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Food web structure in a *Salix subfragilis* dominated wetland in Hangang estuary using stable isotopes and fatty acid biomarkers

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We investigated food webs of a *Salix subfragilis*-dominated wetland in the Janghang wetland in the Hangang estuary, which is very close to the Demilitarized Zone, along the west coast of Korea. Our study focused on understanding sesarmine crab (*Sesarma dehaani*)-related food webs in a *S. subfragilis* forest. For our study, we used carbon and nitrogen stable isotopes and fatty acid biomarkers. We collected samples of plants, animals, and detrital sediment from four quadrats (5×5 m^2) set in the *S. subfragilis* community. Samples were collected from September 2006 to June 2009, except during the winter hibernation period of *S. dehaani*. In the wet season, the sediment showed relatively high δ^{13}C and low δ^{15}N signatures compared with relatively low δ13C and high δ15N signatures in the dry season. Mature S. *dehaani* appeared to feed on fresh leaves and other carbon sources, such as immature individuals or fish, in addition to detrital sediment, which appeared to be the main carbon source for immature crabs. Principal component analysis of fatty acid biomarkers of *S. dehaani* showed a clear difference between immature individuals (10–30 mm) and mature ones (larger than 30 mm), indicating that the main food source for immature crabs was detrital sediment, whereas mature crabs foraged plants in addition to consuming detrital sediment. On the basis of our results from stable isotope and fatty acid analyses, mature *S. dehaani* appeared to feed on detrital sediment and fresh leaves of *S. subfragilis* in summer in addition to engaging in cannibalism of immature individuals.

Keywords: fatty acid biomarkers; food webs; *Salix subfragilis: Sesarma dehaani*; stable isotopes

Introduction

Estuaries generally have a relatively low species diversity and high productivity, and are characterized by low salinity, shallow water depths, high turbidity, and excessive nutrients (Elliot & McLusky 2002). Food webs in estuaries are complex, incorporating both terrestrial and aquatic environments, with organisms engaging in diverse foraging strategies (Haines and Montague 1979). In estuarine ecosystems, the major carbon source for individual food webs is detrital organic matter input from rivers (Mann 1972; Odum et al. 1973).

The Janghang wetland is a tidal willow forest wetland dominated by *Salix subfragilis*. It is located in the upper brackish region of the Hangang River. The primary productivity of *S. subfragilis* is estimated to be as high as 4777 g dry weight (DW) $m^{-2}yr^{-1}$, which appears to be one of highest primary productivities measured in South Korea (Han et al. 2010). The sesarmine crab *Sesarma dehaani* is an important food web component in *S. subfragilis*-dominated estuarine wetlands (Han et al. 2010). It has been suggested that the tunnels made by *S. dehaani* benefit *S. subfragilis* by aeration of the rhizosphere (Han et al. 2010). To fully elucidate the interactions between *S. subfragilis* and *S. dehaani*, it is necessary to understand the trophic relations of the two species.

The traditional approach to food web studies has been gut content analysis (Créach et al. 1997). However, despite considerable time and effort, it has been difficult to quantify trophic relations through gut content analysis. In addition, the traditional trophic level concept has limitations with regard to locating omnivorous species such as *S. dehaani* in food webs (Vander Zanden and Rasmussen 1996). Recently, stable isotopes and fatty acid biomarkers have become popular tools for studying food web structure (Jeong and Park 2010). Stable isotope monitoring can provide an objective and quantitative food web structure when ratios of stable isotopes such as carbon and nitrogen are measured from tissues of biological components in food webs (Vander Zanden et al. 1999). The nitrogen isotope signature, in particular, can be used as an index for quantitative trophic position from the observation that the nitrogen isotope ^{15}N tends to be enriched between prey and predator by $3.4 \pm 0.3‰$ (Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1997; Guest and Connolly 2004; Thimdee et al. 2004). In addition, fatty acid biomarkers can provide additional information about trophic relations. Recent studies have used specific fatty acid biomarkers to understand sources of organic matter or food web structure (Meziane et al. 1997; Meziane et al. 2002; Ruess et al. 2005). A recent report showed that the fatty acid composition of a sesarmine crab, *S. bidens*, is

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similar to that of mangrove plants (Shin et al. 2004). There are new trends that use both stable isotope monitoring and fatty acid biomarkers to study trophic relations or energy flows in food webs (Kiyashko et al. 2004; Ruess et al. 2005; Pond et al. 2006). Since the two approaches provide limited clues about trophic relations, using both approaches would provide us with more information to elucidate complex food webs.

In this study, we investigated trophic relations centered on *S. dehaani* in the *S. subfragilis* community in the Janghang wetland in order to elucidate the interactions between *S. subfragilis* and *S. dehaani* and their roles in an estuarine willow forest-dominated wetland. We used carbon and nitrogen stable isotopes and fatty acid biomarkers for this purpose.

Materials and methods

Study area

The Hangang estuary is a natural estuary facing the Yellow Sea. Although there are diverse brackish wetlands, they are not well studied due to limited access to them in the Demilitarized Zone (DMZ) area. Among these wetlands, 60.668 km^2 between Goyang City, Geonggi-do and Ganghwa County, Incheon Metropolitan City is designated as a wetland protected area of national importance. The Janghang wetland is a riparian wetland with an upper part of brackish water (N 37° 38′ 17″, E 126° 45′ 47″) (Figure 1). This wetland is a forested wetland dominated by *S. subfragilis* and tidal mudflats. Its total area is 7.494 km^2, and a willow forest covers 0.71 km^2, which is 19.6% of the vegetated area.

Sampling

We set four quadrats (5×5 m^2) in a *S. subfragilis* community in the Janghang wetland of Hangang where habitats of *S. dehaani* were in good conditions. Quadrats were approximately 10 m apart. Further details on sampling sites can be found elsewhere (Han et al. 2010). Samples of plants, animals (except for fish and benthos), and detrital sediment were collected monthly from these quadrats between September 2006 and November 2007, except for during the winter hibernation period. Crabs collected from each quadrat were classified into four size groups: 10–20 mm (Age1), 20–30 mm (Age2), 30–40 mm (Age3), and larger than 40 mm (Age4). From each size class, five crabs were randomly selected for stable isotope and fatty acid analyses. Fish and benthic samples were collected using gill-nets between January 2008 and June 2009 from the water and water channel in front of the willow forest in Hangang.

Stable isotope monitoring

Carbon and nitrogen isotope signatures were measured for all organisms collected in the study sites, including *S. subfragilis*, *S. dehaani*, and detrital sediment. For periphytic algae, we collected samples by scraping them from detrital sediment, followed by filtering using glass fiber paper (GF/C, 25 mm; Whatman, Maidstone, UK) pre-combusted at 400°C. Samples from *S. dehaani* were collected from tissue parts inside the carapace, followed by freezing and drying. After drying the filter papers and samples from collected plants and animals at 60°C for more than 1 day, we ground them using pestles and mortars. Ground samples were wrapped in tin discs

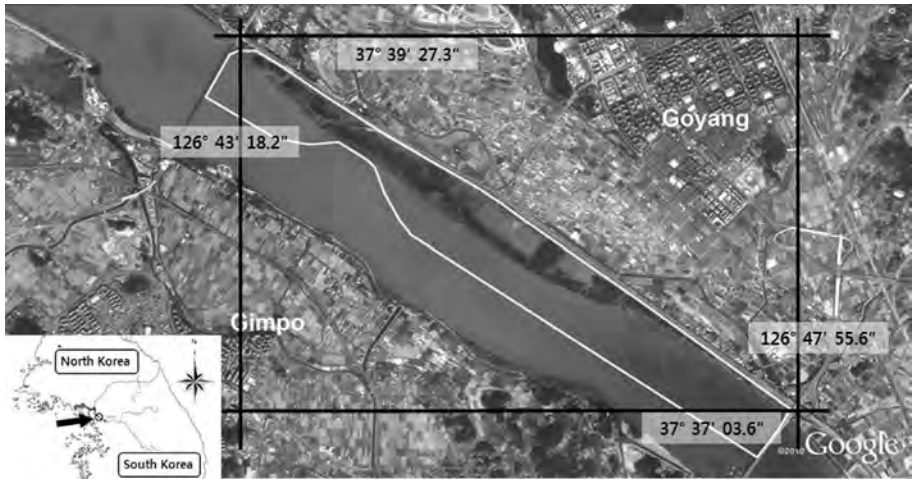

Figure 1. Map of the Janghang wetland in Hangang estuary, South Korea.

(Perkin Elmer, Waltham, USA) into compact spherical shapes with a maximum diameter of 6 mm and stored in well plates until analyzed. Analysis was conducted by the Center for Stable Isotope Biogeochemistry at UC Berkeley, using a Delta Plus XL isotope ratio mass spectrometer, Thermo Fisher Scientific Inc., Waltham, USA). The $d^{13}C$ and $d^{15}N$ values were expressed as ^{13}C to ^{12}C ratio (R) differences in parts per thousand (‰) between samples and standards [Pee Dee Belemnite marine limestone for ^{13}C and atmospheric nitrogen for ^{15}N] as follows:

$$\delta^{13}C \text{ or } \delta^{15}N\,(\text{‰o}) = \left[\frac{R_{sample} - R_{standard}}{R_{standard}}\right] \times 1a0^3$$

$$R = {}^{13}C/{}^{12}C \text{ or } {}^{15}N/{}^{14}N$$

The total carbon and nitrogen contents were analyzed at the same time.

Fatty acid analysis

Since most animals, including crabs, cannot synthesize polyunsaturated fatty acids, they acquire these fatty acids from their diet, resulting in similar fatty acid profiles for these animals (Suprayudi et al. 2004; Chamberlain et al. 2005). Therefore, we can use multivariate analysis such as principal component analysis (PCA) to infer trophic relationships based on similarities in their fatty acid profiles (Dalsgaard et al. 2003).

Samples were frozen using dry ice while transportation to the laboratory and stored in a deep freezer at −80°C until extraction. Frozen samples were dried using a freeze dryer (Model FD2.5; Heto, Waltham, USA) before extraction. These freeze-dried samples were weighed using an electric balance (Model A120S; Sartorius, Goettingen, Germany) to calculate fatty acid content per dry weight (g FA g^{-1}). Dried and weighed samples were wrapped in glass fiber filter paper precombusted at 400°C for extraction. Fatty acids from filter papers were measured to determine the basal amount of fatty acids. We used a mix of 37 fatty acid methyl esters (Supelco Cat. No. 47885-u) and marine source fatty acid methyl esters (Sigma-Aldrich, St. Louis, USA, Cat. No. 47033) to identify fatty acids on the basis of retention time. Further, we used heneicosanoic acid (21:0, 1 mg mL^{-1}) as an internal standard; it was added to the freeze-dried samples immediately prior to the extraction process. Extraction and methylation were performed according to the Kattner and Fricke (1986) method. Extracted fatty acid samples were analyzed using a gas chromatograph (Agilent, Santa Clara, USA, 6890N) with a Programmable-Temperature-Vaporizer and a Flame-Ionization-Detector. Fatty acids were quantified by comparing the area ratios of samples to the internal standard. Response factors for the single fatty acid standards were obtained by comparing quantitative fatty acid standards with the internal standard. The differences between estimated fatty acid concentrations from the internal standard and quantitative standards were within 5%.

Principal component analysis and other statistical analysis

Percentage values of each fatty acid to the total fatty acid amount were compiled to produce a data matrix (18 observations × 35 fatty acid peaks). All fatty acids less than 1% of the total fatty acid amount were removed from the dataset before analysis without recalculating the remaining fatty acid percentage value (Hessen and Leu 2006). Centered fatty acid peak intensity (area) data were standardized to relative abundance to the peaks with the highest intensities prior to PCA. We used log transformation [log (x + 1)] to ensure the homogeneity of variance (Poerschmann et al. 2004). We assigned 0 if there was no matching peak. PCA was conducted using covariance data matrices to reduce their dimensionality. All statistical analyses, including PCA, were performed with S-Plus 6 for Windows (Insightful Corp., Seattle, USA).

Results

Stable isotope signature of detrital sediment, S. subfragilis, *and* S. dehaani

Carbon and nitrogen isotope signatures showed variability with season and crab age (Figure 2). The $\delta^{13}C$ values of *S. dehaani* belonging to Age1 and Age2 were similar to those of detrital sediment, while the $\delta^{13}C$ values of crabs in the Age3 and Age4 group were much higher than those of the Age1 and Age2 groups, indicating carbon sources other than detrital sediment (Figure 2A). The $\delta^{15}N$ values of Age3 and Age4 were significantly higher than those of Age1 and Age2 after July, which, in turn, were higher than those of detrital sediment (Figure 2B). Detrital sediment showed a relatively low $\delta^{13}C$ and relatively high $\delta^{15}N$ value in April 2007, which was the dry season (average temperature: 12.1°C), than in the wet and high temperature season (average temperature: 25.4°C) in August 2007.

Stable isotope signatures of S. dehaani *in the wet and dry periods*

S. dehaani showed very distinctive stable isotope signatures between the dry period (April) and wet period

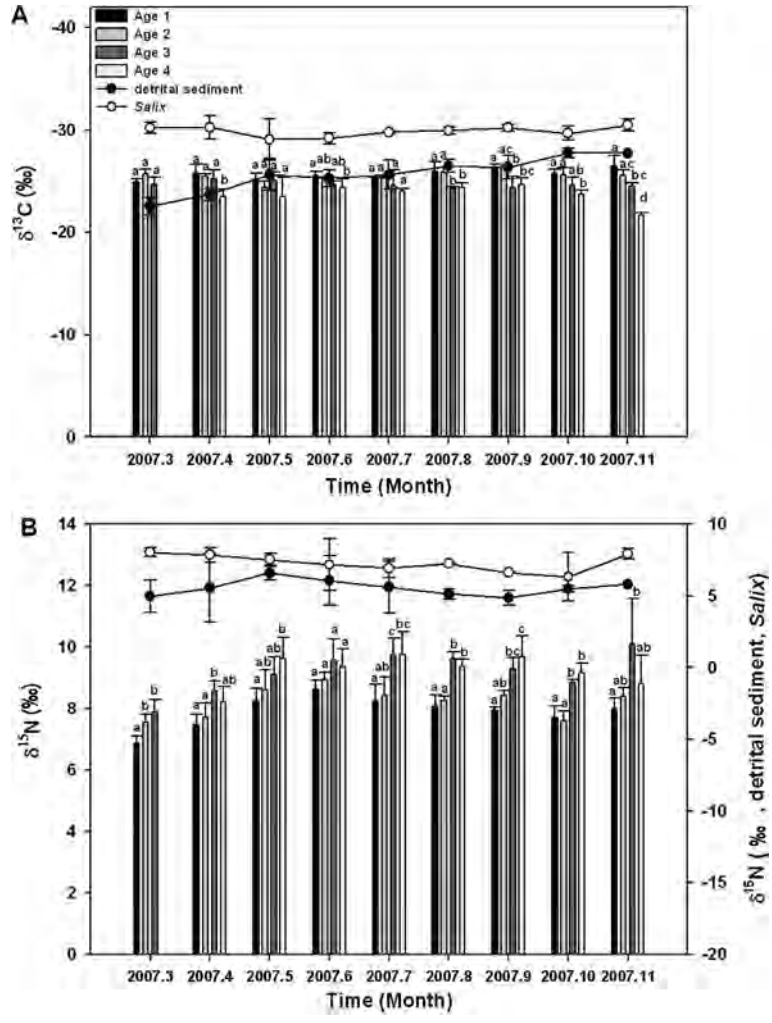

Figure 2. (A) Mean (bar = SD) $\delta^{13}C$ of detrital sediment, *Salix subfragilis*, and *Sesarma dehaani* in the Janghang wetland in 2007. (B) Mean (bar = SD) $\delta^{15}N$ of detrital sediment, *S. subfragilis*, and *S. dehaani* in the Janghang wetland in 2007. a, b, c, and d indicate the results of Tukey multiple comparison.

(August) (Figure 3). In April, the $\delta^{13}C$ value of Age4 was much higher than that of other age classes, which were close to the $\delta^{13}C$ value of detrital sediment. In the wet period (August), the $\delta^{13}C$ values of Age3 and Age4 were clearly higher than those of Age1 and Age2, which were close to the $\delta^{13}C$ values of detrital sediment, indicating that Age3 and Age4 had other carbon sources. The $\delta^{15}N$ values of Age3 and Age4 were higher than those of Age1 and Age2. In the wet period (August), in particular, the $\delta^{15}N$ values of Age3 and Age4 were approximately 1.8% higher than those of Age1 and Age2, supporting the observation that Age3/Age4 cannibalized Age1/Age2.

Food web structure in the Janghang wetland based on a stable isotope signature

To understand the whole food web structure in an *S. subfragilis*-dominated wetland, we included carbon and nitrogen isotope signatures of other organisms such as fish and lugworm collected from near the study site. The $\delta^{13}C$ value of fish such as Gobiidae and flathead mullet (*Mugil cephalus*) were much higher than those of Age3 and Age4, suggesting that these fish were possible carbon sources for Age3 and Age4. Further, the $\delta^{13}C$ value of skin carp (*Hemibarbus labeo*) was close to that of *S. dehaani* (Figure 4).

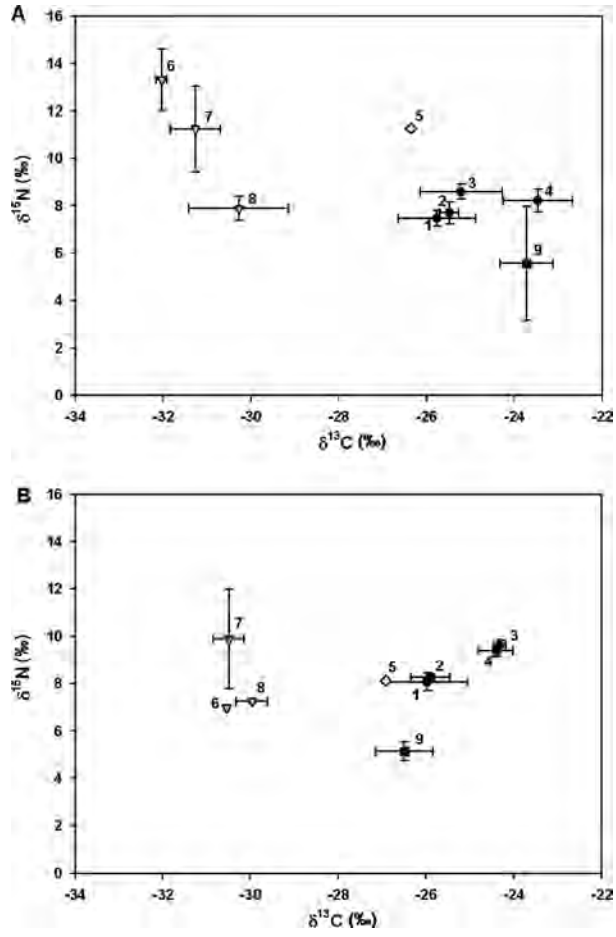

Figure 3. A $d^{13}C$ and $d^{15}N$ diagram of the Janghang wetland in the (A) dry period (April 2007) and (B) wet and humid period (August 2007). 1–4, Crab; 1, Age1; 2, Age2; 3, Age3; 4, Age4; 5, Spider; 6–8, Plant; 6, Monocotyledon; 7, Dicotyledon; 8, *Salix*; 9, detrital sediment.

Fatty acid biomarkers for detrital sediment and S. subfragilis *leaves*

To select useful biomarkers for carbon sources, we analyzed the fatty acid profiles of detrital sediment and *S. subfragilis* (Figure 5). The levels of fatty acids 18:2ω6 and 18:3ω3 appeared to be higher in the fresh leaves of *S. subfragilis* than in detrital sediment. In contrast, 16:1ω7 and 22:2ω6 levels appeared to be higher in detrital sediment than in *S. subfragilis* leaves. Therefore, we selected 18:2ω6 and 18:3ω3 as markers for living plant material and 16:1ω7 and 22:2ω6 as markers for detrital sediment. Individuals of *S. dehaani* in Age1 and Age2 showed relatively high 16:1ω7 content while 18:3ω3 content was relatively high in Age2, Age3, and Age4

Comparison of fatty acid profiles among age classes of S. dehaani

PCA of the fatty acid profiles of each age class of *S. dehaani* showed distinctive grouping between Age1/Age2 and Age3/Age4 along the first principal component (PC1) and second component (PC2) (Figure 6A). PC1 explained 55.2% of the total variance, while PC2 explained 16.9%, covering 72.1% of the total variance together. With regard to PC1, the scores of both Age1/Age2 and Age3/Age4 were located between the scores for detrital sediment and *S. subfragilis* leaves. The PC1 scores of Age1/Age2 were relatively close to that of detrital sediment, while the PC1 scores of Age3/Age4 were relatively close to that of *S. subfragilis* leaves. As *S. dehaani* grows from Age1/Age2 to Age3/Age4,

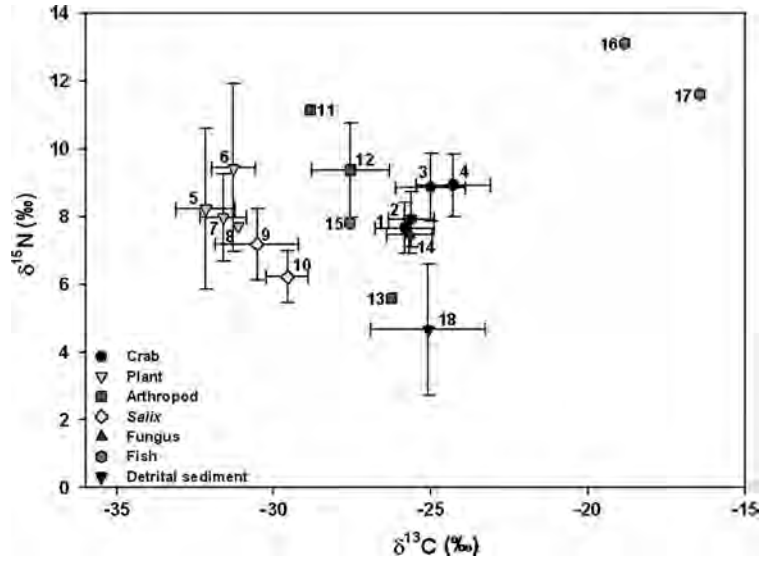

Figure 4. A $d^{13}C$ and $d^{15}N$ diagram of the Janghang wetland, using annual average values and candidate food sources for *S. dehaani*. 1–4, Crab; 1, Age1; 2, Age2; 3, Age3; 4, Age4; 5–10, Plant; 5, Monocotyledon; 6, Dicotyledon; 7, *Sium suave*; 8, Reed; 9, *Salix*; 10, *Salix* (litter); 11–13, Arthropod; 11, Insect; 12, Spider; 13, Lugworm; 14, Fungus, Mushroom; 15–17, Fish; 15, Skin carp; 16, Goby; 17, Flathead mullet; 18, detrital sediment.

16:1ω7, the sediment biomarker, appears to decrease, while 18:2ω6 and 18:3ω3, the *S. subfragilis* leaf biomarker, increases (Figure 6B).

Discussion

Studies on interactions between trees and crabs in forested estuarine wetlands have focused on mangrove forests in tropical and subtropical regions. These studies have found that crabs feed on the leaves or litter of mangroves, detritus, or sediment (Lee 1997; Skov and Harnoll 2002). In these regions, mangrove crabs return organic matter through their excreta, accounting for as much as 24% of mangrove leaf production (Lee 1997), and they feed on 81.3% of mangrove annual production (Inga et al. 2006). However, there are few studies on forested estuarine wetlands in temperate regions. Our previous study found that the secondary productivity of *S. dehaani* was as high as 100.2 g fresh weight (FW) C m^{-2}, indicating that the crabs feed on up to 60% of the organic matter produced by *S. subfragilis* (Han et al. 2010). Results from both stable isotope and fatty acid analyses in the present study indicate that mature *S. dehaani* individuals (Age3 and Age4) feed on both detrital sediment and *S. subfragilis* leaves in the summer in addition to engaging in the cannibalism of younger individuals and decaying fish. In contrast, immature crabs (Age1 and Age2) appear to feed on detrital sediment only. In addition, the ranges of PCA scores on the fatty acid profiles were wider for Age3/Age4 than Age1/Age2, indicating that mature individuals feed on more diverse carbon sources than immature ones.

Our results were well supported by field observations of the feeding behavior of *S. dehaani*. Mature individuals of *S. dehaani* have been observed to feed on diverse fresh and fallen leaves of *S. subfragilis*, litter of *S. subfragilis* in detrital sediment, leaves of *Phragmites communis*, molted carapaces of *S. dehaani*, and dead fish and bivalves. The cannibalistic behavior of mature *S. dehaani* was observed by the authors on several occasions.

Our results indicate that *S. dehaani* experience ontogenic diet changes from sediment feeding to omnivorous feeding. Although ontogenic diet shifts are well known for many aquatic species such as fish, there are few studies on ontogenic diet shift in crabs (Werner and Gilliam 1984). A blue crab, *Callinectes sapidus*, and a portunid crab, *Liocarcinus depurator*, have been reported to show different feeding behaviors depending on size (Laughlin 1982; Freire et al. 1996). However, there are no reports available on ontogenic diet shifts of crabs in woody wetlands such as mangrove ecosystems (Cannicci et al. 2008; Kristensen et al. 2010).

Cannibalism among crustaceans is well documented (Jormalainen and Shuster 1997). Jormalainen and Shuster (1997) summarized four conditions conducive

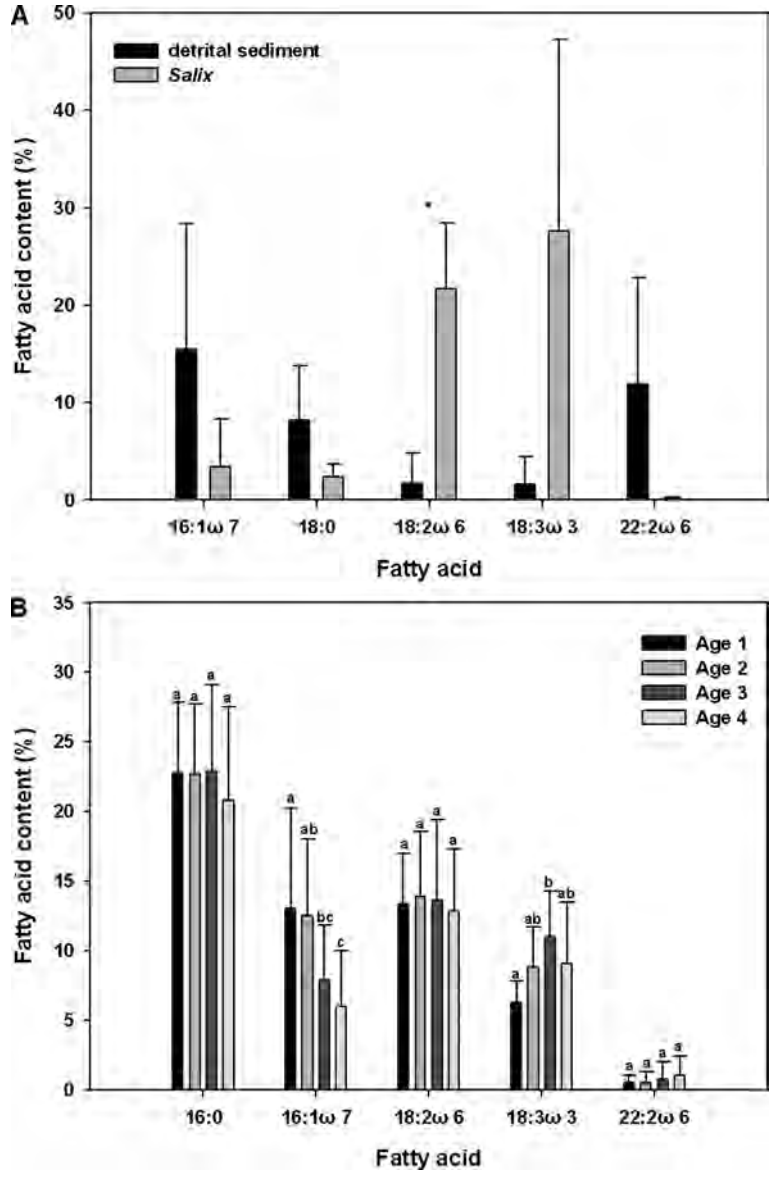

Figure 5. (A) Comparison of important fatty acid contents in detrital sediment and *S. subfragilis* (n = 3). (B) Fatty acid content in each age class of *S. dehaani* in the Janghang wetland (n = 17). Bars indicate average fatty acid content with error bars (±standard deviation). We showed results of t-test with a star (A) and Tukey multiple comparison with a, b, c, and d.

to cannibalism: small habitat, high local population density, food shortage, and structural simplicity of habitats. In addition to these, food quality in terms of carbon to nitrogen (C:N) ratio has been suggested as an important factor for cannibalism (Wolcott and Wolcott 1984). Our results indicate that *S. dehaani* individuals might have experienced nitrogen deficiency during summer and fall since the C:N ratio of *S. subfragilis* leaves dramatically increased to more than 20 after June 2007 (Figure 7A). *S. dehaani* individuals, except for Age4, exhibited increases in C:N ratios after August 2007, indicating that the animals had high C:N diets (Figure 7B). Mature *S. dehaani* individuals, particularly those belonging to Age4, appeared to have managed to keep their C:N ratio low, except in September, possibly by cannibalism of younger individuals (Linton and Greenaway 2007).

Intensive studies on mangrove ecosystems suggest that sesarmid crabs are ecosystem engineers,

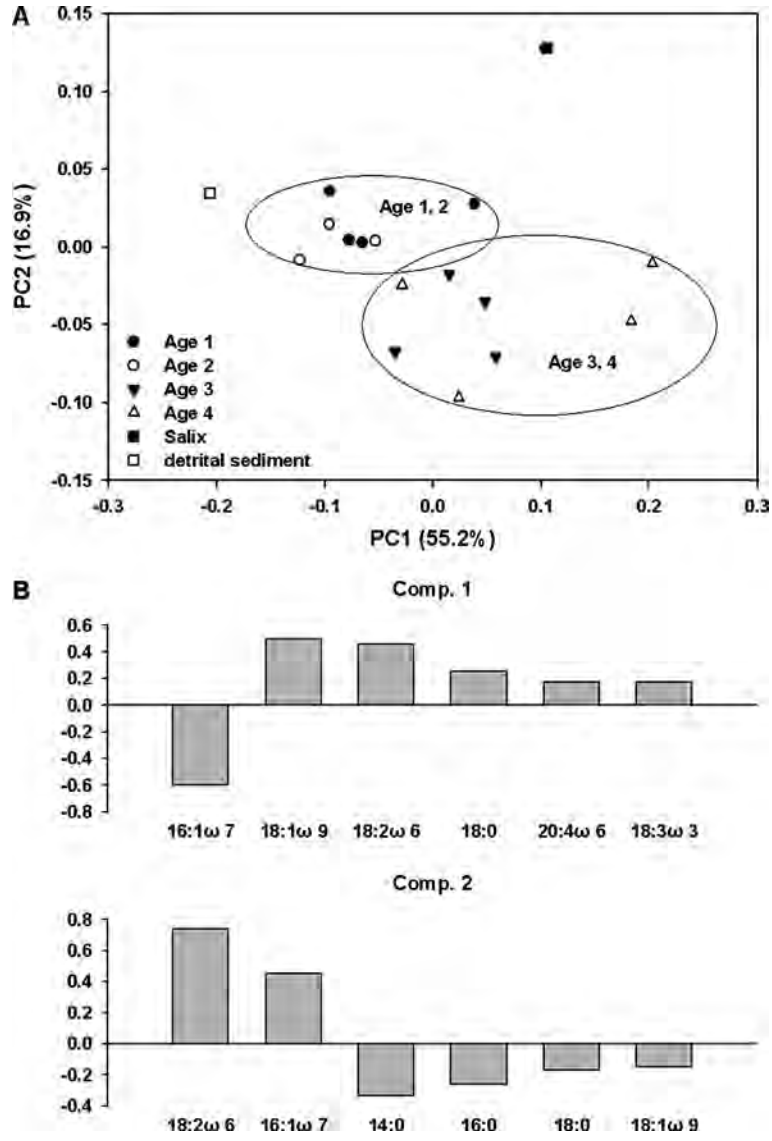

Figure 6. (A) PCA scores based on fatty acid profiles of sediment, *S. subfragilis* and *S. dehaani* of each age class in the Janghang wetland in September 2006, and (B) the most important loading values on the first and second principal components.

responsible for burrowing construction and maintenance, redistribution of organic matter and burial of litter, and exchange between sediment and water/air (Kristensen 2008). Further, herbivorous crabs in mangrove forests have been reported to affect vegetation structure and ecosystem function in various ways: grazing, maintaining high leaf litter turnover rates, recycling mangrove organic production, and propagule predation (Cannicci et al. 2008). We expect that *S. dehaani* plays similar roles in *S. subfragilis* wetlands. Future studies are required to understand the ecological roles of *S. dehaani* in *S. subfragilis* wetland ecosystems.

In conclusion, our results show the differences in the feeding patterns of immature and mature *S. dehaani* individuals through carbon and nitrogen stable isotope signatures and fatty acid biomarkers. Immature individuals appear to feed mainly on detrital sediment, while mature individuals feed on more diverse carbon sources such as fresh and fallen leaves of *S. subfragilis*, fish, and younger individuals of their own species in addition to detrital sediment. Our results provide useful information regarding energy flows and nutrient cycling in *S. subfragilis* forest wetlands and estuarine ecosystems.

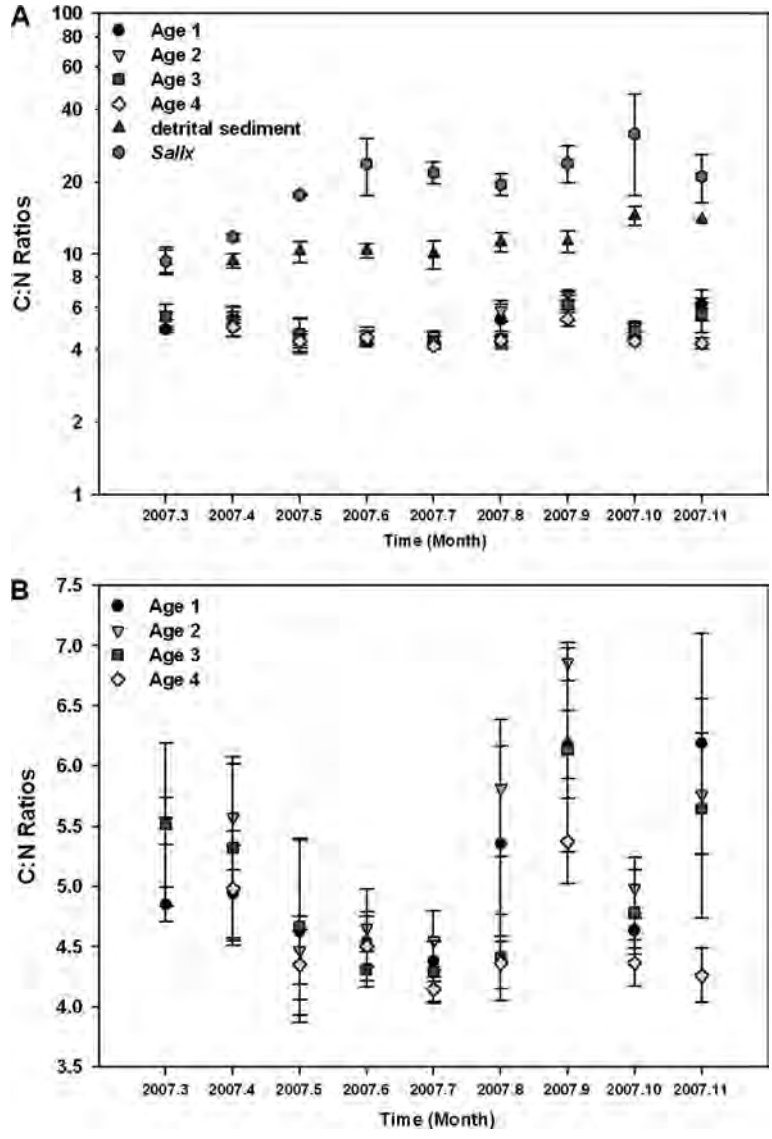

Figure 7. (A) Seasonal changes in C:N ratio in *S. dehaani*, detrital sediment, and *S. subfragilis*. (B) Seasonal changes in C:N ratio in the age classes of *S. dehaani*.

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