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MINIREVIEW

Insights into the Biosynthesis of Nanoparticles by the Genus *Shewanella*

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ABSTRACT The exploitation of microorganisms for the fabrication of nanoparticles (NPs) has garnered considerable research interest globally. The microbiological transformation of metals and metal salts into respective NPs can be achieved under environmentally benign conditions, offering a more sustainable alternative to chemical synthesis methods. Species of the metal-reducing bacterial genus *Shewanella* are able to couple the oxidation of various electron donors, including lactate, pyruvate, and hydrogen, to the reduction of a wide range of metal species, resulting in biomineralization of a multitude of metal NPs. Single-metal-based NPs as well as composite materials with properties equivalent or even superior to physically and chemically produced NPs have been synthesized by a number of *Shewanella* species. A mechanistic understanding of electron transfer-mediated bioreduction of metals into respective NPs by *Shewanella* is crucial in maximizing NP yields and directing the synthesis to produce fine-tuned NPs with tailored properties. In addition, thorough investigations into the influence of process parameters controlling the biosynthesis is another focal point for optimizing the process of NP generation. Synthesis of metal-based NPs using *Shewanella* species offers a low-cost, eco-friendly alternative to current physiochemical methods. This article aims to shed light on the contribution of *Shewanella* as a model organism in the biosynthesis of a variety of NPs and critically reviews the current state of knowledge on factors controlling their synthesis, characterization, potential applications in different sectors, and future prospects.

KEYWORDS biosynthesis, microbial, anaerobic, biofabrication, catalysis, green synthesis, metal nanoparticles, *Shewanella*

Nanotechnology has become increasingly popular with the development of a variety of nanoparticles (NPs) with unique properties for wide-ranging applications across various sectors of science and technology (1, 2). The physical and chemical properties of NPs differ substantially from bulk materials due to their small size (particle size of ≤100 nm), high surface-area-to-volume ratio, and increased presence of defect sites and edges. Owing to these unique properties, the application of NPs is a rapidly growing field of research with diverse applications in a wide range of industries, including farming (3, 4), consumer products (5), coatings (6), cosmetics (7), catalysis (8), chemicals (9), electronics and optics (10), environmental remediation (11, 12), food packaging (13), fuel additives (14), energy (15), textile and paints (16), and next-generation medicine (17).

Worldwide, the area of NP synthesis is growing rapidly, and it is expected that the global market of NPs could reach $25.26 billion by 2022 (18, 19). The physicochemical approaches currently being employed are capital exhaustive and often require the use

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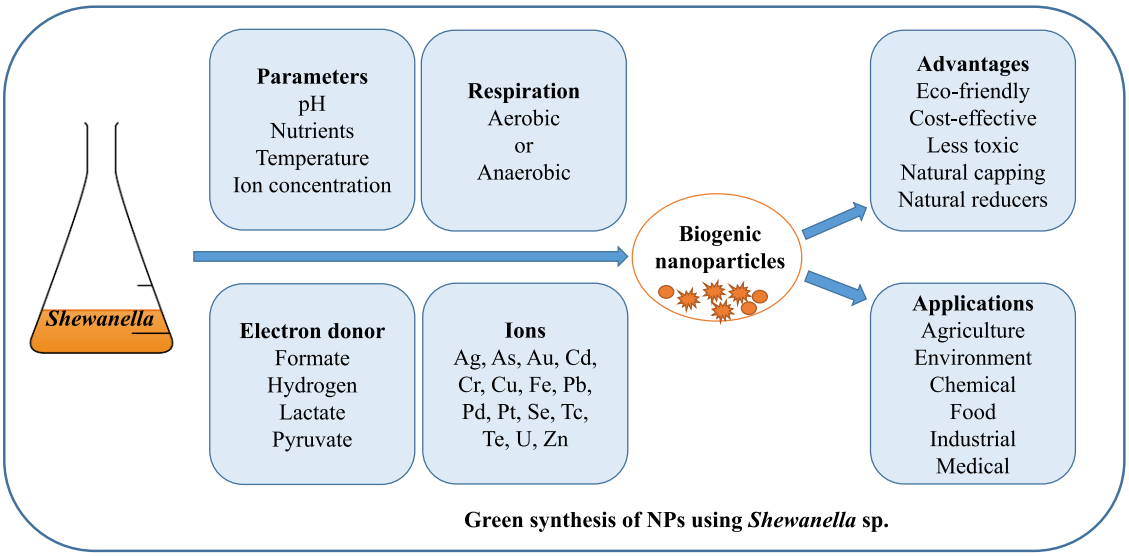

FIG 1 Green synthesis of nanoparticles using *Shewanella* species.

of aggressive reagents and processing conditions (20, 21). Thus, there is a need for cost-effective, clean, biocompatible, and eco-friendly methods for the facile synthesis of NPs. Biological resources, and in particular microorganisms, offer a potential solution as nano-factories for NP synthesis (22, 23). Numerous publications can be found in the literature dealing with the biosynthesis of metal-based NPs using different organisms, including bacteria (24, 25), algae (26), yeasts (27), fungi (28), and plant extracts (29, 30).

Biosynthesis of NPs has several advantages, including high purity, low cost, and sustainable environmentally benign methods. However, consideration must be given to eventual scale-up for mass production via optimization of culture conditions such as pH, incubation time, temperature, and the concentration of the metal ions. Developing an environment-friendly, low-risk approach that effectively modulates the size, morphology, stability, and properties of NPs is an important focus of current research concerned with biogenic NP synthesis. In this minireview, an in-depth critical synthesis pertaining to the application of *Shewanella* as a model microorganism for the green synthesis of NPs is provided, including factors influencing the synthesis and properties of NPs and mechanistic details of electron transfer routes culminating in metal reduction and NPs synthesis. Finally, concluding discussions on potential future opportunities and challenges of microbial synthesis of NPs are summarized.

SYNTHESIS OF NANOPARTICLES USING BACTERIA

Bacteria have attracted significant attention in the green synthesis of NPs due to their ease of cultivation in simple growth media, the large diversity of organisms, and rapid adaptation under changing environmental conditions (31, 32). Extensive studies are available in the literature focusing on the bacterial synthesis of a wide variety of NPs. However, the identification of key bacterial enzymes, metabolic products, and factors affecting the synthesis of NPs is required to develop a systematic understanding of these processes. Among different bacterial taxa, the metal- and sulfur-reducing *Shewanella* spp. have shown promising potential in the fabrication of a variety of NPs for a wide range of applications (33, 34) and are discussed in this minireview. The biosynthesis of NPs using *Shewanella* are generalized in Fig. 1.

Role of *Shewanella* species in the facile synthesis of nanoparticles. *Shewanella* is the sole genus within the family *Shewanellaceae*, belonging to the *Gammaproteobacteria*, a class of Gram-negative bacteria. Among *Shewanella*, *S. oneidensis* MR-1 is often used as a model organism to study the anaerobic reduction of metals. *S. oneidensis* MR-1 (formally *Alteromonas putrefaciens*), was isolated from Lake Oneida, New York, and described with

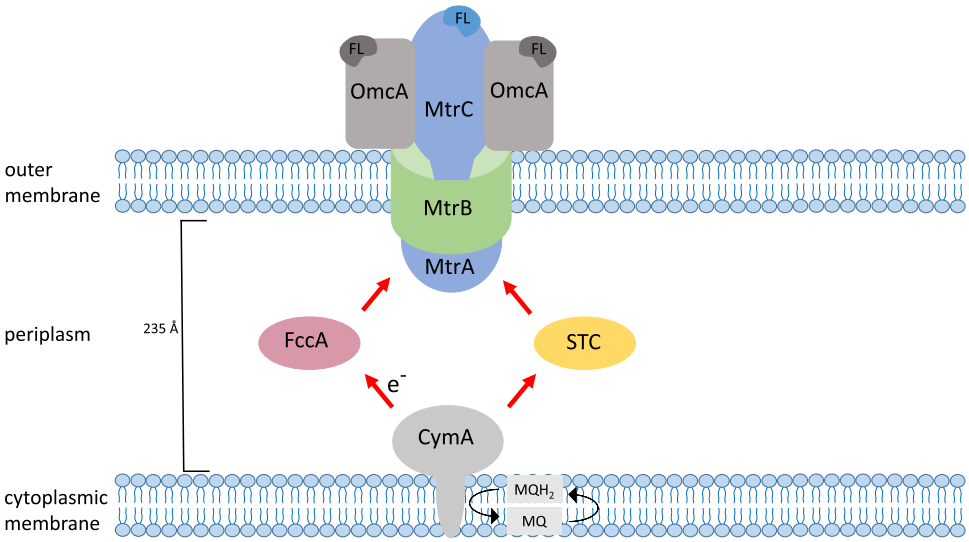

FIG 2 Illustration of the Mtr electron transport pathway in *Shewanella oneidensis* MR-1. Electrons from the menaquinone (MQ) pool are passed to CymA, a cytoplasmic membrane-associated tetraheme cytochrome. The electrons from CymA can be distributed to a range of electron transport pathways with terminal electron acceptors that can be reduced in the periplasm or at the cell surface. In the case of extracellular metal reduction, electrons are transferred from CymA to MtrA via periplasmic *c*-type cytochromes, FccA and STC. MtrA, a decaheme *c*-type cytochrome is located on the periplasmic side of the outer membrane, deeply embedded within the β-barrel protein MtrB. The MtrAB complex connects to MtrC, another decaheme *c*-type cytochrome, located on the external side of the outer membrane, allowing transfer of electron to extracellular electron acceptors. A further decaheme *c*-type cytochrome, OmcA, completes the structure, forming a 2:1 complex with MtrC and facilitating reduction. FL, flavin cofactor of OM cyctochromes. Adapted from Beblawy et al. (128).

the capability of utilizing Fe and Mn as terminal electron acceptors for growth (35, 36). Since then, a variety of other *Shewanella* strains with the capacity for metal reduction have been identified from a range of soil, sediment, and aquatic environments, including, *S. xiamenensis* BC01 (SXM), *S. algae*, *S. putrefaciens*, *S. loihica* PV-4, *S. piezotolerans*, and *S. decolorationis* S12. The versatility of *Shewanella* in reducing metals extends beyond Fe(III) and Mn(IV) to "nonstandard" metals, including U(VI) (37), Cr(VI) (38), Np(V) (39), Tc(VII) (40), Pu(IV) (41), V(V) (42), Se(IV) (43), Te(IV) (43), Au(III) (44), Ag(I) (45), Pd(II) (46), and Cu (II) (47). The reduction of these diverse terminal electron acceptors is facilitated by the complex multicomponent branched electron transport system (ETS) in *Shewanella* which includes inner membrane-localized dehydrogenases, menaquinone, and a multitude of cytochromes (48). Of these electron transport systems, the best characterized is the Mtr pathway of *S. oneidensis*, which is required for the reduction of insoluble metal oxides and electrodes and also plays an important role in the reduction of various soluble electron acceptors (49). Five primary protein components have been identified in the Mtr pathway, the inner membrane-bound CymA, the periplasmic *c*-type cytochrome MtrA, the outer membrane (OM) β-barrel protein MtrB, and the OM-anchored *c*-type cytochromes MtrC and OmcA (Fig. 2). CymA, a tetraheme *c*-type cytochrome, has been described as an "electron transport hub," transferring electrons from menaquinol to a variety of electron transport pathways with terminal electron acceptors that are reduced either within the periplasm or at the cell surface. Electrons from CymA are transferred to MtrA via perisplasmic carriers, including the fumarate reductase (FccA) and the small tetraheme cytochrome (STC) (50).

MtrA is one of three proteins, along with MtrB and MtrC, that form the porin-cytochrome complex, MtrCAB. MtrA is embedded within MtrB, which together span the OM and bind to MtrC on the extracellular side of the membrane (51). Electrons can be transferred directly from MtrA to MtrC and then distributed to various extracellular terminal electron acceptors. OmcA has also been suggested to accept electrons from the MtrAB complex and can facilitate extracellular electron transfer (52). This pathway plays a central role in the bioreduction of many metals and the subsequent formation of metal NPs and is discussed in more detail in the relevant sections.

The current information pertaining to the contribution of different *Shewanella* spp. in the biosynthesis of various metal-based NPs is presented in the following section.

Iron-based nanoparticles. A range of biogenic Fe minerals were produced using *S. putrefaciens* (strain CN32), via reduction of an amorphous hydrous ferric oxide (ferrihydrite) (53). The nature of the resulting biominerals was heavily dependent upon the composition of the aqueous media. In the absence of P in the media, nanoscale magnetite was formed. When an electron shuttle, anthraquinone-2,6-disulfonate (AQDS), was present, the magnetite NPs were highly crystalline, with crystallinity lower in the absence of the electron shuttle (52). *S. oneidensis* MR-1 has also been shown to produce magnetite NPs from a ferrihydrite precursor. These biogenic magnetite NPs were less crystalline than abiogenic magnetite, a feature that could potentially serve as a biosignature for natural magnetites (54). Magnetite NPs have also been produced by a range of other *Shewanella* spp. Ferrihydrite was partially converted to superparamagnetic magnetite nanocrystals by *S. algae* (55). The synthesis of magnetite NPs (>35 nm) by *S. loihica*, a marine psychrotolerant species, resulted in well-formed single-domain magnetite, in contrast to the mostly superparamagnetic magnetite NPs produced by mesophilic species (56), highlighting that strain choice could be important for directing NP properties.

The biosynthesis of doped extracellular magnetite using Fe(III)-reducing bacteria, including *Shewanella*, has also attracted great attention in order to control and exploit the magnetic properties of these biominerals for applications, including remediation, catalysis, drug delivery, and data storage (57). *S. oneidensis* was used to produce Co and Ni doped magnetite NPs (58). The produced $NiFe_2O_4$ contained Ni^{2+}, with at least 80% in O_h coordination, whereas the $CoFe_2O_4$ contained Co^{2+} but with a significant proportion (up to 45%) in T_d coordination. The formation of Ni^{2+}-substituted magnetite NPs from a Ni-doped ferrihydrite precursor was also shown to be promoted by *S. putrefaciens* (59). *S. loihica* was able to facilitate the production of transition metal- and lanthanide-substituted magnetite nanocrystals from a doped iron oxyhydroxide precursor (60, 61). The Mn- and Zn-substituted magnetites had a higher magnetic susceptibility (κ_{RT}) and saturation magnetization (M_S) than pure biogenic magnetite with a maximum κ_{RT} at 0.2 cationic mole fraction, while lanthanide substitution was found to generally decrease M_S, with Gd- and Ho-substituted magnetites having the highest magnetization (61).

Biomineralization of spherical FeS-NPs by *S. loihica* and *S. oneidensis* following bioreduction of iron citrate and thiosulfate has also been demonstrated (62, 63). These extracellular NPs were not directly associated with the cells but were linked to cells via biogenic FeS nanowires which could facilitate long-distance extracellular electron transport.

Copper-based nanoparticles. The role of *S. loihica* in facilitating the synthesis of Cu-NPs possessing antimicrobial activity was reported (63). The authors concluded that the NPs were primarily extracellular, leading them to suggest that extracellular bioreduction could be responsible for their formation (64). However, in a study using *S. oneidensis*, it was demonstrated that key OM cytochromes (OmcA, MtrC, and MtrF) and periplasmic cytochromes (including MtrABCDEF) did not play a role in the bioreduction of Cu(II) by this organism (47). In addition, electron microscopy work clearly demonstrated that Cu-NPs were not restricted to the extracellular environment but were also present in the periplasm and cytoplasm of *S. oneidensis* (47). Although this could indicate that electron transport pathways and characteristics of synthesized Cu-NPs are strain dependent, there was little evidence to support either the involvement of OM cytochromes in *S. loihica* or even that the NPs were indeed extracellular. Furthermore, it was claimed that X-ray photoelectron spectroscopy (XPS) analysis supports the bioreduction of Cu(II) to Cu(0) by *S. loihica*; however, the XPS peaks are more reflective of Cu(II) than Cu(0) (65). The high Cu(II) concentration (1 mM) used in combination with additional salts in the *S. loihica* medium, may have contributed to the abiotic precipitation of oxidized Cu. In contrast, the Cu-NPs produced by *S. onediensis* were confirmed by X-ray absorption spectroscopy to comprise Cu(0). The efficiency of these Cu(0)-NPs as catalysts for "click chemistry" reactions, an important synthesis pathway for new pharmaceuticals (66), was also demonstrated.

S. oneidensis has also been shown to facilitate the synthesis of CuS-NPs when sodium thiosulfate was used as an electron acceptor (66). The CuS-NPs displayed a high photothermal

conversion efficiency, demonstrating the potential for cost-effective and environment-friendly biosynthesis of CuS-NPs by *Shewanella* for possible applications in photothermal therapy for cancer treatment (66). A similar study showed the formation of hollow CuS nanospheres following bioreduction of thiosulfate by *S. oneidensis* and subsequent addition of Cu(II) (67). The CuS shells, located on the cell surface, enhanced the adsorption capacity of *S. oneidensis* toward toxic Cr(VI). These studies demonstrate that the use of an additional electron acceptor, thiosulfate, can lead to the formation of CuS-NPs by *S. oneidensis*, in contrast to the Cu(0)-NPs synthesized where no additional electron acceptor (other than Cu(II)) was used. This highlights the potential for controlling Cu-based NP properties, which could be tailored for specific applications, using a single species of *Shewanella* (*S. oneidensis*).

Gold-based nanoparticles. Synthesis of Au-NPs by *S. oneidensis* from a tetracholoraurate solution was investigated and revealed a synthesis process involving an initial, fast biosorption step followed by a slower reduction step which required the presence of an electron donor (68). While using H_2 as an electron donor, it was found that the location and size of the Au-NPs could be directed. However, as the reduction was also observed in a heat-killed cell control, the synthesis process was considered to be of nonenzymatic nature. The Au-NPs synthesized by *S. oneidensis* were hydrophilic and resisted aggregation even after several months and were not toxic or inhibitory to strains of Gram-negative and Gram-positive bacteria (69). The synthesis of Au-NPs by a biofilm of *S. oneidensis* on the anode of a microbial fuel cell (MFC) and their impact on energy generation were also investigated (70). An anode decorated with the Au-NPs produced a 62.5% higher power density than the MFC containing a plain carbon foam electrode and allowed rapid detection of H_2O_2 at a very low concentration (20 μM) (70).

Photo-induced biosynthesis of Au-NPs by *S. oneidensis* has also been reported (71). The light-induced activation of certain functional groups and extracellular polymer molecules, as revealed by the excision of selected genes, was suggested as the possible mechanism underlying the synthesis of the Au-NPs. Interestingly, light intensity and wavelength were found to influence the rate of Au-NP synthesis. These studies demonstrate several pathways that could induce Au-NP formation in the presence of *Shewanella* spp.; however, the impact of these different pathways on the properties of the resulting Au-NPs has not been studied and should be further investigated so as to identify methods that could produce tailored Au-NPs for specific applications.

Recent work has investigated the synthesis of Au-NPs by *S. oneidensis* and *S. xiamenensis* under various conditions such as pH, initial metal concentration, and cellular biomass of selected anaerobic bacteria (72). *S. xiamenensis* was found to produce a higher yield of Au-NPs, but differences in the properties or characteristics of the NPs produced by the different strains were not reported. The study deciphered the binding of Au ions onto the bacterial OM followed by the precipitation of Au-NPs and presented a viable strategy for metal extraction from large volumes of industrially produced wastes. In a similar study, synthesis of Au-, Pd- and Pt-NPs by an electrochemically active biofilm of *S. loihica* was described (73). Interestingly, cell extracts from *S. algae* were found to produce Au-NPs and nanoplates with H_2 as an electron donor at room temperature and pH 2.8 (33), demonstrating the potential use of *Shewanella* spp. for Au-NP synthesis under harsh conditions, such as those found in metal-rich waste streams.

Palladium-based nanoparticles. The majority of work on *Shewanella*-directed Pd-NP synthesis has focused on *S. oneidensis* and demonstrated the bioreduction of Pd(II) to Pd(0) in the presence of a variety of electron donors (46). Biogenic Pd-NPs have the ability to reductively dehalogenate the contaminant, polychlorinated biphenyl (PCB), with comparable activity to commercial Pd(0) powder (74). The size and reactivity of Pd-NPs synthesized by *S. oneidensis* could be fine-tuned by controlling the Pd/cell weight (dry weight) to tailor catalytic activity toward either PCB or perchlorate (74).

Several studies have sought to elucidate key electron transport pathways involved in Pd(II) reduction and Pd-NP formation, focusing on *S. oneidensis*, with contrasting reports on the roles of hydrogenases and cytochromes. Initial work by Ng et al. (75) suggested that hydrogenases were key enzymes in the reduction of Pd(II), with mutants lacking either the [NiFe]-hydrogenase, HyaB, or [FeFe]-hydrogenase, HydA, displaying decreased Pd

(II) reduction rates relative to the wild type when using formate as an electron donor. On the other hand, a mutant lacking both the OM cytochromes, MtrC and OmcA, did not show any decrease in Pd(II)-reducing capability when either lactate or formate was used as an electron donor (75). It should be noted that the concentration of formate used as an electron donor in this study has been shown to result in abiotic reduction of Pd(II) and so may have contributed to the reduction rates, potentially contributing to differences between the mutant strains (76, 77). More recently, Dundas et al. presented contrasting results showing that the loss of these two OM cytochromes (MtrC and OmcA) did attenuate Pd(II) reduction and were also important in controlling particle size and deposition (78). A minimal decrease in Pd(II) reduction using hydrogenase deletion mutants was also observed (78). In the latter study, transmission electron microscopy (TEM) images revealed clear differences in the cellular location of NPs produced by the different mutant strains. MtrC and OmcA were required for the precipitation of extracellular NPs, with their removal resulting in Pd precipitation in the periplasm, further supporting the role of these OM cytochromes in facilitating Pd(II) reduction. This demonstrated use of mutants to control NP size and localization (78) could prove a valuable tool for the biosynthesis of bespoke Pd catalysts. A difference in buffering capacity used in the two studies could potentially explain the discrepancy in results. Ng et al. (75) used 30 mM HEPES, whereas Dundas et al. (78) used a more heavily buffered medium containing 100 mM HEPES. Dundas et al. (78) suggested that their more strongly buffered system may have better countered pH changes caused by cell metabolism which could, in turn, have affected the results of the study by Ng et al. (75). However, it should also be pointed out that Good's buffers, including HEPES, have been shown to have an effect on aqueous Pd chemistry and at high concentrations (100 mM), and can cause abiotic Pd precipitation, potentially complicating the interpretation in these studies (79). Indeed, Dundas et al. (78) highlighted that they observed decreased reduction rates of Pd(II) with increasing age of the HEPES buffer, further highlighting the importance of buffer chemistry in controlling Pd reduction. A recent study by Yang et al. (77) sought to address these conflicting results and elucidate the role of dehydrogenases and hydrogenases in Pd(II) reduction and NP synthesis. In the presence of formate as an electron donor, the inhibition of NADH dehydrogenases (NADH-DH) resulted in a strong decrease in Pd(II)-reducing capability relative to the wild type with almost no Pd-NPs observed on the OM (77). A smaller decrease in Pd(II) reduction was observed in mutants lacking both the hydrogenases, HydA and HydB. Based on these data, two pathways resulting in Pd(II) reduction in *S. oneidensis* using formate as the electron donor were proposed by the authors (77). Pathway I involves electron transfer from NADH produced by formate dehydrogenases, which couple formate oxidation to NAD^+ reduction (80), via NADH-DH to CymA and the Mtr pathway. This pathway is blocked when NADH-DH is inhibited, resulting in the decrease in Pd(II) reduction and lack of OM-associated NPs observed by Yang et al. (77). Pathway II involves Pd(II) reduction by hydrogen, produced from formate by hydrogenases in combination with formate dehydrogenase. Pathway I, which appeared to be the more dominant mechanism in the study by Yang et al. (77) supports the observation from Dundas et al. (78) that the Mtr pathway, and likely the OM cytochromes, play an important role in Pd(II) reduction. Pathway II supports the earlier observations from Ng et al. (75) that hydrogenases may also be involved in Pd(II) reduction, albeit in a smaller capacity than the cytochromes. It is clear that despite detailed mechanistic work with deletion mutants, the complex electron transport pathways of *Shewanella* require further study focusing on the formation of Pd-NPs to achieve directed control and optimization of NP synthesis. As discussed above, this may also require a deeper understanding of the role of solution chemistry in Pd(II) bioreduction and NP formation (see "Factors Affecting Biosynthesis of Nanoparticles" below).

Recently, *in situ* biosynthesis of Pd-NPs on cells of *S. oneidensis* coated with reduced graphene oxide (rGO), forming a bio-nano hybrid material has been reported (81). The integration of Pd-NPs with rGO and *Shewanella* cells promoted Cr(VI) removal 10 times that of native cells and 5 times that of cells and Pd-NPs without rGO (81). *S. oneidensis* has also been exploited for Pd-NP synthesis in microbial electrolysis cells via bioelectrochemical reduction of the metal on the cathode (82). The size of NPs synthesized via

the bioelectrochemical route was in the range of 10 to 100 nm, in contrast to 200- to 250-nm Pd-NPs generated through an electrochemical reduction process lacking cells. Furthermore, in the same experiment, the bioelectrochemical Pd-NPs also displayed significantly enhanced activity toward hydrogen production by 60% compared to Pd catalysts in the absence of microbial reduction, highlighting the substantial potential of biological routes in producing NPs with smaller size and better catalytic efficiency (82).

Platinum-based nanoparticles. So far, limited investigations have been made regarding the synthesis of Pt-NPs using *Shewanella* spp. A biofilm of *S. loihica* successfully directed the biosynthesis of ultralow-sized Pt-NPs when supplied with acetate as an electron donor (73). The particle size was observed to be influenced by pH, with no Pt-NPs produced at pH 4.0, 2- to 6-nm Pt-NPs produced at pH 7.0, and 2- to 10-nm Pt-NPs produced at pH 9.0 (73). Metal precursor concentration was also found to influence particle size, with higher initial metal concentration producing larger NPs. However, no information on the potential electron transport pathway(s) involved or localization of the Pt-NPs was provided. The bacterium *S. algae* was also found to produce Pt-NPs, with an average diameter of 5 nm, using lactate as an electron donor at ambient temperature and pH 7.0 (83). Resting cells of *S. algae* catalyzed the fabrication of Pt-NPs via bioreduction within 1 h. TEM analysis of thin sections indicated the Pt-NPs were located in the cell periplasm suggesting that periplasmic reductases, such as hydrogenases or periplasmic cytochromes, may be important for Pt reduction. However, further work is required to elucidate the mechanism of Pt reduction in *Shewanella*. The use of deletion mutants, such as those studied in Pd(II) reduction, could prove useful in identifying key Pt reductases. In addition, the catalytic activity of Pt-NPs synthesized by *Shewanella* has not been tested and remains an avenue for further research.

Cadmium-based nanoparticles. Anaerobic synthesis of spherical CdS-NPs by *S. oneidensis*, possessing high activity in the degradation of the diazo dye, trypan blue, was reported (84). When the biogenic CdS-NPs were excited by visible light, the electronic energy transfer (EET) of *S. oneidensis* could deliver electrons to photogenerated holes in the valance band and maintain the ongoing photoexcitation to produce photogenerated electrons and catalyze the photoreduction of trypan blue (84). Participation of *S. oneidensis* has been reported in the synthesis of metastable spherical CdS-NPs in a culture medium containing Na_2S and $CdCl_2$ salts as precursors (32). In abiotic controls, dense precipitates of agglomerated CdS minerals were observed, suggesting that the *Shewanella* cells acted as nucleation sites for CdS-NP precipitation and prevented their agglomeration.

The toxicity of CdS-NPs, synthesized in the presence of *S. oneidensis*, against brain cancer cell lines was demonstrated, thereby offering an environmentally benign biosynthesis method for these important NPs (31). However, the CdS-NPs were largely aggregated which may limit their surface area and potential efficiency for biotechnological applications. A possible solution to problems associated with Cd-NP aggregation was investigated using cells of *Shewanella* to catalyze the synthesis of Cd-based NPs immobilized on polymer supports, resulting in stable and well-dispersed NPs (85).

Silver-based nanoparticles. AgS-NPs synthesized in the presence of *S. oneidensis* displayed enhanced toxicity toward both Gram-negative and Gram-positive bacteria compared to chemically synthesized Ag-NPs (86). Biosynthesis was found to proceed most efficiently in the presence of metabolically active cells, and an increase in the initial concentration of $AgNO_3$ and $Na_2S_2O_3$ from 1 mM to 10 mM was reported to improve the final mass of NPs synthesized (87). Nevertheless, the yield with respect to the concentration of Ag in the medium was observed to decline. The *in situ* synthesis of well-dispersed Ag-NPs on carbon nanotubes assisted by *S. oneidensis* bioreduction was demonstrated, with the resulting NPs displaying satisfactory catalytic activity in the degradation of 4-nitrophenol (88). Studies on Ag-based NP biosynthesis using *Shewanella* spp. were also demonstrated by several other researchers (85, 89, 90).

Composite nanoparticles. Recently, the cost-effective and eco-friendly generation of composite NPs (CNPs) consisting of Cu-NPs and carbon nanotubes (CNTs) assisted by *S. oneidensis*, possessing efficient catalytic activity for the conversion of the environmental pollutant, 4-nitrophenol, was demonstrated (91). Highly crystalline Cu-NPs were formed over the exterior of the CNTs with a size range of 4 to 10 nm. A weight ratio of 3% (Cu-NPs/CNTs)

was found to be the optimal loading before higher Cu-NP loadings started to decrease the catalytic activity, potentially due to increasing NP aggregation. The use of *S. oneidensis* as a bioreducing agent leading to *in situ* fabrication of CNPs consisting of Ag_2S-NPs on the surfaces of TiO_2 nanotubes with a potential application in contaminant degradation was also reported (92). Characterization of the Ag_2S-NPs suggested a relatively uniform distribution on the TiO_2 surface with a particle size of $<$8 nm. The composite materials synthesized by *S. oneidensis* displayed excellent catalytic activity toward the reduction of 4-nitrophenol, and again, the molar ratio of the components was important in maximizing the catalytic efficiency (92).

The biological synthesis of Pt and Pd bimetallic NPs by *S. oneidensis* as catalysts for the reduction of environmental pollutants has been investigated by several authors (93–95). The addition of an electron shuttle was found to decrease the size of bimetallic PdPt-NPs synthesized by *S. oneidensis* and resulted in the increased catalytic activity of these smaller bimetallic NPs relative to their larger counterparts and monometallic Pd- or Pt-NPs (94). The PdPt-NPs could be reused for up to six cycles in the reduction of 4-nitrophenol. Differences in X-ray diffraction (XRD) peaks between the bimetallic PdPt-NPs and monometallic NPs of Pd and Pt were used to infer an alloyed structure (94). Localization of the bimetallic NPs could not be determined in this study. However, a similar study imaging thin-section TEM samples suggested that bimetallic PdPt-NPs synthesized by *S. oneidensis* were present both intracellularly and extracellularly (93), potentially pointing to the involvement of both OM cytochromes and periplasmic enzymes (e.g., cytochromes or hydrogenases) in the metal reduction and NP precipitation process.

S. oneidensis has also been used in the synthesis of PdAg-NPs supported on reduced graphene oxide (rGO). Characterization of the nanocomposites suggested that individual Pd- and Ag-NPs were separated by the rGO. The nanocomposites were catalytically active toward the reduction of 4-nitrophenol with the highest efficiency demonstrated for a 1:1 ratio of Pd to Ag (96). Several authors have also reported the biosynthesis of bimetallic PdAu-NPs using *S. oneidensis* for promising applications in environmental remediation and catalysis. The bimetallic NPs delivered more reproducible results with a broader reaction scope as catalysts for Suzuki coupling compared to monometallic Pd-NPs (97, 98). However, these PdAu-NPs were synthesized under an H_2-containing atmosphere which is known to abiotically reduce Pd and thus may offer less control on NP structure than purely enzymatic synthesis routes (97, 98). This is highlighted in a recent study where the enzymatic synthesis of PdAu-NPs by *S. oneidensis*, in the absence of H_2, resulted in bimetallic NPs with a smaller average size and smaller size range than those seen when H_2 is present as a potential electron donor (99). In the same study, the catalytic activity of these PdAu-NPs was compared against PdAg-NPs and monometallic Pd-NPs in Suzuki-Miyaura cross coupling reactions. The catalytic activity of the NPs was found to follow in the order PdAg$>$PdAu$\gg$Pd, demonstrating the potential application of CNPs in key commercial reactions (99).

The complexes of NPs synthesized by a single *Shewanella* species could foster the development of composite NPs with novel characteristics (82, 92). However, the complexity of multicomponent NP synthesis offers both challenges and opportunities for developing such novel materials.

Other nanoparticles. Apart from the above discussed NPs, *Shewanella* is credited to contribute to the synthesis of a suite of metallic NPs, including Cr, Zn, T, Pb, Se, Te, Tc, U, As, and Mn by numerous researchers (Table 1).

FACTORS AFFECTING BIOSYNTHESIS OF NANOPARTICLES

There are several factors that affect the synthesis and properties of NPs, including solution pH, pressure, temperature, time, types of microorganisms, the concentration of the raw materials and extracts, ionic substances, extracellular materials secreted in the medium, carbon source, precursor salts, composition of growth media, microbial growth phase, and presence of other chemical substances employed in microscopic techniques (100–103).

TABLE 1 Application of *Shewanella* to synthesize various nanoparticles[a]

Produced NPs	Organism	Chemical(s) used	Aerobic or anaerobic	Electron donor	NP size (nm)	Significance	Reference(s)
Arsenic-Fe	*Shewanella* spp.	Na_3AsO_4	Anaerobic	Pyruvate			129
As_4S_4 nanotubes	*Shewanella* sp.	As^{5+} and $S_2O_3^{2-}$	Anaerobic	Lactate		Photoactive	130
As_4S_4-rGO	Strain HN-41	As^{5+}, $S_2O_3^{2-}$, GO	Anaerobic	Lactate		Li ion storage	131
Cadmium sulfide	*S. oneidensis*	$CdCl_2 \cdot 2.5H_2O$	Aerobic		5 ± 1		85
Chromium	*S. oneidensis*	K_2CrO_4	Anaerobic	Lactate	nd		132
Chromium	*S. oneidensis*	K_2CrO_4	Anaerobic	Lactate	nd		133
Cr-Te	*S. oneidensis*	$K_2Cr_2O_7$	Anaerobic	Lactate	10−16	Precipitation of Te(IV)	134
Copper	*S. oneidensis*	$CuSO_4$	Anaerobic	Lactate	20−40	Catalysis	47
Copper	*S. loihica*	$CuCl_2 \cdot 2H_2O$	Anaerobic		10−16	Antibacterial activity	64
Copper	*S. oneidensis*	$CuCl_2$	Anaerobic	Lactate	5	Photothermal agent	66
Gold	*S. algae*	$HAuCl_4$	Anaerobic	H_2	10−20	Intracellular recovery of gold	135
Gold	*S. oneidensis*	$HAuCl_4 \cdot 3H_2O$	Anaerobic	H_2	5−10		68
Gold	EPS of *S. oneidensis*	$HAuCl_4$	Aerobic	Formate	1−8		136
Gold	*S. oneidensis*	$HauCl_4 \cdot 3H_2O$	Anaerobic	Lactate	15		71
Gold	*S. oneidensis*	$HauCl_4$	Aerobic		12 ± 5		69
Gold	*S. haliotis*	$HauCl_4 \cdot 3H_2O$	Aerobic	Lactate	10−30	Degradation of *p*-nitrophenol	137
Iron	*S. oneidensis*	Fe(III) oxide	Anaerobic	Lactate	27−31		138
Lead	*S. putrefaciens*	Pb-jarosite	Anaerobic		113.2	Biogeochemical cycling of Pb	139
Palladium	*S. oneidensis*	Na_2PdCl_4	Aerobic	Formate	nd	Dechlorination of PCB	46
Palladium	*S. oneidensis*	Na_2PdCl_4	Anaerobic	Formate	nd	Dechlorination and degradation of PCBs	74
Palladium	*S. oneidensis*	Na_2PdCl_4	Aerobic	Formate	nd	Dechlorination of lindane	140
Palladium	*S. oneidensis*	Na_2PdCl_4	Aerobic	Formate	nd	Dechlorination of trichloroethylene	122
Palladium	*S. oneidensis*	Na_2PdCl_4	Aerobic	Formate	nd	Remediation of trichloroethylene	141
Palladium	*S. oneidensis*	Na_2PdCl_4	Anaerobic	Formic acid	nd	Pd recovery from waste	76
Palladium	*S. oneidensis*	Na_2PdCl_4	Aerobic	Formate	20−100	Reduction of *p*-nitrophenol	142
Pd-Au	*S. oneidensis*	Na_2PdCl_4 + $HauCl_4 \cdot 3H_2O$	Anaerobic		6.88 ± 5.16	Dechlorination of diclofenac, trichlorethylene	97
Pd-cells-rGO	*S. oneidensis*	Na_2PdCl_4	Anaerobic	Formate	6.8 ± 2.9	Electrocatalyst	143
Platinum	*S. algae*	$PtCl_6^{2-}$	Anaerobic	Lactate	5		83
Selenium	*Shewanella* spp.	$Na_2SeO_3 \cdot 5H_2O$	Anaerobic	Lactate	164 ± 24		144
Selenium	*Shewanella* spp.	SeO_3^{2-}	Anaerobic	Lactate	1−20		145
Selenium	*S. putrefaciens*	$Na_2S_eO_3$	Aerobic		nd	Coreduction of Hg and Se	146
Selenium	*S. oneidensis*	SeO_3^{2-}	Anaerobic	Lactate	20−100		147
Silver	*S. oneidensis*	$AgNO_3$	Anaerobic	Lactate	24, 41	Reduction of methylviologen	148
Silver	*S. oneidensis*	$AgNO_3$	Aerobic		4 ± 1.5	Antibacterial activity	149
Silver on carbon nanotubes	*S. oneidensis*	$AgNO_3$	Anaerobic		20	Nitrophenol catalysis	88
Silver	EPS	$AgNO_3$	Anaerobic		5−35		150
Silver	*S. oneidensis*	$AgNO_3$	Anaerobic		20−50		45
Technetium	*S. oneidensis*	$NH_4{}^{99}Tc(VII)O_4$	Anaerobic	H_2 or lactate			151
Tellurium nanorods	*S. oneidensis*	Na_2TeO_3	Anaerobic	Lactate	100−200		152
Tellurium nanorods	*S. oneidensis*	Te(IV)	Anaerobic	Lactate	25−240	Li ion storage material	153, 154
Uranium	*S. oneidensis*	Uranyl acetate	Anaerobic	Lactate	1–5		155
Uranium	*S. oneidensis*	$UO_2Cl_2 \cdot 3H_2O$	Anaerobic	Lactate	3–5		156
Uranium	*S. oneidensis*	Uranyl acetate	Anaerobic	H_2			157
Uranium	*S. putrefaciens*	$UO_2(NO_3)_2 \cdot 6H_2O$	Anaerobic	Lactate	~3		158

(Continued on next page)

TABLE 1 (Continued)

Produced NPs	Organism	Chemical(s) used	Aerobic or anaerobic	Electron donor	NP size (nm)	Significance	Reference(s)
U nanowires	*S. oneidensis*	Uranyl acetate	Anaerobic	Lactate	2−5		159
U nanowires	*S. oneidensis*	Uranyl acetate	Anaerobic	Lactate	1−4		160
Arsenic sulfide nanotube	*Shewanella* spp.	Thiosulfate, As(V)	Anaerobic	Lactate	20–100		130
Iron sulfide	*S. oneidensis*	Thiosulfate, iron citrate	Anaerobic	Lactate	~100		62
Silver sulfide	*S. oneidensis*	$AgNO_3$, $Na_2S_2O_3$	Aerobic		9 ± 3.5		86
Silver sulfide	*S. oneidensis*	$AgNO_3$, $Na_2S_2O_3$	Anaerobic	Lactate	27, 53	Reduction of methylviologen	148
Silver sulfide	*S. oneidensis*	$AgNO_3$ $Na_2S_2O_3$	Aerobic		4−10		87
Zinc sulfide	*S. oneidensis*	$ZnSO_4$	Anaerobic	Lactate	5	Photocatalytic	161
Mn-doped zinc sulfide	*S. oneidensis*	Mn(IV), Na_2S, $ZnSO_4$	Anaerobic	Lactate	2−70		162
Magnetic	*S. algae*, *Shewanella* spp.	Ferrihydrite	Anaerobic	Lactate	6−26	Superparamagnetic magnetite particles	55
Magnetic	*S. piezotolerans*	Ferrihydrite	Anaerobic	Lactate	4−8	Superparamagnetic magnetite particles	163
Pd/Fe_3O_4	*S. oneidensis*	Na_2PdCl_4	Anaerobic	Lactate	5.5 ± 2.2	Reduction of nitroaromatic compounds	95
Au/Fe_3O_4	*S. oneidensis*	$HAuCl_4$	Anaerobic	Lactate	15.4 ± 6.8	Reduction of nitroaromatic compounds	95
PdAu/Fe_3O_4	*S. oneidensis*	Na_2PdCl_4 and $HAuCl_4$	Anaerobic	Lactate	8.3 ± 3.2	Reduction of nitroaromatic compounds	95

[a]EPS, exopolysaccharide; nd, not determined.

One of the most important factors that influence the size and morphology of NPs synthesized by microorganisms is solution chemistry. For example, pH is known to affect the surface properties of *Shewanella*, controlling metal adsorption and reduction kinetics (104–106). Controlling reaction kinetics through careful selection of pH could offer increased control over NP synthesis by *Shewanella*, as has been well documented for chemical synthesis of NPs (107, 108). The effect of pH on the properties and crucially, the catalytic activity, of NPs produced by *Shewanella* spp. should be explored to optimize reactivity and identify the potential for controlling pH to produce bespoke NPs. As highlighted above ("Palladium-based nanoparticles"), the impact of buffer chemistry can influence the kinetics of metal reduction and must be considered when designing and reporting experiments. Buffering capacity should be carefully considered to minimize potential pH changes from microbial metabolism but also to limit any possible abiotic reduction or precipitation that could complicate interpretation of the results. As reported by Dundas et al. (78) aging of the buffer can also influence reduction kinetics, and so freshly prepared buffer solutions should be used (and reported in methods) to limit this effect and simplify comparisons between studies. Detailed studies on the effects of different buffers on metal precursor chemistry and the subsequent impact on microbial reduction and NP synthesis would greatly enhance our understanding of the role of solution chemistry in NP biosynthesis and enable better comparisons between studies. Additional details, such as the metal precursor used, aging of metal or buffer solutions, and the order of metal and biomass addition to solutions may all influence the reduction kinetics and properties of biosynthesized NPs. Indeed, studies on the abiotic synthesis of NPs highlight how such factors can affect metal ion hydrolysis, formation of polymeric or colloidal species, and precipitation which in turn control the properties of the final NP precipitates (109–111). These factors could also be expected to influence the biosynthesis of NPs by *Shewanella* and other microbes but remain largely unexplored. A wide range of studies has shown that temperature changes over even a relatively narrow window can still influence biological NP synthesis (112–114). The temperature has been shown to affect the kinetics of metal reduction by *S. oneidensis* (106), which could in turn affect the properties of resulting NPs. For example, magnetic NPs produced by the psychrotolerant species *S. loihica* were found to vary in size and shape at temperatures ranging from 0 to 37°C (56).

Variations in the synthesis and storage time may result in aggregation or dissolution of any NPs, potentially affecting their properties (115). However, to our knowledge, there have been limited studies on the effect of prolonged storage on the efficacy of NPs synthesized by any microbe, which may have implications for their contribution in a range of commercial applications.

It was reported that the melting point of NPs is reduced with decreasing NP size (116). The particle shape and size play a vital role in determining the properties of NPs. Although it is often controlled by the synthesis conditions, several postsynthesis processes can also impact these characteristics. The choice of methods used in the purification and separation of the synthesized NPs can also influence their properties. In a number of cases, centrifugation is performed for the separation of NPs based on their gravitational force (100). In other cases, chromatography techniques are described to be used (117).

In the case of *Shewanella*-synthesized NPs, careful consideration must be given to the extraction, separation, as well as purification of the desired NPs to minimize alterations that could negatively affect their performance. This may be particularly important for the separation and extraction of intracellularly precipitated NPs. Physiochemical methods to separate NPs from cells include freeze-thawing, heating processes, osmotic shock, ultrasound treatment, centrifugation, and the use of organic solvents or surfactants (118). However, the impact of these different processing methods on the stability, agglomeration, and oxidation of *Shewanella*-synthesized NPs requires further study to ensure that their functional and structural attributes are conserved.

FUTURE PERSPECTIVES AND CONCLUDING REMARKS

This minireview highlights the versatility of *Shewanella* for the biosynthesis of metal-based NPs. However, several challenges remain before *Shewanella*-based NP synthesis routes could

be considered viable sustainable alternatives to more traditional chemical routes. We believe these challenges center on two primary topics: (i) control of NP physiochemical properties and (ii) scale-up of biological NP synthesis.

Despite the many advantages of microbial synthesis of NPs, traditional chemical synthesis still often provides greater control over the properties of the final NP product. However, recent investigations into controlling NP properties via directing the electron transport pathway involved in metal reduction provide an exciting opportunity to produce tailored biosynthesized NPs. Controlling the electron transfer pathway, for example, using cytochrome or hydrogenase deletion mutants, can preferentially precipitate NPs of a desired size in a desired cellular location (78). Recent studies continue to highlight the complex nature of the branching electron transfer pathways of *Shewanella* involved in metal reduction and NP synthesis and occasionally provide conflicting results on the primary enzymes involved. Strain selection may also prove important in controlling NP properties; however, as highlighted in this minireview, there are only limited comparisons that can be made currently between NPs produced by different *Shewanella* strains. This is perhaps primarily due to a focus of the majority of studies on the model species, *S. oneidensis*. In addition, when other *Shewanella* strains have been investigated, a lack of reported detail on the characteristics and properties of the synthesized NPs makes a comparison between these strains difficult. In our view, this is an important aspect to be rectified in future research. We suggest that in addition to simply expanding the range of *Shewanella* strains studied in NP synthesis, a focus on the electron transport pathways involved and greater characterization of NP properties and reactivity should also be applied to identify optimal pathways for bespoke NP production.

Additionally, the issue of scale-up must also be considered if *Shewanella*-directed biosynthesis of NPs is to replace traditional chemical and physical synthesis processes. While *Shewanella* present an attractive method for the production of biogenic NPs due to their versatility as metal reducers and their potential to tune the physiochemical properties of NPs by carefully controlling reaction conditions (pH, electron donor, etc.), balancing this delicate biological process could also present problems for the biosynthesis of NPs at scale. There is little literature exploring whether these carefully controlled biogeochemical conditions required for NP synthesis can be replicated at scale using *Shewanella*, where heterogeneities in bioreactors could reduce the NP yield and lead to increased heterogeneity in the properties of the biosynthesized NPs (119). However, existing studies have demonstrated the potential for scale-up of Fe-NP (magnetite) production using another model metal-reducing bacterium, *Geobacter sulfurreducens* (120). Like *Shewanella*, *Geobacter* species also contain complex electron transport chains capable of reducing a wide range of metals and producing NPs (121). Cells of *Geobacter* were successfully grown in 50-liter bioreactors, and magnetite was produced in a second stage using biomass at 10-ml to 10-liter scales, producing a maximum of 120 g in under 24 h (120). Crucially, the Fe-NPs retained similar physical properties and catalytic activity at both scales. The successful synthesis of NPs at scale using *Geobacter* could be potentially replicated by *Shewanella* but is yet to be tested. As well as their synthesis at scale, assessing their performance or reactivity at scale is also critical if these NPs are to move from benchtop reactions to industrial or commercial applications. Pd-NPs synthesized by *S. oneidensis* have been demonstrated to successfully treat the contaminant, trichloroethylene (TCE), in a pilot-scale membrane reactor. Under the conditions investigated, a continuous flow reactor containing 20 liters of 50 mg liter^{-1} of Pd-NPs, could remove up to 2,515 mg TCE day^{-1} g^{-1} Pd (122). These studies highlight the potential for scaling up the following: (i) growth of bacterial cells, (ii) synthesis of metal NPs at scale, and (iii) application of these biosynthesized NPs in pilot plant reactors. However, only limited studies have been performed, and significant work is required to be done in this area. Such studies would benefit greatly from industrial collaboration so that engineering and logistical challenges can be addressed in the early designs of pilot-scale reactors.

When considering scale-up, the life cycle analysis of NP synthesis and application will also be crucial to assess the economic viability and environmental sustainability of biosynthesized NPs. A promising direction toward sustainability involves the potential for microbial processes, including the use of *Shewanella* spp., to produce valuable NPs

from metals present in waste streams. This offers potential cost savings by revalorizing existing waste streams and utilizing cheap, readily available feedstocks. In addition, the ability to recover and recycle metals from existing waste offers a possible solution to the security of the supply of critical metals required for industry (123). Recent studies have started to explore the sustainable biosynthesis of Fe-NPs (magnetite) using naturally abundant raw materials or waste products to replace analytical-grade or lab-synthesized precursor materials (124, 125). Interestingly, Sadhukhan et al. (124) reported that when using analytical-grade raw materials, the "state-of-the-art" biosynthesis of magnetite has an increased environmental cost relative to industrial magnetite production. However, when biosynthesis was optimized to reduce raw material use, environmental benefits were generated. These potential environmental benefits were even greater when the analytical raw materials were replaced with naturally abundant or waste materials. These environmental benefits, reported as "fossil resource savings" in the study by Sadhukhan et al. (124), may also translate to economic savings through decreased energy and carbon usage. However, direct comparisons exploring the economic viability of *Shewanella* (or other microbially)-synthesized NPs in relation to established synthesis methods are lacking and must be explored. The potential to produce catalytically active Pd-NPs and Pt-NPs from waste streams has been demonstrated using the bacteria, *Escherichia coli* and *Desulfovibrio desulfuricans* (126, 127). Whether the diverse electron transport pathways of *Shewanella* can be harnessed for the sustainable production of functional NPs from waste or natural sources remains to be investigated. Significant challenges in this area could include the following: (i) difficulty in controlling NP properties under harsh conditions in industrial waste streams, (ii) selectivity of metal recovery and NP precipitation in complex waste streams, and (iii) slow reaction kinetics or reduced NP yield relative to synthetic solutions. However, the possibility of utilizing the metabolic diversity of *Shewanella* toward achieving the goal of a sustainable, circular economy for valuable metals offers great potential rewards.

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We have no conflicts of interest to declare.

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