

摄食和饥饿对大口黑鲈游泳运动能力和低氧耐受的影响

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FEEDING AND FASTING ON SWIMMING PERFORMANCE AND HYPOXIA TOLERANCE OF *MICROPTERUS SALMOIDES*

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摄食和饥饿对大口黑鲈游泳运动能力和低氧耐受的影响

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摘要: 为了研究摄食和饥饿对鱼类游泳运动能力和低氧耐受的影响; 以大口黑鲈(*Micropterus salmoides*)为对象, 在25℃下, 测定对照组(禁食2d)、摄食组(摄食后3h)和饥饿组(禁食16d)实验鱼的日常代谢率(RMR)、活跃代谢率(AMR)、代谢范围(MS)、临界游泳速度(U_{crit})、临界氧压(P_{crit})和失去平衡点(LOE)。研究显示摄食后实验鱼RMR显著提升, AMR没有显著变化, 而MS和 U_{crit} 显著下降($P<0.05$); 饥饿后实验鱼RMR、AMR和MS均没有显著变化, 而 U_{crit} 显著下降($P<0.05$); 摄食后实验鱼 P_{crit} 显著上升, 溶解氧(DO)高于 P_{crit} 时的代谢率(MR)与DO之间的关系的斜率显著大于对照组所对应的斜率, 而LOE没有变化($P<0.05$); 饥饿后实验鱼 P_{crit} 和LOE均没有显著变化, 而DO 低于 P_{crit} 时的MR与DO之间的关系的斜率显著小于对照组所对应的斜率($P<0.05$)。结果表明, 摄食削弱大口黑鲈游泳运动能力是因为“心鳃”系统对其有氧代谢能力的限制; 饥饿后大口黑鲈游泳运动能力下降可能与其无氧代谢能力下降相关; 摄食削弱大口黑鲈的低氧耐受, 而饥饿后其低氧耐受有所增强, 但大口黑鲈低氧耐受总体趋于保守。

关键词: 摄食和饥饿; 能量代谢; 临界游泳速度; 临界氧压; 失去平衡点; 大口黑鲈

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能量代谢是维持有机体高度有序性的基础, 为一切生理活动和生命过程提供了保证^[1]。日常代谢率(Routine metabolic rate, RMR)是指动物在相对安静状态下的代谢率, 常衡量动物的维持能量消耗和整体生理状况^[2]。最大代谢率(Maximum metabolic rate, MMR)是指动物的最大功率输出, 与代谢范围(Metabolic scope, $MS=MMR-RMR$)一并常用以衡量动物的有氧代谢能力^[3, 4]。就大多数鱼类而言, 通过游泳运动能诱导其最大功率输出, 即活跃代谢率(Active metabolic rate, AMR, 在游泳过程中的MMR)^[5]。

游泳运动是鱼类最为重要的生理功能之一, 它与捕食、逃逸、繁殖等密切相关^[6, 7]。临界游泳速度(Critical swimming speed, U_{crit})指鱼类最大持续游泳速度, 反映鱼类有氧运动能力^[8]。由于特殊动力作用(Specific dynamic action, SDA), 摄食后在其消化过程中, 将会提升鱼类的代谢率; 在一些物种,

摄食后由于功率竞争, 其临界游泳能力招致削弱^[9]。由于水体特殊的理化性质, 溶解氧(Dissolved oxygen, DO)具有较大时空异质性, 因此鱼类经常遭遇低氧胁迫。临界氧压(Critical oxygen press, P_{crit})是指能维持鱼类RMR的最低DO水平; 当DO水平低于 P_{crit} 时, 鱼类必须经由无氧代谢提供能量维持生命活动或者被迫降低能量消耗直至身体失去平衡; 因此 P_{crit} 和失去平衡点(Loss of equilibrium, LOE)常作为评估鱼类低氧耐受的指标^[10, 11]。在摄食后, 由于代谢需求的增加, 鱼类的低氧耐受可能被削弱。在鱼类遭受饥饿后, 由于生理机能的下调, 其代谢水平、游泳运动能力等常会下降^[12]。然而, 由于饥饿后鱼类代谢需求也相应下调, 对环境DO要求可能会降低, 进而影响其低氧耐受能力^[13]。

大口黑鲈(*Micropterus salmoides*)原产于北美密西西比河流域, 20世纪80年代引入我国, 现已成为我国淡水养殖业的一种重要经济鱼类。本研究

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以大口黑鲈为对象, 考察摄食和饥饿对实验鱼能量代谢特征、游泳运动能力和低氧耐受的影响, 揭示其生理适应的能量学机制, 旨在为相关领域的研究提供基础资料。

1 材料与方法

1.1 实验鱼及驯化

从重庆长寿区鱼种场购得大口黑鲈(5—10 g), 于循环水槽中进行驯养, 驯养水温(25±1)℃。驯养期间保持水槽中水体氧含量在6 mg/L以上, 氨氮含量在0.005—0.025 mg/L, 保持自然光周期, 每日9:00以鲢(*Hypophthalmichthys molitrix*)肉块饱足投喂1次。所有实验鱼经过21d的驯化后, 选取48尾健康鱼进行实验, 其中16尾(用于游泳运动能力和低氧耐受测试实验鱼各8尾)为对照组(驯化后禁食2d进行实验测试), 16尾为摄食组(投喂3h后进行实验测试), 16尾为饥饿组(饥饿16d后进行实验测试)。

1.2 游泳能力的测定

U_{crit} 和游泳代谢率(MR, metabolic rate)采用鱼类游泳代谢仪(详见参考文献[14, 15])进行测定, 每个处理组测定8尾鱼。在测试前, 将实验鱼转移至代谢仪在6 cm/s的流速下进行适应3h(摄食组鱼类摄食后即进行适应)。在驯化完成后, 将流速调至2 cm/s进行RMR的测定。RMR的测定完成后以每档6 cm/s的流速增量和20min的时间周期测定其临界游泳速度(起始游泳速度亦第一档流速为: 6 cm/s)。每尾鱼临界游泳速度采取以下公式进行计算^[16]:

$$U_{crit} = U_i + (T_i/T_{ii})U_{ii} \quad (1)$$

式中, U_{crit} 为临界游泳速度(cm/s), U_i 是完成设定时间(20min)游泳所具有的最大速度(鱼力竭前一档速度)(cm/s), U_{ii} 是各速度梯度的速度增量(6 cm/s), T_{ii} 是在各速度梯度下设定的持续游泳历时($T=20min$), T_i 是在最大速度下未能完成设定历时的实际持续时间($T_i<20min$)。实验鱼拒绝游泳并停留在游泳管

后置筛板20s以上作为判断其力竭的标准^[17]。

在上述测定 U_{crit} 的同时测定其游泳MR。当游泳管的流速调到设定值后每2min测定溶氧值, 测定仪器为溶氧仪(HQ30d, 美国哈希公司)。实验过程溶氧值始终保持在85%饱和溶氧以上^[18], 温度控制在(25±0.5)℃。每尾实验鱼单位体重游泳耗氧率 $[MO_2, mg O_2/(kg \cdot h)]$ 的计算公式:

$$MO_2 = (S - S_0) \times 60 \times V / m \quad (2)$$

式中, S 和 S_0 [mg O_2 /(L·min)]分别为有鱼和无鱼(细菌耗氧)测定时间(min)与溶氧值(mg O_2 /L)之间经直线拟合后方程的斜率的绝对值, V 为扣除实验鱼体积后的系统总体积(L), m 为实验鱼体重(kg)。在最后一档游泳过程中, 当式2中 $T_i>10min$ 的数据将被采集, 反之则舍去, 不参加游泳MR的分析。实验鱼游泳MR数据详见图1。

1.3 低氧耐受的测定

将实验鱼转移至封闭式呼吸仪(详见参考文献[19])适应3h(摄食组鱼类摄食后即进行适应), 适应结束后将呼吸仪封闭用溶氧仪(HQ30d, 美国哈希公司)以每2 min/次的频率进行溶氧值测定直至身体到达LOE。LOE判别标准为鱼体侧翻或仰泳20s, 此时水中的溶氧量作为该尾鱼的LOE。每个处理组测定8尾鱼。系统温度维持在(25±0.5)℃。根据以下公式计算出每一时间间隔的耗氧率 $[MO_2, mgO_2/(kg \cdot h)]$:

$$MO_2 = ([O_2]_k - [O_2]_{k+1})V / (t \times m) \quad (3)$$

式中, $[O_2]_k$ 为前一时刻点的溶氧值(mg O_2 /L), $[O_2]_{k+1}$ 为相邻后一点时刻的溶氧量读数, V 表示呼吸室内去掉鱼体的体积(L), t 表示前一个点和后一个点的间隔时间(h), m 代表该尾鱼的体重(kg)。根据“双线法(Two-segment linear model)”模型计算每尾鱼的 P_{crit} 和该点的代谢率, 即临界代谢率(CMR, Critical metabolic rate)^[20]。实验鱼低氧耐受测试过程中的MR数据见图2。

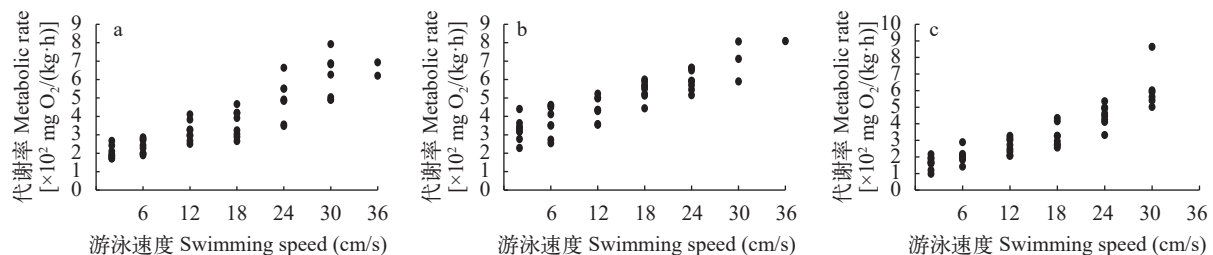


图1 不同处理的大口黑鲈的游泳运动能力

Fig. 1 Swimming performance of largemouth bass with different treatments

a. 对照组; b. 摄食组; c. 饥饿组

a. control group; b. feeding group; c. fasting group

1.4 数据处理

用Excel 2003对所有实验数据作常规计算,用STATISTICS 6.0软件数理统计分析,相同参数不同处理间进行单因素方差分析(ANOVA),方差分析通过后进行“多重比较(Duncan’s test)”。数据结果均以平均值±标准误(mean±SE)表示,显著水平定为 $P<0.05$ 。

2 结果

2.1 摄食和饥饿后大口黑鲈的游泳能力

结果显示,摄食组大口黑鲈RMR显著高于对照组的RMR($P<0.001$),而饥饿组的RMR与对照组间差异不显著($P=0.107$,表1)。对照组、摄食组和饥饿组间实验鱼的AMR差异不显著($P=0.376$,表1)。摄食组的MS显著低于对照组和饥饿组($P=0.033$),而对照组的MS和饥饿组间无显著性差异($P=0.542$,表1)。对照组实验鱼的 U_{crit} 显著高于摄食组和饥饿组实验鱼的 U_{crit} ($P=0.017$),而摄食组与饥饿组间实验鱼的 U_{crit} 差异不显著($P=0.771$,表1)。

2.2 摄食和饥饿后大口黑鲈的低氧耐受能力

结果显示,所有处理组间实验鱼的LOE差异不显著($F_{2,21}=2.319$, $P=0.123$,表2)。摄食组实验鱼的 P_{crit} 显著高于对照组和饥饿组实验鱼的 P_{crit} ($P=0.014$),而对照组和饥饿组间实验鱼的 P_{crit} 差异不显著($P=0.745$,表2)。摄食组实验鱼的CMR显著高于对照组和饥饿组实验鱼的CMR($P<0.001$),而对照组和饥饿组间实验鱼的CMR差异不显著($P=0.355$,表2)。当DO高于 P_{crit} 时,摄食组实验鱼MR与DO间线性关系的斜率显著高于对照组和饥饿组实验鱼所对应关系的斜率($P<0.001$),而对照组和饥饿组间实验鱼所对应关系的斜率无显著性差异($P=0.124$,表2)。当DO低于 P_{crit} 时,饥饿组实验鱼MR与DO间线性关系的斜率显著低于摄食组和对照组实验鱼所对应关系的斜率($P=0.001$),而对照组和摄食组间实验鱼所对应关系的斜率无显著性差异($P=0.826$,表2)。

表 1 摄食和饥饿对大口黑鲈游泳能力的影响(平均值±标准误,样本数=8)

Tab. 1 The effect of feeding and fasting on swimming performance in largemouth bass (mean±SE, n=8)

参数Parameter	分组Group		
	对照Control	摄食Feeding	饥饿Fasting
体重Body mass (g)	7.98±0.56	7.90±0.58	6.07±0.39
体长Body length (cm)	7.38±0.18	7.08±0.18	6.93±0.18
日常代谢率RMR [mg O ₂ /(kg·h)]	203.97±12.22 ^b	328.3±21.86 ^a	157.16±12.60 ^b
活跃代谢率AMR [mg O ₂ /(kg·h)]	643.13±33.04	635.00±31.85	575.18±49.85
代谢范围MS [mg O ₂ /(kg·h)]	439.16±30.73 ^a	306.7±21.62 ^b	418.04±49.24 ^a
临界游泳速度U _{crit} (cm/s)	31.62±1.00 ^a	27.33±1.27 ^b	27.61±0.90 ^b

注:同一行不同字母表示有差异显著($P<0.05$);下同
Note: Values in each row without a common superscript are significantly different ($P<0.05$). The same applies below

表 2 摄食和饥饿对大口黑鲈低氧耐受的影响(平均值±标准误,样本数=8)

Tab. 2 The effect of feeding and fasting on hypoxia tolerance in largemouth bass (mean±SE, n=8)

参数Parameter	分组Group		
	对照Control	投喂Feeding	饥饿Fasting
体重 Body mass (g)	5.73±0.13	6.74±0.37	5.29±0.19
体长 Body length (cm)	6.68±0.05	6.76±0.11	6.44±0.11
失去平衡点 LOE (mg O ₂ /L)	0.94±0.15	0.92±0.06	0.68±0.03
临界氧压 P _{crit} (mg O ₂ /L)	2.03±0.15 ^b	2.52±0.13 ^a	1.97±0.11 ^b
临界代谢率 CMR* [mg O ₂ /(kg·h)]	259.29±25.61 ^b	376.38±19.75 ^a	232.80±11.51 ^b
斜率1 Slope1 [#] [L/(kg·h)]	20.19±4.11 ^b	61.99±4.98 ^a	11.24±2.29 ^b
斜率2 Slope2 [#] [L/(kg·h)]	180.80±13.61 ^a	183.83±7.60 ^a	127.59±5.97 ^b

注: * 表示在临界氧压点的代谢率; # 斜率1和斜率2分别表示溶氧值高于和低于临界氧压时代谢率与溶解氧间关系的斜率
Note: * indicate the metabolic rate at critical oxygen pressure; # the slope1 and slope2 indicate the slopes of the relationships between metabolic rate and dissolved oxygen values above and below critical oxygen pressure, respectively

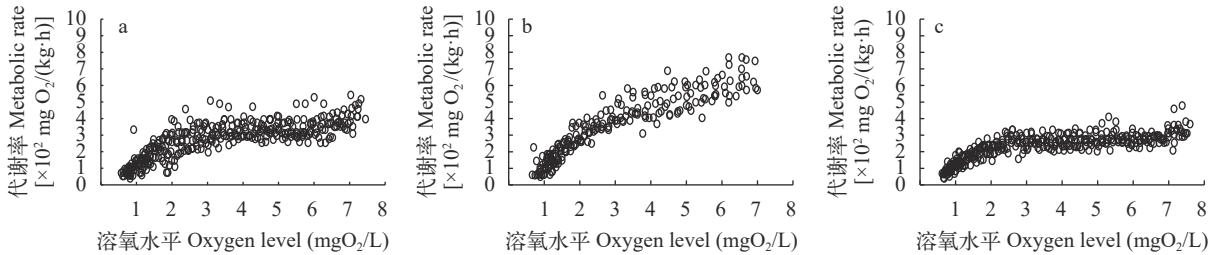


图 2 不同处理的大口黑鲈的低氧耐受能力

Fig. 2 Hypoxia tolerance of largemouth bass with different treatment

a. 对照组; b. 摄食组; c. 饥饿组
a. Control group; b. Feeding group; c. Fasting group

3 讨论

3.1 摄食和饥饿对大口黑鲈游泳运动能力的影响

研究发现, 大口黑鲈摄食后MR显著提升, 这是因为摄食后食物消化、物质合成等过程需要消耗能量, 即“特殊动力作用(SDA)”所致^[21]。当摄食和运动两种生理功能同时进行, 它们必须争夺“心鳃系统”提供的氧气以维持较高的代谢水平^[22]。当鱼类在摄食后游泳, 如果中心“心鳃系统”能力足以支持两种生理活动, 那么这两者间不存在功率竞争, 即摄食和运动可以同时完成^[14]; 摄食后运动其AMR显著增加, 为SDA和非摄食鱼类运动MR之和, 该种模式称为“代谢添加模式(Additive model)”, 如大鳞大麻哈鱼(*Oncorhynchus tshawytscha*)、鲤(*Cyprinus carpio*)、鲈鲤(*Percocypris pingi*)和草鱼(*Ctenopharyngodon idella*)等物种^[23—26]。否则, 要么牺牲运动能力来维持消化[“消化优先模式(digestion prioritization model)”], 例如虹鳟(*Oncorhynchus mykiss*)和南方鲇(*Silurus meridionalis*)等物种^[27, 28]; 要么牺牲消化能力来维持运动[“运动优先模式(Activity prioritization model)”], 如裸盖鱼(*Anoplopoma fimbria*)和中华倒刺鲃(*Spinibarbus sinensis*)等物种^[23, 29]。本研究发现大口黑鲈在摄食后 U_{crit} 显著降低, 而AMR没有变化, 因此大口黑鲈属于“消化优先模式”。此外, 摄食代谢相对较高的物种均为“消化优先模式”, 而摄食代谢较低的鱼类多为“代谢添加模式”, 与系统分类、食性等因素没有直接关联^[30]。

在自然界, 鱼类在面临食物资源短缺时通常有两种应对措施, 一种是通过降低代谢水平减少能量消耗, 以使有限的身体贮能维持更长的生存时间; 另一种是尽可能将代谢保持在相对较高的水平, 以保证在重新获得食物供应或面临其它环境胁迫时能产生适当的应激反应^[31]。在本研究中, 大口黑鲈遭受短期饥饿(16d)后其RMR和AMR与对照组相比并未显著下降; 因此, 大口黑鲈遭受饥饿时可能会选择维持较高的代谢水平来面对环境胁迫。尽管如此, 较高的代谢水平意味着较高的维持消耗; 而在大口黑鲈遭受2周饥饿后, 其 U_{crit} 显著降低, 这可能与能量底物消耗从而导致其无氧代谢能力下降相关。其具体生理生化机制有待进一步研究。

3.2 摄食和饥饿对大口黑鲈低氧耐受的影响

研究发现大口黑鲈摄食后 P_{crit} 和CMR显著上升, 表明摄食后大口黑鲈的低氧耐受能力有所下降, 这是因摄食后大口黑鲈“特殊动力作用”代谢率提升所致^[32]。在各实验组, CMR均高于RMR(仅饥饿组差异显著), 这是因为低氧耐受测试所采用呼吸

室体积远小于游泳代谢测试所采用呼吸室体积, 而所受胁迫更大所致。此外, 当水中DO高于 P_{crit} 时, 摄食组实验鱼MR与DO间线性关系的斜率显著高于对照组实验鱼所对应关系的斜率, 表明摄食后大口黑鲈在遭受“禁闭”的应激反应在饱和氧水平时要强于非摄食实验鱼, 而随溶氧水平的下降, 其这种应激反应有所削弱与非摄食实验鱼趋同。由于大口黑鲈“心鳃系统”供氧能力有限, SDA增加其氧消耗可能导致摄食后动物比空腹动物对“禁闭”和缺氧环境更为敏感^[32]。尽管如此, 大口黑鲈摄食后其LOE与对照组实验鱼LOE并没有变化, 这似乎与其“摄食优先模式”(SDA不可关闭)相冲突; 综合分析表明, 在极端低氧条件下为了生存大口黑鲈消化生理功能仍可关闭。此外, 大口黑鲈的LOE(0.94 mg O₂/L)总体而言高于鲤形目和鲇形目鱼类物种的LOE(0.12—0.80 mg O₂/L), 表明大口黑鲈低氧耐受能力相对较弱^[33]。

在面临低氧胁迫时, 鱼类可能通过降低非必需组织中代谢来满足关键部位的氧气供应; 这与遭受饥饿时机体选择降低代谢水平减少能量消耗类似。当鱼类遭受饥饿和低氧两种胁迫时, 一方面由于代谢需求的下降其低氧耐受可能有所增强; 另一方面, 由于生理调节能力被削弱其低氧耐受又可能下降。本研究发现, 饥饿后大口黑鲈的LOE下降28%($t_{14}=1.790$, $P=0.110$), 与图丽鱼(*Astronotus ocellatus*)研究结果一致^[34]; 并且在DO高于 P_{crit} 时, 饥饿组实验鱼MR与DO间线性关系的斜率显著高于对照组实验鱼所对应关系的斜率。这些结果表明大口黑鲈经饥饿后其低氧耐受能力有所增强。

综上所述, 摄食和饥饿将会削弱大口黑鲈的游泳运动能力; 摄食也将削弱大口黑鲈的低氧耐受能力, 而饥饿对其低氧耐受有所增强; 但总体而言, 大口黑鲈低氧耐受能力趋于保守。

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FEEDING AND FASTING ON SWIMMING PERFORMANCE AND HYPOXIA TOLERANCE OF *MICROPTERUS SALMOIDES*

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Abstract: To evaluate the effects of feeding and fasting on swimming performance and hypoxia tolerance of fish, we tested the routine metabolic rate (RMR), active metabolic rate (AMR), metabolic scope (MS), critical swimming speed (U_{crit}), critical oxygen pressure (P_{crit}) and the point of loss of equilibrium (LOE) of largemouth bass (*Micropterus salmoides*) at 25°C. The fish were divided into 3 groups which include control group (fasting for 2d), feeding group (3h after feeding) and fasting group (fasting for 16d). The results showed that the RMR increased, but the MS and U_{crit} decreased after feeding ($P<0.05$). There was no change in AMR between feeding group and control group ($P>0.05$). There was no change in RMR, AMR and MS between fasting group and control group ($P>0.05$). The U_{crit} of fish was decreased after fasting ($P<0.05$). The P_{crit} was higher in feeding group than that in control group ($P<0.05$). When the dissolved oxygen level was higher than the P_{crit} , the slope of the metabolic rate (MR) and dissolved oxygen (DO) in feeding group was higher than that in control group ($P<0.05$). There was no difference in LOE between feeding group and control group ($P<0.05$); There was no difference in P_{crit} and LOE between fasting group and control group ($P<0.05$). However, when the dissolved oxygen level was below the P_{crit} , the slope of the MR and DO in fasting group was lower than that in control group ($P<0.05$). The results showed that the weakening of swimming performance of largemouth bass in feeding group was caused by the limitation of its cardiobranchial system on its aerobic metabolism ability. After fasting, the weakening of swimming performance of largemouth bass may be related to the decline of anaerobic metabolism ability; Feeding weakens the hypoxic tolerance of largemouth bass, while fasting enhances its hypoxic tolerance. However, the hypoxic tolerance of largemouth bass is conservative.

Key words: Feeding and fasting; Energy metabolism; Critical swimming speed; Critical oxygen pressure; Point of loss of equilibrium; *Micropterus salmoides*