Argopecten 属扇贝种间杂交后代育性决定机制

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摘要: 贝类对全球渔业发展和人类生计至关重要, 其产量约占世界海水养殖产量的 56%。雌雄同体型 *Argopecten* 属海湾扇贝(*Argopecten irradians irradians*)和紫扇贝(*Argopecten purpuratus*)是具有高营养价值和经济价值的贝类, 二者的种间杂交后代表现出极显著的生长优势, 具有巨大的育种潜力。然而, 两者的绝大多数杂交后代都表现为不育, 限制了杂交育种技术的进一步开发和规模化应用。本文从遗传和环境角度综述了两种 *Argopecten* 属扇贝种间杂交不育的潜在机制。线粒体基因和核基因突变、异常核质相互作用、表观遗传修饰失调以及环境因子温度变化引起的能量供应不足、有丝分裂和减数分裂缺陷、高水平的细胞凋亡和活性氧水平以及配子的发生和成熟受阻可能是导致 *Argopecten* 属扇贝种间杂交不育的关键原因。此外, *EGFR* 基因也在杂交贝的育性调控中发挥着重要的作用。本综述为揭示扇贝种间杂交不育的决定机制提供了新的策略和方向, 并为贝类的规模化杂交育种奠定了理论基础, 有望为相关研究提供参考以促进水产养殖业的健康发展。

关键词: 杂交不育; 雌雄同体; *Argopecten* 属扇贝; 细胞凋亡; 能量缺陷; 减数分裂

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水产养殖是优质蛋白质的重要来源, 提供了大约一半的“蓝色食物”[1, 2]。贝类养殖产量在中国海水养殖总产量中占比最高[3]。海湾扇贝(*Argopecten irradians irradians*)作为一种速生型的小型贝, 自 1982 年引进中国后迅速成为主要的养殖品种, 掀起了中国海水养殖的第三次浪潮, 使中国扇贝养殖产量跃居世界第一[4, 5]。然而, 近交衰退导致的种质退化制约了扇贝养殖业的可持续健康发展[6]。紫扇贝(*Argopecten purpuratus*)是速生型的中型贝, 自然分布在秘鲁和智利沿海, 与海湾扇贝亲缘关系接近。为解决海湾扇贝种质退化的产业困境, 王春德等[7]于 2008 年把紫扇贝引入中国并成功将其与海湾扇贝杂交, 种间杂交后代表现出极显著的生长优势, 但绝大多数杂交后代都表现为不育[8]。*Argopecten* 属扇贝雌雄同体的生物学特点制约了规模化种间杂交制种, 幸运的是, 极少量杂交一代个体表现为雌性可育雄性不育, 其卵子和亲本回交后代杂种优势与杂交一代相当, 为突破规模化种间杂交瓶颈提供了有效途径, 但其决定机制尚不明确。

杂交不育广泛存在于生物界中, 研究杂交不育的决定机制在基础研究和杂种利用中具有重要价值。在以往的研究中, 研究人员通过解析和利用杂交不育现象解决了重要的产业问题。例如, 袁隆平院士用野生稻做母本, 用栽培稻做父本进行杂交和多次回交, 利用“远缘杂交”获得了中国的第一个水稻雄性“不育系”, 选用与父本细胞核性质结构相似的雄性水稻植株给不育系授粉得到“保持系”; 选用与母本亲缘关系近的水稻植株给不育系授粉得到“恢复系”打破不育系形成的核质不兼容性, 实现“三系”配套育种体系[9]。通过大规模种植杂交水稻, 中国用仅占世界 7%的土地养活了世界近 1/4 的人口[10]。对籼稻和粳稻杂种花粉不育分子机制的解析破解了水稻

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生殖隔离之谜，促进通过分子标记辅助选择规避花粉败育的问题，从而推进水稻亚种间超强优势利用和高产品种的培育[11]。之前关于杂交不育的报道主要集中在雌雄同株型的植物和雌雄异体型的动物中[12-14]，关于雌雄同体型动物种间杂交不育的报道较少[15, 16]，其机制研究尚不全面。充分利用 *Argopecten* 属扇贝种间杂交后代中“雌性可育雄性不育”的杂交贝，将有助于建立扇贝大规模种间杂交技术，进一步促进扇贝养殖业的发展。解析杂交不育的决定机制也有助于贝类种群资源的利用，并为阐明雌雄同体型动物的生殖演化和新物种形成机制提供新的见解。研究者前期发现了极少数的可育杂交贝，其卵细胞可以正常受精和发育[17, 18]，为 *Argopecten* 属扇贝种间杂交不育机制的解析提供了宝贵研究材料。

在农作物和模式生物中的研究表明，种间杂交不育主要受遗传和环境因素的影响，其中遗传因素主要包括线粒体和核基因组变异、表观遗传修饰以及基因表达失调等[12, 19-21]。主要的环境因素是温度，高温会导致线粒体-核不相容、精子发育缺陷、卵泡损伤和生殖细胞死亡[22-25]。因此，本综述从遗传和环境角度对雌雄同体型海湾扇贝与紫扇贝种间杂交不育的可能决定机制予以概述，以期为扇贝育种产业的可持续健康发展提供理论基础。

1 线粒体基因变异及其与核基因间的相互作用在 *Argopecten* 属杂交扇贝育性决定中的作用

线粒体是能量产生的重要场所，90%以上的 ATP 是通过线粒体中的氧化磷酸化产生的[26]。线粒体基因组通常是环状的 DNA 分子，其进化速度快、突变率高[26, 27]。动物的线粒体基因组通常包含 37 个基因，包括 2 个 rRNA(12S rRNA 和 16S rRNA)、22 个 tRNA 和 13 个蛋白编码基因(所有蛋白编码基因都与内膜的呼吸作用有关)[28]。线粒体基因组中最长的序列是控制区，这是一段极易变异的非编码区[29]。在大多数生物中，线粒体基因组遵循母系遗传，即后代的线粒体 DNA(mtDNA)来源于其母本[30]。但在一些双壳贝类(*Mytilus trossulus*、*Ruditapes philippinarum* 和 *Musculista senhousia*)中存在着双单亲遗传(DUI)的现象，即雌雄性后代的线粒体 DNA 都会遗传自母本，而父本的线粒体 DNA 只遗传给雄性后代[31-35]。父本的线粒体基因组可以直接决定后代的性别和育性[36]。YU 等[37]分别从家系和群体水平以及基因和基因组水平上证实了海湾扇贝与紫扇贝的种间杂交后代的线粒体基因组遵循母系遗传。

在以往关于雌雄同体型植物和雌雄异体型动物的报道中，线粒体异常(尤其是线粒体基因突变、重排和失调)是导致不育的重要因素[12, 38, 39]。线粒体不仅是能量的提供者，也是自由基产生和细胞程序性死亡的诱导者，其功能障碍会导致水稻花粉过早地发生细胞程序性死亡[40, 41]。mtDNA 变异可导致氧化磷酸化系统功能丧失，造成腺嘌呤核苷三磷酸(Adenosine triphosphate, ATP)耗竭和活性氧(Reactive oxygen species, ROS)生成过多，进而诱发进一步的 mtDNA 变异[42]。mtDNA 缺陷和突变会引起小鼠睾丸的减数分裂停滞和凋亡水平升高以及卵巢中卵母细胞的损伤，最终导致小鼠雄性和雌性不育[43, 44]。一般来说，线粒体基因的功能通常需要核基因的参与，特别是那些参与线粒体呼吸链和电子传递链的基因。同样，线粒体基因也可以通过调节参与细胞死亡和凋亡等关键途径的核基因来诱导不育[45-49]。

作为半自主细胞器，线粒体可能在遗传和发育中起重要作用，并可能在种间杂交雌雄同体型动物的不育中发挥关键作用。YU 等[37]首次探索了线粒体基因突变在雌雄同体型 *Argopecten* 属海湾扇贝和紫扇贝种间杂交不育中的作用，并发现杂交一代扇贝性腺中的 ATP 含量显著低于其亲本，这表明能量匮乏可能是杂交扇贝不育的重要原因。在杂交贝的线粒体基因 *CYTB*、*ND4*、*ND2*、*ATP6*、*COX2* 和 *trnD* 中检测到 13 个 SNPs 和 5 个新 SNP 单倍型，这些 SNPs 的等位基因频率在可育亲本扇贝和不育杂交贝之间存在显著差异。与亲本相比，杂交贝中与线粒体 ATP 合成、线粒体呼吸链酶复合物合成以及线粒体凋亡有关的核基因表达水平具有显著差异[37]。表明线粒体 DNA 突变以及线粒体基因与核基因之间的异常相互作用可能通过以下途径引起杂交贝不育(图 1)：(1)*Mfn2* 高表达抑制卵母细胞的成熟；(2)*CDK2* 的表达受到抑制，使卵母细胞的细胞周期停滞在 G1 期；(3)线粒体凋亡诱导细胞凋亡；(4)线粒体能量供应不足；(5)核基因异常表达导致线粒体功能障碍。

2 其他核基因变异在 *Argopecten* 属杂交扇贝育性决定中的作用

与育性调控相关的核基因突变可导致卵母细胞成熟停滞和死亡[50]。与减数分裂相关的核基因中出现

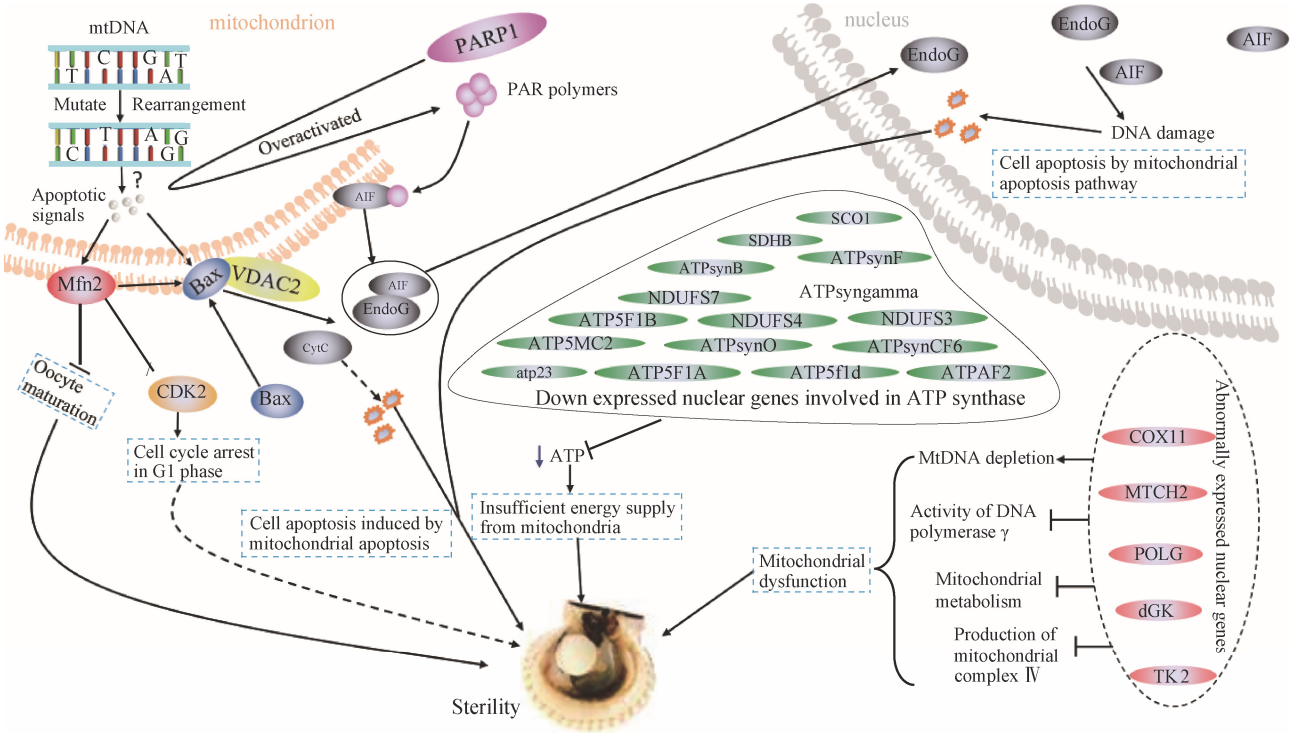

图 1　线粒体突变和异常核质相互作用在 *Argopecten* 属扇贝种间杂交不育中的潜在调控网络(引自 YU 等[37])

Fig. 1　Potential regulatory network of mitochondrial mutations and abnormal nucleocytoplasmic interactions during interspecific hybrid sterility in *Argopecten* scallops (from Yu et al.[37])

SNPs 和 indels 会导致卵母细胞中的双链断裂(DSB)修复失败、同源重组失败和卵母细胞成熟受阻，导致雌性不育[51]。在斑马鱼(Danio rerio)中，*Mlh1* 调控减数分裂，*Mlh1* 雄性突变体表现为不育，雌性后代的畸形率和死亡率高[52]。近年来，高通量测序技术的快速发展为深入探索不同物种的遗传基础提供了有力的工具[53]。全基因组重测序分析可用于全面分析个体基因组中存在的遗传变异，有利于揭示可育和不育个体的遗传差异[54]。转录组测序(RNA-seq)技术可以提供不同组织中所有基因的表达谱并鉴定出差异表达基因(DEGs)，有利于揭示育性相关基因的动态表达模式[55]。转录组测序和全基因组重测序的联合分析在一些物种的不育机制研究中发挥了重要作用，比如在四倍体水稻中鉴定到了与不育相关的基因变异和 DEGs[56]，在鲫鱼(Carassius auratus)中发现与卵细胞发生相关的 DEGs 突变可导致败育[54]。

对可育和不育杂交扇贝的全基因组重测序及转录组联合分析明确了导致雌雄同体型 *Argopecten* 属扇贝杂交不育的候选基因和通路[17]。与可育杂交贝相比，在不育杂交贝中有 24 个携带 246 个变异位点的 DEGs 与育性调控相关，这些基因主要富集在减数分裂和有丝分裂细胞周期、精子发生与发育、错配修复、卵室形成、钙调控信号通路、Wnt 信号通路、Notch 信号通路和 MAPK 信号通路中。这些基因的变异和异常表达可能会促进细胞凋亡，抑制减数分裂和有丝分裂的进程，阻碍杂交贝配子的产生和成熟(图 2)[17]。该研究首次将全基因组重测序技术和转录组测序技术联合应用于扇贝种间杂交的育性解析，为进一步鉴定调控扇贝育性的关键基因奠定了基础。

3　DNA 甲基化对 *Argopecten* 属杂交扇贝育性的调控机制分析

表观遗传修饰在育性调控中发挥着重要作用，它可以在不改变 DNA 序列的情况下引起染色质结构的变化从而改变基因的表达水平[57-59]。DNA 甲基化是最重要的表观遗传修饰之一，能够引起基因转录抑制和基因沉默[60-62]。DNA 甲基化修饰异常已经被广泛认为是导致精子和卵细胞基因表达异常的重要因素[63]。研究表明，雄性和雌性不育与 DNA 甲基化修饰密切相关[64, 65]。精子基因组中 DNA 甲基化水平的改变会严重影响精子的浓度、形态和活力[66-68]。长牡蛎(Carssostrea gigas)*Htatip2* 基因的 DNA 甲基化

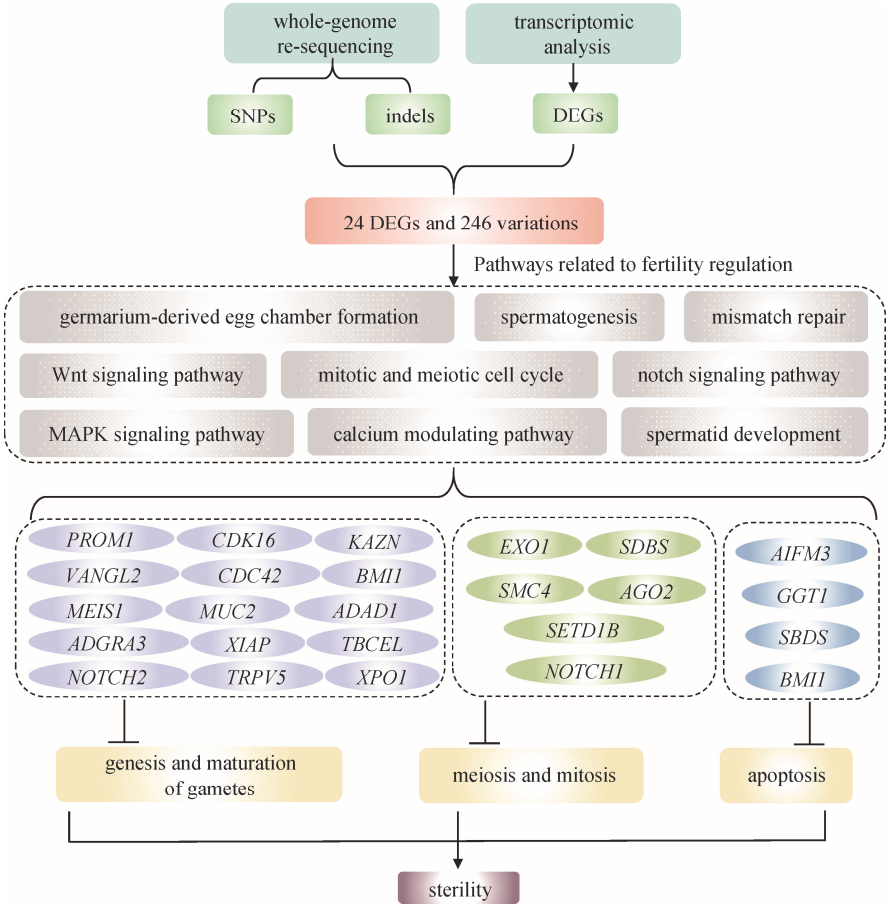

图 2　核基因突变和异常表达在 *Argopecten* 属扇贝种间杂交不育中的潜在作用机制(引自 YU 等[17])

Fig. 2　Potential functional mechanisms of nuclear gene variations and abnormal expression during interspecific hybrid sterility of *Argopecten* scallops (from Yu et al.[17])

可能通过抑制基因表达参与性腺成熟的调控[69]。患有多囊卵巢综合征的女性在基因组高甲基化区域的启动子上具有高密度的 CpG 序列[70]。与可育牦牛(Bos grunnies)相比，不育杂交犏牛 CG 序列环境的甲基化水平显著升高，与减数分裂相关基因的启动子显著高甲基化[71]。启动子上高水平的 DNA 甲基化会对 DNA 复制、转录和修复造成损伤并破坏生精基因的表达，从而导致雌性和雄性不育[72, 73]。甲基化修饰水平的变化会影响基因表达，导致细胞凋亡、ATP 供应不足和败育[74, 75]。细胞凋亡通常会伴随着大量 ROS 的产生，ROS 的积累会引起线粒体 DNA 损伤，导致 ATP 耗竭[76, 77]。此外，ROS 还能通过诱导细胞凋亡和 DNA 断裂来减少配子的数量[78, 79]。DNA 甲基化修饰在虾夷扇贝(Patinopecten yessoensis)的配子发生和长牡蛎的早期性腺发育中发挥着重要的调控作用[80, 81]。

DNA 甲基化修饰在雌雄同体型 *Argopecten* 属扇贝的种间杂交不育中也起着关键的调控作用[18]。不育杂交扇贝的平均甲基化水平高于可育杂交扇贝，特别是在 Chr11P 染色体上表现尤为明显。在不育杂交扇贝中共鉴定出 61 062 个差异甲基化区域(DMRs)，其中有 3 619 个差异甲基化基因(DMGs)和 1 165 个差异甲基化启动子位于 CG 序列环境的 DMRs 中。CG 序列环境的差异高甲基化基因主要富集在 5 个与育性调控相关的 KEGG 通路中，包括非同源末端连接、泛素介导的蛋白水解、错配修复、ECM-受体相互作用和 Notch 信号通路，以上调控通路与之前在其他生物中的研究结果相似[82-89]。共有 24 个与育性调控相关基因的启动子或外显子区域存在高甲基化，它们分别通过调控凋亡和 ROS 生成、ATP 生成以及卵细胞的发生来影响生育能力。不育杂交贝性腺 ATP 含量和 COXI 蛋白的表达水平显著低于可育杂交贝，ROS 生成速率显著高于可育杂交贝。DMGs 可能通过诱导细胞凋亡、提高 ROS 水平、减少 ATP 供应以及抑制卵细胞的发生和成熟来诱导杂交不育(图 3)。

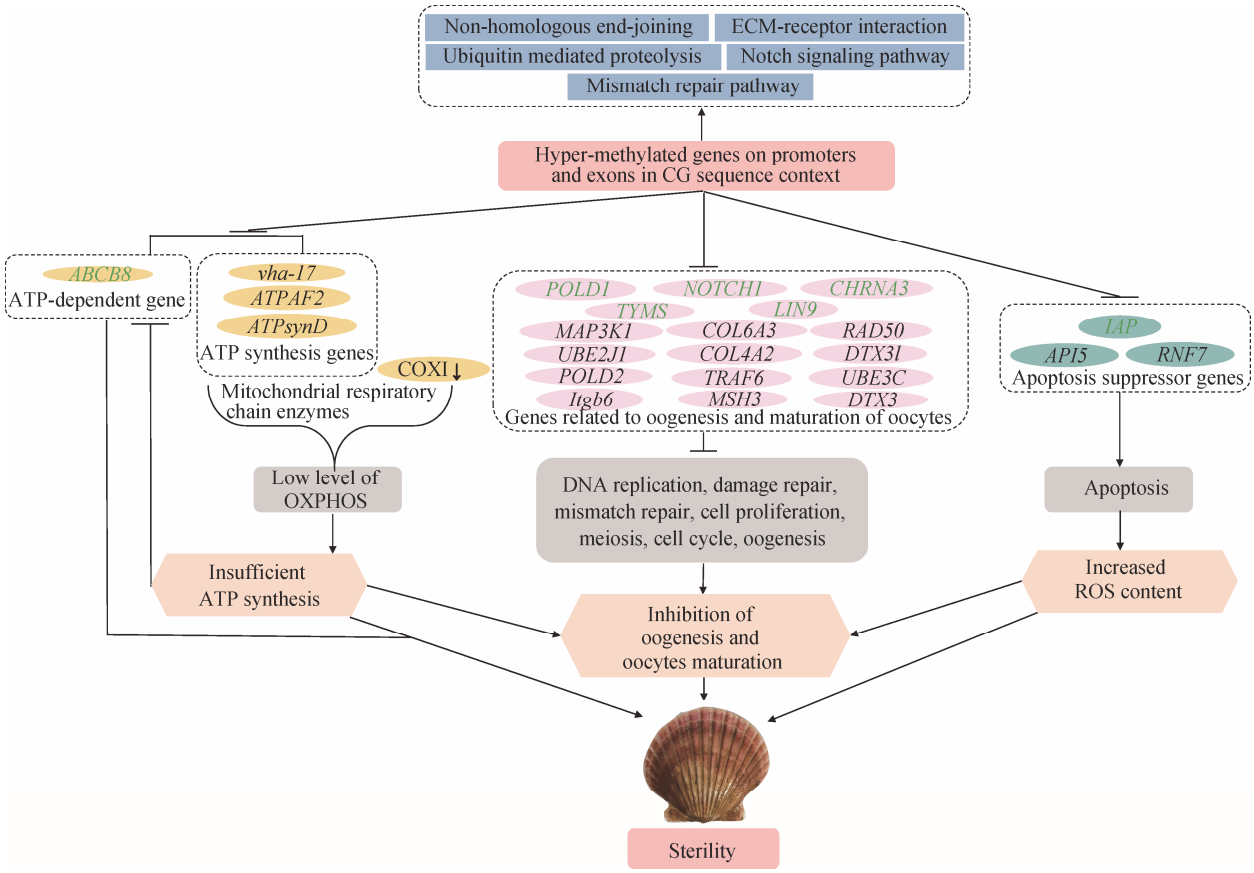

图 3　DNA 甲基化在 *Argopecten* 属扇贝种间杂交不育中的潜在作用机制(引自 YU 等[18])

Fig. 3　Potential functional mechanism of DNA methylation during interspecific hybrid sterility in *Argopecten* scallops (from Yu et al.[18])

4　温度对 *Argopecten* 属杂交扇贝育性的影响

有性生殖对温度的变化非常敏感，温度胁迫是导致不育的关键环境因素[23, 90-92]。温敏性不育是雌雄同株型植物不育症的一种，高温胁迫会破坏雌蕊的抗氧化系统，导致 ROS 过度积累和细胞膜系统受损[93-96]。环境温度升高是导致脊椎动物繁殖力低下的重要原因之一[25, 97]。温度过低或过高都会导致家禽雄性繁殖力下降，而高温则会降低雌性繁殖力[98]。无脊椎动物的繁殖力同样也受温度调节[23, 24]。高温环境会破坏果蝇(*Drosophia subobscura*)的生理代谢和配子发生过程，而在较低温度下饲养的雌性果蝇会产生更多的卵泡细胞[99]。温度升高会诱发秀丽隐杆线虫精母细胞的 DNA 损伤和基因组发生改变[24]。对于水生生物而言，温度也是调节其基因表达、发育和繁殖的重要因素[100, 101]。温度升高会影响硬骨鱼的性别比例、性腺发育和繁殖能力[102]。高温可导致雌性尼罗罗非鱼(*Oreochromis niloticus*)的生殖细胞完全丧失[25]。低温养殖的斑马鱼死亡率较低且性腺成熟延迟，而高温养殖的斑马鱼死亡率较高[103, 104]。低温会改变 ROS 水平，导致减数分裂异常，阻碍 ATP 的产生并最终导致不育[105]。毛蚶(*Scapharca subcrenata*)在经过急性热处理之后导致细胞凋亡率和死亡率增加，超氧化物歧化酶(Superoxide dismutase, SOD)和过氧化氢酶(Catalase, CAT)的活性在急剧增加后降低[106]。双壳类动物可以激活自身的凋亡途径和酶防御系统，将温度变化造成的损害降至最低[100, 107]。

YU 等[108]将 *Argopecten* 属杂交扇贝分别置于 18 ℃、20 ℃、22 ℃、24 ℃、26 ℃和 28 ℃下进行培养，探究了温度对杂交扇贝育性的生理影响。研究表明 18 ℃~22 ℃处理的杂交贝的最终死亡率显著低于 24 ℃~28 ℃处理的杂交贝。随着温度的降低，22 ℃、20 ℃和 18 ℃处理的杂交贝的大小、性腺指数、性腺中的 ATP 含量和大多数与育性调控相关基因的表达量逐渐降低，卵细胞的凋亡率逐渐增加，但性腺中 SOD 和 CAT 的活性在

20 ℃时最高。在 22 ℃和 20 ℃的处理条件下，与海湾扇贝相比，杂交贝性腺中 SOD 和 CAT 的活性显著升高。温度胁迫会产生氧化应激，为保护机体免受损伤，机体通过增加 SOD 和 CAT 等抗氧化酶的活性来清除过量的活性氧[109]。在最低温度 18 ℃时，SOD 和 CAT 的活性显著下降，体内的抗氧化系统遭到破坏，ROS 剧增破坏了生物膜系统并对细胞结构和功能造成严重损害，这与在鲍鱼中的研究结果相似[110]。随着温度的降低，在 22 ℃、20 ℃和 18 ℃下处理的杂交贝的性腺发育速度和成熟卵细胞数目递减，育性逐渐下降。根据基因表达情况，温度可能通过影响细胞凋亡、减数分裂、ATP 产生和损伤修复来抑制生殖细胞的发生和成熟，从而调控 *Argopecten* 属杂交扇贝的育性。

5 *EGFR* 基因在杂交扇贝不育中的作用

近年来单细胞转录组测序(scRNA-seq)技术在配子和性腺发育的研究中得到了广泛的应用[111-113]。与传统的转录组测序技术相比，单细胞转录组测序技术解决了细胞异质性的问题，能够从单个细胞水平分析基因的表达情况，有助于研究者更好地分析、鉴定关键调控基因以及更直观地理解细胞的发育、分化和功能[114]。通过对鲈鱼(Lates calcarifer)卵巢细胞的 scRNA-seq 分析，LIU 等[111]揭示了鲈鱼卵巢发育的分子机制和关键途径。斑马鱼卵巢细胞的 scRNA-seq 检测鉴定出不同的生殖细胞亚群并确定了与卵细胞发育和性别分化相关的基因[115]。

YU 等[116]对雌雄同体型 *Argopecten* 属杂交扇贝成熟期的性腺进行了单细胞转录组测序分析，发现 *EGFR* 基因可能是调控其杂交不育的关键因子。卵细胞在由原始卵泡生成阶段生殖细胞到卵细胞的发育过程中，*EGFR* 基因的表达量在不育杂交贝中逐渐降低，而在可育杂交贝中逐渐升高。对可育和不育杂交贝卵细胞间的 DEGs 进行 GO 和 KEGG 富集分析，其中 *EGFR* 基因主要富集在生殖、雌配子生成、卵细胞构建、ATP 结合、凋亡、钙离子信号通路和 MAPK 信号通路中。通过 RNA 干扰技术特异性降低 *EGFR* 基因的表达水平导致性腺指数降低，性腺中的 ATP 含量降低、ROS 生成速率升高，卵母细胞和性腺发育延迟。与可育杂交贝相比，不育杂交贝性腺中 *EGFR* 基因的表达量和 ATP 含量显著降低，但 ROS 生成速率显著升高，这可能引起卵母细胞发育缓慢、细胞周期停滞、能量供应不足以及细胞凋亡率升高最终导致不育(图 4)。

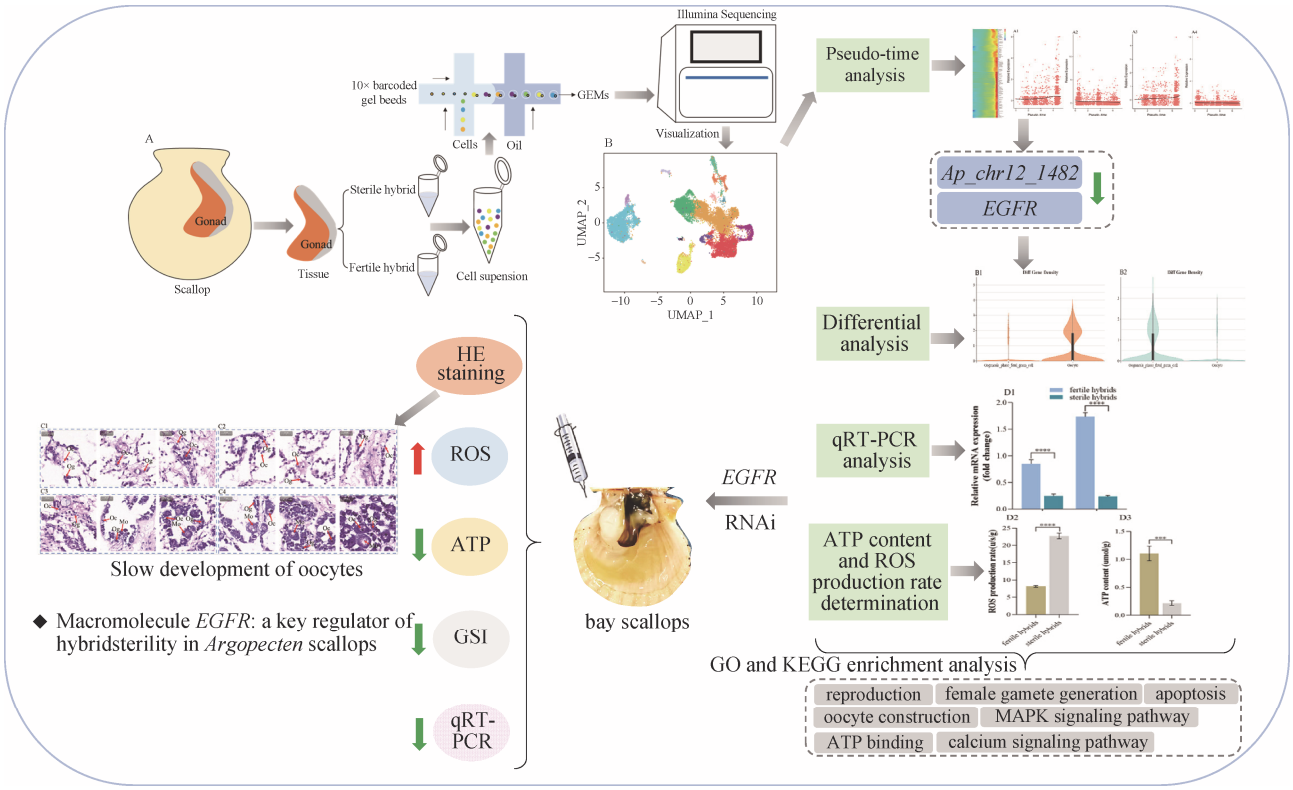

图 4　单细胞转录组测序发现的调控网络(引自 YU 等[116])

Fig. 4　Regulatory network as ascertained by single-cell ribonucleic acid sequencing (from Yu et al.[116])

EGFR 是蛋白激酶超家族中的一员，其在发育、细胞增殖和组织再生中起着多种作用[117]。*EGFR* 基因可以诱导卵细胞的减数分裂，其激活和缺失已被大量报道与一些模式生物的卵细胞成熟和低生育率密切相关[118-120]。表皮生长因子受体信号通路是多种生物过程的关键调节通路，在果蝇中控制着卵细胞发生过程中上皮卵泡细胞的命运[121]。*EGFR* 具有抗凋亡和调节代谢的功能，其可能通过增加能量来增强细胞的运动性[122]。特异性去除 *EGFR* 会引起细胞周期阻滞、去分化或细胞凋亡[123]。在小鼠(Mus musculus)中，*EGFR* 的表达缺失导致其生育能力严重低下[120]。*EGFR* 缺失会导致斑马鱼卵泡的发育完全停止和雌性不育的发生[119]。YU 等[116]的研究结果表明 *EGFR* 基因在 *Argopecten* 属扇贝的种间杂交后代的育性决定中同样起着重要作用。

除了 *EGFR* 基因，可能还存在其他基因在 *Argopecten* 属扇贝种间杂交不育中发挥作用。YU 等[116]在可育和不育杂交扇贝的单细胞转录组测序分析中也筛选到了一个可能参与育性调控的未知基因 *Ap_chr12_1482*，但其功能还需进一步研究。利用线粒体基因组重测序、核基因组重测序、转录组分析以及 DNA 甲基化分析等方法筛选到一些与 *Argopecten* 属扇贝育性调控相关的候选基因，这些基因的作用方式和调控网络还需深入探究[17, 18, 37]。

6 结语

种间杂交后代育性是生殖演化和杂种优势利用研究的前沿热点和难点，育性机制的解析有助于丰富物种演化中生殖隔离和新物种形成机制的新认识。雌雄同体型 *Argopecten* 属杂交扇贝的育性受遗传因素(DNA 甲基化修饰的表观遗传调控、线粒体基因变异、核基因变异、核基因异常表达以及核质互作)和环境因素(温度)的影响，*EGFR* 基因在杂交贝的育性调控中发挥着重要的作用(图 5)。ATP 供应不足、ROS 水平和凋亡水平过高以及减数分裂异常可能是导致 *Argopecten* 属杂交扇贝不育的关键原因。解析 *Argopecten* 属扇贝种间杂交后代育性的决定机制，有助于攻克杂交扇贝育性难题，突破扇贝规模化种间杂交制种的技术瓶颈，有力支持扇贝育种产业的可持续健康发展。

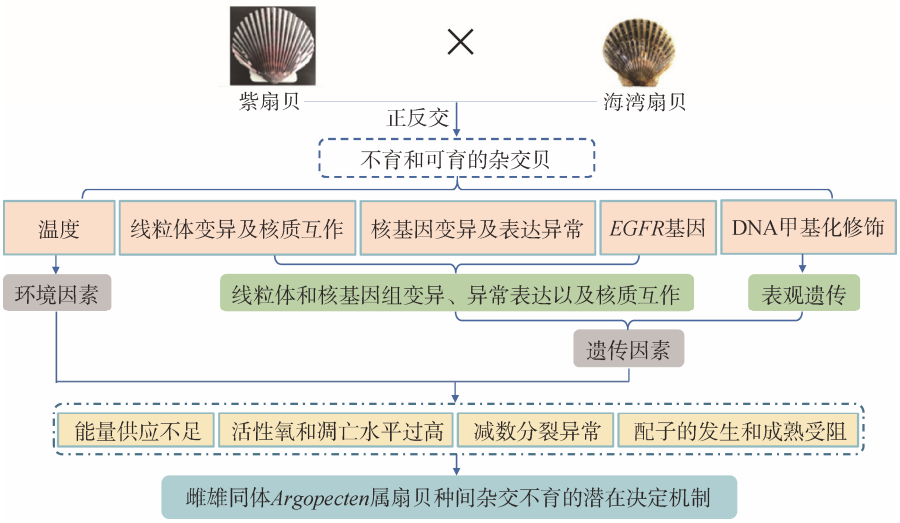

图 5　雌雄同体 *Argopecten* 属扇贝种间杂交不育的潜在决定机制

Fig. 5　Potential determination mechanisms of interspecific hybrid sterility in hermaphroditic *Argopecten* scallops

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Mechanisms determining interspecific hybrid sterility in *Argopecten* scallops

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Abstract: Molluscs are vital to the global fishery industry and livelihood, accounting for approximately 56% of the world's mariculture production. The hermaphroditic bay scallop (*Argopecten irradians irradians*) and Peruvian scallop (*Argopecten purpuratus*) are shellfish with high nutritional and economic value. The interspecific hybrids between the two exhibit remarkable advantages in growth, with *Argopecten* breeding possessing great potential. Nevertheless, most hybrids are infertile, limiting further development and the large-scale application of scallop crossbreeding technology. This review summarizes the potential mechanisms underlying such sterility from genetic and environmental perspectives. Insufficient energy supply, dysregulation of mitosis and meiosis, elevated levels of reactive oxygen species (ROS) and apoptosis, obstruction of gametogenesis and maturation due to mutated mitochondrial and nuclear genes, aberrant nucleocytoplasmic interactions, defective epigenetic modifications, and changes in the environmental temperature may be the most critical reasons. Besides, *EGFR* may also play a key role in regulating fertility in hybrid scallops. This review may provide new insights into understanding the mechanisms determining interspecific hybrid sterility in scallops and lay a theoretical foundation for the large-scale hybrid breeding of shellfish. It is expected to provide related references to promote the healthy development of the aquaculture industry.

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