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卤虫与鲢仔鱼饲喂对开口期鳊消化功能的比较研究

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摘要: 为探索替代开口活饵的适用性, 并评估其对鳊(*Siniperca chuatsi*)消化功能的影响, 本研究以3日龄的鳊仔鱼为对象, 设置对照组(HB, 持续饲喂鲢仔鱼)和卤虫组(AB, 3—6日龄投喂裂壶藻强化的卤虫, 随后转饲鲢仔鱼至9日龄), 比较不同饲喂模式对鳊仔鱼生长和消化机能的影响。结果显示, 尽管经过营养强化, 卤虫的粗蛋白含量仍显著低于鲢仔鱼; AB组鳊仔鱼的全长、特定生长率(SGR)和存活率(SR)均显著低于HB组; 除胃蛋白酶外, AB组的胰蛋白酶、脂肪酶和几丁质酶活性均显著升高, 表现出一定的消化压力; 组织学观察发现, AB组肠道黏膜出现脱落、皱褶紊乱, 肠绒毛缩短且肠壁与绒毛厚度明显增厚。转录组进一步分析显示, AB组富集到多条与免疫炎症及细胞凋亡相关的通路(IL-17、Toll样受体、TNF、NF- κ B及细胞凋亡通路), 关键差异基因(*il17ra1a*、*cxcl19*、*ccl20a.3*、*tnfb*、*casp7*、*casp10*、*bax*)的qPCR验证结果与转录组趋势一致, 且在AB组均显著上调。综上, 尽管营养强化卤虫在短期内具有一定的替代潜力, 但其可能引发鳊仔鱼一定程度的消化压力及肠道应激反应, 从而影响生长和存活。本研究可为鳊开口饵料替代策略的优化及幼鱼消化道健康研究提供参考。

关键词: 开口期; 卤虫; 生长; 消化功能; 鳊仔鱼

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鳊(*Siniperca chuatsi*)隶属鲈形目, 鲴科(Serranidae)、鳊属(*Siniperca*)^[1], 主要分布于东亚, 是一种典型的肉食性鱼类, 也是中国重要的淡水养殖品种, 2024年全国总产量达到54万吨^[2, 3]。鳊的摄食习性十分独特, 一旦开口觅食, 便只摄食活鱼, 拒食死鱼或人工饲料^[4]。因此, 在养殖实践中常需要饵料鱼与鳊繁殖在时间、空间上的耦合。这不仅增加苗种培育成本, 还可能加大病害传播的风险, 成为鳊

产业化发展的主要瓶颈之一^[5, 6]。

为了缓解开口期鳊对饵料鱼的依赖, 开发合适的替代饵料成为鳊苗种培育中的关键问题。目前, 鳊开口期替代饵料的探索主要包括卤虫(*Artemia*)和水蚤(*Daphnia magna*)。已有报道, 鳊仔鱼摄食水蚤后的存活率极低, 应用价值十分有限^[7]。相较之下, 卤虫因其商业化生产成熟、不受季节限制, 且富含蛋白质和多种不饱和脂肪酸, 已被广泛应用于

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多种海、淡水鱼类的早期饲养^[8-10]。在鳃仔鱼中,发现饲喂卤虫可一定程度上促进摄食,虽然表现出一定的替代潜力,但存活率往往低于饲喂饵料鱼组,其适宜性仍有待深入探讨^[7,11]。

基于此,本研究以开口期鳃仔鱼为对象,设置鲢仔鱼(*Hypophthalmichthys molitrix*)和卤虫两种饵料投喂处理,对比分析其对鳃仔鱼生长、存活率和消化功能的影响,探讨卤虫替代受限的可能原因。研究结果有助于深化对鳃仔鱼开口期营养生理需求的理解,并为优化开口饵料替代策略提供理论依据。

1 材料与方法

1.1 活饵培育

本研究的鳃仔鱼与投喂的鲢仔鱼(*H. molitrix*)均来源于重庆市神禹水产引育种股份有限公司青云渔场。卤虫(*Artemia*)卵、裂壶藻(*Schizochytrium*)和螺旋藻(*Spirulina*)粉购于天津丰年水产养殖有限公司。参照马婷等^[12,13]的方法培育卤虫,孵化后长度达到7—9 mm立即投喂。

1.2 实验设计

实验鱼为3 dph (孵化天数)的鳃仔鱼,随机分为2组,每组3个重复,每个重复1000尾,饲养于70 L玻璃缸内。在3 dph之前,两组鳃仔鱼饲养条件一致,若个别鳃仔鱼提前开口,则均投喂鲢仔鱼,未开口个体继续依靠吸收卵黄维持。自3 dph起,鳃仔鱼全部开口后,实施差异化投喂,方案如下(图1):对照组(HB)投喂鲢仔鱼至9 dph,实验组(AB)投喂强化的卤虫至6 dph,再恢复投喂鲢仔鱼至9 dph。实验期间两组鳃仔鱼均按饱食原则投喂,每日投喂3次,卤虫和鲢仔鱼数量充足。投喂后2h及时用虹吸管清除粪便和死亡的仔鱼,记录存活率。投喂密度分别为卤虫4000—5000 个/L^[14],鲢仔鱼200 个/L^[15]。实验期间每天换水1/3,保持水温(29.44±0.89)℃,溶氧量>6.0 mg/L,光周期24h,氨氮<0.02 mg/L, pH 7.6±0.5。

1.3 样品采集与分析

样品分别于3、4、6 和9 dph采集,取样前禁食24h,并用50 mg/L MS-222溶液麻醉处死。每组随

仔鱼年龄(孵化天数) Age of larvae (days post hatch)	3	4	5	6	7	8	9
鲢仔鱼组(HB) <i>H. molitrix</i>							
卤虫组(AB) <i>Artemia</i>							

图1 实验过程中鳃仔鱼的投喂模式

Fig. 1 Feeding pattern of mandarin fish larvae throughout the experiment

机选取330尾鳃仔鱼,其中30尾用于生长指标测量,100尾用于消化酶活性分析,200尾用于转录组分析。受限与开口期鳃仔鱼的体型,消化道难以完整剥离,只能将整鱼置于1.5 mL离心管中液氮速冻,于-80℃保存待测。

增重率(WGR)、特定生长率(SGR)和存活率(SR)按常规方法计算^[16]。胃蛋白酶(A080-1-1)、胰蛋白酶(A080-2)、脂肪酶(A054-1-1)和几丁质酶(A139-1-1)活性的测定,均使用南京建成生物工程研究所提供的酶活试剂盒进行操作,测定原理是通过检测底物显色产物吸光度的变化来定量计算酶活性。测定时,先称量约1 g的整鱼样品,加入9倍体积的匀浆介质,在4℃下匀浆制成10%的组织匀浆液,2500 r/min离心10min,取上清液立即按照说明书要求测定,各酶的检测波长分别为660、253、420和585 nm。每个重复随机选取5尾鳃仔鱼进行组织学切片制备,先将整鱼置于4%多聚甲醛(PFA)固定液中,于4℃固定24h。样品经梯度乙醇脱水、二甲苯透明、石蜡包埋后,使用切片机(Leica, RM 2135)连续切片(厚度5 μm)镜检,每尾鱼选取3张肠道中段的连续切片进行HE染色,在光学显微镜(Leica, DM6000)下拍照,每张切片随机测量5根肠绒毛的长度、厚度及肠壁厚度,使用Image pro Plus 6.0软件测量。肠绒毛长度是绒毛顶端至隐窝交界处的垂直距离,绒毛宽度是绒毛中部的横向宽度,肠壁厚度是黏膜顶端至黏膜下层边界的垂直距离。

1.4 卤虫和鲢仔鱼营养成分分析

取强化后的卤虫和刚开始平游的鲢仔鱼各100 mg,置于1.5 mL离心管中,由青岛科创质量检测有限公司采用AOAC (1984)方法测定两种活饵的营养成分(水分、粗蛋白质、粗脂肪和灰分)^[17]。

1.5 转录组测序

RNA提取 采用TRIzol法对样品进行总RNA提取, Nanodrop检测RNA的纯度和浓度,琼脂糖凝胶检测RNA的完整性^[18]。

cDNA文库测序和数据处理 cDNA文库构建及测序由上海美吉生物医药科技有限公司完成,具体操作流程参照前人所描述的方法^[19]。文库构建完成后,使用Illumina NovaSeq 6000高通量测序平台进行2×150 bp双末端测序。

转录组数据分析 原始测序数据(raw reads)采用fastp (v0.22.0)过滤3'端带接头的序列和低质量序列,最终获得高质量质控数据(clean reads),使用默认参数通过HISAT2 (v2.0)将clean reads与鳃的参考基因组(NCBI Accession: GCF_020085105.1)进行比对^[20,21]。通过将基因序列与GO、KEGG、Pfam、

Swiss-Prot和NR等数据库匹配,从而完成功能注释。使用DESeq2软件筛选差异表达基因,筛选条件设置为表达差异倍数 $|\log_2\text{FoldChange}| > 1$,且 $\text{FDR} < 0.05$,P值经Benjamini-Hochberg方法校正^[22]。对差异基因的GO富集分析采用topGO (v2.50.0),KEGG富集分析采用clusterProfiler (v4.6.0)。

1.6 实时荧光定量PCR分析

根据转录组的富集结果,选取了炎症和凋亡信号通路的关键差异基因进行荧光定量PCR验证。用PrimeScript RT试剂盒(TaKaRa)将RNA反转录为cDNA,以 $rpl13a$ 为内参,利用SYBR[®] Premix Ex Taq[™] II (TaKaRa)试剂盒,通过CFX96 qRT-PCR检测系统(Bio-Rad, USA)进行荧光定量检测,采用 $2^{-\Delta\Delta Ct}$ 法计算基因的相对表达量。引物由上海生物工程股份有限公司合成(表1)。

1.7 数据分析

实验所得数据用SPSS 26.0软件进行 t 检验统计,结果以平均数 $\pm$ 标准误(mean $\pm$ SE)表示。 $P < 0.05$ 为差异显著, $P < 0.01$ 为差异极显著。

2 结果

2.1 强化卤虫和鲢仔鱼的营养成分

对营养强化后的卤虫和鲢仔鱼进行营养成分分析表明,强化后卤虫的粗脂肪和灰分含量显著高于鲢仔鱼,而鲢仔鱼的粗蛋白含量显著高于卤虫($P < 0.05$),二者的水分含量并无显著差异(表2)。

2.2 鳙仔鱼的生长性能

HB组鳙仔鱼的全长、SR和SGR均显著高于AB组($P < 0.05$)。虽然两组的终末均重并无显著差异,但HB组终末均重略高于AB组0.76 mg;HB组的SGR和SR分别是AB组的1.1和1.57倍($P < 0.05$;表3)。不同生长阶段鳙仔鱼WGR和SGR的记录显示(图2),HB组始终高于AB组,尤其在6 dph时,非常显著($P < 0.01$)。

2.3 鳙仔鱼的消化酶活性

随着孵化天数的增加,HB组胃蛋白酶活性急剧下降后便趋于稳定,AB组上升后也逐渐稳定,4 dph时HB组的胃蛋白酶活性显著高于AB组($P < 0.01$);6 dph时AB组的胰蛋白酶活性显著高于HB组($P < 0.01$);AB组脂肪酶活性的变化趋势较明显,呈先上升后下降,在4和6 dph时AB组显著高于HB组,但9 dph时AB组显著低于HB组($P < 0.05$);AB组几丁质酶活性均高于HB组,在4和9 dph时差异显著($P < 0.05$;图3)。

2.4 鳙仔鱼的肠道组织结构

肠道的组织结构如表4所示,HB组鳙仔鱼的肠

绒毛长度显著比AB组长76 μm ,而肠绒毛厚度和肠壁厚度分别显著比AB组薄8.5和58 μm ($P < 0.05$)。HE切片显示(图版I),HB组肠道绒毛结构完整、清晰;上皮细胞和梳状边缘排列整齐,杯状细胞少,肠腔空间大,接触面积大;而AB组鳙仔鱼的肠道黏膜有少许脱落,杯状细胞数目增多,肠道绒毛稀疏,同时还伴随少许破裂,褶皱隆起变少,与食物接触面积变小。

表1 实时荧光定量PCR所用引物

基因 Gene	序列 Sequence (5'—3')
<i>rpl13a</i>	TATCCCCCACCCTATGACA ACGCCCAAGGAGAGCGAAC
<i>il17ra1a</i>	CTGATGACATGCTCACTCCCTT CAGCTTGATTGACTGCGATG
<i>cxcl19</i>	TAACGGTATGCCGCCAATC AACCTTCTCCCCATTACCA
<i>ccl20a.3</i>	ATCACGCTCCTCACCTTTTGT GAACCATTTGTGCTTTGTTCTT
<i>tnfb</i>	ACACAACCGCACTAGGTGAC AGGGCCACAACGAGAATGAG
<i>casp7</i>	GAGGAGGGCATGATCTACGG CGGCAAGCCTGGATGAAGAA
<i>casp10</i>	GAGGGAAGCGTGTGTTGGTG CAGATGGGATGGAGTCTTTAGC
<i>bcl-2</i>	CTCCAAACAGGGCTACGTGT CTCCGGTGGACTAAAGTCGG
<i>bax</i>	ACCATGGACTACCTCCGAGA AACGAATATCCTCCAGCCG

注: *rpl13a*. ribosomal protein L13a, 核糖体蛋白 L13a; *il17ra1a*. interleukin 17 receptor A1a, 白介素17受体A1a; *cxcl19*. C-X-C motif chemokine ligand 19, C-X-C趋化因子配体19; *ccl20a.3*. C-C motif chemokine ligand 20a.3, C-C趋化因子配体20a.3; *tnfb*. tumor necrosis factor beta, 肿瘤坏死因子 β ; *casp7*. caspase-7, 半胱天冬酶7; *casp10*. caspase-10, 半胱天冬酶10; *bcl-2*. B-cell lymphoma 2, B细胞淋巴瘤-2蛋白; *bax* Bcl-2-associated X protein, Bcl-2相关X蛋白

表2 基本营养成分

组分Composition (%)	鲢仔鱼 <i>H. molitrix</i>	卤虫 <i>Artemia</i>
水分Moisture	94.30 $\pm$ 0.71	94.15 $\pm$ 0.15
灰分Ash	0.43 $\pm$ 0.26	1.75 $\pm$ 0.05*
粗脂肪Crude lipid	0.77 $\pm$ 0.09	1.40 $\pm$ 0.01*
粗蛋白Crude protein	3.72 $\pm$ 0.73	1.63 $\pm$ 0.01*

注: *表示同行数据差异显著($P < 0.05$), **表示同行数据差异极显著($P < 0.01$);下同

Note: * indicates significant differences in the same line ($P < 0.05$), ** indicates extremely significant differences in the same line ($P < 0.01$); the same applies below

2.5 转录组测序、组装和注释结果

为了进一步比较两种活饵对开口期鳃仔鱼的影响, 对4、6和9 dph的两组鳃仔鱼进行了比较转录组分析。完成了18个样品的转录组测序, 各样品Q₃₀均在92.76%以上。将得到的clean reads与鳃参考基因组进行比对, 各样品的比对率均不低于94.07% (表 5), 表明测序结果质量较高, 可用于后续分析。

2.6 差异基因的GO富集分析

卤虫组(AB)比鳃仔鱼组(HB)在4、6和9 dph, 分别上调了差异基因为495、468和101个; 分别下调了差异基因为287、671和48个。将各阶段的卤虫组(AB)与鳃仔鱼组(HB)的3827个差异表达基因(上调与下调)合并进行 GO富集分析显示, 多个与肠道屏障、离子转运和免疫应答相关的生物学过程被富集。例如, 细胞间黏附和营养与信号转导相关的生物学过程。此外, 多个免疫相关的通路也被富集, 包括免疫应答激活、补体激活和对其他生物的防御反应等(图 4和图 5)。

2.7 差异基因的KEGG富集分析

KEGG富集分析结果显示, 多条与上皮屏障功

能受损、免疫炎症激活和细胞应激相关的信号通路被富集。其中, 间隙连接、紧密连接和ECM受体相互作用信号通路可能与肠道上皮连接和屏障功能有关; 与此同时, 多条炎症信号通路和细胞损伤及应激相关的通路也均被富集。与饲喂鳃仔鱼相比, 饲喂卤虫可能会诱发鳃肠道炎症, 引发肠道细胞的氧化应激、程序性死亡及自噬等(图 6)。

2.8 炎症免疫和细胞凋亡相关基因表达

基于GO和KEGG富集分析, 筛选出了多个与炎症反应、免疫调节和细胞凋亡密切相关的信号通路。因此我们选取了部分具有代表性的炎症相关基因(*il17rala*、*cxcl19*、*ccl20a.3*和*tnfb*)和凋亡相关基因(*casp7*、*casp10*、*bcl2*和*bax*)进行qPCR验证。参与炎症反应相关的因子*il17rala*、*cxcl19*、*ccl20a.3*和*tnfb*, 在4—9 dph期间, 呈现先上升后下降的趋势或逐渐上升的趋势, 且AB组的相对表达量均高于HB组。这表明鳃仔鱼摄食卤虫后的免疫系统可能会被激活($P<0.05$; 图 7)。同时凋亡相关的*casp7*、

表 3 不同开口饵料对鳃仔鱼生长及存活率的影响
Tab. 3 Effect of different initial feeding regimes on the growth and survival rate of mandarin fish larvae

项目Item	鳃仔鱼组(HB) <i>H. molitrix</i>	卤虫组(AB) <i>Artemia</i>
初始均重 Initial body weight (mg)	1.11±0.02	1.11±0.02
终末均重 Final body weight (mg)	5.84±0.26	5.08±0.37
初始全长 Initial length (mm)	5.17±0.09	5.17±0.09
终末全长 Final length (mm)	8.22±0.10	7.66±0.12 [*]
特定生长率 Specific growth rate (SGR; %/d)	27.61±0.75	25.18±1.13 [*]
存活率 Survival rate (SR; %)	68.72±0.32	43.68±0.10 [*]

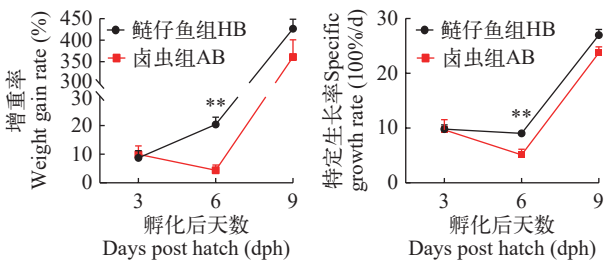


图 2 不同生长阶段鳃仔鱼增重率和特定生长率的变化
Fig. 2 Changes of WGR and SGR of mandarin fish larvae at different growth stages

**表示同行数据差异极显著 ($P<0.01$); 下同

** indicates extremely significant differences in the same line ($P<0.01$); the same applies below

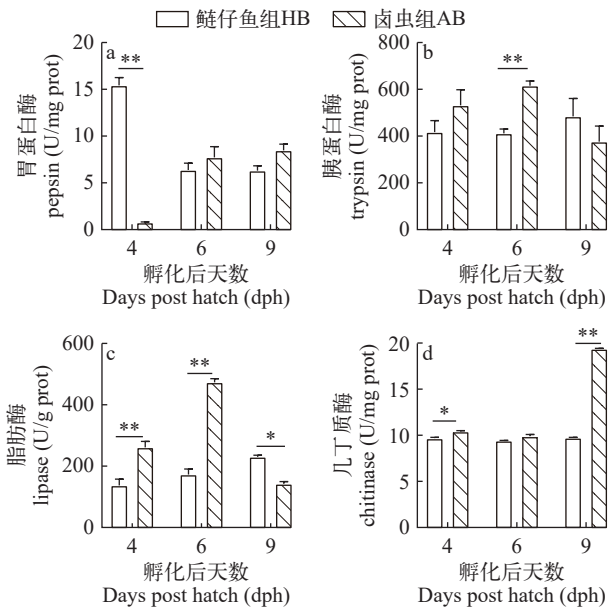


图 3 不同开口饵料对鳃仔鱼消化酶活性的影响
Fig. 3 Effects of different initial feeding regimes on the digestive enzyme activities of mandarin fish larvae

表 4 不同开口饵料对鳃仔鱼肠道组织结构的影响
Tab. 4 Effects of different initial feeding regimes on intestinal histomorphology in mandarin fish larvae

参数Parameter(μm)	鳃仔鱼组(HB) <i>H. molitrix</i>	卤虫组(AB) <i>Artemia</i>
肠绒毛长度 Intestinal villus length	548±0.06	472±0.14 ^{**}
肠绒毛厚度 Intestinal villus thickness	144±0.01	152.5±0.01 ^{**}
肠壁厚度 Intestinal wall high	80±0.02	138±0.04 ^{**}

*casp10*和*bax*的相对表达量显示,在4—6 dph时AB组均显著高于HB组($P<0.05$)。这提示鳊仔鱼摄食卤虫后的肠道上皮组织可能发生了细胞程序性死亡(图8)。以上验证的qPCR结果与转录组的趋势基本一致。

3 讨论

3.1 投喂卤虫和鲢仔鱼对开口期鳊生长和存活的影响

开口期是鳊生长发育过程中最为关键的阶段,开口饵料的营养组成与适宜性直接影响其生长速度、肠道发育及免疫稳态^[23–25]。本研究比较了营养强化卤虫与鲢仔鱼作为开口饵料的效果,卤虫组鳊仔鱼的体重和全长均低于鲢仔鱼组,生长受到一定抑制。本文猜测可能是由于营养强化后的卤虫,其营养成分仍难以满足鳊开口期所需的营养,尤其是在对蛋白质和必需脂肪酸需求量较高的关键窗口期(3—6 dph)。随后的营养成分对比也发现,卤虫的粗蛋白含量显著低于鲢仔鱼。其他研究也认为卤虫的脂肪酸组成及游离氨基酸含量与饵料鱼仍存在些许差距^[26–28]。进一步分析3—9 dph的SGR也发现,卤虫组在各时间段均低于鲢仔鱼组,尤其在3—6 dph阶段差异显著,在7—9 dph阶段,卤虫组SGR较前期有所回升,并逐渐接近鲢仔鱼组,可能与恢复投喂鲢仔鱼有关。存活率方面,卤虫组(43%)

显著低于鲢仔鱼组(69%),可能也与卤虫的营养供给不足有关^[28–30]。与此前报道卤虫替代饵料鱼存在局限性结果一致^[11]。

3.2 投喂卤虫和鲢仔鱼对开口期鳊消化功能的影响

消化酶活性结果显示,4 dph时,鲢仔鱼组的胃蛋白酶活性约为卤虫组的40倍。可能是因为鲢仔鱼蛋白质含量更高(粗蛋白含量约为卤虫的2.28倍),且氨基酸组成更契合鳊仔鱼的营养需求^[31],能有效刺激胃蛋白酶分泌并促进蛋白质高效利用。相比之下,卤虫虽含有一定的优质蛋白,但氨基酸组成不均衡,且外骨骼富含几丁质,降低了蛋白质的可利用性^[28]。在其他研究中也提到,开口期鳊仔鱼对卤虫的消化能力较弱,影响营养的利用效率^[7, 32]。在这种情况下,机体可能会通过增强胰蛋白酶和几丁质酶分泌来弥补消化不足^[33, 34]。本研究在4和6 dph时,卤虫组的胰蛋白酶和几丁质酶活性均高于鲢仔鱼组。这种代偿性增强并不一定代表营养利用率的提高,反而可能反映了消化系统的“消化压力”^[35]。类似现象在其他鱼类研究中也有报道,当饵料营养不均衡或可消化性差时,胰蛋白酶活性升高,但生长效果并不理想^[36]。在4和6 dph时,卤虫组的脂肪酶活性显著高于鲢仔鱼组。这可能由于卤虫中富含的多不饱和脂肪酸(HUFA),能够刺激脂肪酶分泌所致^[37]。总之,卤虫组消化酶的“高活性”更

表5 测序数据质量和比对情况

Tab. 5 Sequencing data quality and alignment

样品 Sample	高质量纯净序列 Clean reads (N_{CR})	高质量纯净碱基 Clean bases	Q_{30} (%)	比对到基因组上的序列数 Mapped reads (N_{MR})	N_{CR}/N_{MR} (%)
D4_HB_1	44401406	6567686584	93.10	42364092	95.41
D4_HB_2	47265942	7027272054	93.45	45254066	95.74
D4_HB_3	42899706	6330900282	92.76	41162948	95.95
D4_AB_1	43259214	6418189994	93.11	41249551	95.35
D4_AB_2	41303018	6117569311	93.28	39362884	95.30
D4_AB_3	43610100	6456979546	93.36	41651197	95.51
D6_HB_1	49654836	7283546202	93.38	46884740	94.42
D6_HB_2	44581410	6581283073	93.43	42563073	95.47
D6_HB_3	49164608	7188126277	93.55	47010644	95.62
D6_AB_1	48538140	7118441087	93.42	46164913	95.11
D6_AB_2	43381474	6414913458	93.57	41370795	95.37
D6_AB_3	48543742	7174056395	93.32	46345619	95.47
D9_HB_1	41581162	6208715302	93.45	39655621	95.37
D9_HB_2	41135532	6094502679	93.53	39028744	94.88
D9_HB_3	43012614	6393430160	93.26	40462133	94.07
D9_AB_1	43449392	6404195684	93.51	41253753	94.95
D9_AB_2	43649106	6452477651	93.48	41615211	95.34
D9_AB_3	41085896	6015927817	93.24	39073820	95.10

多地反映了机体的一种适应性或代偿性反应, 而非消化效率的提升, 这也是卤虫组生长缓慢的原因。

肠道组织学结果发现, 摄食卤虫的鳃仔鱼出现了明显的组织异常, 包括黏膜脱落、杯状细胞数目增多及皱褶缩短等现象, 提示肠道屏障功能可能受到损伤^[33, 38—40]。这种损伤在鱼类早期发育阶段尤为关键, 肠道稳态的破坏会影响整个生长过程中的营养吸收与免疫防御^[41, 42]。卤虫组的肠壁厚度和绒毛厚度显著高于鲢仔鱼组, 但肠绒毛长度却显著低于鲢仔鱼组。这种厚度增加但长度缩短的结构变化, 可能也是一种在应激或损伤状态下的组织重

塑反应^[43, 44]。这说明摄食卤虫会影响鳃仔鱼肠道组织的结构, 类似现象在其他鱼类中也有报道^[45, 46]。

3.3 转录组分析揭示免疫炎症与凋亡相关通路的变化

为进一步探索饵料差异引起的分子响应机制, 本研究对两组鳃仔鱼进行比较转录组分析。差异基因(DEGs)的GO和KEGG富集结果显示, 多条与免疫应激相关的信号通路被富集, 包括IL-17 信号通路、Toll样受体信号通路、TNF 信号通路和NF- κ B 信号通路等。同时也涉及细胞凋亡与细胞衰老的相关通路。为验证转录组结果的可靠性, 选取了部分黏膜免疫相关的代表性差异基因进行qPCR验证, 结果与转录组趋势高度一致。在基因表达层面, 随着饲养时间的增加, 免疫相关基因(*il17ra1a*、*cxcl19*、*ccl20a.3*和*tnfb*)呈先升后降或持续升高的趋势, 且卤虫组的相对表达量显著高于鲢仔鱼组。其中*Il17ra1a*作为白细胞介素-17 (IL-17)的受体亚基, 通过介导IL-17信号激活下游通路, 诱导多种炎症相关基因表达^[47]。已有研究在鲤(*Cyprinus carpio*)感染或炎症状态下也观察到*il17*的上调, 提示其在黏膜免疫应答中的重要作用^[48]。*Cxcl19*和*Ccl20a.3*属于趋化因子(Chemokine), 能够介导免疫细胞向炎症部位迁移^[49, 50]。*Tnfb*作为炎症因子, 则参与免

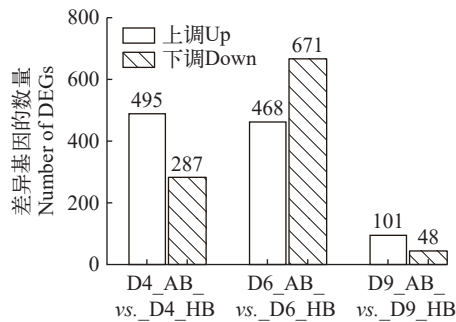


图4 饲喂卤虫组(AB) vs. 饲喂鲢仔鱼组(HB)的差异表达基因
Fig. 4 Differentially expressed genes of feeding *Artemia* vs feeding *H. molitrix*

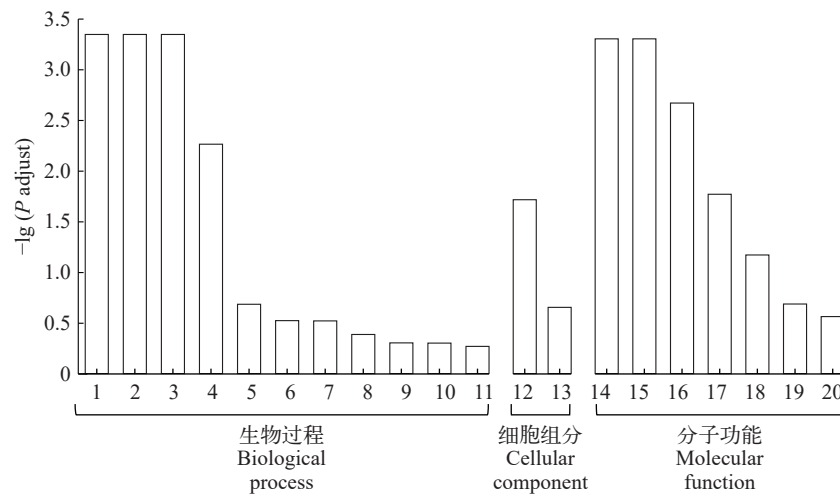


图5 差异基因的GO分析

Fig. 5 GO analysis of differentially expressed genes

1. 通过细胞膜黏附分子介导的同源细胞黏附; 2. 细胞间黏附通过细胞膜黏附分子实现; 3. 离子跨膜转运的调节; 4. 钙离子结合; 5. G蛋白偶联受体活性; 6. 细胞外基质的结构成分; 7. 神经递质转运; 8. 无机分子实体跨膜转运蛋白活性; 9. 分泌囊泡; 10. 氧化还原酶活性; 11. 胰岛素样生长因子结合蛋白; 12. 免疫激活; 13. 含胶原蛋白的细胞外基质; 14. 激素活性; 15. 免疫应答; 16. 免疫正调节; 17. 补体激活; 18. 细胞分裂过程; 19. 单羧酸运输; 20. 对其他生物的防御反应

1. homophilic cell adhesion via plasma membrane adhesion molecules; 2. cell-cell adhesion via plasma-membrane adhesion molecules; 3. regulation of ion transmembrane transport; 4. calcium ion binding; 5. G protein-coupled receptor activity; 6. extracellular matrix structural constituent; 7. neurotransmitter transport; 8. inorganic molecular entity transmembrane transporter activity; 9. secretory vesicle; 10. oxidoreductase activity, acting on the CH-NH2 group of donors; 11. insulin-like growth factor binding; 12. activation of immune response; 13. collagen-containing extracellular matrix; 14. hormone activity; 15. immune response; 16. positive regulation of immune response; 17. complement activation; 18. cytokinetic process; 19. monocarboxylic acid transport; 20. defense response to other organism

疫细胞活性调控,并在过度炎症时通过诱导凋亡维持平衡^[51, 52]。与免疫通路相对应,本研究还检测到凋亡相关基因(*casp7*、*casp10*和*bax*)在卤虫组的表达水平显著高于鲢仔鱼组,而抗凋亡因子*bcl2*在两组间无显著差异。这提示饲喂卤虫可能会激活以Caspase和Bax为主导的促凋亡途径,参与组织稳态调节^[53]。上述结果都表明,饲喂卤虫可能触发了黏膜免疫反应,还可能通过炎症与凋亡途径介导肠道组织损伤,这与HE切片观察到的现象相互印证。

综上所述,裂壶藻强化卤虫在鳊初次摄食阶段具有一定的短期替代潜力。然而,其形态构造和营养成分与鳊早期发育所需的天然饵料鱼存在差异,可能引发一定程度的肠道应激、免疫炎症反应及凋亡活性升高,从而对肠道结构和功能产生影响,进而影响鳊仔鱼的生长和存活。这也提示,在开口期鳊仔鱼饲喂卤虫时,应充分考虑其消化适应性及肠道健康,可结合卤虫去壳处理和饵料鱼联合投喂等策略,以减轻免疫过度激活提高其作为开口饵料的适用性。

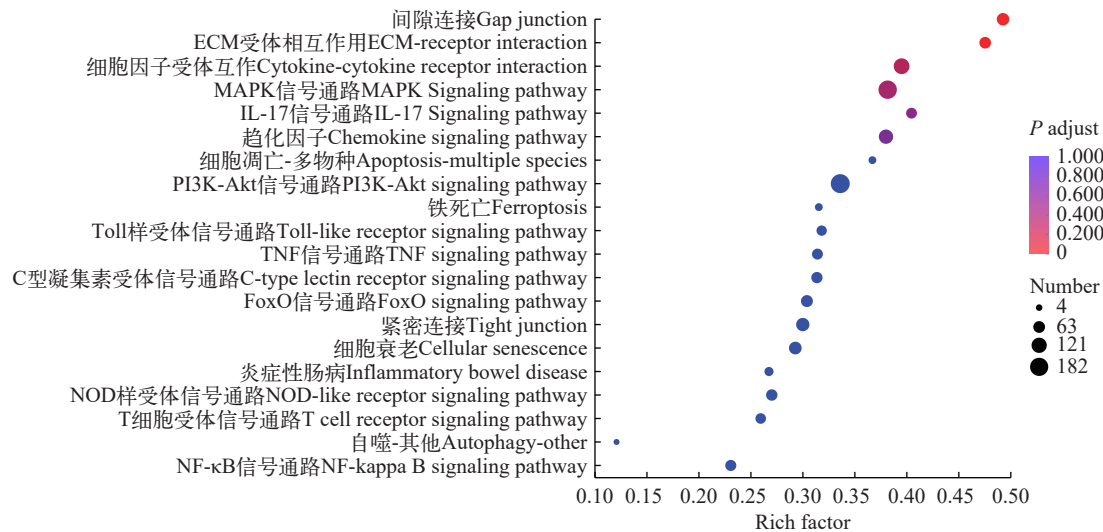


图6 差异基因的KEGG富集分析

Fig. 6 KEGG enrichment analysis of differentially expressed genes

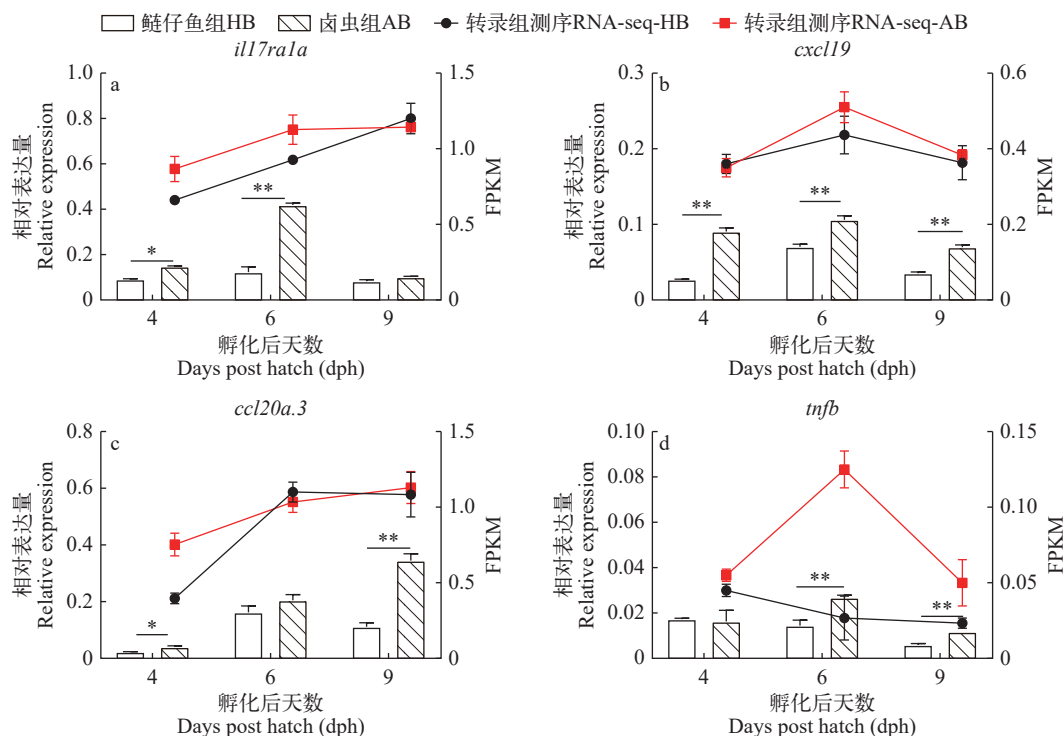


图7 不同开口饵料对免疫相关基因表达量的影响

Fig. 7 Effects of different initial feeding on the expression of genes related to immune response

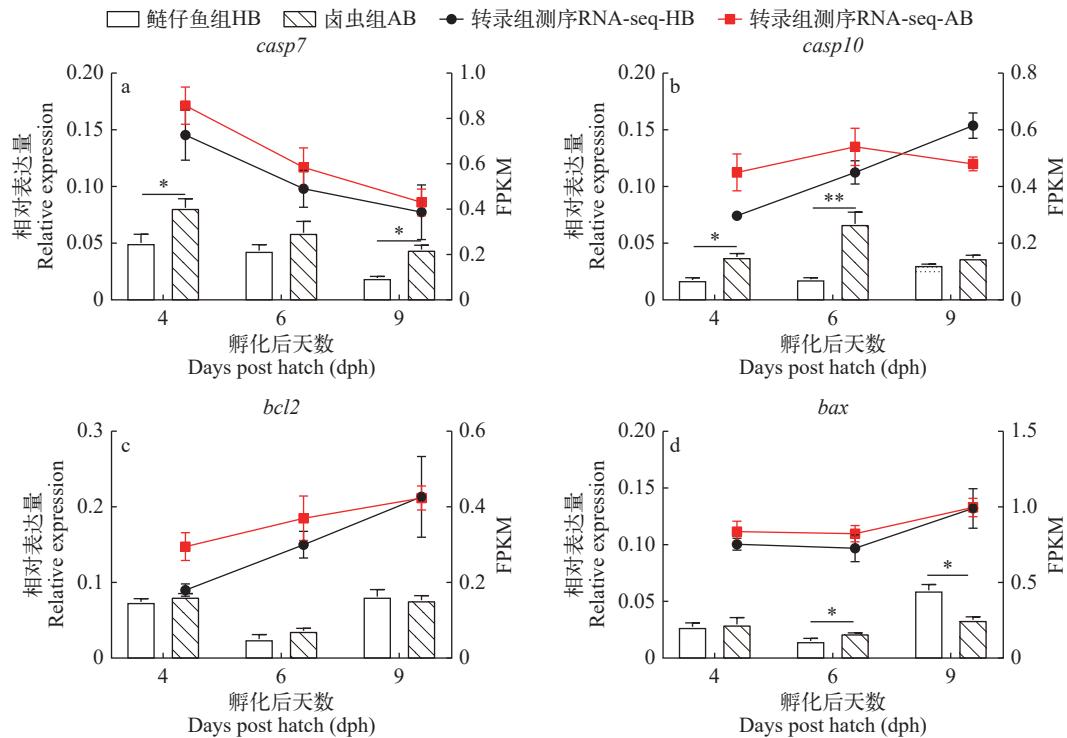


图 8 不同开口饵料对凋亡相关基因表达量的影响

Fig. 8 Effects of different initial feeding on the expression of genes related to apoptosis

(作者声明本文符合出版伦理要求)

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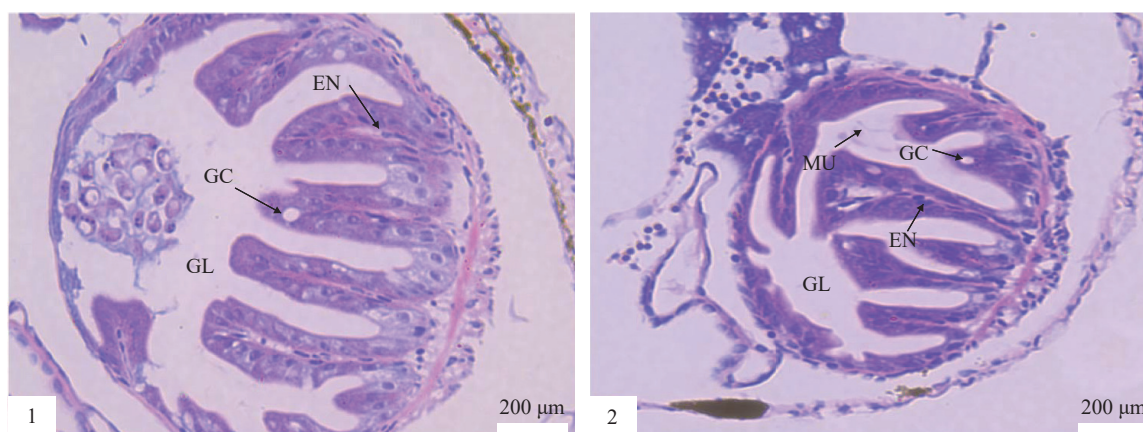
COMPARATIVE STUDY ON THE DIGESTIVE FUNCTION OF MANDARIN FISH (*SINIPERCA CHUATSI*) FED WITH *ARTEMIA* AND SILVER CARP FRY AT THE INITIAL FEEDING STAGE

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Abstract: The characteristic of mandarin fish (*Siniperca chuatsi*) on live prey during the initial feeding stage poses challenges to artificial breeding and increases production costs. To evaluate the feasibility of replacing live prey and to investigate its effects on digestive function, 3 days post-hatch larvae were divided into two groups: a control group (HB) fed continuously with silver carp larvae, and an experimental group (AB) fed *Artemia* enriched with *Schizochytrium* from 3 to 6 days post-hatch, followed by silver carp larvae until 9 days post-hatch. Despite nutritional enrichment, the crude protein content of *Artemia* remained significantly lower than that of silver carp larvae. Growth performance was impaired in the AB group, with total length, specific growth rate (SGR), and survival rate (SR) all significantly reduced compared with the HB group. Except for pepsin, the activities of trypsin, lipase, and chitinase were significantly elevated in the AB group, indicating enhanced digestive stress. Histological examination revealed exfoliation and disorganization of the intestinal mucosa, shortened villi, and marked thickening of both intestinal walls and villi in the AB group. Transcriptomic analysis further demonstrated that differentially expressed genes in the AB group were enriched in immune- and apoptosis-related pathways, including IL-17, Toll-like receptor, TNF, NF- κ B, and apoptosis signaling pathways. qPCR validation confirmed significant upregulation of key genes (*il17ra1a*, *cxcl19*, *ccl20a.3*, *tnfb*, *casp7*, *casp10*, and *bax*), aligning with transcriptomic trends. In conclusion, although nutrient-enriched *Artemia* may have short-term potential as an alternative initial diet, it can induce digestive stress and intestinal responses in mandarin fish larvae, thereby compromising growth and survival. This study provides useful references for optimizing feeding strategies at the initial stage and evaluating intestinal health in juvenile mandarin fish.

Key words: Initial feeding stage; *Artemia*; Growth; Digestive function; Larvae of mandarin fish



图版 I 不同开口饵料对鲟仔鱼肠道组织结构的影响

Plate I Effects of different initial feeding regimes on intestinal histomorphology in mandarin fish larvae

1. 鲟仔鱼组(HB)鲟肠道(400×); 2. 卤虫组(AB)鲟肠道(400×); EN. 上皮细胞细胞核; GC. 杯状细胞; Mu. 肠道黏膜; GL. 肠腔
1. Feeding of *H. molitrix* to the intestines of mandarin fish (400×); 2. Feeding of *Artemia* to the intestines of mandarin fish (400×); EN. epithelial cell nuclei; GC. goblet cell; Mu, Intestinal mucosa; GL. gut lumen