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Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves?

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Abstract Sesamid crabs dominate Indo West-Pacific mangroves, and consume large amounts of mangrove litter. This is surprising, since mangrove leaves have high tannin contents and C/N ratios that far exceed 17, normally taken as the maximum for sustainable animal nutrition. This paradox has led to the hitherto untested hypothesis that crabs let leaves age in burrows before consumption, thereby reducing tannin content and C/N ratio. We excavated burrows of *Neosarmatium meinerti* within high-shore *Avicennia marina* mangroves, and investigated whether burrow leaves had C, N or C/N values significantly different from those of senescent leaves. Leaves were found in <45% of burrows, mostly only as small fragments, and N concentrations and C/N ratios of burrow leaves never varied significantly from senescent leaves. The leaf-ageing hypothesis was therefore not supported. In the field *N. meinerti* and *Sesarma guttatum* fed on sediment in 76% and 66–69% of observations, respectively, and on leaves in <10% of observations. Sediments from two *A. marina* mangroves had a mean C/N ratio of 19.6. Our results, and the literature, show that mangrove leaves are unlikely to fulfil the N requirements of crabs, whether or not leaf ageing takes place. Sediment detritus could be a richer source of N, as shown by lower C/N ratios and regular ingestion by crabs. By fragmenting leaves crabs may be elevating the nutritional quality of the substrate detritus.

Keywords Carbon/nitrogen ratio · Nutrition · Leaves · Burrows · Sediments

Introduction

The importance of grapsid crabs (Crustacea: Grapsidae) to Indo-West Pacific mangrove ecology is unequivocal

(for a review, see Lee 1998). Grapsid communities are highly productive (Hartnoll et al., in press) and may significantly affect soil chemistry and primary productivity (Smith et al. 1991), mangrove zonation and colonisation (Smith 1987; Smith et al. 1989), food web dynamics (Camilleri 1989, 1992; Robertson 1991), nutrient retention, litter decomposition and the offshore export of mangrove production (Robertson 1991; Lee 1995; Skov 2001). Although most grapsids are opportunistic scavengers, many have essentially herbivorous diets, in particular members of the largest subfamily, the Sesarminae (Lee 1998). Multiple field (Camilleri 1992; Micheli 1993b; Twilley et al. 1997) and laboratory (Camilleri 1989; Micheli et al. 1991; Micheli 1993a; Kwok and Lee 1995) studies leave no doubt that sesarmids ingest mangrove leaves. Leaves often comprise >85% of sesarmid stomach contents (e.g. Malley 1978; Leh and Sasekumar 1985; Dahdouh-Guebas et al. 1999), and sesarmids may remove 79–95% of mangrove leaf fall from the forest floor (Robertson and Daniel 1989; Skov 2001). The nutritional rationale of ingesting leaves is nevertheless puzzling. Freshly fallen (i.e. senescent) mangrove leaves have notably high C/N ratios (e.g. Steinke et al. 1983; Wafar et al. 1997) several times in excess of the value of 17 suggested as a general maximum for sustainable animal nutrition (Russell-Hunter 1970). Giddens et al. (1986) proposed that crabs may plaster leaves onto burrow walls to allow tannins to leach and increase the edibility of leaves (Cundell et al. 1979; Neilson et al. 1986). In addition leaf N content increases and C/N ratio decreases during breakdown (e.g. Steinke et al. 1983; Wafar et al. 1997), largely through microbial activity (Gotto and Taylor 1976; Cundell et al. 1979). Thus by not eating leaves immediately, but leaving them to age on the burrow wall, crabs might not only improve the digestibility of leaves (Giddens et al. 1986), but also decrease the C/N ratio of their diet (Robertson and Daniel 1989; Micheli 1993a; Lee 1989). Throughout this paper we refer to this modification of the palatability theory by Giddens et al. (1986) as the “leaf-ageing hypothesis”. A number of studies have indirectly supported this hypothesis

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esis, either by demonstrating that crabs preferred decayed to senescent leaves (Giddens et al. 1986; Camilleri 1989; Lee 1989; Micheli 1993b), or leaves with lowered tannin content (Neilson et al. 1986), or by showing that crabs grew better on aged leaves (Micheli 1993a; Kwok and Lee 1995). Direct evidence for the leaf-ageing hypothesis has, however, not been produced. Although several authors have noted that leaves may occur in crab burrows (Giddens et al. 1986; Robertson 1986), all but one (Steinke et al. 1993) recorded this only qualitatively. We know of no study comparing C/N ratios of burrow leaves to senescent leaves. If burrow-ageing occurs, leaves from burrows should have significantly lower C/N ratios than senescent leaves.

Ólafsson and M. W. Skov (unpublished data) and Bouillon et al. (in press) noted how the stable C isotope ratio of some sesarmids resembled the C signal of sediments more than that of leaves of the resident mangrove, suggesting that sediments may be of higher dietary importance to the crabs. Although several studies have noted that crabs may feed on mud (e.g. Day 1967; McNae 1968; Camilleri 1992), only one has quantified sediment feeding (Micheli 1993b), and none have examined the nutritional basis for this behaviour.

This paper poses three questions:

1. Is there field evidence to support the leaf-ageing hypothesis?

This will be addressed by: (a) examining the frequency of *Avicennia marina* leaves in *Neosarmatium meinerti* burrows, (b) measuring the C/N ratios of burrow leaves and testing the null hypothesis that *the C content, N content or C/N ratio of burrow leaves do not vary significantly from those of senescent leaves.*

2. Do sesarmids display any marked behavioural food-item preference in the field?
3. Might sediment be an important source of N for mangrove sesarmids?

The C/N ratio of sediments from the forest floor, sediment cores and crab burrows is examined.

Materials and methods

Study sites and species

The survey was conducted within the terrestrial fringe [3.6–4.0 m above chart datum (spring tidal range ~4 m)] of two forests on Unguja Island (Zanzibar, Tanzania; 39°12'E, 6°09'S):

1. At Maruhubi mangrove (~100 ha.) the study zone was an almost pure stand of *A. marina* trees in muddy to medium sandy sediments. The commonest crabs were *N. meinerti*, *Sesarma guttatum* and *Uca annulipes*.
2. At Kisakasaka mangrove (<300 ha) the zone was 80% dominated by *A. marina*, and by fine and silty sediments. The most important crabs were *N. meinerti* and *S. guttatum*, with some *Neosarmatium smithi* at lower levels. Feeding activity of *S. guttatum* was also observed within a low-shore *Rhizophora mucronata* stand at Kisakasaka, flooded on 97% of all tides. *S. guttatum* was dominant, though other grapsids occurred (e.g.

Metopograpsus spp. and *Sesarma leptosoma*). More information regarding these mangroves is given elsewhere (Machiwa 1998; Shunula and Whittick 1999; Skov 2001).

The obligate and non-obligate burrowers, *N. meinerti* and *S. guttatum*, are two of the most abundant crabs within East African mangroves (Hartnoll et al., in press). *N. meinerti* [adults: 24–46 mm carapace width (CW)] digs 0.8–1.6 m deep burrows. *S. guttatum* (adults: 11–25 mm CW) is more active, and forages within a few metres of a preferred shelter (Skov 2001). Both species congregate under trees and are avid leaf eaters.

C/N ratio of burrow leaves and senescent leaves

Leaves of *A. marina* were obtained from the burrows of *N. meinerti* as follows. Two 80 m by 40 m transects were laid out 300 m apart in each *Avicennia* mangrove location, and worked during January and March 2000, respectively. Areas were subdivided into 4-m² sub-units, ignoring clearings, drainage channels and sites with trees other than *A. marina*. Six sub-units (quadrats) were randomly selected per transect. Quadrat burrows of *N. meinerti* were numbered, and three randomly selected. Burrows were cast with cement (paint-like viscosity) and excavated 3 days later. The cement structures ensured that individual burrows could be traced into the soil, a task otherwise greatly complicated in areas of high burrow density. All burrows, except those of one Kisakasaka quadrat (subsequently discarded), were found entirely filled with cement upon excavation. In 81% of casts the resident crab (all *N. meinerti*) had been trapped. Casts were wrapped in plastic food-wrapping with ~1 cm of soil still attached. In the laboratory, sediments were separated from the sides of casts, passed through a sieve (2-mm mesh), and leaf fragments extracted. The cement was then broken and leaves removed. Extracted leaves were rinsed of loose sediments before drying (60°C, 48 h). C and N analyses of milled leaves were performed in a Carlo Erba NC 2500 CHN elemental analyser. Elemental concentrations will be reported as percentages of the sample mass. SDs of three aliquots of one leaf sample were ±0.06% and ±0.05% of total C and N contents, respectively.

Thirty senescent *A. marina* leaves were collected from a series of trees. After drying five of these were randomly selected and C/N analysis carried out as above.

Feeding behaviour

Feeding behaviour of *N. meinerti* and *S. guttatum* was observed within the same transects as the burrow casting. Twelve 4-m² quadrats per transect were randomly selected as above, six for a spring and six for a neap tide day. Observations were taken between 07:00 hours and 10:00 hours during February–April 2000. Crab feeding activity was recorded for 30 min per quadrat, and was scored as one of six types: (1) feeding on sediment (mud); (2) scraping or picking material (other than algae) off roots or wooden debris (roots); (3) feeding on, or dragging leaves into burrow (leaves); (4) feeding on, or dragging mangrove propagules into burrow (fruit); (5) feeding on algal mats (algae); or (6) feeding on animal matter. A type of behaviour was scored once for each crab seen showing it. Feeding was defined as continuous when >20 s, with repeated picking at a food source with subsequent transfer to mouthparts. Feeding on animal matter was not recorded in 570 observations and was excluded from the analysis.

C/N ratio of mangrove sediments

Three types of sediments were collected from each burrow-casting quadrat: (1) a surface sample (400 cm², 0.5 cm deep) from the quadrat centre, avoiding digging burrow spoil and faeces (surface); (2) an 18-mm core inserted centrally to the depth of casting burrows (core); (3) a burrow sample from one casting burrow

Table 1 The mean ($\pm 95\%$ confidence interval) C and N contents and C/N ratios (by weight) of *Avicennia marina* leaves and mangrove sediments. Samples originated from Maruhubi (MH) and Kisakasaka (KIS) transects. n =samples (for Burrow leaves: n =burrows with leaves)

Location	Burrows	n	N (%)	C (%)	C/N ratio
Burrow leaves					
MH 1	18	9	1.03 (0.26)	39.5 (1.1)	42.8 (10.2)
MH 2	18	11	0.61 (0.06)	37.4 (0.7)	62.7 (5.9)
KIS 1	15	3	0.66 (0.12)	38.8 (1.6)	59.9 (8.1)
KIS 2	18	8	0.61 (0.13)	35.3 (3.3)	61.9 (8.2)
Mean			0.72 (0.01)	37.3 (1.2)	57.0 (5.1)
Senescent leaves	–	5	0.63 (0.07)	42.6 (1.5)	68.9 (9.0)
Sediments					
MH 1	–	15	0.20 (0.09)	3.47 (1.39)	20.0 (1.9)
MH 2	–	15	0.21 (0.08)	4.36 (1.23)	23.2 (2.6)
KIS 1	–	15	0.16 (0.03)	2.89 (0.57)	18.3 (0.9)
KIS 2	–	15	0.24 (0.04)	4.06 (0.62)	17.1 (0.4)
Mean			0.21 (0.03)	3.70 (0.52)	19.6 (1.0)

(a 5-cm wide, 0.5-cm thick band of soil was scraped from the bottom to the top of the cement cast) (burrow). Sediments were dried, finely ground and a 0.5-g sub-sample taken for C/N analysis. Samples were not acid-treated before elemental analysis, to facilitate like-for-like comparison with mangrove leaves.

Statistical analysis

Statistical analyses were performed following Siegel (1956) and Zar (1984). Mean values are reported with 95% confidence intervals and df will be listed as subscripts to F (ANOVA) values.

The experimental null hypothesis regarding leaf composition (H_0 : burrow leaves=senescent leaves) was tested for N content, C content and C/N ratio. Senescent and burrow leaves were compared by ANOVA with Scheffe's (unequal sample sizes) post hoc multivariate comparisons. Each quadrat that contained leaves was a single replicate: the leaves inside were pooled, and ANOVA conducted on quadrat means. Maruhubi transects 1 and 2 and Kisakasaka transect 2 each had five quadrats with leaves, whereas Kisakasaka transect 1 had three. Adding to these the five senescent leaf samples meant that ANOVA was conducted on a total of 23 samples. The N data needed log-transformation to comply with homoscedasticity.

Results

Leaf chemistry

Sixty-nine *N. meinerti* burrows were cast and excavated by using 500 kg cement. Casting failed in one quadrat in Kisakasaka transect 1 (KIS 1), where results are based on 15 rather than 18 burrows. Leaves were found in 45% of burrows, the majority more than three-quarters eaten. The proportion of burrows per transect that contained leaves was compared by a one-way ANOVA based on quadrat means. There were no significant differences between transects [$F_{(19)}=0.5$; $P=0.7$], indicating that leaf deposition by crabs was consistent between locations and over time.

C and N contents and C/N ratios of leaves are shown in Table 1. C/N ratios of burrow leaves ranged from 25 to 83 with an overall mean of 57, whilst the C/N ratio of senescent leaves ranged from 59 to 84 with an overall mean of 70. C, N and C/N values of leaves were com-

pared by one-way ANOVA followed by Scheffe's multiple comparisons. The null hypothesis (burrow leaves=senescent leaves) was rejected in two cases: burrow leaves in Kisakasaka transect 2 (Scheffe: $P=0.001$) and Maruhubi transect 2 (Scheffe: $P=0.01$) had significantly lower C contents than senescent leaves [$F_{(18)}=8.33$, $P=0.001$]. Nevertheless, although burrow leaves in one transect (Maruhubi transect 1) had an elevated mean N content and lowered C/N ratio compared to senescent leaves, in the remaining three transects, burrow leaves varied little from senescent leaves, and none of the burrow leaves of these transects had N contents or C/N ratios that differed significantly from those of senescent leaves [N: $F_{(18)}=2.75$, $P=0.06$] [C/N ratio: $F_{(18)}=2.78$, $P=0.06$]. Thus the burrow leaves had generally not undergone significant ageing since leaf fall.

Feeding behaviour

The feeding behaviour of *N. meinerti* and *S. guttatum* was observed on eight and ten occasions within transects at Kisakasaka and Maruhubi, respectively (Table 2). *N. meinerti* fed more frequently on mud than on any other food class, irrespective of location, transect or tidal phase. A mean of $75.8 \pm 10.7\%$ of crabs fed on mud, compared to $11.6 \pm 6.3\%$ on roots, $9.5 \pm 9.8\%$ on leaves, $2.6 \pm 2.0\%$ on fruit and $0.5 \pm 1.0\%$ on algae.

The feeding behaviour of *S. guttatum* was observed on the same occasions as that of *N. meinerti*, as well as on 2 days in a low-shore *Rhizophora* stand. Within the combined *Avicennia* habitats, $69.3 \pm 12\%$ fed on mud, $8.1 \pm 8.1\%$ on roots, $16.4 \pm 8.9\%$ on leaves, $4.7 \pm 5.8\%$ on fruit and $1.4 \pm 2.8\%$ on algae. In the *Rhizophora* area, $65.7 \pm 16.6\%$ fed on mud, $24.9 \pm 16.3\%$ on roots, $5.8 \pm 3.9\%$ on leaves, $2.6 \pm 3.0\%$ on fruit and $1.0 \pm 1.9\%$ fed on algae. Clearly *S. guttatum* fed more on mud than on any other food.

Table 2 An overview of observations on *Neosarmatium meinerti* and *S. guttatum* feeding within two *Avicennia* (Maruhubi and Kisakasaka) and one *Rhizophora* stand

Species	Location	Tide	Transects	Quadrats	Feeding crabs
<i>N. meinerti</i>	Maruhubi	Spring	1, 2	12	101
		Neap	1, 2	12	79
	Kisakasaka	Spring	3, 4	12	46
		Neap	3, 4	12	56
<i>S. guttatum</i>	Maruhubi	Spring	1, 2	9	88
		Neap	1, 2	11	35
	Kisakasaka	Spring	3, 4	10	54
		Neap	3, 4	5	6
<i>Rhizophora</i>	Spring	5	6	74	
	Neap	5	7	31	
Total	3		5	96	570

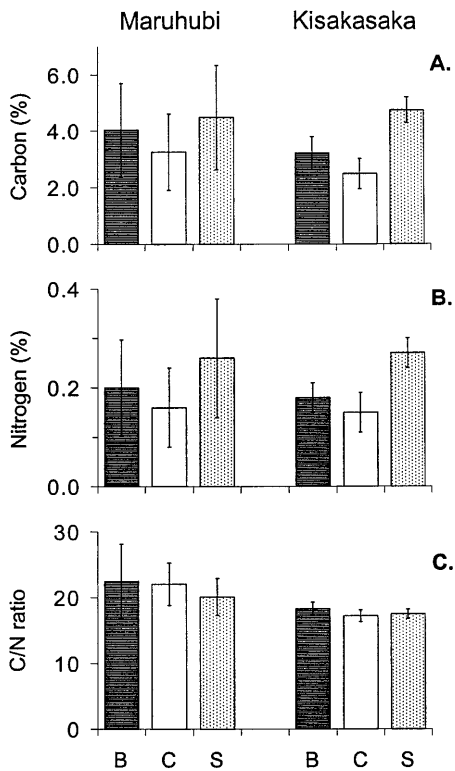


Fig. 1 The mean ($\pm 95\%$ confidence interval) C (A) and N contents (B) and C/N ratios (C) of sediments. Samples (ten per type) originated from *Neosarmatium meinerti* burrows (B), cores (C) or the sediment surface (S)

C/N ratios of sediments

Sediment samples from two Maruhubi quadrats were abandoned due to sudden heavy downpours during excavation, and cement casts in one Kisakasaka quadrat failed. This reduced replication in three transects from six to five quadrats. To ensure equal sample sizes and facilitate nested ANOVA (below) one (randomly selected) quadrat was subsequently discarded from the “full” transect. Figure 1 shows mean values per mangrove and Table 1 shows means per transect. C/N ratios of sediments ranged from 15.1 to 32.7, with an overall mean of 19.6. A nested ANOVA with three levels (location, transect and sediment type) showed the mean C/N ratio of

Maruhubi sediments (21.5) varied significantly from that of Kisakasaka (17.7) ($F_{(1)}=1044.7$; $P<0.001$). This was due to differences between transects, as shown by a significant interaction between location and transect [$F_{(1)}=3.9$; $P<0.03$]. A post hoc Tukey test showed the C/N ratios in the second Maruhubi transect (23.2) were significantly higher than those of any of the remaining transects (20, 18.3 and 17.1) (Tukey: $P=0.001-0.04$). There were no significant differences between the C/N ratios of burrow, core or surface sediments [$F_{(8)}=0.7$; $P>0.5$].

Discussion

The leaf-ageing hypothesis, that sesarmid crabs may plaster mangrove leaves to their burrow walls in order to improve leaf palatability and nutritional quality, has been discussed in the literature for >15 years (Giddens et al. 1986). Nevertheless, despite a substantial research focus into leaf eating by sesarmid crabs (for a review, see Lee 1998), this study is the first to directly test this hypothesis in the field. We excavated 69 burrows of *N. meinerti* to estimate the frequency of leaf burial, and to test the null hypothesis that C content, N content or C/N ratio of burrow leaves do not significantly differ from those of freshly fallen leaves. Leaves of *A. marina* were found in <45% of the excavated burrows, and more than three-quarters of them had been eaten in most cases. Storing of whole leaves by *N. meinerti* was therefore not common. N concentrations and C/N ratios of burrow leaves did not vary significantly from those of freshly fallen senescent leaves, suggesting that significant leaf ageing had not taken place. Few studies have examined the natural occurrence of leaves in crab burrows and none, except the present, have estimated their frequency or chemistry. Steinke et al. (1993) found only small quantities of leaf litter in South African burrows of *N. meinerti*, whereas Alexander and Ewer (1969) found none in the burrows of *Sesarma catenata* and *Cyclograpsus punctatus*. Neither paper reported on the frequency of leaves in burrows, though Steinke et al. (1993) did measure the mass of burrow leaves per square metre. Although Giddens et al. (1986) and Robertson and Daniel (1989) both reported sightings of leaves in crab burrows, neither examined

Table 3 Literature records of C/N ratios in mangrove leaves. Values at leaf fall (*Senescent*), the lowest value recorded (*Aged*) and the times to reach the minimum (*Time*) are given

Species	Location	Senescent	Aged	Time (days)	Reference
		C/N ratio			
<i>Avicennia marina</i>	Australia	44	25	156	Robertson (1988)
	Hong Kong	27	22	14	Kwok and Lee (1995)
	Tanzania	69	49	21	M. W. Skov and R. G. Hartnoll (unpublished data)
<i>A. germinans</i>	Florida	47	17	148	Twilley et al. (1986)
<i>Bruguiera exaristata</i>	Australia	92	84	17	Micheli (1993b)
<i>B. gynorrhiza</i>	S. Africa	74	35	175	Steinke et al. (1983)
<i>Ceriops tagal</i>	Australia	184	66	70	Giddens et al. (1986)
	Australia	80	38	75	Robertson (1988)
<i>Kandelia candel</i>	Hong Kong	49 ^a	17 ^a	56	Lee (1989)
<i>Rhizophora mangle</i>	Florida	91	41	28	Cundell et al. (1979)
	Florida	98	33	148	Twilley et al. (1986)
<i>R. mucronata</i>	Tanzania	109	94	21	M. W. Skov and R. G. Hartnoll (unpublished data)
<i>R. stylosa</i>	Australia	96	93	20	Camilleri (1989)
	India	75	36	160	Wafar et al. (1997)

^a Acid treated before analysis

this critically. Robertson (1986) offered tethered leaves to crabs and found that crabs consumed >78% of tethered leaf material within 6 h of burial. Micheli (1993b), in a similar study, found that *Sesarma messa* and *N. smithi* consumed about 50% of leaves within 24 h and that virtually all leaves had been eaten after 8 days. As burrows were not excavated between the first and the eighth day, it is probable that most leaves were eaten early in that period. Neither the literature, nor the results presented here, therefore, lend support to the leaf ageing hypothesis.

Virtually all studies that have supported the leaf ageing hypothesis have done so through conjecture. Several papers, for instance, have noted how sesarmids in the field (Camilleri 1989; but see Micheli 1993b) and in the laboratory (Giddens et al. 1986; Lee 1989; Micheli 1993b) may prefer to ingest aged leaves rather than senescent leaves. However, the fact that crabs choose a certain decomposition stage over another does not necessarily mean that crabs will store leaves. Competition for leaves is often fierce and forest floors are frequently swept clean by crabs (Robertson 1986; Steinke et al. 1993; Skov 2001). Storing leaves may be a luxury the animal can seldom afford. Micheli (1993b) suggested that leaf storage has the aim of limiting time spent on the forest floor, rather than improving the nutritional qualities of leaves. We hypothesise that storage of leaves is a response that predominates only when leaf litter-fall regularly exceeds the requirement of the forest floor community.

The leaf-ageing hypothesis (Giddens et al. 1986) was based on unpublished observations by Kneipp and Alexander who noticed that “crabs kept in artificial burrows placed leaves on the walls of the burrow instead of eating them” (Giddens et al. 1986). The immediate cause of pasting leaves to walls, it was argued, was probably the more acceptable “taste” of aged leaves since flavolan content reduces during decomposition (Giddens et al.

1986; Neilson et al. 1986). Succeeding literature has carried this further, and questioned whether ageing of leaves by crabs might not also cause significant reductions in the C/N ratio (e.g. Robertson and Daniel 1989; Micheli 1993a), in particular to conform with the paradigm of the Russell-Hunter ratio (e.g. Lee 1989). This contradicts multiple observations showing that mangrove leaves have high C/N ratios even after storage (see Table 3 for examples). The majority of studies have recorded C/N ratios in mangrove leaves that far exceed the Russell-Hunter ratio of 17. Leaves, in general, take a very long time to reach their lowest C/N values, and in most cases the lowest C/N ratios of decayed leaves are still at least double the Russell-Hunter ratio (Table 3).

We examined the surface feeding behaviour of *N. meinerti* and *S. guttatum* within two mangrove biotopes, and found mud feeding clearly predominated. Seventy-six percent of all *N. meinerti* that engaged in feeding activity fed on sediment: in comparison, 12% fed on roots, 10% on leaves, 3% on propagules and <1% on algae. Similarly, *S. guttatum* fed on sediment in 69% (*Avicennia* habitat) and 66% (*Rhizophora* habitat) of feeding observations, respectively. Several studies have noted that mangrove crabs may feed on mud (Day 1967; MacNae 1968; Alexander and Ewer 1969; Robertson 1986; Camilleri 1992; Kwok and Lee 1995), but only one has quantified this: Micheli (1993b) found that *S. messa* spent 5 times longer feeding on mud than on leaves or propagules. This estimate is higher than ours, but her conclusion that mud feeding predominates is the same.

We measured the C and N composition of sediments from the same transects used for the feeding and burrow-leaf studies. The mean sediment C/N ratio varied from 17.7 at Kisakasaka to 21.5 at Maruhubi. These are very similar to those of sites in Kenya (Rao et al. 1994), and are higher than C/N ratios in acid-treated mangrove sediments from Taiwan, Papua New Guinea, Brazil and India

(Alongi et al. 1993; Cheng and Chang 1999; Koch 1999), and lower than those of some north Australian muds (Boto and Wellington 1984). The sediments in the present study had C/N ratios 3 times lower than *A. marina* leaves, indicating that sediments could have higher nutritional value than leaves. We do not know what proportion of the C and N of the sediment could be digested by sesarmids. However, stable isotope studies from Maruhubi (Ólafsson and M. W. Skov, unpublished data) and India (Bouillon et al., in press) indicated that mangrove sediment was an important dietary source for crabs. Robertson (1986) suggested that crabs forage bacteria from the mud surface. Bacteria may certainly reach high densities in mangrove mud (Alongi 1988) and are highly digestible by crabs: *Uca polita* and *U. vocans* feeding on sedimentary bacteria had assimilation efficiencies of 98% (Dye and Lasiak 1987). In comparison, the assimilation efficiency of sesarmids feeding on mangrove leaves is typically 50% or less (Micheli 1993a; Kwok and Lee 1995; Lee 1997; Giddens et al. 1986), although Emmerson and McGwynne (1992) and Skov (2001) have measured assimilation efficiencies of 81–85% in *N. meinerti*.

Why, given high tannin levels, high C/N ratios and low assimilation efficiencies, is there so much evidence that grapsid crabs consume mangrove leaves (for a review, see Lee 1998)? Crabs fragment leaves during feeding and digestion (Malley 1978) with subsequent acceleration of microbial decay (Webster and Benfield 1986) and a decrease in the C/N ratio (Cundell et al. 1979). Lee (1997) fed senescent *R. stylosa* leaves with a C/N ratio of 83 to *S. messa*, and the C/N ratio in fresh crab faeces fell to 49, and after 25 days of decomposition to <28. In comparison, the lowest C/N ratio of 36 for decaying *R. stylosa* leaves was reached only after 160 days in estuarine waters (Wafar et al. 1997). Leaf eating by mangrove crabs may therefore lead to a relative nutrient enrichment of their immediate environment, including the substrate. Similar systems have been described for a wide variety of animals, such as other crustaceans (Lodge et al. 1994; Usio 2000), limpets (Connor and Quinn 1984; Plagányi and Branch 2000), aquatic macroinvertebrates (Wallace and Webster 1996), American voles (Sirotnak and Huntley 2000) and macrograzers of the African savannah (e.g. McNaughton et al. 1997). Where the animals are largely territorial, as is the case for some limpets and sesarmids, the nutritional loop may be quite tight. Could this be why mangrove crabs eat leaves?

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