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VENUS 60 (1-2): 71-78, 2001

Sulfur Nutrition of Gastropods and Bivalves Relevant to the Mangrove Forests: A Case Study from Central Sumatra, Indonesia

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Abstract: Sulfur nutrition of gastropods and bivalves relevant to the mangrove ecosystem from central Sumatra, Indonesia was studied using stable isotopic signature ($^{34}S/^{32}S$ ratios as commonly designated by $\delta^{34}S$ notation, per mil deviation relative to Cañyon Diablo troilite, CDT). The mangroves (*Rhizophora mucronata*, *R. apiculata* and *Bruguiera gymnorrhiza*) assimilate light sulfur (^{32}S) ($\delta^{34}S = -14.4$ to -6.2 ‰) from among sulfides in the substrate sediments ($^{34}S = -20.3$ to -11.9 ‰). The sulfides derive from the reduction of seawater sulfate by activity of sulfate-reducing bacteria under an ample supply of organic matter from mangrove trees. The gastropods (*Terebralia palustris*, *T. sulcata* and *Telescopium* sp.), which feed on the litter of the associated mangroves at low tide, have low $\delta^{34}S$ values ranging from -2.5 to $+9.5$ ‰ in their soft tissues. The present data indicates that of the sulfur assimilated by these species, 40-70 % is derived from mangroves, with the remainder coming from sulfates in ambient seawater ($\delta^{34}S = +21$ ‰), the absolute end-member of sulfur reservoir for marine organisms. The isotopic data provide an overall figure for sulfur nutrition that is difficult to estimate by conventional observation. The common bivalve (*Anadara* sp., $\delta^{34}S = +10.3$ ‰) and a gastropod (*Strombus* (*Euprotomus*) *aurisdianae*, $\delta^{34}S = +14.4$ ‰) obtained from areas of no vegetation in the peripheral regions of the mangrove forests also indicate assimilation of isotopically light sulfur. The isotopically light sulfur would be derived from mangrove leave litter as suspended detritus.

Keywords: gastropod, bivalve, mangrove forest, sulfur nutrition, sulfur isotope, feeding habitat

Introduction

Mangrove forests commonly develop along coastlines where tidal influences prevail, in humid tropical and subtropical climates. The well-developed mangrove forest often features deep, reduced fine deposits (Kira, 1994) in which pyrite and related sulfides predominate due to reduction of the ambient seawater sulfate by sulfate-reducing bacteria in an ample supply of organic debris from mangrove litter (Ogino, 1992). Sulfide-sulfur formed by such microbial activity often depletes ^{34}S ($\delta^{34}S = -20 \pm 10$ ‰; Krouse & Grinenko, 1992) in contrast to the high $\delta^{34}S$ value of the seawater sulfate ($\delta^{34}S = +21$ ‰; Rees *et al.*, 1978). Previous sulfur isotopic studies (Fry *et al.*, 1982; Okada & Sasaki, 1995, 1998) indicate that certain mangroves, particularly the genera, *Rhizophora* and *Bruguiera*, selectively assimilate light sulfide-sulfur from the substrate muds via their root systems as an adaptation to a reductive environment.

World-wide need for sustainable use of mangrove ecosystems has been recognized recently (Tsujii *et al.*, 1994). Several benthic animals, particularly gastropods have been reported from sediment environments under mangrove forests in Indonesia (Wada, 1986; Ogino & Chihara, 1986). Grazing on mangrove litter by *Terebralia palustris* has been recorded (Nishihira, 1983). Compared with crustaceans, few studies have been conducted on the role of gastropods and bivalves in the

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food web under the mangrove ecosystem (Wada, 1989). There are no assessments of the sulfur nutrition of the gastropods and bivalves relevant to *Rhizophora* and *Bruguiera* forests. Here, we report a case study from central Sumatra, Indonesia where the interrelationships between sulfides in the substrate sediment, litter from *Rhizophora* and *Bruguiera* forests and gastropods and bivalves are involved.

Materials and Methods

Study areas

Locations of the study sites in central Sumatra are shown in Fig. 1. A brief description of the analyzed samples is presented in Table 1. The samples include a set of black mud, mangrove leaves of *Rhizophora* and *Bruguiera*, and gastropods and bivalves from the mangrove forests (Fig. 2). Samples were collected in late August, 1999, at low tide. Except for Site 3 at Airbangis, all study sites had been exposed during the sampling.

Three sampling sites, Sites 1, 2, and 3, were selected at Airbangis (Table 1). Site 1 was located in a small inlet with dense *Rhizophora mucronata* stands. The qudrat of Site 1 is 50 m by 150 m. Reduced black sediment (30 cm in thickness) covered this site. This site featured a sparse (less than 1 individual/m^2) *Terebralia palustris* population with medium size individuals (shell length, less than 100 mm). Site 2 was covered by white coral limestone fragments. *Terebralia palustris* (shell length, more than 130 mm) was abundant at this site (more than 10 individual/m^2) under *Bruguiera gymnorrhiza* stands. Site 3 consisted mainly of fine-grained coral limestone frag-

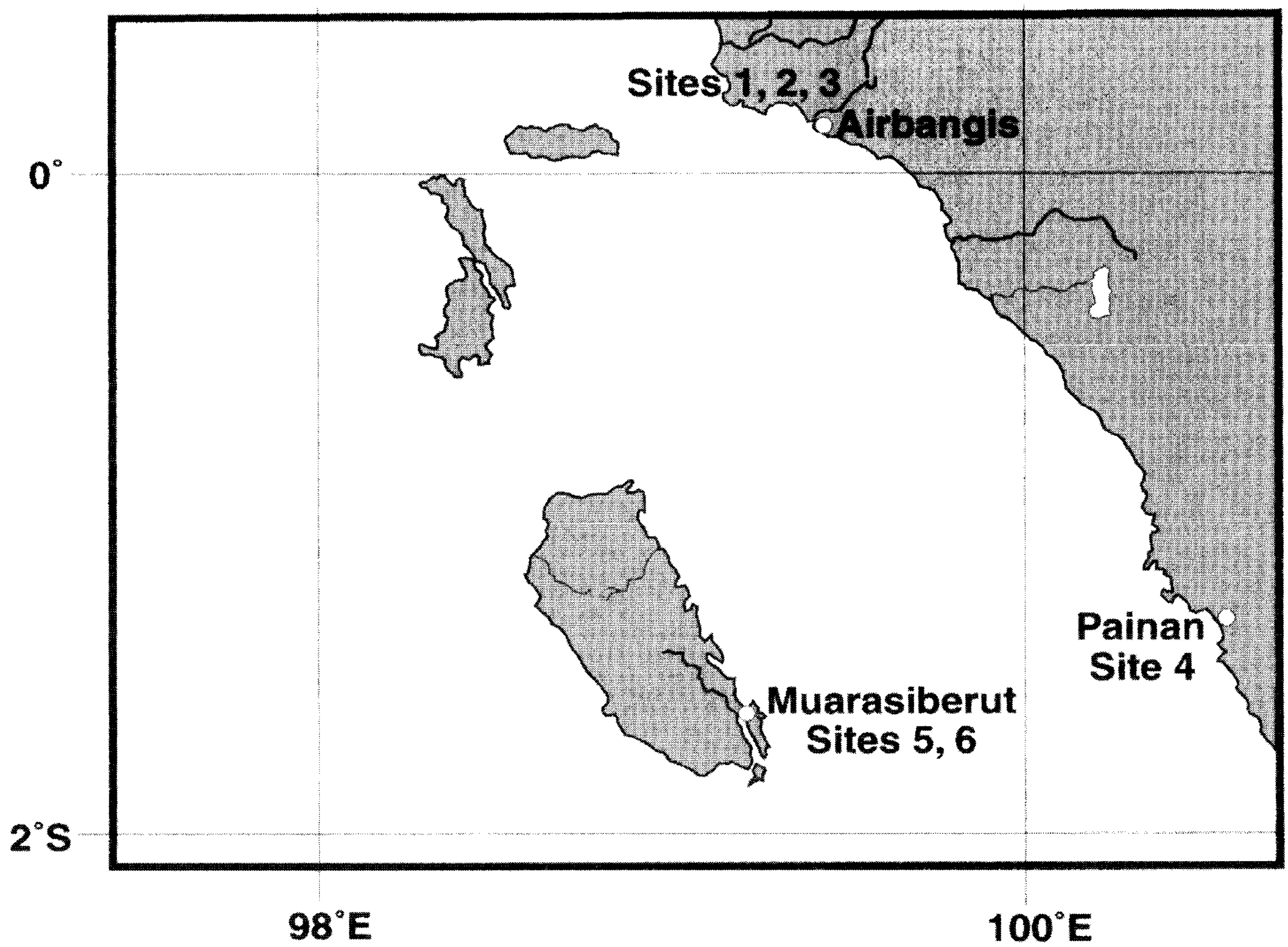

Fig. 1. Locations of the sample site in central Sumatra, Indonesia. Numbers in the figure correspond to sample sites in Table 1.

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Table 1. Sulfur content and isotopic composition of gastropds and bivalves associated with mangrove leaf litter and substrate sediments in central Sumatra, Indonesia.

Location				Benthic animal			Mangrove			Sulfide-sulfur in substrate sediment	
					Sulfur in soft-tissue			Sulfur in leaf			
Region[1]	Site[1]	Latitude	Longitude	Species[3]	Content (%)[4]	$\delta^{34}S$ *vs.* CDT (‰)	Species	Content (%)[4]	$\delta^{34}S$ *vs.* CDT (‰)	Content (%)[4]	$\delta^{34}S$ *vs.* CDT (‰)
Airbangis	1	00°13.436'N	99°18.047'E	*Terebralia palustris* (G)	0.97	-2.5	*Rhizophora mucronata*	0.50	-14.4	3.93	-14.5
	2	00°13.453'N	99°18.046'E	*ditto*	1.18	+0.7	*Bruguiera gymnorrihiza*	0.27	-9.8	-	Not recovered[5]
	3[2]	n d	n d	*Anadara* sp.(B)	0.84	+10.3		-	-	-	-
				Strombus (*Euprotomus*) *aurisdiana* (G)	1.06	+14.4		-	-	-	-
Painan	4	01°13.935'S	100°26.146'E	*Terebralia sulcata*	1.06	+9.5	*Rhizophora apiculata*	0.36	-6.2	1.54	-20.3
Muarasiberut	5	01°33.973'S	99°11.620'E	*Telescopium* sp.(G)	0.67	-0.1	*Rhizophora apiculata*	0.29	-12.7	1.01	-11.9
	6	01°33.820'S	99°11.786'E	*Terebralia palustris*	1.05	+5.0	*ditto*	0.27	-7.3	0.08	-14.1
										0.17	-17.4

[1] Refer Fig. 1.
[2] Peripheral region of the mangrove forest. About 200 m northeast from Site 2.
[3] G = gastropods, B = bivalves
[4] 105°C dry-matter basis.
[5] Sandy calcareous sediments.
nd = not determined.

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ments. A gastropod, *Strombus* (*Euprotomus*) *aurisdianae*, and a bivalve, *Anadara* sp., were collected at site 3, where a few pneumatophores of *Avicenia* sp. were observed.

One sampling site, Site 4, was selected in Painan where *Rhizophora apiculata* was dominant (Table 1). *Terebralia sulcata*, (shell length, less than 40 mm) was the major benthic animal (less than 2 individual/m^2) in this site. The sediments at the mangrove forest floor consisted of gray to dark clayey material which had been washed out from neighboring low hills and terraces.

Two sampling sites, Sites 5 and 6, were selected in Muarasiberut, Siberut Island (Table 1 and Fig. 1). The major mangrove species at these sites was *Rhizophora apiculata,* as at the Painan sites. Site 5 is located in a small inlet with a small river. *Telescopium* sp. (shell length, less than 50 mm, more than 20 individual/m^2) was observed in this site. It was associated with decaying litter from the mangrove trees. Site 6 was located at a small beach open to the Indian Ocean. Thick, black clayey deposits covered the coast around the sample sites. A sparse population of *Terebralia palustris* (less than 1 individual/m^2) was observed there.

Samples for sulfur isotopic analysis

Sediment samples including sulfide-sulfur were collected at a depth of ca. 2 to 15 cm around the rhizosphere of the mangrove trees. The samples were immediately packed into polyethylene tubes with dual stoppers. Biological samples collected from the natural environment are often subject to significant variations. To average such variation, composite samples were prepared as follows. Leaf samples were collected from several individuals of the same mangrove species, and quickly dried in the field under sunlight. The composite samples of the gastropods and bivalves, which were composed of 5 to 10 individuals for each species depending on the size, were first boiled in freshwater to extract the whole soft tissues. Then, all the soft tissue specimens were placed in 80 % ethanol solution.

Analytical methods

The analytical procedures employed in the present study are those described by Mizota *et al.* (1999) and Yamanaka *et al.* (2000). Soft tissue of the collected specimens was transferred into Visking tubes, and dialysed against de-ionized water overnight at 5 °C to eliminate excess seawater sulfates. The salt-free materials were then freeze-dried. A 200 to 500 mg sample of the dry biological material was combusted in a high-pressure oxygen bomb (Parr Bomb #1108, Parr Inc.) to convert all the sulfur compounds into sulfates. Excess seawater sulfate in the substrate sediment was removed by dialysis as similarly described above. Sulfide-sulfur in the sediment was recovered by treatment with warm hydrogen peroxide. All the resulting dissolved sulfates were recovered as a form of $BaSO_4$ by conventional procedure. The dry $BaSO_4$ was mixed with V_2O_5 and silica mixture (1 : 1) to yield SO_2 by thermal decomposition (Yanagisawa and Sakai, 1983). The $^{34}S/^{32}S$ ratios were determined for the SO_2 with a SIRA 10 mass spectrometer (VG Isogas Inc.) installed at the Institute for Study of the Earth's Interior, Okayama University. $^{34}S/^{32}S$ ratios were shown by conventional $\delta^{34}S$ notation, a per mil (‰) variation relative to Cañyon Diablo troilite, CDT. The overall analytical error is ±0.1 ‰.

Results and Discussion

The sulfide-sulfur content of substrate sediments obtained from the habitat varied from 0.08 to 3.93 % (Table 1). The highest content was observed at Site 1 in Airbangis where detritus from the mangroves accumulated because of the topography. $\delta^{34}S$ values of the sulfide-sulfur ranged from −20.3 to −11.9 ‰. Such low $\delta^{34}S$ values are interpreted as being derived from steady state reduction (sulfur isotope fractionation between sulfide and concomitant seawater sulfate; −25 ± 10 ‰; Kaplan & Rittenberg, 1964) of seawater sulfate (Rees *et al.*, 1978 ; $\delta^{34}S$ = +21 ‰) by

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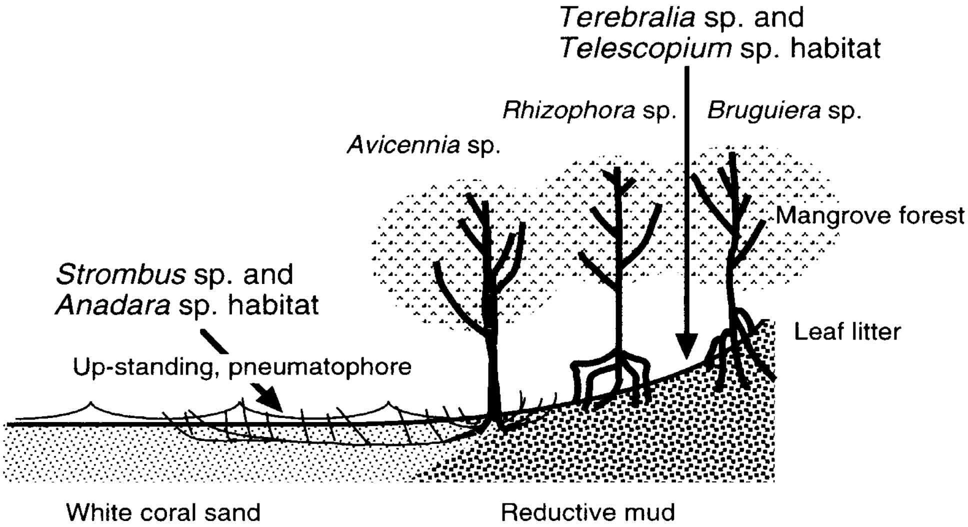

Fig. 2. A schematic illustration of the mangrove forests in Airbangis from central Sumatra, Indonesia.

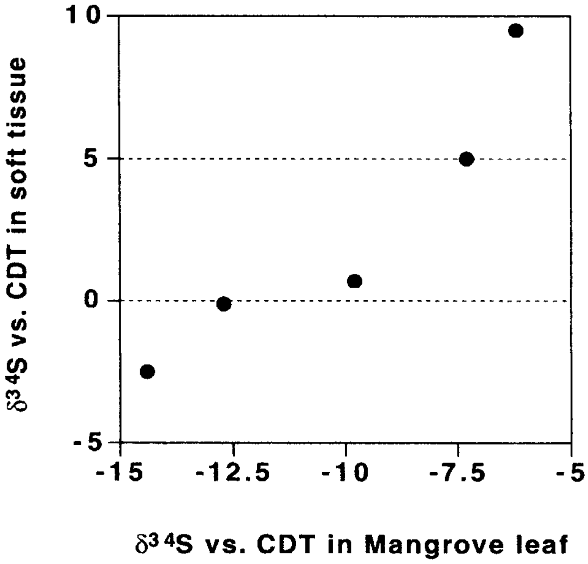

Fig. 3. Relationship between $\delta^{34}S$ values of the gastropods soft tissues and those of mangrove leaves in gastropod habitats from central Sumatra, Indonesia.

sulfate-reducing bacteria in association with sulfur-oxidizing bacteria under aerobic conditions (Yamanaka *et al.*, 2000).

Total sulfur content of the mangrove leaves, at the study habitat ranged from 0.27 to 0.50 % (Table 1). Negative $\delta^{34}S$ values of −14.4 to −6.2 ‰ for the leaves are comparable to those from the associated substrate sediments, indicating incorporation and assimilation of sulfide-sulfur in the substrate sediments around their stands. Okada & Sasaki (1998) reported similar lower values for *Rhizophora apiculata* ($\delta^{34}S$ = −15.6 to −5.8 ‰, n = 3), *R. mucronata* ($\delta^{34}S$ = −2.2 and +2.6 ‰) and *Bruguiera gymnorrhiza* ($\delta^{34}S$ = −15.1 and −5.1 ‰) from Micronesia, Thailand and Japan.

Sulfur content of dry soft tissues of the molluscan samples examined in the present study ranged from 0.67 to 1.18 % (Table 1). The $\delta^{34}S$ values of soft tissues from gastropod samples, *Terebralia palustris*, *T. sulcata* and *Telescopium* sp., varied from −2.5 to +9.5 ‰. These values are clearly higher than those of the associated mangrove leaves ($\delta^{34}S$ = −14.4 to −6.2 ‰). There

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could be seen a weak correlation between the $\delta^{34}S$ values of the soft tissues of the relevant gastropod and those of mangrove leaves within one sample site (Fig. 3). Observation of the feeding habits of the gastropod during the sampling at low tide showed that *T. palustris* actively feeds on the fresh leaf litter of the mangroves, as observed by Nishihira (1983). The other two gastropods (*T. sulcata* and *Teles.* sp.) fed on the decaying litter of the mangroves. Nevertheless, the $\delta^{34}S$ values of the gastropod soft tissues indicate that their sulfur nutriton is not entirely derived from the associated mangroves.

Assuming that the $\delta^{34}S$ values of the gastropod soft tissues could instead be interpreted in terms of a simple mixing of two end-members, i.e., light sulfur derived from mangrove leaf litter and heavy sulfur from ambient seawater sulfate ($\delta^{34}S$ = +21 ‰; Rees *et al.*, 1978), the ratio of each component could be calculated where slight negative kinetic sulfur isotope fractionation associated with assimilatory metabolism of these sulfur sources into body constituents of the gastropod is involved (Yamanaka *et al.*, 2000). The estimated contribution of mangrove leaf sulfur to the total body sulfur of the gastropod varied from 40 % (Site 4 in Painan) to 70 % (Site 2 in Airbangis).

The average litter yield of most mangrove forests is 10 ton/ha/year (equivalent to 60 g/ 25 m^2/day) (Tsujii *et al.*, 1994). Nishihira *et al.* (1988) reported that the daily uptake of leaf litter by a *T. palustris* population amounts to 11.8 g of dry leaf / 25 m^2/ day. That population is composed of 39 juveniles, 6 subadults and 55 adults per m^2, in a mangrove swamp in Nakama River estuary, Iriomote Island, southwestern Japan. Such value would roughly substantiate the validity of our estimations based on the sulfur isotopic composition of the soft tissues from the population of the same species in central Sumatra.

On the other hand, Site 3, where the highest $\delta^{34}S$ values were observed, featured no mangrove leaf litter. Therefore, the organisms there are considered to not depend on mangrove leaves for food. A bivalve, *Anadara* sp., is a suspension feeder, which incorporates major nutrition in the form of suspended particulate matter (Rodelli *et al.*, 1984). A gastropod, *Strombus* (*Euprotomus*) *aurisdianae*, commonly inhabits sandy bottom and feeds on seagrasses (Abbott & Dance, 1982). $\delta^{34}S$ values of *Anadara* sp.; +10.3 ‰ and *Strombus* (*Euprotomus*) *aurisdianae* ; +14.4 ‰ (Table 1), inhabiting the tops of pneumatophores of *Avicennia* sp. on a sandy coast off a mangrove forest (Fig. 2), are still lower than those of the common marine benthic animals ($\delta^{34}S$ = +15 to +19 ‰, Yamanaka *et al.*, 2000). A plankton sample collected by towing a 300-μm mesh net in Woods Hole passage (Massachusetts, USA) gave a value of +18.6 ‰ (Peterson *et al.*, 1985). The isotopic data indicate the positive incorporation of isotopically light sulfur by such animals, even in the peripheral regions where there are no mangrove trees. The source of isotopically light sulfur is considered to be detritus of mangrove leaves which incorporate sulfide-sulfur derived from sulfate-reducing bacteria in the sediments.

Acknowledgments

Field assistance was provided by H. Murano, H. Naitoh, M. Edison, S. Wilson and K. Eni. Sulfur isotopic measurement was conducted at the Institute for Study of the Earth's Interior, Okayama University as a joint research program. Laboratory facilities were provided by Prof. M. Kusakabe. We are grateful to all the above personnel.

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(Received July 21, 2000 / Accepted December 1, 2000)

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マングローブ林下に生息する巻貝および二枚貝の硫黄栄養：安定同位体によるインドネシア・中部スマトラ域についての事例研究

山中寿朗・溝田智俊

要　旨

インドネシア・中部スマトラのマングローブ林下に生息する巻貝および二枚貝の硫黄栄養を安定同位体組成（$^{34}S/^{32}S$ ；$\delta^{34}S$ 表示）を用いて研究した．3 種のマングローブ（ヤエヤマヒルギ *Rhizophora mucronata*，*Rhizophora apiculata* およびオヒルギ *Bruguiera gymnorrhiza*）は，基質泥に含まれる，海水硫酸の微生物還元に由来する同位体的に軽い硫化物硫黄（$\delta^{34}S = -20.3$ から -11.9 ‰）の一部を同化していることが，その低い硫黄同位体組成（$\delta^{34}S = -14.4$ から -6.2 ‰）から推察された。干潮時に盛んにマングローブ落葉および腐朽落葉落枝を摂食している 3 種の巻貝（キバウミニナ *Terebralia palustris*，マドモチウミニナ *Terebralia sulcata* およびセンニンガイ *Telescopium* sp.）の軟組織の硫黄同位体組成（$\delta^{34}S = -2.5$ から $+9.5$ ‰）に基づき，軟組織に取り込まれた硫黄の 40 ～ 70 %がマングローブ葉由来であると推察された。残りの硫黄栄養はおそらく直接，あるは間接的に海水硫酸に由来すると推定された。今回測定した硫黄安定同位体組成から，これらマングローブ林下の底生動物のうち，通常目視観察では推定困難な硫黄栄養源について，直接的な証拠が得られた。マングローブ林下の底泥中で生成された，微生物起源の軽い硫黄源は，近隣海域の一般的な巻貝（マイノソデガイ *Strombus*（*Euprotomus*）*aurisdianae*; $\delta^{34}S = +14.4$ ‰）や二枚貝（アカガイ，*Anadara* sp.; $\delta^{34}S = +10.3$ ‰）にも及んでいることが，その軟組織についての硫黄同位体組成から推察された。

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