Leaf removal by sesarmid crabs in Bangrong mangrove forest, Phuket, Thailand; with emphasis on the feeding ecology of Neoepisesarma versicolor

Nalinee Thongthama, Erik Kristensena,b,*, Som-Ying Puangprasana

Phuket Marine Biological Center, P.O. Box 60, Phuket 83000, Thailand
Institute of Biology, University of Southern Denmark, Campusvej 55, DK-5230 Odense M, Denmark

A R T I C L E   I N F O

Article info:
Article history:
Received 2 June 2008
Accepted 23 September 2008
Available online 4 October 2008

Keywords:
feeding ecology
behavior
leaf removal
mangrove
Neoepisesarma versicolor
Rhizophora apiculata
sesarmid crab

A B S T R A C T

Field measurements on leaf removal by populations of sesarmid crabs at different locations in the Bangrong mangrove forest, Phuket, Thailand, indicated that crabs on average can remove 87% of the daily leaf litter fall by ingestion or burial. The removal rate is correlated positively with the number of crab burrows and negatively with tidal inundation time. The results from the field were supplemented with observations on the behavior of Neoepisesarma versicolor in laboratory microcosms and a mangrove mesocosm. N. versicolor feeds primarily at night and total time spent feeding was up to an order of magnitude higher in the artificial microcosms than under simulated in situ conditions in the mesocosm. Most of the time during both day and night was spent resting near the entrance or inside burrows. N. versicolor mainly feeds on mangrove leaves and scraps of food material from the sediment surface. This is supported by examinations of stomach content, which showed that 62% is composed of higher plant material and 38% of detritus and mineral particles from the sediment. The nutritive value of leaves and detritus is insufficient to maintain crab growth. Sesarmid crabs may instead obtain the needed nutrients by occasional consumption of nitrogen-rich animal tissues, such as carcasses of fish and crustaceans, as indicated by the presence of animal remains in the stomach and the willingness of crabs to consume fish meat. Laboratory experiments on leaf consumption and leaf preferences of N. versicolor indicate that they preferentially feed on brown leaves, if available, followed by green and yellow leaves. If all species of sesarmid crabs in the Bangrong mangrove forest consume leaves at the same rate as N. versicolor, they could potentially ingest 52% of the total litter fall.

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1. Introduction

Tropical mangrove forests produce large amounts of litter, mostly in the form of senescent leaves (Twilley et al., 1992; Jennerjahn and Ittekkot, 2002). The nutrient-poor leaf detritus is ultimately decomposed by the action of bacterial and fungal communities. During the initial phase of the decomposition process, carbon is respired and nutrients are immobilized (Wafar et al., 1997; Ashton et al., 1999). Subsequently, the detritus acts as a major source of nutrients when transported to mangrove waterways and sediments. The mangrove litter is also an important source of food for marine animals in the coastal zone. Thus, most of the primary production in this very productive environment enters the detrital food chain (Wafar et al., 1997), while only a small fraction is exported seaward by tidal currents (Suraswadi, 2002). The subsequent release of nutrients from decaying mangrove litter ultimately forms the basis for primary production in the mangrove environment.

Brachyuran crabs, primarily fiddler crabs (family Ocypodidae) and leaf-eating sesarmid crabs (family Grapsidae), dominate the mangrove fauna in number and biomass (Tan and Ng, 1994; Kristensen, 2008). Leaf-eating sesarmid crabs are abundant in mangrove areas of the Indo-Pacific (Hartnoll, 1975; Ashton et al., 2003), Africa (Emmerson and McGwynne, 1992; Hartnoll et al., 2002) and to some extent America (Abele, 1973; Sheaves and Molony, 2000), whereas the leaf-feeding ocypodid crab, Ucides cordatus, is abundant in mangrove forests of the Central and South America (Nordhaus et al., 2006).

Many studies in Indo-Pacific mangrove forests have shown that sesarmid crabs consume mangrove leaf litter as their major food source (Steinke et al., 1993; Thongtham and Kristensen, 2005) since leaf fragments comprise 55–95% of their stomach content (Malley, 1978; Poovachiranon and Tantichudon, 1991). They consume leaves on the sediment surface or pull them into their burrows for later consumption (Slim et al., 1997). They may even climb trees during the night to consume leaves from the canopy (Fratini et al., 2005).
has been found that sesarmid crabs are capable of consuming >57% of the daily leaf litter production during their active season in Hong Kong mangrove forests (Lee, 1989). A similar trend was observed in Australia, where crabs remove 71–79% of the annual leaf fall to the forest floor (Robertson and Daniel, 1989). More recently, it was found that Ucides cordatus is capable of removing 81% of the litter fall in Brazilian mangrove forests (Nordhaus et al., 2006).

Leaf-eating crabs have a highly significant ecological role by burying or consuming leaves, which would otherwise be exported from the mangrove environment to the adjacent coastal area by tidal currents (Slim et al., 1996; Olafsson et al., 2002). They also assist the decomposer food chain by macerating or fragmenting leaf litter into small particles, providing easier access for microorganisms (Camilleri, 1992). Their faeces are active sites of microbial activity or serve as food for small detritivores and thus contribute to maintain closed nutrient cycles within the mangrove ecosystem (Lee, 1997; Kristensen and Pilgaard, 2001).

As many as 36 species of sesarmid crabs have been found in mangrove forests of Thailand (Majchacheep, 1973; Frith et al., 1976; Tantichodok, 1981). Two of the most common species, Neoposesarma versicolor (Tweedie) and Neoposesarma mederi, are widely caught for human consumption. They are called “salty crab” and are a delicacy for Thai people (Ng and Sivasothi, 1999). Although these leaf-eating crabs are economically important for local people in many mangrove areas of Thailand, their ecological role is not well known.

The objective of this study was to examine the feeding ecology of sesarmid crabs, particularly Neoposesarma versicolor, in the Bangrong mangrove forest, Phuket, Thailand. By a combination of field and laboratory experiments, we clarified central aspects of the feeding behavior of N. versicolor as well as its preference for and consumption of different categories of Rhizophora apiculata leaf litter (green, yellow and brown). The results provide new insight on the diet and feeding rhythm of this threatened sesarmid crab as well as its quantitative role for litter processing in mangrove environments.

2. Materials and methods

2.1. Study area and sampling sites

The field study as well as crab and leaf samplings were carried out from March to April 2000 in the Bangrong mangrove forest, on the northeastern coast of Phuket Island, Thailand (Fig. 1). The climate in the area is monsoonal with an annual precipitation of about 2300 mm. The dry season extends from December to April with air temperature of about 28°C. The vegetation within the forest consists of 3 stations ca. 20 m apart. Transect 1 was located close to a rubber plantation in a high-intertidal area with mixed vegetation of Rhizophora apiculata and Ceriops tagal. The C. tagal dominated transect 2 was located at a transition between the high- and mid-intertidal zone, while transects 3 and 4 were located in R. apiculata dominated mid-intertidal areas (Table 1). At each station, 3 replicate 9 m² plots were marked by plastic strings and further divided into 9 subplots of 1 m². All leaves present on the sediment surface were removed from all plots before the experiment started.

Three categories of Rhizophora apiculata leaves were used: green (fresh), yellow (senescent) and brown (partly decomposed). The green and yellow leaves were picked directly from trees, while brown leaves were collected from the forest floor. Yellow leaves were also defined as those easily abscissed from trees (Giddins et al., 1986). As the appearance and exact color of brown leaves can be classified to different stages of decomposition (Poovachiranon and Tantichodok, 1981), we attempted to choose dark brown leaves at similar stage for the experiment. Rhizophora apiculata leaves were used at all transects for comparative purpose.

Pre-weighed green, yellow and brown Rhizophora apiculata leaves were distributed with 3 leaves of one category in three randomly chosen 1 m² subplots per plot, thus providing 9 replicate subplots containing each leaf category at each station. Leaves were tied by their petiole to a fixed stick using nylon string to avoid loss of leaves by e.g. tidal currents. The strings were long enough to allow crabs taking whole leaves into their burrows. After 24 h, all still tethered leaf remains were collected, rinsed and dried at 105°C for 48 h. Simultaneously, the density of crab burrows were counted. The approximate duration of inundation at each station during the experimental period was determined using tide tables of the Hydrographic Department of the Royal Thai Navy for Bangrong Pier.

The initial fresh weight of leaves was converted to dry weight using regressions between dry (D) and fresh (F) weights obtained from 150 leaves of each category. Thus D/F was 0.34 (r² = 0.94) for green leaves; 0.35 (r² = 0.78) for yellow leaves; and 0.65 (r² = 0.62) for brown leaves. In addition, total carbon and nitrogen contents of the initial leaf material were determined on an Eager 200 CHN analyzer. The removal of leaves by crabs was calculated from the difference between estimated initial dry weight and measured final dry weight. Since litter fall was not prevented during the experiment, crab consumption of newly fallen leaves may have caused a minor underestimate of removal rates.

2.2. In situ leaf removal by crabs

The leaf removal capacity (i.e. immediate ingestion or translocation into burrows) of the sesarmid crab fauna was determined along 4 transects in the mid- to high-intertidal region of the Bangrong mangrove forest (Fig. 1). The transects were adjacent to areas where traps were positioned for simultaneous quantification of litter fall (Suraswadi, 2002). Each transect (60 m long), extended perpendicular from either the main creek or large side creeks into the forest and consisted of 3 stations ca. 20 m apart. Transect 1 was located close to a rubber plantation in a high-intertidal area with mixed vegetation of Rhizophora apiculata and Ceriops tagal. The C. tagal dominated transect 2 was located at a transition between the high- and mid-intertidal zone, while transects 3 and 4 were located in R. apiculata dominated mid-intertidal areas (Table 1). At each station, 3 replicate 9 m² plots were marked by plastic strings and further divided into 9 subplots of 1 m². All leaves present on the sediment surface were removed from all plots before the experiment started.

Observations on the behavior of the leaf-eating Neoposesarma versicolor were carried out both in the laboratory and in a mangrove mesocosm at Phuket Marine Biological Center from December 2000 to January 2001. Neoposesarma versicolor was chosen because it is the largest sesarmid species in the area and therefore easy to observe. The experimental laboratory microcosm consisted of a 50 × 50 × 50 cm glass aquarium containing an 8-cm deep layer of mangrove sediment in half of the bottom area, while the other half was covered by seawater (salinity 15‰) to a maximum depth of 5 cm. A tidal system simulated the natural tidal rhythms using a timer-controlled pump. The crabs were maintained at room
temperature (28–32 °C) and exposed to 12 h light:12 h dark cycles.

Three different leaves (green, yellow and brown) of Rhizophora apiculata were marked and placed on the sediment before a crab was released into the microcosm. The behavior of one crab was monitored continuously for 24 h using infrared video recordings and partitioned into the following activities: Eating (sediment or leaves of the different types), moving limbs, digging, crawling, resting (on sediment, in burrow or in water). The monitoring was done for 10 adult crabs of mixed sex and with a carapace length of 3–3.6 cm (15–35 g wet wt.). The various activities were recorded to the nearest minute and presented as mean percentage of total time during a 12-h light and a 12-h dark period, respectively.

The mesocosm was established in open air close to the seashore in a 2-m i.d. and 1-m high circular concrete frame. The original sediment within the frame was dug out and replaced with mangrove sediment to a depth of 1.5 m. Seawater (salinity 26–32‰) was allowed to pass through the system. About 40 propagules of Rhizophora apiculata were planted in the mesocosm and grown for 14 months before 25 individuals of Neoepisesarma versicolor were released. One month later, a video camera was attached near burrows for observation of crab behavior. The observations were conducted continuously during a 24 h day and night period for each of three crabs. The behavior was separated into the same activity types as in the laboratory microcosm experiment.

2.4. Leaf consumption rate and preference experiments

Leaf consumption (i.e. ingestion and sloppiness) and preference experiments were conducted in the laboratory between November 2000 and January 2001. Specimens of Neoepisesarma versicolor with a carapace width of 3–4 cm and weight between 20 and 43 g were collected in the Rhizophora apiculata dominated part of the Bangrong mangrove area. The crabs were acclimated to the laboratory conditions for two weeks prior to experiments. During this time they were fed fish meat and a mix of different phases of R. apiculata leaves. Only intact crabs having a hard carapace (i.e. in the intermolt stage) and carrying no eggs were used. The carapace width

<table>
<thead>
<tr>
<th>Station</th>
<th>Vegetation</th>
<th>Shading</th>
<th>Sediment</th>
<th>Inundation time (h per d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>R. apiculata</td>
<td>dense</td>
<td>silty-mud</td>
<td>4</td>
</tr>
<tr>
<td>1.2</td>
<td>C. tagal</td>
<td>open</td>
<td>sandy-mud</td>
<td>2</td>
</tr>
<tr>
<td>2.1</td>
<td>R. apiculata, C. tagal</td>
<td>dense</td>
<td>silty-mud</td>
<td>4</td>
</tr>
<tr>
<td>2.2</td>
<td>C. tagal</td>
<td>open</td>
<td>sandy-mud</td>
<td>2</td>
</tr>
<tr>
<td>2.3</td>
<td>C. tagal</td>
<td>dense</td>
<td>silty-mud</td>
<td>4</td>
</tr>
<tr>
<td>3.1</td>
<td>R. apiculata, C. tagal</td>
<td>open</td>
<td>sandy-mud</td>
<td>4</td>
</tr>
<tr>
<td>3.2</td>
<td>R. apiculata</td>
<td>dense</td>
<td>silty-mud</td>
<td>4</td>
</tr>
<tr>
<td>3.3</td>
<td>R. apiculata, C. tagal</td>
<td>open</td>
<td>silty-mud</td>
<td>5</td>
</tr>
<tr>
<td>4.1</td>
<td>R. apiculata</td>
<td>dense</td>
<td>silty-mud</td>
<td>4</td>
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<td>4.2</td>
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<tr>
<td>4.3</td>
<td>R. apiculata</td>
<td>dense</td>
<td>silty-mud</td>
<td>4</td>
</tr>
</tbody>
</table>
and weight of all individuals were measured before the start of experiments.

The experiments were conducted in 25 × 25 × 25 cm glass aquaria supplied with a 5 cm layer of mangrove sediment in half of the bottom and seawater to a depth of 2 cm (salinity 15‰) in the other half. One crab was released into each aquarium. In order to prevent the influence of leaf dimensions on the crab choice, leaves of each category were cut into 2 × 2 cm pieces before being offered to the crab. The initial fresh weight of leaf pieces was converted to dry weight as mentioned above.

In the leaf consumption rate experiment, each crab was offered 10 pieces of only one category (green, yellow or brown) of Rhizophora apiculata leaves. Leaf material remaining after 24 h was collected, rinsed in tap water, dried at 105 °C for 48 h and weighed. Eight replications were applied for each leaf category and the experiment was repeated for 5 consecutive days with the same crab. The consumption rate for each replicate was calculated as the average difference between estimated initial dry weight and measured final dry weight of leaves during the 5 days and expressed as mg dry weight of leaves consumed (g crab fresh wt.)⁻¹ d⁻¹. The leaf preference experiment was conducted similarly to the consumption rate experiment, except that each crab was simultaneously offered 5 green, 5 yellow and 5 brown pieces of Rhizophora apiculata leaves. The leaf material remaining after 24 h was sorted into the 3 categories, rinsed in tap water, dried and weighed. The experiment was done in 10 replications and the entire procedure was repeated 3 times with the same crab. The consumption rate for each replicate and each leaf category was calculated as mentioned above.

2.5. Stomach content of Neoepisesarma versicolor

The natural diet of Neoepisesarma versicolor was assessed from analysis of stomach contents. Sixty-five specimens of N. versicolor (carapace width: 1.7–3.7 cm; fresh weight: 21–37 g) were collected in the Bangrong mangrove forest at night when out of their burrows. The sampled crabs were preserved immediately in 75% ethanol for later stomach content analysis. During dissection of crabs, the approximate volume of stomach contents was determined and only >50% full stomachs were used in the analysis. The stomach was carefully removed from each crab and all material inside was suspended into 5 ml of 70% ethanol. A subsample was transferred to a counting slide (Sedgewick-Rafter slide). Fifty fields of the slide were randomly observed at 200× magnification to identify the presence of food materials in each field. Five replicate slides were examined for each stomach. The average percentage occurrence of various plant materials, animal remains and sediment was determined within one crab and among all crabs (Tirasin and Jørgensen, 1999).

In order to justify the presence of various food items, a frequency of occurrence approach at individual level provides a measure of the regularity by which various food items have been consumed by the crab population. This method has been widely used in diet studies of both fish and crabs (Williams, 1981; Manotelatto and Petracco, 1997) and is recommended when food items of different volumes and digestibility are expected to contribute to the diet (Dahdouh-Guebas et al., 1997).

2.6. Data analysis

The difference between the three types of leaves with respect to elemental composition as well as consumption and removal by crabs offered one type of leaves at the time (both for field and laboratory consumption experiments) were analyzed using standard one-way ANOVA followed by a posteriori Student–Newman–Keul’s test (S–N–K) to investigate significant differences. Due to the lack of independence in the leaf preference experiment where crabs were offered all three leaf types simultaneously, the multivariate Hotelling’s $T^2$ test was applied followed by post hoc analysis for specific pairwise comparisons. The correlation between total removal rate, number, area cover of crab burrows and exposure time was determined by least squares linear regression.

3. Results

3.1. Elemental composition of leaves

The elemental composition of the 3 categories of Rhizophora apiculata leaves reflected their stage of senescence (green versus yellow) and decomposition (yellow versus brown) (Table 2). Green leaves contained significantly more carbon than yellow leaves ($p < 0.01$), indicating that about 5% of the leaf-carbon was lost during senescence. No further change in carbon content occurred during initial decomposition as evident from the similarity between yellow and brown leaves. The significantly lower nitrogen content of yellow than green leaves ($p < 0.001$) indicates that trees remobilized 56% of the total nitrogen, which resulted in a doubling of the C:N ratio. Initial decomposition resulted in 30% higher nitrogen content in brown than yellow leaves ($p < 0.01$).

3.2. In situ leaf removal by crabs

In situ leaf removal ranged from 0.7 to 3.3 (average: $2.1 \pm 0.2$ (SE)) g dry weight m⁻² d⁻¹ for green leaves, 0.4 to 3.9 (average: $1.6 \pm 0.3$ (SE)) g dry weight m⁻² d⁻¹ for yellow leaves, and 0.5 to 4.6 (average: $1.9 \pm 0.4$ (SE)) g dry weight m⁻² d⁻¹ for brown leaves, with no specific trends among and within transects. Since there was no significant preference for any leaf type ($p = 0.171$), all three leaf categories were combined in the considerations below. The density of crab burrows varied by a factor of more than 5 among stations, from 3 to 16 m⁻², respectively. The variation in time of inundation between stations during the experiment reflected the tidal height of the respective stations but varied only from 2 to 5 h⁻¹ (Table 1). The total leaf removal rate, however, correlated positively with density of crab burrows and negatively with tidal inundation time (Table 3).

3.3. Behavior of Neoepisesarma versicolor

Crabs in laboratory microcosms were active (feeding and moving) for 31% of the time during day (06:00–18:00) and 32% during night (18:00–06:00) (Table 4). The crabs rested quietly on the mud surface near burrow openings most of the time during both day and night (59–61%), whereas the time spent inside burrows was of relatively short duration (<5%), particularly during night. They spent most of their active time during the day feeding, digging and burrowing, whereas night activities were dominated by feeding and crawling. About an order of magnitude more time

| Table 2 | Elemental composition of green, yellow and brown Rhizophora apiculata leaves. Values are given as mmol g dry weight⁻¹ ± SE (n = 4) for carbon and nitrogen. |
| Parameters | Categories | Green | Yellow | Brown |
| Carbon | 37.6 ± 0.4 | 35.9 ± 0.6 | 36.3 ± 0.5 |
| Nitrogen | 0.78 ± 0.10 | 0.34 ± 0.01 | 0.44 ± 0.02 |
| C:N | 48.2 ± 6.7 | 105.6 ± 78.6 | 82.5 ± 26.0 |
| Tannin* | 9.0 ± 0.2 | 10.0 ± 0.3 | 7.5 ± 0.2 |

* Data for tannins (mean ± SD of percent dry weight) were obtained from Poovachiranon and Tantichodok (1991).
was spent feeding on sediment and brown leaves than green and yellow leaves (Table 4). Burrowing was almost absent at night. The crabs spent 5–7% of the time in water to clean claws, antennules, antenna and maxillipeds, and probably to moisten their gills.

Crabs in the mesocosm behaved differently from those in the laboratory microcosms. They spent most time inside burrows (65–88%) and less resting on the sediment surface (7–15%), particularly during the day (Table 4). Only 5% of the time during day and 14% during night were spent feeding and moving. Most of the feeding time was devoted to ingesting leaves. Occasionally, the crabs climbed trees to feed on green leaves, as indicated by bite marks on several attached leaves. The crabs never immersed into open water. This important behavior was probably conducted within burrows that extended below the water table and contained water.

### 3.4. Leaf consumption and preference experiments

When kept under laboratory conditions without the possibility of choosing between leaf categories (consumption experiment), sesarmid crabs consumed brown leaves almost twice as fast as green leaves (16.3 ± 0.6 and 8.6 ± 0.5 mg dry weight (g crab ww)^{-1} d^{-1}), and 3–4 times faster than yellow leaves (4.9 ± 0.4 mg dry weight (g crab ww)^{-1} d^{-1}) (Fig. 2). The differences were statistically significant (p < 0.0001).

Brown leaves were also the favorite choice when crabs were offered all 3 categories of leaves simultaneously (preference experiment). Consumption rates ranged from 13.0 ± 0.8 mg dry weight (g crab ww)^{-1} d^{-1} for brown leaves to 5.8 ± 0.3 and 2.0 ± 0.2 mg dry weight (g crab ww)^{-1} d^{-1} for green and yellow leaves, respectively (Fig. 2). The differences were significant (p < 0.01).

### 3.5. Stomach content of Neoepisesarma versicolor

Only 3 of the 65 crabs caught for examination of stomach content had less than half empty stomachs and were discarded. The remaining specimens contained a rich variety of food items in their stomachs (ranging from 10 μm clay particles to 3 mm higher plant fragments). A volumetric quantification of stomach contents revealed that 62% was composed of higher plant material and 38% consisted of detritus and mineral particles. Although other food items were found, they were volumetrically too small to be quantified by this approach. The frequency of crabs containing various food items reveals that all crabs contained materials originating from higher plants, mineral sediment particles and unidentified material (Fig. 3). Many crabs also contained benthic diatoms (86%) and filamentous algae (47%), while only a few had cyanobacteria (5%). Some crabs contained animal remains such as crustacean carcasses (11%) and fish scales (7%). However, the balance between plants and animals by the frequency of occurrence approach may be biased due to differences in digestibility.

### 4. Discussion

Our feeding experiments reveal that *Neoepisesarma versicolor* consumes brown leaves in preference of green and yellow leaves. This is consistent with observations on other sesarmid species (Giddins et al., 1986; Lee, 1989; Camilleri, 1992; Micheli, 1993b). The ingestion rate of brown leaves found in the consumption experiment was comparable to the total leaf ingestion in the preference experiment (Fig. 2). Consequently, the observed consumption rates of 16 and 21 mg dw (g crab ww)^{-1} d^{-1}, respectively can be considered the maximum for *N. versicolor* under the present experimental conditions with ample food supply. Poovachiranon and Tantichodok (1991) reported a comparable rate of total leaf ingestion by individuals of this species from the nearby Ao Nam Bor mangrove forest (~25 mg

### Table 3

Correlation between total leaf removal rate, number of crab burrows and inundation time at the Bangrong mangrove forest.

<table>
<thead>
<tr>
<th>Correlation between</th>
<th>N</th>
<th>r²</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Removal rate, number of crab burrows</td>
<td>12</td>
<td>0.66</td>
<td>19.72</td>
<td>0.0013</td>
</tr>
<tr>
<td>Removal rate, inundation time</td>
<td>12</td>
<td>0.71</td>
<td>24.66</td>
<td>0.0006</td>
</tr>
<tr>
<td>Number of crab burrows, inundation time</td>
<td>12</td>
<td>0.16</td>
<td>1.94</td>
<td>0.1940</td>
</tr>
</tbody>
</table>

### Table 4

Behavior of *Neoepisesarma versicolor* in the laboratory when offered three different categories (green, yellow or brown) of *R. apiculata* leaves and in the mesocosm under natural conditions with occasional litter fall. The elapsed time is presented as feeding, moving and resting. Feeding is separated into ingestion of sediment and various leaf types, moving is separated into activities like moving limbs, digging in the sediment and crawling, whereas resting is separated into the locations where crabs did not move. Values are presented as mean percentage ± SE of total elapsed time for 10 crabs in the laboratory and 3 crabs in the mesocosm. Each crab was monitored for 12 h day and 12 h night periods.

<table>
<thead>
<tr>
<th>Category</th>
<th>Laboratory</th>
<th>Mesocosm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day</td>
<td>Night</td>
</tr>
<tr>
<td>Sediment</td>
<td>4.4 ± 0.7</td>
<td>4.8 ± 0.9</td>
</tr>
<tr>
<td>Green leaves</td>
<td>0.7 ± 0.2</td>
<td>0.6 ± 0.2</td>
</tr>
<tr>
<td>Yellow leaves</td>
<td>0.8 ± 0.5</td>
<td>0.5 ± 0.3</td>
</tr>
<tr>
<td>Brown leaves</td>
<td>5.7 ± 1.4</td>
<td>10.2 ± 2.1</td>
</tr>
<tr>
<td>Moving</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moving limbs</td>
<td>2.7 ± 0.6</td>
<td>2.1 ± 0.4</td>
</tr>
<tr>
<td>Digging</td>
<td>3.3 ± 2.7</td>
<td>1.4 ± 0.7</td>
</tr>
<tr>
<td>Crawling</td>
<td>9.8 ± 1.1</td>
<td>12.3 ± 1.0</td>
</tr>
<tr>
<td>Active sum</td>
<td>31.3</td>
<td>31.7</td>
</tr>
<tr>
<td>Rest</td>
<td></td>
<td></td>
</tr>
<tr>
<td>On sediment</td>
<td>59.1 ± 3.7</td>
<td>60.8 ± 2.4</td>
</tr>
<tr>
<td>In burrow</td>
<td>4.5 ± 2.1</td>
<td>0.6 ± 0.6</td>
</tr>
<tr>
<td>In water</td>
<td>5.1 ± 1.2</td>
<td>6.8 ± 1.1</td>
</tr>
<tr>
<td>Rest sum</td>
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<td>68.3</td>
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<tr>
<td>Total sum</td>
<td>100.0</td>
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</tbody>
</table>

![Fig. 2. Neoepisesarma versicolor ingestion rate when offered leaves “ad libitum” for 24 h. Each crab was offered only one category (green, yellow or brown) of *R. apiculata* leaves in the leaf consumption experiment. In the preference experiment, each crab was simultaneously offered green, yellow and brown leaves of *R. apiculata*. Category was calculated as mentioned above. Values are mean ± SE.](image-url)
immediately after capture in the Bangrong mangrove forest (n = 588). Sesarma messa observed a change in selectivity between laboratory feeding and field studies. Micheli (1993b) also found that the behavior experiment revealed that satiated individuals do not need to feed rapidly when offered food leaves, but at a slower rate than under in situ conditions. Thus, well-fed crabs have more energy available for various activities. On the other hand, individuals kept in the laboratory may be at a higher level of stress because they have limited access to deep burrows. They seem more restless when forced to stay on the sediment surface. Accordingly, crabs in the mesocosm spent 20–100 times longer resting calmly inside burrows. Sediment most of the time. Accordingly, crabs in the mesocosm were less well-fed conspecifics in the mesocosm. This can either be interpreted as a response to the difference in nutritional status. The well-fed individuals in the laboratory were generally 2 and 6 times more active during night and day than their less well-fed conspecifics in the mesocosm. This can either be interpreted as a response to the difference in nutritional status. The well-fed crabs have more energy available for various activities. On the other hand, individuals kept in the laboratory may be at a higher level of stress because they have limited access to deep burrows. They seem more restless when forced to stay on the sediment most of the time. Accordingly, crabs in the mesocosm spent 20–100 times longer resting calmly inside burrows.

As there are no significant relationships between exposure time and burrow abundance, the apparent influence of tidal stage on leaf removal must be related to changes in crab behavior as a function of tidal stage. Since sesarmid crabs retreat to their burrows during tidal inundation (Thongtham and Kristensen, 2003), no leaf removal from the sediment surface will occur at high tide. The extensive crawling that occurs during tidal exposure is probably a behavior for food search. Not all removed leaves are consumed immediately, but are rather pulled into the burrows for later consumption during tidal inundation. The storage of leaves inside burrows is probably also a mechanism to enhance the nutritional value of primarily yellow leaves, which contain less carbon and nitrogen and more tannin than green and brown leaves (Table 2). Microbial growth on the leaf surface during ageing provides essential nutrients, amino acids, fatty acids and vitamins for the crabs (Wolcott and O’Connor, 1992). The physical and chemical characteristics of leaves therefore appear to be important for their palatability and digestibility by most crabs. It must be noted here that some leaf-eating crabs, such as the ocypodid, Ucides cordatus, are not dependent on ageing of leaves as they actually prefer leaves with high tannin content (Nordhaus and Wolff, 2007). Based on the available knowledge it is difficult to assess whether the storage of leaves in the burrows provides crabs with the opportunity to consume fresh leaves during tidal inundation alone or if it is also a mechanism for improving the nutritional value of the leaves. Most likely, it is a combination of both strategies.

Nevertheless, the nutritive value of leaves, even aged brown leaves, is insufficient to maintain crab growth (Thongtham and Kristensen, 2005). The nitrogen content of mangrove leaves is very low with C:N ratios typically ranging from 50 to 80 depending on species (Robertson, 1988). As the theoretical requirement of animal food for maintaining growth is a C:N ratio below 17 (Russell-Hunter, 1970), leaf-eating crabs must supplement their diet with nitrogen-rich food items in order to meet their nitrogen demands (Micheli, 1993a). Stable isotope studies confirm that sesarmid crabs indeed consume other food items than mangrove litter (Bouillon et al., 2002). Microorganisms associated with surface sediment may be one principal source of nitrogen for Neoeopisesarma versicolor. Evidence from the behavior experiment shows that crabs spend almost half of the feeding time browsing material from sediment surface (Table 4). Furthermore, the stomach content of wild-caught crabs always contained sediment and diatoms. Thus, the crabs seem to utilize sediment-associated microalgae and probably bacteria and fungi whereas the dead organic debris in sediments must be considered almost indigestible (Lopez and Levinton, 1987). Recently, however, it has been estimated that crabs must ingest 7–23 cm³ sediment (g ww crab⁻¹) d⁻¹ to fully cover their nitrogen need through digestion of sediment-associated microorganisms (Thongtham and Kristensen, 2005). It is unrealistic to expect that crabs can consume an order of magnitude more sediment than their own body weight per day. Even if crabs are selective during feeding, microalgae must still be considered an insignificant nitrogen source. Leaf-eating sesarmid crabs may instead obtain the needed extra nitrogen by occasional consumption of nitrogen-rich animal tissues, such as carcasses of fish and crustaceans, on the surface or associated with leaf litter (Kwok and Lee, 1995). This assumption is strongly supported by our observations of animal remains in the stomach of N. versicolor and by the fact that our crabs willingly consumed fish meat prior to the feeding experiments. Other mangrove crab species that are regarded as herbivores are also known to supplement their diet with animal material (Giddins et al., 1986; Dahdouh-Guebas et al., 1999; Erickson et al., 2003).

The population of sesarmid crabs remove daily 1.9 ± 0.3 g dw m⁻² d⁻¹ fallen leaves of the dominant tree, Rhizophora apiculata, in the Bangrong mangrove forest. Since the average litter fall in the same area is 2.7 g dw m⁻² d⁻¹, of which 78%
consists of leaf litter (Suraswadi, 2002), the potential leaf removal rate by sesarmid crabs is 87% of daily leaf litter fall. The remainder is decomposed by other organisms or exported to adjacent areas. The much higher leaf removal rates reported by Poochachiranon and Tantichodok (1991) for the nearby Ao Nam Bor mangrove forest (3.4 g dw m⁻² d⁻¹) appears unrealistic as it exceeds the total litter fall of that area (2.2 g dw m⁻² d⁻¹) by almost 50%. In contrast, sesarmid crabs Chironomus onychophorum and Chironomus eumolpe remove 7 and 20–30% of the litter fall in the mid- and high-intertidal zones of a mangrove forest in Malaysia (Leh and Sasekumar, 1985), while 61–81% of the annual leaf litter fall is removed by the ocypodid Ucides cordatus in northern Brazilian mangrove forests (Schories et al., 2003; Nordhaus et al., 2006). In agreement with our results, removal of leaves by sesarmid crabs in high-intertidal mangrove forests of tropical Australia was 1.6–2.2 g dry wt m⁻² d⁻¹, which is equivalent to 70% of the total litter fall in Cetiops and Bruguiera forests (Robertson and Daniel, 1989). However, differences between various studies are expected due to the influence of a number of local factors, including tidal range and frequency of inundation, number and species composition of crabs, density and species composition of mangrove trees and the involvement of other detritivores.

The amount of leaf material that is actually consumed by crabs is less than the removal rate. If it is assumed that all species of sesarmid crabs in the Bangrong mangrove forest consume leaf material at the same rate as observed in our laboratory experiments on Neopisarma versicolor, then the crabs consume 74% of the removed litter or 65% of the leaf litter fall. The remaining is degraded microbially while stored in the burrows. As crabs are known to be “sloppy feeders” and about 20% of the material is lost degraded microbially, while stored in the burrows. As crabs are known to be “sloppy feeders” and about 20% of the material is lost degraded microbially, while stored in the burrows.

Acknowledgements

We are grateful to the staff of the Marine Ecology Unit, Phuket Marine Biological Center for their kind assistance during the field and laboratory work. This work was associated with the Thai-Danish Scientific Cooperative Program (SCP) and supported by DANIDA (Danish International Development Aid) and the Danish Science Research Council (grant no. 21020463).

References


