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脊尾白虾不同蜕皮分期免疫酶、几丁质酶及蜕皮激素的变化*

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摘要 为了研究脊尾白虾(*Exopalaemon carinicauda*)生长蜕皮和生殖蜕皮的差异，本研究对 2 种蜕皮不同分期(间期 C 期、前期 D 期和后期 AB 期)的非特异性免疫指标[酚氧化酶(PO)、超氧化物歧化酶(SOD)、酸性磷酸酶(ACP)、碱性磷酸酶(AKP)、几丁质酶(Chitinase)及蜕皮激素(MH)]进行了差异比较。结果显示，生长蜕皮各分期 PO 活力差异不显著，生殖蜕皮各分期 PO 活性呈先降低后升高的趋势，各分期差异显著；间期时，生长蜕皮和生殖蜕皮 PO 活性差异不显著；前期时，生殖蜕皮显著低于生长蜕皮；后期时，生殖蜕皮显著高于生长蜕皮。生长蜕皮各分期 SOD 活性逐渐升高，且差异显著，生殖蜕皮后期 SOD 活性显著低于间期和前期，间期和前期差异不显著；间期时，生殖蜕皮显著高于生长蜕皮，前期二者差异不显著；后期时，生殖蜕皮显著低于生长蜕皮。生长蜕皮各分期 AKP、ACP 活力均呈先升高后降低的趋势，且各分期差异显著，生殖蜕皮与生长蜕皮变化趋势相同；间期、前期、后期，生长蜕皮都显著高于生殖蜕皮。生长蜕皮时各分期 Chitinase 活力和 MH 激素浓度变化趋势相同，呈逐渐升高趋势，且各分期差异显著，生殖蜕皮时，呈先降低后升高趋势，且各分期差异显著；间期和前期，生长蜕皮显著低于生殖蜕皮，后期生长蜕皮显著低于生殖蜕皮。本文首次对脊尾白虾生长蜕皮和生殖蜕皮进行研究，结果表明，生长蜕皮和生殖蜕皮因为卵巢发育而存在明显不同。本研究结果为虾蟹类蜕皮机制的研究、养殖业苗种的育成提供理论基础和科学依据。

关键词 生长蜕皮；生殖蜕皮；免疫酶；几丁质酶；蜕皮激素

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蜕皮贯穿甲壳类的整个生活史，与其生长、发育、繁殖和附肢再生等密切相关。甲壳类蜕皮发生的关键因素及其调控机制一直是研究的重点(李旭光等, 2014)。甲壳动物蜕皮一般分为以下 3 种类型：发育蜕皮是虾蟹类幼体进行变态发育，每一期蜕皮都会对幼体的形态和生理特点产生重要影响。生长蜕皮在胚胎经过变态发育成幼体后，要经过多次蜕皮，使体长体重逐次增加完成生长。蜕皮不仅是旧壳的更新，还包括胃、鳃、肠等的更新及断肢再生。生殖蜕皮又称青春期蜕壳或终期蜕壳，卵巢发育成熟后，在交配前雌性需要蜕壳，个体的某些部位会发生外部形态的显著变化。例如，雌蟹的腹甲可由三角形蜕变成半圆形(Hartnoll, 1974)。

蜕皮主要由互为拮抗的 Y 器官分泌的蜕皮激素(MH)(Skinner, 1985)和 X 器官窦腺复合体分泌的蜕皮抑制激素(上官步敏等, 1995)共同调节。另外，也需要多种酶的参与，如几丁质酶(Chitinase)。几丁质富含于甲壳动物围食膜及表皮中，其降解与重新合成是蜕皮过程中一个重要的生理过程，而几丁质酶在这一生理过程中起到至关重要的作用(Funke, 1989; Elyakova, 1972; Jeuniaux, 1963)。蜕皮过程会影响到许多生理功能的变化，Hose 等(1992)研究表明，在蜕皮过程中虾体免疫因子会发生改变，很容易受感染。超氧化物歧化酶(SOD)、酸性磷酸酶(ACP)和碱性磷酸酶(AKP)等是体液防御系统中的重要免疫因子。酚氧化酶(PO)也是甲壳动物重要的识别和防御系统，是衡量免疫功能的重要指标(Hernández-López *et al*, 1996; Smith *et al*, 1991)。

脊尾白虾(*Exopalaemon carinicauda*)又名白虾、迎春虾等，系温带海水底栖虾类，在我国沿海均有分布，尤以黄渤海产量最高(李新正等, 2003)。脊尾白虾繁殖盛期一般在 5~6 月和 8~9 月；雌虾无纳精囊结构，所以产卵前需进行交配，交配前雌虾须进行生殖蜕皮。在繁殖期，由于抱卵雌虾在抱卵期间卵巢可以二次发育甚至多次成熟，因此，每尾雌虾在 1 年内可以多次繁殖。本研究以脊尾白虾为对象，从免疫相关的 SOD、ACP、AKP、PO 活力和蜕皮相关的 Chitinase 活力、MH 浓度变化，初步探究了生长蜕皮、生殖蜕皮 2 种不同蜕皮分期之间的差异，为甲壳动物蜕皮调控机制的研究提供理论基础。

1　材料与方法

1.1　实验材料

脊尾白虾取自山东省日照海辰水产有限公司，均为活力好、体长均匀的健康个体，其中，未性成熟个体体长为(3.22±0.21) cm，体重为(0.49±0.04) g，性成熟个体体长为(5.42±0.34) cm，体重为(1.58±0.22) g。将实验用虾暂养于 200 L 的 PVC 桶中，每桶 50 尾，暂养海水盐度为 31，pH 为 8.2，水温为 24℃，24 h 持续充氧。每天早晚 2 次饲喂蛤蜊肉，吸污换水 1/3，连续养殖 10 d 后开始实验。

1.2　实验方法

1.2.1　*2 种蜕皮区分*　　未性成熟的脊尾白虾处于生长期，实验虾的蜕皮为生长蜕皮。性成熟的实验虾分为卵巢发育虾和抱卵虾，其中，卵巢发育且带有腹蓝者的蜕皮为生殖蜕皮。根据中华锯齿米虾(*Neocaridina denticulata sinensis*)(王战芳, 2014)和凡纳滨对虾(*Litopenaeus vannamei*)(Gao *et al*, 2015)的方法进行蜕皮分期，分为蜕皮间期(C 期)、蜕皮后期(软皮期, AB 期)、蜕皮前期(D 期, 取自特征明显的 D2 亚期)。

1.2.2　*样品采集及处理*　　实验用虾暂养 1 周后，挑选活力好、无残缺的个体，用解剖剪剪取尾节末端，置于倒置显微镜观察分期，并拍照。将确定分期的脊尾白虾采集血淋巴：每尾虾取 0.1 ml 血与 0.1 ml 预冷的抗凝剂混合(抗凝剂配方：1.588 g 柠檬酸钠，3.92 g NaCl，4.56 g 葡萄糖，0.66 g EDTA-2Na，200 ml ddH_2O)，4℃ 5000 r/min 离心 10 min 后，留上清液，置于–20℃冰箱保存。每个平行取 3 尾，每个蜕皮分期共 3 个平行。

1.2.3　*样品测定方法*　　PO、Chitinase、MH 测试盒购自上海酶联。应用双抗体夹心法测定标本中酶活及激素水平，测定方法参考试剂盒说明书。ACP、AKP、SOD 测试盒购自南京建成生物研究所。每 100 ml 血清在 37℃与基质作用 30 min 产生 1 mg 酚为 1 个 ACP 或 AKP 活力单位(U)。在反应体系中，SOD 抑制率达 50%时所对应的 SOD 量为 1 个 SOD 活力单位(U)。具体操作见说明书。

1.2.4　*数据分析*　　实验数据均表示为平均数±标准差(Mean±SD)，同种蜕皮不同分期、不同种蜕皮同一分期分别利用 SPSS 21.0 软件进行 Duncan 和独立 *t* 检验，One-way ANOVA 进行单因素方差分析，以 $P<0.05$ 为差异显著性。

2　结果与分析

2.1　酚氧化酶(PO)活力在不同蜕皮分期的变化

PO 在不同蜕皮期的变化见图 1。由图 1 可知，

生长蜕皮各分期的 PO 活力差异不显著。生殖蜕皮各分期的 PO 活力呈先降低后升高趋势，且各分期差异显著(P<0.05)。间期时，生长蜕皮和生殖蜕皮的 PO 活力差异不显著；前期时，生殖蜕皮的 PO 活力显著低于生长蜕皮(P<0.05)；后期时，生殖蜕皮的 PO 活力显著高于生长蜕皮(P<0.05)。

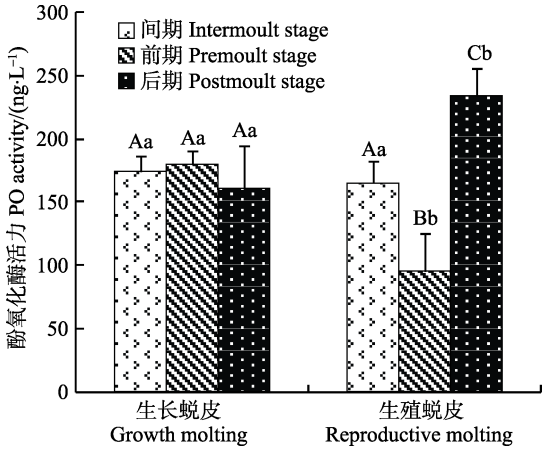

图 1 2 种蜕皮的各分期酚氧化酶活力变化

Fig.1 Variation of the PO activity during different stages of two types of molting

同种蜕皮的不同分期用大写字母表示差异显著性，不同种蜕皮的同一分期用小写字母表示。下同

Capital letters indicated the significance of the difference during different stages of the same molting type, while lower case letters indicated the same stages of different types of molting. The same as below

2.2 超氧化物歧化酶(SOD)活力在不同蜕皮分期的变化

SOD 活力在不同蜕皮期的变化见图 2。由图 2 可知，生长蜕皮各分期 SOD 活力呈逐渐升高趋势，且差异显著(P<0.05)。生殖蜕皮后期的 SOD 活力显著低于间期和前期(P<0.05)，间期和前期 SOD 活力差异不显著。间期时，生殖蜕皮的 SOD 活力显著高于生长蜕皮(P<0.05)，前期二者差异不显著，后期生殖蜕皮的 SOD 活力显著低于生长蜕皮(P<0.05)。

2.3 酸性磷酸酶(ACP)活力在不同蜕皮分期的变化

ACP 活力在不同蜕皮期的变化见图 3。由图 3 可知，生长蜕皮各分期 ACP 活力呈先升高后降低趋势，且各分期差异显著(P<0.05)。生殖蜕皮与生长蜕皮的 ACP 活力变化趋势相同；间期、前期、后期时，生长蜕皮的 ACP 活力都显著高于生殖蜕皮(P<0.05)。

2.4 碱性磷酸酶(AKP)活力在不同蜕皮分期的变化

AKP 活力在不同蜕皮分期的变化见图 4。由图 4

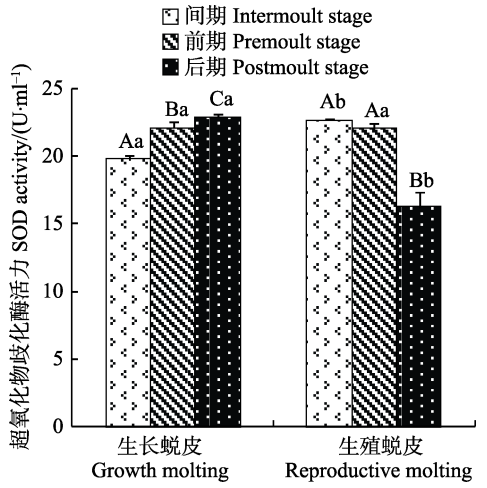

图 2 2 种蜕皮的各分期超氧化物歧化酶活力变化

Fig.2 Variation of the SOD activity during different stages of two types of molting

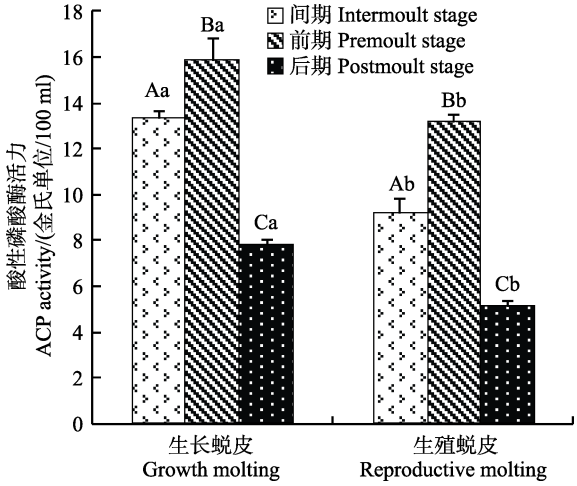

图 3 2 种蜕皮的各分期酸性磷酸酶活力变化

Fig.3 Variation of the ACP activity during different stages of two types of molting

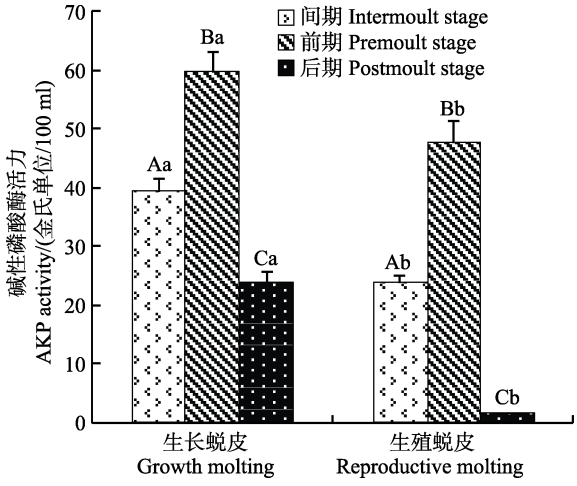

图 4 2 种蜕皮的各分期碱性磷酸酶活力变化

Fig.4 Variation of the AKP activity during different stages of two types of molting

可知，生长蜕皮各分期 AKP 活力呈先升高后降低趋势，且各分期差异显著(P<0.05)。生殖蜕皮与生长蜕皮的 AKP 活力变化趋势相同，间期、前期、后期时，生长蜕皮的 AKP 活力都显著高于生殖蜕皮(P<0.05)。与 ACP 变化趋势相似。

2.5　几丁质酶(Chitinase)活力在不同蜕皮分期的变化

Chitinase 活力在不同蜕皮分期的变化见图 5。由图 5 可知，生长蜕皮各分期 Chitinase 活力呈逐渐升高趋势，且各分期差异显著(P<0.05)。生殖蜕皮的 Chitinase 活力呈先降低后升高趋势，且各分期差异显著(P<0.05)。间期和前期，生长蜕皮的 Chitinase 活力显著低于生殖蜕皮(P<0.05)；后期时，生长蜕皮的 Chitinase 活力显著低于生殖蜕皮(P<0.05)。

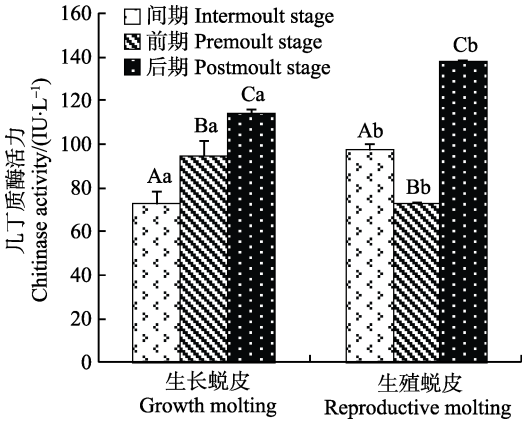

图 5　2 种蜕皮各分期几丁质酶活力变化

Fig.5　Variation of the chitinase activity during different stages of two types of molting

2.6　蜕皮激素(MH)浓度在不同蜕皮分期的变化

MH 浓度在不同蜕皮分期的变化见图 6。由图 6 可知，生长蜕皮各分期 MH 浓度呈逐渐升高趋势，但前期与间期和后期差异不显著，后期 MH 浓度显著高于间期(P<0.05)。生殖蜕皮各分期呈先降低后升高趋势，且各分期差异显著(P<0.05)。间期、前期、后期时，生长蜕皮的 MH 浓度都显著高于生殖蜕皮(P<0.05)。

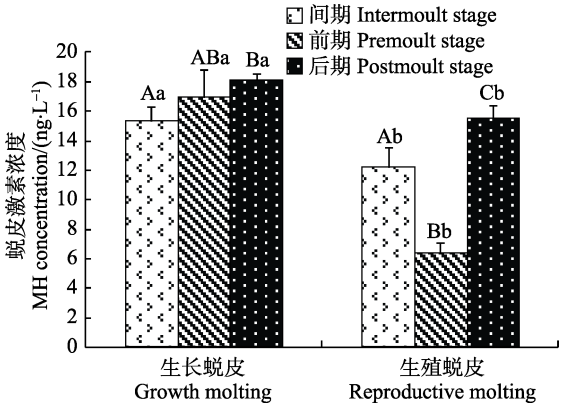

图 6　2 种蜕皮各分期蜕皮激素浓度变化

Fig.6　Variation of MH concentration during different stages of two types of molting

3　讨论

蜕皮是甲壳动物个体发育的一个标志，也是个体生长的一个必要阶段。近年来，甲壳动物蜕皮机制一直是研究的重点。在生产中，诱导蜕皮可以缩短蜕皮周期、体重增长变快、促进抱卵等(张海燕等, 1999; 崔青曼等, 2004)。抱卵虾蟹因外界环境的刺激导致蜕皮，从而使受精卵脱落的现象，严重制约了苗种的生产，给养殖业造成重大损失。脊尾白虾为抱卵繁殖虾类，同步性成熟较困难，人工控制交尾及幼体培育技术尚不完善，苗种大部分来自野采亲虾自然繁殖等问题，全人工繁育技术仍需要进一步研究。雌虾的成熟、交尾与蜕皮密切相关，因此，本文探究了生殖蜕皮与生长蜕皮过程中卵巢发育与蜕皮调控之间的相互关系，可为虾蟹类蜕皮机制的研究提供重要信息，为雌虾同步性成熟、实现全人工繁育提供理论依据。

在甲壳动物中，酚氧化酶原系统在机体对抗外物入侵过程中起着重要作用。伴随着颗粒细胞的脱颗粒和酚氧化酶原系统的激活，酚氧化酶被释放出来，起识别和调理作用。血清酚氧化酶活力是虾类的免疫指标之一(陶保华等, 2000)。在 2 种蜕皮过程中，生长蜕皮变化差异不大，生殖蜕皮在后期酶活性显著升高，可能与蜕皮后排卵有关，这与 Alexander 等(1992)的研究相似。鱼卵中存在着种类丰富的蛋白酶抑制剂成分，除在鱼卵中执行生理调节功能外，在病原生物防御中也起到了重要作用。而蛋白酶抑制剂可以调节酚氧化酶的活性、抗菌肽的合成等(Alexander, 1992; Gregorio *et al*, 2002)。活性氧的产生与耗氧的高低存在着一定的相关性，高的耗氧率往往导致高的活性氧水平，而活性氧再由抗氧化系统清除。SOD 是唯一以活性氧为底物的抗氧化酶，催化其转化为水和氧气。蜕皮前后代谢旺盛、耗氧率高，相应的活性氧也较高，因此，生长蜕皮前期和后期有着较高的 SOD 活力。而生殖蜕皮在间期有着高的 SOD 活力，后期却显著低于生长蜕皮后期，这可能与生殖蜕皮间期卵巢发育代谢旺盛和后期排卵卵巢退化有关。作为溶酶体酶的标志酶，ACP 和 AKP 是甲壳动物的先天免疫反应重要的参与者，同时也是甲壳动物进行酸碱调控的重要因子(Darnell *et al*, 1986; Jiang *et al*, 2015)。生

长蜕皮和生殖蜕皮变化趋势相同，在前期拥有较高活力，但生殖蜕皮各期普遍低于生长蜕皮，这可能与卵巢发育有关。在蜕皮过程中，旧的几丁质外壳被几丁质酶降解。对甲壳动物几丁质酶与其蜕皮间的关系已有不少研究，Espie 等(1995)发现几丁质酶的产生与蜕皮激素分泌量密切相关，几丁质酶 mRNA 的表达会受到蜕皮激素的调节，这与本文中 Chitinase 活力与 MH 浓度变化趋势相一致。而生长蜕皮和生殖蜕皮过程中，Chitinase 活力和 MH 浓度变化却不相同，在生殖蜕皮前期骤降可能与性腺发育有关，这与罗荣生等(1990)的研究结果相似，该研究认为中华绒螯蟹(*Eriocheir sinensis*)摘除双侧眼柄后，血淋巴中 20-羟蜕皮酮含量逐渐增高，在第 10 天后迅速下降，下降可能与性腺发育有关。综上所述，从非特异性免疫、蜕皮相关酶和蜕皮激素 3 项指标的变化结果可知，生长蜕皮和生殖蜕皮因为卵巢的发育而存在明显不同。卵巢发育会导致蜕皮过程中机体免疫力显著升高，而使蜕皮相关酶和激素水平显著降低。

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(编辑 马璀艳)

Changes in Immunity-Related Enzymes, Chitinase Activity, and Molting Ecdysteroid Concentration of *Exopalaemon carinicauda* During Different Molting Stages

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Abstract The present study was conducted to evaluate the differences between the growth and reproductive molting of *Exopalaemon carinicauda*. In this milieu, we analyzed the differences in the representative stages (intermoult C, premoult D, and postmolt AB) of the two types of molting in relation to three parameters: non-specific immune indexes including phenoloxidase (PO), superoxide dismutase (SOD), acid phosphatase (ACP), alkaline phosphatase (AKP), molting-related enzyme (Chitinase), and ecdysone concentration (MH). The activity of PO during different stages of growth molting exhibited no significant difference. While the activity of PO during reproductive molting decreased at first and then increased, and showed significant differences among different stages. At the intermoult stage, the activity of PO of growth and reproductive molting was not significantly different. At the premoult stage, the activity of PO of reproductive molting was significantly lower than that of growth molting. At the postmoult stage, the activity of PO of reproductive molting was significantly higher than that of growth molting. During growth molting, the activity of SOD at all the three stages gradually increased, and demonstrated significant differences. During reproductive molting, the activity of SOD at the postmoult stage was significantly lower than that at the other two stages, and the difference between the intermoult and premoult stages was not significant. At the intermoult stage, the activity of SOD of reproductive molting was significantly higher than that of growth molting. At the premoult stage, there was no significant difference between them, while at the postmoult stage, the SOD activity of reproductive molting was significantly lower than that of growth molting. During growth molting, the activity of AKP and ACP at all the three stages had the same trend, that is they increased at first and then decreased, and the difference was significant. The activity of enzymes during reproductive molting had the same trend as those during growth molting. However, the activity of enzymes at all the three stages during growth molting was significantly higher than that during reproductive molting. At different stages of growth molting, chitinase activity and MH hormone concentration had the same trend, that is they gradually increased, and the difference of the stages was significant. Furthermore, during reproductive molting, they decreased at first and then increased, and the differences between the stages were significant. During the intermoult and premoult stages, chitinase activity and MH hormone concentration of growth molting was significantly lower than those of reproductive molting. During the postmoult stage, chitinase activity and MH hormone concentration of growth molting were significantly lower than those of reproductive molting. The present study conducted is a preliminary study on growth and reproductive molting. The results showed that there was a significant difference between the growth and reproductive molting because of the ovary development. The results provide a theoretical base and a scientific ground for further research on the mechanism of molting and artificial breeding.

Key words Growth molting; Reproductive molting; Immune enzyme; Chitinase; Molting ecdysteroid

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