

# 四指马鲛(*Eleutheronema tetradactylum*)

## 消化系统胚后发育组织学观察

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**摘要** 运用组织学切片技术研究四指马鲛(*Eleutheronema tetradactylum*)出膜后 1–30 d (Day after hatching, DAH)仔鱼的消化系统形态和结构的变化。结果显示,在温度 29–32℃、盐度 25–28、溶氧 4.80–5.5 mg/L、pH 8.0–8.3 条件下,1 DAH 仔鱼消化管尚未分化,由紧贴腹壁和卵黄囊的肠管组成。卵黄囊在 3 DAH 时完全吸收完毕,仔鱼开口摄食,消化管也与外界相通,此后逐渐分化出食道、胃部和肠道,一定程度上能自主消化吸收食物维持自身生长,逐渐从内源性营养期过渡为外源性营养期。15 DAH 时出现幽门盲囊和胃腺,消化道结构和功能成分进一步发育完善,消化能力显著提高,30 DAH 仔鱼消化道具备与成体相似的结构和功能。肝脏和胰腺分别在 2 DAH 和 5 DAH 时分化,随着仔鱼的生长而快速发育,至 30 DAH 时具备与成体相似的结构和功能。四指马鲛消化系统的发育表现为结构与功能密切联系且逐渐发育成熟的特点。本研究根据四指马鲛消化系统的发育特点讨论了育苗过程中的三大危险期并提出应对措施。

**关键词** 四指马鲛; 消化系统; 胚后发育

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四指马鲛(*Eleutheronema tetradactylum*)隶属鲭形目(Mugiliformes)、马鲛亚目(Polynemoidei)、马鲛科(Polynemidae)、四指马鲛属(孙典荣等, 2013), 主要分布于澳大利亚西海岸(Horne *et al.*, 2013; Moore *et al.*, 2011; Newman *et al.*, 2011)、太平洋–印度洋海域(Motomura *et al.*, 2002), 我国东海、南海沿海地区(Wang *et al.*, 2014)也有分布, 是一种生长迅速、营养价值较好的食用鱼类。目前, 该鱼在我国大陆东南沿海地区已有人工养殖。在人工育苗过程中, 掌握幼体

不同时期的适口饵料以及制定合适的投饲策略是提高鱼苗成活率的关键, 而鱼类消化系统在控制食物的消化吸收、能量收支起着关键作用(dos Santos *et al.*, 2014)。研究消化系统结构和功能发育常作为监测仔鱼生长过程中营养需求和消化能力的变化规律的一种手段, 进而优化仔鱼的培育条件(Micale *et al.*, 2010)。关于不同种属鱼类消化系统胚后发育有不少报道(区又君等, 2011、2015; Yang *et al.*, 2010; 关海红等, 2007; 苏友禄等, 2008), 而有关四指马鲛消化道的

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胚后发育观察在国内外尚未见有报道。本研究通过观察出膜后 1–30 d (Day after hatching, DAH)四指马鲛消化道的结构变化,旨在探讨该鱼消化机能发育规律,同时掌握其消化生理和饵料系列更换的特点,从而提高育苗的成活率。

## 1 材料与方法

### 1.1 样本来源

四指马鲛受精卵和初孵仔鱼由本课题组在中国水产科学研究院南海水产研究所珠海试验基地于 2015 年 6–12 月培育所得,仔鱼在室外土池培育,温度为 29–32℃,盐度为 25–28,溶氧为 4.80–5.50 mg/L, pH 为 8.00–8.30, 氨氮含量为 0.20–0.40 mg/L, 亚硝酸盐含量为 0.05–0.015 mg/L。饵料系列为轮虫、小球藻、枝角类(3–15 DAH)→卤虫无节幼体和部分红虫(16–30 DAH)→粉状配合饲料和鱼肉糜或贝肉糜(31–50 DAH)。期间通过对仔鱼 1–30 DAH 阶段进行连续采样,每次采样 30 尾,用 10%甲醛固定。

### 1.2 切片制备

所取样本经过充分的流水冲洗后进行梯度酒精脱水、二甲苯透明、石蜡包埋、切片(5 μm)、HE 染色、中性树脂封片。用 ZEISS 型光学显微镜对已染色的切片进行观察并拍照。

## 2 结果

### 2.1 消化道发育

**2.1.1 1–3 DAH 前期仔鱼** 1 DAH 仔鱼全长为(1.84±0.22) mm,卵黄囊被吸收 1/2,油球渐变为卵圆形,靠近卵黄囊最底部。光镜观察显示,其消化管尚未分化,由紧贴腹壁和卵黄囊的肠管组成,内含细胞比较模糊。此时,口咽腔、肛门尚未形成,卵黄囊体积较大,HE 染色呈深红色(图 1-A)。2 DAH 仔鱼肠管增长,口腔张开形成口裂,卵黄囊体积减少至约为原来的 1/2,肠管向中间扩展,末端与外界形成通路,肠腔内开始形成黏膜上皮层,未见纹缘状结构。靠近卵黄囊前端可见食道原基,其内细胞较密集,外层形成纤维膜,尚未与口咽腔、胃肠道相通。随着卵黄囊的吸收,腹腔体积增大,靠近中部出现胃原基并出现空腔,其内可见黏膜层及单层柱状上皮细胞(图 1-B)。大部分仔鱼在 3 DAH 开口摄食,此时卵黄囊完全消失,消化管道进一步发育,食道接口咽腔和胃部已相通,但仍处于细胞混集阶段,未形成明显的黏膜层。胃肠相连并未完全分化为单独的胃部和肠道,而内部已形成较为丰富的黏膜层并出

现皱褶结构,黏膜上单层柱状上皮细胞清晰可见。

**2.1.2 4–14 DAH 后期仔鱼** 4 DAH 仔鱼消化道与外界相通,口咽腔、食道、胃部、肠道、肛门分化比较明显。食道黏膜分化出复层上皮,末端与胃部形成一个不明显的缢痕。胃腔扩展,肠道增长、增粗,但未形成曲折(图 1-C)。5 DAH 仔鱼食道复层黏膜上皮尤为清晰,未见杯状细胞的分化,与黏膜相连处可见一层较薄的肌肉层(图 1-D);胃部仍无区域的分化,黏膜皱褶变得扁平整齐;肠管黏膜上皮未见杯状细胞,含多量的嗜酸性颗粒(图 1-E)。7 DAH 仔鱼食道变化尤为明显,形成纵行的黏膜皱褶,上皮间出现少量圆形空泡状的杯状细胞(图 1-F),黏膜层以外分化出黏膜下层、肌肉层、外膜,结构已清晰可辨,与胃部连接处黏膜复层上皮过渡为单层柱状上皮;胃部开始贲门、幽门、胃体和盲囊区域的分化,其中,胃体最为膨大,幽门与贲门区和胃体区分界较明显,内含 2–3 条纵行的黏膜皱褶。胃体和盲囊区域由于食物填充而使黏膜平整无皱褶。肠道黏膜皱褶增多。9 DAH 仔鱼食道杯状细胞数量增多,胃肠管壁分化出黏膜下层、肌肉层和外膜(图 1-G, H)。肠道含 12–15 个黏膜皱褶,皱褶明显增高变宽。10–14 DAH 仔鱼消化道变化不大,胃部尚未见胃腺分化(图 1-I, J)。

**2.1.3 15–30 DAH 稚鱼期** 15 DAH 仔鱼消化道出现胃腺和幽门盲囊的分化,消化管管壁包括黏膜层(上皮、固有层、黏膜肌)、黏膜下层、肌肉层(环肌和纵肌)、外膜分化完整。在幽门部与肠道交汇处出现 2 个幽门盲囊管腔,腔内结构与肠道相似,有 3–5 个黏膜皱褶,上皮间已有少量杯状细胞,未见纹缘状结构(图 1-K)。肠道有 2 处明显的曲折,使前、中、后肠分区明显。前肠绒毛最丰富,较为细长,其上分布很多杯状细胞(图 1-L)。中肠和后肠绒毛和杯状细胞数量相当。胃部黏膜皱褶结构极为宽大,除幽门部外均有胃腺的分布,以胃体部区域最为丰富,胃腺均为单管状,分布于黏膜固有层内,与上皮临近(图 2-A),胃腺开口于胃小凹。幽门部肌肉层尤为发达,不含胃腺伸往腔内的黏膜上皮细胞十分整齐密集。17 DAH 仔鱼肠道黏膜分化完整,杯状细胞数量显著增多,但仍含有部分嗜酸性颗粒。20 DAH 仔鱼食道杯状细胞数量极多(图 2-B),黏膜皱褶变得宽长,肌肉层环肌加厚。胃部更为膨大,大量的胃腺与黏膜交织成网状。幽门盲囊管腔增加至 6–8 个,单个管腔增大,内含的皱褶同样变得宽长,上皮杯状细胞增多,肠道绒毛上皮可见纹缘状结构(图 2-C)。23–30 DAH 仔鱼消化道结构成分与成体差异不大,消化管管壁增厚,黏膜皱褶增多,食道和肠道上皮杯状细胞数量继续增多,胃部胃腺、胃小凹增多是基本特点(图 2-D)。

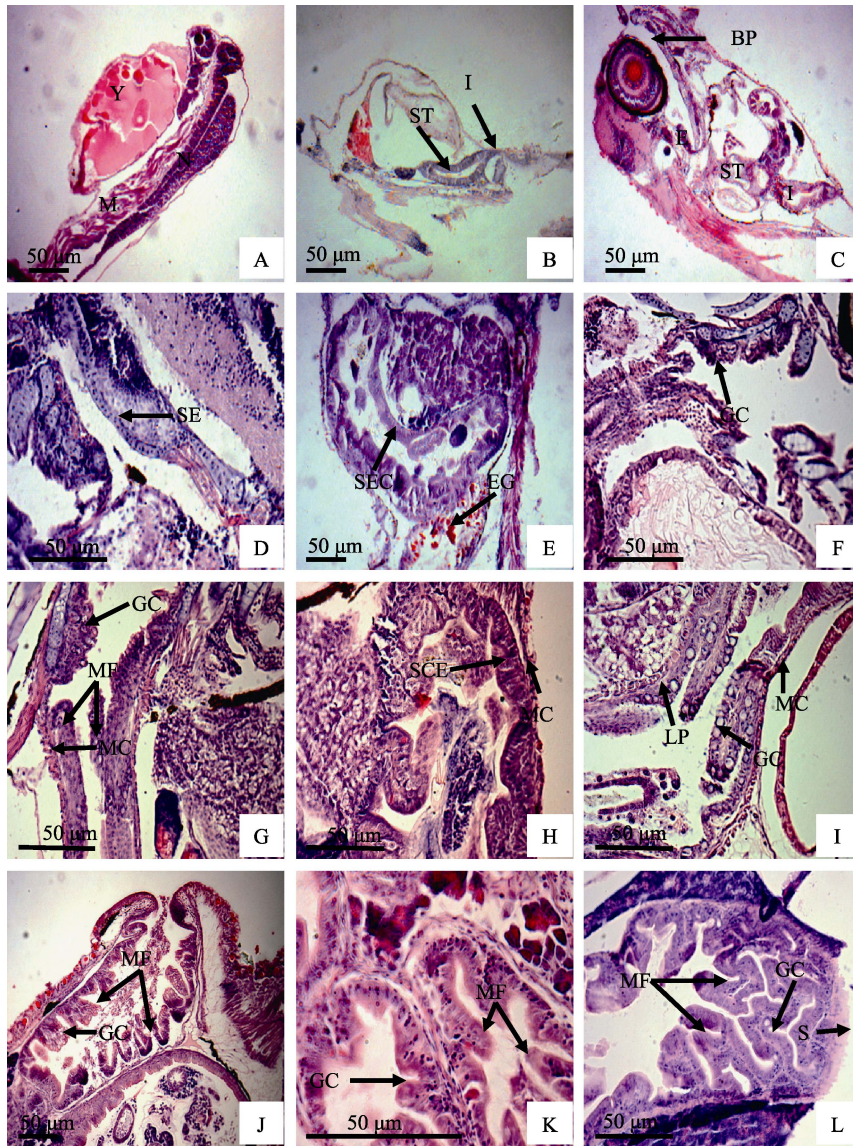


图 1 四指马鲛仔稚鱼消化系统发育组织学结构(HE 染色)

Fig.1 Histological observation of the development of the digestive system of *E. tetradactylum* (HE staining)

A: 1 DAH 仔鱼消化道整体结构, 纵切; B: 2 DAH 仔鱼消化管整体结构, 纵切; C: 4 DAH 仔鱼食道、胃、肠的分化, 纵切; D: 5 DAH 仔鱼食道复层黏膜上皮, 纵切; E: 5 DAH 仔鱼胃单层柱状黏膜上皮以及肠腔内嗜酸颗粒, 纵切; F: 7 DAH 仔鱼食道黏膜上皮杯状细胞的分化, 纵切; G: 9 DAH 仔鱼食道的黏液细胞和黏膜皱褶, 纵切; H: 9 DAH 仔鱼胃黏膜皱褶, 纵切; I: 12 DAH 仔鱼食道杯状细胞和肌肉层, 纵切; J: 12 DAH 仔鱼肠腔内绒毛结构和杯状细胞, 纵切; K: 15 DAH 仔鱼幽门盲囊黏膜皱褶和杯状细胞, 横切; L: 15 DAH 仔鱼肠道绒毛和杯状细胞, 横切

BP: 口咽腔; E: 食道; EG: 嗜伊红颗粒; GC: 杯状细胞; GG: 胃腺; I: 肠道; LP: 固有层; M: 肌肉组织; MC: 肌肉层; MF: 黏膜皱褶; N: 脊索; S: 外膜; SE: 复层上皮; SEC: 单层柱状上皮; SM: 黏膜下层; ST: 胃部; Y: 卵黄囊

A: Longitudinal section of digestive tract of 1 DAH larvae; B: Longitudinal section of digestive tract of 2 DAH larvae; C: Longitudinal section of esophagus, stomach and intestine of 4 DAH larvae; D: Longitudinal section of stratified epithelium in esophagus of 5 DAH larvae; E: Longitudinal section of simple columnar epithelium in stomach and the eosinophilic granular in intestine of 5 DAH larvae; F: Longitudinal section of goblet cells in esophagus of 7 DAH larvae; G: Longitudinal section of mucous cells and mucosal folds in esophagus of 9 DAH larvae; H: Longitudinal section of mucosal folds in stomach of 9 DAH larvae; I: Longitudinal section of goblet cells and muscle layer in esophagus of 12 DAH larvae; J: Longitudinal section of mucosal folds and goblet cells in intestine of 12 DAH larvae; K: Transverse section of mucosal folds and goblet cells in pyloric caeca of 15 DAH larvae; L: Transverse section of mucosal folds and goblet cells in intestine of 15 DAH larvae

BP: Buccopharynx; E: Esophagus; EG: Eosinophilic granular; GC: Goblet cell; GG: Gastric gland; I: Intestine; LP: Lamina propria; M: Musculature; MC: Muscle layer; MF: Mucosal fold; N: Notochord; S: Serosal; SE: Stratified epithelium; SEC: Simple columnar epithelium; SM: Submucosal; ST: Stomach; Y: Yolk sac



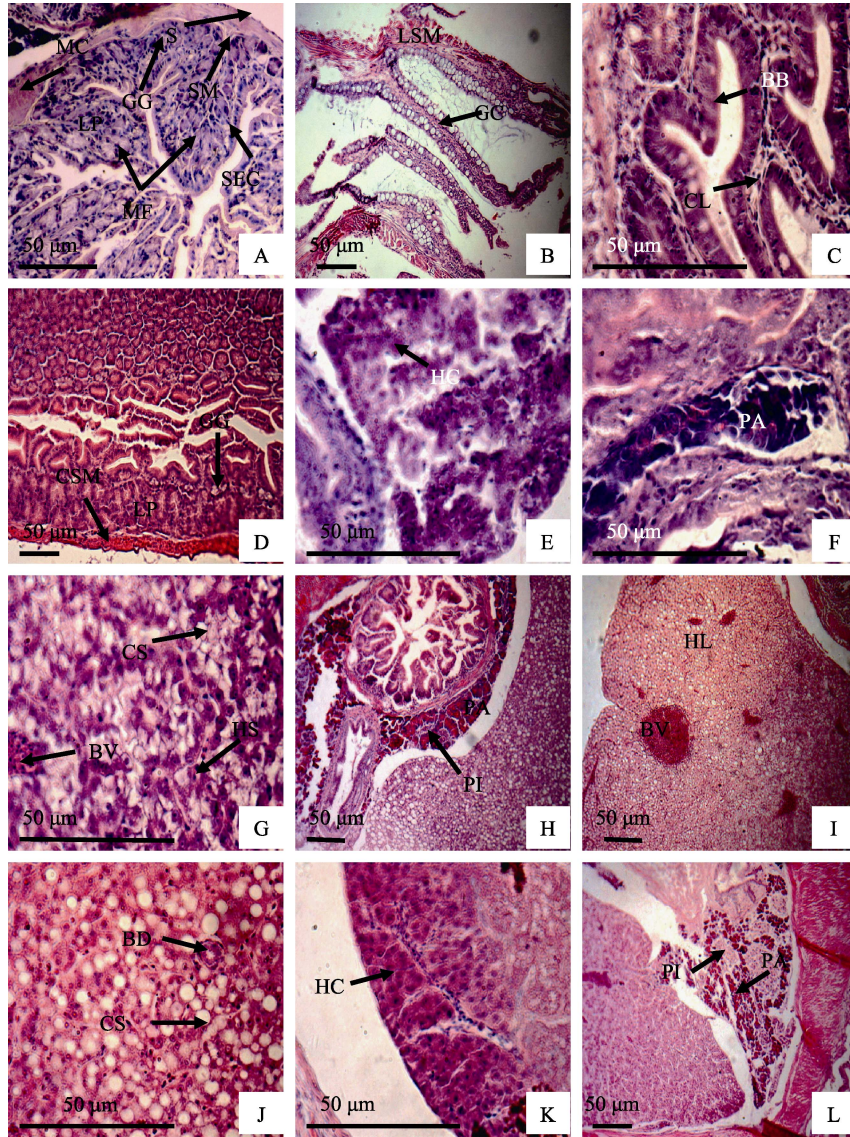


图 2 四指马鲛仔稚鱼消化系统发育组织学结构(HE 染色)

Fig.2 Histological observation of the development of the digestive system of *E. tetradactylum* (HE staining)

A: 15 DAH 仔鱼胃管壁整体结构, 横切; B: 20 DAH 仔鱼食道黏膜和肌肉层结构, 纵切; C: 20 DAH 仔鱼肠绒毛纹缘状结构, 横切; D: 30 DAH 仔鱼胃部胃腺结构, 纵切; E: 5 DAH 仔鱼分化的肝细胞, 纵切; F: 5 DAH 仔鱼胃肠交界处的胰腺组织, 纵切; G: 15 DAH 仔鱼肝脏肝血窦、空泡和血管结构, 横切; H: 15 DAH 仔鱼肝胰脏结构, 纵切; I: 23 DAH 仔鱼肝小叶, 横切; J: 23 DAH 仔鱼肝脏内胆管结构, 横切; K: 30 DAH 仔鱼致密的肝细胞结构, 横切; L: 30 DAH 仔鱼肝胰脏结构, 纵切  
 BB: 纹缘状; BD: 胆管分支结构; BV: 血管; CL: 中央乳糜管; CSM: 环肌; CS: 空泡结构; GC: 杯状细胞; GG: 胃腺; HC: 肝细胞; HL: 肝小叶; HS: 肝血窦; LP: 固有层; LSM: 纵肌; MC: 肌肉层; MF: 黏膜皱褶; PA: 胰腺; PI: 胰岛; S: 外膜; SCE: 单层柱状上皮; SM: 黏膜下层

A: Transverse section of tube wall of stomach of 15 DAH larvae; B: Longitudinal section of mucosal folds and muscle layer in esophagus of 20 DAH larvae; C: Transverse section of brush border in intestine of 20 DAH larvae; D: Longitudinal section of gastric gland in stomach of 30 DAH larvae; E: Longitudinal section of hepatic cells in 5 DAH larvae; F: Longitudinal section of pancreas between stomach and intestine of 5 DAH larvae; G: Transverse section of liver of 15 DAH larvae, including hepatic sinusoid, cavity structure and blood vessels; H: Longitudinal section of hepatopancreas of 15 DAH larvae; I: transverse section of hepatic lobule in 23 DAH larvae; J: transverse section of bile duct in 23 DAH larvae; K: Transverse section of hepatic cells in liver of 30 DAH larvae; L: longitudinal section of hepatopancreas in 30 DAH larvae

BB: Brush border; BD: Branch of bile duct; BV: Blood vessel; CL: Central lacteals; CSM: Circular layers of striated muscle; CS: Cavity structure; GC: Goblet cell; GG: Gastric gland; HC: Hepatic cell; HL: Hepatic lobule; HS: Hepatic sinusoid; LP: Lamina propria; LSM: Longitudinal layers of striated muscle; MC: Muscle layer; MF: Mucosal fold; PA: Pancreas; PI: Pancreas islet; S: Serosa; SCE: Single columnar epithelium; SM: Submucosa

## 2.2 肝脏和胰腺的发育

四指马鲛消化道内无独立的胰脏器官,随着生长发育,在肝脏、胃、幽门盲囊、肠等的系膜交界处呈弥散性分布,其中,与肝脏连在一起的称为肝胰脏,在其余消化管壁系膜分布的为胰腺组织。在2 DAH时形成肝脏原基,原基在卵黄囊近脊椎处,数十个肝细胞排列在一起,呈“三角形”细胞团,细胞之间界限模糊。3 DAH时,肝细胞数量增多,细胞团体积增大。5 DAH仔鱼肝脏器官有了明显的生长,表现为肝细胞体积变大并依次排列形成肝细胞板结构,相邻肝板间有清晰可见的空隙结构,称为肝血窦(图2-E);此时,肝脏周围以及胃和肠系膜交界处出现胰腺细胞团,细胞被染成深紫色,界限比较清晰(图2-F)。9 DAH时,肝脏进一步发育,肝板内细胞增多,排列更为紧密,细胞呈圆形,细胞核很明显,位于中央。肝板周围出现许多空泡结构。肝脏周围的胰腺组织可明显分辨出浅紫色的胰岛区域,胰岛内胰岛细胞形状不规则,胞核不明显,为胰腺内分泌部。胰岛周围是深紫色的外分泌部腺泡,腺泡细胞体积增大,个别可见细胞核。15 DAH时,肝脏开始分出左右两叶,肝细胞数量明显增多、体积变小,呈圆形,肝板结构增多形成肝索结构,肝血窦和肝板之间空泡增多(图2-G),胰腺组织在肝脏周围、胃、肠系膜交界处均有分布,其基本结构变化不大(图2-H)。17 DAH时,肝脏可见中央静脉,局部可见毛细血管和静脉血管管腔,肝血窦内可见红细胞。23 DAH时,肝脏结构发育基本与成体相似,肝细胞紧密连接,血窦增多(图2-I, J),此时,幽门盲囊与肠道交界处以及幽门盲囊管腔之间的胰腺进一步发育,胰腺细胞更为密集。30 DAH时,仔鱼肝脏进一步发育成熟,肝体积增大,肝细胞数量极多,形成致密的肝板结构(图2-K)。胰腺组织结构也基本与成体相似,分布范围不变,但各区域的胰腺区域体积增大,胰腺组织内的外分泌部和内分泌部分化明显(图2-L)。

## 3 讨论

### 3.1 四指马鲛消化道早期发育阶段的划分

本研究发现,四指马鲛消化道的发育具有明显的阶段性特征。1-3 DAH,仔鱼消化道结构简单呈直线状,未与外界相通,表明仔鱼存活所需营养物质全部由卵黄囊提供,为内源性营养期,此阶段仔鱼生长情况是否良好与亲鱼质量和人工孵化技术密切相关。4-14 DAH,仔鱼开口摄食,消化管与外界相通,逐渐分化出口咽腔、食道、胃、肠,同时,肝脏、胰腺

也开始发育,一定程度上能自主消化吸收食物维持自身生长,从短暂的混合营养期(4-7 DAH)过渡为外源性营养期。15-30 DAH为稚鱼期,随着幽门盲囊和胃腺的出现,消化系统结构和功能逐渐发育为与成体相似,消化能力显著提高,进入快速生长阶段。与四指马鲛消化道发育特点类似的还有其他肉食性鱼类。条石鲷(*Oplegnathus fasciantus*)内源性营养期、外源性营养期和稚鱼期的划分分别是1-3 DAH、4-18 DAH和19-35 DAH(区又君等,2014);卵形鲳鲹(*Trachinotus ovatus*)分别是1-2 DAH、6-17 DAH(3-5 DAH为混合营养期)、18-22 DAH(区又君等,2011);鲇(*Silurus asotus*)1-3 DAH为内源性营养期,4-6 DAH为混合营养期,6-8 DAH进入外源性营养期并进入加速生长期,11 DAH出现胃腺,进入稚鱼期(蒲红宇等,2004)。而大黄鱼(*Pseudosciaena crocea*)1-5 DAH为内源性营养期,6-18 DAH为外源性营养期,19-31 DAH为稚鱼期,各阶段持续时间均比四指马鲛略长(徐晓津等,2010)。杂食性鱼类如普安银鲫(*Carassius auratus*)1-2 DAH为内源性营养期,3-4 DAH为混合营养期,5 DAH进入外源性营养期,15 DAH后进入快速生长期(姚俊杰等,2013),而草食性的草鱼(*Ctenopharyngodon idellus*)1-4 DAH为内源性营养期,5 DAH过渡为外源性营养,9-17 DAH为稚鱼期(阮国良等,2012),均与四指马鲛有所不同。由此可发现,鱼类消化道早期发育阶段的划分与种属特性和食性密切相关,另外,普安银鲫和草鱼同为无胃鱼类,其仔稚鱼阶段消化道的形态学变化则主要表现为肠在形态、组织上的进一步分化,而肉食性有胃鱼类进入稚鱼期逐渐形成功能完善的胃,推测胃部和肠道发育的差异也是消化道发育阶段存在差异的原因之一。哲罗鱼(*Hucho taimen*)为凶猛的肉食性鱼类,受精30 d后破膜,要经历较长的内源性营养期(1-24 DAH),直至30 DAH才进入完全外源性营养期(关海红等,2007),可能是由于该鱼喜栖息于冷水环境(孵化温度为7-8℃,仔鱼培育温度为3-14℃),即使在胚胎期已形成原始消化管,但发育速度较慢,仍需借助相当体积的卵黄囊维持较长时间的营养供给以缓解消化道发育缓慢带来的代谢压力。

### 3.2 四指马鲛消化道早期发育的结构特征

鱼类消化道结构与其食性相关,鱼体处于不同发育阶段,其消化功能与其结构相适应。在1-3 DAH内,四指马鲛消化道结构极其简单,仅靠卵黄囊提供营养物质,这与大海马(*Hippocampus kuda*)仔鱼的消化道特点不同,大海马没有经历由卵黄囊提供营养的

内源性营养阶段而直接进入混合营养期,这与其为卵胎生及 1-2 DAH 仔鱼已具有较完善的摄食和消化器官、可独立摄食的特性有关(林强等, 2007)。4-14 DAH 后,四指马鲛开口摄食,消化道有明显变化,逐渐分化出口咽腔、食道、胃、肠、肛门,随着生长,摄食能力加强,消化管扩张,出现黏膜皱褶、杯状细胞等与消化吸收能力匹配的变化,与多种属鱼类仔鱼消化道发育特征相似,如黄尾鲷(*Seriola lalandi*) (Chen *et al.*, 2006)、大菱鲆(*Scophthalmus maximus*) (陈慕雁等, 2006)、军曹鱼(*Rachycentron canadum*) (苏友禄等, 2008)等。食道、胃、肠内形成的黏膜皱褶对于增大食物容纳量及消化吸收面积有重要意义(勾效伟等, 2008),而四指马鲛 5 DAH 仔鱼肠道出现大量的嗜酸性颗粒,是细胞消化的一种方式(Jany, 1976),其食道和肠道分别在 5、9 DAH 时分化出杯状细胞,具有润滑、辅助食物消化的功能,表明在此阶段(4-14 DAH)的仔鱼经过摄食训练和细胞消化协调,机体过渡到完全外源营养模式,此后消化道开始扩张,摄食能力增强,同时分化出基本的功能组分以协助食物的消化。胃腺和幽门盲囊的出现,标志仔鱼进入稚鱼期。胃腺具有分泌黏液和胃蛋白酶原的功能,使消化食物蛋白成为可能,符合肉食性鱼类的消化特点。从四指马鲛仔鱼出现胃腺的时间(15 DAH)判断该鱼为发育迅速的鱼类,与条石鲷(区又君等, 2015) 12-15 DAH、卵形鲳鲹(区又君等, 2011) 17-18 DAH、有名锤形石首鱼(*Atractoscion nobilis*)(Galaviz *et al.*, 2011) 16 DAH 出现胃腺相似,而黄颡鱼(*Pelteobagrus fulvidraco*)(Yang *et al.*, 2010) 3 DAH 即出现胃腺,绯小鲷(*Pagellus erythrinus*)(Micale *et al.*, 2006)和黄鳍鲷(*Sparus latus*)(王永翠等, 2012)胃腺出现则较迟,分别为 28 DAH 和 37 DAH,而黑点圆鲹(*Sphoeroides annulatus*)(García-Gasca *et al.*, 2006)则 32 DAH 还未出现胃腺,这些差异与种属有关,还可能与培育条件、技术和环境等因素有关。此阶段的四指马鲛仔鱼(15-30 DAH),消化管进一步扩张,固有结构(黏膜层、黏膜下层、肌肉层、外膜)逐渐分化完善,似成体状:食道和肠道黏膜皱褶增加,杯状细胞数量显著增多,胃部膨大并形成完善的分化区域(贲门、幽门、胃体和盲囊胃、幽门盲囊),幽门盲囊的出现使机体摄食和消化能力极大提高,消化道结构功能与机体生长发育形成一个正

反馈效应,从而使机体快速生长成为可能。鱼类肝脏和胰腺发育时间存在种属间的差异,四指马鲛肝脏与胰腺发育不同步且胰腺发育比肝脏要迟,与条石鲷(区又君等, 2015)、卵形鲳鲹(区又君等, 2011)相似。有些鱼类如细鳞鲑(*Brachymystax lenok*)(徐革锋等, 2013)、青龙斑(*Epinephelus coioides*♀×*E. lanceolatus*♂)(吴水清, 2014)<sup>1)</sup>的肝脏和胰脏独立存在,前者在胚胎期已出现肝脏原基并在 2 DAH 时肝细胞不断分化,胰脏原基则在初孵仔鱼肠道背侧出现;后者均在 3 DAH 时出现肝脏和胰脏原基。肝脏是机体内最大的消化腺,具有分泌、储存甚至排泄等功能(许晓娟等, 2009),胰腺中则合成和分泌大量的酶(淀粉酶、脂酶和胰蛋白酶等)(陈慕雁等, 2004),肝脏、胰腺的分化和发育在提高仔稚鱼消化能力方面有重要意义。本研究中,四指马鲛 2 DAH 时已分化出肝脏,在 9 DAH 时出现肝脏空泡结构,且随着仔鱼生长,肝脏内空泡结构增多,至 23 DAH 后,肝脏结构基本与成体相似。Boulhic 等(1992)研究指出,这种空泡结构具有储藏肝糖原的作用,表明进入外源性营养阶段的仔鱼消化道的发育速度开始加快,对摄入的食物进行有效的消化吸收并存储营养物质,以适应在同时加速的机体代谢需求。胰腺在 5 DAH 时发生,随着发育的进行,逐渐分化出外分泌部和内分泌部并扩大分布范围,至 30 DAH 时形成具有分泌能力的成熟组织,胰腺的逐渐发育进一步增强仔鱼的消化能力。

### 3.3 四指马鲛消化道发育规律对仔鱼培育的指导意义

根据四指马鲛消化道发育特点,总结出育苗过程的三个危险阶段。第一阶段为卵黄囊期的仔鱼,此阶段仔鱼的存活完全依靠卵黄物质的营养,受精卵质量和孵化技术的优劣决定了子代仔鱼质量的优劣,常因受精卵质量差以及孵化条件如盐度不适宜的原因造成初孵仔鱼及卵黄囊期间存活率降低(柴学军等, 2011)。有研究表明,采用适宜浓度的葡萄糖溶液和维生素对胚胎及卵黄囊仔鱼进行浸泡,可以提高胚胎孵化率和仔鱼存活率,同时,维生素 C 可降低卵黄囊仔鱼机体的损伤,提高免疫力,从而为整个发育过程中正常的代谢提供保障(熊铎龙等, 2014; 蒋左玉等, 2015)。因此,提高育苗成活率,培育优质的亲鱼和建立最适宜的育苗条件是应对措施之一。第二阶段为

1) Wu SQ. Studies on post-embryonic development of Qinglong grouper (*Epinephelus coioides*♀×*E. lanceolatus*♂) and histochemistry and immunohistochemistry of digestive tract in juveniles. Master's Thesis of Shanghai Ocean University, 2014, 26-34 [吴水清. 斜带石斑鱼(♀)×鞍带石斑鱼(♂)杂交子代早期发育及幼鱼消化道组织化学和免疫组织化学的研究. 上海海洋大学硕士研究生学位论文, 2014, 26-34]



开口期仔鱼,从混合营养期过渡到完全外源性营养期,是否有充足的适口饵料以及预防因饵料混有病原微生物而使仔鱼感染,也是提高仔鱼存活率的关键。因为此阶段仔鱼的消化管管径很小以及管壁结构不完善,从而对饵料有较为严格的要求,淡水臂尾轮虫常作为多种鱼类仔鱼的开口饵料,轮虫经孵化后应用小球藻强化培育 3 d 后再投喂,可降低仔鱼因一直摄食未强化培育的轮虫(缺乏高度不饱和脂肪酸)(梁友等, 2011)而造成机体的营养不足甚至死亡的几率。第三阶段为稚鱼变态期,消化器官和功能组分发育基本完善,摄食和消化能力极大提高,同时残食现象以及仔鱼的自身变化与外界环境条件不相适应等也会造成鱼苗的大量死亡(区又君等, 2014)。根据鱼苗摄食情况制定恰当的投饲策略以及适时的分苗培养是关键,可减少鱼苗的死亡。

综上所述,四指马鲛消化系统的发育速度较快并具有明显的阶段性特征,符合肉食性鱼类消化系统发育的规律,体现消化系统结构功能的发育与自身生长发育和外界环境相协调的特点。而在人工育苗过程中,除了重点掌握根据幼体消化能力的变化做好饲喂管理工作外,优化其他培育条件,如良好水质的维持、病虫害的防治等也是必要的。

## 参 考 文 献

- Boulhic M, Gabaudan J. Histological study of the organogenesis of the digestive system and swim bladder of the Dover sole, *Solea solea* (Linnaeus 1758). *Aquaculture*. 1992, 102(4): 373–396
- Chai XJ, Sun M, Xu YJ. Effects of temperature and salinity on embryonic development of *Nibea japonica*. *South China Fisheries Science*, 2011, 7(5): 43–49 [柴学军, 孙敏, 许源剑. 温度和盐度对日本黄姑鱼胚胎发育的影响. *南方水产科学*, 2011, 7(5): 43–49]
- Chen BN, Qin JG, Kumar MS, *et al.* Ontogenetic development of the digestive system in yellowtail kingfish *Seriola lalandi* larvae. *Aquaculture*, 2006, 256(1–4): 489–501
- Chen MY, Zhang XM. Development of the digestive system in larval, juvenile and young turbot *Scophthalmus maximus*. *Acta Hydrobiologica Sinica*, 2006, 30(2): 236–240 [陈慕雁, 张秀梅. 大菱鲆仔稚幼鱼消化系统发育的组织学研究. *水生生物学报*, 2006, 30(2): 236–240]
- Chen MY, Zhang XM. Recent advances in digestive physiology of marine fish larvae-juvenile. *Marine Fisheries Research*, 2004, 25(3): 81–88 [陈慕雁, 张秀梅. 海水鱼类仔稚鱼消化生理学研究进展. *海洋水产研究*, 2004, 25(3): 81–88]
- dos Santos DCM, do Cupertino CM, Fialho MCQ, *et al.* Quantification of endocrine cells and ultrastructural study of insulin granules in the large intestine of opossum *Didelphis aurita* (Wied-Neuwied, 1826). *Tissue and Cell*, 2014, 46(1): 70–77
- Galaviz MA, García-Gasca A, Drawbridge M, *et al.* Ontogeny of the digestive tract and enzymatic activity in white seabass, *Atractoscion nobilis*, larvae. *Aquaculture*, 2011, 318(1): 162–168
- García-Gasca A, Galaviz MA, Gutiérrez JN, *et al.* Development of the digestive tract, trypsin activity and gene expression in eggs and larvae of the bullseye puffer fish *Sphoeroides annulatus*. *Aquaculture*, 2006, 251(2–4): 366–376
- Gou XW, Ou YJ, Liao R. Histochemical study of digestive system of *Rhabdosargus sarba*. *South China Fisheries Science*, 2008, 4(5): 28–36 [勾效伟, 区又君, 廖锐. 平鲷消化系统形态学、组织学及组织化学研究. *南方水产*, 2008, 4(5): 28–36]
- Guan HH, Kuang YY, Xu W, *et al.* Histological observation on the development of digestive system in *Hucho taimen*. *Chinese Journal of Zoology*, 2007, 42(2): 116–123 [关海红, 匡友谊, 徐伟, 等. 哲罗鱼消化系统器官发生发育的组织学观察. *动物学杂志*, 2007, 42(2): 116–123]
- Horne JB, Momigliano P, van Herwerden L, *et al.* Murky waters: Searching for structure in genetically depauperate blue threadfin populations of Western Australia. *Fisheries Research*, 2013, 146(5): 1–6
- Jany KD. Studies on the digestive enzymes of the stomachless bonefish *Carassius auratus gibelio* (Bloch): Endopeptidases. *Comparative Biochemistry and Physiology B: Biochemistry and Molecular Biology*, 1976, 53(1): 31–38
- Jiang ZY, Yao JJ, Xiong HL, *et al.* Effects of glucose and vitamin C on activities of lipoprotein lipase and hepatic lipase during yolk-sac larva development of *Garassius auratus gibelio*. *Acta Hydrobiologica Sinica*, 2015, 39(1): 73–79 [蒋左玉, 姚俊杰, 熊铧龙, 等. 葡萄糖、维生素 C 对普安银鲫卵黄囊仔鱼发育中 LPL 和 HL 活性的影响. *水生生物学报*, 2015, 39(1): 73–79]
- Lin Q, Lu JY, Zhang B, *et al.* Histological studies on post-embryonic development of digestive system of seahorse *Hippocampus kuda*. *Journal of Tropical Oceanography*, 2007, 26(6): 46–51 [林强, 吕军仪, 张彬, 等. 大海马消化系统胚后发育的形态学及组织学研究. *热带海洋学报*, 2007, 26(6): 46–51]
- Liang Y, Ni Q, Wang YG, *et al.* Research on scale manual reproduction techniques of *Epinephelus moara*. *Fishery Modernization*, 2011, 38(5): 31–34, 41 [梁友, 倪琦, 王印庚, 等. 云纹石斑鱼规模化人工繁育技术研究. *渔业现代化*, 2011, 38(5): 31–34, 41]
- Micale V, Garaffo M, Genovese L, *et al.* The ontogeny of the alimentary tract during larval development in common pandora *Pagellus erythrinus* L. *Aquaculture*, 2006, 251(2–4): 354–365
- Micale V, Levanti MB, Germana A, *et al.* Ontogeny and

- distribution of cholecystokinin-immuno reactive cells in the digestive tract of sharpnose sea bream, *Diplodus puntazzo* (Cetti, 1777), during larval development. *General and Comparative Endocrinology*, 2010, 169(1): 23–27
- Moore BR, Stapley J, Allsop Q, *et al.* Stock structure of blue threadfin *Eleutheronema tetradactylum* across northern Australia, as indicated by parasites. *Journal of Fish Biology*, 2011, 78(3): 923–936
- Motomura H, Iwatsuki Y, Kimura S, *et al.* Revision of the Indo-West Pacific polynemid fish genus *Eleutheronema* (Teleostei: Perciformes). *Ichthyological Research*, 2002, 49(1): 47–61
- Newman SJ, Pember MB, Rome BM, *et al.* Stock structure of blue threadfin *Eleutheronema tetradactylum* across northern Australia as inferred from stable isotopes in sagittal otolith carbonate. *Fisheries Management and Ecology*, 2011, 18(3): 246–257
- Ou YJ, Li JE, Ai L. A study on the histology of digestive system in early life stages of *Oplegnathus fasciatus*. *Journal of South China Agricultural University*, 2015, 36(1): 23–27 [区又君, 李加儿, 艾丽. 条石鲷早期发育阶段消化系统组织学研究. 华南农业大学学报, 2015, 36(1): 23–27]
- Ou YJ, He YL, Li JE. Postembryonic development of digestive system of *Trachinotus ovatus*. *Journal of Oceanography in Taiwan Strait*, 2011, 30(4): 533–539 [区又君, 何永亮, 李加儿. 卵形鲳鲹消化系统的胚后发育. 台湾海峡, 2011, 30(4): 533–539]
- Ou YJ, Li JE, Lin F. First maturation and spawning of cultured *Oplegnathus fasciatus* broodstock in the South China Sea. *South China fisheries Science*, 2014, 10(5): 82–86 [区又君, 李加儿, 林锋. 南海区驯养条石鲷亲鱼的初次性成熟和产卵. 南方水产科学, 2014, 10(5): 82–86]
- Pu HY, Zhai BX, Liu HL. Histological studies on post-embryonic development of digestive system in larval catfish *Silurus asotus*. *Journal of Fishery Sciences of China*, 2004, 11(1): 1–8 [蒲红宇, 翟宝香, 刘焕亮. 鲇仔、稚鱼消化系统胚后发育的组织学观察研究. 中国水产科学, 2004, 11(1): 1–8]
- Ruan GL, Yang DQ, Wang WW. Ontogeny of the digestive tracts in grass carp (*Ctenopharyngodon idellus*), yellowcheck carp (*Elopichthys bambusa*) and topmouth culter (*Culter alburnus*). *Acta Hydrobiologica Sinica*, 2012, 36(6): 1164–1170 [阮国良, 杨代勤, 王卫民. 草鱼、鳊和翘嘴鲌消化道组织的早期发育. 水生生物学报, 2012, 36(6): 1164–1170]
- Sun DY, Chen Z. The South China Sea fish to retrieve. Beijing: Ocean Press, 2013: 380–382 [孙典荣, 陈铮. 南海鱼类检索(上册). 北京: 海洋出版社, 2013: 380–382]
- Su YL, Sun XX, Feng J, *et al.* Morphological and histological observations of digestive system of cobia *Rachycentron canadum*. *South China Fisheries Science*, 2008, 4(6): 88–94 [苏友禄, 孙秀秀, 冯娟, 等. 军曹鱼消化系统的形态及组织学研究. 南方水产, 2008, 4(6): 88–94]
- Wang J, Sun P, Yin F. Low mtDNA Cytb diversity and shallow population structure of *Eleutheronema tetradactylum* in the East China Sea and the South China Sea. *Biochemical Systematics and Ecology*, 2014, 55(2): 268–274
- Wang YC, Li JE, Ou YJ, *et al.* Histomorphology observation on digestive tract of larva, juvenile and young yellowfin black porgy (*Sparus latus*). *Journal of Southern Agriculture*, 2012, 43(8): 1212–1217 [王永翠, 李加儿, 区又君, 等. 黄鳍鲷仔、稚、幼鱼消化道形态组织学观察. 南方农业学报, 2012, 43(8): 1212–1217]
- Xiong HL, Yao JJ, An M, *et al.* Effects of glucose and vitamin C on early development of Puan silver crucian carp (*Carassius auratus gibelio*). *South China Fisheries Science*, 2014, 10(6): 88–92 [熊铎龙, 姚俊杰, 安苗, 等. 葡萄糖、维生素 C 对普安银鲫早期发育的影响. 南方水产科学, 2014, 10(6): 88–92]
- Xu GF, Liu Y, Li YF, *et al.* Organogenesis of the digestive system in *Brachymystax lenok* during early development. *Journal of Fishery Sciences of China*, 2013, 20(4): 733–742 [徐革锋, 刘洋, 李永发, 等. 细鳞鲑早期发育过程中的消化系统发生. 中国水产科学, 2013, 20(4): 733–742]
- Xu XJ, Li JE, Ou YJ. Advance in the research on digestive system in fishes. *Fisheries Science*, 2009, 28(6): 350–354 [许晓娟, 李加儿, 区又君. 鱼类消化系统研究进展. 水产科学, 2009, 28(6): 350–354]
- Xu XJ, Wang J, Xie YJ, *et al.* Post-embryonic histological development in digestive system of large yellow croaker *Pseudosciaena crocea*. *Journal of Dalian Fisheries University*, 2010, 25(2): 107–112 [徐晓津, 王军, 谢仰杰, 等. 大黄鱼消化系统胚后发育的组织学研究. 大连水产学院学报, 2010, 25(2): 107–112]
- Yang RB, Xie CX, Fan QX, *et al.* Ontogeny of the digestive tract in yellow catfish *Pelteobagrus fulvidraco* larvae. *Aquaculture*, 2010, 302(1–2): 112–123
- Yao JJ, Liang ZQ, Feng YN, *et al.* Histological studies on post-embryonic development for digestive system of *Carassius auratus*. *Guizhou Agricultural Sciences*, 2013, 41(11): 152–155 [姚俊杰, 梁正其, 冯亚楠, 等. 普安银鲫消化系统胚后发育的组织学观察. 贵州农业科学, 2013, 41(11): 152–155]



## Histological Observation of the Post-Embryonic Development of Digestive Tract of *Eleutheronema tetradactylum*

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**Abstract** *Eleutheronema tetradactylum* is a tropical inshore marine fish species that belongs to the Polynemidae family. It has very high commercial values. Previous studies mainly focused on the stock structure and taxonomy of this species. However, the information about morphology and structural and functional biology has been limited, especially little is known about the development of the digestive system. In this study we applied the histological method to investigate this issue of *E. tetradactylum* aged Day 1 to Day 30 after hatching (DAH 1 to 30). Thus we may develop a better feeding strategy during artificial seedling rearing and improve the survival rate of the larvae. The experimental conditions were temperature 29–32°C, salinity 25–28, dissolved oxygen 4.80–5.5 mg/L, and pH 8.0–8.3. We found that on DAH 1, the digestive tube was not differentiated, and was composed of intestinal tubes that were attached to the abdominal wall and the yolk sac. On DAH 3, the yolk sac was fully absorbed, the larvae began feeding, and the digestive tube started to communicate with the outside. This indicated a switch from the endogenous nutrition to the exogenous feeding, and from this point, the larvae could maintain the growth by relative independent digestion and absorption through the gradually differentiated esophagus, stomach and intestine. The gastric gland and pyloric caeca appeared on DAH 15, which greatly improved the digestion and were the signs of the juvenile stage. On DAH 30, the structure and function of the digestive tract were well developed, which resembled that of the adults. The liver and the pancreas started to differentiate on DAH 2 and DAH 5 respectively, and they developed fast as the larvae grew. These observations suggested that the development of the digestive system was highly associated with the functions. Based on the characteristics of the digestive system, we further discussed issues in three major critical stages in the process of seedling rearing and proposed solutions for each stage.

**Key words** *Eleutheronema tetradactylum*; Digestive system; Post-embryonic development

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