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# 生态学报 (SHENTAI XUEBAO)

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封面图说: 滩涂芦苇及野鸭群——中国的海岸湿地, 尤其是长江入海口以北的海岸线, 多为泥质性海滩, 地势宽阔低洼, 动植物资源丰富, 生态类型独特, 为迁徙的鸟提供了丰富的食物和休息、庇护的良好环境, 成为东北亚内陆和环西太平洋鸟类迁徙的重要中转站和越冬、繁殖地。一到迁徙季节, 成千上万的各种鸟类飞临这里, 尤其是雁鸭类数量庞大, 十分壮观。

彩图提供: 陈建伟教授 国家林业局 E-mail: cites.chenjw@163.com

石小涛, 陈求稳, 黄应平, 刘德富, 庄平. 鱼类通过鱼道内水流速度障碍能力的评估方法. 生态学报, 2011, 31(22): 6967-6972.  
Shi X T, Chen Q W, Huang Y P, Liu D F, Zhuang P. Review on the methods to quantify fish's ability to cross velocity barriers in fish passage. Acta Ecologica Sinica, 2011, 31(22): 6967-6972.

## 鱼类通过鱼道内水流速度障碍能力的评估方法

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**摘要:**鱼类通过鱼道内水流速度障碍能力的量化对鱼道设计有重要理论和实际价值, 其基础是鱼类游泳能力的测定。首先对鱼类游泳能力的研究方法进行了概述总结, 指出了鱼类游泳能力经典测试方法存在测定流场与自然情况相差较大的不足; 分析了关键要素如鱼类行为特征、生理耗能规律及水力特性对鱼类通过水流速度障碍能力的影响; 提出了分析鱼类游泳行为和能力与特征流场的关系, 探讨鱼类通过水流障碍行为规律和生理疲劳恢复特征, 通过研究仿自然流态下的鱼类自由游泳行为、水力计算及生理耗能的关系, 构建多因素鱼类游泳能力关系式, 定量评价鱼类通过鱼道内水流速度障碍的发展方向。

**关键词:**水流障碍; 行为生态; 游泳能力; 模型

## Review on the methods to quantify fish's ability to cross velocity barriers in fish passage

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**Abstract:** Fish passage structures are constructed to facilitate fish moving to suitable habitats that are important during specific life stages. However, whether fish can successfully pass through a passage structure depends on their ability to swim against velocity barriers within the structure. Therefore, quantifying fish swimming ability is essential and to date, this knowledge is lacking for many species. Up to now, there is no widely-accepted method available to determine fish's ability crossing through velocity barriers. Establishment of such methods is important in both theoretical research and practical application. This review first summarized the widely-adopted methods for testing fish swimming ability. Swimming ability is mainly characterized by sustained swimming speed (i. e. the speed a fish can maintained for at least 200 minutes), critical swimming speed (i. e. the speed a fish can reach when using a step-wise protocol of speed increase) and burst speed (i. e. the maximum speed a fish can swim at, and this is usually maintained for <20 seconds). Critical swimming speed is the most common indicator of fish swimming ability. The critical swimming speed, burst speed and sustained speed are often used as references to design the fish passage, together with velocity field that is calculated by mathematical model. However, there are strong arguments that it is not effective to design fish passages according to the above swimming speeds because they are mainly determined in uniform flow condition which is significantly different from the complicated water flows in real passage structures. Unsteady flow (e. g. turbulence), which is a common phenomenon caused by the frictional effects of substrate and other objects in the water that disrupt laminar flow, might bring differences from laboratory results to

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field application. Thus, this review analyzed the key factors which affect fish crossing past velocity barriers, including fish behavior, metabolism, and hydraulics. Fish behavior has important influence on the ability to cross flow barriers, and such behaviors include sprinting, burst-glide, substratum skimming, jumping and flow refuging. Accordingly, researchers have defined the sprinting speed, gait transition speed, burst-glide speed and leaping ability of fishes to quantify their ability cross velocity barriers. Aerobic and anaerobic metabolism provides energy for fish swimming, and the related parameters such as oxygen consumption rate, blood glucose and lactate are effective indicators of a fish's ability to cross passage structures. In recent research, excessive post-exercise oxygen consumption and transport costs are used to measure energy expenditure during and after swimming in order to understand energy utilization and recovery. Hydraulics is another factor affecting fishes' ability to cross velocity barriers. It is observed that turbulence and jet-flows affect fish behavior and metabolism, thus affect passage success. Appropriate flow fields can increase the potential for fish to cross vertical slot fishways and culverts. In summary, a fish's ability to pass through velocity barriers is complicated and depends on several biotic and abiotic factors. Future studies are suggested to (1) analyze the relationships between swimming behavior, swimming ability and hydraulic condition, and (2) quantify the energy cost-recovery rate during fish crossing velocity barriers, and (3) develop mathematical models to describe the probability that a fish can pass through velocity barriers according to the above relationships between hydraulic condition, swimming behavior and energy dynamics.

**Key Words:** velocity barrier; fish ethology; swimming ability; mathematical model

在各种拦水设施阻隔了水利枢纽上下游鱼类的自由交換作用的背景下,鱼道被视为恢复鱼类种群的重要措施<sup>[1-5]</sup>。鱼道建设一直以来受到国外水生态研究者的关注,并在近期逐渐受到我国的重视<sup>[4-5]</sup>。但是,目前各国鱼道的运行远没达到过鱼的预期效果,原因之一为尚不能针对性的设计鱼道水力标准,以满足鱼类克服水流速度及流态造成的水流障碍<sup>[4-5]</sup>。

鱼类的水流速度障碍是指鱼类仅靠有氧呼吸或持续式游泳不能通过的水流<sup>[1-2]</sup>。水流速度障碍广泛存在,鱼类能否通过水流障碍对其完成生活史具有重要意义,如鲑鳟鱼类生殖洄游过程需要克服连续的水流速度障碍才能到达产卵场<sup>[1-2]</sup>。鱼类通过水流障碍能力尚未见系统的定量方法,目前有关研究集中于均匀流场下鱼类游泳能力测试,而较少评估鱼类在自然界通过各种特征流场(射流和涡流等)时的能力<sup>[1, 6-9]</sup>。鱼道为鱼类提供了各种水流速度屏障,鱼类能否通过鱼道与鱼类通过鱼道内水流速度障碍的能力关系密切,本文拟对鱼类通过鱼道内水流障碍能力的评估方法进行分析探讨。

## 1 鱼类游泳能力测试方法

鱼类游泳能力指的是鱼类游泳的持续时间和强度<sup>[10-12]</sup>,是鱼类能否通过水流速度障碍的基础。按照目前国际上广泛认同的分类方法,鱼类的游泳类型分为爆发式游泳、持续式游泳和耐久式游泳<sup>[4, 9]</sup>。对应于各种游泳状态,在密闭空间的均匀流场下,假定鱼类游泳速度与水流速度相等,衡量鱼类游泳能力的指标主要有持久游泳速度、临界游泳速度、爆发游泳速度<sup>[4, 9]</sup>。持久游泳速度用鱼类游泳至疲劳的时间大于200min时的固定水流速度来表达。按照定义,耐久式游泳的指标为鱼类游泳至疲劳的时间小于200 min 大于20 s时的固定水流速度,但实际上由于方法的可操作性,度量耐久式游泳的最常用指标是Ucrit,也称为最大可持续游泳速度,通常用连续时间段增速的方法测定<sup>[6]</sup>。爆发游速则可以衡量鱼类运动的加速能力,测定方式有两种:一种是鱼体从休息状态下在短时间内加速至较大速度;另一种是持续20 s内对应的稳定游速<sup>[6-7]</sup>。

目前,由于测定Ucrit的时间相对较短,方法可控性强,且得到统计上有意义的值所需的鱼数目较少,使用的范围最广。众多学者采用2 min到75 min的时间步长和1/9—1/4 BL/s的流速增量对Ucrit进行定量<sup>[5]</sup>,也有部分学者对测试方法进行了改进,主要集中在时间步长和流速增量上<sup>[12]</sup>,其中一种快速测定法有被越来越多的学者采用的趋势<sup>[13-14]</sup>。如Pettersson等<sup>[11]</sup>在预实验确定粗略Ucrit后,采用快速增速即每2 min增加0.2 m/s的方法,将水流速度调整至75% Ucrit,然后每30 min增加0.3 m/s或0.4 m/s的方法,测试Ucrit。尽

管 Ucrit 得到了学者们的青睐,但学者们同时指出其测定方法存在众多的弊端:首先测定流场与自然界相去甚远,测得的结果不能很好的反映自然状况下的鱼类游泳能力<sup>[15]</sup>,其次,Ucrit 测定时间步长的生理依据不清晰,不能明确无氧呼吸和有氧呼吸的比例<sup>[6, 16]</sup>;最后,游泳状态的时间区分方法不科学,部分鱼类游泳试验证实游泳状态的拐点不应局限于 20 s 到 200 min 的持续游泳时间<sup>[5]</sup>。

尽管鱼类游泳能力经典方法存在缺陷,其仍然被广大学者作为评价鱼类通过水流障碍的依据,主要体现在 Ucrit 在鱼道设计流速过程中的应用<sup>[1, 5]</sup>。这种应用基于两个假设,一是鱼类在鱼道中使用 Ucrit 的速度游泳,二是鱼类通过鱼道的时间与 Ucrit 中时间步长一致,如假设鱼类 Ucrit 为 50 cm/s, 测定时间步长为 30 min, 拟通过 50 m 长的鱼道时, 鱼类的对地游泳速度为  $50 \text{ m} \div 30 \text{ min} = 2.8 \text{ cm/s}$ , 因此鱼道内的最大水流速度不能超过  $50 \text{ cm/s} - 2.8 \text{ cm/s} = 47.2 \text{ m/s}$ <sup>[11]</sup>。Peake 等<sup>[5]</sup>以固定流速下鱼类游泳表现为指标,得到了鲑鱼和鳟鱼的游泳速度模型:  $S = a_0 + a_1 X + a_2 Y + a_3 Z + e$ , 式中 S 为鱼的游速(m/s), X 为鱼的叉长(cm), Y 为水温(°C), Z 为鱼在 S 游速下的耐力(min),  $a_0$ — $a_3$  为模型参数, e 为误差, 并以此模型计算了鱼道流速。但是, 这些使用游泳能力计算鱼道流速的方法存在问题, 因为鱼类自然情况下通过鱼道水流障碍的射流时主要使用的是爆发速度, 通过连续水流障碍时同时需用到耐久式游泳和持续性游泳, 不能仅用 Ucrit 设定鱼道水流标准。为了探讨自由游泳时鱼类的游泳速度与鱼道允许水流速度的关系, Peake 和 Farrell<sup>[17]</sup> 将小口黑鲈 (*Micropterus dolomieu*) 在 25 m 环形跑道进行自由游泳, 发现小口黑鲈游泳速度随着水流速度增加而增加, 按照 Ucrit 估算方法得出的鱼道水流允许速度远小于实际能通过小口黑鲈的水流速度, 并因此指出 Ucrit 不应被用于作为设计鱼道水流速度标准的依据; 另一方面, Peake 和 Farrell<sup>[17]</sup> 同时指出缩短时间步长可能提高 Ucrit, 进而可能更有效的计算鱼道水流速度标准。

## 2 影响鱼类通过水流障碍能力的关键因素

### 2.1 鱼类游泳行为

在自然界中, 游泳运动是一种较不稳定的运动状态, 常与阶段性的持续式游泳运动、暂停及偶而性的爆发游泳运动相互穿插发生<sup>[1, 6, 9]</sup>。以生殖洄游为例, 爆发游速为鱼类越过障碍到达产卵场提供了保障, 持续式和耐久式游泳状态则在鱼类长距离洄游中发挥重要作用<sup>[4, 9]</sup>。在面临不同的水流速度时, 各种鱼表现出来的游泳行为不尽相同, 部分鱼在低流速下使用身体中部的偶鳍, 在应对高流速时转为身体扭动和尾鳍助推, 部分鱼改变身体及尾鳍摆动的频率与幅度或采用一种新的爆发-滑行游泳方式<sup>[9]</sup>, 如短吻鲟 (*Acipenser brevirostrum*) 鱼使用自由游动、侧游(一个胸鳍压住游泳槽底部)、爆发-滑行、连续爆发、底层掠过和固定体位来对抗高的流速<sup>[18]</sup>。游泳行为可能与鱼体本身特性、环境因子和能量代谢等有关, 如个体大小影响鳗鲡在洄游过程中通过水流障碍的成功率<sup>[19]</sup>, 光照影响鲑鱼通过淹没式的水堰<sup>[20]</sup>, 生物力学模型研究表明爆发-滑行是稳定游泳效率的 4—6 倍, 可节省能量<sup>[21]</sup>。考虑到鱼类自主运动下的游泳方式自由选择, Peake<sup>[11]</sup> 指出 Ucrit 测试可能低估了真实的鱼类游泳能力。

基于对上述行为的研究, 学者们提出了步法转换速度(产生推进力的身体部位发生变化时的速度)、爆发-滑行速度、摆尾幅度、摆尾频率、爆发最大加速度、疾游速度(以短时间内游动距离为指标), 以及爆发游泳距离和最大探顶游泳速度等概念<sup>[9-10, 22-23]</sup>。上述各种游泳能力指标与 Ucrit 和 Uburst 等由固定测试方法得出的指标不同, 是以游泳过程中出现的具体行为为标准得出的参数, 无标准的测试方法。如步伐转换速度是在各种游泳过程中身体由胸鳍推动改为尾鳍助推时的速度<sup>[11, 22]</sup>, 疾游速度通过记录鱼类在受刺激后瞬间冲刺速度来测定, 部分学者采用最大冲刺速度作为最大疾游速度<sup>[6, 23]</sup>, 而最大探顶速度目前仅是王萍等针对鱼类应对潮流规律是游泳能力提出的一个概念, 未见具体的测定方法<sup>[10]</sup>。此外, 还有部分鱼类具备跳跃或吸附等特殊行为, 这些行为可能协助鱼类通过水流障碍。Lauritzen 等<sup>[24]</sup>发现红大马哈鱼 (*Oncorhynchus nerka*) 的跳跃是从深水处向水面冲刺。Reinhardt 等<sup>[25]</sup>用 PIT 标记和低照度相机的方法证实七腮鳗 (*Petromyzon marinus*) 在高流速下的吸附行为仅能帮助其固定身体, 而不能协助身体前进。Meixler 等<sup>[26]</sup>以跳跃行为为基础, 得到跳跃高度模型:  $JH = (9L)^2 / 2g$ , 式中, L 为鱼的总长(m), JH 为跳跃高度, g 为重力加速度。我国的鲢

(*Hypophthalmichthys molitrix*) 和鲤 (*Cyprinus carpio*) 具有跳跃行为, 胭脂鱼 (*Myxocyprinus asiaticus*) 有用口咬住底质上的小木棍以对抗水流的行为, 但尚缺乏对这些行为的深入研究。

## 2.2 鱼类游泳过程中的能量代谢

鱼类通过水流障碍时的能量利用方式与爆发速度、持久速度、游泳持续时间、恢复速度和恢复时间等密切相关, 准确评估鱼类行为和运动耗能方式以及生理疲劳恢复的关系对鱼类通过水流障碍尤为重要<sup>[6, 27]</sup>。特别是在鱼类通过连续水流障碍如鱼道时, 必须连续克服多个水流障碍, 其在通过一个水流障碍后到下一个水流障碍冲刺之前的生理恢复可能是鱼类成功穿越鱼道的决定要素之一<sup>[1, 28]</sup>。有关鱼类的运动生理学研究集中于鱼类的耗能机理, 耗能方式, 恢复动力学以及各种生物和非生物因子对能量消耗的影响<sup>[6, 29-30]</sup>。鱼类的运动以能量为动力, 各种情况下的游泳能力与生理状况密不可分, 耗氧率、血糖、乳酸、糖原和皮质醇等指标被学者用于研究能量消耗的过程<sup>[29-32]</sup>。饥饿和饱食状态下, 大西洋鳕 (*Gadus morhua*) 分别会因为弱的分解代谢供能和快的乳酸堆积导致疲劳<sup>[23]</sup>。对鱼类运动耗能 (cost of transport, 耗氧率为指标) 的研究帮助 Burgerhout 等<sup>[33]</sup>采用最适游泳速度 ( $U_{opt}$ , 耗氧效率最高时的速度) 来评价鱼类游泳状态, 并发现个体较小的雄鳗鲡 ( $U_{opt}$  较高) 采用集群游泳的行为减少能耗, 实现与个体较大 ( $U_{opt}$  较低) 的雌鳗鲡同步到达产卵场。力竭性运动后的耗氧量 (Excess post-exercise oxygen consumption, EPOC) 被用于比较鱼类的最大无氧代谢能力, 如 Lee 等<sup>[32]</sup>用 EPOC 比较了不同分布的太平洋鲑鱼的无氧运动能力, 发现洄游距离最长的 Gates Creek 红大马哈鱼的 EPOC 最高。Peake 和 Farre1<sup>[17]</sup>从鱼类采用短时间高速游泳的策略应对厌氧呼吸所需能量的角度解释了小口黑鲈自由游泳时的速度远高于强迫游泳时速度的现象。通过对生理干扰和游泳速度的分析, 部分学者发现圆形水箱中对鱼刺尾 1 分钟进行游泳能力测试是 Ucrit 测试方法的有效替代, 但该方法尚未得到广泛认同<sup>[9]</sup>。

## 2.3 水力因子

水力因子是鱼类通过水流障碍时必须考虑的另一个重要因素, 精细流场和复杂流态下自由游泳时鱼类的游泳行为比强迫游泳形式更丰富, 表明需要探讨鱼类游泳行为 (游泳方式的选择) 和鱼类游泳能力与特征流态的关系<sup>[6, 34]</sup>。水流速度障碍的水力特征与鱼类游泳能力的关系研究集中在鱼道相关领域, 目前国内外较多地选择数值模拟 (Fluent 软件) 并辅以模型试验的方法研究鱼道流速分布以及自由水面特征。曹庆磊等<sup>[35]</sup>和董志勇等<sup>[36]</sup>研究了异侧和同侧竖缝式鱼道模型池中的流速、紊动能、雷诺剪切应力和射流分布形态等。湍动已被证明可以影响鱼类栖息地选择、行为和鱼类游泳能力。经典游泳能力测定方法中限定的均匀流场即是为了减少紊流带来的干扰。多位学者指出过量的湍动如射流、涡流和循环流可能导致鱼类迷失方向、增加耗能<sup>[37]</sup>, 但也有学者指出湍动可节约运动耗能, 如 Liao 等<sup>[38]</sup>发现鲑鱼在通过 D 形障碍物后的涡流时仅需活动身体前侧的肌肉, 降低了耗能。Richmond 等<sup>[39]</sup>用实测数据分析管道式鱼道的流态, 发现鱼道中轴的流态与软件分析的结果一致, 与雷诺系数无关, 但是管道皱纹导致的次生流造就了鱼类喜欢利用的流态。日本公共研究所为了研究鱼类通过鱼道内水流障碍的能力, 用 5 台高速相机和 3D 软件分析鱼类位移、游泳速度和游泳加速度, 并全面分析了水槽流速分布和流量变化, 指出一个 45° 的斜坡可以帮助试验中大多数鱼通过水流障碍<sup>[40]</sup>。由此可见, 流态的细微差别可以影响鱼类行为, 鱼类行为对流态的响应亟待深入研究。

## 3 总结与展望

有关鱼类游泳行为和生理研究一直是国外的热点, 并在最近由于人类活动对鱼类影响加大而加剧了相关研究的迫切程度, 如学者们于 2010 年和 2011 年在西班牙、美国和澳大利亚分别召开了鱼类游泳生理学研讨会 (FitFish 1) 和鱼道研讨会 (Fish Passage 2011 和 5<sup>th</sup> Australian Technical Workshop on Fishways)。目前, 国内外还没有形成广大学者认可的定量评估鱼类生态意义上游泳能力的指标和方法。各种指标和模型共同的缺陷是缺乏对水力、行为和生理的综合考虑, 是假设鱼类在均匀流场里游泳或行为单一或生理状况不变的前提下得出。更能反映自然状况的鱼类通过水流障碍能力评价指标和模型值得期待<sup>[1, 28]</sup>, 是本领域科学发展的方向, 具体需研究内容包括:(1) 鱼类游泳行为和能力与特征流场的关系;(2) 鱼类通过水流障碍行为规律和

生理疲劳恢复特征;(3) 在系统探讨上述问题的基础上,通过仿自然流态下的鱼类自由游泳行为、水力计算及生理耗能的关系,构建多因素鱼类游泳能力关系式来实现鱼类通过鱼道内水流障碍能力定量评价方法。

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