

紫外辐射对鱼类及水生无脊椎动物影响的研究进展

孔清^{1,2}, 宋宏策¹, 魏磊¹, 谢超伊¹, 张钰焯¹, 董美云¹, 高雁³, 王晓通¹

(1. 鲁东大学 农学院, 山东 烟台 264025; 2. 烟台市牟平区渔业技术推广站, 山东 烟台 261499; 3. 烟台市海洋经济研究院, 山东 烟台 264003)

摘要: 全球性的气候变化严重地威胁着自然生态环境间的平衡。在影响生态系统功能的诸多因素中, 太阳紫外辐射的增强逐渐成为最受关注的全球性环境问题之一。太阳紫外辐射对地球生物的生命过程有着举足轻重的影响。生物体一旦吸收了高能量的紫外辐射, 则可对其各种生理过程产生影响, 打破内稳态, 尤其是紫外辐射对 DNA 的损伤作用, 是诱导一系列生物效应的主要原因。本文综述了近年来与鱼类及水生无脊椎动物有关的紫外辐射研究。从紫外辐射对生物不同发育时期的影响、生物对紫外线响应方式、紫外辐射与其他因素复合影响三个层面进行总结。通过总结紫外辐射对鱼类及水生无脊椎动物的影响, 可为预测紫外辐射在水生生态系统中的作用提供助力, 为海洋生物对环境变化的生理响应研究提供参考。

关键词: 太阳紫外线辐射; UVA; UVB; 鱼类; 水生无脊椎动物

中图分类号: S917 **文献标识码:** A **文章编号:** 1000-3096(2024)2-0115-14

DOI: 10.11759/hyxx20220930001

太阳紫外辐射(solar ultraviolet radiation, UVR)是自然界中一种环境威胁和生物压力源^[1-2]。随着地球气候环境的持续变化, 导致到达地球表面的 UVR 不断增强, 且在未来一段时间内将持续上升, 这将对生物造成长久的潜在干扰。UVR 增强可严重影响生物的行为活动及多种生理过程^[3]。

依据波长的不同, UVR 分为 3 种: 长波紫外线(UVA, 400~320 nm)、中波紫外线(UVB, 320~280 nm)和短波紫外线(UVC, 280~100 nm)。其中, UVC 会被平流层臭氧吸收, 无法到达地球表面。而 UVA 和 UVB 可透过臭氧层, 到达地球表面, 对生物造成影响。相较于 UVA, UVB 辐射强度更高, 与生物关系最为密切并且易对生物产生不良影响^[4]。各种紫外辐射均可产生较高的能量, 一定剂量的紫外辐射被生物吸收后, 可对各种生命过程产生一定影响。例如, 紫外辐射增强会抑制植物的光合能力, 减少其生物质产量; 还可影响动物的行为活动, 损伤其 DNA 和蛋白质, 造成免疫功能障碍等^[5]。当前, 紫外辐射对水生动物的影响研究主要在鱼类、棘皮动物、软体动物以及甲壳动物中开展。统计分析显示, 随着紫外辐射的不断增强, 海洋动物的死亡率会随之迅速上升。因此, 未来不断增强的太阳紫外辐射可能会成为海洋生物生存的一大重要威胁^[6]。

1 对生长发育的影响

1.1 配子, 受精及胚胎时期

大多数鱼类及水生无脊椎动物的配子均是排放到海水中, 并在海水中完成受精过程。这种生殖方式很大

收稿日期: 2022-09-30; 修回日期: 2022-12-15

基金项目: 国家自然科学基金项目(41906088, 42076088); 山东省高等学校“青创科技计划”(2019KJF004); 山东省现代农业产业技术体系项目贝类产业创新团队(SDAIT-14-03); 山东省自然科学基金项目(ZR2022QC233, ZR2023QC107); 山东省重点研发计划(农业良种工程)项目(2022LZGC015); 烟台市级以上领军人才专项配套经费资助(202203); 山东省泰山学者专项基金(tsqn201812094)

[Foundation: National Natural Science Foundation of China, Nos. 41906088, 42076088; Plan of Excellent Youth Innovation Team of Colleges and Universities in Shandong Province, China, No. 2019KJF004; Modern Agricultural Industry Technology System of Shandong Province, China, No. SDAIT-14-03; Natural Science Foundation of Shandong Province, Nos. ZR2022QC233, ZR2023QC107; Key Research and Development Program of Shandong, No. 2022LZGC015; Special Supporting Funds for Leading Talents above Provincial Level in Yantai City, No. 202203; the Special Funds for Taishan Scholars Project of Shandong Province, China, No. tsqn201812094]

作者简介: 孔清(1993—), 女, 汉族, 山东烟台人, 硕士研究生, 主要从事海洋生物学研究, E-mail: kongqing23@126.com; 宋宏策(1997—), 共同第一作者, 男, 汉族, 山东聊城人, 硕士研究生, 主要从事海洋生物学研究, E-mail: songhongce@126.com; 魏磊(1984—), 通信作者, 男, 汉族, 黑龙江齐齐哈尔人, 副教授, 主要从事贝类逆境生物学研究, E-mail: lei819@126.com; 高雁(1987—), 共同通信作者, 女, 汉族, 山东烟台人, 工程师, 主要从事水产养殖研究, E-mail: 455386466@qq.com

可能会使动物的配子直接暴露在紫外辐射下。因此, 鱼类及水生无脊椎动物的精子、卵子及胚胎, 常作为生物体受紫外辐射影响研究的焦点对象(表 1)。总结以往的

研究显示, 紫外辐射可损伤配子活力, 增加受精过程的难度, 导致动物受精率降低, 进而对生物体的配子活力、受精效率及胚胎发育产生较大影响。

表 1 紫外辐射对鱼类及水生无脊椎动物配子, 受精及胚胎时期的影响研究

Tab. 1 Effect of ultraviolet radiation on gametes, fertilization, and the embryonic stage in fish and aquatic invertebrates

物种	暴露时间	紫外线暴露类型及强度	受影响生物过程	影响情况	参考文献
<i>Petromyzon marinus</i>	0, 6, 12 s	UV	DNA 断裂片段	↑	[7]
<i>Oncorhynchus mykiss</i>	0, 5, 15 min	UVA, 2 075 mW/cm ²	DNA 断裂片段	↑	[8]
<i>Danio rerio</i>	30, 40 s	UV	畸形率	↑	[9]
<i>Gasterosteus aculeatus</i>	8 h/d	UVA	精子运动速度孵化率	↓	[10]
<i>Carassius auratus</i>	10~70 s	UV	畸形率	↑	[11]
<i>Carassius auratus</i>	0~1 200 s	UV	孵化率	↓	[12]
<i>Crassostrea gigas</i>	60, 70, 80, 90, 120, 150, 180 s	UVC(254 nm)	畸形率	↑	[12]
<i>Chlamys farreri</i>	0, 10, 20, 30, 40, 50, 60, 70, 80, 120 s	UVC(254 nm), 800 μW/cm ²	受精率	↓	[13]
<i>Dreissena polymorpha</i>	0, 2.5, 5, 7.5 min	UVB(290~320 nm), 263 μW/cm ²	精子顶体、鞭毛结构完整性	↓	[14]
<i>Thunnus albacares</i> , <i>Lutjanus campechanus</i> , <i>Rachycentron canadum</i>	10~18.5 hpf	UVA(320~400 nm)	受精率	↓	[15]
<i>Oryzias latipes</i>	15, 30, 60 min	UVA(366 nm), 2 450 μW/cm ²	到达减数分裂时期时间	↑	[15]
<i>Plagopterus argentissimus</i>	14.5 h/d	UVB	胚胎浮力	↓	[18]
<i>Gadus morhua</i>	10 d	UVB	耗氧率	↑	[18]
<i>Macrobrachium olfersi</i>	48 h	UVB, 310 mW/cm ²	能量消耗	↑	[19]
<i>Esox lucius</i>	3, 6 h	UVB	孵化率	↓	[19]
<i>Danio rerio</i>	60, 120, 180, 240 min	UVR	畸形率	↑	[19]
<i>Echinometra lucunter</i>	0~60 min	UVA UVB	死亡率	↑	[20]
<i>Macrobrachium olfersii</i>	30 min	UVB, 310 mW/cm ²	死亡率	↑	[21]
			环丁烷嘧啶二聚体浓度	↑	[22]
			<i>hsp70</i> 基因表达	↑	[23]
			<i>p53</i> 基因表达	↑	[24]
			ABC1 蛋白水平	↓	[25]
			ABCC1 蛋白水平	↓	[25]
			活性氧生成量	↑	[26]
			DRP-1 蛋白水平	↑	[26]

注: UVA 为长波紫外线; UVB 为中波紫外线; UVC 为短波紫外线; ↓表示紫外线暴露引起相应生物过程的下调, ↑表示紫外线暴露引起相应生物过程的上调

在紫外辐射对鱼类配子的影响研究发现, 精子损伤, 生殖能力下降是多数鱼类受到紫外辐射后的主要

表现。利用单细胞凝胶电泳实验(SCGE)观察紫外线照射后鱼类精子的 DNA 损伤情况, 发现海七鳃鳗

(*Petromyzon marinus*)及虹鳟(*Oncorhynchus mykiss*)的精子 DNA 片段显著增加,发生了 DNA 断裂的损伤情况^[7-8]。同时,在斑马鱼(*Danio rerio*)精子的研究中发现 UVB 对精子的损伤进一步导致孵化幼体畸形率的上升现象^[9]。紫外线还可导致三刺鱼(*Gasterosteus aculeatus*)精子运动速度显著下降,降低精子竞争能力,并进一步降低了交配后的繁殖成功率^[10]。另外,紫外辐射可以促使金鱼(*Carassius auratus*)提前产卵,缩短受精卵孵化时间,从而提高孵化率,但随着剂量的增高,孵化率急剧下降,仔鱼畸形率升高,产生致畸效应^[11-12]。在水生无脊椎动物中,其精卵亦会受到紫外辐射的影响。例如:长牡蛎(*Crassostrea gigas*)及栉孔扇贝(*Chlamys farreri*)的精子经过紫外线处理后,其顶体和鞭毛结构受损严重,随着紫外线暴露时间的延长,顶体损伤程度逐渐加重,鞭毛逐渐脱落,从而在一定程度上造成了受精率的逐渐降低^[13-14]。高剂量的紫外线暴露可造成斑马贻贝(*Dreissena polymorpha*)受精率降低,卵子减数分裂时期延迟或停止,从而影响了受精过程^[15]。

紫外辐射对鱼类早期胚胎的影响研究主要从形态学鉴定及分子表达变化等角度入手。相关研究表明紫外辐射可引起动物体早期胚胎的发育延迟,产生致畸效应,甚至造成胚胎死亡^[16]。在鱼类中,随着紫外线暴露时间的延长,早期胚胎的孵化率和出眼率会随之降低,胚胎畸形率会逐渐升高,从而表现出对胚胎发育的强烈损伤效应^[17]。黄鳍金枪鱼(*Thunnus albacares*)、西大西洋鲷(*Lutjanus campechanus*)和军曹鱼(*Rachycentron canadum*)胚胎暴露于环境相关剂量的

紫外线后,显示出胚胎浮力的丧失、耗氧率和能量消耗的增加,进而可能造成胚胎沉降至底层水体死亡^[18]。当辐射剂量达到一定阈值后,则会造成胚胎死亡率的显著升高,如青鳉(*Oryzias latipes*)、伤鳍鱼(*Plagopterus argentissimus*)及大西洋鳕鱼(*Gadus morhua*)的高剂量紫外线暴露^[19-21]。

紫外辐射还可对鱼类及水生无脊椎动物胚胎产生分子层面的影响,在奥氏沼虾(*Macrobrachium olfersi*)、斑马鱼(*D. rerio*)、白斑狗鱼(*Esox lucius*)及梅氏长海胆(*Echinometra lucunter*)的胚胎紫外线暴露研究中,紫外线会通过激活转录因子 *P53* 及热休克蛋白 *Hsp70* 的基因表达,抑制 ABC 转运蛋白(*ABCB1*、*ABCC1*)的活化等分子手段,诱导细胞凋亡甚至细胞死亡,进而降低胚胎发育速度^[22-25]。另外,线粒体可作为显示紫外辐射对胚胎损伤的重要指示性细胞器。例如:在紫外线处理奥氏沼虾(*M. olfersi*)胚胎细胞 30 min 后,发现线粒体中的嵴减少,膜破裂,同时线粒体分裂相关蛋白(*DRP-1*)表达水平显著上升,表明线粒体形态结构被破坏,从而造成了胚胎细胞存活率的下降^[26]。

1.2 幼体时期

由于动物体幼体阶段的形态结构、生理功能及生活习性差异较大,不同时期的幼体对紫外线的敏感性存在一定差异。紫外辐射不仅能影响动物幼体的关键生理过程,而且还会进一步降低存活率,提高死亡率(表 2)。

表 2 紫外线辐射对鱼类及水生无脊椎动物幼体时期的影响研究

Tab. 2 Effect of ultraviolet radiation on the larval stage of fish and aquatic invertebrates

物种	暴露时间	紫外线暴露类型及强度	受影响生物过程	影响情况	参考文献
<i>Plagopterus argentissimus</i>	14.5 h	UVB, 0.15 W/m ²	死亡率	↑	[20]
<i>Oncorhynchus mykiss</i>	15 min/d	UVB	脊椎畸形率	↑	[28]
<i>Danio rerio</i>	60, 120, 150, 180, 240 min	UVR	骨粘连蛋白基因表达	↑	[29]
<i>Solea senegalensis</i>	180, 240, 330 min/d	UV, 1.15 W/m ² , 1.62 W/m ²	生长率	↓	[30]
			游泳行为活动	↓	
			变态畸形率	↑	
<i>Labeo rohita</i>	24 d	UVB(80 μm/cm ²)	生长率	↓	[31]
<i>Salmo trutta caspius</i>	15 min/d	UV	死亡率	↑	[33]
<i>Cyprinus carpio</i>	42 d	UVB	血浆总蛋白浓度	↓	[34]
<i>Oncorhynchus mykiss</i>					

续表

物种	暴露时间	紫外线暴露类型及强度	受影响生物过程	影响情况	参考文献
<i>Odontesthes argentinensis</i>	1~120 min	UVA, UVB	活性氧生成量	↑	[35]
			脂质过氧化物水平	↑	
			环丁烷嘧啶二聚体浓度	↑	
<i>Catla catla</i>	21 d	UVB, 80 $\mu\text{W}/\text{cm}^2$	硫代巴比妥酸反应物生成量	↑	[36]
<i>Gadus morhua</i>	10 d	UVB	超氧化物歧化酶活性	↑	[37]
			超氧化物歧化酶活性	↑	
<i>Cyrtograpsus altimanus</i>	120 min	UVA, 30 W/m^2 ; UVB, 0.76 W/m^2	蜕壳速度	↓	[38]
<i>Neohelice granulata</i>	30 min	UVA, 1.39 mW/cm^2 ; UVB, 1.195 mW/cm^2	脂质过氧化物水平	↑	[39]
			过氧化氢酶活性	↑	
			超氧化物歧化酶活性	↑	
<i>Litopenaeus vannamei</i>	12 h	UVA, UVB, 50 mW/cm^2	谷胱甘肽过氧化物酶活性	↑	[40]
			过氧化氢酶活性	↑	
<i>Pocillopora damicornis</i>	6 h	UVA(395 nm), UVB(320 nm)	存活率	↓	[41]
			变态率	↓	
			沉降率	↓	
<i>Seriatopora caliendrum</i>	5 min	UVA(320~395 nm)	变态率	↓	[42]
			沉降率	↓	
<i>Siphonaria australis</i>	120 h	UVB(290~315 nm)	存活率	↓	[43]

注: UVA 为长波紫外线; UVB 为中波紫外线; UVC 为短波紫外线; ↓表示紫外线暴露引起相应生物过程的下调, ↑表示紫外线暴露引起相应生物过程的上调

紫外辐射可导致鱼类幼体的发育异常并抑制其生长^[27]。例如, 暴露于低剂量紫外辐射的虹鳟(*O. mykiss*)幼体脊椎畸形现象显著增加^[28]。紫外辐射可诱导斑马鱼(*D. rerio*)幼体骨粘连蛋白(osteonectin)异常上调, 进而导致骨骼早期发育异常^[29]。塞内加尔鲷(*Solea senegalensis*)、露斯塔野鲮(*Labeo rohita*)幼体在紫外线暴露后, 出现了生长减缓, 游泳活动减少, 变态畸形等现象^[30-31]。死亡率的增加是水生生物过度暴露于紫外辐射的最严重后果^[16]。相关研究显示鱼类幼体的死亡率与紫外线强度成正相关, 随着紫外线强度的增加, 幼体死亡率会显著升高^[32]。但是, 不同的鱼类幼体对紫外线的抵抗能力存在一定差异^[20]。例如, 伤鳍鱼(*P. argentissimus*)幼体受到低水平紫外辐射(0.15 W/m^2 UVB)的短时间(14.5 h)暴露后, 即会出现较高死亡率^[20], 而暴露在较高紫外辐射(1.3 W/m^2) 9 d 的里海鳟(*Salmo trutta caspius*)幼体, 才会出现相似的死亡率水平^[33]。经紫外线照射后, 鱼类幼体还会出现免疫功能、氧化应激及黑色素沉积等生理功能的变化。鲤鱼(*Cyprinus carpio*)及虹鳟(*O. mykiss*)幼体在进行 6 周低剂量紫外线

暴露后, 发现此两种鱼的淋巴细胞数量, 吞噬细胞的呼吸暴发活性均出现了显著变化, 表明紫外线可能诱导了鱼类幼体的免疫功能的调节^[34]。牙银汉鱼(*Odontesthes argentinensis*)、卡特拉鱼(*Catla catla*)、大西洋鳕鱼(*G. morhua*)幼体在紫外线暴露后均出现了多种抗氧化酶的上调表达, 甚至引发了细胞凋亡及 DNA 损伤^[35-37]。

在 *Cyrtograpsus altimanus* 和张口蟹(*Neohelice granulata*)幼虫的紫外线暴露研究中, 发现其幼虫特有的蜕皮过程出现延迟或者未蜕皮情况, 生长受到抑制, 但是幼虫仍会表现出较强的运动行为能力^[38-39]。此外, 凡纳滨对虾(*Litopenaeus Vannamei*)幼体经紫外线照射后, 发现紫外线可导致相关抗氧化酶活性的升高, 诱导氧化应激响应^[40]。紫外线处理显著降低了鹿角杯形珊瑚(*Pocillopora damicornis*)及浅杯排孔珊瑚(*Seriatopora caliendrum*)幼虫沉降率、变态率及存活率, 并且延长了幼虫浮游的停留时间^[41-42]。长时间的紫外线暴露还可导致 *Siphonaria australis* 幼虫存活率下降, 抑制其生长发育^[43]。

1.3 成体时期

相比于动物配子、胚胎及幼体时期, 动物成体时期受紫外辐射的影响更为多元化, 生物体的多种关

键生理过程均会对紫外辐射做出响应调整, 但是对成体影响大多并不会导致极其严重的后果, 亦或是机体的死亡(表 3)。

表 3 紫外线辐射对鱼类及水生无脊椎动物成体时期的影响研究

Tab. 3 Effect of ultraviolet radiation on the adult stage of fish and aquatic invertebrates

物种	暴露时间	紫外线暴露类型及强度	受影响生物过程	影响情况	参考文献
<i>Danio rerio</i>	24 h	UVB(312 nm)	环丁烷嘧啶二聚体浓度	↑	[47]
<i>Danio rerio</i>	25 h	UVB, 1.28 W/m ² , 1.72 W/m ² , 1.95 W/m ²	谷胱甘肽过氧化物酶活性	↓	[48]
			<i>bcl-2</i> 基因表达	↓	
			<i>p53</i> 基因表达	↑	
<i>Danio rerio</i>	6, 12, 24 h	UVB	<i>xpc</i> 基因表达	↑	[49]
			<i>ddb2</i> 基因表达	↑	
<i>Gasterosteus aculeatu</i>	68 d	UVB(280~320 nm), 0.76 W/m ²	脾脏指数	↓	[50]
			存活率	↓	
<i>Strongylocentrotus intermedius</i>	1 h	UVB, 10 μW/cm ² , 20 μW/cm ²	生殖腺重量	↓	[52]
			生殖腺粗蛋白	↓	
<i>Strongylocentrotus intermedius</i>	1 h	UVB, 10 μW/cm ² , 20 μW/cm ²	摄食能力	↓	[53]
<i>Stichopus japonicus</i>	0, 60, 120, 240, 360 min	UVR	Ca ²⁺ 浓度	↑	[54]
			Ca ²⁺ -ATP 酶活性	↑	
<i>Stichopus japonicus</i>	30 min	UVR	细胞色素 C	↑	[55]
			活性氧生成量	↑	
			活性氧生成量	↑	
			<i>gst</i> 基因表达	↑	
<i>Tigriopus japonicus</i>	24 h	UVB	<i>gr</i> 基因表达	↑	[58]
			<i>gpx</i> 基因表达	↑	
			<i>sod</i> 基因表达	↑	
<i>Daphniopsis tibetana</i>	None	UVR	产卵数量	↓	[59]
			活性氧生成量	↑	
<i>Ucides cordatus</i>	23, 26 min	UVA, UVB	脂质过氧化物水平	↑	[61]
			Caspase 3 蛋白表达	↑	
			DNA 断裂片段	↑	
<i>Ostrea edulis</i>	45 min	UV	细胞质内钙活性	↑	[62]
			线粒体膜电位	↓	
			脂质过氧化物水平	↑	
			谷胱甘肽还原酶活性	↑	
<i>Crassostrea gigas</i>	20 d	UVB(290~320 nm), 2 W/m ²	谷胱甘肽过氧化物酶活性	↓	[64]
			谷胱甘肽 S 移换酶活性	↑	
			活性氧生成量	↑	

注: UVA 为长波紫外线; UVB 为中波紫外线; UVC 为短波紫外线; ↓表示紫外线暴露引起相应生物过程的下调, ↑表示紫外线暴露引起相应生物过程的上调; None 表示研究中未说明具体暴露时间

紫外辐射可对成体鱼类的各种细胞或器官产生影响,主要表现在 DNA 损伤、氧化应激、免疫功能等多个方面^[44-45]。在紫外辐射的压力下,鱼类会出现摄食行为减少、食欲下降、代谢减缓等变化^[46]。到目前为止,以成体斑马鱼(*D. rerio*)为模式生物,已开展了大量的紫外线暴露实验。紫外线暴露后,斑马鱼(*D. rerio*)皮肤组织中环丁烷嘧啶二聚体(CPD)生成增加,引发了 DNA 损伤;肌肉和皮肤组织中谷胱甘肽过氧化物酶(GPX)活性显著下降,诱导了机体的氧化应激;肝细胞中 DNA 修复相关基因 *p53*、*ddb2* 及 *xpc* 的表达上调,抗凋亡基因 *bcl-2* 的表达下调,引起了细胞周期阻滞及活细胞数量的减少^[47-49]。与正常紫外线剂量相比,高强度的紫外线暴露会导致三刺鱼(*G. aculeatus*)脾脏指数(splenic index, SI)的降低,进而抑制了其特异性免疫^[50]。

在水生无脊椎动物中,紫外辐射的研究对象主要为棘皮动物、甲壳动物及软体动物^[51]。在棘皮动物中,以海胆及刺参的研究为代表。中间球海胆(*Strongylocentrotus intermedius*)在紫外线照射后,其存活率、食物消耗量、生殖腺重量及生殖腺粗蛋白均显著下降,进而抑制其生长^[52]。此外,海胆的移动速度、反射时长、翻正时间会明显降低,从而抑制其觅食行为^[53]。紫外线可诱导仿刺参(*Stichopus japonicus*)的自溶过程,并伴随着细胞色素 C 的释放,表明紫外线可能通过线粒体凋亡途径介导海参细胞的凋亡^[54]。对仿刺参(*S. japonicus*)的体腔细胞进行紫外线处理后,发现 Ca^{2+} 浓度显著增加, Ca^{2+} -ATP 酶的活力升高,内质网损伤程度加重,最终亦引发了细胞凋亡及自溶现象^[55]。在甲壳动物中,由于溞科动物的浮游习性,易受紫外辐射影响。因此,开展了大量的紫外线暴露实验^[56-57]。在紫外线照射日本虎斑猛水蚤(*Tigriopus japonicus*)成体的研究中,发现紫外线可诱导其 ROS 生成量上升,刺激机体抗氧化酶(谷胱甘肽-S-转移酶(*gst*)、谷胱甘肽还原酶(*gr*)、超氧化物歧化酶(*sod*)及 *gpx*)相关基因转录及蛋白表达的上调。同时,紫外线还引起 *p53* 基因的表达显著上调,从而诱导了 DNA 损伤^[58]。高剂量的紫外辐射可延长成体西藏拟溞(*Daphniopsis tibetana*)产幼前的发育期,降低产卵量,显著抑制其生长、发育及生殖活动^[59]。针对紫外线处理的西藏拟溞(*D. tibetana*)比较转录组分析发现了 146 个差异表达基因,表明紫外线可能引发了脂质转运和脂质定位等多种生物过程的响应调整^[60]。紫外线暴露招潮蟹(*Ucides cordatus*),则引

起其脑组织内 Caspase 3 蛋白表达增加,从而造成蟹的中枢神经系统细胞凋亡^[61]。在软体动物中,紫外线可造成欧洲牡蛎(*Ostrea edulis*)、紫贻贝(*Mytilus galloprovincialis*)的线粒体形态和功能损伤,并诱导细胞凋亡^[62-63]。紫外辐射可以影响长牡蛎(*C. gigas*)的氧化应激及渗透压调节等生理活动。但是,通过观察成体长牡蛎(*C. gigas*)的开闭壳行为,发现其亦会表现出对紫外辐射的一定适应性行为变化^[64]。

2 响应紫外线的方式

鱼类及水生无脊椎动物对紫外线的响应方式,大致可以概括为 DNA 损伤,氧化损伤,调节免疫及沉积色素等。

2.1 DNA 损伤

紫外线是太阳光中携带能量最高的辐射波段,其高能光子可被生物大分子(主要为核苷酸)所吸收并发生光化学反应,从而造成特定生物功能的损伤或丧失^[65]。紫外辐射可引起 DNA 链上相邻嘧啶分子发生光反应,产生 CPD、嘧啶-嘧啶酮(6-4 PP)^[66],这些光产物则会损伤 DNA 并引发对生物体更为严重的伤害。紫外辐射导致的 DNA 损伤,可扭曲断裂 DNA 结构并中断 DNA 的复制和转录^[67],进而可能造成细胞周期延迟或阻碍、诱变、细胞凋亡和致癌等一系列的严重后果^[68]。在鱼类中,紫外辐射引发 DNA 损伤的现象较多。例如,青鳞(*O. latipes*)、新月锦鱼(*Thalassoma lunare*)和白斑狗鱼(*E. lucius*)经紫外线暴露后均发现,CPDs 生成量上升, DNA 损伤加剧^[23, 68-69]。在紫外线引发 DNA 损伤的同时,生物体亦会借助光修复(photoreactivation repair, PER),即通过 DNA 光解酶与 CPDs 或者 6-4PPs 的结合,逆转紫外线造成的损伤^[70];或者通过核苷酸切除修复(nucleotide excision repair, NER)用未受损核苷酸序列来替代受损残缺部分^[71]。在 DNA 修复过程中,鱼类会减少用于其他活动的能量供应,将更多能量供给 PER 及 NER^[50]。此外,某些关键基因的活化也与修复过程息息相关。例如,紫外辐射后,白斑狗鱼(*E. lucius*)的 *p53* 基因的激活;安氏坑鱼(*Phreatichthys andruzzii*)中 *ddb2* 基因的上调表达;斑马鱼(*D. rerio*)肝细胞中 *apex-1* 基因(*apurinic/aprimidinic endonuclease 1*)的上调表达^[23, 49, 72]。

2.2 氧化损伤

紫外辐射介导的光化学效应,可引起生物体产生

超氧自由基(O_2^-)、过氧化氢(H_2O_2)以及羟基自由基(OH^\cdot)等 ROS 物质,从而进一步引发脂质过氧化等氧化损伤^[36, 73-75]。在紫外辐射暴露斑马鱼(*D. rerio*)后,其体内 ROS 生成量显著升高,游泳能力减弱^[76-77]。此外,紫外辐射产生的过剩 ROS,可以攻击生物膜系统,造成生物膜的通透性和完整性的丧失^[26]。同时,ROS 可与 DNA 发生相互作用,间接引发 DNA 损伤。例如,紫外线暴露造成了斑马鱼(*D. rerio*)、奥氏沼虾(*M. olfersi*)细胞膜的损伤^[77-78]。紫外线照射产生的 ROS 进一步造成了大盖巨脂鲤(*Colossoma macropomum*)、巨骨舌鱼(*Arapaima gigas*)的 DNA 损伤^[79]。

在紫外线引发氧化损伤的同时,鱼类及水生无脊椎动物可以通过抗氧化剂、抗氧化酶类来清除自由基或者增强抗氧化水平来应对紫外线的影响。在鱼类中,紫外线暴露后,斑马鱼(*D. rerio*)的 *sod*, *cat*, *hsp70* 基因表达均显著上调^[80]。在水生无脊椎动物中,紫外线处理后,长牡蛎(*C. gigas*)的 LPO 水平显著上调,抗氧化酶类(GR、GST、GPX)活性发生显著变化^[64]; *Daphnia commutata*、*Pocillopora capitata* 的 GST 活性增加;暗色海葵(*Actinia tenebrosa*)的 CAT 活性增加^[81]; 凡纳滨对虾(*L. vannamei*)的抗氧化酶类(GPX、CAT)活性和 MDA 浓度增加^[40, 82]; 矮小拟镖水蚤(*Paracyclopsina nana*)的 *hsp* 基因显著上调^[83]。

2.3 调节免疫

免疫系统是生物体抵抗细菌,病毒等微生物入侵的重要手段^[84]。过量的紫外辐射则可扰乱生物的新陈代谢平衡,降低对病原体的免疫效力,导致更严重的病原体感染,从而调节生物的先天性或特异性免疫系统。另外,紫外线可以破坏生物的表皮组织,使其受损,生物一旦失去体表的保护机制,如表皮杯状细胞产生的黏液,将变得更易受到病原菌的感染^[85]。例如,暴露于紫外辐射下的虹鳟(*O. mykiss*)幼体,其皮肤黏液细胞数量降低,黏液细胞变性,表皮扁平细胞微核被破坏,进而损伤了皮肤的免疫功能^[86]。在紫外线暴露后三刺鱼(*G. aculeatus*)SSI 的降低,露斯塔野鲮(*L. rohita*)白细胞占比和过氧化物酶水平的降低,凡纳滨对虾(*P. vannamei*)溶菌酶水平的显著降低,均显示出紫外线对生物免疫功能的抑制作用^[31, 50, 82]。但是,紫外线暴露斑马鱼(*D. rerio*)后,多种免疫因子均出现上调表达,如促炎细胞因子(*IL-1 β*),肿瘤坏死因子(*TNF α*)等^[87-88],同样也说明一定剂量的紫外辐射可以增强生物的免疫功能。此

外,在孔雀鱼(*Poecilia reticulata*)亲本的长期紫外线暴露后,其后代亦可产生免疫抑制,更易感染病原菌,表明紫外辐射对鱼类免疫系统调节的遗传性^[75]。

2.4 沉积色素

沉积色素是生物体应对紫外辐射的一种重要手段,通过在体表累积如黑色素、类胡萝卜素、虾青素等色素,可以起到直接屏蔽紫外线的作用。而且随着生物的生长,色素沉积逐渐增加,将逐渐降低紫外线对生物的损伤^[89]。生物体如果缺乏足够色素沉积,将会导致更多的紫外线渗透进入组织中,进而造成更大损伤^[90]。例如,多酚处理可提高斑马鱼(*D. rerio*)胚胎的色素沉着,从而降低了 UVB 诱导的 ROS 水平,减少了细胞凋亡的发生^[91]。紫外线所诱导的桡足类体内类胡萝卜素积累是一种可广泛观察到的光保护机制^[92]。在众多色素中,黑色素的光保护作用最为显著,具有高含量黑色素的生物可表现出对紫外线的较高抵抗能力^[93]。动物体可通过表皮沉积黑色素辅助激活自身修复机制,应对紫外辐射^[94]。例如,紫外辐射可导致斑马鱼(*D. rerio*)胚胎中的黑素小体聚集,造成胚胎黑化^[95]。*Daphnia melanica* 可调节甲壳的黑色素沉着以适应紫外辐射。黑色素含量高的个体,在紫外线诱导后,CPD 生成量及 DNA 损伤程度均更低^[96-97]。另外,真白鲑(*Coregonus lavaretus*)、欧白鲑(*Coregonus albula*)及黑棘鲷(*Acanthopagrus schlegelii*)幼体在紫外线暴露后,黑色素生成量均显著上升,表现出其可能具有较高的紫外线耐受能力^[98-99]。

3 紫外线与其他因素复合暴露

目前,紫外线的复合暴露研究主要集中在两个方面,一方面是与其它环境因素(酸化、温度、缺氧等)复合,另一方面是与水体污染物(化合物、重金属、复合物)复合,此两种类型的复合暴露实验均可产生更大的非加性效应^[100-101],并影响海洋生物的关键生理过程、生长发育或生存状况^[102]。在紫外线与环境因素的复合实验中,关于紫外线与温度的复合暴露研究开展最多。在鱼类中,紫外线和不同温度的处理,可导致斑马鱼(*D. rerio*)的胚胎出现了孵化延迟,畸形率升高,心率降低等影响生长发育的现象,并引起了氧化应激和免疫调节的强烈响应,干扰其正常代谢^[80, 87]。紫外线与温度的暴露还可抑制东部食蚊鱼(*Gambusia holbrooki*)的新陈代谢活动,破坏免疫功能,加剧小瓜虫病感染程度^[103]。在水生

无脊椎动物中,紫外线与温度的复合暴露,可影响 *Bembicium nanum* 和后鳃 *Dolabrifera brazieri* 的发育速度^[104]。

由于紫外线可以通过光敏化及光修饰作用催化水体中污染物产生光致毒性效应,进而导致污染物的毒性增加,造成生物的 DNA、脂质和蛋白的氧化损伤^[105]。因此,与单独毒性相比,在紫外线下的污染物对海洋生物的毒性可增加 2 甚至 1 000 倍以上,从而对海洋生物造成更为严重的影响^[106-107]。紫外线引发的污染物光致毒性作用已在多种海洋生物中被证实,包括甲壳类、鱼类、软体动物、浮游动物^[105]。在紫外线与水体污染物的复合实验中,与各类芳香烃物质的复合实验开展最多,主要以复合原油,多环芳烃(PAHs)为主。在紫外线和原油的复合暴露研究中,发现紫外线可以引起原油毒性的增加,导致黄条鱼(*Seriola lalandi*)及麒麟(Coryphaena hippurus) 胚胎孵化率下降^[108-109];星状海葵(*Nematostella vectensis*)出现大规模的转录应激反应,包括抗氧化酶、DNA 修复酶和紫外线保护基因的上调^[110]。在紫外线和 PAHs 的复合暴露研究中,紫外辐射可被 PAHs 及其衍生物吸收,诱导光毒性,增加 ROS 的产生^[111-112]。同时,紫外辐射还可以催化 PAHs,增加其水溶性,造成生物体胚胎发育畸形甚至死亡^[113]。例如,在紫外线存在下,PAHs 对柔枝鹿角珊瑚(*Acropora tenuis*) 的毒性增加高达 7.1 倍^[114]。紫外线和 PAHs 复合暴露可提高星状海葵(*N. vectensis*) 的死亡率,并伴有细胞和氧化应激反应基因(*cuznsod3*, *copper chaperone of SOD*, *mnsod1*, *hsp70*) 的显著变化^[115]。在紫外线和葱的复合暴露研究中,环境剂量紫外线即可显著提高葱的光致毒性,即便短时暴露,也可造成太平洋鲱(*Clupea pallasii*)及海湾扇贝(*Argopecten irradians*) 的大量死亡^[116-117]。

4 展望

太阳光谱,尤其是紫外线,对生物的影响研究已越来越受到人们的重视。从实验方法上看,目前对水生动物的紫外线暴露,较多采用紫外灯模拟的紫外辐射条件,且暴露条件多为急性或短时的暴露,这与生物所面对的真实自然环境中太阳紫外辐射情况还有较大差异。在研究对象上,则较多的集中在具有游泳习性鱼类及浮游习性溞科动物中。而实际上由于水产养殖技术的迅猛发展,很多养殖对象,如贝类、虾蟹类等均会在滩涂、浅海等地区养殖,这些

物种同样面临着太阳紫外辐射的威胁影响。在研究技术方面,目前多采用形态及行为观察、生理及分子指标测定等方式,较少有结合组学的整合分析研究。因此,太阳紫外辐射的影响研究,急需利用更精准的太阳光模拟器,完善紫外线的暴露条件。从更多层面(基因、蛋白、代谢物),更大尺度(多组学连用)上挖掘水生动物响应紫外辐射的信号通路及生理过程,寻找关键分子并解析对应功能。总之,已有研究均表明紫外线对水生动物的影响是多方面、多层次的,未来针对更多水产养殖品种开展的太阳紫外线暴露影响研究,可充实海洋生物对环境变化的生理响应研究,还可以更好的优化养殖条件并服务养殖生产。

参考文献:

- [1] GIES P, VAN DEVENTER E, GREEN A C, et al. Review of the global solar UV index 2015 workshop report[J]. Health Physics, 2018, 114(1): 84-90.
- [2] ČÍŽKOVÁ K, LÁSKA K, METELKA L, et al. Reconstruction and analysis of erythematous UV radiation time series from Hradec Králové (Czech Republic) over the past 50 years[J]. Atmospheric Chemistry and Physics, 2018, 18(3): 1805-1818.
- [3] JIN P, DUARTE C M, AGUSTI S. Contrasting responses of marine and freshwater photosynthetic organisms to UVB radiation: a meta-analysis[J]. Frontiers in Marine Science, 2017, 4: 45.
- [4] BERNERD F, MARIONNET C, DUVAL C. Solar ultraviolet radiation induces biological alterations in human skin in vitro: relevance of a well-balanced UVA/UVB protection[J]. Indian Journal of Dermatology, Venereology and Leprology, 2012, 78: 15-23.
- [5] BECKMANN M, VÁCLAVÍK T, MANCEUR A M, et al. GLUV: a global UV-B radiation data set for macroecological studies[J]. Methods in Ecology and Evolution, 2014, 5(4): 372-383.
- [6] JIN P, WAN J, ZHANG J, et al. Additive impacts of ocean acidification and ambient ultraviolet radiation threaten calcifying marine primary producers[J]. Science of the Total Environment, 2022, 818: 151782.
- [7] CIERESZKO A, WOLFE T D, DABROWSKI K. Analysis of DNA damage in sea lamprey (*Petromyzon marinus*) spermatozoa by UV, hydrogen peroxide, and the toxicant bisazir[J]. Aquatic Toxicology, 2005, 73(2): 128-138.
- [8] DIETRICH G J, SZPYRKA A, WOJTCZAK M, et al. Effects of UV irradiation and hydrogen peroxide on DNA fragmentation, motility and fertilizing ability of rainbow trout (*Oncorhynchus mykiss*) spermatozoa[J]. Theriogenology, 2005, 64(8): 1809-1822.

- [9] FERNÁNDEZ-DÍEZ C, GONZÁLEZ-ROJO S, LOMBÓ M, et al. Tolerance to paternal genotoxic damage promotes survival during embryo development in zebrafish (*Danio rerio*)[J]. *Biology Open*, 2018, 7(5): bio030130.
- [10] RICK I P, MEHLIS M, ESSER E, et al. The influence of ambient ultraviolet light on sperm quality and sexual ornamentation in three-spined sticklebacks (*Gasterosteus aculeatus*)[J]. *Oecologia*, 2014, 174(2): 393-402.
- [11] 王转斌. 紫外线(UV)对金鱼产卵和受精卵孵化的生物学效应[J]. 曲阜师范大学学报: 自然科学版, 1997, 23(2): 99-103.
WANG Zhuabin. Biological effect of ultraviolet (UV) irradiation on the gold-fish's reproduction and its hatching of fertilized eggs[J]. *Journal of Qufu Normal University*, 1997, 23(2): 99-103.
- [12] 戴桂馥, 吴健, 张凤秋, 等. 紫外线照射对金鱼孵化率的影响[J]. 中国水产科学, 2005(5): 135-138.
DAI Guifu, WU Jian, ZHANG Fengqiu, et al. Effects of UV on hatching rate of goldfish[J]. *Journal of Fishery Sciences of China*, 2005(5): 135-138.
- [13] LI Q, OSADA M, KASHIHARA M, et al. Effects of ultraviolet irradiation on genetical inactivation and morphological features of sperm of the Pacific oyster *Crassostrea gigas*[J]. *Fisheries Science*, 2000, 66(1): 91-96.
- [14] 赵峰, 杨爱国, 刘志鸿, 等. 紫外辐射对栉孔扇贝精子遗传失活及形态结构的影响[J]. 海洋水产研究, 2003, 24(4): 26-31.
ZHAO Feng, YANG Aiguo, LIU Zhihong, et al. Effects of ultraviolet irradiation on genetic inactivation and morphological structure of sperm of scallop *Chlamys farreri*[J]. *Marine Fisheries Research*, 2003, 24(4): 26-31.
- [15] SEAVER R W, FERGUSON G W, GEHRMANN W H, et al. Effects of ultraviolet radiation on gametic function during fertilization in zebra mussels (*Dreissena polymorpha*)[J]. *Journal of Shellfish Research*, 2009, 28(3): 625-633.
- [16] AL-AIDAROOS A M, EL-SHERBINY M M O, SATHEESH S, et al. High mortality of Red Sea zooplankton under ambient solar radiation[J]. *PLoS One*, 2014, 9(10): e108778.
- [17] 吴健, 戴桂馥, 张凤秋, 等. UV辐射对金鱼受精卵和幼胚发育的影响[J]. 辐射研究与辐射工艺学报, 2005(4): 229-232.
WU Jian, DAI Guifu, ZHANG Fengqiu, et al. Effects of UV-C irradiation on development of goldfish embryos[J]. *Journal of Radiation Research and Radiation Processing*, 2005(4): 229-232.
- [18] PASPARAKIS C, WANG Y, HEUER R M, et al. Ultraviolet avoidance by embryonic buoyancy control in three species of marine fish[J]. *Science of the Total Environment*, 2022, 806: 150542.
- [19] SAYED A E D H, MITANI H. The notochord curvature in medaka (*Oryzias latipes*) embryos as a response to ultraviolet A irradiation[J]. *Journal of Photochemistry and Photobiology B: Biology*, 2016, 164: 132-140.
- [20] HOLMQUIST L M, RAY A M, BANCROFT B A, et al. Effects of ultraviolet-b radiation on woundfin embryos and larvae with application to conservation propagation[J]. *Journal of Fish and Wildlife Management*, 2014, 5(1): 87-98.
- [21] BROWMAN H I, VETTER R D, RODRIGUEZ C A, et al. Ultraviolet (280-400 nm)-induced DNA damage in the eggs and larvae of *Calanus finmarchicus* G. (Copepoda) and Atlantic cod (*Gadus morhua*)[J]. *Photochemistry and Photobiology*. 2003, 77(4): 397-404.
- [22] ZENI E C, AMMAR D, LEAL M L, et al. Light-mediated DNA repair prevents UVB-induced cell cycle arrest in embryos of the crustacean *Macrobrachium olfersi*[J]. *Photochemistry and Photobiology*, 2015, 91(4): 869-878.
- [23] VEHNÄÄINEN E R, VÄHÄKANGAS K, OIKARI A. UV-B exposure causes DNA damage and changes in protein expression in northern pike (*Esox lucius*) post-hatched embryos[J]. *Photochemistry and Photobiology*, 2012, 88(2): 363-370.
- [24] CHANG Y, LEE W Y, LIN Y J, et al. Mercury (II) impairs nucleotide excision repair (NER) in zebrafish (*Danio rerio*) embryos by targeting primarily at the stage of DNA incision[J]. *Aquatic Toxicology*, 2017, 192: 97-104.
- [25] DE ARAUJO LEITE J C, DE VASCONCELOS R B, DA SILVA S G, et al. ATP-binding cassette transporters protect sea urchin gametes and embryonic cells against the harmful effects of ultraviolet light[J]. *Molecular Reproduction and Development*, 2014, 81(1): 66-83.
- [26] QUADROS T, SCHRAMM H, ZENI E C, et al. Developmental effects of exposure to ultraviolet B radiation on the freshwater prawn *Macrobrachium olfersi*: mitochondria as a target of environmental UVB radiation[J]. *Ecotoxicology and Environmental Safety*, 2016, 132: 279-287.
- [27] VÁSQUEZ P, LLANOS-RIVERA A, CASTRO L R, et al. UV radiation effects on the embryos of anchoveta (*Engraulis ringens*) and common sardine (*Strangomera bentincki*) off central Chile[J]. *Marine and Freshwater Research*, 2015, 67(2): 195-209.
- [28] DARGAEI Z, SHARIFPOUR I, ZORRIEHZAHRA J. UV-B impacts on morphology and retina of *Onchorhynchus mykiss* larvae[J]. *Iranian Journal of Fisheries*

- ies Sciences, 2014, 13(2): 289-302.
- [29] TORRES NUNEZ E, SOBRINO C, NEALE P J, et al. Molecular response to ultraviolet radiation exposure in fish embryos: implications for survival and morphological development[J]. Photochemistry and Photobiology, 2012, 88(3): 701-707.
- [30] ARAÚJO M J, QUINTANEIRO C, SOARES A M V M, et al. Effects of ultraviolet radiation to *Solea senegalensis* during early development[J]. Science of the Total Environment, 2021, 764: 142899.
- [31] SINGH M K, SHARMA J G, CHAKRABARTI R. Effect of UV-B radiation on the defence system of *Labeo rohita* (Actinopterygii: Cypriniformes: Cyprinidae) larvae and its modulation by seed of devil's horsewhip, *Achyranthes aspera*[J]. Acta Ichthyologica et Piscatoria, 2013, 43(2): 119-126.
- [32] SUCRÉ E, VIDUSSI F, MOSTAJIR B, et al. Impact of ultraviolet-B radiation on planktonic fish larvae: alteration of the osmoregulatory function[J]. Aquatic Toxicology, 2012, 109: 194-201.
- [33] KAZEROUNI E G, KHODABANDEH S. Ionocyte immunolocalization and the effects of ultraviolet radiation on their abundance and distribution in the alenins of caspian sea salmon, *Salmo trutta caspius*[J]. Cell Journal (Yakhteh), 2011, 13(1): 45.
- [34] MARKKULA E, SALO H M, RIKALAINEN K, et al. Long-term UVB irradiation affects the immune functions of carp (*Cyprinus carpio*) and eainbow trout (*Oncorhynchus mykiss*)[J]. Photochemistry and Photobiology, 2009, 85(1): 347-352.
- [35] GOUVEIA G R, TRINDADE G S, NERY L E M, et al. UVA and UVB penetration in the water column of a south west atlantic warm temperate estuary and its effects on cells and fish larvae[J]. Estuaries and Coasts, 2015, 38(4): 1147-1162.
- [36] SINGH M K, SHARMA J G, CHAKRABARTI R. Simulation study of natural UV-B radiation on *Catla catla* and its impact on physiology, oxidative stress, Hsp 70 and DNA fragmentation[J]. Journal of Photochemistry and Photobiology B: Biology, 2015, 149: 156-163.
- [37] LESSER M P, FARRELL J H, WALKER C W, et al. Oxidative stress, DNA damage and p53 expression in the larvae of atlantic cod (*Gadus morhua*) exposed to ultraviolet (290–400 nm) radiation[J]. The Journal of Experimental Biology, 2001, 204(1): 157-164.
- [38] MORESINO R D H, GONCALVES R J, HELBLING E W. Sublethal effects of ultraviolet radiation on crab larvae of *Cyrtograpsus altimanus*[J]. Journal of Experimental Marine Biology and Ecology, 2011, 407(2): 363-369.
- [39] VARGAS M A, GEIHS M A, MACIEL F E, et al. The effects of UV radiation on the visual system of the crab *Neohelice granulata*: a protective role of melatonin[J]. Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology, 2011, 154(4): 427-434.
- [40] FEI F, LIU B, GAO X, et al. Effects of supplemental ultraviolet light on growth, oxidative stress responses, and apoptosis-related gene expression of the shrimp *Litopenaeus vannamei*[J]. Aquaculture, 2020, 520: 735013.
- [41] ZHOU J, FAN T Y, BEARDALL J, et al. Incident ultraviolet irradiances influence physiology, development and settlement of larva in the coral *Pocillopora damicornis*[J]. Photochemistry and Photobiology, 2016, 92(2): 293-300.
- [42] ZHOU J, FAN T Y, BEARDALL J, et al. UV-A induced delayed development in the larvae of coral *Seriatopora caliendrum*[J]. Journal of Photochemistry and Photobiology B: Biology, 2017, 167: 249-255.
- [43] FISCHER J, PHILLIPS N E. Carry-over effects of multiple stressors on benthic embryos are mediated by larval exposure to elevated UVB and temperature[J]. Global Change Biology, 2014, 20(7): 2108-2116.
- [44] RYU H S, CHOI C Y, SONG J A, et al. Effects of UV radiation on oxidative stress in yellowtail clownfish *Amphiprion clarkii*[J]. Ocean Science Journal, 2019, 54(2): 205-212.
- [45] MARTINEZ-LEVASSEUR L M, BIRCH-MACHIN M A, Bowman A, et al. Whales use distinct strategies to counteract solar ultraviolet radiation[J]. Scientific Reports, 2013, 3(1): 1-6.
- [46] ARTS M T, BROWMAN H I, JOKINEN I E, et al. Effects of UV radiation and diet on polyunsaturated fatty acids in the skin, ocular tissue and dorsal muscle of atlantic salmon (*Salmo salar*) held in outdoor rearing tanks[J]. Photochemistry and Photobiology, 2010, 86(4): 909-919.
- [47] ZENG Z, RICHARDSON J, VERDUZCO D, et al. Zebrafish have a competent p53-dependent nucleotide excision repair pathway to resolve ultraviolet B-induced DNA damage in the skin[J]. Zebrafish, 2009, 6(4): 405-415.
- [48] CHARRON R A, FENWICK J C, LEAN D R, et al. Ultraviolet-B radiation effects on antioxidant status and survival in the zebrafish, *Brachydanio rerio*[J]. Photochemistry and Photobiology, 2000, 72(3): 327-333.
- [49] SANDRINI J Z, TRINDADE G S, NERY L E, et al. Time-course expression of DNA repair-related genes in hepatocytes of zebrafish (*Danio rerio*) after UV-B exposure[J]. Photochemistry and Photobiology, 2009, 85(1): 220-226.
- [50] VITT S, RAHN A K, DROLSHAGEN L, et al. Enhanced ambient UVB light affects growth, body condi-

- tion and the investment in innate and adaptive immunity in three-spined sticklebacks (*Gasterosteus aculeatus*)[J]. *Aquatic Ecology*, 2017, 51(4): 499-509.
- [51] MATRANGA V, PINSINO A, CELI M, et al. Impacts of UV-B radiation on short-term cultures of sea urchin coelomocytes[J]. *Marine Biology*, 2006, 149(1): 25-34.
- [52] ZHAO C, ZHANG L, SHI D, et al. Carryover effects of short-term UV-B radiation on fitness related traits of the sea urchin *Strongylocentrotus intermedius*[J]. *Ecotoxicology and Environmental Safety*, 2018, 164: 659-664.
- [53] SHI D, DING J, ZHANG L, et al. Effects of UV-B radiation on fitness related behaviors of the sea urchin *Strongylocentrotus intermedius*[J]. *Journal of Oceanology and Limnology*, 2018, 36(5): 1681-1687.
- [54] SU L, YANG J F, FU X, et al. Ultraviolet-ray-induced sea cucumber (*Stichopus japonicus*) melting is mediated by the caspase-dependent mitochondrial apoptotic pathway[J]. *Journal of Agricultural and Food Chemistry*, 2018, 66(1): 45-52.
- [55] 陈庭家. 紫外线诱导海参自溶过程中体腔细胞钙离子信号与内质网损伤的研究[D]. 大连: 大连工业大学, 2016.
- CHEN Tingjia. Study on calcium signaling and endoplasmic reticulum damage of coelomocytes during UV-induced autolysis in sea cucumber[D]. Dalian: Dalian Polytechnic University, 2016.
- [56] HUEBNER J D, LOADMAN N L, WIEGAND M D, et al. UVB radiation affects growth, reproduction and tissue structure of *Daphnia magna* across several temperatures[J]. *Photochemistry and Photobiology*, 2013, 89(1): 103-110.
- [57] GIRAUDO M, COTTIN G, ESPERANZA M, et al. Transcriptional and cellular effects of benzotriazole UV stabilizers UV - 234 and UV - 328 in the freshwater invertebrates *Chlamydomonas reinhardtii* and *Daphnia magna*[J]. *Environmental Toxicology and Chemistry*, 2017, 36(12): 3333-3342.
- [58] KIM B M, RHEE J S, LEE K W, et al. UV-B radiation-induced oxidative stress and p38 signaling pathway involvement in the benthic copepod *Tigriopus japonicus*[J]. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, 2015, 167: 15-23.
- [59] 赵文, 谢玺, 魏杰, 等. 紫外线辐照对西藏拟溞生长、发育和生殖的影响[C]//中国水产学会. 2012年中国水产学会学术年会论文摘要集. 郑州: 海洋出版社, 2012: 51.
- ZHAO Wen, XIE Xi, WEI Jie, et al. Effect of ultraviolet radiation on growth, development and reproduction of *Daphniopsis tibetana* Sars[C]// China Society of Fisheries. Proceedings of the academic Annual Meeting of Chinese Fishery Society in 2012. Zhengzhou: China Ocean Press, 2012: 51.
- [60] WANG M, ZHAO W, WEI J, et al. Acute effects of UVB radiation on the survival, growth, development, and reproduction of *Daphniopsis tibetana* Sars (Crustacea: Cladocera)[J]. *Environmental Science and Pollution Research*, 2019, 26(11): 10916-10925.
- [61] HOLLMANN G, DE JESUS FERREIRA G, GEIHS M A, et al. Antioxidant activity stimulated by ultraviolet radiation in the nervous system of a crustacean[J]. *Aquatic Toxicology*, 2015, 160: 151-162.
- [62] GERVAIS O, RENAULT T, ARZUL I. Induction of apoptosis by UV in the flat oyster, *Ostrea edulis*[J]. *Fish & Shellfish Immunology*, 2015, 46(2): 232-242.
- [63] ESTEVEZ-CALVAR N, ROMERO A, FIGUERAS A, et al. Genes of the mitochondrial apoptotic pathway in *Mytilus galloprovincialis*[J]. *PLoS One*, 2013, 8(4): e61502.
- [64] SONG H, WEI L, ZHONG M, et al. Ambient ultraviolet B radiation induced valve behavioral acclimation of Pacific oyster which resulted from the different response strategies of smooth and striated adductor muscles[J]. *Ecotoxicology and Environmental Safety*, 2021, 228: 113035.
- [65] HÄDER D P, KUMAR H D, SMITH R C, et al. Effects of solar UV radiation on aquatic ecosystems and interactions with climate change[J]. *Photochemical & Photobiological Sciences*, 2007, 6(3): 267-285.
- [66] IKEHATA H, MORI T, KAMEI Y, et al. Wavelength - and tissue - dependent variations in the mutagenicity of cyclobutane pyrimidine dimers in mouse skin[J]. *Photochemistry and Photobiology*, 2020, 96(1): 94-104.
- [67] SINHA R P, HÄDER D P. UV-induced DNA damage and repair: a review[J]. *Photochemical & Photobiological Sciences*, 2002, 1(4): 225-236.
- [68] SAYED A E D H, MITANI H. Immunostaining of UVA-induced DNA damage in erythrocytes of medaka (*Oryzias latipes*)[J]. *Journal of Photochemistry and Photobiology B: Biology*, 2017, 171: 90-95.
- [69] BRAUN C, REEF R, SIEBECK U E. Ultraviolet absorbing compounds provide a rapid response mechanism for UV protection in some reef fish[J]. *Journal of Photochemistry and Photobiology B: Biology*, 2016, 160: 400-407.
- [70] TUCKER A J, WILLIAMSON C E. The invasion window for warmwater fish in clearwater lakes: the role of ultraviolet radiation and temperature[J]. *Diversity and Distributions*, 2014, 20(2): 181-192.
- [71] DONG Q, SVOBODA K, TIERSCH T R, et al. Photobiological effects of UVA and UVB light in zebrafish embryos: evidence for a competent photorepair system[J]. *Journal of Photochemistry and Photobiology B: Biology*, 2016, 160: 400-407.

- Biology, 2007, 88(2/3): 137-146.
- [72] ZHAO H, LI H, DU J, et al. Regulation of *ddb2* expression in blind cavefish and zebrafish reveals plasticity in the control of sunlight-induced DNA damage repair[J]. PLoS Genetics, 2021, 17(2): e1009356.
- [73] RAMÍREZ-DUARTE W F, KUROBE T, TEH S J. Effects of low levels of ultraviolet radiation on antioxidant mechanisms of Japanese Medaka (*Oryzias latipes*)[J]. Chemosphere, 2017, 181: 304-312.
- [74] LLABRÉS M, AGUSTÍ S, FERNÁNDEZ M, et al. Impact of elevated UVB radiation on marine biota: a meta-analysis[J]. Global Ecology and Biogeography, 2013, 22(1): 131-144.
- [75] GHANIZADEH-KAZEROUNI E, FRANKLIN C E, SEEBACHER F. Parental exposure modulates the effects of UV - B on offspring in guppies[J]. Functional Ecology, 2017, 31(5): 1082-1090.
- [76] HUREM S, FRASER T W K, GOMES T, et al. Sub-lethal UV radiation during early life stages alters the behaviour, heart rate and oxidative stress parameters in zebrafish (*Danio rerio*)[J]. Ecotoxicology and Environmental Safety, 2018, 166: 359-365.
- [77] SEEBACHER F, KAZEROUNI E G, FRANKLIN C E. Ultraviolet B radiation alters movement and thermal selection of zebrafish (*Danio rerio*)[J]. Biology Letters, 2016, 12(8): 20160258.
- [78] MÜLLER Y M R, DE MELO M S, WEISS V M C, et al. Ultraviolet B radiation affects epithelial cell morphology and ultrastructure in the hepatopancreas of the freshwater decapod *Macrobrachium olfersii*[J]. Ecotoxicology and Environmental Safety, 2020, 204: 111096.
- [79] GROFF A A, DA SILVA J, NUNES E A, et al. UVA/UVB-induced genotoxicity and lesion repair in *Colossoma macropomum* and *Arapaima gigas* Amazonian fish[J]. Journal of Photochemistry and Photobiology B: Biology, 2010, 99(2): 93-99.
- [80] LI X, HE Y, XIE C, et al. Effects of UV-B radiation on the infectivity of *Magnaporthe oryzae* and rice disease-resistant physiology in Yuanyang terraces[J]. Photochemical & Photobiological Sciences, 2018, 17(1): 8-17.
- [81] CUBILLOS V M, LAMARE M D, PEAKE B M, et al. Cellular changes associated with the acclimation of the intertidal sea anemone *Actinia tenebrosa* to ultraviolet radiation[J]. Photochemistry and Photobiology, 2014, 90(6): 1314-1323.
- [82] WANG X, LIU B, GAO X, et al. The effects of different UVA photoperiods on the growth performance, immune responses, antioxidant status and apoptosis-related gene expression of the pacific white shrimp (*Penaeus vannamei*)[J]. Antibiotics, 2021, 11(1): 37.
- [83] WON E J, HAN J, LEE Y, et al. In vivo effects of UV radiation on multiple endpoints and expression profiles of DNA repair and heat shock protein (Hsp) genes in the cycloid copepod *Paracyclopsina nana*[J]. Aquatic Toxicology, 2015, 165: 1-8.
- [84] MONTUORI E, DE PASCALE D, LAURITANO C. Recent discoveries on marine organism immunomodulatory activities[J]. Marine Drugs, 2022, 20(7): 422.
- [85] REVERTER M, TAPISSIER-BONTEMPS N, LECCHINI D, et al. Biological and ecological roles of external fish mucus: a review[J]. Fishes, 2018, 3(4): 41.
- [86] ABEDI S, SHARIFPOUR I, MOZANZADEH M T, et al. A histological and ultrastructural study of the skin of rainbow trout (*Oncorhynchus mykiss*) alevins exposed to different levels of ultraviolet B radiation[J]. Journal of Photochemistry and Photobiology B: Biology, 2015, 147: 56-62.
- [87] ICOGLU AKSAKAL F, CILTAS A. The impact of ultraviolet B (UV-B) radiation in combination with different temperatures in the early life stage of zebrafish (*Danio rerio*)[J]. Photochemical & Photobiological Sciences, 2018, 17(1): 35-41.
- [88] BANERJEE S, LEPTIN M. Systemic response to ultraviolet radiation involves induction of leukocytic IL-1 β and inflammation in zebrafish[J]. The Journal of Immunology, 2014, 193(3): 1408-1415.
- [89] FINCH B E, STUBBLEFIELD W A. Photo-enhanced toxicity of fluoranthene to Gulf of Mexico marine organisms at different larval ages and ultraviolet light intensities[J]. Environmental Toxicology and Chemistry, 2016, 35(5): 1113-1122.
- [90] MCFADZEN I, BAYNES S, HALLAM J, et al. Histopathology of the skin of UV-B irradiated sole (*Solea solea*) and turbot (*Scophthalmus maximus*) larvae[J]. Marine Environmental Research, 2000, 50(1/5): 273-277.
- [91] KANG M C, CHA S H, WIJESINGHE W, et al. Protective effect of marine algae phlorotannins against AAPH-induced oxidative stress in zebrafish embryo[J]. Food Chemistry, 2013, 138(2/3): 950-955.
- [92] TARTAROTTI B, ALFREIDER A, EGG M, et al. Seasonal plasticity in photoprotection modulates UV-induced hsp gene expression in copepods from a clear lake[J]. Limnology and Oceanography, 2018, 63(4): 1579-1592.
- [93] SHARMA S, WAGH S, GOVINDARAJAN R. Melanosomal proteins--role in melanin polymerization[J]. Pigment Cell Research, 2010, 15(2): 127-133.
- [94] HÄDER D P, WILLIAMSON C E, WÄNGBERG S Å, et al. Effects of UV radiation on aquatic ecosystems and

- interactions with other environmental factors[J]. *Photochemical & Photobiological Sciences*, 2015, 14(1): 108-126.
- [95] MUELLER K P, NEUHAUSS S C F. Sunscreen for fish: co-option of UV light protection for camouflage[J]. *PLoS One*, 2014, 9(1): e87372.
- [96] TOLLRIAN R, HEIBL C. Phenotypic plasticity in pigmentation in *Daphnia* induced by UV radiation and fish kairomones[J]. *Functional Ecology*, 2004, 18(4): 497-502.
- [97] ULBING C K S, MUUSE J M, MINER B E. Melanism protects alpine zooplankton from DNA damage caused by ultraviolet radiation[J]. *Proceedings of the Royal Society B: Biological Sciences*, 2019, 286(1914): 20192075.
- [98] HAKKINEN J, VEHNIAINEN E, YLONEN O, et al. The effects of increasing UV-B radiation on pigmentation, growth and survival of coregonid embryos and larvae[J]. *Environmental Biology of Fishes*, 2002, 64(4): 451-459.
- [99] FUKUNISHI Y, MASUDA R, ROBERT D, et al. Comparison of UV-B tolerance between wild and hatchery-reared juveniles of red sea bream (*Pagrus major*) and black sea bream (*Acanthopagrus schlegeli*)[J]. *Environmental Biology of Fishes*, 2013, 96(1): 13-20.
- [100] NORDBORG F M, JONES R J, OELGEMÖLLER M, et al. The effects of ultraviolet radiation and climate on oil toxicity to coral reef organisms—a review[J]. *Science of the Total Environment*, 2020, 720: 137486.
- [101] HÄDER D P, BARNES P W. Comparing the impacts of climate change on the responses and linkages between terrestrial and aquatic ecosystems[J]. *Science of the Total Environment*, 2019, 682: 239-246.
- [102] ROBERTS A P, ALLOY M M, ORIS J T. Review of the photo-induced toxicity of environmental contaminants[J]. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, 2017, 191: 160-167.
- [103] CRAMP R L, REID S, SEEBACHER F, et al. Synergistic interaction between UVB radiation and temperature increases susceptibility to parasitic infection in a fish[J]. *Biology Letters*, 2014, 10(9): 20140449.
- [104] DAVIS A R, COLEMAN D, BROAD A, et al. Complex responses of intertidal molluscan embryos to a warming and acidifying ocean in the presence of UV radiation[J]. *PLoS One*, 2013, 8(2): e55939.
- [105] BARRON M G. Photoenhanced toxicity of petroleum to aquatic invertebrates and fish[J]. *Archives of Environmental Contamination and Toxicology*, 2017, 73(1): 40-46.
- [106] BRIDGES K N, LAY C R, ALLOY M M, et al. Estimating incident ultraviolet radiation exposure in the northern gulf of Mexico during the deepwater horizon oil spill[J]. *Environmental Toxicology and Chemistry*, 2018, 37(6): 1679-1687.
- [107] WILLIS A M, ORIS J T. Acute photo-induced toxicity and toxicokinetics of single compounds and mixtures of polycyclic aromatic hydrocarbons in zebrafish[J]. *Environmental Toxicology and Chemistry*, 2014, 33(9): 2028-2037.
- [108] SWEET L E, REVILL A T, STRZELECKI J, et al. Photo-induced toxicity following exposure to crude oil and ultraviolet radiation in 2 Australian fishes[J]. *Environmental Toxicology and Chemistry*, 2018, 37(5): 1359-1366.
- [109] ALLOY M, BAXTER D, STIEGLITZ J, et al. Ultraviolet radiation enhances the toxicity of Deepwater Horizon oil to mahi-mahi (*Coryphaena hippurus*) embryos[J]. *Environmental Science and Technology*, 2016, 50(4): 2011-2017.
- [110] TARRANT A M, PAYTON S L, REITZEL A M, et al. Ultraviolet radiation significantly enhances the molecular response to dispersant and sweet crude oil exposure in *Nematostella vectensis*[J]. *Marine Environmental Research*, 2018, 134: 96-108.
- [111] FU P P, XIA Q, SUN X, et al. Phototoxicity and environmental transformation of polycyclic aromatic hydrocarbons (PAHs)—light-induced reactive oxygen species, lipid peroxidation, and DNA damage[J]. *Journal of Environmental Science and Health, Part C*, 2012, 30(1): 1-41.
- [112] PHILIBERT D A, LYONS D, PHILIBERT C, et al. Field-collected crude oil, weathered oil and dispersants differentially affect the early life stages of freshwater and saltwater fishes[J]. *Science of the Total Environment*, 2019, 647: 1148-1157.
- [113] KNECHT A L, GOODALE B C, TRUONG L, et al. Comparative developmental toxicity of environmentally relevant oxygenated PAHs[J]. *Toxicology and Applied Pharmacology*, 2013, 271(2): 266-275.
- [114] OVERMANS S, NORDBORG M, RUA R D, et al. Phototoxic effects of PAH and UVA exposure on molecular responses and developmental success in coral larvae[J]. *Aquatic Toxicology*, 2018, 198: 165-174.
- [115] TARRANT A M, REITZEL A M, KWOK C K, et al. Activation of the cnidarian oxidative stress response by ultraviolet radiation, polycyclic aromatic hydrocarbons and crude oil[J]. *Journal of Experimental Biology*, 2014, 217(9): 1444-1453.
- [116] 谭海丽, 王玉堃, 唐学玺, 等. 蒎和 UV-B 辐射增强对海湾扇贝早期发育的影响[J]. *海洋环境科学*, 2013, 32(2): 211-215.
- TAN Haili, WANG Yukun, TANG Xuexi, et al. Effects

of anthracene and UV-B radiation on larvae of *Argopecten irradians*[J]. Marine Environmental Science, 2013, 32(2): 211-215.

[117]JEFFRIES M K S, CLAYTOR C, STUBBLEFIELD W,

et al. Quantitative risk model for polycyclic aromatic hydrocarbon photoinduced toxicity in pacific herring following the *exxon valdez* oil spill[J]. Environmental Science and Technology, 2013, 47(10): 5450-5458.

Research progress in the influence of ultraviolet radiation on fish and aquatic invertebrates

KONG Qing^{1, 2}, SONG Hongce¹, WEI Lei¹, XIE Chaoyi¹, ZHANG Yuxuan¹,
DONG Meiyun¹, GAO Yan³, WANG Xiaotong¹

(1. School of Agriculture, Ludong University, Yantai 264025, China; 2. Yantai Muping District Fishery Technology Promotion Station, Yantai 261499, China; 3. Yantai Marine Economic Research Institute, Yantai 264003, China)

Received: Sep. 30, 2022

Key words: ultraviolet radiation; UVA; UVB; fish; aquatic invertebrates

Abstract: Global climate change poses a significant threat to the balance of the natural ecological environment. Among the various factors affecting ecosystem function, the increased exposure of solar ultraviolet radiation (UVR) is emerging as a serious global environmental concern. Solar UVR plays a pivotal role in the life processes of organisms on Earth. However, excessive absorption of UVR by organisms can disrupt their physiological processes and homeostasis. Specifically, UVR has a damaging effect on DNA that induces a range of adverse biological effects. This paper reviews recent research on the impact of UVR exposure on fish and aquatic invertebrates, summarizing the findings from three perspectives: the impact of UVR on different developmental stages, the response mechanisms of organisms to UVR, and the combined effects of UVR and other factors. Therefore, understanding the effects of UVR on fish and aquatic invertebrates can improve our understanding of its future role in aquatic ecosystems and provide a reference for studying the physiological response of marine organisms to environmental changes.

(本文编辑: 杨 悦)