

Tidal marshes as energy sources for commercially important nektonic organisms: stable isotope analysis

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ABSTRACT: Tidal marshes provide nursery habitats for many commercial nektonic species; thus, determining trophic linkages between tidal marshes and aquatic consumers is important for sustaining fishery production in estuarine ecosystems. We examined stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in 4 commercial nekton species (*Chelon haematocheilus*, *Synechogobius ommaturus*, *Lateolabrax maculatus* and *Exopalaemon carinicauda*) in the tidal marshes of the Yangtze River estuary, China. We estimated the frequency and range of potential contribution (0 to 100 %) from different food sources (benthic microalgae, suspended particulate organic matter, the invasive C₄ plant *Spartina alterniflora* and native C₃ plants *Phragmites australis* and *Scirpus mariqueter*) to the nektonic consumers, and then pooled the contributions for primary producers with similar isotope values (giving 3 groups: microalgae, invasive C₄ plant and native C₃ plants). Marsh vascular plants and microalgae were at the base of the food web supporting these nektonic species. For *C. haematocheilus* and *S. ommaturus*, vascular plants constituted a larger fraction of their carbon source than microalgae. *S. alterniflora* contributed more than 50 % of their total organic carbon and was more important than the native C₃ plants. For *L. maculatus* and *E. carinicauda*, intermediate $\delta^{13}\text{C}$ values precluded definitive assignment of a major carbon source. We have shown that tidal marshes provide important food sources for some dominant estuarine nektonic species, and that the exotic plant *S. alterniflora* has been incorporated into aquatic food webs of the Yangtze River estuary.

KEY WORDS: Fish · Food web · *Phragmites australis* · Plant invasion · Prawn · *Spartina alterniflora* · Yangtze River estuary · Nursery habitat

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INTRODUCTION

Tidal marshes are nursery habitats providing food and shelter for many nektonic species (Odum 1980). Though the importance of these habitats for the growth and development of nekton is well established, the degree to which indigenous food source fuels secondary production remains unclear (Dittel et al. 2006). In the past 4 decades, the relative contributions of vascular plants and algae to the nutrition of fish and invertebrates has been largely conjectural. Some studies show that the carbon derived from microalgae is largely assimilated into tidal marsh food webs (Curran et al. 1995, Wainright et al. 2000). Other studies have addressed the important role of vascular plant produc-

tion for macro-invertebrates and fishes (Peterson et al. 1985, Peterson & Fry 1987, Curran et al. 1995, Weinstein et al. 2000, Weis & Weis 2003). There is a variety of estuarine angiosperms and discrepancies exist among reports on the relative contributions of the different primary producers to the food webs (Paterson & Whitfield 1997, Wainright et al. 2000, Curran et al. 2003, Gratton & Denno 2006, Wozniak et al. 2006). It appears that the relative importance of the different sources varies with consumer species, plant species dominance and locality, and that our understanding of this variation is still limited (Deegan & Garritt 1997, Weinstein et al. 2000). Most available information is from the USA (e.g. Curran et al. 1995, Kwak & Zedler 1997, Weinstein et al. 2000, Gratton & Denno 2006,

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Levin et al. 2006, Neira et al. 2006), and the remainder is from France (Créach et al. 1997, Riera et al. 1999, Laffaille et al. 2005), the UK (Wozniak et al. 2006), Australia (Melville & Connolly 2003), South Africa (Schlacher & Wooldridge 1996, Paterson & Whitfield 1997), India (Bouillon et al. 2002) and Japan (Kurata et al. 2001). We know little about the roles of marshes in supporting aquatic food webs in other countries that are rich in tidal marsh habitats, such as China.

The Yangtze River is the largest river in China and third largest in the world. It carries about $928 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$ of water and $468 \times 10^6 \text{ t yr}^{-1}$ of fine sediments into the East China Sea (Chen et al. 1986). More than half of the sediments from the river are deposited in the estuarine area where there are extensive tidal wetlands (Chen et al. 1986). The total area of the tidal wetlands is approximately 800 km^2 and the accretion rate is 15 to $20 \text{ km}^2 \text{ yr}^{-1}$. About a third of the tidal wetland area is covered by vegetation (Yang 1998). The large area of tidal marsh bearing primary producers may contribute significantly to secondary production in the Yangtze River estuary. However, in the past 2 decades, there has been extensive disturbance by reclamation, over-fishing and exotic plant invasions, all of which seriously affect the structure and function of tidal marsh ecosystem in the estuary (Zhao et al. 2004, Chen et al. 2007). Therefore, an understanding of trophic relationships between primary producers and estuarine consumers is essential for effective restoration, management and conservation of tidal marsh habitats in this area.

In this study, we examined food sources of 4 economically important nektonic species (*Chelon haematocheilus*, *Synechogobius ommaturus*, *Lateolabrax maculatus* and *Exopalaemon carinicauda*) in Yangtze River estuary tidal salt marshes using stable isotopes of carbon and nitrogen. According to our pilot investigation, *C. haematocheilus*, *S. ommaturus* and *L. maculatus* are the 3 dominant fish species, and *E. carinicauda* is the dominant decapod within the nekton of Yangtze River estuary tidal marshes (Jin et al. 2007). Asian freshwater goby *S. ommaturus* is a resident fish in the tidal wetland of this estuary and spends its entire life within the shallow water zone. So-iny mullet *C. haematochela*, Spotted sea bass *L. maculatus* and ridgetail prawn *E. carinicauda* stay in the tidal marshes and shallow sub-tidal areas for most of their life histories, and live in deeper coastal waters for a short period during the winter. On flood tides, the 4 nektonic species often enter into the surface marsh and creek system for feeding and shelter. *C. haematochela* is omnivorous and feeds mainly on benthic algae, plant detritus and small fauna (copepods and polychaetes). *L. maculatus* and *S. ommaturus* are carnivores, and their major prey items are small individuals of fish,

prawn and zooplankton. *E. carinicauda* is by far the most widespread white prawn in coastal regions of China; it feeds on organic detritus and zooplankton.

The overall aim of the present study was to assess (using stable isotope techniques) the energy contribution of tidal marshes to secondary production (by nektonic animals) in Yangtze River estuarine food webs. Our specific objectives were to assess the relative importances of (1) vascular plants versus microalgae and (2) native C₃ plants versus an exotic C₄ plant as food sources for nektonic animal species. In addition, we also tested size-dependent effects on the stable isotopic signatures for each nektonic species.

MATERIALS AND METHODS

Study site. The study was carried out on the Dongtan and Jiuduansha marshes of the Yangtze River estuary in China (Fig. 1). These 2 marshes account for 67.0% of the total Yangtze River estuary marsh area (unpublished document from Shanghai Water Authority 2005). There are few plant species in the vegetation of these marshes. The dominant natives are *Scirpus mariqueter* and *Phragmites australis*, both of which have C₃ metabolism. The tidal marshes are now heavily infested with the exotic C₄ plant *Spartina alterniflora*, which makes up 21.4% of total vegetation coverage. Seagrasses are virtually absent in this area and macroalgae were not found during the study. The climate is characterized by an annual precipitation of 1124 mm and a mean temperature of 15.7°C; salinity varied from 1% to 20‰.

Sample collection and processing. Samples of 3 marsh vascular plants (*Phragmites australis*, *Scirpus mariqueter* and *Spartina alterniflora*) were collected from 6 randomly selected stations at Dongtan and Jiuduansha in July and October 2005 (Fig. 1). Leaves of 10 randomly selected plants from 6 sampling stations were pooled to represent one sample for each species. All leaf samples were cleaned with distilled water several times to remove attached detritus, oven dried at 60°C for approximately 48 h to constant weight, and then ground to fine powder.

Phytoplankton (as suspended particulate organic matter, POM) samples were collected during flood tides in tidal creeks or on mud flats. At each of 5 stations in July and 4 stations in October, water samples of 400 l were pre-filtered through a bolting-silk net with a mesh size of 180 µm to remove zooplankton. POM was collected with a plankton net of 35 µm mesh size. The residues in the plankton net were rinsed onto pre-combusted (450°C for 6 h) Whatman GF/F filters. The filters were oven dried at 60°C for at least 48 h and ground to fine powder.

Benthic microalgae (BMI) samples were collected on ebb tide from both vegetated and unvegetated (muddy flat or creek bank) areas. Samples were obtained using a modified version of Riera et al.'s (1999) technique. Commercial sand was pre-soaked in 10% hydrochloric acid for 24 h, rinsed in distilled water and combusted at 450°C for 4 h to remove carbonates and organic matter. On the marsh sites, the sediments were covered with a 5 mm-thick layer of pre-combusted sand, a piece of 63 µm nylon mesh, and another 5 mm-thick layer of pre-combusted sand. During the *in situ* incubations, moisture in treated sediments was maintained with 0.2 µm pre-filtered creekwater. After 3 h, the sand surface was scraped off and mixed with pre-filtered creekwater. The water-sand mixtures were shaken and the supernatants were filtered through pre-combusted Whatman GF/F filters. The filters were oven dried to constant weight at 60°C and ground to fine powder.

Chelon haematocheilus, *Synechogobius ommaturus*, *Lateolabrax maculatus* and *Exopalaemon carinicauda* were captured from tidal creeks extending into stands

of the 3 plant species using fyke nets, or the animals were collected with gill nets from bare mud flats (Table 1). All nekton samples from 6 sampling stations were frozen and returned to the laboratory until further processing. Before dissecting out tissues, we measured body length of the animals. For large fish, approximately equal weights of dorsal white muscle tissue were dissected out from 5 individuals of similar size and pooled as a single sample. For small fish, 10 individuals of a similar size were selected. After the head, tail and viscera were removed, the remainder of the body was retained for isotope analysis as a composite sample. For prawns, the entire cuticle and head were removed, and the remaining tissues of about 20 individuals of similar size were collected as a composite sample for isotope analysis. All fish and prawn tissue samples were oven dried to constant weight at 60°C and ground to fine powder.

All samples (POM, BMI, plant and animal tissues) were treated with 1 N hydrochloric acid to eliminate carbonates using a drop-by-drop technique (Jacob et

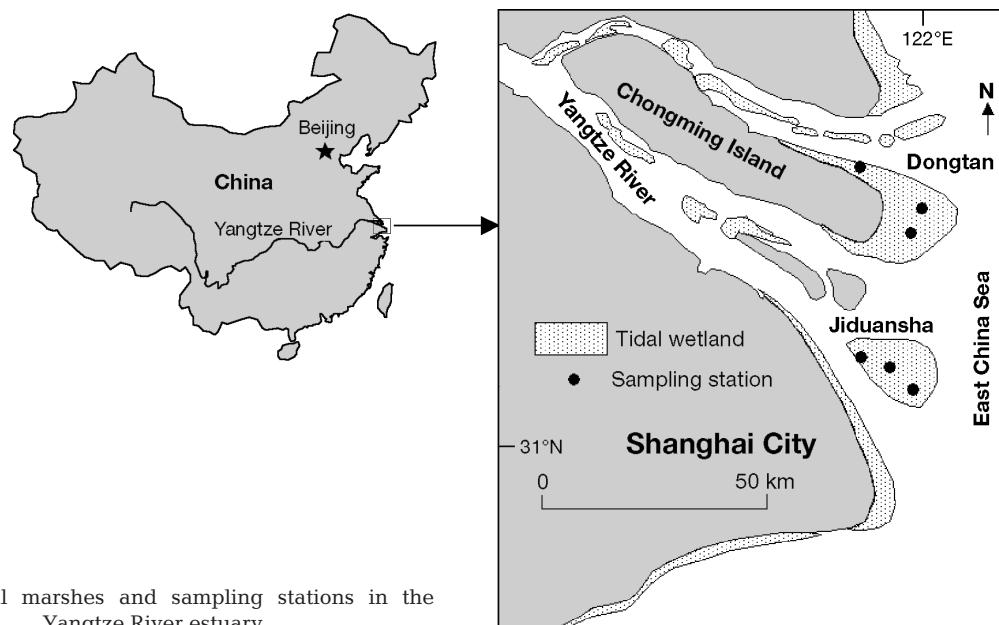


Fig. 1. Tidal marshes and sampling stations in the Yangtze River estuary

Table 1. List of nektonic species, feeding habits, sample sizes (n) and body size ranges (mm)

Nekton	Common name	Order: Family	Feeding type	n	Body size range
<i>Chelon haematocheilus</i>	So-iny mullet	Perciformes: Mugilidae	Omnivore	22	17–315
<i>Synechogobius ommaturus</i>	Asian freshwater goby	Perciformes: Gobiidae	Carnivore	16	50–207
<i>Lateolabrax maculatus</i>	Spotted sea bass	Perciformes: Lateolabracidae	Carnivore	11	70–280
<i>Exopalaemon carinicauda</i>	Ridgetail prawn	Decapoda: Palaemonidae	Omnivore	15	31–83

al. 2005). The acidified samples were oven dried at 60°C and then ground to fine powder. All samples were retained in desiccators prior to isotope analysis.

Stable isotope measurement. Carbon and nitrogen stable isotope ratios were measured on an isotope ratio mass spectrometer (Delta-plus IRMS with Flash EA 1112 Series, Thermo Finnigan) at the Stable Isotope Laboratory for Ecological and Environmental Research, Institute of Botany, Chinese Academy of Sciences, China. Urea and glycine were analyzed as accuracy and precision standards for isotopic ratios. Stable isotope abundance is expressed in δ notation as ‰ difference from an international standard (Vienna Pee Dee Belemnite for carbon, air for nitrogen), which measures depletion or enrichment of the heavy isotope relative to the light isotope in the following relationship:

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

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

Statistical analysis and mixing model. One-way ANOVA (followed by Turkey's HSD post hoc test) was applied to examine the differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among primary producers (*Phragmites australis*, *Scirpus mariqueter*, *Spartina alterniflora*, POM and BMI). To meet assumptions of ANOVA, the stable isotope data were log transformed prior to analysis. Linear regression analysis was carried out to examine the relationship between body length and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values of 4 nektonic species.

A multiple source linear mixing model was used to quantify the food source contribution to nekton. Mean $\delta^{13}\text{C}$ values of 5 primary producers and 4 consumers were used in the IsoSource mixing model (Phillips & Gregg 2003) to calculate feasible solutions that may explain consumer signatures. This model examines all possible combinations of each source's potential contribution (0 to 100 %) in small increments (here 2%). Combinations that summed to within 0.1 ‰ of the consumer signature were considered feasible solutions. The results from the IsoSource model are reported as the contribution of feasible solutions for each autotroph.

For more constrained and interpretable results, an *a posteriori* aggregation method was applied to pool the contributions of primary producers with similar $\delta^{13}\text{C}$ values (Phillips et al. 2005). For each individual solution (isotopically feasible combination of source contributions summing to 100 %), sources were aggregated into 3 logical groups, i.e. C_3 vascular plant (*Phragmites australis* and *Scirpus mariqueter*), C_4 vascular plant (*Spartina alterniflora*) and microalgae (POM and BMI). The IsoSource output file was read into Excel software, where new variables were created, viz. the sums of sources to be combined (e.g. microalgae = BMI + POM;

C_3 plant = *P. australis* + *S. mariqueter*). Possible combinations of the 3 aggregated logical groups' contributions were then re-calculated. Isotope data are presented throughout as means \pm SE.

RESULTS

Stable isotope values of primary producers

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of 5 primary producers are listed in Table 2. *Spartina alterniflora* had a significantly more enriched $\delta^{13}\text{C}$ value (-12.64 ± 0.04 ‰) than other primary producers (1-way ANOVA, $p < 0.05$, Table 2). *Phragmites australis* and *Scirpus mariqueter* were the most depleted in $\delta^{13}\text{C}$, but were not significantly different from one another (1-way ANOVA, $p > 0.05$, Table 2). The microalgae (BMI and POM) had intermediate $\delta^{13}\text{C}$ values, with POM more depleted in $\delta^{13}\text{C}$ (-22.80 ± 0.28 ‰) than BMI (-20.02 ± 0.07 ‰) (1-way ANOVA, $p < 0.05$, Table 2). The $\delta^{15}\text{N}$ values of 5 primary producers ranged from 4.01 to 6.07 ‰, and there were no significant differences among them (1-way ANOVA, $p > 0.05$, Table 2).

Stable isotope values of nekton

Dual isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for *Chelon haematocheilus*, *Synechogobius ommaturus*, *Lateolabrax maculatus* and *Exopalaemon carinicauda* are plotted in Fig. 2. The $\delta^{13}\text{C}$ values of these species ranged from -22 ‰ to -12 ‰ and lay in the enriched half of the range for the autotrophs. *C. haematochiela* and *S. ommaturus* ($\delta^{13}\text{C} -16.23 \pm 0.37$ ‰ and -16.20 ± 0.30 ‰, respectively) had more enriched $\delta^{13}\text{C}$ values than *L. maculatus* and *E. carinicauda* (-18.29 ± 0.49 ‰ and -18.36 ± 0.38 ‰, respectively). The 4 animal species varied greatly in natural abundance of $\delta^{15}\text{N}$ (7.00 ‰ to 14.78 ‰). Mean $\delta^{15}\text{N}$ isotopic values were 8.85 ± 0.22 ‰, 10.34 ± 0.21 ‰, 12.48 ± 0.21 ‰ and

Table 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary producers from the Yangtze River estuary tidal marshes. Data are mean δ values \pm SE and sample size (n). BMI: benthic microalgae; POM: suspended particulate organic matter. Different superscript letters denote significant differences between autotrophs at $p < 0.05$ (Tukey's HSD)

Primary producer	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
<i>Phragmites australis</i>	$-27.12 \pm 0.19^{\text{a}}$	$6.06 \pm 0.52^{\text{a}}$	3
<i>Scirpus mariqueter</i>	$-27.73 \pm 0.35^{\text{a}}$	$5.04 \pm 0.20^{\text{a}}$	4
<i>Spartina alterniflora</i>	$-12.64 \pm 0.04^{\text{d}}$	$6.07 \pm 0.41^{\text{a}}$	3
BMI	$-20.02 \pm 0.07^{\text{c}}$	$4.01 \pm 0.54^{\text{a}}$	3
POM	$-22.80 \pm 0.28^{\text{b}}$	$5.78 \pm 0.77^{\text{a}}$	9

$11.82 \pm 0.28\text{‰}$ for *C. haematochIELA*, *E. carincauda*, *S. ommaturus* and *L. maculatus*, respectively. The consumers were more enriched in $\delta^{15}\text{N}$ than primary producers by a factor ranging from 3.35 to 7.08‰. Given a presumptive +3‰ trophic shift in N assimilation, our results indicate that the nekton species fed approximately 1 to 2 trophic levels above primary producers.

Food source contributions

The ranges of feasible contributions for each primary producer to 4 consumers are shown in Fig. 3. The median contributions of *Spartina alterniflora* were higher than those of POM, BMI, *Phragmites australis* and *Scirpus mariquerter*. Although the median contributions of POM and BMI were lower than those of *S. alterniflora*, the range of their feasible contributions was very broad.

In order to define food source contributions more accurately, we made an *a posteriori* aggregation of autotrophs to show the combined contributions of 3 logical groups including microalgae (POM and BMI), C₃ (*Scirpus mariquerter* and *Phragmites australis*) and

C₄ plants (*Spartina alterniflora*) (Fig. 4). The contributions of *S. alterniflora* were 66% (56–76%) and 68% (52–76%) to *Chelon haematochIELA* and *Synechogobius ommaturus*, respectively (Fig. 4A,B). For these animals, at least half of organic carbon in their tissues was derived from *S. alterniflora*. The contributions of microalgae were 22% (0–44%) and 20% (0–48%) to *C. haematochIELA* and *S. ommaturus*, respectively. The contributions of C₃ plants were 12% (0–24%) to both nektonic species.

For the other 2 consumers *Lateolabrax maculatus* and *Exopalaemon carincauda*, the ranges of feasible contribution of 3 autotrophic groups were very broad and overlapped each other (Fig. 4C,D). Therefore, it was not possible to determine with certainty the major carbon sources assimilated by these species. The contributions of *Spartina alterniflora* were 48% (26–62%) and 48% (24–62%) to *L. maculatus* and *E. carincauda*, respectively, suggesting that at least 20% of organic carbon in these 2 animals was derived from *S. alterniflora*. Microalgae contributed 32% (0–72%) and 34% (0–76%) to *L. maculatus* and *E. carincauda*, respectively, while C₃ plants contributed 18% (0–38%) and 20% (0–38%), respectively.

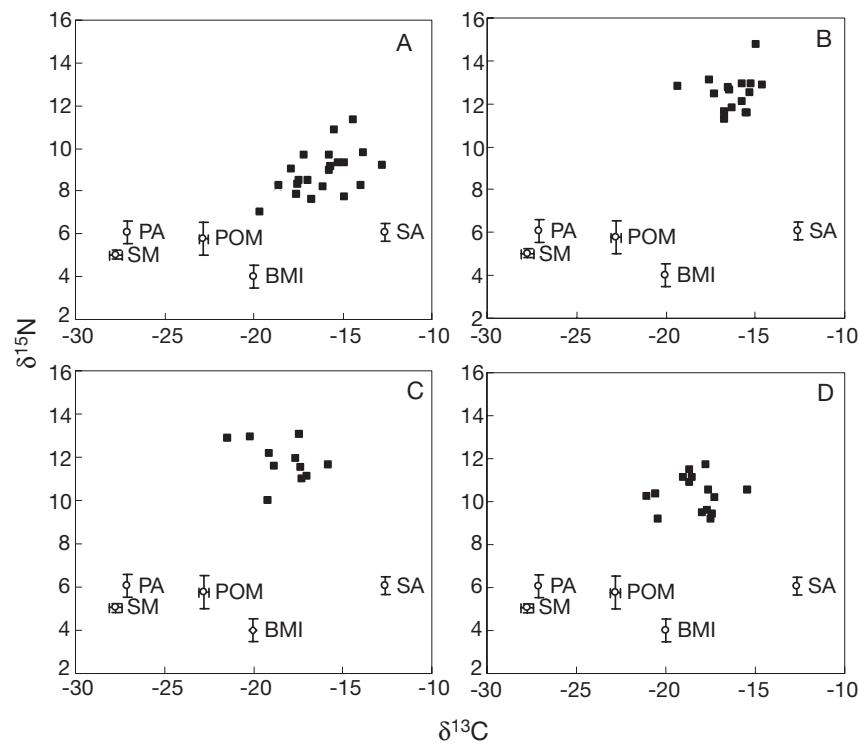


Fig. 2. Dual isotope plots of natural $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures for primary producers (O) and nektonic animals (■) from Yangtze River estuary tidal marshes. Primary producer data are means \pm SE, while animal data are plots of individual samples. (A) So-iny mullet *Chelon haematochIELA*; (B) Asian freshwater goby *Synechogobius ommaturus*; (C) spotted sea bass *Lateolabrax maculatus*; (D) ridgetail prawn *Exopalaemon carinicaud*. Primary producers are *Phragmites australis* (PA), *Scirpus mariquerter* (SM), *Spartina alterniflora* (SA), suspended particulate organic matter (POM) and benthic microalgae (BMI). Horizontal error bars for PA, SA and BMI do not extend beyond symbols

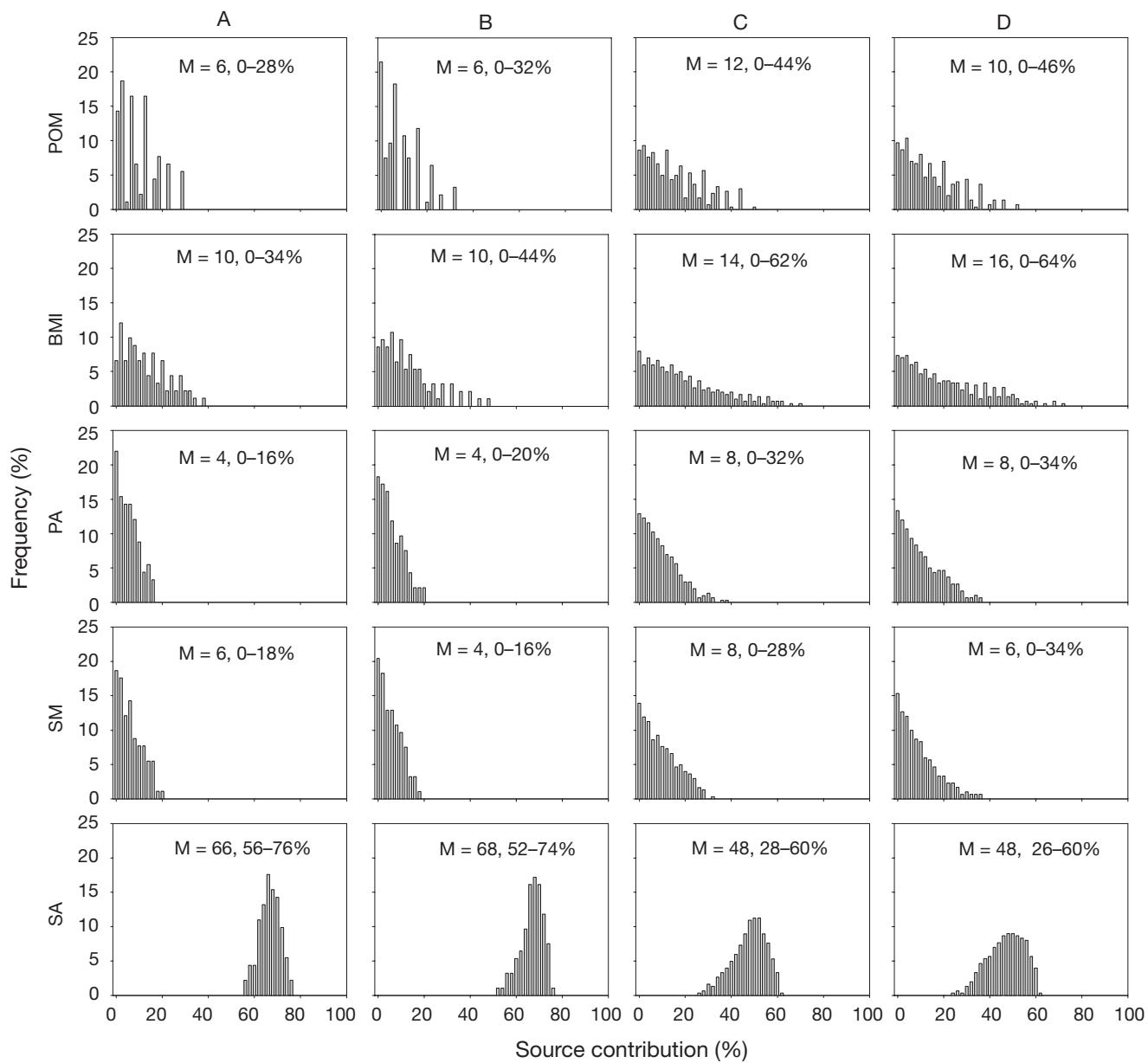


Fig. 3. Frequency distributions of feasible contributions of 5 primary producers to the consumers based on $\delta^{13}\text{C}$ values. M: median; ranges are 1 and 99 percentile values. (A) So-iny mullet *Chelon haematochIELA*; (B) Asian freshwater goby *Synechogobius ommaturus*; (C) spotted sea bass *Lateolabrax maculatus*; (D) ridgetail prawn *Exopalaemon carinicauda*. Primary producers are *Phragmites australis* (PA), *Scirpus mariqueter* (SM), *Spartina alterniflora* (SA), suspended particulate organic matter (POM) and benthic microalgae (BMI)

Size-dependent isotopic values

Regression analysis of body length and stable isotopic values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was used to determine whether or not there were any ontogenetic effects on the stable isotope signatures of nektonic species (Fig. 5). There was a significant positive relationship between body length and stable isotopic values of $\delta^{13}\text{C}$

(Fig. 5A, $p < 0.01$, $n = 22$) and $\delta^{15}\text{N}$ (Fig. 5B, $p < 0.05$, $n = 22$) for *Chelon haematochIELA*. Generally, smaller *C. haematochIELA* individuals had lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than larger individuals. For *Lateolabrax maculatus*, there was no significant relationship between body length and $\delta^{13}\text{C}$ values (Fig. 5E, $p > 0.05$, $n = 11$), while $\delta^{15}\text{N}$ became more enriched as animals increased in size (Fig. 5F, $p < 0.01$, $n = 11$). There were no

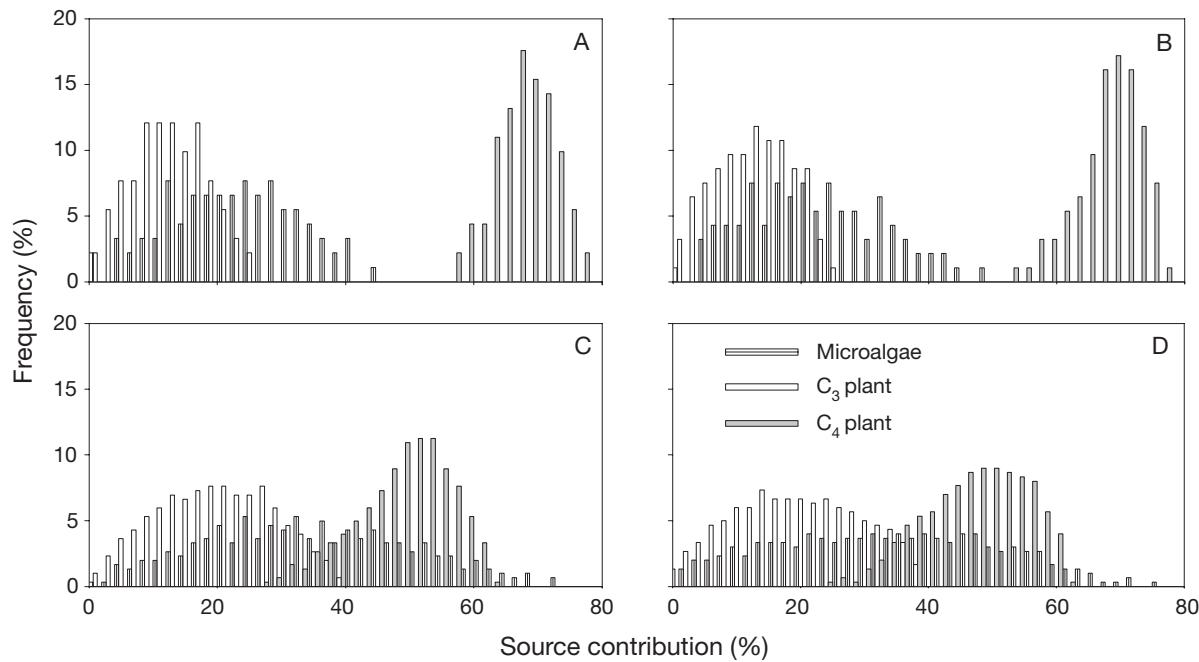


Fig. 4. Frequency distributions of combined contributions from 3 logical autotroph groups (native C_3 plant, exotic C_4 plant and microalgae) to nektonic consumers using an *a posteriori* aggregation method. (A) So-iny mullet *Chelon haematochela*; (B) Asian freshwater goby *Synechogobius ommaturus*; (C) spotted sea bass *Lateolabrax maculatus*; (D) ridgetail prawn *Exopalaemon carinicauda*

significant relationships between body length and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for *Synechogobius ommaturus* (Fig. 5C,D, $p > 0.05$, $n = 16$) or *Exopalaemon carinicauda* (Fig. 5G,H, $p > 0.05$, $n = 15$).

DISCUSSION

Autotroph isotope signatures

Stable isotope signatures of $\delta^{13}\text{C}$ for the marsh vascular plants *Spartina alterniflora* and *Phragmites australis* were similar to those reported in many previous studies (e.g. Peterson et al. 1985, Currin et al. 1995, 2003, Riera et al. 1999, Cheng et al. 2006). The stable carbon isotope signature of *Scirpus mariquerter* ($-27.73 \pm 0.35\text{\textperthousand}$) was close to that reported by Cheng et al. (2006). The stable isotope signature of $\delta^{13}\text{C}$ for BMI ($-20.02 \pm 0.07\text{\textperthousand}$) was similar to the most depleted cases reported in the literature (Peterson et al. 1985, Kwak & Zedler 1997). The $\delta^{13}\text{C}$ values of POM ($-22.80 \pm 0.28\text{\textperthousand}$) fell within the range of those reported from previous studies and were comparable to those reported by Peterson et al. (1985) and Riera et al. (1999). These 5 primary producers had similar $\delta^{15}\text{N}$ values, which may be related to the supply and amount of substrate nitrogen in the habitat studied (Peterson & Fry 1987).

Since *Phragmites australis* and *Scirpus mariquerter* had similar stable carbon isotopic values, it was impossible to distinguish their respective contributions to nekton. It was not our intention to separate these 2 native C_3 vascular plants. Moreover, the relative importance of BMI and POM in fueling food webs was not well resolved in our study because the difference in their $\delta^{13}\text{C}$ values was relatively small. Therefore, emphasis was given to the combined contribution of BMI and POM in the consumers' diets.

Relative contributions of marsh vascular plants and microalgae

There is an ongoing debate as to the relative importance of marsh vascular plants and microalgae to estuarine nektonic species (Currin et al. 1995, Paterson & Whitfield 1997, Bouillon et al. 2002). We showed that marsh vascular plants and microalgae were the bases of the food web supporting nekton, while their relative importance depended on the species of consumer. Litvin & Weinstein (2003) pointed out that species that are pelagic consumers had proportionally greater contributions in their diet from phytoplankton, whereas benthic species depended more on macrophyte detritus and benthic microalgae. Deegan & Garritt (1997)

also showed that benthic fauna has a greater reliance on *Spartina* spp. detritus and benthic microalgae than pelagic species. We found that >50% organic carbon of the 2 benthic fishes *Chelon haematocheilus* and *Synechogobius ommaturus* was derived from marsh vascular plants. This result demonstrates that marsh vascular plants were slightly more important than

microalgae as carbon sources for these 2 consumer species. However, it is rather difficult to determine the major carbon source for the other 2 consumers *Lateolabrax maculatus* and *Exopalaemon carinicauda* due to their intermediate $\delta^{13}\text{C}$ values. Both microalgae and marsh vascular plants are possible major carbon sources for these species.

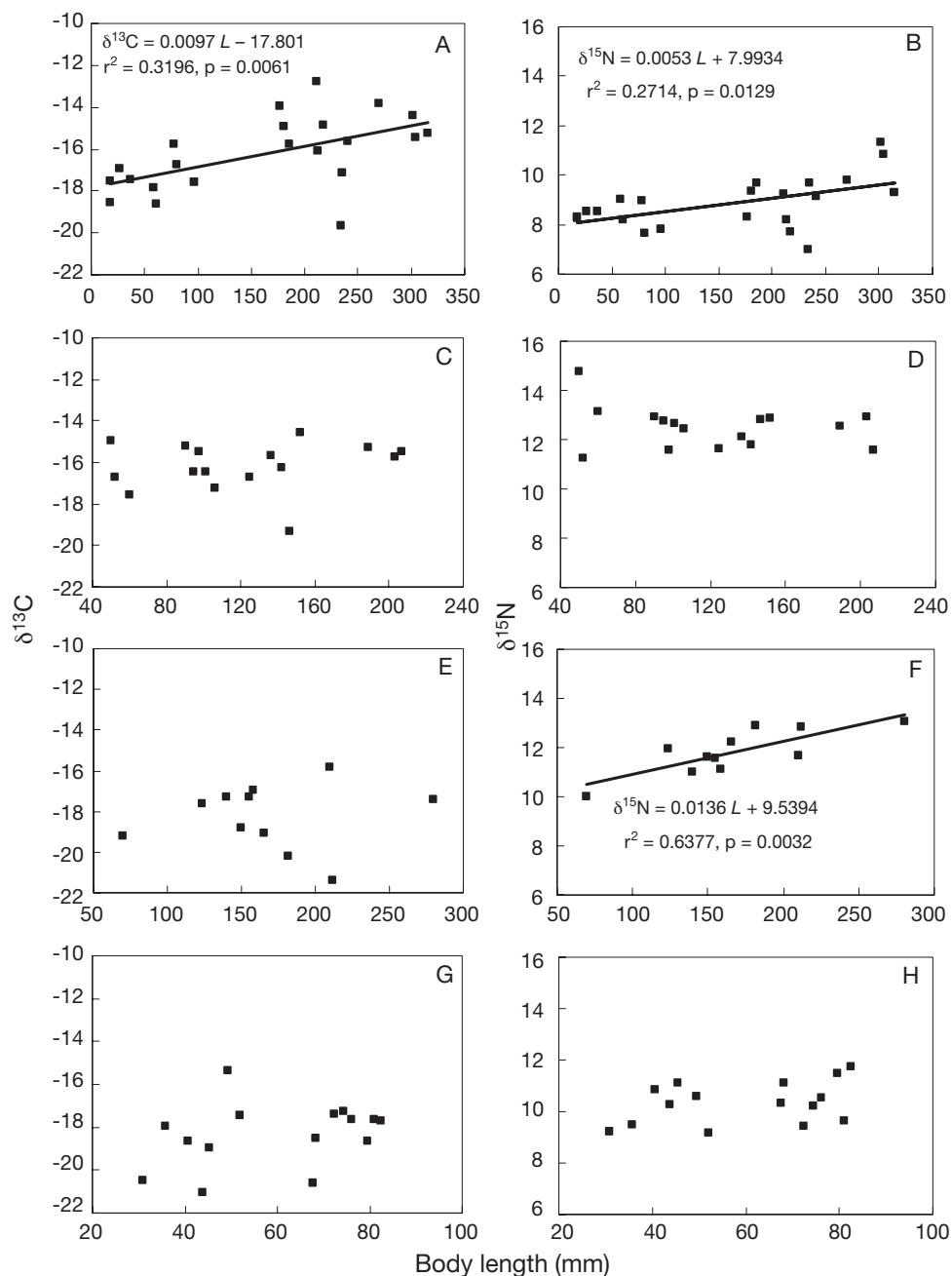


Fig. 5. Individual size (body length L) versus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for 4 consumer species. Linear regression analysis was carried out to examine the relationship between body length and each of the isotopes. (A,B) So-iny mullet *Chelon haematocheilus*; (C,D) Asian freshwater goby *Synechogobius ommaturus*; (E,F) spotted sea bass *Lateolabrax maculatus*; (G,H) ridgetail prawn *Exopalaemon carinicauda*

Relative contributions of C₄ and C₃ plants

In recent years, the ecological consequences of marsh plant invasions have been extensively studied in relation to plant interspecific relationships, local biodiversity changes, habitat degradation and biogeochemistry process alterations (Weis & Weis 2003, Levin et al. 2006). However, rather less information on the trophic contribution of exotic plants has been available until recently. Wainright et al. (2000) found that in native *Spartina alterniflora*-dominated marshes, this cordgrass species supported ca. 39% of mummichog *Fundulus heteroclitus* production, while in invasive *Phragmites australis*-dominated marshes, about 73% of mummichog production is based upon this reed. Weinstein et al. (2000) and Currin et al. (2003) have also shown that the invasion of *P. australis* significantly changed the aquatic food web supporting *F. heteroclitus* production. Levin et al. (2006) have examined the trophic consequences of an invasion by a *Spartina* hybrid into the bare mudflats of San Francisco Bay (USA), and found that the invaded system shifted from an algae-based to a detritus-based food web. Gratton & Denno (2006) suggest that trophic interactions of arthropods in native *S. alterniflora* marshes are characterized by reliance on *S. alterniflora* as a basal resource; however, arthropods in invasive *P. australis*-dominated marshes depend on detritus/algae as basal resources rather than the invading reed. We found that in the Yangtze River estuarine marshes where *S. alterniflora* and native C₃ plants were co-dominant, *S. alterniflora* was the most important food source for *Chelon haematocheilus* and *Synechogobius ommaturus*, with C₃ native plants being utilized only as a minor food source. Like other studies (Wainright et al. 2000, Weinstein et al. 2000, Currin et al. 2003), our results indicate that the exotic plant can be incorporated into aquatic food webs supporting nektonic production.

There are 3 possible reasons for the apparent preferential utilization of the *Spartina alterniflora* by *Chelon haematocheilus* and *Synechogobius ommaturus*. First, the aboveground litter biomass of *S. alterniflora* is much greater than those of *Phragmites australis* and *Scirpus mariquerter* in the Yangtze River estuarine marshes (Liao 2007), thus there is likely a much greater proportion of macrophyte detritus derived from *S. alterniflora* than from the natives. Second, *S. alterniflora* detritus is of higher nutritional quality than detritus from *P. australis* and *S. mariquerter*, or at least of quality equivalent to the latter at some stages (Weis & Weis 2003, Liao 2007). Hence, detritus of *S. alterniflora* may be more readily incorporated into the secondary production. Third, some native consumers may prefer exotic plants, as suggested by the biotic resistance hypothesis (Elton 1958). Parker and Hay (2005) found

that a diverse group of native herbivores generally prefer exotic to native plants in both freshwater and terrestrial ecosystems, suggesting that native generalists may provide biotic resistance to plant invasions. This hypothesis may hold true not only for herbivores but also for some detritivorous species and high trophic level consumers.

For *Lateolabrax maculatus* and *Exopalaemon carinicauda*, we can not discern the relative importance of *Spartina alterniflora* versus native C₃ macrophytes.

Age effects on stable isotopic values

Relationships between age (body length) and stable isotopic signatures have been studied in estuarine and/or coastal fishes (e.g. Currin et al. 2003, Melville & Connolly 2003, Litvin & Weinstein 2004, Rooker et al. 2006), shrimps (Chong et al. 2001) and crabs (Dittel et al. 2006). In some cases there were no significant relationships (Chong et al. 2001); however, other studies have found that large individuals are more enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than small ones, suggesting a gradual shift in dietary origin with increasing body size (Dittel et al. 2006), or show a significantly positive correlation between $\delta^{15}\text{N}$ values and body length, despite the lack of a correlation between $\delta^{13}\text{C}$ values and body length (e.g. Currin et al. 2003, Melville & Connolly 2003, Rooker et al. 2006). We demonstrated that all 3 correlations between body length and stable isotopic signatures existed among the different animal species considered. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values became more enriched with increasing body size in *Chelon haematocheilus*. For *Lateolabrax maculatus*, $\delta^{15}\text{N}$ was more enriched in larger individuals while $\delta^{13}\text{C}$ values remained unchanged. No significant correlation was found between body size and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for *Synechogobius ommaturus* and *Exopalaemon carinicauda*.

The significant changes in stable isotopic signatures with increasing size (age) are often attributable to ontogenetic changes in animals (Currin et al. 2003, Rooker et al. 2006). In the case of mummichog *Fundulus heteroclitus*, Currin et al. (2003) suggest that smaller individuals appear to be cleaner eaters than larger fish and are capable of picking off microalgal grazers such as copepods and polychaetes, while larger fish not only ingest more detrital material, but may also ingest more subsurface deposit-feeders which use detritus to a great extent. These relationships with body size may be applicable to *Chelon haematocheilus* in the present study. However, it has been proposed that differential metabolic fractionation of nitrogen with age also plays roles in the correlations between length and $\delta^{15}\text{N}$ values, especially when a

significant correlation between body length and $\delta^{13}\text{C}$ values is absent (Melville & Connolly 2003). Thus, the differential metabolic fractionation of nitrogen with age is highly possible for *Lateolabrax maculatus* in our study. The relatively small samples for a given size in our study may also account partially for the lack of significant differences in isotope ratios with size; nevertheless, we agree with Melville & Connolly (2003) that the isotope-based interpretations of diet should be limited to individuals of similar size to avoid any potential confounding effects, particularly if different size classes dominate at different locations.

Implications and concluding remarks

The export of organic materials from tidal marshes into estuaries and coastal waters forms the basis for Odum's (1980) outwelling hypothesis. This hypothesis emphasizes the importance of marsh macrophyte production export for utilization in open estuarine food webs. However, the role that transient nekton species play in transporting energy in and off tidal marshes has been neglected by the majority of flux studies (Paterson & Whitfield 1997). Many recent studies indicate that additional export via juvenile nekton is highly possible (Litvin & Weinstein 2004). In the Yangtze River estuary, *Chelon haematocheilus*, *Synechogobius ommaturus* and *Exopalaemon carinicauda* are major prey species for many nearshore carnivorous consumers living in the estuary and coastal areas. Moreover, *C. haematocheilus*, *Lateolabrax maculatus* and *E. carinicauda* move into deeper waters during their life cycles. Since marsh plants were identified as a major organic matter source for dominant nektonic species in this study, we conclude that the tidal marshes in the Yangtze River estuary are important as energy exporters to coastal and nearshore waters.

Determining the importance of marsh grasses for secondary production in estuaries is critical because of the intense human development pressures on coastal ecosystems (Peterson & Fry 1987). In the Yangtze River estuary, such pressure is especially prominent because of the high human population density, rapid urban expansion and economic development in Shanghai. Since 1949, about 750 km² of tidal marsh in the Yangtze River estuary have been reclaimed (Yang 1998). We show here the importance of tidal marshes in providing trophic support for some dominant fishery species. Therefore, it is essential in future wetland reclamations to consider the roles of these habitats in sustaining a huge secondary production.

Whether invaded marshes are functionally equivalent to un-invaded marshes is a hotly-debated issue (Weis & Weis 2003). Gratton & Denno (2006) studied

the effects of *Phragmites australis* invasion on arthropod food web in the Alloway Creek watershed, USA, and demonstrated that the invasive species was not functionally incorporated into the local food web. In our study, the importance of invasive *Spartina alterniflora* exceeded that of the native plants (*Phragmites australis* and *Scirpus mariqueter*) at least in supporting *Chelon haematocheilus* and *Synechogobius ommaturus* production in the Yangtze River estuary. Other studies also indicate that exotic plants provide nutrition for local consumers (Wainright et al. 2000, Weinstein et al. 2000, Currin et al. 2003). More studies are necessary to further examine the nutrient linkage between invasive plants and a spectrum of consumers in diverse ecosystems. Furthermore, changes in local trophic dynamics caused by plant invasions should be taken into consideration when implementing management and restoration strategies.

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LITERATURE CITED

- Bouillon S, Koedam N, Raman AV, Dehairs F (2002) Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. *Oecologia* 130:441–448
- Chen H, Li B, Hu J, Chen J, Wu J (2007) Effects of *Spartina alterniflora* invasion on benthic nematode communities in the Yangtze Estuary. *Mar Ecol Prog Ser* 336:99–110
- Chen JY, Yang QL, Zhao CY (1986) Report of the Shanghai coastal comprehensive investigation. Shanghai Scientific & Technological Publishers, Shanghai
- Cheng XL, Luo YQ, Chen JQ, Lin GH, Chen JK, Li B (2006) Short-term C₄ plant *Spartina alterniflora* invasions change the soil carbon in C₃ plant-dominated tidal wetlands on a growing estuarine island. *Soil Biol Biochem* 38:3380–3386
- Chong VC, Low CB, Ichikawa T (2001) Contribution of mangrove detritus to juvenile prawn nutrition: a dual stable isotope study in a Malaysian mangrove forest. *Mar Biol* 138:77–86
- Créach V, Schrickeea MT, Bertru G, Mariotti A (1997) Stable isotopes and gut analyses to determine feeding relationships in saltmarsh macroconsumers. *Estuar Coast Shelf Sci* 44:599–611
- Currin CA, Newell SY, Paerl HW (1995) The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Mar Ecol Prog Ser* 121:99–106
- Currin CA, Wainright SC, Able KW, Weinstein MP, Fuller CM (2003) Determination of food web support and trophic position of the mummichog, *Fundulus heteroclitus* in New Jersey smooth cordgrass (*Spartina alterniflora*), common reed (*Phragmites australis*), and restored salt marshes. *Estuaries* 26:495–510
- Deegan LA, Garritt RH (1997) Evidence for spatial variability in estuarine food webs. *Mar Ecol Prog Ser* 147:31–47

- Dittel AI, Epifanio CE, Fogel ML (2006) Trophic relationships of juvenile blue crabs (*Callinectes sapidus*) in estuarine habitats. *Hydrobiologia* 568:379–390
- Elton CS (1958) *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago, IL
- Gratton C, Denno RF (2006) Arthropod food web restoration following removal of an invasive wetland plant. *Ecol Appl* 16:622–631
- Jacob U, Mintenbeck K, Brey T, Knust R, Beyer K (2005) Stable isotope food web studies: a case for standardized sample treatment. *Mar Ecol Prog Ser* 287:251–253
- Jin BS, Fu CZ, Zhong JS, Chen JK, Wu JH (2007) Fish utilization of a salt marsh intertidal creek in the Yangtze River estuary, China. *Estuar Coast Shelf Sci* 73:844–872
- Kurata K, Minami H, Kikuchi E (2001) Stable isotope analysis of food sources for salt marsh snails. *Mar Ecol Prog Ser* 223:167–177
- Kwak TJ, Zedler JB (1997) Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia* 110:262–277
- Laffaille P, Pétillon J, Parlier E, Valéry L, Ysnel F, Radureau A, Feunteun E, Lefevre JC (2005) Does the invasive plant *Elymus athericus* modify fish diet in tidal salt marshes? *Estuar Coast Shelf Sci* 65:739–746
- Levin LA, Neira C, Grosholz ED (2006) Invasive cordgrass modifies wetland trophic function. *Ecology* 87:419–432
- Liao CZ (2007) The effects of exotic plant invasions on carbon and nitrogen cycling in ecosystems: case study and meta-analysis. PhD dissertation, Fudan University, Shanghai
- Litvin SY, Weinstein MP (2003) Life history strategies of estuarine nekton: the role of marsh macrophytes, benthic microalgae, and phytoplankton in the trophic spectrum. *Estuaries* 26:552–562
- Litvin SY, Weinstein MP (2004) Multivariate analysis of stable-isotope ratios to infer movements and utilization of estuarine organic matter by juvenile weakfish (*Cynoscion regalis*). *Can J Fish Aquat Sci* 61:1851–1861
- Melville AJ, Connolly RM (2003) Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. *Oecologia* 136:499–507
- Neira C, Grosholz ED, Levin L A, Blake R (2006) Mechanisms generating modification of benthos following tidal flat invasion by a *Spartina* hybrid. *Ecol Appl* 16:1391–1404
- Odum EP (1980) The status of three ecosystem level hypothesis regarding salt marsh estuaries: tidal subsidy, out-welling, and detritus based food chains. In: Kennedy VS (ed) *Estuarine perspectives*. Academic Press, New York, p 485–495
- Parker JD, Hay ME (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecol Lett* 8: 959–967
- Paterson AW, Whitfield AK (1997) A stable carbon isotope study of the food-web in a freshwater-deprived south African estuary, with particular emphasis on the ichthyofauna. *Estuar Coast Shelf Sci* 45:705–715
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:291–320
- Peterson BJ, Howarth RW, Garritt R (1985) Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* 227:1361–1363
- Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136: 261–269
- Phillips DL, Newsome SD, Gregg JW (2005) Combining sources in stable isotope mixing models: alternative methods. *Oecologia* 144:520–527
- Riera P, Stal LJ, Nieuwenhuize J, Richard P, Blanchard G, Gentil F (1999) Determination of food sources for benthic invertebrates in a salt marsh (Aiguillon Bay, France) by carbon and nitrogen stable isotopes: importance of locally produced sources. *Mar Ecol Prog Ser* 187:301–307
- Rooker JR, Turner JP, Holt SA (2006) Trophic ecology of *Sargassum*-associated fishes in the Gulf of Mexico determined from stable isotopes and fatty acids. *Mar Ecol Prog Ser* 313:249–259
- Schlacher TA, Wooldridge TH (1996) Origin and trophic importance of detritus—evidence from stable isotopes in the benthos of a small, temperate estuary. *Oecologia* 106: 382–388
- Wainright SC, Weinstein MP, Able KW, Currin CA (2000) Relative importance of benthic microalgae, phytoplankton and the detritus of smooth cordgrass *Spartina alterniflora* and the common reed *Phragmites australis* to brackish-marsh food webs. *Mar Ecol Prog Ser* 200:77–91
- Weinstein MP, Litvin S, Bosley KL, Fuller CM, Wainright SC (2000) The role of tidal marsh as an energy source for marine transient and resident finfishes: a stable isotope approach. *Trans Am Fish Soc* 129:797–810
- Weis JS, Weis P (2003) Is the invasion of the common reed, *Phragmites australis*, into tidal marshes of the eastern US an ecological disaster? *Mar Pollut Bull* 46:816–820
- Wozniak AS, Roman CT, Wainright SC, McKinney RA, James-Pirri M (2006) Monitoring food web changes in tide-restored salt marshes: a carbon stable isotope approach. *Estuaries Coasts* 29:568–578
- Yang SL (1998) The role of *Scirpus* marsh in attenuation of hydrodynamics and retention of fine sediment in the Yangtze Estuary. *Estuar Coast Shelf Sci* 47:227–233
- Zhao B, Kreuter U, Li B, Ma ZJ, Chen JK, Nakagoshi N (2004) An ecosystem service value assessment of land-use change on Chongming Island, China. *Land Use Policy* 21: 139–148

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