Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*

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Abstract: The feeding behavior of two of the most abundant species of leaf-eating mangrove crabs occurring in North Queensland (*Sesarma messa* and *Sesarma smithii*), was studied during the dry season of 1989. Laboratory feeding choice experiments showed that *S. messa* did not exhibit significant preference for any of the four species of newly fallen mangrove leaves offered, while consuming significantly more decayed than senescent leaves, irrespective of leaf species. *S. smithii* chose *Rhizophora stylosa* mangrove leaves over all other species (*Avicennia marina, Bruguiera exaristata, Ceriops tagal*). The choice of leaves by both crabs was not influenced by any of the leaf properties measured: tannin and water content, $\%$ of organic matter; C:N ratio; and leaf toughness. Crabs displayed no clear pattern of preferential consumption of different species of mangrove leaves in field experiments carried out in five separate forests. However, at all sites significantly greater amounts of *C. tagal* were found shredded and accumulated inside crab burrows compared to the other species of mangroves. Most of the litter accumulated by the crabs in their burrows was consumed within two weeks, before significant changes in the leaf C:N ratio occurred. The lesser selectivity observed in the field than in the laboratory might be the result of a shortage of food in the field during the dry season, when litter fall is minimum. The proportion of leaves shredded and accumulated in the burrows was significantly greater where *S. smithii* was present than at sites where only *S. messa* was found. *S. smithii* is rarely seen foraging on the forest floor and is active only at night. *S. messa*, in contrast, is frequently seen at the surface during day and night. I suggest that litter storage is a consequence of a time constraint to above ground activity for the nocturnal species rather than a mechanism for improving the nutritional characteristics of the food. The fresh mangrove litter most commonly consumed by crabs is characterised by a high C:N ratio and is not likely to meet the crabs' nitrogen requirements. Observations of the foraging activity of *S. messa* in the field, indicated that this species spends most of its feeding time scraping material from the mud surface. Bacteria and microalgae living in the upper layer of the sediment may be the principal source of nitrogen for mangrove crabs. Crabs spent a minor proportion of their time grazing on mangrove leaves and on the benthic algae covering the mangrove prop roots, with no significant preference for either one of these two substrates.

Key words: Feeding ecology; Food preference; Mangrove; Northeastern Australia; Sesarmid crab; *Sesarma messa*; *Sesarma smithii*

INTRODUCTION

The rate of detrital turnover in mangrove forests depends on factors such as degree and frequency of tidal inundation (Odum et al., 1982; Twilley, 1985; Twilley et al.,

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1986), characteristics of the organic material affecting its decomposition rate (Goulter & Allaway, 1979; Robertson, 1988), and species composition and density of the consumer populations (Odum & Heald, 1975; Leh & Sasekumar, 1985; Robertson, 1986).

Investigations of mangrove trophodynamics in Florida showed that most of the mangrove-derived litter is exported by tidal action (Heald, 1971; Odum, 1971; Twilley, 1985). In such systems, nearly all of the forest litter fall is exported to subtidal waters where fragmentation by small detritivores and saprophytic decay take place (Heald, 1971; Odum, 1971; Cundell et al., 1979; Fell & Masters, 1980; Flores-Verdugo et al., 1987). In areas with low frequencies of inundation, mangrove litter is decomposed mainly by bacteria and fungi (Twilley et al., 1986).

Recent studies conducted in eastern Australia, however, have determined that direct grazing of litter by invertebrate herbivores is an important trophic pathway in mangrove forests, and showed that the model of mangrove-based food chains developed in Florida cannot be generalised to other systems (Robertson, 1986, 1987). In the highly diverse mangrove systems of southeast Asia and Australia, sesarmid decapod crustaceans graze on large proportions of mangrove litter (Malley, 1978; Nakasone et al., 1982, 1985; Leh & Sasekumar, 1985; Robertson, 1986; Robertson & Daniel, 1989), consistently reducing the tidal export rates of litter and accelerating its breakdown. In north Queensland, Australia, Robertson (1986) estimated that 28% of the annual litter fall is removed by crabs in low to mid-low intertidal *Rhizophora* sp. forests. In high intertidal forests, removal rates reach 80% (Robertson & Daniel, 1989).

Sesarmid crabs numerically dominate the fauna of mangrove forests (in the Indo-West Pacific, Macnae, 1968, and Hartnoll, 1975; and in eastern America, Abele, 1973). In North Queensland they are represented by more than 30 species (Davie, 1982, 1985; Jones, 1984). Several authors have reported a zonation of sesarmids across the intertidal area, with small sized species generally occupying the lower levels and larger species the high intertidal forests (Macnae, 1968; Warner, 1969; Sasekumar, 1974; Jones, 1984). Different crab species might have different feeding habits and might feed at different rates. Species composition of crab populations may therefore explain the variability in estimates of crab consumption of leaf litter (Robertson, 1986; Robertson & Daniel, 1989) and seeds (Smith, 1987a,b) in different mangrove forests.

Despite their importance in the food web, information on the feeding ecology of *Sesarma* species of the Indo-Pacific is limited (see: Malley, 1978; Leh & Sasekumar, 1985; Nakasone et al., 1985, for gut-content analyses; Robertson, 1986; Lee, 1989, for litter consumption rates in the field; Giddins et al., 1986; Camilleri, 1989, for laboratory ingestion rates and assimilation efficiency). A number of basic questions remain unanswered. For instance, do sesarmids select particular litter types among the range of leaf species available, thus leading to variable turnover rates for different leaf species? How do leaf-eating mangrove crabs cope with the large concentrations of polyphenolic compounds that characterise mangrove leaves (Neilson et al., 1986; Giddins et al., 1986; Robertson, 1988)? Polyphenolics have been shown to deter herbivory by mangrove crabs (Giddins et al., 1986), and a variety of other herbivores

(Swain, 1979; Hay & Fenical, 1992, and references therein). Giddins et al. (1986) found that *Sesarma smithii* had higher ingestion rates and assimilation efficiency when feeding on mangrove leaves of six weeks of age compared with younger litter, and suggested that crabs let the leaves decompose inside their burrows for several weeks before eating them. During this time, polyphenolics are lost through leaching (Robertson, 1988) and the palatability of litter improves.

Storage of mangrove leaves also increases the nutritional properties of litter by increasing nitrogen content through microbial and fungal activity (Goulter & Allaway, 1979; Fell & Masters, 1980; Robertson, 1988). Various sesarmid species accumulate plant material in their burrows (Hogue & Bright, 1971, in Kenya; Robertson & Daniel, 1989; Alexander, unpubl. data, in Australia) but no field data are available on the duration of litter storage or about its function. Storage of mangrove litter within the crab burrows, however, does not seem to be a feature of all sesarmid species found in mangrove forests, suggesting that this behavior might be dictated by ecological constraints other than food quality. Robertson (1986), for instance, found that in low-intertidal Rhizophora spp. forests, where *Sesarma messa* was the dominant crab species, most litter seemed to be consumed by the crabs right away.

A final interesting question yet to be addressed is how mangrove crabs, especially those species that graze on fresh mangrove litter, obtain adequate quantities of nitrogen from their diet. The C:N ratio of mangrove leaves typically ranges from ≈ 50 to 80, according to the species (Robertson, 1988). In all cases, C:N ratios of leaf litter are well above the value of 17, the theoretical requirement for the maintenance of animal tissues (Russel-Hunter, 1970). Leaf-eating crabs may thus be expected to consume nitrogen-rich food items, in addition to mangrove litter, in order to meet their nitrogen requirements.

The experiments reported in the present paper tested (1) whether sesarmids select particular species or ages of litter; (2) whether different crab species exhibit different food preferences; and (3) whether crabs consume litter immediately or after prolonged storage in their burrows. In addition, the foraging activity of *S. messa* individuals was monitored in the field in order to assess the relative importance of mangrove litter, compared with alternative food items, in the diet of mangrove crabs.

METHODS

FIELD SITES AND CRAB SPECIES

Field experiments were carried out during the dry season, April to November, 1989 at Cape Ferguson (19° 17′ S:147°03′ E), near Townsville in North Queensland (sites 1, 2, 3, 4), and at Coral Creek in Missionary Bay (18° 15′ S:146° 12′ E), Hinchinbrook Island, North Qeensland (site 5).

Site 1 is a mixed high intertidal forest dominated by the mangrove species *Bruguiera*

exaristata; sites 2 and 4 are nearly monospecific stands of *Ceriops tagal*, in the mid-high and high intertidal zone respectively; site 3 is in the mid-low intertidal zone and is dominated by *Rhizophora stylosa*; site 5 is also in the mid-low intertidal zone, and is dominated by *R. stylosa* and *Rhizophora apiculata*. Additional information about the study sites are given in Smith (1987a,b), Robertson (1986, 1988) and Robertson & Daniel (1989). Pitfall trapping performed at sites 1 to 4 indicated that *Sesarma messa* was the dominant crab species at all sites, followed by *S. smithii* and *S. fourmanoiri* at site 1, and by *S. smithii* at sites 2 and 4. Robertson (1986) reported that *S. messa* is the dominant leaf-eating crab at site 5.

Sesarma (*Perisesarma*) *messa* Campbell 1967, a species known from the northeastern coasts of Australia (Davie, 1982) and Papua New Guinea (Robertson, pers. comm.), was chosen for the laboratory experiments for two reasons: it is the most abundant species in the study area, and it occurred in all the forests selected as study sites. Food preference experiments were also carried out with *Sesarma* (*Neosarmatium*) *smithii* H. Milne-Edwards 1852, a species found throughout the Indo-West Pacific (Macnae, 1968; Davie, 1982, 1985) in high intertidal mangrove forests and fairly common in the study area (at sites 1, 2 and 4).

The largest individuals captured had carapace lengths of 24 mm for *S. messa*, and 35 mm for *S. smithii*. Both species inhabit systems of interconnected burrows. *S. smithii* is larger and more robust than *S. messa*, it is rarely seen outside its burrow and emerges only at night, while *S. messa* is more slender and active, and is commonly seen at night and during the day wandering on the forest floor or sitting at the entrance of burrows.

LEAF CHARACTERISTICS

Leaf characteristics that might be relevant to the crab leaf preferences were determined for the four mangrove species used in the feeding preference experiments: *Avicennia marina*, *R. stylosa*, *B. exaristata*, and *C. tagal*. Ten senescent leaves (defined as yellow and easily abscissed from the trees, Giddins et al., 1986) of each species were weighed on a Mettler balance to the nearest 0.001 g, oven-dried for 5 days at 65 °C and reweighed in order to determine dry weight/wet weight regressions, for each leaf species (*R. stylosa*: dw = 0.180 + 0.219 ww, $R^2 = 0.923$; *C. tagal*: dw = − 0.05 + 0.265 ww, $R^2 = 0.959$; *B. exaristata*: dw = 0.095 + 0.218 ww, $R^2 = 0.950$; *Avicennia marina*: dw = − 0.013 + 0.460 ww, $R^2 = 0.980$), and water contents. Dry weight-wet weight regressions were used to convert the initial wet weights of the leaves to dry weights.

The dried leaf material was ground to powder and used to determine percent organic matter (muffle furnace, 24 h at 500 °C), percent carbon and nitrogen (Leco 600 C-H-N analyser), and tannin content (Folin-Denis method as described in Allen et al., 1964). The analyses were performed on three replicate leaves of each species. An index of relative toughness of leaves of different species was determined following the procedure described by Robertson & Lucas (1983) and was performed on 18 leaves of each species. Leaves were placed on a Mettler electronic balance. The force necessary to

pierce the leaves with a metal point was estimated by reading the weight recorded by the balance as soon as the point penetrated the leaf.

Carbon and nitrogen content, and leaf toughness were determined also for decayed leaves of *R. stylosa*, *B. exaristata*, and *C. tagal*. Decayed leaves were obtained by placing senescent leaves inside mesh bags (as described in Robertson, 1988) and leaving them in the field for 17 days. Leaves were then retrieved, rinsed in seawater, and analysed as described above.

EXPERIMENTS

Laboratory and field experiments were performed to test crab feeding preferences for different leaf species and ages. In laboratory leaf choice experiments, crabs were offered four species of fresh litter (i.e. senescent leaves) or a combination of senescent and aged leaves. In field leaf choice experiments, senescent leaves of different species were tethered and deployed in the field. Another field experiment was designed to follow the fate of leaves taken down crab holes and to determine which age of litter is consumed at the highest rate in the field.

Laboratory leaf choice experiments

The feeding preference of *S. messa* and *S. smithii* was tested using senescent leaves of four mangrove species. In addition to leaves of the dominant tree species in the study area (*R. stylosa*, *C. tagal* and *B. exaristata*; Smith, 1987a,b), leaves of the less common *Avicennia marina* were used because of their nutritional characteristics (low tannin content and low C:N ratio), which are expected to enhance herbivory (Russel-Hunter, 1970; Giddins et al., 1986). Crab specimens and senescent leaves were collected at Cape Ferguson. Leaf choice experiments were conducted with 47 individuals of *S. messa*. *S. smithii* individuals were virtually impossible to capture by hand, as they would quickly retrieve into their burrows, and were also rarely found in pitfall traps. Due to the difficulty of obtaining large numbers of *S. smithii* specimens, leaf choice experiments were conducted with only 10 individuals of this species.

Sesarma messa and *S. smithii* specimens were kept in the laboratory in individual plastic bowls for one week before the start of the experiment. Seawater was added to the containers up to a level of 0.5 cm. Water was changed every second day and no food was given prior to the beginning of the experiment. All experiments were carried out at a temperature of $21 \pm 0.5\,^\circ C$, with a natural photoperiod.

Senescent leaves were stored at $4\,^\circ C$ (for approximately one day) until the beginning of the experiment. Each leaf was cut through the mid rib; one half was put in a container with a crab, and the other half was put in a separate bowl, containing only seawater, as a control. Both halves were pre-weighed to the nearest 0.001 g. Each animal was offered the four leaf species simultaneously. In order to prevent leaf dimensions from influencing food choice, all the leaves were cut to the same surface area.

Leaf remains were removed from experimental and control containers after 24 h, oven-dried at 65 °C for 5 days, and weighed. Dry weight/fresh weight ratios were calculated for the control leaves and used to convert wet weights of the leaf tissue consumed by the crabs to dry weights. Ingestion rates were expressed as mg dry weight of leaf/g wet weight of crab/24 h (mg dw/g ww/d).

A second experiment was carried out with *S. messa* only to test whether the age of the litter of the most common mangrove species in the study area can affect leaf choice. Twenty-four crabs were offered senescent and decayed leaves of *R. stylosa*, *B. exaristata* and *C. tagal*. Each crab was thus offered six leaf pieces at each trial. Decayed leaves had been allowed to decompose in the field for 17 days, inside 2 mm nylon mesh bags inserted in crab burrows. All other procedures were as described for the first experiment.

Field leaf choice experiments

Leaf choice experiments were performed at all field sites. Leaves of the four mangrove species were tethered by the petiole (as described in Robertson, 1986) and deployed at each site. Senescent leaves of each tree species were weighed within 24 h of collection and tied by the petiole to 1–2 m long pieces of nylon twine which were in turn tied to a prop root or a tree. Twenty replicate leaves of each species were deployed haphazardly at each site.

After 24 h from the beginning of the experiment, the number of leaves taken down the burrows were scored, and the portions of leaves still attached to the tethers were retrieved, rinsed, and oven-dried (65 °C, for 5 days) before being reweighed. Initial fresh weights of the leaves were converted to dry weights using the dry weight-wet weight regressions previously determined for each leaf species (see the section "leaf characteristics"). Leaf consumption by the crabs was quantified as percent dry weight loss. Burrows which contained tethered leaves were excavated, using the twine as a tracer, and all the litter plastered to the burrow walls was collected and taken back to the laboratory, where leaf fragments were rinsed on a 2 mm sieve.

The surface of each leaf had been marked with lines traced with a permanent, non-toxic marker, so that fragments of the tethered leaves dug out from crab burrows were easily identified. A few marked leaves were put inside mesh-bags and buried in crab holes to make sure that the markings did not fade with time (marks were still detectable after 3 weeks). In order to test the effect of the leaf marking on the crabs behavior, a leaf choice experiment was carried out at site 2 with 20 marked tethered *C. tagal* leaves and 20 non-marked ones. The percentage of leaf tissue consumed after 24 h was similar for marked and non-marked leaves, showing that the markings did not affect leaf choice by the crabs (ANOVA: $F = 0.46$, df1 and 38, NS).

Three controls for each mangrove species were also deployed at each site in order to quantify the leaf weight loss due to factors other than crab feeding (leaching, saprophitic decay) and to correct the tethered leaf weight losses. Groups of 3–8 leaves (fresh

weights ranging from 0.5 to 2.0 g) of each species were weighed, put into 2 mm nylon mesh-bags, and left on the mangrove floor for the duration of the experiment. Control leaves were retrieved from the field at the end of the experiment, rinsed, oven-dried, and re-weighed.

Fate of leaves taken down crab burrows

In order to test whether crabs let mangrove leaves decompose inside their burrows before eating them, a tethered leaf experiment was performed at sites 1, 2 and 3 in July–August '89. These sites were selected along an intertidal gradient, at a mid-low (site 3), mid-high (site 2), and high (site 1) intertidal elevation.

Sixty leaves (individually weighed, marked, and tied to 1–2 m long pieces of nylon string, as described above) were deployed at each site. Leaves of the most abundant mangrove species found at each site were used, i.e. *B. exaristata* leaves at site 1, *C. tagal* leaves at sites 2, and *R. stylosa* leaves at sites 3, since these represented the litter types that local crab populations would most frequently store in their burrows. Twenty replicate leaves were retrieved at each sampling date, after 24 h, 8 d, and 17 days from the beginning of the experiment. Burrows were excavated to collect the leaf fragments, as described above. Fragments were sorted into marked and unmarked ones, oven-dried, and weighed.

Controls within nylon mesh-bags were deployed both on the mud surface and inside the crab holes. Three replicate bags were retrieved from each site on each date. Control leaves were oven-dried, reweighed to determine weight loss, ground to powder, and analysed for carbon and nitrogen content.

OBSERVATION OF *S. MESSA* FEEDING BEHAVIOR

In order to asses the relative importance of direct grazing on mangrove leaves vs. deposit feeding in the diet of mangrove crabs, the feeding behavior of 30 individuals of *S. messa* was monitored in the field.

Observations were carried out during October and November 1989 at site 3, during diurnal spring low tides, for ≈ 3 h at the time. Air temperatures ranged from 26.5° to 29.2 °C (average $= 27.5$, $n = 13$), burrow temperatures from 24.6° and 29.1 °C (average $= 25.8$, $n = 13$), and were recorded every 30 min, in the course of the observation period.

The observation of each individual started when the crab emerged from its burrow (i.e. supposedly at the beginning of a feeding cycle) and lasted for 30 min. The type and duration of each activity displayed by the crab during this time (i.e. resting, walking, engaging in aggressive interaction with conspecific, feeding on the sediment surface, grazing on mangrove leaves, feeding on the algae covering the mangrove prop roots) was recorded. Adult male and female of *S. messa* were easily distinguished due to sexually dimorphic chelipeds. Individuals smaller than ≈ 15 mm of carapace length

could not be sexed based on secondary sexual characteristics and are referred to as juveniles. A total of 12 males, 9 females, and 9 juveniles were monitored. Three males that had emerged from their burrow and had sat by the burrow entrance for the whole observation period were excluded from the data analysis.

STATISTICAL ANALYSES

Ingestion rates determined for the laboratory leaf preference experiments were compared with one-way ANOVAs. Prior to analysis, data were tested for homogeneity of variances with the Cochran's test (Underwood, 1981), and square-root transformed when necessary. Since a multichoice experiment was performed (crabs were offered the different species of mangrove leaves contemporaneously), ingestion rates measured for the different leaf species are not independent (Peterson and Renaud, 1989). To circumvent this problem, ingestion rates for each leaf species were drawn at random from the data set, so that only one value was used for each crab tested. Comparison of means, after analysis of variance, was performed using the Student-Newman-Keuls (SNK) procedure (Underwood, 1981). In the field leaf choice experiments, each leaf was treated as a replicate, and a two-way ANOVA (site and leaf species being the fixed factors) was performed on the percent weight loss determined for each leaf. Differences in the duration of leaf storage in burrows were also tested with a two-way ANOVA (with site and date of sampling as fixed factors). Percentages were arcsin transformed prior to analysis. The proportion of time devoted by *S. messa* individuals to different activities (resting, walking, or feeding) and to feeding on different substrates (sediment, mangrove leaves, or prop root surface) was analysed with two-way ANOVAs, with type of activity and crab sex, and feeding substrate and crab sex, respectively, as fixed factors. As for the laboratory experiments (see above), in order to assure independence of the data, the values relative to three individuals of each sex were taken at random and used for each activity type and feeding substrate.

RESULTS

LABORATORY FEEDING PREFERENCE EXPERIMENTS

Sesarma messa individuals had similar ingestion rates of senescent mangrove leaves of the four species offered in the laboratory trials (ANOVA on non-transformed data: $F = 0.63$, df 3 and 43, NS) (Fig. 1). *S. smithii*, on the contrary, significantly selected *R. stylosa* leaves over the other species of mangrove leaves (ANOVA, after sqrt-transformation: $F = 9.29$, df 3 and 6, $p < 0.05$) (Fig. 1), with no significant difference among the latter (SNK: *R. stylosa* > *C. tagal* = *B. exaristata* = *A. marina*, at $\alpha = 0.05$).

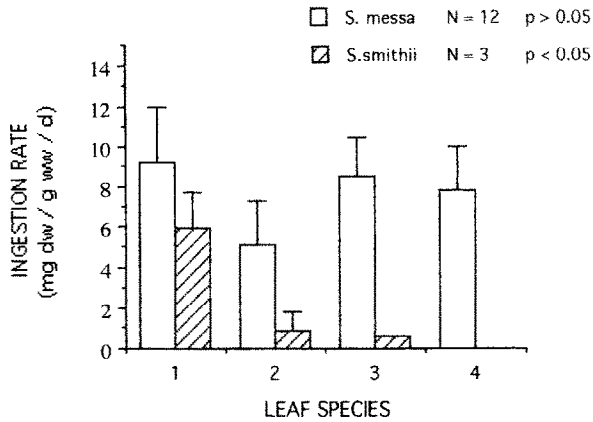For *S. messa*, the sample size was large enough to allow separate analyses of leaf

Fig. 1. Ingestion rates of *S. messa* and *S. smithii* on four species ($1 = R.$ *stylosa*, $2 = C.$ *tagal*, $3 = B.$ *exaristata*, $4 = $ *Avicennia marina*) of senescent mangrove leaves in the leaf choice experiments performed in the laboratory. Error bars represent 1 SE.

choices by male and female crabs. Males and females are likely to have different energy requirements, mirroring the different energetic cost involved in the production of sperm and eggs (Sastry, 1983), and thus might differ in their food preferences. This hypothesis was not supported by the present results, in that neither males nor females preferred any of the leaf species offered (ANOVA on non-transformed data: $F = 0.68$, df 3 and 24, NS, for males; $F = 1.71$, df 3 and 16, NS, for females).

TABLE I

Chemical characteristics and tissue toughness indexes of the leaf species used in the leaf choice experiments. Data are given as mean percentages of leaf dry weight, ± 1 SE (in brackets). Each value is the average of three replicate analyses except for water content and for toughness, where 10 and 18 replicate measurments, respectively, were performed for each leaf species. Results of 1-way ANOVAs performed on non-transformed data are also reported.

Senescent	Leaf species				
	R. stylosa	C. tagal	B. exaristata	A. marina	F. ratio
% Water	72.92 (1.40)	75.15 (1.03)	78.67 (0.80)	55.70 (1.05)	$F_{3,36} = 88.2$***
% Organic matter	74.99 (0.81)	74.09 (0.57)	80.32 (0.69)	79.77 (0.49)	$F_{3,8} = 2.43$***
% Tannins	17.43 (2.33)	11.40 (0.48)	11.13 (2.85)	6.76 (0.42)	$F_{3,8} = 8.67$**
C:N ratio	71.09 (7.40)	87.89 (6.40)	91.62 (2.85)	46.22 (3.39)	$F_{3,8} = 12.45$**
Toughness (g)	122.39 (5.55)	95.94 (5.82)	40.83 (3.83)	132.89 (4.68)	$F_{3,68} = 66.9$***
Aged					
C:N ratio	72.60 (11.92)	57.49 (2.28)	83.87 (6.52)	–	$F_{2,6} = 2.69$ NS
Toughness (g)	51.56 (3.54)	32.89 (2.92)	16.22 (0.90)	–	$F_{2,51} = 42.84$***

NS: $p > 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

TABLE II

Correlation coefficients of ingestion rate-leaf characteristics relationships from the laboratory experiments testing the leaf species choice of *S. messa* and *S. smithii* offered senescent mangrove leaves (experiments 1), and of *S. messa* offered both senescent and aged leaves (experiment 2). Since multiple comparisons were performed, α levels were corrected ($\alpha = 0.01$, for experiment 1, and $\alpha = 0.03$ for experiment 2) (Sokal & Rohlf, 1981). All correlations were not significant.

		df	% Water	% Organic matter	% Tannins	C:N ratio	Toughness
Experiment 1	*S. messa*	2	– 0.06	0.43	0.36	– 0.27	0.00
	S. smithii	2	0.27	– 0.56	0.93	0.03	0.32
Experiment 2	*S. messa*	4	–	–	–	– 0.05	– 0.67

Sesarma messa consumed significantly different amounts of aged and senescent leaves, without any significant effect of leaf species (ANOVA on non-transformed data: $F = 10.51$, df 1 and 18, $p < 0.01$, for leaf age; $F = 1.80$, df 2 and 18, NS, for leaf species; $F = 1.28$, df 2 and 18, NS, for the interaction). Ingestion rates, after pooling results for the different leaf species, were considerably greater for the aged (average = 12.86 mg dw/g ww/d, SE = 3.10, $n = 12$) than for the senescent (average = 1.80 mg dw/g ww/d, SE = 1.77, $n = 12$) leaf material.

Senescent leaves of the four species considered differed for all the characteristics examined (Table I), while aged leaves did not show significant differences in C:N ratios.

No significant correlation was found between leaf characteristics measured (water content, percent organic matter, tannin content, C:N ratio, leaf toughness) and crab ingestion rates in the laboratory (Table II). Crabs of either species seemed not to be affected, in their food choice, by the leaf properties considered here.

FIELD LEAF PREFERENCE EXPERIMENTS

Crabs did not show a clear pattern of leaf preference in the field (Fig. 2). Both leaf species and site had a significant effect on the proportion of leaf material consumed

TABLE III

Results of the 2-way ANOVA testing the effect of site and leaf species on the proportion of leaf material consumed by crabs or shredded and accumulated inside crab burrows.

Source of variation		% Consumed		% Shredded	
	df	SS	F	SS	F
Site	4	8.95	12.19***	0.39	4.75***
Species	3	2.77	5.03**	0.37	5.94***
Site* species	12	4.12	1.87*	0.41	1.63 NS
Error	380	69.75		7.89	

NS: $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.
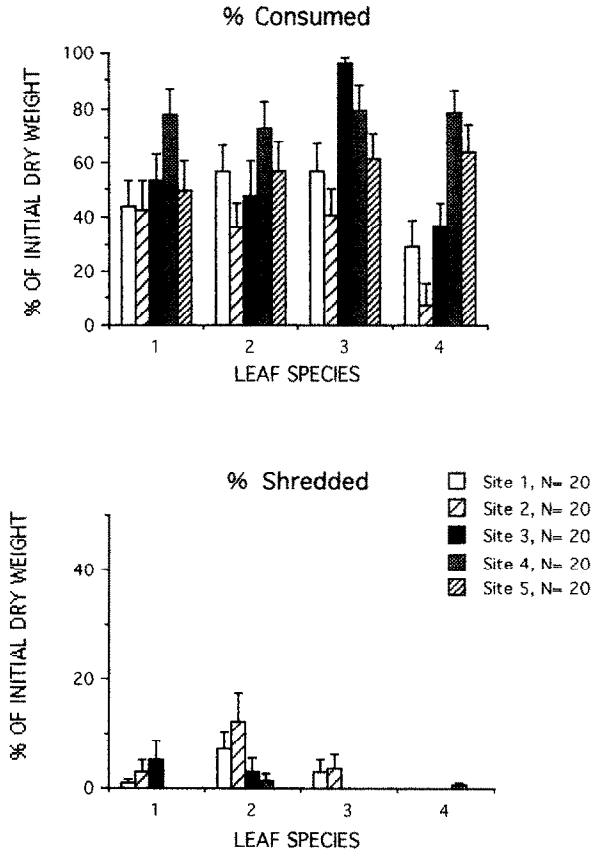
Fig. 2. Percentages of leaf material consumed by mangrove crabs or shredded and accumulated inside burrows after 24 h from the deployment of tethered mangrove leaves of four different species. Error bars represent 1 SE. Leaf species codes as in Fig. 1.

by crabs, with a significant interaction between the two factors, which suggests that crabs had chosen different leaf species at the different sites (Table III). SNK tests perfomed separately for each site, however, showed that none of the leaf species had been consumed significantly more at all five sites (at $\alpha = 0.05$). *Avicennia marina* leaves ranked last at three out of five sites (at sites 1, 2, and 3), although not significantly so, while no trend of preference was evident at the remaining two sites (sites 4 and 5) (Fig. 2).

There were significant species and site effects in the proportion of leaves shredded and accumulated inside the crab burrows, with no significant interaction between the two factors (Table III). At all sites, significantly more *C. tagal* leaves were shredded than all other species (SNK: *C. tagal* > *R. stylosa* = *R. exaristata* = *Avicennia marina*, at $\alpha = 0.05$). Significantly more leaves were shredded and buried at site 2 than at

sites 4 and 5, with no difference between sites 4 and 5, or between the two extremes and sites 1 and 3 (SNK, at $\alpha = 0.05$) (Fig. 2).

After 24 h from the beginning of the experiment, 45.0, 37.5, 38.8, 85.0, and 51.3% of the total number ($n = 80$) of tethered leaves deployed at each site had been carried inside crab burrows at sites 1, 2, 3, 4, and 5, respectively. There was no significant difference in the frequencies at which leaves of different species were carried underground by the crabs ($\chi^2 = 8.78$, df = 12, NS).

FATE OF LEAVES TAKEN DOWN CRAB BURROWS

The percentage of leaves consumed by the crabs were significantly dependent on the time elapsed from the beginning of the experiment and differed among sites (Fig. 3 and
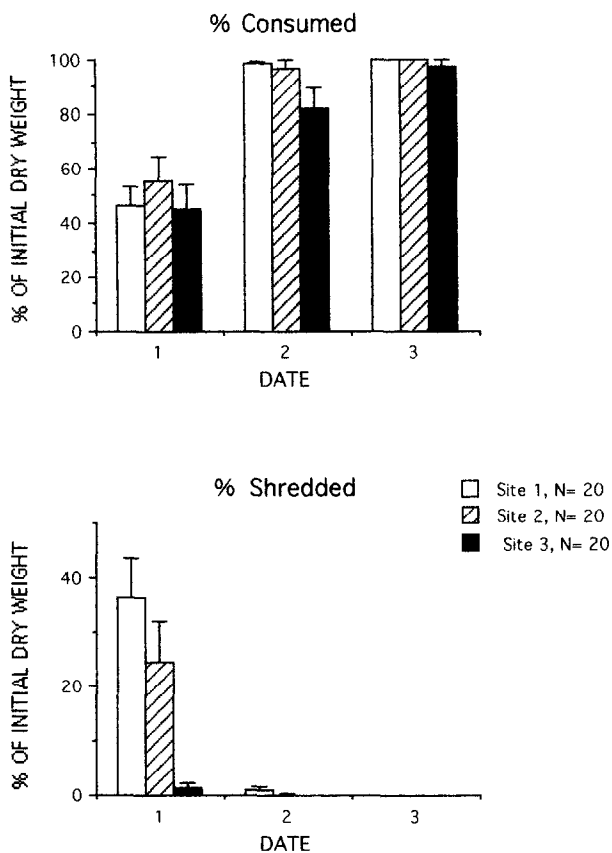

Fig. 3. Percentages of leaf material consumed by mangrove crabs or shredded and accumulated inside burrows after 24 h (date 1), 8 days (date 2), and 17 days (date 3) from the deployment of tethered leaves in the field. Error bars represent 1 SE.

TABLE IV

Results of the 2-way ANOVA testing the effect of site and of time elapsed from the beginning of the experiment on th proportion of leaf material consumed by crabs or shredded and accumulated inside crab burrows.

Source of variation	% Consumed			% Shredded	
	df	SS	F	SS	F
Site	2	0.79	3.14*	1.07	10.75***
Date	2	21.54	85.68***	4.10	41.11***
Site* date	4	0.42	0.84 NS	1.77	8.84***
Error	171	21.50		8.54	

NS: $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Table IV). Significantly lower proportions of leaf material had been consumed after 24 h compared with after 8 and 17 days (SNK: first sampling date < second sampling date = third sampling date, at $\alpha = 0.05$). Lower proportions of leaf material were consumed at site 3, i.e. the *R. stylosa* forest, compared to sites 1 and 2, dominated by *B. exaristata* and *C. tagal*, respectively (SNK: site 3 < site 2 = site 1, at $\alpha = 0.05$).

There was a significant interaction between site and time elapsed from the beginning of the experiment in the proportion of the shredded leaf material retrieved from the crab burrows (Table IV). After 24 h, 36.34% (SE = 7.18, $n = 20$) of the initial leaf weight was retrieved as shredded material from the crab burrows at site 1, while 24.66% (SE = 7.35, $n = 20$) was retrieved at site 2. The amount of marked leaf fragments was insignificant at site 3, on all sampling dates, and at site 1 and 2 after 8 and 17 days from the beginning of the experiment (Fig. 3). There was significantly more leaf material shredded inside crab burrows on the first sampling date compared to subsequent sampling dates at sites 1 and 2 (SNK, $\alpha = 0.05$). There was no significant difference among the three sampling dates at site 3 (SNK, at $\alpha = 0.05$). The proportion of leaf material shredded and accumulated inside crab burrows differed among sites on the first sampling occasion (SNK: site 1 > site 2 > site 3, at $\alpha = 0.05$), but not on the second sampling (SNK: site 1 = site 2 = site 3, at $\alpha = 0.05$). After 17 days, no leaf remains were found inside crab·burrows at the three sites.

The proportions of leaves carried inside crab burrows did not significantly differ between the three sampling dates ($\chi^2 = 1.37$, df = 4, NS), indicating that most leaves were taken underground within the first 24 h from the beginning of the experiment.

Greater amounts of leaf fragments (pooling both marked and unmarked fragments) were dug out of burrows on the second sampling date at the high- and mid-high intertidal sites (sites 1 and 2) ($F = 14.92$, df 2 and 137, $p < 0.001$, among sites; $F = 10.62$, df 2 & 241, $p < 0.001$, among dates; SNK at $\alpha = 0.05$). This date coincided with a spring tide.

The C:N ratios measured for leaves of different mangrove species (*R. stylosa*, *B. exaristata*, and *C. tagal*) had not significantly decreased after 17 days in the crab holes

Results of the 3-way ANOVA testing the effect of leaf species (*R. stylosa*, *C. tagal*, and *B. exaristata*), microhabitat (on the forest floor or inside crab burrow) and time elapsed from the beginning of the experiment (1, 8, and 17 days), on the changes in C:N ratio of mangrove leaves decomposing in the field. ANOVA performed on non-transformed data.

Source of variation	df	SS	F
Species	2	4274.04	17.17**
Microhabitat	1	587.47	4.72*
Date	2	428.12	1.72 NS
Species * microhabitat	2	271.00	1.09 NS
Species * date	4	461.40	0.84 NS
Microhabitat * date	2	7.98	0.03 NS
Species * microhabitat * date	4	959.28	1.93 NS
Error	36	4480.56	

NS: $p > 0.05$; *: $p < 0.05$; **: $p > 0.01$; ***: $p < 0.001$.

(Table V). There was a significant effect of leaf species (leaves of *R. stylosa* had lower C:N ratios than the other species to begin with; Table 1), and of the microhabitat where the aging of the leaves had taken place (sediment surface vs. crab burrow): the burial of the leaves had significantly enhanced their enrichment in nitrogen.

FEEDING BEHAVIOR OF *S. MESSA*

Individuals of *S. messa* spent 50.56% (SE = 9.67, $n = 9$) of their time resting by the entrance of a burrow, at a base of a mangrove seedling or prop root, or on prop roots, without showing any sign of activity. Feeding was carried out for 29.01% (SE = 6.78, $n = 9$) of the time, while 7.28% (SE = 3.76, $n = 9$) of the time was devoted to other activities (namely wandering on the forest floor and interacting with conspecifics). The proportions of time spent in different activities differed among type of activity ($F = 8.17$, df 2 and 18, $p < 0.01$), but not with sex ($F = 0.37$, df 2 and 18, NS), with no significant interaction between the two factors ($F = 0.65$, df 4 and 18, NS).

Crabs spent significantly more time picking unidentified material from the mud surface (average = 27.44%, SE = 7.86, $n = 9$) compared with grazing on the mangrove leaves laying on the forest floor (average = 5.56%, SE = 3.72, $n = 9$) or picking material (possibly algae) from the surface of the mangrove prop roots (average = 5.65%, SE = 3.38, $n = 9$), with no significant difference between these two ($F = 4.60$, df 2 and 18, $p < 0.05$; SNK: mud surface > mangrove leaves = prop root surface, at $\alpha = 0.05$). There was no difference in the proportion of time spent feeding on different substrates between sexes ($F = 0.40$, df 2 and 18, NS) and no significant feeding substrate by sex interaction ($F = 0.34$, df 4 and 18, NS).

DISCUSSION

Two of the most abundant leaf-eating crabs of North Queensland mangroves, *S. messa* and *S. smithii*, consume mangrove leaves before a significant leaching of polyphenolics or decrease in the C:N ratio occur. In addition, these species exhibit absorption efficiencies of non-decayed plant material comparable to those measured for other herbivorous crustaceans on various food items (Micheli, 1993). Further, *S. messa* successfully moults and reproduces when fed adequate amounts of fresh mangrove litter (Micheli, 1993). The capability of directly exploiting the primary production has a greater efficiency than a two-step system, comprising a phase of microbial decay before detritus is consumed (Odum, 1970; Foulds & Mann, 1978). Most of the primary production in mangrove forests is made available to the consumers as litter, thus providing a constantly renewed, though spatially and temporally fluctuating resource (Williams et al., 1981; Boto et al., 1984, Twilley et al., 1986). The high secondary production (Macintosh, 1984; Sasekumar, 1984), the abundance of species (Davie, 1982, 1985; Jones, 1984), and the distribution through the whole intertidal gradient (Macnae, 1968, 1969) of sesarmid crabs in tropical Australia, may be linked to the development of efficient feeding on mangrove litter by these crabs. The grazing on fresh vascular plant material by marine invertebrates has been documented for other crustaceans (in a mysid shrimp, Foulds & Mann, 1978; in a portunid crab, Klumpp & Nichols, 1983; and in the mangrove crab *Aratus pisonii*, Beever et al., 1979), and for the mangrove mollusc *Melampus coffeus* (Heald, 1969).

Ingestion rates of different species of mangrove leaves by *S. messa* and *S. smithii* did not correlate significantly with any of the leaf characteristics considered. Previous studies suggested that grazing of mangrove leaves by sesarmid crabs might be deterred by the high tannin content of fresh mangrove litter (Giddins et al., 1986; Neilson et al., 1986). Crabs may also be nitrogen limited, due to the high C:N ratio of mangrove leaves. Both tannin content and C:N ratios of the leaf species offered to the crabs in the present study, however, did not have any effect on their leaf choice. *Avicennia marina* leaves, in particular, had both the lowest tannin content and the lowest C:N ratio among the species here considered but were not selected by either crab species in the laboratory, and ranked last at three of the five field sites where leaf choice experiments were performed, although such difference was not significant. On the contrary, *S. smithii* significantly preferred *R. stylosa* leaves in the laboratory. *R. stylosa* leaves had the highest concentration of tannins compared with the other species.

Sesarma messa significantly preferred decayed leaves over senescent ones. These results agreed with those of similar experiments using other sesarmid species (Giddins et al., 1986; Camilleri, 1989; Lee, 1989). The tannin content of the aged leaves used in this experiment was not measured. However, Robertson (1988) found that approximately 50% of the original leaf tannin content is lost by leaching during the first 2 weeks. The aged leaves that I used, therefore, were likely to have tannin contents comparable or higher to that of senescent *Avicennia marina* leaves (Table III). Based

on the results of the laboratory leaf choice experiments (see above), tannin content of the leaves does not seem to affect crab preferences for particular leaves, at least within the range of variation of tannin contents considered here (from 6.76 to 17.43%; Table I). The leaching of tannins from decaying mangrove leaves, therefore, seems unlikely to underlie the distinct preference for aged leaves exhibited by the crabs.

No significant decrease in the C:N ratio of the decaying leaf material was observed after 17 days in the field, therefore the hypothesis that crabs select decayed leaves because of their higher C:N ratios was not supported. In fact, there was no significant correlation between ingestion rates of the crabs on the different leaf types offered and the leaf C:N ratios in both laboratory leaf choice experiments. Bacterial and fungal densities on leaves, however, increase early in the decomposition process (Cundell et al., 1979; Fell & Masters, 1980; Robertson, 1988). Even though bacterial and fungal activities do not alter the nitrogen content of litter until later on (significant changes occurred after 20 days, Fell et al., 1975; Robertson, 1988), they may improve the palatability of leaves (Schoth et al., 1968) and/or contribute with their enzymes to the digestion of the plant material by the crabs (Barlocher, 1982; Punja & Jenkins, 1984). In addition, other leaf characteristics might change with the age of leaves. Neilson & Richards (1989) reported that water-soluble pectates complexed with proanthocyanidins account for 15% of dry weight in fresh *C. tagal* leaves. These compounds are readily lost from decaying leaves, possibly improving leaf palatability (Neilson & Richards, 1989). Similarly other compounds contained in mangrove leaves might play a greater role than tannins if affecting herbivory by sesarmid crabs on mangrove litter.

Although particular leaf species (for *S. smithii*) and leaf ages (for *S. messa*) were selected in the laboratory choice experiments, and gave a better rearing performance in longer-term feeding experiments (in *S. messa*, Micheli, 1993), a clear pattern of leaf preference was not observed in the field, suggesting that mechanisms other than food preferences may be operating under natural conditions. Based on the results of the laboratory leaf choice experiments, a greater proportion of *R. stylosa* leaves was expected to be consumed at sites where *S. smithii* was present than at sites were this species was not found. In the field choice experiments, however, *R. stylosa* leaves were never selected over other leaf species at all five sites considered. This result might be explained by the fact that several different crab species are present at the different sites, even though *S. messa* and *S. smithii* seemed to be by far the most abundant. Grazing by crabs of different species might overlap and mask a possible choice exerted by the single species. Alternatively, different species of leaves could be more or less obvious to the crabs in the field, depending on their size or on their contrast with the background colors. The crab food preferences and the probability of encounter with the leaves might interact and produce the lack of selectivity observed.

The dominant mangrove species found at each site (*B. exaristata* at site 1, *C. tagal* at sites 2 and 4, and *Rhizophora* spp. at sites 3 and 5), moreover, seemed to have no effect on the crab leaf choice. Regardless of what leaf species was most commonly found at each site, leaves of all four species were consumed by the crabs at similar rates.

A lack of selective consumption of litter of different qualities in the field was also observed when tethered leaves of *R. stylosa* of 1, 7 and 17 days of age where deployed in a low-intertidal *Rhizophora* spp. forest (A.I. Robertson, unpubl. data). Despite the strong preference exhibited by different crab species for decayed plant material (present study; Giddins et al., 1986; Camilleri, 1989; Lee, 1989), rates of consumption of leaves of the three ages in the field were not significantly different.

In a previous study conducted in this area, crabs consumed significantly more *Avicennia marina* seedlings than all other species in food choice experiments carried out in the field, during the wet season (Smith, 1987a). Since the present field experiments were carried out, on the contrary, during the dry season (August), the lack of selectivity observed could mirror a decrease in food availability at this time of the year (Ivlev, 1961; Beukema, 1968; Werner & Hall, 1974; White, 1978) when the forest productivity is minimum (Williams et al., 1981; Boto et al., 1984). This hypothesis seems to be supported by the trends observed in the leaf choice field experiment. There seemed to be a trend towards a greater selectivity at sites 2 and 3 compared with sites 4 and 5, where grazing had been generally more intense. More tethered leaves, in fact, had been carried in crab burrows at site 4, a *C. tagal* forest, compared with site 2, the other *C. tagal* forest (85.0 vs. 37.5%). The same result was observed for site 5, a *Rhizophora* spp. forest, compared with site 3, the other *Rhizophora* sp. forest (51.3 vs. 38.8%). This may suggest that the crabs were less selective at sites where a greater proportion of litter was consumed, i.e. where competition for food might have been more intense.

The dry season also coincides with higher energy requirements for female crabs, of which a greater proportion are ovigerous at the end of the dry season, in September and October (pers. obs.). Consuming adequate amounts of leaf litter might thus become critical for mangrove crabs during the reproductive season. Previous research carried out in north Queensland showed that nearly all of the litter fall is consumed by crabs during the dry season (Robertson, 1986; Robertson & Daniel, 1989). Litter supply might be a limiting factor for sesarmid crabs at this time of the year, possibly causing them to feed more opportunistically during the dry season than during the wet season. Detritus supply can limit the secondary production of invertebrate populations in other wetland systems. Plant detritus, for instance, proved to be limiting for both fiddler crabs (Genoni, 1985) and molluscs (Stiven & Kuenzler, 1979) in *Spartina* sp. salt marshes of the eastern coast of the United States, despite the high productivity exhibited by these systems (Odum, 1971).

The experiment in which tethered mangrove leaves were sampled on different dates confirmed the observation that *S. messa* immediately consumes litter taken underground (Robertson, 1986). In addition, this experiment indicated that *S. smithii* ate the litter accumulated in its burrows within one week, instead of letting it decompose for weeks, as previously suggested (Giddins et al., 1986). *S. smithii* might accumulate the litter in its burrows coinciding with spring tides, when its above ground activity is the greatest (pers. obs.) and consume it during the following days. Higher amounts of leaf fragments were in fact found in crab burrows coinciding with spring tides.

Crab species that take mangrove leaves underground before consuming them (such as *S. smithii*) are likely to have a more significant impact in decreasing tidal export of litter from mangrove forests than species (such as *S. messa*) that graze on the leaves outside their burrows and leave leaf remains on the sediment surface, where they can be flushed away by the tide. Greater proportions of primary production are thus expected to be kept within mangrove systems as a consequence of the foraging of sesarmid crabs where *S. smithii* is the dominant species rather than in forests where *S. messa* prevails. In the present study, leaves were tethered and thus could not be flushed away by the tide. The proportion of leaf material consumed by the crabs is therefore likely to have been over-estimated, particularly at sites where *S. messa* was the dominant species (at sites 3 and 5).

Litter was almost completely consumed, inside the burrows, before significant changes in the C:N ratios of the leaves occurred, so that the burial of leaves by sesarmid crabs does not seem to have the function of improving food quality. *S. smithii* individuals rarely leave their burrows and it is likely that most activities, feeding and reproduction included, are carried out underground. *S. messa*, on the contrary, is commonly seen outside its burrow, wandering or feeding on the forest floor. Several mating pairs where also seen in the course of this study, indicating that burrow occupation is not critical to the reproductive success of this species. Interspecific differences in the adaptive value of burrow occupation in these two sesarmid species could underlie their different foraging behavior. *S. smithii*, in particular, might carry leaves underground before consuming them in order to reduce the time spent outside its burrow, rather than to improve the litter quality.

Both fresh and decayed mangrove litter is nitrogen-poor. Mangrove crabs, therefore, are not likely to meet their nitrogen requirments from this source. Both crab species occasionally consume nematodes, insects, small crustaceans, and juvenile conspecifics (Giddins et al., 1986; pers. obs.). Field observations of *S. messa* individuals showed that crabs spent considerably longer proportions of time picking material from the sediment surface than feeding on other substrates, suggesting that bacteria and microalgae scraped up from the first millimetres of mud may be a very important source of nitrogen for this species. Crabs also spent comparable amounts of time feeding on mangrove leaves and picking material from the surface of mangrove trunks and prop roots. The macroalgae growing on the lower parts of these surfaces might be a common food item for *S. messa*, and possibly for other grazers. This might indicate that benthic algae significantly contribute to supporting secondary production in mangrove forests, and that the role of benthic algae in the energy flow of the mangrove system deserves further investigation.

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