

群体感应和群体淬灭在藻菌互作中的功能研究进展

杨淋^{1,3}, 王帅^{*1}, 迟旭辉¹, 郑立^{1,2}

1 自然资源部第一海洋研究所 青岛市现代分析与近海生态环境安全保障重点实验室, 山东 青岛 266061

2 青岛海洋科学与技术试点国家实验室 海洋生态与环境科学功能实验室, 山东 青岛 266237

3 自然资源部第四海洋研究所, 广西 北海 536015

杨淋, 王帅, 迟旭辉, 郑立. 群体感应和群体淬灭在藻菌互作中的功能研究进展[J]. 微生物学通报, 2024, 51(5): 1441-1459.

YANG Lin, WANG Shuai, CHI Xuhui, ZHENG Li. Research progress in quorum sensing and quorum quenching in the interaction between microalgae and bacteria[J]. Microbiology China, 2024, 51(5): 1441-1459.

摘要: 群体感应是微生物群体之间的一种交流机制。根据信号分子的识别, 微生物可以进行种群内以及种群间的信息交流, 并调控自身的生理行为。而群体淬灭可以通过打断群体感应信号分子的合成、分泌与识别进程, 从而阻断群体感应。在微藻和细菌的互作过程中, 群体感应和群体淬灭的共同作用调控着微藻和细菌的生理变化, 使得它们达成生态平衡而共存。本文综述了群体感应的发生过程与检测, 并阐述群体感应在微藻和细菌互作中的作用。同时, 论述了群体淬灭的发生机制, 并探讨群体淬灭在微藻和细菌互作中的作用与生态效益。以期为更全面地了解藻菌关系的复杂联系、进一步揭示藻菌互作的分子机制及在海洋生态系统中的作用提供借鉴。

关键词: 群体感应; 群体淬灭; 藻菌互作

资助项目: 国家自然科学基金(41806201, 41776176); 中央级公益性科研院所基本科研业务费专项资金(2021Q10); 泰山产业领军人才工程专项经费(tscx202306084); 国家留学基金(2022)

This work was supported by the National Natural Science Foundation of China (41806201, 41776176), the Basic Scientific Fund for National Public Research Institutes of China (2021Q10), the Taishan Industrial Experts Programme (tscx202306084), and the China Scholarship Council for its 2022 Funding.

*Corresponding author. E-mail: wangshuai@fio.org.cn

Received: 2023-08-15; Accepted: 2023-11-01; Published online: 2024-01-04

Research progress in quorum sensing and quorum quenching in the interaction between microalgae and bacteria

YANG Lin^{1,3}, WANG Shuai^{*1}, CHI Xuhui¹, ZHENG Li^{1,2}

1 Qingdao Key Laboratory of Analytical Technology Development and Offshore Eco-Environment Conservation, Key Laboratory of Marine Eco-Environmental Science and Technology, First Institute of Oceanography, Ministry of Natural Resources, Qingdao 266061, Shandong, China

2 Functional Laboratory for Marine Ecology and Environmental Science, Qingdao Pilot National Laboratory for Marine Science and Technology, Qingdao 266237, Shandong, China

3 Fourth Institute of Oceanography, Ministry of Natural Resources, Beihai 536015, Guangxi, China

Abstract: Quorum sensing is a communication mechanism between microbial populations. By recognizing signal molecules, microorganisms can exchange information within and outside the population and regulate their physiological behaviors. Quorum quenching can block quorum sensing by interrupting the synthesis, secretion, and recognition of quorum-sensing signal molecules. In the interaction process between microalgae and bacteria, quorum sensing and quorum quenching jointly regulates the physiological changes in microalgae and bacteria for their balanced coexistence. This paper introduces the occurrence process and detection of quorum sensing and elaborates on the role of quorum sensing in the interaction between microalgae and bacteria. Furthermore, this paper expounds the occurrence mechanism of quorum quenching and the performance and ecological benefits of quorum quenching in the interaction between microalgae and bacteria. Finally, prospects are put forward for studying the mechanism of the interaction between microalgae and bacteria and the role of the interaction in marine ecosystems.

Keywords: quorum sensing; quorum quenching; algae-bacteria interactions

近年来,随着海洋环境生态研究的逐步深入,海洋生物群落种间关系尤其是藻菌之间的作用及其作用机制研究愈来愈受到重视,从化学生态学层面来认识藻菌作用关系已成为藻类生态学和微生物学研究的前沿和热点。在藻际微环境中,由于微藻和细菌的营养物质、群落结构及其代谢产物的多变性,使得藻菌间相互作用和化学生态过程具有复杂性。一方面微藻共栖细菌和微藻的生长具有相互促进作用,细菌可为微藻的生长提供营养盐和必要生长因子^[1-3],微藻则向环境中释放代谢产物供细菌利用;另一方面微藻共栖细菌也会对微藻产生抑制作用,主要体现在营养竞争以及释放抑藻和溶藻类物质^[4-6],而微

藻则会产生信号分子类似物或信号分子酰基高丝氨酸内酯(*N*-acyl homoserine lactones, AHLs)降解酶进行拮抗作用^[7-8]。近年来,从化学生态学层面探讨群体感应(quorum sensing, QS)和群体淬灭(quorum quenching, QQ)信号介导的微生物群体行为逐渐成为新的研究热点^[9],群体感应和群体淬灭的共同作用不仅影响微生物之间的种内关系,也能影响藻菌间的种间联系,共同维持共栖环境的平衡和稳定^[10-13]。

1 群体感应

群体感应(QS)是指细菌具有典型的密度依赖性,当其数量达到一定密度时可以相互感知

且进行基因表达调控产生某些生理功能的行为, 这些生理功能包括抗生素的产生、化学毒素的释放、孢子的萌发、色素的产生以及生物膜的形成等^[5,14-15](图 1)。

1.1 群体感应的概念

QS 效应在费氏弧菌(*Vibrio fischeri*)的发光现象中首次被提出^[16]。费氏弧菌的发光功能和细菌密度存在密切联系, 在细菌密度低时, 细菌群体不表现出发光现象, 而当群体达到一定密度时, 发光现象才被表现出来^[17]。在这一调节过程中, 细菌自身分泌的自诱导物(autoinducer)充当调控媒介。自诱导物随着细菌密度的增高, 在细菌胞外积累。当自诱导物浓度达到细菌感应阈值时, 自诱导物可以结合到细菌胞内的受体蛋白上, 形成可以调节基因转录的复合物。这也是 QS 常见的调控路径(图 2)。在费氏弧菌的发光现象中, 自诱导物和受体蛋白结合而成的复合物可以激活下游相关发光基因的表达, 从而完成对发光现象的调节^[18]。费

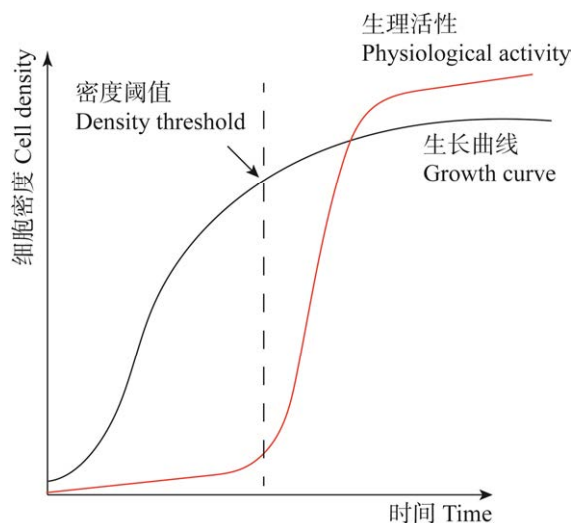


图 1 依赖于细胞密度的群体感应现象
Figure 1 The QS relying on cells density.

氏弧菌通过发光功能给予宿主生存上的帮助, 比如寻找配偶、躲避天敌, 以及在夜间寻觅食物等, 从而稳固自身的寄生环境^[19-20]。因此, QS 调控的发光现象有利于费氏弧菌和宿主的互利共生。

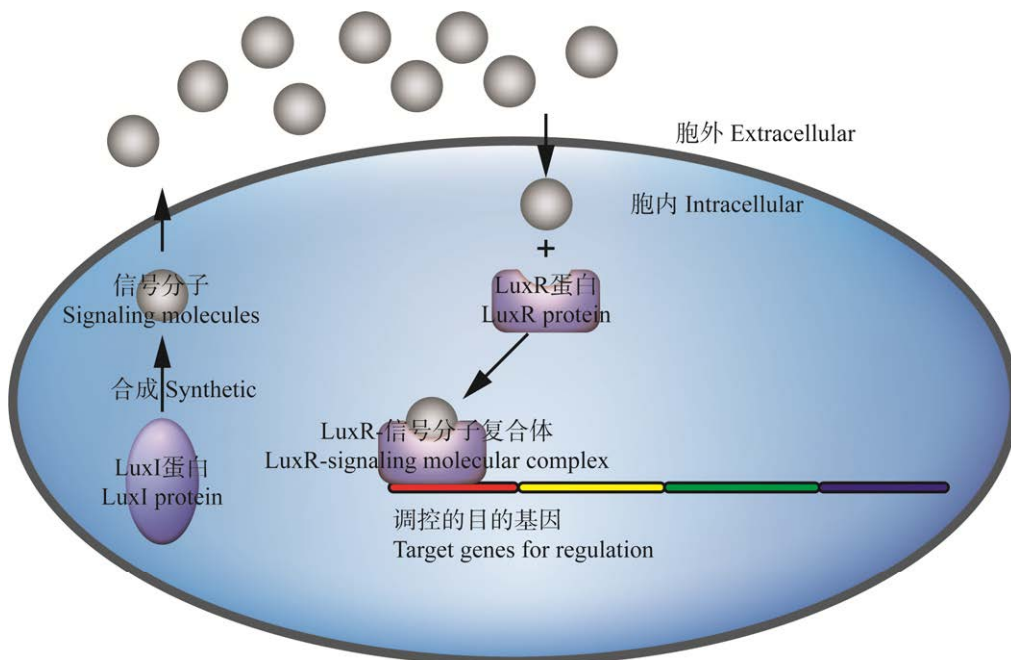


图 2 G^- 细菌中 LuxI/R QS 系统

Figure 2 LuxI/R QS system in G^- bacteria.

1.2 群体感应系统

QS 在不同微生物中的表现可以通过多种 QS 基因系统来实现(表 1)。当微生物具有多种 QS 基因系统时,系统之间可以存在级联关系、平行关系和竞争关系。比如铜绿假单胞菌(*Pseudomonas aeruginosa*)的 LasI-LasR 系统可以调控下游的 RhII-RhlR 系统, LasR-AHL 复合体调节 *rhII*、*rhlR* 基因的表达^[43]。而哈维弧菌(*Vibrio harveyi*)同时具有 LuxM-LuxN、LuxS-LuxQ 和 CqsA-CqsS 三套系统,它们分别具有对应的信号分子和独立调节基因表达^[41]。另外,枯草芽孢杆菌(*Bacillus subtilis*)存在由 ComX 和 CSF (competence and sporulation factor)两种信号分子介导的不同的 QS 系统,两种系统的竞争对细菌感受态和芽孢形态的转变有着调控作用^[44]。

当微生物只具有感受蛋白基因而没有信号分子合成酶基因时,通过感应其他细菌分泌的信号分子,它们可以感受细胞周围其他种类微生物的存在,调控自身基因表达从而对所处环境的生存做出响应。病原菌意大利小海员菌(*Nautella italic*) R11 在侵染宿主前需要形成受控于 QS 的生物膜,但是该菌株的生物膜调控只依靠单独的 VarR 感受蛋白,而没有与 VarR 相配套的信号分子合成酶基因,只能通过感受环境中外来的信号分子而调控 QS 行为^[45]。另外,只具有信号分子合成基因而没有感受蛋白基因的情况也是存在的,在 *Sulfitobacter*、*Ruegeria* 和 *Phaeobacter* 等玫瑰杆菌中,常见 *luxI* 基因单独存在,这可能对微生物群落的动态变化有重要作用,但是具体作用仍未解析透彻^[46]。由此可见,自然界中的 QS 系统是相当多样的。

1.3 群体感应信号分子

随着研究的深入, QS 也被阐述为微生物通过信号分子进行交流的一种途径,不局限于种内的交流,也包括种间的交流^[47];信号分子种

类也随着研究深入而增多(图 3),目前按信号分子种类的不同可将 QS 系统主要划分为 5 类:

(1) 由 G⁻细菌分泌酰基高丝氨酸内酯(*N*-acyl homoserine lactons, AHLs)类化合物介导的 *luxI/R* AI-1 种内信息系统^[35,42,48]; (2) 由 G⁺细菌分泌寡肽(autoinducing peptide, AIP)介导的 AI-1 种内信息系统^[49]; (3) 由呋喃硼酸二酯(furanosyl-borate diester)介导的 *luxS* 种间信息系统 AI-2; (4) 由肾上腺-去肾上腺素介导的 AI-3 信息系统^[50]; (5) 由喹诺酮类(2-heptyl-3-hydroxy-4-quinolone, PQS)、扩散性信号分子(diffusible signal factor, DSF)、二酮哌嗪类化合物(diketopiperazines, DKPs)、弧菌诱导因子(cholerae autoinducer-1, CAI-1)等其他信号分子介导的其他类型^[51-53]。随着研究的发展,更多的信号分子种类正在被发现。

1.4 信号分子检测

由于 QS 是根据信号分子进行介导,因此可以通过检测信号分子的存在来确定 QS 的发生。常用的方法有生物显色法和色谱质谱联用法。生物显色法是利用具有 QS 效应的指示菌株来确定信号分子的存在,比如紫色色杆菌(*Chromobacterium violaceum*) CV026、根癌农杆菌(*Agrobacterium tumefaciens*) KYC55 和大肠杆菌(*Escherichia coli*) pSB536、pAL101 等指示菌株在信号分子存在的环境中可以产生并分泌色素,而在没有信号分子的环境中则不表现色素产生现象^[54]。生物显色法优势在于检出限低、反应灵敏,但是由于需要进行生物培养并受生物活性影响,所以存在精准定量能力差及检测不便等缺点。色谱质谱联用虽然可以直接分析目标分子种类和含量,但是它也存在应用上的缺点,即需要使用标准品对检测物质进行比对,对于未知种类的信号分子还仍需要生物显色法等方法对物质进行功能确认。

表 1 群体感应基因系统及调控行为

Table 1 Quorum sensing gene systems and regulatory behaviors

菌名	调节蛋白	信号分子	调控行为	参考文献
Bacteria	Regulatory proteins	Signaling molecules	Regulatory objects	References
<i>Aeromonas hydrophila</i>	AhyI/AhyR	C4-HSL, C6-HSL	生物膜、胞外蛋白酶、毒力 Biofilm, extracellular protease, virulence	[21-22]
<i>Aeromonas salmonicida</i>	AsaI/AsaR	C4-HSL, C6-HSL	胞外蛋白酶 Extracellular protease	[21]
<i>Agrobacterium tumefaciens</i>	TraI/TraR	3-oxo-C8-HSL	质粒结合 Plasmid conjunction	[23]
<i>Burkholderia cepacia</i>	CepI/CepR	C6-HSL, C8-HSL	胞外酶、生物膜、细胞运动、铁载体、毒力 Extracellular enzyme, biofilm, cell motility, siderophore, virulence	[24]
<i>Burkholderia pseudomallei</i>	CepI/CepR	C8-HSL, C10-HSL, 3-hydro-C8-HSL, etc.	毒力、胞外蛋白酶 Virulence, extracellular protease	[25]
<i>Burkholderia mallei</i>	CepI/CepR	C8-HSL, C10-HSL	毒力 Virulence	[26]
<i>Edwardsiella tarda</i>	EdwI/EdwR, LuxS	BHL, HHL, OHHL, HeHL, AI-2	毒力蛋白、溶血、软骨素酶 Virulence protein, hemolysis, chondroitinase	[27]
<i>Erwinia carotovora</i>	LuxI	3-oxo-C6-HSL	碳青霉烯、胞外酶、毒力 Carbapenem, extracellular enzyme, virulence	[28]
<i>Erwinia chrysanthemi</i>	ExpI/ExpR	3-oxo-C6-HSL	果胶酶 Pectinase	[29]
<i>Escherichia coli</i>	SdiA	C6-HSL	毒力 Virulence	[30]
<i>Pseudomonas aeruginosa</i>	LasI/LasR, RhlI/RhlR	C4-HSL, C6-HSL, 3-oxo-C12-HSL	胞外酶、外毒素、蛋白分泌、生物膜、细胞运动、次级代谢物、毒力 Extracellular enzyme, exotoxin, protein secretion, biofilm, cell motility, secondary metabolites, virulence	[31-34]
<i>Pseudomonas aureofaciens</i>	PhzI/PhzR	C6-HSL	吩嗪类抗生素 Phenazine antibiotics	[35]
<i>Pseudomonas chlororaphis</i>	PhzI/PhzR, AurI/AurR	C6-HSL	吩嗪类 Phenazine	[36]
<i>Pseudomonas putida</i>	PpuI/PpuR	3-oxo-C10-HSL, 3-oxo-C12-HSL	生物膜形成 Biofilm formation	[37]
<i>Pseudomonas fluorescens</i>	PcoI/PcoR	AHL	生物膜 Biofilm	[38]
<i>Rhizobium etli</i>	LuxI/LuxR	Unknown	根瘤数量控制 Nodulation control	[39]
<i>Vibrio anguillarum</i>	VanI/VanR	ODHL	胞外蛋白酶 Extracellular protease	[40]
<i>Vibrio harveyi</i>	LuxM/LuxN, LuxS/LuxPQ, CqsA/CqsS	OHdBHL, AI-2, CAI-1	外毒素、生物发光 Exotoxin, bioluminescence	[41]
<i>Yersinia enterocolitica</i>	YenI/YenR	C6-HSL	细胞运动、胞外蛋白酶、生物膜形成 Cell motility, extracellular protease, biofilm formation	[42]

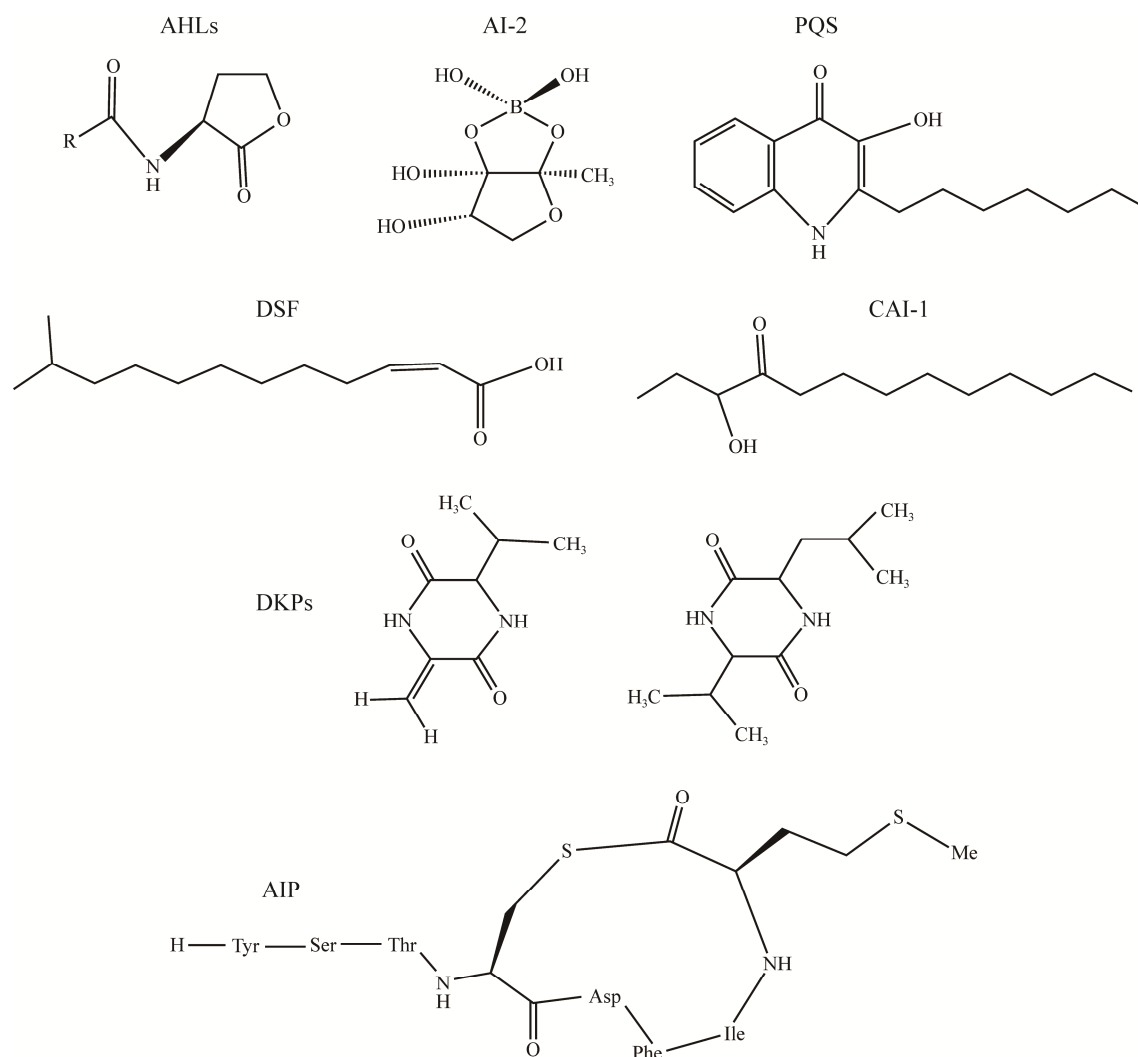


图3 信号分子种类化学结构式

Figure 3 The chemical structure of signal molecules.

目前经常使用的检测技术可以满足对信号分子的定性和定量检测。但是,随着研究的深入,新的信号分子种类也在逐渐被发现,目前对于鉴定新种类仍无较为简便的技术。由于在一些菌株中分泌的信号分子含量低而难以被检测,这也需要检测技术的进步进行弥补。同时存在研究过程中提取信号分子时受到环境因素破坏的情况,因此原位检测技术需要得到进一步关注。

2 群体淬灭

群体感应抑制信号分子以 QS 系统为靶点竞争性地抑制该系统,在不杀死或不干扰细菌正常生命活动的前提下,有效调控菌群的结构和功能的现象被称为群体淬灭(quorum quenching, QQ)。根据 QS 发生的过程,QQ 的途径可以有抑制信号分子的合成、阻断信号的传输和降解信号分子等(表 2)。

表 2 群体淬灭途径与功能

Table 2 The pathways and functions of quorum quenching

菌名 Bacteria	群体淬灭方式 The pathways of quorum quenching	介质 Media	功能 Functions	参考文献 References
<i>Acidobacteria</i> sp.	AHL 内酯酶 AHL lactonase	QlcA	C6、C7、C8-HSL 降解 C6, C7, C8-HSL degradation	[55]
<i>Acinetobacter</i> sp. Ooi24	AHL 酰化酶 AHL acylase	AmiE	3O10-HSL 降解 3O10-HSL degradation	[56]
<i>Agrobacterium tumefaciens</i>	AHL 酰化酶 AHL acylase	AtPVA	(3O)C6-12HSL 降解 (3O)C6-12HSL degradation	[57]
<i>Agrobacterium tumefaciens</i>	AHL 内酯酶 AHL lactonase	AttM, AiiB	广泛降解 Extensive degradation	[58-59]
<i>Anabaena</i> sp. PCC7120	AHL 酰化酶 AHL acylase	AiiC	3OC4-C14-HSL 降解 3OC4-C14-HSL degradation	[8]
<i>Arthrobacter</i> sp. IBN110	AHL 内酯酶 AHL lactonase	AhlD	广泛降解 Extensive degradation	[60]
<i>Bacillus</i> sp.	AHL 内酯酶 AHL lactonase	AiiA	广泛降解 Extensive degradation	[61]
<i>Bacillus megaterium</i> CYP102 A1	氧化酶 Oxidase	P450BM-3 (monooxygenase)	长链 AHL Long-chain AHL	[62]
<i>Brucella melitensis</i>	AHL 酰化酶 AHL acylase	AibP	C12-HSL、3OC12-HSL 降解 C12-HSL, 3OC12-HSL degradation	[63]
<i>Deinococcus radiodurans</i>	AHL 酰化酶 AHL acylase	QqaR	(3O)C8-C14-HSL 降解 (3O)C8-C14-HSL degradation	[64]
<i>Klebsiella pneumoniae</i> KCTC2241	AHL 内酯酶 AHL lactonase	AhlK	C6、OC6-HSL 降解 C6, OC6-HSL degradation	[60]
<i>Kluyvera citrophila</i>	AHL 酰化酶 AHL acylase	KcPGA	(3O)C6-C8-HSL 降解 (3O)C6-C8-HSL degradation	[65]
<i>Ochrobactrum</i> sp. A44	AHL 酰化酶 AHL acylase	AiiO	(3O)C4-C14-HSL 降解 (3O)C4-C14-HSL degradation	[66]
<i>Pectobacterium atrosepticum</i>	AHL 酰化酶 AHL acylase	PaPVA	C10-HSL、C12-HSL 降解 C10-HSL, C12-HSL degradation	[57]
<i>Pseudomonas aeruginosa</i>	AHL 酰化酶 AHL acylase	PvdQ	(3O)C10-C14-HSL 降解 (3O)C10-C14-HSL degradation	[67]
		QuiP	(3O)C7-C14-HSL 降解 (3O)C7-C14-HSL degradation	[68]
		HacB	C6-C14-HSL 降解 C6-C14-HSL degradation	[69]
<i>Pseudomonas syringae</i> B728a	AHL 酰化酶 AHL acylase	HacA	C8-HSL、C10-HSL、C12-HSL 降解 C8-HSL, C10-HSL, C12-HSL degradation	[70]
		HacB	(3O)C6-12-HSL 降解 (3O)C6-12-HSL degradation	[70]
<i>Ralstonia solanacearum</i> GMI1000	AHL 酰化酶 AHL acylase	Aac	C7-HSL、C8-HSL、3OC8-HSL、C10-HSL 降解 C7-HSL, C8-HSL, 3OC8-HSL, C10-HSL degradation	[71]

(待续)

(续表 2)

菌名	群体淬灭方式	介质	功能	参考文献
Bacteria	The pathways of quorum quenching	Media	Functions	References
<i>Ralstonia</i> sp. XJ12B	AHL 酰化酶 AHL acylase	AiiD	3OC8-HSL、3OC10-HSL、3OC12-HSL 降解 3OC8-HSL, 3OC10-HSL, 3OC12-HSL degradation	[72]
<i>Rhodococcus</i> sp.	AHL 内酯酶 AHL lactonase	QsdA	广泛降解 Extensive degradation	[73]
	氧化还原酶 Oxidoreductase		长链 3O-AHL Long-chain 3O-AHL	[74]
	AHL 酰化酶 AHL acylase		广泛降解 Extensive degradation	[74]
	AHL 酰化酶 AHL acylase		C8-HSL、C10-HSL、C12-HSL 降解 C8-HSL, C10-HSL, C12-HSL degradation	[75]
<i>Shewanella</i> sp. strain MIB015	AHL 酰化酶 AHL acylase	Aac	C8-HSL、C10-HSL、C12-HSL 降解 C8-HSL, C10-HSL, C12-HSL degradation	[74]
<i>Streptomyces</i> sp. strain M664	AHL 酰化酶 AHL acylase	AhlM	C8-HSL、C10-HSL、3OC12-HSL 降解 C8-HSL, C10-HSL, 3OC12-HSL degradation	[74]
<i>Streptomyces lavendulae</i> ATCC13664	AHL 酰化酶 AHL acylase	SIPVA	Unknown	[76]

2.1 抑制信号分子的合成

信号分子的合成过程中, 需要前体物质和合成酶的共同参与, 因此可以通过抑制前体物质合成或者抑制合成酶活性来完成抑制信号分子合成。AHLs 类分子酯酰-酰基载体蛋白(acyl carrier protein, ACP)作为前体物质参与到信号分子 AHLs 的合成过程中, 而二氯苯氧氯酚(triclosan)可以阻断该前体物质的形成^[77]。5'-甲基硫腺苷核苷酶的过渡态类似物则可干扰 AI-2 信号分子前体物质之一的 S-腺苷-L-高半胱氨酸(S-ribosyl-L-homocysteine, SRH)形成^[78]。此外, 异戊烯咖啡酸(isoprenyl caffeate)^[79]和姜油酮(vanillylacetone)^[80]可分别抑制紫色色杆菌和铜绿假单胞菌的 AHLs 合成酶活性。SRH 同系物 S-脱水核糖基-L-同型半胱氨酸(S-anhydroribosyl-L-homocysteine)和 S-高核糖基-L-半胱氨酸(S-homoribosyl-L-cysteine)可以与信号分子合成酶 LuxS 结合从而抑制 AI-2 信号分子的合成^[81]。

2.2 阻断信号传输

阻断信号传输的可实现方式则有信号分子拮

抗剂和感受蛋白抑制剂。硫代内酯(thiolactone)^[82]、内酰胺(cyclic azahemiacetals)^[83]、三唑-N-乙酰高丝氨酸内酯(triazole-containing N-acyl homoserine lactones)^[84]和呋喃酮(furanones)^[85]等具有与信号分子 AHL 相似的结构特征, 可以作为信号分子拮抗剂与信号分子竞争结合受体蛋白, 从而阻遏信号分子和感受蛋白的识别结合。同样地, 4,5-二羟基-2,3-戊二酮是 AI-2 途径的重要分子, 它的同系物也能够干扰感受蛋白识别 AI-2 信号分子^[86]。而氟溴酯类^[86]、一些脂肪酸分子^[87]和肉桂醛^[88]等可能通过与感受蛋白结合而成为 AI-2 的抑制剂。而感受蛋白抑制剂比如蛋白 QslA^[89]可以由铜绿假单胞菌表达, 作用于 QS 系统 LasI-LasR 中的感受蛋白 LasR, 使 LasR 蛋白的二聚化不能正常进行, 从而抑制感受蛋白的正常构象形成。

2.3 降解信号分子

信号分子降解的可实现方式则有信号分子降解酶和化学环境的改变。其中信号分子降解酶已在多种细菌中发现, 并且种类多样, 主要

有 3 种降解机制的酶被深入研究,包括 AHL 内酯酶、AHL 酰化酶和 AHL 氧化酶。三种类型的酶可以分别作用于信号分子 AHL 的内酯键、酰胺键和脂肪链。AiiA^[61]和 QsdA^[73]等 AHL 内酯酶可以完成对 AHL 高丝氨酸内酯环的开环化,破坏 AHL 的活性结构。AiiC^[81]、PvdQ^[90]和 QuiP^[68]等 AHL 酰化酶则可以断裂酰胺键而分离 AHL 的内酯环和脂肪链。单加氧酶(monooxygenase) P450^[62]和对氧磷酶 PONs^[91]等 AHL 氧化酶通过氧化还原反应改变 AHL 分子的羰基结构或者脂肪链侧链结构而造成信号分子和感受蛋白无法特异性识别。AHL 信号分子的化学结构在高温和碱性环境中也表现出不稳定的状态,容易造成内酯环开环。在全球变暖和海洋酸化的环境变化下,这些信号分子的稳定状态值得去考虑。在这种环境背景下, QS 交流途径受到的影响以及微生物群落受 QS 变化而变化的程度也研究尚少。

3 群体感应在微藻和细菌互作中的作用

根据 QS 的多样性,微生物依赖 QS 而调节的行为也相当广泛,包括但不限于生物发光,微生物被膜(biofilm)的形成,微生物毒力因子的表达,微生物抗生素的分泌,微生物质粒转移以及其他活性物质的生成等。微生物通过调节生理行为来增强自身对环境的适应能力,以保障自身的生存。微藻和细菌的相互作用过程中也存在受到 QS 调节的行为。

3.1 营养获取

QS 可以参与微藻和细菌的营养获取过程。首先,微藻的生长需要溶解态铁的营养补充^[92]。而在大洋中,以溶解形态存在的铁营养含量并不高^[93],但是存在能分泌胞外体吸附铁元素以

提高其溶解率的细菌存在^[94]。因此,微藻会通过 QS 信号影响这部分细菌的胞外体合成分泌,以此增加自身可吸收利用铁营养的含量^[95]。同时,微藻在生长过程中,可以分泌有机物到其细胞周围,即藻际环境^[96]。这些有机物可以吸引特定类群的细菌前来吸收利用^[97]。由于藻际环境是一个开放型的空间,微藻分泌的物质仅能在短时间、一定范围内保持较高浓度。细菌为了及时利用这些有机物,会通过 QS 信号调节自身群体密度以此增进群体对有机物的利用效率^[98]。另外,细菌还可以通过 QS 机制感应微藻群体密度而改变自身对营养元素代谢的基因表达,比如当普通小球藻(*Chlorella vulgaris*)密度达到高浓度阈值时,藻际细菌将会抑制氮元素固定基因的表达,以此限制微藻对氮元素的吸收^[99]。这或许是细菌和微藻保持群落平衡的一种策略。

3.2 生存环境构建

QS 也可以参与藻菌生存环境的构建,比如生物膜的形成。生物膜具有环境稳态的特性,细菌群落借此能够抵御诸多外界干扰,比如防御捕食者的捕食,增强对抗生素的抗性,提高对紫外线和干燥的耐受程度等^[100-102]。此外,生物膜还可以作为微藻进行生理活动偏好的发生场所。比如,在石莼(*Ulva*)生长过程中,它的游动孢子在固着时偏好于 AHL 含量高的生物被膜环境^[103];珊瑚藻(*Acropora millepora*)的形态变化^[104]以及菱形藻属(*Nitzschia*)等硅藻对附着基质的黏附和释放^[105]等活动也偏好发生于生物膜环境。目前,不少研究证明, QS 可以发生在生物膜环境中,而且作为一个重要的调控途径参与到生物膜的发生过程。铜绿微囊藻(*Microcystis aeruginosa*)通过 AHLs 调节群体中的生物膜形成^[106]。另外,藻类为了防止有害细菌生物膜的侵染,也会分泌 QS 干扰物来控制

生物膜的形成^[107-108]。QS 参与到生物膜的形成过程,说明这种微生物交流机制能够协助微生物更好地抵御环境干扰。QS 可以干扰异源种类的生物膜形成,证实了 QS 可以是一种跨界交流的途径。

3.3 抑藻活性

QS 还可参与微藻和藻际细菌共生关系调节的过程。抑藻细菌的抑藻活性可以受到 QS 的调控。 γ 变形菌 *Hahella* sp. MS-02-063 可以产生对赤潮异弯藻(*Heterosigma akashiwo*)、环状异帽藻(*Heterocapsa circularisquama*)、裸甲藻(*Gymnodinium impudicum*)、塔玛亚历山大藻(*Alexandrium tamarense*)和多环旋沟藻(*Cochlodinium polykrikoides*)具有溶藻活性的 PG-L-1 色素,而色素的产生受到 AHL 介导的 QS 调控^[109]。此外,2-heptyl-4-quinolone (HHQ) 介导的 QS 可以使得杀鱼假交替单胞菌(*Pseudoalteromonas piscicida*)释放溶藻物质作用于赫氏圆石藻(*Emiliania huxleyi*),可使藻细胞裂解^[110]。气单胞菌(*Aeromonas* sp.)分泌的抑藻物质 3-甲基吲哚(3-methylindole)受 C4-HSL 介导的 QS 正调控,而另一种抑藻物质 3-苄基哌嗪-2,5-二酮(3-benzyl-piperazine-2,5-dione)受 C4-HSL 介导的 QS 负调控^[111]。拟菱形藻亚硫酸盐杆菌(*Sulfitobacter pseudonitzschiae*) H46 也具有 QS 系统^[112]。在二甲基巯基丙酸内盐(dimethylsulfoniopropionate, DMSP)环境下,H46 的 QS 系统表达水平下降,同时抑藻活性也出现降低^[113]。H46 表现出偏好抑制 DMSP 产量低的微藻生长^[114]。

3.4 互利互惠

细菌和微藻的互利互惠行为也受到 QS 的调控。在用 DMSP 培养基模拟的微藻高群体密度的藻际环境中,玫瑰杆菌 *Ruegeria pomeroyi* DSS-3 合成的 AHL 信号分子含量增加,并且提

高了细胞的特定代谢物质的合成水平,比如谷氨酰胺(glutamine),维生素 B₂ 等,维生素 B₂ 是微藻生长过程中必需维生素之一^[115]。玫瑰杆菌 *Silicibacter* 分泌的抗生素,一种二硫化物 tropodithietic acid (TDA)可以保护鞭毛藻免受病原菌攻击,而 TDA 的合成受到 AHLs 的调控^[116-120]。小球藻 (*Chlorella* sp.) 共栖细菌农杆菌 (*Agrobacterium* sp.)分泌的 AHLs 对微藻生长具有促进作用^[121]。铜绿微囊藻的生长受到新鞘氨醇杆菌(*Novosphingobium* sp.)胞外多糖的促进,而胞外多糖的产生又由 QS 调控^[122]。同时在信号分子 3-OH-C4-HSL 的影响下,铜绿微囊藻光合作用、辅因子合成的基因表达上调。而 C8-HSL 能够影响微囊藻毒素的合成增多^[123]。

由此可见, QS 调控的微生物行为涉及到多种藻菌互作过程。同时我们也发现, QS 作为微生物获取生存利益的一种手段也逐渐在更多种微生物群落中被发现。然而,仅仅描述现象的存在对于阐明微生物群落中生态关系是远远不够的,我们还需要对现象背后的生态意义进行探究,解释 QS 对微生物自身及其他种类微生物有何生理影响或者生态影响,进一步解释其他种类微生物对 QS 有何反应等,而目前这部分研究在藻菌共生关系中仍较缺乏。

4 群体淬灭在微藻和细菌互作中的表现

在微藻和细菌的交互作用中,微藻会参与到细菌的 QS 系统响应中,可以通过不同的方式抑制细菌的 QS。

4.1 分子拮抗

在微藻和细菌的作用过程中,微藻可以产生信号分子类似物与信号分子竞争受体,从而影响群体感应功能的表现。小球藻 (*Chlorella*

saccharophila)能够分泌代谢物抑制细菌的 QS 现象,包括抑制紫色色杆菌(*Chromobacterium violaceum*)的色素产生,抑制大肠杆菌生物膜的形成,抑制哈维弧菌(*Vibrio harveyi*)的生物发光现象,同时降低哈维弧菌的致病力^[124]。与此相似,莱茵衣藻(*Chlamydomonas reinhardtii*)能够产生可被 AHL 感受蛋白识别的 AHL 模拟物,这种 AHL 模拟物可以阻碍维氏气单胞菌(*Aeromonas veronii*)的生物膜形成,同时也可以被 AHL 内酯酶 AiiA 降解^[7]。另外,颤藻(*Oscillatoria* sp.)也能够产生和 AHL 结构相似的代谢物质,由一个五/六元环以及疏水脂链组成,能够和 AHL 产生拮抗作用而抑制 QS。这些和 AHL 结构相似的物质同时也暗示着跨界信号交流机制的存在^[125]。而对于微藻自身,信号分子类似物也可影响其自身的生理活动。比如呋喃酮的添加可导致铜绿微囊藻培养后期体系的微囊藻毒素水平降低^[123]。

4.2 信号分子降解

另一方面,除了通过分泌 AHL 拮抗剂来抑制 QS 之外,微藻也可以合成信号分子 AHL 降解酶。鱼腥藻(*Anabaena* sp.) PCC7120 能够合成 AHL 酰化酶 AiiC,具有 AHL 降解活性,AiiC 和酰化酶 QuiP 为同系物,具有广泛的酰基链活性。这种酶的产生可能是对它自身的非 QS 信号调节系统的保护,即通过抑制 QS 而保证其他信号交流系统的正常运行^[8]。由此可见,QQ 也存在于藻菌交互作用过程中,但是这些藻菌关系研究大部分只是发现 QQ 的机制存在,而机制存在的生态效应并没有相应研究进行解释。

4.3 群体淬灭的生态意义

当 QQ 作为跨种间的交互作用时,它的生态效应可以是作为不同物种在同一空间生存的平衡机制。细菌可以通过 QS 做出行为调节来适应环境^[53,126-127]。但是当环境中同时出现多种

微生物时,为了竞争生态位或者用于自身防御等意图^[127],微生物可以通过 QQ 抑制其他种类细菌的行为调节,从而使自身更好地生存于该环境。

虽然 QS 和 QQ 是对立关系,但是它们可以共存于同一个个体中。铜绿假单胞菌 MW3A 同时具有 QS 和 QQ 系统,菌株培养上清液含有信号分子 AHL,能够使大肠杆菌生物发光;而同时这一菌株也可以将 AHL 作为碳源,降解 AHL 供自身使用^[128]。同时具有 QS 和 QQ 的微生物种类并不少见^[129],但是这部分既产生 QS 又具有 QQ 系统的微生物,目前在生态效应的了解上,相对于 QS 能够产生明确的个体行为调节,QQ 的实际生态意义并不明确。

有研究认为这种自身的 QQ 是对自身 QS 过度表现时的一种调节。根癌农杆菌在宿主体内表现 QS 过度时,会致使宿主产生应激反应,而根癌农杆菌响应宿主的表现则实行 QQ 机制,以保障自身生存环境,即宿主的安全^[130]。也有观点认为 QQ 是微生物在执行生理功能时的副产物^[67],信号分子降解酶的基因是属于合成一些代谢物质启动子的组成部分,在执行表达代谢物质时顺带表达出了信号分子降解酶。此外,还有观点认为 QQ 是对 QS 的缓和机制^[131],群体响应程度不是固定的,取决于信号分子的产生和降解速率。信号分子被降解可以加快信号分子的流通,以避免信号分子持续刺激感受蛋白,而导致 QS 机制过激。QQ 在不同物种中执行的生态功能会有差异,但目前这方面的研究尚少,尚不能全面地揭示 QS 和 QQ 相互对抗产生的生态效应。为解析更为具体的生态效应,这仍需要深入研究。

同时具有 QS 和 QQ 的抑藻细菌也是存在的,比如菌株 *Ponticoccus* sp. PD-2,虽然尚不能证实抑藻功能与 QS 具有直接联系,然而

PD-2 的抑藻物质分泌会受到 QS 调控^[4], 此外 PD-2 也能表现降解信号分子的能力, 其 QQ 机制对抑藻功能的影响是值得探讨的问题。

5 小结和展望

自“藻际环境”这一概念提出以来, 藻菌互作关系的研究已超过 50 年。目前, 藻菌作用关系未来的研究可在 3 个方向进行尝试: (1) 新的检测技术有待开发。目前的技术集中于生物显色法和色谱质谱联用技术, 这两者各有优缺点, 但是为能够快速筛选新型信号分子种类并同时对其进行定性、定量分析, 仍需结合前两种方法的长处, 研发新的检测技术。 (2) 藻菌互作过程中 QS 和 QQ 的作用机制有待继续挖掘。微藻和细菌相互作用过程受到 QS 和 QQ 调控的作用机制, 结合前文的内容, 我们发现 QS 对微生物自身的生存一般具有积极意义, 而 QQ 对于微生物自身的生存一般为用于防御敌害微生物的 QS 现象。但是对于同时具有 QS 和 QQ 的微生物, 它们的这两种机制是否起到相互拮抗, 或是相互不影响, 仍有待探明。另外, 对于藻际环境中微生物的 QQ 是广泛性地阻断环境中所有的 QS, 抑或是针对性阻断某种生物的 QS, 也仍需探讨。 (3) 由于人为活动影响导致海水环境变化, 比如温度升高、海水酸化等, 而 QS 的信号分子比如 AHLs 结构会受到温度和 pH 变化影响, 在碱性环境等受到内酯环开环而破坏活性, 海水酸化是否导致 QS 退出机制减缓, 而影响微生物群落生理行为等也值得进行探究。

REFERENCES

- [1] EGAN S, HARDER T, BURKE C, STEINBERG P, KJELLEBERG S, THOMAS T. The seaweed holobiont: understanding seaweed-bacteria interactions[J]. FEMS Microbiology Reviews, 2013, 37(3): 462-476.
- [2] de la PEÑA MR. Cell growth and nutritive value of the tropical benthic diatom, *Amphora* sp., at varying levels of nutrients and light intensity, and different culture locations[J]. Journal of Applied Phycology, 2007, 19(6): 647-655.
- [3] 郑天凌, 苏建强. 海洋微生物在赤潮生消过程中的作用[J]. 水生生物学报, 2003, 27(3): 291-295.
ZHENG TL, SU JQ. The role of marine microorganisms in the occurrence and decline of red-tide[J]. Acta Hydrobiologica Sinica, 2003, 27(3): 291-295 (in Chinese).
- [4] CHI WD, ZHENG L, HE CF, HAN B, ZHENG MG, GAO W, SUN CJ, ZHOU GF, GAO XX. Quorum sensing of microalgae associated marine *Ponticoccus* sp. PD-2 and its algicidal function regulation[J]. AMB Express, 2017, 7(1): 1-10.
- [5] 周进, 陈国福, 朱小山, 陈璐, 蔡中华. 赤潮过程中“藻-菌”关系研究进展[J]. 生态学报, 2014, 34(2): 269-281.
ZHOU J, CHEN GF, ZHU XS, CHEN L, CAI ZH. A review of the relationship between algae and bacteria in harmful algal blooms[J]. Acta Ecologica Sinica, 2014, 34(2): 269-281 (in Chinese).
- [6] CHEN WM, SHEU FS, SHEU SY. Novel L-amino acid oxidase with algicidal activity against toxic cyanobacterium *Microcystis aeruginosa* synthesized by a bacterium *Aquimarina* sp.[J]. Enzyme and Microbial Technology, 2011, 49(4): 372-379.
- [7] RAJAMANI S, TEPLITSKI M, KUMAR A, KREDIET CJ, SAYRE RT, BAUER WD. N-acyl homoserine lactone lactonase, AiiA, inactivation of quorum-sensing agonists produced by *chlamydomonas reinhardtii* (*Chlorophyta*) and characterization of *aiiA* transgenic algae[J]. Journal of Phycology, 2011, 47(5): 1219-1227.
- [8] ROMERO M, DIGGLE SP, HEEB S, CÄ;MARA M, OTERO A. Quorum quenching activity in *Anabaena* sp. PCC 7120: identification of AiiC, a novel AHL-acylase[J]. FEMS Microbiology Letters, 2008, 280(1): 73-80.
- [9] 黄昕琦, 蔡中华, 林光辉, 周进. 群体感应信号对“藻-菌”关系的调节作用[J]. 应用与环境生物学报, 2016, 22(4): 708-717.
HUANG XQ, CAI ZH, LIN GH, ZHOU J. Quorum sensing modulating algae-bacteria interactions[J]. Chinese Journal of Applied and Environmental Biology, 2016, 22(4): 708-717 (in Chinese).
- [10] AMIN SA, HMELO LR, van TOL HM, DURHAM BP, CARLSON LT, HEAL KR, MORALES RL,

- BERTHIAUME CT, PARKER MS, DJUNAEDI B, INGALLS AE, PARSEK MR, MORAN MA, ARMBRUST EV. Interaction and signalling between a cosmopolitan phytoplankton and associated bacteria[J]. *Nature*, 2015, 522(7554): 98-101.
- [11] 陈正浩, 张永雨, 杨素萍. 海洋玫瑰杆菌类群研究进展[J]. *生态学报*, 2015, 35(5): 1620-1629.
- CHEN ZH, ZHANG YY, YANG SP. Research progresses of marine *Roseobacter* lineage[J]. *Acta Ecologica Sinica*, 2015, 35(5): 1620-1629 (in Chinese).
- [12] RICLEA R, GLEITZMANN J, BRUNS H, JUNKER C, SCHULZ B, DICKSCHAT JS. Algicidal lactones from the marine *Roseobacter* clade bacterium *Ruegeria pomeroyi*[J]. *Beilstein Journal of Organic Chemistry*, 2012, 8: 941-950.
- [13] 余斌, 方园, 段迎超, 谢智宇, 李洪娟, 张恩, 刘宏民. 微生物群体感应调节信号分子 *N*-酰化高丝氨酸内酯研究进展[J]. *国际药学研究杂志*, 2011, 38(4): 254-262.
- YU B, FANG Y, DUAN YC, XIE ZY, LI HJ, ZHANG E, LIU H. *N*-acyl homoserine lactones as microorganism quorum sensing modulators: research advances[J]. *Journal of International Pharmaceutical Research*, 2011, 38(4): 254-262 (in Chinese).
- [14] HUANG XQ, GAO Y, MA ZP, LIN GH, CAI ZH, ZHOU J. Profile of *Citrobacter freundii* ST2, a multi-acyl-homoserine lactone producer associated with marine dinoflagellates[J]. *Current Microbiology*, 2017, 74(1): 68-76.
- [15] NI NT, LI MY, WANG JF, WANG BH. Inhibitors and antagonists of bacterial quorum sensing[J]. *Medicinal Research Reviews*, 2009, 29(1): 65-124.
- [16] NEALSON KH, PLATT T, HASTINGS JW. Cellular control of the synthesis and activity of the bacterial luminescent system[J]. *Journal of Bacteriology*, 1970, 104(1): 313-322.
- [17] EBERHARD A. Inhibition and activation of bacterial luciferase synthesis[J]. *Journal of Bacteriology*, 1972, 109(3): 1101-1105.
- [18] NEALSON KH. Autoinduction of bacterial luciferase[J]. *Archives of Microbiology*, 1977, 112(1): 73-79.
- [19] RUBY EG. Lessons from a cooperative, bacterial-animal association: the *Vibrio fischeri*-*Euprymna scolopes* light organ symbiosis[J]. *Annual Review of Microbiology*, 1996, 50: 591-624.
- [20] VISICK KL, FOSTER J, DOINO J, MCFALL-NGAI M, RUBY EG. *Vibrio fischeri lux* genes play an important role in colonization and development of the host light organ[J]. *Journal of Bacteriology*, 2000, 182(16): 4578-4586.
- [21] SWIFT S, KARLYSHEV AV, FISH L, DURANT EL, WINSON MK, CHHABRA SR, WILLIAMS P, MACINTYRE S, STEWART GS. Quorum sensing in *Aeromonas hydrophila* and *Aeromonas salmonicida*: identification of the LuxRI homologs AhyRI and AsaRI and their cognate *N*-acylhomoserine lactone signal molecules[J]. *Journal of Bacteriology*, 1997, 179(17): 5271-5281.
- [22] SWIFT S, LYNCH MJ, FISH L, KIRKE DF, TOMÁS JM, STEWART GS, WILLIAMS P. Quorum sensing-dependent regulation and blockade of exoprotease production in *Aeromonas hydrophila*[J]. *Infection and Immunity*, 1999, 67(10): 5192-5199.
- [23] PIPER KR, BECK von BODMAN S, HWANG I, FARRAND SK. Hierarchical gene regulatory systems arising from fortuitous gene associations: controlling quorum sensing by the opine regulon in *Agrobacterium*[J]. *Molecular Microbiology*, 1999, 32(5): 1077-1089.
- [24] LEWENZA S, CONWAY B, GREENBERG EP, SOKOL PA. Quorum sensing in *Burkholderia cepacia*: identification of the LuxRI homologs CepRI[J]. *Journal of Bacteriology*, 1999, 181(3): 748-756.
- [25] LUMJIAKTASE P, DIGGLE SP, LOPRASERT S, TUNGPRADABKUL S, DAYKIN M, CÁMARA M, WILLIAMS P, KUNAKORN M. Quorum sensing regulates *dpsA* and the oxidative stress response in *Burkholderia pseudomallei*[J]. *Microbiology*, 2006, 152(12): 3651-3659.
- [26] EBERL L. Quorum sensing in the genus *Burkholderia*[J]. *International Journal of Medical Microbiology*, 2006, 296(2/3): 103-110.
- [27] HAN Y, LI X, QI Z, ZHANG XH, BOSSIER P. Detection of different quorum-sensing signal molecules in a virulent *Edwardsiella tarda* strain LTB-4[J]. *Journal of Applied Microbiology*, 2010, 108(1): 139-147.
- [28] BAINTON NJ, BYCROFT BW, CHHABRA SR, STEAD P, GLEDHILL L, HILL PJ, REES CED, WINSON MK, SALMOND GPC, STEWART GSAB, WILLIAMS P. A general role for the *lux* autoinducer in bacterial cell signalling: control of antibiotic biosynthesis in *Erwinia*[J]. *Gene*, 1992, 116(1): 87-91.
- [29] NASSER W, BOUILLANT ML, SALMOND G, REVERCHON S. Characterization of the *Erwinia chrysanthemi expI-expR* locus directing the synthesis of

- two *N*-acyl-homoserine lactone signal molecules[J]. Molecular Microbiology, 1998, 29(6): 1391-1405.
- [30] YANG Y, ZHANG X, ZHANG BB, ZHOU MX, DUAN QD, LI ZD, ZHANG XY, ZHU GQ. Quorum sensing-1 signaling of *N*-hexanoyl-L-homoserine lactone contributes to virulence in avian pathogenic *Escherichia coli*[J]. Archives of Microbiology, 2021, 203(10): 6079-6089.
- [31] LATIFI A, FOGLINO M, TANAKA K, WILLIAMS P, LAZDUNSKI A. A hierarchical quorum-sensing cascade in *Pseudomonas aeruginosa* links the transcriptional activators LasR and RhIR (VsmR) to expression of the stationary-phase sigma factor RpoS[J]. Molecular Microbiology, 1996, 21(6): 1137-1146.
- [32] CHAPON-HERVÉ V, AKRIM M, LATIFI A, WILLIAMS P, LAZDUNSKI A, BALLY M. Regulation of the *xcp* secretion pathway by multiple quorum-sensing modulons in *Pseudomonas aeruginosa*[J]. Molecular Microbiology, 1997, 24(6): 1169-1178.
- [33] PEARSON JP, PESCI EC, IGLEWSKI BH. Roles of *Pseudomonas aeruginosa* *las* and *rhl* quorum-sensing systems in control of elastase and rhamnolipid biosynthesis genes[J]. Journal of Bacteriology, 1997, 179(18): 5756-5767.
- [34] GLESSNER A, SMITH RS, IGLEWSKI BH, ROBINSON JB. Roles of *Pseudomonas aeruginosa* *las* and *rhl* quorum-sensing systems in control of twitching motility[J]. Journal of Bacteriology, 1999, 181(5): 1623-1629.
- [35] WOOD DW, GONG F, DAYKIN MM, WILLIAMS P, PIERSON III LS. *N*-acyl-homoserine lactone-mediated regulation of phenazine gene expression by *Pseudomonas aureofaciens* 30-84 in the wheat rhizosphere[J]. Journal of Bacteriology, 1997, 179(24): 7663-7670.
- [36] MOROHOSHI T, WANG WZ, SUTO T, SAITO Y, ITO S, SOMEYA N, IKEDA T. Phenazine antibiotic production and antifungal activity are regulated by multiple quorum-sensing systems in *Pseudomonas chlororaphis* subsp. *aurantiaca* StFRB508[J]. Journal of Bioscience and Bioengineering, 2013, 116(5): 580-584.
- [37] DUBERN JF, LUGTENBERG BJJ, BLOEMBERG GV. The *ppuI-rsaL-ppuR* quorum-sensing system regulates biofilm formation of *Pseudomonas putida* PCL1445 by controlling biosynthesis of the cyclic lipopeptides putisolvins I and II[J]. Journal of Bacteriology, 2006, 188(8): 2898-2906.
- [38] 吴小刚, 付承梅, 张力群. 萤光假单胞菌 2P24 中 PcoI-PcoR 群体感应系统的自体反馈调控[J]. 微生物学通报, 2009, 36(7): 981-987.
- WU XG, FU CM, ZHANG LQ. Auto-induction of PcoI-PcoR quorum-sensing system in *Pseudomonas fluorescens* 2P24[J]. Microbiology China, 2009, 36(7): 981-987 (in Chinese).
- [39] ROSEMEYER V, MICHIELS J, VERRETH C, VANDERLEYDEN J. *luxI*- and *luxR*-homologous genes of *Rhizobium etli* CNPAF512 contribute to synthesis of autoinducer molecules and nodulation of *Phaseolus vulgaris*[J]. Journal of Bacteriology, 1998, 180(4): 815-821.
- [40] MILTON DL, HARDMAN A, CAMARA M, CHHABRA SR, BYCROFT BW, STEWART GS, WILLIAMS P. Quorum sensing in *Vibrio anguillarum*: characterization of the *vanI/vanR* locus and identification of the autoinducer *N*-(3-oxodecanoyl)-L-homoserine lactone[J]. Journal of Bacteriology, 1997, 179(9): 3004-3012.
- [41] HENKE JM, BASSLER BL. Three parallel quorum-sensing systems regulate gene expression in *Vibrio harveyi*[J]. Journal of Bacteriology, 2004, 186(20): 6902-6914.
- [42] THROUP JP, CAMARA M, BRIGGS GS, WINSON MK, CHHABRA SR, BYCROFT BW, WILLIAMS P, STEWART GSAB. Characterisation of the *yenI/yenR* locus from *Yersinia enterocolitica* mediating the synthesis of two *N*-acylhomoserine lactone signal molecules[J]. Molecular Microbiology, 1995, 17(2): 345-356.
- [43] LEE J, ZHANG LH. The hierarchy quorum sensing network in *Pseudomonas aeruginosa*[J]. Protein & Cell, 2015, 6(1): 26-41.
- [44] GROSSMAN AD. Genetic networks controlling the initiation of sporulation and the development of genetic competence in *Bacillus subtilis*[J]. Annual Review of Genetics, 1995, 29: 477-508.
- [45] GARDINER M, FERNANDES ND, NOWAKOWSKI D, RAFTERY M, KJELLEBERG S, ZHONG L, THOMAS T, EGAN S. VarR controls colonization and virulence in the marine macroalgal pathogen *Nautella italica* R11[J]. Frontiers in Microbiology, 2015, 6: 1130.
- [46] CUDE WN, BUCHAN A. Acyl-homoserine lactone-based quorum sensing in the *Roseobacter* clade: complex cell-to-cell communication controls multiple

- physiologies[J]. *Frontiers in Microbiology*, 2013, 4: 336.
- [47] WINANS SC. Bacterial esperanto[J]. *Nature Structural Biology*, 2002, 9(2): 83-84.
- [48] SCHAEFER AL, VAL DL, HANZELKA BL, CRONAN Jr JE, GREENBERG EP. Generation of cell-to-cell signals in quorum sensing: acyl homoserine lactone synthase activity of a purified *Vibrio fischeri* LuxI protein[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 1996, 93(18): 9505-9509.
- [49] WATERS CM, BASSLER BL. Quorum sensing: cell-to-cell communication in bacteria[J]. *Annual Review of Cell and Developmental Biology*, 2005, 21: 319-346.
- [50] READING NC, SPERANDIO V. Quorum sensing: the many languages of bacteria[J]. *FEMS Microbiology Letters*, 2006, 254(1): 1-11.
- [51] WILLIAMS P, WINZER K, CHAN WC, CÁMARA M. Look who's talking: communication and quorum sensing in the bacterial world[J]. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 2007, 362(1483): 1119-1134.
- [52] UROZ S, DESSAUX Y, OGER P. Quorum sensing and quorum quenching: the yin and yang of bacterial communication[J]. *ChemBioChem*, 2009, 10(2): 205-216.
- [53] HMELO LR. Quorum sensing in marine microbial environments[J]. *Annual Review of Marine Science*, 2017, 9: 257-281.
- [54] KALIA VC, KUMAR P, PANDIAN STK, SHARMA P. Biofouling control by quorum quenching[A]//*Springer Handbook of Marine Biotechnology*[M]. Berlin, Heidelberg: Springer Berlin Heidelberg, 2015: 431-440.
- [55] RIAZ K, ELMERICH C, MOREIRA D, RAFFOUX A, DESSAUX Y, FAURE D. A metagenomic analysis of soil bacteria extends the diversity of quorum-quenching lactonases[J]. *Environmental Microbiology*, 2008, 10(3): 560-570.
- [56] OCHIAI S, YASUMOTO S, MOROHOSHI T, IKEDA T. AmiE, a novel *N*-acylhomoserine lactone acylase belonging to the amidase family, from the activated-sludge isolate *Acinetobacter* sp. strain Ooi24[J]. *Applied and Environmental Microbiology*, 2014, 80(22): 6919-6925.
- [57] SUNDER AV, UTARI PD, RAMASAMY S, van MERKERK R, QUAX W, PUNDLE A. Penicillin V acylases from gram-negative bacteria degrade *N*-acylhomoserine lactones and attenuate virulence in *Pseudomonas aeruginosa*[J]. *Applied Microbiology and Biotechnology*, 2017, 101(6): 2383-2395.
- [58] CARLIER A, UROZ S, SMADJA B, FRAY R, LATOUR X, DESSAUX Y, FAURE D. The Ti plasmid of *Agrobacterium tumefaciens* harbors an *attM*-paralogous gene, *aiiB*, also encoding *N*-acyl homoserine lactonase activity[J]. *Applied and Environmental Microbiology*, 2003, 69(8): 4989-4993.
- [59] ZHANG HB, WANG LH, ZHANG LH. Genetic control of quorum-sensing signal turnover in *Agrobacterium tumefaciens*[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2002, 99(7): 4638-4643.
- [60] PARK SY, LEE SJ, OH TK, OH JW, KOO BT, YUM DY, LEE JK. AhlD, an *N*-acylhomoserine lactonase in *Arthrobacter* sp., and predicted homologues in other bacteria[J]. *Microbiology*, 2003, 149(6): 1541-1550.
- [61] DONG YH, XU JL, LI XZ, ZHANG LH. AiiA, an enzyme that inactivates the acylhomoserine lactone quorum-sensing signal and attenuates the virulence of *Erwinia carotovora*[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2000, 97(7): 3526-3531.
- [62] CHOWDHARY PK, KESHAVAN N, NGUYEN HQ, PETERSON JA, GONZÁLEZ JE, HAINES DC. *Bacillus megaterium* CYP102A1 oxidation of acyl homoserine lactones and acyl homoserines[J]. *Biochemistry*, 2007, 46(50): 14429-14437.
- [63] TERWAGNE M, MIRABELLA A, LEMAIRE J, DESCHAMPS C, de BOLLE X, LETESSON JJ. Quorum sensing and self-quorum quenching in the intracellular pathogen *brucellamelitensis*[J]. *PLoS One*, 2013, 8(12): e82514.
- [64] KOCH G, NADAL-JIMENEZ P, COOL RH, QUAX WJ. *Deinococcus radiodurans* can interfere with quorum sensing by producing an AHL-acylase and an AHL-lactonase[J]. *FEMS Microbiology Letters*, 2014, 356(1): 62-70.
- [65] MUKHERJI R, VARSHNEY NK, PANIGRAHI P, SURESH CG, PRABHUNE A. A new role for penicillin acylases: degradation of acyl homoserine lactone quorum sensing signals by *Kluyvera citrophila* penicillin G acylase[J]. *Enzyme and Microbial Technology*, 2014, 56: 1-7.
- [66] CZAJKOWSKI R, KRZYŻANOWSKA D, KARCZEWSKA J, ATKINSON S, PRZYSOWA J, LOJKOWSKA E, WILLIAMS P, JAFRA S.

- Inactivation of AHLs by *Ochrobactrum* sp. A44 depends on the activity of a novel class of AHL acylase[J]. *Environmental Microbiology Reports*, 2011, 3(1): 59-68.
- [67] SIO CF, OTTEN LG, COOL RH, DIGGLE SP, BRAUN PG, BOS R, DAYKIN M, CÁMARA M, WILLIAMS P, QUAX WJ. Quorum quenching by an *N*-acyl-homoserine lactone acylase from *Pseudomonas aeruginosa* PAO1[J]. *Infection and Immunity*, 2006, 74(3): 1673-1682.
- [68] HUANG JJ, PETERSEN A, WHITELEY M, LEADBETTER JR. Identification of QuiP, the product of gene PA1032, as the second acyl-homoserine lactone acylase of *Pseudomonas aeruginosa* PAO1[J]. *Applied and Environmental Microbiology*, 2006, 72(2): 1190-1197.
- [69] WAHJUDI M, PAPAIOANNOU E, HENDRAWATI O, van ASSEN AHG, van MERKERK R, COOL RH, POELARENDs GJ, QUAX WJ. PA0305 of *Pseudomonas aeruginosa* is a quorum quenching acylhomoserine lactone acylase belonging to the Ntn hydrolase superfamily[J]. *Microbiology*, 2011, 157(7): 2042-2055.
- [70] SHEPHERD RW, LINDOW SE. Two dissimilar *N*-acyl-homoserine lactone acylases of *Pseudomonas syringae* influence colony and biofilm morphology[J]. *Applied and Environmental Microbiology*, 2009, 75(1): 45-53.
- [71] CHEN CN, CHEN CJ, LIAO CT, LEE CY. A probable aculeacin A acylase from the *Ralstonia solanacearum* GMI1000 is *N*-acyl-homoserine lactone acylase with quorum-quenching activity[J]. *BMC Microbiology*, 2009, 9: 89.
- [72] LIN YH, XU JL, HU JY, WANG LH, LEONG ONG S, LEADBETTER JR, ZHANG LH. Acyl-homoserine lactone acylase from *Ralstonia* strain XJ12B represents a novel and potent class of quorum-quenching enzymes[J]. *Molecular Microbiology*, 2003, 47(3): 849-860.
- [73] UROZ S, OGER PM, CHAPELLE E, ADELIN MT, FAURE D, DESSAUX Y. A *Rhodococcus qsdA*-encoded enzyme defines a novel class of large-spectrum quorum-quenching lactonases[J]. *Applied and Environmental Microbiology*, 2008, 74(5): 1357-1366.
- [74] PARK SY, KANG HO, JANG HS, LEE JK, KOO BT, YUM DY. Identification of extracellular *N*-acylhomoserine lactone acylase from a *Streptomyces* sp. and its application to quorum quenching[J]. *Applied and Environmental Microbiology*, 2005, 71(5): 2632-2641.
- [75] MOROHOSHI T, NAKAZAWA S, EBATA A, KATO N, IKEDA T. Identification and characterization of *N*-acylhomoserine lactone-acylase from the fish intestinal *Shewanella* sp. strain MIB015[J]. *Bioscience, Biotechnology, and Biochemistry*, 2008, 72(7): 1887-1893.
- [76] TORRES-BACETE J, HORMIGO D, TORRES-GÚZMAN R, ARROYO M, CASTILLÓN MP, GARCÍA LJ, ACEBAL C, MATA I. Overexpression of penicillin V acylase from *Streptomyces lavendulae* and elucidation of its catalytic residues[J]. *Applied and Environmental Microbiology*, 2015, 81(4): 1225-1233.
- [77] HOANG TT, SCHWEIZER HP. Characterization of *Pseudomonas aeruginosa* enoyl-acyl carrier protein reductase (FabI): a target for the antimicrobial triclosan and its role in acylated homoserine lactone synthesis[J]. *Journal of Bacteriology*, 1999, 181(17): 5489-5497.
- [78] GUTIERREZ JA, CROWDER T, RINALDO-MATTHIAS A, HO MC, ALMO SC, SCHRAMM VL. Transition state analogs of 5'-methylthioadenosine nucleosidase disrupt quorum sensing[J]. *Nature Chemical Biology*, 2009, 5(4): 251-257.
- [79] GEMIARTO AT, NINYIO NN, LEE SW, LOGIS J, FATIMA A, CHAN EWC, LIM CSY. Isoprenyl caffeate, a major compound in manuka propolis, is a quorum-sensing inhibitor in *Chromobacterium violaceum*[J]. *Antonie Van Leeuwenhoek*, 2015, 108(2): 491-504.
- [80] KUMAR L, CHHIBBER S, KUMAR R, KUMAR M, HARJAI K. Zingerone silences quorum sensing and attenuates virulence of *Pseudomonas aeruginosa*[J]. *Fitoterapia*, 2015, 102: 84-95.
- [81] ALFARO JF, ZHANG T, WYNN DP, KARSCHNER EL, ZHOU ZS. Synthesis of LuxS inhibitors targeting bacterial cell-cell communication[J]. *Organic Letters*, 2004, 6(18): 3043-3046.
- [82] MCINNIS CE, BLACKWELL HE. Thiolactone modulators of quorum sensing revealed through library design and screening[J]. *Bioorganic & Medicinal Chemistry*, 2011, 19(16): 4820-4828.
- [83] MALLADI VLA, SOBCZAK AJ, MARICIC N, MURUGAPIRAN SK, SCHNEPER L, MAKEMSON J, MATHEE K, WNUK SF. Substituted lactam and cyclic azahemiacetals modulate *Pseudomonas aeruginosa* quorum sensing[J]. *Bioorganic & Medicinal Chemistry*,

- 2011, 19(18): 5500-5506.
- [84] STACY DM, LE QUEMENT ST, HANSEN CL, CLAUSEN JW, TOLKER-NIELSEN T, BRUMMOND JW, GIVSKOV M, NIELSEN TE, BLACKWELL HE. Synthesis and biological evaluation of triazole-containing *N*-acyl homoserine lactones as quorum sensing modulators[J]. *Organic & Biomolecular Chemistry*, 2013, 11(6): 938-954.
- [85] GIVSKOV M, DE NYS R, MANEFIELD M, GRAM L, MAXIMILIEN R, EBERL L, MOLIN S, STEINBERG PD, KJELLEBERG S. Eukaryotic interference with homoserine lactone-mediated prokaryotic signalling[J]. *Journal of Bacteriology*, 1996, 178(22): 6618-6622.
- [86] LOWERY CA, ABE T, PARK J, EUBANKS LM, SAWADA D, KAUFMANN GF, JANDA KD. Revisiting AI-2 quorum sensing inhibitors: direct comparison of alkyl-DPD analogues and a natural product fimbrolide[J]. *Journal of the American Chemical Society*, 2009, 131(43): 15584-15585.
- [87] WIDMER KW, SONI KA, HUME ME, BEIER RC, JESUDHASAN P, PILLAI SD. Identification of poultry meat-derived fatty acids functioning as quorum sensing signal inhibitors to autoinducer-2 (AI-2)[J]. *Journal of Food Science*, 2007, 72(9): M363-M368.
- [88] BRACKMAN G, CELEN S, HILLAERT U, van CALENBERGH S, COS P, MAES L, NELIS HJ, COENYE T. Structure-activity relationship of cinnamaldehyde analogs as inhibitors of AI-2 based quorum sensing and their effect on virulence of *Vibrio* spp.[J]. *PLoS One*, 2011, 6(1): e16084.
- [89] FAN H, DONG YH, WU DH, BOWLER MW, ZHANG LH, SONG HW. QsIA disrupts LasR dimerization in inactivation of bacterial quorum sensing[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2013, 110(51): 20765-20770.
- [90] HUANG JJ, HAN JI, ZHANG LH, LEADBETTER JR. Utilization of acyl-homoserine lactone quorum signals for growth by a soil pseudomonad and *Pseudomonas aeruginosa* PAO1[J]. *Applied and Environmental Microbiology*, 2003, 69(10): 5941-5949.
- [91] YANG F, WANG LH, WANG J, DONG YH, HU JY, ZHANG LH. Quorum quenching enzyme activity is widely conserved in the sera of mammalian species[J]. *FEBS Letters*, 2005, 579(17): 3713-3717.
- [92] COALE KH, JOHNSON KS, FITZWATER SE, GORDON RM, TANNER S, CHAVEZ FP, FERIOLI L, SAKAMOTO C, ROGERS P, MILLERO F, STEINBERG P, NIGHTINGALE P, COOPER D, COCHLAN WP, LANDRY MR, CONSTANTINOU J, ROLLWAGEN G, TRASVINA A, KUDELA R. A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean[J]. *Nature*, 1996, 383(6600): 495-501.
- [93] GEIDER RJ. Complex lessons of iron uptake[J]. *Nature*, 1999, 400(6747): 815-816.
- [94] VRASPIR JM, BUTLER A. Chemistry of marine ligands and siderophores[J]. *Annual Review of Marine Science*, 2009, 1: 43-63.
- [95] AMIN SA. The role of siderophores in algal-bacterial interactions in the marine environment[D]. San Diego: Doctoral Dissertation of University of California, 2010.
- [96] BELL W, MITCHELL R. Chemotactic and growth responses of marine bacteria to algal extracellular products[J]. *The Biological Bulletin*, 1972, 143(2): 265-277.
- [97] AMIN SA, PARKER MS, ARMBRUST EV. Interactions between diatoms and bacteria[J]. *Microbiology and Molecular Biology Reviews: MMBR*, 2012, 76(3): 667-684.
- [98] LEBOULANGER C, ORIOL L, JUPIN HR, DESOLAS-GROS C. Diel variability of glycolate in the eastern tropical Atlantic Ocean[J]. *Deep Sea Research Part I: Oceanographic Research Papers*, 1997, 44(12): 2131-2139.
- [99] WYSS SC. Design of a cross-domain quorum sensing pathway for algae biofuel applications[D]. Athens: Bachelor's Thesis of Ohio University, 2013.
- [100] HALL-STOODLEY L, COSTERTON JW, STOODLEY P. Bacterial biofilms: from the natural environment to infectious diseases[J]. *Nature Reviews Microbiology*, 2004, 2(2): 95-108.
- [101] JEFFERSON KK. What drives bacteria to produce a biofilm?[J]. *FEMS Microbiology Letters*, 2004, 236(2): 163-173.
- [102] MATZ C, KJELLEBERG S. Off the hook-how bacteria survive protozoan grazing[J]. *Trends in Microbiology*, 2005, 13(7): 302-307.
- [103] TAIT K, JOINT I, DAYKIN M, MILTON DL, WILLIAMS P, CÁMARA M. Disruption of quorum sensing in seawater abolishes attraction of zoospores of the green alga *Ulva* to bacterial biofilms[J]. *Environmental Microbiology*, 2005, 7(2): 229-240.
- [104] TEBBEN J, TAPIOLAS DM, MOTTI CA, ABREGO D, NEGRI AP, BLACKALL LL, STEINBERG PD,

- HARDER T. Induction of larval metamorphosis of the coral *Acropora millepora* by tetrabromopyrrole isolated from a *Pseudoalteromonas* bacterium[J]. PLoS One, 2011, 6(4): e19082.
- [105] ZARGIEL KA, SWAIN GW. Static vs dynamic settlement and adhesion of diatoms to ship hull coatings[J]. Biofouling, 2014, 30(1): 115-129.
- [106] ZHAI CM, ZHANG P, SHEN F, ZHOU CX, LIU CH. Does *Microcystis aeruginosa* have quorum sensing?[J]. FEMS Microbiology Letters, 2012, 336(1): 38-44.
- [107] STEINBERG PD, SCHNEIDER R, KJELLEBERG S. Chemical defenses of seaweeds against microbial colonization[J]. Biodegradation, 1997, 8(3): 211-220.
- [108] DWORJANYN SA, DE NYS R, STEINBERG PD. Localisation and surface quantification of secondary metabolites in the red alga *Delisea pulchra*[J]. Marine Biology, 1999, 133(4): 727-736.
- [109] NAKASHIMA T, MIYAZAKI Y, MATSUYAMA Y, MURAOKA W, YAMAGUCHI K, ODA T. Producing mechanism of an algicidal compound against red tide phytoplankton in a marine bacterium *γ-proteobacterium*[J]. Applied Microbiology and Biotechnology, 2006, 73(3): 684-690.
- [110] HARVEY EL, DEERING RW, ROWLEY DC, EL GAMAL A, SCHORN M, MOORE BS, JOHNSON MD, MINCER TJ, WHALEN KE. A bacterial quorum-sensing precursor induces mortality in the marine coccolithophore, *Emiliania huxleyi*[J]. Frontiers in Microbiology, 2016, 7: 59.
- [111] GUO XL, LIU XL, WU LS, PAN JL, YANG H. The algicidal activity of *Aeromonas* sp. strain GLY-2107 against bloom-forming *Microcystis aeruginosa* is regulated by *N*-acyl homoserine lactone-mediated quorum sensing[J]. Environmental Microbiology, 2016, 18(11): 3867-3883.
- [112] HU TY, WANG S, SHAN YS, ZHANG YC, ZHU YJ, ZHENG L. Complete genome of marine microalgae associated algicidal bacterium *Sulfitobacter pseudonitzschiae* H46 with quorum sensing system[J]. Current Microbiology, 2021, 78(10): 3741-3750.
- [113] 杨淋. *Sulfitobacter pseudonitzschiae* H46 在不同藻际环境中的藻菌关系及抑藻机制研究[D]. 青岛: 自然资源部第一海洋研究所硕士学位论文, 2023.
- YANG L. Study on algae-bacteria relationship and algicidal mechanism of *Sulfitobacter pseudonitzschiae* H46 in different phycosphere environments[D]. Qingdao: Master's Thesis of First Institute of Oceanography, Ministry of Natural Resources, 2023 (in Chinese).
- [114] YANG L, HU T, WANG S, ZHANG Y, LI Q, HAN B, ZHENG L. Distinct interactions driven by DMSP between different microalgae and the phycosphere bacterium *Sulfitobacter pseudonitzschiae* H46[J]. Marine Ecology Progress Series, 2023, 710: 15-25.
- [115] JOHNSON WM, KIDO SOULE MC, KUJAWINSKI EB. Evidence for quorum sensing and differential metabolite production by a marine bacterium in response to DMSP[J]. The ISME Journal, 2016, 10(9): 2304-2316.
- [116] BRUHN JB, NIELSEN KF, HJELM M, HANSEN M, BRESCIANI J, SCHULZ S, GRAM L. Ecology, inhibitory activity, and morphogenesis of a marine antagonistic bacterium belonging to the *Roseobacter* clade[J]. Applied and Environmental Microbiology, 2005, 71(11): 7263-7270.
- [117] RAO D, WEBB JS, HOLMSTRÖM C, CASE R, LOW A, STEINBERG P, KJELLEBERG S. Low densities of epiphytic bacteria from the marine alga *Ulva australis* inhibit settlement of fouling organisms[J]. Applied and Environmental Microbiology, 2007, 73(24): 7844-7852.
- [118] GENGHF, BRUHN JB, NIELSEN KF, GRAM L, BELAS R. Genetic dissection of tropodithietic acid biosynthesis by marine roseobacters[J]. Applied and Environmental Microbiology, 2008, 74(5): 1535-1545.
- [119] BERGER M, NEUMANN A, SCHULZ S, SIMON M, BRINKHOFF T. Tropodithietic acid production in *Phaeobacter gallaeciensis* is regulated by *N*-acyl homoserine lactone-mediated quorum sensing[J]. Journal of Bacteriology, 2011, 193(23): 6576-6585.
- [120] THOLE S, KALHOEFER D, VOGET S, BERGER M, ENGELHARDT T, LIESEGANG H, WOLLHERR A, KJELLEBERG S, DANIEL R, SIMON M, THOMAS T, BRINKHOFF T. *Phaeobacter gallaeciensis* genomes from globally opposite locations reveal high similarity of adaptation to surface life[J]. The ISME Journal, 2012, 6(12): 2229-2244.
- [121] 孙文昕. 微藻促生菌群体感应对小球藻的影响机制研究[D]. 西安: 陕西科技大学硕士学位论文, 2023.
- SUN WX. The influence mechanism of quorum sensing of microalgae growth-promoting bacteria on *Chlorella*[D]. Xi'an: Master's Thesis of Shaanxi University of Science and Technology, 2023 (in Chinese).
- [122] WANG ZY, ZENG YH, CHENG KK, CAI ZH, ZHOU J. The quorum sensing system of *Novosphingobium* sp. ERN07 regulates aggregate formation that promotes

- cyanobacterial growth[J]. *Science of the Total Environment*, 2022, 851: 158354.
- [123] 谢雨彤. 信号分子调控铜绿微囊藻合成分泌藻毒素的初步研究[D]. 长春: 东北师范大学硕士学位论文, 2021.
- XIE YT. Preliminary study on signaling molecules regulating the synthesis and secretion of microcystins in *Microcystis aeruginosa*[D]. Changchun: Master's Thesis of Northeast Normal University, 2021 (in Chinese).
- [124] NATRAH FMI, KENMEGNE MM, WIYOTO W, SORGELOOS P, BOSSIER P, DEFOIRDT T. Effects of micro-algae commonly used in aquaculture on acyl-homoserine lactone quorum sensing[J]. *Aquaculture*, 2011, 317: 53-57.
- [125] GERWICK L, BOUDREAU P, CHOI H, MASCUCH S, VILLA FA, BALUNAS MJ, MALLOY KL, TEASDALE ME, ROWLEY DC, GERWICK WH. Interkingdom signaling by structurally related cyanobacterial and algal secondary metabolites[J]. *Phytochemistry Reviews*, 2013, 12(3): 459-465.
- [126] MONTGOMERY K, CHARLESWORTH JC, LEBARD R, VISSCHER PT, BURNS BP. Quorum sensing in extreme environments[J]. *Life* (Basel, Switzerland), 2013, 3(1): 131-148.
- [127] ZHOU J, LYU YH, RICHLIN M, 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.
- [128] WONG CS, YIN WF, CHOO YM, SAM CK, KOH CL, CHAN KG. Coexistence of quorum-quenching and quorum-sensing in tropical marine *Pseudomonas aeruginosa* strain MW3A[J]. *World Journal of Microbiology and Biotechnology*, 2012, 28(2): 453-461.
- [129] TAN CH, KOH KS, XIE C, ZHANG J, TAN XH, LEE GP, ZHOU Y, NG WJ, RICE SA, KJELLEBERG S. Community quorum sensing signalling and quenching: microbial granular biofilm assembly[J]. *Npj Biofilms and Microbiomes*, 2015, 1(1): 15006.
- [130] CHEVROT R, ROSEN R, HAUDECOEUR E, CIROU A, SHELPI BJ, RON E, FAURE D. GABA controls the level of quorum-sensing signal in *Agrobacterium tumefaciens*[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2006, 103(19): 7460-7464.
- [131] UTARI PD, VOGEL J, QUAX WJ. Deciphering physiological functions of AHL quorum quenching acylases[J]. *Frontiers in Microbiology*, 2017, 8: 1123.