

中华双环粒蟹奴寄生对红星梭子蟹蜕皮相关激素和基因表达量

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摘要 [目的] 研究中华双环粒蟹奴寄生对不同蜕皮阶段红星梭子蟹蜕皮激素含量、*MIH* 基因和 *EcR* 基因相对表达量的影响, 为深入研究该类甲壳动物寄生虫的寄生机理提供基础资料。[方法] 采集 200 尾健康和受蟹奴寄生的红星梭子蟹为试验材料进行室内饲养, 观测和记录试验蟹蜕皮间期所需时间, 并分别于 4 个不同的蜕皮阶段抽取血淋巴样品, 开展蜕皮激素和相关基因表达量检测。[结果] 雄性和雌性感染蟹蜕皮间期耗时均大于健康蟹, 分别为 (291.5±115.5) h 和 (342.1±144.5) h; 感染蟹蜕皮间期和前期血淋巴 EH 含量显著低于正常蟹同期水平 ($P<0.05$); 各期感染蟹 *MIH* 基因相对表达量均高于正常蟹, 而 *EcR* 基因相对表达量则呈相反趋势; 血淋巴 EH 含量与 *EcR* 基因相对表达量呈正相关关系, 与 *MIH* 基因相对表达量呈负相关关系。[结论] 中华双环粒蟹奴通过干扰红星梭子蟹蜕皮激素合成和相关基因表达以抑制其正常蜕皮, 主要作用时期为蜕皮间期和蜕皮前期。

关键词 红星梭子蟹; 蜕皮; 基因表达; 中华双环粒蟹奴; 根头目寄生虫

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Effect of the Parasitism of *Diplothylacus sinensis* on the Ecdysteroid Hormone Content and Molting Related Gene Expression from the Three-spot Swimming Crab *Portunus sanguinolentus*

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Abstract [Objective] In order to provide basic data for the parasitic mechanism of rhizocephalan parasites on their crustacean hosts, this paper studied the parasitological effect of *Diplothylacus sinensis* on the content of ecdysteroid hormone (EH) and the expression of *MIH* and *EcR* gene from different molting stages of *Portunus sanguinolentus*. [Method] Two hundred three-spot swimming crabs, including 100 healthy individuals and 100 infected individuals were collected and cultured in experimental ponds equipped with a circular flow system. The duration of intermolt period of crabs was recorded. The haemolymph of crab in different molting stages was drawn off from the third pereopod with syringes, and then the EH content and the *MIH* and *EcR* gene expression were examined. [Result] The duration of intermolt period for male and female infected crabs was (291.5±115.5) h and (342.1±144.5) h, respectively, both of which were longer than healthy crabs. The EH contents of infected crabs in intermolt and premolt period were significantly ($P<0.05$) lower than those of normal crabs. In all of the four molting stages, the relative gene expressions of *MIH* in parasitized crabs were higher than those in healthy crabs, while the *EcR* gene expression showed the opposite trend. In total, the variation of EH content exhibited positive relationship with the *EcR* gene expression, but showed negative relationship with the *MIH* gene expression. [Conclusion] The parasitism of *D. sinensis* mainly affects the host's molting through interfering with the synthesis of ecdysteroid hormone and the gene expression of *MIH* and *EcR* during the intermolt and premolt period.

Key words *Portunus sanguinolentus*; Molting; Gene expression; *Diplothylacus sinensis*; Rhizocephalan parasite

中华双环粒蟹奴 (*Diplothylacus sinensis* Keppen, 1877) 隶属于节肢动物门蔓足下纲根头目粒蟹奴科, 是一种流行于热带、亚热带海区的甲壳类寄生虫, 通常寄生于红星梭子蟹、远海梭子蟹、锯缘青蟹等大型经济蟹类的腹部^[1-2]。受寄生的宿主蟹通常无法正常完成蜕皮周期, 生长受到抑制, 表现出个体小型化、肉质变差、含肉率下降等不良症状, 严重者甚至导致死亡^[3-4]。在蟹类的实际生产养殖中, 蟹奴疾病通常难以防治, 迄今缺乏行之有效的药物能对其进行根治, 蟹奴疾病一旦暴发, 将会造成巨大的经济损失^[5]。

蜕皮是甲壳动物的重要生理现象, 是其生长和发育的标志性特征。但蜕皮是一个十分复杂的过程, 伴随着众多的生理和生化反应, 需要各种器官分泌激素相互协调才能顺利进

行, 蟹类蜕皮的生理调节机制受到了广泛关注^[6]。十足目甲壳动物的蜕皮过程受内分泌系统和生神经系统双重调节, 通过调控 Y-器官 (Y-organ, YO) 合成蜕皮激素 (ecdysteroid hormone, EH) 以及位于眼柄的 X 器官-窦腺复合体 (X-organ sinus gland, XO-SG) 分泌蜕皮抑制激素 (molt-inhibiting hormone, MIH) 相互拮抗而完成蜕壳^[6]。EH 与蜕皮激素受体 (ecdysone receptor, EcR) 相结合构成转录因子, 起着调节甲壳类体内蛋白、糖类物质和矿物质代谢的作用, 从而促进其蜕皮和外骨骼生长^[7]。在不同生长时期, 甲壳动物的蜕皮抑制激素分泌水平会有所不同, 在蜕皮前期, 蜕皮抑制激素含量逐渐降低, 在蜕皮后急剧上升, 与血淋巴中蜕皮激素的含量成反比^[8]。

高血糖激素家族 (crustacean hyperglycemic hormone family) 神经肽是窦腺中含量最丰富的多肽类激素之一, 同时也是甲壳动物类群特有的神经肽, 该家族包括高血糖激素 (crustacean hyperglycemic hormone, CHH)、蜕皮抑制激素、离子转运蛋白 (ion-transport protein, ITP)、性腺抑制激素 (gonad-inhibiting hormone, GIH) 和大额器抑制激素 (mandibular

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organ-inhibiting hormone, MOIH)^[9]。MIH 作为 CHH 家族神经肽的成员之一,主要分布于眼柄端髓 X-器官、胸神经节、腹神经节等中枢神经系统,其作用是通过抑制 Y-器官 EH 的合成与分泌,从而达到抑制甲壳动物蜕壳^[6,9-10]。另外,还有研究表明是诱导甲壳动物肝胰腺卵黄蛋白原(vitellogenin, Vg)基因表达和促进卵巢早期阶段的卵黄发生^[11]。

有研究表明,根头目蟹奴寄生于宿主后,其体内组织会入侵宿主的腹神经节并逐步分解神经内分泌细胞,导致 YO 萎缩或退化,从而抑制宿主的蜕皮行为^[12-13]。为此,笔者以南海沿岸海域中华双环粒蟹奴寄生最为严重的红星梭子蟹(*Portunus sanguinolentus*)为试验对象,聚焦蟹奴寄生前后宿主不同蜕皮阶段的 EH 含量及 *MIH*、*EcR* 表达量分析,了解蜕皮过程蜕皮激素含量变化及基因表达水平。该研究成果可初步掌握蟹奴寄生导致宿主蟹延缓蜕皮或“蜕皮未遂”的成因,为深入探讨蟹奴病害的防控措施及提高我国在蟹奴领域的理论知识水平提供基础资料。

1 材料与方 法

1.1 材料来源 2019 年 10 月,从汕尾红海湾海域底拖网渔船渔获物中采集 200 尾野生红星梭子蟹样品,其中正常蟹 100 尾(对照组),感染蟹 100 尾(试验组,以腹部寄生有中华双环粒蟹奴外体为判断依据,图 1),雌雄比例为 1:1。根据梭子蟹类蜕皮特征,收集处于蜕皮间期的样品,对照组健康无残肢,试验组无蟹奴以外的其他病害。样品蟹规格尽量保持均一,正常蟹甲宽为(62.7±6.0) mm,体重为(13.5±3.5) g;感染蟹甲宽为(63.1±5.5) mm,体重为(13.7±3.0) g。将试验蟹分别置于 200 个容积为 24 L 的吊篮中进行饲养,吊篮悬挂于 2 个 4 m×4 m×2 m 的循环水养殖池内,每天傍晚投喂鲜活缢蛭 1 次,并定时清除篮内残渣。



图 1 受中华双环粒蟹奴寄生的雌性红星梭子蟹

Fig.1 Female *Portunus sanguinolentus* parasitized by *Diplothylacus sinensis*

每天观察感染蟹的存活和蜕皮情况,参照沈洁等^[14]对梭子蟹类的蜕皮分期划分方法,将蜕皮周期分为 4 个时期:蜕皮间期、蜕皮前期、蜕皮期和蜕皮后期。该试验养殖和取样周期耗时 42 d,最终试验组成活 47 尾(蜕皮 40 尾,7 尾蜕皮不遂),对照组成活 60 尾(均正常蜕皮)。

1.2 试验方法

1.2.1 血清样本制备及蜕皮激素测定。记录试验组和对照组每个体蜕皮间期所耗时间,抽取蜕皮间期、蜕皮前期、蜕皮期和蜕皮后期的试验蟹血淋巴样品。各蜕皮期雌蟹和雄蟹均取 5 个样品作为生物学重复,采用注射器从第 3 步足抽取 300 μ L 血淋巴用于血清样品制备。室温自然凝固 15 min,然后 2 500 r/min 离心 20 min,收集上清置于-20 $^{\circ}$ C 保存。各期试验样品的蜕皮激素含量测定参照蟹蜕皮甾体(ecdysteriod)酶联免疫分析(ELISA)试剂盒(上海酶联生物科技有限公司)使用说明书。

1.2.2 总 RNA 提取及基因表达分析。按照“1.2.1”试验样品分组,取各期红星梭子蟹眼柄和血淋巴组织置于液氮中保存。将样品转移至装有 300 μ L Trizol(上海生工)的 1.5 mL 离心管中,按照 Trizol 试剂盒(上海生工)说明对样品总 RNA 进行提取。为保证总 RNA 纯度,采用 DNase I(Takara)去除基因组 DNA,经琼脂糖凝胶电泳检测 RNA 完整性,最后使用超微量分光光度计 Nanodrop 2000C(Thermo Fisher)进行纯度检验。取 1.0 μ g RNA 样品,采用 PrimeScript RT-reagent Kit 试剂盒(Takara)对眼柄和血淋巴总 RNA 进行反转录以获得模板 cDNA。

根据课题组前期已获得的 *MIH* 和 *EcR* 基因序列,利用 Primer Premier Version 6 软件进行荧光(qPCR)定量引物设计(表 1),并选取 β -actin 基因作为内参基因。分别选取眼柄和血淋巴组织的 cDNA 作为模板,利用 Qiagen 荧光定量 PCR 仪器(Qiagen,德国)对目的基因进行序列扩增。qRT-PCR 反应条件:95 $^{\circ}$ C 预变性 5 min,95 $^{\circ}$ C 变性 10 s,60 $^{\circ}$ C 退火/延伸 30 s,共 44 个循环。循环结束后,从 60 $^{\circ}$ C 开始每 5 s 温度上升 0.5 $^{\circ}$ C 直至 95 $^{\circ}$ C,以连续测定样品的荧光强度获得溶解曲线。采用 $2^{-\Delta\Delta Ct}$ 方法计算目的基因表达量,不同蜕皮阶段的基因表达量则以蜕皮后期样品中的 Ct 表达值作为参照,其表达水平以倍数表示^[15]。

1.3 数据处理与分析 采用 SPSS 19.0 软件对试验测得的 EH 含量、*MIH* 和 *EcR* 基因的相对表达量等数据进行统计分析,相关图件使用 Excel 2010、OriginPro v9.8.0 等软件进行绘制。

2 结果与分析

2.1 蜕皮间期持续时间 对感染蟹和正常蟹的蜕皮间期持续时间统计结果表明,感染蟹蜕皮所耗时间相对正常蟹较长,雄性感染蟹($n=14$)、雄性正常蟹($n=23$)、雌性感染蟹($n=26$)和雌性正常蟹($n=37$)蜕皮间期时间分别为(291.5±115.5)、(193.5±35.4)、(342.1±144.5)和(231.1±84.0) h(图 2)。单因素方差分析(One-way ANOVA)结果表明,中华双环粒蟹奴寄生对雌性红星梭子蟹蜕皮间期持续时间影响显著($P<0.05$)。另外,试验组和对照组的雌、雄蟹之间蜕皮间期持续时间差异均不明显。

2.2 蜕皮激素含量变化 图 3 所示为不同蜕皮阶段的红星梭子蟹蜕皮激素含量受中华双环粒蟹奴寄生的影响变化。对照组和试验组血淋巴检测结果均显示,受感染前后各期红

星梭子蟹 EH 含量均表现出显著差异 ($P < 0.05$), 蜕皮间期含量最低, 蜕皮前期含量达到峰值, 随着蜕皮的进行 EH 含量逐渐下降。感染蟹与正常蟹比较, 雌性和雄性感染蟹 EH 含量在蜕

皮间期和前期水平均显著低于正常蟹 ($P < 0.05$), 表明中华双环粒蟹奴的寄生与宿主蟹的蜕皮激素分泌水平相关。此外, 2 种性别红星梭子蟹 EH 含量未见显著差异 ($P > 0.05$)。

表 1 *MIH*、*EcR* 和 β -*actin* 基因 qRT-PCR 引物

Table 1 The primer sequences for real-time quantitative PCR of *MIH*, *EcR* and β -*actin* gene

| 基因 Gene | 正向引物 Forward primer (5'—3') | 反向引物 Reverse primer (5'—3') | 用途 Usage |
|------------------------|--------------------------------|--------------------------------|--------------------------------|
| <i>MIH</i> | GTCCGCATATTCGGGTAATC | CTGTAGACGCCGCAAACG | <i>MIH</i> qRT-PCR |
| <i>EcR</i> | AAAATCTCAGGCTTCCACTACG | TACAGCGGGGCCTTCT | <i>EcR</i> qRT-PCR |
| β - <i>actin</i> | AGTTACTGCCTTCCCCACG | CCTTGATGTCACGAACGATT | β - <i>actin</i> qRT-PCR |

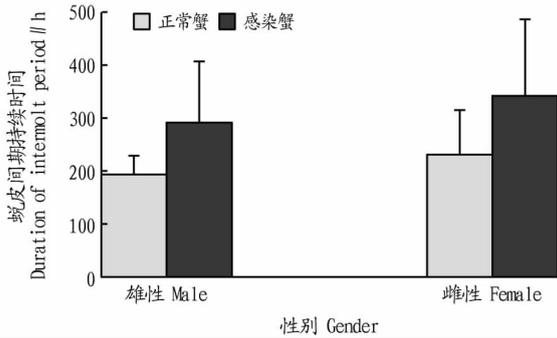


图 2 正常蟹与受中华双环粒蟹奴感染的红星梭子蟹蜕皮间期持续时间

Fig.2 Duration of intermolt period of normal and *D.sinensis*-infected *P.sanguinolentus*

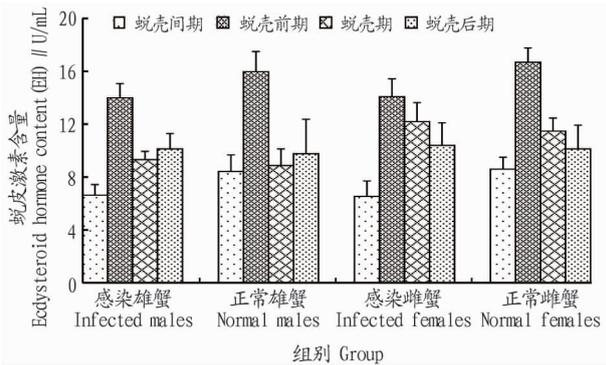


图 3 中华双环粒蟹奴寄生对不同蜕皮阶段红星梭子蟹 EH 含量的影响

Fig.3 Effect of the parasitism of *D.sinensis* on EH content of *P.sanguinolentus* at different molting stages

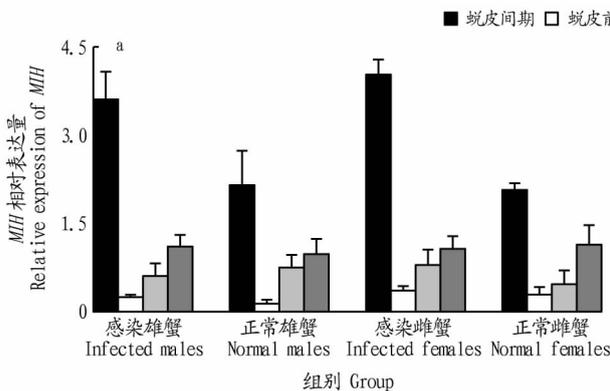


图 4 中华双环粒蟹奴寄生对红星梭子蟹蜕皮相关基因 *MIH* 和 *EcR* 相对表达量的影响

2.3 蜕皮相关基因表达量变化 从图 4a 可看出, 各组感染蟹的蜕皮间期 *MIH* 表达量均显著高于其余 3 个时期 ($P < 0.05$), 其中以雌性感染蟹蜕皮间期 *MIH* 相对表达量最高 ($4.03 \pm 0.26, n = 5$)。蜕皮前期, 各组样品 *MIH* 含量均迅速下降至谷值, 而后随着蜕皮时间的推移逐渐升高。单因素方差分析结果显示, 受中华双环粒蟹奴寄生的红星梭子蟹总体 *MIH* 表达量与正常蟹之间无显著差异 ($P > 0.05$), 但分期比较发现, 雌雄感染蟹蜕皮间期的 *MIH* 表达量均显著高于正常蟹 ($P < 0.05$), 表明该时期是中华双环粒蟹奴抑制宿主蜕皮的关键阶段。

荧光定量分析结果显示, 各组红星梭子蟹不同蜕皮阶段的 *EcR* 基因相对表达量变化与 *MIH* 基因呈相反趋势 (图 4b), 即蜕皮间期表达量最低, 蜕皮前期增加至最高水平, 而后逐渐下降。整体而言, 中华双环粒蟹奴寄生对红星梭子蟹 *EcR* 基因表达量的影响不显著 ($P > 0.05$)。各阶段单因素方差分析结果表明, 雄性和雌性正常蟹的 *EcR* 基因表达量在蜕壳间期均高于感染组, 呈极显著差异 ($P < 0.01$), 而在其他蜕壳时期则未出现显著差异。

2.4 蜕皮激素与蜕皮基因表达相关性分析 将红星梭子蟹各蜕皮时期的 EH 含量与 *MIH*、*EcR* 相对表达量进行两两对比分析, 所得 Pearson 相关系数见表 2。表 2 显示, 感染蟹各蜕皮时期的 EH 含量与同期的 *MIH* 相对表达量均呈负相关关系, 除蜕皮前期外, 其余 3 个时期均呈显著或极显著相关 ($P < 0.05, P < 0.01$), 而不同时期二者含量无显著相关 ($P > 0.05$)。各期感染蟹 EH 含量与 *EcR* 相对表达量比较, 结果均表现显著 ($P < 0.05$) 或极显著 ($P < 0.01$) 正相关关系, 不同

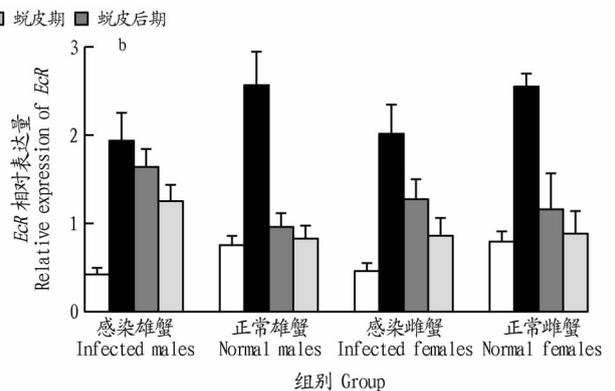


Fig.4 Effect of the parasitism of *D.sinensis* on relative expression of *MIH* and *EcR* of *P.sanguinolentus* at different molting stages

表 2 各期红星梭子蟹 EH 含量与 *MIH*、*EcR* 相对表达量相关性

Table 2 Correlation coefficient of EH content comparing with relative expression of *MIH* and *EcR* at different molting stages of *Portunus sanguinolentus*

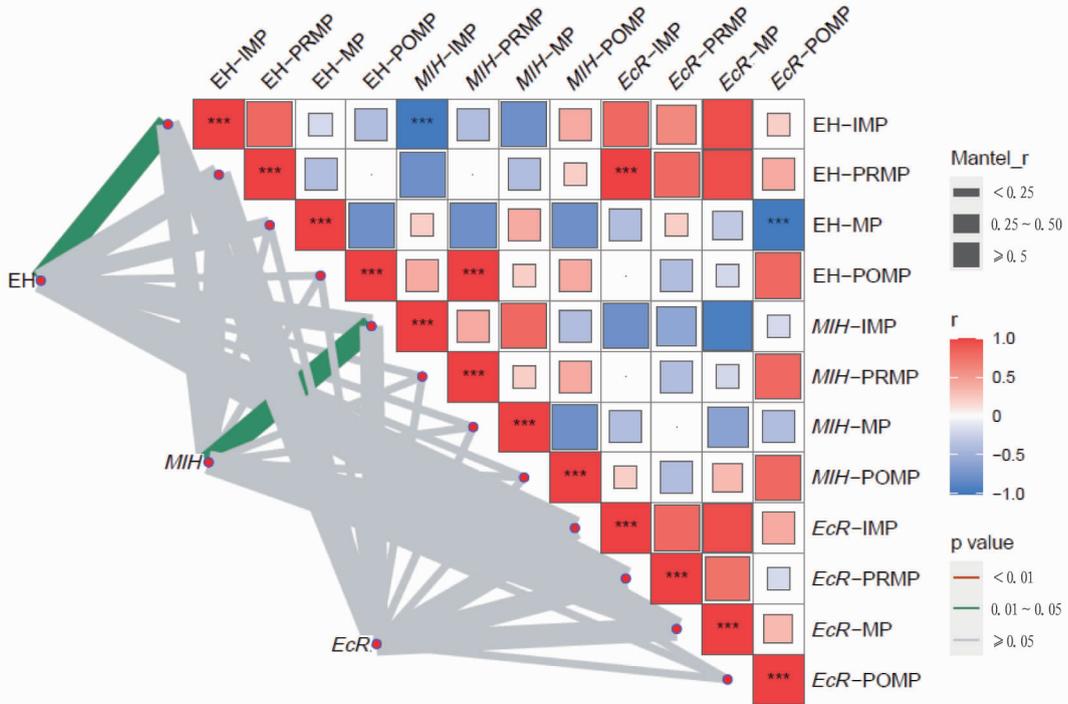
| 指标 Index | 时期 Stage | EH 含量 EH content | | | | |
|--------------------------------------|----------|---------------------------|-----------------------|-------------------|--------------------------|---------------------------|
| | | 蜕皮间期 Deciduous interphase | 蜕皮前期 Prophase molting | 蜕皮期 Molting stage | 蜕皮后期 Anaphase of molting | 蜕皮间期 Deciduous interphase |
| <i>MIH</i> 表达量 <i>MIH</i> expression | 蜕皮间期 | -0.781 ** | -0.355 | -0.102 | 0.57 | -0.954 ** |
| | 蜕皮前期 | -0.421 | -0.528 | 0.042 | -0.203 | -0.287 |
| | 蜕皮期 | 0.438 | 0.228 | -0.956 * | 0.459 | -0.479 |
| | 蜕皮后期 | 0.039 | 0.358 | -0.278 | -0.913 ** | -0.115 |
| <i>EcR</i> 表达量 <i>EcR</i> expression | 蜕皮间期 | 0.777 ** | 0.326 | 0.249 | -0.608 | 0.986 ** |
| | 蜕皮前期 | -0.235 | 0.836 ** | -0.094 | 0.116 | 0.408 |
| | 蜕皮期 | -0.596 | -0.427 | 0.850 * | -0.291 | 0.208 |
| | 蜕皮后期 | 0.079 | -0.252 | 0.430 | 0.868 ** | -0.529 |

注:阴影部分表示感染蟹指标对比,其余表示正常蟹指标对比;*表示差异显著($P < 0.05$),**表示差异极显著($P < 0.01$)

Note:Shaded lattice indicate the correlation coefficients between infected crabs, and the rest lattice indicate those between normal crabs. *.Means significantly different ($P < 0.05$) and ** means extremely different ($P < 0.01$)

时期无显著相关性。由此可见,红星梭子蟹血淋巴中蜕皮激素含量与 *EcR* 相对表达量呈协同作用关系,与 *MIH* 相对表达量则呈拮抗关系。另外,Mantel Test 相关性分析结果表

明,中华双环粒蟹奴对红星梭子蟹蜕皮相关激素和基因表达的影响主要作用于蜕皮间期和蜕皮前期(图 5)。



注:IMP.蜕皮间期;PRMP.蜕皮前期;MP.蜕皮期;POMP.蜕皮后期

Note:IMP.Intermolt period;PRMP.Premolt period;MP.Molting period;POMP.Postmolt period

图 5 受感染红星梭子蟹蜕皮激素与相关基因表达量相关性

Fig.5 Mantel test analyses between EH content and molting-related gene expression of *P.sanguinolentus*

3 讨论

蜕皮是甲壳类动物生长发育必经的重要过程,该过程所需的蜕皮激素由 Y-器官分泌,其分泌量的多寡与蜕皮阶段有关,一般而言呈规律性变化,蜕皮前期分泌量达到高峰期^[16]。该研究中各蜕皮阶段 EH 含量变化趋势与前人研究结果一致^[17-18],表现为蜕皮间期含量最低,蜕皮前期上升至最高值,随后逐渐下降。蜕皮间期是甲壳动物摄食和营养物质储备最活跃的时期,也是蜕皮周期中最稳定且持续时间最长的阶段,而在蜕皮前期则需通过自身调控分泌大量的蜕皮

激素促进表皮回缩,以保证蜕皮活动的顺利进行^[19]。

蟹奴是自然海域和养殖水域常见的蟹类寄生虫,一般于宿主蜕皮期进行入侵,寄生后的内体部分(又称“营养系统”)留存于宿主体内吸取营养,从内体延伸至宿主体外的部分为外体(又称“生殖系统”)^[2]。在一些寄生情形下,蟹奴外体的出现将阻止宿主蟹蜕皮行为的发生^[20-21]。有学者推测,根头目寄生虫可能干扰宿主 Y-器官中 EH 前体的合成或刺激 X 器官-腺囊复合体分泌 *MIH*,以达到抑制宿主蜕皮、保障自身完成寄生周期的目的^[22]。据研究表明,受蟹奴寄生

的哈氏泥蟹 (*Rhithropanopeus harrisii*) 不仅蜕皮行为受阻, 周期明显延长, 其断指再生能力也同样受到抑制^[23], 而在摘除蟹奴外体后, 宿主的蜕皮能力可再次得到恢复^[24]。另外, 一些蟹奴类群 (如 Chthamalphilidae 科和 Peltogastridae 科) 的寄生不会明显阻碍宿主的正常蜕皮, 在外体伴随宿主蜕皮而脱落后, 其基部表皮仍会粘连于宿主新生表皮, 以便继续完成自身寄生生活史^[25]。

EcR 基因是促进甲壳动物蜕皮和外骨骼生长的关键基因, 与 *MIH* 基因共同调控甲壳类的蜕皮行为^[7]。该研究结果表明, 无论是受蟹奴感染的宿主蟹, 还是正常蟹, 其不同蜕皮阶段的 *EcR* 基因和 *MIH* 基因相对表达量均呈现相反的趋势, 即 *EcR* 基因在蜕皮前期表达量最高, 蜕皮间期最低, 而 *MIH* 基因在蜕皮间期含量最高, 蜕皮前期最低, 这与传统的甲壳类蜕皮相关基因表达研究结果相符^[6,11,19]。同时, 各期红星梭子蟹 *EcR* 基因相对表达量与 EH 含量呈正相关关系, 二者之间呈协同作用关系, 且在蜕皮前期最为显著; 蜕皮期的 EH 含量急剧下降, 可能是由于当 *EcR* 表达量高于临界值时, 反而会致使 Y-器官 EH 的合成受到抑制。这与黄妹等^[26] 对于中华绒螯蟹蜕壳基因表达的研究结果一致, 高表达量的 *EcR* 基因对蜕皮激素的合成起到负反馈调控作用。

感染蟹与正常蟹比较, 仅发现中华双环粒蟹奴对蜕皮间期红星梭子蟹血淋巴中 *EcR* 基因和 *MIH* 基因相对表达量影响显著, 表明该时期是蟹奴干扰宿主生理行为的关键阶段。前人有关蟹奴寄生对宿主蜕皮抑制相关机理的报道较少, 有研究指出受蟹奴感染的方形大额蟹 (*Metapograpsus thukuhar*) 血淋巴高血糖激素含量未受影响, 且其 X 器官-窦腺复合体形态仍保持完整^[27], 但可抑制阿拉斯加帝王蟹 (*Paralithodes camtschaticus*) 血淋巴渗透压的正常调节, 促进血蓝蛋白和葡萄糖的合成, 加速代谢并为蟹奴生长和繁殖提供所需能量^[28]。此外, Hsiao 等^[27,29] 研究发现, 扁平蟹奴 (*Polyascus plana*) 寄生可降低宿主血淋巴中乙酰胆碱和甘油三酯的水平, 推测蟹奴可能通过分泌某种化学物质干扰宿主正常的能量代谢, 致使一些受寄生的宿主类群体型偏小, 并产生“性逆转”现象。

甲壳动物蜕皮是一个极其复杂的过程, 除受自身内在因素影响外, 还受外界温度、光照、盐度等诸多因素影响^[30]。蟹奴种类繁多, 不同类群形态各异, 其入侵宿主的途径、繁殖方式和生活史也不尽相同, 对宿主的危害程度也有所差别^[31]。目前大多数研究集中于寄生后宿主的形态、行为以及生理等方面的影响, 因此, 今后有必要针对蟹奴的寄生机理及其影响宿主蜕皮和代谢关键信号通路等方面展开进一步研究。

4 结论

红星梭子蟹的蜕皮行为与其 EH 含量变化密切相关, 中华双环粒蟹奴寄生可在一定程度上干扰宿主蜕皮相关激素分泌和基因表达, 从而抑制或延缓其蜕皮行为。

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螬的较好药剂。

进一步分析它们有效成分的作用机理可以看出,1%氯虫·噻虫胺颗粒剂中的氯虫苯甲酰胺属邻甲酰氨基苯甲酰胺类杀虫剂,其作用机理是高效激活昆虫体内的鱼尼丁(肌肉)受体,过度释放细胞内贮存的钙离子,引起肌肉调节衰弱、麻痹直至最后瘫痪死亡,害虫呈停止取食、活力消失、回吐和肌肉麻痹等中毒症状,最终导致死亡;氯虫苯甲酰胺的主要作用方式为胃毒,同时具有一定的触杀作用,具有良好的内吸性和渗透性,具有作用速度快和持效期长的特点^[11-12]。噻虫胺属第2代烟碱类杀虫剂,其作用机理是与突触后膜上乙酰胆碱受体 AchR 结合,对受体产生抑制作用,从而阻断神经递质乙酰胆碱 Ach 与受体结合,导致害虫出现萎靡而后死亡;噻虫胺的作用方式有触杀、胃毒和内吸作用^[13-14]。氯虫苯甲酰胺和噻虫胺2种药剂的作用机理存在差异,复配制剂在减少用药量、提高防效的同时,能有效延缓害虫抗药性的产生。辛硫磷是一种高效低毒有机磷杀虫剂,以触杀和胃毒为主,无内吸作用。该药施入土中,其残效期很长,可达1~2个月,适合于防治地下害虫,特别是对花生、玉米、小麦的蛴螬、蝼蛄有良好的防治效果^[15]。1%氯虫·噻虫胺颗粒剂和3%辛硫磷颗粒剂这2种颗粒剂对玉米蛴螬均有很好的防效,且持效期较长,可以轮换使用以减缓抗性产生,提高防治效果,降低防治成本。

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萌发有明显的促进作用,但与生产上要求做到胚根与胚芽接近同步发育要求仍有不小的差距。对于流苏种子怎样打破休眠促进萌发,将继续关注国内外有关方面研究成果,汲取新的技术和方法,继续推进有关方面的研究。

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