



Environmental regulation of foraging in the sand fiddler crab *Uca pugilator* (Bosc 1802)

Kathleen A. Reinsel*, Dan Rittschof

Zoology Department and Duke University Marine Laboratory, Beaufort, NC 28516, USA

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Abstract

Sand fiddler crabs *Uca pugilator* (Bosc 1802) live in burrows in the high intertidal to supratidal zones of sandflats and salt marshes. Large groups of crabs regularly leave their burrows to forage on exposed sediments in the low intertidal zone. They are known to forage in response to chemical cues. We hypothesized that environmental factors that vary predictably in field sediment play a role in determining where fiddler crabs forage. To test this hypothesis, we determined the effects of four physical sediment characteristics on chemically mediated feeding behavior in *U. pugilator*: (1) sediment organic content; (2) the salinity of interstitial water; (3) sediment grain size; and (4) sediment water content. Our results indicate that sediment organic content and sediment water content are the most important factors that determine where fiddler crabs forage. Optimal sediment is a mixture of sizes dominated by 0.125 and 0.250 mm sands. This condition is constant across the intertidal zone. Salinity, the most variable of the environmental factors, has no effect upon feeding responses. Optimal conditions for feeding are found in sediment with organic content at or above 1.0% that is fully saturated with water. Complete saturation allows the entire dactyl to penetrate the sediment. Consequently, dactyl chemoreceptors are maximally stimulated. Optimal conditions are found in a band several meters wide immediately above the water. The band moves with the tide. Physical factors (sediment water content), rather than biological factors (food content), are responsible for temporal patchiness of the foraging environment of fiddler crabs.

Keywords: Chemoreceptor; Feeding; Foraging; Functional morphology; Sediment organic; *Uca pugilator*

* Corresponding author.

1. Introduction

Uca pugilator (Bosc 1802) is a semi-terrestrial ocypodid crab that inhabits intertidal sandflats on the Atlantic and Gulf of Mexico coasts of the United States from Cape Cod to southeastern Texas (Crane, 1975). Crabs live in and around burrows that they build in supratidal and high intertidal sediments. They move to forage in the mid to low intertidal zones during periods of sediment exposure (Crane, 1975; Montague, 1980). Crabs feed by bringing pinches of surface sediment to the buccal region with their minor chelae. The mouth appendages process the sediment, scraping off attached particles (Miller, 1961). Rejected sediment collects at the base of the buccal region and is periodically removed and deposited onto the sediment surface in small pellets. Crabs can process about half the surface sediment in the feeding zone during a single feeding period (Robertson et al., 1981).

Stimulation and inhibition of feeding behavior in *Uca* spp. are controlled by both chemical and environmental factors. In the laboratory, feeding behavior, in the form of claw motions from substratum to mouth, is stimulated by hexose sugars, peptides and amino acids (Robertson et al., 1981; Rittschof & Buswell, 1989; Weissburg & Zimmer-Faust, 1991). Solutions of these compounds elicit feeding behavior alone or in combination with sediment. Several *Uca* spp. are most sensitive to glucose (Rittschof & Buswell, 1989). Fiddler crabs also feed in response to pure cultures of diatoms, ciliates and bacteria (Robertson et al., 1981; Weissburg, 1992). These organisms live in and upon the sediment where the crabs feed.

Several ocypodid crabs have been shown to feed in response to sediment food content. Zimmer-Faust (1987) reported that the sand bubbler crab, *Scopimera inflata*, is capable of detecting sediment food quality. However, the threshold level for feeding is lower than food levels in the sediment near the burrows. These crabs forage evenly around their burrow openings. In contrast, *Uca vocans* leave the nitrogen-poor areas near their burrows during low tide to forage in droves upon nitrogen-rich areas closer to the water (Murai et al., 1982). Foraging *U. pugilator* also form droves (Crane, 1975; Salmon & Hyatt, 1983). As the tide falls, crabs leave their burrows in the high intertidal zone and travel downslope across the mid intertidal zone to feed near the water's edge. Robertson et al. (1980) showed an increasing gradient of available food from the supratidal to the low intertidal zones, and suggested that crabs form droves in low intertidal areas in response to increased levels of food in the sediment.

The above studies emphasize the role of food availability in determining where crabs forage. Two field studies have discussed the role of physical sediment characteristics on foraging patterns of deposit-feeding crabs. For example, *Macrophthalmus japonicus* leave the area near their burrows when the sediment there is dry (Henmi, 1989). They "wander" and feed in areas where the sediment is wet. Henmi suggested that in this case sediment water content, rather than food content, can regulate where these crabs feed. In contrast, Christy (1980) determined that sediment moisture content was not important for feeding in sexually active male *U. pugilator*. Sexually active males do not typically forage with the droves, but remain near their burrows (Salmon & Hyatt, 1983). Therefore, crabs that do forage in droves may have a different response to sediment water content.

Studies of feeding behavior in *Uca* spp. have been used to develop and test models of optimal foraging (Weissburg, 1990, 1992, 1993). Optimal foraging models typically incorporate estimates of search time, energy return and handling time for particular prey items (Krebs & Davies, 1987). The models of foraging strategy that have been constructed for *Uca pugnax* feeding on diatoms in the laboratory (Weissburg, 1990, 1992, 1993) are based on measurements of food quality, feeding rates, extraction efficiencies and foraging costs for adult crabs. Handling time of sediment, as it is affected by physical conditions of the sediment, has not been specifically addressed. Fiddler crabs encounter sediment of different food quality and physical conditions as they move across the intertidal zone. In order to fully understand foraging behavior of these crabs, it is important to investigate how they respond to differences in physical conditions as well as differences in food content.

We hypothesize that physical characteristics of the sediment that vary predictably in the field play a role in determining where fiddler crabs forage. In the present study we investigate the effects of four physical sediment characteristics on feeding behavior in *U. pugilator*: (1) sediment organic content; (2) the salinity of interstitial water; (3) sediment grain size; and (4) sediment water content. We show that optimal sediment conditions for crab foraging are: (1) total organic content of at least 1.0%; (2) a mixture of sediment grains dominated by 0.125–0.250 mm sizes; and (3) complete saturation with water. Salinity of the interstitial water has no effect upon feeding behavior. Physical factors (sediment water content), rather than biological factors (food content), are responsible for temporal patchiness of the foraging environment of fiddler crabs.

2. Methods

2.1. Field measurements

Measurements of total organic content, interstitial salinity, grain size and percentage saturation were determined for sediment samples collected on three different dates from areas where crabs foraged. Sediment samples were collected at low tide from three intertidal regions defined by the behavior of the crabs. One set of samples was collected from above the high tide line, in the region containing fiddler crab burrows that are covered with water only during unusually high spring tides (burrow zone). A second set was collected at the lower limit of crab foraging activity near mean low water (feeding zone). The third set was taken at an intermediate distance in the region occupied by feeding crabs at some stage of the tide (transit zone). Approximately 100 g of sediment was scraped from the top 5 mm of sediment at each site. Sediment samples were stored in airtight plastic bags. Total organic content, salinity of the interstitial water, and sediment water content were measured immediately following collection. Mean results for each zone were plotted and compared with either one-way ANOVA (organic content and water content) or the Kruskal-Wallis test (salinity) (Sokal & Rohlf, 1981).

Total organic content was determined for 25 g subsamples from each location on

each sampling date (Dean, 1974). Sediment was dried at 100 °C overnight and weighed dry. It was then ashed at 500 °C for ≈ 4 h and weighed again. Percent by weight of organic material was then calculated from the weight lost during ignition.

To determine the salinity of the interstitial water, sediment samples were weighed wet, then dried at 100 °C overnight. The weight of water lost was converted to volume, assuming that water has a density of 1 g/ml. Samples were rehydrated with some multiple of this volume of deionized water, so that there was water standing over the sample. The sediment was mixed to allow salts to dissolve in the solution. The salinity of this resulting solution was measured with a refractometer, and the salinity of the water in the original sediment sample was calculated. Salinity measurements were repeated on samples collected on three different days to assess temporal variability in sediment salinity.

Standard dry sieving methods (Buchanan, 1984) were used to calculate sediment grain size. The sand fractions, the sand/silt-clay boundary, and the silt fractions were measured. Size divisions within the silt fraction were not determined. Mean ($\pm$ SD) grain size was determined by the method of moments (Folk, 1964).

Porosity, the amount of empty space between grains in sediment (Buchanan, 1984), was used to determine the water content of the sediment samples. Sediment samples were weighed wet, then dried at 100 °C overnight and reweighed. The volume of water in the samples was determined from the weight lost upon drying, as in the salinity measurements. Samples were then ashed at 500 °C for at least 4 h. Deionized water was added to 20 ml of ashed sediment until the sediment was completely saturated. The volume required to fill all empty space, or saturate, is an estimate of the porosity of the sediment, and was called 100% saturation. Percent saturation of field sediment was calculated by dividing the volume of water lost upon drying by the volume required to saturate to 100%. A value $> 100\%$ indicated that water was standing over the sediment when the sample was taken.

2.2. Study animals

Male *U. pugilator* were collected from the Rachel Carson Estuarine Research Reserve, Beaufort, NC and maintained in the laboratory (Rittschof & Buswell, 1989) until used for tests. Previous studies with *U. pugnax* (Weissburg, 1990, 1992, 1993) showed differences in the foraging behavior of male and female fiddler crabs. We used only male crabs to control for potential sex differences in feeding behavior. Crabs were maintained under ambient light and dark cycles in groups of ≈ 150 . Each group was kept in a 120 $\times$ 70 $\times$ 25-cm tank containing a 70 $\times$ 30 $\times$ 2-cm strip of sediment collected from the intertidal zone where the crabs feed. Ambient seawater was provided continuously and covered the bottom of the tank to a depth of several millimeters.

2.3. General design of assays

Laboratory feeding assays were patterned after those used by Rittschof & Buswell (1989) and Sears et al. (1991) for intact crabs. Prior to testing crabs were starved for 12–24 h and stored in plastic containers with 1 cm of seawater that had passed through

a 0.22 μm filter. Between tests, crabs were stored in filtered seawater in glass finger bowls. For any particular assay 30 crabs were tested in groups of five or six. Previous studies (Rittschof & Buswell, 1989) have shown that crabs respond independently whether tested alone or in groups. Crabs were tested in groups to expedite completion of the assays. A test was initiated by placing crabs in a 19 cm finger bowl containing the test solution or sediment in question. Crabs were allowed to settle for ≈ 15 s and then observed through a slit in a blind for 1 min. Each crab that moved its minor cheliped to the buccal region two or more times during the observation interval was counted as responding. The percent responding for each test solution was determined from the number of crabs out of 30 that responded to that test solution. Groups of 30 crabs were tested on a maximum of 21 different test solutions (three dilution series, described below) over a maximum period of 9 h. Repeated handling had no effect on feeding response. Crabs responded identically to dextrose at the beginning and at the end of the maximum test period.

Intact *U. pugilator* exhibit predictable responses to dextrose dissolved in filtered seawater (Rittschof & Buswell, 1989; Sears et al., 1991). The percentage of 30 crabs that responded to dextrose increased with dextrose concentration, with the maximum percentage of crabs (67%) responding to 1 M dextrose. We used the response to dextrose as a basis for determining the effects of salinity, sediment grain size and sediment water content on feeding behavior in *U. pugilator*. Crab responses to a dilution series of dextrose were determined at several salinities, in both natural sediments and in sediments sorted by grain size, and at different levels of water saturation. In addition, responses to dextrose were compared to responses to the total organic content of natural sediments. The details of each series of experiments are described below. Each dextrose dilution series produced a particular response curve. The effective concentration for 50% response (EC_{50}), and 95% confidence limits, were calculated for each response curve with probit analysis using a BASIC computer program (Lieberman, 1980). The 95% confidence intervals for each test condition were then compared to those for the response to dextrose in filtered seawater. Those response curves whose 95% confidence intervals did not overlap were considered to be statistically different (Sokal & Rohlf, 1981). Responses to single dextrose concentrations were compared with the G test (Sokal & Rohlf, 1981) if different crabs were used for the tests involved, or the z-test for proportions (Hardyck & Petrinovich, 1969) if the same crabs were tested on multiple solutions. Multiple comparisons were corrected with the sequential Bonferroni test (Holm, 1979).

2.4. Reagents and materials

Dextrose for feeding assays was dissolved in seawater that had been passed through a 0.22 μm filter or in water purified by reverse osmosis. A 2 M stock solution was made and stored frozen. Test solutions were prepared by dilution immediately before use. The dextrose dilution series included test solutions of: 0; 0.031; 0.062; 0.125; 0.250; 0.500; and 1.0 M. The 0 M treatment was used to determine spontaneous feeding rates. Previous studies (Sears et al., 1991) showed that feeding responses to the different dextrose concentrations were independent of the order in which they were presented.

To aid in data management, we always tested solutions in order of increasing concentration.

For experiments testing responses to salinity changes, dextrose solutions were diluted in artificial seawater that contained: 423.0 mmol NaCl; 9.0 mmol KCl; 9.27 mmol CaCl_2 ; 22.94 mmol MgCl_2 ; 25.50 mmol MgSO_4 ; and 2.15 mmol NaHCO_3 dissolved in water purified by reverse osmosis (Cavanaugh, 1956). Stock solutions of each salt were made and kept refrigerated. Individual test solutions were prepared immediately before testing. Dextrose, KCl, and CaCl_2 were reagent grade from Fisher Chemical Company, Pittsburgh, PA. All other salts were reagent grade from Sigma Chemical Company, St. Louis, MO.

2.5. Experiments

2.5.1. Sediment organic content

Prior to experiments, surface sediment from the crab feeding zone was dried and ashed to remove all organic material (Dean, 1974). This is referred to as “clean” sediment. New sediment from the feeding zone was collected immediately before the experiments and mixed with the clean sediment. Mixtures containing 12.5, 25, 50, and 100% field sediment were tested. A total of 60 ml of sediment was prepared for each test. Field and clean sediments were mixed together and hydrated with filtered seawater to 100% saturation. Prior to testing, 2 ml subsamples were taken from each sediment mixture and analyzed for total organic content by ashing. The organic content of each sediment mixture tested was then used to calculate an effective organic content for 50% response. This was compared with the field measurements of organic content to predict where in the intertidal zone crabs should feed. We used total organic content rather than Chl *a* (Weissburg, 1992) as an estimate of sediment food quality because Chl *a* does not provide information about the bacteria or other organic material in the sediment to which the crabs might respond.

2.5.2. Salinity

Responses of crabs to a dilution series of dextrose were determined at six salinities. Dextrose solutions were in deionized (DI) water (0 ppt) and in artificial seawater (Cavanaugh, 1956) at 0.75, 1, 2, 3, or 4 times natural salinity (35 ppt). For the DI water test, crabs were stored standing in 1 cm of DI water for at least 30 min before the test, and for at least 10 min between test solutions. Feeding response curves were plotted for each of the six salinities and their EC_{50} s were compared with each other and with the response to dextrose in filtered natural seawater.

Feeding responses evoked by field sediment were also tested at different salinities. Sediment from the feeding zone of the crab habitat was collected and immediately mixed with clean sediment to make 240 ml of a 50% mixture. The mixture was divided into four 60 ml portions. Two of these portions were saturated with deionized water (0 ppt). The other two were saturated with $1 \times$ (35 ppt) and $4 \times$ (140 ppt) artificial seawater. Thirty crabs were tested on each of the three sediment-water mixtures. In addition, crabs were tested on water extracted from one of the deionized water mixtures. This extracted sample determined whether addition of deionized water increased the stimulatory capacity of the interstitial water by causing cellular rupture due to

changes in osmotic pressure. Samples of each sediment mixture were taken prior to the experiment and were analyzed for sediment organic content and salinity of interstitial water. Feeding responses to sediments with different salinities were compared with the responses to sediment saturated with filtered natural seawater.

2.5.3. Sediment grain size

Responses of crabs to a dextrose dilution series were determined on several sediment grain size fractions and on natural sediment. Organic-free sediment was separated into five fractions using standard geological sieves. Test sediments were those retained on screens with mesh sizes of: (1) 1 mm; (2) 0.500 mm; (3) 0.250 mm; (4) 0.125 mm; and (5) sediment that passed through a 0.125 mm screen (referred to as <0.125 mm). For each test, 80 ml of sediment was placed in a bowl and 25 ml of the appropriate solution pipetted evenly over the surface. The saturation level of the sediment was 75–80% for all sizes except 1 mm, which had a saturation level of 50%.

The concentration of stimulus required for a 50% response (EC_{50}) was calculated for each of the curves resulting from this set of tests. The feeding response curves were plotted and their EC_{50} values compared for differences in feeding response due to differences in sediment grain size.

A set of experiments determined whether sediment altered the stimulatory capacity of the dextrose solutions. For each combination of grain size and dextrose concentration, a sample of dextrose solution was recovered from the test sediment by vacuum filtration. The extract was tested without sediment on the same groups of crabs used in the original tests. This process was repeated for all dextrose concentrations, including the filtered seawater control, on all grain size groups and on natural sediment. EC_{50} values were then calculated for each “extracted” dilution series and compared with the dextrose series without sediment for that trial.

2.5.4. Sediment water content

Surface sediment (top 5 mm) was collected from *Uca* habitat, rinsed in deionized water to remove salts, dried and ashed at 500 °C for 4 h to remove all potential feeding cues. Preliminary data showed that sediment ashed in this manner did not provide any feeding stimulus to the crabs. Porosity was determined as described for the field measurements. The volume of solution required to cause 25, 50, 75 and 100% saturation was then calculated from the porosity.

Responses of crabs to these four levels of saturation were tested. In any given test, 40 ml of ashed sediment was placed in a bowl and the appropriate volume of a 0.5 M dextrose solution was pipetted evenly over the surface to provide a feeding stimulus. Prior to each sediment series, each group of crabs was tested on 0.5 M dextrose without sediment for comparison. Sediments were tested in order of increasing saturation level. Crabs were blotted dry before being placed on sediment to prevent the addition of water that might alter saturation levels. The proportion of crabs responding to each saturation level was plotted. Since the same crabs were tested several times on different sediment types, differences in responses were analyzed using multiple *z* tests for proportions (Hardyck & Petrinoich, 1969) corrected with sequential Bonferroni tests (Holm, 1979).

2.5.5. Dactyl penetration

The depth to which the crabs' dactyls penetrated the sediment was determined at 25, 50, 75 and 100% saturation. Photographs were taken of 10 crabs as they stood on ashed natural sediment at each saturation level. Photographs of the same crabs standing on glass plates were used to measure the total dactyl length. Measurements of degree of penetration were made from the photographs, and the mean percentage of the dactyl below the sediment surface was calculated. Penetration was related to the feeding response at each saturation level.

3. Results

3.1. Field measurements

3.1.1. Organic content

Sediment organic content (back transformed mean% by weight, 95% confidence limits) increased with decreasing tidal height ($F_{2,6} = 68.89$, $p \leq 0.0001$, one-way ANOVA; Fig. 1a). It was lowest (0.22%, 0.14–0.34%) in sediments from the burrow zone. Transit zone sediment was about three times as rich in organic content (0.7%, 0.56–0.89%). Organic content of sediment in the feeding zone was over 10 times that of the burrow zone (2.9%, 0.98–7.50%).

3.1.2. Salinity

Salinity of intertidal sediment varied both spatially and temporally at low tide, from 0 ppt to the presence of crystalline salt (Fig. 1b). Sediments in the burrow region were the most variable, ranging from 0 ppt on rainy days to sediment covered with precipitated salts during dry periods. Sediment salinity in the transition zone ranged from 52 to 12 ppt. Near mean low water in the feeding zone, the salinity of the sediment was similar, ranging from 40 to 14 ppt. Despite the apparently higher salinity in the upper intertidal, the salinity of interstitial water was not statistically different across the intertidal zone ($\chi^2_2 = 0.62$, $p = 0.73$, Kruskal-Wallis test).

3.1.3. Sediment grain size

There was no difference in mean grain size across the intertidal zone (Fig. 1c). The mean ($\pm$ SD) grain size in the burrow, transit and feeding zones was 0.32 mm (0.22–0.46 mm), 0.25 mm (0.19–0.35 mm) and 0.26 mm (0.20–0.36 mm), respectively. In all zones, >80% of all sediment grains were in the 0.125 and 0.250 mm size fractions. Other size fractions were present in each zone, but none comprised more than 10% of the sediment in any zone.

3.1.4. Sediment water content

There was a strong water content gradient in intertidal sediment at low tide ($F_{2,6} = 15.75$, $p \leq 0.0041$, one-way ANOVA; Fig. 1d). Percent saturation increased with decreasing tidal height. High intertidal sediment in the burrow zone had a mean water content of $9.3 \pm 15.0\%$ saturation. Transit zone sediment was more saturated

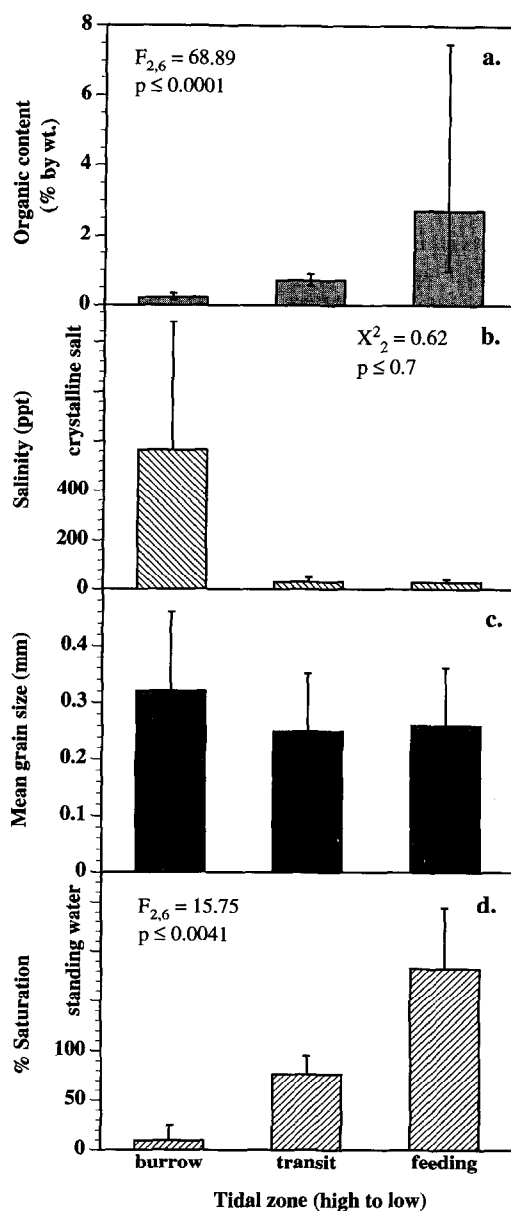


Fig. 1. Characteristics of intertidal sediment in three zones: burrows = in the high intertidal near crab burrows; transit = mid-intertidal zone between burrows and feeding zone; feeding = low intertidal where crabs feed most frequently. Bars are means with: (a) 95% confidence limits; (b–d) 1 SD. (a) Sediment organic content measured by weight lost on ignition. Organic content increased with decreasing tidal height ($F_{2,6} = 68.89$, $p \leq 0.0001$, one-way ANOVA). (b) Salinity of interstitial water. Salinity was highly variable and not significantly different across the intertidal zone ($\chi^2_2 = 0.62$, $p \leq 0.7$, Kruskal-Wallis test). (c) Mean grain size. Grain size distribution was similar across the intertidal zone. (d) Sediment water content measured as % saturation. Saturation increased with decreasing tidal height ($F_{2,6} = 15.75$, $p \leq 0.0041$, one-way ANOVA).

($76.6 \pm 18.1\%$), while feeding zone sediment was 100% saturated and was covered with a few mm of water.

3.2. Experiments

3.2.1. Response to sugar solutions

We confirmed Rittschof & Buswell's (1989) report that *U. pugilator* respond to sugar solutions in the laboratory. The percentage of adult male crabs responding to dextrose increases from 0 in filtered seawater alone to $>60\%$ in 1.0 M dextrose (Fig. 2). The effective dextrose concentration for 50% response (EC_{50}) is 0.223 M with 95% confidence limits of 0.19–0.34 M.

3.2.2. Organic content

Fiddler crabs responded to variations in sediment organic content in the laboratory (Fig. 3). Feeding response increased with increasing organic content from 0% at 0% organics to 60% at 1.3% organics. The effective organic content for 50% response (95% confidence limits) was 1.01% (0.77–1.60%).

Feeding responses to chemical stimuli in field sediment were compared with the feeding response elicited by dextrose. Dextrose concentrations were converted to % organics. The organic content of clean sediment that was 100% saturated with dextrose was determined from the % weight lost on ignition as for field samples. The relation-

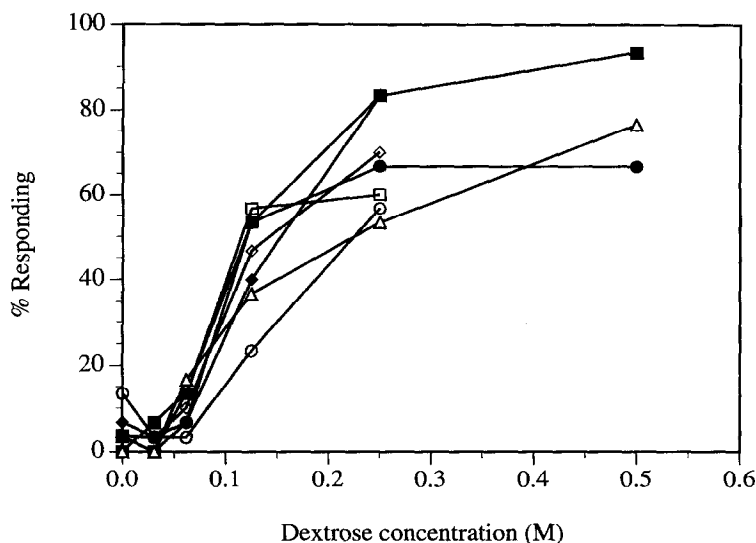


Fig. 2. Feeding responses to dextrose dissolved in artificial seawater of various salinities. ○, DI water; EC_{50} = 0.13 M (0.10–0.16 M); ◆, 0.75x; EC_{50} = 0.25 M (0.19–0.56 M); □, 1x, EC_{50} = 0.16 M (0.13–0.19 M); ◇, 2x, EC_{50} = 0.16 M (0.13–0.23 M); ●, 3x, EC_{50} = 0.16 M (0.13–0.21 M); ■, 4x, EC_{50} = 0.24 M (0.18–0.33 M); △, filtered seawater, EC_{50} = 0.22 M (0.19–0.34 M). % Responding = number of crabs out of 30 that moved the minor cheliped from the test solution to the buccal region at least twice in 1 min. Crabs responded similarly to all solutions.

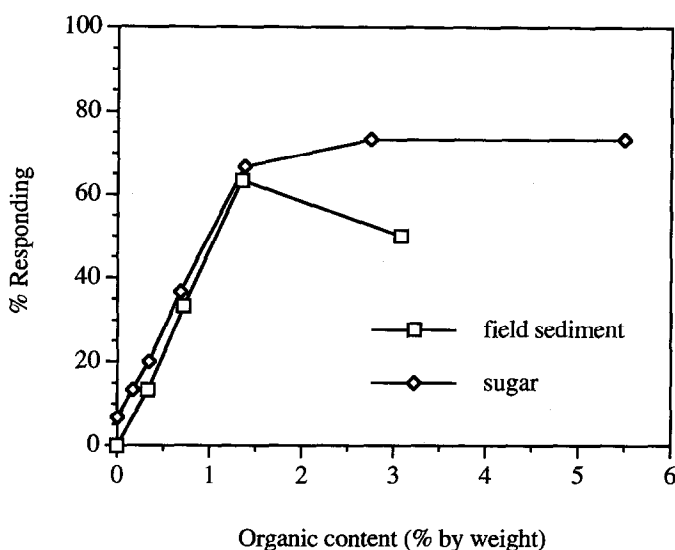


Fig. 3. Feeding response to sediment organic content. Sugar ($\diamond$) is dextrose test solutions converted to organic units (see text). Field sediment ($\square$) is sediment from the feeding zone mixed with ashed sediment to generate different sediment organic contents. Responses to the two stimuli were similar. EC_{50} values (95% confidence limits) are 1.36 M (0.94–2.02 M) for dextrose solutions and 1.01 M (0.77–1.60 M) for field sediment.

ship between dextrose concentration and sediment organic content was then calculated. This relationship is:

$$\% \text{ organics} = 5.5 [\text{dextrose}].$$

Dextrose concentrations from feeding assays were converted to % organic contents using this relationship. Feeding responses to dextrose solutions were then expressed in terms of total organic content. EC_{50} values were determined for responses to sugar in organic units and compared with EC_{50} values for responses to field sediment. The EC_{50} for dextrose solutions was 1.36% organics (0.94–2.02%), while the EC_{50} for field sediment was 1.01% (0.77–1.60%) organics. Thus, the phagostimulants in field sediment were similar in potency to dextrose.

Feeding stimulants in field sediment are bound to the sediment grains. In one test field sediment with an organic content of $0.98 \pm 0.02\%$ elicited 50% response. Interstitial water extracted from the same sediment did not stimulate feeding (0% response). Therefore, unlike the dextrose cue used in the laboratory assays, field phagostimulants are bound to the sediment.

Feeding responses to sediment organic content were independent of pore water salinity (Table 1). The pore water salinity of mixtures saturated with deionized water, 1 $\times$ and 4 $\times$ artificial seawater were 30.7, 38.7 and 80 ppt, respectively. The organic contents of the mixtures saturated with deionized water and 1 $\times$ artificial seawater were near 1.4%, while the organic content of the mixture saturated with 4 $\times$ artificial seawater was 1.09%. The response curve in Fig. 2 predicts that 63.33% of the crabs should

Table 1

Feeding responses to 50% field sediment saturated with solutions of varying salinities

Solution added	Pore water salinity (ppt)	% Organics	Expected response (%)	Response (%)	G value (<i>p</i>)
DI	30.7	1.44	63.33	73.33	1.35 (<i>p</i> > 0.1)
1 ×	38.7	1.39	63.33	66.67	0.15 (<i>p</i> > 0.5)
4 ×	80.0	1.09	50.00	50.00	0.00 (<i>p</i> > 0.9)

DI = deionized water; 1 ×, 4 × = concentrations of artificial seawater. Expected results were generated from the crabs' response to sediment mixtures saturated with filtered natural seawater (Fig. 6).

respond at 1.44% organics. At 1.09% organics 50% of the crabs should respond. The responses to the test mixtures were not different from these expected values ($G = 1.35$, 0.15 and 0, 1 df). Thus, feeding responses to field sediment did not depend upon sediment pore water salinity.

Addition of deionized water did not alter the stimulatory capacity of the interstitial water. Water extracted from the mixture of deionized water and field sediment caused a 6% response. This was not different from the 0% response to pore water extracted from pure field sediment ($G = 2.84$, 1 df).

3.2.3. Salinity

Feeding responses to dextrose were independent of salinity from 0 to 150 ppt. (Fig. 2). EC_{50} values for dextrose dissolved in deionized water and artificial seawater

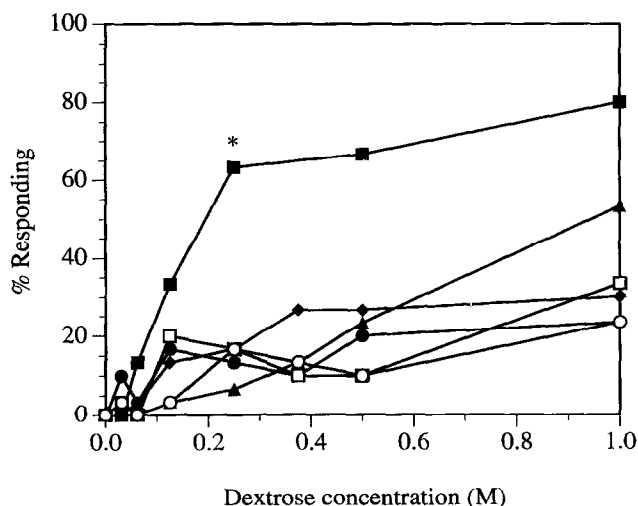


Fig. 4. Feeding responses to sediment fractions of different grain size, saturated to 80% with dextrose solutions: ■, natural mixture of sizes; ●, <0.125 mm; ▲, 0.125 mm; ◆, 0.250 mm; □, 0.500 mm, ○, 1.000 mm. See text for EC_{50} and 95% confidence interval values. Crabs responded more to the natural mixture of sediment sizes than to any size fraction tested individually. * = Significant, G -test for independence.

that was 0.75, 1, 2, 3, and 4 times ambient salinity were not significantly different from each other. EC_{50} values for all salinities were between 0.12 and 0.25 M.

3.2.4. Sediment grain size

Feeding responses to dextrose in the presence of common size classes of field sediments were determined at 80% saturation. Crab feeding response to sediment made up of the natural mixture of sizes was not different from the response to dextrose dissolved in filtered seawater. EC_{50} values (95% confidence limits) for sediment and dextrose in seawater are 0.25 M (0.19–0.34 M) and 0.39 M (0.26–0.66 M), respectively. Feeding responses to all grain size fractions tested alone were lower than the response to the natural mixture of sizes (Fig. 4). The 0.125 and 0.250 mm fractions had the lowest EC_{50} values: 0.97 M (0.73–1.66 M) and 1.98 M (0.98–11.32 M), respectively. The EC_{50} values for the remaining size fractions were all > 5 M and highly variable: < 0.125 mm = 200 M (4.57 – 4.82×10^{16} M); 0.500 mm = 5.92 M (1.66–1010 M) and 1.000 mm = 6.53 M (1.86–1250 M). Crabs responded more to the natural mixture of sediment sizes than to any size fraction tested individually ($G = 5.77$; 1 df, $p < 0.025$ for 0.25 M dextrose). Feeding was inhibited on sediment that was homogeneous in size.

Cleaned sediment did not add or remove chemicals from solutions of dextrose in filtered seawater. Feeding responses to solutions recovered from the sediment were the same as responses to dextrose solutions that had not been exposed to sediment (Fig. 5). EC_{50} values for all size fractions as well as the natural mixture of sizes were not different from each other. Therefore, differences in feeding response to dextrose in the presence of sediment were due to the physical presence of the sediment.

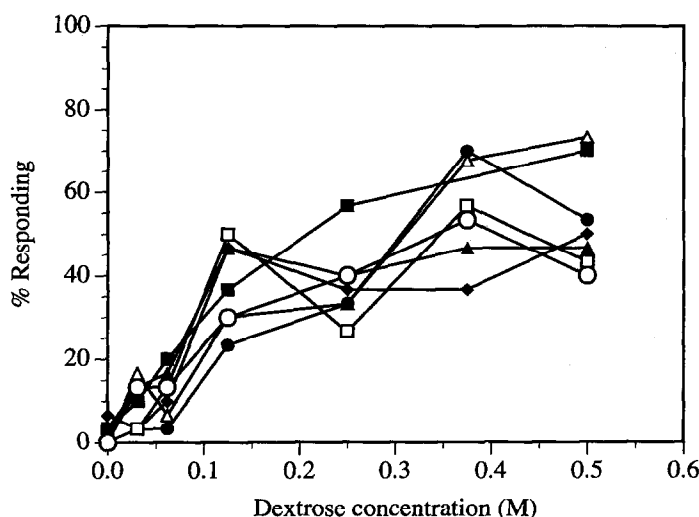


Fig. 5. Feeding responses to dextrose solutions recovered from sediment mixtures: ■, natural mixture of sizes, $EC_{50} = 0.23$ M (0.16–0.35 M); ●, < 0.125 mm, $EC_{50} = 0.28$ M (0.22–0.41 M); ▲, 0.125 mm, $EC_{50} = 0.47$ M (0.26–1.45 M); ◆, 0.250 mm, $EC_{50} = 0.55$ M (0.37–1.00 M); □, 0.500 mm, $EC_{50} = 0.53$ M (0.34–1.03 M); ○, 1.000 mm, $EC_{50} = 0.40$ M (0.28–0.6 M); △ no sediment, $EC_{50} = 0.28$ M (0.16–1.13 M). Crabs responded to all extracts similarly.

3.2.5. Sediment water content

In the presence of sediment, crab feeding responses to 0.5 M dextrose depended upon sediment water content (Fig. 6). Feeding responses were depressed at all saturation levels tested except 100% (z-test for proportions with sequential Bonferroni corrections). Sediment that was 100% saturated with 0.5 M dextrose solution resulted in the highest percentage feeding response (66.7%). This response was identical to the response to 0.5 M dextrose in filtered seawater ($z = 0$, $p > 0.5$). All other saturation levels caused lower response levels that did not differ from each other.

3.2.6. Dactyl penetration

The 10 crabs tested had dactyls ranging from 2.6 to 4.8 mm in length. We define dactyl penetration (% penetration) as the percentage of a particular dactyl that had penetrated the sediment. Penetration was a maximum of 24.1% at any saturation level below 100% (Fig. 7a). At 100% saturation, however, at least 78% of each dactyl measured penetrated the sediment. In 7 of the 10 crabs tested, the entire dactyl (100%) penetrated the sediment. There appears to be a threshold saturation level greater than 75% that allows the dactyls to sink fully into the sediment.

In addition, there appears to be a relationship between the depth to which the dactyls sink and the feeding response at a given saturation level (Fig. 7b). As the degree of penetration increased with increasing saturation level, the percentage of crabs that responded to sediment at those same saturation levels also increased. Maximum feeding response occurred at 100% saturation, when dactyl penetration was near 100%.

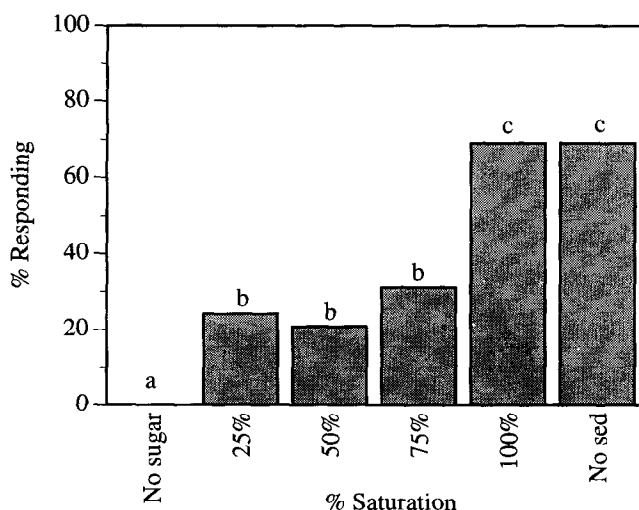


Fig. 6. Feeding responses to cleaned field sediment from the feeding zone at several levels of saturation with 0.5 M dextrose. No sed = response to 0.5 M dextrose in filtered seawater. Saturation levels were determined from sediment porosity. Crabs responded less to incompletely saturated sediments than to 100% saturated sediment or to dextrose solution without sediment. Letters indicate nonsignificant subsets (z-test for proportions with sequential Bonferroni correction).

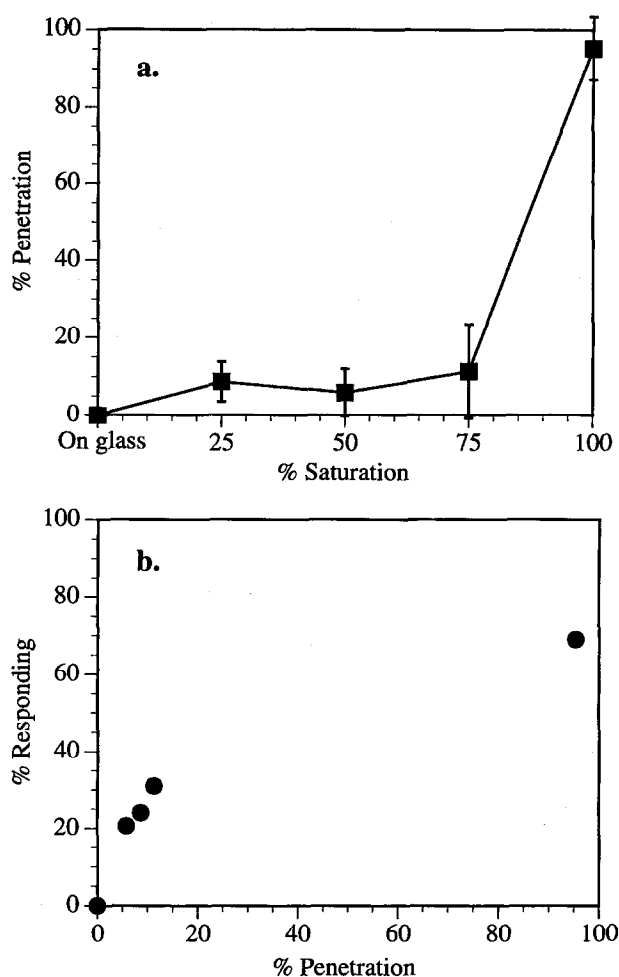


Fig. 7. (a) Percent of dactyl of first walking leg sinking into sediment of different water contents. Symbols are means for 10 adult male crabs with 1 SD. Very little of the dactyl sank into the sediment until 100% saturation. (b) Relationship between dactyl penetration and feeding response for different water contents. The % of crabs that responded to sugar increased as the dactyls sank deeper into the sediment ($r = 0.94$, $p < 0.05$). Maximum feeding occurred when dactyl penetration was near 100%.

4. Discussion

Our data suggest that contact chemical stimulation, physically modulated by sediment grain size and sediment water content, regulates where *U. pugilator* actively forage. Our laboratory studies show that feeding in *U. pugilator* is optimal on sediment with the following characteristics: (1) organic content of at least 1.0%; (2) grain size composition dominated by 0.125 mm and 0.250 mm size classes; and (3) 100% saturation with water resulting in complete dactyl penetration. These conditions are found

in the field in a band several meters wide immediately above the water that moves with the tide. This band can be considered a feeding patch. In contrast, high intertidal sediment is dry, sometimes very salty, and can support little growth of organic material. The burrow zone, then, can be considered to be a patch where feeding does not occur. Thus, physical factors, rather than biological factors, create feeding patches in the intertidal zone.

In the field area studied, grain size does not affect feeding behavior because sediments across the intertidal zone are composed of optimal grain sizes (Fig. 1). Therefore, fiddler crab foraging is controlled by sediment organic content (Robertson et al., 1980; Weissburg, 1992) and sediment water content. Robertson et al. (1980) and Christy (1980) suggested that driving behavior is initiated as a response to low levels of food in the burrow zone. In this study the organic content of sediments in the burrow zone was 0.2% (Fig. 1a), well below the 1.0% required for 50% feeding response. Based on these data, crabs in this location do not feed because chemical stimulation is below the threshold. Based upon sediment water content and dactyl penetration data presented here, crabs will move over dry sediment with organic content above the threshold for chemical stimulation (1.0%, Fig. 3), and will not feed until they encounter sediment of similar organic content that is fully saturated with water. As the tide recedes, crabs follow the water line out of the burrow zone until they encounter sufficient chemical stimuli and moisture content in the transit zone. The crabs stop moving and forage in this zone. As the crabs feed, the level of food decreases (Robertson et al., 1980), but not necessarily below stimulatory levels. However, water content also drops as the tide recedes. The simultaneous drying of the sediments and reduction of chemical stimulation due to reduced dactyl penetration drives feeding crabs down the flat until the water stops receding.

Crabs continue to feed in the low intertidal zone until: (1) levels of chemical stimulants drop below feeding thresholds; (2) the incoming tide forces them back up the beach; or (3) satiation or other factors cause release of a feeding inhibitory peptide (FIF), that inhibits feeding responses to chemical stimulation (Sears & Rittschof, 1991). The length of time spent feeding depends upon the sediment organic content. When organic content is low, but levels are above those necessary for chemical stimulation of feeding, crabs continue to feed until the flooding tide forces them to move higher in the intertidal zone. They then follow the water line back toward the burrow area (pers. obs.). When food is not limiting, and at certain relationships between tide cycles and daylengths (Salmon & Hyatt, 1983) feeding is inhibited physiologically. Animals that are “full” return to the burrow area prior to flooding. Blood levels of a peptide that inhibits chemically stimulated feeding (FIF) are low in crabs moving down the slope to feed and high in crabs returning from feeding (Sears & Rittschof, 1991). Once initiated, movement back toward the burrow area is direct. This movement is facilitated by drier sediments with reduced organic content that have a lower probability of stimulating feeding behavior.

Chemoreceptor function appears functionally tied to conditions that enable efficient sediment processing by the crabs. Chemoreceptors are located on the dactyls (Robertson et al., 1981; Trott & Robertson, 1984). The presence of water in the sediment is important for initial stimulation of these chemoreceptors. Since chemical feeding stimu-

lants are bound to the sediment grains (see Results: Laboratory experiments; Organic content), stimulation requires that the receptors on the dactyls come in contact with the grains (Robertson et al., 1981). The higher the water content, the deeper the dactyls sink into the sediment (Fig. 7a) and the larger the number of chemoreceptors that can contact the stimuli. When the sediment is wet enough and the organic content high enough for a sufficient number of chemoreceptors to be stimulated, the crabs will feed. Routinely the entire dactyl penetrates the sediment at 100% saturation. This allows maximum stimulation of chemoreceptors and maximum feeding response.

Sediment water content is also important for the mechanics of feeding by allowing efficient manipulation, processing and sorting of sediment particles (Miller, 1961). The amount of water in the sediment may determine an optimal texture for manipulation of sediment with the chelae and mouth parts. In the saturation experiments, sediment that was <100% saturated appeared to adhere to the crabs' legs, chelae and mouth parts (pers. obs.). This "sticky" unsaturated sediment may be difficult for the crabs to deliver to their mouths and process. Also, water stored in the branchial chamber is used for flotation of particles in the buccal cavity during sediment processing (Miller, 1961). Some of this water is continually lost as feeding pellets form during sediment processing. Therefore, a nearby water source is vital for efficient foraging. Movement down the beach as the tide recedes provides the crabs with a continuous supply of water. Thus, sediment water content is important for both initiation and continuation of feeding in fiddler crabs.

At first glance, our finding that sediment water content is important in regulating feeding conflicts with Christy's (1980) conclusion that sediment moisture content is not important for foraging in reproductively active male *U. pugilator*. However, closer examination shows that our observations are complementary. The crabs in Christy's study had not fed for several days while guarding burrows. They were hungry and therefore sensitive to chemical cues. The lower intertidal sediment Christy offered to the crabs was rich in organics. The "dry" treatment was, in the worst case, about 25% saturated after drying in the sun for an hour. The wet treatment was close to 100% saturated at the beginning of the experiment. The crabs in our experiments had been starved overnight, so they were also hungry. In our experiments, 7 out of 29 crabs (24%) fed on organic-rich sediment that was 25% saturated, while 20 out of 29 (69%) fed on the same sediment when it was 100% saturated. These results were comparable to Christy's results ($G = 0.179$ for 25% 1 df, $G = 0.359$ for 100%, 1 df). The number of crabs that Christy used was not large enough for him to detect the difference and reach our conclusion. Sediment water content and sediment organic content are both important for feeding in *U. pugilator*. All crabs require adequate organic content for chemical stimulation, but only those that are the most sensitive will feed on sediment that is less than 100% saturated.

We have shown that predictable aspects of the sandflat environment determine and modulate the location of feeding activity in *U. pugilator*. These aspects include sediment organic content, sediment grain size, and sediment water content. Relationships between the controlling variables are complex and involve the mechanics and efficiency of feeding as well as exposure and stimulation of chemoreceptors.

Optimal foraging models typically assume that environments are patchy with respect

to food resources. In the case of fiddler crabs, the food resource (measured by sediment organic content) is continuously distributed across the intertidal zone. Patchiness in the intertidal zone is due to physical factors (sediment water content) that change through time at any location in the intertidal zone. Models of optimal foraging have not considered how physical characteristics of the foraging environment affect foraging strategies. However, at least for deposit feeders like *Uca*, the physical state of the environment plays a critical role in regulating foraging behavior.

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