Herbivory by Caribbean majid crabs: feeding ecology and plant susceptibility

Loren D. Coen

Department of Zoology. University of Maryland, College Park, Maryland, U.S.A.

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Abstract: The present study investigated plant susceptibility, plant quality and food preferences in two small herbivorous mesograzers, the majid crabs Mithrax sculpitus (Lamarck) and Mithrax coryphe (Herbst). Seven plants were chosen based on characteristics hypothesized to influence grazer preferences. These included relative abundance, hypothesized food "quality" (percent ash and water, caloric contents), previous observations on plant susceptibility to herbivorous fishes and sea urchins and inherent structural and chemical traits.

In single preference (day and night) and multiple selection experiments, preferences for both crab species were similar among the seven plants tested and were concordant with those determined previously for fish and urchin grazers on other Caribbean reefs. Mithrax successfully manipulated and consumed both corticated (Laurencia, Acanthophora) and leathery (Padina, Lobophora ruffled form) macroalgae using their spatulate chelae, except where plant secondary chemistry probably reduced consumption (Lobophora decumbent form and Stypopodium). Significant differences in plant calorific, percent organic matter and water values were found among the seven plants and correlations between these variables and feeding preference ranks were negative and highly significant. Curiously, correlations between preference rank and calorific value suggest that crabs were selecting plants with potentially lower net caloric returns. However, when feeding rates were adjusted on a per meal basis, observed grazing rates on "preferred" species may be sufficiently high for crabs to potentially maximize net energy gain.

Key words: Belize; Coral reef; Crab; Feeding preference; Herbivory

INTRODUCTION

Tropical marine herbivore faunas are quite diverse but often fall into fairly discrete functional groupings or guilds (Steneck, 1983; Carpenter, 1986; Menge et al., 1986). However, few field studies (see reviews by Borowitzka, 1981; Lubchenco & Gaines, 1981; Steneck, 1983; Huston, 1985) have examined the possible impact of reef-associated herbivore species other than fishes and sea urchins, exceptions being the work of Carpenter (1986) and Coen (1988) for example.

Herbivores vary in the methods they employ to manipulate and consume plants in the marine environment (e.g., Steneck & Watling, 1982; Steneck, 1983; Gaines, 1985; Lewis, 1985, 1986). In large measure, this results from constraints placed on these
grazers by their morphologies, and to some degree, on selection driven by inherent plant traits (Littler & Littler, 1980; Lubchenco & Cubit, 1980; Paul & Hay, 1986; Targett et al., 1986; Paul et al., 1987; Hay et al., 1988a). These deterrents are not absolute; rather their effectiveness is often dependent upon the herbivore’s feeding apparatus (e.g., Steneck, 1982, 1983; Steneck & Watling, 1982; Gaines, 1985; Padilla, 1985; Coen, 1987). The ability of herbivores to overcome these structural and chemical traits may vary considerably (e.g., Hay et al., 1987a, 1988b). Until recently (Coen, 1987; Hay et al., 1987a, 1988b), morphological and chemical traits as herbivore deterrents in tropical macrophytes have been investigated only with respect to macrograzers (e.g., Hay, 1981a, 1984b; Littler et al., 1983a, b; Lewis, 1985; Morrison, 1986; Paul & Hay, 1986; Targett et al., 1986). Few data are available to test the generality of plant susceptibility patterns for smaller tropical invertebrate herbivores (e.g., mesograzers, Brawley & Fei, 1987; Hay et al., 1987a; Paul et al., 1987).

Herbivorous crustaceans, such as decapod crabs, have been shown to influence semi-terrestrial (e.g., Beever et al., 1979) and marine (e.g., Sousa, 1979; Menge & Lubchenco, 1981; Robles & Cubit, 1981; Menge et al., 1986; Coen, 1988) plant communities in both temperate and tropical habitats. For example, Menge & Lubchenco (1981) and Menge et al. (1986) suggest that the scarcity of fleshy algae in Pacific Panama is in large part a direct result of grazing crabs. Previous studies have shown that live plants (as opposed to just plant detritus) often constitute a large proportion of the diet of many temperate and tropical crabs (Crane, 1947; Hiatt, 1948; Herreid, 1963; Havens, 1974; Hagen, 1977; Warner, 1977; Beever et al., 1979; Hines, 1982; Klumpp & Nichols, 1983; Leber, 1983; Choy, 1986; Coen, 1987), even in families not previously thought to have herbivorous representatives (e.g., Portunidae: Klumpp & Nichols, 1983; Choy, 1986). In spite of this, plant grazing preferences of decapod crustaceans are poorly known (Coen, 1987), except from indirect work exploring decorating (or camouflaging) behavior of a few majid crabs (Getty & Hazlett, 1978; Mastro, 1981; Wicksten, 1983; Kilar & Lou, 1984, 1986).

Here I present results of a study, the objectives of which were: (1) to examine the characteristics of seven species of tropical marine plants chosen for observed differences in relative abundance, susceptibility to fish and sea urchin herbivores and previously identified structural and chemical traits (for macrograzers); (2) to establish preference hierarchies based on comparative grazing rates of two species of Mithrax on this group of commonly encountered (by crabs) plants; and (3) to test whether crab preference patterns conform to those previously observed for macrograzers. Earlier experimental work in Belize on macrograzers provides a framework against which grazing by smaller invertebrate herbivores, such as decapod crabs can be compared.

STUDY SITE AND EXPERIMENTAL ORGANISMS

All collections and experiments were conducted at the Smithsonian Institution’s Carrie Bow Cay field station, Belize, Central America (16°48′N: 88°05′W) during

HERBIVORES

The genus *Mithrax* is one of the most diverse and abundant crab genera in shallow warm-temperate to tropical waters in the Gulf of Mexico, Caribbean Sea and eastern Pacific. Previous work (Warner, 1977; Coen, 1988) has demonstrated that Caribbean *Mithrax* spp. are primarily herbivorous and that they significantly depress algal cover within localized areas (Coen, 1988). *Mithrax sculptus* (Lamarck) and *Mithrax coryphe* (Herbst) are extremely common majid crabs on western Atlantic coral reefs from Florida to Brazil where they are found intertidally to 55 m in cavities in rocks, corals and sponges (Rathbun, 1925; Powers, 1977; Warner, 1977).

In the present study, *M. sculptus* and *M. coryphe* were collected exclusively from small individual *Porites porites* (Pallas) (forma furcata) coral heads in the backreef northeast of Carrie Bow Cay in water < 1.5 m deep. However, both species were locally abundant wherever complex three-dimensional structure (e.g., branching coral colonies, loose and consolidated rubble) was available. *Mithrax coryphe* individuals reached a maximum size of 26 mm carapace width (cw) and a weight of 5.7 g; *M. sculptus* individuals attained a maximum size of 24.6 mm cw and a weight of 7.3 g (Coen, 1987).

ALGAL PREY SPECIES

Experimental plant species were chosen according to local relative abundance and previous differences in herbivore susceptibility as derived from earlier fish and sea urchin studies (i.e., herbivore resistant traits, see Table I and Hay, 1981a, 1984a; Norris & Fenical, 1982; Littler et al., 1983a, b; Lewis, 1985, 1986; Taylor et al., 1986). Distributions of all seven plants overlap those of both species of *Mithrax*. Seven marine plants were used in experiments to examine feeding rates and preferences of the two species of *Mithrax*.

Plants were divided into functional groupings (sensu Littler & Littler, 1980; Steneck & Watling, 1982) consisting of sheet-like, coarsely-branching, corticated, or leathery plants. Experimental macrophytes (Table I) included: two red algae [*Laurenciapapillosa* (Forsskal) Greville and *Acanthophora spicifera* (Vahl) Boergesen], four brown algae [*Padina boergesenii* Allender & Kraft (designated *P. gymnospora* in Taylor 1960), *Lobophora variegata* (Lamouroux) Womersley ruffled form, *Lobophora variegata* decumbent form and *Stypopodium zonale* (Lamouroux) Papenfuss] and a marine vascular plant, turtle grass (*Thalassia testudinum* Banks ex Koenig). An additional *Lobophora* form (encrusting) was also examined. Wet and dry vouchers for all species were deposited in the Algal Collection, National Herbarium, National Museum of Natural History, Smithsonian Institution.
Division RHODOPHYTA (family Rhodomelaceae)

*Laurencia papillosa* — corticated macrophyte, tough, cartilaginous, erect, densely clustered short determinate branchlets, primary axes, 2–3 mm diameter; no unusual secondary chemistry, readily eaten by fishes and sea urchins

*Acanthophora spicifera* — corticated macrophyte, stiff, erect, coarsely branched, spinose, main axes 2–3 mm diameter; no unusual secondary chemistry, readily eaten by fishes and sea urchins

Division PHAEOPHYTA (family Dictyotaceae)

*Padina boergesenii* — lightly calcified, fan-shaped blades, 2–4 cells thick, 60–100 μm thick; no unusual chemistry, readily eaten by fishes and sea urchins

*Lobophora variegata* (ruffled form) — flat to ruffled thallus at margins, usually found in clumps, golden brown, blades 100–180 μm thick; blades split easily; no apparent unusual chemistry, readily eaten by sea urchins and fishes; collected where herbivorous fishes are uncommon

*Lobophora variegata* (decumbent form) — thin flat thallus, dark brown to orange brown, 105–130 μm thick; blades, while easy to tear do not split easily; chemistry under investigation, although previous analysis showed none, rarely eaten by fishes or sea urchins; dominant alga on ridge (> 15 m) east of Carry Bow Cay, but also found in shallow water in shaded microhabitats such as the undersides of patch reefs

*Stypopodium zonale* — leathery macrophyte, thick medulla, iridescent, blades fan shaped to irregularly branched (caused by splitting of the blade), 165–480 μm thick; toxicity demonstrated, essentially untouched by sea urchins and fishes

Division MAGNOLIOPHYTA

*Thalassia testudinum* — vascular plant (seagrass), cortex and epidermis, blades <2 mm thick, 8–12 mm wide; high cellulose and lignin content; tannin-laden cells, grazed, though not extensively by sea urchins and fishes

### MATERIALS AND METHODS

#### GENERAL METHODOLOGIES FOR FEEDING EXPERIMENTS

Two types of feeding experiments were conducted to determine whether *M. sculptus* and *M. coryphe* would mirror fish and sea urchin preference patterns. In the first series of experiments (hence referred to as SP1 and SP2), individual crabs were offered single plants of known weights so that crab preferences could be ranked based on relative amounts consumed. Both day (SP1) and night (SP2) experiments were conducted for *M. sculptus* but only day trials were run for *M. coryphe*. These experiments examined both palatability and ingestion rates for each plant separately (Vadas, 1977; Watanabe, 1984).

In a second series of experiments (hereafter referred to as MP), all 7 plants (species and forms) were presented simultaneously to a group (three) of conspecific crabs (*M. sculptus* and *M. coryphe* separately), thereby allowing herbivores to discriminate among plant species. Plants were then ranked based on relative consumption. Only day trials were conducted. This method is often preferable to single-prey designs (e.g., Vadas, 1977; Nicotri, 1980; Watanabe, 1984) because it requires herbivore discrimination, incorporating both tactile and chemosensory responses.
Epibiont-free plant material was collected immediately prior to each trial. Plants of equal weight were found to vary greatly in size (surface area) due to differences in blade morphology. To control for these potential differences in size, plants of similar area were used. Individual plants were weighed to the nearest 0.01 g, after being shaken twice and patted dry with paper towels. Concurrent controls were run with plants \((n = 5/\text{species/trial})\) placed in similar containers without crabs to allow adjustments for any net weight changes due to growth or respiration. All experiments were conducted under natural light.

At the conclusion of a trial, individual plants were dried as above and reweighed. All fragments torn loose by crabs were carefully collected and weighed along with intact portions. For all experiments, net weight change (pre-weight minus post-weight) was calculated rather than percent change as for example Hay (1984a) did, since the latter method in this case was judged to be sensitive to pre-weight differences within and among plants employed in these experiments (Coen, 1987).

Preliminary experiments showed no size or male–female biases in preference or total consumption among individuals within either herbivore species. Thereafter, all individuals were employed without regard to size or sex. Crabs were starved for a maximum of 24 h prior to a trial and used only once per experimental set. Crabs encountered no problems feeding on unattached plants based on extensive feeding observations with both anchored and unanchored plants. Each crab species experiment was analyzed individually using absolute plant tissue consumed. Comparisons between the two \textit{Mithrax} species were made using relative rankings rather than absolute plant tissue consumed, since the focus of this study was to examine relative preferences and plant susceptibilities.

\textbf{SINGLE-SPECIES FEEDING EXPERIMENTS (SPI, SP2)}

In single-species experiments, individual crabs (\textit{M. sculptus} and \textit{M. coryphe}) fed on each of the seven plants (Table I) singly in 300 ml plastic freezer containers \((n = 30/\text{species})\) for 10 h (SPI, 0930–1930). Observations were made at the beginning and at various times throughout the course of each trial on crab manipulation and subsequent feeding (Coen, 1987). Night experiments (SP2, \textit{M. sculptus}, 2000–0600, \(n = 10\)), were identical to day experiments except that feeding trials excluded \textit{Thalassia}. Concurrent controls were run for both experiments (see general methods). Running sea water was not added during trials; however, no potential dissolved O\(_2\) problems were encountered and only 2 of 450 crabs failed to survive during the feeding trials. Differences in net weight change (for all algae by experiment and herbivore species) were then analyzed by one-way ANOVA after data were square-root transformed to meet homogeneity of variances assumption \((F\text{-max test, Sokal & Rohlf, 1969})\). Multiple comparisons on significant ANOVA \((P < 0.05)\) were performed using a Student–Newman–Keuls test \((\text{SNK experiment-wise error rate, } P < 0.05)\). All statistical analyses used Statistical Analysis System's (SAS Institute, Version 82.3) GLM procedure.
MULTIPLE-SPECIES PREFERENCE EXPERIMENTS

In this experiment, daytime trials (MP, 0930–1430) were conducted offering a crab group (three conspecifics) all seven plant species (Table I) simultaneously in an array. Experimental duration (5 h) was sufficient to allow crabs time to sample all algae, while not consuming 100% of any one alga. As before, control thalli, with crabs excluded, were run concurrently. All seven plants were placed randomly (with respect to nearest species or form) in a circular array in large plastic trays (46 x 31 x 7 cm). No water flowed into arenas during trials, but large surface-area and short trial durations minimized potential dissolved O₂ problems. Each group of crabs was placed within the center of the array and released to reduce positional biases. Observations were made for the first 30 min to observe whether crabs sampled several species or tended to orient immediately to particular species.

The quantity consumed for each plant was then determined after 5 h (n = 30 multiple runs). Mean consumption/intraspecific group/5 h for each crab species was compared using a Friedman non-parametric (Hollander & Wolfe, 1973) two-way test on ranked data. This statistical method avoids the problems (E. Russek-Cohen, pers. comm.) normally encountered with multiple-choice preference experiments (cf. Hay et al., 1988b). Significant among-species differences (P < 0.01) were then calculated by hand using a Friedman multiple comparisons test (Hollander & Wolfe, 1973) at an experimentwise error rate of P < 0.05.

PLANT CALORIC ANALYSES

Samples of all experimental plants were collected at Carrie Bow Cay during July 1985 and split into subsamples for drying. Healthy plants free of epibionts were rinsed in fresh water, patted dry and then weighed on a balance to the nearest 0.001 g for wet weight. They were then dried in an oven (at 60–80 °C) in the field for transport. Upon return to the laboratory, subsamples were dried (≈4 h) to constant weight at 80 °C and reweighed (% water) for calorific and ash-free dry weight analyses. Plants were next frozen with liquid N₂ and pulverized to a fine powder. The resulting powder was pressed into pellets (≈0.20–0.26 g each) for calorimetry. An encrusting form of Lobophora variegata (form c), collected from peat slopes beneath nearby Rhizophora mangle (L.) mangroves (Taylor et al., 1986) was also compared to the two forms of Lobophora already mentioned (Table I).

Calorific values (n = 5/macrophyte) were measured using a Parr Adiabatic Calorimeter (model 1243) with a semi-micro bomb (10 cm fuse) (model 1107) controlled by a Parr computer (model 1720). No corrections for endothermy or mineral oil for combustion were deemed necessary based on preliminary runs. All calorific values are reported in cal/g (wet, dry or ash-free dry weights). Percent ash content (ash-free dry weight) was measured by heating samples (n = 5/macrophyte) to ignition in a muffle furnace at 400 °C for 24 h. Calories per gram ash-free dry weight and calories per gram wet weight were then calculated using calories·g dry weight⁻¹, percent ash and water.
content for each plant. Calorific differences among species were analyzed by one-way ANOVA. Proportional data were arcsin-transformed. All data met the homogeneity of variances assumption (F-max test, Sokal & Rohlf, 1969). Multiple comparisons on significant ANOVA ($P < 0.05$) used a SNK test ($P < 0.05$).

**RESULTS**

**SINGLE-SPECIES EXPERIMENTS**

The observed grazing patterns for both *Mithrax* species can be partitioned into two or three fairly discrete groupings (Table II; Figs. 1, 2) with separation being more pronounced for *M. coryphe* (Fig. 1). Plant species groupings for *M. coryphe* (Table II; Fig. 1) include: a high preference group (greater than 300 mg, *Laurencia* and *Padina*), a second of intermediate preference (150–250 mg, *Acanthophora* and *Lobophora* ruffled form) and a third consisting of species with low or negligible consumption ($< 100$ mg; *Stypopodium*, *Thalassia* and *Lobophora* decumbent form); the latter group was consistently least preferred. No appreciable change in weight for concurrent control plants was detected.

Results for *M. sculptus* feeding (SPI, SP2) conform to this same general pattern, except that *Laurencia* consumption was significantly greater than that of any other species (ANOVA, $P < 0.0001$; SNK, $P < 0.05$; Figs. 1, 2). Species in the intermediate grouping included *Padina*, *Acanthophora* and *Lobophora* ruffled form ($> 100$ mg, Fig. 1). As with *M. coryphe*, species with low or negligible consumption ($< 75$ mg, Fig. 1) included *Stypopodium*, *Thalassia* and *Lobophora* decumbent form; *Stypopodium*, and *Lobophora* decumbent form for night experiments ($< 20$ mg, Fig. 2). Overall, *M. sculptus*

### Table II

Composite crab preference rankings for day single- and multiple-species (SP1 and MP) experiments. Plant species ranked from highly preferred to least preferred (1 to 7).

<table>
<thead>
<tr>
<th></th>
<th><em>Mithrax sculptus</em></th>
<th></th>
<th><em>Mithrax coryphe</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SPI</td>
<td>MP</td>
<td>Sum of ranks</td>
<td>SPI</td>
</tr>
<tr>
<td><em>Laurencia</em></td>
<td>1</td>
<td>1</td>
<td>1 (2)</td>
<td>1.5</td>
</tr>
<tr>
<td><em>Padina</em></td>
<td>2.5</td>
<td>2</td>
<td>2 (4.5)</td>
<td>1.5</td>
</tr>
<tr>
<td><em>Acanthophora</em></td>
<td>2.5</td>
<td>3</td>
<td>3 (5.5)</td>
<td>3</td>
</tr>
<tr>
<td><em>Lobophora</em></td>
<td>4</td>
<td>4</td>
<td>4 (8)</td>
<td>4</td>
</tr>
<tr>
<td>ruffled form</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Stypopodium</em></td>
<td>5</td>
<td>7</td>
<td>6 (12)</td>
<td>6</td>
</tr>
<tr>
<td><em>Thalassia</em></td>
<td>6</td>
<td>5</td>
<td>5 (11)</td>
<td>7</td>
</tr>
<tr>
<td><em>Lobophora</em></td>
<td>7</td>
<td>6</td>
<td>7 (13)</td>
<td>5</td>
</tr>
<tr>
<td>decumbent form</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Numbers in parentheses represent sums of original individual experimental species ranks (e.g., SPI + MP).
day and night rankings were extremely similar (Figs. 1 and 2). Interestingly, both crab herbivores discriminated significantly (SNK, \( P < 0.05 \); Figs. 1, 2) between Lobophora forms (ruffled and decumbent). Mithrax sculp tus day consumption of the ruffled morph was three times that of the decumbent morph (Fig. 1) (six times in night feedings, Fig. 2); for M. coryphe, grazing rates on the ruffled morph exceeded twice that on the decumbent morph.

![Graph](image)

Fig. 1. Mean consumption (untransformed weight change, mg/crab/10 h, \( n = 30 \)) ± 1 SE for Mithrax sculp tus and Mithrax coryphe single-species day experiments (SP1). All raw data square-root transformed to meet homogeneity of variances assumption. Bars with the same letter (lower-case for Mithrax sculp tus and upper-case for Mithrax coryphe) denote non-significant differences by ANOVA (\( P < 0.0001 \)) and SNK (\( P > 0.05 \)). Lp = Laurencia papillosa; Pb = Padina boergeseni; As = Acanthophora spicifera; Lr = Lobophora variegata ruffled form; Sz = Stypopodium zonale; Tt = Thalassia testudinum; Ld = Lobophora variegata decumbent form.

![Graph](image)

Fig. 2. Mean consumption (untransformed weight change, mg/crab/10 h, \( n = 10 \)) ± 1 SE for Mithrax sculp tus single-species night experiments (SP2). All raw data square-root transformed to meet homogeneity of variances assumption. Bars with the same letter denote non-significant differences by ANOVA (\( P < 0.0001 \)) and SNK (\( P > 0.05 \)). See Fig. 1 for plant species legend.
Grazing by *Mithrax sculptus* and *M. coryphe* was similar in both absolute consumption and relative rankings for the three experiments (Table II; Figs. 1, 2), with both exhibiting marked differences in the degree of consumption (over an order of magnitude) among the seven macrophytes. For example, mean plant grazing rates ($\pm$ 1 SE) for *M. coryphe* (mean crab weight = 2.95 g) ranged from $343 \pm 22$ to $38 \pm 7$ mg/crab/10 h (Fig. 1); rates for *M. sculptus* (SP1, mean crab weight = 4.19 g) ranged from $304 \pm 19$ to $30 \pm 6$ mg (for Laurencia and Lobophora decumbent form (Fig. 1).

Net weight change (milligrams consumed) was employed as the dependent variable (cf. Hay *et al.*, 1986, 1987a) in contrast to other studies (Hay, 1981a; Hay *et al.*, 1983; Lewis, 1985, 1986; Lewis & Wainwright, 1985; Paul *et al.*, 1987) which presented percentage change (or loss). Different preference rankings were observed between rankings based on net weight change and those based on percent change for data presented here (cf. Tables II and III, * denotes these changes, Table III). These apparent shifts in rank when employing percentages were due to variation in pre-weights as a consequence of using similar-sized thalli (e.g., Lewis, 1985) from species with very different morphologies (i.e. surface area/unit volume).

### Table III

Mean percent consumption' ($\pm$ 1 SE) and relative rankings for feeding and preference experiments, including rank comparisons with relative consumption calculations.

<table>
<thead>
<tr>
<th></th>
<th><em>Mithrax sculptus</em></th>
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<th><em>Mithrax coryphe</em></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>SNK*</td>
<td>SP1</td>
<td>R1</td>
</tr>
<tr>
<td><em>Laurencia</em></td>
<td>A 71.1 (4.4)</td>
<td>1 83.3 (5.7)</td>
<td>1 A</td>
</tr>
<tr>
<td><em>Padina</em></td>
<td>C 37.8 (4.1)</td>
<td>3** 26.7 (5.7)</td>
<td>3 BC</td>
</tr>
<tr>
<td><em>Acanthophora</em></td>
<td>B 50.7 (5.6)</td>
<td>2** 41.5 (7.5)</td>
<td>2 B</td>
</tr>
<tr>
<td><em>Lobophora</em></td>
<td>D 22.2 (2.5)</td>
<td>5** 14.3 (2.5)</td>
<td>4** CD</td>
</tr>
<tr>
<td>ruffled form</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Stypodium</em></td>
<td>D 16.0 (2.0)</td>
<td>6** 6.6 (2.3)</td>
<td>6 D</td>
</tr>
<tr>
<td><em>Thalassia</em></td>
<td>CD 29.1 (4.3)</td>
<td>4** -</td>
<td>-</td>
</tr>
<tr>
<td><em>Lobophora</em></td>
<td>E 8.1 (1.6)</td>
<td>7** 8.3 (3.1)</td>
<td>5 D</td>
</tr>
<tr>
<td>decumbent form</td>
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</tbody>
</table>

' Mean percent consumption [(weight consumption mg/preweight mg) x 100].

* Raw % data subjected to statistical analysis, $P < 0.0001$, ANOVAs; SNK, on arcsin-transformed data.

** Denotes shift in ranks when compared to original ranks (Table II) which were based on absolute consumption rates not percentage change.

### MULTIPLE-SPECIES EXPERIMENTS

For both *Mithrax* species, mean total plant tissue consumed across all seven plants in multiple species offerings ($n = 30$) was similar; however, separation among plants was somewhat variable (Fig. 3, Friedman multiple comparisons test). Crab preferences are summarized in Table II and Fig. 3. As in the single experiments, *Laurencia papillosa* was the most preferred species (based on consumption), accounting for > 51% of the
total plant tissue consumed by *Mithrax sculptus* or almost 3 times the rate on the second ranked species, *Padina*, which contributed only 22.8% of the total plant tissue consumed.

![Graph](image)

Fig. 3. Mean consumption (untransformed weight change, mg/3 crabs/5 h, n = 30) ± 1 se for *Mithrax sculptus* and *Mithrax coryphe* multiple-species day experiments (MP). Bars with the same letter (lower-case for *Mithrax sculptus* and upper-case for *Mithrax coryphe*) denote non-significant differences by a Friedman two-way test ($P < 0.001$) and its accompanying multiple comparison's test ($P > 0.05$). See Fig. 1 for plant species legend.

In contrast, two species (*Laurencia* and *Padina*) were highly preferred by *M. coryphe* over all others (Friedman multiple comparisons test, $P < 0.05$), each averaging 31 and 44% of total consumption, respectively. For both crab species, these two highly preferred algae collectively accounted for ≈ 75% of the total plant material consumed; including *Acanthophora* (12.1 and 14.2% for *M. sculptus* and *M. coryphe*, respectively), these three preferred species cumulatively were responsible for > 86% of all vegetation consumed in multiple-choice (MP) experiments. None of the remaining species contributed more than 8% to observed total mean consumption. For example, *Thalassia* contributed < 0.2% for *M. coryphe* (Fig. 3). Again, as in the single-species experiments, both *M. sculptus* and *M. coryphe* preferred *Lobophora* ruffled form over the decumbent form (Table II, with rates on form a exceeding 4 times that on form b for *M. sculptus* and 1.5 times for *M. coryphe* (Fig. 3).

Composite rankings (Table II) for *Mithrax sculptus* (SP1 and MP) consistently followed species preference hierarchies derived from individual experiments (exclusive of relative position, ranks 5 to 7 among the three least preferred species, *Stypopodium, Thalassia* and *Lobophora* decumbent form). *Mithrax coryphe* composite rankings (Table II gave even greater concordance with the two individual feeding experiments (SP1, MP).

When single (SP1, 2) and multiple-species (MP) consumption rates were adjusted (using mg/crab/10 h) to facilitate comparisons, *Mithrax sculptus* consumption differed
<table>
<thead>
<tr>
<th>Plant species</th>
<th>% H₂O</th>
<th>N</th>
<th>kcal g ( \text{fw}^{-1} )</th>
<th>SNK</th>
<th>kcal g ( \text{dw}^{-1} )</th>
<th>SNK</th>
<th>%* Ash</th>
<th>SNK</th>
<th>kcal g ( \text{afdw}^{-1} )</th>
<th>SNK</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laurencia papillosa</td>
<td>85.71</td>
<td>5</td>
<td>0.223</td>
<td>f</td>
<td>1.565</td>
<td>g</td>
<td>59.50</td>
<td>a</td>
<td>3.866</td>
<td>c</td>
</tr>
<tr>
<td>Padina boergesennii</td>
<td>84.91</td>
<td>5</td>
<td>0.376</td>
<td>e</td>
<td>2.498</td>
<td>e</td>
<td>37.43</td>
<td>d</td>
<td>±0.002</td>
<td>c</td>
</tr>
<tr>
<td>Acanthophora spicifera</td>
<td>92.94</td>
<td>5</td>
<td>0.151</td>
<td>g</td>
<td>2.140</td>
<td>f</td>
<td>51.07</td>
<td>b</td>
<td>±0.001</td>
<td>ab</td>
</tr>
<tr>
<td>Lobophora variegata ruffled</td>
<td>75.03</td>
<td>5</td>
<td>0.679</td>
<td>a</td>
<td>2.718</td>
<td>d</td>
<td>31.25</td>
<td>e</td>
<td>±0.013</td>
<td>c</td>
</tr>
<tr>
<td>Lobophora variegata decumbent</td>
<td>82.35</td>
<td>5</td>
<td>0.535</td>
<td>d</td>
<td>3.033</td>
<td>c</td>
<td>23.81</td>
<td>g</td>
<td>±0.013</td>
<td>c</td>
</tr>
<tr>
<td>Lobophora variegata encrusting</td>
<td>70.61</td>
<td>5</td>
<td>0.652</td>
<td>b</td>
<td>2.217</td>
<td>f</td>
<td>43.85</td>
<td>c</td>
<td>±0.007</td>
<td>c</td>
</tr>
<tr>
<td>Stylophorum zonale</td>
<td>83.39</td>
<td>5</td>
<td>0.614</td>
<td>c</td>
<td>3.694</td>
<td>a</td>
<td>17.94</td>
<td>h</td>
<td>±0.001</td>
<td>a</td>
</tr>
<tr>
<td>Thalassia testudinum</td>
<td>80.05</td>
<td>5</td>
<td>0.626</td>
<td>c</td>
<td>3.141</td>
<td>b</td>
<td>26.38</td>
<td>f</td>
<td>±0.007</td>
<td>b</td>
</tr>
</tbody>
</table>

All values after the N column are expressed as \( \bar{x} \pm 1 \) SE; fw = fresh weight, dw = dry weight, afdw = ash-free dry weight.

* Within columns, those means followed by the same letter (in the next column) are not significantly different (ANOVA, \( P < 0.0001 \); SNKs, \( P > 0.05 \)). ANOVAs on untransformed data (except % ash on arcsin-transformed proportions). Variances were homogeneous by Cochran's test.

* Ash expressed as % of dry weight (inorganic/total dry weight).
little between SP1, 2 and MP experiments. For example, adjusted mean grazing rates on *Laurencia* were 272 and 262 mg for single night (SP2, Fig. 2) and multiple experiments (MP) (Fig. 3). In contrast, *M. coryphe*’s adjusted consumption for single-species trials always exceeded those from multiple-feeding experiments (for *Laurencia*, 343 versus 181, respectively, Figs. 1 and 3).

**CALORIC ANALYSES**

Caloric values (for dry, ash-free and fresh weights) and percent ash and water content for each macrophyte are presented in Table IV. Significant differences (*P* < 0.0001, ANOVAs) were found among the eight plants for the variables fresh weight (fw), dry weight (dw), and ash-free dry weight (afdw) (kcal per g) and % ash (organics). Plant water content ranged from 70.6% for *Lobophora* encrusting form to 93% for the red alga *Acanthophora spicifera*. Mean percent ash ranged widely from 18% of dry weight for *Stypopodium zonale* to almost 60% for *Laurencia papillosa*. A large proportion of the observed variation among plant species resulted from interspecific differences in percent ash and water content (see Table IV). Mean caloric values ranged from: (1) 0.151 (Acanthophora) to 0.679 kcal/g (*Lobophora* ruffled form) for fresh weight; (2) 1.56 (*Laurencia*) to 3.69 kcal/g (*Stypopodium*) for dry weight, and (3) 3.87 (*Laurencia*) to 4.50 kcal/g (*Stypopodium*) ash-free dry weight.

Spearman rank correlations between caloric and ash data (% ash, kcal/g dw, kcal/g fw, kcal/g afdw) versus the three preference rankings (1–7, most to least preferred; single, multiple and composite) yielded highly significant correlations (Table V) for all but one (*Mithrax sculptus*, SP1, versus kcal/g afdw) of the relationships. However, all correlations were positive (except for % ash) suggesting that crabs tended to prefer species of lower caloric and organic contents such as *Laurencia, Acanthophora* and *Padina*. These highly susceptible species had moderate to high ash and water contents (Table IV) thereby shifting their position to the lower end of the caloric-%, ash species’ distribution.

**Table V**

Spearman rank sum correlation (r.s) between preference rankings* (single (SP1) and multiple (MP) experiments) and mean caloric and ash values.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>% Ash</th>
<th>kcal/g dw</th>
<th>kcal/g fw</th>
<th>kcal/g afdw</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. sculptus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SP1</td>
<td>–0.87*</td>
<td>0.84*</td>
<td>0.60*</td>
<td>0.22 NS</td>
</tr>
<tr>
<td>MP</td>
<td>–0.95*</td>
<td>0.92*</td>
<td>0.58*</td>
<td>0.50*</td>
</tr>
<tr>
<td>Composite ranks</td>
<td>–0.92*</td>
<td>0.86*</td>
<td>0.54*</td>
<td>0.35*</td>
</tr>
<tr>
<td><em>M. coryphe</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SP1</td>
<td>–0.82*</td>
<td>0.88*</td>
<td>0.65*</td>
<td>0.50*</td>
</tr>
<tr>
<td>MP</td>
<td>–0.77*</td>
<td>0.81*</td>
<td>0.61*</td>
<td>0.41*</td>
</tr>
<tr>
<td>Composite ranks</td>
<td>–0.78*</td>
<td>0.84*</td>
<td>0.63*</td>
<td>0.48*</td>
</tr>
</tbody>
</table>

* Ties between ranks were averaged and used in correlation analyses (rankings 1–7, most to least preferred).
* Significant *r*ₜ correlation coefficients (SAS), *P* < 0.05.
However, comparisons of adjusted mean caloric intake (mg consumed × kcal value
fw, dw or afdw) per 10 h of grazing (SP1, SP2; Coen, 1987) suggest that the significantly
greater grazing rates of both Mithrax species on "preferred" plant species (e.g.,
Laurencia, Padina, and to a lesser extent Acanthophora) may be sufficiently high to
maximize potentially available calories on a per meal basis, all other things being equal
(e.g., palatability, handling times, availability). For all four measures (fresh weight, dry
weight, percent organics and ash-free dry weight), Laurencia (e.g., SP1: mean ± 1 SE = 0.476 ± 0.030 kcal/dw), Padina (0.331 ± 0.035 kcal/dw) and Acan-
thophora (0.278 ± 0.030 kcal/dw) were ranked ahead of all others (0.098 ± 0.018,
0.228 ± 0.030, 0.139 ± 0.20 kcal/dw for Lobophora decumbent, Stypopodium and
Thalassia, respectively), with few exceptions (see Coen, 1987, for all experiments and
species).

DISCUSSION

PREFERRED MACROPHYTE SPECIES

Crabs consistently discriminated among and even between forms within macrophyte
(e.g., Lobophora variegata) species (Table II; Figs. 1–3). Marked preferences for
Laurencia papillosa, Padina boergensenii and Acanthophora spicifera were exhibited in
single and multiple choice experiments. These species are among the fastest growing
(Acanthophora, 2–4.5 mm/day, Kilar & Lou, 1986), abundant and most palatable
macrophyte prey on Caribbean reefs (e.g., Hay, 1981b,c; Littler et al., 1983b; Hay,
1984a; Kilar & Lou, 1984, 1986; Lewis, 1985, 1986; Lewis & Wainwright, 1985; Paul
& Hay, 1986; Taylor et al., 1986), being consistently preferred by crabs, fishes and sea
urchins. All three species were grazed upon by Mithrax spp. The crabs either used their
spooned-chelae to tear off portions of plants (e.g., Laurencia and Padina, Coen, 1987)
or manipulated the thallus directly (e.g., Laurencia and Acanthophora) towards the oral
region with several of their eight pairs of oral appendages (primarily the 3rd maxilliped
and mandibles).

LOW PREFERENCE SPECIES AND PLANT TRAITS

It is increasingly evident that parallels may be drawn between terrestrial and marine
plant chemical defense systems (e.g., Norris & Fenical, 1982; Hay, 1984a; Steinberg,
1985; Bakus et al., 1986; Paul & Fenical, 1986; Paul & Hay, 1986; Targett et al., 1986;
Hay et al., 1987a,b; Paul & Van Alstyne, 1988). However, there has been an unfortunate
tendency to equate the presence of "unusual" or "unique" (terminology used in Hay,
1984a; Paul & Hay, 1986) natural compounds as evidence of chemical defense in many
reef-associated macrophytes (e.g., Hay, 1984a; Paul & Fenical, 1986; Paul & Hay,
1986). Relatively few studies until recently (Paul & Fenical, 1983; Targett et al., 1986;
Hay et al., 1987a,b, 1988a,b; Paul et al., 1987) experimentally manipulated plant
effects, thereby adequately testing a deterrence hypothesis.
The plants used in this study are only a small subset of those available to crabs on the reef. However, it now appears that several of the species tested are consistently of low preference to both vertebrate and invertebrate marine herbivores. Few species-specific plant specialists have been identified in marine plant–herbivore systems (e.g., Jensen, 1980; Steneck, 1982; Vermeij, 1983). This apparent lack of specificity may explain observed generalized deterrent patterns seen for many chemically-defended marine plants such as *Stypopodium*, *Caulerpa*, *Halimeda*, and *Lobophora* (Norris & Fenical, 1982; Paul & Fenical, 1983; Hay, 1984a; Littler et al., 1986; Paul & Hay, 1986; Targett et al., 1986; Hay et al., 1988a; Coen & Tanner, unpublished), although recent work suggests that there may be some differences (Hay et al., 1987a, b, 1988). *Stypopodium* and the decumbent form of *Lobophora* have been found previously to be among the least preferred algal species based on field experiments with fishes (Hay, 1981a, 1984a; Hay et al., 1983; Littler et al., 1986; Morrison, 1986; Paul & Hay, 1986; Coen & Tanner, unpublished) and sea urchins (Littler et al., 1983b).

*Stypopodium zonale* may be classified as a tough, leathery macrophyte (Littler et al., 1983b, 1986); however, this morphology does not deter crabs or fishes from tearing or even shredding its uncalcified blades (Coen, pers. obs.). Rather, it appears that palatability is reduced directly by chemical deterrents, in the form of several secondary metabolites (discussed in Gerwick & Fenical, 1981; Littler et al., 1986; Paul & Hay, 1986; Hay et al., 1987b). Similarly, *Lobophora variegata* provokes some interesting questions in regard to herbivore susceptibility. *Lobophora* (probably the ruffled form) is readily eaten by fishes (Hay, 1984a; Lewis, 1985; Morrison, 1986; Coen & Tanner, unpublished), sea urchins (Morrison, 1986; Coen, pers. obs.) and crabs (Figs. 1–3). Elsewhere in the literature *Lobophora* (probably the decumbent form) shows few graze marks and little tissue loss based on numerous field experiments (Hay, 1981a; Hay & Goertmiller, 1983; Morrison, 1986; Paul & Hay, 1986; Coen & Tanner, unpublished). This finding was particularly evident in areas with high fish grazing pressure in Belize (e.g., the outer ridge where the decumbent form dominates the algal community, Lewis & Wainwright, 1985). Both forms are uncalcified and display no obvious morphologically resistant characters, yet both *Mithrax* significantly preferred the ruffled form to the decumbent form (up to 6 times; Table II, Figs. 1–3). An hypothesis presently under investigation (L. Coen & N. Targett) is that some novel secondary chemistry in the decumbent form renders it unpalatable to a phylogenetically diverse group of herbivores. Gerwick & Fenical (1982) have suggested a similar scenario for a related Pacific species, *L. papenjussii*. The chemistry of several forms of *L. variegata* is presently under study (L. Coen, N. Targett & C. Tanner, in prep.).

*Thalassia testudinum* has often been employed in field studies (e.g., Hay, 1981c; Hay et al., 1983; Lewis, 1985; Paul & Hay, 1986; Targett et al., 1986) to estimate local grazing rates. *Mithrax*'s low preference for *Thalassia*, as with *Lobophora* and *Stypopodium*, may similarly be related to plant secondary metabolites. Zapata & McMillan (1979), McMillan et al. (1980), and Harrison & Durance (1985) have found
relatively high concentrations of water-soluble phenolic acids in seagrasses. Others (Bjorndal, 1980; Dawes & Lawrence, 1980) have estimated that > 45% of *Thalassia*'s dry weight is in the form of structural compounds such as cellulose, hemicellulose and lignin. When taken together, these characteristics may render epiphyte-free seagrasses a tough and low-nutritive food that is fairly undigestible to herbivores lacking cellulases (Bjorndal, 1980).

**FOOD PREFERENCES AND PLANT QUALITY**

Positive correlations between preferences and measured plant attributes (Table IV) initially suggested that crabs tended to choose species of lower organic and caloric contents. Similar disparate patterns had been observed in earlier feeding studies (Paine & Vadas, 1969; Carefoot, 1973; Vadas, 1977; Larson et al., 1980; Nicotri, 1980; Watanabe, 1984). However, several of the least preferred species, with significantly greater potential energy returns, also contained chemical feeding deterrents. Thus, these "defended" species may be unavailable to crabs. Alternatively, the plant attributes measured here may not be amongst those employed by crabs in selecting plants (e.g., nitrogen, protein, structural and chemical defenses) (cf. Vadas, 1977; Montgomery & Gerking, 1980; Gaines, 1985; Steinberg, 1985; Hambrook & Sheath, 1987; Hay et al., 1988a). We are currently collecting data on alternative nutritional cues used by *Mithrax*. In line with this, recent findings from terrestrial systems also suggest that herbivore choice may be more related to minimizing secondary metabolites than maximizing nutritive gains (Crawley, 1983).

**METHODOLOGY AND INTERPRETATION**

Analyses based on comparisons of adjusted mean caloric values (see Results and Coen, 1987) suggest that potential available energy (based on calorific contents) from high and low preference species may be equivalent over the course of a meal, due to significantly greater feeding rates on preferred plant species with significantly lower caloric values (see Table IV). Few studies carry the analyses far enough to examine this potential result (Paine & Vadas, 1969; Vadas, 1977). Most do not even calculate potential caloric intake on a fresh weight basis. The remainder have tended not to examine other variables (e.g., toxicity, plant morphology) germane to herbivore choice (but see Steneck & Watling, 1982).

An additional caution for future feeding studies involves the use of relative (or percent) tissue loss among species (e.g., Lewis, 1985). As discussed earlier (see Results and Tables II and III), biases may be generated in feeding experiments employing percentage weight change, when similar-sized plant thalli are used, since natural variation (among species) in thalli weights per unit area is often encountered. Comparisons of the two methods (% change and net weight change, Table III) suggest that rankings and observed percentages may be quite different between the two methods when using larger plants. Low preference species are especially sensitive to these differences. For
example, suppose that a herbivore consumes 2 g of a particular plant. Grazing on an initial 10 g segment would yield a 20% net weight change; however, if the initial weight were decreased to only 4 g, the resulting percentage would be inflated to 50% (ranges are well within those used previously; e.g., 2.65–16.31 g, Hay et al., 1986). For the single-species experiments, over 65% of the ordered rankings changed when the two methods were compared. This included major changes in significant differences among species means for SP1 and SP2 (Table III, \( P < 0.0001 \), ANOVAs on arcsin-transformed data; \( P < 0.05 \), by SNK test). Based on these results it appears that net weight change may be the preferred method to employ over percent change when using more than one prey species and/or form in preference experiments (cf. Hay et al., 1986).

There has been a tendency in marine plant–animal interactions to ask questions concerning community structure by studying large herbivores and using coarse measures of macroherbivore impact such as standing crop, percent cover and species richness across relatively large areas (e.g., Menge & Lubchenco, 1981; Menge et al., 1986). Hence, little is known of the effects of herbivores other than fishes, sea urchins and some molluscs (Lubchenco & Gaines, 1981; Gaines & Lubchenco, 1982; Steneck, 1983). The present study focussed on decapod crab grazing patterns and algal susceptibility in Belize. These results are among the first to demonstrate that these smaller tropical herbivores are capable of feeding on a diverse group of macrophytes ranging in form from filaments to leathery thalli (see Table I and Littler et al., 1983a, b; Steneck & Watling, 1982). Previously (Coen, 1988), I demonstrated that *Mithrax* is able to keep coral (*Porites porites*) heads free of fouling algal epibionts. This, in conjunction with the fact that the plant species employed in this study (see Table I) often constitute the dominant plant species on many Caribbean reefs (Hay, 1981a; Littler et al., 1983a, b; Kilar & Lou, 1984, 1986; Lewis, 1986), implies that the potential small-scale effects of mesograzers, such as herbivorous crabs may be underestimated. Lastly, concordant results of the single and multiple feeding experiments demonstrate that crab choices reflect the feeding patterns observed previously for fish and sea urchin herbivores.

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PLANT SUSCEPTIBILITY TO CRABS


