Macroalgae and seagrass contribution to gastropods in sub-tropical and temperate tidal flats

HIDEYUKI DOI[1], MASATOSHI MATSUMASA[2], MAMORU FUJIKAWA[1], KEIICHI KANOU[1], TAKAO SUZUKI[1] AND EISUKE KIKUCHI[3]

[1]Graduate School of Life Sciences, Tohoku University, 2-1-1, Katahira, Aoba-ku, Sendai 980-8577, Japan, [2]Department of Biology, Centre for Liberal Arts & Sciences, Iwate Medical University, Nishi-Tokuta 2-1-1, Yahaba-cho 028-3694, Japan, [3]Center for Northeast Asian Studies, Tohoku University, Kawauchi, Aoba-ku, Sendai 980-8576, Japan

Macroalgal and seagrass communities are widely distributed in marine and brackish shallow water and have high productivity. The primary production in marine costal areas is often transported to intertidal flats by waves and currents and beached on the flats. Thus, we hypothesized that the macroalgae and seagrasses are food sources for benthic communities on intertidal flats where some gastropod species often dominate. We performed comparisons of food sources among different gastropod species on sub-tropical and temperate tidal flats (26° and 38°N, respectively), and used isotope mixing models using carbon and nitrogen stable isotopes. A mixing model for stable isotopes, IsoSource, revealed that main food sources for three snails were macroalgae (50–56%) and seagrass (39–45%) at the temperate site. The contributions of terrestrial plants, sediment organic matter and benthic microalgae were weaker than those of macroalgae and seagrasses. At the sub-tropical site, snails fed mainly on macroalgae. The differences in food sources between snail species were not remarkable, although the nitrogen values were slightly different. It would thus appear that macroalgae and seagrass play an important role in the food webs not only in their own habitats but also on the adjacent tidal flats.

INTRODUCTION

Recently the importance of organisms to connect spatially isolated ecosystems has been increasingly recognized (Polis *et al.*, 1997; Nakano & Murakami, 2001; Hyndes & Lavery, 2005; Melville & Connolly, 2005; Schindler *et al.*, 2005). Many studies have used stable isotopes to estimate the food sources of benthic consumers in marine ecosystems (e.g. Wainright *et al.*, 2000; Kharlamenko *et al.*, 2001; Riera *et al.*, 2002; Doi *et al.*, 2005; Melville & Connolly, 2005). Estuaries, one of the most productive types of ecosystem (Costanza *et al.*, 1997), are characterized by inputs of terrestrial and marine organic matter in addition to autochthonous production by macroalgae, microalgae, and seagrasses.

Macroalgal and seagrass communities are widely distributed in marine and brackish shallow water and have high productivity in those ecosystems (McRoy & McMillan, 1977; Zieman & Wetzel, 1980; Duarte, 1989). The primary production at marine costal areas is often transported to intertidal flats by waves and currents and beached on the flats, and this sometimes supports relatively high biomass of intertidal gastropods such as limpets (Bustamante *et al.*, 1995; Mann,

2000; Wainright *et al.*, 2000). At our two study sites, one sub-tropical and the other temperate (26°N and 38°N, respectively), high numbers of Batillariid gastropods were observed on green macroalgae (*Ulva* and *Enteromorpha*) and on the leaves of a seagrass *Zostera marina* (Figure 1). Therefore, we hypothesized that the macroalgae and seagrasses are significant food sources for Batillariid gastropods on intertidal flats in both sub-tropical and temperate regions, which have a different composition of snail species. Since little is known about the importance of macroalgae and seagrass to gastropod foraging, and since numbers of gastropod snails are decreasing in Japan due to habitat loss and degradation by human activity, testing the above hypothesis would be an important contribution to conservation of local gastropod populations (Kimura & Kimura, 1999; Kimura, 2005).

Since a few elements can routinely be used for stable isotope analysis, food web studies using isotope data from n stable isotope values (typically two) have often restricted their studies to $n + 1$ organic matter sources by including only those sources either assumed to be most important or shown to be through other types of analyses. Phillips & Gregg (2003) developed isotope mixing model software (IsoSource) that is designed for situations in which n isotopes are being used and more than $n + 1$ sources are likely to be contributing to a mixture. IsoSource mixing model can calculate feasible ranges of source contributions using stable isotope data. We performed comparisons of food sources among

Corresponding author:
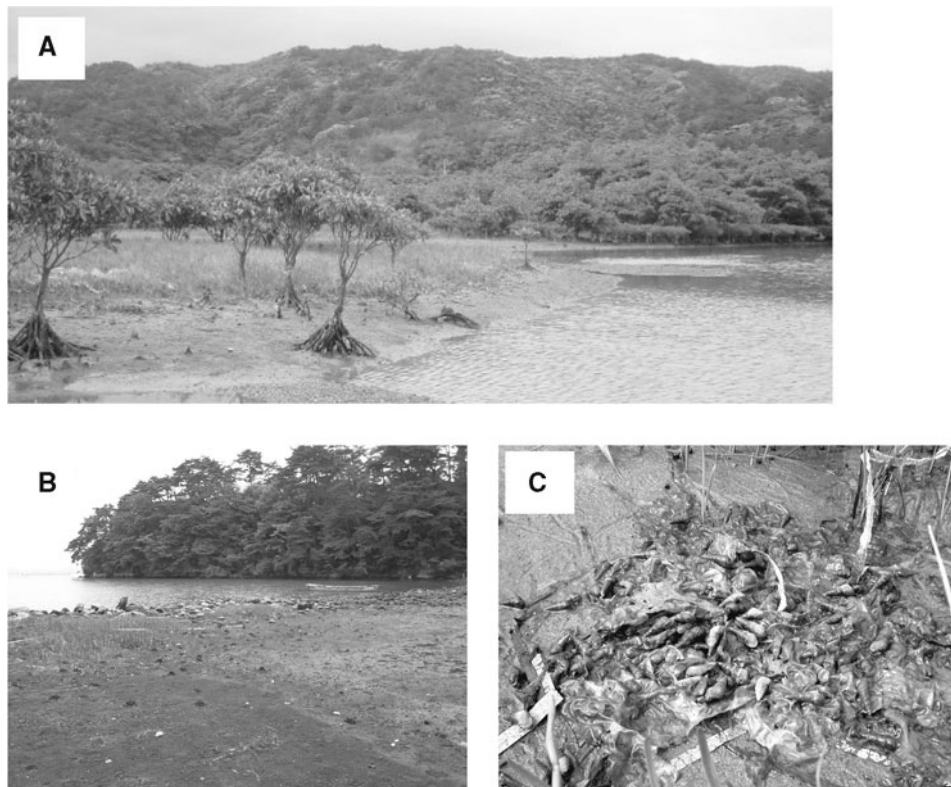H. Doi
Email: h-doi@agr.ehime-u.ac.jp

Fig. 1. (A) Sampling site at Station A in sub-tropical region with macroalga *Enteromorpha* sp. Photograph by M. Matsumasa; (B) sampling site at Station B in temperate region with *Ulva pertusa* and seagrass *Zostera marina*. Photograph by M. Fujikawa; (C) gastropods (*Batillaria multiformis* and *Batillaria cumingi*) were observed on macroalgae *Ulva pertusa* and seagrass *Zostera marina* at Station B. Photograph by M. Fujikawa.

different gastropod species at the sub-tropical and the temperate tidal flats (26°N and 38°N), by the isotope mixing models using carbon and nitrogen stable isotopes.

MATERIALS AND METHODS

Study sites

The sub-tropical site (Station A) is located on a sheltered intertidal flat with a mangrove forest (mainly *Kandelia candel* and *Bruguiera gymnorrhiza*, approximately 300-m away from flat; see Figure 1) in Ohura Bay, Okinawa Island (26°33′N 128°02′E). In March 2004, a green macroalgae *Enteromorpha* sp., which would be transported, covered the tidal flat (Figure 1). The temperate site (Station B) is located on an open intertidal flat with salt marsh plants (mainly *Carex scabrifolia* and *Phragmites australis*) in Matsushima Bay, north-east Honshu Island (38°22′N 141°05′E). There was a seagrass bed (mainly *Zostera marina*) in the coastal zone around Station B, and the tidal flat was covered with beached leaves of the seagrass *Z. marina* and the macroalgae *Ulva pertusa* (Figure 1). The vegetation of seagrass was not found on the tidal flat of Station B. The sediment differed between the two sites: sand and cobbles at Station A, silt and sand at Station B.

Sample collection and preparation for isotopic analyses

The monthly mean air temperature was 16.3°C in March 2004, as recorded at the Japan meteorological observation site nearest to Station A (26°35′N 127°57′E), and 14.5°C in October 2003 at the site nearest to Station B (38°15′N 140°54′E) (data from Japan Meteorological Agency). The choice of sampling periods was made so as to minimize the difference in mean air temperature between the two sites, hence samples were collected at Stations A and B in March 2004 and October 2003, respectively. During the sampling periods, daily tidal amplitude ranged from 82–86 cm at the tidal observation site nearest to Station A (Itoman: 38°18′N 121°70′E), and from 89–96 cm at the site nearest to Station B (Ishihama: 26°80′N 127°40′E).

Three or four replicates of each sample were collected for isotope measurement. From the intertidal areas we collected the dominant adult Batillariidae species (shell lengths > 20 mm): *Cerithidea (Cerithideopsilla) cingulata*, *Cerithidea (Cerithideopsilla) djadjariensis*, and *Batillaria flectosiphonata* at Station A, and *Cerithidea (Cerithideopsilla) rhizophorarum*, *Batillaria multiformis*, and *Batillaria cumingi* at Station B. The stomach contents analysis for *C. cingulata*, *C. djadjariensis*, *C. rhizophorarum* and *B. multiformis* showed that these species fed on micro and macroalgae on the tidal flat (Maki et al., 2002), thus probably the Batillariidae species had a similar trophic niche. In addition, at Station A we collected *C. djadjariensis* and *B. flectosiphonata* from two supralittoral sites to compare the spatial variations in the isotope values of the species. The distance between the supralittoral sites and the intertidal site was approximately 150 m. The substrate compositions of supralittoral sites were similar to that of Station A. These gastropods were the dominant species of the whole benthic community at each station (Motonaga, 1977; Meziane & Tsuchiya, 2000; Fujikawa, M., unpublished data).

We collected the gastropod feet, and foot lipids were removed using a chloroform–methanol mixture (2:1 by weight). We analysed the isotopic signature of each individual.

Sediment samples containing sediment organic matter (SOM) were collected from depths of 0–0.5 cm below the sediment–water interface at each station. The green macroalgae *Enteromorpha* sp. and *Ulva pertusa* were collected on the tidal flat of Stations A and B, respectively, while the leaves of the dominant terrestrial plants *Kandelia candel* and *Carex scabrifolia* were collected at Stations A and B, respectively. In addition, at Station B, we collected the beached leaves of seagrass *Zostera marina* from the offshore area to the tidal flat, but we did not observe any beached seagrass leaves at Station A (Figure 1). Macroalgae and seagrass were washed with dissolved water, and any attached microorganisms and detritus (i.e. benthic diatoms, bacteria, organic matter trapped within mucus secreted by benthos, etc.) were gently scraped off using a tooth brush. Most of the attached microorganisms and detritus were removed by this method (Aikins & Kikuchi, 2002). Crushed and homogenized macroalgae, seagrass, and SOM samples were put in a glass vial and acidified with 1 mol l^{-1} HCl to remove carbonates before the isotope analysis.

Benthic diatoms were collected from the sediment at Station B, making use of their phototactic movement (Couch, 1989; Doi *et al.*, 2003a, b). Sediment samples from a depth of 1 cm were collected and spread in a 1-cm-thin layer on Petri dishes. For each sample, nylon net (75-μm mesh) was placed on the sediment surface and a 2-mm layer of 25- to 65-μm silica powder (precombusted at 500ºC for 2 hours) was spread on the net. The Petri dishes were illuminated for 24 hours by continuous spraying of filtered river water to retain moisture in the silica powder. After 24 hours, the powder was scraped off and mixed with filtered water to suspend the benthic diatoms, which were then decanted into glass vials and freeze-dried. Unfortunately, at Station A we could not collect benthic diatoms because it was difficult to extract them from the muddy sediment using the 75-μm mesh net. This is one limitation of this study, and the reason why the isotope mixing model was performed only for Station B, as described below. Other potential food sources such as other macroalgal species were not observed at Station A (Doi, H., personal observation).

Stable isotope analysis

All the samples were freeze-dried and preserved in a freezer at $-20°C$ prior to isotope ratio and elemental analyses. For nitrogen isotope ratios, the samples were measured without acid-treatment. The carbon and nitrogen isotope ratios of the samples were measured with a mass spectrometer (DELTA plus, Finnigan Mat), and the results are reported using delta notation obtained by $\delta^{13}C$ or $\delta^{15}N = (R_{sample}/R_{standard}-1) \cdot 1000$ (‰), where R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio for $\delta^{13}C$ or $\delta^{15}N$, respectively. As standards, PDB was used for $\delta^{13}C$ and air nitrogen was used for $\delta^{15}N$. The analytical error was ± 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Isotope mixing model and statistical analyses

To determine which of the potential food sources were assimilated by the snails, we estimated the feasible contributions for each food source by isotope mixing models using IsoSource version 1.3.1 software (Phillips & Gregg, 2003). Essentially, the model iteratively creates all possible combinations of source proportions (with each combination equalling 100%) at preset increments (2% in this study) to create a set of predicted mixtures of sources (see Phillips & Gregg, 2003, in detail). For the model, the potential food sources selected were SOM, macroalgae and terrestrial and mangrove plant litter for Station A and SOM, macroalgae, seagrass, benthic microalgae and terrestrial plant litter for Station B. Tolerance was initially set at 0.1‰; if mixture isotope values were out of bounds (i.e. the snails at Station A), we incrementally increased the tolerance value by 0.1‰ up to a maximum of 0.8‰. The carbon and nitrogen isotope enrichments of the snails were $+0.8$ and $+2.3$‰ (France & Peters, 1997 for carbon; McCutchan *et al.*, 2003 for nitrogen).

To compare the isotope values of the potential food sources and snails, we performed one-way analysis of variance (ANOVA) and Tukey multiple comparison. In addition, at Station A we compared the isotope values of the snails at mid-intertidal flats (Station A) and supralittoral flats (Stations A-SF1 and A-SF2) using repeated-measures two-way ANOVA.

RESULTS

Isotopic signatures of the samples

Carbon and nitrogen isotope signatures of the potential food sources varied among the sources at Stations A and B (Table 1; Figure 2). At Station A the mean carbon and nitrogen isotope values of the snails ranged from -14.7 to -13.9‰ and from 11.3 to 12.8‰, respectively. Nitrogen isotope values of the snails at Station A were significantly different among species (one-way ANOVA; Table 1), and those of *Batillaria flectosiphonata* were significantly lower than those of other species (Table 1; Tukey multiple comparison, $P < 0.05$). The carbon isotope values were not significantly different between species (Table 1). Comparison of the isotope values of *Cerithidea (Cerithideopsilla) djadjariensis* and *B. flectosiphonata* between the intertidal and supralittoral sites at Station A (Table 1) revealed that carbon and nitrogen isotope values were not significantly different between the sites (ANOVA, $F = 2.95$ and 0.66, $P = 0.08$ and 0.53, respectively). Thus, the spatial variations of the isotope values of the snails were small over a small horizontal scale at Station A.

At Station B, the mean carbon and nitrogen isotope values of the snails ranged from -12.7 to -12.5‰ and from 10.8 to 11.6‰, respectively. Nitrogen isotope values of the snails at Station B were significantly different between species ($F = 7.58$, $P = 0.02$), and those of *C. rhizophorarum* were significantly lower than those of *B. multiformis* ($P < 0.05$). However, the carbon isotope values were not significantly different ($F = 3.65$, $P = 0.09$). Carbon isotope ratios of benthic microalgae were -23.0 ± 0.2‰. These values are similar to the values (-23.0 ± 0.5‰) obtained at the tidal flats studied by Guest *et al.* (2004).

Contribution of the food sources

Using the IsoSource mixing model, we estimated the contribution of the potential food sources to the snail biomass (Table 2). At Station B, food sources for three snails were

Table 1. Carbon and nitrogen stable isotope values of samples at Stations A and B (Mean ± SE, N = 3 or 4). SOM, mean sediment organic matter. A-SF1 and 2 are two sites on supralittoral flats at Station A. F = mean *F*-value of ANOVA (**, * and non-asterisk indicate $P < 0.01$, < 0.05 and > 0.05, respectively). Tukey multiple comparison results show that different letters indicate significant differences ($P < 0.05$).

| Sites	Samples	Types	δ¹³C (‰)	F	Tukey	δ¹⁵N (‰)	F	Tukey
Sub-tropical								
A	*C. cingulata*	Gastropoda	−13.9 ± 0.0	1.85	a	12.6 ± 0.3	11.0**	a
A	*C. djadjariensis*	Gastropoda	−14.1 ± 0.3		a	12.8 ± 0.2		a
A	*B. flectosiphonata*	Gastropoda	−14.7 ± 0.3		a	11.3 ± 0.2		b
A	SOM		−23.9 ± 0.3			4.4 ± 0.6		
A	*Enteromorpha* sp.	Macroalgae	−16.7 ± 0.5			9.3 ± 0.5		
A	*Kandelia candel*	Terrestrial plant	−27.5 ± 0.3			5.8 ± 0.2		
A-SF1	*C. djadjariensis*	Gastropoda	−14.0 ± 0.4			13.1 ± 0.2		
A-SF1	*B. flectosiphonata*	Gastropoda	−17.1 ± 0.3			11.1 ± 0.8		
A-SF2	*C. djadjariensis*	Gastropoda	−15.1 ± 0.4			12.9 ± 0.3		
A-SF2	*B. flectosiphonata*	Gastropoda	−16.6 ± 0.5			11.7 ± 0.4		
Temperate								
B	*C. rhizophorarum*	Gastropoda	−12.7 ± 0.2	3.65	a	10.8 ± 0.2	7.58*	a
B	*B. multiformis*	Gastropoda	−12.6 ± 0.3		a	11.6 ± 0.6		b
B	*B. cumingi*	Gastropoda	−12.5 ± 0.2		a	11.5 ± 0.5		ab
B	SOM		−19.1 ± 0.6			4.7 ± 1.0		
B	Benthic microalgae		−23.0 ± 0.2			6.7 ± 0.3		
B	*Ulva pertusa*	Macroalgae	−16.5 ± 1.4			9.0 ± 0.1		
B	*Zostera marina*	Seagrass	−10.0 ± 0.3			6.2 ± 0.4		
B	*Carex scabrifolia*	Terrestrial plant	−24.2 ± 0.4			8.4 ± 0.6		
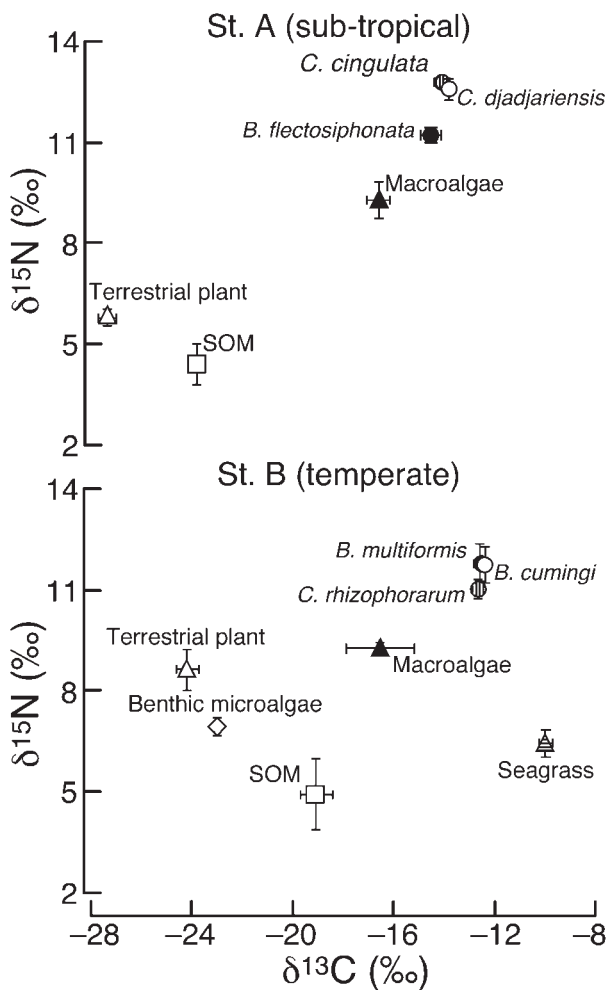
Fig. 2. Carbon and nitrogen stable isotope plots of the snails and their potential food sources at Station A (upper) and Station B (lower). Each symbol shows a mean ± 1 SE.

estimated to be mainly macroalgae (50–56%) and seagrass (39–45%). The contributions of terrestrial plants, SOM and benthic microalgae were smaller than those of macroalgae and seagrass. At Station A, we could not perform IsoSource mixing models to the contributions for snails, since isotope values of the snails were higher isotope values from any potential food sources. This suggested that the snails fed mainly on macroalgae at Station A. We could not detect the remarkable differences in food sources for snail species, since their carbon isotope values were not significantly different, although the nitrogen values were slightly different.

DISCUSSION

At both the sub-tropical and the temperate site (Stations A and B), our results showed the significant contribution of macroalgae and/or seagrass to snails as food sources. In this study, we also observed that snails attached the macroalgal mats of *Enteromorpha* at Station A, and *Batillaria multiformis* and *B. cumingi* attached both the macroalgae and the leaves of seagrass at Station B. Meziane & Tsuchiya (2000), using fatty acid analysis, suggested that *Batillaria zonalis*, always observed on a macroalgal mat, mainly fed on green macroalgae. At Station B, we did not observe *Cerithidea* (*Cerithideopsilla*) *rhizophorarum* colonizing the macroalgae or the leaves of seagrasses. However, the main food sources for *C. rhizophorarum* were estimated to be also macroalgae and seagrass, although its nitrogen isotope value was slightly lower than that of *B. cumingi*.

The results of our mixing model showed the high contribution (39–45%) of seagrass leaves to snails on the tidal flats at the temperate site. Live tissues of marine vascular plants are of limited use as food for marine animals; therefore, other primary producers or the detritus food chain support secondary production in these communities (e.g. Mann, 1972; Fenchel, 1977; Kharlamenko *et al.*, 2001). By observing

Table 2. Contribution of the potential food sources to snails using IsoSource mixing model for Station B. POM, mean particulate organic matter.

Taxon	Macroalgae		Seagrass		Benthic microalgae		SOM		Sediment		Terrestial plants	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
C. rhizophorarum	49.6 ± 4.1	40–62	44.9 ± 2.7	38–52	1.3 ± 1.7	0–8	1.1 ± 1.6	0–6	1.2 ± 1.6	0–6	1.9 ± 2.2	0–10
B. cumingi	56.4 ± 3.8	46–68	38.7 ± 2.8	32–46	1.1 ± 1.6	0–6	1 ± 1.5	0–6	1 ± 1.6	0–8	1.7 ± 2.1	0–10
B. multiformis	56.2 ± 3.5	48–66	39.5 ± 2.6	34–46	1 ± 1.4	0–6	0.9 ± 1.4	0–6	0.9 ± 1.4	0–6	1.5 ± 2	0–8

feeding, Whitlatch & Obrebski (1980) reported that the gastropod *Cerithidea californica* occasionally feeds on large vascular plant fragments. Also, Kharlamenko *et al.* (2001) suggested that the gastropod *B. cumingi* derived on average 50% of its carbon from *Z. marine* in the subtidal seagrass bed. Thus, seagrass species would play an important role as food sources on tidal flats as well as on the seagrass bed of the costal zone.

Increasing attention has focused on benthic microalgae as a food source for the many benthic invertebrates on the tidal flats (e.g. Currin *et al.*, 1995; Doi *et al.*, 2005; Kanaya *et al.*, 2005). For Gastropoda, Page (1997) used stable isotopes to show that *Cerithidea californica*, inhabiting tidal flats, feeds principally on benthic microalgae. In this study, however, the contributions of benthic microalgae to the snails were very low. Using fatty acid analysis, Meziane & Tsuchiya (2000) suggested that the contribution of diatoms to *C. cingulata* was weaker than that of green macroalgae and bacteria at Ohura Bay (Station A in this study). Doi *et al.* (2006) also suggested that deposit-feeding chironomid larvae assimilated green algae more than benthic diatoms. The snails in this study may assimilate the green macroalgae more easily than benthic microalgae (mainly diatoms), and feed mainly on the macroalgae in the algal patches on the tidal flat. In addition, recent studies have suggested that the contribution of terrestrial organic matter is lower than that of other sources in food webs on tidal flats (e.g. Kurata *et al.*, 2001; Doi *et al.*, 2005). Our mixing-model results revealed the lower contribution of mangrove and salt marsh plants to the snails and supported the low contribution of terrestrial organic matter in their systems, although the vegetation of the sub-tropical and temperate sites were quite different.

In conclusion, we showed that macroalgae and seagrass made a greater contribution to snail biomass than the other potential food sources, and thus, that macroalgae and seagrass play an important role as food sources not only at their growing sites but also on tidal flats. We should acknowledge the limitation of this study. This collection was conducted in a season, however, the biomass of macroalgae and seagrass may vary seasonally. Thus, the food source composition of the gastropods would be changed along with biomass of macroalgae and seagrass. Future studies are needed to reveal the seasonal dynamics of the food sources for gastropods. To conserve local gastropod populations, we should consider the connection between tidal flats and coastal marine ecosystems in ensuring their supply of food.

ACKNOWLEDGEMENTS

REFERENCES

Aikins S. and Kikuchi E. (2002) Grazing pressure by amphipods on microalgae in Gamo Lagoon, Japan. *Marine Ecology Progress Series* 245, 171–179.

Bustamante R., Branch G. and Eekhout S. (1995) Maintenance of an exceptional grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* 76, 2314–2329.

Couch C.A. (1989) Carbon and nitrogen stable isotopes of meiobenthos and their food resources. *Estuarine, Coastal and Shelf Science* 28, 433–441.

Costanza R., d'Arge R., Groot R., Farber S., Grasso M., Hannon B., Limburg K., Naeem S., O'Nell R., Paruelo J., Raskin R., Sutton P. and Belt M. (1997) The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.

Currin C.A., Newell S.Y., and Paerl H.W. (1995) The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series* 121, 99–116.

Doi H., Kikuchi E., Hino S., Itoh T., Takagi S. and Shikano S. (2003a) Isotopic (δ13C) evidence for autochthonous origin of sediment organic matter in small, acidic Lake Katanuma, Japan. *Marine and Freshwater Research* 54, 253–257.

Doi H., Kikuchi E., Hino S., Itoh T., Takagi S. and Shikano S. (2003b) Seasonal dynamics of carbon stable isotope ratios of particulate organic matter and benthic diatoms in strongly acidic Lake Katanuma. *Aquatic Microbial Ecology* 33, 87–94.

Doi H., Matsumasa M., Toya T., Satoh N., Mizota C., Maki Y., Kikuchi E. (2005) Spatial shifts in food sources for macrozoobenthos in an estuarine ecosystem: carbon and nitrogen stable isotope analyses. *Estuarine, Coastal and Shelf Science* 64, 316–322.

Doi H., Kikuchi E., Takagi S. and Shikano S. (2006) Selective assimilation of the deposit feeders: experimental evidence using stable isotope ratios. *Basic and Applied Ecology* 7, 159–166.

Duarte C.M. (1989) Temporal biomass variability and production biomass relationship of seagrass communities. *Marine Ecology Progress Series* 51, 269–276.

Fenchel T. (1977) Aspects of decomposition of seagrasses. In McRoy C.P. and Helfferich C. (eds) *Seagrass ecosystems: scientific perspective.* New York: Marcel Dekker, pp. 195–234.

France R.L. and Peters R.H. (1997) Ecosystem differences in the trophic enrichment of 13C in aquatic food webs. *Canadian Journal of Fishery and Aquatic Sciences* 54, 1255–1258.

Guest M.A., Connolly R.M. and Loneragan N.R. (2004) Carbon movement and assimilation by invertebrates in estuarine habitats at a scale of metres. *Marine Ecology Progress Series* 278, 27–34.

Hyndes G.A. and Lavery P.S. (2005) Does transported seagrass provide an important trophic link in unvegetated, nearshore areas? *Estuarine, Coastal and Shelf Science* 63, 633–643.

Kanaya G., Nobata E., Toya T. and Kikuchi E. (2005) Effects of different feeding habits of three bivalve species on sediment characteristics and benthic diatom abundance. *Marine Ecology Progress Series* 299, 67–78.

Kharlamenko V.I., Kiyashko S.I., Imbs A.B. and Vyshkvartzev D.I. (2001) Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulfur stable isotope ratio and fatty acid analyses. *Marine Ecology Progress Series* 220, 103–117.

Kimura S. and Kimura T. (1999) The gastropod fauna of the marshes of the reed (*Phragmites australis* (Cav.))in the estuaries in Mikawa Bay and Ise Bay, Japan. *Japanese Journal of Benthology* 54, 44–56. [In Japanese with English abstract.]

Kimura T. (2005) Marine and brackish water invertebrates in the red data book of Japan. *Japanese Journal of Benthology* 60, 2–10. [In Japanese.]

Kurata K., Minami H. and Kikuchi E. (2001) Stable isotope analysis of food sources for salt marsh snails. *Marine Ecology Progress Series* 223, 167–177.

Maki E., Ohtaki H. and Tomiyama K. (2002) Distribution and substrate preference among four Batillarid and Patamidid species, with observations on seasonal changes in the distribution of *Cerithideopsilla djadjariensis* (K. Martin, 1889) (Gastropoda: Potamididae). *Venus* 61, 61–76. [In Japanese with English summary.]

Mann K.H. (1972) Macrophyte production and detritus food chain in coastal waters. *Memorie dell'Istituto Italiano di Idrobiologia* 29, 353–383.

Mann K.H. (2000) *Ecology of coastal waters: with implications for management*, Second edition. Malden, MA: Blackwell Scientific Inc.

McCutchan J.H., Lewis W.M., Kendall C. and McGrath C.C. (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102, 378–390.

McRoy C.P. and McMillan C. (1977) Production ecology and physiology of seagrasses. In McRoy C.P. and Helfferich C. (eds) *Seagrass ecosystems: scientific perspective*. New York: Marcel Dekker, pp. 53–87.

Melville A.J. and Connolly R.M. (2005) Food webs supporting fish over subtropical mudflats are based on transported organic matter not *in situ* microalgae. *Marine Biology* 148, 363–371.

Meziane T. and Tsuchiya M. (2000) Fatty acids as tracers of organic matter in the sediment and food web of a mangrove intertidal flat ecosystem, Okinawa, Japan. *Marine Ecology Progress Series* 200, 49–57.

Motonaga T. (1977) *Ecological distribution of macrobenthos in Oura mangrove swamp*. Okinawa Master's Report, University of the Ryukyu.

Nakano S. and Murakami M. (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Science of the USA* 98, 166–170.

Page H.M. (1997) Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California salt marsh. *Estuarine, Coastal and Shelf Science* 45, 823–834.

Phillips D.L., and Gregg J.W. (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136, 261–269.

Polis G.A., Anderson W.B. and Holt R.D. (1997) Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28, 289–316.

Riera P., Stal L.J. and Nieuwenhuize J. (2002) $\delta^{13}C$ versus $\delta^{15}N$ of co-occurring molluscs within a community dominated by *Crassostrea gigas* and *Crepidula fornicata* (Oosterschelde, The Netherlands). *Marine Ecology Progress Series* 240, 291–295.

Schindler D.E., Leavitt P.R., Brock C.S., Johnson S.P. and Quay P.D. (2005) Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. *Ecology* 86, 3225–3231.

Wainright S.C., Weinstein M.P., Able K.W. and Currin C.A. (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. *Marine Ecology Progress Series* 200, 77–91.

Whitlatch R.B. and Obrebski S. (1980) Feeding selectivity and coexistence in two deposit-feeding gastropods. *Marine Biology* 58, 219–225.

and

Zieman J.C. and Wetzel R.G. (1980) Productivity of seagrasses: methods and rates. In Phillips R.C. and McRoy C.P. (eds) *Hand-book of seagrass biology: an ecosystem perspective*. New York: Garland STPM Press, pp. 86–116.

Correspondence should be addressed to:
Hideyuki Doi
Graduate School of Life Sciences, Tohoku University
2-1-1, Katahira, Aoba-ku, Sendai 980-8577, Japan
email: h-doi@agr.ehime-u.ac.jp