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外来入侵种克氏原螯虾(*Procambarus clarkii*)和小管福寿螺(*Pomacea canaliculata*)与土著种铜锈环棱螺(*Bellamya aeruginosa*)的生态位比较*

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摘　要: 克氏原螯虾(*Procambarus clarkii*)和小管福寿螺(*Pomacea canaliculata*)是全球广泛入侵的底栖动物,对入侵地水生态系统破坏严重。两者共同出现在同一水生态系统的现象越来越普遍,其对土著底栖动物的影响尚缺乏深入研究。本文通过脂肪酸生物标志物的检测,分析了外来入侵物种克氏原螯虾和小管福寿螺及土著物种铜锈环棱螺(*Bellamya aeruginosa*)在自然水体的食性、生态位宽度及营养级差异,结合两种入侵物种对土著物种的受控捕食实验,探讨克氏原螯虾和小管福寿螺共入侵对铜锈环棱螺的影响。利用主成分分析方法对脂肪酸进行分析,结果显示克氏原螯虾和小管福寿螺的生态位宽度均大于铜锈环棱螺,表明两种入侵物种的食谱更广,在营养资源利用上具有竞争优势;克氏原螯虾的C18:1n-9+C22:6n-3 质量百分比显著高于小管福寿螺和铜锈环棱螺,表明其肉食性特征更强;铜锈环棱螺的 C15+C17 质量百分比显著高于两种入侵物种,表明细菌对其碳源的贡献更高;两种入侵物种的脂肪酸 C18:2+C18:3质量百分比显著高于铜锈环棱螺,表明二者的食物来源主要是维管束植物;此外,入侵物种克氏原螯虾的多不饱和脂肪酸与饱和脂肪酸的比值高于铜锈环棱螺,说明入侵物种克氏原螯虾的营养级高于土著物种铜锈环棱螺,因此在生态位上克氏原螯虾比铜锈环棱螺具有更强的竞争能力。受控捕食实验显示,克氏原螯虾对铜锈环棱螺幼螺的捕食量显著高于对小管福寿螺幼螺的捕食量,而成年小管福寿螺也能捕食铜锈环棱螺幼螺,但捕食量较低。结果表明,克氏原螯虾的生态位宽度高于小管福寿螺,而小管福寿螺的生态位宽度高于铜锈环棱螺,二者共入侵对土著螺的生存负面影响可能更大。
关键词: 克氏原螯虾;小管福寿螺;铜锈环棱螺;共入侵;生态位

Comparative niche analysis of between invasive *Procambarus clarkii* and *Pomacea canaliculata* and native *Bellamya aeruginosa**

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Abstract: The red swamp crayfish, *Procambarus clarkii*, and the golden apple snail, *Pomacea canaliculata*, are globally widespread invasive species that can cause serious damage to aquatic ecosystems in the invaded areas. However, the impact of their co-invasion on native ecosystems has rarely been studied. To explore the niche competition between co-invasive and native species, we investigated a natural pond that was co-invaded by *P. clarkii* and *P. canaliculata*. We used a fatty acid biomarker to analyze differ-

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ences in feeding habits, niche widths, and trophic levels among *P. clarkii*, *P. canaliculata*, and the native snail *Bellamya aeruginosa*. We also conducted indoor predation control experiments to verify that the alien species directly prey on *B. aeruginosa*. Principal component analysis (PCA) of fatty acids in muscles revealed larger areas of the confidence ellipses in *P. clarkii* and *P. canaliculata* compared to *B. aeruginosa*, indicating that the alien species had broader niche widths and superior trophic resource exploitation. Also, the percentage content of C18:1n-9 + C22:6n-3 was significantly higher in *P. clarkii* than in *P. canaliculata* and *B. aeruginosa*, suggesting that the crayfish is more carnivorous. C15 + C17 content was significantly higher in *B. aeruginosa* than in the alien species, suggesting bacteria as the native snail's main carbon source. In contrast, C18:2 + C18:3 content was significantly higher in the alien species, demonstrating that their main carbon source is vascular plant material. Finally, the ratio of polyunsaturated to saturated fatty acids in *P. clarkii* was also higher in the alien species, indicating that they reside at a higher trophic level and exhibit stronger competitive abilities than *B. aeruginosa*. Our indoor predation experiments showed that *P. clarkii* more often preyed on juvenile *B. aeruginosa* than juvenile *P. canaliculata*. We also observed predation of adult *P. canaliculata* on juvenile *B. aeruginosa*, albeit at a lower rate. In summary, by combining the results of fatty acid biomarker techniques and indoor predation control experiments, we demonstrate that the niche width of *P. clarkii* is higher than that of *P. canaliculata*, while *P. canaliculata* exhibits significantly broader niche widths comparing than the native species *B. aeruginosa*. The co-invasion of these two species thus may have a significant negative impact on native snails.

Keywords: *Procambarus clarkii*; *Pomacea canaliculata*; *Bellamya aeruginosa*; co-invasion; niche

外来物种入侵是生态系统风险管理的核心内容[1]。当外来物种进入新的生态环境时,可能会因不适应新环境而被排斥,但更常见的是,由于生活史特征(例如适应能力强、繁殖率高)[2]、缺乏天敌制约等因素[3],它们可能迅速成为优势种群,破坏入侵地原有的生态平衡[4]。入侵物种往往比土著物种表现出更广的摄食生态位宽度(dietary niche breadth)[5]和更强的利用当地营养资源(trophic resource)的能力[6]。这些入侵物种会与土著物种竞争资源和生存空间[7-8],可能导致土著物种的衰退甚至灭绝,进而改变或破坏当地的生态环境,降低生物多样性[9]。入侵物种还可能对农业、林业、畜牧业等产业造成重大的经济损失[10]。在水生生态系统中,许多研究探讨了入侵物种与土著物种之间在食物竞争和捕食关系上的相互影响[11],以及这些因素如何影响系统中种群水平的变化[12],为预测入侵物种入侵的影响提供了科学依据。然而,随着入侵物种的数量不断增加,多种入侵物种共同出现的现象越来越普遍[13],进一步探究多种入侵物种在新环境中的生态位及其与相似生境的土著物种的相互关系,对于揭示生物入侵对生态系统结构和功能的影响至关重要。

多种入侵物种间的相互关系可能是互利、竞争或中性[14],它们在食物网中占据不同的或相似的营养级[15]。荟萃分析显示,两个生态位相似的入侵物种共同入侵的综合影响,与其各自单独入侵的影响具有差异[13]。例如,在美国俄勒冈州的田间试验表明,美国牛蛙(*Rana catesbeiana*)和小口黑鲈(*Micropterus dolomieu*)联合对红腿蛙(*Rana aurora*)蝌蚪的生长和存活的负面影响远大于单一入侵者[16]。在北美北方的自然湖泊中发现,外来物种小口黑鲈和岩鲈(*Ambloplites rupestris*)入侵后导致土著物种鳟鱼(*Salvelinus namaycush*)的营养级下降,鳟鱼的生活习性从沿岸带转变到中上层栖息地[17]。然而,外来物种的入侵也并非全为互利,不同入侵物种间也可能会产生竞争或捕食关系。研究发现克氏原螯虾(*Procambarus clarkii*)与美国牛蛙共入侵时,美国牛蛙对克氏原螯虾的捕食降低了美国牛蛙对土著蛙类的捕食压力,从而减轻了美国牛蛙对土著蛙类的负面影响[18];外来物种黑口虾虎鱼(*Neogobius melanostomus*)和贻贝(*Dreissena polymorpha*、*Dreissena bugensis*)入侵后,改变了土著物种湖鲟(*Acipenser fulvescens*)的生态位,促进了湖鲟的生长和繁殖,增加了湖鲟数量[19]。与单一入侵者的影响相比,在水生态系统中两种共入侵底栖动物与土著底栖动物共存时,对其具体食性和营养级的比较研究较少。这种共入侵情境下的生物间关系尤为复杂,因为可能存在竞争、捕食等多样的种间关系[20],这些关系会对土著底栖动物的生存和生态系统的结构和功能产生不同影响。

外来物种克氏原螯虾和小管福寿螺(*Pomacea canaliculata*)现已广泛入侵亚洲、欧洲等地区[21-23]。克氏原螯虾为杂食性物种[8,24],能摄食碎屑、大型植物,甚至捕食底栖昆虫和螺类等[25],对入侵地的生态系统有显著不利影响[8]。小管福寿螺具有广泛的食物选择性和灵活的摄食策略,能与土著无脊椎动物竞争资源,甚至以一些无脊椎动物为食。研究表明,福寿螺会捕食淡水苔藓虫(*Bryozoans*)、方形环棱螺(*Sinotaia quadrata*)和瘤拟黑螺(*Melanoides tuberculata*)幼螺[26-27]。鉴于克氏原螯虾和福寿螺均能捕食幼螺,因此两者

共入侵可能会对土著螺类产生协同作用。但也有研究发现,在野外环境中,克氏原螯虾也会捕食小管福寿螺幼螺[23,28],这可能会减轻两者共入侵对土著螺类的影响。然而福寿螺有可能因其生长快、体型大的优势而不易被螯虾捕食[29-30],因此三者之间的生态位关系尚待进一步探究。

传统肠道内含物分析和肌肉组织碳、氮稳定同位素技术在研究杂食性消费者的食性及营养级时存在局限性,前者易受消化过程干扰,导致结果不确定性较高,后者则难以精准区分杂食性物种的混合食物来源。研究发现,消费者的脂肪酸主要来源于食物,而极少重新合成[31]。食物资源中脂肪酸的特征性碳链长度模式及双键位置特异性等化学指纹在营养传递过程中保持稳定,形成特异的生物标志物谱系[32]。例如,花生四烯酸(C20:4n-6)、二十二碳六烯酸(C22:6n-3)等多不饱和脂肪酸(EFA)主要源自藻类;奇链饱和脂肪酸和支链脂肪酸(如 C15:0、C17:0及其支链)来源于细菌[33-34];亚油酸/亚麻酸(C18:2+C18:3)来源于维管束植物;而多不饱和脂肪酸(polyunsaturated fatty acids,PUFA)与饱和脂肪酸(saturated fatty acids,SFA)比值可表征消费者的营养级差异(表 1)。基于此,脂肪酸生物标志物不仅能解析种间营养关系[35-36],还可揭示种群内部个体食性差异[37-38]。因此利用脂肪酸生物标志物示踪克氏原螯虾和小管福寿螺在新栖息地的碳源利用策略及其生态位重叠度,能为二者共入侵对土著螺的影响提供新认识。

表 1 水生系统中常见的脂肪酸生物标志物

Tab. 1 Fatty acid biomarkers commonly found in aquatic systems

脂肪酸	表征消费者碳源来源或营养关系
C22:6n-3	甲藻[43]
C18:1n-9	浮游动物[43]
C15+C17	细菌[44]
C18:2+C18:3	维管束植物[45]
C20:4n-6	大型藻类碎屑、底栖微生物[46]
C18:1n-9+C22:6n-3	肉食性[46]
PUFA/SFA 高低	营养级高低[35]

本研究利用脂肪酸生物标志物检测分析了自然池塘中克氏原螯虾和小管福寿螺以及土著物种铜锈环棱螺的生态位关系,探讨了这两种入侵物种对铜锈环棱螺的潜在影响。克氏原螯虾和小管福寿螺广泛分布于长江流域的浅水湖泊[21,39-40],而铜锈环棱螺(*Bellamya aeruginosa*)是我国淡水生态系统的常见物种[41]。野外调查发现铜锈环棱螺与上述两种入侵物种可共享栖息地[42]。基于此,我们提出以下假设:(1)克氏原螯虾和小管福寿螺的营养级高于铜锈环棱螺,且生态位宽度更广;(2)克氏原螯虾能够捕食小管福寿螺和铜锈环棱螺的幼螺,但对铜锈环棱螺幼螺的捕食压力更大。研究两种杂食性底栖动物的共入侵对土著底栖动物的影响,有助于深化对多入侵者效应的理解。

1 材料与方法

1.1 研究区域

研究区域为武汉市新洲区的一个自然池塘(30°39′5″N,114°48′7″E),该池塘毗邻长江,水域面积约为 10000 m^2,平均水深为 1.2 m(0.8~1.6 m)。池塘远离村庄,人为干扰较少。池塘内生长着多种土著沉水植物,包括密刺苦草(*Vallisneria denseserrulata*)、轮叶黑藻(*Hydrilla verticillata*)和金鱼藻(*Ceratophyllum demersum*)。池塘内生长的鱼类主要是鲫(*Carassius auratus*)和麦穗鱼(*Pseudorasbora parva*)。在前期调研中,团队发现该自然池塘已遭到外来物种入侵。这主要是由于周边鱼塘人为引种养殖克氏原螯虾,以及随水生植物引种而无意间带入福寿螺所致,导致克氏原螯虾和小管福寿螺在该池塘内迅速扩张,成为优势种。在产卵季节,池塘周边的挺水植物上可见大量小管福寿螺的卵块,同时通过地笼也可以捕获到大量的克氏原螯虾和小管福寿螺。此外,调查还发现少量我国常见的土著物种铜锈环棱螺与这两种入侵物种在这个池塘里共存。因此,该池塘是研究两种外来水生底栖动物对土著螺类影响的理想场所。

本研究采样起止时间为 2023 年 10 月—2024 年 7 月。针对入侵物种克氏原螯虾和小管福寿螺以及土著物种铜锈环棱螺,每季度采集一次样品用于分析测试脂肪酸。同期,对该池塘内的水质进行了取样分析[47],该池塘水体总氮浓度变化范围为 0.64~1.40 mg/L,总磷浓度变化范围为 0.07~0.29 mg/L,氨氮浓度变化范围为 0.09~0.15 mg/L,叶绿素 *a* 浓度变化范围为 4.9~8.3 μg/L(表 2)。此外,该池塘沉水植物覆盖度常年保持在 80%以上。

1.2 样品采集及分析

1.2.1 脂肪酸分析样品采集与处理　根据 3 种底栖动物活动习性,本研究采用地笼(长 1.7 m,网框 20 cm×

25 cm,网孔 4 mm)捕捉克氏原螯虾、小管福寿螺和铜锈环棱螺。将地笼两端开口系紧并舒展开后,放置于采样点,持续 24 h 后收集地笼中的底栖动物,若单次采集的样品数量不足,则重复该过程直至获得足够样本。随后,挑选出克氏原螯虾、小管福寿螺和铜锈环棱螺带回实验室称重(表 3)。分别取 3 种底栖动物肌肉组织,用蒸馏水冲洗干净后放入 50 mL 离心管中,将离心管置于-80 ℃超低温冰箱冷冻 24 h 后,再用冷冻干燥机将样品冷冻干燥处理。干燥完毕的样品随后用研钵研磨成细粉末,然后将每个粉末状样品通过一个干净的筛子筛选(网孔为 80 μm),把筛分的细粉末样品收集放入 10 mL 离心管中储存于干燥器内,以备后续使用气相色谱—质谱联用仪(GC-MS)进行脂肪酸组成分析[48]。

表 2 采样点不同季节的水质特征

Tab. 2 The chemical characteristics of sampling sites in different seasons

时间	总氮/(mg/L)	总磷/(mg/L)	氨氮/(mg/L)	叶绿素 *a*/(μg/L)
2023 年 10 月	1.28±0.08	0.17±0.04	0.11±0.01	5.9±1.4
2024 年 1 月	0.64±0.07	0.07±0.01	0.09±0.02	4.9±1.3
2024 年 4 月	0.57±0.09	0.14±0.05	0.15±0.03	6.1±1.3
2024 年 7 月	1.40±0.11	0.29±0.02	0.13±0.01	8.3±1.1

表 3 采集的底栖动物个体生物量(湿重均值)

Tab. 3 The size of the collected benthic animals (mean individual wet weight)

时间	克氏原螯虾/g	小管福寿螺/g	铜锈环棱螺/g
2023 年 10 月	19.6±3.8	42.3±11.7	3.1±0.8
2024 年 1 月	25.8±1.7	41.6±19.6	2.8±0.6
2024 年 4 月	16.3±2.7	42.2±9.8	4.0±0.8
2024 年 7 月	15.8±3.6	46.3±10.7	3.7±0.9

1.2.2 脂肪酸组成分析　脂肪酸的组成分析中包括有脂类提取、脂肪酸的甲酯化、甲酯化后的萃取 3 个部分,样品的脂肪酸提取方法参考改进之后的 Folch 法和 Kanzie 法[49-50]:称取样品 50 mg 于 15 mL 离心管中,加入 10 mL 二氯甲烷和甲醇(V∶V=2∶1,含 0.01% BHT)混合提取液,经涡旋混合器充分混合 5 min 后放入超声机,超声 10 min,随后加入 2.5 mL Milli-Q 水,经高速离心机 3000 r/min 离心 10 min,取下层样品转移至 10 mL 样品瓶(瓶盖内垫为四氟垫片),在 40 ℃下用匀速氮气将样品氮吹浓缩,期间控制氮气流速,防止样品飞溅。加入 0.5 mL 二氯甲烷重溶,4 ℃冷藏保存待甲酯化。向样品瓶内加入 2 mL 硫酸—甲醇溶液(含 2% 硫酸)并在氮气保护下于 80 ℃水浴甲酯化 2 h。待样品冷却至室温后加入正己烷 2 mL,萃取上层脂肪酸甲酯化样品。提取后的样品经气相色谱—质谱联用仪(GC-MS)进行脂肪酸组成分析,GC-MS 使用 HP-88 毛细管柱(60 m×0.25 mm×0.2 μm,安捷伦),升温程序为:初始温度为 50 ℃,保持 2 min,然后以 25 ℃/min 的速度升至 175 ℃,再以 7 ℃/min 的速度保持 5 min,直至达到 210 ℃,持续 2 min,最终以 2 ℃/min 升至 275 ℃。其中氦气用作载气,流速为 1 mL/min。

脂肪酸组成以各脂肪酸占总脂肪酸的质量百分比表示。当数据样本多于一个样品时,其数据以平均值±标准偏差的形式表示。脂肪酸由末端甲基(CH_3)、一条碳链以及末端羧基(COOH)组成,脂肪酸的简写表达式为 CA∶Bn-X,其中 A 表示脂肪酸碳链的碳数,B 表示双键的数量,X 表示第一个双键离甲基端的碳数[51]。

1.2.3 脂肪酸生物标志物　本研究依据相关文献把脂肪酸分为 3 个主要类别:饱和脂肪酸、单不饱和脂肪酸(monounsaturated fatty acids,MUFA)和多不饱和脂肪酸(表 1)。饱和脂肪酸不含双键,单不饱和脂肪酸含有一个双键,多不饱和脂肪酸含有两个或以上双键[45]。

1.3 捕食受控实验

基于实验假设,本实验旨在比较成年克氏原螯虾对小管福寿螺和铜锈环棱螺幼螺的捕食强度,以及成年小管福寿螺对铜锈环棱螺幼螺的捕食强度。

1.3.1 实验材料　捕食受控实验所用克氏原螯虾、小管福寿螺和铜锈环棱螺均采集于调研池塘,挑选均匀大小个体用于实验。其中成年克氏原螯虾均重为(25.4±5.9) g,全长为(8.6±0.8) cm;成年小管福寿螺均重为(35.0±5.0) g,壳高为(4.6±0.2) cm;幼小小管福寿螺均重为(0.43±0.1) g,壳高为(1.2±0.1) cm;幼小铜锈环棱螺均重为(0.29±0.1) g,壳高为(0.9±0.3) cm。实验开始时对成年克氏原螯虾和小管福寿螺饥饿处理 24 h。

1.3.2 实验设计　捕食实验在 15 个圆形塑料桶中进行,桶直径 30 cm,高度 50 cm。实验用的成年克氏原螯

虾、小管福寿螺均选择雄性,每个桶水深为 6 cm。实验分为 5 组:(1)10 只小管福寿螺幼螺,(2)10 只铜锈环棱螺幼螺,(3)1 只克氏原螯虾+10 只小管福寿螺幼螺,(4)1 只克氏原螯虾+10 只铜锈环棱螺幼螺,(5)1 只成年小管福寿螺+10 只铜锈环棱螺幼螺。每组设置 3 个重复。实验环境温度为 26 ℃,实验持续周期为 24 h。实验结束后,统计各个实验桶剩余螺数,计算成年克氏原螯虾和小管福寿螺对铜锈环棱螺和小管福寿螺幼螺的捕食情况。

1.4 数据处理及分析

采用 SPSS 27.0 软件进行统计分析,利用 Shapiro-Wilk 检验数据的正态分布,运用 Levene's test 验证方差齐性。符合正态分布和方差齐性的数据采用单因素方差分析(ANOVA)确定组间差异,$P<0.05$ 为有统计学意义。采用最小显著性差异(LSD)法进行物种间的多重比较。若数据在对数转换、平方根转换后仍不齐时采用 Welch's ANOVA,组间存在显著差异时用未假定方差齐性的 Games-Howell 检验进行多重比较[52]。

通过主成分分析(PCA)来降低数据的维数,选择 3 种动物体内占比高于 1% 的脂肪酸作为 PCA 处理的基础数据,然后根据 PCA 分析结果,使用 Origin 2019b 64Bit 中 2D Confidence Ellipse 插件计算置信椭圆面积来表征种群之间的生态位[43,53]。柱状图所有结果均表示为平均值±标准差,组间有显著差异($P<0.05$)用不同小写字母在图上标注。

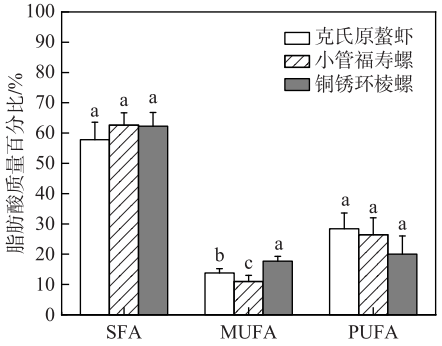

图 1 不同底栖动物脂肪酸质量百分比(误差棒上不同小写字母表示有显著性差异($P<0.05$))

Fig. 1 The percentage of fatty acid content in different benthic animals (Differences between values above the bar graph that share different letters are statistically significant ($P<0.05$))

2 结果与分析

2.1 3 种底栖动物的脂肪酸含量分析

克氏原螯虾和铜锈环棱螺的肌肉中各检测出 22 种脂肪酸,小管福寿螺共检测出 23 种脂肪酸;C16 在 3 种底栖动物的质量百分比均高于 20%,C18 质量百分比均大于 15%,其他种类的脂肪酸质量百分比均小于 15%。克氏原螯虾、小管福寿螺和铜锈环棱螺三者间的饱和脂肪酸(SFA)($P=0.339$)和多不饱和脂肪酸(PUFA)($P=0.140$)之间无显著性差异,而铜锈环棱螺的单不饱和脂肪酸(MUFA)质量百分比显著高于克氏原螯虾($P=0.011$),克氏原螯虾的 MUFA 显著高于小管福寿螺($P=0.046$)(图 1)。

PCA 分析结果显示,PC1 和 PC2 的方差贡献率分别为 31.7% 和 16.3%。置信椭圆面积显示,克氏原螯虾营养生态位面积最大(7.27),其次为小管福寿螺(3.36)和铜锈环棱螺(2.08),表明克氏原螯虾的生态位宽度比小管福寿螺和铜锈环棱螺更广,而铜锈环棱螺生态位宽度最窄(图 2)。

2.2 3 种底栖动物的脂肪酸生物标志物含量

在克氏原螯虾、小管福寿螺和铜锈环棱螺体内均检测到了 C20:4n-6、C18:1n-9、C22:6n-3、C15、C17、C18:2、C18:3。其中,C18:1n-9+C22:6n-3 指征肉食性强度,克氏原螯虾的 C18:1n-9+C22:6n-3 质量百分比显著高于小管福寿螺($P<0.001$)和铜锈环棱螺($P<0.001$);C15+C17 是细菌的脂肪酸标志物,铜锈环棱螺的 C15+C17 质量百分比显著高于克氏原螯虾($P=0.001$)和小管福寿螺($P<0.001$);C18:2+C18:3是维管束植物的脂肪酸标志物,克氏原螯虾($P=0.023$)和小管福寿螺($P=0.003$)的 C18:2+C18:3质量百分比显著高于铜锈环棱螺;C20:4n-6 指征大型藻类碎屑和底栖微生物,3 种生物的 C20:4n-6 质量百分比无显著差异(图 3)。

2.3 3 种底栖动物的营养级比较

PUFA/SFA 比值可以对比各种生物的营养级,克氏原螯虾的 PUFA/SFA 比值均值为 0.51±0.13,显著高于土著物种铜锈环棱螺(0.33±0.11)($P=0.029$);小管福寿螺的 PUFA/SFA 比值均值为 0.43±0.11,但方差分析显示与铜锈环棱螺无显著差异。

2.4 克氏原螯虾对小管福寿螺和铜锈环棱螺的捕食及小管福寿螺对铜锈环棱螺的捕食

在螯虾—福寿螺、螯虾—环棱螺、福寿螺—环棱螺 3 个实验组中,均发现有捕食现象,而无螯虾—福寿螺和无螯虾—环棱螺组的小管福寿螺幼螺、铜锈环棱螺幼螺未发生自然死亡。克氏原螯虾对铜锈环棱螺的捕食量显著高于对小管福寿螺的捕食量($P=0.001$)。在成年小管福寿螺与铜锈环棱螺幼螺的实验桶中,也发现成年福寿螺能够捕食铜锈环棱螺幼螺,但其捕食数量显著低于克氏原螯虾对铜锈环棱螺的捕食量($P<0.001$)(图 4)。

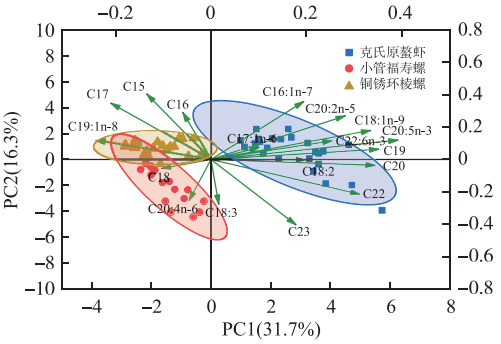

图 2 不同底栖动物脂肪酸的主成分分析

Fig. 2 Principal component analysis of fatty acids in different benthic animals

3 讨论

本研究中入侵物种克氏原螯虾和小管福寿螺的 PCA 置信椭圆面积大于土著物种铜锈环棱螺,表明两种入侵物种的生态位宽度更广。克氏原螯虾的 C18:1n-9+C22:6n-3 质量百分比显著高于小管福寿螺和铜锈环棱螺,表明克氏原螯虾指示肉食性的脂肪酸占比高于小管福寿螺和铜锈环棱螺;铜锈环棱螺的 C15+C17 质量百分比显著高于克氏原螯虾和小管福寿螺,而克氏原螯虾和小管福寿螺的 C18:2+C18:3质量百分比显著高于铜锈环棱螺,表明铜锈环棱螺的碳源主要源于细菌,而克氏原螯虾和小管福寿螺的碳源主要源于维管束植物。

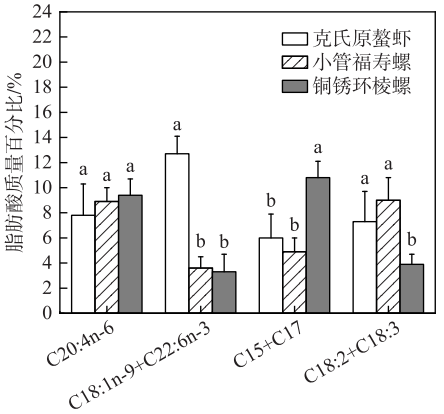

图 3 不同底栖动物脂肪酸生物标志物质量百分比(误差棒上不同小写字母表示有显著性差异($P<0.05$))

Fig. 3 The percentage contents of fatty acid biomarkers in different benthic animals (Differences between values above the bar graph that share different letters are statistically significant ($P<0.05$))

本研究中,在克氏原螯虾和小管福寿螺体内检测到了多种脂肪酸,其中能够指示其碳源主要来自维管束植物、碎屑和微生物的特定脂肪酸含量较高;而铜锈环棱螺的脂肪酸分析结果表明,其基础碳源则更多地来源于细菌,表明铜锈环棱螺直接摄食大型维管束植物的能力弱于两种入侵物种。克氏原螯虾的营养生态位宽度可能因食物来源的可用性和季节变化而变化[24]。克氏原螯虾入侵能力强,这可能与其能够在食碎屑性、食草性和食肉性食物之间转换的摄食可塑性密切相关[54]。小管福寿螺作为一种杂食性底栖动物,能够直接摄食植物、小型无脊椎动物、碎屑等[55],但主要是以植物为食[56]。已有研究表明,铜锈环棱螺主要以附生细菌、附着藻类和碎屑等为食[57-59],克氏原螯虾和小管福寿螺同样也能摄食碎屑、附着藻类和微生物等[56,60],这可能会对以这些资源为食物的土著底栖动物产生负面影响[27]。由于克氏原螯虾和小管福寿螺的食物种类繁多且资源可利用率高[24,55,61],当偏好的资源有限时,它们可以改变觅食方式[26],与土著螺类争夺空间和资源,再加上两个入侵物种可以直接捕食幼螺,因此在与土著螺类共享栖息地时,它们往往能够占据优势地位[5,24,62]。

脂肪酸 PUFA/SFA 比值分析结果表明,克氏原螯虾的营养级高于铜锈环棱螺,且两种入侵物种均可以直接捕食铜锈环棱螺幼螺。先前研究发现鱼类、虾类以及其他底栖动物在克氏原螯虾的食物组成中可占据一半[63]。克氏原螯虾可以直接捕食前鳃亚纲螺类和肺螺亚纲螺类包括小管福寿螺幼螺[64],也会捕食其他软体动物、甲壳类和多毛类等无脊椎动物[65]。本研究中克氏原螯虾对铜锈环棱螺幼螺捕食更多,可能说明

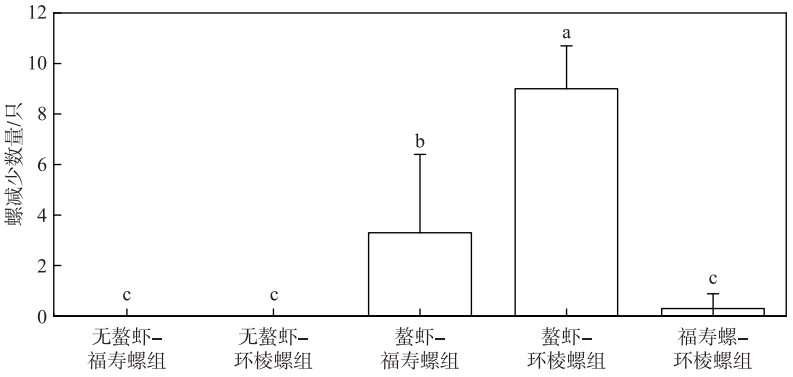

图 4 克氏原螯虾对小管福寿螺和铜锈环棱螺的捕食及小管福寿螺对铜锈环棱螺的捕食
(误差棒上不同小写字母表示显著性差异($P<0.05$))

Fig. 4 The predation of *P. clarkii* on *P. canaliculata* and *B. aeruginosa*, as well as the predation of *P. canaliculata* on *B. aeruginosa* (Differences between values above the bar graph that share different letters are statistically significant ($P<0.05$))

其对土著螺类捕食压力更大。因此,两种外来物种共入侵时,尽管克氏原螯虾也能捕食小管福寿螺幼螺,但由于小管福寿螺往往生长更快,成年个体也更大,其对土著物种的幼螺捕食强度可能更大。需要说明的是,本研究中小管福寿螺幼螺体重比铜锈环棱螺幼螺略大,可能也是造成克氏原螯虾捕食铜锈环棱螺幼螺更多的原因。另一方面,小管福寿螺不仅在碎屑等资源上与土著螺竞争,还会捕食螺类等小型无脊椎动物[66],最终会对螺类的种群数量产生显著的负面影响[67-68]。一些研究表明克氏原螯虾还会捕食福寿螺卵块,且对卵块的捕食率与卵块距离水面的高度呈反比,卵块距离水面的高度会制约螯虾的捕食效果[69]。但小管福寿螺大都产卵于挺水植物或岸边石块上,这会减少小管福寿螺被克氏原螯虾捕食的风险。因此,二者共入侵的叠加作用对铜锈环棱螺的负面影响可能更大,对生物多样性、食物网结构和生态系统过程的负面影响也可能更大[68,70-71]。

克氏原螯虾和福寿螺现已被广泛引入其原栖息地以外的淡水生态系统中[72-73],防止这些物种的入侵以及共入侵是进行生态系统管理和生物多样性保护的重要步骤。本研究的局限在于捕食实验未探讨克氏原螯虾和两种螺共存时的情况,野外调查未对 3 种底栖动物的种群数量动态进行量化。未来研究应进一步探讨克氏原螯虾和小管福寿螺共入侵时入侵物种和土著物种的种群变化及其对水质的影响,这将有助于更全面地评估两种外来物种共入侵对土著螺及其他底栖动物的影响。

4 结论

1)脂肪酸生物标志物分析显示,细菌对铜锈环棱螺的碳源贡献高于两种入侵物种;而克氏原螯虾和小管福寿螺利用维管束植物的碳源比例高于铜锈环棱螺。两种入侵物种的生态位宽度大于土著物种铜锈环棱螺,这表明它们具有更高的营养资源利用能力,从而在竞争中占据优势。

2)克氏原螯虾体内指示肉食性的脂肪酸比例高于小管福寿螺和铜锈环棱螺,其中克氏原螯虾的营养级最高。克氏原螯虾能够捕食小管福寿螺幼螺和铜锈环棱螺幼螺,但对铜锈环棱螺幼螺的捕食压力可能更大,而小管福寿螺也可以直接捕食铜锈环棱螺幼螺。因此,在生态位上,克氏原螯虾和小管福寿螺相较于本土物种铜锈环棱螺具有竞争优势。

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