虫的生理状态

金星幼虫对外界因子或诱导信号的反应程度还依赖于其生理状态(如能量储量和年龄),金星幼虫的生理状态影响它对基质的选择和最终变态的成功[28-29,79]。

2.1 金星幼虫的能量储量

金星幼虫的能量储量是其生理状态的一个决定因子,是其附着变态能否成功的保证,它取决于无节幼体生长经历的条件(特别是食物藻类的数量和质量)[79]。通常采用脂类、核酸、蛋白质的含量作为金星幼虫的营养指标,指示金星幼虫的能量状况。金星幼虫将储存能量的 38%—58% 用于变态,其中脂类占 55%—65%、蛋白质占 34%—44%、碳水化合物占 <2%[80]。

脂类的含量如三酰甘油/固醇(TAG/ST)的比率可指示金星幼虫的能量状况,三酰甘油含量的高低反映了金星幼虫固着成功的可能性[29]。无节幼体食物(藻类)的脂类(三酰甘油 TAG)含量和金星幼虫总的能量储量间存在显著的正相关[79]。金星幼虫 TAG/ DNA 的比率可作为能量储量的另一个指标,这个指标可表示金星幼虫变态能力的大小[79,81]。根据 TAG/DNA 的比率可将金星幼虫分为高、中、低 3 个营养等级,在缺乏成体诱导物时,营养等级高的金星幼虫变态率高于营养等级低的金星幼虫[79,81-82]。

核酸 RNA/DNA 的比率也可作为营养状况的指标。无节幼体的经历可通过 RNA/DNA 这一比率的高低,最终决定金星幼虫的附着变态能力;在同样条件下 20 ℃培养的无节幼体其 RNA 的含量比在 30 ℃培养的明显低,无节幼体 RNA 含量的大小决定了金星幼虫在 5 ℃老化时的存活能力及附着变态能力[83]。

金星幼虫的生理状态还与“金星幼虫主要蛋白”(cyprid major protein,CMP)有关,在金星幼虫附着变态过程中,CMP 是内源的能量来源[84]。纹藤壶 CMP 的分子量为 170 kDa,与卵黄蛋白重链的分子量相同,其生化和免疫特性与卵黄蛋白相似[84-85]。在幼虫发育中 CMP 含量随着无节幼体的发育不断增加,到金星幼虫阶段 CMP 含量达到最高,而后随着金星幼虫虫龄的增大其含量显著下降[84]。

2.2 金星幼虫的生理年龄和保存的环境条件

金星幼虫的生理状况不仅由无节幼体的摄食历史还由其生理年龄[79]和环境条件[11,80]决定。Harder 等[86]发现金星幼虫的年龄影响其附着变态能力,具有相同油脂含量的 3 个年龄(0、3 d 和 6 d)的金星幼虫的固着率间有显著差异;年幼的金星幼虫固着率与其油脂含量间有显著的正相关,而年老的金星幼虫两者间的关系较弱。在 20 ℃培养的金星幼虫在 5℃保存 2—4 d 能成功变态,而 30 ℃培养的金星幼虫在 5℃保存长达 8—16 d 也能成功变态[83]。金星幼虫体内的 CMP 含量变化与保存温度密切相关,在 25、20、15 ℃ 中金星幼虫

CMP 含量随时间的延长显著下降,在 5 ℃时金星幼虫 CMP 的含量保持稳定;但不论在哪个温度组,都以 3 天虫龄的金星幼虫变态率最高,之后随金星幼虫虫龄的增大变态率降低[87],因此金星幼虫的保存温度影响其固着能力。长期以来多认为低温(5、15 ℃)比高温(20、25 ℃)有利于维持其固着能力[87],也有结果表明高温(23 ℃)比低温(6℃)更有利于保持其固着能力[11]。一般认为刚出生的金星幼虫(0d)不具有附着变态能力,金星幼虫的附着变态能力与年龄的关系为:前期随虫龄的增大附着变态能力逐渐提高,后期随虫龄的增大附着变态能力逐渐减弱[11,87]。如 0—3 d 的金星幼虫以第 3 天幼虫的固着率最高,随后随虫龄的增大固着率降低[87];0—10 d 的金星幼虫以第 10 天幼虫的固着率最高,随后固着率降低,至 14—15 d 丧失附着变态能力[11]。一般来说金星幼虫需要一个固着能力获得的时期(刚出生的金星幼虫虽然 CMP 含量最高,但不具有固着能力),之后随时间的延长其脂类或 CMP 含量下降,固着能力逐渐丧失,最终不足以支持附着变态[11,29,87-88]。因此,金星幼虫的生理年龄也与其附着变态能力息息相关,刚诞生的金星幼虫尚未获得固着能力,而虫龄较大的金星幼虫多已丧失固着能力。

3　金星幼虫基质选择的分子机制

在金星幼虫附着变态的过程中,藤壶金星幼虫特异基因 *bcs*-1 和 *bcs*-2 的 mRNAs 的表达降低,而 *bcs*-3,*bcs*-4, *bcs*-5 和 *bcs*-6 的 mRNAs 的表达增加[89]。在诱导物和抑制物的作用下,这 6 个 bcs 基因的表达不同,其中诱导物强烈促进 *bcs*-6 的表达[90-91],而某些抑制物抑制 *bcs*-6 的表达[90],表明这些化学物质通过调节 bcs 基因,特别是 *bcs*-6 的表达参与金星幼虫的附着变态和基质的选择,并在金星幼虫附着变态的调节中起关键作用[90-91]。

芳香族 L-氨基酸脱羧酶能分别促进 5-羟色氨酸、3、4-二羟基苯丙氨酸合成 5-羟色胺、多巴胺。5-羟色胺和成体提取物能明显提高芳香族 L-氨基酸脱羧酶基因 mRNA 在金星幼虫中的表达,说明胞内合成的 5-羟色胺和多巴胺至少部分参与金星幼虫附着变态的调节[58]。通过比较Ⅱ期无节幼体、浮游阶段的金星幼虫、刚附着的金星幼虫和已变态的金星幼虫的蛋白质图谱,可见浮游阶段金星幼虫的蛋白质图谱明显不同于其它阶段[92]。分化表达的蛋白质主要包括信号转导蛋白(腺苷酸环化酶和钙调蛋白)和保幼激素结合蛋白,这些蛋白质在金星幼虫的基质选择,例如信号识别、信号传导和放大以及幼体组织的准备中起关键作用[92]。

蛋白质的磷酸化作用是调节许多胞内快速反应最重要的分子转换机制。研究表明,金星幼虫变态的蛋白质组反应主要变化是蛋白质的磷酸化而不是重新合成蛋白质,对金星幼虫的固着而言,去磷酸化作用是必要的过程,来自适宜基质的诱导信号能激活金星幼虫的磷酸酯酶,最终导致一系列生化变化和随后的附着变态[93]。蛋白质组和磷酸化蛋白质组分析表明,刚形成的金星幼虫(0h)和老化的金星幼虫(24h)的蛋白质表达和翻译后的修饰是高度动态的,与压力和与能量代谢相关的两组蛋白在金星幼虫的发育中分化表达,表明参与压力调节和能量代谢的蛋白质在金星幼虫附着变态的调节中起重要作用[94]。

4　结语与展望

我国海域辽阔,海岸线绵长,海洋环境复杂多样,每年污损生物(包括无柄蔓足类)对我国海洋经济活动和国防建设造成的损失难以估算。国内对无柄蔓足类的种类组成、区系分布、生态特点和防除等方面已有许多研究[4,95-96]。自 70 年代末以来,我国科研人员在藤壶生物学方面也做了一些工作,包括幼虫培养[97-98]、发育[99]、附着[100-101]和藤壶胶[102-103]等方面,但有关藤壶附着变态的生理机制研究较少[97,104]。希望更多的学者能涉及这方面的工作,揭示无柄蔓足类附着变态的机制,为解决蔓足类生物污损这一难题提供理论依据,促进我国海洋经济活动的健康持续发展。

以往海洋污损生物的防除通常是采用化学防污剂手段,由于传统的有机锡类防污涂料对海洋生态系统的污染,目前已被禁止使用,深入了解蔓足类附着变态的机制,开发新型、高效、环保防污剂已成为污损生物防除的一个亟待解决的问题。国外虽然对藤壶金星幼虫附着变态的生理和生态机制进行了多年的研究,明确了藤壶金星幼虫的附着变态需要在各种物理、化学、生物因子的介导及适宜的生理状态下才有可能完成,但有关金星幼虫附着变态机制仍有许多工作需要开展,包括以下几个方面:

(1)藤壶成体提取物和金星幼虫足迹均能诱导金星幼虫的附着变态,其中起决定作用的物质是特殊的糖链,某些凝集素能抑制它的效应。深入研究成体提取物和凝集素之间的相互作用和关系,利用某些凝集素作为防污剂,有可能为我们提供一种新的污损生物防除方法。

(2)金星幼虫的固着由附着、变态两个连续的过程组成,各种神经递质和激素等信号传导物质在金星幼虫附着和变态中所起的作用是不同的,有的参与白垩腺物质的分泌、有的参与附着、有的参与变态、有的促进最终的固着过程。因此,干扰或阻断这些信号传导物质在金星幼虫附着、变态或固着中的作用,可为开发新的无毒防污剂提供一个方向。

(3)生物膜及分泌的胞外产物虽然在金星幼虫附着变态中起重要作用,但这种作用是复杂的,其中起具体作用的物质往往难以确定,应进一步加强有关细菌及其分泌产物对金星幼虫附着变态影响及机制的研究。另外,许多海洋生物如藻类、海绵和珊瑚等的有机提取物及次生代谢产物都被证明对藤壶等主要污损生物幼虫具有明显的抑制作用,这可为天然海洋防污产物的筛选提供另外一个途径。

(4)深入对藤壶胶体的合成、结构组成及固化作用机制的研究。有可能通过人为干扰抑制液态胶的交联聚合过程,阻断其从液态到固态的转变过程,阻碍幼虫的永久固着,从而达到防除污损生物的目标。

(5)目前,从分子水平对金星幼虫附着变态的研究刚刚起步,今后应更多从分子水平(转录组学、代谢组学、蛋白组学途径)追踪影响金星幼虫基质选择的分子路径。从分子水平对各种神经递质和激素的信号通路进行深入的研究,探讨阻断其中某一环节的途径,使金星幼虫不能完成正常的附着变态,可为开发新型、友好、高效的防污剂提供分子靶标和理论依据。

总之,要彻底了解藤壶金星幼虫的附着变态,需要从生态、生理以及分子水平综合入手,阐明藤壶金星幼虫的附着变态机制及其所需条件,通过与物理、化学及材料学等学科的交叉和渗透,期待能开发出高效、环保、无毒的防污技术,最终彻底解决生物污损这一难题。

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