

Trophic importance of meiofauna to polychaetes in a seagrass (*Zostera marina*) bed as traced by stable isotopes

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*Stable carbon and nitrogen isotope ratios of benthic invertebrates and their potential food sources, such as suspended particulate organic matter (POM), benthic microalgae, attached algae and seagrass, were identified in Dong-dae Bay during the winter. The carbon stable isotope ratios demonstrate that filter feeders, such as oysters ($-19.5 \pm 1.0\%$), use benthic microalgae ($-21.2 \pm 0.2\%$) as a major food, and polychaetes such as *Glycera* spp. ($-14.0 \pm 0.6\%$) preferentially use meiofauna, such as nematodes ($-14.0 \pm 0.4\%$) and copepods ($-13.3 \pm 1.0\%$). These meiofauna may feed on mixed resources (including bacteria) with the isotope ratios between benthic microalgae ($-21.2 \pm 0.2\%$) and seagrass ($-9.3 \pm 0.1\%$). These findings are consistent with the trophic enrichment in the nitrogen isotope ratios (by 3–4‰) between consumers and food sources. Moreover, the results of the MixSIR model based on the observed isotope ratios suggest a large seagrass contribution to the food sources of benthic organisms such as meiofauna (~53.7–62.6%) and macrobenthos (~41.1–68%) through the food web. This model additionally suggests a relatively large contribution of benthic microalgae to the food sources of filter feeders (i.e. 26.4% for oysters).*

Keywords: stable isotope, *Zostera marina*, meiofauna, benthic microalgae, MixSIR

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INTRODUCTION

Seagrass beds are widespread in shallow coastal waters and considered to be highly productive and diverse communities (Heck, 1995; Lee *et al.*, 2001; Jaschinski *et al.*, 2008; Ouisse *et al.*, 2012). The *Zostera marina* is a particularly common species in subtidal habitats from the middle to high latitude regions (Jaschinski *et al.*, 2008). Seagrass beds support a high diversity of consumers and most likely become potential food sources for a wide range of consumers (Valentine & Duffy, 2006; Lebreton *et al.*, 2012).

Meiofauna are often characterized by high densities in seagrass leaves (Bell *et al.*, 1984; De Troch *et al.*, 2001) and surface sediments (Escavara *et al.*, 1989; Danovaro & Gambi, 2002). Meiofaunal communities are thought to rapidly respond to organic matter inputs and may be closely coupled with primary production inputs (Escavara *et al.*, 1989; Lebreton *et al.*, 2012). Detrital organic matter constitutes a substrate for the development of bacteria (Anesio *et al.*, 2003; Holmer *et al.*, 2004), which may represent an additional food source for meiofauna (Danovaro, 1996). In particular, bacteria could contribute significantly to the organic carbon pool, and they may dominate the total pool of organic carbon from living microbes in the Mediterranean seagrass system during certain periods of the year (Danovaro *et al.*,

1994; Danovaro & Faviano, 1995). Danovaro (1996) reported a strong relationship between bacterial and meiofaunal abundance, suggesting that bacteria serve as a link that transfers the carbohydrates in detrital particles to benthic consumers. Similarly, Tenore *et al.* (1982) found a highly significant and positive correlation between bacterial abundance and nematode density. Warwick (1987) reported that the structure of the nematode assemblage around the detritus is characterized by selective deposit feeders and suggested that bacteria may be used as suitable food sources for other nematodes.

Stable isotope ratios of carbon and nitrogen have been widely used to identify primary producers at the bases of the food web in several coastal habitats (Fry & Sherr, 1984; Peterson *et al.*, 1987; Bustamante & Branch, 1996; Riera & Richard, 1996; Fry, 2006; Schaal *et al.*, 2008). Moore & Semmens (2008) developed MixSIR, an alternative stable isotope mixing model that uses a Bayesian framework to determine the precise proportional contribution ratio of each source to consumers of interest. Bayesian statistics offer a powerful data interpretation method that incorporates information, integrates sources of uncertainty, and explicitly compares the strength of support for competing models or parameter values (Hilborn & Mangel, 1997; Ellison, 2004).

In this study, we aim to understand the energy flow in the benthic ecosystem around seagrass beds by analysing stable carbon and nitrogen isotope ratios of various primary producers and benthic organisms. Additionally, the seagrass-derived detrital organic matter trophic contribution to the benthic communities is determined by the isotope mixing model (MixSIR mixing model). We evaluate the trophic function of

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meiofauna as a link to transfer the detrital organic matter to higher trophic consumers in the seagrass bed ecosystem.

MATERIALS AND METHODS

Study area

All samples were collected around seagrass (*Zostera marina*) beds in Dong-dae Bay, South Korea (Figure 1). Dong-dae Bay is an inner bay, measuring 5 km long and 1 km wide and covered with the seagrass *Z. marina*. The water depth at the sampling site was 3–12 m at full tide, and the meadow was exposed to air at low tide. The sediment size distribution was sandy-mud (4.3–5.4 Φ). The organic matter content of the sediment was 6.9–7.7%, and the seawater temperature was 4.6–6°C in winter.

Sample collection and isotope analyses

Particulate organic matter (POM), sedimentary organic matter (SOM), benthic microalgae, seagrass, macroalgae (red algae and green), meiofauna (copepods and nematodes), oysters and polychaetes were collected from the intertidal areas every month from December 2004 to March 2005. The POM was collected by filtering 1 l of seawater through pre-combusted filter paper (47 mm GF/F) and stored at -80°C . Sediment samples were taken from the top 0.5 cm of cylinder core samples that were 8 cm in diameter. The sediment was dried at 60°C and completely homogenized. Green algae and new leaves from the seagrass *Z. marina* were collected from the tidal flat, and red algae attached to old leaves of seagrass were isolated using a toothbrush. Macroalgae and seagrass were washed by filtered seawater, and any attached microorganisms and detritus were gently scraped off. Meiofauna (copepods and nematodes) was collected from the surface sediment (above 0.5 cm on top) and separated from the sediment using 20 μm mesh, and approximately 300 individuals were

gathered for stable isotope analysis under a microscope. The oyster *Crassostrea gigas* and polychaetes *Lumbrineris* spp., *Nris* spp. and *Glycera* spp. were additionally hand-collected from this study site. Polychaetes were dissected into the body and internal organs, and only the body was analysed. Benthic shrimps collected from this study area were kept alive overnight in filtered seawater to clear their gut. These consumers and macrophyte samples for stable isotope analysis were dried at 60°C , finely ground with a mortar and pestle, and stored in glass vials at -80°C until the analysis.

Benthic microalgae were separated using a slightly modified method reported by Couch (1989). The details are described by Riera & Richard (1996). Approximately 0.5–1 cm of the surface sediment was used in this study. A sieve (60 μm pore size) was placed on top of the sediment, and silica was spread on the sieve. Then, these samples were exposed to light for 24 h to allow adsorption of the benthic microalgae onto the silica (pre-burned). The collected benthic microalgae and seagrass were preserved at -80°C until analysis. Each sample was put in a glass vial, and inorganic carbon was removed by 1N HCl treatment before measuring the organic stable carbon isotope ratio. This process was not conducted before measuring the stable nitrogen isotope ratio to prevent any change in the isotope ratio during the HCl treatment (Bunn *et al.*, 1995). In this study, the carbon and nitrogen isotope ratios were measured by an elemental analyser coupled to an isotope ratio mass spectrometer (Delta plus, Thermo Fisher Scientific), which was operated by the Alaska Stable Isotope Facility at WERC (Water Environmental Research Center), University of Alaska Fairbanks. V-PDB (Vienna-Pee Dee Belimnite) and AIR (atmospheric nitrogen) were used as reference standards for $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰), respectively.

Mixing model analyses

We estimated the feasible contribution ratio of each food source with the MixSIR model version 1.0.4 and an associated

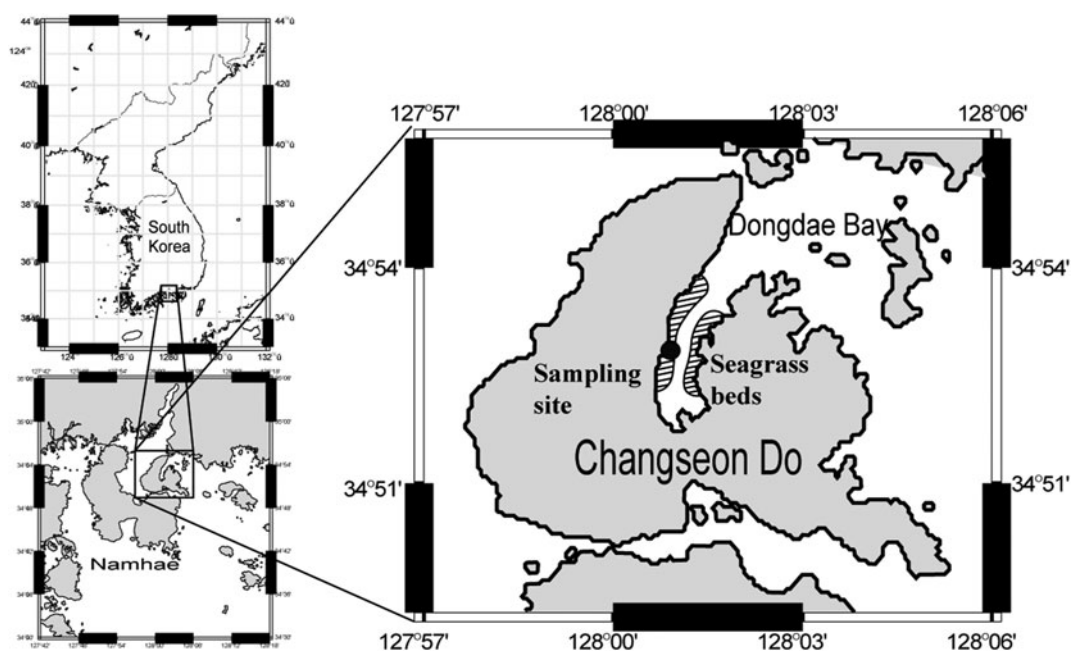


Fig. 1. Map of study area on the southern coast of the Korean peninsula. ●, sampling site at low tide. The shaded portion is the *Zostera marina* meadow.

graphical user interface (GUI) using MATLAB; the number of iterations was 10,000, and we displayed the 0–100% range for each food source (Moore & Semmens, 2008). The dual isotope ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were used after trophic enrichment correction by approximately 0.8‰ for $\delta^{13}\text{C}$ and 3.4‰ for $\delta^{15}\text{N}$ at each trophic level shift.

RESULTS

The average $\delta^{13}\text{C}$ value of POM ($-25.6 \pm 1.7\text{‰}$) in the seagrass beds of Dong-dae Bay was significantly lower than the values of other primary producers in Figure 2. The average $\delta^{13}\text{C}$ value of the SOM was $-19.1 \pm 0.6\text{‰}$, and temporal variation was hardly observed. The average $\delta^{13}\text{C}$ value of the benthic microalgae was $-21.2 \pm 0.2\text{‰}$, which was slightly lower compared with SOM. The $\delta^{13}\text{C}$ values of macroalgae, such as green algae ($-22.3 \pm 0.2\text{‰}$) and attached red algae ($-19.4 \pm 2.4\text{‰}$), were similar to benthic microalgae and SOM, but slightly higher than POM. In contrast, the seagrass *Zostera marina* had a more positive $\delta^{13}\text{C}$ value ($-9.3 \pm 1.0\text{‰}$) compared with the other primary producers. The benthic microalgae, green algae, attached red algae, and SOM primary food sources in the food web had more negative $\delta^{13}\text{C}$ values compared with the seagrass. The POM had the lowest value. The *Crassostrea gigas* oyster, a filter feeder, had an average $\delta^{13}\text{C}$ value of $-19.5 \pm 1.0\text{‰}$, which was slightly higher than benthic microalgae and similar to SOM. In contrast, the meiofauna had $\delta^{13}\text{C}$ values ($-13.3 \pm 1.0\text{‰}$ for nematodes and $-14.0 \pm 0.4\text{‰}$ for copepods) between the benthic microalgae and seagrass. The $\delta^{13}\text{C}$ values of polychaetes such as *Glycera* spp., *Lumbrineris* spp. and *Nris* spp., which are considered to be the highest trophic level organisms in the study area, were close to the meiofauna.

The average $\delta^{15}\text{N}$ value of POM was $3.7 \pm 2.6\text{‰}$, and the values of SOM and benthic microalgae were very similar to each other ($5.5 \pm 0.8\text{‰}$ and $5.7 \pm 1.3\text{‰}$, respectively). However, the $\delta^{15}\text{N}$ value of the seagrass ($6.3 \pm 0.6\text{‰}$) was slightly higher than the values of SOM and benthic microalgae. The primary producers green algae and attached red algae had relatively higher $\delta^{15}\text{N}$ values of $9.0 \pm 1.3\text{‰}$ and $9.3 \pm 0.7\text{‰}$, respectively. The average $\delta^{15}\text{N}$ values of the meiofauna (nematodes and copepods) were $10.4 \pm 0.4\text{‰}$ and $7.9 \pm 1.3\text{‰}$,

respectively) were higher than the primary producers, except for green algae and attached red algae. The $\delta^{15}\text{N}$ values of the oyster ($9.9 \pm 0.4\text{‰}$) were similar to the nematodes (Table 1; Figure 2). The $\delta^{15}\text{N}$ values of the three polychaete species were 3–4‰ higher than the nematodes, reflecting their higher trophic levels (*Glycera* spp., *Lumbrineris* spp. and *Nris* spp. had average values of $14.8 \pm 0.2\text{‰}$, $13.4 \pm 0.3\text{‰}$ and 13.7‰ , respectively). The study period (winter) displayed little temporal variation in the stable isotope ratios for each organism and species.

Based on the $\delta^{15}\text{N}$ values, we assumed the two consumer study groups to be herbivores (trophic level = 2.0, $\delta^{15}\text{N} = \sim 10\text{‰}$, for oyster and two meiofauna) and carnivores (trophic level = 3.0, $\delta^{15}\text{N} = \sim 14\text{‰}$ for polychaetes). In the MixSIR model input, the trophic enrichment in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (0.8‰ and 3.4‰ at each shift of the trophic level, Aberle & Molzahn, 2007; Doi *et al.*, 2011) were corrected for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of these consumers. The MixSIR model shows that the oysters use multiple food sources, including benthic microalgae (26.4 (2.5–62.9%)), POM (19.4 (2.4–43.2%)), red algae (15.8 (1.4–42%)), and green algae (16.5 (1.5–46%)) and seagrass (62.6 (54.2–71%) and 53.7 (41.1–63.3%), respectively) are the dominant food sources for the copepods and nematodes. The model shows that seagrass significantly contributes to the food sources for benthic shrimp (65.9 (54.7–75.7%)) and three polychaete species, *Glyceria* spp. (41.1 (18.7–53.4%)), *Lumbrineris* spp. (48.4 (37.4–57.9%)) and *Nris* spp. (68 (56.8–77.8%)) (Table 2).

DISCUSSION

The role of benthic microalgae as primary food sources

The ^{13}C values of POM were lower than the marine primary producers and sediments, which may reflect large contributions of terrestrial organic matter input from the nearby Sacheon City to the POM in Dong-dae Bay. However, several previous studies reported that carbon sources of terrestrial origin are generally of little importance to estuarine food webs and argued that the influence of terrestrial organic matter input is limited to the riverine or upper estuarine area, potentially due to their poor nutritional quality (Incze *et al.*, 1982; Sinenstad & Wissmar, 1985; Bunn *et al.*, 1989; Deegan & Garritt, 1997; Page, 1997). This small contribution of terrestrial organic matter to estuarine food webs is consistent with the results of the MixSIR model (i.e. relatively small contribution ratio to consumers) in this study (Table 2). It has been reported that re-suspended benthic microalgal biomass in shallow estuaries is largely responsible for the spatial distribution of chlorophyll-*a* and either contributes as much as the total phytoplankton biomass or accounts for most of the chlorophyll-*a* in the water column (Shaffer & Sullivan, 1988; de Jonge & van Beusekom, 1992; Zurburg *et al.*, 1994). Flume experiments and field observations in previous studies have shown variation in re-suspended benthic microalgae in response to stepwise increases in current velocity or wind speed and have identified local deposition of the re-suspended microalgal biomass and rapid settling of fine sediment and microalgae at a low current or wind speed (de

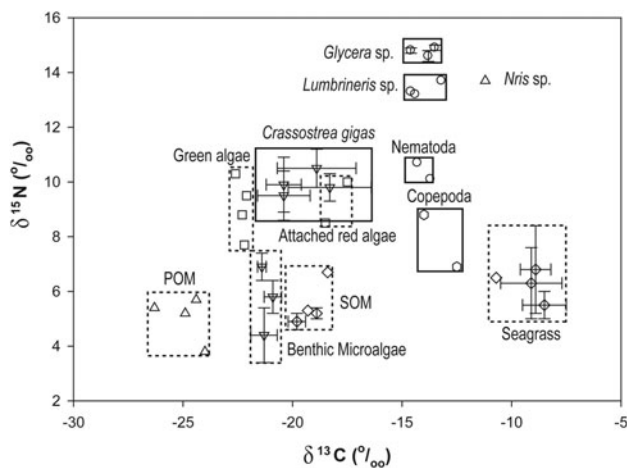


Fig. 2. A cross plot of stable carbon and nitrogen isotope ratios for macrobenthos and their food sources.

Table 1. Stable carbon and nitrogen isotope ratios of primary producers and consumers near the seagrass *Zostera marina* beds in Dong-dae Bay.

Species	Gene	^{13}C (‰)	(\pm SD)	^{15}N (‰)	(\pm SD)	N
POM		-25.6	1.7	3.7	2.6	8
SOM		-19.1	0.6	5.5	0.8	8
Benthic microalgae		-21.2	0.2	5.7	1.3	6
Seagrass	<i>Zostera marina</i>	-9.3	1	6.3	0.6	8
Red algae	(Unidentified sp.)	-19.4	2.4	9.3	0.7	6
Green algae	(Unidentified sp.)	-22.3	0.2	9	1.3	6
Meiofauna	Copepod	-13.3	1	7.9	1.3	2
	Nematoda	-14	0.4	10.4	0.4	2
Oyster	<i>Crassostrea gigas</i>	-19.5	1	9.9	0.4	8
Benthic shrimp	(Unidentified sp.)	-12.3	2.6	10.3	0.9	4
Polychaetae	<i>Glycera</i> sp.	-14	0.6	14.8	0.2	6
	<i>Lumbrineris</i> sp.	-14.1	0.8	13.4	0.3	6
	<i>Nris</i> sp.	-11.2		13.7		1

Jonge & van Beusekom, 1992; Blanchard *et al.*, 1997; Widdows *et al.*, 1998; Herman *et al.*, 2000). In fact, the results in the MixSIR model show that benthic microalgae significantly contribute as a primary food source for oysters (26.4% in diet) and *Lumbrineris* polychaete (14.1% in diet). Additionally, the $\delta^{15}\text{N}$ value of oyster is approximately 4‰ higher than benthic microalgae (Figure 2), which may demonstrate a clear trophic relationship. Most previous studies used approximately 0.8‰ and 3.4‰ as the mean trophic enrichment for carbon ($\Delta\delta^{13}\text{C}$) and nitrogen ($\Delta\delta^{15}\text{N}$), respectively, from diets to consumers (DeNiro & Epstein, 1978, 1981; Minagawa & Wada, 1984; Aberle & Malzahn, 2007; Doi *et al.*, 2011). However, Dubois *et al.* (2007) argue that trophic enrichment for *Crassostrea gigas* should be variable and averaged to 1.85‰ for $\delta^{13}\text{C}$ and 3.78‰ for $\delta^{15}\text{N}$ values because trophic enrichment reflects numerous parameters, including species, diet, environmental conditions, and nitrogenous wasting (Vander Zanden & Rasmussen, 2001; McCutchan *et al.*, 2003; Vanderklift & Ponsard, 2003). Thus, the differences in ^{15}N values between benthic algae and oysters can be simply explained by the contribution of benthic algae as a major food source to oyster in Dong-dae Bay.

Contribution of seagrass detritus as an energy source to the benthic ecosystem

The results of the MixSIR model revealed a significant contribution of seagrass to the diet sources of benthic organisms (except for oyster), particularly meiofauna, which is the likely link between seagrass and macrobenthos (Table 2).

Many previous studies have frequently focused on benthic microalgae as major food sources for various benthic

invertebrates located on the tidal flats (Page, 1997; Kang *et al.*, 2003, 2007; Kanaya *et al.*, 2008). However, Doi *et al.* (2009) reported that seagrass greatly contributes to the food sources of the snail and argued that both macroalgae and seagrass play important roles as food sources at their growing sites and tidal flats. Olsen *et al.* (2011) emphasized that benthic invertebrates consume a large amount of seagrass detritus as food sources at the lower N load estuaries.

It has previously been hypothesized that benthic bacteria are a major carbon source for meiofauna (Montagna, 1984). It has been previously reported that other species of the polychaete *Nephtys incise* could use energy sources derived from aged seagrass detritus (Tenore *et al.*, 1977; Leduc & Probert, 2009). If so, benthic bacteria are likely to be important links that transfer the organic carbon and nitrogen pools from seagrass to meiofauna in the seagrass meadow ecosystem rather than the unvegetated sediment ecosystem. Moreover, $\delta^{15}\text{N}$ values of meiofauna should primarily reflect seagrass and trophic enrichment through the food web. In terms of the energy flow and isotope changes through the benthic food chain, the carbon isotope ratio of bacteria should be close to meiofauna (~ -14 to -13 ‰) if the meiofauna feed on benthic bacteria (Figure 2). Polychaetes (*Glycera* spp., *Lumbrineris* spp. and *Nris* spp.) and their food source meiofauna have similar carbon stable isotope ratios.

Previous investigations of seagrass meadows found that changes in bacterial abundance are closely related to seasonal changes in temperature, food resources (labile organic matter), and primary production (Danovaro *et al.*, 1994; Danovaro & Fabiano, 1995). In the seagrass sediment of Prelo Bay, bacterial abundance was significantly enhanced by organic matter inputs. The highest bacterial biomass was observed during the winter accumulation of vegetal debris

Table 2. Feasible contribution ratio (%) of each food source to the consumer, determined by the MixSIR model using two stable isotopes of carbon and nitrogen (after correcting for trophic enrichment by 0.8‰ for $\delta^{13}\text{C}$ and 3.4‰ for $\delta^{15}\text{N}$) (Moore & Semmens, 2008).

Species	Gene	POM	Benthic microalgae	Seagrass	Red algae	Green algae
Oyster	<i>Crassostrea gigas</i>	19.4 (2.4–43.2)	26.4 (2.5–62.9)	13.5 (3.4–24.9)	15.8 (1.4–42)	16.5 (1.5–46)
Meiofauna	Copepoda	21.7 (8.2–31.5)	6.1 (0.5–25.4)	62.6 (54.2–71)	3 (0.2–11.4)	2.7 (0.2–10.3)
	Nematoda	6 (0.6–18.5)	9.5 (0.9–27.4)	53.7 (41.1–63.3)	14.8 (1.5–36.5)	10.5 (0.9–28.1)
Polychaetae	<i>Glycera</i> sp.	3.8 (0.3–15.2)	6 (0.5–21.3)	41.1 (18.7–53.4)	32.7 (3.8–61.1)	13.6 (1.1–36.4)
	<i>Lumbrineris</i> sp.	9.5 (1–24.2)	14.1 (1.3–35.4)	48.4 (37.4–57.9)	12 (1.1–32.6)	10.2 (0.9–29.1)
	<i>Nris</i> sp.	4 (0.3–13.1)	6.1 (0.5–19.1)	68 (56.8–77.8)	10.3 (0.9–27.8)	6.9 (0.6–19.8)
Benthic shrimp	(Unidentified sp.)	4.3 (0.4–13.9)	6.6 (0.6–20.3)	65.9 (54.7–75.7)	10.8 (1–29)	7.4 (0.7–21)

because fluctuations of bacterial abundance and biomass reflect changes in the sediment's carbohydrate content (Danovaro, 1996). In particular, bacterial abundance that shows a significantly positive correlation with carbohydrates may represent the link between detrital particles and benthic consumers (Danovaro, 1996). Kenworthy & Thayer (1984) reported that structural carbohydrates, which are cell wall constituents in leaves, account for 31.8% of the total carbohydrates in *Zostera marina*. Williams *et al.* (2009) used the isoSource mixing model and reported that seagrass-derived (*Thalassia testudinum*) organic matter explain 13–67% of bacterial-specific $\delta^{13}\text{C}$ signatures. Thus, seagrass detritus may promote bacterial abundance, which is usually transformed by benthic bacteria into useful food sources for deposit feeders. The aboveground biomass of *Z. marina* in this study area is at a minimum in December. The number of spathes per shoot increases from February to the summer, and most leaves and sheathes from *Z. marina* fall in winter (Lee *et al.*, 2005). Thus, seagrass detritus could sufficiently supply organic matter to the bacterial community, and benthic bacteria and meiofauna can survive and grow by consuming the organic matter from fallen *Z. marina* detritus, even in winter.

These stable isotope results demonstrate that filter feeders such as oyster use benthic microalgae as a food source but that polychaetes feed on meiofauna. These meiofauna may feed on benthic bacteria and serve as links that transfer organic carbon and nitrogen from seagrass detritus to the food web. When most of the seagrass leaves had fallen in the study area in winter, the benthic microalgae contribution to the food web may have been limited in the seagrass meadow ecosystem. During this time period, however, seagrass detritus could become an important food source, especially for large deposit feeders (i.e. meiofauna and polychaetes) in this benthic food web. Previous research generally emphasized that the ecological role of seagrass beds is a shelter in a coastal ecosystem. However, the present investigation suggests that seagrass detritus are significant energy source for many consumers, including bacteria and meiofauna that serve as important links in the benthic ecosystem of coastal seagrass beds.

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