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Isolation and Characterization of a High-Efficiency Algicidal Bacterium *Streptomyces violaceorubidus* lzh-14 Against the Harmful Cyanobacteria *Microcystis aeruginosa*

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Abstract

Harmful cyanobacterial blooms (HABs), primarily composed of toxic cyanobacteria like *Microcystis aeruginosa*, pose a significant threat to aquatic ecosystems and human health. Algicidal bacteria had emerged as a promising strategy for HAB control due to their safety and efficacy. In this study, the algicidal bacterium *Streptomyces violaceorubidus* lzh-14, isolated from Cha Lake in Dezhou, China, exhibited strong algicidal activity against *M. aeruginosa*. When bacterial culture was added to algal cultures at a final volume ratio of 10% (*v*/*v*), the algicidal activity reached 94.5% ± 1.8% after 72 h. Moreover, *S. violaceorubidus* lzh-14 showed varying degrees of algicidal activity against other tested cyanobacterial species. Microscopic observation revealed that *M. aeruginosa* cells treated with lzh-14 became deformed and ruptured, resulting in the leakage of cellular contents. The algicidal substance extracted from *S. violaceorubidus* lzh-14 demonstrated strong stability under varying temperatures and pH conditions. Based on these findings, algicidal powder was preliminarily developed. This study confirms that *S. violaceorubidus* lzh-14 and its active substance have potential as effective biocontrol agents against HABs.

Keywords: *Streptomyces violaceorubidus* lzh-14; *Microcystis aeruginosa*; algicidal activity; algicidal spectrum

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1. Introduction

Harmful cyanobacterial blooms (HABs) have been recognized as a global issue in freshwater systems. Their adverse effects are twofold. Firstly, they cause severe environmental degradation, such as elevated turbidity, oxygen depletion, foul odors, and loss of aquatic diversity [1]. Secondly, the associated cyanotoxins pose a direct threat to drinking water safety and human health [2,3]. Over the past three decades, toxic cyanobacterial bloom intensity has increased substantially, degrading water quality in coastal and freshwater systems globally [4]. HABs competitively displace phytoplankton communities for nutrient

resources, progressively dominating aquatic ecosystems [5,6]. *Microcystis aeruginosa* is one of the most common and widespread HABs globally [7–10]. It frequently dominates toxic blooms in freshwater ecosystems, causing significant ecological and public health hazards. This notoriously destructive cyanobacterium induces severe, often near-annual HABs in regions such as China, Canada, Korea, and Japan. The increasing frequency of these blooms represents a critical ecological problem worldwide [11,12]. Consequently, developing urgently needed efficient HAB control technologies is imperative.

Physical and chemical measures were implemented to mitigate HAB damages [13]. Physical HAB mitigation strategies, which involve environmental manipulation (e.g., water mixing, aeration, barriers), are often limited by cost and scale. In contrast, chemical methods rely on algicides, ranging from traditional oxidants like H_2O_2 to newer, more selective compounds, but face challenges with residual effects and specificity. Consequently, exploiting competitive/inhibitory biotic interactions, particularly involving *Actinomycetes*, has emerged as an environmentally prioritized strategy for mitigating HABs [14,15]. *Actinomycetes* secrete diverse algicidal substances during growth, establishing them as potent biocontrol agents against HABs in eutrophic waters [16,17]. Among algicidal *Actinomycetes*, the genus *Streptomyces* are the most extensively reported [14,18,19]. For example, *S. globisporus* G9 kills *M. aeruginosa* exclusively through direct cell-to-cell contact, a novel mechanism unreported in *Streptomyces*, by entangling cyanobacterial cells with hyphae, causing lysis without secreting diffusible algicides [14]. *S. amritsarensis* HG-16 simultaneously lyses *M. aeruginosa* and suppresses microcystin synthesis via light-dependent bioactive metabolites [18]. Likewise, *S. enissocaesilis* M35 exhibits potent algicidal activity against the toxic cyanobacterium *Phormidium angustissimum* through direct contact and bioactive metabolites, achieving >94% removal efficiency under optimized bioreactor conditions [19].

In general, algicidal bacteria typically inhibit algae through two primary mechanisms: direct contact with algal cells or indirect competition for nutrients or the secretion of extracellular active compounds [20–24]. *S. violaceorubidus*, as a species within the genus *Streptomyces*, was identified early on [25–27]. However, most studies for *S. violaceorubidus* have been limited to genomic identification; its their functional roles remain largely unexplored, particularly their inhibitory effects against HABs.

In this study, the algicidal bacterium *S. violaceorubidus* lzh-14 was isolated from Cha Lake in Dezhou, China and demonstrated significant algicidal activity against *M. aeruginosa*. However, the stability of its algicidal metabolites remains poorly characterized. To address this gap, we further investigated the algicidal activity, target range, the mode of action, and the compound stability of *S. violaceorubidus* lzh-14. Based on these findings, algicidal powders were subsequently developed for the future management of *M. aeruginosa* blooms.

2. Materials and Methods

2.1. Algicidal Cultures

The indicator microalgae species were obtained from the Freshwater Algae Culture Collection of the Institute of Hydrobiology, Chinese Academy of Sciences, China (FACHB). The microalgae species included *Synechococcus* sp. FACHB-805, *M. aeruginosa* FACHB-915, *Chlorella* FACHB-8, *Xanthophyta*, *Tribonema* FACHB-1786. The algae were cultured in BG11 medium, which was sterilized by autoclaving at 121 °C for 20 min. The cultures were maintained at 25 °C under a 12 h/12 h light/dark cycle, illuminated with cool white fluorescent lamps at an intensity of 100 μmol photons·m^{-2}·s^{-1}. The flasks were shaken manually three times per day.

2.2. Algicidal Cultures Isolation, and Identification of Bacterium lzh-14

Water samples were collected from Cha Lake in Dezhou, Shandong, China (37°43′44.84″ N, 117°13′32.99″ E). Algicidal bacterium was isolated following a previously described method [28]. After serial dilution with sterile water, a 0.1 mL sample was spread on Gause's medium containing 15 g/L soluble starch, 1 g/L $NaNO_3$, 0.5 g/L K_2HPO_4, 0.5 g/L $MgSO_4 \cdot 7H_2O$, and 0.01 g/L ferrous sulfate. The medium was prepared using deionized water and sterilized prior to use. After inoculation, the plates were incubated at 28 °C for 24 h. Colonies exhibiting distinct morphologies were repeatedly purified to obtain axenic cultures. These pure cultures were stored at –80 °C in 20% (*v*/*v*) glycerol. Strain lzh-14 was cultivated in Gauze's Synthetic Medium No. 1 at 28 °C with shaking at 125 rpm, unless otherwise stated.

To identify the algicidal bacterium lzh-14, it was subjected to taxonomic analysis using conventional physiological and biochemical tests. Genomic DNA was extracted from the bacterium using the TIANamp Bacterial DNA kit (TIANGEN, Beijing, China) according to the manufacturer's instructions. The 16S rRNA gene was amplified by polymerase chain reactions (PCR) using the universal primers 27F (5′-AGAGTTTGATCMTGGCTCAG-3′) and 1492R (5′-GATTACCTTGTTACGACTT-3′) [29]. PCR amplification was performed using a Thermo PCR Thermal Cycler (Thermo Fisher Scientific, Waltham, MA, USA). The 50 µL reaction mixture consisted of 1 µL (approximately 20 ng) of template DNA, 1.5 µL of each primer (10 µM), 25 µL of PCR master mix (TaKaRa Bio Inc., Dalian, China), and 21 µL of double-distilled water. The thermocycling protocol included an initial denaturation at 95 °C for 5 min; 35 cycles of denaturation at 95 °C for 30 s, annealing at 58 °C for 30 s, and extension at 72 °C for 90 s; followed by a final extension at 72 °C for 7 min. PCR products were analyzed by electrophoresis on 1% (*w*/*v*) agarose gel stained with GelGreen, and visualized under UV light. The resulting sequences were assembled and compared with reference sequences in the rRNA/ITS databases using BLAST v2.17 analysis (NCBI, Bethesda, MD, USA) [30].

2.3. Growth Curve of Algicidal Bacterium lzh-14

The growth curve of bacterium lzh-14 was determined turbidimetrically. Bacterium lzh-14 was inoculated into LB liquid medium at an initial concentration of approximately 10^6 CFU/mL and incubated at 28 °C with shaking at 180 rpm. The optical density (OD) of the bacteria culture was measured at 6 h intervals using a spectrophotometer UV2600 (Techcomp, Shanghai, China) for a total duration of 36 h. The growth curve was plotted with OD_{600} on the *y*-axis and time on the *x*-axis. Experiments included three independent biological replicates.

2.4. Algicidal Activity of Bacterium lzh-14 Against M. aeruginosa

Bacterium lzh-14 was inoculated in Gauze's Synthetic Medium No. 1 and incubated for 3 days at 28 °C. To assess algicidal activity, bacterial cultures (2×10^3 cells/mL) were added to *M. aeruginosa* FACHB-915 suspensions (4.6×10^7 cells/mL) at a volume ratio of 10% (*v*/*v*). A control group was prepared by adding an equal volume of sterile medium to the algal culture without the bacteria. All co-culture systems were incubated under the same conditions used for algal cultivation. Algicidal activity against *M. aeruginosa* FACHB-915 was evaluated at 0, 12, 24, 36, 48, 60, and 72 h. Algal cells were counted using a Sail Brand hemocytometer (Mshot, Guangzhou, China) under a light microscope at 40× magnification. The algicidal activity was calculated using the following formula: Algicidal activity (%) = $(1 - N_t/N_c) \times 100\%$, where N_t and N_c represent the cell densities of *M. aeruginosa* FACHB-915 in the treatment and control groups, respectively [31]. Experiments were performed in three independent biological replicates.

2.5. Algicidal Activity of Bacterium lzh-14 Against M. aeruginosa at Different Growth Phase

For each 40 mL sample of *M. aeruginosa* culture (initial cell density: 4.6×10^7 cells/mL) from four distinct growth phases (lag, logarithmic growth, stable, and decline), 4 mL of lzh-14 culture (initial cell density: 2×10^6 cells/mL) was added ($n = 3$). The mixtures were incubated under the same conditions, and algicidal activity (%) was determined as described above [31]. All experiments were conducted with three independent biological replicates.

2.6. Algicidal Range of Bacterium lzh-14

To determine the algicidal spectrum, an exponential-phase culture of the algicidal bacterium was added to a final concentration of 10% (v/v) to test algal cultures (initial algal density: 4.6×10^7 cells/mL) of the following bacteria: *M. aeruginosa* FACHB-915, FACHB-911, FACHB-977; *Synechococcus* sp. FACHB-805; *Anabaena* sp. FACHB-175; *Chlorella* sp. FACHB-5; *Chlorococcum humicola* FACHB-21; *Scenedesmus* sp. FACHB-489; *Tribonema utriculosum* FACHB-2216; and *Cystodinium bataviense* FACHB-1839. A control was prepared by adding an equal volume of Gauze's Synthetic Medium No. 1 to the algal culture. Cellular density was measured 24 h after bacterial inoculation. We repeated each experiment three times independently.

2.7. Algicidal Mode of Bacterium lzh-14

To investigate the algicidal mode of action, 400 mL of the bacterium lzh-14 culture was extracted with ethyl acetate. The extract was then evaporated to dryness and reconstituted in 200 µL of deionized water. The lzh-14 extract, lzh-14 pelleted cells from the fermented culture, and sterile water were separately added into *M. aeruginosa* culture. Cyanobacterial cell density was measured at the indicated time points post-treatment. Experiments included three independent biological replicates.

2.8. Observation on Cell Morphology of Cyanobacteria Attacked by Bacterium lzh-14

Bacterium lzh-14 was added to *M. aeruginosa* FACHB-915 at a ratio of 10% (v/v). Cyanobacterial cells treated for 72 h with either the cell-free filtrate or the whole culture of bacterium lzh-14 were collected by centrifugation at 1000× g for 10 min at 25 °C. The harvested cells were subsequently prepared for light microscope observation. Experiments were performed in three independent biological replicates.

2.9. Stability of the Algicidal Compounds

The cell-free filtrates were exposed to temperatures of −80, −20, 0, 20, 50, 70, and 100 °C for 2 h and then returned to room temperature. Each temperature-treated filtrate was added to algal cultures at a final volume ratio of 10.0% (v/v) and incubated for 72 h to assess algicidal activity. Separately, the pH of cell-free filtrates was adjusted to 3, 5, 7, 9, and 11 using acid or alkali, held for 2 h, and then neutralized back to the original pH. These pH-adjusted filtrates were also introduced into algal cultures at 10.0% (v/v) and incubated for 72 h to evaluate algicidal activity. All experiments were performed in triplicate.

2.10. Algicidal Powder Production and Application

Sawdust was selected as the carrier for immobilizing bacteriumlzh-14. Briefly, the sawdust was sterilized twice, dried, and used as the carrier material. It was then introduced into a stationary-phase culture of bacterium lzh-14 at a concentration of 15% (w/v) and incubated at 28 °C with shaking at 125 rpm for 6 h to facilitate bacterial adsorption. After incubation, the unadsorbed culture was removed by sieving, and the bacterium-loaded sawdust was transferred to a glass Petri dish and freeze-dried for 24 h. The resulting lyophilized powder was stored at 4 °C.

To assess the algicidal efficacy of the powder, 0.1 g of the powder was added to 50 mL of pre-cultured algal suspension (cell density: 10^5 cells/mL). A control was prepared using the same amount of sterile sawdust without bacteria. All treatments were performed in triplicate during the light phase under 25 °C. Algal cell counts were determined after 12 h of treatment, and the algicidal activity was calculated as previously described [31]. Experiments included three independent biological replicates.

2.11. Statistical Analysis

Statistical analyses were performed using two distinct methods to evaluate different aspects of the data. First, one-way ANOVA followed by Fisher's Least Significant Difference (LSD) test was conducted using GraphPad Prism 8 software to compare differences among multiple groups; results are marked with different lowercase letters ($p < 0.05$), with post hoc comparisons carried out in SPSS Statistics 21. Second, Student's *t*-test was applied to assess significant differences between each treatment and the control group, *** $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$, "ns" represents no significance. All data are presented as mean ± standard deviation (SD).

3. Results

3.1. Identification of S. violaceorubidus lzh-14

In our study, we have screened bacterium with potential algicidal activity and named it bacterium lzh-14. The biochemical characteristics of bacterium lzh-14 are summarized in Table S1. The bacterium is Gram-Positive and forms purplish-red colonies that are difficult to isolate; these colonies developed folds on agar plates after 24 h of incubation in Gause's medium (Figure S1). Bacterium lzh-14 was able to grow at temperatures ranging from 10 °C to 40 °C, but not below 5 °C or above 45 °C. Additionally, it did not grow at pH levels below 5 or above 10 (Table S1). Phylogenetic analysis based on the 16S rRNA gene sequence (GenBank accession number: MN099143) revealed that bacterium lzh-14 is closely related to *S. amritsarensis* and was identified as *S. violaceorubidus* lzh-14 (Figure S2). The growth curve of *S. violaceorubidus* lzh-14 is shown in Figure 1. Three distinct growth phases were observed: a lag phase (0–6 h), an exponential phase (6–24 h), and a stationary phase (24–36 h). Interestingly, the growth curve shows an exponential rise at 30–36 h.

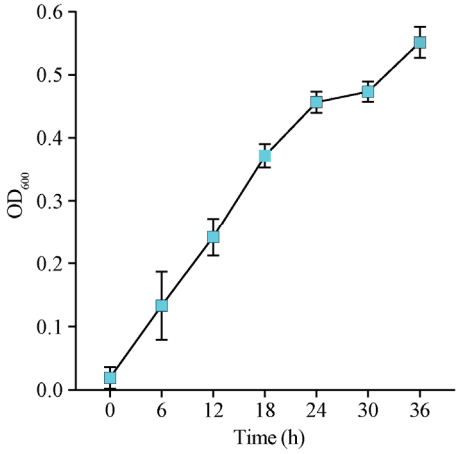


Figure 1. Growth curve of the algicidal bacterium *Streptomyces violaceorubidus* lzh-14. Data are presented as the mean ± SD ($n = 3$).

3.2. Algicidal Activity of S. violaceorubidus lzh-14 Against M. aeruginosa

S. violaceorubidus lzh-14 demonstrated a significant algicidal effect against *M. aeruginosa* FACHB-915 (Figure 2A,B). After application to the algal culture, algicidal activity reached

94.5% ± 1.8% after 72 h. To investigate the algicidal mechanism, both cell-free supernatant and washed bacterial cells resuspended in water were added to the algal cultures and their algicidal activities were evaluated. The results showed that the cell-free supernatant exhibited significantly higher algicidal activity than the resuspended cells (Figure 2C).

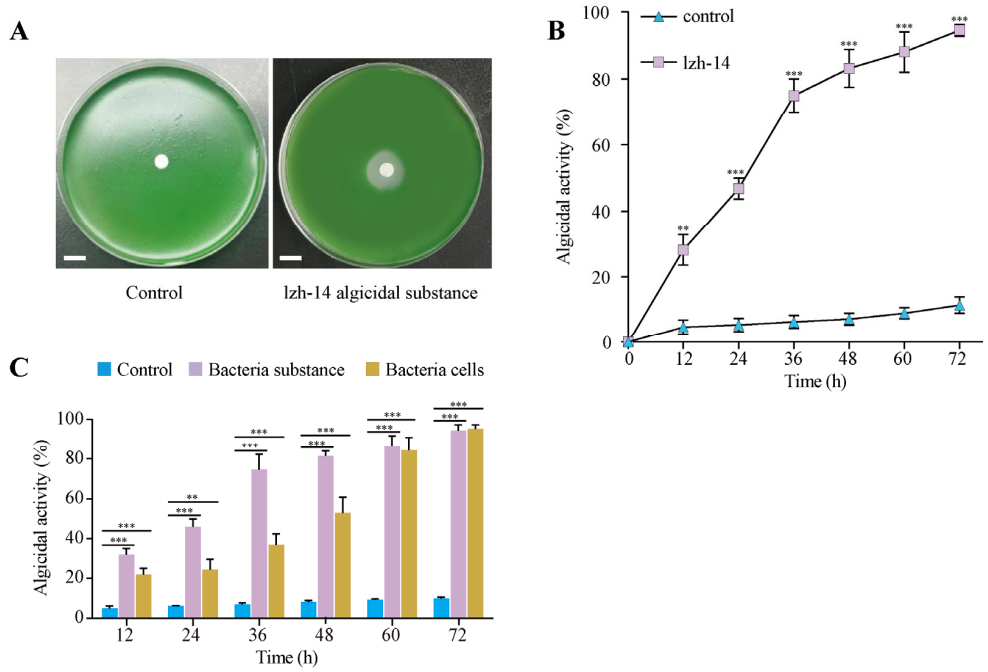


Figure 2. The algicidal effect of *Streptomyces violaceorubidus* lzh-14 algicidal substance against *Microcystis aeruginosa* FACHB-915. (**A**) The algicidal effects of *S. violaceorubidus* lzh-14 on *M. aeruginosa* FACHB-915 were detected using algal plate. Bar: 1 cm. (**B**) The algicidal activities of *S. violaceorubidus* lzh-14 on *M. aeruginosa* FACHB-915 were determined at different times after treatment. (**C**) Comparison of algicidal activities among different fractions of the algicidal substance from *S. violaceorubidus* lzh-14 and whole bacterial cells, based on algal cell density and algicidal rate. Bars represent the mean ± SD (n = 3). Significant differences compared to the control group were determined by Student's t-test, *** $p < 0.001$ and ** $p < 0.01$.

3.3. Analysis of Optimal Application Timing for S. violaceorubidus lzh-14 to Achieve Maximum Algicidal Effect

S. violaceorubidus lzh-14 exhibited significant algicidal activity against *M. aeruginosa*, with its efficacy being influenced by its own growth phase, the co-cultivation time, and the growth stage of the algal culture. As shown in Figure 3A, bacterial cultures harvested during the stationary phase (24–36 h) demonstrated the highest algicidal rate (96.3%), outperforming those from the lag (0–6 h) and exponential (6–24 h) phases. Furthermore, the algicidal activity of *S. violaceorubidus* lzh-14 varied according to its growth phase, reaching a maximum of 98.3% on the 8th day of co-cultivation when stationary phase cells were applied (Figure 3B). Under the same conditions, the algicidal rates for logarithmic growth phase and stationary phases cultures were approximately 85.5% and 96.2%, respectively. The susceptibility of *M. aeruginosa* to *S. violaceorubidus* lzh-14 was also dependent on the algal growth stage. After 4 days of co-culture, the highest algicidal activity (96%) was observed against lag phase algae, followed by logarithmic growth phase (73.2%) and stationary phase (50.4%). No significant algicidal effect was detected against decline phase algae, which is likely attributable to natural cell mortality (Figure 3C).

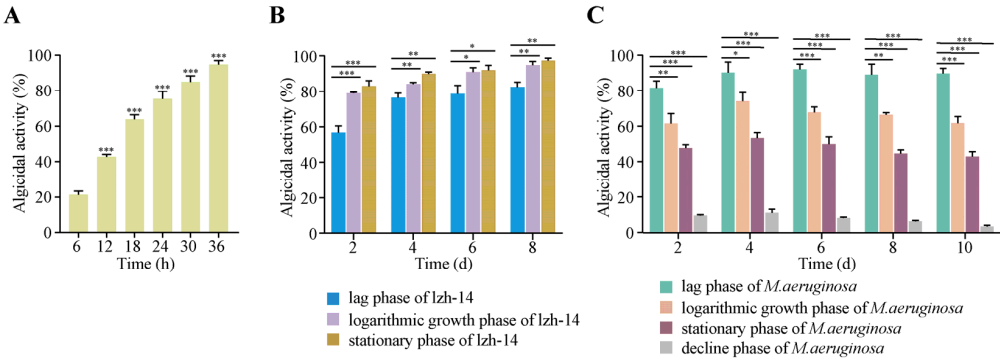


Figure 3. Effect of culture duration of *Streptomyces violaceorubidus* lzh-14 at different growth stages on *Microcystis aeruginosa* FACHB-915. (**A**) Algicidal activity of *S. violaceorubidus* lzh-14 against *M. aeruginosa* FACHB-915 was determined at different time points (0, 6, 12, 18, 24, 30, and 36 h), showing a positive correlation between incubation time and algicidal efficacy. (**B**) Algicidal activity, expressed as the algal-lysing rate, was compared across different growth phases of *S. violaceorubidus* lzh-14 (lag phase, logarithmic growth phase, stationary phase). (**C**) Effect of the growth stage of *M. aeruginosa* FACHB-915 on the algicidal activity of *S. violaceorubidus* lzh-14. Bars represent the mean ± SD (n = 3). Significant differences compared to the control group were determined by Student's t-test, *** $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$.

3.4. Broad-Spectrum Algicidal Activity of S. violaceorubidus lzh-14 Against Harmful Cyanobacteria

To evaluate the algicidal spectrum of *S. violaceorubidus* lzh-14, a total of 10 different algal species were selected for the experiment. The results of co-culture assays testing its algicidal activity against various harmful algal species are presented in Table 1. After 72 h of co-cultivation, *S. violaceorubidus* lzh-14 exhibited algicidal activity exceeding 90% against nearly all tested cyanobacterial species, including *M. aeruginosa* FACHB-915, FACHB-911, and FACHB-977. These results indicate that *S. violaceorubidus* lzh-14 is a broad-spectrum algicidal bacterium against HABs. In contrast, its algicidal effects on *T. utriculosum* FACHB-2216 and *C. bataviense* FACHB-1839 were not significant.

Table 1. Algicidal activity of *Streptomyces violaceorubidus* lzh-14 toward various algal bacteria. Data are presented as the mean ± SD (n = 3).

Algal/Cyanobacteria	Algicidal Ratio (%, t = 72 h)
M. aeruginosa FACHB-915	94.5 ± 1.8
M. aeruginosa FACHB-911	92.1 ± 0.6
M. aeruginosa FACHB-977	90.2 ± 1.3
Synechococcus sp. FACHB-805	93.6 ± 1.1
Anabaena sp. FACHB-175	81.9 ± 1.3
Chlorella sp. FACHB-5	84.1 ± 2.2
Chlorococcum humicola FACHB-21	74.2 ± 0.6
Scenedesmus sp. FACHB-489	76.5 ± 1.8
Tribonema utriculosum FACHB-2216	33.1 ± 0.9
Cystodinium bataviense FACHB-1839	22.4 ± 1.5

3.5. Morphological Alterations in M. aeruginosa Cells Induced by S. violaceorubidus lzh-14

Microscopic analysis revealed that *S. violaceorubidus* lzh-14 significantly altered the morphology of *M. aeruginosa* cells. As shown in Figure 4A, at the beginning of the treatment, *M. aeruginosa* FACHB-915 cells exhibited a spherical and plump morphology with smooth and intact cell surfaces. After 36 h of exposure to the cell-free filtrate from *S. violaceorubidus* lzh-14, the cells lost structural integrity in both the cell wall and plasma membrane (Figure 4B). Following 72 h of treatment, cell rupture and the release of intracellular compo-

nents were observed, suggesting that *S. violaceorubidus* lzh-14 likely kills and decomposes algal cells by secreting extracellular active compounds (Figure 4C).

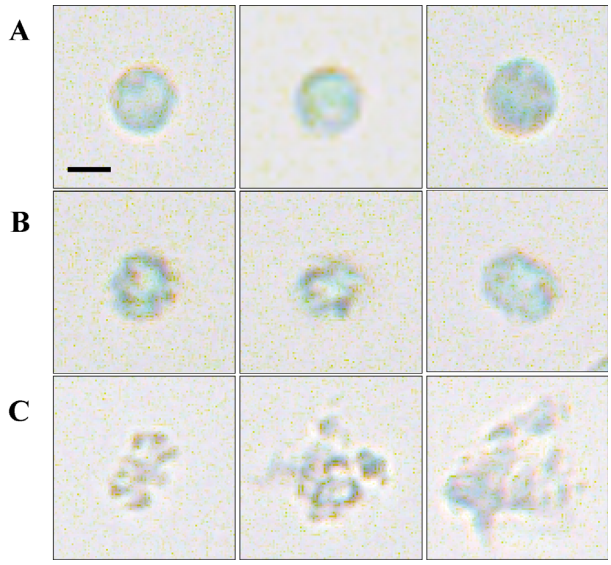


Figure 4. Morphological changes in *Microcystis aeruginosa* FACHB-915 following treatment with the algicidal substance from *Streptomyces violaceorubidus* lzh-14. (**A**) Normal *M. aeruginosa* FACHB-915 cell. (**B**) *M. aeruginosa* FACHB-915 cells treated with *S. violaceorubidus* lzh-14 algicidal substance for 36 h. (**C**) *M. aeruginosa* FACHB-915 cells treated with *S. violaceorubidus* lzh-14 algicidal substance for 72 h. Bar: 100 μm.

3.6. Stability of Algicidal Compounds from S. violaceorubidus lzh-14 Under Various Environmental Conditions

To evaluate the algicidal stability of the active compounds produced by *S. violaceorubidus* lzh-14, their thermal and pH stability were tested (Figure 5). The algicidal activity of the compounds from *S. violaceorubidus* lzh-14 against *M. aeruginosa* was assessed across a range of temperatures (Figure 5A). Although minor variations were observed among treatments, the algicidal rates consistently exceeded 80%, indicating high thermal stability. In addition, we also found that the active compounds retained strong algicidal efficacy under both acidic and alkaline conditions (Figure 5B). Furthermore, the activity was largely unaffected by repeated freeze–thaw cycles, with no significant differences observed between the control and treated groups (Figure 5C). These results confirm that the algicidal compounds produced by *S. violaceorubidus* lzh-14 are relatively stable under diverse environmental conditions.

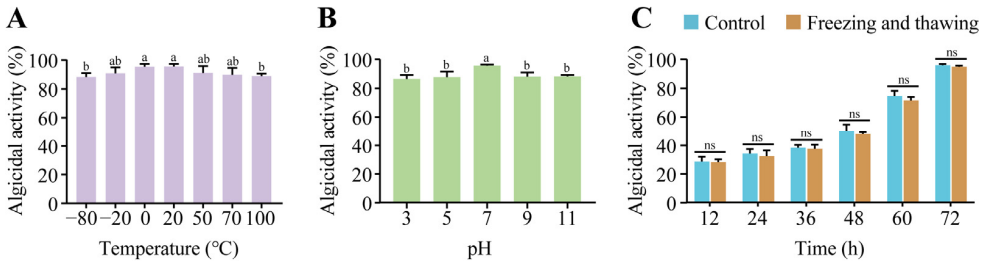


Figure 5. Algicidal stability of the algicidal substance from *Streptomyces violaceorubidus* lzh-14 against *Microcystis aeruginosa* FACHB-915. (**A**) Temperature stability. (**B**) pH stability. (**C**) Stability after repeated freeze–thaw cycles. Data are presented as the mean ± SD of three biological replicates. Different lowercase letters denote statistically significant differences ($p < 0.05$) as determined by one-way ANOVA. "ns" represents no significance.

3.7. Algicide Production and Application of *S. violaceorubidus* lzh-14

The algicidal powder derived from *S. violaceorubidus* lzh-14 was applied to a *M. aeruginosa* culture medium to assess its efficacy. The powder exhibited pronounced algicidal activity at a final concentration of 2% (*v*/*v*) (Figure 6). A complete algicidal effect (100%) was achieved within 24 h. These results not only confirm the strong algicidal capacity of the powder but also validate the feasibility of its production method.

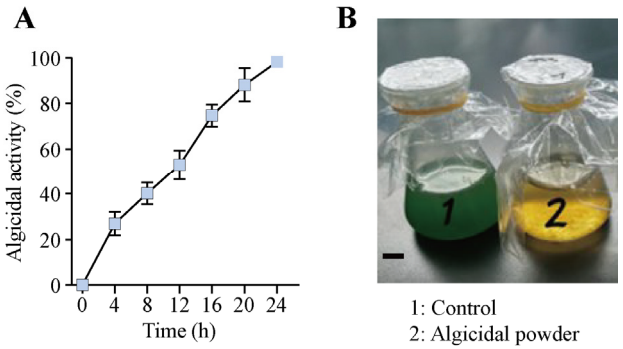


Figure 6. Algicidal effect of a 2% (final concentration) powder derived from *Streptomyces violaceorubidus* lzh-14 on *Microcystis aeruginosa* FACHB-915 after 24 h of continuous treatment. (**A**) Algicidal activity of the powder. (**B**) Efficacy of the powder against *M. aeruginosa* FACHB-915. Data are presented as the mean ± SD (*n* = 3). Bar: 1 cm.

4. Discussion

Cyanobacterial blooms are global environmental issues that threatens freshwater ecosystems worldwide [32]. The toxic cyanobacterium *M. aeruginosa* has a widespread global distribution and is one of the most common bloom-forming species. It frequently dominates HABs in freshwater ecosystems, raising significant ecological and public health concerns [7–10,33]. In efforts to control HABs, algicidal bacteria have gained increasing attention due to their advantageous low-cost and species-specific characteristics [34]. Numerous algicidal bacteria targeting HABs have been isolated and characterized from various environments. For instance, *Qipengyuania* sp. 3-20A1M lyses the harmful alga *Margalefidinium polykrikoides* via the secretion of pyrrole-2-carboxylic acid [35]. Similarly, novel cyclic lipopeptide surfactins from *Bacillus tequilensis* D8 exhibit potent algicidal activity against *Heterosigma akashiwo* blooms by disrupting cell membranes and photosynthetic functions [36]. Furthermore, the algicidal bacterium *Pseudoalteromonas* sp. LD-B6 achieves 90.5% lysis of *Noctiluca scintillans* within 12 h by secreting heat-stable, non-protein extracellular compounds [37]. In this study, we isolated and identified a highly efficient algicidal bacterium, *S. violaceorubidus* lzh-14 (Figure 1). Based on the observed exponential rise in the growth curve of *S. violaceorubidus* lzh-14 between 30 and 36 h, we propose that this phenomenon might represent a diauxic growth pattern, commonly seen in *Streptomyces* [38–41], where a lag phase for the activation of enzymes to decompose complex secondary substrates follows the depletion of a preferred carbon source, leading to a renewed increase in OD. Furthermore, compared to the control, *S. violaceorubidus* lzh-14 exhibited a significant algicidal effect, with its algicidal compounds achieving an activity of 94.5% against *M. aeruginosa* after 72 h of co-cultivation (Figures 2 and 3). These results suggest that *S. violaceorubidus* lzh-14 is a promising agent against HABs.

Algicidal bacteria primarily employed two distinct modes of action: direct and indirect algicidal strategies [32,42]. The direct mode requires physical contact or even invasion between the bacterial and algal cells. A notable example is *Aeromonas bestiarum* HYD0802-MK36, which acts as a specialized direct attacker, exhibiting high specificity toward *M. aeruginosa* through cell-to-cell contact [43]. In contrast, the indirect algicidal mode does not require physical

interaction; instead, bacteria secrete extracellular compounds that inhibit algal growth, induce cell death, or compete with algae for essential resources. For instance, *Enterobacter hormaechei* F2 demonstrates effective algicidal activity against *M. aeruginosa* by producing the red pigment prodigiosin and employing the quorum-sensing molecule PQS (Pseudomonas Quinolone Signal) [44]. In our study, *S. violaceorubidus* lzh-14 exhibited significant algicidal activity against *M. aeruginosa*, primarily mediated by extracellular compounds released into the supernatant (Figure 2). The cell-free filtrate of *S. violaceorubidus* lzh-14 induced loss of structural integrity in the cell wall and plasma membrane of *M. aeruginosa* within 36 h (Figure 4). Previous studies have indicated that *S. amritsarensis* HG-16 produces proteinase K-resistant active substances that exhibit algicidal activity against *M. aeruginosa* [18]. Furthermore, an active algicidal triterpenoid saponin from *Streptomyces* sp. L74 was shown to disrupt the antioxidant systems of *M. aeruginosa* cells [40]. These results indicate that *S. violaceorubidus* lzh-14 likely employs an indirect algicidal strategy by secreting active metabolites to kill *M. aeruginosa*.

Algicidal bacteria have been widely reported to exhibit strong algicidal activity [45–47]. However, studies on the stability of these active bacterial substances remain limited. Our findings revealed that the algicidal compounds of *S. violaceorubidus* lzh-14 were resistant to both acidic and alkaline conditions and remained stable under varying temperature treatments (Figure 5). This observation is consistent with the report by Zhu et al., which showed that the algicidal activity of *Microbulbifer* sp. YX04 supernatant retained stability after exposure to temperatures ranging from −80 °C to 100 °C and pH values between 4 and 12 for 2 h [48]. These results suggest algicidal compounds produced by *S. violaceorubidus* lzh-14 possess remarkable stability under a wide range of extreme environmental conditions. Additionally, existing studies have indicated that aminoclay, as a non-proteinaceous and chemically stable algicide, can disrupt algal cell membranes through electrostatic interactions, leading to rapid cell lysis and thereby exerting algicidal effects [49]. Therefore, given the thermal stability of the algicidal compounds produced by *S. violaceorubidus* Izh-14, they are unlikely to be proteins. This stability, combined with the algicidal potential of these compounds, makes them promising agents for controlling HABs. Moreover, *S. violaceorubidus* lzh-14 demonstrated efficacy against several harmful algal bloom (HAB) species, including *Synechococcus*, *Anabaena*, and *Chlorella* (Table 1), indicating a broad-spectrum algicidal activity and potential utility in controlling HABs caused by these organisms.

A growing number of algicidal agents have been developed for bloom mitigation [30,50]. In this study, the algicidal powder derived from *S. violaceorubidus* lzh-14 exhibited high efficacy against *M. aeruginosa*, achieving 100% algicidal activity within 24 h, confirming both its potent activity and the feasibility of the production process (Figure 6). For future research, it will be essential to isolate and characterize the specific algicidal compounds, and to develop targeted application strategies tailored to specific environmental conditions, such as adapting to variable salinity, temperature, and pH, to enhance practicality and efficiency [51]. Further research should also focus on identifying the effective bioactive compounds produced by *S. violaceorubidus* lzh-14 using mass spectrometry techniques [52–54], and investigating the potential non-target impacts of lzh-14's algicidal metabolites on beneficial microbial communities, such as plant-growth-promoting bacteria [55,56].

5. Conclusions

S. violaceorubidus lzh-14 exhibits potent, broad-spectrum algicidal activity against *M. aeruginosa* and other bloom-forming cyanobacteria via extracellular compounds, demonstrating high stability across extreme environmental conditions. The successful development of an efficacious algicidal powder underscores its practical potential for HAB control.

Future work should prioritize compound identification and field-applicable formulation strategies to enhance real-world utility.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fermentation11100596/s1, Figure S1: Colony of *Streptomyces violaceorubidus* lzh-14 after 24 h of incubation. Bar: 1 cm; Figure S2: Phylogenetic tree based on 16S rRNA gene sequences of *Streptomyces violaceorubidus* lzh-14 and related reference bacteria retrieved from GenBank, constructed using the neighbor-joining method; Table S1: Phenotypic characteristics of *Streptomyces violaceorubidus* lzh-14.

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