



El Colegio de la Frontera Sur

Forrajeo selectivo de *Aratus pisonii* sobre hojas de manglar en experimentos de laboratorio

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Con orientación en Manejo y Conservación de Recursos Naturales

Por

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para obtener el grado de **Maestro en Ciencias en Recursos Naturales y Desarrollo Rural**.

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Resumen

El cangrejo *Aratus pisonii* representa un vínculo importante entre los procesos de degradación de hojarasca y la productividad de manglares. Poco se sabe sobre preferencias y tasas de consumo sobre esta especie. En condiciones de laboratorio se evaluó la tasa de consumo y preferencia alimenticia del cangrejo *A. pisonii* sobre hojas de las especies *Rhizophora mangle* (mangle rojo), *Laguncularia racemosa* (mangle blanco) y *Avicennia germinans* (mangle negro) en dos condiciones foliares (verdes y senescentes). Los experimentos se desarrollaron en períodos de alimentación de 24, 48, 72 y 96 horas. Las muestras de cangrejos y hojas fueron colectadas en mayo de 2016 en manglar de borde de la laguna Mecoacán, Tabasco, México. La tasa de consumo en ambas condiciones foliares no mostró diferencias significativas entre sexo. Por especie de mangle en la condición verde se encontraron diferencias significativas entre *L. racemosa* y *A. germinans* ($P<0.04$). Con hoja senescente todas las especies de mangle mostraron diferencias significativas en la tasa de consumo ($P<0.01$). En la preferencia alimenticia no hubo diferencia significativa entre sexo en la condición verde. Con hoja senescente se encontraron diferencias entre hembras que consumieron *L. racemosa* y machos y hembras que consumieron *R. mangle* y *A. germinans* ($P<0.02$). En la preferencia por especie, en la condición verde *L. racemosa*-*A. germinans* y *R. mangle*-*L. racemosa* fueron significativamente diferentes ($P<0.01$ y $P<0.02$). En la condición senescente *L. racemosa*-*A. germinans* y *R. mangle*-*A. germinans* fueron significativamente diferentes ($P<0.01$ y $P<0.03$). En el contenido nutrimental *L. racemosa* en ambas condiciones foliares presentó mayor contenido de humedad (72.76 y 79.49 g/100 g) y mayor contenido energético (306.65 y 268.97 g/100 g). *A. germinans* y *R. mangle* presentaron el mayor contenido de fibra cruda en ambas condiciones foliares (23.09 y 19.52 g/100 g y 19.44 y 19.92 g/100 g respectivamente). La preferencia de alimentación del cangrejo sobre hojas de *L. racemosa* en ambas condiciones foliares difiere de lo reportado en otras investigaciones.

Palabras clave: preferencia, nutrientes, hoja, consumo, cangrejos

Capítulo I

Introducción

Los manglares son ecosistemas con alta riqueza biológica que proporcionan una gran variedad de recursos y servicios ambientales ocupando así un lugar privilegiado en el país (CONABIO 2008). Este tipo de vegetación se encuentra en la zona de inundación por mareas y forma parte importante de la interface entre el ambiente terrestre y marino (Agraz-Hernández et al 2007). A nivel mundial, México se encuentra entre los cuatro países con mayor extensión de manglares (CONABIO 2013), lo que hace de nuestro país uno de los más ricos en términos de recursos naturales, es decir, un país mega diverso (Llorente-Bousquets y Ocegueda 2008).

Estos sistemas sirven como barrera para el mantenimiento de hábitats costero-marinos y la provisión de alimento y refugio para una gran variedad de organismos a diferentes niveles tróficos. Además, juegan un papel muy importante al mantener la calidad del agua y la estabilidad de la línea de costa (Yáñez-Arancibia et al 1998; CONABIO 2008; 2009).

Las interacciones biológicas pueden influir diversos procesos que se desarrollan dentro de los ecosistemas, por ejemplo el ciclaje de nutrientes y agua, el flujo de energía a través de cadenas tróficas, y la descomposición de la materia orgánica, entre otros. La herbivoría es una actividad que permite a través del consumo de recursos vegetales, transformar esta materia en biomasa y desechos como la producción de heces que permite la transferencia y movimiento de energía a otros niveles tróficos. Lo cual puede influir directamente en la productividad de un ecosistema y sus ciclos de nutrientes (Boege y del Val 2011).

En cualquier ecosistema se desarrollan diversas interacciones biológicas, ya que no existen organismos que estén separados del entorno que los rodea. En el caso de los manglares, una de estas interacciones que tiene gran relevancia para este ecosistema

es la herbivoría. Generalmente, la herbivoría es baja en los manglares, y sólo la realizan organismos como insectos y crustáceos, debido a que estas plantas poseen gran cantidad de sustancias de olor y sabor desagradables, especialmente los taninos, así como la composición química de la hoja, que impiden cierto grado de herbivoría, pues poseen cantidades importantes de lignina y celulosa (Southwell y Bultman 1971; Beever et al 1979; Linton y Greenaway 2007; Kristensen et al 2008; Mchenga y Tsuchiya 2008).

La fauna bentónica asociada con los bosques de manglar está típicamente dominada por diversos decápodos enterradores, como los cangrejos sesármidos y los cangrejos violinistas. Estos son herbívoros que retienen, entierran, maceran e ingieren hojarasca y microalgas (Emmerson y Mcgwynne 1992; Lee 1997; Kristensen y Alongi 2006). Estas actividades previenen la pérdida de nutrientes y promueven los procesos de descomposición, donde la mayoría de los sesármidos y violinistas activamente cavan y mantienen madrigueras en el sedimento. Estas estructuras funcionan como refugio contra depredación y condiciones extremas, y en muchos casos como almacenaje de alimento (Giddins et al 1986; Warren 1990; Dittmann 1996).

En los manglares son abundantes los cangrejos de las familias Grapsidae, Sesarmidae y Ocypodidae (Cannicci et al. 2008), dicha abundancia se puede traducir en cantidades de material foliar que puede ser transformado. Las especies de las primeras dos familias son consideradas como herbívoras funcionales, por la gran cantidad de hojarasca que consumen, y además de consumir hojas del manglar consumen flores, tallos, frutos, raíces y propágulos (Ashton 2002).

En los manglares, la estructura trófica está basada principalmente en la producción de hojarasca y el procesamiento de la materia orgánica (Prahl et al 1990), parte de este procesamiento es realizado por los crustáceos, quienes a través de la fragmentación de la hojarasca, ayudan en el ciclo de nutrientes y el flujo de energía dentro y fuera de los

bosques de manglar (Nordhaus y Wolff 2007). Por ello, los cangrejos son considerados los principales agentes responsables de las tasas de reciclaje de hojarasca en los manglares, es decir, son responsables del movimiento de los nutrientes en las redes tróficas (Lee 2008). Así la acción de los herbívoros puede regular la productividad primaria y secundaria, además de ejercer un papel fundamental en las interacciones tróficas de los bosques de manglar (Robertson y Daniel 1989; Wolff et al 2000; Koch y Wolff 2002; Nagelkerken et al 2008).

Los manglares contribuyen con grandes cantidades de materiales orgánicos en forma de detritus a las lagunas costeras y estuarios, este aporte de detritus lo realizan a través de su defoliación natural (Flores et al 2007). Este detritus se genera rápida y eficientemente gracias a la participación de herbívoros, quienes a partir del consumo transforman la hojarasca y producen heces. Esta transformación de hojarasca en fragmentos pequeños propicia la aparición de hongos y bacterias que aceleran la descomposición de la hoja, representando un recurso alimenticio a otros niveles tróficos dentro y fuera del manglar. Puesto que mucho de esta productividad se exporta en gran parte al medio acuático de zonas adyacente gracias a las corrientes y mareas, incorporando así una fuente importante de alimento para consumidores secundarios y pesquerías adyacentes (Bouillon et al 2008).

Un aspecto importante es la participación del cangrejo sesármido *Aratus pisonii* dentro de las redes alimenticias de los manglares, primero como consumidor primario y después como exportador de energía como presa (Beever et al 1979). El cangrejo *A. pisonii* es uno de los pocos cangrejos que se alimentan de hojas cuando aún están en la copa de los árboles, consumiendo hasta un 30-40 % de la hoja en los árboles (Erickson et al 2003), esta capacidad de alimentarse en el árbol ha cambiado de alguna manera los procesos naturales de descomposición de las hojas, acelerando los procesos de descomposición y dando lugar a un mejor aprovechamiento de los nutrientes en el manglar (Aké-Castillo et al 2006; Bouillon et al 2008; Cannicci et al 2008; Nagelkerken et al 2008).

Las investigaciones acerca del consumo y preferencia de alimentación del cangrejo *A. pisonii* se han basado principalmente de observaciones en campo y experimentos de laboratorio con análisis de contenido estomacal, experimentos de alimentación con diversos recursos alimenticios además de una especie de mangle (Beever et al 1979; Erickson et al 2003; López y Conde 2013), información que podría estar hablando más de comportamiento de alimentación y no de preferencia alimenticia (Underwood et al 2004), sin embargo, trabajos específicos con respecto a tasas de consumo no se han desarrollado.

Dada la importancia del cangrejo dentro de los sistemas de manglar como consumidor, transformador de material foliar y exportador de energía, este trabajo tuvo como objetivo de investigación determinar las tasas de consumo y preferencias alimenticias del cangrejo *Aratus pisonii* sobre las tres especies de mangle: *Rhizophora mangle* (mangle rojo), *Laguncularia racemosa* (mangle blanco) y *Avicennia germinans* (mangle negro) en dos condiciones foliares (verdes y senescentes) de manera experimental.

Este trabajo tuvo como hipótesis general:

Las tasas de consumo y preferencia alimenticia del cangrejo *Aratus pisonii* estará determinada por el grado de senescencia y palatabilidad de las hojas, donde se espera que las hojas senescentes sean preferidas y que la especie de mangle rojo (*Rhizophora mangle*) sea preferida debido a que contiene menor cantidad de lignina y celulosa.

Capítulo II

Artículo enviado

Selective foraging of *Aratus pisonii* on mangrove leaves in laboratory experiments

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Abstract

The feeding rate and feeding preference of the crab *Aratus pisonii* regarding three mangrove species leaves, red (*Rhizophora mangle*), white (*Laguncularia racemosa*) and black (*Avicennia germinans*), under two leaf conditions (green and senescent), were recorded in two laboratory experiments. Feeding rates were determined considering the dry weight of the food before feeding minus the dry weight of the remaining food after feeding, standardised on the fresh weight of each crab. A factor for the conversion of fresh weight to dry weight of each mangrove species and leaf condition was applied in order to obtain the dry weight of the food. Preferences were determined based on the consumption of one of the mangrove species when offered the three species simultaneously, under two leaf conditions. Results showed that the feeding rates of *A. pisonii* were high in the case of the fresh leaves of *A. germinans* ($0.03 \pm 0.06 \text{ g}_{\text{wdl}}/\text{g}_{\text{wwc}}$) and *R. mangle* ($0.02 \pm 0.03 \text{ g}_{\text{wdl}}/\text{g}_{\text{wwc}}$) and of the senescent leaves of *L. racemosa* ($0.05 \pm 0.04 \text{ g}_{\text{wdl}}/\text{g}_{\text{wwc}}$), indicating that the crab chose both green and senescent leaves of the species *L. racemosa*. Regarding sex, the females fed more in all the experiments. Feeding rates were: with fresh leaves, *A. germinans* and *R. mangle* (0.04 ± 0.06 and $0.03 \pm 0.03 \text{ g}_{\text{wdl}}/\text{g}_{\text{wwc}}$ respectively) and with senescent leaves, *L. racemosa* and *R. mangle* (0.06 ± 0.05 and $0.04 \pm 0.04 \text{ g}_{\text{wdl}}/\text{g}_{\text{wwc}}$ respectively). Feeding preferences were: with green leaves, *L. racemosa* ($0.06 \pm 0.06 \text{ g}_{\text{wdl}}/\text{g}_{\text{wwc}}$) and with senescent leaves, *L. racemosa* and *R. mangle* (0.05 ± 0.05 and $0.03 \pm 0.03 \text{ g}_{\text{wdl}}/\text{g}_{\text{wwc}}$ respectively). Under laboratory conditions, the crabs chose both green and senescent leaves of *L. racemosa* as food, and recorded greater feeding rates with fresh leaves of *A. germinans* and *R. mangle* when they had no other feeding option.

Key words: crab; *Laguncularia racemosa*; feeding rate; preference; leaf condition; nutrient cycling

1. Introduction

Mangroves are highly complex ecosystems on which a great number of species depend. Among their many attributes, the production of litterfall is outstanding as it constitutes a source of energy that is fundamental for the resident fauna, as well as for adjacent systems through the transportation of nutrients by currents and tides (Aké-Castillo et al., 2006; Feller and Chamberlain, 2007; Kristensen, 2008). This flow of energy is complemented by the role that several foraging species carry out when they accelerate the processes of energy transference among different trophic levels (Ashton, 2002). In mangrove ecosystems, one of the most important components in this flow of energy, that originates in the production of litterfall, are the diverse species of crabs that live there and participate in the decomposition of leaves through direct foraging, allowing the use of nutrients in the mangrove forest (Webber and Benfield, 1986; Nordhaus and Wolf, 2007). Crabs accelerate the decomposition of leaves through foraging and trituration of litterfall into small particles, allowing the use of nutrients in the mangrove more rapidly and before they are exported by the tides (Wolff et al., 2000; Koch and Wolff, 2002; Nagelkerken et al., 2008). However, the degree and intensity of feeding of the crabs on mangrove leaves depend on the concentration of nitrogen and tannins present. These compounds influence the choice of food, with crabs preferring food items

with low levels of tannins and high levels of nitrogen (Erickson et al., 2004; Nordhaus et al., 2011; Christofoletti et al., 2013).

Crabs are diverse and abundant in mangroves, particularly the species of the families Grapsidae, Sesarmidae and Ocypodidae (Cannicci et al., 2008). These families are considered to be functional herbivores due to the great amount of litterfall they consume, particularly the Grapsidae and Sesarmidae, as they eat flowers, stems, fruit, roots and propagules, apart from leaves (Ashton, 2002; Cannicci, et al. 2008). These crabs are thus considered to be the main agents responsible for recycling mangrove litterfall and for moving nutrients through the food chain (Lee, 2008).

Herbivore activity may regulate primary and secondary productivity, apart from playing a fundamental part in the trophic interactions in mangrove forests (Robertson, 1991; Wolff, Kolch and Isaac, 2000; Koch and Wolff, 2002; Nagelkerken, et al., 2008). Trophic structures in mangroves are based mainly on the production of litterfall and the processing of organic matter (Prahl et al., 1990). Part of this processing is carried out by crustaceans that, through fragmentation of litterfall, contribute to the nutrient cycle and the flow of energy within and outside of the mangroves (Nordhaus and Wolf, 2007).

The purpose of this study was to evaluate the feeding rate of the crab *Aratus pisonii* H. Milne Edwards, (1837), that lives among leaves of red mangrove (*Rhizophora mangle*) L. (Rhizophorae), black mangrove (*Avicennia germinans*) (L.) Stearn (Avicenniae) and white mangrove (*Laguncularia racemosa*) (L.) Gaertn. F. (Combrateceae), in experiments with two leaf conditions (green and senescent), in order to determine the dry weight (in grams) of the leaves that the crab may process in its natural habitat.

Feeding preference regarding the three mangrove species and the two leaf conditions was also examined.

2. Materials and Methods

2.1. Specimen collection

Aratus pisonii specimens were collected from a fringing mangrove in Laguna Mecoacán, Tabasco, at 93°04' - 93°14' W and 18°16' - 18°26' N. The specimens captured were placed in a plastic box measuring 70 x 41 x 33 cm long, wide and deep respectively, together with mangrove branches and water from the estuary for transportation.

In addition, green and senescent leaves of the three mangrove species present in the lagoon, *R. mangle*, *L. racemosa* and *A. germinans*, were collected.

2.2. Laboratory work

2.2.1. Fasting and conditioning

In order to build the microcosms, the method proposed by Salgado-Kent and McGuinness (2008) was applied, using 10 cm diameter and 14 cm high plastic containers. In order to maintain humidity, sponges with water from the estuary (salinity: 14-30 ups) were added. Fasting time before the experimental phase was 48 hours to standardise the level of hunger, and especially to empty the crabs' guts.

2.2.2. Feeding experiments

The method proposed by Salgado-Kent and McGuinness (2008) was modified. Three mangrove species leaves, of *R. mangle*, *L. racemosa* and *A. germinans*, under two leaf

conditions: fresh (green leaves on the tree) and senescent (yellow leaves on the tree), were provided as food at four feeding times (24, 48, 72 and 96 hours).

Before starting the feeding experiments, the leaves were washed under running water. In order to prevent bias due to different leaf size, these were cut into circular sections with a diameter of 2 cm (0.052 ± 0.006 g dry weight).

A total of 120 *A. pisonii* crabs were randomly chosen and placed in individual microcosms. Of these, 10 crabs were used for each type of leaf. The amount of food was one disk for every 24 hours, provided at each feeding time (24, 48, 72 and 96 hours).

At the start of the feeding experiment, the disks were weighed, the crabs were sexed, the female:male ratios were not the same in all the experiments, and the sexed crabs were measured and weighed. The disks were weighed after each feeding time to record the weight difference due to feeding.

The loss of leaf weight through feeding was converted to dry weight using a conversion factor that was calculated after drying 50 disks ($60^{\circ}\text{C}/48$ h) of each mangrove species (*R. mangle*, *L. racemosa* and *A. germinans*), both fresh and senescent. After obtaining the dry weight per species and leaf condition, the difference between the initial wet weight of the disk and the dry weight of the disk per mangrove species and leaf condition was calculated in order to obtain the loss of humidity as dry weight of each mangrove species and leaf condition. Rates of accumulated consumption (T_c) were calculated for each crab considering its initial fresh mass (mf), over the difference

between the initial dry mass and the dry weight of the disk after the feeding time (ms), as established by Nordhaus et al. (2011):

$$Tc = ms_{\text{of the leaf (g)}} / mf_{\text{of the crab (g)}}$$

where:

Tc: rate of accumulated consumption in relation to time

ms: dry mass of the consumed leaf

mf: initial wet fresh mass of the crab

The results were used to calculate the average rates of accumulated consumption per mangrove species, sex and feeding time.

The feeding experiment with senescent leaves was carried out in the same way as that with fresh leaves, choosing crabs randomly. It may be mentioned that the crabs were not used in more than two experiments in order to insure that they were in a good state and that the results of the experiments were not affected (Salgado-Kent and McGuinness, 2008).

2.2.2.3. Feeding preference

A total of 80 crabs were randomly chosen, placed in individual microcosms, and provided simultaneously with leaves of the three mangrove species (*R. mangle*, *L. racemosa* and *A. germinans*), under two leaf conditions (fresh and senescent), for each feeding time (24, 48, 72 and 96 hours). Each experiment had 10 repetitions. The food was provided at the same times as in the previous experiment.

2.3. Proximal chemical analysis of the leaf

A proximal chemical analysis of the mangrove leaves (fresh and senescent) was carried out to determine the nutrient content, humidity (g/100g), ash (g/100g), crude protein (g/100g), crude fiber (g/100g), lipids (g/100g), carbohydrates (g/100g) and energy content (kcal). The methods used were: for humidity: constant weight of the crucibles and drying of samples in a stove at 100°C/4 h (NOM-116-SSA1-1994); for ash: constant weight of the crucibles in a stove at 100°C/4 h and incineration in a muffle at 550°C/6 h (NMX-F-607-NOMRMEX-2002); crude protein: digestion for 100min/393°C, distillation with 1% boric acid and catalyst mixture, titration with 0,0493N valued sulfuric acid solution (METODO INTERNO ET-BR04); lipids: extraction with petroleum ether 7 h; crude fiber: acid/alkaline digestion in a kjeldahl Labconco equipment and use of a gooch crucible (NMX-F-613-NORMEX-2003). Carbohydrates were measured through calculation and the energy content through factors.

2.4. Statistical analyses

Feeding rates per mangrove species, sex and feeding times were analysed with a multiple ANOVA and the R statistical programme (Version 3.1.3). All the *post hoc* tests were carried out with a HSD Tukey test at a significance degree of $P<0.05$.

3. Results

3.1. Experiment I: Feeding rates on fresh and senescent leaves

The results obtained in this study prove that the crab *A. pisonii* eats fresh and senescent leaves of the three mangrove species, although mostly the senescent leaves. No significant differences were detected between females and males regarding feeding rates of fresh and senescent leaves ($P>0.144$ and $P>0.070$ respectively) (Fig. 1). Thus, the results of this first experiment are presented independently of specimen sex.

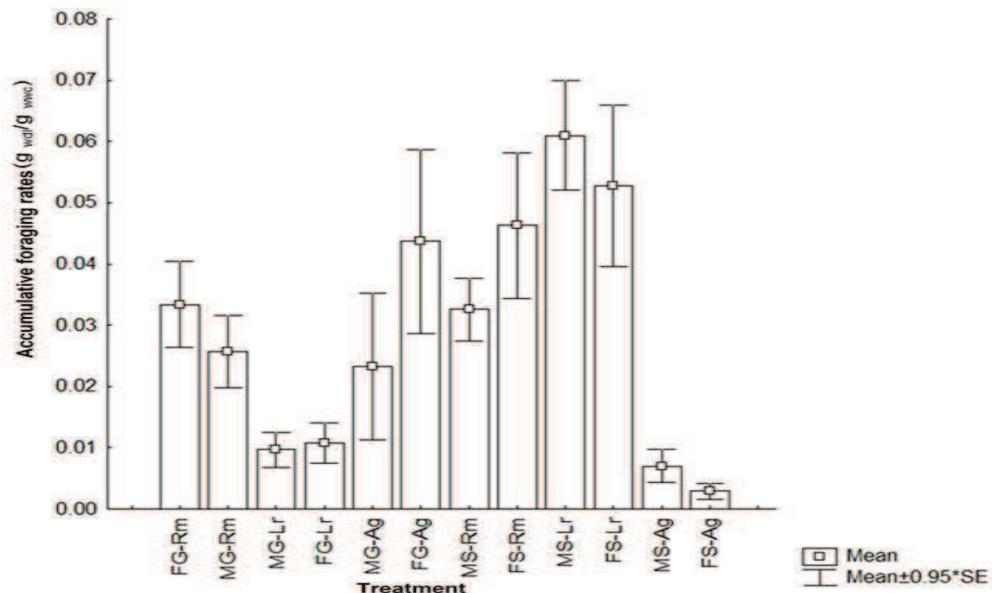


Figure 1. Feeding rate by sex female: (F) and male: (M), leave condition green: (G) and senescent: (S), and mangrove leave (Rm: *Rhizophora mangle*, Lr: *Laguncularia racemosa* y Ag: *Avicennia germinans*) Mean value \pm standard error (M \pm SE).

Regarding the fresh leaves, *A. germinans* and *R. mangle* presented the higher feeding rates (0.03 ± 0.06 and 0.02 ± 0.03 g_{wdl}/g_{wwc} respectively) throughout the experiment,

whereas in the case of the senescent leaves, *L. racemosa* and *R. mangle* had the higher feeding rates (0.05 ± 0.04 and 0.03 ± 0.03 g_{wdl}/g_{wwc} respectively). Significant differences in the feeding rates of the fresh and senescent leaves were obtained ($P<0.01$ and $P<0.00$ respectively). Differences when using the fresh leaves were recorded between *L. racemosa* and *A. germinans* ($P<0.046$), while differences were recorded among the three species in the case of the senescent leaves *L. racemosa-R. mangle*, *R. mangle-A. germinans* and *R. mangle-L. racemosa* ($P<0.01$, $P<0.01$ and $P<0.03$ respectively) (Fig. 2).

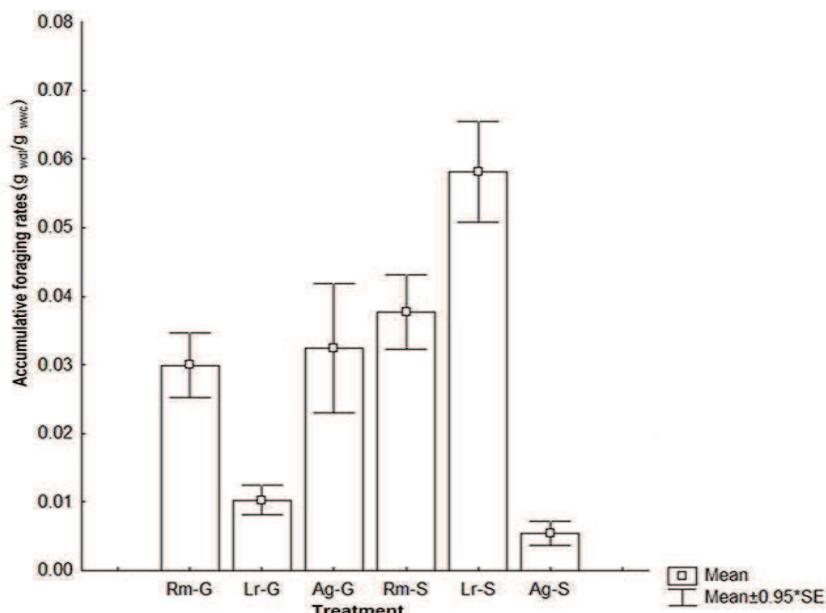


Figure 2. Grazing rate by mangrove leave (*Rm*, *Lr* y *Ag*) and leave condition (G and S) M±SE.

With respect to feeding time, *R. mangle* and *A. germinans* presented the highest feeding rates (0.03 ± 0.02 and 0.02 ± 0.05 g_{wdl}/g_{wwc} respectively) after 96 hours, while the lower

feeding rates were recorded for the fresh leaves of the three mangrove species 24 hours after feeding. In the case of the senescent leaves, feeding rates were high at all feeding times for *L. racemosa* and *R. mangle* (0.05 ± 0.03 and 0.03 ± 0.02 g_{wdl}/g_{wwc} respectively). Significant differences were recorded for the feeding rates of the fresh and senescent leaves ($P<0.01$ and $P<0.01$ respectively) (Fig.3).

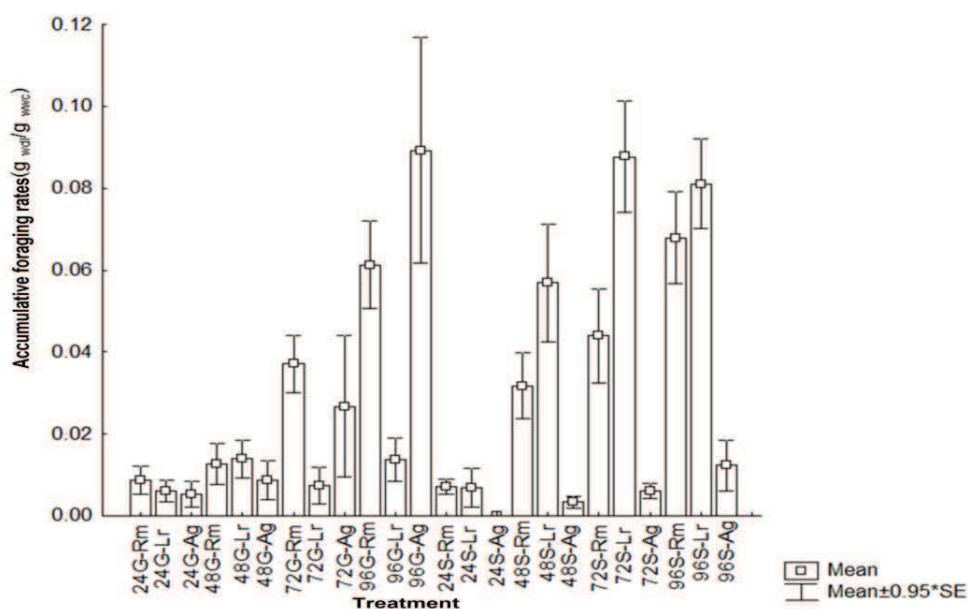


Figure 3. Grazing rate by time period (24, 48, 72 and 96 hours) and leave condition (G and S) M±SE.

3.3. Experiment II: Feeding preference with fresh and senescent leaves

The results obtained for the feeding preference of *A. pisonii* indicated that it preferred senescent leaves of the species *L. racemosa* and *R. mangle* and fresh leaves of *L. racemosa* as food. Regarding sex, a preferential feeding by the crabs showed significant differences with the use of senescent leaves ($P<0.01$), particularly between female: *L.*

racemosa-female: *A. germinans*, male: *A. germinans*-female: *L. racemosa*, male: *L. racemosa*-female: *L. racemosa* and male: *R. mangle*- female: *L. racemosa* with ($P<0.001$, $P<0.001$, $P<0.021$ and $P<0.027$ respectively). No significant differences were recorded for the fresh leaves ($P>0.486$) (Fig. 4).

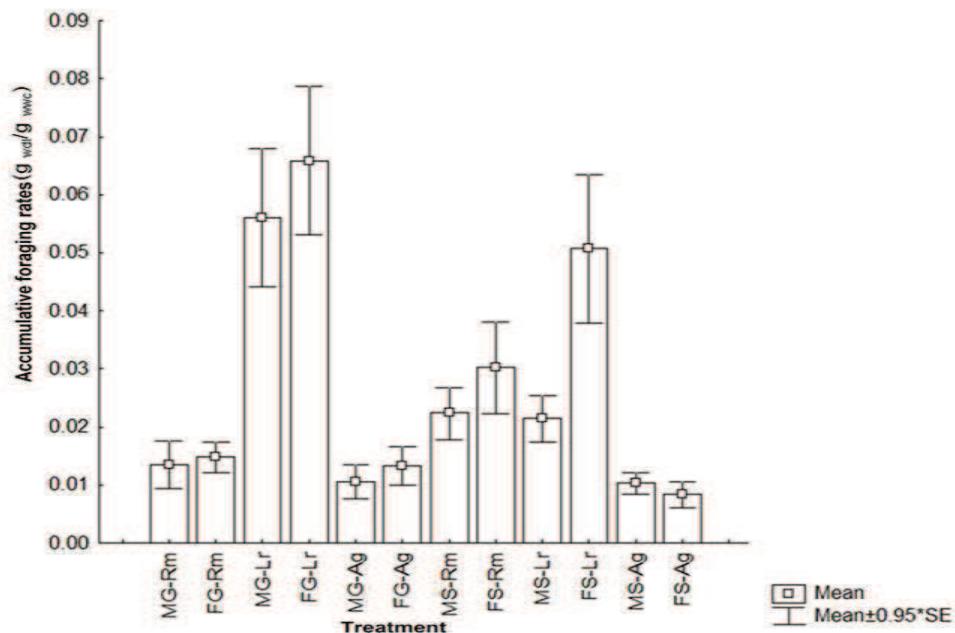


Figure 4. Cumulative grazing rate by crab sex (F and M), leave condition (G and S) and mangrove leave (Rm, Lr and Ag) $M\pm SE$.

The preferential feeding of the crab indicated that with fresh leaves it preferred *L. racemosa* leaves (0.06 ± 0.05 g_{wdl}/g_{wwc}), and with senescent leaves it preferred *L. racemosa* and *R. mangle* leaves (0.04 ± 0.03 g_{wdl}/g_{wwc} and 0.02 ± 0.02 g_{wdl}/g_{wwc} respectively). Differences were recorded in the preferential feeding both on fresh and senescent leaves ($P<0.01$ and $P<0.01$ respectively). Differences among the preferential feeding on the mangrove species with fresh leaves were recorded for *L. racemosa* - *A.*

germinans ($P<0.01$) and with senescent leaves for *L. racemosa* - *A. germinans* and *R. mangle* - *A. germinans* ($P<0.03$) (Fig. 5).

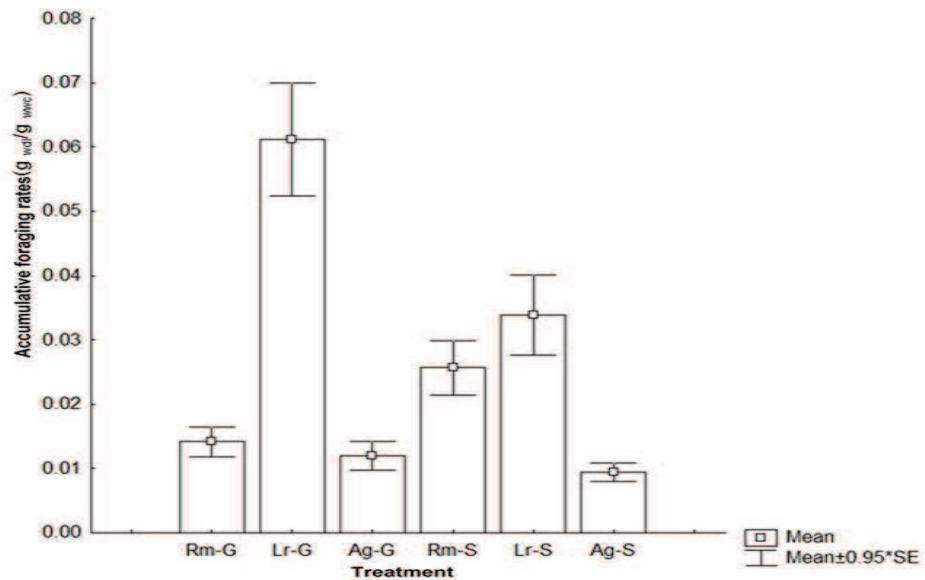


Figure 5. Feeding preference by mangrove leave (*Rm*, *Lr* and *Ag*) and leave condition (G and S) M±SE.

Feeding preference in the case of the fresh leaves was greater for *L. racemosa* at all feeding times (0.06 ± 0.04 g_{wdl}/g_{wwc}), whereas in the case of the senescent leaves, it was greater for *L. racemosa* and *R. mangle* at all times (0.03 ± 0.02 g_{wdl}/g_{wwc} and 0.02 ± 0.02 g_{wdl}/g_{wwc} respectively). The preferential feeding rate with fresh leaves did not present significant differences among feeding times ($P>0.053$), while with combined senescent leaves it did present significant differences ($P<0.001$), proving there were differences among the feeding times at 96:24, 96:48 and 96:72 ($P<0.001$, $P<0.001$ and $P<0.012$ respectively) (Fig. 6).

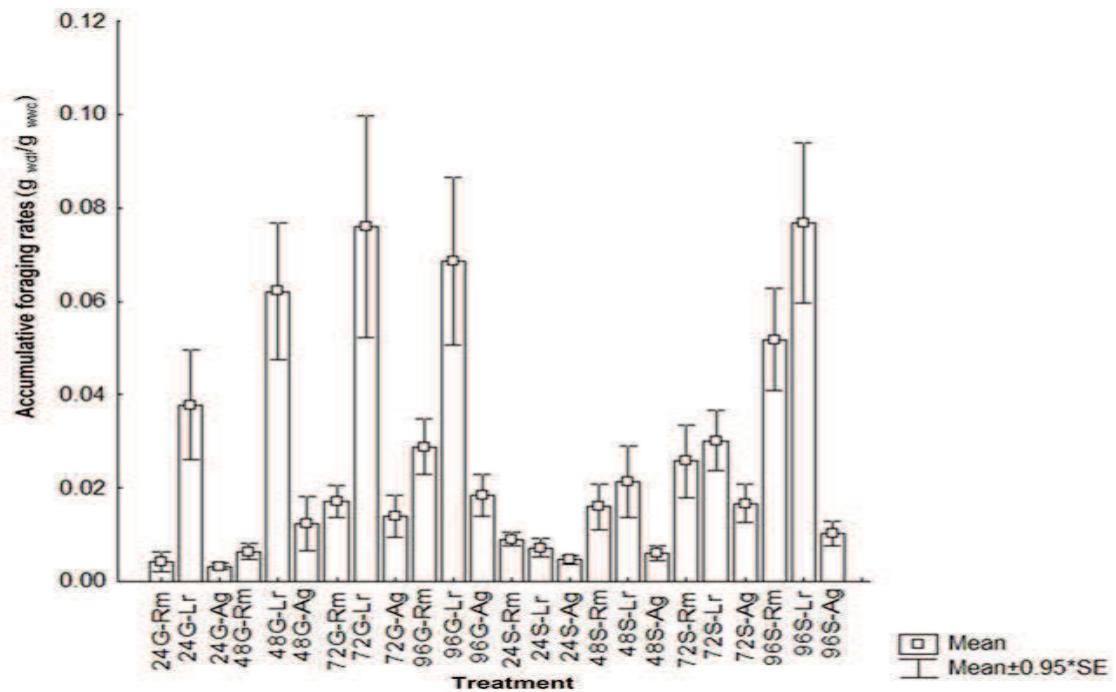


Figure 6. Feeding preference by time (24, 48, 72 y 96 hours), leave condition (G and S) and mangrove leave (Rm, Lr and Ag) M±SE.

3.4. Nutrient and energy content

Maximum values of crude fiber and protein were recorded for *A. germinans* fresh leaves (8.3 and 23.09 g/100g). Maximum values of lipid content were those of the senescent leaves of *R. mangle* (4.85 g/100g). Maximum values of carbohydrates were those of the fresh leaves of *L. racemosa* (63.79 g/100g). And maximum values of energy content were those of *L. racemosa* (306.65 Kcal) fresh leaves (Table 1).

Table 1. Nutritional and energetic content of mangrove leave condition.

Nutritional	<i>Rhizophora mangle</i>		<i>Laguncularia racemosa</i>		<i>Avicennia germinans</i>	
	Green	Senescent	Green	Senescent	Green	Senescent
Leave condition						
Moisture ¹	62.94	65.12	72.76	79.49	63.98	54.74
Ash ¹	10.72	11.58	14.25	22.09	16.89	16.80
Protein ¹	5.07	2.74	5.98	2.70	8.38	3.56
Fiber ¹	19.94	19.92	12.90	15.61	23.09	19.52
Fate ¹	3.62	4.85	3.06	3.96	3.44	4.42
Carbohydrate ¹	60.63	60.89	63.79	55.61	48.17	55.67
Energetic content (Kcal)	295.44	298.20	306.65	268.97	257.26	276.82

¹Equivalent percentage to g/100g

4. Discussion

4.1 Feeding rates

Previous studies on feeding rates of the crab *A. pisonii* feeding on mangrove leaves have mostly focused on feeding preferences based on stomach content analyses (Brogim and Lana, 1997; Erickson et al., 2003; López and Conde, 2013), on field observations and on experiments on preference using only one mangrove species (Beever et al., 1979; Erickson et al., 2008; Riley et al., 2014). This study is the first to carry out an experiment on the feeding rate of *A. pisonii* feeding on three mangrove species.

The results obtained in this study, particularly regarding feeding rates, indicated that both the females and males of this crab feed on the three mangrove species and leaf conditions (Fig. 1). Erickson et al. (2003), in Florida, also recorded both females and males feeding on the three mangrove species, although preferably on *R. mangle*.

Fresh leaves of *A. germinans* and *R. mangle* presented the greater feeding rates of the three mangrove species, with 20 and 17 % respectively. Erickson et al. (2003) recorded 20 to 30% damage to *R. mangle* in the field, through *A. pisonii* feeding. Erickson et al. (2008) established an omnivorous diet for the crab under laboratory conditions, recording a feeding of 5 % on fresh *R. mangle* leaves. Our results establish a capacity to feed via herbivory on mangrove leaves that is reflected in greater transformation or decomposition rates of litterfall in the natural habitat of the crabs via detritus, which then becomes available to organisms in other trophic levels (Bouillon et al., 2008; Kristensen et al., 2008).

The greater feeding rates were recorded with senescent leaves of *L. racemosa* and *R. mangle* at rates of 39 and 24 % respectively. In contrast with fresh leaves, feeding on senescent leaves was greater. According to several authors, the food quality of these leaves increases after they lose part of the chemical components that render them unpalatable to crabs, such as tannins and polyphenols, and their carbon:nitrogen ratio decreases to equal or less than 17:1 in order to become palatable (Russell-Hunter, 1970). This is important, as greater quality food provides the nutrients and energy the crabs require for adaptation and, particularly, reproductive activities (Giddins et al., 1986; Erickson et al., 2004; Nordhaus et al., 2011).

Studies have shown that a leaf, after being in estuarine water for more than 20 hours, begins to lose structural components through lixiviation, and increases in quality and palatability (Erickson et al., 2004; Nordhaus et al., 2013). Regarding our feeding rates and feeding times, the senescent leaves of *L. racemosa* and *R. mangle* presented the

highest feeding rates at all feeding times (24, 48, 72 and 96 hours) and with respect to the degree of feeding (13, 53, 54 and 37%, and 12, 28, 26 and 30 % respectively). In the case of the fresh leaves, feeding rates were greater for *A. germinans* and *R. mangle* after 96 hours, with 39 and 29 % feeding respectively.

4.2 Feeding preference

Other studies on leaf condition carried out with different sesarmid crabs have reported a preference for senescent leaves. For example, Camilleri (1989) recorded that *Sesarma erythrodactyla* ate more senescent leaves of the species *Rhizophora stylosa* and *Brugueira gymnorhiza* than fresh leaves of the same species. Micheli (1993) observed in the laboratory that the crab *Sesarma messa* fed on senescent *Rhizophora stylosa* leaves. Micheli et al. (1991), in Kenia, recorded the crab *Neosarmatium smithii* (=*Sesarma smithii*) feeding more on old leaves than on senescent leaves of *Brugueira gymnorhiza* and *Avicennia marina*, as an indication that a greater degree of leaf decomposition provides a better quality leaf as food for crabs.

Together with recording the feeding rates of *A. pisonii* in this study, feeding preferences regarding the three types of mangrove leaves (*R. mangle*, *L. racemosa* and *A. germinans*) in two leaf conditions (fresh and senescent) were recorded. The preference for senescent leaves presented differences between males and females. *Laguncularia racemosa* was preferred by the females with 28.21% consumption, while the males preferred *R. mangle* with 17.44% consumption. *Avicennia germinans* recorded the lower feeding rates, with 6 and 7% for females and males respectively. In the case of the fresh

leaves, the preferred species of both sexes was *L. racemosa* with 51 and 39 % of the total proportion of food respectively (Fig. 4).

Previous studies have shown that the feeding preference of females and males is determined mainly by the chemical composition of the leaf and by reproductive and physiologic energy requirements. The diet of the females may be different from that of the males considering their adaptations and reproductive activities, while the males may have a wider and more varied food spectrum, although with a lower nutritional quality (Wolcott and O'Connor, 1992; Erickson et al., 2004; Nordhaus and Wolff, 2007). In our case, the preference shown by both sexes for senescent leaves of *L. racemosa* and *R. mangle* is determined mainly by the energy/nutrient content in the leaves. Christofoletti et al. (2013) mentioned that senescent leaves of *L. racemosa* and *R. mangle* had a lower content of lignin, cellulose and hemicellulose than *Avicennia* spp. In the natural habitat, the preference for these mangrove species may determine the rate of nutrient recycling within and outside of the mangrove systems, and the exportation of nutrients to higher levels in the trophic chains of mangroves (Bouillon et al., 2008; Kristensen et al., 2008).

Regarding the preference for fresh leaves, several studies have reported a preferential feeding by *A. pisonii* and other crab species for these, citing as an example the feeding on *L. racemosa* fresh leaves (Faraco and Da Cunha Lana 2004). Christofoletti et al. (2013), in Brazil, found that the crab *Ucides cordatus* preferred as food *L. racemosa* in a mature condition (fresh leaves on the tree) over other mangrove species. However, Beever et al. (1979), in Florida, recorded *A. pisonii* feeding on fresh *R. mangle* leaves

both in the field and in the lab. Erickson et al. (2003) analysed stomach contents in experiments and evaluated the food items of the crab in its natural habitat, recording *A. pisonii* feeding preferably on fresh *R. mangle* leaves and less on those of other mangrove species (*A. germinans* and *L. racemosa*). These results on feeding preference for fresh and senescent leaves provide a view to the ecological implications of *A. pisonii* in mangrove ecosystems, and to the importance of its role as a consumer considering its feeding rates and its preference for a type of food, which affects the recycling of nutrients that are made available through a more rapid decomposition of leaves and feces (Linton and Greenaway 2007; Ingraben and Dittmann 2008).

Christofoletti et al. (2013) worked with three mangrove species, three leaf conditions (fresh, senescent and decomposing) and the crab *Ucides cordatus*, and found that feeding preference was determined by a low polyphenol concentration. Thus, the crab preferred *A. germinans* and *R. mangle* which contain a lower amount of polyphenols, in comparison with *L. racemosa* which has a greater polyphenol content in both the fresh and the senescent leaves (11.97 and 15.68 g/100g). In contrast, in our study *A. pisonii* preferred *L. racemosa* with both leaf conditions. It may be stated that the energy requirements of the different species may differ, and that crabs like *A. pisonii*, that feeds mainly on leaves, have adapted or have developed morphological, physiological and behavioural adaptations in order to be able to feed efficiently as a herbivore (Wolcott and O'Connor, 1992).

4.3 Proximal chemical analysis

Finally, with respect to the nutrient content of the leaf, those that presented a greater energy/nutrient content were in relation to the crude protein in the fresh and senescent leaves of *A. germinans* with 8.389 and 3.562 g/100g respectively. Regarding lipids, all leaves presented similar values (3 to 5 g/100g). For carbohydrates, the maximum values were recorded for the fresh *L. racemosa* leaves (63.79 g/100g) and the fresh and senescent *R. mangle* leaves (60.635 and 60.890 g/100g respectively). This may prove that preference is defined by the nutrient content and chemical composition of the leaf.

The role of crabs in the recycling of nutrients in mangroves directly affects the properties and availability of organic carbon through different mechanisms, one of which is the assimilation and transference of litterfall through feeding. *Aratus pisonii* may cause a 30 to 40% damage to the leaves on the trees through feeding (Erickson et al., 2003). This means that the litterfall they consume later becomes feces that are available to detritivores. Feces pellets of crabs are rich in nitrogen, with particle sizes smaller than the original material (Kristensen et al., 2008; Thongtham et al., 2008).

The fragmentation of leaves also contributes to a faster decomposition of litterfall and to the best use of nutrients within the mangrove (Ashton, 2002; Imgraben and Dittmann, 2008). Nutrients provided by the organic matter that is generated by the decomposition of leaves and feces are incorporated into trophic chains and taken to other trophic levels, apart from representing an important subsidy to adjacent coastal areas (Bouillon et al., 2008; Kristensen et al., 2008).

Hassell and Southwood (1978) defined feeding preference as the proportion of the different food items in the diet, in relation to the proportion of the same foods in the habitat. For this reason, this study focused on testing the feeding and selectivity of the three mangrove species that are common in the areas where the crabs were collected, based on the idea that the crabs are omnivores (Brogim and Lana, 1997; Erickson et al., 2008; López and Conde, 2013; Riley et al., 2014) in order to determine feeding and preference.

As is known, crabs have energy requirements, for which reason a food item with a high level of nutrients (good quality) represents a better food resource (Wolcott and O'Connor, 1992; Erickson et al., 2004; Nordhaus and Wolff, 2007). Thus, together with fresh leaves, senescent leaves in an advanced leaf condition were included considering that, according to the literature, the nutritional quality of these is greater in response to a lower tannin content (Erickson et al., 2004). It is important to emphasise that in order to avoid confusion in the use of the term preference, Singer (2000) established that in order for preference to exist in the choice of food, three main characteristics have to be met: "preference" that describes the choice options of the consumers, "acceptability" that describes food properties, and "selectivity" that describes the properties of the interaction between the consumer and its food. According to Underwood et al. (2004), many ecological publications have reported preferences by organisms for a type of food or habitat, mistaking the term preference for association patterns. Regarding *A. pisonii*, several studies have stated that this species is found mainly in *R. mangle* forests (Beever et al., 1979; Díaz and Conde, 1989) where it prefers this mangrove species as food. This opens the possibility of studying the crab's use of the habitat in order to

determine why it inhabits a particular area. Another opportunity presented here is to quantify the degree and amount of assimilation and transference of energy from litterfall to detritus and to other trophic levels, as well as to other environments such as adjacent lagoons through exportation.

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Capítulo III

Conclusiones

De acuerdo con la hipótesis planteada, ésta se rechaza pues el cangrejo además de consumir *Rhizophora mangle* consumió *Avicennia germinans* en mayor cantidad. Y la preferencia se dió sobre hojas de la especie *Laguncularia racemosa* en ambas condiciones foliares. Estos resultados nos demuestran la plasticidad que posee el cangrejo *A. pisonii* para alimentarse de todas las especies de mangle.

Se demostró que el cangrejo *Aratus pisonii* se alimenta de todas las especies de mangle en condiciones de laboratorio; donde la mayor tasa de consumo se presentó sobre las especies de mangle *A. germinans* y *R. mangle* en condición verde de la hoja, estos datos nos dan un acercamiento sobre la cantidad de material foliar que el cangrejo puede llegar a transformar a partir del consumo en su hábitat natural, además de darnos pautas del importante papel que juega no sólo la especie *A. pisonii* dentro de los flujos energéticos en el manglar, si no de la fauna de cangrejos que ahí habitan.

En condición senescente de la hoja la especie *L. racemosa* presentó mayor tasa de consumo. Esta tendencia en cuanto a consumo por hojas en estado senescente, ha sido reportada por diversos autores, ya que la característica principal de hojas en estado senescente es que representan un recurso alimenticio de buena calidad para los cangrejos y así poder desarrollar actividades fisiológicas, reproductivas y de comportamiento.

Las tasas de consumo en el tiempo de alimentación nos dan un acercamiento de la cantidad de material foliar que el cangrejo puede transformar de manera natural, y en cuanto a las especies de mangle que presentan mayores tasas de consumo, nos indican sobre las especies que representan un recurso alimenticio para la especie *A. pisonii*. En esta investigación se encontró que el cangrejo presenta mayores tasas de consumo a las 96 horas de experimentación con hojas verdes de la especie *A. germinans*. Demostrando entonces que la especie de mangle *A. germinans* es otro

recurso alimenticio para la especie de cangrejo *A. pisonii*, a quien se le ha reportado se alimenta de la especie *R. mangle*.

En la preferencia de la alimentación el cangrejo *A. pisonii* mostró preferencia por hojas verdes de la especie *L. racemosa* con porcentajes de consumo del 51% y 39% para hembras y machos respectivamente. Estos datos nos indican que el cangrejo no prefiere como alimento a la especie de mangle *R. mangle*, como se ha reportado en diversas investigaciones. En este caso, como la preferencia fue hacia otra especie de mangle, posiblemente lo que se ha reportado en otras investigaciones son patrones de asociación de la especie *A. pisonii* hacia la especie *R. mangle* (mangle rojo), por lo que queda la posibilidad de desarrollar investigación especializada en cuanto a usos del hábitat.

Por otro lado, la preferencia de alimentación con hojas senescentes marcó una diferencia entre sexos, pues las hembras prefirieron como alimento hojas de *L. racemosa* (28.21 %) y los machos hojas *R. mangle* (17.44 %). Esta diferencias en la preferencia por sexo, se debe principalmente por los requerimientos energéticos de los cangrejos, la literatura ha descrito que las hembras tienen una dieta especializada en alimentos que pueden cubrir sus necesidades energéticas y los machos pueden tener una dieta más amplia aunque con baja calidad nutricional; en este caso las hojas de *L. racemosa* representó el recurso de mejor calidad para las hembras.

La especie *A. germinans* presentó mayor contenido de proteína cruda en condición verde y senescente con 8.38 y 3.56 g/100g respectivamente. El mayor contenido de carbohidratos lo presentó la especie *L. racemosa* en condición verde con 63.79 g/100 g, y senescentes de *R. mangle* 60.89 g/100 g respectivamente. Cabe mencionar que para poder establecer si existe alguna variación en cuanto al contenido nutrimental, de cada una de las especies de mangle y condición, es necesario desarrollar un trabajo donde se analicen las especies de mangle por temporada, y observar si existe algún patrón de cambio en cuanto a la preferencia y tasas de consumo, ya que en otros trabajos realizados, se ha encontrado que el contenido nutrimental de la hoja puede cambiar con

forme a la temporada del año, y puede modificar los patrones de alimentación de los organismos que se alimentan de hojas de manglar.

Estos resultados reflejan que el cangrejo *A. pisonii* es una especie clave tanto para las redes tróficas del manglar, como para los flujos energéticos en el ecosistema. A partir de estos datos generados se puede desarrollar investigaciones más amplias que incluya todos los componentes faunísticos del manglar, por ejemplo con especies cangrejo arbóreas como *A. pisonii* y especies semiterrestres como algunas especies de las familias Grapsidae, Ocypodidae y Sesarmidae, para poder tener el marco completo en cuanto al papel de los cangrejos desde diferentes niveles de observación, y cómo esta estructuración en el hábitat de las especies de cangrejos repercute directamente en la productividad de los sistemas de manglar.

Finalmente es de vital importancia reconocer el papel de la especie *Aratus pisonii* dentro de los ciclos de nutriente de manglares, su importante rol en las redes tróficas de estos ecosistemas los cuales repercuten de manera directa sobre la productividad de los ecosistemas de manglar, los cuales han sido reconocidos por las grandes aportaciones que hacen vía detrito, pero sin reconocer el papel fundamental de la fauna que participa dentro de estos procesos de transformación del material foliar.

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