

Leaf choice by crustaceans in a mangrove forest in Queensland

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Abstract

The feeding behaviour of leaf eating crustaceans feeding on leaves shed by *Avicennia marina*, *Bruguiera gymnorhiza* and *Rhizophora stylosa* in the mangrove forest at Myora Springs, Queensland, Australia was studied between 1980 and 1984. Individual *Sesarma erythroactyla* (carapace > 9 mm long), one of the most abundant species of crabs in the forest, processed approximately half a leaf from any of the three species of mangroves in 24 h under laboratory conditions. Of the amount of leaf material processed, 20% was lost from the mandibles due to "sloppy feeding", 68% was egested as faeces and 12% converted into crab biomass. Crabs processed more leaf material at 30 °C than at 20 °C. *S. erythroactyla* preferred leaves of *A. marina* to those of the other two species, probably because leaves of *A. marina* have a lower tannin and a higher nitrogen content. Of the other two species, *B. gymnorhiza* was preferred to *R. stylosa*. Among leaves of *R. stylosa*, *S. erythroactyla* exerts a strong preference for aged rather than freshly fallen, and for thick rather than thin leaves. The mesofauna (carapace length < 9.0 mm) which processed dead mangrove leaves comprised juveniles of *S. erythroactyla*, the crab *Ilyograpsus paludicola*, the isopod *Exosphaeroma alata* and the amphipods *Orchestia* sp. and *Melita* sp. These species processed between 0.2 and 24.7 mg dry wt of a leaf per individual over a period of 4 d. Of this, 72 to 85% was egested as faeces. The significance of leaf eating crabs to nutrient cycling in mangrove forests is discussed. I conclude that leaf processing by crustaceans shortens the time span between leaf fall and consumption of leaf material by organisms. This may have the effect of conserving leaf biomass inside the mangrove forest.

Introduction

In the mangrove forest at Myora Springs, Queensland more than 40 species of detritivores feed on dead plant material of mangrove origin, yet the forest is composed of only three species of trees namely, *Avicennia marina*, *Bruguiera gym-*

norhiza and *Rhizophora stylosa* (Camilleri 1984). Since litter is shed during most of the year, yet does not accumulate over the mud in quantities comparable to temperate forests (Staaf 1987), litter is probably always a limiting resource for detritus feeders in mangrove forests. Therefore, it is not trivial that a complex community of detritivores can subsist on litter produced by only three species of trees. Food partitioning may increase the number of food niches for detritivores, provided that the primary food source, namely dead leaves, are processed into a variety of food items having different properties. By shredding leaves into smaller particles crabs, amphipods and isopods make food available for species such as gastropods, crabs and fish.

On the east coast of Australia the crab *Sesarma erythroactyla* is abundant in the mangrove forests from Mackay to Sydney (Macnae 1966). In the mangrove forest at Myora Springs dense populations of *S. erythroactyla* live on mud mounds around roots of mangrove trees, feeding on mangrove litter. Smaller fauna which also feed on dead leaves comprise juveniles of *S. erythroactyla*, the crab *Ilyograpsus paludicola*, the isopod *Exosphaeroma alata*, and the amphipods *Orchestia* sp., and *Melita* sp. They all feed on leaves and process them into small particles. Hence they are a primary link of the marine food web in mangrove forests. In order to assess the rate at which they process leaves, the amount of dead leaf material eaten by these species of crustaceans and the amount of particulate material they produce as a result of the feeding process were measured. Since individual leaves falling to the ground differ morphologically and biochemically, a crab encountering a leaf may exert a choice. Laboratory experiments focused on the influence of four factors on leaf processing by shredders: (1) the properties of leaves of different species of mangroves; (2) the length of time the leaves had been immersed in water; (3) the size of the shredders; (4) temperature.

Materials and methods

Leaves and leaf consumers were collected from the mangrove forest at Myora Springs, North Stradbroke Island,

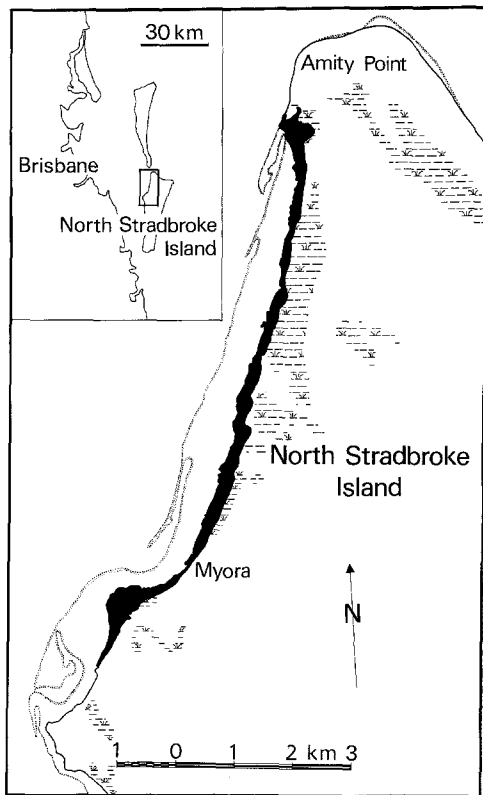


Fig. 1. Mangrove forest (■) at Myora Springs near Brisbane, Queensland, Australia

Brisbane, Queensland (Fig. 1). The annual range of sea water temperature in the forest was 15° to 30°C during the period 1980 to 1984. *Sesarma erythroductyla*, the most abundant crab in the forest, forages opportunistically during low tide. Amphipods and isopods can live in pools and hence escape temperature extremes. Detritivores are active for most of the year, except July and August when temperatures are lowest. In the forest, temperatures are 20°C or higher during most of the year. Therefore, 20° and 30°C were chosen to measure feeding rates of large *S. erythroductyla* and 25°C to measure feeding rates of smaller fauna.

Leaf preference

To test for a possible preference of *Sesarma erythroductyla* for leaves of different types (species, number of days of conditioning in sea water, leaf thickness) four experiments were carried out. Green and yellow leaves of *Avicennia marina*, and yellow leaves of *Bruguiera gymnorhiza* and *Rhizophora stylosa* were hand picked from the trees. Brown leaves of *A. marina* and orange leaves of *B. gymnorhiza* and *R. stylosa* were obtained by ageing leaves on the mud for 20 d in net bags tied to roots. Experimental chambers contained one crab (starved for 24 h) and similar sized pieces of leaf material to be tested. Controls contained leaves but no crabs. Experiments were conducted at 20°C for 48 h, after which the leaf area eaten was measured.

Experiment I

In this experiment each of 14 *Sesarma erythroductyla* was given a choice of one half leaf (produced by splitting a leaf along the midrib), of each of the following types: green *Avicennia marina*; yellow *A. marina*; brown *A. marina*; yellow *Bruguiera gymnorhiza*; orange *B. gymnorhiza*; yellow *Rhizophora stylosa*; orange *R. stylosa*. These leaves represent the whole range of leaf types present on the mud inside the mangrove forest.

Experiment II

In this experiment each of 14 *Sesarma erythroductyla* was given a green, yellow and brown half leaf of *Avicennia marina*.

Experiment III

In this experiment each of 33 *Sesarma erythroductyla* was given one yellow and one orange half leaf of *Rhizophora stylosa*.

Experiment IV

In this experiment each of 14 *Sesarma erythroductyla* was given one thick half-leaf (>0.7 mm thick) and one thin half-leaf (<0.7 mm thick) of *Rhizophora stylosa*. Corresponding half-leaves were weighed, dried at 105°C and reweighed to find the fr wt:dry wt ratio.

Corresponding half leaves from Expts I and III were analysed for carbon, nitrogen and hydrogen content using a Perkin-Elmer Elemental Analyser.

Feeding rates

The amount of leaf material eaten was assessed for large and small shredders in separate experiments.

Experiment V

Sesarma erythroductyla (>9 mm carapace length) were used. Two sets of chambers were set up containing filtered (0.45 µm) seawater: the experimental set contained one crab and one (senescent) half-leaf per chamber; the control chambers contained only one half-leaf per chamber and were used to correct for weight loss of plant material due to leaching and microbial activity. The fr wt:dry wt ratio of leaves was obtained from the second half of each leaf (which was not introduced into experimental or control chambers) by cutting a disk out of the leaf and weighing it before and after drying at 105°C for 24 h. Two treatments were undertaken: one at 20° and one at 30°C. After 24 h (and a tidal rhythm

of low water and darkness and high water and light) the loss in leaf area was measured. The contents in the crabs' chambers were examined, and sorted into faecal pellets and shredded particles produced due to "sloppy feeding". Both types of particles were washed with distilled water to remove any adhering salt, dried at 105 °C and weighed. From these data the following values (as dry wt) were calculated: (1) Wt processed by crab = initial – final wt of leaves – equivalent wt lost in control chambers; (2) wt ingested by a crab = wt processed – wt shredded; (3) wt assimilated by crab = wt ingested – wt egested as fecal pellets.

Experiment VI

Sesarma erythroductyla, *Ilyograpsus paludicola*, *Exosphaeroma alata*, *Orchestia* sp., and *Melita* sp., (<9 mm carapace length) were used. The procedure was as in Expt V, except that between one and five individuals were used simultaneously in the experimental chambers in order to obtain measurable amounts of leaf material processed.

Leaf features

Branches from the canopy of each of five trees of *Avicennia marina*, *Bruguiera gymnorhiza* and *Rhizophora stylosa*, were collected. In the laboratory a sample of ca 40 leaves was used to measure the following features of individual leaves: area, length, width, thickness, wet wt, dry wt. Leaves were analysed for organic matter content in a muffle furnace (550 °C for 1 h), and for energy content using a bomb calorimeter.

Leaf ageing

Green and yellow leaves of *Avicennia marina* and yellow and orange leaves of *Bruguiera gymnorhiza* and *Rhizophora stylosa* were hand picked from the trees and placed in net bags (mesh = 1 mm), each containing six leaves. Twelve bags containing six leaves of each of *A. marina*, *B. gymnorhiza* and *R. stylosa* were placed on the mud and tied to mangrove roots. At intervals of 1, 5, 11 and 36 d three bags of each leaf type were retrieved. They were taken to the laboratory where leaves were washed and subsequently examined under light microscope for change in colour and texture.

Size distribution of crab holes

Since holes of the crab *Helioecus cordiformes* are frequently used as hiding places by *Sesarma erythroductyla*, the size frequency distribution of holes of *H. cordiformes* was assessed in order to obtain an estimate of the number of hiding places available to *S. erythroductyla* of different sizes. Five mud mounds were selected at random. A belt transect equivalent to 10% of the surface area of each mound was marked

and the diameters of crab holes in this transect measured using callipers.

Results

Leaf preference

Experiment I

When given a range of leaf types, *Sesarma erythroductyla* showed a strong preference for leaves of *Avicennia marina* that had been "aged" in seawater and were brown, over the remaining leaf types offered (Table 1).

Experiment II

When given a choice of green, yellow and brown leaves of *Avicennia marina*, crabs chose green (10 out of 14) and brown (8 out of 14) (Table 1).

Experiments III and IV

When offered leaves of *Rhizophora stylosa* only, crabs chose orange (= aged) levels in preference to yellow leaves, and thick (>0.7 mm thickness) over thin leaves (Table 2).

Feeding rates

Large detritivores such as adult *Sesarma erythroductyla* tear bits off the leaf lamina with their chelae and pass them to the mouth where they are shredded by the mandibles. Large particles of organic matter are lost as the mandibles shred the leaf. During passage through the gastric mill in the gut, the ingested matter is further broken down and finally egested as fine organic matter in fecal pellets. The small fauna (<9 mm carapace length) scrape surfaces or pick up small particles with their chelae and pass them to the mouth. Hence little is lost from the mandibles.

Experiment V

When given one half leaf of only one tree species, the amount of leaf material processed by large *Sesarma erythroductyla* (carapace length = 9 to 16 mm) was highest for leaves of *Bruguiera gymnorhiza*, followed by *Avicennia marina* then *Rhizophora stylosa* (Table 3). A two way analysis of variance (ANOVA) showed significant ($p < 0.01$) effects of both the species of mangrove and temperature. For all three species of mangroves the amount processed was higher at 30° than at 20 °C. Of the amount of leaf material processed by crabs, 20% was lost as particulate matter from the mandibles due to "sloppy feeding", 68% was egested as faeces and 12% was assimilated.

Table 1. *Sesarma erythroductyla*. Expt 1, feeding preference in relation to different mangrove half leaves. Numbers are percent dry wt of similar sized leaves processed during 48 h. +: Expt II (leaf colour preference), 20% or more of a half leaf processed by crab. B: brown; G: green; O: orange; Y: yellow leaves. Blanks: no measurable amount of leaf material eaten

Crab no.	Sex	Carapace length (mm)	<i>Avicennia marina</i>			<i>Bruguiera gymnorrhiza</i>		<i>Rhizophora stylosa</i>	
			G	Y	B	Y	O	Y	O
1	M	13.5		+					2
2	M	13.0							15
3	M	12.5	10	+	2				50
4	F	13.0	8	1					
5	F	12.0		+					8
6	F	13.0							40
7	F	11.0							50
8	M	11.5		6	+	2			70
9	M	15.5		+					25
10	M	8.0	10	+					10
11	M	13.0		+					50
12	M	13.5	2	+					10
13	F	12.0		+					75
14	M	11.0	5	+					12

Table 2. *Sesarma erythroductyla*. Feeding preference on *Rhizophora stylosa* leaves. Percent dry wt of half leaves processed in 48 h for females ($n=14$) and males ($n=17$). Leaf thickness: thick = 1.1 ± 0.06 mm; thin = 0.52 ± 0.02 mm. Values are means \pm standard errors

Leaf	Female	Male
Colour (Expt III)		
Yellow	3.61 ± 1.04	2.26 ± 0.53
Orange	15.5 ± 4.43	25.8 ± 4.95
Thickness (Expt IV)		
Thick	31.5 ± 3.80	no data
Thin	3.02 ± 0.78	

Table 3. *Sesarma erythroductyla* (9 to 16.4 mm carapace length). Feeding preference in relation to temperature. Percent dry wt processed in 24 h (Expt V). Data for males and females pooled. Values \pm SE, $n \geq 40$

Temperature (°C)	<i>Avicennia marina</i>	<i>Bruguiera gymnorrhiza</i>	<i>Rhizophora stylosa</i>
20	46.0 ± 4.01	51.1 ± 2.36	33.4 ± 2.59
30	61.9 ± 3.11	71.1 ± 2.15	48.5 ± 2.69

Experiment VI

Juvenile *Sesarma erythroductyla*, *Iliograpsus paludicola*, *Exosphaeroma alata*, *Orchestia* sp. and *Melita* sp. did not produce macroscopic particles by sloppy feeding. Over a period of 4 d the amount of leaf material processed by one individual varied between 0.2 and 24.7 mg dry wt leaf material (Table 4). Of the five species tested, juvenile *S. erythro-*

Table 4. Experiment IV. Amount of dry wt (mg) leaf material processed per individual over 4 d at 25°C. In order to obtain measurable amounts of dry weight eaten, there were 1 to 5 individuals in experimental chambers. Therefore, no standard deviation could be calculated. Values given are mean, range and total individuals used (n)

Species	Carapace length (mm)	Ingested (mg)		
		<i>Avicennia marina</i>	<i>Bruguiera marina</i>	<i>Rhizophora stylosa</i>
<i>Sesarma erythroductyla</i>	2.0–4.5	14.3 (11)	10.29 (13)	5.66 (11)
<i>Iliograpsus paludicola</i>	1.5–4.0	0.7–24.4	0.2–24.7	0.6–10.1
<i>Exosphaeroma alata</i>	4.0–7.0	0.99 (21)	1.13 (9)	1.01 (23)
<i>Orchestia</i> sp.	4.5–7.0	0.50–2.70	0.36–1.90	0.23–2.53
<i>Melita</i> sp.	3.5–6.5	5.30 (5)	2.80 (5)	3.97 (3)
		1.5–11.5	1.0–5.0	1.0–6.9
		12.93 (3)	1.94 (7)	3.74 (13)
		10.0–18.0	0.5–5.0	2.0–6.5
		1.05 (30)	1.97 (24)	0.62 (23)
		0.33–2.50	0.25–8.5	0.1–2.2

Table 5. Leaf characteristics (range or mean) of mangrove trees collected from Myora Springs, Stradbroke Island. Tannin content from Kuthubutheen (1981)

Leaf characteristic	<i>Avicennia marina</i> ($n=24$)	<i>Bruguiera gymnorrhiza</i> ($n=32$)	<i>Rhizophora stylosa</i> ($n=39$)
Water content (%)	46–50	56–74	60–67
Thickness (mm)	0.1–0.5	0.2–0.7	0.1–0.9
Width (cm)	1.5–3.5	3.5–6.5	2.8–7.0
Surface area (cm ²)	2.04–4.08	6.38–18.37	5.00–13.15
Wet wt (g)	1.1–0.75	2.7–6.1	1.9–5.1
Dry wt (g)	0.05–0.4	0.9–2.3	0.7–1.5
Cal g ⁻¹ dry wt (ash free)	5025 ($n=5$)	4931 ($n=5$)	4714 ($n=5$)
Tannin content (%)	3.5	14.6	4.8
Sclereids	absent	present	present

dactyla had the highest processing rates. Of the amount of leaf material processed, *Orchestia* sp. and small *S. erythroductyla* egested 72 and 85% as faeces, respectively.

Leaf features

Leaf features of the three species of mangrove trees growing at Myora Springs are presented in Table 5. Leaves of *Bruguiera gymnorrhiza* are largest and heaviest. They are broad and have a high C:N ratio, a high tannin content, and are rare. Leaves of *Rhizophora stylosa* are intermediate in size and fresh weight. They are also broad, have the highest C:N ratio, a low tannin content, and are abundant. Considerable variation in leaf thickness is exhibited by *R. stylosa*, thick leaves containing more water but not more biomass than thin leaves. Leaves of *Avicennia marina* are smallest and lightest. They are also narrower and thinner, have a lower C:N ratio and a lower tannin content than leaves of the

Table 6. Leaf ageing. Averages (\bar{x}) and standard errors (SE) of carbon, hydrogen and nitrogen content of fresh and aged mangrove leaves ($n=5$ for each leaf type). Green (G) and yellow (Y) leaves were hand picked from trees. Orange (O) and brown (B) leaves were aged in mesh bags tied to mangrove roots for 20 d

Chemical (%)		<i>Avicennia marina</i>		<i>Bruguiera gymnorhiza</i>		<i>Rhizophora stylosa</i>	
		G	B	Y	O	Y	O
Carbon	\bar{x}	46.1	43.8	42.8	42.4	44.8	42.7
	SE	0.54	0.6	0.9	2.28	0.8	0.2
Hydrogen	\bar{x}	5.3	5.5	5.4	5.5	5.53	5.2
	SE	0.21	0.4	0.2	0.25	0.1	0.1
Nitrogen	\bar{x}	1.7	0.8	0.6	0.65	0.5	0.5
	SE	0.04	0.1	0.1	0.1	0.06	0.03
C:N ratio	\bar{x}	30.2	52.7	60.2	70.2	96.3	93.3

other two species and are the most abundant. The nutritional value per g dry wt, as reflected by the caloric content of the leaves, is similar in all three species.

Leaf ageing

Senescent yellow leaves of *Avicennia marina* turn brown, while leaves of *Bruguiera gymnorhiza* and *Rhizophora stylosa* turn pale, then dark orange. The lamina ages in patches. Leaves of *B. gymnorhiza* age faster than those of *R. stylosa*. Eleven days after being shed from trees, all yellow leaves of *R. stylosa* had turned orange and all leaves of *A. marina* had turned brown. After 36 d the mesophyll had become very soft and ca 25% of *A. marina* and *R. stylosa* leaves had lost most of their internal tissue. However the vascular tissue of *A. marina* persisted, probably because it is harder. Small quantities of gas accumulated in empty leaves of *R. stylosa*. In view of these rapid changes it is surprising that the C and N content of leaves changed only slightly during ageing (Table 6).

Size distribution of crab holes

Of the 1 200 crab holes measured, the majority had diameters <12 mm. Only 15.6% of holes were >9 mm and thus suitable as hiding places for large *Sesarma erythroactyla*.

Discussion

This work is one of a series of studies on the structure of the food web and on nutrient cycling in mangrove forests. The aim was to ascertain which properties of mangrove leaves influence the choice exhibited by leaf eating detritivores and how this choice affects the availability of organic particles of different size and structure in the forest. The main results are: (1) in choice experiments, crabs preferred leaves of *Avicennia marina* to those of *Bruguiera gymnorhiza* and *Rhi-*

zophora stylosa, and in *R. stylosa*, aged over fresh leaves and thick over thin leaves; (2) when feeding on leaves, crabs produce particles of different size and texture, ranging from fecal pellets to lamina sections cut from leaves.

Leaf features and leaf choice

The preference for leaves of *Avicennia marina* over those of the other two species may be due to a number of factors. Of the three species, leaves of *A. marina* have the lowest tannin content and C:N ratio. These properties tend to allow richer fungal growth (Fell et al. 1975, Kuthubutheen 1981) which may in turn make the leaf more attractive to crabs. Furthermore, because leaves of *A. marina* are small and narrow they are easier to carry and drag into burrows.

The preference for aged leaves over freshly fallen leaves in *Bruguiera gymnorhiza* and *Rhizophora stylosa* and the use of brown leaves in *Avicennia marina* can be explained by three hypotheses: (1) Unpalatable materials are removed from the leaf during the process of ageing, e.g. tannins may gradually leach out of leaves into seawater (Cundall et al. 1979, Camilleri and Ribí 1986, Neilson et al. 1986, Robertson 1988). Tannin concentrations are high in leaves of *B. gymnorhiza* (14.6%) variable in *R. stylosa* (4.9 to 17%) and low in *A. marina* (3.5%) (Kuthubutheen 1981, Robertson 1988). During leaching the tannin content decreases further so that brown (aged) leaves of *A. marina* would probably contain the least amount of tannin of all leaf types offered. This may in part account for the crabs' preference for aged leaves (Table 1). Alternatively, phenolic compounds are gradually oxidized, rendering aged leaves more palatable to detritivores. The oxidation of phenolic compounds may be achieved by enzymes produced by fungi (Walker 1975), such as *Aspergillus sp.* and *Penicillium sp.*, both of which occur on mangrove leaves (Kuthubutheen 1981), or by enzymes produced by bruised plant tissues (enzymic browning, Burton et al. 1963), or through condensation of tannins and the amino-group of amino acids, a process termed non-enzymic browning (Burton et al. 1963). (2) Chemicals produced in ageing leaves (Misra et al. 1985) may act as an attractant to crabs. It has been shown that fungal colonization of plant material affects its flavour (Schoth et al. 1968). This may provide shredders with feeding cues if such species have appropriate chemoreceptors (Trott and Robertson 1984, De Mott 1986). (3) The nutritional quality of leaves improves during ageing. This could also be achieved by fungi colonizing leaves. This hypotheses is supported by the observation that crustaceans preferred leaves that had been inoculated with fungi (Cummins et al. 1973, Bärlocher and Kendrick 1975), either to use fungi as a source of energy or to aid in the digestion of plant material (Bärlocher 1982, Punja and Jenkins 1984). Fallen mangrove leaves become colonized by several species of marine fungi of which *Phytophthora vesicula* reaches peak abundance after leaves have been immersed in water for 7 d (Fell et al. 1975), at which time leaves of *B. gymnorhiza* and *R. stylosa* are orange. It has been suggested that, as a result of fungal

colonization, the absolute N content of dead leaves increases (Kaushik and Hynes 1971), thus implying that the crustaceans' preference for microbially infected leaves is based on nutritional quality. Fell et al. (1975) also reported that the N content of *R. mangle* leaves increased during ageing. However, it was only after they had lain in seawater for 20 d that the N content began to increase. This is in agreement with my results – that the N content of leaves of three species of mangroves did not increase significantly during 20 d immersion in seawater (Table 6), which implies that leaf preference could not have been influenced by the N content.

Leaves of *Rhizophora stylosa* ranked second in the crabs' preference, thick leaves being selected over thin. Since sesamid crabs do not have adequate means of preventing water loss by evapotranspiration (Kyomo 1986) and are thus subject to desiccation stress, they may partly depend on low salinity fluid provided by leaves of *R. stylosa*.

Feeding rates

Large *Sesarma erythroductyla* have high rates of processing. Of the leaf weight offered to individual *S. erythroductyla*, 33 to 71% was processed in 24 h, indicating high rates of leaf shredding as proposed for detritivores living in freshwater (Mackay and Kalff 1973). Juvenile *S. erythroductyla* also have the highest processing rates, followed by the amphipod *Orchestia* sp. and the isopod *Exosphaeroma alata*. Since *S. erythroductyla* is the only large shredder present in high densities in the forest, it can be considered a key species in the local food web. In contrast, *Ilyograpsus paludicola* and *Melita* sp. have lower processing rates, suggesting that these two species may also utilize other sources of organic matter such as algae.

The low processing rates of *Rhizophora stylosa*, as compared to the other two species of mangroves, may be due to the presence of a hard thick cuticle and sclereids which would make shredding difficult. Nevertheless, the results show that *Sesarma erythroductyla* can shred leaves of *R. stylosa*. The variation in individual rates of processing (as indicated by SD in Table 3) is of ecological interest. If this variation reflects a variation in the ability of claws and mandibles to shred leaf material, then this may be a basis of alternative individual feeding strategies, i.e., fast shredders seek leaves and shred them where found, while slow shredders drag leaves into burrows and feed there.

Of the amount of leaf material ingested, adult *Sesarma erythroductyla* assimilated 12% and egested 68%. Similarly, when *Gammarus* sp. was fed on leaves it assimilated between 5 and 20% of the leaf material ingested (Bärlocher and Kendrick 1975, and references therein). Of the dry wt of elm and maple leaves eaten by *G. pseudolineatus*, 10% was assimilated when leaves were not inoculated with fungi and 42.6 to 75.6% when they were inoculated with fungi (Bärlocher and Kendrick 1975).

It is currently believed that detritivores digest microbial organisms growing on detritus rather than the detritus itself, although a few studies show that plant detritus can supply

nutritional substances (Cammen 1980, Zieman et al. 1984). Evidence for the presence of plant digesting enzymes in invertebrates is scant although they have been shown to occur in some crustaceans following mechanical trituration in the gastric mill (Ray and Julian 1952, Ray 1959, Yasuo and Yokoe 1960). Many crustaceans secrete amylase and fat splitting enzymes (Florkin and Bradley 1970). Chamier and Willoughby (1986) showed that chitinase, cellulase and β -1, 3-glucanase are secreted by the mid gut of *Gammarus pulex*, while Bärlocher (1982) has shown that enzymes produced by saprophytic fungi in decomposing oak leaves contribute to their digestion in the gut of *Gammarus fossarum*. Although no published records of gut enzymes of species mentioned in this paper have been sighted, the observation that parenchyma cell walls gradually became transparent (Camilleri unpublished data) suggests that a chemical alteration of the walls takes place during passage through the crabs' gut.

Energy flow: the role of shredders

Typically, shredders have high ingestion rates and low assimilation values (Sinsabough et al. 1985). Similarly, about 68% of the material ingested by *Sesarma erythroductyla* is egested as small particles and thus made available to species which collect small particles. Both large particles produced by large shredders and fine egested particles are utilized by deposit eating detritivores living on the mud. Since this mechanism continually produces small organic particles associated with the mud in mangrove forests, deposit feeders probably rely on shredders for particulate organic matter (Levinton and Lopez 1977). Furthermore, competition for fine particles may be eased by the fact that some deposit feeders can also utilize larger particles. However, since species which feed on small particles select particles on the basis of physical parameters (particle diameter, weight) rather than on nutritional value (Robertson and Newell 1982), this means that the nutritional quality of particles available to collectors is under the control of the choices made by shredders (O'Hop et al. 1984). Since large shredders have high processing rates, both at high and low temperatures, this has the effect of retaining a substantial amount of leaf material inside the forest during most of the year, rather than it being washed out to sea. Organic matter and nutrients are thus conserved in the forest.

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Literature cited

- Bärlocher, F. (1982). The contribution of fungal enzymes to the digestion of leaves of *Gammarus fossarum* Koch (Amphipoda). *Oecologia* 51: 1–4
- Bärlocher, F., Kendrick, B. (1975). Assimilation efficiency of *Gammarus pseudolineatus* feeding on fungal mycelium or autumn-shed leaves. *Oikos* 26: 55–59

- Burton, H. S., McWeeny, D. J., Pandhi, P. N. (1963). Non-enzymatic browning: browning of phenols and its inhibition by sulphur dioxide. *Nature, Lond.* 199: 659–661
- Camilleri, J. C. (1984). Litter decomposition and resource partitioning in a mangrove forest: a case study in systems ecology and modelling. Ph. D. Thesis. Griffith University, Brisbane, Australia
- Camilleri, J. C., Ribí, G. (1986). Leaching of dissolved organic carbon (DOC) from dead leaves, formation of flakes from DOC, and feeding on flakes by crustaceans in mangroves. *Mar. Biol.* 91: 337–344
- Cammen, L. M. (1980). The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. *Mar. Biol.* 61: 9–20
- Charmier, A.-C., Willoughby, L. G. (1986). The role of fungi in the diet of the amphipod *Gammarus pulex* L.: an enzymatic study. *Freshwat. Biol.* 16: 197–208
- Cummins, K. W., Petersen, R. G., Howard, F., Wuycheck, J., Holt, V. (1973). The utilization of leaf litter by stream detritivores. *Ecology* 54: 36–345
- Cundall, A. M., Brown, M. S., Stanford, R., Mitchell, R. (1979). Microbial degradation of *Rhizophora mangle* leaves immersed in the sea. *Estuar. cstl mar. Sci.* 9: 281–286
- De Mott, W. R. (1986). The role of taste in food selection by freshwater zooplankton. *Oecologia* 69: 334–340
- Fell, J. W., Cefalu, R. C., Master, I. M., Tallman, A. S. (1975). Microbial activities in the mangrove (*R. mangle*) leaf detrital system. In: Walsh, G., Snedaker, S., Teas, T. (eds.) *Proceedings of the International Symposium for the Biology and Management of Mangroves*, Vol. 2
- Florkin, M., Bradley, B. T. (eds.) (1970). *Chemical Zoology*. Vol. V, Arthropoda, Part A. Academic Press, London
- Kaushik, N. W., Hynes, H. B. N. (1971). The fate of the dead leaves that fall into streams. *Arch. Hydrobiol.* 68: 465–515
- Kuthubutheen, A. J. (1981). Fungi associated with the aerial parts of Malaysian mangrove plants. *Mycopathologia* 76: 33–43
- Kyomo, J. (1986). Reproductive activities in the sesarimid crab *Sesarma intermedia* in the coastal and estuarine habitats of Hakata, Japan. *Mar. Biol.* 91: 319–329
- Levinton, J. S., Lopez, G. R. (1977). A model of renewable resources and limitation of deposit-feeding benthic populations. *Oecologia* 31: 177–190
- Mackay, R. J., Kalf, J. (1973). Ecology of two related species of caddis fly larvae in the organic substrates of a woodland stream. *Ecology* 54: 500–511
- Macnae, W. (1966). Mangroves in Eastern and South-Eastern Australia. *Aust. J. Bot.* 14: 67–104
- Misra, S., Dutta, A. K., Choudhury, A., Ghosh, A. (1985). Oxidation of oleandric acid of *Avicennia officinalis* leaves to oleonic acid in the natural environment of sunderban mangrove ecosystem. *J. chem. Ecol.* 11: 339–342
- Neilson, M. J., Giddins, R. L., Richards, G. N. (1986). Effect of tannins on the palatability of mangrove leaves to the tropical sesarimid crab *Neosarmatium smithi*. *Mar. Ecol. Prog. Ser.* 34: 185–186
- O'Hop, J., Bruce, J. W., Haefner, J. D. (1984). Production of a stream shredder, *Peltoperla maria* (Plecoptera: Peltoperlidae) in disturbed and undisturbed hardwood catchments. *Freshwat. Biol.* 14: 13–21
- Punja, Z. K., Jenkins, S. F. (1984). Light and scanning electron microscope observations of calcium oxalate crystals produced during growth of *Sclerotium rolfsii* in culture and in infected tissue. *Can. J. Bot.* 62: 2028–2032
- Ray, D. L., Julian, J. R. (1952). Occurrence of cellulase in *Limnoria*. *Nature, Lond.* 169: 32–33
- Ray, D. L. (1959). Nutritional physiology of *Limnoria*. In: Ray, D. L. (ed.) *Marine Boring and Fouling organisms*. Seattle, University of Washington Press, p. 47–59
- Robertson, A. I. (1988). Decomposition of mangrove leaf litter in tropical Australia. *J. exp. mar. Biol. Ecol.* 116: 235–247
- Robertson, J. R., Newell, S. Y. (1982). Experimental studies of particle ingestion by the sand Fiddler crab *Uca pugilator* (Bosc). *J. exp. mar. Biol. Ecol.* 59: 1–21
- Schroth, M. N., Hildebrand, D. C., O'Reilly, H. J. (1968). Off-flavor of olives from trees with olive knot tumors. *Phytopathology* 58: 524–525
- Sinsabough, R. L., Linkins, A. E., Benfield, E. F. D. (1985). Cellulose digestion and assimilation by three leaf-shredding aquatic insects. *Ecology* 66: 1464–1471
- Staaf, H. (1987). Foliage litter turnover and earthworm populations in three beech forests of contrasting soil and vegetation types. *Oecologia* 72: 58–64
- Trott, T. J., Robertson, J. R. (1984). Chemical stimulants of cheliped flexation behaviour by the western atlantic ghost crab *Ocypode quadrata*. *J. exp. mar. Biol. Ecol.* 78: 237–252
- Walker, J. R. L. (1975) The biology of plant phenolics. In: The Institute of Biology's Studies in Biology, No. 54. Edward Arnold, London
- Yasuo, K., Yokoe, Y. (1960). The cellulase activity in gastric juice and hepatopancreas of crayfish. *J. Fac. Sci. Tokyo Univ.* 9: 31–38
- Ziemann, J. C., Macko, S. A., Mills, A. L. (1984). Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. *Bull. mar. Sci.* 35: 380–392

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