



## Diet choice in an omnivorous salt-marsh crab: different food types, body size, and habitat complexity

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### Abstract

Studies of diet choice by omnivores have the potential to form conceptual links between studies of diet choice by herbivores, frugivores, detritivores, and predators. We examined diet choice in the omnivorous salt marsh crab *Armases cinereum* (= *Sesarma cinereum* (Grapsidae)) in a series of laboratory experiments. *Armases* is sexually dimorphic, with larger males having relatively larger claws than females. In a growth experiment, an invertebrate diet supported better growth than any other single diet; however, growth also occurred on single diets of mud, leaf litter or fresh leaves. Mixed diets provided the best growth. If alternative foods were available, consumption of leaf litter and fresh leaves decreased, but these items were not dropped from the diet completely. In contrast, consumption of invertebrate prey was not affected by the availability of alternative foods. In a predation experiment, crustacean prey (an amphipod and an isopod) were more vulnerable to predation by *Armases* than were two small gastropod species. Only large male *Armases* were able to consume large numbers of gastropods. Environmental structure (plant litter or litter mimics) reduced predation rates, especially on crustaceans, which actively utilized the structure to hide from predators. *Armases* consumes a mixed diet because several factors (prey physical defenses, avoidance behavior of prey, growth benefits of a mixed diet) favor omnivory over a specialized diet.

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Similar factors may promote minor amounts of “omnivory” by species generally considered to be herbivores, frugivores, detritivores, and predators.

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## 1. Introduction

Studies of consumer diet choice have often focused on organisms whose diet is more or less limited to a single broad category of food. Thus, we have studies of diet choice among predators (Elner and Hughes, 1978; Osenberg and Mittelbach, 1989), herbivores (Milton, 1979; Dearing and Schall, 1992; Pennings and Paul, 1992), detritivores (Rushton and Hassall, 1983; Camilleri, 1989; Dudgeon et al., 1990), and frugivores (Levey et al., 1984; Levey, 1987), and these different groups of studies have tended to address different hypotheses using different techniques, putatively because nutritional goals and opportunities differ among consumer types. Because omnivores eat a variety of food types, their foraging decisions may be informed by multiple sets of goals and opportunities. Thus, the various approaches to these different consumer types could potentially be unified by studies of omnivores that require a more comprehensive approach (Klumpp and Nichols, 1983; Bjorndal, 1991; Cruz-Rivera and Hay, 2000).

Omnivores can represent a large proportion of the consumers in many communities (Polis, 1991; Lodge et al., 1994; Polis and Strong, 1996; Cruz-Rivera and Hay, 2000). Moreover, species that are commonly identified as herbivores, detritivores, or frugivores may include some animal material in their diets (Morton, 1973; Mattson, 1980; Dearing and Schall, 1992; White, 1993), and species commonly identified as predators may include some vegetable matter in their diets (Johnson and Boyce, 1990; Kneib and Weeks, 1990; McTigue and Zimmerman, 1991; Kennish, 1996; Stachowicz and Hay, 1999; Martinoli et al., 2001). Because many “detritivores”, “frugivores”, “herbivores”, and “predators” are in fact omnivorous to a greater or lesser degree, studies explicitly focusing on omnivory have the potential to link our understanding of feeding habits in a wide variety of organisms.

Omnivorous feeding habits likely confer both advantages and constraints. By definition, omnivorous organisms have more feeding options, and thus a greater ability to optimize their nutritional balance, than do organisms with narrower diet breadth (Klumpp and Nichols, 1983; Bjorndal, 1991). On the other hand, the constraints imposed on the body plan and feeding apparatus by the necessity of capturing and processing a wide variety of food types may require design compromises such that omnivores are not particularly good at consuming any particular food type. The nature of these compromises may vary within a species as a function of size- or sex-related body-part allometry.

In this paper, we consider the dietary habits of an omnivorous, salt-marsh crab, *Armases cinereum* (Grapsidae) (= *Sesarma cinereum*; hereafter referred to as *Armases*) (Abele, 1992). This small (to about 22 mm carapace width), sexually dimorphic, semi-terrestrial crab is common at the terrestrial border of southeastern salt marshes in the United States (Teal, 1958; Seiple, 1979; Seiple and Mueller, 1992; Pennings et al., 1998). We are unaware of any data indicating that *Armases* has a terminal molt (Williams, 1984; Hartnoll, 1985; K. Anger

and C. Schubart personal communications). *Armases* will eat fresh plant material, leaf litter, fungi, carrion, and organic matter picked from sediments (Seiple and Salmon, 1982; Pennings et al., 1998), but we know little about how different food types rank in preference, ease of handling, or ability to support growth. As a first step toward understanding the feeding habits of *Armases*, we asked four questions. First, how are different food types ranked in preference? Second, how well do different food types support growth? Third, do prey defenses or environmental constraints limit crabs from consuming certain animal prey? Fourth, does sex or body size affect diet? For tractability, we began by examining these questions in the laboratory; however, fully understanding feeding patterns will ultimately require field experiments that consider the numerous factors that may modify laboratory feeding preferences to produce actual patterns of consumption in the field.

## 2. Methods

### 2.1. Study site

The study was conducted at the University of Georgia Marine Institute on Sapelo Island, Georgia, USA (31°27'N; 81°15'W). Animals were collected by hand from marshes surrounding the island and returned to the laboratory for allometry measurements, growth experiments, and feeding trials. Crabs were held in the laboratory in humid tubs with abundant leaf litter for 24–48 h before they were used in experiments. After crabs were sorted by sex (or sex and size), they were randomly assigned to experimental treatments.

### 2.2. Claw size

To document differences in claw size between male and female *Armases*, we collected 175 crabs of a wide range of sizes in March 1996. We measured the carapace width and the height of the propodite of the right chela to the nearest 10th of a millimeter under a dissecting microscope fitted with a calibrated ocular micrometer. We compared the slopes of log–log plots of claw height vs. carapace width, reasoning that a claw structured for crushing strength would have a greater relative height (reflective of a larger flexor  $L_1$  lever length) than one structured, say, for speed or dexterity (Warner and Jones, 1976). This approach vastly oversimplifies the biomechanical complexities that determine crushing strength, but is a reasonable first-order approximation for intraspecific comparisons across sex and body size.

### 2.3. Growth experiment

To determine growth rates of *Armases* fed various diets, we collected crabs of intermediate size (average carapace width 11.1 mm, range 7.9 to 13.3 mm) on 15 June 1997 and housed them individually in 5-l plastic tubs. Each tub had a 10-cm diameter mesh window to allow air circulation and a bowl of seawater to prevent dehydration. Seven male and six female crabs were randomly assigned to each of six diet treatments. The diet treatments, described in detail below, consisted of (1) half of a dead fiddler crab (*Uca pugnax*), (2) mud collected from the *Armases* habitat, (3) leaf litter, (4) fresh leaves,

(5) a combination of all individual diets except *Uca*, and (6) a combination of all individual diets including *Uca*. In every case, food was provided in excess of consumption. The *Uca* diet was chosen to represent a diet of animal tissue, which in the field could be obtained either by consuming carrion or by predation. The mud diet consisted of an undisturbed disk (1.5 cm deep, 7.5 cm diameter) of surface mud from the high marsh. Fresh mud was collected from a single site each time the diets were changed, taking care not to collect in the exact same location. Feeding on mud was not quantified, but crabs were observed to heavily rework the mud with their appendages, suggesting that they were processing the mud for food items. The leaf litter diet consisted of five fallen leaves, one each from *Borrchia frutescens*, *Quercus virginiana*, and *Myrica cerifera*, and two from *Iva frutescens* (this species has small leaves that are highly palatable to *Armases* (Pennings et al., 1998)). Fallen leaves were brown but in the early stages of decomposition. The fresh leaf diet consisted of one green leaf from each species. These four shrubs were chosen because they are common at the marsh border habitat where *Armases* is most abundant, and we knew that *Iva* and *Borrchia* were readily eaten by crabs (Pennings et al., 1998). Diets were replaced every 3 days. Consumption of *Uca*, leaves, and litter was visually estimated to the nearest 10% each time diets were replaced during a 5-week period between 24 June and 28 July 1997 (consumption of diets was not measured during the entire feeding experiment because the measurements were time consuming and feeding patterns appeared stable over the period that they were measured). Crab carapace width was measured at the beginning and end (22 August 1997) of the experiment, and molting recorded when diets were changed. Tubs housing crabs were located under an opaque roof, in full shade, but otherwise exposed to ambient outdoor weather conditions (during the experiment the average daily high, daily mean, and daily minimum temperatures were 31.9, 27.7, and 23.2 °C, respectively). Because growth and feeding in this experiment did not differ by sex ( $P > 0.05$  in all cases), data for male and female crabs were pooled.

#### 2.4. Predation experiment

Although *Armases* readily eats live plants, leaf litter, fungi, sediments, and carrion (Seiple and Salmon, 1982; Pennings et al., 1998), it is unknown whether this species also acts as a predator. To examine the potential for *Armases* to act as a predator, we conducted an experiment in the laboratory during March–April 2000, in which we compared predation rates of four classes of crabs on four potential prey species, in the presence or absence of an alternative food, under two habitat conditions, for a total of 64 treatment combinations. Feeding trials were conducted in plastic arenas (14–17 cm diameter). Prey could not climb out of the reach of crabs. These conditions were chosen to maximize encounter rates with prey so that we could best compare feeding success (determined by attack and success probabilities) given high encounter rates. Each container was provided with 10–20 ml of seawater (15 PSU) to prevent desiccation of organisms.

As potential prey, we used four common small invertebrates living sympatrically with *Armases*: two gastropods, the salt marsh periwinkle *Littoraria irrorata* (= *Littorina irrorata*) and the coffeebean snail *Melampus bidentatus*, and two crustaceans, the common marsh hopper *Orchestia grillus* and the pill bug *Venezillo parvus*. Because we expected that *Armases* would have difficulty consuming large snails, we used only small individuals

Table 1  
 Sizes (mean  $\pm$  SD,  $n$ ) of representative animals used in the predation experiment

<i>Armases cinereum</i>	Carapace width (mm)	Prey	Length (mm)
Large males	18.0 $\pm$ 2.0, 159	<i>Orchestia grillus</i>	12.0 $\pm$ 3.4, 22
Small males	13.4 $\pm$ 1.3, 160	<i>Venezillo parvus</i>	5.2 $\pm$ 0.9, 316
Large females	18.2 $\pm$ 1.2, 167	<i>Littoraria irrorata</i>	6.8 $\pm$ 2.5, 318
Small females	13.7 $\pm$ 1.0, 158	<i>Melampus bidentatus</i>	5.2 $\pm$ 1.4, 320

(Table 1). For the crustaceans, we used animals of the modal size at our collection sites (Table 1). Each trial consisted of 1 crab presented with 10 prey organisms of a single species. To provide alternative food and shelter, we filled arenas with leaf-litter of *Juncus roemerianus*, a common high marsh plant. To provide alternative food without adding shelter, we gave the crabs an artificial diet in a small dish. The artificial diet consisted of 0.3 g granulated agar mixed with 1.0 g ground (< 1 mm) dried *J. roemerianus* leaf-litter, mixed with boiling deionized water and packed into round (2.5 cm diameter, 1.5 cm height) plastic dishes. To provide shelter without an alternative food, we filled arenas with thin strips of plastic to simulate *Juncus* litter.

Crabs were sexed and divided into two size groups per sex based on carapace width to give groups corresponding to immature (average cw = 13.4 mm) and mature (average cw = 18.0 mm) males, with corresponding size treatments of females (Table 1). The experimental design consisted of all 64 combinations of four prey treatments (*Orchestia*, *Venezillo*, *Littoraria*, *Melampus*), two habitat treatments (shelter, no shelter), two alternative food treatments (plant litter available or not), two crab sizes, and two crab sexes. Each combination of treatments was replicated 10 times, for a total of 640 replicates. Trials were allowed to run for 24 h, after which the number of prey consumed was recorded. Crabs of each sex and size class were randomly assigned to diet and habitat treatments, and were used only once and released, whereas uninjured prey were returned to stock colonies and reused. The proportion of prey consumed was arcsine (square-root) transformed to improve normality before testing with ANOVA.

### 3. Results

#### 3.1. Claw size

Both sexes showed significant allometric growth of claws (males:  $n = 127$ ,  $r^2 = 0.96$ , slope  $b = 1.85$ ,  $t = 243$ ,  $P < 0.001$ ; females:  $n = 48$ ,  $r^2 = 0.90$ , slope  $b = 1.22$ ,  $t = 20.1$ ,  $P < 0.001$ ; test for allometry from Zar, 1974). The slope was significantly greater in males than in females ( $t = 100.5$ ,  $P < 0.001$ ), indicating that, with increasing size, males develop disproportionately larger claws than do females.

#### 3.2. Growth experiment

*Armases* fed on each of the four single diets. Feeding on the mud diet could not be quantified, but crabs heavily disturbed the mud and appeared to eat items removed from

the mud. Consumption of *Uca* tended to be reduced in the quadruple-diet treatment compared with when only *Uca* was available, but this trend was not significant (Fig. 1A). Consumption of leaf litter was reduced if alternative foods were available, but some litter was always consumed (Fig. 1B). Consumption of fresh leaves was about half that of litter when each was offered alone (*t*-test,  $P < 0.0001$ ). Consumption of fresh leaves was reduced if alternative foods were available, but some fresh leaf material was always consumed (Fig. 1C).

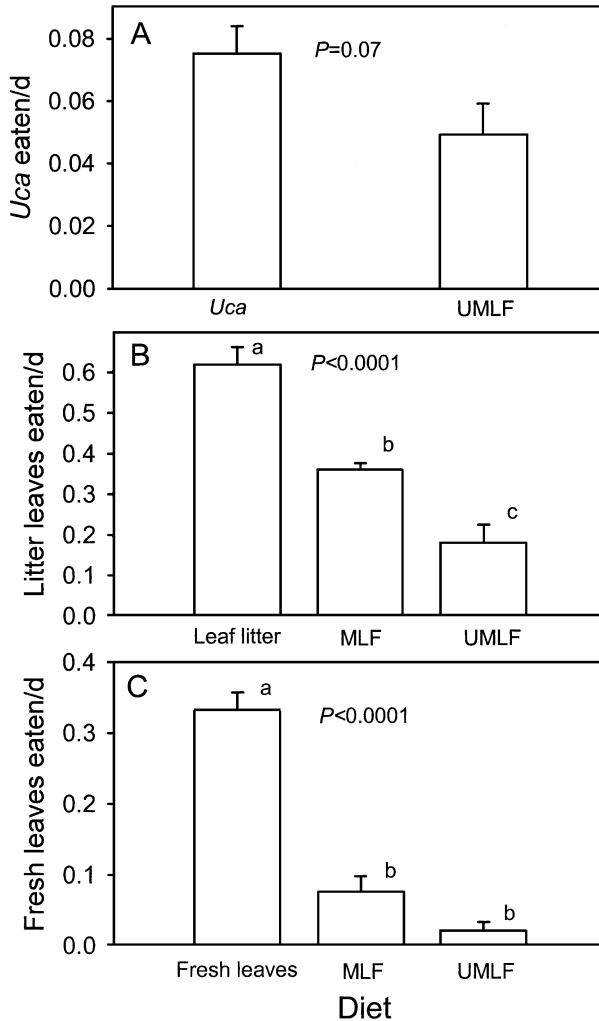


Fig. 1. Number of (A) *Uca*, (B) litter leaves, and (C) fresh leaves eaten by *Armases cinereum* per day in the growth experiment as a function of diet treatment. MLF = diet consisting of a mixture of mud, leaf litter, and fresh leaves. UMLF = diet consisting of a mixture of dead *Uca*, mud, leaf litter, and fresh leaves.  $N = 13$  for each diet.  $P$ -values based on ANOVA. Letters above bars indicate significant differences among means (Post hoc Tukey tests).

Molting of *Armases* peaked in conjunction with full, and to a lesser extent, new moons (data not shown). The proportion of crabs molting during the experiment was high for the *Uca* diet and the two mixed diets, but low for the mud, litter, and fresh-leaf diets (Fig. 2A). Among the single diets, proportional change in carapace width ((final carapace width - initial carapace width)/initial carapace width) was highest on the *Uca* diet and lowest on the fresh-leaf diet; however, the best growth occurred on the mixed diets, whether or not *Uca* was included (Fig. 2B). For crabs, overall changes in carapace width are a function of two independent variables: molting probability and molt increment. Molt increments did not differ among treatments ( $F_{3,25}=0.52$ ,  $P=0.67$ , two treatments with  $n < 3$  omitted); however, this analysis comes with the caveat that the two treatments with the lowest proportion of crabs molting (mud and fresh leaves) by definition had low sample sizes of molt increments, and therefore were not included in the analysis. Nevertheless, as can be seen from Fig. 3, overall changes in carapace width roughly paralleled molting proba-

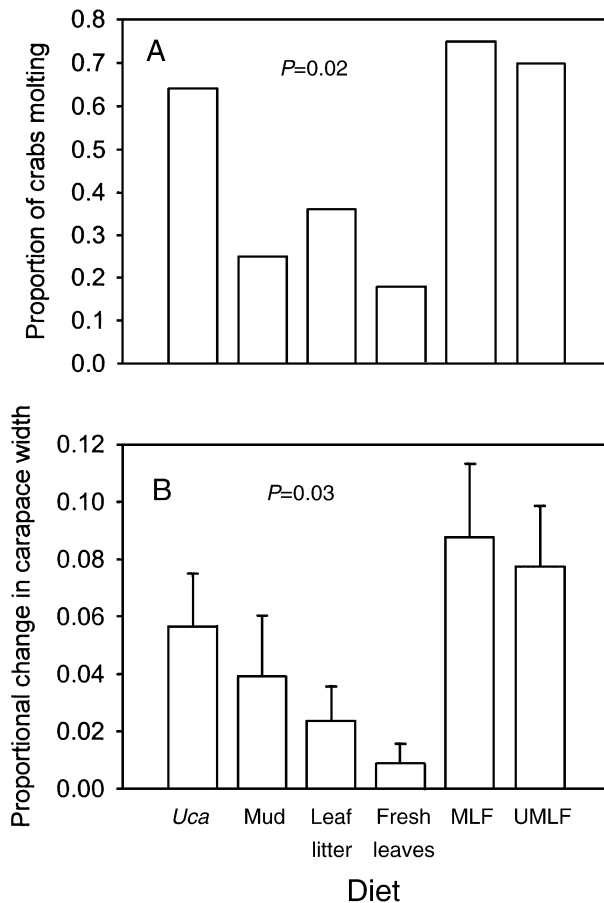


Fig. 2. Growth of *Armases cinereum* fed four single diets and two mixed diets. Abbreviations as in Fig. 1.  $N=13$  for each diet.  $P$ -values are based on (A)  $\chi^2$  test for number of individuals molting and (B) ANOVA.

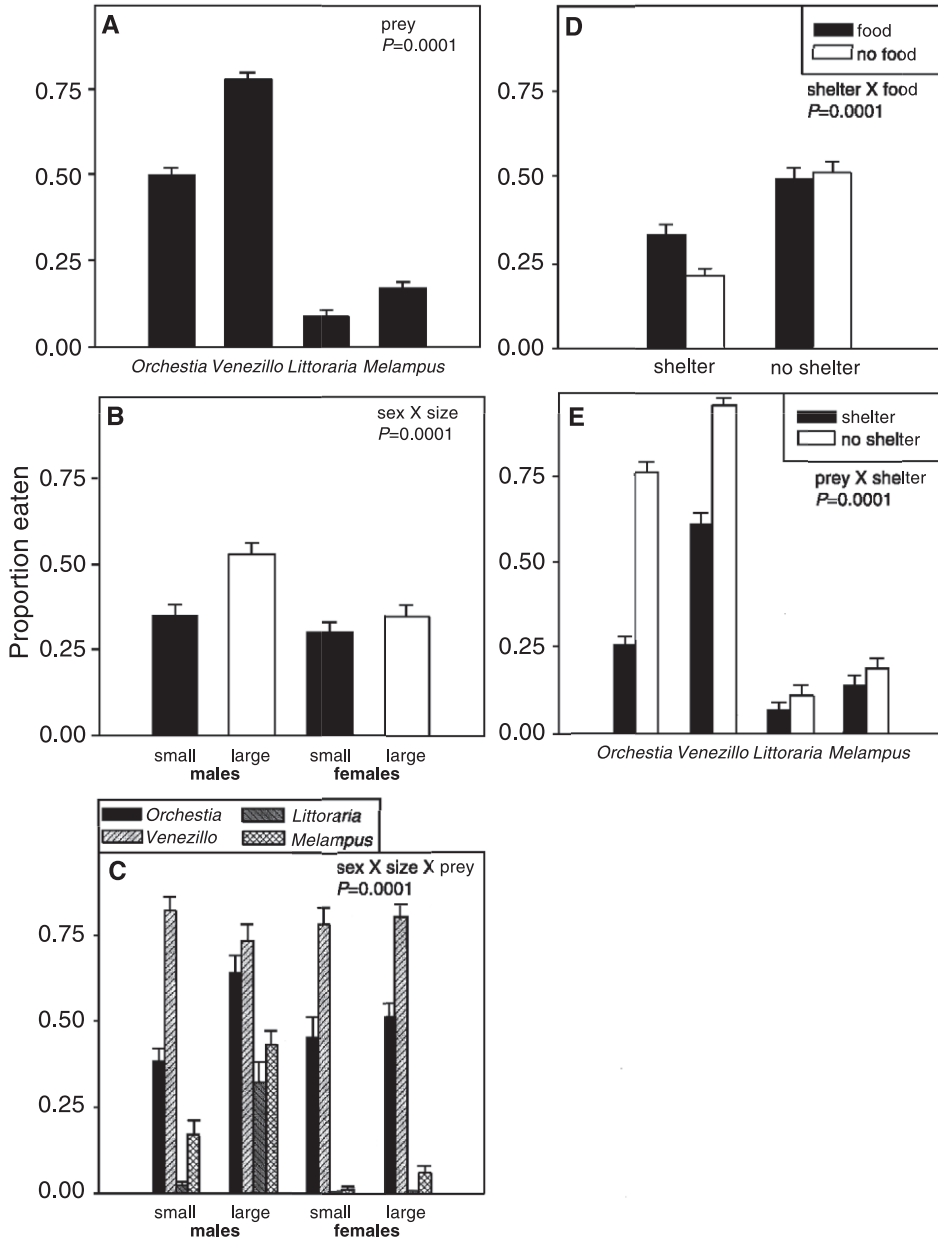


Fig. 3. Proportion of prey (out of 10) eaten by small (<1.5 cm carapace width) and large (>1.5 cm CW) male and female *Armases cinereum* in different habitat (shelter present vs. absent) and food (alternative food available or not) treatments. Each combination of treatments was replicated 10 times for a total of 640 replicates.  $P$ -values for ANOVA interactions.

bilities (both high for the *Uca* and mixed diets; both low for the fresh leaves diet), suggesting that, in this experiment, molting probabilities were the primary factor controlling growth.

### 3.3. Predation experiment

Overall, crabs consumed a greater proportion of the two crustaceans, *Venezillo* and *Orchestia*, than of the two gastropods, *Melampus* and *Littoraria* (Fig. 3A). Greater size offered an advantage in feeding to male crabs only, with large males consuming more prey (averaged over all food types) than small males or either size of females (Fig. 3B). This higher consumption rate of large males was associated with an expansion of diet breadth, leading to a significant interaction between sex, size, and prey species (Fig. 3C). All size-classes of crabs consumed crustaceans in similar amounts, but only males consumed many *Melampus*, and only large males consumed many *Littoraria*.

The effect of an alternative food source (*Juncus* litter) on predation did not interact with crab size or sex (ANOVA,  $P > 0.05$ ). There was a significant interaction, however, between the effect of an alternative food source and the effect of shelter (Fig. 3D). Overall, fewer prey were consumed in the presence of shelter ( $P < 0.0001$ ). Surprisingly, crabs consumed more prey in treatments with both shelter and alternative food available than in treatments that offered shelter but no alternative food. Most likely this was due to subtle differences in the quality of shelter provided by *Juncus* stems vs. plastic strips. The effect of shelter also interacted with prey species, with consumption of the two crustaceans, but not the two snails, reduced in treatments where shelter was available (Fig. 3E).

## 4. Discussion

Our results indicate that in the laboratory *A. cinereum* can act as a predator. We routinely observed crabs stalk and pounce on crustaceans in the experimental arenas, demonstrating well-developed predatory behaviors. Our study does not address what proportion of the diet of *Armases* in the field is obtained by consuming other invertebrates, but it clearly could be considerable. This ability to function as a predator in the field, however, would be expected to be considerably modified by physical defenses of prey and by habitat structure (Kneib, 1995).

Not all potential prey species were equally vulnerable to *Armases* in the laboratory. Crustaceans were rapidly consumed by both sexes, but snails were readily consumed only by large male crabs. Even so, snails were eaten much less often than crustaceans even by large males. Because the snails we used were fairly small (5–7 mm) and in one case relatively thin-shelled (*Melampus*), it seems likely that most salt-marsh molluscs would reach an escape in size from predation by *Armases*. In this regard, *Melampus* is known to reach an escape in size from predation by the marsh killifish, *Fundulus heteroclitus*, at around 7 mm shell length (Vince et al., 1976). Consequently, predation by *Armases* in the field probably focuses on small crustaceans (this paper) and soft-bodied invertebrates such as insect larvae and worms (Pennings, pers. obs.), although newly recruited or small-bodied species of molluscs may be taken occasionally. The Asian shore crab, *Hemigrapsus*

*sanguineus*, also an omnivore, similarly prefers small (<10 mm) vs. large bivalve prey (Brousseau et al., 2001).

There is an extensive literature indicating that increasing environmental structure reduces the ability of predators to capture prey (Vince et al., 1976; Gotceitas and Colgan, 1989; Bartholomew et al., 2000; Lewis and Eby, 2002). Furthermore, the impacts of structure often differ among prey types (Coen et al., 1981; Pennings, 1990; Primavera, 1997). In the present study, crustaceans benefited from habitat structure but snails did not. Our observations suggested that this was due to differences in prey behavior. Crustaceans utilized structure by sheltering under *Juncus* litter or artificial litter provided within the arenas. In contrast, snails crawled openly whether structure was available or not. Because crustaceans are highly associated with plant litter in the field, the ability of *Armases* to capture invertebrate prey in nature may be limited, contributing to its propensity towards an omnivorous diet.

Our study provides experimental support for previous observations (Seiple and Salmon, 1982; Pennings et al., 1998) suggesting that *Armases* is highly omnivorous. Crabs were able to grow on a wide variety of food types, and growth on mixed diets tended to be better than that on single diets (with the possible exception of the *Uca* diet) suggesting that different food types were complementary resources (sensu Tilman, 1988) for *Armases*. In accordance with optimal foraging theory (Schoener, 1971; Pyke et al., 1977), consumption of the single best food type (*Uca*) was not affected by the presence of other foods, although there was a trend towards reduced feeding on *Uca* when other foods were available. In contrast to optimal foraging theory, however, the lower quality food types (fresh leaves and leaf litter) were not completely dropped from the diet when better food types were available. Given the agile foraging behavior of *Armases* and the small size of the experimental arenas, consumption of fresh leaves and litter in the presence of alternative foods was not likely due to constraints on food availability or a need to sample the environment. It could not be due to food limitation either, because all foods were present in excess. Rather, the continued incorporation of plant material in the diet likely indicates that different food types are complementary nutritional resources for *Armases*, with a consequent benefit to a mixed diet (as was seen in the growth experiment where growth was best on a mixed diet). Similar advantages of mixed diets have been shown in a wide variety of taxa (Curtis and Hurd, 1979; MacFarlane and Thorsteinson, 1980; Lobel and Ogden, 1981; Krebs and Avery, 1984; Bjorndal, 1991; Waldbauer and Friedman, 1991; Pennings et al., 1993).

A better understanding of the structure of salt marsh food webs could contribute to our overall knowledge of the ecological and ecosystem functioning of these important habitats. A number of studies have attempted to elucidate the structure of salt-marsh food webs by isotopic analysis of the various component species (Haines, 1976a,b; Sherr, 1982; Fry and Sherr, 1984). Results for *Armases* in these studies have been somewhat variable, with  $\delta^{13}\text{C}$  values varying from  $-12.2$  to  $-19.1$  in different collections, suggesting a variety of diet sources (Haines, 1976a; Haines and Montague, 1979). With the wisdom of hindsight, we can explain this variability in isotopic signature as an expected consequence of the variety of food that *Armases* eats, including several species of live and dead plants, fungi, and other invertebrates (Pennings et al., 1998, this paper). In general, omnivory in food webs may be more prevalent than was

initially appreciated and will ultimately complicate our attempts to understand food web structure and function (Polis, 1991; Polis and Strong, 1996).

Our results indicated that sexual dimorphism in claw structure influences predatory ability in *Armases*. Sexual dimorphism is common in crustaceans (Abelló et al., 1990; Harvey, 1990; Cromarty et al., 1998) and may affect both vulnerability to predators (Lee and Kneib, 1994; Koga et al., 2001) and feeding ability (Valiela et al., 1974; Kyomo, 1992; Brousseau et al., 2001). We did not investigate the factors selecting for sexual dimorphism in *Armases*, nor the various costs that may attend upon the production of large claws in males. Clearly, however, large claws provide a benefit in that they improve utilization of better-defended prey. This benefit may partially compensate for the costs of large claws and thereby reinforce whatever other factors select for sexual dimorphism in this species.

In summary, we found that *Armases* prefers to eat animal tissue over other potential foods and grows best on this diet compared with any other single diet. In the field, however, a variety of constraints may limit the ability of *Armases* to act as a predator. First, only large male crabs are able to eat even fairly small gastropods. Second, crustacean prey are likely able to hide from *Armases* in the plant litter that they associate with in the field. Thus, many marsh invertebrates are likely to have either physical or behavioral defenses against predation by *Armases*. Third, carrion may only be sporadically available in the field. Fourth, because different food types may be complementary nutritional resources for *Armases*, there is likely a growth benefit to consuming a mixed diet. All of these factors will tend to promote omnivory, and casual observations suggest that *Armases* does eat a wide variety of foods in the field (Pennings et al., 1998). We speculate that similar constraints may operate to some degree in almost all taxa. While in many cases the details and strength of the constraints may have favored a high degree of specialization, it is frequently noted that “herbivores” and “frugivores” may include some animal matter in their diet, and that “predators” may include some vegetable matter in theirs. We suggest that this may not simply be an “accident” that happens as the animals consume their primary food, but rather may be favored in order for the consumer to obtain vitamins or nutrients that are lacking in the primary diet. Thus, an increased focus on the costs and benefits of omnivory may lead to a greater understanding of diet choice in a wide variety of consumers.

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