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Different responses of bacterial and archaeal communities in river sediments to water transfer and seasonal changes

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Abstract: Bacteria and archaea participate in and are influenced by processes of substance circulation and energy exchanges in natural environment. Generally, the community changes of bacteria and archaea in sediment are mainly driven by seasonality in mid-latitude regions. But in our study, water diversion to Fen river played a more important role on OTU number, diversity and community structure of bacteria and archaea in sediment than seasonal variation, which was found by 16S rRNA high-throughput sequencing technology. This phenomenon might be caused by external transferred water on the physicochemical water environment and accelerated release of positive nitrogen from sediment caused by rise of water level. Changes of carbon-nitrogen cycle and increase of electrical conductivity (EC) value induced more diversion-responders than season-responders both for bacteria and archaea. Seasonal changes have been influencing bacteria and archaea mildly throughout the whole study reach. After water diversion, the environment indicators relating to bacteria community obviously changed from nutrients to salinity while that for archaea almost disappeared. Our research showed the effects of human activities on the communities of bacteria and archaea outweigh the forcing from natural seasonal changes in mid-latitude regions and revealed the mechanism, highlighting different responses of bacteria and archaea to environmental changes.

Keywords: archaea; bacteria; 16SrRNA high-throughput sequencing; water transfer; seasonal changes; river sediments

1. Introduction

Bacteria and archaea are important components of microorganism, which participate in and were influenced by processes of substance circulation and energy exchanges in natural environment [1-3]. Bacteria and archaea belong to two distinct evolutionary branches. Bacteria are widely distributed in all corners of the earth [2], while the abundance and diversity of bacteria goes down under extreme conditions with archaea becoming main microorganisms [4,5]. In the early days, archaea were thought to be all extremophiles that thrived under high temperature, high salinity, low or high pH, absolutely anaerobic or combinations. Scientists speculated archaea's physiological properties may make them weaker competitors to bacteria in a more general niche.

What turned the tide is the appearance of PCR amplification and Sanger-based sequencing of 16S rRNA genes, which is the beginning of finding archaea in non-extreme environments. Many new archaeal and bacterial lineages (including phyla) have been discovered since then. Recently, studies of comparison between archaea and bacteria in non-extreme environments, including wetlands [6,7], coastal zones [8,9], lakes [10,11] and soil [12,13] attract more and more scientific interest. These results indicate that bacteria and archaea show significant seasonal pattern [14]. For example, the bacteria and archaea in the Alps show obvious seasonal variation, and the abundance of archaea reaches peak in cold spring and winter [15]. Temperature is considered as the main factor driving the seasonal changes of bacterial community in a coastal wetland [16]. Both bacteria and archaea display different community structure and composition in different habitats, and the environmental driving factors are usually different [17].

In river sediments, bacteria and archaea dominate the nitrogen cycle [18-20]. Water diversion projects, especially inter-basin water diversion projects, have a profound impact on the bacterial and archaeal communities, and may lead to a strong heterogeneity of the environment in the water receiving area [21,22]. Most water diversion projects are located in the mid-latitude region with dense population and arid/semi-arid climates. The heterogeneity can be further amplified by seasonal changes. It is expected that bacterial and archaeal communities can sensitively respond to the strong spatial-temporal heterogeneity. Previous studies showed that bacteria in water bodies and sediments affected by water diversion have significant spatial-temporal changes [23]. However, the different responses of bacterial and archaeal communities in river sediments to water diversion and seasonality are currently unknown.

Based on 16S rRNA high-throughput sequencing technology, we determined bacterial and archaeal community compositions in sediments influenced by inter-basin water transfer in the mid-latitude river, and discussed the responses of bacterial and archaeal communities to anthropogenic water transfer and the natural seasonality. We aimed to deepen the understanding of bacteria and archaea communities in a changing environment.

2. Materials and Methods

2.1 Study area and sampling sites

The Fen River, 710 km in length, is the second largest tributary of the Yellow River (Fig.1). The study area located in 38 ° 48 '~ 38 ° 15' N, 111 ° 52 '~ 112 ° 07' E, covering the reach from the river head (Gongjiazhuang) till Fengrun, with a length around 80 km. The research area has a temperate monsoon climate with dry cold winters and wet hot summers. The annual average temperature is about 7℃, with an average temperature of -9℃ in January and 21℃ in June. The annual rainfall is 380 mm to 500 mm, about 70% of which occurs during June to September. The study river reach has been receiving an injection of 320 million m^3/a from the Yellow River water in Toumaying since 2003. The water diversion is usually suspended in February, March, August, and September.

The sampling site of FR01 (Gongjiazhuang) is about 1 km away from the source of the Fen River. The site of FR02 is 100 m upstream of the Yellow River water injection point (Toumaying). The sampling site of FR03 is 4.5 km downstream of Toumaying, with no tributary. The site of FR04 is located about 50 km downstream of FR03. Multiple tributaries are fed in the river reach between FR03 to FR04, although their total runoff is relatively limited. The sampling site of FR05 is located about 6 km downstream of FR04, followed by FR06 about 15 km downstream.

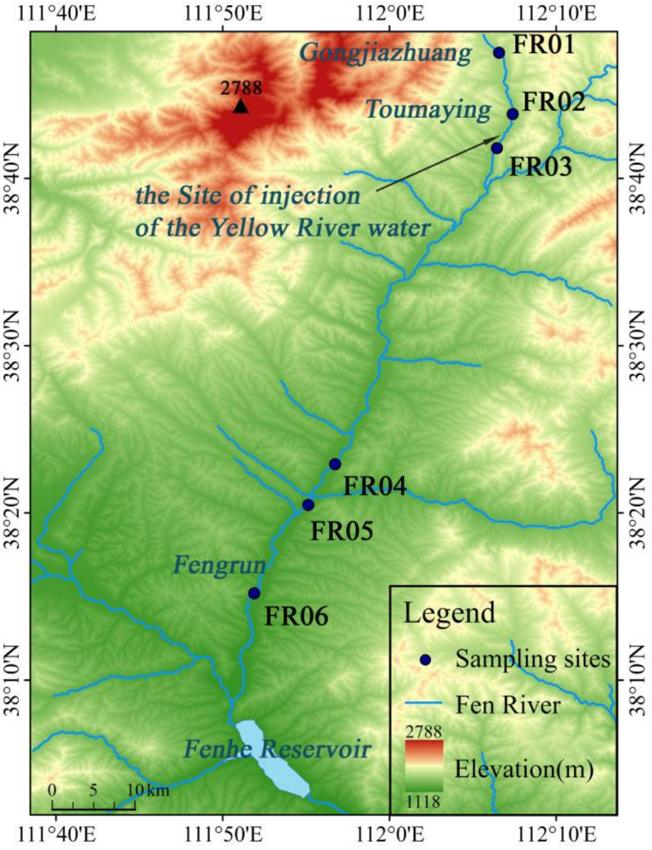

Figure.1 Map of study area and sampling sites

2.2 Sample collection and measurements

Samples were collected from the 6 sampling sites in winter (January) and summer (June) of 2017, respectively. Before sampling, physicochemical parameters, such as water temperature, pH, electrical conductivity (EC), oxidation-reduction potential (ORP) and total dissolved solid (TDS) of the river water, were measured (HORIBA U-51). Then, water samples below 20 cm from the water surface in the center of the river were collected and loaded into three 60 mL high density polyethylene bottles. River sediment samples of 1-2cm below the surface of sediments were collected at three different locations of each site, and then loaded into a 10 mL aseptic centrifugal tube. About 1 kg sediment samples were collected and put into sterile zip-lock bags. All sediment samples were frozen with dry ice immediately after collection.

The contents of Ca^{2+}、Mg^{2+}、Na^{+} and K^{+} in water samples were determined using ICP-OES (PerkinElmer 5300DV), and the contents of Cl^{-}、SO_4^{2-} and NO_3^{-} were determined using Ion Chromatograph (Dionex ICS-900). The contents of HCO_3^{-} were measured by titration on the sampling day. The particle size (PS) of river sediment samples was analyzed by Laser particle size analyzer (Mastersizer 2000). In addition, total nitrogen (TN) , alkeline-nitrogen (AN) , total phosphorus (TP) , total kalium (TK) , olsen-phosphorus (OP) , available kalium (AK) and soil organic matter (SOM) were measured according to standard methods (Kjeldahl method for TN, Alkali solution diffusion method for AN, Sodium hydroxide melting method for TP and TK, Sodium bicarbonate extraction method (Olsen) for OP, Ammonium acetate extraction measurement for AK and H_2SO_4 - $K_2Cr_2O_7$ external heating oxidation method for SOM). The instruments used include Atomic Absorption Spectrometer (Zeenit of jena, Germany 700 p), Spectrophotometer and Kjeldahl Apparatus.

The V3-V4 hypervariable regions of the bacteria and archaea 16S rRNA gene were amplified with primers 338F/806R and 524F10extF/Arch958RmodR by thermocycler PCR system (GeneAmp 9700, ABI, USA). The V3-V4 hypervariable regions of the bacteria and archaea 16S rRNA gene were amplified with primers 338F(ACTCCTACGGGAGGCAGCAG)/806R(GGACTACHVGGGTWTCTAAT) and 524F10extF (5'-TGYCAGCCGCCGCGGTAA-3')/Arch958RmodR(5'-YCCGGCGTTGAVTCCAATT-3') using thermocycler PCR system (GeneAmp 9700, ABI, USA) following the program: 3 min of denaturation of template DNA at 95°C, 27 cycles of 30s at 95°C, 30s for annealing at 55°C, and 45s for elongation at 72°C, and a final extension at 72 °C for 10 min. Three replicates were used for each sample. Sequence determination was completed using MiSeq PE300 sequencer (Illumina). The original paired Illumina MiSeq reads were deposited in the NCBI sequence read archive (accession number: SRP158824). The sequencing results of the sampling points FR01~FR06 in winter and summer were labeled as W1~W6 and S1~S6, respectively.

2.3 Statistical analysis

We used T test to analyze the physicochemical characteristics of river water and sediment by IBM SPSS Statistics 20. To analyze the bioinformation of the high-throughput data, we used QIIME (Quantitative Insights into Microbial Ecology) to classify the sequences into operational taxonomic units (OTUs) using a 97% identity threshold. The α-diversity, Coverage, Chao and Shannon indexes, were calculated using the MOTHUR. Principal component analysis (PCA) was done both for environmental indicators and microbial community by origin2018. Wilcoxon rank-sum test was used to identify species that differ significantly from this group. The ‘pheatmap’ package in R was employed to visually display the correlation between environmental factors and species.

3. Results

3.1 Environmental changes induced by water diversion and seasonality

A part of environmental factors changed significantly in the water-receiving reach compared to the regular river reach (Table 1). The average increase of EC and TDS in the water-receiving reach was about 2.5 times higher than that in the regular river reach. Especially, the concentrations of Cl^- and Na^+ in the water-receiving reach were 1985% and 1725% higher than those in the regular river reach. In January, the contents of most nutrients in the water-receiving reach sediments increased obviously compared to the regular river reach, with an increase of 156% for AN, 125% for AK, 89% for OP, 88% for TN, and 58% for SOM. However, in June, TN, AN, and OP decreased by 44%, 54% and 55% respectively in the water-receiving reach sediments compared to the regular river reach. On average, PS in the sediments of the water-receiving reach decreased by 51% than that in the regular river reach (Table 2).

Table.1 Main water environmental factors affected by Yellow River diversion and seasonal changes

	January		**June**	
	Regular reach¹	**Water-receiving reach²**	**Regular reach¹**	**Water-receiving reach²**
T(℃)	1.44±1.01	1.15±0.52	19.59±0.07*	21.90±0.56*
EC(µs/cm)	535.50±28.50**	1257.50±27.50**	436.00±34.00**	1205.00±32.50**
ORP(mv)	410.00±55.00	366.50±15.25	209.50±26.50	199.75±22.25
TDS(g/L)	0.34±0.02**	0.81±0.02**	0.28±0.02**	0.77±0.02**
NO_3^-(mg/L)	11.95±1.65*	19.65±0.45*	12.35±2.55	11.38±1.69
SO_4^{2-}(mg/L)	70.05±6.65**	205.53±3.66**	121.60±0.90*	400.85±116.28*
Cl^-(mg/L)	6.55±0.75**	132.25±3.78**	7.00±0.40**	150.85±67.63**
Na^+(mg/L)	6.65±0.55**	121.10±3.80**	8.40±1.20**	152.20±3.90**
K^+(mg/L)	1.80±0.00	3.88±0.04	2.39±0.28	4.88±0.57

Mg^{2+}(mg/L)	15.45±0.65**	36.95±0.58**	16.84±1.50*	40.94±0.57*
Ca^{2+}(mg/L)	63.70±0.20	67.60±1.60	76.31±6.94	65.19±3.73

Notes:

[1] Regular reach: FR01~FR02; [2] Water-receiving reach: FR03~FR06.

* represents the value of non-water-receiving reach and water-receiving reach's significant difference were achieved at the 0.05 level; ** represents the value of non-water-receiving reach and water-receiving reach's significant difference were achieved at the 0.01 level.

Table.2 Main soil environmental factors affected by Yellow River diversion and seasonal changes

	January		June	
	Regular reach[1]	**Water-receiving reach[2]**	**Regular reach[1]**	**Water-receiving reach[2]**
PS(um)	105±33	53±18	247±147	116±61
pH	7.80±0.05	8.05±0.16	8.35±0.44	8.91±0.13
SOM(g/kg)	14.65±1.85	23.18±8.28	11.85±3.65	16.03±4.18
TN(mg/kg)	4.40 ±0.00	8.25 ±0.03	11.30 ±0.00*	6.38 ±0.01*
AN(mg/kg)	33.00±2.00*	84.25±23.13*	160.00±29.00*	73.00±8.50*
TP(mg/kg)	464.50±36.50	578.50±45.25	530.00±50.00	589.25±44.38
OP(mg/kg)	5.50±0.50	10.25±3.88	17.00±4.00	7.75±1.75
TK(mg/kg)	2.83±0.01	2.70±0.19	2.82±0.20	2.35±0.14
AK(mg/kg)	48.50±6.50*	109.75±24.25*	69.00±1.00	78.00±15.50

Notes:

[1] Regular reach: FR01~FR02; [2] Water-receiving reach: FR03~FR06.

[3] PS: Particle size; [4] SOM: Soil organic matter; [5] TN: Total nitrogen; [6] AN: Alkali-nitrogen; [7] TP: Total phosphorus; [8] OP: Olsen-phosphorus; [9] TK: Total kalium; [10] AK: Alkali-kalium.

* represents the value of non-water-receiving reach and water-receiving reach's significant difference were achieved at the 0.05 level; ** represents the value of non-water-receiving reach and water-receiving reach's significant difference were achieved at the 0.01 level.

A part of environmental factors showed seasonal variation obviously. From winter (January) to summer (June), the river water temperature, Na^+, Cl^- and SO_4^{2-} in the river water increased 1260.4%, 26.3%, 6.9%, 74.2% and 1804.3%, 25.7%, 14.1%, 94.7%, while ORP decreased 48.9% and 45.5% in the regular reach and water-receiving reach, respectively (Table 1). From winter to summer, PS and pH of the river sediment increased, while SOM decreased 19.0% and 30.6% in the regular reach and water-receiving reach, respectively (Table 2).

The water diversion and seasonality cause significant alteration in environmental factors, which induced microbial community changes. Based on the result of the principal components analysis (PCA) of environmental factors, samples in the regular river reach and the water-receiving reach were separated by the first principal component. The environmental factors, including TDS, EC, Na^+, K^+, Mg^{2+}, Cl^-, and SO_4^{2-}, all responded actively to the water transfer constituting the first principal component. Therefore, the first principal component could recognize the alteration in microbial community induced by the water diversion. At the same time, the second principal component distinguished samples from summer and winter (Fig. 2a). Water temperature and ORP significantly responded to seasons forming the majority of the second principal component. It is considered that the second principal component can identify the alteration in microbial community induced by seasonality. Furthermore, the first principal component explained 41.3% of the total variance of the environment factors, while 20.8% of the total variance was explained by the second principal component. It is indicated that the influence of water diversion on the physicochemical conditions of water and sediments is beyond the influence of seasonality.

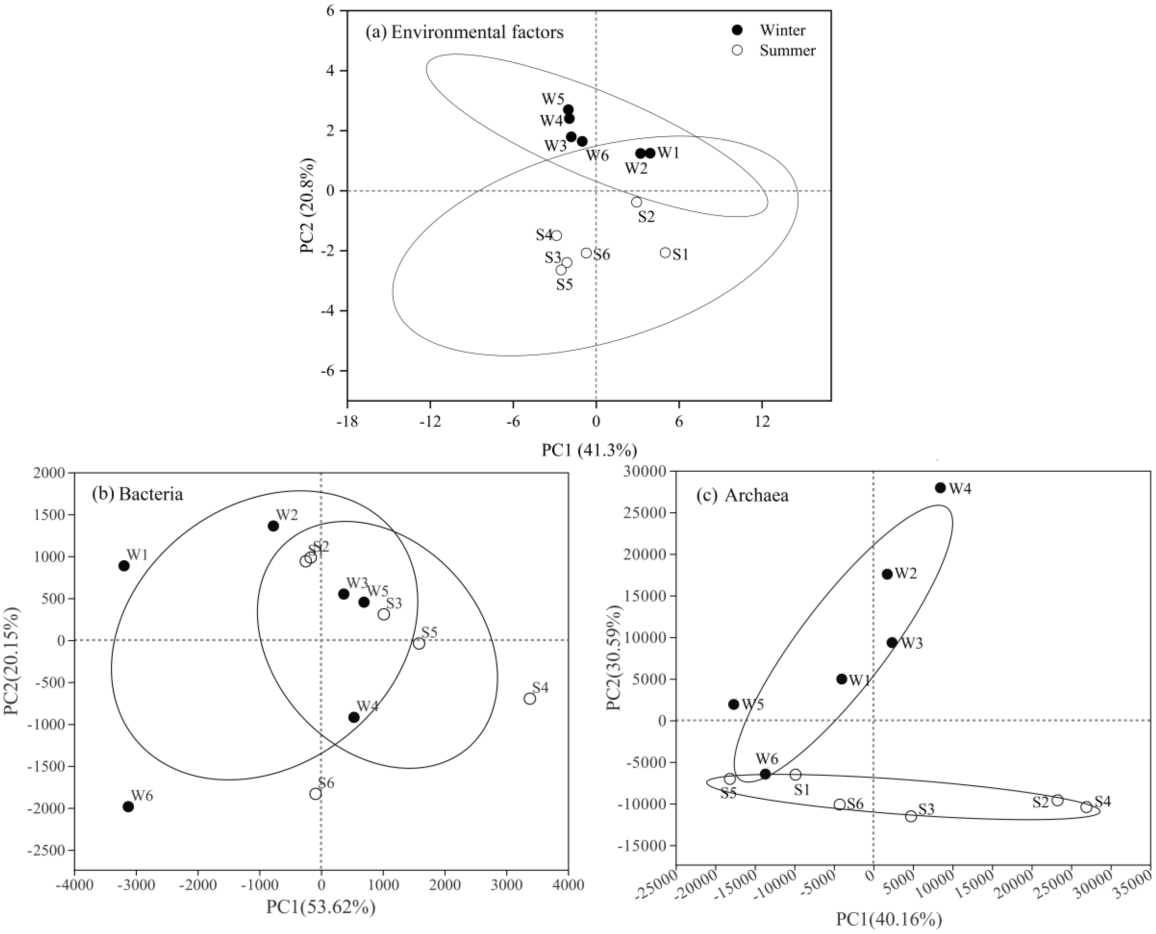

Figure.2 PCA (Principle component analysis) of environmental factors(**a**), bacteria(**b**) and archaea(**c**) in winter and summer. 95% confidence ellipses of sampling groups were showed.

3.2 OTU number and diversity of bacteria and archaea

Under the influence of water transfer, OTU number and diversity of bacteria increased while that of archaea decreased. The average OTU numbers of bacteria were about 2750 and 3329 in the regular reach and the water-receiving reach, respectively (Table 3). The average OTU numbers of archaea were 538 and 335 in the regular reach and the water-receiving reach. The average Shannon diversity index of bacteria were about 6.2 and 6.5 in the regular reach and the water-receiving reach, respectively. The average Shannon diversity index of archaea were about 3.3 and 3.0 in the regular reach and the water-receiving reach.

Table 3 OTU number and α-diversity index of bacteria and archaea

Sample\Estimators	**Season**	**OTUs**		**Shannon Index**		**Chao Index**		**Coverage Index**	
		Bacteria	**Archaea**	**Bacteria**	**Archaea**	**Bacteria**	**Archaea**	**Bacteria**	**Archaea**
FR01	Winter	2822	590	6.06	3.56	3768.44	733.13	0.98	0.99
	Summer	2149	504	5.94	3.32	2859.82	602.89	0.99	0.99
FR02	Winter	3146	512	6.51	3.10	4103.01	610.25	0.98	0.99
	Summer	2884	456	6.42	3.17	3857.02	619.43	0.98	0.99

FR03	Winter	3631	582	6.76	3.26	4722.66	789.59	0.97	0.99
	Summer	3549	392	6.86	2.95	4470.78	553.25	0.98	0.99
FR04	Winter	3659	363	6.77	3.08	4717.44	462.13	0.98	0.99
	Summer	3602	237	6.92	3.03	4479.15	326.44	0.98	0.99
FR05	Winter	3441	288	6.51	2.42	4513.04	380.57	0.98	0.99
	Summer	3737	298	7.01	2.94	4746.85	385.15	0.98	0.99
FR06	Winter	2708	335	5.79	2.89	4044.36	450.93	0.98	0.99
	Summer	2303	348	5.76	3.06	3261.68	461.56	0.98	0.99
Average	Winter	3234.5	445	6.40	3.05	4311.49	580.51	0.98	0.99
	Summer	3037.3	372.5	6.48	3.08	3945.88	491.45	0.98	0.99

The average OTU number of bacteria and archaea was higher in winter than that in summer, which is the same as the result of Chao index, indicating the abundance of bacteria and archaea was higher in winter than in summer. However, Shannon diversity of bacteria and archaea increased from summer to winter in different degrees (1.23% for bacteria, and 0.97% for archaea). The sequencing data are sufficiently representative because the coverage indexes of all the twelve samples were greater than 0.974.

In our case, the water diversion induced greater impacts on the OTU number and diversity of the microbial community than seasonality. Compared to the regular reach, the average of OTU number decreased by 37.7% for archaea, while the average of OTU number increased by 21.1% for bacteria. Moreover, the average of Shannon diversity index increased by 5.1% for bacteria and decreased by 11.3% for archaea because of water diversion. From summer to winter, the average OTU number increased by 6.5% for bacteria and 19.5% for archaea, respectively. Moreover, the average of Shannon diversity index decreased by 2.6% for bacteria and 1.0% for archaea.

The sites of FR02 and FR03 are located close to each other and are respectively distributed in the upstream and downstream of Toumaying where the Yellow River water is injected into the Fen River. The number of bacteria OTU and Shannon diversity index increased in the site FR03 as the result of the water diversion.

3.3 Bacteria and archaea community structure and classification

PCA used sample points and 95% confidence ellipse to represent the similarity and difference of community composition between sample groups. The influence of water diversion on sediment bacteria was beyond the influence of seasonality in the Fen river. The first and second principal coordinates of the weighted analysis accounted for 53.62% and 20.15% of the variation in the data, respectively (Fig.2b). PC1 clearly separated the samples in FR01, FR02 and FR06 from other samples. FR01 and FR02 located at the upstream of the place the Yellow River water injected into Fen river and FR06 after the long-distance self-purification of water bodies so they were not affected by the water diversion project and the bacterial community structures of them were quite different from other sampling sites. PC1 axis represented the influence of water diversion project on bacterial community. Meanwhile, the distribution of bacteria samples was compact in winter and dispersed in summer, indicating that the spatial heterogeneity of bacterial community structure was greater in summer than in winter.

PC1 axis (accounted for 40.16%) separated the samples in FR01, FR05 and FR06 from other samples which indicated PC1 axis represented the influence of water diversion project on archaea community and water diversion project on archaea of Fen river sediments had implications on FR02-FR04 (Fig.2c). The spatial distance of the effect on archaea was less than that on bacteria. The PC2 axis (accounted for 30.5%) failed to separate the samples of the archaea community in different seasons.

3.4 Identification of diversion-responders and season-responders

Responses of bacteria and archaea with 15 highest abundance to the water diversion or seasonal variation were identified by Wilcoxon rank-sum test (Fig. 3). The bacteria and archaea that have p value less than 0.11 were selected as responders [24,25]. The bacteria and archaea that have p value less than 0.25 but more than 0.15 were thought as responded environmental change obviously. For bacteria in the genera level, *Hydrogenophage* and *Cyanobacteria* ($p = 0.1052$), *Comamonadaceae*, *Luteolibacter* and *Nitrosomonadaceae* ($p = 0.2472$, Fig.3a) obviously responded to the water diversion in winter, while *Saprospiraceae* ($p = 0.1052$), *Bacillus*, *Lactococcus*, *Rhodobacter* ($p = 0.2472$ Fig. 3b) can respond distinctly in summer. Diversion-responders are more in winter than in summer. The results of Qv also showed that the bacteria were more responsive to water diversion in winter [23]. The possible reason was that the flow of rivers was more dependent on diversion in winter due to the monsoon climate in the mid-latitudes. No bacteria were selected as season-responders but all bacteria with 15 highest abundance responded seasonality obviously (Fig.3e). *Bacillus*, *Comamonadaceae*, *Flavobacterium* and *Arenimonas* responded significantly to both water diversion and seasonality ($p > 0.05$, Fig.3g). *Bacillus* decreased while *Comamonadaceae*, *Flavobacterium* and *Arenimonas* increased from winter to summer. In our case, the diversion-responders are more than the season-responders.

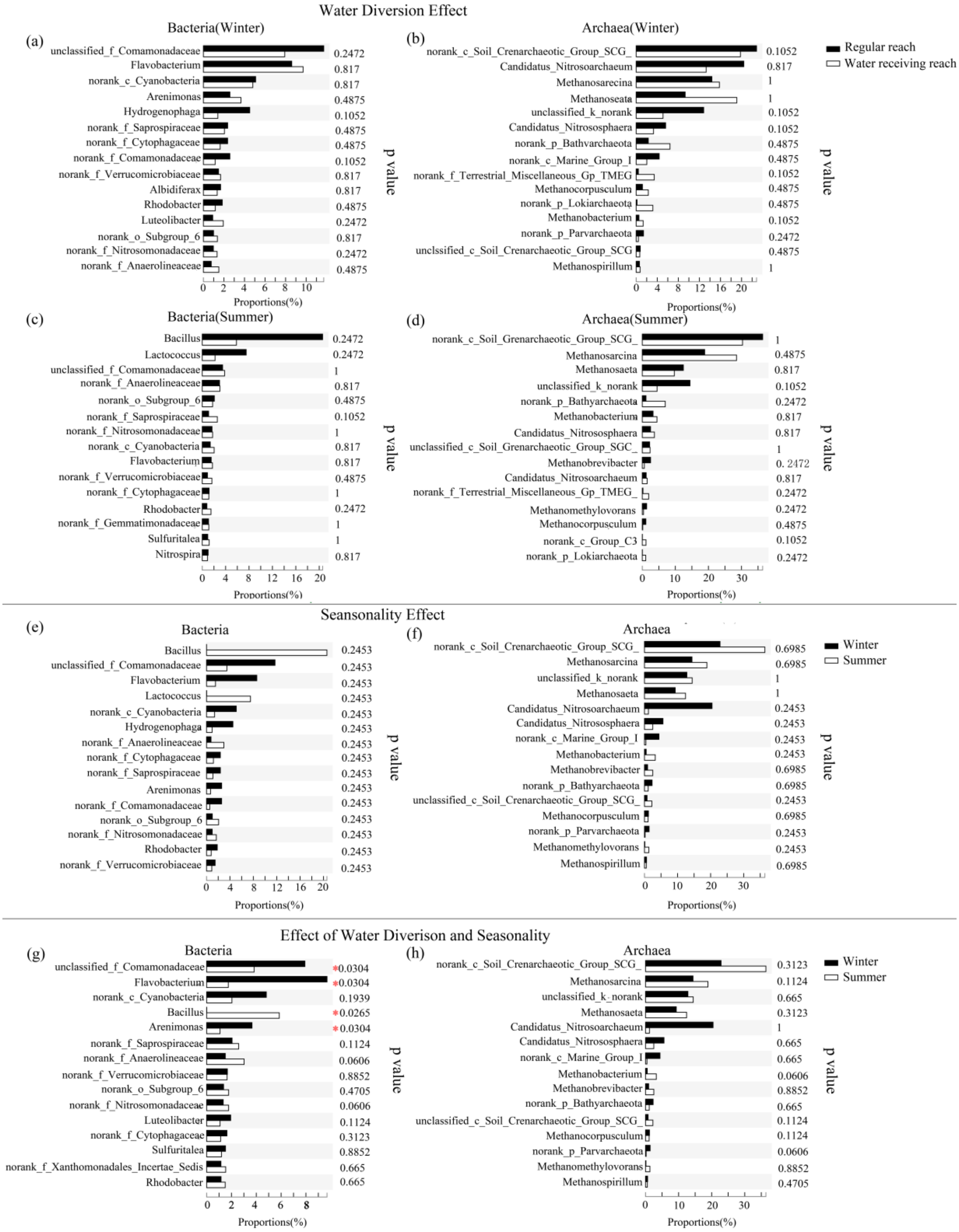

Figure.3 The strength of bacteria(**a**) and archaea(**b**) in winter, bacteria(**c**) and archaea(**d**) in summer responded to water diversion. Strength of bacteria(**e**) and archaea(**f**) in regular reach responded to seasonality. Strength of bacteria(**g**) and archaea(**h**) in water receiving reach responded to water diversion and seasonality by Kruskal-Wallis H test. The significant level was symbolled as: *: $p \leq 0.05$.

The archaea genera responded obviously to the water diversion included *SCG*, *Nitrososphaera*, *Terrestrial Miscellaneous Euryarchaeal Group* (TMGE), *Methanobacterium*, *unclassified_k_norank* (p = 0.1052) and *Parvarchaeota* in winter (p = 0.2472, Fig. 3b). In summer, archaea genera response obviously to the water diversion included *Unclassified_k_norank archaea*, *Methanocorpusculum* (*p* = 0.1052) and *Bathyarchaeota Methanobrevilbacter*, *TMEG*, *Methanomethylovorans*, *Lokiarchaeota* (*p* = 0.2472, Fig. 3d). There were more archaea obviously responding to the water diversion in winter. There were no season-responder archaea in water-receiving reach (Fig. 3f). And no archaea with 15 highest abundance responded significantly to both water diversion and seasonality (Fig. 3h).

The responses of the bacteria and archaea with 15 highest abundance groups to the water diversion were more obvious than that to the seasonal variation. The effect of the water diversion on bacteria and archaea was more obvious in winter. In the regular river reach where seasonal variation factors impacted alone, the response of bacteria with 15 highest abundance was extensive and uniform, while that of archaea with 15 highest abundance was weak. In the water-receiving river reach where seasonal changes and the water diversion impacted simultaneously, the response of 4 genera bacteria was significant, while only one species of archaea showed a relatively obvious response.

4. Discussion

4.1 Water transfer is a more significant driver of microbial community changes than seasonality

Seasonal variation is often the most important factor affecting water system bacteria and archaea in mid-latitudes. Seasonal dynamics had a greater impact on the formation of bacterial communities than the effects of anthropogenic pollution on rivers [26]. The seasonal variation of bacterial and archaeal structures didn’t change after wetland drainage [27]. Significant seasonal changes and non-significant spatial changes can be simultaneously observed in the beta diversity and community structure of sediment bacteria in a mid-latitude lake [28]. The seasonal variation of rainfall was considered as a key factor affecting the abundance and diversity of bacteria and archaea [29]. However, the water diversion is a more significant driver of microbial community OTU number, diversity index, and community structure variation than seasonality in our case.

In this study, the average Shannon index of bacteria and archaea in summer was higher than that in winter (Table 3). Generally, diversity of bacteria and archaea is high in warm seasons and low in cold seasons [30-32]. It was reported that the bacterial diversity in river sediments from five different pollution sites was higher in summer than in winter [33]. Microorganisms always show the best temperature characteristics [34,35]. The composition of bacterial community and archaea community changed with the fluctuation of water temperature. Increased nutrient levels also contribute to the growth of bacterial communities in summer [36]. Seasonality of water temperature and nutrition could play an important role in seasonal variance of bacteria and archaea. It was considered as the reason that the densely growing phytoplankton and benthic plants in summer could stimulate the specific activity, growth efficiency and proliferation of bacterial cells [38,39]. The assimilation material released by these organisms is used by bacteria as a food or energy source, increasing their abundance. Furthermore, farmland irrigation in summer can lead to the increase of nitrogen and phosphorus content in natural channels which could explain the increase of total nitrogen and phosphorus in Fen River (Table 2) [37]. Therefore, the content of nitrifying and desulphurizing bacteria increased [38,39].

Our data also showed the average OTU numbers of bacteria and archaea in summer were lower than that in winter in water-receiving reach (Table 3). It is notable that OTU numbers of bacteria and archaea decline in summer. In previous study, OTU number of bacteria and archaea were also high in summer and low in winter [30-32]. Salinity changes should be responsible for the result. The salinity of water is determined by soil leaching, rock weathering, and pollution [40,41]. The OTU numbers of bacteria and archaea in freshwater ecosystems were significantly positively correlated with EC value of water (as an indicator of salinity) [42]. In our case, water transfer from the Yellow River brought not only nutrients (caused an increase of 43.53% for TN, and an increase of 17.86% for TP) but also salinity (increased by 2.5 times) to the Fen River. The receiving reach of the Fen River was more affected by the water diversion in winter. According to these reports and our results, we speculated this abnormal phenomenon in our case was because water diversion project was a more significant diver of microbial community changes than seasonality.

Responses of bacteria and archaea's community structures to water diversion were more significant than that to seasonality. *P* value represents the possibility of rejecting hypothesis that water diversion or seasonality has no effect on microbial community changes [25]. When water diversion impacted alone, the p value of the sediment bacterial and archaeal community was as low as 0.1052. When the seasonality impacted alone, the p values of that were 0.2472 (Fig.3). The results indicate that the water diversion is more possible factor than the seasonal variation of environment in promoting changes in a microbial community structure.

Under the strong influences of the water diversion, the OTU number and diversity of bacteria and archaea responded more strongly to seasonal variation (Table 3). We could offer two explanations relating with the water transfer for the strong response of bacteria and archaea. One was high concentration of nutrients, EC value and pH value in water body of the Yellow River went into Fen river by water diversion project. It was reported that the TN concentration of the Yellow River sediments (35.3 ~ 1142.5 mg kg^{-1}) was much higher than that of the Fen river sediments. EC value and pH value in the transferred Yellow River was stable above 1000 μS/cm and 8, respectively [43]. Therefore, water diversion obviously increased the TN concentration by 88% in winter (Table 2) and the EC value from 535 μS/cm to 1257 μS/cm in winter and from 436 μS/cm to 1205 μS/cm in summer, pH value of the water-receiving river from 7.8 to 8.05 in winter and from 8.35 to 8.91 in summer (Table 1). Nitrogen is important for nitrifying and denitrifying bacteria and archaea. Most archaea with 15 highest abundance were methanogens (according to Berger's handbook of systematic bacteriology, Fig.3). The number of methanogens obviously decreases with salinity [44]. The increased pH value can obviously inhibit the OTU number of archaea [45]. As a seasonal river, Fen river had low water level and velocity in winter naturally, so water from the Yellow River played a more important role. The other was, in Fen reaches, the influence of water diversion on river water volume and velocity exceeds seasonality. Water from the Yellow River was injected at a rate nearly 15 m3/s, which was roughly 30 times higher than the dry-season flow of the Fen river at this site [46], bringing high water velocity, which strongly dilutes the bacteria in the sediment, thus producing positive nitrogen [47,48]. TN was one of the key factors relating to bacterial community structure and composition which would affect bacteria and archaea obviously [49].

4.2 Diversion-responders more than season-responders

In our case, diversion-responders were more than season-responders in bacteria (Fig.3). Almost all diversion-responders are carbon - nitrogen cycle related. When total nitrogen concentration increasing, these bacteria would respond obviously. *Hydrogenophage* is a kind of denitrifying bacteria and had positive interactions with other denitrifying bacteria [50]. Cyanobacteria is positively corelated to nitrogen concentration [51]. *Comamonadaceae* is a common denitrifying bacterium in water [52]. *Luteolibacter* is independent of the nitrogen cycle and mainly uses iso-$C_{16:0}$ and iso-$C_{15:0}$, which play an important role in the carbon cycle in the environment [53]. *Nitrosomonadaceae* is a typical nitrite oxidizing bacterium [54]. *Saprospiraceae* have the ability to hydrolyze and utilize complex carbon sources, and this bacterium may also play an important role in the decomposition of complex organisms [55]. Compared with conventional denitrification bacteria, the *Flavobacterium* grow well under aerobic conditions and show good denitrification activities [56-59]. *Bacillus* are often used to indicate good quality water bodies [60]. *Bacillus* remained one of the dominant bacteria, although its abundance declined with the onset of winter or water degradation after diversion. Some of the bacteria in this genus were heterotrophic nitrifying bacteria and vulcanized bacteria, which had obvious response to nitrate nitrogen [61]. *Lactococcus* is a pathogenic bacterium capable of causing sepsis in fish and humans [62,63], and is also a common heterotrophic denitrifying bacterium in the environment [64]. *Rhodobacter* contain autotrophic bacteria and heterotrophic bacteria that can utilize carbon sources [65]. Xing [66] used a stable-isotope probing technique and reported that *Arenimonas* is capable of removing nitrate. Denitrification bacteria were dominant in the sediments of the water-receiving reach of Fen River, and the nitrogen in this reach was fractionated [67]. The main reason for the rise in nitrogen concentration in river water is diversion (88 % for water diversion, 39% for seasonal variation, Table 2). Due to that, more responders were sensitive to water diversion.

We had more diversion-responders than season-responders in archaea (Fig.3). We believed the reason diversion-responders were more than season-responders in archaea is that EC value increasing of the water-receiving river. *Methanobacterium*, *Methanocorpusculum*, *Methanobrevilbacter*, *Methanomelovorans* are all typical methanogens [44,68]. Methanogens occupy a unique niche in the anaerobic environment and are the ultimate acceptor of electrons [69]. We speculated that the dominant position of methanogens increased after water transfer, because the increase of water EC provided electrons for methanogens. Possibly, this characteristic of the dominant methanogenic archaea caused more archaea species with a p value of less than 0.2472 than bacteria in the water-receiving reach. *Nitrososphaera* belongs to ammonia-oxidizing archaea, and its response to most inhibitors was weaker than that of ammonia-oxidizing archaea [70]. *TMEG* has been detected many times under extremely acidic conditions, and scientists speculated that this genus of archaea had acidophilic members [71,72]. Some studies have shown that *Parvarchaeota* was only found in acid mine drainage and hot spring habitat, and belongs to microaerobic/anaerobic archaea, which was involved in carbon, nitrogen and iron cycling [73]. However, in the Fen reaches, *Parvarchaeota* emerged as the dominant archaea, indicating that this genus of archaea had a wider habitat distribution than expected. *Bathyarchaeota*, with complex organic proteins, lipids and benzoic acid as the main metabolites, is widely found in the environment [74]. *Lokiarchaeota* is a genus of archaea with a series of pathways involving the carbon, nitrogen, sulfur and phosphorus cycles in its macrogenes [75,76].

4.3 Responses of high-abundance bacteria and archaea to environmental factors reduced by water diversion

When seasonal factors impact alone, ORP, EC, TDS, pH, temperature, SO_4^{2-}, AK, OP and AN significantly affected bacteria. The bacteria with 15 highest abundance showed the opposite response to ORP, EC, TDS and pH, temperature, AK, OP, SO_4^{2-}, AN which was named as niche complementation effect (Fig. 4a). *Bacillus* and *Lactococcus*, *Anaerolineaceae*, *Supgroup_6*, *Nitrosomonadaceae* showed obvious negative correlation to ORP, EC, TDS, and positive correlation to pH, temperature, AK, OP, SO_4^{2-}, AN. *Comamonadaceae*, *Flavobacterium*, *Cyanobacteria*, *Hydrogenophaga*, *Saprospiraceae*, *Cytophagaceae*, *Arenimonas*, *Comaonadaceae*, *Rhodocater* had obvious positive correlation with ORP, EC, TDS, and significant negative correlation to pH, temperature, AK, OP, SO_4^{2-}, AN. In previous studies, temperature was often considered to be one of the key environmental factors that caused seasonal changes in bacterial communities in aquatic ecosystems. Inter-seasonal temperature fluctuations could partly explain seasonal changes in bacterial community structure and diversity [33]. During the rainy season, the warm environment was conducive to the growth of bacteria [77]. Temperature and salinity were the key environmental factors leading to the seasonal dynamics of bacterial communities [78]. Our results demonstrated that the seasonally-driven mechanisms leading to changes of bacterial communities in the river sediments were actually more complex. Nutrients also played an important role on affecting bacteria in seasonal change process. Interestingly, *Verrucomicrobiaceae* exhibited weak or no correlation with the above environmental factors but it was often the dominant bacterium after water transfer [43,79].

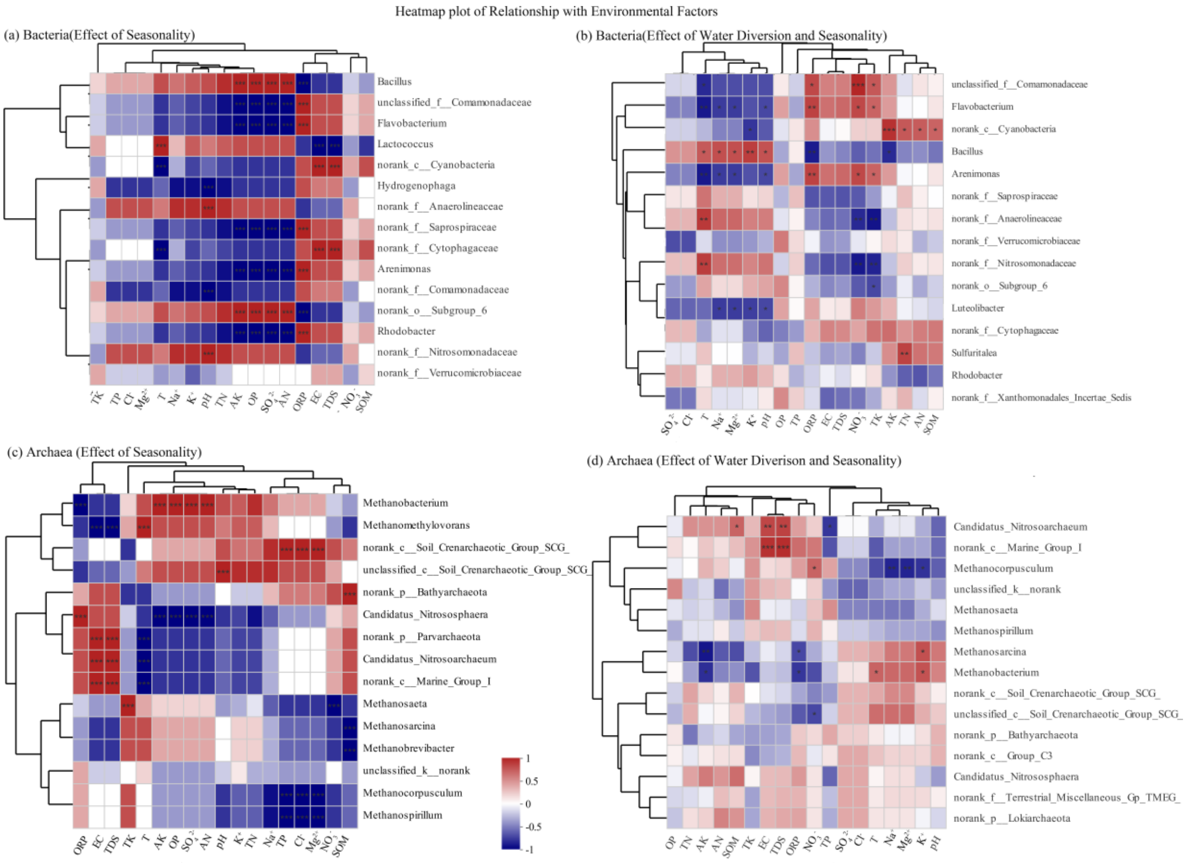

Figure.4 Spearman coefficients between bacteria(**a**) and archaea(**b**) in regular reach, bacteria(**c**) and archaea(**d**) in water-receiving reach and environmental parameters. The significance level was symbolled as: *: $p \leq 0.05$.

When factors of water diversion and seasonal variation impacted collectively, the environmental factors that had a significant impact on the main bacterial communities in water-receiving reach were significantly responsive to water diversion, including temperature, Na^+, Mg^{2+}, K^+, pH, ORP, NO_3^-, and TK (Fig.4b), which indicating water diversion had an important effect on the dominant bacteria. The bacteria with 15 highest abundance in water-receiving reach could be divided into two types that were complementary to the response to environmental factors. The bacteria in the top 15 abundance of water-receiving reach showed opposite responses to temperature, Na^+, Mg^{2+}, K^+, pH and ORP, NO_3^-, TK. Among them, *Bacillus*, *Anaerolineaceae*, *Supgroup_6*, *Nitrosomonadaceae* showed obvious positive correlation to temperature, Na^+, Mg^{2+}, K^+, pH, while presented obvious negative correlation relationship to ORP, NO_3^-, TK. *Comamonadaceae*, *Flavobacterium*, *Arenimonas*, *Luteolibacter* showed significant negative correlation relationship to temperature, Na^+, Mg^{2+}, K^+, pH, presented obvious positive correlation relationship to ORP, NO_3^-, TK. In particular, Cyanobacteria showed obvious negative correlation with temperature, Na^+, Mg^{2+}, K^+ and pH, little correlation with ORP, NO_3^- and TK, and a significant positive correlation with indicators indicating nutrient concentration such as AK, TN, AN and SOM.

Temperature, pH and ORP have been the key environmental factors both in the regular reach and water-receiving reach. Temperature and ORP had a significant response to seasonal change (Table 1), indicating that the influence of seasonal change has been impacting on the whole study reach, which was the same as previous studies [80,81]. Therefore, the species in the top 15 abundance showed obvious response to seasonal changes ($p \geq 0.2472$, Fig.3g). In contrast, EC, TDS, AK, OP, SO_4^{2-}, and AN were no longer the key environmental factors in water-receiving reach. They were transformed into Na^+, Mg^{2+}, K^+, NO_3^-, and TK. Water transfer project made nutrients impact on sediment bacteria was abate, river sediment bacteria mainly controlled by salinity.

In previous studies, *Cyanobacteria* tended to be positively correlated with temperature [82,83]. However, Haakonsson's study [84] proved that this phenomenon only existed in the static water system. The growth promotion effect of temperature rise on the *Cyanobacteria* was greatly weakened in the flowing river [85,80]. The study of Amazon river reach with many tributaries showed that discharge and water salinity were the principal variables for constructing a series of environmental changes [86]. Our results supported both theories. In this study, the abundance of *Cyanobacteria* in winter was much higher than that in summer. We speculated water body was influenced more in winter by the water diversion because of the increase of water flows velocity, a good water circulation and increased the nutrient level in winter, which resulting in weakening of positive correlation between *Cyanobacteria* and temperature. Due to that, *Cyanobacteria* increased in winter and showed negative correlation to temperature. This mechanism also affected *Flavobacterium*, a kind of aerobic denitrifying bacteria, was provided aerobic conditions and food sources by higher water flow velocity after the water transfer, which inhibited the growth of other denitrifying bacteria. Therefore, the *Flavobacterium* had become the dominant bacteria in the water receiving reach and showed the same relationship with environmental indicators as *Cyanobacteria*.

When seasonal factors impact alone, almost all the environmental factors measured could cause significant responses in archaea in the top 15 of abundance (Fig.4c). These archaea could be divided into three categories according to their response to environmental factors. (1) *Methanobacterium*, *Methanomethylovorans* and *SCG* showed obvious positive correlation to temperature, AK, OP, SO_4^{2-}, AN, pH, K^+, TN, Na^+, TP, Cl^-, Mg^{2+} and NO_3^-, while showed obvious negative correlation to ORP, EC and TDS. Among them, the correlation index between *Methanomethylovorans* and Cl^-, Mg^{2+}, NO_3^- was 0. (2) The correlation index of *Norank_c_Soil_Crenarchaeotic*, *Group_SCG_* to EC, TDS and temperature was 0. *Bathyarchaeota*, *Nitrososphaera*, *Parvarchaera*, *Nitrosoarchaeum*, *Marine_Group_I* presented obvious positive correlation to ORP, EC, TDS, and showed significant negative correlation relationship to the temperature, AK, OP, SO_4^{2-}, AN, pH, K^+, TN; (3) *Methanosaeta*, *Methanosarcina*, *Methanobrevibacter*, *Methanocorpisculum* and *Methanospirllum* showed significant negative correlation to AK, OP, SO_4^{2-}, AN, pH, K^+, TN, Na^+, TP, Cl^-, Mg^{2+}, NO_3^-, SOM, for TK was significantly positive correlation.

When factors of water diversion and seasonal variation impacted at the same time, the response mechanism of archaea community to environmental factors in Fen sediments in water-receiving reach became complex (Fig. 4d). There was only a significant correlation between a few environmental factors and a few archaea. After water diversion, the number of environmental factors that could affect the archaea in top 15 abundance decreased at the significance level.

In regular river reach only affected by seasonal factors, the bacteria and archaea in top 15 abundance had obvious responses to environmental factors. In water-receiving reach affected by seasonal factors and water diversion factors, the correlation of microorganism and environmental factors reached significance level decline. At the same time, abundance of microorganism was not sensitive to environmental factors changed of increase. Resulting in microorganism of Fen river sediment with 15 highest abundance response to environmental factors of was weak totally, the response mechanism became more complex. According to Qu [23], after water diversion, the ecological niche range of microorganism (OMI value) in the water-receiving reach increased, competition among dominant species became fiercer, and species' ability to utilize a variety of environmental resources was enhanced. So, the response of a single species to a particular environmental factor was weaker. At the same time, water diversion and seasonal factors impacted together, the species with no obvious response to environmental factors were more likely to become the dominant bacteria.

5. Conclusions

The influence of the water diversion on environmental factors and OTU number，diversity index and community structure of bacteria and archaea in the water-receiving river beyond seasonal variation. We had two explanation of this phenomenon. One was high concentration of nutrients, EC and pH value in water body of the Yellow River went into Fen river by water diversion project. As a seasonal river, Fen river had low water level and velocity in winter naturally, so water from the Yellow River played a more important role. The other was, in Fen reaches, the influence of water diversion on river water volume and velocity exceeds seasonality to producing positive nitrogen. Therefore, water diversion had a greater impact on bacteria and archaea in winter.

According to specific diversion-responders and season-responders were identified, we had more diversion-responders than season-responders both in bacteria and archaea. We speculated the reason diversion-responders were more than season-responders in bacteria is that almost all responders are carbon - nitrogen cycle related. When total nitrogen concentration increasing, these bacteria would respond to them. For archaea, the reason is that EC value increasing of the water-receiving reach. Methanogens dominated archaeal community in Fen river and could be inhibited by high EC value.

Temperature, pH and ORP have been the key environmental factors both in the regular reach and water-receiving reach. After water diversion, the environment indicators could affect bacteria community changed from nutrients to salinity. While the environment indicators could affect archaea community almost disappeared. Interestingly, the correlation between bacteria and archaea and environmental factors was obviously weakened when water diversion and seasonality impact collectively due to the ecological niche range of microorganism (OMI value) increased.

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