Grazing by the intertidal gastropod *Melampus coffeus* greatly increases mangrove leaf litter degradation rates

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ABSTRACT: *Melampus coffeus*, a pulmonate gastropod, forages for mangrove leaf litter at low tide and climbs tree trunks to avoid inundation during high tide. Unlike many grazers, these snails can assimilate mangrove leaf material. At Boca Ceiga Bay, Florida, densities of adult snails were high (>100 snails m^{-2}) throughout a 130 m wide intertidal zone. A mark–recapture study indicated that over the course of 1 mo $48.6 \pm 6.1\%$ of snails returned to their initial tree during high tides, while those that did relocate moved 6.66 ± 0.60 m and were recorded from 33 new trees at high tide. A field experiment comparing tethered leaves with small and large litter bags showed that snail grazing greatly increased the rate of red (*Rhizophora mangle*) and black (*Avicennia germinans*) leaf litter breakdown. Grazing by *M. coffeus* resulted in 90% weight loss in <4 wk (*A. germinans*) and 7 wk (*R. mangle*), compared to slower breakdown in litter bags (12 to 26 wk, *A. germinans*; >26 wk, *R. mangle*). Another experiment showed greater leaf litter accumulation on the forest floor in plots where *M. coffeus* was excluded. The decomposition coefficient (*k*) was 10× greater when *M. coffeus* grazing was allowed than *k* for any studies that enclosed leaves in litterbags. During our experiment, *M. coffeus* consumed an estimated 40.5% of mangrove leaf fall, and 19.8% of leaf litter was exported as particulate or dissolved material. This *M. coffeus* population can produce an estimated 3×10^6 larvae m^{-2} yr^{-1}, which suggests that the larval pathway is an important conduit of mangrove leaf resources to the estuarine food web.

KEY WORDS: Mangrove · Detritivore · Decomposition · *Rhizophora mangle* · *Avicennia germinans*

INTRODUCTION

Despite considerable study, the linkages between mangrove forest detritus and adjacent estuarine water ecosystems are inadequately understood (Odum & Heald 1972, Fell & Master 1973, Snedaker & Lugo 1973, Cundell et al. 1979, Twilley et al. 1986, Boto 1992, Holmer & Olsen 2002). Proffitt et al. (1993) reported that grazing by the intertidal gastropod *Melampus coffeus* L. (Pulmonata: Ellobiidae) in both field and laboratory trials caused very high rates of breakdown of *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa* leaves. They also found differences among mangrove species and with different degrees of leaf senescence (Proffitt et al. 1993) and were the first to suggest that grazing by

invertebrates might account for a large fraction of leaf breakdown in Florida. This important animal–plant interaction was missed by earlier studies of decomposition that excluded *M. coffeus* and other large invertebrate grazers by studying litter enclosed within mesh bags (Heald 1969, 1971, Lugo & Snedaker 1974, Twilley et al. 1986). Laboratory studies by Mook (1986) showed that *M. coffeus* could assimilate large fractions of fresh (79%) and senescent (56%) *R. mangle* leaves. McKee & Faulkner (2000) found high rates of grazing by *M. coffeus* on mangrove leaf litter in both natural and restored forests in SW Florida.

Where *Melampus coffeus* has an abundant and persistent population in mangrove forests, a substantial fraction of mangrove leaf productivity can pass through a snail-mediated pathway to the estuary as

snail biomass, larvae, and feces (Mook 1986, Proffitt et al. 1993). Thus, *M. coffeus* functions as more than just a shredder snail (sensu Newell 1965, Fenchel 1969, 1970, Newell & Barlocher 1993, Barlocher & Newell 1994). Clearly, differences in type of pathway and the rates of litter degradation in mangrove forests may affect predictions about the proportion of mangrove productivity that is re-cycled within the forest relative to that exported. The objectives of the present study were to further quantify the rates of *M. coffeus* grazing on *Rhizophora mangle* and *Avicennia germinans* leaf litter; to couple this with measurements of leaf litter fall and standing crop in order to estimate the rate of this grazing pathway per unit forest area; and to assess *M. coffeus* population densities over time and across the intertidal zone.

Melampus coffeus is abundant in many mangrove forests on both coasts of Florida (authors' pers. obs.) and is present and sometimes abundant elsewhere in the Caribbean (Golley 1960, Heard 1982). In Tampa Bay, *M. coffeus* and *M. bidatentus* co-occur, although the latter is more generally found in salt marshes (Mook 1973). Other studies have indicated the importance of *M. coffeus* in leaf breakdown in SW Florida (McKee & Faulkner 2000) and have suggested that the snail may affect seedling distribution in mangrove forests by consuming *Avicennia germinans* (Smith et al. 1989). Also, other invertebrates can play significant roles in mangrove leaf litter breakdown (Poovachiranon et al. 1986). Crabs have been frequently reported to relocate leaf litter from the forest floor to their burrows in the Indo-Pacific (Macnae 1967, Van der Valk & Attwill 1984, Leh & Sasekumar 1985, Robertson 1986, Lee 1989, Robertson et al. 1992). The crabs then consume the leaves after allowing some time for microbial growth. When leaves are buried under sediment without crab intervention, decomposition is much slower (Holmer & Olsen 2002). Twilley et al. (1997) reported that crabs were important in the removal of litter in some seasons in Ecuador.

Many ellobiid gastropods have a specialized gizzard and stomach system that allows a high efficiency of assimilation of plant matter consumed (Morton 1955). Some molluscs also tend to have a diverse complement of digestive enzymes, often including cellulases (Mason 1974). However the digestive enzymes of *Melampus coffeus* have not been studied. *M. coffeus* preferentially aggregates to green leaves over yellow and brown ones (Proffitt et al. 1993, present study field observations). However, *M. coffeus* apparently requires more time to break through the tough outer cuticle of green leaves. Consequently, there is a lag time before grazing effects are evident, whereas on yellow and brown leaves, grazing effects are seen within hours of exposure (Proffitt et al. 1993). This snail

is an active grazer when the forest floor is exposed at low tide. It escapes being covered by water at high tide by climbing tree trunks, prop roots, taller seedlings, and various emergent debris. The timing of this behavioral rhythm was maintained a number of days when snails were brought in to the lab and kept without any tidal flux (authors' pers. obs.).

Litterfall occurs in seasonal and species specific patterns mainly as yellow senescent leaves, although substantial numbers of green leaves fall episodically during storms (authors' pers. obs.). The rates of grazing of *Melampus coffeus* vary by species and by degree of senescence of the leaves (Proffitt et al. 1993). Thus, the proportion of litter entering the system as green versus yellow leaves, the proportion of leaves that exist on the ground long enough to become brown, and the rates of breakdown of each leaf group all contribute to the nature and pattern of coupling of mangrove forests to adjacent open-water systems and should be considered in models of decomposition and nutrient cycling.

We report here on a 26 wk field experiment of mangrove leaf breakdown in which mangrove leaves were either tethered and thus exposed to *Melampus coffeus* grazing, enclosed in individual small bags, or enclosed with a group of leaves in larger mesh bags that excluded *M. coffeus*. We also conducted a caging study in which litter and snails were removed from one group and litter but not snails from the other and the accumulation of leaf litter over 1 mo was tracked. The hypothesis tested in the first experiment was that leaves enclosed within bags would receive less grazing and therefore degrade less rapidly than tethered leaves exposed to *M. coffeus*. The hypothesis evaluated in the second associated experiment was that litter would accumulate more rapidly on sections of the forest floor that were fenced to eliminate grazing by *M. coffeus*. We also collected litterfall during the caging experiment and measured standing crop of litter in the forest over a 1.5 yr period. Data on mangrove forest structure and *M. coffeus* population densities were also gathered. Grazing rates measured in the litterbag experiment and snail density data were applied to the data on litterfall and standing crop in order to estimate overall amounts of leaf degradation due to *M. coffeus*. The rate of snail movements around the forest were determined in a mark–recapture study to provide information on snail movement and foraging behavior.

MATERIALS AND METHODS

Forest structure, litter standing crop, and litterfall. The study was conducted in Boca Ciega Bay, part of the Tampa Bay estuary system, in the mixed species mangrove forest at War Veterans Park, Pinellas

County, Florida (Fig. 1). Densities of canopy trees, their heights and diameters at breast height (DBH, measured at about 1.3 m above ground) were determined in 3×3 m plots, at stations situated every 10 m along a 130 m long transect extending from shore (0 m) to the upland edge (130 m).

Leaf litter standing crop was collected at stations located 10, 50, and 120 m from shore in 5 replicate 30× 30 cm quadrats 4 times over a year in 1993. Leaf litterfall was collected twice during a 60 d period in the same location during one of the leaf breakdown studies during late summer. Three replicate 0.5×0.5 m collectors made from plastic screen material (1 mm mesh size) were used to collect leaf litterfall at the same location as the decomposition studies. Leaves were separated by species, and dry weights were determined for both standing crop and litterfall.

***Melampus coffeus* population densities.** *Melampus coffeus* densities were recorded in replicate 20×20 cm quadrats (n = 5 to 10) at each station along the forest structure transect during low tide over 33 mo from 1992 to 1994. Density values reported here include only overall transect means (±1 SD) of individuals with shell lengths >4 mm. Smaller individuals 1 to 4 mm in length were present in all months of the year. Separate from the adult population collections, we measured juvenile densities, along with those of adults, on the forest floor in 30×30 cm quadrats (n = 5) at 4 of the stations in February and May. Juvenile and adult densities (square-root-transformed) were analyzed by MANOVA with time (month) and station as independent variables. Also, all quadrats were subjected to paired *t*-test to determine whether mean adult versus juvenile densities differed. Adult and juvenile densities were tested to determine whether they were spatially correlated (Pearson product–moment correlation).

Patterns and rates of snail movement on the forest. We conducted a mark–recapture study of *Melampus coffeus* adults in order to determine their rates of movement around the forest at low tide. During a high tide in May 1993, all snails on 3 *Avicennia germinans* trees approximately 120 m from open water were marked with a different color paint for each tree. The numbers and locations of marked and total snails on tree trunks on subsequent high tides were determined, and the distance of these trees from the starting trees measured.

Leaf tethering and litterbag experiment. The site chosen for the experiment on decomposition of *Rhizophora mangle* and *Avicennia germinans* leaf litter was located 50 to 60 m into the forest from the shoreline. The leaf grazing experiment was initiated in June 1993 and ran for 26 wk. Main factors in the experiment were plant leaf species, grazing treatment, and
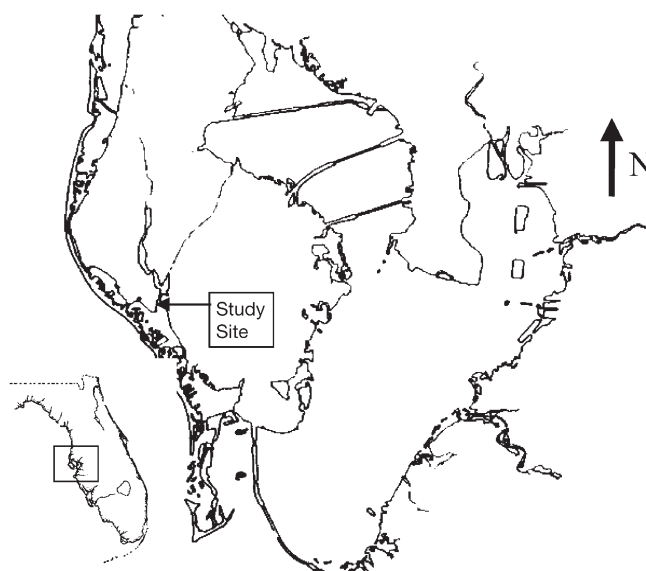

Fig. 1. Map of the Tampa Bay, Florida, estuarine system showing the location of the study site at War Veterans Park in Boca Ciega Bay (27° 48′ N, 82° 46′ W). The state map (left) shows the location of Tampa Bay. Scale: 1 cm is approximately 1.6 km

time. Leaves were collected from trees in the forest for use in the experiment. The grazing treatment had 3 levels: (1) *unbagged*, in which leaves were tethered by their petiole to a wooden stake via monofilament; (2) *small litter bags*, in which single leaves were enclosed in 10×8 cm polypropylene bags held in a cylindrical shape by an internal lattice of larger gauge plastic mesh; and (3) *large litter bags* (30×30 cm), into which 20 g of leaf material (either *R. mangle* or *A. germinans*) was placed. The internal lattice of plastic mesh was used to shape small bags into a cylinder, rather than allowing them to lay flat, in order to reduce the through-the-mesh grazing reported by Proffitt et al. (1993). All bags had a mesh size of 1 mm². Bags were sewn shut with monofilament line. Unbagged (tethered) leaves and bags were tied to wooden stakes (4 to a stake) with 15 cm long strands of monofilament line. Stakes were marked and driven into the sediment at randomly assigned locations ranging from 50 to 60 m from shore, where the canopy was dominated mainly by *A. germinans* with a large number of subcanopy *R. mangle* trees. Sampling was conducted at 4, 7, 12, and 26 wk. Numbers of replicates collected during each sampling were: unbagged = 20, small bags = 20, and large bags = 5. Senescing (yellowing) leaves were used in the experiment.

Collected leaves were carefully washed in the laboratory, and the leaf area showing visible decomposition was measured under a dissecting microscope

following the procedures of Proffitt et al. (1993). This provided 2 measures: (1) areas of holes, where leaf material had completely disappeared, and (2) areas of translucence, where sections of leaves had become noticeably thinner generally (especially in earlier weeks) because of the grazing of layers of cells from the surface. The sum of these 2 measures gave the total area affected by grazing (Proffitt et al. 1993). Dry weight was measured (48 h, 50°C) following area determinations. Dry weights of leaves that were not subjected to field treatments were also measured to allow calculation of percent weight loss occurring under degradation and grazing treatments.

Percent area (translucence and holes) and percent weight remaining were analyzed in a MANOVA with mangrove species, treatment, and time as independent variables. Percent data were arcsine-square-root-transformed following conversion to proportions.

Litter accumulation in cages with *Melampus coffeus* excluded. Open top cages (61×61 cm sides, 50 cm tall, 1 mm mesh size) were constructed at the site of the first experiment. In one set (n = 4) of cages, all litter and snails were removed initially, and any snails re-entering caged areas were removed during a daily check. In the other set of cages, litter was removed but snails were maintained at typical densities (114 snails m^{-2}) by daily checks and addition of snails as needed. After 27 d, all litter was collected from cages, dried and weighed. Mean leaf accumulation by dry weight in cages with and without snails was analyzed by Student's *t*-test.

Calculations and derived variables. *Decomposition coefficient:* The decomposition coefficient (*k*) was calculated from:

$$W_t = W_0 e^{-kt}$$

where W_0 = initial dry weight, W_t = dry weight remaining at time *t*.

Since the proportion of weight remaining is simply $P_W = W_t/W_0$, the equation to calculate *k* can be written as:

$$k = -\ln(P_W)/t$$

k was estimated by regressing the proportion weight remaining on time (in days).

Grazing rates: Leaves exposed to *Melampus coffeus* grazing were staked out among the natural leaf litter of the forest. Therefore, grazing rates calculated from the experimental leaves were applied to the standing crop of leaf litter to provide an estimate of the total amount of material consumed.

Amount consumed per day (C_g) = percent weight grazed/d×litter standing crop (g dry wt m^{-2}). This is a slight overestimate of the total grazing, since litter on the ground varies in age and thus probably palatability. However, Proffitt et al. (1993) showed that both

yellow and brown leaves were consumed at somewhat similar rates after the first few weeks.

Daily leaf litterfall: The amount of the daily leaf litterfall (*L*) that was consumed (C_{LF}) per day was calculated as: $C_{LF} = L - C_g$. Both *L* and C_g are in g m^{-2} d^{-1}.

RESULTS

Melampus coffeus habitat description: forest structure, tidal flooding, litter standing crop, and litterfall

The intertidal region dominated by mangroves was 130 m from open water to upland edge. Unless otherwise specified, values presented in text and graphs are means and one standard deviation. The first 20 m was dominated by *Rhizophora mangle* (3.87 ± 0.86 m tall; DBH 4.2 ± 1.0 cm) (Fig. 2A). *Avicennia germinans* was dominant (Fig. 2A) from 30 m to the upland edge (height 5.12 ± 1.78 m; DBH 6.8 ± 2.9 cm). The region of the forest where leaf decomposition experiments took place was flooded by 252 tides yr^{-1} to monthly mean high depths ranging from 8.1 ± 4.7 to 13.2 ± 5.5 cm. The area near the mangrove-upland edge was flooded by 124 tides yr^{-1}.

The leaf litter standing crop was about evenly split between *Rhizophora mangle* and *Avicennia germinans* leaves within 20 m of open water, but was 83% *A. germinans* and 17% *R. mangle* for the rest of the
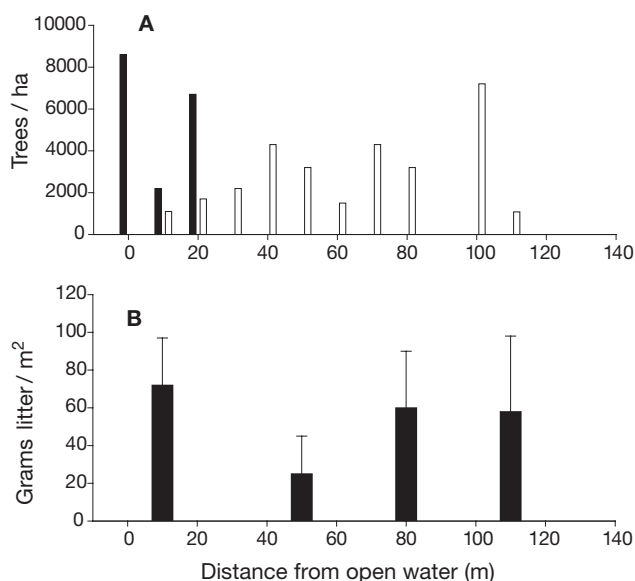

Fig. 2. (A) *Rhizophora mangle* (solid bars) and *Avicennia germinans* (open bars). Relative densities of mangroves from forest-open water edge to upland edge. (B) Standing stock of total mangrove leaf litter at 4 sites along the transect

forest, including the area where the leaf breakdown experiments were conducted (50 to 60 m from open water). The mean standing crop in the forest ranged from 55.2 ± 39.7 to 68.8 ± 27.1 g dry wt m^{-2} over an 18 mo period and was distributed relatively consistently through the 4 stations monitored in the intertidal zone (Fig. 2B). Leaf litterfall over the 60 d of one decomposition experiment was 1.11 ± 0.47 g dry wt m^{-2} d^{-1}.

Melampus coffeus population densities

Melampus coffeus maintained high adult (5 to 19 mm shell length) densities throughout nearly 3 yr of observations (Fig. 3). MANOVA analysis indicated that densities of juveniles varied with season (February vs May: $F = 4.772$, $p < 0.035$) with densities in February being 2× those in May, but adult snails densities did not differ with season ($F = 0.897$, $p = 0.349$). The snails were abundant throughout the intertidal zone (Fig. 3), except for the region within ca. 2 m of

open water. The spatial dispersion pattern on the forest floor was very patchy over small scales as *M. coffeus* tended to congregate on leaf litter and to move toward trees and saplings with rising tide. Very small snails (<4 mm shell length) did not climb to avoid rising water, but rather stayed under leaves or within crevices of driftwood when tides were high. The analysis also showed that both juveniles and adults varied with station (10, 30, 60, 120 m from open water: juveniles, $F = 5.194$, $p < 0.004$; adults, $F = 2.805$, $p < 0.053$). For juveniles, there was also a significant season×station interaction ($F = 4.97$, $p < 0.005$) mainly caused by very low numbers of juveniles at the station farthest from open water (120 m) in February but much higher numbers in May. Juvenile and adult densities were not significantly correlated ($p = 0.09$). Adult densities were significantly greater than juvenile densities (paired t-test, $t = 2.11$, df = 44, $p < 0.04$), although overall mean densities on the forest floor of both groups were relatively high (adults: 142.7 snails m^{-2}; juveniles: 104 snails m^{-2}).

Patterns and rates of snail movement in the forest

Tree DBH and numbers of marked snails on each study tree were: Tree B1, DBH = 4.9 cm, snails = 64; Tree B2, DBH = 5.1 cm, snails = 97; and Tree B3, DBH = 4.8, snails = 34. Distances between these trees were: B1–B2, 2.49 m; B1–B3, 1.64 m; B2–B3, 1.01 m. The total (marked + unmarked) snails on the 3 original trees remained relatively stable over the 31 d of the study (62.1 ± 7.7, range 50.7 to 74.7 snails tree^{-1}). During the study, the 195 total snails marked on the 3 trees relocated to trees up to 6.66 ± 0.60 m away from their initial tree and populated a total of 33 new trees covering an area of the forest floor of 139 m^2 (Fig. 4). However, after 1 mo, 48.6 ± 6.1 % of snails were recorded on the tree where they had originally been marked (Fig. 4C).

Leaf tethering and litterbag experiment

Breakdown of tethered leaves exposed to *Melampus coffeus* grazing was much more rapid when measured either as dry weight loss (Fig. 5) or area of holes grazed leaves (Fig. 6) than was breakdown of leaves in small, single-leaf bags or groups of leaves in large bags that excluded snails. Leaf breakdown was significantly affected by mangrove species, decomposition treatment, and time main effects and most of their interactions (Table 1).

Avicennia germinans decomposition was much more rapid than that of *Rhizophora mangle.* For tethered
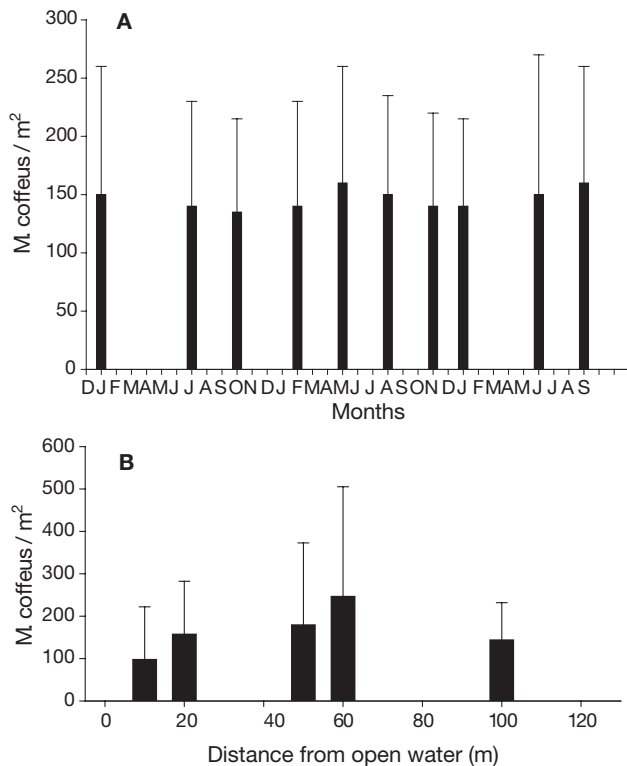

Fig. 3. *Melampus coffeus.* (A) Numbers per m^2 of adult snails in the study forest over nearly 3 yr. (B) Distribution of adult snails at 5 stations in the intertidal zone (130 m wide) in the forest. Distribution of *M. coffeus* observed in the field was from just behind a berm (1 to 2 m in from open water) to the upland edge at about 130 m from open water
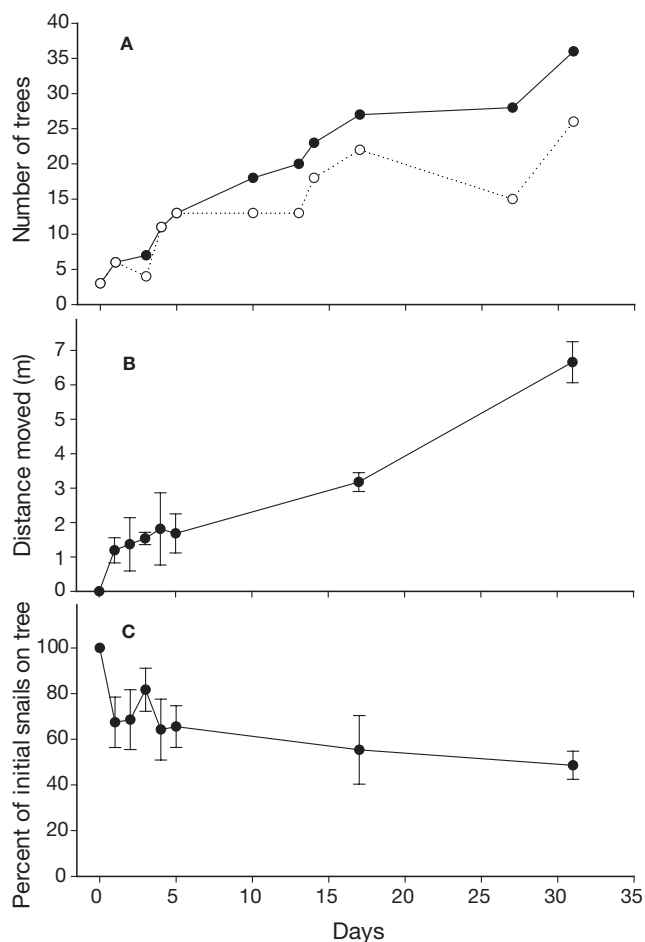
Fig. 4. (A) Number of trees colonized by marked snails over 31 d. (●) Cumulative number of trees with marked snails by that date; (○) number of trees with marked snails on that day of measurement. (B) Distance moved by snails over time. (C) Percent of all snails returning to the initial tree where they were marked at time 0
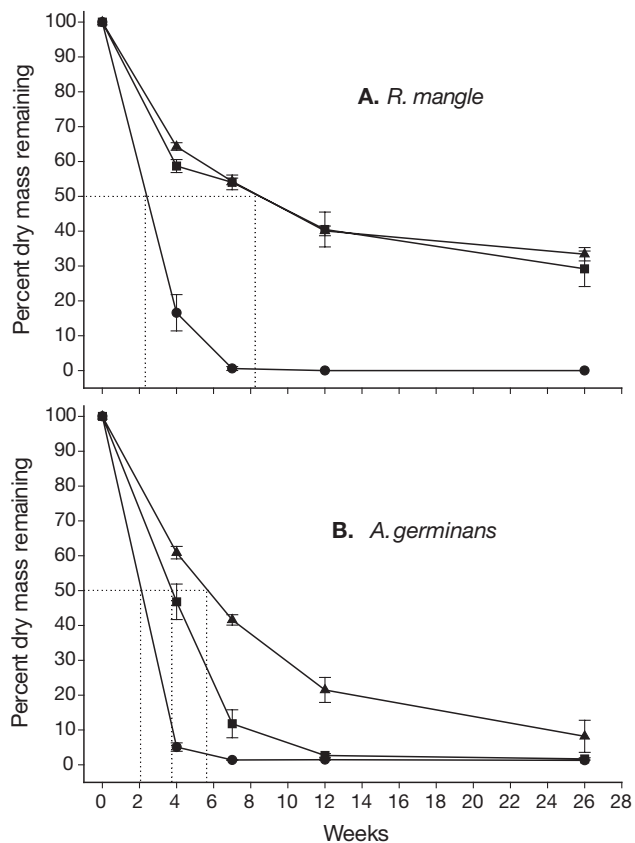

Fig. 5. Percent dry mass remaining for (A) *Rhizophora mangle* and (B) *Avicennia germinans* leaves decomposing under unbagged (●), small individual bag (■), or large bag (▲) conditions. Dashed lines dropping to the *x*-axis indicate the number of weeks for loss of 50% of leaf mass

leaves, 50% weight loss occurred in 2 wk (*A. germinans*) and just over 4 wk (*R. mangle*), while 50% weight loss of bagged leaves for *A. germinans* leaves took about 4 to 6 wk depending on bag size, and for *R. mangle* 50% weight loss of bagged leaves took just over 8 wk (Fig. 5).

Litter accumulation in cages with *Melampus coffeus* excluded

Cages excluding *Melampus coffeus* accumulated significantly more litter over 27 d (17.0 ± 5.03 g dry wt m^{-2}) than did cages in which ambient densities of the snail were maintained (4.44 ± 2.37 g dry wt m^{-2}) (Student's *t*-test, p < 0.025).

Calculated *k* values

Calculated *k* values for *Rhizophora mangle* and *Avicennia germinans* exposed to *Melampus coffeus* grazing were 0.105 and 0.107 d^{-1}, respectively. The *k* values for leaves enclosed in small and large litter bags for both species respectively were: *A. germinans*, 0.022 and 0.014 d^{-1}; and *R. mangle*, 0.006 and 0.005 d^{-1}.

Estimation of amount of standing crop and leaf litterfall consumed by *Melampus coffeus*

Experimental leaves were tethered among the natural leaf litter of the forest. Because *Melampus coffeus* consumes green, yellow, and brown leaves (Proffitt et al. 1993), the rates of grazing measured can be applied to the litter standing crop. Where the decomposition experiment was conducted, mean litter standing crop was 22 g dry wt m^{-2} (18.3 g dry wt m^{-2} *Avicennia ger-*
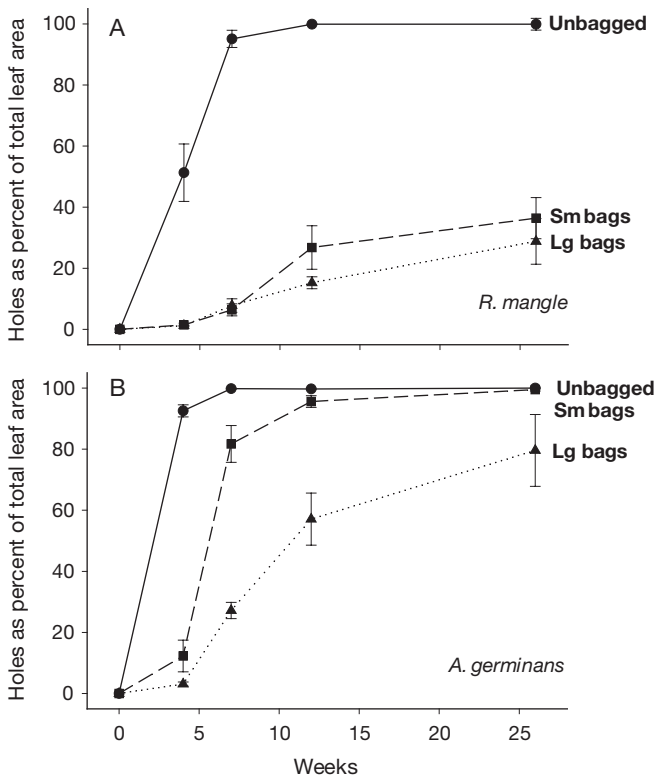
Fig. 6. (A) *Rhizophora mangle* and (B) *Avicennia germinans.* Breakdown, as holes in leaves expressed as a percent of total leaf area, for unbagged (tethered), small (Sm) individual bag, and large (Lg) bag treatments for mangrove leaves

cies provides an estimate of the actual daily loss of mass due to grazing (*R. mangle* = 0.81 % d^{-1}; *A. germinans* = 2.31 % d^{-1}). The dry weight of material grazed per day per m^2 of forest during the experiment was: *A. germinans*: 18.3 g m^{-2}×2.31 % grazed d^{-1} = 0.42 g m^{-2} d^{-1}; *R. mangle*: 3.7 g m^{-2}×0.81 % grazed d^{-1} = 0.03 g m^{-2} d^{-1}.

Since litterfall = 1.11 g m^{-2} d^{-1} and occurred in the same proportions by species as standing crop, the amount of total leaf fall per day that was consumed by *Melampus coffeus* is estimated as 0.45/1.11 = 40.5 %.

The estimated rate of net accumulation of litter in the forest (net litterfall rate – tethered leaf decomposition rates [i.e. grazed vs microbial and physical combined]) is 1.11 – 0.703 = 0.41 g m^{-2} d^{-1}, in which net accumulation is actual accumulation – tidal export. An estimate of gross accumulation was obtained from the measured litter accumulation rate in the cages in which litter and snails were removed (17 g m^{-2}/27 d = 0.63 g m^{-2} d^{-1}) and sides prevented the export of all but smallest particles by tides. Thus, about 0.63 – 0.41 = 0.22 g m^{-2} d^{-1} of litter was exported as particulate material, which was 19.8 % of the leaf litterfall. These estimates are only valid for the time frame of these experiments, and additional studies are needed to examine seasonal effects. Nevertheless, grazing was rapid in late winter–early spring (Proffitt et al. 1993) and summer (present study), and snails were abundant and active in every month of the year. Thus, a high proportion of litterfall appears to be consumed by this *Melampus coffeus* population in all seasons. An additional area for further research is in the per day consumption rates for leaf litter of different age. Proffitt et al. (1993) found in a laboratory study that *M. coffeus* rapidly grazed fresh, yellow, and brown leaves, although at somewhat different rates. Here, we applied the grazing rate from our experimental leaves to the total standing crop of leaf litter. Although we believe that this provides a good estimate of total consumption, further quantifica-

minans and 3.7 g dry wt m^{-2} *Rhizophora mangle* leaves). Conservative estimates of the percent loss per day were made for bagged and tethered leaves from the number of days required for 50 % loss of mass from Fig. 5. These daily loss rates were: *R. mangle* (tethered = 1.7 % d^{-1}, bagged = 0.89 % d^{-1}) and *A. germinans* (tethered = 3.5 % d^{-1}, bagged = 1.19 % d^{-1}). The difference between tethered and bagged values for a spe-

Table 1. MANOVA results for mangrove leaf litter breakdown for leaves that were tethered or placed in small or large decomposition bags. Dependent variables were percent of leaf area that was translucent, holes in leaves as percent of total area, and percent dry weight loss. Independent variables were decomposition treatment, mangrove species, and time. Percent data were converted to proportions and arcsin(square root) transformed prior to analyses

Effect	Holes		Translucent		Weight loss	
	F	p	F	p	F	p
Species	160.1	0.005	18.97	0.005	52.49	0.005
Decomposition treatment	392.98	0.005	32.49	0.005	308.34	0.005
Time	88.28	0.005	13.38	0.005	54.11	0.005
Species×Treatment	59.25	0.005	17.39	0.005	69.55	0.005
Species×Time	2.91	0.03	3.01	0.03	1.78	0.15
Treatment×Time	6.72	0.005	3.85	0.005	7.79	0.005
Species×Treatment×Time	15.92	0.005	11.44	0.005	6.48	0.005

tion in the field of rates of grazing on a broader age range of leaf litter will be necessary to refine this estimate.

In summary, an estimated 40.5 % of leaf fall was consumed by *Melampus coffeus*, where it was converted to snail biomass, eggs and larvae, and snail fecal material. Another 22.8 % of leaf fall biomass was lost to chemical leaching, physical breakdown, and microbial action, and 19.8 % was exported mainly as intact larger pieces of material. Thus, during the experiment, an estimated 16.9 % (0.19 g m^{-2} d^{-1}) of leaf fall was left to contribute to the leaf litter standing crop. An important unknown is the rate of production and nutrition and energy content of snail fecal material. Because fecal matter funnels into the microbial pathway, and since fecal pellets generally adhere to surfaces, this material may be decomposed in the forest rather than being exported to estuarine waters intact.

DISCUSSION

The intertidal air-breathing gastropod *Melampus coffeus* is a critical component in the breakdown of mangrove leaf litter, and it forms an important link between mangrove forest productivity and estuarine food webs. Although a number of other invertebrate species act to accelerate litter breakdown in mangrove and salt-marsh systems (e.g., shredder snails, sesarmid crabs), *M. coffeus* belongs to a smaller group that can directly assimilate the resources in mangrove leaves (Mook 1986). Hence, where *M. coffeus* is a dominant littervore, substantial portions of mangrove leaf material are converted to snail biomass and larvae. Adult snails are preyed upon by white ibis *Eudocimus albus*) (authors′ pers. obs.); juvenile snails may be preyed on by killifish *Fundulus heteroclitus*, which we have observed foraging in the leaf litter at high tide; and larvae are exported to the estuary (Apley 1968).

We found that *Melampus coffeus*, which maintained high population densities throughout most of the intertidal zone over a 3 yr study, was very active in terms of movement and leaf-grazing on the forest floor at low tide. We estimated that 40.5 % of leaf litterfall was consumed by *M. coffeus* during our late summer–early fall decomposition studies. Similar to results of Proffitt et al. (1993), we found that *Avicennia germinans* leaves were consumed more rapidly than *Rhizophora mangle* leaves. Proffitt et al. (1993) also found high grazing rates in a winter field experiment at this same site. McKee & Faulkner (2000) reported high rates of grazing, mainly by *M. coffeus*, at 2 sites in SW Florida and low rates at 2 other sites. They found that leaves of *A. germinans* and *L. racemosa* were consumed more rapidly than those of *R. mangle*, and that grazing dif-

fered between years. The high percentage of litterfall consumed by *M. coffeus* in Florida was similar to values reported for crabs in the Indo-Pacific. Robertson (1986) reported that crabs consumed 28 % of leaf fall in Australia, Lee (1989) found that crabs removed 57 % of leaf litter produced by the mangrove *Kandelia candel*, and Emmerson & McGwynne (1992) showed that 44 % of *Avicennia marina* litter was consumed by crabs. Twilley et al. (1997) reported that a crab harvested most leaves during the rainy season in a forest in Ecuador. Middleton & McKee (2001) compared tethered and bagged leaves in Belize and found that crabs were responsible for considerable fraction of leaf mass loss and that gammarid amphipods also contributed to leaf degradation. The leaf mass consumed per day by crabs in Belize (Middleton & McKee 2001) was less than that consumed by *M. coffeus* in the present study (*R. mangle* leaves: 0.175 vs 0.81 %; *A. germinans* leaves: 0.348 vs 2.31 %). Percent removed per day by crab grazing in the lower intertidal zone in Belize reported by Middleton & McKee (2001) was similar to grazing rates by *M. coffeus* in Tampa Bay averaged over the different species of mangrove leaves in the 2 studies (Belize 1.96 % vs Tampa Bay 1.56 % grazed d^{-1}). However, grazing by *M. coffeus* occurred throughout the intertidal zone, while the high grazing in Belize was restricted to the lower intertidal.

Rates of decomposition (*k* values) of leaves in litterbags in our study were similar to literature values (Fig. 7). The *k* values for both *Rhizophora mangle* and *Avicennia germinans* exposed to *Melampus coffeus* grazing were greater than *k* values from litter in either small or large bags. Comparison of our data with other studies of mangrove decomposition indicates that litterbag studies that exclude detritivores have much slower decomposition rates (Fig. 7). The typical *k* ranges for the 2 species were as follows: 0.0026 to 0.0061 d^{-1} (*R. mangle*) and 0.0037 to 0.027 d^{-1} (*A. germinans*), when measured in litterbags (Fig. 7). Twilley et al. (1997) found differences in the rate of *R. mangle* decomposition in Ecuador between wet (*k* = 0.011 d^{-1}) and dry (*k* = 0.006 d^{-1}) seasons. However, their highest value is 10× less than for leaves exposed to *M. coffeus* in our present study. Twilley et al. (1997) reported that the crab *Ucides cordatus* relocated most leaves to its burrow during the rainy season (January to June) and that the great tidal range transported most leaves to the estuary during the time of reduced crab activity.

The closely related *Melampus bidentatus* produces 33 150 eggs snail^{-1} yr^{-1} (Apley 1968). *M. coffeus* lay similar numbers of eggs in gelatinous masses under leaves and on decaying wood (Russell-Hunter et al. 1972). Since the snails are simultaneous hermaphrodites, it is possible that a population averaging 100 snails m^{-2} could produce some 3×10^6 larvae m^{-2} yr^{-1}.
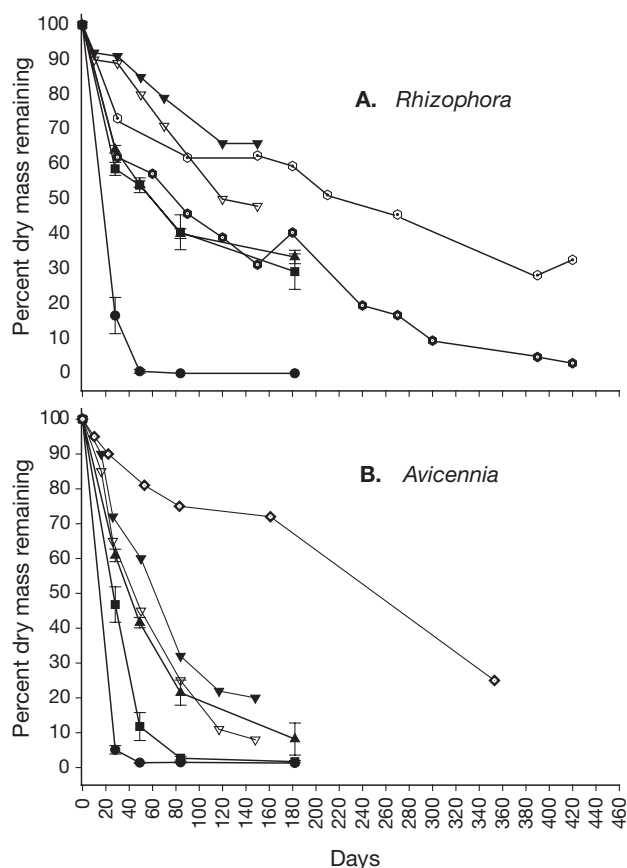
Fig. 7. Percent dry mass remaining for (A) *Rhizophora mangle* and (B) *Avicennia germinans* leaves. Present study data are unbagged (●), small individual bags (■), or large bags (▲). (A) also contains data from Heald (1969) (◉ = dry area, ◕ = wet brackish) and Twilley et al. (1986) (▽ = mixed species plot, ▼ = monospecific plot at Rookery Bay). (B) also contains data from Twilley et al. (1986) (◆ = their RB1 mixed site, ▼ = their RB2 monospecific site, ▽ = their RB2 mixed site), June trials

These larvae are exported via the tide and spend 4 to 6 wk in the planktonic food web of the estuary before the survivors return on a spring high tide to metamorphose into juvenile snails (Apley 1968, Holle & Dineen 1957). Thus, a substantial proportion of the export of nutrient and energy resources from mangrove leaf litter is in the form of snail larvae in the Tampa Bay estuary.

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