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Carbon Sources Supporting Macro-Invertebrate Communities in Restored Mangrove Forests from Hau Loc, Thanh Hoa, Vietnam

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Abstract: Mangrove forests are important in providing habitats for complex communities of terrestrial and marine fauna. Moreover, they are recognized as highly productive ecosystems in providing nutrients to mangrove food webs or exporting them to nearby coastal waters. In the present study, stable isotopes of carbon and nitrogen were applied to examine the changes in the diets of benthic invertebrate communities following mangrove restoration. The isotope signature of invertebrate tissues varied among the forest ages and locations and ranged from 3.7 ± 1.0 to 13.9 ± 1.1‰ and −26.6 ± 0.5 to −15.0 ± 0.4‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively. The results showed that the food source assimilation of macro-invertebrates is slightly altered from a mixture of benthic microalgae and marine phytoplankton in the mudflat to a combination of benthic microalgae and sediment organic matter in the *Sonneratia caseolaris* and the *Kandelia obovata* forests. Therefore, the diets of macro-invertebrates varied following forest ages and the position of the forest in the intertidal zone. These insights from the present study are useful for the effective conservation and restoration of mangrove forests in Vietnam and worldwide.

Keywords: restored mangrove forests; invertebrates; organic carbon; stable isotopes; Vietnam

1. Introduction

Mangrove forests are one of the most productive ecosystems in coastal zones and play a significant role in global carbon (C) sequestration [1,2]. Mangrove forests are known as an important habitat for terrestrial and marine fauna [3], and export a significant amount of primary production to adjacent waters for supporting the food sources of fisheries and coastal water ecosystems [4]. In mangrove forests, benthic invertebrate communities perform a crucial function in the topography and biogeochemistry of the sediments through their burrowing and feeding activities [5,6]. Mangrove litter and subsurface root growth are broken down by benthic invertebrates, such as leaf-eating crab and snail species, and are easy to use for the microbial colonization of the detritus food chain and therefore promote the decomposition of detritus and nutrient cycles in the mangrove ecosystem [7]. Some invertebrates, such as mangrove crabs, can tolerate wide ranges of salinities. Therefore, they can transfer carbon from the landward to the seaward side of mangrove forests [8]. Recent studies have shown that mangrove-derived detritus (tree litter) is a dominant organic carbon (OC) source for the food webs of macro-invertebrates, such as gastropods and crabs [6], while other species primarily feed on benthic

algae for their diets [9,10]. Cloern [11] and Polis, et al. [12] indicated that the food web structure and functions were strongly influenced by significant alterations in land use. However, Viana, et al. [13] showed that the stable isotope composition of food webs present at the river mouth was not affected, although the terrestrial rainforest cover on watersheds was changed due to deforestation.

In the face of mangrove degradation and the effects of climate change, restoration programs have been performed as valuable tools for improving the forest structure and habitat functionality in the coastal zones of tropical developing countries [14,15]. The changes in habitat characteristics following forest restoration, such as the vegetation and physicochemical properties of the sediment, could influence the diversity, abundance, biomass, and community structure of macrofauna communities [16–18]. Other research has shown that the diet of benthic macrofauna in the old-growth forest changes from a homogeneous composition to a heterogeneous [19]. The degree of material exchange with adjacent systems is partially controlled by the complication of food resources in mangrove forests [20]. With restored wetlands, the increase in the diversity of food resource availability is the primary controlling factor in benthic food web succession [21]. Although several related studies have detailed the food web and OC of food sources for macro-invertebrates in mangrove ecosystems, only a few studies concern those of restored mangrove ecosystems. Answering the question of whether macro-invertebrate communities and their diets change in restored mangrove forests is necessary for providing valuable information on the active conservation and restoration of mangrove ecosystems.

Stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are a powerful way of monitoring the trophic interactions between primary producers and primary consumers. Moreover, the application of this technique is vital for examining the diet compositions of primary consumers based on a significant amount of differences in the stable isotope signatures among food sources and consumers [10,22]. Pham, et al. [23] have emphasized that the sedimentary OC correlates with forest maturity and the tidal elevation gradient. As the consequences of changes in the OC cycling in restored mangrove ecosystems, in this paper, we hypothesized that food sources for the assimilation of macro-invertebrates were influenced by the stand development and intertidal zonation of forests. We applied the $\delta^{13}C$ and $\delta^{15}N$ compositions of macro-invertebrates, comprising polychaetes, crustaceans, shrimps, gastropods, bivalves, and potential food sources, to examine the changes in the diets of macro-invertebrates in different ages of restored mangrove forests in Hau Loc, north-central Vietnam.

2. Materials and Methods

2.1. Study Site

The sampling sites were placed in the Hau Loc mangrove forest (HLMF), Thanh Hoa Province, north-central Vietnam (Figure 1), which is recognized as a representative site for succession in mangrove restoration programs in Vietnam. Two dominant mangrove species, *Kandelia obovata (K. obovate)* and *Sonneratia caseolaris (S. caseolaris)*, cover a total of 451.1 ha in the HLMF at an elevation from 0.8 to 2.0 m [24]. Two young stands of *S. caseolaris* and three older stands of *K. obovata* forests are located in the high and low intertidal zones, respectively. This region has a subtropical climate, the average temperature during the period 1980–2009 was 23.8 °C [25], it has an annual precipitation of approximately 1800 mm, and the mean humidity was 85.7% during the period 1997–2001 [26,27]. A dry season continues from May to October, and a rainy season spans from December to February [26]. The HLMF is influenced by mixed diurnal and semi-diurnal tides, with a tidal range of 3 to 4 m for 5 to 7 days a month [28]. The restoration programs in the HLMF started in 1987 after an extensive area of the *K. obovata* forests was converted to plant sedge grass for handicrafts and shrimp ponds in the 1970s. During the restoration, the seedlings and seeds of *K. obovata* and *S. caseolaris* were derived from northern Vietnam for replanting and new planting in the open intertidal zone. The forests area has been continuously expanded until recent years under the funding supports from various restoration programs.

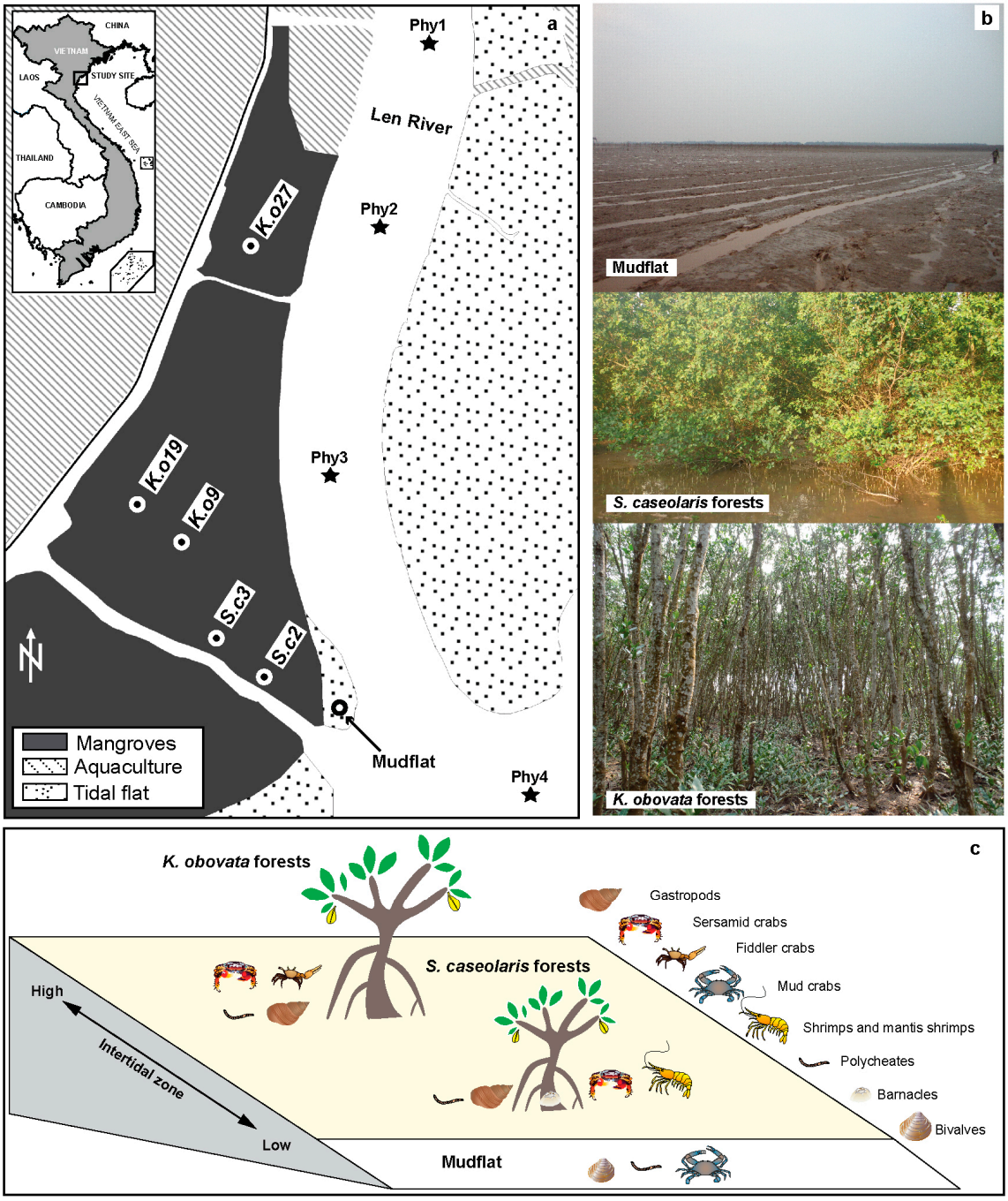

Figure 1. (**a**) The map shows the sampling sites in the HLMF, north-central Vietnam (*K. obovata* and *S. caseolaris* forests with different ages and denoted as *S.c* and *K.o*, respectively; see Section 2.1 for details). (**b**) Figures show the mudflat without plants and the dominant species in the mangrove forests. (**c**) Illustration describes the macro-invertebrate communities collected in the mudflat and the mangrove forests (the macro-invertebrate symbols were collected from the IAN symbol libraries).

The restoration programs in the HLMF have been recognized as having a significant number of benefits, providing forest products such as firewood, fisheries, and honey; and improving the income for local people by catching the mudskippers or collecting mollusks, with estimated earnings of $3.5–8 per day. Additionally, the forests protect shorelines and reduce the disaster risk from 5 to 6 storms per year and the associated floodings. In 2005, the typhoon Damrey destroyed 3 km of the coastal dike, causing inundation of several villages, but 4.7 km of the dike, where it was surrounded

by mangroves, was not affected [24,27]. In November 2018, samples were collected from the 9, 19, and 27-year-olds of the *K. obovata* forests (referred to as *K.o9*, *K.o19*, and *K.o27*), and from the 2 and 3-year-olds of the *S. caseolaris* forest (referred as *S.c2* and *S.c3*). A mudflat is located far from the mangrove forests and has been sampled as a reference site [24,29].

2.2. Field Sampling

Five transects were designed to collect benthic macro-invertebrates and potential food sources in different forest ages and tidal elevations. The transects started from the mudflat toward the mangroves. In isolation in a *K.o27* forest, one transect was established parallel to the river bank to avoid the effect of spatial variation in the C isotope signature of the producers [30]. Along each sampling transect, three sampling plots with sizes of 10 × 10 m were set up, and the specimens of benthic invertebrates were picked by hand during low tides when the plots were not inundated. Brachyuran crabs and mantis shrimps were collected using plastic mesh cages at the border of the *S.c2* forest. The samples were kept in a cool box and transferred to the field laboratory. To collect polychaete, at each sampling plot, a sediment sample of 25 × 25 cm and 20 cm in depth was washed, manually stirred, and sieved through a 500 µm sieve. The fauna specimens retained on the mesh sieve were fixed in 70% ethanol for stable isotope analysis in the field laboratory.

The stable isotope signature of mangrove leaves can be changed under the senescent process [31]. Thus, the samples of mangrove leaves were collected with different senescent statuses, comprising fresh and yellow leaves from the *K. obovata* and *S. caseolaris* trees, and decaying leaves were overlaid on the forest floor. The benthic microalgae (BMA) samples in each sampling plot were collected by scraping off the top layer of sediment, where microbial mats were visible or densely formed, using a stainless-steel spatula. Three surface sediment samples were randomly taken in each plot at a depth of 0 to 2 cm. All the samples were kept in labeled polyethylene (PE) bags and stored in a cool box before processing in the field laboratory. The Phytoplankton (Phy) samples were collected from the sea according to the method outlined in Pham, Luu, Nguyen and Koji [23].

In the field laboratory, the specimens of benthic invertebrate and mangrove leaves were rinsed with distilled water to remove the contaminants of sediment and debris. The polychaete samples were filled with filtered seawater in Petri dishes and maintained alive for 24 h for completely remove the material in their guts. All the samples were enclosed in labeled PE bags and immediately frozen at −20 °C until further processing and analysis in the laboratory.

2.3. Sample Preparation and Analysis

2.3.1. For Potential Food Sources

In the laboratory, mangrove leaves and BMA samples were rinsed with Milli-Q filtered distilled-deionized water and inspected under a microscope to complete the removal of unessential contaminants. Then, all the samples were dried in an electric oven at 60 °C for 48 h. After the drying process, the mangrove leaves, BMA, and sediment samples were ground to a fine powder using a pestle and mortar. With the analysis of the carbon isotope signature of the sediment and BMA samples, an amount of 200 mg of pulverized sample was transferred to an Eppendorf tube and treated with 2 mL of HCl acid 1 N to decarbonate for 24 h. The samples were rinsed three times with distilled deionized water (Millipore Company) to remove the surplus acid completely. Phy filters for stable carbon isotope analysis were exposed to HCl acid 12 N vapor in a glass desiccator for carbonate removal. The sediments and Phy filters were re-dried in a drying oven at 60 °C for 24 h. The top layer of the filters was separated and ground to the powder using an agate mortar and pestle.

2.3.2. For Consumers

The macro-invertebrate samples were first defrosted and gently washed with Milli-Q filtered distilled-deionized water, wiped with laboratory paper, then identified at the species level. After that,

the bodyweight, carapace width and length of the crabs, the shell lengths of the gastropods, the body weight and length of the shrimps, mantis shrimps and bivalves were measured by an electronic microbalance and a digital caliper with an accuracy of 0.1 g and 0.01 mm, respectively. The specimens were carefully dissected, and each white muscle tissue was extracted from the legs, pincers, and adductor muscles for stable isotope analysis. The muscle tissues were dried in an electric oven at 60 °C until it reached a constant weight. Each pulverized sample of potential food sources and consumers was weighed and sealed in a tin capsule and analyzed for the stable isotope signatures of carbon and nitrogen using a gas chromatograph (Sercon, ANCA-GSL) connected to an isotope ratio mass spectrometer (Sercon, Hydra 20-20). The isotope ratios of carbon and nitrogen were reported with the δ-unit notation (‰-per mil) as follows in the equation:

$$\delta X(‰) = \left(\frac{R_{Sample}}{R_{Standard}} - 1 \right) \times 1000 \quad (1)$$

where X is the isotope signature of carbon ($\delta^{13}C$) or nitrogen ($\delta^{15}N$). R is the ratio of either $^{13}C/^{12}C$ or $^{15}N/^{14}N$; R_{Sample} is the ratio of the sample; $R_{Standard}$ is the ratio of the international reference standard (Vienna Pee Dee Belemnite (PDB) limestone carbonate for $\delta^{13}C$ and nitrogen in atmospheric air for $\delta^{15}N$) [32]. During analysis, L-histidine was run concurrently with all the samples as an internal standard to check the analytical accuracy. The $\delta^{13}C$ and $\delta^{15}N$ signatures were measured with precisions of ±0.1‰ and ±0.2‰, respectively.

2.4. Data Analysis

A one-way analysis of variance (ANOVA) and Tukey's post-hoc test was performed to determine the statistical differences in the stable isotope compositions of potential food sources and consumers among differently aged forests. Before the ANOVA test, these data were verified for the normality and homogeneity of variances with the Shapiro–Wilk test and Levene's test, respectively. If the normality assumption and homogeneity of variances were not satisfied, the original data were transformed using an exponential transformation. A Kruskal–Wallis one-way ANOVA rank test and post-hoc multiple comparisons (Dunn's test) were used when the transformed data did not satisfy the homogeneity of variances and normality requirements. A significant level was considered when the *p*-value was less than 0.05. All the statistical analyses were performed using SPSS 21.0 (IBM statistical software for Windows). A biplot and table of $\delta^{15}N$ and $\delta^{13}C$ isotope signatures of the species classified into taxonomic and feeding functional groups were analyzed following the methods in Wang, et al. [33].

3. Results

3.1. The Isotopic Signature of Potential Food Sources

The carbon and nitrogen isotope signatures of potential food sources in the HLMF are shown in Table 1. The variation in the isotopic signatures of phytoplankton from the upper to the mouth of the river has been presented in Pham, Luu, Nguyen and Koji [23]; the $\delta^{13}C$ value of Phy at the river mouth was applied for that of marine phytoplankton in the HLMF. The potential food sources in the mudflat included Phy, BMA, and sediment organic matter (SOM), while those of the *S. caseolaris* and the *K. obovata* forests were Phy, SOM, BMA, and mangrove leaves (Man).

Table 1. The $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± SD) of the primary food sources in the Hau Loc mangrove forest (HLMF).

Primary Food Sources	Acr	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	N
		Mean ± SD	Mean ± SD	
Marine phytoplankton	**Phy**	6.1 ± 0.5	−21.0 ± 0.1	6
Benthic microalgae	**BMA**			
Mudflat		7.4 ± 0.6	−19.9 ± 0.7	5
S. caseolaris forests		6.9 ± 0.5	−21.1 ± 0.7	12
K. obovata forests		3.6 ± 0.1	−24.4 ± 0.1	3
Sediment organic matter	**SOM**			
Mudflat		3.3 ± 0.6	−24.7 ± 0.2	9
S. caseolaris forests		3.8 ± 0.4	−25.0 ± 0.2	18
K. obovata forests		4.2 ± 0.4	−26.5 ± 1.0	27
Mangrove leaves	**Man**			
S. caseolaris forests		4.2 ± 0.4	−29.8 ± 1.4	19
K. obovata forests		2.1 ± 0.8	−31.2 ± 1.9	14

Acr: acronym; N: number of samples; SD: standard deviation values are shown when $n \geq 2$.

The $\delta^{13}C$ and $\delta^{15}N$ values of the BMA were the most enriched, and both signatures decreased in the order: BMA > Phy > SOM > Man. The $\delta^{13}C$ values of SOM ranged from a minimum of −26.5 ± 1.0‰ in the *K. obovata* forests to a maximum of −24.7 ± 0.2‰ in the mudflat ($F_{2,51} = 33.065$, $p < 0.001$). However, the $\delta^{15}N$ values showed an opposite trend, and the lowest value was found in the mudflat ($F_{2,51} = 13.137$, $p < 0.001$) (Table 1). The stable isotope compositions of BMA showed a similar trend to that of SOM, with a significant difference in $\delta^{13}C$ and $\delta^{15}N$ among the sites ($\delta^{13}C$: $F_{2,17} = 47.293$, $p < 0.001$; $\delta^{15}N$: $F_{2,17} = 68.396$, $p < 0.001$). The highest $\delta^{13}C$ and $\delta^{15}N$ values of BMA were observed in the mudflat and were −19.9 ± 0.7‰ and 7.4 ± 0.6‰, respectively. Between two mangrove species, a significant difference was found in the $\delta^{13}C$ and $\delta^{15}N$ ($\delta^{13}C$: $F_{1,31} = 9.302$, $p < 0.05$; $\delta^{15}N$: $F_{1,31} = 38.777$, $p < 0.001$), and the isotopic signatures of the *K. obovata* were lower compared to those of the *S. caseolaris* forests (Table 1).

3.2. The Isotopic Signature of Consumers

The isotopic signatures of C and N for each benthic invertebrate are shown in Table 2 and Figure 2. Three bivalve *Meretrix lyrata*, *Meretrix meretrix*, and *Pharella acutidens* were collected in the mudflat. The isotopic compositions of these species showed a narrow range between 2‰ for $\delta^{15}N$ and 1‰ for the $\delta^{13}C$ (Table 2). On the contrary, eight gastropod species showed a broad range of stable isotope signatures, varying from 3.9 ± 0.2 to 10.1 ± 0.5‰ for $\delta^{15}N$ and from −16.6 ± 0.6 to −26.1 ± 0.3‰ for $\delta^{13}C$.

Among gastropod communities, the wide distribution species such as *Littoraria melanostoma*, *Neritina violacea*, *Onchidiidae* sp., and *Terebralia sulcata* species were caught in the *K. obovata* and *S. caseolaris* forests, while the other species showed a limited distribution. The $\delta^{15}N$ values of *L. melanostoma* fluctuated among the forest ages, ranging from 5.1 ± 2.2 to 7.6 ± 1.1‰ ($H(3) = 9.394$, $p = 0.024$). However, the post-hoc test indicated an insignificant difference in the $\delta^{15}N$ values between the *K.o9* and the *K.o27* forests (Dunn's test, $p > 0.05$), and between the *S.c3* forest and the *K.o19* forest (Dunn's test, $p > 0.05$). Similarly, the $\delta^{15}N$ signatures of *N. violacea* and *Cerithidea obtusa* exhibited fluctuating trends, with no significant difference between the young and older forests (*N. violacea*: $F_{4,15} = 0.959$, $p = 0.458$; *C. obusta*: $F_{2,7} = 0.220$, $p = 0.808$). A slight decreasing trend but insignificant difference in the $\delta^{15}N$ signatures with forest age were observed with two species: *Cassidula aurisfelis*

($F_{1,12}$ = 3.141, p = 0.102) and *Onchidiidae* sp. ($F_{1,3}$ = 0.727, p = 0.456). Otherwise, the *Terebralia sulcata* and *Ellobium aurisjudae* species had lower δ^{15}N values in the old forests compared to those of the younger forests (*T. sulcata*: $F_{3,11}$ = 4.108, p = 0.035; *E. aurisjudae*: $F_{2,7}$ = 2.176, p = 0.184). However, the δ^{15}N values of *Cassidula nucleus* were not different between the *K.o19* and *K.o27* forests ($F_{1,12}$ = 0.149, p = 0.706).

The δ^{13}C signatures of three mangrove snails *L. melanostoma*, *N. violacea*, and *Onchidiidae* sp. tended to decrease with the maturity of the forests, but no significant difference existed among the forest ages (*L. melanostoma*: $F_{3,19}$ = 2.167, p = 0.125; *N. violacea*: $F_{4,15}$ = 0.473, p = 0.755; *Onchidiidae* sp.: $F_{1,3}$ = 0.150, p = 0. 724). A similar trend was found in the δ^{13}C compositions of *C. obtusa*, *E. aurisjudae*, and *T. sulcata* (*C. obtusa*: $F_{2,7}$ = 14.451, p = 0.003; *E. aurisjudae*: H(2) = 7.636, p = 0.022; *T. sulcata*: H(3) = 11.635, p = 0.010). The post-hoc test indicated that the carbon isotope signatures of *C. obtusa* and *T. sulcata* in the *S.c3* forest significantly differed with those of the other forests. However, the δ^{13}C values of the family *Cassidula* had a slight variation between the *K.o19* and the *K.o27* forests, with a small range of δ^{13}C signatures from 0.6 to 0.8‰ (*C. aurisfelis*: $F_{1,12}$ = 1.566, p = 0.236; *C. nucleus*: $F_{1,12}$ = 21.542, p = 0.001).

The crabs *Macrophthalmus depressus*, *Metaplax elegans*, and *Perisesarma bidens* (see the latest taxonomic information of sesarmid crabs in Shih, et al. [34] and Ng, et al. [35]) were the most distributed species in the present study, seen from the low to the high intertidal zone. The nitrogen isotope signatures of these crabs slightly changed with the forest aging, with an approximation of ±1‰. The portunid crab *Scylla serrata* was caught only in the mudflat, and the *S.c2* forest had the highest δ^{15}N value among the benthic invertebrate species. There was a slight change in the δ^{15}N values of *Ilyoplax formosensis*, *M. elegans*, *S. serrata*, *Sersama plicata*, and *Uca arcuata* among the different-aged forests. However, a considerable statistical difference was observed in the δ^{15}N values of *M. depressus* and *P. bidens* (*M. depressus*: $F_{4,14}$ = 5.002, p = 0.010; *P. bidens*: $F_{4,22}$ = 4.155, p = 0.012). The Tukey post-hoc test showed a significant difference in the δ^{15}N values between the *K.o19* and *K.o27* forests (*M. depressus*: Tukey, $p > 0.05$), and between the *K.o9* and *K.o19* forests with other forests (*P. bidens*: Tukey, $p > 0.05$).

The δ^{13}C signatures of crabs ranged from −25.2 ± 0.4 for *S. plicata* to −15.0 ± 0.4‰ for *M. depressus*, with the only significant difference among aged forests for *P. bidens* (*P. bidens*: $F_{4,22}$ = 5.971, p = 0.012). Tukey's post-hoc test identified no difference in the δ^{13}C values among the *S.c3* and other forests (Tukey, $p > 0.05$). Additionally, there was an insignificant statistical difference in isotope compositions between the *S.c2* and the *S.c3* forests for four shrimp species, with higher δ^{13}C and δ^{15}N values compared to those of the crabs. Only one barnacle *Fistulobalanus albicostatus* attached on the *S. caseolaris* trees had a medium isotopic signature among the benthic invertebrate communities, which was 10.1 ± 0.1‰ and −22.4 ± 0.5‰ for δ^{15}N and δ^{13}C, respectively.

Table 2. The $\delta^{15}N$ and $\delta^{13}C$ composition (mean ± SD) of macro-invertebrates in the HLMF.

Species	Acr	Feeding Ecology	$\delta^{15}N$ (‰) (N)						$\delta^{13}C$ (‰) (N)					
			MF	*S.c2*	*S.c3*	*K.o9*	*K.o19*	*K.o27*	MF	*S.c2*	*S.c3*	*K.o9*	*K.o19*	*K.o27*
Gastropods														
Cassidula aurisfelis	*Ca*	Surface feeder					5.3 ± 0.3 ^{a} (8)	4.6 ± 1.0 ^{a} (6)					−25.6 ± 0.5 ^{a} (8)	−25.2 ± 0.8 ^{a} (6)
Cassidula nucleus	*Cn*	Surface feeder					4.7 ± 0.3 ^{a} (5)	4.9 ± 1.0 ^{a} (9)					−26.1 ± 0.3 ^{a} (5)	−25.3 ± 0.3 ^{b} (9)
Cerithidea obtusa	*Co*	Surface feeder			4.2 ± 1.6 ^{a} (3)	3.7 ± 1.0 ^{a} (3)	3.9 ± 0.2 ^{a} (4)				−22.2 ± 0.7 ^{a} (3)	−23.7 ± 0.7 ^{b} (3)	−24.4 ± 0.2 ^{b} (4)	
Ellobium aurisjudae	*Ea*	Surface feeder				8.5 ± 0.7 ^{a} (5)	7.8 ± 0.1 ^{a} (3)	7.5 ± 0.7 ^{a} (3)				−16.6 ± 0.6 ^{a} (5)	−24.5 ± 0.7 ^{b} (3)	−26.6 ± 0.5 ^{c} (3)
Littoraria melanostoma	*Lm*	Grazer			7.0 ± 0.3 ^{a} (5)	7.6 ± 1.1 ^{b} (5)	7.1 ± 0.5 ^{a} (7)	5.1 ± 2.2 ^{b} (6)			−22.9 ± 0.5 ^{a} (5)	−22.3 ± 0.7 ^{a} (5)	−23.0 ± 1.1 ^{a} (7)	−23.7 ± 0.9 ^{a} (6)
Neritina violacea	*Nv*	Surface feeder		7.2 ± 1.0 ^{a} (4)	7.8 ± 1.4 ^{a} (4)	8.3 ± 1.0 ^{a} (4)	7.7 ± 1.5 ^{a} (4)	8.1 ± 1.3 ^{a} (4)		−22.6 ± 1.5 ^{a} (4)	−23.5 ± 2.0 ^{a} (4)	−24.4 ± 0.5 ^{a} (4)	−24.3 ± 1.9 ^{a} (4)	−24.1 ± 1.2 ^{a} (4)
Onchidiidae sp.	*Os*	Surface feeder					6.7 ± 3.4 ^{a} (3)	5.6 ± 2.4 ^{a} (3)					−20.1 ± 4.3 ^{a} (3)	−23.0 ± 1.8 ^{a} (3)
Terebralia sulcata	*Ts*	Surface feeder			10.1 ± 0.5 ^{a} (4)	10.1 ± 0.5 ^{a} (3)	9.2 ± 0.9 ^{a} (3)	9.0 ± 0.4 ^{b} (5)			−22.3 ± 1.7 ^{a} (4)	−24.3 ± 1.3 ^{b} (3)	−24.9 ± 1.6 ^{b} (3)	−26.1 ± 0.1 ^{b} (5)
Crustaceans														
Ebalia malefactrix	*Em*	Predator		14.0 (1)						−20.9 (1)				
Helice formosensis	*Hf*	Deposit feeder						8.4 (1)						−15.7 (1)
Ilyoplax formosensis	*If*	Deposit feeder					8.7 ± 0.5 ^{a} (5)	8.6 ± 0.5 ^{a} (4)					−24.8 ± 1.0 ^{a} (5)	−24.0 ± 1.5 ^{a} (4)
Macrophthalmus depressus	*Md*	Deposit feeder		12.4 ± 0.2 ^{a} (4)	12.5 ± 0.1 ^{a} (3)	12.0 ± 0.4 ^{a} (4)	12.8 ± 0.2 ^{b} (6)	12.9 ± 0.4 ^{b} (3)		−15.0 ± 0.4 ^{a} (4)	−15.4 ± 1.0 ^{b} (3)	−15.6 ± 1.0 ^{a} (4)	−16.0 ± 0.4 ^{a} (6)	−16.4 ± 0.9 ^{a} (3)
Metaplax elegans	*Me*	Deposit feeder		8.2 ± 0.8 ^{a} (3)	8.2 ± 0.6 ^{a} (5)	7.4 ± 1.1 ^{a} (8)	7.5 ± 0.6 ^{a} (4)	7.7 ± 0.7 ^{a} (3)		−25.1 ± 0.7 ^{a} (3)	−24.3 ± 0.9 ^{a} (5)	−24.7 ± 1.0 ^{a} (8)	−25.0 ± 1.0 ^{a} (4)	−25.1 ± 0.3 ^{a} (3)
Metaplax longipes	*Ml*	Deposit feeder					12.2 ± 0.4 (3)						−21.8 ± 0.2 (3)	
Metopograpsus messor	*Mm*	Deposit feeder				13.9 ± 0.2 ^{a} (3)	13.2 ± 0.4 ^{a} (3)	13.3 ± 0.7 ^{a} (6)				−20.2 ± 0.7 ^{a} (3)	−21.7 ± 1.1 ^{a} (3)	−20.5 ± 0.9 ^{a} (6)
Perisesarma bidens	*Pb*	Deposit feeder		6.1 ± 0.7 ^{a} (6)	5.7 ± 0.6 ^{a} (6)	6.9 ± 0.8 ^{b} (6)	6.9 ± 0.6 ^{b} (5)	6.2 ± 0.5 ^{a} (4)		−25.0 ± 0.5 (6)	−25.5 ± 0.2 (6)	−24.9 ± 0.3 (6)	−24.2 ± 0.8 (5)	−24.5 ± 0.4 (4)
Scylla serrata	*Ss*	Predator	13.4 ± 0.6 ^{a} (6)	13.1 ± 0.8 ^{a} (11)					−21.1 ± 0.9 ^{a} (6)	−20.7 ± 1.7 ^{a} (11)				
Sesarma plicata	*Sp*	Deposit feeder					6.5 ± 1.4 ^{a} (4)	5.7 ± 0.5 ^{a} (4)					−25.0 ± 0.2 ^{a} (4)	−25.2 ± 0.4 ^{a} (4)
Uca acuta	*Uac*	Deposit feeder					9.2 (1)	8.3 (1)					−17.3 (1)	−20.5 (1)

Table 2. *Cont.*

Species	Acr	Feeding Ecology	δ^{15}N (‰) (N)						δ^{13}C (‰) (N)					
			MF	*S.c2*	*S.c3*	*K.o9*	*K.o19*	*K.o27*	MF	*S.c2*	*S.c3*	*K.o9*	*K.o19*	*K.o27*
Uca arcuata	*Uar*	Deposit feeder					11.1 ± 1 (3)	9.4 ± 1.1 (5)					−17.5 ± 0.7 (3)	−17.8 ± 2.5 (5)
Varuna litterata	*Vl*	Deposit feeder						8.6 (1)						−23.8 (1)
Barnacles														
Fistulobalanus albicostatus	*Fa*	Filter feeder		10.1 ± 0.1 (5)						−22.4 ± 0.5 (5)				
Bivalves														
Meretrix lyrata	*Ml*	Filter feeder	11.3 ± 0.2 (16)						−21.0 ± 0.4 (16)					
Meretrix meretrix	*Mm*	Filter feeder	11.2 ± 0.1 (4)						−20.9 ± 0.2 (4)					
Pharella acutidens	*Pa*	Filter feeder	9.4 (1)						−23.0 (1)					
Mantis shrimps														
Anchisquilla fasciata	*Af*	Predator		14.4 ± 0.6 [a] (19)	14.4 ± 0.7 [a] (6)					−20.1 ± 0.5 [a] (19)	−19.9 ± 1.4 [a] (6)			
Shrimps														
Alpheus euphrosyne	*Ae*	Omnivore			13.1 ± 1.3 (3)						−21.4 ± 1.9 (3)			
Fenneropenaeus indicus	*Fi*	Omnivore		12.8 ± 0.9 [a] (13)	13.1 ± 1.0 [a] (3)					−21.8 ± 0.8 [a] (13)	−22.2 ± 2.2 [a] (3)			
Lipopenaeus vannamei	*Lv*	Omnivore		14.1 ± 0.8 [a] (5)	13.1 ± 1.4 [a] (3)					−20.7 ± 0.9 [a] (5)	−21.5 ± 1.4 [a] (3)			
Metapenaeus ensis	*Men*	Omnivore		13.0 ± 1.3 [a] (16)	12.4 ± 0.1 [a] (3)					−21.0 ± 1.8 [a] (16)	−20.9 ± 0.5 [a] (3)			
Penaeus monodon	*Pm*	Omnivore			13.9 ± 1.1 (2)						−22.0 ± 1.8 (2)			
Polychaetes														
Diopatra neapolitana	*Dn*	Omnivore	11.8 (1)	12.1 (1)	13.7 (1)				−19.6 (1)	−21.9 (1)	−19.3 (1)			
Nephthys polybranchia	*Np*	Omnivore	11.6 ± 0.3 (4)	12.3 (1)	12.0 (1)	12.7 (1)			−22.4 ± 1.0(4)	−22.4 (1)	−21.3 (1)	−21.8 (1)		
Sternaspis scutata	*Ssc*	Omnivore	10.7 (1)	10.1 (1)		10.7 ± 0.8 (2)			−22.0 (1)	−21.1 (1)		−22.2 ± 1.4 (2)		

SD: standard deviation values are shown when n ≥ 2. Different letters indicate statistically significant differences between groups. Values in brackets indicate the number of analysis samples.

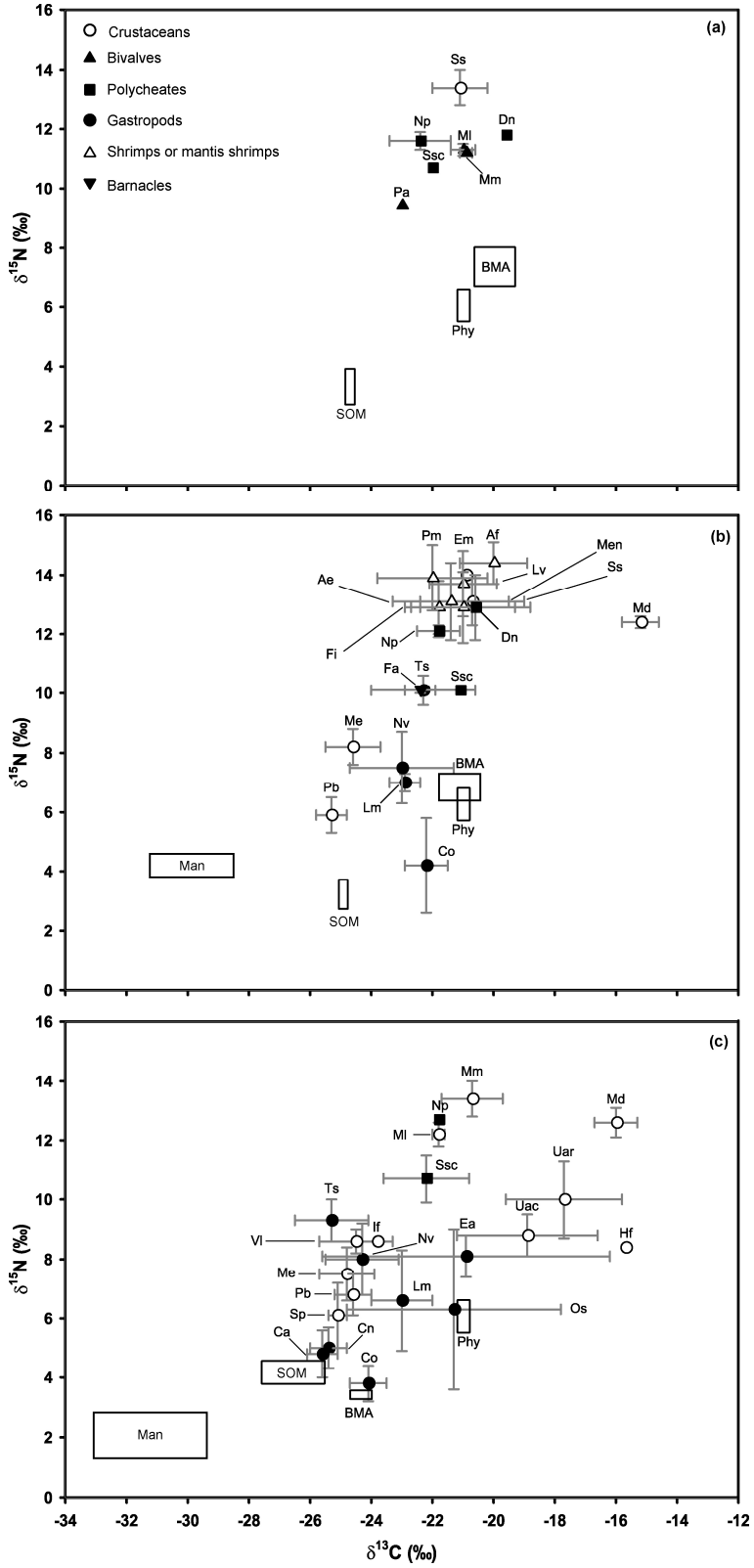

Figure 2. Dual stable isotope plot of the $\delta^{15}N$ and $\delta^{13}C$ (mean ± SD, ‰) values of the potential organic carbon sources and macro-invertebrates in the HLMF. (**a**) Mudflat, (**b**) *S. caseolaris* forests, and (**c**) *K. obovata* forests. Points denote the means and the error bars denote 1 SD. Refer to Tables 1 and 2 for the definitions of acronyms of the potential organic carbon sources and macro-invertebrates, respectively.

3.3. The Isotopic Composition of Macro-Invertebrates at the Community Level

The isotopic compositions at the community level of benthic invertebrates are shown in Figure 3. For the crab predator *S. serrata*, there is no statistical difference in the $\delta^{15}N$ and $\delta^{13}C$ values between the mudflat and the *S.c2* forest (see Section 3.2 for details). Among deposit feeder crab communities, the statistical analysis results showed a statistical significant difference in the $\delta^{15}N$ values and a non-significant statistical difference for the $\delta^{13}C$ values among the different-aged forests ($\delta^{15}N$: $H(5) = 30.045$, $p = 0.001$; $\delta^{13}C$: $H(5) = 8.834$, $p = 0.205$). However, Dunn's test indicated that no significant difference could be found in $\delta^{15}N$ between the mudflat and the *S.c2* forest (Dunn's test, $p > 0.05$), and between the *S.c3* and the *K. obovata* forests (Dunn's test, $p > 0.05$). The highest values of $\delta^{15}N$ and $\delta^{13}C$ were observed in the *K.o19* forest, where the mean values were 10.6 ± 1.0‰ and −17.4 ± 0.5‰, respectively. The lowest values of $\delta^{15}N$ and $\delta^{13}C$ were found in the *S.c3* forest, which were 7.7 ± 2.4‰ and −23.5 ± 0.9‰, respectively. The $\delta^{15}N$ signatures of the grazer gastropods communities (*L. melanostoma*) varied among forests, but no statistically significant difference in the $\delta^{13}C$ values was found. For the surface-grazer gastropod communities, the $\delta^{15}N$ and $\delta^{13}C$ values significantly varied among the mudflat and the mangrove forests ($\delta^{15}N$: $F_{4,106} = 6.254$, $p = 0.001$; $\delta^{13}C$: $H(4) = 38.223$, $p = 0.001$), and had higher values in the *K.o9* forest than those of the other forests, with an average of 7.8 ± 2.3‰ and −21.7 ± 3.7‰, respectively.

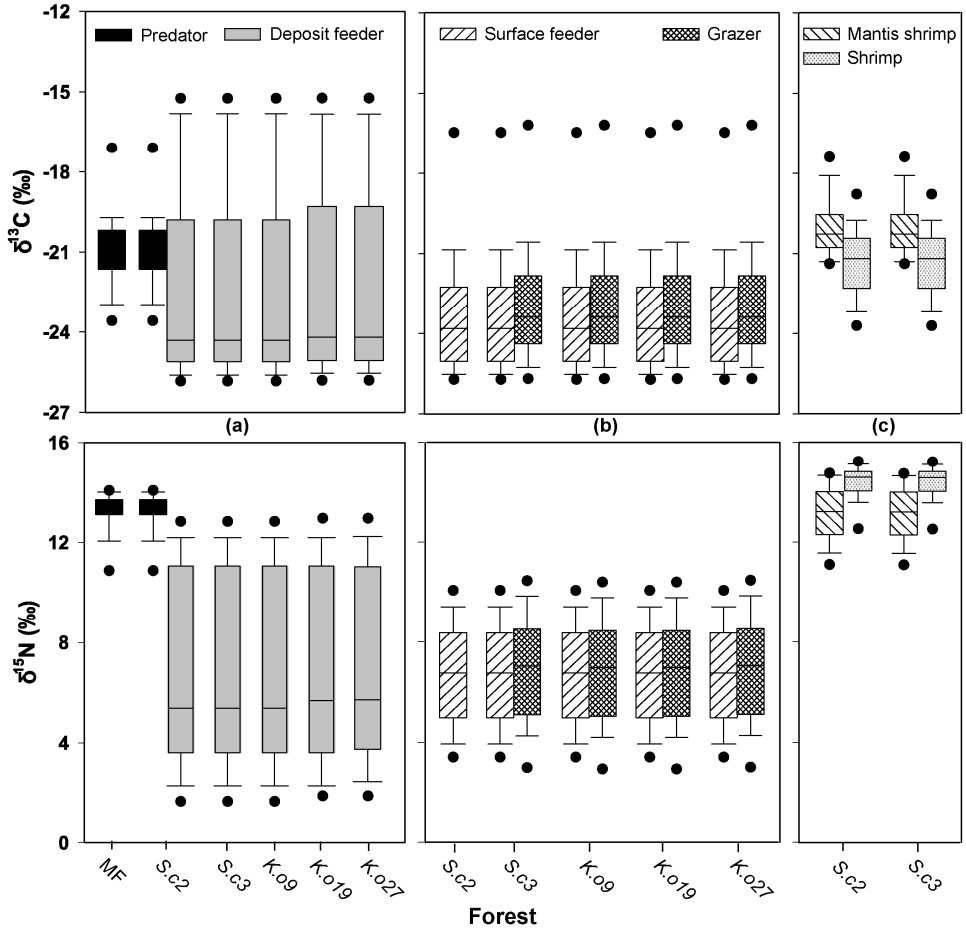

Figure 3. Box and whisker plot of the $\delta^{13}C$ and $\delta^{13}N$ signatures (‰) of (**a**) crab, (**b**) gastropod, (**c**) shrimp, and mantis shrimp communities among the sampling plots in the HLMF (*K. obovata* and *S. caseolaris* forests with different ages and denoted as *S.c* and *K.o*, respectively. MF represents mudflat. See Section 2.1 for details). The feeding ecology of each species was referred from Table 2.

The stable isotope signatures of mantis shrimp were similar between the *S.c2* and the *S.c3* forests ($\delta^{13}C$: $F_{1,14} = 0.342$, $p = 0.568$; $\delta^{15}N$: $F_{1,14} = 0.338$, $p = 0.570$), and were higher than those of other communities. The stable isotope signatures of shrimps were the second-highest among communities, with an average of 13.1 ± 1.0‰ and −21.4 ± 3.7‰ for the $\delta^{15}N$ and $\delta^{13}C$, respectively. The $\delta^{15}N$ values of polychaetes ranged from 11.4 ± 1.3 to 12.9 ± 1.2‰, and the $\delta^{13}C$ values ranged from −22.1 ± 1 to −20.3 ± 1.4‰, without significant differences in the isotopic composition among the mudflat and the *S. caseolaris* and *K.o9* forests ($\delta^{15}N$: $F_{3,10} = 1.326$, $p = 0.320$; $\delta^{13}C$: $F_{3,10} = 1.043$, $p = 0.415$). The variation in the carbon isotope signatures of various food sources indicated the change in the frequency distribution of the $\delta^{13}C$ values of macro-invertebrates from the un-vegetated mudflat to the high mature stage of mangrove in the *S. caseolaris* and *K. obovata* forests.

4. Discussion

4.1. Variation in Isotopic Composition of Primary Food Sources

In the present study, the potential food sources of macro-invertebrates were different among the mudflat and the *S. caseolaris* and *K. obovata* forests. The mudflat was adjacent to the mouth of the river and influenced by tidal flushing and inundation, which limited the accumulation of mangrove-derived organic carbon on the forest floor but had a large input of phytoplankton (Phy) from the sea. Thus, Phy could be recognized as one of the dominant food sources for consumers in the mudflat. The $\delta^{13}C$ value of Phy in the present study was consistent with those reported for mangroves in northern Vietnam [36], but they were slightly higher than the $\delta^{13}C$ values of seston reported for the Setiu Lagoon, Malaysia [37]. The $\delta^{15}N$ value of Phy was more enriched compared to those reported, but they were in the range of data for the Malaysian mangrove forests suggested by Chong, et al. [38]. The $\delta^{13}C$ signatures of mangrove materials were much lower compared to the other sources, indicating that mangrove vegetation uses the C3 photosynthesis pathway [39], but they were lower than the results of mangrove leaves in northern Vietnam [36]. The increasing trend in the SOM $\delta^{13}C$ values from the *K.o27* forest to the mudflat reflected the change in the sources of SOM from mangrove-derived organic carbon to algae (Phy and BMA), or the decomposition process in the unvegetated mudflat [10]. The $\delta^{15}N$ values of SOM and BMA were higher than those previously reported for mangroves in northern Vietnam [36], but they were lower than the results from the mangrove ecosystems in the Zhangjiang Estuary, China [40].

4.2. Food Sources of Macro-Invertebrates in the Restored Mangrove Forests

a. Bivalve and barnacles

In the HLMF, the dominance of hard clam *M. lytara*, Asiatic hard clam *M. meretrix*, and *P. acutidens* in the mudflat was a result of the tidal migration of these species from nearby clam farming [27]. The mean $\delta^{13}C$ and $\delta^{15}N$ values of these bivalves varied slightly and were closer to those of BMA and Phy than other sources, confirming that BMA and Phy were the primary food sources of these bivalves in the HLMF. The sessile filter feeder barnacle *F. albicostatus*, which commonly occupies the trunks and twigs of mangrove trees [41] in the *S.c2* forest, caused a reduction in plant fitness [42]. Their isotopic compositions lay on the range of Phy, reflecting that the mangrove barnacles frequently used Phy in their diets (Table 2).

b. Polychaetes

Only three deposit-feeding polychaete species were found in the sediments from the mudflat and the *S. caseolaris* and *K.o9* forests. This finding was associated with the frequency of tidal flooding and the characteristic of substrates, which changed from the seaward (young mangrove forests) to the landward sites (old mangrove forests) [43]. The $\delta^{13}C$ and $\delta^{15}N$ values of polychaetes varied among the sampling plots, but they were within the range of the Phy and BMA isotopic compositions in the mudflat, and BMA, and SOM in the *S. caseolaris* and *K. obovata* forests. Therefore, the diet of

polychaetes showed a change from the dominance of Phy and BMA to a combination of BMA and SOM under the effects of tidal inundation (Table 2). These results were similar to the suggestions of Hwey-Lian, et al. [44], and proved the functions in the refractory organic matter to the higher trophic level of polychaetes [45].

c. Gastropods

The $\delta^{13}C$ compositions of several gastropod species were relatively smaller, and the $\delta^{15}N$ compositions were larger than those reported for the gastropod community in northern Vietnam [36], while the $\delta^{13}C$ values for them lay within the range of the $\delta^{13}C$ values reported for Malaysian gastropods, with a difference of ±1‰ [46]. Gastropods were mostly distributed in the old forests, reflecting the changes in the light intensity, tidal condition, and sediment properties among the sampling plots [3]. In particular, eight species were caught in the *K. obovata* forests, four species were seen in the *S. caseolaris* forests, and no species was collected in the mudflat. The variation in the $\delta^{13}C$ values at the community level of gastropods may reflect changes in the available food sources on the forest floor. Gastropods in the old mangrove forest tended to consume more mangrove or sediment organic matter than they did at other sites.

The slug *Onchidiidae* sp. was collected only in the *K.o19* and the *K.o27* forests, and it had $\delta^{13}C$ values 2 to 3‰ higher than those of BMA and SOM, suggesting that *Onchidiidae* sp. depended mainly on these sources. The surface grazing gastropods of *C. aurisfelis*, *C. nucleus*, *C. obtusa*, *T. sulcata*, *N. violecia*, and *E. aurisjudae* depended primarily on SOM, BMA, and Phy (in the water column) (Table 2), and were consistent with the previous reports of Abrantes and Sheaves [47] and Bouillon, et al. [48]. Large variations in the $\delta^{13}C$ and $\delta^{15}N$ values of *C. obtusa*, *T. sulcata*, and *N. violecia* were observed among the sampling plots, and they were approximately 1 to 2‰ and 1 to 6‰ for nitrogen and carbon, respectively. These results were consistent with the differences in the geomorphological settings and available food sources, and reflected the heterogeneity of the diets. In the *S. caseolaris* forests, the $\delta^{13}C$ values of these species fell in the range of the BMA and SOM isotopic compositions, and these sources were the dominant food sources of surface-grazing gastropods. In the *K. obovata* forests, the $\delta^{13}C$ values of these species were more depleted than those in the *S. caseolaris* forests, and could be explained by a change in the $\delta^{13}C$ signatures of food sources, with lower C isotope signatures of SOM and BMA. The low $\delta^{13}C$ values of food sources were related to the high contribution of mangrove-derived OM, with low isotopic signatures to the SOC following forest maturity [23]. Moreover, in the old mangrove forests, the higher tree canopy provided larger shaded areas than those in the younger forests, causing a high availability of BMA on the forest floor for gastropod food webs. The BMA was characterized by a highly productive and simpler body structure than mangrove vascular plants [4]. Thus, it was preferentially ingested by gastropods in the *K. obovata* forests.

The generalist grazer *L. melanostoma*, which inhabited the trunk of the mangrove trees, had similar isotope compositions between the *S. caseolaris* and the *K. obovata* forests, with a small range of $\delta^{13}C$ and $\delta^{15}N$ values of about 0.1 and 0.4‰, respectively. However, as mentioned above about the changes in the isotopic compositions of food sources in Section 3.2, the diet composition of *L. melanostoma* varied from the mixing of SOM and BMA in the *S. caseolaris* forests to BMA, which accounted for 85.9% of the diets, but these were inconsistent with the findings from previous studies on the *K. obovata* forests. Lee, et al. [49] revealed that *L. melanostoma* fed on a combination of mangrove trees and other items attached to the trees, such as microalgae and cyanobacteria. The difference pattern could be explained by the locomotor activities of *L. melanostoma* from mangrove trees to the surface sediment to find easy-to-ingest food sources such as BMA in the forests located at the high intertidal zone.

d. Crabs

The portunid crabs *S. serrata* had similar $\delta^{15}N$ and $\delta^{13}C$ compositions between the two sampling plots and were within the range for the BMA and Phy isotope compositions in the mudflat and BMA in the *S. caseolaris* forests, demonstrating the change in primary food sources with tidal elevation.

The *S. serrata* fed on small invertebrates in the mudflat and *S. caseolaris* forests, based on the BMA and Phy food chain. This result was consistent with that of a previous study on the same species in Malaysia [37] (Table 2).

In the HLMF, the sesarmid crabs were functional in processing organic matter derived from mangrove products (roots and litter) and modifying the characteristics of the subsurface sediment [6]. The differences with a broad range of $\delta^{13}C$ values for crabs among the different-aged forests indicated the influences of each food source on each crab species following mangrove restoration. The $\delta^{13}C$ values of the sesamid crabs *M. depressus* and *M. elegans* were relatively lower in the *K. obovata* forests compared to those in the *S. caseolaris* forests. However, they lay in the range of the BMA and SOM isotope signatures, and closer values to these food sources were examined in the *K. obovata* forests, indicating that the two crabs mostly consumed BMA and SOM as food sources. The $\delta^{13}C$ signatures of the sesarmid crab *P. bidens* were 0.3‰ more depleted than those of SOM and Phy in the *S. caseolaris* forests and 0.2‰ more enriched than those of BMA in the *K. obovata* forests, reflecting a change in the dominant food sources of *P. bidens* from a mixture of SOM and Phy to BMA following forest aging. Other sesarmid crabs *M. longipes*, *M. messor*, and *S. plicata* were only caught in the *K. obovata* forests and had $\delta^{13}C$ values that fell in the range of the SOM and BMA isotope compositions, showing that these species assimilated mainly BMA and SOM. The $\delta^{13}C$ compositions of the Ocypodidae family *I. formosensis* and a fiddler crab of the *Uca* genus were close to those of BMA and SOM. Thus, the diets of these fiddler crabs had a significant contribution of BMA and SOM. The species *H. formosensis* showed values more enriched in $\delta^{13}C$ than those of *V. litterata*, but the $\delta^{13}C$ values were within the range of the food sources, indicating an equivalent food source attribution to the diet of crabs.

From the data mentioned above, the diets of crabs tended to change from Phy and BMA in the mudflat to ones dominated by BMA and SOM in the *S. caseolaris*, and there was a higher contribution of these sources in the *K. obovata* forests. However, the dependence of food sources on the BMA was not consistent with the previous report of Nordhaus, et al. [50], which showed that mangrove litter acted as the main food source for mangrove crabs. Several explanations could interpret the difference between them. Firstly, the earlier studies indicated that the fractionation of the $\delta^{13}C$ values between the mangrove leaves and the muscle tissues of leaf-eating crabs was selected at the $\Delta\delta^{13}C$ from 4 to 5‰ at the stepping up of each trophic level [51,52]. After applying this trophic enrichment factor for assessing diet composition using the model, the results showed an increasing trend in the contribution of mangrove litter to the diets of sesarmid crabs. The second explanation was the selection of food sources associated with the feeding behavior and assimilation efficiency of mangrove crabs [53]. Additionally, the nitrogen derived from mangrove leaves does not meet the requirement for the growth and reproduction of the crabs because of their high tannin contents, high C/N ratios, and low assimilation efficiencies. On the contrary, the BMA was documented as a highly productive food source in a mangrove forest with a simpler structure [4], while sediment detritus was a richer source of nitrogen, reflected in the lower C/N ratios than those of the mangrove leaves [53]. Thus, BMA and SOM were more consumed by mangrove crabs than mangrove leaves, and this resulted in an increase in the $\delta^{13}C$ values in their tissues.

e. Other species

The shrimps *A. euphrosyne*, *F. indicus*, *L. vannamei*, *M. ensis*, and *P. monodon* and the mantis shrimp *A. fasciata* were collected only in the *S. caseolaris* forests, and they showed a mean of $\delta^{13}C$ values that were close to that of BMA. Thus, these shrimps and the mantis shrimp mainly consume BMA in their diets.

5. Conclusions

The diets of macro-invertebrates in the HLMF depended on different sources, including SOM, BMA, and Phy in the mudflat and Phy, SOM, BMA, and Man in the *S. caseolaris* and *K. obovata* forests. The $\delta^{13}C$ and $\delta^{15}N$ signatures of the crab and gastropod communities slightly depended on

the forest ages, but no difference could be found in the bivalves, polychaetes, shrimps, and mantis shrimps. The present study showed that the main food sources assimilated by the macro-invertebrates changed from being dominated by BMA and Phy in the mudflat to a mixture of BMA and SOM in the *S. caseolaris* forests and *K. obovata* forests. The diets of macro-invertebrates in the restored mangrove ecosystems were influenced by the mangrove forest ages and the locations of forests in the intertidal zone. The stable isotope analysis results showed that mangrove-derived organic carbon is an important food source for macro-invertebrates in the HLMF. Thus, mangrove restoration plays an important role in providing the food sources of macro-invertebrates in this area. The results from the present study provide important information for the management, conversation, and restoration of mangrove forests in Vietnam and worldwide.

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