TROPICAL LIFE SCIENCES RESEARCH

Feeding Shift of Mangrove Crab Assemblages Revealed Through $\delta^{13}C$ and $\delta^{15}N$ Stable Isotope Ratios in Mangroves of Peninsular Malaysia

Authors:

Nur Hannah Abd Rahim, Khairun Yahya, Syahidah Akmal Muhammad and Shuhaida Shuib*

***Correspondence:** shuhaidashuib@usm.my

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Highlights

- Isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of crabs, sediment, and leaf litter were compared between disturbed (Penang) and less disturbed (Merbok) mangroves in Peninsular Malaysia.

- Sediment and leaf $\delta^{13}C$ and $\delta^{15}N$ were higher in Penang than Merbok, however the $\delta^{15}N$ in crabs was higher in Merbok, suggesting a feeding shift in crabs in Merbok.

- In Penang, $\delta^{13}C$ in crabs was positively correlated with sediment, while $\delta^{15}N$ was positively correlated with both sediment and leaf litter, while no significant correlations were found in Merbok.

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EARLY VIEW

Feeding Shift of Mangrove Crab Assemblages Revealed Through $\delta^{13}C$ and $\delta^{15}N$ Stable Isotope Ratios in Mangroves of Peninsular Malaysia

Nur Hannah Abd Rahim [1,2], Khairun Yahya[1], Syahidah Akmal Muhammad [3,4] and Shuhaida Shuib[1*]

[1]School of Biological Sciences, Universiti Sains Malaysia, 11800 USM, Pulau Pinang, Malaysia
[2]Mangrove Research Unit (MARU), Institute of Oceanography and Environment (INOS), Universiti Malaysia Terengganu (UMT), Kuala Nerus 21300, Malaysia
[3]School of Industrial Technology, Universiti Sains Malaysia, 11800 USM, Pulau Pinang, Malaysia
[4]Analytical Biochemistry Research Centre, Universiti Sains Malaysia, 11800 USM, Pulau Pinang, Malaysia

*Corresponding author: shuhaidashuib@usm.my

Running head: Feeding Shift Mangrove Crab

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Abstract: Crab feeding patterns in mangroves of Peninsular Malaysia were assessed using stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ to identify carbon and nitrogen ratios in crabs, sediment and leaf litter. Sampling of crabs was done using a hand catch method in six chosen sites in Peninsular Malaysia. Three sites were characterized by coastal developments in Penang Island, and three sites from the less disturbed area of Merbok, Kedah. Data were analysed using Welch's t-test to identify differences in $\delta^{13}C$ and $\delta^{15}N$ in samples between Penang and Merbok while Pearson's correlation test was used to determine significant correlations (if any) of isotope signatures among crabs, sediment and leaf litter in SPSS v 27.0. The $\delta^{13}C$ and $\delta^{15}N$ in crabs, sediment and leaf litter differed between Penang and Merbok, except for $\delta^{13}C$ in crabs. Findings showed that the $\delta^{13}C$ and $\delta^{15}N$ in sediment and

leaf litter were significantly greater in Penang compared with Merbok, however the $\delta^{15}N$ in crabs in Merbok was greater than the $\delta^{15}N$ in crabs in Penang. These patterns suggest a feeding shift in crabs in Merbok, possibly caused by low nutrient content in the leaf litter and sediment. In Penang, $\delta^{13}C$ in crabs was positively correlated with sediment, while $\delta^{15}N$ was positively correlated with both sediment and leaf litter, while no significant correlations were found in Merbok.

Keywords: Mangrove, Crabs, Stable Isotope, Feeding Shift, Ratio

INTRODUCTION

Mangrove crabs contribute to nutrient recycling by consuming and processing leaf litter (Koch & Nordhaus, 2010; Thongtham *et al*., 2008; Zhang *et al*., 2024). Leaf litter processing by mangrove crabs is important for the primary and secondary productivity in mangroves (Kristensen, 2008). Despite the importance of crabs in mangroves, there are knowledge gaps in understanding the role of crab activities (Belley & Snelgrove, 2017), such as the trophic role of crabs in the mangrove food web (Le *et al*., 2017). Previous trophic studies conducted based on gut content analysis (Chen *et al*., 2022; Le et al., 2017) were utilized to identify the energy flow from the primary producer to the tertiary or other higher consumer (Acosta-Pachón *et al*., 2022; Odum & Heald, 1975).

Identifying the source of carbon and nitrogen used by crabs using conventional gut content methods can be challenging and time-consuming (Caquet, 2006). Findings from gut content analysis may be unreliable due to difficulties in identifying incomplete or partially digested items, resulting in the inability to determine the source of the consumed food (Polis & Strong, 1996; Xu *et al*., 2024). Furthermore, gut content analysis may be able to provide insights into the diet over a short period of time, whereas stable isotope analysis could indicate the diet of the crabs over weeks to months (Gearing, 1991; Guo *et al*., 2023).

The usage of stable isotopes therefore is to detail nutrient flow in the food web at an elemental level (Guo *et al*., 2023; Le et al., 2017; Xu *et al*., 2024). Stable isotope analysis offers a robust approach for tracing organic matter assimilation into consumer tissues (Gearing, 1991). Previous studies on crab feeding via stable isotope analysis have focused on trophic levels (Sandoval *et al*., 2022; Schwamborn & Giarrizzo, 2015), the role of crab feeding in litter production (Bouillon *et al*., 2008; Werry & Lee, 2005; Zhang et al., 2024) and crab food preferences related to nutrient content in leaves (Nordhaus *et al*., 2011). Crabs, however, have been observed to display changes in their feeding preferences, influenced by the

advantageous benefits derived from various sources of carbon and nitrogen that are more accessible (Nordhaus et al., 2011). The stable isotope approach revealed that in addition to mangrove detrital matter, some crabs have demonstrated an almost omnivorous diet preference which include algae, nematodes or other detrital materials in the sediment to fulfil their nutritional requirements (Nordhaus et al., 2011). For example, some species of *Perisesarma* and *Episesarma* that mainly feed on detritus and mangroves leaves (Nordhaus et al., 2011), supplement their nutrient requirement by feeding on animal matter such as polychaetes (Herbon & Nordhaus, 2013).

The influence of human activities on crab feeding behaviours remains understudied in tropical regions such as Peninsular Malaysia. The extensive mangrove coastlines of Peninsular Malaysia face threats from human-induced nutrient pollution, which can disrupt the delicate balance of carbon and nitrogen in the ecosystem (Mack *et al*., 2024; Molnar *et al*., 2013; Trott & Alongi, 2000). From a nutrient cycling context, effluents from anthropogenic activities (Molnar *et al*., 2013) increases carbon and nitrogen content that could affect mangrove ecosystem negatively (Trott & Alongi, 2000). For example, water quality may decline as concentrations of ammonia, nitrite and phosphate in the water increase, while levels of dissolved oxygen decrease, and pH levels decline (Wear & Tanner, 2007). These excessive nutrients in mangrove sediments may affect mangrove crabs and molluscs that feed on the small particulates in the sediments (Cannicci *et al*., 2009), potentially influencing the feeding strategies of mangrove crabs (Gao et al., 2024; Ramsay et al., 1996).

Despite the potential impact of human induced nutrient enrichment and physical habitat changes on crab populations in mangroves, the extent to which crabs adjust their feeding preferences in response to these factors requires further investigation. Stable isotope signatures have been used in multiple studies to identify the influence of excess nutrients sourced from sewage discharge, tracked through elevated N presence in the environment, trophic transfer, and enrichment in mangrove leaf isotopic values (Medina-Contreras & Arenas, 2023). Recent studies have included using $\delta^{13}C$ and $\delta^{15}N$ to examine the impact of mangrove clearance on mangrove crab feeding activities (Sabeel et al., 2015), extent of waste pollution on crab assemblages in mangroves of North Queensland, Australia (Vermeiren *et al*., 2015), and alteration occurring in the trophic structure of a mangrove food web (Sabeel *et al*., 2015). Isotope signatures in mangrove crab tissue have been used to track shifts in food web structure associated with habitat disturbance and recovery, with detectable changes emerging within 5–15 years of forest clearing (Then et al., 2021). Stable isotope markers in benthic mangrove macroinvertebrates have proven effective at detecting the effects of anthropogenic pressures such as sewage discharge, aquaculture, and urban development on

food web structure (Medina-Contreras & Arenas, 2023). This suggests that isotopic monitoring of crab diet could serve as effective indicators of eutrophication and coastal degradation in mangrove ecosystems. It is essential to address the insufficient understanding of how crab feeding preferences may adapt to environmental changes, particularly with the prevalence of human induced nutrient enrichment in tropical mangroves both now and in the future. This study quantified feeding shifts in mangrove crabs using stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) signatures in crab and potential food sources across sites characterized by different exposure and proximity to anthropogenic activities.

MATERIALS AND METHODS

Study Sites

Samples of crabs, sediment and leaf litter were collected from six mangrove sites from two locations, Penang and Merbok at North-west Peninsular Malaysia. Penang sites were dominated by *Avicennia marina* and *Rhizophora apiculata* (Hamdan *et al*., 2012) and categorized as disturbed due to prevalent deforestation for urbanization and land reclamation activities (Jusoff, 2013). In comparison, Merbok sites that were dominated by *Rhizophora apiculata* and *Bruguiera parviflora* with patches of *Avicennia* and *Sonneratia* (Ong *et al*., 1991) were considered less disturbed than Penang, however, was still impacted by aquaculture and agriculture activities (Latiff & Faridah-Hanum, 2014).

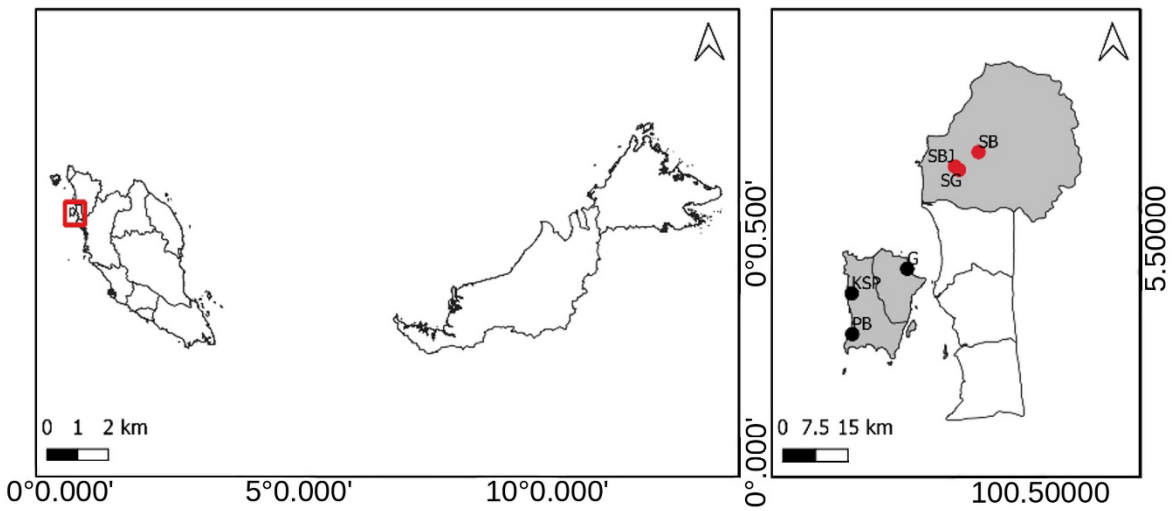


Figure 1. Sampling sites. The sampling sites in Merbok, Kedah; Sungai Bujang (5º 39’11.52” N 100º 24’24.89”E), Sungai Batu (5º 40’58.27” N 100º 27’22.06”E), Sungai Gelam (5º 38’45.18” N 100º 24’55.61”E)) and Penang Island; (Gurney (5º 26’34.42” N 100º 18’30.42”E),

Pulau Betong (5º 18’27.07” N 100º 11’42.47”E), Kuala Sungai Pinang (5º 23’28.58” N 100º 11’38.08”E).

Crabs, Leaf litter and Sediment Sample: Collection and Preparation

This study was conducted to analyse the feeding shift in mangrove crabs based on stable isotope ratio of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) signature in mangrove crabs and potential food sources. Samples were collected across two regions, Penang and Merbok using 36 replicate quadrats per region, yielding a total sample size of N = 72. Crabs were collected by hand in 1 m by 1 m quadrats in 15 minutes (Ashton *et al*., 1999). The leaf litter was collected in 1 m by 1 m quadrats while a subsample of sediment measuring 10 cm by 10 cm was scraped out within the quadrats. The samples were kept in a freezer prior to drying process.

Sample preparation for crabs, sediment, and leaf litter involved different methods based on the presence or absence of carbonate contents. Sediment and crab samples may contain inorganic carbon, therefore a treatment to remove inorganic carbon was necessary before stable isotope analysis (Harris *et al*., 2001). This is crucial as organic carbon reflects the carbon assimilated by consumers from their diet (Yokoyama *et al*., 2005), while inorganic carbon is a non-dietary carbon (Ray *et al*., 2018). Therefore, in this study only stable isotope ratios of organic carbon were studied in assessing crab feeding (Schlacher & Connolly, 2014). Additionally, the presence of even small amounts of inorganic carbon may bias $\delta^{13}C$ values of organic carbon, as inorganic carbon is isotopically heavier than organic carbon in biological samples (Schlacher & Connolly, 2014). Therefore, removing inorganic carbon prior to analysis may prevent any confounding effects to the carbon signature (Harris et al., 2001).

The crabs and the sediment were thawed and dried at 60 °C for a minimum of 24 hours (Bouillon *et al*., 2002b; Carabel *et al*., 2006), then ground into fine powder with a mortar and pestle (Bouillon *et al*., 2002b; Carabel *et al*., 2006). Crab and sediment samples intended for $\delta^{13}C$ analysis underwent acid treatment to remove inorganic carbon in the form of calcium carbonate, via acid fumigation with 1M HCl for 6 hours in a desiccator (Harris *et al*., 2001). Acid fumigation for 6 hours was selected following Harris *et al.* (2001), who confirmed this duration is sufficient to remove carbonate fractions comprising up to 75% of total carbon. Komada *et al.* (2008) found that 6 hours of HCl vapor fumigation is an optimal duration for removing inorganic carbon from coastal sediments, ensuring complete decarbonation while preserving organic carbon integrity.

Leaf litter were analyzed for both $\delta^{13}C$ and $\delta^{15}N$ without acid treatment. This follows the protocol of Carabel et al. (2006), which indicated that acidification is not required for tissues lacking significant inorganic carbon and can instead lead to alterations in N signatures (Schlacher & Connolly, 2014). Samples of leaf litter with the midrib removed were thawed, rinsed in tap water and dried overnight at 60 ºC (Fry & Smith, 2002). After the samples were completely dried, the leaf litter samples were grounded with a blender into fine powder (Muzuka & Shunula, 2006). The powdered samples were then weighed using a microbalance, ranging from 0.5-0.6 mg for crab, 0.3-0.4 mg for leaf litter, and 12.0-13.0 mg for sediment samples.

Stable isotope analysis

The samples were analysed with a Flash 2000 elemental analyzer (ThermoScientific, Waltham, MA) coupled to a Delta V Advantage isotope ratio mass spectrometer (Thermo, Milan, Italy) located at Analytical Biochemistry Research Centre (ABrC), USM. Raw isotope ratios were normalized to international scales via a two-point calibration using 0.5-0.6 mg of USGS 40 (L-Glutamic acid (U.S Geological Survey, Reston, VA 20192)), USGS 41 (L-Glutamic acid (U.S Geological Survey, Reston , VA 20192), while 0.2-0.3 mg of Urea (IVA-Analysentechnik GmbH & Co., Germany) was utilized as an independent quality control standard. The typical precision for the replicated samples was ±0.3‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$. Variations in stable isotope ratios were reported as parts per thousand (‰) deviations from internationally accepted standards which are Vienna Pee Dee Belemnite (VPDB) for carbon, atmospheric nitrogen (AIR) for nitrogen, in the delta (δ) notation, defined using the following equation:

$$\delta\text{-}X\ (‰) = (R_{sample} / R_{standard} - 1)$$

with

X : ^{13}C or ^{15}N

R : ratio of heavy or light isotope content ($^{13}C/^{12}C$ or $^{15}N/^{14}N$).

In stable isotope studies, ratios of carbon and nitrogen are usually reported using a standard δ-notation with the unit of ‰ (Peterson & Fry, 1987). Thus, $\delta^{13}C$ denotes carbon-13 stable isotope ratio while $\delta^{15}N$ denotes nitrogen-15 stable isotope ratio. Another commonly used symbol in stable isotope studies is Δ, which signifies the trophic shift or fractionation that occurs when stable isotope is transferred from food to consumer (Fry, 2006). For example, trophic shift of $\delta^{13}C$ between diet (e.g.; leaf litter) and consumer (e.g.; mangrove crab) is represented as $\Delta\delta^{13}C$, ($\Delta\delta^{13}C$ = $\delta^{13}C$ in mangrove crab - $\delta^{13}C$ in leaf litter) (McCutchan *et al*.,

2003). $\Delta\delta^{13}C$ between consumers and the food source are well conserved or just slightly increased (Fry & Sherr, 1989) while $\Delta\delta^{15}N$ is usually 3 to 4 ‰ enriched between the consumer and its food source (Lau *et al*., 2008).

Statistical Analysis

The total number of replicates was N = 72; however, after excluding one family that occurred in only one region and another represented by only 2–3 individuals per region, the final sample size was (N = 70). Differences in $\delta^{13}C$ and $\delta^{15}N$ between Penang and Merbok were tested for crab, sediment and leaf litter using independent-samples t-tests, with crab families pooled (Penang, n = 34 and Merbok, n = 36). Due to unequal sample sizes and variance, Welch's t-test was chosen to analyze the data. Pearson's correlation test was conducted to assess the correlation between crab and food source isotope signatures.

RESULTS

Range of carbon stable isotope ratio ($\delta^{13}C$) and nitrogen stable isotope ratio ($\delta^{15}N$) of crabs, sediment and leaf litter

Carbon isotopic trophic fractionation (Δ) revealed distinct, family-specific patterns of depletion and enrichment relative to basal resources (Table 1a). In Merbok, all resident crab families exhibited $\delta^{13}C$ values that were enriched relative to both leaf litter and sediment baselines. This trend shifted in Penang, where $\delta^{13}C$ signatures for Sesarmidae and Camptandriidae were depleted relative to the sediment, whereas Dotilidae values reflected the carbon signatures in the sediment, while the remaining families were more enriched (Table 1a).

Table 1a: Carbon stable isotope ratio of crab from different families, sediment and leaf litter, ($\delta^{13}C$) in ‰ (mean ± standard error) from samples collected in Penang and Merbok (n = 72). The "-" denotes crab species was not found in the selected forest.

Samples		Forest	
		Penang	Merbok
Sediment		-25.60 ± 0.33	-26.95 ± 0.17
Leaf litter		-28.20 ± 0.16	-29.11 ± 0.20
Crab family	Camptandriidae	-26.49 ± 0.63	-26.46 ± 0.97
	Sesarmidae	-27.73 ± 0.46	-26.91 ± 0.39
	Dotilidae	-25.60 ± 1.81	-25.72 ± 0.17
	Varunidae	-23.61 ± 0.72	-
	Ocypodidae	-	-24.71 ± 0.62

Table 2b: Nitrogen stable isotope ratio of crab of different families, sediment and leaf litter, ($\delta^{15}N$) in ‰ (mean ± standard error) from samples collected in Penang and Merbok (n=72). The "-" denotes crab species was not found in the selected forest.

Samples		Forest	
		Penang	Merbok
Sediment		5.83 ± 0.61	3.54 ± 0.33
Leaf litter		6.27 ± 0.20	5.31 ± 0.23
Crab	Camptandriidae	6.59 ± 0.41	10.22 ± 0.82
	Sesarmidae	6.04 ± 0.59	8.42 ± 0.61
	Dotilidae	6.64 ± 0.45	6.72 ± 0.35
	Varunidae	7.54 ± 0.21	-
	Ocypodidae	-	8.91 ± 0.89

In Penang, crab $\delta^{15}N$ was similar to or only slightly above the leaf-litter and sediment isotopic signatures, with the exception of Sesarmidae which displayed lower values than the leaf litter. In contrast, crab families in Merbok were consistently more enriched than Penang crabs (Table 1b). In Merbok, the $\delta^{15}N$ in most crab families were more enriched than basal sources, with Camptandriidae and Ocypodidae being the most enriched, while Dotilidae remained closest to the basal resources (Table 1b).

Carbon stable isotope ratio ($\delta^{13}C$) and nitrogen stable isotope ratio ($\delta^{15}N$) of crabs, sediment and leaf litter across region.

Crab $\delta^{13}C$ did not differ between Penang and Merbok (Table 2a), indicating comparable carbon sources. Sediment and leaf litter $\delta^{13}C$ however were significantly different between Penang and Merbok (Table 2b-c), with higher depletion detected in Merbok (Figure 2). The $\delta^{15}N$ of crab and basal sources differed between Penang and Merbok (Table 22-f, Figure 2) with higher crab $\delta^{15}N$ in Merbok despite depleted ^{15}N in basal sources (Figure 2). Sediment and leaf-litter $\delta^{15}N$ were found to be higher in Penang (Figure 2).

Table 2. Independent-samples (Welch's) t-tests of $\delta^{13}C$ and $\delta^{15}N$ by Region (families pooled, N = 70).

	Variable	t	df	p
a.	$\delta^{13}C$ crab	-0.55	67.80	0.583
b.	$\delta^{13}C$ sediment	3.39	49.10	0.001
c.	$\delta^{13}C$ leaf	3.20	65.70	0.002
d.	$\delta^{15}N$ crab	-4.71	61.40	< 0.001
e.	$\delta^{15}N$ sediment	3.26	49.90	0.002
f.	$\delta^{15}N$ leaf	2.96	67.30	0.004

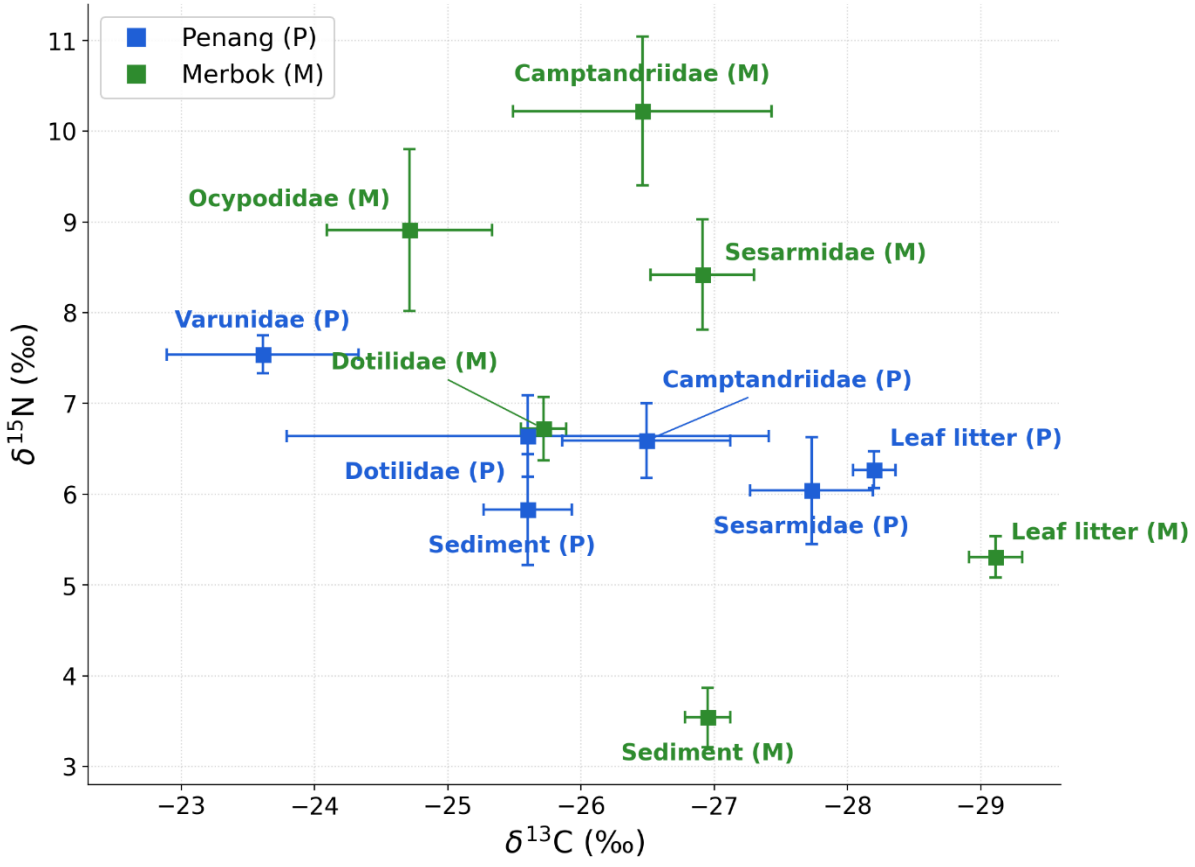


Figure 2: Mean (±SEM) of carbon and nitrogen stable isotope composition in crab, sediment and leaf litter, $\delta^{13}C$ and $\delta^{15}N$ (‰) in (i) Penang (blue) and (ii) Merbok (green).

Isotope values: Correlation between crabs, sediment and leaf litter

In Penang, the $\delta^{13}C$ in crabs positively correlated with $\delta^{13}C$ in sediment (r^2=0.80). No significant correlation was found between $\delta^{13}C$ in crab and $\delta^{13}C$ in leaf litter, or between $\delta^{13}C$ in sediment and $\delta^{13}C$ in leaf litter. There were positive correlations between $\delta^{15}N$ of crabs and $\delta^{15}N$ in sediment (r^2=0.69) and between $\delta^{15}N$ in crabs and $\delta^{15}N$ and in leaf litter (r^2=0.64). $\delta^{15}N$ in sediment did not correlate with the $\delta^{15}N$ of leaf litter. No significant correlations of isotope values between crabs, sediment and leaf litter were found in Merbok.

DISCUSSION

In this study, the range of $\delta^{13}C$ in mangrove crabs, sediment and leaf litter were almost similar to the range that were recorded in previous studies. The $\delta^{13}C$ in leaf litter in Penang and Merbok were similar to the $\delta^{13}C$ in sediment in Trang, Thailand (Kon et al., 2007) and Setiu, Terengganu (Le *et al*., 2017), while the range of $\delta^{13}C$ in sediment was similar to values recorded in Trang, Thailand (Kon *et al*., 2007). However, there were differences in carbon assimilation in specific crab families. Although the $\delta^{13}C$ values found in this study fell within similar range to the $\delta^{13}C$ recorded in previous studies (Kon *et al*., 2007; Le *et al*., 2017), these values differed across different crab families. Camptandriidae, the most dominant crab family, exhibited $\delta^{13}C$ values of -26.49 ‰ ± 0.63 in Penang and -26.46 ‰ ± 0.82 in Merbok, while in comparison a previous study conducted in Singapore recorded $\delta^{13}C$ values of -18.5 ‰ ± 1.0 for Camptandriidae (Zhang *et al*., 2017). In North Queensland, the $\delta^{13}C$ in Camptandriidae ranged between -20 to -14 ‰ (Vermeiren *et al*., 2015). Findings by Zhang *et al.* (2017) and Vermeiren *et al*. (2015) suggests the $\delta^{13}C$ in Camptandriidae in Penang and Merbok were more negative in comparison to these results, indicating the crab sample was more depleted in heavier isotope ^{13}C and enriched in lighter ^{12}C isotope (Fry, 2006).

The greater depletion of $\delta^{13}C$ in Camptandriidae in this present study compared with previous studies might be related to the $\delta^{13}C$ in the sediment and leaf litter, which were the main food source for the crabs in this study. $\delta^{13}C$ stable isotope signatures in the consumer is usually well conserved from its food source (Fry & Sherr, 1989), resulting in a small value of $\Delta\delta^{13}C$ (McCutchan *et al*., 2003). In this study, the $\delta^{13}C$ in Camptandriidae was almost similar to $\delta^{13}C$ in the sediment ($\Delta\delta^{13}C$ = ~1 ‰). Jones & Clayton (1983) found *Paracleistostoma* from the

Camptandriidae crab family preferred to feed on sediment. This may explain why the depleted value of $\delta^{13}C$ in the sediment is similarly depleted in the $\delta^{13}C$ signature in Camptandriidae. Additionally, in this study, specifically in Penang, there was a positive correlation between $\delta^{13}C$ in crab and $\delta^{13}C$ in sediment (r^2=0.80), which might support the findings that $\delta^{13}C$ in food source reflected the $\delta^{13}C$ in *Paracleistostoma*. Bouillon *et al*. (2002a) also found a correlation between $\delta^{13}C$ in crab and $\delta^{13}C$ in sediment. A previous study by Wu *et al*. (2020) shows a close $\delta^{13}C$ value between sediment and epifauna including mangrove crabs. Thus, the negative value of $\delta^{13}C$ in Camptandriidae in this study might reflect the depleted value of $\delta^{13}C$ in sediment.

The depleted value of $\delta^{13}C$ in the sediment might be caused by decline of organic matter such as mangrove litter and algae in the sediment (Ranjan *et al*., 2011). Freshwater and excess carbon flow into mangrove might also lead to $\delta^{13}C$ depletion in sediment (Bouillon *et al*., 2000) as the flow of other terrestrial carbon source such as sewage runoff may increase the ^{13}C-depleted materials in the mangroves instead of increasing the ^{13}C in the sediment (Bouillon *et al*., 2002b). This is attributed to the highly negative $\delta^{13}C$ value of the carbon content in the sewage runoff, which caused the $\delta^{13}C$ in the sediment to be more depleted (Bouillon *et al*., 2002b). Nutrient enrichment can also reduce $\delta^{13}C$ due to decreased photosynthesis by benthic microalgae (Lovelock, 2008). Thus, depletion of $\delta^{13}C$ could indicate the presence of excess nutrients in the mangrove ecosystem.

In comparison the $\delta^{15}N$ values in this study differed from the values found by Kon *et al*., (2007) and Le *et al*., (2017). The $\delta^{15}N$ in crabs, leaf litter, and sediment were mostly greater than the recorded range of $\delta^{15}N$ in previous studies, especially for the $\delta^{15}N$ in sediment and leaf litter from Penang, and $\delta^{15}N$ in crab samples from Merbok. In the Southeast Asia region, Kon et al. (2007) found negative $\delta^{15}N$ values, which was –1.1 ± 0.9‰ for $\delta^{15}N$ in the leaf litter and sediment. Le et al. (2017) found $\delta^{15}N$ that ranged from 3.5 to 3.8 ‰, which was lower compared with the results in this present study. Higher $\delta^{15}N$ were found in leaf litter in Penang at 6.27 ± 0.20 ‰ and 5.31 ± 0.23 ‰ in Merbok. The increase in $\delta^{15}N$ in the samples may be linked to nitrogen originating from urban, aquaculture, and agricultural runoff (Cole *et al*., 2004). Harrington *et al*., (1998) found concentration of $\delta^{15}N$ tend to be greater in effluent runoff from agricultural sites. The enriched $\delta^{15}N$ in the food source from nutrient runoff may account for the greater variability of $\delta^{15}N$ observed in crabs in this study compared with previous studies. Thus, $\delta^{15}N$ values in crabs and potential food sources may serve as effective indicators for assessing the effects of nutrient enrichment, on crab feeding activities (Bouillon et al., 2002b; Schwamborn & Giarrizzo, 2015).

The depleted $\delta^{15}N$ values in sediment and leaf litter compared to $\delta^{15}N$ in crabs in Merbok were consistent with findings by Lau *et al.* (2008) on food web structure investigated using stable isotope analysis. The $\delta^{15}N$ of the consumers were usually 3 to 4 ‰ more enriched compared with the food source (Lau et al., 2008). $\delta^{15}N$ in crab was more enriched as crabs would accumulate ^{15}N and excrete the lighter isotope, ^{14}N (DeNiro & Epstein, 1981; Herbon & Nordhaus, 2013). In this study, some crab families in Merbok such as Camptandriidae was more than 4 ‰ enriched than its food source (i.e. $\Delta\delta^{15}N = 6.68$).

In Penang however, a very small trophic shift was found between $\delta^{15}N$ in crabs and $\delta^{15}N$ in sediment at 0.2 ‰, and between $\delta^{15}N$ in crabs and $\delta^{15}N$ in leaf litter at 0.3 ‰. These findings were similar to previous studies (McCutchan *et al*., 2003; Pasquaud et al., 2008; Xu et al., 2024). McCutchan *et al*. (2003) found values as low as 0.18 ‰ of the trophic shift. The trophic shift varies depending on diet quality, with lower $\Delta\delta^{15}N$ values found in consumers fed high-quality, nitrogen-rich diets sufficient for optimal growth **(**McCutchan *et al*., 2003). In Penang, crabs and its food sources were exposed to elevated ^{15}N caused by anthropogenic nutrient enrichment (Medina-Contreras and Arenas, 2023). Furthermore, a great abundance of high-quality dietary nitrogen may be assimilated by the consumer more efficiently, resulting in lower $\Delta\delta^{15}N$ (McCutchan et al. 2003). This was in contrast with Merbok, where $\Delta\delta^{15}N$ between crab and its diet (sediment and leaf litter) was high. This large difference may be a result of low $\Delta\delta^{15}N$ in the sediment in the less enriched Merbok sites, causing crabs to shift from the sediment to more $\Delta\delta^{15}N$ enriched food sources (Lugendo and Kimirei, 2021).

Crabs in Merbok could have different feeding requirements and strategies compared with crabs in Penang. Isotopic differences between consumers and expected food sources suggest crabs are assimilating nutrients from non-mangrove origins (Fry & Sherr, 1989). The $\delta^{13}C$ and $\delta^{15}N$ assimilated by the crabs in Merbok might have originated from microphytobenthos, localized phytoplankton or marine phytoplankton from adjacent aquatic ecosystems (Bouillon *et al*., 2004; Kawaida *et al*., 2019) that were consumed by the crabs to supplement and meet its nutrient requirement (Nordhaus *et al*., 2011). The microphytobenthos and phytoplankton might contain higher nutrient content than materials derived from mangroves (Bouillon *et al*., 2008). Significantly lower $\delta^{15}N$ and $\delta^{13}C$ in leaf litter and sediment in Merbok compared with Penang indicated low nutrient flow in Merbok might cause the crabs to change its diet from low nutrient leaf litter and sediment to more nutritional food source such as phytoplankton. Furthermore, previous studies showed that phytoplankton was more abundant in sites with lower nutrient input (Costanzo et al., 2004).

It is therefore likely for mangroves such as Merbok that receive less exposure to nutrient effluents from nearby human activities to be categorized as an oligotrophic system (Lugendo and Kimirei, 2021). This pattern of feeding shifts may be observed as a mechanism by macrofauna to supplement a low nutrient diet in a nutrient-limited ecosystem such as mangroves (Bartolini et al., 2011). Generally, crabs and other macrofauna would adopt a diet with more variety (Bouillon et al., 2004), which is a reflection of survival strategies by crabs and other macrofauna in a normally low nutrient mangrove environment, as oligotrophy was considered to be characteristic of mangrove ecosystems (Lovelock *et al*., 2007).

Prolonged and excessive input of nutrients however could upset the fragile balance of a mangrove nutrient cycle. Nutrient loading from aquaculture ponds, agricultural runoff, domestic and industrial activities contain high amount of nutrients such as nitrogen and carbon, is threatening mangrove ecosystems worldwide (Polidoro et al., 2010). In Malaysia, untreated sewage from urban sites and landfills had been discharged into the mangroves (Jusoff, 2013). A study by Lee (2016) had detected the shift in carbon and nitrogen fluxes in South China Sea due to the inflow of sewage effluents from land use conversion of mangrove forests and coastal urbanization from adjacent countries including Malaysia. Thus, greater nutrient loading in Penang based on the higher $\delta^{13}C$ and $\delta^{15}N$ in leaf litter and sediment in Penang compared with Merbok, indicate that Penang was more enriched compared with Merbok.

Short-term nutrient enrichment in mangroves might be beneficial towards macrofauna such as crabs, as observed in this study wherein crab feeding was optimal, with greater crab abundance found in Penang. However, nutrient enrichment might cause the overgrowth of microalgae and bacteria (Meziane & Tsuchiya, 2002), which might lead to eutrophication (Bartolini et al., 2011), and later hypoxic condition in mangroves (Gray et al., 2002). causing adverse effects to mangrove ecosystems (Primavera, 1997). In previous studies, crustaceans such as crabs appeared to be among sensitive benthic animals that react towards hypoxic or low oxygen condition (Penha-Lopes et al., 2009).

CONCLUSION

In conclusion, mangrove crab assemblages in this study reveal dietary flexibility and family specific adaptations to localized nutrient enrichment. Stable isotope analysis identified a spatial mismatch between nitrogen levels in primary food sources and consumer tissues across the two locations. Penang was characterized by highly enriched sediment and leaf litter nitrogen baselines, indicating human-induced nutrient inputs. However, the Merbok crab

communities display higher overall $\delta^{15}N$ enrichment. This pattern points to a reliance on other similarly enriched food sources. Carbon signatures however reveal a link between consumer with sediment, except for Sesarmidae in Penang. Further studies investigating the relationship between stable isotope signatures in crabs and their dietary sources could incorporate a broader range of potential food sources, such as phytoplankton and algae, to achieve a more comprehensive understanding of the local food web. The systematic shifts in dietary preferences and trophic positioning demonstrate that tracking crab tissue isotope signatures in mangroves can be a reliable, early warning bioindicator tool.

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AUTHORS' CONTRIBUTIONS

Nur Hannah Abd Rahim: Methodology, Investigation, Formal Analysis, Writing: Original Draft, Writing: Review & Editing.

Khairun Yahya: Methodology, Investigation, Writing: Review & Editing.

Syahidah Akmal Muhammad: Methodology, Investigation, Formal Analysis, Writing: Review & Editing.

Shuhaida Shuib: Conceptualization, Methodology, Investigation, Formal Analysis, Writing: Original Draft, Writing: Review & Editing.

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