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Isolation and Complete Genome Sequence of a Novel *Pseudoalteromonas* Phage PH357 from the Yangtze River Estuary

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Abstract Phage PH357, a novel lytic *Pseudoalteromonas lipolytica* phage belonging to the Myoviridae family was isolated from the Yangtze River estuary. The microbiological characterization demonstrated that phage PH357 is stable from −20 to 60 °C and the optimal pH 7. The one-step growth curve showed a latent period of 20 min, a rise period of 20 min, and the average burst size was about 85 virions per cell. Complete genome of phage PH357 was determined. Genome of phage PH357 consisted of a linear, double-stranded 136,203 bp DNA molecule with 34.58% G + C content, and 242 putative open reading frames (ORFs) without tRNA. All the predicted ORFs were classified into eight functional groups, including DNA replication, regulation and nucleotide metabolism, transcription, translation, phage packaging, phage structure, lysis, host or phage interactions, and hypothetical protein. A phylogenetic analysis showed that phage PH357 had similarity to the previously published *Pseudoalteromonas* phage PH101 and *Vibrio* phages. Furthermore, the study of phage PH357 genome will provide useful information for further research on the interaction between phages and their hosts.

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Introduction

Viruses are the most abundant biological entities (estimated population of 10^{30}) and encompass a vast genetic diversity in marine ecosystems, and the majority of viruses are bacteriophages [8, 25]. Over the last three decades, viruses, particularly bacteriophages, have received increasing recognition for their importance in marine environments [4]. As a factor of mortality of their hosts, phages can control and regulate the structure of microbial community and play an important role in biogeochemical cycles [7, 8, 32].

The genus *Pseudoalteromonas* is a marine group of bacteria belonging to class *Gammaproteobacteria* [26]. Members of the *Pseudoalteromonas* are motile by a single polar flagellum and have a chemoheterotrophic metabolism [17]. *Pseudoalteromonas* strains are ubiquitous in the ocean including cold environments or other extreme marine habitats, such as deep-sea and polar regions, and many strains have been isolated [21, 26, 27, 31]. *Pseudoalteromonas* strains play an important role in marine ecosystems due to their ability to form marine biofilms and produce large quantities of bioactive compounds with antifouling, antimicrobial, or algicidal activities [3, 20, 34].

Pseudoalteromonas phages represent a significant group of phages in the ocean, which is likely taking a big proportion in the family of unknown phages [7, 12, 29]. And till now, the identified complete genomes of *Pseudoalteromonas* phages rarely occurred in genome dataset. As of March 2017, 22 complete *Pseudoalteromonas* phage

genomes have been submitted to GenBank. Thirteen typical species belong to *Caudovirales*, another one is a corticovirus and the last eight are unclassified viruses.

In this study, *Pseudoalteromonas* phage PH357 was isolated from the Yangtze River estuary of China, and the biological characteristics and complete genome sequence analysis were determined. Present work would provide basic data to further understand the complex phage–host interactions.

Materials and Methods

Location and Sampling

The surface seawater sample was collected from the coastal waters offshore Shanghai City in the Yellow Sea of China at location 32°00′N, 122°32′E on August 22, 2015 (Fig. S1). The seawater sample was stored at 4 °C in the dark before further experiment [26].

Bacterial Strain Isolation and Identification

The host bacterial strain, designated BH357, was isolated from the seawater sample by serial dilution and incubated in liquid Zobell medium at 28 °C [7, 16]. The molecular identification of the bacterial isolate was obtained via 16S rRNA gene sequence analysis [26].

Phage Isolation and Purification

The phage was isolated from the same sample. The seawater sample was filtered through a 0.22-μm Millipore filter to remove the bacteria and phytoplankton, and then plaque assays were performed using the soft-agar overlay method [11]. Phages were purified by picking a single plaque, and suspending the plaque in SM buffer [100 mM NaCl, 8 mM $MgSO_4$, 50 mM Tris HCl (pH 7.5)], incubating for 1 h at 37 °C, titering and plating by the soft-agar overlay method. The purification step was repeated for three times and the purified phages were amplified and stored at 4 °C [7, 16, 26].

Electron Microscopy

The morphology of phages was examined by transmission electron microscopy (TEM). The purified phage particles were negatively stained with phosphotungstic acid (2% w/v, pH 7.2). Stained particles were observed by a JEOL Model JEM-1200EX TEM at 100 kV. Phage dimensions were estimated based on the electron micrographs [16, 26].

Determination of the Multiplicity of Infection (MOI)

The multiplicity of infection (MOI) is the number of virions that are added per cell during infection. MOI was estimated by using the gradient dilution and soft-agar overlay method [11, 26].

Thermal Stability and pH Sensitivity

Thermal control (pH 7.0): the phage suspension was incubated at −20, 4, 20, 40, 50, 60, 70, and 80 °C for 2 h.

pH control: the phage suspension was incubated under a range of pH conditions from 3 to 12 at 37 °C for 2 h.

After treatment, the soft-agar overlay method was used to determine surviving phages at different temperatures or pH [5].

One-Step Growth Curve

For one-step growth curve assay, a modified soft-agar overlay method was used [19]. Briefly, phage suspension and exponential growth phase culture of host bacterium (2×10^8 cfu/ml) were mixed in 1 ml with MOI = 0.1. Phages were allowed to adsorb for 15 min, the mixture was then centrifuged at 13,000 rpm for 30 s. The pellet was resuspended in 5 ml fresh LB to remove the unadsorbed phage. Then sample was taken at 5-min intervals (up to 30 min) and 10-min intervals (up to 90 min), and the phage titer was measured by plaque assays.

Host Range Test

Host range tests were evaluated on a panel of *Pseudoalteromonas* strains, including *Pseudoalteromonas atlantica*, *Pseudoalteromonas marina*, *Pseudoalteromonas shioyasakiensis*, and *Pseudoalteromonas atlantica* by cross infectivity test.

Phage DNA Preparation and Genome Sequencing

Phage DNA extraction was performed by Sangon Biotech Co (Shanghai, China). Purified phage genomic DNA was sequenced using Illumina Miseq 2×300 paired-end sequence by the same company.

Bioinformatic Analysis

After sequencing, raw sequences were processed to remove reads with low quality and adapter. Clean reads were assembled in a single contig using Velvet (Version 1.2.07), and gaps were filled using GapCloser (Version: 1.12) and GapFiller (Version: 1-11) [2]. Sequencing errors were corrected using PrInSeS-G (Version: 1.0.0.beta) [18]. Open

reading frames (ORFs) were predicted using the RAST server (http://rast.nmpdr.org/), and the predicted ORFs sequences were translated using EMBOSS Transeq (Version: 6.5.7). Nucleotide sequence was compared to the NCBI (http://www.ncbi.nlm.nih.gov) reference genomic sequences database using TBLASTX algorithm, and the predicted proteins were compared to the NCBI non-redundant (nr) protein database to predict the functions using BLASTP algorithm [10, 16, 26]. The genome map was performed using the CLC Main Workbench (version 7.7.1).

Phylogenetic analysis with other related phages was carried out by comparing the amino acid sequences of the terminase large subunit (TerL) and phoH using the ClustalW program, and the phylogenetic trees based on the neighbor–joining algorithm were conducted by using the genetic analysis software MEGA (Version 7.0.18) [23].

Nucleotide Sequence Accession Number

The annotated sequence has been submitted to GenBank with Accession Number KX822733.

Results

Host Bacterial Strain Identity

16S rRNA gene sequence of the host bacterial strain BH357 had similarity of 99.71% to the type strain *Pseudoalteromonas* LMEB 39 (T) (Accession Number FJ404721).

Isolation and Morphology of Phage PH357

Phage PH357 was isolated from the seawater sample after three single-plaque purifications. Plaques of phage PH357 were about 1.6 mm in diameter and contained a 3–6 mm aureola zone on the top agar (Fig. 1a). TEM analysis showed that phage PH357 was classified into the *Myoviridae*, consisting of an icosahedral head (106 ± 3 nm of diameter) and a contractile tail (123 ± 2 nm in length and 24 ± 1 nm in width) (Fig. 1b).

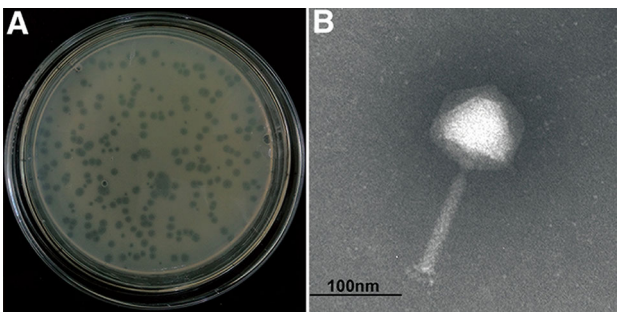

Fig. 1 Isolated *Pseudoalteromonas* phage PH357. **a** Plaques of *Pseudoalteromonas* phage PH357 on *Pseudoalteromonas* BH357. **b** Electron micrographs of *Pseudoalteromonas* phage PH357, magnification at ×200,000. *Bar* represent 100 nm

Optimal MOI

The determination of phage PH357 (Table 1) showed that the optimal MOI of the phage PH357 is 0.1 (MOI = 0.1).

Thermal Stability and pH Sensitivity

The thermal stability test was determined at different temperatures from −20 to 80 °C (Fig. 2), and the pH sensitivity test was investigated under different pH from 3 to 12 (Fig. 3). The curve showed that the biological activity of phage PH357 was relatively stable from −20 to 60 °C, but decreased sharply with increasing temperature at above 60 °C. The pH sensitivity curve showed that the phage PH357 was stable over a board tolerant range of pH from 5 to 10, and the optimal pH was 7. The phage titer decreased sharply when it was acidic (pH 4) or basic (pH 11).

One-Step Growth Curve

The one-step growth curve showed that the phage PH357 had a latent period of 20 min and a rise period of 20 min. The average burst size of the phage PH357 was 85 pfu/cell (burst size is the number of phages produced/infected bacterium) (Fig. 4).

Host Range

Host range tests showed that the phage PH357 could not infect any other *Pseudoalteromonas* strains tested in the cross infection studies.

Genome Analysis of Phage PH357

The genome of phage PH357 was found to consist of a linear, double-stranded 136,203 bp DNA molecule, with a G + C content of 34.58%. A total of 242 ORFs (113 in the positive strand and 129 in the negative strand) were predicted in the phage genome without tRNA. For the predicted ORFs, the average length was 487 bp, the min length was 114 bp, and the max length was 3489 bp. The combined length of all ORFs was 117,312 bp and the coding ratio was 86.13%. 205 (84.71%) ORFs had an ATG start codon, 23 (9.50%) ORFs had a TTG start codon, and 14 (5.76%) ORFs carried a GTG start codon.

BLASTP analysis of the complete genome sequence showed that 98 (40.50%) putative proteins exhibited significant similarity to the viral proteins (*e*-value $<10^{-5}$) in

Table 1 Optimum MOI of phage PH357

No.	Bacterial titer (cfu/ml)	Phage titer (pfu/ml)	MOI	Phage titer (pfu/ml)
1	1×10^8	1×10^{10}	100	3.65×10^9
2	1×10^8	1×10^9	10	4.15×10^9
3	1×10^8	1×10^8	1	1.09×10^{10}
4	1×10^8	1×10^7	0.1	1.32×10^{10}
5	1×10^8	1×10^6	0.01	1.27×10^{10}
6	1×10^8	1×10^5	0.001	1.23×10^{10}

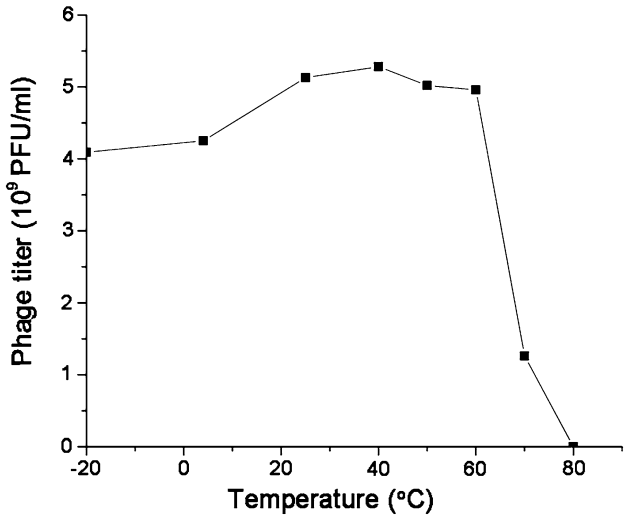

Fig. 2 Temperature stability of *Pseudoalteromonas* phage PH357

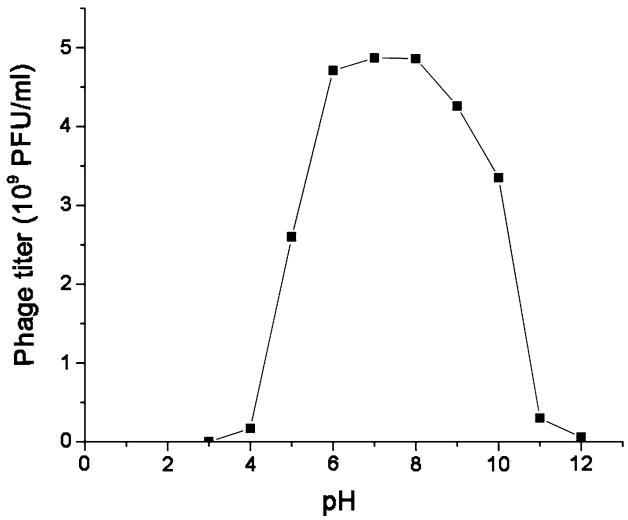

Fig. 3 pH sensitivity of *Pseudoalteromonas* phage PH357

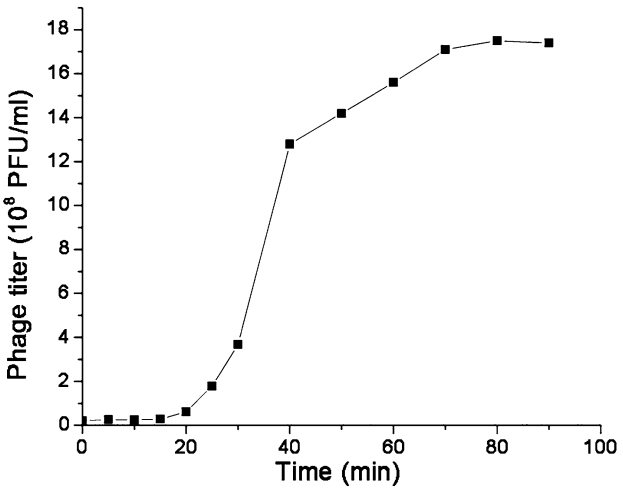

Fig. 4 One-step growth curve of *Pseudoalteromonas* phage PH357

the non-redundant protein sequences database. The remaining 144 (59.50%) hits were not found matched any viral proteins (*e*-value $>10^{-5}$), indicating that putative proteins were new viral proteins.

Among the total 242 ORFs, 29 (11.98%) ORFs could be assigned a putative functional annotation (*e*-value $<10^{-5}$), and the remaining 213 (88.02%) ORFs were supposed to hypothetical proteins. The functions of these unknown ORFs could possibly be deduced from their position in the genome. All the predicted ORFs were then classified into eight functional groups, including DNA replication, regulation and nucleotide metabolism, transcription, translation, phage packaging, phage structure, host lysis, host or phage interactions, and hypothetical protein (Fig. 5). Further conserved protein domain analysis of predicted ORFs showed that 15 conserved domains were detected. The functional groups and conserved protein domain results of phage PH357 are listed in Table S1.

Top ten phages with best match common ORFs with phage PH357 are listed in Table 2. Thirty-five ORFs of phage PH357 had the highest similarity to predicted ORFs from the *Pseudoalteromonas* phage PH101 and 10 ORFs were most similar to predicted ORFs from the *Vibrio* phage qdvp001. Similarity analysis showed that *Pseudoalteromonas* phage PH357 was closely related to *Pseudoalteromonas* phage PH101 (50.3% identity) and *Vibrio* phage qdvp001 (48.7% identity).

To investigate the phylogeny of phage PH357, phylogenetic trees based on the terminase large subunit (TerL) and phoH of selected bacteriophages were constructed by using neighbor-joining analysis (Fig. 6). Phylogenetic tree based on the TerL showed that phage PH357 had no

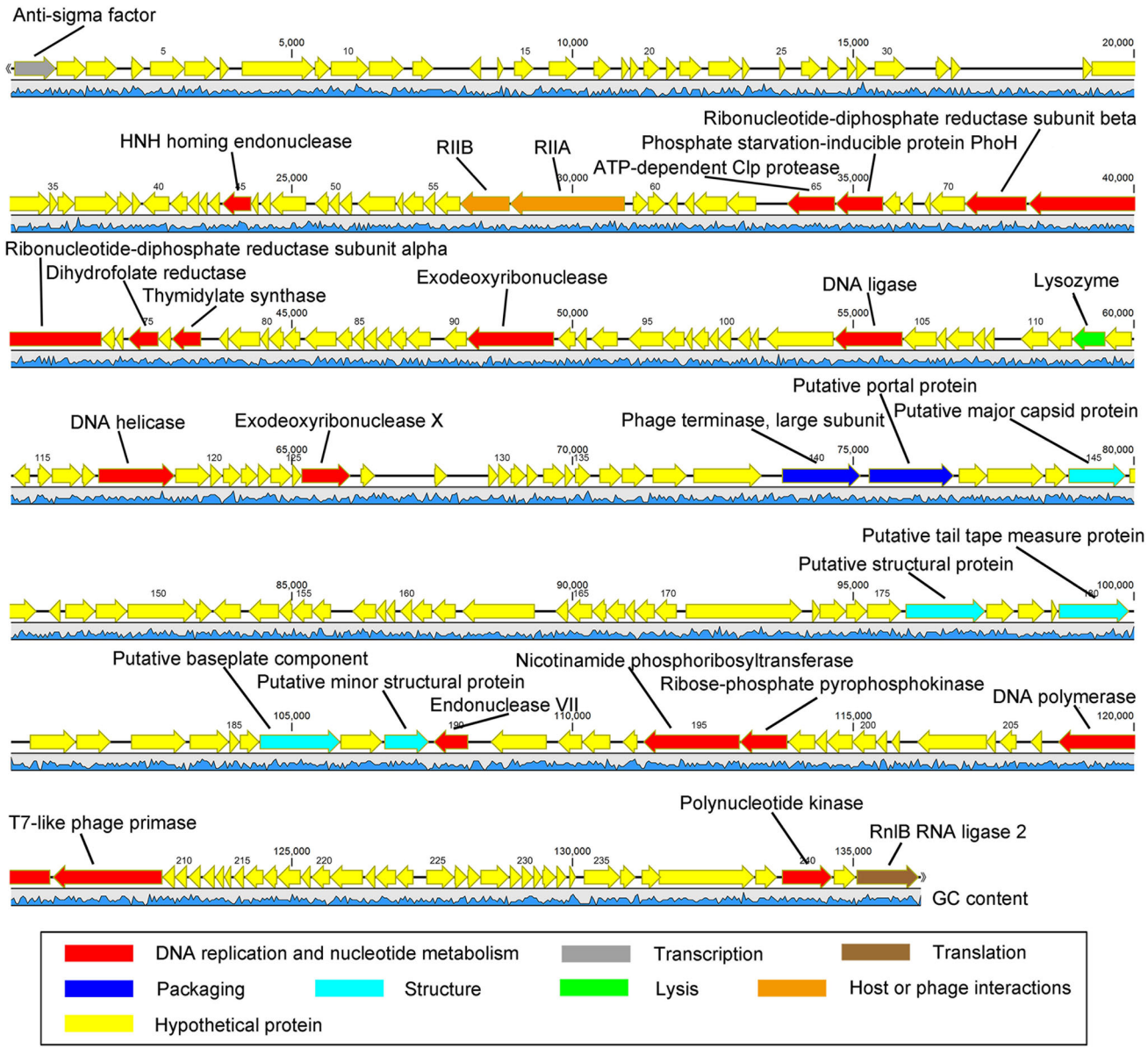

Fig. 5 Annotated genome map of *Pseudoalteromonas* phage PH357. The genome map was performed using the CLC Main Workbench (version 7.7.1). *Arrows* represent predicted ORFs, the *blue line* below the *arrows* indicates the GC content. The color code for gene function is provided in the *bottom* of the figure

obvious similarity to the previously published *Pseudoalteromonas* phages, but it was related to the previously published *Vibrio* phages. However, phylogenetic tree based on the phoH showed that phage PH357 had similarity to the previously published *Pseudoalteromonas* phage PH101 and any *Vibrio* phages.

Discussion

In this study, a novel bacteriophage belonging to the Myoviridae family, PH357, specifically infecting *Pseudoalteromonas lipolytica* was isolated and characterized. The phage PH357 genome adds a new *Myoviridae* genome for marine bacteriophages.

The bioinformatic analysis and gene function analysis extend the knowledge about phages. The DNA replication, regulation, and nucleotide metabolism module of phage PH357 contain at least 17 genes. Most lytic phages have their own replication systems and replication-related enzymes [15]. Among the enzymes directly involved in DNA replication, ORF104 encodes a DNA ligase containing Adenylation_kDNA_ligase_like domain (cd07896), shows homology to DNA ligase in *Shewanella* sp. phage 1/4 (YP_009100328.1) [24]. ORF118 encodes a DNA helicase containing a PIF1 domain (pfam05970), shows

Table 2 Top 10 phages with best match common ORFs with phage PH101 by BLASTP (*e*-value $<10^{-5}$)

Phage name	Phage family	Genome length (bp)	GenBank accession number	Common ORFs with PH357
Pseudoalteromonas phage H101	Myoviridae	131903	NC_029094	35
Vibrio phage qdvp001	Unclassified	134742	NC_029057	10
Vibrio phage 11895-B1	Myoviridae	126434	NC_020843	8
Shewanella sp. phage 1/4	Myoviridae	133824	NC_025436	5
Vibrio phage helene 12B3	Unclassified	135982	NC_021067	4
Shewanella sp. phage 1/40	Myoviridae	139004	NC_025470	4
Vibrio phage PWH3a-P1	Unclassified	129155	NC_020863	3
Vibrio phage ValKK3	Unclassified	248088	NC_028829	2
Vibrio phage ICP1	Myoviridae	125956	NC_015157	2
Aeromonas phage 65	Myoviridae	235229	NC_015251	2

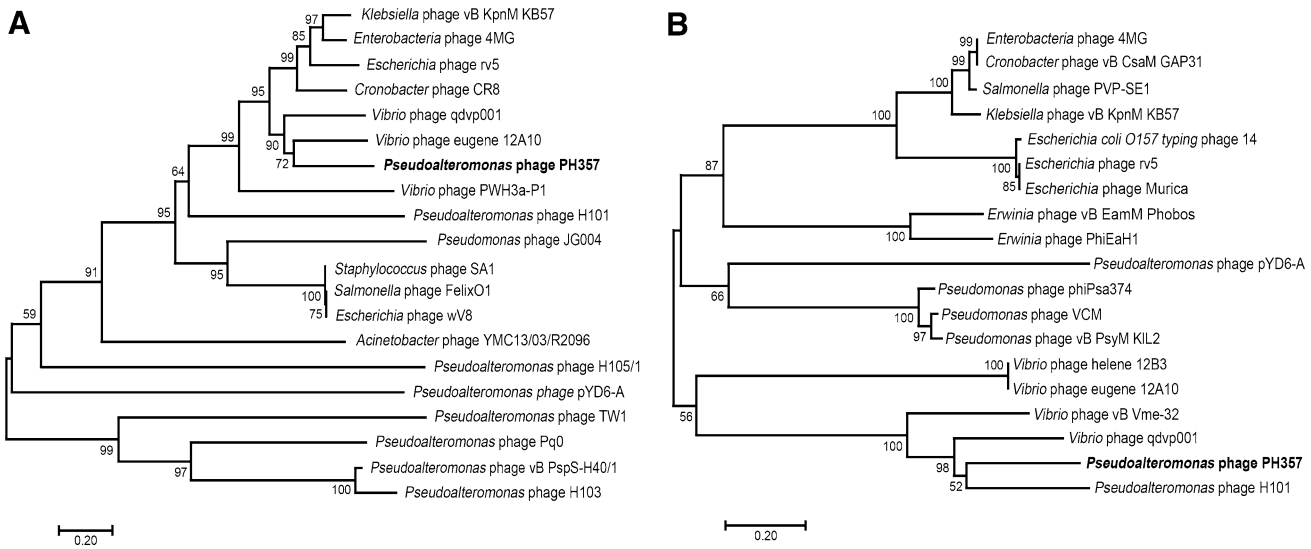

Fig. 6 **a** Phylogenetic tree of various phages having terminase large subunit (TerL). *Pseudoalteromonas* phage PH357 showed highly related to *Vibrio* phages. **b** Phylogenetic tree of various phages having phoH. *Pseudoalteromonas* phage PH357 showed highly related to *Pseudoalteromonas* phage PH101 and any *Vibrio* phages. The *numbers* at the nodes represent the bootstrap probabilities

homology to putative helicase in *Vibrio* phage qdvp001 (YP_009222121.1) [28]. ORF207 encodes a DNA polymerase with a length of 682 amino acids, shows 62% identity with DNA polymerase in *Vibrio* phage qdvp001 (YP_009222199.1) [28]. The T7-like phage primase encoded by ORF208 containing C-terminal GP4d_helicase domain (cd01122) shows similarity to DNA primase in *Vibrio* phage qdvp001 (YP_009222201.1) [28].

The enzymes related to regulation and nucleotide metabolism are HNH homing endonuclease (ORF45), ATP-dependent Clp protease (ORF65), phoH (ORF66), ribonucleotide-diphosphate reductase subunits (beta, ORF71; alpha, ORF72), dihydrofolate reductase (ORF75), exodeoxyribonuclease (ORF91 and ORF126), thymidylate synthase (ORF77), endonuclease VII (ORF190), nicotinamide phosphoribosyltransferase (ORF195), ribose-phosphate pyrophosphokinase (ORF196), and polynucleotide kinase (ORF240). PhoH encoded by ORF66, a protein involved in phosphate metabolism and has been recently developed as a novel marker gene [9]. The ribonucleotide-diphosphate reductase subunit beta encoded by ORF71 containing nrdB domain (PRK09101) shows no similarity to any viral proteins of the database, but its closest homolog in ribonucleotide-diphosphate reductase subunit beta of *Pseudoalteromonas*. The host bacterial strain of phage PH357 belongs to *Pseudoalteromonas*, and that shows phages acting as genetic reservoirs can ensure their reproduction, thus facilitating lateral gene transfer [33].

The phage packaging module of phage PH357 is composed of the large terminase subunit (ORF140) and a portal protein (ORF141), as found in the majority of packaging

modules in phage genomes studied previously [1, 33]. ORF140 encodes large terminase subunit containing a COG5362 domain (COG5362) and shows homology to phage large terminase subunit in *Vibrio* phage eugene 12A10 (YP_009222880.1). The classical terminase consists of a large and a small subunit and involved in DNA translocation inside the capsid, but no small terminase subunit was detected in the phage PH357 genome. This result suggests that the hypothetical protein downstream from ORF140 may play a role as the small terminase subunit [33]. Putative portal protein encoded by ORF141 with a length of 505 amino acids shows 57% identity with portal protein in *Shewanella* sp. phage 1/4 (YP_009100417.1) [24]. The portal protein is a key functional component of the capsid for DNA packaging and genome encapsidation [22]. Additionally, this protein serves as the entrance and exit tunnel for double-stranded DNA and the attachment site for the tail [16, 22].

The packaging module of phage PH357 is followed by the structure module, which including major capsid protein (MCP, ORF145), putative structural protein (ORF176), tail tape measure protein (TMP, ORF180), putative baseplate component (ORF187), and putative minor structural protein (ORF189). Most of the structural proteins (ORF176, ORF180, ORF187, and ORF189) were found to share high similarity with structural proteins from *Pseudoalteromonas* phage PH101 (NC_029094) [26], except for major capsid protein (ORF145), which shows 57% identity with major capsid protein in *Shewanella* sp. phage 1/4 (YP_009100422.1) [24]. TMP is the only one viral tail protein detected in the genome, it plays an important role in phage tails assembling, and is involved in tail-length determination [14, 30].

In many phages, lysis module exists in the genome with the holing gene preceding that of the lysozyme [13]. In phage PH357, lysozyme encoded by ORF112 containing bacteriophage_T4-like_lysozyme domain (cd00735) shows similarity to lysozyme in *Colwellia* phage 9A (YP_006489228.1) [6] but no homolog to a holin was detected. In addition, the hypothetical protein (ORF228) containing LT_GEWL domain (cd00254) which was discovered in many lysozymes shows 46% identity with putative protein in *Pseudoalteromonas* phage PH101 (YP_009225489.1) [26]. It suggests that this hypothetical protein may be a new lysozyme of phages and shows homology of *Pseudoalteromonas* phage PH357 and PH101.

In conclusion, the characterization and genome analysis of PH357 were performed. The phage genome sequence data will provide useful basic information for further research on the interaction between phages and their hosts.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest regarding this study.

Ethical Approval This article does not contain any studies with human participants or animals performed by any of the authors.

References

1. Bai Q, Zhang W, Yang Y, Tang F, Nguyen X, Liu G, Lu C (2013) Characterization and genome sequencing of a novel bacteriophage infecting *streptococcus agalactiae* with high similarity to a phage from s*treptococcus pyogenes*. Adv Virol 158(8): 1733–1741
2. Boetzer M, Pirovano W (2012) Toward almost closed genomes with GapFiller. Genom Biol 13:R56
3. Bowman JP (2007) Bioactive compound synthetic capacity and ecological significance of marine bacterial genus *Pseudoalteromonas*. Mar Drugs 5(4):220–241
4. Cai L, Zhang R, He Y, Feng X, Jiao N (2016) Metagenomic analysis of Virioplankton of the subtropical Jiulong river estuary, China. Viruses 8(2):35
5. Capra ML, Quiberoni A, Reinheimer JA (2004) Thermal and chemical resistance of *Lactobacillus casei* and *Lactobacillus paracasei* bacteriophages. Lett Appl Microbiol 38(6):499–504
6. Colangelo-Lillis JR, Deming JW (2013) Genomic analysis of cold-active *Colwelliaphage*, 9A and *psychrophilic* phage–host interactions. Extremophiles 17(1):99–114
7. Duhaime MB, Wichels A, Waldmann J, Teeling H, Glöckner FO (2011) Ecogenomics and genome landscapes of marine *Pseudoalteromonas* phage H105/1. ISME J 5(1):107–121
8. Fuhrman JA (1999) Marine viruses and their biogeochemical and ecological effects. Nature 399(6736):541–548
9. Goldsmith DB, Crosti G, Dwivedi B, Dwivedi B, McDaniel LD, Varsani A, Suttle CA, Weinbauer MG, Sandaa RA, Breitbart M (2011) Development of phoH as a novel signature gene for assessing marine phage diversity. Appl Environ Microbiol 77(21):7730–7739
10. Huang GT, Le S, Peng YZ, Zhao Y, Yin SP, Zhang L, Yao X, Tan Y, Li M, Hu FQ (2013) Characterization and genome sequencing of phage Abp1, a new phiKMV-like virus infecting multidrug-resistant *Acinetobacter baumannii*. Curr Microbiol 66:535–543
11. Hyman P, Abedon ST (2010) Bacteriophage host range and bacterial resistance. Adv Appl Microbiol 70:217–248
12. Kallies R, Kiesel B, Schmidt M, Kacza J, Ghanem N, Narr A, Zopfi J, Wick LY, Hackermüller J, Harms H, Chatzinotas A (2017) Complete genome sequence of *Pseudoalteromonas* phage vB_PspS-H40/1 (formerly H40/1) that infects *Pseudoal-*

teromonas sp. strain H40 and is used as biological tracer in hydrological transport studies. Stand Genom Sci 12(1):20
13. Kropinski AM, Waddell T, Meng J, Franklin K, Ackermann HW, Ahmed R, Mazzocco A, Yates J, Lingohr EJ, Johnson RP (2013) The host-range, genomics and proteomics of *Escherichia coli*, O157:H7 bacteriophage rV5. Virol J 10(1):1–12
14. Li E, Xiao W, Ma Y, Zhe Y, Li H, Lin W, Wang X, Li C, Shen Z, Zhao R, Yang H, Jiang A, Yang W, Yuan J, Zhao X (2016) Isolation and characterization of a bacteriophage phieap-2 infecting multidrug resistant e*nterobacter aerogenes*. Sci Rep 6:28338
15. Li P, Chen BB, Song Z, Song Y, Yang Y, Ma P, Wang H, Ying J, Ren P, Yang Y, Gao G, Jin S, Bao Q, Yang H (2012) Bioinformatic analysis of the *Acinetobacter baumannii* phage AB1 genome. Gene 507(2):125–134
16. Li Y, Wang M, Liu Q, Song X, Wang D, Ma Y, Jiang Y (2016) Complete genomic sequence of bacteriophage H188: a novel *Vibrio kanaloae* phage isolated from yellow sea. Curr Microbiol 72(5):628–633
17. Liu SB, Chen XL, He HL, Zhang XY, Xie BB, Yu Y, Zhang YZ (2013) Structure and ecological roles of a novel *exopolysaccharide* from the Arctic sea ice bacterium *Pseudoalteromonas* sp. strain SM20310. Appl Environ Microbiol 79(1):224–230
18. Massouras A, Hens K, Gubelmann C, Uplekar S, Decouttere F, Rougemont J, Cole ST, Deplancke B (2010) Primer-initiated sequence synthesis to detect and assemble structural variants. Nat Methods 7:6–485
19. Middelboe M, Chan A, Bertelsen SK (2010) Isolation and life-cycle characterization of lytic viruses infecting *heterotrophic* bacteria and *cyanobacteria*. Man Aquat Viral Ecol 13:118–133
20. Poli A, Anzelmo G, Nicolaus B (2010) Bacterial *exopolysaccharides* from extreme marine habitats: production, characterization and biological activities. Mar Drugs 8(6):1779–1802
21. Qin QL, Li Y, Zhang YJ, Zhou ZM, Zhang WX, Chen XL, Zhang YZ (2011) Comparative genomics reveals a deep-sea sediment-adapted life style of *Pseudoalteromonas* sp. SM9913. ISME J 5(2):274–284
22. Rao VB, Feiss M (2008) The bacteriophage DNA packaging motor. Annu Rev Genet 42:647–681
23. Saitou N, Nei M (1987) The neighbor–joining method: a new method for reconstructing phylogenetic trees. Mol Biol Evol 4:406–425
24. Senčilo A, Luhtanen AM, Saarijärvi M, Bamford DH, Roine E (2015) Cold-active bacteriophages from the baltic sea ice have diverse genomes and virus–host interactions. Environ Microbiol 17(10):392–400
25. Suttle CA (2005) Viruses in the sea. Nature 437(7057):356–361
26. Wang DB, Sun MQ, Shao HB, Li Y, Meng X, Liu ZY, Wang M (2015) Characterization and genome sequencing of a novel bacteriophage PH101 infecting *Pseudoalteromonas marina* BH101 from the yellow sea of China. Curr Microbiol 71(5):594–600
27. Wang P, Yu Z, Li B, Cai X, Zeng Z, Chen X, Wang X (2015) Development of an efficient conjugation-based genetic manipulation system for *Pseudoalteromonas*. Microb Cell Fact 14(1):1
28. Wang W, Li M, Lin H, Wang J, Mao X (2016) The *Vibrio parahaemolyticus*-infecting bacteriophage qdvp001: genome sequence and endolysin with a modular structure. Adv Virol 161(10):2645–2652
29. Wichels A, Biel SS, Gelderblom HR, Brinkhoff T, Muyzer G, Schütt C (1998) Bacteriophage diversity in the North Sea. Appl Environ Microbiol 64(11):4128–4133
30. Xu J, Hendrix RW, Duda RL (2004) Conserved translational frameshift in dsDNA bacteriophage tail assembly genes. Mol Cell 16:11–21
31. Xu XW, Wu YH, Wang CS, Gao XH, Wang XG, Wu M (2010) *Pseudoalteromonas lipolytica* sp. nov., isolated from the Yangtze River estuary. Int J Syst Evol Microbiol 60(9):2176–2181
32. Yu ZC, Chen XL, Shen QT, Zhao DL, Tang BL, Su HN, Wu ZY, Qin QL, Xie BB, Zhang XY, Yu Y (2015) *Filamentous* phages prevalent in *Pseudoalteromonas* spp. confer properties advantageous to host survival in Arctic sea ice. ISME J 9(4):871–881
33. Yuan L, Cui Z, Wang Y, Guo X, Zhao Y (2014) Complete genome sequence of virulent bacteriophage shou24, which infects foodborne pathogenic *vibrio parahaemolyticus*. Adv Virol 159(11):3089–3093
34. Zeng Z, Guo XP, Li B, Wang P, Cai X, Tian X, Wang X (2015) Characterization of self-generated variants in *Pseudoalteromonas lipolytica* biofilm with increased antifouling activities. Appl Microbiol Biotechnol 99(23):10127–10139