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Bioturbation of Burrowing Crabs Promotes Sediment Turnover and Carbon and Nitrogen Movements in an Estuarine Salt Marsh

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Abstract

Ecological functions of bioturbation in ecosystems have received increasing attention over the recent decades, and crab burrowing has been considered as one of the major bioturbations affecting the physical and chemical processes in salt marshes. This study assessed the integrated effects of crab excavating and burrow mimic trapping on sediment turnover and vertical C and N distributions in a Chinese salt marsh in the Yangtze River estuary. Crab burrowing increased soil water content and the turnover of carbon and nitrogen and decreased bulk soil density. Vertical movement of materials, nutrient cycling and reuse driven by crab burrowing might be obstructed by vegetation (*Phragmites australis* and *Spartina alterniflora* communities). The amount of soil excavated by crab burrowing was higher than that deposited into burrow mimics. In *Phragmites* marshes, *Spartina* marshes and unvegetated mudflats, net transport of soil to the marsh surface was 171.73, 109.54, and 374.95 g m^{-2} d^{-1}, respectively; and the corresponding estimated soil turnover time was 2.89, 4.07 and 1.83 years, respectively. Crab burrowing in salt marshes can mix surface and deeper soil over a period of years, accelerating litter decomposition and promoting the efficient reuse of nutrients by plants. Therefore, bioturbation affects soil physical processes and functioning of ecosystems, and needs to be addressed in ecosystem management.

Key words: bioturbation; burrowing crabs; excavation; salt marshes; sediment deposition; soil turnover; transport of soil and nutrients.

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Introduction

As significant biotic components of aquatic and terrestrial ecosystems, soil animals are multipurpose workers, for example, consumers, litter decomposers, and habitat modifiers, which passively and/or actively disturb the substrate. Bioturbation is defined as biological reworking of soils and sediments through animal activities like burrowing and feeding (Meysman and others 2006). Animal bioturbation and its ecological roles in shaping soil ecosystem processes were first appreciated by Darwin (1881) and were described in great detail in his last book *On the Formation of Vegetable Mounds through the Action of Worms with Observations on their Habits*. Invertebrate feeding on resources in the sediments evidently affects key processes, such as organic carbon mineralization (Otani and others 2010), nutrient dynamics (Karlson and others 2007; McHenga and Tsuchiya 2008), sulfur and iron cycling (Gribsholt and others 2003; Nielsen and others 2003), sediment texture modification and particle mixing (Paarlberg and others 2005). The altered soil characteristics might further impact microbial activities (Bertics and Ziebis 2009), zooplankton recruitment (Gyllström and others 2008) and other biotic components (Reinsel 2004; Canepuccia and others 2008), or the spatial heterogeneity might generate niches for smaller organisms (van Nugteren and others 2009). Furthermore, long term functions of bioturbation play important roles in digenetic reaction, and facilitate the development of pristine ecosystems (Herringshaw and Solan 2008). One type of dominant bioturbations in coastal ecosystems is crab burrowing which can transport sediments and modify sediment texture, accelerating ecosystem nutrient cycling.

Salt marshes in coastal wetlands are one of the most productive natural ecosystems (Mitsch and Gosselink 1993) and provide considerable ecosystem services for human society (Costanza and others 1997). The decomposition and transformation of primary products from salt marshes provide nutrients for the growth of marsh plants and for export to adjacent ecosystems, subsidizing oceanic productivity (Odum 1980). Sediment biogeochemical processes play important roles in the metabolism and nutrient cycling of salt marshes (Webb and Eyre 2004).

Burrowing sesarmid (Grapsidae) and fiddler crabs (Ocypodidae) are the most important macroinvertebrates in many salt marshes (Emmerson 1994; Montague 1982). They are often present in large numbers; and their burrowing activities can directly break and transport sediments, decrease the hardness of the soil (Bortolus and Iribarne 1999; Botto and Iribarne 2000; Botto and others 2005), modify microtopography, and increase the density of coarse particles on the soil surface (Warren and Underwood 1986). Crab burrowing also affects soil chemistry and associated microbial processes, increases soil oxygenation, and alters pore water salinity (Fanjul and others 2007). Burrowing crabs significantly affect belowground processes that can impact marsh plants (Bertness 1985; Iribarne and others 1997; Bortolus and Iribarne 1999; Smith and others 2009) in at least three ways. First, crab burrowing increases the passage of liquid and gas between the soil and environment (that is, increase drainage), increasing soil oxidation (Katz 1980; Daleo and Iribarne 2009; Weissberger and others 2009) and the decomposition rate of organic debris (Lee 1998; Reinsel 2004; Fanjul and others 2007). Second, crab burrows can selectively trap sediments that have high organic matter concentrations, finer grain size and low density through the interactions of the burrow opening with tidal water, which can facilitate organic matter decomposition, which can in turn increase nutrient availability and thus, promote their growth (Iribarne and others 1997, 2000; Botto and others 2006). Third, crab excavation transports soil and nutrients from deep layers to the marsh surface (Fanjul and others 2007, 2008), which might accelerate the turnover of soil and nutrients. Soil properties and plant assemblage characteristics influenced by crab excavation and burrow deposition can in turn affect burrowing processes (Neira and others 2006). Few attempts, however, have been made to examine these processes (but see Botto and Iribarne 2000; Gutierrez and others 2006), and the interactive effects of plant communities and crab burrowing remain largely unexplored. Understanding the relative importance of these processes in controlling energy flow and nutrient transformation will enhance our understanding of the ecological roles of crabs in salt marshes.

The objective of this study was to examine the roles of crab burrowing and burrow trapping in sediment turnover, and vertical C and N distributions in a Chinese salt marsh. We specifically examined the following questions. What amounts of soil and C, N nutrients does a crab community vertically transport? How different are the soils of different sources (excavated, deposited, and background) in soil physical and chemical properties? Is vertical transport of sediments and associated C and N affected by crab size, habitat type and environmental conditions? Does crab burrowing controlling vertical transport influence the substrate and nutrient cycling and thus impact ecosystem processes in salt marshes?

Materials and Methods

Study Site

This study was conducted in Dongtan Wetland on Chongming Island in the Yangtze River estuary (31°25′ ~ 31°38′N, 121°50′ ~ 122°05′E). Dongtan Wetland covers 230 km^2, and has 4.62–5.95-m semidiurnal tides (Sun and others 2001, also see Figure A1), with soil pore water salinity ranging from 5 to 35 ‰ (Wang 2007), soil temperatures between 19.7 and 31.5°C during the growing season from May to September (Chen and others 2007), and mean annual precipitation of 1123.7 mm, mostly falling in the summer (Sun and others 2001).

Phragmites australis and *Spartina alterniflora* are the dominant plant species in the high and middle tidal marshes, respectively, often forming respective monocultures (Li and others 2009). The dominant crab species include three Ocypodidae (*Uca arcuata*, *Ilyoplax deschampsi* and *Macrophthalmus japonicus*) and three Grapsidae (*Helice tridens tientsinensis*, *Sesarma dehaani*, *Sesarma plicata*), whose mean densities are given in Table 1. Fiddler crab *U. arcuata* and a small-sized species *I. deschampsi* mainly inhabit mudflats and creek banks, whereas the density of *S. dehaani* is the highest in the *Spartina* marsh (Wang and others 2008). *H. tridens tientsinensis* and *S. plicata* did not show specific preferences for any of the three habitats, whereas *M. japonicus* preferred to select mudflats rather than *Spartina* or *Phragmites* marshes. Both of them construct dense burrows with diverse morphologies that strongly affect the flow of energy and materials in salt marshes (Wang 2008).

Field Sampling

In our sampling areas, mean burrow densities in *Phragmites* marsh, *Spartina* marsh, and mudflats were estimated to be 48.00 ± 3.75 (SE), 42.56 ± 3.70, and 45.22 ± 2.21 burrows m^{-2}, respectively (Wang 2008). For ease of description, we here defined three size classes of burrow opening diameters, that is, small (0–15 mm), medium (15–30 mm), and large (>30 mm). See Figure A2 Supplemental Material for burrow size frequency distributions at the study site.

To estimate the amount of soil excavated by crabs, six randomly selected burrows for each class of opening diameter were labeled in *Phragmites* marsh, *Spartina* marsh, and mudflat habitats, for a total of 54 burrows. Their opening diameters were measured. All the pre-existing superficial soils around these burrow openings were removed before sampling. Excavated soil was collected daily over a 5-d spring-tide period (July 30–August 3, 2007). A total of 270 soil samples (3 sizes × 3 habitats × 5 d × 6 replicates) were taken, oven dried at 60°C to constant weight, and then weighed.

The physical and chemical properties of soil excavated by crabs were quantified. Six groups of burrows were selected in each of the three habitats, each of which consisted of three sizes of burrows. Newly-excavated soil was easily identified by its color (grayish fresh excavation vs. brownish old excavation) and texture (Botto and Iribarne 2000). On August 2, 2007, freshly excavated soil was sampled. A subsample of approximately 50 g from each sample was used to determine soil water content by oven-drying, and 10–20 g was frozen at −10°C for soil NO_3-N and NH_4-N concentrations.

Directly sampling the soil deposited into burrows was impossible because it was impractical to separate soil deposited into burrows from the pre-existing soil in the burrows. Most crab burrows had vertically tubular structures with an opening diameter of up to 50 mm and depth of 10–50 cm (Wang 2008; also see Table A1 Supplemental Material for mean depth data). PVC pipes were used as burrow mimics, as suggested by Gutierrez and others (2006). PVC pipes were inserted into the soil with their upper openings flush with the ground surface. These pipes were 30 cm long and capped at the bottom.

PVC pipes of three sizes (10, 25, 40 mm in diameter) corresponding to the three burrow size classes were used (n = 6/size class). Soil deposited

Table 1. Crab Densities in *Spartina* and *Phragmites* Marshes and Mudflats

Crab species	*Phragmites* marsh	*Spartina* marsh	Mudflat
Whole crab community	72.89 (11.89)[ab]	91.22 (11.26)[a]	39.56 (9.89)[b]
Helice tridens tientsinensis	59.67 (11.59)[a]	47.89 (8.99)[a]	34.78 (10.17)[a]
Sesarma dehaani	12.67 (3.18)[a]	42.22 (7.95)[b]	1.67 (0.65)[c]
Sesarma plicata	0.56 (0.24)[a]	1.00 (0.58)[a]	0.44 (0.34)[a]
Uca arcuata	0[a]	0.11 (0.11)[a]	2.67 (1.18)[b]

The density was expressed using Catch Per Unit Effort (CPUE) in terms of crabs caught per plot (9 m^2) during a period of 7 d. Shown are the mean values with SE in parentheses. Different superscripted letters indicate significant differences between habitat types ($P < 0.05$) (Data from Wang 2008).

into burrow mimics was also collected daily (two tidal cycles) during a 5-d spring-tide period (July 30–August 3, 2007). Again, a total of 270 samples were taken (3 sizes × 3 habitats × 5 d × 6 replicates). We filled PVC pipes with estuarine filtered water to avoid overestimating sediment deposition due to the incoming water. All water and soil in burrow mimics were collected daily in plastic bottles, and stored for 24 h. All supernatants were drawn out, and remaining deposits were oven dried at 60°C to constant weight and weighed.

We combined the samples collected from each burrow or burrow mimic over 5 days for analysis. A total of 54 samples were taken for both excavation and deposition (3 sizes × 3 habitats × 6 burrows or burrow mimics). Total soil N (TN), total soil C (TC) and total organic C (TOC) concentrations, salinity and grain size were measured in the laboratory.

To examine background soil properties, six control samples were taken from the top 5-cm soil (background surface soil) and at a depth of 30 cm (background subsurface soil) in small unburrowed areas in *Spartina* and *Phragmites* marshes and mudflat habitats with a 2-cm-diameter soil corer. The use of the small unburrowed areas for sampling background soil was to avoid sampling errors that might be caused by the differences in other conditions rather than crab burrowing. Thirty-six samples of background soil (6 soil cores × 2 depth × 3 habitats) were taken and used to compare with those of the excavated and deposited soils.

To determine NO_3-N and NH_4-N concentrations, 10–50 g from each of 36 samples were frozen at −10°C until samples were analyzed. The soil for determining inorganic N concentrations was also used to calculate soil water content. Subsamples of approximately 300 mg were used to determine TC, TN and TOC concentrations. The remaining samples were oven dried and used to measure soil salinity and grain size. The total inorganic N (TIN) concentration of the deposited soil was not measured. Consequently, soil TIN, bulk density, and water content were measured only in background and excavated soils.

Determination of C and N Concentrations

To determine TN and TC concentrations, dried soil samples were ground to powder in a mortar to pass through a 100-mesh sieve. C and N analyses were performed on a FlashEA 1112 Series NC Analyzer (Italy). Organic C concentrations were also determined using the NC Analyzer after inorganic C as CO_2 was removed by adding 1:1 HCl and oven-dried to a constant weight.

Soil NO_3-N concentration was determined by KCl extraction colorimetry of fresh soil samples, whereas NH_4-N concentrations were determined by indophenol blue colorimetry on KCl extraction (Liu 1996). Soil grain size was analyzed using a particle size analyzer (Mastersizer 2000, Malvern Instruments, England). Salinity was measured using a Metler SevenEasy conductivity meter.

Statistical Analyses

Three-way ANOVA was used to test the effects of burrow or burrow mimic size, duration of high tide (days since the first day of high tide) and habitat type (*Phragmites*, *Spartina* marshes and mudflats) on the amounts of soil excavated or deposited, deposition efficiency and soil net transport to the ground surface. In this study the soil net transported was calculated as the excavated soil minus deposited soil, collected per day. Burrow mimic trapping, that is soil deposition, is defined as the process in which surface soil and detritus are selectively deposited into burrow mimics through the interaction of burrow mimic openings and tidal water, and burrow mimic deposition is characterized by high organic content, fine grain size and low-density sediments that are easily moved by water flow and transported into crab burrow mimics. Two-way ANOVA was used to test the effects of habitat type and soil source (background surface soil, background subsurface soil, soil excavated or deposited into burrow mimics) on soil properties. In addition, the effects of habitat type and burrow or burrow mimic diameter size on TN, TC, and TOC amounts daily transported were also evaluated using two-way ANOVA tests. One-way ANOVA was used to test the effects of burrow or burrow mimic size on several parameters of soil excavated by crabs and deposited into burrow mimics. Tukey's test was used to determine a posteriori differences at $P < 0.05$. To meet the assumptions of statistical analyses, the data were appropriately examined and transformed prior to statistical analyses as necessary.

The relationships between soil amounts excavated by crabs and deposited into burrow mimics, and between the amounts of soil excavated and burrow diameter were analyzed by linear regression. Analyses of covariance (ANCOVA) were used to test the differences of the above relationships among the three habitats. Linear regression was also used to examine relationships between soil amounts excavated or deposited and soil properties. The effects of soil sources (excavated or deposited) on relationships between soil amounts transported and soil properties were tested with ANCOVA. Data were log (x + 1) transformed prior to regression analysis where necessary to linearize the relationships.

The total amounts of soil nutrients excavated, deposited, and net transported to the surface for each day were calculated by multiplying soil nutrient concentrations by their corresponding soil amounts. The amounts of soil and nutrients transported per unit area were obtained by multiplying the mean amount of transported nutrients per burrow or burrow mimic by burrow density. Soil turnover rates through crab burrowing were also calculated, which are here defined as the total amount of soil transported, that is, excavation plus deposition, by crabs per unit area per day (compare Gutierrez and others 2006).

Within the top 30 cm of soil, soil mass per m^2 was determined by multiplying mean bulk density (for a depth of 0–30 cm) by volume (that is, 0.3 m^3). The soil C stock was calculated by multiplying soil C concentration by soil mass of 0.3 m^3. The calculation methods for TN and TOC stocks were similar to those for TC stocks. The turnover times of soil and nutrients, defined as the time required for crabs to complete a turnover of all the soil or nutrients for the top 30 cm soil, were calculated by dividing the total soil mass, TC, TN, or TOC stocks by corresponding turnover rates. All analyses were performed using a statistical package of Statistica (Version 6.0, StatSoft). All the results of statistic analyses are given in the supplemental Appendices (Tables A2–A7) for this manuscript.

Results

Crab Excavation and Burrow Mimic Deposition of Soil

Four parameters were used to characterize the soil excavating–depositing processes driven by crabs, that is, excavation, deposition, deposition efficiency, and net transport. The deposition efficiency was the amount of deposited soil per unit volume of burrow; and the net transport was the difference between the amount of soil excavated by crabs and that deposited into burrow. Habitat type, duration of high tide, and burrow or burrow mimic diameter all had significant effects on the four parameters. Soils excavated, deposited into burrow mimics, and net transported to the surface increased with the increasing diameter of burrows or burrow mimics, but deposition efficiency decreased with increasing burrow or burrow mimic diameter (Figure 1). The four parameters all increased with increasing duration of high tide (Figure 1). Because crab excavation exceeded burrow mimic deposition, excavating–depositing processes resulted in net transport of soil to the marsh surface. Furthermore, the values of these parameters for mudflats were significantly higher than those for *Phragmites* and *Spartina* marshes.

The soil excavated by crabs was positively correlated with burrow diameter (Figure 2A) and soil deposited into burrow mimics (Figure 2B) in both mudflats and *Phragmites* and *Spartina* marshes, and the regression slopes for mudflats were significantly greater than those for *Phragmites* and *Spartina* marshes.

Effects of Crab Burrowing on Soil Properties

Burrow trapping significantly affected soil physical and chemical properties and texture (Figures 3 and 4). The soil deposited into burrow mimics contained a lower proportion of fine grain and a higher salinity compared to the excavated soil (Figure 3A, B). Excavated soil was characterized by higher water content and lower bulk density (Figure 4D, E). Excavated and deposited soils had higher nutrient concentrations compared to the surrounding background soil. TN, TOC and TOC/TC ratios were all significantly different among the four soil sources and ranked in a descending order of deposited, excavated soil, background surface, and subsurface soil (Figure 3D–F). TC of excavated soil was the highest, followed by that of deposited soil, background surface, and subsurface soil (Figure 3C). The C/N ratio of deposited soil was the lowest whereas that of background soil was the highest (Figure 3G). In addition, NO_3-N, NH_4-N, and inorganic N concentrations of excavated soil were significantly higher than those of background surface and subsurface soil (Figure 4A–C). Although burrow size had no significant effects on the properties of excavated soil, it significantly affected TC, TOC, C/N ratio, and salinity of deposited soil (Table A5 Supplemental Material).

Burrows might interact with physical and chemical conditions of different habitat types, which affected the nutrient concentrations of soil transported. Soil in *Phragmites* and *Spartina* marshes had higher water content and lower bulk density than those in mudflats (Figure 4D, E), although there were no significant differences in soil grain size and salinity among the habitats (Figure 3A, B). Soil in *Phragmites* and *Spartina* marshes had significantly higher TN, TC and TOC, and TOC/TC ratios, and hence, lower C/N ratios compared to those in

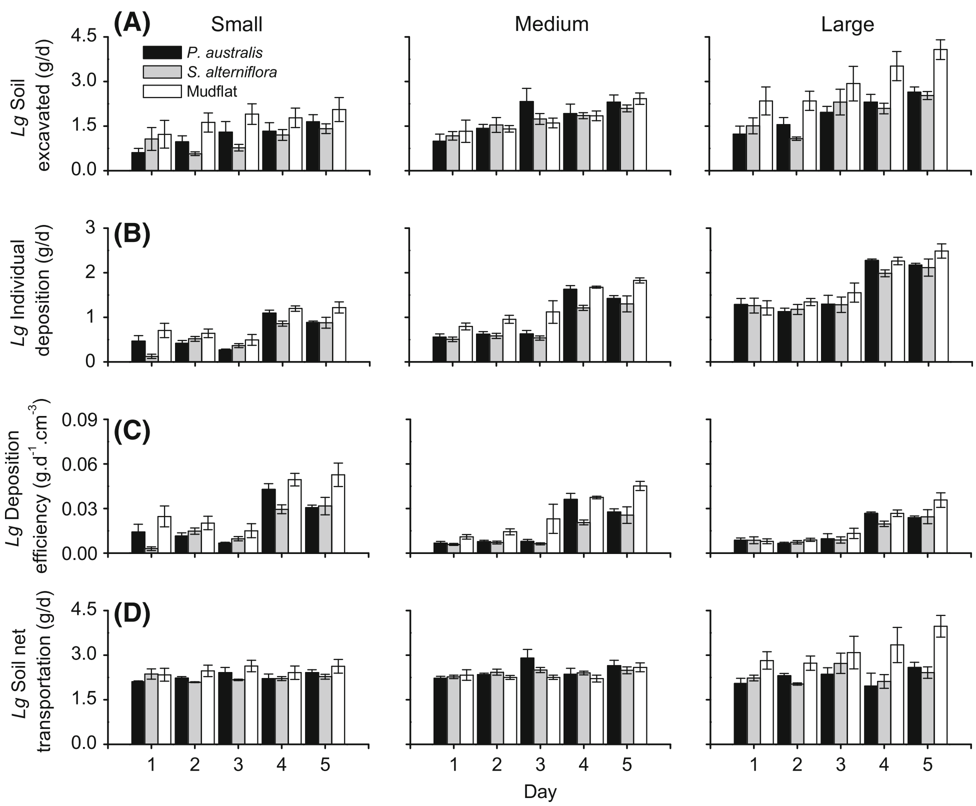

Figure 1. The effects of burrow or burrow mimic opening size on the four parameters reflecting crab excavation and burrow mimic deposition in *Phragmites* and *Spartina* marshes and mudflats over a 5-d sampling period. (**A**) Excavating rate by crabs (g d^{-1}); (**B**) deposition rate per burrow mimics (g d^{-1}); (**C**) deposition efficiency (g d^{-1} cm^{-3}); (**D**) net transport to the marsh surface (g d^{-1}). The data are separately presented for small (diameter: 0–15 mm), medium (diameter: 15–30 mm) and large (diameter: >30 mm) crab burrows.

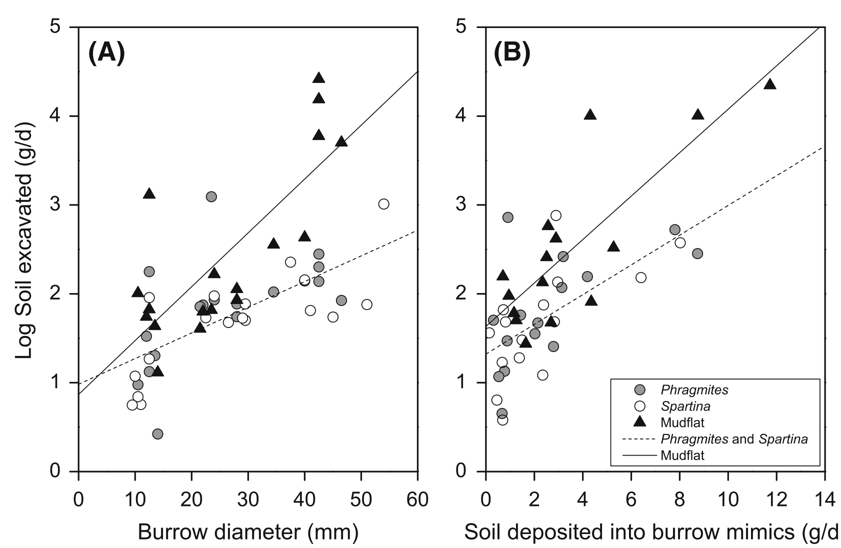

Figure 2. The relationships between soil excavated and burrow mimic diameters (**A**) and burrow mimic deposition (**B**). Shown are the means of six replicates in (**B**). The fitted equations are: (**A**) for *Phragmites* and *Spartina* marshes: $y = 0.98 + 0.03x$ ($r^2 = 0.44$, $n = 36$, $P < 0.001$) and for mudflats: $y = 0.87 + 0.06x$ ($r^2 = 0.60$, $n = 18$, $P < 0.001$); and (**B**) for *Phragmites* and *Spartina* marshes: $y = 1.32 + 0.17x$ ($r^2 = 0.40$, $n = 30$, $P < 0.001$), and for mudflats: $y = 1.63 + 0.24x$ ($r^2 = 0.67$, $n = 15$, $P < 0.001$).

mudflats (Figure 3C–G). Moreover, the interaction between habitat type and soil source was significant (Table A3 Supplemental Material). NH_4-N and TIN concentrations of surface soil in *Phragmites* marshes were significantly higher than those in both *Spartina* marsh and mudflats, but NO_3-N concentration was not different among the three habitats (Figure 4A–C, Table A4).

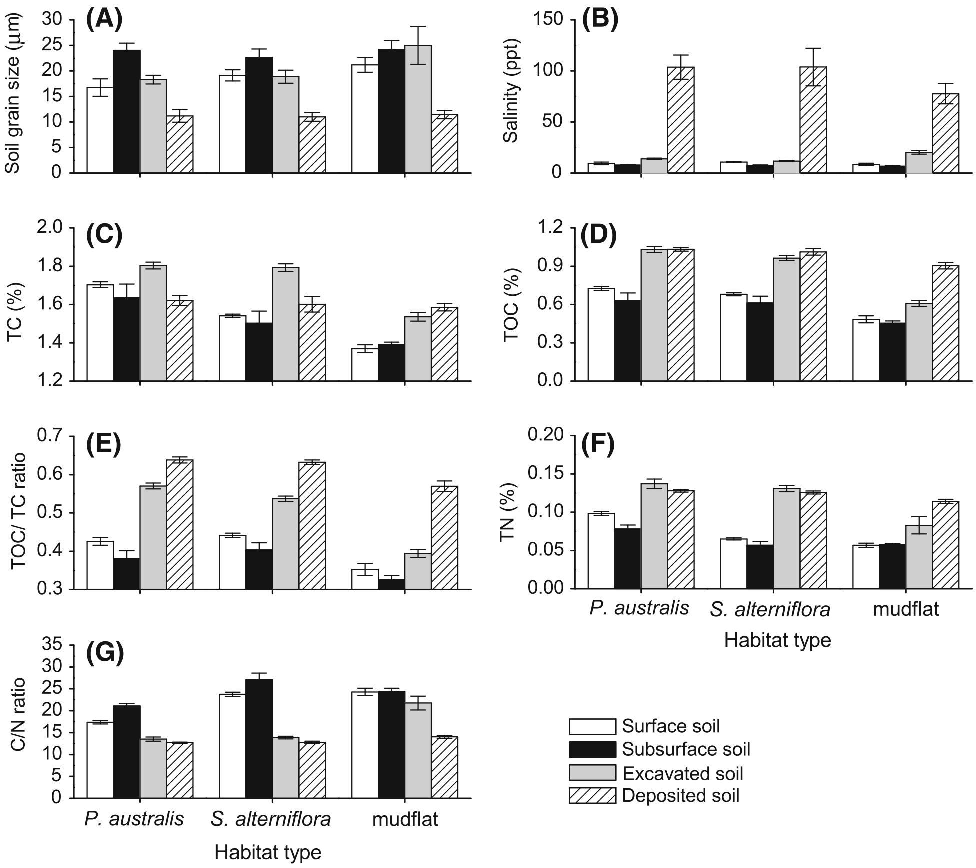

Figure 3. Effects of habitat types (*Phragmites*, *Spartina* marshes, and mudflats) and soil sources (background surface and subsurface soils, excavated, and deposited soils) on soil properties. (**A**) Soil grain size; (**B**) soil salinity; (**C**) soil C concentration; (**D**) soil organic C concentration; (**E**) organic C/total C ratio; (**F**) soil N concentration; and (**G**) soil C/N ratio.

Soil properties correlated with soil amounts transported (Figure 5, Table A6 Supplemental Material). The TN, TC, TOC, and TOC/TC ratio of the excavated soil negatively correlated with the amount of soil transported (Figure 5A–C, E), whereas the C/N ratio positively correlated with soil amount (Figure 5D). For deposited soil, its TN and TOC/TC ratio negatively correlated with amount of soil transported, whereas its TC positively correlated with the soil amount and TOC did not correlate with soil amount. Soil salinity of deposited soil negatively correlated with soil transported, but the correlation for excavated soil was insignificant. Soil grain size did not correlate with the amount of soil transported.

Effects of Habitat Type and Burrow Size on Soil Turnover

TN, TC, and TOC amounts of excavated soil were significantly affected by both habitat type and burrow size. TC and TOC amounts excavated in mudflats were higher than those in *Phragmites* and *Spartina* marshes, but TN amount was not significantly different among the habitats (Figure 6). TN, TC, and TOC amounts excavated all increased with increasing burrow diameter.

Both habitat type and burrow mimic size significantly affected the amounts of soil nutrients deposited, which were also higher in mudflats than in *Phragmites* and *Spartina* marshes. Larger burrow mimics trapped more soil nutrients (Figure 6). The amount of nutrients excavated was much greater than that deposited into burrow mimics, and crab burrowing resulted in a net transport of TC, TN, and TOC to the marsh surface. The net transport of TN and TOC was not significantly different among habitats, whereas that of TC in mudflats was significantly higher than that in the vegetated marshes. Meanwhile, net transport of TN, TC, and TOC to the surface increased with increasing burrow size (Figure 6).

The soil mass, TC, TN, and TOC amounts excavated and deposited into burrow mimics, and net transport to the surface (that is, excavation minus deposition) per unit area were estimated, with these values being the highest in mudflats and the lowest in *Spartina* marshes (Table 2). The soil mass per unit volume was the highest in mudflats and the lowest in *Spartina* marshes. The total C and N per unit volume were the highest in *Phragmites*

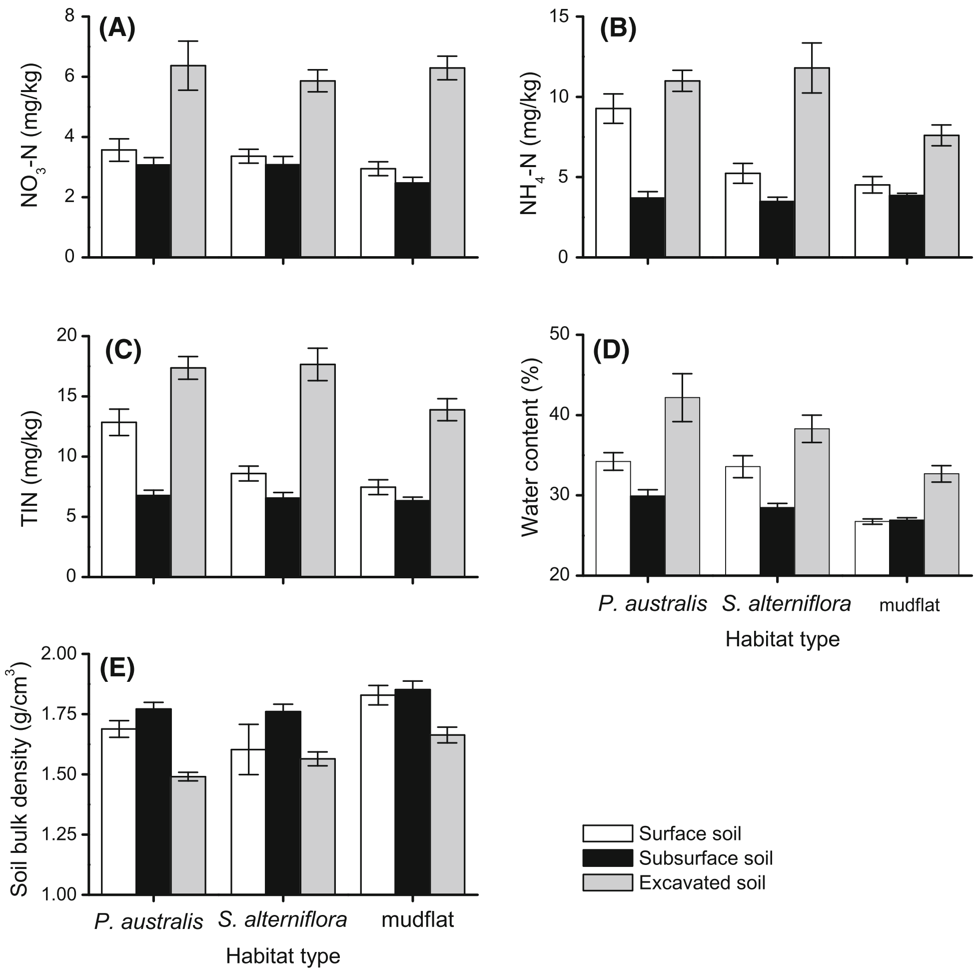

Figure 4. Effects of habitat types (*Phragmites*, *Spartina* marshes, and mudflats) and soil sources (background surface and subsurface soils, and excavated soil) on soil properties.

marshes, whereas those in *Spartina* marshes were the lowest. TOC per unit volume was also the highest in *Phragmites* and the lowest in mudflats (Table 2).

The turnover rates of soil, TC, TN, and TOC through crab burrowing were the highest in mudflats, followed by *Phragmites* marsh and *Spartina* marsh (Table 2). The estimated mean turnover time was 1–4 years in this study (Table 2). The turnover times of soil, TC, and TOC in *Spartina* marsh were the longest, and those in mudflats were the shortest. However, the turnover time of TN in *Phragmites* marsh was longer than that in *Spartina* marsh (Table 2).

Discussion

Crab burrowing is one of the most common bioturbations in salt marsh ecosystems and thus, understanding the movements of soil and associated C and N by crabs and their effects on soil properties is essential to understand how the biotic factors influence material cycling and energy flow. In this study, we considered the roles of bioturbation by a crab assemblage rather than a single dominant crab species in the salt marshes. In such coastal salt marsh ecosystems, crab burrowing does not work alone, but it interacts with tidal flow, which promotes vertical and horizontal transport of sediments and associated carbon and nitrogen. The interactive effects of crab burrowing and tidal flow on soil properties can be conceptualized by Figure 7, based on which our results are discussed below.

Burrowing Effects on the Vertical Transport of Soil Nutrients and Substrate

Our results showed that excavated soil was much greater than that deposited into burrow mimics, which led to a net transport of soil to the surface. The integration of excavating and depositing processes might clarify the burrowing effects in salt marsh more realistically. Botto and others (2006) suggest that burrow beds can significantly hinder the export of organic matter to adjacent ecosystems and serve as reservoirs of organic detritus. Their

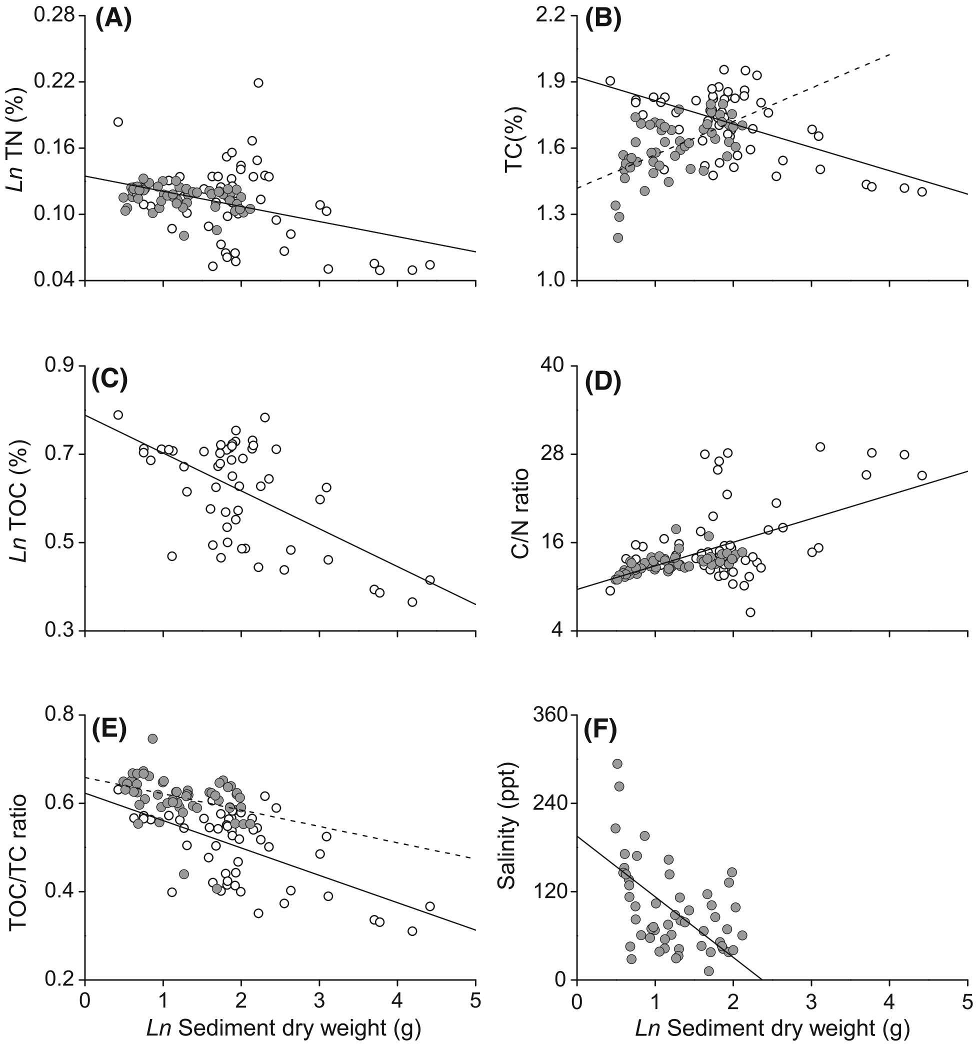

Figure 5. The relationships between soil properties and soil amount transported by crab excavation (*open circles*) or burrow mimic deposition (*solid circles*) over a 5-d sampling period. The equations for significant regressions are given: (**A**) $y = 0.135 - 0.014x$ ($r^2 = 0.16$, $n = 108$, $P < 0.001$); (**B**) solid line: $y = 1.921 - 0.106x$ ($r^2 = 0.32$, $n = 54$, $P < 0.001$); dashed line: $y = 1.42 + 0.15x$ ($r^2 = 0.35$, $n = 54$, $P < 0.001$); (**C**) $y = 0.79 - 0.09x$ ($r^2 = 0.35$, $n = 54$, $P < 0.001$); (**D**) $y = 9.63 + 3.21x$ ($r^2 = 0.32$, $n = 54$, $P < 0.001$); (**E**) solid line: $y = 0.62 - 0.06x$ ($r^2 = 0.35$, $n = 54$, $P < 0.001$); dashed line: $y = 0.66 - 0.04x$ ($r^2 = 0.12$, $n = 54$, $P < 0.01$); and (**F**) $y = 195.37 - 82.35x$ ($r^2 = 0.47$, $n = 54$, $P < 0.001$).

study focuses only on the trapping function of burrows for organic matter without considering re-excavating by crabs to the marsh surface. Gutierrez and others (2006) have similarly found that the excavated soil has lower TC and labile C concentrations than deposited soil in mudflats, which decreases carbon export to estuarine waters by tidal flow. In our study, substrate concentrations of the excavated soil were generally lower than those of the deposited soil except for TC in vegetated marshes (Figure 3C). A higher TC concentration but generally similar TOC of the excavated soil, relative to the deposited soil, suggests that inorganic C was higher in excavated soil than that in deposited soil. This difference also implies that excavating activities accelerated the mineralization of the organic matter from organic C to inorganic C, as observed in previous studies (for example, Otani and others 2010). Alternatively, excavated sediments might be richer in carbon carbonate relative to the deposited ones because of the differences in the selectivity between trapping (selective) and excavating (non-selective) processes (see below for more). In addition, deposition into burrows was repeatedly flooded by tidal water, which resulted in a great loss of carbonate. Thus, the total C concentration of the excavated soil significantly exceeded that of the deposited soil and background soil.

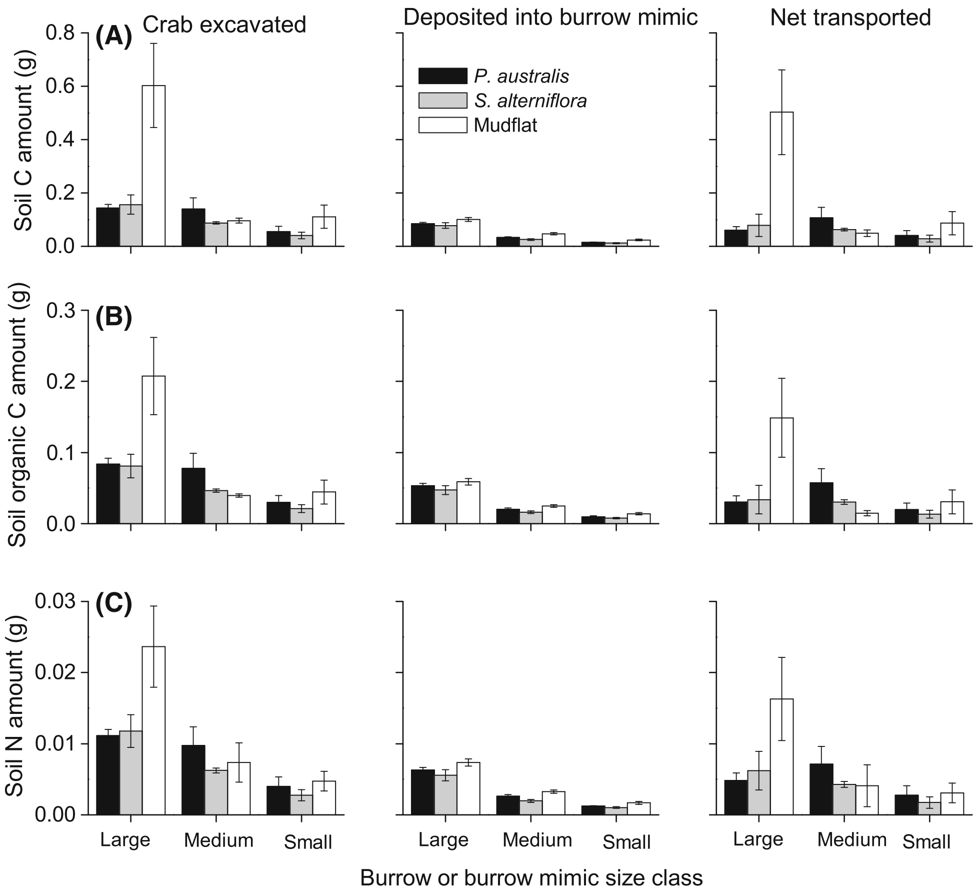

Figure 6. Effects of habitat type and burrow or burrow mimic size on vertical transport of soil nutrients. (**A**) Soil C (g); (**B**) organic C (g); and (**C**) soil N (g).

Soil deposition into burrows is a selective-trapping process mediated by the interactive effects of crab burrows and tidal flow, the former of which collects fine nutrient-rich sediments (Gutierrez and others 2006; Botto and Iribarne 2000). Moreover, crab excavation not only carries deposited soil out of burrows, but also removes the nutrient-poor background sediments during the process of burrow construction and enlargement (Botto and Iribarne 2000; McCraith and others 2003). Thus, the nutrient concentrations of excavated soil were lower than those of deposited soil. As Wolfrath (1992) suggests, crabs excavate deeper nutrient-poor and recently deposited soil to the marsh surface, which might mix sediments from different depths and homogenize the nutrient concentrations of excavated soil. A positive correlation between crab excavation and burrow mimic deposition (Figure 2B) implies that crab excavation and burrow repair were initiated since crab

Table 2. Estimated Turnover Rate and Time of Soil, Total Carbon, Organic Carbon, and Total Nitrogen due to Crab Excavation in *Phragmites*, *Spartina* Marshes, and Mudflats

	Soil	Carbon	Organic carbon	Nitrogen
Total amount (g m^{-3})				
Phragmites	352,925.2	5889.29	2386.36	311.21
Spartina	349,703.6	5321.45	2257.29	212.85
Mudflat	403,932.6	5572.51	1890.33	230.39
Turnover rate (g m^{-2} d^{-1})				
Phragmites	334.68	5.76	3.31	0.42
Spartina	235.67	4.06	2.24	0.30
Mudflat	605.59	9.15	3.80	0.48
Turnover time (year)				
Phragmites	2.89	2.80	1.98	2.02
Spartina	4.07	3.59	2.76	1.97
Mudflat	1.83	1.67	1.36	1.31

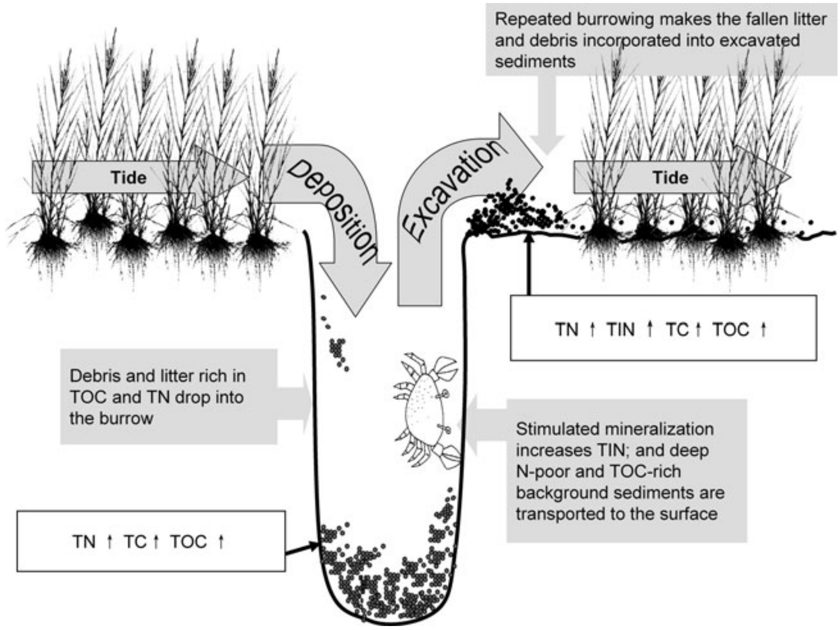

Figure 7. A schematic diagram of interactive effects of tide and crab burrowing on the chemical properties of deep-layer and surface sediments. Tide with debris and litter flows into the crab burrow, increasing the total nitrogen (TN), total carbon (TC), total organic carbon (TOC) of deep soil; and crab excavation might promote the mineralization of soil organic matter and increase the total inorganic nitrogen (TIN) of surface sediments compared to the background soil without crab bioturbation. Crabs may repeatedly use the existing burrows, which incorporates the fallen litter and debris into excavated soil, resulting in more organic matter than background soil.

burrows were filled with muddy slurry brought by the tide. Excavation, which might promote mineralization of soil organic matter, increased the inorganic N concentrations of excavated soil and thus, crab excavation would enhance inorganic N availability to surrounding soil and plants (Mighter and others 1995; Fanjul and others 2007). Moreover, burrow wall sediments provide ideal conditions for denitrification to diminish the effects of anthropogenic nitrogen inputs (McHenga and Tsuchiya 2008). Therefore, crab burrowing significantly affected the functions of salt marshes and the nutrient balance between the marshes and estuarine waters by transporting soil rich in nutrients (that is, TC and TN and TOC) to marsh surfaces for aerobic decomposition and export to adjacent waters.

In addition, our results showed that the soil deposited into burrows had a much higher salinity compared to the excavated soil and background soil that had the lowest salinity. Similarly, Fanjul and others (2007) have found that pore water salinity in crabbed is higher than in non-crabbed areas. Salt burial by crabs may lead only to a slightly local accrual of soil salinity as tidal water has a diluting effect on the salinity of deposited sediments. It is highly likely that the increased salinity has patchy effects on plants and soil biota (for example, soil microbes and nematodes) and associated biogeochemical processes as soil salinity is closely related with pH, conductance, redox state, and denitrification (Fanjul and others 2007). However, quantification of such effects has been scarce. It is highly rewarding to examine the ecological and biogeochemical implications of the net salt burial by crabs and burrowing animals in general.

Interactive Effects of Crab Burrowing and Habitat Type on Bioturbation

The magnitude of bioturbation effects depends on the interactions between the biology of the bioturbators and their environments. Our results show that the crab burrowing effects varied considerably among the three contrasting habitats. In particular, whether vegetation was present greatly affected both quantity and quality of excavated and mimic-burrow deposited soils, and hence determine the burrowing effects.

Crab burrow volume and depth reflected, to a certain degree, the belowground structure of plants (Katrak and others 2008; Wang 2008). Although the biomass of *Spartina*'s rhizomes was significantly less than that of *Phragmites*, that of fine roots in

Spartina marshes was greater than that in *Phragmites* marshes. Crab burrow volume and depth were the lowest in *Spartina* marshes, indicating that these parameters might be limited by the presence of fine roots. Also, the body size of crabs, which largely determines the crab's excavating ability, was generally the largest in mudflats, but the smallest in *Spartina* marsh. As a result, soil excavated in the vegetated marshes was significantly lower than that in unvegetated mudflats. Opening size (diameter) of crab burrows was another important factor influencing burrowing performance. Burrow mimic deposition efficiency decreased with increasing burrow mimic diameter. Small burrows might have substantially contributed to sediment deposition because they were the most abundant at our study site. Dense plant canopies attenuate tidal flows, decreasing sediment transport (Daehler and Strong 1996). Consequently, burrow mimic deposition in *Phragmites* and *Spartina* marshes was significantly lower than that in mudflats.

Plants also affect the properties of soil transported by crabs through increasing plant production and/or altering soil ecosystem processes. Marsh plant communities produce a considerable amount of aboveground litter and detritus and belowground litter and root exudates (Neira and others 2006), which might lead to great soil organic matter content in the vegetated marshes. The presence of plants significantly enhanced the concentrations of total soil N and C, and organic C (Figure 3) although plants might have absorbed some nutrients for their own growth. In general, vegetation can increase the differences in soil properties between upper and deeper soil layers through enhancing nutrient concentrations of upper soil layers and obstructing the vertical movement of materials from crab burrowing. In contrast, vertical mixing of sediments by crabs precludes any obviously vertical stratification of carbon and nutrients (Takeda and Kurihara 1987; McCraith and others 2003; Fanjul and others 2007).

Soil Turnover Rate as Influenced by Crab Burrowing

One of the most important ecological functions of animal bioturbators is to perform soil turnover that in turn causes vertical and horizontal transfer of nutrients in the soil. Several studies have examined the soil-excavating rate of single crab species in salt marshes (Takeda and Kurihara 1987; Iribarne and others 1997; Botto and Iribarne 2000; Gutierrez and others 2006; Fanjul and others 2007). In this study, soil excavated per unit area in *Phragmites* and *Spartina* marshes and mudflats was, respectively 3.11, 2.74, and 4.25 times that deposited into burrow mimics. The ratio for mudflats was slightly higher than that (3.17) estimated by Gutierrez and others (2006). Rates of soil and C transported by crabs in our study (soil excavated: 490.27 g m^{-2} d^{-1}; soil deposited: 115.32 g m^{-2} d^{-1}; total C excavated: 7.33 g m^{-2} d^{-1}; and total C deposited: 1.82 g m^{-2} d^{-1}) were close to those of Gutierrez and others (2006) (soil excavated: 547.08 g. m^{-2} d^{-1}; soil deposited: 172.79 g m^{-2} d^{-1}; total C excavated: 10.28 g m^{-2} d^{-1}; and total C deposited: 4.15 g m^{-2} d^{-1}), but much higher than those reported by Montague (1982) (soil excavated: 6.07 g m^{-2} d^{-1}; soil deposited: data unavailable; total C excavated: 0.65 g m^{-2} d^{-1}; and total C deposited: 0.08 g m^{-2} d^{-1}). However, turnover times (Table 2) in this study are obviously much longer than the estimates given by Takeda and Kurihara (1987). Their estimated turnover time for the top 40 of cm soil by *H. tridens* is 34.4 d.

Why is soil turnover so different among the studies conducted at different sites? Crab species and density largely determine soil turnover. In the salt marshes of Natori River (Japan), *H. tridens* has a larger body size (3 cm in carapace width) and high density (up to 70 burrows m^{-2}), and thus has great excavating ability (Takeda and Kurihara 1987). In Mar Chiquita coastal lagoon (Argentina), the dominant crab species *Chasmagnathus granulatus* also has both large body size (up to 4 cm in carapace width) and high density (ca. 70 individual m^{-2}), and hence exhibits a great excavating ability (Gutierrez and others 2006; Iribarne and others 1997). Although the density of *Uca pugnax* is up to 80 individual m^{-2} in the salt marshes in Georgia (USA), the excavating ability of *U. pugnax* is rather weak due to its small body size, 2.3 cm in carapace width (Montague 1982). In our study site, the dominant crab species in the salt marshes included *S. dehaani*, *Helice tientsinensis,* and *U. arcuata*, all of which had rather large body sizes ($>$3.0 cm in carapace width). Burrow density in the salt marsh was about 40 burrows m^{-2}. Crab communities here showed a medium capacity for soil turnover compared to the crabs examined in other studies. Alternatively, the differences quoted here might be less a characteristic of the crabs than what they might reflect for the differences of the methods and study sites. Measuring methods could, to a certain degree, affect the results. We determined the soil turnover through measuring the amounts of crab excavation, whereas Takeda and Kurihara (1987) determined soil turnover by assuming that the volume of new burrows was equal to the volume of soil carried to the surface by crabs, which might have neglected the contribution of loosening soil and overestimated the turnover rate. Therefore, it is unlikely, with just a few studies done on excavated sediment, to draw any global conclusions about soil turnover through crab burrowing. This is still an open question that is worth answering by setting up the same study in widely varying sites.

It is worth noting that crab excavating ability at our study site was considerably lower than that in Argentina and Japanese marshes perhaps because overharvesting of commercial crabs at Dongtan might have led to reduced diversity and density of crabs, and hence decreased burrowing performance. Although the exact data on commercial crab harvesting at Dongtan are unfortunately unavailable, the harvesting intensity has been so high over the last decades that crab species that used to be common have become less abundant (Xu and Zhao 2005). Obviously, it is urgent to take effective measures against overharvesting crabs so that their bioturbation can be maintained to make the salt marshes function as ecosystem service providers.

Conclusions

Crab burrowing is an important type of bioturbation, which can effectively mix surface and subsurface soil through burrow trapping and crab excavating processes. These processes could stimulate ecosystem C and N cycling. Plants (*P. australis* and *S. alterniflora*) enhanced soil nutrient concentrations, but obstructed the vertical movement of materials driven by crab burrowing, limiting nutrient cycling and reuse. Therefore, crabs directly and indirectly affect ecosystem processes and functioning of the salt marshes, and their roles in the conservation and restoration of coastal wetlands need to be considered.

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