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Bioturbation by sea cucumbers *Apostichopus japonicus* affects sediment phosphorus forms and sorption characteristics

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ABSTRACT: An 84 d experiment was carried out to investigate the impact of sea cucumber *Apostichopus japonicus* (Selenka) bioturbation on different phosphorus forms and phosphorus sorption characteristics in the sediment. Sea cucumbers were cultured in fiberglass tanks (30 × 40 × 50 cm) with 5 cm thick sediment, and were divided into 4 groups according to culture densities, i.e. 0, 4, 6, and 8 ind. tank^{-1}. For each of these 4 densities, 4 replicates of sea cucumbers were cultured. Results showed that the increasing culture density significantly increased the content of NaOH-extractable P (NaOH-P) and decreased the content of organic phosphorus (OP) in sediment. Phosphorus maximum buffer capacity (MBC) and energy adsorption (K_f) values of sediment in the lower density groups (0 and 4 ind. tank^{-1}) decreased significantly with time, while no temporal changes were observed in MBC and K_f values of sediment in the higher density groups (6 and 8 ind. tank^{-1}). Sea cucumbers facilitated the decomposition of OP and the formation of NaOH-P in sediment, and improved the ability and capacity of phosphorus sorption of the sediment with increasing culture density. Our results suggest that the use of sea cucumbers may help to prevent eutrophication in integrated multitrophic aquaculture systems.

KEY WORDS: *Apostichopus japonicus* · Sea cucumber · Bioturbation · Phosphorus forms · Phosphorus sorption characteristics · Holothuroidea

INTRODUCTION

China is now the world's largest aquaculture nation, with aquaculture production of 35.07 million metric tons in 2011, representing 62% of the total world aquaculture production (FAO 2014). However, with the fast development of aquaculture, aquaculture waste has raised many issues related to its effect on the environment, of which nutrient enrichment from aquaculture effluents is perhaps the most serious (Talbot & Hole 1994). In mariculture, amounts of residual diets, animal feces, and biological debris are imported into the water and sediment, resulting in the eutrophication and degradation of water bodies (Lin et al. 1994, Ji et al. 2000). Moreover, wastewater that is rich in organic matter and nutrients and is discharged into coastal estuaries may accelerate eutrophication of adjacent waters (Lin et al. 1994, Ji et al. 2000).

Phosphorus is a major element controlling marine primary productivity and is a major contributor of eutrophication in surface water systems, which influ-

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ences global biogeochemical cycles (Broecker & Peng 1982, Pant & Reddy 2001). Sediment is an important phosphorus sink and source in marine environments (Ruttenberg 1993, Howarth et al. 1995, Cong et al. 2014, Ni & Wang 2015). It provides sites for phosphorus accumulation and regeneration and releases the phosphorus into the overlying water under certain geochemical environmental conditions (Meybeck 1982, Jensen et al. 1995, Cong et al. 2014, Ni & Wang 2015). Phosphorus is deposited in the sediment matrix in the form of calcium, iron, or aluminum complex salts and organic species, or is sorbed onto the surfaces of minerals (Pettersson et al. 1988). Not all of the phosphorus can be released from the sediments (Gonsiorczyk et al. 1998), as the release of phosphorus from sediments depends on the composition of its forms (Zhou et al. 2001). In aquatic ecosystems, the adsorption and desorption of phosphorus by sediment are related to various environmental factors and distribution of phosphorus forms in sediment (Jin et al. 2015). Therefore, the phosphorus forms in the sediment determine the phosphorus sorption characteristics of the sediment, and further affect the concentration of phosphorus and the primary productivity in the water column (Olila & Reddy 1993, Jin et al. 2015). Phosphorus in the sediment in various bound forms has an important potential impact on eutrophication (Hua et al. 2000, Jin et al. 2015).

Benthic deposit feeders, including sea cucumbers, are important components of the benthic environment, and are important environmental factors (Chen et al. 2005). Bioturbation by benthic deposit feeders can modify environmental conditions in the sediment and influence the transport and transformation of phosphorus at the sediment–water interface (Lewandowski et al. 2002, Lewandowski & Hupfner 2005, Papaspyrou et al. 2006, Stockdale et al. 2009, Zhang et al. 2010). Lewandowski et al. (2002) and Lewandowski & Hupfner (2005) discovered that bioturbation by oligochaetes and chironomids could effectively alter the concentration and distribution of NaOH-extractable phosphorus (NaOH-P) in sediment. Zhang et al. (2011) observed that bioturbation by *Corbicula fluminea* increased the NaOH-P content in sediment, while no significant impacts of bioturbation on other phosphorus forms were observed.

The sea cucumber *Apostichopus japonicus* (Selenka) is one of the most commercially valuable species among 1100 sea cucumber species in the world (Okorie et al. 2008). Sea cucumber culturing has rapidly increased in China over the past 20 yr (Chen 2004, Xia et al. 2012). As typical deposit feeders, sea cucumbers mainly ingest microorganisms, organic detritus, including their own feces, and aquatic organisms (Yingst 1976, Moriarty 1982, Uthicke & Klumpp 1998), and they play an important role in the removal, recycling, and repackaging of nutrients, especially organic matter (Jumars & Self 1986). Their trophic position and ability to process sediment enriched and affected by aquaculture activities has led to a strong interest in their use in integrated multitrophic aquaculture systems (IMTAs) worldwide (Zamora et al. 2016). Hence, *A. japonicus* is not only an important economic aquaculture species, but also a valuable species for bioremediation (Yuan 2005). Sea cucumbers influence the transport and transformation of various nutrients such as nitrogen, phosphorus, and carbon due to their movement, feeding, and excretion. Numerous studies have examined changes in the fluxes of nitrogen and active phosphate at the sediment–water interface resulting from sea cucumber farming (Işgören-Emiroğlu & Günay 2007, Zheng et al. 2009). However, to date no quantitative studies about the effects of bioturbation by *A. japonicus* on different sediment phosphorus forms and sorption characteristics of sediment have been reported.

In the present study, the contents of different phosphorus forms and phosphorus adsorption characteristics were investigated to determine the role of sea cucumbers in the transport and transformation of phosphorus at the sediment–water interface. We also aimed to provide a reference for the application of sea cucumbers in IMTAs to prevent eutrophication of aquaculture water and realize the sustainable development of aquaculture.

MATERIALS AND METHODS

Culturing experiment

The experiment was conducted at the laboratory of the Qingdao National Ocean Scientific Research Center, Ocean University of China. Sea cucumbers *Apostichopus japonicus* (Selenka) were collected from a local commercial farm. The experimental sediments were obtained from the natural offshore sea area in Qingdao. In order to better maintain the consistency and homogeneity of the experimental sediments in each glass tank, the experimental sediment was dried and ground to powder in a mortar to pass through a 100-mesh sieve (Nie et al. 2011, Wu et al. 2011a,b, Wang et al. 2015). A 5 cm thick layer of sediment was spread on the bottom of all glass aquaria and fiberglass tanks, and all tanks were filled with seawater. The sediment in each tank was then precipitated and stabilized for 2 wk prior to the experiment. The experimental diets were made of seaweed *Sargassum muticum* powder. Prior to the experiment, the sea cucumbers were cultured in 50 l fiberglass tanks with 5 cm sediment for 14 d to acclimatize to the laboratory conditions. After acclimation, sea cucumbers with initial weights of 15.36 ± 0.23 g were cultured in the glass aquarium tanks (30 × 40 × 50 cm) at 4 different densities, i.e. 0, 4, 6, and 8 ind. tank^{-1} (represented as density groups D0, D4, D6, and D8, respectively), and 4 replicates for each treatment were used in the experiment. Sea cucumbers were fed every 2 d at 16:00 h. The diet was determined based on 5% of the total body weight of all sea cucumbers in the 16 aquaria and divided into 16 approximately equal portions. Each portion was well mixed with water and evenly poured into an aquarium. Water temperature was maintained at 16.5 ± 0.5°C, and salinity ranged from 29 to 31. One-third of the water volume in each tank was exchanged with filtered seawater every 2 d. The experiment was conducted for 84 d (12 wk).

Sample collection

During the 84 d experiment, 3 sampling points were randomly selected in each of the 16 tanks, and 0–1 cm surface sediment samples were collected with a plastic pipe measuring 2 cm in diameter before the experiment began, and then after 4, 8, and 12 wk. All sediment samples were well mixed from the same tank, dried in a lyophilizer (CHRIST LYO Alpha 1-4 LD plus), ground to powder in a mortar to pass through a 100-mesh sieve and kept in a freezer at −80°C before further analysis. Redox potential (E_h) was measured at 1 cm depth intervals at the same time of sample collections using a Pt electrode coupled with an Ag/AgCl reference electrode.

Laboratory analyses

Total nitrogen and total carbon concentrations of sediment samples were determined by a FlashEA 1112 Series NC Analyzer. Total organic matter (TOM) content of the sediment was analyzed using the potassium bichromate-dilution heat colorimetric method (Bao 1999, Lu 2000).

Phosphorus forms in sediment samples were sequentially extracted using the SMT protocol according to the modified Williams protocol (Williams et al. 1980, Ruban et al. 1999, Ruban & Rauret 2001). In this protocol, phosphorus in sediment was separated into NaOH-P, HCl-extractable phosphorus (HCl-P), inorganic phosphorus (IP), organic phosphorus (OP), and total phosphorus (TP).

Phosphorus sorption characteristics experiment

The phosphorus sorption characteristics of the sediment were determined using batch equilibrium experiments based on the method of Nair et al. (1984) to characterize the phosphorus sorption capacity and ability of sediments in different density groups. Sediment samples of 0.2 g were placed into 50 ml centrifuge tubes and treated with 25 ml of standard phosphorus solutions at varying concentrations (0, 0.2, 0.5, 1, 2, 5, 10, 15, 20, and 30 mg l^{-1}). Standard phosphorus solutions were prepared using analytical grade anhydrous KH_2PO_4 in a 0.01 M $CaCl_2$ matrix. Three drops of chloroform were added to inhibit microbial uptake. Centrifuges with 25 ml standard phosphorus solutions and 0.2 g sediment samples were equilibrated at 25 ± 1°C in an end-over-end shaker for 24 h before being centrifuged at 3913 *g* (15 min). The supernatant was then filtered through 0.45 µm Whatman GF/F filters. Phosphorus in the supernatant was determined by the colorimetric molybdenum-blue method (Murphy & Riley 1962).

The amount of phosphorus which was from the standard phosphorus solution and retained by sediment after 24 h equilibrium was calculated as follows:

$$\Delta Q = (C_t - C_0) \times V / W \quad (1)$$

where ΔQ is the amount of phosphorus from the standard phosphorus solution and retained by the sediment after 24 h equilibrium (mg kg^{-1}), C_t is the phosphorus concentration of the solution measured after 24 h equilibrium (mg l^{-1}), C_0 is the initial phosphorus concentration of the solution (mg l^{-1}), V is the volume of the solution, and W is the dry weight (kg).

Sorption parameter calculations

The total amount of phosphorus adsorbed on sediment was calculated as follows:

$$Q = \Delta Q + NAP \quad (2)$$

where Q is the total adsorbed phosphorus in sediment (mg kg^{-1}), ΔQ is the amount of phosphorus which was from the standard phosphorus solution and retained by sediment after 24 h equilibrium (mg kg^{-1}), and NAP is the initial or native absorbed phosphorus in the sediment (mg kg^{-1}).

Since at low equilibrium concentrations, the relationship between ΔQ and C_t is typically linear (Rao & Davidson 1979), the NAP and the linear adsorption coefficient (K_d, l kg^{-1}) could be estimated by a least square fit using the following equation (Reddy et al. 1998, House & Denison 2000, Pant & Reddy 2001, Kerr et al. 2011):

$$\Delta Q = K_d \times C_t - \text{NAP} \quad (3)$$

By plotting the linear form of Eq. (2), the intercept was equal to NAP and the slope was equal to K_d. Equilibrium phosphorus concentration (EPC$_0$, mg l^{-1}), was calculated as follows:

$$\text{EPC}_0 = \text{NAP} / K_d \quad (4)$$

The phosphorus sorption maximum (Q_{max}, mg kg^{-1}) and bonding energy constant (k, l mg^{-1}) were estimated using the Langmuir equation (Pant & Reddy 2001):

$$\Delta Q = (Q_{max} \times k \times C_t) / (1 + k \times C_t) - \text{NAP} \quad (5)$$

The phosphorus maximum buffer capacity (MBC, l kg^{-1}) was calculated as follows:

$$\text{MBC} = Q_{max} \times k \quad (6)$$

Similarly, another phosphorus sorption parameter, the energy of adsorption (K_f, l kg^{-1}), was calculated using the Freundlich equation (Pant & Reddy 2001):

$$\Delta Q = K_f \times C_t^{1/n} \quad (7)$$

where n is a correction factor.

Statistical analysis

In our experiment, for each of the 4 sampling time points, i.e. Weeks 0, 4, 8, and 12, sediment samples were collected from 3 sampling points which were randomly selected in each of the 16 experimental tanks. We did not collect the same sediment samples in Weeks 0, 4, 8, and 12. Instead, for each of the 4 times of sample collection, the sediment samples were randomly collected from each of the 16 experimental tanks. Thus, the samples collected at each of the 4 sampling times were independent, and our experiment was a completely randomized experimental design.

All data were subjected to 2-way factorial ANOVA, with the main factors of culture density and sampling time, followed by a Duncan test for multiple comparisons at a significance level of 0.05. Prior to statistical analysis, raw data were assessed for normality of distribution and homogeneity of variance using the Kolmogorov-Smirnov and Levene's tests, respectively (Zar 1999). All statistical analyses were performed using the statistical software SPSS for Windows (Release 22.0).

RESULTS

Sediment E_h values

Results for the 2-way factorial ANOVA of sediment E_h values of 4 different density groups are given in Table 1. Significant effects of time, density, and their interaction on the sediment E_h values were observed. At the beginning of the experiment, no significant differences occurred in sediment E_h values between the 4 groups. However, in Weeks 4, 8, and 12, the sediment E_h values significantly increased with increasing culture density of sea cucumbers. The sediment E_h value of group D0 was significantly lower than those of groups D4, D6, and D8, and the sediment E_h value of group D8 was significantly higher than those of groups D0 and D4. Significant temporal decreases were observed in E_h values of all 4 groups over the 12 wk experimental period.

Sediment TOM content

The 2-way factorial ANOVA results for TOM content in sediment of the 4 different density groups are summarized in Table 2. The sediment TOM content was significantly affected by time and density, but not by their interaction. TOM decreased significantly with increasing culture density of sea cucumbers. A significant temporal increase was observed in the sediment TOM over the 12 wk experimental period.

Phosphorus forms in sediment

Results of the 2-way factorial ANOVA of various phosphorus forms in sediments of the 4 different density groups are shown in Table 3. Significant effects of time, density, and their interaction on the content of NaOH-P in sediment were observed. At the beginning of the experiment, no significant difference in sediment NaOH-P content was evident between the 4 different density groups; however, in Week 8, the content of NaOH-P in group D8 was significantly higher than in group D0, although no significant difference was observed between groups D4, D6, and D8. In Week 12, the sediment NaOH-P content of group D8 was significantly higher than that of the other groups, and the sediment NaOH-P content of group D0 was significantly lower than that of groups D6 and D8. NaOH-P of groups D0 and D4 showed similar values in Week 12, and the content of NaOH-P in sediment increased significantly with increasing culture density of sea cucumbers in Weeks 8 and 12. Significant temporal increases in sediment NaOH-P of groups D6 and D8 were observed over the 12 wk experimental period. Significant temporal increases in sediment NaOH-P contents of groups D0 and D4 were observed in the first 4 wk, while no significant temporal changes in sediment NaOH-P contents of groups D0 and D4 were found from Week 4 to Week 12.

The sediment HCl-P content was not significantly influenced by time, density, or their interaction. Hence, we found no statistical differences in sediment HCl-P contents between the 4 different density groups at any sampling time. No significant temporal changes in sediment HCl-P contents of the 4 density groups were found throughout the experiment period.

Similarly, the sediment IP content was not significantly influenced by time, density, or their interaction. Hence, we found no difference in sediment IP content between the 4 different density groups at any given sampling time, nor did we find temporal changes in sediment IP content in the 4 groups over the 12 wk experimental period.

We did observe significant effects of time, density, and their interaction on the sediment OP content. At the beginning of the experiment, no significant difference in sediment OP was evident between the 4 groups, but by Week 8, sediment OP was significantly lower in groups D6 and D8 than in groups D0 and D4, while it was similar in groups D0 and D4. In Week 12, sediment OP was significantly lower in group D8 than in groups D0, D4, and D6, and the OP of group D6 was significantly lower than that of groups D0 and D4. Sediment OP decreased significantly with increasing culture density of sea cucumbers in Week 12, although no difference in OP content was found between groups D0 and D4 at

Table 1. Two-way factorial ANOVA for redox potential (E_h) in sediment of different density groups of sea cucumbers *Apostichopus japonicus*. Time indicates the different sampling weeks; D0, D4, D6, D8 indicate 4 different density groups (where 0, 4, 6, and 8 represent the number of ind. tank^{-1}). Data are presented as mean ± SD (n = 3). Different letters in the same row represent significant differences among different sampling times of each specific density group or different density groups in each specific sampling time at a significance level of 0.05; p values in **bold** indicate significant results ($p < 0.05$). See 'Materials and methods' for a detailed description about the statistical methods (ANOVA and multiple comparison procedures)

Source	df	p	Multiple comparison									
				Time					Density			
				0	4	8	12		D0	D4	D6	D8
Dependent variable: E_h												
Time	3	**<0.001**	D0	137.76 ± 11.08^{c}	−70.62 ± 10.68^{b}	−109.74 ± 35.98^{ab}	−138.90 ± 20.06^{a}	0	137.76 ± 11.08^{a}	141.07 ± 4.25^{a}	145.97 ± 14.46^{a}	145.60 ± 3.15^{a}
Density	3	**<0.001**	D4	141.07 ± 4.25^{c}	−0.13 ± 24.18^{b}	−81.33 ± 16.95^{a}	−98.70 ± 11.94^{a}	4	−70.62 ± 10.68^{a}	−0.13 ± 24.18^{b}	16.96 ± 11.95^{bc}	35.14 ± 10.41^{c}
Time × Density	9	**<0.002**	D6	145.97 ± 14.46^{d}	16.96 ± 11.95^{c}	−53.5 ± 18.24^{b}	−83.16 ± 19.56^{a}	8	−109.74 ± 35.98^{a}	−81.33 ± 16.95^{ab}	−53.5 ± 18.24^{bc}	−29.02 ± 11.14^{c}
			D8	145.60 ± 3.15^{d}	35.14 ± 10.41^{c}	−29.02 ± 11.14^{b}	−56.51 ± 18.10^{a}	12	−138.90 ± 20.06^{a}	−98.70 ± 11.94^{b}	−83.16 ± 19.56^{bc}	−56.51 ± 18.10^{c}

Table 2. Two-way factorial ANOVA for the total organic matter (TOM) content in sediment of different density groups of sea cucumbers *Apostichopus japonicus*. Details as in Table 1. Note that only 1 line of data is presented when no multiple comparisons were possible (see 'Materials and methods' for statistical methods)

Source	df	p	Multiple comparison							
			Time				Density			
			0	4	8	12	D0	D4	D6	D8
Dependent variable: TOM										
Time	3	**<0.001**	2.81 ± 0.33^{a}	3.76 ± 1.10^{b}	3.98 ± 0.90^{b}	5.36 ± 1.26^{c}	4.60 ± 1.52^{c}	4.34 ± 1.38^{bc}	3.81 ± 1.12^{ab}	3.17 ± 0.75^{a}
Density	3	**<0.001**								
Time × Density	9	0.286								

Table 3. Two-way factorial ANOVA for the contents of various phosphorus forms in sediment of different density groups of sea cucumbers *Apostichopus japonicus*. NaOH-P: NaOH-extractable P, HCl-P: HCl-extractable P, IP: inorganic phosphorus, OP: organic phosphorus, TP: total phosphorus. Other details as in Tables 1 & 2

Source	df	p	Multiple comparison									
				Time					Density			
				0	4	8	12		D0	D4	D6	D8
Dependent variable: NaOH-P												
Time	3	**<0.001**	D0	37.13 ± 2.21^{a}	42.38 ± 2.34^{b}	43.07 ± 4.22^{b}	43.80 ± 1.60^{b}	0	37.13 ± 2.21^{a}	36.57 ± 1.95^{a}	36.62 ± 1.29^{a}	36.84 ± 2.04^{a}
Density	3	**<0.001**	D4	36.57 ± 1.95^{a}	42.71 ± 5.72^{ab}	44.47 ± 2.14^{b}	45.98 ± 1.48^{b}	4	42.38 ± 2.34^{a}	42.71 ± 5.72^{a}	43.11 ± 2.35^{a}	44.67 ± 2.91^{a}
Time × Density	9	**0.035**	D6	36.62 ± 1.29^{a}	43.11 ± 2.35^{b}	47.20 ± 1.03^{c}	50.03 ± 1.78^{c}	8	43.07 ± 4.22^{a}	44.47 ± 2.14^{ab}	47.20 ± 1.03^{ab}	49.13 ± 2.39^{b}
			D8	36.84 ± 2.04^{a}	44.67 ± 2.91^{b}	49.13 ± 2.39^{b}	55.78 ± 2.81^{c}	12	43.80 ± 1.60^{a}	45.98 ± 1.48^{a}	50.03 ± 1.78^{b}	55.78 ± 2.81^{c}
Dependent variable: HCl-P												
Time	3	0.364		243.06 ± 13.94^{a}	244.50 ± 14.47^{a}	236.63 ± 9.40^{a}	236.78 ± 11.55^{a}		241.52 ± 15.18^{a}	239.47 ± 13.17^{a}	243.24 ± 9.09^{a}	236.74 ± 12.99^{a}
Density	3	0.682										
Time × Density	9	0.935										
Dependent variable: IP												
Time	3	0.482		279.85 ± 14.28^{a}	287.72 ± 12.30^{a}	282.60 ± 9.84^{a}	285.68 ± 10.96^{a}		283.12 ± 15.44^{a}	281.91 ± 11.81^{a}	287.48 ± 8.83^{a}	283.35 ± 11.66^{a}
Density	3	0.743										
Time × Density	9	0.921										
Dependent variable: OP												
Time	3	**<0.001**	D0	52.52 ± 3.48^{a}	65.71 ± 11.97^{b}	78.55 ± 0.77^{c}	94.67 ± 4.30^{d}	0	52.52 ± 3.48^{a}	56.94 ± 4.49^{a}	54.07 ± 2.46^{a}	53.48 ± 3.21^{a}
Density	3	**<0.001**	D4	56.94 ± 4.49^{a}	59.77 ± 10.18^{a}	87.10 ± 10.76^{b}	97.85 ± 3.22^{b}	4	65.71 ± 11.97^{b}	59.77 ± 10.18^{ab}	41.29 ± 8.53^{a}	51.09 ± 10.16^{ab}
Time × Density	9	**0.002**	D6	54.07 ± 2.46^{a}	41.29 ± 8.53^{a}	55.14 ± 11.13^{a}	73.98 ± 3.49^{b}	8	78.55 ± 0.77^{b}	87.10 ± 10.76^{b}	55.14 ± 11.13^{a}	49.64 ± 13.61^{a}
			D8	53.48 ± 3.21^{a}	51.09 ± 10.16^{a}	49.64 ± 13.61^{a}	62.11 ± 5.71^{a}	12	94.67 ± 4.30^{c}	97.85 ± 3.22^{c}	73.98 ± 3.49^{b}	62.11 ± 5.71^{a}
Dependent variable: TP												
Time	3	**<0.001**	D0	334.26 ± 3.48^{a}	346.99 ± 11.97^{b}	359.61 ± 0.77^{c}	383.05 ± 4.30^{d}	0	334.26 ± 3.48^{a}	334.23 ± 4.49^{a}	335.65 ± 2.46^{a}	332.25 ± 3.21^{a}
Density	3	**<0.001**	D4	334.23 ± 4.49^{a}	354.38 ± 10.18^{b}	365.53 ± 10.76^{bc}	375.14 ± 6.06^{c}	4	346.99 ± 11.97^{ab}	354.38 ± 10.18^{b}	333.16 ± 8.53^{a}	334.20 ± 10.16^{a}
Time × Density	9	**0.017**	D6	335.65 ± 2.46^{a}	333.16 ± 8.53^{a}	341.16 ± 11.13^{a}	364.43 ± 3.49^{b}	8	359.61 ± 0.77^{bc}	365.53 ± 10.76^{c}	341.16 ± 11.13^{ab}	334.53 ± 13.61^{a}
			D8	332.25 ± 3.21^{a}	334.20 ± 10.16^{a}	334.53 ± 13.61^{a}	348.72 ± 5.71^{a}	12	383.05 ± 4.30^{c}	375.14 ± 6.06^{c}	364.43 ± 3.49^{b}	348.72 ± 5.71^{a}

that time. Significant temporal increases in sediment OP of groups D0, D4, and D6 were observed over the 12 wk experimental period. In contrast, no significant temporal change in sediment OP content of group D8 was found throughout the experiment.

Significant effects of time, density, and their interaction on sediment TP content were observed. At the beginning of the experiment, we found no significant difference between the 4 different density groups; however, in Week 8, sediment TP of group D8 was significantly lower than that of groups D0 and D4, and no significant difference in sediment TP content between groups D6 and D8 was observed. In Week 12, sediment TP in group D8 was significantly lower than in any other group. Sediment TP was significantly higher in groups D0 and D4 than in groups D6 and D8, while no significant difference was found between groups D0 and D4. Significant temporal increases in sediment TP over the 12 wk experimental period were observed in groups D0, D4, and D6, but not in D8.

Phosphorus sorption characteristics

Results of the 2-way factorial ANOVA of the phosphorus sorption parameters of the 4 different density groups are provided in Table 4. The effects of time, density, and their interaction on the MBC and K_f values of sediment were significant. At the beginning of the experiment, no significant differences in MBC and K_f values were found between the 4 groups; however, the final sediment MBC and K_f values in Week 12 were significantly lower in groups D0 and D4 than in groups D6 and D8. Significant temporal decreases in MBC and K_f values were observed in groups D0 and D4 over the 12 wk experimental period. The final MBC and K_f values of sediment in groups D0 and D4 in

Week 12 were significantly lower than the initial values, respectively. In contrast, we found no significant temporal changes in MBC and K_f values in groups D6 and D8.

We found no significant effects of time, density, or their interaction on the NAP and EPC_0 values of the sediment ($p > 0.05$) and no statistical differences in NAP and EPC_0 values of the sediment between the 4 different density groups at each specific sampling time. No significant temporal changes in NAP and EPC_0 values of the sediment in groups D0, D4, D6, and D8 were found throughout the experimental period.

The sedimentary Q_{max} and K_d values were significantly affected by time, but not by density or their interaction. We found no significant differences in Q_{max} and K_d values of the sediment between different density groups. A significant temporal increase in Q_{max} values and a significant temporal decrease in K_d values were observed over the 12 wk experimental period.

DISCUSSION

Effects of bioturbation by sea cucumbers on sediment parameters

Redox potential and organic matter

Redox potential (E_h) and organic matter are recognized as important controlling factors that affect sediment phosphorus fractions and phosphorus sorption characteristics (Kim et al. 2003, Jin et al. 2006, Liu et al. 2009). Sea cucumbers, being deposit feeders, mainly ingest microorganisms, organic detritus, including their own feces, and aquatic organisms (Yingst 1976, Moriarty 1982, Uthicke & Klumpp 1998). With increasing culture density of sea cucumbers, the TOM content significantly decreased in the present study. This result may indicate that sea cucumbers prevent the accumulation of organic matter by ingestion and digestion. In addition, the significant increase in sediment E_h with increasing culture

Table 4. Two-way factorial ANOVA for the phosphorus sorption parameters in sediment of different density groups of sea cucumbers *Apostichopus japonicus*. K_d: linear adsorption coefficient, NAP: native absorbed phosphorus, EPC_0: equilibrium phosphorus concentration, Q_{max}: phosphorus sorption maximum, MBC: maximum buffer capacity, K_f: energy adsorption. Initial: Week 0; final: Week 12. Other details as in Tables 1 & 2

Source	df	p		Multiple comparison: Time			Multiple comparison: Density			
				Initial	Final		D0	D4	D6	D8
Dependent variable: K_d (l kg^{-1})										
Time	1	**<0.001**		58.41 ± 1.65^b	53.01 ± 3.43^a		56.20 ± 2.48^a	54.68 ± 4.83^a	54.61 ± 4.17^a	57.55 ± 3.52^a
Density	3	0.135								
Time × Density	3	0.271								
Dependent variable: NAP (mg kg^{-1})										
Time	1	0.086		11.54 ± 0.90^a	10.55 ± 1.42^a		10.93 ± 1.62^a	11.45 ± 1.00^a	11.01 ± 0.99^a	10.79 ± 1.59^a
Density	3	0.841								
Time × Density	3	0.881								
Dependent variable: EPC_0 (mg l^{-1})										
Time	1	0.938		0.20 ± 0.02^a	0.20 ± 0.03^a		0.19 ± 0.03^a	0.21 ± 0.02^a	0.20 ± 0.02^a	0.19 ± 0.02^a
Density	3	0.260								
Time × Density	3	0.868								
Dependent variable: Q_{max} (mg kg^{-1})										
Time	1	**0.009**		485.97 ± 63.03^a	563.40 ± 61.11^b		527.97 ± 112.08^a	526.86 ± 71.31^a	505.17 ± 62.83^a	538.75 ± 43.82^a
Density	3	0.834								
Time × Density	3	0.324								
Dependent variable: MBC (l kg^{-1})										
Time	1	**0.002**	D0	81.06 ± 2.69^b	57.18 ± 6.30^a	Initial	81.06 ± 2.69^a	80.90 ± 2.71^a	78.34 ± 5.42^a	79.47 ± 1.10^a
Density	3	**0.003**	D4	80.90 ± 2.71^b	62.64 ± 4.67^a	Final	57.18 ± 6.30^a	62.64 ± 4.67^a	84.07 ± 11.86^b	81.81 ± 2.97^b
Time × Density	3	**0.001**	D6	78.34 ± 5.42^a	84.07 ± 11.86^a					
			D8	79.47 ± 1.10^a	81.81 ± 2.97^a					
Dependent variable: K_f (l kg^{-1})										
Time	1	**0.007**	D0	76.10 ± 0.75^b	62.25 ± 6.64^a	Initial	76.10 ± 0.75^a	77.32 ± 2.24^a	77.05 ± 1.70^a	76.64 ± 1.78^a
Density	3	**0.002**	D4	77.32 ± 2.24^b	65.47 ± 3.04^a	Final	62.25 ± 6.64^a	65.47 ± 3.04^a	80.97 ± 8.44^b	77.64 ± 1.35^b
Time × Density	3	**0.003**	D6	77.05 ± 1.70^a	80.97 ± 8.44^a					
			D8	76.64 ± 1.78^a	77.64 ± 1.35^a					

density of sea cucumbers suggests that mechanical disturbance caused by the activity of sea cucumbers might transport oxygen into the sediment and increase its supply of electron acceptors (van de Bund et al. 1994). Increased E_h in sediment stimulates the decomposition and mineralization of organic matter, thereby reducing the accumulation of organic matter (Aller 1982, 1994).

Different phosphorus forms

NaOH-P represents phosphorus bound to mainly Al and Fe oxides and hydroxides (Ruban et al. 1999, Jin et al. 2006). Olila & Reddy (1997) discovered a strong positive correlation between NaOH-P and redox potential (E_h), whereas Rydin (2000) and Selig (2003) revealed no redox dependence of phosphorus adsorption with aluminum, indicating a refractory character of this pool. Generally, ionic iron states are Fe (II) and Fe (III). Among the 2 forms of iron, the reduced form, Fe (II), is moderately soluble, whereas the oxidized form, Fe (III), is extremely insoluble (Takeda & Fukushima 2004). With increasing E_h, Fe (II) is oxidized to Fe (III) due to the oxygen penetration into the sediment (Yamada et al. 1987, Nguyen 1999). Fe (III) can adsorb a large quantity of phosphorus by forming Fe(OOH)–P complexes or precipitates, such as $\{Fe(PO_4)(OH)_{3-x}\}$ (Zak & Gelbrecht 2002), thereby providing long-term phosphorus retention (Reddy et al. 1996). The significant increases in the NaOH-P content and E_h value in sediment with increasing culture density of sea cucumbers in our study might indicate that the bioturbation caused by sea cucumbers increased the oxygenation of the sediment and the supply of electron acceptors, subsequently facilitating the formation of Fe (III)-P complexes under aerobic conditions, in agreement with the observations reported by Olila & Reddy (1997).

The accumulation of organic matter can change sediment biogeochemistry and facilitate oxygen depletion, subsequently resulting in anoxic conditions in sediment (Liu et al. 2009, Martinez-Garcia et al. 2015). With aerobic sediment being transferred to anoxic conditions, the insoluble Fe(OOH)–P complexes or precipitates can be reduced to soluble Fe (II) (Wildung et al. 1977, Hosomi et al. 1981), which results in the release of phosphorus from the NaOH-P. The sea cucumbers effectively inhibited the accumulation of organic matter in the sediment by mechanical disturbance, ingestion, and digestion, thereby preventing the desorption of NaOH-P. Accordingly, the sea cucumbers effectively increased the content of the NaOH-P in sediment by increasing the E_h value and reducing the content of organic matter in the sediment.

The OP represents the phosphorus fraction bound to organic matter, and can potentially be released. The 'decomposition hypothesis' introduced by Prairie et al. (2001) postulates that mineralization is the most important process driving phosphorus release from OP in many cases. In our study, the increasing culture density of sea cucumbers significantly enhanced the decline in sediment OP content. This indicates that bioturbation by the sea cucumbers increased the E_h and oxygen penetration in sediment, which facilitated the decomposition and mineralization of organic matter, subsequently reducing the concentration of OP (Li & Huang 2010). In the sediment, the OP was released to solution as soluble PO_4 during decomposition and mineralization. Part of the released PO_4 might be adsorbed to Fe (III) by formation of Fe (III)-P complexes under aerobic conditions, while part of it might remain in solution or be recycled into the overlying water (Gächter & Meyer 1993). Thus, sea cucumbers might stimulate the transformation of part of the OP to NaOH-P by bioturbation.

HCl-P is assumed to be an inert and refractory fraction (Psenner & Pucsko 1988, Rydin 2000) and contributes to a permanent burial of P in sediment (Kaiserli et al. 2002, Jin et al. 2006). In sediment, HCl-P is mainly formed through coprecipitation and direct precipitation between calcite and phosphorus, and exists in relatively stabilized forms, such as $Ca_5(PO_4)_3OH$, $Ca_2HPO_4(OH)_2$, $CaHPO_4{\times}2H_2O$, $Ca_3(HCO_3)_3PO_4$, etc. (Cassagne et al. 2000, Berg et al. 2004). In the present study, the sea cucumbers significantly affected the NaOH-P and OP content mainly by mechanical disturbance, ingestion, and digestion, which inhibited the enrichment of organic matter and increased the E_h values in sediment. However, we observed no significant effects by sea cucumbers on the content of HCl-P in sediment, which suggests no redox dependence of the HCl-P (Olila & Reddy 1997).

Phosphorus sorption characteristics

The Freundlich constant K_f is used as a measure to characterize the extent of phosphorus sorption and the energy of phosphorus sorption in sediment (Olila & Reddy 1997, Jalali 2007). The MBC reflects the ability of phosphorus sorption and the phosphorus sorption capacity in general (Wang et al. 2007, He et al. 2011). The MBC and K_f values of the sediment in density groups D6 and D8 were significantly higher than those in groups D0 and D4, which may suggest that the sea cucumbers effectively enhanced the ability and capacity of phosphorus sorption of the sediment with increasing culture density. The accumulation of organic matter could facilitate oxygen depletion and decrease the sediment E_h. With the sediment E_h decreasing, decreases in MBC and K_f values were expected because of the desorption of phosphorus from Fe-P compounds due to the reduction of Fe (III) to Fe (II) (Pant & Reddy 2001). However, the sea cucumbers effectively inhibited the enrichment of organic matter in the sediment by ingestion, digestion, and mechanical disturbance. In addition, mechanical disturbance by sea cucumbers led to an increase in sediment E_h values by transporting oxygen into the sediment. Accordingly, at increasing culture densities, the sea cucumbers effectively enhanced the extent of phosphorus sorption, the ability for phosphorus sorption, and the phosphorus sorption capacity by increasing the E_h value and reducing the content of organic matter in the sediment.

In conclusion, at increasing culture densities, bioturbation by sea cucumbers effectively increased the redox potential (E_h) and inhibited the accumulation of organic matter in the sediment, thus facilitating the decomposition of OP and the formation of NaOH-P in the sediment under aerobic conditions, and improving the ability and capacity of phosphorus sorption of the sediment. Hence, sea cucumbers play an important role in the transport and transformation of phosphorus in sediment. The use of sea cucumbers in IMTAs may help to prevent the eutrophication of aquaculture waters.

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