

Figure 19: Agarose gel (0.8%) showing the restriction digest analysis of recombinant pJet vectors containing phage SHPA DNA fragment inserts between 0.5 and 1.7 kb in length. (A) Lane M, Lambda DNA cut with *Pst*I marker ; Lane 1-19, plasmids cut with *Bgl*II. (B) Lane M, Lambda DNA cut with *Pst*I marker; Lane 20-23, plasmid digested with *Bgl*II restriction enzyme.

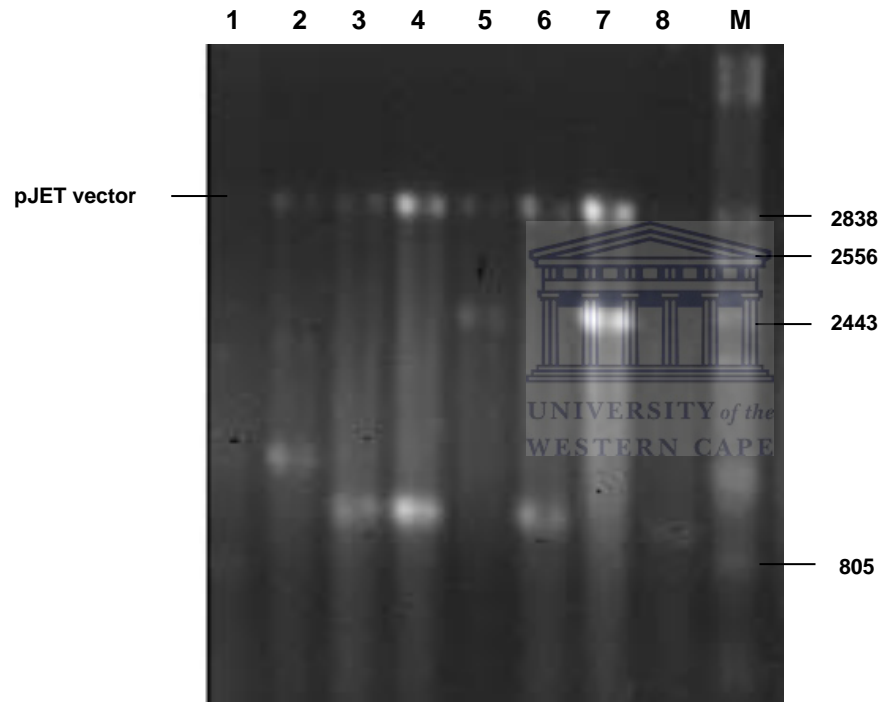


Figure 20: 0.8% agarose gel showing the restriction digest analysis of phage SHPA DNA cloned into the pJet vector. Insert sizes of between 0.8-2.4 kb in length. Lane 1-8, plasmid digested with *Bgl*II restriction enzyme; Lane M, Lambda DNA cut with *Pst*I marker.

3.10. Phage DNA sequence analysis

Sequence analysis indicated that only phage-related proteins were identified. The sequence homologies of the cloned inserts showing the highest sequence hits and phage-related proteins are shown in Table 13. The graphic representations showing the positions of ORFs of phage SHPA sequences are shown in Figure 21 & 22. Sequence homologies of the phage sequences showed that phage SHPA DNA contains both bacterial and phage genes. Lysozyme (on the reverse strand) from *Brevundimonas diminuta* and *Pseudomonas* phage phi15 (*Podoviridae*) was found in clone 1. Lysozyme helps to release mature phage from bacterial cells by breaking down the peptidoglycan layer of the bacterial cell (Santamaria, R.I., Bustos, P., unpublished data). Clone 2 contained three open reading frames (ORFs) (Figure 21), running on the reverse sequence. Two code for a hypothetical protein PaTRP_19434 and a helicase domain-containing protein, both from *Paracoccus* sp. TRP, another codes for a hypothetical protein RAZWK3B_15493 from *Roseobacter* sp. AzwK-3b. Helicases are proteins that play a role in many cellular processes involved in nucleic acid strand separation. These include DNA replication, DNA repair, transcription, translation and recombination. Phages that carried this gene might use the helicase gene product during their own or their host's replication (Jarvis *et al.*, 1996).

Clone 4 contained three possible ORFs (on the reverse strand). The first gene showed high identity to a putative phage head-tail adaptor from *Rhodobacter*

sphaeroides ATCC 17029, the second showed identity to a hypothetical protein NB311A_00470 from *Nitrobacter* sp. Nb-311A, and the third for phage protein DNA packaging protein from *Roseibium* sp. TrichSKD4. Phage head-tail adaptor enzymes help in the attachment of the phage head-tail during phage replication (Copeland, A., Lucas, S., unpublished data). Sequence 5 contained an ORF coding for the phage terminase from both *Rhodobacter sphaeroides* ATCC 17029 and *Achromobacter piechaudii* (running on the negative strand). Terminase is an enzyme that is involved in phage DNA packaging (Copeland, A., Lucas, S., unpublished data). Clone 7 contained two ORFs, phage protein gp12 from *Burkholderia* phage Bcep1 (*Myoviridae*) and hypothetical protein from *Methylobacterium* sp. GXF4, both running on the reverse strand. Phage protein Gp 12 is a tail fiber protein (summer *et al.*, 2006).

Clone 8 contained one ORF coding for either phage-type endonuclease from *Hyphomicrobium denitrificans* ATCC 51888 or phage-related exonuclease from *Liberibacter crescens* BT-1 (on the negative strand). Endonucleases catalyse the hydrolysis of ester linkages within nucleic acids by creating internal breaks. Exonucleases catalyse the hydrolysis of ester linkages within nucleic acids by removing nucleotide residues from the 3' or 5' ends of the DNA molecule (Leonard *et al.*, 2012; Lucas, S., Copeland, A., unpublished data). Clone 10 contained an ORF running on the positive strand, coding for the phage tail fiber protein from *Nitratireductor pacificus* pht-3B. Phage tail fiber proteins help in attachment of the phage to the bacterial cell during phage replication (Lai *et al.*, 2012). Clone 11 contained an ORF coding for the phage major capsid protein, HK97, from *Ruegeria* sp. TM1040 or putative head protein from *Xanthomonas*

phage C1 (running on the positive strand). This protein assists with DNA packaging (Moran *et al.*, 2007).

Phage proteins can be found in bacterial genomes due to lysogenic replication, the process that leads to prophage formation. Bacteriophage genomes are comprised of a high proportion of novel genetic sequences of unknown function (Hatful, 2008). Therefore it is not surprising that the functions of some of the phage genes identified by homology searches in this study are unknown.



Table 13: Bacteriophage SHPA sequence identity results of cloned inserts (June 2013).

Clone no.	Sequence length	ORF Strand	ORF Position	ORF length/ predicted protein length (aa)	Match	Score	E-value	% identity/ similarity	Accession no.
1	726	-	416-721	102/152	Lysozyme [<i>Brevundimonas diminuta</i>]	116	9e-29	42/51	WP_003165060.1
		-	419-718	100/151	Putative N-acetylmuramoyl-L-alanine amidase [<i>Pseudomonas</i> phage phi15]	99.9	3e-22	41/47	WP_016033323.1
2	747	-	187-426	80/83	Hypothetical protein PaTRP_19434 [<i>Paracoccus</i> sp. TRP]	91.3	3e-20	32/65	WP_010400601.1
		-	11-187	59/232	Helicase domain-containing protein, partial [<i>Paracoccus</i> sp. TRP]	72.0	3e-17	23/59	WP_010400602.1
		-	435-719	95/315	Hypothetical protein RAZWK3B_15493 [<i>Roseobacter</i> sp. AzwK-3b]	72.8	4e-12	38/50	WP_007816087.1
3	500	-	268-423	52/774	Xaa-Pro aminopeptidase [<i>Treponema pallidum</i> subsp. pertenue str. Gauthier]	36.2	4.5	31/40	YP_005222753.1
4	773	-	24-302	93/111	Phage head-tail adaptor, putative [<i>Rhodobacter sphaeroides</i> ATCC 17029]	100	2e-23	36/54	WP_011842266.1
		-	509-766	86/196	Phage protein DNA packaging protein [<i>Roseibium</i> sp. TrichSKD4]	60.8	2e-08	33/40	WP_009759185.1
5	781	-	98-778	227/583	Phage terminase [<i>Rhodobacter sphaeroides</i> ATCC 17029]	243	1e-72	52/87	WP_011840500.1
		-	155-778	208/523	Terminase, partial [<i>Achromobacter piechaudii</i>]	182	3e-50	45/79	WP_006228214.1
6	905	-	126-413	96/432	Histidinol dehydrogenase [<i>Crocospaera watsonii</i>]	38.5	2.8	31/33	WP_007303853.1

Table continued

7	745	-	10-276	89/231	Hypothetical protein [<i>Nitratireductor indicus</i>]	155	1e-42	35/78	WP_009756129.1
		-	52-276	75/181	Gp12 [<i>Burkholderia</i> phage Bcep1]	80.9	2e-15	33/53	WP_015974549.1
8	1088	-	27-482	152/214	Phage-type endonuclease [<i>Hyphomicrobium denitrificans</i> ATCC 51888]	209	2e-62	41/64	WP_013214170.1
		-	27-479	151/210	Phage-related exonuclease [<i>Liberibacter crescens</i> BT-1]	196	4e-57	41/61	WP_015272888.1
9	1051	-	205-954	250/541	Hypothetical protein ALIPUT_01592 [<i>Alistipes putredinis</i> DSM 17216]	137	3e-33	46/78	WP_004327624.1
		-	100-684	195/269	Oxidoreductase subunit [<i>Citrobacter rodentium</i> ICC168]	88.2	4e-17	33/84	WP_012905650.1
10	1054	+	61-1032	324/1221	Hypothetical protein Rsph17025_1315 [<i>Rhodobacter sphaeroides</i> ATCC 17025]	263	6e-76	48/92	YP_001168281.1
		+	67-996	310/886	Phage tail fiber protein [<i>Nitratireductor pacificus</i> pht-3B]	229	2e-64	42/88	WP_008599054.1
11	602	+	10-519	170/403	Phage major capsid protein, HK97 [<i>Ruegeria</i> sp. TM1040]	158	5e-41	61/84	WP_011538996.1
		+	61-498	146/394	Putative head protein [<i>Xanthomonas</i> phage CP1]	112	3e-26	51/72	WP_016066045.1

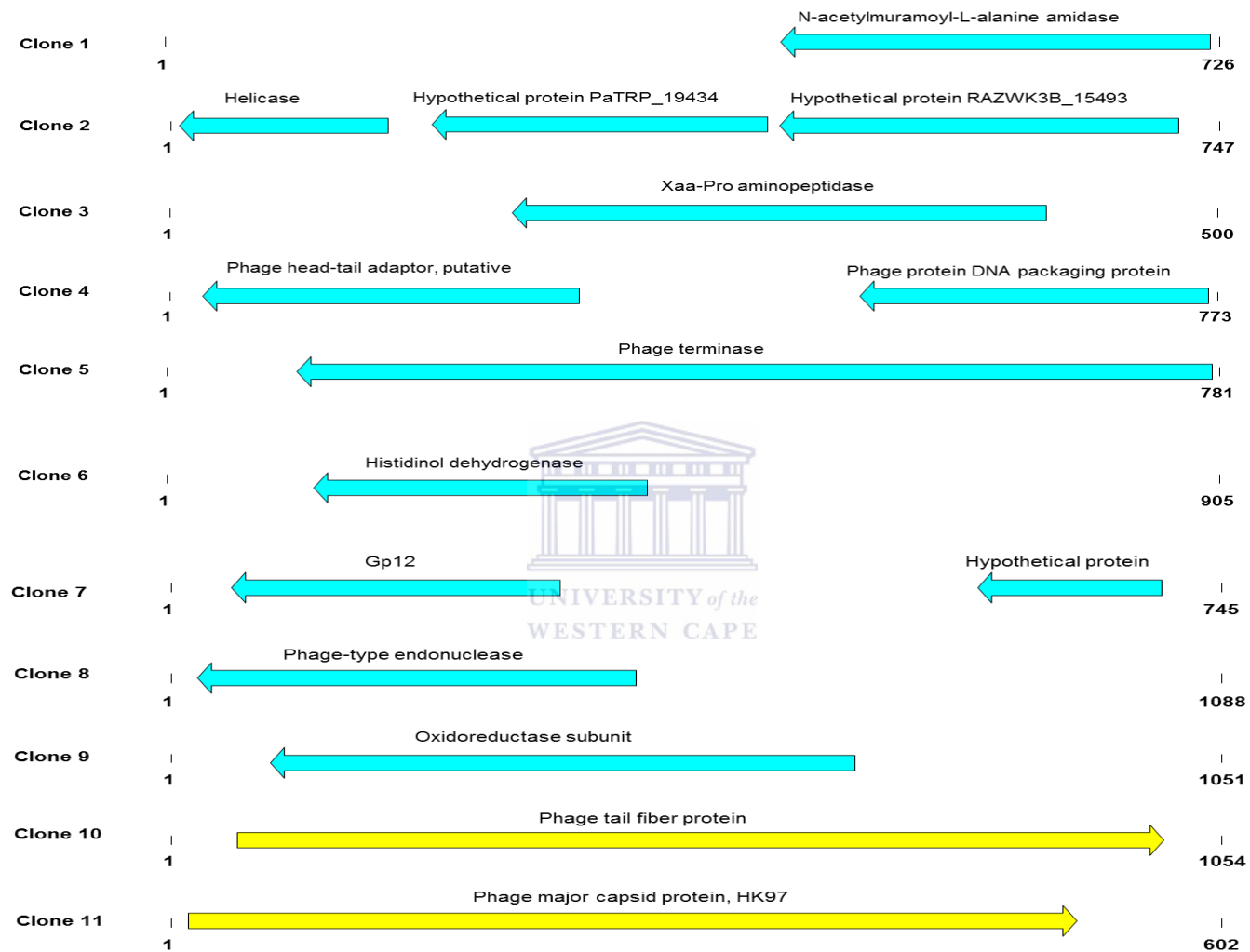


Figure 21: A graphic representation showing the positions of ORFs on phage SHPA DNA sequences. Blue arrow, ORF running on the left strand; yellow arrow, ORF running on the positive strand. The length of the sequences in base pairs (bp).

Chapter 4: General discussion and conclusion

Soda lakes are characterized by a high concentration of sodium carbonate (Na_2CO_3) with varying degrees of salinity and high pH values. Lake Magadi and Lake Shala have NaCl concentrations of approximately 30% and 18% (Jones *et al.*, 1998; Legesse *et al.*, 2004), with pH's of 11 and 9, respectively (Zinabu, 2002; Denson *et al.*, 2010). Despite the extreme conditions soda lakes are well populated almost entirely by prokaryotes (Sorokin & Kuenen, 2005) and are the most productive aquatic environments on earth (Grant, 2003). Phages have been isolated from extreme environments such as thermophilic and psychrophilic sources. Thermophilic and hyperthermophilic lakes have proved to be rich in novel phages (Sharp *et al.*, 1986; Arnold *et al.*, 2000; Rice *et al.*, 2004; Prangishvili *et al.*, 2006). However, in comparison, there are few studies reporting the microbial diversity in soda lakes, and none exist for estimating phage diversity, therefore nothing is known of the phage community in these environments. This largely unstudied phage population may contain a large reservoir of important and unknown genes which probably play a critical role in the microbial population dynamics and geochemical processes.

Haloalkaliphilic microbes are important as they play the role in remineralization of organic matter within the ecosystem. They also play an important role in transforming carbon, sulfur, nitrogenous compounds and metals in nutrient cycling and food webs under aerobic and anaerobic conditions (Joshi *et al.*, 2008). Experimental data and food web models have proved that converting cellular biomass to dissolved organic carbon leads to stimulation of microbial

growth and respiration by viral lysis with a decrease in the transfer of carbon to higher trophic level via grazing, proving that viruses have an effect on carbon flow in soda lakes (Brum *et al.*, 2005). Viruses are capable of species succession, transduction, lysogenic processes and help in the maintenance of microbial diversity (Fuhrman, 1999) and they play an important role in the mortality of their bacterial hosts (Wommack & Colwell, 2000). Because phages can affect their hosts by lysogeny and transduction they effect gene exchange within microbial communities in the environment (Wommack & Colwell, 2000).

Phage classification is based on the morphology and genome type (Nelson, 2004). Unlike bacterial classification, phage classification cannot be based on the analysis of molecular marker sequence like the 16S rRNA gene because no single gene that can be used as the basis for a classification system is shared by all phages (Rohwer & Edwards, 2002). There is a lack of sequence data in the databases because only a few phage sequences mostly related to known phage such as T4 and T7, have been sequenced. At least 50–60% of metagenomic virus sequences have been reported to have no similarities to the current database sequences, indicating that most viruses remain uncharacterized (Kristensen *et al.*, 2010).

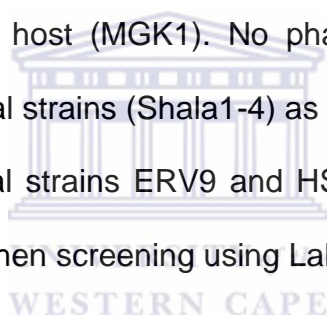
The aim of this study was to isolate and characterize phages from soda lake soil sediment samples. An alkaline medium, Medium A, adapted from Sato *et al.* (1983) was used to isolate these organisms, and the isolates were incubated at 37°C. This medium is similar to the basal medium Horikoshi-I (Horikoshi, 1991). Because the samples were from haloalkaline environments,

the organisms require both high pH and NaCl concentrations for growth. In this study, very few bacteria were isolated using this medium. Although this medium is rich in organic carbon, it is hypothesised that more isolates might have been detected using a medium prepared with lake water. Mwirichia *et al.* (2010) found more novel isolates using different media with varying compositions prepared using soda lake water. As the number of phage isolates depends on the isolated bacteria used to screen them, it is not surprising that very few phages were isolated from both lakes. Metagenomic studies showed that less than 1% of microorganisms in a given environment are culturable (Streit and Schmitz, 2004), therefore culturable isolates represent the minority of the species in microbial communities (Sabet *et al.*, 2006). Unculturability of microorganisms might be part of why so few microorganisms were isolated from both lakes. However, this cannot count for isolating only 5 bacteria in both environments. The samples used in this study had been stored at -80°C for some time, therefore we speculate that significant cell viability was lost, especially since the samples were not stored in glycerol (Gundersen *et al.*, 1996).

Five different bacterial hosts were identified, one bacterial strain (MGK1) from Lake Magadi and four (Shala1-4) from Lake Shala. Two bacterial hosts ERV9 and HS3 from the IMBM culture collection both collected from Lake Shala were also used to isolate phages. All these bacteria were moderately halophilic and alkalitolerant as they were able to grow at up to 10% (w/v) NaCl concentrations with an optimum pH of 10 (Nowlan *et al.*, 2006; Ventosa, 2006).

Morphological characterization and 16S rRNA gene sequencing were used to identify the bacteria. Different bacterial morphologies were identified and the results of 16S rRNA gene sequence showed 96 to 99% identity to existing database sequences. All seven bacterial hosts showed identities to species from four different genera in the database *Bacillus*, *Halomonas*, *Virgibacillus* and *Paracoccus*.

Only one phage (MGBH1) was isolated from Lake Magadi sediment sample, and two different phages (SHBH1 and SHPA) were identified from Lake Shala sediment samples. One phage from Lake Shala (SHBH1) was isolated using the Lake Magadi bacterial host (MGK1). No phage was isolated using the isolated Lake Shala bacterial strains (Shala1-4) as host strains against both soil sediment samples. Bacterial strains ERV9 and HS3 (IMBM culture collection) showed plaque formation when screening using Lake Shala sediments.



Phage images were taken by transmission electron microscopy. Despite the advantages of relatively new approaches such as flow cytometry (Brussaard *et al.*, 2000) and epifluorescence microscopy (Noble & Fuhrman, 1998), TEM remains the principal instrument used to reveal information about virus morphology and size (Pearce & Wilson, 2003). In this study three different viral morphologies were observed: *Siphoviridae*, *Myoviridae* and *Podoviridae* with variously sized capsids and tails. To date over 6000 phages have been examined by electron microscopy (Ackermann, 2011). Most of these phages are tailed, representing 96% of phage and only 3.7% are polyhedral, filamentous or pleomorphic (Ackermann, 2007; 2011). *Siphoviridae* are the

most abundant phages known in the biosphere and have also been extensively characterized (Guttman *et al.*, 2005). About 61% of the isolated *Siphoviridae* and 24.5% of *Myoviridae* phages have been examined by electron microscopy (Ackermann, 2007). As tailed phages are the most commonly found phages in the environment, their sequence information is growing and has strongly influenced the current view of viral genomics (Brüssow & Hendrix, 2002; Pedulla *et al.*, 2003). These dsDNA phages are suspected to infect most if not all bacteria in the biosphere.

Phage genomic analysis and morphological analysis are complementary approaches which provide a more complete picture of phage characteristics. Using one without the other will cause environmental phage diversity to be severely underestimated (Auguet *et al.*, 2006). TEM is also very useful in differentiating phages with a high degree of sequence identity (Jenkins & Hayes, 2006) as it is not possible to describe the viral phenotype from its genomic sequence (Büchen-Osmond, 2003). Although morphological information from electron microscopy alone is unreliable for classifying phages, it is still an important technique used in characterizing viral diversity in the environment (Brum & Steward, 2010).

The smallest phage isolated in this study, phage SHPA (*Podoviridae*), was selected for sequencing. SHPA phage DNA fragments were cloned, and the clones showed homology to some phage related proteins from both phage and bacteria. Phage SHPA is the first phage known to infect *Paracoccus aestuarii*. Although only one phage was sequenced, all the isolated phages may share


similar genetic homology because they are from the same environment. Sabet *et al.* (2006) found that phages from the same environment could share genetic homology as it could relate to increased survivability or better infection in the habitat even though they might infect very diverse hosts.

Podoviruses have linear double stranded DNA genomes of approximately 40-45 kb in length and encodes approximately 55 genes (Zhang *et al.*, 2011; Flores *et al.*, 2012; Karumidze *et al.*, 2012; Kim *et al.*, 2012; Sajben-Nagy *et al.*, 2012). The genome size of phage SHPA was found to be 25 kb, most similar to the genome of *Helicobacter* phage KHP30 isolated from Japanese patients with the size of 26 kb. *Helicobacter* phage KHP30 is a *Podoviridae* that infects *Helicobacter pylori*, a Gram-negative spiral bacterium that is found in the human stomach (Uchiyama *et al.*, 2012). *Podoviridae* are found to infect mostly Gram-negative bacteria (Plunkett *et al.*, 1999; Das *et al.*, 2012; Sillankorva *et al.*, 2012; Abbasifar *et al.*, 2013; Kęsik-Szeloch *et al.*, 2013) with very few infecting Gram-positive bacteria (Kotsonis *et al.*, 2008; Kleppen *et al.*, 2012; Morales *et al.*, 2012).

Most *Podoviridae* that have been classified are from sewage samples (Zhu *et al.*, 2010; Drulis-Kawa *et al.*, 2011; Fan *et al.*, 2012; Karumidze *et al.*, 2012; Kęsik-Szeloch *et al.*, 2013; Thien *et al.*, 2013), while several have been isolated from marine environments (Breitbart *et al.*, 2004; Holmfeldt *et al.*, 2007; Labonté *et al.*, 2009). Although some phage particles have been detected and isolated from Mono Lake, California, USA (a shallow saline soda lake) (Jiang *et al.*, 2004; Sabet *et al.*, 2006), these phage particles have not been classified as

they are not fully characterized. Other than these, no *Podoviridae* from haloalkaline environments have been classified so far. Moreover, only 20% of *Podoviridae* phage genomes have been completely sequenced (Deschavanne *et al.*, 2010). This highlights the scarcity of available information on this family of bacteriophages, and draws attention to the need to conduct further research.

From the sequence analysis of phage SHPA it is evident that this phage, isolated from the extreme environment sediments of Lake Shala, is a novel phage and, like many other environmental viruses (Sabet *et al.*, 2006), it is not fully characterized.



This study indicates that haloalkaline environments such as Lake Magadi and Lake Shala harbour a diversity of phages. A further investigation of haloalkaliphilic phages using culture independent methods such as metagenomic strategies is important to fully understand the diversity of phages in these environments. Another, less costly approach, would be to conduct sequence analysis of representative phage genes. The genetic diversity of specific groups of viruses in different environments has been examined using the sequence analysis of the structural genes *g20* and *g23* (Fuller *et al.*, 1998; Hambly *et al.*, 2001; Short & Suttle, 2002; Dorigo *et al.*, 2004; Filee *et al.*, 2005; Short & Suttle, 2005). Although it is not universally present, family A DNA polymerase has been identified as a good target for examining the diversity of podoviruses (Breitbart *et al.*, 2004). Considering the gap in the number of podovirus sequences with which to conduct genome comparisons, perhaps a diversity survey of structural genes would be useful to identify environments

rich in podoviruses to inform on further analyses of this poorly studied group of phages.



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