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Seasonal Changes in Potential Bioremediation Enzymes Associated with Prokaryotes in Tuz Lake, an Extreme Habitat

Suzan ŞAHIN DOĞAN[1], Aytac KOCABAŞ[2*]

[1]*Biology Department, KO Science Faculty of Karamanoglu Mehmetbey University, 70100, Karaman, Türkiye ORCID: 0000-0002-1554-0080*
[2*]*Biology Department, KO Science Faculty of Karamanoglu Mehmetbey University, 70100, Karaman, Türkiye aytackocabas@kmu.edu.tr ORCID: 0000-0001-7622-1932*

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Abstract

In bioremediation applications, non-extremophilic microorganisms are commonly used. However, when removing organic pollutants in high salt concentrations, non-extremophilic microorganisms typically require a pretreatment process to mitigate the adverse effects of salt. Halophilic microorganisms possess specialized enzymatic structures that enable them to adapt to hypersaline environments. Halophiles are particularly promising as bioremediation agents for organic pollutant removal at high salinity because they can effectively utilize hydrocarbons as their sole carbon and energy sources. In this study, the PICRUSt2 tool was applied to predict bioremediation enzymes from the prokaryotic diversity in Tuz Lake, based on 16S rDNA amplicon sequencing data. The functional analysis revealed the presence of several enzymes related to the bioremediation process in the Tuz Lake metagenome. Enzymes such as arsenite transporter ATPase (EC:3.6.3.16), arsenate reductase (EC:1.20.4.1), (S)-2-haloacid dehalogenase (EC:3.8.1.2), nitrate reductase (EC:1.7.99.4), and catechol 2,3-dioxygenase (EC:1.13.11.2) were found to be highly abundant. Furthermore, significant seasonal differences were observed in the abundance of sequences associated with (S)-2-haloacid dehalogenase, selenite water dikinase, mercury (II) reductase, arsenite transporter ATPase, and 4-hydroxyphenylpyruvate dioxygenase enzymes. (S)-2-haloacid dehalogenase and arsenite-transporting ATPase were found to be highly abundant in spring compared to fall. Atrazine chlorohydrolase, mercury (II) reductase, nitrilase, and nitrate reductase were more abundant in the fall.

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Keywords: PICRUSt2; Extremophilic; Functional genes; Bioremediation enzymes; Seasonal variation.

Ekstrem Bir Habitat Olan Tuz Gölü'nde Prokaryotlarla İlişkili Potansiyel Biyoremediasyon Enzimlerinde Mevsimsel Değişimler

Öz

Biyoremediasyon uygulamalarında genellikle ekstremofil olmayan mikroorganizmalar kullanılmaktadır. Ancak bu uygulamalarda, ekstremofil olmayan mikroorganizmaların yüksek tuz konsantrasyonlarında organik kirleticileri giderimi, olumsuz tuz etkisinin üstesinden gelmek için bir ön arıtma işlemi gerektirmektedir. Halofil mikroorganizmalar, hipersalin ortamlara uyum sağlamalarını sağlayan önemli enzimatik yapılara sahiptir. Halofiller, hidrokarbonları tek karbon ve enerji kaynağı olarak etkili bir şekilde kullanabilmeleri nedeniyle yüksek tuz konsantrasyonlarında organik kirletici giderimi için uygun biyoremediasyon ajanları olarak öne çıkmaktadır. Bu çalışmada, 16S rDNA amplikon dizileme verilerini kullanarak Tuz Gölü'ndeki prokaryotik çeşitliliğin biyoremediasyon enzimlerini tahmin etmek için PICRUSt2 aracı uygulandı. Fonksiyonel analiz sonucunda, Tuz Gölü metagenom verilerinde biyoremediasyon süreciyle ilgili çeşitli enzimler tespit edildi. Arsenit taşıyıcı ATPaz (EC:3.6.3.16), arsenat redüktaz EC:1.20.4.1), (S)-2-haloasit dehalojenaz (EC:3.8.1.2), nitrat redüktaz (EC:1.7.99.4) ve katekol 2,3-dioksijenaz (EC:1.13.11.2) enzimleri yüksek bollukta gözlendi. Ayrıca, (S)-2-haloasit dehalojenaz, selenit su dikinazı, cıva (II) redüktazı, arsenit taşıyıcı ATPaz ve 4-hidroksifenilpiruvat dioksijenaz enzimleriyle ilişkili diziler önemli mevsimsel farklılık gösterdi.

Anahtar Kelimeler: PICRUSt2, Ekstremofilik, Fonksiyonel genler, Biyoremediasyon enzimleri, Mevsimsel değişim.

1. Introduction

Contamination of soil and water due to industrial activities is a widespread issue that impacts both human health and ecological balance. Bioremediation aims to reduce toxicity and pollutants in soil or water through biodegradation or bioconversion [1, 2]. This biotechnological approach is more cost-effective and efficient compared to traditional physicochemical methods [3]. Cytochrome P450, laccases, hydrolases, dehalogenases, dehydrogenases, proteases, and lipases are the key microbial enzymes responsible for the degradation of various pollutants [4].

It has been reported that high concentrations of organic compounds are frequently found in saline environments, resulting from industrial activities or natural processes [5]. The ability of halophilic microorganisms to oxidize hydrocarbons under high salt concentrations is particularly important for the biological remediation of saline ecosystems contaminated by petroleum products. Successful bioremediation of oil spills has been reported in Antarctic, Arctic, and marine environments [6]. Furthermore, it has been suggested that hydrocarbon biodegradation is enhanced at higher salinity levels [7]. Halophilic microorganisms are considered promising candidates for the biodegradation of pollutants in hypersaline conditions because non-halophilic organisms are unable to function effectively at salinities greater than those of seawater due to their molecular structure [8]. Halophilic microorganisms have developed various molecular mechanisms to adapt to hypersaline environments. Typically, halophiles employ two primary strategies to maintain osmotic balance in response to high salt concentrations. The first strategy, known as the "salt-in" strategy, is energetically favorable [9]. Halophiles utilize this strategy by transporting ions into the cell, thereby maintaining an intracellular salt concentration higher than the surrounding environment [10]. The second strategy involves the synthesis or accumulation of intracellular compatible solutes, such as sucrose, ectoine, and trehalose, to preserve osmotic balance under hypersaline conditions [9, 11-13].

Tuz Lake is an ideal natural environment for studying halophilic microorganisms, with a salinity of 32% (w/v). This high salinity makes it one of the most suitable locations for screening microorganisms capable of producing enzymes involved in bioremediation processes. In a previous study, the prokaryotic diversity of Tuz Lake was analyzed by our research team using 16S rDNA amplicon sequencing [14]. In the current study, 16S rDNA amplicon sequencing data were utilized by our research team to assess the bioremediation potential of the prokaryotic community in Tuz Lake, Turkey, using the PICRUSt2 tool. Additionally, the seasonal variation in the activity of enzymes related to bioremediation processes was investigated.

2. Materials and Methods

Samples were gathered from the two main sectors of the Tuz Lake basin (Cihanbeyli and Şereflikoçhisar) over a period spanning late 2018 through early 2020 by our research team (Fig. 1). The samples were aseptically collected and transported to the laboratory under refrigeration at 4°C. Due to a drought occurring in August and September, water samples could not be collected during those months. Consequently, a total of thirteen samples were obtained and used for 16S rDNA amplicon sequencing.

Figure 1: The map of the Tuz Lake where water samples were collected

2.1. Nucleic Acid Extraction and 16S rDNA Amplicon Sequencing

Genomic DNA was extracted using the phenol-chloroform method as outlined in the previous study [14]. Samples were filtered through 0.22 µm membrane filters, pulverized with liquid nitrogen, and treated with 750 µl of extraction buffer. After centrifugation at 15,000 g for 20 minutes, the supernatant was transferred to a clean tube, and RNase was introduced. The supernatant was incubated at 37°C for two hours, followed by RNase inactivation at 65°C for 20 minutes. Phenol:chloroform:isoamyl alcohol (25:24:1, pH 8) was mixed in the supernatant, and the mixture was centrifuged at 15,000 g for 15 minutes. One-tenth volume of 3M sodium acetate was incorporated into the supernatant, and the mixture was stored overnight at -20°C to precipitate nucleic acids. The pellet was rinsed with 70% ethanol and resuspended in 10 mM Tris (pH 8) after centrifugation at 13,000 g.

To amplify the V4 region of the 16S rDNA gene, the PCR protocol established by the Earth Microbiome Project was utilized, employing the primers 515F and 806R as described by Caporaso et al. [15]. The 16S rDNA amplicon sequencing was performed on the Illumina MiSeq platform using the 2 × 300 bp paired-end protocol.

2.2. Bioinformatics Analysis

The Dada2 pipeline was utilized to process the data by filtering, dereplicating, identifying chimeras, and merging paired-end reads. The reads were trimmed to a length of 260 nt (with a Phred score > 20) using the trim-length function. Functional analysis of the reads was performed using the PICRUSt2 pipeline [16], generating tables of feature abundance and representative sequences. These data were then converted to BIOM format for further analysis. The ASVs were assigned to the reference phylogenetic tree using specialized algorithms for sequence placement. Hidden state estimation was carried out with the Castor R package. After estimating the gene family copy numbers in PICRUSt2, the nearest sequenced taxon index (NSTI) values were calculated for each ASV. ASVs with NSTI scores below 2.0 were chosen for further analysis. Metagenomes of the communities were generated, and the contribution of each ASV to the enzyme classes was determined. Finally, the STAMP tool [17] was applied to analyze the functional profile. ANOVA was used to calculate p-values for multiple comparisons, and the Tukey-Kramer test was applied in post-hoc analysis.

3. Results and Discussion

As a result of the functional analysis, various enzymes associated with the bioremediation process were identified from the predicted metagenome data of Tuz Lake. Enzymes such as arsenite transporter ATPase (EC:3.6.3.16), arsenate reductase (EC:1.20.4.1), (S)-2-haloacid dehalogenase (EC:3.8.1.2), and nitrate reductase (EC:1.7.99.4) were found to be present in high abundance (Fig. 2). On the other hand, Oyewusi et al., 2021 indicated that arsenate reductase and molybdate-transporting ATPase, related to bioremediation, were the most abundant in Tuz Lake [18].

Furthermore, enzymes such as molybdate-transporting ATPase, catechol 2,3-dioxygenase, 4-hydroxybenzoate polyprenyltransferase, nitronate monooxygenase, 4-hydroxyphenylpyruvate dioxygenase, haloalkane dehalogenase, selenite water dikinase, mercury (II) reductase, alkane 1-monooxygenase, haloacetate dehalogenase, catechol 1,2-dioxygenase, 3,4-dihydroxyphenylacetate 2,3-dioxygenase, selenite reductase, cyclohexanone monooxygenase, 4-hydroxyphenylacetate 3-monooxygenase, atrazine chlorohydrolase, nitrile hydratase, nitrilase, 4-hydroxybenzoate 3-monooxygenase, and dye decolorizing peroxidase were found to be present in low abundance (Fig. 2). Many of these enzymes involved in bioremediation are produced in response to specific substrates (pollutants or natural compounds) in the environment. If these substrates are not abundant in the environment, there may be a natural decrease in the production of enzymes because of no induction to express related genes [19]. Therefore, it can be said that the accumulation of mercury, atrazine, halogenated compounds, nitrate, and selenite is at low concentrations in Tuz Lake, which is a hypersaline environment. Furthermore, in microbial communities, due to functional specialization, the expression levels of certain enzymes vary according to the genetic structure and metabolic needs of the community as well as environmental factors, including pH, temperature, and oxygen concentration [20–22].

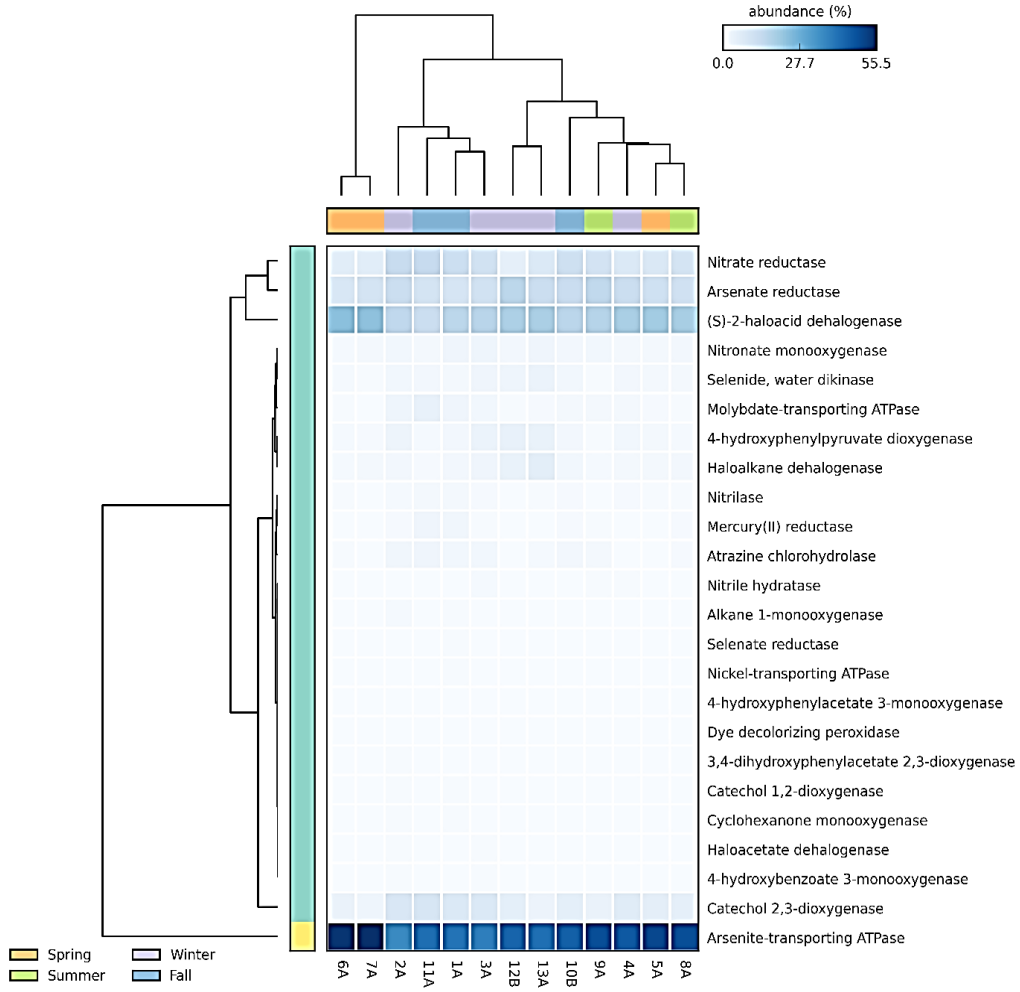
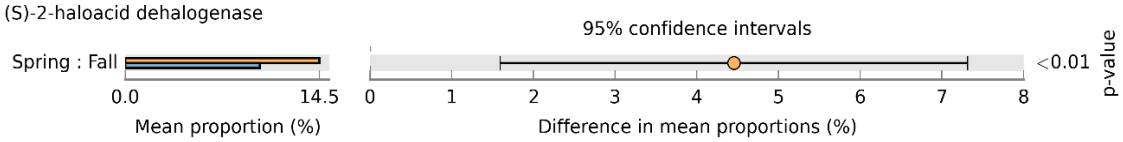


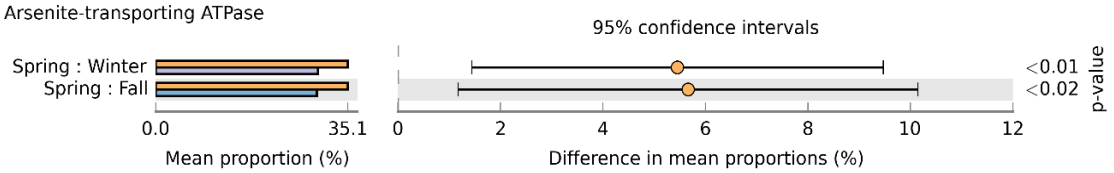
Figure 2: Changes of functional genes related to bioremediation by months with a heatmap graph

(S)-2-haloacid dehalogenase, selenite water dikinase, mercury (II) reductase, arsenite transporter ATPase, atrazine chlorohydrolase, nitrilase, nitrate reductase, and 4-hydroxyphenylpyruvate dioxygenase showed significant seasonal differences (Fig. 2). (S)-2-haloacid dehalogenase and arsenite transporter ATPase were found to be more abundant in spring compared to other seasons (Figs. 3a-3b). Selenite water dikinase and 4-hydroxyphenylpyruvate dioxygenase exhibited significant seasonal variation and were more abundant in winter (Figs. 2c-2d). Atrazine chlorohydrolase, mercury (II) reductase, nitrilase, and nitrate reductase were more abundant in the fall (Figs. 3e-3h). In a previous study, we indicated that microbial abundance and diversity were influenced by environmental parameters, particularly temperature [14]. Temperature changes are known to influence microbial growth and metabolism, gas solubility, and the physical and chemical properties of contaminants [23, 24]. Hu Yop et al. isolated halogen-degrading halophilic bacteria from the hypersaline Salt Lake for use as biodegraders of halogenated compounds and preferring a mesophilic environment [24]. In the present study, (S)-2-haloacid dehalogenase and arsenite-transporting ATPase were found to be highly abundant in spring compared to fall (Fig. 3). In spring, dissolved oxygen, conductivity, and water level are higher compared to fall, whereas temperature is lower

[14]. The analysis revealed that the most abundant arsenite transporter ATPase gene was associated with *Haloquadratum*, the dominant archaeal genus in the Tuz Lake. It has also been observed that the enzyme (S)-2-haloacid dehalogenase is associated with *Salinibacter*, a common bacterial genus in the Tuz Lake [14]. Therefore, the observed fluctuations in enzyme abundance may be related to changes in microbial abundance in Tuz Lake, and consequently, to functional shifts as well as the accumulation of corresponding enzyme substrates. Bacterial populations have been reported to be significantly affected by seasonal changes in environmental factors. Uncovering their impact on microbial diversity and distribution is crucial for the effective utilization of microbiomes in various applications [25].



(a)



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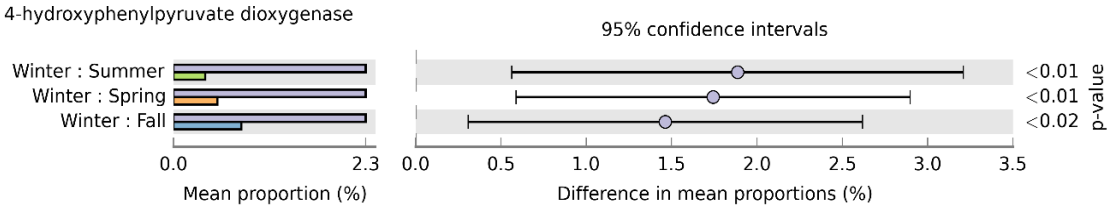

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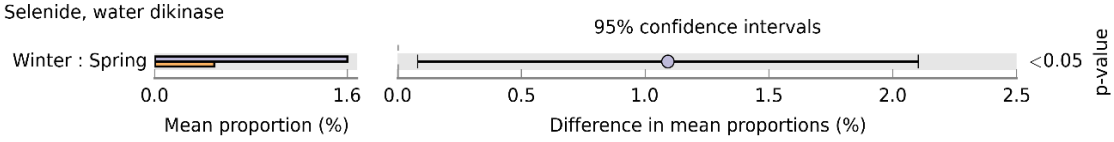

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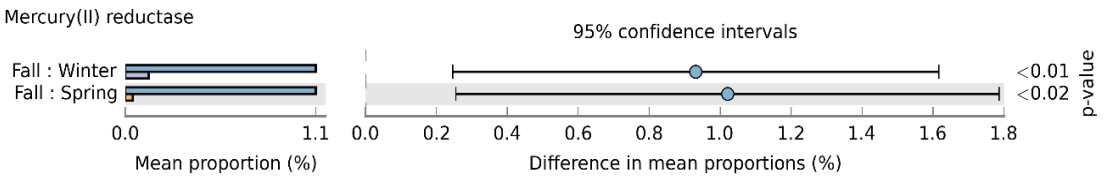

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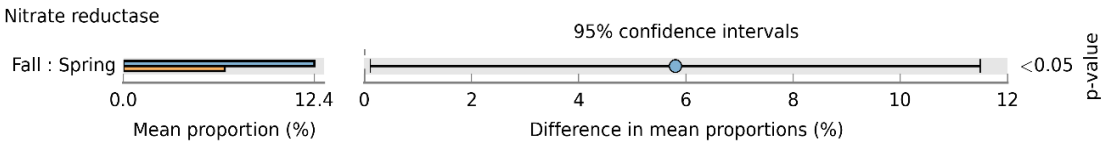
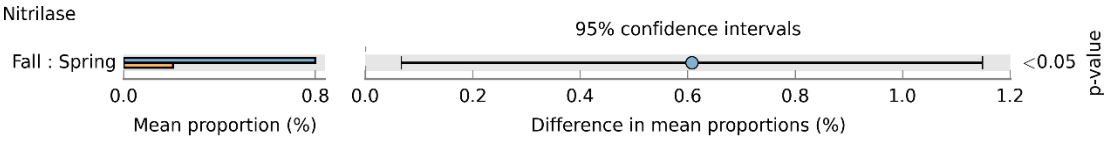
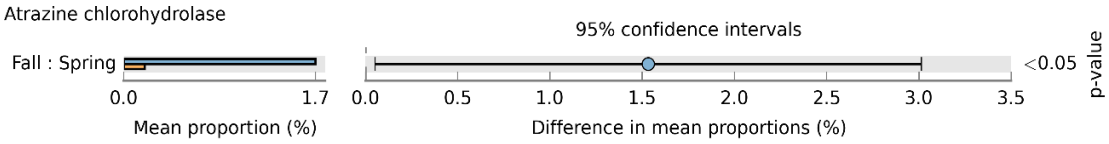


(f)



(g)



(h)

Figure 3: Seasonal variation of potential bioremediation enzymes (a) (s)-2-haloacid dehalogenase (b) arsenite transporter ATPase (c) 4-hydroxyphenylpyruvate dioxygenase (d) mercury (II) reductase (e) selenite water dikinase (f) nitrate reductase (g) nitrilase (h) atrazine chlorohydrolase (Spring:Orange, Fall:Blue, Summer:Green, Winter: Purple)

Functional genes, related taxa, and their abundance are presented in Table 1. According to the pred_metagenome_contrib.tsv file, arsenate reductase is primarily associated with *Chitinophagales_uncultured* and *Salinibacter*, nitrate reductase with *Haloquadratum*, *Natronomonas,* and *Thiohalorhabdus*, with catechol 2,3-dioxygenase and haloalkane dehalogenase with *Salinibacter*, dye decolorizing peroxidase with *Micrococcus*, and alkane 1-monooxygenase with *Marinobacter* (Table 1).

Table 1: Taxonomic units associated with functional profiles

Sample	Function	Taxon	Taxon abundance	Taxon relative abundance	Genome function number	Taxon function abundance	Taxon relative function abundance

10B	EC:3.6.3.16 (Arsenite-transporting ATPase)	*Haloquadratum*	1423	4.9	3	4269	14.6
13A	EC:3.8.1.2 ((S)-2-haloacid dehalogenase)	*Salinibacter*	464	6.5	1	464	6.5
3A	EC:1.14.15.3 (Alkane 1-monooxygenase)	*Marinobacter*	50	0.4	2	100	0.8
1A	EC:1.11.1.19 (Dye decolorizing peroxidase)	*Micrococcus*	109	0.5	1	109	0.5
1A	EC:3.8.1.5 (Haloalkane dehalogenase)	*Salinibacter*	108	0.5	1	108	0.5
12B	EC:1.20.4.1(Arsenate reductase)	*Chitinophagales; D_4__uncultured*	318	8.2	2	636	16.3
12B	EC:1.13.11.27(4-hydroxyphenylpyruvate dioxygenase)	*Salinibacter*	454	11.7	1	454	11.7
3A	EC:1.14.15.3 (Alkane 1-monooxygenase)	*Marinobacter*	50	0.4	2	100	0.8
2A	EC:1.14.15.3 (Alkane 1-monooxygenase)	*Pseudomonas*	261	1.4	1	261	1.4

12B	EC:1.20.4.1 (Arsenate reductase)	*Salinibacter*	454	11.7	1	454	11.7
9A	EC:1.7.99.4 (Nitrate reductase)	*Haloquadratum*	977	3.9	2	1954	7.7
10B	EC:1.7.99.4 (Nitrate reductase)	*Natronomonas*	316	1.1	1	316	1.1
11A	EC:1.7.99.4 (Nitrate reductase)	*Thiohalorhabdus*	26.5	0.1	4	106	0.5

The bioremediation potential of extremophiles has also been demonstrated in studies conducted in various extreme environments. It has been determined that arsenic-reducing microbial communities are commonly found throughout the Atacama Desert, where arsenic concentrations are typically high [26]. In addition, it has been reported that extremely halophilic *Haloferax sp.* decomposes polyaromatic hydrocarbons, while extremely halophilic *Halomonas sp*. reduces selenite to elemental selenium [26]. Wang et al., indicated that *Marinobacter* is capable of phenanthrene degradation at salinities ranging from 3% to 20% [27]. The unique structure of hypersaline habitats, such as Tuz Lake, supports a diverse range of halophilic microorganisms [24]. However, thriving in such extreme environments requires these salt-loving microbiomes to develop specialized adaptation mechanisms [28]. These adaptations enable the microorganisms to withstand the physical stress of high salinity, sustain growth, and perform optimal metabolic functions, making them ideal candidates for the treatment of wastewater generated by coastal aquaculture industries [8].

4. Conclusion

In conclusion, various enzymes associated with the bioremediation process were identified in Tuz Lake through predictive metagenome data. Arsenite transporter ATPase (EC:3.6.3.16), arsenate reductase EC:1.20.4.1), (S)-2-haloacid dehalogenase (EC:3.8.1.2), nitrate reductase (EC:1.7.99.4), and catechol 2,3-dioxygenase (EC:1.13.11.2) enzymes showed highly abundant. Furthermore, some of these enzymes exhibited significant seasonal variations. (S)-2-haloacid dehalogenase and arsenite-transporting ATPase were found to be high abundance in spring compared to fall. The observed fluctuations in enzyme abundance may be linked to changes in microbial abundance in Tuz Lake, and consequently, to their environmental adaptation and functional shifts. The assessment of bioremediation-related enzymes using

PICRUSt2 may serve as a valuable starting point for future ecological and biotechnological research. Furthermore, the predictive functional profile may be useful for identifying candidate microorganisms that produce commercially important bioremediation enzymes.

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