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Absorption Efficiencies of the Intertidal Mangrove Dwelling Mollusk *Melampus coffeus* LINNÉ and the Rocky Intertidal Mollusk *Acanthopleura granulata* GMELIN

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With 1 figure and 5 tables

Key words: Intertidal environment, mangrove swamps, rocky shores, snails, chitons, feeding, Florida, Bahama Islands.

Abstract. The absorption efficiencies of the intertidal mangrove dwelling mollusk *Melampus coffeus* and the rocky intertidal dwelling mollusk *Acanthopleura granulata* were calculated by a modification of CONOVER'S (1966) equation. *M. coffeus* tended to consume fresh mangrove leaves indicating that *M. coffeus* may obtain much of its energy from the actual substrate material rather than from associated bacteria and meiofauna on decaying leaves. Obtaining energy directly from the substrate may be a mechanism for *M. coffeus* to utilize its food source more efficiently. In contrast, chitons (*A. granulata*) may utilize the higher energy components of their limited intertidal microfloral food source. Using the high energy component of a food source may be an additional mechanism by which organisms efficiently utilize a food source.

Problem

Grazing and deposit feeding mollusks are an integral part of the tropical intertidal fauna in both mangrove swamps (BROWN, 1971) where the food supply appears plentiful and on tropical rocky intertidal shorelines (LEWIS, 1960) where food is generally scarce (STEPHENSON & STEPHENSON, 1972). One of the most abundant deposit feeders in the intertidal mangrove swamps of Florida and the Caribbean is *Melampus coffeus* LINNÉ (*Pulmonata*, *Ellobiidae*). The main food of *M. coffeus* in mangrove areas is the freshly fallen and decaying mangrove leaf litter that collects among the prop roots of red mangroves (*Rhizophora mangle* LINNÉ) and the pneumatophores of black mangroves (*Avicennia germinans* LINNÉ). Field observations indicate that *Melampus coffeus* generally consumes the entire mangrove leaf except the midvein, rather than just eating material accumulated on the surface of the leaf as do some detritivores (LOPEZ *et al.*, 1977).

In contrast to the relatively productive mangrove swamps, tropical rocky intertidal shores appear to be characterized by very low productivity (STEPHENSON & STEPHENSON, 1972). Chitons (*Acanthopleura granulata* GMELIN) are common grazers on these shores where their chief food consists of the superficial and endolithic microflora which discolors the intertidal calcium carbonate rocks (MCLEAN, 1967; GLYNN, 1970; HUGHES, 1971). The large amount of calcium carbonate in the fecal material of chitons suggests that these animals ingest the calcium carbonate substrate along with the algae. A similar phenomenon was observed by SCHNEIDER & TORUNSKI (1983) on temperate limestone coasts. Chitons are especially adapted for this type of grazing because their radulae are tipped with magnetite (NEUMANN, 1968; TAYLOR & WAY, 1976).

The purpose of this study is to (1) compare the caloric content of the intertidal mangrove substratum to the caloric content of the tropical rocky intertidal substratum and to (2) determine the absorption efficiencies of energy (calories) by the detritivore *Melampus coffeus* and the intertidal grazer *Acanthopleura granulata*. Since TENORE (1982) cautions against comparing the energetics of different benthic species when their food conditions vary, no direct comparisons are made between the energetics of the mangrove dwelling species and the rocky intertidal species. Throughout the text, the term absorption efficiency will refer to the efficiency of the passage of energy or material across the gut wall (CALOW, 1975). This study makes no attempt to analyse the complex processes that occur within the detrital pool. Many of these processes have been described very well by FELL *et al.* (1980), HOBIE & LEE (1980), CAMMEN (1980), TENORE & RICE (1980) and others.

Material and Methods

1. Mangrove site

Adult *Melampus coffeus* were collected from the leaf litter substratum in a mangrove swamp as well as from red mangrove trunks and prop roots. Both decaying and freshly fallen red mangrove leaves were also collected. Leaves were considered fresh when they were yellow in color or did not crumble when bent. Leaves were considered decaying if they were dark brown or black in color, matted together and easily crumbled when picked up. All mangrove site collections were made in the high intertidal zone of a mangrove island 3.2 km north of Fort Pierce, Florida, U.S.A., on the east side of the Indian River lagoon (Fig. 1).

Fresh and decaying leaves were put into covered fingerbowls (five each) and 10 snails were placed in each fingerbowl to feed. It was not possible to collect fecal material quantitatively, especially from these bowls containing decaying leaves. Fecal material was collected daily, rinsed in fresh water and dried at 50°C until about 500 mg from each group was collected. Aliquots of fresh and decaying red mangrove leaves were stripped of large veins and petioles and washed and dried at 50°C. All samples were ground to a powder in a mortar.

2. Rocky intertidal site

Rocky intertidal collections were made at West End (Bahamas) in December 1981 and Black Rock (Bahamas) in April 1982 (Fig. 1). Fecal material was collected from chitons (*Acanthopleura granulata*) in the intertidal zones. Substrate samples were taken by scrubbing the rock with a wet wire brush and collecting the loosened rock and algal powder with a large bore syringe. Since

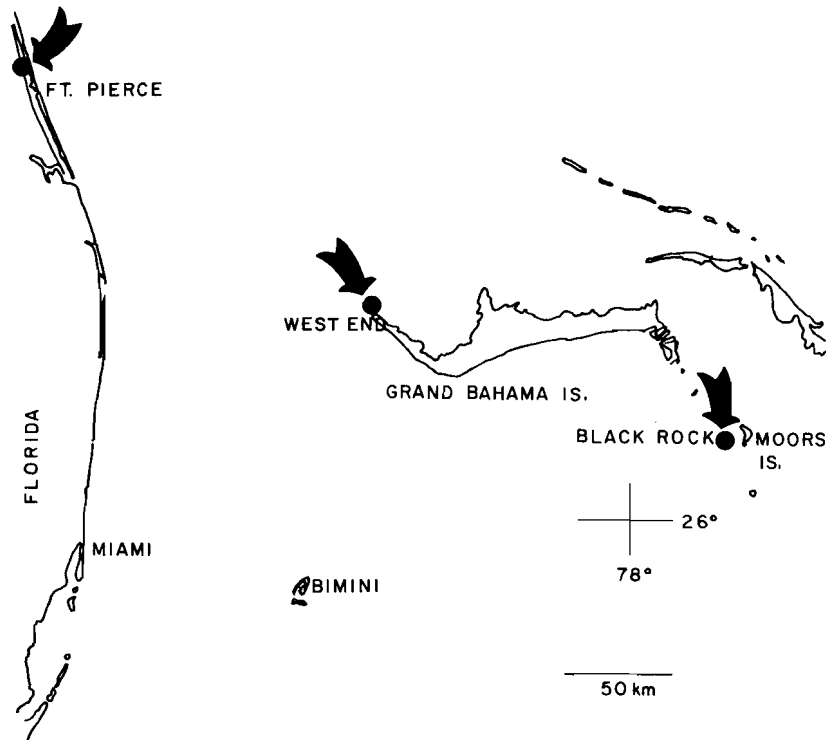


Fig. 1. Arrows indicate location of sampling sites. *Melampus coffeus* material was collected near Ft. Pierce, FL, 27°32.1'N, 80°19.2'W (U.S.A.). Chiton material was collected at West End (26°40.2'N, 78°59.8'W) and Black Rock (26°10.1'N, 77°39.1'W) (Bahamas).

grazing chitons do not penetrate the rock below the external rind of endolithic microflora (<0.5 mm), care was taken not to penetrate this algal rind when sampling with the wire brush. Assuming that the endolithic microflora are more or less evenly distributed in the outer rind of the rock (preliminary microscopic examinations suggest that they are), it is felt that this sampling method approximates what the chiton is ingesting. All fecal and substrate samples were frozen within a few hours after collection. Upon thawing, all fecal and substrate samples were rinsed in fresh water, centrifuged and dried at 50°C.

To determine if there was a significant increase in caloric content of the rocky intertidal substratum when grazers were excluded, a 50 × 50 cm square of 1 mm mesh nitex netting was placed over a portion of the limestone substratum for 5 days. Samples of the substratum were taken at the time nitex netting was placed on the rock. When the netting was removed, substratum samples were again taken from both under and adjacent to the covered area.

3. Energy analysis

Caloric content of all fecal and substrate samples (12 replicates each) was measured in a PHILLIPSON microbomb calorimeter (PHILLIPSON, 1964), and ash weight of all fecal and substrate samples (3 replicates each) was determined by ignition at 450°C for 4 h. All subsamples used for caloric determinations were combined with benzoic acid (50% sample, 50% benzoic acid) to assure complete combustion. Acid production and firing wire corrections were not made because they were considered negligible (WU & LEVINGS, 1978). A sample of reagent grade calcium carbonate was also

combusted in the calorimeter and ignited in the same way as fecal and substrate samples to determine if any corrections were needed for possible calcium carbonate reactions. No corrections were necessary.

To determine caloric (energy) absorption efficiency of the animals, a modification of a standard absorption efficiency equation (CONOVER, 1966) was used so that caloric values, rather than weights of organic matter, could be used. The modified equation is:

$$A = \frac{K_1 I - K_2 N}{K_1 I} \cdot (100 \%)$$

Where A is absorption efficiency, K_1 is the reciprocal of the ash percentage of the food (substrate) and K_2 is the reciprocal of the ash percentage of the fecal material. I and N are the number of calories per unit weight of the food (I) and feces (N).

For the purpose of this study, it is assumed that no significant ash absorption takes place. However, some workers (LASENBY & LANGFORD, 1973) have reported that inorganic absorption does occur in certain organisms. If ash absorption does take place in *Melampus coffeus* or *Acanthopleura granulata*, the values for caloric absorption in this study would be underestimated. As any error that might occur because of ash absorption tends to be minimized when absorption efficiencies are high (CONDREY *et al.*, 1972), the assumption that no significant inorganic absorption takes place most likely does not lead to a large scale underestimation of the animals' absorption efficiency of energy. All comparisons were done with Student's *t* test.

Results

The mangrove leaf substratum contained considerably more energy (calories) than the rocky intertidal substratum (Table 1). Fresh red mangrove leaves had significantly more caloric value than did the decaying mangrove leaves ($P < 0.05$).

Table 1. Caloric content of substrata on which mollusks fed. Fresh mangrove leaves contained significantly ($P < 0.05$) more calories than decayed mangrove leaves.

Substratum	Mean caloric content \pm SE (cal \cdot mg DW ⁻¹) (N = 12)
Fresh mangrove leaves	3.99 \pm 0.13
Decaying mangrove leaves	3.81 \pm 0.16
Rocky intertidal (chitons)	0.25 \pm 0.09

Table 2. Caloric content of fecal material taken from mollusks examined in this study. No significant ($P < 0.05$) differences were detected in caloric value between feces of *Melampus coffeus* fed on decaying leaves and those fed on fresh leaves. The fecal material of *Melampus coffeus* contained significantly more energy than the fecal material of *Acanthopleura granulata*.

Animal	Food	Mean caloric content \pm SE (cal \cdot mg DW ⁻¹) (N = 12)
<i>Melampus coffeus</i>	Fresh leaves	2.94 \pm 0.10
<i>Melampus coffeus</i>	Decaying leaves	2.77 \pm 0.11
<i>Acanthopleura granulata</i>	Algae	0.01 \pm 0.11

Table 3. Absorption efficiencies for carbon and energy of animals examined in this study.

Animal	Food	Absorption efficiency (calories)
<i>Melampus coffeus</i>	Fresh leaves	79 %
<i>Melampus coffeus</i>	Decaying leaves	56 %
<i>Acanthopleura granulata</i>	Algae	96 %

Table 4. Caloric content of rocky intertidal substratum before and after grazers were excluded. After 5 days, the substratum from which grazers were excluded had a significant ($P < 0.05$) higher caloric content than the unprotected control.

Treatment	Mean caloric content \pm SE (cal \cdot mg DW ⁻¹) (N = 12)
Caloric content at beginning of study	0.23 \pm .11
Caloric content under net after 5 d	0.35 \pm .14
Caloric content outside net after 5 d	0.18 \pm .14

No significant difference in caloric value of fecal material was detected between feces of *Melampus coffeus* fed fresh leaves and those fed decaying leaves ($P < 0.05$) (Table 2).

Melampus coffeus that were fed fresh mangrove leaves absorbed energy more efficiently than the *M. coffeus* that were fed decaying leaves. *Acanthopleura granulata* absorbed 96 % of the energy available to it (Table 3).

Protecting the rocky intertidal surface from grazers resulted in a significant ($P < 0.05$) increase in the caloric value of the substratum from 0.18 calories per mg DW to 0.35 calories per mg DW after only 5 d (Table 4).

Discussion

The caloric content of the mangrove leaf substratum is similar to that of many other substrata reported in the literature (Table 5), whereas that of the tropical rocky intertidal substratum is considerably lower. The rapid increase in caloric value of the rocky substratum when grazers were excluded suggests that grazing pressure by chitons and other grazing mollusks may be in part responsible for its low caloric value. UNDERWOOD (1980) found a similar phenomenon on Australian rocky shores and some investigators have suggested that food supply may be a limiting factor for grazing intertidal mollusks (UNDERWOOD, 1976; WELLS, 1978). Other workers (SCHNEIDER & TORUNSKI, 1983; TORUNSKI, 1979; GOLUBIC & SCHNEIDER, 1979; SCHNEIDER, 1976) suggest that the epi- and endolithic microflora are in a balanced trophic relationship with grazers where abrasion of

Table 5. Caloric contents of some biological materials taken from other studies.

Material	Caloric content (cal · mg DW ⁻¹)	Source
Mysis fecal strand	7.04	YOUNGBLUTH, 1982
Alpine meadow	4.71	GOLLEY, 1961
Kelp fronds	4.32	HAYES, 1974
Tropical forest litter	4.05	GOLLEY, 1969
Mangrove forest	3.76	GOLLEY, 1961
Tidal flat sediments	0.15	HUGHES, 1970

the superficial part of the limestone by grazers deepens the compensation depth for endoliths, thus stimulating further endolithic growth. In contrast, the abundance of fallen mangrove leaves in the study area suggests that the feeding activities of *Melampus coffeus* has little impact on its overall food supply.

Unlike many deposit feeders in mangrove areas (HEALD, 1969), *M. coffeus* often utilizes freshly fallen mangrove leaves, which are generally considered a poorer food source than decaying material (FELL *et al.*, 1980; RICE & TENORE, 1981). The higher absorption efficiency for fresh mangrove leaves by *M. coffeus* may be a result of relatively rapid leaching and bacterial decomposition of some of the less refractory compounds from decaying mangrove leaves, leaving a larger proportion of cross-linked celluloses and lignins, which are relatively resistant to decay (HEALD, 1969; RICE & TENORE, 1981). These difficult-to-digest lignins and celluloses may act as a greater "food dilutant" (CALOW, 1975) in decaying leaves resulting in a lower absorption efficiency for these leaves. MORTON (1955) reported that animals of the genus *Melampus* contained well-developed gizzards and highly specialized stomachs; this suggests that they may be capable of specialized digestive processes. Whether *M. coffeus* has any ability to utilize the generally indigestible lignins and celluloses is not known.

Previous studies have suggested that some deposit feeders obtain a certain amount of their nourishment from bacterial and microfauna populations on the decomposing detritus (LOPEZ *et al.*, 1977; YINGST, 1976, 1982); other studies have shown that certain deposit feeders get all (FOULDS & MANN, 1978) or part (TENORE & RICE, 1980; CAMMEN, 1980; HOBBI & LEE, 1980; STUART *et al.*, 1982) of their nourishment directly from the detrital substratum. Field observations indicated that *M. coffeus* feeds on leaf material rather than simply grazing on material accumulated on the leaves. Stomach content studies (MOOK, 1972) revealed mostly leaf material, again supporting present observations that *M. coffeus* feeds directly on the detrital substratum (mangrove leaves) rather than on only the associated bacteria or meiofauna. Obtaining food directly from the freshly fallen mangrove leaf detritus could be a mechanism for a more efficient utilization of a food source by the elimination of one trophic level from the food chain (FOULDS & MANN, 1978; ODUM, 1970). Why an organism such as *M. coffeus*, with a seemingly inexhaustible food supply, would evolve specialized mechanisms to increase the efficiency of its utilization of food is

unclear. The answer may lie in the temporal limitations placed on *M. coffeus* feeding behavior by tides: the snail leaves the substratum and climbs up and down the mangrove trees in synchrony with the high and low tides (HOLLE, 1956; APLEY, 1968). This temporal limitation of food supply coupled with the higher physiological price that *M. coffeus* must pay for its existence on land (RUSSELL-HUNTER *et al.*, 1972; PRICE, 1980) may have forced it to evolve such a more efficient mechanism.

The energy value of the organic components of an organism's food supply varies widely (FINLAY & UHLIG, 1981). Furthermore, the high energy components of the food may not be available because their complex chemical structure may be difficult to break down. *Acanthopleura granulata* absorbs nearly all of the energy it ingests (96%), suggesting that this species has developed the ability to utilize such high energy components. This ability has been demonstrated in other animal groups (CONDREY *et al.*, 1972). In contrast to *Melampus coffeus*, *A. granulata* inhabits areas where the food supply is very limited. However, like *M. coffeus*, *A. granulata* also has temporal limitations on its food supply because of its nocturnal grazing behavior (MOOK, 1983). In this case the utilization of such high energy components could be an adaptation to more efficiently utilize a limited food source.

M. coffeus appears to have developed different mechanisms than *A. granulata* for efficiently utilizing its food source. Possibly the utilization of a lower trophic level in the trophically diverse mangrove swamp is the physiologically least expensive of the several available options. Increased efficiency by consuming food from lower trophic levels has also been reported in several other organisms (*e.g.*, *Mugil cephalus* LINNÉ: ODUM, 1970; *Mysis stenolepis* SMITH: FOULDS & MANN, 1978) and may be a common strategy. Unlike mangrove areas, the tropical rocky intertidal habitat does not offer a variety of trophic levels. Utilizing a higher energy component of the existing food supply may be the only option that chitons have to utilize their limited food source. However, organisms inhabiting trophically more diverse habitats may also select for higher energy components of their food supply (*e.g.*, *Penaeus setiferus* (LINNÉ) and *P. aztecus* IVES: CONDREY *et al.*, 1972) indicating that this strategy is not restricted to trophically simple habitats. The question of how an organism utilizes its food supply and what mechanism it uses offers much potential for future studies.

Summary

Both the chiton *Acanthopleura granulata* and the snail *Melampus coffeus* have developed mechanisms to utilize their food supplies more efficiently. *A. granulata* does this by absorbing nearly all of the available calories in its food whereas *M. coffeus* may more effectively utilize its food supply by directly using fresh mangrove leaf detritus rather than broken down mangrove leaves with their associated bacteria and meiofauna. Utilizing the fresh rather than the broken down leaves may be a mechanism to eliminate a trophic level from the snail's food chain.

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