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溶氧和饲料脂肪水平对罗非鱼生理机能的交互作用*

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摘要　本研究旨在探究溶氧含量和脂肪水平的交互作用对罗非鱼(*Oreochromis niloticus*)的生长性能、肝脏抗氧化能力、免疫指标以及肝组织结构的影响。实验以初始体重为(7.62±0.29) g 的罗非鱼为研究对象，设置低氧[(2.0±0.1) mg/L，A 组]和正常溶氧[(5.0±0.1) mg/L，B 组]养殖环境，并分别饲喂 5 种脂肪水平(1~5 组：1.57%、4.41%、7.61%、10.51%和 13.01%)的饲料，每组 3 个重复，养殖 60 d。结果显示，随着脂肪水平升高，A 组与 B 组的增重率(WGR)、特定生长率(SGR)和饲料效率(FE)呈先上升后下降的趋势，分别在 A2 组、B3 组达到最大值；同一脂肪水平下，B 组 WGR 和 SGR 显著高于 A 组。溶氧和脂肪水平的交互作用显著地影响肝组织中过氧化氢酶(CAT)、总抗氧化能力(T-AOC)和丙二醛(MDA)含量，A 组 CAT 和 T-AOC 活性低于 B 组，MDA 含量高于 B 组；且 A1 组 CAT 活性显著高于其他 A 组。溶氧和脂肪水平的交互作用还显著影响己糖激酶(HK)、丙酮酸激酶(PK)、甘油三酯(TG)和肝脂酶(HL)含量，A 组中 HK、PK 和 HL 均显著低于 B 组，但 TG 含量高于 B 组；A 组免疫球蛋白 M(IgM)、干扰素-γ(IFN-γ)、肿瘤坏死因子 α(TNF-α)、白细胞介素(IL-1β)含量均显著低于 B 组，且不受脂肪水平的影响。随着脂肪水平升高，B 组肝脏组织脂滴空泡逐渐增多，A2 组肝细胞形态结构正常，A3 组、A4 组和 B5 组均有大量的脂滴空泡、细胞核溶解和偏移的现象。综上所述，在本研究范围内，投喂脂肪水平为 4.41%左右的饲料有利于缓解罗非鱼由低氧环境造成的氧化应激，而在常氧环境中，投喂脂肪水平为 7.61%左右的饲料有利于促进罗非鱼的生长。

关键词　罗非鱼；溶氧；脂肪水平；交互作用；肝功能；免疫指标

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罗非鱼(*Oreochromis niloticus*)具有生长快、食性杂、无肌间刺和抗逆性强等养殖优势，同时富含多种必需氨基酸和不饱和脂肪酸，具有较高的营养价值。1976 年，罗非鱼被联合国粮农组织(FAO)列为向世界各国推广养殖的鱼类(肖炜等, 2022; 赵雲等, 2020)。目前，我国罗非鱼的养殖模式正由传统流水模式逐渐向高密度工厂化循环水养殖的方向发展(陈昕等, 2024; 胡俊康, 2021)，而缺氧是导致高密度集约化养殖中鱼类死亡的一个常见因素(张瑜霏等, 2022; Burt *et al*, 2013)，因此，需高度关注养殖环境中溶氧状态。

溶氧是水生动物维持机体正常代谢活动的基础，对水生动物生存、生长发育、免疫功能和能量代谢等

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具有重要影响(Abdel-Tawwab *et al*, 2015; Yuan *et al*, 2023; 王维政等, 2020)。余欣欣等(2024)研究发现，在低氧胁迫下，鱼类机体会产生氧化应激反应，从而造成组织氧化损伤，此时需要机体的抗氧化防御体系来清除活性氧自由基，鱼类通过调节自身抗氧化酶活性缓解低氧胁迫。黄颡鱼(*Pelteobagrus fulvidraco*)、棕点石斑鱼(*Epinephelus fuscoguttatus*)、大菱鲆(*Scophthalmus maximus*)通过提高肝脏抗氧化酶活性来缓解机体因低氧胁迫导致的氧化应激损伤(Wang *et al*, 2021; 段鹏飞等, 2022; 李飞霞等, 2023)。鱼体免疫机能与水体溶氧含量密切相关，低氧会抑制免疫机能，使鱼类患病甚至死亡(Cao *et al*, 2024)。王维政等(2021)通过军曹鱼(*Rachycentron canadum*)幼鱼的研究发现，应激时间过长会降低免疫因子和免疫细胞活性，导致免疫力下降，同时造成组织损伤和影响机体代谢。当鱼类受到低氧胁迫时，会引起其体内非特异性免疫因子(溶菌酶、补体、干扰素和白细胞介素等)活性变化，因此，可根据免疫因子活性反映机体对外界环境的防御能力(王艳玲等, 2020)。

随着鱼类的长期演化，鱼类可以通过一系列生理机制来应对低氧环境(余欣欣等, 2024)。有研究发现，鱼类在急性缺氧应激时以碳水化合物为主要能量来源，而在长期缺氧应激时代谢更多脂质；饲料中高碳水化合物含量可能有助于减少急性缺氧应激的负面影响，饲料中适当增加脂肪含量可能有利于鱼类在缺氧环境中生长(张雷敏等, 2023; Li *et al*, 2018)。据报道，适宜的脂肪水平有助于缓解草鱼(*Ctenopharyngodon idella*)因长期缺氧引起的肝损伤(An *et al*, 2022)。王丽群(2020)研究发现，在低氧条件下提高脂肪水平，可以缓解禾花鲤(*Cyprinus carpio*)应激，并改善生长情况。李梦晓(2018)和 Li 等(2018)研究发现，长期缺氧的罗非鱼会代谢更多的脂质以响应低氧胁迫，饲料中添加适量的脂质有利于鱼类生存，但具体理论依据尚未阐明。因此，本研究探讨不同溶氧和脂肪水平交互作用对罗非鱼生长性能、肝脏抗氧化能力、免疫指标以及肝组织结构的影响，为罗非鱼生产实践提供一定的参考依据。

1 材料与方法

1.1 实验饲料

以大豆油作为脂肪源，按 0%、3%、6%、9%和 12%比例添加到基础饲料中，饲料脂肪水平分别为 1.57%、4.4%、7.61%、10.51%和 13.01%。罗非鱼基础饲料配方组成及基本营养成分组成见表 1。

1.2 实验鱼及实验方案

吉富罗非鱼(GIFT, *Oreochromis niloticus*)鱼苗由广西水产科学研究院良种养殖基地提供，暂养于实验池(1.4 m×1.2 m×1.0 m)中 2 周，以适应养殖环境。养殖水平均水温为(28.2±1.3)℃，溶氧含量为(5.0±0.1)mg/L，pH 为 7.2±0.1。

实验设置低氧[(2.0±0.1) mg/L，A 组]、正常溶氧[(5.0±0.1) mg/L，B 组] 2 种环境和 5 种脂肪水平(1.57%、4.41%、7.61%、10.51%、13.01%)的饲料，完成 2×5 因子实验，即 A1、A2、A3、A4、A5 和 B1、B2、B3、B4、B5 共 10 组，每组 3 个重复，每个重复挑选 40 尾体质健壮的初始体重为(7.62±0.29) g 的罗非鱼，养殖于实验池(1.4 m×1.2 m×1.0 m)中。实验期间每天表观饱食投喂 2 次(09:00 和 17:30)，投喂前称取等量饲料，投喂 1 h 后捞出残饵烘干至恒重称量，残饵量由饲料溶失率校正，换算得到每日投喂量并记录。每 2 周换水 1 次、吸污 2 次，保持水温为(28.2±1.3) ℃，pH 为 7.2±0.1，养殖周期为 60 d。实验期间采用河南科达智能溶氧控制器实时控制水中溶氧，具体参考 Li 等(2020)方法。

1.3 实验样本采集

实验结束，鱼禁食 24 h 后，从每个平行组中随机取 6 尾鱼，用 200 mg/L MS-222 进行麻醉，先称量实验鱼的体重，再测量鱼体长、全长、内脏重、肝重，逐一记录数据。每个平行组中取 6 尾实验鱼迅速在冰上解剖并采集肝脏组织，用 0.85%生理盐水洗净，置于冷冻管中，于–80 ℃冰箱冷冻保存待测。

1.4 生长指标

计算实验鱼生长性能和形体指标公式如下：

增重率(weight gain rate, WGR, %)=$(W_t–W_o)/W_o×100$；

特定生长率(specific growth rate, SGR, %/d)=$(\ln W_t–\ln W_o)/t×100$；

肝体比(hepatosomatic index, HSI, %)=$W_h/W×100$；

脏体比(viscerosomatic index, VSI, %)=$W_v/W×100$；

饲料效率(feed efficiency, FE, %)=$(W_t–W)/W_f×100$；

存活率(survival rate, SR, %)=$N_f/N_i×100$；

式中，W_t 为终末体重(g)，W_o 为初始体重(g)，t 为饲养天数(d)，W_f 为鱼摄入饲料干重(g)，W_h 为样品鱼肝脏重(g)，W_v 为样品鱼内脏重(g)，W 为样品鱼体重(g)，N_f 为终末鱼尾数，N_i 为初始鱼尾数。

表 1　实验饲料配制

Tab.1　Experiment feed proportion (%)

原料成分 Ingredient	脂肪水平 Lipid levels				
	1.57%	4.41%	7.61%	10.51%	13.01%
大豆油 Soybean oil	0	3	6	9	12
鱼粉 Fish meal	8	8	8	8	8
豆粕 Soybean meal	35	35	35	35	35
菜籽粕 Rapeseed meal	22	22	22	22	22
花生麸 Peanut bran	10	10	10	10	10
玉米淀粉 Corn starch	10	10	10	10	10
微晶纤维素 Microcrystalline cellulose	12	9	6	3	0
羧甲基纤维素 Carboxymethyl cellulose	0.40	0.40	0.40	0.40	0.40
磷酸二氢钙 Calcium phosphate	0.80	0.80	0.80	0.80	0.80
食盐 NaCl	0.50	0.50	0.50	0.50	0.50
复合维生素 Vitamins premix	0.50	0.50	0.50	0.50	0.50
无机盐矿物质 Mineral premix	0.50	0.50	0.50	0.50	0.50
防霉剂 Antiseptic	0.10	0.10	0.10	0.10	0.10
抗氧化剂 Antioxidant	0.10	0.10	0.10	0.10	0.10
氯化胆碱 Choline chloride	0.05	0.05	0.05	0.05	0.05
复合酶 Compound enzyme	0.05	0.05	0.05	0.05	0.05
合计 Total	100	100	100	100	100
主要营养成分 Main nutrients					
粗蛋白 Crude protein	35.01	35.24	35.47	35.13	35.52
粗脂肪 Crude fat	1.57	4.41	7.61	10.51	13.01
灰分 Ash	11.37	9.33	7.67	4.33	2.67
水分 Moisture	7.79	7.12	7.17	7.12	7.18
总能 Total energy/(MJ/kg)	18.21	19.97	20.66	22.58	24.47

1.5　生化指标

肝脏过氧化氢酶(catalase, CAT)、总抗氧化能力(total antioxidant capacity, T-AOC)、甘油三酯(triacylglycerols, TG)、丙二醛(malondialdehyde, MDA)和谷草转氨酶(aspartate aminotransferase, AST)指标均采用南京建成生物工程研究所相应指标试剂盒，按照说明书进行测定。肝脂酶(hepaticlipase, HL)、腺苷三磷酸酶(adenosine triphosphatase, ATPase)、含半胱氨酸的天冬氨酸蛋白水解酶-9 (cysteinyl aspartate specific proteinase, Caspase-9)、细胞色素氧化酶(cytochrome c oxidase, CCO)、热休克蛋白-90 (heat shock protein 90, HSP-90)、丙酮酸激酶(pyruvate kinase, PK)以及己糖激酶(hexokinase, HK)均使用江苏酶免实业有限公司试剂盒进行测定。

1.6　免疫指标

肝脏免疫指标：免疫球蛋白 M (immunoglobulin M, IgM)、补体 3 (complement 3, C3)、干扰素-γ (interferon gamma, IFN-γ)、肿瘤坏死因子-α (tumor necrosis factor-α, TNF-α)和白细胞介素(interleukin-1β, IL-1β)均使用江苏酶免实业有限公司试剂盒按照说明书进行测定。

1.7　苏木精–伊红染色

取罗非鱼的肝脏组织后，放置于 4%多聚甲醛中固定 24 h，依次进行脱水浸蜡、组织包埋、切片(厚 4 μm)、脱蜡、苏木精–伊红染色(武汉塞维尔生物科技有限公司)、脱水封片后进行普通光学显微镜(NIKON Eclipse Ci)观察与拍照，采用NIS_F_Ver43000_64bit_E 软件进行图像采集与分析(丁运文, 2018)。

1.8　数据处理与分析

采用 Excel 进行数据计算，SPSS 21.0 软件进行数据分析，不同溶氧含量间的显著性差异使用独立样本 *t* 检验；不同脂肪水平的显著性差异使用 Duncan 氏多重比较法进行比较；再进行双因素方差分析(two-way ANOVA)，以最小显著极差法(LSD)进行比较，实验数值结果以 $P<0.05$ 被认为具有统计学意义，数据用均值±标准差(Mean±SD)表示。

2 结果与分析

2.1 溶氧含量和脂肪水平对罗非鱼生长性能的影响

由表 2 可知，溶氧含量和脂肪水平之间对罗非鱼的 VSI、HSI 均存在显著的交互作用(P<0.05)。在同一溶氧水平，随着脂肪水平的升高 WGR、SGR 和 FE 均先升高后下降，分别在 A2 组、B3 组达到最大值；在低氧 A 组中 HSI 和 VSI 先下降后显著上升(P<0.05)，而在常氧 B 组中 HSI 和 VSI 随脂肪水平增加而升高，B5 组显著高于其他组(P<0.05)。在同一脂肪水平下，B 组的 WGR、SGR 和 VSI 著高于 A 组(P<0.05)，B 组 FE 相对高于 A 组。基于 WGR、SGR 和 FE 与饲料脂肪水平的二次回归模型可知，在常氧环境中投喂 7.61%脂肪水平时，罗非鱼有最大增重率和饲料效率(图 1)。

2.2 溶氧含量和脂肪水平对罗非鱼肝脏组织生化指标的影响

肝脏中的 CAT、T-AOC、AST、Caspase9、CCO 酶活性和 MDA、TG、HL、HK、PK、HSP90 含量均显著受溶氧含量和脂肪水平共同作用的影响(P<0.05)(表 3-1 和表 3-2)，CCO、ATPase 活性只在不同溶氧含量有显著差异(P<0.05)。在同一溶氧水平，随着脂肪水平升高肝脏 AST 活性含量均先降低后升高，A2 组 AST 活性显著低于 A1 组、A4 组、A5 组(P<0.05)，B3 组 AST 活性显著低于 B1 组、B5 组(P<0.05)；B 组 CAT、T-AOC 活性和 A 组 T-AOC 活性均呈现先升高后下降趋势，A 组 CAT、T-AOC 活性低于 B 组；A 组 MDA 含量先下降后升高，而 B 组 MDA 含量逐渐升高，A1 组、A5 组、B5 组显著高于其他组(P<0.05)；A 组中 HK、PK、HSP90 含量和 caspase9 活性显著下降(P<0.05)后趋于平稳趋势，但 B 组中差异不显著(P>0.05)。在同一脂肪水平下，B 组 CCO、ATPase 活性显著高于 A 组(P<0.05)；A 组 AST 活性和 MDA 含量高于 B 组，caspase9 活性和 HK、PK、HSP90 含量显著低于 B 组(P<0.05)。

表 2 溶氧含量和饲料脂肪水平对罗非鱼生长性能的影响

Tab.2 Effects of dissolved oxygen content and dietary lipid level on growth performance of *Tilapia*

溶氧水平 DO level /(mg/L)	脂肪水平 Lipid level /%	生长性能 Growth performance					
		增重率 WGR/%	特定生长率 SGR/(%/d)	脏体比 VSI/%	肝体比 HSI/%	饲料效率 FE/%	存活率 SR/%
A (2)	1(1.57)	2 348.33±141.88^{a}	5.33±0.10^{a}	9.13±0.31^{ab}	2.96±0.04^{b}	57.47±5.11^{a}	100.00
A (2)	2(4.41)	2 892.73±89.31^{b}	5.66±0.06^{c}	8.24±0.01^{a}	2.62±0.30^{a}	83.05±11.65^{b}	100.00
A (2)	3(7.61)	2 861.64±270.16^{b}	5.60±0.2^{bc}	8.70±0.46^{a}	2.64±0.10^{ab}	80.37±21.66^{b}	100.00
A (2)	4(10.51)	2 724.30±79.79^{b}	5.52±0.10^{abc}	9.53±0.41^{bc}	2.72±0.19^{ab}	73.81±4.21^{ab}	100.00
A (2)	5(13.01)	2 682.01±235.68^{b}	5.42±0.16^{ab}	9.79±0.34^{b}	2.81±0.05^{ab}	68.47±5.29^{ab}	100.00
B (5)	1(1.57)	4 332.29±123.78^{ab}	6.32±0.05^{ab}	9.80±0.73^{a}	2.30±0.17^{a}	73.88±5.75^{a}	100.00
B (5)	2(4.41)	4 549.21±234.45^{b}	6.40±0.08^{b}	10.46±0.26^{ab}	2.49±0.10^{ab}	84.06±5.49^{ab}	100.00
B (5)	3(7.61)	4 769.22±316.45^{b}	6.47±0.11^{b}	10.62±0.67^{ab}	2.56±0.12^{b}	95.34±3.11^{b}	100.00
B (5)	4(10.51)	4 673.24±611.37^{b}	6.43±0.21^{b}	10.66±0.32^{ab}	2.84±0.05^{c}	85.77±11.39^{ab}	100.00
B (5)	5(13.01)	3 847.06±333.85^{a}	6.12±0.14^{a}	11.01±0.20^{b}	3.02±0.10^{c}	72.53±11.74^{a}	100.00
双因素方差分析 Two-way ANOVA							
P 值(溶氧) P-value (DO)		0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.046 (*/*/*/*/*)	0.016 (*/*/*/*/*)	–
P 值(脂肪) P-value (lipid)		0.015	0.003	0.001	0.002	0.006	–
P 值(交互) P-value (interaction)		0.115	0.263	0.030	0.001	0.612	–

注：在同一脂肪水平下，不同溶氧组之间的显著性差异用“*”表示，括号内从左至右分别代表 1.57%、4.41%、7.61%、10.51%和 13.01%脂肪水平组，出现“*”表示该脂肪水平下，不同溶氧组之间差异显著。同一溶氧水平下，不同脂肪水平组之间的显著性差异用小写字母表示。下同。

Note: Significant differences between different dissolved oxygen groups at the same fat level are indicated by “*”, with 1.57%, 4.41%, 7.61%, 10.51%, and 13.01% fat level groups represented from left to right in parentheses, and the presence of an “*” indicates that the difference between different dissolved oxygen groups at the fat level is significant. Significant differences between groups of different fat levels at the same level of dissolved oxygen are indicated by lower case letters. The same below.

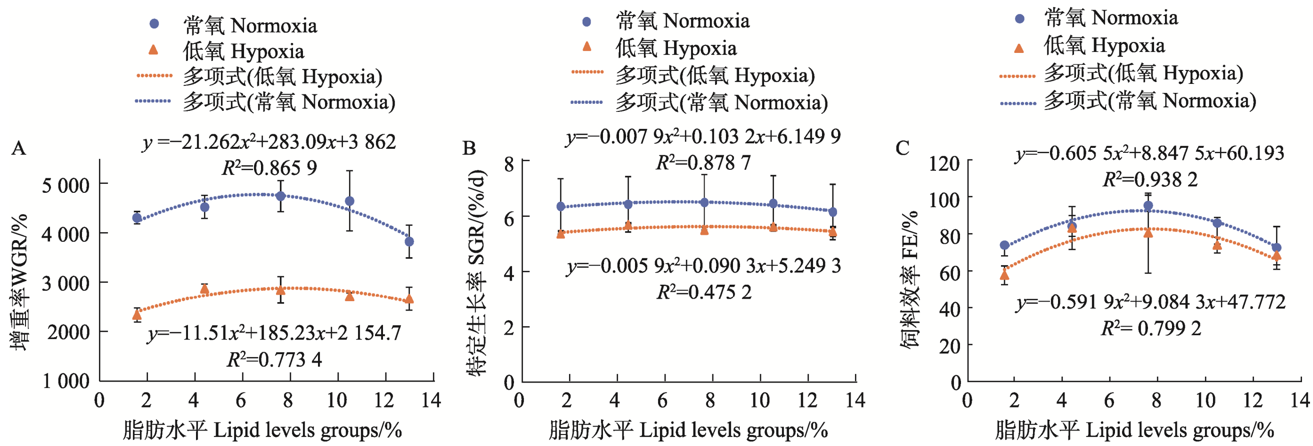

图 1　基于增重率、特定生长率和饲料效率与饲料脂肪水平的二次回归模型

Fig.1　Quadratic regression model of dietary fat level based on WGR, SGR, and FE

2.3　溶氧含量和脂肪水平对罗非鱼肝脏组织免疫指标的影响

由表 4 所示，溶氧含量和饲料脂肪水平分别对罗非鱼肝脏中补体 C3 均具有显著影响(P<0.05)。在 A 组中，随着脂肪水平增加 C3 含量先下降后上升，在 A3 组、A4 组显著低于其他组(P<0.05)，A 组 IFN-γ、IL-1β、lgM、TNF-α 含量显著低于 B 组(P<0.05)。饲料脂肪水平对罗非鱼肝脏免疫指标无显著影响(P>0.05)，2 种因素对免疫指标均不存在交互作用(P>0.05)。

2.4　溶氧含量和脂肪水平对罗非鱼肝脏组织结构的影响

如图 2 所示，在相同溶氧条件下，随着脂肪水平升高，B 组脂滴空泡逐渐增多；A3 组和 A4 组出现大面积的脂滴空泡，但 A5 组中肝组织脂滴空泡有减少，

表 3-1　溶氧含量和饲料脂肪水平对罗非鱼肝脏生化指标的影响

Tab.3-1　Effects of dissolved oxygen content and dietary lipid level on liver biochemical indexes of *Tilapia*

溶氧水平 DO level /(mg/L)	脂肪水平 Lipid level /%	指标 Index 过氧化氢酶 CAT /(U/mg)	总抗氧化能力 T-AOC /(mmol/g)	谷草转氨酶 AST /(U/g)	丙二醛 MDA /(nmol/mg)	甘油三酯 TG /(mmol/g)	肝脂酶 HL /(μmol/L)	细胞色素氧化酶 CCO /(ng/L)
A (2)	1(1.57)	13.27±0.71^{c}	16.31±3.27^{ab}	112.53±9.10^{b}	1.06±0.11^{c}	0.025±0.002^{ab}	105.01±3.06^{a}	239.76±2.66
A (2)	2(4.41)	12.50±0.05^{bc}	19.94±0.91^{b}	73.59±26.54^{a}	0.89±0.06^{b}	0.027±0.001^{b}	105.73±2.58^{a}	243.75±2.47
A (2)	3(7.61)	11.74±0.32^{ab}	15.71±1.14^{b}	98.89±13.54^{ab}	0.75±0.04^{a}	0.030±0.001^{c}	114.10±1.25^{b}	245.39±5.28
A (2)	4(10.51)	10.89±0.88^{a}	15.89±3.43^{b}	116.14±1.27^{b}	0.98±0.06^{bc}	0.032±0.001^{c}	117.30±1.64^{b}	240.70±7.34
A (2)	5(13.01)	11.04±0.47^{a}	15.43±1.76^{a}	157.19±25.11^{b}	1.10±0.08^{c}	0.023±0.001^{a}	106.56±0.18^{a}	237.42±1.07
B (5)	1(1.57)	12.08±0.73^{a}	21.35±2.82^{ab}	78.88±2.71^{b}	0.62±0.06^{a}	0.017±0.001^{a}	123.71±3.01^{a}	292.97±4.52
B (5)	2(4.41)	13.59±0.60^{b}	21.57±2.41^{abc}	56.83±7.17^{a}	0.67±0.10^{a}	0.024±0.002^{b}	129.70±1.12^{b}	280.54±4.68
B (5)	3(7.61)	15.14±0.32^{c}	23.67±2.75^{bc}	57.36±16.12^{a}	0.69±0.09^{a}	0.025±0.002^{bc}	134.65±2.23^{c}	278.90±1.07
B (5)	4(10.51)	11.99±0.59^{b}	25.21±1.81^{c}	65.69±6.36^{ab}	0.74±0.15^{a}	0.027±0.001^{c}	135.04±2.53^{c}	285.23±1.77
B (5)	5(13.01)	11.98±0.59^{a}	18.03±1.36^{a}	133.18±20.20^{c}	1.07±0.12^{b}	0.034±0.001^{d}	136.21±1.91^{c}	282.89±5.58
双因素方差分析 Two-way ANOVA								
P 值(溶氧) P-value (DO)		0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.002 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)
P 值(脂肪) P-value (lipid)		0.001	0.027	0.001	0.001	0.001	0.001	0.170
P 值(交互) P-value (interaction)		0.001	0.024	0.005	0.007	0.001	0.001	0.001

表 3-2 溶氧含量和饲料脂肪水平对罗非鱼肝脏生化指标的影响

Tab.3-2 Effects of dissolved oxygen content and dietary lipid level on liver biochemical indexes of *Tilapia*

溶氧水平 DO level /(mg/L)	脂肪水平 Lipid level /%	指标 Index				
		含半胱氨酸的天冬氨酸蛋白水解酶-9 Caspase 9 /(pmol/L)	己糖激酶 HK /(ng/L)	丙酮酸激酶 PK /(ng/L)	腺苷三磷酸酶 ATPase /(nmol/L)	热休克蛋白-9 HSP 90 /(pg/mL)
A (2)	1(1.57)	32.23±0.08[c]	28.84±0.74[b]	272.03±3.59[b]	1 552.46±39.10	25.42±0.56[c]
A (2)	2(4.41)	26.25±0.62[ab]	23.08±0.54[a]	198.84±4.16[a]	1 596.83±52.20	21.15±0.18[a]
A (2)	3(7.61)	26.53±0.22[a]	22.80±0.25[a]	197.50±2.65[a]	1 550.75±13.55	21.97±0.38[b]
A (2)	4(10.51)	27.17±0.48[b]	23.30±0.48[a]	199.99±4.04[a]	1 562.70±34.85	21.43±0.21[ab]
A (2)	5(13.01)	26.46±0.65[ab]	22.84±0.58[a]	200.76±2.30[a]	1 542.22±56.39	21.50±0.50[ab]
B (5)	1(1.57)	29.94±0.26[a]	26.01±0.64[a]	237.73±1.20[bc]	1 813.55±34.85	23.69±0.36[a]
B (5)	2(4.41)	29.16±0.25[a]	26.32±0.36[a]	232.56±1.33[a]	1 820.38±20.69	23.61±0.36[a]
B (5)	3(7.61)	29.60±0.41[a]	26.01±0.38[a]	236.78±3.83[ab]	1 777.72±30.00	23.43±0.34[a]
B (5)	4(10.51)	29.67±0.35[a]	25.91±0.44[a]	233.14±3.17[ab]	2 132.67±604.58	23.82±0.11[a]
B (5)	5(13.01)	29.48±0.91[a]	26.18±0.65[a]	241.95±1.66[c]	1 827.21±41.90	23.50±0.34[a]
双因素方差分析 Two-way ANOVA						
P 值(溶氧) *P*-value (DO)		0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)
P 值(脂肪) *P*-value (lipid)		0.001	0.001	0.005	0.495	0.001
P 值(交互) *P*-value (interaction)		0.001	0.001	0.001	0.516	0.001

表 4 溶氧含量和饲料脂肪水平对罗非鱼肝脏免疫指标的影响

Tab.4 Effects of dissolved oxygen content and dietary lipid level on liver immune indexes of *Tilapia*

溶氧水平 DO level /(mg/L)	脂肪水平 Lipid level /%	指标 Index				
		干扰素-γ IFN-γ/(ng/L)	白细胞介素 IL-1β/(ng/L)	补体 3 C3/(μg/mL)	免疫球蛋白 M IgM/(μg/mL)	肿瘤坏死因子-α TNF-α/(ng/L)
A (2)	1(1.57)	73.37±1.73	32.20±0.45	356.601.75[b]	3.53±0.02	317.61±8.9
A (2)	2(4.41)	72.33±1.43	32.95±0.86	350.12±8.01[b]	3.53±0.07	317.25±5.06
A (2)	3(7.61)	75.08±0.67	32.29±0.75	341.35±2.88[a]	3.55±0.06	321.66±9.04
A (2)	4(10.51)	71.96±0.67	32.56±0.45	348.98±2.29[a]	3.59±0.06	323.87±12.44
A (2)	5(13.01)	72.25±2.64	32.98±0.23	357.37±4.02[b]	3.55±0.02	311.36±7.99
B (5)	1(1.57)	86.51±2.01	34.83±0.65	411.12±9.73	4.00±0.04	363.25±8.14
B (5)	2(4.41)	86.81±2.02	35.13±0.75	415.69±1.75	3.99±0.06	370.61±6.08
B (5)	3(7.61)	85.99±1.34	34.68±0.51	406.16±3.03	3.99±0.06	369.87±3.37
B (5)	4(10.51)	86.14±0.84	34.74±0.65	414.93±5.40	4.02±0.06	369.14±8.83
B (5)	5(13.01)	86.81±1.36	35.49±0.36	411.12±5.16	4.04±0.03	369.51±8.29
双因素方差分析 Two-way ANOVA						
P 值(溶氧) *P*-value (DO)		0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)	0.001 (*/*/*/*/*)
P 值(脂肪) *P*-value (lipid)		0.588	0.151	0.011	0.476	0.573
P 值(交互) *P*-value (interaction)		0.277	0.952	0.102	0.810	0.610

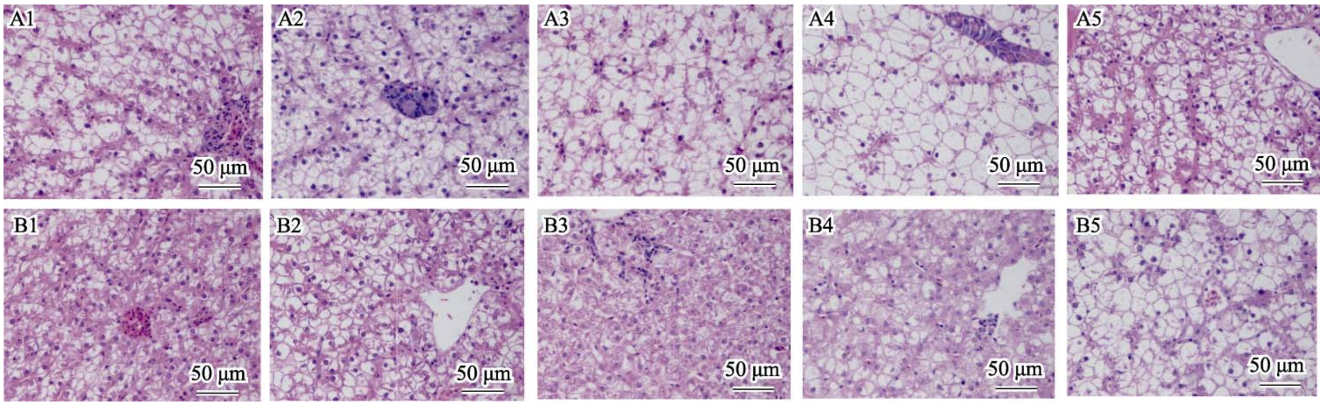

图 2　溶氧含量和饲料脂肪水平对罗非鱼肝组织结构的影响
Fig.2　Effects of dissolved oxygen content and dietary lipid level on hepatic histology of *Tilapia*

A2 组肝细胞形态结构正常。在相同脂肪水平下，A 组肝细胞出现的脂滴空泡比 B 组多，且 A3 组、A4 组和 B5 组细胞核溶解、发生明显偏移的现象。

3　讨论

3.1　溶氧含量和饲料脂肪水平对罗非鱼的生长性能的影响

目前，关于不同溶氧含量和饲料脂肪水平的交互作用对鱼类生理机能的影响研究比较匮乏。但已经有大量研究表明，水中缺氧会降低饲料效率，抑制鱼类的生长。本研究中，低氧组罗非鱼的 WGR、SGR 和 FE 明显降低，与 Thorarensen 等(2010)、Sun 等(2012)和 Yang 等(2015)研究结果一致。实验中 A1 组罗非鱼的 WGR、SGR 和 FE 显著低于其他组，可能跟机体需要消耗更多的能量来抵抗应激，再加上过低的脂肪喂养已经造成机体的营养不良有关，最终导致罗非鱼生长缓慢、肝脏等器官的发育受到限制(Ali *et al*, 2024; 陈德举等, 2019)。当饲料脂肪水平提高至 4.41%时，即 A2 组罗非鱼生长会有明显提高。随着饲料脂肪水平的增加，常氧组、低氧组罗非鱼的生长性能出现先升高后下降的趋势，A2 组和 B3 组罗非鱼分别具有最好的生长性能和饲料效率，与王爱民等(2014)研究结果相似。说明在不同溶氧环境下，适宜的脂肪含量能促进罗非鱼生长。在本研究中，生长性能指标的主效应检验结果显示，溶氧是对罗非鱼生长起主导作用的因子，罗非鱼生长性能提高，原因可能是适宜的溶氧有助于提高罗非鱼的饲料效率，再加上适宜的营养满足机体的需求，使罗非鱼具有更好的生长性能。

3.2　溶氧含量和饲料脂肪水平对罗非鱼生化指标的影响

CAT 具有清除氧自由基(ROS)的能力，可阻止活性氧诱导的氧化应激的产生，保护机体免受过氧化损伤(刘婷婷等, 2019)，而 T-AOC 能反映出机体中各抗氧化分子和酶的总抗氧化能力。熊向英等(2016)研究发现，鲻(*Mugil cephalus*)可以通过提高自身抗氧化应激能力来应对低氧胁迫，以此来缓解氧化应激对组织细胞膜质的损伤。本研究中，A1 组 CAT 活性显著高于其他低氧组，可能是罗非鱼应对低氧极端生存环境和低脂营养条件时采取提高自身的抗氧化能力的应对策略(Lushchak *et al*, 2001)；在常氧 B 组中，随着脂肪水平的升高，CAT、T-AOC 活性均呈现先升高后下降的趋势，与薛晓强等(2018)对血鹦鹉(*Cichlasoma synspilum* ♀×*Cichlasoma citrinellum* ♂)的研究结果类似。说明投喂适宜的脂肪水平饲料可以提高罗非鱼的抗氧化能力。MDA 是反映机体应对氧化应激和机体氧化损伤程度的重要指标，生物机体在正常状态下的 MDA 含量很低(陈莹等, 2024)。本研究中，在常氧条件下，肝脏中 MDA 含量随着脂肪水平的升高而升高，与三倍体虹鳟(*Oncorhynchus mykiss*) (千康康, 2019)、彭泽鲫(*Carassius auratus var. Pengze*)(付辉云等, 2020)和丝尾鳠(*Hemibagrus wyckioides*)幼鱼(张姚铮泰等, 2024)的结果趋势相同。本研究的结果也支持张春暖等(2013)低氧和投喂高脂饲料均会导致肝脏中 MDA 的积累，且在溶氧和脂肪水平交互作用的影响下，低氧的 MDA 含量相对更高，低氧和投喂高脂饲料的叠加效应可能会导致罗非鱼肝脏发生更高的氧化损伤的推测。

PK 和 HK 均是参与糖酵解途径中的关键酶，二者活性变化在维持血糖水平和能量代谢中起重要的调节作用。有研究报道，多鳞四须鲃(*Barbodes schwanenfeldi*) (朱志明, 2014)、鲤(*C. carpio*) (王文娟等, 2023) 以及大黄鱼(*Pseudosciaena crocea* Richardson) (马红娜等, 2016)的 PK 和 HK 含量均随着

饲料脂肪水平的升高而升高，并认为高脂饲料可以提高肝脏糖代谢活性，与本研究结果相似，可能是肝脏营养过剩促进肝脏脂代谢相关酶活性的上升，进而激活肝脏对内源性脂肪的转运和加工，进一步增加了肝细胞能量耗损发生(向枭等, 2013)。郭志雄等(2020)研究发现，急性低氧胁迫后，军曹鱼肝脏中PK、HK含量均升高，ATPase活性显著下降。但本研究结果为在长期缺氧的条件下，肝脏的PK、HK、ATPase均低于常氧组，原因可能是罗非鱼已适应长期缺氧的环境，肝脏组织缺氧状况加重，加强了无氧呼吸供能，而削弱了有氧呼吸代谢(齐明等, 2020)。

TG和HL是脂质代谢中至关重要的指标，含量大幅度变化会引起肝脏功能失常(朱婷婷等, 2018)。军曹鱼幼鱼(王维政等, 2021)、大口黑鲈(*Micropterus salmoides*)(朱婷婷等, 2018)、尼罗罗非鱼(*O. niloticus*)(Li *et al*, 2018)及吉富罗非鱼(Ma *et al*, 2021)等研究发现，TG含量随着脂肪水平升高而显著提高。以上结果均与本研究结果的变化趋势部分相同。但不同的是，在低氧A组中，肝脏TG含量呈现先升高后在A5组显著下降的趋势，结合前面的生化指标，推测是低氧和高脂共同作用下造成的肝组织严重氧化损伤使肝脏脂质代谢能力受损或阻碍。TG浓度受HL影响(黄秀芸, 2015)，张春暖等(2013)研究发现，梭鱼(*Chelon haematocheilus*) HL含量随着饲料脂肪水平的升高显著增高。在本研究中，肝脏HL含量显著受到低氧和脂肪水平的共同作用，低氧组的HL含量显著低于常氧组，提示在低氧环境中投喂过低和过高脂肪水平的饲料可能不利于罗非鱼机体进行脂质的合成与代谢(吕宏波, 2020)。

3.3 溶氧含量和饲料脂肪水平对罗非鱼免疫的影响

实验发现，溶氧含量和脂肪水平的交互作用对lgM、C3、TNF-α、IFN-γ和IL-1β免疫指标均无显著性影响，但这些免疫因子的变化均与溶氧含量显著相关。Welker等(2010)研究发现，斑点叉尾鮰(*Ictalurus punctatus*)在缺氧5 d后，补体CH50和杀菌活性均显著降低，表明低氧会抑制鱼的免疫水平。在本研究中，低氧组中的免疫因子显著低于常氧组，这与Sheng等(2019)和鲁伦文(2011)的研究结果趋势相似，在低氧环境下，鱼类的补体C3和C4等免疫活性显著降低，可能是罗非鱼对长期缺氧环境的适应性，导致这些免疫因子活性受抑制(张雷敏等, 2023)，具体待进一步研究。

3.4 溶氧含量和饲料脂肪水平对罗非鱼肝组织结构的影响

过高的脂质营养会引起肝组织结构的变化和肝组织损伤，严重时造成脂肪肝(孔雨昕等, 2020; 张梦慈, 2017)。本研究中，常氧条件下B组肝细胞空泡逐渐增多、脂肪变性的程度与饲料脂肪水平呈正相关，这与美国红鱼(*Sciaenops ocellatus*)(李雪菲等, 2015)结果相同，说明常氧条件下高脂饲料容易导致脂肪在肝脏中大量的积累。有研究发现，缺氧胁迫会导致肝细胞损伤、细胞核裂解、死亡以及炎症反应(Paternostro *et al*, 2010; 陈世喜, 2016)。在低氧组的罗非鱼肝脏细胞出现脂肪滴，而在低氧和过高饲料脂肪投喂的叠加作用下，加重了肝脂肪堆积，导致肝脏脂肪空泡增多以及细胞核偏移的现象发生。低氧和投喂饲料脂肪含量过高可能造成肝组织的严重损伤和肝脏代谢的紊乱，进而导致机体无法充分合理的利用脂肪和进行机体代谢。A2组肝细胞形态结构正常，未见异常，猜测是投喂中低脂水平(4.41%)饲料可以满足在低氧环境中维持机体的基本代谢。

4 总结

结合生长指标、肝脏生化、免疫指标以及肝脏组织切片结构的观察发现，低氧下低脂和高脂的饲料均会影响脂质营养的有效利用，还会导致更严重的肝脏氧化损伤和脂肪堆积，发生脂质代谢功能障碍和降低免疫能力。在本研究范围内，低氧时投喂脂肪水平为4.41%左右的饲料能促进罗非鱼的生长和改善低氧应激，而在常氧环境中投喂脂肪水平为7.61%左右的饲料有利于罗非鱼的生长。

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Interaction of Dissolved Oxygen and Feed Fat Levels on Physiological Functions of Nile *Tilapia*

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Abstract *Oreochromis niloticus* (Nile *Tilapia*), has the advantages of rapid growth, versatile feeding habits, the absence of intermuscular thorns, and robust stress resistance. Moreover, it is abundant in essential amino acids and unsaturated fatty acids, making it highly nutritious. Since 1976, the Food and Agriculture Organization of the United Nations has recognized *Tilapia* as a suitable fish for global cultivation. The farming model for Nile *Tilapia* in China is gradually shifting from traditional flowing water systems to high-density factory farming systems. However, oxygen deficiency is a common factor that leads to fish mortality in high-density intensive farming settings. Therefore, close attention must be paid to the dissolved oxygen (DO) status of aquaculture environments. DO is essential for maintaining normal metabolic activity in aquatic organisms and significantly impacts their growth, immunity, and energy metabolism. Studies have shown that fish can cope with low-oxygen environments through a series of physiological mechanisms. Under hypoxic conditions, fish utilize stored energy reserves (carbohydrates and lipids) to maintain their activities. Owing to the low utilization rate of carbohydrates in fish, utilizing lipids to provide energy is the optimal choice for them to adapt to low-oxygen environments. Owing to the low utilization rate of carbohydrates in fish, utilizing lipids to provide energy is the optimal choice for them to adapt to low-oxygen environments. *Tilapia* subjected to prolonged hypoxia utilized more lipids in response to hypoxic stress, suggesting that diets supplemented with appropriate lipid levels can enhance fish survival. However, the precise underlying mechanism remains unclear. This study aimed to investigate the interactive effects of DO content and fat levels on the growth performance, hepatic antioxidant capacity, immune parameters, and liver tissue structure of Nile *Tilapia*. The experiment was conducted using *Tilapia* with an initial weight of (7.62±0.29) g as the subjects. Two DO contents: hypoxia [(2.0±0.1) mg/L, group A] and normoxia [(5.0±0.1) mg/L, group B] and five fat levels (groups 1–5: 1.57%, 4.41%, 7.61%, 10.51%, and 13.01%) were applied, including three replicates per group. The culture period was 60 days. The results showed that as fat levels increased, the weight gain rate (WGR), specific growth rate (SGR), and feed efficiency of groups A and B first increased and then decreased, reaching maximum values in groups A2 and B3. At the same fat level, WGR and SGR were significantly higher in Group B than in Group A. Hepatic enzyme activities and content of various parameters, including catalase (CAT), total antioxidant capacity (T-AOC), aspartate transaminase (AST), cytochrome c oxidase (CCO), caspase-9, heat shock protein-90, malondialdehyde (MDA), hexokinase (HK), pyruvate kinase (PK), triglycerides, and hepatic lipase, were significantly affected by the interaction between oxygen levels and fat levels, whereas there was no interaction effects on adenosine triphosphatase (ATPase) activity between the two factors. With the increase in lipid levels, the CAT activity and T-AOC in group B and T-AOC in group A first increased and then decreased; the T-AOC in group A was lower than that in group B, and the B3CAT activity was significantly higher than that in the other groups. MDA content in group B increased gradually with the

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increase in fat level, that in group A decreased first and then increased, and that in group A was higher than that in group B. Under the same lipid level, the CCO and ATPase activities in group B were significantly lower than those in hypoxia group A. AST activity, T-AOC, and MDA content in group A were higher than those in group B, whereas caspase9 activities and HK, PK, and HSP90 contents in group B were significantly lower. Immune indicators, including immunoglobulin M, interferon-gamma, tumor necrosis factor-alpha, and interleukin-1 beta, were significantly lower in group A compared to Group B and were not affected by fat level. DO and dietary fat levels significantly affected complement C3 in the liver of *Tilapia*. In groups A and C3, the content first decreased and then increased with an increase in fat level and was significantly lower in groups A3 and A4 than in the other groups. With increasing fat levels, the number of hepatic lipid vacuoles gradually increased in group B, whereas the cell morphology in group A2 was normal. Groups A3, A4, and B5 showed numerous lipid vacuoles, nuclear dissolution, and displacement. In summary, low oxygen levels and excessive dietary lipid levels lead to severe liver oxidative damage, fat accumulation, dysfunction of lipid metabolism, and reduced immune capacity. Within the scope of this experiment, feeding a diet with a fat content of approximately 4.41% during low oxygen conditions promoted the growth of Nile *Tilapia* and alleviated hypoxic stress, whereas feeding a diet with a fat content of approximately 7.61% in normoxic environments benefited the growth of Nile *Tilapia*.

Key words　*Oreochromis niloticus*; Dissolved oxygen; Fat level; Interaction; Liver function; Immune index