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捕食胁迫对“四大家鱼”幼鱼生理反应的影响*

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摘要 本研究选取乌鳢(*Channa argus*)和南方大口鲶(*Silurus soldatovi meridionalis*)为捕食者, 青鱼(*Mylopharyngodon piceus*)、草鱼(*Ctenopharyngodon idellus*)、鲢(*Hypophthalmichthys molitrix*)、鳙(*Aristichthys nobilis*)幼鱼为猎物鱼, 比较了在无捕食(空白对照)、低捕食(隔网胁迫)和高捕食(直接胁迫)压力下, 胁迫 0、7、14 d 后, “四大家鱼”幼鱼血清皮质醇(COR)水平和血液生化指标的变化。结果显示, 不同捕食胁迫水平下, “四大家鱼”幼鱼的血液生化指标和 COR 水平变化程度不同, 但变化趋势一致。“四大家鱼”幼鱼的 COR 水平随着捕食胁迫程度和胁迫时长的增加显著升高, 表现为无捕食组<低捕食组<高捕食组, 0 d<7 d<14 d。在血液生化指标中, 血清蛋白浓度和总胆固醇(CHO)浓度较为稳定, 各组相比无显著变化; 血糖(GLU)浓度和碱性磷酸酶(ALK)在捕食胁迫下升高, 甘油三酯(TG)则相反, 呈下降趋势。研究表明, “四大家鱼”幼鱼会根据捕食风险来增强自身生存能力的方式及调整生理反应。捕食胁迫处理后, “四大家鱼”幼鱼均产生了应激反应, 与隔网捕食相比, 直接捕食对鱼体生理反应影响更为显著, 且随着胁迫时长的增加应激程度也随之增加。各检测指标中, 血清蛋白和 CHO 可能不是捕食胁迫下鱼类应激的敏感指标; COR 和 GLU 的变化最为显著, 这可能是为了弥补应激期间机体对能量需求的增大。

关键词 捕食胁迫; 皮质醇; 血液生化指标; 四大家鱼

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在自然界中, 鱼类常改变其生理和行为特征以应对不断变化的环境条件, 捕食是影响个体生存的主要环境因素之一(Killen *et al*, 2016; Lima, 1998a; Spiegel *et al*, 2013)。猎物应对捕食者的存在会使其产生生理应激和能量代谢, 已有研究表明, 猎物与捕食者相遇会减少猎物的进食和其他与健康相关的活动(Barcellos *et al*, 2007; Breves *et al*, 2005; Woodley *et al*, 2003)。在捕食胁迫环境下, 鱼在感知到压力后会启

动应激反应, 使其能克服压力恢复体内平衡(Schreck *et al*, 2016)。应激的程度主要取决于压力的强度和持续时间(Lima *et al*, 1999; 张宇婷等, 2021)。若捕食者出现间歇性, 并且猎物鱼在遭遇捕食后生理状态在短时间内恢复正常, 此时的应激反应可以促进猎物鱼的生理改变以更好地适应环境(Cooke *et al*, 2003)。然而, 在压力重复或持续且无法避免的情况下, 猎物鱼的正常生理反应机制可能会受到损害, 生理应激可能

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对免疫系统、生长或繁殖产生长期的负面影响,并降低猎物鱼的适应性和生存能力(Barton, 2002; Colson *et al.*, 2015; Redfern *et al.*, 2017)。已有研究表明,捕食胁迫会对鱼类造成生理应激,但不同鱼种甚至相同鱼种的不同群体对胁迫的应激程度和应激方式都有较大的差异,仍需要更多的物种特异性研究来确定捕食胁迫的长度和强度对鱼类生理应激的影响。

捕食胁迫导致鱼体产生应激反应的一个重要表现为血液中应激激素含量的升高(Clinchy *et al.*, 2004; Frid *et al.*, 2002; Lima, 1998b)。皮质醇是鱼体在受到外界刺激后分泌的一种重要应激激素,能灵敏反映鱼体的胁迫状况(Clinchy *et al.*, 2011; Wendelaar *et al.*, 1997)。鱼类在面临被捕食的风险产生应激并做出行为和生理改变时,鱼体的营养状况和代谢机能也会发生改变(Benson *et al.*, 2019)。因此,捕食胁迫下鱼体应激的另一个重要表现为鱼体内血液生化指标的变化。血液的生化组成包括血糖(glucose, GLU)、血脂、血清蛋白以及酶等成分,是评价环境应激时鱼类的健康状况、营养状况及对环境的适应状况的重要指标(洪磊等, 2004)。GLU 作为鱼体内主要供能物质,其含量与鱼类代谢水平和营养状况直接相关,当其含量不足时,血脂和血清蛋白也会被鱼体利用,三者之间存在着相互转换关系(陈剑杰等, 2009)。除此之外,血清中的许多酶成分也是反映鱼体胁迫状况的重要指标(于森等, 2008)。

青鱼(*Mylopharyngodon piceus*)、草鱼(*Ctenopharyngodon idellus*)、鲢(*Hypophthalmichthys molitrix*)、鳙(*Aristichthys nobilis*)合称为“四大家鱼”,是中国长江流域常见的鲤科(Cyprinidae)鱼类。多年来,由于水力建设、环境污染、过度捕捞等诸多原因导致其野外种群数量急剧下降(Duan *et al.*, 2009; 刘飞等, 2019),此外,在自然水域中,捕食者的普遍存在也对其数量的增长造成威胁。目前,尚不清楚当捕食压力持续存在时,“四大家鱼”幼鱼如何调整其生理过程以应对捕食压力?多数与捕食胁迫相关的研究通常仅选择血液激素中皮质醇(cortisol, COR)水平来反映鱼类生理反应的变化,而没有对捕食胁迫下鱼类的能量代谢进行多方面评估。因此,为了系统探讨鱼类的生理反应和捕食胁迫的内在联系,本研究选取了“四大家鱼”幼鱼为研究对象,分析了不同捕食胁迫水平对血清 COR 和血液生化指标的影响。研究捕食胁迫条件下,“四大家鱼”幼鱼的生理应激和能量代谢对捕食压力的适应性,可为深入研究环境变化引起的机体应激反应提供理论依据,也可为增殖放流前的捕食驯化提供数据参考。

1 材料与方法

1.1 实验鱼来源与驯养

本实验于 2021 年 5—7 月在长江“四大家鱼”监利老江河原种场开展,猎物鱼幼鱼(青鱼、草鱼、鲢和鳙)及捕食者[乌鳢(*Channa argus*)和南方大口鲶(*Silurus soldatovi meridionalis*)]均取自老江河原种场,其中,“四大家鱼”幼鱼为原种场人工繁殖鱼苗。实验鱼分别放入规格为 4 m×2 m×1.2 m 的长方形水泥养殖池中驯养 14 d。驯养期间,“四大家鱼”幼鱼每天 09:00 和 17:00 投喂 2 次商业饲料,投喂量为池内实验鱼体重总和的 3%;乌鳢、南方大口鲶与不用于实验的“四大家鱼”幼鱼混养,不额外投喂饲料,用于混养投喂捕食者的“四大家鱼”幼鱼与用于测定的实验鱼取自同一批次幼鱼,比例及规格均相近。养殖用水取自老江河,驯养温度为 25~29 °C,溶解氧(DO)为 7~8 mg/mL。

1.2 实验设计

14 d 驯养结束后,每种实验鱼各随机选择体长和体重相近的样本[青鱼: (8.81±0.22) cm, (11.73±0.62) g, $n=400$; 草鱼: (8.33±0.19) cm, (10.23±0.72) g, $n=400$; 鲢: (8.43±0.15) cm, (9.10±0.36) g, $n=400$; 鳙: (8.50±0.11) cm, (11.10±0.36) g, $n=400$]分类别按捕食胁迫程度将每种鱼随机分为 3 组,无捕食组(对照组)、低捕食组(隔网胁迫)和高捕食组(直接捕食)共 12 组。为尽量保证除捕食胁迫外的其余因素一致,将低胁迫组与高胁迫组放置在同一水体中。从图 1 可以看出, D、E(D、E 为对照组, D、E 组各放入 100 尾实验鱼)、H(低捕食组)、I(高捕食组)各放入 100 尾同种实验鱼。对照组中,拦网两侧不放入捕食者,捕食组中将乌鳢[(33.64±0.86) cm, (456.82±10.21) g]和南方大口鲶[(35.13±0.64) cm, (421.43±6.12) g]各 1 尾作为共同捕食者一起放入。低捕食组实验鱼与捕食者被拦网隔开,无直接接触;高捕食组实验鱼与捕食者处于拦网同侧,捕食者可直接捕食高捕食组实验鱼(图 1)。捕食胁迫期间,“四大家鱼”幼鱼的投喂同驯养期间一致,捕食者不额外投喂,其食物来源为混养的用于测定的实验鱼。捕食胁迫处理 0、7、14 d 后,随机选取身体健康、大小接近的实验鱼,分别测定其体长、体重、COR 和血液生化指标($n=9$)。捕食胁迫期间为微流水养殖,水深保持在 0.6 m 左右,水温为(27.75±1.05) °C, DO 为(7.82±0.84) mg/L, pH 为 8.16±0.05,氨氮(NH₄⁺-N)含量<0.10 mg/L。

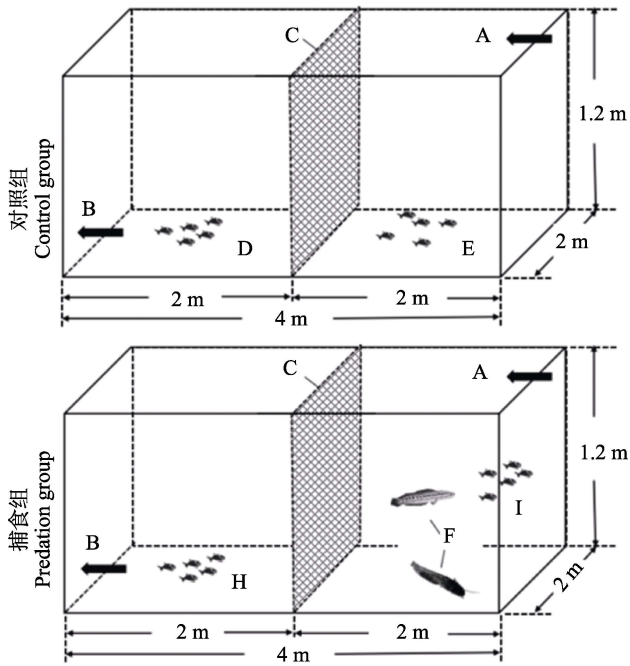


图1 实验装置示意

Fig.1 Schematic diagram of the test device

A: 进水口; B: 出水口; C: 尼龙拦网(孔径为 $0.5\text{ cm} \times 0.5\text{ cm}$); D、E: 无捕食组(对照组), 各放 100 尾实验鱼, 不放入捕食者; F: 捕食者(乌鳢和南方大口鲶各 1 尾); H: 低捕食组, 实验鱼($n=100$)与捕食者分开隔网可见; I: 高捕食组, 实验鱼($n=100$)中放入双捕食者: 乌鳢和南方大口鲶各 1 尾。

A: Water inlet; B: Water outlet; C: Nylon block ($0.5\text{ cm} \times 0.5\text{ cm}$); D and E: No predation group (control group), each with 100 experimental fish, but no predators; F: Predators (one snakehead and one southern catfish); H: Low predation group, experimental fish ($n=100$) and predators were separated by net but can see each other; I: High predation group, two predators, one snakehead and one southern catfish, were added to experimental fish ($n=100$).

1.3 血清制备及生化指标的测定

采样前,将鱼停食 24 h;取样时,先采用 0.1 g/mL 的 MS-222 分别将“四大家鱼”幼鱼麻醉,使用 1 mL 的一次性无菌注射器从实验鱼尾静脉采血,采集的血液于离心管中 $4\text{ }^{\circ}\text{C}$ 下静置 4 h 后, 4000 r/min 低温离心 10 min 至完全分层,收集上层澄清透明的血清。血清生化指标采用英诺华 DS-261 全自动分析仪进行测定。检测指标包括总蛋白(total protein, TP)、白蛋白(albumin, ALB)、球蛋白(globulin, GLB)、GLU、总胆固醇(tholesterol, CHO)、甘油三酯(triglyceride, TG)、碱性磷酸酶(alkaline phosphatase, ALP)。COR 采用酶联免疫法 ELISA 进行测定,试剂盒购自南京建成科技有限公司。

1.4 数据分析

实验数据采用 Excel 2019 软件进行整理和统计,使用 Origin 2021 软件和 SPSS 26.0 软件进行统计分析及绘图。捕食胁迫程度和捕食胁迫时长对 COR 和血液生化指标的影响采用双因素协方差分析(two-way ANOVA),以体重作为协方差。若差异显著,利用 Duncan 法进行多重比较。所有数据结果均以平均值 \pm 标准误(Mean \pm SE)表示, $P < 0.05$ 为差异显著。

2 结果与分析

因考虑到高捕食组存在猎物鱼被捕食情况,捕食胁迫前,各实验组猎物鱼数量在取样所需基础上已增加放养密度,捕食胁迫期间不补充,仅记录各实验组死亡数目。14 d 胁迫实验结束后,统计高捕食组猎物鱼被摄食量并计算被摄食率(表 1)。从表 1 可以看出,各实验组均存在实验鱼死亡现象,主要为较小规格的实验鱼卡在拦网上无法挣脱导致其死亡,除此之外,鱼类无异常行为。

2.1 血清皮质醇(COR)

7 d 胁迫处理后,青鱼、草鱼、鲢和鳙低捕食组 COR 水平升高幅度分别为 9.65%、7.33%、18.71% 和 17.13%。高捕食胁迫组升高幅度分别为 18.57%、26.28%、48.76% 和 46.79%; 14 d 胁迫处理后,低捕食胁迫组升高幅度分别为 36.28%、31.95%、28.29% 和 32.36%,高捕食胁迫组升高幅度分别为 47.39%、54.44%、57.98% 和 49.89%。

在捕食胁迫 7 d 后,低捕食组的 COR 水平升高,但与无捕食组相比差异不显著;高捕食组青鱼、鲢和鳙的 COR 水平显著高于对照组,且高捕食组鲢和鳙的 COR 水平显著高于低捕食组;捕食胁迫 14 d 后,低捕食组和高捕食组的 COR 水平均显著高于无捕食组,其中,高捕食组鲢的 COR 水平显著高于低捕食组。

在不同捕食胁迫时长中,低捕食组“四大家鱼”幼鱼的 COR 水平在胁迫 14 d 后显著高于低捕食 0 d,其中,青鱼和草鱼的 COR 水平在低捕食胁迫 14 d 显著高于低捕食 7 d;高捕食组的 COR 水平在捕食胁迫 7 和 14 d 后均显著高于 0 d,其中,青鱼和草鱼 14 d 捕食胁迫后, COR 水平显著高于 7 d ($P < 0.05$) (表 2 和图 2)。

2.2 营养状况和代谢水平

2.2.1 血清蛋白 不同的捕食胁迫程度和胁迫时长对“四大家鱼”幼鱼的 TP、ALB 和 GLB 浓度影响均不显著(表 2 和图 3)。

2.2.2 CHO 和 TG 不同的捕食胁迫程度和胁迫时长对“四大家鱼”幼鱼的血清胆固醇浓度影响不显著,但 TG 浓度降低。7 d 胁迫处理后,青鱼、草鱼、鲢和鳙低捕食组 TG 浓度的下降幅度分别为 2.25%、4.21%、4.32%和 11.48%;高捕食胁迫组下降幅度分别为 1.82%、5.73%、2.51%和 7.40%;14 d 胁迫处理后,低捕食胁迫组下降幅度分别为 22.41%、33.00%、10.00%和 10.59%,高捕食胁迫组下降幅度分别为 44.93%、39.58%、17.56%和 15.64%。

在不同捕食胁迫中,青鱼、草鱼低捕食组和高捕食组的 TG 浓度与无捕食组相比无显著差异。但在不同的捕食胁迫时长中,低捕食组草鱼和高捕食组的青鱼、草鱼在捕食胁迫 14 d 后的 TG 浓度显著低于 0 和 7 d,其中,0 和 7 d 的 TG 浓度相比差异不显著(表 2 和图 4)。

2.2.3 GLU 7 d 胁迫后,青鱼、草鱼、鲢和鳙低捕食组 GLU 浓度升高幅度分别为 12.43%、20.52%、4.66%和 28.60%,高捕食胁迫组 GLU 浓度升高幅度分别为 26.78%、5.03%、14.96%和 18.68%;14 d 胁迫

处理后,低捕食胁迫组 GLU 浓度升高幅度分别为 64.08%、59.45%、44.36%和 49.05%,高捕食胁迫组血糖浓度升高幅度分别为 81.00%、59.68%、45.02%和 37.06%(表 2)。

在不同捕食胁迫中,捕食胁迫 7 d 后,低捕食组“四大家鱼”幼鱼的 GLU 浓度上升,但与无捕食组相比差异不显著($P>0.05$),高捕食组仅青鱼的 GLU 浓度显著高于无捕食组;捕食胁迫 14 d 后,低捕食组和高捕食组的 GLU 浓度均显著高于无捕食组,其中,高捕食组和低捕食组相比无显著差异($P>0.05$)(图 5)。

在不同捕食胁迫时长中,草鱼的 GLU 浓度升高但差异不显著。低捕食组青鱼和鲢捕食胁迫 14 d 的 GLU 浓度显著高于 0 和 7 d;低捕食组鳙胁迫 14 d 的 GLU 浓度显著高于 0 d。青鱼、鲢和鳙低捕食胁迫 0 和 7 d 的 GLU 浓度相比无显著差异($P>0.05$);高捕食组青鱼捕食胁迫 0、7 和 14 d 的 GLU 浓度随着捕食时长的增加显著升高,高捕食组鲢和鳙捕食胁迫 14 d 的 GLU 浓度显著高于 0 d(表 2 和图 5)。

表 1 捕食胁迫期间“四大家鱼”幼鱼的存活情况
Tab.1 Survival of juvenile “four major Chinese carps” during predation stress

种类 Species	胁迫水平 Stress level	总量/尾 Total number/ind.	死亡数量/尾 Number of deaths/ind.	被摄食量/尾 Number of predated/ind.	被摄食率 Predation rate/%	成活率 Survival rate/%
青鱼 <i>M. piceus</i>	无捕食 No predation	100	3	0	—	97.0
	低捕食 Low predation	100	2	0	—	98.0
	高捕食 High predation	100	4	8	8.0	88.0
草鱼 <i>C. idellus</i>	无捕食 No predation	100	4	0	—	96.0
	低捕食 Low predation	100	2	0	—	98.0
	高捕食 High predation	100	5	6	6.0	89.0
鲢 <i>H. molitrix</i>	无捕食 No predation	100	2	0	—	98.0
	低捕食 Low predation	100	1	0	—	99.0
	高捕食 High predation	100	1	9	9.0	90.0
鳙 <i>A. nobilis</i>	无捕食 No predation	100	1	0	—	99.0
	低捕食 Low predation	100	3	0	—	97.0
	高捕食 High predation	100	2	13	13.0	85.0

表 2 捕食胁迫程度(无捕食、低捕食和高捕食)和捕食胁迫时长(0、7、14 d)对“四大家鱼”幼鱼 COR 和血液生化指标的双因素方差统计分析

Tab.2 Summary of the two-way ANOVA model on serum cortisol and biochemical parameters of juvenile “four major Chinese carps” exposed to different degree (no predation, low predation, high predation) and duration(0 d,7 d and 14 d) of predation stress

测定指标 Index	变量 Variable	青鱼 <i>M. piceus</i>		草鱼 <i>C. idellus</i>		鲢 <i>H. molitrix</i>		鳙 <i>A. nobilis</i>	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
皮质醇 Cortisol/(ng/mL)	协变量(体重) Covariate (Body mass)	0.336	0.570	0.118	0.735	0.051	0.824	2.244	0.152
	胁迫程度 Degree	7.110	0.006*	8.613	0.003*	15.129	0*	14.390	0*
	胁迫时长 Duration	6.782	0.007*	7.527	0.005*	16.970	0*	18.850	0*
	交互作用 Interaction	5.140	0.007*	3.557	0.028*	3.237	0.038*	5.820	0.004*
总蛋白 Total protein/(g/L)	协变量(体重) Covariate (Body mass)	5.285	0.034*	0.233	0.636	0.161	0.694	0.562	0.464
	胁迫程度 Degree	0.919	0.418	0.117	0.891	0.024	0.976	0.360	0.703
	胁迫时长 Duration	1.527	0.246	0.133	0.876	0.209	0.814	0.185	0.833
	交互作用 Interaction	2.090	0.127	0.349	0.841	0.133	0.968	0.388	0.815
白蛋白 Albumin/(g/L)	协变量(体重) Covariate (Body mass)	0.535	0.474	0.497	0.490	0.632	0.438	0.273	0.608
	胁迫程度 Degree	1.056	0.369	0.210	0.812	0.833	0.452	0.090	0.914
	胁迫时长 Duration	3.406	0.057	0.328	0.725	0.397	0.679	0.588	0.566
	交互作用 Interaction	0.687	0.610	0.339	0.848	1.072	0.401	0.205	0.932
球蛋白 Globulin/(g/L)	协变量(体重) Covariate (Body mass)	5.402	0.033*	0.950	0.343	0.605	0.448	0.446	0.513
	胁迫程度 Degree	0.616	0.552	0.096	0.909	0.103	0.903	0.703	0.509
	胁迫时长 Duration	0.814	0.460	0.316	0.733	0.472	0.632	0.396	0.679
	交互作用 Interaction	2.187	0.114	0.400	0.806	0.357	0.835	0.368	0.828
总胆固醇 Tholesterol/(mmol/L)	协变量(体重) Covariate (Body mass)	0.991	0.333	3.442	0.081	0.664	0.427	0.110	0.744
	胁迫程度 Degree	0.132	0.878	1.419	0.269	1.175	0.333	0.961	0.402
	胁迫时长 Duration	0.206	0.816	2.025	0.163	1.245	0.313	0.490	0.621
	交互作用 Interaction	1.502	0.246	0.737	0.579	0.365	0.830	0.210	0.929
甘油三酯 Triglyceride/(mmol/L)	协变量(体重) Covariate (Body mass)	0.194	0.665	0.035	0.854	0.387	0.542	1.759	0.202
	胁迫程度 Degree	2.812	0.088	3.180	0.067	0.288	0.753	0.517	0.606
	胁迫时长 Duration	3.634	0.049*	3.680	0.047*	1.675	0.217	0.236	0.793
	交互作用 Interaction	1.796	0.176	4.644	0.010	0.533	0.713	0.213	0.928
血糖 Glucose/(mmol/L)	协变量(体重) Covariate (Body mass)	0.580	0.457	0.098	0.758	1.363	0.259	0.223	0.643
	胁迫程度 Degree	11.032	0.001*	5.900	0.011*	5.004	0.019*	4.345	0.030*
	胁迫时长 Duration	11.358	0.001*	3.062	0.073	4.431	0.028*	7.323	0.005*
	交互作用 Interaction	4.587	0.011*	1.878	0.161	1.715	0.193	1.006	0.432
碱性磷酸酶 Alkaline phosphatase (King-unit/100 mL)	协变量(体重) Covariate (Body mass)	0.551	0.468	0.010	0.920	0.242	0.629	0.817	0.379
	胁迫程度 Degree	5.934	0.011*	6.373	0.009*	9.300	0.002*	2.276	0.133
	胁迫时长 Duration	3.002	0.076	4.349	0.030*	4.534	0.026*	4.205	0.033*
	交互作用 Interaction	2.109	0.124	1.912	0.155	4.465	0.012	0.558	0.696

注: *表示总体平均值存在显著性差异($P<0.05$)。

Note: * indicates differences in population means ($P<0.05$).

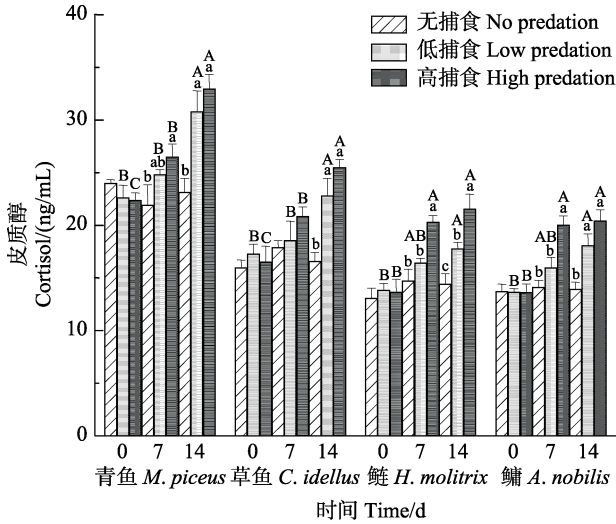


图2 捕食胁迫程度(无捕食、低捕食和高捕食)和捕食胁迫时长(0、7和14 d)对“四大家鱼”幼鱼 COR 水平的影响

Fig.2 The levels of serum cortisol in no predation, low predation, and high predation groups of juvenile “four major Chinese carps” in 0, 7 and 14 d after predation stress

不同大写字母表示在特定的捕食胁迫程度内(无捕食、低捕食和高捕食)不同时长(0、7和14 d)之间显著差异($P < 0.05$);不同的小写字母表示在特定的捕食胁迫时长(0、7和14 d)内不同的捕食胁迫程度(无捕食、低捕食和高捕食)之间显著差异($P < 0.05$)。图中数据为平均值±标准误(Mean±SE),下同。

Different uppercase letters indicated that there were significant differences among different exposure duration (0 d, 7 d and 14 d) within specific predation stress (no predation, low predation, high predation) ($P < 0.05$). Different lowercase letters indicated that there were significant differences among different levels of predation stress (no predation, low predation, and high predation) within the specific duration of predation stress (0, 7 and 14 d) ($P < 0.05$). Data in the figure are mean±standard error (Mean±SE), the same as below.

2.2.4 ALP 与无捕食组相比,ALP在捕食组中浓度升高。在不同的捕食胁迫程度中,“四大家鱼”幼鱼低捕食组的ALP浓度与无捕食组相比无显著差异,鳙的ALP浓度在不同捕食胁迫程度下有升高趋势,但差异不显著($P > 0.05$)。捕食胁迫7 d后,高捕食组青鱼、草鱼和鲢的ALP浓度显著高于无捕食组,且高捕食组鲢的ALP浓度显著高于低捕食组;捕食胁迫14 d后,高捕食组青鱼、草鱼和鲢的ALP浓度显著高于无捕食组,且高捕食组青鱼的ALP浓度显著高于低捕食组($P < 0.05$)。

在不同的捕食胁迫时长中,低捕食组“四大家鱼”幼鱼捕食胁迫0、7和14 d的ALP浓度相比无显著差异。青鱼的ALP浓度在不同捕食胁迫时长中有升高趋势,但差异不显著($P > 0.05$)。高捕食组草鱼、鲢和鳙的ALP浓度在捕食胁迫7 d后显著高于0 d,鳙

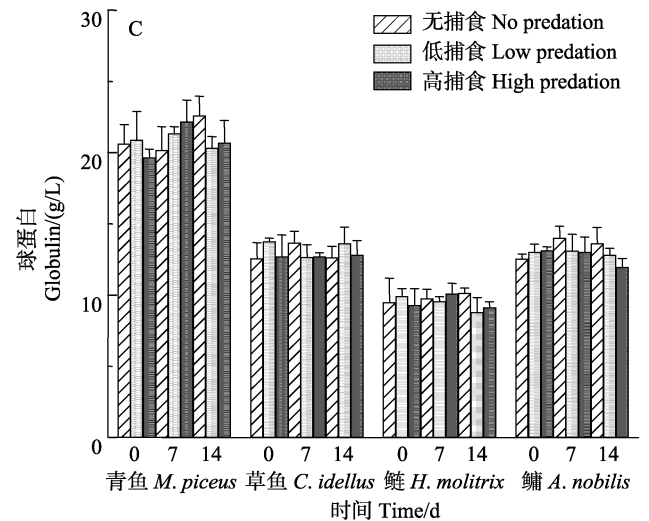
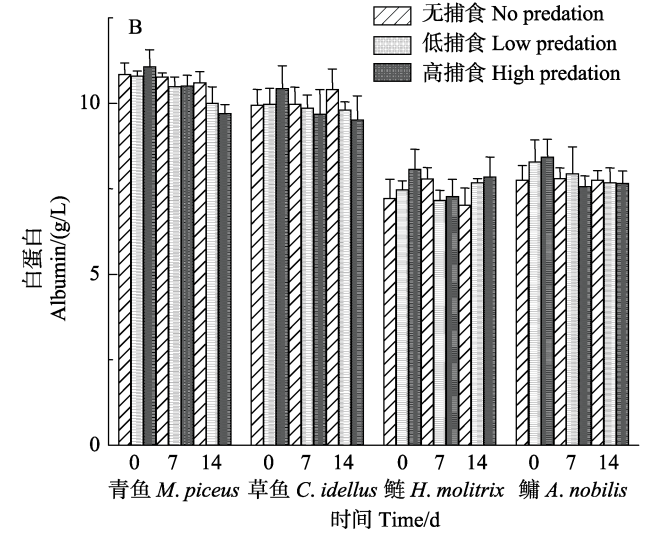
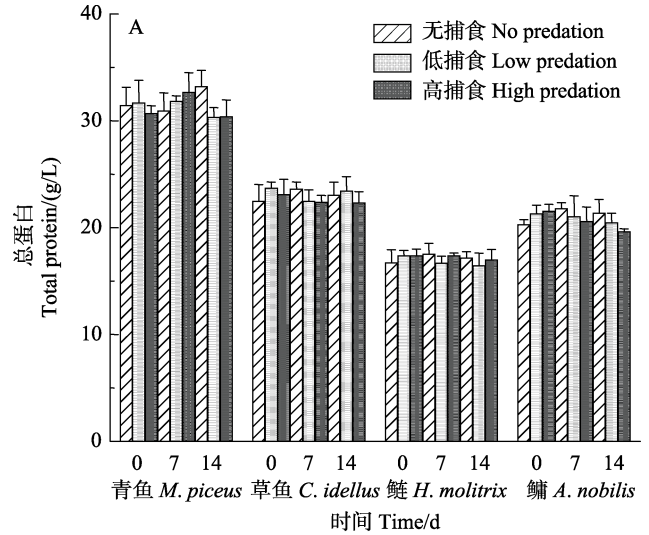


图3 捕食胁迫程度(无捕食、低捕食、高捕食)和捕食胁迫时长(0、7和14 d)对“四大家鱼”幼鱼 TP (A)、ALB (B)和 GLB (C)浓度的影响

Fig.3 The levels of total protein, albumin and globulin in no predation, low predation, high predation groups of juvenile “four major Chinese carps” in 0 d, 7 d and 14 d after predation stress

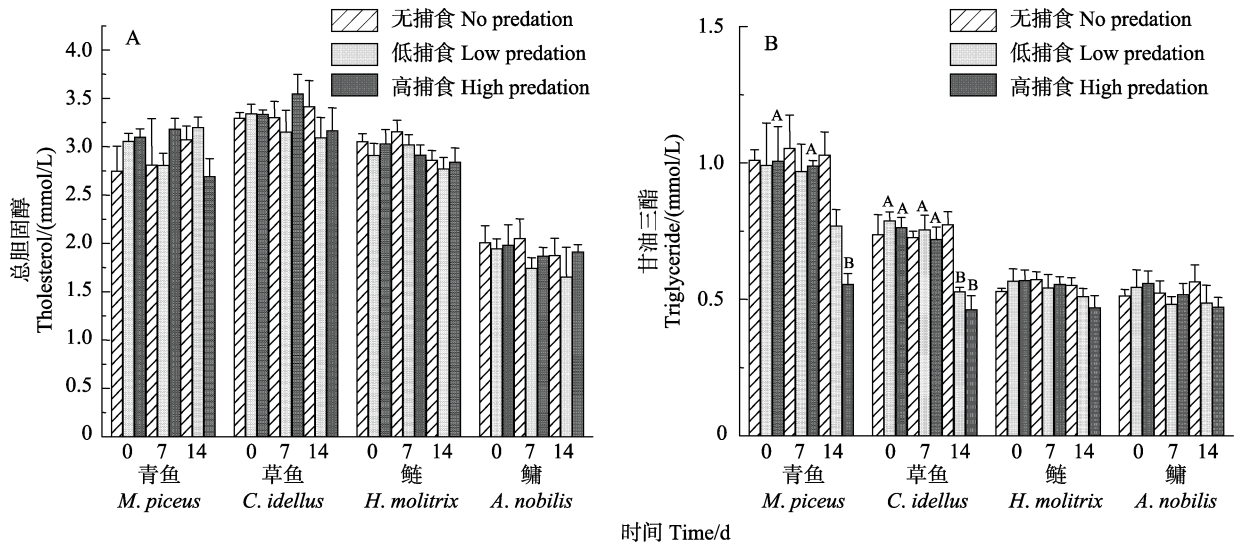


图 4 捕食胁迫程度(无捕食、低捕食、高捕食)和捕食胁迫时长(0、7 和 14 d)对“四大家鱼”幼鱼 CHO (A)和 TG (B)浓度的影响

Fig.4 The levels of cholesterol and triglycerides in no predation, low predation, high predation groups of juvenile “four major Chinese carps” in 0, 7 and 14 d after predation stress .

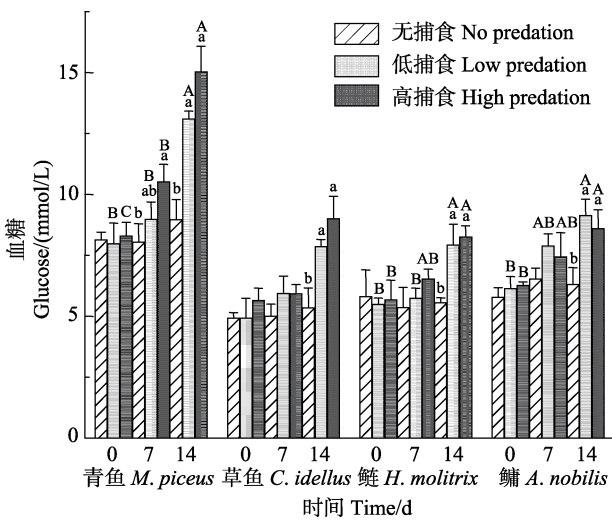


图 5 捕食胁迫程度(无捕食、低捕食、高捕食)和捕食胁迫时长(0、7 和 14 d)对“四大家鱼”幼鱼 GLU 浓度的影响

Fig.5 The levels of glucose in no predation, low predation, high predation groups of juvenile “four major Chinese carps” in 0 d, 7 d and 14 d after predation stress

在 14 d 捕食胁迫后, ALP 浓度降低至无捕食组水平, 草鱼和鲢在 14 d 捕食胁迫后, ALP 浓度呈下降趋势但仍显著高于 0 d ($P < 0.05$) (表 2 和图 6)。

3 讨论

3.1 捕食胁迫下“四大家鱼”幼鱼的 COR 水平的变化

应激反应的核心是下丘脑-垂体-肾上腺(HPA)轴的激活以及随后的糖皮质激素(GC)的分泌(Busch *et al*, 2009; Hansen *et al*, 2016; Tarlow *et al*, 2007)。

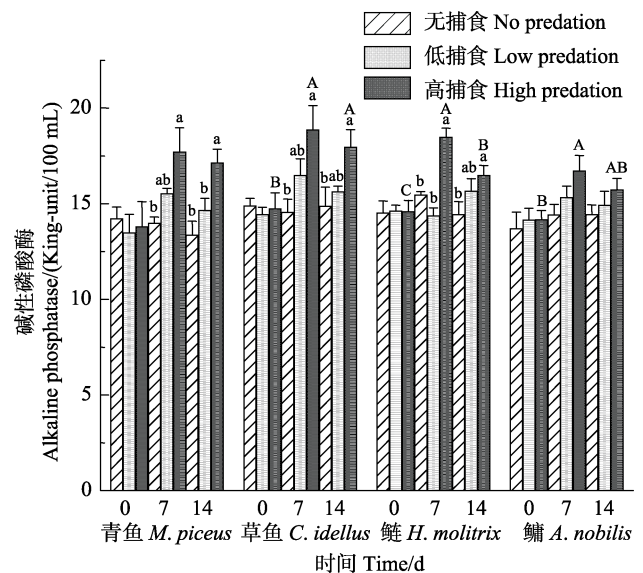


图 6 捕食胁迫程度(无捕食、低捕食和高捕食)和捕食胁迫时长(0、7 和 14 d)对“四大家鱼”ALP 幼鱼浓度的影响

Fig.6 The levels of alkaline phosphatase in no predation, low predation, and high predation groups of juvenile “four major Chinese carps” in 0 d, 7 d and 14 d after predation stress

COR 是关键应激糖皮质激素,其水平的升高被视为鱼类应激的信号(Kortan *et al*, 2011; Oliveira *et al*, 2017; Sapolsky *et al*, 2000)。本研究中, COR 水平随着捕食胁迫程度和胁迫时长的增加显著升高,表明“四大家鱼”幼鱼暴露于捕食者或捕食线索时均产生应激反应,和周龙艳等(2021)对胭脂鱼(*Myxocyprinus asiaticus*)和中华倒刺鲃(*Spinibarbus sinensis*)进行捕食胁迫的研究结果一致。不同捕食压力水平下, COR 水

平表现为无捕食组<低捕食组<高捕食组, 0 d<7 d<14 d, 表明“四大家鱼”幼鱼会根据捕食风险调整其生理反应, 且与捕食者直接接触的应激程度大于嗅觉和视觉等感官接触。COR 水平的增加有利于鱼体抵抗外界不良因子胁迫(Brown *et al.*, 2005)。不同捕食胁迫时长处理后, COR 水平表现为 0 d<7 d<14 d, 这可能是长期压力导致 COR 代谢增加的转变, 进而导致体内基底 COR 水平升高(Dallman *et al.*, 1992; Pottinger *et al.*, 2000), 表明在应激情况下, 猎物鱼倾向于以增强自身生存能力的方式改变生理反应。捕食压力下, COR 水平升高也反映了与应激有关的能量需求的增加(Schreck *et al.*, 1985), COR 升高能刺激糖原(Janssens *et al.*, 1988)、蛋白质(Vijayan *et al.*, 1989)和脂质(Davis *et al.*, 1985)的代谢, 为机体应对捕食胁迫提供能量, 有利于鱼类提高游泳能力和在捕食者攻击下更高的生存率(Fu *et al.*, 2017; Van *et al.*, 1998)

3.2 捕食胁迫下“四大家鱼”幼鱼的能量代谢

鱼类的血液生化指标始终处于动态平衡中, 直接反映了鱼类的内分泌水平和代谢情况(Congleton *et al.*, 2006; Dawood *et al.*, 2017; Wagner *et al.*, 2004)。蛋白质是血清中的重要组成部分, 在鱼类的生理学和免疫系统中发挥重要作用(Kumar *et al.*, 2005)。TP 含量常被用作鱼体对环境应激反应的指示物(Khan *et al.*, 2016; Vaziriyani *et al.*, 2018)。ALB 是重要的特异性蛋白, 被认为是鱼类健康状况良好的指标(Ergonul *et al.*, 2012; Rehulka, 1993)。GLB 是由生物体免疫器官产生的, 其浓度变化反映机体的抵抗力(Xia *et al.*, 2018; Yousefi *et al.*, 2019)。许氏平鲷(*Sebastes schlegelii*)和半滑舌鳎(*Cynoglossus semilaevis*)受到急性高温胁迫后, 血清 TP 和 ALB 水平显著降低, GLB 分泌增多(张亚晨等, 2015; 孙学亮等, 2010)。本研究中, “四大家鱼”幼鱼的血清蛋白浓度(TP、ALB 和 GLB)相比均无显著差异(表 2 和图 3), 表明“四大家鱼”幼鱼的健康状况良好, 免疫功能也并未受到影响。也可能是相比于急性胁迫, 血清蛋白对有较大时间跨度的捕食胁迫敏感程度低, 或者是本研究中捕食胁迫的强度不够, 不足以引起血清蛋白发生显著变化。

血清胆固醇和 TG 是机体重要的能量来源。TG 是脂类代谢的主要物质, 其含量的变化也反映了机体能量的波动(何志刚等, 2016; Peres *et al.*, 2014)。有研究发现, 环境胁迫会促进脂类分解, 导致血清胆固醇和 TG 浓度降低(Vijayan *et al.*, 1990; 张亚晨等, 2015)。本研究中, “四大家鱼”幼鱼的胆固醇浓度与无捕食组相比无显著差异, 表明胆固醇可能不是捕食

胁迫下鱼类应激的敏感指标。TG 浓度随着胁迫时长增加而下降, 其中, 青鱼和草鱼在捕食组胁迫处理后, TG 浓度显著降低(表 2 和图 4B)。一方面可能是捕食压力使鱼类代谢率增加, 导致体内 TG 消耗加快(Lulijwa *et al.*, 2021; Rossi *et al.*, 2017)。青鱼和草鱼相比鲢和鳙 TG 浓度下降显著, 可能是因为青鱼和草鱼的游泳能力更强, 能量消耗需求高(王晓等, 2022); 另一方面可能是由于捕食胁迫下, 鱼类需要花费更多的时间保持警惕, 更少的时间觅食, 进而导致能量摄入减少(Belgrad *et al.*, 2016; Elvidge *et al.*, 2020; 钱云霞等, 2002)。

GLU 是鱼类各种生命活动所需能量的直接来源, 作为鱼体内主要供能物质, 其含量与鱼类代谢水平和营养状况直接相关(Barton *et al.*, 1988)。GLU 在常态下含量比较恒定, 而随着机体的活动和环境的变化, 其含量也会发生变化。本研究中, “四大家鱼”幼鱼的 GLU 浓度显著上升(表 2 和图 5)。在捕食压力下, COR 水平升高促使肝糖原发生糖酵解, 导致 GLU 浓度的上升(Vijayan *et al.*, 2003), 在满足捕食胁迫下, 由于呼吸速率、代谢水平的上升而产生的对能量更高需求(Hawkins *et al.*, 2004; Xu *et al.*, 2019)。此外, GLU 的升高也是“四大家鱼”幼鱼对捕食胁迫作出应激反应的表现(Lawrence *et al.*, 2018), 且随着捕食胁迫程度和胁迫时长的增加, 应激程度也相应增加。

ALP 是一类膜结合糖蛋白, 直接参与磷酸基团的转移和代谢过程, 通常用于评估质膜的完整性(Akanji *et al.*, 1993)。本研究中, “四大家鱼”幼鱼在捕食胁迫后, ALP 浓度升高, 其中, 高捕食组的 ALP 浓度显著升高(表 2 和图 6)。这可能是因为捕食胁迫对“四大家鱼”幼鱼肝脏细胞的 ALP 有激活作用, ALP 浓度升高有助于鱼类在捕食压力下保持细胞膜的完整性, ALP 浓度升高也表明在捕食胁迫下鱼体代谢增强(Kong *et al.*, 2012; Guo *et al.*, 2021)。随着捕食时长的增加, ALP 浓度呈先升高后下降的趋势, 可能是因为鱼体对捕食环境的适应性结果。

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Effects of Predation Stress on the Physiological Responses of Juvenile Four Major Chinese Carps

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Abstract As low-level aquatic vertebrates, fish are highly dependent on the water environment, and general activities such as growth, foraging, and reproduction are easily affected by changes in the external environment. Changes in environmental factors can lead to different degrees of stress response in fish, and trigger a series of physiological changes, which then affect the stability of the organism's internal environment. Predation is one of the main environmental factors affecting the survival of individuals. In nature, almost all species face the risk of predation. Brief encounters with predators can reduce feeding and other health-related activities in prey fish and/or trigger primary and secondary stress responses, including the release of stress substances into the bloodstream. In predation stress, after initially sensing stress, fish initiate a stress response to overcome the stress and restore homeostasis. The degree of physiological stress depends primarily on the intensity and duration of the stress. If the appearance of predators is intermittent, then the physiological state of the prey fish returns to normal quickly, which allows the stress response to promote physiological changes in the prey fish to better adapt to the environment. However, repeated or persistent and unavoidable stress situations cause the normal physiological response mechanisms of prey fish to become compromised. Physiological stress may have long-term negative effects on the immune system, growth, or reproduction, and may reduce the adaptability and survivability of prey fish in the environment. Many studies have confirmed that predation stress can cause physiological stress in fish. Different species of fish and even different groups of the same species vary greatly in the degree of stress and stress mode. More species-specific studies are required to determine the effects of different levels of predation stress on physiological stress in fish.

Black carp (*Mylopharyngodon piceus*), grass carp (*Ctenopharyngodon idellus*), silver carp (*Hypophthalmichthys molitrix*), and bighead carp (*Aristichthys nobilis*) are known as the four major Chinese carps. As common fish species in Chinese inland watersheds, the four major Chinese carps are ecologically and economically valuable. Over the years, many reasons such as hydraulic construction, environmental pollution, and overfishing have led to sharp declines in wild populations. In addition, the prevalence of predators in natural waters also threaten population growth. It remains unclear how the juveniles of the four major Chinese carps adjust their physiological processes to cope with predation stress. We investigate the physiological and energy metabolism adaptations by black carp, grass carp, silver carp, and bighead carp to predatory stress. We selected the common local enemies of natural waters, the snakehead carp (*Channa argus*) and the southern catfish (*Silurus meridionalis*) as predators. The levels of serum cortisol and biochemical parameters in the juveniles of the four major Chinese carps under the stress of no-predation (control), low-predation (indirect stress) and high-predation (direct stress) over 0 d, 7 d, and 14 d were investigated. Changes in the biochemical parameters were analyzed. The effects of

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different predation stress levels on serum cortisol and biochemical parameters were also analyzed. The results showed: (1) under different levels of predation stress, the biochemical parameters and serum cortisol levels of juveniles of the four major Chinese carps varied to different degrees but the trends were consistent; (2) the serum cortisol levels of juveniles of the four major Chinese carps increased significantly with the degree of predation stress and the stress duration, and showed the following patterns: non-predation group < low predation group < high predation group, 0 d < 7 d < 14 d. (3) Among the biochemical parameters, serum total protein concentration and cholesterol concentration were relatively stable and did not vary significantly. Glucose concentration and alkaline phosphatase increased with predation stress, while triglyceride had a decreasing trend. The results showed that juveniles of the four major Chinese carps adjust their physiological responses to enhance their own survivability according to the predation risk. After the predation stress treatment, the juveniles of the four major Chinese carps all underwent a stress response. Compared with indirect predation, direct predation had a more significant effect on the physiological response of fish, and the degree of stress increased with the stress duration. Among the detection parameters, serum total protein and cholesterol may not be sensitive parameters for stress in fish under predation stress. The most significant changes were in cortisol and glucose and may compensate for the increased energy demand by the organism during stress. The adaptation of physiological stress and energy metabolism to predation stress in juveniles of the four major Chinese carps under predation stress conditions provides a theoretical basis for the stress responses of an organism to environmental changes, and can also provide a scientific reference for exploring the ecological interactions between predator and prey.

Key words Predation stress; Cortisol; Serum biochemical parameters; The four major Chinese carps