Marine Environmental Research 144 (2019) 72–83

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

# Does food partitioning vary in leaf-eating crabs in response to source quality?

Tamara Maciel Pereira[a], Gabriel Nuto Nóbrega[b], Tiago Osório Ferreira[c], Cynthia Yuri Ogawa[a], Plínio Barbosa de Camargo[d], José Roberto Feitosa Silva[a], Carla Ferreira Rezende[a,*]

[a] *Departamento de Biologia, Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal do Ceará, Av. Mister Hull s/n, CEP: 60455-760, Fortaleza, CE, Brazil*

[b] *Programa de Pós-Graduação em Geociências (Geoquímica), Departamento de Geoquímica, Instituto de Química, Universidade Federal Fluminense, Outeiro São João Baptista s/n, CEP: 24020-141, Niterói, RJ, Brazil*

[c] *Departamento de Ciência do Solo, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Av. Pádua Dias 11, CEP: 13418-900, Piracicaba, SP, Brazil*

[d] *Centro de Energia Nuclear na Agricultura, Laboratório de Ecologia Isotópica, Universidade de São Paulo, CEP: 13416903, Piracicaba, SP, Brazil*

ARTICLE INFO

*Keywords:*
Trophic ecology
Bayesian mixing models
Stable isotope
Mangrove
Crustacea
Brachyura
Ucididae
Grapsidae
Ecosystem services

ABSTRACT

Mangroves have a relevant ecosystem function due to their efficiency in blue carbon sequestration. Autotrophic carbon conservation in mangroves remains controversial. In this sense, autotrophic nutrient assimilation by crabs can highlight their ecosystem function. This study aims to identify the relationship between quality sources and food partitioning in two leaf-eating crabs, *Ucides cordatus* and *Goniopsis cruentata*. Quantification of the litterfall biomass, analysis of the soil, the C/N ratio and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) were used to evaluate food sources and crab tissues in two mangrove forests. The litterfall and soil C contents and C/N ratios of the Pacoti River (PR) were higher than those of the Jaguaribe River. The higher C/N ratios of the litterfall of the PR led to higher nitrogen ingestion from complementary food sources (soil and omnivorous invertebrates). The nutritional requirements and food partitioning behavior of both species emphasize the ecosystem functions of leaf-eating crabs concerning the assimilation and conservation of autotrophic carbon and nitrogen in mangroves.

## 1. Introduction

The conservation of mangrove ecosystems is crucial for the mitigation of climate change due to their high primary productivity (Bouillon et al., 2008; Kristensen et al., 2008) and efficiency in “blue carbon” sequestration (Nellemann et al., 2009). Carbon from the atmosphere is mostly fixed by vegetation and stored in mangrove soils (~70%) (Donato et al., 2011; McLeod et al., 2011; Kauffman et al., 2018). Autotrophic carbon retention is controversial. First, it was postulated that most of the carbon produced by mangrove forest was exported to the neighboring coastal regions (Odum and Helt, 1975). However, recent studies have shown that most organic matter produced by mangrove species is retained as litterfall (Kristensen et al., 2008; Donato et al., 2011; Alongi, 2014). Although leaf litter is an important source of organic carbon (Kristensen et al., 2008) and its cycling has been extensively described (see Camilleri and Ribi, 1986; Alongi et al., 1999; Dittmar and Lara, 2001; Bouillon et al., 2008; Kristensen, 2008), there is no consensus on the fate of leaf organic matter produced in mangroves (Bouillon et al., 2008).

Leaf-eating brachyuran mangrove crabs have important ecosystem functions in autotrophic carbon conservation (Kristensen et al., 2008, 2017). Ucididae, *Ucides cordatus* (Linnaeus, 1763), and Grapsidae, *Goniopsis cruentata* (Latreille, 1803), crabs are semiterrestrial leaf-eating species abundant in Brazilian mangroves (Coelho and Ramos, 1972). These species are true ecosystem engineers (Araújo et al., 2012) that play an essential role in the carbon cycle by processing litter and organic matter of plant origin (*e.g.*, Robertson and Daniel, 1988; Nordhaus and Wolff, 2007; Bouillon et al., 2008; Claudino et al., 2015). The feeding habits of these crabs consist of macerating litterfall, which accelerates decomposition processes and increases nitrogen enrichment via feces deposition (Lee, 1997; Skov and Hartnoll, 2002). The ingestion of litterfall and vegetal organic matter varies due to leaf palatability (Robertson and Daniel, 1988; Christofoletti et al., 2013) and population abundance (Kristensen et al., 2008). The leaf consumption by crabs can favor carbon assimilation by other animal species (Kristensen, 2008; De Lima-Gomes et al., 2011; Christofoletti et al., 2013) since the digestion

---

[*] Corresponding author.

*E-mail addresses:* tamaramaciel@alu.ufc.br (T.M. Pereira), gabrielnn@id.uff.br (G.N. Nóbrega), toferreira@usp.br (T.O. Ferreira), cynthiaogawa@gmail.com (C.Y. Ogawa), pcamargo@cena.usp.br (P.B. de Camargo), robertofeitosa@ufc.br (J.R. Feitosa Silva), carla.rezende@ufc.br (C.F. Rezende).

https://doi.org/10.1016/j.marenvres.2018.12.005
Received 21 August 2018; Received in revised form 1 December 2018; Accepted 20 December 2018

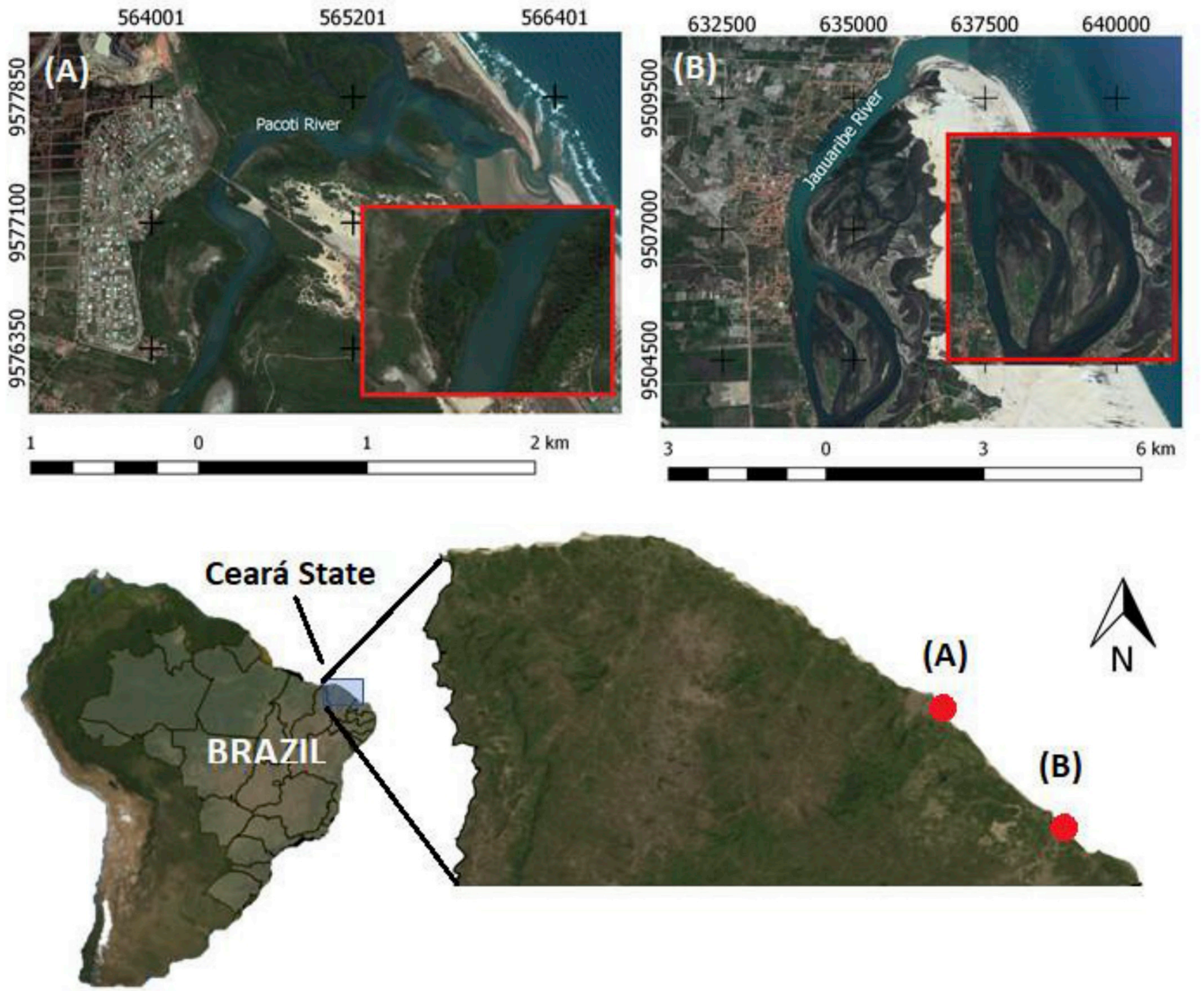

**Fig. 1.** Studied mangroves on the northeastern Brazilian coast and sampling site locations on the Pacoti (PR) and Jaguaribe (JR) rivers.

process contributes to the degradation of cellulose (Skov and Hartnoll, 2002; Christofoletti et al., 2013).

*Ucides cordatus* and *Goniopsis cruentata* predominately feed on litterfall; however, other food items, such as soil, may have high ingestion proportions (Nordhaus and Wolff, 2007; De Lima-Gomes et al., 2011). Stomach content studies have yielded controversial data on feeding on soil as an actual food item or via accidental consumption (*e.g.,* De Lestang et al., 2000; Nordhaus et al., 2006; Nordhaus et al., 2009; De Lima-Gomes et al., 2011). Several studies in the past 20 years on the elucidation of nutrients for leaf-eating crabs have verified carbon and nitrogen sources assimilated by crabs (*e.g.*, Thimdee et al., 2001; Bouillon et al., 2002; Moreno et al., 2010; Giarrizzo et al., 2011; Claudino et al., 2013; Bui and Lee, 2014; Vermeiren et al., 2015; Harada and Lee, 2016; Tewfik et al., 2016; Kristensen et al., 2017; Kristensen et al., 2018). Currently, Kristensen et al. (2017) verified that leaf-eating crabs are capable of supplementing their nutrient-poor leaf diet with nitrogen from alternative sources (i.e., invertebrates and soil). However, studies on the variability in food partitioning and on the assimilation of complementary sources have not been conclusive (Linton and Greenaway, 2007).

This study aims to contribute to the knowledge on the conservation of autotrophic carbon and nitrogen by leaf-eating mangrove crabs. *U. cordatus* and *G. cruentata* were chosen to address the aim of identifying the relationship between quality source and food partitioning.

## 2. Materials and methods

### 2.1. Study site

This study was conducted in two mangrove forests on the Brazilian semiarid coast, along the Pacoti (PR) and Jaguaribe (JR) rivers (Fig. 1). According to the Köppen-Geiger climate classification (Peel et al., 2007), the climate of the study site is Aw, a tropical savanna climate, with two well-defined seasons (rainy and dry) and a mean annual temperature ranging from 26 to 28 °C. The average rainfall is ~950 mm over the PR and ~1400 mm over the JR (IPECE, 2016).

The PR mangrove forest (coordinates 3°49′50″S; 38°25′12″W; Fig. 1A) covers approximately 0.3 $\text{km}^2$ (Maia et al., 2006) and is considered a nearly pristine mangrove ecosystem (Nilin et al., 2013). The JR mangrove forest (coordinates 4°28′45″S; 37°46′38″W) (Fig. 1B), on the other hand, covers an area of 11.6 $\text{km}^2$ (Maia et al., 2006) and is highly affected by effluent discharges from the largest shrimp producer in Brazil (Nogueira et al., 2009; Lacerda et al., 2009).

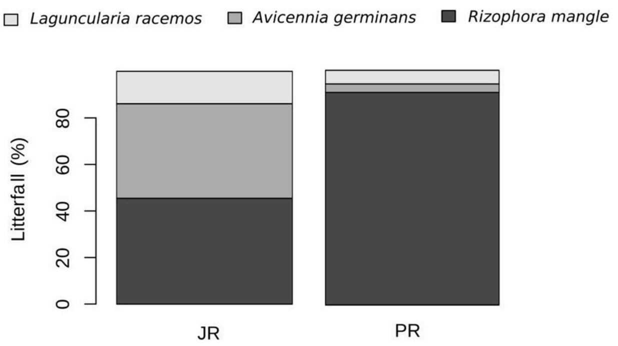

**Fig. 2.** Litterfall biomass of both mangrove forests (JR: Jaguaribe River and PR: Pacoti River).

### 2.2. Sampling procedures

Sampling was performed during low spring tides in December 2015 and March 2016. Soil, litterfall, and invertebrates for the determination of food resources for the brachyura crab species (*G. cruentata* and *U. cordatus*) were sampled in each mangrove forest.

In each mangrove forest, a total area of 2000 $m^2$ was delimited for the quantification of litterfall biomass, soil physicochemical parameters, sample brachyura crab species and their food resources. Crabs were manually collected in the total sampled area of the mangrove forest (34 specimens of *G. cruentata* and 39 of *U. cordatus*). To decrease crab metabolism, specimens were stored immediately after collection in a refrigerated box (4 °C) and transported to the laboratory. At the laboratory, animals were measured, labeled and stored in a freezer for later analysis.

Soil, litter and invertebrate samples for the determination of food resources were collected along ten 50-m long parallel transects, spaced 5 m apart and established 5 m from the river margin. In each transect, six points spaced 10 m apart were marked, for a total of 60 sampling points per area. Thirty of the 60 predefined sampling points were selected for collection of litterfall and macroinvertebrates, which were manually collected from the soil surface, within a 0.25 $m^2$ square (0.5 × 0.5 m). After collection, the samples were stored in plastic bags and transported under refrigeration to the laboratory.

Four soil samples, collected 5, 10, 15, and 20 m from the river, were drilled using PVC tubes (0.05 m in diameter and 0.5 m in length) coupled to a flooded soil sampler (Nóbrega et al., 2014). After sampling, the cores were hermetically sealed and transported at 4 °C to the laboratory in a vertical position, where the soil cores were sectioned at 0–10, 10–20, and 20–30 cm soil depths.

### 2.3. Laboratory procedures

Litterfall samples were classified by species and plant tissue (*e.g.*, leaves, fruit, flowers, and stems), oven dried (60 °C) and weighted to quantify the litterfall biomass from both studied mangroves. The invertebrates were grouped according to their trophic position (herbivorous and omnivorous) based on nitrogen isotopes and feeding habits obtained from the literature (Proffitt et al., 1993; Chrintensen, 1998). Then, the animals were removed from their shells or carapaces and frozen for posterior isotopic analysis.

The physicochemical parameters (*e.g.*, redox potential (Eh) and pH), grain size composition, and soil organic matter content of the soil samples were determined. The Eh was determined with a platinum electrode, and the values were corrected by the addition of the potential of the reference electrode (calomel; +244 mV). The pH was determined with a glass electrode calibrated with pH 4.0 and 7.0 standard solutions. Both parameters were measured using portable electrodes. The grain size composition of soils was determined by the densimeter method (Gee and Bauder, 1986) using a combination of physical (overnight shaking) and chemical (0.015 M Na(PO4)6 + 1.0 M NaOH) dispersal methods and 50 g of dried soil. The sand fraction (0.053–2.00 mm) was obtained by sieving; clay fraction (< 0.002 mm), by reading the densimeter; and silt fraction (0.002 mm–0.053), by determining the difference in the total weight of the sample. Prior to the grain size determination, the soil organic matter ($H_2O_2$, 30% vol.) and soluble salts were removed (ethanol, 60%). Soil organic matter (SOM contents were determined in dried samples by the loss on ignition (LOI; see Nóbrega et al., 2015), whereas total organic carbon (TOC) and total nitrogen (TN) contents were measured using the contents provided by the isotopic analysis. For TOC quantification, dried soil samples were pretreated with hydrochloric acid (HCl, 1 M) to remove inorganic C, whereas TN contents were determined using untreated samples (Howard et al., 2014).

Additionally, solid-phase Fe and P fractionation were performed using sequential extractions. Fe fractionation was performed using a combination of the methods proposed by Tessier et al. (1979), Huerta-Diaz and Morse (1990), and Fortin et al. (1993), yielding six operationally distinct Fe fractions (soluble and exchangeable – $Fe_{Ex}$, Fe associated with carbonates – $Fe_{Ca}$, ferrihydrite Fe – $Fe_{FR}$, lepidocrocite Fe – $Fe_{LP}$, Fe associated with crystalline oxide – $Fe_{CR}$, and pyrite Fe − $Fe_{PY}$; for further details, see Nóbrega et al., 2013; Araújo Júnior et al., 2016). Based on the Fe fractionation, the degree of Fe pyritization [DOP = F6 x 100/(ΣFe1→Fe6)] was also determined.

Phosphorus fractionation followed the method proposed by Paludan and Jensen (1995) and Paludan and Morris (1999), yielding six operationally distinct P fractions (P soluble and exchangeable - $P_{Ex}$, P bound

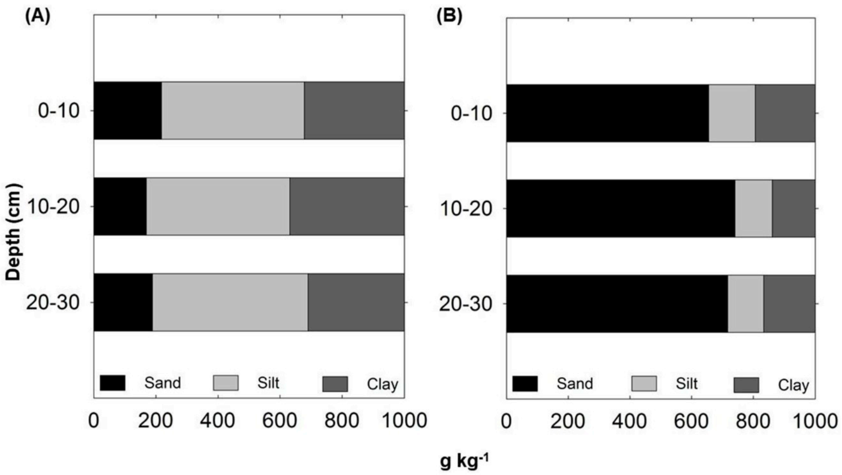

**Fig. 3.** Grain size composition at different soil depths in both mangrove forests: (A) Jaguaribe river and (B) Pacoti river.

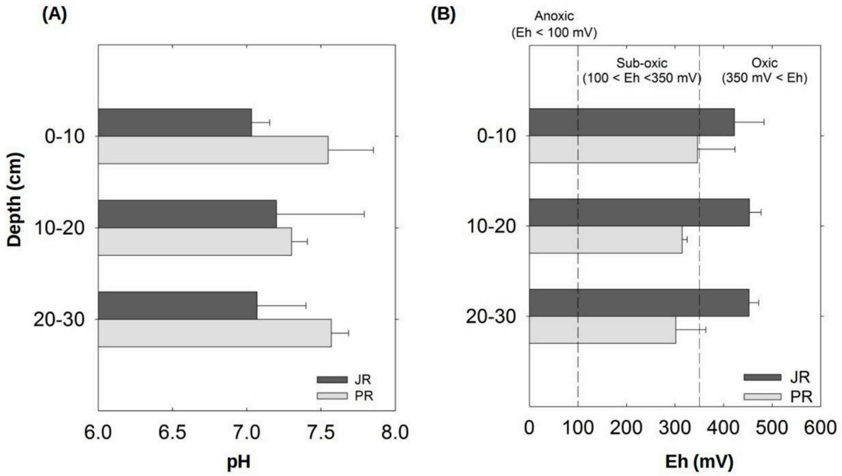

**Fig. 4.** Depth distribution of soil pH (A) and Eh (B) measured at both study sites (JR: Jaguaribe river; PR: Pacoti river).

to Fe-oxyhydroxides - $P_{Fe}$, P bound to Al oxides - $P_{Al}$, P bound to humic acids - $P_{HA}$, P bound to carbonates and apatite - $P_{Ca}$, and P bound to refractory organic matter, i.e., humin - $P_{RES}$; for further details, see Nóbrega et al., 2014).

### 2.4. Isotopic analysis

Oven-dried (60 °C) samples of crab muscle tissue and potential food sources (soil organic matter, litterfall and invertebrates, grouped by trophic position and without carapaces or shells) were ground in an agar mortar for isotopic characterization ($\delta^{13}C$ and $\delta^{15}N$) to assess the food preferences of *G. cruentata* and *U. cordatus.* The isotopic signatures of the soil samples were obtained following the same pretreatment used for TOC and TN quantification.

All samples were then placed in tin capsules and weighed (0.8–1.2 mg for animal material and 2.4–2.7 mg for plant material). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios and the elemental contents of C and N were analyzed by continuous flow-isotope ratio mass spectrometry (CF-IRMS) using a Carlo Erba elemental analyzer (CHN-1110) interfaced to a Delta Plus isotope ratio mass spectrometer in the Isotopic Ecology Laboratory (CENA) of the University of São Paulo (Brazil). The isotopic signatures of carbon and nitrogen were calculated by using the following equation:

$\delta^{13}$ C or $\delta^{15}$:

$$N = \left(\frac{R_{sample} - R_{standard}}{R_{standard}}\right) * 1000$$

where R is the molar ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ in the sample and standard, expressed as delta (δ) per mil (‰) (Fry, 2006). The standards used for nitrogen and carbon were Pee Dee Belemnite (PDB) and atmospheric nitrogen (AIR), respectively. The analytical error of isotope measurements was estimated at 0.3‰ for $\delta^{13}C$ and 0.4‰ for $\delta^{15}N$ using repeated measurements of an internal standard (sugarcane).

### 2.5. Statistical analysis

The Kolmogorov-Smirnov two-sample test was used to study data homogeneity, and Shapiro-Wilk to test normality. Because the litter input and litterfall composition showed a nonnormal distribution, a Mann-Whitney test was used. One-way ANOVA was performed to assess differences between the soil composition of mangrove forests (JR and PR). Student's *t*-test was used to compare the results between brachyuran crabs (*U. cordatus* and *G. cruentata*) and mangrove forests (JR and PR) in terms of %C, %N, C/N ratio, $\delta^{13}C$, and $\delta^{15}N$ for crab tissues and food sources. All tests were considered statistically significant at $P < 0.05$.

Bayesian mixing models were performed using Stable Isotope Mixing Models in R (simmr) (R Core Team, 2018) (Parnell, 2016) to estimate the contribution of possible food sources to the diets of *U. cordatus* and *G. cruentata* in each mangrove forest. Thus, models were run for each species and each mangrove forest. These models allow the inclusion of isotopic signatures, element concentrations and fractionation or trophic enrichment factors. The output of Bayesian mixing models corresponds to a range of solutions on the potential diet, given the available sources and considering uncertainty (Parnell et al., 2010). To use mixing models, the difference in the isotopic composition between animal tissues and diet must be represented by fractionation or a trophic enrichment factor (TEF) (Caut et al., 2009). The most appropriate TEFs were obtained from the literature (Bui and Lee, 2014; Kristensen et al., 2017) (Table A.1).

All statistical analyses (mean comparisons and Bayesian inferences) were performed in the R packages (R Core Team, 2016) Vegan (Oksanen et al., 2013), Redas (Maier, 2015), and simmr (Parnell, 2016), respectively.

## 3. Results

### 3.1. Litterfall biomass

The JR and PR mangrove forests were composed of *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia germinans*. *R. mangle* composed 90% of the total litterfall biomass of the PR. Along the JR, *R. mangle* and *A. germinans* made similar contributions, 45% and 40% of the total litterfall biomass, respectively (Fig. 2).

### 3.2. Soil characteristics

The soils showed significant differences in their grain size composition, with coarser soil textures in the PR (mean values and standard deviations for sand, silt, and clay of 704 ± 158, 130 ± 65, and 166 ± 95 g kg-1, respectively; Fig. 3B) than in the JR (mean values and standard deviations for sand, silt, and clay of 200 ± 38, 462 ± 47, and 338 ± 62 g kg-1, respectively; Fig. 3A). Soils also showed significant differences in their pH and Eh. Slightly higher pH values were recorded in the PR mangrove (mean and standard deviation:

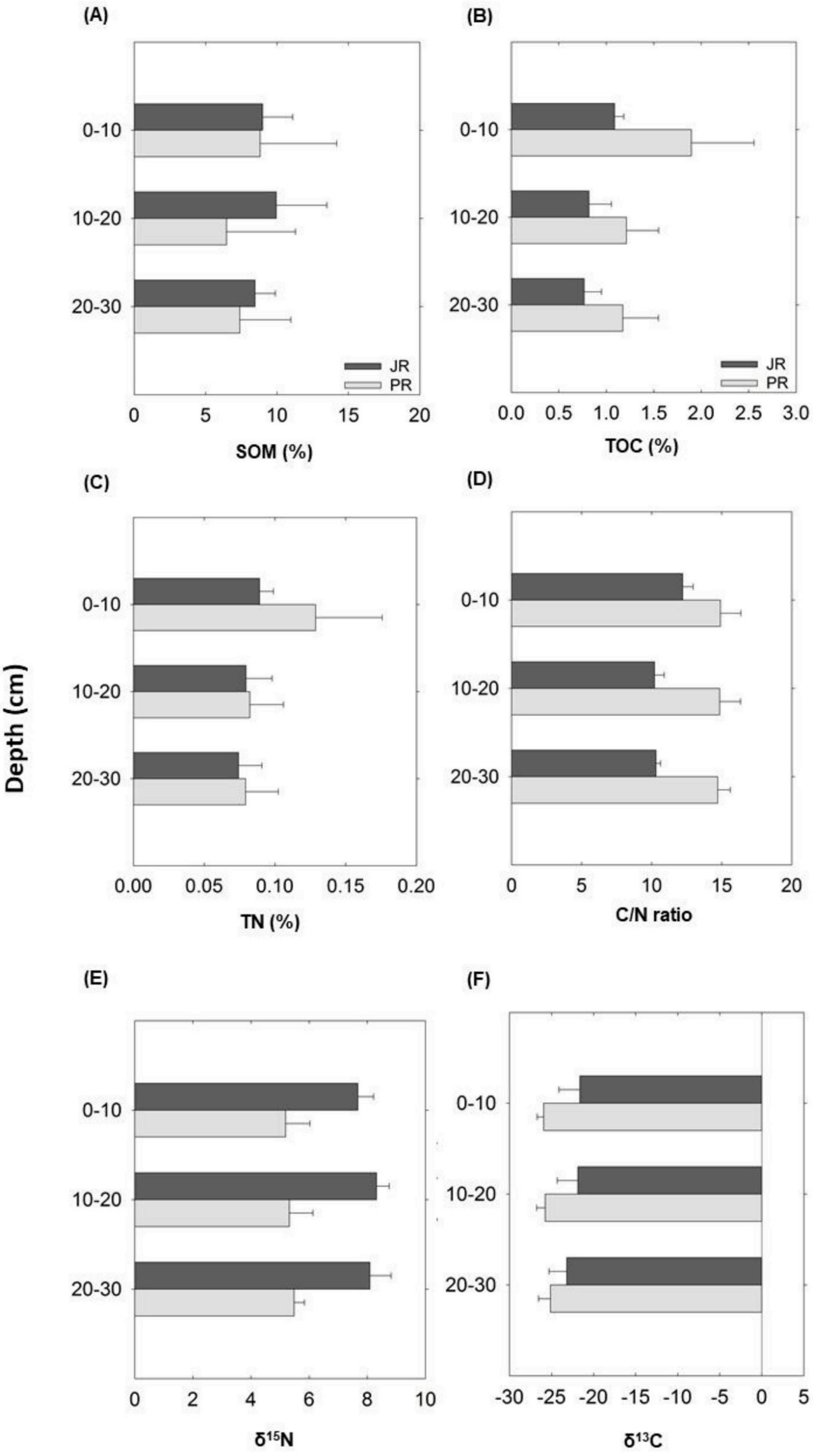

**Fig. 5.** Mean values ( ± standard deviations) of (A) soil organic matter (SOM), (B) total organic carbon (TOC), (C) total nitrogen (TN), (D) the C/N ratio, (E) $\delta^{15}N$, and (F) $\delta^{13}C$ at different depths at both study sites (JR: Jaguaribe river; PR: Pacoti river).

7.4 ± 0.2) than in the JR (mean and standard deviation: 7.1 ± 0.3). Regarding the redox conditions, higher Eh values were found in the JR soils (mean and standard deviation: +445 ± 36 mV) than in the PR soils (mean and standard deviation: +320 ± 55 mV; Fig. 4B).

The soil organic matter (SOM) contents were not significantly different in the studied mangrove forests, with mean values ranging from 8.6 ± 4.5% in the PR to 9.5 ± 2.7% in the JR (Fig. 5A). Significant differences in TOC contents between mangrove forest soils were observed (Fig. 5B), with higher contents in the PR (mean and standard deviation: 1.4 ± 0.6%) than in the JR (mean and standard

**Table 1**
Isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of the food sources in each mangrove forest (JR: Jaguaribe River; PR: Pacoti River).

| Site | Sample | Taxon | | Food source | Mean $\delta^{15}N$ | Mean $\delta^{13}C$ |
|---|---|---|---|---|---|---|
| **JR** | | | | | | |
| | Flower | *Rhizophora mangle* | Magnoliopsida: Rhizophoraceae | Litterfall | 5.32 | −26.95 |
| | Leaf | *Rhizophora mangle* | Magnoliopsida: Rhizophoraceae | Litterfall | 7.31 | −26.33 |
| | Fruit | *Avicennia germinans* | Magnoliopsida: Acanthaceae | Litterfall | 5.03 | −26.05 |
| | Leaf | *Avicennia germinans* | Magnoliopsida: Acanthaceae | Litterfall | 7.32 | −26.50 |
| | Leaf | *Laguncularia racemosa* | Magnoliopsida: Combretaceae | Litterfall | 5.83 | −29.25 |
| | Invertebrate | *Melampus coffeus* | Mollusca: Gastropoda | Omnivorous invertebrate | 5.02 | −19.3 |
| | Invertebrate | *Littoraria angulifera* | Mollusca: Gastropoda | Herbivorous invertebrate | 1.19 | −24.48 |
| | Soil organic matter | | | Soil | 7.76 | −21.21 |
| **PR** | | | | | | |
| | Flower | *Rhizophora mangle* | Magnoliopsida: Rhizophoraceae | Litterfall | 3.61 | −28.35 |
| | Leaf | *Rhizophora mangle* | Magnoliopsida: Rhizophoraceae | Litterfall | 4.24 | −29.65 |
| | Fruit | *Avicennia germinans* | Magnoliopsida: Acanthaceae | Litterfall | 4.36 | −27.46 |
| | Leaf | *Avicennia germinans* | Magnoliopsida: Acanthaceae | Litterfall | 5.53 | −29.04 |
| | Fruit | *Laguncularia racemosa* | Magnoliopsida: Combretaceae | Litterfall | 4.64 | −25.61 |
| | Leaf | *Laguncularia racemosa* | Magnoliopsida: Combretaceae | Litterfall | 5.85 | −27.59 |
| | Invertebrate | *Melampus coffeus* | Mollusca: Gastropoda | Herbivorous invertebrate | 2.48 | −24.71 |
| | Invertebrate | *Littoraria angulifera* | Mollusca: Gastropoda | Herbivorous invertebrate | 1.1 | −23.42 |
| | Invertebrate | *Neritina virginea* | Mollusca: Gastropoda | Omnivorous invertebrate | 8.48 | −21.04 |
| | Invertebrate | Cirripedia | Crustacea | Omnivorous invertebrate | 9.33 | −20.04 |
| | Invertebrate | Ostreidae | Mollusca: Bivalva | Omnivorous invertebrate | 8.39 | −21.45 |
| | Soil organic matter | | | Soil | 5.39 | −25.82 |

deviation: 0.9 ± 0.2%). The TN contents were similar in both soils (mean and standard deviation: 0.1 ± 0.0%; Fig. 5C), whereas the C/N ratios were significantly different (mean and standard deviation: 10.9 ± 1.1 in the JR and 14.8 ± 1.2 in the PR; Fig. 5D). The isotopic compositions indicate a different organic matter composition in the mangrove forests, with the JR samples more enriched in $\delta^{15}N$ than the PR samples (mean values and standard deviations: 8.0 ± 0.6‰ and 5.3 ± 0.6‰ for the JR and PR, respectively; Fig. 5E). Finally, the PR samples were more enriched in $\delta^{13}C$ than the JR samples (mean values and standard deviations: −22.2 ± 2.2‰ and −25.6 ± 1.1‰ for the JR and PR, respectively; Fig. 5F).

All Fe fractions, except for exchangeable Fe ($Fe_{EX}$), were significantly different between the mangrove forests. Higher pseudototal Fe contents ($\Sigma Fe_{EX} \rightarrow Fe_{PY}$; mean and standard deviation: 253.9 ± 41.4 $\mu mol\,kg^{-1}$) and Fe-oxyhydroxide contents (mean values and standard deviations: 24.0 ± 8.3 for $Fe_{FR}$, 111.2 ± 22.1 for $Fe_{LP}$, and 116.4 ± 22.1 $\mu mol\,kg^{-1}$ for $Fe_{CR}$) were recorded along the JR than along the PR (mean values and standard deviations: 17.2 ± 10.4 for $Fe_{FR}$, 62.0 ± 43.9 for $Fe_{LP}$, 45.9 ± 30.6 for $Fe_{CR}$, and 143.2 ± 79.4 $\mu mol\,kg^{-1}$ for pseudototal Fe). On the other hand, the PR showed a higher pyrite content ($Fe_{PY}$; mean and standard deviation: 17.4 ± 17.7 $\mu mol\,kg^{-1}$), resulting in higher DOP levels (14.2 ± 13.1%) than the JR (1.9 ± 1.9 $\mu mol\,kg^{-1}$ for Fe6 and 0.7 ± 0.8% for DOP).

Phosphorus fractionation also showed significantly higher P contents (all fractions) in the JR, except for exchangeable P. The pseudototal P content (sum of all fractions) in the JR was significantly higher (mean values for all depths: 942.3 ± 127.8 $mg\,kg^{-1}$) than that in the PR (mean and standard deviation: 599.0 ± 208.1 $mg\,kg^{-1}$). In the JR, P was mostly associated with humin ($P_{RES}$) (mean of all depths: 228.8 ± 35.4 $mg\,kg^{-1}$), and $P_{Ca}$ was the next most abundant fraction (mean and standard deviation: 228.6 ± 26.0 $mg\,kg^{-1}$). In the PR, the most relevant P fraction was the P associated with Fe-oxyhydroxides (mean and standard deviation: 135.5 ± 70.8 $mg\,kg^{-1}$), followed by $P_{RES}$ (mean and standard deviation: 134.0 ± 78.1 $mg\,kg^{-1}$). The pseudototal P content (sum of all fractions) in the JR was significantly higher (mean values for all depths: 942.3 ± 127.8 $mg\,kg^{-1}$) than that in the PR (mean and standard deviation: 599.0 ± 208.1 $mg\,kg^{-1}$).

### 3.3. *Food source*

The isotopic signatures of the potential food sources were grouped into litterfall, omnivorous invertebrates, herbivorous invertebrates and soil (Table 1). Litterfall was composed of flowers, leaves and fruit that were available on the sampling squares. In the JR, omnivorous invertebrates were composed of *Melampus coffeus,* as evidenced by its high $\delta^{15}N$ value. In the PR, omnivorous invertebrates were composed of *Neritina virginea* and Cirripedia and Ostreidae organisms. Herbivorous invertebrates were composed of one gastropod species *N. virginea* in the PR and two gastropod species (*M. coffeus* and *L. angulifera*) in the JR. *M. coffeus* in the JR was classified as herbivorous due to its lower $\delta^{15}N$ value. This species can change its feeding habits according to the availability of resources (Mook, 1986; Proffitt et al., 1993).

The litterfall showed the highest C contents (Fig. 6A), resulting in the highest C/N ratios. Invertebrates (herbivorous and omnivorous) showed the highest N contents (Fig. 6B), resulting in the lowest C/N ratios. The soil had intermediate C/N values relative to the other food sources (Fig. 6C; Table A.2).

### 3.4. *Crab tissue analyses*

The contents of carbon (C%) and nitrogen (N%) in the crab tissues also differed between species. *U. cordatus* had a higher carbon content (mean and standard deviation: 37.43 ± 2.6%) than *G. cruentata* (mean and standard deviation: 35.84 ± 2.6%) (Fig. A.3). However, *G. cruentata* had higher a nitrogen content (mean and standard deviation: 11.75 ± 0.8%) than *U. cordatus* (mean and standard deviation: 6.16 ± 1.8%) (Fig. A.3). The P contents in crab tissues did not show significant differences between *U. cordatus* (JR mean and standard deviation: 0.09 ± 0.08 $mg\,g^{-1}$; PR mean and standard deviation: 0.44 ± 0.52 $mg\,g^{-1}$) and *G. cruentata* (JR mean and standard deviation: 0.25 ± 0.37 $mg\,g^{-1}$; PR mean and standard deviation: 0.19 ± 0.35 $mg\,g^{-1}$) (Table A.4).

The crab species differed in their isotopic composition (Fig. 7). *G. cruentata* specimens were more enriched in $\delta^{13}C$ (mean and standard deviation: −20.62 ± 1.00‰) and $\delta^{15}N$ (mean and standard deviation: 8.85 ± 1.25‰) than *U. cordatus* ($\delta^{13}C$ mean and standard deviation:

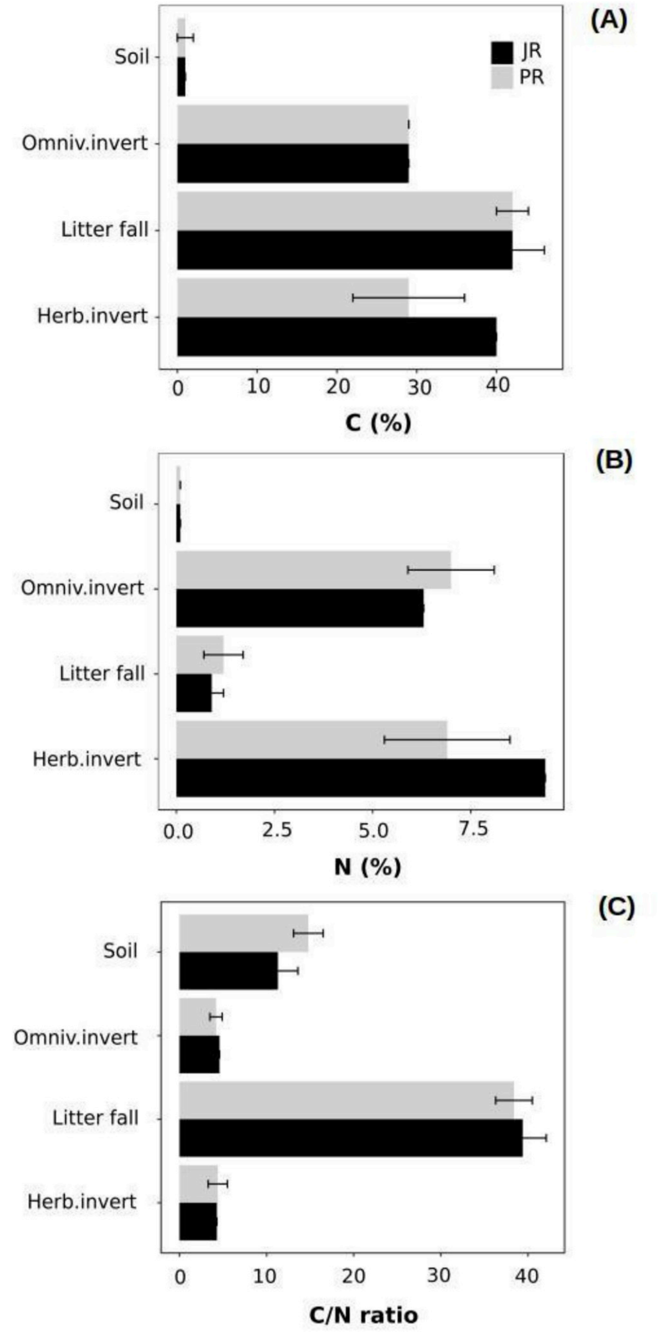

**Fig. 6.** Mean values of C and N ( ± standard deviation) in the food sources (soil, plant material and invertebrates). (A) Carbon percent, (B) nitrogen percent, and (C) C/N ratio in the two mangrove forests (JR: Jaguaribe River; PR: Pacoti River).

−24.47 ± 0.50‰; $\delta^{15}$N mean and standard deviation: 6.16 ± 1.79‰). The $\delta^{15}$N signature of *U. cordatus* was significantly different between mangrove forests (JR mean and standard deviation: 7.27 ± 0.69‰; PR mean and standard deviation: 5.0 ± 1.87‰), with higher values detected in the JR. *G. cruentata* presented significant differences between the mangrove forests in both its $\delta^{13}$C (JR mean and standard deviation: −19.92 ± 0.91; PR mean: −21.31 ± 0.48) and $\delta^{15}$N (JR mean and standard deviation: 9.99 ± 0.54‰; PR mean: 7.8 ± 0.79‰) values, with the highest $\delta^{13}$C and $\delta^{15}$N values recorded in JR crabs.

The analysis of the contributions of food sources (simmr; Stable Isotope Mixing Model in R) showed different results between the mangrove forests and crab species. *U. cordatus* consumed litterfall in a higher proportion in the JR (median: 0.47; Fig. 8A), followed by herbivorous invertebrates (median: 0.31; Fig. 8A). On the other hand, *U. cordatus* in the PR consumed herbivorous invertebrates in a higher proportion (median: 0.70; Fig. 8B) and litterfall in smaller quantities (median: 0.17; Fig. 8B). Soil was the main food source of *G. cruentata* in the JR (median: 0.82; Fig. 8C), whereas in the PR, the omnivorous invertebrate was the main food source (median: 0.70; Fig. 8D), followed by soil (median: 0.11; Fig. 8D).

## 4. Discussion

*R. mangle* composed 90% of the PR litterfall biomass. This species showed a higher C/N ratio (58.52) than *A. germinans* (41.46) and *L. racemosa* (37.55). It was assumed that the PR has a higher litterfall C content than the JR (45% *R. mangle* litterfall biomass) due to the higher C/N ratio of *R. mangle* (Claudino et al., 2015).

The mangrove soil of the PR had a higher TOC content (mean: 1.4 ± 0.6%) and C/N ratio (14.8 ± 1.2) than the JR (TOC%: 0.9 ± 0.2%; C/N: 10.9 ± 1.1). The higher PR organic carbon contents and C/N ratios are probably also related to the high proportions of *R. mangle* in the litterfall biomass. The soil C input results from the decomposition of mangrove plant tissues such as leaves and roots (Thimdee et al., 2001; Giarrizzo et al., 2011; Alongi, 2014).

The lower Eh recorded at the PR site corroborates the higher Fe-pyrite and DOP values, which evidence more reduced soil conditions and a dominance of anaerobic pathways in the decomposition of soil organic matter (i.e., iron and sulfate reductions; Alongi, 2014). These anaerobic pathways favor C accumulation in these soil ecosystems (Howard et al., 2014). On the other hand, the higher Eh values at the JR site indicate an aerobic soil environment (corroborated by the higher Fe-oxyhydroxide contents), resulting in higher organic C oxidation rates and thus the lower TOC soil contents. The oxic conditions observed in the JR (Fig. 4) may result from higher burial activity, which increases oxygen diffusion into the soil (Araújo et al., 2012; Araújo Júnior et al., 2016).

On the other hand, the differences between sites in the soil N and P contents can be related to anthropogenic impacts. The discharge of shrimp farming effluent into the JR is probably associated with the increased P contents in these mangrove soils (Nóbrega et al., 2014). Thus, the lower TOC and higher TN contents in the soil resulted in a lower C/N ratio at the JR site. The nutrient dynamics in mangrove soils are mostly controlled by the flooding frequency, freshwater input, bioturbation, and climatic conditions, which also control the physicochemical status of mangroves (Chapman and Wang, 2001; Laing et al., 2007; Ferreira et al., 2010; Machado et al., 2010; Nóbrega et al., 2016). In fact, the distinct C, Fe and P dynamics observed in the studied mangroves can be associated with the contrasting soil physicochemical conditions between sites.

Invertebrates presented the highest variations in $\delta^{13}$C and $\delta^{15}$N signatures (Table 1). According to their nitrogen isotope signatures, these organisms were grouped into different trophic positions (herbivorous and omnivorous). In contrast, litterfall and soil organic matter showed lower variations in their isotopic signatures (Table 1). The soil isotopic signatures suggest a homogeneous composition, and an intermediate C/N ratio indicates soil as the most nutritious food source. Food sources with high nutritional value must have balanced carbon and nitrogen contents and C/N ratios below 17 (Russell-Hunter, 1970). The soil C/N ratio was three times lower than the litterfall ratio in the JR and twice lower the litterfall ratio in the PR (Fig. 6), showing that soil can have higher nutritional value than leaves. This result corroborates a study carried out in two mangroves on Unguja Island,

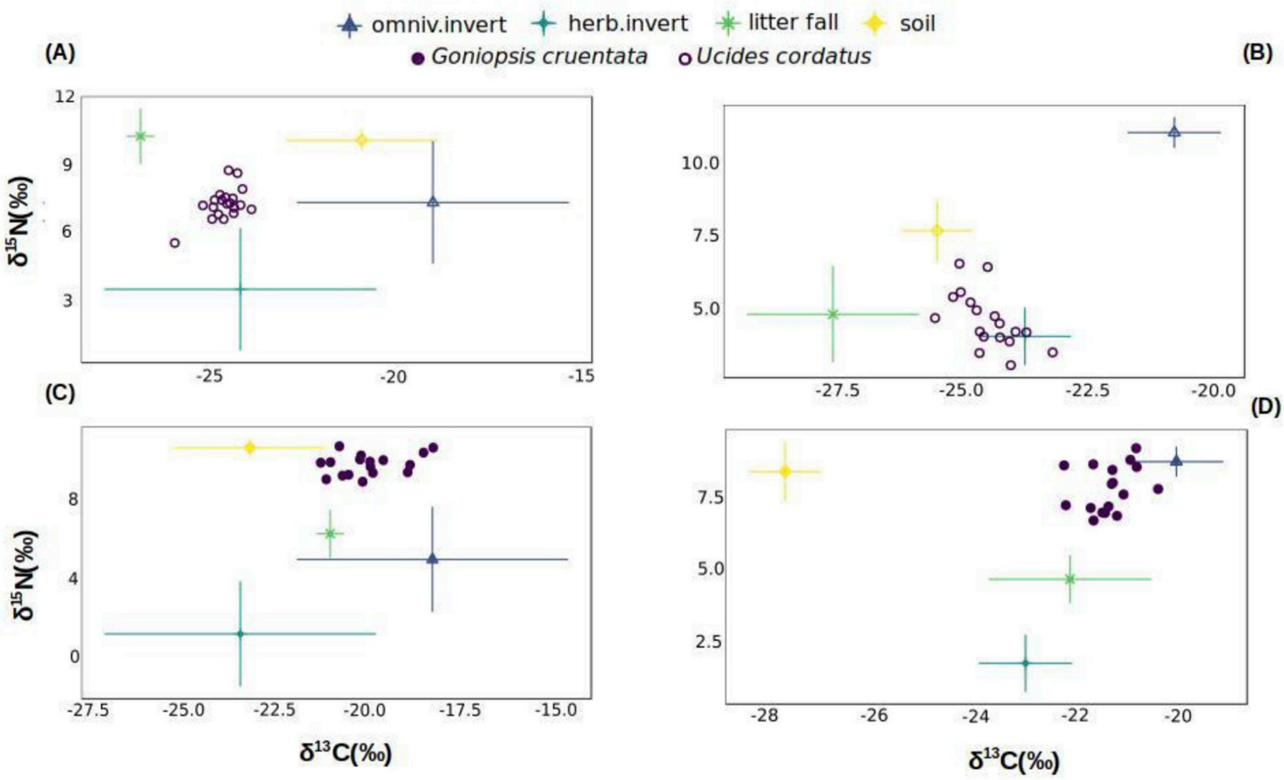

**Fig. 7.** Mean ( ± standard deviation) isotopic signatures ($\delta^{13}$C and $\delta^{15}$N) of Brachyura species: *G. cruentata* (closed circles), *U. cordatus* (open circles), and their food sources (omnivorous invertebrate, herbivorous invertebrate, litterfall and soil) in the studied mangrove forests: (A and C) Jaguaribe River (JR) and (B and D) Pacoti River (PR).

Tanzania (Skov and Hartnoll, 2002), where soil had a lower C/N value than mangrove leaves (Skov and Hartnoll, 2002). Likewise, other authors have observed ingestion of soil as a nutrient source for leaf-eating crabs (Bouillon et al., 2002; Kristensen et al., 2017).

The carbon and nitrogen proportions in *U. cordatus* and *G. cruentata* tissues demonstrate that these species can serve as ecosystem engineers, involved in nutrient conservation. The higher concentration of carbon in *U. cordatus* tissues (mean and standard deviation: 37.43 ± 2.60%) than in *G. cruentata* tissues (mean and standard deviation: 35.84 ± 2.60%) (Fig. A.3) suggests greater carbon recycling by *U. cordatus*. Litterfall consumption and high carbon assimilation demonstrate that leaf-eating crabs have the ability to conserve ecosystem carbon (Kristensen et al., 2008). In addition, their foraging activity facilitates soil heterotrophic microbial activity and improves the nutritional quality of detritivorous organisms (Kristensen, 2008).

However, *G. cruentata* showed higher nitrogen assimilation (tissue mean and standard deviation: 11.75 ± 0.83%) (Fig. A.3). The nitrogen demand of this species is due to its faster growth rate than that of *U. cordatus* (*e.g.,* Pinheiro et al., 2005; Reis et al., 2015, Leite et al., 2014, De Lira et al., 2015). In animals, an investment in growth increases the nitrogen demand during foraging (Sterner and Elser, 2002). The foraging behavior of *G. cruentata* and soil ingestion modify microbial biodegradation, influencing nutrient recycling (De Lima-Gomes et al., 2011).

The species' isotopic signatures varied between mangroves, suggesting an increase in invertebrate ingestion and assimilation in the PR. Differences in species feeding habits between the mangroves may be related to resource availability or quality (Stephens and Krebs, 1986). An increase in benthic invertebrate foraging can occur in habitats where species have higher nitrogen requirements, leading to differences in food partitioning (Zandonà et al., 2011). In the PR, *U. cordatus,* an important litterfall consumer (Nordhaus et al., 2006; Christofoletti et al., 2013), assimilated greater proportions of herbivorous invertebrates, most likely due to the lower quality ( > C/N ratio) of the litterfall. Likewise, *G. cruentata,* classified as a generalist in stomach content studies (De Lima-Gomes et al., 2011), assimilated high proportions of omnivorous invertebrates in the PR. The difference in *G. cruentata* assimilation in the two mangroves is explained by the higher C/N ratios in PR soils. For both species, the higher C/N ratios of the litterfall led to higher nitrogen ingestion from complementary food sources (both soil and omnivorous invertebrates).

## 5. Conclusions

*U. cordatus* and *G. cruentata* assimilated higher proportions of litterfall and *soil organic matter*, respectively, in the JR. In the PR, litterfall and *soil organic matter* were assimilated in lower proportions by the two species. Food source quality ( > C/N ratios) significantly affected food partitioning. Both species assimilated food sources of higher nutritional quality (i.e., invertebrates) in the PR, where the litterfall and soil had low nutritional quality. Both crab species act in carbon and nitrogen conservation, assimilating these nutrients from different sources (i.e., soil, plants, and other animals) according to the source quality. In conclusion, the nutritional requirements and food partitioning behavior of *U. cordatus* and *G. cruentata* emphasize the ecosystem functions of leaf-eating crabs in assimilating and conserving autotrophic carbon and nitrogen in mangrove ecosystems.

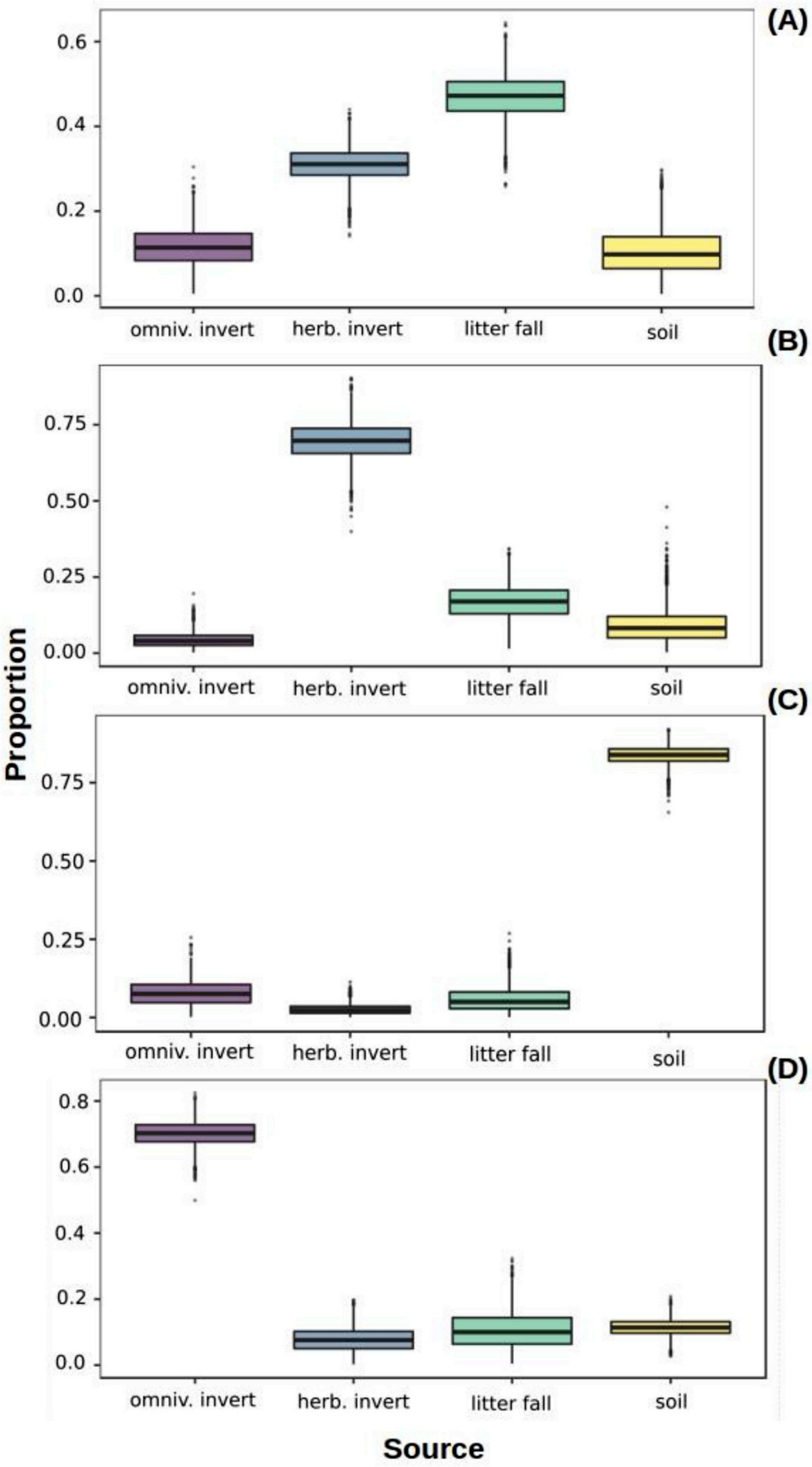

**Fig. 8.** Diet composition for *G. cruentata* and *U. cordatus* according to the simmr (Stable Isotope Mixing Models in R) analysis. (A) *U. cordatus* in the JR, (B) *U. cordatus* in the PR, (C) *G. cruentata* in the JR, and (D) *G. cruentata* in the PR.

## Acknowledgments

This study is part of the first author Master's research (Programa de Pós-Graduação em Ecologia e Recursos Naturais from Universidade Federal do Ceará). The authors were financially supported by grants: TMP (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), CFR (Conselho Nacional de Desenvolvimento Científico e Tecnológico -CNPq, process PQ CNPQ 311627/2015-3), TOF (CNPq, process 308288/2014-9), and CYO (DCR Program from CNPq and Fundação Cearense de Apoio ao Desenvolovimento Científico e Tecnológico). We thank Frederico Alekhine, Felipe Dourado and Keilo Teixeira for field assistance. We especially thank the fisherman (Ronaldo) who collaborated in the field. A collecting permit was issued by the Institute Chico Mendes of Biodiversity Conservations – ICMBio (No 43907–1/2014). We thank Vinicius Neres-Lima for a relevant discussion on mixing models and the two anonymous reviewers for their contributions to improve our manuscript.

## Appendices

Table A.1
Trophical Enrichmente Factor used in the Simmer model for *Ucides cordatus* and *Goniopsis cruentata* in the two mangrove forests (JR: Jaguaribe River; PR: Pacoti River).

| Source | Trophical Enrichment Factor (TEF) | |
|---|---|---|
| | Mean $\delta^{15}N$ | Mean $\delta^{13}C$ |
| ***Ucides cordatus*-JR** | | |
| Omnivorous invertebrates | 2.3 | 0.4 |
| Herbivorous invertebrates | 2.3 | 0.4 |
| Litterfall | 1 | 0.5 |
| Soil | 2.3 | 0.4 |
| ***Ucides cordatus*-PR** | | |
| Omnivorous invertebrates | 2.3 | 0.4 |
| Herbivorous invertebrates | 2.3 | 0.4 |
| Litterfall | 4.0 | −0.3 |
| Soil | 2.3 | 0.4 |
| ***Goniopsis cruentata*-JR/PR** | | |
| Omnivorous invertebrates | 0.0 | 1.1 |
| Herbivorous invertebrates | 0.0 | 1.1 |
| Litterfall | 0.1 | 5.5 |
| Soil | 3.0 | −1.9 |

Table A.2
Maximum and minimum values of percentage of carbon, nitrogen and C / N ratio of food sources in the two mangrove forests (JR: Jaguaribe River; PR: Pacoti River).

| Site | Food source | C (%) | N (%) | C/N ratio |
|---|---|---|---|---|
| **JR** | Omnivorous invertebrate | 29.0–29.0 | 6.3–6.3 | 4.6–4.6 |
| | Herbivorous invertebrate | 40.4–40.4 | 9.4–9.4 | 4.3–4.3 |
| | Litter fall | 46.1–36.1 | 1.1–0.5 | 36.4–41.8 |
| | Soil | 1.2–.5 | 0.1–0.05 | 9.3–12.2 |
| **PR** | Omnivorous invertebrate | 29.0–29.6 | 6.2–7.8 | 3.7–4.7 |
| | Herbivorous invertebrate | 24.7–34.1 | 5.3–8.5 | 3.6–5.6 |
| | Litter fall | 44.5–38.1 | 0.5–2.2 | 35.5–40.8 |
| | Soil | 0.5–2.6 | 0.04–0.2 | 11.1–17.5 |

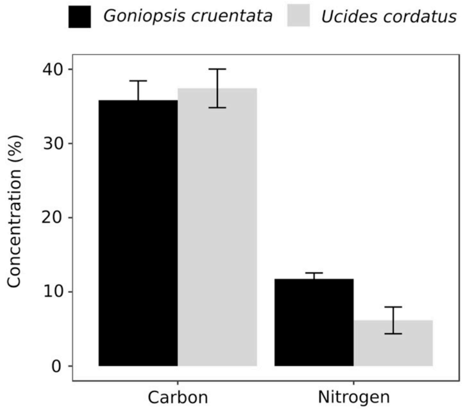

**Fig. A.3.** Mean ( ± standard deviation) concentration of carbon and nitrogen percentage of Brachyura species: *Ucides cordatus* and *Goniopsis cruentata*.

Table A.4
Mean concentration of phosphorus and mean size of Brachyura species at both study sites (JR: Jaguaribe river; PR: Pacoti river).

| Brachyuran species | Mangrove | | | |
|---|---|---|---|---|
| | JR | | PR | |
| | P (mg/g) | Size (mm) | P (mg/g) | Size (mm) |
| *Ucides cordatus* | 0.14 ± 0.05 | 61.68 ± 3.11 | 0.65 ± 0.49 | 63.34 ± 8.08 |
| *Goniopsis cruentata* | 0.03 ± 0.01 | 46.51 ± 2.70 | 0.04 ± 0.02 | 44.82 ± 3.51 |

## References

Alongi, D.M., Tirendi, F., Dixon, P., Trott, L.A., Brunskill, G.J., 1999. Mineralization of organic matter in intertidal sediments of a tropical semi-enclosed delta. Estuar. Coast Shelf Sci. 48, 451–467. https://doi.org/10.1006/ecss.1998.0465.

Alongi, D.M., 2014. Carbon cycling and storage in mangrove forests. Ann. Rev. Mar. Sci. 6, 195–219. https://doi.org/10.1146/annurev-marine-010213-135020.

Araújo, J.M.C., Otero, X.L., Marques, a.G.B., Nóbrega, G.N., Silva, J.R.F., Ferreira, T.O., 2012. Selective geochemistry of iron in mangrove soils in a semiarid tropical climate: effects of the burrowing activity of the crabs Ucides cordatus and Uca maracoani. Geo Mar. Lett. 32, 289–300. https://doi.org/10.1007/s00367-011-0268-5.

Araújo Júnior, J.M. de C., Ferreira, T.O., Suarez-Abelenda, M., Nóbrega, G.N., Albuquerque, A.G.B.M., Bezerra, A. de C., Otero, X.L., 2016. The role of bioturbation by Ucides cordatus crab in the fractionation and bioavailability of trace metals in tropical semiarid mangroves. Mar. Pollut. Bull. 111, 194–202. https://doi.org/10.1016/j.marpolbul.2016.07.011.

Bouillon, S., Koedam, N., Raman, a. V., Dehairs, F., 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. Oecologia 130, 441–448. https://doi.org/10.1007/s004420100814.

Bouillon, S., Connolly, R.M., Lee, S.Y., 2008. Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J. Sea Res. 59, 44–58. https://doi.org/10.1016/j.seares.2007.05.001.

Bui, T.H.H., Lee, S.Y., 2014. Does "you are what you eat" apply to mangrove grapsid crabs? PLoS One 9. https://doi.org/10.1371/journal.pone.0089074.

Camilleri, J.C., Ribi, G., 1986. Leaching of dissolved organic carbon (DOC) from dead leaves, formation of flakes from DOC, and feeding on flakes by crustaceans in mangroves. Mar. Biol. 91, 337–344. https://doi.org/10.1007/BF00428627.

Caut, S., Angulo, E., Courchamp, F., 2009. Variation in discrimination factors (Δ15N and Δ13C): the effect of diet isotopic values and applications for diet reconstruction. J. Appl. Ecol. 46, 443–453. https://doi.org/10.1111/j.1365-2664.2009.01620.x.

Chapman, P.M., Wang, F., 2001. Assessing sediment contamination in estuaries. Environ. Toxicol. Chem. 20, 3–22. https://doi.org/10.1002/etc.5620200102.

Chrintensen, J.T., 1998. Diet in *Littorari*. Hydrobioloia 378, 235–236.

Christofoletti, A.R., Hattori, Y.G., Pinheiro, A.A.M., 2013. Food selection by a mangrove crab: temporal changes in fasted animals. Hydrobiologia 702, 63–72. https://doi.org/10.1007/s10750-012-1307-6.

Claudino, M.C., Abreu, P.C., Garcia, A.M., 2013. Stable isotopes reveal temporal and between-habitat changes in trophic pathways in a southwestern Atlantic estuary. Mar. Ecol. Prog. Ser. 489, 29–42. https://doi.org/10.3354/meps10400.

Claudino, M.C., Pessanha, A.L.M., Araújo, F.G., Garcia, A.M., 2015. Trophic connectivity and basal food sources sustaining tropical aquatic consumers along a mangrove to ocean gradient. Estuar. Coast Shelf Sci. 167, 45–55. https://doi.org/10.1016/j.ecss.2015.07.005.

Coelho, P.A., Ramos, M. de A., 1972. Coelho e Ramos 1972. Trop. Oceonogr. 13, 133–236.

De Lestang, S., Platell, M.E., Potter, I.C., 2000. Dietary composition of the blue swimmer crab Portunus pelagicus L. Does it vary with body size and shell state and between estuaries? J. Exp. Mar. Biol. Ecol. 246, 241–257. https://doi.org/10.1016/S0022-0981(99)00181-1.

De Lima-Gomes, R., Cobo, V., Fransozo, A., 2011. Feeding behaviour and ecosystem role of the red mangrove crab Goniopsis cruentata (Latreille, 1803) (Decapoda, Grapsoidea) in a subtropical estuary on the Brazilian coast. Crustaceana 84, 735–747. https://doi.org/10.1163/001121611X579141.

De Lira, J.J.P.R., Calado, T.C., dos, S., Rezende, C.F., Silva, J.R.F., 2015. Comparative biology of the crab Goniopsis cruentata: geographic variation of body size, sexual maturity, and allometric growth. Helgol. Mar. Res. 69, 335–342. https://doi.org/10.1007/s10152-015-0441-8.

Dittmar, T., Lara, R.J., 2001. Driving forces behind nutrient and organic matter dynamics in a mangrove tidal creek in North Brazil. Estuar. Coast Shelf Sci. 52, 249–259. https://doi.org/10.1006/ecss.2000.0743.

Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. Nat. Geosci. 4, 293–297. https://doi.org/10.1038/ngeo1123.

Ferreira, T.O., Otero, X.L., Souza Junior, V.S., Vidal-Torrado, P., Macías, F., Firme, L.P., 2010. Spatial patterns of soil attributes and components in a mangrove system in Southeast Brazil (São Paulo). J. Soils Sediments 10, 995–1006. https://doi.org/10.1007/s11368-010-0224-4.

Fortin, D., Leppard, G.G., Tessier, A., 1993. Characteristics of lacustrine diagenetic iron oxyhydroxides. Geochem. Cosmochim. Acta 57, 4391–4404. https://doi.org/10.1016/0016-7037(93)90490-N.

Fry, B., 2006. Stable Isotope Ecology, first ed. Springer New York, New York, NY. https://doi.org/10.1007/0-387-33745-8.

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis. In: Klute, A. (Ed.), Methods of Soil Analysis. Part 1. Physical and Mineralogical Methods, second ed. American Society of Agronomy, Soil Science Society of America, Madison, pp. 383–411.

Giarrizzo, T., Schwamborn, R., Saint-Paul, U., 2011. Utilization of carbon sources in a northern Brazilian mangrove ecosystem. Estuar. Coast Shelf Sci. 95, 447–457. https://doi.org/10.1016/j.ecss.2011.10.018.

Harada, Y., Lee, S.Y., 2016. Foraging behavior of the mangrove sesarmid crab Neosarmatium trispinosum enhances food intake and nutrient retention in a low-quality food environment. Estuar. Coast Shelf Sci. 174, 41–48. https://doi.org/10.1016/j.ecss.2016.03.017.

Howard, J., Hoyt, S., Isensee, K., Telszewski, M., Pidgeon, E., 2014. Coastal Blue Carbon: Methods for Assessing Carbon Stocks and Emissions Factors in Mangroves, Tidal Salt Marshes, and Seagrasses. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature, Arlington, VA, USA.

Huerta-Diaz, M. a., Morse, J.W., 1990. A quantitative method for determination of trace metal concentrations in sedimentary pyrite. Mar. Chem. 29, 119–144. https://doi.org/10.1016/0304-4203(90)90009-2.

IPECE–Instituto de Pesquisa e Estratégia Econômica do Ceará, 2016. Perfil Básico Municipal – Aracati. www.ipece.ce.gov.br, Accessed date: 10 August 2018.

Kauffman, J. Boone, Bernardino, Angelo F., Ferreira, Tiago O., Giovannoni, Leila R., Gomes, Luiz Eduardo de O., Romero, Danilo Jefferson, Jimenez, Laís Coutinho Zayas, Ruiz, Francisco, 2018. Carbon stocks of mangroves and salt marshes of the Amazon region. Brazil14Biology Letters. https://doi.org/10.1098/rsbl.2018.0208.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. J. Sea Res. 59, 30–43. https://doi.org/10.1016/j.seares.2007.05.004.

Kristensen, E., Bouillon, S., Dittmar, T., Marchand, C., 2008. Organic carbon dynamics in mangrove ecosystems: a review. Aquat. Bot. 89, 201–219. https://doi.org/10.1016/j.aquabot.2007.12.005.

Kristensen, E., Lee, S.Y., Mangion, P., Quintana, C.O., Valdemarsen, T., 2017. Trophic discrimination of stable isotopes and potential food source partitioning by leaf-eating crabs in mangrove environments. Limnol. Oceanogr. 62, 2097–2112. https://doi.org/10.1002/lno.10553.

Kristensen, E., Quintana, C.O., Valdemarsen, T., 2018. Stable C and N isotope composition of primary producers and consumers along an estuarine salinity gradient: tracing mixing patterns and trophic discrimination. Estuar. Coast. https://doi.org/10.1007/s12237-018-0460-1.

Lacerda, L.D., Santos, J.A., Lopes, D.V., 2009. Fate of copper in intensive shrimp farms: bio- accumulation and deposition in pond sediments. Braz. J. Biol. 69 (3), 851–858.

Laing, G. Du, Vanthuyne, D., Tack, F.M.G., Verloo, M.G., 2007. Management Factors affecting metal mobility and bioavailability in the superficial intertidal sediment layer of the Scheldt estuary Factors affecting metal mobility and bioavailability in the superficial intertidal sediment layer of the Scheldt estuary. Aquat. Ecosys. Health Manag. 10, 33–40. https://doi.org/10.1080/14634980701212969.

Lee, S.Y., 1997. Potential trophic importance of the faecal material of the mangrove sesarmine crab Sesarma masse. Mar. Ecol. Prog. Ser. 159, 275–284. https://doi.org/10.3354/meps159275.

Leite, M. de M.L.L., Ogawa, C.Y., Rezende, C.F., Silva, J.R.F., 2014. Temporal variation in the weight-size relationship of the mangrove crab Ucides cordatus L. (Decapoda: Ucididae) in relation to its life cycle phases. Anim. Biol. 64, 333–342. https://doi.org/10.1163/15707563-00002451.

Linton, S.M., Greenaway, P., 2007. A review of feeding and nutrition of herbivorous land crabs: adaptations to low quality plant diets. J. Comp. Physiol. B 177, 269–286. https://doi.org/10.1007/s00360-006-0138-z.

Machado, W., Villar, L.S., Monteiro, F.F., Viana, L.C. a., Santelli, R.E., 2010. Relation of acid-volatile sulfides (AVS) with metals in sediments from eutrophicated estuaries: is it limited by metal-to-AVS ratios? J. Soils Sediments 10, 1606–1610. https://doi.org/10.1007/s11368-010-0297-0.

Maia, L.P., Lacerda, L.D. de, Monteiro, U.H.L., Souza, M.G., 2006. Atlas dos manguezais do nordeste do Brasil:avaliação das áreas de manguezais dos Estados do Piauí, Ceará, Rio Grande do Norte, Paraíba e Pernambuco. SEMACE: Universidade Federaldo Ceará: Instituto de Ciências do Mar, pp. 2006.

Maier, M.J., 2015. Companion Package to the Book "R: Einführung durch angewandte Statistik". R package version 0.9.3. http://CRAN.R-project.org/package=REdaS.

McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2.

Front. Ecol. Environ. 9, 552–560. https://doi.org/10.1890/110004.

Mook, D., 1986. Absorption efficiencies of the intertidal mangrove dwelling Mollusk Melampus coffeus LINNÉ and the rocky intertidal Mollusk Acanthopleura granulata GMELIN. Mar. Ecol. 7 (2), 105–113. https://doi.org/10.1111/j.1439-0485.1986.tb00150.x.

Moreno, R., Jover, L., Munilla, I., Velando, A., Sanpera, C., 2010. A three-isotope approach to disentangling the diet of a generalist consumer: the yellow-legged gull in northwest Spain. Mar. Biol. 157, 545–553. https://doi.org/10.1007/s00227-009-1340-9.

Nellemann, C., Corcoran, E., Duarte, C.M., Valdés, L., De Young, C., Fonseca, L., Grimsditch, G., 2009. Blue Carbon: a Rapid Response Assessment, Environment.

Nilin, J., Moreira, L.B., Aguiar, J.E., Marins, R., Moledo de Souza Abessa, D., Monteiro da Cruz Lotufo, T., Costa-Lotufo, L.V., 2013. Sediment quality assessment in a tropical estuary: the case of Ceará River, Northeastern Brazil. Mar. Environ. Res. 91, 89–96. https://doi.org/10.1016/j.marenvres.2013.02.009.

Nóbrega, G.N., Ferreira, T.O., Romero, R.E., Marques, A.G.B., Otero, X.L., 2013. Iron and sulfur geochemistry in semi-arid mangrove soils (Ceará, Brazil) in relation to seasonal changes and shrimp farming effluents. Environ. Monit. Assess. 185, 7393–7407.

Nóbrega, G.N., Otero, X.L., Macías, F., Ferreira, T.O., 2014. Phosphorus geochemistry in a Brazilian semiarid mangrove soil affected by shrimp farm effluents. Environ. Monit. Assess. 186, 5749–5762. https://doi.org/10.1007/s10661-014-3817-3.

Nóbrega, G.N., Ferreira, T.O., Artur, A.G., de Mendonça, E.S., de, O., Leão, R. a., Teixeira, A.S., Otero, X.L., 2015. Evaluation of methods for quantifying organic carbon in mangrove soils from semi-arid region. J. Soils Sediments 15, 282–291. https://doi.org/10.1007/s11368-014-1019-9 https://doi.org/10.1007/s10661-013-3108-4.

Nóbrega, G.N., Ferreira, T.O., Siqueira Neto, M., Queiroz, H.M., Artur, A.G., Mendonça, E.D.S., Silva, E.D.O., Otero, X.L., 2016. Edaphic factors controlling summer (rainy season) greenhouse gas emissions (CO2 and CH4) from semiarid mangrove soils (NE-Brazil). Sci. Total Environ. 542, 685–693. https://doi.org/10.1016/j.scitotenv.2015.10.108.

Nogueira, F.N.A., Rigotto, R.M., Teixeira, A.C.D.A., 2009. O agronegócio do camarão: processo de trabalho e riscos à saúde dos trabalhadores no município de Aracati/Ceará. Rev. Bras. Saúde Ocup. 34, 40–50. https://doi.org/10.1590/S0303-76572009000100005.

Nordhaus, I., Wolff, M., Diele, K., 2006. Litter processing and population food intake of the mangrove crab Ucides cordatus in a high intertidal forest in northern Brazil. Estuar. Coast Shelf Sci. 67, 239–250. https://doi.org/10.1016/j.ecss.2005.11.022.

Nordhaus, I., Wolff, M., 2007. Feeding ecology of the mangrove crab Ucides cordatus (Ocypodidae): food choice, food quality and assimilation efficiency. Mar. Biol. 151, 1665–1681. https://doi.org/10.1007/s00227-006-0597-5.

Nordhaus, I., Diele, K., Wolff, M., 2009. Activity patterns, feeding and burrowing behaviour of the crab Ucides cor- datus (Ucididae) in a high intertidal mangrove forest in North Brazil. J. Exp. Mar. Biol. Ecol. 374, 104–112.

Odum, E.P., Heald, E.J., 1975. The Detritus Bases Food Web of an Estuarine Mangrove Community. Estuarine Research. Academic Press, New York, pp. 265–286.

Oksanen, J., Blanchet, F.G., Kindt, R., et al., 2013. Vegan: Community Ecology Package. R Package Version 2.0-10. http://CRAN.R-project.org/package=vegan.

Paludan, C., Jensen, H.S., 1995. Sequential extraction of phosphorus in freshwater wetland and lake sediments: significance of humic acids. Wetlands 15, 365–373.

Paludan, C., Morris, J.T., 1999. Distribution and speciation of phosphorus along a salinity gradient in intertidal marsh sediments. Biogeochemistry 197–221.

Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS One 5, 1–5. https://doi.org/10.1371/journal.pone.0009672.

Parnell, A.C., 2016. Simmr: a Stable Isotope Mixing Model. R Package Version 0.3. https://CRAN.R-project.org/package=simmr.

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644. https://doi.org/10.5194/hess-11-1633-2007.

Pinheiro, M.A.A., Fiscarelli, A.C., Hattori, G.Y., 2005. Growth of the mangrove crab *Ucides cordatus* (Brachyura, Ocypodidae). J. Crustac Biol. 25, 293–301.

Proffitt, C.E., Johns, K.M., Cochrane, C.B., Devlin, D.J., Reynolds, T.A., Payne, D.L., Jeppesen, S., Peel, D.W., Linden, D., 1993. Field and laboratory experiments on the consumption of mangrove leaf litter by the macrodetritivore Melampus coffeus L. (Gastropoda:Pulmonata). Biol. Sci. 56, 211–222.

R Core Team, 2016. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reis, C.R.G., Taddei, F.G., Cobo, V.J., 2015. Growth and reproduction of the mangrove crab goniopsis cruentata (Latreille, 1803) (crustacea: Decapoda: Grapsidae) in southeastern Brazil. An. Acad. Bras. Cienc. 87, 699–711. https://doi.org/10.1590/0001-3765201520130387.

Robertson, A.I., Daniel, P.A., 1988. The influence of crabs on litter processing in high intetidal mangrove forests in tropical Australia. Oecologia 78, 371–375.

Russell-Hunter, W.D., 1970. Aquatic Productivity: an Introduction to Some Basic Aspects of Biological Oceanography and Limnology. Collier-MacMillan, London, UK, pp. 306.

Skov, M.W., Hartnoll, R.G., 2002. Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? Oecologia 131, 1–7. https://doi.org/10.1007/s00442-001-0847-7.

Stephens, David W., Krebs, John R., 1986. Foraging Theory. Princeton University Press.

Sterner, Robert Warner, Elser, James J., 2002. Ecological Stoichiometry: the Biology of Elements from Molecules to the Biosphere. Princeton University Press.

Tessier, A., Campbell, P.G.C., Bisson, M., 1979. Sequential extraction procedure for the speciation of particulate trace metals. Anal. Chem. 51, 844–851. https://doi.org/10.1021/ac50043a017.

Tewfik, A., Bell, S.S., McCann, K.S., Morrow, K., 2016. Predator diet and trophic position modified with altered habitat morphology. PLoS One 11, 22. https://doi.org/10.1371/journal.pone.0147759.

Thimdee, W., Deein, G., Sangrungruang, C., Matsunaga, K., 2001. Stable carbon and nitrogen isotopes of mangrove crabs and their food sources ina mangrove-fringed estuary in Thailand. Benthos Res. 56, 73–80.

Vermeiren, P., Abrantes, K., Sheaves, M., 2015. Generalist and specialist feeding crabs maintain discrete trophic Niches within and among estuarine locations. Estuar. Coast 38, 2070–2082. https://doi.org/10.1007/s12237-015-9959-x.

Zandonà, E., Auer, A.K., Kilham, S.S., Howard, J.L., López-Sepulcre, A., O'Connor, M.P., Bassar, R.D., Osorio, A., Pringle, C.M., Reznick, D.N., 2011. Diet quality and prey selectivity correlate with life histories and predation regime in Trinidadian guppies. Funct. Ecol. 25 (5), 964–973. https://doi.org/10.1111/j.1365-2435.2011.01865.x.