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长江中下游湖泊10种常见鱼类氮磷排泄率特征及其影响因素

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摘要: 为探究长江中下游湖泊鱼类的氮、磷排泄率特征及其影响因素, 于2023年5—6月采集测定了长江中下游湖泊10种常见鱼类的氮、磷排泄率及生态化学计量特征, 并通过模型分析了鱼类氮、磷排泄率关键影响因素。结果表明, 长江中下游湖泊常见鱼类的氮排泄率为0.15—16.24 mg/h, 磷排泄率为0.01—5.73 mg/h。鱼类的氮、磷排泄率与体重呈显著正相关($R^2=0.86$, $P<0.001$; $R^2=0.87$, $P<0.001$), 体型较大的鱼比体型较小的鱼排出更多的氮和磷, 但小体型物种单位体重氮、磷排泄率更高。不同食性鱼类的单位体重氮、磷排泄率存在显著性差异($P<0.001$), 浮游生物食性鱼类单位体重氮、磷排泄率相对较高。鱼类氮排泄率与鱼体氮含量呈显著负相关($R^2=0.10$, $P<0.001$), 磷排泄率与鱼体磷含量不相关。模型结果表明, 体型是预测鱼类氮、磷排泄率的关键因子, 尽管食性和鱼体氮、磷元素含量也会影响鱼类氮、磷排泄率, 但其在模型中的预测效果较差。研究表明生态代谢理论在预测鱼类氮、磷排泄率方面表现优于生态化学计量学理论, 但需考虑物种分类对模型的影响。研究结果对于理解鱼类在湖泊生态系统养分循环过程中的作用具有重要意义。

关键词: 消费者; 排泄; 生态化学计量学理论; 生态代谢理论; 养分循环

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鱼类是水生态系统中的重要消费者, 也是水生生态系统养分循环和能量流动的关键驱动者^[1,2]。作为能主动自由迁移的水生动物, 鱼类能通过多种途径影响水生生态系统的养分循环过程, 如排泄^[3,4]、排遗^[5,6]、捕食^[7]和生物扰动^[8,9]等。研究表明, 鱼类通过排泄释放的溶解性氮、磷等营养物质是初级生产者和微生物的重要养分来源, 并可能在局部空间形成生物地球化学热点, 从而影响水生生态系统的初级生产力和养分循环过程。例如, Vanni等^[10,11]研究发现, 鱼类排泄产生的磷能支持初级生产者磷需求的7%—53%, 并且随着湖泊初级生产力的提

高, 这一养分供应比例也将提高。Williamson等^[12]对一个富营养化水库近20年的监测结果显示, 鱼类在生长季节的氮、磷排泄量对水体营养盐的供给率超过了流域氮、磷输入量, 并且对浮游植物生物量和群落结构组成产生强烈影响。因此, 深入了解鱼类排泄对初级生产者的养分供应与限制作用, 有助于揭示消费者在生态系统养分再循环过程中的重要性。

近年来, 生态化学计量学理论(Ecological Stoichiometry Theory)和生态代谢理论(Metabolic Theory of Ecology)为研究消费者如何调节生态系统养分循

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环提供了两个重要理论框架。生态化学计量学通过解析生物体内碳(C)、氮(N)和磷(P)等关键营养元素的含量和比例,揭示生物体的身体和其饮食化学计量之间的不平衡如何影响其营养排泄率^[13]。而生态代谢理论则从能量代谢角度出发,强调生物体代谢速率主要受体型和环境温度的调控,进而影响其对生态系统中能量与物质循环的贡献^[14]。生物体的排泄活动作为代谢产物的重要释放途径之一,是连接生物体代谢与生态系统养分循环的关键环节。生物体的排泄速率受代谢水平的直接制约,同时也与体内营养元素需求密切相关^[15, 16]。因此,将生态化学计量学理论与生态代谢理论相结合,为预测和解释鱼类等消费者驱动的生态系统养分循环提供理论支持。国外学者如Vanni等^[17]、Allgeier等^[18]、Allen和Gillooly^[19]应用生态化学计量学和生态代谢理论框架在鱼类和无脊椎动物驱动的养分循环研究中取得了重要进展,发现生态代谢理论在预测鱼类和无脊椎动物氮、磷排泄率方面优于生态化学计量学理论,但仍需考虑物种分类对预测效果的影响。相比之下,国内近年来在这领域虽有少量研究^[20–23],但研究对象主要以鲢、鳙为主,而对其他鱼类的研究仍显薄弱。如李培培^[21]测定了千岛湖鲢、鳙的排泄率,定量评价了鲢、鳙在驱动千岛湖营养物质再循环和湖泊营养演化过程中的作用,发现鲢、鳙排泄产生的氮、磷含量占藻类初级生产所需含量的比例较低;唐海滨等^[22]研究了小江流域4种典型食性鱼类排泄及其对初级生产养分循环的作用,发现滤食性鱼类氮排泄率最高,滤食性鱼类和肉食性鱼类磷排泄率相对较高,且水温对鱼类氮、磷排泄率的影响较大。然而这些研究大多集中在特定区域或少数鱼类种类上,且对影响因素的综合分析仍显不足。

因此,本研究以长江中下游湖泊10种常见鱼类为研究对象,解析其氮、磷排泄率特征,并通过整合生态代谢理论和生态化学计量学理论,探讨鱼类氮、磷排泄率的影响因子,并建立预测模型。本研究不仅有助于丰富水生态系统养分循环理论体系,也为湖泊鱼类群落调控和水生态修复提供了科学依据。

1 材料与方法

1.1 排泄率的测定

2023年5—7月,在梁子湖采用插网、地笼等网具收集活鱼样本,并在原位实验网箱中进行暂养。实验鱼的基本情况如表1所示,涵盖了草食性、杂食性、浮游生物食性、鱼食性和碎屑食性5种典型

食性鱼类,且这些鱼类的生活习性和空间分布类型存在显著差异。鱼类氮、磷排泄率测定方法主要参考已建立的方法^[24–26]并进行优化。实验开始前,从网箱中挑选不同体型大小、状态良好且肠道饱满的活鱼备用。根据鱼类的体型,选择尺寸适宜的聚乙烯培养袋用于培养实验,并注入经1.20 μm滤膜(GF/C, Whatman)过滤的湖水(体积0.5—5.5 L)。将经冲洗干净的活鱼放进培养袋,并固定在原位实验网箱中,培养时间为30—60min。同时,设置3个无鱼对照组,用于测定自然环境条件下氨氮(NH₄⁺-N)和可溶性磷(SRP)的浓度变化。在实验开始前,从各培养袋中取水样200 mL作为实验前的对照水样,在培养结束后,再取水样200 mL,并用0.70 μm滤膜过滤(GF/F, Whatman),用于氨氮(NH₄⁺-N)和可溶性磷(SRP)的分析。测定依据《国家地表水质量监测标准》^[27]进行,其中氨氮(NH₄⁺-N)的测定采用纳氏试剂分光光度法(GB.7479-87),可溶性磷(SRP)的测定采用磷钼酸铵分光光度法(GB.11893-89)。各实验组实验前后的氨氮(NH₄⁺-N)和可溶性磷(SRP)含量的差值,经对照组的值校正后即即为鱼类的氮、磷排泄率。

1.2 化学计量特征的测定

在完成鱼类氮、磷排泄率测定后,将鱼收集并测量其体长和体重。随后将鱼去除内脏,清洗干净后,放入烘箱烘干至恒重。烘干后的鱼类样品用研磨机和球磨仪粉碎,再通过100目筛网过筛。称取

表1 长江中下游湖泊10种常见鱼类的基本情况

Tab. 1 Basic information on 10 common fish species in lakes in the middle and lower reaches of the Yangtze River

种类 Species	食性 Trophic guild	样本数 Sample (ind.)	湿重 Wet mass (g)
草鱼 <i>Ctenopharyngodon idella</i>	草食性 Herbivore	13	484.4±120.6
团头鲂 <i>Megalobrama amblycephala</i>	草食性 Herbivore	23	710.6±62.1
鲫 <i>Carassius auratus</i>	杂食性 Omnivore	80	103.7±6.4
鲤 <i>Cyprinus carpio</i>	杂食性 Omnivore	31	589.6±106.4
鳊 <i>Siniperca chuatsi</i>	鱼食性 Piscivore	8	86.3±39.9
翘嘴鲌 <i>Culter alburnus</i>	鱼食性 Piscivore	68	56.1±7.7
鲢 <i>Hypophthalmichthys molitrix</i>	浮游生物食性 Planktivore	14	279.7±68.6
鳙 <i>Aristichthys nobilis</i>	浮游生物食性 Planktivore	8	779.1±193.3
似鲮 <i>Toxabramis swinhonis</i>	浮游生物食性 Planktivore	100	12.0±0.3
黄尾鲮 <i>Xenocypris davidi</i>	碎屑食性 Detritivore	11	32.7±2.0

10—20 mg过筛后的样品,使用元素分析仪(Elementar vario MACRO cube, Germany)测定其碳(C)和氮(N)含量。另外称取0.10—0.30 g过筛后的样品,加入 $H_2SO_4-H_2O_2$ 进行消煮,采用钼锑抗比色法进行磷(P)含量的测定^[28]。

1.3 数据分析

采用Excel进行数据整理, R 4.3.2^[29]进行统计分析和作图。首先通过单因素方差分析(One-way ANOVA)不同物种和不同食性鱼类氮、磷排泄率是否存在显著性差异,并采用Tukey HSD法进行组间多重比较,以 $P<0.05$ 作为显著性水平。采用回归分析拟合体重、鱼体氮、磷含量及其比值与鱼类氮、磷排泄率及其比值的相关关系。根据生态代谢理论和生态化学计量学理论,选择“体重”“食性”“鱼体氮、磷含量”作为预测因子,采用线性模型对鱼类的氮、磷排泄率及其比值进行预测。同时,考虑到物种分类对预测效果的影响,采用线性混合模型对鱼类的氮、磷排泄率及其比值进行预测,并对添加物种分类的线性混合模型和不添加物种分类的线性模型进行了卡方检验。随后,根据物种的分类水平,将“科”“属”“种”三个分类水平作为随机效应,测试了其组合和作为单个随机效应对模型随机斜率、随机截距、随机截距和斜率的影响。根据生态代谢理论,个体的代谢率与其体型大小呈幂律关系,即 $B=B_0 M^{3/4}$ (式中, B 为代谢率, M 为生物体质量, B_0 为常数),因此,将模型得出的随机斜率与0.75进行对比,以验证模型的结果是否支持生态代谢理论。在统计分析前,对氮、磷排泄率及其比值,以及鱼体氮、磷元素含量及其比值分别进行lg转换,以满足正态分布假设。

2 结果

2.1 鱼类氮、磷排泄率特征

本研究共测定10种常见淡水鱼类356尾,不同物种间的氮、磷排泄率差异较大,其中氮排泄率为0.15—16.24 mg/h,磷排泄率为0.01—5.73 mg/h。体型较小的物种似鲮(*Toxabramis swinhonis*)的平均氮、磷排泄率较低,而体型较大的物种鳙(*Aristichthys nobilis*)和团头鲂(*Megalobrama amblycephala*)的平均氮、磷排泄率较高,但小体型物种的单位体重氮、磷排泄率高于大体型物种(表2)。

2.2 鱼类氮、磷排泄率影响因素

体型对氮、磷排泄率的影响 线性回归结果显示(图1),鱼类的氮、磷排泄率与体重呈显著正相关($R^2=0.86, P<0.001$; $R^2=0.87, P<0.001$),氮、磷排泄率比值与体重呈显著负相关($R^2=0.36, P<0.001$)。

表2 10种常见鱼类的氮、磷排泄率(平均值±标准误差)

Tab. 2 Nitrogen and phosphorus excretion rates in 10 common fish species (mean±SE)

种类 Species	氮排泄率 N excretion rate (mg/h)	磷排泄率 P excretion rate (mg/h)	单位体重氮 排泄率 Mass Specific N excretion rate [μg/(g·h)]	单位体重磷 排泄率 Mass Specific P excretion rate [μg/(g·h)]
草鱼 <i>Ctenopharyngodon idella</i>	3.76±0.77	0.71±0.11	10.13±1.28	2.29±0.35
团头鲂 <i>Megalobrama amblycephala</i>	7.99±0.62	1.64±0.15	12.32±0.81	2.35±0.10
鲫 <i>Carassius auratus</i>	1.57±0.10	0.28±0.03	15.68±0.57	2.97±0.29
鲤 <i>Cyprinus carpio</i>	4.40±0.67	1.01±0.21	7.97±0.45	1.47±0.10
鳊 <i>Siniperca chuatsi</i>	1.64±0.30	0.08±0.02	28.12±2.84	1.27±0.09
翘嘴鲈 <i>Culter alburnus</i>	0.97±0.09	0.15±0.02	19.74±0.91	2.92±0.16
鲢 <i>Hypophthalmichthys molitrix</i>	4.87±1.10	1.11±0.20	19.84±1.07	2.35±0.63
鳙 <i>Aristichthys nobilis</i>	5.00±0.93	1.63±0.44	8.06±1.14	2.22±0.32
似鲮 <i>Toxabramis swinhonis</i>	0.53±0.02	0.04±0.01	44.60±1.02	2.96±0.12
黄尾鲮 <i>Xenocypris davidi</i>	0.65±0.09	0.04±0.01	19.18±1.81	1.08±0.07

鱼类的氮、磷排泄率随着体重的增大而增加,氮、磷排泄率比值随着体重的增大而减小。这一结果与异速生长理论相符合,体型较大的鱼比体型较小的鱼排泄出更多的氮和磷,且所有物种的氮、磷排泄率与体重均呈显著正相关(表3)。

食性对氮、磷排泄率的影响 不同食性鱼类之间的单位体重氮、磷排泄率具有显著性差异(ANOVA, $P<0.001$),其中浮游生物食性鱼类的单位体重氮排泄率显著高于其他食性鱼类;浮游生物食性和鱼食性鱼类单位体重磷排泄率显著高于碎屑食性和杂食性鱼类(图2)。

鱼体氮、磷含量对氮、磷排泄率的影响 鱼类氮排泄率与鱼体氮含量呈显著负相关($R^2=0.10, P<0.001$),磷排泄率与鱼体磷含量不相关($P=0.66$),氮、磷排泄率比值与鱼体氮、磷含量比值呈显著正相关($R^2=0.03, P<0.01$; 图3)。鱼类氮排泄率随鱼体氮含量的增加而减小,但磷排泄率不随鱼体磷含量变化而变化。

2.3 鱼类氮、磷排泄率预测模型

线性模型结果显示,预测氮、磷排泄率及其比值的最佳模型均为包含体重、食性、鱼体氮磷含量”的简单线性模型,即生态代谢理论和生态化学

计量理论两者结合的预测因子预测效果最佳(表4)。结果表明,在加入物种分类后,线性混合模型的预测效果优于简单线性模型(表5)。

将科、属、种三个分类水平作为随机效应,其组合和作为单个随机效应对模型随机斜率、随机截距、随机截距和斜率的影响结果。通过对比这些模型,发现氮、磷排泄率及其比值的最佳预测因子均为“体重”,且在“物种”这一分类水平,模型的预测效果最佳(表6)。氮排泄率最佳预测模型的随机效应图显示,只有1个物种的随机斜率95%的置信区间不在0.75范围内(图4);磷排泄率最佳预测模型的随机效应图显示,有3个物种的随机斜率的95%置信区间不在0.75范围内(图4)。预测模型表明,生态代谢理论预测因子(体型)在预测鱼类氮、磷排泄率方面表现优于生态化学计量学理论预测因子(鱼体氮、磷含量和食性),但需考虑物种分类

对模型的影响(图5)。

3 讨论

3.1 长江中下游湖泊常见鱼类氮、磷排泄率特征差异

本研究发现长江中下游湖泊10种常见鱼类的氮、磷排泄率存在显著差异,其中团头鲂(*Megalobrama amblycephala*)和鳙(*Aristichthys nobilis*)的氮、磷排泄率较高,似鳊(*Toxabramis swinhonis*)和黄尾鲮(*Xenocypris davidi*)的较低,但鱼类单位体重氮、磷排泄率则相反,小体型鱼类的单位体重氮、磷排泄率高于大体型鱼类。这与其他研究结果相似,如Shrestha等^[30]研究发现加利福尼亚州海岸带珊瑚礁30种鱼类的氮排泄率随着体重的增加而增大,但单位体重氮排泄率则相反。Oliveira-Cunha等^[31]发现巴西河流中12种鱼类的氮、磷排泄率与体重均呈

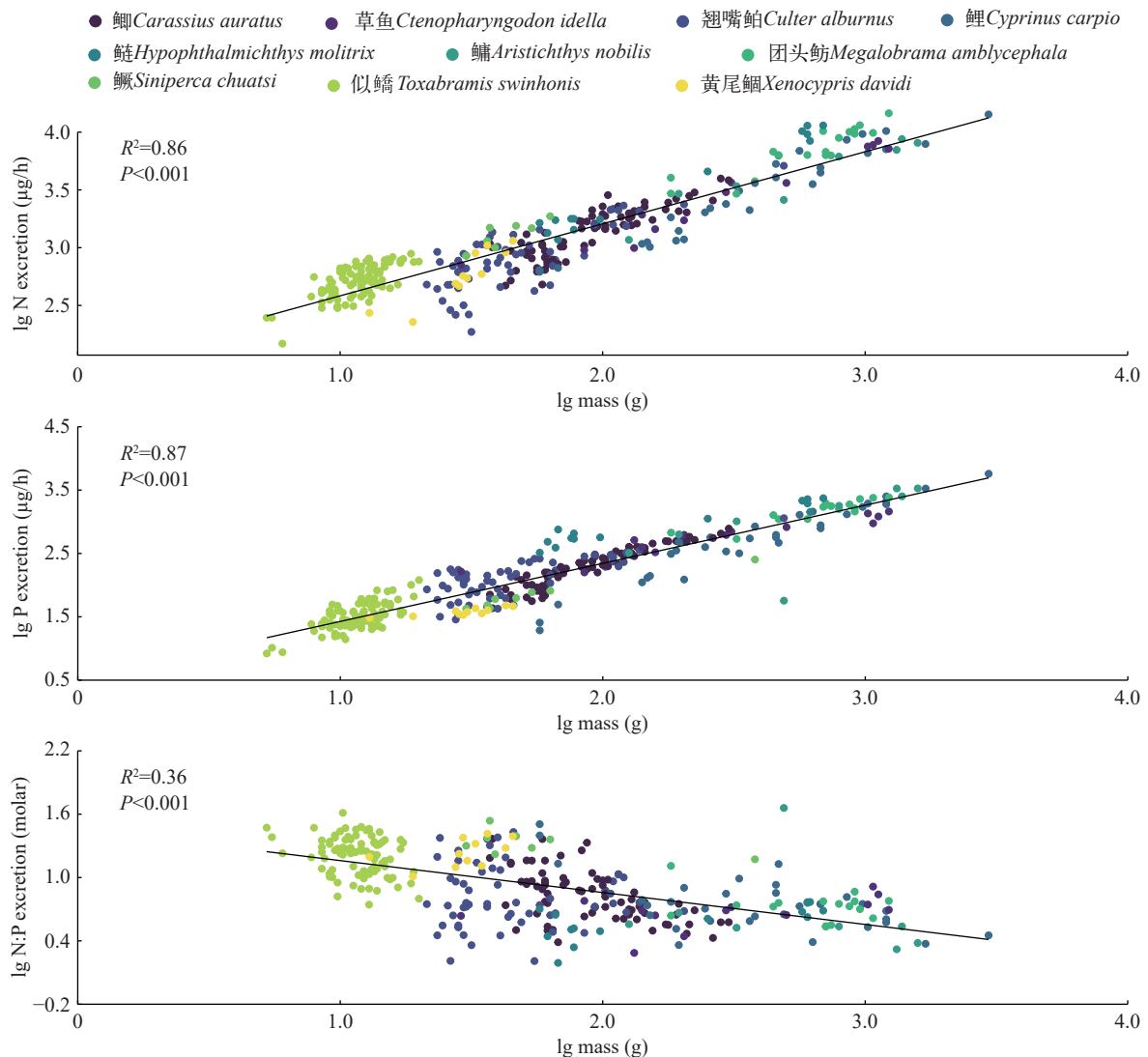


图1 鱼类氮、磷排泄率及其比值与体重的线性回归分析

Fig. 1 Linear regression analysis of nitrogen and phosphorus excretion rates and their ratios of fishes with mass

显著正相关, 体型较小的种(*Phalloceros harpagos*和*Mimagoniates microlepsis*)的单位体重氮、磷排泄率较低, 而体型较大的物种(*Rhamdia quelen*和*Rineloricaria* sp.)的单位体重氮、磷排泄率较高。鱼类生活史策略差异可能是造成这种差异的主要原因^[32, 33]。似鲮是一种快速生长的小型鱼类, 能够在短时间内利用环境资源快速繁殖, 维持种群的增长^[34], 因此, 其生长速度和代谢速度相对较快, 从而导致其单位体重氮、磷排泄率较高。而团头鲂和鳊是体型相对较大的鱼类, 在其生长发育过程中, 生长速度较慢, 代谢速度也相对较低, 进而导致其单位体重氮、磷排泄率较低。此外, 除了生活史策略, 鱼类的食物资源可获得性和栖息生境差异亦可能对其氮、磷排泄率产生显著影响。研究表明, 食物供应的丰富程度和食物质量也可能通过调节鱼类的摄食行为和营养吸收效率, 进而影响其排泄率^[35, 36]。此外, 温度作为影响鱼类代谢和排泄的重

表 3 鱼类氮、磷排泄率与体重的线性回归分析

Tab. 3 Linear regression analysis of nitrogen and phosphorus excretion rates of fishes with mass

物种Species	回归方程Linear regression equation	P	R ²
草鱼 <i>Ctenopharyngodon idella</i>	lg (E _N)=0.73	<0.001	0.94
	lg (mass)+1.63		
	lg (E _P)=0.59	<0.001	0.89
	lg (mass)+1.31		
团头鲂 <i>Megalobrama amblycephala</i>	lg (E _N)=0.73	<0.001	0.81
	lg (mass)+1.83		
	lg (E _P)=0.92	<0.001	0.85
	lg (mass)+0.58		
黄尾鲴 <i>Xenocypris davidi</i>	lg (E _N)=1.31	<0.001	0.81
	lg (mass)+0.84		
	lg (E _P)=0.35	<0.001	0.72
	lg (mass)+1.07		
鲫 <i>Carassius auratus</i>	lg (E _N)=0.84	<0.001	0.72
	lg (mass)+1.50		
	lg (E _P)=1.30	<0.001	0.88
	lg (mass) - 0.26		
鲤 <i>Cyprinus carpio</i>	lg (E _N)=0.89	<0.001	0.92
	lg (mass)+1.19		
	lg (E _P)=1.34	<0.001	0.93
	lg (mass) - 0.75		
鲢 <i>Hypophthalmichthys molitrix</i>	lg (E _N)=0.86	<0.001	0.98
	lg (mass)+1.60		
	lg (E _P)=0.63	<0.001	0.92
	lg (mass)+1.54		
鳊 <i>Aristichthys nobilis</i>	lg (E _N)=0.68	<0.001	0.88
	lg (mass)+1.75		
	lg (E _P)=0.92	<0.001	0.39
	lg (mass)+0.46		
似鲮 <i>Toxabramis swinhonis</i>	lg (E _N)=0.92	<0.001	0.48
	lg (mass)+1.73		
	lg (E _P)=1.41	<0.001	0.48
	lg (mass)+0.01		
翘嘴鲇 <i>Culter alburnus</i>	lg (E _N)=0.78	<0.001	0.61
	lg (mass)+1.60		
	lg (E _P)=0.87	<0.001	0.59
	lg (mass)+0.65		
鳊 <i>Siniperca chuatsi</i>	lg (E _N)=0.52	<0.001	0.87
	lg (mass)+2.25		
	lg (E _P)=0.70	<0.001	0.96
	lg (mass)+0.61		

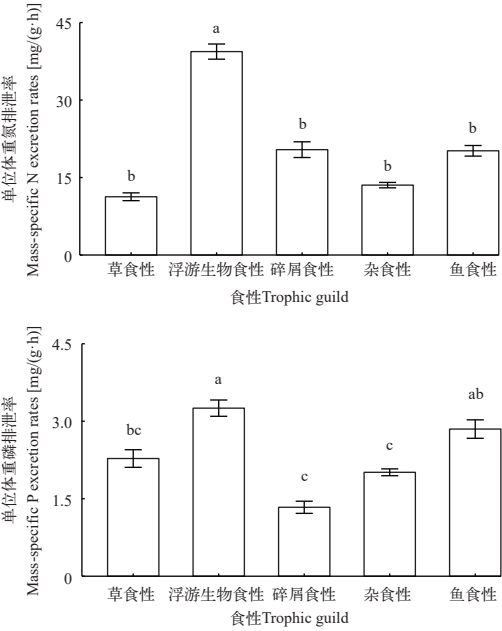


图 2 不同食性鱼类单位体重氮、磷排泄率

Fig. 2 The Mass-specific nitrogen and phosphorus excretion rates of fishes with different trophic guild

要因子, 在较高温度下通常会加速代谢, 从而提高排泄速率^[37]。这些差异反映了鱼类在摄食策略和代谢途径上的深度分化, 表明鱼类的营养物质排泄过程受生活史策略和代谢途径等多种作用的共同影响。

3.2 长江中下游湖泊鱼类的氮、磷排泄率影响因素

本研究发现, 鱼类的体重是影响其氮、磷排泄率的一个重要因素。随着体重的增大, 鱼类的氮、磷排泄率增加, 氮、磷排泄率比值降低(图 1)。与异速生长理论所预测的一样, 较大体型的鱼类排泄出更多的氮、磷, 但比小体型鱼类单位体重排泄的氮、磷更少^[24, 25, 38, 39]。由体型差异引起的氮、磷排泄率的差异可能与生物体的代谢差异和异速生长有关。生物体不同组织的氮、磷元素含量因种类、生长速度和体重等差异而不同。例如, 在无脊椎动物中, 随着生长其体内的磷含量增加^[40]。这一现象在脊椎动物中更为常见, 因为脊椎动物的生长过程中通常需要更多的磷来支持其骨骼或壳的形成^[31, 41, 42]。因此, 不同体型鱼类的氮、磷含量存在差异, 进而导致氮、磷排泄率差异。

其次, 鱼类的食性对其氮、磷排泄率也有显著影响。浮游生物食性鱼类的单位体重氮排泄率显著高于其他食性鱼类; 浮游生物食性和肉食性鱼类单位体重磷排泄率显著高于其他食性鱼类(图 2)。浮游生物食性鱼类主要以浮游植物、浮游动物为食, 这类食物富含易消化的有机物质, 如脂类、糖

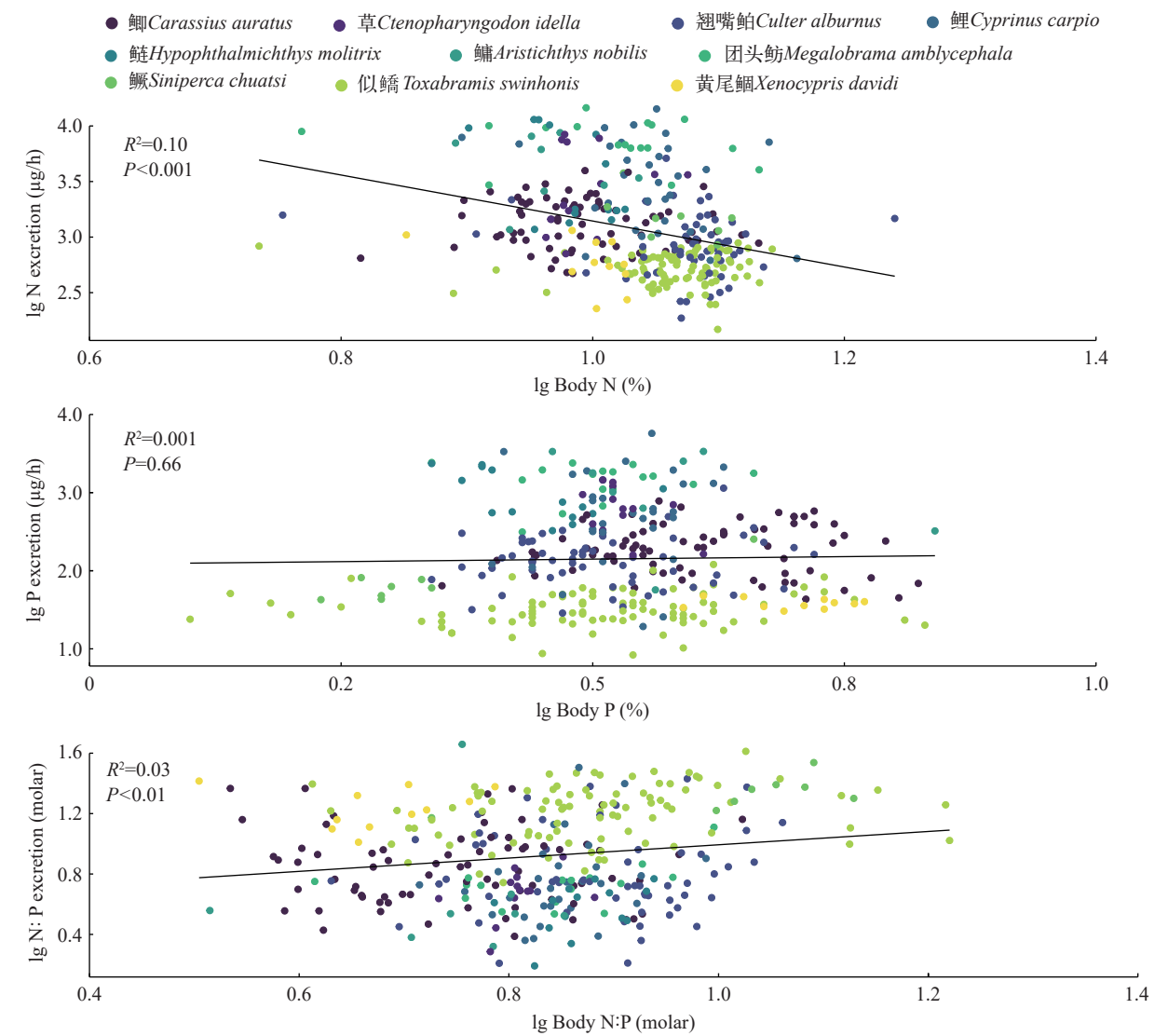


图 3 鱼类氮、磷排泄率及其比值与鱼体氮、磷含量及其比值的线性回归分析

Fig. 3 Linear regression analysis of fish nitrogen and phosphorus excretion rates and their ratios with fish body nitrogen and phosphorus contents and their ratios

表 4 应用生态代谢理论、生态化学计量学理论和两者结合的预测因子预测鱼类氮、磷排泄率及其比值的线性模型比较

Tab. 4 Comparisons of models predicting nitrogen and phosphorus excretion rates and their ratios using predictors from the Metabolic Theory of Ecology, Ecological Stoichiometry Theory, or both

响应变量Response variable	模型类型Model type	预测因子 Predictor factors	AIC	lgLik	RMSE	R ²
氮排泄率N excretion rate	MTE	Mass	-261.6	133.8	0.16	0.86
	ES	Body N, Trophic guild	218.2	-102.1	0.33	0.37
	MTE+ES	Mass, Body N, Trophic guild	-339.0	177.5	0.14	0.89
磷排泄率P excretion rate	MTE	Mass	-57.1	31.6	0.96	0.87
	ES	Body P, Trophic guild	464.5	-225.3	0.99	0.37
	MTE+ES	Mass, Body P, Trophic guild	-96.0	56.0	0.95	0.89
氮磷排泄率比值N:P excretion rate	MTE	Mass	32.8	-13.4	2.24	0.36
	ES	Body N:P, Trophic guild	97.9	-42.0	2.22	0.23
	MTE+ES	Mass, Body N:P, Trophic guild	19.3	-1.64	2.24	0.40

注: 加粗字体表示根据赤池信息标准(AIC)、对数似然(LogLik)和均方根误差(RMSE)选择的首选模型

Note: Bold font indicates the preferred model selected based on the Akaike Information Criterion (AIC), Log-Likelihood (LogLik) and Root Mean Squared Error (RMSE)

表 5 线性模型与线性混合模型的比较

Tab. 5 Comparison between simple linear models and linear mixed models

响应变量 Response variable	线性混合模型Linear mixed models	线性模型Linear models	χ^2	P-value
氮排泄率 N excretion rate	$\text{lmer}(\text{NH}_4^+ \sim \text{Mass} + (1 + \text{Mass} \text{Species}))$	$\text{lm}(\text{NH}_4^+ \sim \text{Mass})$	135.9	<0.001
	$\text{lmer}(\text{NH}_4^+ \sim \text{Body N} + \text{Trophic guild} + (1 + \text{Body N} \text{Species}))$	$\text{lm}(\text{NH}_4^+ \sim \text{Body N} + \text{Trophic guild})$	145.7	<0.001
	$\text{lmer}(\text{NH}_4^+ \sim \text{Mass} + \text{Body N} + \text{Trophic guild} + (1 + \text{Mass} + \text{Body N} \text{Species}))$	$\text{lm}(\text{NH}_4^+ \sim \text{Mass} + \text{Body N} + \text{Trophic guild})$	52.6	<0.001
磷排泄率 P excretion rate	$\text{lmer}(\text{PO}_4^{3-} \sim \text{Mass} + (1 + \text{Mass} \text{Species}))$	$\text{lm}(\text{PO}_4^{3-} \sim \text{Mass})$	129.0	<0.001
	$\text{lmer}(\text{PO}_4^{3-} \sim \text{Body P} + \text{Trophic guild} + (1 + \text{Body P} \text{Species}))$	$\text{lm}(\text{PO}_4^{3-} \sim \text{Body P} + \text{Trophic guild})$	217.7	<0.001
	$\text{lmer}(\text{PO}_4^{3-} \sim \text{Mass} + \text{Body P} + \text{Trophic guild} + (1 + \text{Mass} + \text{Body P} \text{Species}))$	$\text{lm}(\text{PO}_4^{3-} \sim \text{Mass} + \text{Body P} + \text{Trophic guild})$	94.8	<0.001
氮磷排泄率比值 N:P excretion rate	$\text{lmer}(\text{N:P} \sim \text{Mass} + (1 + \text{Mass} \text{Species}))$	$\text{lm}(\text{N:P} \sim \text{Mass})$	71.7	<0.001
	$\text{lmer}(\text{N:P} \sim \text{Body N:P} + \text{Trophic guild} + (1 + \text{Body N:P} \text{Species}))$	$\text{lm}(\text{N:P} \sim \text{Body N:P} + \text{Trophic guild})$	93.5	<0.001
	$\text{lmer}(\text{N:P} \sim \text{Mass} + \text{Body N:P} + \text{Trophic guild} + (1 + \text{Mass} + \text{Body N:P} \text{Species}))$	$\text{lm}(\text{N:P} \sim \text{Mass} + \text{Body N:P} + \text{Trophic guild})$	56.8	<0.001

表 6 不同分类水平下,应用生态代谢理论(MTE)、生态化学计量学理论(ES)和两者结合的预测因子预测鱼类氮、磷排泄率及其比值的模型比较

Tab. 6 Comparison of models for predicting fish nitrogen and phosphorus excretion rates and their ratios using predictors from the Metabolic Theory of Ecology, the Ecological Stoichiometry Theory, and their combination at different taxonomic levels

响应变量 Response variable	模型类型Model type	分类水平 Taxonomic identity	随机效应 Random effect	AIC	lgLik	RMSE	R^2_{marg}	R^2_{cond}
氮排泄率 N excretion rate	MTE	种Species	斜率和截距Slope&Intercept	-372.3	192.1	0.12	0.87	0.94
	ES	属Genus	斜率和截距Slope&Intercept	85.7	-30.8	0.24	0.39	0.75
	MTE+ES	种Species	截距Intercept	-346.1	184.1	0.12	0.83	0.94
磷排泄率 P excretion rate	MTE	种Species	斜率和截距Slope&Intercept	-173.7	92.8	0.96	0.72	0.94
	ES	属Genus	斜率Slope	95.3	-37.7	0.25	0.15	0.73
	MTE+ES	种Species	斜率和截距Slope&Intercept	-156.8	94.4	0.96	0.70	0.94
氮磷排泄率比值 N:P excretion rate	MTE	种Species	斜率和截距Slope&Intercept	-25.2	18.6	2.24	0.15	0.68
	ES	属Genus	斜率Slope	17.4	1.3	2.23	0.12	0.68
	MTE+ES	属Genus	截距Intercept	-5.7	18.9	2.24	0.24	0.77

注: 加粗字体表示根据赤池信息标准(AIC)、对数似然(LogLik)和均方根误差(RMSE)选择的最佳模型

Note: Bold font indicates the preferred model based on the combination of Akaike Information Criterion (AIC), Root Mean Squared Error (RMSE), and Log-Likelihood (LogLik)

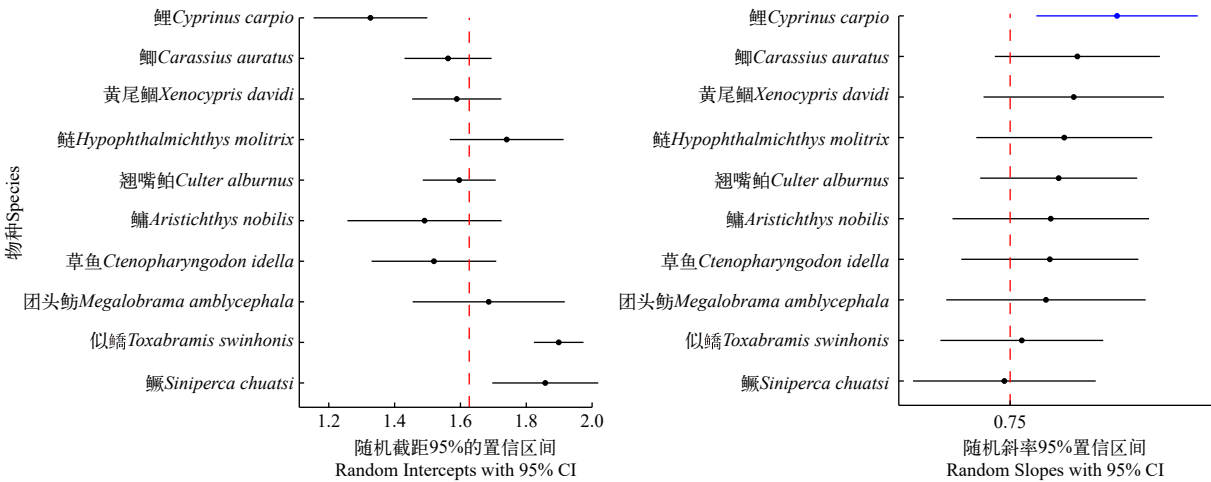


图 4 鱼类氮排泄率与体重线性混合模型中各物种的随机斜率和截距估计值

Fig. 4 Estimated values of random slope and intercept for each fish species in the linear mixed model of fish nitrogen excretion rates and mass

类和蛋白质等, 这些物种通常含有较高的氮、磷等营养元素^[43, 44]。这些富含氮、磷的食物进入鱼体后, 不仅满足了其生长和代谢需求, 也导致了更多氮、磷的吸收和排泄。相反, 碎屑食性、草食性和杂食性鱼类食物中相对较少的氮、磷含量及其较低的可消化性可能是其单位体重磷排泄率较低的主要原因之一。

生态化学计量学理论为解释生物体内营养元素含量与其排泄率之间的关系提供了重要框架, 但也存在一定局限。本研究发现, 鱼类的氮排泄率与鱼体氮含量呈显著负相关, 符合生态化学计量学理论的预期, 即生物体通过减少对某种营养元素的排泄来满足自身营养元素平衡。然而, 鱼体磷含量与磷排泄率之间未发现相关性。根据生态化学计量理论, 生物体通过调节摄食、同化、代谢等过程, 维持身体营养元素的稳定性, 即使在食物营养元素含量发生显著变化时, 也能够通过改变排泄物中的营养元素比例以维持其体内营养元素的平衡^[14]。然而, 鱼类氮、磷排泄率与化学计量特征之间的关系, 可能受食物资源、同化速率、温度变化等多种因素的影响^[45]。这些因素的动态变化可能使理论预测与实际观测结果之间出现偏差。此外, 越来越多的研究表明, 许多生物在化学计量上并不是处于严格的稳态^[46–48], 生物体的发育^[30]、表型可塑性^[49]及遗传变异^[50]等因素均可能影响生物体的化学计量特征及其氮、磷排泄率。因此, 生态化学计量学理论在鱼类氮、磷排泄率时, 可能需要结合更复杂的生理与生态调控机制进行修正。未来的研究可考虑引入多变量模型, 整合鱼类的发育阶段、表型可塑性、遗传背景及其所处环境的温度、食物资源等信息, 从而更全面地预测鱼体的营养元素比例,

及其对氮、磷排泄的影响。

3.3 鱼类氮、磷排泄率预测模型

生态代谢理论和生态化学计量学理论是理解生物如何调节生态系统养分动态和能量流动的两个重要理论框架。本研究测试了生态代谢理论和生态化学计量学理论在预测鱼类氮、磷排泄率及其比值方面的可靠性。通过对比, 发现生态代谢理论预测因子(体型)的表现优于生态化学计量理论预测因子(食性, 鱼体氮、磷含量)。同时, 将物种分类水平融入模型后, 模型的预测效果显著提升。这些结果表明, 鱼类氮、磷排泄率可通过体型和物种的分类水平来预测。这一结果与国外许多研究相似, 例如, Vanni和Mcintyre^[17]对来自全球10534个鱼类、两栖类和无脊椎动物样本的氮、磷排泄率进行了预测, 发现体重是最好的预测因子。Allgeier等^[18]对亚热带沿海102种鱼类和无脊椎动物的氮、磷排泄率的研究结果表明, 体重解释了物种间氮、磷排泄率的大量变化, 并显著高于其他预测因子。然而, 鱼类的食性和鱼体氮、磷含量在预测模型中并未提高模型的解释率。相关研究表明, 鱼类氮、磷排泄率与鱼体氮、磷化学计量特征之间的关系, 可能受食物资源、同化速率、温度变化等多种因素的影响^[31, 45, 47, 51]。这些因素导致鱼类氮、磷化学计量特征与氮、磷排泄率不匹配, 使理论预测与实际观测结果之间出现偏差。

4 结论

本研究系统分析了长江中下游湖泊10种常见鱼类的氮、磷排泄特征及其影响因素, 结果表明鱼类排泄率在种间差异显著, 且受体型、食性和鱼体氮、磷含量的影响。具体来说, 鱼类的氮、磷排泄

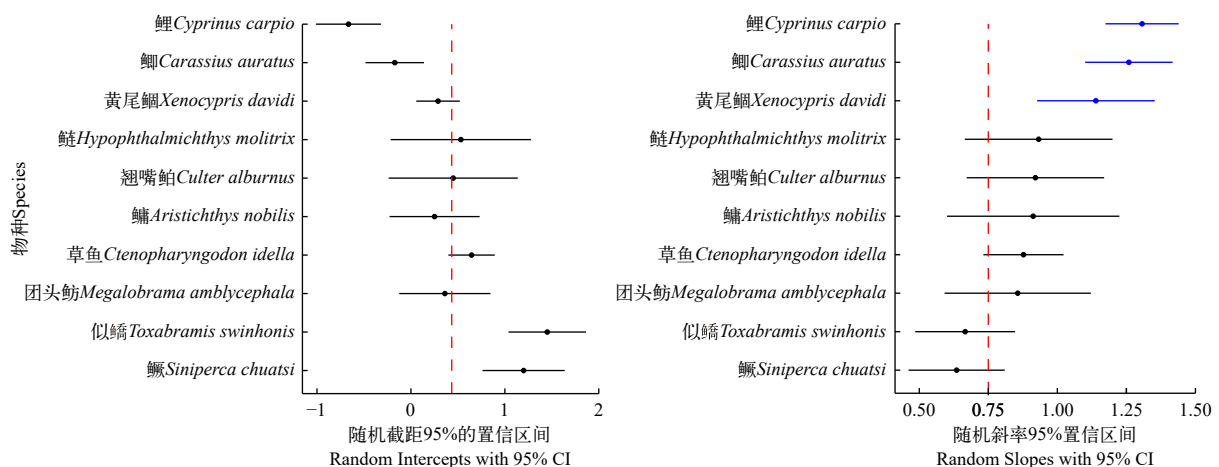


图5 鱼类磷排泄率与体重线性混合模型中各物种的随机斜率和截距估计值

Fig. 5 Estimated values of random slope and intercept for each fish species in the linear mixed model of fish phosphorus excretion rates and mass

率与体重呈显著正相关, 氮、磷排泄率均随体重的增加而增大, 体型较大的鱼类的氮、磷排泄率高于小体型鱼类, 但小体型鱼类的单位体重氮、磷排泄率更高。且不同食性鱼类间的单位体重氮、磷排泄率也存在显著性差异, 浮游生物食性鱼类单位体重氮、磷排泄率相对较高。鱼类氮排泄率与鱼体氮含量呈显著负相关, 磷排泄率与鱼体磷含量不相关。模型结果表明, 生态代谢理论的预测因子(体型)在预测鱼类氮、磷排泄率方面优于生态化学计量学理论预测因子(鱼体氮、磷含量和食性), 但需考虑物种分类对模型的影响。这一发现表明生态化学计量学理论在鱼类氮、磷排泄率时存在一定局限性, 在丰富多样化的鱼类群落中仍存在适用边界, 当前理论尚难充分解释鱼类氮、磷排泄率与鱼体氮、磷含量之间的不匹配现象。未来研究应进一步结合鱼类生活史特征、栖息地差异、营养状态及环境变化, 构建多因子耦合的鱼类氮、磷排泄率预测模型, 从而更全面地理解鱼类在湖泊营养动态中的生态功能。

(作者声明本文符合出版伦理要求)

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CHARACTERISTICS AND INFLUENCING FACTORS OF NITROGEN AND PHOSPHORUS EXCRETION RATES OF 10 COMMON FISH SPECIES IN LAKES OF THE MIDDLE AND LOWER REACHES OF THE YANGTZE RIVER

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Abstract: To investigate the nitrogen and phosphorus excretion rate characteristics of fish in the middle and lower reaches of the Yangtze River and their influencing factors, samples of the nitrogen and phosphorus excretion rates and ecological stoichiometric characteristics of 10 common fish species in the middle and lower reaches of the Yangtze River were collected and analyzed from May to June 2023. Models were employed to analyze the key influencing factors of nitrogen and phosphorus excretion rates. The results showed that the nitrogen excretion rate of common fish species in these lakes ranged from 0.15 to 16.24 mg/h, and the phosphorus excretion rate ranged from 0.01 to 5.73 mg/h. Fish nitrogen and phosphorus excretion rates were significantly positively correlated with body weight ($R^2=0.86$, $P<0.001$; $R^2=0.87$, $P<0.001$). Larger fish excreted more nitrogen and phosphorus than smaller ones, yet the mass-specific nitrogen and phosphorus excretion rates were higher in small-sized species. There were significant differences in mass-specific nitrogen and phosphorus excretion rates among fish with different trophic guilds ($P<0.001$), and planktivorous fish had relatively high mass-specific nitrogen and phosphorus excretion rates. The fish nitrogen excretion rate was significantly negatively correlated with the body nitrogen content ($R^2=0.10$, $P<0.001$), while the phosphorus excretion rate was not correlated with the body phosphorus content. Model results indicated that body size was the key factor in predicting fish nitrogen and phosphorus excretion rates. Although diet and fish body nitrogen and phosphorus elemental content also affected these excretion rates, their prediction in the model was poor. The ecological metabolism theory outperformed the ecological stoichiometry theory in predicting fish nitrogen and phosphorus excretion rates, but the effect of species classification on the model requires consideration. The results of this study are important for understanding the role of fish in the nutrient cycling process in lake ecosystems.

Key words: Consumer; Excretion; Metabolic theory of ecology; Ecological stoichiometry theory; Nutrient cycling

附录 S1 基于生态代谢理论预测因子的预测模型

Appendix S1 Prediction models based on the predictor of the Metabolic Theory of Ecology

响应变量 Response variable	分类水平 Taxonomic identity	随机效应 Random effect	AIC	LogLik	RMSE	R^2_{marg}	R^2_{cond}	模型是否过度 参数化 Overparametrized model
氮排泄率 N excretion rate	科+属+种 Family+Genus+Species	斜率和截距 Slope&Intercept	-362.7	193.3	0.12	0.75	0.94	T
		斜率Slope	-359.7	185.9	0.12	0.85	0.95	T
		截距Intercept	-371.7	191.8	0.12	0.86	0.95	T
	属+种 Genus+Species	斜率和截距 Slope&Intercept	-366.4	192.2	0.12	0.86	0.94	T
		斜率Slope	-361.7	185.9	0.12	0.85	0.95	T
		截距Intercept	-373.6	191.8	0.12	0.87	0.95	T
	种 Species	斜率和截距 Slope&Intercept	-372.3	192.1	0.12	0.87	0.94	F
		斜率Slope	-363.7	185.9	0.12	0.85	0.95	F
		截距Intercept	-375.6	191.8	0.12	0.87	0.95	F
	属 Genus	斜率和截距 Slope&Intercept	-354.1	183.1	0.13	0.85	0.93	T
		斜率Slope	-338.1	173.1	0.13	0.85	0.94	F
		截距Intercept	-351.8	179.9	0.13	0.88	0.93	F
	科 Family	斜率和截距 Slope&Intercept	-236.3	124.1	0.16	0.80	0.84	T
		斜率Slope	-239.5	123.8	0.16	0.84	0.87	F
		截距Intercept	-240.0	124.0	0.16	0.83	0.86	F
磷排泄率 P excretion rate	科+属+种 Family+Genus+Species	斜率和截距 Slope&Intercept	-164.2	94.1	0.96	0.64	0.94	T
		斜率Slope	-113.7	62.9	0.96	0.80	0.92	T
		截距Intercept	-130.5	71.3	0.96	0.84	0.93	T
	属+种 Genus+Species	斜率和截距 Slope&Intercept	-169.4	93.7	0.96	0.72	0.95	T
		斜率Slope	-115.4	62.7	0.96	0.85	0.92	T
		截距Intercept	-132.5	71.2	0.96	0.85	0.93	T
	种 Species	斜率和截距 Slope&Intercept	-173.7	92.8	0.96	0.72	0.94	F
		斜率Slope	-117.4	62.7	0.96	0.85	0.92	F
		截距Intercept	-134.5	71.2	0.96	0.85	0.93	F
	属 Genus	斜率和截距 Slope&Intercept	-158.8	85.4	0.96	0.71	0.94	F
		斜率Slope	-90.8	49.4	0.96	0.85	0.90	F
		截距Intercept	-106.8	57.4	0.96	0.85	0.91	F
	科 Family	斜率和截距 Slope&Intercept	-48.1	30.1	0.96	0.74	0.87	T
		斜率Slope	-52.0	30.0	0.96	0.76	0.87	F
		截距Intercept	-51.3	29.7	0.96	0.80	0.89	F
氮磷排泄率比值 N:P excretion rate	科+属+种 Family+Genus+Species	斜率和截距 Slope&Intercept	-17.4	20.7	2.24	0.07	0.79	T
		斜率Slope	3.4	4.3	2.24	0.05	0.65	F
		截距Intercept	-7.8	9.9	2.24	0.12	0.69	F
	属+种 Genus+Species	斜率和截距 Slope&Intercept	-20.1	19.0	2.24	0.14	0.68	T
		斜率Slope	3.3	3.4	2.24	0.15	0.49	F
		截距Intercept	-7.4	8.7	2.24	0.18	0.50	F
	种 Species	斜率和截距 Slope&Intercept	-25.2	18.6	2.24	0.15	0.68	F
		斜率Slope	2.0	3.0	2.24	0.17	0.49	F
		截距Intercept	-9.0	8.5	2.24	0.19	0.51	F

续表 S1

响应变量 Response variable	分类水平 Taxonomic identity	随机效应 Random effect	AIC	LogLik	RMSE	R^2_{marg}	R^2_{cond}	模型是否过度 参数化 Overparametrized model
	属 Genus	斜率和截距 Slope&Intercept	-23.8	17.9	2.24	0.15	0.68	F
		斜率Slope	2.3	2.9	2.24	0.13	0.49	F
		截距Intercept	-7.9	8.0	2.24	0.16	0.49	F
	科 Family	斜率和截距 Slope&Intercept	34.4	-11.2	2.24	0.14	0.64	T
		斜率Slope	30.6	-11.3	2.24	0.09	0.63	F
		截距Intercept	30.6	-11.3	2.24	0.20	0.65	F

注：加粗字体表示根据赤池信息标准(AIC)、对数似然(LogLik)和均方根误差(RMSE)选择的最佳模型，T表示模型过度参数化，F表现模型没有过度参数化

Note: Bold font indicates the preferred model based on the combination of Akaike Information Criterion (AIC), Root Mean Squared Error (RMSE), and Log-Likelihood (LogLik), T indicates that the model is over-parameterized, and F shows that the model is not over-parameterized

附录 S2 基于生态化学计量学理论预测因子的预测模型

Appendix S2 Prediction models based on the predictor of the Ecological Stoichiometry Theory

响应变量 Response variable	分类水平 Taxonomic identity	随机效应 Random effect	AIC	LogLik	RMSE	R^2_{marg}	R^2_{cond}	模型是否过度 参数化 Overparametrized model
氮排泄率 N excretion rate	科+属+种 Family+Genus+Species	斜率和截距 Slope&Intercept	97.7	-30.8	0.24	0.39	0.75	T
		斜率Slope	98.9	-37.5	0.25	0.15	0.70	T
		截距Intercept	92.8	-34.4	0.25	0.16	0.73	T
	属+种 Genus+Species	斜率和截距Slope&Intercept	91.7	-30.8	0.24	0.39	0.75	T
		斜率Slope	96.9	-37.5	0.25	0.15	0.70	T
		截距Intercept	90.8	-34.4	0.25	0.16	0.73	T
	种 Species	斜率和截距Slope&Intercept	90.3	-33.1	0.24	0.36	0.76	T
		斜率Slope	98.1	-39.0	0.25	0.13	0.69	F
		截距Intercept	92.0	-36.0	0.25	0.15	0.72	F
	属 Genus	斜率和截距Slope&Intercept	85.7	-30.8	0.24	0.39	0.75	T
		斜率Slope	94.9	-37.5	0.25	0.15	0.70	F
		截距Intercept	88.8	-34.4	0.25	0.16	0.73	F
	科 Family	斜率和截距Slope&Intercept	243.6	-109.8	0.32	0.37	0.56	F
		斜率Slope	240.0	-110.0	0.32	0.36	0.45	F
		截距Intercept	240.0	-110.0	0.32	0.36	0.46	F
磷排泄率 P excretion rate	科+属+种 Family+Genus+Species	斜率和截距 Slope&Intercept	262.0	-113.0	0.98	0.18	0.82	T
		斜率Slope	283.1	-129.6	0.98	0.27	0.80	T
		截距Intercept	252.1	-114.0	0.98	0.17	0.81	T
	属+种 Genus+Species	斜率和截距 Slope&Intercept	257.4	-113.7	0.98	0.19	0.82	T
		斜率Slope	281.1	-129.6	0.98	0.27	0.80	F
		截距Intercept	250.1	-114.0	0.98	0.17	0.81	T
	种 Species	斜率和截距 Slope&Intercept	256.3	-116.2	0.98	0.15	0.81	T
		斜率Slope	281.8	-130.9	0.98	0.25	0.81	F
		截距Intercept	252.4	-116.2	0.98	0.17	0.81	F
	属 Genus	斜率和截距 Slope&Intercept	97.50	-36.8	0.25	0.28	0.80	T
		斜率Slope	113.1	-46.6	0.26	0.22	0.74	F
		截距Intercept	95.3	-37.7	0.25	0.15	0.73	F

续表 S2

响应变量 Response variable	分类水平 Taxonomic identity	随机效应 Random effect	AIC	LogLik	RMSE	R^2_{marg}	R^2_{cond}	模型是否过度 参数化 Overparametrized model
氮磷排泄率比值 N:P excretion rate	科 Family	斜率和截距 Slope&Intercept	256.6	-116.3	0.33	0.24	0.62	T
		斜率Slope	253.0	-116.5	0.33	0.28	0.55	T
		截距Intercept	254.2	-117.1	0.33	0.34	0.43	F
	科+属+种 Family+Genus+Species	斜率和截距 Slope&Intercept	32.9	1.6	2.23	0.07	0.72	T
		斜率Slope	24.6	-0.3	2.23	0.08	0.71	T
		截距Intercept	21.2	1.4	2.23	0.07	0.73	F
	属+种 Genus+Species	斜率和截距 Slope&Intercept	27.1	1.5	2.23	0.11	0.67	T
		斜率Slope	23.1	-0.6	2.23	0.11	0.61	T
		截距Intercept	19.3	1.4	2.23	0.12	0.68	F
	种 Species	斜率和截距 Slope&Intercept	23.2	0.4	2.23	0.13	0.67	F
		斜率Slope	24.8	-2.4	2.23	0.09	0.61	F
		截距Intercept	19.2	0.4	2.23	0.13	0.67	F
	属 Genus	斜率和截距 Slope&Intercept	21.1	1.4	2.23	0.11	0.67	T
		斜率Slope	21.1	-0.6	2.23	0.11	0.61	F
		截距Intercept	17.4	1.3	2.23	0.12	0.68	F
	科 Family	斜率和截距 Slope&Intercept	121.2	-48.6	2.22	0.16	0.59	F
		斜率Slope	117.2	-48.6	2.22	0.16	0.58	F
		截距Intercept	117.2	-48.6	2.22	0.12	0.66	F

注：加粗字体表示根据赤池信息标准(AIC)、对数似然(LogLik)和均方根误差(RMSE)选择的最佳模型，T表示模型过度参数化，F表现模型没有过度参数化

Note: Bold font indicates the preferred model based on the combination of Akaike Information Criterion (AIC), Root Mean Squared Error (RMSE), and Log-Likelihood (LogLik), T indicates that the model is over-parameterized, and F shows that the model is not over-parameterized

附录 S3 基于生态代谢理论和生态化学计量学理论所有预测因子的预测模型

Appendix S3 Prediction models based on the predictors of the Metabolic Theory of Ecology and the Ecological Stoichiometry Theory

响应变量 Response variable	分类水平 Taxonomic identity	随机效应 Random effect	AIC	LogLik	RMSE	R^2_{marg}	R^2_{cond}	模型是否过度 参数化 Overparametrized model
氮排泄率 N excretion rate	科+属+种 Family+Genus+Species	斜率和截距 Slope&Intercept	-316.1	186.0	0.12	0.70	0.93	T
		斜率Slope	-333.5	185.8	0.12	0.73	0.93	T
		截距Intercept	-342.1	184.1	0.12	0.83	0.94	T
	属+种 Genus+Species	斜率和截距 Slope&Intercept	-325.5	184.7	0.12	0.83	0.94	T
		斜率Slope	-337.0	184.5	0.12	0.83	0.94	F
		截距Intercept	-344.1	184.1	0.12	0.83	0.94	T
	种 Species	斜率和截距 Slope&Intercept	-337.0	184.5	0.12	0.83	0.94	F
		斜率Slope	-342.6	184.3	0.12	0.84	0.94	F
		截距Intercept	-346.1	184.1	0.12	0.83	0.94	F
	属 Genus	斜率和截距 Slope&Intercept	-316.7	174.4	0.13	0.85	0.92	T
		斜率Slope	-322.5	174.2	0.13	0.85	0.92	F
		截距Intercept	-323.1	172.6	0.13	0.85	0.92	F
	科 Family	斜率和截距 Slope&Intercept	-282.1	157.1	0.14	0.75	0.88	T
		斜率Slope	-288.1	157.0	0.14	0.77	0.88	T
		截距Intercept	-291.1	156.5	0.14	0.81	0.90	F

续表 S3

响应变量 Response variable	分类水平 Taxonomic identity	随机效应 Random effect	AIC	LogLik	RMSE	R^2_{marg}	R^2_{cond}	模型是否过度 参数化 Overparametrized model
磷排泄率 P excretion rate	科+属+种 Family+Genus+Species	斜率和截距 Slope&Intercept	-135.2	95.6	0.96	0.64	0.94	T
		斜率Slope	-136.4	87.2	0.96	0.59	0.95	T
		截距Intercept	-114.4	70.2	0.96	0.77	0.92	T
	属+种 Genus+Species	斜率和截距 Slope&Intercept	-146.8	95.4	0.96	0.70	0.94	T
		斜率Slope	-142.3	87.2	0.96	0.62	0.95	F
		截距Intercept	-116.3	70.2	0.96	0.82	0.92	T
	种 Species	斜率和截距 Slope&Intercept	-156.8	94.4	0.96	0.70	0.94	T
		斜率Slope	-145.8	85.9	0.96	0.64	0.95	F
		截距Intercept	-118.3	70.2	0.96	0.82	0.92	F
	属 Genus	斜率和截距 Slope&Intercept	-146.9	89.5	0.96	0.71	0.93	T
		斜率Slope	-115.4	70.7	0.96	0.54	0.96	T
		截距Intercept	-88.6	55.3	0.96	0.83	0.90	F
	科 Family	斜率和截距 Slope&Intercept	-52.9	42.5	0.96	0.67	0.90	T
		斜率Slope	-58.9	42.5	0.96	0.68	0.91	T
		截距Intercept	-61.2	41.6	0.96	0.77	0.91	F
氮磷排泄率比值 N:P excretion rate	科+属+种 Family+Genus+Species	斜率和截距 Slope&Intercept	16.2	19.9	2.24	0.12	0.80	T
		斜率Slope	12.3	12.9	2.24	0.38	0.93	T
		截距Intercept	11.1	7.5	2.24	0.09	0.76	F
	属+种 Genus+Species	斜率和截距 Slope&Intercept	4.8	19.6	2.24	0.23	0.79	T
		斜率Slope	6.3	12.9	2.24	0.39	0.93	T
		截距Intercept	10.0	7.0	2.24	0.18	0.62	T
	种 Species	斜率和截距 Slope&Intercept	-5.7	18.9	2.24	0.24	0.77	T
		斜率Slope	3.4	11.3	2.24	0.42	0.92	F
		截距Intercept	8.4	6.8	2.24	0.19	0.61	F
	属 Genus	斜率和截距 Slope&Intercept	-3.9	18.0	2.24	0.23	0.78	F
		斜率Slope	1.2	12.4	2.24	0.40	0.93	F
		截距Intercept	10.0	6.0	2.24	0.17	0.62	F
	科 Family	斜率和截距 Slope&Intercept	42.8	-5.4	2.24	0.07	0.74	T
		斜率Slope	37.1	-5.56	2.24	0.10	0.75	T
		截距Intercept	33.8	-5.9	2.24	0.18	0.77	F

注：加粗字体表示根据赤池信息标准(AIC)、对数似然(LogLik)和均方根误差(RMSE)选择的最佳模型，T表示模型过度参数化，F表现模型没有过度参数化

Note: Bold font indicates the preferred model based on the combination of Akaike Information Criterion (AIC), Root Mean Squared Error (RMSE), and Log-Likelihood (LogLik), T indicates that the model is over-parameterized, and F shows that the model is not over-parameterized