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Tidal zone effects on the diet composition of leaf-eating crabs in natural mangrove communities: a stable isotope analysis

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Background: In natural mangrove communities, mangrove species are often distributed zonally. Leaf-eating crabs are one of the most abundant and iconic arboreal brachyurans in mangrove forests, but variation in the composition of crab diets in different mangrove tidal zones is unknown.

Methods: To determine the contributions of mangrove leaves and other organic carbon (C) sources to leaf-eating crab diets, dual stable C and nitrogen (N) isotope signatures (δ13C and 1δ5N) were used in a Bayesian stable isotope mixing model. We conducted experiments at various tidal levels in the Dongzhaigang Bay National Natural Reserve in China. We analyzed δ13C and δ15N of leaf-eating crabs, mangrove leaves, sediment organic matter (SOM), and animal tissues (prey).

Results: The food composition of the dominant crab species, Parasesarma continentale, exhibited significant differences among the four tidal zones. From the margin to the high tide zone, the main food source shifted from predominantly mangrove leaves and SOM to primarily SOM and animal tissues. We observed a significant negative relationship between the C/N ratios of mangrove leaves and the proportion of leaves consumed by leaf-eating crabs. Additionally, as the tidal level increased, the C/N ratio of mangrove leaves also increased, whereas the proportion of leaves consumed by crabs decreased.

Conclusion: Leaf-eating crab diets vary significantly across tidal zones, highlighting the importance of considering tidal zone differentiation when studying consumer diets in mangrove ecosystems.

KEYWORDS

food sources, Bayesian mixing models, stable isotopes, mangrove tidal zones, leaf-eating crabs, mangrove leaf C/N ratio

Introduction

Many benthic invertebrates rely, either partially or entirely, on mangrove habitats to complete their life cycles (Basyuni et al., 2022). They participate in the trophic dynamics of mangrove ecosystems through nutrient cycling, bioturbation, and as prey or predator (Bui and Lee, 2014; Medina-Contreras et al., 2022). Among benthic invertebrates in mangrove forests, leaf-eating crabs play a pivotal role as “ecosystem engineers” (Araújo et al., 2012; Gao and Lee, 2022; Medina-Contreras et al., 2022) because of their top-down role in food web energy flow (Swindells et al., 2017; Xie et al., 2022). Crab activities include feeding, burrowing, and crawling (Lee, 1997). Leaf-eating crabs have downstream effects on mangroves by consuming a substantial portion of annual mangrove primary production (Robertson and Daniel, 1989; Lee, 2008; Medina-Contreras et al., 2022). In the Indo-West Pacific region, species of the Sesarmidae dominate the intertidal zone and rely mainly on mangrove leaves as their food source (Kristensen et al., 1995; Thongtham and Kristensen, 2005; Bui and Lee, 2014; MacKenzie et al., 2020). High leaf consumption rates result in rapid utilization of nutrients in mangrove leaves before they are exported by the tide (Nagelkerken et al., 2008). For instance, leaf-eating crabs living in mangrove forests along the semi-arid coast of Brazil consume more sediment organic matter (SOM) and omnivorous invertebrates to replenish nitrogen, in addition to feeding on mangrove leaf litter because of its high C/N ratio (Pereira et al., 2019). Several studies have shown that leaf-eating crabs supplement their nitrogen-poor diet of leaves by consuming sediment-associated bacteria, microbenthos and fungi, and animal tissues (Kristensen et al., 2010; Oakes et al., 2010; Medina-Contreras et al., 2022). In most mangrove environments, leaf-eating crabs contribute substantially to the detritus-based food chain, resulting in important effects on nutrient cycling, energy flow, litter decomposition, and export of mangrove production (Robertson, 1986; Nordhaus et al., 2006; Chen et al., 2017; Medina-Contreras et al., 2022).

Previous experiments typically explored crab food sources at the estuarine level, primarily in areas dominated by a single mangrove species (Thongtham et al., 2008; Tue et al., 2012; Medina-Contreras et al., 2022). However, mangrove species in natural communities often exhibit zonal stratification (Duke et al., 1998). According to Feng et al. (2017), changes in the structure of mangrove vegetation communities can affect the availability and palatability of food sources for leaf-eating crabs. Van Hieu et al. (2020) discovered that crabs primarily feed on phytoplankton and benthic microalgae in mudflats, while in *Sonneratia caseolaris* and *Kandelia candel* forests, their diet consists mainly of benthic microalgae and sediment organic matter. Past studies have shown differences in the food sources of crabs in mangrove margin areas and forest interior areas (Kruitwagen et al., 2010). However, it remains unclear whether tidal zones composed of different plant communities affect the food composition of leaf-eating crabs.

Previously, it was possible to determine the food composition of leaf-eating crabs by analyzing gastrointestinal tract content (Thongtham and Kristensen, 2005; Kristensen, 2008). Analyzing gastrointestinal tract content has limitations, however, and offers insight into consumer diet composition only in the short term and does not reveal long-term dietary preferences (Gao et al., 2018). Furthermore, the gastrointestinal contents of crabs are influenced by factors such as food digestion rates, food size, and the content of nitrogen, vitamins, and fatty acids in the food (Wolcott and O’Connor, 1992). Stable isotope tracing methods can precisely measure feeding over extended periods and therefore provide a more realistic view of energy flow among organisms in a food web (Mieczan et al., 2015; Preciado et al., 2017; Donázar-Aramendía et al., 2019; Medina-Contreras et al., 2022). Bayesian stable isotope mixing models (SIMMR) based on the Bayesian statistical framework also have been developed to use statistical distributions to characterize the isotopic values of food sources and consumers based on mass-balance mixing models (Moore and Semmens, 2008; Parnell et al., 2010, 2013; Stock et al., 2018; Medina-Contreras et al., 2022). Furthermore, SIMMR can be used to investigate the effects of different food sources on numerous species or populations (Parnell et al., 2013; Stock et al., 2018). However, it is restricted to evaluating the contributions of various foods within the same ecosystem (Parnell et al., 2013).

In this study, we used stable isotopes and C/N ratios to determine variations in food sources among the dominant invertebrate taxon in Dongzhaigang Bay’s mangrove ecosystem: the leaf-feeding crab (*P. continentale*), across different tidal zones. Given the significant ecological role played by leaf-feeding crabs, there is a pressing need for a comprehensive investigation into the intricate interrelationships between leaf-feeding crabs and the tidal zones of mangrove ecosystems. Addressing this knowledge gap is crucial for advancing our comprehension of the dynamics in crab diet.

Materials and methods

Study area

The Dongzhaigang Bay National Natural Reserve, the first mangrove wetland nature reserve established in China, is situated in the northeast of Hainan Island, China (19°55′N, 110°36’E) (Figure 1). Importantly, the mangrove forest in Dongzhaigang Bay remains pristine and is devoid of human-induced influences, such as urban or agricultural runoff. No other systems, such as seagrasses or salt marshes, affect the mangrove forests. The bay covers approximately 3,337 hectares, and this reserve boasts one of the most extensive mangrove forests in China, accounting for 25 distinct mangrove species (Xiong et al., 2017). The mangrove forests within the reserve are predominantly composed of naturally occurring mangrove species. *Avicennia marina* is a pioneer species at forest margins; *Rhizophora stylosa* is in the low intertidal or fringe zone, with frequent flooding by tidal waters; *Bruguiera sexangula* inhabits the intermediate or middle intertidal area; and *Ceriops tagal* is in the high intertidal or landward zone, where tidal inundation rarely occurs. Thus, Dongzhaigang Bay presents a natural laboratory for investigating the food habits of leaf-eating crabs in mangrove forests across diverse intertidal locations. Notably, the mangrove forest zones lack an understory, and in each zone, continuous mangrove leaf litter is the dominant source of litter. Dongzhaigang Bay experiences mixed semidiurnal tides, featuring an average tidal range of 1.6 to 1.8 meters.

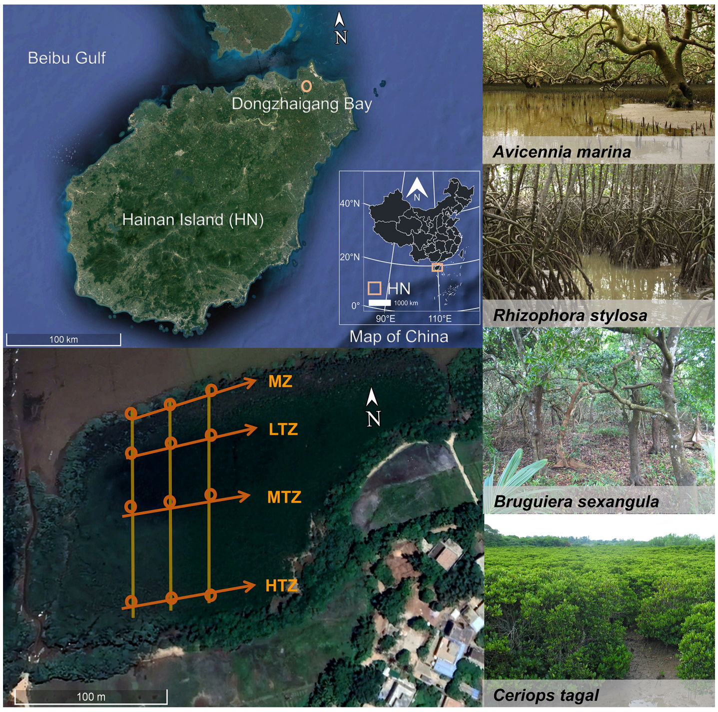

FIGURE 1
Sampling sites along transects in four intertidal zones of the mangrove ecosystem in Dongzhaigang Bay, Hainan Island, China. The locations of sampling sites are represented by circles in the figure. The dominant species in each zone are as follows: MZ, Margin zone (*Avicennia marina*); LTZ, low intertidal zone (*Rhizophora stylosa*); MTZ, middle intertidal zone (*Bruguiera sexangula*); HTZ, high intertidal zone (*Ceriops tagal*).

The bay undergoes two high tides and two low tides of different sizes every lunar day (Zhang et al., 2020). The duration of inundation is short during dry season tides and long during wet season tides. The prevailing climate in the region is characterized as a tropical maritime monsoon, marked by distinct rainy and dry seasons. The rainy season spans from May to October, with an average monthly rainfall of 222 mm and an average monthly air temperature of 27.5°C. Conversely, the dry season persists from November to April, which is accompanied by an average monthly rainfall of 54 mm and an average monthly air temperature of 20.8°C. Salinity levels in the bay exhibit seasonal variations, ranging from 24.9 to 31.8 during the rainy season and from 29.8 to 32.35 during the dry season.

Sampling

In this study, samples were collected monthly during November 2007 and February 2008 (dry season) and May and August 2007 (rainy season). This approach yielded a comprehensive dataset enabling the capture of seasonal and tidal zone variations in the food sources of leaf-feeding crabs. Three repetitive north-south transects were established, each extending approximately 150 meters in length and spaced approximately 50 meters apart, from the mangrove margin to the highest tide mark. Along each transect, sampling sites were strategically chosen across four distinct tidal zones: (1) the margin of the mangrove zone (MZ), where *A. marina* is the pioneer species; (2) the low intertidal zone (LTZ), where *R. stylosa* dominates; (3) the middle intertidal zone (MTZ), where *B. sexangula* is the dominant species; and (4) the high intertidal zone (HTZ), where *C. tagal* prevails (Figure 1). One sampling plot was designated at intervals of 0 m (MZ), 50 m (LTZ), 100 m (MTZ), and 150 m (HTZ) within each tidal zone along each transect. We conducted visual counts of crab populations (1 m × 1 m) within each mangrove tidal zone. The crabs from each tidal zone in three transects were pooled for combined analysis. In our field observations, we've noted that leaf-eating crabs (*Parasesarma continentale*) consume not just mangrove leaves but also soil organic matter (SOM) and animal tissues, including those from *Uca arcuata* and *U. borealis*. During low tide, three individuals of the dominant crab species, *Parasesarma continentale*, were manually captured within each sampling plot. We subsequently cleaned, froze, and stored the leaf-eating crabs at -20°C before transporting them back to the laboratory. Additionally, we collected a total of three individuals of *U. arcuata* and *U. borealis* from each sampling plot. Similarly, the samples underwent cleaning, freezing, and storage at -20°C before being transported back to the laboratory. After thawing the crab samples in the laboratory, muscle tissue was extracted. For *P. continentale*, the chelae from three individuals at each sampling plot were utilized for composite sample analysis. As for *U. arcuata* and *U. borealis*, the gut system was initially removed, and muscle tissue from the body was used, total of three individuals from each sampling plot were pooled to form a single sample. In each sampling plot, we collected three brown mangrove leaves at the stage of decomposition preferred by leaf-eating crabs for composite sample analysis (Lee, 1997; Kristensen et al., 2017). Then, after removing branches, leaves, benthic organisms, animal carcasses, and small rocks, we repeatedly scraped three samples of sediment organic matter (SOM) containing bacteria, microalgae, and fungi at each sampling plot for composite sample analysis.

Sample preparation for stable isotope and nutrient content analyses

Before processing, both leaf and consumer samples underwent a thorough washing with deionized water. Subsequently, all samples were subjected to a drying process at 60°C for 48 h. The dried tissues were then meticulously ground to a fine powder using a mortar and pestle. SOM and plant leaves were analyzed in two subsamples. For $\delta^{13}C$ analysis, subsamples were soaked in 10% HCl to eliminate carbonates. In contrast, subsamples designated for $\delta^{15}N$ analysis did not undergo acid treatment to prevent any impact on $\delta^{15}N$ (Ryba and Burgess, 2002). From each sample, 0.5–1.0 mg was carefully folded into a tin capsule for subsequent analysis. An isotope ratio mass spectrometer (DELTA plus XP, Thermo Finnigan, CA, USA) was used to determine sample $\delta^{13}C$ and $\delta^{15}N$ with a standard deviation of 0.3 per mil for both C and N. Total organic C (TOC) and total N (TN) contents were determined by an elemental analyzer (FLASH EA 1112, Thermo, CA, USA) and used to calculate the C/N ratio. Percentage values of C and N were measured using atropine (Carlo Erba, Milano) as the reference material. The isotopic values were determined against in-house standards, which were calibrated using internationally recognized reference materials: L-glutamic acid USGS 40 (IAEA, Vienna, Austria) and sugar (IAEA-CH-6) for $\delta^{13}C$, and L-glutamic acid USGS 40 and potassium nitrate IAEA-NO3 for $\delta^{15}N$. The uncertainty associated with stable isotopic determinations was 0.3‰ for both $\delta^{13}C$ and $\delta^{15}N$. The detection limit of the method for C and N was 0.6 mmol and 0.9 mmol, respectively. The stable isotope contents were expressed as δ values, following the equation:

$$\delta X_{sample}(‰) = R_{sample}/R_{\text{standard}} - 1) \times 1000$$

where X represents either isotope $\delta^{13}C$ or $\delta^{15}N$ and R is the $^{13}C/^{12}C$ ratio for C or $^{15}N/^{14}N$ for N, using Vienna Pee Dee Belemnite and N_2 in air as the standards, respectively.

Bayesian stable isotope mixing models

The Bayesian SIMMR, which was developed by Parnell and Inger (2016), served as the analytical framework for estimating the contributions of potential food to the diets of leaf-eating crabs (Parnell et al., 2013). This model leverages the Markov chain Monte Carlo (MCMC) method, incorporating a posterior distribution based on 10,000 iterations in this study. The MCMC technique uses random sampling based on prior knowledge of the proportional contributions from different foods and the probability distribution of each input variable (Shang et al., 2020). To assess the model's performance, we employed Gelman–Rubin convergence statistics, with a diagnostic value below 1.1 indicating a satisfactory run (Gelman et al., 2013).

In instances in which a plethora of food sources existed, the model's ability to differentiate between similar sources may have diminished, subsequently amplifying the uncertainty in model results (Phillips et al., 2014). To address this issue, similar food sources can be combined based on *a priori* information such as the isotopic space (Isospace) location of the food source and the results of cluster analysis. Alternatively, for foods that are close ecologically, SIMMR provides a 'combine_sources' function that combines similar sources a posteriori based on the analysis results. Through field observations and literature searches, we identified and selected three primary sources for the model: mangrove leaves, SOM, and animal tissues (prey). This careful selection was based on their ecological relevance and their distinct isotopic signatures, ensuring a robust and accurate representation of the leaf-eating crab's dietary contributions.

Bayesian mixing models assess the likelihood of the proportion of specific foods in a diet by assessing the mean and standard deviation of the stable isotope ratios of producers, as well as the trophic enrichment factor (TEF) for each isotope ratio (Moore and Semmens, 2008; Caut et al., 2009; Ward et al., 2010; Parnell et al., 2013). In our study, we adjusted the isotopic shifts from various food sources to consumers using the "correction_means" parameter in SIMMR, based on mean values of TEF. For leaf-eating crabs, TEF was established as 3.3‰ ± 0.26‰ for $\delta^{15}N$ and 1.3‰ ± 0.3‰ for $\delta^{13}C$ (McCutchan et al., 2003).

Statistical analyses

Before analysis, we checked the variance of the residuals for normality and homoscedasticity using Shapiro-Wilk's ($p > 0.05$) and Levene's tests ($p > 0.05$). Student's *t*-tests were used to compare the differences in stable isotope signatures of leaf-eating crabs between rainy and dry seasons, as well as the differences in stable isotopes of their food sources. We used one-way ANOVA to compare differences in stable isotopes of leaf-feeding crabs across tidal zones in the rainy and dry seasons. To examine variations in the stable isotope signatures of diverse food sources among different mangrove zones, we combined rainy and dry season data in a one-way ANOVA and Tukey HSD as *post hoc* test when differences with ANOVA were detected. We used linear regression analysis to investigate the relationships between C/N ratio of mangrove leaves and their contribution to food, and 95% confidence intervals were determined for the regression. The explanatory power of simple linear regression models was assessed using the modified coefficient of determination R^2. The significance level of linear regressions was set at 0.05 ($p< 0.05$). All reported values are expressed as the mean ± SD.

All statistical analyses and data visualization were carried out using R software v4.0.1 (R Core Team, 2017), with a focus on utilizing the ggplot2 and ggpubr packages for robust analysis and effective data representation (Wickham, 2016).

Results

Carbon and nitrogen isotopic compositions of leaf-eating crabs and food sources

The relative abundance of the leaf-eating crabs (*P. continentale*) exhibited variation among zones, with the highest densities observed in the MZ and LTZ, followed by the MTZ, and the lowest densities recorded in the HTZ (Figure 2). Similarly, we noted variability in prey relative abundance across different zones, with the highest densities found in the LTZ and MTZ, followed by the MZ, and the lowest densities in the HTZ (Figure 2). The stable isotope values for leaf-eating crabs in different mangrove zones are shown in Figure 3. In all four zones, the δ^{13}C signatures of leaf-eating crabs were relatively higher compared to those of mangrove leaves, while the δ^{15}N values of the mangrove leaves were comparatively lower than those of the leaf-eating crabs. Additionally, the δ^{13}C and δ^{15}N values of SOM were comparatively lower than those of the leaf-eating crabs. Conversely, the δ^{13}C and δ^{15}N values of prey were both relatively higher compared to those of the leaf-eating crabs.

In the rainy season, there were no significant differences in the δ^{13}C values of leaf-eating crabs across tidal intervals (p = 0.315, ANOVA) (Supplementary Table S1). However, the δ^{15}N values showed significant differences (p = 0.002, ANOVA) (Supplementary Table S1). *Post hoc* analyses revealed that the MTZ differed significantly from both the HTZ (p< 0.001) and the LTZ (p = 0.042) (Supplementary Table S2). Nonetheless, no significant differences were observed among the other tidal zones. In the dry season, significant variations were observed in the δ^{13}C values of leaf-eating crabs across tidal zones (p = 0.024, ANOVA) (Supplementary Table S1). *Post hoc* analyses indicated a significant difference between the MTZ and HTZ (p = 0.032). However, no significant differences were observed among the other tidal zones. Interestingly, no statistical difference was detected in the δ^{15}N signature of leaf-eating crabs among the zones (p = 0.622, ANOVA) (Supplementary Table S1). The δ^{13}C values of leaf-eating crabs exhibited significant seasonal variations (Supplementary Table S3), with significant differences observed in MZ (p = 0.029, t-test). However, the δ^{15}N values of leaf-eating crabs showed no significant differences between seasons across the four intertidal zones.

Isotopic signatures of the available food sources were categorized into mangrove leaves, SOM, and prey tissues (Figure 3). The δ^{13}C values of mangrove leaves exhibited significant seasonal variations (Supplementary Table S3), with notable differences observed in MZ (p = 0.003, t-test), LTZ (p< 0.001, t-test), MTZ (p = 0.010, t-test), and HTZ (p = 0.017, t-test). However, the δ^{15}N values of mangrove leaves only showed significant differences in LTZ across different seasons (p = 0.041, t-test). Similarly, the δ^{13}C values of SOM varied significantly among different seasons, with notable distinctions observed in MZ (p = 0.015, t-test), LTZ (p = 0.002, t-test), except for MTZ (p > 0.05, t-test), and HTZ (p = 0.042, t-test). However, the δ^{15}N values of SOM only exhibited significant differences in LTZ and MTZ among different seasons (p = 0.011, p = 0.028, t-test). The δ^{13}C and δ^{15}N values of prey showed no significant differences between seasons across the four intertidal zones.

Despite variations in dry and rainy seasons, the trends of δ^{13}C content and δ^{15}N values across different intertidal zones remain consistent. Therefore, to assess differences in food sources across tidal zones, we pooled data from both seasons and conducted ANOVA analysis and *post hoc* tests (Figures 4A, B). The results showed significant differences in the δ^{13}C values of mangrove leaves between the MZ and the LTZ and MTZ, as well as between the HTZ and the LTZ and MTZ. Due to differences in mangrove species, the δ^{15}N values of mangrove leaves decrease with increasing tidal levels. The δ^{13}C values of mangrove leaves and SOM were significantly different in this study (p< 0.001, ANOVA), with SOM enriched by 1.2‰ to 5.9‰ compared with mangrove leaves. The δ^{13}C values of SOM in the MZ were significantly higher than those in the other zones. We did not detect any statistically significant difference in the δ^{15}N values between different tidal zones. The δ^{13}C values of prey in the MZ differed significantly from those in the MTZ and HTZ.

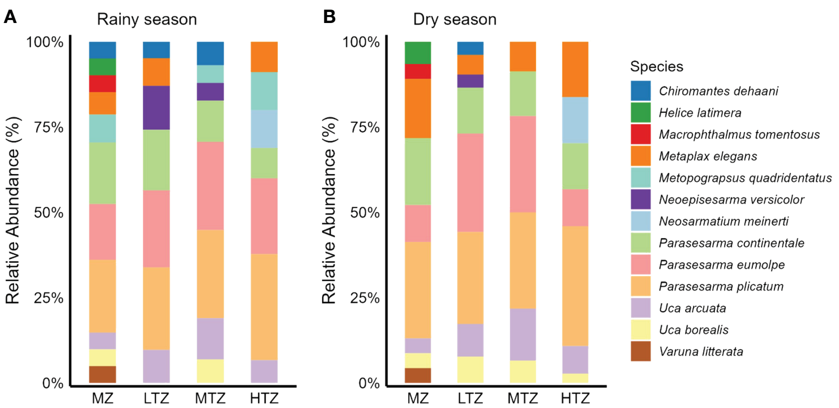

FIGURE 2
Relative abundance of crabs in rainy and dry seasons at different intertidal zones (MZ, margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China. **(A)** Rainy season; **(B)** Dry season.

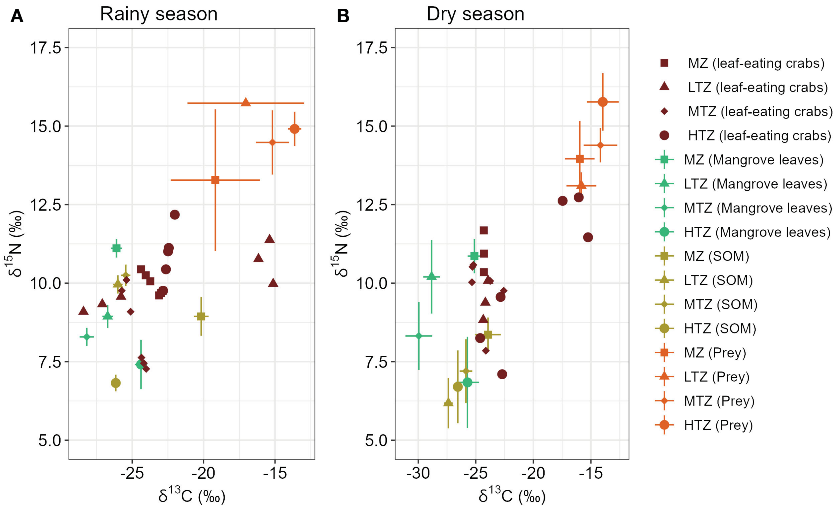

FIGURE 3
Mean ± SD δ^{13}C and δ^{15}N values of leaf-eating crabs, leaves of mangroves, sediment organic matter (SOM), and prey (animal tissues) in different intertidal zones (MZ, Margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China (n = 6). **(A)** Rainy season; **(B)** Dry season. The δ^{13}C and δ^{15}N values were adjusted based on Trophic Enrichment Factor (TEF).

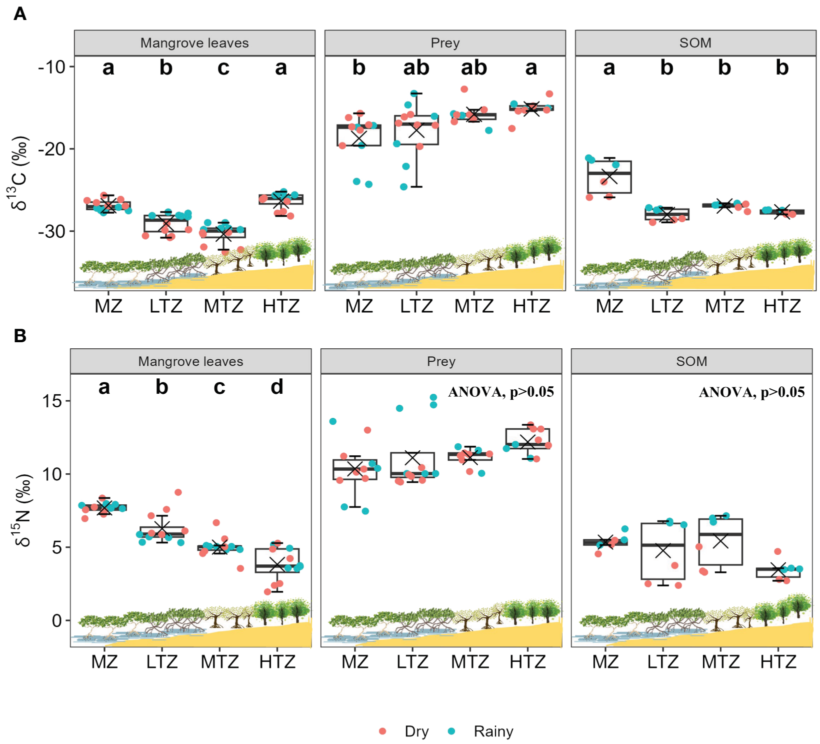

FIGURE 4
Variations in dry and rainy season combinations of data of **(A)** δ^{13}C and **(B)** δ^{15}N values of potential food resources of leaf-eating crabs, including leaf litter of dominant mangrove species (*Avicennia marina* [MZ], *Rhizophora stylosa* [LTZ], *Bruguiera sexangula* [MTZ], and *Ceriops tagal* [HTZ]), prey (animal tissues), and sediment organic matter (SOM), at different intertidal zones (MZ, margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China. Different lowercase letters indicate significant differences in isotope values of a food resource among intertidal zones (*post hoc* tests, $p < 0.05$). Boxes extend from the 25th to 75th percentile, with the black horizontal line indicating the median and the saltire inside boxes indicating the mean. The whiskers extending from boxes represent the highest and lowest values.

Additionally, the $\delta^{15}N$ values of prey increased with increasing tide level, but we did not find any statistically significant difference in the $\delta^{15}N$ signatures among different tidal zones.

Food contribution to leaf-eating crab's diets

The relative contributions of different sources to the diets of leaf-eating crabs as determined by the SIMMR (Figure 5). The highest contribution of mangrove leaves to diets was in the MZ and the lowest was in the HTZ. Mangrove leaves were the primary source of food for leaf-eating crabs in the MZ, especially during the dry season, when leaves accounted for 75.2% of their diet (Figure 5). In the LTZ, the diet mainly consisted of mangrove leaves (48.4% in the rainy season; 30.7% in the dry season) and SOM (41.7% in the rainy season; 39.8% in the dry season). Similarly, in the MTZ, the diet primarily comprised mangrove leaves (63.7% in the rainy season; 43.8% in the dry season) and SOM (24.5% in the rainy season; 28.0% in the dry season). In contrast, the HTZ exhibited the lowest consumption of mangrove leaves (35.6% in the rainy season; 29.7% in the dry season), with prey (24.7% in the rainy season; 41.7% in the dry season) and SOM (39.7% in the rainy season; 28.6% in the dry season) constituting the major sources of crab food. Furthermore, reliance on prey in the crab diet was higher in the dry season compared to the rainy season across all tidal zones.

Relations between carbon to nitrogen ratio and food contribution of mangrove leaves

The linear regression between C/N ratios of mangrove leaves and the proportion of leaves that contributed to diets of leaf-feeding crabs across rainy and dry seasons at different intertidal zones indicated a significantly negative relationship (Figure 6; regression equation: $y = 71.7 - 0.598x$, $R^2 = 0.49$, $p = 0.032$). The 95% confidence interval for the regression coefficient was from −1.125 to −0.072. In the MZ, mangrove leaves had the lowest C/N ratios of 17.84 ± 0.95 and 21.02 ± 1.53 in wet and dry seasons, respectively, and the highest contributions to diet of 52.2% and 75.2% in wet and dry seasons, respectively (Table 1). In the MTZ, mangrove leaves with a C/N ratio of 29.05 ± 0.36 contributed 63.7% to diets in the wet season and those with ratio of 29.67 ± 1.30 contributed 43.8% in the dry season (Table 1). In the LTZ, mangrove leaves with a C/N ratio of 44.83 ± 0.22 contributed 48.4% to diets in the rainy season and those with a ratio of 44.17 ± 3.02 contributed 30.7% in the dry season (Table 1). In the HTZ, mangrove leaves had the highest C/N ratios, with values of 70.37 ± 2.21 in the rainy season and 68.37 ± 0.72 in the dry season. They contributed the least to crab diets, accounting for 35.6% and 29.7% in the rainy and dry seasons, respectively.

Discussion

Stable isotope signatures of leaf-eating crabs and potential crab food sources

The $\delta^{13}C$ signatures of leaf-feeding crabs in MZ (mean = −23.9‰) are consistent with those reported previously in the eastern Pearl River estuary, China (mean = −24.2‰; Lee, 2000). Furthermore, in all four zones, $\delta^{13}C$ signatures of leaf-eating crabs were relatively higher compared with those of mangrove leaves, indicating that leaf-eating crabs did not feed exclusively on mangrove litter. Compared with other leaf-eating crabs of the same genus in previous studies (Lee, 2000; Bouillon et al., 2004), the $\delta^{15}N$ values of *P. continentale* were higher. Their study revealed that the food sources of leaf-eating crabs included mangrove leaves, sediments, particulate organic matter (POM), and microalgae, but did not include animal tissues. Our findings indicated that animal tissues had higher $\delta^{15}N$ values than mangrove leaves. Therefore, leaf-eating crabs supplementing their diet with animal tissues may have had higher $\delta^{15}N$ values than same-genus leaf-eating crabs in other areas. The reliance of Sesarmidae on animal tissues in mangrove ecosystems has been reported previously (Thongtham et al., 2008; Kristensen et al., 2017).

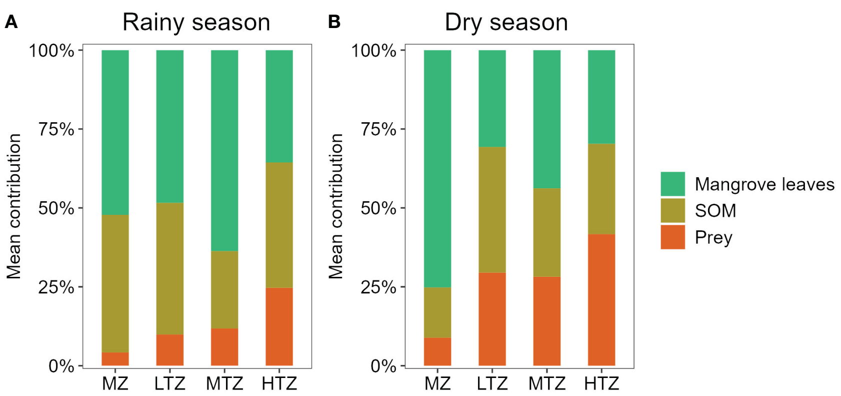

FIGURE 5
Contributions of different food sources to diets of leaf-eating crabs at different intertidal zones (MZ, margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China. SOM, sediment organic matter. **(A)** Rainy season; **(B)** Dry season.

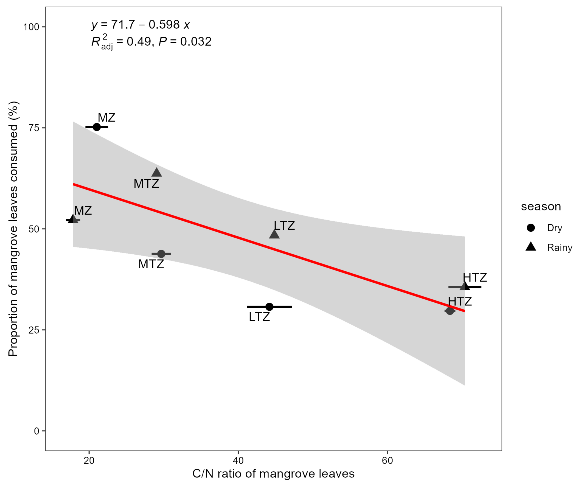

FIGURE 6
Linear regression between mangrove leaf carbon/nitrogen (C/N) ratio (mean ± SD) and the proportion ingested by leaf-eating crabs (mean ± SD, n = 6) across rainy and dry seasons at different intertidal zones (MZ, margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China. R^2_{adj} is the coefficient of determination after correcting for degrees of freedom, and the shaded area indicates confidence intervals.When the SD is not depicted, it indicates that the SD is smaller than the data points being presented.

The $\delta^{13}C$ signatures of mangrove leaves from different mangrove tidal zones (MZ, –26.9‰; LTZ, –29.1‰; MTZ, –30.4‰; and HTZ, –26.4‰; Figure 4A) are within the range of –35‰ to –22‰ reported for mangrove leaves worldwide (Bouillon et al., 2008; Medina-Contreras et al., 2024). In this research, the $\delta^{13}C$ values of SOM were elevated by 1.2‰ to 5.9‰ in comparison to mangrove leaves. This result differs from the observed increase in $\delta^{13}C$ values of SOM compared to mangrove leaves in other mangrove ecosystems. In the Godavari mangrove ecosystem in India, Bouillon et al. (2002) found that carbon isotope composition was enriched by 6‰–8‰ in mangrove sediments compared with mangrove vegetation. Bouillon et al. (2002) found that the Godavari mangrove forest had significant inputs of suspended matter from nearby mangrove creeks and adjacent bays, whereas there was no suspended matter replenishment from other ecosystems in our study area.

The prey (*U. arcuata* and *U. borealis*) exhibited higher $\delta^{13}C$ values compared with the leaf-eating crabs (*P. continentale*). This result was consistent with findings from the same genus observed in Kenya and India (Bouillon et al., 2004), where *Uca* spp. exhibited higher $\delta^{13}C$ values compared to Sesarmidae. Furthermore, the $\delta^{15}N$ values of the prey were higher than those of the leaf-eating crabs, which was in line with the results reported by Kristensen et al. (2017) in the pristine mangrove forests of Pak Meng in southern Thailand. *U. arcuata* and *U. borealis* are omnivorous crabs that primarily consume benthic microalgae and zooplankton (Rianta et al., 2018). The higher $\delta^{13}C$ and $\delta^{15}N$ values of these crabs may be attributed to differences in their food sources compared with the leaf-feeding crab *P. continentale*. Further analysis of the food sources of prey in different tidal zones is necessary to determine their contribution to the diet of leaf-feeding crabs. Despite stable isotope evidence indicating that leaf-eating crabs frequently use C from sources other than mangrove leaves, they can consume and remove a substantial portion of overall mangrove litterfall (Schories et al., 2003; Nordhaus et al., 2006). As a result, leaf-eating crabs can provide an important link between energy flow and nutrient cycling.

TABLE 1 Carbon to nitrogen ratio (C/N) of leaf-eating crab food sources in rainy and dry seasons at different intertidal zones (MZ, margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China.

Intertidal zone	Food source	C/N	
		Rainy season	Dry season
MZ	Mangrove leaves	17.84±0.95	21.02 ±1.53
	SOM	14.73±1.31	13.78 ±1.67
	Animal tissue	4.13±0.07	4.32±0.68
LTZ	Mangrove leaves	44.83±0.22	44.17 ±3.02
	SOM	18.40±0.22	21.59 ±0.37
	Animal tissue	3.69±0.15	3.71±0.10
MTZ	Mangrove leaves	29.05±036	29.67 ±1.30
	SOM	20.62±0.93	21.52±2.1
	Animal tissue	3.88±0.03	3.75±0.06
HTZ	Mangrove leaves	70.37±2.21	68.37 ±0.72
	SOM	22.61±1.05	18.94±2.5
	Animal tissue	3.93±0.01	4.07±0.59

SOM, sediment organic matter; Animal tissue, *Uca arcuata* and *U. borealis.*

Relationship between the C/N ratio and food contribution of mangrove leaves

In this study, we detected a significant negative relation between the C/N ratio of mangrove leaves and the contribution of leaves to crab diets. This result is comparable with that of Sandoval et al. (2022), who found that *Aratus pisonii* had the lowest intake rate of mangrove leaves with a high C/N ratio (155 ± 23) and the highest intake rate of those with a low C/N ratio (51 ± 18). Similarly, Chen and Ye (2008) found that leaf-eating crabs increased feeding rates on leaves with low C/N ratios. Typically, the ingestion of litterfall and vegetal organic matter varies according to the palatability of leaves (Robertson and Daniel, 1989; Steinke et al., 1993; Christofoletti et al., 2013). Christofoletti et al. (2013) concluded that leaf-eating crabs prefer leaves with relatively low polyphenol contents. Furthermore, structural components decrease and palatability increase of mangrove leaves after 20 h of soaking in estuarine water (Erickson et al., 2004; Nordhaus et al., 2011). Hirano et al. (2023) found that herbivory rates in mangroves were moderately affected by the concentration of condensed tannins in leaves and decreased from seaward to landward. This result was consistent with our finding that leaf-feeding crabs were influenced by the C/N ratio in leaves and decreased from low to high tidal zone. Therefore, in the field, leaf-eating crabs may prefer leached, brown leaves with a lower C/N ratio. However, tidal flooding is rare in the HTZ, and complete flooding only occurs during astronomical high tides. Additionally, because the rate of plant litter decomposition decreases as the C/N ratio increases (Enriquez et al., 1993; Almahasheer et al., 2016), relatively recalcitrant mangrove litter may accumulate in the nutrient-limited HTZ.

The environment of mangrove ecosystems is highly complex and variable, and therefore, the consumption of diverse C sources by leaf-eating crabs is expected to vary significantly owing to factors such as geomorphology, tidal amplitude, vegetation type, and biotic influences (Kon et al., 2007; Bouillon et al., 2008).

Food contribution to diets of leaf-eating crabs among mangrove zones

Food contributions to leaf-eating crab diets were different between wet and dry seasons, and this variation might be influenced by tidal cycles (Delong et al., 2001), seasonal abundance of benthic primary producers (Kang et al., 2006), and dietary preferences (Davenport et al., 2011; Rossi et al., 2015). In the field, we observed fewer litter inputs in the HTZ compared with other zones. The decrease in inputs could be a contributing factor to the reduced proportion of mangrove leaves in diets in the HTZ. The highest densities of *P. continentale* were in the LTZ and MTZ, which might be related to the relatively lower C/N ratio of mangrove leaves in the MTZ and the higher density of prey tissue in the LTZ and MTZ. The lower level of tidal scour disturbance in LTZ and MTZ, compared with the MZ which is frequently scoured by the tide, may have been another influencing factor. Therefore, the low and mid-tide zones are the optimum habitats for the leaf-eating crab *P. continentale*.

Sediment organic matter consistently contributed more than 20% to the diet of leaf-feeding crabs across zones and seasons, except in the MZ during the dry season (Figure 5). Similarly, Kawaida et al. (2019) determined that SOM contributed 23.1% to diets of leaf-eating crabs (*P. continentale*) in the spring and 23.3% in the summer. However, sediment is not generally regarded as an important food source, because crabs only assimilate associated refractory detritus and bacteria to a small extent (Thongtham and Kristensen, 2005; Nerot et al., 2009). Sediment organic matter in mangrove estuaries originates from various sources, such as phytoplankton, benthic microalgae, macroalgae, and mangrove detritus (Bouillon and Boschker, 2006). Therefore, the composition of the top 0–2 cm of surface sediment collected for analysis in this study, which includes organic matter from phytoplankton, microphytobenthos, and other components, might be one reason why SOM contributed more than 20% to the diet of leaf-eating crabs.

Further analysis of the chemical of SOM is necessary to determine its contributions to diets of leaf-feeding crabs (Chen et al., 2016) and to understand differences in the contribution at different tidal levels. The components of SOM, such as microalgae and plankton, should be individually sampled to determine their dietary contributions.

Conclusion

This study is the first to analyze the variations in food sources of leaf-eating crabs in different tidal zones. Mangrove leaves were the primary C source for leaf-eating crabs in the forest margin area, and leaves and sediment organic matter were the primary C sources in low and mid tidal zones. By contrast, mangrove leaves had the lowest contributions to the diets of leaf-eating crabs in the high tide zone. With increasing tidal levels, the primary food sources for leaf-eating crabs switched from mangrove leaves and sediment organic matter to sediment organic matter and animal tissues. Thus, the dietary habits of leaf-feeding crabs in mangrove ecosystems were affected by tidal-level zoning.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

XL: Writing – original draft, Data curation, Formal analysis, Methodology. XG: Formal analysis, Methodology, Writing – review & editing. LZ: Data curation, Formal analysis, Writing – review & editing. JZ: Data curation, Writing – original draft. WW: Data curation, Funding acquisition, Methodology, Writing – original draft. MW: Formal analysis, Funding acquisition, Methodology, Writing – original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1351183/full#supplementary-material

SUPPLEMENTARY FIGURE 1
Variations in rainy season of **(A)** $\delta^{13}C$ and **(B)** $\delta^{15}N$ values of potential food resources of leaf-eating crabs, including leaf litter of dominant mangrove species (Avicennia marina [MZ], Rhizophora stylosa [LTZ], Bruguiera sexangula [MTZ], and Ceriops tagal [HTZ]), prey (animal tissues), and sediment organic matter (SOM), at different intertidal zones (MZ, margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China. Different lowercase letters indicate significant differences in isotope values of a food resource among intertidal zones (*post hoc* tests, $p < 0.05$). Boxes extend from the 25th to 75th percentile, with the black horizontal line indicating the median and the saltire inside boxes indicating the mean. The whiskers extending from boxes represent the highest and lowest values.

SUPPLEMENTARY FIGURE 2
Variations in dry season of **(A)** $\delta^{13}C$ and **(B)** $\delta^{15}N$ values of potential food resources of leaf-eating crabs, including leaf litter of dominant mangrove species (Avicennia marina [MZ], Rhizophora stylosa [LTZ], Bruguiera sexangula [MTZ], and Ceriops tagal [HTZ]), prey (animal tissues), and sediment organic matter (SOM), at different intertidal zones (MZ, margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China. Different lowercase letters indicate significant differences in isotope values of a food resource among intertidal zones (*post hoc* tests, $p < 0.05$). Boxes extend from the 25th to 75th percentile, with the black horizontal line indicating the median and the saltire inside boxes indicating the mean. The whiskers extending from boxes represent the highest and lowest values.

SUPPLEMENTARY TABLE 1
Results of the one-way analysis of variance (ANOVA) for the stable isotope values of leaf-eating crabs in different tidal zones.

SUPPLEMENTARY TABLE 2
P-values and *t*-values of Tukey HSD *post-hoc* tests for stable isotope values of leaf-eating crabs among different tidal zones. (MZ, margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China.

SUPPLEMENTARY TABLE 3
P-values of Student's *t*-test for $\delta^{13}C$ and $\delta^{15}N$ of leaf-eating crabs and their food sources in the dry and rainy seasons. (MZ, margin zone; LTZ, low intertidal zone; MTZ, middle intertidal zone; HTZ, high intertidal zone) of a mangrove forest in Dongzhaigang Bay, Hainan Island, China.

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