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嘉陵江下游蛇鮈肠道形态结构及其异速生长模式

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摘要: 对2015—2016年间采自嘉陵江下游合川江段的233尾蛇鮈样本进行肠道形态结构的研究，分析蛇鮈肠道生长模式的特点，并从功能差异的角度探讨其对个体能量需求的适应。结果显示，蛇鮈肠道为Z型盘曲模式，比肠长(RGL)为0.612 8，属肉食性鱼类肠道类型；蛇鮈肠道可分为前肠、中肠和后肠3个分区，各分区在外部形态、内部结构以及肠道指数方面均存在较为明显的差异。Segmented结果分析表明，蛇鮈肠道属异速生长，整体肠道于2龄时出现生长拐点(TL=145.07 mm)，拐点前为快速生长，拐点后为等速生长。同时，肠道各分区的生长模式不尽相同，前肠和中肠始终保持等速生长，仅后肠从快速生长经拐点转换为等速生长。蛇鮈肠道各分区生长模式的差异可能与其功能分化有关，在拐点前，蛇鮈通过后肠的快速增长来提高摄食频率，从而满足其大量的能量需求。本研究不仅能为今后开展蛇鮈的人工养殖提供重要理论依据，同时为探讨鱼类肠道异速生长与食性间关系进行了有益的尝试。

关键词: 蛇鮈；肠道；形态结构；异速生长；摄食频率

中图分类号: S 965.1 **文献标志码:** A

消化道是鱼类营养物质消化和吸收的主要场所[1]，对鱼类的生长、发育和繁殖起着至关重要的作用[2]，其形态和功能受摄食行为(食性、摄食频率)[3-4]、环境条件(温度)[5-6]等多种因素影响。国内外关于消化道的研究主要集中在组织形态、细胞结构、消化机理和微生物等方面[7-14]，而关于消化道发育模式的研究仅有少量报道，如German等[15]和Davis等[16]在相关研究中指出，鱼类消化道属异速生长模式，但拐点位置、模式差异等重要异速生长特点均未提及。

异速生长，又称相对生长，是指受多种因素的影响，身体的不同部位存在不同的生长速率[17-18]。早期有关鱼类异速生长的研究多见于国外报道[19-20]，近年逐渐成为国内前沿热点课题[21-22]。Kramer等[23]认为鱼类肠道长度的异速生长与种间竞争密切相关。国内研究人员通过分析鲈鲤(*Percocypris pingi*)和大麻哈鱼(*Oncorhynchus keta*)仔鱼的感觉、呼吸和游泳等器官的异速生长模式，发现多数器官通过发育早期的快速生长使其在最短的时间内获得与生存密切相关的各种能力，以适应复杂的生存环境[24-25]。

蛇鮈(*Saurogobio dabryi*)属鲤科(Cyprinidae)，蛇鮈属(*Saurogobio*)[26]，为淡水底层鱼类，主要以底栖无脊椎动物为食[27]，是长江水系重要经济鱼类之一，具有营养价值高，肉质鲜美等特点，深受广大群众的喜爱。鲤科鱼类一般无胃[28]，其肠道主要包括前肠、中肠和后肠3个分区，各分区间存在形态结构和功能的差异[29]。目前，关于

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蛇鮈的研究主要集中于繁殖[30]、病理[31]、肌肉组织[32]和两性异形[33]等方面，而对其肠道形态结构及发育模式则鲜有报道。本实验以嘉陵江蛇鮈作为研究对象，观察其肠道的形态结构，分析其异速生长模式特点，并从功能差异的角度探讨其对个体能量需求的适应。研究结果可以为今后探索鱼类肠道发育模式积累经验，同时为蛇鮈的人工养殖提供重要依据。

1 材料与方法

1.1 标本采集

研究用样本采集时间为2015—2016年，采集地点为嘉陵江下游合川江段，采集网具为刺网，共获取样本233尾。样本洗净后，用5%甲醛溶液固定并带回实验室进行形态学观察、测量和解剖。

1.2 实验方法

蛇鮈形态及年龄测定 用数显游标卡尺测定全长(total length, TL)、体长(body length, BL)、头长(head length, HL)、头高(head height, HH)、头宽(胸鳍起点处头部两侧的水平距，head width, HW)、吻长(snout length, SnL)、口宽(口角间距离，mouth width, MW)、眼径(eye diameter, ED)[24]等形态指标(0.01 mm)(图1)，用ALC210.3电子天平测定体质量(body weight, BW)(0.01 g)。选取鳞片在解剖镜(Olympus SZX10)下进行年龄鉴定[3]。

蛇鮈肠道观测 根据无胃鱼类肠道常用分段标准，将蛇鮈肠道分为前肠(foreintestine, FI)、中肠(midintedtine，MI)和后肠(hindintestine，HI)3个分区[25,34]。清洗肠道内容物，观察蛇鮈肠道各分区外部形态及肠壁结构，并测定其长度(gut length, GL)(0.01 mm)及质量(gut weight, GW)(0.01 g)，整体肠道(total intestine，TI)质量和长度分别等于各分区测定数据之和。

采用以下指数对蛇鮈整体肠道及各分区进行描述：

比肠长(relative gut length, RGL)：$RGL=GL/SL$

比肠重(relative gut mass, RGM)：$RGM=GW/BW$

Zihler指数(Zihler index, ZI)：$ZI=GL/10(BW)^{1/3}$

单位长度肠道质量(W/L)：$W/L=GW/GL$

RGL、ZI用于描述肠道长度，RGM、W/L分别反映肠道质量和发达程度。

1.3 数据分析

肠道指数分析 使用SPSS 22.0软件进行单因素方差分析(One-Way ANOVA)，检验各项肠道指数在蛇鮈前肠、中肠和后肠间差异显著性，显著水平设置为P =0.05。

异速生长模式分析 异速生长模型以幂函数方程即$y=ax^b$计算，以TL为自变量x，y为整体肠道或肠道各分区长度，a为y轴截距，b为异速生长指数[35]。为便于计算，在进行数据分析前，先对数据进行log转换，然后确定生长拐点和生长指数[36-37]，使用R软件“segmented”分析包进行相关计算。利用t检验，判断b与1之间差异显著关系，如b与1无显著差异，则肠道为等速生

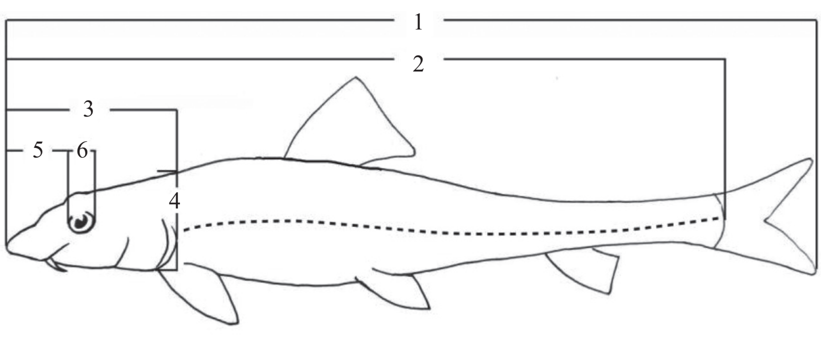

图 1 蛇鮈形态特征

1. 全长；2. 体长；3. 头长；4. 头高；5. 吻长；6. 眼径

Fig. 1 Morphological character of *S. dabryi*

1. total length; 2. body length; 3. head length; 4. head height; 5. snout length; 6. eye diameter

长；b<1，为慢速生长；b>1，为快速生长。使用Origin 8.0软件绘制异速生长模式示意图。

相关形态特征生长模式分析　鱼类头部一些形态特征的生长模式可作为判断其食性是否转变的依据[24-25]，因此分别对蛇鮈HL、HW、HH、SnL、MW、ED的生长模式进行分析，具体计算方法同上。若肠道生长拐点前后，与食性转变相关的形态特征生长指数(b_1、b_2)间差异显著，即生长模式发生显著改变，则其食性有明显转变；反之，则表示蛇鮈食性并无明显变化。

2　结果

2.1　蛇鮈肠道描述

实验用233尾蛇鮈样本，体长为70.53~149.00 mm，全长为80.51~184.00 mm，体质量为3.67~44.40 g。蛇鮈无胃，肠盘曲简单，属于Z型肠道盘曲模式[38]，经2次盘曲开口于肛门。前肠呈膨大的长囊状，包埋于消化腺之中；中肠管状，肠径小于前肠；后肠管状，肠径最小，靠近肛门处肠径逐渐减小。前肠与中肠长度相近，后肠明显长于前肠和中肠。镜检结果显示，前肠肠壁最厚，肠内黏膜褶皱最密集发达，中肠次之，后肠肠壁最薄，肠内黏膜褶皱发达程度相对较低且排列稀疏(图2)。

方差分析结果显示，各分区间肠道指数均差异显著(P<0.05)(表1)。RGL、ZI分析结果均表明，后肠最长，前肠次之，中肠最短，且后肠长度接近前、中肠之和；RGM指数表明，前肠最重，后肠次之，中肠最轻，W/L指数表明，前肠最为发达，中肠次之，后肠发达程度最低。

2.2　蛇鮈肠道异速生长模式分析

t检验结果显示，整体肠道(图3-a)和后肠(图3-d)

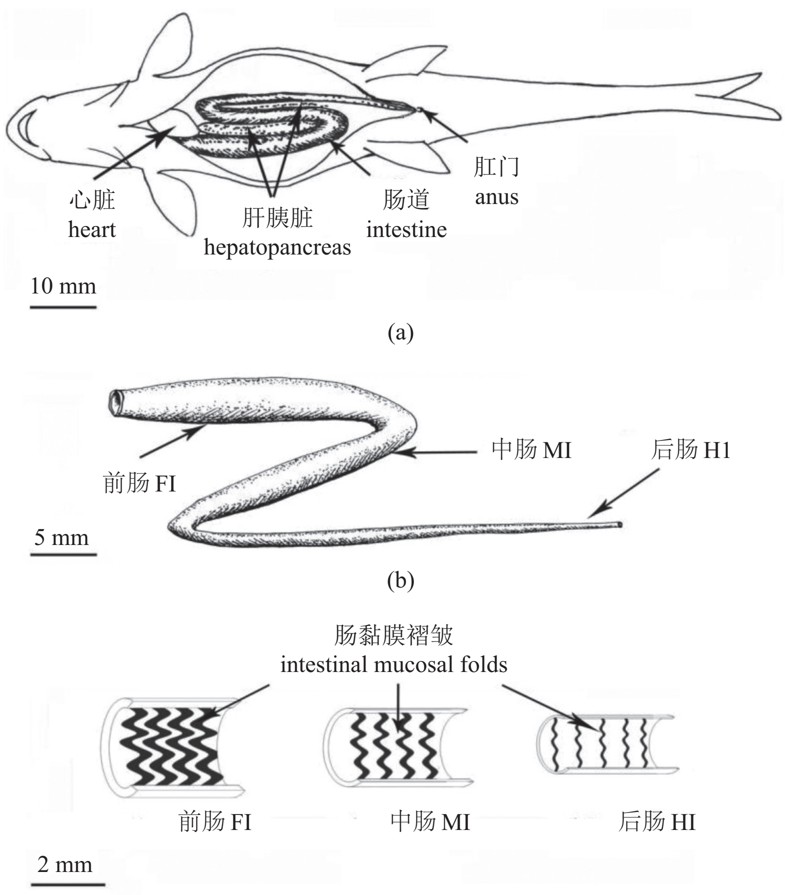

图 2　蛇鮈肠道示意图

(a) 蛇鮈内部器官；(b) 蛇鮈整体肠道；(c) 蛇鮈肠道各分区结构

Fig. 2　Intestine of *S. dabryi*

(a) internal organs of *S. dabryi*; (b) total intestine of *S. dabryi*; (c) structure of every part of *S. dabryi* intestine

表 1 蛇鮈肠道指数

Tab. 1 Intestine index of *S. dabryi*

指标 index	肠道分区 the part of intestine			整体肠道 TI
	前肠 FI	中肠 MI	后肠 HI	
RGL	0.179 9±0.001 9[a]	0.121 3±0.001 7[b]	0.281 6±0.003 2[c]	0.612 8±0.004 9
RGM	0.006 7±0.000 2[a]	0.002 7±0.000 1[b]	0.003 7±0.000 1[c]	0.013 1±0.000 3
ZI	0.796 1±0.021 1[a]	0.669 1±0.007 6[b]	1.245 2±0.013 9[c]	2.710 5±0.021 1
W/L	0.006 1±0.000 2[a]	0.003 0±0.000 1[b]	0.002 2±0.000 1[c]	0.003 5±0.000 1

注：数据采用平均值±标准误，肠道分区数据同行的不同字母表示差异显著(P<0.05)
Notes: the average ± SE was used to express the data, and the different letters meant significant difference (P<0.05)

均在2龄时出现生长拐点，对应TL分别为145.07 mm和148.16 mm(表2)。拐点前生长指数(b_1)分别为1.248 7和1.386 8，均极显著大于1(P<0.01)，即整体肠道和后肠在各自生长拐点前为快速生长。拐点后生长指数(b_2)与1差异不显著。前肠(图3-b)和中肠(图3-c)拐点前后生长指数(b_1、b_2)均与1差异不显著，属等速生长。

2.3 相关形态特征生长模式分析

*t*检验结果显示，在整体肠道和后肠生长拐点(TL=145.07 mm、148.16 mm)前后，蛇鮈相关形态特征的生长模式均无显著改变，说明蛇鮈食性可能并未发生明显变化(表3，表4)。

3 讨论

蛇鮈肠道结构简单，仅有2次盘曲，属Z型肠道盘曲模式[38]，与鮈亚科一些鱼类，如长鳍吻鮈(*Rhinogobio ventralis*)[39]、长蛇鮈(*S. dumerili*)[40]等相似。鱼类肠道形态特征与其食性密切相关[3]，典型的肉食性鱼类肠道结构简单，比肠长一般小于1，如鳗鲡(*Anguilla* sp.)以小鱼、虾、蟹等动物为食[27]，其肠道几乎无盘曲，长度只有体长的1/3[34]；杂食性鱼类或偏重植食性鱼类，比肠长变动于1~3之间；而纯植食性或碎屑食性鱼类，肠道结构复杂，比肠长可大于3[3]，如鲢(*Hypophthalmichthys molitix*)比肠长为6.29~7.77，盘曲高达27次[41]。本研究中蛇鮈肠道较短，比肠长仅为0.612 8，属于肉食性鱼类肠道类型。

鱼类肠道属异速生长模式[15, 20, 42]，许多异速生长器官(如游泳、摄食、视觉等)都具有快速生长阶段，使其能在短时间内形成并完善相应的结构和功能，以适应复杂多变的生态环境[24-25]。本研究表明，蛇鮈肠道发育具备相似特点，这可能与其能量摄入功能密切相关。动物增加能量摄入一般有两种方式，第一种方式是提高摄食频率，如牛、羊等草食性动物，具有发达的胃来储存食物[43]，对于无胃鱼类而言，食物直接进入肠内消化，一次容纳的食物量远不及有胃

表 2 蛇鮈肠道异速生长模式

Tab. 2 Allometric model of intestine in *S. dabryi*

肠道分区 partition	拐点全长 TL	拐点长度 GL	拐点前 before inflexion point			拐点后 after inflexion point			P
			n_1	b_1	P_1	n_2	b_2	P_2	
整体肠道 TI	145.07	76.80	197	1.25	0.001 8	36	0.72	0.386 4	0.167 4
前肠 FI	126.00	19.68	90	1.25	0.133 4	143	0.80	0.406 9	0.136 7
中肠 MI	169.00	18.23	227	1.08	0.376 1	6	4.04	0.073 4	0.288 2
后肠 HI	148.16	36.18	201	1.39	0.000 3	32	0.25	0.120 0	0.019 3

注：n_1，n_2分别表示拐点前后蛇鮈的个体数量；P表示拐点前后生长指数b_1、b_2间差异显著性；P_1、P_2分别表示生长指数b_1、b_2与1的差异显著性水平，显著性水平为0.05；b值显著大于1属快速生长，b值显著小于1属慢速生长，b值与1无显著差异则属等速生长，下同
Notes: n_1, n_2 denote the number of individuals in *S. dabryi* before and after the inflexion point; the b_1, b_2 denote the growth index before and after the inflexion point; P denote the significance of difference between $b_1$and b_2; P_1, P_2 denote the significance of difference between b_1 and 1, b_2 and 1; the significant difference at 0.05 level; b>1 denotes fast growth, b<1 denotes slow growth, if b has no significant difference with 1, the growth model is isokinetic, the same below

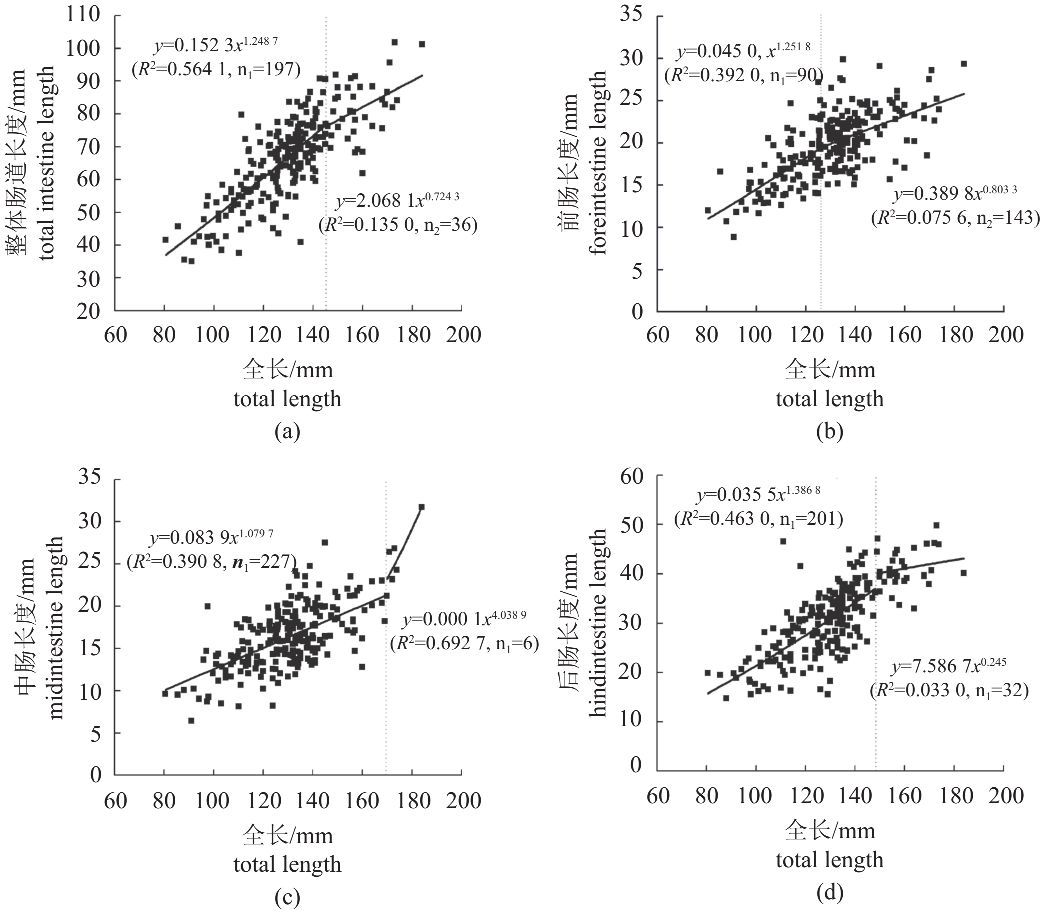

图 3　蛇鮈整体肠道及各分区异速生长曲线及表达函数

Fig. 3　Allometric growth curve and function of total and every part of *S. dabryi* intestines

表 3　相关形态特征生长模式(整体肠道生长拐点)

Tab. 3　Growth models of morphological traits (inflexion point of growth in total intestine)

形态特征 morphological character	拐点前 before inflexion point		拐点后 after inflexion point		P
	b_1	P_1	b_2	P_2	
头长　HL	0.922 7	0.049 8	1.116 7	0.516 7	0.312 3
头宽　HW	1.053 9	0.222 7	1.127 6	0.568 6	0.736 3
头高　HH	1.067 3	0.146 2	1.208 0	0.349 3	0.536 2
吻长　SnL	1.165 3	0.458 2	1.054 3	0.884 3	0.913 7
口宽　MW	0.983 9	0.858 6	1.038 5	0.939 5	0.904 7
眼径　ED	0.727 6	0.005 4	0.443 9	0.193 1	0.547 2

表 4　相关形态特征生长模式(后肠生长拐点)

Tab. 4　Growth models of morphological traits (inflexion point of growth in hindintestine)

形态特征 morphological character	拐点前 before inflexion point		拐点后 after inflexion point		P
	b_1	P_1	b_2	P_2	
头长　HL	0.929 9	0.069 9	1.265 5	0.177 6	0.121 8
头宽　HW	1.073 2	0.097 4	1.324 7	0.170 2	0.312 1
头高　HH	1.086 6	0.062 4	1.398 3	0.072 4	0.227 7
吻长　SnL	1.189 1	0.382 5	1.466 6	0.265 7	0.810 7
口宽　MW	1.000 1	0.998 7	1.243 3	0.673 4	0.637 6
眼径　ED	0.740 9	0.006 8	0.737 0	0.578 0	0.994 1

鱼类[34]，因此，提高摄食频率能显著增加能量摄入；第二种方式是改变食物的类型，通过主动增加食物中蛋白质的比例来满足高能量的需求[11]，如在仔鱼阶段真鲷(*Pagrosomus major*)通过食性的转变来适应高能量的需求[44]。在生长发育过程中，鱼类需要大量的能量来满足身体各器官的快速生长[17，25]，肠道则是无胃鱼类能量吸收的主要场所[45]。本研究中蛇鮈整体肠道和后肠均存在先快后慢的异速生长特点，且与食性相关鱼类头部形态差异分析结果表明，拐点前后食性并无明

显改变，这表明食性的变化可能并不是蛇鮈应对其大量能量需求的主要方式，下一步仍需要从拐点前后蛇鮈的食性差异和摄食频率变化等方面来进一步论证。

另外，蛇鮈肠道各分区生长模式不尽相同，这可能与其功能分化有关，前肠主要行使消化食物的功能，中肠侧重于吸收，而后肠促进消化道内容物的排空[29，38]。相关研究表明，后肠有大量的杯状细胞[29]，其快速增长能提高肠道排空率，从而提高动物的摄食频率[4，46]，说明蛇鮈是通过后肠快速增长从而提高其摄食频率的方式来满足其对大量能量的需求。

适口饵料的组成和合理的投喂频率是投喂模式的主要组成部分，也是水产养殖管理的核心内容之一[47-49]。如肉食性鱼类鳜(*Siniperca chuatsi*)和大口鲇(*Silurus meridionalis*)，在生长发育过程中均存在食物组成的明显变化，其开口饵料的选择和投喂频率的选取(过勤则浪费饵料资源，增加水体污染；过慢则降低鱼类生长速率，甚至会导致个体间自相残食)，很长一段时间都是人工养殖的难点问题[50-54]。本研究表明，蛇鮈属于肉食性鱼类，在生长发育过程中其食性并未发生明显变化，主要通过提高摄食频率来满足大量能量的需求。本研究不仅能为日后开展蛇鮈人工养殖提供重要依据，也为探讨鱼类肠道异速生长与食性间关系进行了有益的尝试。

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Morphological structure and allometric growth pattern of *Saurogobio dabryi* intestine in the lower reaches of Jialing River

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Abstract: To study the intestinal structure characteristics and the relationship with its growth pattern of *Saurogobio dabryi*, a total of 233 individuals were collected from the lower reaches of the Jialing River (Hechuan section) from 2015 to 2016. Morphological observation results showed that the intestinal structure of *S. dabryi* was Z-shaped, and belonged to carnivorous fish gut according to its relative short gut length (RGL) index (0.612 8). Based on its morphological structure, the intestine could be divided into three parts, the foreintestine, the midintestine and the hindintestine, with obvious difference in external morphology, internal structure and intestinal index. The growth pattern of *S. dabryi* intestine was allometry, with 2-year growth inflexion age and 145.07 mm corresponding fish total length (TL). Before and after the inflection point, there was different growth pattern of intestine, *i.e.*, from the fast growth stage to slow growth stage. Meanwhile, the growth pattern of intestine was different between each part. In addition, the results of segmented analysis with R software showed that all of the inflexion points among three parts appeared at the age of 2 years, and their TL were 126.00 mm, 169.00 mm, 148.16 mm respectively; there were obvious differences in intestinal growth pattern among the three parts, with isokinetic growth in the foreintestine and the midintestine, but with significant allometric growth in the hindintestine, which had a fast growth stage before growth inflexion point and then changed to isokinetic growth pattern, based on the growth indices difference analysis between two stages. Thus, the difference of growth pattern of *S. dabryi* among the three parts of intestine might be related to their functional differentiation. Before the inflection point, the *S. dabryi* might improve their feeding frequency by the fast growth stage of the hindintestine, to meet the great demand for energy during the initial growth stage. The results obtained from this research can not only provide important scientific evidence for artificial cultivation of *S. dabryi*, but also offer a new example for studying the relationship between the growth pattern of fish intestine and its feeding habits.

Key words: *Saurogobio dabryi*; intestine; morphological structure; allometric growth; feeding frequency

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