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三种不同游泳习性鱼类骨骼肌的快、慢肌纤维组织学特性*

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摘要　硬骨鱼类的骨骼肌可为其游泳运动提供动力。为认识不同游泳习性鱼类的骨骼肌肌纤维组织学特征，本研究选取 3 种具有不同游泳习性的鱼类：鲐(*Scomber japonicus*)、大黄鱼(*Larimichthys crocea*)和褐牙鲆(*Paralichthys olivaceus*)，采用石蜡切片苏木精–伊红染色法和形态计量法，以形状、直径和密度作为评价指标，对其骨骼肌的快、慢肌纤维组织学特性进行表征，比较 3 种不同游泳习性鱼类的快、慢肌纤维组织学特征差异。组织学观察发现，3 种类型鱼类的骨骼肌快、慢肌纤维横切面均呈不规则形状。营持续式游泳的鲐的快肌纤维呈多角状，慢肌纤维呈多边柱形；营延长式游泳的大黄鱼的快、慢肌纤维呈长椭圆形；营爆发式游泳的褐牙鲆的快、慢肌纤维呈扁椭圆形。形态计量结果显示，3 种鱼类的快肌纤维直径均极显著大于其慢肌纤维($P<0.01$)。大黄鱼的慢肌纤维直径在 3 种鱼类中最大，约为鲐的 1.34 倍、褐牙鲆的 1.14 倍；鲐的快肌纤维直径在 3 种鱼类中最大，约为大黄鱼的 1.41 倍、褐牙鲆的 1.35 倍。3 种鱼类的快肌纤维密度均极显著小于其慢肌纤维($P<0.01$)，其中，快肌纤维密度大小排序为褐牙鲆[(274.60±9.07)根/mm^2]>大黄鱼[(205.43±12.63)根/mm^2]>鲐[(118.92±10.74)根/mm^2]，慢肌纤维密度大小排序为鲐[(1 442.33±28.25)根/mm^2]>褐牙鲆[(1 073.92±39.40)根/mm^2]>大黄鱼[(945.74±19.53)根/mm^2]。进一步分析发现，鱼类的肌纤维形状、直径和密度与鱼类的游泳习性密切相关。上述对不同游泳习性硬骨鱼类骨骼肌的肌纤维形状、直径和密度等组织学特征的描述与差异分析结果，可为进一步开展硬骨鱼骨骼肌的适应性进化和运动生理学研究提供基础性资料。

关键词　骨骼肌；快、慢肌纤维；组织学特征；游泳习性

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游泳对鱼类的生存具有重要意义，直接影响其躲避捕食者和敌害、寻找和捕获猎物、求偶繁殖以及洄游的能力(Martinezl *et al*, 2003; Brian Langerhans *et al*, 2010; Handelsman *et al*, 2010)。鱼类的游泳方式根据

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保持特定速度运动的时间，一般分为持续式游泳(sustained swimming)、延长式游泳(prolonged swimming)和爆发式游泳(burst swimming)三类(Brett, 1964)。鱼类低速进行的游泳运动被称为持续式游泳，其持续的时间一般为数小时或者数天甚至是数月，被形象地称为鱼类的“马拉松运动”(Beamish, 1978)；爆发式游泳只能维持很短的时间(＜20 s)，短期高性能的能力有助于鱼类捕获猎物、躲避捕食者的猎杀(Brian Langerhans *et al*, 2010)；延长式游泳持续时间通常介于持续式游泳与爆发式游泳之间，约为 20 s~200 min (Brett, 1964)。硬骨鱼类游泳运动依靠骨骼肌来支持，其骨骼肌约占鱼体质量的 40%~60% (Bone, 1978)，可为不同速度及不同持续时间的运动提供动力。骨骼肌的基本构成单位是肌纤维(李本相等, 2019)。根据颜色的不同，可分为红肌纤维和白肌纤维(梁婷玉等, 2018)。红肌纤维收缩慢、耐力强，线粒体、糖原和肌红蛋白含量高，以有氧代谢为主，可以有效地利用氧气产生 ATP，也被称为慢肌纤维，其主要功能是为鱼类游泳过程提供稳定和持续的动力；白肌纤维收缩快，但很快会疲劳，以酵解代谢为主，又称为快肌纤维，主要为鱼类的快速游泳行为(如捕食和逃跑)提供动力(Moss *et al*, 1971; Akolkar *et al*, 2010; Jackson *et al*, 2013)。

目前，很多研究指出，鱼类的游泳习性与快、慢肌的构成存在着较强的关联性，例如，有学者对不同游泳习性的淡水硬骨鱼红肌和白肌的比例进行研究，发现持续式游泳的鱼类红肌比例更高(Kiessling *et al*, 2006; Cediel *et al*, 2008)。有研究也指出，红肌适合于持续而缓慢的收缩，白肌适合于快速而短暂的收缩(Zhang *et al*, 2011; Jiao *et al*, 2019)。此外，有研究证明，鱼类缓慢游泳时，只有红肌纤维活跃；而在快速或剧烈运动时，白肌纤维活跃(Drazen *et al*, 2013; Wu *et al*, 2018)。这些研究多集中在对鱼类游泳运动与肌纤维类型相关的研究，对不同游泳习性鱼类的快、慢肌纤维组织学特征差异却鲜见报道。肌纤维的组织学特性主要包括肌纤维的形态、直径和密度等(尹丽卿等, 2015; 关文静等, 2008)，是描述鱼体骨骼肌组织学结构特征的重要指标。

本研究选取以鲐(*Scomber japonicus*)为代表种的持续式游泳习性鱼类、以大黄鱼(*Larimichthys crocea*)为代表种的延长式游泳习性鱼类和以褐牙鲆(*Paralichthys olivaceus*)为代表种的爆发式游泳习性鱼类，利用石蜡切片苏木精–伊红染色法和形态计量法对 3 种游泳类型鱼类的快、慢肌纤维组织学特性进行定性描述和定量分析，旨在比较 3 种游泳习性鱼类快、慢肌纤维组织学结构特征，阐释游泳习性与骨骼肌肌纤维组织学特征的相关性，以期为系统研究硬骨鱼类骨骼肌运动生理学提供基础资料。

1 材料与方法

1.1 实验材料

鲐为采自北黄海的野生样品；大黄鱼为浙江舟山近海网箱养殖；褐牙鲆采自山东威海养殖场。所有实验用鱼均为健康成鱼，每种鱼类各取样 3 尾，基本生物学信息见表 1，取样部位如图 1a、b、c 所示。因尾鳍是鱼类游泳的主要驱动器官，它的运动特征直接影响鱼类的游泳习性(Histand, 1977; Bone, 1966)，研究尾部肌肉组织学特征可以更直接地反映不同鱼类游泳习性的差异。因此，本研究选取尾部(尾鳍前端)快、慢肌组织(图 1d、e、f)，将快、慢肌组织横切成约 0.5 cm×1.0 cm×1.0 cm 的组织块，浸入环保型 GD 固定液(主要成分为福尔马林、冰醋酸和无水乙醇)中，固定 48 h 后保存于 70%酒精中备用。

表 1 实验用鱼的基本生物学信息

Tab.1 Basic biological information of experimental fish

种类 Species	游泳习性 Habits of swimming	样本数 Number	鱼龄 Fish age	体质量 Body weight/g	体长 Body length/mm	全长 Total length/mm
鲐 *S. japonicus*	持续式 Sustained	3	3	298.9±36.7	26.9±1.0	30.6±1.0
大黄鱼 *L. crocea*	延长式 Prolonged	3	3	300.7±14.9	26.4±0.6	29.5±0.7
褐牙鲆 *P. olivaceus*	爆发式 Burst	3	3	774.8±11.6	36.3±1.1	41.8±1.1

注：体质量、体长和全长用平均数±标准差表示。

Note: Data of body weight, body length, and total length were expressed by mean±SE.

1.2 实验方法

1.2.1 组织切片制备　固定的快、慢肌肉组织经 75%、85%、90%、95%、100%和 100%酒精梯度脱水，二甲苯透明，透蜡及包埋后用 LEICA RM 2016 轮转式切片机切片，切片厚度为 5 μm，苏木精–伊红(Hematoxylin-Eosin，HE)染色，中性树胶封片之后在生物显微镜(OLYMPUS BX3，日本)下观察拍照，观察其形态特征。

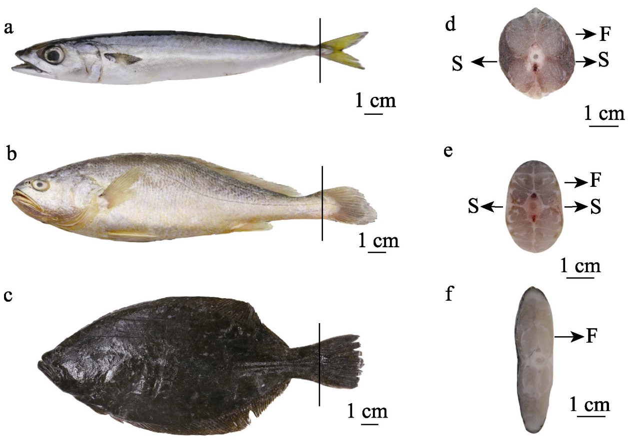

图 1　3 种鱼取样部位示意图
Fig.1　Schematic diagram of sampling sites of the three fish species

a：鲐；b：大黄鱼；c：褐牙鲆；d：鲐尾鳍横截面；e：大黄鱼尾鳍横截面；f：褐牙鲆尾鳍横截面。S：慢肌；F：快肌。
a: *S. japonicus*; b: *L. crocea*; c: *P. olivaceus*; d: Tail fin transverse sections of *S. japonicus*; e: Tail fin transverse sections of *L. crocea*; f: Tail fin transverse sections of *P. olivaceus*. S: Slow-twitch muscle; F: Fast-twitch muscle.

1.2.2　指标测定　肌纤维直径计算参考崔长艳(2017)的指标测定方法，在 10×40 倍光学显微镜下拍照，随机选择 10 个视野，用 ImageJ 直线工具分别测量长轴和短轴，求其平均值为肌纤维直径。肌纤维密度的测量参考崔长艳(2017)的指标测定的方法，在 10×20 倍光学显微镜下拍照，以“记上不记下，记左不记右”为原则，随机选取无重叠、无断裂清晰的 10 个视野，使用 ImageJ 软件统计 10 个视野内的肌纤维面积，统计每个视野内肌纤维的根数，换算成每平方毫米的肌纤维根数，作为被测样本的肌纤维密度。

1.2.3　数据处理　使用 Excel 2019 软件对数据进行前期处理，再用 SPSS 26.0 软件对实验数据进行方差分析及多重比较，实验数据以平均值±标准差(Mean±SD)表示。同一物种内快、慢肌纤维间组织学可量化指标进行配对样本 *t* 检验，3 种鱼类之间肌纤维可量化指标进行独立样本 *t* 检验(unpaired student′s *t*-test)，以 $P<0.05$ 为差异显著、$P<0.01$ 为差异极显著，采用 GraphPad Prism 9 软件作图。

2　结果

2.1　快、慢肌纤维形态特征

3 种鱼的慢肌均分布在侧线位置附近的皮下浅层，快肌分布于躯干深层。但不同的是，鲐的慢肌的横截面呈三角形；大黄鱼的慢肌呈波浪状；而褐牙鲆的慢肌紧靠皮下浅层且颜色浅，所以在横截面上不能明显观察到(图 1d、e、f)。

图 2 为实验所得 3 种鱼类骨骼肌纤维的显微观测结果。肌质内嗜酸性的肌纤维被伊红染成淡红色；细胞核分布在肌质的周边，被碱性染料苏木精染成蓝紫色，每个肌细胞含多个细胞核。3 种鱼类的骨骼肌

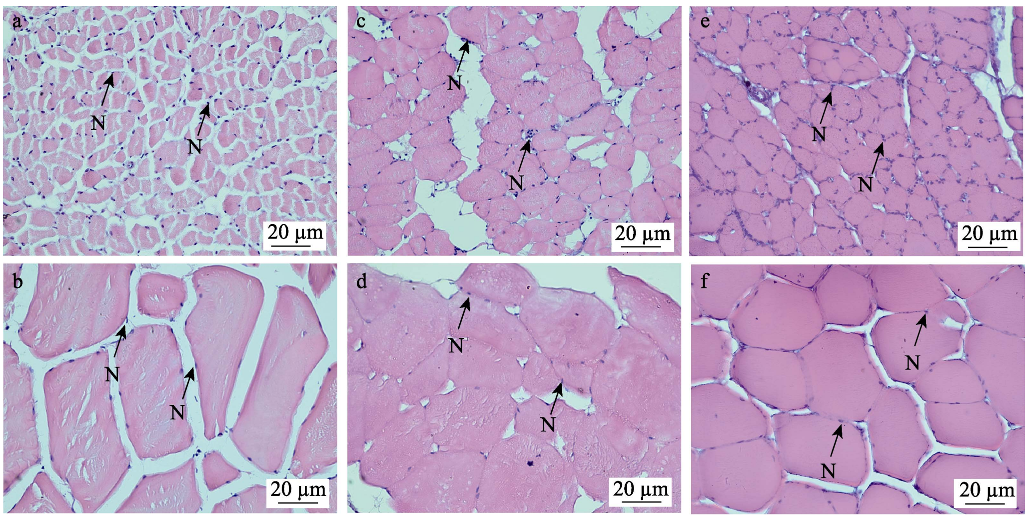

图 2　3 种鱼类骨骼肌纤维光学显微结构
Fig.2　Optical microstructure in muscle of skeletal muscle fibers of three fish species

a：鲐慢肌纤维横切面；b：鲐快肌纤维横切面；c：大黄鱼慢肌纤维横切面；d：大黄鱼快肌纤维横切面；e：褐牙鲆慢肌纤维横切面；f：褐牙鲆快肌纤维横切面；N：细胞核。
a: The slow-twitch muscle fibers transverse section of *S. japonicus*; b: The fast-twitch muscle fibers transverse section of *S. japonicus*; c: The slow-twitch muscle fibers transverse section of *L. crocea*; d: The fast-twitch muscle fibers transverse section of *L. crocea*; e: The slow-twitch muscle fibers transverse section of *P. olivaceus*; f: The fast-twitch muscle fibers transverse section of *P. olivaceus*; N: Nucleus.

细胞形态在组织学水平上可以见到明显差异：3 种鱼的快、慢肌纤维细胞均呈不规则形状，其中，鲐的慢肌纤维细胞呈多角状，快肌纤维细胞呈多边形(图 2a、b)；大黄鱼的慢肌纤维细胞和快肌纤维细胞均呈长椭圆形，且细胞边缘都较圆润(图 2c、d)；褐牙鲆的快、慢肌纤维细胞均呈扁椭圆形(图 2e、f)。此外，与另外 2 种鱼类相比，鲐快、慢肌纤维细胞间隙大，肌细胞排列松散；而褐牙鲆快、慢肌纤维细胞间隙小，肌细胞排列更紧密。

2.2　快、慢肌纤维直径

如图 3 可知，鲐、大黄鱼和褐牙鲆的快肌纤维直径均极显著大于慢肌纤维(P<0.01)。鲐、大黄鱼和褐牙鲆的快肌纤维直径分别约为其慢肌纤维的 4.84、2.57 和 3.07 倍。此外，大黄鱼的慢肌纤维直径约为鲐的 1.34 倍、褐牙鲆的 1.14 倍；鲐快肌纤维直径约为大黄鱼的 1.41 倍、褐牙鲆的 1.35 倍。

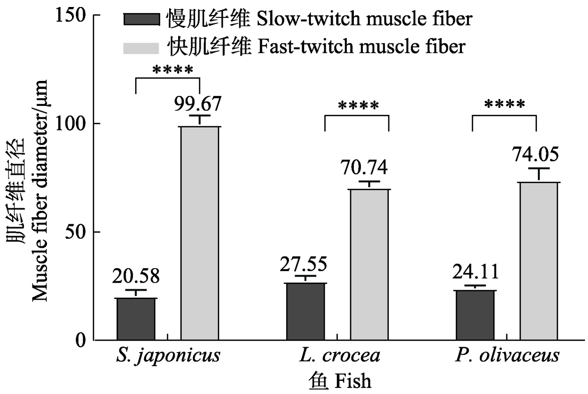

图 3　3 种鱼类快、慢肌纤维直径

Fig.3　Diameter of fast-twitch and slow-twitch muscle fiber of three fish species

****表示差异极显著(P<0.01)。下同。

**** indicates highly significant difference. The same as below.

2.3　快、慢肌纤维密度

由图 4 可知，本研究中的 3 种鱼类的慢肌纤维密度均极显著大于快肌纤维(P<0.01)。鲐、大黄鱼和褐牙鲆的慢肌纤维密度分别约为其快肌纤维的 12.13、4.60 和 3.91 倍。此外，鲐慢肌纤维密度约为大黄鱼的 1.53 倍、褐牙鲆的 1.34 倍；褐牙鲆快肌纤维密度约为鲐的 2.31 倍、大黄鱼的 1.34 倍。

3　讨论

以往骨骼肌纤维多被描述为圆柱形(沈元新等,

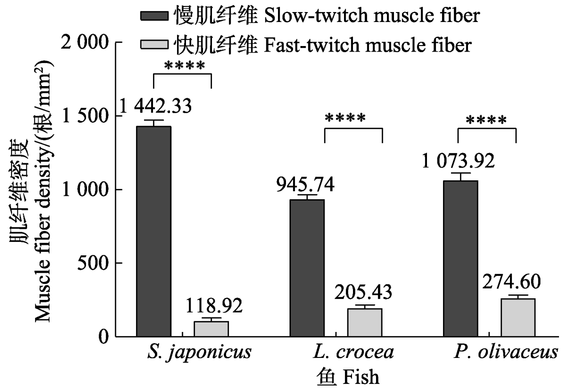

图 4　3 种鱼类快、慢肌纤维密度

Fig.4　Fiber density of fast-twitch muscle and slow-twitch muscle of three fish species

1984; 王力, 2020)，但本研究发现，3 种游泳习性鱼类的快、慢肌纤维形态有别：鲐的慢肌纤维细胞呈多角形，快肌纤维细胞呈多边柱形；而大黄鱼快、慢肌纤维细胞均呈长椭圆形；褐牙鲆的快、慢肌纤维细胞均呈扁椭圆形。这种不同鱼类物种间骨骼肌细胞形态的差异在其他鱼类中也有报道，例如，刘希良(2013)利用琥珀酸脱氢酶(SDH)染色法对翘嘴鳜(*Siniperca chuatsi*)的研究结果显示，翘嘴鳜背肌浅层边缘圆润的肌纤维细胞为慢肌纤维，而呈棱角多边形的深层肌纤维细胞为快肌纤维。梁向阳(2011)利用石蜡切片和电镜切片对 3 种不同倍性鲫的快肌纤维显微结构进行观察时也发现，肌纤维横截面均呈多角形。可见硬骨鱼类骨骼肌的快、慢肌纤维细胞存在多种形态。

本研究中，3 种不同游泳习性鱼类的快肌纤维直径均极显著大于慢肌纤维(P<0.01)，这种快肌纤维直径与慢肌纤维直径的差异在其他鱼类中也有报道。Rowlerson 等(2001)提出，大多数鱼类的快肌纤维的最大直径可达 100~300 μm，而慢肌纤维的直径则相对较小。朱琼等(2011)通过制作石蜡切片对鳜的快、慢肌纤维比较发现，其快肌纤维直径为 50.0~91.5 μm，而慢肌纤维直径为 12.2~44.2 μm。另外，对其他脊椎动物的快、慢肌纤维直径进行研究也发现了差异，例如，白伟良等(2002)研究显示，从犬(*Canis lupus familiaris*)肌纤维横断面观测，快肌纤维直径较大，为(32.7±5.8) μm，慢肌纤维直径较小，为(28.3±7.9) μm。张霖等(1992)利用 SDH 与 AchE 结合染色法对不同负荷训练小鼠(*Mus musculus*)肌纤维组织学的研究结果显示，不同负荷训练模式下其快肌纤维直径均大于慢肌纤维。解祥学等(2011)对不同品种肉牛(*Bos taurus*)肌纤维组织学的研究结果显示，6 个品种牛不同部位均是快肌纤维直径大于慢肌纤维直径。陈宽维等(2002)对 7 个品种肉鸡(*Gallus gallus*)肌纤维的研究结果显

示，快肌纤维直径较粗，且比慢肌纤维粗 20%左右。可见不论是高等脊椎动物还是较低等脊椎动物，肌纤维直径均表现为快肌纤维大于慢肌纤维。

从本研究结果可以看出，3 种游泳习性鱼类的快肌纤维和慢肌纤维在形态、直径和密度上存在差异。3 种鱼的快、慢肌纤维的形状各不相同，3 种鱼的快肌纤维直径均显著大于慢肌纤维。此外，本研究将不同游泳习性鱼类的快、慢肌纤维密度进行对比发现，鲐的慢肌纤维密度最高，而褐牙鲆的快肌纤维密度最高，这种差异可能与快、慢肌纤维的功能有关系。Martinez 等(2003)研究证明，硬骨鱼骨骼肌可为不同游泳速度和持续时间提供动力。慢肌收缩慢，依靠有氧代谢来支持活动，它含有高水平的线粒体以提供稳定和持续的动力；相比之下，快肌收缩速度快、线粒体含量低、爆发力强，更依靠无氧代谢来支持快速游动(Pinte *et al*, 2021)。Jobling 等(1993)研究发现，鱼类在有氧运动训练中主要运用慢肌有氧代谢供能，进行无氧运动训练后主要动用快肌供能。本研究以鲐为代表的持续式游泳习性鱼类所进行的长距离洄游需要有氧运动，因此，鲐的慢肌纤维密度高可能是为了适应这一游泳习性。而以褐牙鲆为代表的爆发式游泳习性鱼类在捕食和避敌中进行的爆发高速的游泳活动则需要无氧运动(李秀明, 2013)，因此，褐牙鲆快肌纤维密度高。

总之，不同种类的鱼类在不同环境和生态条件下适应不同的游泳习性，因此，在肌肉结构和功能方面也会有所差异。这些差异可能是为了更好地适应其生存环境和生活习性而发生的适应性进化。同时，不同种类的鱼类肌肉对不同种类的运动负荷也有不同的适应反应，这也可能会导致肌纤维形态和密度的差异。因此，鱼类肌纤维形态、直径和密度的差异与其游泳习性密切相关。此外，不同物种甚至不同营养水平和环境因素等也可能影响肌纤维特征。比如，野生花鲈(*Lateolabrax maculatus*)的肌纤维密度高于养殖花鲈(Periago *et al*, 2005)；饥饿导致团头鲂(*Megalobrama amblycephala*)的红、白肌纤维细胞小型化，饥饿后再投喂可以使肌纤维细胞加快肥大(陈丽萍, 2013)；缺氧环境也会使鱼类的肌纤维直径增长缓慢(Kiessling *et al*, 1991)。另外，Johnston 等(2000)对大西洋鲑(*Salmo salar*)研究发现，快肌纤维的直径与运动存在相关性，即运动会增加肌纤维的直径。孙文波等(2023)也指出，禾花鲤(*Cyprinuscarpio* var. *Quanzhounensis*)的运动强度大，可引起肌纤维密度变大。因此，本研究结果可为进一步开展硬骨鱼的骨骼肌适应性进化和运动生理学等研究提供重要参考。

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Histological Characteristics of Fast and Slow Muscle Fibers in Skeletal Muscle of Fishes with Three Different Swimming Habits

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Abstract　Swimming is of great significance for the survival of fish and directly affects their ability to avoid predators and enemies, hunt and capture prey, carry out mating and reproduction, and migrate. The skeletal muscles of bony fish, which provide power for swimming and account for approximately 40%–60% of the body mass, can be divided into red and white muscle fibers. Red muscle fibers have a slow contraction, strong endurance, high mitochondria content, glycogen, and myoglobin; mainly employ aerobic metabolism; and effectively use oxygen to produce ATP. They are also known as slow-twitch muscle fibers, whose main function in fish is to provide stable and continuous power for the swimming process. White muscle fibers contract quickly but also tire rapidly and mainly use glycolic metabolism. They are also known as fast-twitch muscle fibers and, in fish, provide power for fast swimming behaviors (such as predation and escape).

Many studies have indicated a strong correlation between fish swimming habits and the composition of slow and fast-twitch muscles. Most of these studies focused on the correlation between swimming motion and muscle fiber types, but differences in the histological characteristics of fast- and slow-twitch muscle fibers of fish with different swimming habits have rarely been reported. The histological characteristics of muscle fibers include shape, diameter, and density, which are important indicators describing the histological structure of the skeletal muscle in fishes. In this study, we selected three species (*Scomber japonicus*, *Larimichthys crocea*, and *Paralichthys olivaceus*) representing different swimming styles, to clarify the histological characteristics of fast- and slow-twitch muscle fibers, and compared them using hematoxylin-eosin staining of paraffin sections and morphometric methods.

The staining showed that the transverse sections of the fast- and slow-twitch skeletal muscle

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fibers were irregular and the diameter of the fast-twitch muscle fibers was larger than that of the slow-twitch muscle fibers. In *S. japonicus*, a species engaged in sustained swimming, the fast-twitch muscles were multi-angular, whereas the slow-twitch muscle fibers were multi-columnar. In *L. crocea*, a species swimming in an extended style, the muscle fibers were long, oval, and had cells with round edges. In *P. olivaceus*, a species engaged in prolonged swimming, the fast-twitch muscle fibers were oblate and had more connective tissues than the slow-twitch fibers. The slow-twitch muscle fibers of *S. japonicus* and the fast-twitch muscle fibers of *P. olivaceus* were finer than the slow-twitch and fast-twitch muscle fibers of these two species, respectively. The longitudinal section of the muscle fibers in the three species were distributed in strips alternating with connective tissue. In addition, the muscle fibers in *S. japonicus* occupied a larger space and were more loosely arranged than those in the other two species. However, the muscular space between fibers of both types was smaller in *P. olivaceus* and the muscle cells were more closely arranged.

Morphometric results showed that the diameters of fast-twitch muscle fibers were significantly larger than those of slow-twitch muscle fibers (P<0.01). The fast-twitch muscle fibers in *S. japonicus* were 4.84 times the diameter of slow-twitch muscle fibers, while that ratio was approximately 2.57 in *L. crocea* and 3.07 in *P. olivaceus*. The diameter of slow-twitch muscle fibers in *L. crocea* was the largest among the three species, approximately 1.34 and 1.14 times that of *S. japonicus* and *P. olivaceus*, respectively. In contrast, *S. japonicus* had the largest fast-twitch muscle fiber diameter, approximately 1.41 and 1.35 times that of *L. crocea* and *P. olivaceus*, respectively. The slow-twitch muscle fiber density in all three species was significantly greater than that of fast-twitch muscle fibers (P<0.01). The density of slow-twitch muscle fibers was 12.13, 4.60, and 3.91 times than that of fast-twitch fibers, in *S. japonicus*, *L. crocea*, and *P. olivaceus*, respectively. The order of the fast-twitch muscle fiber density was *P. olivaceus* [(274.60±9.07) unit/mm^2] > *L. crocea* [(205.43±12.63) unit/mm^2] > *S. japonicus* [(118.92±10.74) unit/mm^2]. The density of the fast-twitch muscle fiber of *P. olivaceus* was 2.31 and 1.34 times that of *S. japonicus* and *L. crocea*, respectively. The order of slow-twitch muscle fiber density was *S. japonicus* [(1 442.33±28.25) unit/mm^2] > *P. olivaceus* [(1 073.92±39.40) unit/mm^2] > *L. crocea* [(945.74±19.53) unit/mm^2]. Furthermore, the slow-twitch muscle fiber density of *S. japonicus* was 1.53 and 1.34 times that of *L. crocea* and *P. olivaceus*, respectively. The above-described methodology and analysis of differences in the shape, diameter, and density in the skeletal muscle fibers of teleost fish with different swimming habits will provide basic data for further studies on the adaptive evolution and movement physiology of this taxonomic group.

Key words Skeletal muscle; Fast and slow muscle fibers; Histological features; Swimming habits