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轮虫和枝角类的种间竞争及其影响因子研究进展

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摘要:轮虫和枝角类是浮游动物群落的重要组成部分和优势类群,它们之间的竞争互作是调节水生态系统结构和功能的主要动力之一。普遍的观点认为,轮虫和大型枝角类难以共存,往往被竞争排斥,而和小型枝角类可以共存;实际上,轮虫和枝角类的种间竞争结局存在一定的不确定性。介绍了轮虫和枝角类的种间竞争方式及其相对重要性,对影响轮虫和枝角类种间竞争结局的因素,包括温度、食物、相对起始密度、个体大小、食物临点、耐饥饿能力、捕食及竞争者和捕食者释放的化感物质等,进行了系统的梳理和分析,并提出了今后亟待解决的科学问题和研究切入点。

关键词:轮虫;枝角类;种间竞争;机理;结局;生物因子;非生物因子

Research advances in interspecific competition and influencing factors between rotifers and cladocerans

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Abstract: Rotifers and cladocerans are important constituents and dominant groups of zooplankton communities. Interspecific competition between them is one of major driving forces regulating structure and function of aquatic ecosystem. It is generally believed that rotifers and large cladocerans are difficult to coexist, and rotifers are often excluded by large cladocerans, while rotifers and small cladocerans can coexist. In fact, the outcome of interspecific competition between rotifers and cladocerans was uncertain to a certain extent. In this review, we briefly introduced the patterns of competition between rotifers and cladocerans and their relative importance, and analyzed in detail the effects of environmental factors, including temperature, food resources, initial density, individual size, threshold food concentration, starvation tolerance ability, predation, allelopathic substances released by competitors and predators on the outcome of competition between rotifers and cladocerans. Finally, we put forward some scientific problems and research breakthrough points.

Key Words: rotifer; cladoceran; interspecific competition; mechanism; outcome; biotic factor; abiotic factor

轮虫和枝角类是浮游动物群落的重要组成部分和优势类群,为水生食物链前端的消费者,可以微藻、原生动物、细菌及有机碎屑等为食物,同时它们本身又是鱼类、猎食性无脊椎动物等其他水生生物的食物,因此,它们在水生食物链当中起着承上启下的作用[1-2]。由于轮虫和枝角类的食性、可摄取的食物颗粒粒径大小及生

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态位均存在重叠,因而它们之间可能会发生因争夺食物资源和生存空间的种间竞争[3-4]。大多数轮虫和枝角类行周期性孤雌生殖、胚胎发育时间短、周转快、内禀增长率高,在外界环境适宜时,可在很短的时间内建立较大的种群[1],但由于枝角类个体较大、滤食率较高,所以枝角类通常是优势竞争者[3-4]。

轮虫和枝角类的生殖及种群增长能力对环境因子变化的敏感性强,但不同种类的轮虫和枝角类对环境因子变化的敏感性差异较大[1,4],因此,它们之间的种间竞争结局可能存在一定的不确定性。轮虫和枝角类的种间竞争结局及其影响因子研究,对于认识浮游动物的种间竞争机理、群落结构特征和功能及动态调节规律和协同进化具有重要的理论意义。本文系统梳理了轮虫和枝角类的种间竞争方式及影响种间竞争结局的主要环境因子,并分析了今后需要进一步解决的科学问题和研究切入点。

1　轮虫和枝角类的种间竞争方式

轮虫和枝角类之间的竞争方式可分为食物资源匮乏时的资源利用性竞争[5-6]、生存空间受限时的机械干涉性竞争[7-9]以及它们释放的化感物质引起的化学干涉性竞争[10-13]。

1.1　资源利用性竞争

轮虫和枝角类均能摄取粒径大小在 1—20 μm 范围内的各类型食物,如果它们所需的食物类型多样、数量以及质量有保障时,那么水体中不同种类的轮虫和枝角类能够共存且能很好地繁殖,反之,就会发生因争夺食物资源的资源利用性竞争,从而抑制竞争者的种群丰度[5-6]。

1.2　机械干涉性竞争

机械干涉性竞争是指动物在捕食或运动的过程中由于身体碰撞造成损伤或潜在的不利影响,对其生殖和种群增长可能产生抑制作用[2]。这种影响常常出现在高密度培养的枝角类之间或枝角类和轮虫之间,而轮虫之间几乎不存在[6]。

Gilbert 和 Stemberger 首次提出了枝角类对轮虫存在机械干涉性竞争[7]。他们发现,在食物非常充足的情况下,大型枝角类(体长>1.2 mm)仍能抑制螺形龟甲轮虫(*Keratella cochlearis*)的种群增长,主要是由于枝角类在摄食时可能会将轮虫带入滤室,从而会使轮虫携带的卵脱落,对其造成机械伤害,甚至致死;轮虫受机械伤害的程度随轮虫被甲的坚硬程度及轮虫在枝角类滤室中停留的时间长短而异,身体纤弱、停留时间长的轮虫种类受到的伤害更大些[2, 7]。Gilbert 进一步证实了轮虫受枝角类的机械干涉伤害程度随轮虫的种类而异,通常个体较大(如独角聚花轮虫 *Conochilus unicornis*)或运动能力较强(如红多肢轮虫 *Polyarthra remata*)从而难以被带入枝角类滤室的轮虫种类,或能够进入滤室但停留时间很短的轮虫种类(如前节晶囊轮虫 *Asplanchna priodonta*、梳状疣毛轮虫 *Synchacta pectinata*),受枝角类的机械干涉伤害较小甚至不受影响;而在滤室中停留时间较长、身体纤弱、个体较小的种类(如螺形龟甲轮虫、长圆疣毛轮虫 *S. oblonga*、无尾无柄轮虫 *Ascomorpha ecaudis*)易受枝角类机械干涉的伤害[2, 8]。

1.3　化学干涉性竞争

即使在食物充足的情况下,由于高密度培养,轮虫和枝角类可能会受到对方释放的化感物质和/或代谢废物的影响,称为轮虫和枝角类之间的化学干涉性竞争[14]。但这些化学物质量少、成分复杂,很难从动物的培养液中提取和分离[15-17],也很难将化感物质和代谢废物区分开来,因此,目前关于轮虫和枝角类之间的化学干涉性竞争研究,均是利用其培养滤液代替其释放的化感物质和/或代谢废物,并且这种竞争作用的影响,究竟是有害的或有利的或几乎无作用,还不能定论,可能取决于轮虫和枝角类的种类、培养滤液中化感物质的量、生活史变量以及温度和食物密度等因素[10-13]。因此,对不同轮虫和枝角类释放的化感物质和代谢废物的区分、有效成分的提取、分离、结构鉴定和功能研究以及化感物质释放量及活性的影响因子研究,将是后续研究亟待解决的问题。

1.4　三种竞争方式的相对重要性

众多的研究表明,大型枝角类通过资源利用性竞争和干涉性竞争的共同作用抑制了轮虫的生殖和种群丰

度,但究竟是哪种竞争方式起主要作用,还难以定论[2]。May 和 Jones 研究发现,大型枝角类对螺形龟甲轮虫种群增长的竞争抑制方式主要为资源利用性竞争[18]。而 MacIsaac 和 Gilbert 则认为,大型枝角类对螺形龟甲轮虫种群增长的竞争抑制方式主要为干涉性竞争[19]。由此展开了关于大型枝角类对轮虫竞争抑制的过程中哪种竞争方式更为重要的争论[2]。大多数的观点认为干涉性竞争更重要[3,9,20-22],也有不少学者认为资源利用性竞争更重要[23-25]。但究竟是哪种竞争方式起的作用更大,可能与大型枝角类和轮虫的种类、个体大小、种群密度及轮虫有无被甲、棘刺等防御性形态特征,以及温度、食物密度、捕食等其他环境因素有关[2]。例如,Conde-Porcuna 等的研究结果表明,大型枝角类对裂痕龟纹轮虫(*Anuraeopsis fissa*)种群丰度的抑制方式主要为资源利用性竞争,而对长圆疣毛轮虫种群丰度的抑制主要是由于干涉性竞争的作用[26]。Fradkin 研究发现,大型枝角类种群密度较低时,对轮虫的作用主要为资源利用性竞争,而种群密度较高时,对轮虫的作用则主要为干涉性竞争[27]。Devetter 和 Seda 研究发现,具被甲轮虫(如螺形龟甲轮虫、矩形龟甲轮虫 *K. quadrata* 和长刺盖氏轮虫 *Kellicottia longispina*)的种群丰度主要受大型枝角类资源利用性竞争的抑制,而身体柔弱的轮虫(如异尾轮虫 *Polyarthra spp.*、喜冷疣毛轮虫 *S. lakowitziana*)可能更容易受到大型枝角类干涉性竞争的抑制[28]。

实际上,以上关于大型枝角类对轮虫的干涉性竞争中,并没有将机械干涉性竞争和化学干涉性竞争区分开来。Flores 等认为,枝角类对轮虫的机械干涉性竞争的作用强度要远远高于化学干涉性竞争[12]。但在群落结构调节机制的研究中发现,化学干涉性竞争的作用更重要,甚至促进了遗传变异[29]。

可见,关于这三种竞争方式在大型枝角类和轮虫的竞争互作中的相对重要性、特别是资源利用性竞争与机械干涉性竞争或与化学干涉性竞争的区分及相对重要性研究还没有形成一致的观点[2],需要考虑更多的环境因子,采用更多种类的枝角类和轮虫为实验对象,设计更加合理的实验方法来进行研究和分析。

2 轮虫和枝角类的种间竞争结局

部分学者认为,自然水体中轮虫的种群丰度与枝角类的个体大小有关,它们的种间关系符合大小效率假说[30]。轮虫与大型枝角类(>1.2 mm)不能共存,而和小型枝角类(<1.2 mm)可以共存[3, 8, 31-36],并且枝角类均表现出更大的竞争优势。Gilbert 认为,轮虫与小型枝角类可以共存的原因主要有:(1)小型枝角类对轮虫的机械干涉性竞争的强度较小;(2)小型枝角类的滤食率不高、繁殖率较低,耐饥饿能力较差,具有较高的食物临点,因此难以消耗太多的食物资源;(3)小型枝角类的种群增长也会受到轮虫资源利用性竞争的抑制;(4)相对于大型枝角类,小型枝角类更容易被无脊椎动物捕食[2-3]。

然而,轮虫和枝角类的种间关系也存在与大小效率假说明显相悖的情况,轮虫表现出比枝角类更大的竞争优势[2]。如螺形龟甲轮虫比含糊溞(*Daphnia ambigua*)的竞争优势更大[32];褶皱臂尾轮虫(*Brachionus plicatilis*)也表现出比蒙古裸腹溞(*Moina mongolica*)[37]和微型裸腹溞(*M. micrura*)[38]更明显的竞争优势;另外,在较高的食物密度下,萼花臂尾轮虫(*B. calyciflorus*)同样表现出比多刺裸腹溞(*M. macrocopa*)更大的竞争优势,并最终竞争排斥了多刺裸腹溞[39]。陈桃英等(2004)认为,褶皱臂尾轮虫在与蒙古裸腹溞竞争的过程中占据明显优势的原因可能是:(1)蒙古裸腹溞个体较小,对褶皱臂尾轮虫的产生机械干涉作用较小;相反,高密度的褶皱臂尾轮虫对蒙古裸腹溞的碰撞可能会导致其从孤雌生殖向有性生殖转变;(2)褶皱臂尾轮虫的耐饥饿能力较强、食物临点较低;(3)褶皱臂尾轮虫个体较小,繁殖较快,在短时间内可达到较高的种群密度,而蒙古裸腹溞幼体发育时间较长,种群增长速度较慢;(4)高密度的褶皱臂尾轮虫可能对蒙古裸腹溞的种群增长产生化感抑制作用[2,37]。而 Huang 等则认为,在较高的食物密度下,萼花臂尾轮虫的种群增长率更高,在很短的时间内就可以达到很高的种群丰度,食物资源被快速消耗,从而通过资源利用性竞争抑制了多刺裸腹溞的种群丰度从而占据了明显的竞争优势[39]。

综上所述,轮虫和枝角类发生竞争时,往往是枝角类占有优势,但也存在一定的不确定性,特别是轮虫和小型枝角类之间竞争结局的不确定性更大,甚至会发生倒转的现象[2]。影响轮虫和枝角类种间竞争结局的

因素很多,究竟哪些是主要因子以及哪些环境条件下何种类群更具有竞争优势等问题,一直是轮虫和枝角类之间竞争关系研究的热点。下面对影响轮虫和枝角类种间竞争结局的主要环境因子及不同环境条件下的竞争关系进行系统梳理,以期为后续研究提供参考。

3　影响轮虫和枝角类种间竞争结局的因素

3.1　温度

温度是影响轮虫和枝角类种群变动的主要环境因子[4],但不同的轮虫和枝角类对温度变化的敏感性存在差异,因此,在不同温度下,特别是在低温和高温下,它们之间的竞争结局可能是不同的[2]。目前,关于温度对轮虫和枝角类种间竞争结局的影响研究,还不多见。

Strecker 等通过对高山无鱼池塘浮游动物的种群变动进行研究后发现,气候变暖是导致螺形龟甲轮虫和独角聚花轮虫等个体较小的轮虫在与蚤状溞(*D. pulex*)等大型枝角类的竞争中表现出更大的竞争优势的主要原因[40]。而 Huang 等在实验室条件下的研究表明,温度的升高并没有改变萼花臂尾轮虫和多刺裸腹溞之间的竞争结局,暗示着两种浮游动物对温度升高的敏感性差异不大,但其竞争强度随着温度的升高而增强[39]。

3.2　食物

轮虫和枝角类生态位相似,均能以各种微藻、细菌、原生动物及有机碎屑等为食,当食物资源匮乏时,它们之间必然会出现资源利用性竞争[2]。资源利用性竞争能力主要取决于竞争者的滤食率[3,20]、食物储存能力[41]、同化率及在低食物水平下的生殖能力等[42]。和轮虫相比,枝角类的滤食率较高,因此,当轮虫和枝角类发生资源利用性竞争时,枝角类往往具有更大的优势[4-5, 39]。

众多的研究表明,食物的数量、质量和类型等对浮游动物的种群丰度、种间竞争结局和多样性都有重要影响[39, 43-45]。不管食物密度如何,模糊网纹溞(*Ceriodaphnia dubia*)和多刺裸腹溞均能竞争抑制十指臂尾轮虫(*B. patulus*)的种群增长,且其竞争强度随着食物密度的上升而增强[46],多刺裸腹溞能够快速的竞争排斥萼花臂尾轮虫,但其竞争强度随着食物水平的上升而减弱[47]。Huang 等研究发现,在低食物密度下,多刺裸腹溞同样竞争排斥了萼花臂尾轮虫,而在较高的食物密度下则与之相反,且其竞争强度随着食物密度的上升而增强[39]。但 Cheng 等研究表明,不管食物丰度如何,缺刺秀体溞(*D. aspinosum*)对圆形臂尾轮虫(*B. rotundiformis*)的种群增长均无影响,两者能够完全共存[35]。

Espinosa-Rodríguez 等研究发现,三刺粗毛溞(*Macrothrix triserialis*)和尖额溞(*Alona glabra*)均能竞争抑制大肚须足轮虫(*Euchlanis dilatata*)的种群增长,但其抑制强度取决于食物类型[45]。食物类型不同,食物质量也可能不同,食物质量对轮虫和枝角类的竞争结局也会产生影响[2],如食物的氮限制削弱了长刺溞(*D. longispina*)对裂痕龟纹轮虫的竞争抑制作用[25]。

另外,食物供给频率对轮虫和枝角类的相对丰度和种间竞争结局也有重要影响。研究发现,当周期性供给高密度食物时,含糊溞竞争排斥了螺形龟甲轮虫,但当持续性供给低密度食物时,两者却可以共存[32]。

3.3　竞争者的相对起始密度

轮虫和枝角类的相对起始密度在一定程度上也影响了两者的竞争结局。Hurtado-Bocanegra 等研究发现,不管轮虫的起始密度如何,模糊网纹溞和多刺裸腹溞均能竞争抑制十指臂尾轮虫的种群增长,但在低食物密度下,轮虫的起始密度较高时,多刺裸腹溞的种群丰度受到轮虫较强的竞争抑制,而模糊网纹溞几乎不受影响[46]。陈桃英等研究表明,不管蒙古裸腹溞的起始密度如何,蒙古裸腹溞均受到了褶皱臂尾轮虫的竞争抑制,而褶皱臂尾轮虫受蒙古裸腹溞的影响不大,褶皱臂尾轮虫的耐饥饿能力较强可能是其重要原因[37]。Larrosa 等研究发现,在螺形龟甲轮虫种群增长的不同阶段引入大型溞(*D. magna*)(部分等同于竞争时的起始密度不同[2]),两者的竞争结局是不同的[48]。张文萍等研究表明,萼花臂尾轮虫种群受到隆线溞(*D. carinata*)的抑制作用随着溞起始密度的增加而增大,而隆线溞种群受到轮虫的抑制作用则随着溞起始密度的增加而降低,当溞的起始密度与轮虫相同时,轮虫对溞的种群增长无明显抑制作用[49]。然而,Xi 和

Hagiwara 发现,不管轮虫的起始密度如何,多刺裸腹溞都能够快速的竞争排斥萼花臂尾轮虫,而溞本身几乎不受影响,究其原因可能是该研究的多刺裸腹溞为成体,其竞争力更强[47]。

3.4 竞争者的个体大小、食物临点和耐饥饿能力

3.4.1 个体大小

枝角类对轮虫的竞争优势随着枝角类个体大小的增大而显著增强[50]。野外研究发现,当水体中只有小型枝角类存在时,往往伴随着大量的浮游性轮虫,而当大型枝角类出现时,轮虫的数量就会快速变少[2]。实验室研究也表明,螺形龟甲轮虫与蚤状溞或大型溞等大型枝角类不能共存,但却能与长额象鼻溞(*Bosmina longirostris*)或网纹溞等小型枝角类长时间共存,并竞争排斥了含糊溞;长圆疣毛轮虫和长额象鼻溞、龟形龟甲轮虫(*K. testudo*)和含糊溞同样均能长时间共存[50]。

大型枝角类对鱼类[30]、群体蓝藻[51]和悬浮粘土颗粒[52]的敏感性高于轮虫。众多的研究表明,大型枝角类通过资源利用性竞争和机械干涉性竞争抑制、甚至竞争排斥了轮虫种群[2-3,9]。大型枝角类对轮虫的机械干涉性竞争的强度随着枝角类个体的增大[53]和轮虫敏感性的上升[8]而增强。如龟甲轮虫对蚤状溞的机械干涉的敏感性随着轮虫个体的增大而降低[8];螺形龟甲轮虫的幼体比成体更容易受到网纹溞的伤害或捕食[54];角突臂尾轮虫(*B. angularis*)和萼花臂尾轮虫的幼体同样也比成体更容易受到蚤状溞和短钝溞(*D. cf. obtusa*)的伤害或捕食[55]。

然而,轮虫和枝角类的个体大小不是恒定不变的,会受到温度、食物和捕食等环境因子的影响[56],从而可能影响其竞争结局。例如,一些轮虫种类可以通过周期变形增大个体或延长棘刺长度来抵御大型枝角类的机械伤害,从而能和大型枝角类长时间共存[57]。

3.4.2 食物临点和耐饥饿能力

许多研究结果支持可以用食物临点和耐饥饿能力来预测浮游动物等植食性消费者之间的竞争结局[2,58],食物临点较低、耐饥饿能力较强的种类通常具有较大的竞争优势[59]。然而,轮虫和枝角类的食物临点或耐饥饿能力可能随着食物颗粒大小[60]、组分[61]和温度[62]等环境因子的变化而变化,从而对其竞争优势可能产生潜在的影响。

3.4.3 个体大小、食物临点、耐饥饿能力之间的关系

有研究表明,浮游性轮虫和小型枝角类的个体大小与食物临点之间呈正相关[63],与耐饥饿能力之间呈负相关[64]。然而,大型枝角类的个体大小与食物临点之间却呈负相关[32, 65]。轮虫和枝角类的食物临点或耐饥饿能力之间的关系还难以定论[2]。有报道显示,轮虫的食物临点高于暖水性浮游枝角类,而个体较小的轮虫和热带小型枝角类的食物临点是相似的[66]。

3.5 捕食

晶囊轮虫[67]、桡足类[68]、昆虫幼体[69]等捕食者对植食性轮虫的捕食,扁形动物[70]、幽蚊幼虫[71]、捕食枝角类[72]和桡足类[73]等捕食者对植食性枝角类的捕食,以及鱼类对轮虫、枝角类或桡足类的大小选择性捕食[30, 74-75],均能直接或间接影响轮虫和枝角类之间的竞争优势。

3.6 竞争者和捕食者释放的化感物质

3.6.1 竞争者释放的化感物质

关于轮虫和枝角类的化感互作研究还很少,仅有的报道是关于以其培养滤液代替其分泌的化感物质对其竞争者种群增长和生活史特征的影响研究[2]。同种轮虫对不同枝角类或不同轮虫对同种枝角类培养滤液响应的差异较大[12],既有促进作用[11, 13],也有抑制作用[10, 13],可能取决于轮虫和枝角类的种类、培养滤液浓度、生活史变量、温度及食物密度等因素。实际上,竞争者释放的化感物质不仅作用于对方,同样作用于自身,因此,轮虫和枝角类的化感互作,是他感和自感的综合影响。

3.6.2 捕食者释放的化感物质

捕食者释放的化感物质对枝角类的形态特征和生活史特征会产生重要影响[76-79],轮虫对捕食者释放的

化感物质也会产生相应的捕食防御反应[80-82],可以预测,轮虫和枝角类对捕食者释放的化感物质的不同响应可能会改变它们之间的竞争结局。

3.7 其他因子

除了上述因子对轮虫和枝角类的竞争结局会产生重要影响外,水体 pH[83-84]、溶氧[85]、光照[86]、紫外线辐射[87]、污染物[88-89]、水文[90]和轮虫的特定行为如逃避[91]或附着在枝角类体表[92]或直接进入枝角类体内[93]等因子也会对枝角类或轮虫产生不同的影响,从而影响它们之间的竞争优势。

4　存在的问题与展望

4.1 轮虫和枝角类种间竞争方式的相对重要性仍存在较大分歧

对于轮虫和大型枝角类的种间竞争方式,大多数的观点认为,干涉性竞争更重要[3,9,20-22],也有不少学者认为资源利用性竞争更重要[23-25]。实际上,干涉性竞争可以区分为机械干涉性竞争和化学干涉性竞争,在早期的研究中,学者们并没有将两者区分开来。

为了避免轮虫和枝角类可能的机械干涉性竞争,随着实验设计的改良,学者们利用枝角类的培养滤液或用滤网将枝角类和轮虫隔开,来研究化学干涉性竞争和资源利用性竞争的相对重要性,但仍然不能形成一致的观点[12, 29, 94]。

轮虫和枝角类种间竞争方式的相对重要性,可能与竞争体系中轮虫和枝角类的种类、个体大小、种群密度、对环境的适应能力、轮虫是否具有逃避机械伤害的形态特征如有无被甲、较长的棘刺或行为特征如逃避、附着特性等因素有关[2]。因此,在将来的研究中,需要在不同生境下,选取更多种类、个体大小不同、具有显著的形态或行为特征差异的枝角类和轮虫作为竞争种,采用更理想的实验设计和装置,来精确区分轮虫和枝角类之间的三种竞争方式的相对重要性。

4.2 轮虫和枝角类种间竞争互作的分子机理尚缺少足够的证据

目前对于轮虫和枝角类种间竞争的机理研究多数还处于种群和个体水平,特别是很少涉及到蛋白组、转录组和基因组水平,更多的开展这方面的研究,将有助于从微观水平更好的分析和理解轮虫与枝角类之间竞争互作的深层次机理。

4.3 轮虫或枝角类释放的化感物质和代谢废物对竞争互作的作用尚不能完全区分

轮虫和枝角类培养液中影响两者竞争互作的物质究竟是化感物质还是代谢废物,目前的实验结果分析基本都来源于推测,很难准确区分和定论;另外,这种化感作用实际上是他感和自感的综合作用。因此,对于化感物质和代谢废物以及他感作用和自感作用的区分将是后续研究的热点和挑战。

4.4 轮虫或枝角类分泌物的提取、分离、纯化、结构鉴定及功效关系研究尚缺少足够的实验数据

随着 HPLC、GC-MS 等高效分离、检测设备及现代分子生物学技术在不同领域的广泛应用,使得轮虫和枝角类培养液中的有效成分的分离、鉴定成为可能。Snell 研究团队对轮虫培养液中的蛋白分析已经做出了重要的成果[17, 95],这为不同轮虫和枝角类培养液中有效成分的分离和鉴定奠定了坚实的基础,对于进一步深入的分析和理解轮虫与枝角类的种间竞争机理具有重要意义。

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