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·综述·

环境丰容技术在鱼类增养殖中的应用研究进展

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摘要：近年来，在野生渔业资源持续衰退、水产养殖规模不断扩大、人们对鱼类福利关注度不断提升等的背景下，环境丰容作为一种全新的技术手段在水产领域受到广泛关注，被认为在野化放流鱼类行为、增加养殖鱼类产量、提升圈养鱼类福利等诸多方面均具有较大的应用潜力。环境丰容是指在增养殖生产中，采用适当方式向圈养或自然水体引入新的环境刺激，提高其异质性和复杂性，从而实现提升鱼类产量、提高鱼类福利、控制鱼类行为、改善鱼类生理目标的环境优化方式。总体来看，国际上围绕环境丰容技术的相关研究结果层出不穷，理论体系不断完善，但国内水产领域的相关研究尚处于起步阶段。本文在简要介绍环境丰容概念和分类基础上，聚焦目前最受关注的物理丰容方式，评述了物理丰容对鱼类打斗行为、生理应激、代谢生长等重要性状和放流后的适应性行为、个体适合度等增殖性状的影响，重点分析了引发研究结果差异的可能原因及其潜在神经可塑性机理，最后探讨了该领域以往研究的不足及今后的研究方向，旨在为我国开展该方面研究提供借鉴，为增养殖苗种高效健康培育与放流鱼类野化训练提供参考。

关键词: 鱼类；增养殖；物理丰容；鱼类行为；鱼类福利；神经可塑性

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近年来，由于过度捕捞、环境污染、生态破坏等原因，海洋渔业资源急剧衰退，面临枯竭的危险[1]。与此相对，世界水产品需求量呈现逐年上升趋势，水产养殖规模不断扩大[2]。同时，随着社会、经济、文化的发展，人们对圈养环境中鱼类福利问题的关注度逐步增加，相关国家和国际组织相继出台一系列政策规定用于保障鱼类福利[3]。出于以上渔业资源增殖放流、水产动物健康养殖和提升圈养鱼类福利等多方面的考虑，需要不断创新水产增养殖模式，优化增养殖技术，提出增养殖新方法，完善增养殖理论。以此为导向，近年来国内外学者围绕如何提高鱼类养殖产量、提升鱼类福利、提高增殖放流鱼类生态适应性等开展了大量理论研究，提出了许多新方法[1, 4-8]。其中，环境丰容 (environmental enrichment) 技术以其操作简易、效果显著、价格低廉等优势，一经引入便受到学术界广泛关注，迅速成为鱼类增养殖领域的研究热点，围绕环境丰容的新理论、新技术、新结果层出不穷[2, 4, 9-14]。而国内该领域研究仅在达氏鲟 (*Acipenser dabryanus*)[15]、许氏平鲉 (*Sebastes schlegelii*)[16-19]、克氏原螯虾 (*Procambarus clarkii*)[20]、大泷六线鱼 (*Hexagrammos otakii*)[21]、稀有鮈鲫 (*Gobiocypris rarus*)[22] 等少数几个物种中做过尝试，秦传新等[23] 对其概念和应用做过介绍。

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因此，亟需对环境丰容的基本理论和研究进展开展系统评述，以为国内水产领域相关研究提供参考和借鉴。

1 环境丰容的概念与分类

1.1 概念

目前，学术界对于环境丰容尚无统一的定义，学者们常根据自己的研究目的、方法和结果给出不同的定义。但总体来看，近年来提出的两种定义为多数学者所采纳。第一种定义在 1995 年提出，认为环境丰容是一种通过优化圈养动物所处环境，以实现改善其生物学功能目标的方法[24]。显然，此定义是“结果导向型”定义，强调环境丰容的结果，只有能改善动物生物学功能的方法才可被认为是环境丰容。第二种环境丰容的定义：对于在感官刺激因子被剥夺的环境中圈养的鱼类，通过刻意提高环境复杂程度，以实现减少鱼类不适应和异常特征的方法[13]。此定义强调进行环境丰容的方式是提高水体环境的复杂程度，但未对环境丰容的结果进行限制，即“即使实验处理未改善(甚至抑制) 动物的生物学功能，只要提高了环境的复杂程度，亦可被认为是环境丰容”，因此，此定义可认为是“过程导向型”定义。值得注意的是，最近有学者将环境丰容定义为通过为圈养鱼类提供新的环境刺激从而满足其生理、行为和心理需要的方法[9]。此定义兼顾了行为、生理与心理状态，强调环境丰容的本质是引入新的刺激因子，尤其是野外生境中存在的诸环境因子。本文综合上述研究观点，重新定义环境丰容：在增养殖生产中，采用适当方式向圈养或自然水体引入新的环境刺激，提高其异质性和复杂性，从而实现提升鱼类产量、提高鱼类福利、控制鱼类行为、改善鱼类生理目标的环境优化方式。

1.2 分类

环境丰容的核心在于向圈养环境引入环境刺激，提高异质性和复杂性，显然，此异质性和复杂性可包括物理、化学、社群等组分水平的差异。在动物园、保护生物学和水产增养殖领域中，常根据环境丰容的方式和目标将其划分为 5 种类型[2, 9, 13-14, 25-27]：①物理丰容 (physical enrichment)，是指提高水体环境的物理复杂度，通常通过向圈养环境引入物理构件、底质等物体来实现；又常常进一步分为结构丰容 (structural enrichment) 和底质丰容 (substrate enrichment) 两种方法。②社群丰容 (social enrichment)，是指提高目标鱼种的种内或种间社群交互行为；比如降低单鱼种驯养密度，多鱼种混养等。③感觉丰容 (sensory enrichment)，是指通过环境丰容达到刺激感觉器官发育的目标；根据所刺激器官的差异，可分为视觉刺激、听觉刺激、化学感觉刺激、肢体感觉刺激等。④训练丰容 (occupational enrichment)，是指通过环境丰容达到降低肢体或精神单调性的目标，此丰容方式常通过运动训练实现，对于水族馆中水生哺乳动物，也常通过引入玩具达到此目标。⑤食物丰容 (dietary enrichment)，是指改变食饵类型或投喂方法。要注意的是，有学者也将营养丰容 (nutrient enrichment) 划为环境丰容的一类，但营养丰容主要通过向食饵中添加营养素来实现，与水产领域中营养与饲料这一方向的研究完全相同，本质上属于营养学的范畴，因此多数学者将营养丰容相关研究排除在环境丰容之外。显然，以上分类并非独立、互斥的，而是在某些情况下交叉、互补的，如向水体引入构造物作为环境丰容措施，直观上应将其划为物理丰容类型，但构造物可能会影响鱼群间的社群交互作用和特定生理过程，进而刺激特定脑区发育，在这种意义上此丰容类型又可归为社群丰容或感觉丰容。在这种情况下，学者常将其认定为最为直观的丰容类型，即物理丰容。就目前来看，物理丰容和基于物理丰容的混合丰容是研究最为广泛的环境丰容类型，因此在相关文献中，广义的环境丰容概念是指上述所有环境丰容，而最为狭义的环境丰容概念则是指物理丰容。本文将主要围绕物理丰容进行综述。

2 增养殖鱼类的界定

总体来看，目前环境丰容技术在水产领域主要有两大应用方向。一是用于提高鱼类生长率和产量，抑制打斗行为和应激反应，这是鱼类育苗和养成阶段最为关注的问题，其中陆基工厂化养殖模式 (包括流水式和循环水式) 是目前最常见的应用场景。其二是用于提高增殖放流苗种在野外各类水体 (包括海洋、湖泊、水库等) 的存活率，即环境丰容是否可以作为一种有效的野化训练方法，用于增强放流苗种的生态适应性，从而促进自然种群的恢复、补充和渔业利用。显然，前者主要针对工厂化养殖鱼类，重点关注生长、代谢、打斗等特征；后者主要针对放流鱼类，重点关注其在野外的生存状态，以自然种群恢复为目标的

保护型增殖放流和以资源量补充为目标的渔业利用型增殖放流均属于环境丰容技术的应用范畴。本文将分别阐述物理丰容对鱼类打斗行为、生理应激、代谢生长等养殖鱼类重点关注的特征的影响及其作用机理，在此基础上，评述物理丰容对增殖鱼类放流后生态适应性的影响，随后从多个角度剖析其可塑性机制，以系统综述环境丰容技术在鱼类增养殖中的研究进展 (图 1)。

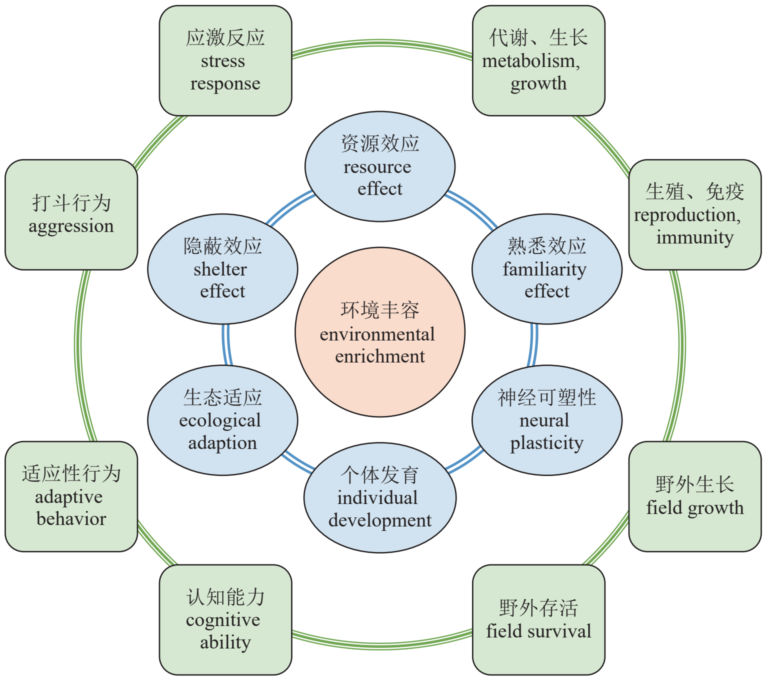

图 1　环境丰容对鱼类的影响及其作用机理

Fig. 1　Effects of environmental enrichment on fish and its mechanism

3　物理丰容对养殖鱼类的影响及其作用机理

3.1　打斗行为

向水体引入构造物，最直接的效应是为鱼体提供隐蔽场所，进而减少打斗行为和肢体损伤[13, 28]。过去通常采用鱼体损伤、鱼鳍损伤、鱼鳍指数等易于观察和统计的指标对此效应加以评估，目前许多研究显示，环境丰容可显著降低鱼类的鱼鳍损伤[29-36]，但也有研究观察到环境丰容的轻微或负面影响[37-38]。有学者指出肢体损伤除了来源于鱼群打斗外，还可能由于鱼体与养殖池壁或其他物理构造物摩擦所致[11, 13]，因此学者们对鱼类的打斗行为进行了直接的观察统计。同样，研究表明环境丰容能够显著减少特定鱼种的打斗频率[39-46]，但同时也在其他为数不少的鱼种中观测到轻微甚至负面结果[47-54]。上述研究显示，适宜的环境丰容在减少鱼类肢体损伤和打斗行为中的潜力，同时表明存在其他因子影响环境丰容对鱼类打斗行为的作用效果。

若想厘清造成研究之间鱼类打斗行为差异的原因，需要先明确环境丰容对鱼类打斗行为的作用机理。综合文献分析，可能存在以下三种机制 (图 1)[55-56]。第一，引入构造物可以为鱼类提供隐蔽场所，同时构造物本身可能阻碍鱼体间的视觉接触[44]，限制领域范围[41]，增加领域数量，减少自发活动[51, 57]，降低鱼体间的相遇频率[58-59]，最终降低打斗频率；这一效应可被称为“隐蔽效应”。第二，既然构造物可作为隐蔽物为鱼类提供保护，那么构造物本身即是一种资源，鱼体间可能为了这一资源发生竞争性打斗[47]，从而提高打斗频率；这一效应可被称为“资源效应”。第三，引入构造物可能重塑鱼群分布格局和社群结构[48, 60]，最直接的结果是鱼群中的优势鱼会占据隐蔽物，而其他鱼则被迫栖息于无构造物的空白区，这一过程可能导致空白区群体密度降低，鱼体间更加熟悉；行为学研究表明，群体密度越小，个体间越熟悉，鱼体间打斗行为越少[61-62]；这一基于社群结构重塑的假说可称为“熟悉效应”。基于以上三种假说，可以合理推测丰容水平是环境丰容影响鱼类

打斗行为的重要调节因子。在引入构造物比较少时，资源效应占主导地位，可能激发鱼群的打斗行为；随着丰容水平逐渐升高，隐蔽效应和熟悉效应逐渐明显，导致打斗行为减少。这一作用过程最近在许氏平鲉和大泷六线鱼中被证实[56, 63]。同时，亦可推测丰容类型、丰容时长、群体密度以及以上各因子间的交互作用均可能影响环境丰容对打斗行为的作用效果[12-13]。例如，丰容类型会影响鱼体隐蔽效果，进而影响鱼体对构造物本身作为资源的价值评估，在影响其隐蔽效应的同时，影响资源效应；丰容时长可能影响熟悉效应；群体密度可能影响竞争效应和熟悉效应等[28, 63]。此外，丰容颜色已被证实会对鱼类打斗行为和生长产生显著影响，特定颜色的底质能够显著降低金头鲷 (*Sparus aurata*) 的打斗频率，促进生长[64-65]；这可能和鱼体生理压力水平与代谢有关，但相关作用机理仍不甚清楚，丰容颜色对行为和生长的影响在其他鱼种中也未被验证。

3.2 应激反应

鱼类应激反应可被分解为行为反应和生理反应两个层次[66-67]。行为反应步骤：当鱼体发现刺激因子后，保存在脑中的记忆被提取，同时本次经历被记录；交感系统被迅速打开，副交感系统被关闭；鱼体立即停止正在进行的其他活动 (如摄食)，将注意力集中于刺激因子；经评估后，决定采取何种行为策略[68]。生理反应较为复杂，通常被划分为三个步骤：首先，下丘脑-垂体-肾上腺肾间组织轴 (hypothalamic-pituitary-interrenal tissue axis, HPI axis) 和下丘脑-交感神经-嗜铬细胞轴 (hypothalamic-sympathetic-chromaffin cell axis, HSC axis) 被激活，分泌皮质类固醇 (在鱼类中主要是皮质醇) 和儿茶酚胺 (主要是肾上腺素和去甲肾上腺素)；第二步是皮质醇和儿茶酚胺引发一系列生理生化反应，如心跳、呼吸率、生理代谢、免疫功能、渗透调节的变化等；最后由此引发整个机体水平的变化，如抗病力和生长等[69-71]。基于以上对应激反应的认识，在研究中常采用一些行为生理指标来评价鱼类的应激反应，如皮质醇、神经递质、血液指标、鳃盖开合频率等。

激烈的社群交互行为被认为与鱼体基础压力水平密切相关，作为对打斗行为的延伸，许多学者探究了环境丰容对鱼体基础生理压力的影响。多数研究表明，环境丰容能够显著降低多种鱼类的基础压力水平 (通常以皮质醇浓度来衡量)[72-74]，但也有部分研究未得到显著结果或具有负面影响[36, 38, 57, 75-76]，这可能与环境丰容对鱼类打斗行为的影响有关，即不同研究中鱼类基础生理压力的差异性反映了打斗行为的差异性。在水产增养殖中充斥着各种人为的或自然的刺激因子，因此更为重要的是鱼体对于急性或慢性刺激的行为和生理恢复能力，即抗逆性。自 Barcellos 等[77] 首次报道环境丰容能够显著降低克林雷氏鲇 (*Rhamdia quelen*) 的应激反应后，其他学者在许多鱼种中也相继证实了这一点[36, 73, 78-81]；但也有学者得到相反的结果[72, 76, 82]。这些差异可能与鱼种、生长阶段、刺激类型、取样时间点、应激指标以及环境丰容模式 (如类型、水平、时长、颜色等) 有关。在生理调控水平，有学者提出鱼类应激反应可能与其基础压力水平有关。Barton 等[83] 通过控制养殖密度探究了长期压力因子 (高密度) 对金头鲷急性应激反应的影响，结果显示，高密度会使鱼体长期处于高压状态 (基础生理压力升高)，最终导致其应激反应能力受损，即空气暴露 30 s 急性刺激 1 h 和 2 h 后，高密度组幼鱼皮质醇水平显著低于低密度组幼鱼。最近的一项研究通过设置不同物理丰容类型和水平，发现实验组间的基础皮质醇浓度和急性应激恢复能力均存在显著差异，且二者存在极显著的相关关系[84]。上述结果表明，环境丰容可能通过调控鱼体基础压力水平，钝化或敏感化与应激反应相关的神经内分泌系统，最终对其应激反应峰值和应激恢复时长产生相应的影响。

3.3 代谢与抗病力

多项研究表明，环境丰容能够显著降低鱼类的标准代谢率和耗氧率[85-89]。从生态和进化的视角来看，在自然条件下栖息于复杂生境中的鱼类具有喜爱复杂和异质环境的天性，因此在圈养水体中引入构造物可满足鱼类的天性，使其感觉被保护、处于安全的水域，进而降低其生理压力和代谢水平[88]。其次，构造物可作为抵抗水流的隐蔽场所，减少鱼类用于游泳、自发活动和保持身体平衡的能量[11]。最后，单一均质的环境常诱发激烈的社群交互作用，可能导致肢体损伤、细菌感染，轻则也会使生理压力上升，在这种情况下代谢升高几乎是必然的[90]。

抗病力是鱼类养殖中极为重要的观测指标，尤其是在集约化养殖条件下，一旦疾病暴发，将

严重影响鱼类成活率、鱼肉品质和养殖效益[91]。目前在实际生产中多采用化学药物防治鱼病，但过多的药物使用量容易引起公众对于鱼肉品质和鱼类福利问题的担忧，因此开发非侵入型的鱼病防控方法具有极为重要的实际意义。如上所述，适宜的环境丰容能够有效抑制鱼体间激烈的社群交互行为、减少自发活动、减少肢体损伤、降低长期生理压力水平，推测能够提高鱼体免疫力、降低疾病暴发和传播几率。但学术界对此问题的关注度极低，仅在少数几个鱼种中进行过尝试[90-93]，且均停留在表型观察层面，深入机理水平的研究尚未见到。值得注意的是，在这几项研究中，环境丰容均能在一定程度上提高鱼体抗病力，取得了较好的效果。鉴于此，未来可在其他鱼种中开展类似的验证性研究，同时在生理和分子水平解析环境丰容对鱼类抗病力的调控机理。

3.4　生长与生殖

生长率在一定程度上直接决定了养殖效益，可能是鱼类养殖中最受关注的性状之一。在环境丰容概念引入水产养殖领域以来的过去 30 年里，学者针对环境丰容对鱼类生长的影响开展了大量相关研究，研究对象覆盖了具有重要经济价值的且对栖息环境复杂度有先天性要求的大多数鱼种[2, 9, 13, 28]。总体来看，多数研究结果显示适宜的环境丰容能够显著促进鱼类生长，但无显著影响或负面影响的结果也较常见，这可能与鱼种、鱼类生长阶段、环境丰容类型、水平、颜色、其他实验设置 (如养殖密度) 以及各因子间交互作用有关，但迄今很少见到验证多因子交互作用的相关研究[9, 13]。综合文献来看，可能有多种途径独立或交互介导了环境丰容对鱼类生长的调控作用。首先，引入构造物会降低鱼类的视力范围，减少自发活动，从而降低摄食成功率和摄食量，对生长产生一定的负面影响[94-95]。另一方面，环境丰容能够减少肢体损伤，削弱社群等级，降低生理压力，这些行为生理过程能够提高鱼类食欲，增加摄食活动[70]；同时较低的行为生理压力可能提高饲料转换效率 (即消化吸收能力)，从而促进鱼体生长[28]；有研究显示环境丰容能够提高血浆生长激素和类胰岛素生长因子含量[76]，这可能也和饲料转换效率提高有关。另外，环境丰容使鱼体代谢消耗降低，也可能节约能量用于生长。显然，上述分析显示出环境丰容对鱼类生长调控过程的复杂性，其中涉及许多行为-生理过程的权衡，这也增加了环境丰容对鱼类生长影响结果的不确定性，因此在开展环境丰容项目 (尤其是以生产为导向的项目) 时，要充分考虑项目的实际情况 (鱼种、密度等)，不宜简单地由某项研究、某个鱼种的结果外推至其他情况。

环境丰容对鱼类生殖成功影响的相关研究极少，目前仅有的几项研究结果各异[59, 96-99]，在这种情况下，很难对环境丰容是否有利于鱼类生殖做出准确的判断。基于环境丰容引发的行为生理效应，推测可能存在以下机制参与调控了鱼类的生殖活动。首先，环境丰容能够降低鱼体自发活动，这意味着雄鱼的生殖搜寻 (mate searching) 和生殖遭遇 (mate encounter) 会相应降低，从而减少了交配几率[58-59]。另一方面，环境丰容会增加领域数量，将水体适当隔离，因此为个体交配提供更为隐秘的空间，降低交配过程中被其他个体打断的几率，有利于交配成功[59]。在生理水平，有研究证实压力激素皮质醇对鱼类生殖轴 (hypothalamic-pituitary-gonadal axis, HPG axis) 具有调控作用[100]，环境丰容能够降低鱼体生理压力，其可能通过进一步调控 HPG 轴对生殖成功产生影响。

4　物理丰容对增殖鱼类的影响

4.1　行为适应性

由于室内行为学实验具有时间和经济成本低廉、鱼类行为表型明显、操作简便可控性强等优点，近年来被广泛用于评估鱼类的放流表现。大量研究表明，环境丰容能够显著提高幼鱼的一种或多种行为适应能力，包括游泳能力[101-103]、探索行为[104-109]、竞争能力[98, 107, 110-113]、伪装行为[114]、隐蔽行为[72, 108, 115]、栖息地忠诚度[115]、捕食能力[104-105, 109]、反捕食能力[102, 109, 116] 以及行为灵活性[104, 117]，但也有少数研究未检测到上述积极影响[118-119]。除上述基础行为适应能力以外，近几年尤其受到关注的是鱼类的高级认知能力 (如学习和记忆能力)。鱼类的学习能力使得鱼类可以从同伴或自身经历中持续不断地吸取教训、积累经验，调整自身行为以更好地适应环境，从而提高个体适合度[120-121]。因此，可以认为学习能力是其他行为能力的基础，是评估鱼类行为适应性强弱更为可靠的指标。自 Strand 等[122] 首次发现环境丰容能够提高大西洋鳕 (*Gadus morhua*) 的社群学习能力以来，研究人员在

多种鱼类中也相继证实环境丰容在提升空间[123-127]、社群[122] 和关联性[128] 学习记忆能力中的作用，同时无明显影响或一定程度的负面影响也在一些研究中被观测到[129-131]。

4.2　个体适合度

行为学研究结果在一定程度上证明了环境丰容提升鱼类生态适应性的潜力，但考虑到野外物理、化学和生物环境的时空复杂性，改善某些特定的行为能力能否显著提升鱼类的个体适合度，即二者作用效果的一致性 (生态效度)，引起了一些学者的担忧，基于此，开展增殖放流实验或半自然的中宇宙实验似乎是必要的[132]。综合利用半自然行为实验、胃含物分析、无线电遥测等方法，Rodewald 等[133]、Hyvärinen 等[134]、Härkönen 等[106] 开展了一系列实验，探究混合环境丰容对大西洋鲑 (*Salmo salar*) 和褐鳟 (*S. trutta*)生态适应性的影响，结果显示，与普通育苗环境中培育的幼鱼相比，丰容幼鱼的不适应性探索行为较少、对自然饵料的摄食率较高、肥满度较高、起始洄游速度较快、放流存活率较高。结合室内行为实验和野外实验，D'Anna 等[116] 也发现物理丰容或反捕食训练能够显著增加沙重牙鲷 (*Diplodus sargus*) 的起始逃逸距离、减少到达隐蔽物的时间，丰容和训练同时处理，可显著增大幼鱼放流存活率、减小扩散距离[116]。类似结果已在大西洋鲑[135-136]、虹鳟 (*Oncorhynchus mykiss*)[110]、褐鳟[137] 中被多次证实，但仍有几项研究显示环境丰容对多种鱼类的放流存活率无显著影响[111, 118, 138-139]，甚至观测到负面影响[140]。以上针对鱼类行为适应性和放流存活率的研究结果说明，环境丰容在鱼类增殖放流中确实具有一定的潜力，但其效果受到多种因素的影响，如环境丰容模式、鱼种和行为指标选择等。目前相关研究多以鲑科 (Salmonidae) 鱼类为对象[2, 28]，针对其他对环境复杂度有先天性要求的领域性海洋鱼类的研究相对较少，未来需要针对这一点开展相关实验，以比较分析鱼类生态习性对于丰容效果的影响。

5　物理丰容对增殖鱼类的作用机理

5.1　生态与进化视角

总体来看，虽然会受到多种因素影响，适宜的环境丰容措施能够提高鱼类的行为适应性和放流存活率[28]。从生态和进化角度来看，可能有多种机制参与调控了环境丰容对鱼类生态适应性的影响过程。首先，物理构件将水体分隔为多个相对独立的空间，加之构件本身的资源效应，使得鱼类有机会表达其天性 (领域性)，维持一定的打斗行为，这种长期的领域性的表达可能提高其竞争能力[11]。第二，这种物理空间的分隔意味着一定程度上的社群交流的分隔，这可能影响个体利用群体或个体信息做决定的能力，据此可以推测，环境丰容个体更倾向于综合利用个体和群体信息做出决策，而未丰容个体更加依赖于群体信息，长此以往可能损害其个体独立生存能力[118]。考虑到增殖放流常在较大范围内开展，个体 (尤其是领域性鱼类) 独自生存的可能性较大，因此环境丰容提升鱼类存活率是可以预期的。第三，环境丰容会提高水体环境的异质性和复杂性，这意味着构造物本身即包含着丰富的视觉空间信息，可能有助于鱼体探索行为、感觉器官和脑组织的发育[141]。

5.2　个体发育视角

从个体发育的角度来看，可以粗略分为形态、生理、行为三个层次的调控过程。在形态水平，环境丰容被多次证实能够减少鱼体损伤、增大鱼鳍长度，这可能有助于提高鱼体游泳能力和敏捷性[102]。另外，环境丰容能够促进褐鳟皮肤斑点的发育[99]，可以作为一种有效的反捕食策略提高放流存活率[142]。最后，环境丰容能够提高放流群体的形态多样性，考虑到自然环境在时间和空间上的异质性和多变性，这种群体形态多样性的提升可能使得整个群体更加适应复杂多变的野外环境[143-144]。在生理水平，最重要的机制可能是环境丰容提高鱼类的抗逆性，即脑组织抗氧化能力、急性应激后的恢复能力等，考虑到野外环境与驯养环境的巨大差异以及放流过程本身充斥着各种刺激因子，较强的抗逆性使得鱼类能够更快地从应激状态恢复至正常生理状态，降低饥饿和被捕食的风险[4]。另外，环境丰容可以降低鱼类基础代谢和呼吸代谢，这意味着鱼体能够分配更多的能量用于神经发育，从而提高其行为可塑性[11]。在行为水平，鱼类行为适应性的优势有助于其野外存活和生长，目前学术界对此已形成共识。

5.3　神经可塑性视角

通常认为，神经可塑性与行为可塑性密切相关[121]。神经可塑性是指由于环境 (或行为) 影响，神经系统在发育过程中所发生的结构和功能上的

修饰，其伴随着鱼类的认知过程而发生，为鱼类调整自身行为、生理，适应复杂环境提供了可能[145-146]。自 Kihslinger 等[147] 首次发现环境丰容能够显著增大虹鳟小脑体积以来，多项研究也证实了这一趋势[124, 148-149]。伴随着啮齿类模式动物环境丰容研究取得突破[150-151]，鱼类该领域研究的重点逐渐转向环境丰容对鱼类神经发生的影响方面。神经发生是指由神经干细胞产生功能性神经元的整个过程，可以划分为脑细胞增殖、神经元分化和迁移、神经元存活等步骤[152-153]。啮齿类的研究已经证实神经发生可能是控制和影响动物行为最重要的基础之一[154-155]。就神经发生而言，哺乳类和鱼类最大的区别在于哺乳类持续整个生命过程的神经发生仅存在于两个脑区，即海马体齿状回颗粒下层和侧脑室下区[152-153]；而鱼类的增殖区在其主要脑区均被发现，相较于哺乳类，具有明显更高的神经发生速率[156-157]。这一区别意味着鱼脑可能更易受到环境的影响，具有更强的神经可塑性。啮齿类的研究发现环境丰容提升动物认知能力的重要机制之一是促进特定的神经发生过程[158]。因此，在近十多年来，多数研究显示，环境丰容能够促进多种鱼类特定脑区的特定神经发生过程和脑细胞数量[57, 123, 126, 159-163]，虽然还没有利用药物活体注射或基因编辑等技术开展进一步功能验证，这些研究结果强烈暗示环境丰容对鱼类生态 (行为) 适应性的提升作用可能是通过神经发生介导的。在这种意义上，评估神经发生的某些分子标志物亦可以作为鱼类生态适应性的良好候选标志分子，当然，这种推测需要后续在多种鱼类中开展大样本量的验证研究。应当注意，有针对斑马鱼 (*Danio rerio*) 和银鲑 (*O. kisutch*) 的研究检验到了负面影响，即环境丰容抑制了神经发生[164-165]；分析认为这可能是该两项研究实验设计不当、样本量过少以及环境丰容设置不当所致，不影响环境丰容促进鱼类神经发生的总体性结论。尽管如此，在其他鱼种中采用不同的分子标志物、构建不同的环境丰容模式继续开展类似的验证性研究仍是必要的，这有助于进一步厘清环境丰容对鱼类神经发生的作用模式及其影响因素。

目前学术界对环境丰容促进鱼类神经发生的机制知之甚少，但通过啮齿类模式动物的研究结果推测，很可能与神经营养因子和生理压力介导的上下游生理过程有关。研究显示，环境丰容能够通过提高啮齿类海马体神经营养因子水平从而促进神经发生，最终改善认知能力[153-154]，但在几种鱼类中均没有检测到类似的趋势[60, 123, 135, 165]。有趣的是，虽然物理丰容未对鱼类神经营养因子产生明显影响，但感觉丰容和训练丰容均能显著提高斑马鱼和大西洋鲑的脑源性神经营养因子 (brain-derived neurotrophic factor, BDNF) 基因表达量[166-167]。这暗示不同环境丰容模式 (类型、水平、时长、颜色等) 可能会对神经营养因子产生明显影响，未来应对此开展深入研究。此外，考虑到环境丰容常显著减少鱼体肢体损伤和打斗行为，生理压力也可能参与介导了环境丰容对神经发生和行为适应性的影响。啮齿类的研究显示，糖皮质激素对神经发生具有极为关键的调控作用[168-169]。有学者认为此作用呈倒 U 形，即适中的压力水平促进神经发生，而压力过大或过小均会产生一定的抑制作用[170-171]；而另一些学者认为糖皮质激素对神经发生的作用主要是抑制性的[172-173]。目前两种观点均有许多证据支持，双方存在一些争论，但是有一点是确定无疑的，即糖皮质激素能够调控啮齿类特定脑区的特定神经发生过程。针对鱼类，已在虹鳟等少数鱼种中证实了皮质醇对神经发生的抑制作用[174]，但是否仅存在抑制作用亦或是倒 U 形作用仍需要进一步研究。

6 总结与展望

近年来随着动物福利观念不断深入人心，环境丰容对增养殖鱼类福利的影响及其作用机理已成为水产领域的研究热点。虽然目前环境丰容可能存在着诸如不便于收集残饵粪便，养殖成本提高，构造物材料、形状、数量、颜色需要分鱼种确定等实际应用中的问题，但该领域研究尚处于蓬勃发展阶段，在促进养殖鱼类生长、提升放流鱼类生态适应性、提高圈养鱼类福利中具有极大的潜在应用价值。应当指出，环境丰容并非适用于所有鱼类，由于环境丰容构造物和底质多布设于水体中下层，其对中上层鱼类的影响较小，因此应充分考虑鱼类种间差异，对于中下层、营底栖生活、具有趋礁性及在整个生活史或某一生长发育阶段具有领域性的鱼类，特别是在自然环境中使用隐蔽物作为必要生存条件的鱼类，在养殖时适当进行环境丰容，可能产生更积极的影响。

以往的研究虽已取得诸多突破性成果，但在环境丰容的概念、模式、效应、机理等方面仍留有许多空白与不足：

①环境丰容的概念。不难发现目前环境丰容主要针对圈养环境而言，向自然水体引入刺激因子是否应视作环境丰容？尤其是在我国大力推进海洋牧场建设的背景下，这一问题更显关键，但截至目前仍没有相关讨论。

②环境丰容模式。在已有的研究中，环境丰容时长从几天到数月、甚至持续数年，开展环境丰容时鱼类的发育时期跨越了卵、仔、稚、幼、成鱼，但专门针对同种鱼类同一环境丰容方式，探究环境丰容时长对不同生长发育时期鱼类影响的研究很少，这对于能否找到“环境丰容敏感期”具有重要意义，值得深入探究。

③环境丰容效应。构造物多作为隐蔽物为鱼类提供避敌场所，但其会否改变养殖环境中的流态效应，进而作用于不与构造物有直接接触的中上层鱼类，至今鲜有类似的报道。环境丰容对放流鱼类适合度影响的现场监测报道相对较少，且野外放流实验结果有时与室内行为学实验结果不一致，那么环境丰容所引发的“行为优势”是否能够转化为“适合度优势”？亟需对此开展深入研究。

④环境丰容作用机理。针对环境丰容对鱼类神经可塑性影响的研究，多集中在脑组织形态、神经发生标志物等方面，深入神经核团、细胞、亚细胞、分子水平的研究仍较少。随着鱼类行为学和神经生物学方法的结合，辅以近年来发展起来的分子生物学方法和高通量测序技术，探究环境丰容对鱼类福利与神经可塑性的影响，定能将本领域研究提升到一个新高度。

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Research progress on application of environmental enrichment techniques in fish aquaculture and stock enhancement

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Abstract: In recent years, the wild fisheries resources have been decreasing, the aquaculture production has been flourishing, and meanwhile the fish welfare has gained increasing attention from the public and scientists. Under these backgrounds, environmental enrichment, as a new technology in the fields of aquaculture and fisheries, has gained wide attention and is considered to have great potential in improving life skills of released fish, increasing the production output of farmed fish, and improving the welfare of captive fish. Environmental enrichment refers to the methods of environmental optimization aimed at increasing production yield, improving fish welfare, controlling fish behaviors and improving physiological status by a deliberate increase in environmental heterogeneity and complexity of water environment. In general, the international studies on environmental enrichment technology has been flourishing, and the theoretical system is constantly improved. However, relevant research in China is still in the initial stage. This paper first briefly introduces the concept and classification of environmental enrichment, and then reviews the effects of physical enrichment (which has received the most attention at present) on fish aquaculture-related traits (such as aggressive behavior, stress response, metabolism, and growth) and adaptive behaviors and individual fitness after release. This review focuses on the possible causes and the potential neuroplasticity mechanism of the differences in results between studies and discusses the shortcomings of the previous studies and future directions of the field. This review aims to provide reference for research in this field and provide valuable information for sustainable aquaculture and stock enhancement programs.

Key words: fish; aquaculture and stock enhancement; physical enrichment; fish behavior; fish welfare; neural plasticity

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