

DOI: 10.5846/stxb201306051343

覃光球, 卢豪良, 唐振柱, 赵鹏, 白雪涛, 彭亮. 水生生态环境中捕食信息素的生态学效应. 生态学报, 2014, 34(10): 2481-2489.

Qin G Q, Lu H L, Tang Z Z, Zhao P, Bai X T, Peng L. Ecological effects of predator chemical cues in aquatic ecosystem. Acta Ecologica Sinica, 2014, 34(10): 2481-2489.

水生生态环境中捕食信息素的生态学效应

覃光球^{1,2,*}, 卢豪良³, 唐振柱¹, 赵鹏¹, 白雪涛², 彭亮¹

(1. 广西壮族自治区疾病预防控制中心毒理所, 南宁 530028; 2. 中国疾病预防控制中心环境与健康相关产品安全所, 北京 102206;

3. 厦门大学环境与生态学院, 厦门 361102)

摘要: 捕食信息素是捕食者释放的, 能够引发猎物反捕食反应的化学信号。在水生生态系统中, 捕食信息素在捕食者和猎物之间信息传递及协同进化过程中发挥着重要的作用, 其生态学效应在国际上受到广泛关注。捕食信息素的来源有多种形式, 研究中常使用养殖过捕食者的水溶液作为捕食信息素的来源。捕食信息素的作用效果受到捕食者和猎物的种类、信息素的浓度、观察的指标等多方面因素的影响。捕食信息素可以对水生生物的行为、形态和生活史特征等方面造成影响。水生生物通过感知捕食信息素来提前预知潜在的被捕食风险, 并作出适应性调整, 以降低被捕食的风险。在某些情况下, 捕食信息素可以与污染物产生交互作用, 从而干扰污染物对水生生物的毒性。对水生环境中捕食信息素的研究现状做了综述, 介绍了当前对捕食信息素来源和理化性质等本质问题的认识, 总结捕食信息素对水生生物行为、形态和生活史特征的影响, 以及捕食信息素对污染物毒性的干扰, 并分析了这一研究领域尚存在的困难和今后的研究方向。加强对捕食信息素的研究, 将为解析水生环境中捕食者和猎物的生态关系提供新依据。

关键词: 捕食信息素; 信息素; 捕食者-猎物交互作用; 生态学效应; 水生生态环境

Ecological effects of predator chemical cues in aquatic ecosystem

QIN Guangqiu^{1,2,*}, LU Haoliang³, TANG Zhenzhu¹, ZHAO Peng¹, BAI Xuetao², PENG Liang¹

1 Institute of Toxicology, Guangxi Center for Disease Prevention and Control, Nanning 530028, China

2 Institute of Environmental Health and Related Product Safety, Chinese Center for Disease Prevention and Control, Beijing 102206, China

3 College of the Environment and Ecology, Xiamen University, Xiamen 361102, China

Abstract: Predator chemical cues are chemical signals released by predators that inform potential prey of the presence of predators. Predator cues allow prey to detect and evade predators from a distance. In aquatic ecosystem, predator chemical cues have been shown to play an important role in information transmission and evolutionary race between prey and predator. The effect of predator cues on aquatic organisms has received increased attention recently. This paper summarized the current understanding on the nature of predator chemical cues and the ecological effects of predator chemical cues on the behavior, morphology, and life-history of aquatic organisms. Recent work on the effects of predator cues on disturbing the toxicity of contaminants was also reviewed. Predator chemical cues origin from the skin exudates, faeces, or injured tissue of predators. It was sometimes confused with conspecific cues since conspecific cues could induce similar responses. Studies examining the effects of predator cues often used predator conditioned water as the sources of predator chemical cues. Although knowledge about the chemical nature of predator chemical cues is still scarce, considerable advances have been made, especially for the identification of cues inducing anti-predator defenses in ciliates and cues originated from fishes. It

基金项目: 中国博士后科学基金(2012M521658); 国家自然科学基金(31000244); 广西自然科学基金(2013GXNSFCA019009); 广西卫生厅科研项目(Z2012218)

收稿日期: 2013-06-05; 网络出版日期: 2014-02-20

* 通讯作者 Corresponding author. E-mail: qinguangqiu@sina.com

<http://www.ecologica.cn>

was found that the effects of predator cues are associated with predator species, predator's diet, concentration of cues, and many other factors. The identification and isolation of predator cues is an important step towards understanding the nature and ecological effects of predator cues. Numerous studies have shown that predator-released chemical cues could induce behavioral, morphological and life-historical anti-predator responses in preys. Behavioral responses to predator cues include avoidance of the area where cues is detected, decreased activity levels or freezing, and increased use of shelter. Behavioral responses of prey to predator cues have been found in cladocerans, gastropods, fishes, and amphibians. Morphological defenses have been found in a wide range of aquatic taxa, including algae, protozoans, rotifers, cladocerans, gastropods, insects, fishes and amphibians. Among them *Chaoborus*-induced morphological defense in *Daphnia* have received the most attention. Life-history responses to predator cues were mainly studied in cladocerans and amphibians, and the responses include adaptive changes in life-history switch points (such as timing of hatching and metamorphosis), longevity and reproduction. The anti-predation responses make prey less vulnerable to predation, and is believed to cause costs that are saved in the absence of predators. Interestingly, it was found that predator cues may interact with contaminants and influence their toxicity to the survival, growth, and life-history of prey. The interaction may be influenced by the sources of predator cues, classes of contaminants and their concentrations, endpoints of prey, and so on. These findings indicate that predatory stress plays an important role in the process of how contaminants exert their effects within the aquatic environment. The mechanisms of interaction between predator cues and contaminants are still unclear. Although considerable progress has been made, several key questions in this area remain. Future studies are needed to explore the chemical nature of predator cues and to examine the signal transmission process in predator-prey interaction. Knowledge of the chemistry and signal transmission process of predator chemical cues may improve our ability to design meaningful experiments, so as to gain better understanding on predator-prey interaction in aquatic ecosystem.

Key Words: predator chemical cues; kairomones; predator-prey interaction; ecological effects; aquatic ecosystem

生物之间的化学信号(infochemicals) 联系是一种普遍存在的生态学现象^[1]。很多生物(包括陆生和水生生物) 都可以接收到源自同类或者潜在捕食者的化学信号, 从而获得周围环境的信息。这类释放到体外、在个体之间传播信息并引发接收者在行为或者生理上反应的化学物质被称为信息素(pheromones)^[2]。在水生生态环境中, 信息素是很多水生生物的一个重要信息来源, 在水生生物的交互作用过程中发挥着重要的信息传递作用^[3]。研究发现, 包括原生动物、甲壳动物、腹足动物、两栖动物和鱼类在内的多种水生生物都能对含量极低的信息素作出反应^[4]。其中, 猎物和捕食者之间的信息素联系是一个受到广泛关注的生态学现象。本文对水生环境中捕食信息素的生态学效应进行综述, 归纳总结当前学术界对捕食信息素的来源、成分、理化性质和受影响因素等方面的认识, 并探讨捕食信息素对水生生物的作用及其潜在影响。

1 对捕食信息素的认识

在水生生态环境中, 猎物和捕食者之间相互沟通的信息素可以分为几类。一类是猎物同类释放的“告警信息素(disturbance cues 或 conspecific cue)”。当猎物受到捕食惊吓或者威胁时, 会释放出这类化学信号, 以警示同类。研究表明, 海胆(*Strongylocentrotus franciscanus*)、小龙虾(*Orconectes virilis*)、细镖鲈(*Etheostoma exile*)、美洲红点鲑(*Salvelinus fontinalis*)、九间始丽鱼(*Archocentrus nigrofasciatus*)、粘杜父鱼(*Cottus cognatus*) 和红腿蛙(*Rana auroa*) 等多种水生生物可以释放这类化学信号^[3]。有研究表明, 尿氨是这类告警信息素的成分之一^[5]。另一类化学信号被称为“损伤信息素(damaged-released alarm cues)”。在捕食行为中, 受伤的猎物会从受损部位释放出化学信息素, 以告知同类捕食行为正在发生。大多数种类的水生生物都会对这类源自受伤同类的信息素产生反捕食反应^[6]。这类反应一般包括行为、形态以及生活史特征的改变, 例如降低活动性、

改变体型大小和发育时间等,其目的都是为了降低被捕食的风险。还有一类化学信号被称为“捕食信息素”或“捕食信号(predator cues 或 kairomones)”。捕食信息素是捕食者释放的,能够引发猎物反捕食反应的化学信号^[3]。猎物通过探知捕食信息素,进而调整自身的反捕食策略,以提高自身的生存几率。由于猎物本身释放出的告警信息素或损伤信息素可以引发与捕食信息素类似的效果,这几类化学信号常常被混为一谈。为了研究方便,下文提及的“捕食信息素”专指捕食者释放的捕食信息素。

捕食信息素可能源自捕食者体表、分泌物、排泄物、或者受伤的组织^[7]。例如,水貂(*Neovision vison*)粪便中含有的信息素可使斑鲮鱼(*Salmo trutta*)产生强烈的规避捕食行为反应^[8]。虹银汉鱼(*Melanotaenia duboulayi*)浸泡液含有的信息素可以影响网纹水蚤(*Ceriodaphnia dubia*)的生活史^[9]。另有报道指出,附着于猎物身上的细菌才是捕食信息素的来源^[10-11]。Ringelberg 和 Van Gool 发现,鲈鱼经过抑菌剂处理之后,水蚤对其产生的捕食信息素的反捕食行为反应减弱,提示捕食信号可能来自与鲈鱼相关的细菌,而非鲈鱼本身^[10]。

将捕食信息素引入试验体系的方法有几种:将笼装的捕食者放在实验体系内(捕食者和猎物同在一个试验体系内,但是被物理分隔,以避免直接捕食行为的发生)^[12-13],使用养殖过捕食者的水样作为信息素处理(即捕食者的浸泡液作为试验溶液)^[14-17],以及在试验体系中引入捕食者的组织提取液^[18]或者排泄物^[8]。使用捕食者的浸泡液作为捕食者信息素的方法是文献中提到常用的方法。

一些研究发现,猎物对来自不同种类捕食者的捕食信息素的反应有所不同^[12,19],提示不同种类的捕食者产生的捕食信息素不尽相同。然而,不同来源的捕食信息素可能引发类似的效果。例如,研究发现,包括同类在内的多种水生生物释放的信息素都能引起小龙虾(*Orconectes virilis*)的捕食规避反应^[20]。目前已知源自舟形虫(*Lembadion* sp.)的一种分子量约为 31500 Da 的蛋白类物质能够引发纤毛虫产生反捕食行为反应^[21];同时,源自直口涡虫(*Stenostomum* sp.)的另一种分子量约为 17500 Da 的蛋白质也能够引发纤毛虫产生类似的反捕食行为反应^[22]。

不同猎物对源自同一种捕食者的信息素的反应可能不同,提示捕食者可能分泌出针对不同种猎物的信息素^[23]。捕食者的食物成分也能影响猎物对其产生的捕食信息素的反应^[3,8,24]。Rosell 等人发现斑鲮鱼对以斑鲮鱼为食的水貂的粪便有明显的反捕食行为反应,而对以鸡肉为食的水貂粪便产生的反应不明显^[8]。Chivers 等人研究了梭鱼捕食信息素对蜻蜓(*Enallagma* spp.)幼虫行为的影响,发现以蜻蜓幼虫和黑头呆鱼(*Pimephales promelas*)为饵料的梭鱼(*Esox lucius*)产生的捕食信息素可以使蜻蜓幼虫的活动性降低,而以粉虫(*Tenebrio molitor*)为饵料的梭鱼产生的信息素不具有这种影响效果^[24]。类似的试验结果提示捕食信息素的效果与捕食者和猎物的物种、捕食者的食物成分等因素有密切联系,同时证明了捕食信息素来源和本质的复杂性。

Hazlett 认为捕食信息素可能为来自尿液或者是腮部释放出的氨类物质^[20],Wisenden 等人的研究结果支持这一观点^[25]。水蚤类生物规避多种鱼类捕食的反应都类似,提示针对水蚤类生物的这种捕食信息素也可能不具有来源特异性^[26-27]。von Elert 等人的报道指出,来源于不同鱼类的捕食信息素具有极其相似的化学特征。他们认为其中的有效成份为一种可溶于水、不挥发、且对温度和 pH 值均相对稳定的低分子物质^[27]。Weber 则认为捕食信息素其实是包含多种成份的复杂混合物^[28]。最近的研究结果表明,胺基类(N-H)和烷基类(CH₃)分子可能是源自鱼类的捕食信息素的主要作用成分^[29]。

捕食信息素的效果会受到一些因素的干扰。目前的研究资料表明,捕食信息素的浓度和其所处的环境将直接影响其对猎物的效果。理论上,较高浓度的捕食信息素预示着较高水平的捕食风险,因此可以预期猎物会根据信息素的浓度或者强度来调整自身的应对策略^[30]。已有研究表明,包括蚊子(*Culex restuans*)^[31]、金鱼(*Carassius auratus*)^[32]、树蛙(*Rana sylvatica*)^[33]在内的数种水生生物会根据捕食信息素的浓度来调整自身反捕食反应的策略,产生类似浓度效应的效果。光照、温度、水质等环境因素也会对捕食信息素的稳定性产生影响,从而对其活性和效果产生影响。例如, Jacobsen 和 Stabell 的研究发现,光照条件影响滨螺(*Littorina littorea*)对捕食信息素的反应^[34]。UV-B 紫外线亦可以影响两栖

动物幼虫对捕食信息素的反应^[35]。Ferrari 等人的研究表明,树蛙(*Rana sylvatica*)产生的捕食信息素在自然条件下的活性只能维持在2h以内^[36]。Smith 等人发现,水体的pH值会影响捕食信息素的活性,同时影响猎物对捕食信息素的识别^[37]。

由于对捕食信息素性质和特征等本质问题的理解尚存在不少疑问和分歧,对其进行的定性定量分析显得非常困难,对捕食信息素在水体中信号传递过程的了解也十分有限。对捕食信息素的来源、成分和理化性质等问题的深入研究,将有助于阐明其信号传递过程并揭示其生态学作用。

2 捕食信息素对猎物的影响

捕食信息素在捕食者和猎物之间信息传递及协同进化过程中发挥着重要的生态学作用。水生环境中,水生生物通过感知捕食信息素来提前预知潜在的被捕食风险,并作出抵抗捕食反应^[4]。水生生物抵抗捕食的策略有很多。例如,通过迁移离开捕食者活跃的区域,改变体色、体型大小和形态、活动性来降低被捕食者发现的可能性,产生休眠卵以延续种群,或者通过调整生活史特征(比如繁殖期和繁殖数)来抵抗捕食^[3]。一般认为,相对于一般情况,捕食胁迫引发的抵抗捕食反应会产生额外的能量损耗,但是相对于被猎食,这是猎物可以选择的较稳妥的保存生命和延续种群的应对措施^[38]。

2.1 捕食信息素对猎物行为的影响

捕食规避反应是猎物在遭遇捕食者的时候做出的一种本能反应。不同种类生物抵抗捕食的行为反应略有差异,通常的行为反应主要包括逃离危险区域、降低活动性以及遮蔽处躲避。研究发现,包括浮游甲壳动物^[39]、腹足动物^[40]、鱼类^[41]和两栖类的蝌蚪^[42]在内的不少种类水生生物能够在检测到捕食信息素时做出捕食规避反应。

捕食信息素可以刺激浮游生物产生逃离^[40]行为,同时可以影响浮游生物的水平或垂直迁移^[44]、趋光反应^[45]等行为。例如,和正常培养的水蚤相比,培养在孔雀鱼(*Poecilia reticulata*)浸泡液中的大型蚤(*Daphnia magna*)对捕食行为更警觉、游速更快^[46]。浮游动物趋光反应或者垂直迁移在通常情况下也会产生,但是有证据表明捕食信息素可以影响这类行为^[15]。例如, van Gool 和 Ringelberg 研究

了捕食信息素对水蚤(*Daphnia galeata*)趋光运动的影响,发现鱼类浸泡液可以显著影响水蚤正常的趋光运动^[16]。捕食信息素甚至可以诱导垂直迁移运动: Neill 发现,幽蚊(*Chaoborus*)浸泡液迅速引发桡脚类动物的垂直迁移游动,而这种垂直游动方式在这类动物身上不常发生^[17]。

鱼类在捕食信息素的刺激下可能产生的行为反应包括降低活动性^[47]、迅速逃离或躲避^[48]、聚集^[49]等。Rosell 等研究发现斑鲮鱼(*Salmo trutta*)会避免游向含有水貂(*Neovision vison*)粪便的水域^[8]。Scheurer 等观察了源自花羔红点鲑(*Salvelinus malma*)浸泡液的信息素对虹鳟(*Oncorhynchus mykiss*)行为的影响,发现捕食信息素对虹鳟在低水层的滞留时间和活动性有显著的影响^[41]。Martin 等发现白斑狗鱼(*Esox lucius*)产生的捕食信息素会使湖拟鲤(*Rutilus rutilus*)往开阔水域游动,而鲈鱼(*Perca fluviatilis*)的捕食信息素会使湖拟鲤躲避于结构复杂的栖息地^[48]。

捕食信息素影响猎物行为方式的情况在其他水生生物身上也能被观察到。Hein 和 Crowl 发现淡水虾(*Atya lanipes*)倾向于远离含有鱼类(*Gobiomorus dormitor*和*Agonostomus monticola*)的捕食信息素的水域^[50]。Epp 和 Gabor 发现捕食者浸泡液显著降低蝶螺(*Eurycea nana*)的活动性^[42]。变形虫(*Amoeba proteus*)分泌的生长激素可以在很短的时间内引发其猎物——纤毛虫(*Euplotes* sp.)的行为反应^[22]。总体上,猎物在捕食信息素刺激下的行为反应被认为是猎物抵御捕食的一种响应方式,有利于提高存活率^[51-52]。

2.2 捕食信息素对猎物形态的影响

捕食信息素的刺激可以引发猎物外表形态的变化。猎物可以根据捕食风险调整自身能量储存分布,而将更多的能量用于调整表型特征^[3]。这种形态上的适应可以降低被捕食的风险。已有的研究表明,水藻^[53-54]、原生生物^[19,55]、轮虫^[56]、浮游甲壳动物^[57]、腹足动物^[58]、水生昆虫^[59]、鱼类^[60]、两栖动物^[61]等多种水生生物均会对捕食信息素产生形态上的响应。

研究发现,水蚤浸泡液中含有的信息素可以诱发绿藻(*Scenedesmus subspicatus*)产生特殊的四细胞到八细胞连体的形态结构,同时在细胞表面长出更

长的针刺^[62]。这种多细胞连体结构增加了水蚤进食绿藻细胞的难度,被认为是绿藻面对捕食压力的一种应对策略^[62]。Lampert 等人证实了这一结果,同时发现水蚤更倾向于进食细胞表面没有针刺绿藻^[63]。Verschoor 等人发现除了水蚤产生的捕食信息素之外,轮虫(*Brachionus calyciflorus*)产生的捕食信息素也可以刺激绿藻产生多细胞连体结构,同时信息素的浓度对这种连体结构有影响^[64]。

蚤状蚤(*Daphnia pulex*)和幽蚊(*Chaoborus*)幼虫是研究捕食信息素引发形态变化的一对模式生物。源自幽蚊幼虫的信息素可以引发蚤状蚤在头颈部生成一种颈针(neck teeth),这种形态上的变化可以大大降低蚤状蚤被幽蚊幼虫捕食的风险^[38, 65]。水蚤在捕食信息素刺激下产生的类似形态还有尾刺(tail spines)、头盔(helmets)、头冠(crests)等。其他水生生物也可以对捕食信息素产生类似的形态上的响应。例如,在含有欧洲鲤(*Tinca tinca*)信息素的环境中,萝卜螺(*Radix balthica*)的外壳会倾向于朝宽扁方向生长,使欧洲鲤不喜以其为食^[58]。

目前的资料显示,捕食者的种类及其食物成分在一定程度上会影响其产生的捕食信息素对猎物形态的影响。例如,Hoverman 等人研究发现,红螺(*Helisoma trivolvis*)对不同种类捕食者的浸泡液产生不同形式的形态反应^[12]。Stabell 等人研究发现,喂食了蚯蚓的鱼类的浸泡液对水蚤的形态没有明显影响,而喂食了水蚤的鱼类产生的捕食信息素可以明显改变水蚤的形态^[66]。Fässler 和 Kaiser 也得发现了类似的现象:他们给螃蟹喂食了不同的饵料,发现喂食了贝类的螃蟹产生的捕食信息素对紫贻贝(*Mytilus edulis*)形态的影响最大^[67]。猎物生长的不同阶段对捕食信息素的形态响应也不同。Hoverman 和 Relyea 将红螺(*Helisoma trivolvis*)饲养于含有负子蝾(*Belostoma flumineum*)的水体中,发现负子蝾产生的化学信号对于不同发育阶段红螺的外壳生长有不同程度的影响^[68]。

2.3 捕食信息素对猎物生活史特征的影响

已知捕食信息素能够引发软体动物^[69]、浮游甲壳动物^[70]、两栖动物^[71]、鱼类^[72]等多种水生生物生活史特征改变。通过改变发育和繁殖策略,猎物可以降低在繁殖前被捕食的几率。对生活史的研究主要集中在研究捕食信息素对水生生物变态发育过程

和繁殖策略的影响上,主要以水蚤和蝌蚪为模式生物。针对水蚤的研究发现,捕食信息素刺激引发水蚤繁殖期提前、繁殖期体型变小、后代体型变小和数量增加^[73]。捕食信息素刺激使水蚤发育迟缓甚至滞育休眠^[74]。通常认为休眠状态是生物在生存环境进一步恶化之前根据已有的预警信息作出的反应,是生物应对恶劣环境条件的一种临时适应措施^[75]。对两栖类的研究发现,某些两栖类通过检测捕食信息素而调整胚胎发育时间,以减低被捕食的风险。例如,在扁虫(*Phagocotus gracilis*)信息素存在的情况下,蝶螈(*Ambystoma barbouri*)胚胎的孵化时间延长以降低幼仔被捕食的风险^[76]。Johnson 等人的研究发现,以蛙卵为食的螯虾(*Procambarus nigrocinctus*)的释放的信息素能刺激缩短豹蚊蛙(*Rana sphenoccephala*)蛙卵的孵化时间,而以蝌蚪为食的蜻蜓(*Anax junius*)幼虫产生的信息素的作用相反,其延长了蛙卵的孵化时间^[77]。

水生生物面临捕食胁迫时作出的行为、形态和生活史等方面特征的响应是互相关联的。例如,水蚤在源自鱼类的捕食信息素刺激下会产生防御性的尾刺(spines),而这种形态变化所产生的能量消耗会明显缩短水蚤的寿命并影响其繁殖策略^[78]。其他研究发现,水生生物应对捕食信息素的防御策略对自身的能量摄入和存储等方面均有显著的负面影响^[79-80]。这进一步验证了水生生物的这些规避捕食反应是对捕食胁迫的妥协和让步,以消耗能量的代价换取生命和种群的延续。需要注意的是,只有在实际收益(降低被捕食的风险)大于付出(能量消耗)的情况下,生物体才会对捕食信息素作出响应,因此,在实际研究中选取合适的指标才能观察到捕食信息素的效果^[81]。

3 捕食信息素干扰污染物毒性

对捕食信息素干扰污染物毒性的早期研究发现,捕食信息素可以干扰杀虫剂对水蚤类生物的毒性。Hanazato 和 Dodson 研究了在幽蚊(*Chaoborus americanus*)幼虫存在的情况下,蚤状蚤(*D. pulex*)对杀虫剂甲萘威(carbaryl)的毒性反应,发现幽蚊幼虫产生的化学信号可以与杀虫剂发生交互作用,干扰杀虫剂对水蚤的生长和发育毒性^[82-83]。Barry^[84-87]和 Rose 等^[9]也做了类似的研究,发现捕食者浸泡液

中的信息素可以与杀虫剂发生交互作用而影响水蚤类生物的形态和生活史特征。随后,Relyea以蝌蚪为研究对象研究了捕食信息素对杀虫剂毒性的干扰,发现红点蝾螈(*Notophthalmus viridescens*)浸泡液中的信息素可以增强某些杀虫剂的致死毒性(最大可增强46倍)^[13]。陆续有研究人员研究了捕食信息素对包括农药、金属、化工产品在内的多种污染物的毒性干扰,并发现捕食信息素可以影响多种污染物对水生生物的致死、生长和发育毒性^[18,88-91]。

捕食信息素对污染物毒性的干扰可能受到捕食信息素来源和种类、污染物的浓度、以及猎物的种类等多方面因素的影响。例如,Campero等人发现太阳鱼(*Lepomis gibbosus*)产生的信息素可以显著增强阿特拉津(Atrazine)对豆娘(*Coenagrion puella*)幼虫食物同化效率的毒性,而对西维因(Carbaryl)这方面毒性的影响不明显^[92]。这一结果提示交互作用的形式可能与农药的种类或者作用机制有关。Qin等人提出污染物的暴露浓度和暴露时间也可能会对捕食信息素干扰污染物毒性的结果产生影响^[14]。

捕食信息素通过何种方式干扰污染物对水生生物的毒性尚不明了。有研究者猜测捕食信息素可能通过物理结合的方式与污染物结合,改变污染物的性质或者生物有效性,从而影响其污染物的毒性;或者通过影响猎物的进食率而影响猎物的能量摄入,最终影响猎物对污染物的解毒或者修复过程^[9]。

4 总结和展望

水生环境中,猎物和捕食者之间的化学信号传递十分普遍。捕食信息素在猎物-捕食者之间间接交互作用的信息传递过程中发挥着重要的生态学作用。虽然目前对其理化性质和分子特征等方面的问题尚存在不少疑问和争议,捕食信息素的存在已经是一个不争的事实。捕食信息素可以影响猎物的行为、形态、以及生活史等多方面的特征,提示猎物可以根据捕食信息素提供的信息来调整自身抵抗捕食的策略,以降低被捕食的风险。捕食信息素在某些情况下可以影响污染物对水生生物的毒性,在一定程度上增加了水生环境污染生态风险评估的不确定性。

我国学者对生物信息素的关注日益增加,在生物间的化学信息联系方面做了不少相关的研

究^[93-94]。在捕食信息素对猎物的影响方面也开展了不少重要的工作^[95-97]。例如,中国科学院水生生物研究所谢平的团队研究了鱼类精液中的信息素对隆线蚤(*Daphnia carinata*)的影响,发现鱼类精液中的化学信号可以影响隆线蚤的生活史特征,而且这种反应具有剂量效应^[95]。中国科学院南海海洋研究所的柯志新和黄良民综述了捕食者释放的化学信息素对溞类的的影响并探讨了其形成机制和生态意义^[95]。

捕食信息素对水生生物的影响已经受到广泛的关注,但是这一研究领域尚存在不少困难和疑点。其中的首要问题是捕食信息素的确切理化信息和结构特征尚未明确。大多数研究者使用养殖过捕食者的水样作为信息素处理,而制备捕食信息素过程中的诸多参数也没有统一的标准,增加了研究结果的不确定性。鉴于捕食信息素在水生生态系统生物间信息交流的重要作用,加强以下几个方面研究将有助于对水生环境捕食信息素的进一步理解:(1)对捕食信息素理化性质和分子特征的研究。对捕食信息素理化性质和分子特征的了解将有助于对其进行定性和定量,从而能在研究中设计更合理而有意义的试验。(2)对捕食信息素受体、信号识别和传递途径的分子机制研究。这方面的研究将有助于了解捕食信息素的作用机制。加强对捕食信息素的研究,将为解析水生环境中捕食者和猎物的生态关系提供新依据。

References:

- [1] Schoepner N M, Relyea R A. Interpreting the smells of predation: how alarm cues and kairomones induce different prey defences. *Functional Ecology*, 2009, 23(6): 1114-1121.
- [2] Karlson P, Lüscher M. 'Pheromones': a new term for a class of biologically active substances. *Nature*, 1959, 183(4653): 55-56.
- [3] Ferrari M C O, Wisenden B D, Chivers D P. Chemical ecology of predator-prey interactions in aquatic ecosystems: a review and prospectus. *Canadian Journal of Zoology*, 2010, 88(7): 698-724.
- [4] Brönmark C, Hansson L A. *Chemical Ecology in Aquatic Systems*. Oxford: Oxford University Press, 2012: 1-22.
- [5] Kiesecker J M, Chivers D P, Marco A, Quilchano C, Anderson M T, Blaustein A R. Identification of a disturbance signal in larval red-legged frogs, *Rana aurora*. *Animal Behavior*, 1999, 57(6): 1295-1300.
- [6] Wisenden B D. Chemically-mediated strategies to counter predation // Collin S P, Marshall N J, eds. *Sensory Processing in the Aquatic Environment*. New York: Springer-Verlag, 2003:

- 236–251.
- [7] Ślusarczyk M , Rygielska E. Fish faeces as the primary source of chemical cues inducing fish avoidance diapause in *Daphnia magna*. *Hydrobiologia* , 2004 , 526(1) : 231–234.
- [8] Rosell F , Holtan L B , Thorsen J G , Heggenes J. Predator-naïve brown trout (*Salmo trutta*) show antipredator behaviours to scent from an introduced piscivorous mammalian predator fed conspecifics. *Ethology* , 2013 , 119(4) : 303–308.
- [9] Rose R M , Warne M S , Lim R P. The presence of chemicals exuded by fish affects the life-history response of *Ceriodaphnia* CF. *dubia* to chemicals with different mechanisms of action. *Environmental Toxicology and Chemistry* , 2001 , 20 (12) : 2892–2898.
- [10] Ringelberg J , Van Gool E. Do bacteria , not fish , produce ‘fish kairomone’?. *Journal of Plankton Research* , 1998 , 20 (9) : 1847–1852.
- [11] Forward R B Jr , Rittschof D. Brine shrimp larval photoresponses involved in diel vertical migration: Activation by fish mucus and modified amino sugars. *Limnology and Oceanography* , 1999 , 44 (8) : 1904–1916.
- [12] Hoverman J T , Auld J R , Relyea R A. Putting prey back together again: integrating predator-induced behavior , morphology , and life history. *Oecologia* , 2005 , 144(3) : 481–491.
- [13] Relyea R A. Predator cues and pesticides: A double dose of danger for amphibians. *Journal of Applied Ecology* , 2003 , 13 (6) : 1515–1521.
- [14] Qin G Q , Presley S M , Anderson T A , Gao W M , Maul J D. Effects of predator cues on pesticide toxicity: Toward an understanding of the mechanism of the interaction. *Environmental Toxicology and Chemistry* , 2011 , 30(8) : 1926–1934.
- [15] Ringelberg J. Enhancement of the phototactic reaction in *Daphnia hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). *Journal of Plankton Research* , 1991 , 13(1) : 17–25.
- [16] van Gool E , Ringelberg J. Light-induced migration behaviour of *Daphnia* modified by food and predator kairomones. *Animal Behavior* , 1998 , 56(3) : 741–747.
- [17] Neill W E. Induced vertical migration in copepods as a defence against invertebrate predation. *Nature* , 1990 , 345 (6275) : 524–526.
- [18] Maul J D , Farris J L , Lydy M J. Interaction of chemical cues from fish tissues and organophosphorous pesticides on *Ceriodaphnia dubia* survival. *Environmental Pollution* , 2006 , 141(1) : 90–97.
- [19] Wicklow B J. Signal-induced defensive phenotypic changes in ciliated protists: morphological and ecological implications for predator and prey. *Journal of Eukaryotic Microbiology* , 1997 , 44 (3) : 176–188.
- [20] Hazlett B A. Source and nature of disturbance-chemical system in crayfish. *Journal of Chemical Ecology* , 1990 , 16(7) : 2263–2275.
- [21] Kusch J , Heckmann K. Isolation of the *Lembdion*-factor , a morphogenetically active signal , that induces *Euplotes* cells to change from their ovoid form into a larger lateral winged morph. *Developmental Genetics* , 1992 , 13(3) : 241–246.
- [22] Kusch J. Predator-induced morphological changes in *Euplotes* (Ciliata) : Isolation of the inducing substance released from *Stenostomum sphagnetorum* (Turbellaria) . *Journal of Experimental Zoology* , 1993 , 256(6) : 613–618.
- [23] Takahara T , Doi H , Kohmatsu Y , Yamaoka R. Different chemical cues originating from a shared predator induce common defense responses in two prey species. *Animal Cognition* , 2013 , 16(1) : 147–153.
- [24] Chivers D P , Wisenden B D , Smith R J F. Damselfly larvae learn to recognize predators from chemical cues in the predator’s diet. *Animal Behaviour* , 1996 , 52(2) : 315–320.
- [25] Wisenden B D , Chivers D P , Smith R J F. Early warning in the predation sequence: a disturbance pheromone in Iowa darters (*Etheostoma exile*). *Journal of Chemical Ecology* , 1995 , 21 (10) : 1469–1480.
- [26] Loose C J , von Elert E , Dawidowicz P. Chemically-induced diel vertical migration in *Daphnia*: a new bioassay for kairomones exuded by fish. *Archiv für Hydrobiologie* , 1993 , 126 (3) : 329–337.
- [27] von Elert E , Loose C J. Predator-induced diel vertical migration in *Daphnia*: enrichment and preliminary chemical characterization of a kairomone exuded by fish. *Journal of Chemical Ecology* , 1996 , 22(5) : 885–895.
- [28] Weber A. More than one ‘fish kairomone’? Perch and stickleback kairomones affect *Daphnia* life history traits differently. *Hydrobiologia* , 2003 , 498(1/3) : 143–150.
- [29] Akkas S B , Kepenek A O , Beklioglu M , Feride S. Molecular approach to the chemical characterization of fish-exuded kairomone: a fourier transform infrared spectroscopic study. *Aquatic Sciences* , 2010 , 72(1) : 71–83.
- [30] Helfman G S. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behavioral Ecology and Sociobiology* , 1989 , 24(1) : 47–58.
- [31] Ferrari M C O , Messier F , Chivers D P. Threat-sensitive learning by the larval mosquito *Culex restuans*. *Behavioral Ecology and Sociobiology* , 2008 , 62(7) : 1079–1083.
- [32] Zhao X X , Ferrari M C O , Chivers D P. Threat-sensitive learning of predator odours by a prey fish. *Behaviour* , 2006 , 143 (9) : 1103–1121.
- [33] Ferrari M C O , Brown G E , Messier F , Chivers D P. Threat-sensitive generalization of predator recognition by larval amphibians. *Behavioral Ecology and Sociobiology* , 2009 , 63(9) : 1369–1375.
- [34] Jacobsen H P , Stabell O B. Predator-induced alarm responses in the common periwinkle , *Littorina littorea*: dependence on season , light conditions , and chemical labelling of predators. *Marine Biology* , 1999 , 134(3) : 551–557.
- [35] Kats L B , Kiesecker J M , Chivers D P , Blaustein A R. Effects of UV-B radiation on anti-predator behavior in three species of amphibians. *Ethology* , 2000 , 106(10) : 921–931.
- [36] Ferrari M C O , Messier F , Chivers D P. Degradation of chemical alarm cues under natural conditions: risk assessment by larval woodfrogs. *Chemoecology* , 2007 , 17(4) : 263–266.
- [37] Smith J J , Leduc A O H C , Brown G E. Chemically mediated learning in juvenile rainbow trout. Does predator odour pH influence intensity and retention of acquired predator recognition?.

- Journal of Fish Biology, 2008, 72(7) : 1750–1760.
- [38] Tollrian R. *Chaoborus crystallinus* predation on *Daphnia pulex*: can induced morphological changes balance effects of body size on vulnerability?. *Oecologia*, 1995, 101(2) : 151–155.
- [39] Hembre L K, Peterson L A. Evolution of predator avoidance in a *Daphnia* population: evidence from the egg bank. *Hydrobiologia*, 2013, 700(1) : 245–255.
- [40] Dalesman S, Rundle S D, Cotton P A. Predator regime influences innate anti-predator behaviour in the freshwater gastropod *Lymnaea stagnalis*. *Freshwater Biology*, 2007, 52(11) : 2134–2140.
- [41] Scheurer J A, Berejikian B A, Thrower F P, Ammann E R, Flagg T A. Innate predator recognition and fright response in related populations of *Oncorhynchus mykiss* under different predation pressure. *Journal of Fish Biology*, 2007, 70(4) : 1057–1069.
- [42] Epp K J, Gabor C R. Innate and learned predator recognition mediated by chemical signals in *Eurycea nana*. *Ethology*, 2008, 114(6) : 607–615.
- [43] Gutierrez M F, Gagneten A M, Paggi J C. Behavioural responses of two cladocerans and two copepods exposed to fish kairomones. *Marine and Freshwater Behaviour and Physiology*, 2011, 44(5) : 289–303.
- [44] Cohen J H, Forward R B. Zooplankton diel vertical migration—a review of proximate control. *Oceanography and Marine Biology*, 2009, 47: 77–110.
- [45] de Meester L, Pijanowska J. On the trait-specificity of the response of *Daphnia* genotypes to the chemical presence of a predator // Lenz P H, Hartline D K, Purcell J E, Macmillan D L, eds. *Zooplankton: Sensory Ecology and Physiology*. Amsterdam: Gordon and Breach Publishers, 1996: 407–417.
- [46] Brewer M C, Dawidowicz P, Dodson S I. Interactive effects of fish kairomone and light on *Daphnia* escape behavior. *Journal of Plankton Research*, 1999, 21(7) : 1317–1335.
- [47] Houtman R, Dill L M. The influence of substrate color on the alarm response of tidepool sculpins (*Oligocottus maculosus*; Pisces, Cottidae). *Ethology*, 1994, 96(2) : 147–154.
- [48] Martin C W, Fodrie F J, Heck K L Jr, Mattila J. Differential habitat use and antipredator response of juvenile roach (*Rutilus rutilus*) to olfactory and visual cues from multiple predators. *Oecologia*, 2010, 162(4) : 893–902.
- [49] Waldman B. Quantitative and developmental analyses of the alarm reaction in the zebra danio, *Brachydanio rerio*. *Copeia*, 1982, 1982(1) : 1–9.
- [50] Hein C L, Crowl T A. Running the predator gauntlet: do freshwater shrimp (*Atya lanipes*) migrate above waterfalls to avoid fish predation?. *Journal of the North American Benthological Society*, 2010, 29(2) : 431–443.
- [51] Ringelberg J, van Gool E. Migrating *Daphnia* have a memory for fish kairomones. *Marine and Freshwater Behaviour and Physiology*, 1995, 26(2/4) : 249–257.
- [52] Gilbert J J, Hampton S E. Diel vertical migrations of zooplankton in a shallow, fishless pond: a possible avoidance-response cascade induced by notonectids. *Freshwater Biology*, 2001, 46(5) : 611–621.
- [53] Yang Z, Kong F X, Yang Z, Zhang M, Yu Y, Qian S Q. Benefits and costs of the grazer-induced colony formation in *Microcystis aeruginosa*. *International Journal of Limnology*, 2009, 45(3) : 203–208.
- [54] van Donk E, Ianora A, Vos M. Induced defences in marine and freshwater phytoplankton: A review. *Hydrobiologia*, 2011, 668(1) : 3–19.
- [55] Lass S, Spaak P. Chemically induced anti-predator defences in plankton: a review. *Hydrobiologia*, 2003, 491(1/3) : 221–236.
- [56] Brandl Z. Freshwater copepods and rotifers: predators and their prey. *Hydrobiologia*, 2005, 546(1) : 475–489.
- [57] Rabus M, Laforsch C. Growing large and bulky in the presence of the enemy: *Daphnia magna* gradually switches the mode of inducible morphological defences. *Functional Ecology*, 2011, 25(5) : 1137–1143.
- [58] Brönmark C, Lakowitz T, Hollander J. Predator-induced morphological plasticity across local populations of a freshwater snail. *PLoS ONE*, 2011, 6(7) : e21773.
- [59] Johansson F, Wahlström E. Induced morphological defence: evidence from whole-lake manipulation experiments. *Canadian Journal of Zoology*, 2002, 80(2) : 199–206.
- [60] Chivers D P, Zhao X X, Brown G E, Marchant T A, Ferrari M C O. Predator-induced changes in morphology of a prey fish: the effects of food level and temporal frequency of predation risk. *Evolutionary Ecology*, 2008, 22(4) : 561–574.
- [61] Gomez V I, Kehr A I. Morphological and developmental responses of anuran larvae (*Physalaemus albonotatus*) to chemical cues from the predators *Moenkhausia dichoroura* (Characiformes: Characidae) and *Belostoma elongatum* (Hemiptera: Belostomatidae). *Zoological Studies*, 2011, 50(2) : 203–210.
- [62] Hessen D O, Van Donk E. Morphological changes in *Scenedesmus* induced by substances released from *Daphnia*. *Archiv Für Hydrobiologie*, 1993, 127(2) : 129–140.
- [63] Lampert W, Rothhaupt K O, von Elert E. Chemical induction of colony formation in a green alga (*Scenedesmus acutus*) by grazers (*Daphnia*). *Limnology and Oceanography*, 1994, 39(7) : 1543–1550.
- [64] Verschoor A M, Van der Stap I, Helmsing N R, Lüring M, Van Donk E. Inducible colony formation within the *Scenedesmaceae*: adaptive responses to infochemicals from two different herbivore taxa. *Journal of Phycology*, 2004, 40(5) : 808–814.
- [65] Dodson S I, Wagner A E. Temperature affects selectivity of *Chaoborus* larvae-eating *Daphnia*. *Hydrobiologia*, 1996, 325(2) : 157–161.
- [66] Stabell O B, Ogbeto F, Primicerio R. Inducible defences in *Daphnia* depend on latent alarm signals from conspecific prey activated in predators. *Chemical Senses*, 2003, 28(2) : 141–153.
- [67] Fässler S M M, Kaiser M J. Phylogenetically mediated anti-predator responses in bivalve molluscs. *Marine Ecology Progress Series*, 2008, 363: 217–225.
- [68] Hoverman J T, Relyea R A. How flexible is phenotypic plasticity? Developmental windows for trait induction and reversal. *Ecology*, 2007, 88(3) : 693–705.
- [69] Crowl T A, Covich A P. Predator-induced life-history shifts in a

- freshwater snail. *Science*, 1990, 247(4945): 949–951.
- [70] Chakri K, Touati L, Alfarhan A H, Al-Rasheid K A S, Samraoui B. Effect of vertebrate and invertebrate kairomones on the life history of *Daphnia magna* Straus (Crustacea: Branchiopoda). *Comptes Rendus Biologies*, 2010, 333(11/12): 836–840.
- [71] Altwegg R. Predator-induced life-history plasticity under time constraints in pool frogs. *Ecology*, 2002, 83(9): 2542–2551.
- [72] Gosline A K, Rodd F H. Predator-induced plasticity in guppy (*Poecilia reticulata*) life history traits. *Aquatic Ecology*, 2008, 42(4): 693–699.
- [73] Reede T. Life history shifts in response to different levels of fish kairomones in *Daphnia*. *Journal of Plankton Research*, 1995, 17(8): 1661–1667.
- [74] Slusarczyk M. Food threshold for diapause in *Daphnia* under the threat of fish predation. *Ecology*, 2001, 82(4): 1089–1096.
- [75] Slusarczyk M. Predator-induced diapause in *Daphnia*. *Ecology*, 1995, 76(3): 1008–1013.
- [76] Sih A, Moore R D. Delayed hatching of salamander eggs in response to enhanced larval predation risk. *The American Naturalist*, 1993, 142(6): 947–960.
- [77] Johnson J B, Saenz D, Adams C K, Conner R N. The influence of predator threat on the timing of a life-history switch point: predator-induced hatching in the southern leopard frog (*Rana sphenoccephala*). *Canadian Journal of Zoology*, 2003, 81(9): 1608–1613.
- [78] Barry M J. The costs of crest induction for *Daphnia carinata*. *Oecologia*, 1994, 97(2): 278–288.
- [79] Morrison L W. Indirect effects of phorid fly parasitoids on the mechanisms of interspecific competition among ants. *Oecologia*, 1999, 121(1): 113–122.
- [80] Downes S. Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology*, 2001, 82(10): 2870–2881.
- [81] Chivers D P, Smith R J F. Chemical alarm signalling in aquatic predator-prey systems: A review and prospectus. *Ecoscience*, 1998, 5(3): 338–352.
- [82] Hanazato T, Dodson S I. Complex effects of a kairomone of *Chaoborus* and an insecticide on *Daphnia pulex*. *Journal of Plankton Research*, 1992, 14(12): 1743–1755.
- [83] Hanazato T, Dodson S I. Synergistic effects of low-oxygen concentration, predator kairomone, and a pesticide on the Cladoceran *Daphnia pulex*. *Limnology and Oceanography*, 1995, 40(4): 700–709.
- [84] Barry M J. Endosulfan-enhanced crest induction in *Daphnia longicephala*: Evidence for cholinergic innervation of kairomone receptors. *Journal of Plankton Research*, 1998, 20(7): 1219–1231.
- [85] Barry M J. The effects of a pesticide on inducible phenotypic plasticity in *Daphnia*. *Environmental Pollution*, 1999, 104(2): 217–224.
- [86] Barry M J. Effects of endosulfan on *Chaoborus*-induced life-history shifts and morphological defenses in *Daphnia pulex*. *Journal of Plankton Research*, 2000, 22(9): 1705–1718.
- [87] Barry M J. Progress toward understanding the neurophysiological basis of predator-induced morphology in *Daphnia pulex*. *Physiological and Biochemical Zoology*, 2002, 75(2): 179–186.
- [88] LaFiandra E M, Babbitt K J, Sower S A. Effects of atrazine on anuran development are altered by the presence of a nonlethal predator. *Journal of Toxicology and Environmental Health, Part A*, 2008, 71(8): 505–511.
- [89] Relyea R A, Edwards E. What doesn't kill you makes you sluggish: how sublethal pesticides alter predator-prey interactions. *Copeia*, 2010, (4): 558–567.
- [90] Giri A, Yadav S S, Giri S, Sharma G D. Effect of predator stress and malathion on tadpoles of Indian skittering frog. *Aquatic Toxicology*, 2012, 106–107: 157–163.
- [91] Kerby J L, Hart A J, Storfer A. Combined effects of virus, pesticide, and predator cue on the larval tiger salamander (*Ambystoma tigrinum*). *Ecohealth*, 2011, 8(1): 46–54.
- [92] Campero M, Slos S, Ollevier F, Stoks R. Sublethal pesticide concentrations and predation jointly shape life history: Behavioral and physiological mechanisms. *Ecological Applications*, 2007, 17(7): 2111–2122.
- [93] Meng X Z. Advances in the research and application of insect pheromones in China. *Entomological Knowledge*, 2000, 37(2): 75–84.
- [94] Li S W. *Ecological Biochemistry*. Beijing: Peking University Press, 2001: 122–145.
- [95] Ke Z X, Xie P, Huang L M, Xu J. Predation risk perception in *Daphnia carinata* induced by the milt of common carp (*Cyprinus carpio*). *Journal of Freshwater Ecology*, 2010, 25(3): 467–473.
- [96] Wang S B, Xie P, Zhu L X. The responses of *Moina micrura* in aquaculture lakes to high concentrations of chemical cues from planktivorous fish: a life table demographic study. *Acta Hydrobiologica Sinica*, 2008, 32(6): 868–873.
- [97] Ke Z X, Huang L M. Advance in the study on the anti-predator phenotypic plasticity of *Daphnia*. *Journal of Lake Sciences*, 2009, 21(6): 758–767.

参考文献:

- [93] 孟宪佐. 我国昆虫信息素研究与应用的进展. *昆虫知识*, 2000, 37(2): 75–84.
- [94] 李绍文. *生态生物化学*. 北京: 北京大学出版社, 2001: 122–145.
- [96] 王松波, 谢平, 朱龙喜. 养殖水体中的微型裸腹溥对高浓度鱼类化学信息素的反应: 以生命表研究为例. *水生生物学报*, 2008, 32(6): 868–873.
- [97] 柯志新, 黄良民. 溥类 (*Daphnia*) 反捕食的表型可塑性及其研究进展. *湖泊科学*, 2009, 21(6): 758–767.