Hydrobiologia (2013) 702:63–72
DOI 10.1007/s10750-012-1307-6

PRIMARY RESEARCH PAPER

# Food selection by a mangrove crab: temporal changes in fasted animals

**Ronaldo A. Christofoletti · Gustavo Y. Hattori · Marcelo A. A. Pinheiro**

Received: 20 August 2011 / Revised: 23 August 2012 / Accepted: 31 August 2012 / Published online: 14 September 2012


**Abstract** The feeding choices of the mangrove crab *Ucides cordatus* for various mangrove plant leaves (*Avicennia schaueriana*, *Laguncularia racemosa*, and *Rhizophora mangle*) at different ages (mature, senescent pre-abscission, and decomposing leaves) were examined. In a controlled experiment set in a mangrove area, we evaluated crab selection for different plant leaves by analyzing foraging rate (number of leaves with predation marks) and leaf consumption. Crabs were housed individually in plastic containers and after a 3-day fast supplied with leaf fragments every 24 h for 72 h. Uneaten leaves were removed before each new food offering. No food selection was observed in the first day, but after this period, senescent leaves, which have a high polyphenol content, were rejected. On the third day, an interactive effect between plant species and leaf age was shown to affect leaf selection, with mature leaves of *A. schaueriana* and *L. racemosa* being more selected than the other treatments. This observation was consistent across crab sexes and ages. Our results show that food selection by this mangrove crab changes through time in fasted animals, suggesting that this variable must be controlled in food preference studies.

**Keywords** Foraging · Herbivory · Mangrove · Ucides · Brazil · Experimental design

Handling editor: Stuart Jenkins

R. A. Christofoletti (✉)
Universidade Federal de São Paulo, Instituto do Mar, Campus Baixada Santista (IMar/UNIFESP); Av. Alm. Saldanha da Gama, 89-Ponta da Praia, Santos, SP 11030-400, Brazil
e-mail: christofoletti@unifesp.br

R. A. Christofoletti · G. Y. Hattori · M. A. A. Pinheiro
UNESP-Univ Estadual Paulista, FCAV, Campus de Jaboticabal, Programa de Pós-Graduação em Zootecnia (Área de Produção Animal), Jaboticabal, SP 14884-900, Brazil

G. Y. Hattori
Instituto de Ciências Exatas e Tecnologia, Universidade Federal do Amazonas, Rua Nossa Senhora do Rosário, 3863, São Jorge, Itacoatiara, AM 69103-128, Brazil

M. A. A. Pinheiro
Campus Experimental do Litoral Paulista (CLP), Grupo de Pesquisa em Biologia de Crustáceos (CRUSTA), UNESP-Univ Estadual Paulista, Praça Infante Dom Henrique, s/n, Parque Bitaru, São Vicente, SP 11330-900, Brazil

## Introduction

Studies on feeding preference elucidate the role that consumers play in food chains (Post et al., 2000; López et al., 2010; Prado & Heck, 2011). Although recent discussions center on experimental designs and types of analyses that improve the assessment of preference (Peterson & Renaud, 1989; Underwood et al., 2004; Underwood & Clarke, 2005, 2006; Manly, 2006; Taplin, 2007), these methods generally neglect the biologic context. For instance, feeding preference is usually assessed in fasted animals to force them to maximize efforts during their search for food (e.g., Micheli, 1993a), but, although it is known that fasting can influence predator behavior (McClintock & Lawrence, 1985; Miyazaki et al., 2000), fasting effects themselves on food selection are disregarded. In a study with an intertidal organism conducted during different post-fasting phases, Christofoletti et al. (2010) showed that fasting may affect food selection, finding only statistically significant selection after 3 days but not before. This suggests that fasted animals forage indiscriminately when they come into contact with food and that after supplying their immediate nutrient needs, start selecting food. Therefore, experiments using fasted animals which do not consider temporal change in selection may be biased due to an influence of fasting. To avoid possible bias, Chen & Ye (2008) suggested that food should be supplied between a fasting period and the experiment, but did not test this hypothesis.

Mangroves are good biologic models for studying food selection, since this ecosystem presents low species diversity and hence few links in the trophic chain. Mangrove leaves are the primary source of food for herbivores in this environment and contribute to the high productivity of mangrove areas due to leaf litter, a primary source of nutrients in ecological interactions (Twilley et al., 1997; Boer, 2000; Clough et al., 2000). Consumers fragment vegetable matter, thereby increasing surface area and promoting colonization by bacteria and fungi, decomposition of undigested particles and soil enrichment (Skov & Hartnoll, 2002). Crustacea are one of the major taxa that participate in litter consumption and removal because of their high biomass and bioturbation capacity and hence make a major contribution to the flow of energy in this ecosystem (Conde et al., 2000; Wolff et al., 2000; Amouroux & Tavares, 2005; Cannicci et al., 2008 and Kristensen, 2008 for review).

A number of studies report factors that influence leaf consumption by mangrove grapsid crabs related to plant distribution and the chemical composition of their leaves (Emmerson & McGwynne, 1992; Slim et al., 1997; Sousa & Mitchell, 1999; Hernes et al., 2001; Skov & Hartnoll, 2002). Leaves are a poor diet because of high carbon to nitrogen content, indigestible structural carbon (cellulose and hemicellulose) and because secondary compounds (tannins) diminish nutrient digestion and absorption (see Linton & Greenaway, 2007 for review). Leaves become more nutritious (C:N) and palatable with age, and crabs may therefore prefer aged leaves to younger ones (Camilleri, 1989; Micheli et al., 1991; Ashton, 2002). Nevertheless, a diet composed predominantly of litter can limit the development of typical herbivorous crabs (Micheli, 1993a, b), prompting Skov & Hartnoll (2002) to question why mangrove crabs eat leaves so abundantly.

*Ucides cordatus* (Linnaeus, 1763) is a semiterrestrial large-bodied crab of ecological and economic importance on the Brazilian coast. This species accounts for 76% of total epibenthic community biomass in mangrove areas (Koch & Wolff, 2002) and consumes nearly 81% of the litter (Nordhaus et al., 2006). The diet of *U. cordatus* consists primarily of vegetable matter (Geraldes & Calventi, 1983; Branco, 1993; Nascimento, 1993; Nordhaus & Wolff, 2007). This crab has a feeding preference for *R. mangle* leaves, which is unexpected due to the low nutrient value of this species (Nordhaus & Wolff, 2007). This would explain the low growth rate of *U. cordatus* described by Pinheiro et al. (2005), since Arthropoda growth can be limited or even interrupted when their diet is rich in tannin or low in calories (Wolcott & Wolcott, 1987; Fleck & Layne, 1990). This crab is one of the main crustacean fishery resources in Brazil, especially in the north and northeast regions (Fausto-Filho, 1968). Population surveys and technical–economic assessment of feasibility of farming *U. cordatus* are required to manage diminishing stocks (Ostrensky et al., 1995; Ivo & Gesteira, 1999; Vasconcelos et al., 1999; Diele & Koch, 2010). A better knowledge of this crabs feeding ecology is also essential to achieve this aim.

This study examined changes in selection of food by *U. cordatus* over time. An experiment was conducted on successive days to detect changes over the post-fasting phases, during which crabs had different energy demands following their recovery from fasting. Tests of selection of leaf food by *U. cordatus* were made based on leaf nutritional character (leaf species and age. The effect of crab sex and maturity on selection was also assessed.

## Materials and methods

The experiments were carried out in a mangrove located in the environmental protection area of

Cananéia-Iguape-Peruíbe, São Paulo State (SP), southeast Brazil, in March 2005. We evaluated food selection by *U. cordatus*, which consisted of leaves obtained from the three main mangrove species in this region (*Avicennia schaueriana* Stapf & Leechman, *Laguncularia racemosa* C.F.Gaertn and *R. mangle* L) at different ages. Leaf age was considered based on stages: mature (green in the trees), senescent (yellow leaves in pre-abscission that dropped from the tree when touched) and decomposing (dark leaves on the ground, clearly undergoing leaching and bacterial decomposition).

The 72 crabs observed were analyzed according to sex and maturity, the latter based on size and abdominal characteristics (Pinheiro et al., 2005) (adult male, adult female, juvenile male, and juvenile female; $N = 18$ for each category). Crabs were housed individually in a plastic container (Ø = 30 cm; height = 15 cm) filled to 2 cm with brackish water and covered with a net. Containers were held in a mangrove area in Ilha Comprida (SP), to provide natural temperature, humidity, and light–dark cycle conditions.

The nine treatments of types of leaves tested (three plant species × three ages) were washed with tap water and cut into same-sized fragments. Leaf fragments were kept at room temperature for less than 24 h before the beginning of the experiment. Crabs were fasted for 3 days to allow complete emptying of the digestive tract. Following fasting, crabs simultaneously received one leaf fragment of each treatment. Leftovers were removed after 24 h and a new set of leaves were offered. This procedure was repeated twice, comprising three consecutive days over a total of 72 h of experiment.

We determined the content of macro and micronutrients, total polyphenols and fibers in the nine leaf types studied. Leaves were individually and thoroughly washed with tap water, dried with a clean cloth and kept cool for a maximum of 48 h. They were then dehydrated in a forced ventilation oven (60°C for 72 h) and ground in a knife mill.

Total polyphenol content was determined colorimetrically by the Folin–Denis method, with the use of a suitable aliquot size for each plant species (1 ml for *L. racemosa*, 10 ml for *R. mangle* and 50 ml for *A. schaueriana*, as determined in preliminary tests). The samples were assayed in triplicate and the mean result (with coefficient of variation under 15%) was used in the subsequent analysis. Dried, ground leaves were analyzed for nutrient content (P, K, Ca, Mg, Fe, Mn, B, Cu, Zn, S, and N) as described by Bataglia et al. (1983) and fiber quantification (lignin, cellulose, and hemicellulose) was performed at the UFSCar (Federal University of São Carlos)—Araras *campus*.

## Data analyses

We assessed crab food selection by the leaf consumption that was measured by the leaf area eaten by the crab. Leaf consumption was evaluated by an ANOVA model with four orthogonal factors: sex and crab maturity (both fixed with two levels each), in addition to mangrove species and leaf age (both fixed with three levels each). In this model, sex and crab maturity test the hypothesis that changes in food selection occur due to biologic characteristics of the consumer (gender and sexual maturity, respectively). Furthermore, the mangrove species term tests the hypothesis that selection by crabs is dependent on species-specific characteristics of the leaf, while the leaf age term tests the hypothesis that this selection is due to changes in leaf characteristics during aging and decomposition processes, independent of mangrove species. Any of the interactive terms will test the hypothesis that selection is dependent on interaction among particular factors. The interactive term between mangrove species and leaf age deserves special attention since it tests if selection by crabs is dependent on changes in leaf characteristics due to aging and decomposition for specific mangrove species.

There were leaves of three different ages from three different mangrove species and hence nine "leaf treatments." All nine treatments were offered at the same time to allow selection among them by crabs. Afterward, we randomly selected only one leaf treatment to be analyzed per crab giving a total of two replicates of each of nine leaf treatments for each crab category (adult male, adult female, juvenile male, and juvenile female). Based on this design, we insured the independence of data among leaf treatments for the ANOVA model, since consumption of the leaf treatment $i$ by the crab $a$ is completely independent of the consumption of the treatment $j$ by the crab $b$. Also, to still insure the independence of data required by the ANOVA, the analyses were conducted for each post-fasting day separately. Thus, the inferences of changes on leaf selection by crabs over time was assessed qualitatively by the comparison among the outputs of the ANOVA models for each separate day.

Cochran's test was used to determine homoscedasticity and transformations were applied when necessary. The post hoc Student–Newman–Keuls (SNK) test was applied for multiple comparisons of the means. Data of macro and micronutrients, total polyphenols and fibers were ordered using Principal Coordinate Analysis (PCoA) (Legendre & Legendre, 1998; Podani, 2000) using Euclidian distances as a similarity measure to analyze the chemical similarities of the leaves in different mangrove species and age/stages.

## Results

The animals' maturity affected leaf consumption, since juvenile crabs consumed a higher amount of leaves compared to adults, during all the experimental days (Table 1: SNK test for "crab maturity" at all 3 days, juvenile > adult; $P < 0.05$). Changes in food selection were detected throughout the experiment (Table 1). In the first post-fasting day, the non-significant effect of leaf species or age show that crabs indiscriminately consumed leaves independent of species and age. In the second post-fasting day, crabs selected leaves according to age and irrespective of plant species. In this case, larger amounts of decomposing leaves and lower amounts of mature and senescent leaves were eaten (Fig. 1). Decomposing leaves generally had a higher content of structural components (lignin and hemicellulose) and Fe and a lower content of polyphenols compared to leaves at the other maturation stages (Table 2; Fig. 2).

Finally, in the third post-fasting day, there was an interactive effect between leaf species and age (Table 1; Fig. 3). *Avicennia schaueriana* leaves were the most consumed, and there was no influence of age for this species. *Rhizophora mangle* leaves were the least consumed, and also there was no influence of age for this species. On the other hand, among leaves of *L. racemosa*, mature leaves were more consumed than senescent ones. When comparing the same age for different species, it was observed that for the mature leaves, *L. racemosa* was more selected than *R. mangle*. For senescent and decomposing ages, *A. schaueriana* was more selected when compared to *L. racemosa* and

**Table 1** Factorial analysis of variance for leaf consumption by the mangrove crab *U. cordatus* in the different post-fasting days and according to sex, maturity, food plant species, and leaf age/stage

| SV | df | Day 1 | | | Day 2 | | | Day 3 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | MS | F | P | MS | F | P | MS | F | P |
| Crab maturity (Ma) | 1 | 709.7 | 4.65 | **0.0378** | 2049.8 | 4.99 | **0.0318** | 4656.3 | 5.98 | **0.0194** |
| Crab sex (sex) | 1 | 240.9 | 1.58 | 0.2170 | 13.8 | 0.03 | 0.8559 | 1252.9 | 1.61 | 0.2126 |
| Leaf species (sp) | 2 | 212.3 | 1.39 | 0.2618 | 520.6 | 1.27 | 0.2938 | 3853.7 | 4.95 | **0.0126** |
| Leaf age (age) | 2 | 206.2 | 1.35 | 0.2717 | 2858.9 | 6.96 | **0.0028** | 552.5 | 0.71 | 0.4984 |
| Ma × sex | 1 | 67.9 | 0.44 | 0.5091 | 111.8 | 0.27 | 0.6051 | 1082.9 | 1.39 | 0.2458 |
| Ma × sp | 2 | 190.6 | 1.25 | 0.2989 | 390.8 | 0.95 | 0.3957 | 2449.3 | 3.15 | 0.0550 |
| Ma × age | 2 | 146.3 | 0.96 | 0.3929 | 882.4 | 2.15 | 0.1314 | 363.5 | 0.47 | 0.6305 |
| Sex × sp | 2 | 177.9 | 1.17 | 0.3232 | 36.4 | 0.09 | 0.9154 | 34.0 | 0.04 | 0.9573 |
| Sex × age | 2 | 37.9 | 0.25 | 0.7815 | 21.7 | 0.05 | 0.9487 | 2279.0 | 2.93 | 0.0663 |
| Sp × age | 4 | 190.4 | 1.25 | 0.3083 | 1012.2 | 2.46 | 0.0625 | 2207.4 | 2.84 | **0.0383** |
| Ma × sex × sp | 2 | 290.8 | 1.91 | 0.1634 | 296.5 | 0.72 | 0.4928 | 29.6 | 0.04 | 0.9627 |
| Ma × sex × age | 2 | 93.9 | 0.62 | 0.5460 | 110.8 | 0.27 | 0.7651 | 1061.7 | 1.36 | 0.2684 |
| Ma × age × sp | 4 | 70.9 | 0.46 | 0.7612 | 306.5 | 0.75 | 0.5670 | 890.5 | 1.14 | 0.3514 |
| Sex × sp × age | 4 | 59.6 | 0.39 | 0.8138 | 116.6 | 0.28 | 0.8865 | 1766.8 | 2.27 | 0.0806 |
| Ma × sex × sp × age | 4 | 113.2 | 0.74 | 0.5698 | 385.2 | 0.94 | 0.4533 | 704.4 | 0.91 | 0.4712 |
| Residual | 36 | 152.6 | | | 410.8 | | | 778.1 | | |
| | | $C = 0.3967$ ($P < 0.01$) | | | $C = 0.2549$ (ns) | | | $C = 0.1785$ (ns) | | |

Bold values correspond to the significant values determined by the statistic analysis

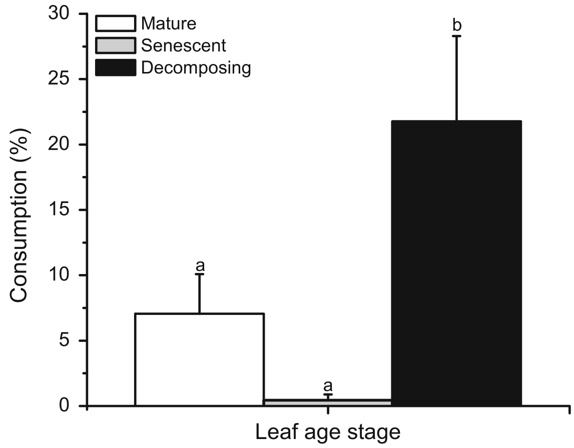



**Fig. 1** Leaf consumption (%) by the mangrove crab *U. cordatus* at the second post-fasting period (24–48 h) according to leaf age

*R. mangle*. The elements N, P, K, Mg, S, and cellulose account for the clustering of the most consumed leaves (Fig. 4). Senescent *L. racemosa* leaves, the least consumed, had the highest polyphenol concentration (Table 2).

## Discussion

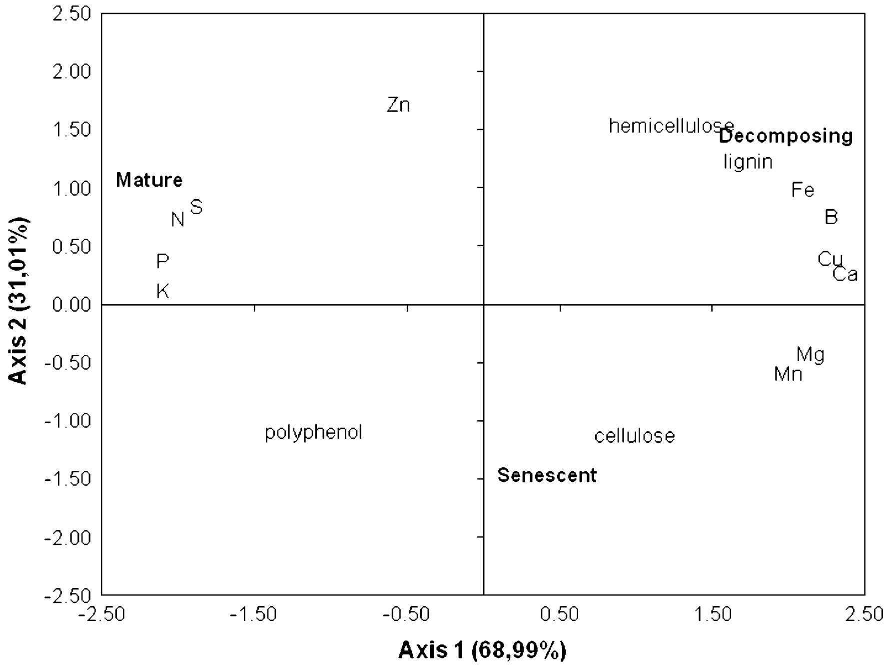
Results show that the mangrove crab *U. cordatus* can alter food selection in the experimental period of post-fasting. Crabs foraged indiscriminately during the first post-fasting day, presumably to rapidly compensate for food deprivation. In the following days, however, they started selecting food, first as a function of leaf age and then according to an interaction between leaf age and mangrove species. Thus, our results suggest, through a qualitative comparison among ANOVA outputs (rather than a formal comparison), that fasting can influence food selection by consumers. We suggest that this biologic influence of pre-experimental fasting should be considered in further studies. Here, we show that consumers can present no selection of food at the beginning due fasting. On the other hand, even in experiments where selection was observed, it would be reasonable to consider the fasting effect where consumers would look for specific nutritional items to satiate the effects of fasting, since it is known that fasting affects both physiology and behavior (Hughes & Dunkin, 1984; Morton & Chan, 1999; Miyazaki et al., 2000). Therefore, results of experiments on food selection disregarding fasting, especially those restricted to a single experimental phase, may present results due to the procedural effect of fasting rather than selection.

In addition to gain a better understanding of fasting effects on feeding ecology, it is necessary that it is included in the discussions of experimental design for feeding preference studies. Based on the ongoing

**Table 2** Chemical composition of mangrove plant leaves at different age/stages (*M* mature, *S* senescent, *D* decomposing)

| | *A. schaueriana* | | | *L. racemosa* | | | *R. mangle* | | |
|---|---|---|---|---|---|---|---|---|---|
| | M | S | D | M | S | D | M | S | D |
| Polyphenol (%) | 0.68 | 1.13 | 0.59 | 11.97 | 15.68 | 5.79 | 7.50 | 10.03 | 2.80 |
| Lignin (%) | 9.52 | 9.76 | 11.64 | 10.16 | 7.36 | 15.56 | 6.88 | 9.24 | 11.12 |
| Cellulose (%) | 13.88 | 20.04 | 22.46 | 10.84 | 11.14 | 5.64 | 10.32 | 9.16 | 8.58 |
| Hemicellulose (%) | 20.4 | 12.5 | 13.1 | 8.7 | 10.3 | 14.6 | 45 | 45.5 | 58.9 |
| N (g $kg^{-1}$) | 22.5 | 9.8 | 8.8 | 13.7 | 6.9 | 6.9 | 15.7 | 7.8 | 6.9 |
| P (g $kg^{-1}$) | 2.1 | 1 | 0.8 | 1.7 | 1.2 | 0.9 | 1.3 | 0.8 | 0.4 |
| K (g $kg^{-1}$) | 28 | 10.2 | 7.6 | 14.1 | 10.1 | 1.6 | 9.3 | 8.1 | 0.7 |
| Ca (g $kg^{-1}$) | 3.3 | 6.6 | 5.9 | 7.4 | 8.1 | 9.4 | 8.3 | 9.7 | 12.5 |
| Mg (g $kg^{-1}$) | 8 | 12 | 13 | 3.1 | 2.4 | 2.6 | 4.3 | 5.1 | 3.5 |
| S (g $kg^{-1}$) | 2.5 | 2.7 | 2.8 | 1.5 | 1.5 | 1.5 | 2.3 | 1.9 | 1.8 |
| B (mg $kg^{-1}$) | 59 | 56 | 63 | 41 | 42 | 44 | 49 | 62 | 74 |
| Cu (mg $kg^{-1}$) | 1 | 0 | 0 | 0 | 4 | 6 | 0 | 0 | 0 |
| Fe (mg $kg^{-1}$) | 191 | 524 | 642 | 887 | 1160 | 3350 | 68 | 94 | 583 |
| Mn (mg $kg^{-1}$) | 133 | 280 | 290 | 119 | 138 | 151 | 280 | 510 | 400 |
| Zn (mg $kg^{-1}$) | 20 | 15 | 8 | 15 | 16 | 27 | 4 | 2 | 3 |

**Fig. 2** Principal coordinate analysis (PCoA) matching data on chemical components of leaves at different age (*M* mature, *S* senescent, *D* decomposing), independent of their species, at the second post-fasting period (24–48 h)




debate regarding such experimental designs (see Peterson & Renaud, 1989; Underwood et al., 2004; Underwood & Clarke, 2005, 2006; Manly, 2006; Taplin, 2007), we assume that we have not tested "preference" in the present study, since we used a multiple-choice experiment and made no test for consumption of a specific treatment offered alone. Thus, our design does not test preference among prey, but the selection of different leaves when available in the same amount and at the same time. However, our results still highlight the changes in selection over time and hence pose important questions which should be considered in discussions of design if artefacts are to be avoided.

Crabs began selecting food in the second post-fasting day, increasing consumption of items that are likely the most palatable and rejecting the least palatable specimens. Therefore, the high polyphenol concentration present in senescent leaves explains why they were less consumed than those at other age/stages. Polyphenols are known to be astringent substances that are part of plant defense mechanisms against herbivores (Godoy et al., 1997; Kandil et al., 2004). Other mangrove crabs prefer leaves with lower polyphenol content (Micheli, 1993a). In the second post-fasting phase, crabs started selecting other leaf characteristics, such as higher N, P, K, and cellulose content.

The crab *U. cordatus* consumed *A. shaueriana* rather than *R. mangle*, in contrast to the results of a study by Nordhaus & Wolff (2007) who reported *R. mangle* as the preferred food species. In the present study, the preference of crabs for decomposing *L. racemosa* leaves and the reduced selection of *R. mangle* leaves show that, in addition to the presence of polyphenols and macronutrients, other factors may have affected food selection, such as texture, color, and even the palatability provided by other chemical components. A more thorough investigation of crab physiology and its energy requirements, as well as detailed studies on the influence of elements such as Fe, Cu, Zn, Mn on leaf palatability, may help to explain food selection. Corrêa et al. (2005) found that Mn and Cr oxides in the environment can affect physiological processes in *U. cordatus*, high Mn levels being toxic to this species. This explains the lower consumption of *R. mangle* leaves by *U. cordatus* in the present study due to their high Mn content in senescent and decomposing leaves. Also, these results highlight the importance of studies on the nutrient value of food rather than their systematic level. In this context, the differences in our findings from those of Nordhaus & Wolff (2007) may be related to geographical changes in nutrients contents for the same plant species. It is also important to consider the influence

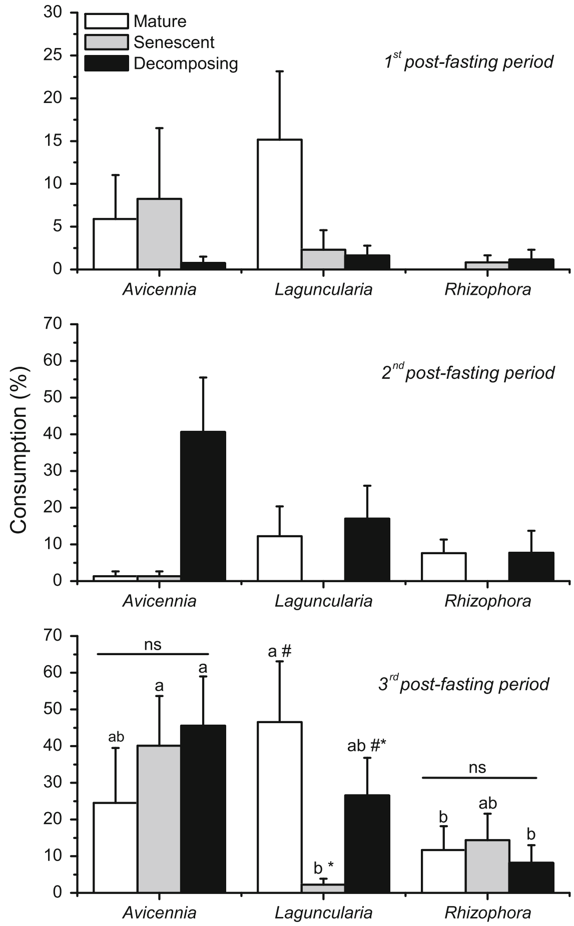



**Fig. 3** Leaf consumption (%) by the mangrove crab *U. cordatus* at the three different post-fasting periods according to the age of leaves from three mangrove species. At the third post-fasting period, SNK for the significant result of the leaf species × leaf age term of the ANOVA model are represented, where symbols indicate comparisons among leaf age for the same mangrove species and *letters* indicate comparison among mangrove species for the same leaf age. In both comparisons, *different symbols/letters* indicate significant differences ($P < 0.05$)

of fasting to standardize experiments to allow better comparisons.

We found that the food selection of *U. cordatus* for mangrove leaves generally followed the pattern observed in other *Grapsidae* and *Sesarmidae* species, in which N, P, and polyphenols are the main variables associated with selection and diet composition (Camilleri, 1989; Lee, 1989; Micheli, 1993a, b; Ashton, 2002). Also, the increased feeding activity of juvenile crabs may be associated with the energy demands needed for growth, since juvenile animals have high molting frequency (Pinheiro et al., 2005). Koch (1999) showed the importance of *U. cordatus* in mangrove energy flow, considering total community biomass, and energy differences between primary production and consumption/respiration of mangrove species. The results of the present study confirm that *U. cordatus* plays a significant role at the bottom of the food chain and in mangrove nutrient cycling. Accordingly, the commercial use of this species must be well planned because overexploitation can diminish its population and cause a serious ecological impact on the mangrove. According to Nascimento (1993), mangrove leaves carried by *U. cordatus* to its burrow are decomposed by fungi and bacteria, which in turn produce proteins that enrich this food. Our captivity experiments with this species reveal a strong association between food preference and the chemical characteristics of leaves, as observed in earlier studies for other species (Camilleri, 1989; Micheli, 1993a; Chan & Ye, 2008; Erickson et al., 2008). Thus, reduced foraging activity in *U. cordatus* could change nutrient content in the mangrove, decreasing decomposition of fragmented organic matter as well as its availability to detritivorous crabs and other components of mangrove fauna.

Given the above-mentioned arguments, we can assert that the feeding choices of *U. cordatus* are mainly driven by low polyphenol levels and high macronutrient content obtained from *A. schaueriana* leaves and mature and decomposing *L. racemosa* leaves. The chemical properties of the leaves as well as space/temporal variations in litter availability and composition can affect the feeding activity of *U. cordatus* in mangrove areas and is certainly associated with the development of this species. More studies on this issue are necessary to assess the effects of specific chemical elements in *U. cordatus* nutrition and provide a background to enable the formulation of a specific and balanced diet that is suitable to optimize crab growth and weight gain in captivity. This may shorten the time required for crabs to reach commercial size, as reported in other studies (Pinheiro et al., 2005; Diele & Koch, 2010). Also, despite leaf age and species choice, mangrove leaves remain an insubstantial diet for some crabs, which require protein from elsewhere (Skov & Hartnoll, 2002). Hence, studies on the physiological capacity of digestion of leaves and also the absorption of protein from other prey are

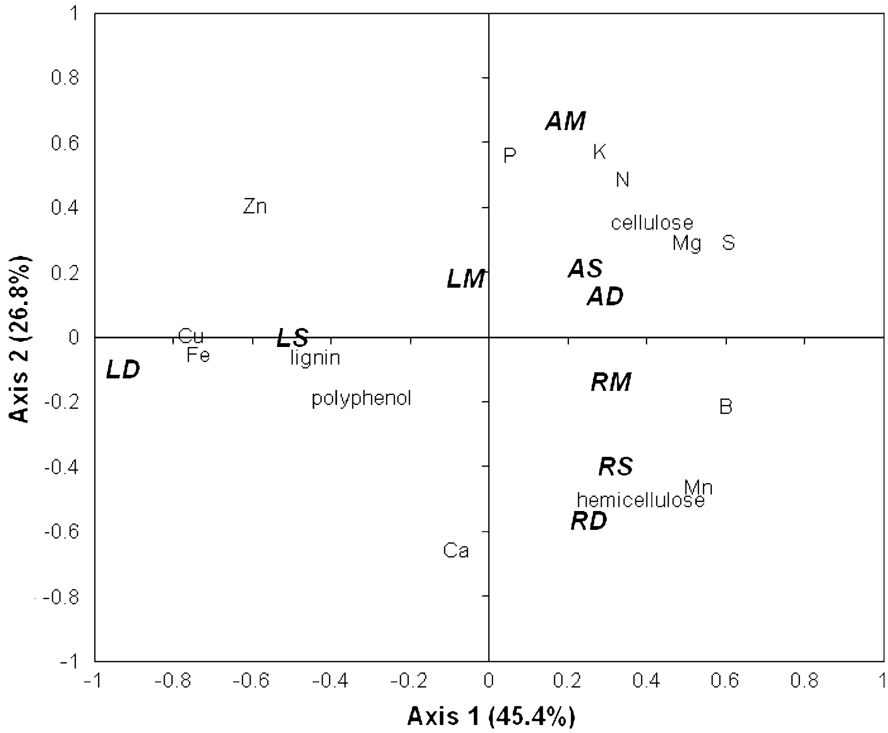



**Fig. 4** Principal coordinate analysis (PCoA) matching data on chemical components of leaves of different species (A = *A. schaueriana*, L = *L. racemosa* and R = *R. mangle*) and at different age (*M* mature, *S* senescent, *D* decomposing) at the third post-fasting period (48–72 h)

necessary in this species, to gain greater understanding of its ecological and phylogenetic importance.

**Acknowledgments** The authors thank all the colleagues who help in both field and laboratory activities, especially B. Sant'Anna, C. Cordeiro, and T. Sabanelli; and the anonymous referees and editor by the valuable suggestions in an early version of the manuscript. Financial support was provided by Fundação de Amparo à Pesquisa do Estado de São Paulo—FAPESP (R.A.C.-# 2002/11580-3; and M.A.A.P. # 2002/05614-2), Fundação Biodiversitas—Programa de Espécies Ameaçadas de Extinção (M.A.A.P. # 020I/012004), and Pró-Reitoria de Pesquisa—PROINTER/PROPe/UNESP (M.A.A.P # 49/2011).

## References

Amouroux, J. M. & M. Tavares, 2005. Natural recovery of Amazonian mangrove forest as revealed by brachyuran crab fauna: preliminary description. Vie et Milieu-Life and Environment 55: 71–79.

Ashton, E. C., 2002. Mangrove sesarmid crab feeding experiments in Peninsular Malaysia. Journal of Experimental Marine Biology and Ecology 273: 97–119.

Bataglia, O. C., A. M. C. Furlani, J. P. F. Teixeira, P. R. Furlani & J. R. Gallo, 1983. Métodos de análises químicas de plantas. Boletim Técnico do Instituto Agronômico de Campinas 78: 48.

Boer, W. F., 2000. Biomass dynamics of seagrasses and the role of mangrove and seagrass vegetation as different nutrient sources for an intertidal ecosystem. Aquatic Botany 66: 225–239.

Branco, J. O., 1993. Aspectos ecológicos do caranguejo *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Decapoda) do manguezal do Itacorubi, Santa Catarina, Brasil. Arquivos de Biologia e Tecnologia 36: 133–148.

Camilleri, J. C., 1989. Leaf choice by crustaceans in a mangrove forest in Queensland. Marine Biology 102: 453–459.

Cannicci, S., D. Burrows, S. Fratini, T. J. Smith III, J. Offenberg & F. Dahdough-Guebas, 2008. Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. Aquatic Botany 89: 186–200.

Chen, G. & Y. Ye, 2008. Leaf consumption by *Sesarma plicata* in a mangrove forest at Jiulongjiang Estuary, China. Marine Biology 154: 997–1007.

Christofoletti, R. A., V. A. Murakami, D. N. Oliveira, R. E. Barreto & A. A. V. Flores, 2010. Foraging by the omnivorous crab *Pachygrapsus transversus* affects the structure of assemblages on sub-tropical rocky shores. Marine Ecology Progress Series 420: 125–134.

Clough, B. F., D. T. Tan & D. X. Phuong, 2000. Canopy leaf area index and litter fall in stands of the mangrove *Rhizophora apiculata* of different age in the Mekong Delta, Vietnam. Aquatic Botany 66: 311–320.

Conde, J. E., M. M. P. Tognella & E. T. Paes, 2000. Population and life history features of the crab *Aratus pisonii* (Decapoda: Grapsidae) in a subtropical estuary. Interciência 25: 151–158.

Corrêa Jr, J. D., M. R. Silva, A. C. B. Silva, S. M. A. Lima, O. Malm & S. Allodi, 2005. Tissue distribution, subcellular localization and endocrine disruption patterns induced by

Cr and Mn in the crab *Ucides cordatus*. Aquatic Toxicology 73: 139–154.

Diele, K. & V. Koch, 2010. Growth and mortality of the exploited mangrove crab *Ucides cordatus* (Ucididae) in N-Brazil. Journal of Experimental Marine Biology and Ecology 395: 171–180.

Emmerson, W. D. & L. E. McGwynne, 1992. Feeding and assimilation of mangrove leaves by the crab *Sesarma meinerti* de Man in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. Journal of Experimental Marine Biology and Ecology 157: 41–53.

Erickson, A. A., I. C. Feller, V. J. Paul, L. M. Kwiatkowski & W. Lee, 2008. Selection of an omnivorous diet by the mangrove tree crab *Aratus pisonii* in laboratory experiments. Journal of Sea Research 59: 59–69.

Fausto-Filho, J., 1968. Crustáceos decápodos de valor comercial ou utilizados como alimento no nordeste brasileiro. Boletim da Sociedade Cearense de Agronomia 9: 27–28.

Fleck, D. C. & J. N. Layne, 1990. Variation in tannin activity of acorns of seven species of central Florida oaks. Journal of Chemical Ecology 16: 2925–2934.

Geraldes, M. G. & I. B. Calventi, 1983. Estudios experimentales para el mantenimiento en cautiverio del cangrejo *Ucides cordatus*. Ciência Interamericana 23: 41–53.

Godoy, S. A. P., M. A. S. Mayworm, V. K. Lo, A. Salatino & Y. Schaeffer-Novelli, 1997. Teores de ligninas, nitrogênio e taninos em folhas de espécies típicas de mangue. Revista Brasileira de Botânica 20: 35–40.

Hernes, P. J., R. Benner, G. L. Cowie, M. A. Goñi, B. A. Bergamaschi & J. I. Hedges, 2001. Tannin diagenesis in mangroves leaves from a tropical estuary: a novel molecular approach. Geochimica et Cosmochimica Acta 65: 3109–3122.

Hughes, R. N. & S. de B. Dunkin, 1984. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. Journal of Experimental Marine Biology and Ecology 77: 45–68.

Ivo, C. T. C. & T. C. V. Gesteira, 1999. Sinopse das observações sobre a bioecologia e pesca do caranguejo-uçá, *Ucides cordatus cordatus* (Linnaeus,1763), capturado em estuários de sua área de ocorrência no Brasil. Boletim Técnico-Científico do CEPENE 7: 9–52.

Kandil, F. E., M. H. Grace, D. S. Seigler & J. M. Cheeseman, 2004. Polyphenolics in *Rhizophora mangle* L. leaves and their changes during leaf development and senescence. Trees 18: 518–528.

Koch, V., 1999. Epibenthic production and energy flow in the Caeté mangrove estuary, North Brazil. Doctor's Thesis of the Center for Tropical Marine Ecology, University Bremen, Bremen: 97 p.

Koch, V. & M. Wolff, 2002. Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. Marine Ecology Progress Series 22: 119–130.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. Journal of Sea Research 59: 30–43.

Lee, S. Y., 1989. The importance of sesarminae crabs *Chiromanthes* ssp. and inundation frequency on mangrove (*Kandelia candel* Druce) leaf litter turnover in a Hong Kong tidal shrimp pond. Journal of Experimental Marine Biology and Ecology 131: 23–43.

Legendre, P. & L. Legendre, 1998. Numerical Ecology, 2nd ed. Elsevier, Amsterdam.

Linton, S. M. & P. Greenaway, 2007. A review of feeding and nutrition of herbivorous land crabs: adaptations to low quality plant diets. Journal of Comparative Physiology B 177: 269–286.

López, M. S., R. Coutinho, C. E. L. Ferreira & G. Rilov, 2010. Predator-prey interactions in a bioinvasion scenario: differential predation by native predators on two exotic rocky intertidal bivalves. Marine Ecology Progress Series 403: 101–112.

Manly, B. J., 2006. On a proposed method for analysing experiments on food choice. Journal of Experimental Marine Biology and Ecology 335: 154–155.

McClintock, J. B. & J. M. Lawrence, 1985. Characteristics of foraging in the soft-bottom benthic starfish *Luidia clathrata* (Echinodermata: Asteroidea): prey selectivity, switching behavior, functional responses and movement patterns. Oecologia 66: 291–298.

Micheli, F., 1993a. Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. Journal of Experimental Marine Biology and Ecology 171: 165–186.

Micheli, F., 1993b. Effect of mangrove litter species and availability on survival, moulting, and reproduction of the mangrove crab *Sesarma messa*. Journal of Experimental Marine Biology and Ecology 171: 149–163.

Micheli, F., F. Gherardi & M. Vannini, 1991. Feeding and burrowing ecology of two East African mangrove crabs. Marine Biology 111: 247–254.

Miyazaki, T., R. Masuda, S. Furuta & K. Tsukamoto, 2000. Feeding behaviour of hatchery reared juveniles of the Japanese flounder following a period of starvation. Aquaculture 190: 129–138.

Morton, B. & K. Chan, 1999. Hunger rapidly overrides the risk of predation in the subtidal scavenger *Nassarius siquijorensis* (Gastropoda: Nassariidae): an energy budget and a comparison with the intertidal *Nassarius festivus* in Hong Kong. Journal of Experimental Marine Biology and Ecology 240: 213–228.

Nascimento, S. A., 1993. Biologia do caranguejo-uçá (*Ucides cordatus*). ADEMA-Administração Estadual do Meio Ambiente, Aracajú: 13–45.

Nordhaus, I. & M. Wolff, 2007. Feeding ecology of the mangrove crab *Ucides cordatus* (Ocypodidae): food choice, food quality and assimilation efficiency. Marine Biology 151: 1665–1681.

Nordhaus, I., M. Wolff & K. Diele, 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. Estuarine, Coastal and Shelf Science 67: 239–250.

Ostrensky, A., U. S. Sternhain, E. Brun, F. X. Wegbecker & D. Pestana, 1995. Análise da viabilidade técnico-econômica dos cultivos do caranguejo-uçá *Ucides cordatus* (Linnaeus, 1763) no litoral paranaense. Arquivos de Biologia e Tecnologia 38: 939–947.

Peterson, C. H. & P. E. Renaud, 1989. Analysis of feeding preference experiments. Oecologia 80: 82–86.

Pinheiro, M. A. A., A. G. Fiscarelli & G. Y. Hattori, 2005. Growth of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) (Brachyura: Ocypodidae) at Iguape, SP, Brazil. Journal of Crustacean Biology 25: 293–301.

Podani, J., 2000. Introduction to the Exploration of Multivariate Biological Data. Backhuys Publishers, Leiden.

Post, D. M., M. E. Conners & D. S. Goldberg, 2000. Prey preference by a top predator and the stability of linked food chains. Ecological Society of America 81: 8–14.

Prado, P. & K. L. Heck Jr, 2011. Seagrass selection by omnivorous and herbivorous consumers: determining factors. Marine Ecology Progress Series 429: 45–55.

Skov, M. W. & R. G. Hartnoll, 2002. Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? Oecologia 131: 1–7.

Slim, F. J., M. A. Hemminga, C. Ochieng, N. T. Jannink, E. C. Moriniére & G. Velde, 1997. Leaf litter removal by the snail *Terebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). Journal of Experimental Marine Biology and Ecology 215: 35–48.

Sousa, W. P. & B. J. Mitchell, 1999. The effect of seed predators on plant distributions: is there a general pattern in mangroves? Oikos 86: 55–66.

Taplin, R. H., 2007. Experimental design and analysis to investigate predator preferences for prey. Journal of Experimental Marine Biology and Ecology 344: 116–122.

Twilley, R. R., M. Pozo, V. H. Garcia, V. H. Rivera-Monroy, R. Zambrano & A. Bodero, 1997. Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador. Oecologia 111: 109–122.

Underwood, A. J. & K. R. Clarke, 2005. Solving some statistical problems in analyses of experiments on choices of food and on associations with habitat. Journal of Experimental Marine Biology and Ecology 318: 227–237.

Underwood, A. J. & K. R. Clarke, 2006. Response on a proposed method for analysing experiments on food choice. Journal of Experimental Marine Biology and Ecology 335: 151–153.

Underwood, A. J., M. G. Chapman & T. Crowe, 2004. Identifying and understanding ecological preferences for habitat or prey. Journal of Experimental Marine Biology and Ecology 300: 161–187.

Vasconcelos, E. M. S., J. A. Vasconcelos & C. T. C. Ivo, 1999. Estudo sobre a biologia do caranguejo-uçá *Ucides cordatus* (Linnaeus, 1763), capturado no estuário do Rio Curimatau (Canguaretama) no Estado do Rio Grande do Norte. Boletim Técnico-Científico do CEPENE 7: 85–116.

Wolcott, D. L. & T. G. Wolcott, 1987. Nitrogen limitation in the herbivorous crab *Cardisoma guanhumi*. Physiological Zoology 60: 262–268.

Wolff, M., V. Koch & V. A. Isaac, 2000. Trophic flow model of the Caeté mangrove estuary (North Brazil) with considerations for the sustainable use of its Resources. Estuarine, Coastal and Shelf Science 50: 789–803.