

doi: 10.7541/2025.2024.0375

CSTR: 32229.14.SSSWXB.2024.0375

秦岭细鳞鲑与拉氏鲮代谢特征及游泳能力的比较

吴奇^{1,2} 王洪³ 王丽英^{1,2} 彭敏锐¹ 郑雪丽¹ 李平⁴
付世建^{1,2} 夏继刚^{1,2}

(1. 重庆师范大学鱼类生态与保护研究中心, 重庆 401331; 2. 重庆师范大学生命科学学院, 进化生理与行为学实验室, 动物生物学重庆市高校重点实验室, 淡水鱼类资源保护与利用重庆市重点实验室, 重庆 401331; 3. 重庆师范大学教师教育学院, 重庆 401331; 4. 中国电建集团西北勘测设计研究院有限公司, 西安 710065)

摘要: 为探究秦岭细鳞鲑(*Brachymystax tsinlingensis*)与其主要猎物鱼拉氏鲮(*Phoxinus lagowskii*)游泳能力的种间差异及其生理机制, 采用鱼类游泳代谢仪, 分别测定了两种实验鱼野生种群有氧运动能力[步法转换速度 Gait transition speed (U_{gait})和临界游泳速度 Critical swimming speed (U_{crit})], 无氧运动能力[匀加速游泳速度 Constant acceleration test speed (U_{cat})], 静止代谢率(Resting metabolic rate, RMR)、最大代谢率(Maximum metabolic rate, MMR)、有氧代谢空间(Aerobic metabolic scope, MS)、运动耗氧率及单位距离运动能耗(Energetic cost of transport, COT)等。结果表明: (1)秦岭细鳞鲑 U_{crit} 和 U_{cat} 高于拉氏鲮($P<0.05$), 但二者 rU_{gait} 、 rU_{crit} 和 rU_{cat} 差异不显著($P>0.05$); (2)秦岭细鳞鲑RMR、MMR、MS等代谢特征均显著高于拉氏鲮($P<0.05$), 并且特定流速下秦岭细鳞鲑运动耗氧率及COT高于拉氏鲮; (3)秦岭细鳞鲑 U_{crit} 与MS、MMR呈现出显著正相关或正相关的趋势, 拉氏鲮 U_{crit} 与其MS和MMR均无显著相关性($P>0.05$)。研究结果提示, 整体上秦岭细鳞鲑与拉氏鲮的相对游泳能力相近, 但秦岭细鳞鲑的游泳效率更低; 秦岭细鳞鲑的代谢潜能更大, 代谢潜能是维持其运动表现的重要动力。

关键词: 临界游泳速度; 有氧代谢空间; 游泳效率; 种间关系; 秦岭细鳞鲑

中图分类号: Q178 **文献标识码:** A **文章编号:** 1000-3207(2025)07-072504-08



由于水体环境的特殊性, 游泳运动作为鱼类集群、洄游、觅食及逃避捕食者等行为实现的主要方式, 为鱼类的生存与繁衍提供了基本保障, 是表征鱼类生存适合度的关键组分, 具有重要的生态学意义^[1-3]。在种内水平上, 揭示鱼类游泳能力及其生理机制有助于阐明物种环境适应性, 可为鱼类资源保护、品种选育与健康养殖、涉水工程鱼道设计等提供重要参考^[4-8]; 在种间水平上, 鱼类群落不同物种游泳能力的变动可能引起种间关系模式的改变, 并潜在影响生态关键鱼类生存适合度与种群动态乃至群落稳定性及水域生态系统生物多样性^[9-11]。

然而, 目前基于自然生态系统具有特定种间关系的鱼类游泳能力及其生理机制的比较研究较为少见。

鱼类的游泳能力与其内在生理功能密切相关, 鱼类游泳过程中对能量的需求主要是通过组织的有氧或无氧代谢来满足的^[1,3]。依据鱼类游泳对水体溶解氧的需求状况可将游泳运动分为有氧运动和无氧运动两种类型^[12]。有氧运动是指以有氧代谢供能、持续时间较长的运动方式, 与鱼类的觅食、洄游等生命活动联系密切, 可通过测定临界游泳速度(Critical swimming speed, U_{crit})和步法转换速度(Gait transition speed, U_{gait})评估鱼类的有氧运

收稿日期: 2024-10-02; 修订日期: 2024-12-30

基金项目: 国家自然科学基金面上项目(32470511); 重庆市自然科学基金(CSTB2024NSCQ-LZX0061); 重庆师范大学“博望学者”领军人才计划; 质兰基金会项目(2024010531B)资助 [Supported by the National Natural Science Foundation of China (32470511); the Natural Science Foundation of Chongqing (CSTB2024NSCQ-LZX0061); the Leading Talent Program for BoWang Scholars of Chongqing Normal University; the Zhilan Foundation Program (2024010531B)]

作者简介: 吴奇(1999—), 男, 硕士研究生; 研究方向为鱼类生理生态学。E-mail: 293688239@qq.com

通信作者: 夏继刚, 男, 教授, 博士生导师; 主要从事鱼类环境适应与保护生态学研究。E-mail: jiggangxia@163.com

动能力^[13–17]。无氧运动则是指鱼类以无氧代谢供能、运动剧烈且时间很短的运动方式,与鱼类穿越激流、伏击捕食与逃避敌害等生命活动密切相关,可通过测定快速启动游泳(Fast-start swimming)、暴发游泳速度(Burst swimming speed)、匀加速游泳速度(Constant acceleration test speed, U_{cat})等来评估鱼类的无氧运动能力^[17–20]。

秦岭细鳞鲑(*Brachymystax tsinlingensis*)隶属于鲑科(Salmonidae)、细鳞鲑属(*Brachymystax*),为我国特有的珍稀濒危鱼类、国家Ⅱ级重点保护水生野生动物,是第四纪冰期自北南移的孑遗物种。其分布地域范围狭窄,对环境变化敏感,被视为秦岭溪流生态系统的顶级捕食者、重要的旗舰物种与环境指示种^[20–23]。秦岭细鳞鲑主要分布在秦岭海拔900 m以上的山涧溪流中,生境特殊,水文地理环境复杂,多高差地貌与湍急激流,不仅需要通过暴发游泳穿越激流甚至堤坝,还需通过长距离游泳完成生殖洄游和越冬洄游,因此游泳能力对其生存至关重要^[20, 24, 25]。作为秦岭细鳞鲑栖息地最为常见的鱼类,拉氏鲮(*Phoxinus lagowskii*)隶属于鲤科(Cyprinidae)、鲮属(*Phoxinus*),为小型野生经济鱼类,杂食性,与秦岭细鳞鲑种间关系复杂、通常被认为是秦岭细鳞鲑主要的猎物鱼,但有时也对秦岭细鳞鲑早期资源构成威胁^[25–28]。值得关注的是,相较于秦岭细鳞鲑显著的洄游性,拉氏鲮则趋于定居性,二者既是研究捕食者–猎物种间关系理想的受试目标,也是研究同域物种适应进化优越的动物模型。

同域物种生态适应与共存机制一直是群落种间关系研究的重要内容与研究热点^[29, 30]。特别是,作为种间关系复杂(兼具捕食和竞争关系)、长期共存于相似生境(秦岭山涧溪流)的同域分布物种^[25, 27],秦岭细鳞鲑和拉氏鲮在代谢生理适应与运动生态表现上是否呈现出相似的生理生态功能特征?目前未见研究报道。为探究秦岭细鳞鲑野生种群与其栖息地主要猎物鱼拉氏鲮游泳能力的种间差异及其生理机制,本研究采用自制鱼类游泳代谢仪^[17, 19, 21],分别测定了两种实验鱼有氧运动能力与无氧运动能力及其代谢特征,以期为秦岭细鳞鲑保护生理学及其群落种间关系研究提供理论参考。

1 材料与方法

1.1 实验鱼

实验鱼种群来自陕西省太白县秦岭细鳞鲑人工繁育试验基地的室外生态池(34°03'N 107°65'E)。生态池河水引流自石头河流域白云峡支流,池内环境与自然河道环境常年保持一致。为避免温度和

摄食状况对实验鱼代谢与游泳能力测定的影响,将两种实验鱼采集后分别置于实验室内循环控温水槽(直径2 m、水深0.6 m)中禁食并驯养适应48h。驯养用水为实验鱼自然栖息地经过沉淀净化处理后的河水,驯养期间实时监测水槽内水温与溶氧的变化,采用温控仪将水温控制在(10.5±0.5)℃,水体溶氧>8 mg/L,采用自然光照。每尾实验鱼仅用于一次实验测定,在测定完毕后,将所有实验鱼置于循环控温水槽中恢复适应24h以上,然后全部放归至室外生态池。

1.2 U_{gait} 和 U_{cat} 测定

采用鱼类游泳代谢仪测定 U_{gait} 和 U_{cat} (表1)。首先,将单尾实验鱼置于游泳管中适应1h,然后将游泳管中的水流速度以0.167 cm/s²的加速度^[24, 31]持续增加(水流速度由计算机程序控制),直至实验鱼到达运动力竭状态。伴随流速的增加,将实验鱼首次出现“暴发–滑行”姿态变化且在水流中相对位置上下移动这一行为时的游泳速度记为 U_{gait} ^[1, 16, 24, 31],将实验鱼力竭时的水流速度记为 U_{cat} 。力竭状态的评判标准为实验鱼无力前进游泳并停留在游泳管末端筛板20s以上^[24, 31]。为减少实验鱼体长对 U_{gait} 和 U_{cat} 测定的影响,将 U_{gait} 和 U_{cat} 分别除以体长得到相对步法转换速度(rU_{gait})和相对匀加速游泳速度(rU_{cat})。

1.3 U_{crit} 及代谢测定

U_{crit} 测定 采用鱼类游泳代谢仪测定 U_{crit} 。在测定前,将单尾实验鱼放入游泳管中过夜适应12h,适应期间游泳管内保持恒定微水流(6 cm/s)。之后,密闭游泳管,将水流从6 cm/s开始每隔20min提升一次流速(流速增量为6 cm/s,流速提升期间短暂打开游泳管后盖换水1次以确保管内的水体溶氧不低于饱和溶氧的80%),直至实验鱼到达力竭状态,力竭状态的判定标准是实验鱼无力前进游泳并停留在游泳管末端筛板20s以上^[17]。为减少实验鱼

表1 实验鱼规格大小(平均值±标准误)

Tab. 1 The body size of the experimental fish (mean±SE)

指标Index	种类Species	体长Body length (cm)	体重Body weight (g)	样本量n
U_{gait} 和 U_{cat} 测定 Measurement of U_{gait} and U_{cat}	秦岭细鳞鲑 <i>Brachymystax tsinlingensis</i>	9.41±1.59	8.58±0.43	8
	拉氏鲮 <i>Phoxinus lagowskii</i>	8.69±0.66	8.39±0.20	15
U_{crit} 及代谢测定 Measurement of U_{crit} and metabolism	秦岭细鳞鲑 <i>Brachymystax tsinlingensis</i>	9.16±0.43	10.98±1.49	15
	拉氏鲮 <i>Phoxinus lagowskii</i>	8.05±0.25	8.18±0.83	15

体长对 U_{crit} 测定的影响, 将 U_{crit} 除以体长得到相对临界游泳速度(rU_{crit})。 U_{crit} 的计算公式^[13]:

$$U_{crit} = U + (t/T)\Delta U$$

式中, U_{crit} 为临界游泳速度, U 为完成设定时间(20min)游泳所游过的最大速度, ΔU 为速度增量(6 cm/s), T 为在各个流速梯度下设定的持续游泳历时(20min), t 为实验鱼在出现力竭状态那一流速梯度下的实际游泳时间(min)。

代谢特征测定 在 U_{crit} 测定过程中, 使用溶氧仪(HQ40, Hach Company, Loveland, CO, USA)持续对游泳管内水体溶氧水平进行测定, 每2min测定1次, 得出实验鱼在不同游泳速度下的耗氧率[Oxygen consumption rate, MO_2 ; mg O_2 /(kg·h)]。 MO_2 的计算公式^[12, 17]:

$$MO_2 = 60(S - S_0)V/m^{0.75}$$

式中, S 、 S_0 分别为游泳管内水体在有实验鱼和无鱼状况下溶氧水平随时间变化的斜率绝对值, V 为游泳管水体系统总体积(3.45 L)减去实验鱼所占的体积(鱼体密度粗略估算为1 g/cm³, 通过体重计算体积), m 为实验鱼体重(kg)。对于单尾鱼游泳试验, MO_2 (y)和游泳速度(x)之间的关系一般可以用如下方程进行描述^[32-34]:

$$y = ae^{bx}$$

式中, a 为流速为0时的 MO_2 , 即静止代谢率(Resting metabolic rate, RMR); b 是一个常数。将 U_{crit} 测试期间最大 MO_2 定义为最大代谢率(Maximum metabolic rate, MMR), 通过MMR减去RMR计算得出有氧代谢空间(Aerobic metabolic scope, MS)^[17, 34]。

游泳效率测定 通过测定游泳运动单位距离能量消耗(Energetic cost of transport, COT)来反映游泳效率, COT (J/m)越大则游泳效率越低^[35]。COT的计算公式^[17, 34]:

$$COT = 13.56MO_2/(U \times 36)$$

式中, MO_2 为不同游泳速度 U 下的耗氧率, 13.56为氧热当量系数(J/mg O_2)^[34, 35]。

1.4 数据分析与处理

使用Excel 2010对数据进行整理后, 采用SPSS软件(SPSS 22.0 Inc., USA)对数据进行统计分析。首先对实验数据进行正态性检验(Shapiro-Wilk), 之后, 采用 t -检验或Mann-Whitney U检验分别分析数据满足和不满足正态性时两物种代谢特征与游泳能力的种间差异, Pearson或Spearman相关分析检测实验鱼 U_{crit} 与MMR和MS的关联。数据以

平均值±标准误表示, 显著性水平设为 $P<0.05$ 。

2 结果

2.1 两种实验鱼游泳能力的比较

秦岭细鳞鲑与拉氏鲮 U_{gait} 差异不显著($z=-1.549$, $P=0.121$), 二者 U_{cat} ($t=3.091$, $P=0.006$)和 U_{crit} ($t=3.345$, $P=0.002$)差异显著(图1)。秦岭细鳞鲑的 U_{cat} 和 U_{crit} 显著高于拉氏鲮(图1)。秦岭细鳞鲑与拉氏鲮 rU_{gait} ($t=1.003$, $P=0.327$)、 rU_{cat} ($t=1.869$, $P=0.076$)和 rU_{crit} ($z=-1.224$, $P=0.233$)均无显著差异(图1)。

2.2 两种实验鱼代谢特征与游泳效率的比较

秦岭细鳞鲑与拉氏鲮RMR ($t=2.380$, $P=0.024$)、MMR ($t=4.320$, $P<0.001$)和MS ($t=3.622$, $P=0.001$)均存在显著差异(图2)。秦岭细鳞鲑RMR、MMR和MS均显著高于拉氏鲮(图2)。

不同流速下秦岭细鳞鲑与拉氏鲮的代谢水平

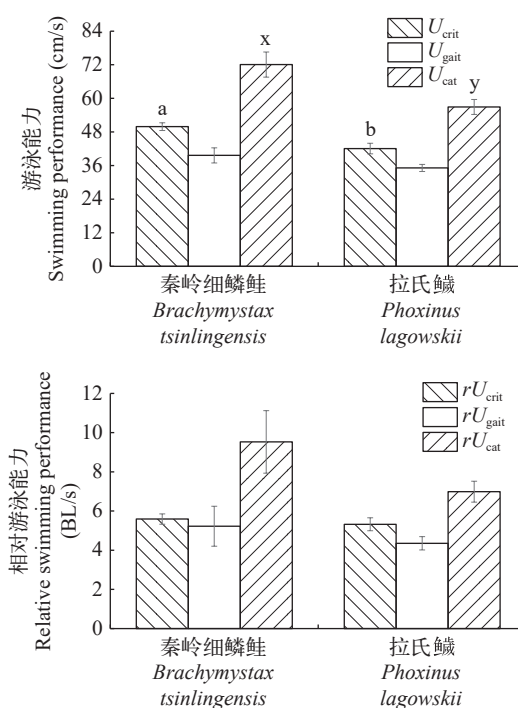


图1 秦岭细鳞鲑与拉氏鲮游泳能力的比较

Fig. 1 Comparison of swimming performance between *Brachymystax tsinlingensis* and *Phoxinus lagowskii*

U_{crit} : 临界游泳速度; U_{gait} : 步法转换速度; U_{cat} : 匀加速游泳速度; rU_{crit} : 相对临界游泳速度; rU_{gait} : 相对步法转换速度; rU_{cat} : 相对匀加速游泳速度; a—b, x—y上标字母不同分布表示两物种 U_{crit} 和 U_{cat} 种间差异显著

U_{crit} : Critical swimming speed; U_{gait} : Gait transition speed; U_{cat} : Constant acceleration test speed; rU_{crit} : Relative critical swimming speed; rU_{gait} : Relative gait transition speed; rU_{cat} : Relative constant acceleration test speed; Different letters on a—b and x—y indicate significant interspecific differences in U_{crit} and U_{cat} , respectively

(耗氧率 MO_2)见图3,二者 MO_2 随游泳速度变化的曲线拟合方程: $y = 44.543e^{0.0318x}$ 和 $y = 34.546e^{0.0303x}$ 。不同游泳速度下秦岭细鳞鲑与拉氏鲮游泳运动的单位距离能量消耗(COT)见图4。

2.3 两种实验鱼游泳能力与代谢特征的关联

秦岭细鳞鲑 U_{crit} 与其MS显著正相关($R=0.575$, $P=0.025$), 与其MMR呈现出正相关的趋势($R=0.459$, $P=0.085$; 图5); 拉氏鲮 U_{crit} 与其MMR ($R=0.164$, $P=$

0.559)和MS ($R=0.156$, $P=0.579$)均无显著的相关性(图5)。

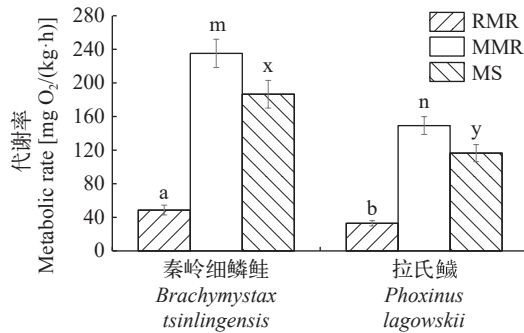


图2 秦岭细鳞鲑与拉氏鲮代谢特征的比较

Fig. 2 Comparison of metabolic characteristics between *Brachymystax tsinlingensis* and *Phoxinus lagowskii*

RMR. 静止代谢率; MMR. 最大代谢率; MS. 有氧代谢空间; a—b, m—n, x—y上标字母不同分布表示两物种RMR、MMR和MS种间差异显著

RMR. Resting metabolic rate; MMR. Maximum metabolic rate; MS. Aerobic metabolic scope; Different letters on a—b, m—n, and x—y indicate significant interspecific differences in RMR, MMR and MS, respectively

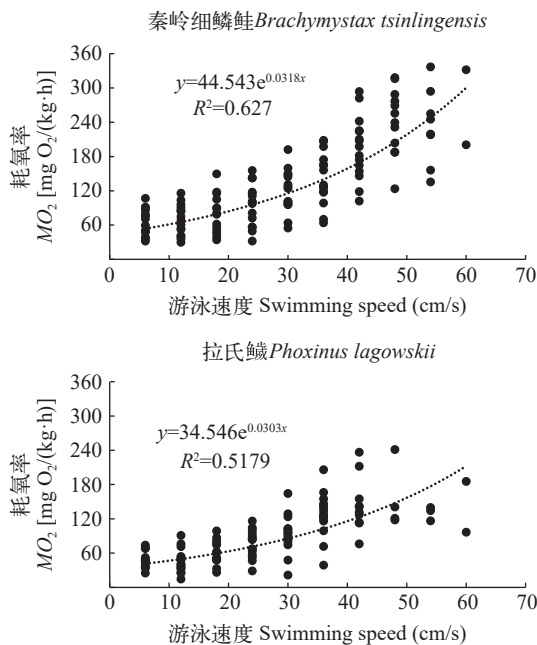


图3 不同游泳速度下秦岭细鳞鲑与拉氏鲮的耗氧率 MO_2

Fig. 3 The oxygen consumption rate (MO_2) of *Brachymystax tsinlingensis* and *Phoxinus lagowskii* at different swimming speeds

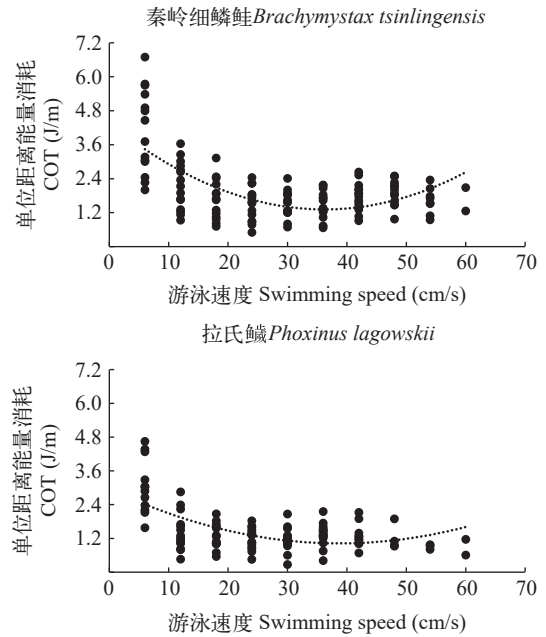


图4 不同游泳速度下秦岭细鳞鲑与拉氏鲮游泳运动的单位距离能量消耗(COT)

Fig. 4 The energetic cost of transport (COT) of *Brachymystax tsinlingensis* and *Phoxinus lagowskii* at different swimming speeds

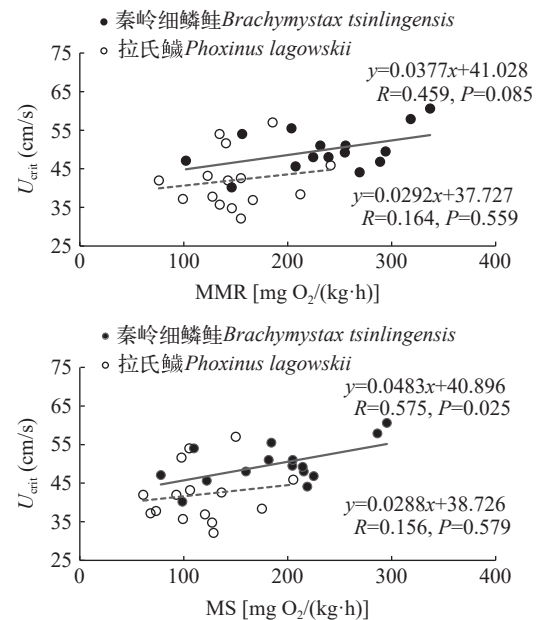


图5 秦岭细鳞鲑和拉氏鲮游泳能力与其代谢特征的相关性

Fig. 5 Correlations between swimming performance and metabolic characteristics in *Brachymystax tsinlingensis* and *Phoxinus lagowskii*

U_{crit} . 临界游泳速度; MMR. 最大代谢率; MS. 有氧代谢空间

U_{crit} . Critical swimming speed; MMR. Maximum metabolic rate; MS. Aerobic metabolic scope

3 讨论

捕食者-猎物种间关系是影响群落构成及其动态的核心要素,对洞察区域内物种应对策略、开展濒危物种保护、预测群落稳定性及生态系统可持续性具有重要意义^[10, 36, 37]。当捕食者的能量摄入超过其能量需求,且猎物的生长速度抵消了捕食压力,理论上群落中捕食者-猎物动态应该是稳定的^[38]。对于鱼类而言,捕食者-猎物相互作用的结果通常由它们的相对感觉运动表现来决定^[9, 39]。秦岭细鳞鲑作为秦岭溪流生态系统的顶级捕食者,以捕食拉氏鲮、底栖动物和各类昆虫为主。本研究首次比较研究了捕食者秦岭细鳞鲑及其同域分布的主要猎物鱼拉氏鲮野生种群代谢与游泳能力的种间差异。研究发现,表征秦岭细鳞鲑无氧运动能力的 U_{cat} 和表征有氧运动能力的 U_{crit} 均显著高于拉氏鲮, U_{cat} 和 U_{crit} 分别为拉氏鲮的1.27和1.19倍,表明作为捕食者秦岭细鳞鲑的游泳能力强于其猎物鱼拉氏鲮,为其有效捕食提供了功能基础;但秦岭细鳞鲑的相对游泳能力 rU_{gait} 、 rU_{cat} 和 rU_{crit} 与拉氏鲮相比均无显著差异,表明对于特定大小的群体,二者在整体运动性能上表现出了趋同适应。研究结果提示,尽管拉氏鲮通常被认为是秦岭细鳞鲑主要的猎物鱼,但二者种间关系很大程度上是个体大小与生活史状态依赖的。我们前期调研中也发现,处于被捕食地位的拉氏鲮也能够对秦岭细鳞鲑胚胎造成捕食压力,并对早期生活史阶段秦岭细鳞鲑幼体在食物资源和生存空间等多方面构成竞争^[25]。未来研究中进一步深入探究环境变动(限制)条件下秦岭细鳞鲑与拉氏鲮种间互作模式及其机制是必要的。

代谢率体现了能量吸收、转化和分配的速率,是基本生物学速率,体现了鱼类的整体生理性能^[40-43]。代谢功率的配置在一定程度上反映出鱼类的适应策略^[1]。其中,MS为MMR与RMR差值,是鱼类各种生理功能可能占用的潜在代谢空间,体现了鱼类应对环境变化的代谢潜能^[44, 45]。MS较高的鱼类通常能够更快地从无氧运动中恢复,因此具有较大MS的鱼类更能够担负与代谢恢复相关的能量成本,在逃逸反应中表现出更优的响应性或逃逸性能^[46, 47]。另一方面,RMR高的鱼类在高食物资源环境中往往更占优势且生长更快^[46],并且代谢水平较高的动物在能量分配上更倾向于维持警觉状态,在面对有利环境资源或潜在威胁时能够更快速地做出相应反应^[46-48]。Killen等^[47]发现,金灰鲷幼鱼(*Liza aurata*) 在遭遇捕食风险时,反应潜伏时间与运动力竭后的代谢恢复时间负相关,表明提高警惕性和代谢需求

之间存在权衡;此外,黄粉虫(*Tenebrio molitor*)的RMR与其捕食风险下的反应潜伏期呈正相关,与总静止时间负相关,表明代谢水平高的个体具有更高的警觉性^[48]。在本研究中,秦岭细鳞鲑的RMR显著高于拉氏鲮,前者为后者的1.48倍,这可能与该物种野生种群相较于拉氏鲮具有更高的环境敏感性和警戒性有关,与上述研究结果相一致^[47, 48]。秦岭细鳞鲑的MS和MMR均显著高于拉氏鲮,MS和MMR分别为拉氏鲮的1.60和1.58倍,表明与拉氏鲮相比秦岭细鳞鲑具有更大的代谢潜能。

COT表示单位体重鱼类运动一定距离的能量消耗^[35, 49]。从COT和 MO_2 随游泳速度变化的拟合曲线可以看出(图3和图4),随游泳速度的增加, MO_2 呈指数式增长,而COT呈先较快下降后缓慢上升的变化规律、趋于近U形,表明两种实验鱼在低速和高速游泳下的能耗高、游泳效率低。进一步分析发现,不同流速下秦岭细鳞鲑的代谢耗能更大、单位距离能量消耗更多、游泳效率更低。各流速下秦岭细鳞鲑的COT显著高于拉氏鲮,其中以低流速下(小于30 cm/s)更为显著(图4),推测秦岭细鳞鲑在捕食能量分配上主要采取高速追击或伏击的捕食策略而不是低速搜寻食物的对策。此外,鱼类代谢表型如何影响其运动能力一直是生理生态学者关注的科学问题^[17, 50]。通常认为MMR或MS较高的个体应该具有更高的 U_{crit} ,然而相关的实证研究案例较少^[46]。本研究中,秦岭细鳞鲑 U_{crit} 与其MS和MMR呈现出显著正相关或正相关的趋势,由于秦岭细鳞鲑常需要通过游泳完成捕食、洄游与栖息地选择,推测其代谢潜能可能主要供给于游泳运动,代谢潜能是维持其运动表现的重要动力;而拉氏鲮 U_{crit} 与其MS和MMR均不相关,推测其代谢潜能可能并不主要供给于运动(可能是有利于适合度提升的摄食、消化、生长、繁殖等其他方面)。

综上,本研究初步揭示了秦岭细鳞鲑及其同域分布的猎物鱼拉氏鲮野生种群代谢与游泳能力的种间差异。二者在整体相对运动性能上表现出了趋同适应,但秦岭细鳞鲑的游泳效率更低。另一方面,二者在代谢特征上表现出了趋异适应,秦岭细鳞鲑维持能量消耗更高、代谢潜能也更大,代谢潜能是其运动性能的重要支撑。研究结果可为秦岭细鳞鲑保护生理学及其水域生态系统种间关系动态研究提供理论参考。

(作者声明本文符合出版伦理要求)

参考文献:

- [1] Fu S J, Cao Z D, Zeng L Q, et al. Fish Locomotion:

- Strategies and Adaptive Evolution [M]. Beijing: Science Press, 2014. [付世建, 曹振东, 曾令清, 等. 鱼类游泳运动—策略与适应性进化 [M]. 北京: 科学出版社, 2014.]
- [2] Blake R W. Fish functional design and swimming performance [J]. *Journal of Fish Biology*, 2004, **65**(5): 1193-1222.
- [3] Langerhans R B, Reznick D N. Ecology and Evolution of Swimming Performance in Fishes: Predicting Evolution with Biomechanics [M]//Domenici P, Kapoor B G (Eds.), 2010. Fish Locomotion: an Etho-ecological Perspective. British Isles: Science Publishers, 2009: 200-248.
- [4] Cooke S J, Bergman J N, Twardek W M, *et al.* The movement ecology of fishes [J]. *Journal of Fish Biology*, 2022, **101**(4): 756-779.
- [5] Cai L, Katopodis C, Johnson D, *et al.* Case study: Targeting species and applying swimming performance data to fish lift design for the Huangdeng Dam on the upper Mekong River [J]. *Ecological Engineering*, 2018(122): 32-38.
- [6] Chen X F, Liu S K, Wang Y M, *et al.* Restoration of a fish-attracting flow field downstream of a dam based on the swimming ability of endemic fishes: A case study in the upper Yangtze River basin [J]. *Journal of Environmental Management*, 2023(345): 118694.
- [7] Tran H Q, Van Doan H, Stejskal V. Does dietary *Tenebrio molitor* affect swimming capacity, energy use, and physiological responses of European perch *Perca fluviatilis* [J]? *Aquaculture*, 2021(**539**): 736610.
- [8] Allen P J, Brokordt K, Oliva M, *et al.* Physiological insights for aquaculture diversification: Swimming capacity and efficiency, and metabolic scope for activity in cojinoba *Seriolella violacea* [J]. *Aquaculture*, 2021(531): 735968.
- [9] Domenici P, Allan B J M, Lefrançois C, *et al.* The effect of climate change on the escape kinematics and performance of fishes: implications for future predator-prey interactions [J]. *Conservation Physiology*, 2019, **7**(1): coz078.
- [10] Domenici P, Claireaux G, McKenzie D J. Environmental constraints upon locomotion and predator-prey interactions in aquatic organisms: an introduction [J]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2007, **362**(1487): 1929-1936.
- [11] Fulton C J, Bellwood D R, Wainwright P C. Wave energy and swimming performance shape coral reef fish assemblages [J]. *Proceedings of the Royal Society B: Biological Sciences*, 2005, **272**(1565): 827-832.
- [12] Reidy S P, Kerr S R, Nelson J A. Aerobic and anaerobic swimming performance of individual Atlantic cod [J]. *Journal of Experimental Biology*, 2000, **203**(2): 347-357.
- [13] Brett J R. The respiratory metabolism and swimming performance of young sockeye salmon [J]. *Journal of the Fisheries Board of Canada*, 1964, **21**(5): 1183-1226.
- [14] Dalziel A C, Vines T H, Schulte P M. Reductions in prolonged swimming capacity following freshwater colonization in multiple threespine stickleback populations [J]. *Evolution*, 2012, **66**(4): 1226-1239.
- [15] Nelson J A, Gotwalt P S, Reidy S P, *et al.* Beyond U_{crit} : matching swimming performance tests to the physiological ecology of the animal, including a new fish 'drag strip' [J]. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 2002, **133**(2): 289-302.
- [16] Peake S J. Gait transition speed as an alternate measure of maximum aerobic capacity in fishes [J]. *Journal of Fish Biology*, 2008, **72**(3): 645-655.
- [17] Yan G J, He X K, Cao Z D, *et al.* An interspecific comparison between morphology and swimming performance in cyprinids [J]. *Journal of Evolutionary Biology*, 2013, **26**(8): 1802-1815.
- [18] Domenici P, Blake R. The kinematics and performance of fish fast-start swimming [J]. *Journal of Experimental Biology*, 1997, **200**(8): 1165-1178.
- [19] Huang Y, Peng M R, Xia J G. Effects of temperature on different eco-physiological properties in *Spinibarbus sinensis*: testing the beneficial acclimation hypothesis [J]. *Acta Ecologica Sinica*, 2021, **41**(6): 2496-2504. [黄艳, 彭敏锐, 夏继刚. 温度对中华倒刺鲃不同生理生态性能的影响: 驯化有益假说的验证 [J]. 生态学报, 2021, **41**(6): 2496-2504.]
- [20] Zhao Y H, Zhang C G. Threatened fishes of the world: *Brachymystax lenok tsinlingensis* Li, 1966 (Salmonidae) [J]. *Environmental Biology of Fishes*, 2009, **86**(1): 11-12.
- [21] Xia J G, Ma Y J, Fu C, *et al.* Effects of temperature acclimation on the critical thermal limits and swimming performance of *Brachymystax lenok tsinlingensis*: a threatened fish in Qinling Mountain region of China [J]. *Ecological Research*, 2017, **32**(1): 61-70.
- [22] Xia J G, Peng M R, Huang Y, *et al.* Acute warming in winter eliminates chemical alarm responses in threatened Qinling lenok *Brachymystax lenok tsinlingensis* [J]. *Science of the Total Environment*, 2021(764): 142807.
- [23] Xia J G, Chen M, Xiao J, *et al.* The metabolism and hypoxia tolerance of *Brachymystax lenok tsinlingensis* in relation to temperature acclimation [J]. *Acta Hydrobiologica Sinica*, 2017, **41**(1): 201-205. [夏继刚, 陈梅, 肖静, 等. 秦岭细鳞鲃代谢及低氧耐受能力对温度驯化的响应 [J]. 水生生物学报, 2017, **41**(1): 201-205.]
- [24] Peng M R, Zheng X L, Li P, *et al.* Effects of temperature and repeat measurement on fast-start, swimming performance and post-exhaustion metabolic characteristics in *Brachymystax lenok tsinlingensis* [J]. *Acta Ecologica Sinica*, 2021, **41**(6): 2505-2514. [彭敏锐, 郑雪丽, 李平, 等. 温度和重复测定对秦岭细鳞鲃快速启动反应、游泳性能及力竭后代谢特征的影响 [J]. 生态学报, 2021, **41**(6): 2505-2514.]

- [25] Deng C K, Huang Q F, Li P, *et al.* Comparative studies on burst swimming performance of *Brachymystax tsinlingensis* and sympatric *Phoxinus lagowskii* in different life history stages [J]. *Acta Ecologica Sinica*, 2024, **44**(9): 3999-4008. [邓楚可, 黄青峰, 李平, 等. 不同生活史阶段秦岭细鳞鲑与同域物种拉氏鲮爆发游泳能力比较研究 [J]. 生态学报, 2024, **44**(9): 3999-4008.]
- [26] Tao Y Z, Wang L Y, Huang Q F, *et al.* Distribution patterns and habitat environmental characteristics of *Brachymystax tsinlingensis* larval fish [J]. *Acta Hydrobiologica Sinica*, 2024, **48**(10): 1716-1723. [陶渝镇, 王丽英, 黄青峰, 等. 秦岭细鳞鲑仔稚鱼分布模式及其栖息地环境特征 [J]. 水生生物学报, 2024, **48**(10): 1716-1723.]
- [27] Wang L Y, Xia J Y, Deng C K, *et al.* Comparative studies on light color preference of Qinling lenok *Brachymystax tsinlingensis* and sympatric fish *Phoxinus lagowskii* in different life history stages [J]. *Acta Ecologica Sinica*, 2024, **44**(17): 7859-7870. [王丽英, 夏静怡, 邓楚可, 等. 秦岭细鳞鲑与同域物种拉氏鲮的光偏好: 生活史阶段效应及种间差异 [J]. 生态学报, 2024, **44**(17): 7859-7870.]
- [28] Gou N N, Jin T Z, Zhang J L, *et al.* Population characteristics and seasonal variation of *Brachymystax lenok tsinlingensis*'s main bait organism *Lagowskiella lagowskii* in national nature reserves of rare aquatic wildlife of Heihe River [J]. *Acta Agriculturae Boreali-occidentalis Sinica*, 2018, **27**(9): 1258-1264. [苟妮娜, 靳铁治, 张建禄, 等. 黑河国家级自然保护区秦岭细鳞鲑主要饵料生物—拉氏鲮种群特征及其季节变化 [J]. 西北农业学报, 2018, **27**(9): 1258-1264.]
- [29] Lear K O, Whitney N M, Morris J J, *et al.* Temporal niche partitioning as a novel mechanism promoting coexistence of sympatric predators in marine systems [J]. *Proceedings of the Royal Society B: Biological Sciences*, 2021, **288**(1954): 20210816.
- [30] Büchi L, Vuilleumier S. Coexistence of specialist and generalist species is shaped by dispersal and environmental factors [J]. *The American Naturalist*, 2014, **183**(5): 612-624.
- [31] Pang X, Yuan X Z, Cao Z D, *et al.* The effect of temperature on repeat swimming performance in juvenile qingbo (*Spinibarbus sinensis*) [J]. *Fish Physiology and Biochemistry*, 2015, **41**(1): 19-29.
- [32] Webb P W. Hydrodynamics and energetics of fish propulsion [J]. *Bulletin of the Fisheries Research Board of Canada*, 1975(190): 1-159.
- [33] Roche D G, Binning S A, Bosiger Y, *et al.* Finding the best estimates of metabolic rates in a coral reef fish [J]. *Journal of Experimental Biology*, 2013, **216**(11): 2103-2110.
- [34] Fu C, Fu S J, Yuan X Z, *et al.* Predator-driven intra-species variation in locomotion, metabolism and water velocity preference in pale chub (*Zacco platypus*) along a river [J]. *Journal of Experimental Biology*, 2015, **218**(2): 255-264.
- [35] Tucker V A. Energetic cost of locomotion in animals [J]. *Comparative Biochemistry and Physiology*, 1970, **34**(4): 841-846.
- [36] Nuismer S L, Harmon L J. Predicting rates of interspecific interaction from phylogenetic trees [J]. *Ecology Letters*, 2015, **18**(1): 17-27.
- [37] Zhang N, Elvidge C K, Li Q, *et al.* Does mutualism provide additional indirect benefits? Behavioral indicators of chemical communication in a temporally dynamic fish-mussel mutualism [J]. *Behavioral Ecology and Sociobiology*, 2024, **78**(2): 21.
- [38] Vasseur D A, McCann K S. A mechanistic approach for modeling temperature-dependent consumer-resource dynamics [J]. *The American Naturalist*, 2005, **166**(2): 184-198.
- [39] Cooper W E, Blumstein D T. Escaping from Predators: an Integrative View of Escape Decisions [M]. UK: Cambridge University Press. 2015.
- [40] Brown J H, Gillooly J F, Allen A P, *et al.* Toward a metabolic theory of ecology [J]. *Ecology*, 2004, **85**(7): 1771-1789.
- [41] Bigman J S, M'Gonigle L K, Wegner N C, *et al.* Respiratory capacity is twice as important as temperature in explaining patterns of metabolic rate across the vertebrate tree of life [J]. *Science Advances*, 2021, **7**(19): eabe5163.
- [42] Pettersen A K, Metcalfe N B. Consequences of the cost of living: is variation in metabolic rate evolutionarily significant [J]? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2024, **379**(1896): 20220498.
- [43] Gvoždík L. Individual variation in thermally induced plasticity of metabolic rates: ecological and evolutionary implications for a warming world [J]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2024, **379**(1896): 20220494.
- [44] Jutfelt F, Norin T, Åsheim E R, *et al.* 'Aerobic scope protection' reduces ectotherm growth under warming [J]. *Functional Ecology*, 2021, **35**(7): 1397-1407.
- [45] Clark T D, Sandblom E, Jutfelt F. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations [J]. *Journal of Experimental Biology*, 2013, **216**(15): 2771-2782.
- [46] Metcalfe N B, Van Leeuwen T E, Killen S S. Does individual variation in metabolic phenotype predict fish behaviour and performance [J]? *Journal of Fish Biology*, 2016, **88**(1): 298-321.
- [47] Killen S S, Reid D, Marras S, *et al.* The interplay between aerobic metabolism and antipredator performance: vigilance is related to recovery rate after exercise [J]. *Frontiers in Physiology*, 2015(6): 111.

- [48] Krams I, Kivleniece I, Kuusik A, *et al.* High repeatability of anti-predator responses and resting metabolic rate in a beetle [J]. *Journal of Insect Behavior*, 2014(27): 57-66.
- [49] Hinch S G, Rand P S. Optimal swimming speeds and forward-assisted propulsion: energy-conserving behaviours of upriver-migrating adult salmon [J]. *Canadian Journal of Fisheries and Aquatic Sciences*, 2000, 57(12): 2470-2478.
- [50] Fu S J, Dong Y W, Killen S S. Aerobic scope in fishes with different lifestyles and across habitats: trade-offs among hypoxia tolerance, swimming performance and digestion [J]. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 2022(272): 111277.

COMPARATIVE STUDY OF METABOLIC CHARACTERISTICS AND SWIMMING PERFORMANCE BETWEEN *BRACHYMYSTAX TSINLINGENSIS* AND *PHOXINUS LAGOWSKII*

WU Qi^{1,2}, WANG Hong³, WANG Li-Ying^{1,2}, PENG Min-Rui¹, ZHENG Xue-Li¹, LI Ping⁴,
FU Shi-Jian^{1,2} and XIA Ji-Gang^{1,2}

(1. Fish Ecology and Conservation Research Center, Chongqing Normal University, Chongqing 401331, China; 2. Laboratory of Evolutionary Physiology and Behavior, Animal Biology Key Laboratory of Chongqing Education Commission, Chongqing Key Laboratory of Conservation and Utilization of Freshwater Fishes, Chongqing Normal University, Chongqing 401331, China; 3. School of Teacher Education, Chongqing Normal University, Chongqing 401331, China; 4. Power China Northwest Engineering Corporation Limited, Xi'an 710065, China)

Abstract: Qinling lenok *Brachymystax tsinlingensis*, a threatened salmonid species endemic to the Qinling Mountain Range, is a second-class state-protected wild animal in China Red Data Book of Endangered Animals. This species is landlocked and adapted to cold-water environments, specifically occurring in Qinling streams together with *Phoxinus lagowskii*. In order to explore the interspecific differences in swimming performance and metabolic characteristics between *B. tsinlingensis* and their main prey fish *P. lagowskii*, the anaerobic exercise ability (i.e., constant acceleration test speed, U_{cat}), aerobic exercise ability (i.e., gait transition speed, U_{gait} , and critical swimming speed, U_{crit}), resting metabolic rate (RMR), maximum metabolic rate (MMR), aerobic metabolic scope (MS), and the energetic cost of transport (COT) of wild populations of both species were measured using a Brett-type swimming tunnel respirometer. The results showed that: (1) the U_{crit} and U_{cat} of *B. tsinlingensis* were higher than those of *P. lagowskii* ($P < 0.05$), but there was no significant difference in the relative swimming abilities (including rU_{gait} , rU_{crit} , and rU_{cat}) between the two species ($P > 0.05$). (2) The RMR, MMR, and MS of *B. tsinlingensis* were significantly higher than those of *P. lagowskii* ($P < 0.05$). Moreover, both the oxygen consumption rate and COT of *B. tsinlingensis* at a specific swimming speed were higher than those of *P. lagowskii*. (3) The U_{crit} of *B. tsinlingensis* showed a significant positive correlation or a trend of positive correlation with MS and MMR, while the U_{crit} of *P. lagowskii* was not correlated with either MS or MMR ($P > 0.05$). The results suggest that the relative swimming performance of *B. tsinlingensis* is similar to that of *P. lagowskii*, whereas the swimming efficiency of *B. tsinlingensis* is lower. On the other hand, *B. tsinlingensis* have greater metabolic potential, which is an important driving force for supporting their swimming performance. These findings are expected to provide a theoretical reference for studying the conservation physiology of *B. tsinlingensis* and understanding the dynamics of interspecific relationships in Qinling stream ecosystems.

Key words: Critical swimming speed; Aerobic metabolic scope; Swimming efficiency; Interspecific interactions; *Brachymystax tsinlingensis*