

# 海洋浮游生物介导的弧菌传播扩散机制研究进展

林建楠<sup>1,2</sup>, 明红霞<sup>2</sup>, 张庆利<sup>3</sup>, 樊景凤<sup>\*1,2</sup>

1 上海海洋大学海洋生态与环境学院, 上海 201306

2 国家海洋环境监测中心 国家生态环境保护近岸海域生态环境重点实验室, 辽宁 大连 116023

3 中国水产科学研究院黄海水产研究所, 山东 青岛 266071

林建楠, 明红霞, 张庆利, 樊景凤. 海洋浮游生物介导的弧菌传播扩散机制研究进展[J]. 微生物学通报, 2023, 50(10): 4681-4693.  
LIN Jiannan, MING Hongxia, ZHANG Qingli, FAN Jingfeng. Marine plankton-associated transmission of vibrios: a review[J].  
Microbiology China, 2023, 50(10): 4681-4693.

**摘要:** 弧菌在全球范围内广泛存在, 弧菌病的暴发和流行不仅给海水养殖业造成巨大的经济损失, 还严重威胁人类健康。一些弧菌可以通过与环境中浮游植物和浮游动物的相互作用提高自身存活率和环境持久性, 并进行跨海域传播。本文综述了海洋浮游生物作为部分弧菌物种储库的作用及影响因素, 以及气候变化和人类活动等因素驱动下浮游生物间接介导的弧菌传播扩散特性; 并重点介绍了弧菌特定的结构、代谢途径和次级代谢产物在其与浮游生物互作过程中发挥的独特作用及其机制; 提出今后应从分子层面深入解析浮游生物与弧菌的相互作用机制, 从全球尺度阐释浮游生物介导的弧菌跨海域传播机制, 建立弧菌疾病传播预测模型和预警系统, 为浮游生物介导的弧菌传播扩散风险的防控提供重要信息。

**关键词:** 弧菌; 浮游生物; 相互作用; 扩散

## Marine plankton-associated transmission of vibrios: a review

LIN Jiannan<sup>1,2</sup>, MING Hongxia<sup>2</sup>, ZHANG Qingli<sup>3</sup>, FAN Jingfeng<sup>\*1,2</sup>

1 College of Marine Ecology and Environment, Shanghai Ocean University, Shanghai 201306, China

2 State Environmental Protection Key Laboratory of Coastal Ecosystem, National Marine Environmental Monitoring Center, Dalian 116023, Liaoning, China

3 Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Qingdao 266071, Shandong, China

**Abstract:** Vibrios are ubiquitous in aquatic environments. The outbreaks of vibriosis cause

资助项目: 辽宁省民生科技计划(2021JH2/10300001); 辽宁省“百千万人才工程”千层次人才项目; 大连市高层次人才创新支持计划(尖端和领军人才项目)(2021RD04); 国家重点研发计划(2017YFC1404500)

This work was supported by the People's Livelihood Science and Technology Project of Liaoning Province (2021JH2/10300001), the Millions of Talent Projects of Liaoning Province, the Dalian High Level Talent Innovation Support Program (2021RD04), and the National Key Research and Development Program of China (2017YFC1404500).

\*Corresponding author. E-mail: jffan@nmemc.org.cn

Received: 2023-03-02; Accepted: 2023-05-04; Published online: 2023-06-09

substantial economic losses to the mariculture industry and seriously threaten human life and health. Some vibrios can improve their survival and environmental persistence and spread across the ocean through interactions with phytoplankton and zooplankton. We describe the role and influencing factors of marine plankton as reservoirs of some vibrios and the plankton-associated transmission characteristics of vibrios upon climate change and human activities. Focuses are put on the unique roles and mechanisms of the specific structures, metabolic pathways, and secondary metabolites of vibrios in the interactions with plankton. Further research should focus on the molecular mechanism of interactions between plankton and vibrios and the mechanism of plankton-associated spreading of vibrios on the global scale. This review provides meaningful information for preventing and controlling the risk of plankton-associated transmission of vibrios.

**Keywords:** *Vibrio*; plankton; interaction; transmission

弧菌(*Vibrio*)是水生环境的自然居民,广泛存在于河口、海湾、近岸海域的海水和海洋动物体内,其中多种弧菌能引发人类和海洋动物疾病,如霍乱弧菌(*Vibrio cholerae*)、创伤弧菌(*V. vulnificus*)、副溶血弧菌(*V. Parahemolyticus*)、鳃弧菌(*V. anguillarum*)、哈维氏弧菌(*V. harveyi*)、非 O1 型霍乱弧菌(non-O1 *V. cholerae*)、费氏弧菌(*V. fischeri*)、弗利斯弧菌(*V. furnissii*)、河弧菌(*V. fluvialis*)、美人鱼弧菌(*V. damsela*)、病海鱼弧菌(*V. ordalii*)、杀鲑弧菌(*V. salmonicida*)、灿烂弧菌(*V. splendidus*)、拟态弧菌(*V. mimicus*)、飘浮弧菌(*V. natriegens*)、远洋弧菌(*V. pelagius*)、火神弧菌(*V. logei*)、粘性弧菌(*V. viscosus*)和鱼肠道弧菌(*V. ichthyornteri*)等。近年来,美国<sup>[1]</sup>、澳大利亚<sup>[2]</sup>、中国<sup>[3]</sup>和坦桑尼亚<sup>[4]</sup>等多个国家报告了沿海水域环境中致病性弧菌的出现,并且其流行范围在逐步扩大。例如,立陶宛首次报告了具有潜在致病性的霍乱弧菌和创伤弧菌<sup>[5]</sup>,英国首次从贝类中检测出重要的水产养殖病原体轮虫弧菌(*V. rotiferianus*)和杀岩龙虾弧菌(*V. jasicida*)<sup>[6]</sup>。因此,了解弧菌在水生环境中的环境持久性可以更有效地监测和管理弧菌疾病的风险。

以往的研究主要集中于弧菌属或单一弧菌物种本身以及非生物因素对弧菌的影响,而忽视了环境中其他生物的作用。法国的一项研究显示,托泻湖中大牡蛎弧菌(*V. crassostreae*)的动态似乎是由温度和浮游生物群落组成共同驱动的,而塔斯曼尼亚弧菌(*V. tasmaniensis*)的动态似乎只由浮游生物群落组成驱动<sup>[7]</sup>。一些弧菌可能通过与浮游生物的相互作用来增加其在环境中的存活率和持久性。例如,研究人员发现桡足类动物在墨西哥沿海地区霍乱弧菌的发生和分布中具有重要作用,而西班牙近海副溶血弧菌的发生几乎完全与浮游动物有关<sup>[8]</sup>;对巴西港口所采集样品的检测发现,浮游生物相关的弧菌比自由生活的弧菌丰度高 2-4 个数量级<sup>[9]</sup>;在韩国巨济岛采集的中型浮游动物样品中副溶血弧菌和创伤弧菌的检出率均高于其相应海水样品<sup>[10]</sup>。浮游生物很可能在水环境中充当部分弧菌的环境储库,从而促进弧菌传播<sup>[11-14]</sup>。

在海洋中,浮游生物与弧菌的相互作用受到多种环境因素的影响,如温度、溶解氧、盐度等<sup>[15-17]</sup>。自 20 世纪 60 年代至 21 世纪初,大西洋东岸海水中总弧菌浓度持续增长,弧菌在浮游生物相关细菌群落中的占比有所提高,海水变

暖可能是这一长期变化的主要驱动因素<sup>[16,18]</sup>。20世纪90年代初,南美洲霍乱的出现时间和空间上都与重大厄尔尼诺事件相吻合,并且霍乱发病率与海面温度升高之间存在显著相关性<sup>[19-20]</sup>。海水变暖、厄尔尼诺等全球气候事件很可能会增加浮游生物介导的弧菌传播风险<sup>[1,21]</sup>。同时,跨国航行等人类活动以及以浮游生物为食物的水鸟很可能为弧菌提供了跨海域传播的便利。浮游生物相关的弧菌在水生环境中的持久性受到自身与环境多种因素的调节<sup>[22]</sup>,阐明不断变化的环境因素如何影响浮游生物相关弧菌病原体传播以及相互作用机制,可以为浮游生物介导的人类和海洋生物致病性弧菌防控提供重要信息。

## 1 浮游动物直接介导弧菌的传播扩散

### 1.1 弧菌与浮游动物的相互作用

大量研究报道了弧菌与产生几丁质的浮游动物之间具有密切的联系。大多数弧菌物种都能够通过降解几丁质获得氮(N)和碳(C),与几丁质降解相关的基因几乎存在于所有已测序的弧菌属细菌中<sup>[23]</sup>。例如,在孟加拉国南部,霍乱弧菌的检出和霍乱病例的发生始终与该海域的桡足类、轮虫和枝角类等浮游动物存在相关性<sup>[24]</sup>。霍乱弧菌和副溶血弧菌能够通过附着于活的桡足类动物体表而显著延长其在水中的存活时间,且不会对桡足类动物产生明显的不利影响<sup>[11]</sup>。Abd等<sup>[25]</sup>将棘阿米巴和霍乱弧菌共培养,发现棘阿米巴抵抗不利的温度、pH和多种化学药品的能力为其胞内的霍乱弧菌提供重要的保护作用。浮游动物是一些弧菌在水环境中的重要宿主,浮游动物可以充当附着底物,为弧菌提供庇护,从而促进弧菌的环境持久性、水平基因转移以及弧菌疾病的传播<sup>[26-27]</sup>。在清洁水源有限的地方,通

用过纱布布料过滤受污染的水可以去除99%的浮游生物和附着其上的霍乱弧菌,从而显著降低霍乱的发病率<sup>[28]</sup>。

### 1.2 弧菌与浮游动物相互作用的影响因素

弧菌通过多种机制附着于浮游动物,不同弧菌与浮游动物组合间的相互作用存在显著差异,这些差异可能反映了这些生物所处生态环境的不同<sup>[29-30]</sup>。已有许多研究表明弧菌的丰度和检出率与温度、盐度等环境因素密切相关<sup>[31-32]</sup>,尤其是当这些弧菌与浮游生物相关时<sup>[15,33]</sup>。海水中弧菌的丰度表现出强烈的季节性,在夏季水域较温暖的月份最为丰富。当水温超过15℃、盐度在5-25之间时,副溶血弧菌的丰度通常会增加,如果这些副溶血弧菌与浮游生物有关,丰富的有机分泌物会刺激副溶血弧菌种群迅速增长<sup>[34]</sup>。在全球范围内,水环境中的非O1/O139霍乱弧菌(non-O1/O139 *Vibrio cholerae*, NOVC)菌株及其相关的人类感染呈上升趋势,并且这一趋势与水温和盐度的持续变化密切相关<sup>[35]</sup>。

环境因素通过多种方式影响弧菌与浮游动物的相互作用。温度上升会增强副溶血弧菌和霍乱弧菌的结构基因 *mshA* 的表达,产生较高水平的甘露糖敏感血凝素(mannose-sensitive haemagglutinin, MSHA),促进弧菌在几丁质表面的定殖,这是温度影响弧菌附着浮游动物的主要机制之一<sup>[36-37]</sup>。霍乱弧菌冷休克基因 *cspV* 通过调节第二信使环二鸟苷酸来控制生物膜的形成,并以温度依赖的方式调节VI型分泌介导的种间杀伤,这种种间杀伤能改变浮游动物表面微生物群落的组成,进而对浮游动物的生理产生影响<sup>[38]</sup>。霍乱弧菌生长的最佳盐度在5-25之间,但在有足够溶解有机质存在时,霍乱弧菌也可以在接近45的盐度下正常生长<sup>[39]</sup>。因此,浮游动物很可能通过提供溶解有机质增强部分弧菌物种在高盐度环境中的存活能力。

### 1.3 弧菌与浮游动物的相互作用机制

对几丁质的附着是弧菌与浮游动物相互作用的重要基础,结合几丁质的能力使弧菌能够附着于浮游动物的体表、口器和肠道等部位,规避捕食压力<sup>[11]</sup>。几丁质结合蛋白(chitin-binding proteins, CBPs)在环境和临床弧菌菌株中普遍存在, CBPs 介导弧菌细胞识别和不可逆黏附几丁质底物的过程,在弧菌与几丁质表面的相互作用中发挥重要作用<sup>[15,40]</sup>。*gbpA* 基因在霍乱弧菌中普遍存在且高度保守,其表达产物 N-乙酰氨基葡萄糖结合蛋白(N-acetylglucosamine-binding protein A, GbpA)已被证明在霍乱弧菌定殖于海洋几丁质和哺乳动物肠道粘蛋白的过程中发挥重要作用<sup>[41]</sup>。在海洋环境中, GbpA 的结构域 1 和结构域 4 提供了对不同类型结晶几丁质的多种结合特性,使弧菌能够附着并定殖于一系列甲壳类动物<sup>[42]</sup>。

IV型菌毛 MSHA 是促成霍乱弧菌黏附浮游动物的重要因素<sup>[36,43]</sup>,并且和几丁质调节菌毛 PilA 等其他IV型菌毛共同介导了副溶血弧菌对几丁质的黏附和生物膜的形成<sup>[44-45]</sup>。MSHA 菌毛在介导霍乱弧菌与浮游动物的附着方面比 GbpA 有效得多<sup>[41]</sup>。霍乱弧菌使用极性鞭毛和 MSHA 菌毛协同作用,在附着之前对几丁质表面进行机械性扫描,而后 MSHA 菌毛与几丁质表面结合,这对于阻止表面附近的细胞运动以及过渡到表面附着和生物膜的形成至关重要<sup>[46]</sup>。

弧菌并不只是简单地附着在浮游动物上,它们通过多种途径利用浮游动物。桡足类动物相关的弧菌可以使用碱性磷酸酶分解源自桡足类动物的有机磷酸酯来应对环境中磷营养的限制,桡足类动物可能会将这些弧菌带到更多需要表达碱性磷酸酶的生物体表面,促进这些弧菌的扩散<sup>[47]</sup>。近年有研究发现,霍乱弧菌在光照条件下会增加其宿主甲壳类浮游动物 *Daphnia*

*pulicaria* 的活跃性,这可能使宿主个体更容易被鱼类等捕食者捕获,弧菌可以借此进入水生食物链进一步扩散<sup>[48]</sup>。对于 *D. pulicaria* 种群而言,消除受感染的个体能降低其他个体被感染的可能性,因此从某种意义上说,这种相互作用对弧菌和宿主都是有益的。在液体环境中,副溶血弧菌集群可以持续释放细胞,释放的冒险细胞具有较强的游动能力,能够趋化至几丁质化合物并最终附着在几丁质表面<sup>[49]</sup>。弧菌在浮游动物体表形成生物膜后多个基因的表达水平发生变化,其传播能力、毒力和抗生素耐药性显著增强<sup>[50-51]</sup>。

浮游动物也不是被动地作为弧菌的环境载体,而是与弧菌相互作用,影响其丰度和活性。例如,河口桡足类动物近亲真宽水蚤(*Eurytemora affinis*)暴露于弧菌后,其包括皂素类和 C 型凝集素在内的多个基因表达发生变化<sup>[52]</sup>。皂素可以作为形成跨膜孔隙的抗菌肽应对微生物感染<sup>[53]</sup>,结合甘露糖的 C 型凝集素可以作为模式识别蛋白,承担从环境中获取共生细菌的功能<sup>[54]</sup>。但高度保守的系统性先天免疫途径的组成部分,如 Toll 和 IMD 信号通路并未被上调表达,这表明弧菌引起的免疫反应具有特异性,近亲真宽水蚤很可能通过有针对性地调节免疫元件对弧菌的反应主动识别和维持共生弧菌<sup>[52]</sup>。弧菌与浮游生物间多种相互作用的分子基础尚不明确,仍需要更多的研究来阐明其中的机制,并揭示温度、盐度等环境因素如何参与调节这些过程。

## 2 浮游植物直接介导的弧菌传播扩散

### 2.1 弧菌与浮游植物的相互作用

越来越多的证据表明,一些弧菌与浮游植物存在密切的联系。Constantin 等<sup>[55]</sup>通过卫星和原位测量仪发现印度加尔各答发生霍乱的时间与

较高的叶绿素 a 浓度存在显著相关性;较高的叶绿素 a 浓度反映了强烈的藻华,藻华促进甲壳类、桡足类等浮游动物种群的增长,进而促进霍乱弧菌的传播。Michotey 等<sup>[56]</sup>的研究发现,马尾藻的生长速度是影响弧菌发生的重要因素,所有有利于马尾藻生长的区域都有可能成为弧菌的潜在来源,而桡足类等浮游动物的存在则不利于马尾藻相关弧菌的出现。这表明浮游植物不只是通过促进浮游动物的生长间接地影响弧菌种群,浮游植物与弧菌之间还存在直接的相互作用。

浮游植物也是弧菌的重要环境宿主。弧菌通过与浮游植物结合来增加其在环境中的存活率和持久性<sup>[57]</sup>。Main 等<sup>[58]</sup>通过定量 PCR 分析了在美国特拉华州内陆海湾形成藻华的甲藻、硅藻和针藻,结果表明,颗粒吸附型弧菌丰度与这些浮游植物存在显著相关性。在美国南卡罗来纳州海域,创伤弧菌和副溶血弧菌的丰度与鞭毛藻藻华显著正相关<sup>[59]</sup>。Asplund 等<sup>[60]</sup>研究了印度西南沿海水域与浮游植物相关的细菌群落,发现浮游植物的高生物量和高多样性有利于弧菌的生长。这些研究共同表明,浮游植物与弧菌之间的关系以正相关为主,并且藻华很可能强化了它们之间的相互作用。阐明弧菌群落与浮游植物之间的相关性将有利于评估海洋生态系统的生态效应和公共卫生风险。

## 2.2 弧菌与浮游植物相互作用的影响因素

弧菌与浮游生物群落的相互作用影响着海洋生态和人类健康<sup>[1]</sup>。弧菌与浮游植物之间的相互作用受到海水中多种非生物因素的影响,包括温度、盐度、溶解氧、总有机氮、磷酸盐等,这些非生物因素被认为是浮游植物相关致病性弧菌生长和分布的主要驱动力<sup>[2,61]</sup>,并且在藻华期间这些因素对浮游植物和弧菌之间相互作用的影响比藻华前后都更明显<sup>[62-63]</sup>。

弧菌属的总体变化趋势并不一定反映单个弧菌物种的趋势。副溶血弧菌和创伤弧菌往往受温度的影响更大,而霍乱弧菌与特定浮游植物的相关性可能比非生物变量更强。特定弧菌与浮游植物的联系必须在二者共同环境生态偏好的背景下评价。许多研究表明,创伤弧菌与营养物质、藻华之间均存在强相关性<sup>[59]</sup>,但 Rosales 等观察到创伤弧菌与鞭毛藻和甲藻之间存在弱相关性,这表明不同弧菌和浮游植物组合之间的关系是特异性的,并且很可能受到特定营养物质的影响<sup>[63]</sup>。硅藻与高丰度副溶血弧菌、高温、高盐度显著正相关,但与创伤弧菌负相关<sup>[58]</sup>。这可能是由于它们的环境偏好不同,副溶血弧菌的丰度与较高的盐度有关,而创伤弧菌与较低盐度有关<sup>[1]</sup>。共同的环境条件调节着浮游植物与弧菌的相互作用,使得弧菌对藻华的反应表现出高度异质性。

## 2.3 弧菌与浮游植物的相互作用机制

浮游植物可能通过提供营养丰富的微环境而在弧菌的生态中起着至关重要的作用。Stabili 等<sup>[64]</sup>在意大利南亚得里亚海发现弧菌数量增长的高峰往往在浮游植物藻华后约 1-2 月出现,即使承受原生动物的强烈捕食压力,藻华期间颗粒吸附型的弧菌丰度仍迅速增加<sup>[59]</sup>。浮游植物大量繁殖期间释放的溶解有机质很可能导致弧菌在海水中的爆炸性生长,并促进弧菌的扩散<sup>[12,62]</sup>。在印度和孟加拉国地区,已有研究人员尝试利用卫星传感器测量的叶绿素 a 浓度(指示浮游植物生物量)和海面温度数据建立霍乱的预测模型<sup>[55]</sup>。

Eiler 等<sup>[65]</sup>将霍乱弧菌、创伤弧菌、副溶血弧菌、溶藻弧菌(*V. alginolyticus*)接种于模拟波罗的海微型生态系统中,在提供不同浓度蓝藻来源有机物的条件下,产生了不同的弧菌群落,随着有机物浓度升高,霍乱弧菌数量增加,而其他弧菌数量减少。在海洋环境中,霍乱弧菌与蓝藻的

正相关性以及创伤弧菌、副溶血弧菌与蓝藻的负相关性已在其他研究中得到验证,然而溶藻弧菌与蓝藻却呈现显著的正相关<sup>[2,5]</sup>。这表明存在其他因素参与调节浮游植物与弧菌互作关系。尤其是在藻华期间,藻华扰乱了浮游植物和弧菌的原始栖息地,使更多的营养和生物因子参与调节浮游植物和弧菌的生长和种群动态<sup>[66]</sup>。浮游植物可以分泌多种碳源,为异养弧菌生存和生长提供重要底物<sup>[67-68]</sup>。然而,存在浮游植物来源的溶解有机质情况下,弧菌的生长响应具有高度异质性<sup>[69]</sup>。这可能是因为弧菌能选择性地利用特定底物来增强自身对环境胁迫的耐受性。藻华期间弧菌与浮游植物之间的相互作用受到活性化合物和代谢物的严格调节<sup>[62]</sup>。Amin 等<sup>[67]</sup>在藻华中检测到弧菌与群体感应相关的 LuxS 蛋白和调节细胞密度的转录调控因子 AphA,表明部分弧菌可以协调其群体行为以响应藻华体系的转变;而某些藻类也能通过分泌物影响弧菌,例如利用甘露醇诱导霍乱弧菌中生物膜基因的转录<sup>[70-71]</sup>。

一些浮游植物通过与弧菌共生应对不利的环境条件。例如,在硝酸盐有限的环境中,弧菌的硝酸盐异化还原成铵(dissimilatory nitrate reduction to ammonium, DNRA)作用可能在弧菌和浮游植物之间的互利共生中发挥关键作用,这种微生物介导的氮转化反应可能会改变总体氮的可用性以及氮的形态,从而影响浮游植物的氮供应<sup>[72]</sup>。一些弧菌菌株对有机磷的矿化作用可以在原位富集无机磷,并增加磷对浮游植物的生物利用度,从而有助于藻华的形成<sup>[73]</sup>。但弧菌与浮游植物之间并不总是互惠的,溶藻弧菌能产生具有强杀藻活性的胞外物质,裂解某些浮游植物的细胞或抑制其生长<sup>[74]</sup>。弧菌与浮游植物分泌的代谢物是它们相互作用的重要途径,进一步开展研究来表征这些相互作用中涉及的生理

生化过程,将有可能推动弧菌成为预测海洋环境和生态变化的生物指标或控制有害藻华的生物工具。

### 3 浮游生物间接介导的弧菌跨海域传播扩散

弧菌与浮游生物间的紧密联系很可能会增加沿海居民和游客在娱乐海域活动时感染病原性弧菌的可能性<sup>[31]</sup>。海洋浮游生物是悬浮在水体中的生物群,主要在水流作用下被动移动。当河流流量较低时,潮汐入侵很可能将浮游生物相关的致病性弧菌带到内陆,引发弧菌疾病的局部流行<sup>[55]</sup>。秘鲁的一项研究显示秘鲁沿海出现了先前只在亚洲发现过的副溶血弧菌遗传变体,并且基因组分析结果表明这类副溶血弧菌在南美的引入与浮游生物有关<sup>[19]</sup>。这表明在其他因素(如人类活动、其他生物或非生物因素)的作用下,浮游生物也可能间接参与介导弧菌的跨海域传播,在弧菌的跨海域传播过程中发挥重要作用。

#### 3.1 气候变化影响下的弧菌传播

在全球变暖的长期趋势下,全球海洋持续变暖<sup>[75]</sup>。一项时间跨度长达半个世纪的研究显示,在海水变暖的影响下,大西洋北海南部与浮游生物相关的细菌群落结构发生了重大变化,包括霍乱弧菌在内的弧菌属优势度显著增加<sup>[18]</sup>。海水变暖影响细菌的生长、可培养性、致病性和基因表达以及浮游动物的发育、物候、大小、结构等,这可能会增强弧菌与浮游动物间的相互作用并导致弧菌疾病在更大范围内传播<sup>[76]</sup>。例如,Doni 等<sup>[77]</sup>发现 2016 年大堡礁区域的海洋热浪事件对海水表层浮游生物群落产生了重大影响,并促进了潜在致病性弧菌的传播,对该地区的海洋生物多样性构成了威胁。因此,近几十年来海洋温度

的上升被认为是人类弧菌感染发病率增加的最重要驱动因素之一。

Gil 等<sup>[20]</sup>在 1997 年 10 月至 2000 年 6 月研究了秘鲁沿岸海水和浮游生物中霍乱弧菌的发生和分布,观察到霍乱病例的增加与秘鲁沿岸海面温度之间存在显著相关性,霍乱弧菌的扩散发生在与厄尔尼诺现象相关的温度升高期间。Martinez-Urtaza 等<sup>[78]</sup>分析了厄尔尼诺事件与副溶血弧菌引发的疾病发生率之间的关联,认为厄尔尼诺的发生很可能推动了副溶血弧菌在南美的引入和传播。厄尔尼诺现象会导致暖水从太平洋西侧向东侧带状位移,太平洋西侧的浮游生物很可能随着海水的运动到达秘鲁和智利。浮游生物提供的营养来源和保护使同样来自太平洋西侧的弧菌能够方便地搭载进入秘鲁沿岸<sup>[19]</sup>。目前仍需更多跨海域研究和基因组学证据来阐明全球气候变化促进浮游生物相关弧菌跨海域传播的可能性和潜在风险,以便及时采取防范措施。

### 3.2 跨国航运影响下的弧菌传播

跨国航行等人类活动也可能助推了浮游生物相关弧菌的跨海域传播。船舶压载水是沿海海洋物种的一种潜在转移机制(载体),在全球数百起有记录的海洋生物入侵事件中,至少三分之一与船舶压载水有关<sup>[79-80]</sup>。已有研究表明弧菌在压载水中并不常见<sup>[81-83]</sup>,例如,巴西港口船舶压载水样品中弧菌的检出率显著低于港口地区的海水样品,这可能与压载水中浮游动物死亡率增加伴随的几丁质底物损失有关<sup>[9]</sup>。但压载水中与浮游生物相关的弧菌丰度很可能被低估了。一方面,死亡的浮游动物最终会沉降到底部沉积物,浮游动物的尸体能为弧菌提供保护,使其免受环境压力的影响<sup>[11]</sup>;另一方面,一些浮游生物(例如硅藻)可以在低光或黑暗的压舱水中存活很长时间,为弧菌提供附着底物和营养物质<sup>[84]</sup>。一旦

跨国货船受污染的压载水排放入环境,致病性弧菌种群可能会与本地种群发生遗传上的相互作用,从而为霍乱等弧菌疾病的暴发创造条件<sup>[9]</sup>。因此,对压载水排放的管理有必要将浮游生物相关弧菌的风险纳入考虑。

### 3.3 水鸟介导的弧菌传播

由于其迁徙特性,水鸟很可能充当跨海域传播病原体的媒介,对人类和海洋生物的健康产生重要影响。桡足类动物等浮游生物可以从外部附着在鸟的体表和羽毛上,水鸟可能直接携带受弧菌污染的浮游生物迁徙<sup>[85]</sup>。

霍乱弧菌可以附着在鱼类肠道上皮并形成微生物落,在肠道中参与几丁质的降解,因此,鱼类宿主与霍乱弧菌可能存在共生关系<sup>[86]</sup>。鱼类以桡足类动物为食,这可能是鱼类体内弧菌的重要来源。已有研究表明,一些桡足类动物和弧菌可以在几种水鸟的肠道中存活,水鸟食用与弧菌共生的鱼类后,其肠道内很可能存在活的弧菌,这些弧菌可以随排泄物从水鸟体内排出<sup>[87]</sup>。许多水鸟在海洋和淡水流域之间活动,它们很可能在短时间内在大陆内部和大陆之间传播霍乱弧菌、副溶血弧菌等致病性弧菌<sup>[88-89]</sup>。目前,上述结果仅是基于已有研究的一种推测,仍需要进一步的证据明确水鸟在浮游生物相关弧菌跨海域传播中的作用。

## 4 总结与展望

作为一些弧菌物种重要的环境储库,浮游生物在水环境中为弧菌提供附着底物和营养物质,在促进弧菌的环境持久性、弧菌疾病传播等方面起重要作用。弧菌可以利用几丁质结合蛋白或IV型菌毛附着于浮游动物的几丁质外壳,并且附着过程受到温度的显著影响。浮游植物大量繁殖期间释放的溶解有机质为弧菌的生长提供营养来源,这可能是浮游植物与弧菌间高度异质性相互

作用的重要基础。弧菌与浮游生物之间的相互作用不仅取决于浮游生物的丰度,而且还取决于海水中存在的特定浮游生物类群。但弧菌与浮游生物宿主的分子相互作用信息仍然缺乏,大多数关于弧菌与浮游生物间联系报道只是描述性的,难以确定相关弧菌疾病暴发的起源以及监测弧菌的传播。未来应充分应用分子遗传学和基因组学方法检测浮游生物种类和弧菌物种间的特定关联,尤其是应从分子层面解释浮游生物与弧菌的相互作用机制,包括温度、盐度等环境因素调节二者相互作用的机制。

以往的研究大多以月或年为采样间隔,无法了解弧菌和浮游生物群落的短期动态。后续应考虑结合实验室和野外的观察数据,在较短的时间尺度上分析弧菌和浮游生物的短期变化及涉及的机制。然而在全球气候变化的背景下,需要在更长的时间尺度上对区域内浮游生物影响下弧菌多样性的变化趋势进行比较性的观察和描述,包括弧菌种群遗传多样性的变化。全球尺度的气候变化如何影响浮游生物与弧菌的相互作用,以及利用基因组学技术分析浮游生物介导弧菌的跨海域传播的途径也是该领域未来重要的研究方向。相关的研究成果可能会为预测海洋生态系统中弧菌的发生提供重要的信息。建议未来建立国际研究合作网络,收集世界范围内浮游生物与弧菌间可能的互作关系以及浮游生物相关弧菌的长期或短期动态,开发一个数据库,实现全球数据共享,便于后续研究的开展。同时可为相关部门进一步建立弧菌疾病传播预测模型和预警系统,及时调整公共卫生规划和决策等提供重要参考,进而有效管控浮游生物相关弧菌的传播风险。

## REFERENCES

- [1] DINER RE, KAUL D, RABINES A, ZHENG H, STEELE JA, GRIFFITH JF, ALLEN AE. Pathogenic *Vibrio* species are associated with distinct environmental niches and planktonic taxa in southern California (USA) aquatic microbiomes[J]. *mSystems*, 2021, 6(4): e0057121.
- [2] PADOVAN A, SIBONI N, KAESTLI M, KING WL, SEYMOUR JR, GIBB K. Occurrence and dynamics of potentially pathogenic vibrios in the wet-dry tropics of northern Australia[J]. *Marine Environmental Research*, 2021, 169: 105405.
- [3] MING HX, MA YJ, GU YB, SU J, GUO JL, LI JY, LI X, JIN Y, FAN JF. Enterococci may not present the pollution of most enteric pathogenic bacteria in recreational seawaters of Xinghai bathing Beach, China[J]. *Ecological Indicators*, 2020, 110: 105938.
- [4] HOUNMANOU YMG, LEEKITCHAROENPHON P, HENDRIKSEN RS, DOUGNON TV, MDEGELA RH, OLSEN JE, DALSGAARD A. Surveillance and genomics of toxigenic *Vibrio cholerae* O1 from fish, phytoplankton and water in Lake Victoria, Tanzania[J]. *Frontiers in Microbiology*, 2019, 10: 901.
- [5] GYRAITE G, KATARYT M, SCHERNEWSKI G. First findings of potentially human pathogenic bacteria *Vibrio* in the south-eastern Baltic Sea coastal and transitional bathing waters[J]. *Marine Pollution Bulletin*, 2019, 149: 110546.
- [6] HARRISON J, NELSON K, MORCRETTE H, MORCRETTE C, PRESTON J, HELMER L, TITBALL RW, BUTLER CS, WAGLEY S. The increased prevalence of *Vibrio* species and the first reporting of *Vibrio jasicida* and *Vibrio rotiferianus* at UK shellfish sites[J]. *Water Research*, 2022, 211: 117942.
- [7] LOPEZ-JOVEN C, ROLLAND JL, HAFFNER P, CARO A, ROQUES C, CARRÉ C, TRAVERS MA, ABADIE E, LAABIR M, BONNET D, DESTOUMIEUX-GARZÓN D. Oyster farming, temperature, and plankton influence the dynamics of pathogenic vibrios in the Thau Lagoon[J]. *Frontiers in Microbiology*, 2018, 9: 2530.
- [8] LIZÁRRAGA-PARTIDA ML, MENDEZ-GÓMEZ E, RIVAS-MONTAÑO AM, VARGAS-HERNÁNDEZ E, PORTILLO-LÓPEZ A, GONZÁLEZ-RAMÍREZ AR, HUQ A, COLWELL RR. Association of *Vibrio cholerae* with plankton in coastal areas of Mexico[J]. *Environmental Microbiology*, 2009, 11(1): 201-208.
- [9] RIVERA ING, SOUZA KMC, SOUZA CP, LOPES RM. Free-living and plankton-associated vibrios: assessment in ballast water, harbor areas, and coastal ecosystems in Brazil[J]. *Frontiers in Microbiology*, 2013, 3: 443.



- [10] YANG JH, MOK JS, JUNG YJ, LEE KJ, KWON JY, PARK K, MOON SY, KWON SJ, RYU AR, LEE TS. Distribution and antimicrobial susceptibility of *Vibrio* species associated with zooplankton in coastal area of Korea[J]. Marine Pollution Bulletin, 2017, 125(1-2): 39-44.
- [11] HUQ A, SMALL EB, WEST PA, HUQ MI, RAHMAN R, COLWELL RR. Ecological relationships between *Vibrio cholerae* and planktonic crustacean copepods[J]. Applied and Environmental Microbiology, 1983, 45(1): 275-283.
- [12] MOURIÑO-PÉREZ RR, WORDEN AZ, AZAM F. Growth of *Vibrio cholerae* O1 in red tide waters off California[J]. Applied and Environmental Microbiology, 2003, 69(11): 6923-6931.
- [13] ERKEN M, LUTZ C, McDOUGALD D. Interactions of *Vibrio* spp. with zooplankton[J]. Microbiology Spectrum, 2015, 3(3): 3.3.02.
- [14] ISLAM MS, ZAMAN MH, ISLAM MS, AHMED N, CLEMENS JD. Environmental reservoirs of *Vibrio cholerae*[J]. Vaccine, 2020, 38: A52-A62.
- [15] PRUZZO C, CRIPPA A, BERTONE S, PANE L, CARLI A. Attachment of *Vibrio alginolyticus* to chitin mediated by chitin-binding proteins[J]. Microbiology, 1996, 142(8): 2181-2186.
- [16] VEZZULLI L, GRANDE C, REID PC, HÉLAAOUËT P, EDWARDS M, HÖFLE MG, BRETTAR I, COLWELL RR, PRUZZO C. Climate influence on *Vibrio* and associated human diseases during the past half-century in the coastal North Atlantic[J]. Proceedings of the National Academy of Sciences of the United States of America, 2016, 113(34): E5062-E5071.
- [17] NAIR S, ZHANG ZH, LI HM, ZHAO HS, SHEN H, KAO SJ, JIAO NZ, ZHANG YY. Inherent tendency of *Synechococcus* and heterotrophic bacteria for mutualism on long-term coexistence despite environmental interference[J]. Science Advances, 2022, 8(39): eabf4792.
- [18] VEZZULLI L, BRETTAR I, PEZZATI E, REID PC, COLWELL RR, HÖFLE MG, PRUZZO C. Long-term effects of ocean warming on the prokaryotic community: evidence from the vibrios[J]. The ISME Journal, 2012, 6(1): 21-30.
- [19] MARTINEZ-URTAZA J, TRINANES J, GONZALEZ-ESCALONA N, BAKER-AUSTIN C. Is El Niño a long-distance corridor for waterborne disease?[J]. Nature Microbiology, 2016, 1(3): 16018.
- [20] GIL AI, LOUIS VR, RIVERA ING, LIPP E, HUQ A, LANATA CF, TAYLOR DN, RUSSEK-COHEN E, CHOOPUN N, SACK RB, COLWELL RR. Occurrence and distribution of *Vibrio cholerae* in the coastal environment of Peru[J]. Environmental Microbiology, 2004, 6(7): 699-706.
- [21] LIANG JC, LIU JW, WANG XL, LIN HY, LIU JL, ZHOU S, SUN H, ZHANG XH. Spatiotemporal dynamics of free-living and particle-associated *Vibrio* communities in the northern Chinese marginal seas[J]. Applied and Environmental Microbiology, 2019, 85(9): e00217-19.
- [22] HARTWICK MA, BERENSON A, WHISTLER CA, NAUMOVA EN, JONES SH. The seasonal microbial ecology of plankton and plankton-associated *Vibrio parahaemolyticus* in the northeast United States[J]. Applied and Environmental Microbiology, 2021, 87(15): e02973-20.
- [23] PRUZZO C, VEZZULLI L, COLWELL RR. Global impact of *Vibrio cholerae* interactions with chitin[J]. Environmental Microbiology, 2008, 10(6): 1400-1410.
- [24] MAGNY GC, MOZUMDER PK, GRIM CJ, HASAN NA, NASER MN, ALAM M, SACK RB, HUQ A, COLWELL RR. Role of zooplankton diversity in *Vibrio cholerae* population dynamics and in the incidence of cholera in the Bangladesh sundarbans[J]. Applied and Environmental Microbiology, 2011, 77(17): 6125-6132.
- [25] ABD H, WEINTRAUB A, SANDSTRÖM G. Intracellular survival and replication of *Vibrio cholerae* O139 in aquatic free-living amoebae[J]. Environmental Microbiology, 2005, 7(7): 1003-1008.
- [26] MAUGERI TL, CARBONE M, FERA MT, GUGLIANDOLO C. Detection and differentiation of *Vibrio vulnificus* in seawater and plankton of a coastal zone of the Mediterranean Sea[J]. Research in Microbiology, 2006, 157(2): 194-200.
- [27] NEOGI SB, ISLAM MS, NAIR GB, YAMASAKI S, LARA RJ. Occurrence and distribution of plankton-associated and free-living toxigenic *Vibrio cholerae* in a tropical estuary of a cholera endemic zone[J]. Wetlands Ecology and Management, 2012, 20(3): 271-285.
- [28] NOORIAN P, HOQUE MM, ESPINOZA-VERGARA G, McDOUGALD D. Environmental reservoirs of pathogenic *Vibrio* spp. and their role in disease: the list keeps expanding[J]. Advances in Experimental Medicine and Biology, 2023, 1404: 99-126.
- [29] LI D, HE Y, ZHENG Y, ZHANG S, ZHANG H, LIN L, WANG D. Metaproteomics reveals unique metabolic

- niches of dominant bacterial groups in response to rapid regime shifts during a mixed dinoflagellate bloom[J]. *Science of the Total Environment*, 2022, 823: 153557.
- [30] ALMADA AA, TARRANT AM. *Vibrio* elicits targeted transcriptional responses from copepod hosts[J]. *FEMS Microbiology Ecology*, 2016, 92(6): fiw072.
- [31] 明红霞, 张颖雪, 金媛, 苏洁, 石岩, 樊景凤. 大连典型浴场海水中粪源指示细菌和土著病原弧菌的流行分布[J]. *生物学杂志*, 2020, 37(2): 52-56.  
MING HX, ZHANG YX, JIN Y, SU J, SHI Y, FAN JF. Distribution of fecal indicator bacteria and indigenous pathogenic vibrio in the seawater of Dalian typical bathing beach[J]. *Journal of Biology*, 2020, 37(2): 52-56 (in Chinese).
- [32] 郭建丽, 王玥, 李江宇, 明红霞, 苏洁, 关道明, 王斌, 樊景凤. 大连重要海水增养殖区粪便污染指示菌和弧菌的时空分布[J]. *海洋环境科学*, 2017, 36(6): 813-819.  
GUO JL, WANG Y, LI JY, MING HX, SU J, GUAN DM, WANG B, FAN JF. Spatial and temporal distribution of fecal indicator bacteria and vibrios in the mariculture zones of Dalian[J]. *Marine Environmental Science*, 2017, 36(6): 813-819 (in Chinese).
- [33] WANG XL, LIU JW, LI B, LIANG JC, SUN H, ZHOU S, ZHANG XH. Spatial heterogeneity of *Vibrio* spp. in sediments of Chinese marginal seas[J]. *Applied and Environmental Microbiology*, 2019, 85(10): e03064-18.
- [34] TAKEMURA AF, CHIEN DM, POLZ MF. Associations and dynamics of Vibrionaceae in the environment, from the genus to the population level[J]. *Frontiers in Microbiology*, 2014, 5: 38.
- [35] VEZZULLI L, BAKER-AUSTIN C, KIRSCHNER A, PRUZZO C, MARTINEZ-URTAZA J. Global emergence of environmental non-O1/O139 *Vibrio cholerae* infections linked with climate change: a neglected research field?[J]. *Environmental Microbiology*, 2020, 22(10): 4342-4355.
- [36] STAUDER M, VEZZULLI L, PEZZATI E, REPETTO B, PRUZZO C. Temperature affects *Vibrio cholerae* O1 El Tor persistence in the aquatic environment via an enhanced expression of GbpA and MSHA adhesins[J]. *Environmental Microbiology Reports*, 2010, 2(1): 140-144.
- [37] BILLAUD M, SENECA F, TAMBUTTÉ E, CZERUCKA D. An increase of seawater temperature upregulates the expression of *Vibrio parahaemolyticus* virulence factors implicated in adhesion and biofilm formation[J]. *Frontiers in Microbiology*, 2022, 13: 840628.
- [38] TOWNSLEY L, SISON MANGUS MP, MEHIC S, YILDIZ FH. Response of *Vibrio cholerae* to low-temperature shifts: CspV regulation of type VI secretion, biofilm formation, and association with zooplankton[J]. *Applied and Environmental Microbiology*, 2016, 82(14): 4441-4452.
- [39] SINGLETON FL, ATTWELL R, JANGI S, COLWELL RR. Effects of temperature and salinity on *Vibrio cholerae* growth[J]. *Applied and Environmental Microbiology*, 1982, 44(5): 1047-1058.
- [40] VEZZULLI L, PEZZATI E, REPETTO B, STAUDER M, GIUSTO G, PRUZZO C. A general role for surface membrane proteins in attachment to chitin particles and copepods of environmental and clinical vibrios[J]. *Letters in Applied Microbiology*, 2008, 46(1): 119-125.
- [41] STAUDER M, HUQ A, PEZZATI E, GRIM CJ, RAMOINO P, PANE L, COLWELL RR, PRUZZO C, VEZZULLI L. Role of GbpA protein, an important virulence-related colonization factor, for *Vibrio cholerae*'s survival in the aquatic environment[J]. *Environmental Microbiology Reports*, 2012, 4(4): 439-445.
- [42] WONG E, VAAJE-KOLSTAD G, GHOSH A, HURTADO-GUERRERO R, KONAREV PV, IBRAHIM AFM, SVERGUN DI, EIJSINK VGH, CHATTERJEE NS, van AALTEN DMF. The *Vibrio cholerae* colonization factor GbpA possesses a modular structure that governs binding to different host surfaces[J]. *PLoS Pathogens*, 2012, 8(1): e1002373.
- [43] CHIAVELLI DA, MARSH JW, TAYLOR RK. The mannose-sensitive hemagglutinin of *Vibrio cholerae* promotes adherence to zooplankton[J]. *Applied and Environmental Microbiology*, 2001, 67(7): 3220-3225.
- [44] FRISCHKORN KR, STOJANOVSKI A, PARANJPYE R. *Vibrio parahaemolyticus* type IV pili mediate interactions with diatom-derived chitin and point to an unexplored mechanism of environmental persistence[J]. *Environmental Microbiology*, 2013, 15(5): 1416-1427.
- [45] KHAN F, TABASSUM N, ANAND R, KIM YM. Motility of *Vibrio* spp.: regulation and controlling strategies[J]. *Applied Microbiology and Biotechnology*, 2020, 104(19): 8187-8208.
- [46] TESCHLER JK, ZAMORANO-SÁNCHEZ D, UTADA AS, WARNER CJA, WONG GCL, LININGTON RG, YILDIZ FH. Living in the matrix: assembly and control of *Vibrio cholerae* biofilms[J]. *Nature Reviews Microbiology*, 2015, 13(5): 255-268.
- [47] SHOEMAKER KM, McCLIMENT EA, MOISANDER

- PH. Copepod-associated gammaproteobacterial alkaline phosphatases in the north Atlantic subtropical gyre[J]. *Frontiers in Microbiology*, 2020, 11: 1033.
- [48] HINOW P, NIHONGI A, STRICKLER JR. Statistical mechanics of zooplankton[J]. *PLoS One*, 2015, 10(8): e0135258.
- [49] FREITAS C, GLATTER T, RINGGAARD S. The release of a distinct cell type from swarm colonies facilitates dissemination of *Vibrio parahaemolyticus* in the environment[J]. *The ISME Journal*, 2020, 14(1): 230-244.
- [50] MEZA-VILLEZCAS A, CARBALLO-CASTAÑEDA RA, MORENO-ULLOA A, HUERTA-SAQUERO A. Metabolomic profiling of the responses of planktonic and biofilm *Vibrio cholerae* to silver nanoparticles[J]. *Antibiotics*, 2022, 11(11): 1534.
- [51] WANG QY, WANG PF, LIU PP, OU J. Comparative transcriptome analysis reveals regulatory factors involved in *Vibrio parahaemolyticus* biofilm formation[J]. *Frontiers in Cellular and Infection Microbiology*, 2022, 12: 917131.
- [52] TURNER JW, GOOD B, COLE D, LIPP EK. Plankton composition and environmental factors contribute to *Vibrio* seasonality[J]. *The ISME Journal*, 2009, 3(9): 1082-1092.
- [53] ROEDER T, STANISAK M, GELHAUS C, BRUCHHAUS I, GRÖTZINGER J, LEIPPE M. Caenopores are antimicrobial peptides in the nematode *Caenorhabditis elegans* instrumental in nutrition and immunity[J]. *Developmental & Comparative Immunology*, 2010, 34(2): 203-209.
- [54] BULGHERESI S, SCHABUSSOVA I, CHEN T, MULLIN NP, MAIZELS RM, OTT JA. A new C-type lectin similar to the human immunoreceptor DC-SIGN mediates symbiont acquisition by a marine nematode[J]. *Applied and Environmental Microbiology*, 2006, 72(4): 2950-2956.
- [55] CONSTANTIN de MAGNY G, MURTUGUDDE R, SAPIANO MRP, NIZAM A, BROWN CW, BUSALACCHI AJ, YUNUS M, NAIR GB, GIL AI, LANATA CF, CALKINS J, MANNA B, RAJENDRAN K, BHATTACHARYA MK, HUQ A, SACK RB, COLWELL RR. Environmental signatures associated with cholera epidemics[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2008, 105(46): 17676-17681.
- [56] MICHOTÉY V, BLANFUNE A, CHEVALIER C, GAREL M, DIAZ F, BERLINE L, Le GRAND L, ARMOUGOM F, GUASCO S, RUITTON S, CHANGEUX T, BELLONI B, BLANCHOT J, MÉNARD F, THIBAUT T. *In situ* observations and modelling revealed environmental factors favouring occurrence of *Vibrio* in microbiome of the pelagic *Sargassum* responsible for strandings[J]. *Science of the Total Environment*, 2020, 748: 141216.
- [57] HUQ A, COLWELL RR, CHOWDHURY MAR, XU B, MONIRUZZAMAN SM, ISLAM MS, YUNUS M, ALBERT MJ. Coexistence of *Vibrio cholerae* 01 and 0139 Bengal in plankton in Bangladesh[J]. *The Lancet*, 1995, 345(8959): 1249.
- [58] MAIN CR, SALVITTI LR, WHEREAT EB, COYNE KJ. Community-level and species-specific associations between phytoplankton and particle-associated *Vibrio* species in Delaware's inland bays[J]. *Applied and Environmental Microbiology*, 2015, 81(17): 5703-5713.
- [59] GREENFIELD DI, GOOCH MOORE J, STEWART JR, HILBORN ED, GEORGE BJ, LI Q, DICKERSON J, KEPPLER CK, SANDIFER PA. Temporal and environmental factors driving *Vibrio vulnificus* and *V. parahaemolyticus* populations and their associations with harmful algal blooms in south Carolina detention ponds and receiving tidal creeks[J]. *GeoHealth*, 2017, 1(9): 306-317.
- [60] ASPLUND ME, REHNSTAM-HOLM AS, ATNUR V, RAGHUNATH P, SARAVANAN V, HÄRNSTRÖM K, COLLIN B, KARUNASAGAR I, GODHE A. Water column dynamics of *Vibrio* in relation to phytoplankton community composition and environmental conditions in a tropical coastal area[J]. *Environmental Microbiology*, 2011, 13(10): 2738-2751.
- [61] MING HX, FAN JF, LIU JW, SU J, WAN ZY, WANG YT, LI DW, LI MF, SHI TT, JIN Y, HUANG HL, SONG JX. Full-length 16S rRNA gene sequencing reveals spatiotemporal dynamics of bacterial community in a heavily polluted estuary, China[J]. *Environmental Pollution*, 2021, 275: 116567.
- [62] XU QS, WANG PB, HUANGLENG JH, SU HQ, CHEN PY, CHEN X, ZHAO HX, KANG ZJ, TANG JL, JIANG G, LI ZT, ZOU SQ, DONG K, HUANG YQ, LI N. Co-occurrence of chromophytic phytoplankton and the *Vibrio* community during *Phaeocystis globosa* blooms in the Beibu Gulf[J]. *Science of the Total Environment*, 2022, 805: 150303.
- [63] ROSALES D, ELLETT A, JACOBS J, OZBAY G, PARVEEN S, PITULA J. Investigating the relationship between nitrate, total dissolved nitrogen, and phosphate

- with abundance of pathogenic vibrios and harmful algal blooms in Rehoboth Bay, Delaware[J]. *Applied and Environmental Microbiology*, 2022, 88(14): e0035622.
- [64] STABILI L, CAROPPO C, CAVALLO RA. Monitoring of a coastal Mediterranean area: culturable bacteria, phytoplankton, environmental factors and their relationships in the Southern Adriatic Sea[J]. *Environmental Monitoring and Assessment*, 2006, 121(1-3): 303-325.
- [65] EILER A, GONZALEZ-REY C, ALLEN S, BERTILSSON S. Growth response of *Vibrio cholerae* and other *Vibrio* spp. to cyanobacterial dissolved organic matter and temperature in brackish water[J]. *FEMS Microbiology Ecology*, 2007, 60(3): 411-418.
- [66] ZHOU J, RICHLIN ML, SEHEIN TR, KULIS DM, ANDERSON DM, CAI ZH. Microbial community structure and associations during a marine dinoflagellate bloom[J]. *Frontiers in Microbiology*, 2018, 9: 1201.
- [67] AMIN SA, PARKER MS, ARMBRUST EV. Interactions between diatoms and bacteria[J]. *Microbiology and Molecular Biology Reviews: MMBR*, 2012, 76(3): 667-684.
- [68] ZHOU J, LYU YH, RICHLIN ML, ANDERSON DM, CAI ZH. Quorum sensing is a language of chemical signals and plays an ecological role in algal-bacterial interactions[J]. *Critical Reviews in Plant Sciences*, 2016, 35(2): 81-105.
- [69] KING K, BRAMUCCI AR, LABBATE M, RAINA JB, SEYMOUR JR. Heterogeneous growth enhancement of *Vibrio cholerae* in the presence of different phytoplankton species[J]. *Applied and Environmental Microbiology*, 2022, 88(17): e0115822.
- [70] DITTAMI SM, AAS HTN, PAULSEN BS, BOYEN C, EDVARSDEN B, TONON T. Mannitol in six autotrophic stramenopiles and *Micromonas*[J]. *Plant Signaling & Behavior*, 2011, 6(8): 1237-1239.
- [71] YMELE-LEKI P, HOUOT L, WATNICK PI. Mannitol and the mannitol-specific enzyme IIB subunit activate *Vibrio cholerae* biofilm formation[J]. *Applied and Environmental Microbiology*, 2013, 79(15): 4675-4683.
- [72] KIM DD, WAN LL, CAO XY, KLISAROVA D, GERDZHIKOV D, ZHOU YY, SONG CL, YOON S. Metagenomic insights into co-proliferation of *Vibrio* spp. and dinoflagellates *Prorocentrum* during a spring algal bloom in the coastal East China Sea[J]. *Water Research*, 2021, 204: 117625.
- [73] THOMSON B, WENLEY J, CURRIE K, HEPBURN C, HERNDL GJ, BALTAR F. Resolving the paradox: continuous cell-free alkaline phosphatase activity despite high phosphate concentrations[J]. *Marine Chemistry*, 2019, 214: 103671.
- [74] DUNGCA-SANTOS JCR, CASPE FJO, TABLIZO FA, PURGANAN DJE, AZANZA RV, ONDA DFL. Algicidal potential of cultivable bacteria from pelagic waters against the toxic dinoflagellate *Pyrodinium bahamense* (Dinophyceae)[J]. *Journal of Applied Phycology*, 2019, 31(6): 3721-3735.
- [75] CHENG LJ, ABRAHAM J, TRENBERTH KE, FASULLO J, BOYER T, MANN ME, ZHU J, WANG F, LOCARNINI R, LI YL, ZHANG B, YU FJ, WAN LY, CHEN XR, FENG LC, SONG XZ, LIU YL, RESEGHETTI F, SIMONCELLI S, GOURETSKI V, et al. Another year of record heat for the oceans[J]. *Advances in Atmospheric Sciences*, 2023, 40(6): 963-974.
- [76] VEZZULLI L, PEZZATI E, BRETTAR I, HÖFLE M, PRUZZO C. Effects of global warming on *Vibrio* ecology[J]. *Microbiology Spectrum*, 2015, 3(3): 3.3.18.
- [77] DONI L, OLIVERI C, LASA AD, Di CESARE A, PETRIN S, MARTINEZ-URTAZA J, COMAN F, RICHARDSON A, VEZZULLI L. Large-scale impact of the 2016 Marine Heatwave on the plankton-associated microbial communities of the Great Barrier Reef (Australia)[J]. *Marine Pollution Bulletin*, 2023, 188: 114685.
- [78] MARTINEZ-URTAZA J, HUAPAYA B, GAVILAN RG, BLANCO-ABAD V, ANSEDE-BERMEJO J, CADARSO-SUAREZ C, FIGUEIRAS A, TRINANES J. Emergence of Asiatic *Vibrio* diseases in South America in phase with El Niño[J]. *Epidemiology*, 2008, 19(6): 829-837.
- [79] HEWITT CL, CAMPBELL ML. Mechanisms for the prevention of marine bioinvasions for better biosecurity[J]. *Marine Pollution Bulletin*, 2007, 55(7-9): 395-401.
- [80] SOLEIMANI F, TAHERKHANI R, DOBARADARAN S, SPITZ J, SAEEDI R. Molecular detection of *E. coli* and *Vibrio cholerae* in ballast water of commercial ships: a primary study along the Persian Gulf[J]. *Journal of Environmental Health Science and Engineering*, 2021, 19(1): 457-463.
- [81] NG C, GOH SG, SAEIDI N, GERHARD WA, GUNSCH CK, GIN KYH. Occurrence of *Vibrio* species, beta-lactam resistant *Vibrio* species, and indicator bacteria in ballast and port waters of a tropical harbor[J]. *Science of the Total Environment*, 2018, 610/611:

- 651-656.
- [82] NG C, LE TH, GOH SG, LIANG L, KIM Y, ROSE JB, YEW-HOONG KG. A comparison of microbial water quality and diversity for ballast and tropical harbor waters[J]. PLoS One, 2015, 10(11): e0143123.
- [83] WANG Q, CHENG F, XUE J, XIAO N, WU H. Bacterial community composition and diversity in the ballast water of container ships arriving at Yangshan Port, Shanghai, China[J]. Marine Pollution Bulletin, 2020, 160: 111640.
- [84] TURNER JW, MALAYIL L, GUADAGNOLI D, COLE D, LIPP EK. Detection of *Vibrio parahaemolyticus*, *Vibrio vulnificus* and *Vibrio cholerae* with respect to seasonal fluctuations in temperature and plankton abundance[J]. Environmental Microbiology, 2014, 16(4): 1019-1028.
- [85] LAVIAD-SHITRIT S, IZHAKI I, HALPERN M. Accumulating evidence suggests that some waterbird species are potential vectors of *Vibrio cholerae*[J]. PLoS Pathogens, 2019, 15(8): e1007814.
- [86] SENDEROVICH Y, IZHAKI I, HALPERN M. Fish as reservoirs and vectors of *Vibrio cholerae*[J]. PLoS One, 2010, 5(1): e8607.
- [87] LEE JV, BASHFORD DJ, DONOVAN TJ, FURNISS AL, WEST PA. The incidence of *Vibrio cholerae* in water, animals and birds in Kent, England[J]. Journal of Applied Bacteriology, 1982, 52(2): 281-291.
- [88] HALPERN M, SENDEROVICH Y, IZHAKI I. Waterfowl—the missing link in epidemic and pandemic cholera dissemination?[J]. PLoS Pathogens, 2008, 4(10): e1000173.
- [89] MUANGNAPOH C, TAMBOON E, SUPHA N, TOYTING J, CHITRAK A, KITKUMTHORN N, EKCHARIYAWAT P, IIDA T, SUTHIENKUL O. Multilocus sequence typing and virulence potential of *Vibrio parahaemolyticus* strains isolated from aquatic bird feces[J]. Microbiology Spectrum, 2022, 10(3): e0088622.