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Possible Food Sources of Macrozoobenthos in the Manko Mangrove Ecosystem, Okinawa (Japan): A Stable Isotope Analysis Approach

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Abstrak: Mengenal pasti sumber makanan berpotensi di dalam ekosistem paya bakau adalah suatu proses yang kompleks kerana penerimaan pelbagai input daripada darat dan laut. Kajian ini, yang telah dijalankan di ekosistem paya bakau Manko, Okinawa, Jepun, telah mengenal pasti komposisi isotop stabil δ^{13}C dan δ^{15}N dalam pengeluar primer dan makrozoobentos untuk menganggarkan sumber makanan berpotensi yang telah diasimilasi dan untuk mengetahui aras trofik sasaran makrozoobentos. Kami telah mengukur penanda-penanda dua isotop stabil oleh tiga gastropod (*Cerithidea* sp., *Cassidula mustelina, Peronia verruculata*), dua ketam (Grapsidae sp., *Uca* sp.), daun pokok paya bakau (*Kandelia candel*) dan endapan dari ekosistem paya bakau tersebut. Keputusan tanda isotop karbon dan nitrogen masing-masing adalah seperti berikut: –22.4‰ dan 8.6‰ untuk *Cerithidea* sp., –25.06‰ dan 8‰ untuk C. *mustelina,* –22.58‰ dan 8‰ untuk *P. verruculata*, –24.3‰ dan 10.6‰ untuk Grapsidae yang tidak dikenal pasti, –21.87 ‰ dan 11.5 ‰ untuk *Uca* sp., –29.81‰ dan 1‰ untuk *K. candel,* dan –24.23‰ dan 7.2‰ untuk endapan. Penanda asimilasi isotop stabil makrozoobentos menunjukkan endapan sebagai sumber makanan. Melihat kepada aras trofik, nilai isotop stabil juga boleh menunjukkan bahawa lima spesies makrozoobentos tersebut ialah pengguna sekunder atau lebih tinggi.

Kata kunci: Sumber Makanan, Isotop Stabil, Aras Trofik, Ekosistem Paya Bakau, Makrozoobentos

Abstract: Identifying potential food sources in mangrove ecosystems is complex because of the multifarious inputs from both land and sea. This study, which was conducted in the Manko mangrove ecosystem of Okinawa, Japan, determined the composition of the stable isotopes δ^{13}C and δ^{15}N in primary producers and macrozoobenthos to estimate the potential food sources assimilated and to elucidate the target trophic levels of the macrozoobenthos. We measured the two stable isotope signatures of three gastropods (*Cerithidea* sp., *Cassidula mustelina, Peronia verruculata*), two crabs (Grapsidae sp., *Uca* sp.), mangrove tree (*Kandelia candel*) leaves, and sediment from the mangrove ecosystem. The respective carbon and nitrogen isotope signature results were as follows: –22.4‰ and 8.6‰ for *Cerithidea* sp., –25.06‰ and 8‰ for C. *mustelina,* –22.58‰ and 8‰ for *P. verruculata*, –24.3‰ and 10.6‰ for unidentified Grapsidae, –21.87 ‰ and 11.5 ‰ for *Uca* sp., –29.81‰ and 11‰ for *K. candel,* and –24.23‰ and 7.2‰ for the sediment. The stable isotope assimilation signatures of the macrozoobenthos indicated sediment as

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their food source. Considering the trophic levels, the stable isotope values may also indicate that the five macrozoobenthos species were secondary or higher consumers.

Keywords: Food Source, Stable Isotope, Trophic Level, Mangrove Ecosystem, Macrozoobenthos

INTRODUCTION

Mangrove ecosystems serve significant ecological functions, particularly in providing food sources for various terrestrial and marine animals (Field 1998; Hsieh *et al.* 2002; Hogarth 2007; Nagelkerken *et al.* 2008). The forms of carbon and nitrogen that are found in the food sources in mangrove ecosystems are complex; these food sources are derived from external ecosystems and are transported by river and tidal movements (such as land plants and seagrass) or from ecosystems, such as phytoplankton and micro- or macro-algae (Marguillier *et al.* 1997; Bouillon *et al.* 2004; Kristensen *et al.* 2008).

Many types of macrozoobenthos have been shown to consume mangrove-derived material and its associated biota, such as detritus, microphytobenthos, filamentous algae, diatoms and sediment (Wada & Wowor 1989; Marguillier *et al.* 1997; Hsieh *et al.* 2002; Bouillon *et al.* 2004; Muzuka & Shunula 2006; Nordhaus & Wolff 2007; Pape *et al.* 2008; Penha-Lopes *et al.* 2009; Nordhaus *et al.* 2011).

The food sources of macrozoobenthos can be identified using four methods: direct observation in the field and examination of the digestive system (Nordhaus & Wolff 2007; Davenport *et al.* 2011), biomarkers (fatty acids) (Meziane & Tsuchiya 2000; Meziane *et al.* 2002; Dalsgaard *et al.* 2003; Alfaro *et al.* 2006), stable isotopes (Wada *et al.* 1991; Marguillier *et al.* 1997; Kasai *et al.* 2004; Alfaro 2008; Vonk *et al.* 2008; Nordhaus *et al.* 2011) and DNA molecular composition (Blankenship & Yayanos 2005).

Stable isotope (*i.e.,* carbon and nitrogen isotopes) analysis has been widely used in marine ecosystems to understand ecological processes, including to elucidate the origin of dissolved organic matter in mangrove ecosystems (Marguillier *et al.* 1997; Bouillon *et al.* 2002; Hsieh *et al.* 2002; Kasai *et al.* 2004; Alfaro 2008; Vonk *et al.* 2008; Nordhaus *et al.* 2011); to differentiate different food web paths; to determine the trophic levels of the community (Vander Zanden *et al.* 1999; Pasquaud *et al.* 2007; Abrantes & Sheaves 2009); to trace food sources, the origin of water contamination, nutrient and animal migration patterns, nutrient input, and species' body size (Jardine *et al.* 2003; Fry 2006); and to study the physiology of marine biota (Lorrain *et al.* 2002). In addition, stable isotope analysis can be used to study mangrove photosynthesis (Muzuka & Shunula 2006), to assess the levels of nitrification (Sulzman 2007), and to study bio-indicators in marine ecology (Fukumori *et al.* 2008).

Stable isotopes of carbon in consumers have signatures that are identical to or reflective of their food source (DeNiro & Epstein 1978), and nitrogen in animals can provide information on the composition of nitrogen in their food sources (DeNiro & Epstein 1981). Carbon and nitrogen assimilation by consumers indicates the degree of fractionation or transfer of carbon and nitrogen ($\Delta\delta^{13}C$ and $\Delta\delta^{15}N$) (DeNiro & Epstein 1978, 1981; Dubois *et al.* 2007). The signatures of the ratio of carbon assimilation from food sources by consumers are usually in the range of –2 to +2‰ (Bouillon *et al.* 2008).

This study, which was conducted in the Manko mangrove ecosystem of Okinawa, Japan, had the following goals: (1) to determine the stable isotopic ratios of carbon, $\delta^{13}C$, and nitrogen, $\delta^{15}N$, in primary producers and five species of macrozoobenthos; (2) to elucidate the potential food sources assimilated by the macrozoobenthos; and (3) to estimate the trophic level position of the macrozoobenthos.

MATERIALS AND METHODS

Study Site

The research site was a Manko mangrove ecosystem on Okinawa Island, Japan (26°11'N, 127°40'E) (Fig. 1) that contains several species of mangrove trees, including *Kandelia candel*, *Bruguiera gymnorhiza*, *Rhizophora stylosa* and *Excoecaria agallocha*. The mangrove ecosystem is dominated by *K. candel* (Mchenga *et al.* 2007) growing in black, soft clay or sandy mud (Islam *et al.* 2004). Various macrozoobenthos, such as crustaceans, molluscs, fishes and polychaetes, are found distributed according to their required habitats (Islam *et al.* 2002).

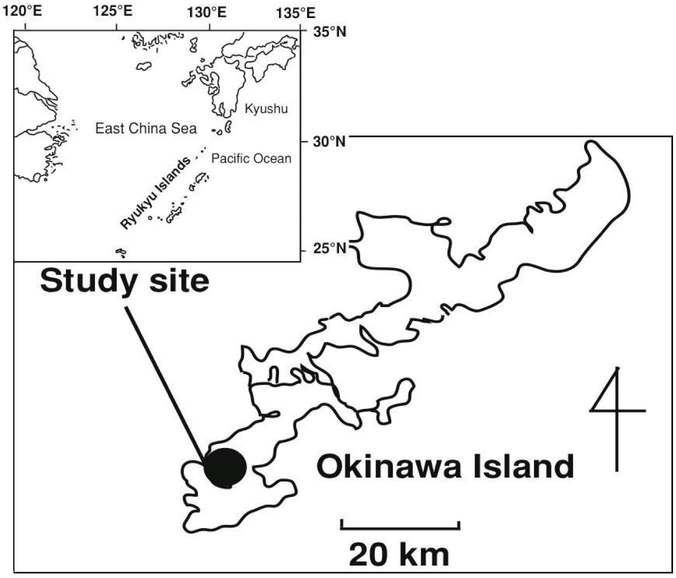

Figure 1: Map showing the research site, which is located on the main island of the Ryukyus Archipelago. The black circle indicates the location of the Manko mangrove ecosystem.
Source: Modified from Khan *et al.* (2009).

Five species of macrozoobenthos, *i.e.*, three gastropod species (*Cerithidea* sp., *Cassidula mustelina, Peronia verruculata*) and two crabs (Grapsidae sp. [an unidentified grapsid crab], *Uca* sp.), were selected as the fauna targets. Mangrove leaves (*K. candel*) and sediment were also analysed as potential food sources of the macrozoobenthos.

Sample Collection and Preparation for Stable Isotopes Analysis

The macrozoobenthos were collected during low tide. Mangrove leaves and surface sediment samples were collected near the benthic collection site to minimise bias (Bouillon *et al.* 2004). Samples were placed in plastic containers and then stored in a cool box containing dry ice during transportation to the Laboratory of Marine Biology and Coral Studies (Marine and Natural Science Department, University of the Ryukyus). Samples of macrozoobenthos were divided into two parts; one part was for identification purposes, and the other part was for stable isotope analysis. The macrozoobenthos were identified according to the procedure of Okutani (2000) and Sakai (1976). In the laboratory, all samples were stored in a freezer at –18°C to minimise any changes in the $\delta^{13}C$ and $\delta^{15}N$ isotope signatures (Kaehler & Pakhomov 2001; Carabel *et al.* 2006).

Macrozoobenthos Preparation

Sample preparation followed the method described by Carabel *et al.* (2006), Ng *et al.* (2007), and Jaschinski *et al.* (2008). Each macrozoobenthos sample was washed with Milli-Q water; in addition, for the gastropods, the soft tissue was removed from its shell. For crustaceans, the carapace was excluded. These samples were then washed with 1.2 N hydrochloric acid (HCl) to remove carbonate ($CaCO_3$) until air bubbles were no longer observed. Finally, the samples were rinsed three times with Milli-Q water.

Sediment Preparation

Sediment samples were filtered using a 0.25 mm sieve (No. 60 mesh size) to remove large particles and non-sediment materials. The samples were then soaked with 1.2 N HCl for 6 h to remove carbonates, followed by rinsing with Milli-Q water. Subsequently, they were soaked with 6 N HCl for 24 h to ensure the complete removal of the carbonates. Finally, they were rinsed three times with Milli-Q water and then centrifuged to separate the water and the sediment sample (Carabel *et al.* 2006; Ng *et al.* 2007; Jaschinski *et al.* 2008).

Mangrove Leaf Preparation

Samples of mangrove leaves were washed with Milli-Q water (Carabel *et al.* 2006; Ng *et al.* 2007; Jaschinski *et al.* 2008) and then dissected into small pieces. All samples were freeze-dried for 24 h, ground with a mortar and pestle, and then placed in tin capsules (Santis 5 × 9 mm, SÄNTIS Analytical AG, Switzerland) with three replicates for analysis.

Stable Isotope Analysis

The $\delta^{13}C$ and $\delta^{15}N$ isotopes were analysed using a mass spectrometer (Delta V Advantage IRMS, Thermo Scientific, Germany) connected for elemental analysis

(NA-2500, CE Instruments, Rodano, Italy). The analytical precision of the instrument was ±0.15‰. The isotope ratios (*R*) are expressed according to the following formula (Hoefs 2009):

$$\delta^{13}C \text{ or } \delta^{15}N = (R_{sample}/R_{standard} - 1)\ 1000\ (‰), \tag{1}$$

where R_{sample} and $R_{standard}$ are the $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratios of the sample and standard, respectively. The $\delta^{15}N$ values are reported relative to atmospheric N_2, and the $\delta^{13}C$ values are expressed relative to the Vienna Pee Dee Belemnite (VPDB).

The assimilation of food biota ($\delta^{13}C$ or $\delta^{15}N$ ratio) was determined using the following formula (DeNiro & Epstein 1978, 1981):

$$\Delta_{Animal\text{-}Diets} = \delta^{13}C_{animal} - \delta^{13}C_{diet} \text{ or } \delta^{15}N_{animal} - \delta^{15}N_{diet} \tag{2}$$

where Δ is the signature of $\delta^{13}C$ or $\delta^{15}N$ assimilation. The food sources assimilated by the macrozoobenthos can be determined if the Δ value falls between –2‰ and + 2‰ (Bouillon *et al*. 2008).

The trophic level (TL) position was estimated according to the following formula (Post 2002; Won *et al.* 2007):

$$TL = \lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{mean\ producer})/3.4 \tag{3}$$

where λ is the signature for the TL primary producers (Post 2002), $\delta^{15}N_{mean\ producer}$ is the average signature of the primary producers, *i.e.*, 3.9‰, and 3.4 is the average trophic enrichment of the $\delta^{15}N$ signatures (Minagawa & Wada 1984; Post 2002). A TL value approaching 1 indicates primary consumers, and a value >2 indicates carnivorous species or higher consumers (Won *et al.* 2007). In addition to the mangrove leaves and sediment from the study site, potential food sources from the results of other studies were considered when determining the food assimilation by the macrozoobenthos.

RESULTS AND DISCUSSION

Stable Isotope Composition in Mangrove Leaves and Sediment

The mean (range) $\delta^{13}C$ signature of *K. candel* leaves was –29.81‰ (–27.83 to –31.80‰), and that of the sediment was –24.23‰ (–21.39 to –25.94‰) (Table 1). The mean $\delta^{15}N$ was 11.0‰ (8.6–15.2‰) in *K. candel* leaves and 7.2‰ (6.8–7.6‰) in the sediment.

Table 1: Mean and standard deviation (SD) of the signatures of $\delta^{13}C$ and $\delta^{15}N$ of two potential food sources of macrozoobenthos in the Manko mangrove ecosystem, Okinawa, Japan.

Potential food sources	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
	Mean	SD	Mean	SD
K. candel leaves	–29.81	1.98	11.00	3.61
Sediment	–24.23	2.48	7.20	0.44

The mean signature of $\delta^{13}C$ for *K. candel* leaves has been reported in several previous studies. The research conducted in Taiwan by Hsieh *et al.* (2002) and in the Ohura area, Okinawa, by Doi *et al*. (2009) found $\delta^{13}C$ values in *K. candel* of –28.3 and –27.5‰, respectively. Other mangrove species have produced comparable results for $\delta^{13}C$, including –28.8‰ in *Avicennia marina* (Penha-Lopes *et al.* 2009), –27.8‰ in *Avicennia officinalis* (Nerot *et al.* 2009), –27.9‰ in *Excoecaria agalocha* (Bouillon *et al*. 2002), and –27.5‰ in *Rhizophora mucronata* (Penha-Lopes *et al.* 2009).

The $\delta^{15}N$ measured in our study appears to be higher than the previously reported values; Doi *et al*. (2009) measured 5.8‰ in *K. candel* leaves in the Ohura area. Furthermore, *A. marina* and *R. mucronata* and a non-mangrove species (*Suaeda* sp.) exhibited smaller $\delta^{15}N$ values (Bouillon *et al.* 2002, 2004; Nerot *et al.* 2009; Penha-Lopes *et al.* 2009).

The range of $\delta^{13}C$ in the sediment in the Manko mangrove ecosystem was –21.39 to –25.94‰, which is comparable to the $\delta^{13}C$ values reported for other mangrove or intertidal areas (e.g., Bouillon *et al.* 2002; Hsieh *et al.* 2002; Doi *et al*. 2009). The $\delta^{15}N$ in the Manko mangrove sediment was enriched by ~6‰ compared with the major vegetation in the Manko mangrove ecosystem. Although the value was higher than that of the sediment in Ghazi Bay, Kenya (Bouillon *et al.* 2004), it was similar to the range found in sediment from the mangrove ecosystem of Inhaca Island, Mozambique (Penha-Lopes *et al.* 2009).

Stable Isotope Composition of Macrozoobenthos

The $\delta^{13}C$ and $\delta^{15}N$ signatures in the five macrozoobenthos were found to vary by species (Table 2). *C. mustelina* had the lowest $\delta^{13}C$, although it exhibited a wide range in $\delta^{15}N$. However, *Uca* sp. exhibited a wide range in $\delta^{13}C$ and an even wider range in $\delta^{15}N$.

Table 2: Mean and SD of the signatures of $\delta^{13}C$ and $\delta^{15}N$ of five macrozoobenthos species in the Manko mangrove ecosystem, Okinawa, Japan.

Macrozoobenthos	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
	Mean	SD	Mean	SD
Cerithidea sp.	–22.40	0.32	8.60	0.34
C. mustelina	–25.06	0.63	8.00	0.29
P. verruculata	–22.58	1.69	8.00	0.83
Grapsidae sp.	–24.30	0.70	10.60	0.32
Uca sp.	–21.87	2.54	11.50	3.30

The δ^{13}C and δ^{15}N values in the three gastropods (*Cerithidea* sp., *C. mustelina, and P. verruculata*) in this study were within the range of *Cerithidea cingulate* (–21.3‰ and 6.2‰, respectively) and *Cerithidea decollate* (–21.6‰ and 4.7‰, respectively) (Bouillon *et al.* 2004), C. *mustelina* in India (–25.4‰ and 5.9‰, respectively) (Bouillon *et al.* 2002), *Onchidium* sp. in the Coringa Wildlife Sanctuary, India (–23.4 to –23.7‰ and 1.7 to 5.7‰, respectively) (Bouillon *et al.* 2002, 2004), and *Terebralia palustris* (Family Potamididae) (–22.2‰ and 11.8‰, respectively) (Penha–Lopes *et al.* 2009). However, Doi *et al.* (2009) reported δ^{13}C and δ^{15}N values in *Cerithidea djadjariensis* of –14.1‰ and 12.8‰, respectively.

For the benthic crustaceans, the δ^{13}C value of the grapsid crabs in the Manko mangrove ecosystem were similar to those found in other locations, with the exception of δ^{15}N (*e.g.*, Hsieh *et al.* 2002; Kristensen *et al.* 2010). The grapsid crab *Helice formosensis,* for example, had a mean carbon isotope signature in its body tissue of –21‰ (Hsieh *et al.* 2002), and *Neoepisesarma versicolor* had mean δ^{13}C and δ^{15}N signatures of –24.3‰ and 7.15‰, respectively (Kristensen *et al.* 2010). Fukumori *et al.* (2008) suggested that the differences in the carbon and nitrogen isotope signatures among benthic species may be influenced by their food sources. In addition, Miyazaki *et al*. (2011) found that the δ^{13}C and δ^{15}N values in benthic fauna were species specific.

Food Sources of Macrozoobenthos and the Trophic Level

The variability of δ^{13}C in various macrozoobenthos provides a possible indication of their food sources via the relationship between the Δ-isotope values in the δ^{13}C of the macrozoobenthos and those of the possible food materials. Bouillon *et al.* (2008) found that sediment, microphytobenthos, and micro-epiflora were the food sources of invertebrates, with Δ-values (signature assimilation values) in the range of approximately –2 to +2‰. In the present study, *Cerithidea* sp. and C. *mustelina* exhibited Δ-values that were closely related to those of the sediment compared with those of other materials, such as mangrove leaves, microphytobenthos, and micro-epiflora (Table 3). The Δ-values of the gastropod (*P. verruculata)* and of the two crab species were closely related to those of both the sediment and the mangrove leaves. This result indicates that the sediment was likely a food source for these benthic organisms. Moreover, the graph of δ^{13}C and δ^{15}N shown in Fig. 2 indicates that the plot of the five species is closer to the sediment, which further supports the conclusion that the sediment was a food source for these macrozoobenthos.

Figure 2 also shows the relationship between the macrozoobenthos and the trophic level in the Manko mangrove ecosystem. C. *mustelina* displayed the strongest relationship to the sediment, and *Uca* sp. displayed the weakest relationship. This result is likely due to the different degrees of mobility of the two species. *Uca* sp. is more mobile and thus has more food source options. In general, no macrozoobenthos in this area exhibited δ^{13}C and δ^{15}N values close to those of the mangrove leaves. Sediment consists of both organic and inorganic components. Many microbial products are accumulated in the sediment, and they may be derived from other autotrophic organisms, such as microphytobenthos and micro-epiflora. A comparison of these findings with data reported by Bouillon *et al.* (2002, 2004) indicates that none of the macrozoobenthos sampled in our study had $\delta^{13}C$ and $\delta^{15}N$ values close to the values of these autotrophic organisms. The area likely developed with microflora or phytobenthos, which were decomposed microbially to form the sediment. Benthic organisms, such as *P. verruculata* and Grapsidae sp., likely consumed these decomposition products of microphytobenthos and micro-epiflora. However, the enrichment of $\delta^{15}N$ in the macrozoobenthos indicates that they must have consumed other nitrogen-containing material, such as microfauna (Kristensen *et al.* 2010). However, *C. mustelina*, as the organism with the $\delta^{13}C$ and $\delta^{15}N$ values closest to those of the sediment, may be a scavenger.

Table 3: The ratio of the signatures of $\delta^{13}C$ and $\delta^{15}N$ of macrozoobenthos assimilated food sources and the trophic level in the Manko mangrove ecosystem, Okinawa, Japan.

Macrozoobenthos	Food source	$\Delta_{\text{Animal-Diets}}$		Trophic level
		$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	
Cerithidea sp.	Sediment	1.34	1.83	2.4
	Mangrove leaves	–2.37	7.41	
	Benthic microalga[a]	6.90	–5.10	
	Microphytobenthos[b]	6.70	–0.30	
	Micro-epiflora[b]	11.00	1.80	
C. *mustelina*	Sediment	0.80	–0.83	2.2
	Mangrove leaves	–2.91	4.75	
	Benthic microalga[a]	6.40	–7.76	
	Microphytobenthos[b]	6.20	–2.96	
	Micro-epiflora[b]	10.50	–0.86	
P. verruculata	Sediment	2.52	1.65	–0.5
	Mangrove leaves	–1.19	7.23	
	Benthic microalga[a]	8.10	–5.29	
	Microphytobenthos[b]	7.90	–0.49	
	Micro-epiflora[b]	12.2	1.61	
Grapsidae sp.	Sediment	3.39	–0.06	1.0
	Mangrove leaves	–0.32	5.51	
	Benthic microalga[a]	9.00	–7.00	
	Microphytobenthos[b]	5.40	–2.20	
	Micro-epiflora[b]	9.70	–0.10	
Uca sp.	Sediment	4.22	2.37	3.2
	Mangrove leaves	0.51	7.94	
	Benthic microalga[a]	9.80	–4.57	
	Microphytobenthos[b]	9.60	0.23	
	Micro-epiflora[b]	13.90	2.33	

Source: a = Bouillon *et al.* (2002), b = Bouillon *et al.* (2004)

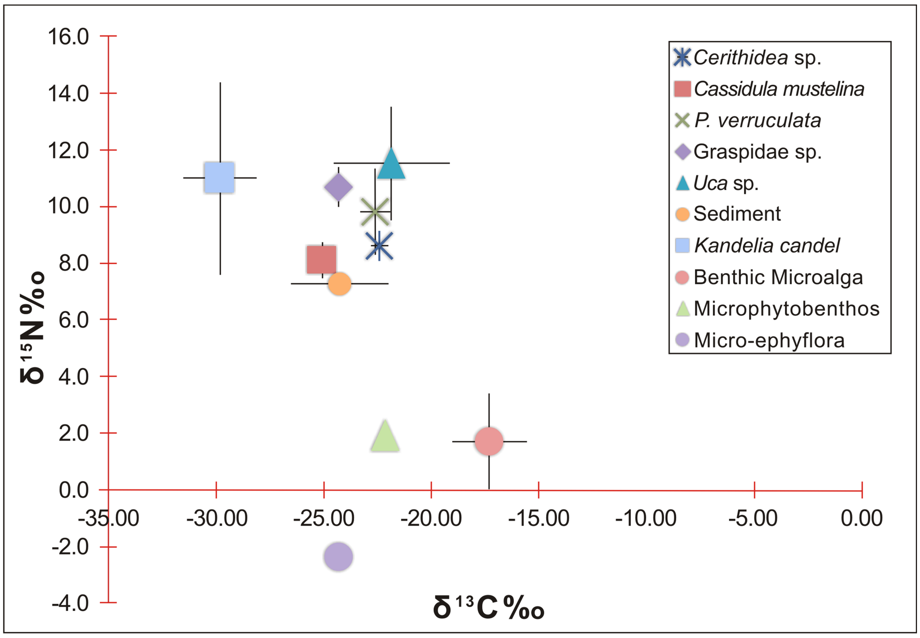

Figure 2: δ^{13}C and δ^{15}N signatures (error bars indicate mean±SD, n = 3) of macrozoobenthos and the primary producers in the Manko mangrove ecosystem. Benthic microalgae data from Bouillon *et al.* (2002), and micro-epiflora and mikrophytobenthos data from Bouillon *et al.* (2004).

Many studies have shown that macrozoobenthos consumed autotrophic organisms, such as the gastropod *Onchidium* sp. (from the same family as the species *P. verruculata*) (Bouillon *et al.* 2002), and other materials, including mangrove litter, algae growing on bark (Hogarth, 2007), phytoplankton (Kurata *et al.* 2001; Bouillon *et al.* 2002; Antonio *et al.* 2010), microalgae, zooplankton, mangrove tissue (Alfaro 2008), and epiphytic plants on mangrove trees (Penha-Lopes *et al.* 2009). The species *T. palustris* (Family Potamididae) consumed mangrove leaves (Marguillier *et al.* 1997; Fratini *et al.* 2004, 2008; Penha-Lopes *et al.* 2009), but it also consumed diatoms (Pape *et al.* 2008). However, Nordhaus *et al.* (2011) found that the grapsoid crab was omnivorous.

In our study, *Uca* sp. was categorised as a secondary or higher consumer. This categorisation was confirmed by Nordhaus and Wolff (2007), who demonstrated that *Uca* sp. consumed dead organisms. Other studies have demonstrated that *Uca* sp. food sources were derived from benthic microalgae (Currin *et al.* 1995), a mixture of benthic microalgae and particulate organic matter (POM) sediment (Hsieh *et al.* 2002), diatoms, green algae, mangroves, and food pellets (Meziane *et al.* 2002), diatoms and cyanobacteria (Bouillon *et al.* 2002; 2004), and plant material, detritus, sediment, and mangrove leaves (Nordhaus & Wolff 2007).

CONCLUSION

The macrozoobenthos in the Manko mangrove ecosystem appear to consume the sedimentary material derived from various decomposed autotrophic organisms can thus be categorised as secondary or higher consumers. Variations in the $\delta^{13}C$ and $\delta^{15}N$ compositions provide a possible indication of the degree of mobility of organisms within the ecosystem.

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