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The complete genome sequence of the archaeal isolate *Halomicrobium* sp. ZPS1 reveals the nitrogen metabolism characteristics under hypersaline conditions

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Abstract

Purpose: As a potential tool for the biodegradation of nitrogen contaminants, including nitrate, nitrite, and ammonium, in pickled foods with high salinity, the halophilic and denitrifying archaeal strain *Halomicrobium* sp. ZPS1 was isolated from edible salt particles.

Methods: Under anaerobic and static culture conditions, *Halomicrobium* sp. ZPS1 could simultaneously degrade nitrate, nitrite, and ammonium in liquid medium with 18% salinity and generate N_2O. To gain insight into these physiological characteristics, the complete genome of *Halomicrobium* sp. ZPS1 was sequenced to reveal the mechanism of nitrogen metabolism associated with salt-tolerance.

Result: The complete genome sequencing revealed a genome size of 3,094,203 bp with a circular chromosome and a GC content of 65.64%. Based on gene annotation, 3191 CDSs, 6 rRNA genes, and 76 tRNA genes were identified. Moreover, 28 genes were annotated as related to salt tolerance, ammonium assimilation, and a truncated denitrification pathway.

Conclusion: The annotated functional genes indicate that *Halomicrobium* sp. ZPS1 could be a candidate strain for the simultaneous removal of nitrate, nitrite, and ammonia in extremely high salt environments.

Keywords: *Halomicrobium* sp., Salt tolerance, Ammonia assimilation, Denitrification

Introduction

Various vegetables, which contain an abundance of nitrate and ammonium resulting from excessive nitrogen fertilization, can be pickled into various table food in China and other Asian countries. The nitrate contained in plant tissues can be reduced to nitrite, which causes anoxia poisoning and cancer (Zhong et al. 2002). Ammonium contained in plant tissues is also harmful to human health (Yusof et al. 2010). Therefore, the removal of excessive nitrate, nitrite, and ammonium is critical for the production of salted vegetables. Spoilage bacteria have been considered to reduce nitrate to nitrite in pickled vegetables, and lactic acid bacteria are considered to be powerful microbial barriers to the degradation of nitrite in pickled vegetables (Oh et al. 2004; Yan et al. 2008). For the removal of ammonium, some bacteria belonging to *Planctomycetes* are considered to completely oxidize ammonium to produce nitrogen through Anammox processes (Jetten et al. 2001). However, the high salinity in salted vegetables inhibits the normal growth and metabolism of these microorganisms (Carr et al. 2002) and limits their capability of removing nitrogen contaminants.

Haloarchaea, a group of halophilic archaea, could thrive in hypersaline environments from 1 M to 5.3 M NaCl (Aharon 2002; Pfeifer 2015), and it is widely

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distributed on edible salt particles (Henriet et al. 2014). It has been reported that some haloarchaea, such as *Haloferax mediterranei* (Cheung et al. 1997), *Haloferax volcanii* and *Haloferax denitrificans* (Torregrosa-Crespo et al. 2019), and *Haloarcula marismortui* (Yoshimatsu et al. 2000), possesses denitrification genes and could perform denitrification or truncated denitrification pathways. Simultaneously, we found that haloarchaea can grow in medium with ammonium as the only nitrogen source (data not shown). Thus, we considered that haloarchaea could be a candidate microorganism for the simultaneous removal of nitrate, nitrite, and ammonia through assimilated and dissimilated nitrogen metabolism in a hypersaline environment. Here, the archaeal strain *Halomicrobium* sp. ZPS1 was isolated from edible salt particles produced in the Zhangpu Salt Field of China and was shown to be capable of degrading nitrate, nitrite, and ammonium under high salinity conditions. We describe the complete genome of *Halomicrobium* sp. ZPS1 to gain insight into the mechanism of nitrogen metabolism in extreme salt environments. The result may improve the theoretical basis and practical applications of haloarchaea in the removal of nitrogen during salted vegetable production, as well as other high salinity environments.

Materials and methods

The removal capability of nitrogen contaminants

Halomicrobium sp. ZPS1 was cultivated in HNM medium for 96 h, and 1 ml of culture was transferred to vials containing modified HNM medium, which contained 18% (w/v) NaCl and $NaNO_3$, $NaNO_2$, and NH_4Cl at a final concentration of 1 mM. The final pH was 7.0. After replacing the air with Ar, the vials were sealed with rubber septa and aluminum cap (Torregrosa-Crespo et al. 2019). During an observation period of 84 h, liquid and gas samples were collected every 12 h to determine the concentrations of nitrate, nitrite, ammonium, N_2O, and N_2. The concentration of nitrate and nitrite was measured by using cadmium column reduction and the *N*-(1-naphthyl)-ethylenediamine dihydrochloride spectrophotometric method (Ozdestan and Uren 2010; Ding et al. 2018). The concentration of ammonium was determined by the phenol-hypochlorous acid method (Ngo et al. 1982). Gas components were detected by gas chromatography with a TCD and ECD detector (SHIMADZU-2014).

Sample preparation and genome DNA extraction

The strain *Halomicrobium* sp. ZPS1 was cultured in NOM liquid medium at 37 °C and enriched to the mid-logarithmic phase. We used the SDS method to extract the genomic DNA of *Halomicrobium* sp. ZPS1 and determined the quality and quantity of the DNA by agarose gel electrophoresis and Qubit 2.0, respectively.

Genome sequencing and assembly

The genome of *Halomicrobium* sp. ZPS1 was sent to Beijing Novogene Bioinformatics Technology Co., Ltd., and sequenced by Pacific Biosciences RS II single-molecule real-time (SMRT) sequencing technology and high throughput Illumina sequencing technology (Mardis 2017; Hebert et al. 2018). We obtained low-quality reads after filtering raw data from the PacBio RS II and Illumina PE150 sequencer, and the reads were filtered by SMRT Link 5.0.1 (https://www.pacb.com/support/software-downloads/) (Ardui et al. 2018; Reiner et al. 2018) to generate contigs.

Analysis of genome composition

We used GeneMarkS4.17 (Besemer et al. 2001) to predict protein-encoding genes, RNAmmer (Lagesen et al. 2007) to predict ribosomal RNA (rRNA) genes, tRNAscan-SE 1.3.1(Lowe and Eddy 1997) to predict transfer RNA (tRNA) genes, and BLAST in the Rfam database to predict small nuclear RNAs (snRNA) (Gardner et al. 2008). The Genomics Islands were predicted through the IslandPath-DIOMB program (Hsiao et al. 2003), and the transposons were predicted through transposon PSI (http://transposonpsi.sourceforge.net/). PHAST (Zhou et al. 2011) was used for prophage prediction, and CRISPRFinder (Grissa et al. 2007) was used for CRISPR identification. The interspersed repetitive sequences were predicted through TRF (Tandem Repeats Finder, Version 4.07b) (Benson 1999).

Genome annotation

Five databases were used to predict gene functions: GO (Gene Ontology) (Ashburner et al. 2000), KEGG (Kyoto Encyclopedia of Genes and Genomes) (Kanehisa et al. 2004; Kanehisa et al. 2006), COG (Clusters of Orthologous Groups) (Galperin et al. 2014), NR (Non-Redundant Protein Database databases) (Li et al. 2002), and CAZy (Carbohydrate-Active enzyme database) (Cantarel et al. 2008). A whole-genome blast search, which had an *E* value of less than 1e−5 and a minimal alignment length percentage larger than 40%, was performed against above the five databases. In addition, we used Mega7.0, and DNAMAN software to analyze sequences of 16S rRNA and enzymes.

The assessment of potential secondary metabolites

To assess the potential secondary metabolites of *Halomicrobium* sp. ZPS1, we used antiSMASH (Medema et al. 2011) to predict the number of biosynthetic gene clusters (BGCs).

Data deposition

The complete genome sequence of *Halomicrobium* sp. ZPS1 has been deposited in GenBank under the accession number CP045142.

Results

Nitrogen metabolism pathway of *Halomicrobium* sp. ZPS1 under high salinity conditions

Under the condition of 18% salt concentration, the degradation rate of NO_3^- in the medium reached 95.1% in 60 h, and the degradation rate of NO_2^- reached 98.3% in 84 h after fluctuating. NH_4^+ continued to decline, and the degradation rate reached 52.2%at 84 h. Gas detection results showed that a large amount of N_2O was generated without N_2 production. These results suggest that the strain *Halomicrobium* sp. ZPS1 has the ability to simultaneously metabolize NO_3^-, NO_2^-, and NH_4^+ to N_2O under high salt and anaerobic conditions (Fig. 1).

General genome features of *Halomicrobium* sp. ZPS1

After filtering the raw data, we obtained clean data and 108,469 reads with 1,028,063,020 nucleotides, and the mean read length was 9477 bp. Then, the raw data were assembled through SMRT Link v5.0.1, generating one contig. We obtained a complete genome sequence of *Halomicrobium* sp. ZPS1, which contained a circular chromosome of 3,094,203 bp in length and a G+C content of 65.64%. Meanwhile, 6 rRNA operons, 76 tRNA genes, 10 genomics islands, 1 CRISPR system, 2 prophages, and 3191 protein-coding genes (CDSs) were identified (Fig. 2 and Table 1). The results of genome annotation showed that 1426 CDSs could be annotated by the KEGG database, 2212 CDSs could be annotated by the COG database, and 1967 CDSs could be annotated by the GO database.

Functional annotation of *Halomicrobium* sp. ZPS1

To identify the gene functions of *Halomicrobium* sp. ZPS1, the genome was functionally annotated with five databases. The GO classification results revealed that the number of genes encoding biological processes is more than those encoding molecular functions and cellular components (Additional file 1: Fig. s1). Based on the analysis of COG, we can classify the 2212 protein-encoding genes into 24 categories. The result indicates that the number of matched protein-coding gene numbers of R (general function prediction only) is much higher than those of other categories, including J (translation, ribosomal structure, and biogenesis), E (amino acid transport and metabolism), K (transcription), and H (coenzyme transport and metabolism) (Fig. 3).

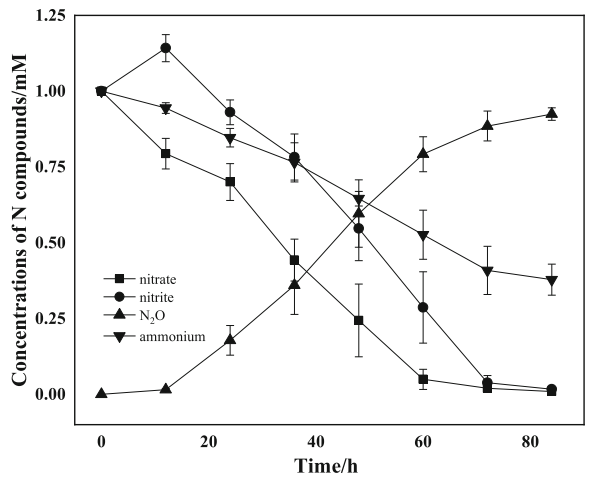

Fig. 1 Degradation of nitrate, nitrite, and ammonium by *Halomicrobium* sp. ZPS1 at NaCl concentration of 18%

The KEGG pathway results show that 813 protein-coding genes are associated with 133 KEGG pathways. Among the 555 protein-coding genes, 7 genes are related to cellular processes, 79 genes are related to environmental information processing, 171 genes are related to genetic information processing, 1 gene is related to human disease, 554 genes are related to metabolism, and 1 gene is related to organismal systems. Most genes are associated with metabolism, and the number of genes related to amino acid metabolism (137), carbohydrate metabolism (110), metabolism with cofactors and vitamins (93), nucleotide metabolism (78), and energy metabolism (58) is more than those of other pathway-related genes (Additional file 1: Fig. s2).

According to the results of BLASTP searches in NR databases, 1161 genes were annotated, and the two 16S rRNA sequences of *Halomicrobium* sp. ZPS1 showed the highest identity with *Halomicrobium mukohataei* (100%) (Additional file 1: Fig. s3).

The mechanism of salt tolerance

In addition, through COG annotation of the complete genome sequence of *Halomicrobium* sp. ZPS1, 13 genes related to Na^+/K^+ transportation were also found, which means that *Halomicrobium* sp. ZPS1 could exist in saline or hypersaline environments through the enrichment of potassium ions and discharge of sodium ions, also called the "salt-in" strategy (Table 2). *Halomicrobium* sp. ZPS1 balanced the osmotic pressure of the medium by accumulating intracellular K^+ to a high concentration through a K^+ transport system and pumping Na^+ through an electrogenic Na^+/H^+ antiporter (Mnh). Moreover, the Na^+/H^+ antiporter also plays an essential role in the homeostasis of intracellular pH (Aharon 1999).

Genes involved in nitrogen metabolism

By comparing the amino acid sequence of *Halomicrobium* sp. ZPS1 with the COG database, we obtained a total of 2213 genes encoding different functional enzymes, and at least 10 reductase genes involved in nitrogen metabolism were obtained, including nitrate reductase-, nitrite reductase-, nitric oxide reductase-, nitrate/nitrite transporter-, nitrous oxide reductase-, glutamate dehydrogenase-, glutamate

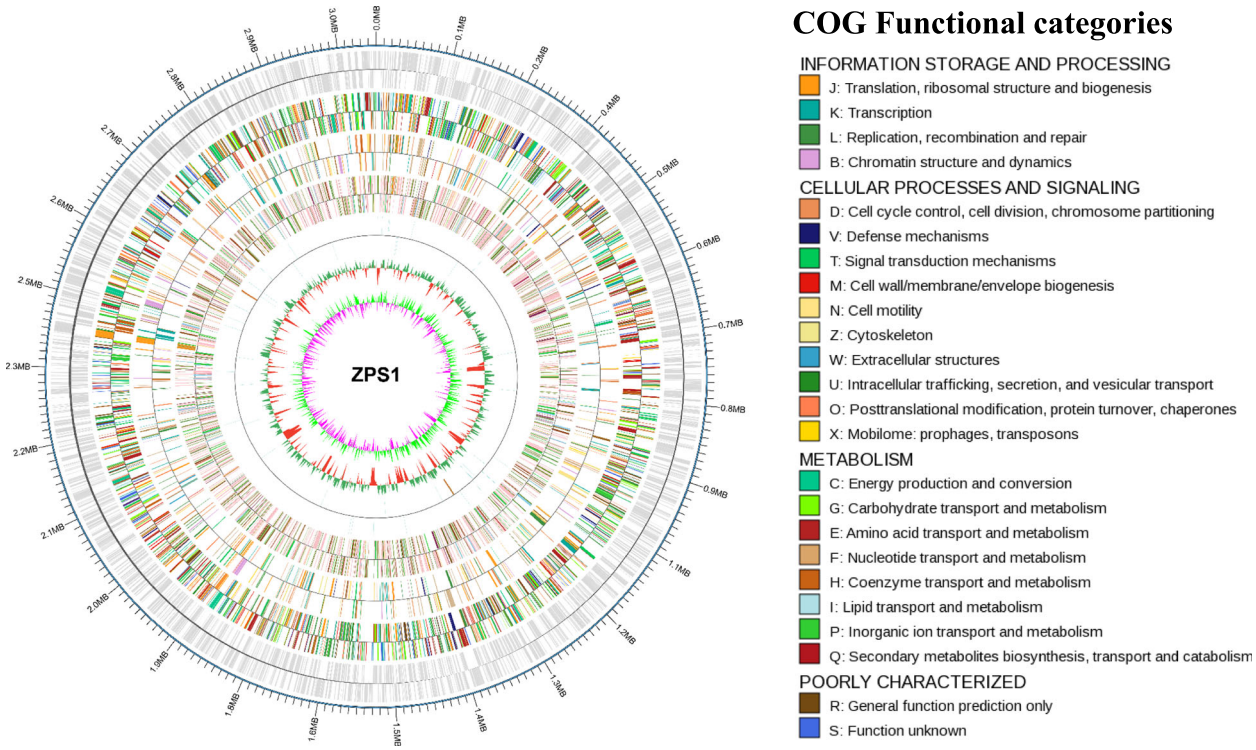

Fig. 2 Genome map of *Halomicrobium* sp. ZPS1. From the outer cycle to the inner cycle, circle 1 indicates the total base pairs and the position coordinates of the genomic sequence; circle 2 shows the coding genes; circles 3, 4, and 5 represent the gene functional annotation results colored according to COG, KEGG, and GO, respectively; circle 6 shows the ncRNAs; circle 7 indicates the genomic GC content; and circle 8 illustrates the genomic GC skew value distribution

Table 1 Overview of genomic features of *Halomicrobium* sp.ZPS1

Attributes	Characteristics
Genome size(Mb)	3.09
GC content(%)	65.64
CDS	3191
tRNA genes	76
rRNA genes	6
snRNA genes	0
Secondary metabolite BGCs	3
Genes assigned to COG	2212
Genes assigned to KEGG	1426
Genes assigned to GO	1967
Genes assigned to CAZy	47
Genes assigned to NR	1165
GenBank accession number	CP045142

synthase-, and ammonia channel protein-encoding genes (Table 2). However, through the comparison with other denitrifiers, we found that the gene encoding the nitrous oxide reductase in *Halomicrobium* sp. ZPS1 was *nosL*, which might be a remnant of a complete operon, and this gene did not transcribe a protein with synthesize nitrous oxide reductase (Lycus et al. 2017). We consider that *Halomicrobium* sp. ZPS1 could perform a truncated denitrification pathway, reducing nitrate or nitrite to nitrous oxide.

Based on the analysis of the KEGG database, the nitrogen metabolism pathways are performed (Fig. 4), and *Halomicrobium* sp. ZPS1 could reduce nitrate or nitrite to nitrous oxide through truncated denitrification under salty environments. Nitrate is first reduced to nitrite by nitrate reductase, then to nitric oxide by nitrite reductase, and finally to nitrous oxide by nitric oxide reductase. In the assimilatory nitrate reduction pathway, nitrite existing in salted vegetables could be transported into the cells through nitrate/nitrite transporters and further reduced to NH_4^+ by assimilatory nitrite reductase.

Discussion

Haloarchaea exist in saline or hypersaline environments where other microorganisms hardly exist, and they could

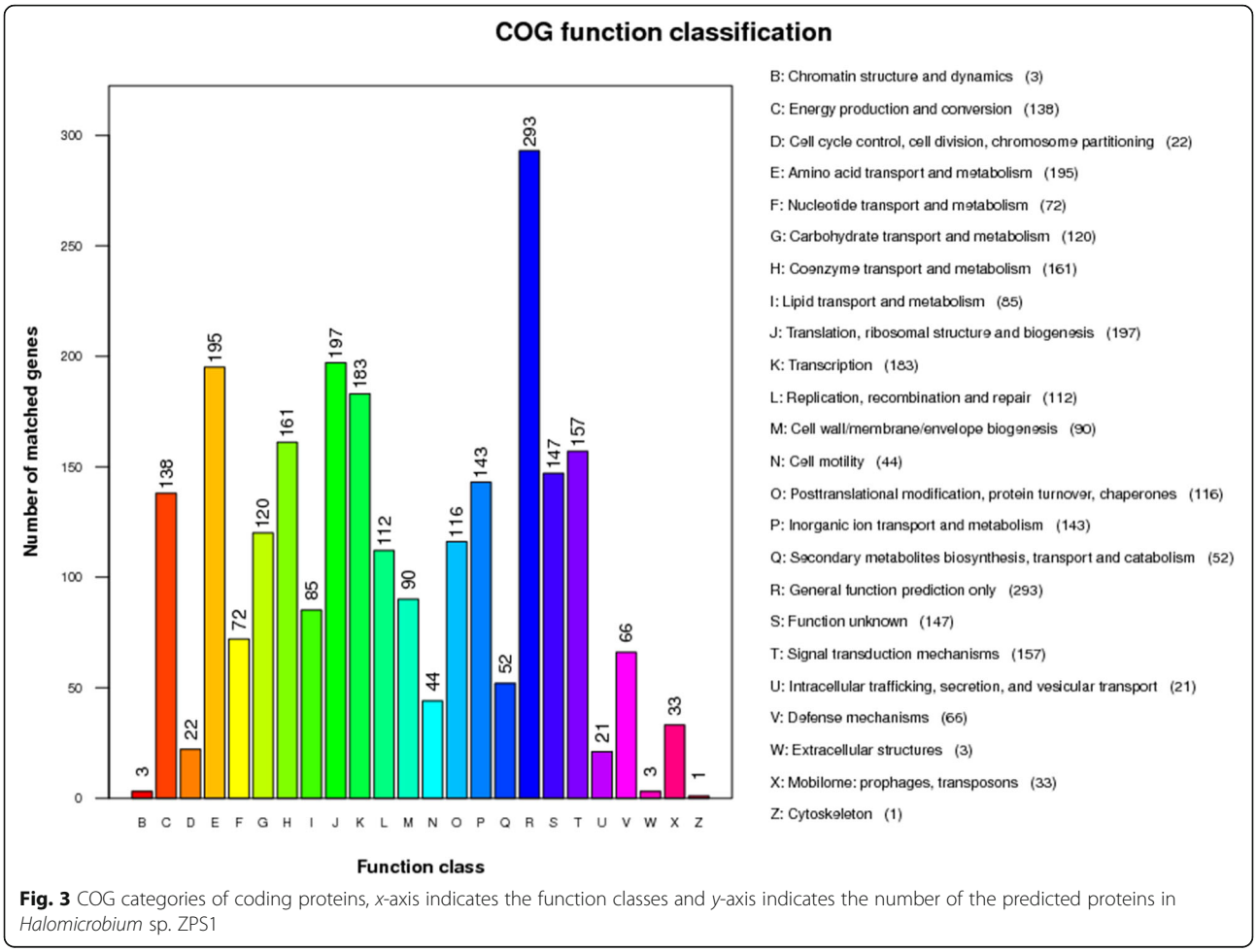

Fig. 3 COG categories of coding proteins, *x*-axis indicates the function classes and *y*-axis indicates the number of the predicted proteins in *Halomicrobium* sp. ZPS1

maintain normal growth and metabolism in these environments. It has been found that the intracellular ionic composition of haloarchaea is different from the outer extracellular environment; the environment contains NaCl as the main salt, while the cytoplasm contains more KCl than outside environment (Aharon 1999). This could be regarded as a salt-in strategy, which is expected to provide the ability to survive in high salt environments. In this study, we annotated genes related to the K^+ transport system and Na^+/H^+ antiporter (Mnh), which indicates that *Halomicrobium* sp. ZPS1 grows in high salinity environments through a "salt-in" strategy, and K^+ existing in the medium is critical for the growth and metabolism of *Halomicrobium* sp. ZPS1.

Under the condition of 18% salt concentration, the growth and metabolism of *Halomicrobium* sp. ZPS1, the concentration of NO_3^-, NO_2^-, and NH_4^+ could be decreased, and N_2O was simultaneously produced; however, no N_2 was produced. Based on these physiological characteristics, we can speculate that the degradation of nitrate and nitrite is attributed to truncated denitrification.

Denitrification in microorganisms is a dissimilatory process in which nitrate or nitrite is reduced to nitrogenous gas (Wei et al. 2015); this process includes four steps, $NO_3^-\rightarrow NO_2^-\rightarrow NO\rightarrow N_2O\rightarrow N_2$ (Verstraete and Focht 1977), and these four steps are catalyzed by four different kinds of enzymes, nitrate reductase (Nar), nitrite reductase (Nir), nitric oxide reductase (Nor), and nitrous oxide reductase (Nos) (Philippot 2002). Through the annotation of the complete genome of *Halomicrobium* sp. ZPS1, the *nar*, *nir*, and *nor* were found but *nos* was not, which means that ZPS1 could perform a truncated denitrification pathway, and nitrate and nitrite could be reduced to nitrous oxide and released to the atmosphere, making salted vegetables free of nitrate or nitrite residues.

Moreover, according to the previous physiological characteristics, we can also speculate that the degradation of ammonium is achieved by ammonium assimilation. Through the annotation of the complete genome of *Halomicrobium* sp. ZPS1, genes related to ammonium assimilation and ammonia transportation, including glutamine synthetase-, glutamate dehydrogenase-, and

Table 2 The denitrification related genes in COG database

	Identity (%)	*E* value	COG gene ID	Functional description	Functional class	Class description
ZPS1 GM001562	100	0.00E+00	YP 003176769	Nitrate reductase gamma subunit	CP	Energy production and conversion Inorganic ion transport and metabolism
ZPS1 GM002221	47.9	1.40E−96	YP 008376898	Nitrate/nitrite transporter NarK	P	Inorganic ion transport and metabolism
ZPS1 GM003113	100	1.00E −223	YP 003178284	Nitrate reductase beta subunit	CP	Energy production and conversion Inorganic ion transport and metabolism
ZPS1 GM003113	100	1.00E −223	YP 003178284	Nitrate reductase beta subunit	CP	Energy production and conversion Inorganic ion transport and metabolism
ZPS1 GM003114	100	0.00E+00	YP 003178285	Nitrate reductase alpha subunit	CP	Energy production and conversion Inorganic ion transport and metabolism
ZPS1 GM000464	45.9	5.20E−07	YP 007284710	Ferredoxin subunit of nitrite reductase or a ring-hydroxylating dioxygenase	PQ	Inorganic ion transport and metabolism Secondary metabolites biosynthesis, transport and catabolism
ZPS1 GM000538	100	9.60E−77	YP 003178896	Ferredoxin subunit of nitrite reductase or a ring-hydroxylating dioxygenase	PQ	Inorganic ion transport and metabolism Secondary metabolites biosynthesis, transport, and catabolism
ZPS1 GM001048	100	7.90E−97	YP 003176228	Ferredoxin subunit of nitrite reductase or a ring-hydroxylating dioxygenase	PQ	Inorganic ion transport and metabolism Secondary metabolites biosynthesis, transport, and catabolism
ZPS1 GM002618	100	0.00E+00	YP 003177800	Nitric oxide reductase large subunit	P	Inorganic ion transport and metabolism
ZPS1 GM001012	100	6.60E −102	YP 003176191	Nitrous oxide reductase accessory protein NosL	P	Inorganic ion transport and metabolism
ZPS1 GM001342	100	2.10E −261	YP 003176547	Glutamine synthetase	E	Amino acid transport and metabolism
ZPS1 GM000568	100	3.10E −235	YP 003178926	Glutamate dehydrogenase/leucine dehydrogenase	E	Amino acid transport and metabolism
ZPS1 GM000588	100	6.00E −239	YP 003178946	Glutamate dehydrogenase/leucine dehydrogenase	E	Amino acid transport and metabolism
ZPS1 GM000589	100	0.00E+00	YP 003178947	Glutamate synthase domain 3	E	Amino acid transport and metabolism
ZPS1 GM001552	100	1.50E −253	YP 003176759	Ammonia channel protein AmtB	P	Inorganic ion transport and metabolism
ZPS1 GM000021	100	2.50E −251	YP 003178383	Na^+-dependent transporter, SNF family	R	General function prediction only
ZPS1 GM000159	99.7	7.80E −187	YP 003178520	ABC-type Na^+ efflux pump, permease component	CP	Energy production and conversion Inorganic ion transport and metabolism
ZPS1 GM000311	100	1.30E −180	YP 003178669	Multisubunit Na^+/H^+ antiporter, MnhE subunit	P	Inorganic ion transport and metabolism
ZPS1 GM000312	100	1.30E−42	YP 003178670	Multisubunit Na^+/H^+ antiporter, MnhF subunit	P	Inorganic ion transport and metabolism
ZPS1 GM000313	100	6.40E−55	YP 003178671	Multisubunit Na^+/H^+ antiporter, MnhG subunit	P	Inorganic ion transport and metabolism
ZPS1 GM000315	100	7.20E−81	YP 003178673	Multisubunit Na^+/H^+ antiporter, MnhB subunit	P	Inorganic ion transport and metabolism
ZPS1 GM000316	99.2	3.50E−59	YP 003178674	Multisubunit Na^+/H^+ antiporter, MnhC subunit	P	Inorganic ion transport and metabolism

Table 2 The denitrification related genes in COG database *(Continued)*

	Identity (%)	*E* value	COG gene ID	Functional description	Functional class	Class description
ZPS1 GM000318	100	0.00E+00	YP 003178676	Formate hydrogenlyase subunit 3/Multisubunit Na^+/H^+ antiporter, MnhD subunit	CP	Energy production and conversion Inorganic ion transport and metabolism
ZPS1 GM000779	100	1.10E −262	YP 003175955	Na^+-dependent transporter, SNF family	R	General function prediction only
ZPS1 GM001320	100	4.10E −279	YP 003176524	Na^+-driven multidrug efflux pump	V	Defense mechanisms
ZPS1 GM003089	100	2.20E −158	YP 003178260	Predicted Na+-dependent transporter	R	General function prediction only
ZPS1 GM001370	100	0.00E+00	YP 003176577	Trk K^+ transport system, NAD-binding component	P	Inorganic ion transport and metabolism
ZPS1 GM002514	99.8	1.10E −293	YP 003177697	Trk-type K^+ transport system, membrane component	P	Inorganic ion transport and metabolism

ammonia channel protein-encoding genes, were also found in the complete genome. This means that ammonia could be transported into the cytoplasm from the periplasm through the ammonia channel protein (amtB) and further assimilated to L-glutamate from L-glutamine (Fig. 4), which could maintain the normal growth of *Halomicrobium* sp. ZPS1. This means that NH_4^+ produced from nitrite or that existed in the vegetables could be involved in carbon metabolism by the glutamine synthetase/glutamate synthase pathway, and maintain the growth of *Halomicrobium* sp. ZPS1 without additional carbon and nitrogen sources, and it makes it possible to eliminate nitrate, nitrite, and ammonia simultaneously.

Oxalic, malate, malonic, erythorbic acid, glutamic acid, and other organic acids are present in radish (Gutiérrez and Perez 2004). Genes involved in the reductive tricarboxylic acid (TCA) cycle were obtained through the KEGG database except 2-oxoglutarate dehydrogenase-encoding genes, which means that malate could act as an electron donor and carbon source for cells, allowing the cells to maintain growth. The energy for *Halomicrobium* sp. ZPS1 to synthesize fumarate and succinate

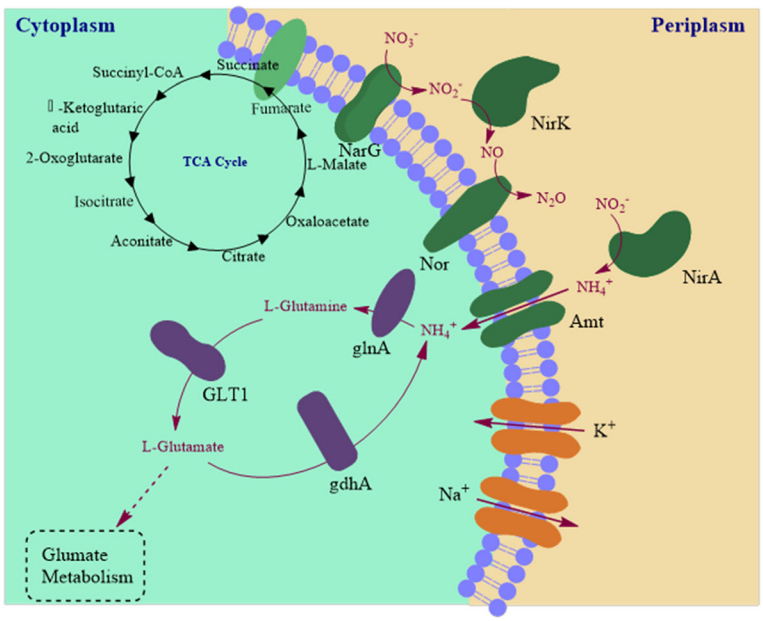

Fig. 4 Genome-based nitrogen metabolism pathways of *Halomicrobium* sp. ZPS1. Nitrate and nitrite could be reduced to nitrous oxide through a truncated denitrification pathway. Ammonium existing in the vegetables or formed by nitrite assimilatory could be transported into the cytochrome and transformed to L-glutamate, formed L-glutamate, which could participate in glutamate metabolism. *Halomicrobium* sp. ZPS1 could perform a reductive TCA cycle, and electrons generated from succinate to fumarate could be transferred to denitrification pathways. NarG, nitrite reductase; NirK, cooper-containing nitrite reductase; Nor, nitric oxide reductase; NirA, ferredoxin-nitrite reductase; Amt, ammonia channel protein; glnA, glutamine synthetase; GLT1, glutamate synthase; gdhA, glutamate dehydrogenase

comes from metabolizing the malate in salted vegetables, and the transformation of fumarate and succinate provides electrons for the truncated denitrification pathway (Fig. 4). Thus, nitrate, nitrite, and ammonium could act as nitrogen resources, and organic acids present in salted vegetables act as carbon resources to provide electrons and energy for cells; therefore, the cells are able to maintain respiration and growth and remove nitrogen contaminants without additional carbon and nitrogen resources.

The safety of haloarchaea applications for food has not been confirmed so far, mainly because it is impossible to simulate the high salt environment in which that haloarchaea inhabit in mice. Edible sea salt and mineral salt contain a large amount of haloarchaea; however, cells could rupture and die due to the osmotic pressure of the normal human body; therefore, it is difficult to find haloarchaea in the human body. If the safety of haloarchaea can be confirmed, they can provide a feasible solution for the complete removal of nitrogen contaminants from high-salt vegetables. *Halomicrobium* sp. ZPS1 could be a potential resource for the elimination of nitrite and nitrate in salted food.

Conclusion

This study reports the complete genome sequence of *Halomicrobium* sp. ZPS1 isolated from a salt mine in China. The phylogeny analysis indicates that ZPS1 is closely related to *Halomicrobium mukohataei*. By assembling and annotating the complete genome, we considered that ZPS1 could grow in a high salinity environment by using a "salt-in" strategy and ammonium assimilation and reduce nitrate into N_2O via a truncated denitrification pathway. The results indicated that *Halomicrobium* sp. ZPS1 might be a candidate strain for the simultaneous removal of nitrate, nitrite, and ammonia in the process of salted vegetable production, as well as in other high salinity environments.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s13213-020-01575-8.

Additional file 1: Figure S1. GO classification of genome function in *Halomicrobium* sp. ZPS1. **Figure S2.** KEGG categories of coding proteins in *Halomicrobium* sp. ZPS1. **Figure S3.** Phylogenetic tree based on 16S rRNA sequences of *Halomicrobium* sp. ZPS1. Bootstrap values greater than 50% are shown. Scale bar represents substitutions per nucleotide.

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Competing interests

The authors declare that they have no competing interests.

Research involving human participants and/or animals

N/A

Informed consent

N/A

Authors' contributions

All the authors designed this study. XyH performed the experiment and drafted the manuscript. XyH, CIZ, KI, KS and LZ analyzed and performed the data. ZzH, YW and QX contributed reagents/materials/analysis tools. The author(s) read and approved the final manuscript.

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