Effects of invasive cordgrass on crab distributions and diets in a Chinese salt marsh

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ABSTRACT: The effects of invasive cordgrass *Spartina alterniflora* on burrowing crab communities in the salt marshes of the Yangtze River Estuary, China, were studied. Crab abundance, distribution and diets were compared in native *Phragmites australis* and invasive *S. alterniflora* stands. *Spartina*-invaded stands had 42% higher crab density than did native *P. australis* stands, largely because 2 dominant grapsoid crabs, *Helice tientsinensis* and *Chiromantes dehaani*, thrived in *S. alterniflora* stands. Sediment grain size, water content and vegetation stem height were the main factors correlated with crab distributions. Crab diet analyses revealed that crab stomach fullness was similar in stands of different plant species, indicating that in *Spartina*-invaded stands crabs can find compatible food quantity as in native plant stands. Both *H. tientsinensis* and *C. dehaani* from *S. alterniflora* stands had significantly higher δ^13C values than those from *P. australis* stands, suggesting that the crabs consumed *S. alterniflora* in the invasive marshes. This non-selective feeding may be driving the success of *H. tientsinensis* and *C. dehaani* in invasive *Spartina* stands.

KEY WORDS: Herbivores · Invasive species · *Spartina alterniflora* · *Phragmites australis* · Feeding habits · Gut contents · Stable isotopes · Yangtze River estuary

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INTRODUCTION

In salt marsh ecosystems, burrowing crabs influence sediment, plants and other marsh organisms physically. Fiddler crabs can enhance the growth of *Spartina alterniflora* and the abundance of meiofauna by aerating the sediment (Hoffman et al. 1984, Bertness 1985). *Helice* spp., a common and widely distributed crab in saltmarsh habitats, might prevent the outflow of primary products of *Phragmites australis* from the salt marsh to open shores (Takeda & Kurihara 1987). Substrate excavation by burrowing crabs can turn over marsh sediments, bring buried material to the marsh surface, expose the sediments to oxygen, change the amount of material that is imported or exported by tidal flushing and, thus, play an important role in the circulation of nutrients within the salt marsh ecosystems (McCraith et al. 2003, Minkoff et al. 2006, Escapa et al. 2008, Fanjul et al. 2008).

Salt marshes are vulnerable to various disturbances including biological invasions (Grosholz 2002, Levin et al. 2006). The introduction of exotic plant species in salt marshes has occurred worldwide, and has affected native invertebrate communities (Talley & Levin 2001, Posey et al. 2003, Neira et al. 2006). The changes in vegetation type that instigate changes in sediment properties might influence the abundance and distribution of burrowing crabs as well as the services they provide to the marsh systems. The effects of plant invasions on burrowing crabs, however, have not received much attention. To date, only 2 studies assessed the influence of plant invasions on marsh crabs and each emphasized a certain crab species. Jivoff & Able (2003) reported that the feeding molt stage of juvenile blue crabs *Callinectes sapidus* preferred native cordgrass *Spartina alterniflora* to invasive *Phragmites australis* in marshes of Delaware Bay, USA. Wang et al. (2008) found that the abundance and biomass of *Sesarma dehaani* (i.e. *Chi-*

romantes dehaani) were significantly greater in the invasive *S. altniflo*ra than in native *P. australis* stands in the Yangtze River estuary, China. The effects of plant invasions on crab communities are still largely unknown. Since different crab species influence sediment properties differently, understanding the modification of whole crab communities and their functions induced by plant invasions is important.

To mitigate erosion control and enhance sediment accretion, *Spartina alterniflora* was intentionally introduced from North America to China in 1979. This led to a rapid range expansion along the Chinese coast (Li et al. 2009). *S. alterniflora* became a dominant plant in wetland ecosystems at Dongtan on Chongming Island in just over 10 yr since its introduction, and its effect on native biodiversity has become evident (Wang et al. 2006, Chen et al. 2007). Wang et al. (2008) investigated the influence of *S. alterniflora* invasions on the crab *Chiromantes dehaani* by using traps. However, how the crab communities respond to the exotic *S. alterniflora* remains unclear.

Plant communities provide food, living habitats and nursery grounds for benthic organisms; therefore, the mechanisms underlying the shifts in zoobenthic communities due to plant invasions are site and species specific. Among these mechanisms, the feeding habits of organisms are undoubtedly one of the most important. Saltmarsh crabs can be important grazers, predators or deposit feeders with different selectivity on various food types (Bertness 1999). However, the relationship between the feeding preference and the distribution of crabs is still unclear (Bertness & Miller 1984, Bortolus et al. 2002). By studying crabs in adjacent native *Phragmites australis* and exotic *Spartina alterniflora* stands and quantifying crab diets, the present study examined: (1) whether the distribution of crabs is influenced by the *S. alterniflora* invasion of the Yangtze River estuary salt marshes and (2) whether the modifications of crab distributions are related to their feeding activities.

MATERIALS AND METHODS

Study site. The study was conducted at the Chongming Dongtan National Nature Reserve (121° 50′ to 122° 05′ E, 31° 25′ to 31° 38′ N) on the Yangtze River
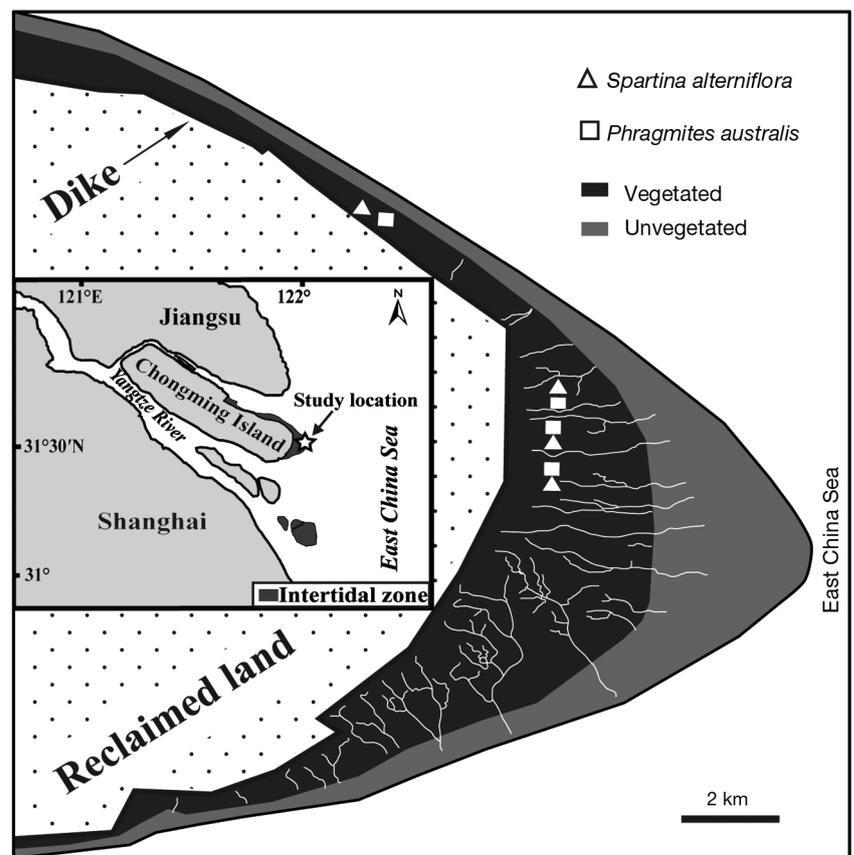

Fig. 1. Chongming Dongtan at the Yangtze River estuary showing locations of sampling sites

estuary in eastern China (Fig. 1). The study site (241.55 km^2) is characterized by a warm, humid, subtropical monsoonal climate, with annual mean temperature and mean precipitation of 15.3°C and 1022 mm, respectively. The intertidal areas are flooded by semidiurnal tides with a maximum range of 4.62 to 5.95 m and an average tidal height range of 1.96 to 3.08 m. The invasive plant species *Spartina alterniflora* has rapidly expanded at Dongtan marshes by forming pure stands that constitute up to 33.1% of the total vegetation coverage (Huang et al. 2005).

Sampling design and crab sample processing. Common borrowing crab species at the studied marshes include 3 species from the family Ocypodidae (*Uca arcuata*, *Ilyoplax deschampsi* and *Macrophthalmus abbreviatus*) and 3 species from Grapsidae (*Helice tientsinensis*, *Chiromantes haematocheir* and *C. dehaani*) (Xu & Zhao 2005). These crabs have various feeding habits and potential food sources include vascular plants, microalgae and animal items.

Within the intertidal marshes of the reserve, 4 blocks were chosen at an elevation of ~3.8 m from which to collect crabs (Fig. 1). In each block, there were monoculture patches of both native *Phragmites australis* and

invasive *Spartina alterniflora*. The diameter of each monoculture patch was >50 m. Sampling was done at spring tides on 20 November 2007, and on 18 January, 2 April and 25 June 2008, to represent autumn, winter, spring and summer, respectively. In each block at each sampling date, 3 randomly placed 50 × 50 cm quadrats were selected in *P. australis* and *S. alterniflora* monocultures. From within the quadrat, crabs were collected from the sediment surface, and those in burrows were obtained by digging them out (Spivak et al. 1996, Bas et al. 2005). Additional crabs were also collected seasonally for stomach content analyses. All crabs captured were preserved in 10% formalin in labeled plastic bottles. In the laboratory, crabs were identified, counted and weighted. The nomenclature of crabs followed Ng et al. (2008).

Environmental parameters. Sediment temperature and electrical conductivity were measured directly at 10 cm depth in each crab sampling quadrat. One sediment sample was collected from each quadrat with a PVC tube 3.2 cm in diameter to a depth of 10 cm for water content and grain size analyses. In the laboratory, water content was assessed by drying the samples at 80°C for 48 h. Sediment grain size was determined using a LS100Q laser grain sizer. Live plant stem densities were recorded by counting the shoots from 3 additional 25 × 25 cm quadrats, and stem height was determined by measuring 15 random stems per plant species per block.

Stomach content analyses. Stomachs of the 2 dominant crab species were excised from specimens collected during the 4 seasons. Stomach fullness was visually assessed according to the criteria of Johnston & Freeman (2005) and placed into 5 classes: 1 = empty, 2 = 25%, 3 = 50%, 4 = 75% and 5 = 100% full. For stomach content analyses, 10 crabs with stomach fullness from 50 to 100% were selected for each vegetation area in each season. The stomachs were cut open and the contents were washed with distilled water into a 10 cm diameter dish. The contents in the dish were stirred evenly and examined under a binocular microscope (Olympus SZ-CTV). For each specimen, 10 visual fields were chosen randomly and photos were taken under an 11× ocular objective with the photo system (NIS-Elements D 2.20). A grid (100 × 100 µm) was added simultaneously to the image by means of the photo system. The relative abundance of each dietary item was counted in the field they occupied and 4 categories of food types from stomach contents were determined. Animal materials included gastropods, insects, isopods, crustaceans, fish and invertebrate eggs and scales. Plant materials included rhizomes/roots, stems, leaves, inflorescence, seeds and buds. Unidentified organic matter was placed in the organic debris category, and inorganic debris mainly

consisted of sand, clay, plastic and other unidentified materials.

Stable isotope analyses. Samples for stable isotope analyses were collected in July and October when the plants had the highest biomass. Samples of *Phragmites australis* and *Spartina alterniflora* were collected by hand at ebb tides. Leaves from 10 plants were pooled as a single sample.

Benthic microalgae (BMI) samples were collected from the monocultures of the 2 vegetation types at ebb tide by the modified technique of Riera et al. (1999). Briefly, the sediment surface was covered with a 5 mm thick layer of pre-combusted commercial sand, a piece of 63 µm nylon mesh and another 5 mm thick layer of pre-combusted sand and left to incubate for 3 h. After 3 h, the sand layer was scraped off and mixed with pre-filtered creek water. The water–sand mixture was shaken and the supernatant was filtered through pre-combusted GF/F filters (Whatman).

Crabs for stable isotope analyses were collected from vegetated zones of the marshes. Muscle tissue from approximately 10 individuals of each crab species from each plant monoculture type were pooled for analysis.

All plant and animal materials were first treated with 1N HCl to eliminate the carbonates and then were oven dried at 60°C. Stable carbon and nitrogen isotope ratios were measured by continuous-flow isotope ratio mass (IRM) spectrometry using a Finnigan Delta-plus IRM spectrometer interfaced with a Flash EA 1112 Series at the Institute of Botany, Chinese Academy of Sciences. Urea and glycine were used as accuracy and precision standards for isotopic ratios. All stable isotope abundances are expressed using the δ notation as ‰ differences from an international standard (Vienna Pee Dee Belemnite for carbon, air for nitrogen):

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3,$$

where X is ^{13}C or ^{15}N, and R is the corresponding isotope ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The analytical precision of these measurements was 0.20‰ for $\delta^{13}C$ and 0.30‰ for $\delta^{15}N$.

Since the exotic *Spartina alterniflora* and the native *Phragmites australis* are C_4 and C_3 plants, respectively, the $\delta^{13}C$ value for *S. alterniflora* is expected to be higher than that for *P. australis*. If the crabs are nonselective in feeding and can consume *S. alterniflora* in exotic marshes, they would have higher $\delta^{13}C$ values than those from native marshes.

Data analyses. Nested 2-way ANOVA with 2 main factors (Plant type and Season) was used to evaluate the effects of plant type and season on sediment properties, plant traits and crabs. Proportional data were arcsine(x)-transformed before analysis. When effects were significant, multiple comparisons between plant types were made based on least square means. Differ-

ences were regarded as significant at p < 0.05. The
BIO-ENV procedure was used to identify the environ-
mental variables that best explained variations in crab
communities (Clarke & Ainsworth 1993). The BIO-
ENV analysis used Spearman's rank correlation be-
tween the resulting ranked similarity matrices of crabs
and the rank similarity matrix obtained through
Euclidean distances using the standardized environ-
mental variables. All analyses were performed using
Statistica 7.0 and PRIMER 5.

Two-way ANOVA was performed to test the effects
of season and habitat on crab stomach fullness. The
differences in relative abundance of each dietary item
in crabs from different plant communities were ana-
lyzed by a *t*-test. Before analysis, the proportional data
were arcsine(x)-transformed. One-way ANOVA was
applied to test the difference in $\delta^{13}C$ and $\delta^{15}N$ values
among autotrophs and among crabs. Differences were
regarded as significant at p < 0.05.

RESULTS

Environmental factors

The proportions of different sediment grains, sedi-
ment water content, temperature, stem density and
height differed significantly between the 2 plant types
(Table 1). Silt and clay constituted the majority of sedi-
ment (>90%) in most samples. The sediment in
Spartina alterniflora patches had a lower proportion of
silt than that in *Phragmites australis* patches. The tem-
perature in *S. alterniflora* stands was generally higher

than in *P. australis* stands except in April. Sediment
water content ranged from 27.92 to 37.41%; signifi-
cantly higher water content was found in *S. alterniflora*
compared with *P. australis* communities in most
months. The stems of *S. alterniflora* were generally
denser than those of *P. australis*. In April, *S. alterniflora*
had higher stems than *P. australis*. After June, *P. aus-
tralis* exceeded *S. alterniflora* in stem height.

Crab communities

During the study, a total of 308 crabs belonging to 4
species from 3 families were captured; 181 crabs were
collected in *Spartina alterniflora* and 127 crabs in
Phragmites australis communities (Table 2). The den-
sity and biomass of the total crabs differed signifi-
cantly between *S. alterniflora* and *P. australis* mono-
cultures, with higher values found in *S. alterniflora*
patches (Table 3). No significant difference in species
richness was found between the 2 plant types. BIO-
ENV analysis revealed that the stem height was the
environmental variable that best explained the varia-
tions in the crab communities (correlation coefficient
= 0.129). In combination, 4 environmental variables
(temperature, water content, sand proportion and
stem height) were closely correlated with the varia-
tions in crab communities, with the maximum correla-
tion coefficient of 0.143.

Numerically, *Helice tientsinensis* and *Chiromantes
dehaani* were the dominant crab species in both
Spartina alterniflora and *Phragmites australis* commu-
nities, together constituting over 75% of the total crab

Table 1. Sediment properties and vegetation characteristics of *Spartina alterniflora* (SA) and *Phragmites australis* (PA) marshes in each
sampling month. Shown are the mean values with SE in parentheses and the summary of nested 2-way ANOVA (*F*-values with significance
levels in parentheses; significant differences p < 0.05 are indicated in **bold** text). Blocks were nested within plants and time. Different
superscript letters (a, b) indicate significant differences between SA and PA in each month (p < 0.05)

Mo	Plant	n	Clay <4 μm (%)	Silt 4–63 μm (%)	Sand >63 μm (%)	Temperature (°C)	Water content (%)	Electrical conductivity (mS cm^{-1})	Stem density (ind. m^{-2})	Stem height (cm)
Nov	SA	12	22.43 (3.17)[a]	63.74(2.91)[a]	13.83 (4.57)[a]	12.97 (0.29)	31.34 (0.68)		592 (45)	131.5 (14.7)[a]
	PA	12	27.59 (2.97)[b]	69.80(2.26)[b]	2.61 (0.78)[b]	12.89 (0.38)	32.70 (1.17)		524 (43)	151.4 (25.8)[b]
Jan	SA	12	29.28 (1.00)	70.26(0.84)	0.46 (0.19)	12.78 (0.52)[a]	33.62 (1.43)[a]		308 (33)[a]	112.6 (15.4)[a]
	PA	12	27.83 (0.49)	71.66(0.40)	0.51 (0.15)	11.55 (0.55)[b]	29.71 (0.93)[b]		252 (47)[b]	165.2 (20.8)[b]
Apr	SA	12	29.79 (0.85)[a]	69.70(0.78)[a]	0.51 (0.14)[a]	11.72 (0.31)[a]	32.09 (0.91)[a]	5.82 (0.45)	374 (67)[a]	19.4 (4.32)[a]
	PA	12	26.06 (0.69)[b]	72.64(0.46)[b]	1.30 (0.27)[b]	12.47 (0.13)[b]	28.26 (0.39)[b]	5.29 (0.26)	142 (12)[b]	17.81 (2.85)[b]
Jun	SA	12	31.90 (1.30)[a]	67.80(1.23)[a]	0.30 (0.09)	23.31 (0.16)	37.41 (1.51)[a]	5.62 (0.31)	238 (24)	100.3 (14.36)[a]
	PA	12	27.32 (0.89)[b]	72.03(0.76)[b]	0.65 (0.16)	23.25 (0.13)	27.92 (0.71)[b]	5.17 (0.38)	196 (19)	161.0 (36.64)[b]
Summary of nested 2-way ANOVA										
Plant			6.81 (0.011)	**39.31 (<0.001)**	**10.07 (0.002)**	**5.04 (0.028)**	**104.68 (<0.001)**	3.874 (0.058)	**64.18 (<0.001)**	**355.04 (<0.001)**
Time			**37.57 (<0.001)**	**10.78 (<0.001)**	**86.27 (<0.001)**	**3442.00 (<0.001)**	**7.04 (<0.001)**	0.406 (0.529)	**98.70 (<0.001)**	**1947.58 (<0.001)**
Plant × Time			**37.68 (<0.001)**	**2.77 (0.049)**	**42.18 (<0.001)**	**40.66 (<0.001)**	**32.07 (<0.001)**	0.022 (0.883)	**12.62 (<0.001)**	**28.08 (<0.001)**
Block (Plant × Time)			**37.50 (<0.001)**	**8.71 (<0.01)**	**24.79 (<0.001)**	**44.02 (<0.001)**	**10.17 (<0.001)**	**5.013 (<0.001)**	**10.84 (<0.001)**	**18.41 (<0.001)**

Table 2. Crab species captured in *Spartina alterniflora* and *Phragmites australis* communities during the study. Shown are abundance (individual), biomass (g) and percentage contribution of abundance (%)

Family	Crab species	—— *Spartina alterniflora* patches ——			—— *Phragmites australis* patches ——		
		Abundance	Biomass	Percentage	Abundance	Biomass	Percentage
Varunidae	*Helice tientsinensis*	85	648.91	46.96	51	411.625	40.16
Sesarmidae	*Chiromantes dehaani*	80	912.25	44.20	48	604.584	37.79
	Parasesarma plicatum	9	60.87	4.97	15	96.885	11.81
Ocypodidae	*Uca arcuata*	7	58.19	3.87	13	121.519	10.24
Total	4	181	1680.22	100	127	1234.613	100

Table 3. Species richness (expressed per quadrat), density (ind. m^{-2}) and biomass (g m^{-2}) of all crabs and 2 numerically abundant species, *Helice tientsinensis* and *Chiromantes dehaani*, from *Spartina alterniflora* (SA) and *Phragmites australis* (PA) monocultures at each sampling time. Shown are the mean values with SE in parentheses and the summary of nested 2-way ANOVA (*F*-values with significance levels in parentheses; significant differences p < 0.05 are indicated in **bold** text). Blocks were nested within plants and time. Different superscript letters (a, b) indicate significant differences between SA and PA in each month (p < 0.05)

Mo	Plant	n	Species richness	——————— Density ———————			——————— Biomass ———————		
				All crabs	*H. tientsinensis*	*C. dehaani*	All crabs	*H. tientsinensis*	*C. dehaani*
Jan	SA	12	1.67 (0.26)	12.00 (1.64)[a]	8.00 (1.12)[a]	3.00 (1.12)	108.76 (18.48)[a]	66.20 (9.52)[a]	64.68 (31.16)
	PA	12	1.08 (0.19)	6.68 (1.12)[b]	3.68 (0.92)[b]	2.32 (1.36)	55.68 (12.76)[b]	25.28 (7.12)[b]	26.36 (14.48)
Apr	SA	12	1.25 (0.18)	19.68 (3.60)[a]	5.68 (2.12)	12.68 (3.68)[a]	190.00 (37.76)[a]	43.12 (16.32)	138.12 (39.84)[a]
	PA	12	1.83 (0.21)	9.68 (1.36)[b]	4.00 (0.68)	3.68 (1.16)[b]	102.72 (17.88)[b]	33.48 (7.76)	44.84 (15.92)[b]
Jun	SA	12	1.58 (0.26)	18.37 (3.56)	5.68 (1.92)	10.68 (2.72)	174.48 (37.12)	32.96 (11.60)	126.80 (32.68)
	PA	12	2.08 (0.31)	17.00 (2.84)	4.68 (1.36)	7.68 (1.60)	170.24 (33.96)	38.52 (13.56)	104.40 (27.84)
Nov	SA	12	1.25 (0.22)	10.32 (1.92)	9.00 (1.64)[a]	0.32 (0.32)	86.84 (14.92)	74.00 (14.40)[a]	1.76 (1.76)
	PA	12	1.50 (0.23)	9.00 (1.92)	4.68 (1.48)[b]	2.32 (1.24)	82.92 (20.28)	39.92 (12.16)[b]	25.88 (14.88)
Summary of nested 2-way ANOVA									
Plant			2.455 (0.122)	**17.254 (<0.001)**	**10.704 (0.002)**	**9.395 (0.003)**	**9.997 (0.002)**	**7.832 (0.007)**	**6.368 (0.014)**
Time			**3.263 (0.027)**	**13.917 (<0.001)**	1.037 (0.382)	**20.184 (<0.001)**	**14.714 (<0.001)**	1.812 (0.154)	**12.593 (<0.001)**
Plant × Time			**4.960 (0.004)**	**3.621 (0.018)**	1.025 (0.388)	**7.266 (<0.001)**	**2.993 (0.037)**	2.332 (0.082)	**3.544 (0.019)**
Block (Plant × Time)			**4.434 (<0.001)**	**6.489 (<0.001)**	**2.679 (<0.001)**	**6.257 (<0.0001)**	**6.333 (<0.001)**	**2.579 (0.001)**	**4.383 (<0.001)**

individuals (Table 2). The density and biomass of both species differed significantly between *S. alterniflora* and *P. australis* communities (Table 3). *S. alterniflora* patches contained significantly more *H. tientsinensis* than *P. australis* in November and January, and significantly more *C. dehaani* than *P. australis* in April.

Feeding habits of dominant crabs

For both *Helice tientsinensis* and *Chiromantes dehaani*, 2-way ANOVA showed that the stomach fullness of crabs did not differ significantly between *Spartina alterniflora* and *Phragmites australis* communities. Both crab species had significantly higher stomach fullness in summer than in the other seasons (Fig. 2). However, in spring *H. tientsinensis* tended to eat more in *S. alterniflora* stands than in *P. australis* stands, whereas the results were opposite in summer and autumn. In contrast, *C. dehaani* tended to have

higher stomach fullness in *P. australis* stands than in *S. alterniflora* stands in spring with the opposite trends occurring in the other seasons.

Among the 160 crab specimens examined 99.4% contained plant materials, and only 31.9% contained animal materials. In spring, the relative abundance of plant material in the stomachs of *Helice tientsinensis* from *Spartina alterniflora* stands was significantly greater than that from *Phragmites australis* stands (Table 4). *H. tientsinensis* from *P. australis* areas ingested significantly more inorganic debris than in *S. alterniflora* areas. Significantly more plant material was found in the stomachs of *Chiromantes dehaani* from *S. alterniflora* stands than those from *P. australis* stands in autumn. *C. dehaani* generally ingested more inorganic debris in *S. alterniflora* areas than in *P. australis* areas, with a significant difference observed in autumn (Table 4).

Among plant materials, leaves were the most common (98.75%) items, followed by rhizomes/roots. In
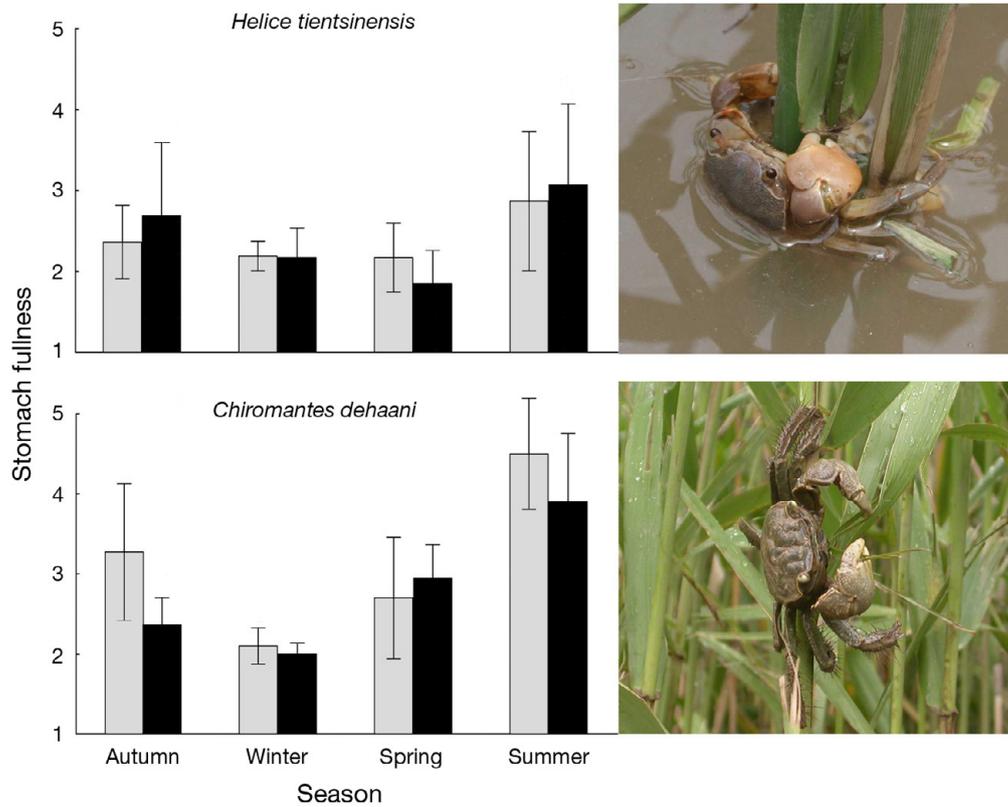
Fig. 2. *Helice tientsinensis* and *Chiromantes dehaani*. Stomach fullness analyses of 2 dominant crab species and photos showing their feeding behavior. (■) Crabs from *Phragmites australis* patches; (▨) crabs from *Spartina alterniflora* patches. Error bars indicate SE (n = 10 to ~22, depending on specimens available)

Table 4. *Helice tientsinensis* and *Chiromantes dehaani*. Stomach contents of the 2 most numerically abundant crab species from *Spartina alterniflora* (SA) and *Phragmites australis* (PA) monocultures. Relative abundance (mean ± SE) of each food item are expressed as the proportional area of the food item in stomach contents mounted on microscope slides. Different superscript letters (a, b) indicate significant differences between SA and PA in each season determined from *t*-tests (p < 0.05)

Season	Vegetation	n	Relative abundance of each food category (%)			
			Animal material	Plant material	Organic debris	Inorganic debris
Helice tientsinensis						
Autumn	SA	10	6.59 ± 6.59	73.47 ± 9.15	8.00 ± 3.92	11.94 ± 3.39[a]
	PA	10	8.08 ± 6.49	55.66 ± 9.64	3.61 ± 1.37	32.65 ± 8.11[b]
Winter	SA	10	2.46 ± 2.46	34.81 ± 6.58	3.85 ± 1.55	58.88 ± 6.67[a]
	PA	10	10.59 ± 6.53	50.88 ± 9.34	2.81 ± 1.02	35.72 ± 7.32[b]
Spring	SA	10	6.24 ± 6.24	64.09 ± 7.30[a]	6.89 ± 2.82	22.78 ± 4.68[a]
	PA	10	3.59 ± 3.08	37.64 ± 8.23[b]	16.76 ± 6.30	42.01 ± 7.56[b]
Summer	SA	10	0.55 ± 0.41	75.85 ± 4.26	7.36 ± 3.84	16.23 ± 4.23
	PA	10	4.60 ± 2.88	83.99 ± 3.86	2.72 ± 0.89	8.69 ± 2.19
Chiromantes dehaani						
Autumn	SA	10	0.18 ± 0.18	84.16 ± 2.96[a]	1.46 ± 0.57	14.20 ± 2.64[a]
	PA	10	0.32 ± 0.31	61.51 ± 8.21[b]	2.86 ± 0.84	35.31 ± 7.81[b]
Winter	SA	10	9.19 ± 6.28	59.05 ± 7.31	2.00 ± 0.89	29.84 ± 3.67
	PA	10	10.11 ± 9.70	55.60 ± 7.87	1.91 ± 0.56	32.33 ± 5.54
Spring	SA	10	0.71 ± 0.29	61.39 ± 6.74	3.03 ± 0.99	34.87 ± 6.92
	PA	10	5.15 ± 2.66	52.77 ± 8.22	4.16 ± 1.21	37.92 ± 8.03
Summer	SA	10	1.17 ± 0.41	83.67 ± 3.25	3.43 ± 0.96	11.74 ± 2.78
	PA	10	1.02 ± 0.47	70.15 ± 6.31	2.67 ± 0.91	26.16 ± 6.73

Table 5. *Helice tientsinensis* and *Chiromantes dehaani*. Composition of plant materials in stomach contents of the 2 most numerically abundant crab species from *Spartina alterniflora* (SA) and *Phragmites australis* (PA) monocultures. Relative abundance (mean ± SE) of each plant part is expressed as the proportional area within plant materials detected in stomach contents mounted on microscope slides. Different upper case letters (a, b) indicate significant differences between SA and PA in each season determined from *t*-tests (p < 0.05).

| Season | Vegetation | n | Relative abundance of each plant part among plant materials (%) | | | | | |
			Rhizome & root	Stem	Leaf	Flower & inflorescence	Seed	Bud
Helice tientsinensis								
Autumn	SA	10	35.55 ± 8.20[a]	9.48 ± 4.15	48.70 ± 8.47[a]	0	0	6.26 ± 6.26
	PA	10	8.10 ± 3.93[b]	12.96 ± 7.36	73.37 ± 6.60[b]	2.58 ± 1.84	2.66 ± 1.50	0.33 ± 0.33
Winter	SA	10	32.34 ± 9.73	0	61.67 ± 11.41	0	0[a]	6.00 ± 5.59
	PA	10	29.54 ± 9.59	0.61 ± 0.61	54.23 ± 8.60	0	12.99 ± 5.62[b]	2.63 ± 2.63
Spring	SA	10	19.84 ± 9.54	4.12 ± 2.05	76.04 ± 9.48	0	0	0
	PA	10	24.30 ± 6.09	2.13 ± 2.13	73.57 ± 6.78	0	0	0
Summer	SA	10	13.12 ± 4.91	12.15 ± 4.22	74.72 ± 5.62	0	0	0
	PA	10	14.70 ± 9.54	2.89 ± 1.44	82.04 ± 9.38	0.38 ± 0.38	0	0
Chiromantes dehaani								
Autumn	SA	10	0.22 ± 0.12[a]	6.30 ± 1.71	92.87 ± 1.88[a]	0	0.30 ± 0.30	0.32 ± 0.32
	PA	10	32.91 ± 9.92[b]	19.69 ± 7.09	47.14 ± 9.35[b]	0	0.27 ± 0.27	0
Winter	SA	10	26.42 ± 8.17	0	69.89 ± 8.12	0	0	3.69 ± 2.60
	PA	10	17.36 ± 6.17	7.01 ± 3.80	57.68 ± 10.07	0	7.91 ± 5.32	0
Spring	SA	10	18.05 ± 7.09[a]	6.68 ± 4.09	75.28 ± 6.94[a]	0	0	0
	PA	10	0.49 ± 0.22[b]	3.46 ± 1.52	95.04 ± 2.22[b]	0.63 ± 0.63	0.12 ± 0.12	0.25 ± 0.25
Summer	SA	10	4.01 ± 1.58	10.64 ± 3.61	85.35 ± 4.71	0	0	0
	PA	10	3.00 ± 0.99	4.36 ± 2.72	91.66 ± 2.60	0.33 ± 0.33	0.66 ± 0.66	0

autumn, *Helice tientsinensis* ate more roots in *Spartina alterniflora* stands and more leaves in *Phragmites australis* stands. In spring, *Chiromantes dehaani* ate more roots and fewer leaves in *S. alterniflora* areas than in *P. australis* areas, whereas the opposite occurred in autumn (Table 5). In winter, the crabs ate seeds of *P. australis* but not of *S. alterniflora*.

Of the producers, the exotic *Spartina alterniflora* had a significantly higher $\delta^{13}C$ value than the other primary producers, whereas *Phragmites australis* had the lowest $\delta^{13}C$ value (Table 6). Benthic microalgae had significantly lower $\delta^{15}N$ values than did the vascular plants. *Chiromantes dehaani* and *Helice tientsinensis* from *P. australis* monocultures had similar $\delta^{13}C$ values, and were significantly depleted compared with those from *S. alterniflora* patches (Fig. 3, Table 6). The $\delta^{15}N$ values of *H. tientsinensis* were generally higher than those of *C. dehaani*.

Table 6. Stable isotope $\delta^{13}C$ and $\delta^{15}N$ values of main primary producers and crabs as consumers. Data are expressed as mean ± SE. Different superscript lower case letters (a, b, c) denote significant differences between plant autotrophs; different superscript upper case letters (A, B) indicate significant differences between crab species. PA: *Phragmites australis*; SA: *Spartina alterniflora*

Sample	Sample size (n)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Producers			
Phragmites australis (PA)	4	−26.92 ± 0.23[a]	6.09 ± 0.37[a]
Spartina alterniflora (SA)	4	−12.65 ± 0.03[b]	6.02 ± 0.29[a]
Benthic microalgae (BMI)	6	−22.99 ± 0.19[c]	4.47 ± 0.22[b]
Consumers (crabs)			
Helice tientsinensis from PA	6	−21.63 ± 0.31[A]	8.25 ± 0.39[A]
Helice tientsinensis from SA	6	−17.52 ± 0.68[B]	8.04 ± 0.38[A]
Chiromantes dehaani from PA	6	−22.67 ± 0.58[A]	7.54 ± 0.21[A,B]
Chiromantes dehaani from SA	6	−16.07 ± 0.63[B]	6.96 ± 0.38[B]

DISCUSSION

Effects of plant type on crab communities

This is the first study to reveal the effects of an invasive saltmarsh plant on crab communities and relate the changes of crab distributions to their feeding habits by means of gut contents and stable isotope analyses. Our study showed that the *Spartina alterniflora* invasion has had a positive effect on borrowing crab populations in the salt marshes of the Yangtze River estuary, mainly because the 2 dominate grapsoid crabs, *Chiromantes dehaani* and *Helice tientsinensis*, preferred *S. alterniflora* over the native *Phragmites australis* communities as habitats. Other in-
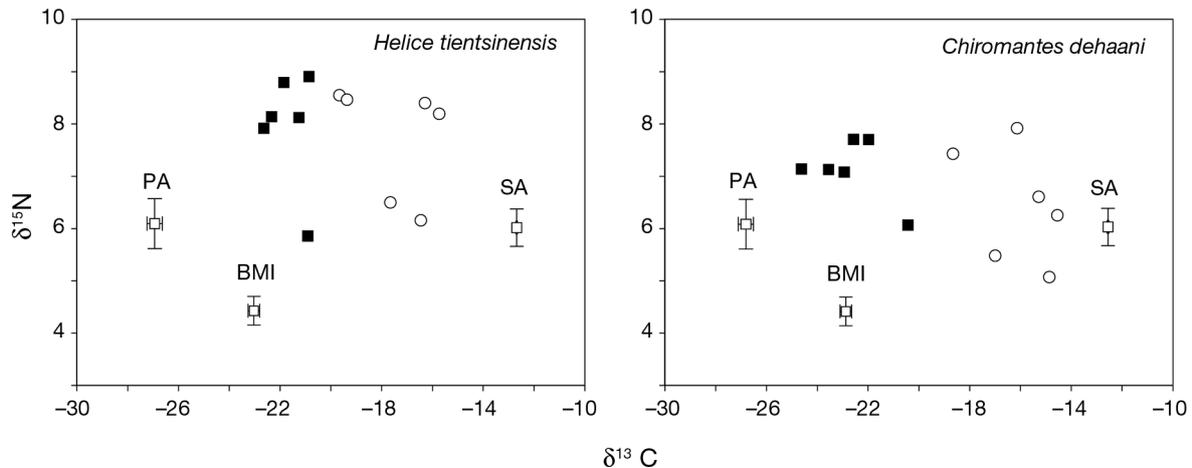
Fig. 3. *Helice tientsinensis* and *Chiromantes dehaani*. Dual isotope (δ^{13}C and δ^{15}N) plots of primary producers and crab consumers. Primary producer (□) data are shown as means ± SE, whereas crab data are shown as individual plots. (■) Crabs from *Phragmites australis* (PA) monocultures; (○) crabs from *Spartina alterniflora* (SA) monocultures. BMI: benthic microalgae

vestigations also indicated that the *S. alterniflora* communities are more favorable for crabs than are *P. australis* communities. In Delaware Bay, USA, where *P. australis* has invaded *S. alterniflora* communities, the blue crab *Callinectes sapidus* prefers *S. alterniflora* over *P. australis* habitats (Jivoff & Able 2003). Wang et al. (2008) reported that the invasive *S. alterniflora* enhanced densities of *C. dehaani* compared with the native *P. australis*, which was confirmed in this study.

Environmental factors influencing the crab distribution

Vegetation might affect crab communities through a series of physical, chemical and biological changes in the benthic systems (Nomann & Pennings 1998, Peterson et al. 2001). Our study identified sediment grain size, water content and vegetation canopy structure (e.g. stem height) as the main factors influencing the crab distributions.

Density variations in intertidal crabs were shown to be related to sediment grain size (Katrak et al. 2008, Wang et al. 2009). Seiple (1979) found that *Sesarma cinereum* habitats were characterized by sandy substrates, whereas *S. reticulatum* inhabited substrates with high silt content. Bertness et al. (2009) found that the burrow density, depth, and complexity of *S. reticulatum* were higher on peat substrate than on sand or mud substrate. The highest *Helice crassa* densities corresponded to soft and muddy substrata in New Zealand estuaries (Jones & Simons 1983). In our study area, *Chiromantes dehaani* and *H. tientsinensis* densities were higher in *Spartina alterniflora* communities, which tended to accumulate more fine-grained parti-

cles than did the adjacent *Phragmites australis* marshes.

Plant canopy characteristics such as stem height and density are important determinants of macrofauna community structures (Netto & Lana 1999). The distribution and abundance of fiddler crab *Uca pugnax* were found to be related to the density of *Spartina* root mats (Ringold 1979, Bertness & Miller 1984). In our study, *Spartina alterniflora* had higher stem density and lower height than did the native *Phragmites australis*. This implied that *S. alterniflora* may provide a more benign habitat for crabs than *P. australis*. *S. alterniflora* has 70% greater root biomass than *P. australis* (Liao et al. 2007); therefore, the belowground structure of *S. alterniflora* would also have effects on the distribution of crabs. Wu (1959) reported that *Chiromantes dehaani* prefers moist environments. The moister environment provided by *S. alterniflora* may be one of the reasons why more crabs were found in patches of this plant.

Feeding activities of the 2 dominant grapsoid crabs

The stomach fullness of *Chiromantes dehaani* and *Helice tientsinensis* from the invasive *Spartina alterniflora* and the native *Phragmites australis* communities were similar. This suggests that the crabs found similar amounts of food in communities composed of different plant species.

Plant materials were the major component in the diet of both *Chiromantes dehaani* and *Helice tientsinensis* from both *Spartina alterniflora* and *Phragmites australis* marshes. Therefore, both crabs were primarily herbivores based on their natural diets. *C. dehaani* is

generally reported to be an herbivore (Feng & Guan 1964), but it also eats juvenile crabs and can consume 80 to 85% in animal foods in laboratory feeding experiments (Feng & Guan 1964, Kneib et al. 1999). The feeding habits of *H. tientsinensis* are unknown to date. However, the congener *H. tridens* has been reported to rely mostly on plant matter (Kuroda et al. 2005); and *H. formosensis* is primarily regarded as a carnivore, consuming 75.1 to 82.5% in animal materials (Mia et al. 2001). Our field observations found that both *H. tientsinensis* and *C. dehaani* attacked other crabs, fish and crustaceans. Animal materials, including gastropods, isopods and crustaceans, were also detected in their stomachs. Therefore, these helicid and sesarmid crabs are probably omnivores, but have flexible diets depending on food availability. The present study revealed that *H. tientsinensis* and *C. dehaani* did not shift their feeding habits in marshes of different plant species, and both ingested plants as a major food category. This was confirmed by similar δ^{15}N values for *H. tientsinensis* and *C. dehaani* from different stands of plants.

Among the vascular plant materials consumed by the crabs, leaves were the major items and rhizomes/roots were next in importance in both *Spartina alterniflora* and *Phragmites australis* stands. Plant rhizomes/roots were probably a substitute for leaves. In autumn, for example, *Helice tientsinensis* consumed more leaves and fewer rhizomes/roots in *P. australis* communities than in *S. alterniflora* communities, but they consumed more rhizomes/roots and fewer leaves in *S. alterniflora* communities. In contrast, *Chiromantes dehaani* ate more rhizomes/roots and fewer leaves in *P. australis* communities in autumn, but ingested more leaves and fewer rhizomes/roots in *S. alterniflora* communities in this season. The sympatric occurrence of crabs at high densities is common in estuaries and salt marshes. The coexistence of different crab species may be achieved by intraguild predation or niche partitioning (Kuroda et al. 2005). Our study may reflect the feeding strategies of 2 grapsoid crabs, *H. tientsinensis* and *C. dehaani*, that are able to coexist by alternatively feeding on leaves and rhizomes/roots. These 2 species probably exerted different top-down effects on the plant productivity.

A number of studies have reported that animals exhibit dietary shifts between native and invaded coastal habitats. Some of these studies have shown that benthic infaunal animals do not use invasive plants as a major carbon source (Brusati & Grosholz 2007, Demopoulos et al. 2007). However, Wainright et al. (2000) reported that the mummichog *Fundulus heteroclitus* largely (73%) relied on *Phragmites australis* in exotic *P. australis*-dominated marshes. In our study, as reported previously (e.g. Quan et al. 2007), *Spartina*

alterniflora had significantly more enriched δ^{13}C values than did *P. australis*. For both *Chiromantes dehaani* and *Helice tientsinensis*, crabs from *S. alterniflora* patches were significantly more enriched in δ^{13}C values than those from *P. australis* patches. This finding suggested that the crab consumers were likely to eat vegetation materials of different plant species. Through a feeding preference experiment, *C. dehaani* was found to prefer *S. alterniflora* to *P. australis* (Wang et al. 2008). Together these results suggest that the invasive *S. alterniflora* can provide as significant a carbon source for herbivorous crabs as that provided by the native plant species.

CONCLUSION AND IMPLICATIONS

In conclusion, stands of invasive *Spartina alterniflora* supported about 42% higher crab densities than was supported in adjacent native *Phragmites australis* stands, mainly because 2 dominant grapsoid crabs, *Chiromantes dehaani* and *Helice tientsinensis*, preferred *S. alterniflora* communities. Because the plant stems of *S. alterniflora* were generally denser and lower than those of *P. australis*, *S. alterniflora* may provide more benign environmental conditions than does *P. australis*. Dietary analyses revealed that the crabs did not change their feeding habits and continued to act as herbivores in invasive vegetation, and stable isotope analyses revealed that crabs use *S. alterniflora* as an important carbon source. Levin et al. (2006) reported a relationship between diet and tolerance to invasion and hypothesized that species that can consume invasive plants are more likely to inhabit invaded sediments than those that do not shift their diet. Our study supports this hypothesis and indicates that the non-selective feeding activities of *H. tientsinensis* and *C. dehaani* might be an important explanation for why they inhabit the invasive *S. alterniflora* stands.

The presence of crab burrows affects soil aeration, soil organic matter decomposition rates and material exchange between marshes and coastal waters (Minkoff et al. 2006, Daleo et al. 2007, Xin et al. 2009). With the invasion of *Spartina alterniflora* more crabs and more burrows will possibly lead to changes in sediment dynamics of the Yangtze River estuarine marshes. Our previous studies at Chongming Dongtan indicated that the macroinfauna density tended to decrease in the invasive *S. alterniflora* communities (Chen et al. 2009). Because the presence of intertidal crabs is known to depress macrofaunal activities (Neira et al. 2006), the decreased infaunal densities in *S. alterniflora* patches may partly be related to the increased crab abundance. The marsh crab larvae are one of the important food sources for estuarine fish and

are regarded to be an essential biological export of marsh elements when released (Wooldridge & Loubser 1996, Costa et al. 2009). The enhanced crab densities at the Yangtze River estuarine salt marshes and the shifted carbon sources in their diets would possibly affect the carbon export from the marshes to the open water through the crab larvae.

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