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· 综述 ·

鱼类环境耐受性与抗逆性育种研究进展

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摘要：随着高密度集约化水产养殖业的发展，溶解氧、水温和氨氮等水环境因子胁迫已成为制约渔业高质量发展的限制性因素，抗逆水产新品种的培育成为重要的解决途径之一。本文综述了鱼类对温度、低氧、氨氮、亚硝态氮、盐碱胁迫的响应机制，以及环境耐受性鱼类新品种的育种现状，提出充分利用第一次全国水产养殖种质资源系统调查结果发掘优异种质资源，建立高通量表型和基因型精准鉴定技术，深入解析鱼类响应环境因子胁迫的机制，利用分子标记辅助育种、全基因组选择育种、基因编辑育种和分子设计育种等现代分子育种技术进行高效精准抗逆新品种的培育，为鱼类抗逆性新品种培育提供参考。

关键词: 水产种业；水产养殖；环境胁迫；抗逆育种

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中国水产品产量连续 33 年位居世界首位，2021 年全国水产品总产量为 6 690.29 万 t，其中鱼类养殖产量 2 824.66 万 t，为人民群众提供了大量的优质蛋白[1]。近年来，养殖模式由粗放型向集约型转变，养殖环境已经成为制约渔业发展的“瓶颈”，环境因子的胁迫严重限制鱼类生长，降低鱼类抗性，增加病害的易感性，给水产养殖业造成重大经济损失。通过挖掘环境因子和鱼类之间的互作机制，解析应答胁迫的关键基因及调控元件，进而对抗逆性状 (如耐低氧、抗寒、耐高温、耐盐碱等) 进行遗传改良，培育耐受性强的新品种是解决这一挑战的重要途径。本文通过综述环境因子和鱼类互作机制研究以及抗逆性育种现状，分析鱼类环境响应与抗逆性育种研究趋势，探讨未来抗逆育种发展方向，为鱼类种业创新提供新思路，为种业振兴提供参考。

1　鱼类环境胁迫响应机制研究

我国地理气候差异大，加之近年来全球气候

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变化多样，极端天气频现导致水环境极不稳定，鱼类需要不断增强对不同水环境的耐受性以应对生境变化。环境耐受性状一般属于数量性状，易受到外界环境的影响，筛选出鱼类环境响应的主效基因和调控元件、解析作用机制及调控网络是抗逆育种的理论基础。

1.1 鱼类对温度胁迫的响应机制

鱼类属于低等变温脊椎动物，生理活动易受外界温度影响[2]，温度胁迫下丘脑-垂体-肾间组织轴迅速合成分泌大量皮质醇 (COR)[3-7]，进而调节糖代谢及免疫反应，增强抵御环境胁迫的能力。温度胁迫导致鱼类糖代谢发生变化以应对能量需求的改变，通常热应激下机体血糖水平升高[8-10]，而冷胁迫导致下降[11-12]。温度对鱼类糖代谢的影响可能主要通过糖原磷酸化酶、己糖激酶和丙酮酸激酶等酶活性和基因表达的变化而实现[13-17]。脂质代谢也是鱼类应对低温胁迫的重要途径，低温下过氧化物酶体增殖激活受体 (PPARs)信号通路调节 β-氧化相关酶基因表达 [4,18-21]，硬脂酰辅酶1(SCD1) 提高体内脂肪酸不饱和度以增加细胞膜的流动性[8, 22]。

温度对鱼体能量代谢和生长的影响主要取决于酶活性的变化，低温抑制酶活性，温度升高则增加酶活性，但温度过高又导致酶变性失活，黄鳍鲷 (*Sparus latus*) 和条石鲷 (*Oplegnathus fasciatus*) 幼鱼肠蛋白酶、胃蛋白酶和淀粉酶活性随温度的升高而先升后降[23-24]；尼罗罗非鱼 (*Oreochromis niloticus*) 淀粉酶活性随温度 (20~32 °C) 的升高而升高[25]；黄尾鰤(*Seriola lalandi*) 18 °C 时消化胰蛋白酶、脂肪酶和 α-淀粉酶活性显著高于 22 °C 时[26]。同样地，鱼类摄食率、食物转化率和生长率在一定温度范围内随水温的升高而升高，高于或低于最适温度都会使生长受到抑制[6, 27-29]。调控鱼类生长的生长激素/胰岛素样生长因子 (GH/IGF) 轴对温度也较为敏感，相对低温环境鱼类血清 IGF-1 水平随温度上升而显著升高，如银大麻哈鱼 (*Oncorhynchus kisutch*) 和虹鳟 (*Oncorhynchus mykiss*)[30-31]。温度对 GH/IGF 轴的影响可能主要通过调节葡萄糖、氨基酸和脂肪酸等代谢产物水平直接或间接影响 GH 的分泌，最终调控鱼类生长[32]。

温度胁迫诱导鱼体表达多肽类蛋白分子家族热休克蛋白 (HSP)，保障蛋白分子的正确折叠、加工和转运，保护细胞免受温度应激引起的损伤[4, 6, 33-34]，提高机体对温度应激的耐受性，如高温环境下斑马鱼 (*Danio rerio*)*Hsp70* 基因表达上调[35]，低温胁迫下尼罗罗非鱼和吉富罗非鱼肝脏 *Hsp70* 表达量先升后降[10,36]，暗纹东方鲀(*Takifugu obscurus*) 肝脏中 HSP90 也被证实为低温诱导的关键蛋白[37]。

1.2 鱼类对低氧胁迫的响应机制

鳃作为与水体进行气体交换的主要器官，缺氧时鳃通气量和呼吸频率增加，以提高氧气的摄取[38-40]。“鳃重塑”是低氧胁迫下鱼类通过组织结构变化提高摄取氧能力以应对缺氧的重要策略，在鲫 (*Carassius auratus*)、青海湖裸鲤 (*Gymmocypris przewalskii*)、团头鲂 (*Megalobrama amblycephala*) 等鱼类中都得到证实，鳃适应性变化表现为上皮变薄、鳃小片上皮延伸及表面积扩大[41-45]。严重缺氧或窒息会导致鳃小片扭曲变形、鳃弓表面微脊数量增加、鳃细胞肿胀、细胞质收缩、线粒体扩张以及细胞凋亡增加[45-48]。鱼类还能通过增加血液中红细胞数量、血红蛋白或血铁水平提高血液转运氧能力应对低氧胁迫，如鲫、长丰鲢 (*Hypophthalmichthys molitrix*)、黑鲮脂鲤 (*Prochilodus nigricans*) 和金鱼等 [42, 49-54]。

低氧胁迫诱导高浓度氧自由基 (ROS) 和 COR 导致丙二醛 (MDA) 含量增加造成组织应激损伤[40, 44, 48, 55-58]，鱼类通过提高抗氧化酶 (过氧化氢酶 CAT、超氧化物歧化酶 SOD、谷胱甘肽过氧化物酶 GPx) 活性或抗氧化物 (还原型谷胱甘肽 GSH 等) 水平保护自身免受低氧胁迫损伤[45, 59-64]。然而，严重缺氧或长时间缺氧时抗氧化系统无法抵御胁迫，体内抗氧化酶和抗氧化物被大量消耗而显著下降[65-68]，溶解氧为 1 mg/L 和 2 mg/L 时鲫脾脏和肾脏抗氧化酶 (SOD、CAT、GPx) 活性均显著降低，而溶解氧 4 mg/L 时肾脏中 SOD 和 CAT 活性以及脾脏中 GPx 和 CAT 活性显著升高[69]；在溶解氧 (0.27±0.06) mg/L 时鲢血清和肝脏中 SOD 和 CAT 活性显著下降[62]。

低氧条件下，鱼类有氧代谢减弱，无氧代谢相关的乳酸脱氢酶活性显著增强[44, 70-73]，同时脂代谢增加导致肝脏甘油三酯消耗下降[63, 74]。Sun 等[75] 发现低氧时大口黑鲈 (*Micropterus salmoides*) 肝脏中参与脂肪酸代谢相关的溶质载体家族 (SLC27A6)、过氧化物酶体增殖物激活受体 (PPARA)、AMP 激活蛋白激酶 β 亚基 (PRKAB) 以及糖代谢上游的胰

岛素受体底物 2(IRS2)、磷酸肌苷-3 激酶、调节亚基 1(PIK3R1)、丝氨酸/苏氨酸激酶 2(MKNK2) 和 HIF1α 基因编码的蛋白在激活肝脏糖脂代谢方面发挥作用。鱼类还通过增强线粒体内腺苷三磷酸 (ATP) 酶活性直接调节能量供应满足低氧胁迫时能量需求[59, 76-79]。

HIF 调控的靶基因参与血管和红细胞的生成、糖代谢、细胞生长、血管舒张及收缩等适应低氧生理反应，低氧胁迫下鱼类可能主要通过 HIF 调控机体适应性变化[40, 46, 53, 80-81]，穴居墨西哥脂鲤 (*Astyanax mexicanus*) 过表达 *Hif-1* 及其调控通路基因来响应低氧[82-83]；敲除 *Hif-1α* 的斑马鱼低氧时死亡率显著升高[84]；持续低氧 (2.5 mg/L) 和间歇性低氧 (12 h 7.5 mg/L，12 h 2.5 mg/L) 下黄尾平口石首鱼 (*Leiostomus xanthurus*) 肌肉组织中的 HIF-1α 浓度增加，且间歇性低氧比持续低氧产生更高的 HIF-1α 蛋白浓度[85]；低氧、半窒息和窒息条件下鲢可通过 HIF-1 调节获取更多的氧气[46]。

1.3　鱼类对氨氮胁迫的响应机制

氨氮是影响水产养殖的重要环境因子，高浓度氨氮抑制鱼类的生长、危害健康，甚至导致死亡[86-87]。鳃将体内代谢产生的 90% 以上的氨排出，NH_3 主要通过自由扩散，而 NH_4^+ 主要依赖鳃上 Na^+/NH_4^+ 交换系统；海水鱼还以细胞旁路排出部分 NH_4^+[88-90]。水体氨氮也通过鳃进入体内，导致血浆氨水平升高，引起氨中毒[87, 91-93]。体内高水平氨氮引起鱼类发育迟缓及生长速度下降[94-96]，且通过 GH/IGF 轴和甲状腺轴抑制生长，其中 GH/IGF 轴在抑制鱼类生长方面发挥了更重要的作用[97-99]。高水平氨氮也引起鱼类氧化应激，导致 COR 和 ROS 水平升高，造成组织氧化损伤[100-102]，如鳃小片融合、上皮增生及出血；肝脏空泡化、肝细胞水肿 [103-105]。

鱼类通过提高抗氧酶活性 (CAT、SOD、GPx) 以及 GSH 含量以增强机体抗应激能力，维持氨氮应激下机体正常生理功能[86, 100, 106-108]。核因子 E2 相关因子 2(Nrf2)/Kelch 样环氧氯丙烷相关蛋白 1(Keap1) 信号通路在氨胁迫下参与调节抗氧化酶基因表达，氨氮胁迫下金鲳 (*Trachinotus ovatus*) 肝脏抗氧化酶基因表达水平与 *Nrf2* 和 *Keapl* 表达分别呈正相关和负相关[109]，其中 *Nrf2* 可诱导抗氧化基因表达，而 *Keapl* 阻碍 *Nrf2* 发挥调控作用。鱼类也通过降低蛋白质水解和/或氨基酸分解代谢速率减少自身氨生产、利用氨氮合成尿素、谷氨酸和谷氨酰胺等方式抵御高氨胁迫[109-114]。

1.4　鱼类对亚硝态氮胁迫的响应机制

水体中亚硝态氮主要以亚硝酸根 (NO_2^-) 和亚硝酸盐形式存在，鳃氯细胞上 NO_2^-通过与氯化物竞争吸收进入细胞导致毒性反应[115-121]。NO_2^-主要与血红蛋白反应生成高铁血红蛋白而降低红细胞的携氧能力[116, 122-127]，同时破坏鳃结构 (细胞增生、毛细血管扩张、充血) 而降低对氧气的摄取[128-131]，最终造成机体缺氧。NO_2^-也可以被血红蛋白转化为 NO_3^-排出体外，高铁血红蛋白还原系统 (高铁血红蛋白还原酶、还原型谷胱甘肽和抗坏血酸) 又将高铁血红蛋白转化为功能血红蛋白[132-135]。体外实验证实红细胞血红蛋白在有氧条件下可以与 NO_2^-反应生成高铁血红蛋白和 NO_3^-，但缺氧的红细胞难以将 NO_2^-氧化为 NO_3^-[136]。

NO_2^-引起机体内 COR 和 MDA 含量显著升高导致组织损伤，亚硝态氮胁迫后斑马鱼肝脏以及暗纹东方鲀血液内 MDA 含量均显著升高[137-141]。鳙 (*Hypophthalmythys nobilis*)、团头鲂、红鳍东方鲀(*Takifugu rubripes*)、大黄鱼 (*Larimichthys crocea*) 和大菱鲆 (*Scophthalmus maximus*) 等通过提高抗氧化酶活性应对亚硝态氮胁迫导致氧化应激损伤[127, 137-138, 142-144]。细胞水平发现亚硝态氮胁迫下草鱼 (*Ctenopharyngodon idella*) 肝细胞通过 Nrf2/Keap1 信号通路调节抗氧化酶基因的表达以增强抗氧化能力[145]。也有研究表明，亚硝态氮通过 Caspase 依赖凋亡通路、c-jun 氨基末端激酶 (JUK) 信号通路和 p53-Bax-Bcl-2 通路促进细胞凋亡[130, 137-138,144]。

1.5　鱼类对盐碱胁迫的响应机制

鱼类对盐胁迫的响应　盐度超过鱼的耐受范围会破坏体内离子平衡引起渗透胁迫，鱼类会通过改变组织结构来调节离子转运和吸收，进而维持渗透压稳定。低盐导致鳃组织中鳃丝和鳃小片宽度增加、泌氯细胞数量减少，而高盐条件下泌氯细胞数量和体积增加[146-153]；肾脏低盐环境下肾小球发达，而高盐下出现萎缩[149, 151, 154]。硬骨鱼渗透压调节主要依赖 Na^+和 Cl^-，鳃中含众多 Na^+/K^+-ATP 酶的泌氯细胞对盐度响应较为显著[155-158]，高盐下鳃、肾和肠道中 Na^+/K^+-ATP 酶活性均显著升高以调节渗透压平衡[159-162]。此外，对 Na^+/K^+-ATP

酶具有抑制作用的催乳素 (PRL) 在红鳍东方鲀低盐 (25% 海水) 胁迫下表达显著升高，而对 Na^+/K^+-ATP 酶具有促进作用的 GH 被显著抑制，盐度胁迫下 PRL 和 GH 分别参与渗透压高调节和低调节作用[163-164]。水通道蛋白 (AQP) 在鱼鳃、肾和肠组织适应不同盐度环境时通过调节水运输发挥渗透调节作用[165-166]。

盐度胁迫引起丙二醛 (MDA) 水平升高造成鱼体氧化损伤，鱼类则通过抗氧化系统抵御氧化应激损伤[149,167-168]。低盐通常激活抗氧化系统[169-173]，黄河鲤 (*Cyprinus carpio*) 鳃组织 SOD、CAT、GPx 活性在盐度 6 时显著升高，许氏平鲉(*Sebastods schlegelii*) 血液 SOD 和 CAT 活性随着盐度 (5~40) 下降而升高，点篮子鱼 (*Gold Saddle rabbitfish*) 移入淡水 3 h 后肝脏 SOD、CAT 和 GPx 活性明显升高，小黄鱼 (*Larimichthys polyactis*) 肝脏 SOD 活性在盐度 (5.0±0.3) 条件下也显著升高；而高盐则会抑制抗氧化系统，鲤鳃 SOD、CAT 和 GPx 活性在盐度 15 和 20 条件下显著下降[170]，同样盐度 9、12 和 15 条件下黄河鲤鳃组织中酶活性被抑制[167]。

鱼类对碱胁迫的响应　碱胁迫不仅具有渗透胁迫，还会引起高 pH 的应激。碱胁迫会引起鱼体内 Na^+、Ca^{2+}等浓度升高，导致体内渗透压升高以及碱中毒[174-176]。鱼类能适应一定范围的碱度胁迫，1.5 g/L 和 3.0 g/L $NaHCO_3$ 下尼罗罗非鱼血液 Ca^{2+}、K^+和 Na^+浓度随时间的延长先升高后降低[177]。鱼类通过增加鳃上氯细胞体积和数量、上调 Na^+/ K^+-ATP 酶活性，调节碱胁迫下机体离子平衡[175-176, 178-180]，且耐高盐碱水淡水鱼类鳃组织结构特化为类似于海水鱼鳃的结构，氯细胞数量多呈蜂窝状、鳃丝上分布少量微绒毛；肾脏的肾小球萎缩退化[176, 181]。鳃和肠道组织中 Na^+/Cl^-、Na^+/HCO_3^-和 $Na^+/K^+/2Cl^-$共转运体以及碳酸氢盐转运体基因 *Slc4a1*、*Slc4a2*、*Slc26a5*、*Slc26a6* 通过分泌和排泄机体内积累的碱补偿因水环境中盐碱度升高而造成的渗透及酸碱失衡，这也是耐碱鱼类的重要调节途径[176, 178]。

氨中毒是碱胁迫鱼类重要的表现形式，盐碱环境中高 pH 导致鱼体内 pH 上升，H^+大量减少使得 NH_3 与 NH_4^+平衡改变，同时 Na^+/NH_4^+转运蛋白被破坏导致体内的氨无法有效的排出，造成体内氨累积[179, 182-184]。鱼类通过提高氨排泄相关基因 (*Rhcg*) 表达、增加氨转化为尿素和谷氨酰胺，或减少体内代谢中氨的产生，应对高碱胁迫导致的氨中毒[182-183, 185-188]。

2　鱼类抗性育种现状

截止 2022 年，通过全国水产原种和良种审定委员会审定的水产新品种 266 个，鱼类新品种 134 个，其中抗逆性鱼类新品种培育也取得了重要进展。

2.1　温度耐受性鱼类新品种培育

我国南北气候差异大，东北地区冬季气候寒冷，低温冰期长 (冰下水温 0~2 °C 长达约 5 个月)，而南方广东、海南夏季炎热，水温高达 40 °C 以上，但我国主要养殖鱼类适宜生长水温 15~32 °C。抗寒和耐高温品种培育一直是鱼类遗传育种的重要方向。2011 年前，抗逆育种主要是鲤耐低温育种 (表 1)，利用德国镜鲤通过混合群体选育和家系选育培育出抗寒能力提高 33.8% 的德国镜鲤选育系，选育出的松浦镜鲤 1 龄鱼比亲本越冬率高 8.86% [189]；利用建鲤通过群体选育获得在北方地区成功越冬的津新鲤[190]。通过选择育种结合杂交育种和人工雌核发育技术培育出松荷鲤和荷包红鲤抗寒品系自然越冬存活率高达 95% 以上；培育出的松浦红镜鲤越冬成活率较荷包红鲤抗寒品系高 8% 以上[189-192]。利用杂交育种、细胞工程技术培育出在水温 10 °C 以下能够正常摄食生长的湘云鲤和湘云鲫，培育出的湘云鲫 2 号可在水温更低的春、冬季保持生长[193-195]。选择育种和杂交育种在鱼类抗性育种方面发挥了重要作用，多种育种技术相结合是抗性品种选育的有效途径。2013 至今，通过选择育种和杂交育种又相继培育出多个抗寒和耐高温新品种 (表 1)，通过群体选育获得能在 12 °C 以上正常摄食，越冬率提高 11.8% 的暗纹东方鲀 “中洋 1 号” [196]；以及 6 °C 条件下存活率比普通鱼苗高 22.5% 的大黄鱼“东海 1 号”新品种[197]。此外，通过杂交培育出的奥尼鱼的致死温度低至 5.8~8.3 °C[198]，以及杂交育种技术结合群体选育培育出能在北方地区自然越冬的乌斑杂交鳢[199-200] 和耐高温的大菱鲆“多宝 2号” [201]。目前，鱼类温度耐受性新品种的育种方式仍多为传统的选择育种和杂交育种为主。

鱼类环境耐受性状受微效多基因控制，分子标记辅助选育是高效选育的有效途径。目前，鱼类中已经筛选出一些温度耐受性相关标记，并进行了相关耐受基因在基因组中的定位 (QTL)(表 2)。

表 1　抗逆鱼类新品种

Tab. 1　New varieties of environmental tolerance fish

序号 number	品种 varieties	登记号 registration no.	第一选育单位 first breeding organization	抗逆性状 anti-abiotic stress traits
1	荷包红鲤抗寒品系	GS-01-006-1996	中国水产科学研究院黑龙江水产研究所	耐低温
2	德国镜鲤选育系	GS-01-007-1996	中国水产科学研究院黑龙江水产研究所	耐低温
3	奥尼鱼	GS-02-001-1996	广州市水产研究所	耐低温
4	湘云鲫	GS-02-002-2001	湖南师范大学	耐低温、耐低氧
5	湘云鲤	GS-02-001-2001	湖南师范大学	耐低温
6	红白长尾鲫	GS-02-001-2002	天津市换新水产良种场	耐低氧
7	蓝花长尾鲫	GS-02-002-2002	天津市换新水产良种场	耐低氧
8	松荷鲤	GS-01-002-2003	中国水产科学研究院黑龙江水产研究所	耐低温
9	津新鲤	GS-01-003-2006	天津市换新水产良种场	耐低温
10	异育银鲫“中科3号”	GS-01-002-2007	中国科学院水生生物研究所	耐盐碱
11	松浦镜鲤	GS-01-001-2008	中国水产科学研究院黑龙江水产研究所	耐低温
12	湘云鲫2号	GS-02-001-2008	湖南师范大学	耐低氧
13	“吉丽”罗非鱼	GS-02-002-2009	上海海洋大学	耐高盐
14	长丰鲢	GS-01-001-2010	中国水产科学研究院长江水产研究所	耐低氧
15	松浦红镜鲤	GS-01-001-2011	中国水产科学研究院黑龙江水产研究所	耐低温
16	芦台鲂鲌	GS-02-002-2012	天津换新水产良种场	耐低氧
17	大黄鱼“东海1号”	GS-01-001-2013	宁波大学	耐低温
18	乌斑杂交鳢	GS-02-002-2014	中国水产科学研究院珠江水产研究所	耐低温
19	莫荷罗非鱼“广福1号”	GS-02-002-2015	中国水产科学研究院珠江水产研究所	耐高盐
20	暗纹东方鲀 “中洋1号”	GS-01-003-2018	江苏中洋集团股份有限公司	耐低温
21	团头鲂“浦江2号”	GS-01-002-2020	上海海洋大学	耐低氧
22	大菱鲆“多宝 2 号”	GS-02-004-2022	中国水产科学研究院黄海水产研究所	耐高温

鲤中成功鉴定出与耐低温显著相关的 12 个随机扩增多态性 DNA(RAPD) 和 2 个微卫星标记 (SSR)，且 5N145lc 标记定位在第 5 号连锁群中。大黄鱼和红鳍东方鲀中分别筛选出 3 个和 4 个 SSR 与耐低温显著相关标记，其中 SSR 标记 KPC43 (AY957409) 可能与大黄鱼耐低温性状相关基因连锁，并通过改变核心序列的重复次数控制相关基因表达。红鳍东方鲀中确定 6 个 QTL 区间与耐低温性状相关联，分别定位在 LG7、LG10、LG15、LG16 和 LG22，其中 LG10 具有最大 LOD 值 (5.87)，同时筛选出 16 个 SNP 位点与耐低温相关；暗纹东方鲀中也筛选出尚需在耐寒极端群体中验证的 13 个 SNP 位点 (表 2)。大菱鲆中鉴定出的耐高温显著相关 SSR(Sma-USC38、3/9CA15、HLJDLP33、Saml-125INRA、Sam-USC86、L12144、Sma-USC81) 和 SNP(S22) 位点已进行了准确的 QTL 定位 (表 2)，在牙鲆、大黄鱼和白斑狗鱼耐高温分子标记鉴定方面也取得了一些进展。

随着高通量测序技术的发展，可以获得高密度的 SNP 图谱，更加准确的定位到与目的性状相关的候选基因，进而确定 SNP 位点最佳基因型，为耐受性育种应用提供理论依据 (表 3)。斑马鱼谷胱甘肽巯基转移酶 M(*Gstm*) 基因上鉴定出 1 个 SNP 位点的 DD/DE/EE 3 种基因型均与耐低温性状显著相关，DD 型在耐低温组占优势 (频率 50%)，而 DE 型在不耐低温组占比较大 (频率 51%)[221-223]。尼罗罗非鱼 *Hsp70* 和 TCP-1 的 eta 亚型基因 (*Tcp-1-eta*) 分别鉴定出 35 和 8 个 SNP 位点与耐寒性状相关，进而得到 16 个与罗非鱼抗寒性状显著相关的 SNP[224]。牙鲆中 *Hsp70*、高速迁移蛋白 1(*Hmgb1*)、Y 盒结合蛋白 1(*Yb-1*) 和冷诱导 RNA 结合蛋白 (*Cirp*) 基因中分别筛选出与耐低温相关的 SNP 分子标记，其中 *Hsp70* 中 SNP 8(location 1 797) 等位基因 G 和单倍型 TTG 以及 *Hmgb1* 中 SNP 7(location 725) 等位基因 TT 和 T 以及单倍型 ATG 与耐低温性状显著相关；同时 *Hsp70* 中还筛选出 51 个 SNP 与耐热性状相关，其中 SNP02:-587CG 和

表 2　鱼类耐温分子标记和 QTL 定位

Tab. 2　Molecular markers and QTL mapping related to temperature tolerance traits in fish

性状 trait	物种 species	标记类型 marker type	标记数 marker number	标记 marker	QTL数 QTL number	QTL所在染色体或连锁群 chromosome or linkage group
耐低温 low temperature tolerance	鲤[202-205] *Cyprinus carpio*	RAPD	12	5N1451c、RAG20、AL04$_{986}$、AR02$_{788}$		LG5
		SSR	2	HLJ578、HLJ580		LG5
	红鳍东方鲀[206-207] *Takifugu rubripes*	SNP	16		6	LG7、LG10、LG15、LG16、LG22
		SSR	4	fms45、fms82、fms100、fms182		
	暗纹东方鲀[208] *Takifugu fasciatus*	SNP	13			
	大黄鱼[209-211] *Larimichthys crocea*	SSR	1	KPC43		
		SSR	1	LYC0015		
		SSR	1	LYC0002$_{112bp}$		
耐高温 high temperature tolerance	大菱鲆[212-215] *Scophthalmus maximus*	SSR	4	Sma-USC25 478bp、Sma-USC24 106bp、Sma-USC17 286bp、Sma-USC31 135bp		
					3	LG17
		SSR/SNP			7	LG17、LG20、LG21、LG4、LG6
		SSR/SNP	7/1	**SSR：** Sma-USC38、3/9CA15、HLJDLP33、Saml-125INRA、Sam-USC86、L12144、Sma-USC81 SNP：S22	1	C9
	牙鲆[216-217] *Paralichthys olivaceus*	AFLP/SSR	5/2	AFLP：A1(AAC/CCA)、A2(AGA/CTA)、A3(AAC/CAC)、A4(ACT/CTC) SSR：S1:Po25A、S2:205TUF		
		SSR	1	Po42		
	大黄鱼[218-219] *Larimichthys crocea*	SNP	38			
		SSR	3	LYC0148、LYC0200、LYC0435		
	白斑狗鱼[220] *Esox lucius*	SNP	9	HT1、HT2、HT3、HT4、HT5、HT6、HT7、HT8、HT9		Chr3、Chr15、Chr4、Chr8、Chr24、Chr17、Chr1、Chr7、Chr4

SNP04:I2-67TA 呈显著相关性。这些 SNP 位点和单倍型可以作为潜在的分子标记辅助筛选温度耐受性品系。

2.2　鱼类耐低氧育种

我国养殖鱼类窒息含氧量一般高于 0.30 mg/L，如鲤、草鱼、鲢、鳙、团头鲂窒息点溶解氧分别为 0.30~0.34 mg/L、0.30~0.51 mg/L、0.34~0.68 mg/L、0.34~0.72 mg/L 和 0.35~0.64 mg/L，鲫窒息点溶解氧为 0.10~0.15 mg/L 具有较强的耐低氧能力[225-229]。目前，累计选育出 7 个具有耐低氧性状的新品种(表 1)，翘嘴红鲌与团头鲂杂交育成的芦台鲂鲌临界窒息点溶解氧低至 0.36~0.48 mg/L[230]；杂交育种结合细胞工程技术育成的湘云鲫窒息点溶解氧为 0.11~0.22 mg/L，育成的湘云鲫 2 号在一定范围的缺氧下通过长时间浮头用嘴呼吸而避免缺氧死亡[195, 231]；观赏鱼新品种蓝花长尾鲫和红白长尾鲫临界窒息点溶解氧分别为 0.135 mg/L 和 0.142 mg/L[232]。通过低氧胁迫技术经 4 代群体选育出的团头鲂“浦江 2 号”耐低氧能力比团头鲂“浦江 1 号”提高 27%[233]。中国水产科学研究院长江水产研究所育成的长丰鲢耐低氧能力提高了 22.2%[234]。

目前，鱼类中已筛选出一些与耐低氧性状相关 SSR 和 SNP 分子标记，并进行了准确的 QTL 定位 (表 4)。金鲳和大黄鱼中分别鉴定出 4 个 SNP 位点与耐低氧性状相关。牙鲆中筛选出 9 个 SSR 与耐低氧性状显著相关，分布在 LG4、LG7、LG10、LG17和 LG24 连锁群中[236]。瓦氏黄颡鱼、团头鲂、尼罗罗非鱼和斑点叉尾鮰中成功鉴定出

表 3　鱼类耐温性状相关基因 SNP 位点

Tab. 3　SNP markers of temperature tolerance traits in fish

性状 trait	物种 species	基因 gene	SNP位点数 SNP number	显著相关SNP位点 SNP site
耐低温 low temperature tolerance	牙鲆[221-222] *Paralichthys olivaceus*	*Hsp70*	9	SNP 2 (locus1524)、3 (locus1623)、8 (locus1797)
		Hmgb1	21	SNP 7 (locus 725)
		Yb-1	10	
		Cirp	4	274CT、275TA、277TC、294AT
		Hmgb1	2	725TC、839CT
	斑马鱼[223] *Danio rerio*	*Gstm*	1	5`UTR
	尼罗罗非鱼[224] *Oreochromis niloticus*	*Hsp70*	35	HP700108249、HP700108292、HP700408304 、HP700108306、HP700108443、HP700608460、HP700610225、HP700610273、HP700610306、HP700612464、HP700614224、HP700614272、HP700614462
		Tcp-1-eta	8	TCP11314313、TCP11314319、TCP11314421
耐高温 high temperature tolerance	牙鲆[217] *Paralichthys olivaceus*	*Hsp70*	51	SNP02:-587CG、SNP04:I2-67TA

多个耐低氧 QTL 位点 (表 4)，其中团头鲂 *Egln2*、*Hif-3α*、*Hif-1* 和 *Plin2* 基因中具有耐低氧性状显著相关的 SNP 位点，且亲本中鉴定出 Plin2-A1157G 和 Hif-3α-A2917G的 SNPs 位点与耐低氧性状显著相关，但在子代群体中没有发现同样结果，分子标记仍需验证和开发[226]。Li 等[243] 鉴定了 4 个尼罗罗非鱼耐低氧的 QTLs，QTL 区间的 G 蛋白偶联受体 b2(*Gprb2*) 和 ATP 结合盒亚家族 G 成员 4 (*Abcg4*) 基因外显子的 SNPs 与耐低氧性状显著相关。

2.3　鱼类耐盐碱育种

罗非鱼是我国淡水养殖的重要对象，在盐度 22.5 的环境中仍有良好的生长性能[247]。目前，培育出的吉丽罗非鱼新品种可在 15~25 盐度池塘养殖，致死盐度为 57.9[248]；莫荷罗非鱼“广福 1 号”可在盐度 30 的水域正常生长[249]。异育银鲫“中科三号”幼鱼碱度的半致死浓度 (LC 96 h) 为 46.26 mmol/L，碳酸盐碱度的安全浓度高达 13.20 mmol/L[250]。

尼罗罗非鱼 chrLG4 和 chrLG18 上鉴定出两个耐盐性状的显著 QTL 区间，其中一个 QTL 区域位于 chrLG18 的 23.0 Mb 解释了 79% 的表型变异，进而鉴定出 chrLG18 位点上耐盐性相关的 QTL 包含的烟酰胺核苷激酶 (*Nmrk22*)、F 型蛋白酪氨酸磷酸酶受体 (*Ptprf*) 和鸟嘌呤核苷酸交换因子 18 (*Arhgef18a*)3 个主要耐盐相关基因，且 *Ptprf* 基因中的 3 个 SNP 与耐盐显著相关[251-254] (表 5)。刘峰等[255] 获得 15 个尼罗罗非鱼耐盐 QTL，认为钠钾氯协同转运蛋白 2(*Nkcc2*) 基因可作为耐盐育种候选基因，且雄性在耐盐能力上高于雌性，单性育种也可能是提高鱼类环境耐受性有效途径。瓦氏雅罗鱼中鉴定出 325 个与盐碱适应相关的 InDels 位点，关联到 176 个候选基因，并在达里湖 (碱水) 和松花江 (淡水) 的瓦氏雅罗鱼杂交 F2 中筛选出 2 个 EST-SSR 标记与耐碱性状显著相关[256]。

2.4　鱼类耐氨氮和亚硝态氮育种

随着高密度集约化养殖发展，氨氮和亚硝态氮已成为限制渔业发展重要因素，国内尚无针对氨氮和亚硝态氮耐受培育出的鱼类新品种，但在分子标记开发方面取得了一些进展，石斑鱼中筛选得到 25 个 SNP 与耐氨性相关，大部分定位在 9 号和 16 号染色体上，进而获得与耐氨性状显著相关的候选基因 7 个，其中血清/糖皮质激素调节激酶家族成员 3(*Sgk3*) 发挥着关键的作用[258]；尼罗罗非鱼中也成功获得与氨氮耐受性相关的 chrLG1 QTL，这都为氨氮耐受性育种提供了借鉴[259]。

3　鱼类环境胁迫研究和抗性育种未来发展方向

利用现代分子生物学技术研究鱼类对养殖环境因子的响应机制，培育优质、高效、多抗的鱼类新品种，将是支撑水产种业振兴，实现水产养殖业高质量发展的重要研究方向[260-261]。

表 4　鱼类耐低氧分子标记和 QTL 定位

Tab. 4　Molecular markers and QTL mapping related to hypoxia-tolerance traits in fish

物种 species	标记类型 marker type	标记数 marker number	标记/基因 marker/gene	QTL数 QTL number	QTL所在染色体或连锁群 chromosome or linkage group	显著SNP位点 SNP site
瓦氏黄颡鱼[235] *Pelteobagrus vachelli*				11	LG4、LG5、LG10、LG12、LG19、LG21、LG23	
牙鲆[236] *Paralichthys olivaceus*	SSR	14			LG4、LG7、LG10、LG17、LG10、LG34	
团头鲂[237−240] *Megalobrama amblycephala*	SNP	47		1	Chr17	
	SNP	2	*Egln2*			397TC、715TG
	SNP	1	*Hif-3α*			Hif-3α-A2917G
	SNP	1	*Plin2*			Plin2-A1157G
	SNP	3	*Hif-1*			−402T/A、 −106G/T、 +1557C/T
尼罗罗非鱼[241−243] *Oreochromis niloticus*				2	LG3、LG14	
				3	LG3、LG14、LG23	
	SNP	5	*Gprb2*			LG3_3701444、 LG3_3701533、 LG3_3701699、 LG3_3701708
	SNP	3	*Abcg4*			LG14_594184、 LG14_594237、 LG14_594483
斑点叉尾鮰[68, 244] *Ictalurus punctatus*				4	LG5、LG6、LG10、LG12	
	SNP	40		4	LG2、LG4、LG23、LG29	
金鲳[245] *Trachinotus ovatus*	SNP	4	SNP24101852、 SNP9934726、 SNP28384758、 SNP24194184			
大黄鱼[246] *Larimichthys crocea*	SNP	4	chr13:2535902、 chr15:11774198、 chr18:20360178、 chr24:9514192			

表 5　鱼类耐盐碱分子标记和相关 QTL 定位

Tab. 5　Molecular markers and QTL mapping related to saline-alkali tolerance traits in fish

性状 trait	物种 species	标记类型 marker type	标记数 marker number	标记/基因 marker/gene	QTL数 QTL number	QTL所在染色体或连锁群 chromosome or linkage group	显著SNP位点 SNP site
耐盐 saline tolerance	尼罗罗非鱼[251-255] *Oreochromis niloticus*				2	chrLG4、chrLG18	
		SNP	10		3	chrLG3、chrLG5、chrLG18	
		SSR	190		15		
		SNP	3	*Ptprf*			chrLG18_23 422 794(T>C)、 chrLG18_23 422 749(T>C)、 chrLG18_23 422 735(A>G)
		SNP	5	*Epc1*			chrLG18_23 095 656(C>G)、 chrLG18_23 095 729(A>C)、 chrLG18_23 095 745(C>T)、 chrLG18_23 095 746(G>A)、 chrLG18_23 095 751(C>T)
		SNP	34	*Transferrin*			
耐碱 alkali tolerance	瓦氏雅罗鱼[256-257] *Leuciscus waleckii*	SSR	2	HLJYLe289、 HLJYL100			
		inDels	325				

3.1　环境胁迫研究

厘清不同养殖水体水质变化规律　虽然我国水资源总拥有量位居世界前列，但人均拥有量严重不足，提高水产养殖效率，发展绿色健康养殖，充分利用现有养殖水体资源至关重要。持续对池塘养殖、循环水养殖、稻田综合种养、盐碱水养殖、高原地区养殖以及深远海养殖等不同养殖模式下的养殖水体进行监测，摸清不同养殖模式下水体的温度、pH、盐度、碱度、氨氮等水环境因子的变化规律，探明不同因子之间的相关性，为环境因子养殖风险评估以及培育专门化水产新品种提供依据。

评价多环境因子之间的交互特性　养殖水体环境因子相互制约、相互依存，目前对鱼类响应环境胁迫的研究主要集中在单一环境因子的影响，不能准确反映实际养殖环境下鱼类对多因子胁迫的综合响应。双因素交互作用研究日益受到重视，但三因素乃至多因素相互作用研究还很匮乏。今后需开展不同养殖模式下多种水质因子对鱼类影响交互作用研究，解析不同因子间的作用机理，精准评估不同养殖环境下限制鱼类健康养殖的环境因子，为鱼类耐受性育种提供支撑。

解析鱼类环境胁迫应答分子机制　鱼类对环境的耐受性由环境和基因共同决定，且耐受性状往往是由多基因共同决定，目前对于耐受基因的挖掘还十分有限。今后可建立基于不同水体及养殖对象的鱼类高通量表型和基因型精准鉴定评价技术和分析平台，通过多组学贯穿分析深入挖掘鱼类环境响应的主效基因、调控元件和分子标记，构建鱼类耐受性基因分子模块，系统挖掘分子模块在鱼类抗逆性状调控潜力，阐明鱼类对环境胁迫应答的分子基础。

3.2　耐受性鱼类育种

开展精准鉴定，发掘育种潜力　我国鱼类种质资源丰富，养殖环境多样，不乏环境耐受性的优异种质资源。对第一次全国水产养殖种质资源系统调查数据进行充分挖掘，探明我国鱼类种质资源本底，深入解析遗传本底与地理环境的相关性，挖掘适应特殊生境的优异种质。建立水产种质资源高通量表型和基因型精准鉴定技术，解析环境抗性关键基因和功能元件，充分发掘种质资源的育种潜力。

提升育种技术水平，实现精准育种　鱼类抗逆性状是受微效多基因控制的数量性状，传统的育种技术效率较低，选育进展缓慢。随着育种技术的不断发展和完善，分子标记辅助育种、全基因组选择育种、基因编辑育种和分子设计育种等育种技术为鱼类耐受性精准育种提供了重要途径，未来应突破传统育种技术，综合利用现代分子育种技术，研发抗逆品种选育共性技术，实现耐受性新品种的精准育种。

构建育种平台，提升育种效率　鱼类耐受性状通常由基因型和环境共同决定，随着生物大数据的发展和应用，未来可结合组学技术与数据超算分析技术，加快建设“耐受性状-基因型-环境型”的“DT+BT”鉴定与育种技术平台，大幅提升育种的精度和深度，培育出适合不同养殖模式、不同养殖水体的专门化鱼类新品种。

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Advances in environmental tolerance and resistance breeding in fish

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Abstract: With the development of high-density and intensive aquaculture, the water environmental factors stress such as dissolved oxygen, water temperature and ammonia nitrogen has become the restricting factor. The harmful environmental conditions severely decrease the fish growth rate, reduce fish resistance and increase the susceptibility to diseases, which ultimately causes significant economic losses in aquaculture industry. The cultivation of new resistance fish varieties is one of the important solutions and attracting more attention which is becoming the research hot. In this review, we summarize the response mechanisms to environment stress including the temperature, hypoxia, ammonia nitrogen, nitrous nitrogen and saline-alkali stress from the physiology to molecules. Furthermore, the breeding progress of new fish varieties with environmental tolerance and the molecular markers (gene, SNP, SSR and so on) related to environmental tolerance traits are presented. Finally, we point out that the first national aquaculture germplasm resources investigation should be applied to explore excellent germplasm resources. The research on the integrated response mechanism of fish under multiple environmental factors stress should be strengthened. Meanwhile, the efficient and precise breeding technology of the new varieties of environment-tolerance fish should be established based on the modern molecular breeding technologies such as molecular marker-assisted breeding, genome selection breeding, gene editing breeding, molecular module design breeding and so on. This review will provide the reference for the new fish varieties breeding with resistance.

Key words: aquaculture; environmental stress; resistance breeding; aquaculture seed industry

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