SCIENCE CHINA
Earth Sciences

•RESEARCH PAPER•

February 2019 Vol.62 No.2: 459–472
https://doi.org/10.1007/s11430-017-9269-3

# Responses of benthic foraminifera to changes of temperature and salinity: Results from a laboratory culture experiment

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Received August 30, 2017; revised July 7, 2018; accepted July 11, 2018; published online December 4, 2018

**Abstract** The effects of temperature and salinity on intertidal foraminiferal community under laboratory conditions are poorly understood. We designed a two-factor crossed experiment in which foraminiferal communities were cultured at different temperatures (6, 12, and 18°C) and salinities (15, 20, 25, and 30 psu) for 10 weeks. In total, 2616 living (stained) specimens were obtained and analyzed. Foraminiferal abundance ranged from 9 to 202 individuals/10 g wet weight of sediment. The highest abundance was obtained at 12°C, 25 psu and the lowest at 6°C, 15 psu. Statistical results demonstrated that temperature affected foraminiferal community more significantly than salinity. Most foraminiferal community parameters (abundance, species richness, Margalef index, and Shannon-Wiener diversity) were significantly positively correlated to temperature, but not to salinity, whereas Pielou's evenness was significantly negatively correlated to both temperature and salinity. The interactive effect of temperature and salinity on foraminiferal abundance was significant. In addition, with increasing temperature, the species composition shifted from hyaline Rotaliida to porcellaneous Miliolida. The abundance of dominant species (e.g., *Ammonia aomoriensis*, *A. beccarii*, and *Quinqueloculina seminula*) showed significant positive correlations to temperature. Our study indicated that the intertidal foraminiferal community responds sensitively and rapidly to the changes of salinity and, especially, temperature by shifting foraminiferal species composition and altering the community parameters.

**Keywords** Benthic foraminifera, Community parameter, Temperature, Salinity, Culture experiment, Intertidal zone

**Citation:** Dong S, Lei Y, Li T, Jian Z. 2019. Responses of benthic foraminifera to changes of temperature and salinity: Results from a laboratory culture experiment. Science China Earth Sciences, 62: 459–472, https://doi.org/10.1007/s11430-017-9269-3

## 1. Introduction

Benthic foraminifera are widely used as paleoenvironmental proxies because of their high sensitivity to environmental changes and excellent preservation potential in sediment (Kitazato and Bernhard, 2014; Murray, 1991). In intertidal environment, benthic foraminifera are abundant, widespread, and diverse, which have been extensively studied (Culver and Buzas, 1995; de Rijk, 1995; Horton et al., 1999; Murray, 2006). Intertidal environments are particularly sensitive to environmental changes, such as climatic change, heavy rain, river input, sea level rise, and human activities (de Rijk, 1995; Hayward et al., 2004; Scavia et al., 2002). Especially in the temperate zone, intertidal environments are subjected to seasonal changes in climate, and it is reasonable to expect that the biotic community is affected by this (Murray and Alve, 2000).

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Some studies, most of which were field studies, have investigated the foraminiferal distribution, community structure, and seasonal change in intertidal areas (Alve and Murray, 2001; Berkeley et al., 2007; Hayward et al., 2004). Some relationships between environmental factors and foraminifera have been established to explain the changes in benthic foraminiferal community (Nigam, 2005; Papaspyrou et al., 2013; Saad and Wade, 2016) and reconstruct paleoenvironments (e.g., the past sea level and monsoon change) (Berkeley et al., 2007; Horton et al., 1999; Scott and Medioli, 1978).

Despite numerous ecological studies, the influence of environmental factors on benthic foraminiferal community is still poorly understood (Li et al., 2015). The mechanisms underlying the results observed in past foraminiferal studies remain largely unexplained, and the response of foraminiferal community to environmental factors may be region-specific. For example, Basson and Murray (1995) found a dramatic change in foraminiferal abundance and diversity in an intertidal area of Bahrain, Arabian Gulf between July and August 1992, but the cause was unknown. Alve and Murray (2001) found that seasonal cyclicity was strongly exhibited by species diversity but not by foraminiferal abundance in Hamble Estuary, England. Buzas et al. (2002) found that their tested environmental factors provided little explanation about the changes in foraminiferal densities in Indian River Lagoon, Florida. Environmental factors are not independent, and the responses of foraminifera usually reflect the combined effects of the measured environmental factors and other unknown biotic and abiotic factors in the field. Therefore, it is difficult to discern cause-effect relationships between environmental factors and changes in benthic foraminiferal community in field studies, especially with interactive effects. Therefore, a laboratory culture experiment is the most direct and effective method to study the effects (or interactive effects) of one or more factors while keeping the others under constant control (Nardelli et al., 2013). Some culture experiments for individual foraminiferal species have been performed, establishing relationships between environmental factors and benthic foraminifera, e.g. *Ammonia* sp. (Dissard et al., 2010; Haynert and Schönfeld, 2014), *Amphistegina* sp. (Prazeres et al., 2016; Schmidt et al., 2011), *Elphidium* sp. (Allison et al., 2010), and *Rosalina* sp. (Nigam et al., 2008; Saraswat et al., 2011). However, culture experiment for individual species could not explain the relationships between environmental factors and foraminiferal community. Therefore, a laboratory culture experiment with a complete foraminiferal community in a natural sedimentary environment may be the best method to address this problem. Few studies have reported culture experiments with a complete foraminiferal community (Goldstein and Alve, 2011; Gross, 2000; Haynert et al., 2014; Weinmann and Goldstein, 2016). However, many of them studied community response to several environmental factors (e.g., temperature, salinity, site, oxygen, food availability, and $pCO_2$) separately and none focused on the interactive effect of environmental factors.

Salinity could affect the osmoregulation of a cell and lead to a change in foraminiferal distribution (Bé and Hutson, 1977; Debenay et al., 2000). Temperature could affect enzyme activity and consequently, foraminiferal growth (Lombard et al., 2009; Prazeres and Pandolfi, 2016). Temperature and salinity may be key environmental factors regulating foraminiferal community in intertidal areas. In addition, foraminifera are frequently used as temperature and salinity key proxies to reconstruct paleoenvironments.

To investigate the responses of intertidal benthic foraminiferal community to temperature and salinity, we conducted a laboratory culture experiment for benthic foraminiferal community from Qingdao Bay. Qingdao Bay (36°00′N, 120°30′E; Appendix Figure S1, http://earth.scichina.com) is a muddy-sand intertidal flat, located on the southern coast of the Shandong Peninsula in the eastern China, where foraminifera are abundant and widely distributed (Lei and Li, 2016). Previous studies have provided substantial background information about the distribution, composition, and community parameters of foraminifera in Qingdao Bay (Lei and Li, 2016; Lei et al., 2017a), but no culture experiment has been reported. Our study aimed to determine the response of benthic foraminiferal community to changing environmental factors (temperature and salinity) under laboratory culture conditions and to establish the relationships between foraminiferal community and environmental factors.

## 2. Materials and methods

### 2.1 Sample collection

Surface sediments (top 5 mm) over an area of approximately 1 $m^2$ were collected from a silt-sand beach using a spoon. The sediments samples were collected at low tide from Qingdao Bay on July 15, 2014. Sediment temperature was measured using a spirit thermometer (precision: 1°C) and was 23°C. Salinity was measured with a portable refractometer (precision: 1 psu) and was 30 psu. No specific permits or approvals were required to collect sediments at this site. The sample site was not privately owned or protected in any way. No endangered or protected species were involved.

### 2.2 Experimental design

After collection, sediments were transported to the laboratory in 500-mL plastic bottles filled with *in situ* seawater. In the laboratory, the sediments were mixed carefully and

thoroughly using a spoon in a plastic wash-basin, and 10 g (wet sediment) aliquots were scooped using a lab spoon, weighted using a balance, and then randomly placed in a series of columnar glass cylinders (9-cm diameter, 5-cm height), along with 150-mL of filtered (through 0.22-μm-pore filter) *in situ* seawater. To reduce evaporation during the experiment, the glass cylinders were sealed using parafilm with a few tiny holes. All materials were acid-cleaned in 2 M HCl for 24 h and thoroughly rinsed with deionized water prior to their use in the experiment. *Nitzschia closterium* was separated from sediment previously collected from Qingdao Bay and cultured to serve as food in an f/2-medium at 18°C under 2000 lux, with a 12-h light/dark cycle (Lee et al., 1961; Lei et al., 2016).

For this study, we used three constant temperatures (6, 12, and 18°C) and four constant salinities (15, 20, 25, and 30 psu). Each treatment was performed in triplicate, yielding 36 glass cylinders (3 temperatures×4 salinities×3). All treatments were kept in temperature-controlled incubator (precision: 1°C) with artificial lighting (2000 lux with a 12-h light/dark cycle) to promote algal growth in the sediments. The seawater was changed twice weekly (salinity was unchanged). All treatments were simultaneously fed with 1-mL of concentrated *N. closterium* (approximately $1\times10^8$ cells $mL^{-1}$).

The salinity of *in situ* seawater was altered by adding deionized water or evaporating at room temperature to reach the desired salinity. The measurements were made using a portable refractometer (precision: 1 psu).

Before the experiment, three additional samples (10 g wet weight of sediment) were preserved as *in situ* assemblages. These samples were treated using the following sample treatment procedures.

### 2.3 Sample treatment

After 10 weeks of culturing, all samples were treated according to the Chinese National Standards of GB/T 34656-2017. The samples were fixed using 95% ethanol mixed with 1g $L^{-1}$ Rose Bengal for 48 h such that live and dead specimens could be distinguished. Each sample was dried at 50°C in the oven and weighed. Subsequently, it was sieved through 150-μm meshes. The foraminiferal specimens were concentrated by an isopycnic separation technique using tetrachloromethane ($D$=1.59), and the residues were carefully checked for omissions. Specimens >150 μm in size were picked with a fine brush and stored on micropaleontological slides to be used for species identification, counting, and enumeration. Microscopic observation and species identification were performed using a stereomicroscope (Olympus SZX16), with continuous zooming up to a maximum magnification of 115×. Species identification was based on Loeblich and Tappan (1988) and Lei and Li (2016).

We used the Rose Bengal staining method, but the reliability of its result has been challenged (Bernhard, 2000), mainly because the cytoplasm of dead foraminifera may get stained with the Rose Bengal several weeks after an individual's death (Bernhard, 1988, 2000). Nevertheless, it is still a sufficiently reliable method and offers a close estimate for the living assemblages, especially in oxygenated environments and superficial sediment samples (Fontanier et al., 2002). Moreover, it is also quick and inexpensive and is widely used in ecological studies (Bernhard et al., 2001; Frontalini et al., 2013; Murray and Alve, 2000; Papaspyrou et al., 2013; Weinmann and Goldstein, 2016). In our study, only the surface sediments (top 5 mm) were used and no anoxic phenomena were observed. In addition, strict staining criteria were applied to reduce the subjective interpretation of the staining of benthic foraminifera in our study. For hyaline taxon, specimens with all but the last few chambers stained brightly pink were counted as live. However, porcellaneous and agglutinated taxa were non-transparent, and thus, their stained protoplasm was difficult to observe. For both porcellaneous and agglutinated taxa, each specimen was thoroughly wetted with water, and the specimens with a tint of pink color were counted as live.

In this study, we analyzed only large foraminifera (>150 μm) to allow for direct comparison with the field study performed by Lei et al. (2017a). Other previous studies have also focused only on the large size fraction of >150 μm (Duros et al., 2014; Fontanier et al., 2002; Goineau et al., 2011, 2015; Stefanoudis et al., 2017). Smaller individuals (63–150 μm) were preserved for future studies; this group (63–150 μm) usually includes some small species or juveniles, which were difficult to identify. We analyzed the triplicates of each treatment; therefore, the result obtained in our study are relatively reliable and comprehensive reflections of the living species composition.

### 2.4 Statistical analysis

Only living foraminifera were included in statistical analyses. Community parameters were calculated using PRIMER v6.1.13 (Plymouth Routines in Multivariate Ecological Research); these included abundance ($N$, number of individuals (ind.) per 10 g wet weight (WW) of sediment), species richness ($S$, number of species), Margalef index ($D$), Shannon-Wiener diversity ($H'$), and Pielou's evenness ($J'$). The Margalef index assumes a logarithmic distribution of species abundances and is an index of species richness. The Shannon-Wiener diversity is a predictive index of species diversity based on the weighted means of proportional abundances. Pielou's evenness shows species evenness (Al-Sabouni et al., 2007). These factors were calculated as follows: Margalef index was measured using the equation $D=(S-1)/\ln N$, where $S$ is total number of species and $N$ is

total number of individuals; Shannon-Wiener diversity was measured using the equation $H' = -\Sigma Pi \ln Pi$, where $Pi$ is the proportion of total number of species made up of the $i$th species; Pielou's evenness was calculated using the equation $J' = H' / \ln S$, where $H'$ is Shannon-Wiener diversity and $S$ is total number of species. Species constituting no less than 5% of the community abundance were defined as dominant species.

According to Loeblich and Tappan (1988), foraminiferal species are divided into three taxa by shell structure: hyaline, porcellaneous, and agglutinated taxa. Coincidentally, in the present study, the three taxa of shell structure corresponded exactly to the three foraminiferal orders studied: Rotaliida, Miliolida, and Textulariida, respectively. Therefore, we analyzed them together, that was hyaline Rotaliida, porcellaneous Miliolida, and agglutinated Textulariida.

The submodule BIOENV was used to find a subset of the abiotic parameters (temperature and salinity) that most closely matched the biotic matrix to determine the comprehensive effects of environmental factors. The biotic Bray-Curtis similarity matrix (square root transformed) was generated from foraminiferal species-specific abundances and community parameters (community abundance, species richness, Margalef index, Shannon-Weiner diversity, and Pielou's evenness). The mean values of the triplicates of each treatment were used. The normalized environmental Euclidean distance matrix was generated from the data of temperature and salinity. The significance of biota-environment correlations was tested using the routine RELATE (Clarke and Gorley, 2006).

A two-way factorial ANOVA was used to test the effects of temperature and salinity on foraminifera. Tukey's honestly significant difference (HSD) post hoc test was used to check for differences between groups. Differences were considered statistically significant at $p<0.05$. When the interactive effect of temperature and salinity was statistically significant ($p<0.05$), the SAS program of "Contrast Statement" in "GLM (General Linear Model) Procedure" was performed to do pairwise comparison in different temperature when salinity was fixed and vice versa. In addition, univariate correlations (Spearman's $r$ values) between biotic and abiotic factors were analyzed. These analyses were performed using SAS for Windows version 9.2 (SAS Institute Inc., 2009).

## 3. Results

### 3.1 *In situ* assemblages

*In situ* foraminiferal assemblages collected from the intertidal area of Qingdao Bay contained 89 living (stained) specimens belonging to five species (Appendix Figure S2; Table S1). The corresponding assemblage abundance was on average 30 ind./10 g WW of sediment, with an average species richness of four. The Margalef index, Shannon-Wiener diversity, and Pielou's evenness were on average 0.89, 1.01, and 0.76, respectively. *In situ* assemblages were composed of on average 38.87% hyaline Rotaliida, 59.21% porcellaneous Miliolida, and 1.92% agglutinated Textulariida. The dominant species were *Ammonia aomoriensis*, *A. beccarii*, and *Quinqueloculina seminula*, representing on average 18.58%, 19.18%, and 59.21%, respectively.

### 3.2 Foraminiferal abundance

At the end of the experiment, foraminiferal abundance ranged from 9 to 202 ind./10 g WW of sediment and averaged 70 ind./10 g WW of sediment in all treatments. Foraminiferal abundance varied greatly among treatments, with 12°C and 25 psu (on average 162 ind./10 g WW of sediment) yielding the highest abundance and 6°C and 15 psu (on average 12 ind./10 g WW of sediment) yielding the lowest abundance (Figure 1). Both temperature and salinity had a statistically significant effect on foraminiferal abundance ($F$=84.18, $p$=0.0001 for temperature and $F$=16.06, $p$=0.0001 for salinity) (Table 1). The results of HSD post hoc test are shown in Table 2. As for temperature, the average abundance was higher at 18°C (102 ind./10 g WW of sediment) than at 12°C (96 ind./10 g WW of sediment) and was the lowest at 6°C (13 ind./10 g WW of sediment). As for salinity, the average abundance was higher at 25 psu (98 ind./10 g WW of sediment) than at 20 psu (80 ind./10 g WW of sediment) and 30 psu (63 ind./10 g WW of sediment) and was the lowest at 15 psu (40 ind./10 g WW of sediment).

However, with increasing temperature (from 12 to 18°C), the highest abundance occurred at medium salinity (from 25 to 20 psu). With increasing salinity (from 20 to 30 psu), the highest abundance occurred at medium temperature (from 18 to 12°C) (Figure 1). This was caused by the significant interactive effect of temperature and salinity ($F$=9.39, $p$=0.0001) (Table 1). To analyze the interactive effect of temperature and salinity, the multiple comparison was performed for temperature and salinity, respectively (Tables 3 and 4). There was no difference between these salinities at the lowest temperature (6°C), and temperature other than salinity was the key factor controlling foraminiferal abundance at 6°C. With temperature increasing to 12 and 18°C, the differences between salinities were significant. There were fewer differences between these temperatures at salinities of 15 and 30 psu than those at salinities of 20 and 25 psu. The results showed that higher abundance occurred at the warm temperatures (12–18°C) and medium salinities (20–25 psu).

### 3.3 Foraminiferal species richness

Species richness ranged from 2 to 8 and showed an in-

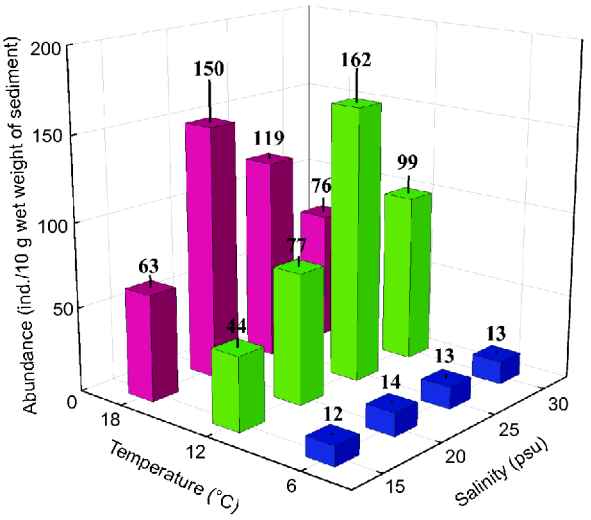


**Figure 1** Community abundance (Mean±SE) of foraminifera from experimental treatments plotted against temperature and salinity.

creasing trend with increasing temperature (Figure 2a) with average of 3, 5.58, and 6.33 at 6, 12, and 18°C, respectively. An overall increasing trend in species richness with increasing salinity was also observed (Figure 2b). Species richness was on average 4.56, 4.67, 5.33, and 5.33 at 15, 20, 25, and 30 psu, respectively.

Temperature had a significant effect on species richness ($F$=28.11, $p$=0.0001), but not salinity ($F$=1.21, $p$=0.3265>0.05). In addition, the interactive effect of temperature and salinity was not significant ($F$=0.70, $p$=0.6507>0.05) (Table 1). Tukey's HSD post hoc test showed that species richness was significant higher at 18 and 12°C than at 6°C ($p$<0.05) (Table 2).

### 3.4 Foraminiferal Margalef index (*D*)

The Margalef index increased with increasing temperature (Figure 2c) with average of 0.80, 1.03, and 1.18 at 6, 12, and 18°C, respectively. As for salinity, from 15 to 20 psu, the mean Margalef index decreased from 1.02 to 0.86. The Margalef index increased with continuous increase in salinity and was on average 1.04 and 1.11 at 25 and 30 psu, respectively (Figure 2d).

Temperature had significant effect on the Margalef index ($F$=3.41, $p$=0.0498), but not salinity ($F$=0.76,

**Table 1** $p$-values for effect of temperature (Tem) and salinity (Sal) on foraminiferal community parameters[a)]

| Factor | Tem | Sal | Tem * Sal |
|---|---|---|---|
| Abundance | **0.0001** | **0.0001** | **0.0001** |
| Species richness | **0.0001** | 0.3265 | 0.6507 |
| Margalef index | ***0.0498*** | 0.5263 | 0.8632 |
| Shannon-Wiener diversity | **0.0001** | 0.7120 | 0.2439 |
| Pielou's evenness | **0.0010** | ***0.0113*** | 0.5613 |

a) Table entries are $p$ values (marked in bold when $p$<0.01; marked in italic and bold when $p$<0.05) from two-way factorial ANOVA. There are two degrees of freedom for the temperature effect, three for the salinity effect, and six for the temperature and salinity interaction

**Table 2** Results of Tukey's honestly significant difference (HSD) post hoc test for the mean values of foraminiferal community parameters at different temperatures and salinities[a)]

| Factor | Temperature (°C) | | | Salinity (psu) | | | |
|---|---|---|---|---|---|---|---|
| | 6 | 12 | 18 | 15 | 20 | 25 | 30 |
| Abundance | 12.92$^{\dagger}$ | 95.67$^{*}$ | 102.00$^{*}$ | 39.44$^{\ddagger}$ | 80.22$^{*\dagger}$ | 98.22$^{*}$ | 62.89$^{\dagger\ddagger}$ |
| Species richness | 3.00$^{\dagger}$ | 5.58$^{*}$ | 6.33$^{*}$ | 4.56 | 4.67 | 5.33 | 5.33 |
| Margalef index | 0.80$^{\dagger}$ | 1.03$^{*\dagger}$ | 1.18$^{*}$ | 1.02 | 0.86 | 1.04 | 1.11 |
| Shannon-Wiener diversity | 0.88$^{\ddagger}$ | 1.18$^{\dagger}$ | 1.40$^{*}$ | 1.14 | 1.14 | 1.22 | 1.11 |
| Pielou's evenness | 0.84$^{*}$ | 0.71$^{\dagger}$ | 0.76$^{\dagger}$ | 0.81$^{*}$ | 0.80$^{*}$ | 0.78$^{*\dagger}$ | 0.69$^{\dagger}$ |

a) Different superscript letters (*, † and ‡) indicate significant differences ($p$<0.05) between temperatures or salinities

**Table 3** Multiple comparison of foraminiferal abundance for temperature[a)]

| Contrasts | 15 psu | 20 psu | 25 psu | 30 psu |
|---|---|---|---|---|
| 6°C vs. 12°C | ***0.0475*** | **0.0004** | **0.0001** | **0.0001** |
| 6°C vs. 18°C | **0.0027** | **0.0001** | **0.0001** | **0.0004** |
| 12°C vs. 18°C | 0.2192 | **0.0001** | **0.0098** | 0.1409 |

a) Table entries are $p$ values (marked in bold when $p$<0.01; marked in italic and bold when $p$<0.05)

**Table 4** Multiple comparison of foraminiferal abundance for salinity[a)]

| Contrasts | 6°C | 12°C | 18°C |
|---|---|---|---|
| 15 psu vs. 20 psu | 0.8972 | ***0.0379*** | **0.0001** |
| 15 psu vs. 25 psu | 0.9314 | **0.0001** | **0.0012** |
| 15 psu vs. 30 psu | 0.9143 | **0.0013** | 0.4046 |
| 20 psu vs. 25 psu | 0.9657 | **0.0001** | 0.0593 |
| 20 psu vs. 30 psu | 0.9828 | 0.1640 | **0.0001** |
| 25 psu vs. 30 psu | 0.9828 | **0.0004** | **0.0093** |

a) Table entries are $p$ values (marked in bold when $p<0.01$; marked in italic and bold when $p<0.05$)

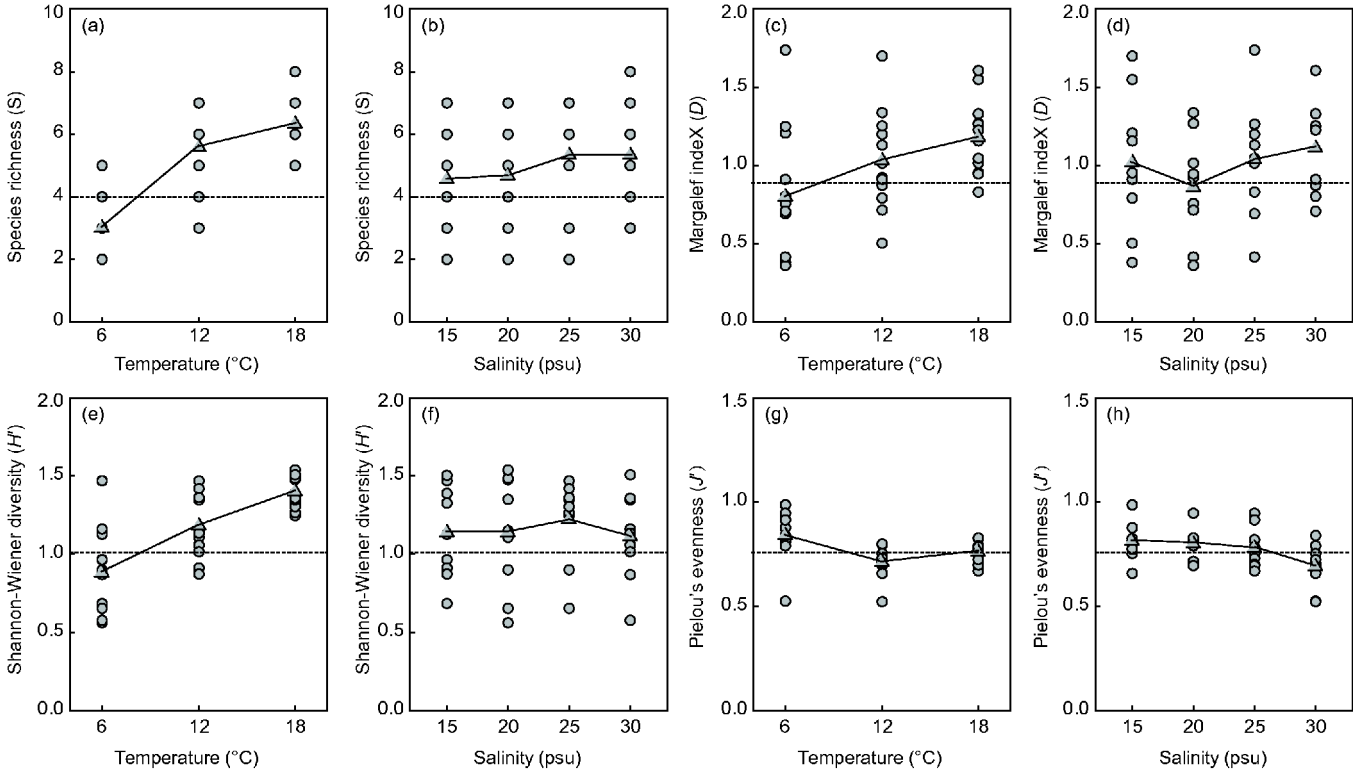


**Figure 2** Foraminiferal community parameters plotted against temperature and salinity. (a), (b) Species richness; (c), (d) Margalef index; (e), (f) Shannon-Wiener diversity; (g), (h) Pielou's evenness. Gray circles represent values from each experimental treatment and triangles represent the mean values at the same temperature or salinity. Horizontal dashed lines represent the mean value of *in situ* assemblages.

$p$=0.5263>0.05). In addition, the interactive effect of temperature and salinity was not significant ($F$=0.41, $p$=0.8632>0.05) (Table 1). Tukey's HSD post hoc test showed that the Margalef index was significant higher at 18°C than at 6°C ($p$<0.05) (Table 2).

### 3.5 Foraminiferal Shannon-Wiener diversity (*H'*)

Shannon-Wiener diversity increased with increasing temperature (Figure 2e), with average of 0.88, 1.18, and 1.40 at 6, 12, and 18°C, respectively. The diversity was constant at 1.14 for salinity from 15 to 20 psu, but increased to 1.22 for salinity from 20 to 25 psu. As salinity increased continuously, the diversity decreased, reaching 1.11 at 30 psu (Figure 2f).

Temperature had a significant effect on Shannon-Wiener diversity ($F$=19.87, $p$=0.0001), but not salinity ($F$=0.46, $p$=0.7120>0.05). In addition, the interactive effect of temperature and salinity was not significant ($F$=1.43, $p$=0.2439>0.05) (Table 1). Tukey's HSD post hoc test showed that the Shannon-Wiener diversity was significant higher at 18°C than at 12 and 6°C ($p$<0.05). The diversity was significant higher at 12°C than at 6°C ($p$<0.05) (Table 2).

### 3.6 Foraminiferal Pielou's evenness (*J'*)

Pielou's evenness initially decreased at temperatures from 6 to 12°C and then slightly increased from 12 to 18°C, with average of 0.84, 0.71, and 0.76 at 6, 12, and 18°C, respec-

tively (Figure 2g). The evenness decreased with increasing salinity and was on average 0.81, 0.80, 0.78, and 0.69 at 15, 20, 25, and 30 psu, respectively (Figure 2h).

Both temperature and salinity had significant effect on Pielou's evenness ($F$=9.38, $p$=0.0010 for temperature and $F$=4.58, $p$=0.0113 for salinity). However, the interactive effect of temperature and salinity was not significant ($F$=0.83, $p$=0.5613>0.05) (Table 1). Tukey's HSD post hoc test for temperature showed that Pielou's evenness was significant higher at 6°C than at 12°C and 18°C ($p$<0.05), whereas for salinity, it showed that the evenness was significantly higher at 15 and 20 psu than at 30 psu (Table 2).

### 3.7 Species composition

A total of 18 living benthic foraminiferal species were observed across all experimentally grown assemblages (Appendix Figure S2, Table S2). The experimentally grown assemblages were composed of the following average proportions of the three taxa: hyaline Rotaliida, 65.61%; porcellaneous Miliolida, 28.56%; and agglutinated Textulariida, 5.83%.

Ternary plots of the three taxa revealed almost no overlap among temperature treatments (Figure 3), with the main difference being the percentage of hyaline Rotaliida and porcellaneous Miliolida within the assemblages. Living assemblages cultured at 6°C were almost exclusively composed of hyaline Rotaliida (on average 92.32%). Assemblages cultured at 12°C included a large proportion of porcellaneous Miliolida (on average 51.95%) and were largely comparable to *in situ* assemblages. Compared with assemblages cultured at 12°C, those cultured at 18°C included an increasing proportion of hyaline Rotaliida (on average 64.08%) and a decreasing proportion of porcellaneous Miliolida (on average 30.26%). The proportion of agglutinated Textulariida was on average 4.21%, 7.62%, and 5.66% at 6, 12, and 18°C, respectively. The proportion of agglutinated Textulariida was the lowest (on average 5.83%) among the three foraminiferal taxa and almost constant at all temperatures.

The proportions of the three taxa did not show a distinct pattern with changes in salinity. The proportion of hyaline Rotaliida initially increased at salinity from 15 to 20 psu, and then decreased from 20 to 30 psu. The proportion of hyaline Rotaliida was on average 68.46%, 71.02%, 63.14%, and 59.82% at 15, 20, 25, and 30 psu, respectively. In contrast, the proportion of porcellaneous Miliolida initially decreased from 15 to 20 psu, and then increased from 20 to 30 psu. The proportion of porcellaneous Miliolida was on average 27.77%, 22.85%, 25.08%, and 38.54% at 15, 20, 25, and 30 psu, respectively. The proportion of agglutinated Textulariida initially increased slightly from 15 to 25 psu, and then decreased from 25 to 30 psu. The proportion of agglutinated Textulariida was on average 3.77%, 6.14%, 11.77%, and 1.64% at 15, 20, 25, and 30 psu, respectively.

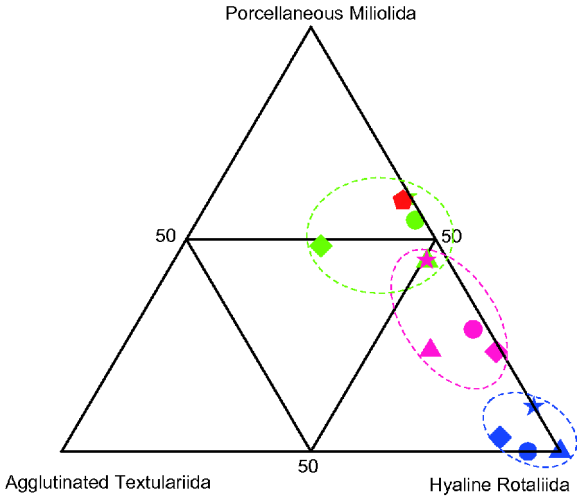


**Figure 3** Ternary plots of foraminiferal shell structure and taxa composition (mean values of three replicates). Circles, triangles, diamonds, and stars represent salinities levels of 15, 20, 25, and 30 psu, respectively. Blue, green, and pink represent temperatures levels of 6, 12, and 18°C, respectively. Red pentagon represents the *in situ* assemblages. Blue, green, and pink dashed circles mark the treatments at 6, 12, and 18°C, respectively.

The dominant species in experimentally grown assemblages included *A. aomoriensis*, *A. beccarii*, and *Q. seminula*, representing on average 32.47%, 28.42%, and 28.53% of the assemblages, respectively. The sum of the proportions of the three dominant species constituted no less than 70% in each experimentally grown assemblage (Figure 4).

The abundances of the three dominant species showed an overall increasing trend with increasing temperature (Figure 5a). The abundance of *A. aomoriensis* was on average 7, 19, and 25 ind./10 g WW of sediment at 6, 12, and 18°C, respectively. The abundance of *A. beccarii* was on average 5, 15, and 32 ind./10 g WW of sediment at 6, 12, and 18°C, respectively. The abundance of *Q. seminula* was on average 0, 50, and 29 ind./10 g WW of sediment at 6, 12, and 18°C, respectively. No distinct pattern was observed in the abundances of dominant species with changes in salinity (Figure 5b). The abundance of *A. aomoriensis* was on average 11, 31, 14, and 12 ind./10 g WW of sediment at 15, 20, 25, and 30 psu, respectively. The abundance of *A. beccarii* was on average 11, 14, 29, and 14 ind./10 g WW of sediment at 15, 20, 25, and 30 psu, respectively. The abundance of *Q. seminula* was on average 14, 23, 36, and 32 ind./10 g WW of sediment at 15, 20, 25, and 30 psu, respectively.

### 3.8 Correlations between community parameters and environmental factors

We conducted Spearman's correlation analysis between foraminiferal community parameters (community abundance, species richness, Margalef index, Shannon-Wiener

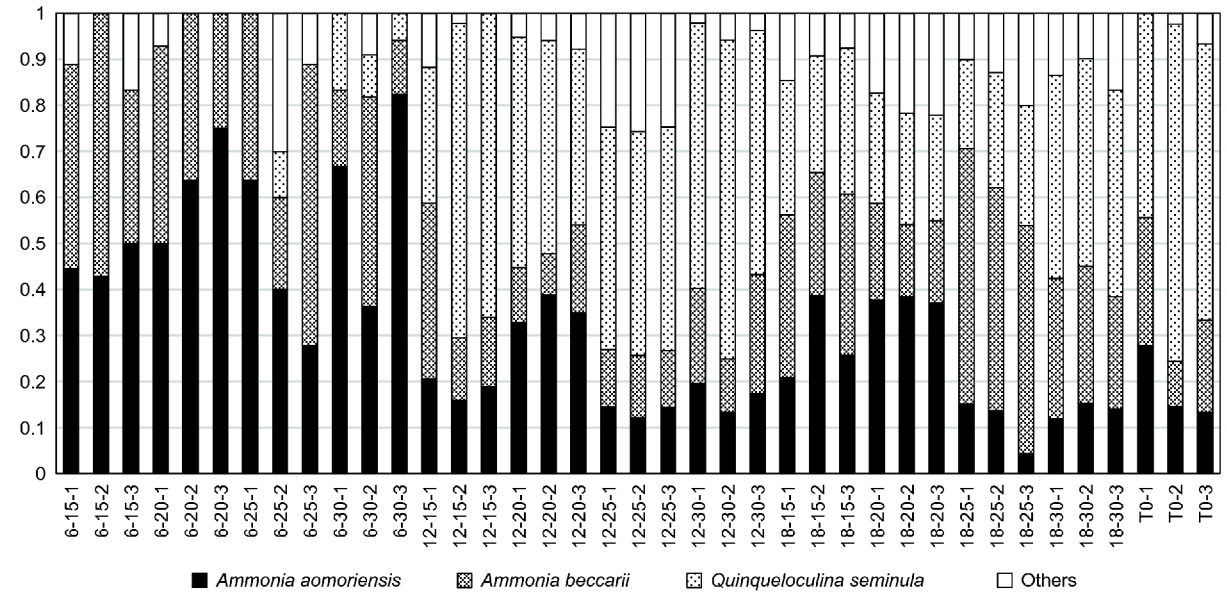


**Figure 4** Proportion of dominant species in all foraminiferal assemblages. Treatment abbreviations code for temperature (6, 12, or 18°C), salinity (15, 20, 25, or 30 psu), and replicate (1, 2, or 3). T0 represents the *in situ* assemblages (replicate 1, 2, 3).

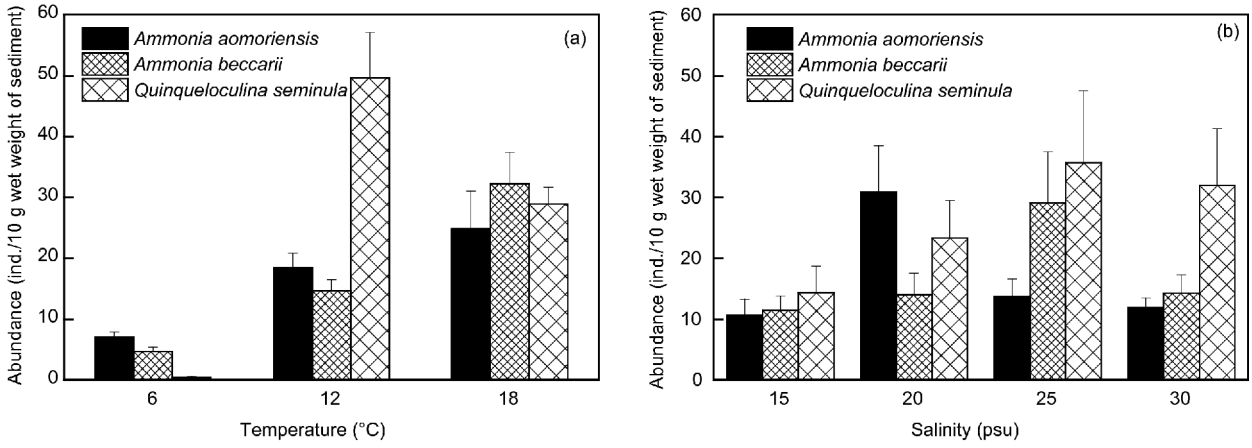


**Figure 5** Abundance (Mean±SE) of dominant species plotted against temperature (a) and salinity (b).

diversity, and Pielou's evenness) and environmental factors (temperature and salinity). Statistical analysis showed that correlations were stronger between community parameters and temperature than between community parameters and salinity. For example, foraminiferal abundance, species richness, Margalef index, and Shannon-Wiener diversity were significantly positively correlated to temperature; Pielou's evenness was significantly negatively correlated to temperature. However, only Pielou's evenness was significantly negatively correlated to salinity. No correlation between other parameters and salinity was significant (Table 5).

### 3.9 Correlations between species compositions and environmental factors

We conducted Spearman's correlation analysis between the abundances of three dominant species and environmental factors (temperature and salinity). Statistical analysis showed that the abundances of three dominant species were significantly positively correlated to temperature ($r$=0.5569, $p$=0.0004 for *A. aomoriensis*; $r$=0.8555, $p$=0.0001 for *A. beccarii*; and $r$=0.5749, $p$=0.0002 for *Q. seminula*), but not significantly correlated to salinity ($r$=0.0132, $p$=0.9391 for *A. aomoriensis*; $r$=0.1223, $p$=0.4773 for *A. beccarii*; and $r$=0.3284, $p$=0.0505 for *Q. seminula*) (Table 6).

We also conducted Spearman's correlation analysis between the proportions of three foraminiferal taxa (hyaline Rotaliida, porcellaneous Miliolida, and agglutinated Textulariida) and environmental factors (temperature and salinity). Statistical analysis showed that the proportion of Rotaliida was significantly negatively correlated to temperature ($r$=−0.4853, $p$=0.0027), and that of Miliolida was significantly

**Table 5** Correlations (Spearman's $r$ values) between foraminiferal community parameters and environmental factors[a)]

| Factor | Temperature | Salinity |
|---|---|---|
| Abundance | 0.7273 (**0.0001**) | 0.2201 (0.1971) |
| Species richness | 0.7404 (**0.0001**) | 0.1811 (0.2906) |
| Margalef index | 0.4831 (**0.0028**) | 0.1387 (0.4197) |
| Shannon-Wiener diversity | 0.7074 (**0.0001**) | −0.0227 (0.8953) |
| Pielou's evenness | −0.3832 (***0.0211***) | −0.4006 (***0.0155***) |

a) The $\alpha$-level is 0.05. $p$-values (marked in bold when $p<0.01$; marked in italic and bold when $p<0.05$) are listed in the parentheses

**Table 6** Correlations (Spearman's $r$ values) between the abundance of dominant species and environmental factors[a)]

| Dominant species | Temperature | Salinity |
|---|---|---|
| *Ammonia aomoriensis* | 0.5569 (**0.0004**) | 0.0132 (0.9391) |
| *Ammonia beccarii* | 0.8555 (**0.0001**) | 0.1223 (0.4773) |
| *Quinqueloculina seminula* | 0.5749 (**0.0002**) | 0.3284 (0.0505) |

a) The $\alpha$-level is 0.05. $p$-values (marked in bold when $p<0.01$) are listed in the parentheses

positively correlated to temperature ($r$=0.4972, $p$=0.0020). However, the proportion of Textulariida was not significantly correlated to temperature ($r$=0.2920, $p$=0.0840). No correlation between the three taxa and salinity was significant (Table 7).

The results from BIOENV analysis indicated that the best match of the biotic matrix with foraminiferal species composition was obtained for temperature, followed by the combination of temperature and salinity (Table 8). The environmental factor that revealed the best match between the biotic matrix and foraminiferal community parameters was also temperature, followed by the combination of temperature and salinity. However, salinity did not show a significant correlation to the biological matrix.

## 4. Discussion

### 4.1 Foraminiferal species composition

In coastal areas, the proportion of hyaline, porcellaneous, and agglutinated species can be used as indicator of environmental factors (Jorissen et al., 2007). Debenay (2012) found that the proportion of hyaline species increased with increasing depth and mud content in the sediment, and that of porcellaneous species decreased with increasing contamination in New Caledonia. However, the relationships between these taxa and temperature/salinity are unknown.

*In situ* assemblages included on average 38.87% hyaline Rotaliida, 59.21% porcellaneous Miliolida, and 1.92% agglutinated Textulariida; these results were comparable to those of the field study (in July) reported by Lei et al. (2017a). In experimentally grown assemblages in our study, foraminiferal assemblages included on average 65.61% hyaline Rotaliida, 28.56% porcellaneous Miliolida, and 5.83% agglutinated Textulariida, indicating that the proportion of hyaline Rotaliida and agglutinated Textulariida increased but that of porcellaneous Miliolida decreased. This was explained mainly by the difference in temperature. The environmental temperature for *in situ* assemblages was 23°C, whereas experimentally grown assemblages were maintained under lower temperatures (6, 12, and 18°C). A similar change was observed within experimentally grown assemblages, i.e., with decreasing temperature, the proportion of hyaline Rotaliida increased but that of porcellaneous Miliolida decreased. This shift reflected the responses of different foraminiferal taxa to the change of temperature; that was, the hyaline Rotaliida could tolerate low temperature and the porcellaneous Miliolida preferred the warm temperature. This was consistent with our observation in Qingdao Bay: more hyaline Rotaliida occurred in spring and winter, but more porcellaneous Miliolida occurred in summer and autumn. Statistical analysis showed that the proportion of rotaliids was significantly negatively ($r$=−0.4853, $p$=0.0027) correlated to temperature, whereas that of miliolids was significantly positively ($r$=0.4972, $p$=0.0020) correlated to temperature. No significant correlation was found between the three foraminiferal taxa and salinity. Reportedly, benthic foraminifera had a narrow range of preferred salinity (Kurtarkar et al., 2011; Nigam et al., 2006). However, the salinities in this experiment had a large range of variation (15 to 30 psu). Therefore, the range of salinity used in our study may be largely beyond the narrow range of preferred salinity that foraminifera experienced. Although the correlation between salinity and the proportions of three taxa was not statistically significant, salinity may have affected foraminifera (de Rijk, 1995; Haynert and Schönfeld, 2014; Kurtarkar et al., 2011; Nigam et al., 2006). These relationships could be used to indicate the changes in environmental factors and reconstruct paleoenvironment.

In experimentally grown assemblages, Rotaliida species

**Table 7** Correlations (Spearman's $r$ values) between the proportions of three taxa and environmental factors[a)]

| Foraminifera | Temperature | Salinity |
|---|---|---|
| Rotaliida | −0.4853 (**0.0027**) | −0.1724 (0.3146) |
| Miliolida | 0.4972 (**0.0020**) | 0.1767 (0.3025) |
| Textulariida | 0.2920 (0.0840) | −0.1267 (0.4614) |

a) The $\alpha$-level is 0.05. $p$-values (marked in bold when $p<0.01$) are listed in the parentheses

**Table 8** Summary of results from BIOENV analysis showing all matches of environmental factors with foraminiferal species-specific abundance and community parameters at all treatments[a)]

| Foraminifera | Rank | $R$ | Environmental factors | $p$ |
|---|---|---|---|---|
| Species composition | 1 | 0.709 | Temperature | **0.001** |
| | 2 | 0.375 | Temperature & salinity | **0.008** |
| | 3 | −0.178 | Salinity | 0.974 |
| Community parameters | 1 | 0.653 | Temperature | **0.001** |
| | 2 | 0.373 | Temperature & salinity | **0.009** |
| | 3 | −0.129 | Salinity | 0.883 |

a) The $\alpha$-level is 0.05. $p$-values (marked in bold when $p<0.01$) are listed in the last column. Community parameters: community abundance, species richness, Margalef index, Shannon-Weiner diversity and Pielou's evenness. The mean values of three replicates for each treatment are used

were predominant, followed by Miliolida and Textulariida species, which was consistent with the findings of some previous studies in intertidal areas (Berkeley et al., 2008; Debenay et al., 2006; Ghosh et al., 2009; Horton et al., 1999). As for the shell structure, hyaline species constituted the highest proportion, followed by porcellaneous and agglutinated species, which was also consistent with the proportions reported by some previous studies (Dorst and Schönfeld, 2013; Frontalini et al., 2013; Murray and Alve, 2000).

In both *in situ* and experimentally grown assemblages, the dominant species were *A. aomoriensis*, *A. beccarii*, and *Q. seminula*. The *Ammonia* and *Quinqueloculina* species usually appeared in shallow-water environments worldwide. They could tolerate stressful conditions (Weinmann and Goldstein, 2016) and had the ability to reproduce and grow rapidly, making them predominant in all assemblages under different temperatures and salinities in our study.

In addition, the abundances of three dominant species were significantly positively correlated to temperature but not significantly correlated to salinity. However, Lei et al. (2017a) found that the abundances of *A. aomoriensis* and *A. beccarii* were significantly negatively correlated to temperature and that of *A. aomoriensis*, *A. beccarii*, and *Q. seminula* were significantly positively correlated to salinity in their field study. The different results between culture experiment and field study can be explained by the complex effects of environmental factors beyond temperature and salinity in the field, which will be discussed in the next section. It is worth noting that the abundance of *Q. seminula* was higher at 12°C than at 18°C. This may be due to competition with *Ammonia* species at 18°C. With the changes of temperature, the proportion of *Ammonia* species decreased and that of *Quinqueloculina* species increased dramatically, especially from 6 to 12°C (Figure 4). This reflected that *Ammonia* species had stronger tolerance to low temperature than *Quinqueloculina* species. Therefore, the proportions of *Ammonia* and *Quinqueloculina* species could be used as indicators of environmental factors in paleoenvironmental reconstruction. The species composition showed no obvious trends with the changes of salinity.

Some foraminiferal species (e.g., *Ammonia* species) had wide tolerance range of salinity (Alve and Murray, 1999). Debenay et al. (2000) also showed that some foraminiferal species had powerful osmotic regulation and occurred in both hypersaline and hyposaline environments. In this study, the foraminifera in the culture experiments may have almost adapted to the changes of salinity (15–30 psu) and showed few correlations to salinity.

### 4.2 Foraminiferal community

Overall, the foraminiferal abundance of experimentally grown assemblages (ranging from 9 to 202 ind./10 g WW of sediment and averaged 70 ind./10 g WW of sediment) was higher than that of *in situ* assemblages (ranging from 18 to 41 ind./10 g WW of sediment and averaged 30 ind./10 g WW of sediment). This indicated that foraminifera reproduced and grew dramatically under experimental conditions. In experimentally grown assemblages, the low abundance occurred at the lowest temperature (6°C) and salinity (15 psu). Overall, the abundance increased with increasing temperature and salinity. However, owing to the significant interactive effect of temperature and salinity, a high abundance occurred at combinations of warm temperatures (12–18°C)

and medium salinities (20–25 psu). The highest abundance was obtained at 12°C and 25 psu. A high abundance indicated rapid growth and reproduction rate. Therefore, temperatures of 12–18°C and salinities of 20–25 psu were suitable conditions for the development of foraminiferal community in the laboratory culture experiment.

In another culture experiment, Weinmann and Goldstein (2016) also found a similar result that foraminiferal abundance increased with increasing temperature and salinity, but did not report any interactive effect. It is notable that the interactive effects of different factors are almost impossible to determine in field studies, making experiments with controlled environmental factors the only tractable way forward. The results obtained from culture experiments can help explain the combined effects of environmental factors in field studies.

However, previous field studies have shown that high foraminiferal abundance occurred in winter (<10°C) (Lei et al., 2017a), which was partly in conflict with our result. We recognize our laboratory experiment do not completely simulate natural conditions. The difference was partly because of the lack of consistent dissolved oxygen levels, a single food supply, and the potential decrease in pH due to the addition of deionized water. In addition, the differences may be partly attributed to the uncertainty and complexity of environmental factors in field studies. Environmental factors are not independent, and the responses of foraminifera usually reflect the combined effects of measured environmental factors and other unknown biotic and abiotic factors in the field. In culture experiments, apart from the factors studied, other environmental conditions are controlled. Therefore, it is not surprising that the effects of environmental factors on foraminifera may differ between field and laboratory studies. During the sampling season, the intertidal area of Qingdao Bay was severely affected by the local tourism (especially from April to November) and the summer blooms of drifting green tide (*Enteromorpha prolifera*) (Lei and Li, 2016). Tourism brought in more trampling and digging activities in intertidal area, and the sediment was disturbed severely, which may inhibit the growth and reproduction of foraminifera. In addition, the blooming of green tide would result in anoxia, which may also contribute to the low foraminiferal abundance in summer in field study. We speculate that the conflicting field results of foraminiferal abundance in Qingdao Bay were complex effects of environmental factors, human activities and the blooming of green tide.

Species richness, Margalef index, and Shannon-Wiener diversity increased sharply with increasing temperature. Higher temperature may have facilitated the occurrence of rare species. In addition, the rapid growth of algae at high temperature offered abundant food, which may have reduced competitions between species. The Margalef index and Shannon-Wiener diversity increased with the increase in species richness and abundance. Foraminiferal communities were more diverse. Our results were similar with those of some previous studies. For example, Goldstein and Alve (2011) and Weinmann and Goldstein (2016) found that foraminiferal community abundance and diversity increased at high temperature; Ongan et al. (2009) found that high diversity of foraminiferal community occurred in high-salinity area. However, Pielou's evenness decreased slightly with increasing temperature, probably because the increasing abundance of dominant species resulted in an unbalance in the community. The community parameters demonstrated no obvious trend with changes in salinity.

Because of the limitation of temperature control equipment, we did not culture the foraminiferal communities at temperatures >18°C. The monthly sediment temperature ranged from 3 to 25°C in Qingdao Bay, and the range of experimental temperature in present study covered the most changes of temperature in Qingdao Bay. Therefore, our study still represented a normal change of temperature at least in most temperate intertidal areas. The monthly seawater salinity ranged from 31 to 38 psu in Qingdao Bay. In present study, the salinity of seawater for culturing foraminiferal communities ranged from 15 to 30 psu to simulate a low salinity condition that may result from heavy rain, freshwater input, and sea level rise. The experimental period in our study was 10 weeks. Previous studies have shown that the environmental changes could lead to rapid reaction in foraminiferal community in only a few weeks (Goldstein and Alve, 2011; Weinmann and Goldstein, 2016). Moreover, our result showed that the foraminiferal community changed with the changes of temperature and salinity over the 10 weeks.

### 4.3 Linkage between foraminiferal community and environmental factors

In the present study, Spearman's correlation analyses showed close correlations between foraminiferal community and temperature/salinity, especially temperature. Foraminiferal abundance, species richness, Margalef index, and Shannon-Wiener diversity were significantly positively correlated to temperature. Pielou's evenness was significantly negatively correlated to temperature. Pielou's evenness was significantly negatively correlated to salinity, and no other parameter showed any significant correlation to salinity (Table 5). BIOENV analysis also showed that temperature and the combination of temperature and salinity were the significant factors influencing the foraminiferal species composition and community parameters. However, salinity alone was not a significant factor (Table 8). Some relationships between foraminifera and salinity have previously been established in local area (Lei and Li, 2015; Lei et al., 2017b).

Therefore, a further study of laboratory culture experiment for foraminiferal community at a much wider range of salinity should be performed to determine the potential relationships between foraminiferal community and salinity.

The relationships between foraminifera and environmental factors were usually used to develop the transfer function or biotic index on foraminiferal studies (Horton et al., 1999; Lei et al., 2017a). Based on our results, five biotic indices, namely abundance, species richness, Margalef index, Shannon-Wiener diversity, and Pielou's evenness could be potentially used for this calculation (Table 5). In addition, foraminiferal taxa (i.e., Rotaliida and Miliolida) and dominant species (i.e., *A. aomoriensis*, *A. beccarii*, and *Q. seminula*) were positively or negatively correlated to temperature (Tables 6 and 7). These relationships could also be used for the calculation (Lei and Li, 2015; Lei et al., 2017b). For example, a finding of increasing community abundance may indicate an increase in temperature and a finding of increasing proportion of Rotaliida may indicate a decrease in temperature.

## 5. Conclusions

Benthic foraminiferal communities from intertidal sediment were cultured at three temperatures (6, 12, and 18°C) and four salinities (15, 20, 25, and 30 psu) for 10 weeks. It is inferred that:

(1) Temperature was a key factor affecting community structure. As temperature increased, most community parameters (abundance, species richness, Margalef index, and Shannon-Wiener diversity) significantly increased and only Pielou's evenness decreased. Salinity had relatively weak influence on community parameters. Only Pielou's evenness was significantly negatively correlated to salinity.

(2) Temperature had more effects on species composition than salinity. The abundances of three dominant species (*Ammonia aomoriensis*, *A. beccarii*, and *Quinqueloculina seminula*) were significantly positively correlated to temperature. The proportion of rotaliids and miliolids showed significantly negative and positive correlations to temperature, respectively. However, no significant correlation was detected between the species composition and salinity.

(3) The intertidal foraminiferal community responds rapidly to the changes of temperature and salinity, especially temperature. The relationships between foraminiferal community and environmental factors established in our study can be used to indicate the changes of environmental factors and reconstruct the paleoenvironment.

**Acknowledgements** *We thank the two anonymous reviewers for constructive comments on the earlier version of this manuscript. The authors thank to the Jiaozhou Bay Marine Ecosystem Research Station, Chinese Academy of Sciences for sharing the voyage and providing CTD data. This work was supported by the National Natural Science Foundation of China (Grant Nos. 41476043, 41630965 & 41830539), the Strategic Priority Research Program of the Chinese Academy of Sciences (Grant No. XDA11030104), the National Program on 'Global Change and Air-Sea Interaction' (Grant No. GASI-03-01-03-01), the Continental Shelf Drilling Program of China (Grant No. GZH201100202), the Paul Brönnimann Foundation 2014.*

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(Responsible editor: Huayu LU)