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Research Article

The Changes of Phenotypic Characteristics of *Shewanella putrefaciens* under Cold Adaptation

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Shewanella putrefaciens (*S. putrefaciens*) is frequently detected as a serious threat to food safety because it causes spoilage of aquatic products during cold chain transportation. Here, we studied phenotypic changes in *S. putrefaciens* at low temperatures to discuss the specific behavior of its spoiled aquatic products. *S. putrefaciens* was found to grow considerably through the growth curve at 0–30°C. In order to investigate the strong putrefaction of aquatic significant amounts under cold storage at 0–10°C, SEM was used to examine the microstructure of *S. putrefaciens* that had been cultivated at various temperatures. At low temperatures, it was discovered that the cell membrane surface of *S. putrefaciens* was smoother. FITC-labeled fluorescence microscope was used to view the results. Analysis of *S. putrefaciens* cultivated at various temperatures revealed that the integrity and permeability of the cell membrane deteriorated with the drop of culture temperature; however, the downward trend slowed down when the temperature was below 10°C. In addition, as the temperature continued to drop below 10°C, the capacity of *S. putrefaciens* to build biofilms did not diminish noticeably. The findings demonstrate that *S. putrefaciens*'s cold adaptation mechanism at low temperatures involves modifications to the morphological and phenotypic characteristics of cell membranes, plays a significant role in the organism's ability to corrode aquatic products at low temperatures, and provides an important target for prevention and control of *S. putrefaciens*' ability to contaminate aquatic products and cause financial losses.

1. Introduction

The environment in which microorganisms grow is subject to a variety of unfavorable conditions, and when those conditions are stressful, they activate a number of self-protection mechanisms in order to resume normal growth by adjusting to environmental changes. Researchers have focused a great deal of interest on the methods by which microorganisms might create resistance or adaption responses to challenging conditions [1]. The process by which microorganisms withstand the effects of a harmful external environment is complicated, and many of these systems remain poorly understood. *S. putrefaciens* is a typical specific spoilage bacterium in aquatic products, and due to its adaptability and spoilage at low temperatures, a thorough study of the mechanism underlying *S. putrefaciens*' cold adaptation during temperature reduction is required to lay the theoretical groundwork for applications involving the preservation of aquatic products.

The majority of current research on *Shewanella's* ability to adapt to cold has been on the interaction between cold-adapted proteins and enzymes and temperature. For instance, Jian et al. [2] knocked down the HNS gene in *Shewanella Pizotolerans* and discovered that the histone-like protein HNS was responsible for the transcriptional activation of cold-adapted lateral flagellar genes. The research also revealed that the 4°C culture was effective. In their study of 19 species of *S. putrefaciens*, Karpinets et al. [3, 4] found that the Antarctic bacteria *Shewanella gelidimarina's* cytoplasmic nitrate reductase alters microbial low-temperature environmental sensors by locally altering hydrophobic and hydrogen-bonding networks. The K14-2 tryptophan synthase subunit (SfTSA) of *Shewanella frigidimarina* has a large cavity volume and a low number of ion pairs and also

does not have a hydrogen bond close to ring B, according to research by Mitsuya et al. [4], who investigated the molecular basis of enzymatic cold acclimation in *S. putrefaciens*. These characteristics make it more conformationally flexible, and this flexibility forms the basis for microbial low-temperature catalytic activity and cold adaption.

The cell membrane is a crucial component in the development and metabolism of microorganisms, as well as in their ability to adapt to changes in their environment. The ability of the cell membrane to control fluidity and permeability allows it to respond to changing environmental conditions [5, 6]. To make sure that bacteria maintain a proper development state, good membrane fluidity and permeability are crucial. The fatty acid composition is crucial for cell membrane fluidity [7] and transcription factors FabR and FadR change cell membrane fluidity by controlling the production of unsaturated fatty acids in *Shewanella oneidensis* [8]. According to Hassan et al. [9], polyunsaturated fatty acids were only produced at specific low temperatures and that the proportion of branched-chain fatty acids grew dramatically upon temperature reduction, while the proportion of straight-chain fatty acids declined. Zhang et al. [10] studied *Escherichia coli* ATCC43889 and discovered that the weaker the membrane fluidity, the higher the stress temperature. This finding has been linked to the idea that there is a relationship between the alteration of microbial phospholipid phase transition temperature and cell membrane fluidity and permeability. By generating biofilm at low temperatures, *S. putrefaciens* was also able to control how sensitive it was to the environment [11, 12].

In brief, SEM, fluorescence microscopy, and the 96-well microplate method were used to investigate the growth curve, cell membrane fluidity, permeability, integrity, phospholipid phase transition temperature, and biofilm generation ability of *S. putrefaciens* cultured at different temperatures in this paper. We also looked at how *S. putrefaciens*' cell membranes changed in response to variations in low temperature, and we found that these modifications helped the bacteria adapt to their low-temperature stress environment.

2. Materials and Methods

2.1. Media, Strains, and Culture Conditions. S. putrefaciens ATCC8071* is from the American Type Culture Collection (ATCC), frozen in glycerol tubes at −80°C in the laboratory. Tryptic Soy Broth (TSB, OXOID) was used to culture *S. putrefaciens* ATCC8071* strains at 30°C, 220 rpm.

2.2. Growth Curves. S. putrefaciens ATCC8071* glycerol tubes were incubated overnight at 30°C in TSB solid medium after being frozen at −80°C. From the solid medium, single colonies were selected and cultured in TSB liquid medium at 200 rpm with shaking for 16 hours at 30°C. A 35 ml portion of new TSB medium was injected with 1 ml of the overnight culture before being incubated at various temperatures. Every 24 hours, 100 μl of sterile TSB medium was obtained to calculate the OD600 as a blank control.

2.3. Changes in Individual Cell Morphology. The following procedures were followed while taking *S. putrefaciens* ATCC8071* in logarithmic phase (incubation temperatures of 0, 4, 10, 20, and 30°C) for processing and microscopic examination: 2.5% glutaraldehyde phosphate buffer wash for two hours; three 15-minute phosphate rinses; 1% osmium acid fixative for two hours; three 15-minute phosphate rinses; 50% ethanol wash for 15 minutes, 70% ethanol wash for 15 minutes, 90% ethanol wash for 15 minutes, 100% ethanol wash for 15 minutes, and 100% ethanol : amyl acetate for 1 : 1 wash for 30 minutes, amyl acetate wash for 30 minutes, wash for 30 minutes, dry for 1 hour, spray for 30 minutes, and detection.

2.4. Membrane Permeability. The logarithmic growth phase was centrifuged, the bacteria in 800 mL of 0.02 mM PBS were resuspended, and it was repeated again, OD600 was adjusted to 0.4, 200 mL of bacteria was incubated per tube at 0°C, 4°C, 10°C, 20°C, and 30°C, 10 g/mL of PI was added and dipped at 4°C for 20 minutes and again centrifuged, the supernatant was discarded, and the bacteria were resuspended again. 10 mL of bacterial solution should be used, and the film should be sealed with antifluorescent quenching sealer. The film should then be examined and photographed using a fluorescence microscope and 546 nm excitation light.

2.5. Biofilm Formation Assay. Three replicates of each strain were incubated for 36 hours at various temperatures using 10 L of an overnight culture that had been injected onto 96-well plates that contained 100 L of TSB medium. After 36 hours, the medium was aspirated, cleaned twice with sterile water, fixed for 15 minutes with 100 L of methanol, thrown away, and dried. Then, 100 L of 1% crystalline violet was added for 5 minutes, excess crystalline violet was washed away, and 100 L of 33% glacial acetic acid was added. The medium was then incubated for 30 minutes at 37°C, and the absorbance value was determined by OD590.

2.6. Statistical Analysis. When $p < 0.05$, which was used to assess all data using the standard deviation, the data are considered to be statistically different. GraphPad Prism 8 software was used to perform *t*-test, one-way and two-way ANOVA analyses on two-group data, single-line graph, and multigroup data, respectively.

3. Results and Discussion

3.1. Growth of S. putrefaciens ATCC8071 Cells.* At lower temperatures, microorganisms typically stagnate or barely develop, decreasing their ability to communicate with the outside world and their ability to synthesize nonessential proteins and other materials to conserve nutrients and survive the harsh environment [13, 14]. In order to do this, the study compared the growth of *S. putrefaciens* at various temperatures, including the optimal culture temperature of 30°C, suboptimum temperatures of 20°C and 10°C, low storage temperatures of 4°C, and freezing temperatures of

0°C. *S. putrefaciens* grew faster and had a significant logarithmic growth period at 20°C and 30°C, whereas it grew slower at 10°C and 4°C (Figure 1). When the bacteria were at 0°C, *S. putrefaciens* grew the slowest and the number of bacteria did not significantly increase. The growth of *S. putrefaciens* was not inhibited at low temperatures, as evidenced by the faster growth rates at 4 and 10°C than 0°C and the OD600 reaching about 1 on day 6; however, there was no significant logarithmic growth period, which is also the reason why *S. putrefaciens* can still cause low temperatures at low temperatures. One of the main causes of the continued deterioration of aquatic items stored and transported at low temperatures is *S. putrefaciens*. The growth rate of *S. putrefaciens* increased gradually, as the temperature rose, and when it reached 20°C and 30°C, it significantly accelerated. From day 1 to day 2, the growth of *S. putrefaciens* was in a significant logarithmic growth period, with a slight decline in OD600 from day 2 to day 6, and from day 6 on, the OD600 decreased more significantly than on day 2 and stayed close to OD600 = 2. This might be because of the population growth, which led to a lack of nutrients to support a large number of bacteria. As a result, some bacterial lysis caused OD600 to drop, allowing a few bacteria to survive and continue to proliferate when additional nutrients came.

These byproducts adversely affect the sensory of aquatic products and result in significant yearly economic losses. In this study, we looked at the growth curves of *S. putrefaciens* ATCC8071* at 0°C, 4°C, 10°C, and 30°C for 0–10 days. We discovered that when the temperature was lower than 10°C, *S. putrefaciens* was still able to proliferate and its OD600 kept climbing, indicating that *S. putrefaciens* has a strong growth and reproduction ability under low temperature. These findings imply that *S. putrefaciens* can reproduce in considerable quantities at temperatures higher than 4°C. This result provides the need for defensive measures and guided storage times for the transportation and storage of fish products at low temperatures.

3.2. The Morphology of Individual S. putrefaciens ATCC8071 Cells.* Microorganisms can change in their individual morphology in response to environmental changes, physicochemical factors, and other influences, and under harmful external impacts, individual morphology is typically disturbed or physiologically altered 10 [15]. We used scanning electron microscopy to examine the cellular microstructure of *S. putrefaciens* ATCC8071* at various temperatures, in order to determine the impact of temperature on the individual morphology of *S. putrefaciens* cells (Figure 2). By gradually lowering the temperature from 30°C to 0°C, the differences in its individual cell shape were not very noticeable. The *S. putrefaciens* cell wall membrane generally had waves of folds, and this morphology could increase the surface area of the bacterium, which was more favorable for the quick exchange of different substances between the bacterium and the environment, increase the absorption of nutrients, and promote its growth and reproduction as well as signal communication between the individuals of the

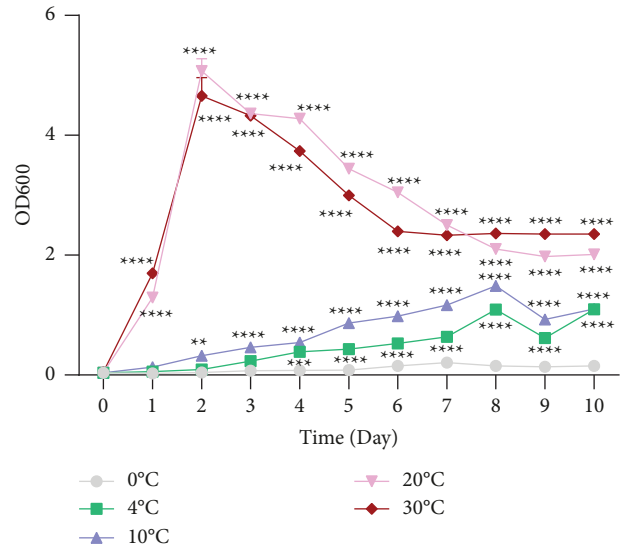


Figure 1: Growth curve of *S. putrefaciens* ATCC8071* cultured at different temperatures. OD600 of *S. putrefaciens* at 0, 4, 10, 20, and 30°C. Three repeats at each time point to detect.

population [16, 17]. Although the surface stickiness of the bacterium is obviously reduced when cultured at 0°C and 4°C compared with 30°C, the cell wall of the strain under low temperature culture is relatively soother compared to that at room temperature. As the culture temperature decreases, the sticky material on the cell wall also decreases.

This may be caused by a decrease in biofilm components secreted by bacteria into the extracellular matrix at low temperatures, such as extracellular polysaccharides, proteins, and other components. This result is consistent with the phenotype of reduced biofilm formation capacity of *S. putrefaciens*, presumably because the morphological characteristics of *S. putrefaciens* cultured at different temperatures were better understood. *S. putrefaciens* cell surface area decreases at low temperatures, which reduces the contact surface with unfavorable environments while maintaining basic nutrient exchanges with the external environment as a means of adapting to the unfavorable effects of low temperatures on its growth, a phenomenon consistent with the findings of Yang et al. [18]. This result provides a better understanding of the morphological characteristics of *S. putrefaciens* at low temperatures.

3.3. Cell Membrane Integrity of S. putrefaciens ATCC8071.* The integrity of the cell membrane was further investigated to see if it changed because the cell surface of *S. putrefaciens* displayed morphological alterations at low temperatures. *S. putrefaciens* was used to further investigate the integrity of the cell membrane at various culture temperatures, and it was discovered that, as the culture temperature dropped, the degree of membrane integrity gradually reduced (Figure 3(a)). As shown in Figure 3(a), *S. putrefaciens* ATCC8071* cells maintained high levels of cell membrane integrity when cultured at 20°C and 30°C, but the rate of cell membrane integrity loss was faster when the temperature was lowered from 30°C to 10°C. Conversely, when the

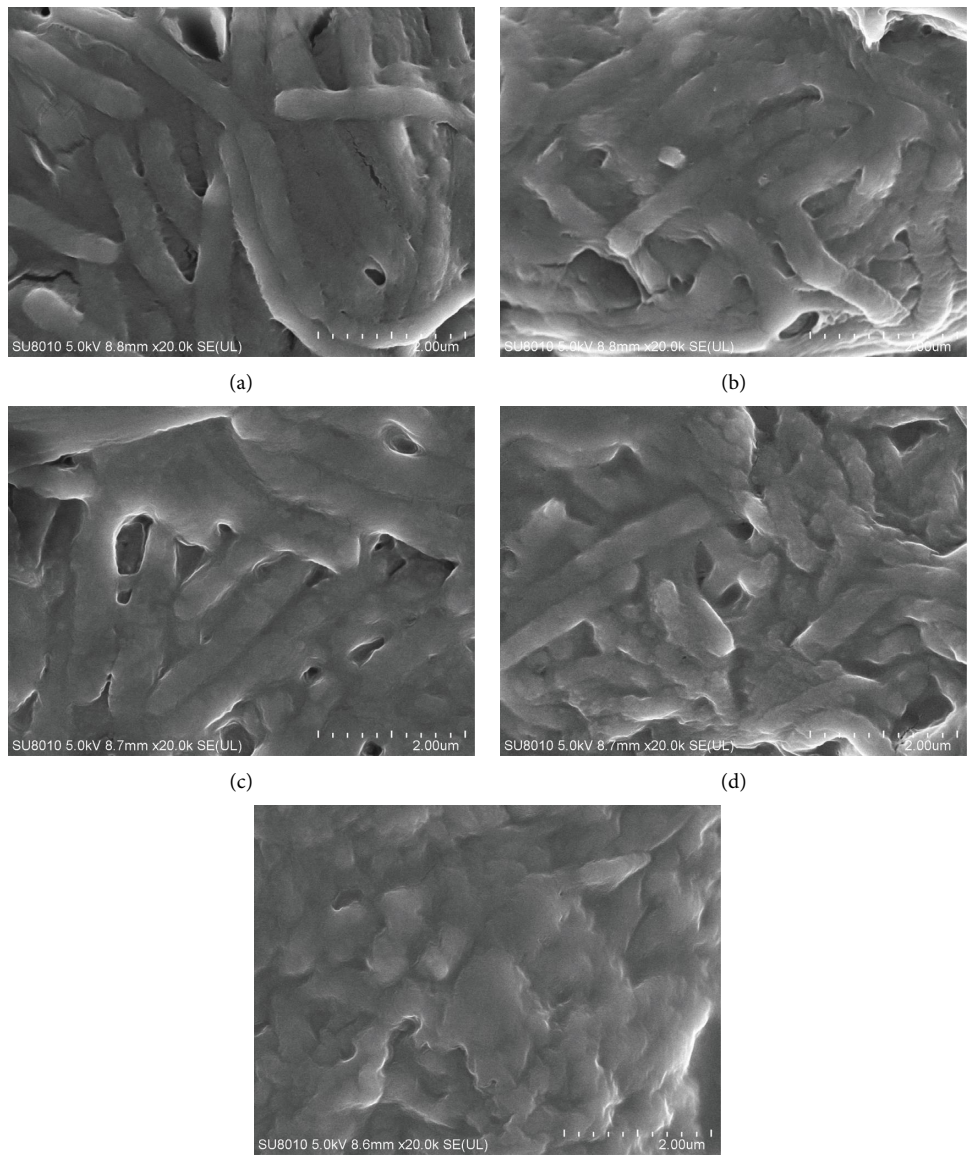


Figure 2: Scanning electron microscopic structure of *S. putrefaciens* ATCC8071* cells cultured at different temperatures. Electron micrographs of incubation temperatures of (a) 0°C; (b) 4°C; (c) 10°C; (d) 20°C; (e) 30°C, respectively.

temperature was lowered to 4°C and 0°C, the rate of cell membrane integrity loss significantly decreased, but the rate of decrease slowed down significantly, presumably due to this. *S. putrefaciens* felt the cold stimulation of the environment when the temperature fell below 10°C and underwent specific stress responses to alter the cell membrane components by modulating intracellular gene expression, metabolic rate, and metabolic pathways, which preserved the integrity of its own bacterium's cell membrane and stopped apoptosis and the leakage of cell contents brought on by low temperature in order to support its own existence. The cell membrane's integrity serves as a barrier between the bacterium and the outside world and is connected to substance exchange transport, receptor response, and cellular signaling [19–21]. Changes in cell surface morphology at low temperatures may be associated with changes in characteristic cell membrane properties. The results of the cell membrane integrity of *S. putrefaciens* at low temperatures showed that integrity decreased with decreasing temperature compared to those in normal culture, but when the temperature reached below 10°C, this decrease in integrity to prevent apoptosis and leakage of contents tended to moderate, a result that is presumed to be a manifestation of self-protection by the microorganism due to the stress response caused by the lower culture temperature [22].

S. putrefaciens ATCC8071* was fluorescently labeled in FITC to examine the permeability of the cell membrane at various culture temperatures. Figure 4 depicts the consequences of altering the permeability of the cell membrane, which caused the cells to emit green fluorescence. The cells of

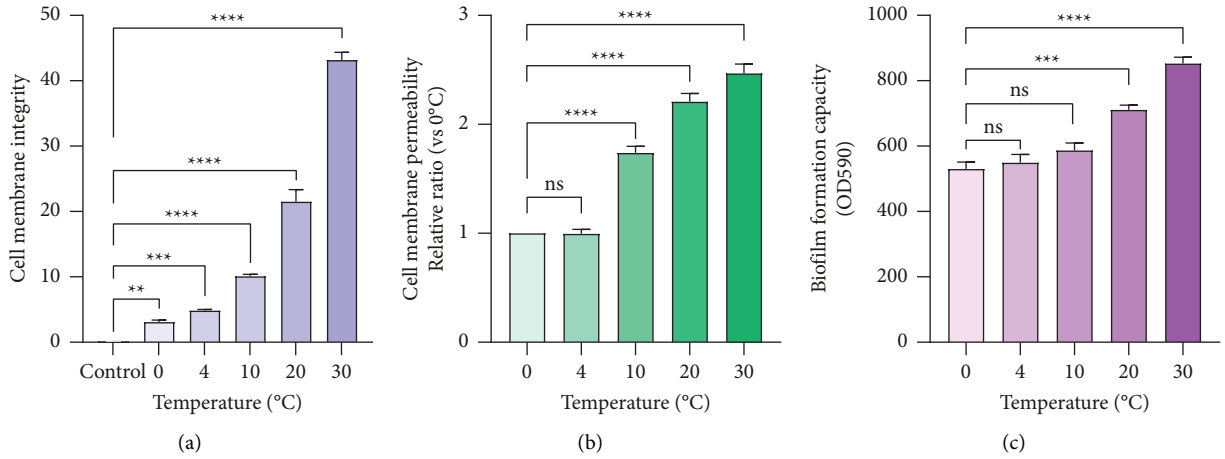


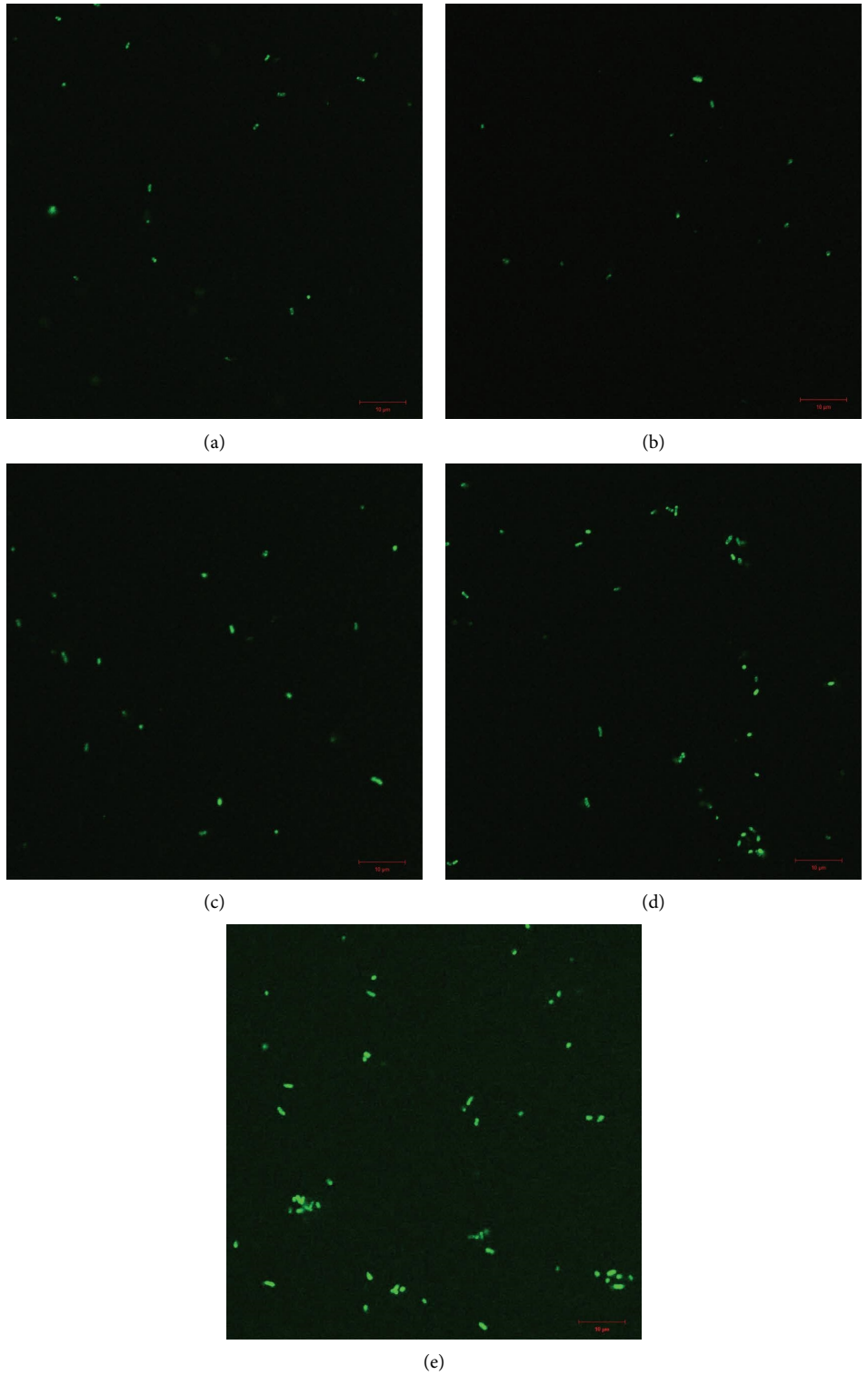
Figure 3: Changes of *S. putrefaciens* ATCC8071* in cell membrane phenotype at different temperatures. (a) Cell membrane integrity. (b) Cell membrane permeability. (c) Biofilm formation capacity. Three repeats at each time point to detect.

the strains that were cultivated at temperatures ranging from 0°C to 30°C all displayed fluorescence, or were labeled by FITC fluorescent tagging, demonstrating that the cells kept up some amount of material exchange and signal communication with extracellular. The permeability of *S. putrefaciens* ATCC8071* demonstrated a decreasing trend during the process of lowering the culture temperature from 30°C to 4°C, while the cell membrane permeability slowed this decreasing trend during the process of lowering the culture temperature from 4°C to 0°C. Indicating that the cell membrane permeability and cell-environment communication were at their lowest point at this temperature, the cell membrane permeability stopped decreasing when the temperature was lowered below 4°C (Figure 3(b)).

Cell membrane permeability decline with decreasing temperature and stopped declining when the temperature was lowered below 4°C, indicating that cell membrane permeability and cell-environment communication decreased to a minimum at this temperature. On the other hand, it may be caused by changes in some amino acids and metal ions that control osmosis. It is hypothesized that this phenomenon is caused by a decrease in cell membrane fluidity due to low temperature and the decrease in the rate of material movement, resulting in a decrease in cell membrane permeability with the decrease in temperature, thus the bacteria becomes more tolerant of low temperature while it is at a lower temperature, by reducing the impact of low temperature on cell membrane permeability. In combination with the findings of the study on cell membrane integrity, it was hypothesized that, as the temperature drops, the cell membrane undergoes stress changes in order to resist outside disturbances, maintain a constant level of permeability for the exchange of intracellular and extracellular materials, maintain the uptake of nutrients and the release of metabolites, and promote the growth and division of *S. putrefaciens* [23]. In addition, it has been demonstrated that variations in ion concentration can affect membrane potential and permeability, which in turn has an impact on ATP and NADH levels [24]. These changes can affect how well *S. putrefaciens* ATCC8071* is able to withstand the external low-temperature environment by providing the energy needed.

In order for bacteria to colonize a particular habitat or object surface, extracellular polysaccharides and biofilms are crucial structures. These structures can significantly improve bacterial adhesion, resistance to antibiotics, and resilience to severe environments [25]. We tested *S. putrefaciens* ATCC8071*'s capacity to build biofilms at various temperatures. In this experiment, the ability of each strain to produce biofilm was determined by subtracting the OD590 value measured for each strain from the OD590 value of the blank control. As seen in Figure 3(c), *S. putrefaciens*' ability to produce biofilms steadily diminished, as temperature dropped, which might be related to the metabolism-slowing effects of low temperatures. In addition, the decline in biofilm formation capacity started to slow down rather than drop proportionally when the temperature fell below 10°C, which suggests that *S. putrefaciens* increases resilience through biofilm development, in line with the findings of Hu et al. [26]. In addition, based on the results of the experiment, *S. putrefaciens* ATCC8071* had a tendency to produce less biofilm as the incubation temperature dropped, demonstrating that the low temperature prevented the formation of biofilms. This decreasing trend started to become moderate when the temperature was lowered to 4°C, demonstrating that the bacterium's stress response in response to low-temperature stimulation only kept the bacterium in a planktonic state and did not cause it to develop into a biofilm. In addition, it is hypothesized that these phenomena may also be connected to cell density, since bacteria may grow more slowly at low temperatures and may not reach the necessary cell density to produce a dense and thick biofilm.

The significant colony shape known as biofilm is created by bacteria in harsh conditions. It has been demonstrated that the formation of bacterial biofilms and bacterial population sensing are closely related. For instance, in *Pseudomonas aeruginosa*, the population bacterial concentration



(a) (b) (c) (d) (e)

Figure 4: Fluorescence microscopy of *S. putrefaciens* ATCC8071* for cell membrane permeability. The fluorescence photos of FITC labeling at (a) 0°C; (b) 4°C; (c) 10°C; (d) 20°C; (e) 30°C, respectively, and the fluorescence intensity gradually increased with the increase of incubation temperature.

threshold influences the formation of population sensing, and transcription factors connected to population sensing can control the expression of genes related to biofilm formation, such as the phenazine biosynthesis-related phz, pqs, and phn gene clusters, which in turn regulate the production of biofilms [26, 27]. Numerous microorganisms have also been demonstrated to be capable of forming biofilms, and the development of biofilms is frequently a sign of microbial

adaptation to changes in the external environment, which can increase microorganisms' resistance to harmful external influences and serves as a form of self-defense [28]. When the temperature dropped below 10°C, the capacity of S. putrefaciens to build biofilm began to slow down, indicating that the bacteria increased resilience to adversity by forming a specific quantity of biofilm [29].

4. Conclusions

In order to understand the mechanism of *S. putrefaciens*' cold acclimation, the growth curve, individual morphology, cell membrane integrity, cell membrane permeability, and biofilm formation capacity of *S. putrefaciens* ATCC8071* were measured at various culture temperatures. The results show that *S. putrefaciens* ATCC8071* is able to regulate its own cell wall membrane when the culture temperature drops. These results imply that *S. putrefaciens* ATCC8071* can regulate its cell wall membrane to resist the harm of a low-temperature environment when the culture temperature decreases, which offers a new idea and target for studying *S. putrefaciens*' cold adaptation mechanism and targeting to prevent *S. putrefaciens* from reproducing at low temperatures.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

Conflicts of Interest

The authors declare that they no conflicts of interest.

Authors' Contributions

B.L. and J.X. conceptualized the study. X.G. developed the methodology M.S. provided the software. X.G., M.S., and B.L. performed validation. X.G. contributed to formal analysis. X.G. performed investigation. X.G. provided the resources. X.G. performed data curation. B.L. wrote the original draft. B.L. reviewed and edited the article. J.X. contributed to visualization. M.S. performed supervision. B.L. provided project administration. J.X. provided funding acquisition. All authors have read and agreed to the published version of the manuscript.

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