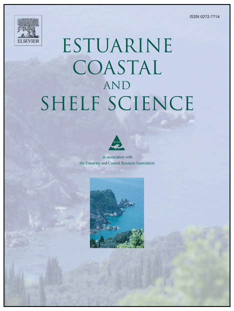

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Effects of Short-term Hydrological Processes on Benthic Macroinvertebrates in Salt Marshes: A Case Study in Yangtze Estuary, China

ABSTRACT

Understanding the effects of hydrological processes on the benthic macroinvertebrates in salt marshes can provide theoretical basis for species diversity restoration, coastal environment protection, and comprehensive exploitation and utilization of salt marsh ecosystems. In this study, 4 fixed-point sampling sites were set up in the salt marsh of the East Nanhui tidal flat in the Yangtze Estuary for benthic macroinvertebrate survey, hydrological monitoring and sedimentary parameter collection over two short-time scales (semidiurnal and fortnightly cycles). Based on the results of these surveys, we analyzed the effects of hydrological processes on the benthic macroinvertebrates over different timescales. The results showed that benthic macroinvertebrates assemblages varied significantly over the semidiurnal and fortnightly tide periods but not between sites. The number of species and the abundance of the benthic macroinvertebrates during spring tide period were significantly lower than that during neap tide period, although the biomass during both tidal periods were not significantly different. There was no significant variation in the number of species, abundance, and biomass of benthic macroinvertebrates over the semidiurnal tidal scale in general with few exceptions. However, there were significant differences in most of the hydrological and sedimentary parameters between the spring and neap tide periods, as well as between semidiurnal tides in these two periods. Two principal components, the intensity of hydrological processes (PC1) and the physicochemical properties of water and sediment (PC2), were derived from principal component analysis on hydrological factors and sedimentary physicochemical parameters. The results show that PC1 had a significant effect on abundance of benthic macroinvertebrate community; while PC2 had a significant effect on biomass. The best combined environmental factors, which exhibited significant correlations with the characteristics of the benthic macroinvertebrates and also their taxonomic classes, varied across the sampling periods. This study indicates that short-term hydrological processes can not only directly affect the benthic macroinvertebrates, but also indirectly affect the communities by altering sedimentary physicochemical factors. There were significant differences in the effects of the hydrological processes on the benthic macroinvertebrate community over the semidiurnal and fortnightly tidal scales, and it could be inferred that the scale effect still exists in the short-time scale.

Keywords: Benthic macroinvertebrate community; East Nanhui tidal flat; Hydrological process; Salt marsh; Short timescale

1. Introduction

Salt marshes, which are widely distributed in coastal areas across middle- and high-latitude, are one of the most productive ecosystems in the world (Mitsch and Gosselink, 2011). Benthic macroinvertebrates are key links in the food chains of salt marsh ecosystems (Moseman *et al*., 2004). Specifically, macroinvertebrates are often a food source for birds, fish and mammals (Levin *et al*., 2001; Cardoso *et al*., 2008). Macroinvertebrates also play important roles in the material circulation and energy flow of the ecosystems, they can contribute to the decomposition of organic matter in the sediment (Stief, 2013; Signa *et al*., 2015). As the benthic macroinvertebrates are sensitive to environmental changes, they are often employed as important indicators in environmental monitoring and assessment (Rakocinski, 2012; Do *et al*., 2013). Therefore, variation of benthic macroinvertebrates in salt marshes has also been described as a function of biotic and abiotic variables (e.g., vegetation type, sediment substrates and organic matter content) (Tong *et al*., 2013).

Hydrological processes are dynamic processes of the continuous or periodic variation of hydrological elements. Salt marshes are located in the transition zone between terrestrial and marine ecosystems. They are influenced by precipitation and runoff, and also by tide and tidal currents. Regional hydrological processes are important driving forces for shaping and sustaining the structure and function of salt marsh ecosystems, including the benthic macroinvertebrate communities (Barbone and Basset, 2010; Hughes *et al*., 2012; Wal *et al*., 2017). In past decades, there have been many studies on the influence of hydrological elements on the benthic macroinvertebrate communities in salt marshes. Warwick and Uncles (1980), who firstly established a direct correlation between tidal stress and macroinvertebrate communities, pointed out that high velocity flow can lead to significant reductions in some species. Some studies indicate that changes in flow velocity can cause variations in the transportation of benthic macroinvertebrate larvae and their food, which, in turn, can affect biomass, density and diversity of the benthic macroinvertebrates in salt marshes (Turner *et al*., 1997; Norkko *et al*., 2000; Coco *et al*., 2006). Ysebaert *et al.* (2003) found that water depth was one of the most important factors affecting the spatial distribution of macroinvertebrates communities in Scheldt estuary, NW Europe. It was reported that abundance and biomass of the benthic macroinvertebrates in the intertidal zone was significantly higher than the corresponding values in the subtidal zone. Norkko *et al*. (2001) and Nishijima *et al*. (2013) found that regional variations in water salinity could negatively affect the biomass and abundance of the benthic macroinvertebrates. Similar conclusions were reached by Kneib (1984) and Partyka and Peterson (2015). Other authors have also reported that change in water turbidity and temperature can also affect the abundance and biomass of macroinvertebrate communities (Salen-Picard and Arlhac, 2002; Salen-Picard *et al*., 2003; Blanchard *et al*., 2013).

In addition to the hydrological elements, many sedimentary physical and chemical factors, including sediment pH, bulk density, water content, and grain size etc., affected by hydrological processes can also influence the benthic macroinvertebrate communities (Lamptey and Armah, 2008; Tong *et al*., 2013; Takada *et al*., 2015). From these studies, we can find that many studies have investigated separately the influence of hydrological elements or sedimentary factors (physical and chemical) on the benthic macroinvertebrate communities, but less is known about the synergistic effects of hydrological elements and sedimentary factors on benthic macroinvertebrates after hydrologic processes.

Scale effect is a core issue in modern ecology. When studies are based on different scales, different processes and patterns can be detected and different results are obtained (Schneider, 2001). The effects of hydrological processes and sedimentary factors on benthic macroinvertebrate communities appeared to vary across different temporal scales. It was found that variation in water salinity and sediment grain size had significant effects on benthic macroinvertebrate communities on an annual scale (Edgar and Barrett, 2002; Ysebaert and Herman, 2002; Grilo *et al*., 2011; Dittmann *et al*., 2015), while the effects of water salinity and temperature appeared to be more obvious over monthly or seasonal scales (Eyre and Ferguson, 2006; Lamptey and Armah, 2008; Nishijima *et al*., 2013). Only a few studies have considered the dynamics of benthic macroinvertebrate communities with the change of water depth in the diurnal tide (e.g., Cruz-Motta, 2005), while the effects of hydrological processes on benthic macroinvertebrate communities over semidiurnal or fortnightly tidal scales have been largely ignored, although they are basic processes for the longer term hydrological processes in salt marshes. Understanding the effects of short-timescale hydrological processes on benthic macroinvertebrate communities in salt marshes can provide a theoretical basis for rapid species diversity restoration, coastal environmental protection, and comprehensive exploitation and utilization of salt marsh ecosystems.

In this study, we focused on the following two objectives: 1) identify the characteristics of the effects of short-term hydrological processes on the benthic macroinvertebrate community in the salt marshes of East Nanhui tidal flat in the Yangtze Estuary, and the corresponding hydrological elements and sedimentary factors; and 2) determine whether there were any differences in the effects of the hydrological processes on the benthic macroinvertebrate community over the semidiurnal and fortnightly tidal scales. We hypothesized that short-term hydrological processes would directly affect the benthic macroinvertebrates, and could also affect them indirectly by influencing sedimentary factors. We also hypothesized that scale effects could also exist over the semidiurnal and fortnightly tidal scales. In order to test our hypotheses, we carried out surveys on the benthic macroinvertebrates, hydrological processes and sedimentary factors at the fixed sampling sites on semidiurnal and fortnightly tidal scales.

2. Materials and methods

2.1. Study area and field site selection

The study was carried out on the East Nanhui tidal flat (Fig. 1) in the Yangtze Estuary, the largest estuary in China, characterized by a typical three-level bifurcation and a four-outlet configuration. The tides inside the estuary are irregular semidiurnal tides. The East Nanhui tidal flat is located in the southern part of the entrance to the Yangtze Estuary, on the south side of the third branch of the southern channel, at the junction of the Yangtze Estuary and the Hangzhou Bay. It was formed by the long-term accumulation of sediment in the Yangtze Estuary. The average tidal range in the East Nanhui tidal flat area is 2.7 m, reaching approximately 4 m during the spring tide period (Li *et al.*, 2012). The area has a subtropical maritime climate with an average annual temperature of 15–16 °C and an average annual rainfall of 1.2×10^3 mm (Niu *et al.*, 2013). The sediment mainly comprises clayey silt and silt (Huang *et al.*, 2008; Ma *et al.*, 2012). The East Nanhui tidal flat area is one of the most important reclamation areas of the Yangtze Estuary. Since the 1990s, several dams and reclamation efforts have been put in place (Ma *et al.*, 2012). The sea-side of the levee is mainly mudflats, with 50 m-wide vegetation belts between the levee and the digue. The main plant species in the area are native species *Phragmites australis* (Cav.) Trin. ex Steud., *Scirpus mariqueter* Tang & F. T. Wang and the invasive species *Spartina alterniflora* Lois.

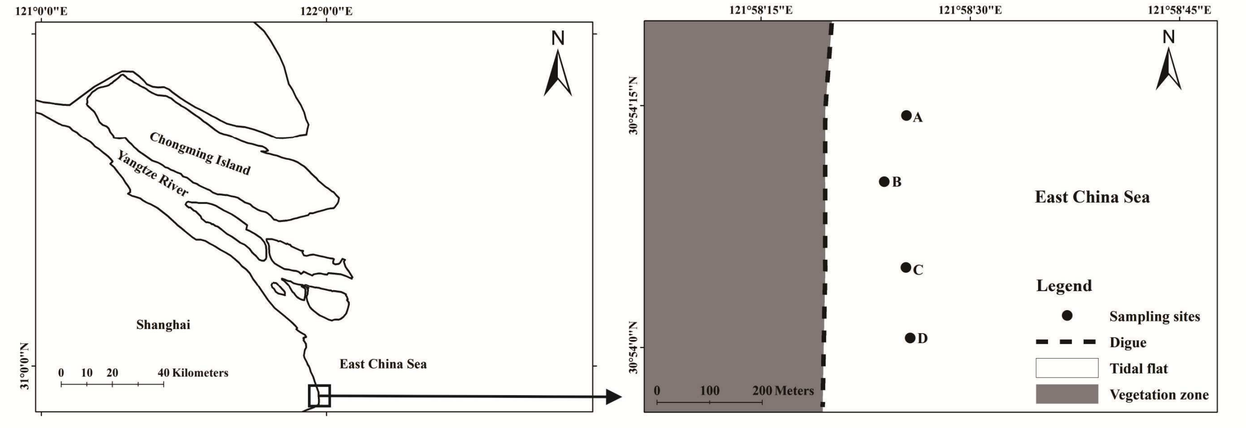


Fig. 1. Study area showing the sampling locations in the salt marsh of the East Nanhui tidal flat in the Yangtze Estuary.

Four 20 m × 20 m square sampling sites (A, B, C and D) were set up about 200 m away from the digue, and the distance between each sampling site was approximately 200 m (Fig. 1). The relative elevation of the diagonal center of each site was measured using the Total Station (GTS-102N, Topcon, Beijing Ltd., Beijing, China), and the bias of relative elevation between the sites was controlled within 10 cm to ensure that changes in the community were not due to natural elevation differences between the zones. Four 2m×2m sampling plots were established at each site as each corner of the square contained one.

2.2. Sample collection and processing

Benthic macroinvertebrates and sediments were sampled at low tide after each semidiurnal tide during the spring tide period (20th, 21st, 22nd, 6 samplings) and the neap tide period (27th, 28th, 29th, 6 samplings) in July 2016. Two replicates were collected in each plot every time. Benthic macroinvertebrates were collected using 25 cm × 25 cm quadrats. During each sampling, benthic macroinvertebrates on the sediment surface were collected first, and then sediment samples were collected down to a depth of approximately 20 cm using a shovel. The infauna were collected after the sediments were sieved through a 0.5-mm mesh sieve. All of the collected specimens were preserved in 10% (v/v) formalin solution *in situ*. Two replicate sediment cores ($h = 2$ cm; $r = 2.25$ cm) were collected at each time using a syringe sampler for laboratory analysis.

At the same time during the sampling, sediment pH was measured twice at each plot with a portable pH meter (IQ150, Zealquest Ltd., Shanghai, China) in the field. A set of hydrological instruments was arranged at the diagonal center of each sampling site to monitor the hydrological processes, and the height of each instrument was approximately 10 cm from the sediment surface. An electromagnetic current meter (ALEC-Infinity, ALEC Ltd., Tokyo, Japan) was used to record the flow velocity, while an optical backscatter turbidity sensor (OBS-3A, Campbell Ltd., Utah, USA) was used to record the temperature, salinity, turbidity, electrical conductivity, and water depth at each site. All hydrological data were sampled every 10 seconds during the spring and neap tidal periods (5 tidal cycles in spring tides, 5 tidal cycles in neap tides). The period of water depth > 0 is used as the data pool to calculate the average and maximum values of hydrological data.

In the laboratory, the macroinvertebrates were identified to species (Liu and He, 2007) and counted, then dried at 60 °C for more than 48 h to a constant weight, and weighed to the nearest 0.0001 g to obtain the dry weight (DW) of the biomass. After the wet weight of each sediment sample was determined, all the sediment samples were dried at 60 °C for more than 48 h to a constant weight and weighed to the nearest 0.1 g. The water content and bulk density of the sediment samples were calculated from these weights. The median grain sizes (d_{50}) of the sediments were measured using a Malvern laser particle size analyzer (MS2000, Malvern Ltd., Malvern, UK).

2.3. Data analysis

We used relative abundance (%N), relative biomass (%B), and Pinkas index of relative importance (IRI) to reflect the composition of the benthic macroinvertebrate communities (Tong，2012; Wu and Tong, 2017).

Relative abundance: $$\%N = \frac{n_i}{N} \times 100 \quad (1)$$

Relative biomass: $$\%B = \frac{b_i}{B} \times 100 \quad (2)$$

Pinkas index of relative importance: $$IRI = (\%N + \%B) \times f_i \quad (3)$$

where n_i and b_i indicated the individual number and biomass of the species i respectively; f_i indicated the occurrence frequency of the species i at each site; N and B indicated the total individual number and total biomass at each site, respectively.

PERMANOVA (permutational analysis of variance) was performed on the benthic macroinvertebrates assemblage datasets in R statistical programming language v2.15.1 to determine the main sources of variation of the data, with three explanatory variables (a fixed factor TIDE (2 levels: neap and spring tide), a fixed factor TIME (6 levels, nested in TIDE: 6 samplings after each semidiurnal tidal cycle, T1 to T6) and a random factor SITE (4 levels: A, B, C and D)) (Anderson, 2005). 4,999 permutations, using raw data were carried out in all cases. All interactions were included ($P < 0.05$ was considered statistically significant,

$P < 0.001$ was considered statistically extremely significant).

IBM SPSS Statistics v.21 was used to analyze how benthic macroinvertebrate communities, hydrological elements and sedimentary factors change after semidiurnal or fortnightly hydrological processes. The environmental factors data that did not meet the requirement of homogeneity of variance were square root transformed before analysis. We used Student t-test to analyze the variations of number of species，abundance，biomass of community and environmental factors between spring and neap tide periods, and used one-way ANOVA and the least significant difference (LSD) for multiple comparisons to test for significant differences of these parameters between different sampling sites and also in semidiurnal tides ($P < 0.05$ was considered statistically significant, $P < 0.001$ was considered statistically extremely significant) (Tong *et al.*, 2013).

Principal component analysis (PCA) was used to reduce the dimensions of the environmental factors (eigenvalue = 1) (Griffith *et al.*, 2005), and linear regression analysis to reveal the effects of the principal components (PCs) on the benthic macroinvertebrate communities (Li *et al.*, 2012). The number of species, abundance, and biomass of the benthic macroinvertebrate communities were taken as the dependent variable, while the PCs were the independent variables.

Primer 5.2.8 was employed to carry out nonlinear regression analysis to find the best matches between the combined environmental factors and the benthic macroinvertebrate community characteristics. The data for abundance or biomass of the benthic macroinvertebrate communities were fourth root transformed to down-weighting the importance of the highly abundant species. The relevant data for environmental factors were standardized transformed to avoid the effects of dimensional differences (Tong *et al.*, 2013). Then, Bray-Curtis similarity indices were used to build the similarity matrices of the communities and Euclidean distances dissimilarity indices were used to build the dissimilarity matrices of the environmental factors; The BVSTEP procedure was used to determine the best combination of environmental factors matching the characteristics of the benthic macroinvertebrate communities, and also the correlation coefficient, then the

RELATE procedure was used to test the significance of the correlation ($P < 0.05$ was considered statistically significant, $P < 0.001$ was considered statistically extremely significant) (Tong, 2013).

3 Results

3.1. Characteristics of benthic macroinvertebrate communities

A total of 19 species of benthic macroinvertebrates, belonging to three phyla, three classes, seven orders and 11 families, were recorded during the surveys (Table 1). All recorded species are native species. Over the survey period, *Potamocorbula amurensis* Schrenck and *Corbicula fluminea* Muller appeared to be the dominant species (IRI>10), while *P. amurensis* also happened to have the highest relative abundance and biomass. During the spring tide period, a total of 12 species of benthic macroinvertebrates was recorded. The dominant species were also *P. amurensis* and *C. fluminea* (IRI>10), and *P. amurensis* also had the highest relative abundance and biomass. During the neap tide period, all 19 benthic macroinvertebrate species were recorded. The dominant species were still *P.amurensis* and *C.fluminea* (IRI>10), while *C. fluminea* appeared to have the highest relative abundance, and *P. amurensis* had the highest relative biomass.

Table 1

Characteristics of the benthic macroinvertebrate communities in the different tidal periods in the salt marsh of the East Nanhui tidal flat.

Groups and species	Spring tide			Neap tide			Total		
	N%	B%	IRI	N%	B%	IRI	N%	B%	IRI
Bivalvia									
Potamocorbula amurensis Schrenck	39	90.5	129.5	29.06	87.96	102.39	34.03	89.23	115.94
Corbicula fluminea Muller	13.9	0.51	10.8	35.35	3.26	35.39	24.63	1.88	23.1
Moerella iridescens Benson	1.54	0.14	0.21	0.24	0.06	0.01	0.89	0.1	0.11
Sinonovacula constricta Lamarck	0.77	2.12	0.12	0.24	1.34	0.07	0.51	1.73	0.09
Malacostraca									
Crandidierella japonica Stephens	14.67	0.07	8.6	13.08	0.11	8.79	13.87	0.09	8.69
Corophium volutator Pallas	8.49	0.04	4.62	3.39	0.02	1.56	5.94	0.03	3.09
Macrophthalmus abbreviates Manning Holthuis	4.63	6.09	4.02	3.15	5.6	3.65	3.89	5.85	3.83

Parasesarma pictum De Haan	0	0	0	1.45	0.01	0.36	0.73	0	0.18
Synidotea laevidorsalis Miers	0	0	0	0.48	0	0.04	0.24	0	0.02
Philyra pisum De Haan	0	0	0	0.48	1.31	0.15	0.24	0.66	0.07
Cleantioides annandalei Tattersall	0	0	0	0.48	0	0.04	0.24	0	0.02
Exopalaemon Annandalei Kemp	0.77	0	0.06	0.73	0.01	0.06	0.75	0.01	0.06
Exopalaemon modestus Heller	0	0	0	0.24	0	0.01	0.12	0	0.01
Polychaeta									
Notomastus latericeus Sars	6.95	0.1	3.23	2.91	0.05	0.98	4.93	0.07	2.11
Branchionmma cingulatum Grube	2.32	0.02	0.49	1.94	0.12	0.6	2.13	0.07	0.54
Glycera chirori Izuka	0	0	0	1.45	0.03	0.31	0.73	0.02	0.15
Dentinephtys glabra Hartman	6.18	6.09	2.63	3.15	0.07	1.07	4.66	3.08	1.85
Tylorrhynchus heterochaetus Quatrefages	0	0	0	0.73	0.03	0.06	0.36	0.01	0.03
Perinereis nuntia Savigny	0.39	0.01	0.02	0.73	0.02	0.09	0.56	0.01	0.05

Table 2

PERMANOVA results for the macroinvertebrates. *df* represents degrees of freedom, *SS* represents square sum, *M*S represents mean sum, *F* represents Fisher's univariate *F* statistic, *P*(MC) represents *P* values using Monte Carlo permutations.

Source	*df*	*SS*	*MS*	*F*	*P*(MC)
Time	5	3.68	0.74	3.45	＜0.001
Tide	1	2.34	2.33	10.95	＜0.001
Site	3	0.97	0.32	1.51	＞0.05
Time×Tide	5	2.19	0.44	2.05	＜0.05
Time×Site	15	4.86	0.32	1.52	＜0.05
Tide×Site	3	0.88	0.29	1.37	＞0.05
Time×Tide×Site	15	4.89	0.32	1.52	＜0.05
Residual	93	19.84	0.21		
Total	140	39.64			

PERMANOVA indicated that two explanatory variables (time and tide) were governing sources of variation in the macroinvertebrates assemblages. The interaction terms, such as time×tide, time×site, time ×tide ×site, were also significant (Table 2). The interaction term tide× site was not significant.

In the fortnightly tide period, the difference of number of species (*df*=47; *F*=1.435; *P*> 0.05), abundance (*df*=47; *F*=1.685; *P*> 0.05) and biomass (*df*=47; *F*=2.151; *P*> 0.05) of benthic macroinvertebrates at different sampling sites were not significant. However, there were significant differences in species and abundance between individual sampling sites (Fig.2). There was also no significant difference in the number of species, abundance and biomass of benthic macroinvertebrates at different sampling sites during the spring and the neap tide periods, but also some significant differences exist in number of species and abundance between individual sampling sites (Fig.2).

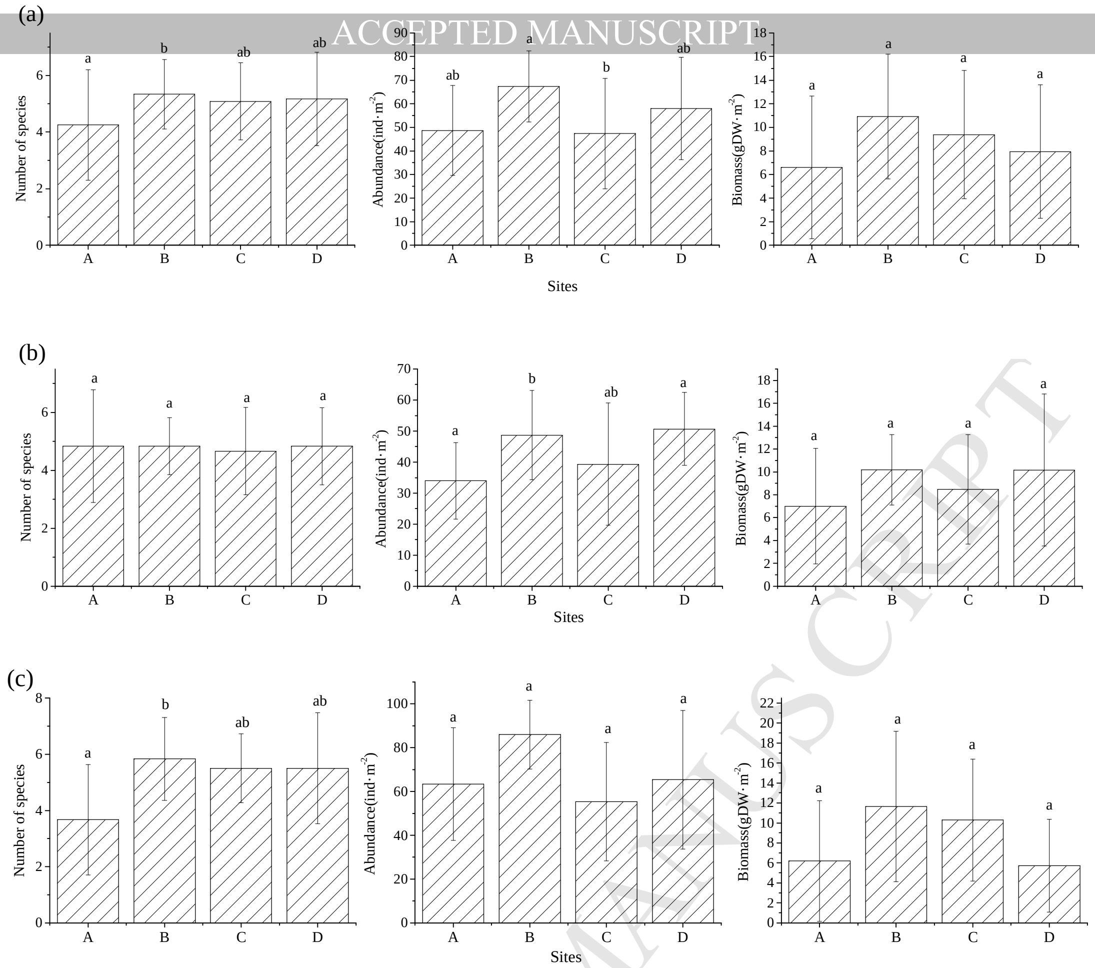


Fig.2. The number of species, abundance and biomass of the benthic macroinvertebrate communities (mean±se) at Site A, B, C and D in the salt marsh of the East Nanhui tidal flat during the fortnightly tide period (a), spring (b) and neap (c) tide periods. Any two columns with the same letter are not significantly different following one-way ANOVA (P>0.05).

The variations in characteristics of number of species, abundance and biomass of benthic macroinvertebrates during the spring and neap tide periods were very different (Fig.3). The number of species (df=46; t=-3.729; P<0.05) and the abundance (df=46; t=-2.522; P<0.05) of benthic macroinvertebrates in the spring tide period were significantly lower than that in the neap tide period. In contrast, there was no significant difference in the biomass of benthic macroinvertebrates between the spring and neap tide periods (df=46; t=1.046; P＞0.05).

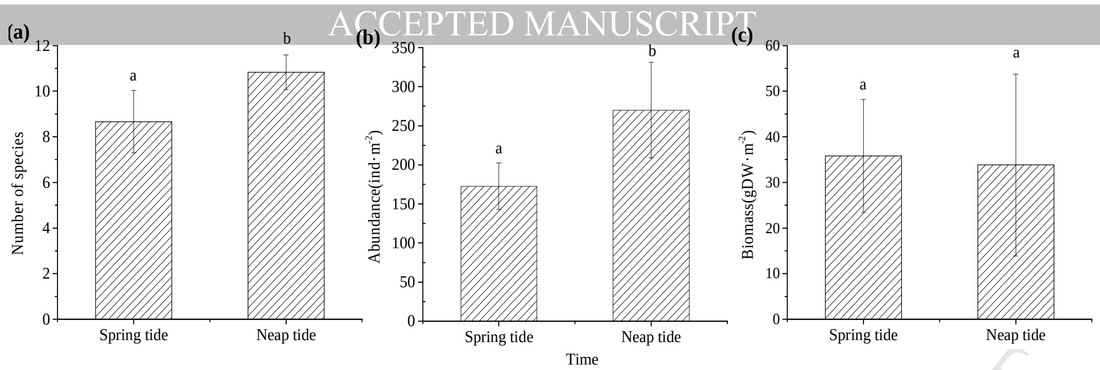
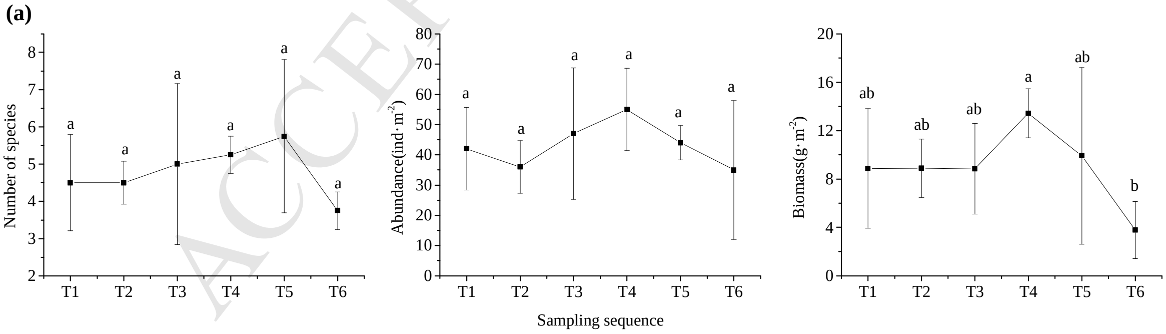


Fig. 3. The number of species (a), abundance (b) and biomass (c) of the benthic macroinvertebrate communities (mean±se) in the salt marsh on the East Nanhui tidal flat during the spring and neap tide periods. Any two columns with the same letter are not significantly different following Student t-test (*P*>0.05).

The characteristics of semidiurnal variation in the number of species, abundance and biomass of benthic macroinvertebrate communities during the spring tide period were different (Fig. 4). There were no significant differences in the number of species (*df* =23; *F*=1.020; *P*＞0.05), abundance (*df*=23; F=0.807; *P*＞0.05) or biomass (*df*=23; *F*=1.897; *P*＞0.05) of benthic macroinvertebrates among the spring tides. There were also no significant differences in the number of species or abundance of benthic macroinvertebrate communities between individual semidiurnal periods, while there were significant differences in biomass between some semidiurnal periods.



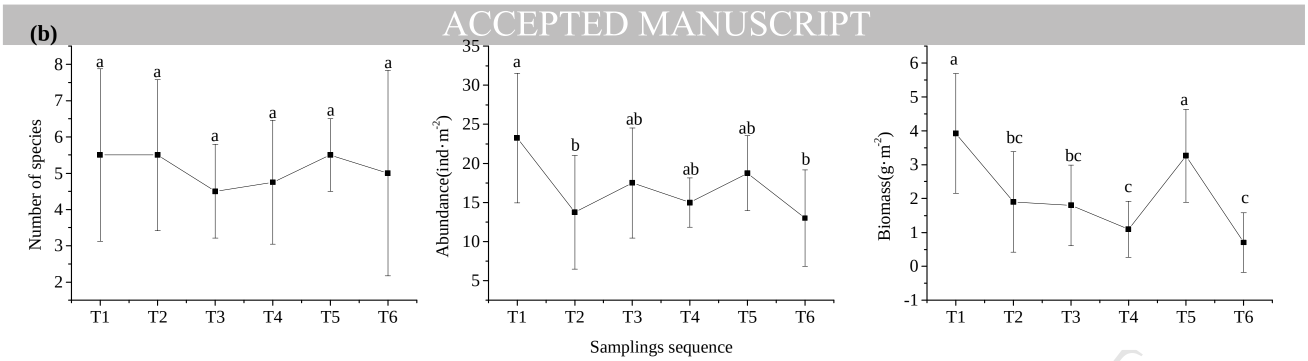


Fig. 4. Semidiurnal variations in the number of species, abundance and biomass of benthic macroinvertebrate communities (mean±se) in the salt marsh on the East Nanhui tidal flat during the spring (a) and neap (b) tides. T1–T6 represent the six sampling events during the ebb tide between the successive semidiurnal tides. Any two samples with a common letter are not significantly different following one-way ANOVA (P>0.05).

The characteristics of semidiurnal variation in the number of species (df=23; F=0.131; P＞0.05), abundance (df=23; F=0.197; P＞0.05) and biomass (df=23; F=1.442; P＞0.05) of benthic macroinvertebrate communities in the neap tide period were different (Fig. 4). The number of species, abundance and biomass were largely similar across successive semidiurnal tidal cycles, however, there were significant differences in abundance and biomass between some semidiurnal tidal periods (df=23; F=3.707; P<0.05).

3.2. Characteristics of hydrological and sedimentary factors

Variations characteristics of the environmental factors during the spring and neap tide periods were different (Table 3). Most hydrological elements and sedimentary factors differed significantly between the spring and neap tide periods. The average water depth, maximum water depth, average water flow velocity and maximum water flow velocity during the spring tides were all significantly higher than those in the neap tides (P<0.001). The sediment water content in the spring tide period was significantly higher than in the neap tide period (P<0.05), while the water temperature, conductivity, salinity, and sediment bulk density in the neap tide period were all significantly higher than those in the spring tide period (P<0.001). The water turbidity and sediment pH values in the neap tide period were also significantly higher than those in the spring tide period (P<0.05). There were no significant differences in flooding duration or sediment grain size between the spring and neap tide periods.

Average water depth, maximum water depth, flooding duration, water turbidity, water temperature, conductivity, salinity, sediment water content and sediment bulk density in the spring tide periods varied significantly during tidal cycles (P<0.001) (Table 3); Average flow velocity and sediment pH changed significantly with tidal stages (P<0.05), whereas the maximum flow velocity and sediment grain size did not show significant variation. Results from LSD Multiple comparison showed that there were dramatic variations in the water turbidity, salinity, conductivity, and water content of sediment in the spring tide period, with the differences being significant (P<0.05) or extremely significant (P<0.001) between individual semidiurnal tides. There was no significant change in the maximum flow velocity in the spring tide period between individual semidiurnal tides. Significant differences also occurred in some other environmental factors between certain individual semidiurnal tides (P<0.05).

There were extremely significant temporal variations in water temperature, conductivity, salinity, sediment pH and bulk density in the neap tide period (P<0.001) (Table 3). Average water depth, maximum water depth, flooding duration, maximum flow velocity, and sediment water content showed significant temporal variations (P<0.05). Unlike in the spring tide period, water turbidity, average flow velocity, and sediment grain size in the neap tide period did not vary significantly with tides. Multiple comparison results showed that the water salinity in the neap tide period changed dramatically, and significant (P<0.05) or highly significant differences (P<0.001) occurred between the individual semidiurnal tides. No significant difference occurred in water turbidity, average flow velocity or sediment grain size between every two semidiurnal tides in the neap tide period. There were significant differences in some other environmental factors between certain individual semidiurnal tides (P<0.05).

Table 3

Variations in environmental parameters during different tidal periods in the salt marsh on the East Nanhui tidal flat. *F* value and *P* value represent the significant level of overall environmental parameters variations during spring tide and neap tide periods following one-way ANOVA；W1–W5 represent the environmental factors in each semidiurnal tide in spring and neap tide periods (mean±se); *P**and *t* * value represent the significant level of overall environmental factor variation between spring tide and neap tide period following Student t-test. Total represents the average values of environmental factors during spring and neap tide periods (mean±se).

Environment factors	Tide period	*F* value (*df=23)*	P value	W1	W2	W3	W4	W5	*t**value (*df*= 38)	P*value	Total
Hydrology											
Mean water depth (m)	Spring	68.9	*P*<0.001	1.00±0.03^{a}	1.52±0.07^{b}	1.13±0.06^{c}	1.65±0.07^{b}	1.17±0.07^{c}	5.703	*P**<0.001	1.30±0.26^{a}
	Neap	3.4	*P* <0.05	0.95±0.14^{a}	0.86±0.13^{ab}	0.97±0.13^{a}	0.71±0.14^{b}	1.03±0.16^{a}			0.90±1.66^{b}
Max water depth (m)	Spring	66.2	*P*<0.001	1.51±0.11^{a}	2.35±0.11^{b}	1.67±0.11^{c}	2.55±0.11^{b}	1.76±0.10^{c}	5.421	*P**<0.001	1.97±0.43^{a}
	Neap	5.06	*P* <0.05	1.41±0.18^{a}	1.30±0.18^{ab}	1.46±0.119^{a}	1.05±0.18^{b}	1.60±0.18^{a}			1.37±0.25 ^{b}
Submergence time (day)	Spring	43.3	*P*<0.001	0.23±0.01^{a}	0.28±0.01^{b}	0.23±0.11^{a}	0.29±0.01^{b}	0.24±0.01^{a}	-0.929	*P**>0.05	0.25±0.03 ^{a}
	Neap	5.53	*P* <0.05	0.25±0.02^{ab}	0.25±0.02^{ab}	0.27±0.02^{bc}	0.23±0.02^{a}	0.29±0.02^{c}			0.26±0.03 ^{a}
Water turbidity (NTU)	Spring	99	*P*<0.001	562.51±41.36^{a}	724.91±6.02^{b}	497.04±37.27^{c}	982.45±53.45^{d}	860.35±47.24^{e}	-2.567	*P**<0.05	725.45±188.7^{a}
	Neap	1.11	*P* >0.05	772.19±125.86^{a}	865.95±103.81^{a}	817.08±156.79^{a}	1013.38±255.2^{a}	1001.32±254.5^{a}			873.68±176.4^{b}

Water temperature (℃)	Spring	99.7	$P<0.001$	29.36±0.09^{a}	29.44±0.06^{b}	30.06±0.10^{c}	29.38±0.05^{ab}	30.20±0.08^{c}	-7.581	$P*<0.001$	29.69±0.38^{a}
	Neap	397.4	$P<0.001$	31.97±0.04^{a}	30.13±0.13^{b}	32.44±0.10^{c}	30.29±0.14^{b}	31.93±0.04^{a}			31.35±0.97^{b}
Water conductivity (mS·cm^{-1})	Spring	900.9	$P<0.001$	0.61±0.01^{a}	0.67±0.01^{b}	0.95±0.05^{c}	2.06±0.12^{d}	4.74±0.20^{e}	-3.519	$P*<0.001$	1.81±1.60^{a}
	Neap	197.5	$P<0.001$	2.32±0.07^{a}	2.81±0.15^{b}	2.65±0.10^{b}	3.75±0.22^{c}	4.85±0.25^{d}			3.27±0.95^{b}
Water salinity (‰)	Spring	947.6	$P<0.001$	0.27±0.01^{a}	0.29±0.01^{b}	0.42±0.02^{c}	0.97±0.06^{d}	2.28±0.10^{e}	-3.234	$P*<0.001$	0.85±0.78^{a}
	Neap	137.1	$P<0.001$	1.03±0.03^{a}	1.30±0.07^{b}	1.17±0.04^{c}	1.77±0.10^{d}	2.26±0.13^{e}			1.50±0.47^{b}
Mean flow velocity (cm·s^{-1})	Spring	4.29	$P<0.05$	22.86±1.85^{a}	24.94±1.64^{ab}	23.45±0.99^{a}	26.68±0.77^{b}	23.67±1.73^{a}	8.634	$P*<0.001$	24.32±1.90^{a}
	Neap	0.33	$P>0.05$	18.57±0.15^{a}	18.66±0.14^{a}	20.05±1.49^{a}	19.14±1.32^{a}	18.67±3.78^{a}			19.02±1.97^{b}
Max flow velocity (cm·s^{-1})	Spring	0.16	$P>0.05$	42.14±0.52^{a}	41.28±1.23^{a}	40.94±4.51^{a}	41.24±3.57^{a}	42.41±3.65^{a}	5.684	$P*<0.001$	41.60±2.82^{a}
	Neap	5.35	$P<0.05$	34.59±5.81^{a}	31.31±0.69^{a}	33.36±1.96^{a}	34.16±0.85^{a}	42.18±5.02^{b}			35.12±4.95^{b}
Sediment											
pH	Spring	75.34	$P<0.05$	8.16±0.75^{ab}	7.91±0.62^{ab}	8.60±0.80^{b}	6.70±0.90^{c}	7.31±0.42^{a}	-1.747	$P*<0.05$	7.74±0.93^{a}
	Neap	18.14	$P<0.001$	8.84±0.50^{a}	6.55±0.53^{c}	9.98±1.17^{b}	8.97±0.12^{ab}	9.26±0.33^{abc}			8.72±1.31^{b}
Median grain size (d$_{50}$)	Spring	2.7	$P>0.05$	56.27±4.67^{abc}	53.54±3.67^{ac}	60.71±4.82^{b}	52.24±4.53^{c}	59.05±3.91^{ab}	1.159	$P*>0.05$	56.36±5.06^{a}
	Neap	0.55	$P>0.05$	51.44±6.61^{a}	52.38±6.58^{a}	54.69±7.06^{a}	51.32±5.15^{a}	57.30±6.72^{a}			53.43±6.20^{a}
Water content (%)	Spring	30.27	$P<0.001$	24.84±0.82^{a}	24.21±0.73^{b}	26.15±0.61^{c}	28.13±0.61^{d}	30.15±0.55^{e}	1.751	$P*<0.05$	0.46±004^{a}
	Neap	3.27	$P<0.05$	24.48±0.42^{a}	28.15±0.81^{b}	27.94±0.89^{b}	26.43±0.82^{ab}	26.55±0.61^{ab}			0.26±0.01^{b}

Bulk density (g·cm^{-3})	Spring	30.85	*P*<0.001	1.27±0.04^{a}	1.21±0.05^{a}	1.25±0.03^{a}	1.19±0.03^{b}	1.18±0.01^{b}	1.812	*P**<0.001	1.23±0.04^{a}
	Neap	30.85	*P*<0.001	1.27±0.03^{a}	1.42±0.05^{b}	1.45±0.03^{b}	1.61±0.08^{c}	1.48±0.15^{c}			1.48±0.15^{b}

3.3. Effects of hydrological processes on benthic macroinvertebrate communities

Two principal components were obtained through principal component analysis on hydrological factors and sedimentary physicochemical factors (Fig. 5). The cumulative contribution rate of the two PCs extracted was 74.9% indicating that these two components comprehensively generalized the 13 main indexes. The contribution rate of PC1 was 52.8%, which encompassed the average water depth, maximum water depth, average flow velocity, maximum flow velocity and flooding duration, which together could be generalized as the intensity of hydrological processes (Table 4). The contribution rate of PC2 was 22.1%, which encompassed water salinity, conductivity, turbidity, sediment bulk density, water temperature and other factors (Table 4). Thus, PC2 could be summarized as the physical and chemical properties of both water and sediment.

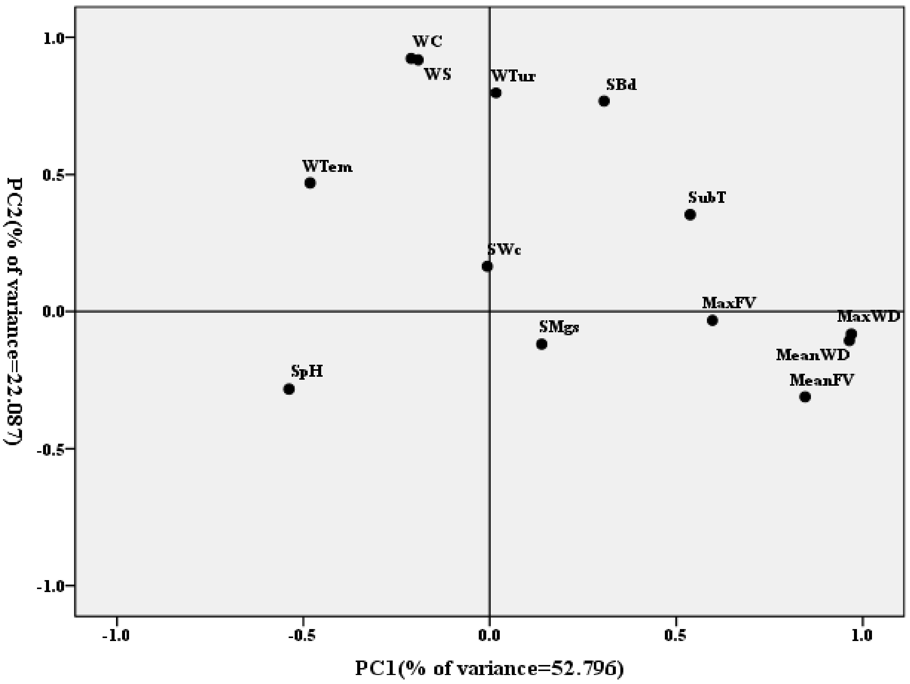


Fig. 5 PCA of hydrological elements and sedimentary parameters in the salt marsh of the East Nanhui tidal flat. MeanWD: Mean water depth; MaxWD: Maximum water depth; SubT: Submerge time; WTur: Water turbidity; WTem: Water temperature; WC：Water conductivity; WS: Water salinity; Mean FV: Mean flow velocity; Max FV: Maximum flow velocity; SpH: Sediment pH; SMgs: Sediment median grain size; SWc: Sediment water content; SBd: Sediment

bulk density.

Table 4

Eigenvector values of the environmental factors of PC1 and PC2. The abbreviations in the table were same to Fig.5

	PC1	PC2
MeanWD	0.965	-0.1
MaxWD	0.97	-0.076
SubT	0.535	0.357
WTur	0.012	0.798
WTem	-0.484	0.467
WC	-0.217	0.922
WS	-0.197	0.917
MeanFV	0.847	-0.305
MaxFV	0.597	-0.029
SpH	-0.537	-0.286
SMgs	0.14	-0.117
SWc	-0.007	0.165
SBd	0.302	0.769

The correlations of the number of species, abundance and biomass characteristics of the overall benthic macroinvertebrate communities with the two PCs are very different (Table 5). PC1 has no significant effect on the number of species or biomass of the benthic macroinvertebrate communities (*P*>0.05), but does significantly influence the abundance (*P*<0.05); PC2 has no significant effect on the number of species or abundance of macroinvertebrate communities, but does have a significant effect on the biomass (*P*<0.05).

Table 5

The correlations between the number of species, abundance and biomass characteristics of the benthic macroinvertebrate communities and the two PCs in the salt marsh of the East Nanhui tidal flat. The significant correlations are shown in bold.

	PC	P value	Correlation coefficient
Number of species	PC1	0.222	-0.199
	PC2	0.484	-0.113
Abundance	**PC1**	**0.011**	**-0.396**
	PC2	0.669	0.070
Biomass	PC1	0.608	0.078
	PC2	**0.014**	**-0.389**

The best combination of selected factors which correlate significantly with the abundance and biomass of the benthic macroinvertebrate communities vary widely across the sampling periods (Table 6). In the entire fortnightly tide period, the combined environmental factors which have significant effects on the abundance of the benthic macroinvertebrate communities appear to include the average water depth, maximum depth, water salinity, maximum flow velocity, and sediment grain size (r=0.216, P<0.05), while no such combined environmental factors exhibit a significant correlation with the biomass of the benthic macroinvertebrate communities. The abundance of bivalves is significantly correlated with the combination of average water depth and sediment bulk density (r=0.447, P<0.05), whereas there is no significant correlation between the combined environmental factors and the biomass of the community. There is also no significant correlation between the combined environmental factors and the abundance or biomass of malacostracans. In contrast, the biomass of polychaetes is significantly positively correlated with the combination of average flow velocity, sediment bulk density and flooding duration (*r*=0.084, *P*<0.05), but there is no significant correlation between the same combined factors and the abundance of the community.

The biomass of the benthic macroinvertebrates in the spring tide period is significantly correlated with the combination of water temperature and maximum flow velocity (*r*=0.379, *P*<0.05), whereas there is no significant correlation between the combined environmental factors and the abundance of the community. The results imply that the bivalve abundance is not significantly affected by either the hydrological elements or sedimentary parameters that we investigated in the spring tide period, whereas their biomass is significantly positively correlated with the combination of maximum water depth, water turbidity, water salinity, and sediment bulk density (*r*=0.369, *P*<0.05). Neither the abundance nor the biomass of either the malacostracans or the polychaetes in the spring tide period are significantly correlated with the hydrological elements or sedimentary parameters in this study.

The biomass of the benthic macroinvertebrates during the neap tide period is significantly correlated with the combination of average water depth, average flow velocity, and sediment grain size (*r*=0.251, *P*<0.05), whereas there is no significantly correlation between the combined environmental factors and the abundance of the communities. The abundance of the bivalves was not significantly correlated with either the hydrological elements or the sedimentary factors in the neap tide period, whereas their biomass was significantly positively correlated with the combination of average water depth, average flow velocity, and sediment grain size (*r*=0.251, *P*<0.05). Neither the abundance nor the biomass of the malacostracans or the polychaetes during the neap tide period is significantly correlated with the hydrological elements or the sedimentary parameters.

Table 6

Correlations between the benthic macroinvertebrate communities and environmental factors in the salt marsh on the East Nanhui tidal flat. The significant correlations are shown in bold.

Tidal periods	Community parameters		Correlation coefficient	Selected factors	P value
Fortnightly tides	Total	Abundance	**0.138**	**1,2,7,9,11**	**0.023**
		(Biomass)	(0.194)	(1,3,8)	(0.130)
	Bivalve	Abundance	**0.447**	**1,13**	**0.008**
		(Biomass)	(0.270)	(1,2,12,13)	(0.122)
	Malacostracan	Abundance	0.033	4,12	0.332
		(Biomass)	(0.103)	(1)	(0.093)
	Polychaete	Abundance	0.044	2,8,13	0.167
		(Biomass)	(**0.084**)	(**8,13**)	**(0.040)**
Spring tides	Total	Abundance	0.047	7	0.381
		(Biomass)	**(0.379)**	**(1,2,4,7,8)**	**(0.006)**
	Bivalve	Abundance	0.141	7	0.174
		(Biomass)	**(0.369)**	**(2,4,7)**	**(0.007)**
	Malacostracan	Abundance	0.036	1,2,4,7	0.629
		(Biomass)	(0.011)	(1,2,12)	(0.085)
	Polychaete	Abundance	0.093	7,9	0.218
		(Biomass)	(0.085)	(8,13)	(0.090)
Neap tides	Total	Abundance	0.302	1,7,11	0.220
		(Biomass)	(**0.251**)	(**1,8,11**)	(**0.024**)
	Bivalve	Abundance	**0.494**	**1, 9,11,13**	**0.023**

	(Biomass)	**(0.259)**	**(1,8,11)**	**(0.005)**
Malacostracan	Abundance	0.072	1,11	0.631
	(Biomass)	(0.378)	(5,7,13)	(0.068)
Polychaete	Abundance	0.010	7	0.853
	(Biomass)	(-0.093)	(7,8,12)	(0.658)

Notes: Environmental factors 1: Mean water depth; 2: Max water depth; 3: Submergence time; 4: Water turbidity; 5: Water temperature; 6: Water conductivity; 7: Water salinity; 8: Mean flow velocity; 9: Max flow velocity; 10: Sediment pH; 11: Sediment median grain size; 12: Sediment water content; 13: Sediment bulk density. The bold type signifies significant correlations (P<0.05).

4 Discussion

4.1. Effects of hydrological processes on benthic macroinvertebrates in salt marshes

The roles of hydrological processes as important as physical processes in salt marsh ecosystems and their effects on organisms, including the benthic macroinvertebrates, have attracted much attention in the past decades (Cardoso *et al*., 2010; Paavo *et al*., 2011). Previous studies have shown that hydrological elements in the salt marshes, including water flow velocity, depth, salinity and turbidity (Warwick and Uncles, 1980; Salen-Picard *et al*., 2003; Ysebaert *et al*., 2003; Tomiyama *et al*. 2008), as well as sediment grain size, pH, bulk density and other sedimentary factors (Lamptey and Armah, 2008; Tong *et al*., 2013; Takada *et al*., 2015) have different effects on the composition, number of species, abundance and biomass of benthic macroinvertebrates community. Our results showed that hydrological processes have significant effects on compositions, number of species and abundance of the benthic macroinvertebrates, but not on the biomass, which was consistent with the results found in previous studies. For example, Conde *et al*. (2013) found that strong hydrological processes resulted in a significant decrease in the abundance of benthic macroinvertebrates, but not in the biomass. They declared that the increase in abundance and biomass of the opportunistic species resulted in the stable biomass of the benthic macroinvertebrates. In our study, we found that hydrological processes mainly affected the biomass of the relatively small-sized malacostracans and polychaetes, while the bivalves, which had relatively higher individual biomass values, appeared to be more stable. This was likely the reason that the biomass of the benthic macroinvertebrates did not vary significantly.

Our hypothesis, which is that hydrological processes can directly affect the benthic macroinvertebrate communities, has been supported by our results. In this study, the intensity of the hydrological processes appeared to be the first principal component of the related environmental factors, which had significant correlation with the abundance of the benthic macroinvertebrates. Water depth and flow velocity appeared in the combined environmental factors which had significant correlation with the benthic macroinvertebrate communities in both semidiurnal and fortnightly timescales. These results were consistent with those previous studies (Warwick and Uncles, 1980; Ysebaert *et al*., 2002). According to a study by Warwick and Uncles (1980), tides and tidal currents can directly disturb the benthic macroinvertebrates, the intensity of this effect mainly depended on the water flow velocity and depth.

In this study, furthermore, water salinity and turbidity appeared to have the highest contribution to the second principal component of the environmental factors，and these two factors proved to have significant correlation with the biomass of the benthic macroinvertebrates. This indicates that the change of physicochemical parameters of water in hydrological process is as important as the intensity of hydrological process. These conclusions are supported by previous studies. For example, Norkko *et al*. (2001) and Nishijima *et al*. (2013) concluded that large volumes of low-salinity water flowing into the salt marshes might lead to a decrease in the number of species, abundance and biomass of the benthic macroinvertebrates. Salen-Picard *et al*. (2003) reported that a dramatic increase in water turbidity could cause feeding difficulties for the suspension feeders, which could, in turn, lead to the decrease in their abundance. Therefore, we can conclude that the direct effects of hydrological processes on benthic macroinvertebrates depend mainly on the intensity of the processes and water physicochemical properties. It is suggested that the restoration of the benthic macroinvertebrates community can be carried out by adjusting the intensity of hydrological processes, physicochemical characteristics of water and sediment.

In this study, we observed that hydrological processes could also influence the benthic macroinvertebrates indirectly by affecting sedimentary factors. Hydrological processes can significantly alter bulk density, water content and pH of the sediments. Previous studies have shown that hydrological processes can drive transportation, deposition and redistribution of the sediments, which, in turn, affect the sediment grain size (McCave, 1978; Gao *et al*., 1994). Agitation of the sediment by hydrological processes could change its consolidation state, thereby affecting the bulk density and water content of the sediments (Shi *et al*., 2014). In addition, it has been shown that variation in flooding conditions can have significant effects on pH of the sediments (Portnoy, 1999). In this study, it is found that hydrological processes have no significant effect on sediment grain size. A possible explanation is that the hydrological processes varied less in such a short time during our study period. Our previous study has also shown that sediment bulk density is one of the most important factors affecting the benthic macroinvertebrates (Tong *et al*., 2013). In this study, bulk density appeared repeatedly in the combined environmental factors which have significant effects on the benthic macroinvertebrates. The results suggested that hydrological processes can indirectly affect the benthic macroinvertebrates by influencing the bulk density of the sediments. It is also found in this study that sediment grain size correlates significantly with the abundance and biomass of the benthic macroinvertebrates, which is consistent with the results from the previous studies (Cahoon, 1999; Yuan and Lu, 2001; Tomiyama *et al*., 2008).

In addition, the effects of hydrological processes on the benthic macroinvertebrates can vary with the different taxonomic classes. In this study, it is found that environmental factors, including water depth, flow velocity, salinity, turbidity, sediment grain size and bulk density, have significant correlations with the abundance and biomass of bivalves. Similar results have been reported in previous studies. For example, Tomiyama *et al*. (2008) found that the abundance of bivalves in the Natori River estuary were higher in areas with high salinity and low sediment clay content, and Coco *et al*. (2006) reported that bivalves could not survive in water with high turbidity. In the Yangtze Estuary, bivalves usually gathered in areas where the sediments have coarse grain size (Fang *et al*., 2006). In this study, the combination of water flow velocity and sediment bulk density was found to have significant correlations with the polychaetes, while previous studies reported that the important factors included water salinity, dissolved oxygen, sediment grain size, clay and organic matter content (Omena and Creed, 2004; Pillay and Perissinotto, 2008; Tomiyama *et al*., 2008; Musale and Desai, 2011). In this study, there found no significant effects on malacostracans due to environmental factors related to hydrological processes. However, previous studies showed that water salinity and temperature as well as other factors could have important effects on this group (Pérez-Castañeda and Defeo, 2001; Posey *et al*., 2005; Beguer *et al*., 2012). The differences in lifestyle of the different classes should be considered to be one of the most important reasons for this phenomenon (Tong *et al*., 2013; Lin *et al*., 2015), which may need further investigation.

4.2. Effects of scale on the studies

When the temporal and spatial scales of surveys change, the system will exhibit different characteristics (Crawley and Harral, 2001; Byers and Noonburg, 2003; Kallimanis *et al*., 2008; Reif *et al*., 2008).The results from this investigation showed that the scale effects also exists over the shorter time scale, which supports our hypothesis. In this study, we found that the composition，number of species，abundance of the benthic macroinvertebrates changed significantly over the fortnightly scale, whereas only the composition of benthic macroinvertebrates community changed over the semidiurnal scale. Moreover, previous studies have shown that hydrological processes have significant effects on the composition, number of species, abundance and biomass of benthic macroinvertebrates over longer timescales (Edgar and Barrett, 2002; Ysebaert and Herman, 2002; Eyre and Ferguson, 2006; Nishijima *et al*., 2013). It can be inferred that the effects of hydrological processes on benthic macroinvertebrates in the salt marsh are much more obvious over the longer timescale, in which the hydrological processes may vary more significant, and their effects may be extended over time. The mechanisms are beyond this study, but it is worthy of further investigation.

According to the results from this study, the combined environmental factors, which significantly affect the benthic macroinvertebrates may differ from timescales. Over the semidiurnal tidal scale, the important factors appeared to be water depth, flow velocity, water salinity and turbidity during spring tide period, but water depth, flow velocity, sediment grain size and bulk density during the neap tide periods. On the fortnightly tidal scale, the combination included not only the intensity characteristics of hydrological processes, but also the physicochemical factors of water and sediment. A few previous studies reported similar effects over the longer timescales. In the monthly or seasonal scale, water salinity and temperature appear to be the most important factors to the benthic macroinvertebrates (Eyre and Ferguson, 2006; Lamptey and Armah, 2008; Nishijima *et al*., 2013), while variations in water salinity and sediment grain size caused by the runoff changes are more important over the annual scale (Edgar and Barrett, 2002; Ysebaert and

Herman, 2002; Grilo *et al*., 2011; Dittmann *et al*., 2015). Furthermore, the characteristics of the hydrological processes also vary over different time scales. For example, the runoff of the river usually varies over months, seasons or even years, which, in turn, affects water salinity, sediment grain size,etc. (Détriché *et al*., 2011; Ghezzo *et al*., 2011; Garcia *et al*., 2012; Zhu *et al*., 2012; Yu *et al*., 2014).

The current study provides a better understanding of the effects of hydrological processes on benthic macroinvertebrates, and has highlighted that the effects of short-timescale hydrological processes on benthic macroinvertebrate communities in salt marsh should not be ignored in future studies. It is necessary to replicate the experiment of this study in different months, seasons and years to ensure these findings. More in-depth research on the effects of hydrological processes on benthic macroinvertebrate communities needs to be carried out to provide a theoretical basis for species diversity, restoration and comprehensive exploitation and utilization of salt marsh.

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Highlights:

1. Continuous hydrological processes had significant effects on the number of species and abundance but not on biomass of the benthic macroinvertebrates .

2. Hydrological processes could not only directly affect the benthic macroinvertebrates, but also indirectly affect the communities by influencing sedimentary physiochemical factors.

3. The effects of hydrological processes on benthic macroinvertebrates over shorter timescales still showed scale effects.