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FEEDING PREFERENCES OF A GENERALIST SALT-MARSH CRAB: RELATIVE IMPORTANCE OF MULTIPLE PLANT TRAITS

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Abstract. Few studies have evaluated the relative importance of multiple plant traits to herbivore diet choice, especially with an experimental approach. Moreover, although circumstantial evidence points to plant toughness and silica content as important determinants of diet choice, few studies have experimentally demonstrated that these factors actually deter feeding by herbivores. We examined feeding preferences of a generalist salt-marsh crab, *Armases cinereum*, for all the common angiosperms in its habitat. We took an experimental approach to evaluating the importance of toughness, secondary chemistry, silica, salt, and protein in determining feeding preferences.

Consumption of plants by *Armases* in two experiments was correlated with decreasing toughness. Consumption was more equitable when plants were ground up and reconstituted in agar discs, with reduced differences in toughness. In four pairwise choice tests, *Armases* always preferred the softer plant of the pair, but in three of four cases exhibited no preference when the same plants were presented in reconstituted discs. Several plant extracts significantly stimulated or deterred feeding by *Armases*, but these effects were not consistent with and could not be used to predict overall preferences for fresh plants. Salt in artificial diets stimulated feeding by *Armases*. Silica had no effect on feeding in two experiments and stimulated feeding in a third. *Armases* was mildly stimulated to feed by high levels of protein in artificial diets, but these levels were above those found in plants, and the protein content of plants did not correlate with feeding preferences.

Our results point towards plant toughness as most important in determining feeding choices of *Armases*. Since *Armases* is omnivorous, it may escape dietary constraints that affect feeding choices of pure herbivores. The dogma that silica defends plants against herbivory needs to be re-examined with additional experimental studies.

Key words: *Armases*; chemical defenses; crab; decapod; feeding preferences; herbivory; plant-herbivore interactions; plant defenses; plant toughness; salt marsh; silica.

INTRODUCTION

The determinants of herbivore feeding preferences remain an unresolved issue for students of plant-animal interactions. In contrast to the field of predator-prey interactions, where optimal foraging approaches have been strikingly successful in providing a simple, general theoretical approach to predicting diet choice (Schoener 1971, Pulliam 1974, Stephens and Krebs 1986), studies of herbivore diet choice remain to some extent a series of special cases, from which few strong generalities have emerged.

A wide variety of plant traits are known to influence herbivore feeding choices. Plant secondary metabolites are extremely important in numerous cases (Rhoades 1979, 1985, Ehrlich and Murphy 1988, Schultz 1988).

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However, efforts to create a general theory of diet choice based on plant secondary metabolites have been hampered by variable responses of different herbivores to some compounds (Barbosa 1988a, Hay and Fenical 1988, 1992), by the lack of a clear link between unpalatability and toxicity (Bernays 1990, 1991, Hay and Fenical 1992, Steinberg and Van Altena 1992), and by weak structure-function relationships (Hay and Fenical 1988, 1992). Early attempts to develop general theory based on differentiating broad classes of secondary metabolites (e.g., Feeny 1976, Rhoades and Cates 1976) have largely been discounted as oversimplifications (Zucker 1983, Hay and Fenical 1988, 1992, Karowe 1989, Bernays et al. 1989). Attempts to predict herbivore diet choices based on plant energy or nitrogen content have also had limited success (Paine and Vadas 1969, Vadas 1977, Milton 1979, Bryant and Kuropat 1980, Belovsky 1981, 1984, Owen-Smith and Novellie 1982, Stephens and Krebs 1986, Horn 1989, Dearing and Schall 1992, Dearing 1996). Other factors such as mineral content (Littler et al. 1983a, b, Lewis 1985,

Paul and Hay 1986, Gali-Muhtasib et al. 1992, Pennings and Paul 1992, Hay et al. 1994, Schupp and Paul 1994), spines and thorns (Cooper and Owen-Smith 1986, Myers and Bazely 1991), toughness (Tanton 1962, Steneck and Watling 1982, Coley 1983, Padilla 1985, 1989, Raupp 1985, Bernays 1986, Pennings and Paul 1992), and natural enemies (Lawton 1978, Damman 1987, Bernays and Graham 1988, Bernays 1989, Hay 1992) may affect diet choice but have received less experimental attention.

Although numerous studies have assessed the importance of single plant traits to herbivore feeding, relatively few have compared the importance of multiple plant traits (e.g., Milton 1979, Coley 1983, Hay 1984, Steinberg 1985, Paul and Hay 1986, Damman 1987, Duffy and Hay 1991, Pennings and Paul 1992, Dearing 1996, Pennings et al. 1996), and only a subset of these have taken an experimental approach. We favor an experimental, multifactorial approach for two reasons. First, diet choices of many herbivores may be determined by a combination of factors, such that an approach examining multiple plant traits may be most successful (Belovsky 1984, Barbosa 1988b, Duffy and Paul 1992, Hay et al. 1994, Dearing 1996). Second, different plant traits may be of primary importance to different herbivores (Schupp and Paul 1994, Pennings et al. 1996). Determining which plant traits matter most to which herbivores could allow the development of theory explicitly based on between-herbivore variation (Lubchenco and Gaines 1981). Steps toward such a theory have been taken by classifying herbivores based on body size (Steneck 1982, Hay et al. 1988, 1989, Hay 1992), mouthpart strength (Steneck and Watling 1982, Bernays 1986, Hay 1991), gut environment (Appel 1993, 1994, Schupp and Paul 1994), and history (Estes and Steinberg 1988, Spencer 1988, Steinberg and Van Altna 1992). To encourage further development of theory, additional studies are needed on which plant traits matter most to a variety of herbivores.

Pennings and Paul (1992) experimentally examined the importance of algal toughness, calcification, and secondary metabolites in determining diet choices of a generalist gastropod, *Dolabella auricularia*, and concluded that toughness was most important. *Dolabella* sequesters secondary metabolites from its diet (Faulkner 1988, Pennings and Paul 1993) and probably is well adapted to algal secondary metabolites. Here, we took a similar approach to studying diet choice of an omnivorous crab feeding on salt-marsh angiosperms. We experimentally examined the importance of toughness, secondary chemistry, silica, salt, and protein in determining feeding choices. Coastal salt marshes are ideal for such a study because they contain few plant species, making it possible to study virtually the entire plant community. Moreover, although salt marshes are common coastal ecosystems (Chapman 1960, Ranwell 1972), the factors determining diet choices of salt-marsh herbivores have rarely been studied (but see

Buchsbaum et al. 1984, Hacker and Bertness 1995). A number of herbivores occur in coastal marshes (e.g., Smalley 1960, Parsons and de la Cruz 1980, Smith and Odum 1981, Ellison 1987, 1991, Stiling et al. 1991, 1992, Furbish and Albano 1994). We chose to study a crab because it was common year-round, catholic in its diet, and easy to work with in the laboratory. Our work focused on laboratory studies with the goal of understanding what plant traits determined diet choice when foods were equally available and factors such as temperature stress and natural enemies were unimportant. To what extent the plant traits we studied interact with other factors to control dietary patterns, population dynamics, and/or evolution in the field is an open question for future studies.

METHODS

Study site and species

Research was conducted on Sapelo Island, Georgia (31°27' N; 81°15' W). The marshes around this barrier island are typical of the southeastern Atlantic coast (Pomeroy and Wiegert 1981, Wiegert and Freeman 1990). The plant community is dominated by cordgrass, *Spartina alterniflora*, and needlerush, *Juncus roemerianus*, with sea oxeye, *Borrchia frutescens*, and marsh elder, *Iva frutescens*, common at the terrestrial border. High-marsh soils commonly become hypersaline, in which case saltwort, *Batis maritima*, saltgrass, *Distichlis spicata*, and glasswort, *Salicornia virginica*, are present in the understory or as monospecific stands. Because they make up >99% of the angiosperm biomass in the marsh, we used these seven species as the test plants in our study. A handful of other plant species (e.g., *Aster tenuifolius*, *Limonium carolinianum*, *Salicornia bigelovii*, *Salicornia europaea*) are recorded in the marsh but are comparatively rare.

The wharf crab *Armases cinereum* (= *Sesarma cinereum*, henceforth *Armases*) (Crustacea: Decapoda: Grapsidae) occurs throughout the marsh but is most abundant at the terrestrial border where it digs burrow networks (Seiple 1979, 1981, Abele 1992). This highly motile, semiterrestrial crab is often found up to 100 m inland from the marsh (some report it to be a garden pest) or climbing in vegetation. Like some mangrove grapsid crabs (Beever et al. 1979, Micheli 1993a, b), *Armases* is omnivorous, feeding on fresh plant material, leaf litter, mammal feces, small fiddler crabs (*Uca* spp.), terrestrial basidiomycetous fungi, and marsh sediments (S. C. Pennings et al., *personal observations*; S. Y. Newell, *personal communication*). Fragments of plant material with obvious cell walls comprised $39 \pm 24\%$ (SD) of crab gut contents ($n = 50$). Forty percent of crabs ($n = 600$) observed over 12 d were climbing in vegetation as opposed to on the marsh surface.

We collected *Armases* from the terrestrial border of the marsh at several locations. Animals (carapace widths 10–22 mm, ~2:1 female : male sex ratio) were

collected fresh daily for each experiment. To avoid re-collecting individuals, we did not collect near locations where we released crabs. In a sample of 75 crabs of both sexes, live mass was correlated with carapace width [$\ln(\text{mass}) = 3.17 \ln(\text{carapace width}) - 8.14$, $r = 0.98$]. We used this equation to estimate crab mass from carapace width and included crab mass as a covariate in appropriate analyses. However, because of the relatively small range of crab sizes and the relatively high between-crab variability in feeding rates, the covariate usually had little effect on the statistical tests.

General feeding experiment methods

Unless otherwise indicated, feeding experiments involved housing crabs singly in loosely capped 500-mL glass jars. Seawater (10–20 mL) was available in a small bowl or covering the bottom of the jar. Diets were weighed before and after feeding trials. In all cases, no-crab replicates (Peterson and Renaud 1989) were run to measure mass changes of diets in the absence of crabs and to correct the apparent amount eaten by crabs.

Feeding preferences

To determine which plants were eaten by *Armas*, we conducted a multiple-choice preference experiment. Each replicate crab was offered each of the seven plant species; cut basal ends of plants were submerged in seawater in the bottom of the jar. Experimental replicates ($n = 27$ crabs) and paired no-crab controls were terminated after 4–11 d when at least one species of plant had been substantially grazed (>33% consumed). For each replicate, the mass eaten was calculated for each plant as “change in mass of plant exposed to crab” minus “change in mass of no-crab control” and compared to zero with a one-sample t test. We also visually inspected plants for obvious feeding marks.

Physical attributes of plants

To determine whether feeding preferences of crabs were related to physical attributes of plants, we measured the water content, thickness, and toughness of each species. The water content of plants was determined by weighing 10 samples of each species, drying at 60°C to constant mass, and weighing again. The thickness of leaves (or photosynthetic stems in *Salicornia*) was measured with calipers ($n = 15$ samples/species).

We measured plant toughness using three techniques. None of these techniques precisely mimicked the way that crabs feed. However, we reasoned that the combination of the three would provide a useful guide to the relative challenge that crabs experience in feeding on different plants, especially if the three techniques gave similar results. First, we measured the force required to punch a 3 mm diameter metal rod through the plant leaf or photosynthetic stem. Plant material (n

$= 15$ samples/species) was clamped between acrylic plates over a 7 mm wide groove, and the metal rod, topped by an attached plastic beaker, was placed so that the plant supported it over the groove. Sand was slowly added to the beaker until the rod punched through the plant, at which point the sand, beaker, and rod were weighed. Second, we measured the force required to rip a pin through a leaf or photosynthetic stem. Plant material ($n = 15$ samples/species) was supported with the axis horizontal and a safety pin inserted in a standard position just below the middle of the leaf or photosynthetic stem. A beaker was hung from the safety pin by a string. Sand was slowly added to the beaker until the pin ripped free from the plant, at which point the sand, beaker, string, and pin were weighed. The maximum force generated by this apparatus was 3.41 N (newtons), which was sufficient to rip all plants except *Juncus*. Third, ~1-g samples of plant material ($n = 10$ samples/species) were weighed, added to 150 mL distilled water in a blender, and blended for 10 s. Contents of the blender were poured through a coffee filter, and the retained plant material was dried at 60°C and weighed. Paired control replicates ($n = 10$ samples/species) that were not blended were weighed, dried at 60°C, and weighed again. Wet mass: dry mass data from control replicates were used to calculate the proportion of blended plant material that passed through the filter.

To obtain further data on feeding preferences of *Armas* and to determine whether these preferences depended upon the physical structure (i.e., toughness) of the plants, we conducted a single-choice feeding experiment using all seven plants in both fresh and reconstituted form. To create reconstituted plants, plant material was lyophilized, pulverized in a blender or mill, and reconstituted in a diet composed of agar plated onto a filter paper disc (for physical support). Plant powder (0.1 g) was placed inside a 55 mm diameter petri plate, 3 mL of a 4% agar solution were pipetted into the petri plate, and the mixture was gently stirred to suspend the plant powder. Filter paper discs (Whatman 1, 0.21 g) were placed snugly on top of the mixture. Once the diet had cooled and set, the disc was removed from the petri plate and cut into 4–6 pieces for use in experiments. This diet had a water content of 88%, comparable to that of *Batis*, *Borrchia*, and *Salicornia* (Table 1). Because of the contributing mass of the filter paper and agar, the dry mass of the diet was 24% plant powder. Crabs ($n = 20$ crabs/diet) were offered a single food item pinned to a rubber stopper and allowed to feed for 2 d. We hypothesized that if toughness was important, *Armas* consumption would differ more between fresh plants than between reconstituted plants. Although the process of reconstituting plants might alter more than just toughness, alternative experimental approaches were not obvious, and the results were in agreement with our correlative results. Data were analyzed using ANOVA, with species and

TABLE 1. Physical attributes of plant species. Plants are listed in order of increasing average toughness. Superscript letters indicate groups within columns that are not significantly different (ANOVA with Tukey comparisons). All data are means ± 1 SD, except for overall toughness rank, which was determined by averaging ranks from three toughness measures.

Species	Toughness measures					Water content (proportion water)	Leaf/stem thickness (mm)
	Penetrometer (force in newtons)	Ripping (force in newtons)	Blender assay (proportion passing through filter)	Overall rank (soft to tough)			
<i>Iva</i>	1.2 ^a \pm 0.2	0.2 ^a \pm 0.1	1.00 ^a \pm 0.00	1	0.78 ^c \pm 0.028	0.39 ^{bc} \pm 0.07	
<i>Borrichia</i>	1.5 ^a \pm 0.4	0.5 ^a \pm 0.3	0.87 ^b \pm 0.17	2	0.84 ^b \pm 0.013	0.44 ^c \pm 0.08	
<i>Batis</i>	4.2 ^b \pm 1.0	1.1 ^b \pm 0.4	0.65 ^c \pm 0.11	3	0.86 ^a \pm 0.015	1.98 ^d \pm 0.34	
<i>Salicornia</i>	6.4 ^c \pm 1.8	1.2 ^b \pm 0.6	0.65 ^c \pm 0.09	4	0.86 ^{ab} \pm 0.011	2.59 ^e \pm 0.18	
<i>Distichlis</i>	4.4 ^{bc} \pm 1.3	1.6 ^b \pm 0.7	0.20 ^d \pm 0.08	5	0.50 ^f \pm 0.040	0.27 ^a \pm 0.09	
<i>Spartina</i>	17.9 ^d \pm 2.9	3.1 ^c \pm 0.9	0.31 ^d \pm 0.07	6	0.68 ^d \pm 0.014	0.31 ^{ab} \pm 0.08	
<i>Juncus</i>	30.3 ^e \pm 3.7	3.4 ^{c†} \pm 0.0	0.22 ^d \pm 0.07	7	0.57 ^e \pm 0.018	2.03 ^d \pm 0.32	
	$F_{6,97} = 437,$ $P < 0.0001$ ($n = 15$ samples except <i>Spartina</i> , $n = 14$)	$F_{6,98} = 87,$ $P < 0.0001$ ($n = 15$ samples)	$F_{6,63} = 91,$ $P < 0.0001‡$ ($n = 10$ samples)		$F_{6,63} = 442,$ $P < 0.0001‡$ ($n = 10$ samples)	$F_{6,98} = 335,$ $P < 0.0001§$ ($n = 15$ samples)	

† All readings were greater than the capacity of the instrument (3.4 N).

‡ Data were arcsine(square root) transformed before analysis to improve normality.

§ Data were log transformed before analysis to improve homogeneity of variance.

presentation mode (fresh vs. reconstituted) as main effects.

To explore further the role of toughness in determining feeding preferences, we offered *Armases* a choice between all four possible pairwise combinations of two soft (*Batis*, *Iva*) and two tough (*Spartina*, *Juncus*) plants. Additionally, we offered *Armases* the same set of pairwise choices using reconstituted plants. Based on the notion that toughness was governing preference, we hypothesized that *Armases* would prefer to eat the softer plant of each pair, but that these preferences would disappear when plants were reconstituted as comparatively soft diets. Reconstituted plants were prepared as above except that 0.2 g of lyophilized plant material was added to give a diet that was 83% water and whose dry mass was 38% plant powder. Replicates (initially $n = 20$ replicates/trial) were stopped when approximately half of one diet had been eaten; animals that did not feed sufficiently within 2 d (2–7 replicates/trial) were dropped from the experiment.

Plant extracts

Plants were collected from around Sapelo Island. Each collection of healthy leaves or green shoots was composed of numerous individuals from several locations. Plant material was coarsely chopped in a blender in methanol (MeOH), extracted three times in a 1:2 mixture of MeOH and dichloromethane, and then extracted twice in 70% aqueous MeOH. The organic extract was reduced to dryness on a rotary evaporator. The MeOH and aqueous MeOH extracts were combined, the MeOH removed on a rotary evaporator, and the remaining extract lyophilized. The plant material remaining after extraction was dried at 60°C and weighed in order to calculate yields.

Extracts were incorporated into the agar-filter paper artificial diet at natural concentrations based on dry mass (Table 2). Aqueous methanol extracts were added to petri plates and mixed into warm agar as described above for plant powders. Organic extracts were dissolved in 50 μ L of ether and painted onto the filter paper before it was added to the agar. Pieces of filter paper for blanks were painted with equal amounts of ether. We let the ether evaporate before filter papers were added to agar. Crabs were offered two pieces of artificial diet, one containing a single extract and the other a blank. Replicates (initially $n = 20$ replicates/trial) were stopped when at least half of one diet had been eaten; animals that did not feed within 2 d (0–4 replicates/trial) were dropped from the experiment.

Silica

Silica is common in some plants, especially wetland grasses such as *Distichlis* and *Spartina* (Lanning and Eleuterius 1983, 1985). To test the hypothesis that silica in plants affected feeding by *Armases*, we obtained silica from three sources: *Distichlis*, *Spartina*, and a chemical supply house. Plant material was collected from several locations, pooled within each species, dried, ashed (450°C, 12 h) in a muffle furnace, washed 5 times in 2 mol/L HCl, rinsed 5 times in distilled water, and then dried (modified from Lanning and Eleuterius 1983, 1985). Examination of the remaining material under a light microscope revealed intact, clean portions of silica "skeleton," suggesting that all organic material had been removed. We also obtained pure SiO₂ (240 mesh) from Fisher Scientific (Atlanta, Georgia). Because silica occurs in *Distichlis* and *Spartina* at ~2–4% of dry mass (Lanning and Eleuterius 1983), we

TABLE 2. Extract yields and energy and nitrogen contents of fresh plant material. Plants are listed in order of increasing toughness. For energy and nitrogen, superscript letters indicate groups within columns that are not significantly different from each other (ANOVA with Tukey tests).

Species	Organic extract yield (% dry mass)	Aqueous MeOH extract yield (% dry mass)	Energy (kJ/g dry mass)		Nitrogen (mg/g dry mass)	
			<i>n</i>	Mean ± 1 SD	<i>n</i>	Mean ± 1 SD
<i>Iva</i>	4.8	12.8	14	16.17 ^c ± 0.96	12	23.7 ^a ± 2.5
<i>Borrighia</i>	4.8	22.5	24	14.92 ^{cd} ± 1.32	22	17.1 ^{bc} ± 4.2
<i>Batis</i>	1.3	37.9	13	9.48 ^e ± 0.88	12	16.2 ^{bc} ± 1.3
<i>Salicornia</i>	1.8	41.3	6	12.72 ^d ± 3.31	5	11.6 ^c ± 7.2
<i>Distichlis</i>	1.7	6.4	12	20.65 ^{ab} ± 2.79	11	21.0 ^{ab} ± 5.8
<i>Spartina</i>	3.6	19.9	16	18.38 ^b ± 0.81	15	18.3 ^b ± 2.0
<i>Juncus</i>	3.0	14.3	16	21.02 ^a ± 2.72	16	17.3 ^{bc} ± 5.1

$F_{6,94} = 69.41, P < 0.0001$ $F_{6,86} = 7.37, P < 0.0001$

tested it at 4% dry mass to approximate the upper end of this range.

Silica was incorporated into the agar-filter paper artificial diet by gently mixing into the warm agar. Crabs were offered two pieces of artificial diet, one containing silica and the other a blank. Replicates, initially 13 (commercial SiO₂), 20 (*Spartina* silica), and 13 (*Distichlis* silica), were stopped when at least half of one diet had been eaten; animals that did not feed within 2 d (0–3 crabs/trial) were dropped from the experiment.

Salt

Some salt-marsh plants accumulate high concentrations of salt in their tissues (Lanning and Eleuterius 1985). We hypothesized that *Armas* might avoid eating plants with high internal salt concentrations. To test this hypothesis, we conducted a single-choice feeding assay with seven different salt concentrations. Agar-filter paper artificial diets were prepared as above with NaCl added at 0–50% of the dry mass of the diet. The saltiest diet had a “salinity” of 108 ppt, or >3 times the salinity of seawater. Crabs (*n* = 8 crabs/diet) were offered single diets; replicates were terminated after 2 d.

Since the above experiment showed a trend towards crabs eating more of saltier diets, we conducted a paired-choice assay to explore further the role of salt in feeding. Crabs (*n* = 14) were offered a choice between artificial diets containing 0 and 50% NaCl; all replicates were stopped within 2 d when at least half of one diet had been eaten.

Energy and nitrogen content of plants

To determine protein (expressed as nitrogen) and energy content of different plant species, replicate plant samples were lyophilized, ground to a powder, and analyzed on a model NA 1500 CN analyzer (Carlo Erba, Italy). To convert carbon values to kilojoules, we used bomb calorimetry to measure the energy content of 20 of the same samples and empirically derived a single

conversion factor of 1 g C = 30.87 kJ (*n* = 20 samples, *r* = 0.86).

Protein

To determine whether the protein content of food affected feeding by *Armas*, we conducted a single-choice feeding assay with seven different protein concentrations. Casein was added to agar-filter paper diets, as described above for other powders, at 0–60% of the dry mass of the diet (well above that found in the plants: maximum ~15% assuming protein = 6.25 × nitrogen, Table 2). Replicates (*n* = 12 replicates/diet) were terminated after 2 d.

Statistics

All analyses were done using Statistix 4.0, Analytical Software (Tallahassee, Florida). We used Spearman's rank order correlations to correlate plant traits with feeding preferences in the multiple-choice feeding assay since amounts consumed were not independent and were not normally distributed. Pearson's correlations were used in the single-choice feeding assay since these constraints did not apply.

RESULTS

Feeding preferences

When offered a choice between fresh material from seven plant species, *Armas* displayed strong feeding preferences (Fig. 1A). *Batis* and *Iva* were unambiguously consumed by the crabs (*t* tests of mass eaten vs. zero, both *P* < 0.0001). *Borrighia* and *Salicornia* appeared to be eaten in modest amounts, but the results were variable enough that the mass eaten was not or was barely significantly different from zero (*P* = 0.27 and 0.048, respectively). *Spartina*, *Juncus*, and *Distichlis* appeared not to be eaten at all (*P* > 0.24 in all cases). A plot of the number of replicates in which each species of plant had feeding marks resulted in an almost identical rank of preferences (Fig. 1B). *Batis* and *Iva* had feeding marks

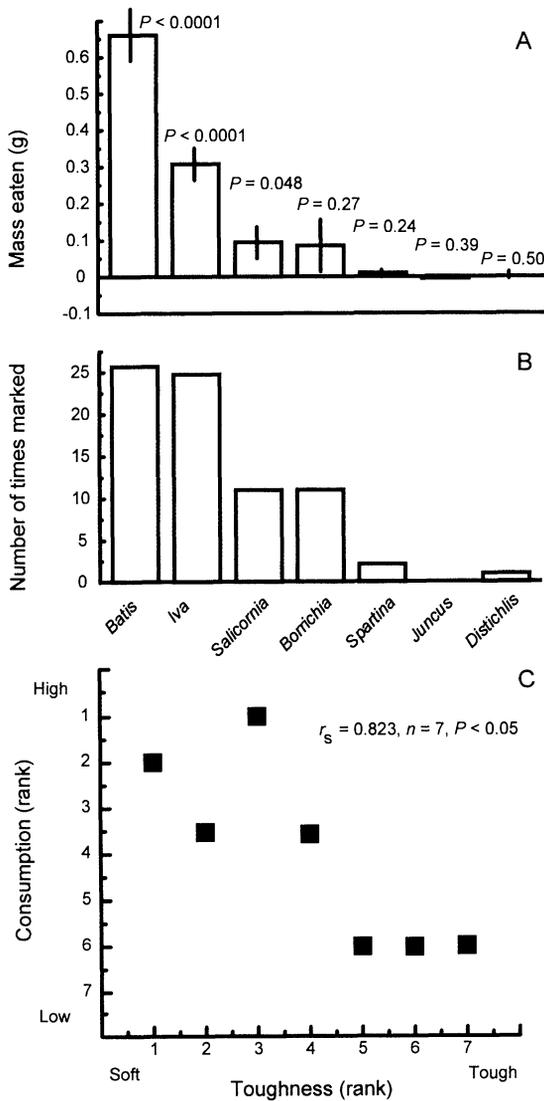


FIG. 1. Consumption of seven species of salt-marsh plants by *Armases* in a multiple-choice feeding assay ($n = 27$ replicates). (A) Mass eaten by crabs. Data are means ± 1 SE, P values are for t tests comparing mass eaten with zero. (B) Number of replicates out of 27 in which plants had feeding marks. (C) Rank consumption as a function of rank toughness (from Table 1).

in most cases, *Salicornia* and *Borrighia* about one-third of the time, and *Spartina*, *Juncus*, and *Distichlis* only rarely. For the purposes of correlations, we assigned a single set of rank preferences to the plants based on an integration of Fig. 1A and B, with tied ranks being assigned to species with similar levels of consumption: *Batis*-1, *Iva*-2, *Borrighia*, and *Salicornia*-3.5, *Spartina*, *Distichlis*, and *Juncus*-6. Preference ranks of plants common at the terrestrial border of the marsh (*Iva*, *Borrighia*, *Juncus*) and plants common in the remainder of the marsh (*Batis*, *Dis-*

tichlis, *Salicornia*, *Spartina*) did not differ (rank sum test, $P = 0.86$).

Physical attributes of plants

Water content, thickness, and toughness all differed among plant species (Table 1). Rankings from three techniques for measuring toughness were similar (Spearman's rank-order correlations, $P < 0.05$ in all cases), and we used a ranking that integrated the three techniques (Table 1) for all further calculations. *Iva* and *Borrighia* were consistently the softest plants by all three measures, and *Spartina* and *Juncus* the toughest (Table 1). In the two techniques that measured force, the force required to damage *Juncus* was over an order of magnitude greater than the force required to damage *Iva*.

Feeding by crabs in the multiple-choice feeding assay was positively correlated with increasing water content ($r_s = 0.80$, $n = 7$, $P < 0.05$) and decreasing toughness (Fig. 1C, $r_s = 0.82$, $n = 7$, $P < 0.05$), but not with thickness (Table 1, $r_s = 0.32$, $n = 7$, $P > 0.05$). Low-preference plants could be either thick or thin (*Juncus* and *Distichlis*, respectively) as could high-preference plants (*Batis* and *Iva*, respectively).

Patterns of consumption of different species of plants in the single-choice assays were affected by whether plants were presented fresh or reconstituted in agar

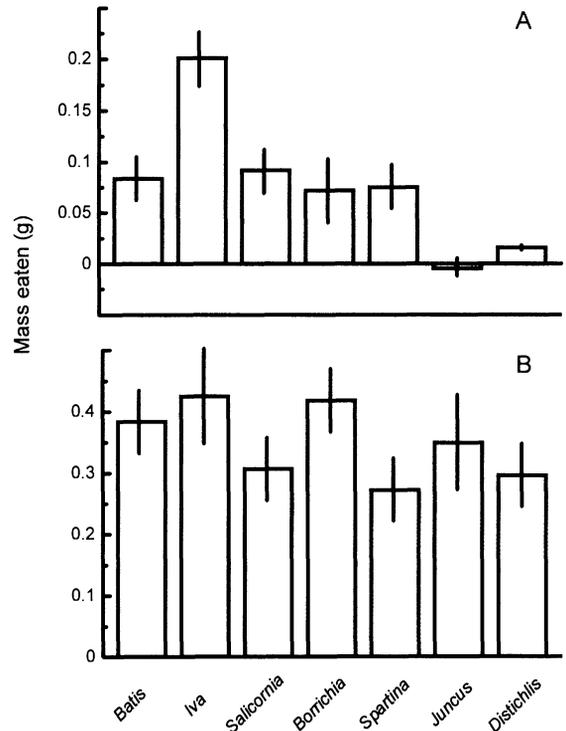


FIG. 2. Consumption of seven species of salt-marsh plants by *Armases* in single-choice feeding assays. Data are means ± 1 SE; $n = 20$ replicates/diet. (A) Fresh plants. (B) Reconstituted plants.

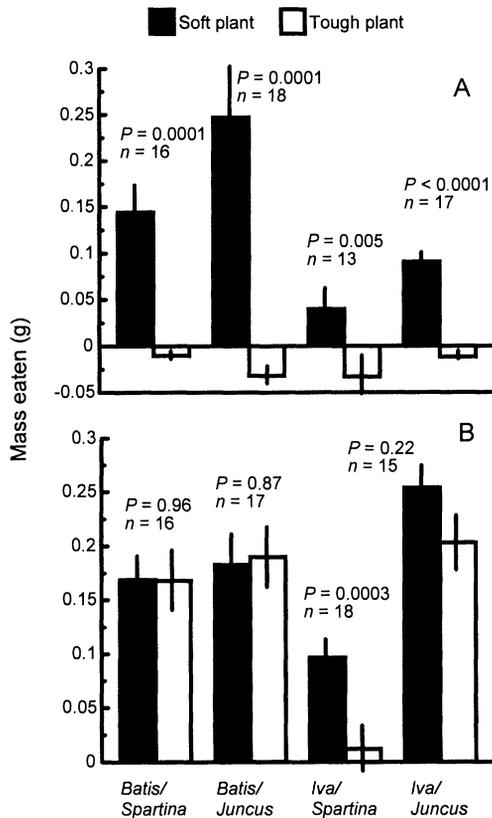


FIG. 3. Effect of pulverizing plants on feeding preferences for soft (*Batis*, *Iva*) vs. tough (*Spartina*, *Juncus*) plants. Data are means \pm 1 SE. (A) Fresh plants. (B) Reconstituted plants.

(Fig. 2, ANOVA: species \times presentation mode, $F_{6,264} = 2.57$, $P = 0.02$). Crabs presented with fresh plant material fed heavily upon *Iva*, and very little upon *Distichlis* and *Juncus* (Fig. 2A). In contrast, crabs presented with reconstituted plant material did not have strong feeding preferences (Fig. 2B). Consumption of fresh plants in this experiment was correlated with toughness ($r = 0.81$, $P = 0.03$), as in the multiple-choice experiment, but not with water content or thickness ($P > 0.05$ in both cases).

When offered pairs of soft and tough plants, *Armases* strongly preferred to eat the softer species in all four cases (Fig. 3A); however, *Armases* showed no preference in three of four comparisons between reconstituted plants (Fig. 3B).

Plant extracts

Several plant extracts affected feeding by *Armases* (Fig. 4), but these results did not explain the crab's preferences among fresh plants. In particular, there was no indication that extracts from highly preferred plants consistently had a positive effect on feeding, nor that extracts from low-preference plants consistently had a negative effect. Extracts of *Batis* (high preference) and

Juncus and *Distichlis* (low preference) all had little effect on feeding. Organic extract of *Salicornia* stimulated feeding and aqueous methanol extract of *Borrichia* deterred feeding, but these results shed little light on the intermediate palatability of these plants. Extracts of *Iva* (high preference) and *Spartina* (medium to low preference) gave mixed results. The aqueous methanol extract of *Iva* stimulated feeding, but the organic extract deterred feeding. The aqueous methanol extract of *Spartina* deterred feeding, but the organic extract stimulated feeding.

Silica

Silica did not deter feeding by *Armases* when incorporated into artificial diets in three different trials (Fig. 5A). On the contrary, although silica from *Spartina* had no effect on feeding, silica from *Distichlis* stimulated feeding and commercial SiO_2 showed a trend towards stimulating feeding.

Salt

Feeding by *Armases* did not differ among seven salt treatments (Fig. 5B, ANOVA, $F_{6,48} = 1.28$, $P = 0.29$); however, there appeared to be a trend toward higher consumption of the saltier diets. When offered a choice between salty food and a blank, crabs strongly preferred to eat the salty diet (Fig. 5B).

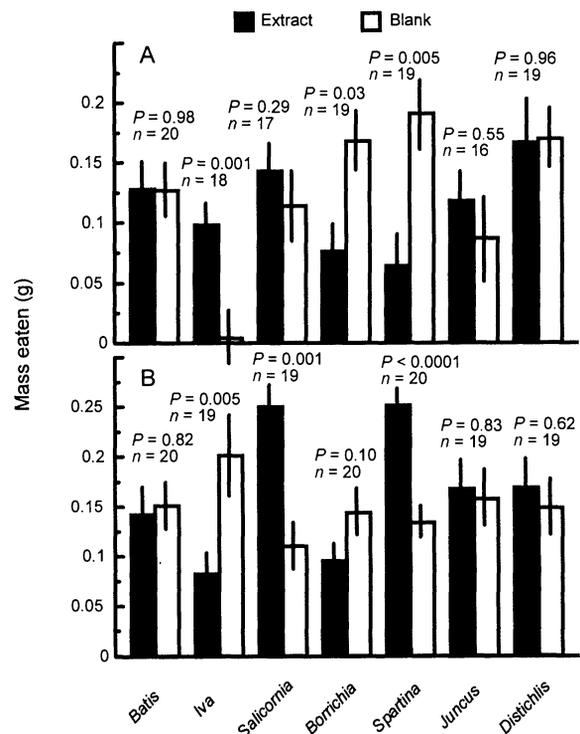


FIG. 4. Effect of plant extracts on feeding by *Armases* in paired assays. Data are means \pm 1 SE. (A) Aqueous methanol extracts. (B) Organic extracts.

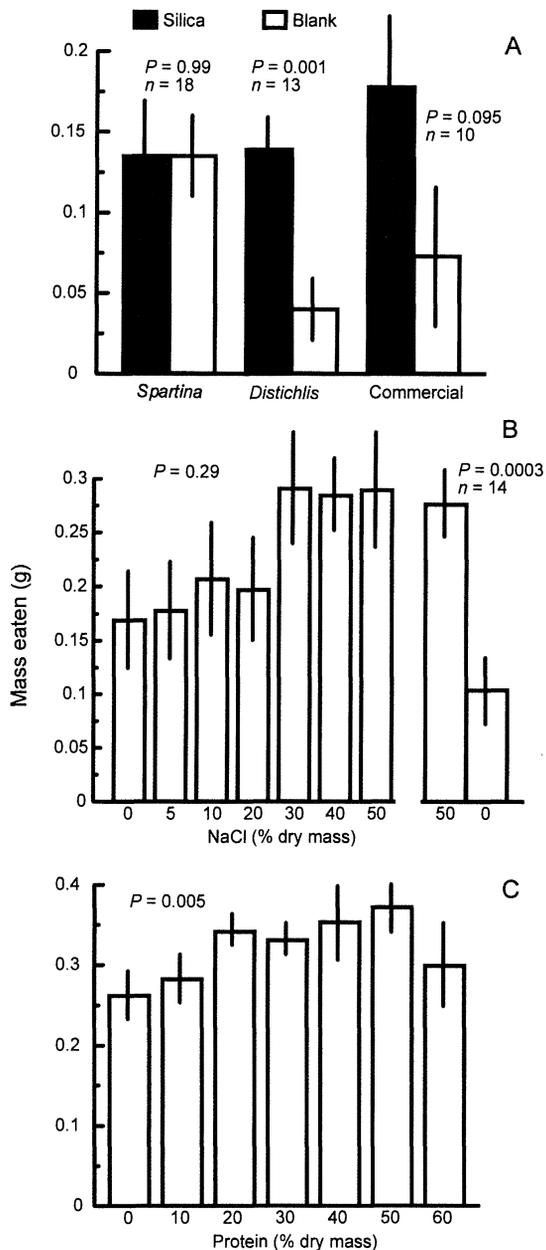


FIG. 5. Effect of silica, salt, and protein on feeding by *Armases*. Data are means \pm 1 SE. (A) Effect of silica from three sources in paired assays. (B, left) Effect of salt in single-choice assays, $n = 8$ replicates/diet. (B, right) Effect of salt (50% dry mass) in paired assays. (C) Effect of protein in single-choice assays, $n = 12$ replicates/diet.

Energy and nitrogen content of plants

Energy content differed between plants (Table 2); however, crabs did not prefer to feed on energy-rich species. Energy content was negatively correlated with preference in the multiple-choice experiment ($r_s = -0.84$, $P < 0.05$) but was not correlated with preference in the single-choice experiment ($r = -0.50$, $P > 0.05$).

Nitrogen content differed between plants (Table 2); however, feeding by crabs was not correlated with N content in either preference experiment (multiple choice: $r_s = 0.30$, $P > 0.05$; single choice: $r = 0.31$, $P > 0.05$). Plants with high N levels could rank either high (*Iva*) or low (*Distichlis*) in preference, and the plant with the lowest N levels, *Salicornia*, was of intermediate preference.

Protein

Feeding by *Armases* in single-choice assays was influenced by the protein content of the diet (Fig. 5C, ANOVA, $F_{6,76} = 3.38$, $P = 0.005$), with the highest feeding rates occurring at protein levels of 20–50%.

DISCUSSION

Our results suggest that plant toughness is the most important factor, of those we tested, in determining feeding preferences of *Armases* in the laboratory. Although other traits affected feeding in individual experiments, only toughness consistently explained the patterns of preference among fresh plants. We focused on understanding feeding preferences in the laboratory given that plants were equally available. In the field, additional factors such as plant abundance, architecture (height, branching, flexibility), heat and desiccation, and natural enemies might interact with preferences to affect consumption rates (Lubchenco and Gaines 1981). Whether the same factors that affect feeding choice in the laboratory also mediate dietary patterns, population dynamics, or evolution of *Armases* in the field is an open question, requiring additional studies.

Theory suggests that dietary specialization is most likely among very small, sedentary herbivores with low feeding rates and large costs of moving among plants (Steneck 1982, Steneck and Watling 1982). Costs of moving for *Armases* might be both small and inescapable because it is highly mobile and regularly returns to its burrow. If so, selection should favor a generalized diet because specialization would limit feeding opportunities without reducing costs. Since *Armases* is omnivorous, it may escape some dietary constraints affecting pure herbivores and be more sensitive to others.

Studies of the effect of toughness on feeding have a long history (Tanton 1962), a simple but compelling mechanistic and theoretical framework (Littler and Littler 1980, Steneck and Watling 1982, Littler et al. 1983a, b, Raupp 1985, Bernays 1986), and a record of success in predicting patterns of herbivory in some taxa (Dirzo 1980, Coley 1983, Pennings and Paul 1992, Sagers and Coley 1995, but see Hay 1984, Steinberg 1985). Difficulty in removing and masticating plant material will directly limit feeding rate, and this effect should logically be reinforced by a preference for foods that are easier to process. Nevertheless, the potential effect of toughness on feeding has been overshadowed in the plant-herbivore literature by a focus on plant secondary chemistry and/or nutritional content and has

rarely been evaluated with an experimental approach. We suggest that the possible role of toughness as a primary factor determining herbivore feeding choices deserves increased attention. Plant toughness is overcome by specialized, robust feeding appendages (Steneck and Watling 1982, Bernays 1986). Since *Armasas* is omnivorous, its feeding appendages must be able to handle a wide variety of food types, perhaps limiting their ability to process very tough plants.

Consideration of plant toughness in marine systems has often been guided by a functional form approach (Littler and Littler 1980, Steneck and Watling 1982, Littler et al. 1983a, b). Although this approach has the virtue that it is easy to rapidly assign plants to functional form categories based on visual inspection, it suffers from the fact that toughness may vary considerably within each category and may not always vary as predicted between categories (Padilla 1985, 1989, Duffy and Hay 1991). For this reason, we suggest that studies of the importance of toughness will benefit from measuring plant toughness directly, rather than relying on functional form as an indicator of toughness.

Plant secondary chemistry is often thought to play a preeminent role in herbivore diet choice (Rhoades 1979, 1985, Ehrlich and Murphy 1988, Schultz 1988). High concentrations of tannins have been both negatively and positively correlated with diet preferences of mangrove crabs in different correlative studies (Camilleri 1989, Micheli 1993b). In our experiments, plant extracts sometimes stimulated or deterred feeding by *Armasas*, but there was no pattern that reflected the overall preference hierarchy of *Armasas* among fresh plants. In particular, there was no pattern for extracts of highly preferred plants to consistently stimulate feeding, or for extracts of low-preference plants to consistently deter feeding. This suggests that plant secondary chemistry is not the primary factor determining feeding choices of *Armasas*.

Plant secondary chemistry may have been important in one case, when *Iva* was preferred over *Spartina* in both whole-plant form and when reconstituted. This result may represent the peak of chemical effects in this system because both extracts (aqueous methanol and organic) of both plants had strong and significant effects on feeding. Since aqueous methanol and organic extracts of each of these plants had opposite effects on feeding, more complicated experiments using combinations of extracts would be necessary to unambiguously determine the net effect of plant chemistry on feeding. Such experiments might reveal that the net effects of *Iva* and *Spartina* chemistry on feeding were, respectively, positive and negative, in which case chemistry would partially explain the high- and low-preference rankings of these two plants. In all other cases, however, the results of trials with plant extracts offered no insight into the palatability of the fresh plants. In particular, neither *Batis*, a highly preferred plant, nor *Distichlis* or *Juncus*, low-preference plants,

yielded extracts that had any significant effect on feeding.

Theory suggests that smaller herbivores should preferentially feed on plants where they are less at risk of predation or of incidental consumption by large herbivores. Since such plants are likely to be chemically defended, small herbivores should evolve resistance to chemical defenses (Hay and Fenical 1988, 1992, Hay et al. 1988, 1989, Hay 1992). Although *Armasas* is relatively small, it is agile enough that it is unlikely to be eaten accidentally by deer or horses feeding on marsh plants. *Armasas* probably suffers predation from raccoons and birds; however, it is unclear whether its risk varies substantially depending upon which plant it is in. *Armasas* does not appear cryptic on any plants, and we have no reason to believe that it can sequester secondary metabolites from its diet. Its primary response to human collectors is rapid flight, suggesting that it does not gain protection from residing in any particular plant. Consequently, theory suggests that *Armasas* should be relatively sensitive to plant chemical defenses. Since very little work has been done on the chemical defenses of salt-marsh plants, we cannot compare our results to other studies. *Armasas* was deterred from feeding by extracts of three of seven plants, indicating that it is not completely indifferent to chemical defenses; however, other traits appeared more important in determining feeding preferences.

Silica is present in many angiosperms where it has been thought to function as a defense against herbivory (reviewed in McNaughton and Tarrants 1983). Recent challenges to this view point to inconsistencies between correlative studies and to a lack of manipulative experiments (Hochuli 1993, Vicari and Bazely 1993). To our knowledge, only one study to date has directly manipulated silica content and demonstrated that it reduces feeding (Gali-Muhtasib et al. 1992). In our experiments, silica did not deter feeding. In contrast, it appeared to stimulate feeding in some trials. It may be that only certain types of herbivores are deterred from feeding by silica, just as calcium carbonate in seaweeds appears to have different effects on different herbivores (Pennings and Paul 1992, Hay et al. 1994, Schupp and Paul 1994). Alternatively, our experiments with silica may have introduced artifacts. For example, even although we were as gentle as possible with our silica collections from fresh plants, and retained much of the original "skeletal" structure, we inevitably created an agar disc in which the silica "fibers" were oriented randomly, rather than in structured bundles as they would be in vivo. In any case, we suggest that the defensive properties of silica remain to be conclusively demonstrated against a variety of herbivores and that this issue deserves more experimental attention.

Attempts to predict herbivore diet choices based on N or energy content of foods have generally had limited success (Paine and Vadas 1969, Vadas 1977, Milton 1979, Bryant and Kuropat 1980, Belovsky 1981, 1984,

Owen-Smith and Novellie 1982, Stephens and Krebs 1986, Horn 1989, Dearing and Schall 1992, Dearing 1996). Correlative studies of mangrove crab diets have associated high-preference foods with either high or low N content (Camilleri 1989, Micheli 1993*b*). The palatability of different plants to *Armases* in this study did not correlate positively with N or energy content. Although feeding increased with protein in the laboratory, peak levels of feeding occurred at protein levels much higher than those found in plants. Since we examined only C and N content, it is possible that more complex aspects of nutritional quality such as amino acid ratios or lipid composition might play a role in *Armases* feeding choices. Alternatively, since *Armases* is omnivorous, it may rely upon animal foods for its nitrogen needs and choose among plants based on other criteria.

Salt-marsh plants often accumulate high levels of salt in their tissues (Lanning and Eleuterius 1985). We hypothesized that *Armases* would avoid salt in its diet in order to reduce problems of osmoregulation, but this was not the case, at least in our short-term experiments. In view of *Armases*' semiterrestrial lifestyle in which it experiences soils that vary widely in water content and pore water salinity, its osmoregulatory abilities are likely excellent. Consequently, short-term intake of dietary salt may not be a problem. Whether this tolerance would extend over longer terms is a matter for future studies.

Comparatively few studies have examined the relative importance of multiple plant traits in determining herbivore feeding preferences within a single system (Milton 1979, Coley 1983, Hay 1984, Steinberg 1985, Paul and Hay 1986, Damman 1987, Pennings and Paul 1992, Duffy and Hay 1991, Dearing 1996, Pennings et al. 1996). These studies did not reach a consensus. Some found plant toughness to be most important (Coley 1983, Pennings and Paul 1992, Sagers and Coley 1995); others indicated a preeminent role for secondary chemistry (Hay 1984, Buchsbaum et al. 1984, Steinberg 1985, Paul and Hay 1986) or natural enemies (e.g., Duffy and Hay 1991, Hacker and Bertness 1995). The relative importance of different plant traits to herbivores might vary predictably based on herbivore traits such as body size, mouthpart strength, or diet breadth, and on plant community traits such as successional stage, selection pressure experienced from consumers, availability of nutrients, etc. (Lubchenco and Gaines 1981). If so, it might be possible to use these traits to assign herbivores to groups that will predictably use different criteria to select their diets. Evaluating this possibility will require multifactor experimental studies with a variety of herbivores, but could lend a new level of generality to plant-herbivore theory.

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