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海水养殖鱼类仔、稚鱼骨骼发育与畸形发生

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摘要: 骨骼畸形可导致鱼类运动困难、摄食能力降低、生长缓慢、成活率低, 因此, 畸形鱼苗的出现将增加生产成本、影响养殖的经济效益。在海水鱼类人工育苗阶段, 骨骼畸形现象普遍存在, 严重制约了海水鱼类养殖产业的可持续发展。本文首先系统总结了卵形鲳鲹、黄尾鲷、尖吻鲈等经济海水鱼类颌骨、脊柱、尾骨的早期发育时序及特点, 比较了仔、稚鱼骨骼畸形发生的部位、时间及发生规律。之后针对仔、稚鱼阶段影响骨骼发育的主要因素, 从遗传、环境、营养等方面进行了剖析, 以期寻找降低人工养殖条件下海水鱼类仔、稚鱼的骨骼畸形提供启示。

关键词: 海水仔、稚鱼; 骨骼发育; 骨骼畸形

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大多数海水鱼类的初孵仔鱼都处于发育不完善阶段, 会经历众多重要的功能和形态上的发育变化, 外界环境因子可能影响其正常发育而出现骨骼畸形。仔、稚鱼骨骼畸形往往表现为脊柱畸形、颌骨畸形等, 可导致摄食能力低, 运动能力弱, 生长缓慢, 成活率低等问题^[1], 即使畸形鱼长成商品规格, 但由于外观不佳, 市场价值很低, 甚至无法销售。仅 2007 年, 鱼苗畸形给澳大利亚黄尾鲷(*Seriola lalandi*)繁育、养殖生产造成直接经济损失达 100 万澳元^[2]; 据 Hough^[3]统计, 养殖鱼的畸形每年给整个欧洲水产养殖业带来的经济损失超过 5000 万欧元。笔者近年来对海南、广东等南方地区主要养殖海水鱼类的调研发现, 其畸形率在 17.5%~25.9%, 骨骼畸形问题已经成为困扰这些地区海水鱼类养殖的主要问题之一。

由此可见, 仔、稚鱼骨骼发育畸形在世界范围内已经成为制约海水鱼类养殖业发展的主要瓶颈之一。本文结合近年来笔者对卵形鲳鲹(*Trachinotus ovatus*)*骨骼发育及骨骼畸形发生的研究成果, 系统总结了海水养殖鱼类骨骼早期发育的特点, 仔、稚鱼畸形发生的部位及发生规律, 并针对仔、稚鱼阶段影响骨骼发育的主要因素进行了剖析, 以期寻找降低人工养殖条件下海水鱼类仔、稚鱼骨骼畸形提供启示。

1 仔、稚鱼骨骼发育

在发育初期, 大多数海水鱼仔鱼具有相似的颌骨结构, 由米克尔氏软骨、下舌软骨、基鳃软骨等构成(图 1)。海水鱼类颌骨的早期发育时序在种属之间差异很大。例如, 卵形鲳鲹的颌部骨骼

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*国内所指卵形鲳鲹(*Trachinotus ovatus*)实际为狮鼻鲳鲹(*Trachinotus blochii*)的误鉴.

骨化开始于孵化后第 7 天(体长为 3.50 mm), 而在孵化后第 11 天, 体长达到 4.33 mm 时即骨化完成^[5]。黄尾鲷(*Seriola lalandi*)颌骨骨骼(前颌骨、上颌骨等)在体长为 6.6 mm 时开始骨化, 当体长达 16.1 mm 时矿化完成^[7]。尖吻鲈(*Lates calcarifer*)在开口后 58 h 齿骨、前颌骨和下颌骨便开始骨化, 在开口后 158 h, 颌部骨骼骨化基本完成^[6]。

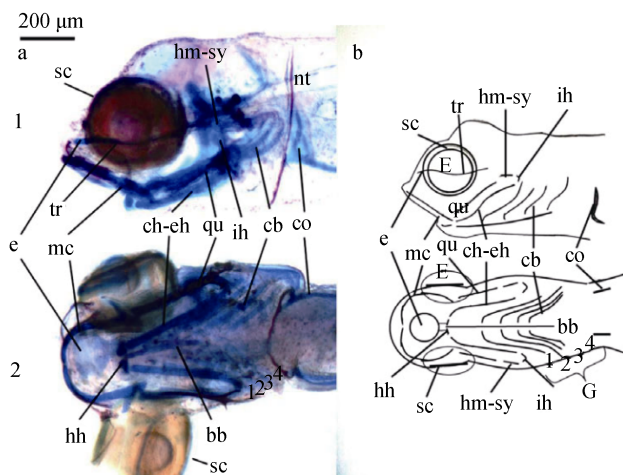


图 1 孵化后第 5 天卵形鲳鲹头部骨骼结构

a. 双染色结构图; b. 手绘结构图^[5]。bb: 基鳃软骨, cb: 角鳃软骨, ch-eh: 上舌舌骨角软骨, co: 喙状肩胛骨软骨, e: 筛骨板, E: 眼, G: 鳃弓, hh: 下舌软骨; hm-sy: 舌颌软骨对, ih: 茎舌骨软骨, mc: 美氏软骨, nt: 脊索, qu: 小翼软骨, sc: 巩膜软骨, tr: 小梁软骨。

Fig.1 Skeletal structure of normal larvae at 5 days post hatching
a. Double-staining to reflect the structure; b. Diagrammatic of the cephalic cartilages^[5]. bb: basibranchial cartilage, cb: ceratobranchial cartilage, ch-eh: ceratohyal-epihyal cartilage, co: coracoid-scapula cartilage, e: ethmoid plate, E: eye, G: gill arch, hh: hypohyal cartilage, hm-sy: hyomandibular-symplectic cartilage, ih: interhyal cartilage, mc: Meckel's cartilage, nt: notochord, qu: quadrate cartilage, sc: sclerotic cartilage, tr: trabecula cartilage.

与颌骨骨骼的发育类似, 仔、稚鱼脊柱骨骼发育时间在不同种属之间存在显著差异。例如, 对高体鲷(*Seriola dumerili*)脊柱骨骼发育的研究表明, 其体长为 4.6 mm 时脊柱开始发育, 而其脊柱的矿化开始于体长为 4.8 mm 时, 体长为 9.1 mm 时脊柱矿化完成^[7]。当黄尾鲷体长为 4.78 mm 时, 鱼体开始出现软骨组织, 而当体长达到 10.10 mm 时, 鱼体骨骼矿化基本完成^[8]。卵形鲳鲹体长为 3.49~4.00 mm 即孵化后 7~9 d 时, 尾部骨骼和脊柱开始

发育, 表现为脉棘和髓棘的矿化以及尾部构件的分化; 而在孵化后第 18 天, 即体长达到 9.12 mm 时矿化完成^[9]。

相关研究表明, 不同鱼类尾部骨骼构成存在异同, 大部分海水鱼类尾部包含有 5 片大小不一的尾下骨(Hy), 但尾上骨等存在差异^[10-13]。卵形鲳鲹尾部骨骼由 5 片尾下骨、3 片尾上骨(Ep)、1 片尾神经骨构成(图 2)。半滑舌鲷(*Cynoglossus semilaevis*)、金头鲷(*Sparus aurata*)、重牙鲷(*Diplodus sargus*)以及遮目鱼(*Chanos chanos*)尾部骨骼也同样存在 5 片尾下骨, 这与卵形鲳鲹相同, 但半滑舌鲷尾部缺少尾神经骨而与卵形鲳鲹相异^[11]。大部分的鱼类含有 2 片或 2 片以上尾上骨, 如金头鲷、重牙鲷均有 3 片尾上骨, 而半滑舌鲷仅有 1 片尾上骨。研究发现, 卵形鲳鲹尾上骨为 3 片。卵形鲳鲹仔、稚鱼尾部在构造上与其他海水鱼类存在一定差异, 但尾下骨发育顺序与其他鱼类保持一致, 均是按照从 Hy1 至 Hy5 的发育顺序依次出现在尾部。然而各片尾下骨的形成时间又存在一定差异。半滑舌鲷尾部 Hy1 和 Hy2 出现在孵化后第 13 天(体长 4.4 mm), 而 Hy5 的出现时间不早于孵化后第 18 天(体长 5.6 mm)^[10]; 重牙鲷长度为 5.2 mm 时, Hy1 和 Hy2 即已经开始分化出来, 并在体长为 7.8 mm 时 Hy5 出现^[14]。

鱼类早期骨骼发育时序的不同与仔、稚鱼的胚后发育和对环境的适应性密切相关^[12]。例如, 塞内加尔鲷(*Solea senegalensis*)在孵化后第 12~13 天脊柱和尾骨开始发育, 此时底栖生活习性形成^[10]。类似的观点亦在对牙鲆(*Paralichthys olivaceus*)的研究中得到证明^[15]。相关研究表明, 刀鲚(*Coilia nasus*)的胸鳍早在卵黄囊阶段便开始发育, 这是为了其能够在油球完全消耗完之前具备自主摄食功能^[16]。而青鳉(*Oryzias latipes*)的骨骼发育早在孵化之前就开始, 这保证了其在仔鱼阶段能够自主游泳和摄食^[17]。在鲷科鱼类中脊柱和尾部骨骼发育较早, 这表明鲷科鱼类具有发育速度快、适应能力强的特点^[5, 7, 8, 18]。例如, 卵形鲳鲹在孵化后第 7~9 天时, 颌部骨骼矿化已经开始, 脊柱和尾部骨骼开始矿化^[19], 此时卵形鲳

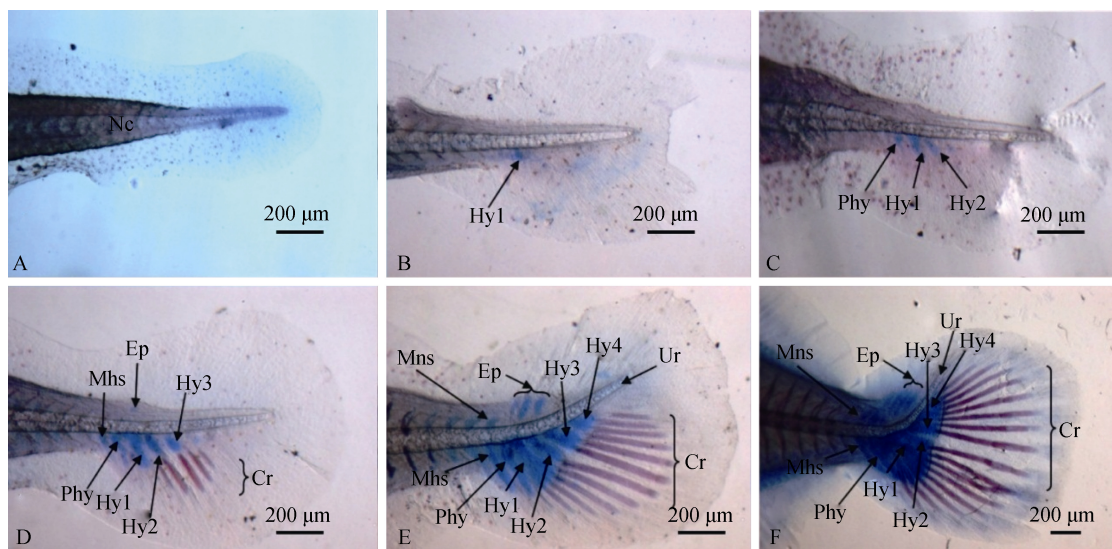


图 2 孵化后 1~15 d 卵形鲳尾部骨骼特征^[4]

A. 孵化后第 5 天, 标准体长(SL)=3.38 mm; B. 孵化后第 7 天(SL=3.8 mm), Hy1 出现; C. 孵化后第 9 天, Hy1 和 Hy2 及 Phy 均出现; D. 孵化后第 11 天, Ep、Mhs 和 Hy3 出现, Cr 已分化出现, Ur 轻微上翘; E. 孵化后第 13 天(SL=5.14 mm), Hy4 和 Mns 出现, Ur 进一步上翘, Ep 增至 3 片, 并出现在 Ur 上翘内侧, Cr 增至 12 条; F. 孵化后第 15 天(SL=6.1 mm), Ur 上翘程度增加, Ep 轮廓变清晰, Cr 数目增至 17 条。Cr: 尾鳍鳍条; Ep: 尾上骨; Hy: 尾下骨; Mhs: 脉棘; Mns: 髓棘; Nc: 脊索; Phy: 尾下骨旁骨; Ur: 尾杆骨。

Fig.2 Characteristics of caudal skeletons in golden pompano larvae of 1–15 day post hatching (dph)^[4]

A. 5 dph [standard length (SL) = 3.38 mm]; B. 7 dph (SL = 3.8 mm), Hy1 appeared; C. 9 dph, Hy1, Hy2 and Phy all appeared; D. 11 dph, Eps, Mhs and Hy3 appeared, with Cr coming out; E. 13 dph (SL = 5.14 mm), Hy4 and Mns appeared, with Ur upward bending, three Eps appeared beside the corner; F. 15 dph (SL = 6.1 mm), Ur bent upward further, Eps became more distinct, 17 Crs appeared. Cr: Caudal fin rays; Ep: Epural; Hy: Hypural; Mhs: Modified haemal spine; Mns: Modified neural spine; Nc: Notochord; Phy: Parhypural; Ur: Urostyle.

鲳在处于由生物饵料的过渡期(由摄食轮虫转向摄食卤虫无节幼体)^[20]。骨骼的迅速发育使卵形鲳鲳仔、稚鱼能够具有较强的游泳与摄食能力, 这也表明了鱼类骨骼发育是对环境和生理功能适应的产物。

2 仔、稚鱼骨骼畸形

颌骨畸形是一种常见的鱼类骨骼畸形, 在人工养殖条件下和野生条件下均可被发现且出现频率较高^[21]。鱼类颌骨畸形主要表现为上下颌短小、缺失, 舌弓下沉, 下颌扭曲等(图 3)。米克尔氏软骨弯曲作为一种常见颌部畸形, 已经在黄尾鲷、尖吻鲈、大西洋鲑等的仔、稚鱼的骨骼畸形研究中被报道^[22–24]。在卵形鲳鲳中, 米克尔氏软骨弯曲在孵化后第 3 天即被检测到, 这与黄尾鲷骨骼发育和骨骼畸形的研究结果相类似^[23]。在针对尖吻鲈的相关研究中发现, 米克尔氏软骨扭曲可在孵化后第 18 天被检测出^[25], 而在卵形鲳

鲳发育过程中, 孵化后第 5 天即表现出来, 同时该样品伴有严重的发育迟缓^[19]。条纹婢鲷仔、稚鱼(*Latris lineata*)的颌骨畸形主要表现为颌部无法闭合, 且这种畸形在其初始摄食阶段即可观测到^[26]。最近的研究发现, 条纹婢鲷仔、稚鱼的颌骨畸形与其沿养殖缸壁运动行为呈正相关^[26]。

脊柱和尾部骨骼是养殖鱼类骨骼畸形发生频率最高的部位^[27]。脊柱畸形主要表现形式有脊柱前弯、脊柱萎缩等, 而尾部畸形则主要表现为尾上骨、尾下骨融合、尾椎骨畸形等(图 4)。脊柱畸形是发生率最高的骨骼畸形类型, 但在变态后由于体表被皮肤覆盖, 一些轻微的脊柱畸形容易被忽略。在针对卵形鲳鲳仔、稚鱼骨骼畸形的研究中发现, 脊柱畸形平均占比为 18.72%, 此畸形发生率水平和金头鲷(*Sparus aurata*)、绯海鲷(*Diplodus puntazzo*)、斑马鱼(*Brachydanio rerio*)、欧洲鲈(*Dicentrarchus labrax*)等类似^[28–32]。早期的脊柱畸形会对后期养成阶段鱼类的生长与存活造

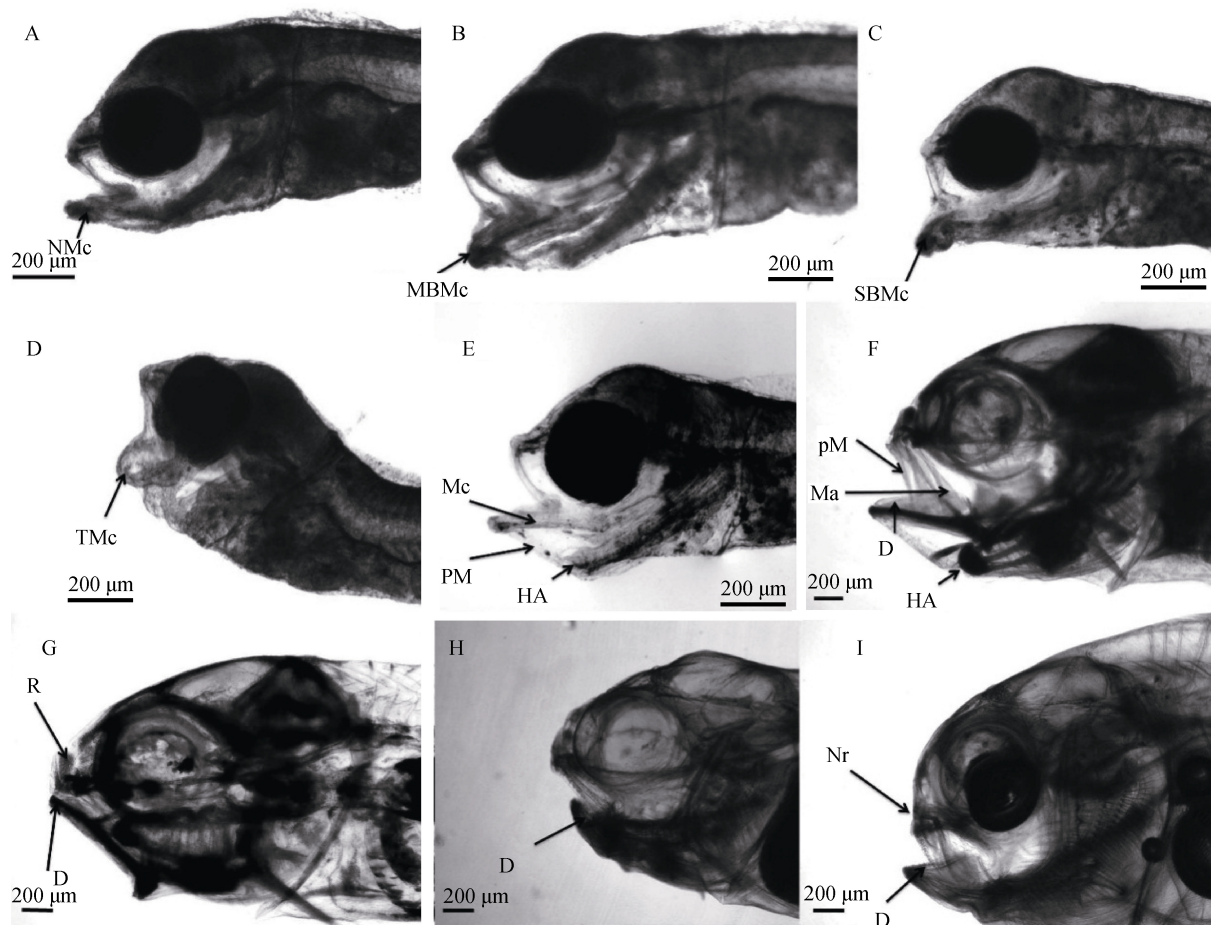


图 3 卵形鲳鲹仔、稚鱼颌部畸形示例^[5]

A. 正常颌部结构(5 d); B. 米克尔氏软骨中度畸形(5 d); C. 米克尔氏软骨严重畸形; D. 下颌扭曲(5 d); E. 舌弓下沉(16 d); G. 正常颌部结构(17 d); H. 下颌短缩(22 d); I. 颌骨畸形。

Fig.3 Head view of *Trachinotus ovatus* larvae at different developmental stages

A. Normal jaw structure (5 dph); B. Mediate bending on Meckel's cartilage (5 dph); C. Severe bending on Meckel's cartilage (5 dph); D. Twisted lower jaw (5 dph); E. Lowered hyoid arch (5dph); F. Lowered hyoid arch (16 dph); G. Normal jaw structure (17 dph); H. Shorten lower jaw (22 dph); I. Pugheadness (29 dph).

成显著的影响^[33-35]。因此, 对鱼类发育早期阶段脊柱畸形的检测与控制至关重要。

仔、稚鱼阶段骨骼畸形出现的时间依物种的不同而有所差异, 产生这种差异的原因被认为与种属间骨骼发育时序不同有关^[4, 25]。在大西洋鲑颌骨早期发育过程中, 颌骨骨骼畸形在软骨期即可被发现^[24]。与大西洋鲑有所不同, 条纹婢鲷在孵化后第 44 天才出现颌部骨骼畸形, 此时颌部骨骼骨化已经完成^[36]。在卵形鲳鲹颌部骨骼发育过程中颌部软骨组织在孵化后第 3 天出现, 孵化后第 4 天即出现米克尔氏软骨弯曲的颌骨畸形现象^[5]。对同属于鲹科的黄尾鲷的研究结果也有类似的发现^[23],

这表明包括卵形鲳鲹在内的部分鲹科鱼类的颌骨骨骼畸形在早期颌部软骨发育过程中形成。

3 仔、稚鱼骨骼畸形的影响因素

截至目前, 虽然对引起骨骼畸形的因素有所了解, 但骨骼畸形仍是阻碍海水鱼类养殖的一个主要问题^[21, 37-75]。引起鱼类骨骼畸形的主要因素有遗传因素、环境因素、营养因素、疾病因素等。但在人工养殖条件下遗传因素、环境因素及营养因素对仔、稚鱼早期骨骼发育影响较显著^[1, 38-39]。环境因素包括温度、盐度、溶解氧以及水流速度等物理参数, 被证实可引起鱼类骨骼发育异常^[40-43]。

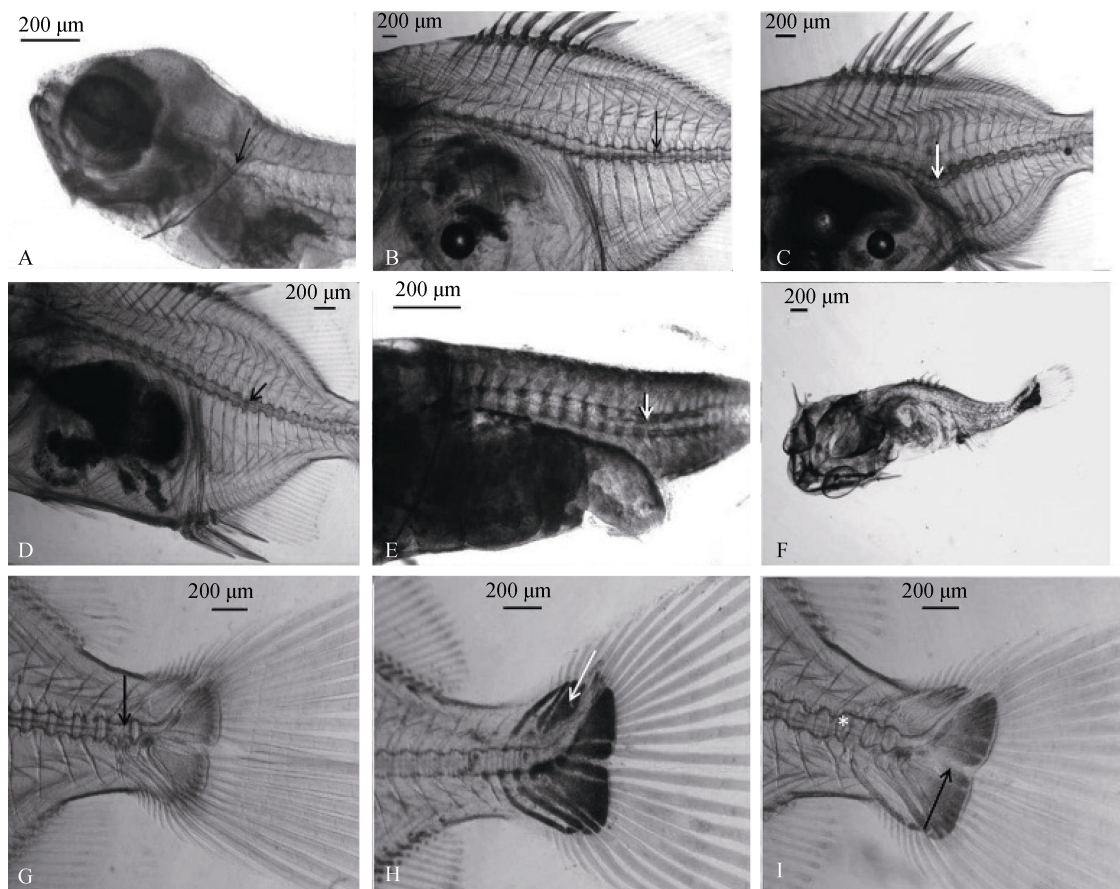


图 4 卵形鲳鲹脊柱畸形及尾骨畸形示例^[9]

A. 脊索畸形(3 d); B. 椎骨异位(31 d); C. 脊柱 V 型弯曲(31 d); D. 椎骨萎缩(31 d); E. 椎骨融合(11 d); F. 脊柱侧凸(16 d); G. 尾椎骨萎缩; H. 尾上骨畸形; I. 尾下骨畸形。

Fig.4 Some typical deformity samples detected in different body parts of fish^[9]

A. Notochord deformity on 3 dph; B. Malposition of vertebrae on 31 dph; C. Severe deformed vertebral column individual on 31 dph (V-shape); D. Atrophy of vertebrae on 31 dph; E. Fusion between vertebrae on 11 dph; F. Scoliosis (16 dph); G. Preural vertebrae deformities; H. Epural deformities; I. Hypural deformities.

而饵料中包括高度不饱和脂肪酸、维生素、矿物质等必需营养成分的不均衡,亦会导致骨骼畸形发生率增高^[44-45]。

3.1 遗传因素

在仔鱼内源营养阶段,发育所需营养物质主要依赖于卵黄囊与油球的供给^[46]。因此,亲鱼产前营养状态对于子代的发育具有显著影响。相关研究表明,黄尾鲷和卵形鲳鲹在孵化后的第 4 天即表现出一定的畸形发生率,此时仔鱼正处于由内源性营养阶段向外源性营养阶段转变中,畸形的发生与其亲鱼的营养状态及遗传关系密切^[4, 23]。Ma 等^[47]研究发现,黄尾鲷不同生殖群体中子代出现颌骨畸形时的体长有所不同。最近的研究结

果表明,大西洋鲑三倍体后代出现的畸形子代显著多于二倍体^[48]。这些研究结果都表明鱼类子代的骨骼发育及骨骼畸形发生受亲本遗传因素的影响。

3.2 环境因素

已知研究结果表明,温度、盐度、溶解氧及水流速等环境因子能引起鱼类的骨骼发育畸形。环境因子对鱼类骨骼发育的影响主要表现在以下两个方面:一是环境因子可以对鱼体的神经或肌肉产生干涉,导致骨骼畸形^[49];二是环境因子可以通过干涉骨骼成分或者发育过程,导致骨骼畸形发育^[50-52]。

3.2.1 温度 水温是影响鱼类骨骼发育重要因素之一^[53]。已有研究表明,孵化后鱼类在从内源性

营养转化到外源性营养过程中, 对环境温度较敏感^[54-57]。温度过高或过低都会对仔、稚鱼骨骼发育及畸形发生产生显著影响^[58-59]。在温度对比试验中, 欧洲鲈在 15℃ 水温下鳃盖骨的畸形发生率显著高于同批次 20℃ 的处理组^[53]。温度对鱼类骨骼畸形发生的部位具有选择性影响。例如, 在不适宜的水温下养殖的日本鳎的颌骨畸形发生率显著升高, 但对如头部骨骼畸形和脊柱骨骼畸形等其他类型的骨骼畸形无显著影响^[60]。笔者在研究温度对卵形鲳鲹仔、稚鱼畸形的影响中发现, 随着温度的升高, V-形脊柱畸形显著升高, 但其他类型的骨骼畸形在不同温度处理下无显著差异。这种现象的发生被认为是温度对鱼类骨骼发育顺序的一种干扰作用^[61]。有研究表明, 温度会对水产动物包括骨骼形成和代谢作用等发育过程进行干扰, 而且这种干扰是决定性的且不可逆^[62-63]。不仅如此, 由于不同鱼类骨骼发育时序存在差异, 温度对其畸形发育的影响也随之不相同。

3.2.2 溶解氧 在人工养殖条件下, 溶解氧是导致鱼类畸形的一个重要因素。研究表明, 溶氧量低是诱导动物细胞凋亡的关键因子^[64-65]。在低溶氧量环境下, 碳水化合物的厌氧反应是鱼体获得能量的主要途径, 大量碳水化合物的消耗会造成仔鱼发育阻滞, 生长迟缓^[66]。相关研究表明, 低溶氧量条件下仔鱼体长显著低于对照组, 且对脊索发育造成严重影响^[42]。在斑马鱼发育过程中, 低溶氧量能够导致畸形发生率增加 77.4%^[67]。以 60% 饱和溶解氧浓度对初孵大西洋鲑进行处理(饱和溶解氧作为对照)发现, 大西洋鲑的畸形发生率与低氧处理时间呈正相关, 且处理组的仔鱼在脊柱矿化和脊索直径等方面均较对照组迟缓^[42]。

3.3 营养

3.3.1 脂肪酸 鱼类自身缺乏合成长链脂肪酸的能力, 只能从食物中摄入来满足鱼体需要, 其中以 DHA(二十二碳六烯酸)、EPA(二十碳五烯酸)和 ARA(二十碳四烯酸)最为重要^[68]。这些必需脂肪酸是参与机体组成的重要营养成分, 并为代谢调控提供物质基础^[69]。必需脂肪酸的代谢受控于

包括 PPAR、RXR 和 RAR 等在内的核内受体, 这些受体能够通过组合形成同源或异源二聚体, 实现对下游基因的调控^[70-71]。而这些下游基因, 如骨形态发生蛋白(bone morphogenetic protein)^[72]、类胰岛素生长因子(insulin-like growth factors)^[73]等, 广泛参与机体的生长和发育。因此, 不平衡膳食脂肪酸的摄入会影响仔、稚鱼骨骼发育, 导致骨骼畸形的发生^[74-75]。研究表明, 投喂经 DHA 强化的轮虫能够有效降低遮目鱼(*Chanos chanos*)仔、稚鱼鳃盖畸形发生率^[76]; 同样以 DHA 强化后的轮虫喂养赤鲷(*Pagrus pagrus*), 脊柱畸形的发生率较未强化组降低 50%。不仅如此, DHA、EPA 和 ARA 等不饱和脂肪酸在膳食中的相对含量对鱼类发育亦具有影响, 例如, 当饵料中 EPA 含量较高而 DHA 含量较低时, 仔、稚鱼体内的包括膜的流动性等生理功能会失衡^[77], 导致发育畸形的现象。

3.3.2 维生素 维生素 A 是鱼类骨化及骨量代谢的关键营养因子^[78]。它不仅能够对仔、稚鱼阶段骨骼发育产生影响, 还能对成鱼的骨骼代谢起到调控^[79]。维生素 A 的代谢是通过两组核内受体, 即 RAR(RA receptor)和 RXR(retinoid X receptor)而进行。这两个受体又都分别有 3 个亚型, 分别为 α 、 β 和 γ ^[80]。这些受体能够与维生素 D 受体或 PPAR 形成多聚体的功能单元, 并与骨化或骨骼代谢相关基因的 DNA 结合区域结合, 对其进行调控^[81]。研究表明, 以 RA 处理处于发育中的牙鲆仔鱼, 能显著影响其颌骨发育^[82]。饵料中高剂量维生素 A 同样会对仔鱼的骨骼发育产生负面影响^[83]。例如, 在斑马鱼仔鱼饵料中添加超剂量的维生素 A, 将导致其椎骨出现椎骨融合等异常发育^[84]。

维生素 D 是维持骨骼中钙和磷平衡、维护骨骼完整的脂溶性激素原物质^[85]。该激素通过与肠道内的包括钙结合和转运蛋白等在内的维生素 D 受体相互作用来调节钙元素的摄取, 以保持一定血钙含量, 维持骨骼中矿物元素稳态。除此之外, 维生素 D 还能直接参与成骨细胞的分裂、分化以及矿化作用等过程^[86]。研究表明, 维生素 D 的缺乏和过量添加均会造成初仔鱼脊柱和鳃骨发育异常^[87]。不仅如此, 维生素 D 的存在形式亦会影响

鱼类的功能性发育。例如, 1, 25-(OH)₂D₃ 能够使莫桑比克罗非鱼(*Sarotherodon mossambicus*)骨骼去矿化, 促进骨骼生长^[88], 但对于大西洋鲑仔稚鱼没有显著影响^[89]。

维生素 C 是鱼类重要的微量营养物质, 它是合成骨胶原的必须成分^[90]。维生素 C 缺乏症会引起鱼类骨骼去矿化, 引起鳃骨畸形^[91]。维生素 E 与维生素 C 均为抗氧化剂。研究表明, 在缺乏维生素 E 的情况下, 维生素 C 可以在一定程度上起到补偿作用, 从而降低黄鲈(*Perca flavescens*)骨骼畸形发生率^[92]。

维生素 K 通过参与骨钙素的羟化过程将其激活^[93]。骨骼中的骨钙素是一种维生素 K 依赖蛋白, 活化后的骨钙素与 Ca⁺的亲合力提升, 并能够与羟基磷灰石结合, 进而使骨骼矿化^[94-95]。骨钙素又是鱼类脊柱中含量最丰富的非胶原蛋白^[96]。试验表明, 维生素 K 的缺乏能够导致底鳉(*Fundulus heteroclitus*)幼鱼脊柱畸形率显著增高^[97]。饵料中维生素 K 的添加能够提高鱼类骨骼质量^[50]。

3.3.3 矿物元素 鱼类骨骼中含有大量的钙和磷元素化合物, 因此, 钙和磷元素的摄入不平衡会导致鱼类骨骼发育不良以及骨骼代谢异常^[98]。鱼类所需的钙元素可以从水体中获得, 但水体中供鱼类直接吸收的磷元素含量很少, 需要从饲料中摄入^[99]。因此, 对于鱼类来说, 钙的缺乏症不常见, 但磷元素的缺乏却能导致一系列的骨骼发育异常, 包括骨骼矿化障碍、头骨畸和脊柱侧凸等^[51, 100-101]。造成这些畸形的原因是磷的缺乏会导致鱼类骨骼无法骨化、脆度增加^[102]。

3.3.4 蛋白质 蛋白质包括氨基酸和多肽, 为鱼类的生长发育提供必须营养, 而骨骼的发育也必须以其作为营养基础^[103]。试验表明, 虹鳟(*Oncorhynchus mykiss*), 大马哈鱼(*Oncorhynchus keta*)在缺乏色氨酸的营养条件下, 会出现脊柱侧凸^[104], 而以短肽来替代海鲈饲料中的蛋白水解产物, 其骨骼畸形发生率随短肽添加量的升高而降低^[105]。目前关于蛋白质类营养物质(氨基酸、多肽等)对海水鱼类仔、稚鱼骨骼畸形影响的研究尚少, 有待进一步深入研究。

4 小结

养殖鱼类骨骼畸形问题已经成为影响海水鱼类养殖健康发展的一个重要问题。研究鱼类早期骨骼发育和骨骼畸形发生具有重要的科学意义和实际应用价值。一方面, 可以深入探讨鱼类骨骼发育的过程, 丰富鱼类发育学基础理论; 另一方面, 骨骼畸形的发生可以揭示出鱼类在养殖过程中, 可能受到来自营养、环境或者遗传等诸多因素的胁迫, 可以通过遗传改良、调整养殖参数达到降低畸形率的目的。在仔、稚鱼养殖阶段, 遗传、营养、环境因子是影响鱼类骨骼早期发育的主要因子。由于鱼类早期发育种属间的特异性, 不同种类骨骼畸形发生的时间、部位会有所差异, 因此, 对于特定养殖品种骨骼畸形的研究需要进行有针对性的定性、定量研究。

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Skeletal ontogeny and deformities in commercially cultured marine fish larvae

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Abstract: Skeletal malformations are often associated with limited movement, reduced feeding capacity, depressed growth, and a high mortality rate. Deformed fish have a low market value and represent wasted time and effort. Skeletal malformations are observed frequently in hatchery-reared marine finfish larvae and juveniles. Such malformations continually hinder development of marine finfish aquaculture. This study summarizes early bone development (including jaw skeleton, vertebral column, and caudal vertebra) characteristics of commercial marine fish, such as golden pompano, yellowtail kingfish, and Asian sea bass, and compares bone malformation position, time of occurrence, and frequency in fish larvae. We also review genetic, environmental, and nutritional factors that regulate skeletal development in marine fish larvae to help reduced skeletal deformities during marine larval fish culture.

Key words: marine fish larvae; skeletal ontogeny; skeletal deformities

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