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鱼类早期发育阶段异速生长及核酸、消化酶变化的研究进展

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摘要: 鱼类早期发育阶段是其生活史中的关键时期之一, 生理、形态学变化剧烈, 死亡率极高。研究鱼类早期发育阶段的生长规律及其生理特性, 可为了解鱼类早期阶段的致死因子提供理论依据, 有助于提高苗种阶段的生长率和成活率, 也对制定合理的早期培育策略具有重要的指导意义。异速生长模式对确定仔鱼的养殖模式有重要的指示作用, 鱼类在早期阶段会优先发育与生命活动关系较密切的器官, 以期达到较高的早期成活率。RNA/DNA 是评价鱼类早期发育阶段生长率的有效指标, 也可用于评价仔稚鱼的生长潜力、营养状况、饲料营养水平以及确定关键期。研究仔稚鱼消化酶的发生和演变有助于深入了解鱼类在个体发育早期的消化生理, 有助于选择适口饵料和制定投喂策略。因此, 本文综述了鱼类早期发育阶段的异速生长模式、核酸及蛋白含量变化规律以及消化酶的发生和变化, 为鱼类早期阶段健康养殖的发展提供依据。

关键词: 早期阶段; 异速生长; 核酸; 消化酶; 演变
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鱼类早期发育阶段的生长规律及生理特性, 是解释鱼类早期生活史发生机理途径的重要基础, 也是提高鱼类苗种培育技术的重要理论依据。有关鱼类早期发育过程中的相关研究, 包括形态结构、生态习性、消化生理和免疫特性等是成功建立人工繁育技术和健康养殖理论与技术的基础。鱼类早期阶段的生理、形态变化剧烈, 通常伴随着高死亡率[1−2], 而饥饿和被捕食是造成仔鱼死亡的重要原因[3], 准确评价仔稚鱼的营养状况、生长率以及早期阶段的变化规律有助于发现和调控影响鱼类早期成活率及生长率的因子, 提高生长率和成活率[4]。因此, 研究鱼类早期发育阶段的生长及生理特性对提高鱼苗早期成活率及制定合理的早期培育策略均具有重要意义。本文综述了鱼类早期发育阶段的异速生长模式、核酸及蛋白含量变化规律以及消化酶的发生和演变, 为鱼类早期健康养殖提供基础资料。

1 鱼类早期阶段的生长模式及异速生长

在早期发育中, 鱼类各个功能器官发生了剧烈的生理和结构变化, 各部分的生长速度也不同步, 这种现象叫异速生长(allometric growth)[5]。异速生长保证了重要器官的优先发育, 影响了仔稚鱼的生长、运动、摄食等生理活动及存活率[6]。研究鱼类早期阶段的异速生长是研究鱼类早期生活史的重要部分之一[7], 对鱼类分类、物种保存具有重要意义[8], 同时形态学指标对确定仔鱼的养殖模式也有重要的指示作用[9]。

鱼类体长−体重关系(length-weight relationship, LWR)在渔业管理和生态学研究中应用非常广泛[10]。鱼类早期生活史阶段具有不同的生长模式和体长−体重关系[10−11], 但是其在鱼类早期生活史研究中的应用并不多[11]。鱼类体长−体重关系一般为指数关系 $W=aL^b$, Boukal 等[12]详细综述

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了鱼类生长模式的各种函数关系, 但也有许多其他生长模型[13–17], 如产后生长曲线[18]、von Bertalanffy 生长曲线[19]等。鱼类 LWR 虽然是较为基础的资料, 但其具有重要意义, 相关的研究较多[20–23]。

研究鱼类生长模式及异速生长需要测量鱼体的各种形态学参数, 如体长、全长、体重、头长、头高、体高、鳍长、眼径、须长等等。异速方程广泛用于分析鱼类早期发育阶段的生长模式[24]。就规格来说, 鱼体某一部分的规格 y 与另一部分的规格 x 之间的关系一般为 $y=ax^b$。其中，指数 b 可反映两部分生长速度之间的差异, $b<1.0$ 表示负异速生长, $b>1.0$ 表示正异速生长, $b=1.0$ 则表示等速生长[25–26]。通常情况下会将数据进行对数转化后来评价异速方程的参数, 转化之后异速方程会变成直线回归曲线, b 值为异速方程的截距。近年来, 国内外相关的研究报道很多, 如细点牙鲷(*Dentex dentex*)[26]、北美牙鲆(*Paralichthys californicus*)[27]、黍鲱(*Sprattus sprattus*)[11]、中吻鲟(*Acipenser medirostris*)[28]、大西洋鳕(*Gadus morhua*)[29–30]、金头鲷(*Sparus aurata*)[24]、斑带副鲈(*Paralabrax maculatofasciatus*)[9]、鮸(*Miichthys miiuy*)[31]、甲鲇(*Corydoras aeneus*)[32]、红鲱脂鲤(*Hyphessobrycon serpae*)[33]、白梭吻鲈(*Sander lucioperca*)[34]、尖吻重牙鲷(*Diplodus puntazzo*)[35]、施氏俯海鲇(*Cathorops spixii*)[36]、真鲷(*Pagrus pagrus*)[37]、金眼短鲷(*Nannacara anomala*)[38]、奥比尼亚石脂鲤(*Brycon orbignyanus*)[39]、江鳕(*Lota lota*)[7]、阿氏冠鲇(*Lophiosilurus alexandri*)[8]及大鳞副泥鳅(*Paramisgurnus dabryanus*)[40]等。

鱼类早期阶段的异速生长具有一定的规律性, 简单来说就是鱼类在早期阶段会优先发育与生命活动关系较密切的器官, 以期达到较高的早期成活率[9, 41–42]。而头部是鱼类呼吸、摄食的重要部位, 因此通常来说这一部位在鱼类中均是较早发育的, 在早期阶段呈现正异速生长, 而且大量的研究结果也证明了这一结论, 如红鲱脂鲤[33]、尖吻重牙鲷[35]、泥鳅(*Misgurnus anguillicaudatus*)[43]、中吻鲟[28]、阿氏冠鲇[8]、甲鲇[32]、黄尾鰤(*Seriola lalandi*)[44]、奥比尼亚石脂鲤[39]等。大脑、鳃以及摄食器官的优先发育保证了仔稚鱼应对外界环境压力的能力。其次是视觉器官, 视觉与仔稚鱼摄食[45–46]及避敌[47]之间具有显著的相关性, 在多数仔稚鱼中均为正异速生长[24, 32, 36, 38, 43–44]。躯干部是鱼类消化系统的重要部位, 但在多数鱼类中却为负异速生长[7, 33, 38–39, 44, 48–49], 仅有少数鱼类中发现其为正异速生长[50], 这有可能是因为仔鱼孵化之后首先以卵黄囊作为主要营养源, 其消化系统的发育则相对滞后, 因此多数仔鱼躯干部为负异速生长。

2　鱼类早期阶段核酸及蛋白含量的变化

鱼类早期阶段对环境变化极为敏感, 精确测定这些细微变化是非常困难的[51–52]; 仔鱼个体小, 传统评价鱼类生长变化的指标不适合于仔鱼[53]。研究表明生化指标能很好地反映仔鱼的生长、体重以及形态学指标[1], 因此, 生化指标被用于评价仔鱼的生长及营养状况。这主要是由于鱼类生化成分对环境、食物等外界条件变化的反应非常敏感且迅速, 相对来说鱼体生长对外界条件变化的反应则相对滞后[54–55]。生化指标已用于评价生长速度较慢鱼类仔稚鱼的生长及未能在生长上体现的营养差异[56]。

核酸测定可作为评价仔稚鱼生长的指标, 其理论基础是有共识的。动物细胞内脱氧核糖核酸(DNA)含量是基本恒定的, 而核糖核酸(RNA)主要存在于核糖体中(约占总 RNA 的 85%~90%), 而且与蛋白合成速率密切相关[2]。这种方法可避免重复测定生长缓慢的仔稚鱼的体长及体重的误差, 并且可用于一些无法测定生长指标的研究中。有些研究报道, 可利用核酸测定来评价仔稚鱼的生长[3, 53, 57]、生长潜力[2, 58]、营养状况[59–60]、饲料营养水平[61]及确定仔稚鱼的关键期[62]。

测定鱼类早期发育阶段的核酸水平, 有助于了解仔稚鱼的生长及营养状况。常用的评价指标有 RNA 含量、DNA 含量、RNA/DNA 比以及蛋白质/DNA 比。核酸指标测定能更好地评价仔稚鱼的生长和营养状况主要是由于生化指标对环境变化的敏感性高于机体的生长[54]。RNA 主要存在于生长迅速的组织中[1], 其含量常用于评价蛋白质合成能力, 即仔稚鱼的生长, 美洲拟鲽

(*Pseudopleuronectes americanus*)和隆头鱼(*Tautoga onitis*)早期阶段 RNA 含量均与特定生长率之间存在显著性关系[57]，仔鱼早期阶段一般都表现为 RNA 和蛋白含量升高伴随着快速的生长，关于太平洋蓝鳍金枪鱼(*Thunnus orientalis*)[2]和大菱鲆(*Scophthalmus maximus*)[53]的研究都遵循这一规律。DNA 含量的增加主要是由活跃的细胞分化造成的，而活跃的细胞分化通常伴随着器官的发育与分化。如太平洋蓝鳍金枪鱼在孵出后 10~15 d，牙齿、幽门盲囊及胃腺开始分化；在孵出后 15 d 时，DNA 含量最高[2]。蛋白质/DNA 比是反映仔稚鱼细胞重量或细胞大小的指标[63]，鱼类早期仔鱼蛋白质/DNA 比的增加是由于该阶段的生长以细胞增大为主[2, 53]。相对地，DNA 含量的增加则被认为是细胞增生引起的，因为单个细胞的 DNA 含量比较恒定[53]。根据这些指标的变化趋势可以判断鱼类早期阶段的发育规律。在对美国红鱼(*Sciaenops ocellatus*)的研究中发现，其早期阶段细胞水平上的发育过程从孵化到卵黄囊耗尽主要表现为细胞数量的增生，初次摄食之后则是以细胞体积、质量的增大为主[62]。而牙鲆(*P. olivaceus*)[55]和大菱鲆[53]早期阶段细胞水平上的发育则是一个细胞增生和增大循环的过程。RNA/DNA 比与生长速度明显相关[53]，但却与鱼体规格没有显著相关[64]。对牙鲆[65]、大西洋鳕[66]、美洲拟鲽[67]及大鳞副泥鳅[68]等的研究中都发现了 RNA/DNA 比与瞬时生长率之间具有明显的正相关性，说明 RNA/DNA 比是评价鱼类早期发育阶段生长率的有效指标。

此外，RNA/DNA 比对确定仔稚鱼关键期也具有重要的意义[2, 69]，RNA/DNA 比值低意味着生长速度慢、营养状况差及死亡率高[70]。而 RNA/DNA 比是反映仔鱼状况的可靠指标[3, 62, 71]，因此了解鱼类早期阶段核酸的变化是非常重要的。一般认为鱼类早期阶段 RNA/DNA 比的急剧变化发生的时间段是仔鱼的关键期，在这一阶段应提供足质足量的饵料，确保仔稚鱼能安全度过关键期。

3 鱼类早期阶段消化酶活性的变化

鱼体内消化酶的发生并不是完全同步的，而是随着动物体的生长发育而演变的。消化酶活性演变主要是个体生长及器官、组织发育，而不是对摄食量变化的应答，也不是由饵料成分的变化引起的[72]。但也有学者认为，活饵料量和组成的改变[73–74]、生长引起的可溶性蛋白含量变化[75]及幼体代谢变化引起的不同酶表达的变化[76]都会导致蛋白酶活性的变化。研究鱼类个体发育时期消化酶的演变有助于了解鱼类各生长阶段的饵料利用情况及营养需求，对鱼类饲料开发具有重要意义。

国内外主要从生物化学的角度来定量测定鱼类各个体发育期的消化酶活性，评价其消化能力，并作为仔鱼营养及饲料配备的参考依据[77]。Ribeiro 等[78]测定了塞内加尔鳎(*Solea senegalensis*)从孵化到 30 d 主要消化酶及碱性磷酸酶活性的变化，并认为其适合使用人工配合饲料。Comabella 等[72]研究了古巴雀鳝(*Atractosteus tristoechus*)幼鱼发育期间消化酶活性的变化，他们认为古巴雀鳝适合以人工饲料来养殖。相似的研究还有很多，如庸鲽(*Hippoglossus hippoglossus*)[79–80]、河鲈(*Perca fluviatilis*)[81]、北美牙鲆[82]、黄尾鰤[83]、大西洋鳕[80]、斑带副鲈[76]、细点牙鲷[84]、波斯鲟(*Acipenser persicus*)[85]、军曹鱼(*Rachycentron canadum*)[86]、鲤(*Cyprinus carpio*)[87]、双斑绚鲇(*Ompok bimaculatus*)[88]、真鲷[89]等。

仔稚鱼消化酶活性的演变可以反映出鱼类消化系统发育及营养需求的变化。对蛋白酶来说，一般初孵仔鱼即可检测出较高的胰蛋白酶活性，但却无法检出胃蛋白酶活性[78, 84, 90]，胃蛋白酶会在发育一段时间后检出，各种鱼类的检出时间不同(表 1)。随着仔鱼的发育，胰蛋白酶活性持续上升，达到峰值后开始迅速下降，这是脊椎动物包括鱼类个体发育的明显特征[81, 85, 91]。胃蛋白酶的出现，标志着胃功能的发育，而且随着胃蛋白酶活性的升高，一般胰蛋白酶的活性会降低[76, 78, 80–81, 85]，这标志着蛋白质的消化由碱性消化转化为酸性消化。在此之前，胰蛋白酶[76, 78, 85, 91–92]和胞饮作用[80, 93]对仔稚鱼消化食物中的蛋白质至关重要。

一般认为脂肪酶受基因调控[72, 85]，初孵仔鱼可检出较高的脂肪酶活性，但也有不一致的结果，

表 1　不同鱼类胃蛋白酶的检出时间
Tab. 1　Testing time of the appearance of pepsin in different fish species

种类 species	检出时间*testing time*	养殖温度 rearing temperature	参考文献 reference
丝尾鳠 *Mystus nemurus*	1	未提及 not mentioned	[94]
波斯鲟 *Acipenser persicus*	5	17~18℃	[85]
大雀鳝 *Atractosteus spatula*	5	未提及 not mentioned	[95]
大菱鲆 *Scophthalmus maximus*	9	18~19℃	[96]
大西洋白姑鱼 *Argyrosomus regius*	15	20.0~22.0℃	[97]
双斑绚鲇 *Ompok bimaculatus*	15	27℃	[88]
卵形鲳鲹 *Trachinotus ovatus*	15	27~29℃	[98]
北美牙鲆 *Paralichthys californicus*	18	(18.2±0.2)℃	[82]
细点牙鲷 *Dentex dentex*	19	(19.2±0.5)℃	[84]
墨西哥笛鲷 *Lutjanus guttatus*	20	(26.7±0.21)℃	[99]
条石鲷 *Oplegnathus fasciatus*	22	(24.0±1.0)℃	[100]
军曹鱼 *Rachycentron canadum*	22	未提及 not mentioned	[86]
舌齿鲈 *Dicentrarchus labrax*	24	18~19℃	[101]
尖吻重牙鲷 *Diplodus puntazzo*	32	19.0~23.0℃	[90]
大鳞副泥鳅 *Paramisgurnus dabryanus dabryanus*	35	(24.4±0.4)℃	[102]
漠斑牙鲆 *Paralichthys lethostigma*	37	(18.5±0.5)℃	[103]
金头鲷 *Sparus aurata*	40	19℃	[74]

注: *表示检出时间为仔鱼孵化后天数, 单位为 DAH.
Note: * means testing time is the days after hatching (DAH).

如高眼丽体鱼(*Cichlasoma urophthalmus*)[104]直至 13 d 才检测出脂肪酶。其变化规律及机制并不清楚, 在不同鱼类中的表现也不一致。在牙鲆[105]、斑带副鲈[76]及细点牙鲷[84]中表现为初次摄食之后开始下降, 在北美牙鲆[82]中表现为逐渐上升至平衡, 而在波斯鲟[85]中表现为持续上升。普遍的观点是鱼类仔鱼存在两种脂肪酶, 一种涉及卵黄囊中脂肪的消化, 另一种则与食物中脂肪的消化相关[106], 初次摄食之后两种脂肪酶转化可能会造成脂肪酶活性的不稳定变化。

淀粉酶与脂肪酶相似, 初孵仔鱼即可检出, 多数学者认为其也是受基因调控[76, 81, 92]。淀粉酶的变化规律与胰蛋白酶相似, 都表现为先上升后下降, 这是鱼类及其他脊椎动物发育的规律[78, 91]。在古巴雀鳝[72]、塞内加尔鳎[78]及大雀鳝(*A. spatula*)[95]中, 淀粉酶的活性在内源性营养向外源性营养转变期和仔鱼向稚鱼转变期这两个时间点有明显的峰值。但其变化机制却没有定论, Cahu 等[91]认为饲料中 12%的淀粉含量可显著诱导舌齿鲈(*Dicentrarchus labrax*)淀粉酶活力升高; Oozeki 等[106]推测外源性淀粉酶增加了鱼体淀粉酶的活力; 张云龙等[107]认为消化系统快速发育引起的消化能力增强导致了泥鳅仔鱼淀粉酶活力的增强; 而淀粉酶活力降低则可能是随着仔鱼的发育, 其对蛋白质和脂肪的利用增加而降低了对糖类的需求[93], 或者是淀粉酶分泌系统功能终止[78]。

仔稚鱼的肠分泌酶主要是碱性磷酸酶以及一些氨基肽酶, 这些酶主要位于肠上皮刷状缘膜[78, 90, 108], 常作为指示营养物质吸收和肠上皮细胞分化的指标[109]。肠酶通常是作为评价仔稚鱼进入成鱼消化模式的指标[78, 110]。许多研究结果表明, 仔鱼在孵出后的最初几周内刷状缘膜酶活力会显著增加[85, 104, 111], 但随后会出现一个明显的下降趋势, 这可能是由可溶性蛋白含量的急剧增加引起的[80], 而不是其消化酶活性和消化能力的降低导致的。碱性磷酸酶是一种膜结合金属酶, 分布于鱼类肠上皮纹状缘上, 对脂类、葡萄糖、钙及无机磷的吸收有促进作用, 碱性磷酸酶活性越高表明该区域的吸收能力越强[108]。磷酸酶最主要的作用是水解无机磷酸盐作为营养物质以及转运营养物质[76]。草鱼(*Ctenopharyngodon idellus*)仔鱼肠道中碱性磷酸酶的分布与脂肪、氨基酸及

糖类在肠道中的吸收位置紧密相关[112]。研究表明，碱性磷酸酶与肠道吸收及营养物质转运有关，碱性磷酸酶活性高意味着高的肠吸收能力强[72]；碱性磷酸酶的增加也标志着肠道刷状缘的发育[78]。碱性磷酸酶与鱼类消化间接相关，其作用机制是通过改变氨基酸的磷酸链来促进其他消化酶的活性，从而通过 Ca^{2+}转运的方式增加营养物质的吸收[113]。在鱼类早期发育阶段，碱性磷酸酶活性的显著上升被认为是鱼类肠吸收功能发育完全的标志[72, 76, 78, 80, 109]，也是仔鱼向成鱼消化模式转变的关键步骤[114]。

参考文献

[1] Park S U, Lim H K, Han H S. Changes in RNA/DNA ratio and growth of slime flounder, *Microstomus achne*, larvae until metamorphosis[J]. J Appl Ichthyol, 2008, 24(1): 50–54.

[2] Tanaka Y, Gwak W S, Tanaka M, et al. Ontogenetic changes in RNA, DNA and protein contents of laboratory-reared Pacific bluefin tuna *Thunnus orientalis*[J]. Fish Sci, 2007, 73(2): 378–384.

[3] Ramírez T, Cortés D, García A, et al. Seasonal variations of RNA/DNA ratios and growth rates of the Alboran Sea sardine larvae (*Sardina pilchardus*)[J]. Fish Res, 2004, 68(1–3): 57–65.

[4] Caldarone E M, St Onge-Burns J M, Buckley L J. Relationship of RNA/DNA ratio and temperature to growth in larvae of Atlantic cod *Gadus morhua*[J]. Mar Ecol Prog Ser, 2003, 262: 229–240.

[5] van Snik G M J, van den Boogaart J G M, Osse J W M. Larval growth patterns in *Cyprinus carpio* and *Clarias gariepinus* with attention to the finfold[J]. J Fish Biol, 1997, 50(6): 1339–1352.

[6] Rodriguez A, Gisbert E. Eye development and the role of vision during Siberian sturgeon early ontogeny[J]. J Appl Ichthyol, 2002, 18(4–6): 280–285.

[7] Kupren K, Trąbska I, Żarski D, et al. Early development and allometric growth patterns in burbot *Lota lota* L.[J]. Aquacult Int, 2014, 22(1): 29–39.

[8] Guimarães-Cruz R J, Veloso-Júnior V C, Sales N G, et al. Allometric growth patterns in hatchery-reared larvae of the catfish *Lophiosilurus alexandri* (Pisces: Pseudopimelodidae)[J]. Arq Bras Med Vet Zootec, 2014, 66(1): 284–288.

[9] Peña R, Dumas S. Development and allometric growth patterns during early larval stage of the spotted sand bass *Paralabrax maculatofasciatus* (Percoidei: Serranidae)[J]. Sci Mar, 2009, 73(S1): 183–189.

[10] Froese R. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations[J]. J Appl Ichthyol, 2006, 22(4): 241–253.

[11] Peck M A, Clemmesen C, Herrmann J P. Ontogenic changes in the allometric scaling of the mass and length relationship in *Sprattus sprattus*[J]. J Fish Biol, 2005, 66(3): 882–887.

[12] Boukal D S, Dieckmann U, Enberg K, et al. Life-history implications of the allometric scaling of growth[J]. J Theor Biol, 2014, 359: 199–207.

[13] Charnov E L, Turner T F, Winemiller K O. Reproductive constraints and the evolution of life histories with indeterminate growth[J]. Proc Natl Acad Sci USA, 2001, 98(16): 9460–9464.

[14] Kozlowski J. Optimal allocation of resources to growth and reproduction-implications for age and size at maturity[J]. Trends Ecol Evol, 1992, 7(1): 15–19.

[15] Kozlowski J, Teriokhin A T. Allocation of energy between growth and reproduction: the Pontryagin maximum principle solution for the case of age- and season-dependent mortality[J]. Evol Ecol Res, 1999, 1(7): 423–441.

[16] Lester N P, Shuter B J, Abrams P A. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction[J]. Proc R Soc Lond Ser B-Biol Sci, 2004, 271(1548): 1625–1631.

[17] West G B, Brown J H, Enquist B J. A general model for ontogenetic growth[J]. Nature, 2001, 413(6856): 628–631.

[18] Kerkhoff A J. Modelling metazoan growth and ontogeny[M]//Sibly R M, Brown J H, Kodric-Brown A. Metabolic Ecology: A Scaling Approach. Hoboken, New Jersey: John Wiley & Sons, 2012: 48–56.

[19] von Bertalanffy L. A quantitative theory of organic growth[J]. Hum Biol, 1938, 10(2): 181–213.

[20] Vicentin W, Costa F E dos S, Súarez Y R. Length-weight relationships and length at first maturity for fish species in the upper Miranda River, southern Pantanal wetland, Brazil[J]. J Appl Ichthyol, 2012, 28(1): 143–145.

[21] Gaygusuz Ö, Aydın H, Emiroğlu Ö, et al. Length-weight relationships of freshwater fishes from the western part of Anatolia, Turkey[J]. J Appl Ichthyol, 2013, 29(1): 285–287.

[22] Lim K C, Chong V C, Lim P E, et al. Length-weight relationship of stingrays in Kuala Selangor, Malaysia[J]. J Appl Ichthyol, 2014, 30(5): 1096–1098.

[23] Zeng Y, Huang Y Y, Chen Y B, et al. Length-weight relationships of fishes in the Wujiao nature reserve and adjacent areas, China[J]. J Appl Ichthyol, 2014, 30(5): 1099–1100.

[24] Çoban D, Kamaci H O, Suzer C, et al. Allometric growth in hatchery-reared gilthead seabream[J]. N Am J Aquac, 2009, 71(3): 189–196.

[25] Katsanevakis S, Thessalou-Legaki M, Karlou-Riga C, et al. Information-theory approach to allometric growth of marine organisms[J]. Mar Biol, 2007, 151(3): 949–959.

[26] Koumoundouros G, Divanach P, Kentouri M. Ontogeny and allometric plasticity of *Dentex dentex* (Osteichthyes:

Sparidae) in rearing conditions[J]. Mar Biol, 1999, 135(3): 561–572.
[27] Gisbert E. Morphological development and allometric growth patterns in hatchery-reared California halibut larvae[J]. J Fish Biol, 2002, 61(5): 1217–1229.
[28] Gisbert E, Doroshov S I. Allometric growth in green sturgeon larvae[J]. J Appl Ichthyol, 2006, 22(S1): 202–207.
[29] Árnason T, Björnsson B, Steinarsson A. Allometric growth and condition factor of Atlantic cod (*Gadus morhua*) fed to satiation: effects of temperature and body weight[J]. J Appl Ichthyol, 2009, 25(4): 401–406.
[30] Wold P A, Hoehne-Reitan K, Rainuzzo J, et al. Allometric growth and functional development of the gut in developing cod *Gadus morhua* L. larvae[J]. J Fish Biol, 2008, 72(7): 1637–1658.
[31] Shan X J, Cao L, Huang W, et al. Feeding, morphological changes and allometric growth during starvation in miiuy croaker larvae[J]. Environ Biol Fishes, 2009, 86(1): 121–130.
[32] Huysentruyt F, Moerkerke B, Devaere S, et al. Early development and allometric growth in the armoured catfish *Corydoras aeneus* (Gill, 1858)[J]. Hydrobiologia, 2009, 627(1): 45–54.
[33] Celik P, Cirik S. Allometric growth in serpae tetra (*Hyphessobrycon serpae*) larvae[J]. J Anim Vet Adv, 2011, 10(17): 2267–2270.
[34] M'Hetli M, Ben Khemis I, Hamza N, et al. Allometric growth and reproductive biology traits of pikeperch *Sander lucioperca* at the southern edge of its range[J]. J Fish Biol, 2011, 78(2): 567–579.
[35] Çoban D, Suzer C, Yıldırım Ş, et al. Morphological development and allometric growth of sharpsnout seabream (*Diplodus puntazzo*) larvae[J]. Turk J Fish Aquat Sci, 2012, 12(4): 883–891.
[36] Lima A R A, Barletta M, Dantas D V, et al. Early development and allometric shifts during the ontogeny of a marine catfish (*Cathorops spixii*-Ariidae)[J]. J Appl Ichthyol, 2012, 28(2): 217–225.
[37] Andrade C A P, Nascimento F J A, Nogueira N, et al. Allometric growth in red porgy larvae: Developing morphological indices for mesocosm semi-intensive culture[J]. North Am J Aquac, 2013, 75(1): 42–49.
[38] Kupren K, Prusińska M, Daniel Ż, et al. Early development and allometric growth in *Nannacara anomala* Regan, 1905 (Perciformes: Cichlidae) under laboratory conditions[J]. Neotrop Ichthyol, 2014, 12(3): 659–665.
[39] Nogueira L B, Godinho A L, Godinho H P. Early development and allometric growth in hatchery-reared characin *Brycon orbignyanus*[J]. Aquac Res, 2014, 45(6): 1004–1011.
[40] Zhang Y, Wu Q, Hu W, et al. Morphological changes and allometric growth in hatchery-reared Chinese loach *Paramisgurnus dabryanus* (Dabry de Thiersant, 1872)[J]. Chin J Oceanol Limnol, 2016, 34(4): 757–762.
[41] Khemis I B, Gisbert E, Alcaraz C, et al. Allometric growth patterns and development in larvae and juveniles of thick-lipped grey mullet *Chelon labrosus* reared in mesocosm conditions[J]. Aquac Res, 2013, 44(12): 1872–1888.
[42] Russo T, Costa C, Cataudella S. Correspondence between shape and feeding habit changes throughout ontogeny of gilthead sea bream *Sparus aurata* L., 1758[J]. J Fish Biol, 2007, 71(3): 629–656.
[43] Gao L, Duan M, Cheng F, et al. Ontogenetic development in the morphology and behavior of loach (*Misgurnus anguillicaudatus*) during early life stages[J]. Chin J Oceanol Limnol, 2014, 32(5): 973–981.
[44] Martínez-Montaño E, González-Álvarez K, Lazo J P, et al. Morphological development and allometric growth of yellowtail kingfish *Seriola lalandi* V. larvae under culture conditions[J]. Aquac Res, 2016, 47(4): 1277–1287.
[45] Shand J, Chin S M, Harman A M, et al. Variability in the location of the retinal ganglion cell area centralis is correlated with ontogenetic changes in feeding behavior in the black bream, *Acanthopagrus butcheri* (Sparidae, Teleostei)[J]. Brain Behav Evol, 2000, 55(4): 176–190.
[46] Uemura M, Somiya H, Moku M, et al. Temporal and mosaic distribution of large ganglion cells in the retina of a daggertooth aulopiform deep-sea fish (*Anotopterus pharao*)[J]. Philos Trans R Soc Lond B Biol Sci, 2011, 355(1401): 1161–1166.
[47] Kunz Y W, Ennis S, Wise C. Ontogeny of the photoreceptors in the embryonic retina of the viviparous guppy, *Poecilia reticulata* P. (Teleostei): An electron-microscopical study[J]. Cell Tissue Res, 1983, 230(3): 469–486.
[48] Gisbert E. Early development and allometric growth patterns in Siberian sturgeon and their ecological significance[J]. J Fish Biol, 1999, 54(4): 852–862.
[49] Gisbert E, Asgari R, Rafiee G, et al. Early development and allometric growth patterns of beluga *Huso huso* (Linnaeus, 1758)[J]. J Appl Ichthyol, 2014, 30(6): 1264–1272.
[50] Gisbert E, Merino G, Muguet J B, et al. Morphological development and allometric growth patterns in hatchery-reared California halibut larvae[J]. J Fish Biol, 2002, 61(5): 1217–1229.
[51] Gwak W S, Tanaka M. Changes in RNA, DNA and protein contents of laboratory-reared Japanese flounder *Paralichthys olivaceus* during metamorphosis and settlement[J]. Fish Sci, 2002, 68(1): 27–33.
[52] Mercaldo-Allen R, Kuropat C, Caldarone E M. A model to estimate growth in young-of-the-year tautog, *Tautoga onitis*, based on RNA∶DNA ratio and seawater temperature[J]. J Exp Mar Biol Ecol, 2006, 329(2): 187–195.
[53] Tong X H, Liu Q H, Xu S H, et al. Changes in RNA, DNA, protein contents and growth of turbot *Scophthalmus maximus* larvae and juveniles[J]. J Fish Biol, 2010, 77(3): 512–525.
[54] Folkvord A, Blom G, Johnnessen A, et al. Growth-de-

Growth-dependent age estimation in herring (*Clupea harengus* L.) larvae[J]. Fish Res, 2000, 46(1–3): 91–103.
[55] Gwak W S, Tanaka M. Developmental change in RNA: DNA ratios of fed and starved laboratory-reared Japanese flounder larvae and juveniles, and its application to assessment of nutritional condition for wild fish[J]. J Fish Biol, 2001, 59(4): 902–915.
[56] Haines T A. An evaluation of RNA-DNA ratio as a measure of long-term growth in fish populations[J]. J Fish Board Can, 1973, 30(2): 195–199.
[57] Kuropat C, Mercaldo-Allen R, Caldarone E, et al. Evaluation of RNA concentration as an indicator of growth in young-of-the-year winter flounder *Pseudopleuronectes americanus* and tautog *Tautoga onitis*[J]. Mar Ecol Prog Ser, 2002, 230: 265–274.
[58] Vinagre C, Fonseca V, Maia A, et al. Habitat specific growth rates and condition indices for the sympatric soles *Solea solea* (Linnaeus, 1758) and *Solea senegalensis* Kaup 1858, in the Tagus estuary, Portugal, based on otolith daily increments and RNA-DNA ratio[J]. J Appl Ichthyol, 2008, 24(2): 163–169.
[59] Rosa R, Nunes M L. RNA, DNA and protein concentrations and amino acid profiles of deep-sea decapod *Aristeus antennatus*: An indication for seasonal variations of nutrition and growth[J]. Aquat Living Resour, 2004, 17(1): 25–30.
[60] Tanaka Y, Satoh K, Yamada H, et al. Assessment of the nutritional status of field-caught larval Pacific bluefin tuna by RNA/DNA ratio based on a starvation experiment of hatchery-reared fish[J]. J Exp Mar Biol Ecol, 2008, 354(1): 56–64.
[61] Zehra S, Khan M A. Dietary lysine requirement of fingerling *Catla catla* (Hamilton) based on growth, protein deposition, lysine retention efficiency, RNA/DNA ratio and carcass composition[J]. Fish Physiol Biochem, 2013, 39(3): 503–512.
[62] Westerman M, Holt G J. RNA: DNA ratio during the critical period and early larval growth of the red drum *Sciaenops ocellatus*[J]. Mar Biol, 1994, 121(1): 1–9.
[63] Fukuda M, Yano Y, Nakano H, et al. Protein and nucleic acid changes during early development stages of cresthead flounder[J]. Bull Jpn Soc Sci Fish, 1986, 52(6): 951–955.
[64] Islam M S, Tanaka M. Nutritional condition, starvation status and growth of early juvenile Japanese sea bass (*Lateolabrax japonicus*) related to prey distribution and feeding in the nursery ground[J]. J Exp Mar Biol Ecol, 2005, 323(2): 172–183.
[65] Fukuda M, Sako H, Shigeta T, et al. Relationship between growth and biochemical indices in laboratory-reared juvenile Japanese flounder (*Paralichthys olivaceus*), and its application to wild fish[J]. Mar Biol, 2001, 138(1): 47–55.
[66] Peck M A, Buckley L J, Caldarone E M. Effects of food consumption and temperature on growth and biochemical-based indicators of growth in early juvenile Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*[J]. Mar Ecol Prog Ser, 2003, 251(1): 233–243.
[67] Mercaldo-Allen R, Kuropat C, Caldarone E M. An RNA: DNA-based growth model for young-of-the-year winter flounder *Pseudopleuronectes americanus* (Walbaum)[J]. J Fish Biol, 2008, 72(6): 1321–1331.
[68] Zhang Y L, Hu W H, Wu Q W, et al. Ontogenetic changes in RNA, DNA and protein contents of Chinese loach, *Paramisgurnus dabryanus* (Dabry de Thiersant, 1872), larvae and juveniles[J]. J Appl Ichthyol, 2015, 31(5): 876–882.
[69] Clemmesen C M. Importance and limits of RNA/DNA ratios as a measure of nutritional condition in fish larvae[M]//Watanabe Y, Yamashita Y, Oozeki Y. Survival Strategies in Early Life Stages of Marine Resources. Rotterdam: A. A. Balkema, 1996: 141–151.
[70] Canino M F. Effects of temperature and food availability on growth and RNA/DNA ratios of walleye pollock *Theragra chalcogramma* (Pallas) eggs and larvae[J]. J Exp Mar Biol Ecol, 1994, 175(1): 1–16.
[71] Ferron A, Leggett W C. An appraisal of condition measures for marine fish larvae[J]. Adv Mar Biol, 1994, 30: 217–303.
[72] Comabella Y, Mendoza R, Aguilera C, et al. Digestive enzyme activity during early larval development of the Cuban gar *Atractosteus tristoechus*[J]. Fish Physiol Biochem, 2006, 32(2): 147–157.
[73] Morais S, Cahu C, Zambonino-Infante J L, et al. Dietary TAG source and level affect performance and lipase expression in larval sea bass (*Dicentrarchus labrax*)[J]. Lipids, 2004, 39(5): 449–458.
[74] Moyano F J, Díaz M, Alarcón F J, et al. Characterization of digestive enzyme activity during larval development of gilthead seabream (*Sparus aurata*)[J]. Fish Physiol Biochem, 1996, 15(2): 121–130.
[75] Cara J B, Moyano F J, Cárdenas S, et al. Assessment of digestive enzyme activities during larval development of white bream[J]. J Fish Biol, 2003, 63(1): 48–58.
[76] Alvarez-González C A, Moyano-López F J, Civera-Cerecedo R, et al. Development of digestive enzyme activity in larvae of spotted sand bass *Paralabrax maculatofasciatus*. 1. Biochemical analysis[J]. Fish Physiol Biochem, 2008, 34(4): 373–384.
[77] Kolkovski S. Digestive enzymes in fish larvae and juveniles--implications and applications to formulated diets[J]. Aquaculture, 2001, 200(1–2): 181–201.
[78] Ribeiro L, Zambonino-Infante J L, Cahu C, et al. Development of digestive enzymes in larvae of *Solea senegalensis*, Kaup 1858[J]. Aquaculture, 1999, 179(1–4): 465–473.
[79] Gawlicka A, Parent B, Horn M H, et al. Activity of digestive enzymes in yolk-sac larvae of Atlantic halibut (*Hippo-*

glossus hippoglossus): indication of readiness for first feeding[J]. Aquaculture, 2000, 184(3–4): 303–314.

[80] Kvåle A, Mangor-Jensen A, Moren M, et al. Development and characterisation of some intestinal enzymes in Atlantic cod (*Gadus morhua* L.) and Atlantic halibut (*Hippoglossus hippoglossus* L.) larvae[J]. Aquaculture, 2007, 264(1–4): 457–468.

[81] Cuvier-Péres A, Kestemont P. Development of some digestive enzymes in Eurasia perch larvae *Perca fluviatilis*[J]. Fish Physiol Biochem, 2002, 24(4): 279–285.

[82] Alvarez-González C A, Cervantes-Trujano M, Tovar-Ramírez D, et al. Development of digestive enzymes in California halibut *Paralichthys californicus* larvae[J]. Fish Physiol Biochem, 2006, 31(1): 83–93.

[83] Chen B N, Qin J G, Kumar M S, et al. Ontogenetic development of digestive enzymes in yellowtail kingfish *Seriola lalandi* larvae[J]. Aquaculture, 2006, 260(1–4): 264–271.

[84] Gisbert E, Giménez G, Fernández I, et al. Development of digestive enzymes in common dentex *Dentex dentex* during early ontogeny[J]. Aquaculture, 2009, 287(3–4): 381–387.

[85] Babaei S S, Kenari A A, Nazari R, et al. Developmental changes of digestive enzymes in Persian sturgeon (*Acipenser persicus*) during larval ontogeny[J]. Aquaculture, 2011, 318(1–2): 138–144.

[86] Salze G, McLean E, Craig S R. Pepsin ontogeny and stomach development in larval cobia[J]. Aquaculture, 2012, 324–325: 315–318.

[87] Farhoudi A, Abedian Kenari A M, Nazari R M, et al. Changes of digestive enzymes activities in common carp (*Cyprinus carpio*) during larval ontogeny[J]. Iran J Fish Sci, 2013, 12(2): 320–334.

[88] Pradhan P K, Jena J, Mitra G, et al. Ontogeny of the digestive enzymes in butter catfish *Ompok bimaculatus* (Bloch) larvae[J]. Aquaculture, 2013, 372–375: 62–69.

[89] Caruso G, Denaro M G, Caruso R, et al. Changes in digestive enzyme activities of red porgy *Pagrus pagrus* during a fasting-refeeding experiment[J]. Fish Physiol Biochem, 2014, 40(5): 1373–1382.

[90] Suzer C, Aktülün S, Çoban D, et al. Digestive enzyme activities in larvae of sharpsnout seabream (*Diplodus puntazzo*)[J]. Comp Biochem Physiol A: Mol Integr Physiol, 2007, 148(2): 470–477.

[91] Cahu C, Zambonino Infante J L. Early weaning of sea bass (*Dicentrarchus labrax*) larvae with a compound diet: effect on digestive enzymes[J]. Comp Biochem Physiol A: Physiol, 1994, 109(2): 213–222.

[92] Lazo J P, Mendoza R, Holt G J, et al. Characterization of digestive enzymes during larval development red drum (*Sciaenops ocellatus*)[J]. Aquaculture, 2007, 265(1–4): 194–205.

[93] Kim B G, Divakaran S, Brown C L, et al. Comparative digestive enzyme ontogeny in two marine larval fishes Pacific threadfin (*Polydactylus sexfilis*) and bluefin trevally (*Caranx melampygus*)[J]. Fish Physiol Biochem, 2001, 24(3): 225–241.

[94] Srichanun M, Tantikitti C, Vatanakul V, et al. Digestive enzyme activity during ontogenetic development and effect of live feed in green catfish larvae (*Mystus nemurus* Cuv. & Val.)[J]. Songklanakarin J Sci Technol, 2012, 34(3): 247–254.

[95] Mendoza R, Aguilera C, Montemayor J, et al. Studies on the physiology of *Atractosteus spatula* larval development and its applications to early weaning onto artificial diets[C]// Cruz-Suárez L E, Ricque-Marie D, Tapia-Salazar M, et al. Avances en Nutrición Acuícola VI. Memorias del VI Simposium Internacional de Nutrición Acuícola. 3 al 6 de Septiembre del 2002. Cancún, Quintana Roo, México, 2002.

[96] Tong X H, Xu S H, Liu Q H, et al. Digestive enzyme activities of turbot (*Scophthalmus maximus* L.) during early development stages under culture condition[J]. Fish Physiol Biochem, 2012, 38(3): 715–724.

[97] Suzer C, Kamacı H O, Çoban D, et al. Functional changes in digestive enzyme activities of meagre (*Argyrosomus regius*; Asso, 1801) during early ontogeny[J]. Fish Physiol Biochem, 2013, 39(4): 967–977.

[98] Ma Z H, Guo H Y, Zheng P L, et al. Ontogenetic development of digestive functionality in golden pompano *Trachinotus ovatus* (Linnaeus 1758)[J]. Fish Physiol Biochem, 2014, 40(4): 1157–1167.

[99] Moguel-Hernández I, Peña R, Nolasco-Soria H, et al. Development of digestive enzyme activity in spotted rose snapper, *Lutjanus guttatus* (Steindachner, 1869) larvae[J]. Fish Physiol Biochem, 2014, 40(3): 839–848.

[100] He T, Xiao Z Z, Liu Q H, et al. Ontogeny of the digestive tract and enzymes in rock bream *Oplegnathus fasciatus* (Temminck et Schlegel 1844) larvae[J]. Fish Physiol Biochem, 2012, 38(2): 297–308.

[101] Zambonino-Infante J L, Cahu C L. Development and response to a diet change of some digestive enzymes in sea bass (*Dicentrachus labrax*) larvae[J]. Fish Physiol Biochem, 1994, 12(5): 399–408.

[102] Zhang Y L, Wu Q W, Hu W H, et al. Changes in digestive enzyme activities during larval development of Chinese loach *Paramisgurnus dabryanus* (Dabry de Thiersant, 1872)[J]. Fish Physiol Biochem, 2015, 41(6): 1577–1585.

[103] Faulk C K, Holt G J. Early weaning of southern flounder, *Paralichthys lethostigma*, larvae and ontogeny of selected digestive enzymes[J]. Aquaculture, 2009, 296(3–4): 213–218.

[104] López-Ramírez G, Cuenca-Soria C A, Alvarez-González C A, et al. Development of digestive enzymes in larvae of Mayan cichlid *Cichlasoma urophthalmus*[J]. Fish Physiol Biochem, 2011, 37(1): 197–208.

[105] Bolasina S, Pérez A, Yamashita Y. Digestive enzymes

activity during ontogenetic development and effect of starvation in Japanese flounder, *Paralichthys olivaceus*[J]. Aquaculture, 2006, 252(2–4): 503–515.
[106] Oozeki Y, Bailey K M. Ontogenetic development of digestive enzyme activities in larval walleye pollock, *Theragra chalcogramma*[J]. Mar Biol, 1995, 122(2): 177–186.
[107] Zhang Y L, Fan Q X, Peng C, et al. Changes of digestive enzymes and alkaline phosphatase specific activities in *Misgurnus anguillicaudatus* during the development of early larval ontogeny[J]. Freshwater Fisheries, 2013, 43(1): 19–23. [张云龙, 樊启学, 彭聪, 等. 泥鳅仔稚鱼发育期间消化酶及碱性磷酸酶比活力的变化[J]. 淡水渔业, 2013, 43(1): 19–23.]
[108] Tengjaroenkul B, Smith B J, Caceci T, et al. Distribution of intestinal enzyme activities along the intestinal tract of cultured Nile tilapia, *Oreochromis niloticus* L.[J]. Aquaculture, 2000, 182(3–4): 317–327.
[109] Zambonino-Infante J L, Cahu C L. Ontogeny of the gastrointestinal tract of marine fish larvae[J]. Comp Biochem Physiol C: Toxicol Pharmacol, 2001, 130(4): 477–487.
[110] Martínez-Lagos R, Tovar-Ramírez D, Gracia-López V, et al. Changes in digestive enzyme activities during larval development of leopard grouper (*Mycteroperca rosacea*)[J]. Fish Physiol Biochem, 2014, 40(3): 773–785.
[111] Uscanga-Martínez A, Perales-García N, Álvarez-González C A, et al. Changes in digestive enzyme activity during initial ontogeny of bay snook *Petenia splendida*[J]. Fish Physiol Biochem, 2011, 37(3): 667–680.
[112] Stroband H W J, van der Meer H, Timmermans L P M. Regional functional differentiation in the gut of grass crap, *Ctenopharngodon idella* (Val.)[J]. Histochemistry, 1979, 64(3): 149–156.
[113] Copeland R A. Structural component of enzymes[M]//Enzymes: A Practical Introduction to Structure, Mechanism, and Data Analysis. New York: John Wiley & Sons, Inc., 2002: 35–65.
[114] Zambonino-Infante J L, Gisbert E, Sarasquete C, et al. Ontogeny and physiology of the digestive system of marine fish larvae[M]//Feeding and Digestive Function of Fishes. New Delhi: Oxford & IBH Publishing Co. Pvt. Ltd, 2008.

Allometric growth and ontogenetic changes in nucleic acids and digestive enzymes during the early life stage in fish species: A review

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Abstract: The early life stage is a critical period in fish species since complicated physiological and morphological changes and often massive mortalities occur at this stage. Studies of the growth patterns and physiological characteristics during the early life stage often uncover lethal factors in this stage, and the information gained can lead to improvements in survival rates during larval production. Allometric growth can be used as an indicator for larval production, and fish experience a change in shape in relation to increases in their ability to perform vital biological functions needed for survival during their early life stage. The RNA/DNA ratio is a sensitive indicator of growth rates, which can be used to evaluate growth potential and nutritional condition, as well as to determine critical periods in the larval stage. Specifically, studies on the development of the digestive tract and digestive capability of the organism can be used as an indicator of nutritional status at an early life stage, thereby providing information useful either for improving feeding protocols in larviculture, suggesting more suitable food items, or designing feasible larval rearing procedures. Through a review of previous studies, this article summarizes information on allometric growth and ontogenetic changes in nucleic acids and digestive enzymes during the early life stage of fish species. It is hoped that this review might revive interest in conducting investigations of the early life stage of fish species, and accordingly we provide some basic information meant for future studies

Key words: early life stage; allometric growth; nucleic acids; digestive enzymes; ontogeny

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