AHLs-produced bacteria in refrigerated shrimp enhanced the growth and spoilage ability of *Shewanella baltica*

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Abstract *Shewanella baltica* is the predominant bacteria in spoiled shrimp (*Litopenaeus vannamei*), however, the spoilage ability and the mechanism of *S. baltica* is still unknown. *S. baltica* can't produce the signal molecule of acyl-homoserine-lactones (AHLs), so the aim of this study was to investigate how wild type *S. baltica* SA03 (WT SA03) eavesdrop exogenous AHLs to enhance its spoilage ability through LuxR receptor. The results indicated that *Aeromonas* spp. (Aer), *Acinetobacter* spp. (Aci) and *Serratia* spp. (Ser) isolated from refrigerated shrimp can produce different AHLs. WT SA03 can eavesdrop the AHLs of Aer (C4-HSL), Aci (O-C6-HSL) and Ser (C6-HSL, O-C6-HSL) to enhance its growth, especially Ser. Exogenous C4-HSL and C6-HSL enhanced biofilm formation of WT SA03, and C6-HSL and O-C6-HSL enhanced thioredoxin reductase *trxB* mRNA expression. However, the *luxR* mutant of WT SA03 ($\Delta luxR$ SA03) lost or weakened the role of using environmental AHLs. In vivo experiments, the lag time of WT SA03 was shortened by 6.4 h, 6.2 h and 14.4 h by co-inoculated with Aer, Aci and Ser, respectively. The total volatile basic nitrogen (TVB-N) were significantly enhanced in the samples co-inoculated with WT SA03 and Aer (or Aci, Ser) than those of $\Delta luxR$ SA03 and Aer (or Aci, Ser) ($p < 0.05$). The results showed that *S. baltica* SA03 can utilize AHLs produced by other bacteria

to enhance its growth and spoilage ability through LuxR receptor system. Quorum sensing based on AHLs of bacteria might as the potential targets for food spoilage control.

Keywords *Shewanella baltica* · Quorum sensing · Eavesdropping · Acyl-homoserine-lactones · Spoilage ability

Abbreviations

WT SA03	Wild type <i>Shewanella baltica</i> SA03
$\Delta luxR$ SA03	The <i>luxR</i> mutant of <i>Shewanella baltica</i> SA03
Aer	<i>Aeromonas</i> spp.
Aci	<i>Acinetobacter</i> spp.
Ser	<i>Serratia</i> spp.
C4-HSL	<i>N</i> -butanoyl-L-homoserine lactone
C6-HSL	<i>N</i> -hexanoyl-L-homoserine lactone
C8-HSL	<i>N</i> -3-hydroxyoctanoyl-L-homoserine lactone
O-C6-HSL	<i>N</i> -(3-oxohexanoyl)-L-homoserine lactone
O-C8-HSL	<i>N</i> -(3-oxo hydroxyoctanoyl)-L-homoserine lactone

Introduction

Quorum sensing (QS) is bacteria communication in a cell-density-dependent manner by producing and responding to small diffusible molecules named autoinducers. The QS system based acetylated homoserine lactones (AHLs) consists of two components, an autoinducer synthase (LuxI) and a transcriptional regulator (LuxR) (Waters and Bassler 2005). In recent years, many studies have shown that food spoilage is related to the QS of bacteria (Rul and Monnet 2015). Christensen et al. (2003) reported that the

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spoilage behavior of *Serratia proteamaculans* B5 was regulated by QS, and the *sprI* (responsible for the production of AHLs) mutant of *S. proteamaculans* B5a lost the spoilage ability in the milk. AHLs were also detected in spoiled shrimp, and the enhancing AHLs accelerate the spoilage process of shrimp (Zhu et al. 2015).

However, some bacteria do not produce AHLs (solo LuxR) but can use AHLs produced by other bacteria to regulate their own metabolism, which phenomenon is called QS eavesdropping. Hudaiberdiev et al. (2015) found that 2698 of 3550 LuxR in prokaryotes are solo LuxR without the AHL synthase (LuxI). Solo LuxR from *Pseudomonas putida* can sense exogenous AHLs (Subramoni and Venturi 2009). Solo LuxR (SmoR) from *Stenotrophomonas maltophilia* binds exogenous AHLs and regulates their ability of swimming (Martínez et al. 2015). The solo LuxR in *Pseudomonas syringae* (PsaR) and *Escherichia coli* (SdiA) can also sense exogenous AHLs and regulate their pathogenicity (Patel et al. 2014; Smith et al. 2011).

Shewanella baltica are the predominant bacteria in many fish and shrimp (Fonnesbech et al. 2005; Zhu et al. 2015; Zhang et al. 2016). *S. baltica* can't produce AHLs, and it contains solo LuxR which can eavesdrop on AHLs to improve its spoilage ability (Zhu et al. 2018). *Aeromonas* spp. (Aer), *Acinetobacter* spp. (Aci) and *Serratia* spp. (Ser) are the important components of the microbiota in spoiled *L. vannamei* (Zhu et al. 2015), and all of them have the ability to produce AHLs (Kim and Park 2013; Zhang et al. 2016). The previous studies have shown that *S. baltica* can utilize AHLs produced by *Acinetobacter* through LuxR system (Zhu et al. 2018; Jie et al. 2018). However, little is known about what kind of AHLs can be utilized by *S. baltica* to enhance its spoilage potential. The purpose of the study was to elucidate how *S. baltica* eavesdrops AHLs produced by other bacteria to enhance its growth and spoilage ability by comparing the wild type *S. baltica* (WT SA03) with the *luxR* mutant of *S. baltica* ($\Delta luxR$ SA03).

Materials and methods

Materials and bacterial strains

AHLs standards (*N*-butanoyl-L-homoserine lactone, C4-HSL; *N*-hexanoyl-L-homoserine lactone, C6-HSL; *N*-3-hydroxyoctanoyl-L-homoserine lactone, C8-HSL; *N*-(3-oxohexanoyl)-L-homoserine lactone, O-C6-HSL, *N*-(3-oxooctanoyl)-L-homoserine lactone, O-C8-HSL), X-Gal (5-bromo-4-chloro-3-indol-yl- β -D-galactopyranoside) were purchased from Sigma-Aldrich Co. (St. Louis, MO, USA). The wild type *Shewanella baltica* (WT SA03), *Aeromonas* spp. (Aer), *Acinetobacter* spp. (Aci)

and *Serratia* spp. (Ser) were isolated from spoiled refrigerated *Litopenaeus vannamei* using agar plate method and kept in our laboratory. The *luxR* mutant of *S. baltica* SA03 ($\Delta luxR$ SA03) was constructed using the *att*-based fusion PCR method and kept in our laboratory (Jie et al. 2018). *Agrobacterium tumefaciens* A136 and *Chromobacterium violaceum* CV026 were presented by Professor Mclean (Texas State University, USA).

AHLs assays

The qualitative assay of AHLs was performed according to the method of Ravn et al. (2003). Briefly, the samples were spotted onto the thin-layer chromatography plate and separated with methanol–water (60:40, v/v.), and the chemically synthesized AHLs (C4-HSL, C6-HSL, O-C6-HSL) were used as the standard. *A. tumefaciens* A136 and *C. violaceum* CV026 were used as bioreporter strains.

AHLs in shrimp samples were quantified by assaying β -galactosidase induction in cellular lysate of *A. tumefaciens* A136 (Kawaguchi et al. 2008). The sterile medium was used as the negative control. The AHLs levels were expressed as β -galactosidase activity ($U = OD_{635}$ of the sample/ OD_{635} of the negative control).

Bacterial growth assay

The growth assay was performed according to the method of Jie et al. (2018). The strains were pre-cultured in LB medium at 30 °C for 12 h, then inoculated into fresh AB medium (1%) with or without the exogenous AHLs (C4-HSL, C6-HSL, O-C6-HSL, final concentration of 10 μ mol/L) for 16 h at 30 °C. The control added equivalent dimethyl sulfoxide. Bacterial population was estimated by the measure of OD_{600} using a spectrophotometer in 2 h intervals.

Biofilm formation assay

The biofilm formation assay was performed according to the method of Zhang et al. (2016). The surface-attached biofilms were stained with crystal violet (0.1 g/L) for 15 min. Crystal violet-stained biofilm matrices were resuspended with 95% ethanol and the absorbance was measured at 570 nm. The relative biofilm formation was expressed as OD_{570} .

Thioredoxin reductase *trxB* gene expression assay

The relative expression of thioredoxin reductase *trxB* gene was measured according to the method of Fu et al. (2018). The primers of *trxB* (F: GCTGTGATCGGTGGCGGTAAC; R:GTGTCACGACGGTGGATCAGATG) and 16S

rRNA (F: GTCGAGTTGCAGACTCCAAT-CCG; R:CGTGCTTCAATGGCGAGTACAGAG) were designed and synthesized by Sangon Biotech (Shanghai, China). The relative quantitation of *trxB* gene expression was used to evaluate the activity of spoiled enzyme thioredoxin reductase.

Spoilage ability assay

The sterilized shrimp: Live *Litopenaeus vannamei* with an average weight of 14 ± 2.7 g were purchased from a local market. The peeled shrimp soaked in 2% formalin for 30 s and washed with sterile water 3 times for sterilization. Then, the sterilized samples were randomly assigned into different groups (each group 6.0 ± 0.2 kg) and each subjected to process in triplicate (Zhu et al. 2015; Wang et al. 2016).

The sterilized samples were mono-inoculated with 1.0×10^4 cfu/mL WT SA03, *AluxR* SA03, Aer, Aci and Ser, and the shrimp samples were co-inoculated with WT SA03 and Aer (WT SA03 + Aer), WT SA03 and Aci (WT SA03 + Aci), WT SA03 and Ser (WT SA03 + Ser), *AluxR* SA03 and Aer (*AluxR* SA03 + Aer), *AluxR* SA03 and Aci (*AluxR* SA03 + Aci), *AluxR* SA03 and Ser (*AluxR* SA03 + Ser). For the co-inoculation, the volume ratio of the two strains was 1:1 (v/v), and the concentration of the two strains was 1.0×10^4 cfu/mL. The sterilized sample without inoculation was appointed as the control. All treated samples were air packaged and stored at 4 ± 1 °C for 7 days. Average 500 g samples were taken from each group for analysis at each sampling point. The experiments were performed in triplicate.

Total viable counts and total volatile basic nitrogen assay

Total viable counts (TVC) were enumerated using nutrient agar incubated at 37 °C for 24 h and the H₂S-producing bacteria were determined by iron agar (Gu et al. 2013). The results were expressed as log₁₀ colony-forming units (cfu) per g of the sample. The microbial growth kinetics was described using the modified Gompertz model (Zwietering et al. 1990; Zhu et al. 2015). Total volatile basic nitrogen (TVB-N) values of the samples were measured according

to the method of Botta et al. (1984). The results were expressed as mg per 100 g sample.

Statistical analysis

Statistical analysis were done using SPSS software version 19.0 (SPSS, Inc., Chicago, USA) and OriginPro 8.0 software (OriginLab Co., Northampton, USA). The microbial growth dynamics were fitted using the modified Gompertz model by Origin8.0. All experiments were performed in triplicates (n = 3). The data are expressed as the mean $\pm$ standard deviation (SD).

Results and discussions

WT SA03 and *AluxR* SA03 eavesdropping on AHLs of Ser, Aer and Aci

Thin-layer chromatography assays indicated that the bacteria Aer, Aci and Ser can produce the signal molecules of C4-HSL (Fig. 1a), O-C6-HSL and O-C8-HSL (Fig. 1b), C6-HSL and O-C6-HSL (Fig. 1c), respectively. The results of Aci were consistent with the reports of Sun et al. (2015), which indicated that O-C6-HSL and O-C8-HSL were detected in the Aci culture. Our previous study has found that *Shewanella baltica* are incapable of producing AHLs but it could eavesdrop on the AHLs of Aci (Zhu et al. 2018). These results further confirmed that *S. baltica* SA03 can eavesdrop on the AHLs of all the three strains (Aer, Aci and Ser) in the co-cultivation on shrimp (Table 1, based on the β -galactosidase activity). However, the *luxR* mutant of *S. baltica* (*AluxR* SA03) lost or weakened the role of eavesdropping on the AHLs (accumulation higher levels of AHLs), which indicated that LuxR receptor of *S. baltica* play an important role in eavesdropping and utilizing the AHLs.

Effects of exogenous signal molecules on the growth of WT SA03 and *AluxR* SA03

To evaluate the effect of eavesdropping on the AHLs of Aer, Aci, Ser on the growth of *S. baltica*, the exogenous

Fig. 1 Thin-layer chromatography assays for AHLs production of Aer (a), Aci (b), Ser (c). *C. violaceum* CV026 (a, c) and *A. tumefaciens* A136 (b) were used as reporter strains

Table 1 The AHLs levels (β -galactosidase activity) changes in shrimp mono-inoculated with WT SA03 ($\Delta luxR$ SA03, Aer, Aci and Ser) and co-inoculated with WT SA03 ($\Delta luxR$ SA03) and Aer, Aci and Ser

Groups	Treatments	AHLs levels (U)
<i>S. baltica</i>	WT SA03	1.64 $\pm$ 0.34
	$\Delta luxR$ SA03	1.89 $\pm$ 0.51
Aer	Aer	18.23 $\pm$ 0.81 ^a
	WT SA03 + Aer	6.62 $\pm$ 1.82 ^c
	$\Delta luxR$ SA03 + Aer	13.20 $\pm$ 1.39 ^b
Aci	Aci [#]	17.00 $\pm$ 1.11 ^a
	WT SA03 + Aci [#]	3.90 $\pm$ 0.25 ^b
	$\Delta luxR$ SA03 + Aci	–
Ser	Ser	20.11 $\pm$ 1.11 ^a
	WT SA03 + Ser	6.95 $\pm$ 1.36 ^c
	$\Delta luxR$ SA03 + Ser	11.63 $\pm$ 0.51 ^b

Data with different letters (a, b and c) in the same group indicates significant difference ($p < 0.05$)

[#]Zhu et al. (2018)

signal molecules (i.e., C4-HSL, C6-HSL and O-C6-HSL) were added in the incubation of WT SA03 and $\Delta luxR$ SA03. The results indicated that the growth of WT SA03 was significantly increased upon adding 10 $\mu\text{mol/L}$ C4-HSL, C6-HSL and O-C6-HSL in AB medium ($p < 0.05$), and there was no significant difference of the growth of $\Delta luxR$ SA03 with or without exogenous signal molecules (Fig. 2), which indicated that *S. baltica* can promote its growth by eavesdropping all the three signal molecules (C4-HSL, C6-HSL and O-C6-HSL). These results agreed with reporting by Zhang et al. (2014, 2017), which showed that the growth of *Pseudomonas aeruginosa* and *Shewanella putrefaciens* increased upon adding AHLs. However, the exogenous AHLs had no effect on WT SA03 and $\Delta luxR$ SA03 in LB medium (data not shown). The reason may be attributed to the nutrient stress of the AB medium. Ravn et al. (2003) reported that the bacterial growth regulated by QS was influenced by the environment, and *S. baltica* has a more competitive advantage under nutrient stress conditions (Zhu et al. 2018), indicating that *S. baltica* might have the ability of eavesdropping exogenous AHLs through LuxR receptor to regulate their growth according to the environmental conditions.

Effects of exogenous signal molecules and co-incubation on the metabolism of WT SA03 and $\Delta luxR$ SA03

Biofilm formation represents a protected growth pattern that allows bacteria to survive and spread to new niches in harsh environments (Hall-stoodley et al. 2004), and biofilm

Fig. 2 Effects of exogenous signal molecules on the growth of WT SA03 and $\Delta luxR$ SA03 in vitro

formation is usually regulated by QS systems (Zhu et al. 2015). The *trx* gene (encoded thioredoxin reductase) is involved in the production of sulfides, which is also associated with QS (Fu et al. 2018). The results indicated that C4-HSL and C6-HSL enhanced the biofilm formation (incubation of 36 h) of WT SA03, and C6-HSL and O-C6-

Fig. 3 Effects of exogenous signal molecules on the biofilm formation (a) incubation for 36 h) and thioredoxin reductase *trxB* mRNA expression (b) incubation for 12 h) of WT SA03 and *AluxR* SA03 in vitro. (n = 3, ***p* < 0.01)

HSL promoted the *trxB* gene expression (incubation of 12 h) of WT SA03 ($p < 0.05$) (Fig. 3a, b). However, the biofilm formation of *AluxR* SA03 has no changes with or without exogenous signal molecules, and the increase of *trxB* mRNA expression in *AluxR* SA03 upon adding exogenous signal molecules was significantly lower than that of WT SA03 ($p < 0.05$). Based on the results, we deduce that *S. baltica* might have the ability of utilizing exogenous AHLs through LuxR receptor to regulate their biofilm formation, *trxB* mRNA expression even spoilage ability, and different signal molecules play different roles in spoilage potential of *S. baltica*.

Effects of mono- and co-inoculation on the spoilage ability of WT SA03 and *AluxR* SA03

To test the spoilage ability of *S. baltica* in vivo, WT SA03 and *AluxR* SA03 were mono- and co-inoculated in shrimp with AHLs-produced bacteria (Aer, Aci and Ser). The results indicated that total viable counts (TVC) of all treatments increased with storage time. The TVC of the samples showed no difference between the mono-inoculation with WT SA03 and *AluxR* SA03. As for the co-inoculation with Aci and Ser, the TVC values of the WT SA03 co-inoculation groups were significantly higher than that of *AluxR* SA03 co-inoculation groups after 6 days ($p < 0.05$), but the TVC values showed no significant difference between the WT SA03 co-inoculation group and *AluxR* SA03 co-inoculation group when co-inoculated with Aer (Fig. 4).

Shewanella baltica in the samples co-inoculated with WT SA03 and Aer (Aci and Ser) exhibited shorter lag time compared with the mono-inoculation WT SA03, and the lag time of WT SA03 was shortened by 6.4 h, 6.2 h, 14.4 h when co-inoculated with Aer, Aci and Ser, respectively ($p < 0.05$) (Table 2). However, the lag time of the samples co-inoculated with *AluxR* SA03 and Aer (Aci and

Ser) showed no significant changes compared with *AluxR* SA03. The maximum growth rate of WT SA03 was enhanced only co-inoculated with Ser. We concluded that WT SA03 could eavesdrop the AHLs of Aer, Aci and Ser to improve its growth. Different signal molecules play different roles in the spoilage potential of *S. baltica*, and the AHLs of Ser were more capable of promoting the growth of WT SA03. Bacteria are the major cause of spoilage food, and extending lag time of bacteria may extend the shelf-life of seafood products (Remya et al. 2017). Thus, we suggested that LuxR receptor was involved in the spoilage ability of *S. baltica*, and AHLs-produced bacteria (Aer, Aci and Ser) could enhance the spoilage ability of *S. baltica*.

Previous studies reported that exogenous AHLs (C7-HSL, C8-HSL) significantly increased TVB-N production of surimi juice (Zhao et al. 2018). Meanwhile, the AHL-negative strains or mutant lost or weakened their spoilage ability in the meat storage (Bruhn et al. 2004). As shown in Fig. 4, the TVB-N values of all treatments increased with storage time. The TVB-N of the samples showed no difference between the mono-inoculation with WT SA03 and *AluxR* SA03, which were in agreement with total viable counts.

These indicated that there was no difference in the spoilage ability between WT SA03 and *AluxR* SA03. However, the TVB-N of the WT SA03 co-inoculation groups were significantly higher than those of *AluxR* SA03 co-inoculation groups after 6 days. In the samples of co-inoculated with Aer (or Aci, Ser), the TVB-N increased by 3, 7, 12 mg/100 g, respectively ($p < 0.05$). These trends were in agreement with the changes of total viable counts, indicating that WT SA03 have more strong spoilage ability than *AluxR* SA03 through eavesdropping AHLs of Aer, Aci and Ser, and Ser were more capable of promoting the spoilage ability of *S. baltica* among the three strains.

Fig. 4 Total viable counts in shrimp mono-inoculated with WT SA03 (or $\Delta luxR$ SA03, Aer, Aci and Ser) and co-inoculated with WT SA03 (or $\Delta luxR$ SA03) and Aer, Aci and Ser

Conclusion

In summary, *S. baltica* could utilize exogenous AHLs through LuxR receptor to regulate their growth, biofilm formation and *trxB* mRNA expression in vitro. The *luxR* mutant of *S. baltica* lost its sensitivity to AHLs. *S. baltica* could eavesdrop on AHLs produced by *Aeromonas*,

Acinetobacter and *Serratia* to enhance their spoilage ability and accelerate the shrimp spoilage in vivo. Different signal molecules play different roles in the spoilage potential of *Shewanella baltica*, and the AHLs of Ser were more capable of promoting the growth and spoilage ability of *S. baltica*. The results suggested that the quorum sensing

Table 2 The lag time and the maximum growth rate of *S. baltica* in shrimp mono-inoculated with WT SA03 ($\Delta luxR$ SA03) and co-inoculated with WT SA03 ($\Delta luxR$ SA03) and Aer, Aci and Ser

Groups	Treatments	$\mu_{\max}$ /h	Lag/h	R ²
WT SA03	WT SA03	0.060 ± 0.001	66.2 ± 2.04	0.994
	WT SA03 + Aer	0.056 ± 0.006	59.8 ± 1.13**	0.994
	WT SA03 + Aci	0.059 ± 0.001	60.0 ± 2.40**	0.988
	WT SA03 + Ser	0.078 ± 0.001**	51.8 ± 0.74**	0.997
$\Delta luxR$ SA03	$\Delta luxR$ SA03	0.060 ± 0.001	55.4 ± 0.31	0.985
	$\Delta luxR$ SA03 + Aer	0.061 ± 0.001	55.2 ± 2.74	0.980
	$\Delta luxR$ SA03 + Aci	0.061 ± 0.001	57.1 ± 0.74	0.981
	$\Delta luxR$ SA03 + Ser	0.065 ± 0.001*	56.7 ± 1.75	0.999

Lag is the lag time (hour). $\mu_{\max}$ is the maximum growth rate (per hour). R² is the coefficient of determination. (n = 3, * p < 0.05; ** p < 0.01)

based on AHLs might as the potential targets for developing novel preservative strategies.

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Compliance with ethical standards

Conflict of interest The authors declared that they have no conflict of interest.

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