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Cultural optimization and metal effects of *Shewanella xiamenensis* BC01 growth and swarming motility

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Abstract

Background: *Shewanella* species belonging to dissimilatory metal bacteria were found to decolorize most textile dyes and had also attracted great interests in regard to bioremediation. However, studies have rarely been reported on *Shewanella xiamenensis* BC01, which was isolated as a biodecolorization and bioelectricity strain recently. In this study, the effect of cultivation conditions on *S. xiamenensis* BC01 was studied to explore how environmental conditions may influence *S. xiamenensis* growth and swarming motility.

Results: *Shewanella xiamenensis* BC01 grew over a wide range of pH (5.0–9.0) and mild temperatures (25–42 °C). The optimal conditions for cell growth were using Luria-Bertani (LB) as medium with shaking at 150 rpm, 37 °C, and pH 8.0 which had been confirmed by shift pH and temperature. *S. xiamenensis* BC01 was able to resist 1 mM concentrations of various metal ions, i.e., Ca^{2+}, Mg^{2+}, Cu^{2+}, Zn^{2+}, Mn^{2+}, Fe^{3+}, and Al^{3+}, respectively. As shown in scanning electron microscopy (SEM) analyses, cell morphologies were slightly changed under metal stress. Swarming motility showed that the velocity ranking at 80 μM and 1 mM of metal was Al > Cr > LB > Zn > Fe > Cu and Mg > Mn > Ca, respectively.

Conclusions: This study evaluates the impact of cultivation methods and metal ions on the activity of *S. xiamenensis* BC01 and provides an alternative to bioremediation of heavy metal-containing wastewaters by utilizing this strain.

Keywords: *Shewanella xiamenensis*; Optimization; Heavy metal; Swarming motility

Background

With the rise in industrialization and manufacturing activities, a lot of harmful substances are released daily into the atmosphere in large quantities. For example, environmental pollution, especially heavy metal pollution, represents an important problem due to the toxicity, and their accumulation throughout the food chain leads to serious ecological and health problems. However, many microorganisms demonstrated resistance to metals in water, soil, and industrial waste [1] and were intimately involved in metal biogeochemistry with a variety of processes determining mobility and therefore bioavailability [2]. Some microorganisms could enzymatically reduce a variety of metals in metabolic processes that are not related to metal assimilation, conserving energy to support growth by coupling the oxidation of simple organic acids and alcohols, H_2, or aromatic compounds to the reduction of Fe(III) or Mn(IV) [3]. In particular, dissimilatory metal-reducing bacteria (DMRB) would reduce various metals and radionuclides, including sediment-abundant Fe(III) and Mn(III/IV) and aqueous species of U(VI), Cr(VI), Co(III), and Tc(VII) [3–8].

Dissimilatory metal reduction was proposed to be an early form of microbial respiration [9]. As the reduction of metals by bacteria was generally coupled with the oxidation of organic matter [9, 10], the ability to reduce metals could be exploited not only for the bioreduction or immobilization of many toxic metals, including cobalt, chromium, uranium, and technetium, but also for the biotransformation of organic contaminants to benign products such as carbon dioxide [11, 12]. Several physicochemical methods existed for the treatment and remediation of metal-contaminated environments. The

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conventional methods for heavy metal removal included chemical precipitation, chemical oxidation or reduction, ion exchange, filtration, electrochemical treatment, reverse osmosis, membrane technologies, and even evaporation recovery [13, 14]. These technologies, however, had some disadvantages such as the requirement for high energy and high facilities input. Another major disadvantage is the production of toxic chemical sludge, and its disposal or treatment becomes a costly affair and is not eco-friendly. Therefore, removal of toxic heavy metals to an environmentally safe level in a cost-effective and environment-friendly manner assumes great importance.

Microorganisms were found in different habitats and had developed the capabilities to protect themselves from heavy metal toxicity by various mechanisms such as adsorption, uptake, methylation, oxidation, and reduction [13, 15, 16]. A number of metal-reducing bacteria have been isolated and characterized from a variety of habitats, and much work had focused on *Shewanella* and *Geobacter* spp. [17]. The genus *Shewanella* was first described two decades ago [18]. In general, shewanellae are members of the γ-proteobacteria that are gram-negative rods 2–3 μm in length, 0.4–0.7 μm in diameter, and motile by flagellum [19]. *Shewanella* species were widely distributed and had been isolated from various environments such as marine and freshwater, spoiled food, and oil field wastes and were capable of dissimilatory reduction of solid iron and manganese oxides [20]. Previous research revealed that the hallmark features of the members of this genus include unparalleled respiratory diversity and the capacity to thrive at low temperatures [21].

The strain used for this study, *Shewanella xiamenensis* BC01, is a newly isolated strain collected from sediment near Xiamen, China [15]. Phylogenetic analysis and identification of 16S rRNA sequences of BC01 showed that it was similar to *S. xiamenensis* sp. nov. S4, a novel recently classified *Shewanella* species with distinct characteristics [22]. To date, there is no literature cited for swarming effect under metal stress by using BC01. The purpose of this study is to find out the effect of cultivation conditions on the growth, such as optimal pH, temperature, and conditions. Moreover, cell morphology and swarming motility of *S. xiamenensis* BC01 under the response to different metal ions were further investigated and accelerated the application of this strain.

Materials and method

Bacterial strain

Shewanella xiamenensis BC01 has been deposited in the Bioresources Collection and Research Center (BCRC; Hsinchu, Taiwan) as BCRC80598 [15].

Chemicals and reagents

All chemical reagents used were of analytical grade without further purification. Stock solutions (100 mM) using deionized water (10 ml) were prepared from the following metal salts: $AlCl_3{\cdot}6H_2O$, $MnSO_4{\cdot}H_2O$, $MgCl_2{\cdot}6H_2O$, $FeCl_3{\cdot}6H_2O$, $ZnSO_4{\cdot}7H_2O$, $CuSO_4{\cdot}5H_2O$, $AgNO_3$, $CaCl_2$ anhydrous (Sinopharm Chemical reagent Co., Ltd), and $K_2Cr_2O_7$ (Sigma-Aldrich, USA). Other reagents used include Luria-Bertani (LB) and marine broth 2216, purchased from BD Difco (Difco, USA).

Cultivation condition

The isolated microorganism was grown on a LB agar plate at 30 °C and maintained at 4 °C for long storage. To culture *S. xiamenensis* BC01 (SXM), the cells inoculated from a loopful of seed colony were cultured overnight in 50 ml LB broth at 30 °C, 150 rpm for 12 h. Then, 0.5 ml (1 %, *v*/*v*) cells in the late log growth phase were transferred into 50 ml fresh sterile LB media. Incubation proceeded for 24 h at 30 °C with shaking under aerobic conditions. The pH, determined using a pH meter (Mettler-Toledo, Switzerland), and optical density at 600 nm (OD_{600nm}; SpectraMax M5, Molecular Device, USA) were monitored over the experimental time course. Cell concentrations were determined by extrapolating optical density readings at 600 nm to dry biomass values.

Static and shaking cultures

The same inoculation and cultivation procedure was done as described above. Fifty milliliters of LB broth was taken in sterilized 250-ml conical flasks and inoculated with 0.5 ml logarithmic-phase culture of the bacterial isolate. The medium was then incubated for 24 h at 30 °C with orbital shaking (150 rpm). For the static cultures, all tests were carried out in stationary mode at 30 °C. Bacterial growth was monitored by measuring the pH and optical density at 600 nm. Similar experiments were performed using marine broth 2216 (normally used for the cultivation of marine heterotropic bacteria), instead of LB, as the growth medium to determine the effect of culture media on the growth kinetics of the bacterium.

Determination of optimum growth conditions

For optimum growth of the bacterium, two parameters, i.e., temperature and pH, were considered. Four sets of flasks were incubated at 25, 30, 37, and 42 °C, respectively. Incubation proceeded for 24 h at 30 °C with shaking under aerobic conditions. The pH was measured with a pH meter (Mettler-Toledo, Switzerland), and OD_{600nm} was monitored in a spectrophotometer (SpectraMax M5, Molecular Device, USA) over the experimental time course. To determine the optimum pH, 250-ml flasks, each containing 50 ml LB, were prepared. The pH was adjusted to 5.0, 6.0, 7.0, 8.0, and 9.0, and then

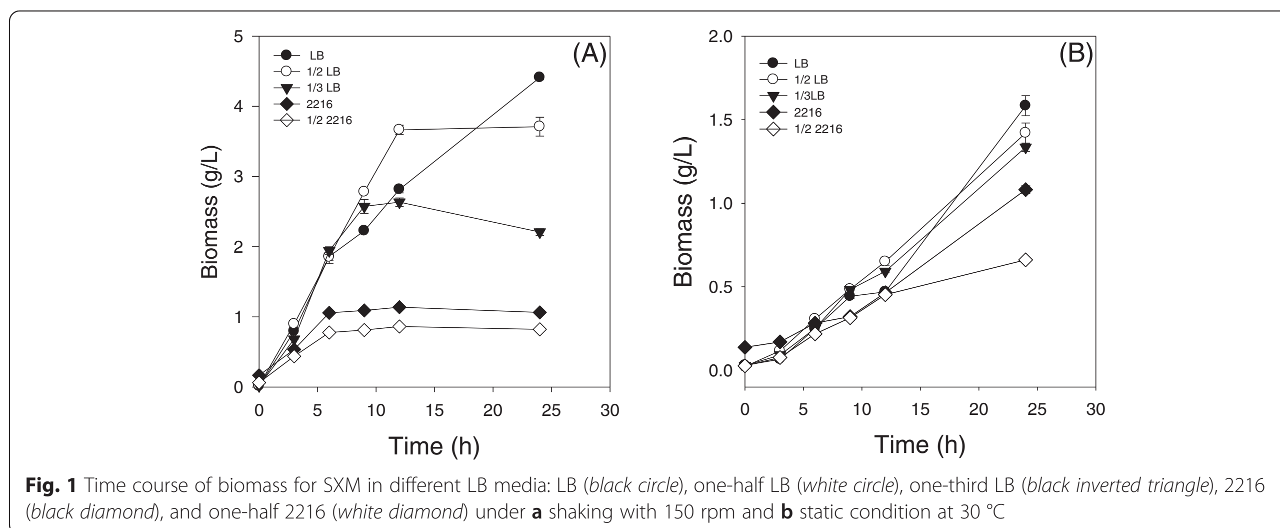

Fig. 1 Time course of biomass for SXM in different LB media: LB (*black circle*), one-half LB (*white circle*), one-third LB (*black inverted triangle*), 2216 (*black diamond*), and one-half 2216 (*white diamond*) under **a** shaking with 150 rpm and **b** static condition at 30 °C

flasks were autoclaved (121 °C for 20 min). These flasks were also inoculated as described above with the same culture conditions. The pH and growth of the bacteria were monitored periodically (0, 3, 6, 9, 12, and 24 h) by measuring the OD at 600 nm.

Culture with addition of metal ions

Resistance of SXM to nine metal ions, i.e., Al^{3+}, Mn^{2+}, Mg^{2+}, Fe^{3+}, Zn^{2+}, Cu^{2+}, Ag^{+}, Ca^{2+}, and Cr^{6+}, was checked by addition of the respective metal salts in the LB medium. Metal ions were filter-sterilized (0.2 μm) and added separately in the culture media. Stock solutions of 100 mM concentration of the metals were prepared, except for Cr (4 mM). A final concentration of 1 mM of all the metals except Ag (80 μM) and Cr (150 μM) was added in treated culture flasks containing 50 ml LB medium. Another flask without metal ions was used as the control. The culture flasks and metal ions were inoculated with 0.5 ml overnight bacterial culture and incubated at 30 °C for 24 h. Aliquots of culture were taken out in oven-sterilized tubes, at regular intervals of 0, 4, 8, 12, and 24 h, and growth was measured as optical density at 600 nm.

Swarming motility in LB agar plate with metal addition

The LB media used in swarming assay with SXM consisted of a final concentration of the following metals: Mg, Ca, and Mn at 1 mM; Cu, Zn, Fe, and Al at 80 μM; and Cr at 150 μM. Another plate containing only LB agar was used as the control. The swarming motility assay was done as described elsewhere [23] except that LB was used as the culture medium instead of 2216E (marine agar). For the motility assay, 0.2 μl from overnight culture grown at 30 °C was placed on the swarming plates (LB medium with 0.7 % agar). The agar media were air-dried for 30–45 min before use. Swarming efficiency was dramatically improved when cells were inoculated onto the center of swarm plates [24]. All experiments were conducted in triplicates, and each set of plates was given the same amount of time to dry prior to inoculation. The plates were incubated at 30 °C for 7 days, and the motility was measured by examining the migration distance of the bacteria from one side to another side of the colony edge. Cultures were spotted onto each plate for 3 days, and the swarming distance was measured as the diameter of zone traveled by bacteria every day for 7 days. The plates were photographed at the third and seventh day to document differences between each plate.

SEM analysis

Whole amounts for scanning electron microscopy (SEM) were prepared by placing a small drop of a washed SXM suspension on a formvar-coated cover glass. Excess solution was wicked away using a piece of filter paper. Samples were fixed for 2 h by the addition of glutaraldehyde (final concentration of 2.5 %) and then dehydrated using a graded ethanol series and 100 % *tert*-butyl alcohol. All samples were fixed, embedded, and sectioned under anaerobic conditions to avoid oxidations of redox-sensitive components. Whole amounts were examined using Hitachi S4800 (Hitachi, Japan) operating at a 10-kV accelerating voltage.

Table 1 The pH values of *Shewanella xiamenensis* BC01 in different culture media with shaking at 150 rpm and 30 °C

Time (h)	LB	One-half LB	One-third LB	2216	One-half 2216
0	7.22	7.18	7.19	7.53	7.53
3	7.36	7.49	7.56	7.47	7.47
6	7.64	7.74	7.92	7.61	7.78
9	7.90	7.93	8.19	7.78	8.00
12	8.32	8.46	8.41	7.91	8.30
24	8.51	8.93	9.00	8.44	8.81

Results and discussions

Effect of media and culture condition on growth of SXM

To determine a suitable culture medium that supports rapid cell growth and good metal-reducing activity, two different media, marine broth 2216 and LB, were compared. The media were also diluted to one-half LB, one-third LB, and one-half 2216, to determine the effect of nutrient concentration on the biomass of the microorganism. As shown in Fig. 1, SXM could grow and be cultivated in 2216 marine broth; however, the biomass only attained a low level (≤1 g/l). In contrast, the LB medium showed the highest growth rate as the cell density was highest in the LB medium with 4.5 g/l at 24 h. At 9 and 12 h, respectively, one-third LB and one-half LB reached the highest biomass values before the growth ceased or decreased. This phenomenon can be attributed to the fact that the

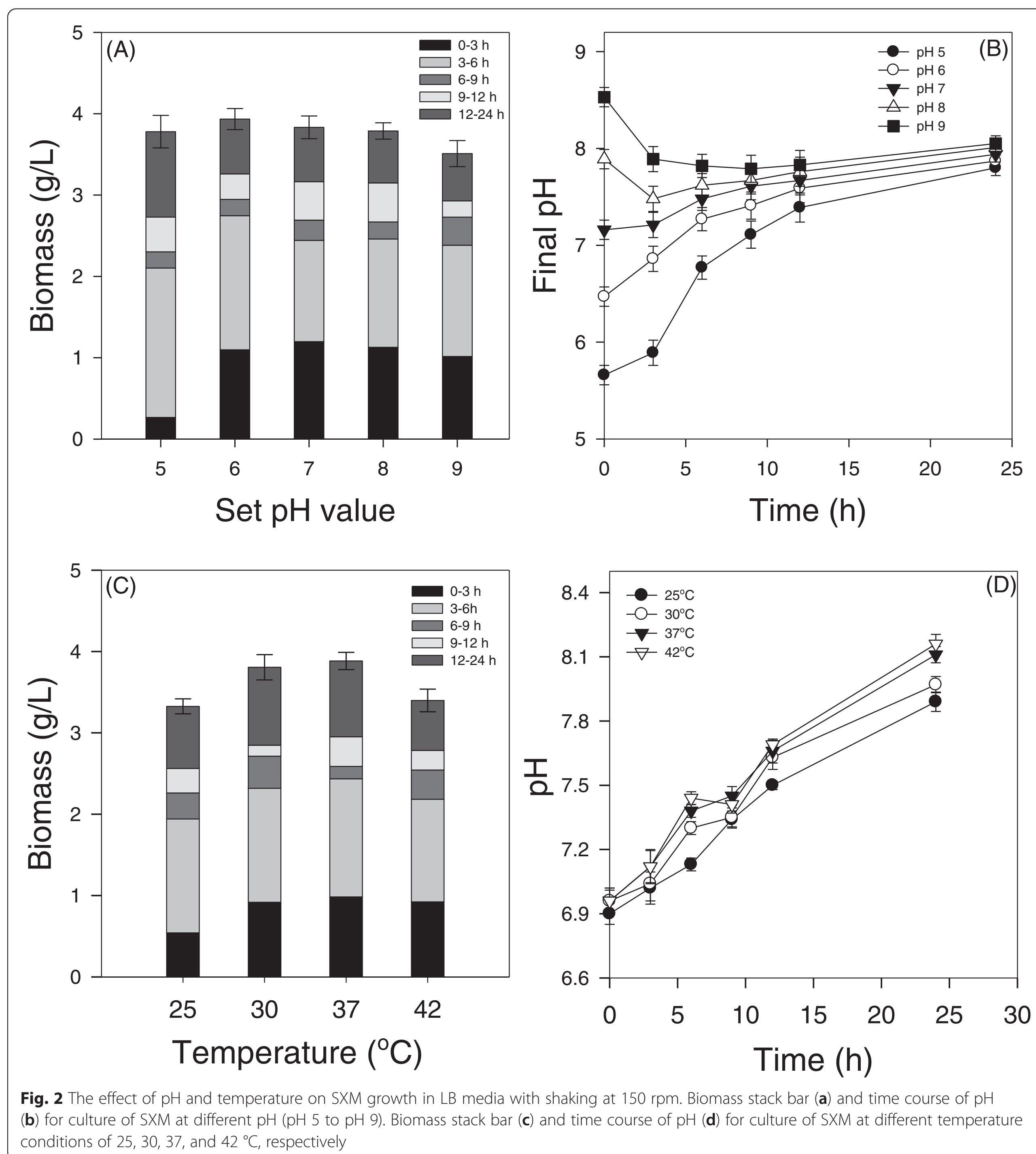

Fig. 2 The effect of pH and temperature on SXM growth in LB media with shaking at 150 rpm. Biomass stack bar (**a**) and time course of pH (**b**) for culture of SXM at different pH (pH 5 to pH 9). Biomass stack bar (**c**) and time course of pH (**d**) for culture of SXM at different temperature conditions of 25, 30, 37, and 42 °C, respectively

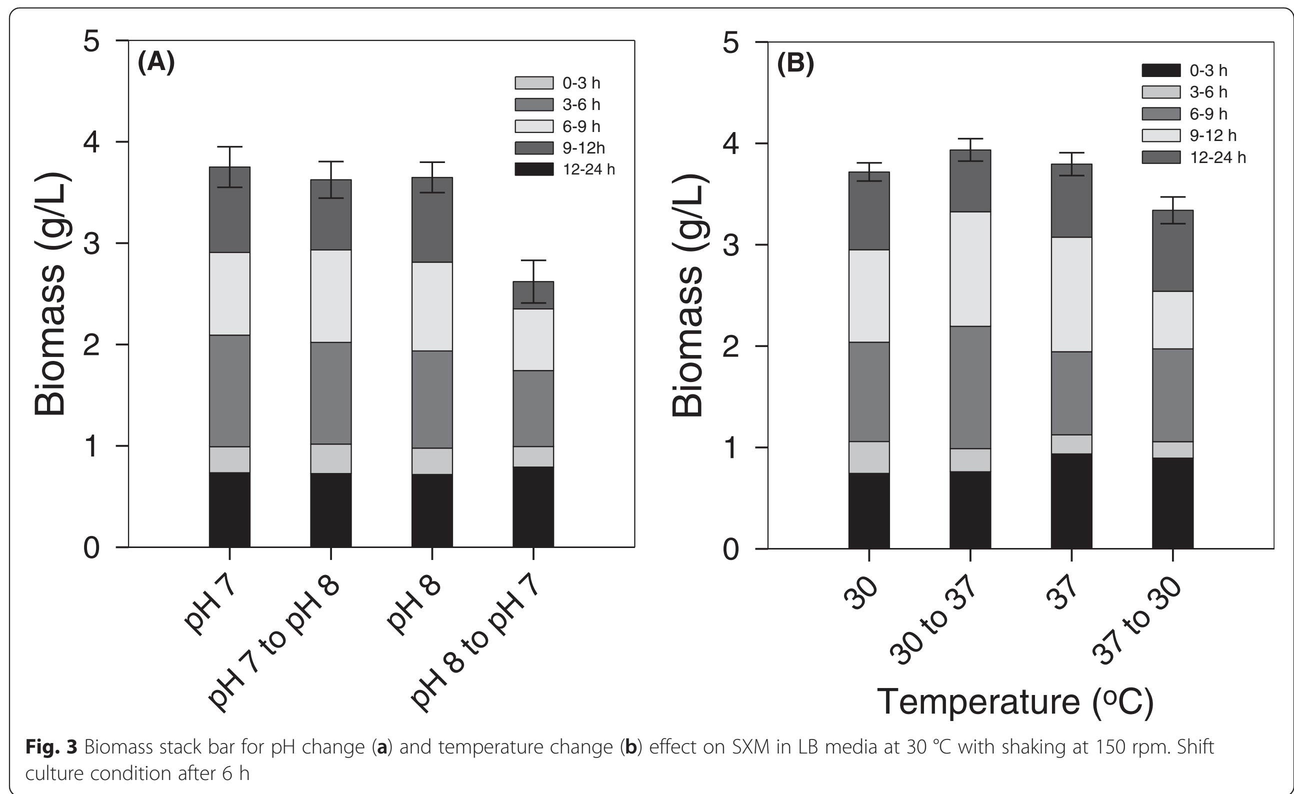

Fig. 3 Biomass stack bar for pH change (**a**) and temperature change (**b**) effect on SXM in LB media at 30 °C with shaking at 150 rpm. Shift culture condition after 6 h

nutrients in the media have been depleted and thus the organism's growth impeded. Examination of SXM growth is important for bioremediation applications, since heavy metal reduction rates have been shown to be directly related to total biomass [25].

The growth curve pattern under static conditions (Fig. 1b) was significantly different from that of shaking. Under shaking conditions, SXM attained more biomass yield compared to the yield under static conditions. The pH values of SXM in different media under shaking

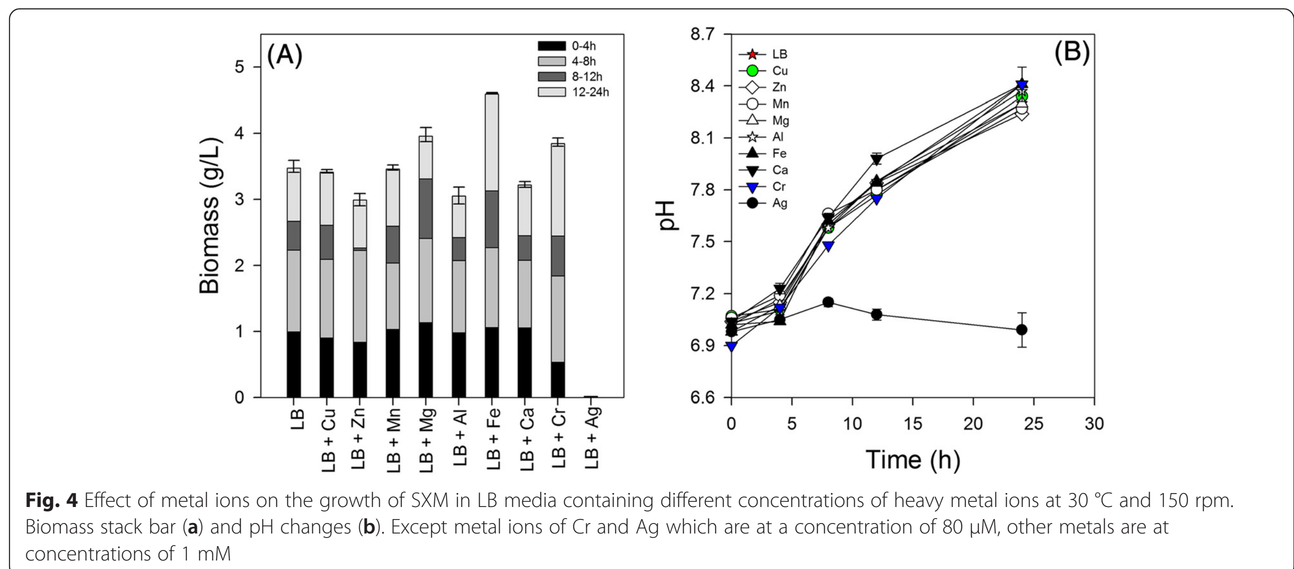

Fig. 4 Effect of metal ions on the growth of SXM in LB media containing different concentrations of heavy metal ions at 30 °C and 150 rpm. Biomass stack bar (**a**) and pH changes (**b**). Except metal ions of Cr and Ag which are at a concentration of 80 μM, other metals are at concentrations of 1 mM

conditions are shown in Table 1. From the table, it can be seen that the pH measurement under shaking conditions showed consistency with time, increasing with concomitant increase in cultivation time. This showed that increase in biomass might be correlated with a corresponding increase in pH. On the other hand, pH under static conditions (data not shown) showed a different pattern, decreasing at first before a slow, gradual increase occurs. This can

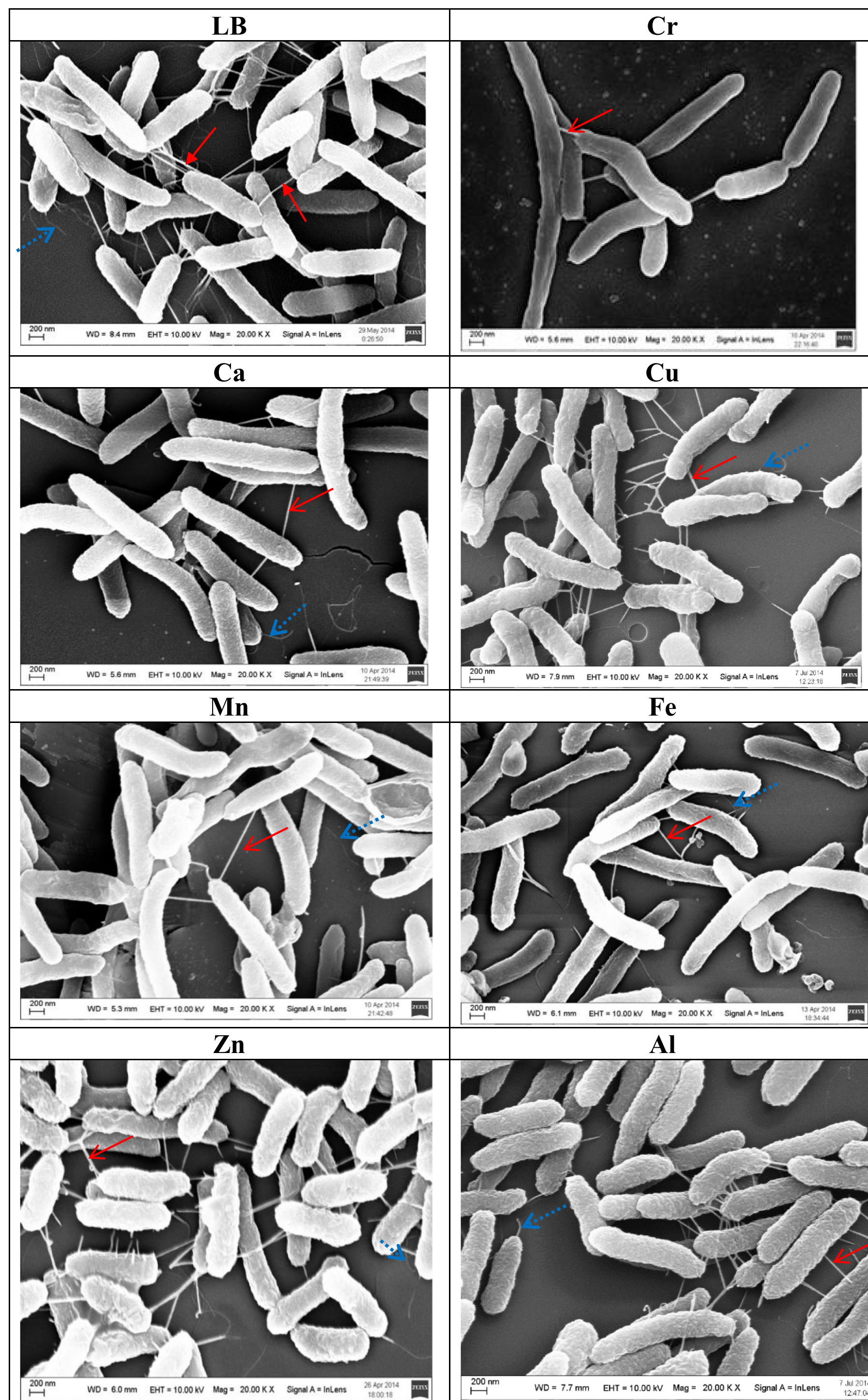

Fig. 5 Scanning electron microscopy (SEM) analysis of SXM cultured in LB medium with different metal ions. All cells were grown for 24 h at 30 °C. SXM produced flagellum (indicated by *blue dot arrows*), and nanowires (indicated by *red arrows*) were observed

be attributed to the fact that under static cultivation technique, essential parameters directly impacting organism physiology are poorly described. These parameters, which include nutrient availability, specific growth rate, and poor mixing, lead to cultural/environmental heterogeneity [26]. The increase in optical density measured during the course of the experiment under shaking conditions reflected the metabolic variability between cultures and may result from increased variability in the mass transfer kinetics in poorly mixed cultures compared to shake flask. Shaking, therefore, results in an optimal mass transfer and more consistent metabolic activities within cultures.

Optimum pH and temperature conditions

Figure 2a shows the effect of pH on the growth of SXM. It was observed that growth occurred at a pH range of 5.0–9.0, but an optimum growth was observed at pH 8.0. SXM exhibited a slight increase in growth over the temperature between 25 and 37 °C and with maximum at 37 °C (Fig. 2c). From Fig. 2b, d, the pH of SXM showed a trend towards basic condition (i.e., pH 8.0) indicative of its marine habitat. However, extreme pH (9.0) restricted the bacterial growth.

Figure 3a shows the effect of pH fluctuations on biomass. Here, the initial pH values of 7.0 and 8.0 were, at 6 h, changed from 7.0 to 8.0 and vice versa. A pH decrease from 8.0 to 7.0 had a negative effect on SXM biomass whereas an increase from 7.0 to 8.0 led to no changes on biomass yield, showing that pH 8.0 is the optimum pH.

As shown in Fig. 3b, the temperatures were changed from 30 to 37 °C and vice versa at 6 h. Even though SXM could grow well at both temperatures, the biomass increased exponentially after a temperature increase from 30 to 37 °C. In contrast, a reduction from 37 to 30 °C

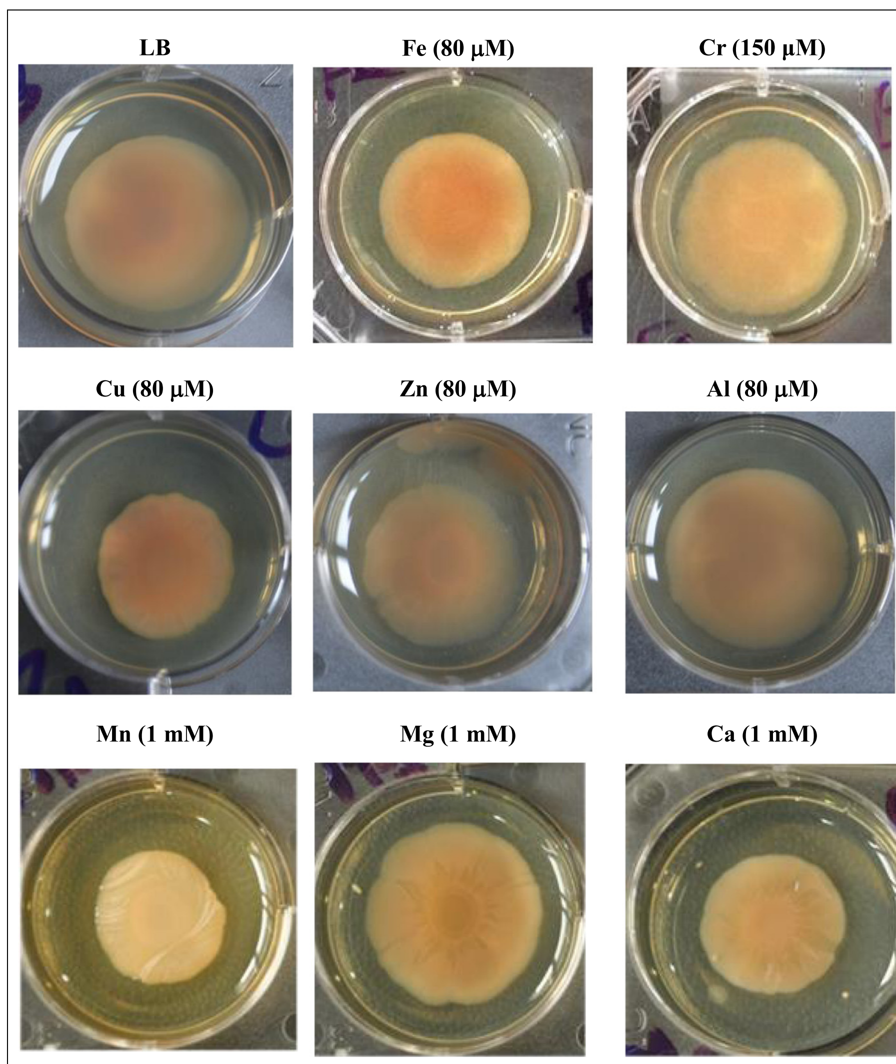

Fig. 6 Swarming motility of SXM after 7 days of cultivation in LB agar supplemented with different metal ions at 30 °C and 150 rpm

showed a reduction in biomass yield. This confirms the fact that SXM attains the highest possible biomass at 37 °C.

Resistance to heavy metal ions

SXM was tested for its resistance to various metals, such as Ca, Mg, Mn, Cu, Zn, Al, Ag, Cr, and Fe. Relative growth of the strain in different metal-containing media is shown in Fig. 4. It was evident that SXM was resistant to all the metals except Ag. It showed that the strain was incapable of growing in the presence of Ag as it was significantly inhibitory for growth. SXM also showed that maximum resistance against 1 mM of metal ion with regard to the biomass was $Fe^{3+} > Mg^{2+} > Mn^{2+} > Cu^{2+} > Ca^{2+} > Al^{3+} > Zn^{2+}$, respectively.

Inhibition of microbes by heavy metals has been reported earlier. *Enterobacter cloacae* was completely inhibited by low concentrations of Hg^{2+} (1 μM), Cu^{2+} (390 μM), Mn^{2+} (480 μM), and Zn^{2+} (0.3 μM) [27]. Wang et al. [28] showed that at high concentrations, Ag(I) can penetrate the cell and potentially impact on several areas of metabolism, most notably lipid metabolism and membrane integrity in *Shewanella oneidensis.* Heavy metal uptake processes by biological cells are generally referred to as biosorption and include both passive adsorption of heavy metals to the cell walls and metabolically mediated uptake. This uptake of heavy metals by live cells has become one of the most attractive means for bioremediation of industrial wastes and other metal-polluted environments [16]. Tolerance to other metals has an added advantage of withstanding the presence of different metallic ions while performing the desired activity. Therefore, we suggest that metal tolerance was due to bioaccumulation of heavy metals by the bacterium.

The SEM image of SXM revealed that it had a long rod shape with a diameter of 1.5–2.0 μm, was motile by means of a single polar flagellum (indicated by blue dot arrows), and had nanowires (indicated by red arrows) cross-linked between the cell systems (Fig. 5). Also, the morphology of SXM on LB agar plate showed that plum-red pigments are secreted from the cell (Fig. 6). However, the cell morphologies varied under different growth conditions and metal stress. In metals like Cu, Cr, and Ca, the cells were narrower, slender, and elongated, with less condensed and fewer cells. Similar morphologies were observed in cells grown in Mn and Fe, as they showed an aggregation of slender, elongated cells. Zn showed shorter but robust cells.

Previous experiments report that *S. oneidensis* MR-1 can utilize extracellular nanowires of mineral forms as the electron acceptor for dissimilatory metal reduction [29, 30]. Moreover, bacterial nanowires present important and logical implications for enzymatic reduction of solid-phase iron and manganese oxides by DMRB, such as *Shewanella* and *Geobacter*. Bacterial nanowires are extracellular appendages that have been suggested as pathways for electron transport in phylogenetically diverse microorganisms. In this study, pilus-like appendages are produced by SXM and they can represent nanowires.

Effects of metal ions on the swarming motility

The motility of SXM was monitored for 7 days at 30 °C. Various metals with different concentrations were tested for their inhibition of or effect on SXM swarming (Fig. 6). The growth curve of external diameter and swarming distance were calculated and shown in Fig. 7.

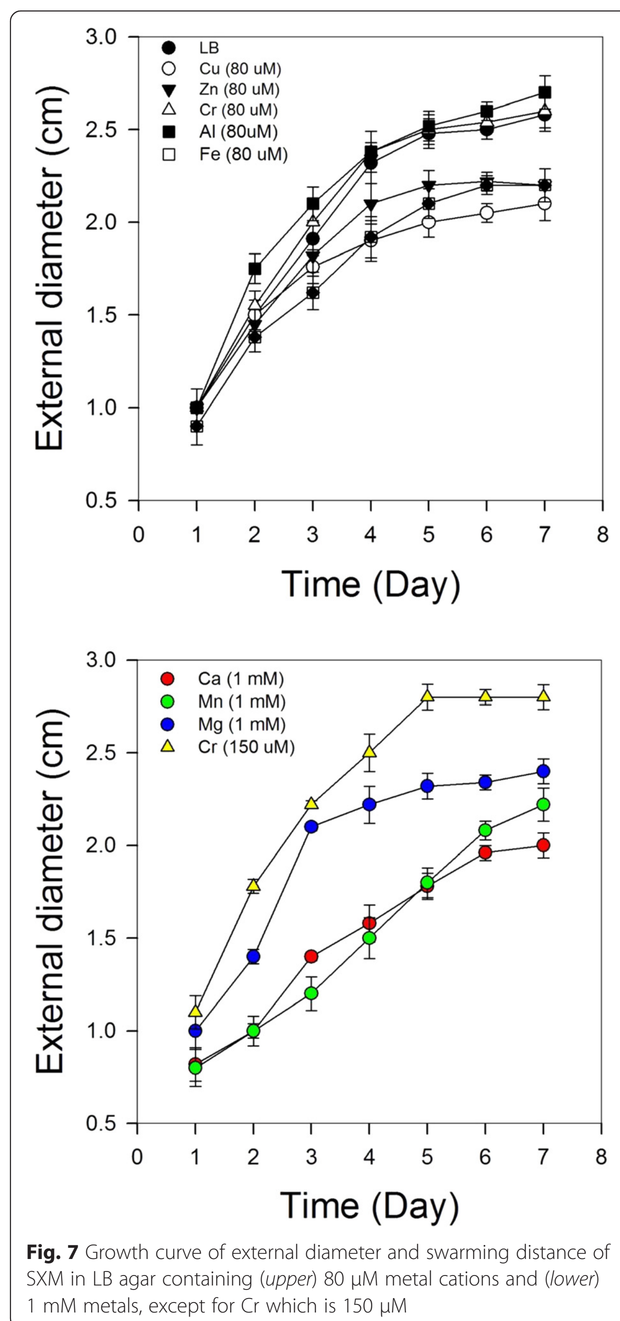

Fig. 7 Growth curve of external diameter and swarming distance of SXM in LB agar containing (*upper*) 80 μM metal cations and (*lower*) 1 mM metals, except for Cr which is 150 μM

SXM showed a strong tendency to engage in swarming behavior, even at the 150 μM of Cr in the LB agar plate. Results of the experiments showed significant differences in swarming behavior between various metals, including differences not only in the size of the swarm zone but also in the tendril formation and the behavior at the edge of the swarm zone (Fig. 6).

SXM with Al exhibited the most swarming, followed by Cr. SXM with Mn showed the least swarming after the first day (data not shown), moving only a few inches beyond the point of inoculation after 7 days (Fig. 6). Interestingly, most of the metals, especially Cu, Ca, Fe, and Zn, showed a reduction in swarming behavior after 4 days, while at final concentrations of 1 mM of Cu, Zn, Fe, and Al on SXM, it displayed no swarming activity on the agar plate (data not shown). Swarming is a powerful means of rapidly colonizing nutrient-rich environments, facilitating colony spread, and accelerating biomass production [31]. Cell density, surface contact, and physiological signals all provide critical stimuli, and close cell alignment and the production of secreted migration factors facilitate mass translocation [31]. Another study had shown that different bacteria exhibit swimming or swarming or both types of motility [32], in which *S. oneidensis* MR-1 displayed swimming in complex media but no swarming across surfaces was observed. Swarming is different from swimming which is dependent only on flagella and occurs in a liquid medium or solid medium with lower concentrations of agar [33]. Swarming, however, is a surface phenomenon. In addition to flagella, swarmer cells require an increased production of certain extracellular components (known as wetting agents) that reduce surface friction and enable the smooth migration of a group of cells on viscous surfaces [34]. Swarming is a multicellular type of motility and is considered as a model of bacterial social behavior and had been shown to be associated with virulence and resistance to antibiotics in some species.

Metals could inhibit the swarming of bacteria either by reducing the wetness of the colony or by suppressing the activity of the wetting agent or rhamnolipid biosynthetic pathway. Members of the *Shewanella* genus are mostly isolated from seas and sediments and grow at low temperatures [22]; thus, swarming is most likely the dominant motility pattern of cells in such habitats. Our hypotheses are that variations in swarming may be directly related to rhamnolipid production and also swarming defects may be due to inadequate wetness required for the swarming movement under different metals.

Conclusions

Shewanella xiamenensis BC01 can grow over a wide range of pH and mild temperatures, which is an adaptive mechanism considering the fact that aquatic environments are warmed either naturally or by power plant effluents and other heated wastes. Many studies have shown that *Shewanella* has the ability to use various terminal electron acceptors, allowing them to survive in extreme and harsh environments such as the absence of oxygen or very low temperatures. The results indicate that *S. xiamenensis* BC01 activity may be sensitive to environmental factors present in the culture medium. Also, in its interaction with metals, it can be assumed that *S. xiamenensis* BC01 has the capability of accumulating and transforming these metals to nontoxic forms. Thus, this strain has potential in bioremediation and detoxification of heavy metals in industrial wastewaters.

Abbreviations

DMRB: dissimilatory metal-reducing bacteria; LB: Luria-Bertani; SEM: scanning electron microscopy; SXM: *Shewanella xiamenensis* BC01.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

IN designed the experiments and wrote the manuscript. NCI performed all the experimental works. XW and YZ interpreted the results. All authors read and approved the final manuscript.

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